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Autumnal Reproduction in *Cumberlandia monodonta*  
(Unionoidea: Margaritiferidae)

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**Abstract.** Gill marsupia of *Cumberlandia monodonta* were observed to contain early developmental stages on 27 October 1982. This occurrence, in conjunction with histological examination of gonads from several specimens, documents the first record for autumnal reproductive behavior in *C. monodonta*, and lends credence to previous speculation that biannual periodicity occurs in this species.

Smith (1976, 1978, 1988) systematically examined gametogenesis and reviewed brooding periodicity within the North American Margaritiferidae. However, information concerning margaritiferid reproductive biology remains sparse. Howard (1915) reported a single vernal brooding female of *Cumberlandia monodonta* (Say, 1829) and briefly described that individual's glochidia (also see Surber, 1915). These data are augmented by the discovery of an autumnal brooding female *C. monodonta* and histological examination of gonadal tissues from several preserved specimens collected at different localities.

MATERIALS AND METHODS

Several individuals of *Cumberlandia monodonta* (obtained from Meramec River, Times Beach access, 3 km east of Eureka, St. Louis County, Missouri, 27 October 1982) were maintained for several days in aquaria. During this period, one individual discharged large quantities of a mucus-like substance from its excurrent siphon. This material was collected immediately and examined microscopically. Forty additional specimens in collections of the University of Massachusetts at Amherst (UMA), Thomas M. Freitag (TMF), and one of the authors (MEG) were available for histological analysis of gonad activity (Table I). Mussels had been preserved either by fixation in 10% formalin, followed by 70% ethanol, or in alcohol without previous fixation. A portion of the viscera of each specimen was embedded in paraffin and sectioned at 8  $\mu$ m. Five sections from each specimen were hydrated to water, stained with Ehrlich's hematoxylin and eosin, dehydrated, and mounted.

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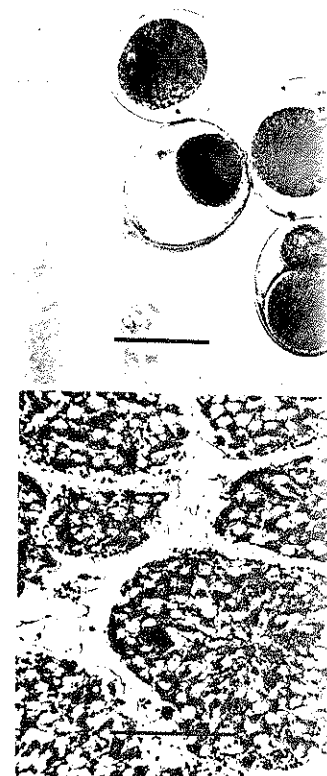
TABLE I  
Chronological list of collection data and deposition of histological specimens

Date	Location	Number of specimens	Collection
17 September 1964	Gasconade River; Missouri, Gasconade Co., Mt. Sterling	16	UMA MO. 1106
19 June 1978	Mississippi River; Iowa, Muscatine Co., Muscatine	1	TMF
18 August 1978	Mississippi River; Illinois, Rock Island Co., Rock Island	1	UMA MO. 1426
7, 12 August 1979	Clinch River; Tennessee, Hancock Co., Kyles Ford	16	UMA MO. 1143
August 1979	Mississippi River; Illinois, Rock Island Co., Foster	1	TMF
8 May 1980	Mississippi River; Iowa, Muscatine Co., Muscatine	1	TMF
18 July 1981	Clinch River; Tennessee, Hancock Co., Kyles Ford	1	MEG
27 October 1982	Meramec River; Missouri, St. Louis Co., Eureka	3	UMA MO. 1425, TMF

#### RESULTS AND DISCUSSION

Margaritiferids often abort marsupial contents following tactile stimulation (Howard, 1915; Smith, personal observations). Consequently, extruded material from the Meramec River specimen was composed primarily of early embryonic forms (ova through morulae, Figs. 1, 2) suspended in a globular, acellular matrix. Howard (1915) reported both ova and glochidia simultaneously in the marsupial mass, indicating considerable developmental asynchrony (see Matteson, 1948; Yeager and Neves, 1986; Yokley, 1972). Observed variations between embryonic stages might represent minor deviations in fertilization or ovulation rates, but such occurrences may reflect extended periods of spawning in both sexes or low fertilization efficiency.

The presence of eggs in marsupia was corroborated by histological examination of male and female specimens collected with the same individual described above. Gonads of both sexes showed onset of spawning as indicated by spaces, formerly occupied by gametes, appearing in the thin-walled follicular acini (Figs. 3, 4). Ovarian eggs of *Cumberlandia monodonta* averaged 43  $\mu\text{m}$  in diameter, being slightly larger than the average for those of *Margaritifera margaritifera* (Linnaeus, 1758) (Smith, 1978). Diameters of discharged ova reached 115  $\mu\text{m}$ , or about twice those of glochidia (55–65  $\mu\text{m}$ ; see Howard, 1915; Surber, 1915), but varied considerably owing to quantitative disparities in yolk deposition (Fig. 1). Embryonic sac diameters measured up to 160  $\mu\text{m}$ . Although inconsistent with glochidial dimensions given by Smith (1976), Howard (1915) contended that larvae of *C. monodonta* were slightly larger than those of *M. margaritifera*. If compared with figure dimensions of Smith (1976, fig. 1), our data supports Howard's (1915) observation.



FIGS. 1, 2. *Cumberlandia monodonta* (ova and embryos obscured by matrix globules) and glochidia (Fig. 1) represent 115  $\mu\text{m}$ . FIGS. 3, 4. Gonads of male (Fig. 3) and female (Fig. 4) specimens. Scale bars

Previous records of reproduction of *C. monodonta* (Lea (1842)<sup>2</sup> and Howard (1915)) from the Mississippi River near Missouri contained both ova and glochidia, indicating spawning was occurring and that the material had not been held over from the previous year, probably produced two years ago (e.g., Baker, 1915; spawner; however, gravidity was not observed (e.g., Buchanan, 1980). Although the female in late October suggests a biannual reproductive period.

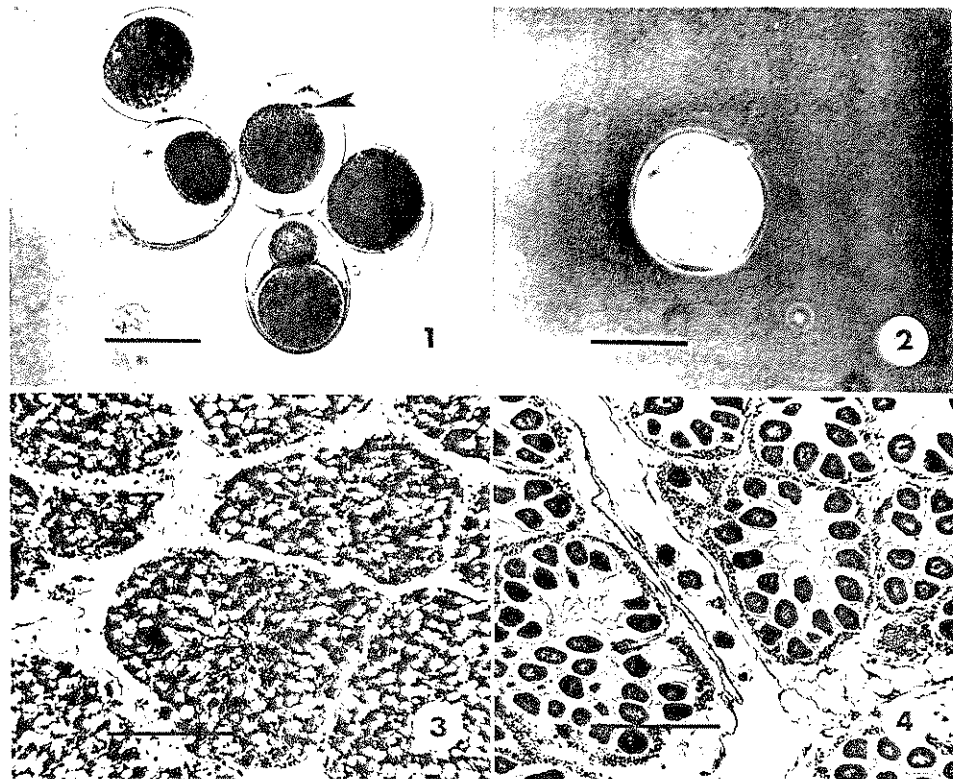
<sup>2</sup> Lea (1842) included seven specimens collected between 19 September and 19 October in the marsupia, Lea (1863, p. 422) notes that the material was collected. He did not list a specific date of collection.

ological specimens

Collection
UMA MO. 1106
TMF
UMA MO. 1426
UMA MO. 1143
TMF
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FIGS. 1, 2. *Cumberlandia monodonta*. Fig. 1. Ova (polar body indicated by arrow, but partially obscured by matrix globules) and one early cleavage stage. Fig. 2. Eight-cell stage. Scale bars each represent 115  $\mu\text{m}$ . FIGS. 3, 4. Gonads of *C. monodonta* collected with gravid specimen. Fig. 3. Male. Fig. 4. Female. Scale bars each represent 150  $\mu\text{m}$ .

Previous records of reproductive behavior for *C. monodonta* include Lea (1842)<sup>2</sup> and Howard (1915, a single brooding female collected 2 May 1912, Mississippi River near Moline, Illinois). Marsupial gills of the latter specimen contained both ova and incompletely developed glochidia, indicating that spawning was occurring at that time. Howard (1915) stated that larvae had not been held over from the previous autumn and speculated that *C. monodonta* probably produced two broods of glochidia annually. Various subsequent publications (e.g., Baker, 1928; Oesch, 1984) listed *C. monodonta* as a biannual spawner; however, gravidity in May has been interpreted to represent bradytaxis (e.g., Buchanan, 1980). Although inconclusive, our current record of a brooding female in late October substantially supports Howard's (1915) contention that biannual reproductive periodicity occurs in *C. monodonta*.

<sup>2</sup> Lea (1842) included seven specimens of *Cumberlandia monodonta* in a list of nongravid mussels collected between 19 September and 13 November 1838. In a brief anatomical description of gill marsupia, Lea (1863, p. 422) noted that "No ova were found here, but they were in the ovarium." He did not list a specific date of collection for his specimens.

A slight asynchrony in gonad activity was evident between Illinois and Tennessee populations during August. Histologically, the gonads of female specimens from the Mississippi River in Illinois were developmentally more advanced (e.g., free oocytes in acini) than females from the Clinch River, Tennessee (e.g., developing oocytes still embedded in wall of each acinus). Such differences in developmental rates might be attributed to latitudinal variations in temperature between the two localities.

In addition to latitudinal variation in ovarian development, water temperature probably initiates or closely mediates unionoid spawning behavior (see Yokley, 1972). A temperature of 14°C (Meramec River, 27 October 1982) is within a range to be expected for the Mississippi River near Howard's (1915) locality for late April and early May. Biannual reproduction would suggest that there probably are critical upper and lower thermal limits controlling spawning.

Based on duration of glochidial retention within marsupia, reproductive cycles of North American Unionoidea have been classified as tachytictic (short-term or summer brooders) or bradytictic (long-term or winter brooders) (Baker, 1928; Gordon & Layzer, 1989; Lefevre & Curtis, 1912; Ortmann, 1911; Sterki, 1895). Available data for Margaritiferidae indicate tachytictic reproductive behaviors, but with temporal variations referable to species-specific and possibly geographical/environmental bases (see also Smith, 1978). Biannual gametogenesis and gravidity also were demonstrated for some species. Unfortunately, our histological data are restricted to May through October, and, despite Howard's (1915) observations, cannot conclusively address the question of whether a biannual cycle occurs or not. Post-spawning features are evident from May through June, which probably indicate May spawning, but might reflect a delay in gonadal recovery from the previous fall.

Another phenomenon relevant to reproductive biology of *C. monodonta* is the possible occurrence of hermaphroditism. Van der Schalie (1966) reported occasional hermaphrodites in *C. monodonta*, but in a later expanded account (Van der Schalie, 1970) mentioned no hermaphrodites. The specimens examined by us were gonochoristic. Hermaphroditism (hence the possibility of self-fertilization) probably is not an important characteristic of *C. monodonta*.

Available data indicate that breeding cycles are variable within the Margaritiferidae (see Smith, 1978). Other unionoid species, which generally have been classified bradytictic, have been shown to exhibit tachytictic responses (e.g., *Anodonta*, see Heard, 1975; W. R. Hoeh, personal communication; Lewis, 1985; Surber, 1915). Other supposed tachytictic species spawn during seasons that may be considered atypical and, in some instances, resulted in their classification as bradytictic (e.g., Heard & Guckert, 1970; Howard, 1915). With respect to variations in unionoid reproductive behavior, general concepts of tachytictic and bradytictic classification apparently warrant re-examination (Gordon & Layzer, 1989).

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