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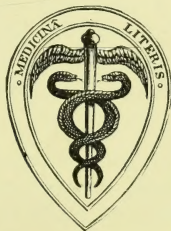LATE FELLOW OF ST. JOHN'S COLLEGE, CAMBRIDGE;

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The "Sexual Season" of Mammals and the Relation of the "Pro-œstrum" to Menstruation.

By

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Contents.

Introduction.

THE following paper is concerned with certain phenomena which affect reproduction and which occur in female mammals prior to the fertilisation of the ovum.

The times of propagation of the species and the behaviour of many female mammals during certain portions of the

breeding season have been noted by zoologists, but the changes which take place in the female generative system prior to gestation require examination which it is impossible to extend, with few exceptions, to mammals in the wild state, and almost all that is known on this matter is derived from a study of domesticated mammals and of some few wild animals kept in captivity. But little attention, however, has been paid to the subject at all by scientific students, while the only attempt, so far as I am aware, which has been made to treat it from a comparative point of view is that of Wiltshire, whose "Lectures on the Comparative Physiology of Menstruation" were published in the 'British Medical Journal' (1883).

The subject is of importance in proportion to the light it may throw upon the evolution of the functional phenomena of breeding. To attack such a subject by means of data obtained from the highest groups of animals may seem to many to be beginning at the wrong end of the story, and there is, of course, much truth in that view; but knowledge of the physiology of the lower animals is at present very limited, and information regarding the habits of most of them at times of reproduction extremely scanty;[1] on the other hand, we have available some knowledge of the habits of many classes of mammals and of the variety of sexual phenomena exhibited by them.

The data for a comprehensive comparative account even in mammals does not exist; at the same time there is sufficient material at hand, in my opinion, to permit of a foundation being laid, upon which it will be more easy to arrange facts in the future. It is, therefore, not with any idea of finality, but with the purpose of suggesting a wide field of inquiry, and with the hope of assisting therein, that this chapter on the comparative physiology of breeding has been written.

In the first place, with regard to the terms to be used; at present there is great confusion regarding those used by breeders; the same terms are used for both male and female

[1] In this relation Dr. Lo Bianco's papers in the 'Mitth. Zool. Stat. Neapel,' vol. viii, 1888, and vol. xiii, 1899, are of great value.

animals when they should not be so used, the same terms are used for different processes and conditions in female mammals, and it is necessary for a clear understanding of the subject that the limits of their use should be defined, and where needful new terms adopted.

One of the most fertile sources of confusion is, disregard of the fact that the history of the generative phenomena exhibited by female mammals is different when reproduction takes place and when it does not take place; it is essential that this fact should be kept in mind.

The remainder of this Introduction I have devoted to a definition of the terms used in the following pages, and to an endeavour to show wherein they differ or are in accord with those now in use.

Reproductive Period.—I have used this expression to denote the whole of that period in the life of a mammal, whether male or female, during which its generative organs are capable of the reproductive function; and in contrast to the Pre-reproductive and Post-reproductive periods which severally precede and follow it, during which the generative organs are either not fully developed or are degenerate.

The bearing of young, however, is not possible at all times during the reproductive period. In the course of that period there are intervals during which the generative organs of all mammals exhibit, on the one hand special activity, and on the other hand a fallow condition. This variation is periodic, and is due, not to a periodic degeneration from a stable condition, but to the periodic accession of a special stimulus, culminating in sexual desire, and resulting in coition and in gestation in the female when conception takes place.

The periodicity of this stimulus is very variable, and is influenced by many factors of both extraneous and internal origin.

Breeding Season is adopted to denote the whole of that consecutive period during which any male or female mammal is concerned in the production of young, and it is not applicable to any isolated portion of that period.

Although the part which the male takes in breeding is confined to the insemination of the female, while the whole of the rest of the process is carried on by the female, and in spite of the fact that the word " breed " carries with it, in its original sense, as I understand it, the giving of nourishment, and might perhaps in that sense be confined to the female, it is impossible to avoid including the male. The extent of the breeding season of a male depends upon the length of time during which he is preparing for, and is capable of, inseminating a female ; while the extent of the breeding season of a female mammal depends upon the extent of the sexual season, during which her generative organs are preparing for conception, plus the time occupied by gestation, or the gestation period.

The term has been used to describe specially the season when mammals copulate, or, again, it has been used to specially designate the period of gestation in the female; but it is not applicable as a definitive of either of these periods separately, and must be used for the whole consecutive breeding period experienced, and in this sense is applicable to both male and female mammals.

The term " breeding " is also frequently used in connection with the rearing of the young after birth, and this has given rise to confusion, inasmuch as while the mother is providing nutriment for young already born, she may or may not be bearing others. It is obviously inconvenient to include the period of suckling in the " breeding season," for which reason I have called it the Nursing Period.

Sexual Season is a term I have used to designate, for both male and female mammals, the particular time or times of the year during which their sexual organs exhibit special activity.

Some mammals experience only one sexual season each year, some experience more than one ; in some it is a brief period, in others it occupies a much longer time ; in some the sexual season of the female may be interfered with by gestation, in others it is not.

It is a convenience to be able to use one term for this phenomena in both sexes, but it is to be noted in the first place, that the sexual season of an individual male and individual female of the same species is not necessarily coincident, either with regard to time or with regard to extent; and in the second place, that the phenomena exhibited are different in the two sexes. For this reason special terms are used for each sex.

The Male Sexual Season.

Rutting Season.—This term is used to describe all seasons of special activity of the generative organs of the male, during which he is desirous of coition and normally capable of inseminating the female. In some animals these seasons are of short duration and at long intervals; in others the intervals may be shorter or the duration of the season longer; while in others, again, there would appear to be little or no cessation of the generative power.

It is necessary here to remark that the term "rut" (German "Brunst," French "rut") is used by German and French authors frequently, and by some English writers, to designate the conditions obtaining in both male and female mammals during the sexual season. This is an error; it is essentially a word which should be confined to the phenomena exhibited by the male; it has its origin in the Latin word "rugire," to roar or bellow, and is, I believe, strictly applicable only to such animals as stags and boars. There are, however, other male animals to which the term may be applied in its original sense, as, for instance, the bull elephant in a condition of "must," and it will be convenient to extend the use of the term "rut" to the males of all animals which exhibit seasons of special generative activity; to those, on the other hand, who are capable of inseminating the female at all times of the year, the term is not applicable.

The Female Sexual Season.

In the case of the female the activity of her generative

organs and the form which that activity takes is modified by conception, and it is necessary to consider the subject under two heads : (1) when reproduction does not take place, that is in the absence of the male, or when coition does not result in conception ; and (2) when reproduction does take place.

Under either of these circumstances the changes which take place in the generative system are both complex and variable, and for purposes of comparative study must be identified.

(1) When Reproduction does not take place.—In the first place we will consider the changes which take place in the simplest form of the female sexual season, and afterwards indicate the nature of the more complicated processes.

Pro-œstrum, or the Pro-œstrous Period, is the term I have adopted to describe the first phases of generative activity in the female mammal at the beginning of a sexual season ; it is identical with the period spoken of by the more accurate breeders as the time during which an animal is " coming on heat," or " coming in season." During this period certain changes take place in the generative organs which, while in some animals they are more drastic, in some more complete than in others, are based on the same plan, have the same object, and the same effect in all. They result in a condition which I have called—

Œstrus.—This is the climax of the process ; it is the special period of sexual desire of the female ; it is during œstrus, and only at that time, the female is willing to receive the male and fruitful coition rendered possible in most, if not in all, mammals.

Œstrus may be a brief period and exist for only a few hours, or it may extend for days, or apparently even for weeks; it is possible, however, normally, only as a result of the active changes which take place in the generative organs during pro-œstrum.

The period of œstrus is referred to by various writers as " Brunst," " rut," " heat," " season," " brim," or

" œstrum ; " as I have before remarked, some of these terms
are used also to designate the rutting season of the male, and
most of them are used indiscriminately for both the periods
of pro-œstrum and œstrus, which I seek now to establish
for the female. In comparing, therefore, the writings of
former investigators with the statements made in the follow-
ing paper, it must be recollected that the various terms
hitherto used are not necessarily homologous with those used
by me, and are not necessarily descriptive of the sexual
season or of the breeding season of female mammals, as I
understand these processes. Much of the confusion and
misunderstanding which exists, regarding breeding phe-
nomena, is due to the indiscriminate use of the terms above
noted, and it is essential that their use should be restricted,
or given up altogether.

There is one point which I should briefly refer to here. I
have said above that œstrus, the period of desire, normally
follows pro-œstrum ; but there are times when the females of
certain, probably of many, mammals are anxious to receive
the male without the pro-œstrum having taken place.

This condition may occur in various mammals during
pregnancy, and has frequently been noticed in most species
of domestic mammals during that period, while it is evident
in a considerable number of animals also at other times. This
may be called abnormal œstrus. Normal œstrus, as we
shall see below, occurs in conjunction with certain changes
in the uterine tissue, and this is accompanied by congestion
and stimulation or irritation of the copulatory organs ;
whether the congested condition of the latter organs is in
itself sufficient to induce œstrus, or whether the presence of
some peculiar substance in the blood, or other influences, are
essential for that purpose, is not known ; however that may
be, congestion is invariably present, and is an essential
condition.

So also in abnormal œstrus, congestion of the copulatory
organs takes place, but the changes in the uterus which are
evident in normal œstrus are apparently absent. When

œstrus occurs during pregnancy it is probably due to a temporary diversion of a superabundant supply of placental blood ; when it occurs at other times, the highly nutritious food, with which the animals which experience it appear to be generally supplied, or the condition resulting therefrom, is possibly largely responsible for it.

Metœstrum, or the Metœstrous Period.—If conception does not take place during œstrus the activity of the generative organs gradually subsides during a definite period, which I have called the metœstrum ; and this is followed, in the simple form which we are now considering, by a long period of rest.

Anœstrum, or the Anœstrous Period, is the name I have given to this period of rest. It may last two or three or eleven or possibly more months, and during that time the generative organs lie fallow in the non-pregnant female. It is eventually succeeded by a new pro-œstrum, and the four periods, pro-œstrum, œstrus, metœstrum, and anœstrum, constitute what I have designated as the anœstrous cycle.

By some this period of anœstrum is called the non-breeding season, but this is not correct, for although conception cannot take place during this period it may be occupied partially or wholly by the period of gestation, and inasmuch as gestation is included in the breeding season, the anœstrum cannot be considered as a non-breeding season.

We now have to consider a more complicated form of sexual season. In this case the sexual season is ushered in as before, with the pro-œstrum, œstrus follows, and is succeeded by metœstrum, but instead of the anœstrum, a short quiescent period now occurs which I have called the—

Diœstrum, or the Diœstrous Period.—This is a brief period lasting only a few days, at the most probably not more than twelve or fourteen days, while in some animals four to six days may be its duration. It is followed at once by a new pro-œstrum, and the four periods, pro-œstrum, œstrus, metœstrum, and diœstrum, I have designated the diœstrous cycle.

In those animals which experience the diœstrous cycle the sexual season (when conception does not take place) consists of a series of such cycles, two or more; and may occupy any length of time from one month to the whole year. In the former case it is limited to a definite portion of the year only, while in the latter case it may be coincident with the whole reproductive period [human female, under certain conditions]. But when the recurrence of the diœstrous cycle is limited to a definite portion of the year, the sexual season is, of course, also limited to that period, and there is consequently a period of rest, which is the anœstrum.

In such cases the non-pregnant female experiences a series of diœstrous cycles during the sexual season, at the end of which, instead of diœstrum following metœstrum, the latter is succeeded by anœstrum, which persists until the next sexual season occurs.

In order to distinguish between the two classes of female mammals into which the occurrence or absence of diœstrum divides them, I have called those which experience a single œstrus during each sexual season, or in other words those in which the anœstrous cycle only occurs, monœstrous mammals; while those whose sexual season is occupied by a series of diœstrous cycles, or in other words those who experience a series of recurrent œstri, I have called polyœstrous mammals.

The complication into which an otherwise simple story is thrown is due, therefore, to variation in the quiescent period. In some animals this may be a very brief period, never lasting more than a few days; in others it may occupy from two to eleven months each time it occurs; while in others again both these conditions are experienced at different times of the year.

Functionally, no doubt, these two varieties of the quiescent period are homologous, the one is a modification of the other; and the modification is probably due, as will be shown below, to an increased or decreased power of reproduction. At the same time, for the purposes of the present paper, the difference between them is essential, and their relation to the sexual

season renders it necessary to discriminate clearly between
them.

The result of the foregoing may be summarised thus :
when the male has not access to the female during the sexual
season, or when insemination at that time does not result in
the fertilisation of an ovum, pro-œstrum and œstrus are
followed by metœstrum and, if the animal be polyœstrous,
diœstrum is followed by another pro-œstrum, and such di-
œstrous cycles continue so long as the sexual season lasts ;
whereas if the animal be monœstrous, or if the diœstrous
cycles of the polyœstrous animal be ended, anœstrum follows,
and persists until a new sexual season occurs.

A few examples will render the foregoing somewhat more
clear. Among monœstrous mammals is the wolf, which, in
the wild state, experiences only one sexual season at a
particular time each year ; in her case pro-œstrum and œstrus
are followed, when conception does not take place, by met-
œstrum, and the whole of the remainder of the year is
occupied by anœstrum. She therefore experiences a single
anœstrous cycle each year.

Another monœstrous animal is the domestic bitch ; but in
her case, in the absence of gestation, the anœstrous cycle
may recur two, three, or even four times each year.

Among polyœstrous mammals the mare may be taken as
an example ; during a certain portion of the year, of variable
extent, she undergoes a series of diœstrous cycles when she
is not pregnant ; this portion of the year is her sexual
season ; when it is over anœstrum occurs and lasts until the
commencement of the same time the following year.

The human female, who is also a polyœstrous mammal,
under certain circumstances has a continuous series of
diœstrous cycles throughout the year when she is not preg-
nant, and is thus subject to a sexual season during the whole
of her reproductive period.

(2) When Reproduction does take place.—In this
case the pro-œstrum is followed by œstrus, during which
period insemination occurs and the ovum or ova are fer-

tilised ; gestation results and persists until parturition takes place.

After parturition there may be a considerable interval of rest ; this interval may occupy only what remains of the anœstrous period which the same animal would experience in case it had not borne young, or it may persist during a nursing period which extends beyond the normal limits of such anœstrous period, or it may be even still further prolonged. On the other hand, parturition may be followed almost immediately, and in spite of the nursing period, by pro-œstrum, œstrus, insemination, and renewed gestation. While finally, the same animal may at one time of the year exhibit a recurrent gestation, while at another time of the year its generative organs may continue fallow for the remainder of that interval which represents the anœstrous period.

Such briefly are the different types of breeding phenomena exhibited by female mammals during their reproductive period; the following account will show that they all conform to one plan, and that the variability, which altered conditions of life induce therein, clearly indicates the origin of these types. On this account the subject is likely to be of considerable interest to students of variation, and the collection of facts which bear thereon is urgently needed.

The Sexual Season of Male Mammals.

It is unnecessary to do more than mention here that males may be divided into two classes : those which rut (stag), and those which do not rut (dog). Rutting males have a special sexual season ; those which do not rut experience sexual capability all the year round.

The sexual season of some males in captivity [1] is capable

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[1] Information regarding wild animals in captivity, unless otherwise stated, has been obtained from certain keepers in the Zoological Gardens of London, whose statements appear to me to be reliable. The reference given in the text is (Zoo.).

of modification similar to that of certain females under the same conditions; for instance, wapiti stags under natural conditions have a special limited rutting season, but in captivity (Zoo.) they rut all the year round except during the season when they cast their antlers and until those structures grow again.

When rutting exists it is probably excited by similar influences to those which induce the advent of œstrus in the female ; on the other hand, when the sexual season of a male is a permanent characteristic, either all the females of that species have a sexual season all the year round or individual females have different times for their sexual season.

As examples of these two conditions it may be pointed out that the camel in the Zoological Gardens of London ruts at much the same time as the female camels experience œstrus in Mongolia, namely, early in spring (Prejevalsky, 1876), although in the Gardens there are no female camels ; while the sexual passions of the dog, on the other hand, are excited by œstrus of the bitch and may be called forth at any time of the year.

At the same time the proximity of the two sexes may stimulate both œstrus and rutting. The stimulation of œstrus is noticed in some of the larger carnivora in the Zoological Gardens by the presence of the male, while I have noticed rut in Semnopithecus entellus, in the Calcutta Zoological Gardens, stimulated by the female; and rut in the domestic rabbit stimulated by a doe under the influence of œstrus.

It is interesting to observe that while the sexual activity of domestic mammals (Müller, 1838) and of wild animals in captivity (Heck, 1899) may be more frequently exhibited, it is not so violent as is shown by animals in the wild state.

For the purposes of this paper, this is all that need be said specially, regarding the generative phenomena exhibited by the male ; although the activity of his generative organs may be to some extent influenced by the presence or absence of the

female, the general scheme of his reproductive period, and breeding, sexual or rutting season, remains the same.

The Breeding Season of Female Mammals.

The breeding season of mammals should rightly be considered after the sexual season has been discussed, but, owing to the fact that the term " breeding season " has been so universally used to designate the sexual season as well as the gestation period of breeding mammals, it is necessary to say a few words here in order to make the following account clear.

The occurrence of a breeding season depends upon the occurrence of a sexual season, and those factors which influence the former, influence also the latter, and will be treated under that head.   The same is true for the recurrence of both the breeding and the sexual seasons.

The recurrence of the sexual season may be interfered with by the bearing of young, both gestation and nursing may so interfere, but that does not remove a consideration of the question, under such circumstances, out of the realm of the sexual season ; the effect of these processes, of bearing young and of nursing young, on the sexual season, must be considered in relation to that period, and must not be supposed to have relation only to the remainder of the breeding season.

Questions regarding the breeding season of mammals concern what happens during both the sexual and the gestation periods jointly, and, as I have before stated, the expression is a term used to define the period passed through by an animal which experiences both these processes ; it is not applicable as an expression or term which may be used for the occurrence of either of them separately, nor for the effect one of these processes may have upon the other.

A breeding season may include only one sexual season and one gestation period ; this is true for all monœstrous mammals, of which the bitch will serve as an example, and it may

be also true for certain polyœstrous mammals, as, for instance, the mare, under certain circumstances. On the other hand it may include several sexual seasons and several gestation periods, a condition to which only certain polyœstrous mammals can attain, of which the rat is an example.

The time occupied by a breeding season is very variable, from a few weeks (bitch) to several months (mare), and even more than a year (elephant). There may be only one breeding season in the course of several years, as shown by the walrus (Bell, 1874), elephant, and probably rhinoceros (Willoughby, 1889). There may be one breeding season each year (mare) or more than one (domestic bitch and cat).

The result of a breeding season may be the birth of one young one (mare usually), one litter of young ones (bitch), or many litters (rat).

There may be great variation in the period of gestation of different species of the same order of mammals. For instance, among Rodents, the rat goes twenty-one days in young, the rabbit thirty-two days, the guinea-pig sixty-three days. Among Equidæ, mares carry their foals eleven months, asses from three hundred and fifty-eight to three hundred and eighty-five days, and Burchell's zebra over thirteen months (Tegetmeier and Sutherland, 1895). Among Ovidæ the Barbary wild sheep goes from twelve to fifteen weeks in young (Zoo.), while the domestic sheep in this country averages about twenty-one weeks.

There may even be variation in the period of gestation in varieties of one species; for instance, Merino sheep average 150·3 days' gestation, while Southdowns average 144·2 days (Darwin, 1875), and different breeds of cows apparently vary from 277 to 288·75 days' gestation (Varigny, 1892).

The supply of food available may influence the length of time occupied by gestation. A correspondent who is a sheep-breeder informed me that his ewes, when run on poor land, experience an appreciably longer gestation period than those run on rich land; and I am strongly inclined to think investigation will show that the supply of food, and the

quality of that food, have very marked effects not only upon breeding seasons and gestation periods, but upon fertility generally, upon the mother and upon the fœtus (Latarte, 1891).

It is with such questions as these that the consideration of the breeding season as a whole is concerned ; with them the following paper does not deal, and it is obvious that before they can be profitably discussed, not only the sexual season, but the gestation period must be examined separately.

The Sexual Season of Female Mammals.

In dealing with this subject we have to discriminate between mammals under three different conditions : namely, wild animals in a state of nature, wild animals in captivity, and domesticated animals ; and this is necessary, because the generative system of wild animals is affected by the conditions attending captivity, because the effect of captivity is not necessarily the same as the effect of domestication, and because wild animals cannot be examined so closely as the others and less is known about them.

In dealing with wild animals in captivity it is necessary to bear in mind the fact that good food, warmth, and shelter have a very great effect on the increase of the generative powers of some animals, while on others a strange climate, confinement, want of violent exercise, and probably the absence of opportunity for periodic gorging of freshly killed food, or of a sufficient variety of food, have the opposite effect.

As an example of the former the deer and cattle in the Zoological Gardens may be quoted, as an example of the latter some of the larger carnivora will stand.

In dealing with domesticated animals we do not know what the original conditions were, and we have to take the facts as they stand. At the same time we may assume that animals which do not show themselves to be prolific under domestication are rarely domesticated, and that a very long

course of artificial selection, added to the plentiful supply of food, with warmth and shelter inseparable from domestication, has no doubt greatly increased their power of reproduction.

As has been already stated, there are two forms of sexual season evident in female mammals ; the monœstrous, in which there is only a single œstrus at one or more particular times of the year (bitch), and the polyœstrous, in which there are two or more concurrent diœstrous cycles at a particular time of the year (mare).

The sexual season may be influenced by the climate of the region in which the animal lives, by the seasons of the year when these are of marked variation, and by the supply of food, or possibly by the nature of the food, obtainable. These may be called climatic influences.

It may also be influenced by special nervous, vascular, and secretory peculiarities of the individual and by its habits of life. These may be called individual influences.

It may also be influenced by the length of gestation, the claims of the newly-born offspring on the mother (i. e. nursing), and by her powers of recuperation. These may be called maternal influences.

Such influences may affect the time of year when the sexual season occurs, its recurrence, and its duration. The influences which affect the time of year when the sexual season occurs, concern both monœstrous and polyœstrous mammals, and are essentially governed by climatic considerations, including the supply of food. The recurrence and duration of the sexual season on the other hand are affected either by climatic, individual, or maternal influences, and are also experienced both by monœstrous and polyœstrous mammals, though in a somewhat different way by each.

In order to understand this difference it is necessary to examine briefly what occurs in these two classes of animals. Among monœstrous animals there are a variable number of sexual seasons each year, one or more, each composed of a single œstrous of variable duration. So that the result of the

different influences which affect the sexual season may be either to increase or decrease the periodicity of that season, or to increase or decrease the duration of each one.

Among polyœstrous animals there is usually one sexual season per annum, which is composed of two or more diœstrous cycles, and the result of these influences on such animals may be, either to increase or decrease the number of consecutive diœstrous cycles in any one sexual season, or to increase or decrease the duration of each cycle.

The effect of these influences in both cases is to increase or decrease the reproductive power of the animals, and they act in monœstrous animals by affecting both the periodicity and duration of the sexual season, in polyœstrous animals chiefly by affecting the duration, but in two different ways, namely by increasing or decreasing both the number of consecutive diœstrous cycles and the duration of the œstri which occur therein.

Modification of the periodicity of the sexual season, therefore, is chiefly found among monœstrous animals ; while modification of its duration is common to both monœstrous and polyœstrous animals. It would seem possible to simplify these conditions if it were assumed that the polyœstrous arose from the monœstrous condition ; if it were assumed, in point of fact, that polyœstrum is simply a condition arrived at by the concentration of several monœstrous sexual seasons.

There might seem to be some reason for this when such animals as the red deer, for instance, are considered ; in the wild state this animal is apparently monœstrous, while in captivity it is polyœstrous, at any rate in this country.

But it may equally plausibly be argued that monœstrum is simply decentralised polyœstrum. There are instances among domesticated animals of monœstrous animals with a tendency to polyœstrum (bitch), and of polyœstrous animals with a tendency to monœstrum (mare). So also among wild animals there are instances of animals which are monœstrous in one climate and apparently polyœstrous in another (Sciurus vulgaris) (compare Bell, 1874, and Lataste, 1887).

I doubt if, in the present state of our knowledge of the subject, it is possible to determine which is the original of these two conditions. The behaviour of animals in captivity and under domestication inclines one to believe that monœstrum is the original form; then, again, it is the simplest form, and on that ground may be thought the more archaic. But, on the other hand, it is the lower animals which are the most prolific breeders, and, for many reasons, we may perhaps expect the ancestral mammal to have been more prolific than wild animals are now.

If this should be true, the increased capacity for reproduction, shown by domesticated animals, would indicate reversion to ancestral powers, due to the removal of such obstructions as must be inseparable from the struggle for existence. Thus all we can be certain of is the close similarity between these two forms of sexual season.

A further complication is introduced by certain breeds of domesticated sheep and by pigs; these are polyœstrous animals when domesticated, and they may also exhibit more than one sexual season each year. Such a condition appears to be exceptional, and I have not included this form of variation in the foregoing account for that reason; but I am quite prepared to believe a more exact knowledge of what takes place among domesticated animals will show a similar variation among individuals of other classes of animals.

Variation in the periodicity of sexual seasons is brought about by an increase or decrease in the persistence of the anœstrum, and has nothing to do, necessarily, with variation in the œstrus cycle itself; while, on the other hand, variation in the duration of a sexual season is brought about by an increase or decrease in the number of consecutive diœstrous cycles (polyœstrous mammals), or by an increase or decrease in the persistence of the œstrus (monœstrous and polyœstrous mammals), the anœstrum being only secondarily affected in consequence thereof.

The effect of an increase in the periodicity of sexual seasons may be twofold; it permits of reproduction at differ-

ent times of the year, and, when gestation is of sufficiently short duration, of reproduction more than once a year. An increase in the duration of the sexual season may also have two effects ; it gives increased opportunity for successful coition, highly advantageous to those animals which live an isolated life, while, among animals which experience a sufficiently short period of gestation, it gives them opportunity for reproducing several times in each season. On the other hand, a decrease in the periodicity or duration of the sexual season has an opposite effect.

It would seem highly probable that the method of increasing or decreasing the opportunities of reproduction varies with the habits of animals, the claims of maternity, and the climate in which they live. The different methods are not necessarily peculiar to particular groups or classes of animals, and they may vary, within limits, in the same species in different localities and in the same individual under different circumstances. Climatic and maternal influences may be observed in wild, captive, and domesticated animals ; but individual influences can only be noted in the two latter classes, and especially in domestic mammals.

It has been freely stated, originally by Aristotle and subsequently by numerous biologists, that the sexual seasons are governed by the requirements of the newly born young ; in other words that the season for conception is regulated by the length of gestation and the time of year which is most favourable for the birth of the young ; and it is argued, that the different times of the year during which the sexual seasons of similar animals occur is sufficient ground for that view.

I cannot agree with this opinion ; if it were so, why should some bats experience a sexual season in the autumn and not produce young until about June (Beneden, 1880, and others, see below), although not more that two months are required for gestation and these animals are active for that length of time in the spring, before parturition takes place ? Again, why should roe deer, in Germany, have their sexual season

in early autumn, when the embryo does not develop beyond the segmentation stage until the following spring? (Bischoff, 1854). Why should the seal take eleven to twelve months for gestation, while a large dog only requires three months? If there was a great difference in the size of these animals the variation might to some extent be accounted for, but it is not so. It is true that the newly born seal is a far more perfect animal than the newly born puppy, but it cannot be that the whole of the difference in the time of gestation, namely, eight to nine months, is required for the extra development of the more perfect seal embryo, other factors being equal.

Again, how is it that an unusual change of climate will affect the sexual season of an animal? This is constantly observed among domesticated animals, and a very marked case is recorded of cows, in Skye, after an exceptionally severe winter (Youatt, 1834).

And how is it that the sexual season, for instance, of the fox (Bischoff, 1863) and red deer (Cameron, 1900), is modified in accordance with the nature of the country in which it lives, whether high or low ground, in accordance with the age of the animal, and probably also in accordance with its bodily condition?

There seems to me ample reason for the belief that the sexual season is governed directly by the influences detailed above— climatic, individual, and maternal; and that variation in the rate of development of the embryo, in the length of gestation, and in the powers of nursing, are quite sufficient to provide for the launching of the young at a favourable time of the year.

The origin of the sexual season is another matter; for a solution of this question a comparative study of the phenomena in the lower animals is necessary.

That it is the result of a stimulus which may be effected through the alimentary canal is demonstrated by the effect upon ewes of certain stimulating foods; the sexual season of ewes may be thus forced by "flushing" them, as it is called by flockmasters.

In the same way it is stated that a quart of milk, drawn

from a cow "in season" (i. e. during œstrus), but which has
not had the bull, will, if drunk by another cow, bring on the
sexual season of the latter (Youatt, 1834).

That it is associated with a stimulus which is manifested
by exceptional vigour and exceptional bodily "condition"
is demonstrated by the pugnacity of the males at such times,
by the restless activity of the females, by the brilliant
colouring of such widely divergent animals as, for instance,
annelids, amphibia, birds, and mammals, by the condition of
the plumage of birds, and of the pelage or skin of mammals.

That it is associated with nutrition, and that it is a stimulus
which is gradually collected, is indicated by the increased
frequency of the sexual season among domesticated mammals
as compared with nearly allied species in the wild state.

That it is manifested by hypertrophy and by congestion
of the mucous tissue of the generative organs, and of various
other organs, such as the wattles and combs of birds, the
crest of the newt ; and by the activity of special glands, the
affection of all of which may be exceedingly severe, is true.

These, and many other similar facts, are well known, but they
do not assist in the elucidation of the origin of the function.

The most that they do is to show that the sexual instinct is
seasonal, and that nutrition, whether affected by external or
internal factors, plays an important part in its manifestation.

The Periodicity of the Sexual Season in Monœstrous Mammals in the Absence of the Male.

In the absence of gestation most mammals would appear to
experience at least one sexual season per annum, under natural
conditions, but there is great variation in the periodicity of
the sexual season in captive and domesticated mammals, the
variation being extended not only to varieties of a species,
but also to individuals of that species under domestication.

Among certain wild animals which are known to undergo
parturition only during a very circumscribed time, the
monœstrous condition may be assumed as probable, and the
periodicity of the sexual season calculated ; but it must be

recollected that without accurate observation, during the absence of the male, it cannot positively be asserted that such animals are monœstrous.

In the case of the bitch, in Danish Greenland the bitch generally experiences only one sexual season per annum, though sometimes she may have two (Rink, 1877).

In this country, as a rule, the bitch has two sexual seasons each year, one in the spring and one in the autumn, but there are wide variations to this rule. She may have only one sexual season per annum, or it may occur every eleven, ten, nine, eight, seven, six, five, or four months (Stonehenge, 1887). It seems probable the sexual season recurs less frequently in breeds of large dogs as a rule; a correspondent (Dr. Inmann), who breeds St. Bernard dogs, informs me this is his experience, and I have had information from other breeders of large dogs, mastiffs and bloodhounds, which shows there is an obvious tendency in this direction; at the same time it does not appear to be by any means a universal rule. Again, while the spring and autumn are the usual times when the sexual seasons of dogs occur, the sexual seasons of each bitch have a more or less exact periodicity peculiar to herself.

Finally, the sexual seasons of any bitch may be interfered with to the extent even of complete cessation, if she is systematically prevented from breeding.

The bitch may be considered a case of extreme variation in the periodicity of the sexual seasons of a monœstrous domesticated mammal. The normal two sexual seasons experienced in this country are reduced usually to one in Danish Greenland, probably owing to the effect of climatic influences, while the variations which exist in this country indicate the effect of individual influences, which are largely stimulated by artificial selection and domestication.

The wolf, jackal, and fox are monœstrous like the dog, and in captivity in the Zoological Gardens they show two sexual seasons per annum, like the normal dog in this country.

Bears are also monœstrous, but they have only one sexual season per annum in the Zoological Gardens.

Badgers also are probably monœstrous, but there is great uncertainty regarding their breeding (Harting, 1888; Denwood, 1894).

The same is true for the Barbary wild sheep; they are said to be monœstrous and to have one sexual season per annum in captivity in this country (Zoo.).

The red deer, fallow deer, and roe deer are probably monœstrous in the wild state; they have only one sexual season of very limited duration (Bell, 1874). The same may be said for the ibex, Markhor, Barasingh, and Hemitragus jemlaicus in Cashmir (Laurence, 1895), possibly also the American bison (Allen, 1876), and various other species of Bos, Ovis, and Capra (Lydekker, 1898); also the black-tailed deer in Montana (Roosevelt, 1893), and several antelopes (Sclater and Thomas, 1900).

The truth regarding these animals is not, however, known; their monœstrous condition is rendered probable from the known very limited sexual and calving seasons, but it is by no means certain.

The genus Sorex, some of the Mustela, Myoxus avellanarius, Arvicola amphibius, and Sciurus vulgaris, in this country (Bell, 1874) are probably monœstrous in the wild state, as are also the wild cat and the fox, and they have only one sexual season.

Phoca vitulina, P. hispida, P. grœnlandica, Cystophora cristata, and Halichœrus gryphus have all a very limited sexual season, occurring once only in the year, and it is highly probable they also are monœstrous (Bell, 1874, and Turner, 1875).

Variation in the periodicity of the sexual season of various domesticated animals, in comparison with nearly allied species in the wild state, has been observed in a few cases.

The cat in the wild state has one (Hamilton, 1896)—some say two (Mivart, 1881), though this seems doubtful—sexual season per annum, while the domestic cat may have three or four sexual seasons each year.

The sow has only one sexual season in the wild state in

France (Beever, 1870), but it is not clear whether she is
monœstrous or polyœstrous; when domesticated, however,
she is polyœstrous (Fleming, 1878; see also Aristotle).

Certain wild sheep, O. argali, O. burrhel, O. poli,
have only one sexual season per annum, and are probably
monœstrous (Prejevalsky, 1876); whereas domesticated sheep
are polyœstrous, and may have such an extended series of
diœstrous cycles that they are capable of producing young
almost at any time of the year; such, for instance, are Dorset
Horns in the south of England and Hampshire Downs in
some parts of Ireland (compare also Aristotle). As a rule,
however, sheep in this country have a much more limited
polyœstrous season,—as, for instance, the Scotch black-faced
sheep, which has only two recurrent periods of œstrus
(Cameron, 1900).

Variation in the periodicity of the sexual season of wild
animals, as compared with individuals of the same species
in captivity, has been noted in but few cases. Some of the
large carnivora in the Zoological Gardens exhibit great irre-
gularity in their sexual seasons, but too little attention has
been paid to the subject in these animals to allow of more
being said than that, in some cases, their generative activity
appears to have been stimulated, in others checked.

The wolves in the Zoological Gardens have two sexual
seasons, while the Tibet wolf (L. chanco) has only one (Pre-
jevalsky, 1876) in a wild state; in New Mexico also, I am told
by a keen sportsman familiar with the country, wolves bear
young only once each year (W. Ruston). The same is true
for the foxes in the Zoological Gardens; they have two sexual
seasons, while the Tibet fox (Prejevalsky, 1876) and the
English fox (Bell, 1874) have only one in the wild condition.

The wild cat, on the other hand, in captivity does not
experience more sexual seasons than when in a feral state,
namely one (Hamilton, 1896); and the tame cat, when it
becomes wild, has apparently only one sexual season, whereas
the same animal under domestication has from two to four
sexual seasons per annum.

Among the deer in the Zoological Gardens their generative activity appears to have been universally stimulated—they will be referred to under the heading of "Duration of the Sexual Season in Polyœstrous Mammals,"—for it would seem that their normal (as I have considered it) monœstrous sexual season is increased by the conditions of captivity until it may become a continuous polyœstrous sexual season.

The Barbary wild sheep, on the other hand, does not appear to be affected by captivity; it exhibits a single monœstrous sexual season only, each year (Zoo.), and that is probably its condition in the wild state if we may judge from what is known of O. argali, and O. burrhel in Tibet (Prejevalsky, 1876).

It is with some hesitation I have included among monœstrous mammals deer, sheep, and pigs in the wild state; their retention in this class is doubtful; but if these animals were omitted there remains a remarkable series of examples of the variability of the sexual season of monœstrous mammals under various conditions.

The Duration of the Sexual Season in Polyœstrous Mammals in the Absence of the Male.

The duration of the sexual season in these animals depends upon two factors, the length of the diœstrous cycle and the number of times it recurs. Both factors may be different in different species of animals, and either may be different in different individuals of some species, or variable in the same individual at different times.

Knowledge of polyœstrum in animals in a wild state in this country is limited to certain rodents. The rat (M. decumanus), mouse (M. musculus), and the rabbit in this country are known to experience a recurrence of the diœstrous cycle. It is probably recurrent also in M. minutus, M. sylvaticus, M. rattus, Arvicola agrestis, A. glareolus, and Lepus timidus; while possibly Mustela vulgaris and Lepus variabilis, under favourable circumstances, may also experience a recurrence of the diœstrous cycle, judging from the account given of them by Bell (1874).

In Southern Europe and Algiers polyœstrum is apparently usual amongst rodents (Lataste, 1887). It appears to be ascertained for Sciurus vulgaris living in that part of the world—though the same animal is probably monœstrous in this country—for Eliomys quercinus, Gerbillus hirtipes, Dipodillus campestris, D. simoni, Meriones shawi, M. longifrons, Mus musculus, M. rattus, M. decumanus, and to be probably true also for several other species.

The animals on which these observations were made by Lataste were kept in captivity, but there is good reason to think that the conditions under which they were kept did not interfere with their habits in this respect.

Among domesticated animals polyœstrum occurs in horses, cattle, sheep, and pigs. While for wild animals in captivity it has been observed (Zoo.) in the gayal and bison; in wapiti, axis and red deer; in the gnu, eland, nilghau, and waterbuck; in Gazelle dorcas, in giraffes, in elephants, and probably in kangaroos.

In its most complete form polyœstrum occurs in certain monkeys and in the human female; probably most monkeys are similarly affected, and possibly also lemurs; in these animals there is a regularly recurrent series of diœstrous cycles throughout the year.

The Duration of the Diœstrous Cycle varies from five days (exceptional in rodents, Lataste, 1887) to as much as two months (exceptional in mares, and in various wild animals in captivity from time to time, Zoo.).

The usual length of the diœstrous cycle for rodents is ten to twenty days, and in other animals in which the phenomena has been observed from three to four weeks. In the rodents observed by Lataste (1887) the diœstrous cycle was usually ten days, and in the rat and mouse in this country the same may be said to be approximately true. In the domestic rabbit, however, I find great variability; while some individuals exhibit œstrus every three weeks fairly regularly, others do so every ten days; on the whole I think ten to fifteen days is the usual length of their diœstrous cycle.

In the domestic mare and cow three to four weeks, and in the domestic sheep and pig two to four weeks is said (Fleming, 1878) to be the length of the dicestrous cycle, while another authority (Ellenberger, 1892) regards three to four weeks as the usual time for all these animals.

In wild cattle, deer, and antelopes in captivity (Zoo.) three weeks is the usual time. In monkeys it appears to be about one month in duration (Heape, 1894, 1897, Keith, 1899). In the human female, while twenty-eight days is the normal length of time occupied by the dicestrous cycle, it is frequently experienced every three weeks or every five weeks, while occasionally even shorter or longer periods are known. Aristotle is represented to have made the extraordinary statement that few women menstruate every month, while most menstruate every three months. It would seem possible that the opposite is what he meant; at the same time it should be remarked that various observers (Wiltshire, 1883) have recorded their opinion that the women of certain tribes in different parts of the world menstruate only at long intervals (see also Ellis).

The recurrence of the Dicestrous Cycle is also very variable; exact knowledge on this point is not possible for wild animals; only those under observation, captive or domestic, can supply the requisite information.

The known limitations of the sexual season among certain wild animals, however, admit of a fairly accurate idea being gained of the recurrence of their dicestrous cycles, although not accurately enough to enable one to determine with certainty whether an animal is moncestrous or polycestrous. For instance, the American bison (Allen, 1876) experiences a sexual season from some time in July until some time in August. In the Cashmir ibex it persists during parts of November and December. In the Markhor and Hemitragus jemlaicus in Cashmir it occurs in December, while in the "Barasingh" in that country from September 20th to November 20th it has been observed (Laurence, 1895).

In Scotland the red deer's sexual season lasts three weeks,

during September and October, according to Cameron (1900) six weeks, while in this country September is the sexual month for the fallow deer, and July and August the time when the roe deer will receive the male.

In all these cases there can be little over three weeks during which copulation takes place, and the extremely limited period during which parturition occurs strongly corroborates the view that this is the extent of the usual time during which sexual intercourse is possible. The fact that in captivity three weeks is the usual period which intervenes between two œstri in such animals, and the extreme probability that individual females do not all experience œstrus at exactly the same time (Cameron, 1900), predispose one to believe that they are monœstrous in the wild state; but, if the limit of time for coition is three weeks, there is still just time for the females to undergo two diœstrous cycles, and it is this possibility which prevents positive assertion on the matter.

Among captive animals (Zoo.) not more than two diœstrous cycles have been observed in the gnu during one sexual season. Gazelle dorcas has two or three; the giraffe about three; while the eland, nylghau, and waterbuck have a series of diœstrous cycles, each lasting three weeks, during May, June, and July each year.

The gayal and bison, the axis and wapiti deer, on the other hand, experience a continuous series of diœstrous cycles all the year round, at intervals of about three weeks.

The hippopotamus at present in the Gardens is an old animal; for long she showed no signs of a sexual season, but lately she has done so at irregular intervals; no doubt in her case captivity has checked the generative function, for a former specimen which bore three young while there is said to have exhibited monthly sexual excitement (Wiltshire, 1883).

Among wild rodents in this country, recurrent diœstrous cycles last about two months, probably, in Lepus variabilis; about three months, probably, in Arvicola agrestis; from four to six months, probably, in Mus minutus; about nine

months in Mus rattus; and even longer, perhaps, in Mus musculus and M. decumanus.

Bell (1874) appears to think that, under favourable circumstances, the diœstrous cycles may continue all the year round in these latter animals and in the rabbit, but I am inclined to think such a condition is unusual in this country among wild rodents, since it is exceptional to find any of them pregnant during the winter months.

Among domesticated animals the period during which the diœstrous cycles recur, in the absence of the male, lasts from one month to as many as eight months for the mare, about five to six months for the rabbit, from one to three months for the sheep (with certain exceptions), and about two months for the pig. So far as the domestic rabbit is concerned, no doubt, if they are kept warm, carefully fed, and their breeding carefully regulated throughout the spring and summer, they may exhibit œstrus also in winter, but it must be recollected that here we are treating of œstrus independent of pregnancy, which is a very different matter.

Among certain monkeys, probably in most of them, the diœstrous cycle recurs all the year round (Geoffroy, St. Hilaire and Cuvier, Ehrenberg, 1833, Numan, 1838, Heape, 1894, 1897, Keith, 1899; compare also Rengger, 1830, Sutton, 1880, and Ellis). In the human female, as a rule, this is also the case; there appear, however, to be exceptions to this rule, for instance, the women of the Esquimaux peoples living between the seventy-sixth and seventy-ninth parallel do not always menstruate during the winter months. It is said (Cook, 1894) that not more than 10 per cent. of these women menstruate during the long dark winter months, and it is possible to imagine that the peculiar conditions of life they experience during that time may well be responsible for their peculiarity. If this be so, a true anœstrous period may be experienced by women.

Rink's (1877) account of the origin of these people, if correct, precludes the probability that the occurrence of an anœstrous period is a racial characteristic, and emphasises the view that it is a variation due to climatic conditions.

It is held by some writers, several of which are quoted by Wiltshire (1883), that the women of various savage tribes exhibit the menstrual flow only at intervals of several months; and the same author remarks on the fact that girls at puberty in this country menstruate only at intervals of three, four, or six months; and that it may be this condition is an indication of an ancestral habit. Ellis also quotes various authors who state that menstruation takes place at long intervals in women of Lapland, Greenland, the Faroe Islands, Tierra del Fuego, and among the Guaranis of Paraguay.

The effect of captivity or domestication on the duration of the sexual season in mammals is very remarkable.

As has been already pointed out, wild sheep have only a very limited sexual season per annum (O. argali, burrhel and poli, in Tibet, Prejevalsky, 1876), a condition which is maintained by the Barbary wild sheep in captivity in this country (Zoo.); whereas the domestic sheep has a much longer sexual season, and in addition has for many centuries (Aristotle) been capable of reproducing twice in each year under favourable circumstances.

Again, the wild goat has a very limited sexual season (Lydekker, 1898), whereas the domesticated goat will receive the male at almost any time (Low, 1845). A more remarkable example is that of certain deer in captivity (Zoo.). Wild red deer have a special sexual season, extending little over three weeks (Bell, 1874), and including certainly not more than two diœstrous cycles; whereas in captivity (Zoo.) the sexual season of these animals extends over most of the year, and consists of an extensive series of diœstrous cycles.

A similar condition prevails with the wapiti deer in the wild state (Roosevelt, 1893), while in captivity (Zoo.) the possibility of pregnancy at any time of the year is only prevented by the fact that the male does not rut during the casting and growth of his antlers; and it is asserted that park-fed wapiti stags in America are able to beget offspring even after their horns are shed (Caton, 1881).

Wild cattle in captivity (Zoo.) are also capable of repro-
duction at any time of the year, and they also experience a
remarkable increase in the recurrence of their diœstrous
cycles, from what we are led to infer, by the limited
calving season, is the case among similar animals in the
wild state.

Among domesticated mammals similar modifications are
evident, not only in animals of different species, but in indi-
viduals of the same species, as, for instance, in cattle and
horses.

Mares may have only one period of œstrus in the year, in
which case they are purely monœstrous animals, but this is a
rare condition ; rarely, also, they may have two diœstrous
cycles, but usually they have many.   In the latter case œstrus
may recur every three weeks, or the interval may be longer.
As a rule among thoroughbred mares the history of the
sexual season shows a series of diœstrous cycles, each occupy-
ing about three weeks and recurring throughout the spring
and often until the early autumn, as many as seven or eight
months being in some cases thus occupied.

Although these animals—horses, cattle, and deer—either
in captivity or under domestication, experience such an ex-
tensive increase in the consecutive recurrence of the diœstrous
cycle, it is not a condition natural to them ; it is due, in all
probability, to the care and attention paid to them by man ; in
the same way, it may be argued, that the stimulated power
of reproduction evinced by certain rodents is also due to the
advantages derived from their intimate relations with the
luxuries of civilisation (rat and mouse).

The only animals, so far as is at present known, which
experience a continuous series of diœstrous cycles in a state
of nature are certain monkeys.

The fact that it is possible to induce such an enormously
increased capacity for œstrus in any animals, prepares one to
consider the regular recurrence of the diœstrous cycle in
monkeys, and in the human female also, as a very slight step
in advance ; and when the whole of the evidence is considered,

it will, I believe, be found that the regularly recurrent diœstrous cycles of the Primates are strictly homologous with the more or less regular diœstrous and anœstrous cycles of the lower animals.

The Sexual Season in Monkeys.—The consideration of this subject introduces a further complication, and that is, while monkeys may have a continuous series of diœstrous cycles, they are not all of them fitted for reproduction at all times of the year.

Some monkeys in tropical countries may be in a condition to become pregnant at all times of the year; though this is by no means certain it is not an impossible fact, but others are certainly not so. For instance the chimpanzee and gorilla are said to have a special sexual season in West Africa (Garner, 1896).

Semnopithecus entellus, from the jungles on the south bank of the Hugli, has a definite time for reproduction (Heape, 1894); and Macacus rhesus, the area of whose geographical distribution is very large, apparently produces young at different and definite times in different districts (Heape, 1897).

There is every reason to believe, however, that these animals experience regular recurrent diœstrous cycles throughout the whole year.

If the diœstrous cycle of a monkey is homologous with the anœstrous cycle of a dog—and that this homology exists will be apparent when the question is considered from a histological point of view—it is obvious that we are naturally led to suppose that an increased number of œstri should result in an increased number of opportunities for pregnancy, precisely as in the case of the mare, deer, etc. But this is not so, and the result is that there exist certain mammals which, while they exhibit a continuous recurrence of the diœstrous cycle, have a circumscribed season for conception.

As I have shown elsewhere (Heape, 1894, 1897), this result is due to the fact that, although menstruation recurs regularly, ovulation does not; or, in other words, that ovula-

tion is not necessarily coincident with the œstrus in these animals.

This opens up a wide question, which I hope to treat of in a separate paper, but it is necessary to refer to it here in order to point out, that the limited season for conception in some monkeys is no reason for regarding their diœstrous cycle as in any way different from that of other animals.

Briefly, we may say that both ovulation and œstrus are due to stimulating influences. But they are not necessarily co-incident in the lower animals, and they are not necessarily both induced by the same means, nor at the same time.

In the virgin domesticated rabbit I find that ovulation does not occur in consequence of œstrus alone; while various observers have shown that in the bat ovulation may occur at quite a different time of year from œstrus, in some cases probably as much as six months may intervene between the two functions in this animal (Benecke, 1879; Eimer, 1879; Fries, 1879; Beneden and Julin, 1880).

Again, as I have already noted, there may be abnormal œstrus in many animals, it may occur during gestation and be independent of ovulation; while finally, it is quite certain that many animals which usually experience ovulation during œstrus, sometimes fail to become pregnant at that time in consequence of the failure of the function of ovulation.

Such being the case, it may truly be said the period of œstrus is not invariably identical with the period of ovulation; the two are separate functions, possibly closely asso-ciated, but also possibly widely divergent.

In monkeys we have an instance of animals in which the rhythm of ovulation may be different from the rhythm of œstrus, but it must not be supposed, on this account, that either of these processes is not homologous with the same process in other animals in which the rhythm may be identical. It would seem as if the sexual activity of these animals had been developed more than, and out of propor-tion to, the ovarian activity; or, in other words, that their sexual powers were greater than their powers of reproduction.

The ideas on this subject which have for so long prevailed and which even now are taught, namely, the identity of "menstruation"[1] and of œstrus with ovulation, would make this view impossible; but since it is known that, in various animals, either "menstruation" or œstrus may take place without ovulation, and that ovulation may occur without the coincidence of "menstruation" (Leopold and Mironoff, 1894) or of œstrus (bat), the possibility of isolating these functions is demonstrated. Thus it is no longer impossible to suppose that, while they are both due to similar stimulating influences, one of them may be developed in excess of the other. In this respect monkeys stand in an intermediate position between the lower mammals and man.

The Sexual Season in Man.—In the human female this question of the simultaneity of ovulation and œstrus ("menstruation," as it has been wrongly called) has given rise to wide discussion. I have referred to the question somewhat fully elsewhere (Heape, 1894, 1897, 1898), and have shown that the majority of modern writers on the subject are in favour of the view that the two functions are not necessarily coincident in the human female, the correctness of which conclusion it seems to me impossible to doubt.

With regard to the existence of a special limited sexual season or seasons, it is interesting to note that there is some evidence of such in the human female; evidence both of a time in the past when such special seasons were common to all, and of a time in the present day to which certain peoples confine such matters and during which most peoples exhibit special generative activity.

Here again we are upon the edge of a very wide field of research which it is impossible to do more than touch. I may, however, briefly draw attention to certain facts which in my opinion throw some light upon the matter.

Feasts, similar to the erotic feasts which were indulged in by the ancients—Babylonians, Phœnicians, Egyptians, Greeks, and Romans (Ploss, 1887),—were still practised to

[1] " Menstruation " is used here in its original sense.

some extent in the sixteenth century in Russia (Kowalewsky, 1890 and 1891), and in some parts of India at a much more recent date (Rousselet, 1876), while such customs as " gwneyd Bragod" (Owen, 1886) and possibly our own " bean feasts" may not improbably be the modern representatives of these ancient customs in our own country.

Again, it is worthy of note that the erotic feasts of more civilised peoples are not greatly dissimilar to the sexual feasts and dances of the savage peoples of Australia, Polynesia, West Africa, South America, New Britain, and West Asia (Ploss, 1887). Apart from the fact that many of them surely have some reference to phallic worship, as in the case of the maypole, the origin of these feasts—shrouded as they are in the mists of ancient customs now but little understood, and of laws long since forgotten, complicated as they are by customs, religions, and laws of a later growth—is not definitely known.

It is indeed a matter of the greatest difficulty to trace, justly, the true relation and likeness of any one of these customs to another, however similar they apparently may be. At the same time the universality of such customs is very remarkable, and may, I think with some justice, prepare one to believe that in prehistoric times man was impelled to indulge, if not wholly, at least more freely, in sexual intercourse at certain seasons rather than at other times of the year.

Hill (1888) attempts to trace the apparent survival of a human pairing season, by the customs of the Hindus and the proportions of births in each month of the year; while Westermarck (1891) records customs and statistics which certainly point even more strongly in the same direction. Ploss (1887) also gives many valuable statistics for Russia, Germany, Italy, and France; and Haycraft (1880) does the same for Scotland. It is remarkable that the statistics brought forward by these authors in all cases show a considerable rise in the birth rate at certain seasons. In Scotland, Haycraft oints out that from 1866 to 1875 a marked

increase of births occurred with striking regularity in April, showing that a maximum of conceptions takes place in July.

Hill says that ten years' statistics of the district in which he lived in India show that the maximum of conceptions occurs in December, when food is cheapest and the salubrity of the country at its best; while the minimum of conceptions occurs in September, towards the end of the hot season, when food is most scarce and malaria rife.

Ploss shows that in Russia the maximum of conceptions takes place in autumn, in Germany during May and December, while in Italy and France May is the month responsible for most conceptions. This author also points out that in Russia religion affects the birth-curve, and he traces the cause to fasting seasons.

Westermarck goes very fully into this matter, and has collected a great many facts bearing upon it which are of great interest. The sexual instinct in civilised man, he concludes, has two special seasons of activity—spring and autumn, but it is most active towards the end of spring as a rule, in the south of Europe this activity being most marked somewhat earlier than it is in the more northern countries.

Illegitimate births, it is remarked, are comparatively more numerous in early spring, and this, it is suggested, is due to an increase of sexual instinct during May and June.

These conclusions are interesting inasmuch as they indicate a season or seasons which may be the original sexual seasons; but it is the evidence he produces of the sexual seasons of more savage peoples which is of special interest here.

Some of the Indians of California are stated to have a regular sexual season, spring being a literal St. Valentine's Day with them.

The Watch-and-dies of West Australia and the Tasmanians have sexual feasts in the middle of spring-time.

The Hos, an Indian hill tribe, have a similar feast, which becomes a saturnalia during which absolute sexual freedom is indulged in, in the month of January; while among the Santals, another hill tribe, marriages mostly take place in

January.   Among the lower castes of the Panjas in Jeypore
a festival in January is kept up for a month, during which
promiscuous sexual intercourse is allowed.   The Kotars, a
tribe in the Neilgherries, have a similar feast marked by
similar licence and debauchery; and the same may be said
for the Keres in New Mexico, the Hottentots, and some
tribes near Nyassa.

In New Caledonia November (that is late spring) used to
be the time when marriage engagements were made, and
among the Rajputs of Mewar the last days of spring are
dedicated to the god of love.

Among the Kaffirs of Cis-Natalian Kafirland more children
are born in August and September than in any other month,
and it seems probable this is due to certain feasts during
which there is unrestricted intercourse between the un-
married people of both sexes.

Among the Bateke—Stanley Pool—most children are born
in September and October—the season of the early rains,—
and it is said the same is the case among the Bakongo.

In Chili the maximum of births occurs in September.

Dalton (1872) gives an account of the Miris, an Indian
hill tribe, which shows that at one season of the year
sexual relations between the unmarried are specially counte-
nanced and indulged in.

My friend Mr. Caldwell tells me that the Queensland
natives with which he was brought in contact have a distinct
sexual season in September (that is spring), and that they
cannot be prevailed upon to do any work for some weeks at
that time of the year.

Cook (1894) records that the Esquimaux which inhabit the
country lying between the seventy-sixth and seventy-ninth
parallels, exhibit a distinct sexual season, which recurs with
great intensity at the first appearance of the sun, and that
little else is thought of for some time afterwards : an account
which is in agreement with statements made by Bosquet
(1885) regarding other Esquimaux.

Finally Man (1882) notes that the children of the natives

of the Andaman Islands are said to be born mostly at a particular time of the year—during the rains.

I have not done more here than simply to indicate the bearing of a very considerable literature which deals specially or incidentally with this subject; one section of this literature demonstrates by means of statistics, for countries where such are available, an excessive birth rate in special seasons; the other shows that the habits and customs of the less civilised peoples indicate that their sexual and reproductive functions are specially stimulated at definite times of the year.

While there is some variation in the season for special sexual activity indicated by the above statements, spring is obviously the most usual time. Hutchinson (1897) seeks to show that the time of marriage among certain widely divergent people is largely governed by times of agricultural plenty; for economic reasons this might reasonably be expected, though the evidence he brings forward is not at all conclusive. But it does not seem to me to be an important point. Many reasons, religious or otherwise social, may have arisen to interfere with such a rule, supposing it ever was a rule. The importance of the evidence consists in the proof that any time is or was specially conducive to sexual disturbance, and this, I think, has been proved. (See also Laycock [1840] and Ellis's very interesting résumé of this question.)

The wide variation in the time of the year during which the sexual season of the lower mammals occurs in different parts of the world, renders it not surprising that there should be wide variation in man also in this respect, in different geographical areas.

However that may be, the fact remains that there is much evidence in favour of the view that special sexual seasons were, at one time, universally experienced by the various races of man, a fact of great importance from a comparative point of view.

But not only is there evidence of a circumscribed period for reproduction in the ancestral human being, and in those

peoples who occupy a low position in the scale of civilisation, but there is also evidence that the latter produce smaller families.

In some cases this is ascribed to the practice of infant marriage, to the strain of child-bearing on a mother who requires for herself all the nourishment she is capable of assimilating; but comparatively small families are usual in many savage peoples whose women do not become mothers at a very early age (Westermarck, 1891).

In these cases the result is probably due not only to prolonged lactation, or to infant mortality, but to inability to produce more children; for, as the practice of polygamy shows, the advantage of large families is fully recognised, and each individual woman will be required to reproduce as frequently as possible.

It would seem highly probable, therefore, that the reproductive power of man has increased with civilisation, precisely as it may be increased in the lower animals by domestication; that the effect of a regular supply of good food, together with all the other stimulating factors available and exercised in modern civilised communities, has resulted in such great activity of the generative organs, and so great an increase in the supply of the reproductive elements, that conception in the healthy human female may be said to be possible almost at any time during the reproductive period.

We have come to believe that it is to the regular monthly menstrual periods, which the human female generally experiences, that this great reproductive power is due. But the evidence of a regular menstruation with a limited conception period in monkeys, shows that this is certainly not so. As in monkeys, so in man, these two functions are not necessarily equally developed.

I think it may fairly be stated that an increase in the frequency of menstruation is not necessarily a sign of an increased power of reproduction among women, and that there is no indication that women who menstruate every two or three weeks are more prolific than those who menstruate

every month; in fact, the reverse is probabl true, and the excessive activity of the menstrual organ, if it ; not developed at the expense of the reproductive power, n many cases results in lessened fertility.

We are here doubtless in the region of pathological conditions, since when there is a considerably increased menstruation, either by increase of the amount of the menstrual flow or by decrease of the intra-menstrual peric], it is accompanied by exhaustion and the evils which res lt therefrom.

If the above be true, it would appear that ivilised woman has reached the limits of reproduction compatible with her mode of life, and it may be concluded that increased reproductive power will not arise until her power; of assimilation are increased to a sufficient extent, and unti the products of that assimilation are devoted more exclusi ely to the reproductive function.

The Duration of the Œstrus in Monœstrous and Polyœstrous Mammals in the Absence of the Male.

There is very little known regarding this point except in certain domesticated animals. The œstrus of monœstrous mammals may last a short or a long time. In the Barbary wild sheep in captivity (Zoo.) it only lasts a few hours. In the bitch it lasts a variable time, variable both in different individuals of the same species and in the same individual at different times. The winter œstrus of the bitch does not last so long as the summer œstrus in certain breeds; a well-known breeder (Dr. Inman) has assured me this is the case with his bitches. The usual time is probably from seven to nine days.

A most careful observer, however, tells me that a bitch which he had for many years usually remained in a condition of œstrus for nine days, but sometimes it persisted in her for fourteen days. Other breeders have informed me they have had bitches undergoing œstrus for even a longer period than this, but it is undoubtedly an exceptional experience.

In certain bloodhounds a well-known breeder (Mr. Brough) has observed œstrus to last twenty-one days, but only very exceptionally, and not as a characteristic of any particular bitch.

There can be little doubt the persistence of œstrus in bitches may be influenced by their temperament, by their food, and by the particular conditions of existence experienced by each bitch.

Wolves, jackals, and foxes in the Zoological Gardens have about the same duration for œstrus as the average bitch, from seven to nine days. In the cat œstrus lasts nine to ten days (Hamilton, 1896); in tigers in captivity (Zoo.) for eight days at the longest. In bears, on the other hand (Zoo.), œstrus appears to last continuously for two to three months; it must be recollected, however, that this occurs with females kept together with males under conditions which, while they may very probably excite sexual feelings, do not result in gestation.

Among wild animals the duration of the œstrus can only be assumed by comparison with other individuals of the same species in captivity; although the duration of the sexual season may be inferred from the known season during which parturition takes place, the duration of the œstrus cannot be so determined.

Among polyœstrous mammals there is not such great variation in the duration of œstrus, since, instead of a long period of œstrus, these animals exhibit a recurrence thereof; still there is some difference apparent : the domestic sheep has œstrus for only a few hours, say twelve hours; the cow for not more than twenty-four hours as a rule; while antelope, deer, and wild cattle in captivity (Zoo.) closely imitate domestic cattle and sheep in this respect.

The mare endures œstrus probably for a slightly longer period as a rule, but this depends very much on the temperament of the individual mare, and the conditions under which she is kept.

The elephant in the Zoological Gardens has persistent œstrus for probably three to four days.

In monkeys the œstrus has not usually been carefully noticed, but I am assured that the Moor macac in confinement (Zoo.) has a definite œstrus which lasts two or three days ; and in a few other monkeys a similar condition has been from time to time noticed (Ellis).

In the human female there is not wanting evidence of a similar condition (Aristotle ; Martin, 1888 ; Haycraft, 1880), and on this point information has been supplied to me by various experts, which leads me to think it will probably be found that those women who are most robust, and who suffer least from the enervating effects of civilised life, experience a condition comparable to that of œstrus in the lower mammals (confer also Ellis).

The Effect of Maternal Influences on the Sexual Season and on Œstrus.

Maternal influences may or may not completely disorganise the sexual season ; this depends upon whether or not they interfere with its recurrence or with that of œstrus.

Gestation.—Gestation may or may not interfere with the recurrence of one or other of these factors. In the dog it does not do so, because the dog has only one œstrus during each sexual season, and the period between two sexual seasons, i. e. the anœstrum, is longer than the period of gestation. In the elephant it does do so, because the gestation period is longer than the anœstrous period. So also with badgers this appears probable (Denwood, 1894). In camels, whose gestation occupies thirteen months, the sexual season is interfered with by gestation, and is on that account put off for another year. The camel conceives every two years (Swayne, 1895). In the rat, on the other hand, gestation does not interfere with the recurrence of the sexual season, but does interfere with that of œstrus, because the rat has a series of diœstrous cycles in each sexual season, and she may also undergo a series of gestation periods during that time, and because the maternal generative cycle (twenty-one days) is longer than the diœstrous cycle (ten days).

But whenever gestation occurs it encroaches upon, if it does not entirely absorb, the anœstrum; that is to say, it reduces the period during which the generative organs would lie fallow if the sexual season were a barren one. Thus in the case of the mare, a barren sexual season may consist of a series of diœstrous cycles lasting for as long as six months, in which case the anœstrum lasts six months also, after which another sexual season again begins.

A reproductive sexual season, however, results in a period of eleven months' gestation; interfering not only with the diœstrous cycles which would have recurred if conception had not taken place, but also absorbing practically the whole of the anœstrum; for, nine days after parturition, the majority of mares again experience œstrus.

Nursing.—Nursing also may or may not interfere with the recurrence of the sexual season and of œstrus. The rat suckles her new-born litter of young while pregnant with another litter; so also does the domestic rabbit and guinea-pig, and probably many rodents. The mare also, as a rule, readily becomes pregnant while suckling her newly born foal. Here, however, there is some evidence of variation, for I am informed, by a breeder of large shire horses in the west of England, that many of the mares in his stud become pregnant only once every two years; the drain on the system, in consequence of gestation and nursing, in these large animals being, apparently, too great to admit of the immediate recurrence of another sexual season. Another breeder of shire horses, however, assures me that he gets a foal each year from his mares.

On the whole there is some reason to believe that, unless these large mares are exceptionally carefully tended, they are liable to miss bearing annually, from time to time.

A few instances may be given here of animals in the wild state which do not bear young every year. The grizzly bear in British Columbia bears young only every second year (Somerset, 1895). The wild yak in the Tibetan desert only produces a calf every second year (Prejevalsky, 1876), and

the same is probably true for the Greenland musk ox (Lydekker, 1898); while the walrus, which goes nearly twelve months with young, nurses her calf or provides it with food for two years (Bell, 1874), and during that time ancestrum appears to persist.

Similar evidence of variation is to be found in the human female. Among the Esquimaux in high latitudes children are nursed from four to six years, and women bear children about every four years (Cook, 1894). It is not uncommon to hear of women of various tribes purposely prolonging the nursing period in order to avoid too frequent breeding. The Waganda women nurse their children until two years of age, and live apart from their husbands from the time of conception until the child is weaned (Felkin, 1885). The Andaman Island native women nurse their children as long as they can (Man, 1882). On the other hand, it is recorded that among the North-west Central Queensland natives nursing may go on for three, four, or five years, and a mother is frequently seen with two children of different ages at the breast (Roth, 1897). Among more civilised women menstruation is frequently in abeyance during the nursing period, nevertheless many women menstruate while lactation is still possible. Such a possibility is not confined to women among menstruating animals. I have seen a monkey, Macacus cynomolgus, in the gardens of the Zoological Society at Calcutta, which menstruated regularly while still suckling a young one.

The whole question of lactation and its relation to sexual phenomena, more especially gestation, is of great interest, all the more perhaps when it is remembered that virgin bitches frequently secrete milk in sufficient quantities to interfere with their work (foxhounds), while mules have been known to nurse successfully the foal of a mare; but for our present purpose sufficient has been said, and in conclusion it may be argued that when nursing encroaches upon the sexual season, the recurrence of the latter depends upon the vigour of the mother and her powers of recuperation.

The Pro-œstrum.

The pro-œstrum, as I have already stated, is the forerunner of œstrus. Evidence of it is to be seen in each of the large groups of the Vertebrata, fishes, amphibia, reptiles, birds, and mammals (Wiltshire, 1883), and it must be regarded in all of them as a sign of the preparation of the generative system for the sexual act.

Pro-œstrum is usually associated, in the minds of breeders, with reproduction, to an extent which entails the supposition that the same stimulus which incites the former also causes the latter ; but the fact that pro-œstrum may occur normally without the concurrent production of ova shows that the two functions are not always interdependent, and that what serves as sufficient stimulus for sexual desire is not necessarily sufficient for reproduction.

A consideration of these relationships belongs rather to the study of ovulation than to the subject-matter of the present paper. I would merely remark here that while the ovary probably does participate to some extent in the excitement evidenced by pro-œstrum, this function in mammals must be considered as evidence mainly of sexual rather than of reproductive power.

Pro-œstrum is first evident in the tissue of the external generative organs and the surrounding parts, and while it increases in intensity there, it extends to the uterus ; during this time certain changes (to be mentioned below) take place in the uterine tissue, and they are followed by the subsidence of the disturbance, first in the uterus and finally in the external generative organs.

The length of time during which pro-œstrum lasts is extremely difficult to determine ; there seems to be considerable variation in different animals, and in the same animal at different times ; but that may be due to variation in the intensity of the external evidence rather than to variation in the duration of the pro-œstrum itself.

In the rabbit I have observed this period lasts, probably,

one to four days; in the bitch seven to twelve days (Stone-henge, 1887); in the chimpanzee six to eight days (Keith, 1899). In cattle and sheep the external evidence of pro-œstrum is difficult to determine, and œstrus appears to follow very quickly upon the former, about one day after or less. Pigs, on the other hand, exhibit external signs of pro-œstrum somewhat longer, while mares are very variable in this respect.

A further consideration of the subject is divided into the external and internal evidence of pro-œstrum.

The External Evidence of Pro-œstrum in Mammals.—The first sign of pro-œstrum noticed, in the lower mammals, is a swollen and congested vulva, and a general restlessness, excitement, or uneasiness. There are other signs familiar to breeders of various mammals, such as the congested conjunctiva of the rabbit's eye, and the droop-ing ear of the pig, which are considered by some as even more reliable indications of the probability or capability of conception than is afforded by the vulva alone. Many monkeys (Heape, 1894, 1897, Keith, 1899) exhibit conges-tion of the face and nipples, as well as of the buttocks, thighs, and neighbouring parts; sometimes they are congested to a very marked extent, and in some species a swelling, occa-sionally prodigious, of the soft tissues round the anal and generative openings, which is also at the time brilliantly congested, indicates the progress of the pro-œstrum.

The Pro-œstrous Discharge and Menstrual Flow. —Following the swelling and congestion of the external generative organs, there is, in most animals, a discharge from the generative canal. The discharge may consist merely of mucus from the uterine glands and from the glands of the cervix and from those in the neighbourhood of the vaginal orifice, of the products derived from the breaking down of epithelial tissue, and of fragments or small masses of pave-ment epithelium from the vagina; such a discharge is usually to be seen in the rat and mole.

In addition, fragments or small masses of columnar uterine epithelium may be observed in various animals. Again, to

the above, blood may be added for a large number of animals, some of which rarely, some frequently, and some always suffer from a loss of blood. While, finally, more or less compact masses of uterine stroma tissue are included in the discharge of the Primates and some of the lower mammals. Blood has been observed in the discharge during pro-œstrum in the mare, ass, cow, sheep, goat, pig, cat, rabbit (Aristotle ; Ellenberger, 1892 ; Fleming, 1878 ; Wiltshire, 1883), and rat (Lataste, 1887) ; it is also recorded as having been observed in marsupials (Wiltshire, 1883) ; in the bitch it is almost invariably present, and so also it would appear to be in Pachyuromys duprasi, Dipodillus simoni, Meriones shawi (Lataste, 1887), and in Tupaja javanica and Tarsius spectrum (Stratz, 1898). In most of these animals there is only enough blood to tinge the discharge more or less, but in the bitch, and probably T. javanica and T. spectrum, there is a flow of blood almost as concentrated as that recorded for monkeys (Heape, 1894, 1897).

It has been recorded for a large herd of highly bred Alderney or Jersey cattle in the south of England, that a discharge of blood is of regular recurrence among them (Wiltshire, 1883) ; but so far as I can learn this is exceptional, although its occurrence in individuals is by no means rare. It has been suggested that bleeding in the lower mammals during pro-œstrum is confined to domesticated species, but this is not true (Lataste, 1887 ; Stratz, 1898 ; Wiltshire, 1883) ; at the same time it is not improbable that the circumstances attending domestication tend to increase the flow of blood from the uterus, and that highly bred domesticated animals are more liable to experience it than those which are hardier, less carefully attended to, and less luxuriously fed.

The pro-œstrous discharge, then, varies in quality in different animals, and not only is this true, but it varies at different times in the same animal, both as to quantity and quality. There is ample evidence of this in various human tribes (Holder, 1892, Ellis) and in individuals. Among

domesticated animals, mares, cows, sheep, and rabbits do not always experience a loss of blood; further, individual animals of these species sometimes experience a much more profuse flow than at other times, or they may experience a profuse flow only rarely or not at all.

The Internal Phenomena of Pro-œstrum.—It will be convenient first to abstract the account I have given elsewhere (Heape, 1894) of the changes which take place in the uterus of the monkey during pro-œstrum, and then to compare these changes with those which occur at that time in the human female on the one hand, and in the lower animals on the other.

A. Period of Rest.—Stage I. The resting stage. This is the period before pro-œstrum occurs, and at that time the uterine mucosa is a shallow bed, opaque, white, and anæmic.

B. Period of Growth.—Stage II. The growth of stroma. It is now that pro-œstrum first becomes apparent; the uterine stroma thickens, hypertrophy takes place, and it becomes semi-transparent, soft, and flabby.

Stage III. The increase of vessels. The growth of the stroma tissue is rapidly followed by an increase in the number and size of the vessels of the stroma, the whole becomes richly supplied with blood, and the surface is flushed and highly vascular. This process goes on until the whole of the uterine stroma becomes tense and brilliantly injected with blood.

C. Period of Degeneration.—Stage 4. The breaking down of vessels. The walls of the superficial vessels now break down, and the blood contained therein is extravasated throughout the superficial portion of the mucosa.

Stage V. The formation of lacunæ. The extravasated blood becomes gradually collected in lacunæ, which at first lie within the stroma, but gradually become enlarged and project as rounded hillocks, bounded superficially by the uterine epithelium, into the cavity of the uterus.

Stage VI. The rupture of lacunæ. The superficial mucosa cells, isolated or in patches, now begin to degenerate; they

are cut off, as it were, by the extravasated blood, from the deeper mucosa cells, and they shrivel up and die. Soon the uterine epithelium follows suit and, with the degeneration of its cells, loses its continuity and ruptures, thus allowing the blood hitherto contained to pour into the uterine cavity.

Stage VII. The formation of the menstrual clot. With the blood which is poured out from the ruptured lacunæ is mixed also degenerated epithelium cells, isolated or in strings ; and as the tissue below is laid bare, the extravasated blood in the deeper parts of the mucosa, together with stroma tissue and the superficial portion of uterine glands, also collects in the uterine cavity, and the whole forms therein a more or less dense clot. Some of the blood and degenerate uterine tissue oozes out through the os uteri to the vagina and thence to the exterior while the process is in progress, but there is frequently left behind until a later stage a clot, which in some cases entirely fills the uterine cavity.

D. Period of Recuperation.—Stage VIII. The recuperative stage. While the clot is still within the uterus, a new epithelium begins to grow over the, now much reduced, uterine stroma. At the same time new capillary vessels are formed, the extravasated blood which still remains in the tissues is collected therein, and brought back into the circulatory system. During this period the clot is expelled, and subsequently the uterus assumes again the appearance first described, and eventually becomes again at rest. It is at or towards the close of this period that œstrus normally occurs.

For the human female the histology of pro-œstrum (menstruation) has never been so fully worked out in healthy normal uteri. Many observers have described isolated specimens, and most of them have had recourse to material which has either been obtained some time after death, or from individuals suffering from diseases which may well have produced pathological changes in the uterine tissue. Then, again, the extent of menstruation varies in different peoples and individuals, and in the same individual at different times. The amount of the menstrual flow and the quality of that flow also

varies, to such an extent, indeed, that, while some women lose a large amount of blood at each pro-œstrum, others sometimes and some never lose any at all. It is not surprising, therefore, to find that while some observers hold that no change takes place in the uterine tissue during pro-œstrum, others state that highly specialised decidual tissue is formed at that time; while some deny that even a portion of the uterine epithelium is lost by denudation during pro-œstrum, others maintain that the whole of the mucosa layer is discarded during that process.

The question has been somewhat fully discussed by me in a former paper (Heape, 1894), where an account is also given of the more important literature of the subject. Here it is only necessary to add the conclusions arrived at, which are that in all essential points the menstruation or pro-œstrum of the human female is identical with that of monkeys. More recently I have described (Heape, 1898) two menstruating human uteri, the first of which shows congestion and is closely comparable to Stage IV of the monkey, while the second shows denudation, and appears to be practically identical with Stage VII of the monkey.

A slightly earlier condition of denudation in the human uterus has been described and figured by Minot (1892), and again supports the view above expressed.

Among lemurs, Stratz (1898) has described what he calls bloody "menstruation" for Tarsius spectrum. I gather that, in this animal, denudation of the epithelium of the uterus takes place and that Stage VII exists; but there is no proof that denudation extends to the stroma tissue, and therein possibly lies the difference between lemurs and monkeys, otherwise there can be little doubt of the homology of the process in these two animals.

Stratz has also described the existence of a blood-clot and a "menstrual"[1] flow in Tupaja javanica, and here again the

[1] The use of the term "menstrual" flow, as it is here used, to denote a flow of blood from the uterus, without regard to the periodicity of that flow, is to be deprecated.

tissue contained in the clot apparently consists only of desquamated epithelium.

Retterer (1892) has given a more detailed account of what happens during the pro-œstrum of the bitch. During period A, of rest, Stage I, the mucosa of the uterine horns is firm, pale, and of a thickness of ·3 to ·5 mm.; but with the commencement of pro-œstrum, period B, there is a well-marked Stage, II, in which the mucosa grows rapidly to three or four times its original thickness, and becomes soft and spongy. Stage III is also well marked, and the mucosa becomes injected with numerous vessels distended with blood. Then period c occurs, and Stage IV is marked by the breaking down of the vessels and extravasation of the blood in the mucosa tissue. Lacunæ are formed, Stage V, which, during Stage VI, rupture, and pour the contained blood into the uterine cavity.

So far the similarity of the progress of the pro-œstrum in the bitch is practically identical with that of monkeys, but there is no blood-clot formed, and Retterer's account renders it doubtful whether any denudation, even of epithelium, takes place. He himself thinks not. I have myself worked out the history of the pro-œstrum of the bitch to some extent, and have satisfied myself that Retterer's account is true in all essential details.

I have also failed to find any area of the uterine mucosa which has been denuded of epithelium, and do not believe that this process occurs to any extent; at the same time, where lacunæ rupture there must be loss of epithelium, though I think denudation is confined to these spots.

The pigmentation of the uterus, described by Altmann (1878), is further evidence of the probability that much of the extravasated blood is not discharged into the uterine cavity, but is retained in the uterine tissue and absorbed from thence.

The homology of this process in the bitch with that already described for monkeys is absolutely certain, and if nothing more were known, would establish the identity of the pro-

œstrum in these animals ; or, in other words, the homology between the pro-œstrum (so-called "heat") of the lower mammals and the menstruation of the Primates.

The absence of Stage VII, the menstrual clot, is not to be wondered at in a large bifid uterus ; the denudation of tissue in sufficient quantity to form a clot would be a very severe operation in such a comparatively large organ.

The only other paper dealing with this subject, for the bitch, with which I am acquainted (Johnstone, 1888), treats of what the author calls the "corpuscular development" of the mucosa of the bitch during the pro-œstrum, but I do not gather the author has satisfactorily demonstrated the truth of the view he advocates (see also Johnstone, 1895).

Pouchet's description of the changes in the uterus of the sow during pro-œstrum shows the existence of Stages II and III (Wiltshire, 1883) ; he does not describe the breaking down of vessels or the formation of lacunæ, but his description of the histology of the uterine discharge shows that it contains, besides mucus, both blood and uterine epithelium. Stage IV, therefore, is assuredly represented, and there can be little doubt that Stages V and VI are also passed through, since there must have been rupture of the uterine tissue in order that pieces of it should be contained in the discharge.

Ellenberger's (1892) account of the changes which take place during pro-œstrum in domestic mammals includes Stages II and III ; he also does not describe Stages IV, V, and VI, but he records the presence of both blood and epithelial cells in the discharge, and these stages must therefore have been passed through, although denudation is in all probability very slight. Fleming (1878) adopts the view that, among ruminants, the blood which finds its way to the exterior exudes from the cotyledons ; while Ellenberger describes pigmentation there, and states it is caused by the blood left behind in that tissue after pro-œstrum has occurred.

Bonnet (1892) also describes Stages II and III in various domestic mammals during pro-œstrum, but he also adds

Stage IV for ruminants, horse and pig, and where external bleeding is seen in these animals the occurrence of the equivalent of Stages V and VI is essential.

Kazzander (1890) notes the existence of extravasated blood (Stage IV) in the sheep's uterus during pro-œstrum, at a period before external bleeding is noted; so that when the latter occurs, a condition equivalent to Stage VI is passed through by this animal.   Both this author and Bonnet (1880, 1882), whom he quotes, describe pigmentation in the uterine mucosa of the sheep, and consider it is due to the extravasated blood which is not discharged during the pro-œstrum.

Lataste (1887) describes desquamation of uterine epithelium in several Muridæ, and states that it takes place independently of pro-œstrum (or, as he calls it, " rut "), during which Stages II and III are noted, and at the close of which a bloody discharge (which he calls "menstruation") is evident.   Stages IV, V, and VI are therefore probably also passed through in the case of these animals.

I find it difficult to determine exactly what this author means, but I gather it is his opinion that in these animals there is a periodic shedding of uterine and superficial vaginal epithelium, and that this precedes and is independent of the pro-œstrous discharge (p. 163); if this be so it is quite different from anything which has been already described for any other of the lower mammalia, and is comparable only to that somewhat rare phenomenon, exfoliation of the vagina, in the human female.   The same author declares (1893) there is a rhythmical transformation of the epithelium of the vagina in certain of the lower mammalia, which is in connection with rhythmical generative changes; he describes the denudation of this epithelium, and its recuperation from the lower layers.

The subject has been very rarely investigated in the lower mammals, and still more rarely has it been attacked from a histological point of view; isolated specimens have been described with more or less detail, but no attempt has been made to work out the history of the process by any one, so far as I know, but Retterer.

For this reason the evidence available is fragmentary, but it is remarkably consistent; and although further researches may, and probably will, show variations in detail, the broad fact of the homology of the internal process of pro-œstrum in all mammals is sufficiently demonstrated.

This we may summarise as follows: the uterus of all mammals during the quiescent period is comparatively anæmic, and its mucosa is a thin layer; it has at that period the appearance of lying fallow.

During pro-œstrum hypertrophy of the mucosa first takes place, and is followed by congestion, which results usually in the rupture of the superficial vessels and consequent extravasation of the blood into the surrounding tissue; in some cases this extravasated blood finds its way into the cavity of the uterus and thence to the exterior, with either more or less denudation of the superficial mucosa, while in other cases there is no external hæmorrhage, and the extravasated blood is absorbed in situ. While, therefore, neither the discharge of blood nor the extravasation of blood is an essential feature of the pro-œstrum, the hypertrophy and congestion of the mucosa is invariably present in all mammals, a condition which we may confidently expect to find also in the lower Vertebrata.

The Period of Œstrus.

The period of normal œstrus, as I have stated in the introduction to this paper, occurs as a result of pro-œstrum.

As a rule breeders regard œstrus (the period of desire) as an attendant condition of pro-œstrum rather than as a result thereof; where there is no discharge evident there is some excuse for this view, especially as, even when a discharge does occur, œstrus may happen before the discharge completely ceases. Œstrus, however, is possible only after the changes due to pro-œstrum have taken place in the uterus. A wave of disturbance, at first evident in the external generative organs, extends to the uterus, and after the various phases of pro-œstrum have been gone through in that organ,

and the excitement there is subsiding, it would seem as if the external organs gain renewed stimulus, and it is then that œstrus takes place. If the uterine changes are confined to Stages II and III, that is simply hypertrophy and congestion of the mucosa, œstrus rapidly follows the first external signs of pro-œstrum ; but if more elaborate disturbance takes place in the uterus, the period of œstrus is delayed.

Thus it is during the subsidence of the uterine disturbance that œstrus takes place. The period during which the discharge continues is not, however, a true indication of the permanence of the uterine disturbance. In comparatively large uteri, especially in those which extend as long horns from the corpus uteri, the area of denudation or hæmorrhage may be situated far from the vagina ; and the products of that hæmorrhage and of denudation may take a considerable time to find their way to the exterior; this is especially the case where there is little blood and much mucous discharge.

We have seen above that in the monkey, Stage VIII, a new epithelium is formed over the surface of the newly denuded uterus before the blood-clot is evacuated ; and in the same way, before the discharge from long-horned uteri reaches the exterior, the uterine disturbance is largely allayed, and renewed stimulus may be supplied to the external generative organs.

In all animals which have been investigated, coition is not allowed by the female until some time after the swelling and congestion of the vulva and surrounding tissue is first demonstrated, and in those animals which suffer from a considerable discharge of blood, the main portion of that discharge, if not the whole of it, will be evacuated before sexual intercourse is allowed.

Thus in Pachyaromys duprasi, which experiences hæmorrhage, coition is not allowed during the flow (Lataste, 1887).

Bitches, except rarely, receive the dog only after bleeding is over (Stonehenge, 1887), although a mucous discharge, which frequently continues after the discharge of blood

ceases, may be still in progress at the time coition is permitted by the bitch (Millais).

The Moor macæ in the Zoological Gardens has a definite œstrus, which always occurs shortly after the menstrual discharge ceases, and which lasts for two or three days; and there is strong reason for believing this is also the case with various other monkeys, as, for instance, the orang-utang (Ellis).

The human female frequently experiences œstrus with marked strength after menstruation is over (Martin, 1888), more especially, it would appear, in those individuals who do not suffer from excessive menstruation,—in other words, in those whose generative system is least disturbed by the consequences of civilisation and social life. This special time for œstrus, in the human female, has very frequently been denied, and no doubt civilisation and modern social life do much to check the natural sexual instinct where there is undue strain on the constitution, or to stimulate it at other times, where extreme vigour is the result.

For these reasons a definite period of œstrus may readily be interfered with, but the instinct is, I am convinced, still marked. Ellis quotes various authors who hold a similar view, but they do not all agree as to the time when œstrus occurs; if, therefore, the views which I have advocated here are correct, it would seem probable that abnormal œstrus has been mistaken for true œstrus in many of these cases.

Summary and Conclusion.

Introduction.—After criticising the terms commonly used to denote the various stages of the "sexual season" of mammals, I have defined the terms used in the present paper.

Female mammals are divided into two classes, "monœstrous" and "polyœstrous" mammals, and I have explained that, in the absence of the male, "pro-œstrum," "œstrus," and "metœstrum" are followed by "diœstrum" in polyœstrous mammals, during the recurrence of the "diœstrous

cycles," and by " anœstrum " in monœstrous mammas
always, and in polyœstrous mammals at the close of the
sexual season.

The difference between the diœstrous or anœstrous cycles
in the absence of the male, and the " maternal generative
cycle " when œstrus is followed by insemination, fertilisation
of the ovum, and gestation, is drawn attention to.

The occurrence of abnormal œstrus is noted.

The Breeding Season of Mammals is merely touched
upon ; inasmuch as it concerns what happens during both the
sexual season and the gestation period jointly, its full con-
sideration is not possible in this paper.

The Sexual Season of Male Mammals.—Males are
divided into two classes, those which have a special sexual
season, " rut," and those which are sexually capable all the
year round. The influence of captivity is touched upon, and
it is shown that, while sexual activity is not so violent in
captive animals as in those in the wild state, it may be
much more frequently or continuously exhibited.

The Sexual Season of Female Mammals.—This is
considered in wild mammals in a state of nature, in those
which are captive, and in domestic mammals ; and the effects
of climatic, individual, and maternal influences are drawn
attention to.

Among monœstrous mammals the effect of these influences
may be to increase or decrease the periodicity or the duration
of the sexual season, while among polyœ   ammals the
effect may be to increase or decrease the number of diœstrous
cycles in each sexual season or the duration of each cycle ;
the effect in both classes of animals being to increase or
decrease their reproductive power.

It is pointed out that the knowledge at present available
throws no light on the origin of the sexual season ; but that
it is due to a stimulus which appears to be gradually collected,
that it is associated with nutrition, and is manifested by excep-
tional vigour and bodily " condition " seems assured.

The Periodicity of the Sexual Season in Monœs-

trous Mammals in the Absence of the Male.—This is shown to be affected by climatic and by individual influences, to be more frequent in domesticated than in wild animals of the same species, and to be variously affected by captivity.

The Duration of the Sexual Season in Polyœstrous Mammals in the Absence of the Male.—The sexual season in these animals is affected by the duration and the recurrence of the diœstrous cycle; as in monœstrous mammals, it is shown to be affected by climatic and individual influences, by domestication and captivity.

It is here that we are first brought into contact with monkeys and man, and I have endeavoured to show that the sexual season which undoubtedly exists in monkeys, exists also in certain human peoples in the present day, while there is some evidence that, in the past, all peoples were similarly affected, and that a definite sexual season was the rule. The fact that, in spite of the regular recurrence of the œstrus, monkeys have only a limited season during which conception is possible, is drawn attention to. It is pointed out that this is due to the fact that the ovary is not active all the year round, and evidence is brought to show that the function of ovulation is also not necessarily coincident with œstrus in various other mammals. This condition is apparently due to the want of sufficient energy for both œstrus and ovulation.

The Duration of the Œstrus in Monœstrous and Polyœstrous Mammals in the Absence of the Male.—Knowledge of this point is practically confined to domesticated mammals and to certain animals in captivity, and the evidence, which a study of these animals renders available, shows that the duration of œstrus is very variable, not only in different species, but also in different individuals of the same species, and in the same individuals at different times.

There is greater variation in this respect among monœstrous than among polyœstrous mammals, as a rule.

The Effect of Maternal Influences on the Sexual Season and Œstrus.—These may or may not completely

disorganise the sexual season, and this depends on whether or not they interfere with its recurrence or with that of œstrus.

The above is true for both monœstrous and polyœstrous mammals, for both gestation and nursing ; but whereas gestation interferes with the recurrence of the œstrus, only if it extends over the time which would otherwise be a sexual season, the interference of nursing depends upon the vigour of the mother and her powers of recuperation.

The Pro-œstrum.—Evidence of pro-œstrum is to be seen in all Vertebrata, and is the forerunner of œstrus. It is first noticeable in mammals in the external generative organs, and extends thence to the uterus.

The essential manifestations thereof are first hypertrophy, and secondly congestion of the tissues affected, and this is very usually, indeed probably always, followed by a discharge.

The discharge always consists partly of mucus from the uterus, and partly of desquamated vaginal epithelium and the products of broken-down epithelial tissue.

In some animals always, and in others sometimes, blood is also evacuated, which has its origin from the uterine mucosa, in which case there is always more or less of uterine tissue also contained in the discharge.

There is very considerable variation in the extent of both hypertrophy and congestion of the tissue in various mammals, but it is essential to note that these phenomena are to some extent always present, and are frequently combined with the rupture of the congested vessels in the mucosa, and also, more rarely, with a discharge of blood from, and still more rarely a denudation of, the superficial uterine mucosa.

The evolution of the pro-œstrum in its most advanced form, that is to say the menstruation of the Primates, from the simplest form, as it appears in such animals as the mole, is traced, and menstruation is shown to be identical with " heat."

The Period of Œstrus.—This is possible only after

the active changes due to pro-œstrum have taken place in the
uterus; it is always present, under normal conditions, in the
lower mammals at that time, and is much more frequent then
in the Primates than is generally supposed.

Conclusion.

The conclusions I draw from the evidence detailed above
are then, very briefly, as follows :

A sexual season is common to all female mammals; its
recurrence may be interfered with in consequence of climatic,
individual, or maternal influences, and it may be modified by
the influences attending captivity, domestication, or civilisa-
tion.

The modification brought about by one or other of these
various influences is not necessarily the same in different
species of the same genus, nor in different individuals of the
same species, nor even in the same individual at all times ;
but whatever differences there may be, they are merely
modifications of the same plan.

The sexual season of all mammals is evidenced by a series
of phenomena which constitute, in the absence of the male,
one œstrous cycle (monœstrous mammals) or a series of
œstrous cycles (polyœstrous mammals); animals usually
monœstrous may, under certain circumstances, show a
tendency to polyœstrum ; in the same way animals usually
polyœstrous may show a tendency to monœstrum.   These two
conditions are very closely related, and the main difference
between them is the method by which the reproductive power
is increased.

The various constituent parts of an œstrous cycle are in-
variably demonstrated in all mammals; there is in all of them
a period during which the generative organs are hypertro-
phied and congested (pro-œstrum), followed by a period of
desire for coition (œstrus), which, in the absence of the male,
gradually dies away (metœstrum), and results in a period of
rest (diœstrum or anœstrum).   When this period of rest
merely separates two recurrent diœstrous cycles it is brief,

and I have called it the diœstrum; but where it serves to separate two sexual seasons it persists for a considerable length of time, and I have called it the anœstrum.

The pro-œstrum is always associated with hypertrophy and congestion of both external and internal sexual organs and the uterus, and with a discharge from the generative orifice. These phenomena are common to all mammals; they may, however, be further complicated. These complications may include rupture of the congested vessels of the hypertrophied superficial uterine mucosa, and extravasation of the blood contained therein; they may include a discharge of this blood into the uterine cavity, and from thence to the exterior; and even more or less denudation of the mucosa may take place, leading to the formation of a menstrual clot.

The rupture of the vessels of the mucosa and the subsequent phenomena are not experienced by all mammals; they are supplementary to the essential factors of pro-œstrum, and occur in part rarely in some animals, in part always in some animals, and in a complete sequence only, so far as is known, in Primates.

That the pro-œstrum of Primates is identical with the pro-œstrum of other mammals does not, however, admit of any doubt; there is ample evidence of this in the various intermediate conditions of other mammals, by means of which, and bearing in mind the influence of domestication and civilisation on polyœstrum, the evolution of the menstruation of monkeys and of the human female from the pro-œstrum of the lower mammals can be surely traced. A further evidence of this is the time of the occurrence of œstrus. It is manifested at a certain period after pro-œstrum, and has a certain relation to it—that is, it follows and is not coincident with pro-œstrum in the lower mammals, as is usually supposed.

In some monkeys the same relation of œstrus to pro-œstrum obtains, and in others it is probably so, while in the human female there is evidence of a similar condition, especially, probably, among normally strong individuals who lead a healthy life.

Thus the human female may exhibit a sexual season, a pro-œstrum, and a period of œstrus, precisely like any other mammal, and the homology of these processes in all mammals is, in my opinion, established.

A review of the literature which treats of the relation between " heat" or " rut," as it is usually called, and menstruation, resolves itself practically into an enumeration of those who deny there is any ground for comparison, and those who assert they are identical processes. I do not propose to enter into a detailed criticism of the voluminous literature which bears upon the subject, but will content myself with quoting the essence of the most frequent assertions which are made for and against the homology of these processes, and with briefly replying to them.

Those who uphold the homology do so because—

I. There is congestion of the generative organs during both " heat" and menstruation.

II. There may be a recurrence of " heat" as there is a recurrence of menstruation.

III. The discharge during " heat" may be of a menstrual character.

IV. From a phylogenetic point of view the homology is to be expected.

These statements may be disposed of together ; so far as they go they are true enough, but they are not in themselves, separately nor collectively, conclusive evidence.

Those who deny the homology do so because—

1. The discharge during " heat" in the lower animals is said to be mucus, while in the human female it is mostly blood.

2. The time of " heat" is said to be the only time the lower animals will permit of coition, while sexual union during menstruation is a very rare occurrence.

3. " Heat" or " rut" is said to occur in both males and females in the lower animals and to depend upon the seasons, whereas in the human species it is said to be not so.

4. After " heat" the female of the lower animals is said

to refuse the male, whereas in the human female sexual desire is not confined to the time of menstruation.

5. " Heat" is necessary to the production of the species in the lower animals, while in woman " desire" is said to be not essential to conception.

6. In the lower animals the ovaries are said to contain ripe ova only during the time of " heat," whereas ripe ova are said to be found in the human ovary at all times without reference to menstruation.

7. There is said to be no proof of the identity of the two conditions.

I think these propositions fairly cover the ground over which those who deny the relationship of what they call "heat" to menstruation have hitherto travelled.

It will be seen at a glance that the denials originate, in most instances, in misconception of the facts, and that many of the errors are due to the misuse of terms.

It will be worth while, however, to answer each of them separately, and the following replies are numbered to correspond with the numbers of the above objections.

1. The discharge in many animals during the pro-œstrum contains blood and sometimes uterine tissue ; it is not always solely mucus, and when blood is absent it has been shown that its absence is due to a modification of, and not to any radical difference in, the process.

2. The term " heat " is here wrongly used ; it is made to include both the pro-œstrum and the œstrus in the lower mammals, and is compared in that extended sense with the term menstruation, which is an error. The time the lower animals will permit of coition is not during pro-œstrum, which is synonymous with menstruation, but during œstrus, which immediately follows the pro-œstrum. I have shown above that there is not wanting evidence that the same may be true for the human female.

3. Although the time for sexual intercourse among human beings is not universally confined to particular seasons, I have shown that in some cases this is so, and that in all

peoples there is a marked disposition to indulge in sexual intercourse at particular times of the year, which are undoubtedly comparable to the so-called " breeding seasons " of the lower mammals. Further, in certain domesticated animals and certain wild animals kept in captivity the males do not " rut " only at certain times of the year, but are prepared to propagate at all times (dog) or almost at all times (captive cattle or deer) throughout the year.

4. There is some truth in this objection; but it must not be forgotten that, among the lower mammals, while captivity and domestication reduce the violence of the sexual passion, they increase its frequency; and that in civilised woman, in all probability, it is this variation of the function still further exaggerated which is responsible for the difference (see also 2).

5. Here again the objection is largely due to a mistaken use of the term " heat," which in this case is used to denote œstrus.

Menstruation, that is pro-œstrum, in women is as necessary to the production of the species as pro-œstrum in the lower animals can be; the fact that œstrus is less pronounced in the former is true, but it is not altogether absent, and has already been referred to in the replies to propositions numbered 2 and 4.

6. This objection has reference to the question of ovulation, which has not been treated of in this paper; with regard to it I would merely say, that ovulation in certain of the lower mammals is not necessarily coincident with œstrus, while in some of them œstrus and ovulation are quite separate functions. Ripe ova are not found at all times in each human female, and the fact that they may be found at times which are not coincident with menstruation, is merely further evidence that these functions are independent also in women. Further, the degree of independence which these two functions assume is apparently variable in the human female.

7. The answer to this objection is contained in the foregoing paper.

In spite of the fact that the evidence I have brought forward is fragmentary, and notwithstanding that only the fringe of a vast subject has been touched upon, I venture to hope enough has been said to show that the wide variations in the sexual functions exhibited by various mammals are variations in degree, not variations in kind; and I venture to think that the evidence of the homology, not only of pro-œstrum and menstruation, but of each of the various sexual phenomena dealt with in the various types, is incontrovertible.

One word with regard to the future development of the subject. It is the cause of the sexual season which requires determination.

Much stress has been laid upon the rhythmical nature of all breeding processes; this has been carried furthest by Lataste (1887 and 1891), and by Beard in a very suggestive paper on gestation (1897). So far as the sexual season is concerned, its rhythm is no explanation of its origin. It may, I suppose, be asserted that all forces are exerted rhythmically, that is a condition; whereas what is required here is knowledge of the nature of the force itself, and the causes which govern or limit its rhythm.

These are questions for the comparative physiologist, in whose hands, as it seems to me, lie so many of the great biological problems of the day.

Speaking generally, the rhythm of the sexual season and the power of breeding is seasonal, it is governed by external forces which are exerted in consequence of seasonal change, and by internal forces which are dependent upon individual powers; further there is abundant evidence that nutriment, and the capacity for storing nutriment, and the energy resulting therefrom are essential factors.

I differ from those who, like Beard, consider the ovary the seat of the governing power of the breeding function; ovulation and the œstrus cycle are not necessarily coincident, the stimulus sufficient to induce the one is apparently not sufficient in all cases to induce the other, and it would appear that the requisite initiative is independently produced.

I am tempted to suggest the probability that there is
present in the blood from time to time what may be called
an œstrus toxin, to suggest that its presence is due to the
external and internal forces mentioned above, and to relegate
to it the power which stimulates the activity of the sexual
season, and brings about the actual production of those
generative elements which nutrition has enabled the animal
to elaborate.

It appears to me that research in this direction would be
likely to be rewarded; it would not only be of great theo-
retical interest, but might well lead to increase of knowledge
regarding some of the causes of sterility, and prove of enor-
mous practical value.

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A Description of Ephydatia blembingia, with an Account of the Formation and Structure of the Gemmule.

By

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With Plates 1—4.

Contents.

Part I.—The Morphology, etc., of Ephydatia blembingia.

I. INTRODUCTION.

Ephydatia blembingia is a fresh-water sponge which Mr. Annandale came across in a small pool of water while in search of snails. It was collected and preserved by me on the 23rd of July last year.

The specific name blembingia has been applied to it on account of its locality. Blembing is a small Malay village which was visited by the members of an expedition sent out by Cambridge University to the Siamese Malay States, and which is situated on a small river of the same name. The river Blembing is a tributary of the Pergau, which in its turn empties itself into the Kelantan River.

The pool of water in which the sponge, now described for the first time, was found, was situated in a comparatively dense jungle at a distance of a few yards from the bank of the river. The trees growing around it were so big, and their foliage so thick, as to admit of only a small amount of light ever passing through them. Consequently the pool of water in which Ephydatia blembingia was found was always in a deep shade.

The material which I collected was preserved in the following reagents :

(1) Flemming's solution (weak fluid).

(2) Saturated solution of corrosive sublimate (92 volumes) and glacial acetic acid (8 volumes).

(3) Absolute alcohol.

(4) Rectified 70 per cent. spirits.

II. DESCRIPTION OF EPHYDATIA BLEMBINGIA.

(1) Colour, Habits of Growth, and External Form.— Ephydatia blembingia is almost colourless, or to use a term which was used many years ago by Professor Lankester (11) to describe the colour of Spongilla from the Thames, it is " pale flesh-coloured." Knowing as we do that Spongilla

lacustris and Ephydatia fluviatilis, denizens of our own rivers, are green in colour only when they grow in bright sunlight, this is what we would have expected in the case of a sponge which grew in a pool of water scarcely ever brightened by direct sunlight.

The habits of growth of Ephydatia blembingia are peculiar. In reality it is an encrusting sponge, though some specimens have a massive appearance. But this is due to the habit of growing on such supports as blades of grass and branching weeds of various kinds which inhabit the same pool of water as the sponge. It never seems to produce independent branches, which, when present, give a sponge a kind of bush-like appearance, as Spongilla lacustris does. If, at first, a specimen appears to branch, on closer examination the apparent branching reveals itself as the result of creeping over a branched support. Consequently, in spite of its massive appearance, Ephydatia blembingia is an encrusting sponge. The biggest specimens measure no more than about an inch across (Pl. 1, fig. 1).

The surface texture of the preserved sponge is somewhat woolly, an appearance caused by the spicule fibres which support the otherwise smooth dermal membrane. The fibres often penetrate the membrane, owing undoubtedly to its being rubbed off their extreme points.

To sum up, Ephydatia blembingia may be described as a pale flesh-coloured sponge, with encrusting habits, creeping over branched vegetable supports, and consequently irregular in shape and woolly in texture.

The oscula, not to speak of the dermal ostia, are so small as to be invisible without the aid of the microscope. The openings represented in fig. 1 are those of the inhalant canals seen through the dermal membrane.

(2) Skeleton.—The skeleton consists almost entirely of spicules, which I shall now proceed to describe.

A. Spicules.—In order to facilitate the description of this most important element of the skeleton, I shall arrange the spicules under three heads.

(*a*) The first group of spicules consist of diactinal monaxons or amphioxea, which are usually curved, though straight specimens are occasionally seen (Pl. 1, fig. 3, *a—e*).

(*b*) The second group also consists of curved amphioxea, but for reasons which will be stated further on they are separated from the first group (Pl. 1, fig. 3, *f*).

(*c*) The third group consists of amphidiscs, which may be present in a fully developed or in an immature form (Pl. 1, figs. 3, *g—m*, 4, *a—c*).

(*a*) The amphioxea belonging to the first group taper gradually to a sharp point. They are never provided with a swelling at the middle point of the shaft, and scarcely ever are they malformed or modified in any way. In both respects, therefore, they differ most strikingly from the spicules of Spongilla moorei, a description of which was published in this journal a year and a half ago. They appear to be invariably covered with small spines.

(*b*) The amphioxea belonging to the second group are invariably curved and covered with small spines. In fact, they present the same characters as the spicules of the first group, but differ from them in being only half as long and less than half as thick. They are not found in the general tissues of the sponge or in its membranes, but are grouped together round small bodies[1] which are embedded in

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[1] The bodies above mentioned seem to possess a definite outline, and to lie in cavities of their own, much in the same way as the gemmules (Pl. 4, fig. 17). I have no conception what these bodies are, but several solutions have suggested themselves. Unfortunately I have been unable to find them in thin sections, and consequently cannot speak of their internal structure.

The first suggestion, with regard to their nature, to present itself was that they were a second kind of gemmule. The arrangement of the spicules round them reminds us of that of the spicules round the gemmules of Spongilla lacustris, and is, so far, in favour of the supposition that these bodies are some kind of gemmules. But apart from the fact that Ephydatia blembingia possesses another kind of gemmule, these structures are much more transparent than ordinary gemmules are at any stage in their development or when they are mature. If they were gemmules their basket-like shape could be easily explained as the result of contraction under the action of preserving reagents, owing to the cuticular coat being extremely thin. Apart from the

the deeper tissues, and which present a kind of basket-shaped form.

(c) The last class of spicules to be considered consists of the amphidiscs (Pl. 1, fig. 4, b). The diameter of the hat-shaped disc is about three times that of the shaft. The two discs are exactly similar in size and shape. The surface situated away from the shaft is smooth and convex, while the other surface is concave. Their margins are very finely serrated. The shaft is covered with spines which are conical in shape and placed at right angles to the axis of the amphi-discs.

In addition to the fully mature forms, all the stages of development are represented, from the simple rod slightly

fact that, if the supposition here made were true, it would cut at the very root of the system of division into sub-families, now adopted, of the so-called Spongillidæ, the reasons given above seem to be sufficiently weighty to compel us to lay aside this possible view of the nature of these enigmatical bodies.

The second supposition that suggests itself as a solution of the problem is that these structures are a kind of symbiotic or parasitic sponge. This supposition is not so unreasonable as it would at first appear, for we already know that Spongilla bohmii is parasitic on Spongilla nitens (17). Besides, it must be remembered that all the spicules in connection with these bodies are quite different from those which form the sponge skeleton, being, as has been stated already, only half as long and less than half as thick. It is no argument to say that they are incompletely developed, for they are all of equal size, which would not be the case if they were merely young spicules. However, if these bodies are of the nature of a parasitic sponge, there are, at present, no data by which its position among the Spongillidæ can be determined.

There is still left another possible solution of the problem, namely, that the bodies here discussed are the result of parasitism on the part of some animal other than a parasitic sponge. If this supposition were true, these bodies would have to be considered as a kind of gall, by means of which the sponge endeavoured to protect itself from the action of an unwelcome intruder. But there are two facts which go against this view. In the first place, though I have examined several of these bodies, I have so far failed to find any animal inside them. In the second place, though there are many parasites in the sponge, not one of them has as yet been found to possess such a coat as these bodies would provide.

Though it must be left an open question what the nature of these bodies are, for the reasons given above I am inclined to adopt the view that they are parasitic sponges.

swollen at both ends to the fully-formed amphidiscs. Their development, however, will be considered along with that of the gemmule.

B. The Arrangement of the Spicules to form Fibres, etc. (Pl. 1, fig. 2).—The spicule fibres are poorly developed, and consequently stand in a most marked contrast with those of some other fresh-water sponges. I have never seen more than three spicules situated side by side in a spicule fibre, and scarcely ever saw more than two. As often as not, the spicules seem to be arranged end on in a single file. In the deeper parts of the sponge, fibres are almost non-existent, the spicules lying about freely and presenting no particular arrangement. Nearer the surface, however, the fibres are better developed, and traverse the strands of tissue which separate the various compartments of the sub-dermal cavity from one another. On the outer ends of the fibres is situated the dermal membrane, which is often pierced owing merely to the wear and tear of the life which the sponge lives. Owing to the absence of flesh spicules or microscleres, the skeletal fibres formed of megascleres present an evident tendency to run in the vicinity of the membranes which line the canals and cavities of the sponge.

As has been stated above, spicules of the class b take no part in the formation of the skeleton, but this is not true of those belonging to class c, i. e. the amphidiscs. The latter are found in all stages of development scattered about in the general tissues of the sponge, while the former are limited to the walls of the enigmatic bodies described above. Special stress must be put on the fact that the developing stages of the amphidiscs have been seen in the sponge tissues, and not in the gemmule wall.

c. Spongin.—It is scarcely necessary to mention spongin in connection with Ephydatia blembingia, for it is almost completely absent. In this respect the sponge here described strongly contrasts with some fresh-water sponges. In Spongilla moorei the spicule fibres and the dermal membrane are covered with this substance (7), but in Ephy-

datia blembingia there is no spongin on the surface, and
the spicule fibres are, at most, provided with a very small
amount at the junction of the spicules.

This difference is explained by the dissimilarity in the con-
ditions of life. On the one hand, Ephydatia blembingia
lives in a small pool of water which probably dries up for the
greater part of the year; while Spongilla moorei, on the
other hand, lives at the bottom of Lake Tanganyika. There-
fore, the former may be described as an annual, while the
latter—so to speak—is a perennial spongilla. If this differ-
ence in the conditions of life under which these two sponges
live were to have any effect at all, we would naturally expect
the spongin part of the skeleton to suffer most.

(3) The Canal System.—Owing to the presence of gem-
mules in all stages of development, the canal system could
hardly be in such a condition as to be capable of minute
description, for the formation of gemmules is accompanied by
the breaking down of the sponge tissue. Besides, we know
of no preserving fluid that does not admit of a considerable
amount of disassociation of the tissue cells of the Monaxo-
nida. Though they be preserved with the greatest care, and
with the best reagents known, free cells are found in great
abundance in the interior of the sponge tissues. The presence
of so many amœboid cells is conducive to this state of things.
Consequently our remarks on the canal system must be meagre
at best.

As has been stated above, the dermal ostia are micro-
scopically small but comparatively numerous. They open as
usual into the subdermal cavities, which are large and ex-
tensive (fig. 2), and which are lined by cells which possess
granular nuclei. These in their turn open into the inhalant
canals, which are also well developed, but decrease in size
towards the surface of fixation of the sponge. The flagellated
chambers are small and numerous, lying about in the extremely
loose tissues of the sponge. The exhalant canals, though at
first of fine calibre, assume comparatively huge proportions.
The oscula, however, by which they open to the exterior are

small. The membranes which line the canals are not pro-
vided with special spicules, but are supported by the spicule
fibres, which are situated close to the lining membranes.

4. The Structure of the Gemmule.—The gemmules
are scattered about singly throughout the whole tissue of the
sponge. They are found, on the one hand, near the surface,
and on the other hand, quite close to the vegetable supports
of the sponge. They are never found in groups. Each gem-
mule occupies its own cavity (Pl. 1, fig. 2, *gem.*).

I shall here describe only the structure of the mature gem-
mule, the development of which will be described in Part II.
Nevertheless, it must be remembered that the sponge con-
tained gemmules in all stages of development at the time it
was collected.

The gemmule is oval in shape, being, as a rule, slightly
flattened on the side on which the opening is situated. The
external opening or pore is placed at the bottom of a small
depression surrounded by a rosette-like structure, which is
raised up, and into the composition of which all the layers of
the gemmule coat enter (Pl. 1, fig. 7).

The contents of the gemmule consist of a number of glo-
bular cells which are full of oval-shaped food granules. The
cells are all alike, and the whole mass possesses no membrane
of any kind save the gemmule coat, which I shall now proceed
to describe.

The gemmule coat consists of three layers which differ
from one another, to a considerable degree, both in structure
and extent of development.

The inner layer of the gemmule coat completely surrounds
the cells which are situated in the interior. It presents the
general shape of the gemmule and is prolonged round the
aperture to form a kind of a tube, the passage through which
is interrupted by a chitinous membrane situated about the
middle. The cellular contents of the gemmule extend into
the inner half, and the second layer of the gemmule coat to
the outer half of this tube. In structure this layer is chitinous,
and resists the action of all ordinary reagents, save the mineral

acids. It often happens, that, in sections, it splits in two, a result brought about by the weakening produced through the inner ends of the amphidiscs being embedded in it, and not lying upon it as is usually described in the gemmules of Ephydatia. The line along which the splitting takes place is that in which the discs are situated (Pl. 4, fig. 17, *a*).

The middle layer of the gemmule coat is by far the thickest and approximately extends over the whole length of the shafts of the amphidiscs. It is clear in structure, and presents in section the appearance of ordinary parenchyma with very small granules at the nodes. In the fully developed gemmule there are no lines of division indicative of the different cells out of which it was originally formed (Pl. 4, fig. 17, *a*).

The outer layer of the gemmule coat is thinner than either of the other two, and in it are embedded the outer ends of the amphidiscs. It consists of the same substance as the inner layer but is much more granular. In the mature gemmule it is often rubbed off, and consequently the outer discs of the spicules protrude from the gemmule coat (Pl. 4, fig. 17, *a*).

The amphidiscs lie partly in the three layers. The inner disc lies in the corresponding layer, the shaft in the middle layer, and the outer disc in the thin outer layer. They are so closely packed that the discs overlap one another and consequently are not on the same level. Their shafts never seem to cross one another, but lie approximately parallel.

III. The Affinities of Ephydatia blembingia.

The presence of gemmules in the material at my disposal made the task of determining the systematic position of the fresh-water sponge here described a comparatively easy one. The possession of gemmules excludes it from the sub-family Lubomirskinæ, which is a sub-family created for the purpose of grouping together a number of fresh-water sponges in which the gemmule, if it does exist, has not yet been discovered. Further, the existence of the thick coat which surrounds the gemmule cells and which contains, embedded

in it, a thickly-set layer of amphidiscs separates it, on the one hand, from the sub-family Spongillinæ, and on the other hand places it among the Meyeninæ. Again, its generic position is not difficult to determine. The equality of size of the amphidisc rotules separates it from both Tubella and Parmula, the serrated edge of the rotules from Trochospongilla, the equality in length of all the amphidiscs from Heteromeyenia, and the absence of any kind of filament or appendage, attached to the chitinous tube, from Carterius. Consequently the sponge, which is described in this paper, belongs to the genus Ephydatia. Of the species contained in this genus, the sponge to which the name Ephydatia blembingia has been given seems to approach Ephydatia plumosa (Carter, 2) more closely than it does any other well-marked species. Several species of the genus Ephydatia are provided with amphioxea, which are covered with small spines, and are the constituent elements of the skeletal fibres. In Ephydatia fluviatilis (17) both smooth and spined spicules occur together. It follows, therefore, that the presence or absence of small spines on the skeletal spicules is not distinctive as a specific character. Potts (17) seems to consider this difference so unimportant that he describes an American sponge, to which he has given the name palmeri, as a mere variety of the Indian sponge plumosa; though the skeletal spicules in the former are covered with small spines, while in the latter they are smooth. The skeletal spicules of Ephydatia blembingia agree with those of palmeri, and not with those of plumosa.

The amphidiscs seem to be closely similar in plumosa, palmeri, and blembingia, though the rotules appear to be more deeply notched in the two sponges mentioned first than they are in blembingia. If these were all the differences that could be enumerated the sponge now discussed would have to be considered a slight variety of the species plumosa, if, indeed, not actually identical with the variety palmeri. However, there still remains to be mentioned another most important difference, namely, the absence from blembingia

of the flesh spicules so characteristic of both plumosa and palmeri. Though this is a negative character, combined with the other differences it seems to be a sufficient reason for the formation of a new species, to which I have given the name blembingia.

IV. Summary.

Ephydatia blembingia is an encrusting sponge which grows on vegetable supports. It is pale flesh in colour, and loose in texture. The skeletal spicules are covered with small spines. Flesh spicules are absent unless the small amphioxea (*b*) be considered to belong to such a category. The spicule fibres are poorly developed, and in the deeper parts of the sponge the spicules, as a rule, lie about irregularly arranged in the tissues. Spongin is present only in very small quantities. The gemmules are numerous, but not aggregated in groups. They are situated—each one occupying a cavity of its own—near the surface as well as deeper down in the tissues of the sponge. They are oval in shape, and possess an opening resembling that of a bottle, which is obstructed by a chitinous septum. They are provided with a thick and well-developed coat, in which amphidiscs of equal lengths are arranged in a single layer. The shaft of the amphidiscs is furnished with conical spines, large in size and situated at right angles to the longitudinal axis. The outer surface of the discs is convex, and the margin is slightly serrated. Amphidiscs, in all stages of development, are scattered about in the sponge tissue where they are formed.

Part II.—The Formation of the Gemmule of Ephydatia blembingia.

I. Introduction.

When I took the description of Ephydatia blembingia in hand I had no intention of describing the development of

the gemmule; but when I saw that the material at my disposal contained gemmules in all stages of development I thought it would be a mistake not to describe it. Further, I was encouraged to do so by Professor Weldon, to whom I am greatly indebted both for the free use of his laboratory and all its resources, and for much invaluable assistance, especially in connection with the literature on the subject. I shall first give a summary of what is already known of the gemmule. I shall then proceed to describe my own observations, the method followed being that of tracing the origin and subsequent changes of the various cells which take part in the process, this method being considered simpler and more intelligible than that of giving a complete description of the different stages of development. The reader can easily make out for himself, by examining the figures 8, 9, ... 17, the true relation of the changes in the different parts of the developing gemmule much better than by reading the best possible description. Finally, I shall review previous accounts and compare my own conclusions with them.

II. Historical Review.

Carter (2), who was the first to attempt an explanation of the origin of the gemmule, which he terms the seed-like body, writes as follows :—" At the earliest period of development in which I have recognised the seed-like body it has been composed of a number of cells, united together in a globular or ovoid mass (according to the species) by an intercellular substance. In this stage, apparently without any capsule, and about half the size of the full-developed seed-like body, it seems to lie in a cavity formed by a condensation of the common structure of the sponge immediately surrounding it. It passes from the state just mentioned into a more circumscribed form, then becomes surrounded by a soft, white, compressible capsule ; and finally thickens, turns yellow, and develops upon its exterior a firm crust of siliceous spicules." He says with regard to the origin of the gemmule, "I do not

wish it to be inferred that I am of opinion that the seed-like
body is but an aggregate of separate sponge-cells;" and
further, after describing certain cells of the sponge, he says:
" It may, perhaps, be one of these cell-bearing cells which
becomes the seed-like body."

Lieberkühn (**12**), in the year 1856, published an account
of the origin and structure of the gemmule.   He found in
the deeper parts of the sponge shiny white gemmules, which
on the whole appeared like ordinary brown gemmules, and
which possessed exceedingly plain amphidiscs.   He also found
other gemmules, distinguished by their very delicate trans-
parent shells, also possessing very obvious amphidiscs.   These,
he said, had a superficial layer of a substance feebly refrac-
tile, and a central mass brilliantly refractile.   The feebly refrac-
tile cells separated easily, while the others only did so with
difficulty.   In these bodies he was not able to find the delicate
transparent encrusting layer, which he had seen round the
white gemmule ; but found a layer of cell-like spherules which
resembled the ordinary sponge-cells in the arrangement of
their granules and of their nucleolus ; while others contained
the amphidiscs.   Some of the enclosed amphidiscs had exactly
the shape of those found surrounding the ordinary gemmule.
Others, he said, did not possess the two discs, but in the
interior of each cell-like structure there was a delicate rod
with a slight knob-like swelling at each end.   In others a
series of very fine spicules radiate from the terminal swelling.
He derived the amphidiscs by imagining these spicules to
become broader, and the axial rod to become thicker.   The
contours of the cells containing the spicules were described
as being as sharp as those of ordinary sponge-cells.   He could
find no nuclei in these cells.   He finally concluded that these
bodies were incompletely developed gemmules.   He also
found certain bodies which he described as white aggregations
of sponge-cells, possessed of the same size and shape as
ordinary gemmules.   In the same year he published a second
paper, in which he summed up as follows (**13**) :—" That the
gemmules are derived from a heap of ordinary sponge-cells

we can very plainly see in that branched sponge which has
gemmules with smooth shells. In a longitudinal section of a
suitable piece we find—(1) Gemmules which are completely
developed, and possess a smooth shell containing a large
number of the rounded masses accurately described by Meyen.
Each of these masses is spherical, and contains in its interior
an albuminous fluid and many strongly refractive spherules.
It is about as large as a sponge-cell, and quickly disintegrates
in water. (2) Gemmules with an obvious shell, which con-
tains Meyen's spherical masses and also contains bodies which
have Meyen's masses, but are distinguished from these by
sending pseudopodia like the ordinary sponge-cells. (3)
Gemmules in which the shell and the pore are obvious, con-
taining only cellular bodies which send out pseudopodia.
Some of these contain a nucleus and a nucleolus like sponge-
cells, and are distinguished from these only by the fact that
they contain in their interior the refracting spherules already
alluded to. (4) Spherical heaps corresponding in size to the
gemmules which consist of the above-mentioned bodies,
sending out pseudopodia, and of undoubted sponge-cells. The
sponge-cells have an obvious nucleus and nucleolus, and they
contain besides a mass of very fine granules, which may be
scattered through the whole cell-body or may be collected
in small spherical masses. These spherical masses are of the
same size as the refracting spherules already described, and
one or two such spherules are often found in the sponge-cells.
Round some of these spherical heaps of cells a very fine
structureless membrane can be recognised. The spherical
masses of Meyen which are commonly found in gemmules
are nothing else than altered sponge-cells ; by compressing the
contents of the gemmule under the cover-slip we can find a
nucleus and a neucleolus in every such mass ; but nucleus and
nucleolus are so hidden by the strongly refractile contents of
the Meyen's masses that they can only be demonstrated by a
process of pressure. These nuclei and nucleoli do not espe-
cially differ from those of ordinary sponge-cells."

Lieberkühn again, in a third paper (**14**), speaks as follows

of the gemmule :—" The gemmules are not eggs, but a sort of cyst or capsule, out of which the same individual which built them ultimately creeps through the pore."

In a later publication (**3**) Carter describes the seed-like bodies as being globular in shape, and consisting of a coriaceous membrane enclosing a number of delicate, transparent, spherical cells, more or less filled with ovules and granular matter, while an incrustation of gelatinous matter charged with small spicules peculiar to the species surrounds the exterior of the coriaceous membrane. " It has also been shown," he adds, " that at an early period of development the spherical masses, which we shall henceforth call ovi-bearing cells, are polymorphic—identical, but for the ovules, with the ordinary sponge-cells—and surrounded by a layer of peculiar cells equally polymorphic, which I have conjectured to be the chief agents engaged in constructing the capsule."

Again, in a later publication (**4**), he speaks of the "ova"— preferring the term "ovum" to "seed-like body"—of Spongilla as follows :—" At an early period of the ovum the spherical cells, though already filled with the refractive granules, are few in number and sub-polymorphic ; hence it may be reasonably inferred that their multiplication as the ovum increases in size is produced by fission ; the younger the ovum the more polymorphic and resistent are these cells, while the older it becomes the more they are attenuated, and the more rapidly they burst by endosmose after liberation."

In the year 1874 he further writes of the gemmules as follows (**5**) :—" It may be a question whether the entire body may not be the ovarium of a Spongozoon in the first place ; while, as in hundreds of instances of the same kind in the animal kingdom, all the other parts have perished, their function having ended when sufficient nutriment had been gathered and assimilated to support the reproductive elements until they could do this for themselves." Further on he adds, " It is an assemblage of ova which are at once developed together into a young Spongilla."

In his final communication (**6**) on the gemmule, he views it

" as a simple ovum with modified form to meet the require-
ments of the case."

It seems Carter was always uncertain as to the origin of
the gemmule, and at one time or another he appears to have
had four views. First, that the gemmule was a mere aggre-
gation of sponge-cells; secondly, that it was an aggregation
of cells produced from one cell, the "ovi-bearing" cell;
thirdly, that it was a single ovum, which was his final view;
and fourthly, that it was a single "ovarium" of a dead
" spongozoon."

In the year 1884 Marshall published an account of the de-
velopment of the gemmule of Spongilla·lacustris (**15**).
He says that the first sign of the gemmule consists of a
number of amœboid cells, which are found in the neighbour-
hood of the inhalant canals and the ciliated chambers, and
which he terms the "trophophores." They fill themselves
with reserve material, and wander together in groups. They
become round and give up water, so that they look like
masses of reserved food material. Very early round the
pseudomorula formed in this way there appears a delicate
structureless membrane, a cuticle, the matrix of which should
be probably looked for on the surface of the pseudomorula
itself. The "mesoderm" outside this cuticle builds at first
an endothelium which deposits on the cuticle further layers
of horny substance and delicate siliceous structures, in this
case spiny tangential needles.

In the year 1886 appeared Goette's account of the develop-
ment of the gemmule of Spongilla fluviatilis (**10**). He
says that the first rudiment of the gemmule is formed by an
aggregation of ordinary parenchyma cells in a nearly spheri-
cal area of $36-44\,\mu$ in diameter; really, the flagellated
chambers and canals of this region become enclosed in the
aggregation, which is produced through hypertrophy of the
cells. In this aggregation of cells the formation of two
layers quickly takes place; a central mass of cells, con-
taining a great number of yolk-granules, and an outer sheet
of cells, which become club-shaped and form a kind of

columnar epithelium round the central mass. This sheet secretes a cuticle round the central mass, and its cells form the amphidiscs. Subsequently the club-shaped cells migrate outwards, and secrete a second cuticle outside the amphidiscs.

In the same year as Goette, and independently of him, Wierzejski described the development of the gemmule (**19**). He describes the first rudiment of the gemmule as a group of naked amœboid cells. He says that the cells of the mother-sponge can migrate to the body of the gemmule and thus increase its volume. The heap of cells brought together through migration from the sponge tissue become differentiated into a central mass and a peripheral layer. Shining spherules and granules are deposited in the cells of the central mass, those of the peripheral layer becoming columnar. The amphidiscs are not developed in the peripheral cells, but in the surrounding tissues, and only subsequently migrate to the columnar layer.

In the year 1892 Zykoff published an account of the development of the gemmule (**21**). This account adds little, if anything, to what was known before of the formation of the gemmule. He found, among the ordinary amœboid cells of the parenchyma, cells which contained a number of refractive granules of a very definite form, which he describes as boat-shaped. He considers the appearance of refractive yolk-substance in a few amœboid cells of the mesenchyme as the first step in the development of the gemmule. These amœboid cells have the protoplasmic structure of Fiedler's amœboid "Fresszellen," but the nuclear structure of his "Nahrzellen." He disagrees with Goette and supports Wierzejski on the question of the origin of the first rudiment of the gemmule. He denies Goette's statement that the flagellated chambers and the epithelial lining of the canals participate in the formation of the gemmule. The rudiment of the gemmule soon becomes differentiated to a central mass of yolk-cells, among which amœboid cells of the mesenchyme occur, and a peripheral stage which consists of one or two concentric layers

of mesenchyme cells of the sponge. The peripheral cells be-
come club-shaped and not columnar. This change takes place
gradually, not all at once. The club-shaped cells secrete the
inner cuticle, and the amphidiscs migrate from the sponge
and take up their position among the club-shaped cells, which
subsequently migrate outwards, secrete the outer cuticle, and,
finally losing their club-shaped form, gradually become re-
sorbed.

In the year 1893 Weltner published a short paper (**18**), in
which he brings together the different views expressed as to
several important points in connection with the structure and
development of the gemmule, and from his own observations
draws his own conclusions. Having discussed the use of the
protective coat; the presence of a thin membrane, which he
does not believe to exist, round the reproductive portion of
the gemmule; the number of nuclei in each cell, of which he
has seen more than one in several cases, he finally deals with
the question of the origin of the cells of the gemmule, in the
first rudiment of which he finds three kinds of cells, namely
cells which have yolk-bodies alone, cells which display fine
granules of equal size and a distinct nucleolus, and cells
which have large granules of unequal size. The third class
of cells are different from the cells with granules of unequal
size found in the parenchyme.

He comes to the conclusion that the development of the
gemmule is not yet sufficiently known, and that a fresh
inquiry should be instituted as to two main points: first,
the origin and nature of the cells which form the first rudi-
ment of the gemmule; secondly, to ascertain the fate of
these cells.

He suggests that their origin and nature should be exa-
mined with a view to the following possibilities :

Is the first rudiment of the gemmule formed from a single
cell which has the value of an egg ? Then the gemmule
should be a group of segmenting cells.

Or, does the inner mass of the gemmule arise from one class
of cells derived from the previous mesoderm ?

Or does it arise from more than one class of mesoderm cells?

Or, finally, is it built from different germ layers (two or three)? The gemmule should then be considered a bud.

In Section III of the second part of this paper I shall give an account of the development of the gemmule in Ephy-datia blembingia, reserving criticism of whatever kind to Section IV. In Section III I shall include nothing but a simple description, followed by a few conclusions. This course will be pursued in order to make the account more available and more intelligible to the reader than it would be if it were mixed up with critical remarks and conclusions scattered about throughout the paper.

III. Descriptive Account of the Development of the Gemmule of Ephydatia blembingia.

(1) Origin and Further Development of the Repro-ductive Part of the Gemmule.—The first sign of prepara-tion for the formation of the gemmule consists in the presence of single cells or small groups of cells scattered about chiefly in the dermal membrane; the strands of tissues which support the dermal membrane; and in the tissues situated immediately below the subdermal cavity.

The protoplasm of the cells in question is uniformly clear, and the nucleus is granular and not vesicular (Pl. 2, fig. 8). I have been unable to detect a karyokinetic figure in any of these cells. Consequently I am of opinion that the constituent cells of these groups seldom divide during the early stages of formation of the gemmule, which is contrary to what must have been the case if the cells of the repro-ductive part of the gemmule were derived from one mother-cell.

The cells in virtue of their power of wandering travel through the dermal membrane, and strands of tissue which support the membrane, and become aggregated in groups situated either deep in the tissues of the sponge or even in the strands of tissue above mentioned (Pl. 2, fig. 8).

The protoplasm soon loses its uniformly clear appearance and becomes unevenly granular (Pl. 2, fig. 9), a feature which rapidly becomes more accentuated (Pl. 2, fig. 10). The contained granules or irregular blotches at this stage lie in round, clear spaces in the protoplasm, but they soon increase in size to such an extent as to fill the spaces above mentioned. At the same time they acquire an oval or spherical form and exhibit a certain amount of internal structure, in the form of unevenly distributed granules of very small size (Pl. 2, fig. 11a). The subsequent change in the interior of the spherical granules or yolk bodies, as they may be termed henceforth, consists in the differentiation of a peripheral layer or coat which sometimes, though not always, contains fine granules, from a centre which invariably seems to possess a finely granular structure (Pl. 3, fig. 13d). The yolk bodies have at this stage attained their ultimate structure, and fill the cell in which they have been formed.

While these changes are going on a curious change takes place in the character of the nucleus. At first granular, it now becomes vesicular, or perhaps more correctly it presents an appearance intermediate between the typical vesicular nucleus with a solid nucleolus and a granular nucleus (Pl. 3, fig. 13d, nu.). The cells seem never to possess more than one nucleus.

The yolk cells, as they may be termed henceforth, have increased slightly in size during the changes above described. However, they retain their individuality, though owing to the pressure which they exert on one another they are often polygonal in shape. In the fully developed gemmule they are so pressed against one another that their individual outline can be seen only with difficulty, which is in no way a remarkable thing seeing that at no stage do they possess a definite cell wall though having a well-defined cell limit.

The yolk cells collectively, or the reproductive part of the gemmule, as they may be termed, at no stage possess a membrane, though in the fully mature gemmule they are so pressed against the inner chitinous layer of the protective

coat as to present a perfectly smooth and membrane-like appearance.

(2) The Origin and Subsequent Changes of the Cells which produce the Ground Substance of the Protective Coat of the Gemmule.—These cells, after having wandered from the general sponge tissues, appear in the neighbourhood of the gemmule as a loosely arranged layer situated outside the future yolk cells. Fig. 11a (Pl. 2) shows how they travel towards the developing gemmule and how they become concentrated to form a layer.

Their general protoplasm is clear, but they contain a number of granules or yolk bodies which resemble those of the yolk cells. In addition, they often contain a much bigger spherical body which seems to be of the same nature as what I have described in my account of the structure of the larva of Spongilla lacustris as nutritive vacuoles. The cells which develop to yolk cells seem never to contain either of the above bodies at their first appearance. At first they are spherical in shape, but soon become columnar, though never club-shaped. However, their outer end may be round and not flat during certain stages (Pl. 3, fig. 13, and Pl. 4, fig. 15a). They assume the columnar form, at first, only on one side of the reproductive mass of cells, the columnar layer so formed gradually increasing in extent until it completely surrounds the yolk cells. The point at which the columnar layer is finally completed marks the position of the future pore of the gemmule.

Subsequent to the assumption of the columnar form, these cells begin to secrete the inner chitinous layer, which in its formation follows the same course as the columnar layer did, which is a proof that the layer in question is secreted by the columnar cells and not by yolk cells (Pl. 3, fig. 13; Pl. 4, figs. 14 and 15).

Soon after the amphidiscs have taken up their position among the columnar cells—a phenomenon which takes place soon after the formation of the columnar layer—the latter grow out and before long appear outside the outer ends of

the amphidiscs (Pl. 4, fig. 16). While this is going on their inner ends situated between the amphidiscs become transformed to the parenchyma-like substance situated in the mature gemmule between the inner and outer chitinous coats. During the elongation of the columnar cells outwardly the nucleus is carried along. After their inner moiety has been modified and the nucleus has passed to the outer portion they secrete the outer chitinous layer and ultimately break off, and so becoming liberated they pass back again to the sponge tissue (Pl. 4, fig. 16a). The nucleus at the close of these changes, as at the beginning, is vesicular.

The outer chitinous coat is much thinner and less homogeneous than the inner. In the fully mature gemmule the greater part of it is lost, so that the outer ends of the amphidiscs are uncovered.

(3) The Origin, Migration, and Final Modification of the Scleroblasts, inside which the Amphidiscs are developed, and their Migration from the Sponge Tissue into the Columnar Layer.—At the outset special emphasis must be laid on the point that incompletely developed amphidiscs were never seen in the protective coat of the gemmule, whether during the early or later stages. The amphidiscs situated in the gemmule coat are always fully developed, while in the sponge tissues incompletely developed stages as well as fully developed ones are plentiful.

The first stage observed in the formation of the amphidiscs consists of a rod-like structure swollen at both ends (Pl. 1, fig. 3, m, and fig. 6, a), in which respect they differ essentially from the young stages of the amphioxea, which are always pointed (Pl. 1, fig. 5). Both kinds make their first appearance in cells with vesicular nuclei, which soon become transformed and become granular, especially in the mother-cells of the amphidiscs. The next change consists in the development of a more or less conical form by the ends of the above-mentioned rods, the cone-shaped end at the same time becoming surrounded by a rim (Pl. 1, fig. 6, b). The cone-shaped end, together with its slightly developed rim, ulti-

mately grows to the hat-shaped disc. Throughout the process of formation of the amphidisc both ends are of the same shape. If one end is incompletely developed, the other is equally so. The spicules retain their position inside the scleroblast until they have reached their definitive form, and there seems to be no reason for supposing that, were the scleroblast in any way injured, the spicule could ever attain full development. The amphidiscs thus described assume their ultimate form while yet in the general tissues of the sponge. It is important to remember that they are developed in cells which are essentially amœboid. When gemmules are being developed, the scleroblasts in virtue of their inherent power of locomotion move towards them. They travel along the strands of tissue which have been described above as passing from the general sponge tissue to the somewhat loose membrane which surrounds the gemmule. Ultimately they make their way among the columnar cells which surround the gemmule (Pl. 4, figs. 14 and 15b). Fig. 15b (Pl. 4) is particularly interesting in that it shows the last spicule that has entered the columnar layer as well as one situated in a strand of tissue close by. The latter is on its way to take up its position alongside the former spicule among the columnar cells. When the amphidiscs, still situated inside the scleroblasts, have reached their final position, at first they are longer than the columnar cells, which lie completely inside their outer ends. At this stage the scleroblasts, though already considerably modified, can be distinctly seen. In the fully grown gemmule, however, they are indistinguishable from the parenchyma-like substance produced from the modified inner ends of the columnar cells.

The scleroblasts with their contained amphidiscs first push their way in among the columnar cells at that point where the columnar layer and the inner chitinous coat made their first appearance. They become more numerous and gradually increase in number until finally they envelop the whole gemmule (Pl. 4, figs. 15 and 16). There are, therefore, three distinct structures at least which first appear on the same

side of the central cells, i. e. on the side opposite the point which later on will be occupied by the pore, and all three increase in extent in a similar way. They ultimately form complete layers, though one of them, viz. the columnar layer, is no longer found in the mature gemmule.

The migration of scleroblasts, or cells that would become scleroblasts, is not a new idea to zoological literature. Mr. Bourne described such migration of the calicoblasts in Heliopora cœrulea (1), and Professor Minchin has given a full account of the migration of the epithelial cells in the Ascons to the interior, and the subsequent formation of spicules inside them (16). It is true that in both these cases the migration to the interior is previous to the formation of spicules, while in Ephydatia blembingia the amphidiscs are fully formed before the change of position takes place. This difference does not in any way tend to minimise the importance of the facts described above. The amphidiscs are so small as compared with ordinary spicules, and their ends are rounded, consequently there is no inherent improbability in the view that they are carried from one place to another by the scleroblasts.

(4) The Origin, Structure, and History of the Trophocytes.—The trophocytes are large round cells with vesicular nuclei, the chromatin of which is for the most part aggregated in small granules either round the spherical central corpuscle or against the nuclear membrane, the intervening space being, as a rule, occupied by only a few small granules. In the immediate neighbourhood of the nucleus there are innumerable small and irregularly shaped granules which give the cell a dirty-looking appearance, the peripheral portion being exceptionally clear and devoid of granules of any kind. A negative feature of these cells is seen in the absence of both yolk bodies and nutritive vacuoles.

The trophocytes originate from the sponge as a separate class of cells, like the three other classes which have been already considered. They migrate from the sponge tissue at the same time as, and along with, the cells which become columnar. While the columnar cells always remain outside

the yolk-cells, the trophocytes pass in among them. They are incapable of passing through the columnar layer after it has been completely formed, but seem to be able to push their way through when the cells in question are arranging themselves and becoming elongated. Not all of them pass among the yolk-cells, some, as it appears, only entering among the developing columnar cells and turning back. The majority of them, however, seem to pass among the yolk-cells. As a rule, they pass through the developing columnar layer singly, but occasionally groups of several cells are witnessed making their way in. After the trophocytes have entered among the yolk-cells they distribute nutritive material to them, pro- bably in solution. They take no part in the formation of the reproductive portion of the gemmule further than to supply it with nutritive material which the yolk-cells store up in the yolk-bodies. When the inner chitinous layer is about half formed (Pl. 3, fig. 13[1]), the few remaining trophophores are seen travelling towards that part of the gemmule where the pore will appear. They pass out and become scattered about round the gemmule (Pl. 3, fig. 13c). It is not difficult to understand why the trophocytes travel all in the same direc- tion, i. e. away from the portion that is already formed of the inner chitinous layer, for it is undoubtedly the direction of least resistance.

5. Summary of Conclusions.—(1) Four classes of cells, each of which is derived independently from the sponge, take part in the formation of the gemmule; first, the mother- cells of the yolk-cells which, alone, constitute the reproduc- tive portion of the gemmule; secondly, the mother-cells of the columnar cells which pass back to the sponge; thirdly, the mother-cells of the amphidiscs, "scleroblasts," which

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[1] The sections represented in figs. 13—13d (Pl. 3) were cut from material preserved in Flemming's weak solution, while those represented in all the other figures were from material preserved either in absolute alcohol or in a mixture of 92 parts of saturated solution of corrosive sublimate and 8 parts of glacial acetic. This explains the absence of the dirty-looking granules from all the trophocytes except those represented in figs. 13—13d (Pl. 3).

become modified and form a part of the intermediate layer of
the protective coat of the gemmule ; and fourthly, the tropho-
cytes, whose function is to supply both the columnar and the
yolk cells with food material, and which, like the columnar
cells, pass back to the sponge.

(2) The yolk-cells and the columnar cells draw their food
material in solution from the trophocytes; the yolk-cells
storing it up as a reserve in the yolk bodies; the columnar
cells using it in such a way as to enable them to secrete the
inner chitinous layer, to grow and pass out between the
outer ends of the amphidiscs, their inner ends being modified
to form the greater part of the ground substance of the pro-
tective coat of the gemmule, and finally to secrete the outer
chitinous layer ; processes which mean that there is an enor-
mous amount of metabolism going on.

(3) The amphidiscs are developed in cells, the scleroblasts,
which carry them through strands of the sponge tissue to
their ultimate position in the protective coat of the gemmule.

IV. Critical Review of Previous Accounts.

On perusal of the historical section of this paper it will be
seen that the views which have been expressed as to the first
appearance of the gemmule are numerous and conflicting.
The only thing certain is that a group or aggregation of cells
is formed.   How it is formed and whence it is derived no one
seems to know, though every one has a theory to put forward.
Again, it is equally uncertain whether the gemmule is formed
from the group which first appears, or whether this group in
order to build up the gemmule structure acquires recruits
from among the sponge cells and tissues.

Probably the first question that should be discussed is
whether the group of cells above mentioned is the product of
cell migration to one spot, or of cell division either of a single
cell or of a group of cells.

In his first attempt to explain the origin and structure of
the gemmule in the year 1849 (**2**), Carter expressed himself

in favour of the view that the gemmule is derived from what he calls an "ovi-bearing cell." In the year 1886 Goette supports the view that this group of cells is the product of cell proliferation (hypertrophy) (**10**).

In reply to both of these views it will suffice to point out that at no stage during the early development of the gemmule are there any signs of cell division. Though during the very earliest stages the cells are absolutely clear (Pl. 2, fig. 8) I am totally unable to find the least sign of nuclear division, not to speak of fragmentation. In all cases the nuclei seem to be well formed, and in no way modified. Carter had not the facts required to support his view, while Goette seems to have merely figured a piece of ordinary sponge, indifferently preserved, as the first rudiment of the gemmule. For fig. 31 (**10**) can hardly be explained in any other way. It must be admitted as certain that he saw flagellated chambers and canals in the specimen represented in the above-mentioned figure, but it seems almost equally certain that what he saw was not the rudiment of a gemmule, for the gemmule at its first appearance offers no points of comparison with Goette's representation. From the consideration of the absence of cell division, the view that the gemmule rudiment is formed by that means may be set aside— to say the least—as a most highly improbable one.

The second view of the origin of the gemmule rudiment to be considered is the one according to which it contains collar cells and flat epithelium cells, or, as Weltner expresses it, that it consists of cells from two or three germ layers. This view has its most influential advocate in Goette. It was held by Carter also at one time, and probably by Lieberkühn, who says of the spherical heaps of cells he found in the sponge tissue, that, besides containing Meyen's masses, they also contain undoubted sponge cells.

If the explanation given above of Goette's fig. 31 (**10**) is correct—and it seems that it must be—it easily explains how he arrived at the conclusion that all the sponge layers participate in the formation of the gemmule. Besides, it is quite

possible that those who hold this view of the origin of the
gemmule are mentally dominated by the principles of the
" Germ Layer Theory." If so, this would be a splendid
example of an otherwise good theory leading to false conclu-
sions. Further, it is more than probable that Carter, Lieber-
kühn, and Goette never saw the first signs of the formation
of the gemmule. This is undoubtedly the most charitable
view to take of the conclusions they arrived at.

Now that the above-mentioned views have been disposed
of, there remain for consideration two more views, one of
which can be set aside after only a few remarks. The view
in question is the one according to which the gemmule is
derived from a group of cells, all of which are alike. This
view has not found favour with those who have investigated
the structure and formation of the gemmule. Carter at one
time held it (**5**), thinking that the gemmule was an ovarium
of a " Spongozoon," a name which he gave to his imaginary
sponge-animal. However, in a later publication he gave his
support to another view. In fact, a single glance at a good
section of the gemmule during some of the early stages is
enough to cause one to recoil from the idea that only one
class of cells take part in its formation. Consequently there
remains only one view, namely, that the gemmule originates
from a number of cells belonging to various classes. This
view, in one form or another, is supported by Marshall (**15**),
Wierzejski (**19**), Zykoff (**21**), and Weltner (**18**).

Marshall's account does not concern us as much as those of
the other authors above mentioned do, for the reason that he
worked on the gemmule of a species belonging to a different
genus. There is, however, one point which must be men-
tioned. The point in question is that he derives the gem-
mules from two classes of cells at least; namely, the cells
which he terms " trophophores," and which give rise to the
contents of the gemmule, that is the reproductive part, as
well as to the delicate structureless membrane surrounding
it ; and the " mesoderm " cells, which give rise to the outer
shell as well as to the spicules. The importance of this dis-

covery lies in the fact that the reproductive part of the gemmule and its protective coat are respectively formed from classes of cells which are absolutely different, a conclusion which is endorsed in the present paper, though the existence of Marshall's " delicate membrane " round the central mass is here denied.

Wierzejski, evidently, has observed some phenomena which he did not understand. According to this author a first heap of naked amoeboid cells becomes differentiated to a central mass of yolk containing cells, and a peripheral layer of columnar cells. But he also states that the cells of the mother sponge can even migrate to the body of the gemmule, and thus increase its size. In the light of the facts which have been described in the foregoing section of this paper, it seems certain that Wierzejski discovered the migration of cells, on the one hand, to form the columnar layer, and on the other hand to feed the mother-cells of the reproductive cells of the gemmule. Wierzejski in describing the first group of cells uses the term " pseudomorula," and, probably knowing that a true morula always becomes differentiated to two classes of cells, he comes to the conclusion, as it appears, that his " pseudomorula " must do the same. Consequently he commits the mistake of describing the columnar layer of cells as originating by differentiation from his pseudomorula instead of by further migration from the sponge tissue. Not only this, he was also unfortunate in not being able to discover the true nature of the cells which migrated to the interior of the gemmule, as he says, to increase its size. His failure was probably due to the method of preservation he used.

Before proceeding any further, it is necessary to refer to Fiedler's account of the cells which he found during his investigations of Ephydatia fluviatilis (9). Fiedler describes and figures two kinds of cells (9, pl. xi, figs. 3 and 4, and pl. xii, figs. 36 and 37). One kind, which he terms " amoeboid Fresszellen," has granules of equal size in its protoplasm, and a nucleus the chromatin of which is arranged in a network. The other kind, which he terms " amoeboid

Nahrzellen," has granules of unequal size in its protoplasm, and a nucleus with a distinct nucleolus.

Zykoff, who writes in the light of Fiedler's discoveries, considers the appearance of refractive yolk substance in a few amœboid cells of the mesenchyme as the first development of the gemmule. He finds these cells belong to neither of Fiedler's classes of cells, for they have the protoplasm of the "amœboid Fresszellen" and the nucleus of the "amœboid Nahrzellen." These cells, together with others like them, but without yolk substance, are described as creeping together to form a spherical heap of cells, which differentiates to a central mass which consists of yolk-cells, amongst which here and there are scattered amœboid cells of the mesenchyme, and to a peripheral sheet of mesenchyme cells without yolk, which pass to the general mesenchyme of the sponge. Zykoff has described Wierzejski's figures as being diagrammatic and far from the truth. His figures, however, might with a certain amount of propriety be described in the same terms, and Weltner's criticism that they are not natural is quite true. Zykoff, however, is in error when he says the cells of the peripheral sheet above mentioned do not contain yolk. It is true that there are cells among them without spherical bodies in them, the trophocytes of the present paper ; but it is equally true that the greater number of them contain bodies which are in all respects similar to the "re-fractive yolk substance" which Zykoff professes to have seen "in a few amœboid cells of the mesenchyme," which he describes as the appearance of the first development of the gemmule. Zykoff has here failed to distinguish between two classes of cells, and consequently the description he has given of them is not true of either. The cells which he found to contain yolk-bodies in the sponge tissue, and which, he assumes, become the yolk-cells, develop, as it appears, to the columnar cells, and do not fall under the category of "amœboid Fresszellen," or that of "amœboid Nahrzellen." They form a separate class, while the other cells found among them as well as among the yolk-cells must be placed in a class by

themselves. In the present account they have been termed
"trophocytes," and seem to be identical with Fiedler's
"Nahrzellen." Zykoff found the cells in question among the
yolk-cells, but does not properly account for their absence
from that position in later stages. It seems certain that
Zykoff never saw the first stages in the development of the
gemmule. His first figure has not the remotest resemblance
to the first rudiment of the gemmule. If he never saw the
first stages, this explains how he missed the cells with nuclei
the chromatin of which is arranged in a network at first, but
later on presents the appearance of a modified vesicular
nucleus. However, there seems to be little doubt but that
these cells form a different class from the above-mentioned
classes, and correspond when they are coming together in all
respects to Fiedler's "Fresszellen." Consequently, at the
time the peripheral layer of cells appears the whole group
consists of three classes of cells : first, the mother-cells of the
yolk-cells; secondly, the mother-cells of the columnar cells;
and thirdly, the "trophocytes." The first class consists of
Fiedler's "amœboid Fresszellen," the third class of his
"amœboid Nahrzellen," while the second class consists of
those cells which, according to Weltner, belong to neither of
Fiedler's classes, and, according to Zykoff, occupy a position
between the two.

Now that the somewhat difficult questions of the origin and
fate of the cells above discussed seems to have been solved,
there remain but few points to be considered in connection
with the formation of the protective coat of the gemmule.

At no stage in the formation of the gemmule was a delicate
coat or membrane, situated internally to the inner chitinous
layer, found to exist. It often happens, however, that the
outer limit of the reproductive portion of the gemmule is
sharp, smooth, and well defined. But there is no membrane,
the sharpness of contour being merely the result of the pres-
sure exerted by the mass of cells on the inner chitinous layer.

The cells of the outer layer are columnar in form, and not
club-shaped. This, however, is a small point hardly worthy

of all the importance attached to it by Zykoff. The columnar
cells during their transference from the inner to the outer
side of the external ends of the amphidiscs grow out rather
than migrate out. The result is that the spaces between the
amphidiscs are partly occupied by the inner moiety of the
cells, which moiety, being more or less cut off by the outer
ends of the amphidiscs, becomes transformed to the paren-
chyma-like substance which occupies that position in the
mature gemmule. That this is true can be easily seen on
examination of fig. 15b (Pl. 4), where the inner ends of the
columnar cells are already undergoing the above-mentioned
transformation, though the amphidiscs are not yet in position.
Consequently the origin of this layer need no longer be con-
sidered unknown, as has been done by Goette and Zykoff.

The next question to be considered is the origin of the
amphidiscs. Lieberkühn describes the amphidiscs as being
developed in some of the cells of the peripheral layer (see
p. 83). Goette figures a developing amphidisc in one of
these cells, and describes these spicules as being formed from
within outwards. As has already been pointed out, incom-
pletely developed amphidiscs are never seen in the gemmule
coat (p. 92), but are abundant in the sponge tissue. They
seem to be invariably symmetrical in form, one end being the
exact counterpart of the other. Goette seems to have been
in error on both these points.

Zykoff merely confirms Wierzejski's view that the amphi-
discs are formed outside the gemmule, but neither of them
was able to find the scleroblast, which is most surprising,
seeing that Lieberkühn says that the outlines of the cellular
structures containing the amphidiscs are as sharp as those of
ordinary sponge cells. Zykoff discusses at considerable length
the mode of migration of the amphidiscs from the sponge
tissue to the gemmule coat, and arrives at the somewhat
amusing conclusion that they are pushed from one position to
the other by the sponge cells, much in the same way, I should
imagine, as a colony of ants carries away bits of food which
are too heavy a bundle for one. The presence of amphidiscs

in the scleroblasts, both in the sponge tissue and in the gemmule coat, disposes of the necessity of such a supposition. It seems that it may be considered as finally established that the amphidiscs are carried to their ultimate position by the scleroblasts which secrete them.

In conclusion I wish to offer my sincerest thanks to Professor Weldon for the free use of his laboratory and all its resources, as well as for much invaluable assistance in relation to the literature of the subject; to Professor Minchin for reading the proof sheets; to the Government Grant Committee of the Royal Society for their kind and timely assistance; and to the Principal and Fellows of Jesus College, Oxford, for further help.

THE DEPARTMENT OF COMPARATIVE ANATOMY,
THE MUSEUM, OXFORD.

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EXPLANATION OF PLATES 1—4,

Illustrating Mr. Richard Evans' paper on " Ephydatia blembingia, and the Development of the Gemmule in the same Species."

All the figures from 2—17 *a*, both inclusive, have been drawn with the camera lucida.

SIGNIFICANCE OF THE LETTERING.

am. wand. cell. = *fut. yo. cells.* Amœboid wandering cells which later on in the development become the yolk-cells. *Am. wand. cells* = *fut. col. cells.* Amœboid wandering cells which later on in the development become the columnar cells. *Amphid.* Amphidiscs. *chit. sept.* Chitinous septum. *col. cells.* Columnar cells. *col. lay.* Columnar layer. *d. m.* Dermal membrane. *in. chit. lay.* Inner chitinous layer. *nu.* Nucleus. *ou. chit. lay.* Outer chitinous layer. *mod. sclerob.* Modified scleroblast or spicule cell. *sclerob.* Scleroblast. *s. d. c.* Sub-dermal cavity. *spic.* Spicule. *sp. fib.* Spicule fibre. *tropho.* Trophophore. *v. s.* Vegetable support of the sponge. *yo. body* Yolk-body. *yo. cell.* Yolk-cell.

PLATE 1.

FIG. 1 ($\times$ 1$\frac{1}{5}$).—Ephydatia blembingia growing on vegetable supports, *v. s.*

FIG. 2 ($\times$ 28).—A section showing diagrammatically the structure of the sponge, especially the dermal membrane (*d. m.*) and its supports, which are traversed by the spicule fibres; the large sub-dermal cavities (*s. d. c.*); the poorly developed spicule fibres (*sp. fib.*), the great number of spicules, both amphioxea and amphidiscs, scattered about more or less loosely in the tissues, and the gemmules (*gem.*) which are never found aggregated together in groups.

FIG. 3 ($\times$ 225).—A representation of the various kinds of spicules. *a—e* represent the amphioxea which on the one hand form the spicule-fibres, and on the other hand lie about loosely in the sponge-tissues. *f* is one of the spicules which are seen grouped together in fig. 7. *g—i* are the amphidiscs. *g* and *h* are fully formed; *i* and *k* are intermediate in size, while *l* and *m* represent the early stages.

Fig. 3 was drawn from specimens cleaned with nitric acid.

FIG. 4 ($\times$ 575).—A more highly magnified representation of some of the

spicules shown in Fig. 3. a represents m of Fig. 3; b is an enlarged drawing of g of Fig. 3; and c shows the end of the amphidisc when looked down upon. Note the serrated edge.

FIG. 5 ($\times$ 665).—A young amphioxea shown inside the scleroblast. It should be specially compared with the Fig. 6, a, which represents the early stage of the amphidisc. Both are drawn on the same scale, and on comparison it will be clearly seen that the spicule represented in Fig. 6, a, cannot be a young amphioxea.

FIG. 6 ($\times$ 665).—A representation of an early stage, a; intermediate stage, b; and a fully-grown stage, c, of the amphidisc. Each spicule is situated inside the scleroblast which produced it. The cells themselves are amœboid in character.

FIG. 7 ($\times$ 225).—This figure represents a side view of the somewhat problematic body discussed in the footnote on p. 74, and described as having a basket-like form. It is covered with spicules ($sp.$) of the amphioxea type belonging to group b (compare Fig. 3, f).

PLATE 2.

FIG. 8 ($\times$ 565).—A representation of the cells which later on in the development become the yolk-cells of the gemmule. On the left side of the figure the cells are seen coming together in virtue of their power of wandering. On the right side a portion of a much bigger group of cells is seen. The group in question is situated in the interior of one of the columns of tissue which support the dermal membrane. Note that the protoplasm of the cells is absolutely clear, and that the nucleus is not vesicular.

FIG. 9 ($\times$ 950).—A representation, more highly magnified, of a slightly later stage than that shown in Fig. 8. Note that the protoplasm is becoming slightly granular.

FIG. 10 ($\times$ 950).—A representation of a slightly later stage than that shown in Fig. 9. Note that the protoplasm has become still more granular.

FIG. 11 ($\times$ 130).—A representation of the gemmule at a stage slightly later than that shown in Fig. 10. Note that the granules in the cells have increased to a considerable extent in size, but that their internal structure is not so dense as at later stages. Also note that a great number of cells possessing different characters are aggregated round the central cells ($yo.$ $cells$). These cells seem to have been derived from the sponge at a later stage than the yolk-cells, and constitute a different class both as regards their origin and fate.

FIG. 11 a ($\times$ 950).—A representation, more highly magnified, of a portion of the section shown in Fig. 11. Note the yolk-cells ($yo.$ $cells$) with their

yolk-oodies (*yo. body*), also the columnar cells which are as yet only an aggregation of amœboid wandering cells with food vacuoles and yolk-bodies, also the " trophophores " which possess clear protoplasm, but no yolk-bodies or food vacuoles.

Fig. 12 (× 130).—A representation of a stage slightly later than that shown in Fig. 11. Note that the amœboid wandering cells outside are becoming columnar, especially on one side, also that the outer cells are becoming separated, from those which are becoming columnar, to form a kind of loose membrane (cf. Fig. 14).

Fig. 12*a* (× 950).—A representation, more highly magnified, of the amœboid wandering cells, which are becoming columnar on one side of the section shown in Fig. 12, and also, on the left side of the figure, of the cells which begin to form the loose membrane.

PLATE 3.

Fig. 13 (× 130).—A representation of a stage slightly later than that shown in Fig. 12. Note that the columnar layer is complete except over a small portion at which, later on, the pore will appear, and at which alone the " trophocytes " (*troph.*) are found ; also that the inner chitinous layer is being formed from the same position, i. e. from the bottom, as the columnar layer of cells was formed.

Fig. 13*a* (× 1150).—A representation of a portion of a section similar to the one shown in Fig. 13. Note the group of six trophocytes (*tropho.*) which are making their way to the interior of the gemmule, also the " trophocyte " which has already reached that position. This group is an unusually large one, and was found opposite one of the strands of tissues which pass from the sponge tissue to the loose membrane which surrounds the gemmule. The " trophocytes " appear to travel chiefly along these strands of tissue.

Fig. 13*b* (× 1150).—A representation of a similar portion to that shown in Fig. 13*a*. Note that the " trophocytes " (*troph.*) are scattered about among the amœboid wandering cells, which later on become the columnar cells. On the left of the figure is seen the end of one of the strands of tissue along which the trophocytes travel. Also note the trophocyte on the right of the figure. This cell is just passing among the yolk-cells (*yo. cell*).

Fig. 13*c* (× 960).—A representation of a portion from the top of a section similar to the one shown in Fig. 13. Note that the " trophocytes " (*troph.*) are arranged chiefly outside the columnar cells, but that there are some situated still among the yolk-cells. Those outside have already travelled out while those inside are in the process of doing so. In the lower part of the section there were no " trophophores."

Fig. 13*d* (× 1150).—A representation of a yolk-cell from the same section as Fig. 13*c*. Note the large, central, vesicular nucleus (*nu.*).

PLATE 4.

Fig. 14 (× 130).—A representation of a stage slightly later than that shown in Fig. 13. Note that the columnar layer is complete, and that the loose membrane which surrounds the gemmule is almost complete and is connected by strands of tissue, in which amphidiscs are found, with the general sponge structure. Further, note that there are neither amphidiscs nor trophophores among the columnar cells.

Fig. 14a (× 960).—A representation, more highly magnified, of a portion of the columnar layer and loose membrane shown in Fig. 14.

Fig. 15 (× 130).—A representation of a stage slightly later than that shown in Fig. 14. Note that there are amphidiscs (*amphi.*) over half the extent of the columnar layer of cells, while the other half is as yet free of them. Also note that the inner chitinous layer is still incomplete at the point where the pore will be formed; but the yolk granules in the interior are fully formed. The outer end of the amphidiscs extends beyond the columnar cells.

Fig. 15a (× 665).—A representation, more highly magnified, of the amphidiscs (*amphid.*) lying inside the modified scleroblast (*mod. sclerob.*) which has lost its nucleus, and of the columnar cells lying between the amphidiscs. Note that the inner ends of the columnar cells are becoming clear, as is shown in Fig. 15.

Fig. 15b (× 665).—A representation of the inner chitinous layer (*in. chit. lay.*), the columnar layer (*col. cell.*), the loose membrane, and one of the strands which pass to the membrane, the whole being taken from the region intermediate between the one occupied by amphidiscs and the one devoid of them in a gemmule similar to that shown in Fig. 15. Both amphidiscs are shown inside their scleroblasts, and the one in the strand of tissue outside is being carried to its position alongside the other amphidisc among the columnar cells.

Fig. 16 (× 130).—A representation of a stage slightly later than that shown in Fig. 15. Note that the spicular layer and the inner chitinous layer are complete. Further, note that the columnar cells have passed out and are situated externally to the outer end of the amphidiscs, their inner ends having been modified to form the parenchyma-like substance situated between the amphidiscs.

Fig. 16a (× 665).—A more highly magnified representation of the gemmule coat shown in Fig. 16. Note that the columnar cells are forming the outer chitinous layer and are becoming separated preparatory to their passing back to the sponge.

Fig. 17 (× 130).—A representation of the fully-developed gemmule, showing the contents passing up the pore as far as the chitinous septum (*chit.*

sept.) ; the inner chitinous layer (*in. chit. lay.*) ; the amphidiscs (*amphid.*) ; and the not strongly developed outer chitinous layer (*ou. chit. lay.*).   Note that the columnar cells are no longer present.

FIG. 17*a* (× 665).—A more highly magnified representation of the gemmule coat, showing the several parts indicated in the description of Fig. 17. Note the parenchyma-like structure of the substance situated between the amphidiscs (*inter. lay.*), that is, the intermediate layer of the protective coat of the gemmule.
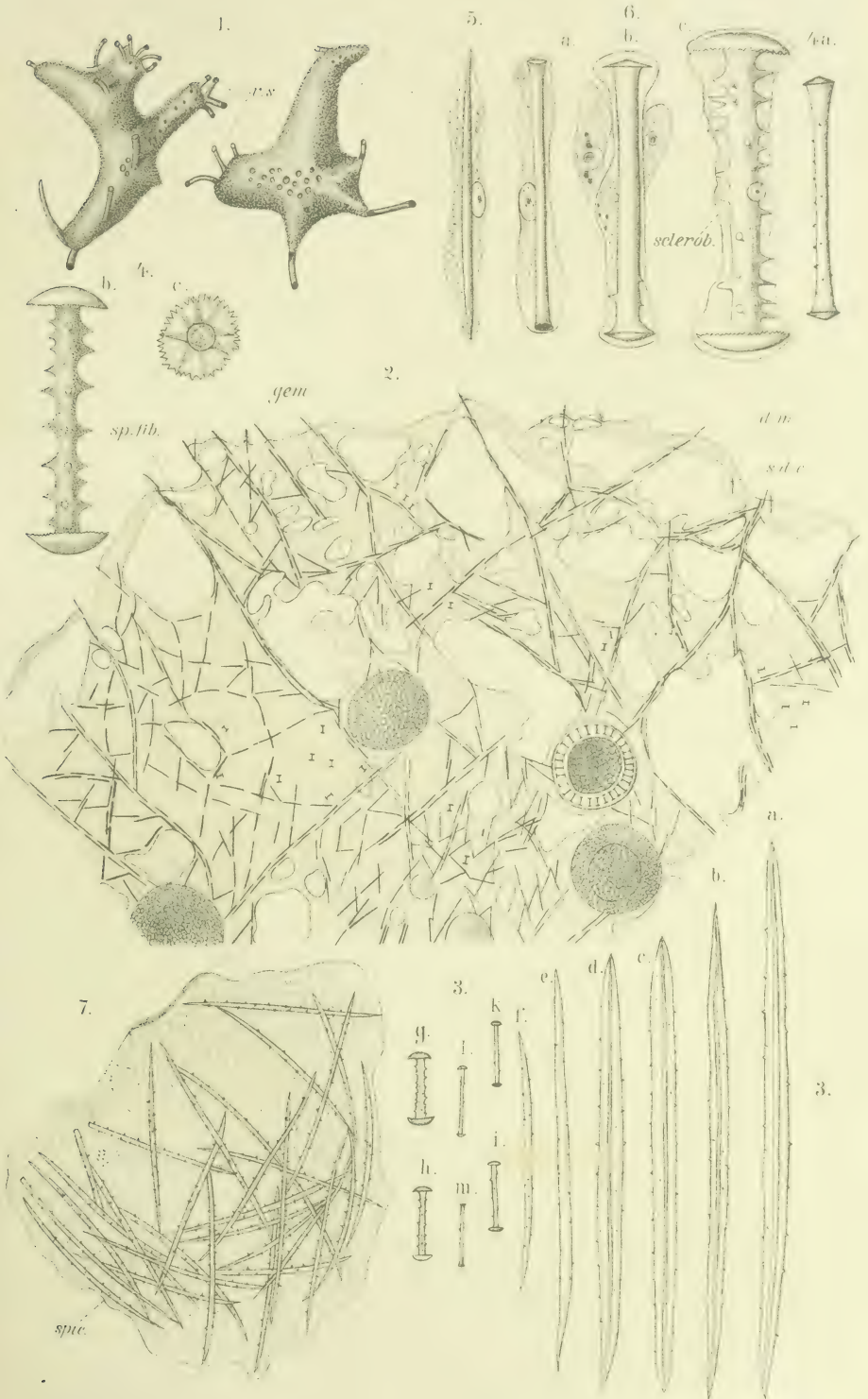
8.

d.m.

am.wand.cells
= fut.yo.cells

9.

10.

11.

12.

yo.
cells

col.cells.

am.wand.
cells.fut.
col.cells

yo.cells

am.wand.cells
= fut. yo.cells

11ª

am.wand.cells
fut.yo.cells

12ª

troph.

col.
cells

col.
cell.

troph.

yo.cells

yo.body

13.   troph.   13ᵇ

yo.cells.

col.lay.   in.chit.lay.

13ᵃ   troph.

col.cells.
yo.cell.

yo.body

troph

yo.cell.
yo.body.

yo.cell.
yo.body.

nu.

troph.

col.cell.

13ᵈ
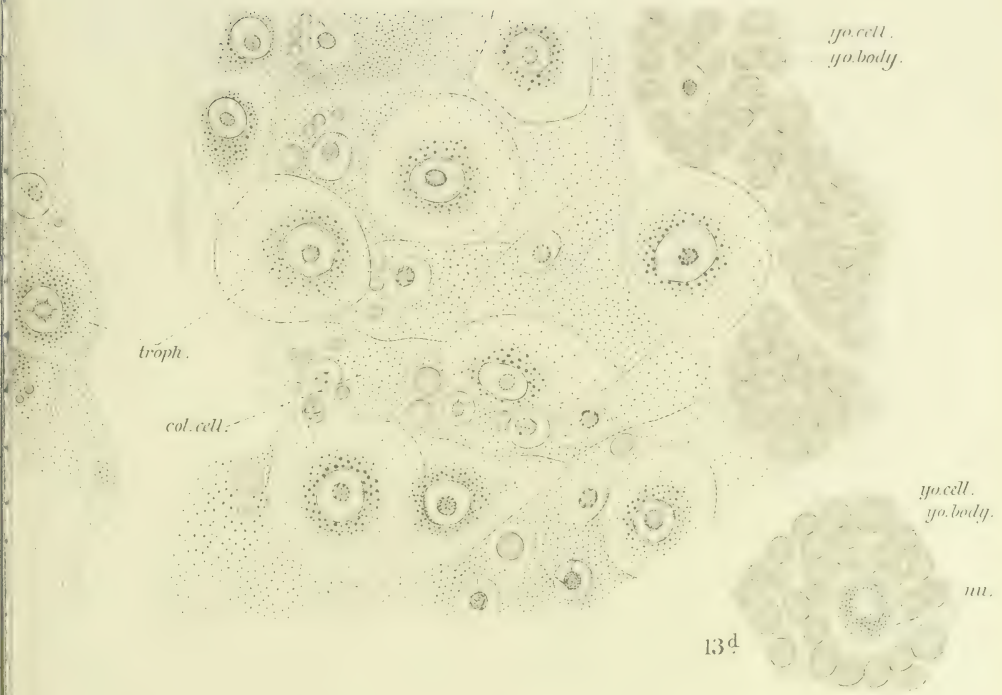
13ᶜ

troph.

col.cell.

troph.

14.

14 a

vo.cell.

col.cells.

in.chit.lay.

16.

col.cells.

17.

pore

15 a

in.chit.lay.

Amphid.

out.chit.lay.

vo.cells

col.cell.

Amphid.

Mod.sclerob.

Evans del. ad nat

16ᵃ

col. cells.

sclerob.

Amphid.

15ᵇ

Amphid.

Broken
young
Amphi.

Amphid.

col. cells.

ol. cell.

sept.

in. chit. lay.

Amphid.

in. chit. lay.

Amphid.

in. chit. lay.

intr. lay.

col. cells.

15.

17ᵃ

Amphid.

out. chit. lay.

Mod. sclerob.

Amphid.

interlay.

in. chit. lay.
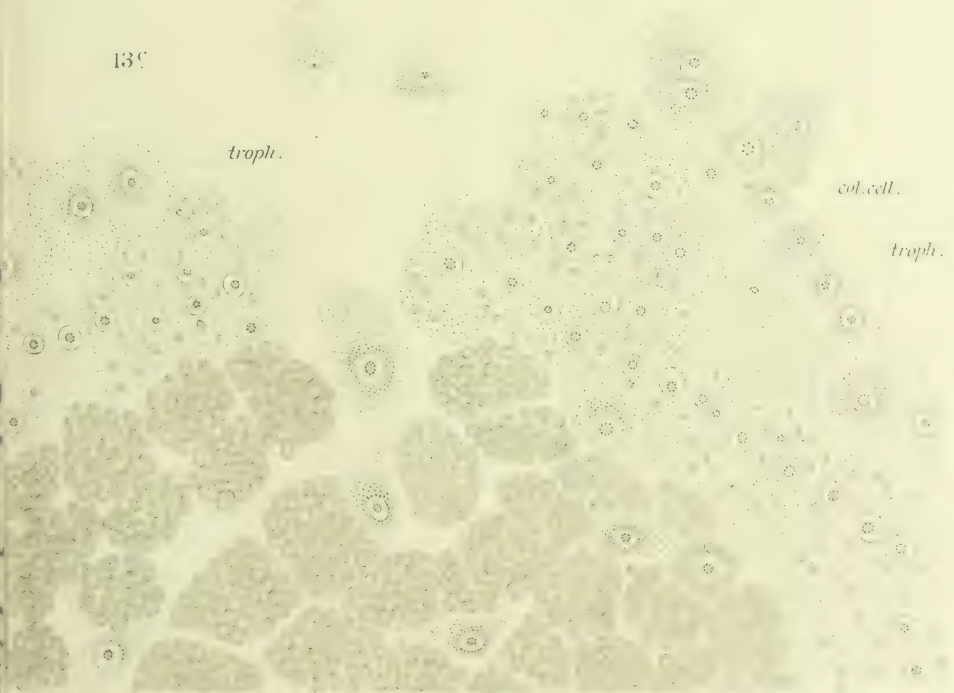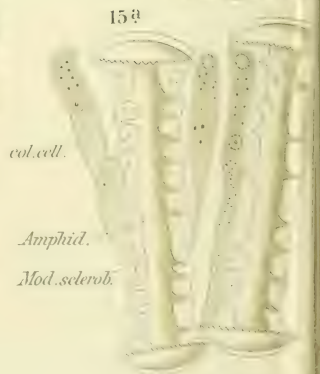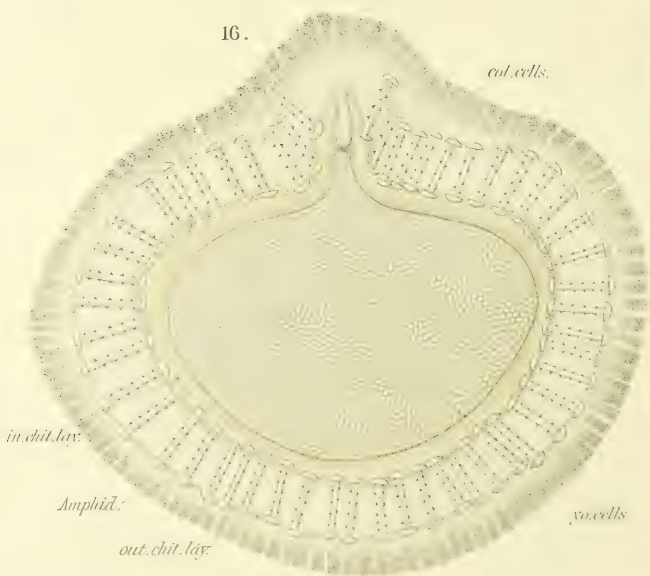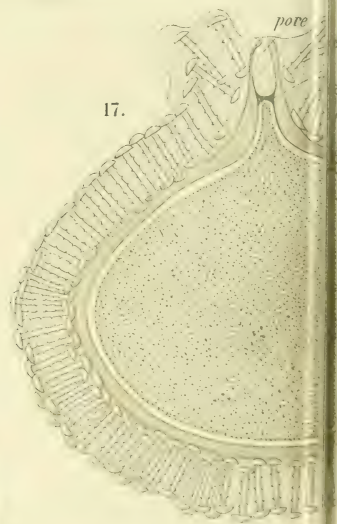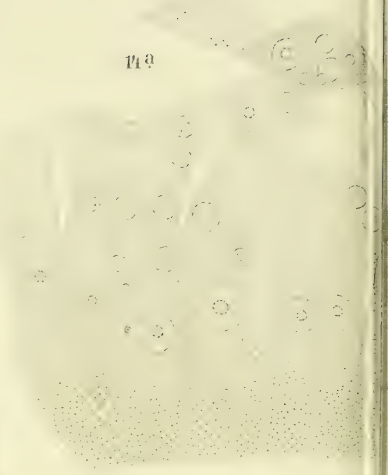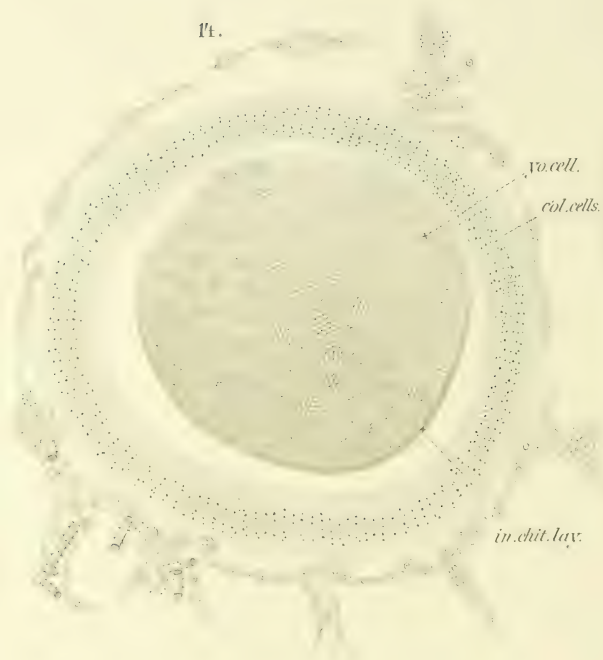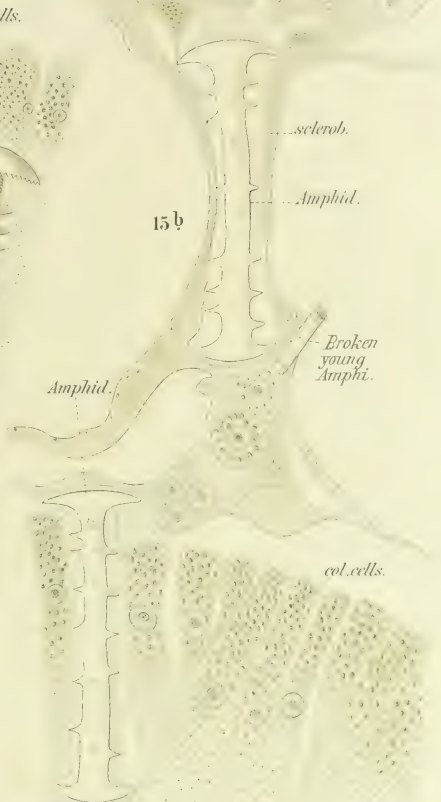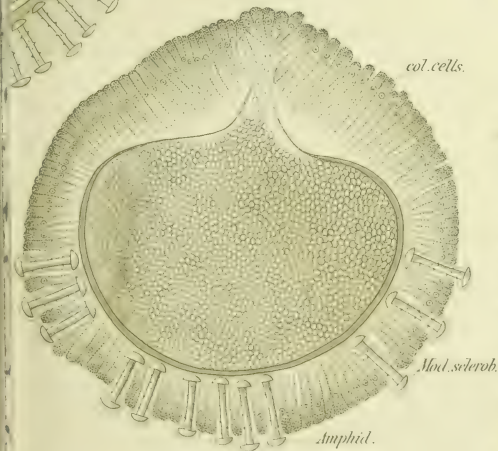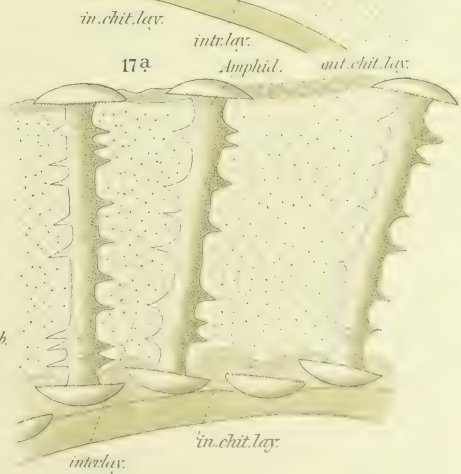
On a Collection of Nemerteans from Singapore.

By

R. C. Punnett, B.A.

With Plates 5—8.

THE Nemerteans described below were collected by Mr. F. P. Bedford and Mr. W. F. Lanchester during a year's stay in and near Singapore. They comprise ten species, nine of which have not hitherto been described. All belong to the order Heteronemertini, whilst eight out of the ten come into the family of the Lineidæ. It is worthy of note that no specimens of Drepanophorus were found, seeing that in collections from adjacent seas, previously described by Bürger (1) and myself (7), they form a marked constituent of the Nemertean fauna. It will be noticed that I have assigned all the Lineidæ here described to the genus Cerebratulus. This I have done not because I am convinced that they approximate more closely in every case to the forms already placed in that genus, but because of the difficulties of distinguishing, in preserved specimens only, the three genera, Lineus, Cerebratulus, and Micrura. This difficulty was dealt with in Hubrecht's case (5) by recognising in the family only the single genus Cerebratulus. As, however, the family already contains more than eighty species, with the probability of large additions in the near future, it seems expedient to adhere to the present arrangement of genera, in spite of its unsatisfactory character, until the accumulation of anatomical data be sufficient to warrant revision. The caudal appendage forms the chief distinction between the genus Lineus on the one

hand and Cerebratulus and Micrura on the other (the small genera Borlasia and Langia being sufficiently well marked to be left out of account here). Though its presence shows its possessor to be either a Cerebratulus or a Micrura, its absence does not necessarily establish the specimen in question as a Lineus, unless a large amount of material is forthcoming, since it is a delicate structure which may easily be broken off. In his monograph Bürger (**3**) attempts to place these genera on a firmer basis by taking into account certain anatomical features, such as the sidefolds usually characteristic of Cerebratulus, the presence or absence of a diagonal muscle layer, and of neurochord cells. Based mainly on a study of the Neapolitan forms, the attempt is for them fairly successful. For exotic forms, however, it is less so. Thus C. natans, which closely resembles many of the Mediterranean forms in its general form, its well-marked side-folds, and its swimming habits, differs markedly from them in the absence of neurochord cells and of a diagonal muscle layer. Again, C. brunneus agrees with the genus Micrura in the absence of sidefolds and a diagonal muscle layer, whilst its comparatively large size and stoutness of build incline one to associate it rather with the genus Cerebratulus. The small and slender C. erythrus, again, with its absence of a diagonal muscle layer, might be relegated to the genus Micrura, were it not for the presence of small side-folds and of neurochord cells. Other instances might be taken, but the above are enough to show that Bürger's system is not altogether satisfactory. However, before we can hope to improve upon it more anatomical evidence must be forthcoming. And, indeed, on many important points much yet remains to be made out in the species inhabiting our own shores. Especially is this the case with the excretory system, its range, topography, and the position and number of its ducts. We are only acquainted with these details in two of the thirty odd species of Cerebratulus, and in six or seven cases in nearly the same number of species of Lineus. The figures at the end of this paper will give some idea of the diversities shown by this system, even

in members of the same genus. Other features which may prove of taxonomic value, and to which I venture to draw attention in the following list, are :

(1) The presence or absence of a frontal organ.
(2) The presence or absence of a cephalic vascular loop.
(3) The extent of the rhynchocoelom.
(4) The minute structure of the cutis.
(5) Structure of the cerebral organ.

Moreover it would greatly facilitate the labours of the systematists in this group if collectors were able to make a coloured sketch of the living animal, and to make particular note as to the presence or absence of a caudal appendage whilst the animal is still living. A word on preservation may not be out of place here.

Excellent results are to be obtained by stupefying the worms in a 1 per cent. solution of chloral hydrate in sea water, and subsequent treatment with saturated corrosive sublimate. Particular care should be taken that the anterior few centimetres of the animal are preserved as straight as possible by killing the animal on a glass slide or some other such means. Since this region must be cut into serial sections the labour-saving importance of this precaution can hardly be exaggerated.

HETERONEMERTINI.

EUPOLIIDÆ.

Eupolia melanogramma, mihi (= E. quinquelineata, Bürger).

Five specimens of this large and striking worm were obtained, showing considerable variation in the completeness of the five dorsal black lines.

(1) Specimen, 32 × 6 mm., having the five lines well marked for the whole length of the body except near the posterior end, where the outer two are occasionally broken. All lines of nearly equal thickness.

(2) Specimen, 52 cm. × 6 mm., agreeing very closely with last specimen.

(3) Specimen, 36 cm. × 4 mm., with the three median lines well marked, of equal thickness and unbroken. The two outer ones are present only along the anterior half of the body, and even here are finer than the others and much broken.

(4) Specimen, 15 cm. × 5 mm., with only three broad inner lines except for the anterior 2 cm., where there are two fine outer lines.

(5) Specimen, 54 cm. × 7 mm., with three dorsal lines only, except for an exceedingly fine trace of an outer one for a distance of about ½ cm. on the right side only.

From which it may be seen that these five form a series, at one end of which there is a specimen with five well marked lines of equal thickness throughout almost the whole length, whilst at the other there is a specimen which shows only three lines (excluding the faint trace mentioned above). In this connection it is interesting to note that Bürger (2) has described a single specimen with seven dorsal lines on which he founds a new species, E. septemlineata, but concerning whose inner organisation he gives no details. With almost equal justice the specimen last described above might be christened E. trilineata. Since, in the light of the above facts, it seems reasonable to look upon Bürger's new species as a variety, I would venture to suggest the name melano-gramma for the species as a whole, restricting the terms quinquelineata, septemlineata, etc., to denote varieties where such a proceeding is thought desirable.

With regard to the inner organisation of this form, I am able to confirm the special features given by Bürger (2), and also to add a few points of interest omitted by him.

The epithelium is high, and its external portion contains a number of anucleate (fig. 5) unicellular glands containing minute yellowish bodies. Beneath the epithelium is a struc-tureless basement membrane. Below this, again, is a layer of longitudinal muscle fibrils, mixed up with which, in the

region of the black lines, is the pigment, which in sections is seen to be brown.   The cutis glands are well marked and their contents stain deeply with thionin, though not at all with carmalum.   The gelatinous layer of the cutis is rich in circular fibrils.

The vascular system in the snout shows the wide horizontal lacunæ characteristic of the genus.   These bend round beneath the dorsal ganglion at its commencement, and, taking an upward course, come to lie between the latter and the proboscis sheath at the level where the proboscis is attached (fig. 1, *a*).   These lacunæ then extend dorsally, and at the posterior limit of the ventral commissure unite to form the dorsal vessel, and also envelop the top of the dorsal ganglion (fig. 1, *b*).   In this region a small diverticulum projects into the tissue between the dorsal and ventral ganglia.   This diverticulum becomes separated off, and a few sections later is seen to unite with its fellow of the opposite side, forming the median ventral œsophageal vessel (Schlundgefass) (fig. 1, *c*).   At this level the lacuna which earlier enveloped the dorsal portion of the dorsal ganglion is now seen to lie upon the dorsal surface of the cerebral organ.   Still more dorsally a portion of the lacuna has separated off, and this later unites with the median œsophageal vessel on each side (fig. 1, *d*), and the common lacuna so formed is continued into the œsophageal lacunæ.

The alimentary canal is characterised by the great thickness of the glandular tissue beneath the epithelium of the œsophagus.   In the intestinal region the lumen is wide. The intestinal diverticula alternate in depth, every other one being nearly twice the depth of those directly behind and in front.   The deeper set are not so deep as the width of the lumen of the intestine.   There is no ventral gutter.

The proboscis shows a layer of diagonal muscles between the circular and longitudinal layers.   The longitudinal fibres are characteristically arranged, recalling the condition seen in transverse sections of Lumbricus.

The proboscis sheath extends rather less than one third

of the length of the body. In a specimen 36 cm. in length,
it came to an end 10·5 cm. from the anterior end.

The excretory system commences soon after the mouth,
and extends as far as the commencement of the intestine.
Anteriorly small portions of it show a tendency to become
isolated from the rest (cf. E. multiporata [7]). It possesses
a number of openings to the exterior, and also presents the
unique condition of ducts opening into the œsophagus (fig. 2).
In this way the lumen of the alimentary canal is indirectly
placed in communication with the exterior medium. That
such a condition is not pathological but normal in this species
is shown by the fact that it was found in another specimen,
the anterior portion of whose body was cut. The subjoined
tables show the position of the various ducts (see pp. 118 and
119). The sections were of a uniform thickness of 8 μ, and
commence with the anterior extremities of the animals.

It will be noticed that the ducts are in some cases rudi-
mentary, i. e. they do not form a communication with the
excretory system, but end blindly when they reach the
circular muscle layer. It is also interesting to notice that
in several cases they pass through the ganglion-cell layer of
the side stem (fig. 3) ; and also that in one instance the duct
passed beneath the side stems, the only instance, as far as
I am aware, of such a condition occurring in the group.

The genital sacs were devoid of sexual cells.

The main features of the nervous system have been
touched upon by Bürger. An interesting point, however, is
to be made out with regard to the anal commissure. In this
species it is very strong and ventral to the gut. In this case
the pigment lines afford an infallible criterion of orientation,
and there can be no question of a twisting of the body such
as described by Hubrecht in the case of E. delineata, though
he states that the commissure is also ventral in this case (5)
(p. 11). Oudemans (6) (p. 41) mentions the commissure of E.
curta as being dorsal. In the species of Eupolia next de-
scribed in this paper there is no commissure. How far such
divergent conditions may be due to injury and subsequent

regeneration seems to the writer a subject better fitted for experimental inquiry than for morphological speculation.

Eupolia pholidota, n. sp.

A single specimen of this worm was taken, and in the preserved state measured 19 cm. in length. The posterior two thirds or so were very slender, being barely half as thick as the anterior portion of the worm, which was about 3 mm. in diameter. The record of its appearance in lifetime shows it to have been " white with reddish-black spots." The only indication of such markings left are faint yellowish blotches (fig. 7). These do not extend beyond the head furrow anteriorly.

The epithelium is high and in its outer portion lacks the small granular cells which characterised that of the preceding species. The basement membrane (fig. 8, *bm*) is exceedingly thick, and beneath it is a well-marked layer of longitudinal muscle fibrils. The cutis glands are of the usual Eupolia type.

The muscular system presents no peculiarities.

The vascular system resembles that described above for E. melanogramma. The lacunæ round the cerebral organ are, however, more complete, and the vessels forming the buccal commissure (fig. 9, *bbvc*) are seen in section to pass round the outer side of the cerebral organ instead of the inner side as in the preceding species.

In the alimentary canal the glandular tissue beneath the œsophageal epithelium is comparatively thinner than is usual in most members of the family. The œsophagus terminates about 4·25 mm. from the tip of the snout. In the intestinal region the lateral diverticula are small and there is a deep ventral gutter.

The proboscis is extremely slender.

The generative sacs are full of spermatozoa, most of which are ripe. Ducts are present.

The excretory system commences at about ·85 mm. from

Specimen No. 1.

	RIGHT SIDE.			LEFT SIDE.		
	External openings.	Internal openings.			External openings.	Internal openings.
			231—257 {			240
			270—352 {	295		332
		317				
		413				
		430				450
		458				493
		485				529
		548				564
256—860 {			355—860 {	598 (through n.c.)		
						617
						630
				638		
	647					678
	681					685
	706	706		702		717
	720					
	732	751				
		756		753 (incomplete)		762
	775	761				769
						772
						791
		807		828		
	829 (below n.c.)					
	830 (through n.c.)					
	834 (through n.c.)					
	842					
	855 (incomplete)			859		

SPECIMEN No. 3.

	RIGHT SIDE.			LEFT SIDE.	
	External openings.	Internal openings.		External openings.	Internal openings.
319—364 {	329		362—375 {		
425—457 {		455			
476— {	571 583	513 525	485— {		615
		749			
	839	816			775 786 800 829

the tip of the snout, and the ducts commence about this level
also. The system is interrupted in many places. These ducts
are exceedingly numerous, far exceeding in number those of
any other Nemertine known. On one side I was able to count
nearly a hundred ducts, and even then the excretory system
had not come to an end. Another feature peculiar to this
worm, and one which, so far as I am aware, occurs in no other
member of the group, is the backward extent of the excretory
system into the intestinal region, where the generative sacs
and their ducts also occur. Their extent may be more easily
recognised by a glance at the table below giving the levels
at which various systems commence or terminate. All sections
are 5 μ in thickness.

Commencement of brain .	. Section	31
Commencement of cerebral organ .	,,	60
Termination of cerebral organ .	,,	77
Commencement of excretory system .	,,	170
Termination of œsophagus .	,,	850
Commencement of generative region .	,,	1250
Excretory system still found in .	,,	2120

In the generative region the excretory tubules have almost
disappeared, though traces of them may still be recognised
(fig. 10 *). The excretory ducts are in this region often
incomplete, not penetrating the circular muscle layer. Their
external opening, however, appears to be always present. As
these ducts and the gonads are found in the same region, it
seemed possible that the former might, where present, act as
the ducts of the latter. Such a view, however, appears to be
negatived by the following considerations :

(1) The ducts which are seen to be in connection with the
gonads show a different histological structure, being composed
of long fibrillated cells with slender rod-like nuclei (fig. 10,
gd.). The excretory ducts do not present this fibrillated
structure, and their nuclei are smaller and slightly oval
fig. 10, *exd.*).

(2) The excretory ducts generally show a certain amount of expansion in the circular muscle layer, the gonadial ducts never.

(3) Spermatozoa may often be detected in the gonadial ducts though not in the excretory ducts.

(4) The excretory ducts generally pass out just over the side stem, and take a more or less horizontal course through the body-wall. The gonadial ducts, on the other hand, are usually given off somewhat more dorsally, and their later course is directed more vertically than is the case with the former (fig. 9).

Such considerations appear to show conclusively that, although these two sets of ducts co-exist in the same region in this particular worm, there is no connection between them; moreover, they point to the improbability of any homology being established between the two sets of ducts, whose chief feature in common appears to be that of repetition.

With regard to the nervous system the brain is small for the size of the animal. The ventral ganglion is small compared with the dorsal (fig. 6). The œsophageal commissure is well marked and contains ganglion-cells (fig. 6 a, onc.). The side stems end blindly near the anus without forming a commissure above or below the rectum. Possibly this may be owing to injury and subsequent regeneration, but it is impossible to say without more material.

The cerebral organ is small. The gland cells form a peculiar process directed inwards and ventralwards (fig. 6a, gcorg).

The cerebral canal opens to the exterior laterally and somewhat ventrally.

Eyes are apparently absent, as careful search over sections through the precerebral portion of the groove failed to reveal any structures which might be construed as such. With the exception of E. rugosa (7) all the other species of the genus known possess these sense organs.

The head glands are well marked (fig. 6, hg.) and stretch back over and under the brain well into the œsophageal region.

LINEIDÆ.

Cerebratulus natans, n. sp.

Five specimens of this worm were procured from shallow water during the night time by the use of the tow-net. Mr. Bedford informs me that he has observed what was probably the same species swimming with eel-like movements near the bottom during the day time.

C. natans is from 8—10 cm. long. The anterior 2 cm. are rounded and about 4 mm. in diameter. Posteriorly it becomes much flattened dorso-ventrally, and the width increases to as much as 8 mm., which is about six times the depth at this portion of the body. A caudal appendage is present (fig. 11). The snout is blunted, and is marked by a black patch above and below the proboscis pore (fig. 12). Mr. Bedford informs me that in life dorso-lateral longitudinal reddish lines were to be seen. As there is no trace of pigment to be seen in this region after preservation, either in the epithelium or the cutis, it is probable that such an appearance was due to the coloration of the intestinal pouches viewed through the pale whitish-brown integument of the living animal (cf. Verrill [**8**], p. 435). The head slits are well marked, and are about 2·5 mm. in length. The mouth commences rather before the posterior end of the head slits, and is about 2·5 mm. long. A shallow ventral groove runs along the flattened portion of the body, commencing about 15 mm. from the anterior end of the worm (figs. 11 and 15, vgr.).

The cutis in the œsophageal region shows a well-marked nervous layer directly beneath the epithelium (fig. 21, nep.). Below this is found a thin layer of circular muscle fibres (mcc.). The longitudinal muscle layer of the cutis is very highly developed, and in it are imbedded the large cutis glands (cgl.), which have a strong affinity for staining re-agents such as carmalum. The connective tissue layer (cn.) is fairly well developed though it is to a great extent invaded by fibres from the external longitudinal muscular coat (mlo.).

The muscle layers in the œsophageal region are well developed, the external longitudinal layer (*mlo.*) being more than double the thickness of the circular layer (*mc.*), whilst this in turn is about twice as thick as the internal longitudinal layer (*mli.*). Further back the circular layer becomes relatively smaller, and near the posterior end the outer longitudinal layer becomes very sparse. The horizontal layer over the mouth is well marked. The dorso-ventral muscles between the intestinal diverticula are strong. There is no diagonal muscle layer.

The vascular system anteriorly forms a well-marked head loop. There is in addition a small dorsal portion separated off. The rest of the vascular system is formed on the usual type for the family as described by Oudemans (**6**) and Coe (**4**). The proboscis vessel leaves the proboscis sheath about 6·5 mm. from the anterior end.

The alimentary canal is of the usual type. The intestinal diverticula are very deep, and with a very narrow lumen (fig. 15). There is no ventral gutter posteriorly.

The proboscis shows the usual three layers of muscles, i. e. outer longitudinal, circular, and inner longitudinal, the last named being the thickest. Outside the circular muscles is a well-marked nerve layer. There are two muscle crosses (fig. 13, *mcr.*) dorsally and ventrally. The epithelium either dorsally or ventrally (which it is impossible to determine) is considerably thickened and highly glandular. The outer borders of the cells are here rendered conspicuous by the presence of a dark greenish pigment.

The proboscis sheath extends to within a millimetre of the posterior end, though it is here much reduced.

The generative organs appear as thin-walled sacs between the intestinal diverticula. There is no trace of sexual products.

The excretory system commences about 3 mm. from the tip of the snout, and extends over the same distance. The tubules, except at the anterior portion, are exclusively ventral to the level of the side stems. Anteriorly there is a single

duct on each side opening just over the level of the side stems (fig. 37).

The nervous system exhibits the usual type. The median dorsal nerve is not greatly differentiated from the nervous sheath enclosing the circular musculature.

The cerebral organ is well developed, and is rounded in shape though somewhat flattened dorso-ventrally. The ventral glands are well developed, but dorsally they are almost absent. The dorsal lobe of the dorsal ganglion ceases before either the ciliated canal effects a junction with the ventral lobe or the appearance of gland cells round the former.

A frontal organ of the typical threefold arrangement is present at the tip of the snout.

Eyes are absent.

The head glands are well marked, reaching ventrally beyond the commencement of the brain. Both dorsally and ventrally they merge into the cutis glands.

Cerebratulus brunneus, n. sp.

The single specimen procured measured about 12 cm. in length and 4 mm. at its greatest breadth. In shape it was rounded anteriorly, though somewhat flattened posteriorly. The snout was much blunted. The mouth was small and rounded. A caudal appendage was present. The colour was darkish chocolate in life, slightly paler ventrally. It persisted to a great extent after preservation.

The epithelium is very thick, and near the basement membrane are a number of deeply staining, small, unicellular glands. The circular muscle layer of the cutis is thin, and beneath it is a comparatively thick though sparse layer of longitudinal fibres (fig. 40, *mlc.*). The cutis glands form a compact, thick, and continuous layer, beneath which may be seen traces of the connective-tissue layer which is almost absent in this species.

The muscle layers are strong, the outer longitudinal layer

being more than double the thickness of the circular layer, whilst this in turn is about four times as thick as the inner longitudinal layer. There is a layer of longitudinal fibres between the proboscis sheath and alimentary canal (cf. Lineus versicolor, Bürger [**3**], p. 638). There is no diagonal muscle layer.

The vascular system anteriorly shows a network of small lacunæ instead of a head loop. From this network the main cephalic vessel, just before the brain, is situated dorsally to the proboscis sheath (as in the Eupoliidæ). The œsophageal vessels are merged into a single large lacuna on each side in the posterior region of the œsophagus, about 8 mm. from the tip of the snout.

The alimentary canal presents no special features. A ventral gutter is present in the intestinal region, which commences about 1·5 cm. from the tip of the snout. It is very conspicuous.

The proboscis is extremely thin. It contains no muscle crosses.

In the proboscis sheath the circular layer is extremely thick in the mouth region. The proboscis sheath is not found in the posterior 3 cm. of the body.

The generative sacs contain developed ova.

The excretory system commences 3·4 mm. behind the snout, and extends over 3·8 mm. The tubules do not extend much, either dorsally or ventrally, over the level of the side stems. There are ten ducts on the left side and five on the right (fig. 35). They open to the exterior just above the level of the side stems.

The nervous system is built on the usual type. The median dorsal nerve is well marked.

The cerebral organ is well developed and rounded in transverse section. The dorsal glands are more strongly developed than the ventral (fig. 27, a—d). The connective tissue contains a bright yellow pigment (pg.). The dorsal lobe of the dorsal ganglion stretches over the anterior portion of the organ. The head slits are deep, though not reaching

to the brain. They are continued beyond the level where the ciliated canal is given off.

Frontal organ and eyes are both absent.

Cerebratulus robustus, n. sp.

A single specimen only was procured. It is a short, thick form 7 cm. long and about 7 mm. broad in the middle, with a depth of about 4 mm. The snout is very blunted. The mouth is small and the head slits rather short. No caudal appendage could be observed, but this may have been due to an accident. Unfortunately no record was made of the colour in the living form. In the preserved specimen it is a uniform pale buffish brown.

The epithelium is separated by a fine line (possibly the expression of a delicate membrane) into an outer portion containing a few unicellular glands but no nuclei, and an inner nuclear portion also containing unicellular glands (fig. 20, ep.).

The cutis, which is separated from the epithelium by a fine basement membrane, possesses a thin layer of circular and longitudinal muscle fibres, contains a moderately well-developed layer of glands. Beneath these, again, the connective-tissue layer is well marked in the œsophageal region, being thicker than the rest of the cutis.

The muscular system is of the normal type. A diagonal layer is present between the circular layer and the nervous layer.

The vascular system anteriorly forms a well-marked head loop. The blood lacunæ in the œsophageal region are extremely small, and a single one is present in each of the ventral œsophageal folds. There is no well-marked anastomosis among them, as in most cases. Otherwise the arrangement is typical.

The alimentary canal in the œsophageal region (fig. 16) presents a well-developed glandular layer beneath the epithelium ventrally—recalling somewhat the condition found in the Eupoliidæ. The intestine commences about 1·3 cm. from the anterior end.

The proboscis is very thin and without muscle crosses.

The proboscis sheath reaches nearly to the posterior extremity of the animal.   The rhynchodæum is very small.

The generative sacs contain immature ova.

The excretory system commences about 2·5 mm. from the tip of the snout, and extends over about 5 mm.   It lies wholly ventral to the level of the side stems.   There are no excretory ducts opening to the exterior.   Moreover, I have been unable to discover any openings into the alimentary canal, and as the series of sections was quite complete, I can only conclude that in this instance the excretory system is without any openings (cf. (**7**) Eupolia hemprichi).

The nervous system is built on the usual type.   The upper lobes of the dorsal ganglion are considerably larger than is general.   The median dorsal nerve stands out well from the nervous layer beneath the outer longitudinal muscle layer.   The ventral commissure is very strong, and where they separate the ventral ganglion is nearly as large as the dorsal.

The cerebral organ is of moderate size and rounded in shape, though posteriorly its outline becomes more oval (fig. 31, *d*).   The dorsal gland cells are few, though the ventral are well developed.   The organ is further removed from the ventral nerve cord than is usually the case (fig. 31, *b*).   The dorsal lobe of the dorsal ganglion ends before the canal enters the ventral lobe.

The head slits reach nearly to the brain, but cease very abruptly externally at the level of the anterior limits of the brain.

A frontal organ is present, but it is small.

Eyes are absent.

The head glands are well developed, and extend backwards nearly as far as the brain.

Cerebratulus erythrus, n. sp.

Several specimens of this worm were procured, the average length being between 6 and 7 cm.   The shape is rounded

throughout, though small side-folds could be made out. The snout is rather sharply pointed. The head slits do not extend beyond the commencement of the mouth, except as very shallow depressions. A small caudal appendage is present. The colour in life was bright red, and is fairly well preserved in a glycerin specimen.

The epithelium contains small, non-staining, unicellular glands in its outer portion, and also small deeply-staining ones nearer the basement membrane. A circular muscle layer cannot be made out in the cutis, and the longitudinal layer (fig. 22, *mlc.*) is feebly developed. The composite glands of the cutis (*cgl.*) are small and rounded, and do not stain appreciably with carmalum. The connective-tissue layer is thick, and contains a few longitudinal muscle fibres. In front of the brain this last layer is small.

Of the muscle layers, the external longitudinal in the œsophageal region is about twice as thick as either the circular or the internal longitudinal layer, which are of approximately equal thickness. There is a well-marked horizontal layer over the mouth. In the snout the longitudinal fibres are very diffuse. There is no diagonal muscle layer.

The vascular system is of the usual type, a well-marked head loop being present. The dorsal vessel leaves the proboscis sheath about 4 mm. behind the tip of the snout (fig. 42).

The alimentary canal presents no special features. The intestine commences about 8 mm. behind the tip of the snout. The ventral gutter is large and the gut pockets small.

The proboscis is in all cases missing.

The proboscis sheath reaches very nearly to the posterior extremity.

The generative sacs contain no sexual cells.

The excretory system commences at the level of the posterior border of the mouth, and extends some way above and below the level of the side stems. A single excretory pore occurs on each side near the hind end of the system.

The nervous system is of the ordinary type, the dorsal

commissure being, as usual, much thinner than the ventral. The latter is found somewhat behind the former.   The median dorsal nerve is well marked.

The cerebral organ is small.   Both dorsal and ventral glands are well developed.   The dorsal lobe of the dorsal ganglion (fig. 6a, *ddg.*) does not end until the glands of the cerebral organ have made their appearance.

The head slits are wide and shallow, not reaching more than halfway to the brain.

The frontal organ is exceedingly well developed, being very conspicuous in sections through the snout.   At the base of each of its three divisions are a number of small cells with large nuclei, bearing a great resemblance to the ganglion cells of the brain (*gf.*), though whether they are of such a nature it is impossible to state definitely.   A nervous connection between the frontal organ and the brain could not be traced.

Eyes are not present.

The head glands are well marked, falling anteriorly into three divisions round the frontal organ.   Posteriorly these merge into one surrounding the head loop.   They take a light stain with carmalum, and do not become continuous with the cutis glands.   Neither do they reach backwards as far as the brain.

Cerebratulus sordidus, n. sp.

The shape is rather rounded anteriorly, more flattened behind.   The length is about 6 cm., but the tail was somewhat damaged, for which reason it is not possible to say whether a caudal appendage was present.   The head slits extend beyond the mouth region as shallow depressions.   The colour in life was a dirty yellow-brown.

The epithelium contains greenish unicellular glands superficially, and small more deeply staining ones near the basement membrane.   The cutis presents a fine layer of delicate longitudinal muscle-fibrils, but no circular ones.   A layer of composite lightly-staining cutis glands occurs (fig. 23, *cgl.*), beneath which there is a layer of connective tissue

containing muscle-fibrils. These glands become much smaller posteriorly.

In the muscular system the horizontal layer over the mouth is well marked. There is no diagonal layer.

The vascular system is of the regular type, except that the head loop is replaced by a network of lacunae.

The alimentary canal shows no special features. The intestine commences about 6·5 mm. from the tip of the snout. Ventral gutter very small.

The proboscis is missing.

The genital sacs contain ova, which, however, are not mature.

The excretory system reaches forwards to the point where the cerebral organ ends. It extends some way dorsally and ventrally to the level of the side stems, the tubules of the opposite sides nearly meeting at places in the mid-ventral line. The paired ducts open from the middle of the system, and the position of the pores is somewhat dorsal.

The nervous system is of the usual type.

The cerebral organ is considerably elongated dorso-ventrally (fig. 32, c.) owing to the large development of both the dorsal and ventral glands. The dorsal lobe of the dorsal ganglion ends before the organ starts, and the ventral lobe becomes greatly diminished in size before entering into its composition (fig. 32, d.). The head slits reach nearly to the brain.

The frontal organ is well developed.

Eyes are not present.

The head glands are very small, and rapidly merge into the cutis glands.

Cerebratulus bedfordii, n. sp.

A single specimen of this species was obtained by Mr. Bedford, with whose name I have much pleasure in associating it. It was about 16 cm. long and 3 mm. broad, being rounded in shape all through. The anterior end is sharply pointed. The head slits are about 2·5 mm. long, and the mouth, which

is small and round, commences after their termination.   No
record was preserved of the colour in lifetime.   In the
preserved specimen it is of a pale dirty brown throughout,
and the animal resembles, both in this respect and in its
shape, the smaller C. erythrus.   No caudal appendage was
observed, the posterior end being damaged.

The epithelium is almost destitute of the small unicellular
glands so characteristic of the group.   A few deeply staining
ones occurred near the basement membrane.   The basement
membrane itself differs markedly from that of all the other
species here described in that it is of great thickness, and
almost unaffected by staining reagents (fig. 24, *bm.*).   Both
circular and longitudinal muscle layers are present in the
cutis.   The cutis glands are small, and stain deeply with
carmalum.   The connective-tissue layer is well marked,
becoming very strong posteriorly.   Its fibres are to a great
extent oblique.

Of the muscle layers the outer longitudinal in the
œsophageal region is more than double the thickness of the
circular layer, which in its turn is thicker than the inner
longitudinal layer.   The horizontal musculature over the
mouth is very feeble, and there is a trace of longitudinal
fibres between the alimentary canal and the proboscis sheath.
Circular fibres surround the cephalic lacunæ, and a ventral
muscle-cross occurs (fig. 18).   There is no diagonal layer.

The vascular system presents no head loop.   Instead
there is a network of lacunæ separated by fibrillated tissue
containing very large oval nuclei.   The two lateral vessels
are not formed until the brain is reached.   The dorsal vessel
does not leave the proboscis sheath until 1·2 cm. behind the
tip of the snout.

The alimentary canal is of the usual type.   The intes-
tinal diverticula commence about 2 cm. from the tip of the
snout.   A ventral gutter is well marked.

The proboscis is about 12 cm. long and very stout.
Two muscle-crosses are present (fig. 17, *mcr.*).   The epi-
thelium is in part much thickened, and contains a number of

mushroom-shaped bodies conspicuous by their deep green pigment. They appear to contain numbers of small "rhabdites." To the naked eye the proboscis shows two longitudinal deep green bands in this position. The nervous layer is considerably thickened here.

The proboscis sheath reaches to within 5 cm. of the posterior end.

The genital sacs contain nearly ripe ova.

The excretory system commences about 5 mm. from the tip of the snout, and extends over 7 mm. The excretory ducts are numerous, there being twenty-two on one side and eighteen on the other. As they pass through the circular muscle layer they show a bladder-like expansion, which disappears when they emerge into the outer longitudinal layer.

The nervous system is of the usual type, with the exception that the cephalic nerves are very strong and well marked, and are accompanied with a few ganglion cells externally (fig. 18). The median dorsal nerve stands out distinctly from the nervous layer.

The cerebral organ is very small, and to a great extent overlapped by the dorsal lobe of the dorsal ganglion, which, however, is not well marked, and does not make its appearance until after the ciliated canal has entered the brain (fig. 30, c.). The gland cells are not numerous, and a separation of a dorsal and ventral portion does not occur. The head slits are very shallow and wide.

Frontal organ and eyes are absent.

The head glands are small but compact, and appear to be merely a rather specialised portion of the deeper cutis glands.

Cerebratulus insignis, n. sp.

Two specimens of this species were procured, one of which was about 7 cm. and the other about 10 cm. long. The shape is rounded, the side folds being small but marked. The mouth is small, and the head slits are continued beyond

it as shallow depressions. A caudal appendage is present. The colour is olive-green above, becoming slightly paler below. A broad white transverse band occurs round the snout near the tip. The tip of the snout is nearly black (fig. 14).

The epithelium contains numerous greenish unicellular glands (fig. 25, *ep.*). The cutis contains the usual circular and longitudinal layers of muscle fibrillæ. Cutis glands are absent except for two longitudinal streaks anteriorly at the level of the head slits (fig. 25, *a.* and *bcgl.*). These glands do not stain appreciably with hæmalum, but take a vivid stain with eosin. The connective-tissue layer is well marked, and contains a few muscle-fibrils except beneath the cutis glands. Behind the œsophageal region there are no gland cells in the cutis.

The muscle layers are of the usual order, the outer longitudinal layer being considerably thicker than the other two together. A horizontal layer occurs over the mouth. There is no diagonal layer.

The vascular system is of the usual type, and there is a well-marked head loop.

The alimentary canal presents no special features. The dorso-ventral musculature is very weak. The ventral gutter is very small.

The proboscis is missing in both cases.

The generative organs contain immature ova.

The excretory system commences before the termination of the cerebral organ, and lies, for the whole of its short extent, entirely dorsal to the level of the side stems. The excretory duct is given off about the middle (fig. 40).

The nervous system shows no special features except that the brain lobes are rather high and short. The median nerve is indistinguishable.

The cerebral organ is large compared with the size of the brain, its extent from before backwards being rather greater than that of the brain. The dorsal lobe of the dorsal ganglion ends just as the cerebral organ commences. Dorsal and ventral glands are both well developed (fig. 29,

b—e). The organ is ovoid in shape, its dorso-ventral diameter being the larger. The head slits reach nearly to the brain.

A frontal organ is present.

Eyes are absent.

The head glands are diffuse, and soon become continuous with the cutis glands laterally.

Cerebratulus ulatiformius, n. sp.

The single specimen obtained is rather flattened throughout and about twice as wide as deep. The side folds are marked. The length is just over 6 cm. The mouth commences just behind the head slits, which end abruptly shortly before the commencement of the former. The proboscis pore is not terminal, but is found on the ventral surface 1 mm. behind the tip of the snout. No caudal appendage was observed. Colour a uniform orange-red. The name bestowed on this worm is derived from the native word "ulat," which Mr. Bedford informs me is a term applied to such creatures.

The epithelium contains small unicellular unstaining gland cells. The cutis shows the usual circular and longitudinal muscular fibrillæ. The composite cutis glands (fig. 26, $cgl.$) are well marked in the œsophageal region, but almost cease posteriorly.

The muscle layers are of the usual type, the outer longitudinal being considerably the thickest, especially laterally, where the side folds are developed. There is no diagonal muscle layer.

The vascular system shows a large well-marked head loop. The dorsal vessel leaves the proboscis sheath 2·5 mm. behind the tip of the snout.

The alimentary canal is of the usual type, the intestinal diverticula commencing about 5 mm. from the tip of the snout. The animal is remarkable in having food inside its intestine, but the remains are too problematical to make it

worth venturing a suggestion as to their origin. A ventral gutter is not present.

The proboscis is lacking.

The proboscis sheath ends rather more than 1 cm. from the posterior extremity.

The generative sacs contain nearly mature ova.

The excretory system commences before the end of the cerebral organ. The system is short, and opens by a duct on each side which passes a little dorsal to the side stem.

The nervous system is in no way remarkable. The dorsal lobe of the dorsal ganglion is large, but does not reach as far as the cerebral organ.

The cerebral organ is short, and the dorsal glands are not strongly developed (fig. 34, a—d).

The frontal organ is well marked.

Eyes are not present.

The head glands are fairly strong, and reach backwards about halfway to the brain, where they end abruptly.

Before bringing this paper to a close it may be as well briefly to summarise the points of more general interest which have arisen in connection with this collection.

(1) A considerable amount of variation occurs in the striking and characteristically marked Eupolia melanogramma, and such variation appears to be continuous rather than discontinuous.

(2) The excretory system of E. melanogramma possesses the hitherto unique feature of ducts opening into the alimentary canal.

(3) In E. pholidota the excretory ducts reach back into the intestinal region, thus co-existing in the same region with the gonidial ducts. Histological evidence tends to show that these two sets of ducts are not homodynamous.

(4) In the same genus (Eupolia) the lateral nerve-stems may form a commissure either above or below the anus, or else may end blindly.

(5) In the Lineidæ great variations occur in the range and topography of the excretory system, and also in the number of ducts. Neither here nor in the Eupoliidæ is to be found that incipient metamerism of the ducts which Oudemans claims to have shown.

(6) The vascular system of the Lineidæ shows but little variation in the different species, except in so far as in the precerebral region there may be either a well-marked head loop or else a vascular network—a fact already pointed out by Bürger. It is worthy of note that there appears to be some correlation between the extent of the excretory system and the point of exit of the dorsal vessel from the proboscis sheath. The vessel in all the species here described (except in one case where the preservation was not sufficiently good to determine this point) leaves the sheath within a few micromillimetres of the hinder termination of the excretory system wherever the ducts of the latter may be situated (cf. figs. 35—42).

(7) The frontal organ which characterises the Lineidæ is not always present.

(8) The structure of the cerebral organ and of the cutis is characteristic for the different species.

Gatby Marine Laboratory,
St. Andrews, N.B.;
March, 1900.

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EXPLANATION OF PLATES 5—8,

Illustrating Mr. R. C. Punnett's paper "On a Collection of Nemerteans from Singapore."

Reference Letters.

ac. Anal commissure. *al.* Alimentary canal. *blv.* Buccal vessel. *blvc.* Commissure of buccal vessels. *blc.* Blood lacuna of cerebral organ. *bm.* Basement membrane. *c.* Cutis. *cap.* Caudal appendage. *cc.* Ciliated canal of cerebral organ. *cgl.* Cutis glands. *corg.* Cerebral organ. *cu.* Connective-tissue layer of cutis. *dbv.* Dorsal blood-vessel. *dc.* Dorsal commissure. *ddg.* Dorsal division of dorsal ganglion. *dg.* Dorsal ganglion. *ep.* Epithelium. *exd.* Excretory duct. *exdi.* Internal excretory duct. *ext.* Excretory tubule. *fc.* Fibrous core of cerebral organ. *fuc.* Fibrous core of side stem. *fr.* Frontal organ. *g.* Ganglion cells. *gcu.* Gelatinous connective-tissue layer of cutis. *gcorg.* Gland-cells of cerebral organ. *gd.* Genital duct. *go.* Glandular layer of œsophagus. *hf.* Head furrow. *hg.* Head glands. *hl.* Cephalic lacuna. *hs.* Head slit. *id.* Intestinal diverticulum. *lbv.* Lateral blood-vessel. *m.* Mouth. *mc.* Circular muscle layer. *mcc.* Circular muscles of cutis. *mcn.* Muscle-fibres and connective tissue. *mcr.* Muscle-cross. *ml.* Longitudinal muscles of proboscis sheath. *mlc.* Longitudinal muscles of cutis. *mli.* Inner longitudinal muscle layer. *mlo.* Outer longitudinal muscle layer. *nc.* Lateral nerve-cord. *nd.* Dorsal median nerve. *nep.* Subepithelial nervous layer. *nh.* Cephalic nerves. *ns.* Nervous sheath. *ol.* Œsophageal lacunæ. *ps.* Proboscis sheath. *r.* Rectum. *rhc.* Rhynchocœlom. *t.* Testis. *tbv.* Transverse blood-vessel. *tg.* Glandular (?) tissue round cephalic lacunæ. *vc.* Ventral commissure. *vdg.* Ventral division of dorsal ganglion. *vg.* Ventral ganglion. *vgr.* Ventral groove. *vgt.* Ventral gutter of intestine.

FIG. 1, *a—d*.—Eupolia melanogramma. Transverse sections, illustrating the arrangement of the blood-vessels in the region of the brain.   × 45.

FIG. 2.—E. melanogramma. Portion of a transverse section, showing an excretory tubule opening into the œsophagus.   × 110.

FIG. 3.—E. melanogramma. Showing an excretory duct piercing the lateral nerve-cord.   × 110.

FIG. 4.—E. melanogramma. Transverse section, showing ventral position of anal commissure.   × 60.

FIG. 5.—E. melanogramma. Transverse section of body-wall in œsophageal region.   × 110.

FIG. 6.—E. pholidota. Transverse section through brain just behind the commissures.   × 45.

FIG. 6*a*.—E. pholidota. Transverse section through cerebral organ and neighbouring structures.   × 45.

FIG. 7.—E. pholidota. Dorsal view of anterior end.   × 2.

FIG. 8.—E. pholidota. Transverse section through outer body-wall in the œsophageal region.   × 160.

FIG. 9.—E. pholidota. Transverse section through anterior portion of intestinal region.   × 45.

FIG. 10.—E. pholidota. Portion of a section from about the same level as the preceding, but more highly magnified.   ×

FIG. 11.—Cerebratulus natans. From spirit specimen. Natural size.

FIG. 12.—C. natans. Anterior extremity, showing pigment patches. From a formol specimen. Natural size.

FIG. 13.—C. natans. Transverse section of proboscis.   × 45.

FIG. 14.—C. insignis. Anterior end.   × $\frac{5}{2}$.

FIG. 15.—C. natans. Transverse section through intestinal region. × 32.

FIG. 16.—C. robustus. Section through one of the œsophageal folds.   × 110.

FIG. 17.—C. bedfordii. Transverse section through proboscis.   × 45.

FIG. 18.—C. bedfordii. Section through snout.   × 45.

FIGS. 19—26. Sections through the outer portion of the body-wall in the œsophageal region. All × 160.

    Fig. 19.—C. brunneus.

    Fig. 20.—C. robustus.

    Fig. 21.—C. natans.

    Fig. 22.—C. erythrus.

    Fig. 23.—C. sordidus.

Fig. 24.—C. bedfordii.

Fig. 25.—C. insignis.

Fig. 26.—C. ulatiformius.

FIGS. 27—34.—Sections taken at intervals of 50 μ through the cerebral organs of the above species.   All × 45.

Fig. 27.—C. brunneus.

Fig. 28.—C. natans.

Fig. 29.—C. insignis.

Fig. 30.—C. bedfordii.

Fig. 31.—C. robustus.

Fig. 32.—C. sordidus.

Fig. 33.—C. erythrus.

Fig. 34.—C. ulatiformius.

FIGS. 35—42.—Diagrammatic reconstructions of the various systems in the anterior of the body in the above members of the Lineidæ.   All × 10.   The proboscis and sheath are omitted.

Fig. 35.—C. brunneus.

Fig. 36.—C. bedfordii.

Fig. 37.—C. natans.

Fig. 38.—C. robustus.

Fig. 39.—C. ulatiformius.

Fig. 40.—C. insignis.

Fig. 41.—C. sordidus.

Fig. 42.—C. erythrus.

Fig. 1ᵃ

Fig. 1ᵇ

Fig.
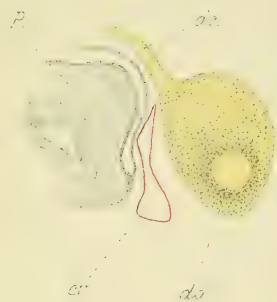
Fig. 2.

Fig. 3.

Fig. 4.

Fig. 8.

Fig.
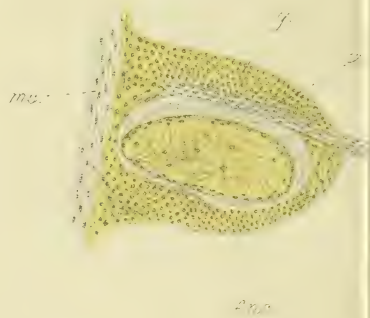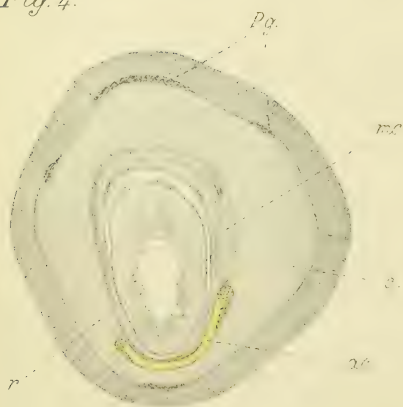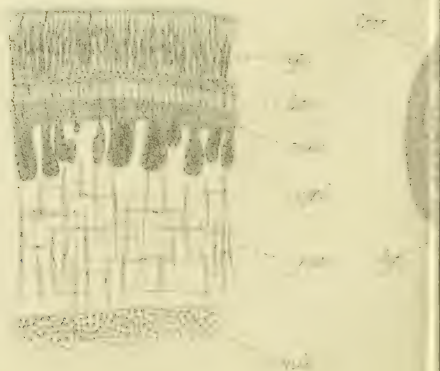
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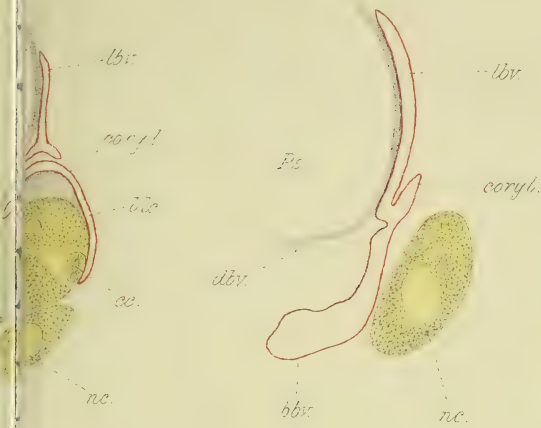
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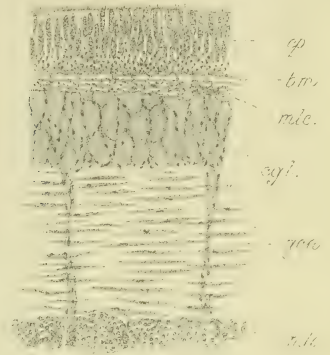
Fig. 6.ᵃ

Fig. 7.

Fig. 9.

Fig.10.

Fig.14.

t.

*

n.li.

gd.

m.lo.

e.rd.

m.c.

n.c.

n.c.

Fig.13.

ep.¹

Fig.12.

h.s.

h.s.

Fig.11.

r.s.

m.f.

m.an.

Fig.15.

var.

cap.

ol.

g.

ci
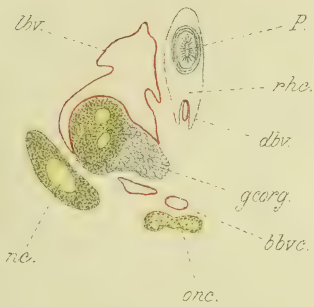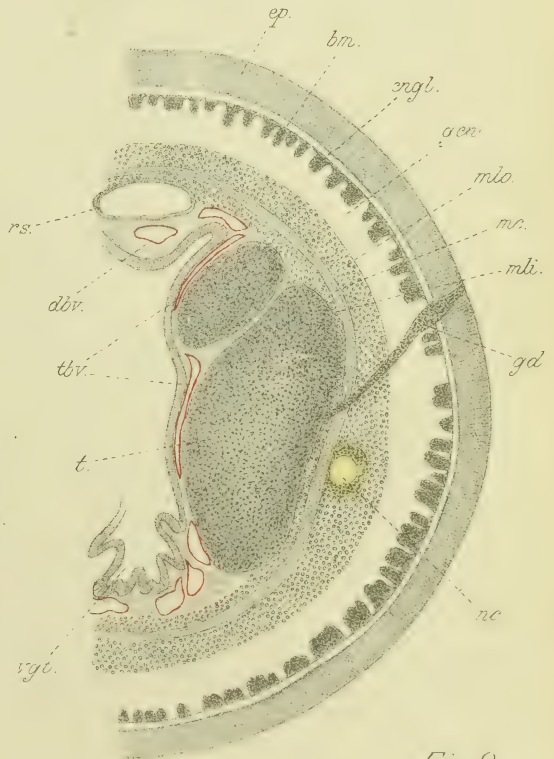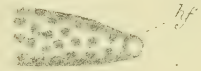
Fig. 15.

Fig. 17.
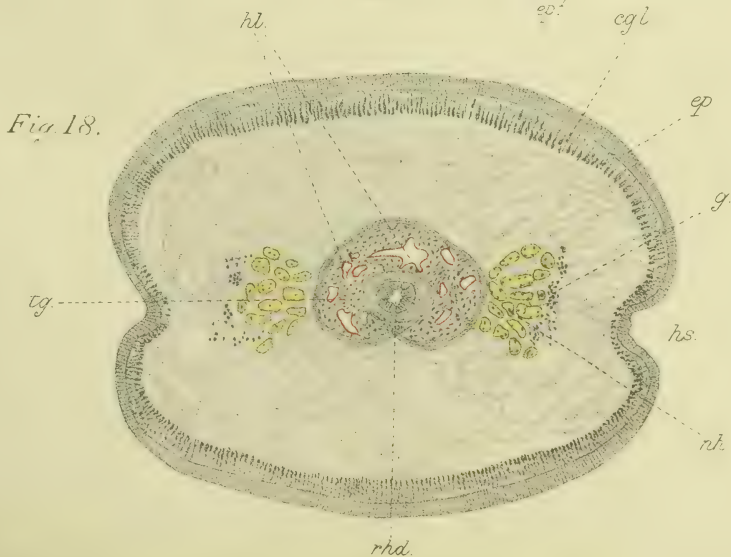
Fig. 18.

Fig. 19.
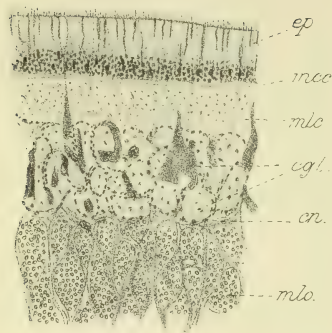
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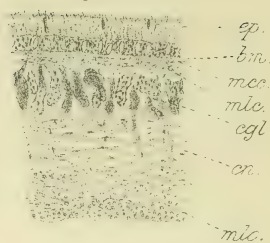
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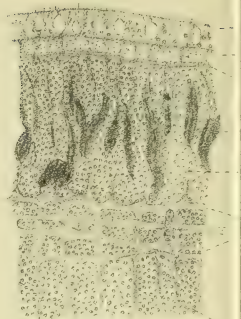
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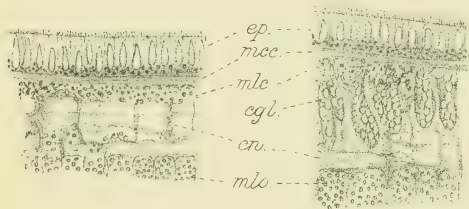
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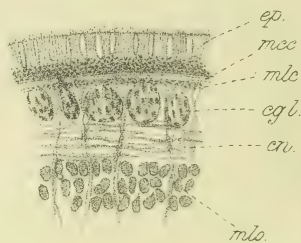
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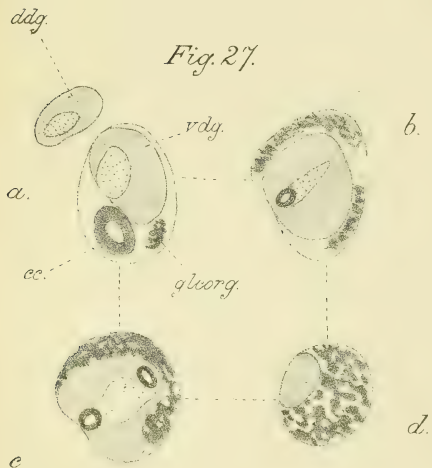
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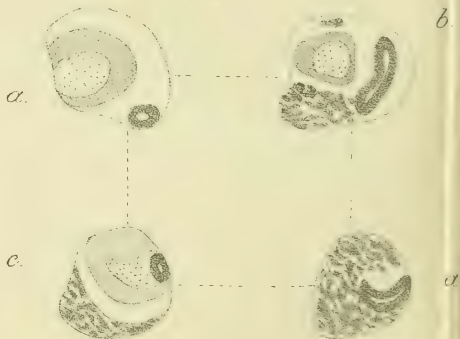
Fig. 34.

Fig. 22.
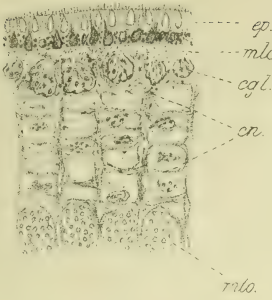
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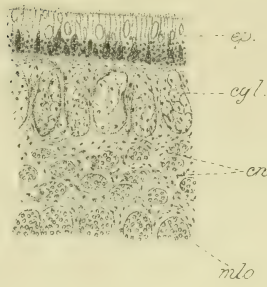
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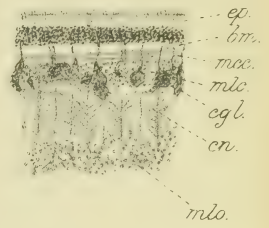
Fig. 29.

Fig. 30.

Fig. 31.
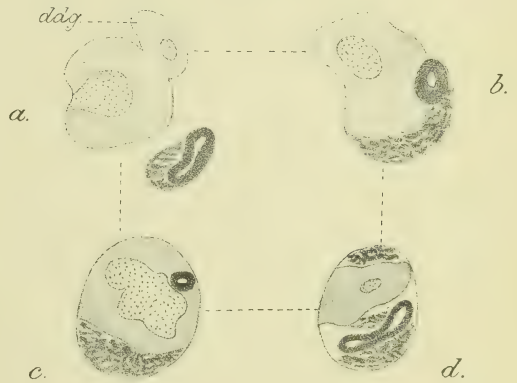
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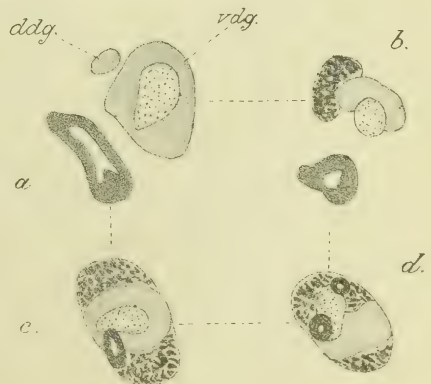
Fig. 33.
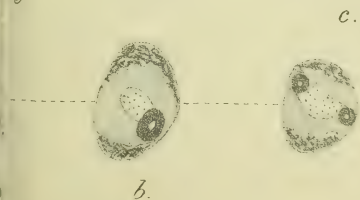
C. brunneus.

Fig. 35.
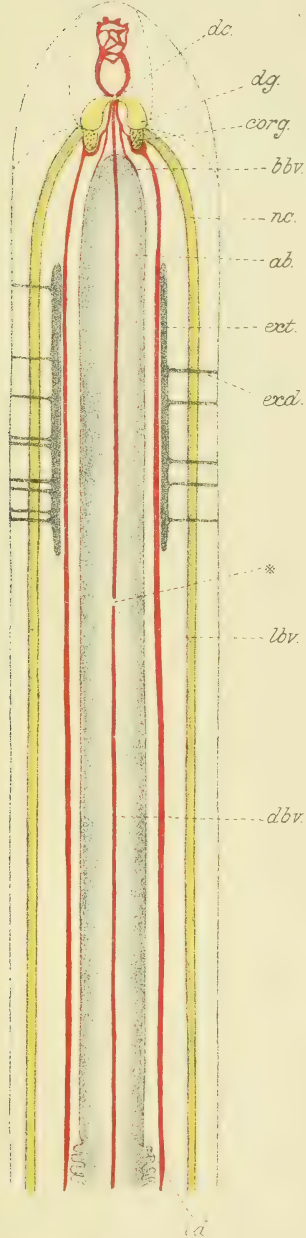
C. bedfordii.

Fig. 36.
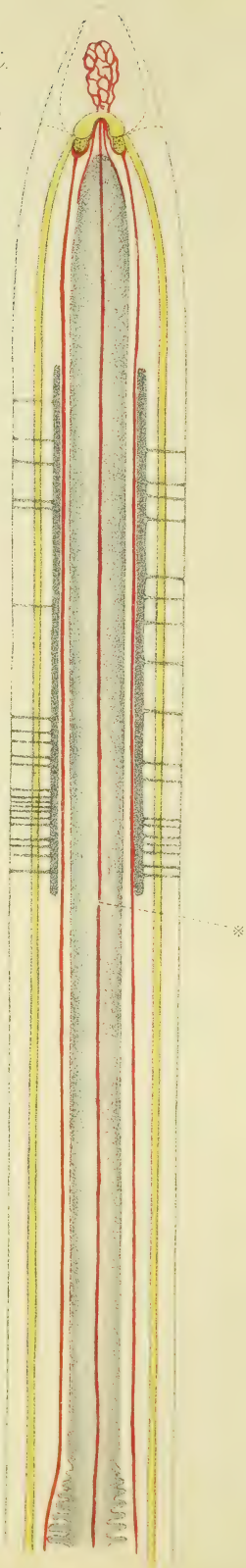
C. natans.

Fig. 37.
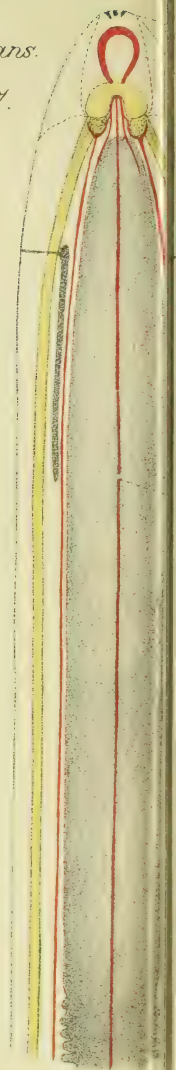
C. ulatiformius.

Fig. 39.

dc.
dg.
corg.
bbv.
nc.
ab.
ext.
exd.
*
lbv.
dbv.
a
*

C. robustus

Fig. 38.

C. sordidus.

Fig. 41.

C. erythrus.

Fig. 42.

C. insignis.

Fig. 40.

On the Protostigmata of Molgula manhattensis (De Kay).[1]

By

Arthur Willey.

With Plate 9.

INTRODUCTION.

IN the case of several species of simple Ascidians with relatively alecithal eggs, it is known that the larva, at or about the time of fixation, possesses two pairs of gill-clefts or primary branchial stigmata. The period during which the stigmatic system of the young Ascidian is represented by these two pairs of clefts alone may be one of considerable duration, thus constituting a definite stage of development. This is succeeded by another well-marked stage, characterised by the presence not of three but of four stig-

[1] Molgula manhattensis is one of the commonest Ascidians on the coast of New England. Whereas other Ascidians are eclectic in their distribution, this species, as Verrill and Smith ('Report upon the Invertebrate Animals of Vineyard Sound,' Washington, 1874) have shown, is at home in all kinds of places. In New Bedford it occurs or occurred in large clusters on the piles of a wharf. I sent specimens to Professor Herdman, who has kindly informed me that he is satisfied that they are true Molgulæ. The species is the Molgula manhattensis of American authors, and the generic name Bostrichobranchus, given to it by Traustedt, must rest upon some misunderstanding which ought to be cleared up. Professor Herdman suggests (in lit.) that the specific name manhattensis may be misapplied. It may be so, but I think the burden of proof rests upon the author of the genus Bostrichobranchus.

There should be no doubt concerning such a common and easily obtainable Ascidian.

mata on each side of the pharynx. In the next stage there are five pairs of stigmata; and, finally, the last stage of the infantile or nepionic period of development is heralded by the appearance of a sixth pair.

The primary branchial stigmata become greatly drawn out in the transverse direction (i. e. dorso-ventrally), and eventually become subdivided to form secondary branchial stigmata, which, in their turn, undergo elongation in the longitudinal direction, and again become subdivided to form the tertiary branchial stigmata of the adult.

In some cases, therefore, it is highly probable that the entire stigmatic system of the adult is derived by subdivision from six pairs of primary branchial stigmata.

Thus the nepionic period of development comprises four stages, which it is necessary to particularise, because each of them requires or may require separate morphological treatment; and, moreover, young Ascidians in one or other of these stages may be collected in the open, and so constitute specimens requiring diagnosis.

The stages may be named and tabulated as follows, attention being again drawn to the singular absence of a stage presenting three pairs of stigmata :

Nepionic period . . . $\begin{cases} \text{1. Distigmatic stage.} \\ \text{2. Tetrastigmatic stage.} \\ \text{3. Pentastigmatic \quad ,,} \\ \text{4. Hexastigmatic \quad ,,} \end{cases}$

Young Ascidians may often be collected in the hexastigmatic stage. It is often difficult to know what is meant by stages of development, but it is not difficult in this case, the stages being quite definite.

The above enumeration of stages refers to species belonging to the family Ascidiidæ, and also, as I shall proceed to show, to at least one member of the Molgulidæ. The table does not apply to such forms as Perophora, Clavelina, Distaplia, etc., where, as shown (and the observation is capable of ready confirmation) by the researches of Giard (1872),

Seeliger (1885), and Lahille (1890), the rule is that the definite stigmata arise each by separate perforation of the pharyngeal wall.

A method of formation of the stigmata intermediate in character between that followed by a form like Ciona on the one hand, and Clavelina on the other, is afforded by Botryllus, as shown by Mr. Garstang, to whose researches I shall again refer.

Meanwhile I pass on to a brief recapitulation of my previous

Observations on Ciona intestinalis.[1]

1. Distigmatic Stage.—I could not detect any difference in the time and manner of formation of the two protostigmata which characterise this stage. They appeared to me to arise simultaneously, and to resemble one another in all respects. Accordingly, to account for this similarity and simultaneity, I suggested a certain interpretation (namely, the precocious subdivision of a single branchial pouch) which I do not relinquish, but do not now wish to press further.

In a recent publication Professor Julin[2] dissents from my version of affairs regarding this stage. As he reserves full details for a future occasion it is not desirable to enter upon an extended discussion, and I will only touch upon one point. M. Julin states definitely that the stage now under consideration is preceded by a stage in which only one pair of primary stigmata is present; in other words, that the two pairs of stigmata which characterise this stage do not arise simultaneously, but one after the other.

These two pairs of stigmata arise before the change of axis of the body of the larva (which ensues after fixation) has

[1] See this Journal, vol. 34, January, 1893, p. 317; also in 'Proc. Roy. Soc.,' vol. li, 1892, p. 513.

[2] Charles Julin, 1899, "Contribution à l'histoire phylogénétique des Tuniciers;" "Recherches sur le développement du péricarde, du cœur, et les transformations de l'épicarde chez les Ascidies simples;" 'Miscellanées biologiques,' Trav. Stat. Zool. Wimereaux, t. vii, see p. 336.

taken place; and the consequence is that they do not at first occur one behind the other in the longitudinal direction along lines parallel to the longitudinal axis of the larva, but they lie somewhat obliquely in a subvertical or dorso-ventral direction, one being dorsad of the other, i. e. one of them is nearer the oral or dorsal side of the body, while the other is nearer the ventral side (cf. my Pl. 30, fig. 2, op. cit.).

The figures 1 to 5 on pl. xxi of M. Julin's memoir (op. cit.) represent transverse sections through a tailed larva of Ciona intestinalis, preserved fifteen hours after hatching. This larva is described as possessing one pair only of primary branchial stigmata, in the form of a nearly transverse branchial tube on each side, opening by an internal aperture into the pharynx and by an external orifice to the exterior. This branchial tube is regarded by M. Julin as the primordium of the corresponding half of the peribranchial chamber.

In M. Julin's fig. 1 the right branchial tube is seen to open internally at the extreme dorso-lateral angle of the pharynx, whereas in fig. 2, which we are told represents the next section in the series, it passes through the external (atrial) orifice of the right side, and the same branchial tube opens internally through the middle of the wall of the pharynx i. e. at quite a different (lower) level. I cannot understand how the right internal orifice of the branchial tube shown in M. Julin's fig. 2 can be identical with the right internal orifice of fig. 1. Remembering the primary axial relations of the two first-formed stigmata, and their slightly oblique position, one being below and somewhat behind the other, I should rather interpret M. Julin's figs. 1 and 2 as passing respectively through the two branchial stigmata of the right side, these stigmata in their turn communicating with the exterior by way of the right atrial chamber.

It will soon be evident that the two first-formed stigmata have identical properties and identical fates, thereby creating a strong presumption in favour of the identity of their origin.

The distigmatic stage of Phallusia mammillata was described by Krohn ('Müller's Archiv,' 1852), who also ad-

mitted the simultaneous origin of the two first-formed gill-clefts.

2. Tetrastigmatic Stage.—This stage has been observed by Krohn (1852) for Phallusia mammillata, by Ed. van Beneden and Julin (1884) for Ascidiella scabroides, and by me (1892) for Ciona intestinalis, and again (1893) for Molgula manhattensis (see below).

The inauguration of this stage or the transition from the preceding to this had not been observed before my account of the process in Ciona.

The ventral ends of the two primordial stigmata of each side bend towards one another, and their walls even come into contact; each of them, then, forms by constriction a small diverticulum, that from the first stigma being directed backwards, and that from the second stigma forwards. The two diverticula from the primordial stigmata thus come to lie in the primary interstigmatic space and are finally cut off from the parent stigmata. In this quite unexpected way is the tetrastigmatic stage of Ciona intestinalis introduced.

The second stigma of the distigmatic stage becomes, after the abstriction of the two intercalary stigmata, the fourth of the series of protostigmata in the present stage.

3 and 4. Penta- and Hexastigmatic Stages.—These can be considered together, because in Ciona intestinalis the fifth and sixth protostigmata arise successively by independent perforation. A pentastigmatic stage was described by Krohn for Phallusia mammillata and a hexastigmatic stage by van Beneden and Julin for Ascidiella scabroides.

The description of the hexastigmatic stage of the last-named species given by van Beneden and Julin was the only one with which I could compare the corresponding stage observed by me in Ciona. In making the comparison I was influenced by Krohn's statements regarding Phallusia mammillata, and consequently assumed too great a uniformity in the method of formation of the protostigmata of simple Ascidians.

Van Beneden and Julin found that the protostigmata of Ascidiella scabroides were of unequal and irregular sizes,

and thought it probable that the size of the stigmata was an indication of their order of formation. It may or it may not be so in this particular case, but nothing can be affirmed without special investigation.

In his valuable "Étude de la branchie chez Ascidiella scabroides," M. de Selys Longchamps [1] criticises my statements concerning the independent perforation of protostigmata V and VI in Ciona. He says (p. 121):

"En fait, rien n'est plus difficile que d'établir qu'un stigmate est né par perforation; je me demande même sur quel fait positif Willey se base, pour attribuer une origine indépendante aux protostigmates V et VI chez Ciona."

To this I can reply that, apart from the general conviction resulting from the comparison of numerous specimens, the positive observation which demonstrated to me the fact of the independent perforation of protostigma V is illustrated in my Pl. XXX, fig. 14 (op. cit.). Here it will be seen that the ventral ends of the protostigmata I and IV are inclined respectively towards their derivatives II and III, while V appears as a minute perforation apart, and is later followed by VI without any indication of abstriction.

Moreover Molgula manhattensis will afford collateral evidence in corroboration of my former account of Ciona.

5. Adolescent Period.—If it be thought useful to recognise different periods of development it is necessary to be precise. Fortunately this is comparatively easy with the simple Ascidians, which exhibit five well-marked periods, namely:—1. Embryonic. 2. Larval. 3. Nepionic. 4. Adolescent. 5. Adult.

The nepionic period obviously commences with the fixation of the larva, but there is a slight difficulty as to its termination, due to the fact that there is no such abrupt contrast between the nepionic and adolescent periods as there is between the former and the larval period. It is a question whether it should be regarded as ending with the establishment of the six protostigmata or with the subdivision of these

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[1] 'Archives de Biologie,' xvi, 1899, pp. 117—171.

to form six rows of secondary branchial stigmata.   I take the latter view, while recognising its arbitrary nature.

The adolescent period would then be inaugurated by the change in the long axis of the secondary stigmata (cf. my pl. xxxi, fig. 18, op. cit.), and characterised by the formation, by subdivision from the secondary stigmata, of the definitive or tertiary branchial stigmata; and by the development of the reproductive organs from the genital primordium.

It is satisfactory to note that collateral evidence in confirmation of the account which I gave (1) as to the increase in the number of stigmata in a transverse row, and (2) as to the increase in the number of transverse rows in Ciona, has been forthcoming on the part of M. de Selys Longchamps[1] in respect of Ascidiella scabroides:—" La règle générale est la même ici que chez Ciona intestinalis; tout nouveau stigmate d'une rangée n'est autre chose qu'une partie séparée d'un stigmate préexistant." And again :—" L'augmentation du nombre des rangées transversales de stigmates ne résulte pas de l'apparition de rangées nouvelles entre les rangées préexistantes, mais du dédoublement de ces rangées préexistantes, ainsi que Willey l'a décrit et représenté fig. 22, chez Ciona."

The formation of the intercalary stigmata in a transverse row of Ascidiella scabroides as described by de Selys Longchamps differs in detail from the method which prevails in Ciona in that minute diverticula are budded off from the ends of the pre-existing stigmata in a manner which strikingly recalls the mode of origin of protostigmata II and III in Ciona.[2]

OBSERVATIONS ON MOLGULA MANHATTENSIS.

My observations on Molgula manhattensis were made during the long vacation of 1893, in the Marine Biological Laboratory at Woods Holl, Mass., where I was privileged to

[1] Op. cit., pp. 124—126.
   De Selys Longchamps, op. cit., pl. viii, figs. 5—7.

occupy a table. I collected the material myself in the company of a friend from the piles of a wharf at New Bedford.

All the nepionic stages of Ciona, which I observed at Naples, were reared in jars from artificially fertilised eggs ; those of Molgula manhattensis were collected in the open. I gave the gist of my observations on the protostigmata of the latter species in the book entitled 'Amphioxus and the Ancestry of the Vertebrates,'[1] which I prepared for the Columbia University Biological Series, and intended to let that suffice. For various reasons, however, I have come to the conclusion that it would be desirable to furnish further details, and that is the object of the present contribution.

As previously noted by Kingsley,[2] this species is viviparous, in so far that the embryonic development, during which the embryo is surrounded by the follicular membrane, takes place within the peribranchial chamber of the parent.

In the urodele larva the organ of fixation assumes the form of a hollow lobe at the anterior end of the body, much as in Ciona, where I identified it as a præoral lobe. The main body of the larva is so opaque that the internal structures cannot be made out in any detail without sections. I could not see the buccal and atrial orifices in the larva before fixation ; but after fixation there appeared, in addition to the buccal orifice, a single median atrial siphon. It would be interesting to have it established exactly at what moment the mouth breaks through, since this crucial event appears to vary in relative time of occurrence in different species. In another Molgulid, Lithonephria eugyranda Giard, Julin[3] finds that the mouth is formed long before the hatching of the larva.

In the larva of M. manhattensis, at the time of fixation, the præoral lobe elongates as a stolon-like tube, and at the

[1] 1894, see pp. 232—233.

[2] J. S. Kingsley, "Some Points in the Development of Molgula manhattensis," 'Proc. Boston Soc. Nat. Hist.,' xxi, 1882, pp. 441—451. The account of the segmentation stages was erroneous.

[3] Op. cit., see pp. 355–6.

same time three or four hollow ectodermic processes grow out at different points from the main body, and project into the test (cf. Pl. 9, fig. 3). These processes are contractile, and their somewhat dilated extremities may sometimes be seen to execute a prominent systole; they are still to be seen at the end of the nepionic period (fig. 12).

Under certain imperfectly known circumstances the larva may undergo a portion of its metamorphosis while still enclosed within the follicle, so that it passes through no freeswimming stage.[1]

I am quite unable to say whether such precocious metamorphosis is a normal variant, but even if it is a teratological phenomenon it is of some interest, and would have a more definite significance if (1) the exact circumstances under which it takes place were determined, and (2) it were ascertained whether any of the individuals attained maturity.

In fig. 2 a larva is shown whose tail is in regression within the follicle. One point of special interest in this larva is the great development of the præoral lobe (organ of fixation), which extends as a hollow tube containing loose mesenchyme, close beneath the follicular membrane between the latter and the embryo. In this position it appears likely that it would fulfil a respiratory function, since I observed it to contract and expand. In the same larva (fig. 2) there were two round pigmented bodies in the larval brain. Often only one spot is present; one only was observed by Kingsley in this species, and one by Julin in Lithonephria. I found reason for supposing that the presence of two spots might be due to the fragmentation of a single one. What has been

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[1] This indication of precocious metamorphosis is of importance in comparison with the development of other Molgulids, in which, according to the observations of Lacaze-Duthiers and Kupffer, the urodele stage is omitted from the ontogeny. It also recalls to my mind some experiments which I made on species of Styelidæ some years ago, when I succeeded in hastening the preliminary stages of the metamorphosis by cutting off the tails of the larvæ. [A. Willey, "Report on the Occupation of the Table of the British Association at the Marine Biological Laboratory, Plymouth, during August and September, 1891," 'Rep. Brit. Ass. (Edinburgh),' 1892.]

said is enough to show that the larva of Molgula manhattensis is well worth further study, and the teratological side should not be neglected. I now pass on to the description of the nepionic stages, which is the special purpose of this paper.

1. Distigmatic Stage (Pl. 9, fig. 3).—Owing to the opacity of the larvæ the earliest stage at which the two first-formed stigmata could be recognised is that which is represented in fig. 3. In this case the details of the neuro-hypophysial system could not be made out in the object viewed as a whole. It is noteworthy that we have here a median dorsal atrial aperture in place of paired apertures, an observation which accords with that of Julin on Lithonephria.

Now if we follow the growth of the two stigmata, which we may distinguish by the letters A and B, we find that they increase in size principally in the dorso-ventral direction, A being generally somewhat in advance of B (fig. 4). Having attained a certain transverse diameter, their ventral ends (i. e. the ends directed towards the endostyle) become bent backwards towards the fundus of the pharynx (fig. 5). Next the recurved ventral ends of the stigmata A and B double round in the dorsal direction so that each of the originally simple clefts become biramous, having a larger anterior and a smaller posterior arm (figs. 6 and 7).

2. Tetrastigmatic Stage (fig. 8).—A young Molgula manhattensis collected in the open is shown in fig. 8, illustrating the commencement of the tetrastigmatic stage.

Here we note that the posterior arm of stigma A has become separated by constriction from the parent cleft, while in the case of B the abstriction of its posterior arm has not yet taken place. This specimen was fortunately in a state of complete expansion when the sketch was taken, and it presents the facies of a typical Ascidian. I took special pains to note that the stigmata were in precisely the same condition on the right side as that in which they are here represented to be on the left.

The fact that the growth of stigma A is in advance of that of B is a detail of some interest in comparison with the behaviour of the homologous stigmata in Ciona intestinalis, where B tended to take the priority of A.

Thus stigmata A and B produce by abstriction two new stigmata, C and D. These latter arise, as the figures show, not in the form of minute diverticula of A and B, as is the case in Ciona, but as large reduplications equal in longitudinal diameter to the parent clefts, though less in their transverse (dorso-ventral) diameter. Moreover, whereas in Ciona the stigma D was the third in the definitive series of protostigmata, here it becomes the fourth of the series, owing to the fact that its abstriction from B takes place in the opposite direction to that observed for Ciona.

3. Pentastigmatic Stage.—I regret that among the drawings which I still possess relating to M. manhattensis I can find none illustrating this stage, so that I must refer to the composite diagram reproduced on Pl. 9, fig. 10, which was drawn at the time that the observations were made in 1893.[1]

After the establishment of the tetrastigmatic stage by the abstriction of C and D from A and B, a fifth protostigma, E, arises by independent perforation. In M. manhattensis, by observing many specimens, noting the curvature of the already formed stigmata (cf. fig. 11), and seeing a new stigma at its first appearance as a minute perforated disc, it is possible to demonstrate beyond reasonable doubt that the fifth protostigma is formed independently of the rest. This being the case, it is the more singular to find that the fifth protostigma, E, subsequently behaves in exactly the same manner as A and B did, namely, it doubles round upon itself at its ventral end, and the recurved arm is the primordium of the sixth and last protostigma, F.

4. Hexastigmatic Stage (Pl. 9, figs. 11 and 12).—The appearance of the protostigmata shortly after the abstriction of the sixth from the fifth (F from E) is shown in fig. 11.   Here it

[1] Cf. 'Amphioxus and the Ancestry of the Vertebrates,' 1894, pp. 232–3.

is to be noted that while the primitive relations of each couple of stigmata are indicated by the slight curvature of their ventral ends, yet the actual order of their formation could not be deduced from their appearance and size. For example, D appears larger than B, from which it in reality was derived.

A later condition of the protostigmata is shown clearly in the specimen represented in fig. 12. Here we still see the long-drawn-out dorso-ventral clefts, but the first one has undergone subdivision into four approximately equal secondary branchial stigmata. The method of division by the growth of a tongue-like projection across the primitive cleft is shown in fig. 13.

The vascular trabeculæ, which traverse the wall of the pharynx in the longitudinal direction, pass across the protostigmata independently of the tongue-like bridges which subdivide them. In the specimen represented in fig. 12, only the first protostigma is subdivided, but there were four longitudinal vascular trabeculæ passing from the buccal region to the fundus of the pharynx, crossing over the stigmata, and, in the case of the first stigma, not corresponding with the true subdivisions of the cleft. They have been omitted from the lithographed drawing for the sake of clearness.

It should further be noted that at the time when the first protostigma is subdivided, the sixth is still quite small. I am unable to say whether any fresh perforation occurs after the formation of the series of protostigmata, but certainly the bulk of the secondary branchial stigmata arise by subdivision of and abstriction from the protostigmata.

The transverse rows of secondary stigmata do not long retain the simple form which they present in fig. 12. They soon become arched in the manner shown in fig. 14, where it is seen that the concavities of the arches face one another. Next occurs the abstriction of small tertiary stigmata, which take part in the formation of the intercalary rows (fig. 15). Finally, by differential growth, the stigmata gradually assume the spiral disposition which is so characteristic of the Molgu- loid pharynx.

I desire to lay special stress upon the protostigmata A, B, C, and D.   It is often difficult to distinguish between an actual observation and an interpretation of one.   There is not the slightest doubt in the world that the origin of the protostigmata C and D from A and B in Molgula manhattensis takes place in the manner described in the preceding lines.

There are perhaps two main points of interest which are brought out by comparing the protostigmata of M. manhattensis with those of Ciona intestinalis.   The first is a question of homology, and the second is one of homodynamy. The stigma D is the third protostigma in C. intestinalis and the fourth in M. manhattensis.   It arises from abstriction from B in both cases, but in reversed senses.   We have, therefore, here a special instance of enantiomorphism.

The point of homodynamy relates to the two protostigmata which are the first to be formed, namely A and B.   In my judgment the behaviour of these clefts both in Ciona and Molgula, and also in Phallusia, shows them clearly to be homodynamous formations.   Protostigma A is obviously homodynamous with protostigma B.   This is my contention, but it is not the opinion of Professor Julin.

In the work to which reference has already been made (above, p. 143) M. Julin, in developing an idea previously expressed by him in conjunction with Professor E. van Beneden (1887), maintains that the first primary branchial stigma is quite distinct in its origin and fate from the second, being essentially concerned, in its capacity of branchial pouch, with the formation of the peribranchial chamber.   According to Julin,[1] the peribranchial chamber is essentially formed by dilatation of the walls of the first pair of primary branchial stigmata, and the part taken by the atrial involutions is quite subordinate, if not altogether negligible.

[1] It should be stated that M. Julin's observations relate principally to Ciona intestinalis, Lithonephria eugyranda, and Styelopsis grossularia.   In the last two species there is at no stage a paired atrium, the cloacal aperture being unpaired and median from the beginning.   I do not attempt to contradict his observations on these species, but his interpretation is open to discussion.

M. Julin's work overlaps mine in regard to Ciona intes-
tinalis, and it follows inevitably from his statements, although
he does not say it in so many words, that protostigma A is
not homodynamous with protostigma B. I think these two
protostigmata are homodynamous structures, and that is how
the matter rests.

The comparison of the protostigmata in M. manhattensis
and C. intestinalis may be tabulated as follows, the stig-
mata being denoted by Roman numerals in their serial, and
by capital letters in their individual capacities :

Protostigmata.	Ciona intestinalis.	Molgula manhattensis.
I	A	A
II	C	C
III	D	B
IV	B	D
V	E	E
VI	F	F

GARSTANG'S OBSERVATIONS ON BOTRYLLUS.[1]

If it is desired to form any idea as to the probability of one
method of formation of the branchial stigmata of Ascidians
having a more primitive character than another, it is necessary
to take note of Garstang's observations on the formation of
the stigmata in the oozoid and blastozoid of Botryllus.
Reference has been made above (p. 142) to the known fact
that in Clavelina and other Ascidians the definitive stigmata
arise by separate perforations, without the intervention of
protostigmata. Here, therefore, we have two different methods
to consider, and to decide between them which is the more
primitive. The question can only be approached from a basis
of probability, and in this sense it has been answered un-
equivocally by Garstang to the effect that the formation of
protostigmata is a primitive character. Garstang found that

[1] W. Garstang, "On the Development of the Stigmata in Ascidians,"
'Proc. Roy. Soc.,' vol. lii, 1892, p. 505. In this paper the term protostig-
mata was first introduced.

in the oozoid of Botryllus the definite stigmata were pre-
ceded by protostigmata, while in the blastozoid protostigmata
were never formed in any generation of buds, but the definite
stigmata arose separately as small rounded perforations.

The earliest stage observed by Garstang was the tetrastig-
matic stage. He describes (loc. cit., p. 509) the pharynx as
being provided with "four pairs of transversely elongated
stigmata, whose transverse diameters are nine times as great
as their antero-posterior diameters. . . . . They are not
exactly of equal size, but decrease slightly in width in regular
order from before backwards."

In the next stage observed "the pharynx possesses, in
place of the four pairs of transversely elongated stigmata,
four transverse rows of small stigmata on each side." Even-
tually a fifth row is added. Garstang further remarks (p. 510)
that "the primary stigmata—if an inference may be drawn
from their relative sizes—arise one after another in regular
order from before backwards, and that they are subsequently
subdivided in the same order." If this is so—and it seems
probable that it is so—we should have the following sequence
in Botryllus to be compared with the table given above
on the preceding page:

I	.	.	.	.	.	A
II	.	.	.	.	.	B
III	.	.	.	.	.	C
IV	.	.	.	.	.	D
V	.	.	.	.	.	E

Having decided that protostigmata are primitive, the dis-
cussion becomes narrowed down to a consideration of the proto-
stigmata themselves. The logic is simple, but of course not
demonstrative. Protostigmata are primitive; the origin of the
definite stigmata by subdivision of protostigmata is indirect as
compared with the direct method of independent perforation;
the formation of protostigmata by abstriction is indirect as com-
pared with the direct perforation in regular order from before
backwards, which probably occurs in Botryllus; therefore

the formation of protostigmata by abstriction is probably primitive. From this point of view it may be concluded that subdivision of protostigmata has dropped out of the ontogeny of Clavelina, while abstriction of protostig- mata no longer occurs in Botryllus.[1]

RECTIFICATION.

In my former studies on the Protochordata, published in this Journal,[2] the main object of which was to obtain an inde- pendent basis of comparison between the Ascidians and Amphioxus, I referred incidentally to certain points which did not fall within the strict limits of my thesis, among these being the pericardium and heart of Ciona. With regard to the cavity of the heart, it seemed to me to arise by a splitting apart of the two layers of what I described as a pericardial septum. In the memoir quoted above, Professor Julin denies the existence of this septum, and says that the heart arises in Ciona, as in all Ascidians, by invagination of the wall of the pericardium. In a form such as Clavelina, where a longitu- dinal invagination of the dorsal wall of the pericardium occurs, the lips of the involution finally come together and coalesce to form a longitudinal cardiac raphe. Now in Ciona there is a ventral raphe as well as a dorsal one, as shown in my fig. 30, Pl. 31, vol. 34, and in some of Julin's figures. If, as M. Julin states, the heart of Ciona arises by invagination and not by the splitting of a septum, then it is necessary to give an explanation of the double cardiac raphe which has been observed in this Ascidian.[3]

The question as to the exact origin of the heart in Ciona is not, however, the special matter to which the heading of this section of the present paper refers.

[1] Garstang states (p. 511) that in the Polystyelid Thylacium sylvani "eight protostigmata arise on each side of the pharynx, and become sub- divided, in regular order from before backwards, to form a corresponding number of rows of secondary stigmata."

[2] Vols. 34 and 35, 1893.

[3] See note on p. 158.

The point which requires rectification relates to the epi-cardium. With regard to this important structure I wrote as follows:[1]—"I have seen the epicardium in Clavelina, which was described by van Beneden and Julin, but no trace of such an organ in Ciona, although it was held as probable by these authors that it occurred in all Tunicates." A few months later, in vol. 35 of this Journal, appeared a paper by Mr. Newstead describing the communication of the capacious perivisceral cavity of Ciona with the cavity of the branchial sac by means of a pair of retro-pharyngeal orifices.[2] More recently M. Damas[3] has shown (1) that the perivisceral cavity of Ciona is paired, and (2) that it is the homologue of the epicardium of Clavelina. Finally, Professor Julin (op. cit.) has described the development of this structure from the beginning to the end.

When it is known that the epicardium (or rather the homo-logue of the epicardium) is larger in Ciona than in any other Ascidian, it may seem unaccountable that I should not have seen it. As a matter of fact, however, Damas finds nothing surprising therein, since, according to his observations, the epicardial diverticula occur at a later stage than those examined by me.

Damas and Julin have shown that the epicardial diverticula in Ciona are the direct extensions of the fundus of the pharynx on either side of a ridge called the retro-pharyn-geal crest, which is in continuity with the right lip of the endostyle (Julin). Throughout the nepionic period the epi-cardial diverticula are little more than the somewhat deepened pharyngeal fundus; in fact, the latter is shown by Julin to be the primordium of the epicardium.

In Clavelina, as shown partly by Seeliger (1885), and

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[1] This Journal, vol. 34, pp. 351, 352.

[2] A. H. L. Newstead, "On the Perivisceral Cavity of Ciona," 'Quart. Journ. Micr. Sci.,' vol. 35, July, 1893, pp. 119—128, Pl. 8. The author confirms van Beneden's and Julin's suspicion that the perivisceral cavity of Ciona represents the epicardiac tubes of Clavelina.

[3] D. Damas, "Les formations épicardiques chez Ciona intestina is," 'Archives de Biol.,' vol. xvi, 1899, pp. 1—25, pl. 1—3.

finally by van Beneden and Julin (1887), the pericardium and epicardium are developed from a common primordium. Damas, who saw the origin of the epicardial diverticula in Ciona, found them in complete independence of the pericardium.

Thus Damas describes the origin of the epicardium apart from the pericardium, while I referred to the latter in ignorance of the former.

It seems quite clear that the epicardium of Ascidians is a very important morphological entity, and, in fact, this has already been recognised in a practical manner by M. Giard, who has instituted an interesting comparison between the Tunicate epicardium and the post-branchial bodies of Vertebrates.[1]

NOTE.—As a matter of fact my original account of the double nature of the pericardial primordium in Ciona, and of the origin of the heart by splitting of the pericardial septum, has been fully confirmed quite recently by Dr. Marc de Selys Longchamps (" Développement du cœur, du péricarde, et des épicardes chez Ciona intestinalis," 'Bull. Ac. Belgique,' No. 6, June, 1900). In another article in the same bulletin, by Selys Longchamps and Damas (" Recherches sur le développement post-embryonnaire et l'organisation de Molgula ampulloides, P. J. Van Beneden "), the following passage occurs :—" Ce stade à six protostigmates que nous avons observé chez l'ampulloïde rappelle un moment correspondant du développement des autres Ascidies simples. Son origine n'ayant pas encore été mise complètement hors de doute, nous ferons remarquer la complète ressemblance de la présente description avec celle fournie par A. Willey (1) chez la Molgule des îles Manhattes."

[1] Alfred Giard, " Sur l'homologie des thyroïdes latérales (corps post-branchiaux, Verdun) avec l'épicarde des Tuniciers," 'Comptes rendus Soc. Biol.,' April, 1898.

EXPLANATION OF PLATE 9,

Illustrating Mr. Arthur Willey's paper "On the Protostig-
mata of Molgula manhattensis (De Kay).

Letters of Reference.

at. Atrial or cloacal orifice. *Boj.* Organ of Bojanus (renal organ). *c.* Cardio-
pericardiac vesicle. *cc.* Central canal of medullary tube. *cv.* Cerebral vesicle
with pigment-globule. *d.t.* Dorsal tubercle. *end.* Endostyle. *ep.* Ecto-
dermal processes. *e.v.* Endodermic vesicle. *f.* Follicle. *g.* Ganglion. *m.*
Mouth. *n.* Notochord. *o. e.* Œsophagus and its orifice. *p. b.* Peripharyngeal
band. *p.l.* Præoral lobe (organ of fixation). *sn.g.* Subneural gland. *st.*
Stomach. *t.* Tail. *t.b.* Tongue dividing cleft. *t.c.* Testa cells. *v.t.* Vascular
trabecula.

All the figures refer to Molgula manhattensis.

Fig. 1.—Anterior portion of urodele larva (tadpole) after hatching.
Zeiss 3 D.

Fig. 2.—Urodele larva undergoing precocious metamorphosis within the
follicle. The tail is seen in regression at its insertion into the body, where
there is a mass of histolytic residua. 3 D.

Fig. 3.—Distigmatic stage, after fixation. A and B are the two primordial
stigmata. The pigmented globule (eye-spot) marks the position of the cerebral
vesicle now in regression. 3 D.

Figs. 4—6.—Successive stages in the growth of the primordial stigmata of
the right side.

Fig. 7.—Condition of protostigmata rather later than that shown in Fig. 6,
from the left side.

Fig. 8.—Commencement of the tetrastigmatic stage from the left side.
Between the mouth and the peripharyngeal band are seen four pericoronal
tentacles. 3 A.

Fig. 9.—Protostigmata of preceding.

Fig. 10.—Composite diagram illustrating the mode of origin of the six
protostigmata. [From Willey, 'Amphioxus and the Ancestry of the Verte-
brates,' 1894, p. 233.]

Fig. 11.—Protostigmata of the right side at the hexastigmatic stage.

Fig. 12.—Entire individual viewed as a transparent object at the hexastig-
matic stage. The first protostigma has become subdivided into four secondary

stigmata. The organ of Bojanus contains a renal calculus. 2 C, reduced by one third.

Fig. 13.—First two protostigmata at a slightly earlier stage than preceding, showing the first in process of subdivision. From the right side.

Fig. 14.—Change of shape of stigmata in the early adolescent period. The figure represents a portion of the third and fourth rows of the right side of an individual possessing eight rows on the right side, and six on the left.

Fig. 15.—Formation of intercalary stigmata by abstriction (the figure does not show the actual process of abstriction). From left side; about ten rows of stigmata present in specimen.
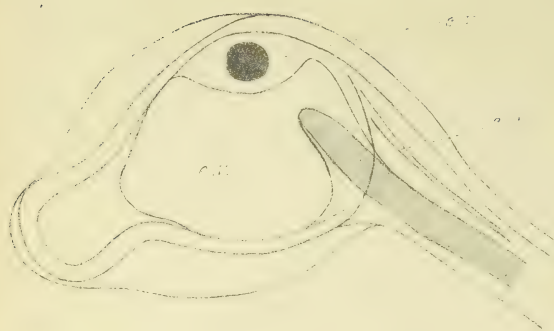
Fig 1.

Fig. 2.

Fig. 8.

Fig. 7.

A
C
B
D

A
C
B
D
E
F

Fig. 11

Fig. 3.

Fig. 4.

Fig. 5.

Fig. 6.

Fig. 9.

Fig. 10.

Fig. 12.
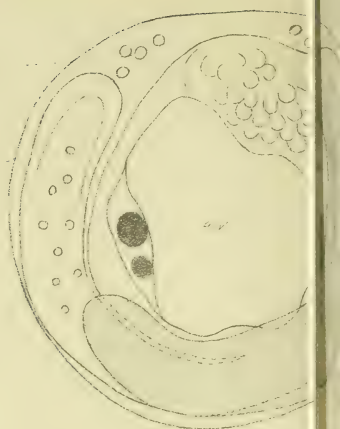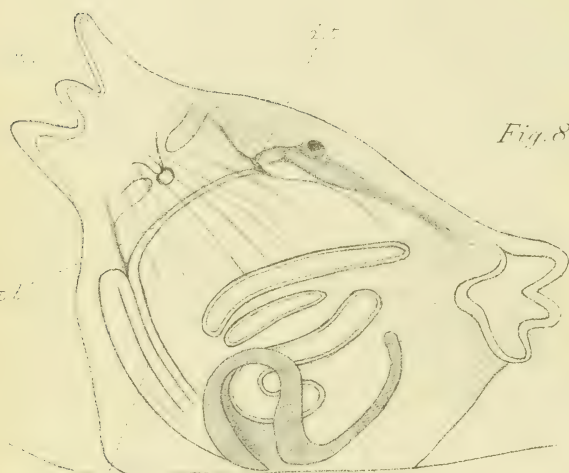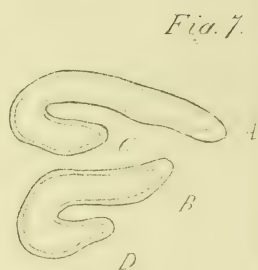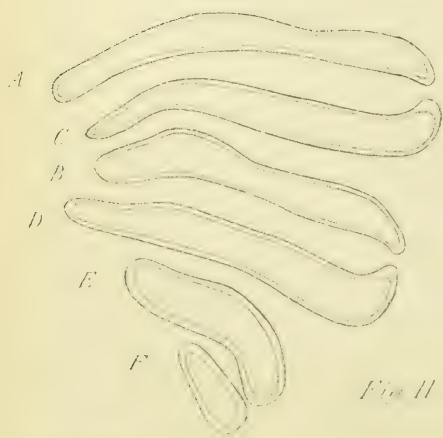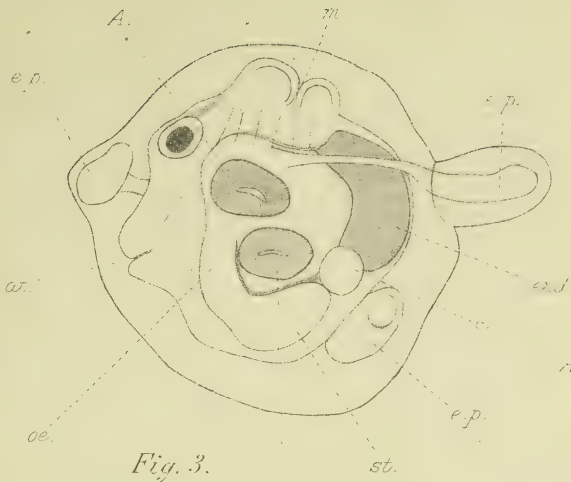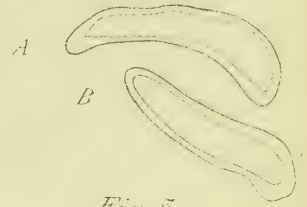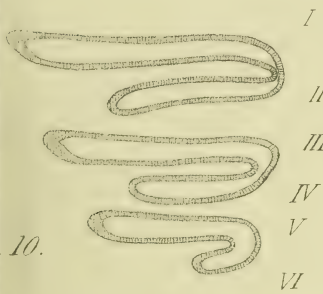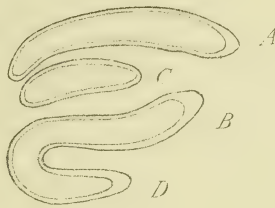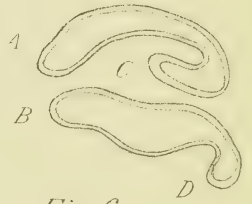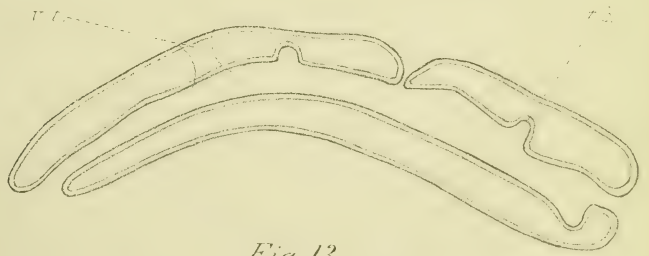
Fig. 13.
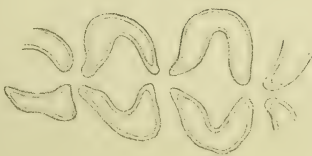
Fig. 14.
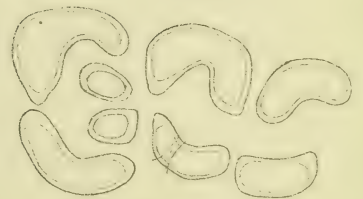
Fig. 15.

The Development and Succession of Teeth in Hatteria punctata.

By

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With Plates 10—12.

INTRODUCTION.

THE dentition of Hatteria presents certain peculiar and characteristic features, which have always attracted attention, and many of which have not yet received adequate explanation. I need only mention here such points as the structure of the premaxillary and anterior mandibular teeth, the irregularity in occurrence and number of vomerine teeth, and the part taken by the edges of the jaws when the teeth have become worn down. Other matters on which uncertainty exists are the presence or absence of enamel, and the extent of the tooth change, which is usually stated not to occur at all. Owing to the great difficulty of obtaining embryos and young, our knowledge on these points is incomplete. However, Professor Dendy has recently to a large extent overcome this difficulty, and most of the material on which this investigation is based was sent to England by him. In my endeavours to clear up the points at issue, I have been greatly indebted to Professor Howes and

Mr. Swinnerton, who have generously placed at my disposal all the slides and preparations made for their research on the development of the skeleton, and who have also granted me the privilege of examining their manuscript and figures. My thanks are also due to Professor Howes for suggesting this research and for the use of a table in his laboratory, and to Mr. M. F. Woodward for much friendly criticism and advice.

Historical.

The first account of the adult dentition of Hatteria is that given in 1867 by Günther (1), where he emphasises the acrodont character, and points out the important part played by the edges of the dentigerous bones when the teeth have become worn down. He gives a full account of the macroscopic features of the dentition of the adult, but appears to have examined no individuals with vomerine teeth. He also describes a young specimen (seven inches long) in which each of the premaxillary teeth of the adult was represented by two, and each of the large anterior mandibular teeth by three separate teeth. In this young specimen he could distinguish no polished surface on the "alveolar" edges, but does not speak positively on this point.

The discovery of the occurrence of vomerine teeth was made by Baur (2) in 1886. His specimen was 210 mm. in length, and had a tooth on each vomer.

In 1890 Professor Howes (3) examined nine specimens for vomerine teeth. In five of these no such teeth were to be found; in one they were bilaterally symmetrical, in one the last traces could be detected, in one there was a tooth on the right side only, and in another the right tooth was larger than the left. In no case did they project into the cavity of the mouth. Even when teeth were wanting he found a ridge of the mucous membrane in the proper position on the vomer. He suggested finally that the vomerine teeth are vestigial structures, and are undergoing suppression from left to right.

Siebenrock (**4**) in 1893 described a specimen having two vomerine teeth on the right side and one on the left.   This was the only instance of teeth occurring on the vomer out of nine specimens examined.   He states that the tips were covered with enamel.

In the same year Röse (**5**) stated that he could find no tooth replacement in Hatteria, although he apparently found an "Ersatzleiste."   He says " . . . trotzdem findet sich, besonders im Oberkiefer, hinter den functionirenden Zähnen eine wohl entwickelte Zahn- oder Ersatzleiste.   Am hinteren Ende derselben findet zeitlebens eine fortwährende Neubildung von Zähnen statt."   It is, however, difficult to say from the context whether he is referring to Hatteria, or Chamæleo, or both.   Later, also, he says that in Chamæleo, "und vermutlich auch bei Hatteria," there is behind the functional teeth "eine gänzlich functionlose[1] aber wohl entwickelte Zahn- oder Ersatzleiste."

Burckhardt (**6**) in 1896, in a review of our knowledge of the dentition of the Sauropsida, expresses his belief that the form of the anterior teeth of Hatteria is due to concrescence.

About the same time Baur (**7**) examined the skull of a young Hatteria (25 mm. from premaxilla to occipital condyle), and found two separate teeth in each premaxilla, an outer larger and an inner smaller one, the latter having at its base a replacing tooth, which, however, he says does not become functional.   In speaking of the maxilla also, he says, "Der fünfte Zahn besitzt wie der Innere des Premaxillare einen Ersatzzahn, und der letzte steht frei in einer Alveole." He found a well-developed tooth on each vomer, and in addition an anterior small one on the left side.   He states that the second tooth in the mandible has an "Ersatzzahn," and concludes that Hatteria has an incomplete set of successional teeth, which, however, are never functional.   He does not give his reasons for the latter part of his conclusion.

Osawa (**8**), in 1897, stated that the teeth of Hatteria consist chiefly of dentine.   He could find no enamel, and to its

[1] The spacing is mine.—H. S. H.

presumed absence he attributes the early wearing down of
the teeth. He found no true cement; but bone corpuscles
and dentine tubules occur side by side, so that at this point
he considers we have to do with osteodentine.

In 1899, in his paper on the "Outlines of the Development
of Hatteria," Dendy (**9**) first described the presence of three
separate teeth in each premaxilla and on each side of the
mandibular symphysis, at a period just before hatching. He
suggests that fusion takes place later, the result being the
formation of the four anterior teeth of the adult.

Howes and Swinnerton (**10**), in a paper at present in the
press, point out that the middle premaxillary tooth on each
side ceases to grow after a certain stage (Stage S), and is
in all probability shed. They also figure the replacing tooth
lying lingually to it, but owing to lack of material they
do not venture to decide whether this does or does not be-
come functional. They discuss Baur's observations, and
draw attention to the alternation in size of the teeth in the
embryos and young. They found no calcified vomerine
teeth in any of the embryonic stages investigated. As
regards the substance on the exposed surfaces of the denti-
gerous bones, they accept Tomes's (**11**) view that it consists
of true bone, and they have therefore introduced a new term
—"hyperacrodont"—for describing the secondarily theco-
dont condition produced in some of the teeth by the dis-
position of this bone round their bases.

Material and Observations.

I have examined complete series of sections taken in
various planes, through embryos and young of several stages,
ranging from about the third month of incubation (Q) to a
period some months after hatching. I have also examined
preparations, dissections, and specimens of young and adult
animals. In describing the stages I shall make use of letters
and numbers in the same sense as Dendy, and as Howes
and Swinnerton, adding such other data as may be desirable.

Stage Q.

Embryo Q, 52a, in about the third month of incubation. The skeleton is mainly cartilaginous, but along the upper border of Meckel's cartilage, and in several other regions, a considerable amount of ossification has taken place. Length of head as measured from sections 5 mm.

The epithelium along the upper and lower jaws has grown down into the mesoderm in the form of a well-marked dental lamina, consisting of an outer limiting layer of columnar cells, and a central core of more irregular ones (fig. 1, *d. l.*). The line of ingrowth is marked on the surface of the epithelium by a shallow groove, the dental furrow (fig. 1, *d.f.*), such as has been described in many other vertebrates. The dental lamina is on the whole less developed in the lower than the upper jaw, and in the former is quite indistinguishable for some little distance in the middle line anteriorly ; in the latter, also, it is not conspicuous in this region.

The most interesting feature of this stage is the presence of minute teeth, which are perhaps homologous with the early (embryonic) dentition described by Röse (**12, 13**) in the Crocodile, by Leche (**14**) in Iguana tuberculata, and by others in various fishes and Amphibians.

The best developed tooth of this first series is shown in fig. 2. Here we see that the tooth is formed just below the epidermis, and has a well-defined enamel organ, although I have been unable to detect any enamel. The presence of the tooth produces a prominent papilla. The dentine is formed by the activity of odontoblasts, which do not become so elongated as do those of the next set of teeth, but the process of dentine formation is apparently the same in the two cases. In fact, except for the minute size and the position immediately below the epidermis, the members of the first series of teeth are very similar to those of the functional set. Referring to fig. 1, we see that at the labial attachment of the dental lamina to the epithelium there is

an enamel organ, in which the deepest layer of cells is
beginning to assume the character of an enamel epithelium,
part of the cells belonging to the epithelium of the jaw at
this point, while the others belong to the labial side of the
dental lamina. There is as usual a great accumulation of
mesodermal cells below the epidermal cap, and also in the
region towards which the dental lamina is growing. This
enamel organ belongs to the first series, and its position is
obviously labial to the dental lamina; with the exception
of the palatine teeth of this series the dental lamina always
occupies this relative position. As Röse (**12**) says of the
Crocodile, "liegen die verkalkten Zähnchen der ersten Serie
nach aussen von der Zahnleiste." Leche also (**14**) says of
the embryonic teeth of Iguana tuberculata, "Es ist
besonders hervorzuheben dass die fraglichen Zähne nur im
Bereiche der Schmeltzleiste entstehen." In this specimen
of Hatteria I found a pair of calcified teeth of the first series
in both upper and lower jaw; in each case these were the
second in order, the anterior pair above and below being
represented by enamel organs. Of the latter, I found on
each side eight above and seven below, a number which
corresponds fairly well with the number of calcified teeth
occurring at a later stage. This is considerably more than
have been found in Iguana or Crocodilus.

The presence of an enamel organ usually produces an
epidermal papilla, which is probably what Röse (**13**) found
in the Crocodile and described as follows:—"Die ersten
Zahnanlagen der Krokodile zeigen sich ganz ähnlich wie
die Placoid-schuppen und ersten Zähne der Selachier in
Form von frei über die Kieferschleimhaut hervorstehenden
Papillen." He says also, "Die ersten Zähnchen entstehen
ganz ähnlich wie bei Selachiern durch Verkalkung von frei
über die Schleimhautoberfläche hervorragenden Schleim-
hautpapillen." Although I should scarcely describe the pro-
cess of formation of the first teeth in Hatteria in these
terms, I am inclined to think there is no fundamental point
of difference between this and Crocodilus. Röse in the same

paper refers to "Epithelwucherungen," which are formed before the ingrowth of the dental lamina and which project above the surface of the mucous membrane; it is not easy to be sure when he is speaking of these, and when of the papillæ produced by the presence of an enamel organ of the first series.[1] In a recent paper, Laaser (15), in describing the development of the dental lamina in Spinax niger, says: "Die ersten Zähne liegen also meist am Uebergang vom äusseren Zahnepithel zur Zahnleiste;" and his fig. 4, showing the enamel organ of such a tooth, is almost a fac-simile of my fig. 1. Here, then, we have a Selachian whose first teeth originate in the same way as do those of Hatteria, and in neither case can we accurately speak of development "durch Verkalkung von frei über die Schleimhautoberfläche hervorragenden Schleimhautpapillen."

In addition to the marginal teeth of the upper and lower jaws, there are present in a position slightly posterior and external to the choanæ, two calcified teeth of the first series, one on each side. As is seen from an examination of later stages, this situation corresponds to the anterior extremity of the line along which the palatine dental lamina is subsequently formed. It is interesting that each of these teeth is situated within a prominent papilla, but owing to the lack of sections showing their development I am unable to say what is the time of origin of the papilla, i. e. whether before or after the tooth is formed.

Taking all points into consideration, the teeth of this series seem to resemble more closely those of Iguana tuberculata than those of the Crocodile. The latter in particular, according to Röse, form a "Cementsockel," and are eventually removed by absorption within the mesoderm. In Hatteria, on the contrary, no such substance is produced, and instead of passing deeper into the mesoderm the teeth are moved

[1] In Hatteria the apex of most of these papillæ is certainly in the form of a small group of cells (not shown in my fig. 1), which suggest "Epithelwucherungen." These may correspond to what Röse describes, but my specimens do not enable me to say whether they arise before the enamel organs are formed.

into the epidermis, and are finally shed about the time of
hatching (see later stages and fig. 12). In these features
Iguana appears to agree with Hatteria.

The general resemblance to the functional teeth which is
exhibited by these embryonic teeth in their development
and structure, causes me to doubt their special homology
with the placoid scale, and I prefer to describe them as
simply belonging to the first or embryonic dentition, which is
no longer functional, but which, no doubt, was so when the
incubation period of Hatteria was shorter than it is at present.

At Stage Q the teeth of the future functional series have
not yet begun their development.

Stage R.

Embryo R, 142, in about the fifth month of incubation.
Length of head from occipital condyle to premaxilla 6·5 mm.

This embryo shows a very considerable advance on the last.
The teeth of the first series are now all calcified, and show
some degree of degeneration, inasmuch as many of them have
become solid nodules of dentine, lying immediately below the
epidermis, and having lost their pulp. The enamel epi-
thelium in some cases is still distinct, and an unmistakable
tendency to the formation of stellate tissue is occasionally to
be seen. The teeth number about fourteen above and fourteen
below, in addition to the palatine pair. We found in Stage
Q that there were only six of these teeth in a calcified con-
dition, the others being represented by a slightly greater
number of enamel organs than there are teeth at this stage.
In dealing with vestigial structures of this kind, little
morphological importance can probably be attached to such
differences in time of development, but it is interesting to
note that the first marginal teeth to calcify are those four which
lie near the anterior angles of the jaws, and which, in a
young animal, would be most useful in catching small prey.

The teeth and enamel organs belonging to the future
functional series of the young animal are at this stage con-

spicuous structures. Many of them are well advanced in calcification, and a deposit of enamel has commenced. In fig. 3 is shown the enamel organ of the first premaxillary tooth of the right side. The mesodermal papilla indents the deepest portion of the dental lamina at this point, and there is no indication of a lingual continuation of the latter. The enamel epithelium is conspicuous, and evidences of the stellate tissue are seen, while the mesoderm shows a tendency to form a capsule. In this tooth no calcification has yet occurred, and the odontoblasts are still undifferentiated mesoderm cells. In the second premaxillary tooth, however, there is a considerable degree of calcification, and an indication of a prolongation of the dental lamina on the lingual side can be detected. In both these points the third premaxillary resembles the first. Comparing these three teeth with the corresponding anterior three on each side in the lower jaw, we find that similar relations obtain, i. e. that the second is more advanced than the other two, and shows indications of a lingual prolongation of the dental lamina. I shall have more to say on these points in the sequel. Each maxilla has ten teeth, most of which are more or less calcified; but here, again, there is a well-marked alternation in the degree of calcification. As sagittal sections only of this embryo were at my disposal, I am unable to give the precise relations of the dental lamina in the lateral regions of the jaws. The mandibular teeth posterior to the first three (eight in number on each side) are, as regards the first six, well calcified, the two posterior only slightly so.

The anterior end of the palatine tooth-bearing regions is indicated by the presence, on each side, of the tooth of the first series, mentioned in the last section. The dental lamina bears three enamel organs, which show no calcification.

Embryo R, 162, in about the eighth month of incubation. Although this is apparently so much older than the last embryo, the stage in development is actually not much more advanced, for Dendy (loc. cit.) has pointed out that, for a long period during the winter months, very little progress

made, and embryos from the fifth to the ninth or tenth month of incubation may all be included in his Stage R.

The teeth of the first series have become less tooth-like in form, and some of them are enclosed in the epidermis (fig. 4, *pal.* 1). They are not so numerous as in the last embryo described, and perhaps some of them have already been shed. They occur as far back in the jaw as the ninth maxillary teeth of the future functional series.

As regards the future functional teeth, there are in each premaxilla three teeth, the first being smaller and less developed than the other two, and the second being the most advanced.

Each maxilla has ten teeth, and, as in the last embryo, these exhibit an alternation similar to that already described, but in this case I am able to give a more detailed description. Before doing so I wish to refer to fig. 11, where the alternating series of the maxilla at Stage S is shown. Here a large tooth alternates with a small one, and the larger differ somewhat in shape from the smaller. A comparison of figs. 6 and 7 will illustrate the condition found in frontal sections at Stage R. Fig. 6 shows a tooth having a considerable development of dentine, a lingual prolongation of the dental lamina (*r. d. l.*), stellate tissue much broken down and only separated from the exterior by two or three layers of flattened cells. Fig. 7, on the other hand, shows a tooth in which the amount of dentine is much less, though the enamel organ as a whole is larger; there is no lingual prolongation of the dental lamina; the stellate tissue is more intact, and is separated from the exterior by several layers of cells; the whole structure is obviously in an earlier stage of development. Fig. 6 is the eighth maxillary tooth of the right side, and fig. 7 is the tooth immediately anterior to it; the former represents one of the smaller teeth of the alternating series shown in fig. 11, the latter one of the larger. This alternation of character, as seen in sections, prevails throughout the maxillary series, and it is difficult to avoid coming to the conclusion that we are here dealing

with two dentitions, the smaller tooth representing an earlier set, and the larger a later one. The same is true of the premaxillary teeth, where only the second belongs to the earlier set. The interpretation of the epithelial strand lingual to the smaller teeth (fig. 6, *r. d. l.*; fig. 4, *r. d. l.*) as a residual dental lamina seems to me to be justifiable, although at later stages, and at this stage in the lower jaw (fig. 5, *man. lin.*), epithelial ingrowths of a different nature arise, which produce some uncertainty. The fifth pair of maxillary teeth form an exception to the regular alternation, inasmuch as though they resemble the larger teeth in most respects, they have an apparent residual dental lamina. This fact has an interest in view of the development of a successional tooth at this point at a much later stage.

Labially to the enamel organs the epidermis is beginning to grow down into the mesoderm in the form of a band of cells more or less closely connected with the enamel organs or with the dental lamina in the intermediate regions (figs. 4, 5, 6, 7, *m. lab.*). This is the labio-dental strand, and its further development will be seen in later stages.

The most anterior indication of the palatine dental lamina occurs at the level of the sixth pair of maxillary teeth. The epidermal ingrowth is anteriorly a solid roundish mass of cells, which, traced backwards, is found to assume in section a crescentic form, the attachment to the epithelium being by the convex side of the crescent. The inner limb is the one more closely related to the enamel organs, and represents the dental lamina. The outer limb, on the other hand, is more independent (figs. 4 and 5, *p. lab.*), and represents a glandular ingrowth, the relations of which will be presently described. The most anterior tooth of the palatine belongs to the first (embryonic) dentition, and is situated lingually to the dental lamina (fig. 4, *pal.* 1). It is a more or less triangular fragment of dentine, completely enclosed in epidermis, and on the point of being shed. Its position is exceptional, as the teeth of this series are usually labial to the dental lamina; but I do not attach much importance to

this divergence from the rule, as this particular tooth is formed before the dental lamina, and may easily have reached its present relative position through the growth of the epidermis. The palatine dental lamina of each side has four enamel organs, of which the first two only have partially calcified teeth (fig. 4, *p. e. o.*; this section passes through the anterior portion of the first enamel organ). The second is the only one having an epidermal strand lingual to the enamel organ. Between the teeth the dental lamina is continued as a well-marked strand of cells (fig. 5, *d. l.*) in both palatine and maxilla: in the maxilla it terminates without becoming separated from the epidermis; in the palatine the dental lamina and the lingual epidermal ingrowth run together behind (as they arise together in front), and form a roundish knob of cells attached to the epidermis, which, again, is continuous posteriorly with a groove in the roof of the mouth.

In the mandible of the last embryo described we saw that of the first three teeth on each side the second was more advanced than the other two, and this is the case in the present specimen. It has the same claim to be considered a member of an earlier series than the others as has the second premaxillary. There are now ten pairs of calcified cheek teeth, and a pair of enamel organs without calcification on the posterior free prolongations of the dental laminæ. A reference to fig. 11 will show that the mandibular teeth exhibit an alternation in size similar to, though not so conspicuous as, that seen in the maxilla. I have been unable, however, to convince myself that there is a corresponding difference in their period of development; and as the mandible is in a more advanced stage than the maxilla as regards the epidermal ingrowths which are so conspicuous at a later stage, the evidence of a possible residual dental lamina cannot be relied upon. As a matter of fact, each of these mandibular teeth has a well-marked epidermal ingrowth on its lingual side (fig. 5, *man. lin.*), but the interpretation of this structure as a residual dental lamina is hardly justi-

fiable, since at a later stage a similar ingrowth is found opposite each tooth in the upper jaw, with the position and appearance of a dental lamina, though the result of its further development is mainly a glandular groove. On the whole I regard the alternation in size of the mandibular teeth as indicative of the presence of teeth belonging to the two dentitions, which I have shown to be probably represented in the premaxillæ, maxillæ, and palatines. I shall have occasion to refer to this point again in the sequel.

Posteriorly the dental lamina (which is probably already involved in the ingrowth mentioned above) leaves the epidermis and runs back for some distance deep in the mesoderm, until it terminates between the coronoid and dentary. This portion of it is probably entirely dental in character, and bears one enamel organ.

In view of the complexity of the epidermal down-growths into the mesoderm at this and following stages, it will be conducive to clearness if a short account of the arrangement of the parts of the mouth in the adult in the neighbourhood of the teeth be given here.

In both upper and lower jaws the lips and teeth are, as is usual, separated by a deep groove, for which we may use the term labio-dental groove. In the lower lip there is a sort of glandular shelf running along the internal face, and the groove itself has glands on the face looking towards the teeth (figs. 14 and 19, *l. d. gr.*). The groove is developed from the labio-dental strand (figs. 4—9, *m. lab., man. lab.*). Running along the inner or lingual face of both jaws is a prominent fold or ridge of mucous membrane, reaching almost as high as the apices of the teeth. That of the lower jaw is the crista gingivalis inferior (**8**), that of the upper the crista gingivalis lateralis. The deep groove between the crest and the mandible may be called the mandibular (internal) dental fossa, and that in the corresponding position in the upper jaw the maxillary (internal) dental fossa. In Hatteria these grooves are formed from epidermal ingrowths, situated lingually to the teeth (and

already mentioned), which are superposed on the denta. laminæ in such a way as to lead to great difficulty in distinguishing the respective limits (see figs. 5, 8, *man. lin.*; 9, *m. lin.*; 14 and 19, *lin. gr.* and *r. d. l.*). As in the labiodental groove, the side facing the teeth is glandular.

Lying between palatine and maxillary series is a ridge similar to the others described (crista gingivalis medialis), and the internal face of the palatine is covered by another ridge (crista gingivalis palatinæ), the two being connected anteriorly. The palatine has, therefore, grooves on its outer and inner faces, and they are continuous anteriorly. We may call these the internal and external palatine fossæ. The latter corresponds to the labio-dental groove, and is formed from an independent ingrowth of the epidermis (figs. 5 and 9, *p. lab.*), whereas the former is developed from an ingrowth of cells bearing the same relationship to the teeth and dental lamina as I have just described in the case of the mandibular and maxillary lingual ingrowths.

As in the two following stages it is not always possible to distinguish between the dental laminæ and the superposed ingrowths, I have made use of descriptive terms having no morphological significance.

Stage R—S.

This embryo was intermediate between the Stages R and S, as defined by Dendy, and was 6·3 cm. in length. It was found dead in the egg, and its preservation therefore leaves something to be desired.

In all three tooth-bearing regions there are now present both external and internal (labial and lingual) epidermal ingrowths, having extremely varying and perplexing relationships to the enamel organs. It is no longer possible to indicate with certainty any of the dental laminæ, although they are no doubt represented in the lingual strands (fig. 8, *man. lin.*; fig. 9, *m. lin., p. lin.*). In some cases these are attached to the lingual sides of the enamel organs

(fig. 9, *p. lin.*), and in others they are quite independent of the latter (fig. 8, *man. lin.*; fig. 9, *m. lin.*).

In the maxillary region we find that the labial ingrowth appears in sections at or near the middle of any one of the posterior teeth, in the form of a more or less lobed projection from the side of the enamel organ (fig. 9, *m. lab.*). In the space between two teeth it arises independently from the epidermis, and this is also the case opposite the anterior maxillary teeth. Its deepest portion is close to the developing maxilla, and the intervening mesoblast is denser than elsewhere. The lingual ingrowth appears anteriorly in the form of a simple band of cells projecting from the sides of the enamel organs, and having here the appearance of a residual dental lamina. Posteriorly it is free from the enamel organs (fig. 9, *m. lin.*). The alternating character of the maxillary teeth is now expressed chiefly in their sizes.

The anterior indication of the palatine ingrowths is found as a mass of cells attached to the epidermis, and already unmistakably glandular in arrangement. These cells can be traced backwards into the labial and lingual ingrowths, and in the space between these the enamel organs and teeth appear. The relation is, as before, closest between the lingual ingrowth and the enamel organs, and fig. 9, *p. lin.*, represents the condition for all four palatine teeth. The labial ingrowth is more conspicuous than the lingual, and is throughout independent of the enamel organs. The two fuse posteriorly, and are continued backwards for a little distance as an epidermal groove, as in Stage R. In the maxilla there is a short continuation of the ingrowths posteriorly, free from the epidermis.

The teeth are well calcified, and have a conspicuous layer of enamel (figs. 8 and 9, *en.*). They are not yet fused with the bone, but are in close proximity to it.

In the lower jaw the teeth are more advanced than in the upper, and are separated from the bone by a very short interval, especially on the outer side. The line of subsequent union is indicated by a band of mesodermal cells. On each

side of the teeth are the labial and lingual epidermal ingrowths (fig. 8, *man. lin., man. lab.*), which are now broad bands of cells projecting down into the mesoderm beyond the deepest point reached by the enamel organs; in fact, as seen in section, they embrace between them the edge of the dentary as well as the base of the teeth. In the section figured (fig. 8) the relations of the epidermal ingrowths are very simple, but in some sections we may find anterior and posterior portions of two enamel organs, the labial ingrowth appearing as a process of one of them, and the lingual as a process of the adjacent one. In the anterior and middle regions of the jaw the enamel organs are mainly free from the lingual ingrowth, but the posterior younger enamel organs are found with an internal connection with it.

Posteriorly the labial and lingual strands fuse, separate from the epidermis, and pass backwards, as in Stage R, into the space between coronoid and dentary. The fifteenth mandibular tooth, the last at this stage, makes its first appearance on this portion.

Stage S.

This stage embraces the later period of incubation.

In a skull measuring 13·5 mm. from premaxilla to occipital condyle the condition of the teeth is as follows (see also figs. 10 and 11):

The premaxillary teeth (fig. 10) are three in number on each side, the third being considerably the largest. The maxillary teeth (fig. 11) show a conspicuous alternation in size, Nos. 1, 3, 5, 7, 9, on the left, being larger than the intermediate teeth, although the first is smaller than the others of the larger series. On the right side the first three are small, the middle one being the largest, while Nos. 4, 6, 8, 10, correspond to the larger teeth of the left side. We see, then, that although the alternation is regular, there is a tendency for the first two or three to be small, whichever series they may belong to, and also that the two sides do not correspond in this specimen.

Each palatine has four teeth, three anterior larger and one posterior smaller.

In the mandible, number 3 is much larger than the first two; in the middle line over the symphysis is left a gap into which the two first premaxillary teeth are received. The third mandibular "bites" posterior to the third premaxillary tooth. In the cheek teeth (10 and 11 respectively on the two sides), the alternation in size is less regular and conspicuous than in the maxilla, and the average size is also less.

The teeth are not simple cones, but are elongated along the line of the jaw, and overlap one another to some extent. The large maxillary teeth are markedly rounded on their external faces, the internal one being flattened; the converse is the case with the palatine teeth, the flattened faces being turned towards the maxilla. The mandibular teeth more closely approach the conical form, as do the smaller ones of the upper jaw.

All the teeth are more or less triangular in side view; the apices of the larger ones in the upper jaw, however, point slightly backwards.

Embryo S, 2.—7·5 cm. in length, and was prematurely hatched. The length of skull as measured from sections was 11·5 mm., slightly smaller than the last.

There are very few teeth of the embryonic series now remaining, and these are evidently being forced to the exterior by the growth of the epidermis. The epidermal cells form a more or less regular capsule, and the tooth usually shows no signs of absorption, being probably shed entire (fig. 12, *T*. 1).

In the functional series, we find the first premaxillary tooth smaller than the other two and further removed from the surface.

The maxillary teeth are about equal in number to those in the skull just described, and show a similar alternation. Posteriorly the dental lamina takes a curious upward then forward course (fig. 16, *d. l.*), previously losing its direct connection with the epidermis. The eleventh and twelfth

teeth are borne on this portion (fig. 16, *e. o. f.*; this is the eleventh), as is shown in the figure. The twelfth is only indicated in the section drawn by a slight swelling anterior to the eleventh.

In number and size the palatine and mandibular teeth show no special features, and correspond with those of the skull described. The mandibular dental lamina (fig. 16, *d. l.*) has a free posterior continuation, as in earlier stages, and this bears a small, slightly calcified tooth and the enamel organ of another (neither shown in fig. 16).

The most interesting observation I have made in this embryo relates to the vomerine dentition. I have shown in the historical portion of this paper that the occurrence of vomerine teeth is comparatively rare, and that considerable variation and inconstancy obtains in their relative size and even in their number.

In the present embryo I find on the left side, very near the middle line, a longitudinal thickening of the epithelium of the palate, situated below the posterior portion of the vomer. Indenting the middle portion of this thickening is a mesodermal papilla and a well-marked early enamel organ formed from the overlying epithelium (fig. 13, *V. e. o.*). Between this structure and the bone there is a dense mass of flattened mesodermal cells. In a corresponding position on the right side is a slight epidermal thickening, but only a faint though unmistakable indication of an enamel organ and papilla. The condition on this side is, I believe, degenerate as compared with the other, and it is not a case of later development.

Returning to the teeth of the future functional series in the upper and lower jaw, we find that the labial and lingual epidermal ingrowths are now very conspicuous structures, and the former at least is beginning to form large cavities and to show a lobed character, indicative of the future glandular structure of a portion of its constituent cells. The cavities are the first stages in the formation of the labio-dental groove, which is found in the next embryo (fig. 14, *l. d. gr.*).

The teeth themselves have not yet cut the gum, but they cause conspicuous projections from the surface of the jaws.

In the lower jaw fusion with the bone is on the point of taking place in some cases and has already occurred in others. Tomes, as the result of the study of several reptiles (**17, 18**), stated that the occurrence of cement in this class is comparatively rare. Santa Sirena (**19**) mentions a "falsche" cement in Lacerta agilis, and in Bronn's Tierreich (**20**) cement is described as differing from dentine in the absence of dentinal tubules and the presence of "so-called" bone cells. I have not succeeded in finding a satisfactory account of the development and structure of cement in reptiles, and Hatteria in this respect confirms Tomes's results in the slowworm and green lizard. Up to the stage immediately before fusion the respective territories of the osteoblasts and the odontoblasts are well defined. When dentine and bone are almost in contact there is a layer of flattened osteoblasts intervening, and these become included in the bone or pushed to one side, fusion taking place without the production of any third substance whatever. The bone is very simple in structure, and the dentine at the base of the tooth usually has its dentinal tubules indistinctly shown, so that, as we shall see in the next embryo, the transition from tooth to bone is not an abrupt one as far as appearance is concerned, though the presence of bone corpuscles is of course diagnostic (fig. 15). I do not agree with Osawa's use of the term "osteodentine" for the transitional region.

Another very interesting feature shown in this embryo is the fusion of teeth in the lower jaw. Most of the cheek teeth have here begun to fuse with their anterior and posterior neighbours, the enamel organs however apparently remaining distinct from one another. The odontoblasts are congregated in great numbers at the points of fusion. We have here an undoubted case of concrescence in the wider sense of the term. This process does not occur, at any rate to the same extent, in any other tooth-bearing region, and we shall see that it is the probable cause

of an important difference between the dentary and the other dentigerous bones as regards their tooth supply.

Embryo S, 19A.—This was a newly-hatched individual and considerably more advanced than the last. In transverse sections through the lower jaw the fully formed teeth are seen to be firmly united with the jaw, and many have cut the gum (fig. 14). The internal surface of the tooth is lined by a layer of slightly flattened odontoblasts (fig. 15, *od.*). The labio-dental and the internal dental grooves are now formed, and the glandular structure is evident (fig. 14, *l. d. gr.*, *lin. gr.*, *gl.*). At the base of the internal groove is a ridge of cells which is non-glandular in structure, and probably represents the persistent dental portion of the labial ingrowth (*r. d. l.*). The crista gingivalis (*c. g.*) has also become cut off by the formation of the internal fossa. At the junction of tooth and bone the attachment of the inner limb of the ∨-shaped sides of the labio-dental groove to the calcified tissue is very intimate (fig. 15), and the same is the case to a less extent with the corresponding limb of the internal groove, although in the section (fig. 15) it had broken away. There is a thin layer of mesoderm between the epithelium and the bone, below the attachment of the former, and this is concerned in the formation of new bone lamellæ at later stages.

The teeth are at this stage typically acrodont, and in the lower jaw their fusion in a longitudinal direction can clearly be seen.

The enamel has been completely removed by decalcification in the tooth figured.

Stage T and later.

Stage T includes young individuals, from a few weeks to a few months old, measuring 15—17 cm. in length.

In a skull measuring 19 mm. from premaxilla to occipital condyle, on the right side the condition of maxillary and palatine teeth is much the same as in the skull of Stage S, but the general size is somewhat larger. The chief interest

lies in the premaxillary teeth (figs. 17 and 20). Here we find that the second tooth has remained of about the same size as at Stage S, whilst the first has grown considerably. The third is still the largest. A stained and mounted preparation of the premaxilla shows that No. 2 is evidently about to be shed, and that there has been a large absorption of bone at its base internally. From the evidence of sections of this stage (see below), there was no doubt a successional tooth at this point, unfortunately removed in making the preparation (fig. 20).

In the lower jaw the teeth have increased to sixteen on each side. The alteration in size is fairly regular, except in the case of the first five teeth. There is a short gap anteriorly between the teeth of the two sides over the mandibular symphysis.

Sagittal sections of the premaxilla of another individual of this stage show that the labio-dental groove has been formed; the internal dental fossa is not typically developed in this region (fig. 18). From the deepest portion of the epithelium of the internal fossa a dental lamina projects into the mesoderm. This is found in the whole premaxillary region, and opposite the second functional tooth it bears a well-developed enamel organ with a calcified tooth (fig. 18, *t. s.* 1). A similar condition of the dental lamina is found in the lower jaw at this stage (fig. 19, *r. d. l.*), but there are at present no signs of successional teeth. The second premaxillary is shown to be separated from the inner table of the bone, absorption having taken place at the base of the tooth. In some sections a portion of bone is seen to be still attached to the latter, and is probably cast away with it, perhaps representing what Tomes ('Manual of Dental Anatomy') calls "bone of attachment." On the labial side also bone absorption has commenced. As is seen in fig. 20 the absorption on the lingual side extends to the bases of the first and third teeth, and in addition, sections show that there is a separate small area of absorption at the base of the third. I shall prove later that each of these three teeth

is shed, and that successional teeth arise at different times to fill their places.

The number of teeth in the maxilla at this stage is eleven, of which the last two are behind the others in development, and are attached to a posterior free prolongation of the dental lamina. The labio-dental and the internal maxillary grooves with their glands are now obvious structures, and the dental lamina arising from the deepest part of the internal groove has a posterior prolongation, to which the last tooth is still attached. The palatine has six teeth, the last two resembling the corresponding maxillary teeth in their state of development.

The fifteen teeth of the mandible are succeeded posteriorly by two enamel organs, the posterior of which is in a very early stage of development, the anterior being well calcified.

My observations had reached this stage when, through the further kindness of Professor Howes, I was enabled to examine two fine young specimens, measuring respectively 17·8 cm. and 21·2 cm. in total length. These, which filled the gaps in the Howes-Swinnerton series, were by a fortunate coincidence received at the very moment I was in need of them. They were the gifts of Professor A. W. P. Thomas, of Auckland, New Zealand, and from their study I am able to show that there is not only a development of successional teeth in Hatteria, as was first stated by Baur, but also an actual tooth replacement, denied by him and others. We may consider first the smaller specimen, 17·8 cm. total length, 7·2 cm. from anterior border of pelvis to snout.

In place of the three premaxillary teeth on each side, as seen in Stage T (figs. 17 and 20), we find in this specimen only two. It is clear that at any rate the second tooth (counting from the middle line) has been shed. Not only so, but the first has also fallen out, and the successional tooth (figs. 18 and 20, t. s. 1.) has replaced them both, as seen in an entire preparation of the right premaxilla (fig. 21). In the same preparation (and figure) we see that No. 3 is

becoming detached from the bone by absorption at its base internally, and also that there is a further absorption of bone at some depth, a developing tooth (*t. s.* 2) being found at this point. Serial sections through the left premaxilla confirm all these observations, and show that in all essential respects the second successional tooth resembles the first (fig. 18, *t. s.* 1) in its relations to the neighbouring parts. Comparison of figs. 20, 21, and 22, will make clear the order of tooth change in the premaxilla up to the stage of my largest young specimen.

The number of maxillary teeth on each side, visible without dissection, was thirteen, regularly alternating in size throughout, although the three anterior differed somewhat in size from the following teeth. Microscopic examination shows that the first tooth is one which has only recently been formed (fig. 23, *t. s.* 1). Its pulp cavity is wide, its enamel is almost undamaged, it is not yet fused with the bone, and it has evidently just grown up from the area (indicated in the figure by lighter shading), where bone absorption had been proceeding. There is no doubt as to the successional character of this tooth, although I have not found its early stages in any of my specimens. I am unable to say whether it replaces two or only one of the preceding teeth.

The palatine teeth are six in number on each side, some being large and others small, but they show a less definite alternation than do the marginal teeth.

In the lower jaw we find on each side three anterior teeth, the outer being a little larger than the other two. Posterior to these are thirteen teeth alternating in size, but all of them small, and further back still are three or four larger teeth of uniform size. Here, then, we see that whereas in the maxilla all the teeth belong to the alternating series, in the mandible there is already a commencement of a posterior uniform series. In this specimen I found no indication of replacing teeth in the lower jaw.

In the middle line of the roof of the mouth, about opposite the ninth maxillary tooth, and just anterior to the line joining

the first palatine pair, I found a conspicuous longitudinal oval swelling, about 3 by 1 mm., having a whitish appearance in the spirit specimen. Closer examination showed that in the anterior portion of this swelling were two small teeth, one on each side the middle line, and about 1 mm. apart, the left being slightly anterior to the right. Both had their apices directed backwards and inwards, and they had not broken through the oral epithelium. These were, of course, the vomerine teeth, of which the only other indications I have found occurred in a specimen of Stage S (see fig. 13).

Fig. 24 represents a section passing through the middle of the right vomerine tooth, and through the posterior part of the left. Considering the former, we see that it is a well-developed tooth firmly fused with the underlying bone and showing no signs of degeneration. As regards the left tooth, however, the structure is different. In the figure it appears in two portions, this being due in part to the backward curve of the tooth; but its shape in this section is also influenced by the fact that there is a large aperture on the outer side, through which the surrounding meso-derm is in free communication with the pulp cavity. In other sections, also, the tooth is seen to have a somewhat irregular shape and imperfect construction. These facts point to a condition of degeneracy, and it seems possible that the gap in the dentine arose from a similar imperfection of the enamel organ. I have not found any enamel on either of the teeth, but this may have been entirely removed by decalcification. Siebenrock, who described a specimen with vomerine teeth, stated that the tips were covered with enamel, and this may very well have been the case in the present instance. Reference to fig. 24 will show that there are large ingrowths of epidermis closely applied to the internal faces of the teeth. These are, however, continued anteriorly and posteriorly into more or less glandular structures. How far we should be safe in assuming the possibility of a tooth change in this case may be inferred from the previous

observations on the subject of such ingrowths. Here on the vomers there are several of these structures at various points. Anterior to each tooth is a thin, flat band of epithelial cells lying freely below the epidermis, and continuous posteriorly with the epidermal cells in contact with the teeth. I am inclined to regard this as dental in its nature, and as perhaps giving rise to the occasional anterior small vomerine tooth described (on one side only) by Baur (**7**) and Siebenrock (**4**). There are no indications of this tooth in my specimen.

The larger specimen of the last two examined measured 21·2 cm. in total length, and 9 cm. from tip of snout to anterior border of pelvic girdle.

In this individual, as in the last, each premaxilla has two teeth projecting beyond the gum. A microscopic preparation of the right side, however, shows that they are not the same in the two specimens (fig. 22). The following is my interpretation of the tooth change here, although it is possible that other successional teeth may have intervened between the conditions shown in figs. 21 and 22. I believe that No. 3 of the newly-hatched animal has now been shed, and is replaced by the second successional tooth (*t. s.* 2). The first successional is still in place, but it is on the point of being shed to make way for the third (*t. s.* 3), which is nearing the surface. I have confirmed the appearances seen in this entire preparation by sections through the left premaxilla.

In the maxilla there are thirteen and fourteen teeth respectively on the two sides (fig. 27, for the left side). Throughout the whole length a large alternates with a small tooth. An entire preparation of the left side shows that the anterior portion is undergoing tooth change. In addition to the first successional (*t. s.* 1) seen in the last specimen, the second in order is now also a successional tooth (*t. s.* 2). Judging from its size and extent it has replaced two teeth of the earlier set. Finally, there is a third successional tooth (*t. s.* 3) lying deeply seated above the fourth in order, and pointing with its apex towards the fifth. I have not found any indication of a tooth change posterior to this point up to

this stage. In sections of the right maxilla I have found that at the base of the first successional tooth a successor has commenced to form. The indications of an active tooth change in this portion of the maxilla are therefore very marked. The third successional mentioned here is no doubt the one discovered by Baur (7) in the specimen in which he found also the first successional tooth in the premaxilla, and the first in the mandible (to be presently described). He appears, however, to have worked from dissection only, and it is difficult to see how he arrived at the conclusion that these teeth never become functional. The "alveolus" he alludes to as containing the teeth was no doubt the cavity caused by bone absorption. His specimen was evidently slightly younger than the one under consideration.

From the foregoing it is clear that there are at least four successional teeth developed in the anterior part of the maxilla. Sections through the posterior maxillary tooth show that this is large, well developed, and completely fused with the bone. The dental lamina is continued beyond this point for a short distance, but has no traces of enamel organs. From this fact, and other considerations to be presently adduced, I conclude that there is a halt in the formation of maxillary teeth, commencing when about sixteen [1] of the alternating series have been produced, and lasting for a con- siderable period beyond the stage of the specimen now described. It follows that these teeth (all of the alternating series) or their vertical successors, when present, are functional during a large part of the period of growth of the animal. Subsequently new teeth are added from behind forwards, and these are uniform in size. At this stage they have not commenced their development.

Each palatine has seven teeth, which show differences in size but no very regular alternation. In a series of sections through this region I find the enamel organ of a succes- sional tooth situated lingually to the second functional, the usual absorption of bone being in progress. The dental

[1] Probably more, 18—19. See Addendum.

lamina dies out immediately posterior to this point. The seventh palatine tooth is, like the last maxillary, fully formed and fused with the bone. In this case the dental lamina, which reappears here and is continued some little distance backwards, bears two enamel organs, both in the earliest stages. Here, again, we have an indication of a cessation of tooth formation, but from the condition in the adult, and from the above observations, this is much less prolonged than in the maxilla. The two early enamel organs are doubtless destined to form teeth of the uniform series, which are in the adult proportionately much more numerous here than in the maxilla, commencing their formation as we see at an earlier period.

I have found no signs of v o m e r i n e t e e t h in this specimen.

The number of teeth in the two halves of the m a n d i b l e are twenty and twenty-one respectively. Although we may still single out three more conspicuous front teeth on either side, these are not the same as those of the newly-hatched animal, or even of the last specimen. The second is clearly a successional tooth (fig. 26, t. s. 1), and a comparison shows that it has replaced Nos. 2 and 3. In Baur's specimen it was still below the gum. In addition to this, as fig. 26 shows, I found a second successional tooth, deeply seated below the fourth and fifth in order. I have confirmed these points in sections, and find that the first tooth in order shows signs of being deciduous. There is a conspicuous dental lamina attached to the side of the internal fossa nearest the tooth. It extends round the anterior curve of the jaw, and dies out just posterior to the fifth in order. It has a swelling between the second and third teeth, which is perhaps an early enamel organ. I have found no other indications of tooth change in the mandible. Returning to the macroscopic features of the mandibular teeth we find that, posterior to the first two, there are thirteen teeth belonging to the alternating series. Posterior to these, again, are five larger teeth uniform in size. In the last specimen we found also thirteen alternating teeth, and three

or four of the uniform series. We see, then, that, whereas in the maxilla the uniform series of teeth has not yet commenced its development, and is represented by two early enamel organs in the palatine, the teeth are already being rapidly produced in the mandible as the jaws lengthen. The only evidence of the cessation of tooth formation in the mandible was found at Stage T (see p. 180), when there were sixteen teeth of the alternating series, followed posteriorly by one early enamel organ. Stated briefly, then, the position is as follows :—at a stage (differing secondarily, as I believe, in point of time) in the dentition of the three bones under consideration, when the mandible and maxilla have in the alternating series about sixteen teeth each and the palatine six or seven, there is a more or less prolonged cessation of tooth development, this being longest in the maxilla, shortest in the mandible, and intermediate in the palatine. Up to this stage the teeth have shown the alternation in size so often mentioned here, this characteristic being least marked in the palatine. After this period of inactivity, there is a renewed formation of teeth from behind forwards,[1] commencing earliest in the mandible, latest in the maxilla, and continuing during the whole period of growth of the animal. I shall attempt to explain these facts in the next section.

There remain to be discussed a few points of special interest with regard to the succession of teeth. In my description of Stage R, I put forward the view that the smaller teeth of the alternating series represent an earlier set than the larger. The evidence for this was more conclusive in the upper jaw and in the anterior part of the lower than in the posterior part of the latter, where, in my specimens, size alone suggested any difference in the nature of the teeth. I also found that the second palatine gave marked indications of belonging to the earlier dentition. The mandibular alterna-

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[1] The posterior teeth of the alternating series are also, as we have seen, formed on backward prolongations of the dental laminæ. In the case of this series, however, there is no cessation of tooth formation until the set is complete.

ting teeth are subject to great modifications in later stages, and this has no doubt affected their earlier development, so that we may well consider them as originally similar to the rest. At Stage R, then, No. 2 premaxillary, Nos. 2, 4, 6, 8, 10 maxillary (though here this is not quite constant as far as the first five are concerned), No. 2 palatine, and Nos. 2, 4, 6, 8, 10 mandibular, belong to the earlier set of smaller teeth. It is, I consider, a support to this view, that amongst the first successional teeth to be developed are those formed lingually to No. 2 premaxillary, and No. 2 mandibular, the first palatine successional tooth being also lingual to the second in order. In the maxilla the relations are not so clear, though the third successional is lingual to one of the smaller teeth, the first and second giving no indications of their exact place of origin in any of my specimens. The second successional of the mandible lies at the base of two teeth, though from its relations I believe it to have originated lingually to the smaller one. I have already noted that these successional teeth replace, undoubtedly in three cases, and very probably in two others, two deciduous teeth of the alternating series. Now according to my view, in the premaxillæ of Hatteria the following dentitions are represented:

First, or embryonic—those shed during incubation.

Second,—the smaller teeth of the alternating series (i. e. the second in order).

Third,—the larger teeth of the alternating series (i. e. the first and third).

Fourth,—the first and second successional.

Fifth,—the third successional (which, as is required by my theory, evidently replaces only one of the preceding dentition).

I have chosen the premaxillæ for illustration, because they retain their successional teeth in greater number than do the other dentigerous bones, as far, at least, as my specimens enable me to decide.

I have endeavoured to correlate and account for the foregoing anomalies of tooth succession by means of the following

theory :—During the phylogeny of Hatteria there was pro-
bably a period when emergence from the egg occurred much
earlier than it does at present. The presence in ontogeny of a
complete though degenerate set of embryonic teeth, reaching
their maximum of development so long as nine months before
the end of incubation, has already suggested this to us.   Let
us now proceed on the assumption that at one time incubation
terminated at this stage, and that the young animal was set
free with a set of these small teeth.   In the ordinary course
these would be followed by a second set, which are now
represented by the smaller teeth of the alternating series, and
these would in their turn be displaced by the third set, now
appearing as the larger teeth of the alternating series.   After
these would follow, as in more normal reptiles and lower
types, a constant succession of teeth.   For some reason the
period of incubation became greatly lengthened—perhaps
owing to difficulty in obtaining food during the winter months
or to changed climatic conditions,—and the embryo, instead
of remaining about five months in the egg, had the period
prolonged to thirteen months, as at present.   The embryonic
dentition, together with the two dentitions now represented
by the alternating series, were thus developed during the
intra-capsular period.   The first set of teeth became use-
less, and were shed before hatching.   The second set, con-
sisting of much larger teeth, were retained, owing probably
to the disadvantage of shedding or absorbing them within the
egg, as would be necessary if the third set were to take their
places.   These latter, being thus unable to take their proper
positions, were forced to occupy the intervening spaces.   The
animal therefore left the egg with a set of teeth
(called in this paper the alternating series) repre-
senting the second and third dentitions.[1]   The pos-
terior members of both dentitions, however, suffered a
retardation in development, especially in the maxilla, so that
several of them do not now appear till some time after hatch-

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[1] The number of teeth of the first dentition, as compared with those of
the second and third (as seen in the alternating series), is shown in the

ing. The crowding together of these two dentitions on a
small length of jaw, caused in the mandible that early inti-
mate fusion with each other which we observed at Stage S.
Probably, also, this process was associated with an upgrowth
of bony tissue round the bases of the teeth such as we find
at the present time in many of them. All this would render
the process of tooth change more expensive, and it has
therefore become much reduced, confined to the anterior
region of the jaws, and restricted to the period of imma-
turity, when the amount of bone absorption is much less
than it would be in the adult. The reason for the retention
of an active tooth change in the anterior regions of the jaws
is perhaps due to the necessity for an efficient dental arma-
ture in the front of the mouth.

The following diagrams will help to explain my views of
the relations of the tooth change in the premaxillary region
to the normal types of succession. Incidentally they suggest
a possible explanation for that obliquity of position notice-
able in the youngest mandibular and maxillary successional
teeth, where these are seen to lie at the base of a small tooth
(second dentition), and point towards a large one (third den-
tition), both of which they probably replace. The explana-
tion suggested is, of course, that the teeth of the third
dentition being forced to come up between two of their pre-
decessors, gradually came to develop with their apices
pointing in this direction, and that this change also affected
the teeth of the fourth dentition. It must be understood that
the condition found in the first diagram is never realised, the
second set at the present time always alternating with the
first, from the earliest stages. It will be seen that, accord-
ing to my view, the premaxilla had primitively only one

following table. Only the marginal teeth of one side are given, the pre-
maxillary and anterior mandibular being included.

	Upper jaw.	Lower jaw
Stage Q (enamel organs and teeth of first dentition)	9	8
Alternating teeth (second and third dentitions)	17—19	16

tooth,[1] with a constant series of successors, the outer one in
b and *c* being really a maxillary tooth. The dotted tooth of
the fifth dentition has not been found in any of my specimens,
but I believe it will be found to occur in slightly older
individuals.[2]

We are now called upon to account for the presence of
the posterior uniform series, and for the lack of synchronism
in its first appearance in the different dentigerous bones.

That the uniform series must be regarded as a later ac-
quirement than the other teeth, I consider has been suf-
ficiently proved by the facts adduced as to the occurrence of
a cessation of activity when the alternating series have
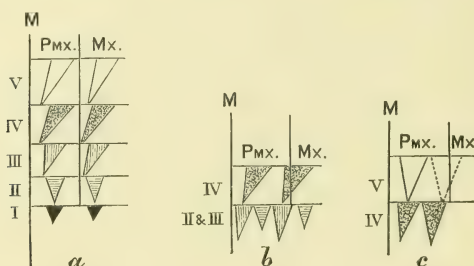
Diagrams to illustrate the dentitions represented in the premaxillary teeth up
to the stage of my largest specimen (compare with figs. 20, 21, and 22).
Dentitions :—I, black; II, horizontal lines; III, perpendicular lines;
IV, dotted; V, blank. *Mx*, maxilla. *Pmx*, premaxilla. *M*, middle line
of jaw. *a*. Purely theoretical, showing all the successional teeth at one
time. *b*. Modified from figs. 20, 21, and 22 of Stage T, and a little
later. *c*. As seen in my largest specimen, with hypothetical tooth added
(dotted outline).

been completed. What was the cause of the development of
this new set of teeth can only be conjectured. It may have
been due to a general increase in size of the animal, or to the

[1] In this connection it is interesting to note that in Zittel's 'Palæontology'
(23) Homœosaurus of the Jurassic, which is placed next to Hatteria in
the family Sphenodontidæ, is stated to have the "Zwischenkiefer paarig
am Vorderrand mit einem einfachen schneidenden Zahn besetzt."

[2] See Addendum.

modifications caused by the lengthening of the incubation period.

The reason for the early appearance of the uniform teeth in the mandible as compared with the maxilla and palatine is undoubtedly to be found in the concrescence described in Stage S; this fusion causes the whole of the mandibular alternating series (not including the first three on each side) to assume the character of a single multicuspid tooth, thus preventing any adaptation to the growth in length of the jaw. As will be seen from the comparative measurements given below, the region in question does not increase in length from Stage T onwards. In the adult it is represented by a short apparently toothless ridge immediately posterior to the large anterior tooth. When this fusion occurred during the phylogeny of Hatteria, the formation of the uniform teeth was hastened, and hence their early appearance at the present time. I have not observed any concrescence in the palatine teeth, but it probably occurs to some extent, as here the uniform series begins its development much earlier than in the maxilla, though later than in the mandible.

The following is a comparative table of the number of, and space occupied by, the alternating teeth or their vertical successors in maxilla and mandible (three anterior teeth not included) at various stages. It is usually impossible to detect the separate teeth of this series in the adult mandible, so that the number inserted is only an approximation. The other figures are averages where possible. It will be found that the number of teeth of this series is less in the adult than in the young. This is partly due to the fact that successional teeth, in some cases at least, replace two of their predecessors, and partly to some of the teeth having become indistinguishable. In the anterior mandibular region also the alternating series is encroached on by the formation of the two compound teeth. I have added to the table the number of uniform teeth.

Comparison of dentition of young with that of adult.—We are now in a position to consider the relation

STAGE.		MAXILLA.		MANDIBLE.	
		Alternating.	Uniform.	Alternating.	Uniform.
S {	Number of teeth	9—10	0	10—11	0
	On length of jaw of	6 mm.	—	5·5 mm.	—
T {	Number of teeth	10—11	0	12—13	0
	On length of jaw of	7 mm.	—	7 mm.	—
Specimen of { 17·8 cm.	Number of teeth	13	0	13	3
	On length of jaw of	10·3 mm.	—	6 mm.	—
Specimen of { 21·2 cm.	Number of teeth	14 (16)[1]	0	13	5
	On length of jaw of	12 mm.	—	6 mm.	—
Adult {	Number of teeth	11	5	7	12
	On length of jaw of	15 mm.	—	5 mm.	—

between the dentition of the last specimen described and that of the adult.

The great majority of adult Sphenodons show two large " cusps " to each incisor. In some cases there are in addition one or two minute projections, which have sometimes been taken for cusps. I believe, however, that these are merely portions of an overgrowth of bone that occurs round the base of many of the adult teeth. It appears certain that there are only two teeth concerned in the formation of each adult premaxillary tooth. Knox (**21**), it is true, stated that he found a specimen with three cones to each, but his description is very brief and not at all clear. I have shown that in my largest young animal the third successional tooth is on the point of replacing the first. All the three teeth of the newly-hatched animal are lost. In the absence of other young specimens I prefer to reserve judgment as to whether the two main teeth of my specimen (i. e. the second and third successional, see figs. 21, 22) are the two components of the adult tooth. On the whole, I think it is very probable that there may be a constant succession of teeth in this region

[1] If the two successional teeth have each replaced two of the alternating series, 16 would be the correct number. All the figures given are approximate, as sometimes the two sides differ slightly. (See also Addendum.)

until the jaws have practically stopped growing. However, most of the teeth of Hatteria retain their odontoblasts in an active condition during the greater part of the life of the animal, and it is possible that no further tooth change takes place.[1] Burckhardt's opinion that the form of the premaxillary teeth is due to concrescence is quite erroneous, if by this term he means the fusion of dentine with dentine before the tooth is fully formed; still more so if he intends to imply the fusion of one enamel organ with another to produce a compound tooth, as has been described in the Chamæleon. The anterior teeth of Hatteria at the last stage I have investigated are successional teeth developed quite independently of one another, and their fusion is produced by the formation of bone round their bases, which even passes some little distance down their sides. The premaxillary bones also grow down, so as to cause their apical tooth-bearing edge to project considerably beyond the gum.

In the maxillæ of a full-grown specimen now before me there are anteriorly on one side three, on the other four, well-defined teeth. The insertion of these on the jaw is not at the same level as that of the teeth posterior to them. The appearance suggests that a small strip of the tooth-bearing edge has been removed, and the teeth inserted along the exposed surface. This is in effect what has happened. As may be seen from several of my figures, when a tooth is shed a large absorption of bone takes place, and the new tooth is inserted at a different level from the old one. The assumption that each of these anterior teeth is a successional one seems quite justifiable, in view of the fact that I have myself found four successional teeth in various stages of development in this region. Assuming, also, that each of these teeth has replaced two others of the alternating series, the number of teeth now left will agree approximately with the original number (say sixteen) of the latter in the maxilla. Posterior to these anterior teeth there is, as I have intimated, a distinct

[1] See Addendum.

step in the dentigerous edge of the bone, and on this higher
level are the much worn members of the original alternating
series. The first three on the one side, and two on the
other, judging by the space occupied by a smooth ridge, are
worn down to the bone, and posterior to this are four teeth
in each case alternating in size. Allowing each successional
tooth to equal two of the original set, and including the
teeth that are obviously worn away, the totals are thirteen
and fourteen respectively. The relationships are not always
so simple as this, but I believe it will be found that tooth
change is confined to the anterior third of the jaw, the first
four maxillary teeth being usually successional. This skull
has on the two maxillæ respectively four and five teeth of
the uniform series. My remarks on the subject of the con-
tinuance of tooth change in the premaxillæ during further
growth will also apply to the maxilla. It is possible, though
not probable, that successional teeth are formed further back
than I have described, but at my latest stage there is no
independent residual dental lamina in the middle region of
the maxilla. This argument, however, in the case of Hatteria
has little weight in view of what we have seen in other
regions, where the dental epidermal ingrowth may remain
latent, as it were, in the face of the internal groove which is
attached to the teeth.

The right palatine of the same adult specimen has a large
anterior tooth, showing the same indications of its succes-
sional nature as do the first three or four maxillary. The left
palatine, on the other hand, terminates in a slightly sinuate
ridge. The successional tooth of the right side no doubt
corresponds with the one shown in fig. 28, and has replaced
Nos. 1 and 2 in order. In another adult skull I find that the
large anterior palatine tooth is present on both sides. It is an
interesting example of the greater variability of the palatine
dentition, that whereas in the first of the adult skulls I have
described the proportion of uniform teeth in maxilla and
palatine respectively is 5 : 7, in the other it is 6 : 5. I be-
lieve that the tooth-change in the palatine will be found to

be restricted to the replacement of Nos. 1 and 2 by a succes-
sional tooth, and that even this may not always occur.

Passing on to the teeth of the lower jaw, we find that the
anterior region, which in the adult is occupied by a large
tooth on either side, has in the newly-hatched animal three
separate teeth in the corresponding positions. We have seen,
also, that the posterior two of these are replaced by a succes-
sional tooth, and that there are signs of the deciduous nature
of the first. My material does not take me far enough to
decide whether any of the teeth of the last young individual
described take part in the formation of the adult tooth. The
presence of a well-developed residual dental lamina in this
region at this stage proves that further change may occur.
Concerning the second successional, it is quite possible that
it may be a component of the adult compound tooth, which
I believe is formed partly at the expense of the anterior teeth
of the alternating series, their vertical successors taking part
in its constitution. In any case I believe the constituent
teeth to be three in number on each side, though in the adult
this is rarely evident.[1] Newman (**22**) appears to have had a
specimen in which the middle cusp was especially distinct.
The "fusion" is produced in the same manner as in the case
of the large incisors. In the adult jaw the large anterior
tooth is succeeded by a short ridge, which is the representa-
tive of the posterior portion of the alternating series. The
teeth are practically worn down to the bone, which is there-
fore, as in some parts of the upper jaw, the functional equi-
valent of the teeth. From the attachment of the large
anterior teeth to the jaw there is a marked step to the level
of this ridge. I have observed that in the falling out of
deciduous teeth in the lower jaw, the amount of bone that is
separated along with the tooth by absorption is very great.
The alternating series of the lower jaw very soon cease
growth, and are hence worn away at an early stage, the
bone here growing very rapidly and becoming dense and
solid. This cessation of growth is no doubt due to their

[1] Two. See Addendum.

early concrescence, which by preventing separation at the base materially interferes with any increase in size. There are in all probability no successional teeth represented in this portion of the jaw. The posterior uniform teeth we have already considered, and a reference to the table on page 194 will show the number present at various stages. I believe that these teeth have never possessed a successional set, and they have no vertical predecessors.

Leaving out of account the uniform series, we are justified in stating that there are at least three dentitions represented in the functional teeth of the adult, viz. a second and third in the persisting members of the alternating series, and a fourth or fifth, or even some later dentition, in the anterior teeth of both jaws. Perhaps members of the later dentitions exist side by side in the adult (as they do in the premaxilla of the young), and if so, there may be four or more dentitions represented in the adult.

The vomerine teeth are undoubtedly in course of sup-pression, as suggested by Howes (3). This is evident from the infrequency of their occurrence (especially as paired structures), and their small size in the adult when present : this view is supported by the evidently degenerate condition of one of the teeth in the specimen I have described. When they occur they seem to begin their development about the end of the incubation period, and I have found no indications previous to Stage S. It is possible that they represent the surviving members of two longitudinal series, as in two cases one vomer has been found to possess two teeth, a smaller one anterior to the larger ; there are also traces of an anterior prolongation of the dental lamina on both sides in one of my specimens.

Contrary to the usually accepted statement, the teeth of Hatteria have a well-developed outer coat of enamel. I have seen this in its earliest stages of develop-ment, and I give a figure of a portion of the fully formed tooth, showing the dentinal tubules branching near their

terminations, and being in many cases continued into the enamel as far as its outer limit (fig. 28). This continuation of the tubules into the enamel has been described in many vertebrates. If a young tooth of Hatteria is treated with 3 per cent. HNO_3 in alcohol, the enamel is in the course of an hour or two completely dissolved, and the dentine is then seen to be surrounded by a fringe of short processes, representing the ends of the dentinal tubules, perhaps still containing the odontoblast processes. As will be seen in fig. 28, the enamel is characterised by the presence of alternate light and dark lines, running approximately parallel to the long axis of the tooth. I have not isolated the enamel prisms, but from the course of the dentinal tubules, from the marked tendency to fracture at right angles to the surface, and from the appearances in early stages of development, I believe these are at right angles to the surface of the tooth, if, indeed, they exist at all as elements possible of isolation.

The first teeth to fuse with the bone show the typically acrodont condition, as seen in fig. 14 of a mandibular tooth of Stage S. At later stages, however, secondary overgrowths of bone occur round the bases of many of the teeth, which thus come to be firmly fixed in a socket with which they are fused at all points externally, as well as at their base. Howes and Swinnerton have used the term "hyperacrodont" for this condition, and it is a very convenient one, inasmuch as we are dealing with a type of attachment which is undoubtedly derived from the acrodont; it would be inaccurate to use here the term "thecodont," since although the base of the tooth is in a socket, the origin of the socket and its relations to the tooth do not indicate a morphological identity with the thecodont type. The bony upgrowth is of a rather peculiar structure. It consists of a number of thin, closely-applied lamellæ, which in transverse sections of the decalcified jaw give the appearance of a number of fibres converging on the base of the teeth. The extent to which the upgrowth actually surrounds the latter varies in different regions. It may be conspicuously seen embracing a considerable portion

of the tooth in the palatines, for instance. This bony over-
growth assists in the "fusion" of the anterior teeth of both
upper and lower jaws, and its outer layers are similar in struc-
ture to the specialised bone described in the next paragraph.

A conspicuous feature of a prepared skull of Hatteria is
the polished appearance of the edges of the jaws for a con-
siderable distance above or below the insertion of the teeth.
Tomes found this outer layer to be true bone, but gives no
details of his preparations. In a ground section of the lower
jaw (transverse) I found the superficial layer to present the
appearance shown in fig. 29. The similarity to enamel is
striking, and this is in some places increased by its tendency
to fracture at right angles to the surface. I have found,
however, that weak acids do not dissolve it, and in some cases
I have been able to trace it into continuity with bone lamella
containing bone corpuscles. These are wanting in the fully-
formed material. In addition to this, it is not so highly
refractive as enamel, though more so than bone, and it seems
to be more affected by weak acids than does the latter. I
therefore conclude that it is a specialised layer of bone,
owing its similarity in appearance (in ground sections) to
enamel to a similar method of deposition by osteoblasts. It
apparently contains more calcareous matter than true bone,
and by its hardness enables the edges of the jaws to
functionally replace the teeth when these are worn away.
As this material is formed by the mesoderm (the process
commences at Stage T), the overlying epithelium moves
further from the teeth, until its line of attachment to the
jaws is separated from the bases of the teeth by a very con-
siderable interval. The intervening bony surface is covered
with this outer specialised layer. It is of interest to note
that in this retreat of the epithelium from the bases of the
teeth, the potential dental laminæ are removed to a great
distance from the latter, so that the succession of teeth in
the adult could only be effected at the cost of an immense
absorption of bone, which is here very dense, particularly in
the mandible. Whether this has been a factor in the partial

suppression of tooth replacement, or whether it has only been concomitant with it, I do not venture to decide.

Summary and Conclusions.

1. The first dentition of Hatteria consists of a set of minute teeth, about thirty-six in number, which originate immediately below the epidermis, labial to the dental lamina. They subsequently pass into the epidermis, and are shed about the time of hatching. The period of their best development is about the fifth month of incubation. They are never functional, and form no connection with the bone. The anterior end of each palatine dentigerous region is first indicated by the development of one of these teeth, formed before the dental lamina. Amongst other reptiles Crocodilus porosus and Iguana tuberculata possess a somewhat similar, though less extensive, functionless dentition, the members of which closely resemble the first teeth of some Selachians as regards place of origin.

2. The dental lamina arises as in other Vertebrates, and its position is at first indicated externally by a dental furrow.

3. At an early stage (R) the dental laminæ and the enamel organs (of the future functional teeth of the newly-hatched animal) in all the main tooth-bearing regions, become involved in epidermal ingrowths, which much obscure the primary relationships of the parts. In each case there is a lingual and a labial ingrowth, and the former carries with it the dental lamina, which is thus for a long period indistinguishable as an independent structure. Towards the end of incubation the lingual ingrowth is mainly converted into a glandular groove; the side attached to the base of the tooth, however, remains in the condition of a stratified epithelium, and may project as an epithelial ridge beyond the deepest part of the groove; it is from the cells of this portion that the enamel organs of the successional teeth are developed in the young animal. The labial ingrowths (labiodental strands) of the premaxillæ, maxillæ, and mandible,

form the labio-dental grooves, that of the palatine an external
groove bounded labially by a prominent ridge (crista medi-
alis) between maxilla and palatine.

4. The teeth which are developed on the dental
lamina during the incubation period, and which
function during the early life of the young animal,
are almost certainly the members of two distinct
dentitions (the second and third), the later teeth
instead of displacing the earlier coming to alter-
nate with them. The chief arguments in favour of this
view are—(a) In the upper jaw, at Stage R, every alternate
tooth is small, is further advanced in development, and has
a lingual prolongation of the dental lamina; these belong to
the second dentition. The other teeth, on the contrary, have
larger enamel organs, are in an earlier stage of development,
and have no lingual prolongation of the dental lamina (third
dentition). In the lower jaw it is chiefly the alternation in
size which indicates the two dentitions. (b) The number of
teeth in the alternating series is eventually approximately
double that of the first set. (c) The first successional teeth
of the young animal, in several cases, each replace a large
and a small tooth of the alternating series. That is, a member
of the fourth dentition displaces not only a member of the
third, but also one of the second. On the other hand, as
seen in the premaxilla, a member of the fifth has only one
predecessor of the fourth.

5. Successional teeth make their first appearance in the
premaxillæ some months after hatching. In this region
there are in all five distinct sets of teeth repre-
sented during development to a length of 21·2 cm.,
commencing with the first or embryonic series. Each pre-
maxilla originally bore one tooth only, with a constant suc-
cession; the presence of three in the newly-hatched animal
is due to the second and third dentitions functioning at the
same period, the premaxilla then having also a tooth of the
third dentition belonging to the maxilla. The number is
reduced to two by the displacement of the premaxillary teeth

of the second and third dentitions by one of the fourth dentition. In my oldest specimen the fourth is the functional dentition in the premaxilla, though there is one of the fifth on the point of displacing its predecessor of the fourth. It is quite possible that more successional teeth will be found in this region on examination of later stages.[1] Each adult "incisor" tooth has two components, but the union is not due to concrescence, being caused by intimate fusion with the bone, which embraces the bases of the teeth and also grows down beyond the gums, thus increasing the apparent size of the compound tooth. Hatteria does not foreshadow the heterodont condition of higher types, but is truly homodont.

6. In the maxillæ the anterior alternating teeth are subject to replacement by members of the fourth dentition, each of these replacing, in some cases at least, two of the alternating series. I have found one successional tooth which I believe to represent the fifth dentition in the maxilla. The first four teeth of the adult maxilla are usually successional (i. e. belong to the fourth or a later dentition).

7. The only successional tooth I have found in the palatines was situated lingually to No. 2 (second dentition). It replaces in all probability both Nos. 1 and 2, and may be seen in many adult specimens as a large tooth at the commencement of the palatine series, if, indeed, this does not represent a still later dentition, e. g. fifth or sixth.

8. The vomerine teeth are in course of suppression. They may be paired or unpaired, and one may show signs of degeneration in structure. In some cases two teeth have been found on one side. In most specimens they are completely absent, probably during the whole of development. The dental lamina is not a conspicuous structure, but appears to have a short prolongation anterior to the teeth. We are perhaps here dealing with the surviving members of two longitudinal series.

9. The anterior portion of the mandible at one stage

[1] See Addendum.

possesses successional teeth belonging to the fourth dentition, replacing, in one case at least, two of the alternating teeth. The number of components of the large front teeth is probably three in each case,[1] the union being produced in the same way as in the premaxillary. I am uncertain how many or which dentitions are represented here in the adult, as I believe further change takes place in larger young individuals than I have examined. In the adult there is posterior to the large front teeth a ridge of bone frequently to all appearance edentulous. This represents the posterior teeth of the alternating series, which, owing to concrescence at Stage S, are unable to adapt themselves to the increasing length of jaw, and lose their power of growth, becoming, therefore, worn down at an early stage. There are probably no teeth of the fourth or later dentitions represented here, those which are formed anteriorly in the young animal taking part in the compound anterior teeth.

10. In the main dentigerous regions there is a more or less prolonged cessation of tooth development when the alternating series is complete. Subsequently a renewed formation of teeth takes place from behind forwards, and these are uniform in size. In the lower jaw this halt is of short duration, and the uniform teeth make their appearance long before those of the palatine and maxilla. In fact, there are already five uniform teeth in the mandible, when in the maxilla this series is not even represented by enamel organs, and in the palatines only by the first stages of two dental germs. This set of teeth is no doubt a more recent acquisition, and has, I believe, like the permanent molars of mammals, no vertical predecessors or successors. The want of synchronism in its appearance in the different regions is due to the fact that the concrescence of the alternating series in the lower jaw prevents the teeth from adapting themselves to the growth in length, as do those of the maxilla, and of the palatine (to a less extent). During the period

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[1] More probably two. See Addendum.

of growth of the animal there is a constant succession of these teeth from behind forwards, the series having once commenced.

11. All the teeth except those of the first dentition have an outer coating of enamel, which, however, does not extend as far as the base of the fully formed teeth. It contains prolongations of the dentinal tubules. The odontoblasts of many of the teeth remain in activity for a considerable period, probably at least till the animal is full-grown.

12. The teeth of the very young animal are typically acrodont in their attachment. Later, through a secondary formation of bone round their bases, many of them come to lie in shallow alveoli, apparently similar to those described in some fossil Rhynchocephalians, such as Proterosaurus and Champsosaurus. Since the teeth are firmly fused with the base and sides of the alveoli, we are not justified in calling them thecodont, and the condition is best described by the use of the term " hyperacrodont," suggested by Howes and Swinnerton.

The sides of the jaws are covered with a specialised layer of bone, apparently more highly calcified than the rest. In the adult a large part of the jaw is exposed, and when the teeth are worn down this outer layer assists the exposed portion to functionally replace the teeth. In some of its macroscopic and microscopic features it resembles enamel.

13. The evidence of the tooth development and succession suggests that the long incubation period of Hatteria (thirteen months) is a comparatively recently acquired character.[1] This view affords us an explanation of the possession, after about five months of incubation, of a complete (though degenerate) dentition,

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[1] This view is also supported by several of Dendy's discoveries. The presence of a characteristic pattern on the skin, after about five months' incubation, and its almost complete disappearance before hatching, is very suggestive. So also is the very early development of the epidermal shell-breaker on the snout.

which is shed before hatching, as well as of the fact that the succeeding set is approximately double the number of the first, and therefore (as is strongly supported by many other arguments) represents two dentitions, which in consequence of their development within the egg have come to form an alternating series. The crowding together of these on too short a length of jaw explains the concrescence which takes place in the mandible : this, again, is the cause of the early appearance of the uniform teeth in this region and their greater number in the adult. It is possible also that the origin in phylogeny of the uniform series, and the other irregularities of tooth succession, may be traced to this lengthening of the incubation period.

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Addendum.

Some time after the foregoing paper was sent to press, I was enabled, through the kindness of my chief, Professor W. N. Parker, to examine the prepared skull of a young Hatteria, whose total length was 24·6 cm. The skull measures 3·5 cm. from premaxilla to occipital condyle. The dentition forms an interesting intermediate stage between the last described and that of the young adult, and a study of it has caused me to slightly modify some of my previous opinions.

The character and disposition of the teeth is shown in the following table, one side only being given. The smaller teeth of the alternating series are so worn, even at this stage, as to be difficult of identification.

	Successional.		Alternating.		Uniform.
Premaxilla .	2	...	—	...	—
Maxilla .	3	...	10—12	...	—
Palatine .	1	...	4—5	...	2
Mandibular .	2	...	7	...	8

In the premaxilla the outer tooth has obviously only

recently cut the gum, whereas the inner is older and more worn. The latter is no doubt the third successional, shown still below the gum in my fig. 22, whilst the former is a fourth successional, belonging, like the third, to the fifth dentition. It is indeed the tooth represented as hypothetical in my diagram c. The bone has not yet grown down with the teeth to any extent.

Of the three successional teeth of the maxilla, the anterior is the least worn and the middle one the most. The posterior is the third successional shown deeply seated in fig. 25 (t. s. 3), the middle one is the second successional (t. s. 2), whilst the anterior is a fourth successional (which I have mentioned but not figured), and represents the fifth dentition, having replaced the first successional (fourth dentition). Posterior to these three anterior teeth are from ten to twelve of the alternating series, but there are as yet no indications of the uniform series. The number of teeth in the upper jaw belonging to the second and third dentitions is slightly greater than I had supposed from my earlier specimens.

Taking the maximum of twelve as the number remaining at this stage, and adding two for each of the successional (maxillary and premaxillary), we arrive at twenty-two as the number of alternating teeth represented on each side of the upper jaw. This would give us eleven each of the second and third dentitions, whereas the first has only nine in the corresponding region. The discrepancy does not, however, constitute any serious objection to the view that the ancestors of Hatteria at one period possessed a dentition consisting of a definite number of teeth, about ten (marginal)[1] on each side above and below, and that these were replaced regularly by vertical successors, without increase in number. As I have already said, the uniform series is almost certainly a later acquisition.

[1] The number of palatine teeth was probably 3—4 on each side, though the evidence here is not so satisfactory as in the case of the marginal teeth. The number of vomerine teeth at this period is quite uncertain.

The anterior palatine tooth is clearly the successional tooth I mentioned in describing my last specimen, and judging from the space it occupies, has replaced at least two of the alternating series. Of the latter there are four to five, posterior to which are two of the uniform series, these being no doubt the representatives of the two enamel organs described in my 21·2 cm. specimen.

The left vomer has a small though well-developed tooth.

In the mandible the anterior region is beginning to assume the appearance characteristic of the young adult, that is to say, the teeth and bone are becoming related to one another in such a way as to foreshadow the two large anterior "teeth." At this stage the components are clearly two in each case, the anterior being the first successional (fig. 26, t. s. 1), while the posterior is the second successional (t. s. 2). The latter is a very large tooth, and, from comparison of this stage with adult individuals, I have come to the conclusion that it eventually forms practically the only actual dentinal portion of the adult compound tooth, the remainder consisting of bone. In the body of this paper I have stated that I consider these front teeth to have each three components. I am now of opinion that there are only two concerned, and that the anterior of these is worn away at a stage very little beyond that we are now considering. The most anterior tooth of fig. 26 is not to be found in the present specimen, and has probably been shed.

Posterior to the large successional tooth are the remaining members of the alternating series, now only seven in number. Since there were originally sixteen alternating teeth on each side, it is evident that the space formerly occupied by nine teeth is now taken up by two only. From this comparison, and from the space in the jaw occupied by the second successional, the latter has obviously displaced six or seven of the alternating series. This would at first sight appear to be very contradictory to my view that a tooth of the fourth dentition usually replaces two teeth, one each of the second and third. The conspicuous irregularity in this case is, how-

ever, probably due to two causes : (1) the fusion of the alternating teeth, which has caused them to occupy less than their proper space on the jaw ; and (2) the large size of the successional tooth in question, due to its importance as the main constituent of the anterior compound tooth.

Posteriorly are eight fully formed teeth of the uniform series, and one in course of development below the gum.

From a comparison of numerous adults with the specimen just described, I believe that very little further tooth change takes place. In most adults, however, the first four maxillary teeth are clearly successional. The fifth is the latest dentition I have been able to trace in any of my specimens, and this is represented in the premaxillæ and maxillæ of the present one.

LITERATURE.

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DESCRIPTION OF PLATES 10—12,

Illustrating Mr. H. Spencer Harrison's paper on "The Development and Succession of Teeth in Hatteria punctata."

LIST OF REFERENCE LETTERS.

Ant. Anterior. *ad.* Adamantoblasts. *b. v.* Blood-vessel. *cav.* Artificial space. *c. g.* Crista gingivalis inferior. *d.* Dentine. *den.* Dentary. *d. l.* Dental lamina. *en.* Enamel. *e. o.* 1. Enamel organ of tooth of first (embryonic) series. *ep.* Epithelium of buccal cavity. *gl.* Gland. *Lab.* Labial side of section. *Lin.* Lingual side of section. *l. d. gr.* Labio-dental groove.

lin. gr. Mandibular (internal) dental fossa. *man.* Mandible. *man. lab.* Epithelial ingrowth labial to mandibular teeth (labio-dental strand). *man. lin.* Epithelial ingrowth lingual to mandibular teeth. *max. f.* Maxillary tooth of functional series. *mes.* Mesoderm. *mk.* Meckel's cartilage. *m. lab.* Epithelial ingrowth labial to maxillary teeth (labio-dental strand). *m. lin.* Epithelial ingrowth lingual to maxillary tooth. *m. p.* Mesodermal dental papilla. *p. lab.* Epithelial ingrowth labial to palatine teeth. *p. lin.* Epithelial ingrowth lingual to palatine teeth. *pmx.* Premaxilla. *post.* Posterior. *r. d. l.* Residual dental lamina. *st.* Stellate tissue of enamel organ. *t. s.* Successional tooth.

(Outlines of all sections drawn with camera lucida.)

FIG. 1.—Section of the enamel organ of a tooth of the first series (first, left, upper), with dental lamina on the lingual side. *d. f.* Dental furrow. (Embryo Q, 52A. Sagittal section. × 240.)

FIG. 2.—Section of the second tooth of the first series, which is already well calcified. (From same series of sections as fig. 1. × 240.)

FIG. 3.—Section through the enamel organ of the first premaxillary tooth (right), belonging to the future functional series. (Embryo R, 142. Sagittal section. × 240.)

FIG. 4.—Section through enamel organ of the right anterior palatine tooth, and the sixth maxillary, of the functional series. The small palatine tooth of the first series is seen lying lingually to the palatine, enclosed in epidermis. The epidermal ingrowth labial to maxillary (labio-dental strand) is just becoming evident. *p. e. o.* Enamel organ of palatine tooth of functional series. *pal.* 1. Palatine tooth of first series. (R, 162. Frontal section. × 60.)

FIG. 5.—Section through left maxillary, palatine, and mandibular dental regions, immediately posterior to first palatine tooth, and through the seventh mandibular. (From same series as fig. 4. × 60.)

FIG. 6.—Section through eighth maxillary tooth of right side. This is one of the smaller teeth of the alternating series (cf. fig. 11), and is more advanced than the seventh (cf. fig. 7). (R, 162. Frontal section. × 240.)

FIG. 7.—Section through seventh maxillary tooth of right side, for comparison with fig. 6. (R, 162. Frontal section. × 240.)

FIG. 8.—Section through the eighth mandibular (left). (R—S. Frontal section. × 60.)

FIG. 9.—Section through right palatine and maxillary teeth to show the relations of the epidermal ingrowths at this stage. *pal. f.* Palatine tooth of functional series. *max.* Maxilla. (Embryo R—S. Frontal. × 60.)

FIG. 10.—View of premaxillary and anterior mandibular teeth at Stage S, from a prepared skull. × 5.

FIG. 11.—Lateral view of teeth at Stage S, to show the conspicuous alter-

nation in the maxillary and the less marked one in the mandibular teeth. Palatine teeth not shown. × 5.

Fig. 12.—Section of a lower tooth of the first series at Stage S. *T.* 1. Tooth of first series. *ep. s.* Capsule of flattened cells. (S. 2. × 240.)

Fig. 13.—Section of palate passing through the enamel organ of the vomerine tooth of left side. *Vo.* Vomer. *V. e. o.* Enamel organ. (S. Sagital. × 240.)

Fig. 14.—Section of mandibular tooth, with bone of jaw. In this section are also figured the labio-dental groove (*l. d. gr.*), formed from the corresponding strand of cells by splitting ; also the mandibular dental fossa, formed in the same way from the lingual ingrowth, cutting off a ridge of mucous membrane (with a core of mesoderm), which runs between the inner face of the jaw and teeth and the tongue (cf. also figs. 5, 8, 19). The glands on the sides of the grooves and on the lower lip (*l. l.*), together with the shelf of the latter, are shown. The enamel of the tooth has been removed in the process of preparation. At the base of the internal dental fossa a solid ridge of epithelial cells (*r. d. l.*) remains non-glandular, and no doubt represents the dental lamina, which has been carried down by the glandular ingrowth (cf. figs. 19, *r. d. l.*, and 18, *t. s.*[1]). (Embryo S, 19A. Frontal section. × 60.)

Fig. 15.—Section of junction of tooth and bone at Stage S. On its internal surface the dentine has a more recently formed layer (unshaded). On the labial side the close attachment of the epithelium to the tooth and bone is shown. *b. c.* Bone-corpuscles. *ep. gr.* Epithelium of inner limb of labio-dental groove. (S, 19A. Frontal section. × 240.)

Fig. 16.—Sagittal section through posterior part of right upper and lower jaws at Stage S, to show the posterior continuation of the dental laminæ of maxilla and dentary. Three large teeth have been cut through, and one small one on the upper dental lamina. *e. o. f.* Enamel organ of tooth of alternating series. (S 2. Sagittal. × 60.)

Fig. 17.—Anterior view of premaxillary and anterior mandibular teeth at Stage T, to show the relative reduction in size of the second premaxillary on each side. × 5.

Fig. 18.—Sagittal section through the second premaxillary tooth of one side, to show the development of a successional tooth, which arises from the epithelium near the deepest part of the internal dental fossa (*lin. gr'.*). The glandular portion of the latter is not evident, and the labial side of the section is damaged. The functional tooth is seen to be attached to the bone on the labial side only. *pmx. t.* Second premaxillary tooth. *t. s.* 1. First successional tooth. (Stage T. Sagittal section. × 60.)

Fig. 19.—Section through third mandibular tooth of one side, showing a well-defined mass of epithelial cells at the base of the internal dental fossa. The interpretation of this as a dental lamina is justified by the formation of

successional teeth on its lingual side at a later stage (see also fig. 18). (Stage T.   × 60.)

Figs. 20, 21, 22.—Three stages in the development and succession of teeth in the premaxilla (right) of specimens 17 cm., 17·8 cm., and 21·2 cm. in length.   1, 2, 3 are the teeth of the newly-hatched animal; *t. s.* 1, 2, and 3, are the successional teeth in the order of their formation.   (*t. s.* 1 in fig. 20 was missing in the preparation figured, but was inserted from sections). × 10.

Fig. 23.—Inner view of the anterior maxillary teeth of left side, from a specimen 17·8 cm. in length.   *t. s.* 1 is the first successional tooth of the maxilla, which has cut the gum but is not yet fused with the bone.   × 14.

Fig. 24.—Transverse section across the vomers (*vo.*), cutting the two vomerine teeth (*l. v. t., r. v. t.*) more or less longitudinally.   The left tooth had a considerable backward curve, which partly accounts for its division into a free and an attached portion.   From the same specimen as the last figure. × 50.

Fig. 25.—Inner view of anterior maxillary teeth of left side, from specimen 21·2 cm. in length.   *t. s.* 1, 2, and 3 are the successional teeth, the last being still deeply seated.   × 14.

Fig. 26.—Inner view of anterior mandibular teeth of left side, showing two successional teeth.   *t. s.* 1 no doubt replaced two of the earlier set (from same specimen as last figure).   × 14.

Fig. 27.—Outline of marginal teeth of 21·2 cm. specimen.   The uniform series in the lower jaw already occupies considerable space, whereas all the maxillary teeth are of the alternating series or their vertical successors (the same may be said of the palatines at this stage).   × 5.

Fig. 28.—Portion of ground longitudinal section through the base of a young tooth, to show the branching dentinal tubules (*d. t.*) with their prolongations into the enamel (*d. t'.*).   × 300.

Fig. 29.—Portion of a ground section through the specialised outer layer of bone, on the lingual side of the adult lower jaw, to show the close resemblance to enamel.   *b. c.* Bone-corpuscles.   × 300.

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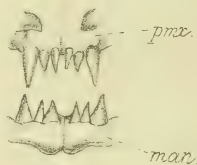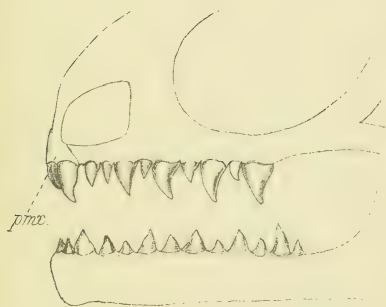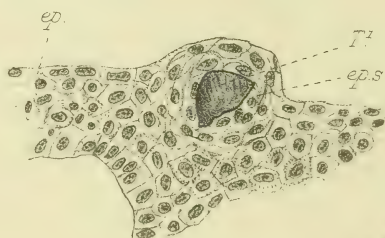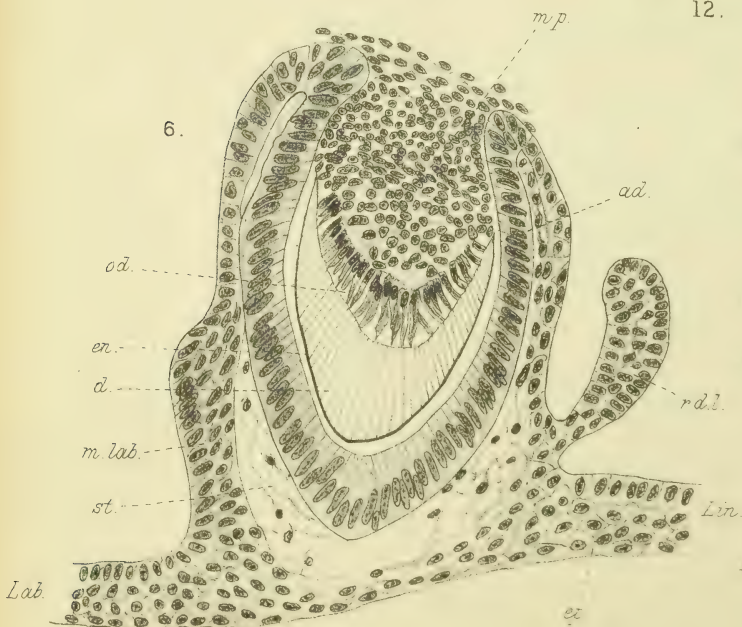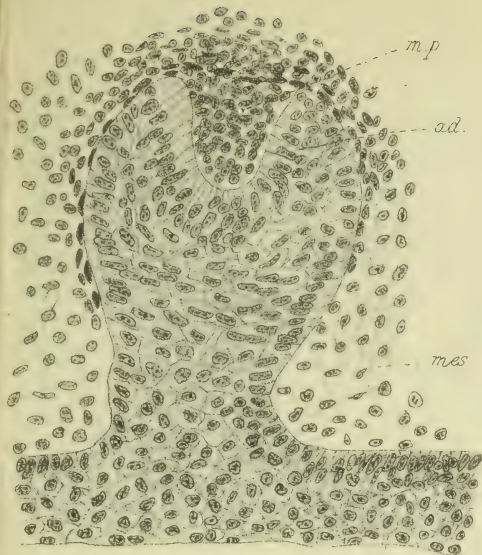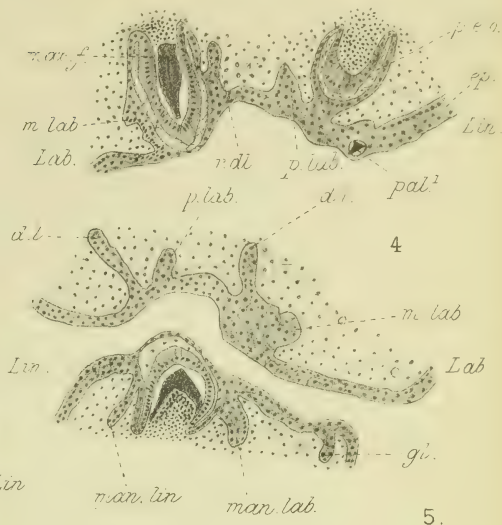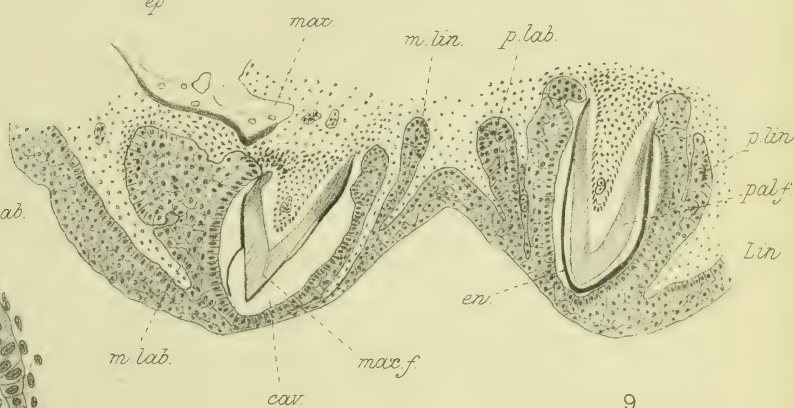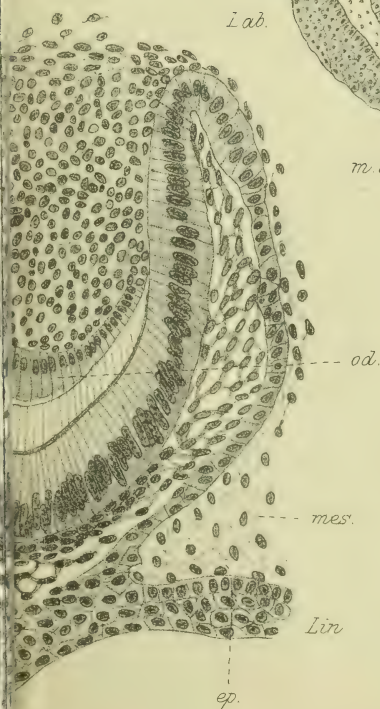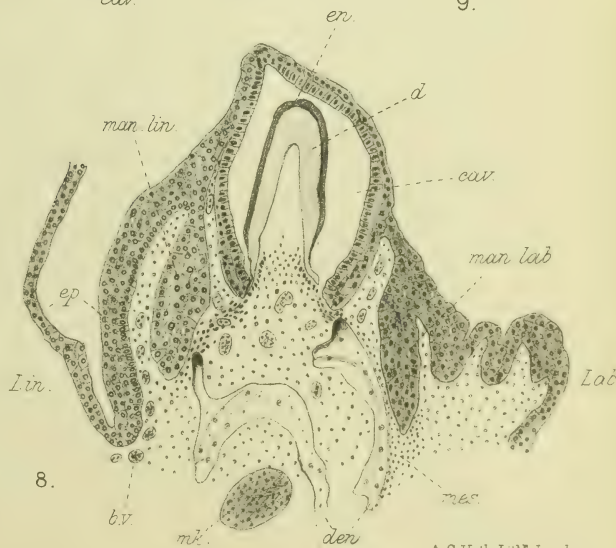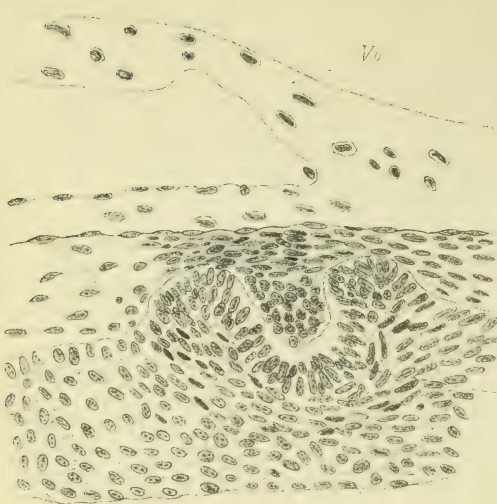
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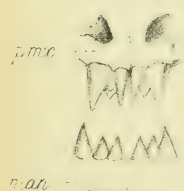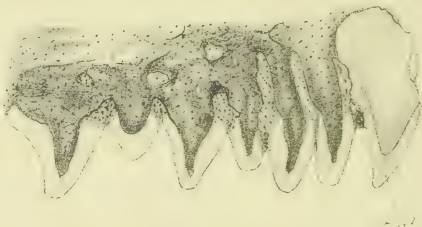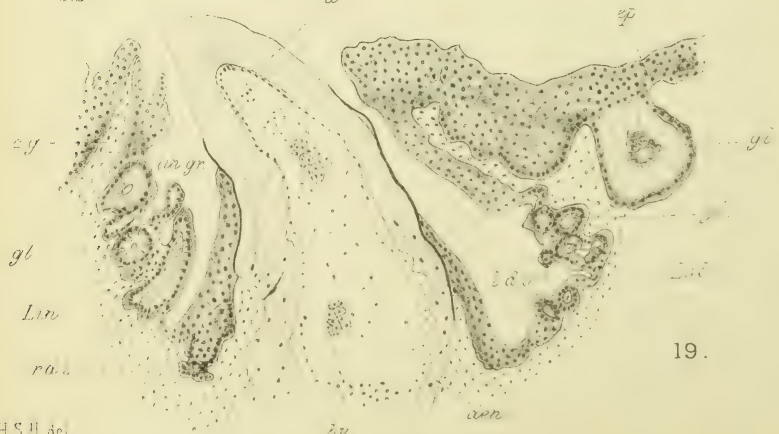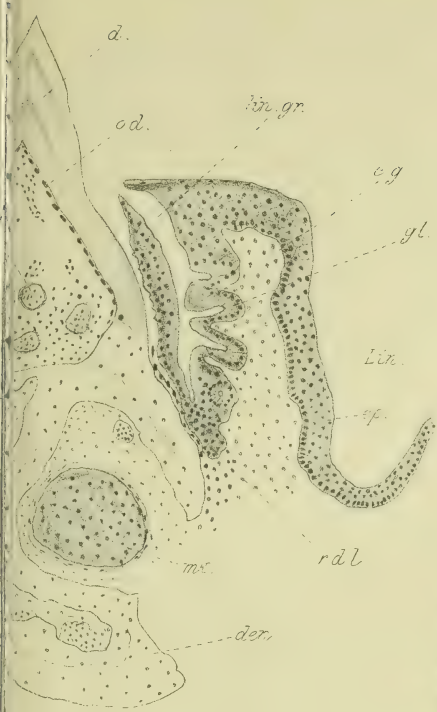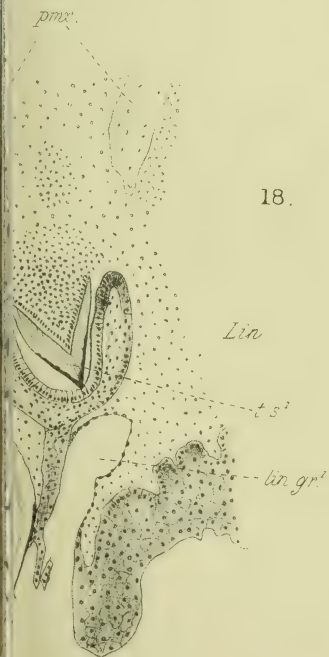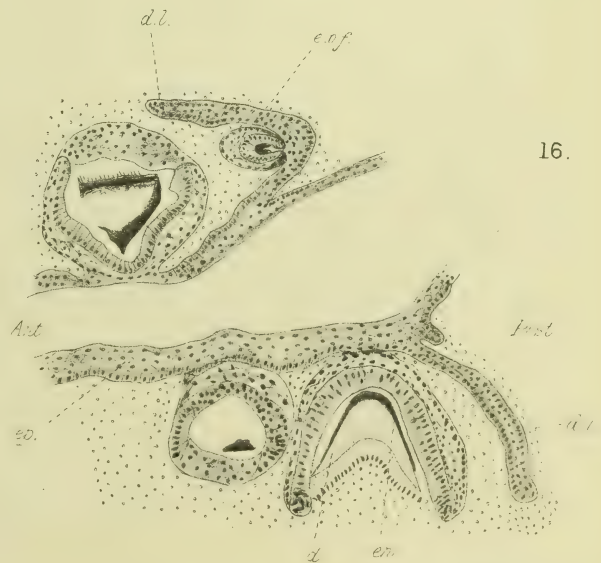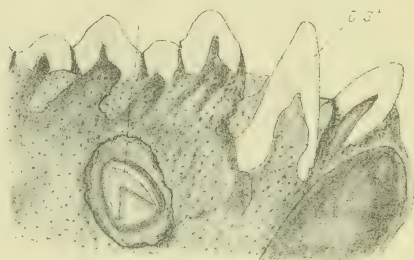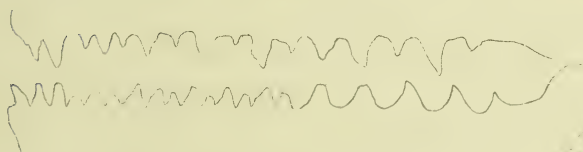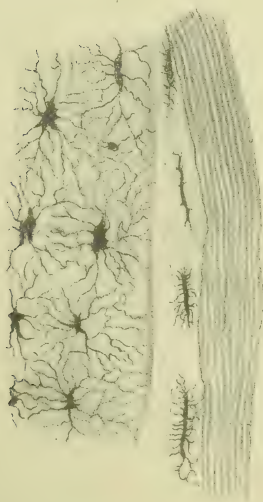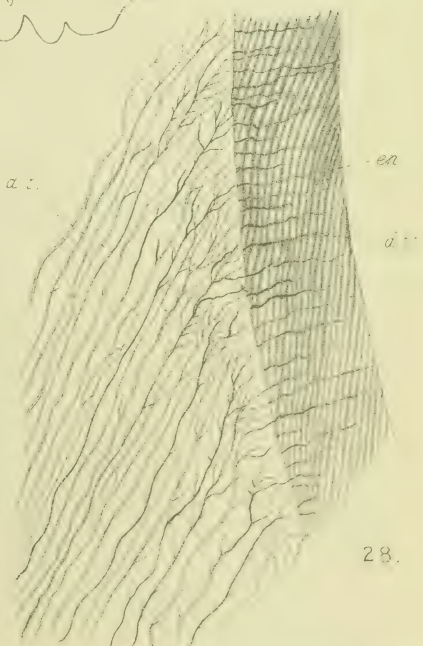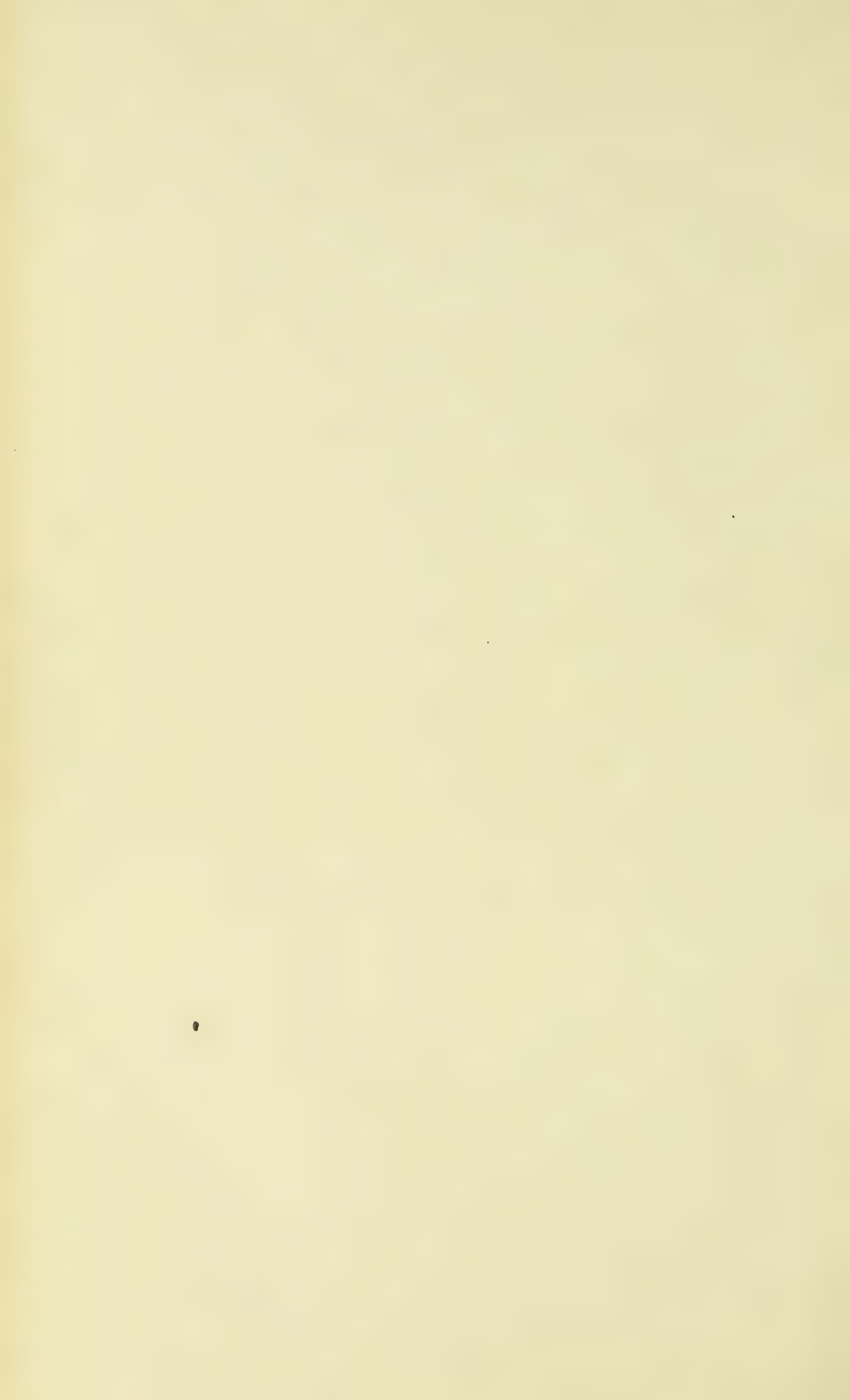
The Anatomy of Pleurotomaria Beyrichii, Hilg.

By

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With Plates 13—16.

THE vast antiquity which characterises the genus Pleuro-tomaria—for no one can doubt the identity of the living and fossil shells which are customarily grouped together under this name—has justly endowed this mollusc with great interest for those studying the ancestry of the Prosobranchia. When, therefore, a living example was obtained by Agassiz in 1871, and later in 1879 several specimens of both P. Quoyana and P. Adansoniana were dredged by the United States steamer "Blake," the result of an investigation of the anatomy of these forms was awaited with great interest. Unfortunately, however, the specimens all turned out to be in a bad state of preservation, and although falling into such skilled hands as those of Dr. Dall, it was found impossible to make out much of their anatomy. Dall, how-ever, published [1] figures and descriptions of the external characters of the animals, of the radulæ and of some few points in connection with the pallial complex, the rest of the body being too much decomposed for investigation.

During the last few years a further examination of one of

[1] "Report on the Mollusca dredged by the United States steamer 'Blake,'" 'Bull. Mus. Comp. Zool., Harvard,' vol. xviii, 1889.

the specimens of P. Quoyana obtained by the "Blake" has
been made by Fischer and Bouvier,[1] and these authors have
made a still more detailed examination of the radula of this
form, and also of the nervous system, which had not previ-
ously been examined. These investigators have published a
most exhaustive history of the genus, giving in addition a
complete list of the recent specimens obtained up to the year
1898, and they further append a full literature relating to
this mollusc. Since it is not my intention to enter into these
branches of the subject, I must refer the reader to Messrs.
Bouvier and Fischer's paper.[2]

Through the kindness of the Director of the Natural
History Museum I had placed at my disposal an example of
the animal of P. Beyrichii obtained off Boshu, in Japan.
The animal was beautifully preserved, but unfortunately it
declined to part company with its shell save in pieces, so that
my first investigation was much retarded by having to build
up the anatomy of the animal from these fragments. Fortu-
nately, however, two more specimens were obtained by the
Museum and handed over to me by Professor E. Ray Lan-
kester, whom I have to thank for entrusting their examina-
tion to me. Without these additional specimens my results
would have been very incomplete, since the first specimen,
though in much the best state of preservation, was in so
many fragments that it was extremely difficult if not impos-
sible to make out the exact relations of some of the organs.
Although my investigations are largely based on an examina-

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[1] "Étude monographique des Pleurotomaries actuel," 'Archiv. Zool. éxp.'
(3), vol. vi, 1898. Reprinted in 'Bull. Mus. Comp. Zool., Harvard,' vol.
xxxii.

[2] Since the publication of Bouvier and Fischer's monograph at least five
new specimens of P. Beyrichii have been obtained. These all came from
the Boshu, Japan, being captured alive in nets set at the bottom at a depth
of seventy to eighty fathoms; they were preserved in spirit with the animal.
One of these specimens has been described by Rolle ('Nachrbl. Deutsch.
Malak. Ges.,' 1899) as a new species under the name of P. salmiana. I
think, myself, that is only a variety of P. Beyrichii. An additional shell of
P. Adansoniana has also been obtained.

tion of the fragmentary specimen, they have in every case been verified by a comparison with the two complete specimens.

The External Characters.—The first example which came into my hands was the identical specimen whose external characters were described by Professor Mitsukuri in the 'Annotat. Zool.,' Japan, vol. i, p. 67; consequently I cannot do better than quote his description in extenso.

"The animal was not very lively and could not be persuaded to extend itself fully. At the utmost we were able to see the foot and a part of the head. The sole of the foot was straw-yellow. The side of the foot and the throat were mottled with large and small patches, and streaks of deep carmine-red on the ground colour of reddish yellow. The proboscis was uniformly deep carmine-red. The left tentacle had a small branch near the tip. On the sides and the posterior aspect of the foot we were able to make out two lobes, one standing up from each side of the foot and applied to the shell. It seemed probable to me that when fully extended these lobes enveloped the shell to a greater extent, a supposition which is strengthened, as was first pointed out by Mr. Namiye, by the fact that the shells of Pleurotomaria hitherto found are all extremely clean, and have never barnacles, worm-tubes, etc., attached to them. The mantle was not at all visible, and we were thus not able to see how it is related to the slit on the outer lip."

It will be seen from the above account that Mitsukuri makes no mention either of the presence or absence of an operculum—a strange omission when we remember that an operculum had been described by Dall as present in both P. Quoyana and P. Adansoniana. When I received the specimen I found that it had no operculum, nor could I find, after a careful examination, any suggestion that the operculum had been torn away. The only indication of the possible presence of this organ was a minute lobe (fig. 2, *op. l.*) situated on the dorsal side of the foot in the position of the opercular lobe of Trochus. The arrival of the

second specimen, however, showed that P. Beyrichii, like the two other species mentioned above, possessed a fairly stout though somewhat small operculum attached to the foot by a large circular lobe (figs. 3 and 4). We are, however, still unable to determine whether the first specimen had lost its operculum during its free life, or if it had been born without one. Judging from the presence of the opercular lobe, I should be inclined, in spite of its small size, to suggest that the operculum had been present, but accidentally lost either through disease, or mishap, early in life.

The operculum (fig. 4) is nearly circular in outline, measuring, in the largest specimen, 14·5 mm. in diameter; in character it is trochiform, consisting of about twenty closely coiled whorls, strongly marked with line of growth. It is apparently composed solely of dark brown horny (chitinous) matter, and for its size is very thick and strong, retaining its thickness quite to the margin.

The mouth of the shell from which the operculum was taken measured 40 mm. in transverse and 30 mm. in vertical diameter. Hence it will be seen that the operculum can be of very little use in closing the aperture, and thus protecting the retracted animal; it may, however, be of some service in protecting the upper surface of the foot from mechanical injury which might be caused by the rubbing of the shell when the animal was fully extended, since under these conditions the shell rests, as in the Trochidæ and Turbinidæ, directly upon the operculum.

Compared with the opercula of P. Quoyana and P. Adansoniana, the operculum of P. Beyrichii appears to most nearly resemble that of the first-named species, although Dall in his description does not mention what is such a striking feature in P. Beyrichii, the thickness of the operculum. In P. Adansoniana the operculum is very much larger and thinner, and still more closely resembles the opercula of the Trochidæ.

The small size of the operculum in two of the three specimens, and its absence in the third, suggests that this organ

is of very little importance to P. Beyrichii, and that possibly it will disappear in the near future.

The Foot.—The foot, although contracted in my specimens, is still very large, and is evidently capable of great extension.   As is the case with many Prosobranchs its anterior margin is double (figs. 1, 2, and 7), the upper surface of the foot being separated from the sole by a well-marked transverse groove. We are quite at a loss to account for this structure, which is evidently of great importance since it is present in so many Gastropoda.

The lateral surfaces of the foot are finely rugose, being closely beset with minute papillæ (figs. 1 and 2).   These papillæ are wanting on the dorsal surface, which is separated from the lateral surfaces by the paired epipodial folds (ep.). At the anterior extremity of the dorsal surface is situated the opercular lobe (figs. 2 and 3, op. l.); this in its functional condition is circular and nearly as large as the operculum.   On the right side it is produced out into a little lobe, which is in turn attached to the upper surface of the foot, and marks the growing point of the multispiral operculum. Behind the opercular lobe a median longitudinal groove leads to the posterior end of the foot; on either side of this is a modified area due to the presence of numerous transverse grooves originating from the median one; some of these are symmetrically arranged, but others are unpaired (fig. 2).

This somewhat ᴠ-shaped modified area is bounded in front by a couple of longitudinally-placed bands running back from under the opercular lobe; these, however, only extend for about one third of the length of this area, which is elsewhere bounded by a groove marking the commencement of the epipodium.   A similar modified area was found by Dall in P. Adansoniana, but strangely enough this appears to be quite wanting in P. Quoyana, a point upon which Dall lays some stress. This is a very curious fact, for in other respects, notably in the operculum and in the radula, as we shall see later, P. Beyrichii is more closely related to P. Quoyana than to P. Adansoniana, a relationship which

had already been noted by Crosse and Fischer from a study of the shells, and expressed by the institution of the section Perotrochus for the first two species.

This peculiar specialised area is also to be met with in the Trochidæ (notably in T. [Gibbula] magus and T. [Callio-stoma] zizyphinus); but though so commonly present, I am unable to offer any suggestion as to its function.

The Epipodium.—This structure, which is so charac-teristic of the majority of the Diotocardia, or of that sub-division for which Fischer proposed the name Thysanopoda, is not conspicuously developed in P. Beyrichii. It takes the form of a couple of folds, one on either side of the body. They start a short distance behind the head and attain their maximum development in the region of the operculum; whence they extend back in the posterior extremity of the foot, practically meeting in the middle line behind the median dorsal groove. These folds, which are evidently somewhat contracted in the spirit specimen, are like the rest of the body covered with minute papillæ, and are entirely devoid of those accessory lapets and tentacles so characteristic of the epipodia of the Trochidæ, Haliotidæ, and other Thysanopoda. Judging by the figures given by Dall (op. cit., pl. xxx, figs. 1, 4, and 5) of the living animal of P. Adansoniana, the epipodium would be more conspicuous in the living animal in P. Quoyana; Fischer and Bouvier even speak of it as being largely developed. In comparison with the Trochidæ and Haliotidæ, however, I should rather conclude that the epipodium was feebly developed in Pleurotomaria.

I do not think there is any evidence to support the view advanced by Mitsukuri that these lobes partly envelop the shell, although they are apparently closely applied to its base, and I would rather account for the clean nature of the shell by the habitat of the animal being in deep water—seventy to eighty fathoms,—where life, both animal and vegetable, is not so abundant as in the littoral zone inhabited by the Trochidæ, whose shells are so generally encrusted with foreign matter.

The Head.—The head is large and produced into a somewhat cylindrical snout, bent downwards as in the Trochidæ. On the under surface, which is abruptly truncated, is situated the mouth, surrounded by a horseshoe-shaped lip, the gap in the lip being placed ventrally. The head and anterior part of the body are much smoother than the foot, being practically devoid of papillæ. The tentacles are situated low down on either side of the head. In form they are cylindrical, with roughly pointed extremities ; they are highly muscular and evidently much contracted. The only peculiar feature about them is the tendency which they show to become branched at their free ends ; this is most marked in the left tentacle of the first specimen examined (fig. 1), but the second specimen also showed indications of a similar condition in both tentacles, although to a lesser degree, while the right tentacle of the third specimen shows no less than two accessory branches.

The Eyes.—The eyes, which are small and inconspicuous, are situated, each on a slight elevation, at the posterior side of the base of the tentacle. Examination with a lens shows the cornea to be perforated, as in Trochus and most Diotocardia.

An examination of sections (fig. 20), however, shows that they are simple in constitution ; like those of Trochus the central cavity is only partially filled by a vitreous body, the rest of the space being occupied by sea-water.

The eyes, as may be supposed, are not specially well preserved, but one can see that the retina consists of a series of pigmented rods, turned towards the optic cup, and an external layer of ganglionic cells. I was unable to make out the clear distal segments of the rods, such as are figured for other Diotocardia. The retina is bounded by a delicate capsule, outside which we see the optic nerve and a few mesodermal pigment cells. The retinal pigments extend out through the perforation in the optic cup into the adjacent epidermis. The structure of the vitreous body suggests that is secreted by the individual rod-cells.

The Mantle.—In the contracted state of the dead animal the mantle-slit, so characteristic of this genus, is inconspicuous, and appears more like a broad, shallow sinus than a deep narrow slit ; even in the living animal Mitsukuri was unable to observe its relation to the shell-slit. Its true relation is, however, well seen in Dall's figures of P. Quoyana and P. Adansoniana taken from the living animal. In these forms we see that the margins of the mantle-cleft are closely applied to the margins of the shell-slit, through which they may slightly protrude. The free edge of the mantle is thickened and closely beset with numerous small papillæ, which are evidently slightly protrusible, although not to the extent seen in Haliotis. The mantle-fold completely encircles the body, but is only feebly developed behind, and in this region its margin is quite smooth.

The Pallial Complex.—Owing to the bad state of preservation of the specimens collected by the "Blake," Dall was unable to give us much information concerning the organs falling under this category ; he was further unfortunate in his attempts to identify these badly preserved parts, and consequently, beyond a slight knowledge of the gills, we were quite in the dark as to the relations of the kidneys and the genitalia, since the structures to which Dall, and after him Fischer and Bouvier, applied these names, have quite different significances.

The Ctenidia.—The gills are very large and conspicuous, and possess the form characteristic of the Scutibranchia (figs. 5, 6, 7 and 14). The two gills, though symmetrically placed, are not equally developed, that on the left side being very much larger than that on the right (cf. figs. 5 and 7). This is a very interesting feature, which is obviously connected with the dextral coiling of the shell, and one which is of great significance when studying the phylogeny of the Azygobranchia. Each gill is characteristically bipectinate, consisting of an axis which takes the form of a long and somewhat stout septum, containing the efferent and afferent branchial vessels, and two sets of gill-filaments, which have the

form of triangular plates, whose surfaces bear a number of
fine plications (fig. 14).   In each gill the inner or under set
of plates are somewhat smaller than the outer set, a con-
dition leading towards the more specialised one seen in the
Trochidæ.   As in other Scutibranchs, the anterior end of
each gill is not attached to the mantle, but projects freely
into the mantle-cavity, and, in the contracted state of the
mantle, almost beyond the anterior margin of that fold.

Structure of the Gill-plates.—A careful study of
sections of the gill taken through the three principal planes,
i. e. transverse to the long axis, longitudinal sections parallel
to the gill-septum, and horizontal sections, enables us to
construct a diagram (fig. 15) showing the circulation of the
blood in the gill-plates.   The afferent branchial vessel (*a. b.*),
as we have already seen, is situated at the ventral edge of
the gill-septum under a thickened ridge of glandular epi-
dermis; this vessel gives off on either side small branches,
which enter one into each of the very thin gill-plates.   The
vessel then spreads out as a delicate film between the two
laminæ which together constitute the plate.   After the blood
is aërated by being brought into such close proximity to the
sea-water it leaves the plate near its dorsal attachment, this
efferent channel joins across the septum with the corre-
sponding vein from the opposite plate, the conjoint vessel runs
up the septum and enters the efferent branchial vessel (*e. b.*),
which lies at the junction of the septum and mantle.   It must
not, however, be supposed that the space between the two
laminæ of a gill-plate is as simple as represented diagrammati-
cally on the left of fig. 15; such is not the case, the space
being broken up into numerous small channels by the pre-
sence of great numbers of interlaminar connections (*i. l. c.*,
figs. 15, 16, and 18), extending across the space and joining
the two laminæ which compose the gill-plate.   The blood thus
takes a very sinuous course among these connections.   A
somewhat larger channel is, however, present all round the
margin of the gill-plate.

The extremely delicate nature of the gill-plates is well seen

in fig. 16, which represents vertical sections across two gill-plates. The ventral and dorsal margins are seen to be dilated, as also are the blood-spaces nearer the dorsal margin, in which region also the interlaminar connections are larger and fewer, whence the dotted appearance seen in fig. 14. The curious crumpling shown in the ventral part of these plates (fig. 16) represents transverse sections through the folds seen in the surface view of gill-plate (fig. 14); this appearance suggests that the margin of the gill-plate is too short to surround the central area without the latter becoming puckered. The gill-plates present another interesting feature in the presence along their outer margins of a couple of supporting rods (*s. r.*), the relations of which are well shown in figs. 15 and 18. From an examination of a transverse section of these rods (fig. 18) it will be seen that they are flattened structures, closely applied to the base of the epidermal cells, and enclosing between them portions of the blood-space of the gill-plate. A section taken parallel to the gill septum and passing through the dorsal junctions of the gill-plates with the septum (fig. 17) shows that the two rods in each plate are perfectly independent of one another, and that each rod is related to two gill-plates. In other words, each rod is a U-shaped structure which embraces the space between two gill-plates, one limb extending into each of these plates, a condition which at first sight reminds one of the relation of the gill-skeleton in the Lamellibranchia. The epithelium covering the margin of the gill-plates is thickened and specialised; that covering the ventral margin is ciliated (fig. 16), so, too, is that covering the outer border of the plate (fig. 18). Specially long cilia are present near the outer margin in two bands, one on either side of the plate a short distance from the free margin (figs. 16 and 18); the cells bearing these cilia are particularly large, and are closely related to the supporting rods.

Comparison with the Lamellibranch Gill.—The general structure and relation of the gill as seen in the zygobranchiate Diotocardia is highly suggestive of that

met with in the more lowly Lamellibranchs, viz. the Proto-
branchia (Mitsukuri [1]). Consequently one might naturally
expect to find a similar resemblance in the finer structure of
these two organs. In this, however, one is doomed to disap-
pointment, for although at first sight there appears to be a
great resemblance (cf. Mitsukuri, op. cit., pl. xxxiv, figs. 6
and 8, and my figs. 17 and 18), yet when we examine this
more carefully we find that instead of a resemblance, there is
in reality a very marked difference. Thus in Nucula the
supporting rods lie along the ventral border of the gill-plates
and meet along the ventral edge of the gill-septum, whereas
in Pleurotomaria, as we have seen, the gill-skeleton is
situated along the outer or dorso-lateral margin of the plates,
and the connections between the adjacent rods take place at
the dorsal attachment of the plates to the septum. Simi-
larly, the modified ciliated epithelium, which is closely related
to these rods, is dorso-lateral in the Gastropod, and ventral in
the Lamellibranch. We thus see that there is a very strik-
ing and fundamental difference in the relation of the gill-
skeleton in the two groups, and one which must tend to throw
back the common ancestor of the two to a still earlier period
than that generally assigned to it.

The dorso-lateral position of the supporting rods is, how-
ever, found in another great Molluscan order, the Cephalopoda.
Thus in Sepia Burne [2] has described cartilaginous rods, one to
each gill-plate, strengthening the supporting lamella, in a
position corresponding to the outer and dorsal margin of the
gill-plate of Pleurotomaria. This is an interesting point,
for, as we shall see later, the Diotocardia appear to approach
the Cephalopoda further in the relation of the spiral stomach-
cæcum. The skeletal difference between the gills of the
Diotocardia and the Protobranchia is, however, far more
surprising than the resemblance of the former to the Cepha-
lopoda, for, in addition to the general form and relation of

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[1] "On the Structure and Significance of some Aberrant Forms of Lamelli-
branchiate Gills," 'Quart. Journ. Micr. Sci.,' vol. xxi, 1881.

[2] 'Proc. Mal. Soc.,' vol. iii, p. 53.

the gill, Nucula approaches the Diotocardia in so many other respects that one would naturally have expected a very close agreement on this point. In the face of the unexpected difference one feels some doubt as to the full value of generally accepted views on the relations of these forms.

The Branchial Ganglia.—On the outer side of each gill and close to its anterior point of attachment is situated a very conspicuous hemispherical swelling (figs. 5, 6, and 7, *bn. g.*). These protuberances, which were described by Dall as blood-sinuses, are caused by the presence of a large ganglion, situated on the branchial nerve. The branchial ganglia are the most conspicuous ganglionic swellings on the nervous system. In section (fig. 19) they exhibit a great accumulation of nerve-cells, arranged in two layers round the periphery of the ganglion, a narrower outer and a broader inner layer, the two being separated by a very narrow band of fibrous tissue. The centre of the ganglion is occupied by a great mass of fibrous tissue, the bundles of which run in various directions. Near the periphery of the central mass are some curious dim bodies, which at first sight suggest large ganglionic cells ; but the entire absence of nuclei and the want of sharpness of outline lead me to conclude that they are in reality bundles of fibre, rather more closely packed than usual.

A very large nerve is given off from the ganglion to the gill, and from this is derived that very conspicuous layer of nerves (fig. 15, *n. l.*) following the course of the efferent branchial vessel.

The Osphradium.—Dall has figured a small hemispherical structure, situated somewhat nearer the middle line than is the branchial ganglion (blood-sinus of Dall), which he thinks may represent the osphradium. His description of the position of this organ is, however, not very clear ; and a comparison of his figure (op. cit., pl. xxx, fig. 2) with my fig. 6 suggests that the gill he represents is the right gill seen from below, in which case his osphradium would in reality be situated externally to the branchial ganglion, its

more median position being only an apparent one due to the displacement of the mantle in the dissection. However this may be, I have utterly failed to find any such structure, either internally or externally to the branchial ganglion ; and if I am correct in my identification of the osphradium I cannot help doubting the osphradial nature of the structure to which Dall assigns this significance in P. Adansoniana.

While examining a series of transverse sections through the free end of the gill I noticed a thickened patch of epithelium situated on the ventral or external border of the gill, and extending from near the point of attachment to the free end (figs. 5—7, *os*.). An examination of these sections shows that this thickened patch of epithelium overlies the great branchial nerve, and receives numerous branches from it. The epithelium itself has all the character of a sensory one, consisting as it does of delicate fusiform cells supported by more columnar ones, and also exhibiting a few pigment cells. Although a few gland cells are to be seen they are much less numerous here than in the adjacent epithelium. At times there is even a suggestion of the bunching together of these cells into oval masses, not unlike the taste bulbs of the Vertebrata and the sensory organs of Acavus Waltoni, as described by the Sarasins.

The identity of this strip of sensory epithelium with the osphradium is confirmed by a comparison with the latter organ, as seen in Haliotis. In this genus the osphradium, as described by Spengel, has precisely the same relationship and form as the strip of sensory epithelium found in Pleurotomaria Beyrichii, which last we may, I think, safely identify as the osphradium.

At the posterior end of each gill the afferent and efferent branchial vessels may be seen (figs. 5 and 7, *a. b.* and *e. b.*). The former, springing from a sinus (figs. 7 and 23, *v. s.*) situated ventrally to the rectum and ureter, run forward near the former structure and diverge outward to the gills ; while the latter, passing on either side of the mantle-cavity, converge on the heart. As we have already seen, the afferent

vessel lies near the free margin of the gill-septum, while
the efferent vessel is situated at its base.

The Hypobranchial Mucous Glands.—One of the
most striking features in the mantle-cavity is a large oval
glandular structure, which, occupying a median position,
extends from the posterior limit of the mantle-slit along the
roof of the mantle-cavity to about the level of the posterior
end of the right gill (figs. 5, 6, and 7, *m. g.*).

In one specimen this gland still retained a pinkish colora-
tion. This gland is partially divided by a median longitudinal
furrow into two halves, each of which is marked by a number
of more or less interrupted grooves which converge on the
median one. The whole structure presents an appearance
not unlike the venation of a leaf. Anteriorly, however, the
two halves of the gland slightly separate from one another,
and end in a couple of pointed structures, in which Dall
thought he could perceive openings which he took to be the
renal apertures. In this supposition he was mistaken, for
the renal organs have a perfectly normal position, and the
gland, as may be seen from a microscopic examination, is a
true mucous gland : further, if we examine Haliotis we
shall find a gland, the hypobranchial mucous gland, occu-
pying a precisely similar position; and I think there can
be no question as to the homology of these two structures
and of the similarly named gland of the Monotocardia.

Two additional mucous glands are found in the roof of the
mantle-cavity behind the large hypobranchial gland (figs. 5
and 7, *mg'.* and *mg''.*) ; these are situated one at the base of
each gill, that on the left being much the largest, a further
example of the asymmetry which we have already seen fore-
shadowed in the gills, and which affects the whole pallial
complex.

The rectum is situated somewhat to the right side, and
extends forward over the hypobranchial gland in a variable
manner (cf. figs. 5 and 7) ; but in neither of my specimens
does it extend so far forward as in the P. Adansoniana
figured by Dall.

The Kidneys.—As in the majority of the Diotocardia, there are two kidneys, a right and a left one, which exhibit very different structure and perform different functions. The left kidney or papillary sac is situated in the left-hand upper corner of the mantle-cavity. In form it is somewhat oval, and it opens by a wide slit-like aperture into the mantle-cavity near the rectum (figs. 7, 23, and 26, *l. k. a.*). On cutting open this sac it is found to have a large central cavity bounded by thick walls, whose epithelium is thickened and forms numerous rounded papillæ; the outer wall is, moreover, folded. As in Trochus and Haliotis, this left kidney alone communicates with the pericardium, the reno-pericardial pore taking the form of a long canal, which runs along the floor of the papillary sac and opens into it near its external aperture by a ciliated slit (figs. 24—26, *r. p. c.*). The structure of this kidney and the relation of the reno-pericardial pore closely resemble that seen in Trochus, the only difference being that in the latter the reno-pericardial canal is distinctly shorter, about half as long, but otherwise it has the same relation. Unlike the condition seen in Patella (Goodrich[1]), it is the aperture leading into the kidney which is ciliated in Trochus, and not that leading into the pericardium.

A microscopic investigation of the papillary sac shows that this organ is highly vascular, but I have been unable to ascertain whence this blood-supply is derived. According to Perrier[2] the vascular system of the left kidney of the Diotocardia is directly connected with the auricle or auricles, is, we may fairly assume, a similar condition for Pleurotomaria. The folds and papillæ which project into the central cavity are invariably supplied with conspicuous blood-lacunæ, which break up into a rich capillary system; this lies embedded in a connective-tissue framework containing large quantities of

[1] "On the Reno-pericardial Canals in Patella," 'Quart. Journ. Micro. Sci.,' vol. xli, 1899.

[2] "Recherches sur l'Anatomie et l'Histologie du rein des Gastéropodes prosobranches," 'Ann. Sci. Nat.,' (7) Zool., tom. viii, 1889.

leucocytes. The whole papilla is covered by an epithelium whose cells are somewhat conical; the free expanded bases of these cells are crowded with yellowish granules, which, since they are also seen in some of the leucocytes, are probably waste matter taken up by phagocytes in different parts of the body, and carried to the papillary sac to be discharged.

The right kidney is very large and complicated, and probably forms the more important excretory organ, beside serving to transmit the genital products. This kidney opens into the mantle-cavity through a glandular tube, which, from a situation to the right of, has now come to lie almost ventrally to the rectum. This thick-walled glandular tube passes behind into a thin-walled funnel-shaped structure, which may be termed the ureter (*u.*), but is really the commencement of the kidney-chamber (*k. c.*); this passes back beneath the pericardium, and enlarges behind this structure to form a wide chamber with thick walls, the posterior portion of the right kidney (*p. r. k.*). The walls of this chamber project into the cavity in the form of a series of deep semilunar folds, covered with glandular epithelium and richly supplied by a plexus of blood-vessels containing venous blood. This, however, only forms a part of the right kidney, a very large portion running forward below the floor of the mantle-cavity between the crop and the intestine as far forward as the point where the brown tint stops, and marked *a. r. k.*, fig. 7. We may speak of this portion as the anterior lobe of the right kidney (figs. 23, 25, and 26, *a. r. k.*); its cavity communicates with the kidney-chamber near the anterior boundary of the pericardium. Like the posterior lobe it is richly supplied with venous blood, since it receives all the blood coming from the anterior part of the body and from the foot on its way to the gills.

The right kidney has thus a very complicated form, and one that will be best understood by an examination of the diagrams given in figs. 25 and 26.

The Genital Organs.—Of the three specimens examined two were females and the third a male. The genital gland, which presents a similar appearance in both sexes, forms as

in other Prosobranchia a fairly thick investment to the dorsal surface of the liver (fig. 7, *g. g.*), extending to the top of the spire.

The origin of the efferent duct from the gland was not to be made out owing to the upper part of the body being slightly damaged in removal from the shell, but I think there can be no doubt that the genital products are shed into a series of thin-walled remnants of the true cœlom, which in turn unite to form the somewhat thickened duct (*g. d.*) shown in figs. 23—26. This duct, which is present in both sexes, runs on the inner side of the spire, and communicates by a slit-like opening (*g. a.*) with that portion of the right kidney-chamber which we termed the ureter (*u.*). The conclusion that this is the genital duct is supported by a comparison with Trochus, where the undoubted genital duct has precisely the same relationships.

In the male this constitutes the whole of the genital system, there being no accessory organs, the genital products passing out directly through the unmodified right ureter. In the female, however, the distal portion of the ureter which serves to transmit both the excretory and genital products becomes much modified, owing to the enormous development of glandular tissue in its walls; the latter become so much thickened that it is by no means easy to find the lumen of this tube, which may now be called the oviduct (*ov. d.*).

The presence of this modified oviduct places Pleurotomaria about on the level with the Trochidæ, and indicates a somewhat more specialised condition than that met with in many Diotocardia, for in these latter the genital products are discharged into the mantle-cavity through the unmodified right kidney duct,—in some cases, it is thought, without the intervention even of the simple genital duct seen above.

The Alimentary Canal.—The mouth communicates with a thick-walled buccal cavity situated in the free portion of the head. This buccal mass, which is slightly constricted by the nerve-ring, is closely attached to the body-wall by numerous short radiating muscle-fibres (figs. 6, 7, and 8), which

are, however, less developed posteriorly where the salivary gland (fig. 8, *sl. g.*) occupies the roof of this structure.

On opening the buccal cavity a couple of laterally placed folds, covered with horny matter, will be seen (fig. 9,*j.*). These folds, which undoubtedly correspond to the jaws of other Gastropods, are but feebly developed in Pleuroto-maria, and probably serve, as Dall suggested, to protect the soft wall of the buccal cavity from the scraping action of the radula. The structure of one of these is shown in fig. 54. In front of the horny jaws a number of small flattened papillæ, also covered with horny matter, are to be seen (fig. 9, *h. p.*). Between and behind the jaws the ventrally placed odontophore may be seen bearing the chitinous radula (*rd.*), the functional portion of which when at rest appears somewhat V-shaped when viewed from above, and thus only covers the central portion of the odontophore, the sides of which are covered by the lateral extension of the radular membrane. Thus the whole of the buccal cavity is more or less protected by a lining of chitin.

The Salivary Glands form a compact mass in the roof of the alimentary canal, at the junction of the buccal mass and the crop (figs. 6—8, *s. g.*) ; their ducts (*sl. d.*), which are closely related to the buccal nerves, run forward within the thickness of the wall of the buccal mass, and open into the buccal cavity just above the odontophore (fig. 10). The gland, which is a much branched one (fig. 8), was not well enough preserved to enable me to study its histology.

The odontophore is enormously developed, being highly muscular, and further strengthened by the odontophoral cartilages. When at rest it forms a comparatively slight projection into the buccal cavity, but, on the other hand, it projects as a great muscular mass into the hæmocœle (fig. 7, *od.*). Between it and the crop the enormous radular sac (*r. s.*) will be seen extending back for two or more inches, and becoming involved in the anterior lobe of the right kidney.

The Musculature of the Buccal Mass.—As in other Odontophora, the muscles of the buccal mass can be divided

into the extrinsic and the intrinsic muscles; the former being concerned more in the movement of the mass as a whole, while the latter are specially related to the movements of the odontophore.

Extrinsic Muscles.—Curiously enough, these seem to be mainly protractor muscles, the retractors being but feebly developed.

(1) The lateral protractors. Three laterally placed vertical sheets of muscle arising from the side wall of the head, and inserted towards the posterior end of the buccal mass (fig. 30 A, $l.\,pr.$).

(2) The ventral protractors. A large paired muscle arising from the region of the lower lip, and inserted upon the basal cartilages (fig. 30 H, $v.\,pr.$).

(3) The lateral retractors (? divaricators of the cartilages). Five or six small strands of muscles arising from the side wall of the head, and inserted upon the main odontophoral cartilage just below the edge of the radular membrane (figs. 9 and 30 A, $l.\,r.$).

(4) The ventral retractors (?). A pair of short longitudinal sheets of muscle arising from the body-wall just above the pleuro-pedal cords, and inserted upon the radular sac as it emerges from the odontophoral mass (figs. 29 and 30 A, $v.\,r.$).

(5) The depressor muscle (figs. 30 B and D, $d.\,m.$). A small muscle inserted upon the main cartilage, just in front of the insertion of No. 3, and passing down to the ventral side of the head.

I have called Nos. 3 and 4 retractors because when the buccal mass is protruded their fibres would be on a stretch, but I think that this is probably only part of their function. Thus if the right and left portion of No. 3 contracted together they would separate the main odontophoral cartilages, and No. 4 may also function to prevent too great a displacement of the growing part of the radula.

Intrinsic Muscles.—These, again, fall under two heads : those concerned in the movements of the radula itself by

acting directly upon it, or upon the infra-radular membrane; and those concerned in the movements of the odontophoral cartilages.

On examination of the odontophore from the side, after removal of the extrinsic muscles, three muscles will be seen (fig. 30 B). One of these ($d.\,l.\,m.$) runs from the outer edge of the infra-radular membrane to the upper border of the main odontophoral cartilage, the fibres being arranged somewhat obliquely to the length of the cartilage. This muscle must by its contraction serve to flatten, $i.\,e.$ expand, the radula, and at the same time slightly pulls it back over the odontophoral cartilages. It is the largest and most powerful of the intrinsic muscles, and may be termed the dorsal or postero-dorsal longitudinal muscle. Three muscles are antagonistic to this; one of these ($v.\,l.\,m.$) is a small ventro-lateral band attached in front to the antero-ventral edge of the infra-radular membrane, and behind to the accessory basal odontophoral cartilage. This muscle, which we may term the ventral or antero-ventral longitudinal muscle, serves to pull the radula over the odontophoral cartilage, and also to flatten the anterior part of the radula. The second of these muscles is not seen in this dissection, since it lies on the inner side of the main cartilage; it is, however, shown in the median, the ventral and dorsal aspects (fig. 30 E, F, G, $i.\,l.\,m.$). This muscle is attached to the under side of the radula and to the infra-radular membrane, where it underlies the middle functional part of the radula, its insertion forming an oblique line, starting near the median ventral line, and passing upwards and outward until it ends on the edge of the basal membrane of the radula; posteriorly this muscle is attached behind to the accessory basal cartilage. The contraction of this muscle causes the radula to assume once more its V-shaped grooved character, and in addition it acts as a powerful retractor. It may be termed the internal longitudinal muscle. The third muscle is a very small one (fig. 30 D, x.) attached to the infra-radular membrane laterally, and running forwards it is inserted up the anterior portion

of the odontophoral cartilage; it pulls the radula forwards and inwards.

The remaining muscles only act indirectly upon the radula through the movements of the odontophoral cartilages.   One of these lies at the side of the main cartilage, to which it is attached by a long fleshy insertion (fig. 30 *C, l. l. m.*) ; it then runs back as a flat muscular band, and takes its origin from the outer border of the basal cartilage.   The contracture of this pair of muscles causes the anterior ends of two main cartilages to diverge, and so tends to flatten the anterior part of the radula.   The second of these two muscles is situated ventrally, and is the only unpaired muscle in the buccal mass; it consists of a transverse band of fibres running from the outer border of one main cartilage to the corresponding surface of the other, and thus by its contraction approximates the cartilages (fig. 30 *G* and *H, v. t. m.*).

The odontophoral cartilages are four in number.   Of these two are very large and laterally compressed, constituting the main cartilages which support the radula.   The remaining two are the small basal plates presenting concave surfaces for articulation with the former.   In spite of the small size of the basal plates, they appear to be the relatively fixed points for insertion of the majority of the muscles of the buccal mass.

The radula itself will be considered later.

Owing to the complicated nature of the movements of the radula we commonly find that the muscles of the odontophore are similarly complicated.   Unfortunately it is not easy to ascertain with any degree of precision the exact nature of the movements produced by the contraction of a given muscle, and consequently it is inadvisable in the present state of our knowledge to give them very precise names.

It is interesting to find that the arrangement of the odontophoral muscles of Pleurotomaria compares very closely with that described as occurring in Patella by Geddes.[1]

[1] "On the Mechanism of the Odontophore of certain Mollusca," 'Trans. Zool. Soc.,' vol. x, 1879.

Thus we find in both forms similarly placed lateral and ventral protractors among the extrinsic muscles, while among the intrinsic the dorsal, ventral longitudinal muscles connected with the infra-radular membrane are similar, as also is the transverse ventral muscle. The remaining muscles, however, differ, as, moreover, do the cartilages, since there are three pairs of cartilages in Patella and only two pairs in Pleurotomaria.

The Crop.—As in most Diotocardia, the first portion of the œsophagus is much dilated and saccular, and may be thus spoken of as a crop. It is closely connected with the body-wall by fine bundles of muscle-fibres, making the removal of the latter very difficult, and giving the crop a villous appearance. Its internal structure also is very characteristic, its walls, as in Haliotis, being thickly covered by numerous papillæ (figs. 9 and 10). These papillæ are, however, wanting in front where the crop and buccal cavity join, and in the morphological dorsal and ventral middle line. The epithelium covering these papillæ is highly glandular, and the centre of each papilla is a blood-lacuna. The presence of the papillæ thus causes an increase of the secretory epithelium.

Situated immediately behind the odontophore is a somewhat oval thickening. At a little distance from this structure we find on either side a slit-like depression (fig. 10, $lp.$ $lp^1.$), which we may term the lateral œsophageal pouch. Each of these depressions is bounded by a couple of folds (lettered in fig. 10, 1 and 2 on the left side, and 3 and 4 on the right). Tracing these structures back, we find that by their enlargement and rotation they cause the crop to assume a very complicated form. Thus the two ventral folds 2 and 3, enclosing between them the ventral median area, pass first to the right side and then gradually ascend until they assume a dorsal position; this causes a corresponding displacement of the two dorsal folds (1 and 4), which pass down the left side until they attain a ventral position. At the same time the lateral pouches become enlarged, and undergo a corresponding displacement; thus the original left pouch ($lp.$) now constitutes

the ventral and right half of the crop, while the right pouch
(lp^1.), which is somewhat smaller, forms the dorsal and left
portion of the same.

The non-papillate median dorsal and ventral areas remain
small, and are practically reversed in position.   The position
of these folds and pouches is shown in figs. 10 and 11, the
latter being a diagrammatic transverse section of the crop,
from which it will be seen that the enlargement of the crop is
practically confined to the lateral pouches.

Tracing the crop still further back it is found to gradually
diminish in size and complication, until it assumes the form
of a simple tube with rather thick walls, which we may speak
of as the œsophagus (fig. 7, o. e.).

The Stomach.—The œsophagus extends back a little
behind the heart, and then suddenly debouches into the
stomach, which, as a large **U**-shaped cavity, lies below and
behind the right kidney (figs. 7 and 12, st.).   The cavity of
the stomach is large and divided by a marked constriction
into a right and left portion, the former receiving the
œsophagus, while the latter receives the bile-duct (b. d.), and
gives origin to the intestine and the spiral cæcum (sp. c.).
The œsophageal aperture is very narrow and guarded by a
sphincter, while the intestinal orifice is large (fig. 12).   The
bile-duct (b. d.) opens by a wide slit situated immediately to
the left of the semilunar fold which grows in from the floor
of the stomach and separates the two chambers.

The spiral cæcum (sp. c.) opens on the dorsal wall imme-
diately above the bile-duct, but the structure which may be
described as the columella of the spiral cæcum is prolonged
down to the floor of the stomach, and forms the anterior lip
of the constriction between the two stomach-chambers.   The
cæcum itself forms a perfect helicoid spiral situated dorsally,
and overlying the two halves of the stomach.

A spiral stomach-cæcum is a very characteristic feature of
those Diotocardia possessed of a spiral shell, being specially
well marked in Trochus (fig. 13), Turbo, and Phasianella;
it is also developed in Haliotis, and in a very much modified

form in Scutum and Fissurella. Traces of this organ are
also found in that primitive tænioglossan, Nassopsis.
The almost universal occurrence of this organ in the Dioto-
cardia suggests that it is a structure of great antiquity and
functional importance, although we are unable to ascribe any
special physiological function to it.

This cæcum is in most cases connected with the postero-
dorsal wall of the stomach (postero-ventral in Phasianella),
and its lips are invariably related to the opening of the bile-
duct. Regarding the stomach as a U-shaped structure
composed of an œsophageal and an intestinal chamber, the
cæcum invariably arises close to the junction of the two, but
essentially belonging to the intestinal chamber, and is closely
associated with the bile-ducts.

This structure has no homology with the crystalline style sac
of other Gastropoda or of the Lamellibranchia; the two struc-
tures are undoubtedly co-existent in Nassopsis (Moore [1]),
and possibly in some Diotocardia. It is, however, extremely
suggestive of the spiral cæcum present in the Cephalopoda,
which, like the cæcum described above, is a postero-dorsal
outgrowth from the stomach, closely related to the bile-ducts
and to the point of origin of the intestine.

An attempt to homologise the spiral cæcum found in two
such distinct orders of Mollusca as the Gastropoda and the
Cephalopoda may at first sight seem unjustifiable, but the rela-
tions of the two organs to the alimentary canal are so precisely
alike that one cannot help being struck with their similitude.

It is, moreover, generally accepted that the Cephalopoda
and Gastropoda are descended from a common ancestor, so
that presence in the two groups of a spiral stomach-cæcum
is not so surprising, and would only suggest that this struc-
ture was present in that ancestral form. Unfortunately we
know nothing of the connecting type, which is not astonishing
when we remember that both the Cephalopoda and the Dioto-
cardia extend back to the Cambrian epoch. The only group

[1] "The Molluscs of the Great African Lakes. IV. Nassopsis and Bytho-
ceras," 'Quart. Journ. Micro. Sci.,' vol. xlii, 1899.

which is sometimes regarded as representing the primitive molluscan stock, viz. the Amphineura, does not exhibit this organ; but, on the other hand, they do not extend back so far in time, the earliest chiton being only found in the Ordovician; and further, the components of this group, while retaining many primitive features, are obviously specialised along a particular line, so that I do not think the absence of this spiral cæcum in the Amphineura can be regarded as disproving the homology of the two cæca seen respectively in the Cephalopoda and Diotocardia.

From a consideration, therefore, of the similar structural relations of the spiral cæcum in these two groups, I conclude that the two structures are homologous.

The intestine (figs. 7 and 12, *int.*) is very simple. It runs forward until within about half an inch of the salivary glands, and then forming a ∪-shaped bend, it passes back towards the stomach, whence it curves dorsally, perforating the pericardium and the ventricle, and bending once more on itself, it enters the mantle-cavity, to the roof of which it is attached, at first slightly to the right of the middle line, but gradually assuming a more median position (figs. 5 and 7, *r.*). It is attached below the hypobranchial gland, and opens into the mantle-cavity by the anal orifice situated some considerable distance from the posterior limit of the mantle-slit, and therefore very differently from the condition observed by Dall in P. Adansoniana.

The Vascular System.—The heart, which is enclosed in a spacious pericardium (figs. 7 and 23—26), is that of a typical Zygobranch, consisting of a muscular ventricle (*v.*) surrounding the rectum, and a pair of thin-walled auricles (*l. au.* and *r. au.*), which receive the blood from the long efferent branchial vessels.

A common aorta springs from the posterior portion of the ventricle, and soon divides into an anterior and a posterior artery; the former (figs. 6, 7, and 28, *a. a.*) is distributed to the anterior and ventral parts of the body, while the latter supplies the stomach, liver, and genital gland.

The venous system takes the form of series of more or less well-marked canals and sinuses, which are specially conspicuous in the region of the right kidney. The blood from the foot and anterior parts of the body is apparently collected into a series of channels, which run in close connection with the excretory epithelium of the anterior lobe of the kidney, while that from the liver and stomach passes through the posterior lobe. These various renal veins eventually open into a large sinus situated ventrally to the ureter, genital duct, pericardium, and rectum (figs. 7 and 23, *v. s.*), from which the afferent branchial vessels arise.

The body-cavity of the adult is very inconspicuous, owing to the great development of the crop with its radiating muscle-fibres. This cavity represents part of the venous system, and is of the nature of a hæmocœle. The true cœlom is only represented in the pericardial, renal, and genital cavities.

The Nervous System.—An examination of fig. 27 will show at a glance that the nervous system of P. Beyrichii presents all the essential features of that of a typical Diotocardian, this being especially noticeable in the practical absence of distinct ganglia; for although on the removal of the dense connective-tissue sheath a certain amount of orange colour is noticeable in the cerebral and pedal centres, thus indicating an accumulation of nerve-cells, yet an examination of a series of sections through these regions and the intervening connectives shows (fig. 22) that while the nerve-cells are more abundant in these coloured areas, yet they are not confined to these regions, but are distributed, though in smaller numbers, throughout the whole length of the connectives, commissures, and even many of the nerves. The orange-coloured areas where the nerve-cells are more abundant correspond with the cerebral centres (*cb. g.*), the points of origin of the visceral loop (*pl. c.*), and the anterior portion of the pleuro-pedal cords. This distribution of the nerve-cells along the connectives makes it extremely difficult to localise the individual ganglia, and forces us to rely rather upon the points of origin of certain nerves than upon the

definite accumulation of nerve-cells met with in other Proso-
branchs.

Fischer and Bouvier seem to have been misled, either by
this coloration or by the slight swelling of the cords in
certain of these regions, into the belief of the existence of
definite ganglionic areas, and they indicate such regions by
means of dots in their figures ; they appear to have over-
looked the presence of nerve-cells along the connectives, and
the still more important, though slight, accumulation and
coloration at the point of origin of the visceral nerve.

The Cerebral Ganglia.—The circum-œsophageal nerve-
ring is much enlarged on either side of the anterior part of
the buccal cavity, and since the tentacular and certain other
nerves which are characteristic of the cerebral ganglion of
other Prosobranchs arise from this region, we may regard it
as representing that ganglion. The cerebral ganglia are,
then, a pair of elongate band-like structures widening out
below ; they are connected together above the buccal mass by
a slightly narrow region (*cb. c.*), which represents the
cerebral commissure of more specialised forms, but which
here is indistinguishable from the ganglia themselves, since
both in its size and in the number of its ganglionic cells it
passes imperceptibly into the laterally placed ganglionic
areas. The cerebral ganglia give origin to five pairs of
nerves supplying the lips (figs. 21, 22, and 29), and to a pair
of laterally placed tentacular nerves (*t. n.*), from which in
turn the optic nerve arises. Arising with the most ventral of
these labial nerves is a broad nerve which runs downwards
and below the buccal mass (figs. 21 and 29) ; this nerve
gives off a sixth lip-nerve, and is then continued ven-
trally to the mouth and close to the lips, to meet and fuse
with a similar nerve from the opposite side of the body, thus
constituting the labial commissure (*l. c.*) so characteristic of
the Diotocardia and archi-Tænioglossa.

Yet another nerve arises from the ventral continuation of
the cerebral ganglion, but in order to see this properly the
mesial aspect of the ganglion must be examined. Such a

view (fig. 21) shows a nerve arising just between the fourth
and fifth lip-nerves; this nerve, the buccal nerve (*b. n.*),
curves sharply up over the muscular odontophore, giving off
branches on its course. After ascending for some distance
it bends sharply back and becomes greatly enlarged, and
may now be spoken of as the buccal ganglion (figs. 8 and 29,
b. g.). This ganglion is a curiously elongate structure, and
gives off branches anteriorly and ventrally; while the main
mass is continued back under the radular sac, where it unites
with its fellow from the opposite side (fig. 27). A very con-
spicuous branch arises from the middle of the dorsal border of
the ganglion, which curving upwards and backwards runs along
the salivary duct and supplies the salivary gland (figs. 8 and 29).

From the posterior border of the cerebral ganglia two very
large cords arise, these represent the cerebro-pleural and
cerebro-pedal connectives; of these the former and more
posterior cord is as usual much the larger. As with the
other parts of the nervous system, ganglionic cells are
scattered along the length of these cords, more especially at
the periphery, and more abundantly in the cerebro-pleural
than in the cerebro-pedal connective (fig. 22).

The cerebro-pedal connective passes back, taking at first a
somewhat horizontal position, but eventually curving down-
ward to join the great scalariform pleuro-pedal cords. It is
closely followed by the cerebro-pleural connective, and the
two become reunited near the posterior border of the great
odontophoral muscular mass. The combined pleuro-pedal
mass then enters the foot, where it becomes connected by
a transverse commissure with the corresponding structure
from the opposite side (figs. 21 and 27). This transverse
commissure contains elements derived from both the pleural
and pedal systems (fig. 21).

The Pleuro-pedal Cords.—Although the pleural and
pedal cords are now closely connected, they can still be dis-
tinguished from one another by the presence of a groove
which runs along the whole length of the combined pleuro-
pedal cord (figs. 28 and 29).

This separation is probably only an external one, since sections through the cords fail to reveal any continuous layer of connective tissue separating the two, and bundles of nerve-fibres apparently pass from the ventral to 'the dorsal moieties of the cord, and vice versâ.

The right and left pleuro-pedal cords now diverge slightly from one another and run back within the substance of the foot, each cord lying in a slight blood-sinus situated below and on either side of the main pedal sinus.

The cords extend to the posterior extremity of the foot, and are furthest apart near the middle of the foot ; toward the posterior end they become somewhat approximated (fig. 27). These cords, along which ganglionic cells are fairly evenly distributed, are, as we have seen, equally derived from the pedal and pleural systems : in width each cord at its anterior extremity is but very slightly if at all larger than the cerebro-pleural and cerebro-pedal connectives when closely approximated, i. e. there is no marked swelling indicative of a great accumulation of ganglionic cells (fig. 22). In fact, there is but a slight increase in number of these cells in this region, and that mainly in the ventral or pedal portion. It becomes then very difficult if not impossible to speak of a pedal, and, as I shall endeavour to show later, inadvisable to attempt to identify a pleural ganglion in this pleuro-pedal cord.

These ganglionic pleuro-pedal cords are connected at intervals by transverse commissures : the first of these, as already mentioned, is derived from both the pleural and pedal moieties ; but the posterior ones, of which there are at least twelve, at first sight would be considered as derived exclusively from the pedal portion of the cord. An examination of sections, however, reveals the fact that a bundle of nerve-fibres comes down from the dorsal portion of the pleuro-pedal cords and enters the commissure, which is therefore derived equally from both portions of the cord.

The laterally placed pedal nerves arise like the above from both portions of the cord. The double root of these nerves is often very conspicuous (fig. 21, p^2.), somewhat resembling

the dorsal and ventral roots of a vertebrate spinal nerve. In addition to these large latero-ventral nerves there are present certain small nerves, which apparently arise from the pleural portion of the cord and pass to the dorsal pedal muscles. When, however, we remember that the distinction between these two portions of the cord is practically only an external one we shall probably be right in concluding that all the nerves derived from these cords are connected with both subdivisions.

In connection with the apparent separation of the pleuro-pedal cords into two distinct portions by means of a longitudinal groove it is interesting to note that Haller[1] had already come to the conclusion that this groove has no morphological significance; thus he found in other Rhipidoglossa, as I have found in Pleurotomaria, that transverse sections of this cord failed to reveal any line of separation between the pleural and pedal portions of nerve tracts running from one into the other.

Visceral Commissure.—As suggested by Bouvier and Fischer from the study of an imperfect specimen, Pleurotomaria exhibits a typical streptoneurous condition in its visceral loop (figs. 6, 27, and 28); but at the same time this mollusc is most peculiar among the Diotocardia in the point of origin of its visceral nerves.

If the cerebro-pleural connective on either side of the body be examined, it will be seen that between its origin from the cerebral ganglion and its fusion with the pedal system it gives rise to a very large nerve, whose relations at once identify it with the visceral nerve, that on the right side being the supra- and that on the left the sub-intestinal nerve.

As already mentioned, the points of origin of these nerves appear, after the removal of the thick nerve-sheath, slightly orange-coloured, owing to the presence of a considerable number of nerve-cells which are continued, though in smaller numbers, from this point up to the branchial ganglion. The

[1] " Untersuchungen über marine Rhipidoglossen. II. Textus des Central-nervensystem und seiner Hüllen," ' Morph. Jahrb.,' Bd. xi, 1886.

origin of the visceral nerves alone would suggest that we were here dealing with the pleural centres—a view which is greatly strengthened by the presence of an accumulation of nerve-cells, and to which we shall refer again.

The right half of the visceral loop arises fairly close to the cerebral ganglion, whereas the left half originates very much closer to the pedal ganglion (cf. figs. 21, 22, and 27), thus producing a marked asymmetry.

The supra-intestinal nerve passes over the alimentary canal immediately behind the salivary gland (figs. 6, 10, and 29), whereas the subintestinal passes below the crop and radular sac. Both of these nerves perforate the muscular body-wall, and come to lie in the mantle close to its junction with the former (figs. 6 and 28). Each nerve then bifurcates, one portion running back parallel with the gill to complete the visceral loop by uniting with its fellow in a blood-sinus just below the right kidney duct (figs. 23 and 27), while the other portion runs out and gives rise to the immense branchial ganglion, which forms a large round swelling close to the point of attachment of the gill, which it innervates. There is no distinct abdominal ganglion such as was surmised by Fischer and Bouvier.

In addition to the great visceral nerves a number of smaller nerves arise from the pleural connectives, the presence of which strengthens the view that the pleural ganglia are not yet condensed in Pleurotomaria, and that this mollusc is a fairly primitive one, for in most other Gastropods there is a tendency for these nerves supplying the muscles of the side wall of the head and posterior parts of the mantle to take the form of one large nerve arising in fairly close connection with the pleural ganglion.

So far as I can ascertain about four moderately conspicuous nerves arise from the two cerebro-pleural connectives to be distributed to the side walls of the head (fig. 21). From the connective behind the origin of the visceral loop, to which I apply the term pleuro-pedal connective, and before it fuses with the cerebro-pedal connective, there arise two

fairly large nerves (figs. 21, 22, 28, 29); one of these runs forwards between the cerebro-pleural and cerebro-pedal con- nectives (fig. 22) to the muscles of the side of the neck, while the other runs up to the body-wall above the crop to the floor of the mantle cavity; this last may be Bouvier and Fischer's pallial nerve, although it does not arise at the same spot. I do not feel at all certain about the identity of these nerves, since I have not been able to trace any of them to the free mantle-fold, and consequently am not inclined to call any of them pallial nerves. Still less am I satisfied concern- ing the presence of the primary pallial nerves of these authors, and I take it that they rather assume that such nerves must be present. An examination of their fig. C, op. cit., p. 170, will show two large nerves arising from the upper part of the pleuro-pedal cords, the anterior of these corre- sponding with the nerve marked with an asterisk in my figs. 21 and 22; the nerve runs up parallel to my pleuro-pedal connective, branching repeatedly, and is eventually lost in the muscle of this portion of the body: it is possible that some of its finer fibres may penetrate into the mantle. With regard to the second, which they represent as co-extensive with the pleuro-pedal cords, I can only say that it does not exist in P. Beyrichii. Behind the last-mentioned nerve a series of four small nerves are seen to arise from the pleural portion of the pleuro-pedal cords, between the point of origin of the first and second pedal nerves (figs. 21 and 22, $p.^1$ and $p.^2$). These nerves, which are distributed to the muscles on the dorsal surface of the foot where the latter joins the body, —i. e. to the commencement of the columella muscle (fig. 28) —are the only nerves which occur in the region corre- sponding to that whence Bouvier and Fischer's great hypo- thetical pallial nerve springs; they are, however, quite small, and I have not been able to trace them beyond the columella muscle. Since I cannot think that there is likely to be any great difference between the different species of Pleuroto- maria in this respect, I can only conclude that the great primary pallial nerve of Bouvier and Fischer does not exist

in Pleurotomaria. Even in Trochus I think they greatly overrate the size and importance of this nerve, which so far as I can find is a small nerve distributed to the posterior portion of the mantle, and probably to the secretory epithelium of that region.

A few small nerves arise from the cerebro-pedal commissure, these being distributed to the muscles between the under lip and the foot.

The Sense-organs.—The eyes and osphradia having been already described, it only remains to draw attention to the otocysts. These latter take the form of a pair of large vesicles, situated just above and in front of the pleuropedal cords (fig. 27). The actual otocyst is not very large, but it is surrounded by a very tough, thick, concentric arranged sheath of connective tissue (fig. 31 A). The otoconia are small and numerous; typically they are spherical bodies, varying much in size and often fusing together to form reniform structures (fig. 31 B).

The Radula (figs. 32—52).—The radula of Pleuroto maria Beyrichii is extremely complex, and exhibits the same type as that described for P. Adansoniana by Dall, and P. Quoyana by Fischer and Bouvier. In the number and character of its teeth it more closely approximates to the latter species—a fact which strongly supports the view advanced by Crosse in 1882, from the study of the shells, that these two species should be grouped together as a section or sub-genus of Pleurotomaria, for which group P. Fischer proposed the name Perotrochus.

The radula is very large, one example measuring 62 mm. long by 5 mm. wide. The greater portion of the radula is of course not functional, but lies buried in the radular sac, which extends up to the anterior lobe of the right kidney.

In fig. 32 I have given a view of half a transverse row, which, as mentioned by Fischer and Bouvier, does not run straight across the radula, but has a somewhat V-shaped course.

The number of teeth in a transverse row is 223; one of

these being unpaired occupies the centre of the row, and on either side of this are situated 111 teeth. So far as I can see from the examination of many rows this number is quite constant. The lateral teeth exhibit a number of different types, at least five, which, however, merge imperceptibly into one another. For convenience' sake we may, however, follow Fischer and Bouvier, and divide them into the following groups :—(1) The central teeth, (2) the lamellate teeth, (3) the hooked teeth or uncini, (4) the brush or tufted teeth, (5) flabelliform teeth.

The Rhachian or Unpaired Tooth.—This tooth (figs. 32 and 33) has a very curious form. Viewed from above (fig. 32), it appears to consist of a somewhat pointed oval or lanceolate lamella, which overlaps the adjacent central teeth. When, however, the rhachian tooth is isolated and viewed from the side (fig. 33), it is seen that this more or less horizontally placed lamella is attached to a longitudinally placed vertical plate, the posterior half of which is thickened, and forms the base of attachment of the tooth to the basal membrane. The tooth thus consists of two pieces—a flat horizontal lamella, and a vertical plate strengthening and attaching the former to the radular membrane.

The Central Pairs.—On either side of the rhachian are situated three large teeth (fig. 32), which, while asymmetrical in form, nevertheless approximate somewhat in structure to the symmetrical rhachian tooth, forming a gradation between this tooth and the more laterally placed lamellate teeth. It is very difficult, if not impossible, to draw a line between these central pairs and the lamellate teeth, and we only separate them for the convenience of description. In the central teeth (figs. 34—36) the vertical plate has greatly increased in size, while the horizontal lamella, so characteristic of the rhachidian, is much reduced, and only present on the outer side of the vertical plate near the base of attachment ; it still, however, overlaps the tooth immediately external to it (fig. 32). The portion corresponding to the vertical plate of the rhachian is now no longer placed vertically, but has become

inclined to the basal membrane, and its anterior extremity is much widened. The form of these teeth may be best understood by an examination of figs. 32—36.

The Lamellate Teeth.—It will be seen from figs. 32 and 36 that the central teeth are not sharply marked off from the more laterally placed lamellate teeth, but pass imperceptibly into them. Thus, owing to its size, the first lamellate tooth might be almost equally well classified with the central teeth.

There are twenty-one teeth which may be grouped under this head. Though varying in size, they are, on the whole, the smallest teeth in the radula, and present very uniform characters. The free end of each of these teeth is abruptly truncated, and the upper border is generally straight, while the under margin is either convex or angulated, and the base of attachment is small (figs. 32, and 37 *A, B, C, D*). The lamellate teeth are far more complicated than would appear at first sight, so much so that it is very difficult indeed to gain any idea of their form from a written description. I have therefore thought it better to give several drawings of one of these teeth in different positions (see fig. 37 *A, B, C, D*), and to these I must refer the reader who desires to obtain an idea of the form of these very characteristic teeth.

The first five or six of these teeth present a slightly concave free border, and thus approach the central pairs, which they further resemble in the greater development of the outwardly flexed free margin, which evidently represents the last trace of the overlapping lamella of the central teeth.

As we pass outward the lamellate teeth increase in size, and thus approximate to the hooked teeth (figs. 32 and 38).

The Hooked Teeth or Uncini.—The gradation between the lamellate and the hooked teeth is completed by the twenty-fifth tooth (fig. 38), which, though only slightly larger than the preceding tooth, approximates in form to the more lateral hooked teeth. It will be seen to present a double curvature in its free margin, and a slightly hooked free extremity. The twenty-sixth tooth (fig. 39) is much larger

than the above, and shows a well-marked hook at its extremity, and a small cusp a little below this; this cusp is still visible on the twenty-seventh (fig. 40) but completely disappears on the succeeding teeth, which have the form of long massive hooks (figs. 41 and 42), and constitute the largest teeth on the radula. After the thirtieth, the teeth, while still remaining long, become much slighter (fig. 42), and soon (about the thirty-seventh) begin to show signs of the development of two additional cusps (fig. 43), which attain their full development on the forty-ninth tooth (fig. 44). The teeth have now the form of long delicate sickles, the free end of which exhibits two deep notches. The last one or two hooked teeth are somewhat shorter than the earlier ones, and thus lead to the distinctly shorter brush teeth.

I have somewhat arbitrarily drawn the line separating the hooked and the brush teeth between the forty-first and forty-second tooth, thus making seventeen hooked teeth.

The Brush Teeth.—The forty-second tooth at first sight does not appear to differ materially from the forty-first, but a more careful examination shows that it possesses on either side on a level with the lowest cusp two minute bristles (fig. 45). On the next tooth these bristles are longer, and one or two more are appearing (fig. 45); and if we examine the feature as we pass outward in the row of teeth (figs. 47—52) we find that the bristles steadily increase in number and length, until by the forty-ninth tooth they form a considerable brush reaching to the free end of the tooth. Thus it will be seen that it is impossible to separate the forty-second tooth from the true brush teeth; and although it is more closely approximate in general appearance to the hooked teeth, yet, in the presence of the two minute hairs on either side, it already shows the essential feature of the brush teeth.

The brush teeth are sixty-three in number, and they form the most characteristic feature of the radula of Pleurotomaria.

A tooth taken from the middle of this series (fig. 50) shows

a decided reduction in the length of the hooked portion of
the tooth, the three cusps being now somewhat closely
crowded near the free end of the tooth.   The tuft of bristles
now appears to be inserted lower down on a ridge placed
transversely to the axis of the tooth, and the bristles them-
selves, forming a compact brush, extend considerably beyond
the free end of the tooth (figs. 50—52).   With the reduction
of the hooked portion of the tooth the two sets of bristles meet
behind, and now form a horseshoe-shaped brush embracing
the end of the tooth.   Passing outward the teeth become
still more delicate, and the cusps smaller and smaller, until they
completely disappear.   Traces of the cusp-bearing lobe are,
however, still distinctly visible on the 101st tooth, although
it is now only a narrow slightly notched process.   The same
structure, but still smaller and devoid of notches, may be seen
on the 102nd and 103rd teeth, and I think on all the
remaining teeth, in the form of a slight process on upper
border of the teeth.

As the upper tooth-bearing lobe becomes reduced, the two
sets of bristles run together and form a single clump, and
gradually approach the free upper border of the tooth.   This
latter condition is accelerated by the development on 101st—
104th of a lamina springing from the back of the tooth, and
foreshadowing the flabelliform tooth (fig. 53).

The bristles remain well developed after the disappearance
of the cusps, and even the 103rd tooth possesses a good brush.
The 104th, however, shows a marked reduction in its bristles,
and this is the last of the brush teeth, since the 105th tooth
is entirely devoid of these structures.   In other respects the
difference between these two teeth is slight, their general
form being very similar.

The Flabelliform Teeth.—There are seven of these
teeth (the 105th to the 111th inclusive), which have the form
of delicate narrow lamellæ, arranged like the rays of a fan;
they all bear a slight notch at their free end, corresponding
to the point of attachment of the bristles in the brush teeth,
and possibly representing the tooth-bearing lobe.

The Radula as a Whole.—If we recognise the five divisions described above, we may express the arrangement and number of teeth on the radula by the following numerals : —7, 63, 17, 20, 3 ; R. 3, 20, 17, 63, 7 ; there being, as we have seen, a single rhachian, 3 central pairs, 20 lamellate, 17 hooked, 63 brush, and 7 flabelliform teeth.

One of the most noticeable features in this radula, however, is the great difficulty which its teeth offer to our attempts to arrange them in groups, this being due to the presence of intermediate forms between each two adjacent groups of teeth, thus causing them to merge into one another, and making it almost impossible to draw any sharp line between them.   Nevertheless there are a number of very marked types of teeth in this radula, notably the lamellate, the hooked, the brush, and the flabelliform teeth ; of these the lamellate and the brush teeth are very striking and peculiar, and not apparently met with in any other mollusc.

It is somewhat difficult to understand the function of the lamellate and brush teeth, especially the former, and in order to do so we require to know more about the habits and the nature of the food of Pleurotomaria.   An examination of the contents of the stomach of two specimens revealed a large quantity of sponge spicules, both megascleres and microscleres, belonging to one of the Halichondrina (? a species of Amphilectus).   From the fact that many of these spicules appeared to be bound together by tissue, I conclude that Pleurotomaria feeds on the living sponge.   For this purpose the hooked teeth would be useful in tearing away great pieces of the sponge, and the brush teeth might at the same time rasp away some of the flesh from the spicules ; but one is still at a loss to understand the action of the lamellate teeth.

Another peculiar feature in this radula is the presence of what Bouvier and Fischer term the accessory basal plates.   These structures take the form of little chitinous plates, somewhat of the same shape as the basal plates of the teeth themselves, which are attached to the radular mem-

brane.   These accessory plates, of which there are about thirty-seven on each side of the middle line in each row of teeth, are situated about in the middle of each half-row of teeth, commencing with the twenty-seventh and extending out as far as about the sixty-fourth tooth.   They appear to alternate with the true bases of the teeth in front, whereas posteriorly they underlie them.   The row represented in fig. 32 would underlie the next posterior row of teeth.

Comparison with the Radula of P. Quoyana and P. Adansoniana.

The radulæ of the three species of Pleurotomaria, of which the animals have been examined, stand apart from those of all other Diotocardia in the absence of that sharp division into regions which is so characteristic of the majority of this group.   They are further to be distinguished by the character of their central teeth, and in the possession of brush teeth.

Of the two species, P. Quoyana much more nearly approaches P. Beyrichii in the character of its radula than does P. Adansoniana.   The radula of the former, according to Bouvier and Fischer, may be expressed as follows :— R. 3, 24, 13, 63, 6, there being 109 teeth on either side of the rhachian.   Except in the number of the teeth in the different groups there is very little difference indeed between the two species, the resemblance being so close that one might almost match the individual teeth in the two radulæ ; thus the rhachidian, the central pairs, and the lamellate are very similar, the only difference being in the greater number of lamellate teeth (twenty-four) in P. Quoyana.   The thirtieth tooth of the latter species forms an exact match with the twenty-sixth of P. Beyrichii, and the fiftieth with the forty-third.

This close resemblance between the radulæ of these two species is strong argument in favour of the retention of these two forms in a sub-section of the genus Pleurotomaria (section Perotrochus, Fischer).   Since P. Bey-

richii so closely resembles P. Quoyana in its radula, it
differs equally with the latter species from P. Adanso-
niana, the radula of which, according to Dall, shows a
rhachian, 15 laterals, 5 tufted uncini, 4 denticulate uncini,
and 45 simple uncini, or 69 teeth on either side of the
rhachian.   An examination of his figure would lead us to
interpret the teeth somewhat differently, but since the num-
bering of the teeth in the plate and account given in the text
are at variance a detailed comparison becomes difficult.   It
is obvious, however, that this form differs considerably in its
radula from the section Perotrochus, and thus justifies
Fischer's creation of the section Entemnotrochus.

A comparison of the Pleurotomarian radula with that of
other Diotocardia is almost impossible, for while the former
is a typical rhipidoglossate radula, yet it is so peculiar that
we can find no other living form which at all approximates
to it.   This is, perhaps, not so surprising when we consider
the great antiquity of this form, on which account we might
expect that Pleurotomaria would show either a very
primitive type, or if, on the other hand, the radula had
undergone much change, that it would show a very spe-
cialised one.

When we attempt to decide the question as to the primi-
tive or specialised nature of this radula, we are at once at
fault, for we have not one particle of evidence to show us
what the nature of the pro-rhipidoglossate radula was.   All
the evidence we possess tells us that the Diotocardia are un-
doubtedly the most primitive of living Prosobranchia, and
that they all possess the highly developed rhipidoglossate
type of radula.   Of the early Diotocardia, Pleurotomaria
is the only form of which we have any knowledge, all the
other living zygobranchiate Diotocardia being comparatively
modern forms, and this genus also shows us a rhipidoglos-
sate radula.   It is true that the radula of Pleurotomaria
differs from that of all other Diotocardia in the absence of
those sharply marked regions which are so characteristic of
the majority of the rhipidoglossate radulæ.   The question

then arises as to whether, taking into consideration the antiquity of Pleurotomaria, we are justified in regarding this feature as a primitive one.

Considerable stress has been laid by Troschel, Moore, and others upon the breaking up of the rhipidoglossate radula into zones, three on either side of the rhachian tooth, and on the occasional replacement of the great group of marginal laterals by one large tooth, which, however, generally retains sufficient traces of the individuals which it replaces to suggest that it represents a fusion of teeth, a view which is supported when we find that this takes place in undoubtedly specialised forms (notably in Addisonia and Cocculina among the Rhipidoglossa, and certain Cyclophoridæ among the archi-Tænioglossa). Such a condition has led some to suppose that the tooth arrangement met with in the Tænioglossa might be derived from the Rhipidoglossate radula by a fusion of the elements of the three zones, thus giving a formula of 1.1.1.1.1.1.1, a view which the condition of the archi-Tænioglossate Cyclophoridæ seems to support.

If, then, this subdivision of the row of teeth into sharply marked zones is a foreshadowing or a tendency in the direction of the condition met with in the Tænioglossa, it seems only natural to conclude that this in turn was derived from a radula in which all the teeth in a transverse row were similar. Such a stage has not been preserved to us, but in Pleurotomaria we have an approximation to this condition, inasmuch as all the various specialised tooth areas merge imperceptibly into one another, and this in my opinion is a very primitive character.

I therefore conclude that, in spite of its very specialised brush teeth, the radula of Pleurotomaria exhibits the most primitive type among all existing Gastropods.

Considerations regarding the Primitive Nature of Pleurotomaria.—If we are justified in concluding, as I have done above, that in its radula Pleurotomaria is a most primitive form, then we might naturally expect to find indications of this primitive character in other of its organs.

We have already in dealing with the different organs suggested that certain of them presented primitive characters, —for example, the eye, the spiral cæcum in the stomach, and still more notably the characters of the nervous system.

The morphology of the nervous system has already been dealt with at length by Bouvier and Fischer, especially with reference to the relation of the pleuro-pedal cords to the origin of the visceral connectives from the conditions seen in Chiton. Personally, however, I do not think Pleurotomaria throws any fresh light on this branch of inquiry. This, nevertheless, does not rob the nervous system of the mollusc of all interest, for, as we have already seen, in the very uniform distribution of the nerve-cells through the connectives and commissures, and the consequent practical absence of distinct ganglia, we have retained in Pleurotomaria, no matter what view we take of the origin of the molluscan nervous system, a very primitive feature.

The second point of interest, which taken in connection with the above yields to no other feature in the anatomy of Pleurotomaria in its importance, concerns the position of the pleural centres. In the Gastropoda the pleural ganglia may be defined as the accumulations of nerve-cells related to both the cerebral and pedal ganglia, and giving origin to the visceral connectives, these being the only constant features presented by the pleural centres. In position the pleural centres may vary from one close to the cerebral ganglia, as exemplified by the majority of the Monotocardia, to one close to the pedals as in Haliotis and Trochus, but in each case the visceral nerves arise direct from these ganglia. In Pleurotomaria, however, these nerves arise as we have seen from the connective joining the cerebral with the pleuro-pedal cords, so that if Bouvier and Fischer are correct in their localisation of the pleural centres at the anterior end and on the upper surface of the pleuro-pedal cords, we should have the very peculiar and absolutely unique condition of the visceral nerve arising from the cerebro-pleural connective quite independent of the pleural centre;

but, as I have pointed out above, although there is a certain amount of concentration of nerve-cells in this region, yet it is mainly in the ventral half of the pleuro-pedal cords, i. e. in the region of the pedal ganglion. Moreover, while the nerve-cells are distributed along the whole pleural connective, yet they are distinctly concentrated to a small extent round the origin of the visceral nerve sufficient to give it a slightly orange colour, an appearance which distinctly suggests the localisation of the pleural centre at this point, a condition which would be in harmony with what we find in many other Gastropoda. From these considerations I am forced to the conclusion that the pleural ganglion, such as figured by Fischer and Bouvier, does not exist, and that a distinct pleural ganglion has not yet evolved in Pleurotomaria. Nevertheless we can distinguish a pleural centre in the point of origin of the visceral nerves, and it is here that a pleural ganglion would form by an aggregation of nerve-cells, supposing a form were to arise from Pleurotomaria possessed of distinct ganglia.

The above conclusion is of great importance in considering the phylogeny of the Tænioglossa, for with the exception of Cyclophorus and Ampullaria—two very aberrant archi-Tænioglossa, all the remaining members of the great tænioglossate group exhibit a condition in which the pleural ganglia are more nearly approximated to the cerebral ganglia than to the pleuro-pedal cords. The connection of these forms with the typical nervous system of the Diotocardia has been sought in the Cyclophoridæ and in the Trochidæ, but a careful consideration of both these well-known types of nervous system will show that they are both specialised along a different line from that characteristic of the Tænioglossa, by a tendency of the pleural ganglion to mount up the visceral nerve (see Bouvier and Fischer's diagram, figs. D and E). On the other hand, in Paludina, the form which, so far as its nervous system is concerned, appears to me to be the only true archi-tænioglossan, the pleural ganglion giving origin to the visceral nerve is little more than a swelling

along the course of the posterior connective joining the cere-
bral to the pleuro-pedal cords. This condition is practically
the same as that seen in Pleurotomaria if we imagine a
crowding together of the ganglionic cells at the point of
origin of the visceral nerve, and is the natural outcome of
that tendency towards a shortening of the nerve-tracts and
concentration of the nerve-cells into ganglia which is so
characteristic of the Gastropoda.

From the condition seen in Paludina it would be very
easy to derive, by a shortening of the cerebro-pleural con-
nective, the condition of all other Tænioglossa, with the
possible exception of the Cyclophoridæ and Ampullaria,
which are probably special and independent derivatives of
more specialised Diotocardia.

From the above consideration I conclude that Pleuro-
tomaria in its nervous system, as in some other points in
its anatomy, is the most primitive of existing Diotocardia,
and presents a condition from which that of the majority of
the Tænioglossa may be derived,—possibly also that of the
other Diotocardia, the form in the latter being attained by a
shortening of the pleuro-pedal connective, thus causing the
pleural centres to be approximate to the pedal ganglia; thus
the condition seen in Haliotis, Trochus, Fissurella, and
Patella would be a derived and not a primitive one.

While it is fairly easy to derive the Monotocardian type of
nervous system, radula, gill, and reproductive system from
the corresponding organs of existing Diotocardia, yet in the
conformation of the kidneys we meet one of the greatest
stumblingblocks in our attempt to derive the former group
from the latter.

All the Diotocardia with the exception of the aberrant
Neritinoid group possess two kidneys, and in the majority
these two organs differ markedly in structure and function.[1]

[1] In Fissurella and Patella, both of which, however, are specialised
forms, the two kidneys, though differing in size and relationship, are both
excretory in function; but the left kidney, as in other Diotocardia, derives its
blood-supply from the auricles.

The left characteristically forms the papillary sac, and alone (save in Patella) communicates with the pericardium: this organ is not truly excretory, but serves as a reserve organ, and only removes foreign matter by phagocytosis ; thus if insoluble powder-like carmine be injected into the body it is removed by phagocytes which discharge through the papillary sac (Pelseneer[1]). This left kidney has also a peculiar and characteristic blood-supply, being directly connected with the auricle or auricles (Perrier, op. cit.), and thus receives arterial blood.

The right kidney, on the other hand, is very large, and characteristically situated between the pericardium and stomach, being also at times extended below the former into the anterior part of the hæmocœle. This kidney, which receives the venous blood on its way to the gills, is the true excretory organ, since it alone removes the soluble waste products. The right kidney further serves to transmit the genital products, its duct being frequently modified and glandular in this connection.

In the adult Monotocardian a single kidney alone is present. The position occupied by this gland is somewhat intermediate between that of the two seen in the Diotocardia, being placed in the majority between the pericardium and stomach. It opens normally (where no secondary ureter is developed) by a slit-like orifice between the rectum and gill near the posterior limit of the mantle-cavity, much as does the left kidney of the Diotocardia, and it further resembles that organ in the fact that its cavity communicates with the pericardium ; but at the same time it is a true kidney, and functions like the right kidney of the Diotocardia. Closely pressed between this organ and the pericardium is a glandular mass, often spoken of as the renal gland ; the last organ has the peculiar blood-supply found in the papillary sac of the Diotocardia, which it further resembles in function (Perrier).

We see, then, that the kidneys of these two great sub-

[1] " Les reins, les glandes génitales, et leurs conduits dans les Mollusques," ' Zool. Anz.,' Bd. xix, 1896.

divisions of the Streptoneura are very differently developed, and it is consequently not surprising that a considerable diversity of opinion has been expressed concerning the homology of the single kidney of the Monotocardia.

A consideration of the position of the orifice of this organ in the Monotocardia and its possession of a reno-pericardial pore at once suggests a comparison with the left kidney or papillary sac; but on the other hand in the position of the gland itself, in the nature of its activity, and in the actual presence of the peculiar renal gland, it more nearly approximates to the corresponding right organ of the Diotocardia.

Ray Lankester appears to have been the first to seriously attempt to seek for the homology of the single kidney of the Monotocardia in the left kidney of the Diotocardia, and this view, which is now practically universally accepted, has been further supported by the embryological works of v. Erlanger on Paludina,[1] and on comparative grounds by Pelseneer. Practically the only opponents of this view in recent years have been Haller[2] and Perrier.

The first view, which is based mainly upon the consideration of the relation of the kidney to the rectum and the presence of a reno-pericardial pore, receives additional support from v. Erlanger's ontogenetic observations. An examination of these latter shows them to be much less satisfactory than one would gather from the account given in the average text-book, since the only trace of the supposed missing kidney, the adult right, is an angulation and faintest indication of an outgrowth from the pericardium (cœlom) on the opposite side to that at which the functional kidney is developing. This vestigial structure disappears very speedily without ever attaining any characters which would stamp it as a kidney, so that the support afforded to this theory by v. Erlanger's ontogenetic researches is very meagre. A similar unsatisfactory condition is attached to his surmise—

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[1] "Zur Entwicklung von Paludina vivipara," 'Morph. Jahrb.,' Bd. xvii, 1891.

[2] "Beiträge zur Kenntniss der Niere der Prosobranchia," 'Morph. Jahrb.,' Bd. xi, 1886.

for it is no more—that the genital duct of Paludina arises from the right secondary ureter, a structure which is not known to be present in any living mollusc, and whose existence we have no reason to presuppose.

If, however, we may rely upon these ontogenetic researches, then the single kidney of the adult Monotocardia would be the left kidney or papillary sac of the Diotocardia, a view which is supported by the presence of a reno-pericardial pore.

Against this view we have the position of the kidney in relation to the stomach and pericardium in the majority of the Monotocardia (Paludina being an exception), and the necessity, if we accept it, to seek our ancestral Monoto-cardian in some very archaic Diotocardian, one in which the left kidney has not attained the specialised character of a papillary sac.[1]   Moreover the acceptance of this view does not explain the presence of the peculiar renal gland in the Monotocardia, which has much the character of, and which possesses the peculiar vascular relation of the papillary sac.

Perrier, who made a very exhaustive investigation on the molluscan kidney, believes that the single kidney of the Monocardia contains representatives of both the kidneys of the Diotocardia, and he sees in the renal gland of the former group the representative of the papillary sac of the latter group.   This view, which is an extremely suggestive one, has not met the consideration which it deserves, most zoo-logists apparently accepting Erlanger's statements on the development of these organs in Paludina as conclusively proving that the monotocardian kidney is the papillary sac.

It is, however, possible to approach this subject from ano-ther standpoint, and to endeavour to reconstruct the stages which must have occurred in the displacement of the kidney following upon the disappearance of the right gill and the consequent displacement of the heart and pericardium, and

[1] It might be thought that Fissurella or Patella among living Dioto-cardians presented us with the condition we want, but these forms are too obviously specialised in other respects to serve as the ancestors of the Mono-tocardia.

it appears to me if this view be carefully followed out that it is possible to derive the Monotocardia from such an existing Diotocardian as Pleurotomaria.

If we examine the condition of these organs in one of the Azygobranchia we shall find that with the loss of the right auricle and gill the pericardium becomes displaced to the left, and consequently the two kidneys approach one another very nearly, so much so that Haller thought he found a communication between the two. It appears, however, doubtful if such a connection was present in the forms he examined, but at the same time it seems extremely probable to me that such a condition was attained in the early Monotocardia, as the pericardium shifted further to the left to take up a position at the end of the left gill, and the two kidneys consequently came into close contact. Supposing a perforation to occur in the wall intervening between the two kidneys, a condition would be attained that would be of the greatest advantage to the mollusc, as it would enable it to discharge the secretion of the right kidney through the cavity of the left, while the old right kidney-duct would now serve to transmit the genital products unmixed with excreta.

By a diminution in size of the glandular portion of the papillary sac, and a complete severance of the right kidney duct as a genital duct, we arrive at the condition of the Monotocardia, in which we find a kidney situated in the position of the right kidney, but whose cavity communicates with the pericardium, and whose aperture suggests that of the papillary sac; while packed in between this kidney and the pericardium is the degenerate glandular portion of the papillary sac forming the renal gland.

I would thus regard with Perrier the single kidney of the Monotocardia as representing the excretory part of the right kidney of the Diotocardia plus the cavity, external aperture, and reno-pericardial pore of the papillary sac; while the glandular part of the latter structure persists as the renal gland, and the duct of the right kidney becomes the genital duct.

If these conclusions regarding the homology of the kidney of the Monotocardia have any truth in them, then it would be quite possible to derive the Monotocardia from a Diotocardian having the type of kidney seen in Pleurotomaria, Trochus, or Haliotis.

As I have already pointed out, the nervous system of Pleurotomaria would serve as an excellent starting-point from which to derive that characteristic of the Tænioglossa, better by far than that of Trochus, which in the character of its gills more nearly approaches the Monotocardia.   The general lowly character of Pleurotomaria, especially of its nervous system and radula, and slight reduction of the right gill, taken together with its great antiquity, justifies us, I think, in regarding it as a very primitive form, and one from which the great monotocardian group may very possibly have arisen, and possibly also some of the subdivisions of the Diotocardia.

The following is a brief summary of some of the conclusions at which I have arrived.

Summary.

1. Pleurotomaria is a typical example of a zygobranchiate Diotocardian.

2. In the absence of sharply marked specialised regions in the radula Pleurotomaria Beyrichii and P. Quoyana are distinctly primitive among the Rhipidoglossa.

3. In the reduction of the right gill Pleurotomaria tends to approach the azygobranchiate Diotocardia.

4. In the uniform distribution of the ganglionic cells through the connectives, the commissure, and even the large nerves, and the consequent absence of distinct ganglia, Pleurotomaria is extremely primitive.

5. In the position of the point of origin of the visceral loop (roughly halfway between the cerebral and pedal regions) Pleurotomaria approaches the archi-tænioglossate Paludina and Nassopsis.

6. The pleural ganglion probably arises at the point of

origin of the visceral loop by a further concentration of the ganglionic cells.

7. There is no special concentration of the ganglionic cells just above the future pedal ganglion, such as Bouvier and Fischer identify as the pleural ganglion.

8. That in the position of the supporting skeleton of the gills and the possession of a spiral stomach-cæcum Pleurotomaria shows signs of a common ancestry with the Cephalopoda.

9. That Perrier is correct in regarding the single kidney (including the renal gland) of the Monotocardia as representing both the right and left kidney of the Diotocardia.

10. That Pleurotomaria may be regarded as a form very closely related to the stock from which the Monotocardia originated.

July, 1900.

DESCRIPTION OF PLATES 13—16,

Illustrating Mr. Martin F. Woodward's paper on "The Anatomy of Pleurotomaria Beyrichii, Hilg."

List of Reference Letters.

a. a. Anterior aorta. *a. b.* Afferent branchial vessel. *a. p.* Pedal artery. *a. r. k.* Anterior lobe of right kidney. *b. d.* Bile-duct. *b. g.* Buccal ganglion. *b. n.* Buccal nerve. *bn. g.* Branchial ganglion. *cb. c.* Cerebral commissure. *cb. g.* Cerebral ganglion. *cb. p.* Cerebro-pedal connective. *cb. pl.* Cerebro-pleural connective. *cr.* Crop. *d. l. m.* Dorsal longitudinal muscle. *d. m.* Depressor muscle. *e. b.* Efferent branchial vessel. *ep.* Epipodium. *g'., g''.* Right and left gills. *g. a.* Genital aperture. *g. d.* Genital duct. *g. g.* Genital gland. *h. p.* Horny buccal papillæ. *i. l. c.* Interlaminar connections. *i. l. m.* Internal longitudinal muscle. *int.* Intestine. *i. r. m.* Infra-radular membrane. *j.* Jaw. *k. c.* Kidney chamber (right). *l.* Liver. *l. au.* Left auricle. *l. c.* Labial commissure. *l. k.* Left kidney (papillary sac). *l. k. a.* Left renal aperture. *l. l. m.* Lateral longitudinal muscle. *l. m.* Longitu-

dinal muscle of gill-septum.   *l. p.*, *l. p.*[1] Lateral œsophageal pouches.   *l. pr.* Lateral protractor.   *l. r.* Lateral retractor.   *m.* Mouth.   *ma.* Mantle.   *m. c.* Mantle cavity.   *m. g.* Mucous (hypobranchial) gland.   *m. g'.*, *m. g''.* Accessory mucous glands.   *m. s.* Mantle-slit.   *n. l.* Nerve-layer in gill-septum.   *od.* Odontophore.   *od. c'.*, *od. c''.* Odontophoral cartilages.   *œ.* Œsophagus.   *o. n.* Optic nerve.   *op. l.* Opercular lobe.   *os.* Osphradium.   *ot. n.* Otocyst nerve. *ovd.* Oviduct.   *p'.*, *p''.* First and second pedal nerves.   *p. r. k.* Posterior lobe of right kidney.   *pc.* Pericardium.   *pl. c.* Pleural centre.   *pl. p.* Pleuro-pedal connective.   *rd.* Radula.   *r.* Rectum.   *r. au.* Right auricle.   *r. k. a.* Right kidney aperture.   *r. k. d.* Right kidney duct.   *r. p. c.* Reno-pericardial canal. *r. s.* Radular sac.   *s. r.* Supporting rods.   *sb. int.* Subintestinal nerve.   *sl. d.* Salivary duct.   *sl. g.* Salivary gland.   *sp. a.* Supra-neural artery.   *sp. c.* Spiral cæcum.   *sp. int.* Supra-intestinal nerve.   *st.* Stomach.   *t. n.* Tentacular nerve.   *u.* Ureter (right kidney duct).   *v.* Ventricle.   *v. b.* Vitreous body. *v. l. m.* Ventral longitudinal muscle.   *v. pr.* Ventral protractor.   *v. r.* Ventral retractor.   *v. s.* Venous sinuses.   *v. t. m.* Ventral transverse muscle.

The figures, unless otherwise stated, are of the natural size.

PLATE 13.

Figs. 1—12. Pleurotomaria Beyrichii.

Fig. 1.—Anterior part of the body viewed from the left side, showing the bifid left tentacle.

Fig. 2.—Anterior part of the body viewed from above, to show dorsal surface of foot. This specimen had lost its operculum.

Fig. 3.—Opercular lobe of normal specimen.

Fig. 4.—Operculum.

Fig. 5.—Dorsal wall of mantle cavity, with gills, mucous glands, and rectum ; viewed from below.

Fig. 6.—Dissection of the anterior part of the body; mantle divided and reflected, floor of mantle cavity and dorsal surface of head removed, to show the relations of the anterior viscera.

Fig. 7.—General dissection from the right side, showing the mutual relations of the alimentary canal, nervous system, heart, and pallial complex. The forward extension of the right kidney is indicated by a brown shade.

Fig. 8.—Side view of the buccal mass, showing the salivary gland with its duct, the cerebral ganglia, and the buccal nerves. Enlarged.

Fig. 9.—Dissection of the buccal cavity, showing the radula, jaws, and horny papillæ.

Fig. 10.—Dissection of the buccal mass and crop : 1 and 2 the left, 3 and 4 the right œsophageal folds.

Fig. 11.—Diagrammatic transverse section across the crop.

Fig. 12.—Dissection of the stomach with its spiral cæcum, from above.

Fig. 13.—Dissection of the stomach of Trochus zizyphinus, from above. Enlarged.

PLATE 14.

P. Beyrichii.

Fig. 14.—Transverse section of the gill and branchial ganglion, showing the gill-plates in surface view. Somewhat diagrammatic. × about 12.

Fig. 15.—Transverse section of the gill, showing the circulation of the blood in the gill-plates. Diagram constructed from sections. × about 13.

Fig. 16.—Section across two gill-plates, taken along the line *a b*, Fig. 14. × about 36.

Fig. 17.—Section parallel to the last, but passing through the dorsal junction of the gill-plates with the septum. × 170.

Fig. 18.—Horizontal section across the outer margin of a gill-plate. × 500.

Fig. 19.—Section through the branchial ganglion at the origin of the branchial nerve. The ganglion is slightly contracted away from the connective tissue of the mantle. × 50.

Fig. 20.—Section through the eye. × 60.

Fig. 21.—Anterior portion of the nervous system from the left side of the body viewed from within, showing the cerebral ganglion and its connections with the pleuro-pedal cords, together with the origin of the subintestinal nerve and the principal nerves to the head and side-walls of the anterior part of the body. The first transverse pedal commissure is seen to be formed from both the pleural and pedal cords, as also is the second pedal nerve. × $2\frac{1}{2}$.

Fig. 22.—The corresponding portion of the nervous system from the right side of the body, viewed from without. Drawn from a dissection with the portion of the nerve-cells indicated diagrammatically from microtome sections. × 6.

PLATE 15.

Fig. 23.—Dissection of the kidneys and pericardium, showing the extent of the right kidney and its relation to the genital duct; also the great venous sinus.

Fig. 24.—Dissection showing the relation of the left kidney to the pericardium.

Fig. 25.—Semi-diagrammatic representation of the two kidneys, the pericardium, reno-pericardial canal, and genital duct.

Fig. 26.—Schematic representation of the same.

Fɪɢ. 27.—Diagram of the nervous system viewed from above.

Fɪɢ. 28.—Dissection of the head, foot, and mantle, showing the relations of the nervous system on the right side of the body; also the anterior aorta and supra-neural and pedal artery.

Fɪɢ. 29.—Enlarged view of the brain, cerebro-pleural, and cerebro-pedal connectives, and the relation of the nerves to the lips and buccal mass.

Fɪɢ. 30.—*A—H.* Eight views of the musculature of the buccal mass. *A.* Dorsal view. *B.* Side view, with the lateral protractor (*l. pr.*) reflected. *C.* Ditto, with the ventral longitudinal muscle (*v. l. m.*) reflected. *D.* Ditto, after the removal of the lateral longitudinal, the radula, and greater part of the infra-radular membrane (*i. r. m.*). *E.* Ditto, after the removal of the main odontophoral cartilage, exposing the internal longitudinal muscle (*i. l. m.*). *F.* Dorsal dissection, showing the cartilages on the left, and the muscles and infra-radular membrane on the right. *G.* Viewed from below, showing the transverse muscle (*v. t. m.*). *H.* Diagrammatic transverse section.

Fɪɢ. 31.—*A.* Entire otocysts.   × 50. *B.* Isolated otoconia.   × 400.

PLATE 16.

Fɪɢ. 32.—Half a transverse row of teeth, including the rhachidian.   × 50.

Fɪɢ. 33.—Rhachian tooth, side view.   × 66.

Fɪɢ. 34.—First central tooth, side view.   × 66.

Fɪɢ. 35.—Second central tooth, side view.   × 66.

Fɪɢ. 36.—Third central, with first and second lamellate tooth.   × 66.

Fɪɢ. 37.—Four views of a typical lamellate tooth, from the left side of the radula. *A.* Viewed from the outer side. *B.* Normal view. *C.* Edge on. *D.* Viewed from below.   × 140.

Fɪɢ. 38.—Twenty-fifth tooth.   × 60.

Fɪɢ. 39.—Twenty-sixth tooth.   × 60.

Fɪɢ. 40.—Twenty-seventh tooth.   × 60.

Fɪɢ. 41.—Thirtieth tooth.   × 60.

Fɪɢ. 42.—Thirty-fourth tooth.   × 60.

Fɪɢ. 43.—Thirty-seventh tooth.   × 60.

Fɪɢ. 44.—Thirty-ninth tooth.   × 60.

Fɪɢ. 45.—Forty-second tooth.   × 120.

Fɪɢ. 46.—Forty-third tooth.   × 120.

Fɪɢ. 47.—Forty-fourth tooth.   × 120.

Fɪɢ. 48.—Forty-seventh tooth.   × 120.

Fɪɢ. 49.—Forty-ninth tooth.   × 120.

Fɪɢ. 50.—Type of tooth between the fiftieth and the sixtieth.   × 120.

FIG. 51.—Seventy-fourth tooth. × 120.

FIG. 52.—Ninety-seventh tooth. × 120.

FIG. 53.—Last four brush teeth and the seven flabelliform teeth, i. e. the 101st to the 111th tooth, from the left side of the radula. × 120.

FIG. 54.—Left jaw, from its inner side. × 9.

15.

17.

14.

19.

V.

22.

cb.g.

cb.pl

pl.c.

sp.int.

cb.p.

20.

s.r.

v.b.

o.n.

6.

cb.c.

cb.g.

m.

b.n.

l.c.

pl.p.

cb.pl

cb.p.

21.

l.c.

s.r.

i.l.c.

sb.int.

pl.c.

18.

p.

*

*

*

23.

24.

28.

29.

32.

33.

A.

B.

41.

42.

54.

53.

Martin Woodward del.
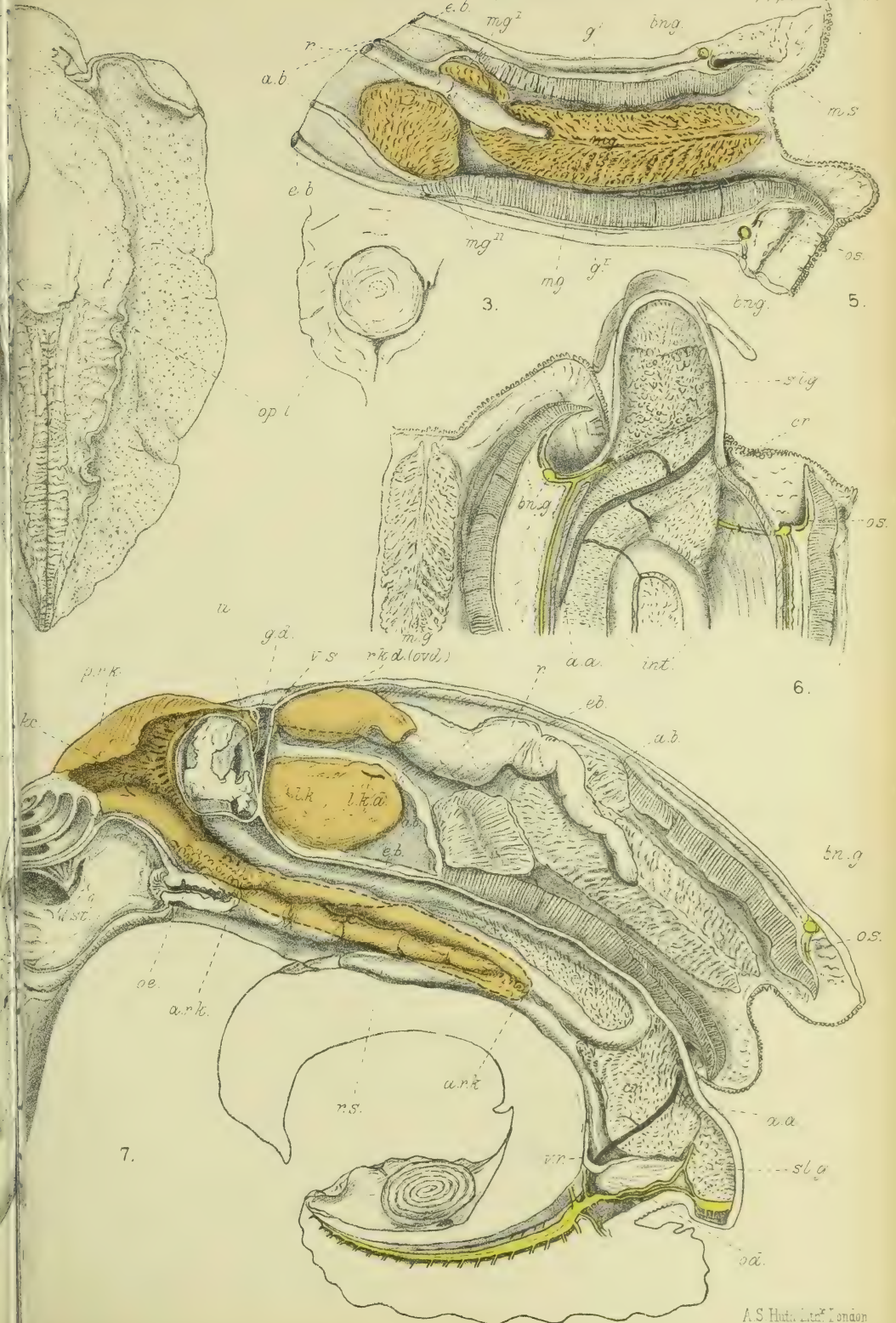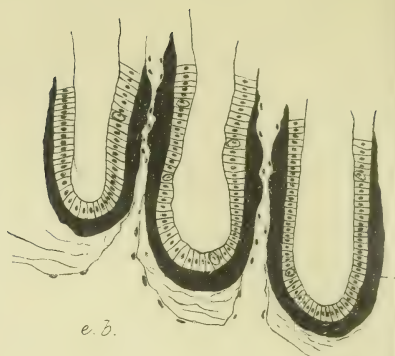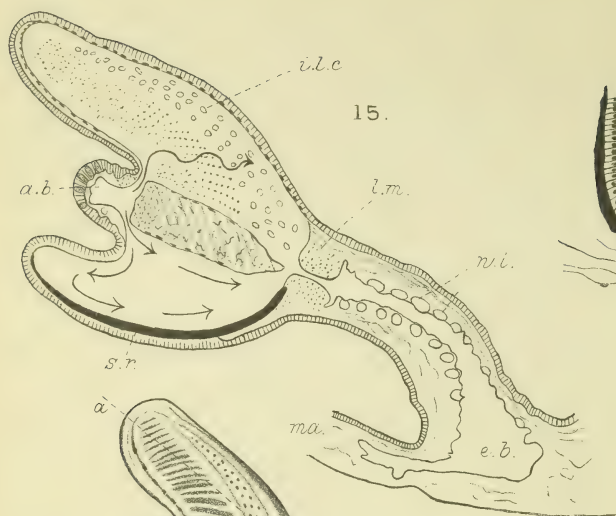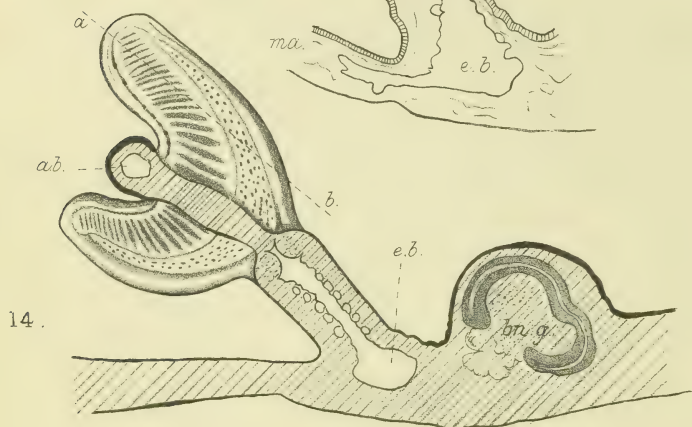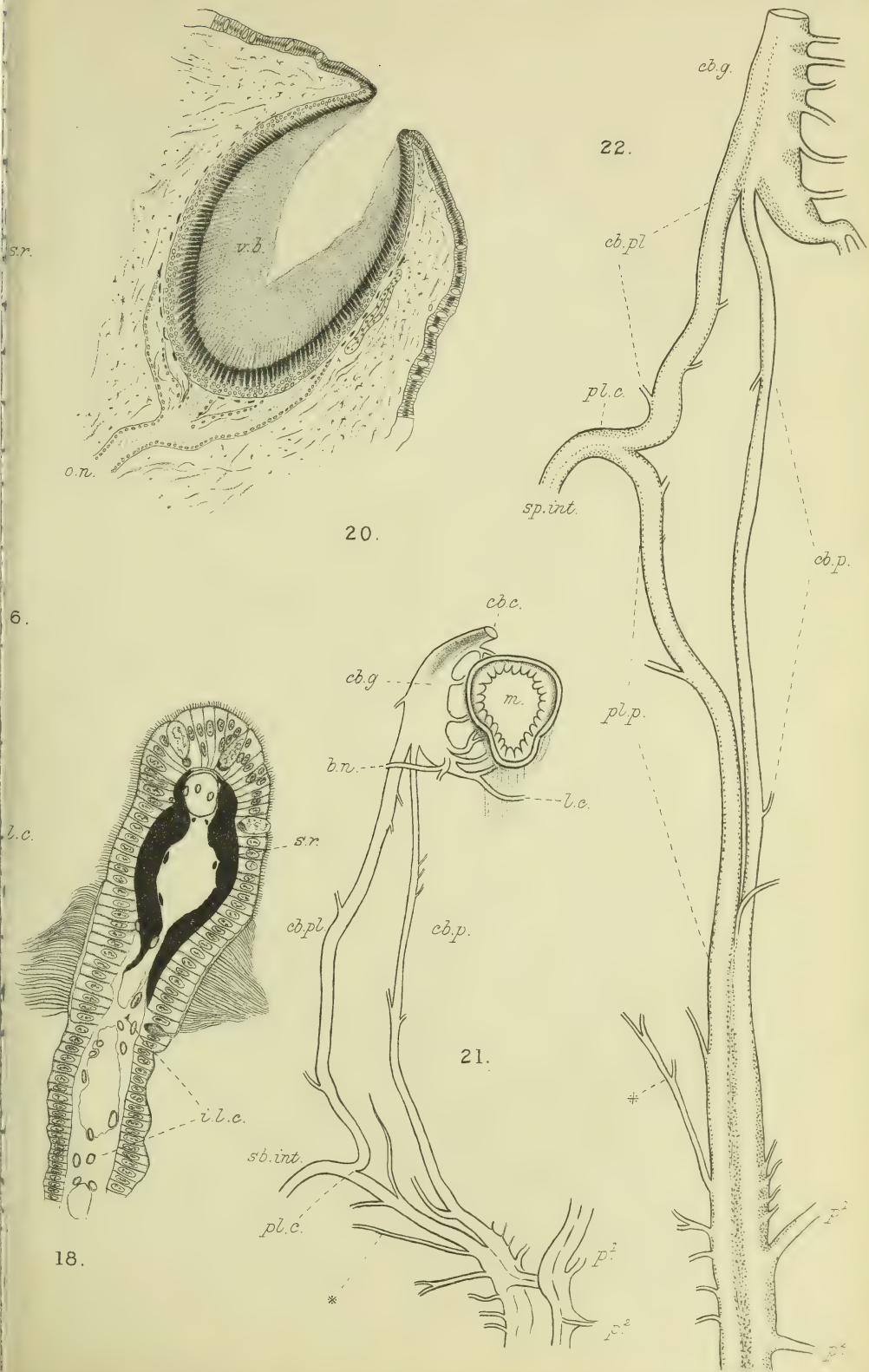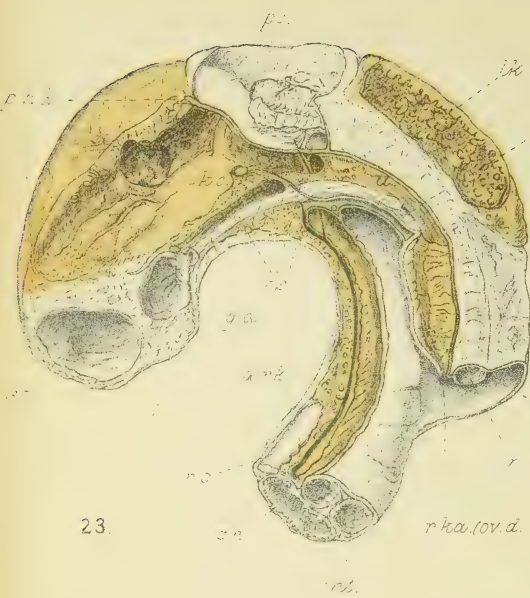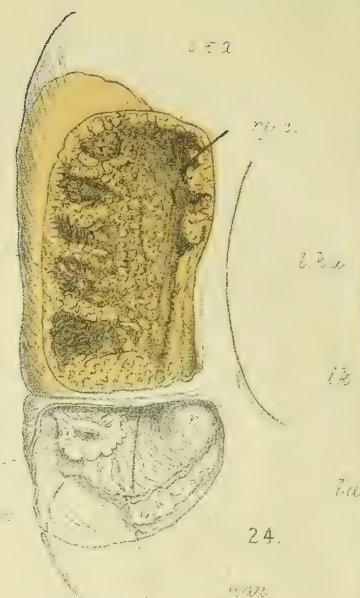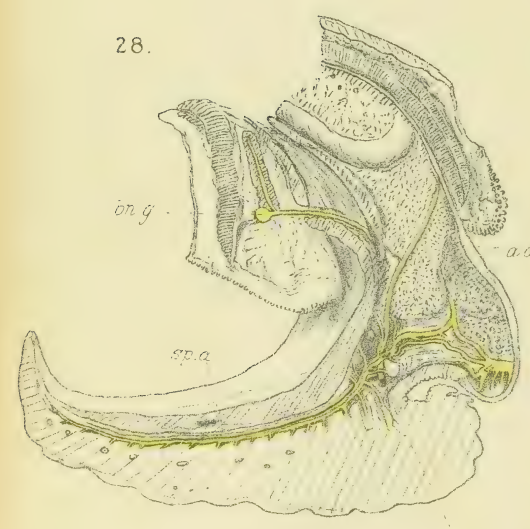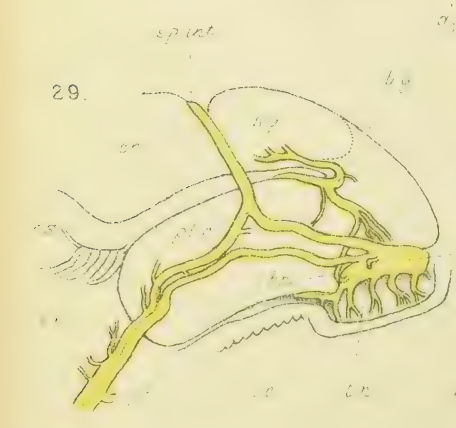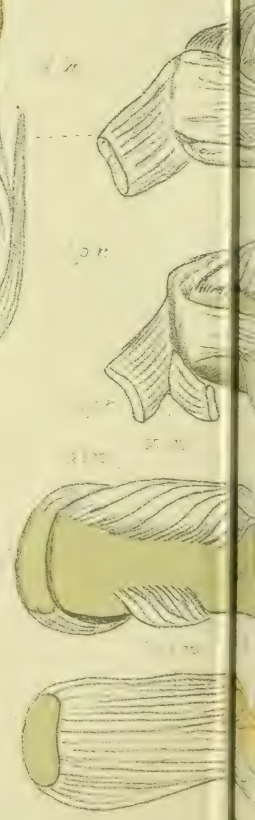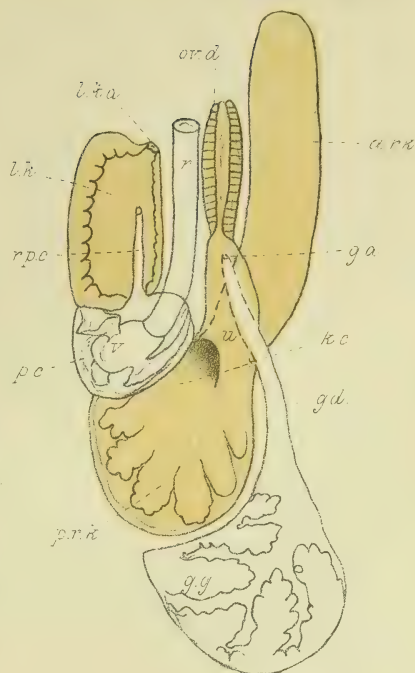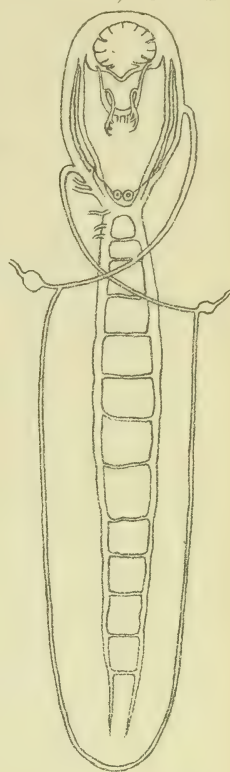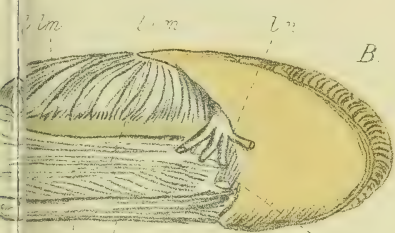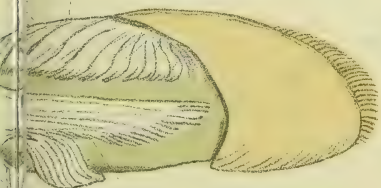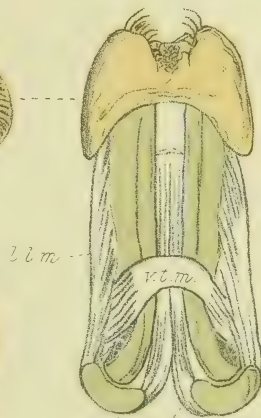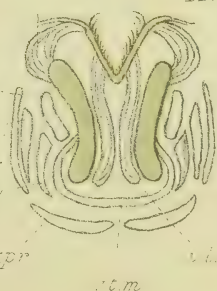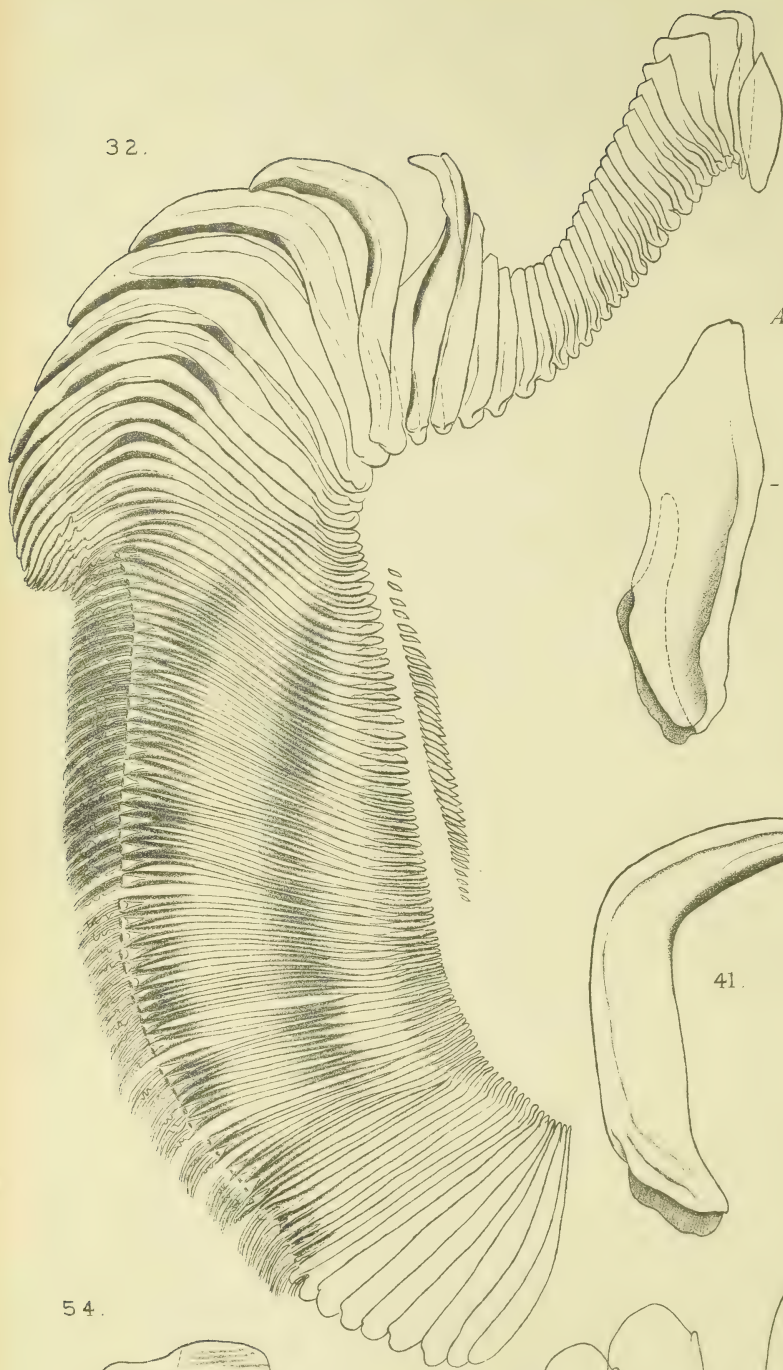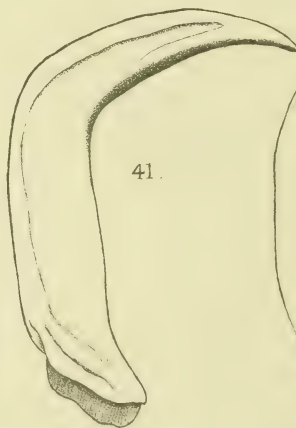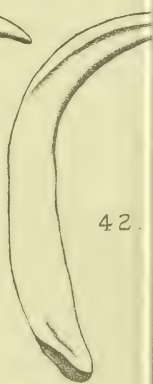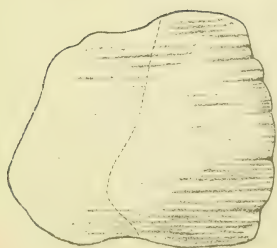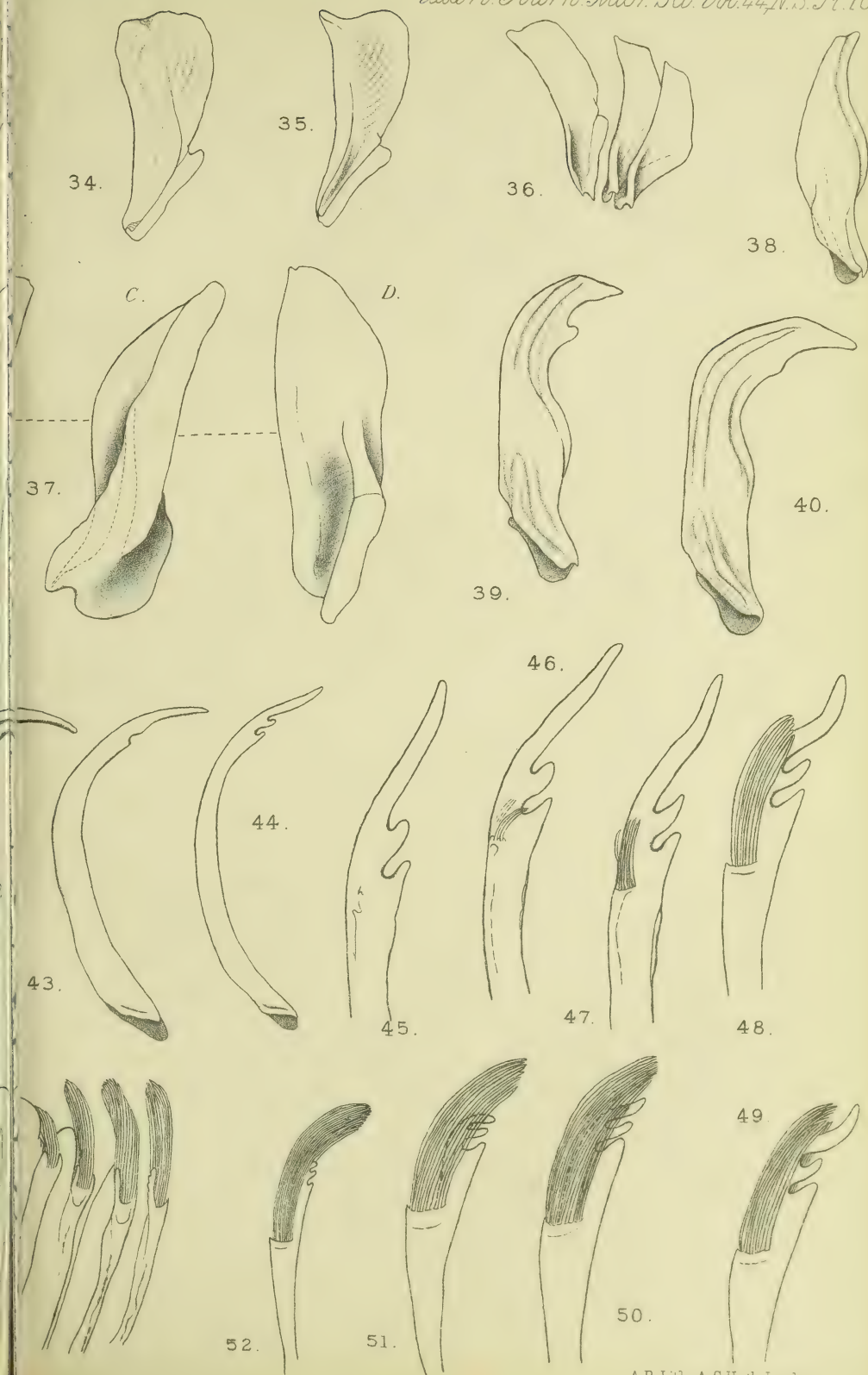
Dolichorhynchus indicus, n. g., n. sp.
A New Acraniate.

By

Arthur Willey.

In the collection of Polychæta made during the voyages of
H.M.S. "Investigator," in the Indian Ocean, under the
direction of Dr. Alcock, there is a tube containing several
specimens of an Amphioxus, which on inspection has
proved to be the type of a new sub-genus of the genus Bran-
chiostoma.

Not one of the specimens appears to be in a condition of
sexual maturity, in spite of the fact that the largest attains a
length of 25·75 mm. The body is elongated, slender, late-
rally compressed, and tapering gradually towards the posterior
end. There are seventy-one myotomes, and the formula is
42—14—15.

The feature which at once differentiates it from all other
known forms of Amphioxus is the great length of the præ-
oral lobe, close upon 2 mm. measured from the anterior
termination of the neurochord, or equal in length to the first
six myotomes (Fig. 1). The metapleural folds terminate sym-
metrically some distance behind the atriopore on either side
of the ventral fin, a fact which denotes the systematic posi-
tion of the species in the absence of data afforded by the
gonads (Fig. 2). There are about forty-five ventral fin cham-
bers behind the termination of the metapleural folds, and
four or five in front of this point. In the specimen figured
the tentacular cirri (buccal cirri) are mostly concealed within
the vestibule of the mouth, but the ends of several are pro-
jecting from beneath the oral hood in front.

The dorsal fin is well marked, being about one fifth the

total height of the body. In the single specimen cut for the examination of the ventral fin rays they do not appear as paired structures, but as massive median expansions of the hyaline laminar tissue.

It will be noticed that the modification which characterises this species, namely, the prolongation of the notochord and cephalic fin in front, is of an exactly opposite nature to that

Fig. 1.
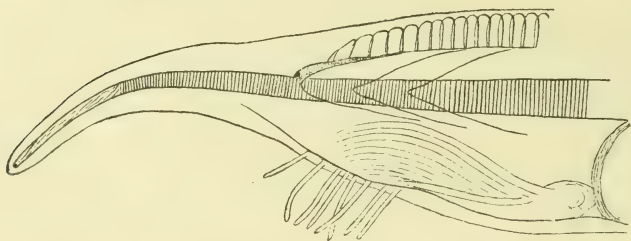
Anterior region of D. indicus, comprising the oral hood and præ-oral lobe from the left side. The anterior end of the neurochord with the eye-spot projects in front of the first myotome.

Fig. 2.
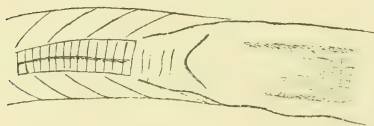
Region of the atriopore of D. indicus in ventral view, to show the symmetrical termination of the metapleural folds on either side of the ventral fin behind the v-shaped atriopore.

which distinguishes Asymmetron, where the notochord and caudal fin extend far behind the posterior limit of the myotomes.

Locality.—Off Black Pagoda, Orissa Coast ; 11 fathoms ; January 15th, 1889.

The following tabulation of the genera and sub-genera of Amphioxus will serve to show the systematic position of the new form.

Genus I.—Branchiostoma, Costa, 1834.
      With biserial gonads.
    Sub-genus 1.—Amphioxus, Yarrell, 1836.
        Type, A. lanceolatus (Pallas).
    Sub-genus 2.—Dolichorhynchus, n. g.
        Type, D. indicus, n. sp.
Genus II.—Heteropleuron, Kirkaldy, 1895.
      With uniserial gonads.
    Sub-genus 1.—Paramphioxus, Haeckel, 1893 [in Semon's 'Forschungsreise,' Bd. i, p. xiii].
        Type, P. bassanus (Günther).
    Sub-genus 2.—Epigonichthys, W. Peters, 1876.
        Type, E. cultellus, Peters.
    Sub-genus 3.—Asymmetron, E. A. Andrews, 1893.
        Type, A. lucayanum, Andrews.

Of the above sub-genera the three which are most peculiar in external form, namely, Dolichorhynchus, Epigonichthys, and Asymmetron, are monotypic if we consider Asymmetron caudatum, Willey, 1896, to be merely of subspecific rank, as would seem to be the case.

Heteropleuron hectori, the New Zealand Lancelet.

By

W. Blaxland Benham, D.Sc., M.A., F.Z.S.,
Professor of Biology in the University of Otago.

With Plate 17.

By the kindness of Sir James Hector I have been able to examine a couple of specimens of an " Amphioxus " that have been for some years past in the Colonial Museum at Wellington, N.Z. The specimens are referred to by Captain Hutton in his ' Catalogue of the Fishes of New Zealand,' published by the Colonial Museum and Geological Survey Department in 1872.

On p. 88 of this catalogue, under the title of " Branchiostoma lanceolatum," a brief series of measurements are given, but without any details to enable one to judge that they are different from the type of the family. At that period, and for some years later, indeed, even Dr. Günther believed that the various specimens from extra-European seas belonged to this same species, as is evident from the account of the lancelet in his ' Study of Fishes ' (1880). Since Hutton's reference to them they seem to have been entirely overlooked by recent writers, for no mention is made of any New Zealand representative of the family either by Andrews, by Willey, or by Kirkaldy, in their respective accounts of this animal.

This New Zealand Lancelet is the type of a new species of

the genus Heteropleuron, for which I propose the name H. hectori.

The specimens had apparently been preserved in osmic acid, for they are dark grey; and though they had received various slight injuries to the side of the body and to the fins, they are in sufficiently good condition to enable me to make out all the important specific characters. One of the specimens I was permitted to open, doing as little damage to it as possible; and afterwards I cleared it in oil of cloves for more detailed examination of certain parts.

The extreme tips at both ends of the body in each specimen were more or less injured, but by comparing the two I have been able to reconstruct, with some confidence, these ends. The injury affects the tip of the caudal fin, and part of the rostral, which was folded round the side : in the case of the latter the outlines are in the drawings represented by dotted lines, as there is some doubt as to the exact form of the fin; while the general curvature of the upper and lower margins of the caudal fin, preceding the injury, suffices to show that probably the fin is naturally of the form shown in the drawing.

Heteropleuron hectori, n. sp., has a length of about two inches, the actual measurements being 48 mm. and 49 mm. respectively.

The myotomes number 84 or 85, and the myotome formula is 53 + 19 (20) + 12, i. e. there are 53 myotomes from the anterior end to the hinder margin of the atriopore, 19 or 20 thence to the posterior margin of the anus, and the remaining 12 are post-anal. The last two or three are very small, and the usual difficulties in deciding as to the exact number of myotomes between atriopore and anus were encountered. But from careful examination of the two specimens, I believe that the above formula (which, as Kirkaldy's paper [1] shows, is subject to individual variation in all species) is correct.

The dorsal fin is very shallow over the greater part of its

[1] " Revision of the Branchiostomidæ," 'Quart. Journ. Micr. Sci.,' xxxvii.

extent, though rather higher over its anterior quarter; while shortly before the level of the atriopore it again gradually rises to form the caudal fin. The fin rays cease at the level of the anus. The rostral fin—as I have remarked—is only indicated in the drawing with some hesitation; but it appears to be rhomboidal in outline, rising suddenly from the dorsal. The ventral fin, or pre-anal region of the median fin, is short and low; it contains about a dozen unpaired fin-ray boxes, which are, however, without fin rays, as is the case, too, in H. cultellum. At first these boxes are quite distinct, but after twelve or fourteen complete ones the outlines become less and less distinct, and soon disappear altogether.

The caudal fin rises quite gradually from the dorsal, at about the level of the atriopore, without any abrupt angle, such as is seen in H. bassanum and H. cingalense; but in this respect it resembles H. cultellum. Its lower moiety is, however, deeper than the upper, and rises relatively far forwards—about the seventh myotome behind the atriopore.

It attains its greatest height at about the fourteenth post-atrioporal myotome, that is some distance anterior to the anus. Posteriorly the upper and lower margins slope gradually, and equally and regularly backwards, and appear to pass in the same curve to a point a short distance behind the notochord.

On examining the transparent specimen I noted a series of short brownish chitinoid rods along the ventral base of the caudal fin, extending outwards from the lower ends of the muscles for a distance equal to about one fourth the depth of the fin (fig. 5). Each rod spreads out slightly near its distal end, and becomes thinner and more transparent— losing itself in the tissue of the fin. These rods I traced backwards to the end of the body, whilst forwards there is a great gap between them and the ventral fin-ray boxes, the walls of which have quite a different aspect from the rods, which do not appear to be optical sections of transverse walls, but appear to be definite, solid, rod-like structures.

Along the upper base of the caudal are also a few shorter and less distinct rod-like structures, but I do not feel sure that in this case they are not the transverse walls of empty fin-ray boxes ; the animal was lying in an awkward position, and though there was a gap between the dorsal rod-like structures and the hindermost distinct fin-ray boxes, yet the higher surface of the body was here slightly injured and torn, so that it was not possible to trace the continuity of the two series.

At first I imagined that we had in this species an interesting vestige of the peculiar caudal fin rays of the early larva, as figured in Lankester and Willey's memoir[1] (pl. xxix, fig. 1). But on examining the tail of a specimen of H. bassanum I found that it was unnecessary to explain the appearance in this temptingly interesting manner ; for in H. bassanum I find that the fin rays of the ventral fin are continued past the anus along the under surface of the body to the antepenultimate myotome (fig. 6) : it is true they and their " boxes " are smaller here than in the true ventral fin, anterior to the anus, but they are perfectly distinct right along the base of the caudal fin.

These ventral rays extend further backwards than do the dorsal fin rays, which are here only represented by a series of empty boxes and irregular "lymph-spaces ;" in fact, the " rods " in H. hectori are the shallow transverse walls of the empty fin-ray boxes. This post-anal extension of the fin rays does not appear to have been noted[2] in any other member of the group; and in A. lanceolatus Lankester states definitely that they cease in front of the anus, and I have examined mounted specimens myself and can confirm this statement.

In connection with H. bassanum I have to correct what appears to be an error in Kirkaldy's diagnosis of this species, where it is stated (p. 314) that the ventral fin-ray

[1] Lankester and Willey, "Development of the Atrial Chamber in Amphioxus," 'Quart. Journ. Micr. Sci.,' xxxi.

[2] "Contributions to the Knowledge of A. lanceolatus," 'Quart. Journ. Micr. Sci.,' xxix, p. 373.

chambers contain " paired fin rays." In specimens collected in Port Phillip, and presented to me by Prof. Dendy, I find, on the contrary, most definitely only a single series of fin rays in the ventral fin in this species.

This continuity of the fin rays post-anally seems to show the probability that the "ventral fin " is a part of the " median fin," as is suggested by Lankester and Willey (p. 456), in opposition to the earlier view by the former author that the ventral fin is the result of fusion of a paired structure (3, p. 373). It becomes more evident that the double fin rays of A. lanceolatus are secondary, arising perhaps as a result of splitting of single rays.

The pre-oral hood is much deeper on the right than on the left side, so that when viewed from the latter aspect both margins and their cirri are visible (fig. 2), and the vestibule opens distinctly on the left side of the animal. This is even better seen in a ventral view (fig. 4), where the right hood is seen passing obliquely forwards to be continued into the ventral fin, while the left margin disappears from view as it curves dorsally upwards.

In the drawings of Heteropleuron and Asymmetron given by Kirkaldy and Andrews[1] the vestibule and its opening are represented as being quite symmetrical. It is of interest that in this new species a condition is retained which is a distinct reminiscence of the larval state of affairs. Further, the cirri on the right side are somewhat shorter than those on the left. These cirri number nineteen on each side, with one median ventral, which is shorter than the lowest of the lateral series ; these commence as long filiform structures, and gradually diminish in length as the series approaches the dorsal termination.

The gonads, present only on the right side, appear to be about eighteen in number, but as they dropped away from the body-wall as it was turned aside there may have been a few more.

[1] "An Undescribed Acraniate—Assymmetron lucayanum," 'Stud. Biol. Lab., J. H. Univ.,' v.

It is scarcely necessary to state that the right metapleur is continuous with the ventral fin, as that is one of the characters of the genus.

Locality.—East coast of the North Island of New Zealand.[1]

From this brief but sufficient survey of the external characters of the New Zealand species, it will be seen that it differs from each of the previously known species of Hetero-pleuron.

In form this new species seems, from the drawings available, to be somewhat stouter than other species, while the tapering anteriorly is comparatively sudden (fig. 1). The greatest height, measured from the upper edge of the dorsal fin to the lower margin of the metapleure, is 5 mm., which is about one tenth of the total length. These measurements are, of course, liable to variation according to the condition of preservation ; my specimens, however, are not shrunk in the way that occurs when living specimens are plunged into strong alcohol, but have retained a form similar to that of A. lanceolatus preserved in picric acid, and though some-what soft are not in any way " rotten." Therefore I think the form given in the plate, which is drawn to scale, is as nearly as possible true to life. It must be borne in mind, however, that the pre-oral hood is retracted, while in the most reliable drawing of Amphioxus, viz. that given by Pro-fessor Lankester, this hood hangs down as a nearly semi-circular membrane. The left metapleural ridge can be traced in my specimens right forwards above the hood, which has shrunk upwards below it (see fig. 2).

The distance between the atriopore and the anus is one sixth of the total length, and the distance of the anus from the end of the body is one sixteenth of the total.

In size it exceeds the largest, which is H. bassanum,

---

[1] According to a verbal communication by Sir James Hector, these two specimens were collected at Awanui, just south of the East Cape ; whilst Hutton in the ' Catalogue' gives as the locality " Poverty Bay," which is a little further south.

with a length of 43 mm.; in total number of myotomes, too, it exceeds any Amphioxid hitherto described—the nearest approach being seventy-nine in "A. elongatum" of Sandeval, and seventy-eight in H. bassanum.

It is perhaps worth noting that this excess is chiefly due to an increase in the number of pre-atrioporal segments; for the post-anal segments in other species are from eight in H. cingalense to fourteen or even seventeen in H. bassanum, with an interporal number of ten to seventeen in the various species.

In regard to the caudal fin, there is equally sufficient evidence of distinctness, for whereas in H. bassanum it commences behind the anus, in H. cingalense it arises immediately in front of it, and is very short; while in H. cultellum, though it begins at a point further forward, yet this point is some distance relatively behind its point of origin in H. hectori, while the position of the greatest depth is behind the anus in all three, instead of being anterior to it, as in the present species.

The sea surrounding Australia and the neighbouring islands is evidently rich in species of Branchiostomidæ, for already four species belonging to each of the three known genera have been recorded,—viz. Amphioxus belcheri, Gray, from Torres Straits, as well as from the coast of Borneo; Heteropleuron cultellum, Peters, from Torres Straits and further east coast of Australia; Asymmetron caudatum, Willey, from the Louisiade Archipelago,[1] due east of the Torres Straits; and H. bassanum, Günther, from the south of Australia, from Bass's Straits. The present species thus makes the fifth in these southern seas; its habitat is two thousand miles or more distant from each of these localities. These seas appear to be the home of the asymmetrical species, and one is tempted to think that these may be the more primitive of the family, especially as my species presents one, perhaps two survivals apparently of a larval condition.

[1] 'Quart. Journ. Micr. Sci.,' vol. xxxix, p. 210.

I regret that I have been unable to make a fuller examination of this interesting species, and look forward to obtaining living specimens ; but it appeared worth while to rescue these individuals from their obscurity when it was found that they differed from those of the neighbouring seas.

DUNEDIN;
  August 25th, 1900.

EXPLANATION OF PLATE 17,

Illustrating Professor Blaxland Benham's paper on " Heteropleuron hectori, the New Zealand Lancelet."

FIG. 1.—Heteropleuron hectori, n. sp. (× 2). *a*. Metapleur. *b*. Floor of atrium. *c*. Atriopore. *d*. Anus.

FIG. 2.—Heteropleuron hectori. Side view of the anterior end (× 8). *a*. Left metapleur. *b*. Floor of the atrium. *c*. Right metapleur. The outline of the rostral fin is dotted, as there is some doubt as to its true shape and size.

FIG. 3.—Hinder end of the same (× 8). *a*. Left metapleur. *b*. Atriopore. *c*. Ventral fin. *d*. Anus.

FIG. 4.—Ventral view of the anterior end of the same, showing the vestibule opening distinctly on the left side of the animal. *a*. Left metapleur. *b*. Floor of atrium. *c*. Right metapleur. *d*. Ventral fin.

FIG. 5.—A portion of the ventral base of the caudal fin of a transparent specimen, seen under a low power. *a*. Muscles. *b*. Fin. *c*. Rod-like structures, the walls of empty fin-ray boxes.

FIG. 6.—View of the tail of H. bassanum, cleared in clove oil, showing the post-anal continuation of the ventral fin rays. The myotome marked 3 is the antepenultimate segment, beyond which the fin rays are absent. *a*. Ventral caudal expansion of median fin, the edge of which is folded. *b*. Fin rays. *c*. Dorsal portion of the caudal fin, along the base of which empty " boxes " and lymph-spaces are seen.

FIG. 7.—A view of a portion of the per-anal part of the ventral fin of H. bassanum. The lower part of the body was cut off, cleared and mounted ; it is seen from below, and shows a single series of fin rays.
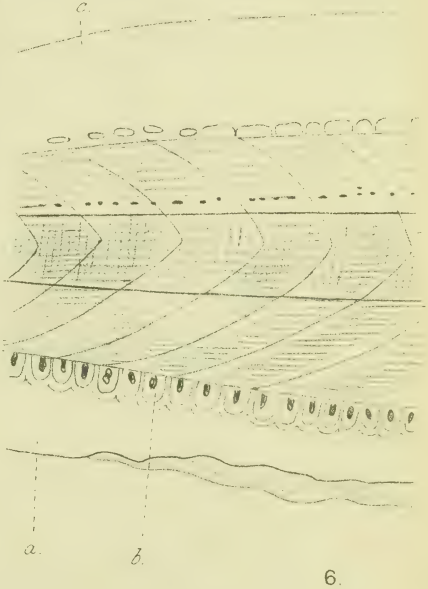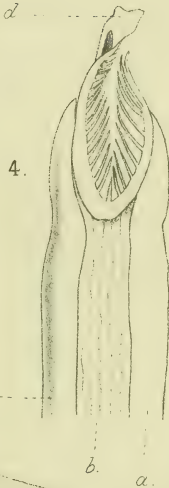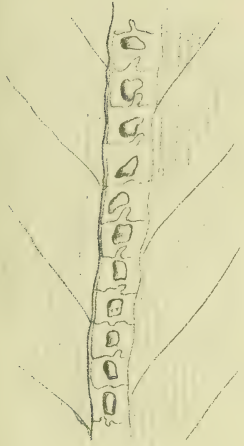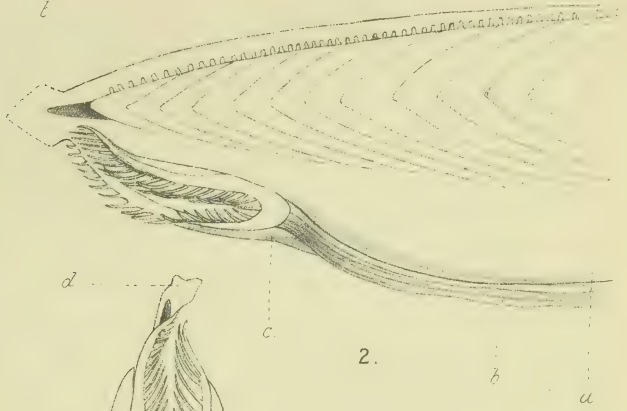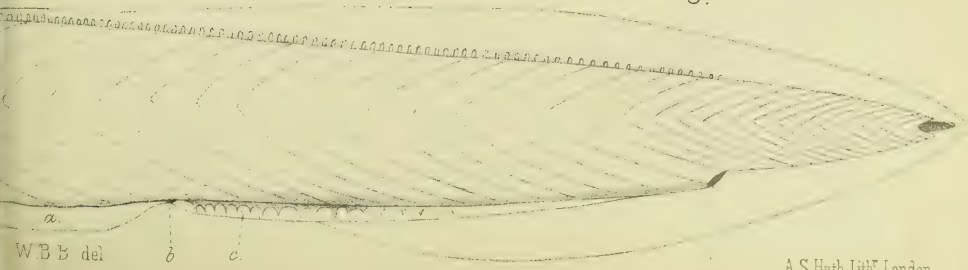
On some Parasites found in Echinus esculentus, L.

By

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With Plate 18.

I. TURBELLARIA.

THE interesting parasite, Syndesmus, was first observed
by Patrick Geddes,[1] who, however, beyond drawing attention
to its partly Turbellarian, partly Trematode characters, made
no attempt to describe it. He found it in the perivisceral
cavity of Echinus esculentus, L.

W. A. Silliman[2] in the following year gave a description
of the external features of the parasite, and suggested the
generic name Syndesmus. He found it living on a large
green nematode, which seemed to him to be a parasite of E.
esculentus taken at Roscoff.

Five years later Ph. François[3] in the same Proceedings
records the occurrence of this animal in the intestine of
Strongylocentrotus lividus, Lam., and of E. acutus,
Lam., at Banyuls. His description, however, differs mate-
rially from that of Silliman,—so much so, indeed, that Braun[4]

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[1] 'Arch. Zool.,' exp. 1, ser. viii, 1879–80, p. 483.
[2] 'C. R. Ac. Sci.,' xciii, 1881, p. 1087.
[3] Ibid., ciii, 1886, p. 752.
[4] 'Central. Bakter.,' v, 1889, p. 41.

remarks that one might think that the two authors were observing different species. François suggests the specific name echinorum.

The animal is again recorded in 1892–3 by L. Cuénot,[1] who draws attention to the fact that it corresponds well with the character of the family VORTICIDA of von Graff, and indeed to his sub-family VORTICINA PARASITICA, which includes another parasitic genus of Turbellaria, A noplodium, also found in echinoderms. Silliman, François, and Cuénot all promise full accounts with figures of the anatomy, but as far as I can find out these have not yet appeared.

Last autumn my friend Mr. W. F. Cooper brought me eleven specimens of this parasite which he had found, ten in the alimentary canal, and one lying on the genital gland in the perivisceral cavity of a specimen of Echinus esculentus, L., that he was dissecting at the Marine Biological Laboratory at Plymouth. This winter I have worked out the anatomy of the form and made numerous drawings. After I had completed the work I discovered that Professor Russo[2] had been over very much the same ground ; he has, I believe, anticipated me in many details, but as the parasite is very interesting, and is now recorded from the British area, and as the periodical in which Professor Rosso's full paper appears is very inaccessible—I have not been able to find a copy in any of our libraries—I have thought it not useless to publish the following general account of the anatomy of Syndesmus echinorum, Franç.

Anatomy: External Features.—The eleven specimens vary from 1 mm. to 2 mm. in length, and their greatest breadth is one half of their length. These dimensions are considerably less than those recorded by François. His specimens were nearly twice this size. In shape the animals are leaf-like, and have a tendency to be hollowed out ventrally. The anterior end is more rounded than the posterior, but in

[1] ' Rev. biol. Nord France,' v, 1892–3, p. 1.

[2] ' Ric. Labor. anat. Roma,' v, 1895, abstracted in ' Monit. Zool. ital.,' vii, 1896, p. 6.

some cases the latter is produced into a small papilla caused by the evagination of the penis.

The mouth leads into a well-marked sucker-like pharynx. It is situated on the ventral surface in the middle line, about one eighth of the body-length from the anterior end of the animal. The opening of the vas deferens, the vagina, and the uterus are all at the posterior end of the body, and open by a common pore (figs. 4 and 5).

There are no tentacles, or papillæ, or hooks, or spines, and as far as I could observe no skin-glands.

Histology.—The whole body is covered with a thin but distinct cuticle of uniform thickness (fig. 6). This is continued into the mouth and genital openings, but soon disappears. Externally this cuticle bears numerous small processes, very minute, but sufficient to give a rough appearance to the outside surface under a high power of the microscope. These are almost certainly the cilia described by all authors who have observed the animal alive.

The cuticle is secreted by a single layer of ectoderm cells with large, clear, spherical nuclei (fig. 6). In some sections these ectoderm cells showed fairly definite cell limits, and in that case each cell was about as broad as it was long; in other cases the limits of the cell could only be guessed by observing the nuclei placed at regular intervals. In all the specimens I cut the ectoderm of the dorsal and ventral surfaces had separated from the subjacent tissues, leaving a considerable space, but it had retained its normal position along the edges of the animal.

Beneath the layer of ectoderm cells is a basement membrane, which seems, however, to belong rather to the underlying parenchymatous cells than to the ectoderm; it gives a smooth and clearly defined outline to the body where the ectoderm has broken loose from it.

The muscular system described by some authors was not visible in my sections.

The parenchyma of the body presented different appearances in accordance with the different state of preservation of the

specimens. It consists in the more typical form of a
number of large, more or less cubical cells, full of a densely
granular protoplasm. The cells take every variety of shape,
owing to mutual pressure and the various strains and stresses
which affect them. In life their outline cannot remain
constant for any length of time. In the more poorly pre-
served specimens the granular protoplasm had shrunk away
from the firmer exterior of all but one surface of the cell,
leaving a large but irregular vacuole. The firm external
part of the cell, with from time to time patches of contracted
protoplasm adhering to it, gives the parenchyma the appear-
ance of a network with considerable vacuoles. When this
firmer exterior is a little more emphasised it forms the base-
ment membrane, which underlies the ectoderm and surrounds
the various parts of the reproductive system ; it is, however,
very noteworthy that no such basement membrane surrounds
the alimentary canal or intestine.

The Digestive System.—The mouth is ventral, in the
middle line and situated about the distance of one eighth or
one tenth of the body-length from the anterior end of the
body (fig. 4). It leads by a very short passage, lined by
cuticle, and bearing as far as I could make out no glands of
any sort, into a spherical pharynx. This organ is of the
type found in Vortex or Plagiostoma. The minute lumen
is lined by a uniform cuticle, and the bulk of the thick
wall is built up of radial muscle-fibres, among which a few
large nuclei stand out in stained sections (fig. 7). From the
inner end of the pharynx a very short œsophagus provided
with numerous glands—the so-called salivary glands—leads
to the digestive sac.

The stomach or intestine, or, as I prefer to call it, the
digestive sac, is a rod-like organ extending along the middle
line of the animal, and so close to the dorsal surface that
there is practically none of the parenchymatous tissue which
serves as a packing for the various organs of the body be-
tween it and the epidermis (fig. 2). The axis of the lumen of
the mouth, pharynx, and œsophagus is a dorso-ventral one, but

where the last-named passage joins the digestive sac it forms a right angle with the lumen of the alimentary canal.   Anteriorly the digestive sac extends a little way in front of the level of the entrance of the œsophagus, and when looking through a series of transverse sections it comes into view before any trace of the pharynx makes its appearance. Posteriorly the digestive sac extends to near the end of the body, coming to an end at a distance of perhaps one tenth or one twelfth of the total body-length from the end.

The digestive sac is lined by a very definite layer which is in the main a plasmodium, though it shows here and there traces of division into cell areas (fig. 6).   The limit of the tube is clearly defined, but the basement membrane is very thin, and in places the outer edges of the endoderm plasmodium rests against the packing cells of the body.   Internally the lining is produced into many apparently amœboid processes or pseudopodia, which project loosely into the cavity, and the free ends of which often are cut off and lie as isolated pieces of stained protoplasm in the sections.   It is along the inner boundary from which these processes arise that evidence of cell structure is most evident, since the chinks between the bases of the pseudopodia are continued by fine lines, which pass a little way into plasmodium, dividing it as it were into cell areas.

Throughout the plasmodium deeply staining nuclei are distributed, and numerous vacuoles are scattered ; some apparently contain drops of fluid, probably oil or fat ; others contain uniformly staining spheres of unknown nature.

I have not been able to find any trace of a secretory apparatus ; neither canals nor pore could be made out in any of my sections.

Nervous System.—The nervous system consists of a well-marked ganglion, situated just anterior to the mouth ; it is somewhat rectangular in outline, and a nerve is given off from each angle.   The anterior pair of nerves soon disappear ; the posterior, which bend backwards, are stained, but I failed to follow them very far down the body.   In one stained

specimen a median nerve seemed to leave the ganglion between
the anterior two nerves. It is probable that this nerve
divides into two branches.

Reproductive System.—The external opening of the
vas deferens and of the uterus lie side by side, close to one
another, at the posterior end of the body.

The male reproductive organs consist of paired branching
testes. Each half presents some ten or twelve twigs lying on
either side of the anterior end of the digestive sac, and ex-
tending in front of the mouth (fig. 5). These twigs fill up most
of the sides of the body, from in front of the mouth to the region
of the yolk-glands. The several branches of each half of the
testis unite and open into a pair of tubes, which may be termed
the vasa efferentia. These soon fall into one another, and
form a long median and anteriorly much-coiled tube. This
vas deferens makes a well-marked loop forward to the left of
the mouth (fig. 4). In its hindermost part, however, the
tube is straight, and is provided with thick muscular walls
lined with a cuticle.

Russo describes a complicated penis. I have not been able
to follow all his details, but there is undoubtedly a protrusible
intromittent organ present.

The histology of the male reproductive organs presents little
worthy of notice. The branches of the testis were outlined
by a very thin basement membrane, but beyond this they
presented no special investiture. Their contents were cells
of some size with large nuclei and conspicuous chromatin.
Near the end next the ducts, bundles of tailed spermatozoa
are to be seen. The vas deferens is a long and much-coiled
duct, so that, as a rule, portions of it are seen several times in
any one section. It has a smooth internal wall or cuticle,
and apparently a thin muscular lining; at the posterior end
the wall of the tube is very much thickened by a stout
muscular sheath, and this portion is protrusible, and indeed in
one specimen is protruded as a penis.

The ovary, like the testis, is double and branched; each half
is compared by François to a hand with the fingers extended.

Each branch of the ovary contains, as a rule, a single row of large angular ova, with very large spherical nuclei. The ova are mostly bounded by flat sides. They show some tendency to squeeze one another out of the single row, and when this is the case the row appears double. The ova at the end of each branch next the outlet are markedly bigger and more rounded than those near the top, where they are very small, and apparently it is here that they arise.

The coating of the ovary is thin, and it is continued in each side into a short duct which unites with its fellow, and at or near the point of union the ducts of the yolk-glands open.

The yolk-glands are large and branching; they lie on each side of the body between the testes and the ovary,—on the whole, more dorsal than the ovaries (fig. 2). The tissue of the yolk-glands is dense, and stains deeply near the tips of the branches; but it becomes much vacuolated and stains less deeply near its opening, which leads into the duct of the yolk-glands.

The two oviducts of each side and the two ducts of the yolk-glands open into a common chamber of somewhat angular shape.

The shell-glands are paired, and occupy much of the posterior end of the body. The numerous little glands which constitute the organ are unicellular and generally somewhat angular in shape, packed away as they are amongst the interstices of the parenchyma. Each is crowded with fine granules, and leads by a very delicate duct, which, converging towards each side of the uterus, does not open into the yolk-gland ovary complex, but as far as I can make out into the uterus.

In each specimen the uterus contained a beautiful golden egg, oval in outline and continued posteriorly into a long filament. This filament is bent and curved so as to form a tangled skein in the centre of the body; gradually it becomes finer, and its end, which is of extreme tenuity, lies in the neighbourhood of the external opening of the uterus. The

contents of the golden egg-shell stained uniformly and deeply, so that no nucleus could be detected. In bulk the egg in the egg-shell surpassed the ripe ova in the yolk-gland ovary complex by some five or six times; this is almost certainly due to the addition of the yolk. On the other hand, the golden case may have been an egg capsule, and contained more than one egg. I rather gather that Russo takes this view.

II. Nematoda.

In 1854 Dr. Leydig[1] described some nematodes belonging to the genus Oncholaimus which he had found in the alimentary canal of Echinus esculentus. The parasites were 4 mm. long, thread-like and pointed at both extremities. The oral cavity was provided with a certain toothed and ridged armature in the shape of thickenings of the cuticle prolonged from the firm cuticle covering the body. The œsophagus was long, and posteriorly enlarged, but nowhere did it form a bulb. The intestine ran in a straight line to the anus at the base of the tail, and had a brown colour due to pigmented granules which crowded the cells. The ovary had an anterior and a posterior branch, and each branch terminated in a line which doubles back and ends near the genital opening about the middle of the body. The ripe egg was of considerable size and of oval shape. The oviducts united to form a sharply defined vagina. The cuticle had longitudinal striations.

Dr. Leydig suggested the name Oncholaimus echini for this parasite.

The only other nematode that I find mentioned as coming from within the body of Echinus esculentus is the large green nematode of Silliman, which presumably—it is not quite certain—came out of one of these creatures taken at Roscoff.

A year or two ago Mr. A. J. Smith, assistant at the Marine Biological Laboratory at Plymouth, found two or three very long nematodes in the perivisceral cavity of an E. esculentus at Plymouth, which he sent to me for investiga-

[1] 'Müller's Archiv,' Jahrgang 1854, p. 291.

tion.   Unfortunately I did not undertake this at once, and when I came to look at the specimens a short time ago I found that, owing to a piece of iron being in the bottle in which they were preserved, the nematodes had become coated with rust, and in freeing it from rust their structure was so injured that nothing of their histology could be made out. The larger worm had further been injured in extracting it from the shell of the host.

Beyond the facts that the longest nematode is some 46 cm. in length, a little under 1 mm. in average diameter, and the smaller specimens were some 6 cm. in length; that both ends of the animals taper, but more particularly the anterior; that the posterior end is recurved, as is so usual amongst male nematodes; and that the alimentary canal was visible through the skin in the line specimens as an opaque strand, I can say nothing.   Enough is not known to warrant the suggestion of any specific characters, and I mention the parasite only in the hope that it may attract attention to it and lead to its being found again, carefully preserved, and investigated.

ZOOLOGICAL LABORATORY, CAMBRIDGE;
        April, 1900.

EXPLANATION OF PLATE 18,

Illustrating Mr. Arthur E. Shipley's paper "On some Parasites found in Echinus esculentus, L."

LIST OF ABBREVIATIONS.

c. Cuticle.   *c.g.* Cerebral ganglion.   *egg.* Egg in uterus.   *ep.* Epidermis. *g.d.* Genital duct.   *g.p.* Genital pore.   *hyp.* Amœboid plasmodium lining intestine.   *i.* Intestine.   *m.* Mouth.   *ov.* Ovary.   *par.* Parenchyma.   *sc.* Sucker.   *s.gl.* Salivary gland.   *sh.gl.* Shell-gland.   *t.* Testis.   *v.* Vagina. *v.d.* Vas deferens.   *y.g.* Yolk-gland.

FIG. 1.—A longitudinal horizontal section through Syndesmus echinorum near the ventral surface.

Fig. 2.—A transverse section through about the centre of the body of Syndesmus echinorum.

Fig. 3.—A longitudinal horizontal section through Syndesmus echinorum. This section is cut in a somewhat oblique plane, the anterior end being nearer the dorsal surface, the posterior nearer the ventral surface.

Fig. 4.—A sketch of a stained and mounted specimen of Syndesmus echinorum. The parts shown can be identified by a reference to Fig. 5.

Fig. 5.—A diagram to explain the anatomy of Syndesmus echinorum.

Fig. 6.—A small portion of the epidermis and intestinal wall of Syndesmus echinorum, very highly magnified to show the nature of the plasmodium lining the alimentary canal.

Fig. 7.—A transverse section of Syndesmus echinorum through the region of the mouth and pharynx. To the left the anterior loop of the vas deferens is shown.

Fig. 8.—Large nematode extracted from the cœlom of Echinus esculentus. × 1.

Fig. 1.
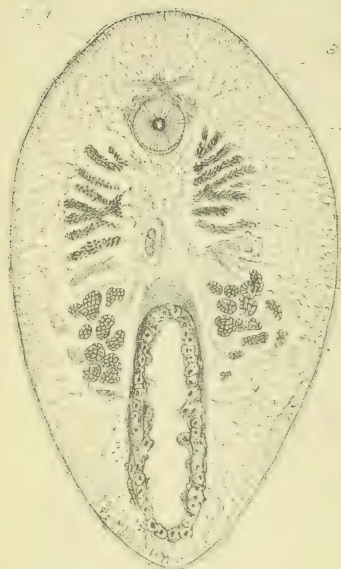
Fig. 2.

Fig. 3.
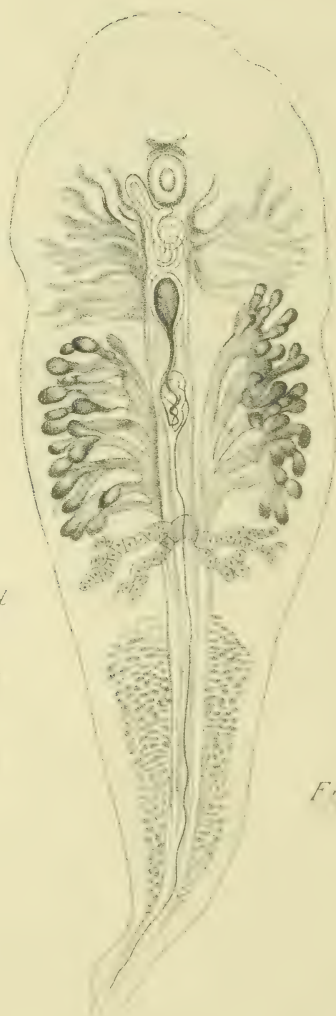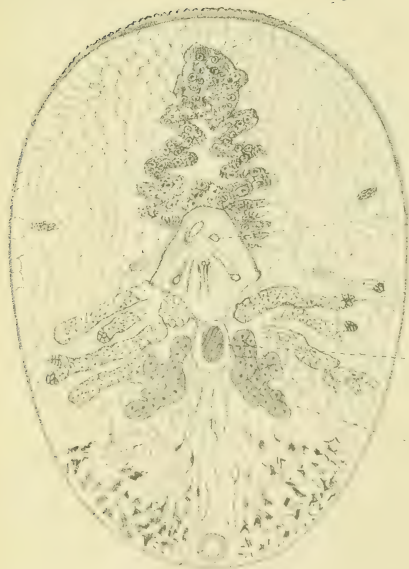
Fig. 4.

Fig. 5.

Fig. 8.
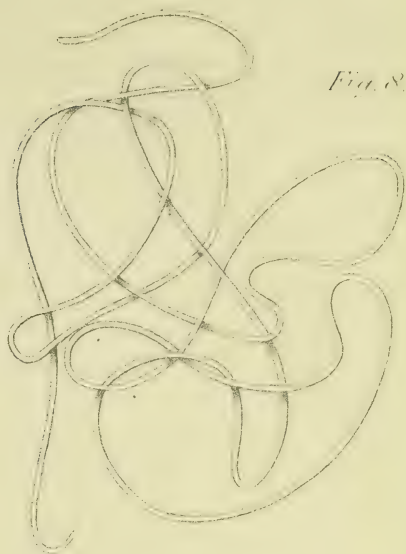
Fig. 6.

Fig. 7.

The Scottish Silurian Scorpion.

By

R. I. Pocock.

With Plate 19.

1. Introductory Remarks.

Our knowledge of the existence of scorpions in marine beds of Upper Silurian age dates from the publication of an announcement to this effect in the 'Comptes rendus de l'Académie des Sciences,' Paris, in December, 1884, wherein Professor Lindström and Dr. Thorell gave an account of the discovery of the well-preserved remains of a fossil scorpion at Gotland in Sweden, proposing for the new form the name Palæophonus nuncius. This important find in palæontology attracted wide-spread interest, and was discussed in various journals, scientific and popular. In 1885 it was followed by an exhaustive memoir on the fossil by Lindström and Thorell ('Kongl. Sv. Vet.-Akad. Handl.,' xxi, No. 9, 1885). Prior to the appearance of this memoir an article entitled "Ancient Air Breathers," by Mr. B. N. Peach, was printed in 'Nature' (vol. xxxi, pp. 295—298, 1885). In this a preliminary description was given of a second Upper Silurian scorpion, which had been unearthed in the summer of 1883 at Lesmahago, in Lanarkshire, and formed part of the rich collection of fossils belonging to Dr. Hunter. The value of this second specimen was enhanced by the circumstance that it fortunately lies with its ventral surface exposed, and is thus the complement, as it were, of the Gotland fossil, of which

the dorsal surface, at all events, of the anterior half of the body is uppermost.

For those who hold that the terrestrial Arachnids are descended from marine ancestors allied to Limulus and the Eurypterida, and recognise genetic affinity instead of "fortuitous coincidence" and "convergence" in the many deep-seated structural resemblances between the two groups, these archaic scorpions have, since their discovery, been vested with a peculiar interest, largely in view of the possibility of their supplying fresh evidence in support of this relationship. Little in this direction was yielded by the memoir on the Gotland scorpion ; and Peach's description of the Scotch specimen, although containing many important anatomical observations, was by no means exhaustive, and the figure that accompanied it not all that could be desired. Hence it has for many years been felt that a complete and properly illustrated account of this unique fossil would make a valuable addition to zoological literature.

In July of last year Prof. Ray Lankester wrote for the loan of the specimen to the authorities of the Kilmarnock Museum, where it has been preserved since the death of Dr. Hunter. The authorities not only kindly and promptly acceded to the request, but most generously permitted the specimen to be kept for three months at the Natural History Museum. I gladly avail myself of this opportunity to express my sincere thanks to Professor Lankester for placing the specimen in my hands for investigation. I am also indebted to Miss G. M. Woodward for the trouble and time she devoted to the lithograph, her skill and experience in interpreting fossils being most helpful in the present instance.

2. Description of the Specimen.

So far as the disposition of the various members is concerned, my restoration agrees with that of Mr. Peach in most particulars. I think, however, that the second leg on the right side lies distally across the anterior portion of the

" hand " of the chela, and not across its posterior portion as shown in the figure in 'Nature.' One or two other particulars in which I differ from him are referred to in the following pages.

The specimen gives the following measurements in millimetres :—Total length on stone 32·5, actual total length when extended 35·5, trunk 16·5, tail 19.

The Gotland specimen is considerably larger, measuring 62 mm. in total length, the tail being at least 26 mm.

Prosoma.—Owing to the outward displacement of the chelæ the anterior portion of the carapace is visible between the basal segments of these appendages, and in front of those of the first pair of legs. Its surface is thickly granular, its anterior border lightly concave, as is the Gotland specimen, and its antero-lateral angles subquadrate.

Eyes.—In the Gotland specimen no trace of eyes, either median or lateral, is discernible, though the median ocular tubercle of recent scorpions is represented by a relatively large and longitudinally oval elevation, situated in the anterior third of the carapace, and separated from its anterior edge by a space equalling about one half the length of the elevation. Judging from the figure, this tubercle is preserved in its entirety; hence there is no reason to doubt that if eyes had been borne upon it, some trace of them at least would have been preserved.

In the Scotch specimen also there is no sign of the lateral eyes. If, however, as is possible, these organs existed, and were placed behind the level of the median eyes, as is the case in the normal Pedipalpi, and, as is alleged, in the Carboniferous Anthracoscorpii, they would be concealed from view beneath the basal segments of the anterior legs, which on each side overlie that portion of the carapace immediately behind the median eyes. The median eyes are very distinctly represented by a pair of elliptical impressions situated close together, one on each side of the middle line, and scarcely more than their own long diameter from the anterior border of the carapace. There is no evidence that these eyes were

elevated upon a tubercle. If, indeed, such a tubercle existed as is exhibited in the Gotland specimen, the eyes must have been situated on its extreme anterior border. The presence of these median eyes, and the probable absence of the tubercle, are two important structural differences to distinguish the Scotch specimen from the Swedish.

Appendages.—The six pairs of prosomatic appendages (i—vi, Pl. 19) are preserved in a state of greater or less completeness, those on the left side being on the whole more clearly defined than those on the right.

The chelicerae or mandibles are, as in the Gotland specimen, very large as compared with those of recent scorpions. The left chelicera, crushed out of shape and position, shows no recognisable feature but a portion of the immoveable digit. The right, on the contrary, is well preserved and occupies its normal position, projecting straight forwards from the fore-part of the prosoma. The immoveable digit is slender, pointed, and nearly straight; the moveable is equally slender and pointed, but is lightly curved and armed in the middle of its lower edge with a single tubercular tooth.

It is noticeable that the digits of the chelicera are thinner, and overlap at the apex to a much greater extent than in the Gotland fossil.

Owing to the distortion and displacement of the left chelicera a portion of the matrix is displayed between the bases of the two appendages just in front of the middle line of the anterior border of the carapace. Presumably it is this portion of matrix which Mr. Peach describes—I think erroneously—as "a fleshy labrum (camerostome) between the bases of the chelicerae."

Chelae.—As in the Gotland specimen, these appendages do not appear to differ in any essential respects from those of recent scorpions. Their basal segments are too badly preserved for delineation—a particularly regrettable circumstance in view of the fact that in the Gotland specimen they are concealed from view. Hence it is impossible to surmise whether they took a greater, less, or an equal share in masti-

cation as compared with those of existing forms. The second segments project on each side of the antero-lateral angles of the carapace, and are granularly sculptured. The anterior surface of the third segment is apparently normally crested above and below, and the fourth segment of the left side shows traces of the basal prominence so noticeable in living species. Granules are observable along the anterior side of both these segments. The fifth segment (hand) of the left side differs in shape from that of the right, being more oval in form, with its posterior border in approximately the same straight line as that of the distal segment, the bulge being confined to the anterior surface as in the Gotland specimen and recent species. On the right side the hand is unusually globular, its posterior surface, probably owing to crushing, being abnormally swollen. The fingers are thinner, more taper, and straighter than in the Gotland specimen and recent scorpions. No distinct joint between the finger and hand is discernible, although presumably it is the under side of the hand and of the moveable finger that is exposed to view, both on the right and left sides. It is possible that the shallow median longitudinal groove observable on the finger of the right chela represents the line along which the two fingers meet when closed. The finger of the opposite side is similarly marked with a fine sculptured ridge.

Legs.—So far as can be ascertained the legs resemble those of the Gotland specimen in length, strength, and segmentation. As in other scorpions, and typically in all orders of Arachnida, they increase in length from before backwards, the fourth pair being nearly half as long again as the first. They consist, moreover, of what is doubtless the primitive number of segments—namely, seven. Primitiveness of segmentation is also shown by the subequality in length of the individual segments—a character which, in conjunction with the sharply pointed, practically clawless terminal segment, serves to distinguish the legs of Palæophonus from those of all other scorpions, living or fossil. I say

practically clawless because Thorell detected a minute claw-like structure at the tip of the seventh (tarsal) segment in
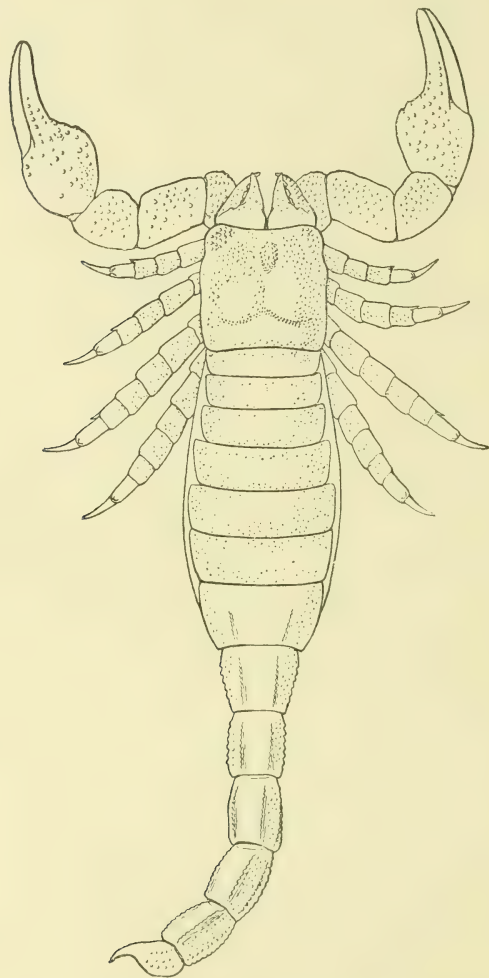
Fig. 1.—Restoration of Palæophonus nuncius.
Dorsal view (after Thorell).

the Gotland specimen. Although no trace of such a struc-ture was found in the Scotch fossil, no great value must be

attached to its apparent absence, in view of the chances against the preservation of an organ so delicate.

Nor was I able to detect a sign of the presence on the fifth segment of any of the legs of that spur so clearly shown on the first, second, and third pairs in the Gotland fossil, and described and figured by Thorell (see cut, p. 296). The interest invested in this spur depends upon the probability of its direct homology with the so-called " tibial spur " found upon the arthrodial membrane at the distal end of the fifth segment in some recent Buthoid scorpions. Certain genera of this family (e. g. Buthus, Lychas) possess it upon the third and fourth legs, one alone (Babycurus) retaining it only on the fourth leg. Assuming that the spurs in the genera just mentioned are homologous to those found in the Swedish Palæophonus, their presence upon the third and fourth, or upon the fourth leg in the former, and upon the first, second, and third legs in the latter, suggests that scorpions primitively possessed them upon all four legs. In that case the absence of the spur from the fourth leg in the type of Palæophonus nuncius may be a natural characteristic of the species, or may be due to a mere accident of preservation. The same may be said of the apparent total absence of this spur from the legs of the Scotch specimen.

There is, however, a still deeper interest attached to this spur, on account of its apparent presence upon the fourth leg (sixth prosomatic appendage) of Limulus. The first and second appendages of this animal agree in structure and in the number of segments with those of scorpions, the former consisting of three and the latter of six segments. But the third, fourth, and fifth appendages of Limulus also consist apparently of six segments, resembling in all particulars those of the second pair. In the scorpions, on the contrary, these appendages, as well as the sixth pair, consist of seven segments, the distal being furnished with a pair of moveable claws. Careful examination of these appendages in Limulus, however, shows that the fourth segment is encircled in its basal

half with a sutural impression, which represents, I believe,
the line of union between two segments, the portion on the
proximal side of the line being the fourth, that on the distal
side the fifth segment of the appendage. If this interpre-
tation be correct there is the same number of segments in
these appendages in both Limulus and the scorpions. Now
in the fourth leg of Limulus (except in L. rotundicauda)
the fifth segment, according to this new method of enumera-
tion, is furnished beneath distally with a spur like those
described above in the scorpions. Again, at the extremity
of the sixth segment in Limulus there are four moveable
lobate sclerites, which spread out like the fingers of a hand
when the leg is plunged into the mud. At the extremity of
the sixth segment in the scorpion's leg, or rather on the
arthrodial membrane between it and the seventh, there are
either one or two " pedal " spurs, which represent, I suggest,
the lobate sclerites in the same position on the leg of
Limulus. Lastly, there is attached to the distal extremity
of the seventh segment in Limulus a pair of short moveable
sclerites, forming a small nipper. Similarly there is a pair
of moveable sclerites or claws articulated to the distal
extremity of the seventh segment in the scorpion's leg. The
annexed figure (Fig. 2) will make these suggested homologies
clear.

Whether Palæophonus possessed any structures com-
parable to the pedal spurs of recent scorpions and to the
lobate sclerites of Limulus is doubtful. I can detect
nothing comparable to them in the Scottish specimen, but
the figure of the Gotland specimen suggests the possibility
of the presence of one or more spurs at the distal end of the
sixth segment.

It is a matter for regret that the exact structure of the
basal segments of the legs, and the relation of these segments
to one another, are not with certainty interpretable, owing to
the crushing and displacement of the parts composing the
ventral area of the prosoma, and of the anterior somites of
the mesosoma. Hence too much reliance must not be placed

upon the accuracy of the attempted restoration of these structures.
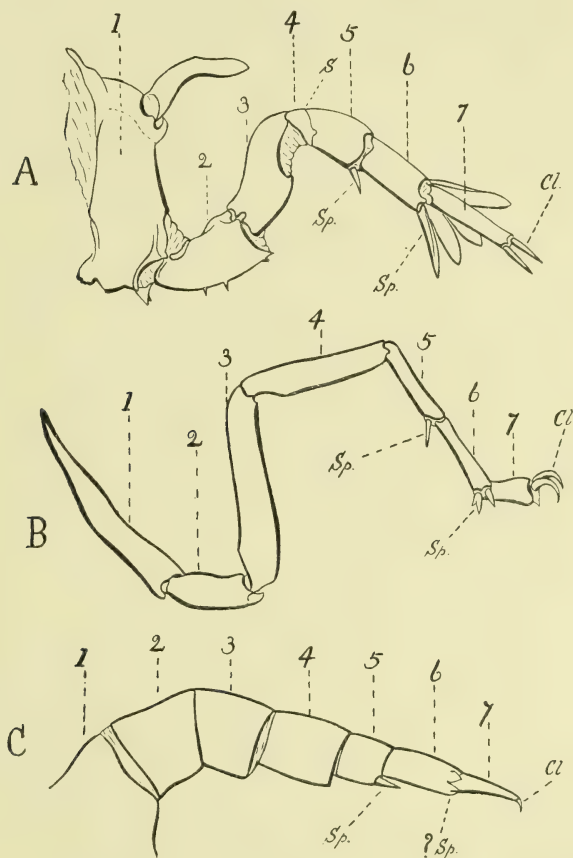
FIG. 2.—A. Fourth leg of Limulus moluccanus. B. Fourth leg of a recent scorpion (Buthus australis). C. Third leg of Silurian scorpion, Palæophonus nuncius, after Thorell.

1—7. Segments. s. Suture between fourth and fifth segments of the leg in Limulus. sp. Spurs and lobate sclerites. ? sp. Processes possibly representing the point of attachment of spurs in Palæophonus. cl. Claws in the scorpion, and pair of sclerites forming a nipper in Limulus.

In existing scorpions the basal segments (coxæ) of the legs of the first and second pairs are furnished with a for-

wardly directed sterno-coxal or maxillary process, the coxæ
of the second leg meeting each other in the middle line in
front of the prosomatic sternum, and sending forwards these
processes, which are in contact throughout their length, to
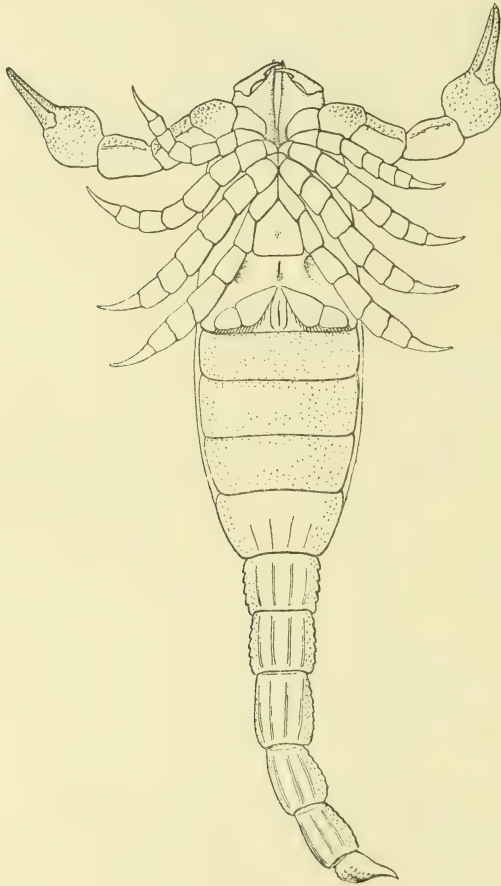
Fig. 3.—Restoration of Palæophonus Hunteri (ventral view).

underlie the mouth.   The coxæ of the third and fourth legs,
on the contrary, are devoid of sterno-coxal processes, and are
separated from each other in the middle line by the sternal
plate, against the sides of which they abut.

A very different state of things appears to obtain in Palæophonus. No trace of a sterno-coxal process is discoverable upon the first leg. On the second, however, a small one seems to be present. This lies transversely, and meets its fellow of the opposite side in the middle line. On the third leg a process similar in its form and relations is also indicated, and the segment that bears it, instead of abutting against the sternum, is mesially in contact with its fellow. The probability of the correctness of this conclusion is enhanced by its tallying with Peach's opinion. I cannot, however, quite agree with this author in believing that the legs of the fourth pair are basally separated by the sternum as in recent scorpions. On the left side of the specimen, where the leg is well preserved, the segments seem to be traceable right up to the middle line, the basal segment being sharply defined. On the right side, however, this is not so clearly indicated, on account of a displacement which has resulted in the overlap of the proximal end of the fourth leg by that of the third.

The sternum (*st.*, Pl. 19) does not stand out as a sharply defined plate with clean-cut edges, but is merely represented by the subpentagonal area that lies between and behind the two proximal segments of the fourth leg of the left side, and those of the third and fourth legs of the right side. It shows a faint central circular depression answering presumably to the similarly shaped sternal depression in Chærilus, and to the median groove in other recent scorpions.

The above-described arrangement of the skeletal pieces, forming the ventral surface of the prosoma, offers many points of morphological importance in view of the differences that obtain in this particular between the recent scorpions and Limulus or one of the Eurypterida. The relations of the sternum to the coxæ and the coxæ to each other in the scorpions have already been described. Those of Limulus and the Eurypterida may be stated in a very few words. In the latter the basal segments of all the appendages, ex-

cepting those of the first pair, acted as jaws, and were frequently armed with teeth, the greatest share in crushing and masticating food falling to the coxæ of the fourth pair, which were especially enlarged for the purpose. Behind, and partially concealing them from the ventral side, lay a large plate, the so-called " metastoma," the homologue of the scorpion's sternum. To all intents and purposes the same arrangement is found in Limulus, except that the coxæ of the fourth are less masticatory in function, and the " metastoma " is represented by a pair of moveable sclerites, the " chilaria," set immediately behind and between the bases of the legs of the fourth pair.

In Palæophonus the sternal plate of the prosoma lies apparently behind the basal segments of the fourth legs as in Limulus, and, as in the latter and in the Eurypterida, the basal segments of all the appendages were in contact or capable of meeting in the middle line. On the other hand, the coxæ of the fourth were small and functionless so far as the mouth was concerned, and food was probably crushed by those of the chelæ as in recent scorpions, the sterno-coxal sclerites of the second and third pairs assisting in this process, and preventing the escape of nutritive juices. Thus, so far as the parts now under discussion are concerned, this archaic scorpion presents a condition of things intermediate in many particulars between that of the typical scorpions and of Limulus or Eurypterus.

Mesosoma.—The ventral portion of the first somite of the mesosoma is represented by a relatively short but wide area lying behind the sternal region of the prosoma. This area is marked in the middle line with a short longitudinal groove (*gen.*, Pl. 19), representing in all probability the divisional line between the right and left halves of the genital operculum. On each side this area is impressed with a shallow but conspicuous indentation, which from its position seems hollowed out for the reception of the third segment of the fourth leg, perhaps in order that this portion of the appendage might be insunk to the level of the generative

orifice, so that its prominence should offer no obstacle to the act of copulation.

A short distance behind the genital cleft a similar but larger and more conspicuous median cleft is visible. This is flanked on each side by a narrow longitudinally elongate plate or lobe (*end.*, Pl. 19), somewhat resembling one half of the genital operculum of recent scorpions. On the outer side of the right-hand lobe lies a bisegmented appendage (*pect.*, Pl. 19), which may be regarded as the homologue of a recent scorpion's pecten or comb. Along the posterior border of this appendage are traceable a number of fine striæ occupying the position of the pectinal teeth. Similar striæ are traceable upon the left-hand side, although the pecten itself is obliterated.

Peach regarded the cleft between the two above-described lobes as the generative aperture, a conclusion it is impossible to accept in view of the improbability of the backward movement of this aperture on to the somite that bears the pectines. The opinion, which I here put forward, that the generative aperture is represented by the slit which, although not mentioned by Peach, appears on his published figure immediately behind the pentagonal prosomatic sternite, seems on morphological grounds far more likely to be correct. Thorell, moreover, suggested that the pair of lobes lying between the pectines correspond to the small, sometimes longitudinally grooved pectinal sternite of recent scorpions. This may be the true interpretation; but the shape of the lobes, the length and depth of the groove that separates them, and their relations to the pecten, suggest that they have another significance, and are probably to be regarded as the inner branches of an appendage of which the pecten is the outer branch. From this standpoint the appendage may be compared with the mesosomatic appendages of Limulus, and of the archaic spider Liphistius. In the former the appendages (except in the case of the genital operculum of the Eastern species) consist of a broad foliaceous trisegmented external branch, and of a slender trisegmented internal

branch. In Liphistius also there are two branches, the inner slender and unsegmented, the outer stout and composed of two principal segments. Although in general form the inner lobes (*end.*, Pl. 19) of Palæophonus resemble those of Limulus, they differ from the latter, and approach those of Liphistius in being unsegmented. The outer branch is broad and flattened, and is somewhat like that of Limulus, except that it is relatively smaller, and lies with its axial line directed, not longitudinally, but obliquely outwards and backwards like the comb of a typical scorpion. It shows, however, no signs of segmentation into so-called "fulcra" and "intermediate lamellæ," such as are found in the combs in the majority of species. Structurally, in short, it is inter-mediate between a typical comb and the outer branch of one of the mesosomatic appendages of Limulus. Furthermore, the fine striæ which fringe its posterior edge are, in my opinion, too delicate to be the remains of teeth comparable in shape and size to those of recent scorpions. Rather would I suggest that they are portions of the edges of branchial lamellæ which were affixed like those of Limulus to the posterior side of the appendage, with their lines of attach-ment lying at right angles to its longitudinal axis.

These appendages overlie and almost completely conceal the sternite of the third mesosomatic somite. The stern-ites of the fourth, fifth, and sixth somites, however, are fully exposed and well preserved. They are granular, and resemble the corresponding plates in recent scorpions but for the absence of the muscular impressions and, so far as my observations go, of the stigmata. Peach, however, declares most emphatically that "all four sterna exhibit on the right side undoubted slit-like stigmata at the usual places." It is true that the sternites are somewhat wrinkled laterally, and, as shown on Pl. 19, exhibit certain shallow impressions, which, especially in the case of the fourth and fifth sternites, might be mistaken for stigmata; but it is hard to believe that slits as conspicuous as the stigmata of recent scorpions should be so indistinctly preserved on sternites in such an

admirable state of conservation that even their granulation is still apparent. Nevertheless it must be borne in mind that Peach's opinion on this point is in complete agreement with Thorell's regarding the Gotland specimen.

According to Thorell this specimen exhibits on its right side a portion of a displaced sternal plate, upon which a distinct stigma is visible. This sternal plate he assigns to the third somite of the mesosoma ; but a glance at his drawing shows that the greater part of it lies at the sides of and beneath the tergite of the second somite, and that at all events a large part of the third sternite is situated on the left-hand side beneath its corresponding tergite. To hold that this third sternite has been fractured and displaced to the extent that Thorell's interpretation demands appears to me to be an opinion based on an improbability. From the position of the fragment that protrudes on the right-hand side, I judge that it belongs to the second mesosomatic somite— a somite which in all known scorpions bears the pectines but is without stigmata,—and that it is part of its pleural membrane. This interpretation, if correct, involves the conclusion that the " spiraculum " described by Thorell is a fortuitous crack in the integument. There is one other point, too, bearing indirectly upon the question of the presence or absence of stigmata, in which, without further evidence, I find it impossible to accept Thorell's decision. The Swedish specimen is broken in two by a transverse fracture, crossing the fourth somite of the mesosoma. The posterior half thus contains the fifth and sixth mesosomatic somites and the metasoma. It is admitted—and there is no reason to doubt—that the ventral surface of the metasoma is exposed. According to Thorell, however, the two mesosomatic somites which go to make up the severed portion of the body lie back uppermost. This supposition implies the belief that the severed portion of the specimen was itself completely divided into two at the junction of the mesosoma and metasoma, that the latter was overturned, and was so accurately fitted into place that perfect continuity between it and the mesosoma was restored. That

the uninterrupted outline presented by the somites in question, which imparts so natural an appearance to this region, is thus the result of pure accident I find hardly credible. In fact, there is, I think, no reason to doubt that the fifth and sixth mesosomatic somites were united to the metasoma, and shared its unmistakable inversion. Hence the plates in question are sternites. The important point attached to this conclusion is the absence of stigmata on these sternites. Perhaps it was this fact which led Thorell to his decision as to their tergal character.

The above-given reasons justify a sceptical attitude towards the alleged existence of stigmata in the Gotland Palæopho-nus, at all events until a further examination of the specimen settles the points now under dispute. And since I found no distinct traces of stigmata in the Scotch specimen, I am in-clined to believe that Peach fell into error on this point perhaps influenced in part by the alleged presence of stigmata in the Gotland example, perhaps in part by the assumption that a form so closely resembling recent scorpions in other structural details must also resemble them in the nature of its respiratory organs.

To the belief in the presence of stigmata, implying the existence of organs fitted for aërial respiration, coupled with the knowledge of the terrestrial habits of all living scorpions, is traceable the conviction evinced by most previous writers that these Silurian scorpions lived on the land. This belief is less easy to reconcile with the facts that both the known specimens are relatively in an admirable state of preservation, and were met with in strata of undoubted marine origin, containing abundance of admittedly marine organisms, than the belief, which I hold, that Palæophonus lived in the sea, probably in shallow water, its strong, sharply pointed legs being admirably fitted, like those of a crab, for maintaining a secure hold amongst the seaweed or on the jagged surface of rocks, and for resisting the force of the rising and falling waves.

Respiration, as already suggested, may have been effected

by means of the appendages of the second mesosomatic somite, although it must be admitted they appear too small to have performed this office for the whole organism without help from other organs. It is possible that there were such organs in the form of small appendages bearing branchial lamellæ attached to the mesosomatic sterna. But if so, no definite trace of such has been preserved. Or, indeed, it is possible that the ventral plates, above regarded as mesosomatic sternites, may have been broadly laminate mesosomatic appendages, closely pressed down against the ventral surface of this region, and bearing branchial lamellæ on their posterior surfaces. This suggestion gains some support from the fact that the laminate mesosomatic appendages of the Eurypterida are generally indistinguishable from sternal plates.

Metasoma.—This region of the body in the Scotch specimen closely resembles that of the Swedish specimen, the same surface, namely the ventral, being in each case uppermost. Peach, however, states that the dorsal surface of the posterior caudal segments is in part exposed. According to my interpretation, on the contrary, in all the segments it is the area lying between the inferior lateral keel on the left side (inf. lat. and sup. lat., Pl. 19) and the superior lateral keel on the right that is exposed. Both of these keels are granular. As in most recent scorpions, a pair of median keels (inf. med., Pl. 19) lie along the lower surface of the tail, between the inferior lateral keels on the first four segments of the tail. Keels corresponding to these four inferior medians and inferior laterals are traceable upon the first metasomatic sternite, and also, I think, upon the sixth (fifth caudal segment). This last fact, if true, is of some interest, inasmuch as it shows a more primitive arrangement than is found in recent scorpions, where the two median keels have invariably coalesced into one. The inferior median keels on the posterior caudal segments appear to be smooth. In the Swedish specimen they are granular. The lower side of the vesicle is granular in both, but the aculeus in the Scotch example is

apparently less curved, less circular in section, and more tri-
angular than in recent scorpions and the Swedish specimen.

3. Description of the Species, with Notes on the other known Silurian Scorpions.

The preceding description of the Scottish fossil, and the
comparisons that have been made between it and the Swedish
specimen, have revealed some noticeable structural differ-
ences between the two, which leave no other course open
than to regard the former as the representative of a distinct
and undescribed species. This I propose to dedicate to Dr.
Hunter, and to diagnose as follows :

Palæophonus Hunteri, sp. n.

Differing from P. nuncius in its much smaller size, being
35·5 mm. as compared with 62 mm. in total length, in
possessing a pair of median eyes set close to the anterior
border of the carapace, in having the digits of the cheliceræ
longer and thinner, and the moveable more curved, and the
chelæ very much lighter in build, with the digits nearly
straight; in the absence of a spur from the fifth segment of
the first, second, and third pairs of legs, and in the smooth-
ness of the inferior median keels on the posterior segments
of the tail.

In addition to the specimens discussed in the preceding
pages, two other scorpions have been recorded from Silurian
strata, namely, Proscorpius Osborni and Palæophonus
loudonensis. The first was described by Whitfield
('Science,' vi, p. 88, 1885; 'Bull. Amer. Mus. Nat. Hist.,' i,
No. 6, pp. 181 to 190, 1885), and was based upon a fairly
well preserved specimen, with the dorsal surface exposed,
from rocks referred to the middle of the Upper Silurian.
Like the Swedish and Scotch specimens, it was associated
with fossil remains of Pterygotus, Eurypterus, and other
marine organisms.

The specimen was examined by both Whitfield and

Scudder.   The latter (Zittel's ' Handbuch der Paläontologie,'
ii, p. 739, 1885) classified it with the Carboniferous scorpions
on account of the alleged presence of a pair of claws at the
extremity of the anterior leg of the left side.   This classifi-
cation was endorsed by Whitfield, who based the genus
Proscorpius mainly upon these claws, declaring them to
be very similar to those of living forms.   His figure shows
no such similarity.   The apical segment of the leg is simply
bifid at the tip, a feature which may be due to fracture, or
may represent a pair of sclerites like those borne at the tip
of the distal segment of the fourth leg of Limulus; or may
be explained on the supposition that the end segment ter-
minated in a sharp point as in Palæophonus, and was
furnished near the tip with a moveable spine or spur.   Since,
however, there is no agreement between Scudder and Whit-
field as to whether the segment stated to possess these claws
is numerically the third or sixth from the base, it seems idle
to discuss the matter further.   If Scudder's interpretation
of the numbers of the segments is correct, these "claws"
are situated at the end of the third or fourth segment, and
cannot be compared with the tarsal claws of other scorpions.

Apart from the leg, the chief points of interest connected
with Proscorpius Osborni are the presence of a pair of
eyes on a median ocular tubercle, and of a row of lateral eyes
(not shown in the figures, by the way) on each side of the
carapace.   The rounded median tubercle projects in the
middle line of the fore border of the carapace, the lateral
angles of which are also rounded.   Hence the trilobate
appearance of the anterior border of this plate, which forms
such a contrast to the even emargination seen in the Swedish
and Scotch Palæophonus.   It is further to be noticed that
the dorsal integument is smooth, and not granular as in
Palæophonus nuncius.

Along the right-hand side of the specimen, both Scudder
and Whitfield agree that six (five mesosomatic and one
metasomatic) abdominal sternites are exposed.   The first of
these belongs to the second mesosomatic somite, which in

recent scorpions bears the pectines and has no appreciable sternal area.

But there appears to me to be no reason for regarding this so-called sternal area other than as the pleural membrane of the second somite of the mesosoma.

Mr. Whitfield could find no satisfactory evidence for the existence of stigmata, and infers from this fact, and from the nature of the strata in which the specimen was preserved, that the species was "aquatic in habits," and furnishes a "link between the true aquatic forms like Eurypterus and Pterygotus and the true air-breathing scorpions of recent periods."

Of Palæophonus loudonensis, described by Laurie, from the Upper Silurians of the Pentland Hills ('Tr. Royal Soc. Edinb.,' xxxix, p. 576, pl. i, fig. 1, 1889), little need be said, the specimen being too imperfectly preserved to yield satisfactory data for discussion. That the specimen was specifically distinct both from P. nuncius and P. Hunteri cannot be doubted if the great length of the carapace and the slenderness of the tail in the fossil are not attributable to imperfection of preservation. As in P. Hunteri, there are a pair of median eyes close behind the fore border of the carapace, which is emarginate.

No genuine stigmata were discovered, but on some of the mesosomatic somites a curved ridge running obliquely outwards and backwards on the sides of the segments was traceable. The ridge on the second somite Laurie interprets as the impression of the outline of the pecten, those on the others as the outline of a plate-like gill-bearing appendage.

4. RECAPITULATION.

From a morphological point of view, perhaps the most important results obtained by the examination of this fossil are those connected with the structures of the basal segments of the prosomatic appendages, and their relation to the sternal area of this region, and those connected with the

structure of the appendage of the second somite of the mesosoma.

If the above-given interpretation of the arrangement of the parts constituting the ventral side of the prosoma is correct—and I do not think it is likely to be very far wrong —Palæophonus occupies an intermediate position between Limulus and the Eurypterida on the one hand, and recent scorpions on the other, standing, if anything, rather nearer to the former than to the latter.

The same may be said of the structure of the second mesosomatic appendage, which with its outer and inner branch is like the corresponding appendage in Limulus; while the outer branch itself, although in general form and size resembling the pecten of a scorpion, offers some interesting structural features in which it differs from that organ, and resembles the outer branch of a mesosomatic limb of Limulus.

On the whole, it must be admitted that Palæophonus Hunteri supplies a few more links to the chain of evidence pointing to the descent of the scorpions from marine Limuloid ancestors.

EXPLANATION OF PLATE 19,

Illustrating Mr. Pocock's paper on "The Scottish Silurian Scorpion" (Palæophonus Hunteri).

The figure gives a magnified view of the specimen of Palæophonus Hunteri, Pocock, from the Upper Silurian of Lesmahago, Lanarkshire. It was formerly in the collection of Dr. Hunter, and is now in the Kilmarnock Museum. This lithograph was executed from the specimen itself by Miss G. M. Woodward, under the supervision of Mr. R. I. Pocock, in October, 1900.

I—VI. Prosomatic appendages. *st*. Sternal area of prosoma. *gen*. Genital cleft. *pect*. Pecten, or external branch of appendage of second somite of mesosoma. *end*. Internal branch of appendage of second somite of mesosoma. *sup. lat., inf. lat., inf. med.* Superior lateral, inferior lateral, and inferior median crests of fourth somite of metasoma.

The Life-History of Nucula delphinodonta (Mighels).

By

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With Plates 20—25.

THE material upon which these observations were made was secured at Casco Bay, Maine, during the summers of 1897 and 1898. Nucula delphinodonta is a small form, seldom growing to be more than 4 mm. in length, and as it lives below low-tide mark it is not very well known by collectors. By using a sufficiently fine dredge, however, unlimited numbers of adult and young specimens may be procured. Individuals may be found living under very different conditions; in inlets and protected places, and exposed to the open sea, and from near low-tide mark to a depth of several fathoms. The principal habitat, however, is in the shallow inlets and near the heads of sounds, where the bottom is composed of fine mud, mixed with some sand, broken shells, and decaying vegetable matter. Individuals are most numerous just outside of the eel grass which skirts the shore where the bottom is of this character, in water which at low tide is from one to three fathoms deep. The mud in which they live is much like that inhabited by Yoldia limatula, except that it is not so free from shore débris. Although some specimens may be obtained where Yoldia is most abundant, they are generally more numerous

somewhat nearer the shore, and they may be very numerous at considerable distances from places where Yoldia is known to thrive.

In picturing the conditions under which these animals live along the coast of Maine, the reader should not fail to take into account the average tide of about ten feet, which keeps the water very pure over a comparatively foul bottom. The fauna and flora of these bottoms are very abundant and diversified, but have not been carefully catalogued. Diatoms of several species abound, and form a large part of the food of Nucula. Other Algæ, Ostracods, Foraminifers, small Lamellibranchs, and Gastropods are also very abundant, and small individuals of most of these forms are occasionally found in the stomachs of preserved specimens.

While I have never succeeded in getting individuals to form brood-sacs in captivity, they live well in aquaria, and may be kept for several weeks either in vessels containing the mud in which they normally live, or in vessels without this mud. It is not even essential that the water be changed very frequently.

When placed in vessels containing mud they bury themselves, and seem never to come to the surface to stay for any considerable time. They are at all times comparatively sluggish, and seem to wander around in the mud by slow thrusts and retractions of the foot, which is a very perfect burrowing organ. When placed in mud that is just sufficiently deep to cover them, their movements can be followed fairly well by the movements of the mud. To see them feeding it is necessary to use only a very thin layer of mud. The action of the palp appendages can then be observed. They perform the same function that is performed by similar appendages on the palps of Yoldia (1), that is, they are food collectors. Nucula delphinodonta seems normally to feed beneath the surface of the mud, so feeding cannot be observed as easily as it can be in the case of Yoldia (Text-fig. T).

The movements of the foot are best observed by placing

specimens in shallow dishes of sea water.   When specimens are placed on mud they bury themselves so promptly that the movements of the foot cannot be carefully followed. The movements are all such as would be of service in burrowing in mud.   Although specimens have been kept under observation under different conditions for long periods of time, I have never known one to execute movements that could be interpreted as creeping.   In 1853 Forbes and Hanley, in describing Nucula nucleus (4), made the following statement :—"The foot is white, and as if pedunculated and deeply grooved, so as to expand into a broad leaf-shaped disc with serrated margins ; by means of this organ it can creep like a Gasteropod, and we have seen it walk up the sides of a glass of sea water."   This seems to be the only observation of this kind on record, although many students have worked on this and related forms.   The authors who have adopted the view that the foot functions as a creeping organ in members of this group have, in nearly every case, had only preserved material to work upon, and perhaps have been influenced by finding so many characters that seem to them to denote generalised structure.   Some Lamellibranchs are able to pull themselves over smooth surfaces, but my observations lead me to believe that the form and structure of foot found in this group is especially poorly adapted for such a purpose (3).   The expanded foot of Nucula delphinodonta is relatively very large, and the almost spherical shell is frequently turned from one side to the other, but nothing comparable to creeping has been observed.

Although many Lamellibranchs carry their eggs and developing embryos, I think this is the first case reported where a special external sac is formed for the purpose.   This sac (fig. 1) is composed of a mucus-like material, mixed with foreign bodies, and is attached to the posterior ends of the valves of the shell.   Although the process of making the sac has never been observed, it seems probable that the mucus-like material is secreted by the hypobranchial glands.

This material is probably passed posteriorly by the action of the cilia on the mantle, and very likely the respiratory currents of water swell it into a sort of bubble that remains attached to the posterior ends of the shell-valves, and, while still soft, adheres to the foreign particles with which it comes in contact.

That the hypobranchial glands are concerned in the formation of the material from which the brood-sac is formed is indicated by their appearance before and after the sacs have been formed. In females in which the ovaries are still full of eggs, the cells of the hypobranchial glands are large and gorged with secretions, while in females that have formed the brood-sacs the cells are shrivelled and almost devoid of secretions.

The eggs are deposited in the brood-sac (fig. 1), and in it the embryos are carried until they reach an advanced stage in development, probably for a period of three or four weeks.

The eggs of this species are brown, opaque, few in number, and correspondingly large. From about twenty to seventy may be found in a sac, and they average about ·21 mm. in diameter. Each egg is enclosed in a membrane that is probably secreted by the egg, but its formation has not been observed. Fertilisation is probably accomplished in the brood-sac. Eggs and young embryos do not live well after they are removed from the brood-sacs, so the ages of the various stages have not been determined. Processes of maturation and cleavage proceed slowly. The time between the appearance of the first and the second polar body is frequently as much as two hours, and the time between cleavages seems to be nearly or quite as long. It is not beyond doubt, however, that the removal of the eggs from the brood-sacs influenced the length of time. That development is slow is not to be doubted. Embryos taken from the brood-sacs of specimens kept under as nearly natural conditions as possible for a month, had only reached the stage where two gill-lobes were formed.

It seems probable that the polar bodies may be formed by

eggs that have not been fertilised. Eggs were sometimes obtained that formed polar bodies and developed no further.[1]

Just before each polar body is formed, a more or less distinct, and frequently a very pronounced swelling, makes
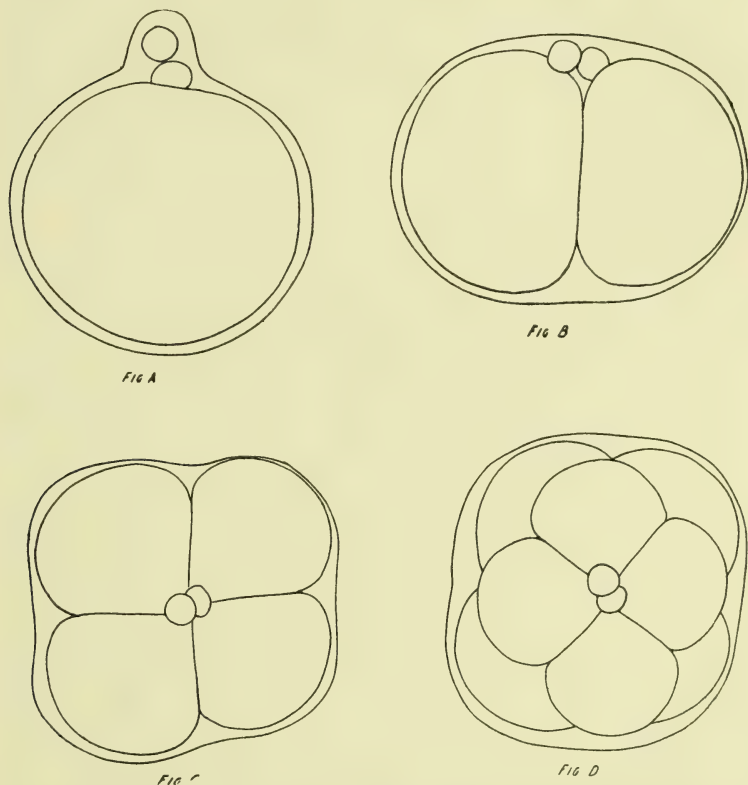
TEXT-FIGS. A, B, C, and D.—Early stages in the development of Nucula delphinodonta.

its appearance on the side of the egg opposite the point

[1] Most of the eggs of an isolated specimen of Nucula proxima, a form that throws its eggs free into the water, formed the polar bodies, and a few eggs cleft the first time. It is possible that some sperm were in the water, but the water had not been changed for nearly twenty-four hours before the eggs were laid, and sperm of this species do not seem to retain their vitality for nearly so long a time.

where the polar body will appear. In the preparation for the first cleavage a similar swelling is formed on the side opposite the polar bodies. When the egg divides, the dividing wall passes to one side of this swelling. The two blastomeres are accordingly rather unequal in size. The difference in the size of the two blastomeres seems to depend upon the size of the swelling that precedes their formation. Cleavage into four and eight cells (Text-figs. C and D) are typical. The polar bodies retain their position on the animal pole until the embryo acquires cilia, when they are rolled around on the inside of the membrane. No attempt has been made to follow out the fate of the individual cells.

In the sixteen-celled stage, figs. 2 and 3, a small cleavage cavity is present. Later this becomes slightly more pronounced. The cells on one side of the blastula divide more rapidly than those on the other side, and push over them in the form of a cap (fig. 4). A pocket appears between the large cells at such a point as is indicated by the asterisk in fig. 4. Just how this pocket is formed is still a matter of some doubt, but it seems to be formed by the separation and division of some of the larger cells. This pocket (fig. 8) can now be compared with the invaginate portion of a gastrula. It represents the first appearance of the gut.

About the time that the pocket is formed most of the smaller surface cells acquire cilia (fig. 6), and the embryo begins to roll around in the membrane. The cilia are all short, similar in appearance, and seem to be evenly scattered over the surfaces of the cells. In whole mounts the boundaries of the surface cells are not very distinct, but the cells do not seem to have a very definite arrangement.

From these small surface cells, that at this stage appear very much alike, the test,[1] the apical plate, and the cerebral ganglia are formed.

The large cells near the blastopore do not bear cilia, at

[1] I use the term "test" here, as in former publications, to designate the surface cells that bear cilia and may be homologised with the velum of other forms.

least none could be found on preserved specimens. They are concerned in the formation of the shell-gland.

The embryo is still nearly spherical, and so opaque that, while alive, internal changes cannot be followed. A few cells, probably the beginning of the mesoderm, lie above and by the sides of the gut. About this time some of the surface cells around the blastopore divide, and push in to form a stomodæum. Other cells near the blastopore become enclosed by the surface cells, and together with cells probably derived from those forming the stomodæum, finally form a portion of the new ectoderm, that soon covers the body of the embryo inside of the test. When the ectodermal layer is complete it joins, but does not enclose, the stomodæum. In position as well as origin the stomodæum is ectodermal.

Before the ectodermal layer is complete the embryo begins to elongate, and the surface cells close in over the shell-gland from the sides and anterior end. At the same time the surface cells become arranged in rather definite rows. It is very difficult to get satisfactory views of these cells in whole mounts, but there seem to be five rows, beside a group at the anterior end that forms the apical plate. Two or three of the posterior rows are interrupted in the region of the shell-gland, but this interruption disappears as the shell-gland becomes closed in. Closing is never complete. A small opening is left dorsal to the blastopore, separated from it by the width of one test cell (fig. 15). The anus comes to lie near this opening at a later stage (fig. 24). Before the shell-gland is covered the gut turns towards the dorsal side (fig. 11, *mg.*), and the mesoderm cells take up a position near the posterior end of the embryo. Two of the mesoderm cells are large, and have very large and conspicuous nuclei. These cells are far posterior, and lie side by side.

Soon after the shell-gland is covered, the gut begins to grow posteriorly, almost, if not quite, in contact with the shell-gland dorsally, and separated from the stomodæum ventrally by a few mesoderm cells (fig. 15). A small space appears among these mesoderm cells that later becomes con-

nected with a space that is formed between the gut and the shell-gland.

At no stage in its development is the shell-gland invaginated. From the time of its formation it arches dorsally to some extent (figs. 7 and 9, *sg.*). Just before it becomes covered by the test it flattens somewhat (figs. 11 and 12), but it soon arches dorsally again and becomes quite convex (fig. 17, *sg.*).

The cells that give rise to the cerebral ganglia are few in number (fig. 15, *cg.*), and lie ventral to the anterior end of the stomodæum. They frequently come to the surface, but
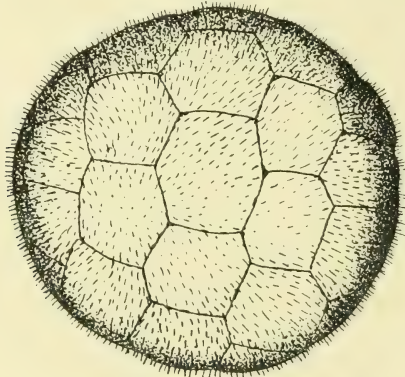
Text-fig. E.—Surface view of a young embryo of
Nucula delphinodonta.

they may be entirely covered by test cells. A more or less distinctly recognisable test cell lies between the cerebral ganglia and the apical plate, but beneath this test cell the cerebral ganglia and the apical plate are in contact. The two cerebral ganglia seem to originate from a single mass of cells. There is no indication of the formation of cerebral pouches, as in Yoldia (Text-fig. V). The position occupied by the developing body of Nucula does not make it necessary for the cerebral ganglia to shift their position from the point of their formation until the test is shed.

The apical plate is composed of a number of cells, the walls

of which are rather indistinct (fig. 15, *ap.*). They bear cilia that in size and distribution resemble those that cover the test cells.

Under favourable conditions the test cells can be seen to be arranged in five rows; occasionally part of a sixth row is present. As in other stages, the boundaries between the test cells are poorly marked, and it is quite impossible to sketch them accurately. Text-fig. E shows their general arrangement, but it must be understood that this is quite diagrammatic. The cilia on the test cells of this species are not collected into bands as they are in Yoldia (Text-fig. F),
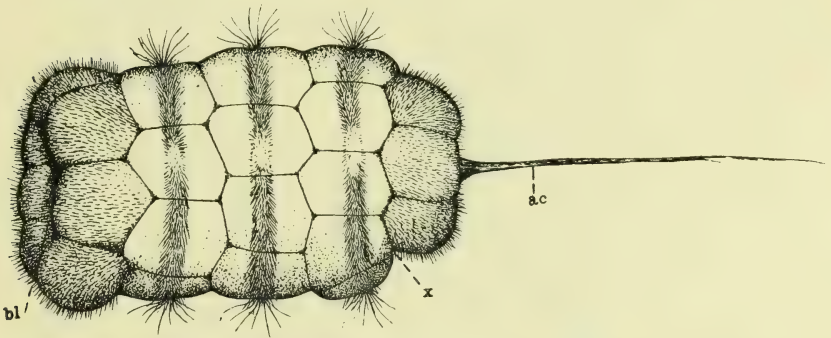
TEXT-FIG. F.—Surface view of a forty-five hour embryo of Y oldia l imatula. *ac.* Apical cilia. *bl.* Blastopore. *x.* Depression where the cells that form the cerebral ganglia come to the surface.

but are evenly scattered over their surfaces. The embryo becomes free from the egg membrane about the time that the shell-gland becomes covered by the test, but the cilia are barely powerful enough to slowly move the embryo on the bottom of a dish. The absence of the bands of cilia, and of the long tuft of apical cilia, is probably due to the protected life of the embryo. Nucula proxima lays its eggs free in the water, where they are fertilised and develop. These embryos have to shift for themselves, and are very active. Here, as in Yoldia, the cilia on each of the three intermediate rows of test cells are long and collected into a band (Text-
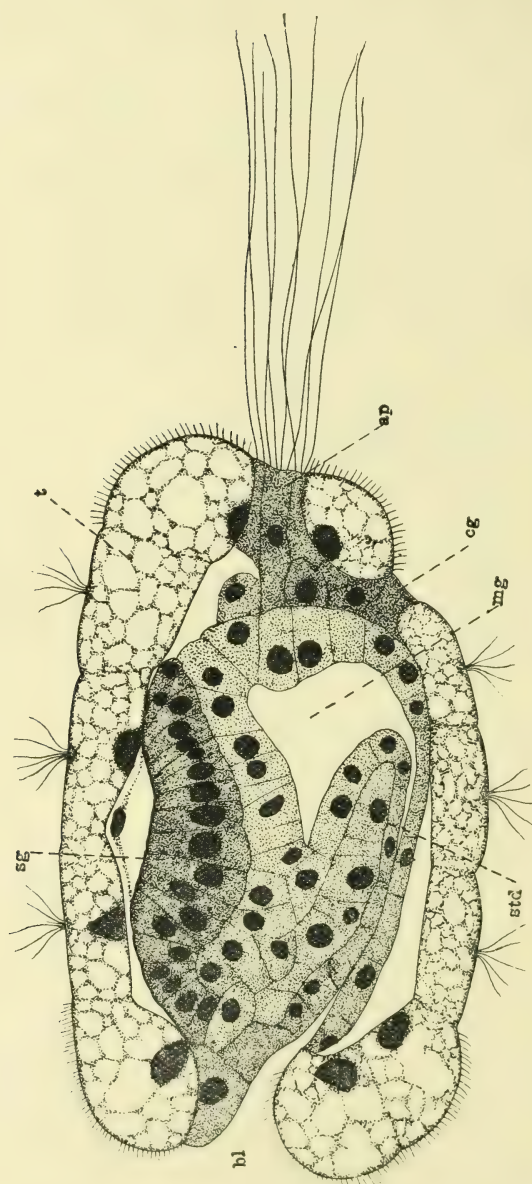
TEXT-FIG. G.—Median sagittal section of a thirty-six hour embryo of Yoldia limatula. *ap.* Apical plate. *bl.* Blastopore. *cg.* Cells from which the cerebral ganglia are formed. *mg.* Mid-gut. *sg.* Shell-gland. *std.* Stomodæum. *t.* Test.

fig. H).   Sometimes part of a fourth band is present.   The
end rows of test cells have the cilia evenly scattered over
their surfaces.   The apical cilia are long and bunched into a
sort of whip that precedes the embryo when it swims.   In
fact, the embryo resembles that of Yoldia so closely that,
except for a difference in size and a slight difference in shape,
a description of the surface appearance and movements of
one will do very well for the other also.

The cilia on the embryos of N u c u l a   d e l p h i n o d o n t a
may then be regarded as arrested in their development.
Life in the protecting brood-sac makes active locomotion
unnecessary and even dangerous, inasmuch as active embryos
would be likely to find their way out of the brood-sac, and
so be exposed to outside dangers.

The embryos continue to elongate and begin to flatten
slightly laterally (fig. 23).   In the living embryo, viewed by
transmitted light, this stage is marked by the appearance of
a light spot near the dorsal margin.   A smaller, much less
distinct light spot has been present near the ventral margin
for some time, and corresponds in position to the cavity that
was mentioned as appearing in the mesoderm, ventral to the
gut.   This space has enlarged considerably (fig. 24), but is
covered laterally by rather thick walls of ectoderm and by
some mesoderm, so it is not very distinct.   The dorsal space
is formed by the arching up and flattening out of the cells of
the shell-gland, which are now beginning to form the mantle
lobes (fig. 20).   It is bounded dorsally, laterally, and poste-
riorly by the mantle, anteriorly by the mantle and the apical
plate, and ventrally by the gut and by the body-wall.   A
few cells, apparently mesodermal, lie in this space, generally
attached to the mantle or to the gut.

At a little later stage (fig. 25) two fibre-like cells stretch
from the anterior end of the gut posteriorly and dorsally to
the mantle.   They are quite conspicuous in living embryos,
and they retain their position until after the test is thrown
away.

About this stage the gut, which has grown posteriorly,
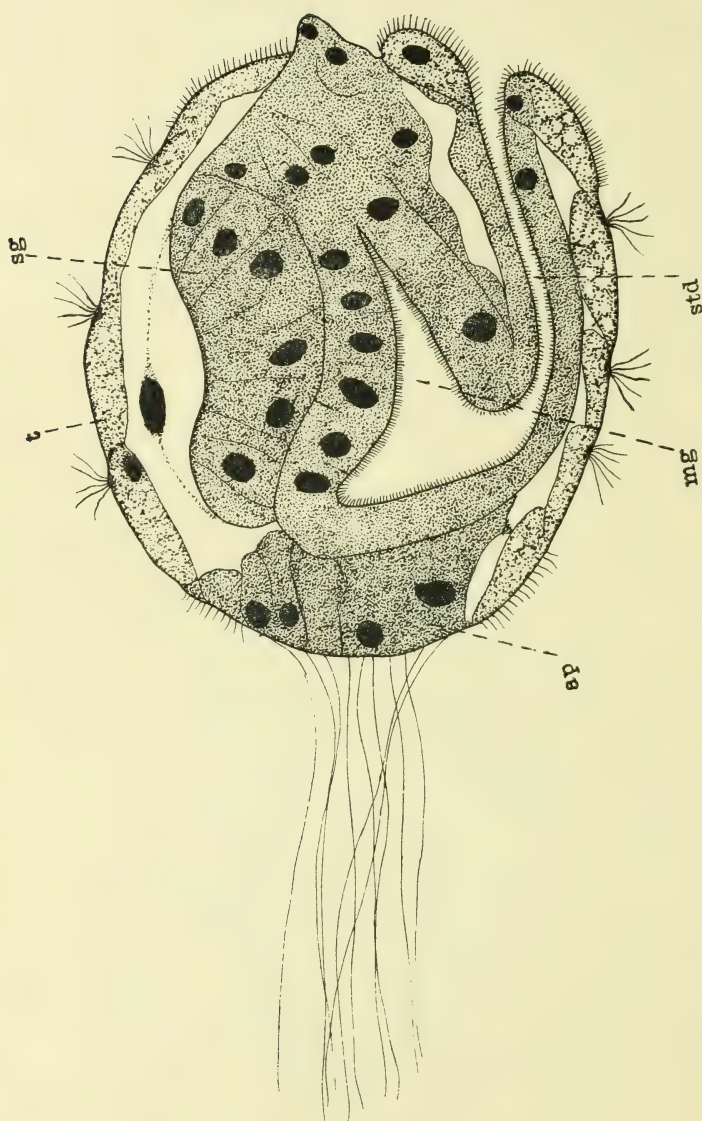
TEXT-FIG. H.—Median sagittal section of a twenty-five hour embryo of Nucula proxima. *ap.* Apical plate. *mg.* Mid-gut. *sg.* Shell-gland. *std.* Stomodœum. *t.* Test.

acquires an anus (fig. 24). The anus is not directly applied to the pore that opens between the test cells, but it opens into a cavity that is continuous laterally with that portion of the embryo that, as the mantle continues to grow, becomes the mantle chamber. This communication will be described in a later stage.

The embryo flattens laterally until its thickness equals about two thirds of its dorso-ventral width, and the dorsal space becomes considerably enlarged (fig. 25). Near the anterior end of this space the anterior adductor muscle (aa.) makes its appearance. At first it consists of a very few fibres, and is not conspicuous. The anterior enlarged portion of the gut takes on the distinctive characters of the stomach (sto.), and the liver grows out as paired right and left pouches (l.). The anterior end of the stomach is carried dorsally, and a more or less distinct bend is made where it joins the intestine.

The relationship of the various cavities in the embryo to each other, and of the anal pore in the test to the mantle chamber, can be best understood by comparing the sagittal, horizontal, and transverse sections of embryos, represented on Plate 22, with the reconstruction of an embryo at the same stages of development (Plate 21, fig. 25). The position of the horizontal and transverse sections are indicated on fig. 25 by numbers that correspond to the numbers of the figures.

The dorsal cavity is separated from the ventral cavity by the gut (fig. 28). In some sections the two cavities communicate around the sides of the gut. This may be due to shrinkage, but it seems more likely that the two portions are parts of a single cavity. It is just possible that the cleavage cavity never entirely disappears, and that this cavity can be traced back to the blastocœle, but I am of the opinion that it is a later formation, and represents a schizocœle. Its fate is of interest, and will be referred to in later stages.

The lobes of the mantle are now well formed, a distinct shell-cuticle has been secreted, and some lime salts have been deposited. The stomodæum for most of its length is joined,
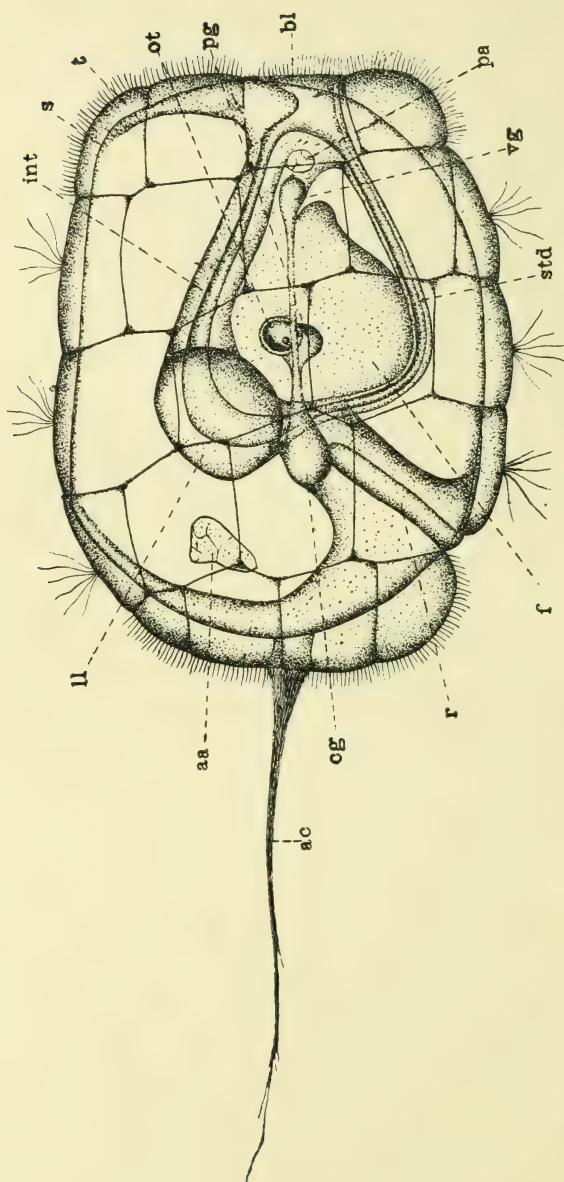
TEXT-FIG. I.—Reconstruction of an embryo of Yoldia limatula at a stage just before the test is cast off. The embryo is seen from the left side. Specimens are ·2 mm. long without the apical cilia. *aa*. Anterior adductor muscle. *ac*. Apical cilia. *bl*. Blastopore. *cg*. Cerebral ganglion. *int*. Intestine. *ll*. Left lobe of the digestive gland. *ot*. Otocyst. *pa*. Posterior adductor muscle. *pg*. Pedal ganglion. *r*. Pouch leading from the surface to the cerebral ganglia. *s*. Shell. *std*. Stomodeum. *t*. Test. *vg*. Visceral ganglion.

but is not enclosed by the body ectoderm (fig. 28), which in this region forms the walls of the foot (*f.*). Near its external opening the stomodæum has become free, and is more or less closely jointed to the test cells.

The relation of the anal test pore to the mantle chamber can now be understood. As shown by a sagittal section (fig. 26), this pore opens into a small cavity that receives the anus. This cavity is bounded anteriorly by the posterior wall of the foot, and ventrally either by the stomodæum or by cells covering the dorsal portion of the stomodæum. Transverse (fig. 27) and horizontal (fig. 31) sections show that this cavity spreads out laterally, and becomes continuous with that portion of the mantle chamber posterior to the foot. At this stage the foot is very imperfectly formed, and contains the cavity that has been referred to as the ventral cavity. The cavity soon disappears, and the ectoderm on the two sides of the foot fuse ventrally, dorsal to the stomodæum. The foot is still very small, and shows no sign of its future activity. At a corresponding stage the foot of Yoldia is quite well developed (Text-fig. I). This is about the condition of the embryo when the test is thrown away.

It takes several hours for embryos of this species to cast the test, a process that with Yoldia limatula and Nucula proxima is completed within a very few minutes after it is begun. The test cells in the region of the anal pore break apart, and the whole mass is frequently pushed forward to the region of the apical plate. This stripping forward carries the outer end of the stomodæum forward to some such position as is shown by fig. 34. The cilia on the test cells remain feebly active for a considerable time. While the test cells, stomodæum, and apical plate still adhere to the embryo, the stomach and liver pouches are drawn some distance dorsally into the schizocœle (fig. 34, *sto.* and *l.*). Whether the fibres extending from the stomach to the mantle are important in effecting this movement is not known. Their position is suggestive, but I have no direct evidence that they contract. The position now occupied by the stomach

causes the bend where the intestine joins the stomach to become quite abrupt.

At the same time that the stomach moves dorsally, the cerebral ganglia (fig. 34, *cg.*), which are still a mass of rather undifferentiated cells, are carried up, and come to lie posterior and a little ventral to the anterior adductor muscle (*aa.*). The foot (*f.*) retains its position beneath the intestine and
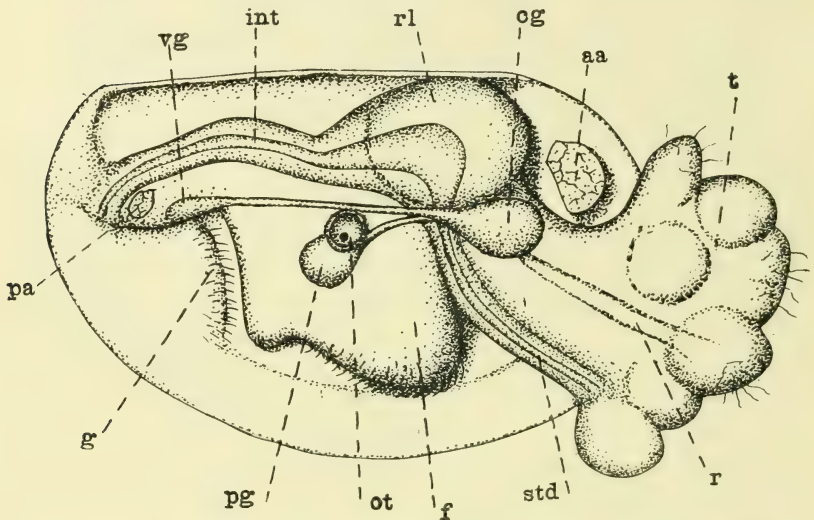
TEXT-FIG. J.—Reconstruction of an embryo of Yoldia limatula at a stage during casting. Represented as seen from the right side, with the right shell-valve and mantle lobe removed. *aa.* Anterior adductor muscle. *cg.* cerebral ganglion. *f.* Foot. *g.* Rudiment of gill. *int.* Intestine. *ot.* Otocyst. *pa.* Posterior adductor muscle. *pg.* Pedal ganglion. *r.* Pouch that leads to the cerebral ganglia. *rl.* Right lobe of the digestive gland. *std.* Stomodæum. *t.* Adhering test cells. *vg.* Visceral ganglion.

stomach, and in the general dorsal movement is carried a little further from the margin of the shell. A similar stage for Yoldia is represented by Text-fig. J. At the end of several hours the stomodæum (fig. 34, *std.*) breaks across near the tip of the foot, and together with the apical plate and the remnants of the test cells is thrown away. From appearances I am inclined to believe that the whole of the apical

plate is thrown away, but this may not be the case. The test cells may or may not remain attached to the apical plate and stomodæum until these are thrown away. Generally many of them break loose or go to pieces before this change occurs, but some of them nearly always remain.

After casting is completed (fig. 35) the stomach (*sto.*) and the liver lobes (*l.*) are drawn further into the schizocœle, and the liver lobes begin to be flattened out against the mantle. The cerebral ganglia (*cg.*) lie almost directly posterior to the anterior adductor muscle (*aa.*), and the ectodermal thickenings that result in the formation of the pedal and visceral ganglia soon begin to form (fig. 36).

Thus far in the development of the animal the shell-valves have remained gaping, but after the removal of the apical plate and the stomodæum they are free to close. This is effected by the contraction of the anterior adductor muscle, and materially diminishes the space between the shell-valves.

The closing of the shell is accompanied by important changes in the liver pouches, changes similar to those that have been described for Yoldia (**1**). Apparently as the result of the mechanical pressure the liver pouches go to pieces, and the large cells of which they were composed become rounded and scattered through most of the schizocœle (fig. 36, *z.*). The posterior portion of the schizocœle is not filled by the scattered liver-cells. This persists and finally becomes the pericardium.

The foot (fig. 39, *f.*) grows and soon executes feeble movements. The pedal ganglia (*pg.*) and visceral ganglia (*vg.*) take on definite form; the posterior adductor muscle (*pa.*) appears; and the invaginations that result in the formation of the otocysts are formed. Very possibly commissures connect the ganglia at this time, but I have not been able to distinguish them from the surrounding tissue until a somewhat later stage. A thickening on the inner surface of the posterior end of each lobe of the mantle indicates the beginning of the formation of the gill (fig. 39, *g.*).

About this time a little invagination on the mid-line of the

ventral portion of the foot, just anterior to the heel-like projection, makes its appearance (fig. 39, *bg.*). This develops into the byssal gland. It grows rapidly until it becomes proportionately very large (fig. 45, *bg.*), then ceases to grow, and possibly shrinks somewhat. In the adult it is comparatively insignificant (fig. 48). No signs of byssal threads have ever been observed, nor have the secretions ever been seen to protrude from the duct of the gland.

The foot grows rapidly, and the projection that looks like a heel becomes more marked (fig. 40, *f.*). Anterior to this
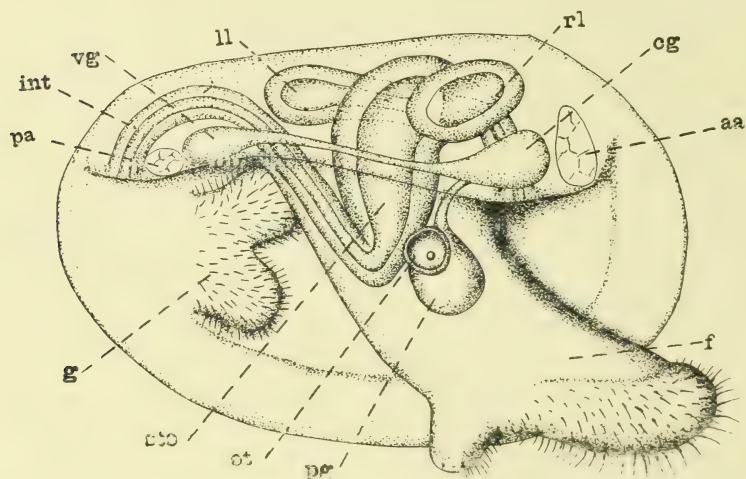
TEXT-FIG. K.—Reconstruction of a ten-day embryo of Yoldia limatula. Represented as seen from the right side with the right shell-valve and mantle lobe removed. *aa.* Anterior adductor muscle. *cg.* Cerebral ganglion. *f.* Foot. *g.* Gill. *int.* Intestine. *ll.* Left lobe of the digestive gland. *ot.* Otocyst. *pa.* Posterior adductor muscle. *pg.* Pedal ganglion. *rl.* Right lobe of the digestive gland. *sto.* Stomach. *vg.* Visceral ganglion.

projection the sides grow ventrally faster than the intermediate portion, and finally from the side flaps that are so characteristic of the foot of the adult. Movements of the foot now become energetic.

The gill (fig. 40, *g.*) becomes more pronounced, and soon

unequal growth causes it to be divided into two lobes. The dorsal wall of the stomach re-forms, and the liver-cells begin to be rearranged. The commissures between the ganglia are distinctly visible. The otocysts (*ot.*) are quite large, and contain granules. Although adults have canals leading from the otocysts to the exterior, I have not been able to demonstrate their existence in this or somewhat older stages. The presence of the otocystic canal had been explained (**13**) as the persistent opening of the otocyst, which was formed as an invagination from the surface of the body. This seems to be the natural explanation, but if canals are present at this stage they are certainly very small. I am inclined to regard the exceedingly small size or absence of these canals as evidence against the view that the otoliths are foreign particles.

Thus far most of the embryos have been carried in the brood-sacs, but many of them now become free. They are not set free by any act of the mother, but they individually find their way into the mantle chamber of the mother and so to the exterior.

Frequently younger embryos become free, but they generally do not live long. Many embryos remain in the brood-sacs until a much later period, but they do not seem to be in need of its protection after the stage that has just been described. The brood-sacs frequently remain intact after all of the embryos have left them.

The more dorsal of the gill lobes elongates into a finger-like process, and the ventral lobe broadens and becomes divided into two lobes (fig. 41, *g.*). New lobes are thus formed as the result of unequal growth of the most ventral lobe.

About the time that the third lobe of the gill begins to form a few papillæ appear along the margins of the side flaps of the foot (fig. 41, *f.*). The liver lobes also become hollowed out and lose most of the rounded cells. Part of these cells seem to go to pieces much as if digested (fig. 43), and it seems quite possible that this is the case.

The heart (fig. 41, *h*.) is apparently formed from meso-dermal tissue that collects to form a strand, that runs across the pericardium from one side to the other. I have found no indication of its being formed as paired pouches, as described by Ziegler (**20**) for Cyclas cornea, nor have I found any evidence that it originates as two masses that grow toward each other. Its first appearance seems to be in the form of a mesodermal strand of tissue that soon hollows out and encloses the intestine. The fact that the heart forms around the intestine, and not dorsal to it, is of interest, and will be discussed under the head of the Circulatory System.

The growth of the kidneys, which are now present as small tubes, seems later to force the sides of the heart up around the intestine (fig. 68), so that the ventral portion of the ventricle becomes drawn out into a trough in which the intestine lies. As the kidneys grow the trough becomes deeper. By gradually closing in dorsal to the intestine at the anterior and posterior ends, the trough is shortened, and the intestine finally becomes free from the heart and lies ventral to it (fig. 69). This is accomplished by a very slow process, and is not completed until after the animal has become sexually mature.

I am inclined toward the opinion that the kidneys are formed by the differentiation of mesodermal tissue. When they first appear each is a very narrow tube, and extends from its external opening in the mantle chamber to the mid-line of the body. I have not succeeded in demonstrating the inner pericardial openings of the kidneys in this or in later stages. The cells soon become large and vacuolated, and the kidneys grow rapidly and crowd anteriorly ventral to the pericardium, where they become coiled and sac-culated.

With the formation of the fourth lobe of the gill (fig. 45) processes make their appearance on the bases of the lobes, between them and the mantle lobe to which the gill is attached. These processes grow to form what have been called the outer gill plates, but in this species their position

is better described as posterior than outer. The lobes, at
the bases of which the outer plates are formed, develop into
the inner plates. Viewed from the side, both sets of plates
are visible. The gills of Yoldia hang so that in a side view
the outer plates hide the inner plates, which lie directly
behind them (Text-fig. L). When viewing Nucula from the
side we see that portion of the gill that corresponds to the
ventral portion in Yoldia.

The labial palps appear as patches of cilia on embryos with
three gill lobes (fig. 41). The outer palps soon begin to grow
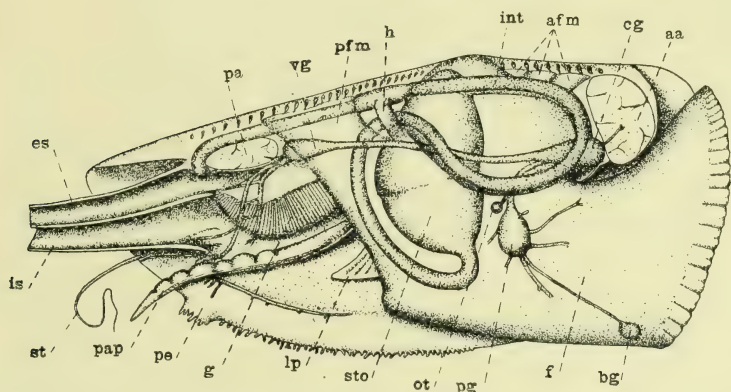
TEXT-FIG. L.—Adult specimen of Yoldia limatula. Represented as seen
from the right side. Reconstructed to show internal organs. Fully
grown specimens may be 6 cm. long. *aa.* Anterior adductor muscle.
afm. Anterior foot muscles. *bg.* Byssal gland. *cg.* Cerebral ganglion.
es. Exhalant siphon. *f.* Foot. *g.* Gill. *h.* Heart. *int.* Intestine. *is.*
Inhalant siphon. *lp.* Labial palp. *ot.* Otocyst. *pa.* Posterior adductor
muscle. *pap.* Palp appendage. *pe.* Posterior expansion of the margin
of the mantle. *pfm.* Posterior foot muscle. *pg.* Pedal ganglion. *st.*
Siphonal tentacle. *sto.* Stomach. *vg.* Visceral ganglion.

out as flaps (fig. 45, *lp.*), and by the time that the fifth pair
of gill plates are formed the inner palps are present as folds.
The formation of the ridges on the ciliated surfaces of the
outer palps begins with embryos having six pairs of gill
plates, and the palp appendages are formed soon after

(figs. 55 and 56). The development indicates that each palp appendage (fig. 56, *pap.*) is to be regarded as a pair of ridges with an enclosed groove, developed and modified so that it may be extended beyond the edges of the shell.

Little remains to be described in this general sketch of the development, further than to call attention to the formation of the loops of the intestine, that are indicated in different stages of development by Text-figs. M to S; to the formation of the cartilage pit and teeth on the valves of the shell; to the formation of more gill plates and foot papillæ as these organs continue to grow; to the appearance of the otocystic canals about the time that the sixth pair of gill plates are formed; and to the formation of the genital organs.

Mention should be made of a peculiar closed pouch (figs. 40, 48, and 63, *v.*), of unknown function, that lies just anterior to the anterior adductor muscle. It makes its appearance in embryos that are just getting the second gill lobes, and is fairly conspicuous in adult animals.

Germ Layers.

An almost spherical embryo is formed as the result of the first few cleavages (fig. 5), the cells on one side of which are much larger than those on the other side. The large cells extend far into the interior of the embryo, and the smaller cells form a cap over the larger ones (fig. 4).

In reaching this stage of development the embryo has passed through a blastula stage, in which the cleavage cavity was very small (fig. 3). As the cells become arranged in the manner described, the greater part of the cleavage cavity disappears. It has not been determined whether any of it remains or not. A depression appears near one side of the group of larger cells at a point corresponding to the asterisk in fig. 4. This depression seems to be formed by the separation and further division of some of the large cells, and results in the formation of the gut (fig. 8, *mg.*).

The surface cells may now be regarded as ectoderm, and at least two kinds may be distinguished: small ones, which

finally form the test, the apical plate, the cerebral ganglia, the stomodæum, and a considerable portion of the future ectoderm of the embryo; and large ones that form the shell-gland.

The endodermal pouch is carried further into the interior by the division and pushing in of ectodermal cells in the region of the blastopore (figs. 9 and 11, *mg.*). In this way a long stomodæum is formed on the ventral side of the developing embryo. The ectodermal covering of the later embryo, exclusive of that derived from the shell-gland, seems to be formed in connection with the formation of the stomodæum, by cells that wander in from the region of the blastopore, and perhaps from cells derived from the stomodæum itself.

About the time that the stomodæum begins to form, a few cells, two of which are quite large and conspicuous, make their appearance by the sides of the endodermal pouch, and extend between it and the shell-gland. These are mesodermal cells. Their exact origin has not been traced. As the embryo elongates, the two large cells come to lie near the posterior end of the embryo (fig. 19). They probably correspond to similar cells that have frequently been described for other forms. Similar cells are found in Yoldia in a corresponding position.

Test.

As the result of the first few cleavages a number of large cells become covered on one side by a cap of smaller cells (fig. 4). A part of the smaller cells become covered with cilia, about the time that the gut is formed (fig. 8); others near the blastopore divide rapidly and form the stomodæum (figs. 9 and 11); still others form the cerebral ganglia; while others in the region of the blastopore wander in and form a part of the future ectoderm.

The cells that bear cilia are concerned in the formation of the test and apical plate. These cells soon cover the surface that is not occupied by the shell-gland and the cerebral ganglia. Both the apical plate and the cerebral ganglia are

small at this stage, consist of a very few cells, and can hardly be distinguished from the surrounding cells. The apical cells acquire cilia about the time that the test cells do (figs. 9 and 11), and for some time they cannot be distinguished from them. Later the apical plate may be told by its shape and position (figs. 15 and 24, *ap.*).

As development proceeds the test begins to close in over the shell-gland from the sides and anterior end (figs. 10—13). Five rows of test cells can now be seen under favourable conditions, but their outlines are very hard to determine. Until the shell-gland is covered, two or three of the posterior rows are incomplete dorsally. A small pore is left near the posterior end, separated from the blastopore by the width of one test cell (fig. 15). The anus comes to lie near this opening (fig. 24).

The five rows of cells are now arranged much as shown in Text-fig. E. From the formation of the test until its ultimate disappearance its cells are evenly ciliated with short cilia. In this respect the embryos differ from those of Yoldia limatula (Text-fig. F) and Nucula proxima (Text-fig. H). Both of these forms have the cilia on each of the three intermediate rows of test cells collected into a band. Sometimes a fourth more or less complete band is present. The cilia on the end rows of the test cells of all of the forms are short and evenly scattered over the surfaces of the cells.

In this connection it is of interest to observe that the cilia on the apical plate of Nucula delphinodonta are short and independent, while those on the apical plates of Yoldia limatula and Nucula proxima are long and bunched together. They all seem to have a rather scattering origin, and when animals are killed the cilia become separated from one another.

In both species of Nucula the embryo differs from that of Yoldia limatula in having a posterior opening in the test, dorsal to the blastopore (fig. 15, and Text-figs. G and H). This difference might easily be accounted for by a slight difference in the closing in of the test over the shell-gland.

The ciliated embryos of Nucula delphinodonta, unlike those of the other two forms, are not able to swim freely in the water. At the most they are barely able to move on the surface of a glass dish. This is probably the result of their being carried in a protecting brood-sac. It seems but natural that the bands of strong cilia and the apical tuft of cilia would not be developed by embryos such as these, were there no need for active locomotion, and where active locomotion would be dangerous. It is for the best interest of embryos that they remain in the brood-sacs, where they are protected from many enemies. Were they capable of active movement, many would probably escape and perish. In the two related forms, Nucula proxima and Yoldia limatula, the embryos have to depend on their own activities for their existence.

It is highly probable that the embryos of the ancestors of Nucula delphinodonta led an active, free-swimming existence. The rearing of embryos in protecting brood-sacs is very possibly connected with the present life of the animal beneath the surface of the mud, and, in any case, has probably been acquired at a comparatively recent day. Again, the test in its present condition is of no appreciable value to the embryo, and no doubt is to be regarded as a vestige of a once functional organ.

Young embryos of Nucula delphinodonta when taken from the brood-sacs do not live well, and it is accordingly difficult to determine how long the test is retained. As near as could be judged, it seems to be retained about two weeks. Its cells then begin to break apart near the posterior end of the embryo, and many of them move toward the anterior end, where they remain attached to the apical plate and the stomodæum (fig. 34). Sometimes most of the cells of the test seem to thus accumulate at the anterior end, but they frequently become detached and go to pieces before reaching this position. In any case they, together with the apical plate, and the stomodæum, to the position of the future mouth, are finally thrown away (fig. 35). In many cases the

process of casting occupies several and sometimes as many
as fifteen hours. The process is much more rapid for both
Yoldia limatula and Nucula proxima (**2**). It is quite
possible that the difference in the length of the time occu-
pied by the different embryos is connected with the differ-
ence in the conditions under which they develop.

Further study has tended to confirm my view that the test
should be regarded as the homologue of the velum of other
forms. In a former publication (**1**) I made the statement
that "in either Dentalium or Patella, if we imagine the
velum to be stretched posteriorly over the shell-gland dor-
sally, and the foot ventrally, so as to enclose the body, the
œsophagus will be pulled out into a narrow tube ventral to
the foot, and the position of the blastopore will correspond
to its position in Yoldia. Furthermore the position of the
foot and shell-gland will correspond, and the alimentary
canal will be bent in the same way." This states the case
backward, and may be a little confusing. If we begin with
the condition found in Yoldia and Nucula, and imagine the
test to shrink until it consists of a band of ciliated cells sur-
rounding the embryo anterior to the mouth, the condition
would be comparable to that shown by embryos of Den-
talium and Patella.

As in the case of Yoldia, the closest resemblance to the
test, outside of the group, is shown by Dondersia. Although
Pruvot's (**15**) account of these embryos is very short, and
only three figures are given, there is quite a striking external
resemblance. In both cases the surface cells are arranged
in five rows, all of which bear cilia. They are both provided
with apical plates, and with both the test is finally thrown
away. The bodies of the embryos of Dondersia protrude
posteriorly during development. A slight posterior protru-
sion of the body of Nucula sometimes takes place through
the opening dorsal to the blastopore.

The resemblances shown by embryos of Dentalium
(**8** and **9**) and Patella (**12**) are not so striking, but they are
somewhat similar. The apparent posterior protrusion of the

body in each of these forms is such as might be produced if the body of Nucula were to grow and protrude to a corresponding extent. In such a case the test of Nucula would occupy a corresponding position to that occupied by the velum in the other forms.

Apical Plate.

At an early period the cells of the apical plate cannot be distinguished from those that form the test, but as development proceeds they become marked off as a rather definite plate at the anterior end of the embryo (figs. 11, 15, and 24, *ap.*). This plate is relatively large and thick, and extends posteriorly as far as the stomach. The cells from which the cerebral ganglia are formed lie ventral to it (figs. 15 and 24, *cg.*). Beneath the test the cerebral ganglia and the apical plate are in contact.

The cells of the apical plate are evenly ciliated with short cilia, like those borne by the test cells (fig. 15). In this respect this species differs from both Nucula proxima and Yoldia limatula. Both of these forms have long apical cilia (Text-figs. G and H) that during life are bunched together (Text-fig. F). Nucula proxima has an apical plate that in extent may be compared to that of Nucula delphinodonta, but the apical plate of Yoldia is comparatively very small. The short, diffuse cilia on the apical plate of Nucula delphinodonta are probably the result of the conditions that make active locomotion at this stage both unnecessary and dangerous. (See what is said regarding this under the head of Test.) Certainly most of the apical plate, and probably all of it, is cast away when the test is shed (figs. 34 and 35).

Shell.

Some lime salts are deposited soon after the cuticle of the shell begins to be secreted, which takes place about the time that the lobes of the mantle begin to form (fig. 20). When the test is shed (figs. 34 and 35), the shell-valves are white,

glossy, and quite transparent. They do not correspond to the adult valves in shape (fig. 50), and they do not have the long, straight hinge-line of the prodissoconch of Yoldia (Text-fig. K). The hinge-line is not very definitely marked off from the rest of the shell, but it can be distinguished as a nearly straight or slightly curved portion on the dorsal margin (fig. 36). The difference in the shape of the prodissoconches of Nucula and Yoldia is quite marked, more marked than might have been expected for forms so closely related, when there is so much resemblance between the prodissoconches of many Lamelli-branchs (**6**). They both conform to the same type, how-ever.

At first the valves are thin and have neither cartilage pit nor teeth. Soon after casting, a little knob of cartilage (fig. 36, *ca.*) makes its appearance near the middle of the hinge-line. The teeth do not form until a much later stage (fig. 46). About the time that the fifth pair of gill plates are formed, a tooth appears on each valve in front of the cartilage pit. This is soon followed by another, which is added anteriorly. The teeth posterior to the cartilage pit begin to appear about the time that the third tooth anterior to the cartilage pit is formed. New teeth in the posterior series are added pos-teriorly. Only about half as many teeth are formed posterior to the cartilage pit as anterior to it. Apparently as long as the shell continues to grow in size new teeth are added. Shells of fully grown specimens are about 4 mm. long, but they sometimes occur nearly 5 mm. long.

Each shell-valve is very convex (figs. 50 and 51), slightly oblong, and moderately thick. The beaks are directed pos-teriorly and placed far back on the shell. This gives an appearance quite the reverse of most Lamellibranch shells, which have the beaks nearer the anterior than the posterior ends, and directed forward. The cuticle of the shell differs in different specimens from horn colour to dark brown or nearly black. It may be considerably broken near the beaks, but it is generally quite perfect and smooth. Unlike most Lamellibranchs, the shells of this species contain so much

animal matter that they retain their forms after the lime salts have been dissolved away. The material is quite tough, and frequently causes much trouble in cutting series of sections.

Each valve of the shell of fully adult animals has from ten to twelve teeth in the series anterior to the cartilage pit and five or six posterior to it (figs. 50 and 51). All of the teeth are more or less conical, pointed, curved toward the dorsal margin of the shell, and distinctly grooved on the side away from the cartilage pit. Each series of teeth forms a ridge some distance from the dorsal margin of the shell, which disappears dorsal to the adductor muscle-scar. The teeth of the two valves interlock so completely that it is frequently quite impossible to separate the valves without breaking some of them. The cartilage pit is large and deep. The adductor muscle-scars and pallial lines are faintly marked.

Mantle.

The shell-gland is formed early. About the time that the gut is formed it consists of a number of large cells that lie near the blastopore, on what may be distinguished as the dorsal side of the embryo. Its cells do not seem to bear cilia, but only preserved material was at hand for the determination of this point. The surrounding ciliated cells, those that form the test, begin to grow over the shell-gland from the sides and anterior end (figs. 10, 11, 12, and 13, sg.). At the same time the shell-gland flattens slightly, and the cells along its margins push up and form a slight ridge, that keeps the surface of the shell-gland separated from the overgrowing test. Soon after the shell-gland is covered by the test, it arches dorsally, and the two come to lie close together (figs. 17 and 18, sg.). As the embryo flattens laterally the shell-gland arches dorsally still more (fig. 20), and a space appears between it and the intestine. This space seems to be formed by the multiplication and flattening of the cells of the shell-gland, which arches dorsally and becomes separated from the intestine. Lateral folds (fig. 20, m.), the beginnings of the

mantle lobes, are soon formed. About this time the shell cuticle is secreted and some lime salts are deposited.

Soon after casting has been completed, swellings, the beginnings of the gills (fig. 39, *g.*), are formed near the posterior margin of each lobe of the mantle. The gills are thus formed as appendages of the mantle.

The mantle now has the adult structure and appearance, except that at a later stage a portion of its inner epithelium, and of the epithelium covering the suspensory membranes of the gills, becomes converted into the hypobranchial glands. These glands are present in both sexes, but just before the breeding season they are much better developed in the females than in the males, and there is considerable evidence that they furnish most, if not all, of the material from which the brood-sacs are formed. The margins of the mantle lobes remain thickened and contain the glands that secrete the cuticle of the shell. Some cells along the ventral and posterior borders of the mantle lobes bear cilia. Pallial muscles are attached to the shell-valves, and extend out to the margins of the mantle. These serve to retract the margins of the mantle when the shell is tightly closed.

Foot.

At a stage such as is represented by figs. 14 and 15, a group of cells lie between the gut and the stomodæum. These cells, together with the ectodermal side walls, are concerned in the formation of the foot. The side walls of the foot are continuous with the general ectodermal covering of the body beneath the test. The cells lying between the gut and the stomodæum are apparently mesodermal, and enclose a small space (figs. 15 and 24). The shell-gland spreads out, arches dorsally, and folds laterally to form the mantle, and a large space is left between it and the stomach and intestine (figs. 20, 24, and 26). In some transverse sections the space between the stomodæum and the intestine, and the space dorsal to the intestine, are more or less connected. This connection may be due to shrinkage caused by pre-

servatives, but it seems probable that the two spaces are naturally more or less definitely connected around the sides of the stomach and intestine, and that they may be regarded as a single cavity—a schizocœle.

The side walls of the foot join the stomodæum, and are not continuous with each other ventrally (figs. 20 and 28). Just before the test is cast away they begin to unite dorsal to the stomodæum, and the stomodæum becomes comparatively free. This change begins at the posterior end of the foot and works forward.

The process of casting is slow, and includes a large part of the stomodæum. When it is completed, the foot consists of a small mass of tissue, lying ventral to the stomach and intestine (figs. 34 and 35, $f.$). It is not capable of executing movements, and for a period of about a day, or even longer, the embryo lies perfectly quiet with the shell-valves tightly closed. At first I supposed that this comparatively immature condition of the foot at the time of casting was connected with the protected life of the embryo. The foot of Yoldia executes movements before the test is shed, and burrowing is begun almost as soon as the process is completed. It seemed natural to conclude that the greater development of Yoldia at this time depended upon the necessity for self-preservation. It was surprising, then, to find that at a corresponding time the foot of Nucula proxima is no better developed than is the foot of Nucula delphinodonta. This seems very remarkable to me, for Nucula proxima inhabits muddy and shelly bottoms over which flow quite strong tidal currents. Under these conditions it would seem that such perfectly helpless embryos would surely perish.

The foot of Nucula delphinodonta grows rapidly, and by the second day (fig. 36) performs feeble movements, but it is not thrust out of the shell for some time. It becomes provided with cilia (figs. 39 and 40), but they are not as powerful as those on the foot of Yoldia (Text-fig. K), and they are of but little service in locomotion.

The first movements of the foot are feeble twitches. These

in time become more frequent and powerful. Finally the foot
is thrust out of the shell, stretched ventrally and anteriorly,
swelled up at the end, and held more or less rigid while the
cilia vibrate. After being held in this position for a few
seconds it is withdrawn, either to remain quiet for some time,
or to be immediately thrust out again. The earlier move-
ments are not very energetic, and as the side flaps have not
been formed, they are not like the movements of the adult.

The first indication of the side flaps consists of a slight
longitudinal groove on the mid-line of the ventral surface of
the foot. On each side of this groove the foot grows to form
flaps (figs. 40 and 61) that lie side by side.

Soon after the test is shed, a rounded knob develops on
the postero-ventral portion of the foot (fig. 36). This grows
quite rapidly, and forms the prominence that appears like a
heel (figs. 40 and 41). It soon stops its rapid growth, and
in the adult is comparatively small (figs. 48 and 49). In
this species it is comparatively much larger in the adult
animal than in any of the other species that I have studied.

The side flaps at first have smooth margins (fig. 40), but
papillæ soon begin to be formed (fig. 41). The anterior
papillæ are formed first, and new ones are added posteriorly
as the foot grows, until as many as thirteen pairs have been
formed (fig. 48). The number differs with the size of the
individual. Sexually mature specimens may be found with
no more than eight pairs. The papillæ are large, conical,
more or less pointed, and very sensitive to mechanical stimu-
lation.

The movements of the foot of this species when compared
with the movement of the foot of Yoldia are very deliberate,
but the foot is so large, and the muscles so powerful, that
burrowing is quite rapid. Individuals of this species seem
normally to live entirely covered by mud, in which they
wander around by slow thrusts and retractions of the foot.
Specimens do not seem to come to the surface of the mud to
remain for any considerable time, and it seems probable that
the greater part of the lives of individuals are passed beneath

the surface of the mud. Observations made on specimens kept in dishes of sea water in which there was no mud show that individuals of this species execute movements very similar to those executed by Yoldia (1), but that in all cases they are much more deliberate (3). Leaping movements are absent, but slow thrusts with the flaps extended may frequently be observed. In former publications attention has been called to the characteristic movements of the foot, and they need not here be redescribed (1 and 3). As in the case of other members of this group, the movements of burrowing are very effective. The somewhat spherical shape of the shell, and the relatively large size of the foot, make it possible to raise the shell from the bottom of a dish, and occasionally to keep it balanced for a few seconds over the expanded foot. My observations lead me to believe that the animals never creep.

As in Yoldia, the foot is supplied with complicated and powerful muscles (1 and 3). It is attached to the shell by three pairs of muscles, and by a few fibres that lie ventral to the genital mass and liver. The posterior pair of foot muscles is very powerful. These muscles are attached to the shell at the bases of the teeth, just anterior to the posterior adductor muscle, and extend along the sides of the foot in an anterior and ventral direction. They are the powerful retractor muscles of the foot. Fibres from them are extended into the muscular flaps, and are important in spreading them apart.

The two anterior pairs of foot muscles correspond to the three anterior pairs of foot muscles in Yoldia. They are inserted on the shell close together along the bases of the teeth, just posterior to the anterior adductor muscle. The most anterior pair has much the same distribution as the two anterior pairs in Yoldia, and in some cases each muscle seems to be slightly separated into two near its origin. They spread out along the sides of the foot, and are distributed to its posterior and ventral portions. These muscles seem to be closely connected with the muscle-fibres that are attached

along the sides of the shell ventral to the genital mass and liver. The more posterior of the two anterior pairs of foot muscles passes between the pair just mentioned, and is distributed to the anterior and ventral portions of the foot.

In the foot all of the muscles are closely bound together by their own fibres and by interlacing fibres, so that many movements occur that cannot be explained by direct pulls of one or more muscles. It should constantly be borne in mind that the attachments of the fibres are all along the sides of the foot, and that many, if not most of the muscle-fibres pull from one portion of the body-wall to another, without changing the relation of the body to the shell. Thus the flaps can be spread apart after the shell has been removed. By compressing the blood contained in the large spaces of the foot, many movements, especially those connected with protruding the foot, may be performed.

As in the case of Yoldia, the foot muscles are so large that they are attached along a considerable portion of the dorsal surface of the shell. I regard this as the result of the size of specialised muscles, and do not agree with Pelseneer (13) that it should be regarded as a primitive character.

Byssal Gland.

The byssal gland is formed as an invagination, just anterior to the posterior projection of the foot, about the time that the side flaps of the foot begin to form (fig. 39). Although there is but a single external opening, the gland at first consists of right and left pouches that extend into the foot near its posterior side. The cells forming the upper portion of the gland soon become somewhat swollen, and do not stain very well with hæmatoxylin. The lumen of the gland soon shows traces of a secretion, but the secretion has never been seen protruding from the duct.

The gland soon enlarges to a remarkable extent, becomes quite irregular, and the paired appearance disappears. At this stage, which extends from about the time that the gill acquires its third lobe (fig. 41) until about the time that it

acquires its fifth pair of plates (fig. 45), the byssal gland extends through a considerable portion of the foot, and in the posterior side of the foot it may extend to a position somewhat dorsal to the pedal ganglia. The cells of the gland during this stage are greatly swollen and vacuolated, and have thin, almost indistinguishable walls. They are crowded together so as to almost obliterate the lumen of the gland. The result is that stained sections of the gland have the appearance of a fibrous or reticular mass that is so mixed up as to be hardly intelligible.

As the embryo gill begins to acquire its fifth pair of plates the byssal gland generally becomes less extensive. In the adult it is reduced to a small pouch (fig. 48, *bg.*) that opens in the median groove of the foot, just anterior to the heel-like projection. The dorsal, blind end of the pouch consists of comparatively large cells with small nuclei, and seems to contain some secretions. They are not generally distended with secretion, and the duct is generally quite empty. Nothing comparable to byssal threads have been observed. Towards the opening of the gland the cells become smaller and bear cilia.

I have described the adult condition that seems most frequently to prevail. In a few specimens the gland cells are much shrunken, and seem to contain little or no secretion. In some specimens of Nucula proxima the gland is more extensive and the cells are greatly distended. This would seem to indicate that the gland is functional, but not as an organ for the formation of threads. The present use of such a secretion is problematical.

It is very natural to compare this gland to the mucus-secreting glands of Gastropoda, but there seems to be little direct evidence that they are homologous.

Alimentary Canal.

There is a stage when the embryo resembles an epibolic gastrula (fig. 4). A pouch appears between the large cells, at a point corresponding to the asterisk, that seems to be formed

by the separation of some of the larger cells, accompanied
by their division into smaller cells. This pouch is the first
indication of the alimentary canal (fig. 8, *mg.*). Partly by
the division of cells forming it, and partly by the addition of
ectodermal cells around the blastopore, the gut is carried
further into the interior (figs. 9 and 11), and comes to lie at
the end of a narrow tube, the stomodæum (fig. 15, *std.*). The
blastopore never closes, so from its first appearance the
stomodæum is connected with the gut.

The blind end of the gut turns dorsally beneath the shell-
gland (fig. 11, *mg.*), and soon begins to grow posteriorly
(fig. 15, *int.*). It finally comes to the surface at the posterior
end of the embryo at a point ventral to the shell-gland and
dorsal to the blastopore (fig. 24), where the anus is formed.
The anus does not open directly to the exterior, but opens
into the mantle chamber near an external opening in the test.

The alimentary canal at this stage consists of three distinct
parts (fig. 24) : a slender tube, the stomodæum (*std.*), opening
through the blastopore and extending forward nearly to the
apical plate that is formed from the ectoderm ; a rather thick-
walled stomach (*sto.*) that lies dorsal to the anterior end of
the stomodæum, and ventral to the shell-gland ; and the
intestine (*int.*), which joins the posterior end of the stomach,
and at first has rather thick walls.

Dorsal to the stomach and intestine, between them and the
shell-gland, a cavity makes its appearance that communicates
by lateral passages with another cavity that lies ventral to
the stomach and intestine, between them and the stomodæum.
The ultimate fate of these cavities has been referred to in the
sketch of the life-history, and in connection with the foot,
and will again be referred to in connection with the peri-
cardium. For some time they are rather large, and a portion
of the alimentary canal is left quite free from surrounding
tissue, except where it seems to rest on the walls of the
developing foot (fig. 28). A short time before the test is shed
the liver pouches make their appearance (fig. 25, *l.*). These
are formed from the sides of the anterior end of the stomach.

The cells of the epithelial walls of the stomach are of two kinds.   Those at the anterior end of the stomach carry comparatively few cilia, and those at the posterior end carry many cilia.   At this stage some of the cells on the dorsal side of the stomach, near its anterior end, begin to secrete a mucus-like material that extends posteriorly in the lumen of the stomach as a small rod that probably represents the crystalline style (fig. 26).   Later the posterior portion of the whole dorsal division of the stomach (the part that at this stage is the dorsal part of the anterior portion) is given over to secreting this material, but a definite rod may not be present.

About the time that the embryo casts its test the stomach grows dorsally into the space above it, so that a ventral bend is formed where the stomach joins the intestine (fig. 26). This is the beginning of the abrupt bend that marks this portion of the alimentary canal in later life.   Two fibre-like cells stretch across the dorsal space from the anterior end of the stomach to the mantle (fig. 25).   Their position suggests that they may aid in moving the stomach into the more dorsal position, but there is no direct evidence that this is the case.

When the test is cast away and the adductor muscle pulls the shell-valves together, the stomach is crowded further into the dorsal space, and the bend in the intestine becomes more pronounced (figs. 34 and 35).   The same pressure apparently causes the liver pouches to go to pieces.   Their cells become more or less separated, and fill the larger part of the cavity dorsal to the stomach (figs. 36—39, z.).   The same changes have been noticed in embryos of Yoldia limatula and Nucula proxima.   In all of these forms the changes occur in connection with the closing of the shell.   Until the test is shed, tissue lies between the valves of the shell so that they cannot be shut together.   When the tissue is removed, and the shell is closed, there is no longer room for the liver pouches to lie on the sides of the stomach and retain their original shape.   They are accordingly flattened and pressed

into the unoccupied space dorsal to the stomach. The cells are no longer arranged to form definite walls (figs. 36—39, z.), but later some of them seem to form liver pouches again (figs. 42—44). A small portion of the space into which the stomach and liver are crowded is not filled, and finally forms the pericardium (figs. 39—41).

The rupture of the liver pouches leaves the dorsal part of the stomach without side walls, and the dorsal wall is commonly broken (figs. 37 and 39). The dorsal wall is formed again before the liver pouches regain their cavities (fig. 40). Some of the separated liver cells find their ways into the open stomach (figs. 37 and 38), and together with mucus practically fill it. For a period of two or three days after casting, the animal is not active, and it is doubtful if it feeds. At the end of this time the walls of the stomach begin to re-form, and the mass of material that has filled the stomach has largely disappeared. For a number of days the liver does not form definite pouches. The rounded and scattered cells are finally collected into two masses (figs. 40 and 42) that finally form new liver lobes. The left is slightly larger than the right mass, but the masses are more nearly equal in size than is the case with Yoldia. In both cases it seems that the difference in the size of the two liver lobes causes the developing loops of the intestine to take up a position on the right side. Cavities gradually extend out into the liver pouches from the stomach (figs. 43 and 44). In the formation of the cavities some of the rounded cells seem to go to pieces in much the same way as they would if digested.

The elongation of the intestine that results in the formation of the loops begins about the time that the embryo acquires its fourth pair of gill plates (fig. 45). This elongation carries the portion of the intestine that lies dorsal to the posterior adductor muscle toward the posterior wall of the stomach and nearer the dorsal margin of the shell. The end of the loop is forced over to the right side, and is extended anteriorly nearly to the anterior wall of the stomach. At this stage (Text-fig. O) the loop of the intestine is much like

the loop that occurs in adult Yoldia limatula (Text-fig. L).
The dorsal bend now begins to elongate and project ante-
riorly (Text-fig. P). This continues until the loop is ex-
tended between the limbs of the loop that was made first
(Text-fig. Q). The lower limb of the loop begins to elongate
(Text-fig. R), and the adult condition is soon reached (Text-
fig. S and fig. 48).

The heart makes its appearance some time before the loops
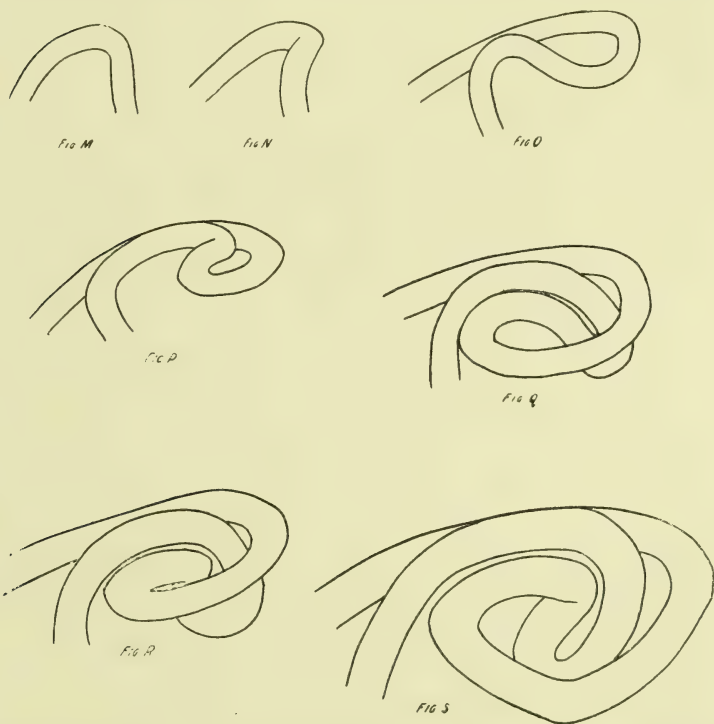
TEXT-FIGS. M, N, O, P, Q, R, AND S.—Stages in the development of the
loops of the intestine in Nucula delphinodonta.

of the intestine begin to be formed (fig. 41). From the first
appearance of its cavity the heart surrounds the intestine.
This condition continues for a long time, until the loops of
the intestine have been formed, and, in fact, until after the

animal has reached sexual maturity. At first the intestine passes through the middle of the heart (fig. 67). The sides of the heart seem later to be forced dorsally by the growth of the kidneys, and the intestine becomes applied to the ventral wall of the heart. By the continued growth of the kidneys the ventral portion of the ventricle is drawn out into a trough, in which the intestine lies (fig. 68). The growth is continued until the trough is considerably deeper than the width of the intestine. By gradually closing in dorsal to the intestine at the anterior and posterior ends the trough is shortened, and the intestine finally becomes free from the heart and lies ventral to it (fig. 69).

In the adult animal (fig. 48) the œsophagus is a rather broad and long, nearly cylindrical tube, that opens between the palps just posterior to the anterior adductor muscle. I find no indication of anything that can be interpreted as salivary glands at any stage in the development (13). Throughout its length it is evenly ciliated and quite devoid of ridges. The corners of the mouth are continuous with the groove between the two labial palps. The stomach is large, somewhat spindle-shaped, and extends from near the dorsal margin of the shell to the level of the pedal ganglia. Near its middle there is a nearly complete ridge of elongated epithelial cells, and frequently a more or less well-marked external groove that divides it into a dorsal and a ventral portion. The posterior and part of the lateral walls of the dorsal portion of the stomach are formed by long and slender epithelial cells that stain but slightly. They secrete a mucus-like material that stains deeply, and probably corresponds to the crystalline style. In adults this secretion seldom takes the form of a rod, but in embryos a rod is commonly present (figs. 26, 28, 30, and 64). The remaining cells in the dorsal portion of the stomach are short, stain deeply, and are evenly ciliated. The ducts from the liver open in the dorsal end of this portion of the stomach. The epithelial cells of the ventral portion of the stomach are short, stain deeply, and carry a quantity of short cilia.

Leaving the ventral end of the stomach, the intestine bends dorsally, and follows the posterior walls of the stomach nearly to its dorsal end. Here the loops already described are formed. From the loops the intestine passes posteriorly ventral to the heart, bends around the posterior side of the posterior adductor muscle, and opens in the mantle chamber. It is composed of short ciliated cells that stain deeply. Its lumen varies greatly in size, according to the amount of matter it contains.

Labial Palps.

Soon after the embryo acquires its second gill lobe the epithelium around the mouth, and for a short distance along the sides of the body, becomes ciliated (fig. 41). This ciliation precedes the formation of the palps, and, to a certain extent, marks out the region where they will form. The cilia are more numerous immediately anterior to the mouth than they are immediately posterior to it, and they soon extend along the sides of the body for about half the width of the foot. The position of the ciliated patches on the body-wall is such that the dorsal portion of each tends to lie horizontally, and the ventral portion tends to the vertical position (fig. 62, *lp.*). The groove thus formed becomes the groove between the outer and the inner palps. The portion above the groove forms the outer palp, and that below the groove the inner palp. This is accomplished by the growth and folding of the body-wall. The outer palp begins to grow first, and in such a way that the line marking the dorsal limit of the cilia becomes the free margin of the palp. This leaves the inner surface of each outer palp covered with cilia, and the outer surface unciliated. The two outer palps are continuous anterior to the mouth, where they form a slight ridge (figs. 54 and 63).

For some time after the outer palps form folds, the inner palps are represented by ciliated ridges (fig. 54), that reach some distance beyond the posterior ends of the outer palps. These ridges grow so that the lines marking the ventral limit

of the cilia become the free margins of the inner palps. The two inner palps are continuous posterior to the mouth, where they form a slight ridge (figs. 55 and 63). Like the elevation anterior to the mouth, this never becomes prominent.

The inner surface of each outer palp becomes folded near its anterior end to form ridges and grooves (fig. 55), and the postero-ventral portion protrudes to form a lobe. This lobe is the beginning of the formation of the palp appendage. The edges of this lobe soon begin to thicken, and a groove is left between the ridges thus formed. This is accompanied by a considerable growth in length (fig. 56, *pap.*). At this stage of development the palp appendage is seen to correspond to two of the ridges on the general surface of the palp, with a groove enclosed between them.

Posterior and dorsal to this appendage another smaller appendage is formed (fig. 56). This is also on the outer palp, and consists of two ridges with a groove between them. It never grows to be very long, but resembles the large appendage that lies ventral to it in its formation.

As development proceeds the larger appendage (fig. 56, *pap.*) twists, so that its groove opens dorsally and posteriorly (fig. 57, *pap.*), and the smaller appendage twists so that its groove opens ventrally. This double twisting brings that portion of the small appendage that was dorsal nearly or quite in contact with that portion of the large appendage that was ventral, so that for a short distance the two grooves together form a tube that opens anteriorly between the two palps (fig. 57). During the development of the palp appendages both outer and inner palps have grown to be quite large, and their ciliated surfaces have been thrown into series of ridges and grooves.

The palps on each side of an adult animal consist of two large, somewhat triangular folds of tissue (fig. 48, *lp.*), united to each other along their dorsal margins, and suspended from the body-wall by a thin membrane. The outer palps on the two sides of the body are connected in front of the

mouth by a small ridge that occupies the position of an upper lip. In the same way the inner palps are connected by a ridge posterior to the mouth that is comparable to a lower lip. The corners of the mouth are continuous with the space between the two palps of each side. The opposed surfaces of the palps are densely ciliated, and thrown into a series of ridges and grooves that tend to lie opposite each other on the two palps. Near the free margins this arrangement may be considerably broken. Large blood-spaces follow along these ridges. Each outer palp is supplied with two grooved appendages that originate near its dorsal margin. The most ventral of these appendages (fig. 48, *pap.*) can be extended far beyond the margin of the shell, and is used to elevate mud with the contained food. The dorsal appendage sets over the anterior end of the groove of the ventral appendage, and with it forms a short tube that opens between the palps. Each ventral palp appendage is supplied with longitudinal muscles (fig. 66, *lm.*), that are continued in from the body-wall; with a large nerve (*pn.*) that originates in a cerebral ganglion, and runs posteriorly along the united dorsal margins of the outer and inner palps; and with a continuous blood-space (*bs.*). The epithelium lining the groove of the appendage is very thick, and is densely covered with cilia. The nuclei of these epithelial cells are very long and slender. The muscles in the palp appendages are so placed that their contraction causes the appendages to curl, as shown in fig. 48, *pap.*

It is not easy to observe individuals of this species while they are feeding, as they normally live entirely covered by the mud. If specimens are placed in a dish of sea water, in which there is only a thin layer of mud, the action of the palp appendages may be observed. It is well to use as much mud as possible without affording the animals an opportunity to bury themselves, and to use specimens that have not been in mud for several days and are accordingly hungry. The mud is passed along the grooves of the palp appendages by the action of the cilia, and finally conducted

between the palps, where the cilia carry it to the mouth. Very few specimens have shells that are transparent enough to allow observation of processes carried on inside of the shell, but there can be no doubt as to the path taken by the mud after it has started up the grooves in the palp appendages.

Feeding is much more easily observed in the case of Yoldia limatula. In this species the animal has fre-
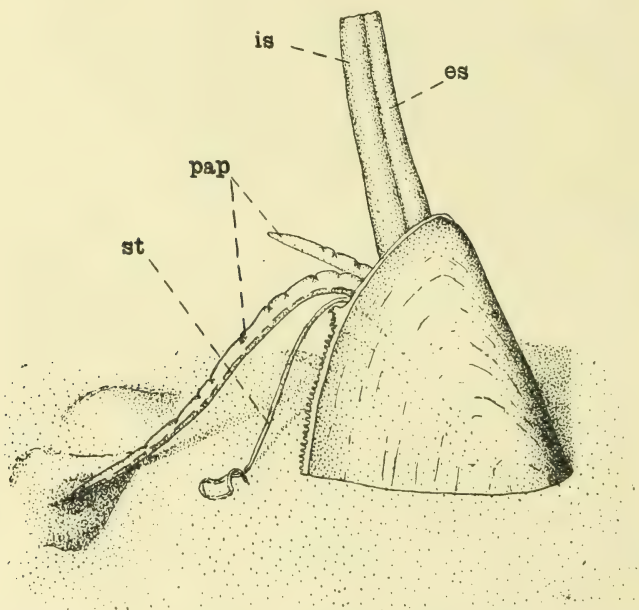
TEXT-FIG. T.—An adult specimen of Yoldia limatula as it appears while feeding. *es*. Exhalant siphon. *is*. Inhalant siphon. *pap*. Palp appendages. *st*. Siphonal tentacle.

quently as much as one third of the posterior end of the shell above the mud while feeding (Text-fig. T). The palp appendages are protruded, and one at least bends over and inserts its tip in the mud. By the action of the cilia in the longitudinal groove, large quantities of mud and food are elevated. There is no reason to suppose that the palp appendages of

Nucula are not as effective as those of Yoldia, but the method of life makes observation more difficult. As suggested by Mitsukuri (**11**), it seems probable that the large palps with their numerous large blood-spaces may be important respiratory organs.

Gills.

A short time after the embryo sheds its test, a portion of each lobe of the mantle near its posterior border begins to thicken (fig. 39, *g.*) and then to project anteriorly. These thickenings are the beginnings of the gills. They grow rapidly, acquire cilia, broaden dorso-ventrally, and each begins to divide into two lobes (fig. 40, *g.*). The formation of the lobes is due to unequal growth more than to constriction. Each lobe is at first a little knob that is flattened slightly laterally. As growth proceeds the ventral lobe broadens and flattens along its anterior border preparatory to the formation of another lobe. Coincident with these changes in the ventral lobe, the dorsal lobe grows anteriorly, and forms a rather long finger-like process or filament, that closely resembles the filaments of the developing gills of other Lamellibranchs (fig. 41, *g.*). New lobes are added to the gill by the unequal growth and division of each ventral lobe in its turn, and as the new lobes are formed the more dorsal lobes lengthen.

Throughout life the gill occupies a decidedly dorso-ventral position, but growth carries the ventral end some distance toward the posterior end of the animal, so that the adult gill lies somewhat diagonally (fig. 48, *g.*). In Yoldia (Text-fig. L) the gills lie more nearly parallel to the long axis of the body.

The chitinous support of the gill makes its appearance when the gill is still in the two-lobed condition. At first it consists of a thin plate lying just beneath the epithelium on the anterior border of the gill, and is continued from one lobe into the other. Its ends lie near the anterior extremity of each lobe. As the ventral lobe flattens the chitinous plate is extended along its anterior border, so that with the

formation of the third lobe the plate is extended into it. In this way, as new lobes are formed, the chitinous plate is extended into each, and continues to be connected throughout the length of the gill. As the lobes grow to form filaments, the chitinous plates extend with them, and each becomes trough-shaped with the open side of the trough directed away from the corresponding lobe of the mantle. Later the free edges of the trough are brought near together, and the support in each filament practically assumes the form of a tube that extends out nearly to the tip of each filament. The tubes that support the different filaments are united at their bases, so the chitinous support is continuous throughout the gill.

As the lobes elongate to form filaments, the cilia on each becomes restricted, so that the side that is turned away from the lobe of the mantle to which it is attached becomes quite free from them. On the remaining sides the cilia are long and powerful.

About the time that the fourth division of the gill is formed the mantle begins to thicken at the bases of the filaments, between them and the shell (fig. 45). These thickenings are generally opposite the bases of the filaments, and connected with them, but as there are sometimes more plates on one side of the gill[1] of the adult animal than on the other, the thickenings are probably not always formed in this position.

They represent the beginnings of the outer plates of the gill. The filaments, at the bases of which these thickenings are formed, form the inner plates of the gill.

For a considerable time the outer plates remain much smaller than the inner plates, and they never quite equal them in size (fig. 53). As the outer plates of the gill are formed, the chitinous support is carried out into them as branches from the portion that runs lengthwise of the gill.

[1] The term gill is for convenience applied to the respiratory organ on one side of the animal, although writers agree that it probably corresponds to tne two gills found on each side of most Lamellibranchs.

These branches become trough-shaped, with the open part of the trough directed away from the inner plates. Finally, the free edges of the troughs come close together, as described in connection with the other set of filaments or plates.

The chitinous material at the bases of the two sets of plates also becomes trough-shaped, and has the open portion of the trough directed away from the plates. Thus the chitinous support of the gill consists of two series of troughs, bent so as to form tubes, each of which is connected by one end to the side of a larger trough that runs lengthwise of the gill. The whole might be compared to a large trough with a series of spouts leaving each side, the individual spouts of the two series being placed opposite each other. Later, bridges are built across the main trough in the intervals between the side spouts. The whole system is in direct communication with the blood-spaces of the gill, but probably is not concerned with the circulation of the blood.

The two sets of plates do not lie parallel to each other, but they grow away from each other at an obtuse angle. The inner plates grow almost in an anterior direction, and the outer plates grow laterally and a little posteriorly, so that the angle formed by the two sets of plates on the two sides of the gill is visible when the animal is viewed from the side. The suspensory membrane, formed by the growth of the mantle at the base of each gill, makes it possible for the gill to take up this position.

The filaments begin to grow into flattened triangular plates about the time that the fourth division of the gill is formed. This is accomplished by slow, unequal growth, and throws no light on the phylogeny of the gill. It seems to be a matter of individual opinion whether each of the plates should be considered to be homologous with a descending filament of an ordinary Lamellibranch gill, or whether it should be considered to be homologous with both a descending and an ascending filament.

The adult structure of the gill of Nucula has been so carefully and accurately described by others, that were it not for

the sake of completeness, it would not be necessary to describe it here. Mitsukuri's (**11**) description of the gill of Nucula proxima holds good in all essentials for the gill of this species, and since his description was published others have verified and supplemented his results (**7, 13**, and **16**) until our knowledge of the structure is comparatively complete.

The adult gill of Nucula delphinodonta is suspended from the body-wall by a fold of tissue, the suspensory mem-
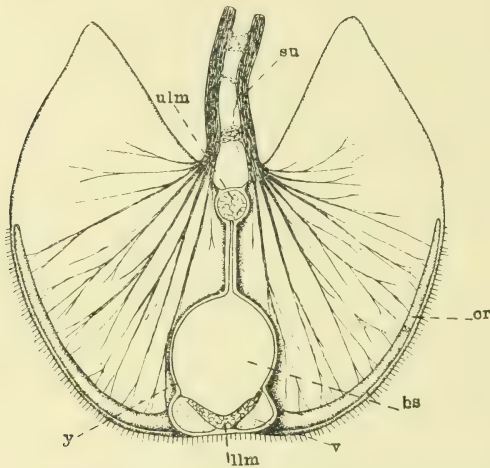
TEXT-FIG. U.—A pair of plates from a gill of Yoldia limatula. *bs.* Blood-space. *cr.* Chitinous rod. *llm.* Lower longitudinal muscle. *su.* Suspensory membrane. *ulm.* Upper longitudinal muscle. *v.* Cut surface of a chitinous rod. *y.* Cut wall of the gill plate where it bends to join the plate anterior to it.

brane (fig. 53, *gs.*), that was originally a fold on the inner surface of the mantle lobe. The suspensory membrane contains between its walls a large blood-space that communicates near its anterior end with the auricles of the heart, and throughout its length communicates with blood-spaces in the mantle. At intervals it communicates with similar spaces in the body proper. Unlike the suspensory membrane of Yoldia (Text-fig. U), this membrane is not very muscular, but some

muscle-fibres are always present. The epithelium covering the outer surfaces of the suspensory membranes, those surfaces that are turned away from the mid-line of the body, is modified to form a portion of the hypobranchial glands.

Each suspensory membrane bears two series of gill plates that generally lie opposite to each other. Occasionally a gill occurs in which there are more plates on one side than on the other, but even in these cases the order is interrupted only for a short distance. The number of plates differs with the size of the individual, but about twenty pairs seems to be common for well-grown specimens. Each plate is thin and triangular, and is composed of epithelial walls, between which there are loose connective tissue, large blood-spaces, and the chitinous framework. The epithelial walls on the edges of the plates that are directed away from the suspensory membranes are thickened and covered with strong cilia. This thickened ciliated epithelium extends between the plates for a short distance, but most of the epithelium is quite thin and destitute of cilia. The wall of each plate is continuous with the wall of the plate that lies in front of it, with the wall of the plate that lies behind it, and with the plate on the other side of the gill that lies opposite to it. Near the border furthest from the suspensory membrane, the opposing walls of the two series of gill plates are separated so as to form a large blood-space (fig. 53, bs.), that runs the whole length of the gill. This space is continued as a narrow slit to the base of the suspensory membrane. Thus the blood-space in the suspensory membrane is in direct communication with the blood-space of each plate, and in the gill the blood is free to flow from one part to another.

The chitinous framework consists of a bridged trough that occupies the bottom and part of the sides of the blood-space that lies between the two series of plates, and of two series of side spouts that project into the plates on the two sides, and lie in contact with the thickened epithelium. Although the chitinous framework is arranged as a system of troughs and spouts that, from their position, must be filled with

blood, they are probably not directly concerned in the circulation of the blood.

Between the chitinous trough and the suspensory membrane there is a small bundle of muscle-fibres that are continued the whole length of the gill (fig. 53, *lm.*). This bundle lies in the open part of the chitinous trough, and probably corresponds to the large bundle that occupies a similar position in the gill of Yoldia (Text-fig. U, *llm.*). A second longitudinal bundle of muscles is found in the gill of Yoldia (*ulm.*), but this does not seem to be present in this species. A few of the muscle-fibres in the suspensory membrane seem to be continued into the plates. They are not numerous, and they have not been carefully followed. The gill of this species is so small that it is not favourable for the determination of minute details.

The gills probably act as respiratory organs, but their small size, together with the blood-supply of other parts, makes it seem probable that other organs, such as the mantle and the palps, are also concerned in respiration. The opaque character of the shells of adult animals makes it quite impossible to observe the normal movements of the gills. They can be seen to move slightly, however, and it seems probable that the suspensory membranes contract slightly at intervals. Such movements would be useful in causing movements in the contained blood, but they are not sufficient to cause strong currents of water. The shape of the gills is not such as would make them efficient pumping organs. (Compare fig. 53 and Text-fig. U.) Inasmuch as these animals live entirely covered by mud, the production of strong currents of water could not be beneficial. As the animal wanders around in the mud the fæces naturally drop out of the open mantle chamber.

It would be a matter of some interest if the exact relationship of the gills of Nucula and Yoldia could be determined. It would seem to be a comparatively easy task to account for the changes in the shape and structure of the gill of Yoldia if we were to start with a gill such as has been described for

Nucula. The habits of Yoldia are such as to render the formation of strong currents of water absolutely necessary, for otherwise the mantle chamber would become clogged with fæces and dirt. The gill of Yoldia might have been perfected for pumping water from a Nucula-like gill. It would, however, be equally easy to account for the reverse modifications when we consider what the formation of strong currents of water by an animal entirely covered by a soft, slimy mud would mean. If we follow the generally accepted theory of the gill, the former change would seem more likely than the latter, though it is quite possible that nothing like a direct change from one to the other has taken place. The generally accepted theory of the gill has grown up as the result of structural and embryological considerations, and but scant attention has been given to probable modifications for the special purposes of the animals. Until we have much more detailed knowledge regarding the habits of most of the Lamellibranchs that have plate gills, and of some of the supposed near relatives of these Lamellibranchs, it seems to me that we lack the necessary data to give the derivation of the gill with anything like accuracy. There is much in the structure and embryology of Nucula that points to a gene-ralised type, and in this much it seems natural to look at the gills as primitive; but the gills of Yoldia—its undoubted near relative—are so remarkably well adapted for the performance of a special function, that it hardly seems safe to regard them as slightly modified gills until there are more careful observa-tions on the habits of other forms. I recognise fully the mass of evidence in favour of the primitive form of the plate-like gill. My only plea is for caution.

Hypobranchial Glands.

The epithelium on the inside of the posterior end of each lobe of the mantle, and on the outer side of a corresponding portion of the suspensory membrane of each gill, is glandular, and has been termed the hypobranchial gland. When these glands are present in Lamellibranchs, their secretions seem to

correspond very closely to mucus, and they are generally referred to as mucus glands. During the greater part of the year the hypobranchial glands of both sexes of Nucula delphinodonta are rather small and inconspicuous. They contain rounded or oblong masses of a refractive material that takes no stain. The cells themselves are small, and do not seem to be secreting actively. The hypobranchial glands of specimens of males seem to have the appearance that has been described, no matter what time of the year they are collected. As the breeding season approaches, the hypobranchial glands of the females become greatly distended with secretions. The rounded or oblong masses that are common at other seasons of the year are now seldom found, and the cells are packed full of rather large granules. Immediately after the brood-sac is formed, the cells of the hypobranchial glands appear shrunken and free from granules, and the glands have the appearance of having discharged their secretions. After examining a large number of specimens, I have become convinced that the hypobranchial glands furnish nearly all of the material from which the brood-sacs are formed. Specimens kept in aquaria do not form brood-sacs, and accordingly the processes of their formation have not been observed, but it seems probable that the secretions from the glands are passed posteriorly by cilia on the mantle, and probably swelled out into a bubble by the respiratory current of water. While the material is still soft it adheres to the foreign bodies with which it comes in contact.

Well-developed hypobranchial glands are present in only a limited number of Lamellibranchs, and their special function is hard to determine. It is interesting to find that they are concerned in the formation of the brood-sacs in this species, but this is the first instance that has been reported where such a sac is formed. It may be that other forms that possess especially large hypobranchial glands will be found to form similar brood-sacs, but this will not hold true for all. Nucula proxima has rather large hypobranchial

glands, and I find that it does not form brood-sacs. Such a case as this, where it is known that brood-sacs are not formed, seems to indicate either that the glands have some function to perform other than providing the material for the formation of brood-sacs, and that Nucula delphinodonta has adapted them to this purpose; that they are retained from forms that originally formed brood-sacs, in which case we must suppose that the ancestors of all forms that possess hypobranchial glands formed brood-sacs; or that in forms where brood-sacs are not formed the glands are, when present, mere vestiges, and are not now functional.

The latter explanation seems unlikely, as the glands of Nucula proxima are better developed than vestiges are likely to be. If the second explanation is accepted, we must regard the rearing of embryos in brood-sacs as more primitive, for this group at least, than throwing the eggs in the water where the embryos have to take care of themselves. From the standpoint of specialisation this seems to be very unlikely, and the fact that the embryos of Nucula delphinodonta possess tests that seem to serve no purpose, while similar tests function as organs for locomotion in other forms, points clearly to a condition when all of these embryos depended on their own activities for protection. It seems most likely that Nucula delphinodonta has made use of already existing glands to furnish the secretions for the formation of its brood-sacs, and that they may have other functions to perform.

Pericardium.

A short time before the shell-gland begins to fold at the sides to form the lobes of the mantle, a space appears between the stomodæum and the gut, and a little later a space begins to form between the shell-gland and the gut (fig. 24). These two spaces are separated by the gut, but in preserved material they are frequently connected around the sides of the gut. While these connections may be due to

shrinkage caused by the treatment with preservatives, it seems most likely that the spaces are normally connected with each other. It is just possible that these spaces may be traced back in their formation to the blastocœle, but it is more probable that the blastocœle entirely disappears, and that they represent a schizocœle. At first the space ventral to the gut is larger than that dorsal to it, but the latter grows as the mantle arches dorsally, and the ventral space remains practically unchanged.

As the foot begins to take form the ventral space becomes quite small, and about the same time that the embryo sheds its test it disappears altogether. A short time before the test is shed the dorsal space reaches its greatest size (figs. 25 and 26). About the time that the test cells begin to break apart, the stomach is carried dorsally some distance into this space (fig. 34). Two fibres, that in shape suggest muscle-fibres, extend from the anterior end of the stomach to the mantle. Their position suggests that they may aid in moving the stomach dorsally, but of this I have no proof. As the stomach moves dorsally they become shorter and thicker, but there is no evidence that they are moving factors. Until casting is completed, the apical plate and the stomodæum lie between the edges of the shell-valves, and keep them from being closed. When they are removed, the contraction of the adductor muscle closes the shell, and the body, which has until now been lying between gaping valves, is made to change its shape and position. The stomach and liver pouches are forced into the dorsal space until the dorsal end of the stomach comes in contact with the mantle.

This divides the space into anterior and posterior parts (fig. 35). There is no longer room for the liver pouches to retain their form and position, and as the body continues to move dorsally they are flattened out and soon go to pieces (fig. 36). Most of the cells that formerly composed their walls become scattered and rounded, and the anterior space becomes entirely filled (fig. 39). The posterior space, some-what diminished in size, persists, and finally becomes the

pericardium (figs. 40 and 41). The pericardial space is not smooth as it has been necessary to represent it in the figures. Mesoderm cells project into it from the surrounding tissue, and others lie comparatively free within it. As yet it lies almost wholly dorsal to the intestine, but just before the heart is formed it is extended beneath the intestine, and begins to have a rather definite epithelial lining. The epithelial lining seems to be formed by the change in shape and position of cells in the immediate vicinity. I find no indication that the pericardium originates as a pair of pouches, as has been described by Ziegler for Cyclas cornea (**20**).

Vascular System.

Small connected cavities are present throughout the body from an early time, but a true vascular system, with a heart and anything like a definite circulation, is not to be distinguished until much later, and a closed system of vessels with capillaries is never present.

The heart is formed about the time that the gill becomes well divided into two lobes, or just before the third lobe is formed. It seems to be formed by the hollowing out of a strand of mesoderm that stretches across the pericardial cavity. I have seen nothing that would indicate that the heart has a double origin, as Ziegler has described for Cyclas cornea (**20**). Mesoderm cells in the pericardial cavity and along its walls arrange themselves to form a strand that becomes hollow and begins to pulsate. From the first appearance of its cavity the heart surrounds the intestine (figs. 41 and 67). Most specimens show the heart collapsed with its walls in contact with the intestine, but some specimens have it distended with blood. In all cases it is easy to determine that the heart is perforated by the intestine, but it is especially evident in specimens where the heart is distended. In most of these cases the intestine lies nearer the ventral than the dorsal wall of the heart, and in many cases it lies directly in contact with this wall. At this stage the heart is not separated into auricles and ventricle (fig.

67, h.). It is in the form of a bent spindle, the two ends of which communicate with the blood-spaces of the gill. The larger median portion arches dorsally and surrounds the intestine. Anterior and posterior aortæ leave the heart, but no attempt has been made to follow them, until the adult stage is reached.

For a considerable time after its formation there is no appreciable change in the heart. About the time that the eighth pair of gill plates are formed it begins to be separated into ventricles and auricles. The auricles are at first very small and narrow. They extend only a short distance from each gill, and are separated from the ventricle by slight constrictions. There has been no change in the relative positions of the heart and intestine. At a slightly later stage, when the gill has about ten pairs of plates, the ventricle of the heart begins to change its shape. This seems to be due to the growth of the kidneys, which push anteriorly ventral to the pericardium. As the kidneys grow, the two sides of the heart are pushed dorsally, while the middle part of its ventral wall is held in its original position by the intestine. In this way the ventral wall is pulled out into a sort of trough in which the intestine lies (fig. 68, h.). Continued growth deepens the trough until it is considerably deeper than the intestine is wide. The heart gradually closes in, dorsal to the intestine, at the anterior and posterior ends of the trough, until it becomes free from the intestine, and lies dorsal to it (fig. 69). This is a very slow process, and is not completed until after the animal has reached sexual maturity.[1]

The adult heart consists of a ventricle and a pair of auricles, separated from each other by constrictions that are much deeper on the dorsal than on the ventral surface (fig. 69, h.). The openings between the auricles and the ventricle are so small that they must be quite obliterated

[1] Every specimen of Nucula proxima that I have examined has its heart perforated by the intestine. The specimens are all of good size, and many of them are the same ones from which I obtained eggs and sperm.

during contraction.   A band of muscle occurs near the end of each auricle, that keeps the blood from flowing back into the spaces of the gills.   Each auricle is somewhat conical, small where it joins the gill, and considerably enlarged at the end next to the ventricle.   The ventricle is swollen at the ends next to the auricles, and flattened over the intestine. The swollen ends of the auricles and the corresponding ends of the ventricle make right and left enlargements that superficially might be mistaken for two hearts.

A blood-vessel leaves the anterior end of the ventricle on the left side of the intestine, and not in contact with it. Another blood-vessel leaves the posterior end of the ventricle above the intestine and in contact with it.   The anterior vessel is somewhat larger than the other.   It runs forward over the dorsal end of the stomach and sends branches to the liver and genital organs, to the stomach and loops of the intestine, to the foot, to the labial palps, and to the anterior portions of the lobes of the mantle.   The vessel that leaves the ventricle posteriorly is at first dorsal to the intestine, but it soon becomes ventral to it, and is distributed to the posterior part of the body.

All of the blood-channels seem to end in rather large connected spaces, that ramify throughout the body.   The course of the blood cannot be traced in these spaces.   The blood-spaces of the foot, beside providing for the ordinary blood-supply, serve as reservoirs in which blood can be forced to extend the foot.   By suppressing some channels and squeezing blood into others different results may be obtained.   Blood must undergo respiratory changes in the gills, the mantle lobes, and the palps.

The opinions of writers on Lamellibranch morphology, regarding the primitive form and position of the heart, are very different.   Milne-Edwards (10) thought that the double appearance of the heart of Nucula and Arca pointed toward a primitive condition in which the heart was double.   Thiele (19), basing his conclusions on Ziegler's observations on the formation of the heart of Cyclas, holds that the heart was

probably originally a double organ, and that upon uniting in the median line it has taken up the various positions in regard to the intestine. Grobben (5) considers the single heart primitive, and thinks that the double condition is the result of changes in the position of retractor muscles. Pelseneer (13) and others, depending largely upon the position of the heart in Nucula and Arca, have considered the dorsal position of the heart to be the primitive position. Stempell (17) rightly holds that the ventral position of the heart of Malletia chilensis destroys the oundation of Pelseneer's reasoning, inasmuch as Nucula and Malletia are closely related forms. Stempell apparently considers the perforated heart to be the most primitive. From this position the heart may become dorsal or ventral to the intestine by a comparatively simple process.

The development of the heart of Nucula seems to indicate that the perforated heart is more primitive than the dorsal heart in this group. While, as Stempell holds, it seems most reasonable to consider a perforated heart that may become either dorsal or ventral by comparatively simple changes as more primitive than either a dorsally or a ventrally placed heart—where, in order to reach the opposite extreme, the heart would have to enclose the intestine, and then become free on the other side,—there is still nothing to prove that the ventral position of the heart is not primitive. The development of the heart of Malletia would accordingly be of considerable interest.

As neither the pericardium nor the heart of this Lamellibranch seems to be formed as a paired structure, there is nothing here to further the view of Thiele (19) that the position of the heart in regard to the intestine depends simply upon the position of two lateral hearts, that may, as a matter of convenience, fuse dorsally, ventrally, or around the intestine.

Nervous System.

The cerebral ganglia are formed in direct contact with the apical plate. The cells from which they originate can first

be distinguished as a group soon after the surface cells that
form the test become ciliated (fig. 15, *cg.*).   They frequently
remain as surface cells for some time, and they doubtless
originate as surface cells in all cases.   The group of cells is
not distinctly paired, and does not invaginate as it does in
Yoldia. Each cell becomes much larger at the inner end than
at the end that comes to the surface. Although a test cell lies
between the cerebral ganglia and the apical plate they still
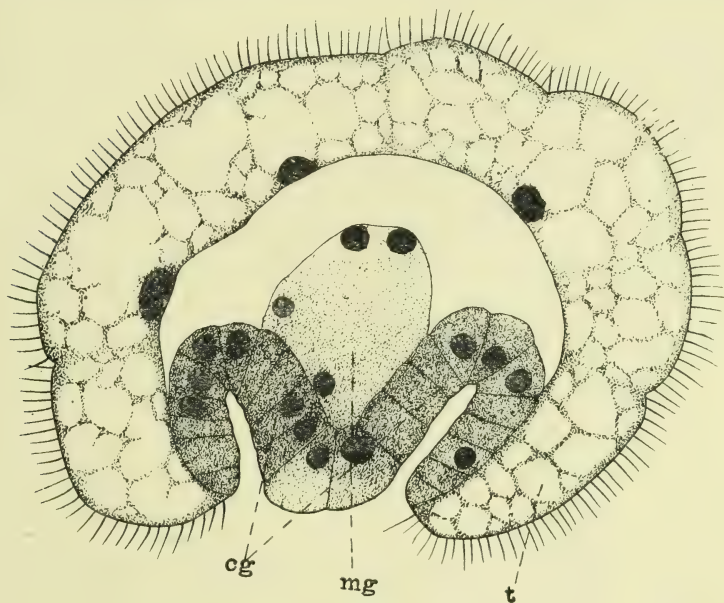
TEXT-FIG. V.—Transverse section of a forty-five hour embryo of Yoldia
    limatula, taken through the cerebral pouches. *cg.* Cerebral pouches.
    mg. Anterior wall of the mid-gut. *t.* Test.

remain in contact beneath this cell.   Little change occurs in
the appearance, size, or position of the cerebral ganglia until
the test is cast away, and until then no other part of the
nervous system can be distinguished.

When the test cells break apart and accumulate near the
anterior end of the embryo (fig. 34) a portion of the body of
the embryo is carried dorsally at the expense of the large

dorsal space. This dorsal movement includes the cerebral ganglia (cg.). When casting is completed, and the valves of the shell are closed, a further dorsal movement occurs, that results in the filling of the greater part of the dorsal space. This movement places the cerebral ganglia in position posterior to the anterior adductor muscle (figs. 35 and 36, cg.). The foot now begins to grow quite rapidly, and the pedal and visceral ganglia begin to form (fig. 36, pg. and vg.). Both pairs of these ganglia are formed as thickenings of the surface ectoderm. The thickenings that give rise to the pedal ganglia begin to form first, but both pairs of ganglia are in process of formation at the same time. Owing to the character of the embryonic tissue it is very difficult to determine how the commissures that connect the ganglia arise. They are first found very close to the surface, almost, if not quite, in contact with the ectoderm. Later they sink deeper into the body. The cerebro-visceral commissures are quite thick, and differ from the cerebro-pedal commissures in having much the same structure as the ganglia themselves. In the earlier stages I have been able to demonstrate only a single cerebral origin for each cerebro-pedal commissure. This may be due to the difficulty of tracing commissures in embryonic tissue. Later stages show two separate origins very distinctly.

The double origin of the cerebro-pedal commissures has been regarded by Pelseneer (13) as an indication of the presence of cerebral and pleural ganglia in each anterior nerve-mass. Furthermore, Pelseneer and others find that each mass is divided by a constriction into two rather distinct parts. I have not been able to satisfy myself that there is a distinct separation into cerebral and pleural ganglia, either in this or the other forms that I have studied.

The cerebral and pedal ganglia are about equal in size, but they differ in shape (fig. 48). The visceral ganglia are smaller than the cerebral ganglia, but compare pretty well with them in shape. Each cerebral ganglion is large at its anterior end, and tapers posteriorly into the cerebro-visceral

commissure. The commissure that connects the two cerebral ganglia is a broad, somewhat flattened band, that passes between the œsophagus and the anterior adductor muscle, and joins their anterior ends. The cerebral ganglia give rise to a number of nerves. A large nerve leaves the ventral side of each near its anterior end, passes ventrally along the posterior and ventral surfaces of the anterior adductor muscle, to which it sends branches, and is distributed to the anterior and ventral portions of the corresponding lobe of the mantle. Just posterior to the origin of the pallial nerve, and a little closer to the median line, another nerve, about equal to the pallial nerve in size, leaves each cerebral ganglion. This nerve follows along the fold of tissue that suspends the labial palps and is continued into the palp appendage. Other nerves from these ganglia are distributed to the visceral mass and to the dorsal portions of the foot muscles. Posterior and still further toward the median line than the palp nerve, the two portions of each cerebro-pedal commissure leave each cerebral ganglion, one a little anterior and ventral to the other. The two portions run posteriorly a short distance, and join to form a single commissure that is continued to the pedal ganglion of the same side. A nerve leaves each cerebro-pedal commissure dorsal to the corresponding otocyst, and is continued to it. This nerve is generally supposed to have its origin in the cerebral ganglion, and the angle at which it issues from the commissure indicates that this is probably the case. The otocystic nerve is about equal in size to the posterior division of the cerebro-pedal commissure. Stempell (18) finds that each otocystic nerve of Solemya togata leaves the cerebral ganglion direct, and runs an independent course to the otocyst. He also finds that each cerebro-pedal commissure leaves the cerebral ganglion as a single strand. He thinks that this is a double commissure, because it receives fibres from what he considers cerebral and pleural ganglia.

It seems more likely to me that the nervous systems of all molluscs have been derived from some such a generalised

type as is found in Chiton, and that each class has developed ganglia according to its needs, than that the ancestors of Lamellibranchs possessed the comparatively complex system of ganglia found in Gastropods. If this is true, it is easy to understand why Gastropods with their complicated head apparatus should develop ganglia for which Lamellibranchs have no need. Accordingly the necessity to homologise all of the ganglia in the two classes disappears.

In most Lamellibranchs the otocystic nerves spring from the cerebro-pedal commissures, and they are supposed to originate in the cerebral ganglia. In Solemya togata, Stempell finds that the otocystic nerves leave the cerebral ganglia direct, and are not included in the cerebro-pedal commissures in any part of their length. Is it not possible that the posterior root of the cerebro-pedal commissure, in forms where there are two roots, is the central end of the otocystic nerve ?

The pedal ganglia (fig. 48, *pg.*) are rounded and nearly equal to the cerebral ganglia in size. They lie close together, and they are connected by a moderately large commissure. The nerves from the pedal ganglia supply the muscles of the foot. They need no special mention.

The visceral ganglia (fig. 48, *vg.*) are the smallest of the three pairs of ganglia. In shape they resemble the cerebral ganglia, but they are turned in the opposite direction. Each visceral ganglion is elongated, and gradually tapers anteriorly into the cerebro-visceral commissure. The two ganglia lie far apart, and are connected near their posterior ends by a long and rather thick commissure. A rather large nerve leaves the posterior end of each ganglion, runs posteriorly ventral to the posterior adductor muscle, and, besides giving branches to this muscle, supplies the posterior and ventral portions of the corresponding lobe of the mantle. Anterior and ventral to the posterior pallial nerves another rather large nerve leaves each ganglion. This nerve runs along the inner side of the suspensory membrane of the corresponding gill nearly to its posterior end.

Otocysts.

The otocysts are formed soon after the embryo sheds its test. They originate as invaginations in the body-wall, a little posterior and dorsal to the pedal ganglia. The invaginations deepen and close over to form what seem to be closed sacs, that soon come to lie near the pedal ganglia in the interior of the foot. As in the case of Yoldia, these sacs are apparently entirely closed. Soon after the otocysts are formed, before the gills acquire their second lobes, otoliths appear. The otoliths have the appearance of little crystalline fragments, but I am inclined to think that they are formed in the otocysts, and are not introduced through the otocystic canals, as has been held by some writers. The particles seem to be too large to have been introduced through canals that, at this stage, I am unable to find. Again, the otocysts never seem to contain diatoms. Diatoms are very abundant in the brood-sacs in which the embryos are carried, and form a large part of the animal's food. Many of them are well shaped to pass through small openings, and one would expect to find them occasionally in the otocysts, if the contained material consists of foreign bodies that have gained access through the otocystic canals.

About the time that the gills acquire their sixth pair of plates the otocysts can be seen to be connected with the surface of the foot (figs. 46 and 64, *ot.*). At first the connection seems to be solid, but a little later openings can be traced from the otocysts to the exterior. These tubes, the otocystic canals, are quite slender near the otocysts, but widen toward the surface of the foot. From each otocyst the canal passes anteriorly, laterally, and a little dorsally to open to the exterior (figs. 46 and 64, *ot.*).

The position of the external opening is not just what might be expected if the otocystic canals are remnants of the invaginations that formed the otocysts. The otocysts are formed just posterior and a little dorsal to the pedal ganglia. As they develop, they sink into the interior of the foot and

become permanently settled near the ganglia at points nearly opposite their points of origin. As the same relation between organs in this region is retained during the whole of the development, there is no reason to think that growth is more from one side than from another. If, then, the otocystic canals are remnants of the original invaginations, we might expect them to run almost perpendicular to the surface instead of opening so far anterior and dorsal. It might be thought that the development of the anterior foot muscles has crowded the stomach, ganglia, and otocysts posteriorly,
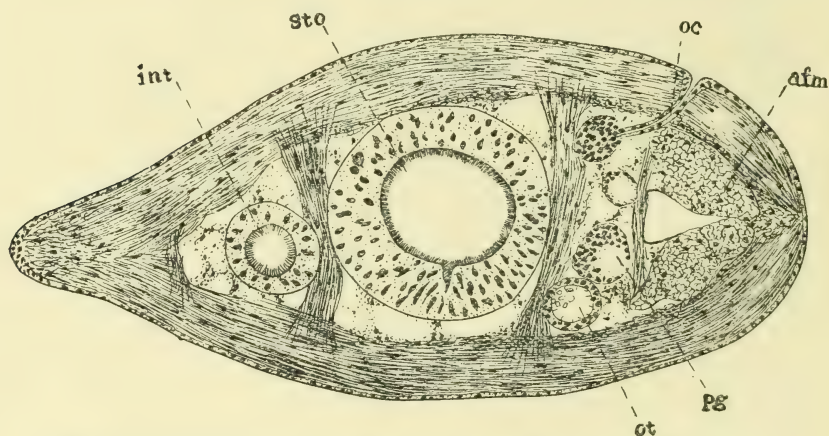
TEXT-FIG. W.—Horizontal section of the foot of an adult Nucula delphi-
nodonta. The otocystic canals leave the dorsal side of the otocysts, so
that in this section only the dorsal wall of the otocyst is seen on the side
where the canal is present. *afm.* Anterior foot muscles. *int.* Intestine.
oc. Otocystic canal. *ot.* Otocyst. *pg.* Pedal ganglion. *sto.* Stomach.

and caused the otocystic canals to take up this position, but reference to fig. 64 will show that before these muscles become very large the otocystic canals open further toward the anterior than when these muscles become highly developed (Text-fig. W). This seems to show that the muscles, as they develop, project anteriorly, and do not affect the organs lying behind them.

In a former publication (1) I have described the imperfect

otocystic canals of Yoldia limatula. The canals are short and do not reach the surface of the foot. Frequently a number of closed pouches are connected with the end of each otocystic canal by a strand of fibrous material (Text-fig. X). Stempell reports that the otocystic canals of Leda pella are very rudimentary. He has never been able to trace them with certainty to the surface skin (**17**). The conditions illustrated by these two forms can easily be explained as the result of degeneration, but there is no direct evidence that this is the case. If the canals are not remnants of the original invaginations, the imperfect canals may be structures that have never been perfect canals, or they may indicate the degeneration of canals that have at some time been perfect.

The nerve-supply of the otocysts has been discussed in connection with the nervous system. It seems possible that
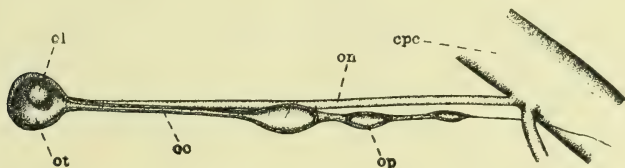
Text-fig. X.—Otocyst of Yoldia limatula. *cpc.* Cerebro-pedal commissure. *oc.* Otocystic canal. *ol.* Otolith. *on.* Otocystic nerve. *op.* Otocystic pouch. *ot.* Otocyst.

the dorsal roots of the cerebro-pedal commissures may be the central ends of the otocystic nerves.

Muscular System.

For convenience in treating the subject the muscles may be grouped into those concerned in shutting the shell, in moving the foot, in propelling blood, in retracting the margins of the mantle, in retracting the palp appendages, and in raising the gills. Beside these muscles, there are many scattered and interlacing fibres that are concerned in making many of the movements.

The anterior adductor muscle (figs. 25 and 36, *aa.*) is formed somewhat earlier than the posterior adductor muscle, and throughout life the former is larger than the latter (fig. 48). When the anterior adductor muscle is first formed (fig. 25, *aa.*), it occupies a position at the anterior end of the dorsal space, very near the apical plate. Soon after the test is shed, it becomes surrounded by tissue that is drawn up around it (figs. 35 and 39, *aa.*). The posterior adductor muscle is formed soon after the test is shed (fig. 39, *pa.*). It lies ventral to the intestine, and posterior to the visceral ganglia, and from its first appearance is surrounded by other tissue.

In the adult the adductors are attached to the shell, with their dorsal borders very near the ends of the rows of teeth. The function of these muscles is simply to close the shell. The contraction of the muscles, and the consequent closing of the shell, compresses an elastic pad known as the cartilage, that lies in the cartilage pit. As soon as the adductor muscles relax, the expansion of this piece of cartilage opens the shell. The epidermis is not thickened to form a prominent external ligament.

The foot is attached to the shell by three pairs of well-developed foot muscles, and by a number of fibres that form a more or less connected series on each side, ventral to the genital organ and liver. Of the three pairs of foot muscles, one is posterior and two are anterior. The posterior muscles are inserted on the shell along the bases of the teeth, anterior and dorsal to the posterior adductor muscle. They extend anteriorly and ventrally along the sides of the foot, and form the strong retractors of the foot. The two pairs of anterior foot muscles are attached to the shell close together, along the bases of the teeth, posterior and dorsal to the anterior adductor muscle. In distribution, the anterior pair of these muscles correspond to the two anterior pairs in Yoldia. They spread out along the sides of the foot, and are distributed to its posterior and ventral portions. The more posterior of the two pairs of muscles passes between the pair

just mentioned, and is distributed to the anterior and ventral portions of the foot.

All of these muscles are closely bound together by their own fibres and by interlacing fibres, so that many movements occur that cannot be explained by direct pulls of one or more muscles. It should be remembered that the attachments of the fibres are all along the sides of the foot, and that many, if not most of the muscle-fibres, pull from one part of the body-wall to another, without changing the relation of the body to the shell. Thus the muscular side flaps of the foot can be spread apart after the animal has been removed from the shell.

Between the muscles, loose connective tissue and large blood-spaces occur. Many of the movements, especially those that result in the protrusion of the foot, seem to depend on the action of muscles on the fluids of the body, more especially upon the blood contained in the spaces of the foot. By obliterating some channels and forcing blood into others, different results may be obtained.

The muscle-fibres that are attached to the shell along the ventral border of the genital mass and liver are distributed to the body-wall. They are not as numerous as they are in Yoldia. I have found no indication of a special muscle at the posterior end of each series, as is the case with Yoldia (**3**).

The heart is largely made up of interlacing muscle-fibres. Each auricle is separated from the ventricle by a constriction (figs. 68 and 69, *h.*). It seems probable that, when the ventricle begins to contract, the contraction of the muscles in these constrictions closes the openings between the ventricle and the auricles so that the blood cannot flow back into them. Where the auricles join the blood-spaces of the gills and mantle lobes, the muscles probably act in the same way.

There are some muscle-fibres in the suspensory membranes of the gills that probably contract at intervals. The opaque shells make it impossible to watch the movements of the gills, but it will be seen that such movements as are made must

force some of the blood out of the blood-spaces of the sus-
pensory membranes. The movements are not enough to form
strong currents of water, such as are formed by Yoldia (1).

The margins of the lobes of the mantles are never pro-
truded far beyond the margins of the valves of the shell, and
the pallial muscles are accordingly not excessively developed.

Each of the large palp appendages is supplied with a
rather large muscle that is continued into it from the body-
wall. It occupies the ventral (morphologically outer) side of
the appendage (fig. 66, *lm.*), and is continued to its tip. This
muscle serves to retract the appendage. Its position in the
appendage is such that when the appendage is strongly
retracted it is curled as shown in fig. 48. The muscle seems
to be homologous with fibres that extend into the membrane
that suspends the palps from the body-wall.

Excretory Organs.

Just before embryos reach the stage where the second gill
filaments begin to flatten, preparatory to forming the third
gill filaments, a pair of narrow tubes appear just anterior to
the visceral ganglia and ventral to the pericardium. The
two tubes touch each other on the median line of the body,
but their cavities do not seem to communicate. Laterally
they are extended to the surface of the body, where they open
into the mantle chamber. This is the earliest stage in which
I have been able to distinguish the kidneys. I have not
succeeded in determining whether the external openings are
present from the beginning, or whether they are formed later.
I am inclined toward the view that the kidneys are meso-
dermal in their origin; but this view is based simply on the
length and narrowness of the tubes when they can first be
distinguished. They may be formed as invaginations from
the surface.

The cells forming the walls of the kidneys soon become
large and vacuolated. This character is retained throughout
the life of the animal, and makes the tracing of their cavities

in some places a very difficult matter.   Near the outer end of each kidney the cells are smaller, and the lumen is more easily traced.   As the kidneys grow, they extend anteriorly and crowd dorsally beneath the pericardium and heart.   As growth continues they become bent into loops, and numerous side pouches are formed.

Although much time has been spent in trying to find the inner, pericardial openings of the kidneys, I have not succeeded in placing them.   Cavities leading from the pericardium have frequently been traced nearly to the kidneys, but the vacuolated condition of the cells that compose their walls makes it very difficult to trace cavities with accuracy. I have no reason to suppose that the pericardial openings do not exist.   I have simply been unable to find them.

In the adult, the ducts of the genital organs pass close to the lateral extremities of the pericardium.   Near its end each duct turns toward the median line, meets the outer end of the kidney on the same side of the body, and opens with it into the mantle chamber.   This connection is easy to demonstrate. Whether the genital ducts also communicate with the pericardium, or with the inner ends of the kidneys, I am not prepared to say.

Genital Organs.

The genital organs appear after the animal has become adult in most other respects.   Each genital organ consists, at first, of a short and rather narrow tube that lies close to the pericardium, for the most part in contact with it. Whether this tube originates from the pericardium, or whether it is formed in some other way, has not been determined.   The genital organs grow rapidly, and extend anteriorly and dorsally over and among the lobules of the liver, which are now very numerous.   Soon the eggs and sperm begin to be formed, and the sexes can be distinguished.   The eggs are few in number, but they are large and brown.   The sperm are very numerous, of moderate size, and pale yellow.

These colours are imparted to the genital organs.   As their
products begin to mature, the genital organs become very
extensive and crowd between and around other organs, until
all available space is filled.

The genital ducts of the adult, as in the young, connect
with the outer ends of the kidneys, and with them open into
the mantle chamber.

Summary.

The young embryos of Nucula delphinodonta and
Yoldia limatula resemble each other in most respects.
They differ considerably in appearance, because of the dif-
ference in the size and distribution of the surface cilia.   In
the case of Yoldia the apical cilia are long and bunched to-
gether, and the cilia on the three intermediate rows of test-
cells are collected into bands (Text-fig. F).   In Nucula
delphinodonta all of the cilia on the surface of the embryo
are short and evenly scattered (Text-fig. E).   The embryos
of Yoldia swim freely in the water, and have to depend on
their own activities for safety.   The embryos of Nucula
delphinodonta develop in a protecting brood-sac (fig. 1).
It is to the advantage of these embryos to remain in the
brood-sac, so active locomotion would not only be of no
value, but it would be a positive danger.   The possession of
a test that is not functional as an organ of locomotion pro-
bably indicates that the embryos of the ancestors of Nucula
delphinodonta were free-swimming.   They then probably
corresponded closely in appearance to the embryos of Yoldia
limatula and Nucula proxima, both of which have the
apical tuft and the bands of cilia.

The presence of a separate anal opening in the test, an ex-
tensive apical plate, and the formation of the cerebral ganglia
without invaginations (fig. 24), are points in which Nucula
delphinodonta differs from Yoldia.   Nucula delphino-
donta sheds its test when the foot is very immature.

The development of many of the organs of Yoldia has not

been traced. The following is a brief review of the organs of Nucula delphinodonta.

Test.—The test consists of five rows of flattened cells, that together cover the greater portion of the body of the embryo. The cilia on the test are short and evenly distributed. The size and distribution of the cilia are probably the result of the protection afforded the developing embryo by the brood-sac. The test is finally thrown away. It is probably homologous to the velum of most Lamellibranch embryos. (See pp. 335—339, and figs. 11, 24, 25, 34, and 35.)

Apical Plate.—The apical plate is quite extensive, and bears short diffuse cilia that resemble the cilia on the test cells. The size of the apical cilia is probably also the result of the protection afforded the developing embryo by the brood-sac. The apical plate is thrown away with the test. (See p. 339, and figs. 11 and 24.)

Shell.—The shell begins to form some time before the test is shed. The prodissoconch has a rounded outline and a short straight hinge-line. The adult shell is very robust. (See pp. 339—341, and figs. 20, 36, 50, and 51.)

Mantle.—The mantle lobes are formed by the growth and folding of the shell-gland. There are no tentacles on the margins of the mantle, and no siphons are formed. (See pp. 341, 342, and figs. 8, 17, 20, 48, and 69.)

Foot.—The foot is formed by the growth of tissue that, at first, lies between the stomodæum and the gut. At the time the test is shed it is very small and cannot be moved. The side flaps are developed as the result of unequal growth of the ventral side of the foot. The foot is a remarkably good burrowing organ, and it seems never to be used in creeping. (See pp. 342—346, and figs. 25, 28, 34, 36, 39, 40, 41, 48, 49, and 69.)

Byssal Gland.—The byssal gland is formed as an invagination on the ventral surface of the foot soon after the test is shed. It becomes very extensive, but in the adult is quite small. It seems never to form fibres. (See pp. 346, 347, and figs. 39, 40, 41, 45, and 48.)

Alimentary Canal.—The primitive gut is formed by the separation and division of cells on one side of the embryo. It is carried further into the interior by the addition of cells around the blastopore. These cells form the stomodæum. Later the gut grows posteriorly, beneath the shell-gland, and forms the stomach and intestine. The anus opens into the mantle chamber near the anal pore in the test. The future shape of the intestine seems to depend upon the position of certain organs during its elongation. (See pp. 347—353, and figs. 8, 9, 11, 15, 24, 25, 34, 36, 40, 45, 46, 47, and 48, and Text-figs. M to S.)

Labial Palps.—The labial palps are marked out as patches of cilia about the time that the third lobe of the gill begins to form (fig. 41). The ciliated patches along the sides of the body are bent so as to form grooves (fig. 62, *lp*.); the dorsal portions of the patches form the outer palps, and the ventral portions the inner palps. The palp appendages are formed by unequal growth of the posterior portion of the outer palps, and each corresponds morphologically to a pair of ridges with a groove between them. They can be extended beyond the margins of the shell, and they are used as food collectors. (See pp. 353—357, and figs. 41, 45, 47, 48, 54, 55, 56, 57, 58, 59, 60, 62, and 66.)

Gills.—The gills are formed as folds on the inner sides of the lobes of the mantle. The folds form lobes that grow to form filaments and finally plates. The inner plates are formed first. The outer plates are formed by growth at the bases of the inner plates. A study of their development throws no light on the phylogeny of the gills. (See pp. 357—363, and figs. 39, 40, 41, 45, 48, 52, and 53.)

Hypobranchial Glands.—The hypobranchial glands are formed about the time that the animals become sexually mature. They seem to furnish the secretions from which the brood-sac is formed, and they may have other functions. (See pp. 363—365.)

Pericardium.—The pericardium is a remnant of a cavity that probably represents a schizocœle. Its epithelial lining

seems to be formed by the rearrangement of mesodermal cells. (See pp. 365—367, and figs. 24, 26, 28, 34, 35, 36, 39, 41, and 48.)

Vascular System.—The heart is formed as a mesodermal strand that stretches across the pericardium from one side to the other. There is no indication that it is formed by the fusion of either a pair of pouches or two masses of cells. It seems to be single in its origin. It is formed around the intestine, but later becomes free and dorsal to it. This seems to show that for this group, at least, the dorsal position of the heart as found in the adult is not primitive. The vascular system consists largely of spaces that occur in all parts of the body. (See pp. 367—370, and figs. 41, 48, 67, 68, and 69.)

Nervous System.—The cerebral and pedal ganglia are about equal in size, and the visceral ganglia are considerably smaller. The cerebro-visceral commissures are very large, and contain many scattered nuclei. The cerebro-pedal commissures show ordinary structure. It is suggested that the smaller, dorsal roots of the cerebro-pedal commissures may be the central ends of the otocystic nerves. (See pp. 370—374, and figs. 24, 34, 36, 40, 46, and 48.)

Otocysts.—The otocysts are formed as invaginations from the body-wall soon after the test is shed. They seem to be entirely closed off, but canals connecting them with the surface are present in the adult. The otoliths are irregular bodies, but they are probably formed in the otocysts themselves. (See pp. 375—377, and figs. 40, 46, 48, and 64, and Text-fig. W.)

Muscular System.—The muscular system is well developed, and resembles the muscular system of Yoldia in most respects. The extensive attachments of the foot muscles to the dorsal portion of the shell is accounted for by the great development of these muscles. (See pp. 377—380.)

Excretory Organs.—The vacuolated character of the cells of the excretory organs makes it difficult to trace some portions of the cavities of these organs. The inner peri-

cardial openings are hard to find. The outer end of each excretory organ opens into the mantle chamber, in connection with the genital duct of the same side. (See pp. 380, 381.)

Genital Organs.—The genital organs are formed after the animal is adult in most other respects. They can first be distinguished as short tubes that lie very close to, or in contact with, the pericardium, and open into the mantle chamber in connection with the outer ends of the kidneys. The genital organs become very extensive in the adult. The sexes are separate. (See pp. 381, 382.)

Most of the work necessary for the preparation of this paper was done in the Biological Laboratory of the Johns Hopkins University. To many that are now or formerly were connected with that laboratory, and especially to Professor W. K. Brooks, I am indebted for suggestions and encouragement. I also desire to express my appreciation of the courtesies extended to me by Professor C. O. Whitman, at the Marine Biological Laboratory. I am particularly indebted to my wife, who has, among other things, performed a great share of the work connected with the care and preservation of material. Beside the work at the sea-shore, embryos obtained in June were kept alive in Baltimore from October 1st until January 1st, with water sent from the sea.

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EXPLANATION OF PLATES 20—25,

Illustrating Mr. Gilman A. Drew's paper on " The Life-History of Nucula delphinodonta (Mighels)."

Reference Letters.

aa. Anterior adductor muscle. *aas.* Anterior adductor muscle-scar. *ap.* Apical plate. *bg.* Byssal gland. *bs.* Blood-space. *ca.* Cartilage. *cg.*

Cerebral ganglion. *cp.* Cartilage pit. *cs.* Chitinous support. *ec.* Ectoderm. *f.* Foot. *g.* Gill. *gs.* Suspensory membrane of gill. *h.* Heart. *int.* Intestine. *ip.* Inner plate of the gill. *ilp.* Inner labial palp. *k.* Kidney. *l.* Liver. *lm.* Longitudinal muscle. *lp.* Labial palp. *m.* Mantle. *mg.* Midgut. *mo.* Mouth. *oes.* Œsophagus. *olp.* Outer labial palp. *op.* Outer plate of the gill. *ot.* Otocyst. *pa.* Posterior adductor muscle. *pap.* Palp appendage. *pas.* Posterior adductor muscle-scar. *pg.* Pedal ganglion. *pn.* Palp nerve. *sg.* Shell-gland. *std.* Stomodæum. *sto.* Stomach. *t.* Test. *tc.* Cavities in the mantle caused by teeth on the shell. *v.* An organ of unknown function. *vg.* Visceral ganglion. *y.* Cut wall of gill plate. *z.* Scattered cells of the disorganised liver.

PLATE 20.

Fig. 1.—Adult specimen with the brood-sac attached. The brood-sac is torn open to show the eggs inside. × 10.

Fig. 2.—Sixteen-celled stage. × 150.

Fig. 3.—Section of an embryo in the sixteen-celled stage. × 275.

Fig. 4.—Section of a later cleavage stage that corresponds to an epibolic gastrula. The asterisk (*) marks the position where the gut is formed. × 275.

Fig. 5.—An embryo that is slightly older than the one represented in section by Fig. 4. × 150.

Fig. 6.—Lateral view of an embryo in which the gut has been formed, represented as a slightly transparent object. From the study of preserved material I am inclined to think that the shell-gland does not bear cilia, but this has not been determined on living material. The line marked 7 indicates the plane in which the section, Fig. 7, was taken. × 150.

Fig. 7.—Transverse section of an embryo in the stage represented by Fig. 6. The line 7, on Fig. 6, indicates the plane of the section. × 275.

Fig. 8.—Sagittal section of an embryo in the stage represented by Fig. 6. × 275.

Fig. 9.—Sagittal section of an embryo slightly older than the embryo of which Fig. 8 is a section. It represents the beginning of the formation of the stomodæum. × 275.

Fig. 10.—Dorsal view of an embryo in which the test is growing over the shell-gland. The lines numbered 11, 12, and 13 indicate the planes of sections represented in corresponding figures. × 150.

Fig. 11.—Sagittal section of an embryo in the stage represented by Fig. 10. The line 11 on Fig. 10 indicates the plane of the section. × 275.

Figs. 12 and 13.—Transverse sections of an embryo in the stage represented by Fig. 10. The lines 12 and 13 on Fig. 10 indicate the planes of the sections. × 275.

PLATE 21.

FIG. 14.—Lateral view of an embryo in which the test is fully formed, represented as a slightly transparent object. The lines numbered 16, 17, 18, and 19 indicate the planes of sections represented in corresponding figures. × 150.

FIG. 15.—Sagittal section of an embryo in the stage represented by Fig. 14. The anterior ends point in opposite directions in the two figures. × 275.

FIGS. 16, 17, 18, and 19.—Transverse sections of an embryo in the stage represented by Fig. 14. The lines 16, 17, 18, and 19 on Fig. 14 indicate the planes of the sections represented by these figures. × 275.

FIGS. 20, 21, and 22.—Transverse sections of an embryo older than the one represented by Fig. 14, and a little younger than the embryo represented by Fig. 23. The lines 20, 21, and 22 on Fig. 23 represent planes that correspond to these sections. × 275.

FIG. 23.—Lateral view of an embryo in which the mantle is beginning to form, represented as a slightly transparent object. The lines 20, 21, and 22 indicate the planes of sections represented in corresponding figures, but the embryo represented in Fig. 23 is slightly older than the one from which these sections were obtained. × 150.

FIG. 24.—Sagittal section of an embryo in the stage represented by Fig. 23. × 275:

FIG. 25.—Lateral view of an embryo that would soon shed its test. The test cells, indicated in outline, are very indistinct, and are not accurately drawn. Cilia have been indicated along the margins only. They cover the whole of the surface. The organs are more clearly shown than in preceding figures of embryos. They are not visible in whole mounts, but have been reconstructed from sections. The lines 27, 28, 29, 30, 31, 32, and 33 indicate the planes of sections represented by these figures. (See Plate 22.) × 150.

PLATE 22.

FIG. 26.—Sagittal section of an embryo in the stage represented by Fig. 25, Pl. 21. × 275.

FIGS. 27, 28, and 29.—Transverse section of an embryo in the stage represented by Fig. 25, Pl. 21. The lines numbered 27, 28, and 29 on Fig. 25 indicate the planes of sections represented by these figures. × 275.

FIGS. 30, 31, 32, and 33.—Horizontal sections of an embryo in the stage represented by Fig. 25, Pl. 21. The lines numbered 30, 31, 32, and 33 on Fig. 25 indicate the planes of the sections represented by these figures. × 275.

PLATE 23.

FIG. 34.—Lateral view of a reconstruction of an embryo that has just com-

pleted the first step in the process of casting. The test cells, apical plate, and stomodæum still adhere to the anterior end of the embryo.   × 150.

FIG. 35.—Lateral view of a reconstruction of an embryo that has completed the process of casting.   × 150.

FIG. 36.—Lateral view of a reconstruction of an embryo in which the liver pouches have begun to go to pieces.   × 150.

FIG. 37.—Sagittal section of an embryo in the stage represented by Fig. 36.   × 275.

FIG. 38.—Transverse section of an embryo in the stage represented by Fig. 36, taken through the stomach just posterior to the pedal ganglia.   × 275.

FIG. 39.—Lateral view of a reconstruction of an embryo that is just beginning to form the gills.   × 150.

FIG. 40.—Lateral view of a reconstruction of an embryo in which each gill is beginning to form two lobes.   × 150.

FIG. 41.—Lateral view of a reconstruction of an embryo in which each gill is beginning to form its third lobe.   × 150.

FIG. 42.—Horizontal section of an embryo in a stage represented by Fig. 40, taken through the dorsal end of the stomach and the re-forming lobes of the liver.   × 200.

FIG. 43.—Horizontal section of an embryo in the stage represented by Fig. 41, taken through the dorsal end of the stomach and the re-forming lobes of the liver.   × 200.

FIG. 44.—Horizontal section of an embryo in the stage represented by Fig. 46, Pl. 24, taken through the dorsal end of the stomach and the re-formed lobes of the liver.   × 150.

PLATE 24.

FIG. 45.—Lateral view of a reconstruction of an embryo in which each gill has four pairs of plates.   × 125.

FIG. 46.—Lateral view of a reconstruction of an embryo in which each gill has six pairs of plates.   × 125.

FIG. 47.—Lateral view of a reconstruction of an embryo in which each gill has eight pairs of plates.   × 110.

FIG. 48.—Lateral view of a reconstruction of an adult specimen.   × 30.

FIG. 49.—Adult specimen with the foot protruded and the side flaps spread apart.   × 10.

FIG. 50.—View of the inside of an adult left shell-valve.   × 15.

FIG. 51.—Left shell-valve seen obliquely from the dorsal margin.   × 15.

FIG. 52.—A nearly horizontal section of an embryo in the stage represented by Fig. 46, cut to show the developing outer plates of the gills.   × 150.

Fig. 53.—A pair of adult gill plates. The suspensory membrane, the continuous chitinous trough, the longitudinal muscle, and the walls of the plates that join the plates next in succession have all been cut across in removing the plates from the gill. (Drawn from a study of sections.) × 250.

PLATE 25.

Figs. 54, 55, and 56.—Stages in the development of the labial palps. The palps have been carefully drawn, but for the sake of clearness they have in each case been represented with the outer palp on the right side turned away from the corresponding inner palp. The foot is represented as cut off, and the specimen is turned so that the mouth can be seen between the palps. × 125.

Fig. 57.—The posterior portions of the right outer and inner palps of an adult specimen. The two palps are represented as spread apart and placed in a position that corresponds with Fig. 56. × 65.

Figs. 58, 59, and 60.—Successive sections of the labial palps of a specimen that has six pairs of gill plates. The sections are taken transverse to the embryo. The stage is much the same as is represented by Fig. 54. Fig. 58 is near the mouth, Fig. 59 is near the posterior end of the outer palp, and Fig. 60 is posterior to the outer palp. × 150.

Fig. 61.—Transverse section of an embryo with four pairs of gill plates (see Fig. 45, Plate 24) taken through the mouth. × 200.

Fig. 62.—Transverse section of an embryo with four pairs of gill plates, taken just anterior to the stomach. × 200.

Fig. 63.—Sagittal section of the antero-dorsal portion of an embryo that has eight pairs of gill plates. × 150.

Fig. 64.—Horizontal section of the foot of an embryo that has six pairs of gill plates, taken just ventral to the mouth. × 150.

Fig. 65.—Horizontal section of the foot of an embryo that has six pairs of gill plates, taken through the mouth. × 150.

Fig. 66.—Transverse section of the palp appendage of an adult specimen. × 200.

Fig. 67.—A nearly transverse section of an embryo that has five pairs of gill plates, taken through the heart. × 200.

Fig. 68.—A diagonal section of an embryo that has nine pairs of gill plates, taken through the heart. × 90.

Fig. 69.—A diagonal section of an adult specimen, taken through the heart. × 45.

Fig. 1.

Fig. 2.

Fig. 5.

Fig. 6.

Fig. 9.

Fig. 10.

Fig. 11.

Fig. 4.

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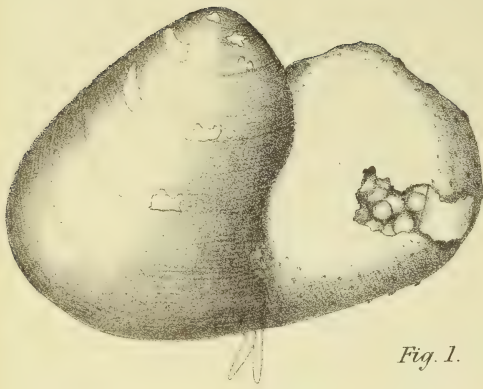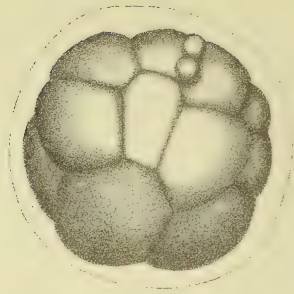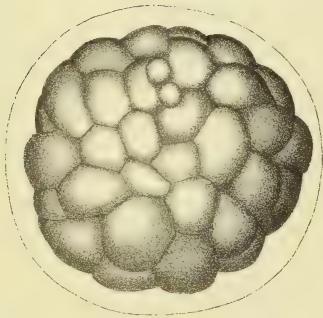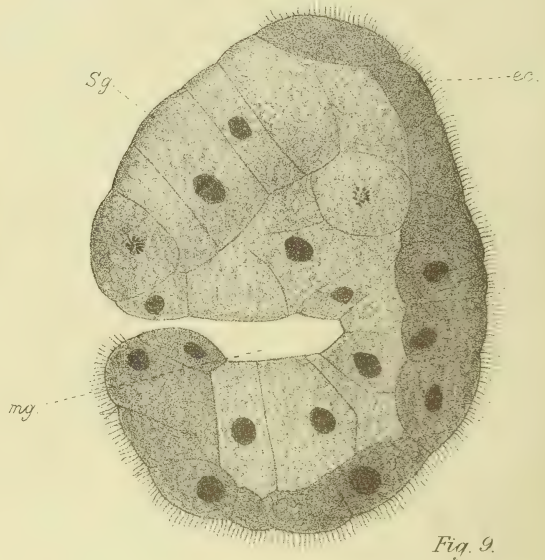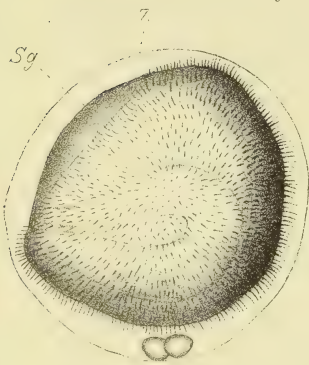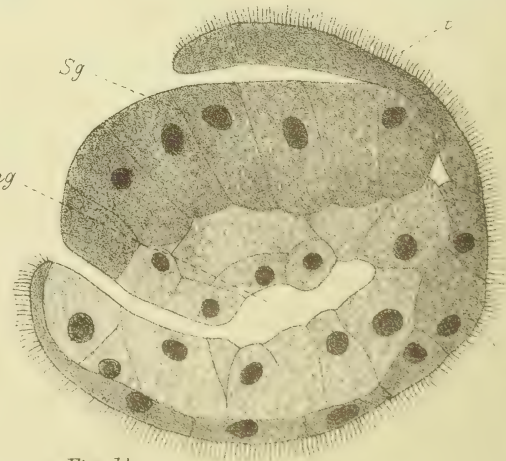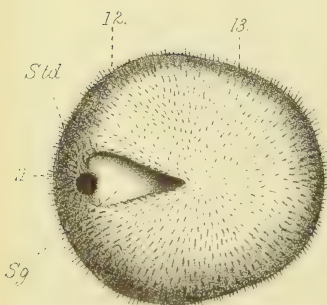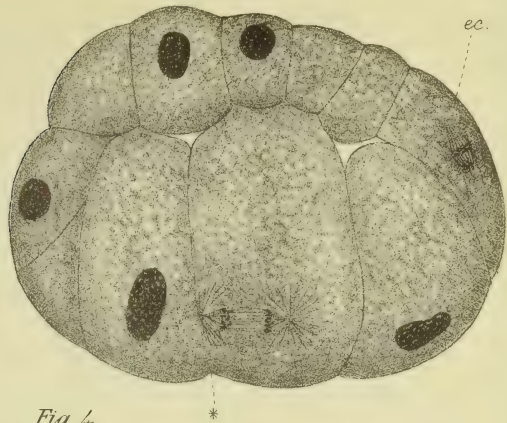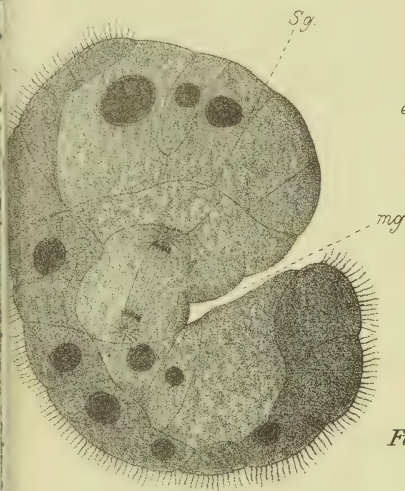
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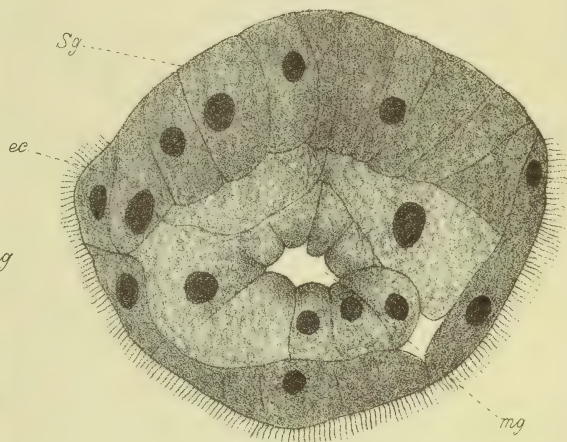
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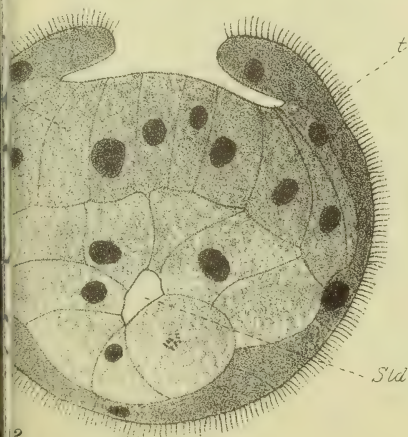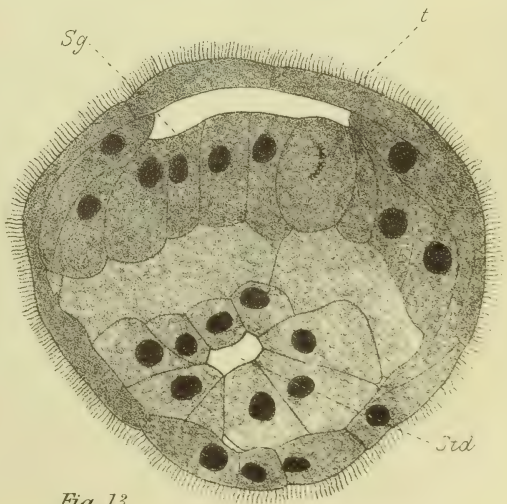
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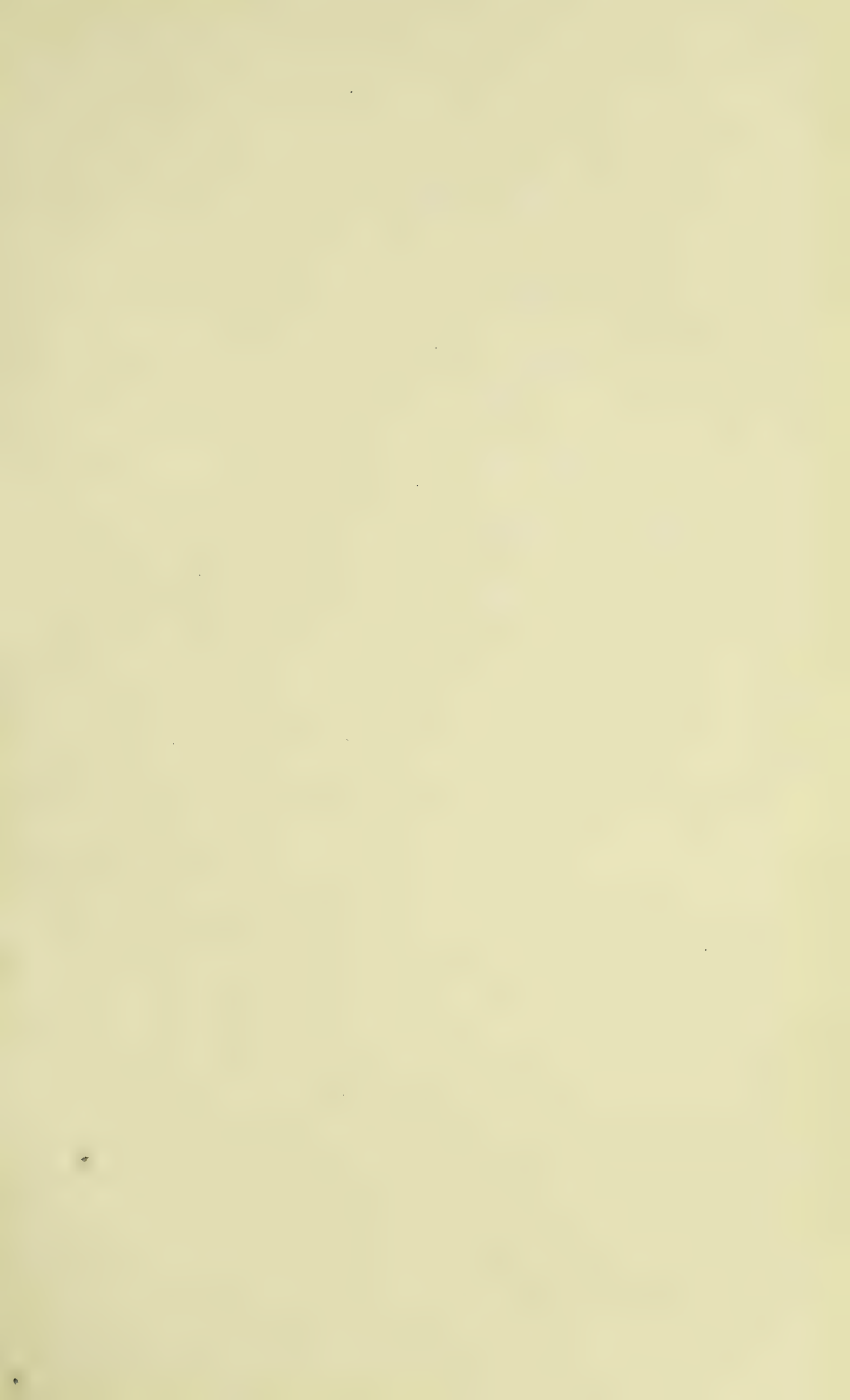
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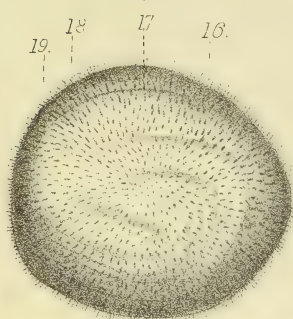
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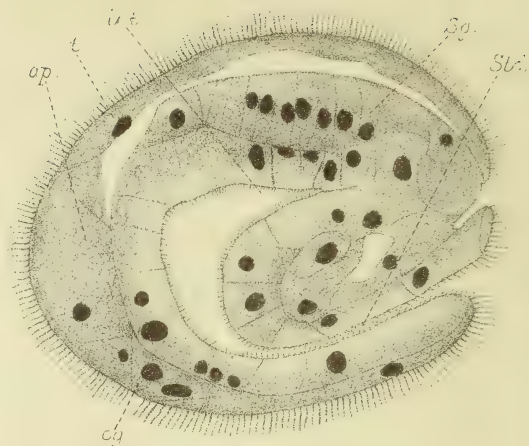
Fig. 23.

Fig. 24.

Fig. 25.

Fig. 22.

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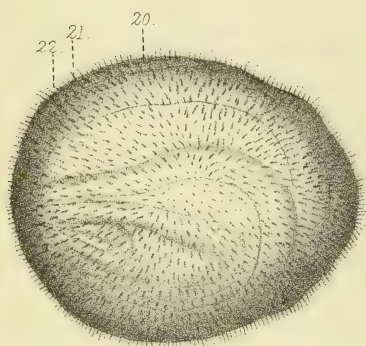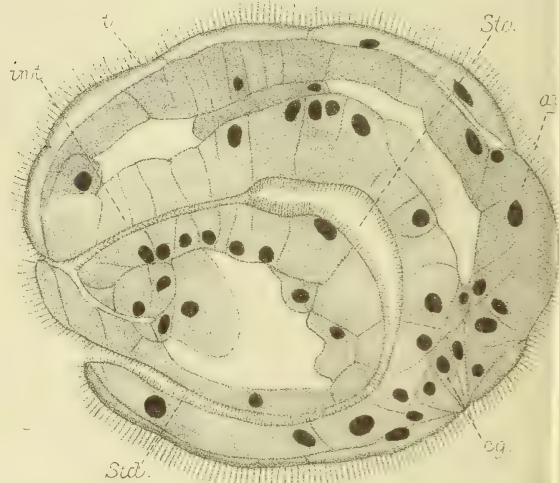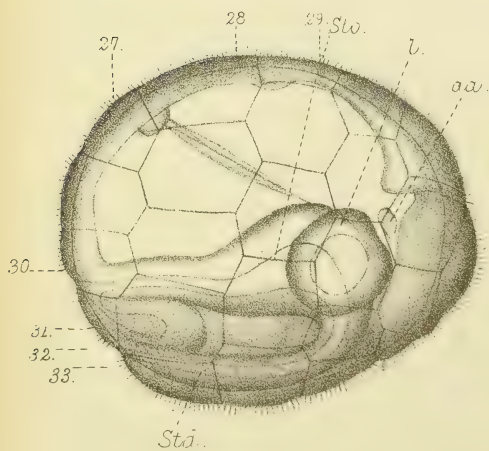
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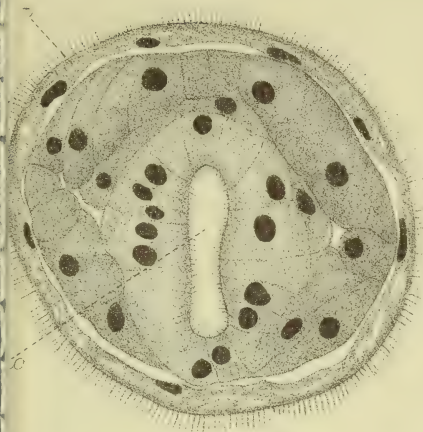
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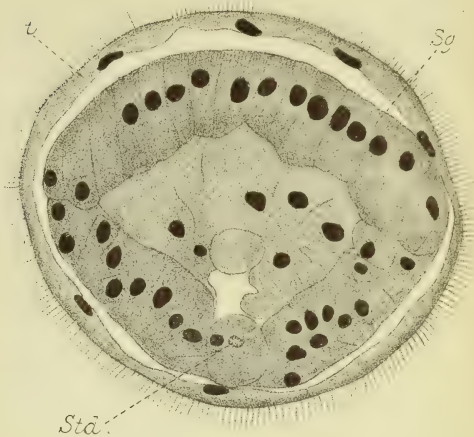
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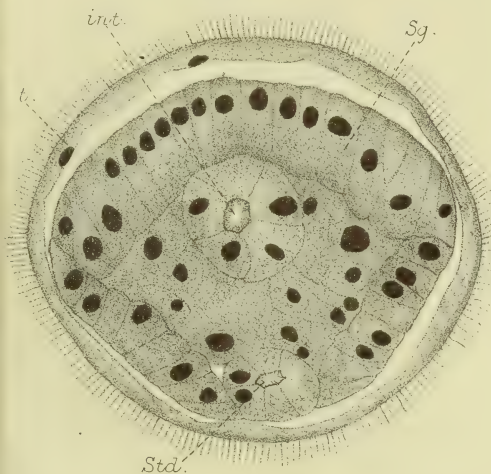
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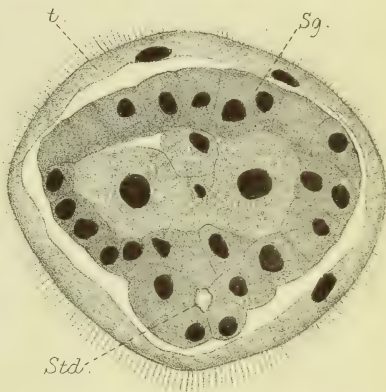
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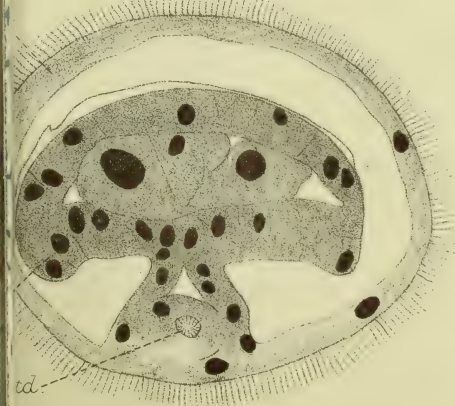
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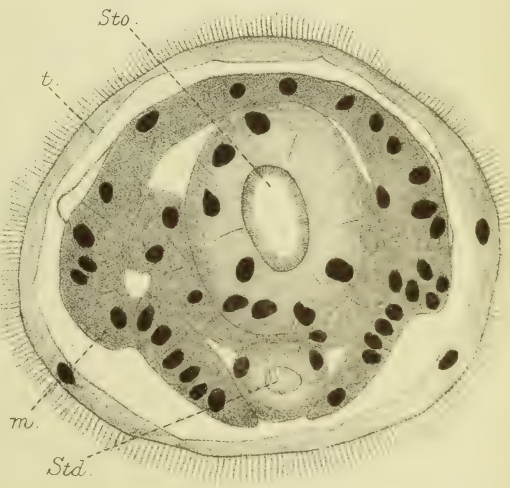
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Fig. 27.

Fig. 30.

Fig. 31.

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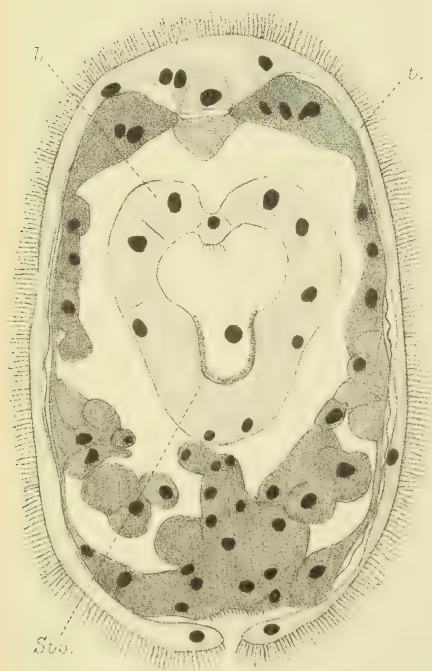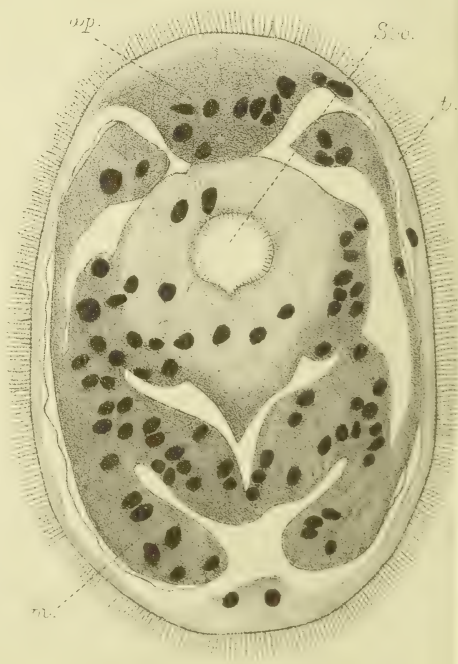
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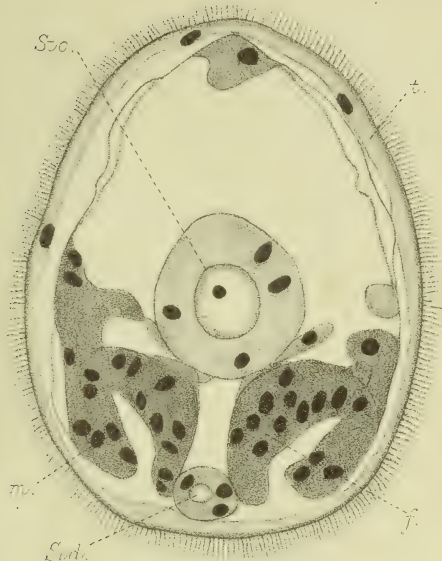
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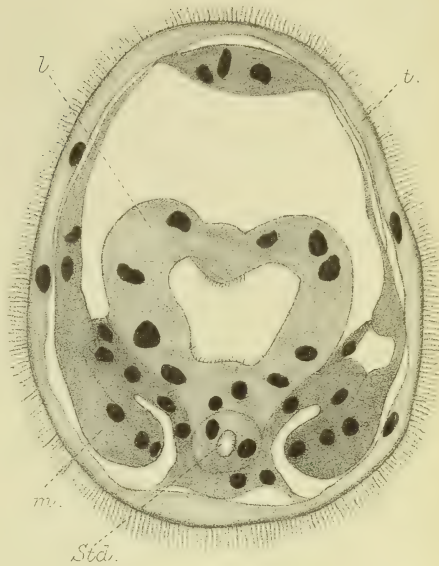
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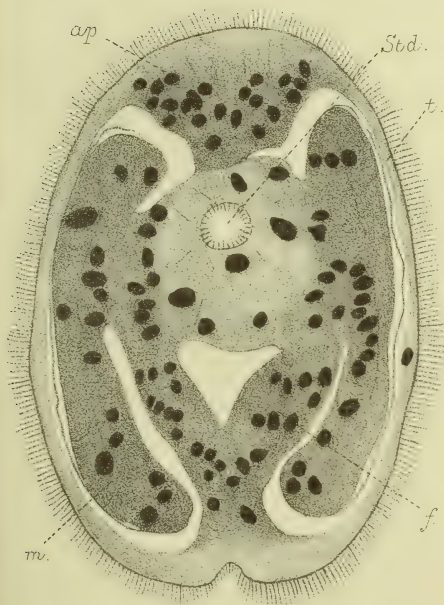
Fig. 33.

Fig. 34.

Fig. 35.

Fig. 36.

Fig. 38.

Fig. 39.

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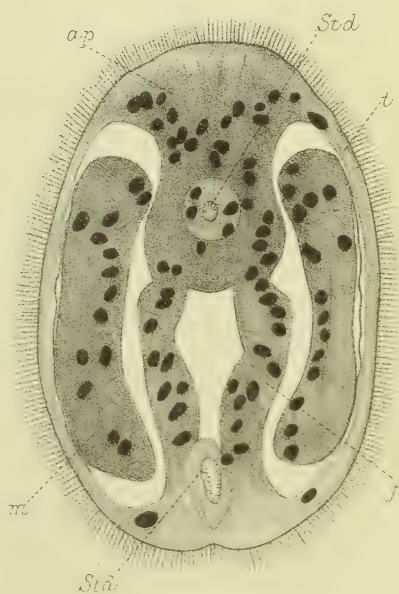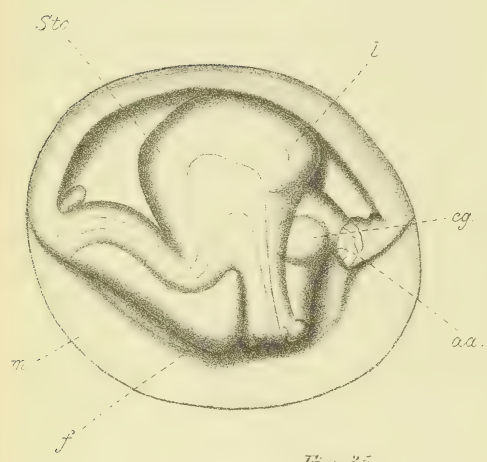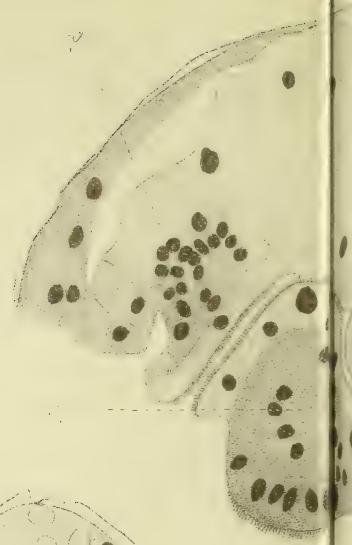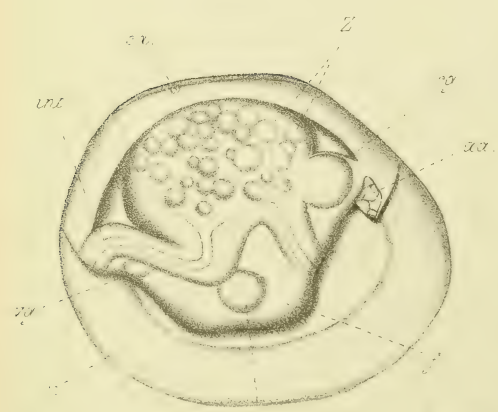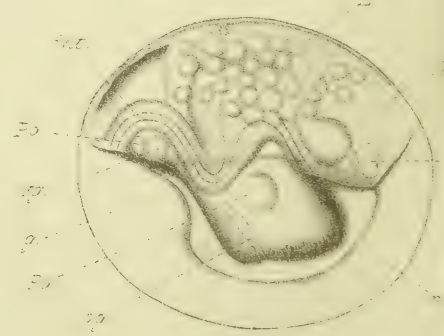
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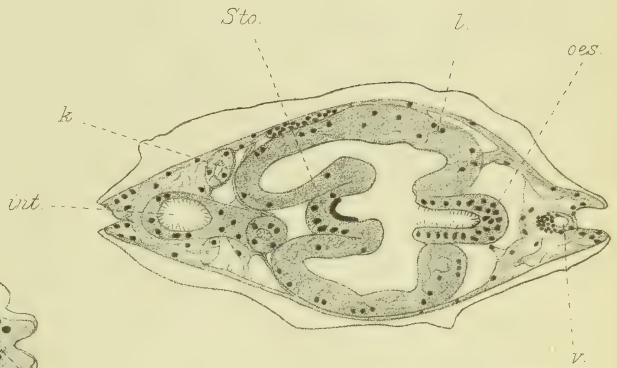
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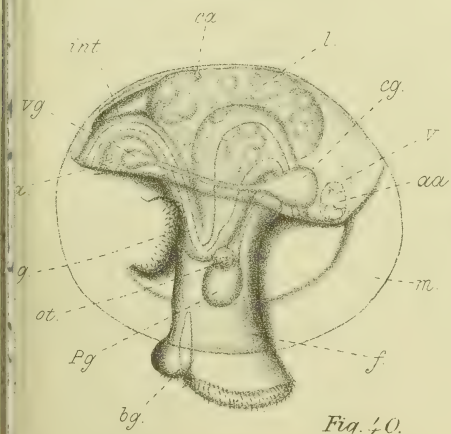
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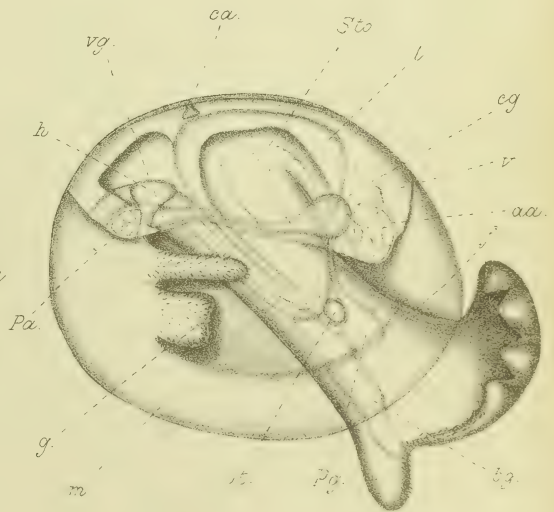
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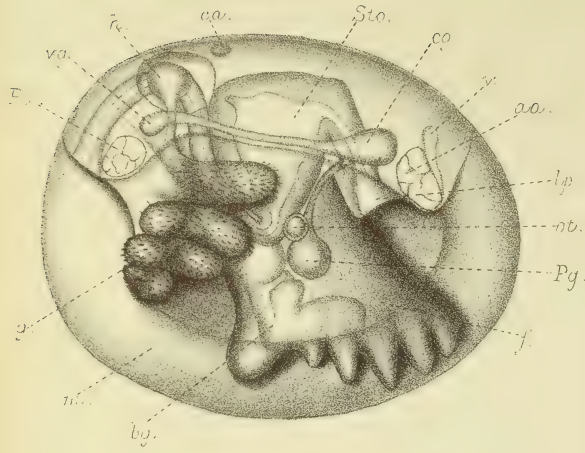
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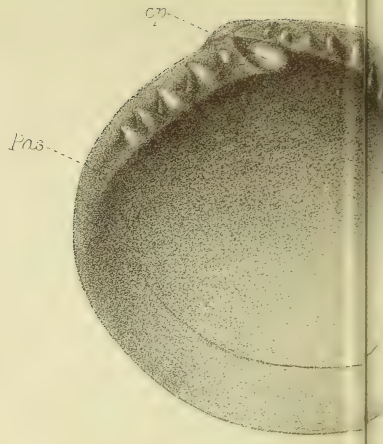
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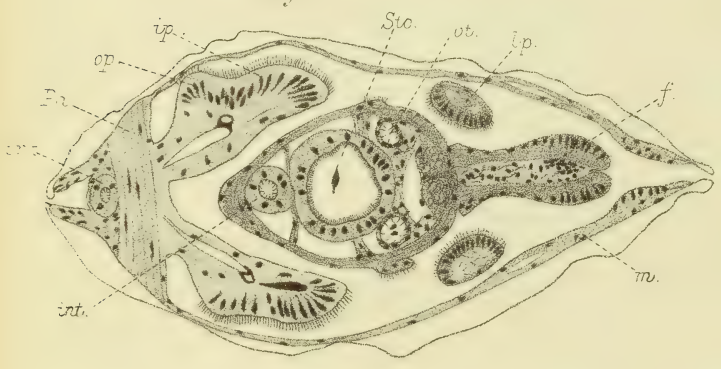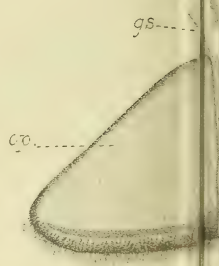
Fig. 48.

Fig. 49.

Fig. 46.

Fig. 51.

Fig. 47.

olp.

ilp.

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f.

Fig. 54.

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olp.

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f.

Fig. 55.

Pn

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Fig. 66.

Sto.

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Fig. 65.

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Fig. 67.

Fig. 68.

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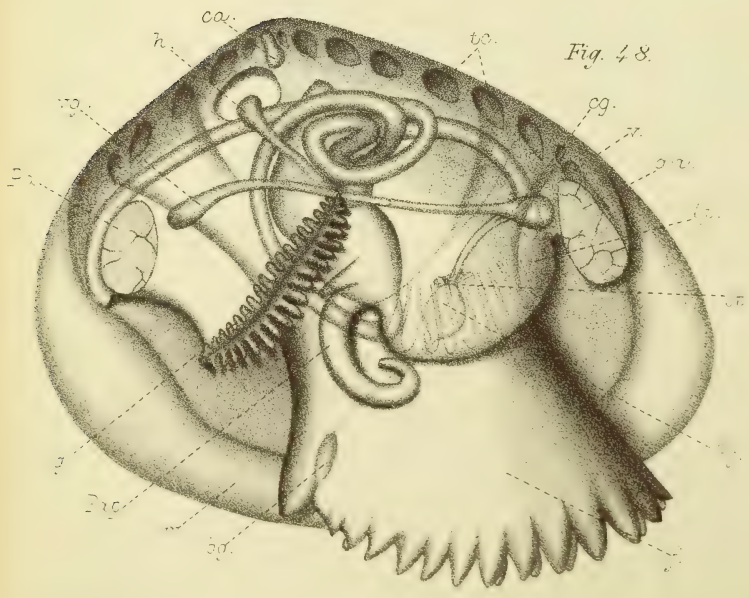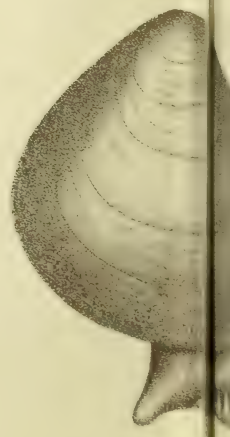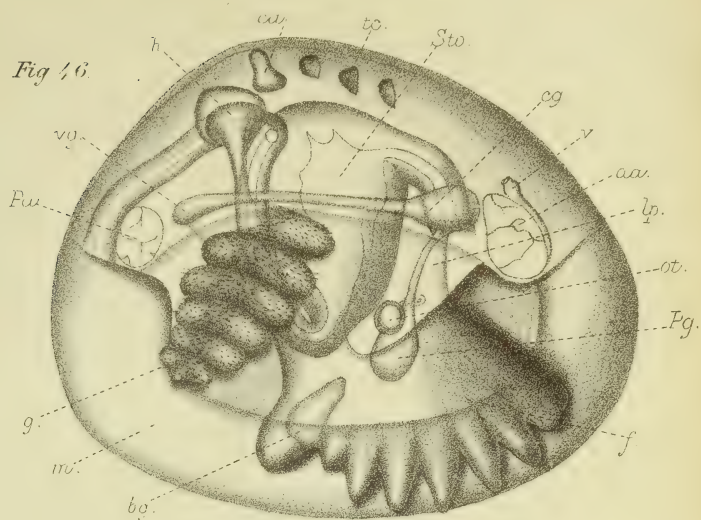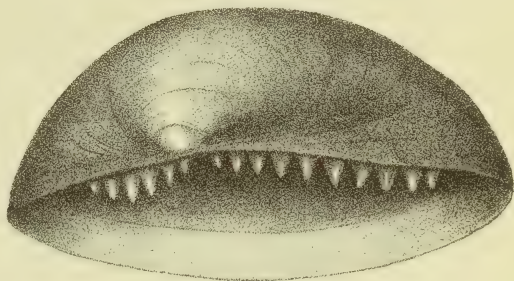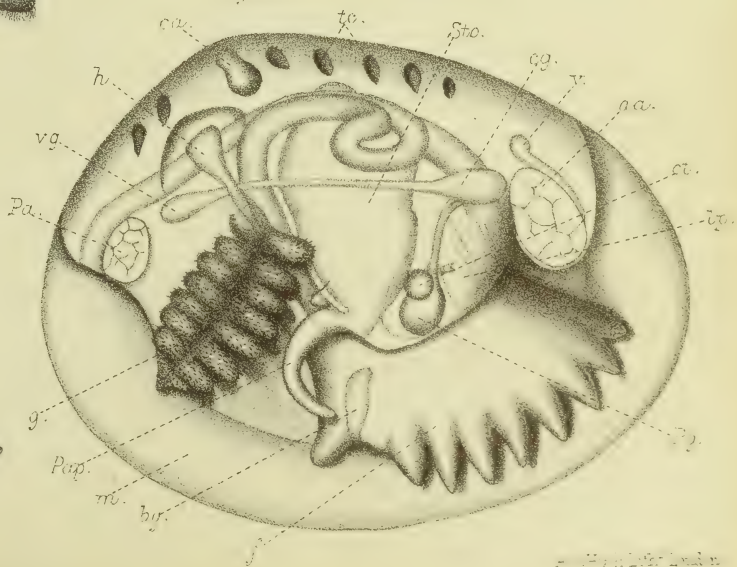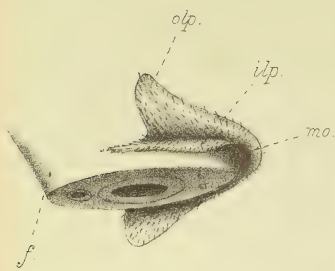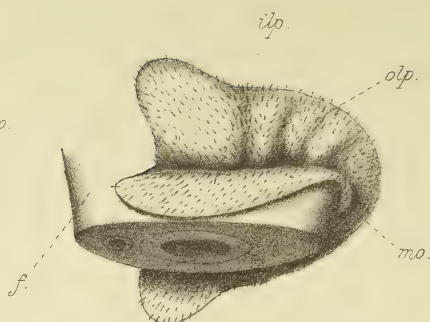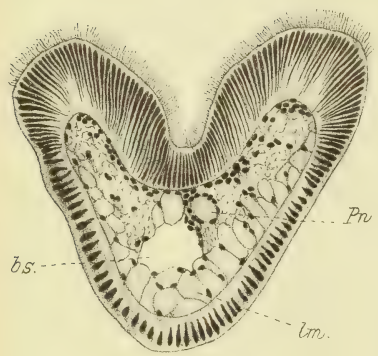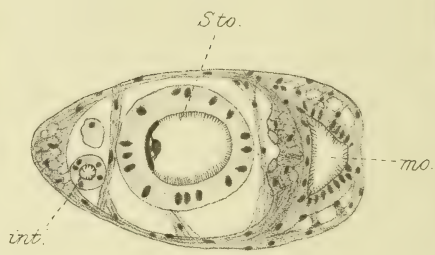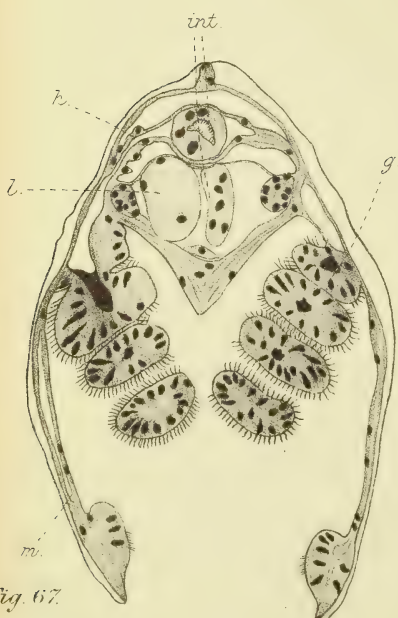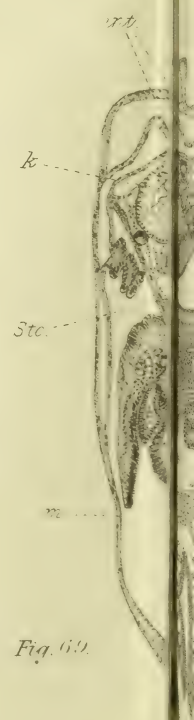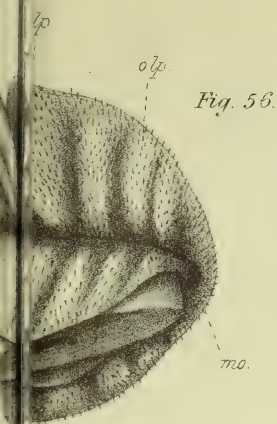
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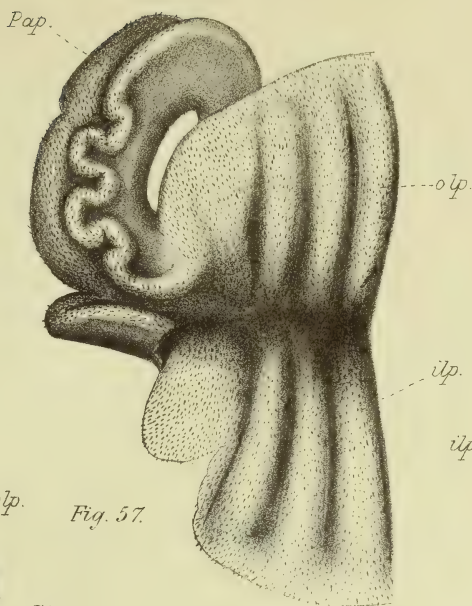
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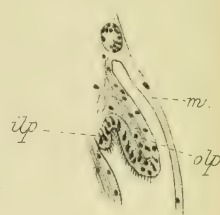
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Fig. 59.

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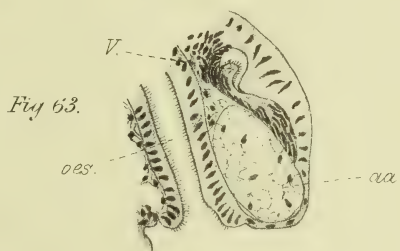
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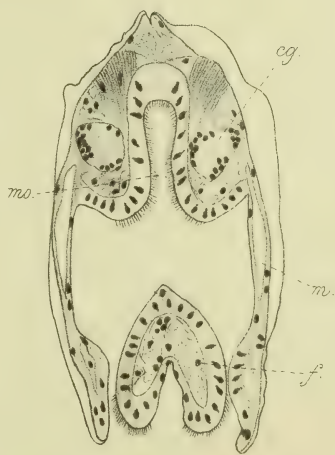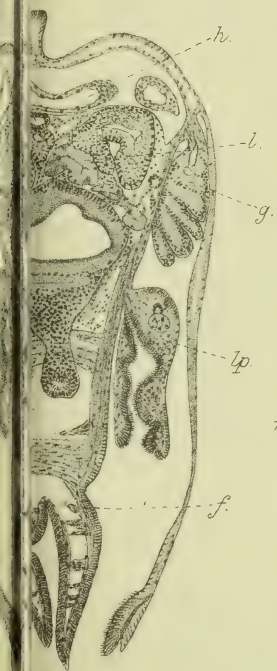
Fig. 61.

Fig. 62.

A.S. Huth. Lith⁵ London
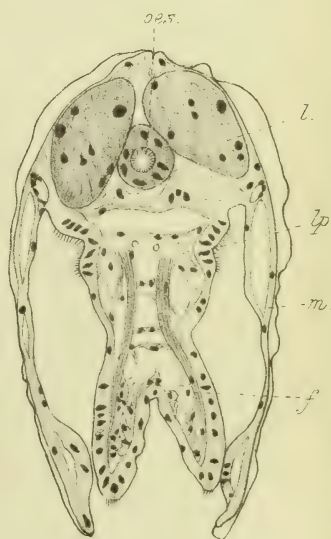
On the Structure of the Hairs of Mylodon Listai and other South American Edentata.

By

W. G. Ridewood, D.Sc., F.L.S.,

Lecturer on Biology at the Medical School of St. Mary's Hospital, London.

With Plate 26.

THE interest attaching to the discovery of portions of well-preserved skin of a great Ground Sloth, very closely allied to if not identical with Mylodon, was considerably increased when it was found that the hairs do not agree in their minute structure with those of the Tree Sloths, Bradypus and Cholœpus. While agreeing with the latter in the absence of a definite medulla, they are destitute of the extra-cortical layer which characterises the hairs of Bradypus, and have not the fluted surface which is such a distinctive feature of the hairs of Cholœpus. The characters of the hairs have been commented upon by several authors in the course of their remarks upon the remains of this ground sloth, but the subject has never been treated exhaustively; and Professor Ray Lankester suggested to me that the matter was worthy of further inquiry, and that it was desirable to compare the newly discovered hairs not only with those of Bradypus and Cholœpus, but also with those of the ant-eaters and armadillos.

The order Edentata, as at present constituted, will probably prove to be an unnatural assemblage of animals, and it may become necessary, when our knowledge is more complete,

to remove the Old World forms Manis and Orycteropus, to constitute two new orders by themselves. For the present purpose, however, the relationships are not material, except for the fact that the late traveller Ramon Lista saw and shot at a curious animal in South America, which he likened to a hairy and scaleless Pangolin. It is generally denied (Ameghino [1], Lönnberg [7, p. 168]) that this " pangolin " was the Mylodon of which the skin and bones have more recently been found.

Accounts of the various pieces of skin discovered have been published by Ameghino (1), Lönnberg (7), Roth (14), Smith Woodward and Moreno (18), and Smith Woodward (19). The locality from which Dr. Ameghino obtained his specimen is not stated, but the other pieces of skin were found on different occasions in the loose earth of a cavern near Consuelo Cove, Last Hope Inlet, Patagonia. The deposit in which they were found is regarded as of Pampean age, and there can be no doubt that these ground sloths were contemporaneous with man, if not actually living in the cavern in a state of domestication.

Concerning the generic name, there appears to be no valid reason why Mylodon should not be used. The genus was first established by Owen in 1840 (11, p. 68), the type species being Mylodon Darwinii. Two years later Owen (12) described a nearly complete skeleton of a ground sloth which he called robustus, and referred to the same genus. Reinhardt (13), writing in 1879, showed that the two species were generically distinct, and renamed the earlier specimen Grypotherium. If, however, the rules of priority are to be observed at all, the term Mylodon should be retained for the species Darwinii, and the robustus should be accorded a new generic name. The argument that the species robustus was fully described, whereas Darwinii was represented only by a fragment of jaw, is obviously inadmissible, for if the fragment is sufficiently perfect to enable Reinhardt's specimen and those recently discovered to be regarded as generically identical with it, it is sufficiently perfect and important to

act as the type of the genus. Glossotherium, a genus founded by Owen in 1840 (**11**, p. 57), is admitted by himself (**12**, p. 154) to be identical with Mylodon Darwinii, and this genus may thus be dismissed as a synonym of Mylodon. The same fate befalls Neomylodon, since the newly discovered specimens to which the name was applied are widely regarded as generically, if not specifically (Nordenskjöld [**10**]), identical with Owen's Mylodon Darwinii. Until, however, the specific identity has been more fully established it is preferable to retain Ameghino's specific name of Listai for these remains.

The hairs of Mylodon Listai have been described by Lönnberg (**7**), Jacob (**4**), and Smith Woodward (**18** and **19**), and transverse sections have been figured by the first two authors. The descriptions presuppose a knowledge of the hair structure in Bradypus, the ant-eaters and armadillos, and so in the present communication the consideration of the Mylodon hairs and the criticism of the views of these three authors are left till the last.

The method adopted for the examination of the hairs was in all cases the same. The hairs were arranged with the roots pointing one way and the free ends the other; they were tied up in bundles, stained with a weak alcoholic solution of magenta, washed and dehydrated. The bundles were then soaked in xylol, and transferred to hard paraffin. After cooling the paraffin was cut into convenient blocks, and the sections were made by hand with a sliding motion of the razor. It was found that better results were obtained in this way than by the employment of any form of microtome. Some of the sections were mounted in glycerine jelly, but the majority in Canada balsam, since the former medium has the disadvantage of dissolving out the stain. A few hairs of each of the species studied were stained and mounted whole. For the Mylodon hairs I am indebted to the kindness of Dr. F. P. Moreno; the hairs of the other Edentata were obtained from dried specimens in the Natural History Museum, London.

Bradypus tridactylus.

The hairs of Bradypus are oval in section, and exhibit a central clear area and a darker marginal area (fig. 3). The central area stains very faintly if at all with magenta, and being brittle is apt to crack in the cutting. It is marked by a small number of minute air spaces, the true shape of which is fusiform. The long axis of each spindle is parallel to the length of the hair, and consequently the transverse sections of the spaces are larger or smaller according as they are cut through the middle or near the ends of the spindles. The outer substance stains deeply, and is thickly marked with dark granules, and exhibits at the same time two sets of radiating lines—a set of very fine and closely set lines around the outer edge, and a set of coarser and more irregular lines branching out from the central mass. The average size of the transverse section is $240\,\mu \times 145\,\mu$.

The outer substance is a layer not represented, or at least not in this form, in the hair of any other mammal. It does not extend the full length of the hair, but stops short near the free end, and is absent from the basal third of the hair. In optical section (fig. 4, upper part) it exhibits an oblique striation. The terminal portion of the hair (the " Endfaden " of Welcker [17]) has the normal structure of a non-medullate hair with a scaly cuticle, but at a certain distance from the point the diameter increases quite suddenly by the addition of this new layer (fig. 2). The diminution in the width of the central core at this point is probably not real, but an optical effect due to the refrangibility of the external layer. The figure represents an optical section, not an actual slice taken from the middle of the hair. The basal third of the hair is thin as compared with the distal part, and measures only $64\,\mu$ across (fig. 6) ; it appears transparent when the hair has been clarified and mounted whole. In addition to the minute fusiform air spaces it frequently has larger air-filled cavities, blunt ended, and about $60\,\mu$ long and $6\,\mu$ broad. The transverse section of this part of the hair is nearly

circular (fig. 5).   In all parts of the hair of Bradypus the
cuticular scaling can be seen by suitable staining and accu-
rate focussing.

That the central part of the hair of Bradypus is a cortex,
and not medulla, as Eble supposed (2, Bd. ii, p. 440, and
Taf. x, fig. 111), and that the peripheral part is extra-cortical,
has been ably shown by Welcker (17), who applied the name
" Belegschicht " to it.   The relation which the extra-cortical
layer bears to the normal cuticle is very difficult to determine.
A careful examination of the part of the hair where the
transition occurs between the normal terminal portion and the
part provided with the extra-cortex (fig. 2) shows that the
arrangement of the imbricate scales of the cuticle is con-
tinued without interruption upon the exterior of the extra-
cortical layer, thus seeming to show that the cuticle is con-
tinued over the outer surface of this layer.   The extra-cortex,
however, is very friable in old hairs, and comes away readily,
leaving the central column of cortical substance bare ; and it
is then seen that the surface of the column is marked by lines
taking a more or less transverse course, and suggesting
forcibly that the cuticular scaling is continued on the surface
of the cortex beneath the extra-cortical layer.   There is yet
a third possibility, which may eventually prove to be the
correct interpretation, since it accounts for both sets of
appearances.   It is that the extra-cortical layer is the cuticle
itself, enormously thickened and distinctly cellular, instead
of more or less homogeneous and structureless.   The
arrangement of the cells would account for the markings on
the external surface of the hair, and the scaly appearance of
the cortical rod when laid bare would be due to the impress
left by the extra-cortical cells.   The appearances presented
by that basal part of the hair where the extra-cortex is just
dwindling away certainly favours the third supposition.   The
cells of the extra-cortex get thinner and thinner, and come to
resemble the scales of the cuticle.   They become more firmly
adherent to one another and to the cortex, they appear more
homogeneous, and they stain less deeply.   The figure given

by Welcker (**17**, Taf. ii, fig. 11) of the young hair in its follicle at a time when the extra-cortex is forming would appear to allow of no alternative proposition. Yet Welcker was disposed to regard the Belegschicht as a new tissue intercalated between the cuticle and the cortical rod (**17**, p. 44) ; and the effect obtained by macerating the hair in water, and thus causing a thin cuticular layer to peel off (**17**, Taf. ii, fig. 14), lends support to his view. But this effect is very possibly due to the excessive cuticularisation of the outer parts of the external cells, and not to any morphological distinction of layers.

Leydig (**6**, p. 687) took the extra-cortex, or at least a part of it, to be the cuticle, for he observed that, contrary to the generalisation made by Reissner and Reichert, the hair cuticle does contain pigment granules in one mammal, namely, Bradypus. Waldeyer (**16**, p. 186) supported, in the main, Welcker's contention, and regarded the " Rindenmantel " as a layer peculiar to the sloths, and lying below the cuticula ; and Leche (**5**, p. 934) is probably only adopting Welcker's suggestion when he remarks of the " Umkleidungsschicht " that " sie besteht aus einer zwischen Cuticula und Rindensubstanz gelegenen pulpösen, lufthaltigen Zellenschicht." Maurer (**8**, p. 278), on the other hand, holds that the thickening of the distal part of the hair of Bradypus is mainly effected by the cuticle (Oberhautchen). His account, however, is very confusing, since he speaks of a medulla extending two thirds of the length of the hair, and of the cortical cells being pigmented ; and although he gives the title of Welcker's classical paper in his bibliography, he fails to contrast his own observations with those which this author had already placed on record.

The biological significance of the extra-cortical layer is full of interest, and has been made known by the writings of Welcker (**17**) and Sorby (**15**). The layer has a tendency to crack in a transverse direction, and in the cracks there come to lodge unicellular algæ, to which Kühn (**17**, p. 66) has given the name Pleurococcus Bradypi. The moisture of

the climate in which Bradypus lives enables the alga to live and propagate in this curious position, and the sloth acquires a general green tint, which must render it very difficult to distinguish as it hangs among the green foliage.   In thick transverse sections of the hair these algal bodies show up very clearly, since they stain deeply, and have a sharply defined, circular or slightly oval outline.   Unless the hair is much broken they are confined to the outer parts of the extra-cortical layer.

In addition to the larger hairs just described, Bradypus has a set of shorter and much finer hairs, constituting the under-fur.   These hairs have a diameter of $24\,\mu$, and consist of a column of cortical substance traversed by fine fusiform air spaces, and covered by an imbricated cuticle (fig. 7). Like the larger hairs of the body, they have no medulla.

Cholœpus didactylus.

The hairs of Cholœpus are no less remarkable than those of Bradypus, but in a totally different way.   The bulk of the hair is composed of cortex, the surface of which is fluted or channelled.   The grooves, as is well known, are occupied by strands of extra-cortex, in which lives an alga—the Pleuro-coccus Cholœpi of Kühn (17, p. 66).   Even from the hairs of dried museum specimens a green solution, giving the absorption bands of chlorophyll, can be obtained by boiling first in water and then in alcohol.

When seen in transverse section (fig. 8) the outline is oval, and measures about $150\,\mu \times 90\,\mu$.   The cortical substance is in some cases quite clear and hyaline, but in others it is marked by brown spots—differences presumably related to the age of the hairs.   In both cases this cortical substance does not stain with magenta.   But running throughout, except towards the summits of the superficial ridges of the hair, are irregular branching lines, which stain deeply, and are discernible in unstained sections by reason of their different refrangibility.   In very thin sections these lines are

seen to be empty tubes, with a deeply staining lining. These
conditions do not appear to be paralleled in the hair of any
other animal. The branching tubes may possibly represent
a diffused medulla, for in most hairs the medulla stains deeply
and becomes largely infiltrated with air. This is the view
taken by Waldeyer (**16**, p. 187), who writes that the hair
shows " einen grossen centralen Markstrang, der aber durch
Balken von Rindenschicht vielfach durchsetzt ist," and by
Welcker (**17**, p. 55), according to whom " diese Markröhre
ist, wie bereits Erdl [**3**] erwähnt, innerhalb des dickeren Thiels
des Haars nicht circumscript, sondern in eigenthümlicher
Weise mit Rindenschicht untermischt." Maurer's account of
the hair structure in Cholœpus (**8**, p. 278) is as unintelligible
as his description of that of Bradypus. He speaks of the
cortex being thin in the broad part of the hair, thereby
implying that a compact central medulla is present.

The cuticle is present, and it is imbricate, as can be seen
by the serrated appearance of the edge of the hair when
viewed in optical section. By staining rapidly, and washing
before the deeper parts of the hair have become affected, the
edges of the scales can be seen when the surface of the hair
is in focus. This is particularly the case with the hairs of
the under parts of the body, which have fewer longitudinal
grooves than those on the back. On the summit of the
ridges the cuticle is thick and highly refractive, but how the
cuticle is continued from one ridge to the next it is difficult
to determine. In very thin sections the cuticle can be traced
down the sides of the groove, becoming thinner and thinner,
and disappearing at the bottom. The grooves would thus
seem to be morphologically outside the hair. Yet it can be
seen in many places that the grooves are not perfect, as if
made with a plough, but are discontinuous ; and each portion
is canoe-shaped, open to the exterior at its middle, but covered
in at the two ends. Sections taken across the end of such a
segment of the groove show a continuous cover of cuticle
(see *a*, fig. 8), and in surface view, with carefully stained
specimens, the edges of the cuticular scales can be traced

across. It is no uncommon thing to find a ragged flap of cuticle overhanging the groove, as at *b* in fig. 8. These facts tend to show that the grooves are subcuticular; Welcker, in fact, goes so far as to state (**17**, p. 56) that the cuticle bridges over the grooves except in certain places, and his fig. 21 lends support to this view. And yet there is no denying the fact stated above, that the cuticle can be traced down the side of the groove. The logical conclusion, therefore, to which these facts point is that the grooves are morphologically intra-cuticular, a view which is in complete accord with the third suggestion offered in the case of the extra-cortex of Bradypus—that the cells are those of the cuticular layer, more numerous and less cuticularised than usual.

The hairs of Cholœpus are as a rule coarse, and with a single curve extending over the greater part of the length, while the basal fourth or so is wavy; but in young specimens, and in some apparently adult specimens from Costa Rica, the hair is very delicate and soft, and sinuous from base to point. The differences may be specific,[1] or due to age, season, or sex. However, in these forms the hairs are only about $42\,\mu$ across, and have only two or three furrows instead of the more usual nine, ten, or eleven. The algæ, also, are quite absent from many of the grooves. When such an empty groove is examined in optical section (fig. 12) it exhibits the outlines of obsolete extra-cortical cells, the edges of which are conterminous with those serrations of the margin which indicate the edges of the cuticular scales. In baby specimens more than half of the hairs are slender, non-medullate cylinders, with very distinct scaly cuticle, and no grooves on the surface. They are only slightly shorter than the two- or three-grooved hairs just referred to, and constitute the nearest approach to an under-fur found in Cholœpus.

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[1] The species didactylus and Hoffmanni were supposed to differ in the number of cervical vertebræ. Although this distinction has broken down, Cholœpus Hoffmanni may still prove to be a good species. Until more accurate knowledge is available concerning the geographical range and internal anatomy of the so-called species of Cholœpus the point must remain open.

In Cholœpus, as in Bradypus, the hairs are very thin at their basal ends (60 μ). The flutings of the surface die away on the basal sixth of the hair, and here the structure is that of a normal non-medullate hair (figs. 10 and 11). The cortex is not marked by the deeply staining branched tubes, but is rendered slightly granular by the presence of a number of fine air spaces, some spherical and scattered, some spherical and arranged in series of five or six, like strings of beads, and some fusiform, as though formed by the coalescence of such series of smaller cavities. The cuticle is thin and distinctly imbricate.

There are in Cholœpus no fine hairs to constitute a proper under-fur, and Welcker has remarked (**17**, p. 70), " Der Gegensatz von Stichelhaaren und Wollhaaren fehlt bei Cholœpus;" but de Meijere (**9**, p. 361) has described some flattened, stiff, and slightly curved hairs, much shorter than the ordinary hairs, and possessed of large medullary cells, surrounded by a very thin cortical layer. These hairs I have searched for in vain.

Myrmecophaga jubata.

The hairs of the great ant-eater are much flattened, and resemble a ribbon which is thinner in the middle than toward its edges. The actual measurements are—breadth 400 μ, thickness in the middle 110 μ, thickness near the edge 170 μ. The cuticle is thin for the size of the hair, and exhibits, rather indistinctly, the usual imbricate or serrate appearance, according as a surface view or an optical section is taken. The cortex is full of air spaces (fig. 14), which are provided with a deeply staining lining after the manner of the branching tubes which permeate the cortex of the Cholœpus hair. These spaces, however, can hardly be regarded as a diffused medulla, since a true medullary region is here differentiated ; and the suggestion made to this effect in the case of Cholœpus thus receives by analogy a partial refutation. When the hair is examined from the side the cortical vacuoles are

seen to consist of rows of six or seven spherical spaces arranged in the direction of the length of the hair. The middle spaces of each series are the largest, and the terminal ones the smallest, so that the general effect is that of a segmented spindle. In the pigmented parts of the hairs the pigment granules are disposed mainly around the smallest air spaces at the ends of the spindles. The central part of the hair is occupied by a slit-like air space partially filled with a highly refractive substance, which shows no traces of its cellular origin as the medulla so frequently does. The basal part of the hair is more cylindrical in shape than the middle part; and the medullary cavity dwindles gradually away, to disappear altogether in the part of the hair within the follicle, or just outside it. The basal parts are transparent, owing to the reduction in the number and size of the air vacuoles. A section of the hair taken about 3 mm. outside the follicle is shown in fig. 15.

Tamandua tetradactyla.

In this ant-eater the hairs are less coarse than in Myrmecophaga, and have the form of slightly compressed cylinders. The transverse section is oval in form, measures 140 μ × 90 μ, and exhibits a solid, non-medullate area of cortex, marked with numerous brown spots arranged in groups (fig. 16). The cortex is enclosed within a thick and tangentially stratified cuticle of clear, highly refractive aspect. Examined from the side the cuticle shows the usual imbricate markings. The basal part of the hair is more circular in section; it is free from the brown granules, and contains only a few scattered air spaces of minute size.

Cyclothurus didactylus.

The two-toed ant-eater has in addition to the principal hairs of the body a well-developed under-fur of much finer hairs. The whole pelage is soft and fluffy. The principal hairs, although much smaller than those of Tamandua, do

not differ from these in any essential respect. They have a fairly thick cuticle, but no medulla. They are broadest at about one sixth of their length from the free end, and in this part the cortex is coloured brown by numerous granules; whereas in the basal half or more these are wanting, and the hair appears quite clear, with just an odd air vacuole here and there.

The scaling of the cuticle is very strongly marked on the basal part of the hair, but in the pigmented portion it is less easy to distinguish. In the fine hairs of the under-fur the cuticular scaling is the most obvious feature. The greatest width of the larger hairs is 70 μ; that of the supplementary hairs 20 μ. There is, however, no rigid distinction between the two kinds of hair, and transitional forms are fairly common.

Chlamydophorus truncatus.

The soft fur of Chlamydophorus is made up of fine non-medullate hairs, the average breadth of which is 17 μ. The cortex is transparent and unpigmented, and contains only a few scattered granular markings. The scales of the cuticle project considerably, and give a ragged appearance to the surface of the hair (fig. 17).

Dasypus sexcinctus and villosus.

In both species the hairs are coarse, brown, and oval in section. When examined from the side they show a fine and close longitudinal striation, due to the arrangement of highly refracting granules in fusiform series. The cuticular scaling is close, and can be made out only with difficulty. In Dasypus villosus (fig. 19) the section is less perfectly oval than in Dasypus sexcinctus (fig. 18), since it tends rather towards the rectangle in shape. There is a distinct slit-like medullary cavity in D. villosus, but this is wanting

in D. sexcinctus;[1] the cuticle, also, is considerably thicker. In both species the granules in the cortex are most thickly set at some little distance from the margin, thus leaving a central part and a peripheral part of the cortex relatively clear. The long diameter of the oval measures about 230 μ in both species.

Tolypeutes conurus.

Tolypeutes has solid hairs provided with a thin, finely scaled cuticle. The minute structure very closely resembles that of the Dasypus hairs; in fact, except for their lighter colour, these hairs might be considered as of intermediate character between those of the two species of Dasypus examined. The sections are oval in shape (fig. 20), and there is a central clear area suggesting a medulla such as occurs in Dasypus villosus, but it has no cavity, and does not stain differently from the cortex. The cortex contains bright granules, not of a brown colour, disposed most thickly around the central clear space. Nearer the base of the hair the section is circular (fig. 22), and has no central clear area. The width of an average hair at its broadest part is 200 μ.

Tatusia novemcincta and pilosa.

The hairs of Tatusia are clear, solid, and non-medullate, with a sharply marked cuticular scaling and a very faint longitudinal striation. In transverse section the cortex appears very clear, and contains only a few highly refractive colourless granules (fig. 23). These are uniformly distributed, and are particularly scarce in Tatusia novemcincta. The sections of the hairs of T. pilosa are oval, and measure 115 μ × 95 μ; while those of T. novemcincta are circular in shape, and measure 130 μ across.

Mylodon Listai.

The hairs of Mylodon Listai are solid, and without any

[1] Lönnberg (7, p. 162) speaks of D. sexcinctus as though its hairs possessed a central pith.

trace of medulla. The width is very uniform, and measures
170 μ throughout the middle six eighths of the hair. The
basal eighth is slightly narrower, and the free end tapers
gradually to a blunt point, which is missing from most of the
hairs. A perfect hair measures about 6 cm. in length.[1] The
cortex would be quite clear and homogeneous but for the few
short, fusiform air spaces, which are visible both from the
side and in transverse sections. The vacuoles are uniformly
distributed in all my preparations, and I have been unable to
discover the peripheral clear zone of the cortex mentioned and
figured by Jacob (**4**, p. 62 and fig. 2). Transverse sections
from different parts of the hair are all similar in character
(fig. 24).

The cuticle is moderately thick, and stains deeply. When
the hair is examined from the side the cuticular scaling is
very clearly observable on the basal third (fig. 25), but
cannot be seen over the rest of the hair. This fact, together
with a certain anxiety to make this ground sloth conform in
its hair structure with the tree sloths, has led Lönnberg (**7**)
to conclude that the hairs of Mylodon Listai, as we know
them, are but the central cores of hairs which were provided,
like those of Bradypus, with a more perishable extra-
cortical layer. The fragments of adhering material, however,
which he alludes to as the remains of the extra-cortex, are,
judging by my own preparations, nothing but foreign matter
such as dried mud or portions of the shrivelled root-sheath.
On the basal part of the hair of the human head organic
cellular substance, probably derived from the inner root-
sheath, is commonly found attached to the cuticle long after
that part of the hair on which it is found has emerged from
the follicle. The fact of the cuticular scaling showing
only on the basal part of the hair appears at first sight to
support Lönnberg's view, for in Bradypus the extra-cortex

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[1] The observations were made upon the specimen described by Smith
Woodward and Moreno in 1899 (**18**). In a more recently discovered speci-
men, less well preserved, the hairs are much longer. See Smith Woodward
(**19**).

is wanting on the basal part, and the scaling there is particularly clear. But in Mylodon the transition is very gradual, the scaling becoming fainter and fainter, and giving place to a uniformly stained external layer, whereas in a damaged Bradypus hair the scaling disappears in sharply outlined patches which do not stain at all.

Lönnberg writes (7, p. 162) that in tangential sections of the skin he saw around some of the hairs two rings, the outer of which was the epithelial hair-sheath, while the inner he took to be the "loose outer bark of the hair"—the extra-cortex, in fact. Since, however, in the fully grown hairs of neither Bradypus nor Cholœpus is the extra-cortex found within the follicle or anywhere near it, the argument fails to carry as much weight as he evidently intended it to do. His remarks on the following pages concerning the rings of dried epithelial substance around the exposed bases of the hairs are equally unfortunate. On the drying of the skin the hairs become protruded, and that region of each which in life was flush with the surface and closely surrounded by the general epidermis is pushed some distance out, a millimetre or so, dragging up the stratum corneum into the form of a cone. As the cone dries it cracks horizontally at a little below the summit, leaving an annulus attached to the hair. This is the kind of thing which can be seen by examining with a lens almost any museum skin of a mammal with a thick skin and stiff hair.

Again, a glance at the transverse section of the Bradypus hair taken through its broad part (fig. 3) is sufficient to show that, were the extra-cortex removed by disintegration or rough treatment, the central core would present a very ragged, unstainable edge, quite unlike the uniform, smooth, and deeply staining cuticular border of the transverse section of the Mylodon hair (fig. 24). And lastly, the reappearance of the cuticular scaling at the tip of the Bradypus hair (fig. 2) is not paralleled in the hair of Mylodon. The bulk of the evidence appears, therefore, to be against Lönnberg's theory, and we must consider the hairs of Mylodon to be preserved

to us in their completeness. They will bear a very close comparison with the hairs of Tatusia (fig. 23), and are not remarkably different from those of Tamandua (fig. 16) and Dasypus sexcinctus (fig. 18).

It is a curious fact that in all the American Edentates examined any characteristic features which each kind of hair may possess is absent from the basal portion. The basal parts of the hairs of Bradypus (figs. 5 and 6), Cholœpus (figs. 10 and 11), Myrmecophaga (fig. 15), and Tolypeutes (fig. 22) agree with one another, and furnish a generalised type of hair structure, with which the whole hairs of Tatusia, Tamandua, and Dasypus sexcinctus conform. Since the hairs of Mylodon are in such close agreement with this generalised type, it seems wiser to accept them as of primitive and generalised structure than to attempt to establish a parallelism between them and those of the tree sloths, especially in view of the fact that these latter are extremely aberrant, and differ so remarkably inter se. There is no need to conclude that Mylodon is the less a sloth, and more related to the ant-eaters and armadillos, because its hairs fail to possess an extra-cortex.

As regards the arrangement of the hairs in the skin there is not much to be said. The hairs are, as has been pointed out by Smith Woodward (18, p. 149) and Lönnberg (7, p. 164), all of one kind, there being no under-fur, and they are uniformly distributed, without any signs of symmetrical grouping. In Bradypus the follicles of the small hairs are clustered around those of the principal hairs, as Leydig (6, p. 707), Welcker (17, pp. 68—70, and pl. i, fig. 4), and de Meijere (9, p. 361) have shown; while in Cholœpus the hairs are arranged in bundles of two, though occasionally solitary, and there is no proper under-fur.

Appended to Dr. Sorby's remarks on Bradypus (15, p. 339) is a foot-note by the editor [1] of the ' Linnean Society's Journal,' which reads, "There is a small sloth, however, in which the larger hairs are smooth and solid." It is much to

[1] The late Mr. E. R. Alston.

be regretted that he did not mention the species he had in mind. The existence of a sloth with such hair would, of course, be of the greatest interest in the present connection, and so I examined the hair of every species of sloth available at the Natural History Museum. The results, however, do not enable me to confirm the editor's remark.

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EXPLANATION OF PLATE 26,

Illustrating Dr. W. G. Ridewood's paper "On the Structure of the Hairs of Mylodon Listai and other South American Edentata.

al. Alga. *co.* Cortex. *cu.* Cuticle. *eco.* Extra-cortex. *m.* Medulla.

Fig. 1.—Bradypus tridactylus. Hair, one and a half times natural size.

Fig. 2.—Terminal portion of hair (A in Fig. 1). × 100.

Fig. 3.—Transverse section taken through the thickest part of the hair (B in Fig. 1). × 100.

Fig. 4.—Corresponding part of hair seen longitudinally; the upper part in optical section, the lower part with the surface in focus. × 100.

Figs. 5 and 6.—Transverse section and side view of basal part of hair taken in the position indicated by c in Fig. 1. × 100.

Fig. 7.—Portion of one of the fine hairs of the under-fur, and a transverse section of the same. × 100.

FIG. 8.—Cholœpus didactylus. Transverse section through the middle of the length of the hair. The superficial grooves are occupied by shrivelled extra-cortex and algæ. At *a* the groove is completely, and at *b* partially closed over by cuticle. × 150.

FIG. 9.—Portion of the hair seen from the side. × 150.

FIGS. 10 and 11.—Transverse section and side view of the hair at a point one eighth of the total length from the base. × 150.

FIG. 12.—Optical section of a hair of a soft-furred specimen of Cholœpus didactylus, showing in the groove, which is in focus on the right side of the figure, the cell outlines of the extra-cortex. × 150.

FIG. 13.—Transverse section of the same hair. × 150.

FIG. 14.—Myrmecophaga jubata. Transverse section through the middle of the length of the hair. × 100.

FIG. 15.—Transverse section through the hair at about 3 mm. above the surface of the skin. × 100.

FIG. 16.—Tamandua tetradactyla. Transverse section through the middle of the length of the hair. × 150.

FIG. 17.—Chlamydophorus truncatus. Hair seen in transverse section and from the side. × 600.

FIG. 18.—Dasypus sexcinctus. Transverse section through the middle of the hair. × 100.

FIG. 19.—Dasypus villosus. Transverse section through the middle of the hair. × 100.

FIG. 20.—Tolypeutes conurus. Transverse section through the middle of the hair. × 100.

FIG. 21.—Middle part of the hair seen from the side; upper part in optical section, lower part with the surface in focus. × 100.

FIG. 22.—Transverse section through the hair at about one quarter of its length from the base. × 100.

FIG. 23.—Tatusia pilosa. Transverse section through the middle of the length of the hair. × 150.

FIG. 24.—Mylodon Listai. Transverse section through the middle of the hair. × 100.

FIG. 25.—Portion of the hair about one quarter of the total length from the basal end; surface in focus to show the cuticular scaling. × 100.
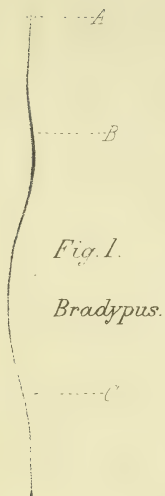
Fig. 1.

Bradypus.
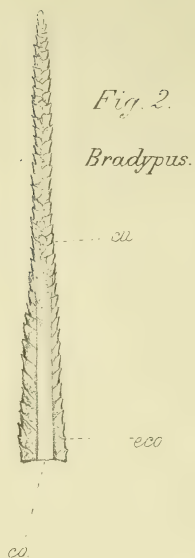
Fig. 2.

Bradypus.
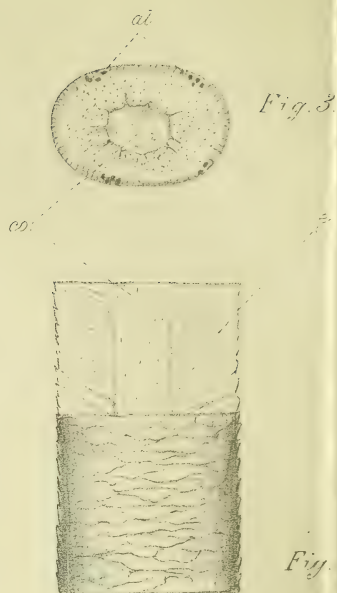
Fig. 3.

Bradypus.

Fig. 10.
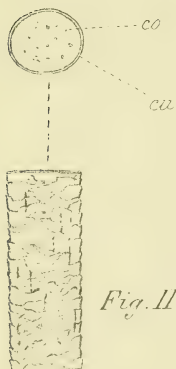
Fig. 13.

Fig. 11.

Fig. 12.

Choloepus

Choloepus.

Fig. 17.

Chlamydophorus.

Fig. 14.
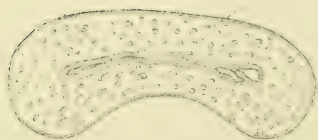
Fig. 15.

Myrmecophaga.

Myrmecophaga.

co.

Fig. 5.

cu.
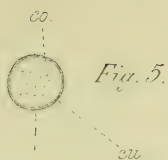
Fig. 6.

Bradypus.

Fig. 7.

Bradypus.

al. *cu.*

Fig. 8.

h.

Fig. 9.
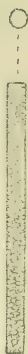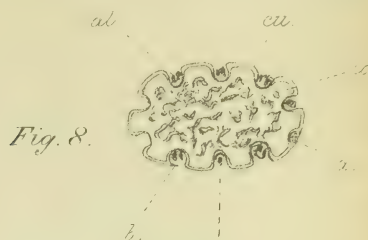
Choloepus.
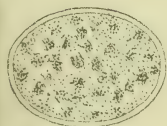
Fig. 20.

Tolypentes.

Fig. 16.

Tamandua.
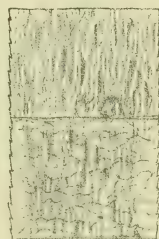
Fig. 21.

Tolypentes.

Fig. 23.

Tatusia.
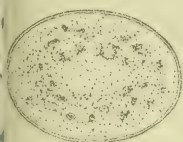
Fig. 18.

Dasypus.

Fig. 24.

Mylodon.

v.

Fig. 19.

Dasypus.

Fig. 22.

Tolypentes.

Fig. 25.

Mylodon.

On the Structure and Affinities of Saccocirrus.

By

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With Plates 27—29.

WHEN studying the morphology of the excretory organs of the Polychæta, I thought it advisable to investigate those few cases of worms in which the true nephridia have been alleged to function as genital ducts. Of these Polychætes, Saccocirrus papillocercus, Bobr., is one of the most interesting ; and whilst occupying for a short time last winter, at the Zoological Station at Naples, a table kindly placed at my disposal by the committee of the British Association, I had an opportunity of studying its structure.

Unfortunately the results are somewhat disappointing, since I have not been able to discover any facts of such decisive significance as to settle the difficult question of the morphological value of the organs which contribute to form the complex genital apparatus of this little worm. However, as I was able to complete and to correct the accounts of previous authors in many points of detail, I publish this paper as a small contribution to the subject, and have appended some general remarks concerning the validity of the group " Archi-annelida."

Marion and Bobretzky,[1] in 1875, published an excellent account of the structure and habits of Saccocirrus, from material studied at Marseilles (**10**). Since then Langerhans

[1] Bobretzky's original paper (**1**) I have not been able to consult.

(8) has mentioned this worm in a paper on the fauna of Madeira, and Fraipont has made a detailed study of its nervous system (3).

External Characters.—I have nothing to add concerning the external morphology of Saccocirrus, excepting with regard to its parapodia and chætæ. Unlike what has been described by Marion and Bobretzky, the parapodia in my specimens do not extend all the way from the second[1] to the last segment; but there is at the posterior end of the animal a variable number of segments (from ten to twelve), on which neither parapodia nor chætæ are present. The transition from the region with parapodia to the region without is marked by one or two segments in which the parapodia and chætæ are rudimentary. In every bundle of chætæ, besides the ordinary chætæ described with blunt ends, I find one long needle-like chæta, the tip of which is divided into three sharp prongs (fig. 9).

It is of course possible that the Saccocirrus of Naples is not of the same species as the worm described by Marion and Bobretzky from Marseilles; but on the whole this seems unlikely, since Saccocirrus papillocercus has also been found in the Black Sea by its original describer, and at Madeira by Langerhans. The discrepancies in the descriptions may vanish on a closer inspection of specimens from the other localities.

Nervous System.—It is well known that the central nervous system consists of a brain in the prostomium, from which two nerve-cords run along ventrally above the epidermis on either side of the body. Fraipont also found, extending along the œsophagus, two strands, which he conjectured must be of nervous nature, although he was unable to follow them to the brain. In my series of sections these two nerves can be plainly seen to arise from the ventral surface of the brain, more towards the middle line, but quite near to the origin of the main nerve-cords (fig. 2). They pass backwards along the roof of the buccal cavity (fig. 16)

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[1] The "first segment" is probably formed of two fused segments.

and the sides of the œsophagus (figs. 17, 18, and 19), below which they join to form a complete loop just behind the muscular pharyngeal sac (figs. 20 and 2). A few nuclei, especially in this region, indicate the presence of ganglionic cells. Obviously this loop represents the stomatogastric system.[1]

A small knob with sensory hairs is situated behind each parapodium.

Alimentary Canal.—Hitherto the alimentary canal of Saccocirrus has been described as quite simple, without special muscular pharynx. In my specimens, however, I find a well-developed muscular pharyngeal sac below the œsophagus,[2] opening forwards into the buccal cavity (figs. 1 and 2), and extending backwards into the third segment. The roof of this diverticulum is thin, and the floor is thickened into a sort of muscular pad (figs. 1, 19, and 20). Special muscles, passing from the hinder lip of the mouth backwards round the sac, and then forwards to be attached dorsally to the wall of the œsophagus, serve no doubt to push the sac and its pad forwards and outwards; but I have never seen this apparatus in action.

The inside of the sac is lined with rather thick cuticle, and is not ciliated like the rest of the digestive tract. Behind this organ is the glandular region with muscular walls, representing the digestive stomach. It reaches, as already described by Marion and Bobretzky, to about the fourteenth segment. Following on this is the long sacculated intestine, the absorptive region, covered externally with chloragogen cells.

Vascular System. — Of the blood-vascular system, Marion and Bobretzky only found the dorsal vessel; Fraipont figured a ventral vessel (3). Langerhans had previously described this ventral vessel, and a vessel passing into the

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[1] Surely it is to such a stomatogastric system that the subœsophageal ganglion of Rotifers is to be compared, and not to the ventral nerve-cords of the body-wall as urged by Eisig ("Zur Entwicklungsgeschichte der Capitelliden," 'Mitth. Zool. Stat. Neapel,' vol. xiii, 1898).

[2] The sac is absent in two out of a dozen series of sections.

tentacles (**8**). I can confirm this author's discovery of the
two main longitudinal vessels, but not that of a tentacular
vessel. The dorsal vessel divides below the brain into two
branches, which run down on either side of the œsophagus
to join below, and behind the pharyngeal sac to form the
ventral vessel (figs. 17 to 21).

Cœlom.—Marion and Bobretzky described the spacious
cœlom, subdivided by median dorsal and ventral mesenteries
and by transverse septa, and traversed by the oblique muscle
strands. Fraipont has figured the cœlom as filled with a fine
reticulum of stellate cells (**2** and **3**). It may be the case that
at a certain age, or at a certain time of the year, the cavity
of the body is so filled; but I have never observed this con-
dition myself, and I am inclined to believe that Fraipont has
been somewhat misled by appearances brought about by the
coagulating action of fixatives, or by studying sections taken
in the region of a septum, or close to the head, where nu-
merous tissue strands extend from the anterior end of the
œsophagus to the body-wall, as in worms generally.

The wall of the intestine is covered externally with large
irregular cells projecting far into the cœlom, and filled with
coloured granules (fig. 5). The cœlomic epithelium lining
the other parts of the body-cavity is composed of cells, which
often are so filled with vacuoles that they project consider-
ably into the cœlom (fig. 9). When a Saccocirrus is viewed
compressed under a cover-glass the body-cavity may appear
to be almost obliterated, but this appearance is deceptive.

Head Cavity.—Amongst the most peculiar characters of
Saccocirrus may be reckoned the possession of a special
closed cavity in the head, consisting of a right and left
ampulla, situated in the peristomial segment, passing forwards
into canals which run up the prostomial tentacles (figs. 1, 2,
and 17). A transverse communicating canal runs across
beneath the posterior edge of the brain (fig. 16). The walls
of this system are provided with muscles—longitudinal in the
tentacular canal, circular as well in the ampulla. Its cavity
is filled with a fluid and lined by an epithelium.

Marion and Bobretzky correctly described the head cavity, and believed its function to be erectile; contraction of the ampullæ driving the contained fluid into the tentacular canals, and so straightening out the tentacles. This interpretation is very probably correct, but I have never myself observed any very manifest signs of such action. Langerhans added the observation that the wall of the head cavity is provided with an outer cuticular lining. Staining with nigrosin shows the covering coloured dark blue like the cuticle. Fraipont has figured transverse sections of the system, the lumen being drawn as if filled with a reticulum.

Whilst fully confirming most of these authors' statements, it may be added that the contents seemed to me to be not colourless, as described, but pale pink; and further, that the " fluid " is really composed chiefly of large cells with granular and very fluid contents closely packed together (figs. 1 and 17). No doubt there is some intervening liquid, but it does not appear in sections.

The morphological significance of this head cavity is not easy to determine. It seems to me probable that it represents the specialised cœlomic cavity of the peristomial segment (see p. 404).

Excretory and Genital Organs.—Our knowledge of these organs is due entirely to the observations of Marion and Bobretzky, some of which Langerhans confirmed. This description, on the whole, is remarkably good, but it is incomplete and incorrect in a few points.

These authors found that the sexes are separate; that the testes and ovaries are developed from the cœlomic epithelium on the posterior surface of the septa; that in the male there is, in the region behind the œsophagus, on either side of each segment a protrusible penis with sheath, leading into a ciliated duct which enlarges to form a vesicula seminalis, continued into an open funnel, " disposé d'après la forme typique des organes segmentaires " (**10**). In the œsophageal region they found ordinary nephridia opening at the same level as the penis. Naturally they believed that the male

ducts were merely modified nephridia : " Nous croyons que le Saccocirrus est jusqu'ici le premier exemple, parmi les Annélides Polychètes, de vers dans lequels les organes segmentaires du mâle se transforment et deviennent de véritables appareils de copulation."

In the female they described nephridia, as in the male, which they believed to open to the exterior near the parapodium, and to function as oviducts in the genital region, Bobretzky having seen the nephridial canal dilated with eggs in ripe specimens. Besides these, a pair of spermathecæ were found in every genital segment opening ventrally by a narrow duct, with cilia producing a current inwards. To explain how fertilisation takes place, Marion and Bobretzky added that " il faut supposer que ces vésicules [spermathecæ] s'ouvrent dans la grande chambre où les ovules s'accumulent."

Now when this investigation was begun I hoped to find this internal opening, and to interpret the excretory organs of the female as true nephridia, and the spermathecæ as cœlomostomes (5). But such an opening does not appear to exist. The spermatheca consists of a pear-shaped sac, with a long duct passing straight through the ventro-lateral longitudinal muscles (figs. 14 and 21) to open to the exterior. The wall of the duct is formed of ordinary ciliated epithelium (figs. 3 and 13) ; but the cilia do not reach far into the sac, where the epithelium soon becomes altered in character. Near the base of the sac, surrounding the entrance of the duct, is a cup-shaped region where the lining is formed of very large granular cells containing yellow granules, and at their inner ends large irregular angular bodies of yellow refringent matter (figs. 3, 4, and 13). Similar bodies are distributed in the epithelium lining the swollen end of the sac, and together with the granules give the spermatheca its yellow tinge. What the function of these bodies can be it is difficult to guess ; possibly they serve as a reserve of food material for the spermatozoa. There is no reason to consider them as of an excretory nature.

The nephridium in the female is a slender tube running in the angle between the oblique muscles and the body-wall, to open forwards into the cœlom through a septum (figs. 3 and 22). In the genital segments (intestinal region), when it reaches a point nearly opposite the spermathecal pore, the nephridium turns sharply downwards, passing between the epidermis and the longitudinal muscles, until it touches the spermathecal duct, into the very base of which it opens (figs. 3, 6, 21, and 14). This downward limb of the nephridium becomes very narrow, having a much diminished lumen towards the minute opening. The wall of the nephridium is formed of granular, much vacuolated protoplasm; a few cilia are seen in the lumen (fig. 3). There is no projecting lip to the funnel, which merges rapidly into the epithelium covering the septum (in my specimens, which were not quite mature). Round the opening are long cilia passing down into the lumen of the canal (fig. 3).

In the male the cavity of the penis is lined with granular cells, and its wall is strengthened by a number of delicate refringent cuticular rods pointed at both ends (figs. 8 and 9). The sperm-sac and nephridium do not form one continuous duct, as described by Marion and Bobretzky. Coming off from the penis is a ciliated duct, which soon widens out into a pear-shaped sac lying, unlike the spermatheca, entirely in the lateral chamber of the cœlom (figs. 9, 10, 11, and 14). This sperm-sac contains ripe spermatozoa, and ends blindly at its swollen extremity. In the genital segments the nephridia, quite similar organs to those of the female in their general structure, open into the duct of the sperm-sac near its entrance into the penis. The funnel in these segments is much enlarged, richly ciliated, and spreads for a considerable distance over the anterior face of the septum (figs. 9, 12, and 14).

Small-funnelled nephridia are found in both sexes in the segments of the œsophageal region, beginning after the first bundle of chætæ (fig. 15). But whereas in the male they open dorsally, at the level of the penis in the more posterior

segments, in the female they open ventrally as in the genital segments.

It will be seen that the general relations of the genital organs is really much the same in both sexes; that the sperm-sac can be compared to the spermatheca; and that if an invagination similar to that which has given rise to the penis took place in the female at the mouth of the spermatheca, a condition would be brought about almost identical with that which obtains in the male. Whether the sacs themselves are formed from invaginations of the skin can only be decided by a study of their development; on the whole, it seems probable that this is the case.

As to the morphological value of the excretory organ, whether it be a true nephridium with a nephridiostome, or a nephromixium formed of a cœlomostome grafted on to a nephridium (5), only a knowledge of development can here again help us to decide. The structure of the male organ especially seems to lend itself readily to the latter interpretation. The main part of the canal appears to be undoubtedly of nephridial nature, comparable to the very similar nephridia of the Polygordiidæ (2 and 5). On the other hand, the funnel has very much the appearance of being derived from the cœlomic epithelium (figs. 9 and 12).

Summary and Conclusion.

The chief additions to our knowledge of the structure of Saccocirrus recorded in the foregoing pages may be briefly enumerated as follows:—the parapodia and chætæ are absent from the last ten or twelve segments; in each bundle of chætæ, besides the ordinary blunt bristles, is one long slender chæta, ending in three prongs; there is a stomato-gastric nervous system, consisting of two nerves passing backwards from the brain, and joining below the œsophagus; the buccal cavity is prolonged into a muscular diverticulum below the œsophagus, which forms a ventral pharyngeal pouch, lined with cuticle, and probably eversible; the dorsal blood-vessel divides below the brain into two branches,

which pass down on either side of the œsophagus to join below it in the ventral vessel; in the male genital region the nephridia which open into the cœlom by wide funnels spreading over the front of the septa, pass backwards to open by a narrow tube into the ducts of the sperm-sacs before their entrance into the penes; the penis is provided with a number of supporting cuticular rods in its wall; in the female the nephridium of the genital region opens in front by a small cœlomic funnel, and runs backwards to open by a minute pore into the base of the spermathecal duct.

Although we cannot hope, in the present state of our knowledge, to definitely determine the affinities of Saccocirrus, yet a general review of the question may be made with some profit.

Marion and Bobretzky (10) considered Saccocirrus to be allied to Polygordius; Hatschek (6), followed by Fraipont (2), believing the Polygordiidæ to represent an Archi-annelidan group outside the Polychæta, places Saccocirrus at the beginning of the Polychætes, between the Archi-annelids and the Opheliidæ.[1] It is obvious that to determine the position of Saccocirrus, we must first of all inquire into the affinities of the Polygordiidæ. The Polygordiidæ comprise the two genera Polygordius and Protodrilus. The characters on which Hatschek founds his opinion that these worms form a group ancestral to the remainder of the Annelida are the following:—the absence of parapodia and chætæ; the homonomy of the segments, and the fact that segmentation is chiefly internal (a statement which scarcely agrees with the structure of Protodrilus, however); the restriction of the pharynx to the buccal segment; the close connection of the nervous system with the epidermis; the absence of ventral ganglia; the simplicity of the musculature, there being no circular muscles (except in Polygordius Villoti, described by Perrier [11]); the presence of dorsal and ventral mesenteries, and the simplicity of the

[1] Perrier, in his 'Traité de Zoologie' (1897), places the Polygordiidæ near the Phyllodocidæ.

vascular system.   To these characters Fraipont added the simple primitive structure of the nephridia running in the body-wall, below the cœlomic epithelium.

That the general organisation of Polygordius and Protodrilus is simple cannot be denied ; but that this simplicity is necessarily of an archaic nature remains to be proved.   To a great extent it may be due to a general tendency to simplification shown in the smaller representatives of many families of Polychætes, especially amongst sand-inhabiting forms. It is well known that in the smaller Syllids, Opheliids, Eunicids, etc., the nerve-cords are closely connected with the epidermis.   The intimacy of the connection between the epidermis and the nerve-cords in the Polygordiidæ appears to me to have been a little exaggerated by Fraipont (**2**). Protodrilus I have not studied ; but in Polygordius the distinction between the two does not seem to me to be much less marked than in many small Polychætes (in Saccocirrus a line of demarcation can always be made out separating the nerve-cord from the epidermal cells).   However, the absence of ganglionic concentrations may certainly be archaic ; but the presence of ganglia in such forms as Dinophilus and Histriodrilus, animals considered by some authors to be allied to the Polygordiidæ, tends to show that it is a character of no very fundamental importance.

Again, with regard to the absence of circular muscles ; not only have they been expressly stated to exist in Polygordius Villoti by Perrier (**11**), but surely if we consider how well developed they are in Nemertines and Platyhelminths, the assumption that their absence is primary and not secondary does not seem to be justified.   The peculiar development of the oblique muscles in the Polygordiidæ is much more like what we find in many Polychæta where the parapodia are reduced (Arenicola, Capitellidæ, Opheliidæ, etc.), than anything we know of in the lower classes of Cœlomata.

Moreover little importance can be attached to the position of the nephridia ; in almost all Polychæta these organs are

primarily covered by the cœlomic epithelium—even in the adult; and in Polygordius the nephridia are not always in the body-wall, as stated by Fraipont, but may run (as in Poly-ophthalmnus, for instance) along the oblique muscles crossing the cœlom, as shown in fig. 7. The persistence of both mesenteries is probably a truly archaic character. This and the absence of the parapodia and chætæ are the only points of first-rate importance common to Polygordius and Proto-drilus in the list of alleged primitive characters. It is, then, to the absence of parapodia and chætæ that we must turn our attention.

Let us try, for the sake of argument, to conceive what sort of creature the common ancestor of the Annelida (Polychæta, Oligochæta, Hirudinea, Echiuroidea, and Myzostomaria) must have been. It may safely be conjectured that it was a creeping segmented worm, with a skin, whether ciliated or not, covered by a cuticle; with metameric bundles of chætæ, longitudinal ventral nerve-cords; circular, longitudinal, and dorso-ventral muscles, septa, and mesenteries; with seg-mental nephridia (probably not opening into the cœlom), cœlomic cavities and cœlomostomes (genital ducts) leading to the exterior. Such may have been approximately the structure of the Annelid common ancestor in pre-Cambrian times. This primitive Annelid must have been itself derived from a form which, we may presume, to some extent ap-proximated to the plan of structure now elaborated along the Nemertine and Platyhelminth lines of descent. In other words, it was probably derived from worms in which the muscles and parenchyma were well developed, but in which the cœlom and internal segmentation were not so well differ-entiated, and which were provided with nephridia ending in flame-cells.

Now this is just the position the Polygordiidæ occupy according to the Archi-annelid theory. Can it be truly said that they fit in the place assigned to them? Moreover can it be believed that these little modified ancestral forms have persisted to the present day, and live happily together with

the highly modified Chætopods, which are supposed to be derived from them, in the Bay of Naples? The absence of parapodia and of chætæ are the only characters which seriously entitle the Polygordiidæ to such a bold claim. Therefore, if it can be shown that both chætæ and parapodia have been reduced or even lost in other cases; and if, further, it can be shown that the Polygordiidæ are quite nearly related to a form possessing parapodia and chætæ, the "Archi-annelid theory" will be severely shaken.

That parapodia may disappear more or less completely is shown in many families of Polychætes. One may mention especially the Scalibregmidæ, Chlorhæmidæ, Sternaspidæ, and the Opheliidæ, to which family McIntosh (9) and Giard (4) believe Polygordius to be closely related. The Oligochæta exhibit an example of the total loss of chætæ (Anachæta and the Discodrilidæ?), and of course in almost all the Hirudinea they have entirely vanished; but amongst the Polychæta it may be pointed out that in Arenicola a considerable region of the body is devoid of both chætæ and parapodia. In Tomopteris also no chætæ are present on the trunk segments.

More important still is the near relationship which undoubtedly exists between the Polygordiidæ and Saccocirrus. Already Marion and Bobretzky, as mentioned above, remarked on this affinity, and Fraipont has further insisted on it. But the most convincing evidence seems to have been brought forward by Langerhans (8); curiously enough it appears to have escaped the notice of later writers on this subject. The piece of evidence to which I refer concerns the very remarkable contractile head cavity of Saccocirrus, hitherto generally supposed to be unique.

Describing Protodrilus (Polygordius) Schneideri, Langerhans says, "Innen von den Gefässen liegt, ganz wie bei Saccocirrus, in den Tentakeln ein grösserer Hohlraum (Fig. 47), welcher im Kopf zwischen Quergefäss und Hirn mit dem der anderen Seite zusammenhängt, von diessem Verbindungstück geht ein kleiner dorsaler Forsatz ab

(Fig. 48).[1] Durch die lebhaften Bewegungen der Fühler werden in diesen Hohlräumen lose Zellen hin und her getrieben" (p. 126 [**8**]). Moreover Uljanin evidently figures a similar cavity in the head of Protodrilus flavocapitatus (figs. 5, *h.*, *h'.*, and 15, *sch.* [**12**]). Hatschek himself, in describing Protodrilus Leuckartii, mentions a cavity in the peristomial segment which runs up the tentacles, and is filled with reddish fluid (the blood is colourless). There seems to be no doubt, then, that in Protodrilus, as in Saccocirrus, there exists a special " head cavity " in connection with the tentacles, a cavity which, in fact, I believe to be the modified cœlom of the first segment.

All known species of the genus Protodrilus are provided with a ventral, muscular, pharyngeal sac below the œsophagus. As further evidence in favour of the close affinity advocated above, one may bring forward the discovery of a very similar sac, lined with cuticle and with muscular walls, in Saccocirrus. In the details of its structure the pharyngeal sac of Saccocirrus seems to be more like that described in Protodrilus Schneideri than like that of Protodrilus Leuckartii.

In the presence of these facts we are forced to the conclusion that in some important respects Protodrilus is much more closely allied to Saccocirrus than to Polygordius! Wherever we put Protodrilus in our system of classification, there also we must place Saccocirrus. On the other hand, that Polygordius and Protodrilus are nearly related seems to be almost equally certain. There remains, therefore, no alternative but to unite all three genera in one group. And if we do this, many of the list of supposed primitive characters of the "Archi-annelida" (Polygordiidæ) are struck off at one blow. No longer can we enumerate as characters of this group the absence of parapodia and chætæ, of external segmentation, of circular muscles, or even of muscles in the wall of the gut, for these statements do not apply to Saccocirrus. And, moreover, it may be added that in this worm the segments are not homonomous, and the pharyngeal sac extends into the third segment.

[1] I have observed a similar dorsal process of the wall in Saccocirrus.

This group, containing the genera Polygordius, Protodrilus, and Saccocirrus, to which Lankester's name Haplodrili might still be applied, we should regard not as ancestral to all the Annelida, but as composed of specialised offshoots of the Annelid stem (probably, indeed, of the Polychæte stem itself), in some respects primitive, in other respects highly specialised.[1] As specialised characters we may reckon the development of a contractile " head cavity " (Protodrilus and Saccocirrus), of a very complex genital apparatus (Saccocirrus), and the partial (Saccocirrus) or total loss of parapodia and chætæ (Polygordius and Protodrilus). All three genera possess two prostomial tentacles.

If it be objected that in the foregoing pages I have tacked much theoretical speculation on to very little fact, my excuse must be that I have endeavoured not so much to add to the number of existing theories as to diminish it, and so to bring back the question of the affinities of Polygordius and Saccocirrus to the position it occupied before the " Archiannelid theory" was put forth.

The remarkably close affinity which has been shown to exist between Saccocirrus and Protodrilus seems to force on us the conclusion that the absence of parapodia and chætæ in the Polygordiidæ is not primitive, but secondary.

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[1] Giard seems to me to have been very near the truth when he wrote of Polygordius, " C'est un type d'Annélide archaïque et aberrant " (**4**).

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EXPLANATION OF PLATES 27—29,

Illustrating Mr. Edwin S. Goodrich's paper "On the Structure and Affinities of Saccocirrus."

All the figures, excepting No. 7, are of Saccocirrus papillocercus.

FIG. 1.—Nearly median sagittal section of the anterior end, showing the root of the tentacle and the pharyngeal sac. Cam. D, oc. 2.

FIG. 2.—Somewhat diagrammatic representation of the anterior end, drawn from living specimens and preparations. The internal organs are seen by transparency; the nervous system is coloured yellow.

FIG. 3.—View of a portion of a genital segment of a female. The nephridium and spermatheca are shown in optical section. From the living. Oil im. $\frac{1}{12}$.

FIG. 4.—Highly magnified view of a small portion of the wall of the spermatheca in optical section.

FIG. 5.—Similar view of a portion of the wall of the intestine.

FIG. 6.—Highly magnified view of a small region of the ventral surface of a genital segment of a female, showing beneath the transparent skin the junction of the spermathecal and nephridial ducts. Oil im. $\frac{1}{12}$.

Fɪɢ. 7.—Portion of a transverse section of Polygordius neapolitanus showing the nephridium lying on the oblique muscles. Cam. D, oc. 3.

Fɪɢ. 8.—One of the supporting rods of the penis.

Fɪɢ. 9.—Portion of three genital segments of a male, seen under pressure from above. The internal organs are represented in optical section. From the living. Oil im. $\frac{1}{12}$.

Fɪɢ. 10.—Portion of a transverse section passing through a penis. Cam. D, oc. 2.

Fɪɢ. 11.—Part of a similar section passing through the nephridium and sperm-sac. Cam. D, oc. 2.

Fɪɢ. 12.—Section through the septum and edge of the funnel in a male genital segment. Cam. Oil im. $\frac{1}{12}$, oc. 3.

Fɪɢ. 13.—Section through the spermatheca and its duct from a longitudinal series. Cam. Ap. 4 mm., oc. 3.

Fɪɢ. 14.—Diagram of the male and female excretory and genital ducts, seen in transverse section.

Fɪɢ. 15.—Portion of a sagittal section of several segments in the œsophageal region of a female, showing the nephridia opening into the cœlom. Cam. D, oc. 2.

Fɪɢs. 16, 17.—Two transverse sections of one series, the first taken through the posterior end of the brain, the second across the mouth. Cam. D, oc. 2.

Fɪɢs. 18—20.—Three transverse sections of one series, showing the position and structure of the ventral pharyngeal sac. Cam. D, oc. 2.

Fɪɢ. 21.—Transverse section of a genital segment of a female. Cam. D, oc. 2.

Fɪɢ. 22.—Small part of a similar section, showing the position and structure of the nephridium. Cam. Oil im. $\frac{1}{12}$, oc. 3.

Fig. 1.

prostomium nuchal organ epidermis oesophagus

tentacle

head cavity

lip

mouth

muscular pad prot...

Fig. 2.

prostomium ampulla stomatogastric nerve oesophagus

tentacle

lip

muscular pharyngeal sac ventral ve...

refringent bodies

coelomic epithelium

Fig. 4.

Fig. 5.

Fig. 3.

septum

nephridium

spermatheca

body-wall

external
pore

parapodium

ovum

parapod
ium

nephridial canal

Fig. 6.

spermathecal
duct

epidermal
glands

external pore

10.

septum

funnel

spermatozoa

penis

intestine

testis

12.

nephridium

oblique muscles

nephridium

♂   ♀   14.

nephridium   nephridium

penis

sperm. sac   intestine   spermatheca

11.

sp.

13.

15.

septum   coelom

chaeta   epidermis   nephridia

external

7.

nephridium

penis
extruded

9.

intestine

longit!
muscles

developing
spermatozoa

nephridium

sperm - sac

ac

8.

penis sheath

body-wall

coelom

spermatheca

parapodium

septum

Fig.16.

brain

transverse
canal

epidermis

stomatogastric
nerve

tentacle
muscle

oesophageal
commissure

stomatogastric
nerve

dorsal vessel

Fig.19.

Fig.17.

ampulla

epidermis

stomatogastric
nerve

Fig.18.

ampulla

oesphageal
commissure

buccal cavity

lateral
vessel

Fig.20.

stomatogastric
nerve

oesophagus

ventral diverticulum

muscular pad

Fig.22.

hagus

dorsal longit.[l]
muscles

cuticle

epidermis

oblique muscles

nephridial
canal

ventro-lateral longit.[l]
muscles

stomatogastric
nerve

Fig.21.

coelom

intestine

ova

chaetae

nephri-
dium

atheca

longit.[l]
muscles

spermathecal
duct

spermathecal
duct

chaetae

On the Question of Priority with Regard to certain Discoveries upon the Ætiology of Malarial Diseases.

By

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THOUGH it has long been a popular belief in certain countries that malaria is communicated to man by means of mosquitoes, experimental proof was lacking until a recent date. The history of the mosquito-malaria theory has been amply discussed elsewhere by the writer, to whose papers the reader is also referred for a detailed description of the experimental work on the part played by mosquitoes in the propagation of malarial diseases.[1]   It is not the object of this paper to discuss these matters in detail.

Persons who read the medical literature of but one country will naturally become biassed in their judgment. This accounts for the fact that at present different investigators receive the credit of having definitely established the part played by mosquitoes in malarial diseases. In view of the confusion which will naturally result from the claims made

[1] Nuttall, G. H. F. (1899–1900). I. "On the Rôle of Insects, Arachnids, and Myriapods as Carriers in the Spread of Bacterial and Parasitic Diseases of Man and Animals: a critical and historical Study;" 'Johns Hopkins Hospital Reports,' vol. viii, pp. 1—154, 3 plates (Bibliography). II. "Die Mosquito-Malaria-Theorie," 'Centralbl. f. Bakteriologie,' vol. xxv, pp. 162—170, 209—216, 245—247, 285—296, 337—346 (Bibliography). III. "Neuere Forschungen über die Rolle der Mosquitos bei der Verbreitung der Malaria: Zusammenfassendes Referat;" 'Centralbl. f. Bakteriologie,' vol. xxvi, pp. 140—147, and vol. xxvii, pp. 193—196, 218—225, 260—264, 328—340 (exhaustive Bibliography).

in various quarters, it seems eminently desirable to give a brief impartial summary of the experimental work which has been done, relying solely upon published researches, these being cited in their chronological order. With the facts thus marshalled before him every reader is at liberty to draw his own conclusions.

The study of the hæmocytozoa begins with the discovery by Ray Lankester in 1871 of Drepanidium ranarum. Human malarial parasites were seen, but their significance not comprehended until Laveran published his investigations in November, 1880. Following upon the fundamental work of Laveran, the most important discovery was that of Golgi (November, 1885), who demonstrated the relationship existing between the life-cycle of the parasites within the human body and the occurrence of the febrile attack. With regard to these investigations there has never been any dispute on the question of priority, but this is far from being the case with the discoveries which followed. Any further disputes regarding the priority of subsequent discoveries should be disposed of by such a chronological record as that which follows, in which not only the year, but also the month and even day of publication are given.

Chronology relating to certain of the more Important Recent Researches on Malaria.

1893 and 1895, Sacharoff demonstrated the presence of chromatic substance within the "flagella" of certain avian parasites by means of the Romanowsky stain.

December 17th, 1895, Ross observed the process of "flagellation" of crescentic parasites to occur in the stomach of mosquitoes (species not determined) fed on the blood of a malarial patient.

1896, Bignami and Dionisi report the negative results of two experiments made in 1893–4 with mosquitoes (species uncertain) collected in malarious localities, the insects being permitted to bite healthy persons. They attribute the failure of the experiment to the dispersion of

the insects in the room where they were liberated, and to the experiment not having been continued long enough. They cite Calandruccio as having observed the degeneration of malarial parasites in the stomach of mosquitoes (species not stated).

November 13th, 1897, MacCallum, in Baltimore, found that the "flagella" of Halteridium and of æstivo-autumnal parasites constitute the male element, and serve to impregnate the "pigmented spheres" or female element. In the case of Halteridium the impregnated spheres became converted into motile "vermicules." This transformation was, however, not observed in the human parasites.

December 18th, 1897, Ross fed mosquitoes upon human blood containing crescentic parasites. The experiments were made at Secunderabad, and were reported upon at the time as follows :

After examining hundreds of mosquitoes fed on malarial blood, always with negative results, he obtained a few which belonged to a species with spotted wings, which he had hitherto not used. As Ross distinctly describes the egg of this species, there is no doubt whatever but that he was dealing with a species of Anopheles. The insects were bred from larvæ, and fed with blood containing crescentic parasites. Four to five days later peculiar pigmented cells were observed lying within the walls of their stomachs. These cells were round or oval; they measured $12-16\,\mu$ on the fourth, and $20\,\mu$ on the fifth day after feeding, and the pigment they contained was similar to that within the malarial parasites in the blood upon which the insects had been fed. Such bodies could not be found in control mosquitoes. Ross concluded that he had found the mosquito which served as a host for the parasite.

February 26th, 1898, Ross refers again to his experiments with crescentic parasites. After examining some scores of "dapple-winged" mosquitoes unfed or fed with healthy blood, all the results were negative until

" at last two of this species were persuaded to feed on a
patient with crescents.   One of them was killed next
day ;   no pigmented cells could be found.   The second
was killed forty-eight hours after feeding ;   numerous
pigmented cells were present.   They were all small,
much smaller than epithelial cells, ovoid, about
7 μ in the major axis, and each contained about
twenty granules of typical pigment, which were
often arranged circumferentially, just as in the malarial
parasite."   Though it is not stated in this publication
that he raised these mosquitoes from larvæ, reference to
Ross's previous paper (p. 1786) will show this to have
been a part of the method he employed.

Experiments with Tertian Parasites.—" A hundred or more grey or
  ' barred-back' mosquitoes, unfed or fed on healthy or crescent blood,
  have been dissected without finding the pigment cells.   At last one was
  observed feeding on a patient whose blood that morning had been seen
  to contain numerous mild tertian parasites."   Killed on the third
  day, the insect contained many pigmented cells measuring
  8—25 μ.   (Ross subsequently discarded this experiment, as it was
  possible that the insect which was not raised from the larva had become
  infected with some other parasite.)

May 21st, 1898, Experiments on Proteosoma.—Work-
    ing in Calcutta, Ross observed the development of
    Proteosoma in a species of Culex (subsequently
    determined as C. fatigans, Wied.), the insects being
    fed on the blood of infected crows, larks, and sparrows.
    The parasites found in the external coat of the insects'
    stomachs measured 6 μ after thirty hours, 60 μ after six
    days.   " Successive feeds by the same mosquito on the
    same bird are followed by fresh crops of young coccidia.
    . . .   Similar pigmented cells " had been previously
    observed in mosquitoes fed on human parasites.   Ninety-
    four per cent. of the mosquitoes fed on blood containing
    mature Proteosoma became infected.
September 24th, 1898.—Manson reported to the British

Medical Association Meeting at Edinburgh (July) on behalf of Ross regarding further experiments with Proteosoma. These observations showed that the encapsulated parasites, on reaching a certain size, ruptured and emptied their contents into the cœlom of the insect. The contents of the ruptured capsules consisted of minute spindle-shaped bodies, and these bodies subsequently accumulated in the salivary gland of the insect. When this had occurred the insects were capable of communicating the proteosomal infection to healthy birds. Of twenty-four sparrows exposed to the bites of insects fed on mature parasites, twenty-two became infected.

October 1st, 1898, Grassi reported that he had reason for suspecting three species of Culicidæ as being carriers of malarial infection, claiming that they were confined in their geographical distribution to those regions where malaria was prevalent in Italy. The three species were Culex penicillaris, Anopheles claviger (syn. A. maculipennis), and a purported new species, Culex malariæ.[1] It has since been proved that only

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[1] In his paper in the ' Policlinico ' (October 1st, 1898), Grassi writes : " In conclusione, io sono d' avviso che il Culex penicillaris e l' Anopheles claviger o per lo meno il Culex penicillaris, fors' anche il Culex malariæ, nella malaria si comportano come le zecca nella febbre del Texas." Grassi therefore makes a misstatement in a later paper (December 1st, 1900) when he writes, " Proclamai come indiziati due specie di culex, ma sopratutto l'Anopheles claviger." It is curious that Grassi should subsequently have continued to lay stress upon the geographical coincidence having led him to the discovery of Anopheles claviger being a host of malarial parasites, for two out of three species which he for this reason supposed must be hosts were afterwards proved not to be such. He certainly considered A. claviger at first to be of quite secondary importance ; we have his own words for it : " Certi casi di malaria sviluppatisi in Settembre a Locate Triulzi, nei quali gli Anopheles di certo o non punsero o soltanto rarissime volte, denunciano decisamente come trasmissore il Culex penicillaris, enormamente comune in tutti i luoghi malarici." (The italics are Grassi's.) It is but fair to Ross to state here that Grassi in his paper of the 1st of October refers to the experiments made by Smith and Kilborne upon Texas fever, and by Ross upon avian malaria as having been a " forte argumento "

the second of the three species named can serve as a
host for human malarial parasites. The coincidence in
the geographical distribution of ague and malaria-bear-
ing mosquitoes in Italy, as claimed repeatedly by Grassi,
has been disproved by Celli. The claim that this geo-
graphical agreement would probably be found to hold
in other parts of the world has been disproved by Nut-
tall, Cobbett, and Strangeways-Pigg (1901) in England.
We cannot, therefore, accept Grassi's statement that he
discovered the malarial mosquito because of its geo-
graphical distribution, pretty and ingenious as the
hypothesis seemed in the beginning. It seems certain
that Grassi was after all entirely guided by Ross's pub-
lication of December 18th, 1897, in which he describes
an insect with spotted wings and eggs like those which
characterise Anopheles.

November 6th, 1898, Infection Experiment on Man.—
Grassi mentions that Bignami had made an infection
experiment by means of mosquitoes (the three species
above named were employed) collected at Maccarese,
a malarious locality. The result was positive in this
case, the person acquiring æstivo-autumnal fever.
(Several infection experiments were subsequently car-
ried out by Bignami, Bastianelli, and Grassi in colla-
boration, these being reported in various papers of
later date. The first experiment did not prove which
species harboured the parasites, and of itself was insuf-
ficient to establish the theory on a firm basis.)

December 4th, 1898, Bastianelli, Bignami, and Grassi
observed the development of crescentic parasites
in Anopheles claviger, the appearances correspond-
ing to those described by Ross for Proteosoma on the

in favour of the mosquito-malaria hypothesis. In the paper read on the next
day at the Accademia dei Lincei, under the same title as that which appeared
in the 'Policlinico,' Grassi omits to mention Ross, though he refers to what
was known regarding Texas fever. The paper, published in the 'Transac-
tions' of the Accademia, differs in several respects from that which appeared
in the 'Policlinico.'

fourth day in Culex. Referring to his experiments with
human parasites, they write, "Verisimilmente i due
mosquitos coli ali macchiate nei quali il Ross in India
trovo stadi di sviluppo simili a quelli del proteosoma (3°
giorno circa) appartenevano pure alla specie Anopheles
claviger, Fabr." (This statement is of interest in view
of Grassi's subsequent claim that Ross might very well
have been working with insects belonging to the genus
Culex, and not with Anopheles at all.) They, more-
over, consider that Ross had not certainly determined
the development of the crescents in his mosquitoes, for
his observations had been broken off at too early a date;
besides which the insects might have infected themselves
with hæmatozoa from some other animal. We have seen
that the latter supposition is unwarranted, because Ross's
Anopheles were raised from larvæ. Moreover they
themselves neglect to state that they raised their Ano-
pheles from larvæ, so we must presume that they did
not.

Infection Experiment on Man.—In a foot-note to the
above publication it is reported that the authors had
successfully infected a person with tertian fever by
means of infected A. claviger, collected at Maccarese.

December 22nd, 1898, Grassi, Bignami, and Bastianelli
follow the development of crescentic parasites
in Anopheles claviger to the formation of "sporo-
zoites," the escape of the latter into the cœlom of the
insect, and their accumulation in the salivary gland.
The development was found to be slower at 20° to 22°
than at 30° C. The fully developed capsules measured
70 μ, the sporozoites measured 14 μ. The process of
development, the size of the fully developed capsules,
and of the sporozoites, were the same as Ross had
observed in Proteosoma.

The development of tertian parasites was observed to
take place in A. claviger up to the fifth day.

February 2nd, 1899, Koch published a preliminary note

upon the results of the investigations conducted by the German Malaria Commission, consisting of himself, R. Pfeiffer, and H. Kossel. Further details will be found in a publication which appeared September 8th, 1899. The Commission observed the development of Proteosoma in Culex nemorosus, from the formation of the "vermiculi" described by MacCallum for Halteridium to their appearance in the salivary gland of the insect. The process of fertilisation was found to occur in Proteosoma, as MacCallum had found for Halteridium and human crescentic parasites. Healthy birds were successfully infected by means of infected insects. The later publication, which is illustrated by excellent microphotographs, completely confirms the observations of Ross and others.

February 5th, 1899, Grassi, Bignami, and Bastianelli observe the development of quartan parasites in A. claviger. Ross (September 2nd, 1899) observed the development of quartan parasites in a species of Anopheles in Sierra Leone.

January 23rd, 1899, Daniels reported to the Royal Society that he had been able to confirm Ross's observations with Proteosoma. He followed their development in a species of Culex, and successfully infected healthy birds by means of infected insects. He added nothing to what Ross had already found.

April 19th, 1899, Bastianelli and Bignami reported further studies upon the development of tertian parasites in Anopheles claviger, and describe three successful infection experiments on man by means of A. claviger previously fed on tertian parasites.

May 7th, 1899, Grassi, Bignami, and Bastianelli report to the Accademia dei Lincei that they had observed the development of tertian and crescentic parasites in Anopheles bifurcatus.

June 18th, 1899, Grassi observed the development of tertian and crescentic parasites in Anopheles

pseudopictus, but not in various species of Culex. The latter result again obtained later (October 4th, 1899).

June 28th, 1899, Ross stated that Proteosoma scarcely developed in Culex at 21°, and that the growth of the parasites was already slowed at 27° C. in Calcutta. The development of tertian parasites in spotted-winged mosquitoes raised from larvæ was also observed (letter dated February 22nd, 1899, to Nuttall; see 'Centralbl. f. Bakteriologie,' vol. xxv, p. 908).

September, 1899, Bastianelli and Bignami give a detailed description of tertian and crescentic parasites, the publication being accompanied by the best coloured plates hitherto published, illustrating their development. They prove that a single infected Anopheles claviger may communicate malaria (tertian) to man.

May 4th, 1900, Ziemann, working in Cameroon, observes the development of the parasites of tropical malaria in two species of Anopheles, as also the development of tertian parasites in one species of Anopheles. He followed the development to the appearance of sporozoites in the salivary glands of the insects. He subsequently (November 22nd, 1900) found that the parasites would not develop in Cimex lectularius nor in sandflies.

September, 1900, van der Scheer and van Berlekom, in Holland, observe the development of tertian parasites in A. claviger.

September 29th, 1900, Manson reported a positive infection experiment with tertian-infected Anopheles (spec. ?) imported from Rome, the insects being permitted to bite his son in London.

October 6th, 1900, Rees reports a similar experiment to the former.

After perusing the above chronology, and remembering the question most disputed—the discovery of the develop-

ment of human parasites in Anopheles, we must conclude
that the pigmented encapsulated bodies observed by Ross in
" spotted-winged mosquitoes " at Secunderabad were cres-
centic parasites in early stages of development.   In his first
paper Ross definitely states that he raised the imagos from
larvæ kept in bottles ; that the parasites which subsequently
developed within them contained a pigment similar to that
of the parasites in man ; and his description of the insects'
eggs leaves no room for doubt but that they were Ano-
pheles.   (In their paper of December 4th, 1898, Bastianelli,
Bignami, and Grassi even made the statement that it is
extremely likely that Ross's spotted-winged mosquito was
A. claviger !)   The work done subsequently on Proteo-
soma quite rightly confirmed Ross in his belief.   We are,
however, indebted to the Italian investigators named for
completing the study of the further development of human
parasites in various species of Anopheles, these studies
being subsequently pursued by still other investigators in
other countries.[1]   Ross is perfectly justified in laying stress
upon the fundamental importance of his discoveries in the
development of Proteosoma, and there can be no doubt
whatever about his work having served as a guide to sub-
sequent investigators.   There is no denying that both the
human and avian parasites referred to offer great points of
similarity throughout.   The assumption was, therefore, per-
fectly justified that the further stages in the development of
crescentic parasites such as Ross had observed at Secunder-
abad would be identical with what he saw in the case of
Proteosoma afterwards in Calcutta.

    In conclusion we must not forget to mention the name of
Patrick Manson, who until recently took no part in the
experimental solution of the problem, but who throughout
Ross's investigations, which he stimulated, did much to
further the studies which in one direction at least have
reached such a satisfactory conclusion.

        [1] It has not been deemed necessary to refer to all of these.

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Studies in the Retina: Rods and Cones in the Frog and in some other Amphibia.

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With Plates 30 and 31.

Part II.[1]

The first part of this paper was devoted to showing that the structures called " cones " in the amphibian retina were the earlier stages in the development of the new rods required by growth, and that they force their way in wherever there is room for them between already existing rods. The forms of these elements with the positions of their nuclei[2] were alone dealt with. In this paper it is proposed to give some account of the intimate structure of the amphibian rod. The minute details to be described will necessitate some discussion of the physiological processes which, so far as I have been able to interpret them, underlie their forms.

Little success has so far attended the attempts of naturalists to unravel the finer structure of the rods. Indeed, the subject seems to have been temporarily closed by the classical researches of Max Schultze in the sixties, for since that time little or no advance has been made. The earlier

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[1] The final revision of this MS. was kindly undertaken by my friend Mr. Martin Woodward, during my temporary absence from England.

[2] On page 44 I inadvertently attributed to Borysiekiewitz an observation of my own. This will be fully dealt with in Part III.

literature is, however, full of scattered observations, and it is possible that some of them may have been overlooked by me or far too briefly noticed. I do not pretend to have mastered the whole of the literature on the retina. I do not wish, therefore, to make any claims to priority, but simply to describe my observations, referring briefly to those of former students, so far as I know of any covering the same ground.

And here I should add that, while confining myself in this paper solely to the Amphibia,[1] these researches have extended over other Vertebrates, and that the general conclusions arrived at are not drawn solely from the facts here described.

Enveloping Membranes.—While the existence of the membrane investing the inner limb of the rod requires no demonstration, it has been much disputed whether the outer limbs possess any such envelope or not. Apart from the fact that such a covering is difficult to demonstrate, it is possible that the conception of the rod as a cuticular structure may have strengthened the doubt. It has long been known that the outer limbs of the rods can be made to divide up transversely into discs, and that on such a dissolution no investing membrane can be seen (cf. Max Schultze's figures, ' Arch. mikr. Anat.,' Bd. iii, pl. xiii, figs. 11 c, etc.).

Merkel[2] found membranes wherever he looked for them except in the Amphibia, while Landolt[3] figured very thick homogeneous membranes covering the rods (frog and newt) and the cones (newt). I am not aware that these have ever been confirmed, and I doubt their existence. He figures them even passing in between outer limb and ellipsoid. Something like what he figures may be seen in my fig. 13, c—i, the significance of which will be discussed later on. In the meantime I may state that I do not regard the thick rind there shown as an outer covering.

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[1] The following forms have been examined:—Rana temporaria, Bufo vulgaris, Molge cristata and M. vulgaris, Salamandra maculosa, and Siredon pisciformis.

[2] ' Arch. Anat. u. Phys.,' 1870, pl. xiv.

[3] ' Arch. mikr. Anat.,' Bd. vii, 1871, p. 81, pl. ix.

That enveloping membranes occur in the outer limbs of Amphibian rods is certain, both on theoretical grounds and because they can be demonstrated.

As we saw in Part I of this paper (this Journal, p. 29), the rods are primarily protoplasmic vesicles protruded from the retina. The walls of the vesicles are of extraordinary delicacy and transparency, and it will be a triumph of microscopic technique when retinas can be fixed so as to show them intact. They are best seen in their very earliest stages of protrusion, before any rods are formed and the pigment is only just being forced away from the retina by their increase in number and size. From this early stage we traced them through their principal form-phases till they became normal rods, and all these phases were not only consistent with their being long, membranous sacs, but even confirmatory of this conception of their essential structure. Lastly, the persistence of the membrane covering the inner limbs has, as we have seen, long been an established fact.

But granted that in all the earlier stages of the rods we have a wall to the vesicle—a wall which persists in the inner limb,—we have still to ask whether that is the case with the outer limb when the rod is complete. May not the protoplasmic wall merge in the substance which fills up the interior of the outer limb and lose its individuality, so that it would be impossible to speak of any investing membrane? This is, of course, quite possible; and, moreover, it is certain that even if it preserved its individuality one would rarely expect to demonstrate the existence of such a delicate film of transparent protoplasm round the outer limb of the amphibian rod, with its usually refractive contents. Actual observations, however, show clearly that the protoplasmic wall does retain its individuality, and that to the last the rod is a thin protoplasmic vesicle filled up with matter, the origin and nature of which will be discussed in the following pages.

As demonstration of this persistence of the protoplasmic wall of the vesicle, I will call attention to Pl. 30, fig. 2, which is taken from the retina of a toad. All the rods in this

retina are obviously bags which have, under pressures and strains, lost their normal cylindrical shapes, and are now pulled out or crushed together into every variety of form, from short, rounded sacs to long, thin clubs with round knobs at the tips.[1] Endless, too, are the instances in which the inner and outer limbs have been pulled somewhat apart, and the stretched or torn membrane becomes visible under good microscopic powers. Important, also, in this connection is Pl. 30, fig. 1, from a newt, in which in one spot all the rods were broken away, but their basal portions persisted emptied of all contents except the remains of the ellipsoids. This last is a fortunate observation, because it shows that, in essence, the inner and outer limbs are simply two sacs separated by a thin wall, and that the great differences seen between them must be referred entirely to their contents. To this we shall return later.

Lastly, I have sections of a newt's retina in which the thin coverings of the rods have taken stain, and are quite demonstrable in optical sections.

External Markings.—The longitudinal striation of the outer limbs of the rods has long been seen, but its nature has never been satisfactorily settled. Max Schultze regarded it as a furrowing of the surface, and figured the cross-sections of the rod as having an outline like that shown in Pl. 30, fig. 8.

With regard to the inner limbs of the rods in Amphibia, exact records of striation are few. The well-known "Faserkorb" of Max Schultze was found by him, " essentially the same," in all the classes of Vertebrates, including the Amphibia. He records finding it in the axolotl, and he figures it in the newt.[2] Hoffmann also figures the upper ends of these or similar threads round the bases of the inner limbs of amphibian rods, and forming a ring of needle-like points similar to those figured by Max Schultze as projecting from

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[1] Max Schultze gives a somewhat similar figure, viz. the sac-like rod of a pike, produced artificially ('Arch. mikr. Anat.,' Bd. iii, pl. xiii, fig. 18 a).

[2] 'Arch. mikr. Anat.,' Bd. v, p. 379, pl. xxii, fig. 2 a.

the membrana lim. externa when the rods and cones are broken away (cf. Hoffmann's figures [Bronn's 'Thierreich; Amphibien,' pl. xxiii, 11—18, and pl. xxiv, 2—8] with Max Schultze's ['Arch. mikr. Anat.,' Bd. v, pl. xxii]). The latter author traced the threads of his "Faserkorb" proximally into the connective tissue of the outer nuclear layer, but inasmuch as distally they ran on to the outer limbs of the rods, he clearly wished to see in them the ends of the nerves (cf. Stricker's 'Handbuch'). Hoffmann, who figures the basal threads as running only a short way down the inner limbs of the Amphibia, and then only loosely applied, apparently regarded them as nothing more than hair-like prolongations of the membrana lim. externa. Further, as stated, Max Schultze described a continuation of his "Faserkorb" a short way down the outer limbs. Hoffmann (loc. cit.) also figures somewhat similar threads running on to the outer limbs of amphibian rods; these he could not explain because his basal threads were not supposed to run the whole length of the inner limbs.

There seems, then, to have been a distinct tendency to attribute to the inner limbs in the Amphibia a system of longitudinal fibres, though apparently not so pronounced or complete as the "Faserkorb" of the inner limbs of the human rods and cones.

We may say, then, that the rods are thought to be longitudinally striated, but while the inner limbs are externally striated with fibrils the outer limbs are marked by furrows. My own observations entirely confirm the existence of longitudinal striæ; but those on the inner limb and those on the outer limb are not distinct in kind from one another, but are parts of one system.

Long before I had succeeded in discovering the true relations of these striations to one another, I had noticed that the markings on the outer limbs consisted far more of longitudinal rows of dots than of furrows. The rows, though mostly continuous, are not always strictly parallel; and the dots only occasionally fall into circular series running nearly

evenly round the rod. I find in my notes that at times two series of dots at right angles to one another are recorded as marking the exterior of the rods. The dots were usually slightly drawn out longitudinally. Fig. 3, *a*, *b*,[1] are from my earlier drawings. It was noticed that the dots appeared almost as if they raised the surface of the rod, and that, hence, between the rows there were slight furrows, but on this point I have never satisfied myself; if any furrowing exists, it must be very slight. While these longitudinal rows of dots on the outer limbs were clear with any well-preserved retinas stained in Ehrlich's hæmatoxylin, it was not till I employed the iron-alum hæmatoxylin method of staining that I saw any striation of the inner limbs, and then, while that on the outer limbs was very strong and regular, that on the inner limbs was hardly ever regular, often indeed not recognisable as a system of striæ at all. Further, I then found, as stated, that the two are not distinct phenomena, but that the fine staining threads which run down in the walls of the inner limbs are continued on to the outer limbs, as Max Schultze observed: but they do not stop short, as he supposed; on the contrary, they run down the whole way, swelling into small clumps of staining matter at short distances from one another, these clumps being the rows of dots I had seen all along.

Fig. 11 shows diagrammatically the arrangements of this system of threads, while figs. 13, *a*—*d*, and 29, *a*, *b*, *e*—*j*, are from actual preparations of retinas from different Amphibia. Beginning usually faint near the nucleus, and seldom as a distinct system, the arrangement gets more pronounced distally. It may be very pronounced indeed near the ellipsoid (e. g. in the toad, fig. 13, *a*, *b*). Here it passes on to the outer limbs, and, where inner and outer limbs are stretched a little apart, may be seen as a nearly regular ring of smooth, thin threads,

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[1] Cf. Max Schultze, 'Arch. mikr. Anat.,' Bd. iii, pl. xiii, fig. 11, where he shows a rod covered with " pigment granules ; " another figure occurs in Bd. v, pl. xxii, fig. 17 *a*. The dots above referred to are quite distinct from pigment granules, one of which I have drawn in fig. 3, *b*.

not free, like Max Schultze's needle-like prolongations of his "Faserkorb," but rather as thickenings of the stretched membrane. On these threads clumps of staining matter soon appear (fig. 13, c). In the diagram, fig. 11, the system is drawn very symmetrically from the nucleus outward, but this is not by any means usually the case. The nearest approach to it has been found in the axolotl, preparations of which inspired this diagram. Fig. 29, b, represents more truly the ordinary conditions. We have a gradual formation of the symmetrical system of striæ towards the distal ends of the inner limbs (though usually quite irregularly), and when formed it passes on to the outer limbs. There is some evidence that this is also what takes place in the human rods and cones, for the "fibrillation" is said to be limited to the outer portions of the inner limbs (cf. 'Quain's Anatomy,' 1894, vol. iii, part 3, p. 49, fig. 52, after Schwalbe).

Some variation seems to occur in the numbers of the longitudinal threads on the outer limbs; they are sometimes very numerous (e. g. newt, fig. 30), at others very sparse; and this is not only the case in different Amphibia, but in different specimens of the same. Figs. 3 and 6 are from different frogs; in one case the threads are crowded, and in the other quite far apart: the rods in this latter case have been greatly stretched, but one does not see why that should lessen the number of striæ. The significance of some of the irregularities of this system of striæ[1] will be better understood when we have described the connection between these threads and the contents of the vesicles in whose walls they occur.

The rods, then, are delicate protoplasmic vesicles, in the thin walls of which staining threads occur. In the walls of the outer limbs these threads are usually more or less beaded with clumps of staining matter. The claim made by Max Schultze and Hoffmann (see the figures and plates re-

[1] The spiral twist of the striæ on the outer limbs has been rightly attributed to torsion. I have only seen it, and then very marked, on rods broken off like that shown in fig. 13, c.

ferred to above) that the outer limbs of the cones are also striated will be discussed later.

The Contents of the Rods. — According to Max Schultze the outer limbs of the rods are built up of discs joined together by some cementing substance. This description, propounded by so great an observer, seems to have had the effect of turning away attention from Hensen's figures of cross-sections of rods of the frog,[1] which clearly showed some definite internal structure. It must, however, be admitted that Hensen's cross-sections differed among themselves; there were two kinds (see Pl. 30, figs. 7, *a, b*, which reproduce them), and they were not easy to reconcile with one another. Nevertheless I think it cannot be doubted that the discs of Max Schultze, which are, I believe, artificial phenomena, helped to consign them to temporary oblivion. As a matter of fact, Hensen's figures, which were optical sections and hence hazy, come near the truth, and are, as we shall see presently, reconcilable with my own observations. It seems fairly clear, for instance, that his two sections may compare with my own figs. 9, *b*, 13, *g*, and 12, 13, *k*, respectively. Hensen, however, was too anxious to discover nerve-endings, and was therefore prepared to see fibrils in any clear space or small refractive portion of the section. In the case of fig. 7, *a*, he thought the meshes of the reticulum round the periphery of the sections were fibrils of doubtful significance, but in fig. 7, *b*, those in the centre were regarded as nerves,— three, he thought, in the centre of each rod.

With regard to the contents of the inner limb of the rod, its most conspicuous element, the " ellipsoid," has long been known; it has been regarded as the organ in which the nerves end (cf. fig. 23, on the right), and deserves a separate section. This is readily accorded, inasmuch as it admits of being described separately, and what follows will be clearer if we temporarily ignore it. At the same time we shall find it necessary to discuss the contents of both outer and inner limbs together, passing by for the present this particular body.

[1] Virchow's ' Arch. path. Anat.,' Bd. xxxix, 1867, pl. xii, figs. 7 and 8.

For a clear understanding of the description and figures relating to the contents of the rods to be here given, it is worth while turning once more to their development, and noting that, in essence, they are protoplasmic vesicles extruded from the retina. As seen in the first part of this paper, the early stages of these vesicles are seldom found intact, but when they are they usually appear clear, and apparently with only fluid contents. Faint traces of delicate protoplasmic networks may occasionally be seen (see Part I, Pl. 3, fig. 16). Networks are, again, found in well-preserved and properly stained preparations in the large basal vacuoles of the cones (see Pl. 31, figs. 23, 27, 28). Later we find distinct networks in the inner limbs of cones and rods, with usually a certain number of very pronounced threads running down in their delicate walls (see above and figs. 29, a, h, i, j) ; so also in the outer limbs—which, as we saw in Part I of this paper, began as fluid vesicles at the tips of the cones— a protoplasmic reticulum ultimately appears. The staining reticulum in the outer limbs is not often found as a simple meshwork, but this is sometimes the case, and we may assume that it first appears as such. Two instances are shown in the figures (4, b, and 6). We gather from these cross-sections that the clumps on the longitudinal threads running down the rods are the points of attachment of this internal reticulum to the walls of the vesicle. As a rule this reticulum is not evenly distributed ; we find a tendency for it to be compressed into the axis of the rod, always, however, remaining attached by its threads to the wall fibrils. As this compression increases the threads of the internal axial portion get very thick, coarse, and matted together. The compression may go so far that the reticulum merely consists of an axial strand with a few meshes in it, while the attaching threads are lengthened so as, in cross-section, to look like the spokes of a wheel (see figs. 12 and 13, k, and also cf. Hensen's optical section reproduced in my fig. 7, b).

So far, then, the rods are protoplasmic vesicles, each

divided into two compartments by a cross-membrane ;[1] and
as they assume their definitive shapes they become gradually
filled with a staining reticulum, which, omitting the ellipsoid,
develops especially strongly in the outer and, in the adult
Amphibian rod, more important of the compartments.

This account seems to justify the description of the rods as
prolongations of the " visual cells." It is obvious that each
may be regarded as a prolongation of the cytoplasm belong-
ing to each rod nucleus, a prolongation at first filled with
fluid, but sooner or later containing also the usual reticulum
which ramifies through the cytoplasm of ordinary cells. My
only objection to this description is to the term "visual
cells." My researches long ago compelled me to abandon
the usual conception of the retina as composed of cells, and I
now regard it as a syncytium, in which the nuclei
are arranged in layers, not as fixed morphological
units, but solely as centres of physiological acti-
vities which may at times require them to migrate
outwards, ultimately, if life lasts long enough, to
become rod nuclei. The evidence for this is, to my mind,
so convincing that I have no hesitation in making the state-
ment, even though it stands in such startling contrast to the
conclusions of nearly all the most recent workers on the
retina, such as Ramón y Cajal, Dogiel, and others, and though
a criticism of the method and results of these authors is here
out of the question. In the first part of this paper, p. 43, I
referred to the migration of nuclei from the middle nuclear
layer to the outer nuclear layer, and showed that, even if we
could not see evidence of it in our sections, it would be
necessary to assume it ; and I here add figures of nuclei
passing through the outer reticular layer in different Am-
phibia (figs. 21—23, 25, 26) ; while, again, in fig. 24 one or
perhaps two nuclei have moved outwards together, leaving a
space vacant in the middle nuclear layer, and apparently

[1] I have not yet been able to ascertain for certain the time of appearance
of this membrane. As we shall see below, it probably appears before the
ellipsoid.

dragging the cytoplasmic reticulum after them. Such figures might be multiplied indefinitely, and, moreover, taken from nearly every retina that is closely enough examined. I reserve full discussion of this somewhat revolutionary conception of the retina as a syncytium for another communication. But in the meantime I feel compelled to state my conviction that the rods are not the prolongations of "visual cells," but protrusions of the cytoplasm of the retinal syncytium, each, at least in the Amphibia, dominated by a nucleus.

Passing on from this digression, and regarding it for the moment as indifferent how we describe the rods in their relations to the nuclei, the evidence is abundant, as I shall now endeavour to show, that these nuclei are the centres of the physiological activity which gives rise to the rods.

In the first place, a great part, if not all of the fluid or hyaline matter, here always spoken of as fluid, which first causes the vesicle to protrude, comes from the associated nuclei.

Fig. 17 can hardly admit of any other interpretation than that fluid is extruded by the nuclei into the inner limbs of rods. If it is objected that these figures might as easily be interpreted as representing phenomena due to the stimulation of fixing agents, this argument will not apply to fig. 23, where we see a " double cone,"[1] in which one nucleus is still large and vesicular, while the other is collapsed, because its fluid contents have been discharged into the base of the cone belonging to it. Indeed, a study of cones with their basal vacuoles makes it very evident that the fluid of these vacuoles has been derived from their nuclei. Large vesicular nuclei in the position of cone-nuclei, i. e. well within the membrana limitans externa, are very common and in striking contrast to the more condensed rod-nuclei (figs. 16, *a*, *b*, and 18). The same contrasts may also be found in the other nuclear layers, but here, again, it is impossible to give in this paper

[1] For the correct interpretation of "double cones" in the Amphibia see Part I, p. 33.

an extended account of the observations made relating to this subject. Selecting one more instance, I would refer to fig. 20, in which a large fluid vesicle has been discharged from its associated nucleus, and apparently has not found a way down as a young cone between the adjoining rod-nuclei, or, if part of it has succeeded in doing so, that part did not come into the optical field. Lastly, fig. 19 shows a rod thrust outwards by an increase in size of its basal vacuole.

In the second place, the staining reticulum of each rod is also certainly derived from its associated nucleus. Not only can the reticulum of the inner limbs be seen in direct connection with the linin network of the nucleus (see figs. 29, a, i, j), but a thick stream can be seen descending from the nucleus on to the ellipsoid (figs. 10, 23, 27), a phenomenon to which we shall refer more fully later on. Indeed, if the form of the cone or young rod (figs. 13, d, 15, b, 23, 29, a[1]) with its nucleus surmounting its narrow basal neck be kept in mind, it is difficult to conceive of any other origin than the nucleus for the large amount of staining material which finds its way outwards into what was certainly originally a fluid vesicle, with, at the most, a few delicate reticular strands. The longitudinal fibrils running down the outer limbs are, in their shape and arrangement, evidence for this outward movement, while the clumps of staining matter along the whole length of their threads, and the density of the reticulum in the interiors of the rods, are witnesses of the immense quantity of this staining matter required.

Actual demonstration of the derivation of this reticulum of the outer limb from that of the inner limb, and both from the nuclear reticulum, can be seen in the figures. For instance, there occur, in different parts of the inner limb, often in the wall low down and partly apparently embedded in the ellipsoid, deeply staining refractive bodies, usually globular, and, what is more important to note, always surrounded by clear zones as if they were the centres of small fluid vacuoles (figs. 15, a, and 29, c—g). These are certainly

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[1] Many more are figured in Part I, Pl. 3.

chromatin globules, and are usually found in young rapidly growing retinas.[1] In well-stained preparations it is common to find that, from these bodies, fine threads run down the walls of the outer limb. In one figure of a developed rod this thread was the only one which took the stain (fig. 29, c). In another figure, two staining and rather straggling threads came from one of these bodies, which had apparently been flattened out against the membranous partition between inner and outer limb (fig. 15, a). To this phenomenon, i. e. this membrane acting as a barrier between inner and outer limb, we shall return.

Even where there are no such bright globules of chromatin, the derivation of the reticulum of the outer limb from that of the inner can be at once seen if we study the figures of the developing cones shown in fig. 29, e—j. These figures are merely a selection, and might be multiplied indefinitely. They show quite clearly that the staining material within the outer limb appears where the thin threads from the inner limb come down on its wall. This fact shows that the striation of the outer limbs of the cones figured by Max Schultze and Hoffmann may exist, not as a complete system as they represented it, but as the first beginnings of the subsequent striation of the rods.

Unfortunately none of these figures (29) seem to show the true tips of the cones; still, enough is here seen to demonstrate the point we have immediately in hand.

Lastly I would refer to fig. 26, which is by no means an uncommon phenomenon. A nucleus is seen passing through the outer reticular layer and about to join the outer nuclear layer (that of the rods and cones). It is preceded by a fluid space, while from it a very delicate reticulum streams outwards. This I interpret as representing a very early stage in the formation of a rod, being still entirely within the

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[1] The only other figure I know of which shows such a body is one by Hensen (l. c., fig. 7, c), who, as we have seen, came so near discovering the structure of the rods, having failed apparently for the want of better microscopic technique.

retina. The fluid vesicle in the ordinary course of things would, on approaching the mem. lim. externa, form the usual conical protrusion, and into it the staining reticulum would follow. On the other hand, it is only fair to note that streams of very delicate staining reticulum occur elsewhere; one other, for instance, is shown running up from the left-hand rod-nucleus in fig. 27. The explanation of this must be deferred until I can at the same time give the evidence in full on which it rests, and this I hope to be able to do in the near future.

Further Contents of the Rod.—So far, then, we have described the origin and structure of the rod as a protoplasmic protrusion from the retina, containing the usual staining network very strongly developed in the outer limb, and with some clear fluid in the meshes or interstices.

This network and this fluid are not, however, the sole contents of the normal rod, and the striking difference between inner and outer limbs, apart from the difference in shape and density of the reticulum, is found in the fact that while the former remain protoplasmic vesicles, with apparently soft, flexible walls filled with these elementary constituents which we have described (passing over for the moment the ellipsoid), the outer limbs become filled with some highly refractive substance, which renders them turgid.

The change from the loose, long terminal bag found at the tip of the advanced cone (c_4) to the outer limb of the rod (r_1) (see Part I, Pl. 3, fig. 4) is seen to consist not only in the squeezing outwards of the staining matter to the distal end of the inner limb, but also in the filling up of the outer limb. Now while we have traced to its source some of the matter which helps to fill the outer limb, viz. the staining reticulum, this will not account for the refractive contents which now seem to make them turgid and cylindrical. Further, we saw that the outer limbs of the rods lengthened (from r_1 to r_3), and hence apparently continued to take in more of this refractive constituent of their contents; and not only lengthened, but as a rule became also much thicker. I have

noticed also that the outer limbs of Schwalbe's rods (r_1 and r_2) were in most cases rather more deeply stained than the longer, thicker definitive rods, although I lay no great stress on this. The accidents which can never be eliminated from our technical methods are too numerous to allow conclusions to be based upon mere variations in diffuse staining. I mention the point, however, just because it is possible that the proportion of the refractive matter to the staining reticulum might be expected to be less in an outer limb, just beginning to fill up, than in a large swollen rod. It is this refractive matter which gives the rods their characteristic appearances, and which has led to their being classed among cuticular structures.

The source of this refractive matter is to be seen in the pigment epithelium into which the tips of the rods are plunged, and it is largely composed of pigment granules, probably with some portion of the protoplasm of the epithelial cells. At least the absorption of cytoplasm as well as pigment by the rods can actually be shown to take place under special circumstances, as we shall presently see.

In the first place, dealing for the moment with general considerations, I again refer to the development of the rod ; a fluid vesicle is thrust into the pigment layer, and slowly becomes filled with refractive matter. Both the vesicle and the epithelial cells are, so far as we can see, naked protoplasm in the very closest contact with one another,—indeed, tightly interlocked, the pigment cells constantly forcing a passage up between the packed rods.[1] Between these some interaction is almost certain to take place. This interaction is, I contend, in part at least an absorption of pigment by the rods. The pigment of the epithelial cells is constantly recruited by an outward streaming of granules from the choroidal layer adjacent to it, a streaming which can be seen in every successful preparation. So that we may conclude that pigment is being used up and as constantly replaced. The only other alternatives to this view are either that the refractive matter in the outer limbs of the rods comes from

[1] For the evidence that the rod layer is normally compact see Part I.

the retina, or that it is manufactured in situ within the rods.

That it does not come from the retina, from which we can easily trace the fluid and the staining network, we gather from the total absence of any refractive matter in the inner limb except in the ellipsoid; and, as we shall presently see, the position of this body forms additional evidence that the source of the refractive matter is from without inwards towards the retina, and not from the retina outwards.

That the matter is not manufactured in situ we gather from the microscopic appearances, which show very clearly that it is forced in through the walls. The evidence for this is to be seen in the changes already described, which take place in the character of the reticulum within the outer limb of the rod. Figs. 4, b, and 6, b, show this reticulum simply diffused equally across the section; figs. 13, c—k, and 12 show different stages in its compression towards the axis of the rod. Now it is difficult to explain this compression except on the assumption of some matter passing in through the walls and crushing it inwards, stretching, or perhaps merely lengthening the threads which attach it to the walls. Fig. 13, j, shows the process as being irregular, while fig. 14 shows that it may take place locally, i. e. along one side of a rod and not on the opposite side. This observation is important, because it is in keeping with the fact that the tongues of the pigment cells run up lengthwise between the rods. Fig. 13, i, shows that at times the reticulum, though compressed towards the axis, may retain some of its concentric threads, the refractive matter passing them by. The refractive layer was here $1·5\ \mu$ thick, the whole rod being $9\ \mu$.[1]

Again, in eyes in which, after exposure to light, the pigment has been forced up to the membrana limitans externa, individual granules can be seen remaining behind after the general retreat of the pigment, and sticking to the clear protoplasmic walls of the inner limbs. Many of them can

[1] Zenker ('Arch. mikr. Anat.,' iii, 1867, p. 259) discovered that the outer layer of the rod is more highly refractive than the axial portion.

then be seen obviously fading away, the shape being re-
tained, but the bright colour and sharpness of contour have
disappeared, and the whole appearance suggests their being
slowly absorbed. Although, as above stated, with the excep-
tion of the ellipsoid (and the oil globule in the cones of the frog),
I have never found refractive matter in the inner limbs in
Amphibia, cases occur elsewhere in the animal kingdom in
which large inner limbs become filled with it, but in a manner
entirely confirmatory of my argument that its source is the
pigment epithelium. The clinging of pigment granules to
the protoplasmic walls of cones was noted in Part I.

Again, in a series of sections of retinas of animals which
had been exposed for three hours to the light of an arc lamp,[1]
the heat rays being screened off as far as possible, one
interesting result is conspicuous. The pigment epithelium
is here and there disorganised, and isolated pigment cells
have forced their way up to various heights among the rods.
These can be found in all stages of losing their pigment;
some appear as nuclei still thickly enveloped in pigment,
others with only a trace of pigment, while here and there
nuclei alone persist from which all the pigment and the
protoplasm have disappeared. Fig. 12 shows in a tangential
section, selected because of the cross-sections of the rods,
such a nucleus, bereft of all its pigment, embedded among
rods, and in these latter the reticulum has been compressed
into the axis, which, as above suggested, indicates the absorp-
tion of extraneous matter through the walls.

Other effects of this exposure to such a fierce light have
still to be studied. For instance, the contents of the rods
have a singularly blotchy appearance, but I cannot satisfy
myself whether this lies in the object or in the accidents of
staining.

While these arguments are, I think, sufficient for the

[1] I am indebted to my friend Mr. George Newth, of the Royal College of
Science, not only for the use of the necessary apparatus, but also for indis-
pensable advice and assistance in making a series of experiments with pure
monochromatic light, the results of which are still being worked out.

present demonstration that the refractive matter within the outer limbs is absorbed by the rods from the pigment, I should like to mention two points on which I am in great uncertainty. It has appeared to me more than once as if the pigment granules could pass bodily into the rods, and, at least for a time, maintain their individuality. I do not see why this should not occasionally happen; indeed, I cannot explain some of the phenomena on any other hypothesis. Still, the evidence shows conclusively that this is not the normal method, but that the pigment granules are absorbed as a colourless or nearly colourless refractive and amorphous matter. The occasional finding of retinas in which the colour of this refractive matter within the rod is the same as that of the pigment granules without (I have seen this in sections of the retinas of the pigeon and of frog tadpoles, etc.) may be mentioned, in passing, as additional evidence of the origin of the former from the latter.

One appearance suggestive of pigment granules within the rod seen in osmic acid preparations must be familiar to all students of the retina. It is the " disc " formation on which Max Schultze laid so much stress. I now, however, refer this to a transverse flaking of the internal reticulum, perhaps a kind of coagulation of the same, as Max Schultze himself suggested. The transverse flakes are usually deeply coloured by osmic acid, and often appear exactly like layers of intruded pigment granules. In preparations not treated with osmic acid the appearance is not to be found.

The second point is the relation of the phenomena here detailed to the visual purple. This is said to be produced in the dark through the interaction of the rods and the pigment epithelium, i. e. when the epithelium is only in contact with the tips of the rods, and, further, it is said to be bleached by the light, i. e. when the rods should, according to my own observations, be absorbing clear refractive matter from the epithelial cells, which are then in intimate association with the rods, inasmuch as tongues of the cells then travel up between the rods. I am of course aware that it is frequently

maintained that fine protoplasmic processes of the pigment cells are permanently advanced as far forward as the membrana limitans externa, and are thus always in contact with the rods. Not in any single one of the retinas of some twenty-five vertebrates I have yet examined, and their number must, I think, now amount to fully one hundred, fixed and stained by all the latest methods, and examined with the best available microscopic lenses, have I been able to find a trace of these processes of the epithelial cells permanently interlocking with the rods. On the contrary, when the pigment is retracted the contour of the pigment cells is perfectly straight or rounded as the case may be. Had such processes existed, I am convinced that at least some evidence of their presence would have forced itself on my attention long ago.

I have, therefore, so far no point of connection to offer between the physiological details here described and the visual purple, which appears when, according to my own observations, the rods should be getting rid of the matter absorbed when last the light forced the pigment cells into close contact with them, and is bleached when they ought to be absorbing, and at the same time clarifying, the warm colouring matter of the pigment. A reconciliation of these observations will doubtless some day be forthcoming, and there the matter must be left for the present.

The Ellipsoid.—This somewhat inappropriate name is usually applied to the body found in the inner limbs of the Amphibia where these limbs abut against the outer limbs. Max Schultze regarded it as a plano-convex lens; the name here adopted was suggested by Krause ("Opticus Ellipsoid"). It is here preferred robbed of its prefix "opticus," so as not necessarily to suggest special functions.[1] So far as the terms describe form alone, "plano-convex" is preferable to ellipsoid for the Amphibia, for that is the most usual definitive form assumed in the adult rod, i.e. when the rod is not very large and thick, as it is in the axolotl, in

[1] Krause thought it was the nerve-end organ ('Anat. Untersuch.,' 1860)

which case the body is usually an irregular flattened disc (fig. 23).

As a matter of fact, the body is of very various shapes. Fig. 15 shows a series of cones and rods (salamander) in which only in a young cone is the body egg-shaped, in others it takes the shape of the tip of the swollen inner limb of the cone: if the latter is large, the body is large; if narrow, the body is narrow, while in the definitive rod it is uniformly plano-convex. It thus seems quite plastic in its earlier (cone) stage, and only assumes a definite form in the full-grown rod.

Dealing, then, with this body as we have with the other contents of the rod, we must regard it as an aggregation of these contents which, for some reason or other, rests permanently against the transverse membrane separating the inner and outer limbs.

It varies greatly in its staining. It is sometimes intensely stained, at others it is comparatively clear and refractive. In this latter case a dense stream of staining matter is very frequently seen descending upon it from the nucleus (see figs. 10, 23, 27). We cannot be far wrong, then, if we refer the variation in the intensity with which the body takes stain to the relative proportions of staining matter and refractive matter which compose it. For out of these two substances, which, as we have seen, together constitute the visible contents of the rods, it must surely consist.

Regarding it for the moment in its definitive plano-convex form, it seems to me that we have, both in its shape and in its position, striking confirmation of our conclusion as to the origins of the contents of the rod. On the one hand, we have an outwardly streaming reticulum of staining matter which, so far as we can see, only manages to get further, i. e. into the outer limb by way of the outer walls. There certainly seems to be some condensation of the reticulum against the blind end of the inner limb (see fig. 27, left-hand figure). On the other hand, coming into the rods from the opposite direction, viz. from the pigment epithelium, we have the re-

fractive matter. This, as we have seen, is absorbed by the walls of the rods filling them up till they are turgid. This matter would thus find its way inevitably up against the transverse membrane separating inner from outer limb, and, seeing that it passed through the outer wall into the rod, there is no apparent reason why it should not pass through this transverse membrane from the outer limb into the inner limb. This, then, I believe, is what takes place, the very form of the ellipsoid being suggestive of its having been forced through to form a kind of drop on the proximal side of the transverse membrane. Confirmatory evidence will later be adduced from other retinas, but sufficient to establish the point will be found in what follows.

When we come to the ellipsoid in the cones (see figs. 15, *c—e*) it would seem that the explanation we have given of it in the rod could hardly apply. There appears to be a transverse membrane (fig. 29, *f, j*), but there is no swollen outer limb filling up with refractive matter. Nevertheless the explanation of the ellipsoid is practically the same, as we can gather from the conditions seen in the frog. In the cones of the frog there is invariably a round refractive globule at the junction of the basal and the conical portion. In well-stained specimens a mass of staining matter is generally seen abutting against this globule, as if they mutually blocked the way for one another. We thus get practically the same condition as in the rod, though in this case we do not know exactly where the transverse membrane is, i. e. whether the refractive globule is on its inner or outer side.

This parallel assumes (1) that the refractive globule of the cones of the frog is of the same substance and has the same source as the refractive matter in the rod, and (2) that this refractive globule and the adjacent staining matter will later fuse together to form the definitive ellipsoid.

The former of these assumptions is, I think, fully justifiable. We have seen how readily pigment granules cling to the thin protoplasmic walls of the cones, and can be seen fading away on the fine membranous walls of the inner limbs

of the rods, as if in the act of being absorbed. Hence it is but natural to assume that some of the refractive matter which later fills these vesicles to overflowing should early find its way into the tips of the cones and be squeezed out by the lateral pressure described in Part I as existing in the rod layer, so as to appear as refractive globules just above the line where the pressure of the rods ceases, i. e. on a line between the junctions of the inner and outer limbs. The secondary thrusting back again of these globules in cones (c_3), described in Part I of this paper, needs no comment.

Then, again, I mentioned in Part I that in young tadpoles it was possible at times to see these globules actually disappearing in the ellipsoids of young rods (see Pl. 3, fig. 15), showing clearly that, in this refractive globule of the cone with its adjoining staining matter, we really have the elements of the future ellipsoid, though not blended together. Further, in one of my slides of a young frog tadpole the refractive matter absorbed by the rod is not always discoloured ; globules of bright reddish-brown matter exactly resembling the pigment in colour occur high up in the rod, near the transverse membrane, while as a complete confirmation of the argument, globules of exactly the same colour can here and there be found in the ellipsoids of the same rods.

The condition found in the cones of the frog thus helps us to understand the ellipsoid in the cones of the other Amphibia here dealt with. It has long been known that the refractive globule was absent from the cones of the toad, an absence which was disconcerting to the earlier investigators, who would attribute to it an important dioptric function. It is also absent from the cones of the salamander and the axolotl. In these cases, from our point of view, it is not so much that the refractive matter is absent, but that it never really forms as a distinct globule ; it is mixed with the staining matter to become the ellipsoid as fast as it collects.

In the case of the newt, all students will remember that

Max Schultze, and others after him,[1] described and figured a combination of two "lenses," a biconvex and a plano-convex, as a higher specialisation than the simple plano-convex "lens" (the ellipsoid) of the frog, toad, salamander, etc. Max Schultze even claimed that this lens could be isolated. The body which he figured can be seen frequently enough, but not by any means always in the shape of a biconvex lens. It is nothing but a fluid vacuole, more sharply defined than usual. Fig. 30 shows two rods of a newt side by side ; in one there is a well-defined vacuole resting on the ellipsoid, and in the other a quite undefined vacuole like that usually found in other Amphibia. The former is interesting because its origin from the nucleus can be seen, a second one appearing ready to escape. Most of the nuclei in this preparation have vacuoles about the same size as shown in fig. 30. Further, in very many of the outer limbs of the rods rows of fluid globules of different sizes can be seen. Compare the views as to the origin of the fluid on p. 453.

Let us sum up the conclusions so far arrived at, forbearing to enter more fully into the physiological results obtained till the corroborative evidence yielded by the eyes of vertebrates other than Amphibia can be prepared for publication.

The rods in the Amphibia are specialised protrusions of the retina, consisting of extremely delicate protoplasmic vesicles, each divided by a transverse membrane into an inner and an outer compartment. The staining reticulum which traverses these vesicles is especially developed in the outermost, into which it finds its way in threads down the walls. These threads, at short distances, give off other threads from small nodes into the interiors of these outer vesicles. These latter further become filled with refractive matter absorbed from the pigment epithelium, and certainly largely obtained from the pigment granules. This matter absorbed through the walls condenses the mass of the reticulum into the axes

[1] Cf. 'Arch. mikr. Anat.,' Bd. v, 1869, pl. xxii, fig. 2 *a*. See also ' Bronn's Thierreich ' (Amphibia).

of the rods. A portion of this refractive matter **exudes** through the transverse membrane, where it mixes with the staining matter of the inner limb, and forms the body infelicitously termed the ellipsoid.

<p align="center">(To be continued.)</p>

<p align="center">EXPLANATION OF PLATES 30 and 31,</p>

Illustrating Part II of Mr. H. M. Bernard's "Studies in the Retina : Rods and Cones in the Frog and in some other Amphibia."

<p align="center">PLATE 30.</p>

Fig. 1.—The basal portions of two rods (newt) with remains of ellipsoids, and showing the relations of inner and outer limb as two vesicles separated by a thin membrane.

Fig. 2.—Part of an adult rod (toad) distorted, and showing its sac-like character, the contents having ruptured down the middle. Cf. Max Schultze's Fig., 'A. M. A.,' iii, pl. xiii, fig. 18d (Pike).

Fig. 3.—a, b. Two surface views of rods (frog, Flemming), showing the dotted appearance of the longitudinal striation. b. With a pigment granule to show relative size of dots.

Fig. 4.—a. Rod of young salamander (boiling corrosive sublimate), showing the longitudinal striation straggling irregularly. b. Cross-section of a rod of same eye, showing a simple reticulum attached to the dots in the walls.

Figs. 5 and 6.—Parts of rods and cross-sections from retina of frog (exposed to osmic vapour); in Fig. 6, a, the rod was abnormally stretched.

Fig. 7.—a, b. Two cross-sections of rods (frog) according to Hensen. a. "Optical section of a fresh rod." b. "Optical section of a rod fixed with osmic acid."

Fig. 8.—A cross-section of the same according to Max Schultze.

Fig. 9.—Part of a rod (a), with cross-section (b), and a small piece cut off tangentially (c) from retina of axolotl; note the density of reticulum near the tip of the rod. Cf. b with Hensen's section, Fig. 7, a.

Fig. 10.—Upper portion of rod of same (Perenyi), partly in optical section, showing part of nucleus and inner limb ; the reticulum of the latter can be seen (1) coming from the nucleus, (2) condensing on what is called the ellip-

soid (cf. Figs. 23 and 27), and (3) passing in fine threads on to the outer limb ; the striæ which continue them are obscured by the internal reticulum.

FIG. 11.—A diagram of the same showing the surface arrangement of the threads ; the symmetry is, however, seldom so complete on the inner limb. The threads thicken towards the tip of the rod.

FIG. 12.—Tangential section through a group of rods of a salamander after three hours' exposure to intense light. The cross-sections compare with Hensen's section, Fig. 7, b. Among the rods is the nucleus of a dislocated pigment cell, from which all the cytoplasm and pigment have been absorbed.

FIG. 13.—From a toad fixed in boiling corrosive sublimate. a, b, show a thick basket-like reticulum ("Faserkorb") of inner limb near the ellipsoid ; c, part of a rod broken away, and showing the longitudinal threads beaded with dots of staining matter ; d, a Schwalbe's rod with threads apparently running over the deeply stained ellipsoid and on to the outer limb ; e, f, g, sections of rods cut at different angles ; from c to f what appears to be a homogeneous rind is seen ; h, a rod 9 μ thick, with a "rind" 1·5 μ thick ; part of the same in i, as interpreted when examined under high magnification (1500 times; apoch. 2 mm.; N.A. 1·4, comp. oc. 12) ; j, a part of a cross-section, showing the material of the rind fitting into irregular spaces of the reticulum ; k, cross-section of a narrow rod 5 μ thick.

FIG. 14.—Optical section of a rod from the other eye of the same animal ; the "rind" seen only on one side.

FIG. 15.—Salamander (boiling corrosive sublimate) : a, the upper parts of a rod, showing dark body in or on ellipsoid, flattened like the latter against the transverse membrane (see Fig. 1), and from this body two staining threads descend on the outer wall of the rod ; b, ellipsoid, egg-shaped in young cone ; c, the same with its shape adapted to its position, and with mass of staining material in contact with it ; d, e, the same ; f, g, ellipsoids in rods and in their definitive shapes, with dense staining matter condensing on them (cf. Fig. 10).

FIG. 16.—Toad (strong alcohol) : a, two condensed rod-nuclei protruding through the mem. lim. externa, and a vesicular cone-nucleus in contact with the outer reticular layer ; b, the same, with similar vesicular nuclei, one in the middle, and one in the outer, nuclear layer.

FIG. 17.—The same, condensed rod-nuclei with fluid vacuoles in the inner limbs, as if exuded by these nuclei.

FIG. 18.—Axolotl (Perenyi) ; a condensed rod-nucleus with a much larger vesicular nucleus above it (cf. also Fig. 23).

FIG. 19.—The same ; a rod forced farther than its neighbours into the pigment, apparently by the intrusion of fluid into the inner limb, thereby displacing the ellipsoid.

FIG. 20.—Frog (Flemming); a nucleus in position of cone-nuclei, but condensed, with a vacuole near it and apparently discharged from it.

FIG. 21.—Frog (Flemming); two nuclei passing, with amœboid changes of shape, through the outer reticular layer.

FIG. 22.—Axolotl, showing the similarity of the cone-nuclei to those of middle nuclear layer.

PLATE 31.

FIG. 23.—The same, showing a nucleus passing through the outer reticular layer; a double cone, one with condensed and the other with vesicular nucleus (cf. Fig. 18, right-hand nuclei).

FIG. 24.—The same, showing a spot where one nucleus, or perhaps two nuclei, have passed outwards, and apparently dragged the tissue outwards with them and left a large gap in the middle nuclear layer.

FIG. 25.—Salamander (Perenyi), showing three nuclei, two working outwards through the outer reticular layer.

FIG. 26.—Frog (Flemming); a nucleus passing through the outer reticular layer, preceded by a fluid space and an exquisitely fine staining network.

FIG. 27.—Axolotl (Perenyi); a large nucleus with a similar fine staining network above it, and the reticulum condensing at the distal end of its inner limb; on the right is a small condensed rod-nucleus, with the reticulum of the inner limb condensing on the ellipsoid (cf. also Figs. 10 and 23).

FIG. 28.—Frog (Flemming), showing upper end of a cone with a reticulum traversing the basal vacuole.

FIG. 29.—*a—j*, a series of figures from the retina of a young salamander (seven weeks old, Perenyi), showing in developing cones and in rods the origin of the staining reticulum of outer limbs from that of the inner limbs, and sometimes from bright round masses of chromatin. The connection of the reticulum with that of the nucleus is shown in *a, i, j* (cf. *c, d, e, f, g,* with Fig. 15, *a*).

FIG. 30.—Two rods from the retina of the newt. The very delicate longitudinal striation of the outer limbs is shown, and in connection with the outermost rim of the coarsely granular ellipsoid. Above the ellipsoid is a fluid vesicle very variously developed, but not infrequently slightly flattened (Max Schultze's "biconvex lens"). Fluid vesicles or vacuoles are also very commonly seen in the nuclei and in the axes of the rods.

Fig 1.

Fig. 2.

a

b

Fig. 3.

a

b

Fig. 9.

a

b

Fig. 7.

Fig. 8.

a

Fig. 15.

a

b

a

b

c

d

e
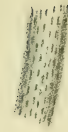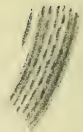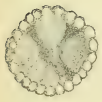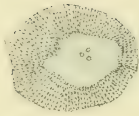
Fig. 16.
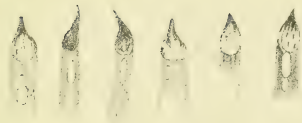
Fig. 17.

Fig. 19.

Fig. 18.

a

b

Fig. 21.

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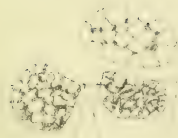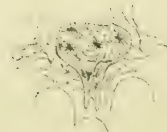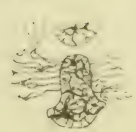
Fig. 4.

Fig. 5.

Fig. 6.

Fig. 10.

Fig. 11.

Fig. 12.
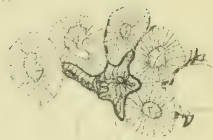
Fig. 13.

Fig. 14.
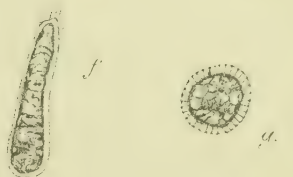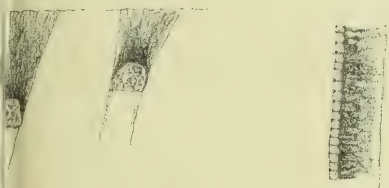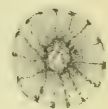
Fig. 22.
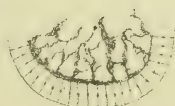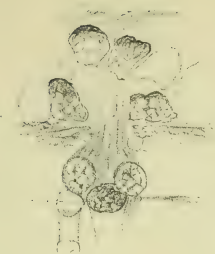
Fig. 24.

Fig. 23.

Fig. 25.

Fig. 26.

Fig. 30.

Fig. 27.

Fig. 28.

a

b

c

d

Fig. 29.

e

f

g
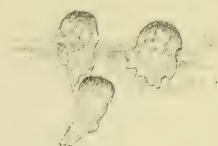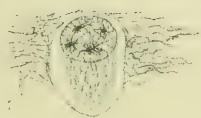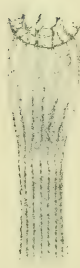
h

i

j

Staining with Brazilin.

By

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Beyer Professor of Zoology in the Owens College, Manchester.

BRAZILIN is extracted from the wood of Cæsalpinia echinata, growing in South America. Formerly, under the name Brazil-wood, it was used commercially as a dye ; but of recent years it has been superseded by other colouring substances, and practically driven out of the market.

Chemically it has considerable resemblance to hæmatoxylin, which is also extracted from the wood of a tree belonging to the order Leguminosæ, but brazilin ($C_{16}H_{14}O_5$) differs from hæmatoxylin ($C_{16}H_{14}O_6$) in having one hydroxyl less. Further information concerning the chemistry of brazilin may be found in the papers by Professor Perkin and Dr. Gilbody published in the 'Proceedings of the Chemical Society' during the past four or five years.

Brazilin has been tried as a stain for animal tissues by Flechsig and Breglia, but apparently the results were not very satisfactory. Their methods, though mentioned in the third edition of Lee's 'Microtomist's Vade-Mecum,' are omitted from the fourth edition.

Brazilin is mentioned as a chromatin stain in Rawitz's 'Leitfaden für histologische Untersuchungen,' p. 98, but it is not mentioned in the elaborate 'Tabellen zum Gebrauch bei mikroscopischen Arbeiten,' by W. Behrens, published in 1898, nor in Böhm and Oppel's 'Taschenbuch der mikroscopischen Technik,' published in 1896.

My first experiment was to attempt to use brazilin instead of hæmatoxylin in the method suggested by Heidenhain,

and now widely used in England and elsewhere under the name of the "Iron-Hæmatoxylin method." This experiment did not give results that were at all satisfactory. Another series of experiments which have been made in the Owens College laboratory by Mr. Wadsworth, under my direction, have shown that the most satisfactory results are obtained by the following method :—" The sections are placed in a solution of iron-alum (1 per cent. iron-alum in 70 per cent. alcohol) for one to three hours, and then placed, after slight washing in 70 per cent. alcohol, in a ½ per cent. solution of pure brazilin in 70 per cent. spirit."

Brazilin stains much more slowly than hæmatoxylin, and we have found that generally it takes several hours (three to sixteen) to give a good sharp definition. After staining, the sections are washed in pure 70 per cent. spirit, passed through the usual stages, and mounted. There is seldom any need to wash the sections in iron-alum after staining. It will thus be seen at the outset that this method possesses two advantages over iron-hæmatoxylin,—the sections are never taken down into water, and the number of washings is considerably reduced.

The results are, to my mind, eminently satisfactory ; for not only is brazilin a definite chromatin stain, but in nearly all tissues some parts of the cytoplasm are also stained, though of a different colour. It is in most cases a double stain, but with some tissues it is a treble stain.

We have used as a test object a series of sections through the body of a larval newt. Each of these sections exhibits so many subjects of histological interest that it is impossible to describe them briefly. I think it would be admitted, however, by all observers that nearly, if not all the tissues are well stained. The chromosomes in the cells that are dividing in the skin and ovary are very sharply defined and of a deep purple colour, while the granules in the cytoplasm are brown. On making a comparison of our preparations of newt's testis stained by the iron-brazilin method and by the iron-hæmatoxylin method, it was found that the karyokinetic figures

were equally well defined in the two preparations ; but the iron-brazilin showed an advantage in that the spermatozoa were triple stained, the head, middle piece, and tail being clearly of different colours.

A preparation of the sciatic nerve of a dog stained in brazilin exhibits the neurokeratin remarkably clearly, but the axis-cylinder is not well stained.

Our method has great advantages in showing the blood-supply of an organ, the red blood-corpuscles being stained very deeply. Preparations of ovary of a cat and kidney of a dog exhibit the capillary plexus excellently.

It is, however, principally in cytological work I think that the new method will be valuable, as we have found after many experiments, in our investigations on the very delicate nuclear structures of the Suctorian Dendrocometes, that it gives us by far the best general results.

It is obvious that a good deal more must be done before an opinion can be expressed as to the general value of this method, but I have thought it right to bring it before the notice of workers in various branches of microscopic science at the present time, because I feel that it is a method well worthy of further trial.

In conclusion I may say that the somewhat severe test of exposing slides to the action of direct sunlight for several months has not indicated any appreciable fading effect.

I am indebted to Professor W. H. Perkin, jun., F.R.S., for much valuable advice and assistance in working out this method.

On Two New Species[1] of Onychophora from the Siamese Malay States.

By

Richard Evans, M.A., B.Sc.,

Of Jesus College, Oxford.

With Plates 32—37.

Part I.

CONTENTS.

[1] The discovery of the two species here described was announced in 'Nature,' vol. lx, p. 591, by E. B. Poulton, Esq., M.A., F.R.S., Hope Professor of Zoology in the University of Oxford.

I. Introduction.

Peripatus, although found in the islands of the Malay and Melanesian Archipelagos, in Sumatra and New Britain, has not been hitherto discovered on the mainland of the Asiatic continent. Dr. R. Horst (**8**) recorded a specimen from Sumatra in 1886. The specimen in question was subsequently named P. sumatranus by Sedgwick (**15**). Several years (1898) afterwards Dr. Arthur Willey described a species which he himself collected in New Britain (**17, 18**).

The general characters of the Sumatran species are those common to all the Neotropical forms of Peripatus. But Dr. Willey points out that, though New Britain is geographically an intermediate locality between Sumatra and the Neotropical region, the New Britain species does not possess a single external character of importance in common with the Neotropical forms, although by a singular coincidence the female has the same number of claw-bearing legs—twenty-four pairs—as the alleged Sumatran specimen. Dr. Willey further remarks that under the circumstances the evidence that the latter was found in Sumatra, which Sedgwick regards as inconclusive, must appear more than ever worthy of suspicion. The material which will be described in the present account will show that the doubt expressed by Mr. Sedgwick, and subsequently by Dr. Willey, was not well founded, though it was, under the circumstances, justifiable. While the New Britain species possesses no single external feature in common with the Neotropical forms, the Malay species described in the following pages, on the contrary, agree in almost all the most important external characters with the Neotropical forms as well as with the Sumatran. This fact of itself goes far to prove that Dr. Horst's specimen really came from Sumatra.

At one time it was supposed that the various species of Peripatidæ could be arranged in groups in accordance with their geographical distribution (**15**). Mr. Sedgwick described

three groups, namely, the Neotropical, the Australasian, and the Ethiopian. Dr. Willey, in correspondence with this nomenclature, states that the New Britain form may be designated Melanesian (**18**). M. Bouvier has already shown that such a grouping of the Peripatidæ has no foundation in fact (**4**). The discovery in the Malay peninsula of a number of species which, as above mentioned, agree with Neotropical forms in almost all their most important characters, will effectually dispose of the above supposition.

Conditions under which Peripatus was obtained in the Malay Peninsula.—The material at my disposal consisted of thirteen specimens, six males and seven females. I obtained my first specimen on the 5th, and the second on the 6th, of May, 1899. We were then camping on the side of a mountain 3300 feet high, the position of our camp being about 2250 feet above sea level. The mountain in question is designated Bukit besar, in the native tongue, and is situated on the boundary line between the States of Nawngchick and Jalor, a full day's journey from the town of Patani. The first specimen was brought me by a Malay, who carried it between the prongs of a split stick. When I took hold of the stick and began to handle the animal between its prongs, it suddenly squirted a whitish, sticky slime to a distance of fully eighteen inches. My hands were covered with it, and though it did not stick to the body of the animal itself, I only succeeded in getting it off with a considerable amount of difficulty. This slime, though fluid when first squirted out, solidifies almost immediately. When in a semi-solid state it can be drawn out in threads, much in the same way as the juice of the rubber tree. The natives, when they saw the slime being squirted, were much frightened. This whitish secretion is considered to be poisonous, and accounts for the manner in which they brought me the animal.

We had, unfortunately, arranged to leave Bukit besar next morning. It was, however, agreed among the members of the expedition that I should spend the day on the moun-

tain in search of Peripatus, and make the descent towards
the evening, so as to be ready to leave the neighbourhood on
the following day. I took with me the man who brought me
the first specimen, in the hope that he would be able to find
some more. The day's work resulted in the capture of one
more individual. The Malay who was with me searched all
day on the ground under leaves, but was unable to find any
more specimens; while I myself turned but a few leaves and
spent almost the whole time in splitting and chopping dead
tree trunks. Knowing, as I did, that the natives were ac-
quainted with Peripatus, and had a name for it (Ulat
chelawah), I considered, at the time, that the Malay's persis-
tence in turning over leaves was probably significant of the
habits of the animal. Later, however, I learnt that this was
not so, for all my specimens were found in dead wood. The
one specimen which I obtained on the 6th of May was found
in a stump of a tree about six feet in height. The stump
in question was almost completely dry, and, situated in its
interior, at a height of four to five feet from the ground, I
came across Peripatus in its usual habitat for the first time.
It was in a torpid state, and endured a considerable amount
of handling before it realised—as it were—what was taking
place. However, it was not long before it began to squirt
with celerity and great force its slimy secretion from the
slime-glands, which open at the tips of the oral papillæ.

The remaining eleven specimens were obtained more than
three months later at Kuala Aring, in the State of Kelantan,
a distance of at least one hundred and twenty miles in a
southerly direction from Bukit besar. The first batch,
consisting of five specimens, was found on the 18th of August
in a dead tree, which for the most part was exceedingly damp;
but the exact spot in which they were found was dry. They
were discovered by Mr. Skeat's Javanese "boy," who, to-
gether with the other Malay servants, had been carefully
instructed by me several months previously as to the import-
ance of Peripatus. This native happened at the time to be
out collecting with Mr. Laidlaw, who brought the specimens

to me.   On the following day the same man found an additional specimen in the very tree in which he had discovered the other five on the previous day.   On the same morning another Malay servant came across five more specimens in another fallen tree, which was almost completely dry and rotten.   On the day in question I myself was with the men who discovered the specimens, and am able to testify as to the nature of the places in which they were found.   The kind of place which they seem to prefer for hiding during the daytime is the interior of dry rotten wood.

Preservation.—Of the thirteen specimens obtained five were preserved in a mixture composed of ninety-two volumes of saturated solution of corrosive sublimate in water, and eight volumes of glacial acetic acid ; three specimens in absolute alcohol ; four specimens in Flemming's weak solution ; and one specimen in four to five per cent. formaline, that is, in a mixture of one volume of the commercial formaldehyde with seven of water.   All the specimens save the one preserved in formaline were cut by a longitudinal incision, either dorsally or dorso-laterally, so as to preserve the internal organs.   Unfortunately, however, it happened—as if by the irony of fate—that only male specimens were preserved in Flemming's solution, all the female specimens having been preserved either in absolute alcohol or in the corrosive and acetic mixture. This was a great misfortune, for the material preserved in Flemming's fluid was almost perfect, while that treated with the other solutions was far from reaching the same standard of excellency.

II. The Classification of the Onychophora.

Before I proceed to describe the species here considered, it seems necessary to give a historical account of the views which have been put forward of the classification of the Onychophora.

Mr. Sedgwick, as was mentioned above, pointed out that the Onychophora fell into three groups, namely, the

African, the Neotropical, and the Australian, though he did not consider the differences in character between these groups of sufficient importance to entitle them to the rank of three distinct genera. Consequently all the species then known were described by Mr. Sedgwick in his Monograph under the genus Peripatus (**15**). Later, however, the genus Peripatus, thus constituted, was broken up by Mr. Pocock, and arranged in three genera, corresponding to Mr. Sedgwick's three groups. Mr. Pocock retained the name Peripatus for the Neotropical forms, and gave the names Peripatoides and Peripatopsis to the Australian and African forms respectively.

In the year 1898 Dr. Willey published a complete description of a species which he had discovered in New Britain, and gave it the name Paraperipatus Novæ-Britanniæ. Willey, however, considers the three genera formed by Pocock, as well as Paraperipatus, worthy only of subgeneric rank, and prefers along with Mr. Sedgwick to include all the species in one genus. Prior to the publication of Willey's account of P. Novæ-Britanniæ, M. Bouvier gave a short account of P. Tholloni, for which Dr. Willey justly remarks a new sub-genus must be formed if the other sub-generic names—as he describes them—are to be retained ; in other words, he is of opinion that P. Tholloni, from a classificatory point of view, is equivalent to any one of the other four sub-genera, a view which is adopted in the present paper, with the difference that Willey's sub-genera are accorded generic rank. Because the species Tholloni is intermediate in character between the genus Peripatus (Pocock) on the one hand, and the genus Peripatopsis (Pocock) on the other hand, I propose to give it the generic name Mesoperipatus.

In addition to the above-mentioned genera a new genus, designated Opisthopatus, has been established by Purcell, to include those African species which in some respects approach the Australian forms (**13**).

In a recent number of this Journal, M. Bouvier published

the results of a thorough and complete study of a great number of species, and embodied the classificatory results at the close of his paper in a tabular form, from which the following is taken (**5**).

I. Peripatus .   .   . (1) Genus.
II. { Peripatoides .   . (2)   ,,
     { Opisthopatus .   . (3)   ,,
III. Peripatopsis . . . (4)   ,,
IV. Paraperipatus .   . (5)   ,,

In the above classification the genus Peripatus includes the species Tholloni and Sumatranus.   In the present paper the former of these two species is placed in a genus by itself, and is called by the generic name Mesoperipatus; the latter, together with the Malayan species, constitutes a new genus, to which the name Eoperipatus will be given.   Bouvier has shown that M. Tholloni is intermediate in character between the Neotropical and the African species, and that it is more closely related to the former than to the latter.   From the description given in the present paper it will be seen that the Malay forms are more nearly akin to the Neotropical genus than to any other, and that the genus Mesoperipatus is intermediate between the Malay and African species.   By dividing the genus Peripatus, as constituted by Bouvier, into three genera, the differences between the Malayan, African, and Neotropical forms contained in it will be emphasised.   Bouvier has already united together the genera Peripatoides and Opisthopatus, this indicating the belief that they are closely related.   In the same way the close relationship existing between the genera Peripatus, Mesoperipatus, and Eoperipatus may be indicated by placing them together in one sub-family.

The following classification seems to be a fair expression of our present knowledge both of the anatomy and development of the Onychophora.   It will undoubtedly be improved upon as our knowledge of the class advances.

Class ONYCHOPHORA.

Family I. Peripatidæ.

    Sub-family 1. Peripatinæ.

        Genus 1. Eoperipatus[1] (gen. nov.).

          ,,   2. Peripatus (Pocock) (**12**).

          ,,   3. Mesoperipatus (gen. nov.).

    Sub-family 2. Peripatoidinæ.

        Genus 4. Peripatoides (Pocock) (**12**).

          ,,   5. Opisthopatus (Purcell) (**13**).

    Sub-family 3. Peripatopsinæ.

        Genus 6. Peripatopsis (Pocock) (**12**).

    Sub-family 4. Paraperipatinæ.

        Genus 7. Paraperipatus (Willey) (**17**, **18**).

The above classification follows the same lines as that of Bouvier. In fact, it amounts to little else than the breaking up of Bouvier's genus Peripatus into three genera, and the formation of a number of sub-families by the grouping together of the genera.

The feature which has been considered in the formation of sub-families is the gradual degeneration of the last two pairs of legs, and the position of the genital openings. These characters formed the basis of Mr. Sedgwick's division into groups, and later of Mr. Pocock's formation of three genera, as well as of M. Bouvier's four divisions.

I shall now proceed to give a formal definition of the above four sub-families.

1. Peripatinæ:—The genital orifice is situated between the penultimate pair of legs. There is a slight reduction in size, but no actual degeneration in structure of the last two pairs of legs, further than that they do not possess the full number of pads.

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[1] I am indebted to J. W. Jenkinson, Esq., M.A., of Exeter College, Oxford, for the term Eoperipatus, as expressive of the distribution of the genus in the East.

2. Peripatoidinæ:—The genital orifice is situated between the last pair of legs which are not reduced in size. The hindermost pair, found in the Peripatinæ, is obsolete.

3. Peripatopsinæ:—The genital orifice is situated between the last pair of legs (anal papillæ), which are much reduced in size and degenerate in structure. According to Purcell the anal papillæ may be obsolete (**13**).

4. Paraperipatinæ:—The genital orifice is situated behind the last pair of legs. The vestigial pair found in the Peripatopsinæ has completely disappeared, and the last existing pair, which is pregenital in position, is reduced in size.

Now that the sub-families have been defined, it seems necessary to sum up the main characters of the genera. It is impossible to form concise definitions of them, because in several cases some of the more important characters are common to more than one genus—a fact which points to the desirability of arranging the genera on a wider plan than the one which has been adopted, and of giving the rank of families to the groups here described as sub-families. It is highly probable that future investigation and more extensive knowledge of the class Onychophora will tend towards the adoption of the course above suggested. However, it may be useful to give a summary of the leading features of the several genera here recognised.

Genus 1. Eoperipatus :—The legs have either four or five pads. The renal papillæ of the fourth and fifth pairs of legs are situated either in the middle of the proximal pad, that is, the fourth pad, or on its proximal side. The legs in question have only four pads. The feet are provided with two papillæ situated on their distal margin, one in front and one behind. There are four ventral prominences on the feet, which are provided with one or more spines, similar to those found on the erect distal papillæ, and pointing downwards. The outer blade of the jaw has two accessory teeth on the inner side of the main tooth. The inner blade may have three accessory teeth on the inner side of the main tooth.

The inner blade has a diastema followed by a row of small denticles. The male genital pore has the shape of a cross. The ductus ejaculatorius is very long and forms a loop. The male accessory glands open to the exterior by a median pore situated between the last pair of legs. The female opening is a transverse slit. Receptacula ovorum and seminis are present. The ovary is large, and spreads out over the other organs. The ova are large, full of yolk, and exogenous. The developing embryos have no kind of placental structure, and measure 20—27 mm. in length at birth.

Genus 2. Peripatus:—The legs have either four or five pads. The renal papillæ of the fourth and fifth pairs of legs are situated either on the proximal side of the third pad or in the groove between the third and fourth pads. The feet have a variable number of papillæ; the hinder margin having either one or two, while the anterior margin has from one to three. The outer blade of the jaw has one or two accessory teeth, the inner blade has the same number followed by a diastema and a row of small denticles. The ductus ejaculatorius forms a very long loop. The male accessory glands (anal glands) open beside the anus into two pouches, which have the same structure as the rectum. Receptacula seminis and ovorum are present. The ovary is small and compact. The ova are endogenous and devoid of yolk. The young are provided with a nutritive organ which has been called the " placenta," and measures 20—25 mm. in length at birth.

Genus 3. Mesoperipatus :—The legs have only three pads. The renal papillæ of the fourth and fifth pairs of legs make a slight indentation in the proximal pad, that is, the third pad. The number of legs varies from twenty-two to twenty-five pairs. The two blades of each jaw have an accessory tooth on the inner side of the main tooth, and the inner blade has a long row of denticles. The ridges of the skin are continuous across the back. The female has a pair of receptacula seminis ; presumably there are no receptacula ovorum.

Genus 4. Peripatoides :—The legs have three pads.

The renal papillæ of the fourth and fifth pairs of legs are continuous with the proximal pad (the third), but do not divide it in two. The feet carry three papillæ near the edge, one in front, one behind, and one dorsally. The outer blade of the jaw has lost its accessory denticle, the inner blade has no diastema and the denticles are few. The ductus ejaculatorius is almost as long as in Eoperipatus. Male accessory glands open to the exterior by one or two openings situated between the genital pore and the anus. When there are two they are widely separated. The genital opening (female) is round. There is a pair of receptacula seminis, but no receptacula ovorum. The ova are large, full of yolk, and exogenous. Development may take place in the uteri, or ova are discharged. When development takes place in the uteri the young at birth measure 5 mm.

Genus 5. Opisthopatus :—The legs have three pads. The renal papillæ of the fourth and fifth pairs of legs are situated in the proximal pad. The feet carry three papillæ, one in front, one behind, and one dorsally. The outer blade of the jaw has a small denticle inside the bigger one; the inner blade has no diastema, but a row of small denticles. Male unknown. The female genital opening is a transverse slit. No receptacula seminis or ovorum. The young at birth are large in size. They are of different ages in the uteri.

Genus 6. Peripatopsis :—The legs have three pads, and the excretory papillæ of the fourth and fifth pairs of legs are situated in the proximal pad. Feet have three papillæ near the apex, two on the anterior side, and one on the posterior side. The outer blade of the jaws has a small accessory tooth at the base of the main tooth; the inner blade has no diastema, but has a row of small denticles. The ductus ejaculatorius is shorter than in genera 1, 2, and 4. The male accessory glands open into the ductus ejaculatorius. The female genital pore is a longitudinal slit. There are no receptacula ovorum or seminis. The ova are large, devoid of yolk, and arise exogenously. The young at birth are of

medium size. All the embryos in the uteri are of the same age.

Genus 7. Paraperipatus:—The legs have three pads. The renal papillæ of the fourth and fifth pairs (sometimes the sixth as well) are situated in the proximal pad, completely dividing it into two. The feet carry three papillæ, one on the anterior side, one on the posterior side, and one variable in position. The outer blade of the jaws is simple, without a small accessory tooth at the base. The inner blade has no diastema, but has a row of small denticles. The male genital pore is at the tip of a conical papilla. The ductus ejaculatorius is short and median. The male accessory glands ("pygidial glands") debouch into a bulbus, which opens to the exterior by a median pore above the anus. There are no receptacula ovorum. There are two receptacula seminis. The ova are small, devoid of yolk, and arise exogenously. The young at birth are of medium size. During the early uterine development they are provided with a trophic sac, which becomes completely enclosed in the later stages.

III. Some Notes on the Type Specimen of E. sumatranus.

In order to compare the two species here described with E. sumatranus (Horst), at the end of the summer I visited the Leyden Museum. There I met with every courtesy on the part of Dr. Horst, who first described the species in question (**8**), and under whose care the type specimen is at present. He kindly gave me every facility in its examination.

The following notes made at the Leyden Museum confirm, add to, and to some extent correct Dr. Horst's description.

The colour of the dorsal surface of E. sumatranus is dark brown, while that of the ventral surface is considerably lighter. The white spots found on the dorsal surface are due almost entirely to the broken condition of the large primary papillæ. The ventral surface completely lacks the pink

found in the species Horsti. There is a dark line along the middle of the back, as in the Malay forms. The line in question is due to the greater development of pigment in the papillæ situated on either side of the non-pigmented but narrow line which occupies the mid-dorsal position, as in the Malay species. The segmentally arranged areas situated on the ventral surface in the species from the peninsula are scarcely visible in the Sumatran form, although, having previously seen them in the former, I was able to find traces of them in the latter.

The mouth, genital orifice, and the anus are situated in the same position, and have the same structure as in E. Horsti. Between the genital orifice and the anus, i.e. between the last pair of legs, is found the common opening of the male accessory glands. This opening was mistaken by Dr. Horst for the anus, which is a small longitudinal slit situated very slightly subterminal.

The antennæ have the same shape as in the Malay species, and very nearly the same number of rings, although some of these are small and consequently very difficult to count. It seems that there are in all about fifty or fifty-one rings.

The disposition of the legs, of which there are twenty-four pairs, is practically the same as in the species Horsti. The distance between the successive pairs in the anterior part of the body is not much greater than that between similarly situated pairs in the posterior part. There are four crescentic pads on every leg of the first twenty-two pairs, the penultimate pair having only three, and the last only two on each leg. The crural grooves are all closed, but are easily made out on all the legs except the last two pairs, though they are smaller on the three anterior pairs. On the last two pairs of legs in the species sumatranus there is no sign of the papillæ, which are supposed to represent the whitish lips of the reduced crural grooves.

The feet in E. sumatranus have the two papillæ found in Weldoni and Horsti. The two distal papillæ, one in front and one behind, are divided into two parts, the top

part carrying the usual spine. The spines were not observed on the four ventral prominences; they were probably rubbed off.

The opening of the renal organ of the fourth and fifth pairs of legs is situated on the top of a papilla, which completely divides the proximal pad in two. In this feature Sumatranus agrees with the species Weldoni, and not with Horsti. The structure of the skin, however, has no resemblance to that of Weldoni, but is very similar to that of Horsti. The papillæ are arranged on the transverse ridges, and are scarcely ever found in the grooves between them. The transverse ridges rise up suddenly, and the grooves are well marked. Owing to the broken condition of the skin papillæ it is almost impossible to distinguish in all cases between primary and accessory papillæ, save in so far as this can be done by noticing the difference in situation and size. The primary papillæ consist of a truncated base, with a cylindrical part on top of it, the latter carrying a spine. The primary papillæ occupy the whole width of the ridge on which they are situated, while the accessory ones are placed more or less laterally, and are less numerous than in the species Horsti, to be described in the present memoir.

IV. DESCRIPTION OF THE TWO SPECIES,

EOPERIPATUS WELDONI AND EOPERIPATUS HORSTI.

A. Introduction.

Of the thirteen specimens at my disposal only two of them —both females—belong to the species Weldoni; the remaining eleven belong to the species Horsti, and consist of six males and five females. The former are the specimens obtained on Bukit besar, the latter are those obtained at Kuala Aring in Kelantan. The proportion between the number of males and females of the species Horsti is rather a commentary on the statement generally made, that the females are more numerous than the males. In order to

avoid repetition the two species will be described together
as far as possible, and the features in which they differ will
be pointed out as they arise.

B. External Characters.

Colour.—The colour of the two species here described is
slightly different, especially on the ventral surface. The
dorsal surface of the species Weldoni is coloured dark
brown, while that of the species Horsti is lighter; that is,
it is warmer in tone, as if there were a certain amount of
pink mixed with the brown. The mid-dorsal position in
both species is occupied by a very dark chocolate-coloured
line, of a much deeper hue than the neighbouring parts. It
extends uninterruptedly from close to the anterior end
almost to the terminal anus. The appearance of a dark line
is brought about by the greater development of pigment in
the papillæ situated on either side of a completely non-pig-
mented but exceedingly narrow line which occupies the
median position. The dorsal surface, especially in the species
Weldoni, has pale spots, distributed with a certain amount of
regularity all over it. This appearance results, on the one hand,
from broken primary papillæ, and, on the other hand, from
the primary papillæ containing less pigment than the others,
and consequently presenting a yellowish-white appearance.

The ventral surface in the species weldoni is coloured
yellowish-grey with small spots of brown. In the species
Horsti it may be almost as in Weldoni, or it may have a
decidedly pink appearance, which in some cases may even
push between the legs towards the dorsal surface. In both
species there is a row of whitish areas, segmentally arranged
along the mid-ventral line between the legs of each pair.
They correspond to, and lie below, the ventral organs, which
in the genus Eoperipatus do not completely degenerate in
the adult condition.

Dimensions.—The two species here described differ con-
siderably in size, Weldoni being much larger than Horsti.

The average length of the specimens belonging to the species Weldoni is 58 mm., and average breadth is 6·25 mm., while the average length of the female specimens of Horsti is only 35·4 mm., and average breadth is 4·6 mm.; and of the male specimens the average length is 33·5 mm., and average breadth 3·8 mm. If the eleven specimens of Horsti be taken together, the average length is 34 mm. and average breadth is 4·16 mm. Therefore, in whichever way the comparison is made, the size of Horsti is to that of Weldoni approximately as three is to four. Another fact brought out by the above measurements is that the females of Horsti are both longer and broader than the males. However, these measurements must not be taken as the maximum length and breadth of the species Horsti; for one female in my collection measures 46 mm. in length and 5·5 mm. in breadth, and one male 40 mm. in length and 4·5 mm. in breadth.

The last fact mentioned seems to dispose of the specific difference in size, but such is not really the case, for the larger specimen of Weldoni is 65 mm. long and 7·5 mm. broad, and therefore exceeds the largest specimen of Horsti in length by 19 mm., and in breadth by 2 mm.

The Skin.—The skin is thrown into folds, of which there are about twelve between each successive pair of feet in the middle part of the body. An examination of figs. 10 and 13 will serve better than the best possible description to emphasise the most characteristic difference between the two species here described. When the skin is examined with a hand lens the folds appear continuous across the back, but when looked at through the microscope a narrow, non-pigmented line is revealed. On these folds are found the papillæ which are one of the constant features of the Peripatidæ. In the Malay forms, as well as in the Sumatran species, they resemble in structure the papillæ of the Neotropical forms. Among the dorsal papillæ are found both primary and accessory ones, the former consisting of a basal portion which varies in shape between a cylinder and a cone (figs. 7 and 8),

and an apical part which may be either conical, cylindrical, or spherical in form, and carries on its top a pointed spine; the latter consisting merely of a conical elevation of the skin. The basal portion of the primary papillæ almost invariably stretches across the folds of the skin from one groove to the other, while that of the accessory papillæ only occupies a portion of that area. The scales which cover the basal portion of the primary papillæ, and correspond to the epidermal cells of the skin, are shorter and broader than those which cover the apical part.

In the species Weldoni all the papillæ have a somewhat polygonal and distinct basal outline, and the consecutive folds of the skin come so close together as almost to obliterate the grooves between them (fig. 10); while in the species Horsti the papillæ have a round and indistinct basal outline, and the grooves between the folds are at least half as wide as the folds themselves (fig. 13). In Weldoni it is not unusual to find secondary papillæ situated in the grooves; while in Horsti they scarcely ever occupy that position; in the former the grooves are narrow and shallow, and the folds rise up gradually; in the latter the grooves are broad and deep, and the folds rise up suddenly.

The Median External Openings:—In the female there are only three median openings, while in the male there are four. The latter has an opening which does not occur in the female, and which is situated between the last pair of legs. It was described by Horst as the anus, which he said was subterminal (8).

The Mouth:—The mouth is surrounded by a ring of yellowish-white papillæ of large size. Inside the ring, and in front of the actual mouth-opening, are situated four pairs of large papillæ, which become smaller in size from in front backwards. Between these internal papillæ the so-called tongue appears, and carries a number of complex denticles (fig. 4 and fig. 14).

The Anus:—The anus is a small, longitudinal slit-like opening, situated at the terminal end of the animal. In

describing the species s u m a t r a n u s Horst missed it, and described the above-mentioned opening found in the male as the anus (fig. 5 and figs. 15 and 16).

The Genital Orifice:—The genital opening in the female is situated between the penultimate pair of legs (fig. 5 and fig. 15), and has the form of a deep, transverse slit, surrounded by tumid lips, which consist of whitish papillæ similar in characters to those which surround the mouth.

The genital opening of the male of the species Horsti is cross-shaped, the cross lines lying in the longitudinal and transverse axes of the animal. The lobes situated in the angles of the cross are made up of numerous papillæ, which are fused together to form four masses, on the top of which occurs a small circular pit. The position of the male genital orifice is between the penultimate pair of legs, as in the female. The characters of the genital openings constitute an unfailing external difference between the male and female of the species Horsti (fig. 16).

The Accessory Pore:—The opening of the male accessory glands is situated between the last pair of legs. It is triangular in shape, but its sides are slightly concave towards the exterior. Papillæ similar to those which surround the male genital orifice form its boundary. Its presence absolutely distinguishes the male from the female (fig. 16).

The Number of Appendages:—The two specimens belonging to the species Weldoni have twenty-four pairs of legs. The number of legs possessed by the young taken from the uteri of these two specimens varies between twenty-three and twenty-five pairs.

Of the eleven specimens belonging to the species Horsti two females have twenty-five pairs ; three females and one male have twenty-four pairs, and five males have twenty-three pairs. Out of five females two have twenty-five pairs, and three twenty-four pairs ; while out of the six males only one has as many as twenty-four pairs, the remaining five

possessing only twenty-three pairs. As a rule, the male of the species Horsti has only twenty-three pairs of legs, while the female has at least twenty-four, and as often as not it has twenty-five pairs. The net result of the above facts is that the male has fewer legs than the female by at least one pair. Another fact brought out by this small collection is the variability in number of legs possessed by both male and female —a feature which is more characteristic of the Peripatinæ than of any other sub-family.

Antennæ:—The antennæ taper gradually as far as the thirty-fourth or thirty-fifth ring, but from that position onwards they increase in circumference so as to become club-shaped. All the rings, as far as the position above mentioned, have the same thickness ; but a considerable number of the last fifteen rings may be either thicker or thinner than the rest. The presence of the thin ones makes it almost impossible to count the number of rings which constitute the antennæ, which are scarcely ever fully extended. On this account the number that can be counted varies between forty-six and fifty, or perhaps in some instances fifty-one.

The Jaws:—The jaws are different from those of any species that has been so far described. The outer blade has two denticles on the inner side of the main tooth. As a rule, in the genera Peripatus and Peripatopsis there is only one denticle ; while in Paraperipatus and Peripatoides there are none in this position. Similarly the inner blade has two denticles on the inner side of the main tooth, which are followed by a diastema, on the inner side of which is found a row of smaller denticles—nine or ten in number. There seems to be no essential difference between the jaws of the two species Weldoni and Horsti. Two vestigial denticles, however, were noticed at the inner moiety of the diastema of the inner blade in one specimen of the species Horsti (fig. 12 a). They are not constant, for the inner blade of the other jaw of the same specimen did not possess them. Nevertheless, they are interesting in that they point to the series being at one time continuous, much as it is at

present in P. capensis, in which the reduction in number
seems to have taken place at the inner end of the series and
not in its middle, as in the Peripatinæ (figs. 11 a and 11 b ;
figs. 12 a and 12 b).

The Oral Papillæ :—The oral papillæ, situated at the
sides of the mouth, consist of two rings, which do not carry
skin papillæ, and of a knob-like end-piece which is provided
with skin papillæ, chiefly on the dorsal aspect. The opening
of the slime-gland is slightly sub-terminal, and is surrounded
by four large papillæ, similar in character to those forming
the ring round the mouth. The oral papillæ seem to be
extremely contractile, and are scarcely ever fully extended
in preserved specimens (fig. 4).

The Legs :—The legs, which vary in number from twenty-
three to twenty-five pairs, are short and stumpy. There is a
marked difference between the arrangement of the legs in
the two species. In the species Weldoni they are crowded
towards the posterior end, the distance between the successive
pairs in the anterior moiety being much larger than in the
posterior one. In the species Horsti they are almost evenly
distributed along the whole length of the body, except in the
region of the last two or three pairs.

The Leg-pads:—With the exception of those of the last
two pairs, every leg carries four pads. The last pair has
only two on each leg, and it often happens that they are in
no way well marked from each other. The penultimate pair
has only three, of which the proximal one is often a mere
vestige. Similarly the fourth pad of the antepenultimate
pair of legs may be fully developed.

The Crural Grooves :—Crural grooves may occur on all
the legs, but on the first and last two pairs they are very
feebly developed, and there is often no trace of them. The
grooves on the second and third pairs of legs are much
smaller than on those further back. They extend from the
third row of papillæ, counted from the proximal pad of the
leg, to a considerable distance on the ventral surface of the
body.

In connection with the crural grooves there are whitish structures of variable size and shape, according to the part of the body to which the leg belongs and according to the species considered.

In the male of the species Horsti there is a whitish papilla of round shape on every leg of the last two pairs, where there is hardly a trace of the crural grooves. On the legs of the genital segment the crural groove is surrounded by a thin and irregularly-shaped fold, white in colour. It is specially thickened round the distal angle of the groove. The same arrangement occurs on seven or eight pairs of legs in front of the genital segment (fig. 16), but as we pass forwards the proximal ends of the folds become less marked. On the next six or seven pairs the white folds are reduced to two papilla-like structures, situated close together at the distal angle of the crural grooves, and sometimes fused together to form an U-shaped body. There are no signs of white papillæ or folds on the anterior five pairs of legs.

In one female of the species Horsti whitish sucker-like structures were observed on all the legs, with the exception of the five anterior pairs. On the last two pairs of legs they were smaller in size than on those in front. These structures in the female present an appearance which is remarkably like that figured in Mr. Sedgwick's monograph, and described as occurring in P. Edwarsdii (compare Pl. 28, fig. 12 [15]). In another female of the same species the legs were so contracted that the structures described above could not be seen, the crural grooves appearing as narrow slits. Whether in the male or in the female the renal pores are situated proximally to the above structures, even in those legs of the female where they are only partially developed.

In the female of the species Weldoni the sucker-like structures, described above in the female Horsti, do not occur. On the last two pairs of legs there is a round papilla similar to that found on the male of the species Horsti. On the legs of the genital segment, as well as on all those situated in front, with the exception of those of the first pair,

there is an **U**-shaped papilla, which surrounds the outer angle of the crural groove. Such a structure was not found on all of them, but it was observed on the second, the fourth, the seventh, and other pairs of legs. Its occurrence on some of the legs of the anterior five pairs contrasts with the condition found in Horsti, where the whitish papillæ do not appear on the legs situated in front of the sixth pair, which is supplied with them in both male and female. In the anterior half of the female Weldoni the **U**-shaped bodies are often divided into two papillæ, situated close together and flattened against each other—a condition found to occur on the sixth to the twelfth pair of legs in the male Horsti.

The Renal Apertures:—The openings of the renal organs are situated in the crural grooves at the junction of the legs with the body, except in the fourth and fifth pairs, in which they are removed to the vicinity of the proximal pad of the leg.

The actual position of the renal papillæ of the fourth and fifth pairs of legs differs in the two species here described. In the species Weldoni they are situated in the proximal pad, and therefore divide it into two (fig. 9); but in the species Horsti they are situated on the proximal side of the pad (fig. 21). The position of these openings in E. Sumatranus agrees with that of the species Weldoni, and not with that of Horsti.

The position of the renal papillæ of the fourth and fifth pairs of legs in Eoperipatus is different from that found in any other genus of the Onychophora. It is more primitive than even that found in the genus Peripatus, which is its closest ally.

Renal pores do not occur on the penultimate or on the last pair of legs in the males. They are found, however, on the last pair of legs in the female of the species Horsti, in which there is a large renal organ in the segment behind the genital one. They were not seen in the adult female of the species Weldoni, in which the outer end of the renal duct of the penultimate segment seems to disappear in the adult.

The Openings the Crural Glands:—Crural glands only occur in the males, and open into the crural grooves, so close to the aperture of the renal organs that they may be said to debouch into a common pit in the groove. They occur only in the two pairs of legs situated in front of the genital orifice, and are placed on the outer side of the renal pores. There are two openings, corresponding to the couple of glands found in every leg of the two pairs above mentioned. It is just possible that, were a sufficient number of specimens examined, they would be found still further forwards, as is the case in P. Edwardsii (**7**).

The Feet:—The feet present the same general structure as in all the Peripatidæ. They are provided with a terminal pair of sickle-shaped claws and a number of papillæ. Dr. Horst described them in E. sumatranus as being provided with only two papillæ, and as having their ventral surface divided by a longitudinal and a transverse groove into four elevations (**8**). Mr. Sedgwick pointed out that, if Horst's description was correct, E. sumatranus was unique; for in all other species of Peripatidæ the foot was provided with at least three papillæ (**15**).

Renewed examination of E. Sumatranus has proved the correctness of the above description as far as it goes. It is equally applicable to the feet of the species from the Malay Peninsula, which have only two primary papillæ situated one on the anterior and one on the posterior distal margin. The four elevations on the ventral surface seem to be four papillæ which are but slightly raised above the general surface, and are pressed against the sides and ventral surface of the foot. The elevations in question carry at least one spine which was not mentioned by Horst in the species Sumatranus, but has been described by Bouvier in some American forms (P. Geayi, Bouvier). As a rule the distance between the erect papillæ and the distal one of the above elevations equals that between the two ventral elevations on each side of the foot; but occasionally the distal elevation is displaced, and becomes located near the erect papillæ which are situated on

the distal margin. This displacement only takes place on either the anterior or posterior aspect of the foot, or on both together. In such cases the foot presents an appearance which has a certain resemblance to the condition found in other Peripatidæ where it is provided with more than two papillæ.

c. Internal Anatomy.

(a) Introductory Remarks:—The internal anatomy of all the Peripatidæ presents a great degree of resemblance; consequently it is not necessary to describe at length the whole anatomy of the species here considered; but as they, together with E. sumatranus, constitute a new genus, it is advisable to describe some systems of organs at greater length than would be otherwise necessary.

The muscular and vascular systems call for no special remark. The nervous system resembles that of other genera to such a degree that there is no need to describe it further than to mention one or two points which seem to demand attention. One of the points in question is the difference between the male and the female nervous systems immediately in front of the genital orifice. In the male the cords are provided with specially enlarged swellings or ganglia in the above-mentioned position (fig. 35), while in the female there is no such swelling beyond that which occurs opposite each pair of legs (fig. 33). The second point is the well-developed condition, even in the adult, of the strands of nervous matter which pass from the lateral nerve-cords to the ventral organs. These strands contrast strongly with the nerves given off from the nerve-cords to the body-wall and the legs, in that they consist of cells in the more or less undifferentiated state in which they are found in the lateral nerve-cords (fig. 34).

(b) Ventral Organs.—As the ventral organs have been mentioned already, it is advisable to describe them at the present juncture. They occur between each pair of legs in the mid-ventral line, and correspond to the segmentally

arranged spots mentioned in describing the external cha-
racters.   Even in the adult they are not as degenerate as
usually represented in other genera.   In section they are
seen to consist of a group of long cells with oval nuclei
situated near their internal end.   In a median section the
cells seem to be arranged fan-wise round what appears to be
a cavity which apparently communicates with the exterior.
If this is not the case, the cuticle covering the skin clearly
dips down into the space situated inside the group of cells
constituting the ventral organ.

(c) The Salivary Glands :—The salivary glands present
the same general arrangement as in the other genera of the
Peripatidæ.

Their cœlomic end-sacs are of enormous size, and spread
themselves, chiefly in a dorso-ventral direction, under the
lateral longitudinal muscles.   Their walls are thick, and
consist of cells which present no definite cell outlines, and
which are supplied with large nuclei and highly vacuolated
cytoplasm.

From the postero-dorsal corner of the cœlomic end-sacs
a short duct passes and opens into the tubular part of the
slime-gland on its dorsal aspect, on a level with the first pair
of legs.   The tubular parts of the glands lie in the lateral
body-cavity immediately above the nerve-cords.   Towards
their posterior end they are circular in transverse section,
but anteriorly they are triangular, the apex of the triangle
being wedged in the upper angle of the lateral body-cavity. As
a rule their lining cells are tall and columnar, but in places
they are short, especially on the lower side of the triangular
section and towards the anterior end of the glands.   They
open into the anterior outer corner of two rather large sacs
which are situated, one under each of the nerve-cords.
These sacs have not been seen in any other genus.   They
certainly do not exist in P. capensis, or else Balfour and
Sedgwick would have seen them in sections, for in Eoperi-
patus they are the most prominent feature of a section
passing through that region.   From the inner anterior corner

of each sac a short duct passes into the posterior outer corner of the median diverticulum of the buccal cavity.

Shortly before the tubular glands pass into the above-mentioned sacs there is a sudden, well-marked change in the characters of the lining cells. The lining of the glandular part in this region consists of short columnar cells with no well-defined cell outlines, and with nuclei in the centre, while the lining of the portion which enters the sacs consists of tall columnar cells with large nuclei situated at their free ends and with well-defined cell outlines. In both respects the lining of the sacs resembles the latter, which is a proof that they are mere diverticula of the ectodermal ducts (fig. 32). The lining of the backward diverticulum of the mouth, that is, the so-called common duct of the salivary glands, consists of much shorter cells with nuclei in the centre, but the linings of the two regions pass gradually into each other.

The sharp distinction between the lining cells shown in figure 32 probably marks the external limit of the meso-dermal portion of the gland.

Mr. Sedgwick describes the elongated glandular portion as being produced by the backward extension of the duct, and since the duct is mesodermal in origin the gland must be so too (14). If we judge from the histology of the parts in question, there seems to be no doubt but that the tubular gland, which runs along at least two thirds of the length of the body, is mesodermal. Kennel would probably consider it ectodermal, but the histology of the salivary glands, the renal organs, the genital organs, and finally of the male accessory glands, all of which appear to be homologous organs, tends to disprove Kennel's view of the nature of the renal and genital ducts, as well as of the salivary duct, from which the salivary gland is produced by a backward exten-sion.

(d) The Renal Organs:—Renal organs occur in all the leg-bearing segments except the genital one. However, a complete duct was not found in the last segment provided

with legs in either the adult female of the species Weldoni, or the adult male of the species Horsti; though in the female of the latter species the duct was very highly developed (fig. 34).

A typical renal organ is usually said to consist of four parts: namely, the cœlomic end-sac; the thickened funnel; the coiled tube; and the bladder. It appears, however, that there is a fifth part which is, most probably, as constant as any other part, without making an exception even of the cœlomic end-sac, which is always present. The part in question is the ectodermal duct which puts the cœlomic portion of the organ in communication with the exterior. It varies in length according to the position of the renal organ; in that of the ninth segment, which is represented in fig. 26, this ectodermal duct is short; but in the one from the fourth leg-bearing segment which is shown in fig. 25 it is much longer. Of the other parts, the bladder, the funnel, or the coiled duct may be absent. In the renal organ of the fourth and fifth leg-bearing segments the bladder is wanting, while in those placed in the first, second, third, and the two prægenital segments, there is neither a differentiated funnel nor a bladder, and the coiled tube is represented only by a short, straight duct.

A typical renal organ from the ninth leg-bearing segment, with the five parts above mentioned, is shown in fig. 26. The short duct situated externally to the bladder in the above-mentioned figure is a well-marked structure, and its distinctive histological characters are clearly seen in fig. 31. The lining cells of this ectodermal duct resemble exactly those which cover the external body wall, while the lining cells of the bladder approach much nearer to those of the coiled tube. The bladder, it would appear, is nothing more than a dilated portion of the outer end of the coiled tube. In the renal organ, shown in fig. 25, which has no dilated bladder, the short duct represented in fig. 26 appears as a much elongated tube which stretches from the level of the nerve-cord to the renal papilla situated on the proximal side

of the fourth pad. Fig 24 represents the renal organ of the second pair of legs. The only parts represented here are the cœlomic end-sac, and an undifferentiated short duct which passes from it to the exterior. Figs. 27 and 28 show a similar reduction of the renal organs of the two pairs of legs situated in front of the genital orifice. In both cases they consist of a small cœlomic end-sac and a short narrow duct which passes to the exterior. The examples given above suffice to show that there is a considerable amount of difference in the structure of the renal organs in the various parts of the body. The most prominent feature is the simplification of structure towards either end of the animal.

The cœlomic end-sac presents in section an irregular and collapsed appearance, but is easily demonstrated in the adult. In the middle part of the body it extends through several sections, but is much smaller towards either end of the animal. Its walls are thin and seem to consist of two layers of cells, which are flattened out though not to any great extent (figs. 29 and 30).

The funnel has a rim which projects into the cavity of the cœlomic end-sac, and is never provided with cilia. Its walls consist of an internal lining of closely packed columnar cells with deeply staining nuclei, and an external layer of flattened cells (figs. 29 and 30).

The coiled tube and the bladder have practically the same structure as the cœlomic end-sac; the lining cells of the former, however, are less flattened than those of the end-sac, while those of the bladder are more so, and strongly contrast with those lining the short duct which passes from the bladder to the exterior (fig. 31).

(e) The Female Reproductive Organs :—When an adult female is opened the first structures visible are either the stomach or the coils of the uteri, and the ramifications of the slime-glands, which extend backwards as far as the ovary. In some cases the coils of the uteri are above the stomach and completely conceal it, but in others they are below it and are hidden by it. In either case the branches of the slime-

glands intertwine with the uterine coils. The ramifications of the slime-glands seem to vary considerably in size, especially in transverse section—a variation which is probably due to the condition of the glandular secreting cells which line the interior, and to the amount of secreted matter in the lumen of the glands. The length of the lining cells of the slime-glands is variable, sometimes long, sometimes short, but always more or less columnar. Their nuclei are large, granular, and clear, and on this account a section of one of the finer branches of the slime-glands is distinguished with ease from other small tubes, such as the finer coils of the vasa deferentia. The clot of slime, also, which they usually contain, helps to distinguish them (fig. 41, *s. g.*).

The Ovary :—The ovaries in the two species here considered resemble each other in their most essential features to such an extent that there is no need to describe them separately. In both cases the ovary is situated dorsally in the region of the third and fourth pair from the posterior end of the body. It is found under the floor of the pericardium, and is attached to it not by a single ligament, but by an extensive surface, thus differing from all the genera as yet described. This feature of itself makes it almost impossible to dissect it out. Not only is it attached to the pericardium, but it spreads out over the rectum and uteri like a saddle, and pushes itself into any space that may be unoccupied, both between as well as outside the uteri. It becomes closely adherent to the uterine walls on the one hand, and to the peritoneal lining of the body-cavity (hæmocœle) on the other hand. Thus the fusion of the ovary wall with two or three other structures makes it almost impossible to remove it in an unbroken condition.

In the adult the ovary consists of a shapeless sac with an immense cavity which presents no sign whatever of its double origin. Its walls are folded and carry follicular outgrowths which are suspended in the body-cavity, and contain ova in various stages of development. The ovarian cavity communicates by means of a large, irregularly shaped opening with the oviducts. The opening in question is situated, as a

rule, at the posterior end of the ovary, the oviducts [1] passing forwards from it.

No essential difference could be made out between the oviduct and the proximal part of the uteri by looking at a complete preparation; but when sections were examined a most marked difference was immediately noticed; but there seems to be no sharp line of demarcation between the two parts (compare fig. 50, *ovid.*, with fig. 51, *ut.*).

It is difficult to make out that the cells lining the oviducts are columnar, because the cell outlines are not easily seen, and the nuclei may take up any position whatever in the cells; that is, they may be found at the base, in the middle, or at the free end of the cell (fig. 50). Another feature of the cell-lining of the oviduct is the sharp and well-defined limit which the cells present towards the lumen of the duct, which is in no way narrower than that of the proximal portions of the uteri.

The cells which line the uteri are quite different in character from those which line the oviducts. In those portions where there are no embryos they are distinctly columnar, with well-marked cell outlines, with nuclei invariably situated at their base, with granular cytoplasm, and their free ends rounded and separate from one another; the result being the absence of a well-defined limit towards the cavity of the duct. The cells lining the uteri, whether near the receptaculum seminis or towards the exterior, possess glandular and secreting characters.

Up to the present time such a difference as has been shown to occur between the lining of the oviduct and that of the uteri in Eoperipatus has been found only in Paraperipatus Novæ-Britanniæ, discovered and described by Dr. Willey (**17, 18**).

The oviducts have thick walls, consisting of the same

[1] The term oviduct is restricted in the present account to that portion of the genital duct which is situated between the ovary and the receptaculum seminis; the term uterus being used to designate the portion of the genital duct in which the embryos develop, and which is situated between the receptaculum seminis and the exterior,

layers as the uterine wall, namely a peritoneal investment, a tunica muscularis, a tunica propria, and a lining epithelium. The first, second, and fourth of these layers are very distinct in Eoperipatus, but the tunica propria is not well developed either in the oviducts or in the uteri.

The ova in both species are large and full of yolk. In size and structure they resemble those of the New Zealand forms, and differ most of all from those of the genus Peripatus; although as far as external characters are concerned Eoperipatus is more closely related to that genus than to any other. When this feature of the ovum is considered in connection with the external characters, it is impossible not to accept Mr. Sedgwick's conclusion (14), and to reject that of Kennel (9) and Willey (18), who think that the yolk-bearing condition of the ovum is not a primitive but a secondary feature. This question, however, will be discussed further on, as well as the question as to which is the most primitive genus of the Peripatidæ.

The Receptaculum seminis :—In Eoperipatus there are a couple of well-developed receptacula seminis, such as are found in the genera Peripatus, Paraperipatus, and Peripatoides. In the genus Paraperipatus, the "infundibulum," which corresponds to what has been called the oviduct in the present memoir, passes directly into the receptaculum seminis, and the uterine canal starts from the opposite side of the same. The "infundibulum" and the uterine canal are put into communication with each other by means of a narrow secondary duct (18). In the genus Peripatus, on the other hand, the main duct passes alongside the receptaculum seminis, and seems to communicate with it only in an indirect way, by means of a couple of narrow ducts opening into the receptaculum seminis on either side, and into the main duct by a common aperture. The condition occurring in Eoperipatus is exactly parallel to that found in the genus Peripatus. The main canal passes alongside the receptaculum seminis, and communicates with it only in an indirect way by means of two diverging narrow ducts,

which for the greater part of their course are embedded in the wall of the sac (fig. 51).

The wall of the receptaculum seminis is thin, and consists of two layers of cells. The outer layer is made up of flattened cells belonging to the peritoneal epithelium; the inner layer consists of short cells, with rather large nuclei and clear cytoplasm. They contrast in the most marked way with the columnar lining of the adjacent genital ducts (fig. 51). The two narrow ducts of the receptaculum seminis lie for the most part in its walls, and are lined with short columnar cells provided with small and closely set nuclei. The receptaculum seminis seems to be a storehouse, in which the spermatozoa are kept until they are wanted. In Eoperipatus copulation appears to take place, and the spermatozoa must pass up the uterine canal into the receptaculum seminis. In one speci-men which was sectionised the lower parts of the uteri were absolutely full of sperm-cells, enough, it would seem, for a lifetime. Indeed, it is difficult to understand how fecunda-tion can take place in Eoperipatus once the ova have entered the genital ducts, and have started on their journey down the uteri. Embryos in all stages of development are found in the uteri, and probably go on developing all the year round, so that the uteri are never empty. The natural conclusion come to is that fecundation takes place only once ; that is, before the ova have ever entered the uteri. The receptacula seminis should be considered as a couple of sacs formed for the purpose of retaining the sperma-tozoa, which are transmitted into the female uteri during copulation, which takes place before any ova have ever passed down the oviducts to the uteri.

The Receptaculum Ovorum :—In Eoperipatus there are two receptacula ovorum with thick walls, exactly like those figured and described by Gaffron as open funnels (7), and by von Kennel as closed sacs (9). They occur only in the genera Peripatus and Eoperipatus. Paraperi-patus, Mesoperipatus, Opisthopatus, Peripatopsis, and Peripatoides have no receptacula ovorum. In Eo-

peripatus they are situated close to the ovarian opening of the oviducts, with which they communicate. Their free end, which was described by Gaffron in the genus Peripatus as an open funnel, is closed by a thin membrane. The lining of the diverticulum in the region situated close to the above-mentioned membrane consists of columnar cells, which present a certain amount of resemblance to the lining cells of the renal funnels communicating with the cœlomic end-sac of the renal organs ; but the lining of that part which opens into the oviduct presents the characters possessed by the lining of the latter (fig. 50).

Willey is of opinion that the presence or absence of receptacula ovorum is correlated with the occurrence of what he describes as " epithelial ova " and " follicular ova " respectively. The presence in Eoperipatus of "follicular ova " as well as receptacula ovorum, proves Willey's suggestion to be unsound. It seems, however, that there is no reason for supposing that the so-called receptacula ovorum function as such in Eoperipatus. It is much more probable that here, as in all forms which possess follicular ova, the stalks of the follicles, as Willey expresses it, represent so many secondary ducts discharging into the main ovarian cavity, which in Eoperipatus is of immense size, and which plays the part of the receptacula ovorum.

There seems to be in the literature of the Peripatidæ a certain amount of confusion as to the exact meaning of Mr. Sedgwick's suggestion of the homology of the parts under consideration. Having said that Kennel distinctly states that he does not regard the receptaculum ovorum as homologous with the funnel of the renal organ, apparently because the thin-walled vesicle closes its free end, Mr. Sedgwick proceeds to explain his view of the homology of the parts in question. He draws the conclusions that the thin-walled vesicle of the receptaculum ovorum is homologous with the cœlomic end-sac of the renal organs, and that the diverticulum—Ovarian-trichter of Gaffron—is homologous with the so-called funnel of the renal organs ; two conclusions which derive support

from the histological details of the parts under consideration in Eoperipatus.

The only desirable modification of the above conclusions is that not the whole, but a portion, of the canal passing from the thin-walled vesicle to the oviduct is homologous with the renal funnel—the part situated nearest the oviduct, of which, though it is curved, it seems to be a continuation, being homologous with a portion of the coiled tube of the renal organs.

To recapitulate, the homology of the parts seems to be as follows :—The thin-walled vesicle or membrane closing the ovariantrichter of Gaffron is homologous with the cœlomic end-sac of the renal organs; the portion of the diverticulum which is situated nearest the thin-walled vesicle corresponds to the renal funnel; the remaining portion of the diverticulum, the oviducts, and the uteri, would be homologous with the coiled tube and the dilated bladder; and finally, the ectodermal portion of the female genital system would correspond to the short, ectodermal duct of the renal organ.

On the above view of the homology of the parts here considered the receptaculum ovorum is the direct continuation of the oviduct into the terminal end of which it leads. It follows that the renal funnel is not represented by the pore leading from the oviduct into the diverticulum. It may be so represented in other genera of the Peripatidæ, but certainly it is not so in Eoperipatus.

It does not follow from the above view that the cavity of the ovary is a mere continuation of the oviduct. Sedgwick describes the "germinal nuclei" as appearing in the sixteenth to the twentieth somite, both inclusive. The twenty-first pair of somites, in which germinal nuclei do not appear, are completely used up in the formation of the genital ducts. In this case the ovary formed from the dorsal cœlom of several somites becomes grafted—so to speak—on the twenty-first somite. Consequently it can in no way be described as a mere continuation of the oviduct which is developed independently from a different pair of somites.

Kennel, differing from Sedgwick, has described the ovary

and oviducts as being developed from the genital somite
alone in the genus Peripatus.

It is quite possible that there is a difference in this respect
in the Peripatidæ; but it is necessary to point out that the
position of the ovary in the adult of the genus Peripatus, as
well as of other genera, tends to show that Kennel is in error,
for the ovary is located in the prægenital segment, just where
we should expect to find it had it been developed from the
dorsal portion of a prægenital somite. If this be so, the
ovary with its oviduct is a composite structure even in the
genus Peripatus, as is certainly the case in the genus Peri-
patopsis. But, though Kennel may be in error in deriving
the ovary from the genital somite alone in the genus Peri-
patus, it is highly improbable that it is formed from as many
somites as in the genus Peripatopsis; for to make a mistake
with regard to one somite is quite different from falling into
error regarding six somites. It would seem that there is a
difference between Peripatopsis and Peripatus in this
respect; a difference which points to the possible participa-
tion of a great number of somites in the formation of the
ovary in the ancestral Peripatus. In the genus Eoperi-
patus the ovary is formed from the dorsal portion of the
four pairs of somites situated immediately in front of the
genital segment, which, it would seem, takes no part in the
formation of the ovary.

The Uteri:—This term is applied to the main part of the
generative ducts, that part which extends from the receptacula
seminis to the vagina, and contains the developing embryos,
if there are any. The uteri present no constant arrange-
ment, and it is impossible to say whether any particular one
is predominant. In the specimens shown in figs. 22 and 23,
the arrangements are exceedingly different. In both cases
the uteri contain a number of embryos. In the specimen
shown in fig. 22, the oldest embryo in the left uterus is on
the right side, and the one in the right uterus is on the left
side—a result brought about by the crossing of the uteri close
to the vagina.

In the specimen represented in fig. 23 the uteri do not cross one another ; consequently the embryo in the right uterus is on the right side, and the one in the left is on the left side. In the two specimens represented in figs. 22 and 23, there is another marked difference in the topography of the uteri. In fig. 22 the uteri are packed under a loop of the posterior end of the stomach, and do not extend forward on either side of the alimentary system; while in figure 23 they are placed on the right side of the stomach, and extend forward as far as the first pair of legs. The stomach in this case has no loop at its posterior end, and this may be the cause of the forward extension of the uteri.

As has been stated above, the ovary is constant in its position. The proximal ends, that is, the ovarian ends of the uteri, always pass forwards to a greater or less distance ; the middle portions are intricately coiled among themselves, and may form one or two loops round the stomach ; the posterior ends descend and pass on the outer side of the nerve-cords to the short vagina (figs. 22, 23, and 33).

The thickness of the uterine wall is highly variable. It may be thick and consist of a well-developed peritoneal investment, a tunica muscularis, a tunica propria—which is usually very thin,—and a lining of tall columnar cells (figs. 51, 52, and 54), or it may be thin, when it seems to consist of thin layers of cells. This difference, however, is more apparent than real, for it is due to the expansion of the uterus brought about by the increasing volume of the developing embryos, as well as the secretion of nutritive material by the lining cells, and consequent diminution in size. That there is no actual loss or destruction of the lining cells is amply proved by the way the columnar cells which line those portions of the uteri situated between the several embryos gradually pass into the flattened layer which lines the portions of the uteri in which the embryos are found (fig. 53).

In mature specimens the uteri contain a variable number

of embryos which represent a number of stages in the development. It seems that not all the ova which pass into the uteri develop. Many of them, either for want of room or for some other reason, fail to advance beyond the segmentation stages, even if they do segment at all, and as the embryos which are successful in the struggle for existence elongate, the unsuccessful ones become wedged in between the continually growing young.

There seems to be no evidence in favour of the view, which has been put forward more than once, that accompanying parturition there is a resorption of the terminal ends of the uteri. When the pigmented embryo, which measures from 20 to 27 mm. in length, is born, that portion of the uterus which contained such an embryo must contract; consequently the wall must thicken and the flattened cells of the lining, being no longer called upon to secrete nutritive material, once more assume their normal form. The embryos are always entirely free in the uterus, that is, there is no organic connection between the developing young and the uterine wall, though they are in close contact with each other. From what can be seen in Eoperipatus, it seems much more reasonable to suppose that the embryos pass gradually down the uteri than that the uteri are resorbed at their vaginal ends.

(f) The Male Reproductive Organs:—Though the female reproductive organs of Eoperipatus differ considerably from those of the genus Peripatus, the male reproductive organs of the former present a peculiar agreement with those of the latter.

The tubular testis communicates with the seminal vesicle by means of a short duct which opens into the latter near its anterior end. Close to the posterior end of the seminal vesicle the vas deferens [1] arises and coils about in the body-cavity (hæmocœl). The vasa deferentia pass backwards, and

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[1] No distinction is made here between vas efferens and vas deferens, because there seems to be no satisfactory reason for drawing such a distinction.

on reaching the level of the antepenultimate pair of legs, leave the dorsal aspect of the animal and pass in an oblique direction towards the ventral surface. The right vas deferens makes its way under the corresponding nerve-cord and the ductus ejaculatorius. As a rule, the left vas deferens passes under the corresponding nerve-cord, but, in some cases, it does not do so. The vasa deferentia unite to form a common duct, the point of union being situated either on the inner or on the outer side of the left nerve-cord, according as the left vas deferens does or does not make its way under the cord. When the point of union is on the outer side of the cord, the right vas deferens passes under it so as to unite with the left. After the vasa deferentia have united, they pass forwards in a common sheath to the level of the antepenultimate pair of legs, where the canals themselves unite.

The common duct runs forward as far as the third præ-genital pair of legs, and there, turning round, makes its way backwards to the genital orifice. When the point of union of the vasa deferentia is on the outer side of the left nerve-cord, the ductus ejaculatorius in passing to the genital opening has to make its way under the cord; but when the point of union is inside the nerve-cord, the ductus ejaculatorius does not pass under it (figs. 36 and 37).

The testes are provided with a peritoneal investment and a lining of tall columnar cells, with nuclei at their base, and a sharp cell outline. The nuclei are comparatively large, and the cytoplasm is clear (fig. 38). The duct which passes from the testis to the seminal vesicle has the same two layers as the testis, together with an intervening muscular layer (fig. 39). Its lining cells are columnar in form and are provided with basal nuclei, well-defined cell outlines, and clear cytoplasm. The wall of the seminal vesicle presents close resemblance to that of the receptaculum seminis. The vas deferens at its commencement has much the same appearance in section as the short duct which passes from the testis to the seminal vesicle, with the difference that the intermediate or muscular layer is thicker (fig. 40).

Further along the vasa deferentia, however, the wall becomes thinner, the muscular coat less developed, and the lining cells less columnar. This feature becomes more and more emphasised towards the point of union of the two genital ducts, as can be seen on comparing figs. 40, 41, and 42. At the above-mentioned point, however, there is a sudden change in the characters of the lining cells as well as in the muscular coat. In both the ascending and descending limbs of the common duct the lining cells become columnar and, as a rule, the cell limits are well marked. The muscular coat of the ascending limb, however, remains comparatively thin, and even in the descending limb it only becomes greatly thickened at the level of the antepenultimate pair of legs. From that position onwards it is extremely thick, and the term ductus ejaculatorius should be confined to this thickened portion of the common duct (figs. 46, 47, and 48).

The most interesting character of the male genital organs of Eoperipatus is the great length of the unpaired duct, which almost equals in extent that of the genus Peripatus. The variation that occurs in the length of the unpaired portion of the male organs in the Peripatidæ is a very interesting feature. It is longest in the genera Peripatus and Eoperipatus (7). In the genus Peripatoides it is not so long (16), and is still shorter in Peripatopsis (2); but is shortest of all in Paraperipatus, in which, according to Willey, the unpaired portion of the male duct is hardly any longer than the vagina (18). Whether this feature of Paraperipatus is primitive may well be doubted, when the fact that there are no spermatophores in this genus is taken into consideration. As in the genera Peripatus and Peripatoides, there is in the unpaired duct of Eoperipatus an enormously long spermatophore, which, however, lacks the horny coat described by Miss Sheldon in P. Novæ-Zealandiæ (16), and by Gaffron in P. Edwardsii (7). It is nevertheless provided with a horny cap, which covers its foremost end, and this seems to be the only advance which it has made, in the direction of forming a coat, from the condition described

by Professor Lankester many years ago in two species of the genus Tubifex (**11**). In this Annelid genus the tails of the spermatozoa project freely from the wall of the spermato- phore, and are found in the living state in continual vibration. In Eoperipatus the tails were not observed to project freely from the body of the spermatophore, but it must be remem- bered that it was not examined in the fresh state. If it were examined fresh, it is quite possible that the tails of the spermatozoa would be found to project freely into the cavity of the duct. In the spermatophore of Eoperipatus as in that of Tubifex the spermatozoa are arranged radially round a central core, which is free of them, as was figured in Tubifex by Professor Lankester (**11**). It is evident that the spermatophore of Eoperipatus is but little in advance of that found in the Annelid Tubifex. The next stage in the evolutionary series is found in the genera Peripatus and Peripatoides, where both the head and the body of the spermatophore are provided with a horny coat (**7**) (**16**). The genus Peripatopsis would supply a still further stage in the series; a stage in which the long spermatophore of the other genera has been broken up, and is represented by a number of small oval bodies each consisting of a thin case full of spermatozoa (**15**). The last stage would be represented by the condition of things found in Para- peripatus, where the male genital ducts are described by Willey as "containing abundant loose felted spermatozoa" (**18**).

If, on the one hand, the above account represents cor- rectly the phylogenetic history of the spermatophore in the Peripatidæ, and if, on the other hand, as Willey seems to think (**18**), the presence or absence of a long unpaired duct is in correlation with the formation of a long spermatophore, it seems that there are good reasons for doubting the con- clusion that the condition of the genital ducts in the genus Paraperipatus is primitive, though on à priori grounds it appears to be so. This explanation of the features presented to us enables us to place the Malay and Neotropical genera

nearer the base of the Onychophoron branch of the great Arthropodan phylum than the African, New Zealand, and Australian genera. This agrees with the arrangement to which we are forced on other grounds, which will be discussed later.

(g) The Male Accessory Glands.—These are a pair of glands which occur only in the male (fig. 35, m. a. g., and fig, 36, m. a. g.). Their external opening has already been described (p. 490). The general course which they take is the following. They start as straight tubes, occupying a cavity of their own situated in the dorso-lateral aspect of the body. Their position is shown in fig. 35, which represents a transverse section passing just in front of the male genital pore, from the level of which they pass obliquely downwards on the outer side of the nerve cords to the common opening which is situated between the last pair of legs. In passing round the nerve cords they press against them in such a way as to become partially embedded in them.

The inner ends of the male accessory glands have thin walls and a fairly large lumen, which is circular in shape (fig. m. a. g.), and which is not lined by a chitinous intima. The lining cells of this part are short and columnar; the peritoneal investment consists of much-flattened cells, and the intervening layer is thin. The walls of the portion situated nearer to the exterior which passes round the nerve cords are much thicker, and the lumen, which may be of any shape, and small, is lined with a chitinous intima. It consists of the same three layers as the thinner portion situated more internally, but the middle or muscular layer is much thicker.

It is difficult to say what the homology of these glands may be, as their development has not been worked out; but it seems necessary to discuss the possibilities of the question, were it only to clear the ground. The great difficulty of the subject lies in the different positions occupied by the external openings of a pair of glands which are found more or

less closely related to the male genital system in the different genera of the Peripatidæ.

In Peripatus Edwardsii the "anal glands" open on either side of the anus as shown by Gaffron (**7**). In Peripatoides Novæ-Zealandiæ, according to Miss Sheldon, the "accessory glands" open outside the nerve-cords near the posterior end of the body (**16**). In Peripatoides leuckarti, Fletcher describes the "accessory glands" as opening close together between the generative pore and the anus (**6**). In Peripatopsis capensis, according to Balfour, the "male accessory glands" open into the ductus ejaculatorius (**2**). Willey describes the "pygidial glands" of Paraperipatus Novæ-Britanniæ as debouching into a much-thickened bulbus, which in its turn opens to the exterior above the anus (**18**). In Eoperipatus the male accessory glands debouch into a median opening situated between the last pair of legs.

From the above short statement it will be seen that the glands found at the posterior end of the Peripatidæ open to the exterior in half a dozen different positions. As to their homology two views have been put forward, and obviously two views are possible. Balfour thought the male accessory glands of P. capensis were homologous with the crural glands (**2**). Kennel thinks that the anal glands of P. Edwardsii are homologous with the renal organs (**9**), and Willey seems to accept this view (**18**). The latter author in his most brilliant account of the anatomy and development of Paraperipatus Novæ-Britanniæ writes as follows of the "pygidial glands:"—"There are a pair of glands . . . . homologous with the 'accessory glands' of the African and Australian species, and with the 'anal glands' of the Neotropical species." On another page he has the following expression:—"It is advisable to give separate names to structures, even though obviously homologous, when they have such very different anatomical relations." (In both of the above quotations the italics are mine.) Dr. Willey has brought forward few or no reasons in favour of the view that all these glands are "obviously homologous." At the

present juncture it is proposed to examine the known facts of anatomy and development in order to see how far such a statement is justified.

Gaffron's description of the "anal glands" of P. Edwardsii, and Willey's account of the "pygidial glands" of P. Novæ-Britanniæ are in agreement in so far as that they show that the glands consist of two parts, which Gaffron designated the "ectodermal" and the "entodermal" portions, and which Willey describes as "ectodermal" and "mesodermal." The same distinction occurs in Eoperipatus, though it is perhaps not so well marked. So far, then, there is in these three genera an agreement between the accessory glands—to use one term for all of them—and the renal organs, which consist of an ectodermal portion, however short, and a mesodermal or cœlomic portion. It must be pointed out, however, that too much importance should not be attached to the difference between the so-called ectodermal and mesodermal portions of these glands, because the lining cells of the cœlomic portions of the renal organs differ widely from one part to another; for example, the lining of the funnel differs more from that of the coiled tube or of the cœlomic end-sac than the lining of the two parts of the accessory glands do from one another. It follows that the argument derived from histology in favour of the view that the accessory glands consist of ectodermal and mesodermal parts homologous with the similarly situated parts of the renal organs is not a very strong one. It seems that the only point of any importance is the existence of a chitinous intima lining the so-called ectodermal portions, which are always short.

Kennel described the development of the anal glands in P. Edwardsii as taking place from the apodal anal segment; that is, the second segment behind the genital one, and also found a vestigial representative of them in the young female. The conclusion which naturally follows is that the anal glands of P. Edwardsii are homologous with the renal organs and genital ducts.

In Peripatoides Novæ-Zealandiæ the accessory

glands open by the sides of the nerve cords, near the posterior end, that is, they open almost exactly where we should expect a renal organ to open, and so far this is in favour of their homology with the renal organs; but we know nothing of their development. It is not known whether they belong to the anal segment, as in P. Edwardsii, or to another segment situated between the anal and the genital segment, which in P. Novæ-Zealandiæ has lost all traces of its appendages. If they belong to the former there is a very close relation between them and the anal glands of P. Edwardsii, but if they belong to the latter, the most that can be said is that they are thus homologous in the same sense that the renal organs of the various segments are homologous with them.

In P. Leuckarti the "accessory glands" differ from those of P. Novæ-Zealandiæ only as regards their external openings, which are situated close together near the middle line, between the genital orifice and the anus—a position reached by a very slight amount of shifting towards the mid-ventral line. It seems probable, when other genera are taken into consideration, that in the above two species which belong to the genus Peripatoides, the "accessory glands" are derived from the anal somite.

The condition existing in P. Leuckarti leads naturally to that found in Eoperipatus, where the accessory glands open into a common pit situated in the mid-ventral line between the genital pore and the anus; that is, the external opening is placed exactly where we should expect to find it if the accessory glands belonged to the somite of the last leg-bearing segment. But if the accessory glands of Eoperipatus are homologous with the renal organs, they cannot belong to the last leg-bearing segment; for in both male and female there exists a well-developed renal organ in that segment, though in the adult male the external portion of the duct is not found. It follows that the accessory glands of Eoperipatus must be either the renal organs of the anal segment as in P. Edwardsii, or the crural glands of the last leg-

bearing segment. Their position is in favour of the view that they are crural glands which have passed from the outer to the inner side of the renal organs. This would be possible, because the renal openings on this segment have moved slightly forward, as can be seen from the section represented in fig. 34, which, though passing through the renal opening, is taken in front of the last pair of legs. Their structure, however, is in favour of the view that they are derived from the apodal anal segment, and contain a cœlomic element, but that their openings have moved both forwards and inwards, and have united together in the mid-ventral line. Of the two views above suggested the latter seems the more probable, because the accessory glands of Eoperipatus and the anal glands of Peripatus would on that view belong to the same somite.

The next form to be considered is Paraperipatus, in which the glands open dorsally above the anus. In Paraperipatus the penultimate pair of legs has completely disappeared, and the genital segment is apodal. As the development of the " pygidial glands " is unknown, it is not at all certain whether they are crural glands or renal organs which have been modified. Their structure is certainly in favour of the latter view. Again, supposing that they are modified renal organs, it is not known whether they are derived from the somite next the genital somite or from the one which follows, namely, the anal somite ; the position of their external opening, however, is in favour of the latter view.

In all the above forms it is probable that the accessory glands belong to the apodal anal segment—a statement, however, which is far from having been proved. As regards their external openings, there seems to have been a gradual shifting probably in two directions. If these glands represent renal organs it is only natural that they should have opened at first in the same position as the renal organs. In fact, the position of their openings in P. Novæ-Zealandiæ closely resembles that of the renal organs, and a slight shifting forwards and inwards would produce the condition found in

P. Leuckarti, and finally in Eoperipatus. If instead of
shifting forward they had shifted backwards, the condition
found in P. Edwardsii would result, and by shifting up-
wards that found in Paraperipatus would be brought
about. It seems that there are two reasons for this shifting;
first, the slightly subterminal position of the anus; secondly,
the shortening of the anal cone. Probably the latter was the
more potent element in driving the opening to the mid-dorsal
line in Paraperipatus, the question of space becoming a
determining factor in bringing about the change of position
of the openings. In Paraperipatus, as the anus and
genital orifice approached each other, the glands and their
openings were forced towards the dorsal aspect of the animal.

We may conclude that it is possible to homologise the
anal glands of Peripatus, the pygidial glands of Para-
peripatus, and the accessory glands of Peripatoides and
Eoperipatus with the renal organs, and with one another,
without violently twisting the facts known about them,
though in many respects we are still treading on uncertain
ground.

There remains to be considered, however, one well-known
form, namely, Peripatopsis capensis. In this form the
male accessory glands open into the terminal portion of the
ductus ejaculatorius. In this feature Peripatopsis is quite
unique. In fact, in this genus the relation of the male
accessory glands to the ductus ejaculatorius is exactly what
it should be, on the view that they are the crural glands of
the genital segment. In Balfour's posthumous works the
following expression occurs:—"The accessory gland in the
male is probably a modification of one of these organs;" i. e.
of the crural glands (1). Mr. Sedgwick in his account of
the development of the species under consideration writes as
follows:—"There are rudiments of two pairs of somites
behind the somites of the anal papillæ in Stage E. One
of these is just visible in Stage F. They vanish completely
at the end of Stage F. No appendages or rudiments of such
are developed in connection with them" (14). From this

passage it seems absolutely clear that the somites behind the genital segment do not give rise to the male accessory glands of P. capensis. It follows from this that the glands in question cannot in any way be described as modified renal organs, unless the genital somite is capable of giving rise to two sets of similar organs, one of which is modified as the genital ducts, and the other as the male accessory glands— an absolutely gratuitous supposition, for the body segments of the Peripatidæ, as far as is known, never give rise to more than one renal organ or its modified homologue. It seems, therefore, that the "obvious homology" of the male accessory glands of P. capensis with the anal glands of P. Edwardsii, the pygidial glands of P. Novæ-Britanniæ, and the accessory glands of P. Novæ-Zealandiæ, P. Leuckarti, and Eoperipatus, is far from being proved, and that the possibility of their being merely modified crural glands must not be lost sight of. It may be that, when we shall have learnt more about the origin of these glands in the different genera, they will be shown to be homologous; but for the present we must at least suspend judgment, as the formation of a premature conclusion tends to obscure the problem which has to be solved, and the view that they are homologous is still sub judice.

(h) The Crural Glands.—The occurrence of these glands has already been mentioned in describing the position of their external apertures. There are four pairs of them; two in each of the first and second prægenital pairs of legs. They are tubular glands which almost exactly equal in size the renal organs of the segments in which they occur (figs. 27 and 28). They are lined internally with a thin chitinous layer, under which are found the short columnar cells, which are supported by a thin muscular coat and a peritoneal investment. The occurrence of two crural glands, in each of the legs in which they occur, is a feature in which Eoperipatus Horsti resembles P. Edwardsii. It appears, however, that they occur in a far greater number of legs in the latter than in the former (7).

V. THE STRUCTURE OF THE OVUM.

In no group of comparatively small size does the structure of the ovum vary as in the Onychophora. In Peripatoides and Eoperipatus the ovum is large and full of yolk; in Peripatopsis it is large and devoid of yolk; in Peripatus and Paraperipatus it is small and free from yolk.

With regard to the primitive condition of the ovum there are two views—the one put forward by von Kennel (**9**), and recently supported by Dr. Willey; the other held by Mr. Sedgwick (**15**), and adopted by Korschelt and Heider in their 'Text-book of Embryology.' Von Kennel's view, so frequently adopted by Dr. Willey, is that the ancestral Peripatus had a small yolkless egg, which it laid in water; Mr. Sedgwick's view, adopted by Korschelt and Heider, is that the ancestral form had a large egg full of yolk. Kennel, with whom the first view originated, thought that the course of embryonic development in the Peripatidæ had followed two divergent lines of evolution, the one leading towards the type of development occurring in the genus Peripatus, the other towards that found in the genus Peripatoides; the ovum remaining yolkless in the former, but developing yolk in the latter—a feature which is considered by Willey to be a secondary one, which culminates in the oviparity of P. oviparus (Dendy). Sedgwick, disagreeing with Kennel, sees only one line of evolution; according to him the yolk-bearing egg of Peripatoides is primitive, the vesicular egg of Peripatopsis is intermediate, while that of Peripatus represents the end result of a series of modifications (**15**, p. 463).

Dr. Willey has recently expressed himself very strongly on these questions. Even with regard to the condition found in P. capensis, he declares that the opposite view to that of Sedgwick could be sustained with equal force, though he admits "there is no means at present known of deciding between the two views in this particular case," and "both of them seem to

be equally possible." In the case of the egg of Paraperi-patus, as well as in that of the Neotropical forms, he goes even further and says, "There is no reason whatever to suppose that there has been a secondary loss of yolk in these cases" (**18**). He does not stop to argue and consider the point, but gives us his conclusions unsupported by either fact or argument of any kind. He begins the paragraph from which the above quotations are taken as follows:—" I will not attempt to discuss this very difficult subject."

Since Dr. Willey did not consider it advisable to make us acquainted with the line of thought which led him to adopt the above conclusions, he can hardly find fault with us for not accepting them, and perhaps for trying to supply the reasons which induced him to adopt them.

The view has been held for many years, and is being held to-day—most probably quite correctly—that of all the forms of Peripatidæ hitherto known, the Neotropical ones are the most primitive. Kennel, probably thinking that an animal which is in several respects primitive must be so in every respect, came to the conclusion that, since the Neotropical forms are primitive as regards general characters, they must also possess a primitive ovum; that is, as he thought, a small yolkless ovum. Dr. Willey may have unconsciously fallen into the same error, for he mentions several features which he considers primitive in Paraperi-patus, for example, the structure of the male genital ducts, and it is quite possible that for such reasons he has accepted von Kennel's view of the original condition of the ovum in the Peripatidæ.

Evidently there are two ways of explaining the structure of the ovum of P. capensis. The condition of the ovum in this species may be a vestigial one, the yolk having been lost, but the spaces in which the yolk was found in the not very distant past, being still retained, as well as the comparatively large size of the ovum; or it may be a case of what may be described as prophetic adaptation in phylogeny, the egg preparing itself—so to speak—for the reception of

yolk which is to be stored in it in the not very distant future,
such as is now found in the ovum of both Eoperipatus and
Peripatoides. The first explanation is the one put forward
by Sedgwick, and seems to be the only possible one; for the
second alters the sequence of events in such a way that the
effect precedes the cause. The cause of the large size of all
ova seems to be the presence of yolk in one form or another.
But there is no yolk in P. capensis if we are to accept
Sedgwick's account of the structure of the ovum in that
species. From these considerations it seems fairly evident
that it is not equally possible to explain the structure of the
ovum of P. capensis in both ways, and that the only
possible explanation of it is the one put forward by Mr.
Sedgwick. It has been pointed out above that the main
reason for assuming the ovum of the Neotropical genus,
Peripatus, to be primitive as compared with that of the
New Zealand genus, Peripatopsis, is the generally primitive
character of the former, and Dr. Willey might justifiably say
that there is no such difficulty in explaining the structure of
the ovum of Peripatus and Paraperipatus as is raised
by the explanation of the case of Peripatopsis.   But
now that the Malay forms have been discovered, forms
which in all respects are as primitive, and in some respects
more primitive, than the Neotropical genus;—e. g., in the
position of the renal opening of the fourth and fifth pairs of
legs; the presence in the species Horsti of a well-developed
renal organ in the last pair of legs, and in the species
Weldoni of a vestigial one,—a new difficulty crops up, for we
have two groups, to which the dignity of genera has been
accorded in the present memoir,—which are closely related in
all their external and internal characters except in those of
the ovum, ovary, and mode of development. In the genus
Peripatus the ovary is small and compact, and the ova
arise endogenously and are devoid of yolk, but in the
genus Eoperipatus the ovary is large and spreads out, and
the ova arise exogenously and are full of yolk. It becomes
necessary to decide which of these conditions is the more

primitive. If there was no difficulty in accepting Kennel's view before Eoperipatus was discovered, there certainly seems to be a difficulty now that this genus has to be considered, and that of such a nature as cannot very easily be put aside. When the genera Peripatus and Peripatoides are compared from this point of view, it seems less difficult to adopt Kennel's view, because in Peripatoides the young are born small in size, or are hatched from ova outside the body ; but when Peripatus and Eoperipatus are compared this reason no longer exists. In both Peripatus and Eoperipatus the young measure from 22 to 27 mm. in length at birth, and are coloured much in the same way as the adult.

If Kennel's and Willey's view be correct, the ovum of Eoperipatus must have acquired its yolk since it took to uterine development, and the condition of the ovum in the genus Peripatus would in this case be primitive ; but if Sedgwick's view be the correct one, the structure of the ovum in Eoperipatus has been inherited from an ancestor which discharged a yolk-bearing egg either in water or on land, and the condition of the ovum in the genus Peripatus would be a secondarily acquired one.

The above seems to be a fairly clear statement of the facts of the problem discussed. If Kennel's view be correct, it seems that we have to consider the question, what advantage would it be to Eoperipatus, once it had taken to nourishing its young in the uteri, to produce yolk in its egg as well? It is difficult enough to explain the presence of yolk in the egg of Eoperipatus on the supposition that it has been inherited from a former ancestor which discharged a yolk-bearing egg ; for we should expect to find the yolk disappearing, as in the genus Peripatopsis, when uterine development became habitual ; but when we are asked why yolk was produced after the uterine method had become the habitual mode of development, we find it impossible to answer, simply because we cannot conceive of any advantage that would accrue to the animal in the struggle for life from

the adoption of such a course. In fact, it seems a decided disadvantage for an egg which develops inside the mother, within easy reach of any amount of food material in the form of secretion from the tubular walls of the oviducts and uteri, to have to move along from the ovary to the uteri carrying with it a mass of yolk of an immense size, of which it has no need. The improbability of the view held by Kennel and Willey when applied to Eoperipatus, the young of which measure 22 to 27 mm. in length at birth, is so great that we are forced to reject it, and to adopt Sedgwick's view of the primitive condition of the ovum in the ancestral form.

Having reached this position by a method of reasoning which appears to be perfectly legitimate, the explanation which Sedgwick gave of the structure of the ovum in P. capensis follows naturally, and the ovum of Peripatoides would have to be explained in the same way as that of Eoperipatus. The next conclusion of necessity follows, which is, that the oviparity of P. oviparus is primitive and not secondarily acquired.

To sum up, the following seem to be the stages in the evolutionary changes of structure of the ovum, as its development became more and more confined to the uterus. Peripatoides represents a primitive condition, and produces a yolk-bearing egg, which either develops within the uterus to a small embryo, or is discharged and develops outside. The second step is met with in Eoperipatus, which has a very large yolk-bearing egg, from which is developed an embryo measuring from 22 to 27 mm. in length at birth. Peripatopsis supplies the third step, with a large egg possessing highly vacuolated cytoplasm, and produces an embryo of medium size in the uterus. Paraperipatus represents the fourth step, with a yolkless egg, much reduced in size, and gives rise to an embryo of medium length. The genus Peripatus seems to present the culminating point in these changes, for it not only produces a yolkless egg, but seems to possess what is a highly modified mode of development.

It has been mentioned above as a general principle that animals which are primitive in some respects need not of necessity be so in all respects. The primitive genus Eoperipatus has the most primitive kind of ovum, while the almost equally primitive genus Peripatus has completely lost its food-yolk, and in consequence the embryo has assumed an entirely secondary mode of obtaining nutriment. This seems to be equally true of Paraperipatus, where one portion of the ovum is turned into a kind of trophic sac, which comes in contact with the uterine wall and draws nutritive material from it, by means of which the young embryo develops and increases in size.

We now pass on to discuss the relations of the various genera to one another.

VI. The Relations of the Various Genera of the Peripatidæ to one another, together with some Phylogenetic considerations.

M. Bouvier, in his recently published memoir, has put forward the view that the most primitive forms are those which show the least amount of degeneration of the two pairs of legs situated posteriorly (**5**). He is of opinion that there is a gradual degeneration of the last and penultimate pairs of legs, and from this point of view the family Peripatidæ naturally falls into four sub-families (see pp. 480 to 484). This view is accepted without reserve in the present memoir. It seems so well founded that there is no need to say anything in its favour. However, it may not be out of place to point out one embryological fact which supports this view, namely, the presence in P. capensis of two vestigial somites behind the somite of the anal papillæ or last pair of legs (**14**). This is the exact number that is wanted in that species to represent the segments found by Kennel in the Neotropical forms. They completely disappear in the former, but in the latter the hinder somite, that is, the anal somite, gives rise to a vestigial renal organ in the female, and to the anal glands

in the male (**9**). This goes far to prove that the genus Peripatus is more primitive than the genus Peripatopsis, and that the ancestral form possessed two somites behind the genital one. This view assumes the position of the genital orifice to remain constant, that is, between the originally penultimate pair of legs—an assumption which is supported by embryology and anatomy. Taking the condition of the last two pairs of legs as the basis of our classification, the Peripatidæ fall into four groups, the first of which contains three genera which show only a slight diminution in size of the last pair of legs; in the second there are two genera in which the last pair has disappeared, but the last but one is still well developed; in the third there is only one genus, in which the second pair of legs is very much reduced; and in the fourth there is one genus in which there are no signs whatever of the originally penultimate pair, the genital pore being situated behind the last existing pair of legs, which is reduced in size.

In a group so small and so widely distributed it would hardly be expected that one genus could be derived from another. The consequence is that any kind of branching arrangement intended to show their phylogenic relations seems impossible, for in one genus one primitive character has been retained while in another genus another such character is found, and comparison of the several features of the genera lead to the most divergent results. Hence the gradation which can be traced among the several genera of the Onychophora only represents steps which have been reached by each genus more or less independently. If these gradations be considered, as has already been done in the case of the male accessory glands, the male ducts and spermatophores, the ovum, and finally the genital orifice and the last two pairs of legs, we arrive at a different result in almost every case—a fact which justifies the statement that no branching arrangement can possibly represent the phylogenetic relations of the different genera, which appear to have developed more or less independently from a common

ancestor, which is more closely represented in Eoperipatus than in any other genus; for this genus combines the most complete development of the two posterior pairs of legs with what seems to be the most primitive ovum. Peripatoides lacks the last pair of legs, though its development is as primitive as that of Eoperipatus, and, even more so, in that oviparity occurs. However, the actual development is so little changed in Eoperipatus, that it may well lay claim to being, on general grounds, the most primitive genus among the Peripatidæ.

Before bringing the present part of my account of Eoperipatus to its close, it seems necessary to make a brief reference to the geographical distribution of the Peripatidæ.

About two years ago M. Bouvier published a preliminary note on the geographical distribution and the evolution of Peripatus (4), in which he came to the following conclusions: first, that the African, American, and Australasian groups are definitely related to the Continents the names of which they bear; secondly, that it appears quite certain that Central America and the Caribbean Region have been the centre of origin and migration of the species of Peripatus. From the above-mentioned regions they are supposed to have travelled towards the east to Africa, and towards the west to Australia.

The first conclusion has been adopted in the present memoir, and the discovery of the Malay forms considerably strengthens it. But the same discovery seems to weaken the second conclusion, which, to say the least, has been prematurely formed.

The only feature in which the American species seems to be more primitive than the Malay ones is the possession of a greater number of segments in all of them. The number of denticles in each blade of the jaws of P. tuberculatus (Bouvier) seems in some respects to show a more primitive condition than that which occurs in the Malay forms; but in other respects the jaws of the latter seem to present the more

primitive structure. The greater number of denticles in the outer blade of the jaws of P. tuberculatus seems the more primitive, but of the inner blades those of the Malay species, containing in all a greater number of denticles, seem to approach nearer the original arrangement. In the position of the renal papillæ of the fourth and fifth pairs of legs, the arrangement occurring in Eoperipatus is decidedly the more primitive, and in the structure of the ovary and the ova, as well as in their method of development, the condition found in the Malay species is nearer the ancestral arrangement than that found in the genus Peripatus.

In the same communication Bouvier says that it would be possible to believe the species of Oceania to be derived from those of Africa; but, seeing that they have some primitive features, e. g. the position of the sexual orifice and of the nephridial pores of the fourth and fifth pairs of legs, he says that it may be supposed that the dispersal of the group took place in both directions at the same time; towards the east in the case of Africa, and towards the west as regards Australia and the adjacent region. In a later publication Bouvier does not seem so definite in his opinion; for he uses the word certain in his first paper (4), while in the second he uses the word probably (3). Curiously enough, the description given by Bouvier of P. Tholloni in the paper in which he argues the American origin of the Peripatidæ is exactly what was wanted to prove the possibility of the origin of the Australian forms from Africa; for it does away with any force there may be in the argument based upon the possession of primitive features by the latter. The probability of the African origin of the Australian forms is strengthened by the discovery of the genus Opisthopatus by Purcell—a genus which Bouvier himself has placed beside the Australian genus Peripatoides because the genital orifice is between the last pair of legs (5). When to all this is added the argument drawn from the primitive structure of the Malay species, the view that the Peripatidæ originated in Central America and the Caribbean Region seems well-nigh impossible.

On looking through the list of sub-families given on page 8, we note that three of them are represented in Africa, which is a rather significant fact, while only one of them is found in America. If it were granted that Central America and the Caribbean Region were the centres from which the Peripatidæ dispersed, the presence in the Malay Region of such primitive forms would be a problem of great difficulty, which would have to be solved. Besides, the Australasian forms are much more closely allied to the Malay species than to the Neotropical ones—another telling fact which tends to make Bouvier's view impossible.

It seems that there are two views to choose between, each of which seems more satisfactory than the one adopted by Bouvier. It may be concluded that the centre of origin of the Peripatidæ was somewhere in Africa, and that they travelled in one direction towards America and in another to the Malay Region, and finally to Australasia; or it may be concluded that the ancestral Peripatus had an exceedingly wide distribution, ranging over a tract of land stretching from South and Central America to South Africa, and across to the Malay Region. When this tract of land became partly submerged, the widely distributed Peripatidæ became separated in groups corresponding to the unsubmerged continents. Every group then developed along one or more lines of evolution. The American forms kept to one line of evolution; the African species seem to have branched off in three directions; the Malay forms adhered to one plan of development; the Australasian species, likewise, followed one course, and finally the New Britain form has gone along a line of its own.

It seems that there are at present no means of deciding between the above-mentioned views. The adoption of the latter view would certainly enable us to explain the occurrence of one primitive feature in one, and of another in another genus. It seems that we must wait until more is known of the specific characters of the Peripatidæ before we can decide with certainty between the two views above

formulated, though from our present knowledge of them it appears that Bouvier's view must be dismissed.

ADDENDUM.

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EXPLANATION OF PLATES 32—37,

Illustrating Mr. Richard Evans' paper on " Two New Species of Onychophora from the Siamese Malay States."

Figs. 2, 6, 10, 16, 17, 18, 36, and 37 were drawn by Mr. Bayzand, the able artist in the Department of Comparative Anatomy, at Oxford; all the remaining figures were drawn by the author.

Figs. 24, 25, 26, 27, 36, and 37 were drawn from reconstructions by the author of series of sections.

SIGNIFICANCE OF THE LETTERING.

a. p. Accessory papilla. *cav.* Cavity of the ovary. *c. e. s.* Cœlomic end-sac. *c. g.* Crural gland. *d. ej.* Ductus ejaculatorius. *fl.* Funnel. *g. o.* Genital orifice. *h.* Heart. *L.* Left uterus. *l. v. d.* Left vas deferens. *m. a. g.* Male accessory glands. *m. d. l.* Mid-dorsal line. *n. c.* Nerve-cord. *op.* Opening of the oviduct to the ovarian sac. *ovid.* Oviduct. *p. c.* Pericardium. *p. p.* Primary papilla. *R.* Right uterus. *re. o.* Receptaculum ovorum. *re. s.* Receptaculum seminis. *r. o.* Renal organ. *r. v. d.* Right vas deferens. *s. g.* Slime-gland. *sp.* Spermatozoa. *ut.* Uterus. *v. o.* Ventral organ.

PLATE 32.

FIG. 1 (× 2).—Dorsal view of Eoperipatus Weldoni.

FIG. 2 (× 2).—Ventral view of Eoperipatus Weldoni.

PLATE 33.

FIG. 4.—Ventral view of the anterior end of Eoperipatus Weldoni.

FIG. 5.—Ventral view of the posterior end of Eoperipatus Weldoni.

Fig. 6.—Lateral view of one of the legs of Eoperipatus Weldoni. Note the two distal papillæ situated on the distal margin, one in front and one behind. Each of these papillæ is divided into a basal and an apical piece, the latter of which carries a spine. Also note the ventral prominences or ridges which have the appearance of two recumbent papillæ pressed against the latero-ventral aspect of the foot. Every prominence carries a spine similar to the one on the distal papillæ.

Fig. 7.—A primary papilla from the dorsal surface of Eoperipatus Weldoni. Note the conical basal part.

Fig. 8.—A primary papilla from the dorsal aspect of the leg shown in Fig. 6. Note the cylindrical basal part, and compare with the conical basal part of the papilla shown in Fig. 7. Intermediate stages between the papillæ represented in Figs. 7 and 8 are very common.

Fig. 9.—A ventral view of the fourth and fifth legs of Eoperipatus Weldoni. Note the position of the renal papilla, on the top of which the renal pore is situated. Note that by its position it divides the pad into two pieces.

Fig. 10.—This figure represents a portion of the skin of the dorsal surface of Eoperipatus Weldoni. Note that the primary papillæ (p. p.) have a polygonal or perfectly irregular outline, and that they stretch across the ridges from one groove to the other. The grooves between the ridges are exceedingly narrow, and the accessory papillæ are often situated in the grooves as well as on the ridges. The accessory papillæ are very numerous, and their outlines are quite distinct. At the lower left-hand corner of the figure there is no special arrangement of the papillæ, though the position in question is situated above the leg. The position marked m. d. l. represents the mid-dorsal line.

Fig. 11.—The inner (11a) and the outer (11b) blades of the jaws of Eoperipatus Weldoni. Note that there are two denticles on the inner side of the large tooth in each blade. The inner blade has a diastema, followed by a number of smaller denticles.

PLATE 34.

Fig. 12.—The inner (12a) and the outer (12b) blades of the jaws of Eoperipatus Horsti. Note that they have almost the same characters as those figured on the previous plate, though they are different in size.

Fig. 13.—This figure represents a portion of the skin of the dorsal surface of Eoperipatus Horsti, and should be compared with Fig. 10 on the previous plate. Note the well-defined transverse ridges and grooves. The primary papillæ have not the sharp, irregularly shaped outline found in

Eoperipatus Weldoni. The accessory papillæ, which are here much less numerous, and are scarcely ever found in the grooves, lose their individuality in that of the transverse ridges which rise up suddenly from the general surface. The middle of the back is occupied by a clear narrow line. At the lower right-hand corner of the figure is represented the special arrangement of ridges and grooves which exists in relation to the leg. This should be compared with the lack of arrangement in the lower left-hand corner of Fig. 10.

Fig. 14.—Ventral view of the anterior end of Eoperipatus Horsti.

Fig. 15.—Ventral view of the posterior end of Eoperipatus Horsti (female).

Fig. 16.—Ventral view of the posterior end of Eoperipatus Horsti (male).

Fig. 17.—This figure represents an antero-ventral view of one of the feet of Eoperipatus Horsti. Note the two distal papillæ and the four ventral prominences or ridges. The two distal papillæ, as in E. Weldoni, are divided into basal and apical portions, and carry a spine. The ventral prominences also carry a spine.

Fig. 18.—Postero-dorsal view of the same foot, as shown in Fig. 17.

Fig. 19.—A primary papilla from the dorsal surface of Eoperipatus Horsti.

Fig. 20.—A primary papilla from the dorsal aspect of one of the legs of Eoperipatus Horsti. Note the same difference between the basal portions of the papillæ shown in Figs. 19 and 20, as was noticed between those represented in Figs. 7 and 8.

Fig. 21.—Ventral view of the fourth and fifth legs of Eoperipatus Horsti. Note the position of the papillæ which carry the renal openings as compared with that which occurs in Fig. 9.

Figs. 22 and 23.—These figures represent two dissected females of Eoperipatus Weldoni. Note the difference in the arrangement of the uteri in the two figures. In Fig. 22 the uteri, full of embryos, are packed near the posterior end, under the loop of the intestinal canal, while in Fig. 23 they are arranged on the right side, and extend forward as far as the first pair of legs.

PLATE 35.

Fig. 24.—The renal organ of the second pair of legs of Eoperipatus Horsti. There is neither a terminal bladder nor a differentiated funnel. The cœlomic end-sac is well developed.

Fig. 25.—The renal organ of the fourth pair of legs of Eoperipatus Horsti. There is no terminal bladder, but the funnel is well developed. The renal duct, as a whole, is very long and coiled.

Fig. 26.—The renal organ of the ninth pair of legs of Eoperipatus Horsti. All the parts of a typical renal organ are represented here, namely, a dilated bladder, a coiled duct, a well-developed funnel, and a cœlomic end-sac. The dilated bladder above mentioned is not close to the renal pore.

Fig. 27.—The renal organ and the crural glands of the fourth last pair of legs of Eoperipatus Horsti (male).

Fig. 28.—The renal organ and the crural glands of the third last pair of legs of Eoperipatus Horsti (male).

Fig. 29.—The funnel and cœlomic end-sac of the renal organ of the fourth pair of legs of Eoperipatus Horsti.

Fig. 30.—A section through the fourth leg of Eoperipatus Horsti. Note especially the cœlomic end-sac (c. e. s.), the funnel (fl.), and the renal duct, which passes down the leg to the papilla situated on the proximal side of the fourth pad.

Fig. 31.—A section through the outer portion of the renal duct shown in Fig. 26. Note the difference in the arrangement and character of the cells. In the upper portion, which represents the wall of the bladder, the cells are large and extended, and their nuclei are far from one another. In the lower portion the cells are small and columnar, and their nuclei are closely packed together, as they are in the layer of cells covering the external surface. Note especially that there is no gradual transition between the two portions above mentioned, but that there is a sharp rim.

Fig. 32.—A section of the duct of the salivary gland of Eoperipatus Horsti. Note the difference in the characters of the lining cells. The tall columnar cells with large nuclei at their free end line the portion nearest the buccal cavity. The short cells with small nuclei line the portion nearest the gland.

Fig. 33.—This figure represents a transverse section passing through the anterior edge of the female genital orifice of Eoperipatus Horsti, the actual opening being found in the third section from the one drawn. The uteri (ut.) pass on the outer side of the nerve-cords (n. c.), and are full of spermatozoa (sp.). The nerve-cords (n. c.) are widely separate. The heart (h.) is still a well-developed tube lying in the pericardium. The section passes through one of the ridges of the skin—a fact which explains the presence of the large number of papillæ.

Fig. 34.—This figure represents a transverse section passing immediately in front of the last pair of legs of the female of Eoperipatus Horsti. From the nerve-cords (n. c.), which are still widely separate, nervous strands (n. s.) pass to the ventral organ (v. o.). The heart no longer exists. The most noticeable feature of the section is the large renal organ (r. o.) with its cœlomic end-sac (c. e. s.).

PLATE 36.

Fɪɢ. 35.—This figure represents a transverse section passing immediately in front of the penultimate pair of legs of E. Horsti. The left vas deferens (*l. v. d.*) is cut across twice, the right one (*r. v. d.*) passes under the nerve-cord (*n. c.*), and is cut across twice on the right side. The nerve-cords (*n. c.*) approach each other below the rectum (*rt.*), and present a kind of a ganglionic swelling situated immediately in front of the male genital orifice. In the dorso-lateral part, in cavities of their own, are seen the male accessory glands (*m. a. g.*). The ductus ejaculatorius with its much-thickened wall appears on the left side immediately under the left nerve-cord. In order to understand the topographical relations of the male genital ducts and the nerve-cords, Figs. 35—37 should be compared.

Fɪɢ. 36.—An enlarged representation of the male genital organs of Eo-peripatus Horsti. The small numbers (38—48) placed outside the figure, and at the ends of lines crossing the genital ducts in various positions, refer approximately to the positions of the sections drawn in Figs. 38—48. The rectum (*rt.*), which passes between the coils of the vasa deferentia, is repre-sented as having been cut close to the posterior end of the stomach on the one hand, and near the anus on the other. Note that the ductus ejacula-torius is drawn out into a long loop on the left side, the lines bearing the numbers 44—48 cross it at various places. The male accessory glands (*m. a. g.*) are shown as two small tubes situated between the terminal end of the ductus ejaculatorius and the posterior end of the rectum.

Fɪɢ. 37.—This figure shows the relations of the nerve-cords, which are represented in black, to the various organs shown in Fig. 36, which in the present figure are drawn only in outline.

Fɪɢ. 38.—A transverse section of the testes of Eoperipatus Horsti. See number 38 in Fig. 36.

Fɪɢ. 39.—A transverse section of the duct passing from the testes to the seminal vesicle of Eoperipatus Horsti. See number 39 in Fig. 36.

Fɪɢ. 40.—A transverse section of the vas deferens, close to the seminal vesicle, of Eoperipatus Horsti. See number 40 in Fig. 36.

Fɪɢ. 41.—A transverse section of the much-coiled vasa deferentia of Eoperipatus Horsti. The tube marked *s. g.* represents one of the branches of the slime-gland. In the tubes on the left of the figure are several loosely-arranged spermatozoa, but in those on the right they are arranged in a compact and characteristic way round a common centre. See number 41 in Fig. 36.

Fɪɢ. 42.—A transverse section of the vasa deferentia of Eoperipatus Horsti. The ducts have a common sheath, but their lumen are still separate. The spermatophores are completely formed. See number 42 in Fig. 36.

Fɪɢ. 43.—A transverse section of the common genital duct close to the

union of the vasa deferentia. The spermatophores have not yet fused. See number 43 in Fig. 36.

Fig. 44.—A transverse section of the common genital duct at some distance from that shown in Fig. 43. The spermatophores have fused together, but in the arrangement of the spermatozoa there are signs of a double origin. See number 44 in Fig. 36.

Fig. 45.—A transverse section of the descending limb of the common genital duct of Eoperipatus Horsti. The head of the spermatophore has been cut through twice, and the spermatozoa are arranged in two groups round two centres. The wall of the duct is as yet comparatively thin. See number 45 in Fig. 36.

PLATE 37.

Fig. 46.—A transverse section of the ductus ejaculatorius of Eoperipatus Horsti. The wall is greatly thickened, but the lining cells are tall and columnar. See number 46 in Fig. 36.

Fig. 47.—A transverse section of the ductus ejaculatorius of Eoperipatus Horsti. The wall is very thick, but the lining cells, though columnar, are much shorter. See number 47 in Fig. 36.

Fig. 48.—A transverse section of the ductus ejaculatorius of Eoperipatus Horsti. The wall is extremely thick, and the lumen is correspondingly small. See number 48 in Fig. 36.

Fig. 49.—This figure represents a dissected-out ovary, etc., of Eoperipatus Weldoni. It shows the ovary enormously spread out, one receptaculum ovorum (*re. o.*), and two receptacula seminis (*re. s.*), as well as the commencement of the two uteri. The ova are also seen suspended in thin-walled sacs, which hang freely in the vascular body-cavity. The lines bearing the numbers 50, 51, and 52 mark the position of the sections shown in Figs. 50, 51, and 52.

Fig. 50.—This figure represents a section along the line marked 50 in Fig. 49. It passes through the receptaculum ovorum (*re. o.*) and through one oviduct (*ovid.*). The other oviduct is not cut across, as the section goes through the opening passing from the extended cavity (*cav.*) of the ovary to the oviduct.

Fig. 51.—This figure represents a section through the receptaculum seminis (*re. s.*) and the proximal end of the uterus (*ut.*). Note the highly columnar lining of the latter, and the comparatively thin wall of the former. One of the ducts passing to the receptaculum seminis is shown embedded in its wall, and lined by cells with small nuclei.

Fig. 52.—This figure represents a section across the uterus at the position marked by the line bearing the number 52 in Fig. 49. Note the comparatively thick wall and columnar lining.

Fig. 53.—This figure represents a section across the uterus in the neighbourhood of one of the embryos contained in it. Note that on one side the lining cells are columnar, while on the other side they are becoming flattened; that is, there is a gradual transition from the tall and columnar condition to the flattened one. There is no destruction or loss of cells in any way.

Fig. 54.—This figure represents a transverse section of one of the uteri of Eoperipatus Weldoni. The section is from close to the posterior end, and should be compared with the representation of the uterine walls of Eoperipatus Horsti shown in Fig. 33.
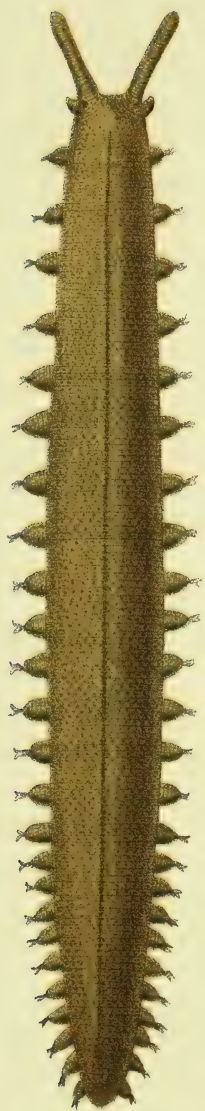
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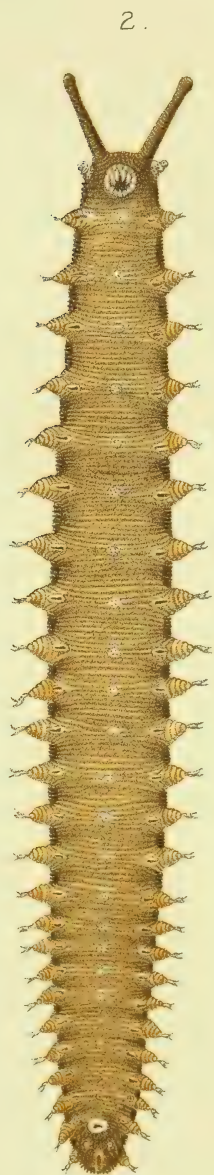
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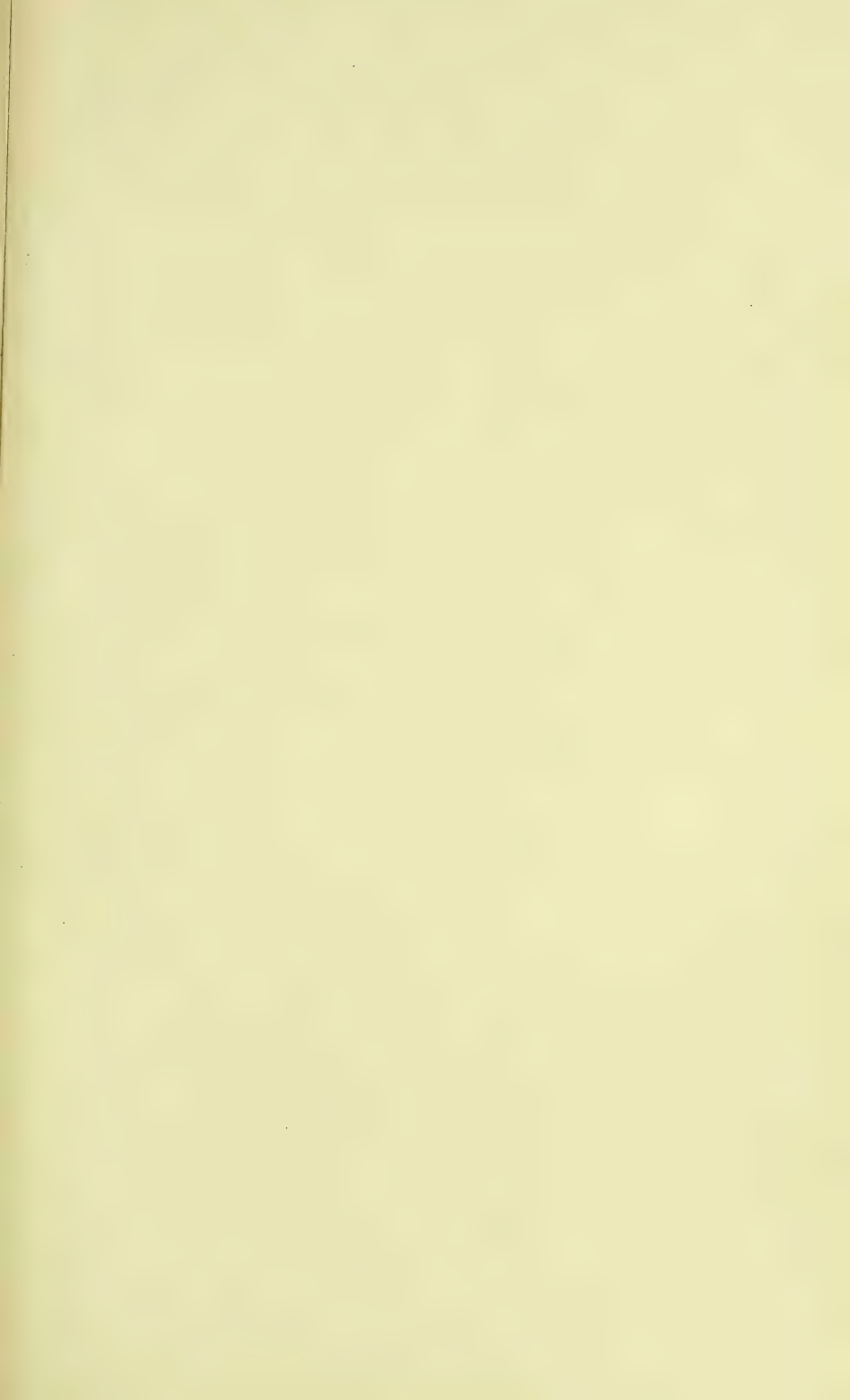
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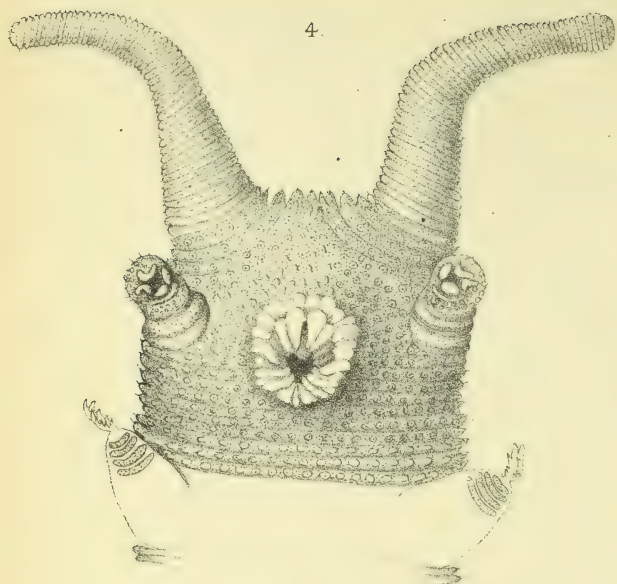
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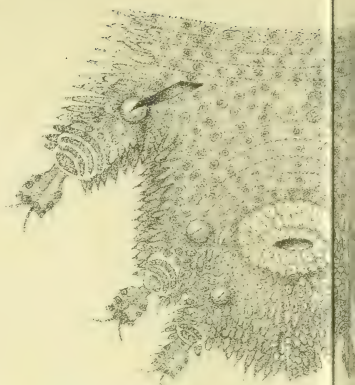
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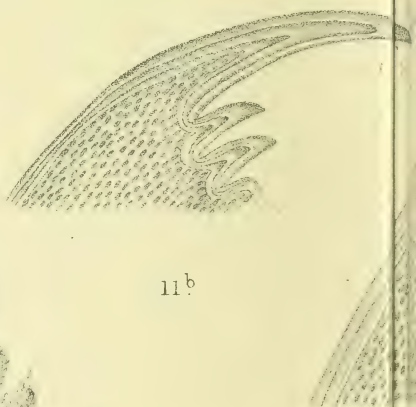
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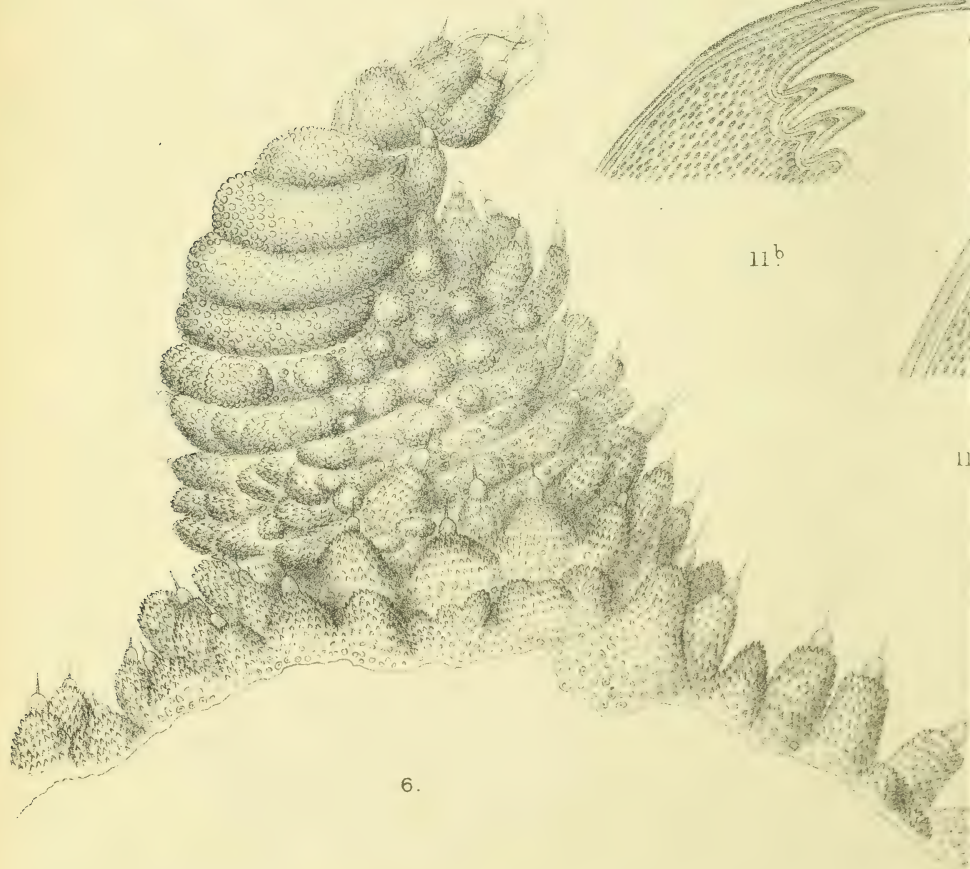
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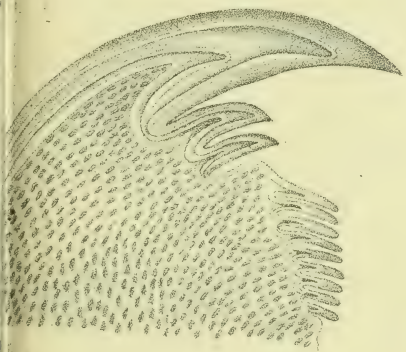
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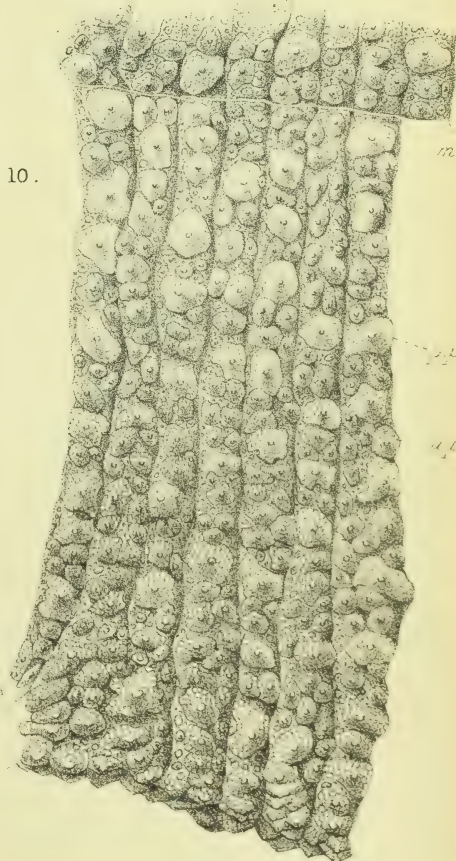
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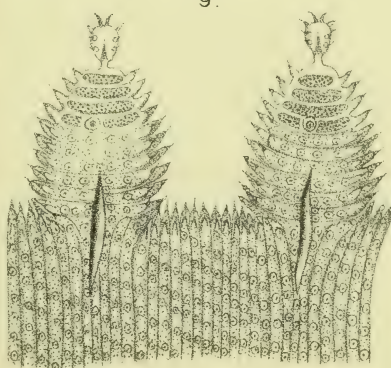
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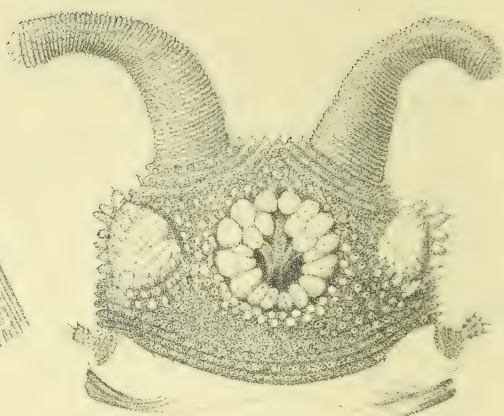
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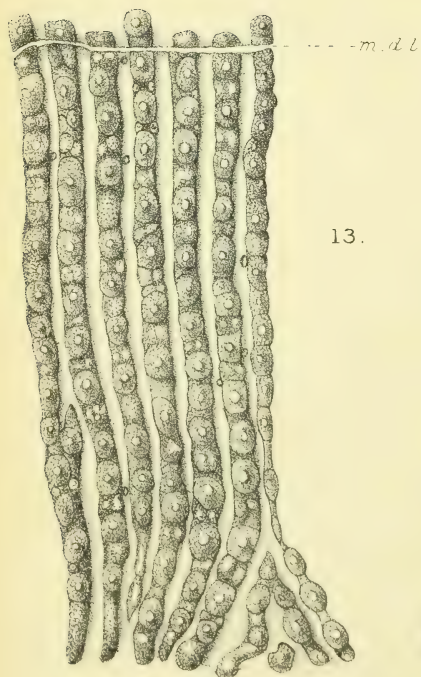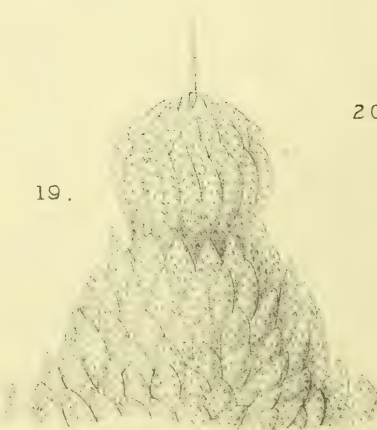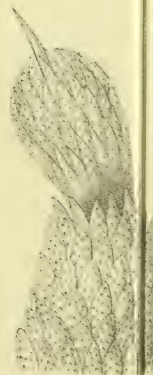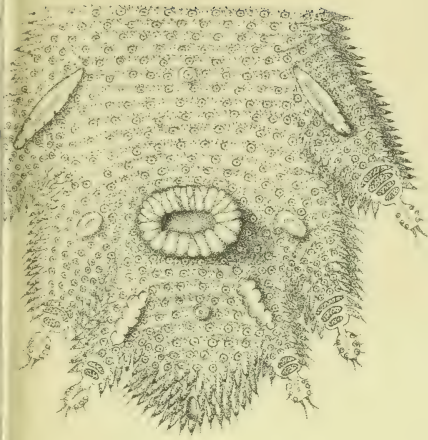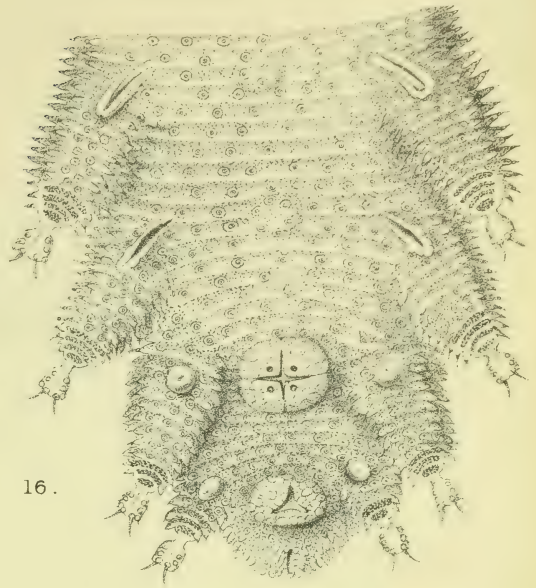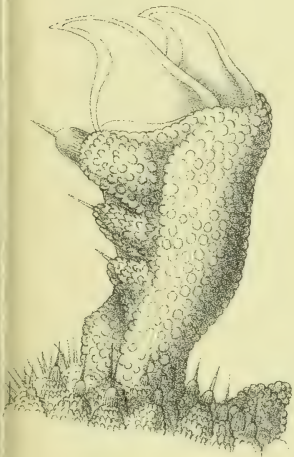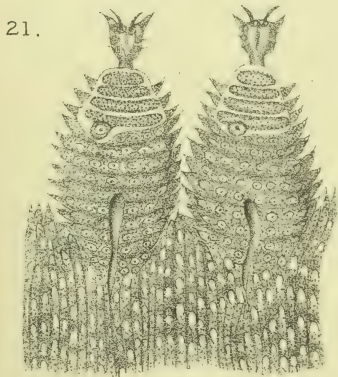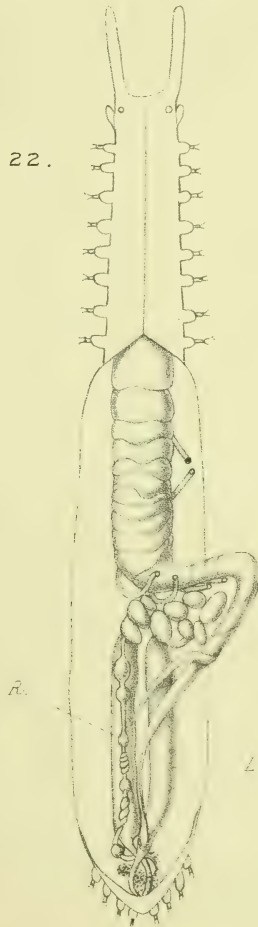
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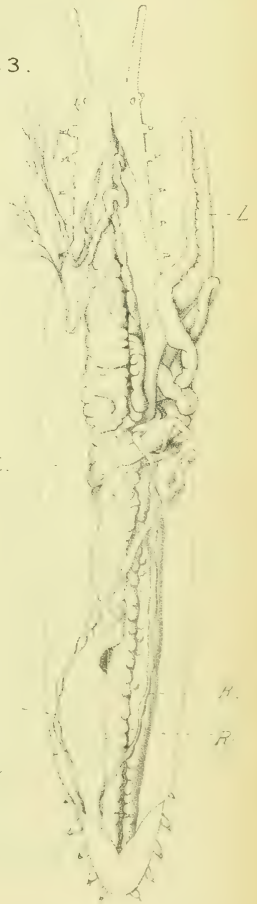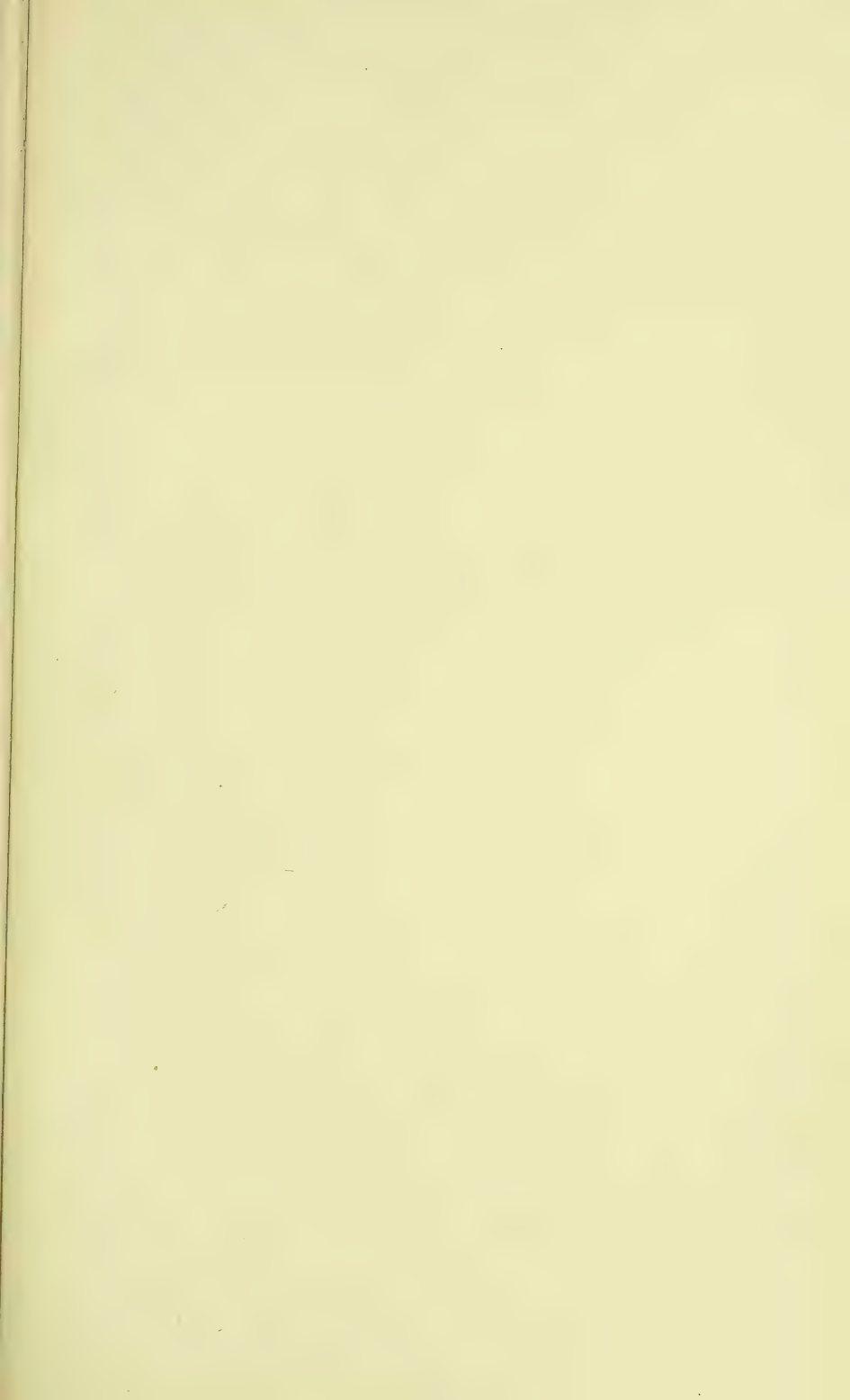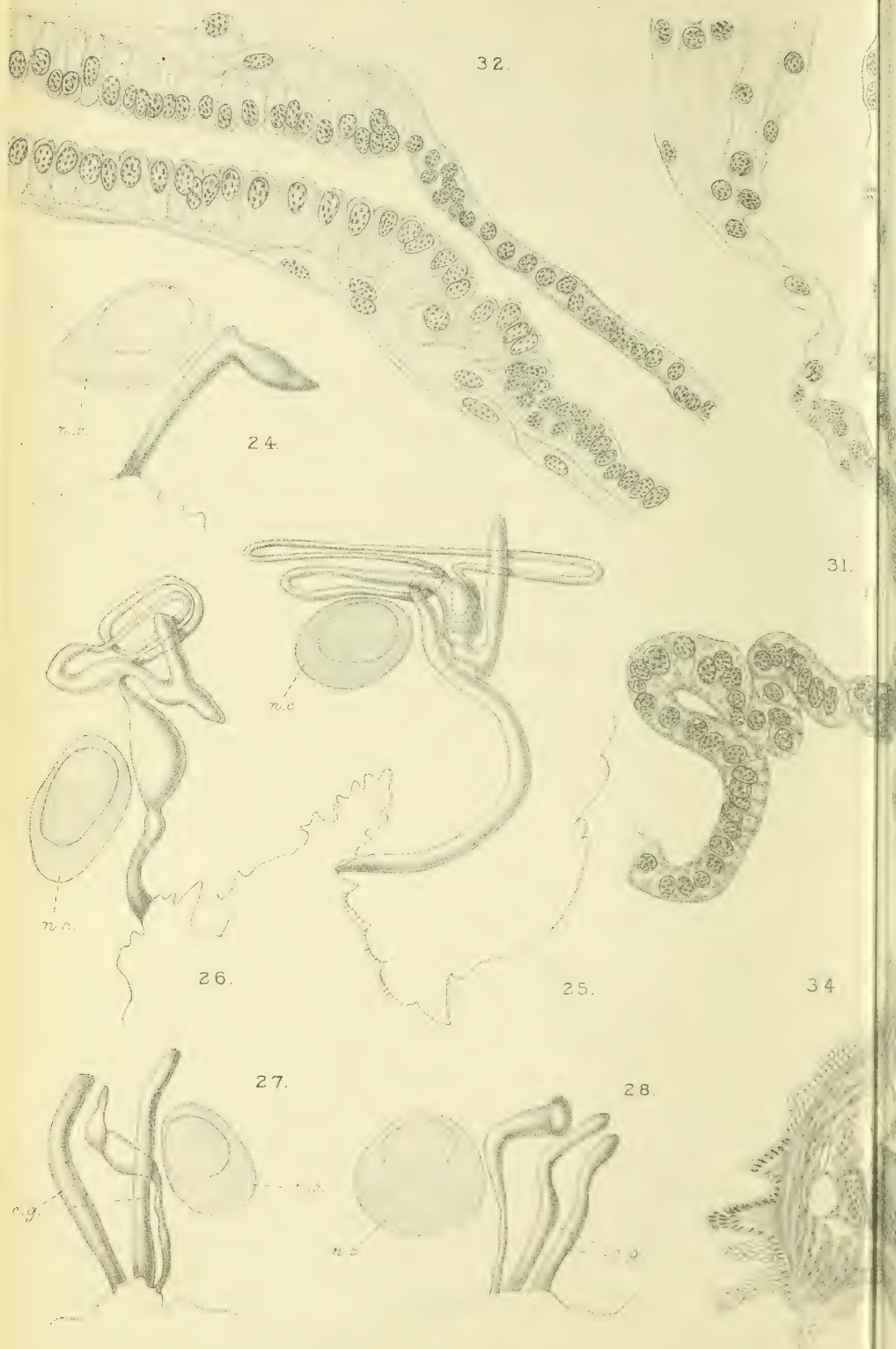
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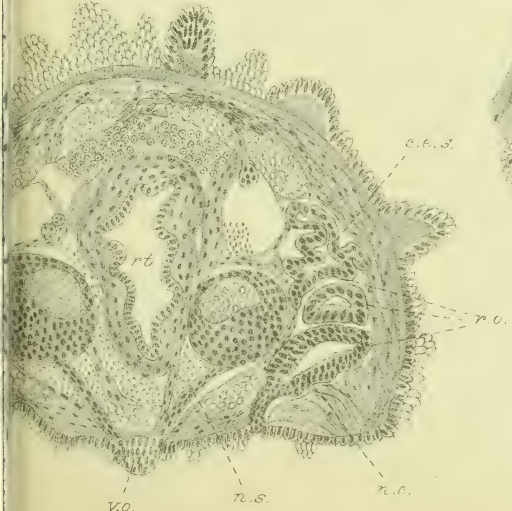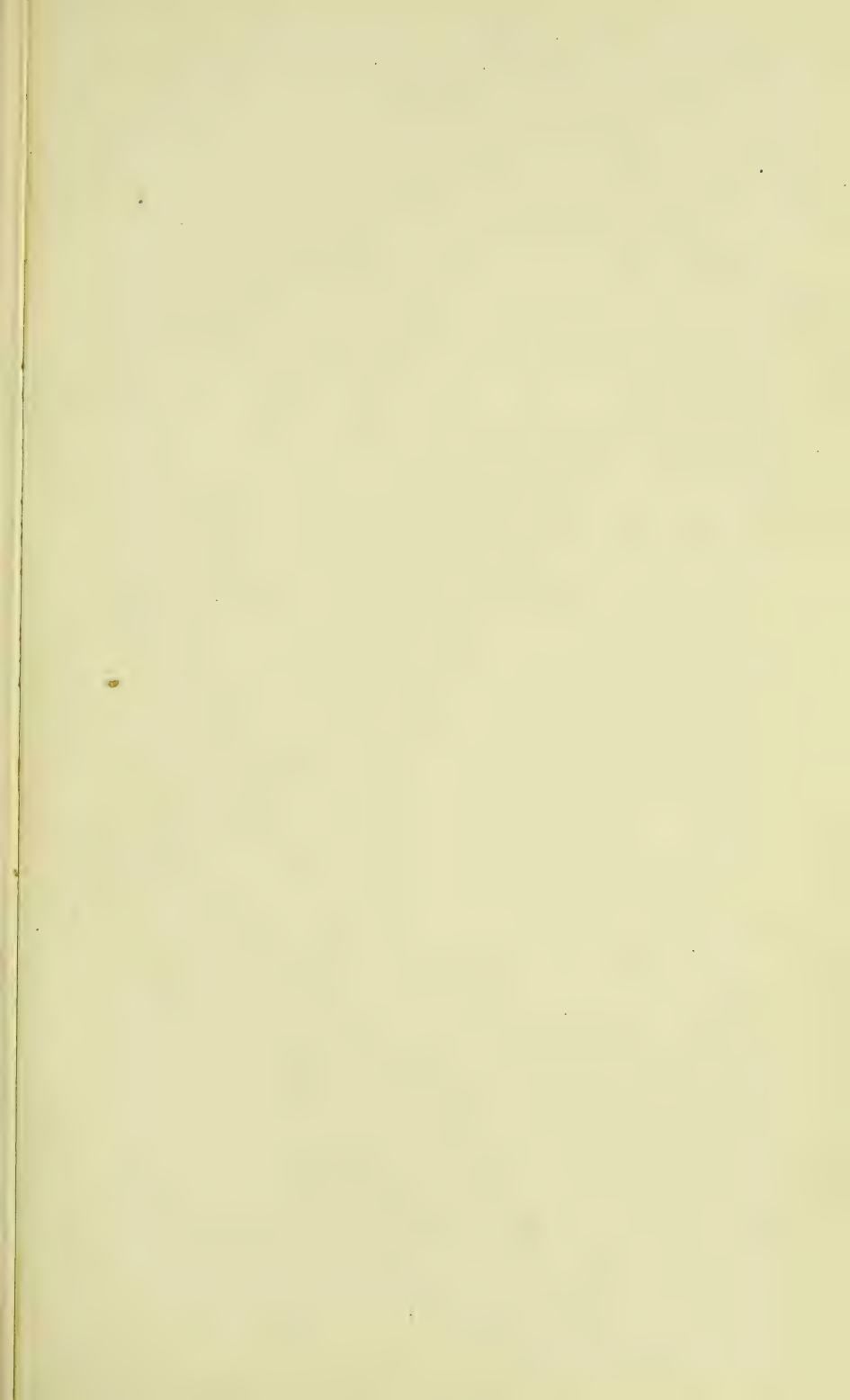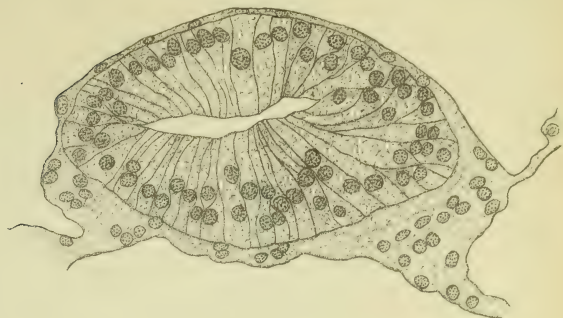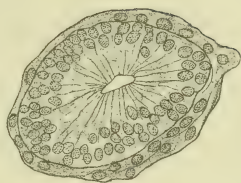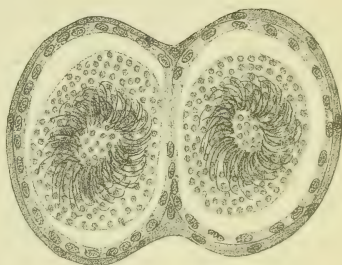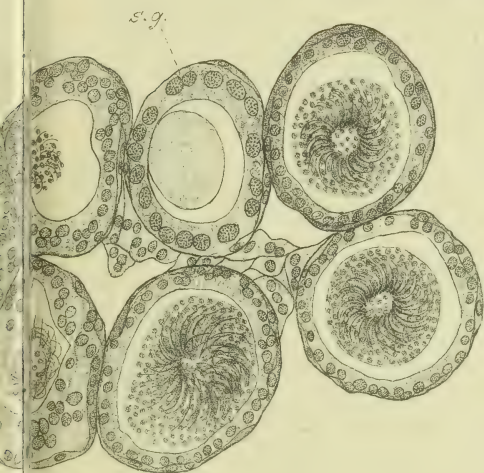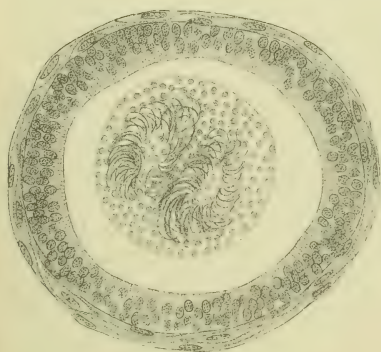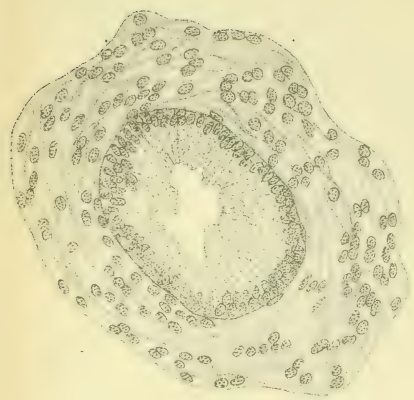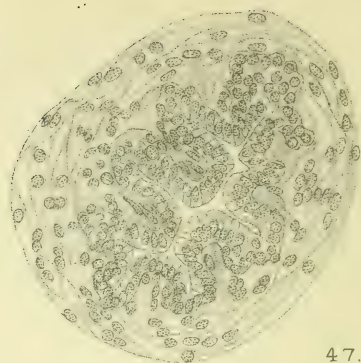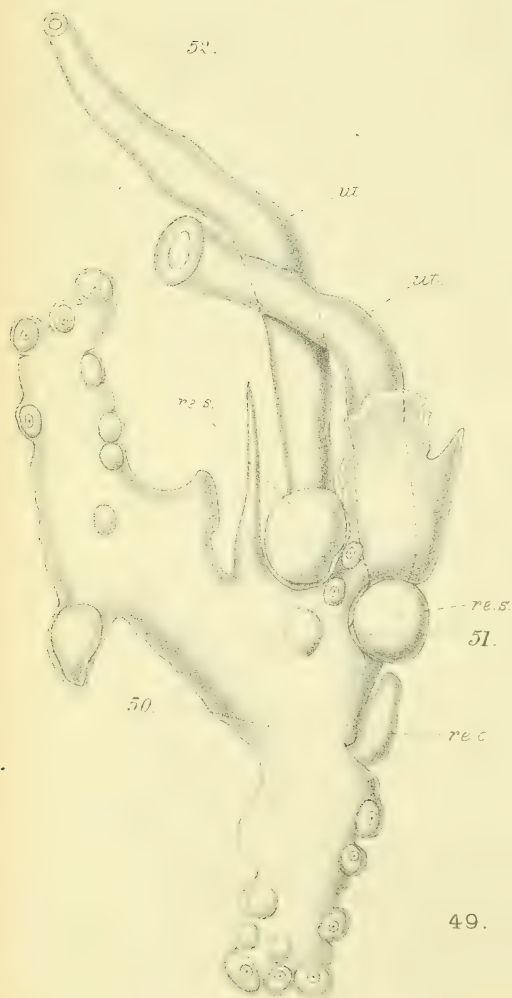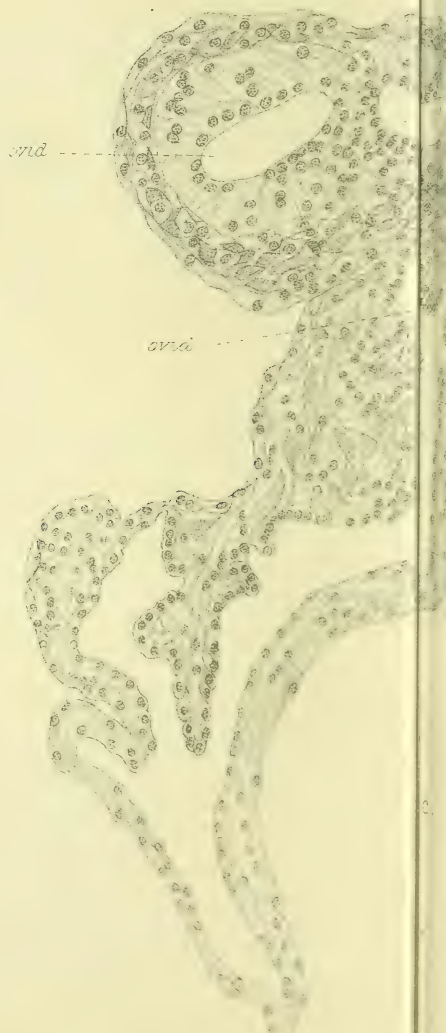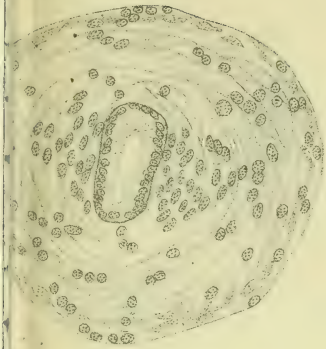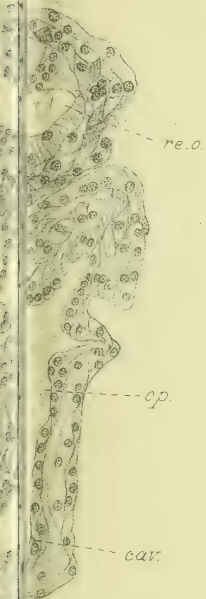
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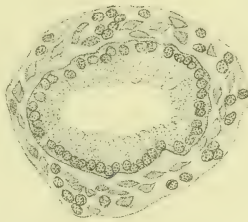
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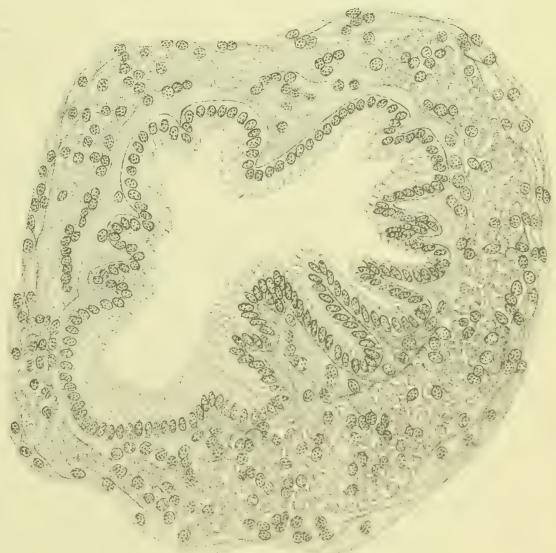
Eoperipatus Butleri (nov. sp.).[1]

By

Richard Evans, M.A., B.Sc.,

Of Jesus College, Oxford.

With Plate 38.

Contents.

I.—INTRODUCTION.

THE material described in this paper consists of one female specimen, which was kindly sent me by Mr. R. I. Pocock, on the suggestion of Professor Ray Lankester, Director of the British Museum (Natural History). Mr. Pocock obtained it from Mr. A. M. Butler, Curator of the Museum at Selangor,

[1] This short paper is considered as a supplement to the foregoing memoir "On the Two New Species of Onychophora from the Siamese Malay States," rather than as an independent paper, and must be read in connection with that memoir; for in the description given here of E. Butleri, especially in comparing it with the other species, constant allusion is made to the facts recorded in the above-mentioned paper, in which alone a list of references is given.

Straits Settlements, who discovered it on Larut Hills at the height of 4000 feet. In accordance with a suggestion made by Mr. Pocock, I have given it the specific name Butleri in honour of its discoverer.

II.—Description of Eoperipatus Butleri.

(a) Colour.—The dorsal surface is coloured dark brown, with pale spots scattered about with a certain amount of regularity over the whole of the animal's back. These spots represent the large primary papillæ, which contain less pigment than the other parts of the skin, and which in almost all cases have lost their apical part. The mid-dorsal position is occupied by a dark chocolate-coloured line, which extends from the region of the first pair of legs nearly as far back as the anus. When the skin is examined with the microscope a narrow, non-pigmented line is seen to occupy the centre of the dark line, as in the other Malay forms. The colour of the dorsal surface is remarkably like that of Eoperipatus Weldoni. The colour of the ventral surface is slightly paler than that of the dorsal, though the difference is in no way well marked. The segmentally arranged spots, which correspond to the ventral organs, are very evident, owing to their yellowish white appearance. Eoperipatus Butleri contrasts strongly with E. Weldoni as regards the colour of the ventral surface. In the latter it is grey with sparsely scattered brownish spots, while in the former it is not very different from the dorsal surface. It also contrasts with the greater number of my specimens of the species Horsti, for it absolutely lacks the pink found in that species.

(b) Dimensions.—The specimen here described measures 52 mm. in length, 6 mm. in greatest breadth, and 5 mm. in greatest dorso-ventral diameter.

(c) The Characters of the Skin.—The skin is thrown into folds, of which there are about fourteen to each segment in the middle part of the body. The folds, when examined with a hand lens, seem continuous across the back, but when looked at through the microscope they are seen to be divided

by a narrow, non-pigmented line similar to that found in other
Malay species. The folds of the skin exhibit a varying degree of
continuity on the latero-dorsal aspect, for those which corres-
pond to the intervals between the legs are continuous, while
those which are situated above the legs are discontinuous and
often break up, so that the papillæ display a diffuse arrange-
ment in patches of varying shape and size. Comparison of
figs. 4 and 5 will probably help the reader to understand the
difference and appreciate the distinction which has been made
above.

The conformation of the ridges and the arrangement of the
papillæ on them near the mid-dorsal line resemble those found
in E. Weldoni, in which the folds rise up gradually, and are
covered with primary and accessory papillæ. The primary
papillæ are few in number and extend over the greater part
of the width of the ridge or fold, while the accessory ones are
very numerous and occupy only a portion of the width. The
grooves between the folds are somewhat wider in E. Butleri
than they are in E. Weldoni. On the sides between the
successive pairs of legs the folds display exceedingly different
characters from those which have been described above. In this
position they resemble much more closely those of E. Horsti
than of E. Weldoni. They rise up suddenly, and are pro-
vided almost exclusively with large primary papillæ. The
accessory papillæ, which are few in number in the region
under consideration, tend to lose their individuality in that
of the ridges, a feature which seems to accompany the forma-
tion of folds of this particular kind, for it also occurs in
E. Horsti. The primary papillæ are provided with apical
portions, which are differentiated from the basal ones. In
E. Weldoni and E. Horsti, as a rule, the apical portion is
either oval or subspherical in form, and is comparatively
large in size, but in the species Butleri the apical part is
conical in shape and small in size. Even on the dorsal aspect
of the leg, a position in which the apical part attains its
greatest development in E. Weldoni and E. Horsti, it is
almost impossible to see it in E. Butleri.

(d) The Median External Openings.—There are three of these openings, namely, the mouth, the genital orifice, and the anus.

The Mouth :—The mouth is in an exceedingly extended condition, and consequently all the papillæ surrounding it are clearly seen (Pl. 38, fig. 1). The incomplete circle of inner papillæ consists of four pairs symmetrically arranged on either side of the anterior moiety of the mouth. The outer circle, which is complete, has a pair of papillæ symmetrically situated in front of the mouth, and a median one behind. The latter seems to be composed of three papillæ which are united together. The papillæ placed laterally to this median one are specially enlarged, and, like those of the incomplete ring situated in front, form the boundary of the buccal cavity. Owing to the extruded condition of the mouth it is possible to make out three pairs of papillæ in the interior of the buccal cavity behind the jaws. The tongue, situated in front of and between the jaws, carries a number of complex denticles. All the papillæ surrounding the mouth are provided with one or more spines.

The Genital Orifice.—The genital orifice is situated between the penultimate pair of legs. It has the form of a transverse opening surrounded by tumid lips, made up of numerous white papillæ, similar to those which surround the buccal cavity.

The Anus :—The anus is a slit-like aperture situated at the terminal end of the short anal cone. It inclines towards the dorsal surface rather than towards the ventral, a result brought about probably by contraction.

(e) Antennæ, Jaws, Oral Papillæ, Legs and Feet. The Antennæ :—The antennæ present the same general characters as in the other species of the genus Eoperipatus. The club-shaped appearance of the distal extremity is much less marked. The number of rings that can be counted with certainty is forty-seven, as in E. sumatranus and in some of the specimens of E. Horsti and E. Weldoni. It seems, however, that there are a few small rings intercalated among

the larger ones in the distal third, which would bring the number of rings—both large and small—up to fifty or fifty-one.

The Jaws.—The outer blade of the jaws has the same structure in E. Butleri as in E. Horsti and E. Weldoni; that is, there are two small denticles on the inner side of the main tooth (fig. 6). The inner blade, however, differs from that of the above-mentioned species in that it has three small denticles, instead of two, between the main tooth and the diastema, as well as fourteen smaller denticles on the inner side of the diastema instead of the nine or ten found in E. Weldoni and E. Horsti (fig. 7). The jaw-blades are larger in E. Butleri than in the other species.

The Oral Papillæ.—The oral papillæ are in no way peculiar. They consist of two rings which do not carry papillæ, and of an end-knob which is provided with papillæ mainly on the dorsal aspect. The opening of the slime-gland is slightly sub-terminal.

The Legs.—There are twenty-four pairs of legs, which are arranged as in the species Horsti, with almost the same distance between the successive pairs of feet along the whole length of the body, with the exception of the last two or three pairs; a feature which distinguishes E. Butleri, even at a glance, from E. Weldoni, in addition to the fact that the legs are shorter and stouter. The legs, with the exception of the last two pairs, are provided with four pads, and many of those situated behind the fifth pair have a vestige of an additional one (fig. 2). The penultimate pair has only three pads, which are reduced on the last pair to two. On neither of the last two pairs of legs are the pads well separated from one another.

Crural grooves occur on all the legs, but are least developed on the first pair, where they are hardly visible. On the distal angle of these grooves there is a whitish structure, which may consist of two papillæ lying close together, or of an U-shaped body formed by the fusion of the two papillæ on their distal side. They seem to occur on all the legs, though owing to

the contracted state of the latter, in many cases they are drawn into the grooves.

The Feet:—The feet have almost the same structure as in the other species belonging to the genus Eoperipatus. They carry only two primary papillæ on the distal margin, one in front and one behind. Each papilla consists of a basal and an apical part, the latter being provided with a pointed spine. The ventral elevations or ridges are not so well marked as in the species Weldoni and Horsti. The proximal pair of these elevations agrees with those of the above-mentioned species in that they carry only one spine, but the distal pair differs, for they are provided with two spines to each elevation (fig. 2). Lest the second spine should have been missed, a renewed examination of the feet of both Weldoni and Horsti was made, but only to confirm the conclusion previously reached.

III. Conclusion.

In conclusion, my best thanks are due to Professor Lankester and to Mr. Pocock, who sent me for examination the first specimen obtained in this country from the Malay Peninsula, of the species here described, and for allowing me to dissect it as far as was necessary to determine its specific characters.

EXPLANATION OF PLATE 38,

Illustrating Mr. Richard Evans' paper "On Eoperipatus Butleri" (nov. sp.).

All the figures were traced with the camera lucida.

Fig. 1.—This figure represents the mouth opening and the papillæ which surround it. It is in a beautifully expanded condition, and will serve to show the general arrangement of the papillæ round the mouth in all the Malay

species which agree with one another to a wonderful extent as regards their accessory structures. The figure was carefully traced with the camera lucida by the author, and very carefully finished by Mr. P. Bayzand.

Fig. 2.—This figure represents the latero-ventral aspect of the sixth leg of the right side. Note the presence, in addition to the usual four crescentic pads, of a vestige of a fifth pad; the two papillæ on the distal margin of the foot, and the four ventral prominences. Note that each prominence of the distal pair carries two spines, those of the proximal pair being provided with only one each.

Fig. 3.—This figure represents the crescentic pads of the fifth leg of the right side. Note that there is no trace of a fifth pad, and that the renal papilla is situated in the fourth pad, and divides it into two halves.

Fig. 4.—This figure represents a portion of the skin of the dorsal surface. Note the narrow, clear line which occupies the mid-dorsal position; the large primary papillæ which stretch almost across the ridges from one groove to another; the numerous accessory papillæ which are scattered among the primary ones, and which follow no definite arrangement; and finally, the narrow fold with small papillæ which fails to reach the mid-dorsal line.

Fig. 5.—This figure represents a portion of the skin taken from the area situated immediately above one of the legs, the upper limit of which is shown at the lower end of the figure, where the papillæ are arranged in oblique rows. Note that the ridges above the leg break up into patches. Compare the two ridges, one on either side of the figure, with those shown in the previous figure, and note the gradual diminution in number of the accessory papillæ.

Fig. 6.—This figure represents the outer blade of the jaw.

Fig. 7.—This figure represents the inner blade of the jaw. Note the three small denticles situated on the inner side of the main tooth, and the great number of smaller denticles on the inner side of the diastema. Note the large size of the jaw-blades as compared with those of E. Weldoni, and especially of E. Horsti.

1.

2.

3.

4.

5.

6.

7.
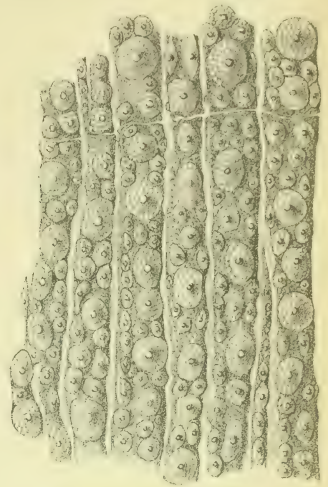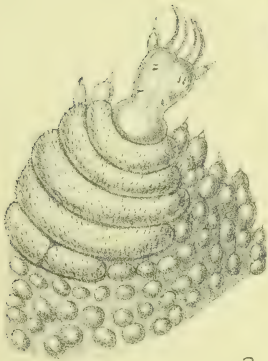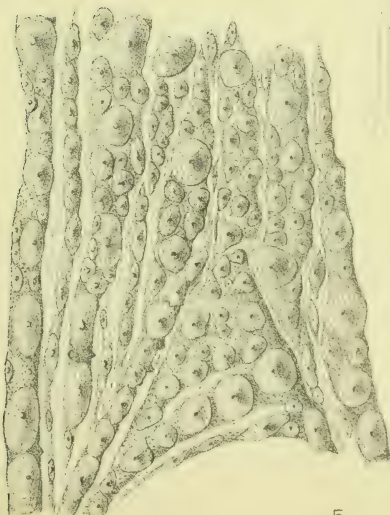
On Two New British Nemerteans.

By

R. C. Punnett, B.A.

With Plates 39 and 40.

THE two new species of Heteronemerteans described below each form a new genus. Both were found at Plymouth. The first, Microella rufa, was found by myself whilst digging in the mud of the river Yealm at low water mark. Amongst other forms dug up at the same time may be mentioned Carinella superba, Nemertes echinoderma, together with species of Synapta, Nephthys, Solen, and Capitellidæ. For two preserved examples of the second form I am indebted to the kindness of Mr. W. I. Beaumont, who discovered it among some dredge material from near the Mewstone, and with whose name I have much pleasure in associating it. As will appear below, it has seemed advisable to create a new genus to receive it. Consequently its full name appears as Oxypolia beaumontiana. A third and larger example has recently been sent to me alive from the same locality. By means of it I have been able to confirm the observations Mr. Beaumont made upon his specimens when alive.

Microella rufa belongs to the family of the Lineidæ, Oxypolia beaumontiana to that of the Eupoliidæ.

Fam. LINEIDÆ.

Micrella, nov. gen.

Body elongated, slender and dorso-ventrally flattened posteriorly. No side folds present. Caudal appendage present.

Rhynchocœlom to posterior end, and with pockets in the œsophageal region. Proboscis two-layered and with muscle crosses. Excretory system with long duct and a single pair of openings at the posterior end. No neurochord cells. Side organ present just behind excretory pore.

Micrella rufa, n. sp.

Two specimens were obtained, one of which lacked the anterior end. The perfect specimen was about 18 cm. long when alive and extended, and about 2—3 mm. broad. In colour it was of a bright vermilion, shading off into yellow near the anterior end. Through the orange-coloured head the brain showed bright red. In the intestinal region the gut and its pockets showed brown through the body-wall. The head was somewhat pointed in life, a feature which became more marked as the animal essayed to burrow through the bottom of the glass vessel which contained it. The larger and imperfect specimen was probably, before the severance of the anterior end, about twice the size of the above.

The epithelium is crowded with unicellular glands, which stain readily with picric acid. They are wanting only on the tip of the head, in the head slits and side organs, on the ventral surface of the caudal appendage, at the junction of the caudal appendage with the trunk, and in sundry patches ventrally near the posterior end. The epithelium rests on a fine basement membrane. Beneath this is an exceedingly delicate layer of circular muscle-fibrils. The large cutis glands lie in the outer longitudinal muscle layer, and in the œsophageal region they reach inwards as far as the delicate nervous sheath surrounding the circular muscle layer (fig. 2). Shortly after the œsophageal region they entirely disappear.

The muscular system in front of the brain consists mainly of longitudinal fibres. Those directly surrounding the rhynchodæum and cephalic vascular lacunæ are surrounded by a thin layer of circular muscle. Of the three muscle layers in the œsophageal region, the inner longitudinal

is the thickest, and this relation obtains throughout the body. In the posterior œsophageal region the alimentary canal is completely surrounded by a layer of longitudinal muscles, separated off from the inner longitudinal layer. The inner longitudinal layer also separates the circular layer and the proboscis sheath. Dorso-ventral fibres occur in the posterior œsophageal region as well as between the intestinal pouches. The last are, however, but poorly developed. There are a few horizontal fibres above the mouth. The outer longitudinal layer is feeble in the œsophageal region, owing possibly to the great development of the cutis glands. It becomes more strongly marked in the anterior part of the intestinal region, but entirely disappears towards the posterior end of the animal. The caudal appendage contains prolongations of the circular and internal longitudinal layers (fig. 8).

The proboscis sheath possesses an outer circular and an inner longitudinal layer of muscles. It extends throughout the length of the animal, though it does not reach into the caudal appendage. In the œsophageal region occur diverticula (figs. 1 and 11, *rhc. p.*) from the proboscis sheath in which the muscle layers are absent. These diverticula are closely embraced by the lateral vascular lacunæ in this region. They are crowded with large rhynchocœlomic corpuscles, which are oval in shape and greatly flattened (fig. 9). Each contains a nucleus in which the chromatin is arranged in four small circular masses, all connected by a more or less circular thread. Similar corpuscles are to be found in the cavity of rhynchocœlom, and also in the vascular lacunæ in this region. The proboscis is not long. In its middle portion it is composed (when retracted) of an outer longitudinal muscle layer directly beneath the rhynchocœlomic epithelium, containing two muscle crosses (fig. 4) formed by fibres from the thinner circular layer directly beneath it. Beneath this again is the high and glandular proboscis epithelium. Just inside the circular muscle layer are several nerves on either side; that is to say, if the proboscis is

so orientated that the muscle crosses are dorsal and ventral, the nerves are then lateral in position. There is no continuous nervous layer such as occurs in the majority of the group.

The alimentary canal presents no features of special interest in its structure. The œsophageal epithelium contains unicellular glands, and unicellular glands also form a layer round it. In the intestinal region the gut pockets are deep, and there is a well-marked ventral gutter. The gut pockets are continued to the anus, which is a comparatively large opening at the posterior end of the body on the dorsal surface just in front of the caudal appendage. For the last millimetre or so the alimentary canal and its pockets are devoid of gland cells. The whole canal is richly ciliated throughout.

The vascular system (fig. 11) in the snout consists of a large lacuna which divides just in front of the brain. At the level of the brain commissures these unite ventrally, and then again divide into two lateral and a median dorsal vessel. The lateral vessels form lacunæ round the cerebral organ. At this level they again communicate by the buccal commissure, though no buccal vessels are formed. Behind the cerebral organ the lateral vessels pass backwards to the œsophagus, where they form the œsophageal lacunæ characteristic of the order. This lacunar network is co-extensive with the excretory tubules. As soon as the tubules cease the œsophageal lacunæ are gathered into a very large lacuna on either side (fig. 1). This condition lasts until just after the level of the excretory pore, when the lacunæ become constricted and surrounded with the peculiar parenchymatous tissue found in the rest of the Heteronemertini. The median dorsal vessel runs in the proboscis sheath until the level of the excretory pore,[1] when it emerges and becomes surrounded by parenchymatous tissue like the lateral vessels. In the intestinal region the lateral

[1] In a previous paper I have already drawn attention to the curious fact that the dorsal vessel almost invariably leaves the proboscis sheath at the level of the hind end of the excretory system, whatever may be the extent of the latter. ('Quart. Journ. Micr. Sci.,' vol. 44, p. 136.)

vessels communicate in the usual way with the median dorsal
vessel. Just in front of the caudal appendage the median
dorsal vessel ends, while the lateral vessels form a ventral
commissure, from which arise two minute vessels. These soon
fuse, forming a cord of cells which is continued into the caudal
appendage.

The excretory system consists of a duct on each side,
into which run a number of tubules. The tubules lie in close
relation with the œsophageal lacunæ, and extend both dorsally
and ventrally to the level of the nervous side stems. After
the tubules come to an end the large duct is continued back-
wards, and opens by a single pore on either side just above the
side stems. It is remarkable that at least half the total ex-
tent of the excretory system is taken up by the large duct
unaccompanied by any excretory tubules.

The gonads were in each case testes alternating with the
intestinal pouches. The ducts are much nearer to the median
dorsal line than to the side stems. No gonidial pouches are
found in the caudal appendage.

The nervous system is formed on the usual Lineid type.
Of the four different kinds of ganglion cells enumerated by
Bürger, all are present with the exception of the neurochord
cells. These are also absent from the side stems. The
cerebral organ is not very strongly developed. Its glandular
epithelium reaches forwards dorsally over the hinder part of
the dorsal ganglion (fig. 10). The epithelium of the ciliated
canal is not so highly differentiated as in the rest of the
members of the family in which it has been described. The
large and characteristic cells found on the external side of
canal are not present in Micrella, the whole canal being lined
by epithelium similar to that found on the inner side of the
ciliated canal of other Lineidæ. The head slits are not deep,
extending only halfway to the brain. They end abruptly at
the level where the ciliated canal comes off.

With regard to the other sense-organs, both eyes and
frontal organ are absent. There is, however, a lateral sense-
organ on either side (fig. 2) shortly behind the excretory pore.

In the preserved animal it is conspicuous as a small longitudinal slit (fig. 5) about ·75 mm. long on either side. It is lined with characteristic glandular epithelium resembling that found in the head slits (fig. 6).

The head glands are feebly developed.

The foregoing account shows that Micrella presents several features which separate it from the rest of the Lineidæ, and it may be profitable to consider them in rather more detail. In his monograph (5, p. 713) Bürger derives the Heteronemerteans from such Protonemerteans as Carinella. The Carinellidæ are characterised by a side organ in the neighbourhood of the excretory pore, a feature which is shown only by Zygeupolia (7, p. 151) and Micrella among the Heteronemerteans. Its position and structure in the lastnamed forms would lead us to infer that it is homologous in both cases with that in Carinella. The excretory system again in Micrella, whilst typically Heteronemertean in the arrangement of the tubules closely connected with the œsophageal lacunæ, resembles that of Carinella in the size and length of the main duct, and in the single pair of very posteriorly situated pores (cf. Bürger [5], pl. xxviii, fig. 2). The proboscis also shows a Protonemertean feature in the absence of a continuous nervous layer and the presence of but two muscular layers. It differs, however, from that of a Carinella in having muscle crosses, a feature hitherto only found among the Heteronemerteans.

The cutis, again, is not so highly differentiated as is usually the case in the group where the outer longitudinal muscle layer is usually separated by connective tissue from a cutis containing muscle fibrils and glands. It is hardly possible to speak of a cutis in Micrella, which shows a condition similar to that described by Bürger[1] for Lineus lacteus (5, p. 621, and pl. xxii, fig. 37).

With regard to the vascular system also the œsophageal

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[1] A somewhat similar condition occurs in a fragment christened Cerebratulus medullatus by Hubrecht (vide " Nemertea," in 'Challenger Reports,' vol. xix, p. 39, and pl. xii, fig. 10).

lacunæ have not nearly so great an extent as in the majority of the group, where they reach almost or quite to the intestinal region.

Again, the epithelium lining the ciliated canal shows a lower degree of specialisation than is the case in any other Lineid.

Though possessing many apparently primitive features tending to connect the Lineidæ with the Carinellidæ, Micrella yet shows evidence of specialisation in other organs.

The extent of the rhynchocœlom over the whole length of the body is a feature common enough in the Lineidæ, though never found in a Protonemertine. The curious rhyncho-cœlomic pockets find their closest parallel in those of certain Metanemertines, such as [1] Drepanophorus, though the intimate connection established between rhynchocœlom and lateral blood lacuna seems to suggest a comparison with the lateral rhynchocœlom vessels found in Carinella, Carinoma, and Cerebratulus (cf. Bürger [5], pl. xii, fig. 7; pl. xiv, fig. 4; pl. xxiii, fig. 6). Whilst, however, in all these cases the blood-vessel projects into the rhynchocœlom, in Micrella the rhynchocœlom projects into the blood lacuna.

A caudal appendage is a feature characteristic of many Lineidæ, though what its significance may be is very doubtful. Bürger regards it as "das stark und meist plötzlich verjüngte hintere Körperende" (5, p. 238), which apparently remains in a more or less embryonic state, possibly reminiscent of an ancestral condition in which the body was relatively much longer. He holds that it contains prolongations of all the organs and layers found in the intestinal region with the single exception of the rhynchocœlom. Further, he finds that the anus opens at its tip. Coe, however (4, p. 493), found that the anus in Cerebratulus lacteus opened at the posterior end of the body just below where the caudal

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[1] Somewhat similar diverticula have been recently described by Montgomery for another genus of Metanemerteans—Proneurotes. Here however they arise as ventral outgrowths of the proboscis sheath. ('Zool. Jahr. Abt. f. Syst.,' 1897, p. 4.)

appendage joined it. He gives no account of the structure of the organ, though one would suppose that it contained no portion of the alimentary canal.

In Micrella, on the other hand, the appendage joins the body ventral to the anus, and contains neither gonidial pouches, intestine, nor outer longitudinal muscle layer, whilst the vascular system in it is rudimentary. In the light of such conflicting evidence it can only be conjectured that we are probably not dealing with homologous structures in each case, but that the caudal appendage in Heteronemerteans may have an entirely different morphological significance—unless, indeed, the anus is not homologous in the different members of the group. Owing to the fact that the primary subdivisions of the great family of the Lineidæ are based upon the presence or absence of a caudal appendage, the study of its structure in a number of forms would be of the highest importance for the systematist, whilst at the same time it might be expected to throw some light upon the morphological significance of a very puzzling and enigmatical formation.

One of the most interesting features connected with Micrella is the light which it throws upon the relations of the two Heteronemertean families—the Eupoliidæ and the Lineidæ. In his monograph (p. 715) Bürger has sketched a family tree of the group. From it may be seen that he derives the Lineidæ directly from a form such as Eupolia. In the last-named genus we find an excretory system with many ducts, such as occurs in many Lineidæ. Micrella alone in this family presents a condition of this system approaching that of the Protonemerteans, from which all the Heteronemerteans are probably to be derived. But Micrella already possesses the characteristic head slits, consequently we must suppose that the Lineidæ branched off the common stock before the type of excretory system with many ducts had been evolved, and that this latter type has arisen independently in the two families. The family tree given by Bürger must therefore be amended somewhat in the way which the accompanying scheme indicates.

Rest of
Lineidæ.

Eupoliidæ.

Micrella.

Heteronemertini.

Protonemertini.
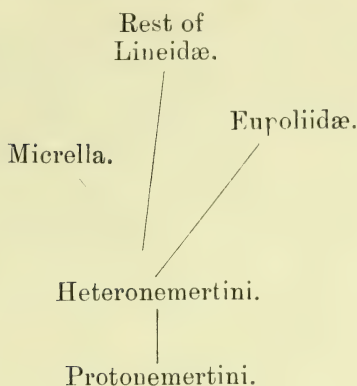
Fam. EUPOLIIDÆ.

Oxypolia, nov. gen.

Short and stout in build, and with pointed head. Proboscis pore ventral. Circular ciliated groove round head just in front of mouth. Rhynchocœlom to end of body. Excretory system with many ducts. Cerebral organs small and not surrounded by blood lacunæ. Proboscis with three muscle layers, but without muscle crosses.

Oxypolia beaumontiana.

The largest specimen of this worm, which was sent me in the living state from Plymouth, measured about 12 cm. in length and about 5 mm. in breadth. When extended the whole worm became greatly flattened. In contraction this was much less noticeable, the anterior portion of the body becoming quite cylindrical. The colour was pure white in the anterior portion, whilst the intestinal region was of a pale rose-colour. The following notes on the live animal were made by Mr. Beaumont, who kindly gave them to me together with the two specimens which he had procured:—" Anterior half milk-white (and this part is rounder in section than the rest), whilst the remaining portion has a brownish look about it, and shows more opaque rings, not very regular,

about 3—4 mm. apart. Head shaped like a spear-head, but not quite as wide as the succeeding portion of the body. It is very flat, as is the animal throughout, especially the posterior part of the body, which is almost oar-like. When squeezed the brain was noted as a small yellowish mass in front of the mouth opening. The gonads were regularly arranged. The proboscis extended over nearly half the length." On preservation the anterior portion becomes cylindrical, though the posterior half of the body remains somewhat flattened.

The epithelium is not high. It is crowded with nuclei, and contains a number of unicellular glands which stain vividly with picric acid. There is a fine but well-marked basement membrane in the œsophageal region, beneath which is a well-developed layer of circular muscle-fibres (fig. 17). Underneath this again is a thick layer of gelatinous-like connective tissue, which stains deeply with nigrosin, though faintly with carmine, thionin, or picric acid. It contains a number of small glands (fig. 15) whose contents stain deeply with thionin, and whose secretion can, with the help of this reagent, be traced through the epithelium The layer bears some resemblance to the gelatinous connective-tissue layer found in Eupolia, though in that genus the cutis glands are aggregated nearer the outer surface. In the intestinal region the basement membrane disappears, the cutis glands become smaller, and the connective-tissue layer more fibrillated in appearance. The epithelium of the circular head groove is characterised by the absence of the unicellular glands and the rich ciliation.

The muscle layers of the body-wall are well developed. The internal longitudinal layer is thicker than the circular. In the œsophageal region it forms a well-marked layer dorsal to the alimentary canal, between the latter and the proboscis sheath. It is also continued dorsally round the proboscis sheath, completely separating the latter from the circular muscle layer. The outer longitudinal muscle layer is considerably thicker than either of the other two. There are no

horizontal muscles above the mouth. The dorso-ventral muscles are feebly developed.

The proboscis sheath extends to within a millimetre of the posterior end. It is composed of the usual outer circular and inner longitudinal muscle layers.

The proboscis is very stout and well developed. The rhynchocœlomic epithelium which covers it externally (in the retracted state) rests on a well-developed basement membrane (fig. 14). This basement membrane is succeeded by an outer longitudinal and a circular muscle layer, both of which are very thin. Just inside the circular muscles is the nervous layer, beneath which is the exceedingly thick inner longitudinal muscle layer upon which rests the thin and almost aglandular epithelium of the proboscis.

As regards the alimentary canal, the mouth is behind the brain and the anus terminal. In the œsophageal region the epithelium contains but few glands. In the intestinal region the epithelium is very granular. In the posterior part of the intestine the epithelium is but slightly glandular, whilst the intestinal diverticula become much shallower in depth and less compressed.

The vascular system in front of the brain shows wide lacunæ dorsal to the rhynchodæum as in the genus Eupolia. These reach forwards in front of the proboscis pore (fig. 16). The lateral vessels give off no diverticula embracing the cerebral organs (fig. 19, *a*—*e*, and fig. 22). There is a large buccal commissure behind the commissure whence the median dorsal vessel arises, but no buccal vessels arise from it. The rest of the system is on the usual Heteronemertean plan. The œsophageal lacunar network extends to the beginning of the intestinal region.

The excretory system closely resembles that described by Bürger (**5**, p. 181) for Eupolia. The tubules extend some way dorsally and ventrally to the level of the side stems. There are a number of ducts on either side (fig. 22), many of which are incomplete, not piercing the circular muscle layer. The number of ducts is not, however, so great as in

most species of Eupolia (cf. **8**, pp. 116 and 120, **10**, p. 577, and **2**, p. 44).

The gonads in both the specimens sectioned contained minute ova in various stages. They alternate with the intestinal pouches, and open to the exterior by well-marked ducts just above the side stems. The cavities in which the young ova lie are not lined by any kind of epithelium, but are merely somewhat indefinite spaces in the gelatinous mesenchymatous tissue Probably the ova arise from the mesenchyme cells, as has been suggested by Montgomery in the case of Cerebratulus lacteus (**6**, p. 17).

The brain is somewhat high in comparison with its length (fig. 20). The side stems form a well-marked ventral commissure beneath the anus. The œsophageal commissure and nerves are small. The arrangement of the dorsal nerve shows a peculiar feature (fig. 18). After rising from the dorsal commissure it passes backwards for some distance between the outer longitudinal muscle layer and the cutis. It is not until the intestinal region is almost reached that it dips down and joins the median dorsal thickening of the nervous layer surrounding the circular muscle layer. The median dorsal thickening just outside the circular muscle layer is found in all Heteronemerteans springing from the dorsal brain commissure there (Rückennerv of Bürger [**5**, p. 363]). In Oxypolia this nerve is well marked, but does not reach forwards as far as the brain (fig. 18, *nd*.). The arrangement in this genus finds a close parallel in Carinoma armandi (**5**, p. 364, pl. xiv, figs. 4—8). Apparently the so-called median dorsal nerve of other Heteronemerteans must be regarded as containing two elements: (1) the true median dorsal nerve springing from the dorsal commissure, and (2) a specialised thickened portion of the nervous layer surrounding the circular muscles. In Oxypolia both have round them a few nuclei of what are apparently ganglion cells. Just beneath the circular muscles in Oxypolia is found the " untere Rückennerv."

The cerebral organ is small and considerably flattened

both dorso-ventrally and in an antero-posterior direction
(fig. 19, *b—e*, and fig. 20). It is not embraced by a blood
lacuna. The epithelium of the ciliated canal (as is usual
among the Heteronemerteans) contains specialised large cells
externally, seven in number, as seen in transverse section.
The ciliated canal arises dorso-laterally from the ciliated
circular ring surrounding the head just in front of the mouth.

Neither eyes nor frontal organ are present.

The head glands are largely developed, as in Eupolia.
They reach backwards dorsally, and to a less extent ventrally
past the brain, lying in the outer longitudinal muscle layer.
Their substance stains deeply with thionin.

At the time when Bürger's monograph was published the
Eupoliidæ contained but three genera, viz. Eupolia,
Valencinia, and Poliopsis. Since then three other
genera (including the present one) have been added, viz.
Parapolia (Coe [4]), Zygeupolia (Thompson [7]), and
Oxypolia; consequently I have thought it advisable to add
a table showing the main differences presented by the six
genera which now form the family.

From this table it will be seen that Oxypolia holds a
position more or less intermediate between Valencinia and
Eupolia. It is more closely related to the former genus,
though, in addition to characters given above, it may be dis-
tinguished by the following :

(1) The body is shorter and stouter in build than in Va-
lencinia. Moreover in Oxypolia the posterior portion is
not thicker than the anterior.

(2) There is no circular ciliated head furrow in Valen-
cinia.

(3) Whilst the head glands in Oxypolia exactly resemble
those of Eupolia, those of Valencinia, according to
Bürger (5, p. 186), are slighter in build, recalling those of
many Lineidæ.

(4) The cephalic vascular lacunæ in Valencinia form a
broken ring anteriorly (2, pl. ii, fig. 53). In Oxypolia
they are quite horizontal as in Eupolia.

	Eupolia.	Valencinia.	Oxypolia.	Poliopsis.	Parapolia.	Zygeupolia.
Position of proboscis pore	pro- Subterminal	Ventral[1]	Ventral	Terminal	Ventral	Subterminal
Extent of rhynchocoelom	Not nearly to hind end	Nearly to hind end	To hind end	?	To hind end (?)[2]	To hind end
Head glands	Present	Present	Present	?	Absent	Absent
Gelatinous cutis layer	Present	Absent	Present	Similar tissue present. Much vacuolated	Absent	Absent
Nephridial ducts	Many[3]	Many	Many	?	One pair	One pair
Cerebral organs	Large and embraced by blood lacuna	Small and partly embraced by blood lacuna	Small and not embraced by blood lacuna	Large	Small and not embraced by blood lacuna	Large and embraced by blood lacuna
Side organ	Absent	Absent	Absent	Absent (?)	Absent	Present
Eyes	Present[4]	Absent	Absent	Present	Absent	Absent
Proboscis musculature	Two-layered[5]	Two-layered	Three-layered	?	Three-layered	Two layered

[1] I have followed Bürger's account of the anatomy of Valencinia, which differs somewhat from that of Joubin (3, p. 508), especially in the account of the proboscis musculature. The Valencinia lineformis of McIntosh (1, p. 207) is probably not a Heteronemertean, but a Mesonemertean.

[2] Miss Thomson (7) states that Parapolia resembles Zygeupolia in the extent of the rhynchocoele. Coe, however (4, p. 519), mentions that both his specimens were fragmentary.

[3] Bürger states that there is only one pair of ducts in E. delineata, but this is probably an error (cf. 9, p. 826).

[4] Eyes are not invariably present in this genus, cf. E. pholidota (8, p. 121).

[5] The proboscis of Eupolia may occasionally possess more than two muscle layers, as in E. melanogramma (8, p. 115), where a diagonal layer is interposed between the other two.

(5) The peculiar arrangement of the median dorsal nerve noted above only occurs in Oxypolia.

Oxypolia also shows affinities with Parapolia, though the absence of a head gland and the single excretory pore readily distinguish this genus from it. With regard to the relative positions of the six genera in the genealogical tree, it seems probable that the six genera fall into at least two groups.

On the one hand, the American genera Zygeupolia and Parapolia stand together somewhat apart from the rest. Three of the features which bring them together—i. e. the absence of a specialised gelatinous connective layer in the cutis, the absence of peculiar head glands, and the presence of but a single excretory pore—seem at the same time to point to their more primitive nature if we accept Bürger's view that the group is derived from a Carinella-like form. This view is emphasised by the presence of a side organ in Zygeupolia, an organ only found elsewhere in Carinella and the primitive Lineid Micrella. Again, the three genera Eupolia, Valencinia, and Oxypolia form a group characterised by the presence of peculiar head glands, the thick gelatinous cutis layer (except in Valencinia), and an excretory system with many ducts. Of the position of Poliopsis it is impossible to speak while so many points in its anatomy remain unknown.

Summary.

1. Description of two new genera of Heteronemerteans belonging to the families Eupoliidæ and Lineidæ, viz. Oxypolia and Micrella.

2. Micrella rufa is the most primitive member of the Lineidæ, showing great resemblance to the Carinellidæ, more especially in its excretory system and in the presence of a side organ.

3. The structure of the caudal appendage in Micrella rufa differs from that of any other Heteronemertean yet

described, and throws doubt on the homology of that organ throughout the group.

4. The presence in a Heteronemertean of rhynchocœlomic pouches comparable to those of Drepanophorus among the Metanemerteans.

5. The arrangement of the median dorsal nerve in Oxypolia is peculiar, as it runs for some way outside the external longitudinal muscle layer.

6. A comparison of Oxypolia with the other genera of the Eupoliidæ.

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EXPLANATION OF PLATES 39 and 40,

Illustrating Mr. Punnett's paper on " Two New British Nemerteans."

ABBREVIATIONS IN PLATES.

a. Anus. *b. c.* Buccal commissure. *b. m.* Basement membrane. *c.* Cutis. *c. c.* Ciliated canal of cerebral organ. *cer.* Cerebrum. *c. org.* Cerebral organ. *c. org. gl.* Glands of cerebral organ. *c. t.* Connective tissue. *cu. gl.* Cutis glands. *d. b. v.* Dorsal blood-vessel. *d. c.* Dorsal commissure of brain. *d. g.* Dorsal ganglion. *e. p.* Epithelium. *ex. d.* Excretory duct. *ex. p.* Excretory pore. *ex. t.* Excretory tubules. *g.* Gonad. *h. s.* Head slit. *i. d.* Intestinal diverticulum. *l. b. l.* Lateral blood lacuna. *l. b. v.* Lateral blood-vessel. *m. c.* Circular muscle layer of body-wall. *m. c. c.* Circular muscles of cutis. *m. c. p.* Circular muscle layer of proboscis. *m. cr.* Muscle cross. *m. d. v.* Dorso-ventral muscles. *m. l. i.* Inner longitudinal layer of body-wall. *m. l. i. p.* Inner longitudinal muscles of proboscis. *m. l. o.* Outer longitudinal muscles of body-wall. *m. l. o. p.* Outer longitudinal muscles of proboscis. *n. c.* Lateral side stem. *n. d.* Median dorsal nerve. *n. l.* Nervous layer. *n. p.* Proboscis nerve. *o. d. n.* Superior median dorsal nerve (in Oxypolia). *œs.* Œsophagus. *œs. e.* Œsophageal epithelium. *œs. l.* Œsophageal lacunæ. *p. ep.* Proboscidial epithelium. *r.* Rhynchodæum. *r. ep.* Rhynchocœlomic epithelium. *rhc. p.* Rhynchocœlomic pocket. *s. o.* Side organ. *v. g.* Ventral ganglion. *v. v. c.* Ventral vascular commissure.

FIG. 1.—Micrella rufa. Transverse section through the œsophageal region just behind the termination of the excretory tubules. × 45.

FIG. 2.—M. rufa. Transverse section through the level of the side organ. × 45.

FIG. 3.—M. rufa. Transverse section through the level of the anus. × 80.

FIG. 4.—M. rufa. Transverse section through the proboscis about the middle. × 160.

FIG. 5.—M. rufa. Side view of anterior end of the animal after preservation. × 2.

FIG. 6.—M. rufa. Section through the side organ. × 160.

FIG. 7.—M. rufa. Section through outer portion of ventral body-wall in œsophageal region. × 160.

Fig. 8.—M. rufa. Section through caudal appendage. × 80.

Fig. 9.—M. rufa. Corpuscles from rhynchocœlom pocket, two of which are seen sideways. × 530.

Fig. 10, a—c.—M. rufa. Transverse sections through brain, cerebral organ, and head slit taken at intervals of 30 μ. × 45.

Fig. 11.—M. rufa. Diagrammatic reconstruction of the anterior end of the animal. Only a small portion of the proboscis sheath is shown, viz. the portion which gives off the pockets. × 20.

Fig. 12.—Oxypolia beaumontiana. Sketch of live animal. Somewhat reduced.

Fig. 13.—O. beaumontiana. Sketches of anterior end made by Mr. W. I. Beaumont from the live animal. Enlarged.

Fig. 14.—O. beaumontiana. Section through a portion of the proboscis. × 110.

Fig. 15.—O. beaumontiana. Section through a portion of the skin in the œsophageal region. From a thionin preparation to show the cutis glands. × 160.

Fig. 16.—O. beaumontiana. Section through anterior end near proboscis pore. × 45.

Fig. 17.—O. beaumontiana. Section through body-wall in œsophageal region. × 80.

Fig. 18.—O. beaumontiana. Diagram showing arrangement of median dorsal nerve.

Fig. 19, a—e.—O. beaumontiana. Section through brain and cerebral organ. Distance between a and b = 69 μ; between the succeeding sections = 25 μ. × 45.

Fig. 20.—O. beaumontiana. Two views of brain from model reconstructed from sections. (a) Seen from the side. (b) Seen from behind. × 15.

Fig. 21.—O. beaumontiana. Longitudinal horizontal section through intestinal region. × 45.

Fig. 22.—O. beaumontiana. Diagrammatic reconstruction of anterior end, showing the arrangement of the various systems. The proboscis sheath is omitted. × 10.
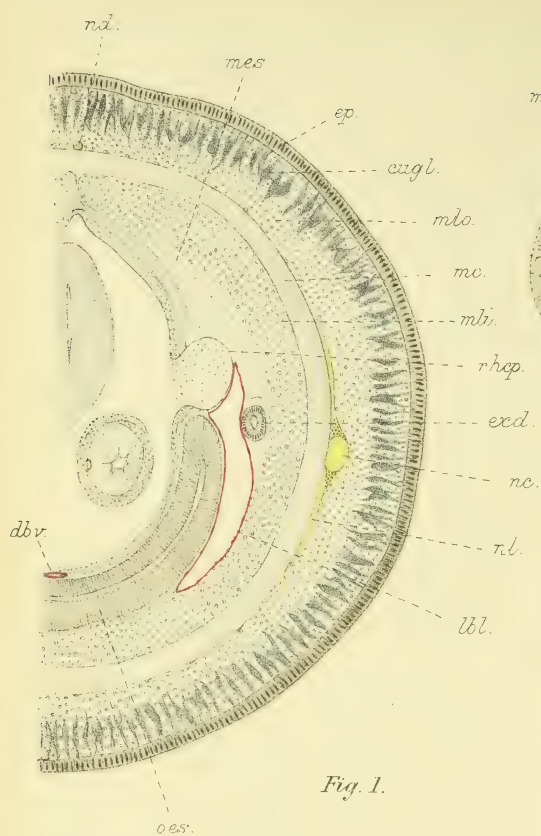
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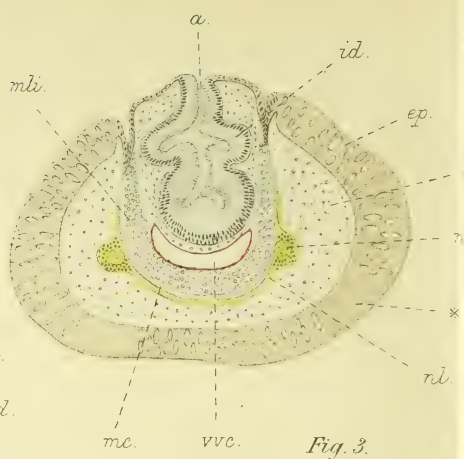
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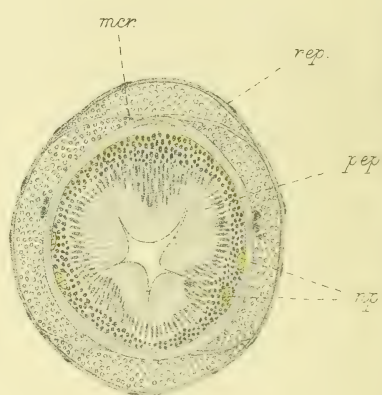
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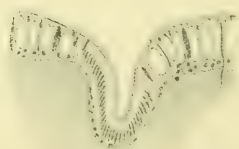
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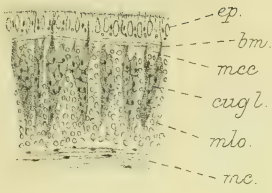
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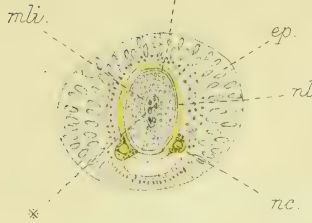
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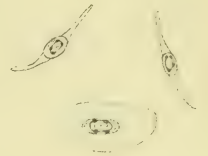
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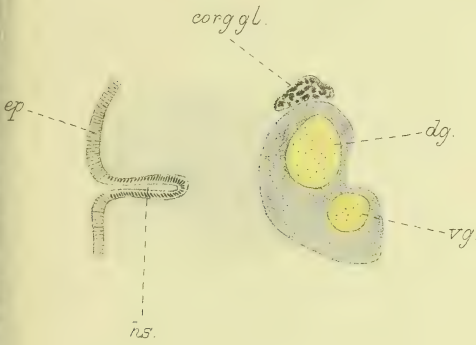
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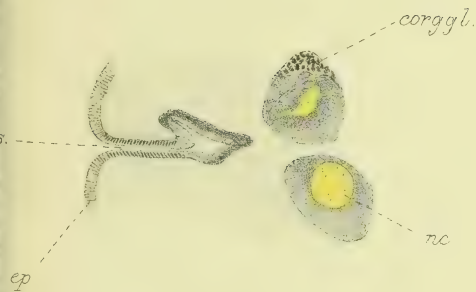
Fig. 10.ᵇ

Fig. 10.ᶜ

Fig 11.

Fig. 13.

Fig. 14.

rep.
bm
mli
mcp
mlip.
pep

Fig. 12.

dc.   odn   nd.

vc   nc.

ri.

Fig. 18.

Fig. 19.

dg.

dg.

dg.

cc

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corggl

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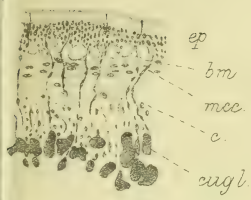corggl

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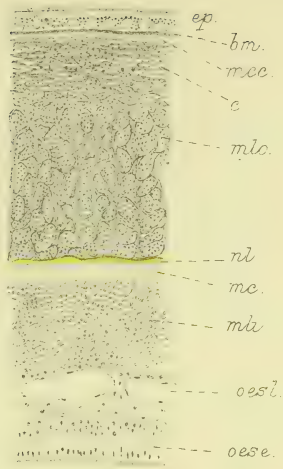
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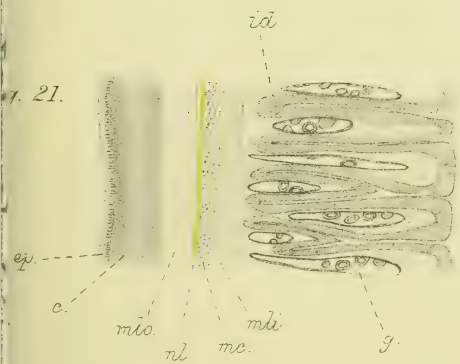
Fig. 19.ᵈ

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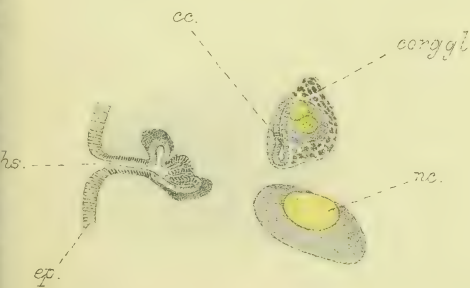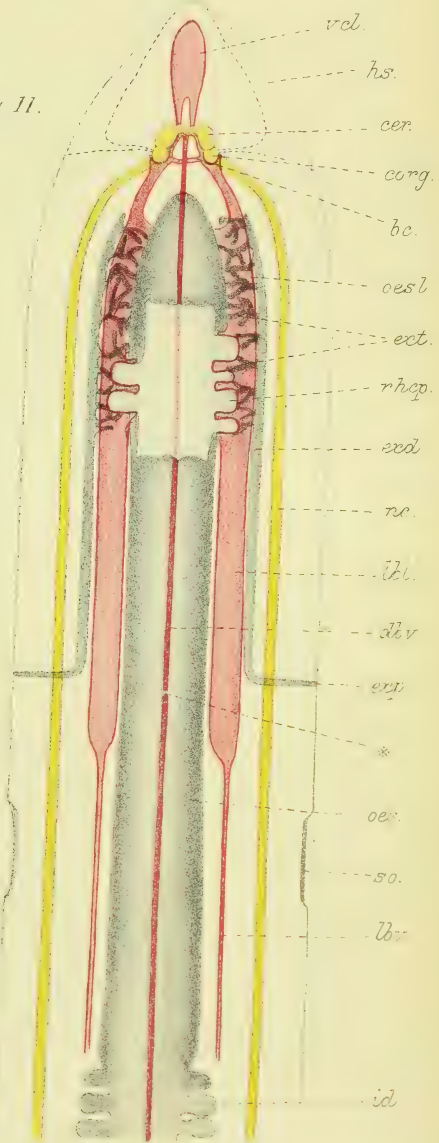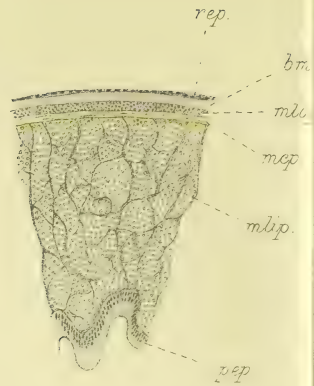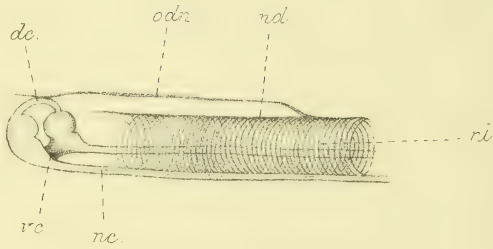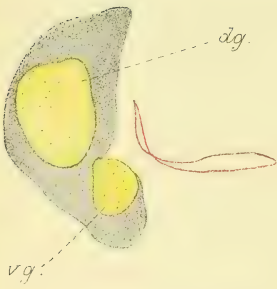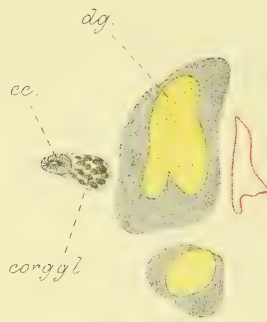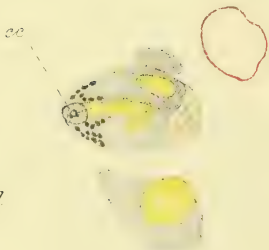
Fig. 19.ᵉ

Fig. 15.

Fig. 17.

Fig. 16.
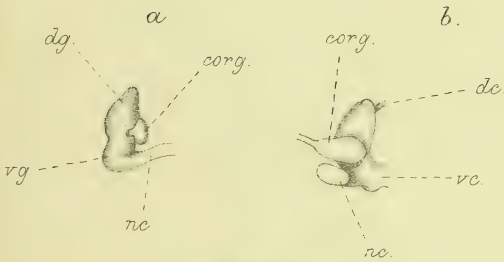
Fig. 22.

Fig. 20.
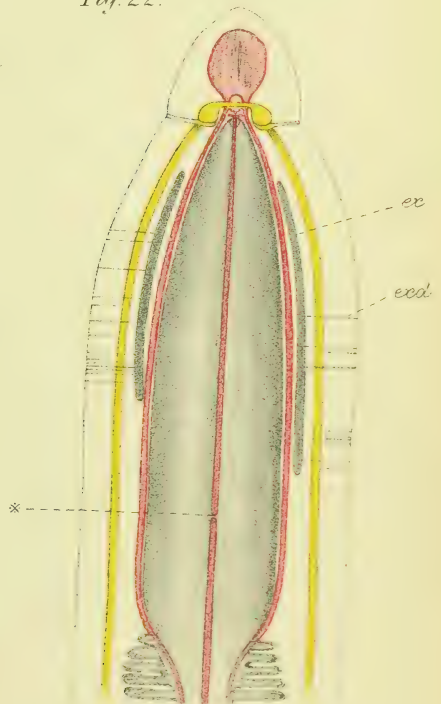
Fig. 21.

The Cœlomic Fluid in Acanthodrilids.

By

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With Plate 41.

THE corpusculated fluid contained in the cœlom of European earthworms belonging to the family Lumbricidæ has been the subject of a memoir by Dr. Rosa—from whose careful studies we have learnt that, in certain species of the genus Allolobophora, the corpuscles are of a varied character—differing somewhat in different species; and, moreover, that the commonly accepted account of the formed elements of the fluid is not only very incomplete, but more or less erroneous. The usual description refers to this fluid as " a colourless fluid with numerous amœboid corpuscles." This is an imperfect truth, for, in addition to "amœbocytes," there are, in the commoner species of Allolobophora, numerous " Eleocyte " cells containing refringent oily globules, which are, however, absent in species of the genus Lumbricus, where, it seems, their place is taken by " vacuolated lymphocytes," which are not endowed with amœboid movement.

Soon after my arrival in New Zealand, in 1898, I was surprised to note, in the fluid of Octochætus multiporus Beddard—which served my students as the type of an earthworm—not only very abundant cells, recalling the eleocytes of Rosa, but curious " thread-containing cells," similar to those then recently described by Goodrich as a constituent of the cœlomic fluid of Enchytræus hortensis,

This observation led me to commence a detailed study of the cœlomic fluid in various species of our New Zealand earthworms; the work has been interrupted from time to time, owing to a variety of causes, but it seems at least worth while to bring together such facts as I have gathered with regard to this species, and to leave aside, for the present, the less perfect observations on other species.

Octochætus multiporus has become familiar to zoologists from the various memoirs of Mr. Beddard, dealing with the peculiar and exceptional situation of the gonads on the posterior wall of their segments, the interesting condition of the nephridia, and so forth.

The worm is one of our largest species and, like the three other species[1] of the genus, is pale, indeed almost white, owing to the absence of pigment in the body wall, which allows the opaque white fluid contents of the cœlom to show through. The worm is curiously sluggish and inert; if one be taken in the hand it makes no attempt to wriggle out of it, but, by the contraction of the longitudinal muscles the worm shortens itself, and at the same time the circular muscles are contracted, so that it becomes quite tense and firm to the touch. When placed upon a table it remains quiescent, and is extremely dilatory in making an effort to escape. In a pie-dish the worm seems to lack the strength to raise its body up the sides—in the way so familiar to students of most earthworms.

But when handled roughly a small amount of cœlomic fluid issues from the dorsal pores. When the worm is placed in weak alcohol or vapour of acetic acid for the purpose of killing it the discharge from the dorsal pores is abundant, and a similar fluid is copiously discharged from the mouth, which, on examination, is found to be cœlomic fluid, with all the usual cells. Whether this fluid enters the buccal

[1] The account of the fluid here given refers especially to O. multiporus, but I have examined the fluid of two other species of Octochætus and find a close similarity in the constituent cells, as well as in Acanthodrilus annectens,

region of the gut by way of the peptonephridia—which are known to be provided with funnels in the young (Beddard, **2**), though these structures have not been recognised in the adult —remains to be discovered ; the alternative is a rupture of the buccal wall.

If the surface of the worm be touched with corrosive sublimate, or if an incision be made in the tense wall, the discharge of the white milky fluid from the dorsal pores at once becomes active. In the latter case the discharge only takes place from a few pores in the immediate neighbourhood of the incision.

This fluid is opaque-white, resembling cream in appearance ; it has a varying consistency, but generally that of a thick gum-mucilage or clotted cream. It does not " flow " from an incision over the surface of the body, but spreads slowly over it. So, too, when a drop is placed upon a glass slip, it seems to " set " at once, forming a mass of sufficient consistency to support the cover-slip, for it does not—as the fluid of Lumbricus does—flow over the slide to form an even sheet. This property necessarily makes the passage of reagents somewhat difficult, but the use of normal salt solution obviates this.

The fluid discharged into a dish soon " coagulates " to form a dirty white sticky and slimy sheet.

In the case of Acanthodrilus annectens (Beddard), the slightest handling of the worm leads to a very copious discharge of the cœlomic fluid through the dorsal pores. The fluid is cream coloured when fresh, and of the consistency of a thick gum solution ; it very soon becomes firm, and in a few minutes hardens to form a pale yellow chalky mass. It is so tenacious that it clogs scissors, sticks the fingers together, forms a cake on the scalpel, and, in fact, is quite unpleasant to deal with. Its great density renders the examination of its micro-chemical reactions even more difficult than in Octochætus, especially as normal salt solution does not readily mix with it. The plasma coagulates almost at once, and forms a clot, through which fluids

do not pass. The cells die very much more readily than in the case of Octochætus, the amœbocytes soon forming a "plasmodium," which Rosa has shown to be precedent to death—one stage in degeneration.

The method of observation of the fluid naturally varied according to the object to be attained. For the investigation of the form and structure of the living elements a hanging drop of the fluid was examined, the cover-slip being supported on a ring or by some other means. In this way no pressure on the cells occurred; but the exposure to air, even for a very brief moment, has—as Rosa has noted—certain effects upon the cells, and I found it advisable to support one side only of the cover, so that various depths of fluid could be observed. The cells in the centre being protected from air, and at the same time being subjected to a minimum pressure—if any,—were probably in a normal condition. This method, too, allowed the use of various reagents.

In fixing the cells I followed Rosa's suggestion of killing them as they issue from the dorsal pore; by touching the body with a drop of corrosive sublimate the fluid is discharged and fixed.

The Cellular Elements of the Fluid.

The cells in the cœlomic fluid are extremely abundant, the plasma being, relatively, as little as in the blood of a frog, for example. Thus the cells are crowded together, and seem to exert a certain degree of mutual pressure upon one another.

I recognise four distinct kinds of cells (Pl. 41, fig. 1), viz. :

1. Amœbocytes.—Naked, more or less granular cells, capable of thrusting out pseudopodia, in fact typical "leucocyte-like" elements.

2. Eleocytes.—Large rounded cells with a distinct limiting pellicle, and incapable of forming pseudopodia. The cytoplasm is filled with highly refringent oily globules.

3. Lamprocytes.[1]—Large rounded cells with a distinct pedicle; without pseudopodia. The cytoplasm is occupied by numerous "vacuoles," each of which usually contains a small, highly refringent "granule."

4. Linocytes.[2]—Smaller clear cells, containing one or more thread-like products.

The relative proportions occupied by these four kinds of cell varies; but the "lamprocytes" are the most abundant, and in a drop of fluid fill almost the entire field (fig. 1). The "linocytes" are usually the fewest in number, but I have evidence that they are more abundant in some worms than in others; but whether this is a seasonal or physiological or an individual peculiarity I am at present unable to determine.

The amœbocytes are only moderately numerous; and they also vary in numbers.

While in Octochætus these cells remain distinct and separate, those of Ac. annectens adhere together to form clumps, so that when a drop of the fluid is placed on the slide one sees what at first appear to be enormous cells, visible to the naked eye. But examined under the microscope—and especially after the use of iodine—these large cells are seen to be groups of cells adhering closely to one another.

A variable number of cells occur in each group—usually from six to twelve, but sometimes even more—and in each group there is generally one linocyte, one or two eleocytes, and the rest lamprocytes.

1. Amœbocytes.—These appear under two forms, depending on the character of the granules and of the pseudopodia.

The most usual form has a spherical, rather coarsely granular body, with few, clear, filamentary pseudopods, chiefly arising from one side (fig. 2). Whether or not this form of pseudopods is the true and normal condition assumed during the life of the cell in the body of the worm I am

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[1] λαμπρος = shining, in reference to the highly refringent granules.
[2] λινον = thread.

unable to state ; certain it is that this is the form presented
by an amœbocyte examined under the ordinary conditions—
either fresh in its own fluid, or after the addition of salt
solution. But Rosa denies that such is the true form of the
corpuscle within the body—as Cattaneo and others have done
in the case of Arthropods and molluscs. According to him
this form, usually described and figured, is only assumed
under abnormal conditions.

He describes the true amœbocyte of the common earth-
worms (Lumbricus and Allolobophora species) as consist-
ing of a small central body, surrounded by more or less
numerous " petaloid pseudopods," each of which consists of
a firmer margin and an extremely transparent central portion,
so that the pseudopods look like a number of loops (see Rosa,
fig. 41).

I have certainly observed similar amœbocytes in Octo-
chætus (Pl. 41, fig. 3) ; nevertheless, I have—even after
taking the precautions suggested by Rosa, of fixing the cells
with osmic acid or corrosive sublimate as the fluid issues
from the pores—observed corpuscles with a form represented
in fig. 2.

Some of these amœbocytes contain yellow globules of
chlorogogen ; though it does not seem necessary to distin-
guish these as an independent kind of cell.

In Acanthodrilus annectens some of the amœbocytes
contained both these yellow globules or granules of chloro-
gogen, and in addition some clear refringent globules ; these
also have short pseudopods, and few of them.

In addition to these more or less spherical amœbocytes I
have noted in Octochætus—though as rarities in the dis-
charged fluid—some much elongated, spindle-shaped cells,
with clearer cytoplasm, containing finer granules; the pseudo-
pods are few, at the ends of the cell (fig. 4).

These long cells I found in considerable numbers by scrap-
ing gently the inner surface of the body-wall, along which
they appear to be creeping. These appear to correspond with
the " spindle-shaped cell " described by Ling Boom Keng in

his account of the 'Cœlomic Fluid of the Common English Earthworm' (pl. 4, fig. 15). It bears some resemblance to the "mucocyte" of Allol. mucosa, figured by Rosa (fig. 23), but that cell is much larger than the eleocyte; further, his account of the "mucocyte" shows it to be a very different cell.

A good deal of work has in the last few years been done in the staining reaction of the granules of amœbocytes in various animals; amongst them, Ling Boom Keng has described the various forms of amœbocyte in Lumbricus terrestris. I have not made any observations on those of Octochætus, and am, therefore, not in a position to confirm any of his statements; but it is to be regretted that he did not give a more detailed account of the living cell.

2. Eleocytes (Pl. 41, fig. 5).—These cells are moderately abundant, of relatively large size, irregularly oval or circular in outline, and measure, on the average, 40 μ.

The cell is more or less spherical, but owing, perhaps, to mutual pressure the cells assume irregular shapes. I have not been able to detect any "diffluence" or automatic change of outline, and it appears to me that cytoplasm so loaded with endoplastic products could scarcely retain sufficient energy to move so large a mass.

The cytoplasm is transparent (i. e. very finely granular) in the living cell, and relatively small in amount; it is limited externally by a very definite pellicle or cell-membrane, which remains when, by the action of various reagents, the cytoplasm has been rendered absolutely transparent or has been destroyed.

The characteristic feature of this cell is the presence of numerous clear, colourless globules of oil, which crowd the cytoplasm; and—unlike those recorded for Allolobophora— are not limited to the periphery, but occur through the entire depth of the cell. These globules are highly refringent, and conceal the nucleus and cytoplasm in the living state.

The nucleus is excentric, circular in outline, and is em-

bedded in a central mass of cytoplasm, the rest of which is reduced to delicate threads ramifying between the globules.

I found iodine a useful reagent whereby to stain the cytoplasm,—which takes on a sherry-brown tint—contrasting therein with the cytoplasm of the other cells of the fluid; it presents the appearance of groups of brown granules between the globules, which are unaffected. This colour disappears on warming, or rather becomes much lighter; but there is no reappearance of the dark tint on cooling. I conclude, therefore, that these granules are not glycogen.

These eleocytes, however, contain in some cases highly refringent granules in addition to the oily globules; only rarely do the latter occur by themselves; but generally the "granules" are few in number; in a few cases, however, they preponderate. I will return to them in describing the "granule cells."

It will be convenient now to describe the reactions of these oily globules.

Firstly, with respect to stains:

Rosa finds that gentian violet colours the globules in the eleocytes of Allolobophora blue, the nucleus being violet. The globules in Octochætus do not stain in a solution of gentian violet in normal salt; the nucleus, however, stains violet, but much less readily than do the other cells of the fluid.

But if the cells be first killed in corrosive sublimate, and the stain run in, the oily globules take on a blue tint.

Cyanin, too, is recommended for fat; and in the fresh condition I find that the oil globules become coloured blue with this reagent.

The Action of Acids, Alkalis, etc.—Nitric acid (strong) causes the cells to swell, thus exhibiting very clearly the pellicle, which is seen to be folded and creased on its surface—evidence of a membrane of some toughness. The oil globules swell up, gradually losing their refringency as they do so; but after the prolonged action of the strong acid, and even after boiling the acid, they remain undissolved.

Hydrochloric acid gives a similar reaction.

Sulphuric acid reacts at first like the preceding; but the globules are dissolved, leaving a coagulated network (? cytoplasmic) pervading the cell, whose pellicle, however, persists.

Acetic acid (glacial) does not dissolve the globules, which are equally insoluble in oxalic acid.

[The slide is heated over a bunsen till bubbles appear, and the thin film of fluid boils more or less fiercely.].

When caustic potash (70 per cent.) reaches the cell, the globules rapidly disappear one after the other; they are, in fact, instantaneously dissolved.

Ether dissolves the globules.

Absolute alcohol, when poured suddenly and in considerable quantity on a cover-slip, leaves many of the globules undissolved; but when it is run in below the cover, I have seen the globules disappear.

3. The Lamprocytes are the most abundant of all the elements in the fluid (Pl. 41, fig. 6). They resemble in size and general outline the preceding eleocytes, but are, as a matter of fact, rather flattened—as can be seen as they roll over in a current of reagent; the oval or roundish outline is more or less irregular, and I believe the cells are capable of a certain degree of diffluence. At any rate, they are very readily capable of being compressed, and of again resuming the normal form.

The cytoplasm—bounded by a definite pellicle—is clear and transparent; it is crowded with clear, colourless, circular, vacuole-like structures, most of which contain a small but very highly refringent body. This "granule" differs chemically as well as physically from the "vacuole," and each differs from the globule of the eleocyte.

I have used the expression "vacuole-like," for I feel doubt as to whether we are here dealing with true vacuoles in the cytoplasm; when the cell is broken these structures are freed and retain their form. They seem to be of firmer consistency than the cytoplasm, but have no definite "membrane;" each

seems to be a droplet of some fluid, but not of an oily character; there is no marked refringency, and reagents point to different substance.

The "granules," which are somewhat greenish in colour, are contained within the vacuoles, as can most certainly be recognised in crushed cells (see fig. 6, a), and each granule exhibits "Brownian movement" therein, whether the vacuole be still within its cell or isolated. As a rule each vacuole contains a small granule, and never more than one, but frequently the vacuole contains none. I have not seen any granule independent of a vacuole; the two are genetically related, but whether the granule is formed within the vacuole, or the fluid of the vacuole arises as a result of solution of the granule I cannot determine.

These vacuoles are fairly constant in size, but the granules vary within small limits and in different cells, while the number in different cells is also subject to considerable variations. The resemblance in size that a vacuole bears to a globule naturally suggests some relation between the two, but, as will be seen below, there is a chemical difference between these things, though it seems probable that there is a genetic bond connecting them in a series.

I have already mentioned that most of the eleocytes contain, also, a few "granules" in vacuoles; sometimes the characteristics of the two cells, which for convenience I refer to by separate names, are united in a single cell (see fig. 7). There is therefore little doubt as to the relation of one to the other, and in some specimens of Octochætus the resemblance is still closer, in that some of the "lamprocytes" contain "vacuoles" which are without granules.

We thus have, if we regard the eleocytes and lamprocytes as derivatives one from the other, four conditions:

(a) Cells containing nothing but oily globules.

(b) Cells chiefly with globules, with few or many granules in vacuoles.

(c) Cells with only one granule in each vacuole.

(d) Cells with vacuoles only.

I am, however, unable to say which of the two cells is derived, or which is the earlier stage in the history.

In Ac. annectens these lamprocytes contain much larger "granules," about twice the size of those in Octochætus; they have a much higher refringency, and are so abundant that, when viewed by transmitted light, the whole cell appears opaque and nearly black. The granule nearly fills the vacuole.

Actions of Reagents.—Stains.—Gentian violet, in the fresh, stains the nucleus deep violet: the cell membrane is also stained, though less so than the nucleus. The cytoplasm is scarcely tinted, while the vacuoles become a very pale violet, so that in a glycerine mount they show up very distinctly.

Iodine.—The cytoplasm is stained only a very faint yellow —quite different from the brown colour exhibited by the eleocyte. The "vacuoles" also share in this yellow coloration, as is best seen in those isolated and freed from the cytoplasm, but the granules remain uncoloured.

Acids, Alkalies, etc.—When treated with nitric acid the "vacuoles" burst after swelling; the granules are thus released, but soon dissolve, accompanied by a good deal of turmoil in the cell. Though I could not detect any actual bubbles, yet the cell-contents seemed to be "on the boil," as Goodrich has expressed it in regard to the action of certain reagents on cells of Vermiculus.

Hydrochloric and sulphuric acids have the same effect.

Acetic acid (glacial) dissolves the granules after first causing the "vacuoles" to swell and disappear. The granules are insoluble in oxalic acid.

In potash the entire cell swells, and the contents disappear instantaneously on the arrival of the reagent.

Neither absolute alcohol nor ether dissolve the granules.

4. Linocytes.—These thread-containing cells are, without doubt, the most interesting and puzzling of the cell-constituents of the fluid, and, though bearing some resem-

blance to the "thread-containing cells" of Vermiculus, described by Goodrich, differ in a few details.

The relative number varies somewhat in different worms, and the appearance of the cell and degree of development of the thread within are subject to considerable variation; though whether this is due to individual or other causes I am as yet uncertain.

When a drop of the cœlomic fluid is examined under a low power there are seen, amongst the refringent cells just described, a few clear, almost transparent, and somewhat yellowish cells (fig. 1, d.), much larger, as a rule, than the granular amœbocytes, and sometimes nearly as large as the eleocytes. If this fluid has been mounted without any precautions, but merely taken from the cœlom, this clear cell will show, either immediately or after a short time, a circular vacuole within—or sometimes more than one vacuole,—which may be circular, or oval, or irregular. The margin of the vacuoles is clear and slightly more refringent than the cytoplasm, and has the appearance of a ring, which becomes more evident after the death of the cell. This "ring," when carefully examined, appears to be made up of a coiled fine thread, which is faintly yellow, but prolonged study modified this conception of a "coiled thread." Before discussing the interpretation to be put upon this cell-product, it will be convenient to describe an average form and some less usual types.

Usually, the linocyte (fig. 9) is spherical, of about half the size of an eleocyte. The cytoplasm is finely but regularly granulated, and forms a superficial envelope to the contents, and it is bounded externally by a distinct envelope. The nucleus is oval, and lies in the peripheral cytoplasmic coat, which is thicker in its neighbourhood than elsewhere. The greater part of the cell is occupied by a slightly refringent, clear, faintly yellowish inclusion—which for convenience may be termed a "coiled thread," for even in the most carefully mounted preparations the refringent outline of the inclusion, be it oval or circular, soon shows

minute concentric fibrils ; and moreover, the refringency is not limited to the outline of the inclusion, but crosses the "vacuole" in curved lines, each of which presents the same appearance of fibrillation, and, as one focusses this strange inclusion, the whole resembles a coil or tangle of cotton.

The use of certain reagents renders the thread more distinct, and separates the fibrils from one another, so that the tangle appears to be unravelled before one's eyes (see fig. 25) ; but I have failed, after long search, to detect a free end ; nor is there any regular spiral arrangement such as both Goodrich and Eisen have indicated.

Whereas the majority of the cells have but one such "coil of thread," a few cells (or in one specimen, at least, the majority of the cells) contain several threads, which are of different sizes and degrees of development. Thus, on July 11th I noted a great variety in the form of the coil, as these figures well illustrate (see figs. 18, 19, 20). One particularly curious cell is figured (fig. 21) ; it shows two coils, a circular and an hour-glass shaped one, which is further represented enlarged at the sides. But generally, in the case of the several small "coils," each lies in one plane, is simple, and more or less circular ; whereas, in the case of what I think may be regarded as normal linocytes, the "coil" is spheroidal, and complicated by crossings and "intertwinings" as it were.

From a series of observations, made at two different seasons of the year, in worms of different degrees of sexual maturity I have been able to trace the development of this curious cell-product.

The linocyte is at first a spherical, colourless, non-amœboid cell, filled with cytoplasm only, and bounded by a delicate but distinct membrane (fig. 10).

The cytoplasm is very finely granular, and is occupied by numerous very small, circular vacuoles, so regularly arranged as to deserve the descriptive term "honeycomb." The nucleus, even in the younger cell noted by me,[1] is peripherally

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[1] It is probable that a still earlier phase of this linocyte bears some rela-

situated just below the cell membrane ; moreover, even in
the earlier phase observed, there is a larger more centrally
placed vacuole, the outline of which is at first not specially
distinct. This vacuole gradually increases in size, but I
could not determine whether this results from the union of
the smaller vacuoles with one another, which appears pro-
bable. With this increase of the vacuole the cytoplasmic
envelope becomes thinner and loses its "honeycomb" ap-
pearance, etc. (fig. 11). At first, and for some little time,
the outline of the vacuole, though distinct, exhibits no pecu-
liarity ; but after a time it becomes more definite, and
appears as a gradually thickening wall, which then becomes
refringent. This refringency (fig. 12) commences to be evi-
dent at one side, sometimes on the side next the nucleus,
but as often at any other point. This refringent arc gradu-
ally extends so as to become crescentic (fig. 13), the ends
always thinner than the central region ; and by a continua-
tion of this procedure the central vacuole becomes completely
surrounded by a circular refringent ring (fig. 14). These
stages were particularly well exhibited in a fully mature
individual examined in November.

This ring now continues to thicken, so that the vacuole
becomes constantly reduced ; and as it does so, the ring
seems to become differentiated into irregularly concentric
layers, alternately more and less refringent ; in this way the
fibrils of the thread are established (fig. 15). But mean-
while the contents of the vacuole have also become con-
centrated and refringent along transverse lines, giving rise
to curved loops passing from one side of the ring to the
other ; and in this way the "coil" represented in fig. 9 is
brought about.

In this history there are many points of resemblance to
the development of a nematocyst within a cnidoblast ; and at
an early stage the likeness of the young linocyte to a fat cell
is very evident. The fibrillation of the "ring" is not evident

tions to an amœboid cell; or at least to some indifferent cell with a centra
nucleus.

in absolutely fresh cells, but when the cell is examined in salt solutions or even after exposure to air, soon becomes marked, and is still more intensified by the use of reagents. The inclusion seems, then, to be a semi-solid spheroidal structure, which is easily disintegrated into a " thread."

Turning now to the less frequent condition where a multiplicity of "rings" exists (as observed in certain immature specimens examined in July). The earlier phases are identical with the one first described, but in place of a single, large, central vacuole two, or more, smaller and irregularly distributed vacuoles make their appearance (fig. 16) ; each of which, then, becomes surrounded by a refringent ring, which usually remains simple (fig. 17, etc.).

Action of Reagents.—Stains.—Gentian violet stains the thread and the fluid in the vacuole very rapidly a bright blue ; it is the first of the cells of the fluid to take the stain ; the nucleus is stained violet.

Iodine stains the thread a bright yellow, much more deeply than the cytoplasm.

Acids, Alkalies, etc.—Nitric acid.—At the first contact the cell membrane shrinks somewhat, and the thread becomes more evident. But soon the cytoplasmic envelope becomes coagulated, the transparency being replaced by opaque granulations that conceal the thread within. The cell swells, and these granules then give place to a series of radial lines (fig. 23) ; while the thread is concealed, and in the first experiments I believed that it had been reduced to granules which are more refringent than those of the cytoplasm ; finally, the cell membrane becomes ruptured, and the thread issues in loops from the margin (fig. 24), sometimes at one point only, though usually at several points round the circumference. The radial lines observed in the cytoplasmic envelopes are probably caused by the "unravelment" of the thread, and represent the limbs of the loops that ultimately burst out of the cell.

Boiling nitric acid reduces the whole thread to granules, which are not dissolved by further action.

The action of hydrochloric and of sulphuric acid is similar.

In acetic acid the thread cell becomes transparent; the thread gradually swells and loses its distinctness till it finally disappears; while oxalic acid reduces the thread to granules, but does not dissolve it.

In caustic potash (30 per cent.), just at first the thread becomes more evident; the cell swells and bursts, leaving the thread behind. This now in its turn swells up, and the fibrillation becomes more and more definite, the thread, indeed, has the appearance of becoming gradually unravelled, so that the ring is replaced by a coil, which becomes looser as the action of the reagent is prolonged (see fig. 25, a, b, c). By this method it is possible to ascertain the existence or non-existence of a "free end." I have been quite unable to see anything of the kind; nor is the thread, as represented by its fibrils, coiled in a spiral.

The process of unravelling continues, but the potash has no further action upon it. Even after boiling the preparations the thread remains undissolved, and appears as a continuous thread in the form of a chain or a wreath of loops of varied shapes; but even now retains it refringency and definiteness (fig. 26).

In earlier experiments, where the potash was weaker, the cell after swelling simply burst, and the thread issued in loops, much as in the reaction with mineral acids.

Absolute alcohol does not dissolve the thread, though it shrinks a good deal, forming a refringent, irregular mass in the cell.

Ether converts the thread into granules.

Osmic acid has an action similar to absolute alcohol, and does not sensibly brown the thread.

Remarks on the Cœlomic Fluid in general.

The fluid, as already stated, is milky to creamy in colour, owing to the great abundance of the eleocytes and lampro-

cytes. The great consistency, and the absence of ready flow, which is so noticeable a feature, as compared with the fluid of Lumbricids, is related no doubt to the abundance of cell elements and small proportion of liquid plasma. But this plasma itself must be much less fluid than blood-plasma, for, as above mentioned, a drop of the fluid is sufficiently firm to support a cover-slip, and yet the cells are protected from bursting or injury; indeed, they are but slightly compressed except at the margins of the drop.

The fluid appears to " coagulate " rapidly, but I have been unable to detect any fibrin-like threads except after exposure to air for some time.

The stuff is sticky; adheres to the glass, or dish, or fingers.

The dish in which the worm was kept during examination of the fluid soon became coated at the bottom with a tenacious slime, becoming slightly buff coloured after a time. This slime when lifted seems stringy, and fine threads, fibrin-like, hold the corpuscles together. But these have no relation, so far as I could discover, to the threads in the linocytes. I imagine they are chemically produced in the plasma.

Octochætus multiporus and O. antarcticus are highly photogenic or phosphorescent, and when handled in the dark it is at once seen that this light has its seat in the cœlomic fluid as it issues from the dorsal pores and slowly spreads over the surface of the worm. The effect is much more brilliant if the worm be stimulated by a little vapour of acetic acid; then the abundantly discharged fluid gleams with considerable brilliance.

It has been suggested (Beddard, ' Nature,' vol. lx, p. 52) that the photogeny of Microscolex modestus and of Allolobophora fœtida is due to photogenic bacteria; but as I have indicated (loc. cit., p. 591) there is reason to believe that the phenomenon is connected with the eleocytes of the fluid. It is well known that in a number of animals photogeny occurs in direct association with cells containing fatty matters; and that it is by no means always or necessarily associated with the presence of bacteria (for example,

the glowworm, and firefly, and others). It has long been regarded as connected with metabolism and rapid oxidation of fat. Radziszewski has carried out a series of experiments with various organic chemical substances, such as fats, ethereal oils, hydrocarbons, and alcohols; and (I quote from Max Verworn's 'General Physiology,' p. 256) he "found that a whole series of organic bodies emit light when they are slowly combined with oxygen in an alkaline solution." Further, Verworn states, "It is in the highest degree probable that the luminosity of living substances depends upon analogous processes;" and he comes to the conclusion, as others have before him, that the photogenic substance is produced in cell-metabolism.

Now in the eleocytes of the cœlomic fluid, it seems to me, we have just the very conditions for the emission of light, and we need not summon bacteria to their aid. As a matter of fact, I have seen no bacteria in this photogenic fluid.

The cells possess considerable vitality and power of resistance to pressure and to drying, for after several hours' exposure such a slime shows abundant cells of all kinds. In one instance a living worm was first operated on at about 10.30 in the morning by a small incision; it remained alive in the dish, being repeatedly incised for fluid, all day, and the slime, when examined at 4.30 the same afternoon, exhibited all the usual cells apparently alive; at any rate the amœbocytes were still moving, thrusting out pseudopods as actively as when freshly extruded from the worm; the cells presented their normal appearance, and there was no evidence that the linocytes discharge the thread, for the cells were present in the usual proportion, and nothing resembling empty cells existed.

Again, the bottom of the tin in which several worms had been kept for a week or more in grass, was covered with slime, mixed with earth that had been discharged through the anus. This dirty slime, when examined, also contained uninjured cells; but I was unable to detect many of the linocytes. Some I saw, but apparently they were not as abundant

as in the fluid.   However, it is not an easy matter to explore a fluid thick with finely comminuted dirt, and I do not think any conclusion can be drawn from the apparent fewness of the linocytes here.

Comparison of the Cells with those of other Oligochætes.

In his monograph Beddard gives but little information as to the formed constituents of the cœlomic fluid.   On p. 26 he states that "in the higher Oligochæta" the corpuscles are " apparently of two kinds : " viz. amœboid cells, and large spherical cells loaded with granules; these " are probably merely stages in growth."

On p. 27 he says, "among earthworms there is generally not such a great abundance of corpuscles" (as in the Naiads and Enchytræids), but he mentions the milky-white appearance of certain Eudrilids as being due to the great abundance of cells.

Beddard himself, in studying the development of Octochætus multiporus, observed a large quantity of corpuscles ; for in the later stages the cœlom " was almost completely filled with granular corpuscles (i. e. lamprocytes), which represent a further development of the small non-granular cells " (i. e. amœbocytes) (**2**, p. 509).   In his monograph he considers this fact " related to rapid growth and excretion ; " but it is curious that in his various studies on the anatomy of the adult, his attention had not been attracted to the flaky, white substance that in preserved specimens fills the cœlom ; but even if it had been examined, it is improbable that much additional information could have been derived from it.

Since Kükenthal's account of the "lymphoid cells " of Annelids, the most detailed description of the cœlomic corpuscles is contained in Rosa's memoir, to which reference has already been made.   He finds in most of the species of Lumbricids three kinds of cells—amœbocytes, eleocytes, and " vacuolated lymphocytes."

I have referred to the amœbocytes above. The eleocytes of Octochætus differ but slightly from those described by Rosa ; and, indeed, different species of Allolobophora contain eleocytes that differ slightly amongst themselves. Thus in some cases (e. g. A. fœtida) the oily globules fuse with one another when the cell is exposed to the air, giving rise to a peripheral halo of oil round a central nucleus ; whereas in A. putris this fusion does not occur. I have not been able to detect the " centrospheres " which, though absent in some species, seems to be a very conspicuous feature in other eleocytes.

The " vacuolated lymphocytes," which exist in those species in which eleocytes are less abundant—as in A. caliginera, Lumbricus and sp.—differ chiefly from the "lamprocytes" in the absence of the refringent granules. Rosa notes also their slow coloration with gentian violet.

It may be mentioned here that Rosa has shown that these refringent globules in eleocytes—which are yellow in some species—are easily distinguished from chloragogen globules by various reactions; and he shows the error of the idea—due originally, I believe, to Prof. Ray Lankester,[1] and later on to Kükenthal's work—that these spherical cells are simply amœbocytes gorged with chloragogen granules ; a view that has crept into a number of text-books, from its plausibility and from the ready way in which the function of the cells was thereby explained.

Cuénot, too, confused the eleocytes with chloragogen cells, but explained their history rather differently.

There seems, according to Rosa, to be no doubt as to the distinction between the oily globules and the chloragogen. But in the " granules " of the lamprocytes occurring in Octochætus we have quite a different substance, resembling some form of chloragogen in its insolubility in absolute

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[1] The view that the chloragogen cells are metamorphosed into free cells of the cœlomic fluid is due to d'Udekem, who in his monograph on "Tubifex rivulorum" ('Mem. Couron. Acad. Belg.') develops this view and gives figures in support of it.—E. R. L.

alcohol, in ether, and in potash; and this opens up another question—the relation of the two kinds of cells.

To this I am not prepared with any suggestion, but it is fairly evident that one is derived from the other.

Before leaving these eleocytes, reference may be made to Mr. Picton's observations on the corpuscles of the cœlomic fluid of Amphitrite, of which he figures (figs. 50, 52) examples, which appear to agree closely with those of Oligochæta. Further, he states that in some of the eleocytes in which little fat has accumulated there are " strongly defined granules of yellow pigment " (p. 290), which are represented in his fig. 51, where each appears as a highly refringent granule in the centre of a " vacuole," similar to the condition noted in the " lamprocytes " of Octochætus; in fact, the figure of the whole corpuscle, with its vacuolated structure, might stand for such a cell.

In this paper the author gives an account of the series of chemical tests applied by him to the cell-contents of heart-body and other cells, in a series of Polychæta.

With regard to the linocyte or thread-containing cells :— these seem to have been observed in cœlomic fluid for the first time by Goodrich—in Enchytræus hortensis. His account of the reactions of the thread agrees very closely with those enumerated above; but he states, with some apparent doubt, that the thread is dissolved in boiling potash. The form of the cell and of the thread itself is different, however. The " thread-containing cell " of Enchytræus agrees with the " granular cells " in containing highly refringent globules, and he states (p. 58) " that the thread itself appears to be formed at the expense of the granules," though he allows that the appearance upon which he relies may be deceptive.

In Octochætus it does not appear that there is any relation between either the " granules " or the globules on the one hand and the " thread " on the other; we have seen that the characters of the cells are entirely different, and while the " eleocyte " and the " lamprocyte " may be, and

probably are, related to one another, I am of opinion that the "linocyte" is quite an independent cell.

Still more recently "thread-containing cells" have been noted by Eisen in certain Oligochæta. He uses the term "nematocytes" in describing them—a term which I think is not altogether suitable, in view of the familiar "nematocyst" of the Cnidaria. His account of these "thread-containing cells" is based upon sections, and this has, I believe, led him to certain erroneous conclusions as to the form and character of the cell and thread.

In Ocnerodrilus panamaensis he finds such cells, and he states (p. 131) that "the whole cytoplasm is filiform, and takes the shape of a single, continuous, narrow strand, wound regularly, like a coil of rope." . . . "The beginning and end of the thread could be clearly seen" (p. 132). "There is no cytoplasm visible either inside or outside the cytoplasmic thread, which does not fill the centre of the cell, there being always a space there." I think, from his description and figures (pl. xi, fig. 116), that the discrepancy between this account and my own may be explained by the fact that he examined no fresh material.

But I cannot accept his suggestion that "the rope may serve to catch bacteria, sperm fragments, or other foreign substance in the lymph." Had he examined the fluid fresh I believe that he would not have hazarded the suggestion. At the same time I am not in a position to form any idea as to the functions of the thread.

In this paper Eisen also gives some account of other kinds of cœlomic corpuscles occurring in various earthworms, but, since this account is founded on observations of preserved material only, I have no occasion to refer to it more specially.

With regard to the chemical nature of these cell-products, I regret that I have not been able to form any definite conclusion, owing to my ignorance of micro-chemistry and the lack of available literature dealing with the subject.

As will be seen in the above notes, I have used the same

MICRO-CHEMICAL REACTIONS OF THE CELL-PRODUCTS.

The sign + indicates that the product is dissolved.
The sign — ,, ,, ,, not dissolved, even on boiling.
The sign * ,, ,, ,, reduced to granules, but undissolved.

	Absolute Alcohol.	Ether.	Potash. 30 %	Acetic Acid.	Oxalic Acid.	Nitric Acid.	Hydro-chloric Acid.	Sulphuric Acid.	Water.
Globules in eleocyte	+ (partially)	+	+	+	—	—	—	+	—
Granules in lamprocyte	—	—	+	+	—	+	+	+	—
Thread in linocyte	—	*	—	+	*	*	*	*	—

Note.—After treatment with acetic acid a quantity of small crystals—some diamond-shaped, others like short rods—were noted in the preparation.

series of reagents as Goodrich employed, under the advice of Professor Gotch ; and I will tabulate the results obtained by me for ready comparison with Goodrich's results.

The observations of Schaeppi, of Picton, and of several others, on the intra-cellular products of Polychæta, point to the great variety of these cell-contents. But, in order to obtain some further light upon this difficult problem, it seems to me desirable that the whole question should be dealt with by a competent chemist. It is, at present, somewhat difficult to correlate the various results, or to form a definite opinion as to the function performed by these cells—whether excretory or otherwise,— or the stages by which the varied chemical substances are built up. The whole subject is one of great interest and importance, and I can only give my results for what they are worth.

A comparison of this table with that given by Goodrich shows that these "granules" agree with the "white granules" in the lymphocytes of Enchytræus hortensis, which are neither mucin nor chitin. They do not appear to agree with "Chloragogen"—a word of very wide application.

DUNEDIN ;
November 30th, 1900.

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EXPLANATION OF PLATE 41,

Illustrating Professor W. Blaxland Benham's paper on " The Cœlomic Fluid in Acanthodrilids."

Fig. 1.—A group of cœlomic corpuscles of Octochætus multiporus, fresh, without reagent. (Camera. × 375.) *a*. Amœbocyte. *b*. Eleocyte. *c*. Lamprocyte. *d*. Linocyte.

Fig. 2.—A granular amœbocyte (*a* of Fig. 1), the appearance described in ordinary preparations, with short, clear, digitiform pseudopods.

Fig. 3.—An amœbocyte with petaloid processes; seen when the greatest care is taken to obtain a preparation in a natural condition.

Fig. 4.—Spindle-shaped, faintly granular amœbocyte; found creeping along the inner surface of the body-wall.

Fig. 5.—An eleocyte, slightly compressed, but without having been acted upon by any reagent. In addition to the characteristic oily globules, it contains a few refringent granules; the vacuole in which each lies is not seen.

Fig. 6.—A typical lamprocyte, slightly compressed, fresh; the vacuoles, with their highly refringent granules, are also shown at 6, *a*, as seen when a cell is broken up.

Fig. 7.—A cell intermediate in character, combining the features of both eleocyte and lamprocyte, slightly compressed, fresh.

Fig. 8.—A lamprocyte stained with gentian violet. (Camera. × 700.) The vacuoles and granules are represented of their real size. The nucleus is shown and the creasing of the cell-membrane.

Fig. 9.—A typical linocyte, from discharged fluid, slightly compressed and dead, showing nucleus and complex "thread-coil."

Fig. 10.—A young linocyte, showing the honeycomb appearance of the cytoplasm, and the great central vacuole and peripheral nucleus.

Fig. 11.—A slightly older linocyte, with enlarged vacuole; the honeycomb appearance of the cytoplasm no longer exists.

Figs. 12—15.—Sketches of four linocytes in different stages of development, showing the method of origin of the "thread" within the vacuole. These sketches are slightly diagrammatic, but represent faithfully the appearance of the thread.

Fig. 16.—A young linocyte in which several large vacuoles exist, in each of which a thread-coil will arise (fresh).

Fig. 17.—A linocyte with several independent rings or thread-coils.

Figs 18—20.—Living linocytes with more than one thread-coil, to illustrate the variety of form assumed by this cell product. The details of the cytoplasm are not fully represented.

Fig. 21.—A linocyte with a single thread-coil and three large vacuoles, in which probably threads will appear later on.

Fig. 22.—A linocyte (dead) containing two thread-coils, one of which has an exceptional form, which is further indicated at a ; n is the nucleus.

Fig. 23.—A linocyte after the addition of nitric acid to the preparation. The thread is indistinct, but a series of radiating lines occupy the peripheral region of the cell, which are possibly parts of the disentangled thread.

Fig. 24.—A linocyte after further action of nitric acid ; the cell membrane has become ruptured, and the unravelling thread is issuing in the form of loops.

Fig. 25.—The thread-coil after potash has dissolved the cytoplasm. As the reagent acts the thread undergoes the changes represented at $a, b, c,$ the thread-coil or ring swells up, and the fibrils separate from one another.

Fig. 26.—Three sketches of threads left after the action of boiling potash, to illustrate the continuity of the thread.

Fig. 1.
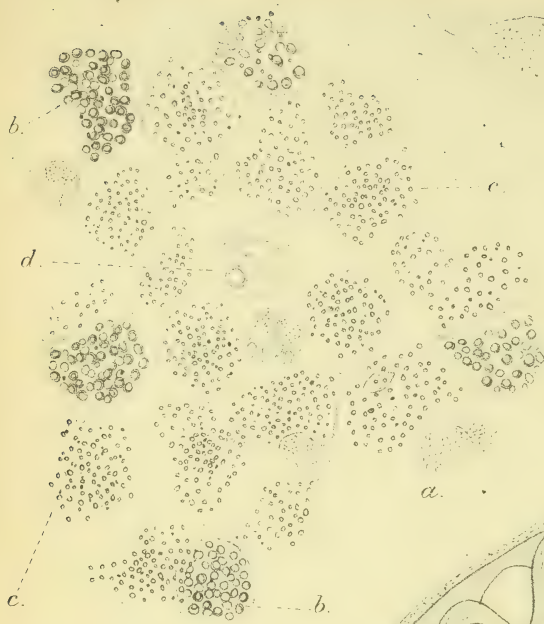
Fig. 4.
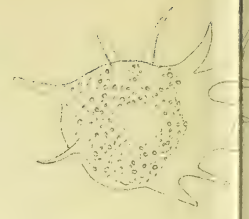
Fig. 2.

Fig. 16.

Fig. 10.
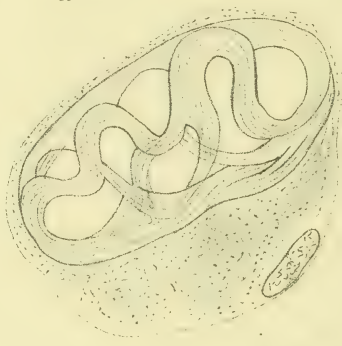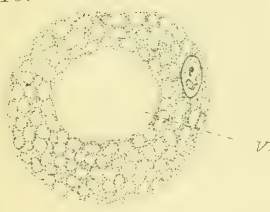
Fig. 9.

Fig. 11.

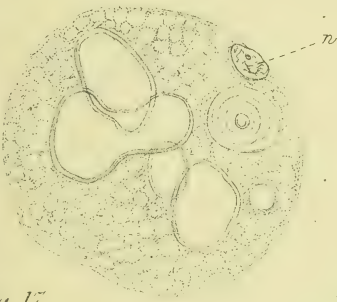Fig. 20.

Fig. 12.

Fig. 14.

Fig. 15.

Fig. 22.

Fig. 13.

W.B.B. del.

Fig. 5.

Fig. 6.

a.

Fig. 3.

Fig. 8.
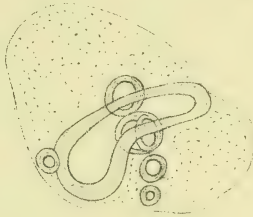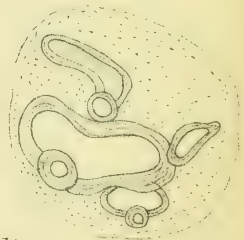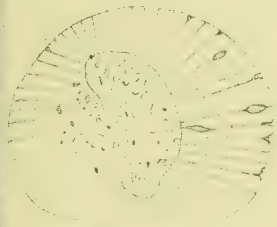
Fig. 7.

n
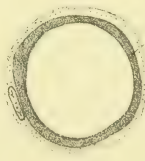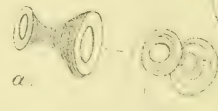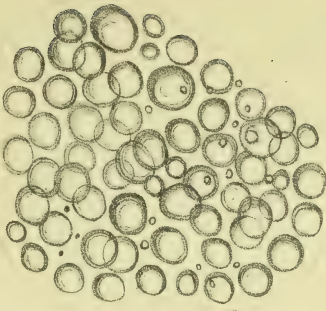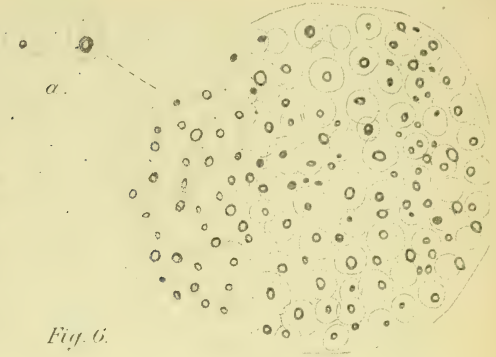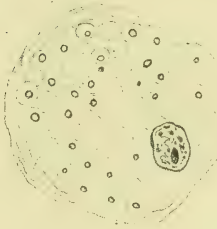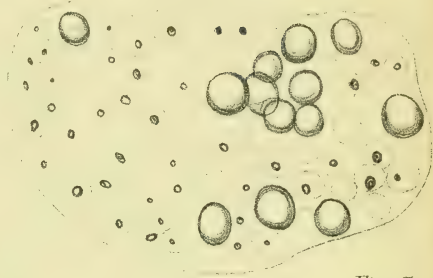
Fig. 17.

Fig. 18.

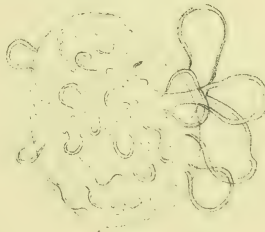Fig. 19.

Fig. 23.

Fig. 21.

Fig. 26.

a.

b.

c.

Fig. 25.

The Crystalline Style of Lamellibranchia.

By

S. B. Mitra,

Of Calcutta, late of University College, London.

With Plate 42.

FOUR hypotheses have been framed with regard to what the crystalline style of the Lamellibranchia is and does : (1) Gegenbaur thought it was a secretion from the enteric epithelium ('Elements of Comparative Anatomy,' English translation, p. 359). (2) Balfour suggested that it was to be considered as a rudiment of the radular sac of the Glossophora (see Professor Lankester's article on "Mollusca," in the 'Encyclopædia Britannica,' ninth edition, p. 685). (3) Claus regarded it as an excretion of the enteric epithelium. (4) Sedgwick thinks it is to be regarded as a "reserve of nutriment" ('Student's Text-book of Zoology,' vol. i, p. 335). We may say at the outset that of all the hypotheses Gegenbaur's was the nearest to the truth, for it is in reality a secretion, a digestive ferment whose function it is to digest starch, i. e. to convert starch into a reducible sugar.

The crystalline style cannot be regarded as a rudimentary structure representing the radular sac of the Glossophora, for the following reasons :[1]

(1) Its comparative size is not like that of a rudimentary structure. It is fully three fourths as long as is the animal

[1] A structure apparently identical in nature with the crystalline style of Lamellibranchs co-exists in some Gastropoda with the radula. If the identity of the Gastropod's and Lamellibranch's crystalline styles be admitted there can be no question of relationship to the radula.—E. R. L.

itself (Anodon). A structure of such a comparatively great
length cannot be regarded as a vestigial structure unless
there are cogent reasons for taking it in that light; but there
are none.

(2) The cæcum (a diverticulum of the alimentary canal
starting from the pyloric end of the stomach), in which in
some Lamellibranchs the style is lodged, and which the
hypothesis under consideration would take to represent the
sac proper of the radula of a glossophorous Mollusc, is lined
with epithelial cells bearing active cilia which are much
longer and better developed than the cilia of the epithelial
cells that line the alimentary canal itself. Here we might
say parenthetically that the alimentary canal of the Lamelli-
branchia is lined throughout with ciliated epithelium. Now,
as cilia always perform an important function in the economy
of the organism that possesses them, we should, if the cæcum
were really a vestigial structure, expect to see either that it
was not lined with ciliated epithelium at all, or that if it
was lined with ciliated epithelium at all, the cilia were shorter
and less well developed than the cilia of the cells that line
the alimentary canal itself. The fact that the epithelial
cells lining the cæcum bear such highly active and longer
cilia, suggests forcibly the idea that the cæcum performs
some important function, and so cannot be regarded as a
vestigial structure. In fact, there are reasons (as we shall
see later on) for regarding it as a higher stage in the evolu-
tion of the receptacle for the lodgment of the crystalline
style, the more primitive stage being still found in some
species of the Lamellibranchia.

(3) The cæcum in which the crystalline style is lodged in
some Lamellibranchs starts from the pyloric end of the
stomach, whereas the radular sac is formed by a diverticulum
of the wall of the œsophagus. If the former represented the
latter, we should expect to see the cæcum start from some
part of the œsophagus. We admit that, taken alone, this
reason is not very forcible, as there may be considerable
change in the position of the same fundamental structure in

the different species of the same group of animals; but taken in conjunction with the other reasons, it must be allowed to possess some value.

(4) We invariably found in literally hundreds and hundreds of the fresh-water mussels and other Lamellibranchs that a considerable quantity of food material surrounds and is embedded in that end of the crystalline style that projects into the stomach (see figs. 2, 4, 6). This is very suggestive to say the least.

(5) The fact that the crystalline style is periodically renewed (Claus, Sedgwick) does not fit in well with the idea that it is a rudimentary structure. Why should a vestigial structure be formed and vanish again and again, say once a day (about that is the frequency of renewal that I found to obtain amongst the mussels which I kept in an aquarium)? It rather suggests the idea that the style is somehow connected with some important function that is performed by some organ of the animal. And we have found that that is the case. It is connected with the digestive function. Whenever digestion is going on actively in the animal, as evidenced by the presence of undigested and half digested food material in the stomach and first portions of the intestine, and of excrementitious matter in the last portion, one is sure to find the style. When that function is for any reason in abeyance, one fails to find it. This is shown by the following observations. I used to get my supplies of mussels in batches of about 200 each. After they had been taken out of a pond they were kept and brought to me in a very small quantity of water in a pail-like vessel. About ten hours elapsed from the time they had been taken out of a pond and the time they reached me. All this time their position in the vessel was anything but natural. They lay in the vessel like a mass of pears in a basket,—some horizontally, some vertically, others obliquely, every one being in contact with the surrounding ones. Moreover, during the transit from the country to the town they had to undergo a considerable amount of jostling and rubbing against one

another. All these circumstances were unfavourable for the proper functioning of their digestive organs. Now, on their arrival at my place, I used to open some fifty at a time, and found the crystalline style in none. I could also at the same time see that their digestive function was naturally enough in abeyance. The remaining mussels I would then put into a fresh-water aquarium, where there was plenty of space, good water, and food material. After two or three hours I used to open some fifty more of the same batch, taken fresh from the aquarium. Then I invariably found the crystalline style in one and all of these fifty mussels, and at the same time noticed that the digestive function in them had just begun again. An interesting experiment proving the same thing—that is, the existence of a connection between digestion and the crystalline style—got performed over and over again, one might almost say of itself, in one of my aquaria. This aquarium had a leak, and the water in it would gradually drain away in the daytime. During the night there would not be left sufficient water to enable the mussels to set up the well-known in-going and out-going currents and so carry on respiration and digestion actively. On the next morning at about 7 o'clock there would be left no water at all in the aquarium. At 8 a.m. every day for two months I examined some twenty mussels, and found the crystalline style in none, and the digestive function in abeyance in them. At about 9 a.m. the tap was turned on every day, and the aquarium filled with water. Two or three hours afterwards, on opening twenty other mussels taken fresh from the same aquarium and from the same batch, I invariably found the crystalline style in them all, and at the same time noticed that digestion had begun again in all of them. These observations show conclusively that a functional relationship exists between digestion and the crystalline style,—that the style either somehow aids digestion, or else is a product or waste-product of digestion. And we shall see presently that it aids digestion in a very important way.

(6) But the most convincing, the most irrefragable proof

that the crystalline style cannot be regarded as a rudimentary structure, is that it is an active amylolytic ferment, as we shall see presently. Only if we could regard the ptyalin or the pepsin of other animals as a rudimentary structure, could we take the crystalline style as a rudimentary structure.

Let us now describe and state fully the physical, chemical, and physiological characteristics of the crystalline style, that is to say, see what it really is and what it really does. After we have done that we shall dispose of the third and the fourth hypotheses.

A fully-formed crystalline style that has been shed some twelve hours is a flexible, solid transparent body that is thicker at one end than at the other. Broadly speaking its form is like that of a slender cone (see figs. 1, 2, 4, 5, 6). Under the microscope it is seen to be longitudinally striated (see figs. 4, 6). The striation is due to the fact that the style is composed of concentric or rather co-axial (placed round a common axis) layers of a colloid substance of greater and lesser density. A cross section of a fully formed style looks under the microscope like the cross section of an onion (see fig. 3). We must state here that very often one notices in the style of Anodon a central much softer core, which is much less perfectly striated, and which has embedded in it particles of food material (see fig. 5). In a freshly formed style in Anodon, that has been shed a few minutes ago, this central core forms a very marked feature. Under the microscope it is seen to occupy three fourths or more of the space occupied by the whole style, that is to say, to possess a diameter that is three fourths or more as long as the diameter of the whole style at the corresponding part; to be a viscous liquid of a finely bubbly appearance; and to be surrounded by a comparatively thin nearly homogeneous sheath-like layer (fig. 5). In fact, such a freshly formed style may briefly be said to be formed of a viscous liquid that has got formed round it, apparently through condensation of its own substance, a thin sheath-like layer. This observation is very important, as showing that a fully-formed style is not pro-

duced as a tough, solid substance, but is shed as a viscous, finely bubbly liquid, which in the receptacle gradually gets thicker and thicker in consistency, till it becomes a flexible solid. It should be stated here that occasionally one notices in a pretty freshly formed style in Anodon, an axial zone that consists chiefly of particles of food material. Such a zone is never found in fully formed styles in Anodon, and its occasional presence in a freshly formed style in that animal would seem to point to the imperfection of the method of storing the ferment, and passing on the food material that obtains in this species of the Lamellibranchia. It is interesting to note in this connection, that such a zone is never found in the style of a species of Pholas examined by me, in which the style is lodged in a cæcum, and not in the alimentary canal itself. The style, let us add, in this species of Pholas always possesses a central, liquid, finely bubbly core (fig. 6), which never contains a particle of food material. In fact, the main body of the style of this Pholas is always free from a single particle of food material—an assertion that cannot be made with regard to the style of Anodon. Under these circumstances one is surely justified in thinking that the complete freedom of Pholas' style from food particles is due to a superior, more differentiated mechanism for storing the ferment and passing the food material through the alimentary canal.

As is well known, the style is lodged in some species in the alimentary canal itself (Anodon), in others (fig. 9) in a diverticulum (cæcum) of the canal, which starts from the pyloric end of the stomach (Pholas). But the most curious fact in this connection, that has never before been observed, is that in Anodon the first portion of the intestine—the portion that lodges the style—is divided into two longitudinal compartments by two longitudinal ciliated ridges that project into the lumen of the canal. A cross section of the canal at this part, seen from behind, is represented diagrammatically in the figure 7. One ridge is placed dorsally, the other ventrally. The two compartments may, therefore, be called

one the right and the other the left compartment. They
are open at both ends : but the stomach-ends of both are
guarded by a cuticular value. It is in the left compartment
that the style is lodged. Now what is the use of the right
compartment ? It took me some time to find out. It is
through the right compartment that food material is, as a
rule, passed on from the stomach into the rest of the alimen-
tary canal. By careful dissection of the animals when they
are digesting food actively, one can see with the naked eye
particles of food material forming a very slender cord (figs
7, 8), and being hurried along through this compartment by
the action of the cilia. It is easy to see that if there were no
such division of the lumen into compartments there would be
no proper storage of the ferment, and food material might be
passed on without being properly mixed up with the ferment.
It is not out of place to mention here that the cæcal
diverticulum in Pholas that lodges the crystalline style
arises from the same point of the stomach as the intestine,
that it runs parallel with the first portion of the intestine,
and that it is placed to the left of the same portion (fig. 9).
These facts with regard to the point of origin and the position
of the cæcum in Pholas, coupled with the undoubted fact
that Pholas is a more highly specialised form than Anodon,
and the fact mentioned above, that the crystalline style when
it is lodged in a cæcum is completely free from food particles,
whereas, when it is lodged in the alimentary canal itself
food particles are occasionally found in its substance, force
the idea on one's mind that this blind cæcum is only a
differentiated part of the first portion of the intestine, and
that it has been evolved from the left compartment of the
first portion of the intestine of Anodon by the permanent
coalescence of the ciliated ridges and shutting up of the
distal end of the compartment. It is to be remembered here
that this phenomenon—viz. the permanent coalescence of two
ciliated surfaces—must have taken place extensively and over
and over again in the evolution of the more complicated
forms of the Lamellibranch gill-plate,

Here also the important fact should be stated definitely, that one end of the crystalline style, whether it is lodged in a cæcal diverticulcum or in the alimentary canal itself, invariably projects a little into the stomach, and that this end is as invariably surrounded by and has embedded in its substance a very considerable quantity of food material (fig. 8). In fact, one can see that this projecting end is slowly and gradually dissolved in the stomach, and is there mixed up with food material, which then is passed on into the intestine (fig. 8). In Anodon the thicker end projects into the stomach, in Pholas the thinner end.

One more fact should be mentioned here, and that is that there is no cellular element in the style, and that it is composed entirely of a colloid substance.

Let us now describe the chemical properties of the style. The style is soluble in distilled water, but this solubility is due to the presence in the style of a minute quantity of salts. The solution is neutral. That it is a proteid substance is proved by the following colour reactions. It gives the xanthoproteic reaction with nitric acid and ammonia or caustic potash; the Millon's reaction with Millon's reagent; and gives violet coloration with copper sulphate and caustic potash (Piotrowski's reaction). Its solution in distilled water coagulates on heating. (The solution must be concentrated, otherwise this result cannot be obtained.) The solution in distilled water is precipitated by nitric acid. The precipitate is not dissolved by heat. The solution is also precipitated by tannin, ammonium sulphate, magnesium sulphate, sodium chloride, and alcohol.

It is important to know to what class of proteids the style belongs. It belongs to the globulin class—the class to which fibrin-ferment, which has been proved to be a proteid, belongs. It is not an albumin, because its solution in water is completely precipitated by saturation with magnesium sulphate. It is not an acid or alkali-albumin, because its solution in water is neutral, and coagulates on heating. There is no peptone in the style, because when its solution in water is

saturated with ammonium sulphate and filtered, the filtrate does not give the characteristic reaction of a peptone. Nor are there any albumoses in the style, because when its solution in water is precipitated with alcohol, and the precipitate has been kept under absolute alcohol for six months, and is then treated with water, the water does not dissolve the slightest quantity of the precipitate, and does not give the characteristic reactions of albumoses. The method of exclusion, therefore, shows that the proteid of the style must belong to the globulin class, and it shows the characteristics of that class. It is soluble in dilute saline solutions, and insoluble in concentrated solutions of NaCl, Mg SO_4 and Am_2 SO_4. Its solution in water, as has been stated above, is precipitated by heat.

Analysis shows that there is about 88 per cent. of water in the style, about 12 per cent. of a proteid (globulin), and about 1 per cent. of salts. As far, therefore, as the proportion of water to the solids goes, the composition of the style is not far different from that of the pancreatic secretion of the dog.

Let us now examine the physiological properties of the style. If two styles from fresh-water mussels are added to thirty minims of starch solution, all the starch will be converted into reducible sugar in about three hours. If seven styles are dissolved in distilled water, and the solution added to thirty minims of the same starch solution, all the starch will be transformed into a reducible sugar in about twenty minutes. These very simple experiments show that there is an amylolytic ferment in the style. An intermediate product of the nature of dextrin is formed, just as it is formed during the conversion of starch into sugar by saliva. In fact, all the stages of this transformation of starch into sugar in salivary digestion are noticeable during the conversion of starch into sugar by the crystalline style. It should be stated here that the style can also transform raw starch into sugar, but more slowly. It also acts on glycogen as ptyalin does, converting it slowly into sugar. We could not detect any action of the

crystalline style on a proteid such as egg-albumin, boiled egg fibrin, muscular fibres, etc.

But granted, it may be said, that there is an amylolytic ferment in the style, still the proteid in the style may serve as a reserve of proteid nutriment. And so, it may be said, the fourth hypothesis may still be regarded to embody, not the whole truth it is true, but part of the truth. But this idea is negatived by several considerations and facts. In the first place a proteid matter (like that of the style) reserved as a food material in an adult animal is practically unknown in the animal kingdom. Then, if the style solution in water is precipitated by alcohol, and the precipitate, consisting of a globulin, kept under alcohol, it is seen that while the supernatant alcohol contains no ferment matter, the more insoluble the precipitate becomes, the less is the ferment-activity of the precipitate; until at last, when the precipitate becomes completely insoluble in water, its ferment-activity is also lost completely. This points strongly to the conclusion that the proteid of the style and the ferment are identical. But the most striking proof that they are identical is furnished by the fact that the temperature at which the proteid in a watery solution of the style coagulates, and so loses its distinctive characteristics, is the same as that at which the solution loses its ferment-activity completely. Under the circumstances the proteid of the style and the ferment must be regarded as identical. This being so, one cannot regard that proteid as a reserve of nutriment.

After all this, it is hardly necessary to say that the third hypothesis, that the style is to be regarded as an excretory matter, is quite untenable. It is not an excretion in the strict sense of the word, because it is a ferment, and a very active and important ferment too. Besides, we know that it performs an important function in the organism by coming into contact with the food material in the stomach and acting on it.

The style cannot be regarded as a product of digestion, because there is neither acid-albumin, nor alkali-albumin, nor any albumose, nor any peptone in it.

Now the important question arises, Where does the crystal-line style come from? There are grounds for believing that it is secreted by the so-called liver. The chief ground is that there is in the liver an amylolytic ferment exactly like the ferment of the style. The ferment in the liver behaves exactly as the style ferment does. On the other hand, we could hardly detect any amylolytic ferment in the enteric epithelium. The very small quantity that may occasionally be detected may be due to the adherence to the epithelium of a minute quantity of the ferment from the outer surface of the style. There is also another fact, which must be allowed to have some force in this connection. It is that yellow pig-ment cells from the liver are occasionally seen to form the axial zone of freshly formed styles (fig. 10). If this fact does not show anything else, it shows at least the possibility of a product of the liver being carried easily into the recep-tacle in which the style is lodged. If pigment-fed cells from the liver may pass into the receptacle, a secretion of the liver may do so too.

The crystalline style has been found in Mactra, Donax, Unio, Anodon, in a species of Pholas, in a species of Mytilus, and in other species. Considering the high importance of the ferment, one is justified in predicting that future obser-vation will reveal its presence in all the species of the Lamellibranchia. Its presence in the Lipocephala is pos-sibly connected with the absence in them of specially differ-entiated salivary glands, just as it is possible to connect this absence of special salivary glands with the absence of a buccal mass. But the styles and cords which appear to represent it in Gastropoda should be now examined afresh, both as to their origin and chemical properties.

The conclusion that is to be drawn from the foregoing observations and experiments is, that the crystalline style is an active amylolytic ferment; that it is secreted as a viscous liquid, most probably by the liver; that it is stored up as a flexible solid in the cæcum, or in a compartment of the alimentary canal itself; that the end of it that projects into

the stomach is slowly and gradually dissolved there, and is mixed there with particles of food material, the starchy portion of which is transformed by it into a reducible sugar.

DESCRIPTION OF PLATE 42,

Illustrating Mr. S. B. Mitra's paper on "The Crystalline Style of Lamellibranchia."

Fɪɢ. 1.—Crystalline style of Anodon, natural size.

Fɪɢ. 2.—Enlarged drawing of another specimen.

Fɪɢ. 3.—Transverse section of the crystalline style of Anodon to show the laminated structure.

Fɪɢ. 4.—Greatly enlarged view of a style of Anodon, showing the longitudinal striation and attached food particles.

Fɪɢ. 5.—Optical longitudinal section of a similar specimen.

Fɪɢ. 6.—Optical longitudinal section of a crystalline style of Pholas.

Fɪɢ. 7.—Transverse section, showing the right and left compartments of that portion of the intestine which lodges the crystalline style in Anodon (which has no special cæcum for the style as has Pholas).

Fɪɢ. 8.—Diagram showing the crystalline style in the left compartment of the intestine of Anodon with the stream of food particles in the right compartment.

Fɪɢ. 9.—Diagram showing the separate cæcum and intestine of Pholas, formed by completion and fusion of the dividing ridges seen in Fig. 7.

Fɪɢ. 10.—Crystalline style of Anodon, showing pigmented liver-cells in the axis.

N.B.—Details are explained by the lettering on the Plate. All the Figs. except Fig. 6 and Fig. 9 represent the crystalline style of Anodon.

Food-material (alga).

Food-particles (protozoa and algae).

The substance of the thicker end of the style dissolved in the stomach.

Food-particles (algae) lying in the dissolved substance of the style.

Striated portion striation disappearing gradually towards the thinner end.

Fig.1.

Longitudinal striation.

Homogeneous sheath-like layer.

Food-material surrounding the thicker end.

Finely bubbly viscous liquid substance.

Fig. 2.

Fig. 6.

(Pholas.)

Fig.4.

Fig. 5.

Fig. 3.

The thinner end dissolved in water.

The thinner end that has got dissolved in water.

Some food-particles on the outer surface.

Ciliated epithelium.

The dorsal ridge.

Fig. 7.

The right compartment.

The left compartment.

Food-particles.

The ventral ridge.

The crystalline style.

The stomach

The oesophagus

Fig. 9.

(Pholas.)

Pigment cells from the liver.

The caecum

The central liquid core.

The first portion of the intestine.

The stomach.

The oesophagus.

Mass of food-particles in the stomach mixed up with the dissolved substance of the projecting end of the style.

The thicker end of the style projecting into the stomach.

Stream of food-particles in the right compartment.

Stream of food-particles in the oesophagus.

The first portion of the intestine.

Fig. 10.

The crystalline style.

Food-material.

Fig. 8.

Food-particles.

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