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HERMAPHRODITISM IN *ELLIPTIO* (PELECYPODA: UNIONIDAE)[1]

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ABSTRACT

The gonadal organizations and the spacings of interlamellar septa are described for 22 monoecious animals found among 1026 *Elliptio arctata, E. buckleyi, E. complanata* and *E. icterina* examined histologically. Samples of 152 *E. crassidens* s.s., *E. c. downiei, E. hopetonensis, E. jayensis* and *E. mcmichaeli* contained only males and females.

The gonads of a total of 18 hermaphroditic *Elliptio arctata, E. buckleyi, E. complanata* and *E. icterina* contained a preponderance of testicular tissue, and those of four *E. complanata* and *E. icterina* contained about as much or more ovarian tissue. Eleven *E. arctata, E. buckleyi, E. complanata* and *E. icterina* had intermingled zones of male and female acini, and 10 animals of these same four species had regionally distinct and separate male and female acini; one *E. icterina*, with a preponderance of testicular tissue, had a few monoecious acini.

Outer, marsupial demibranchs of females had about 3-10 filaments on each side of the water-tubes (short), and non-marsupial demibranchs of females and males had about 20 filaments (long water-tubes). The hermaphrodites possessed eight different combinations of gonadal constitution and sizes of water-tubes (long, intermediate and short) in the four demibranchs, and gravid animals displayed two of those combinations.

The cause(s) of the variable expressions of hermaphroditism in *Elliptio* are unknown, but the low frequencies of monoecious animals indicate that hermaphrodites do not contribute significantly to reproduction within their populations.

INTRODUCTION

Van der Schalie (1970) found only males and females among six *Elliptio buckleyi* (Lea), five *E. complanata* (Lightfoot), 22 *E. crassidens* (Lamarck), eight *E. fraterna* (Lea), six *E. strigosa* (Lea) [=*E. arctata* (Conrad), *fide* Johnson (1970)], and six *E. tuomeyi* (Lea) [=*E. icterina* (Conrad), *fide* Johnson (1970)], but reported two hermaphrodites among 68 *E. dilatata* (Rafinesque) and one hermaphrodite among nine *E. productus* (Conrad) [=*E. lanceolata* (Lea), *fide* Johnson (1970)].

The ovotestes of both monoecious *Elliptio dilatata* consisted predominantly of ovarian tissue with some hermaphroditic acini being present, and one of the animals was gravid, whereas the non-gravid monoecious *E. productus* contained a preponderance of testicular tissue (interpretations from legends to van der Schalie's (1970) figs. 5-7). However, it is unknown whether the outer demibranchs of these three animals were of marsupial or non-marsupial structural organization, i.e., possessed either densely spaced interlamellar septa and therefore longitudinally short water-tubes (interlamellar spaces) or distantly spaced septa and long water-tubes, respectively.

The only other reported case of hermaphroditism in this genus was one predominantly ovarian animal among 150 *Elliptio complanata* (Matteson, 1948); details of demibranch organization were not given, nor was it noted whether the animal was gravid.

Hermaphroditism in freshwater mussels is seemingly most widespread in the unionid subfamily Anodontinae Ortmann, and especially so in *Anodonta* Lamarck (see van der Schalie, 1970; Heard, 1975). Bloomer (1934) reported that in *A. cygnea* (Linnaeus) in England the structure of an individual's outer demibranchs was not always correlated with the nature of

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the gonads, and he concluded that sex-reversal occurs in that species. In contrast, Heard (1975) found that in several North American *Anodonta* the outer demibranchs were always marsupial in females and "female-hermaphrodites" (ovarian tissue approximating or greatly exceeding the amount of testicular tissue) and always non-marsupial in males and "male-hermaphrodites" (predominance of testicular tissue). In addition, female-hermaphrodites were found in gravid condition, but male-hermaphrodites were never gravid.

The purposes of this report are to record additional occurrences of hermaphroditism in *Elliptio* Rafinesque, and to provide a description of the nature of the gonads and structure of the demibranchs in the monoecious animals.

MATERIAL EXAMINED

Elliptio arctata (Conrad). North Mosquito Creek adjacent to Florida State Hospital, Chattahoochee, Gasden County, Florida. Animals from 12 consecutive monthly collections: June 1976 to May 1977. 62 ♂, 60 ♀ and 4 ⚥.

Elliptio buckleyi (Lea). Myakka River at Myakka River State Park, about 27 km southeast of Sarasota, Sarasota Co., Fla. Six bimonthly collections: January, March, May, July, September and November 1965. 26 ♂, 30 ♀ and 3 ⚥.

Elliptio complanata (Lightfoot). Spring Creek at Federal Highway 90, 3.2 km southeast of Marianna, Jackson Co., Fla. Thirteen consecutive monthly collections: March 1976 to March 1977, each with two forms; shell of *form A* posteriorly inflated and with incurved ventral margin (67 ♂, 71 ♀ and 2 ⚥), and shell of *form B* compressed and with rather straight or slightly convex ventral margin (62 ♂, 62 ♀ and 2 ⚥).

Elliptio crassidens crassidens (Lamarck). Population 1: Apalachicola River at Chattahoochee, Gadsden Co., Fla.; 14 May 1977 (9 ♂ and 15 ♀). Population 2: Chipola River at State Road 167, 1.6 km north of Marianna, Jackson Co., Fla.; 16 November 1973 (3 ♂ and 7 ♀).

Elliptio crassidens downiei (Lea). Satilla River at Federal Highway 301, 4.8 km south of Hortense, border of Wayne and Pierce counties, Georgia; 11 October 1973. 14 ♂ and 16 ♀.

Elliptio hopetonensis (Lea). Ohoopee River at State Road 56, 3 km southwest of Covena, Treutlen Co., Georgia; 25 October 1973. 17 ♂ and 15 ♀.

Elliptio icterina (Conrad). Population 1: Little (= South Prong of) St. Marys River at Federal Highway 90, 1.6 km west of Macclenny, Baker Co., Fla.; 10 December 1973 and 10 May 1974 (25 ♂, 26 ♀ and 3 ⚥). Population 2: same North Mosquito Creek locality as for *E. arctata*; 19 consecutive monthly collections: April 1976 to September 1977 (107 ♂, 101 ♀ and 3 ⚥). Population 3: Steinhatchee River at Federal Highway 19, 26.4 km northwest of Cross City, border of Dixie and Taylor counties, Fla.; monthly collections from March 1976 to April 1977, except in January and February (154 ♂, 151 ♀ and 5 ⚥).

Elliptio jayensis (Lea). Black Creek at State Road 209, 10.7 km northwest of Green Cove Springs, Clay Co., Fla.; 16 October 1977. 11 ♂ and 9 ♀.

Elliptio mcmichaeli Clench & Turner (? = *E. fraterna sensu* van der Schalie, 1970). Choctawhatchee River at State Road 20, Ebro, border of Walton and Washington counties, Fla.; 20 November 1971. 20 ♂ and 16 ♀.

Shells from each of these populations have been deposited as voucher specimens in the Museum of Comparative Zoology, Harvard University.

METHODS

The animals described herein were discovered during a survey of seasonal gonad activity in the *Elliptio* in the Mosquito, Myakka, Spring and Steinhatchee localities, findings on which will be published elsewhere. Five animals with provisionally identified marsupial outer demibranchs and five with non-marsupial outer demibranchs were taken from each monthly collection, and sections of the gonads were made from each of these individuals. Frontal sections of the outer and inner demibranchs of several known males and females, and of each hermaphrodite, were made. In order to assess the accuracy of identification of the kind of outer demibranch, the gonads of all 310 individuals of Steinhatchee River *E. icterina* were sectioned, as were those of all animals from the other sites not named above. Histological sections of gonads and demibranchs were prepared according to the methods used by Heard (1975).

Septal spacing was determined by counting the number of ordinary filaments along the sides of water-tubes, i.e., between consecutive interlamellar septa. Demibranchs with comparatively low numbers of filaments per water-tube were considered to be marsupial, and those with comparatively high numbers were treated as non-marsupial.

FINDINGS

Gonadal constitution

Just 22 of the 1178 individuals examined histologically, viz., 1.87%, were monoecious (see Table 1). The gonads of 18 of those hermaphrodites contained predominantly testicular tissue (Fig. 1), whereas four contained about as much or more ovarian tissue (Fig. 2). In 16 animals the kind of gonadal tissue that was least abundant lagged in gametogenic development (Fig. 3). The six exceptions are: four animals in which the least abundant gonadal tissue was of more advanced development, viz., those with much ovarian tissue; one in which both kinds of tissue were of equal development; and one in which the most abundant kind was the most developed. Fifteen of the 22 hermaphrodites were found during the breeding season of the specific populations, although the relative states of development of the two kinds of gonadal tissue were not consistently related to the time of year.

Eleven hermaphrodites had intermingled zones of male and female acini, and 10 displayed regionally distinct and separate male and female acini (see Table 1). *Elliptio complanata* form A showed only the former condition, whereas form B had just the latter; *E. arctata, E. buckleyi* and all three populations of *E. icterina* contained animals of both conditions. The single animal with monoecious acini contained a vast predominance of testicular tissue, with eggs present in just four adjacent acini (Fig. 4).

Demibranch structure

Frontal sections of female outer demibranchs confirmed Ortmann's (1911) report of unipartite marsupial organization in *Elliptio*, i.e., of simple, vertically undivided interlamellar septa and water-tubes. The non-marsupial demibranchs, viz., the inner ones of females and all four in males, were also of unipartite organization, although they were distinguished from the marsupial demibranchs by more distantly spaced septa and therefore longitudinally longer water-tubes that were flanked on each side by a greater number of filaments. Marsupial water-tubes had about three to five filaments on each side in *E. arctata, E. buckleyi, E. complanata* (both forms), *E. icterina* and *E. jayensis*, and about 7-10 in *E. crassidens* s.l., *E. hopetonensis* and *E. mcmichaeli*; non-marsupial water-tubes of all species had about 20 filaments on each side (Table 2).

All demibranchs of all hermaphrodites were likewise of unipartite structure, but septal spacing varied more in them than in males and females. Eleven hermaphrodites had long water-tubes in all four demibranchs: one *Elliptio buckleyi*, four *E. complanata* (two of each form), one Little St. Marys River *E. icterina*, three Mosquito Creek *E. icterina* and two Steinhatchee River *E. icterina*; all of these animals except one each of the two forms of *E. complanata* contained mostly testicular tissue (Table 1). Three other hermaphrodites had short water-tubes in the outer demibranchs and long water-tubes in the inner demibranchs: one *E. arctata* with mostly testicular tissue, and two Little St. Marys River *E. icterina* with much ovarian tissue. The remaining seven monoecious animals, all with predominantly male gonads, had intermediate-sized water-tubes in the outer demibranchs; four of them also had intermediate-sized water-tubes in the inner demibranchs (one *E. arctata*, two *E. buckleyi* and one Steinhatchee River *E. icterina*), and three had long water-tubes in the inner demibranchs (one *E. arctata* and two Steinhatchee River *E. icterina*).

TABLE 1. Relative proportions of testicular and ovarian tissue in each hermaphroditic *Elliptio* examined, and the number of filaments (mean ± 1 standard deviation) along each side of the water-tubes in different demibranchs of those individuals. Ten water-tubes were studied in each demibranch. LSMR: Little St. Marys River; MC: Mosquito Creek; SR: Steinhatchee River.

Species	Spn.	% of gonads		Outer demibranchs		Inner demibranchs	
		Testicular	Ovarian	Mean ± S.D.		Mean ± S.D.	
E. arctata	1[r]	>95	<5	11.70	3.16	17.50	1.90
	2[i]	>95	<5	3.80	0.63	15.30	2.00
	3[r,d]	>95	<5	–	–	–	–
	4[r]	>95	<5	9.00	1.56	13.60	2.01
E. buckleyi	1[r]	>95	<5	17.00	2.87	16.80	4.52
	2[i]	>95	<5	7.70	1.16	12.00	3.06
	3[i]	>95	<5	11.30	1.70	9.70	1.06
E. complanata							
form A	1[i]	25	75	19.50	2.27	18.80	2.57
	2[i]	>95	<5	18.40	3.86	19.40	3.03
form B	1[r]	>95	<5	21.10	2.47	19.30	2.26
	2[r,g]	<5	>95	21.10	2.85	20.20	3.33
E. icterina							
LSMR	1[i]	55	45	7.10	1.73	20.50	2.99
	2[r]	>95	<5	19.40	1.58	20.30	3.53
	3[r,g]	<5	>95	5.50	1.35	19.80	1.69
MC	1[m]	>95	<5	19.60	4.97	20.30	3.06
	2[i]	>95	<5	20.80	3.26	20.40	3.75
	3[i]	>95	<5	20.40	3.17	20.20	4.21
SR	1[i]	>95	<5	19.10	1.79	19.50	1.65
	2[i]	>95	<5	19.50	2.51	17.70	4.19
	3[i]	>95	<5	10.90	2.02	19.00	3.65
	4[r]	75	25	9.20	1.62	20.00	4.64
	5[r]	>95	<5	10.40	1.71	11.80	2.04

[d]Discarded before demibranchs could be examined.

[g]Gravid.

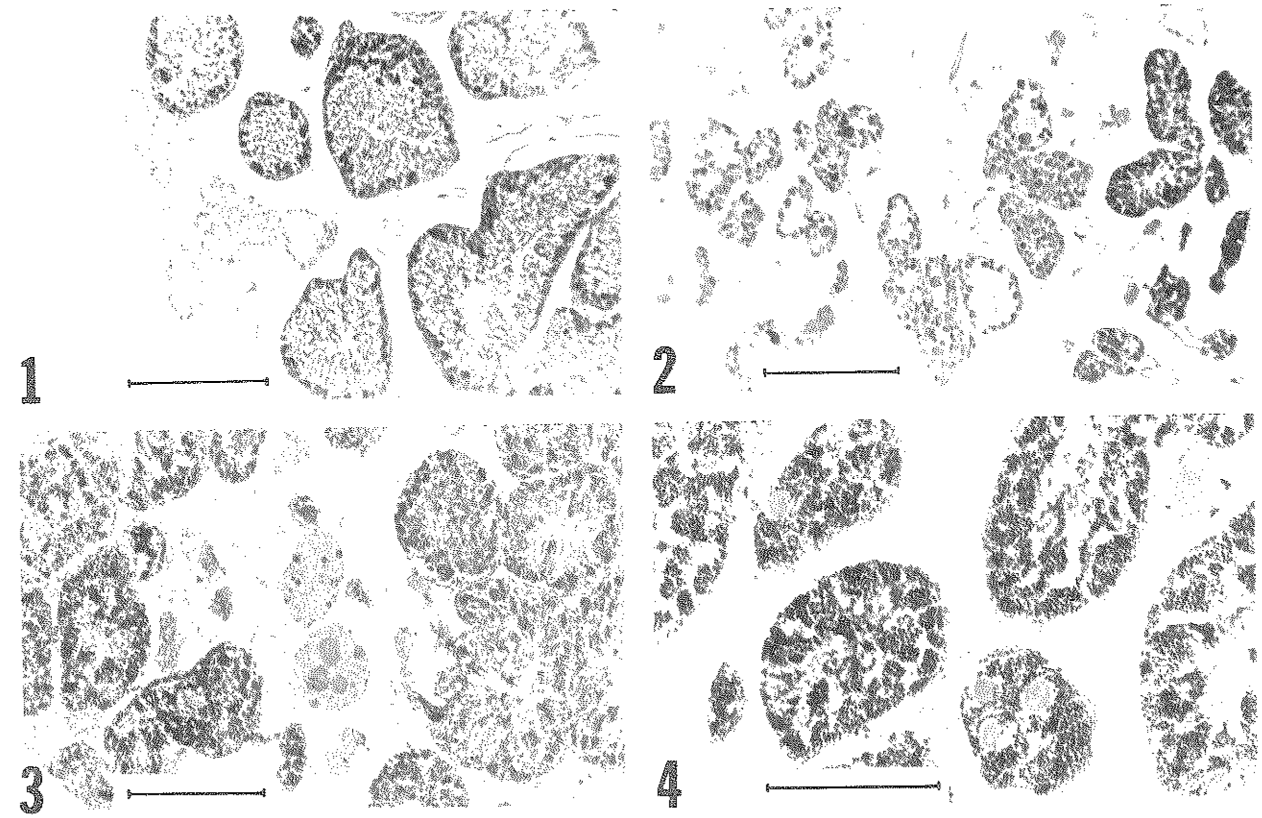
[i]Intermingled zones of male and female acini.

[m]With a few monoecious acini.

[r]Regionally distinct and separate male and female acini.

TABLE 2. Number of filaments (mean ± 1 standard deviation) along each side of the water-tubes in different demibranchs of female and male *Elliptio*; 30 water-tubes were studied for each condition. AR: Apalachicola River; CR: Chipola River; other abbreviations as in Table 1.

Species	Outer demibranchs				Inner demibranchs			
	Female		Male		Female		Male	
	Mean	± S.D.	Mean	± S.D.	Mean	± S.D.	Mean	± S.D.
E. arctata	3.30	1.15	19.70	2.32	19.70	2.60	19.07	2.62
E. buckleyi	3.33	0.76	19.17	3.63	16.13	2.84	17.73	4.18
E. complanata								
form A	3.57	1.22	19.10	2.41	18.40	2.03	19.40	2.72
form B	4.53	1.43	20.10	3.00	20.53	2.84	20.90	3.61
E. crassidens s.s.								
AR	8.47	1.48	18.87	3.03	21.43	3.33	18.10	3.53
CR	10.50	2.27	22.57	3.95	23.57	3.40	24.67	2.76
E. c. downiei	6.83	1.58	19.67	3.53	20.70	4.06	20.00	4.03
E. hopetonensis	8.07	1.78	21.87	3.96	20.60	3.48	21.50	3.31
E. icterina								
LSMR	4.97	1.71	20.47	3.77	19.67	3.18	21.67	2.91
MC	2.80	1.00	19.87	2.03	21.00	3.21	20.03	2.65
SR	4.20	1.10	20.63	3.15	19.50	2.15	20.20	3.12
E. jayensis	5.47	1.28	19.23	2.64	19.97	3.64	18.90	3.11
E. mcmichaeli	8.43	1.76	20.17	3.76	20.27	4.45	20.20	4.11



FIGS. 1-4. Photomicrographs of hermaphroditic gonads in *Elliptio*. FIG. 1. *E. arctata* with predominantly testicular tissue (see Table 1: specimen 3). FIG. 2. *E. complanata* form A with much ovarian tissue (Table 1: spn. 1). FIG. 3. Steinhatchee River *E. icterina* with least abundant, ovarian tissue lagging behind testicular tissue in gametogenic development (Table 1: spn. 2). FIG. 4. Mosquito Creek *E. icterina* with a few monoecious acini in a predominantly testicular individual (Table 1: spn. 1). Scale in Figs. 1-3: 50 µm; and in Fig. 4: 20 µm.

DISCUSSION

Van der Schalie's (1970) two monoecious *Elliptio dilatata* were, according to the criterion of gonadal constitution (= "visceral sex" *sensu* Heard, 1975), female-hermaphrodites; in addition, each contained some hermaphroditic acini, a state found here in one Mosquito Creek *E. icterina* with mostly testicular tissue. His monoecious *E. productus* was a gonadal male-hermaphrodite, seemingly with intermingled zones of male and female acini. That state occurred here in a total of 11 individuals. Regionally distinct and separate male and female acini, found in 10 animals, constitute a condition hitherto known only in *Anodonta imbecilis* Say among all other ectobranchous freshwater mussels (= Unionidae *sensu* Heard & Guckert, 1970).

Mature eggs and sperm were not simultaneously present in any of the 22 monoecious animals described herein, and thus none could be termed functional hermaphrodites *sensu* Coe (1943). All of the animals were "occasional", "partial" and "sporadic" hermaphrodites *sensu* van der Schalie (1966, 1970).

Unlike that in the investigated North American *Anodonta*, septal spacing in the outer demibranchs of monoecious *Elliptio* was not consistently correlated with gonadal constitution. As a consequence, a wide range of monoecious conditions is now known in *Elliptio*: (1) nine gonadal male-hermaphrodites had distantly spaced septa and thus long water-tubes in all four demibranchs, i.e., were evidently functional males, and (2) two gonadal female-hermaphrodites had densely spaced septa in the outer demibranchs and distant septa in the inner demibranchs, i.e., would seem to have the capacity to function as both male and female. The remaining hermaphrodites displayed four combinations of gonadal constitution and septal spacing: (3) mostly testicular tissue and intermediate septal spacing in all four demibranchs; (4) mostly testicular tissue, intermediate septal spacing in the outer demibranchs, and distant septal spacing in the inner demibranchs; (5) mostly testicular tissue, dense septa in the outer demibranchs and distant septa in the inner demibranchs; and (6) much ovarian tissue and distant septa in all four demibranchs. Moreover, there are two kinds of animals with monoecious acini: (7) one with mostly testicular tissue and (8) one with predominantly ovarian tissue. Finally, it is possible for hermaphroditic *Elliptio* with either (9) marsupial or (10) non-marsupial outer demibranchs to be gravid.

The monoecious state has been suggested to occur more commonly in cases of existence in standing waters (Weisensee, 1916), restricted contact with potential breeding partners (Cole, 1954; Ghiselin, 1969), small, genetically isolated populations (Ghiselin, 1969), beneficial size dimorphism between different sexes (Ghiselin, 1969), survival and dispersal advantage if the individual has the capacity for autofecundation (Heard, 1975). Although Heard (1975) found a greater frequency of monoecious *Anodonta peggyae* Johnson in flowing water, there is available concerning freshwater mussels little or no other empirical information bearing on these postulates. In terms of size, however, it was noted in this study that large male *Elliptio icterina* from Mosquito Creek were more frequent than females of the same size class. The hermaphrodites in all species (and populations) were of large size, and the condition was not confined to smaller individuals that might have been undergoing sex-reversal.

The detection of hermaphroditic freshwater mussels might be a matter of chance, or it could reflect relative commonness of the condition. Whether van der Schalie's (1970) finding of one gravid female-hermaphrodite in a sample of just three *Lasmigona complanata* (Barnes) truly indicates that monoecious animals are more common in that species than in Steinhatchee River *Elliptio icterina* (only five hermaphrodites among 310 individuals examined) is a moot question. Hermaphrodites were not found here in *E. crassidens* s.l., *E. hopetonensis*, *E. jayensis* and *E. mcmichaeli*, but such animals, if rare, might occur in larger samples.

The low frequencies of hermaphrodites in *Elliptio arctata, E. complanata* and *E. icterina* suggest that those animals play an insignificant role in contributing to breeding in their populations. Still, the existence of hermaphroditism and the cause(s) of it are curious. To better understand sexual expression in hermaphrodites, it will first be necessary to determine the mechanism of sex determination and expression in dioecious animals.

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