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HERMAPHRODITISM IN *ANODONTA GRANDIS*,  
A FRESH-WATER MUSSEL

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It is stated in standard works dealing with the invertebrates that among the Unionidae the sexes are usually separate and that hermaphroditism is as a rule confined to relatively few species. Nevertheless, actual histological examination of the gonads for sex determination has been made for less than a half dozen species of the group. In some species the majority of individuals observed during the course of general collecting was gravid. It was this preponderance of gravid females which led Sterki (1898b: 87-88) to investigate the sex of *Anodonta imbecillis* and to establish that in this species (as stated by Ortmann, 1911) hermaphroditism is the normal condition. A similar observation on the part of the late A. E. Boycott and C. Oldham led the former to suggest that H. H. Bloomer investigate further the sex of *Anodonta cygnea* in the British Isles. Several papers by Bloomer dealing with this subject have appeared during the past ten years, and recently he (1939: 294) summed up his work on *cygnea* as follows: "(6) In *A. cygnea* (*sensu lato*) hermaphroditism is quite common and reveals different phases, the extent of which has yet been only partly explored."

Bloomer's studies of *cygnea* suggested to us the desirability of an investigation into the sex of *Anodonta grandis*, one of

the most common and widespread North American Naiades. Accordingly, as soon as the mussels in our local Michigan lakes became active in the spring (i.e., when the water temperature rose above 10° C.) specimens were collected for a study of the gonad tissue.

Vogt and Yung (1888: 756) in their work with *Anodonta anatina* stated that the testes and the ovaries resemble one another so much that one should examine them microscopically in order to distinguish between them. In the more recent work of Orton with *Ostrea edulis* and Bloomer with *Anodonta cygnea* microscopic examinations of gonad smears were made. At the beginning of our work we also attempted to make smear preparations. Although the advantage due to the rapidity with which smears are obtained is appreciated when large series of specimens are to be examined, the advisability of serial sectioning was soon obvious. Our smears were often contaminated with extraneous materials and in the light of information gathered later from our serial sections of the visceral mass it is quite likely that in many smears one may fail completely to detect the hermaphroditic condition. As a consequence, we finally used dorsoventral sections of the visceral mass almost exclusively in our studies of the gonads. We are well aware that the number of specimens examined is few, but we are convinced that our use of serial sections made possible an accurate diagnosis in each case.

The animals used were removed from their shell by cutting the adductor muscles and carefully releasing the mantle along the pallial line. The visceral mass was fixed in Bouin's fluid, mounted in paraffin, and sectioned at 6  $\mu$ . The sections were stained with Heidenhain's iron-haematoxylin. At first eosin was used as a counter stain, but it was found later that satisfactory differentiation of the eggs and the sperm was obtained without the use of a counter stain.

Fourteen sexually mature specimens of *A. grandis* were sectioned and studied in the spring of 1940 (Table I). Of these nine were males, three were females, and two were hermaphrodites. Another specimen with but a single annulation on its

shell was sexually immature, which indicates that *grandis* possibly does not become sexually mature till it has reached its second year of growth. Further studies, however, should be made on the relation of sexual maturity to age.

TABLE I  
DISTRIBUTION OF THE SEXES IN *Anodonta grandis* SECTIONED AND  
EXAMINED FOR HERMAPHRODITISM

Locality	Date	Male	Female	Hermaphro- dite
Portage Lake, Wash- tenaw Co., Michigan	April 22	6 (2, 2, 4, 5, 7, 11)*	1 (4)	1 (5)
Zukey Lake, Living- ston Co., Michigan ...	May 11	2 (4, 5)	1 (6)	1 (7)
Creek entering Lake Huron, Lambton Co., Ontario .....	May 18	1 (3)	.....	.....
Pond near Huron River, Ypsilanti, Michigan .....	May 25	.....	1 (7)	.....
Totals .....		9	3	2

\* Numbers in parentheses indicate the number of annulations present on the shells and the approximate age of the specimens in years.

The gonad appears to be made up of clusters or acini of sperm and eggs distributed throughout the connective tissue of the visceral mass (Pls. I-III). Ventrally and laterally, the gonad is surrounded by the muscles of the foot. Antero-dorsally, it extends to the lobules of the liver or digestive gland, and posterodorsally to the top of the foot. The sperm and developing egg masses are separate (see figures), and there is no evidence from the material studied that both sperm and eggs are produced by the same gland at different seasons. In this respect *A. grandis*, as well as *A. imbecillis*, differs from *Ostrea edulis* as reported by Orton (1937: 85). Each acinus produces either eggs or sperm, and no acini were found which contained both sex elements.

The acini containing eggs are decidedly different from those containing sperm (Pls. I and II). The egg masses are irregular in outline and usually contain a few large eggs in the lumen with many smaller developing ones irregularly scattered throughout the wall of the acinus. As the eggs grow they are carried into the lumen on a stalk (Pl. I, Figs. 2 and 3; Pl. III, Fig. 3). An occasional sustentacular cell has been observed accompanying the egg as it passes from the wall of the acinus into the lumen (Pl. III, Fig. 3). Among the ova which are in the lumen a prominent double nucleolus is usually present (Pl. II, Fig. 3). The sperm masses are dense in appearance and have a more regular outline and a much less clearly defined lumen. The sperm also develop in the walls of the acini, and in the process of spermatogenesis they form dense masses of sperm morulae (Pl. I, Fig. 3; Pl. II, Fig. 3). As a contrast to our hermaphroditic specimens of *A. grandis*, sections of the normally hermaphroditic *A. imbecillis* are presented in Plate III. Although there are several minor points of difference between the sex elements of these two species, as shown in the plates, they are fundamentally very similar. The points of difference might briefly be stated as follows: in *imbecillis* the sperm acini are distributed along the lateral walls of the visceral mass, but in *grandis* they are scattered about more or less irregularly; the sperm are also further developed in the specimen of *imbecillis* shown; in *grandis* the egg masses are more dense than they are in *imbecillis*.

The development of both sex elements in the specimens examined indicates, in a general way, that in *A. imbecillis* there is an almost equal amount of male and female tissue, whereas the two observed hermaphroditic specimens of *A. grandis* are essentially males. In the latter species, however, the relative development of both eggs and sperm does not suggest a protandric condition. Additional study of the sexes throughout the year may throw further light on this; however, we are justified in concluding that there is now definite evidence that *Anodonta grandis* may be hermaphroditic.

Whether or not both eggs and sperm (see figures of the

hermaphroditic *A. grandis*) will continue to develop and will remain functional, is a question which our investigation leaves unanswered. Okkelberg (1921) found a hermaphroditic condition in the young of the brook lamprey, but as the animals matured one of the sex elements disappeared, leaving the adult to function as either male or female. Since both hermaphroditic specimens of *A. grandis* investigated were mature individuals of five and seven years of age respectively, it is possible that in this species both eggs and sperm may continue to develop, thus permitting the hermaphroditic condition to persist.

Although we were not able to determine the sex of *grandis* without microscopic examination of the gonads, some investigators express their ability to determine the sex of *grandis* by merely examining the relative obesity of the shell. The method obviously is not dependable, and we even question the accuracy of sex determinations on the basis of the presence or absence of glochidia in the gills during periods when the gills are normally charged with them.

H. H. Bloomer (1935: 304-8), following the work of De Blainville and Duméril, gave an interesting history of hermaphroditism in the naiads. From his account, as well as from information available in other studies, there appears to be some indication that representatives of each of the major subfamilies within the Unionidae may be hermaphroditic. Among the Unioninae, Sterki (1898a: 31) claimed to have observed a specimen of *Fusconaia flava* (= *Unio rubiginosus*) "with a few acini producing ova in the gonad charged with copius sperma." He also reported two specimens of *Pleurobema cordatum pyramidatum* (= *Unio pyramidatus*) that were hermaphroditic. Among the Anodontinae both *Anodonta imbecillis* and *henryana* (a southern form of *imbecillis* whose systematic status is as yet uncertain) were reported as hermaphroditic by Sterki (1898a). More recently Ortmann (1911: 308) added *Lasmi-gona compressa* to this group. Bloomer added *Anodonta cygnea* and *anatina*, and we may now append *Anodonta grandis*, thus bringing the total known hermaphroditic species

in this subfamily to approximately five. Among the Lampsilinae the preponderance of females as shown by gravid specimens led Sterki (1898a) to state that *Carunculina parva* (= *Lampsilis parvus*) is hermaphroditic. The former association of *parva* with the genus *Lampsilis* rather than with *Carunculina* is unfortunate, since there is actually no evidence that any of the members of the genus *Lampsilis* are hermaphroditic, although there is every reason to believe that hermaphroditism is common in *Carunculina parva*. Consequently, it may be more common to the *Carunculina* group than to species of *Lampsilis*.

In conclusion, it is clear that hermaphroditism occurs in *Anodonta grandis*, just as Bloomer reported it in *A. cygnea*. The seasonal variation in the condition of the gonads, the differences that may exist in various age groups, the role played by abundance or scarcity of food in influencing sex (since food is known to influence sex in the oyster), and many similar problems are still awaiting investigation.

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PLATE I

- FIG. 1. An hermaphroditic specimen of *Anodonta grandis* Say, with a vertical section of the visceral mass enlarged about three times. A part of gonad from which microphotographs in Figures 2 and 3 were taken is marked by a small square. This specimen had seven annulae and was collected from Zukey Lake, Livingston County, Michigan, on May 11, 1940.
- FIG. 2. Microphotograph of the section in Figure 1 taken under low power. Acini containing sperm, to the right, and eggs, to the left.
- FIG. 3. Microphotograph under high power of a part of Figure 2. Sperm morulae, on the right, and an acinus containing eggs, on the left.



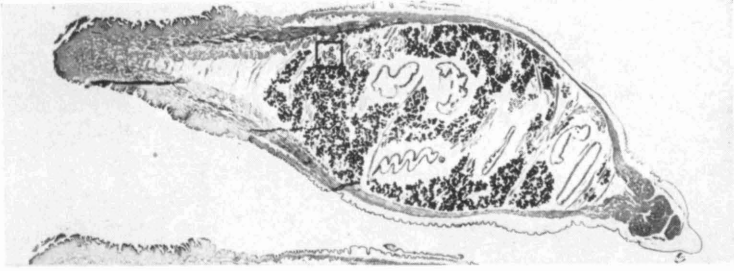


FIG. 1

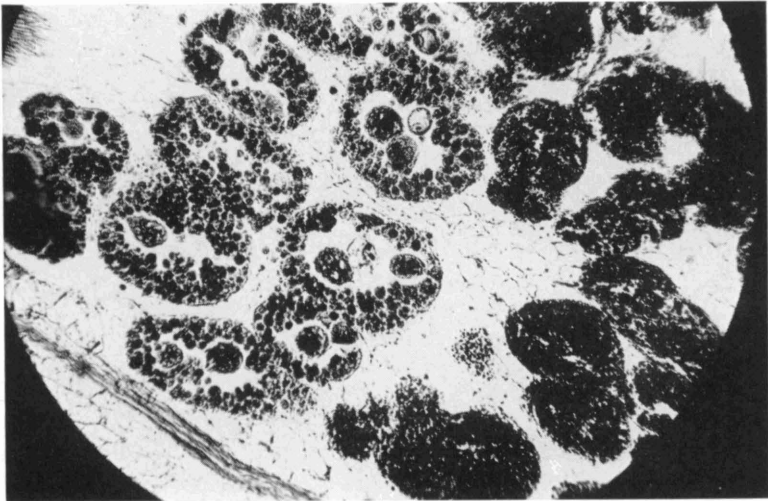


FIG. 2

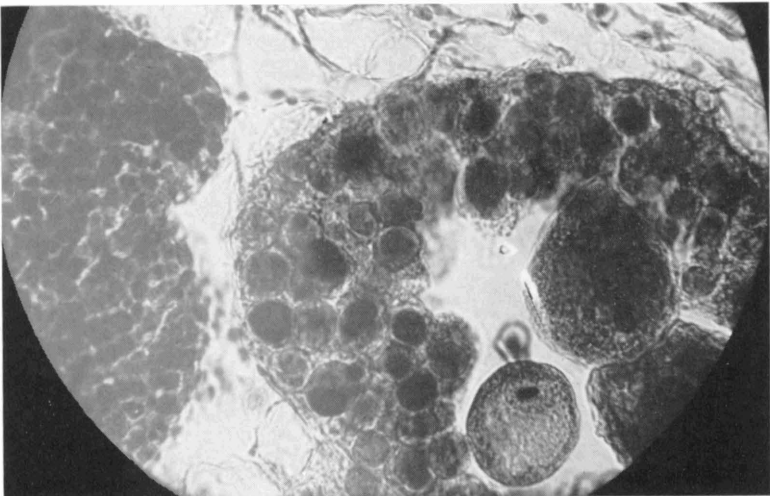


FIG. 3

*Henry van der Schalie and Fred Locke*

PLATE II

- FIG. 1. An hermaphroditic specimen of *Anodonta grandis* Say, with a vertical section of the visceral mass enlarged about three times. A part of gonad from which microphotographs in Figures 2 and 3 were taken is marked by a small square. This is a more anterior section of the same specimen shown in Plate I.
- FIG. 2. Microphotograph of the section in Figure 1 taken under low power. Acini containing sperm, on the right, and eggs, on the left.
- FIG. 3. Microphotograph under high power of a part of Fig. 2. Sperm morulae, on the right, and an acinus containing developing eggs, on the left. Note dark double nucleolus in the *gg* which is free in the lumen.

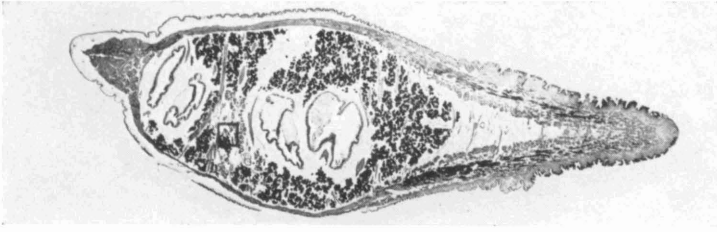


FIG. 1

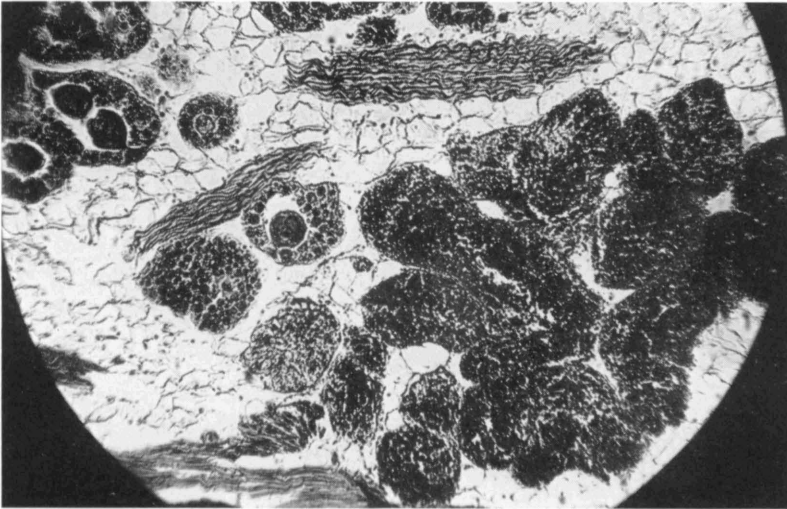


FIG. 2

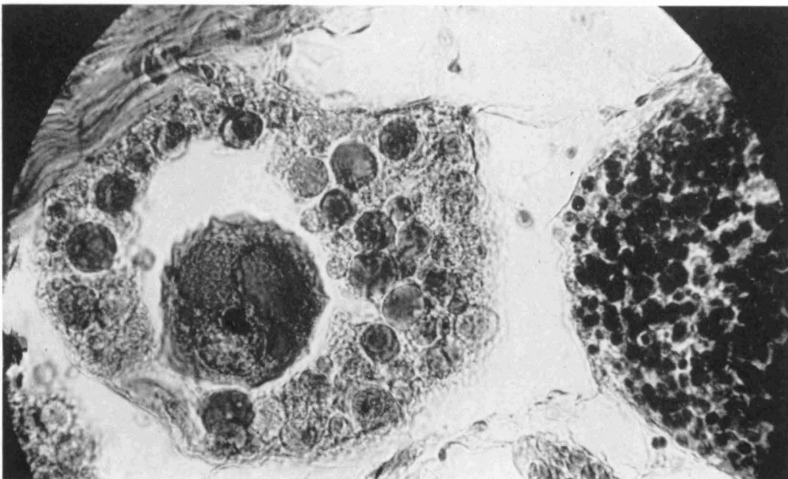


FIG. 3

PLATE III

- FIG. 1. Vertical section of the visceral mass of the normally hermaphroditic *Anodonta imbecillis* Say. Section enlarged about three times with the two small squares indicating parts from which microphotographs shown in Figures 2 and 3 were taken. This specimen had five annulae and was collected from a pond adjoining the Huron River, at Ypsilanti, Michigan, on May 25, 1940.
- FIG. 2. Microphotograph of the section on left in Figure 1 taken under low power. Acini containing sperm (upper part of picture) and those with eggs (lower part of picture).
- FIG. 3. Microphotograph under high power of section on right in Figure 1. Sperm morulae, at the left, and an acinus with developing eggs, to the right. Note the large sustentacular cell on which the egg rests and the stalk which is produced as the egg leaves the wall of the acinus to enter the lumen.

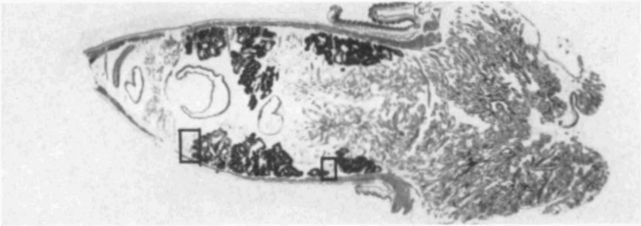


FIG. 1

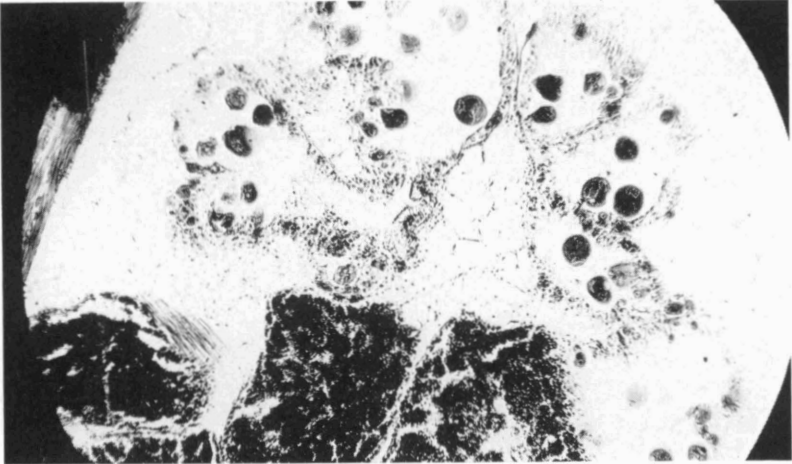


FIG. 2

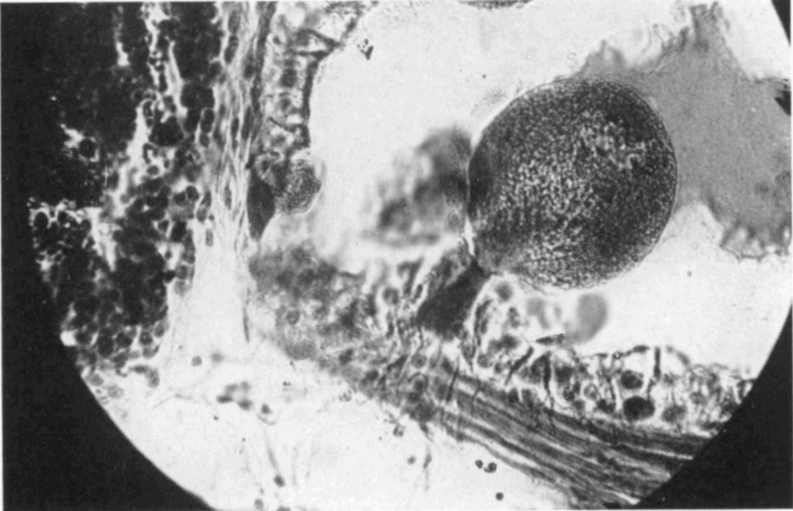


FIG. 3

