PART IV.—BIONOMICS.[1]

By R. B. SEYMOUR SEWELL.

The Life-history.

The breeding season of *Vivipara bengalensis*, that is to say the period during which the young are born, commences early in the year and seems to extend throughout the whole of the hot-weather and monsoon periods up to and probably beyond September; but the period of most intense reproduction is from April

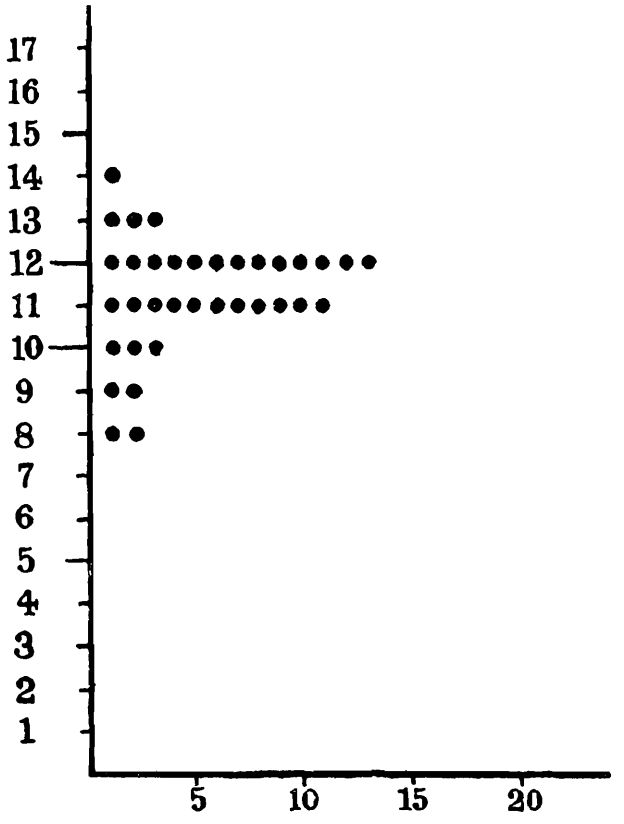

FIG. 20.—Length measurements of 35 examples of young *Vivipara bengalensis*, born in experimental tanks, at the age of 3 months old.

to July. During this period the uterus of a mature female is crammed with eggs, containing young in varying stages of development, but young Viviparidae are to be found *in utero* at all seasons of the year. I have even found them to be present in examples that had buried themselves in the mud at the bottom of a tank in Lahore at the onset of the cold weather and were dug up in December. Examples of *Lecythoconcha lecythis*, dug from

[1] In compiling this section I am greatly indebted to Dr. Annandale for many additional notes and observations.

dried mud at the edge of a swamp in Manipur, and brought to Calcutta in March, produced living young when placed in water.

Newly born examples of *V bengalensis* are comparatively well-developed and already show $3\frac{1}{2}$ turns of the spiral in the shell. In a preceding part of this paper Dr. Annandale has described the young shell.

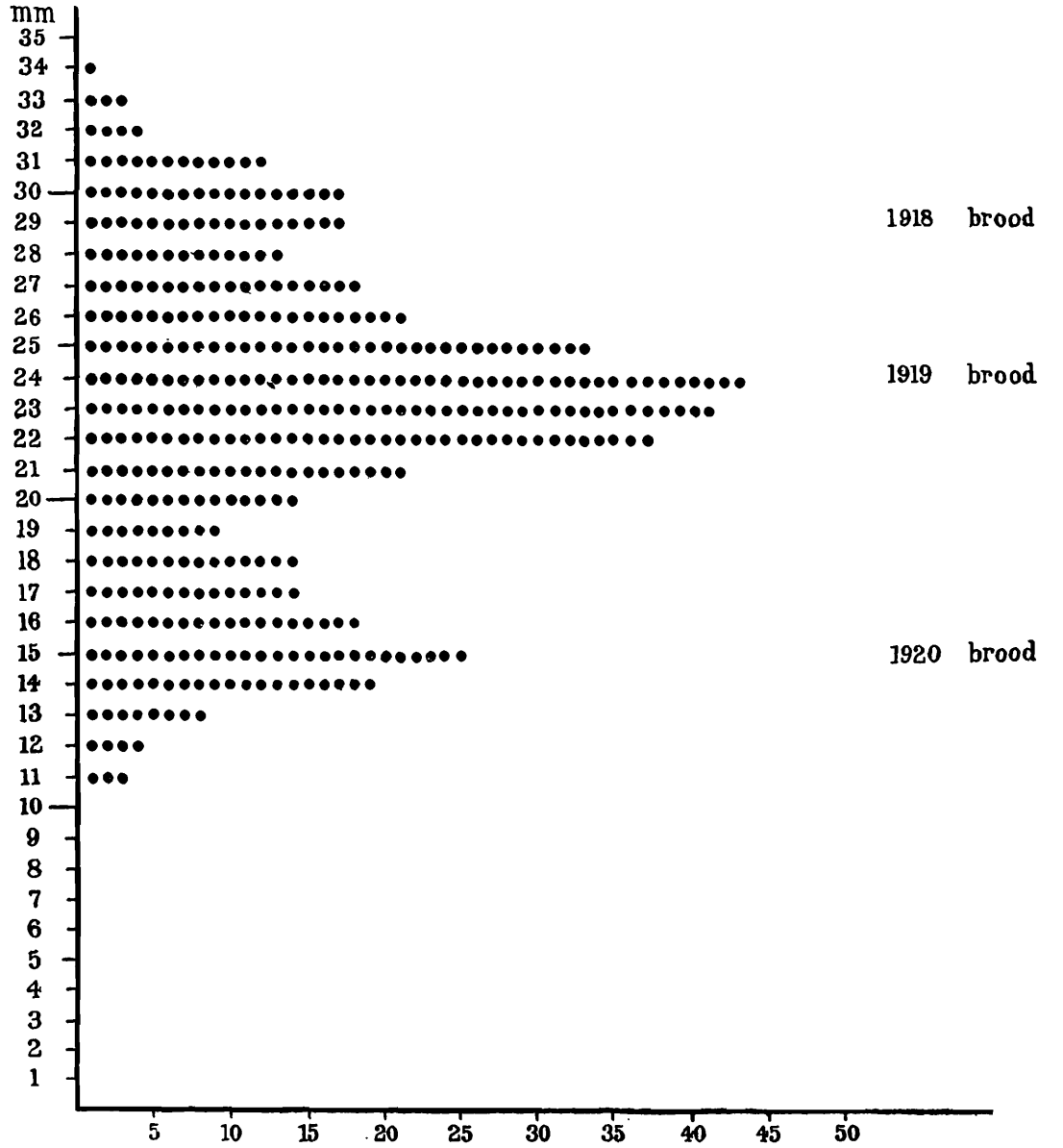

FIG. 21.—Length measurements of 409 examples of *Vivipara bengalensis*, taken from the tank in the Indian Museum compound, July 26th to August 2nd, 1920.

Growth at first proceeds rapidly. Newly born individuals measure approximately 3 mm. in maximum height from the apex of the shell to the margin of the peristome, but in less than three months a complete extra whorl has been added and the height of the shell is now approximately 15 mm. During May and August, 1919 a number of examples of *Vivipara bengalensis* were kept under observation in experimental tanks in the Indian Museum. These adults were introduced into the tanks between the 2nd and 23rd of May, 1919. Young were deposited in large

numbers and at the end of July several were collected and measured, and the results obtained are given in fig. 20. The measurement taken was the maximum height as defined above, and the individuals fall into a well-defined regular group, the measurement ranging from 8 mm. to 14 mm. and having an average of 11·3 mm. Since all these examples were less than three months old, we get some idea of the very rapid growth that takes place in early life. At the same time a number of adult examples from the pond in the Museum compound were measured and were found to fall into a group having a length measurement of 20 mm. to 27 mm. This I believed to represent the size attained after one year of life, and, in order to check this, between July 26th and August 2nd, 1920, 409 examples from the same pond of all sizes except the very smallest, which had obviously only recently been born, were collected and measured. The results are given in fig. 21. It will be seen that we have two well-defined groups with their maxima corresponding to a height measurement of 15 mm. and 24 mm. respectively.

The members of the first group correspond very closely both as regards size and degree of development with the examples hatched and reared in the experimental tanks in 1919. They are somewhat larger, but the experiments of Semper (1874), De Varigny (1894), and others have shown that growth is more rapid under favourable conditions and in large areas of water with efficient natural aeration than it is under artificial conditions in small aquaria, and it seems reasonable to conclude that the individuals comprising the group of the 1920 brood were approximately three months old and had been born about April. This rapid rate of growth, from 3 mm. in height when born to 12–15 mm. at approximately three months, corresponds closely with the results obtained by Lyon (*vide* Baker, 1911, p. 51) in which examples of *Limnaea* (*Galba*) *reflexa*, measuring 2·00 mm. at 6 weeks old, attained to a height of 5–10 mm. at 12 weeks and 26·0–28·5 mm. at one year old, or by Woodruff (*loc. cit.*) who found that examples of *Limnaea* (*Radix*) *auricularia* increased from 0·75 mm. in height when born to 11·50 mm. at 4 weeks. As age progresses, the rate of growth naturally becomes slower, since other and equally important processes are going on in the young individual, especially the attainment of sexual maturity.

The second group, having an average height of 24 mm., corresponds exactly with the adult examples taken from the pond in August, 1919.

It seems clear that these two groups of *Vivipara bengalensis* correspond respectively to the 1919 and 1920 broods, but there are indications of a still further group having an average height of 29–30 mm.; this however does not appear very clearly in the chart owing to overlapping with the group of the 1919 brood. These large individuals, which were much fewer in number than those of the preceding group, I take to represent individuals who have survived for a further period of one year and who represent the

1918 brood. The great majority of these large examples show a well-marked 'varix' across the middle of the body whorl of the shell, thus indicating that there has been a period of arrested growth followed by a subsequent increase in size. The distance from the apex of the shell to the umbilical end of the varix measures approximately 24 mm. which corresponds closely to the average height attained by examples that are one year old, and it is evident that the period of arrested growth corresponds to the second winter of their life-history. The maximum length of life of any individual appears then to be two years, but the vast majority of individuals die after one year. Each year towards the end of the rains there is a very heavy mortality among the molluscan fauna of the ponds and tanks, etc., in this country. This was first noticed in a period of exceptional drought by Dr. Annandale, who called attention to it in his preliminary report to the Government of India on the mollusc survey of the Madras Presidency, but he attributed it to the partial drying up of the pools and the consequent foulness of the remaining water. The same mortality, however, occurred, though perhaps on not quite so large a scale, in ponds in Calcutta in August, 1919, where no such causative agent could be suspected, and it appeared to be a natural phenomenon affecting many different genera of molluscs, including *Vivipara*.[1] In *V bengalensis*, the vast majority of individuals born in the preceding year die during this period, only a few surviving for a second year. This heavy annual mortality among the freshwater molluscs is a phenomenon of considerable antiquity, for Annandale (1920 (*a*), p. 53) has adduced evidence that it was in existence in the Intertrappean (late Cretaceous) beds of this country.

The sexual differences in the antennae of *Vivipara bengalensis* render it easy to carry out an investigation regarding the influence of sex on the individual. I have been quite unable to detect any difference in the shape of the shell, but measurement of a number of individuals of both sexes, collected haphazard from the pond in the Indian museum compound[2] shows very clearly that there is a quite appreciable difference in height. In fig. 22, I have given the measurements of 147 female and 57 male examples and it shows that the average height of females of one year old is 25·0 mm. and of two years old 30·0 mm., whereas males of the corresponding length of life have an average height of only 22·0 and 27·0 mm. respectively.

Difference in size in the two sexes of *Vivipara vivipara* was noticed as long ago as 1695 by Lister, and more recently Wood-Mason (1881, p. 86) has recorded the same sexual character in

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[1] *Vide* Annandale and Sewell "Progress report on a Survey of the Freshwater Gastropod Molluscs of the Indian Empire and of their Tremetode Parasites." *Ind. Journ. Med. Research* VIII, p. 119.

[2] Examples living in this pond are considerably smaller than those found in certain other localities.

examples of *Vivipara crassa* (Hutton) that he obtained and examined in Sylhet. This difference in size is also known to occur in other genera and according to Cooke (1895, p. 134) "is markedly the case in *Littorina*, *Buccinum*, and all the *Cephalopoda*." It is generally assumed that the difference in the two sexes is related to the viviparous habit and is dependent on the necessity for

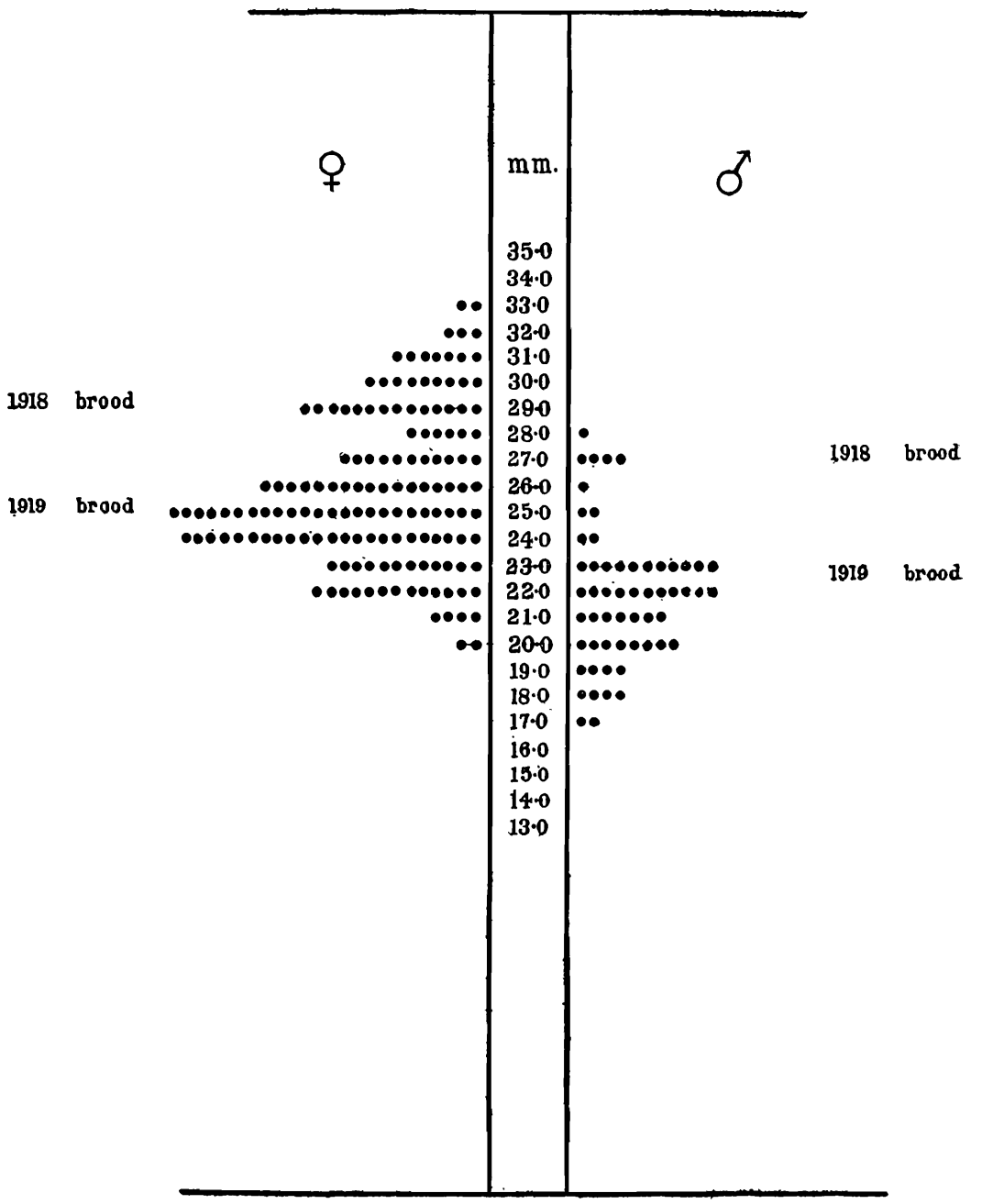

FIG. 22.—Measurements of 147 ♀ examples and 57 ♂ examples of *Vivipara bengalensis*.

increased space in the shell of the female in order to accommodate the large numbers of contained young in utero. If this were the sole causative agent, one would expect to find the condition constantly present, but this expectation is not fulfilled in the Viviparidae of this country, for in certain species no difference can be detected in the two sexes, while in others there is a difference

in the shape of the shell though not in height. In *Vivipara oxytropis* (Benson) Annandale found that while there was no difference in the height of the shell of the two sexes in the adult, the female shell was considerably broader than the male. In *Lecythoconcha lecythis* (Benson) also large shells were of the same height, but the whorls of the spire increased in size more gradually in the female. In the genus *Taia* Annandale (1918, p. 137) found that there was very little sexual variation in the shell in *T intha*, though he found specific differences in sexual variation in the genus as a whole. In *Lecythoconcha* and *Taia* the young *in utero* are relatively large as compared with *Vivipara bengalensis* but this is not so in *V oxytropis*. It appears probable, therefore, that there is some reason other than the mere necessity of increased space for the accommodation of young to account for this difference in height of the shell in the two sexes, and a possible cause may be found in the natural antagonism between bodily growth and the attainment of sexual maturity. In *Vivipara bengalensis* and probably in many other species of mollusc in this country sexual maturity is attained at a very early date. Whitfield (1882) states that examples of *Limnaea* (*Bulimnaea*) *megasoma* Say, which he hatched out from the egg and managed to rear successfully in the United States, America, became sexually mature at the age of one year. According to Baker (1911, p. 50) "the duration of life in the family Limnaeidae is from three to four years, full maturity being reached in about two years," and though I have no information regarding other genera in temperate regions it is probable that they much resemble the Limnaeidae in this respect. In this country and in Egypt, however, the general condition is vastly different. Manson-Bahr and Fairley (1920, p. 65), who were engaged in investigations regarding Schistosomiasis in Egypt, state that in that country examples of *Bullinus* and *Planorbis* become sexually mature at the early age of three months, and the same undoubtedly occurs in examples of *Vivipara bengalensis* in India. Dissection of fifty examples belonging to the 1920 brood, during July, showed that already many of them were sexually mature, and this was especially so in the males. In many cases the gonad was well developed and was full of ripe spermatozoa. In the females, only comparatively few were sexually mature. The smallest sexually mature male measured 13 mm. in height, while the smallest female with eggs and young *in utero* was 16 mm. Two others of the same height had a quantity of seminal fluid in the egg-shell gland, so that copulation had taken place. Assuming that the rate of growth is equal in both sexes up to the onset of sexual maturity, it would appear that the males become mature at an earlier date than the females, and the antagonism between growth and the attainment of sexual maturity occurs when the males are smaller, thus producing a disparity in size between the two sexes. In spite of their increased bulk females of the age of two years are remarkably less fertile than those of only one year old. In only three examples out of a total of fourteen

belonging to the 1918 brood and examined by me in August, 1920 were eggs, in which development was in an early stage, found *in utero*; in five others the uterus contained a few embryos in a comparatively advanced stage, with 3 to 3½ whorls in the spire; and in the remaining seven the uterus was empty. The average production of these examples was 2·8. On the other hand nine females belonging to the 1919 brood yielded an average of 12·0 eggs or developing young, so that in spite of their greater size, examples of the age of two years show very distinct evidence of senile decay, and it is not improbable that in many cases the young offspring found *in utero* had been retained since the previous breeding season.

Under certain conditions of cold, drought, etc., *Vivipara bengalensis* appears to be capable of undergoing 'hibernation.' In December, 1919 I examined a series of examples that had been obtained during that month by Mr. Sunder Lal Hora from the mud, in which they had buried themselves, at the bottom of a pond in Lahore. In every case the uterus contained a certain number of live young, which must obviously have been the product of the previous breeding season, and which would doubtless have been set free during the following season, in the event of the parent having been able to survive. Annandale has pointed out that *V bengalensis* is less modified, especially in the structure of the operculum, for resisting drought than the species of the *V dissimilis* group (sub-genus *Idiopoma*, Pilsbry). In a bottle full of specimens of *V bengalensis* and *V dissimilis*, recently brought to Calcutta from the Ganjam district of Madras, the difference in the behaviour of the two species as the water became foul was very marked. The individuals of *V bengalensis* crowded round the edge at the top of the water with the aperture of the branchial chamber above the surface and widely open, as though inhaling air, while those of *V dissimilis* closed their opercula tightly and sank to the bottom.

A further interesting point brought out by a study of the two sexes is the greater mortality among males during the period following the attainment of sexual maturity. Out of the fifty examples of the 1920 brood that were examined the proportion of the sexes was 24 ♂ and 26 ♀, so that at this period of life the numbers are approximately equal. A reference to fig. 21 shows that at the end of the first year of life the proportion of the sexes was 203 ♀ to 51 ♂ or roughly 4 : 1. While at the end of the second year of the life the proportion had become still greater and there were as many as 44 ♀ to 6 ♂ or 8 : 1. Wood-Mason (1881, p. 87), when examining a series of examples of *Vivipara crassa*, found that in seventy-six specimens forty-six were females and only thirty were males. He was, however, doubtful whether this difference in the numbers was due to an actual minority in the males or was merely the result of his collector having naturally tried to secure the largest possible specimens, but in view of the figures obtained by me in *V bengalensis* I am inclined to believe that we get a similar disproportion of the sexes in both these

species. This disparity in numbers is not, however, of universal occurrence in the Viviparidae for Dr. Annandale informs me that in the Loktak Lake adult females of *Lecythoconcha lecythis* were at least as numerous as adult males, whereas in the case of *Vivipara oxytropis* females were distinctly less numerous than males.

As I have already mentioned, examination of 50 examples of the 1920 brood in July, taken from the pond in the Indian Museum, showed that the proportion of ♂ to ♀ was 24 : 26. A further examination of 35 examples from the same source in August gave a corresponding proportion of only 15 : 20, so that there had already been a considerable drop in the proportion of ♂ examples present. I give below a table showing the proportion of the two sexes in individuals of different sizes.

TABLE 1.—*Showing the proportion of sexes in individuals of different sizes from the pond in the Indian Museum.*

Length of shell.	11 mm.	13 mm.	14 mm.	15 mm.	16 mm.	17 mm.	18 mm.
♀	3	3	2	5	4	2	1
♂	1	...	1	1	5	4	3

This shows clearly that in the larger examples the proportion of ♂ sex is high whereas the exactly opposite condition prevails among the smaller examples. We have already seen that individuals of 11 mm. in length are of an age of three months or less, and these must therefore have been born about the beginning of June, whereas those having the greater length of 18 mm. were almost certainly born in April or earlier. It seems clear, then, that at the commencement of the breeding season there is a very distinct tendency to produce ♂ offspring, whereas later in the season it is mostly ♀ examples that are produced. I am inclined to attribute this alteration in sex-production to the variation in external conditions. I know of no data that would enable one to form an estimate of the length of the period of gestation, during which the developing embryo is retained within the uterus, and it probably varies at different periods of the year, but it seems likely that offspring born in April are derived from ova that became mature and were fertilized during the winter season, whereas offspring born later in the year will be derived from eggs that became mature during the warmer weather. If this be so, we have here another example of the influence of adverse surroundings in the production of male offspring.

Food.

A study of the contents of the stomach of a number of examples, as well as observations carried out on living specimens,

show that the normal food of *Vivipara bengalensis* consists almost entirely of algae and minute particles of vegetable matter which are rasped off from the surface of submerged plants, stones, decaying vegetable matter, etc. Along with these fragments of vegetable origin, a considerable quantity of fine mud and sand is ingested and swallowed in consequence of which the bulk of faecal material is very large. After passing up the oesophagus the food is mixed in the stomach with the bile which is poured out by the hepatic ducts, so that the stomach contents have a brown appearance and are liquid in character. As the contents are passed down the intestine, they become more and more solid and are finally moulded into small oval pellets which are at first usually rounded at one pole and more or less acutely pointed at the other. Later on, however, both poles become rounded. Finally these pellets are ejected through the anus into the syphonal tube and are forcibly swept out of the body by the outflowing current of water.

At times individuals have been found whose stomach and intestine were crowded with enormous numbers of a species of *Volvox*. These invariably contained within the parent colony a number of daughter colonies, and it is interesting to note that although the superficial cells of the parent colony were digested, the daughter colonies, being more deeply seated, entirely escaped digestion, and passed out of the body in the faeces in apparently a perfectly healthy condition. Gravely (*vide* Annandale, 1911, p. 216) has noted a somewhat similar phenomenon in the fresh-water polyzoon, *Plumatella repens*.

If aquatic vegetation is not available, as was the case where examples were kept in earthen basins or glass bowls, the animals could frequently be seen rasping off the algae that were growing on each others shells.

Although normally vegetable feeders, this *Vivipara* is by no means averse to a carnivorous diet, and feeds on the bodies of other dead snails. This habit appears to be by no means uncommon in molluscs that are normally vegetable feeders. Benson (1829, p. 363 and 1830, p. 126) has called attention to the carnivorous habits of a species of *Paludina*, under which generic term *Vivipara* was formerly included, but from his description of the animal it seems probable that he was referring to a species of *Bithynia* or *Amnicola*. Baker (1911, p. 42) has also pointed out that *Limnaea* is at times carnivorous though normally a vegetable feeder, but his statement that "the part they play as natural scavengers renders their presence in water-troughs and other sources of drinking water highly desirable" seems to overlook the fact that the presence of these snails may be and almost certain would be highly dangerous as a source of trematode infection.

More recently Annandale (1920 (*b*), p. 1) has noted that *Pachylabra* (Ampullariidae) is occasionally carnivorous.

Parasites and Incolae.

Amongst the normal inhabitants of the alimentary canal of *Vivipara bengalensis* and probably of other species of the same genus are several different types of ciliate protozoa, and it seems worth putting on record that in almost every individual examined. I have found what appear to be Spirochaetes in both stomach and intestine. There appear to be two different forms. One of these measured 0·026–0·028 mm. in length and shows 6–7 curves in the spiral; it is highly refractile and quite easily seen under a high power. It moves backwards or forwards with equal facility. At times individuals are met with which show a narrow thin portion in the middle of their length, while short individuals having a length of 0·014 mm. and only 3 curves in the spiral are occasionally met with. It appears that these short forms are produced by transverse fission of the larger individuals. The second form of Spirochaete occurs in the rectum and measures 0·014–0·016 mm. in length, it is of a robust type and has two or three wave like bends in the course of its length.

In addition to the above, there is a rich bacterial flora, consisting of diplococci, rod-like bacilli, etc., in both stomach and intestine.

Vivipara bengalensis rarely acts as the *primary* mollusc host for the development of Trematodes. In this respect it forms a marked contrast to other species of the same genus, for *Vivipara fasciata* Müll. has been recorded as the primary host of nine different cercariae, and *V vivipara* (L.) harbours as many as eleven. Out of a total of 283 examples of *V bengalensis* I have only succeeded in finding cercariae on two occasions and in both individuals it was the same form that was present. This cercaria belongs to the group of Xiphidiocercariae, and was developing in small oval sporocysts.[1] In both cases the host was a male and development was taking place in the testis.

On the other hand, it is often extremely difficult to find an example that is not acting as an intermediate host. Two kinds of Agamodistomes[2] infect and become encysted in this species and each has a very distinct anatomical distribution. One type of cyst, which is circular in shape, is found in the auricle of the heart. These cysts enclose a stage in the development of an Echinostome. The other cyst is found in the gill-bars, it is oval in shape, and usually of a pale brown colour and enclosed within it is a small Agamodistome, that judging from its structure is derived from a Xiphidiocercaria. I am unable to say whether this Agamodistome represents a further phase of the life-history of the cercaria noted above, but the two are extremely closely related and both possess

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[1] For a description of this Cercaria see Sewell, "Cercariae Indicae," *Indian Journal of Medical Research* (in the press).

[2] Dollfus (*Mem. Soc. Zool. France* XXV p. 87, Paris, 1912) has introduced the term 'Metacercaria' to describe the stage in the life-history of a Trematode between the free-living cercaria and its final establishment in its definitive host.

exactly the same type of excretory system. Infection with these two cysts appears to occur in different stages of the life-history of the mollusc host. Even in examples of so early a stage as 10 mm. in length, the gills have already become infected with the cysts of this Xiphidiocercaria; and out of 36 examples examined of sizes ranging from 10 mm. to 18 mm. in length only two were apparently free from this parasite. With regard to the Echinostome cysts in the auricle, however, infection appears to occur much later, and further the proportion of infection is extraordinarily different in the two sexes in early life.

TABLE. 2.—*Showing the percentage infection with Echiniostome cysts in the two sexes of examples of* 1920 *brood.*

Sex.	No. examined.	No. infected.	Percentage of infection.
♂	39	24	61·5 %
♀	46	15	32·6 %

The table shows that infection is twice as frequent in young males as it is in young females. No case of infection was found in examples that measured less than 14 mm. in shell length. I have already mentioned that sexual maturity is attained in this species when the individuals reach approximately the length of 13 mm. in the ♂ and 16 mm. in the ♀ Manson-Bahr and Fairley (1920, p. 66) have stated, and my own observations on the cercariae of this country have corroborated their statement, that "snails do not become infested with cercariae till they have reached maturity, that is about the third month." I have elsewhere put forward the view that infection by miracidia is probably largely dependent on the establishment of a chemotactic stimulus at the time when sexual maturity is attained in the mollusc host, and it seems possible that we are dealing here with a similar phenomenon. Certainly such an explanation would account for the higher percentage of infection in the males, which become sexually mature at an earlier stage of their life-history than do the females, and would also account for the freedom of infection of young immature examples. On the other hand infection of these molluscs by the Xiphidiocercaria and the production of cysts in the gill-filaments shows no evidence of any such phenomenon.

Turning now to the presence of these cysts and the degree of infection in adult individuals of either sex, I have given in the table below the results obtained from a careful examination of fifty examples, 25 aged 1 year and 25 aged 2 years. The point to which I wish to call attention is the very large percentage of ♂ examples that show a heavy infection with both Xiphidio-

cercaria and Echinostome cysts at the end of the 1st year of life, whereas at the end of the second year there is no such distinction between the two sexes. In cases where infection is heavy the auricle is so packed with cysts that it is a matter for wonder that it is able to perform its function at all, and in the case of the gills their physiological activity must be very seriously interfered with, leading to impaired vitality and a lowered resistance to adverse conditions. It is not improbable that we have here, if not the sole explanation, at least a contributory cause towards the marked progressive reduction in the proportionate numbers of adult males during the period of life succeeding the attainment of sexual maturity that, as we have already seen, occurs in this species.

TABLE 3.—*Showing the degree of infection present in adult examples aged one and two years.*

	AGAMODISTOME CYSTS IN GILL-FILAMENTS.				ECHINOSTOME CYSTS IN AURICLE.			
Degree of Infection.	1st year.		2nd year.		1st year.		2nd year.	
	♂	♀	♂	♀	♂	♀	♂	♀
Absent ...	8%	13%	...	...	46%	42%	50%	30%
Slight ...	8%	31%	50%	47%	8%	48%	25%	45%
Heavy ...	84%	56%	50%	53%	46%	10%	25%	25%

The occurrence of Echinostome cysts in the auricle is by no means restricted to *Vivipara bengalensis*, nor is it confined to any particular district or country. Filippi (1855, p. 345) has recorded the occurrence of similar Echinostome cysts in the auricle of *Vivipara vivipara*, and he has further noted "qu'il ne m'a jamais été possible de voir la moindre trace de ces parasites dans les foetus des Paludines; mais que les jeunes individus, pourvu qu'ils aient vécu quelques mois en liberté dans l'eau du lac en sont déjà enrahis." His results obtained in Europe agree, therefore, closely with the observations made in India. The occurrence of these cysts has also been noted by Moulinié (1886, p. 193).

As regards the geographical distribution in India, I have found these cysts present in examples of *V bengalensis*, taken from five different areas of water in the Calcutta district. It is worth noting, however, that in examples of the phase *annandalei*, taken from a tank in Baliaghatta, this infection was absent in ten specimens that I examined: other examples from the same source were placed in experimental tanks, and when they were examined about 2 months later in every case cysts were present, so that infection had occurred during their sojourn in the experimental tanks. Extremely similar, if not absolutely identical cysts were found in identically the same situation, namely the auricle,

in two out of six examples of *Vivipara dissimilis* taken from swamps near Bombay, and in nine out of eighteen examples of this species taken from a small ditch at Rambha, Ganjam; but in these latter cases the cysts were degenerating.

Yet another trematode may find a temporary resting place in Indian species of Viviparidae. Examples of *Lecythoconcha lecythis* and *Vivipara oxytropis* brought from the Loktak Lake, and of an undescribed species allied to *V oxytropis* from Dimapore, Assam, were infected with trematode cysts in the mantle. These cysts were oval in shape, and were situated beneath the external or shell surface just behind the thickened mantle margin. The cyst-wall was thick and gelatinous and appeared to open by a single aperture on the shell surface of the mantle. Contained within these cysts were small examples of a species of *Urogonimus* Mont. [=*Leucochloridium* Carus]. I am elsewhere publishing an account of this species (*vide* Sewell, "Cercariae Indicae," *Ind. Journal Med. Research*); suffice it to say here that these trematodes measure 2–3 mm. in length, are of a deep orange-red colour and have a prominent ventral sucker with a diameter twice that of the oral sucker. Filippi (1855, p. 353, footnote) has recorded finding free distomes, which possess all the above characters, in examples of *Vivipara vivipara* taken from the Lake of Varese, Italy. As regards their distribution in the mollusc host he remarks, "Ils n'ont pas de place fixe, et souvent je les ai vu sur le manteau de l'animal." It is of course impossible to be certain on the point, but it seems by no means unlikely that he was also dealing with an intermediate stage in the development of a species of *Leucochloridium* in the European *Vivipara*.

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