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THE DISTRIBUTION, ECOLOGY, AND LIFE HISTORY OF THE MUSSEL, *ACTINONAIAS ELLIPSIFORMIS* (CONRAD), IN MICHIGAN

BY HENRY AND ANNETTE VAN DER SCHALIE

AFTER a series of careful stream surveys of the mussels in Michigan drainage systems some years ago, when these rivers still yielded an abundance of naiades, it was shown (H. van der Schalie, 1938, 1939, 1941, 1945, and 1948) that mussel distribution can serve to interpret post-glacial stream confluences. In spite of the large amount of factual information adduced, there are still some (W. J. Clench and D. F. McMichael in Ann. Rpt. Amer. Mal. Union for 1954:12) who would prefer to have birds or other passive agents account for the patterns of distribution. In an effort to understand better the biology of a key species such as *Actinonaias ellipsiformis* and to relate these data to its striking distribution pattern in Michigan (Fig. 1), additional information on its life history and ecology has been obtained. Originally this study was intended to be sufficiently broad in scope to include the fish-host relations and, if possible, a life history of the mussel in a flow-system in our laboratory. That venture has, as yet, not been possible, but sufficient data have been obtained on the development of these animals, based on field work and many serial sections of the gonads, to provide an understanding of the periods when eggs and sperm are formed and of the season when the glochidia are shed to infect the proper fish host.

The site for most of the collections has been Ore Creek, a small creek below Hartland, Livingston County, Michigan. One is always impressed in traveling north, from the Huron River drainage to the Saginaw system, by the low, almost imperceptible, divide between those drainage systems. It is even more impressive to realize that *Actinonaias ellipsiformis* has never crossed that low divide to enter any of the streams of southeastern Michigan, nor has *Lampsilis fasciola* managed to leave the latter region to enter the Saginaw, or any of the west-flowing streams of Michigan (Fig. 1). This faunal relationship is definite, but there is need to emphasize a difficulty that arises when those not familiar with naiad systematics misidentify species that superficially appear similar. *Actinonaias ellipsiformis* is often mistaken for a common, wide-ranging small species, *Micromya iris* (more recently named *Villosa iris*), in Michigan. It is important that these species be differentiated. To assist in keeping them separate, they are figured here (Plate I). Some of the essential shell characters are as follows: *A. ellipsiformis* has a thicker shell, heavier hinge teeth, a fine and almost imperceptible beak sculpture, a ray pattern consisting of many fine wavy rays, and a post-basal margin that dips (mainly in females). All these characters separate this shell clearly from *Micromya iris.*

Over the years *Actinonaias ellipsiformis* has been known under a variety of names. Conrad (1836) described it as *Unio ellipsiformis,* while Lea (1845) used *Unio spatulatus.* Call (1900) used the latter

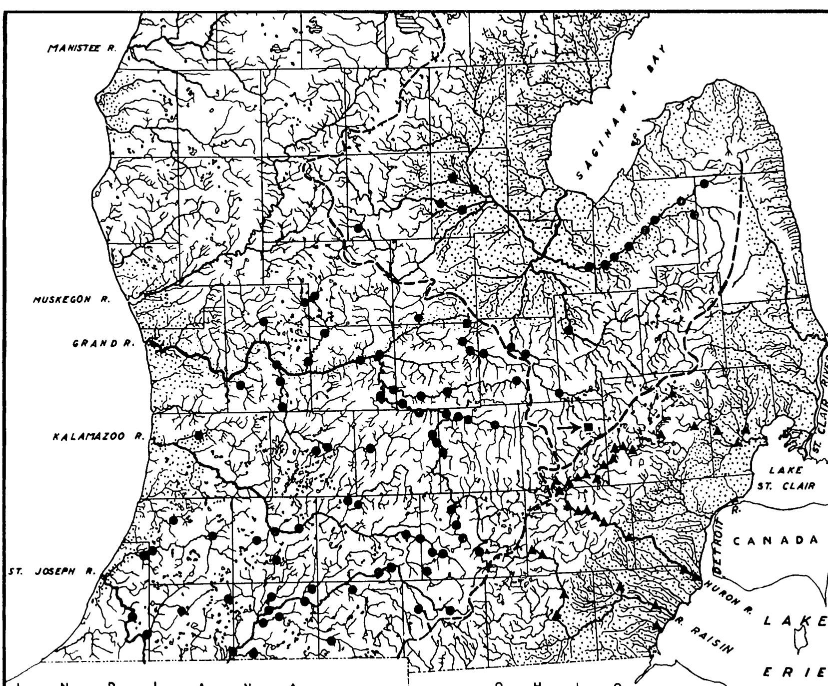

FIG. 1. Distribution of *Actinonaias ellipsiformis* (Conrad), circles, and *Lampsilis fasciola* Rafinesque, triangles, in Michigan. The dark square represents the region in the Ore Creek drainage at Hartland, the site from which specimens were taken for gonadal studies. Note proximity of streams in the drainages and the strikingly separate distribution patterns.

name; F. C. Baker (1898) also used *spatulatus*, but referred it to the genus *Lampsilis*. Simpson (1900; 1914) adopted *Lampsilis ellipsiformis* (Conrad). Most authors since then have used the species name *ellipsiformis*, but there has been more than the usual amount of disagreement as to the proper genus to which this species should be referred. The choices seem to range from *Lampsilis* (Scammon, 1906) to *Nephronaias* (Utterback, 1916) to *Eurynia* (*Micromya*) *venusta* (Lea) (Ortmann, 1918) to *Ligumia* (Grier and Mueller, 1923; F. C. Baker, 1928). The generic status of the species in the Lampsilinae remains an open question since too little is known, as yet, of the details that relate to the anatomy of these genera. However, there is no question but that the characters of the shell of this species relate it more with *Actinonaias* than with what is generally considered a typical *Lampsilis* or *Ligumia* or *Micromya* (*Eurynia* or *Villosa*). Call (1900), Utterback (1916), and others have referred to the error often made when this species is mistaken for the young of *Actinonaias carinata* (Barnes), the well-known "Mucket" in the button industry.

The distribution pattern outside of Michigan deserves more attention than hitherto given it. Since this mussel usually inhabits small rivers and does not attain a size that would make it useful for button manufacture, it has not generally been cited in the papers that deal with mussel surveys. Bryant Walker (1892), in an early account of the shell-bearing mollusks of Michigan, indicated that Conrad's type specimens were originally from Michigan. The records available in our collections and those cited in the literature reveal that it occurs in northern Indiana, Illinois, Wisconsin, Iowa, Kansas, Missouri, Oklahoma and Arkansas. Dawley (1947) did not record it in Minnesota. It does not occur in the Mississippi River proper except as a rather rare species in the region of Lake Pepin (Grier and Mueller, 1923; H. and A. van der Schalie, 1950). In the west and southwestern part of its range, some clarification is necessary since Ortmann (1918) has expressed the opinion that *"Lampsilis" venusta*, *L. ellipsiformis*, and *L. pleasi* are all the same; Frierson (1927) lists them as separate species.

In order to understand better the life history of *A. ellipsiformis*, collections were made to determine the size, age, sex, and the state of gonadal development during each month of the year, but only a few animals were collected in the very coldest period (December to April) when little activity and development is in evidence in this latitude. While most of the animals were taken from Ore Creek below Hartland, Livingston County, Michigan (Fig. 1), specimens for comparison were collected also in Cranberry Creek, near its junction with the Shiawassee River at Byron, and in the headwaters of the Grand River above Jackson (Flansburg Road). The data obtained from specimens in these collections were tabulated to determine: locality, date, length of shell in millimeters, number of annuli, and whether or not gravid. This information is given here only in summary form.

As a member of the Lampsilinae, *Actinonaias ellipsiformis* has a typical long-term (bradytictic) breeding cycle in which the gills become gravid in the late summer and early fall and the glochidia are shed in late spring or early summer. It is not unusual to find some specimens becoming gravid while others have not entirely shed the glochidia of the past year. In any case, the gills become highly modified so that it is relatively easy to count the number of ovisacs present in the posterior portion of the outer gills. F. C. Baker (1928:264) stated: "Marsupium occupying posterior half of outer gills, consisting of about 20 ovisacs." Our data permitted a comparison between the size of the females and the number of ovisacs in the gill on one side of the animal. When these figures are compared (Table 1) it is evident that there is a relation between the size (or age) of the animal and the number of ovisacs. The average of 20 on one gill given by Baker is a good average for females that are 5 years or older (between 45 and 52 mm. long).

Among the many specimens sectioned it was evident that the gonads remained in an undeveloped state until the third year; it was not possible to determine the sex of animals in their second year. The distribution of age classes in the 218 specimens of *Actinonaias ellipsiformis* studied was as follows: Age, 2 (number, 12); 3 (38); 4 (52); 5 (58); 6 (30); 7 (12); 8 (9); 9 (2); 10 (3); 11 (0); 12 (2). As indicated, the range in age of the mussels collected throughout the active portion of the year is 2 to 12 years with most of the group in the 3- to 6-year range. It has always been a matter of concern in collecting fresh-water mussels that so few young appear at many of the stations. In those situations the distribution of the age groups as represented may reflect unfavorable conditions that are becoming more and more accentuated as many Michigan rivers are increasingly subjected to adverse influences, such as power dam construction, pollution, and silting. For example, Ore Creek has changed considerably in the seven-year period during which specimens were collected for these studies. While early in the program (1954) one could find an abundance of *A. ellipsiformis* in the creek just below the dam at Hartland, the construction of a superhighway has almost eliminated the fauna from the

TABLE 1

RELATION OF SIZE (LENGTH IN MM.) TO NUMBER OF OVISACS (ON ONE GILL) IN *Actinonaias ellipsiformis*

Size (length in mm.)	Number of Ovisacs on one gill									Average
32	9									9.0
33										
34	10									10.0
35	10	11	10							10.3
36	10	9	16	9						11.0
37	11	9	14							11.3
38	15	12								13.5
39	12	13	13	12	12	14	15	15	14	13.3
40	11	13								12.0
41	16	14								15.0
42	15	18	15	19	17					16.8
43	16	15	18	16						16.3
44	18	16	19	20	16	20	18	18	20	19.4
45	18	20	18	18	21	19	20			19.1
46	21	22	19	23	18	18	20			21.3
47	17	15	18	22	24	20	18			19.1
48	20	22	22	21						21.2
49	20	20	20	20	20					20.0
50	20	20								20.0
51	19	20	20	17						19.0
52	20									20.0
53	23	20								21.5
54	23									23.0
55	25									25.0

stream there. More recently a dam has been constructed on this creek below Parshallville so that an extensive zone in the valley has now been formed into a lake. A species conditioned to life in riffles is not likely to persist with such a drastic change in its ecology.

It has become increasingly important to find a means to determine the age of mussels, especially in studies in which they ("clams") are used to measure the amount of contamination in fallout with Strontium 90 (D. J. Nelson, 1962). The method employed here has been to count the number of annuli shown on the shell. In some groups, such as those that live in lakes, the prominent annular growth rests shown on the shell are relatively easy to see, but in a small species such as *A. ellipsiformis* the growth increments are small and among the older specimens it is almost impossible to make an accurate count of the annuli. For practical purposes, the aging as shown in our tables is reasonably accurate, but there is a need for the development of techniques that would give better results.

Only occasionally is it impossible to determine whether an animal is a female since they normally have marsupia distended with glochidia. One sectioned gonad of a specimen (Pl. I, lower right) shows how the tissue of a female can be so crowded with developing trematode parasites (in this case with growing *Macrocercus*-like cercariae) that the animal becomes sterile and eggs then fail to reach the marsupia of the gills. Of the 218 mussels previously listed only 4 were parasitized, all of them from one locality near Byron, Michigan. In the case of a male (Pl. I, lower left), the infestation was relatively light and large numbers of sperm were still being produced. Undoubtely there are sites where infection might run high and most of the females could be rendered sterile by parasites.

Whether male or female, sexual maturity is usually not attained until the animal reaches the third year. Such immature animals appear as unsexed in the tables. Although most of the animals collected were sectioned to enable an analysis of sex and its development, only one hermaphrodite was discovered. This case was so unusual that it warrants special consideration and it will be discussed in a current study dealing with hermaphroditism among the freshwater mussels. Although random samples from several sites produced a preponderance of one sex over the other, the sex ratio of the total number studied clearly gave an almost one to one ratio—130 males to 108 females (Table 2).

Development of Male Gonad.—Many males were sectioned. The amount of sperm produced is prodigious. The illustrations (Pl. II) indicate that spermatogenesis can be found during all months of the year. During the active and growing season, which in Michigan is between April and late October, mature sperm are most common from the middle of May into July. In August, the sectioned specimens again indicated that most of the gonadal tissue was active with the acini functioning to produce early stages in spermatogenesis. These sperm remain in a developing state and evidently are shed as mature sperm in late spring and early summer.

Development of Female Gonad.—While the glochidia of the previous year are still carried in the ovisacs of the outer, posterior gills of females, the gonads in April (Pl. III, upper left) contain many eggs in early stages of development. In this condition the walls of the acini are usually thick and have many eggs and nurse cells in early stages of development. The eggs enter the lumen of the acinus in increasing numbers, but it is only towards June that they begin to show an encasing vitelline membrane (Pl. III, upper right). By the middle of July most of the eggs, still in an unfertilized state, have moved to the gills where they are fertilized and carried until the following spring and early summer. In August the gonad again shows many eggs in early development and the marsupial gills become charged with developing eggs and glochidia.

The many gonads examined appeared to be in an active state throughout most of the year. As a consequence, there is a virtual overlap in the gravid state of females so that one can find individuals in

TABLE 2

NUMBER AND SEX RATIOS OF *Actinonaias ellipsiformis* (CONRAD) COLLECTED OVER EIGHT SEASONS (1954–1962) IN SOUTHERN MICHIGAN.*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Gravid (♀)	..			17	21	28	1	4	17	19	1	..	108
Not Gravid (♂)	3	.	.	6	13	40	12	8	35	5	8	..	130

* In all, these numbers represent 18 collections made throughout the year yielding a total of 238 specimens. The proportions of males and females taken at any one of the stations were not at all in a one to one ratio, but when the total number is considered they are in about equal numbers. The few gravid specimens found in the summer (July and August) is a characteristic pattern for such a long term breeder. It is unfortunate that one never finds more than a few at a station and when one visits the site at monthly intervals the problem of depleting the fauna becomes a real one.

August that have not yet completely shed glochidia produced from eggs of the previous year, while other females in the same collection may be starting to become gravid with eggs produced during the ensuing year. Consequently, with the typical modification of posterior outer gills among the females, it is usually easy to determine the sex of animals without sectioning them. Most of the specimens examined, measured, and aged, were found to have been properly sexed by examining the gills for marsupia and the branchial mantle edge for papillae. In addition to the modified marsupia (many of them gravid), there are papillae present on the mantle edge back of the branchial siphon where the mantle itself not only is thickened but usually has a black or brown pigmentation.

The glochidium (Pl. I, center left) of *Actinonaias ellipsiformis* has not hitherto been figured. It compares very favorably in outline and general appearance with that of *Actinonaias carinata* (formerly *Lampsilis ligamentina*) as illustrated by Suber (1912, pl. II, fig. 18). His measurements for that species are: 0.220 $\times$ 0.260 mm; an average of 7 glochidia of *A. ellipsiformis* mounted and measured with an ocular micrometer by us was 0.237 $\times$ 0.285. The glochidia of this species, which is considerably smaller in its adult stage, are, nevertheless, larger than those of *A. carinata,* a species known as the "Mucket," and one of the best button-producing shells.

Like many fresh-water mussels, *A. ellipsiformis* occupies a very definite ecologic niche. As can be seen by examining the map of general distribution (Fig. I), it appears to be most common in small rivers and creeks. This observation is strengthened by data obtained in a survey of the main portion of the Grand River (H. van der Schalie, 1948:6–7) where it is clearly shown to be very rare in the main portion of the river between Muir and Grand Rapids. During the past seven years many collections (marked by a square in Fig. 1) were made in Ore Creek, the stream that served as a main source of supply for specimens used in the seasonal studies of gonadal development. Only those portions of that creek where the bottom was rough gravel and sand, with swift to moderate current, yielded numbers sufficient for the series needed in these studies. The specimens were obtained usually by dragging a heavy meshed screen, mounted on a pole, through the bottom to remove the gravel substrate and sieving it vigorously; small series of mussels were found among the stones and gravel.

In view of the well established relationship between mussels and fish hosts, on which they must develop, it was suspected that a fish might be found, in riffles flowing over a coarse rocky bottom, that would have a distribution pattern in Michigan similar to that observed for this mussel (Fig. 1). If there were such a fish, it would be possible to test it as a possible normal host. The work of completing the life history of *A. ellipsiformis* would then be made much easier. It turned out that none of the species of fish that are known to occur with this mussel, nor any species of fish of known distribution in Michigan, actually shows a pattern that could be superimposed on, or could match, that of the mussel; most of them have a far wider range in Michigan. By the same token, it is now evident that in its characteristic pattern this mussel is far more conservative in extending its range than is its fish host. While in this case judgment may be premature, it has been evident from most studies of mussels and their relation to former stream confluence that, because of demands for timing in their life cycles, mussels are indeed very helpful in establishing pre- and post-glacial drainage relationships (van der Schalie, 1963).

On 25 June 1959, fish were seined in Ore Creek, just below Hartland, Livingston County, Michigan. This seining was done under ideal conditions with the weather sunny and fair. The following 16 species of fish were taken: *Lepomis megalotis* (Long-eared Sunfish), *Lepomis gibbosus* (Pumpkinseed), *Notropis cornutus* (Common Shiner), *Notropis heterolepis* (Blacknose Shiner), *Semotilus atromaculatus* (Creek Chub), *Campostoma anomalum* (Stoneroller), *Hybopsis biguttatus* (Hornyhead Chub), *Catostomus commersoni* (White Sucker), *Pimephales notatus* (Bluntnose Minnow), *Poecilichthys caeruleus* (Rainbow Darter), *Boleosoma nigrum* (Johnny Darter), *Catanotus flabellaris* (Fantail Darter), *Perca flavescens* (Yellow Perch), *Umbra limi* (Mud Minnow), *Labidesthes sicculus* (Brook Silversides), *Esox lucius* (Northern Pike).

SUMMARY AND CONCLUSIONS.—In Michigan, *Actinonaias ellipsiformis* has a circumscribed distribution pattern; formerly it occurred only in streams of the southern half of the Lower Peninsula which flowed toward Lake Michigan. During periods of confluence it entered the Saginaw Bay drainage, but it has not migrated into any of the streams of southeastern Michigan draining into Lake St. Clair or Lake Erie. This mussel inhabits mainly small streams and in this respect it complements the only other species of the genus in Michigan, *Actinonaias carinata*, which usually inhabits the large rivers. Within the small streams it appears to be restricted to zones with firm bottom conditions consisting of sand and coarse gravel which are subjected to moderate or strong current. Although it was not possible to determine the fish host among sixteen species seined in the habitat, it is likely that the natural host will be a fish that frequents a stony bottom in the riffles. None of the fish seined have the restricted range of this mussel.

Over a period of seven years specimens of *A. ellipsiformis* were collected during the seasons when the animals were active to permit histological examination of the developmental conditions of the gonads. This species is a typical long-term (bradytictic) breeder; the males have developing sperm in most seasons with mature sperm appearing especially in the spring; the females produce eggs in the fall and spring. The eggs pass to the ovisacs in the gills in late summer; here they develop into glochidia that are shed in late spring and early summer of the following year. The gravid periods of the females often overlap. The animals do not become sexually mature until the third

year of growth; the largest individuals reach a length of about 55 mm.; and most individuals in the population die before the tenth year. The number of ovisacs varies with the size (age) of the individuals; they range from 9 per outer gill in the youngest to 25 in the oldest examined.

The rapid changes in streams of Michigan make it increasingly difficult to find sites for carrying out life history studies of a species such as this one. A field and laboratory study designed to determine the normal fish host is contemplated.

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PLATE I

UPPER LEFT: Characteristic appearance of shell of *Actinonaias ellipsiformis* (Conrad).

UPPER RIGHT: The shell of *Micromya iris* (Lea), more recently named *Villosa iris* (Lea), showing the differences as compared with *A. ellipsiformis*.

CENTER LEFT: Glochidia of *A. ellipsiformis,* × 40. Actual size, 0.237 × 0.285 mm.

CENTER RIGHT: Glochidia of *A. ellipsiformis* as seen in a section of a gravid gill, × 40.

LOWER LEFT: Gonad of a male *A. ellipsiformis* showing the way spermatogenic tissue is crowded out by a developing trematode parasite, × 40.

LOWER RIGHT: Female gonad of *A. ellipsiformis* with trematode parasite development crowding out developing eggs. This animal also did not have glochidia in its gill marsupia while those not parasitized did, × 40.

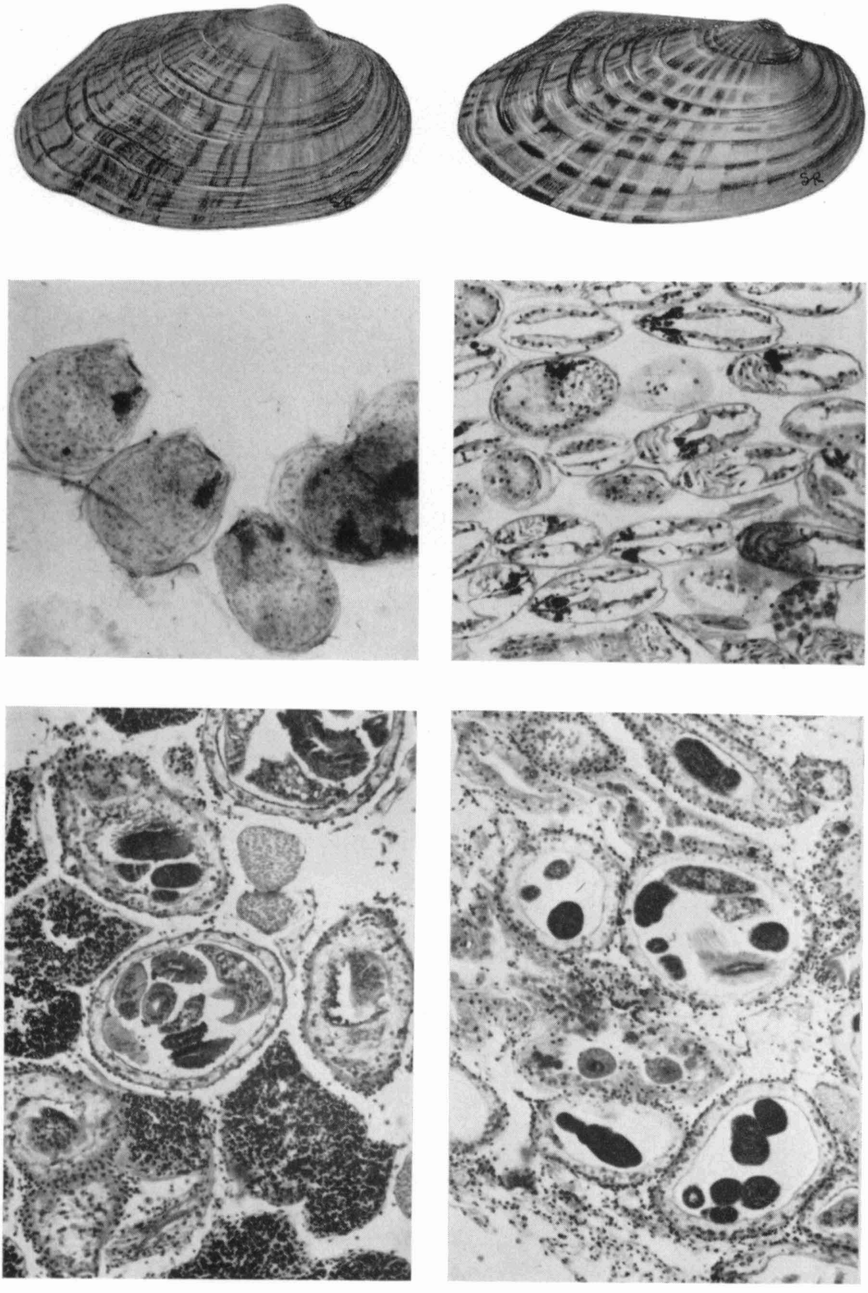

PLATE I

PLATE II

Upper Left: Male gonad showing early spermatogenesis in a specimen killed and fixed 26 April, 1962; note that mature sperm do not yet occur in these acini, ×40.

Upper Right: Male gonad in early summer as seen in a specimen killed and fixed on 25 June, 1959; note that many mature sperm occupy the center of the acini with spermatogenesis taking place only in the outer, peripheral regions, × 40.

Lower Left: Male gonad in early fall (30 September, 1954) with all of the mature sperm shed and spermatogenesis starting in preparation for the next season, × 40.

Lower Right: Male gonad in the late fall (21 October, 1960) with very active spermatogenesis leading to the condition shown in the upper left of this plate, × 40.

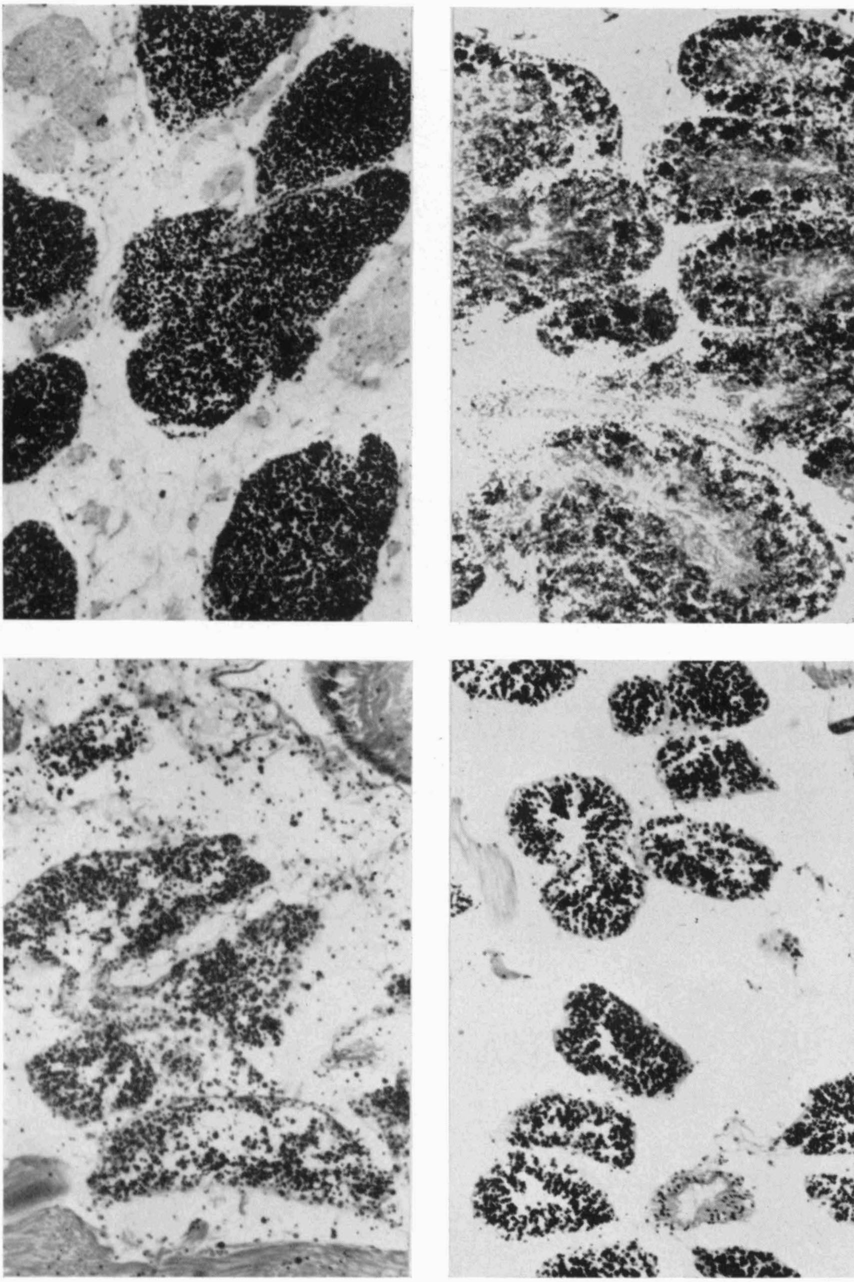

PLATE II

PLATE III

UPPER LEFT: Gonadal acini of an animal in the spring (fixed 7 April, 1960); note that the walls are relatively thick and many eggs are budding into the lumen, × 40.

UPPER RIGHT: Section of a gonad of an animal in early summer (25 June, 1959) showing that the walls of the acini become thin and the eggs are surrounded by vitelline membranes, × 40.

MIDDLE LEFT: An enlarged acinus showing crowding of eggs in gonad during the summer; the spaces between eggs result from shrinkage in the process of dehydration, × 200.

MIDDLE RIGHT: Mature egg of gonad at left, × 400.

LOWER LEFT: Early fall (30 September, 1954) condition of gonad with oogenesis at an early stage with the walls of the acini again becoming thickened but only a few eggs are entering the lumen, × 40.

LOWER RIGHT: Later fall (21 October, 1960) condition of female gonad with the walls of the acini again thickened and approaching the condition (upper left) found in the spring of the year, × 40.

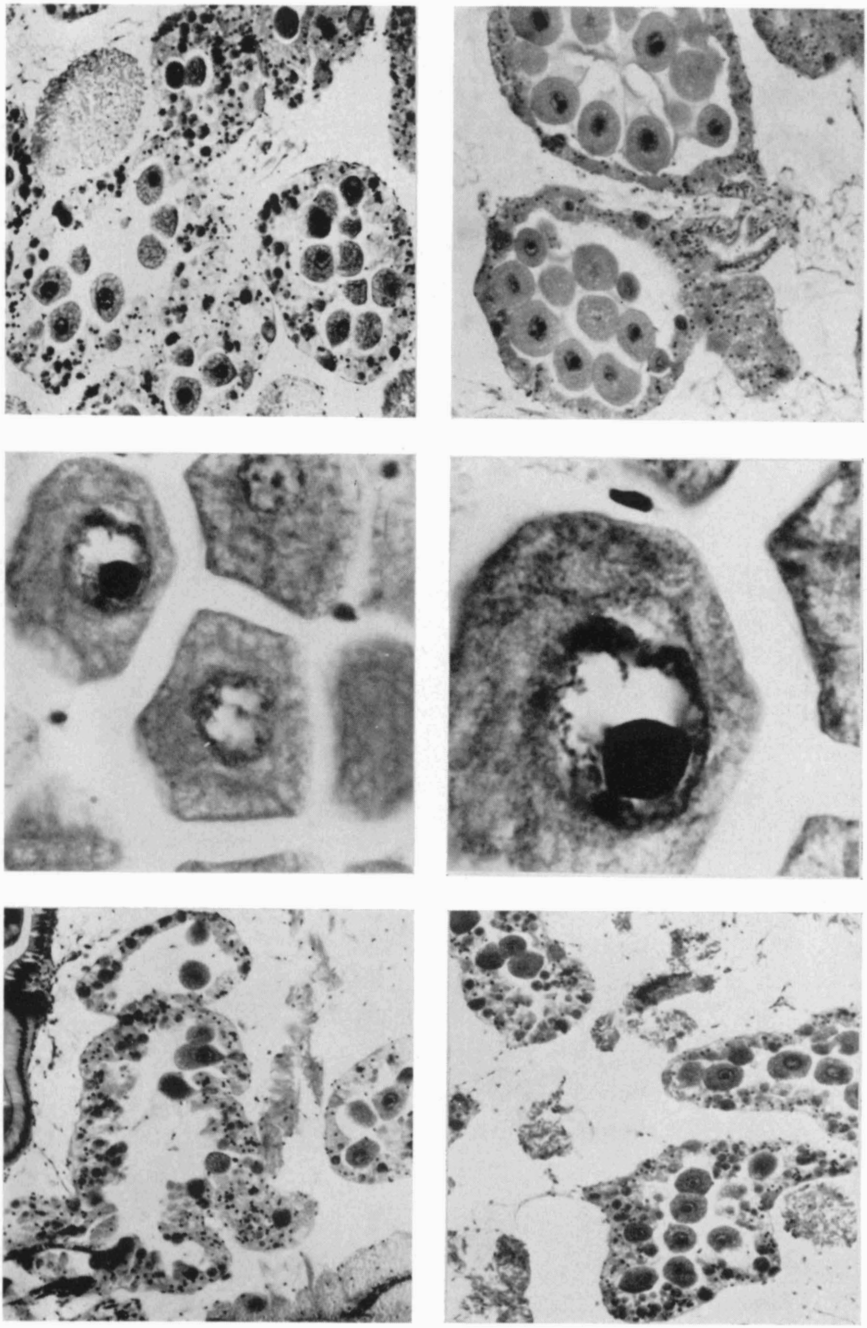

PLATE III