

Some Observations on Acinetaria.

By

C. H. Martin, B.A.,

Demonstrator in Zoology at Glasgow University.

With Plate 15, and 6 Text-figures.

Part 3.—The Dimorphism of Ophryodendron.

CONTENTS.

	PAGE
(1) Introduction	629
(2) Historical	631
(3) Material and Methods	637
(4) The Structure of the Proboscidiform Individual	638
(5) The Structure of the Vermiform Individual	642
(6) The Feeding of Ophryodendron, with a Note on Nematocysts in some other Protozoa	644
(7) The External Budding of Ophryodendron	648
(8) The Ciliate Embryos	652
(9) Conclusions	655
(10) Summary of Results	661

1. INTRODUCTION.

Instances of heteromorphism are fairly common amongst Protozoa, especially in the case of parasitic forms, but in all the known cases, as far as I am aware, where this occurs in free living forms, the differences are comparatively slight. These differences can often be connected with the Schizogonous and Amphigonous stages of a complicated life history (e. g. the megalosphæric and microspheræic forms of Foraminifera), whereas in the case of parasites, in which the differ-

ences are often very great, there is frequently the additional factor of the change of host (e. g. Hæmosporidia). In the case of the animal *Ophryodendron* of which some description is given in the following pages, such an explanation of the dimorphism in terms of the Amphigonous and Schizogonous stages of a life cycle is absolutely excluded. For although conjugation has never been described in this form (Koch's theory will be dealt with later), yet from the presence of a micronucleus there is very reason to predict, that as in other Acinetaria, conjugation will be found to occur of a kind absolutely similar to the process of conjugation in the Ciliates.

And it is again interesting to observe that *Ophryodendron* is the only free living heterokaryote (i. e. Ciliate or Acinetarian)—in which dimorphism¹ has been observed.

Ophryodendron is a somewhat aberrant Acinetarian frequently found as an ectoparasite on Hydroids, and also, though more rarely, on Crustacea. As has long been known, it occurs under two remarkably different forms; (*a*) the probosciform individual, and (*b*) the vermiform or Lageniform individual.

The probosciform individual is characterised (1) by the more or less pyriform shape of the body (in *Ophryodendron sertulariæ* the body is compressed),

(2) By the absence of a stalk (this may be present in some forms, e. g. *Ophryodendron trinacria*), and

(3) By the presence of a long, very contractile proboscis furnished with rows of tentacles.

The vermiform individual is characterised—

(1) By its elongate cylindrical body,

(2) By the presence of a long solid stalk which passes into the posterior end of the body, and

(3) By the absence of a proboscis.

It is obvious that the difference between the two dimorphic forms in the case of *Ophryodendron* is very great (so

¹ By the term dimorphism the occurrence of two different reproductive forms in the same species is here meant.

great in fact that two at least among its observers, Strethill Wright and Robin, have described the vermiform animal as a parasite), in the one case as a Gregarine, in the other as a Nematode worm, but before proceeding to give any further account of the life-history of the animal, it will be necessary to examine shortly the very discrepant views as to the relations between the two individuals put forward by earlier workers on this animal.

2. HISTORICAL.

Ophryodendron abietinum was first discovered by Claparède and Lachmann in 1855 on *Campanularia* from the North Sea. Their account of this animal is in many respects by far the best which has yet appeared since they saw and figured the free ciliated embryo.

On the other hand, although they recognised the difference in external form between the vermiform and the probosciform individuals, they finally concluded that in the vermiform individuals the proboscis was retracted, and that therefore there was no fundamental difference between the two forms (p. 143, "l'extrémité antérieure de ces espèces de vers présentait une espèce d'enfoncement spécial, que nous crûmes d'abord devoir considérer comme une bouche ou comme une ventouse de succion, mais que nous reconnûmes bientôt n'être qu'une fossette indiquant l'ouverture d'une cavité dans laquelle était logé un long organe rétractile que nous aurons à décrire plus loin").

They recognised in the interior of some animals both of the vermiform and probosciform type small corpuscles "tout à fait semblables aux organes urticants des Campanulaires" (p. 144), but as all their efforts to surprise the animal at the moment of feeding were vain (p. 145), they concluded that "les corpuscles particuliers qu'ils renferment sont peut être comparable aux trichocystes d'autres infusoires." They thought it probable that the probosciform individuals could

bud externally, but were not in a position to positively affirm this statement.

They describe and figure two forms of ciliated embryos, a large and a small, but as in each case the buds were freed from the parent by pressure they were never able to follow their development into the fixed form.

In 1859 Strethill Wright described shortly under the name of *Corethra sertulariæ* the species at present known as *Ophryodendron sertulariæ*. In two further short papers he identified his form wrongly with the *Ophryodendron abietinum* described by Claparède and Lachmann, and added some further details on the movements of the animal.

Strethill Wright was at first inclined to regard the vermiform individuals as Gregarine Parasites, but in his later paper he considered that they were probably gemmæ. He also figures in his paper in the 'Annals and Magazine of Natural History' for 1861, the ciliate embryo, which he "freed from the parent form by a somewhat troublesome midwifery," and described very fully the movements of the proboscis.

In 1873 Hincks published some observations on *Ophryodendron abietinum*, and on a new species *Ophryodendron pedicellatum*. He was the first observer to point out clearly that *Ophryodendron* is a dimorphic form, and that (p. 4) the vermiform individual cannot be regarded as a probosciform individual with a retracted proboscis. He says (p. 8), "If my view of the history then be correct, the *Ophryodendron* is a dimorphic animal, that which may be called the primary zooid giving origin by gemmation to bodies unlike itself which, on becoming free, group themselves around the parent organism and lead with it an associated life." Hincks failed to see the ciliated embryo, and could find no trace of any corpuscle resembling the thread cells of the hydroid even in *Ophryodendron abietinum*.

In 1876 von Koch published a paper on a supposed new species, *Ophryodendron pedunculatum*, which he found on *Plumularia* from Messina. (This species is probably

synonomous with Hinck's *Ophryodendron pedicellatum*). von Koch describes the proboscidiiform and vermiform individuals which he terms respectively forms A and B. He does not describe the ciliated embryos, but he puts forward the novel view that the cases of association between the individuals A and B which Claparède and Lachmann and Hincks considered as probable cases of budding, were rather to be regarded in the inverse order, as the gradual stages of a complete copulation between the individual A and B, which would probably result in the formation of internal buds, as may be seen from the following passage: "Aus den Embryonen entwickeln sich die zwei verschieden gestalteten Formen A und B. B (the vermiform individual) lost sich nach eine gewisse Zeit von seinem Stiel ab, und es verschmilzt Protoplasma und Kern mit denselben Theilen von A (the proboscidiiform individual). Nach dieser Verschmelzung werden von A und B endogene Embryonen erzeugt. Gegen diese Deutung lässt sich aus meinen Beobachtungen keine Einwendung machen."

Koch's principal reason for this interpretation seems to have been the fact that he could not recognise any trace of the stalk in the full-grown vermiform individuals which he saw in contact with the proboscidiiform.

The reason for this, as will be shown later, is that the stalk is usually only formed after the vermiform individual has become free from the proboscidiiform parent.

Fraipont, in 1877, returned to the original view of Claparède and Lachmann, that the vermiform individuals are a stage in the development of the proboscidiiform individuals, though he describes the vermiform individuals as characterised "par l'absence de trompe proprement dite, et de sucoirs prehenseurs" (p. 783). It is very difficult to form a clear conception as to his views on external budding. On p. 791 he states that, "Les Proboscidiens donnent naissance par bourgeonnement externe à des individus semblables à eux soit directement soit après qu'ils ont passé par la phase d'individus Lagènimiformes." Whereas on p. 789 the following

passage is found :—“ Constatons d'abord que l'on ne trouve jamais chez mon espèce des individus Lagèniiformes fixés sur les Proboscidiens.”

Fraipont failed to see the ciliated buds (p. 785, “ Quant à moi, je n'ai remarqué chez mon espèce la reproduction gemmipare”), and he regards the corpuscles found in the animal as “ un produit du protoplasme de l'organisme et qu'ils doivent être comparés aux trichocystes que l'on connaît chez plusieurs infusoires ” (p. 778).

Robin in 1879 published an account of an Ophryodendron under the name of *Ophryodendron abietinum*, though there can be no doubt, from his excellent figures, that the animal he observed was *Ophryodendron sertulariæ*. He considers the vermiform individual to be a true parasite, as is shown by the following passage on p. 540 :—“ Les faits qui suivent montrent que cet animal est une larve d'Helminthe d'espèce encore indéterminée.” He was unable to show the multicellular nature of the animal, but on p. 541 he states—“ On ne saisit sur ce parasite ni bouche, ni anus, ni le tube digestif au moins en voie de formation, qu'on trouve dans les larves filariennes de beaucoup de Nématoides, auxquelles ils ressemblent morphologiquement et par la constitution de son contenu et de son tegument.

“ Classifier cet animal et lui donner un nomme serait risquer de faire double emploi et premature tant que les phases de sa développement, près ou loin des *Ophryodendron* n'auront pu être suivies.”

Robin was not able to see either the ciliated embryos or the nematocysts, and, although he gives accurate drawings and description of the proboscidiform individual, he concludes that even the proboscidiform individual cannot be regarded as an Acinetarian because the tentacles “ n'ont aucun des caractères des rayons ou scoirs des acinètes ” (p. 536).

Saville Kent, in his monograph of the Infusoria, published in 1882, agrees with Fraipont that “ the non-proboscidiform or vermiform zooids must be regarded as the larval or transitional condition of the fully developed zooids provided with

their characteristic probosces. . . . Although the further development of the vermiform into the proboscidiform zooids has not so far been determined, it is clear that little beyond the everting of the neck-like anterior region of the former is requisite to bring about such a result."

As regards the process of feeding, Saville Kent put forward a somewhat novel view (p. 850):—"No evidence has, however, yet been adduced showing that these filaments or the extensile proboscis itself possesses a similar suctorial capacity, nor indeed is it known in what manner the animal grasps or incepts its food. Pending the satisfactory elucidation of this most important point, it seems most reasonable to premise that food substances are seized by the brush-like filamentous tuft or distal end of the proboscis itself, and then withdrawn with it into the parenchyma of the body."

As regards the ciliate embryos and the nematocysts, Saville Kent seems to have made no original observations; but he describes the latter as "navicula-shaped bodies" which "are apparently of an adventitious nature."

Gruber, in his account of the Protozoa of the Harbour of Genoa (1884), described a new species—*Acineta* (*Ophryodendron*) *trinacria*—attached to a copepod. He puts forward no theory as to the relations between the vermiform and proboscidiform individuals, but notes the absence of nematocysts. This form is shortly described under the name of *Acineta trinacria* by Daday, who found it on a copepod, *Tisbe furcata*, in the Bay of Naples, and he again apparently regards the vermiform individuals as developmental stages of the proboscidiform individual, although he does not bring forward any evidence to support this view.

In 1886 Milne published a short paper in the 'Proceedings of the Glasgow Philosophical Society' on *Ophryodendron trinacria*, which he described as the type of a new genus, *Stylostoma Forrestii*. The paper is of very unequal value, since he regards the macronucleus as an ovary which can be fertilised by fragments of Nucleoli; but there is one

valuable observation showing that *Ophryodendron trinacria* feeds upon free swimming ciliate infusoria.

He considers the vermiform zooids "to be immature and midway between the ciliated embryo and the adult arm-bearing form," but cannot bring forward any proof of this theory.

In 1889 Bütschli gave an excellent summary of the earlier literature in his account of the Protozoa in Bronn's 'Thierreich'; he had apparently no opportunity of examining the animal himself, but after a careful account of the conjugation theory of Koch, and the parasitic theories of Strehl and Wright and Robin, finally accepts Hincks' theory of dimorphism as an explanation of the relations between the vermiform and proboscidiform individuals.

On p. 1916 he says: "Es scheint mir aber keine Bedingung der Knospungshypothese zu sein, dass die Form B (vermiform individual), in A (proboscidiform individual) übergehe, vielmehr deutet wohl alles darauf hin, dass es sich um zweierlei dimorphe Individuen handelt. Bedenklich macht mich namentlich auch die Erfahrung, dass bei den übrigen Suctorien, wie gesagt, die geschlechtlichen Verjüngungsprocesse partielle Conjugationen sind, während es sich hier entschieden um einfache Copulation handelte, wenn Koch's Deutung richtig wäre. . . ."

"Gegen die Knospungslehre spricht namentlich, dass bei ihrer Annahme zweierlei wesentlich verschiedene Fortpflanzungsvorgänge bei *Ophryodendron* vorkämen, wofür keine andere Suctorie sichere Analogien bietet. Doch ist auch dieser Umstand nicht so gewichtig, da ja *Ophryodendron* auch die einzige Gattung mit dimorphen Individuen ist. Ohne Analogie wäre es ferner, dass die freien Knospen nicht in den Schwärmerzustand übergingen.

"Doch spinnen wir diese, bei der Unvollständigkeit der Beobachtungen doch resultatlosen Erwägungen nicht weiter aus. Hätte sich einer der Beobachter bemüht die angeblichen Knospen längere Zeit fortdauernd zu verfolgen, so wäre wohl

die langathmige Erörterung unnöthig geworden. Hoffentlich wird dieses bald nachgeholt."

Sand, in his 'Étude Monographique sur le Groupe des Infusoires Tentaculifères,' published in 1901, returns to Claparède and Lachmann's original view. On p. 76 he states:—"Nous croyons tout simplement qu'il n'y a pas plus de différence entre un Proboscidiien et un Lagèníforme qu'entre un Dendrocometes dont les bras sont étalés et un Dendrocometes qui les a retractés. Souvent il est vrai la forme extérieure des deux variétés d'Ophryodendron n'est pas identique mais ce caractère n'est pas constant: nous avons vu des Lagèníformes identiques à des Proboscidiens et des Proboscidiens analogues à des Lagèníformes."

He did not succeed in watching the ciliate embryos or the animal feeding, but he states (p. 35): "D'après nos observations, les corpuscules naviculaires d'Ophryodendron belgicum sont identiques, comme dimensions et comme aspect aux granulations de l'ectosarc des Hydroïdes sur lesquels les Ophryodendron sont fixés."

To his further observations, especially those dealing with the structure of the vermiform individual, with most of which I can find no point of agreement, it will be necessary to return in the special part.

3. MATERIALS AND METHODS.

It will now be necessary to give my own observations on Ophryodendron, most of which were, to a large extent, controlled by work on the living animal. Most of the work was done on Ophryodendron abietinum (Claparède and Lachmann) which was found growing on Clytia during the months of July and August at Plymouth, and on Obelia during the months of October, November, and December at Millport in a particularly mild winter.

I should like to thank the staff at both these laboratories for the readiness with which they assisted me in obtaining material, and for the facilities they gave me for working it

through. I have also examined *Ophryodendron trinacria*, which I found on a copepod (*Tisbe*) at Naples, and I am indebted to Mr. Grosvenor, of New College, Oxford, for some preparations of *Ophryodendron multicapitatum* from an *Idotea* found at Plymouth, with some notes on the living animal.

The *Ophryodendron* were usually fixed with Flemming, which was washed out by H_2O_2 in 70 per cent. alcohol, or in corrosive acetic. The whole preparations were stained either with alum carmine or by borax carmine, followed in some cases, according to Hertwig's method, by picric acid. The last method was the only one by which the nematocysts could readily be demonstrated in whole preparations.

The sections were stained with hæmatoxylin followed by eosin to show the structure of the proboscis and the nematocysts.

General.

For convenience sake I have decided to divide my observations under the following headings :

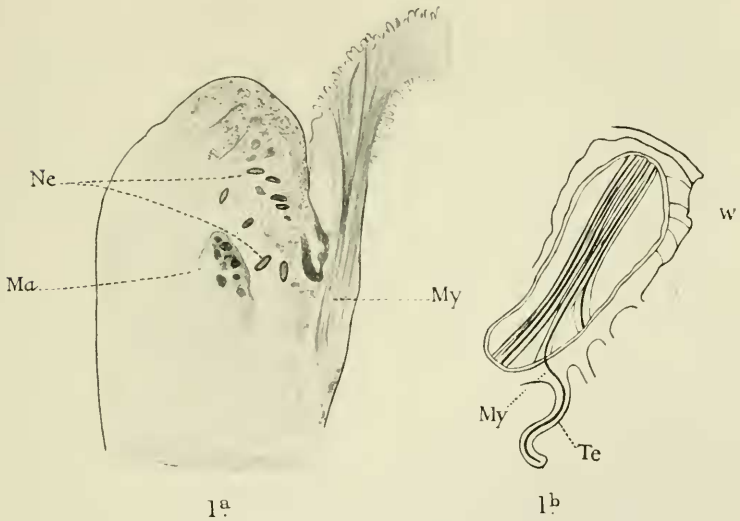
- (4) The structure of the probosciform individual.
- (5) The structure of the vermiform individual.
- (6) The feeding of the *Ophryodendron*, with notes on nematocysts in some other protozoa.
- (7) The external budding of *Ophryodendron*.
- (8) The ciliated buds.

In the following pages, unless definite reference is made to another species, the observations deal with *Ophryodendron abietinum* (Clap. and Lach).

4. THE STRUCTURE OF THE PROBOSCIFORM INDIVIDUAL.

The Probosciform individual of *Ophryodendron abietinum* is roughly pyriform in shape, the basal portion of the animal in the neighbourhood of its attachment being small (Pl. 15, fig. 6). In a section at right angles to the longest axis of the animal it will be seen that the animal is much

flattened in a direction at right angles to that in which the attachment of the proboscis lies, and it is probable that the proboscis arises from the surface which is ventral in the ciliate embryo. The base of the animal is directly attached to the supporting hydroid, as may be readily seen in longitudinal sections.



TEXT-FIGURE 1 *a*.—Part of a longitudinal section of a Proboscidian individual of *Ophryodendron abietinum*, to show the origin of the proboscis.

1 *b*.—Part of a longitudinal section of the distal portion of a proboscis to show the relations of the tentacles to the proboscis.

Ma. Macronucleus. *My*. Myonemata. *Ne*. Nematocysts.
Te. Tentacles. *W*. Wall of proboscis.

The proboscis takes its origin rather low down on one surface of the animal (text-fig. 1*a*), and passes forward between two lateral thickenings which I shall term the apical lobes. It is from these apical lobes that the vermiform buds take their origin. During life the proboscis is in constant motion, expanding and contracting rapidly. In an ordinary Proboscidian individual the proboscis in the contracted condition measures about 66μ , but when fully expanded

it can attain a length of over $332\ \mu$. In the contracted condition the outer wall of the proboscis is thrown into a series of wrinkled folds, and as a rule only the tentacles at the anterior end are visible; but when the proboscis is fully expanded these folds disappear, and the proboscis then is seen as a long ribbon-shaped structure with a row of tentacles on either side down the greater part of its length.

As a rule even in the expanded proboscis only the apical tentacles are fully expanded, but a series of short knobs can be seen down the rest of the proboscis with the exception of a short basal portion indicating the positions of the retracted proximal tentacles (Pl. 15, figs. 1 and 2). As the proboscis moves backwards and forwards, the apical tentacles move also, actively to and fro, so that the anterior end of a contracting or expanding proboscis looks rather like a portion of an active centipede.

In sections of the proboscis each tentacle is found to pass as a continuous tube down the whole length of the proboscis (text-fig. 1*a*). Near the origin of the proboscis a large number of bands, which stain very lightly in eosin, arise. A single band passes up each tentacle tube in the proboscis, and is probably instrumental in the shortening of the tentacles and the proboscis (text-fig. 1*b*). These bands seem analogous to the myonemes of the stalk of a Vorticellid, and similar structures can be found in sections of the tentacles of other acinetaria, e. g. *Ephelota*.

The investigation of the nuclei is rendered very difficult in fully grown forms by the presence of numerous masses of chromatin, the so-called Tinctin-körper in the cytoplasm. The origin of these masses from the nuclei of the cells ingested during the process of feeding will be dealt with in a later section. In a young proboscidiform individual the macronucleus is a rod-shaped structure lying parallel to the animal's long axis, in the later stages of growth it generally becomes more or less T-shaped, the two branches passing up into the apical lobes.

In the young individuals a single micronucleus can always

be found lying near the distal end of the macronucleus. In section the macronucleus of both the proboscidiform and the vermiform individuals is found to possess a distinct membrane. In sections of material fixed in both Flemming and corrosive acetic the chromatin in the resting nucleus is massed in a number of minute granules, an arrangement which seems quite different from that in any acinetarian I have hitherto examined.

In well-fed individuals the vacuolar cytoplasm is completely blocked with nematocysts, the origin of which will be described in the section on feeding.

In *Ophryodendron sertulariæ* the body is more or less disc-shaped, with a marked flattening on its lower surface (text-figure 6a). The proboscis takes its origin from the lower surface of the animal, and bends upwards to end freely in the bunch of tentacles. This is by far the most common of all the species of *Ophryodendron*, but its extremely flattened form, coupled with the fact that it usually lies closely applied to the theca of a sertularian in such a way that only the edge of the animal is presented to the observer, render it an exceedingly unsatisfactory object for detailed work.

I have only had one opportunity of examining *Ophryodendron trinacria* in a living condition.

The proboscidiform individual is more cylindrical than the proboscidiform individual of *Ophryodendron abietinum*, and the three proboscides arise near the distal end. The proboscis does not show any trace of the wrinkling which is so characteristic of the contracted proboscis of the other species of *Ophryodendron*, and, in fact, seems to approach far more closely a simple apical prolongation bearing tentacles such as is found in some species of *Acineta*. The tentacles are rather long, few in number, and distinctly knobbed. There is a short hollow stalk, of quite a different structure to the solid rod-like stalk which will be described in the section on the vermiform individual.

I have never seen *Ophryodendron multicapitatum* in

the living condition, but in stained preparations the numerous proboscides seemed to resemble the proboscis of *O. sertulariæ*.

5. STRUCTURE OF THE VERMIFORM INDIVIDUAL.

The fully grown vermiform individual of *Ophryodendron abietinum* is roughly cylindrical in shape, tapering somewhat towards the free distal end. The stalk is a solid rod, attached at its basal end by a slight thickening to the hydrotheca of the hydroid, and passing in the opposite direction to end in a sharp point buried in the cytoplasm of the *Ophryodendron*. During life the animal is in almost constant motion, swinging in various directions on its stalk.

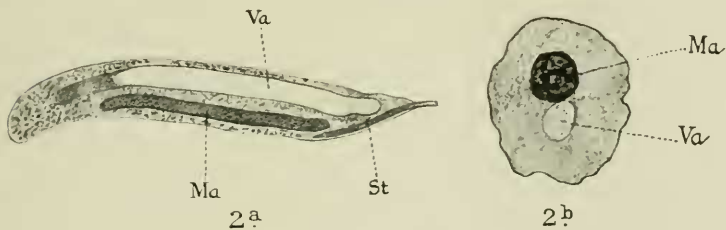
It is extremely difficult to make out the structure of the anterior end, the shape of which in the living animal is constantly changing. At one time the anterior end will show a distinct thin lip surrounding a large cavity, a little later this lip may be rolled back over the free surface of the animal, then the whole apical end may become swollen and the lip disappear.

That this lip can actually exert a powerful sucking action is shown by some observations on vermiform individuals which were still attached by their basal end to their proboscidiform parents. Under these conditions the vermiform individual would frequently attach its anterior end to the stalk of the hydroid and pull its parent over to one side. If the anterior end of the vermiform individual is carefully examined, a slender tube is found opening to the surface in the centre of the depression, and at the other end into a long vacuole, which in sections is seen to pass almost to the proximal end of the animal (text-fig. 2).

It is possibly worth noting that the first sign of disintegration in a living proboscidiform individual is furnished by the appearance of drops of cytoplasm at the end of the tentacles, whereas in the vermiform individual a similar

drop makes its appearance on the free apical surface. The cytoplasm of the vermiform individual may be crowded with the nematocysts and "Tinctin-körper" which have been previously mentioned in the account of the proboscoidiform individual. The macronucleus is usually a more or less dumbbell-shaped structure lying generally rather to one side in the posterior half of the animal.

The vermiform individuals of *Ophryodendron sertulariæ* and *Ophryodendron multicapitatum* (vide Saville Kent, p. 855) closely resemble in shape and move-



TEXT-FIGURE 2 *a*.—Oblique longitudinal section through the basal portion of a vermiform individual of *Ophryodendron abietinum*, showing the stalk (*St*), macronucleus (*Ma*), and long vacuole (*Va*). (2 Searcher, comp. oc.+2 mm. apochromat.)

2 *b*.—Transverse section through a vermiform individual, showing macronucleus (*Ma*), and vacuole (*Va*). (6 comp. oc.+2 mm. apochromat.)

ments the vermiform individuals of *Ophryodendron abietinum*, from which the vermiform individual of *O. sertulariæ* only differs in the fact that the internal end of the stalk may end in short hooks (vide Robin).

The vermiform individual of *Ophryodendron trinacria* seems, however, in the case of the few individuals which I examined, to possess a rather peculiar method of movement, by which the animal becomes contracted into a short spiral, and then slowly elongated again.

There is one curious feature in Milne's account of the vermiform individual of *O. trinacria*, the presence of a series of "setæ or cilia" at the anterior end of the vermi-

form individual. In one of Milne's figures, three of these structures are shown, and in another eight, but on the only occasion on which I examined a living *Ophryodendron trinacria* I saw no trace of these structures.

It is now necessary to refer to a rather remarkable statement by Sand that the vermiform individual of *Ophryodendron belgicum* is attached, not by a rod-like stalk but by a tentacle (p. 336). "Le pedicule du Lagéniforme est chez cette espèce un tentacule ordinaire capité, analogue à celui d'un suceur quelconque." This species was first found by Fraipont and it is rather remarkable that no mention is made in his long account of *Ophryodendron* of this remarkable structure.

Saville Kent remarks (p. 853) that "apart from its size (*Ophryodendron abietinum*, P. 1.75"—1.30". V. 1.50" to 1.30". *O. belgicum*, P. 1.400". V. 1.400") and habitat (*O. belgicum* is described as occurring on *Clytia volubilis*) the chief distinction between this type and *O. abietinum* would seem to subsist in the less luxuriant development of the tentacular appendages of the proboscis."

Bütschli also believed that the species *Ophryodendron belgicum* was identical with *Ophryodendron abietinum*. I myself worked partly on a form occurring on *Clytia* and partly on a form occurring on *Obelia*, and could find no essential difference between them and until further evidence is adduced than Sand's Pl. 13, fig. 9, it would seem impossible to credit this very abnormal state of affairs, especially as the structure figured looks far more like a stalk than a tentacle.

6. THE FEEDING OF OPHRYODENDRON.

Ophryodendron abietinum is to a very large extent a true external parasite of the hydroid to which it is attached, as will be shown by the observations on the living animal detailed below. I have, however, on two occasions, seen it

attack and suck small ciliate infusorians, the tentacles of the proboscis behaving in the same way as the ordinary acinetan tentacle.

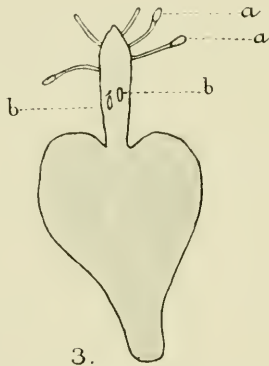
It is probable that the food of the species of *Ophryodendron* which live upon crustacea is derived entirely from ciliate protozoa in this way, as has been shown by Milne (loc. cit.). *Ophryodendron sertulariæ*, in its method of feeding would seem to resemble *Ophryodendron abietinum*, though it is probable that it is not so exclusively parasitic in its diet as *Ophryodendron abietinum*.

I found *Ophryodendron sertulariæ* growing on *Sertularia pumila* in 30 fathoms at Plymouth in July crowded with the nematocysts of *Sertularia*, and the nematocysts were very common in *Ophryodendron sertulariæ* collected from the shore at Millport in November. On the other hand, there were very few nematocysts in some *Ophryodendron* of the same species collected from the shore at Plymouth in July.

On examining fixed preparations of *Ophryodendron abietinum* by far the greater number of individuals is found grouped around the opening of the hydrotheca of the hydroid, but a few are found scattered over the main stem. In the case of the latter, it is at first sight rather difficult to believe that the tentacles of the *Ophryodendron* can reach the ectoderm of the hydroid, but it must be remembered that the tentacles of the hydroid in the living condition are usually held back well over the base of the hydrotheca, and that the proboscis which in the living resting form of *Ophryodendron* measured about $66\ \mu$ in length, when expanded measured $332\ \mu$.

In an *Ophryodendron abietinum* which was drawn while feeding, it was noticed that the tentacles of the *Ophryodendron* were wrapped around the tentacles of the hydroid. After a short time the proboscis of the *Ophryodendron* was retracted, and the nematoblasts with their contained nematocysts could be seen sticking for some time in the aperture of the tentacles, giving the tentacles a curious knobbed appearance. It is this appearance that is possibly responsible for the figures of knobbed tentacles in *Ophryodendron*.

The nematoblasts could now be seen passing down the proboscis into the body of the animal with a peculiar gliding motion. In the course of this passage the long axis of the nematocyst was always parallel to the long axis of the proboscis; and when the nematoblasts passed simultaneously down the proboscis they followed parallel paths, thus indicating a feature that has already been described in the sections of the proboscis, the prolongation of the tentacles as separate



TEXT-FIGURE 3.—Living feeding Proboscidiform individual with contracted proboscis, only a few of the tentacles are shown. *a.* Nematoblasts still fixed in the aperture of the tentacles. *b.* Nematoblasts passing down the proboscis.

tubes down the proboscis. The first stage in feeding is shown in Pl. 15, figs. 1 and 2, in which one nematoblast has been pulled out of its position in the ectoderm of the hydroid, the later stage is shown in a drawing from a living specimen, text-fig. 3, and from a stained preparation, Pl. 15, fig. 3. It would seem that the size of the nematoblasts prevents their passage down the tentacles as long as the proboscis is in its fully extended condition.

After passing down the proboscis the ingested ectodermal cells may be found (Pl. 15, fig. 3) lying in the cytoplasm of the Ophryodendron, and in some cases the whole body is absolutely blocked by them. The cytoplasm of these cells seems to undergo fairly rapid digestion, but the nucleus is far

more resistant; in early stages the nucleus retains its characteristic shield-shape and vacuolar appearance, but under the influence of the digestive enzyme its structure breaks down, and finally the only trace left of it is a number of dots of darkly-staining matter lying in small vacuoles dotted through the cytoplasm of the animal. (The characteristic Tinctin-körper of the Acinetaria.)

There seems to me a strong probability that the so-called chromidia of many protozoa may possess a similar origin from the remains of the nuclei of their prey, and I believe that a really careful study of this process of digestion of a typical metazoan nucleus in the cell-body of a protozoan might have a salutary influence on some of the extreme upholders of the chromidial hypothesis.

The nematocysts which remain after the nematoblast itself has been completely digested can readily be seen in the living animals, and can, by crushing the Ophryodendron, be readily exploded. In whole preparations stained with carmine and picric acid, and in sections stained with hæmatoxylin followed by eosin, the nematocysts are easily seen. In some cases the whole cytoplasm of the Ophryodendron is absolutely blocked with them (text-fig. 1), and it is noticeable in such cases that the embryonic mass cut off in the formation of the ciliated embryos, which will be described later, is relatively far freer from nematocysts than the remaining husk of the parent individual.

Whether the adult Ophryodendron has any means of ridding itself of these structures must remain an open question, but on one occasion I found a proboscidiform individual which had thrown off a mass of cytoplasm containing an enormous number of nematocysts which had exploded on contact with water. This individual seemed perfectly healthy next morning, so that it is possible that the process is a normal one. This is the only occasion on which I have found a free Ophryodendron with exploded nematocysts.

It is thus clear that the nematocysts of Ophryodendron are derived from its host, and this explains the fact that

nematocysts have never been found in the other species of *Ophryodendron* which live upon Crustacea.

The case of the nematocysts of *Ophryodendron* is, of course, paralleled by that of the nematocysts of *Æolids*, as has been shown by Grosvenor, and by that of the nematocysts of *Turbellaria*. I have had an opportunity of observing two analogous cases amongst *Infusoria* :—

(1.) In some *Kerona* which were found on a rather morbid *Hydra* at Glasgow, the three characteristic *Hydra* nematocysts were present.

(2.) During a stay at Naples I found that a holotrichous infusorian on *Endendrium*, which seemed to agree in all essentials with the *Holostoma* described by Entz (*loc. cit.*), was full of the two very characteristic nematocysts of the hydroid in an unexploded condition.

It is far more difficult to arrive at a clear conception of the process of feeding by direct observation in the case of the vermiform individual. During life the vermiform individual is in constant swaying motion on its stalk, touching with its anterior extremity all objects within reach. That the anterior end of the vermiform individual possesses considerable power of suction is shown by the fact that an external vermiform bud which has not yet become completely detached from the parent probosciform individual, can often be seen applying its anterior end to the stalk of the hydroid, and pulling its parent right over. At the same time, nematocysts are always found in the vermiform individual, and in fixed preparations I have found cases in which a vermiform individual had its anterior end closely applied to the ectoderm of a hydroid, whilst the nuclei of freshly ingested ectodermal cells were to be seen in its cytoplasm.

7. THE EXTERNAL BUDDING OF OPHRYODENDRON.

In following the external budding of *Ophryodendron* on the living animal, as far as my experience goes it is essential that the *Ophryodendron* should be kept in a fairly deep

watch-glass, and not under a coverslip. In a typical case a short piece of hydroid was placed in a flat-bottomed watch-glass at 5 p.m. on Saturday, and the positions and appearance of all the *Ophryodendron* on it were carefully noted. The proboscidiform individual showed the commencement of the formation of a vermiform bud. On Sunday morning the vermiform bud was fully grown, but was still in direct continuity with the proboscidiform. At 5 p.m. on Sunday the vermiform bud was active, and was almost free, and at 5.30 p.m. it was quite free and attached to the hydroid stem.

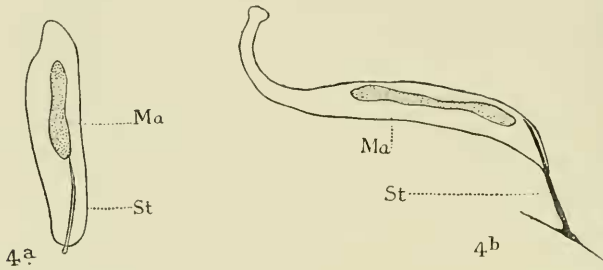
The young, free vermiform individual can travel considerable distances in a leech-like fashion, using its ends as suckers. The observations were repeated on other individuals with the same result. The internal details of this process of budding are shown in Pl. 15, figs. 4 and 5.

In Pl. 15, fig. 4, a proboscidiform individual is shown, in which the right apical lobe is prolonged, indicating the first stage in the formation of an external vermiform bud; on the left side there is a fully developed vermiform bud, which has not yet become free.

In section it is easy to see that the bud is formed as a hollow outgrowth, a fact which explains the rapidity of the early stages in its development, as well as the enormous apparent disparity in mass which is sometimes seen between the bud and its proboscidiform parent.

In Pl. 15, fig. 5, the last stage in the division of the macronucleus between the proboscidiform and the vermiform bud is shown. At this stage the vermiform individual is always much swollen at its apical end, and it is only later that the vermiform individual becomes elongated, and a distinct lip is developed round the anterior end. The young vermiform bud now becomes active, and finally pulls itself away from the parent individual. At this stage the vermiform individual creeps up the stem of the hydroid, finally becoming attached by its posterior end and developing its characteristic rod-like stalk. At first the stalk is quite short, and the greater length is hidden in the posterior end of the animal

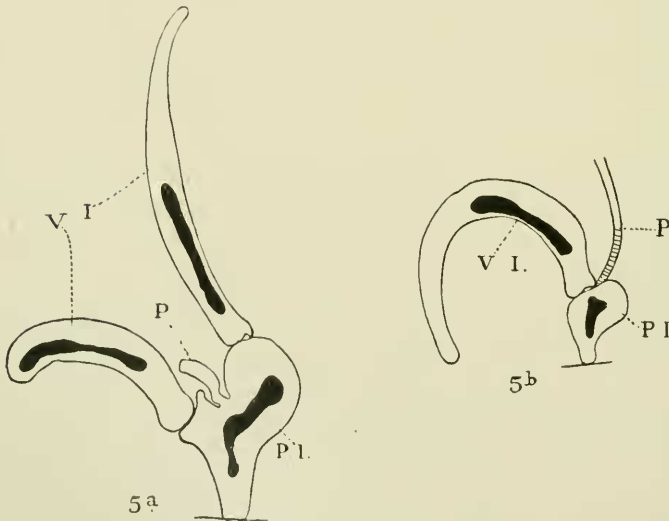
(text-fig. 4*a*), but later it elongates and assumes the appearance characteristic of the adult individual. I do not know whether the adult vermiform individual can leave its stalk



TEXT-FIGURE 4.—Vermiform individuals of *Ophryodendron abietinum*.

4 *a*.—Showing development of the rod-like stalk (*St*).

4 *b*.—With fully developed stalk. *Ma*, Macronucleus. (2 Searcher, comp. oc. + 2 mm., apochromat.).



TEXT-FIGURE 5 *a*.—A large Probosciform individual with a late Vermiform bud on the right side, and an earlier Vermiform bud on the left.

5 *b*.—A small Probosciform individual with a late Vermiform bud on the left side.

P, Proboscis. *P.I.*, Probosciform individual. *V.I.*, Vermiform bud. (± comp. oc. + 4 mm. apochromat.).

and wander to a fresh position, but the bare stalks of the vermiform individual are often found attached to the hydroid.

Fraipont and Sand's view that the vermiform individual can develop into a proboscidiform individual will be examined in the concluding section, but it may be well to state here that I have never been able, either in continuous observations on the living animal or in fixed preparations to find the slightest evidence for this transformation.

There is one interesting fact as regards the budding of the vermiform individual which I think points clearly to the conclusion that the vermiform individual is a distinct dimorphic individual. The size of the proboscidiform individual is very variable, whereas that of the budded vermiform individual is singularly constant even in those cases in which the parent proboscidiform individual is quite small (see text-fig. 5).

This absence of correlation between the size of the parent proboscidiform and that of the attached vermiform bud is shown in the following table¹:

	Proboscidiform individual.		Vermiform bud.	
	Greatest length of the body, excluding the proboscis.	Greatest breadth.	Greatest length.	Greatest breadth.
Small Proboscidiform	34	20	138	11
Medium Proboscidiform	48	33	142	23
Large Proboscidiform	92	46	184	13

These figures do not really express the difference in mass between the two individuals since the vermiform individual is cylindrical, and its width is more or less uniform throughout the greater part of the animal's length, whereas in the proboscidiform individual, owing to its pyriform shape, the greatest width is far greater than the mean width.

¹ Measurements in μ .

The only method of reproduction I have found in the vermiform individual is by the formation of internal ciliated buds, which will be described later (Pl. 15, fig. 10).

Hineks puts forward the possibility of the vermiform individual giving rise to other vermiform individuals, but the single preparation on which this interpretation is based is not convincing, and I have never been able to see anything of the kind in any of the vermiform individuals I have examined.

8. THE CILIATE EMBRYOS.

It is rather remarkable that the only observations on the free ciliated embryo are due to the earliest workers on this form—Claparède and Lachmann and Strethill Wright. In both these cases, however, the embryos were released by an operation, and it is to this fact that Claparède and Lachmann's statement that the embryos in *Ophryodendron* are of two sizes is probably due, since the large ciliated embryos divide in the broad pouch to give rise to the normal small free embryos (Pl. 15, fig. 7). Ciliate embryos are formed both in the proboscidiform and the vermiform individuals of *Ophryodendron abietinum*. I have only seen the ciliated embryos of the proboscidiform individual actually escape on five occasions, although, especially at Plymouth, I wasted much time in watching for it. This was partly due to the fact that a considerable period, over twelve hours, during which the embryos divide, intervenes between the time at which the cilia of the embryos in the brood pouch become active and the final escape of the embryos, and partly possibly to the evil effect of the coverslip. Probably the best method would be to keep the *Ophryodendron* in a watch-glass, but here the extremely small size of the embryos would present a great difficulty, though it is possible that this might be partly obviated by the use of a water immersion objective.

The first sign of the formation of the ciliate embryo is the rounding off of a central block of protoplasm (Pl. 15, fig. 6),

the embryonic mass which contains the greater part of the nucleus of the parent. This embryonic mass gives rise to usually about six to eight oval blocks measuring about $46\ \mu$ long, by about $14\ \mu$ wide, which develop cilia and swim actively about in the brood pouch.

A rather small proboscidiform individual was found to contain six large active ciliate embryos at 5.45 p.m., and at 8.35 p.m. one of these measuring $46\ \mu$ long was seen to show signs of a division, which was complete by 10 p.m., the two products of the division measuring $24\ \mu$ long. By the next morning all the embryos in the brood pouch had divided.

Just before the ciliate embryos escape, they exhibit paroxysms of activity, during which they swim over and over each other in the brood pouch, these periods of intense activity being interspersed by long rests, during which the cilia beat very languidly.

In the case of a small proboscidiform individual, of which the six embryos were very active at 3.30 p.m., they broke through at 5 p.m., measuring $28\ \mu$ long by $14\ \mu$ by $10\ \mu$. On the other hand, a large proboscidiform individual, seen at 4 p.m. to contain a large number—over 30—of active embryos which escaped at 4.50 p.m., and which measured $20\ \mu$ by $10\ \mu$ in the stained preparation. These embryos were fixed at once, and one of them is figured (Pl. 15, fig. 11).

The embryos seemed always to escape from a lateral opening not far from the animal's point of fixation. Nearly all the cytoplasm and nuclei is used up in the formation of the embryonic masses, and in most cases in which an individual contained a large number of embryos, the parent, after the escape of the embryos, is left a mere shell which soon perishes. The free embryos are more or less oval animals with a decidedly flattened ciliated ventral surface, and a convex dorsal surface. On the animal's left side there seems to be a flap overhanging the ventral surface. In the ventral region there are large vacuoles which often contain nematocysts, and there is a single small contractile vacuole. They move in a curious hesitating manner with the narrow end

forward, far more slowly than the ciliate embryos of *Acineta papillifera*, halting at intervals on their posterior end to make a half left turn. In the case of some embryos which were seen to escape at 5 p.m., they were almost stationary at 6.35 p.m., and were fixed at 7 p.m.

The embryos attach themselves by their posterior end, and the proboscis makes its appearance as a projection on the anterior ventral surface.

Claparède and Lachmann's drawings (11, *a* and *b*), seem to show very faithfully the appearance of the free living ciliate embryo; (*a*) being a ventral view, and (*b*) a lateral one.

I have never succeeded in observing the escape of the ciliate embryo from the vermiform individual, though I have often seen the cilia slowly beating in the large earlier embryo, and on one occasion I saw six small embryos in very active motion in a vermiform individual. The shape and size of the ciliated embryo in the latter case coincided with those of the normal free embryos developed from a proboscidiform individual. There appears to be, however, a constant difference between the number of ciliated embryos in the vermiform and the proboscidiform individuals; in the former I have never seen more than six embryos, whereas in the large individuals of the latter the number may be great—over 30 (Pl. 15, fig. 10).

I believe that the embryos of both the proboscidiform and the vermiform individuals always gives rise on fixation to young proboscidiform individuals, since while small proboscidiform individuals of about the same bulk as the ciliate embryo are often met with (Pl. 15, fig. 12), the smallest vermiform individual I have seen with a well-developed stalk measured $115\ \mu$ long by $18\ \mu$ at its widest point.

RESULTS OF EARLIER WORKERS.

The chief conclusions of the earlier workers can be summarised in tabular form :—

	Relations between Proboscidiform and Vermiform Individuals.	Ciliate Embryo.	Nematocysts.
Claparède et Lachmann, 1855 (<i>O. abietinum</i>)	P. is identical with V. (the proboscis being retracted)	Saw two kinds	Trichocysts.
Strethill Wright, 1861 (<i>O. sertulariæ</i>)	(a) V. is a Protozoan parasite. (b) P. buds V.	Saw one kind	No mention.
Hincks, 1873 (<i>O. pedicellatum</i>)	P. buds V.; also V. buds V.	Not seen	Not seen.
Koch, 1876 (<i>O. pedunculatum</i> = <i>pedicellatum</i> Hincks)	Contact between V. and P., a process of copulation resulting in formation of ciliate	Not seen, but presumed to give rise to P. and V.	No mention.
Fraipont, 1877 (<i>O. abietinum</i>)	V. is a developing P.	Not seen	Trichocysts.
Robin, 1879	P. not a true acinetarian. V. a parasitic worm	„	Not seen.
Kent, 1882	Agrees with Fraipont	„	Possibly external origin.
Sand, 1901	Agrees with Fraipont	„	„

9. CONCLUSIONS.

Ophryodendron abietinum is to a large extent a true external parasite on its supporting hydroid, and the nematocysts which it contains are derived from its host on which it preys. In some cases I have seen the proboscidiform individual attack and suck small ciliates, and it is probable that the species of *Ophryodendron* which are attached to Crustacea obtain their nourishment entirely in this way.

The study of the nuclei is much obscured by the presence

in the animal of masses of chromatin (Tinetin-körper) derived from the nuclei of the ingested nematoblasts, but in the ciliated embryos and in the young fixed proboscidiform individuals there is always to be found a minute sphere of chromatin surrounded by a clear area which, from its position and behaviour, must be regarded as a micronucleus.

It will now be necessary to examine the theories of the earlier workers as to the relation between the two individuals of *Ophryodendron* in the light of the observations detailed above.

(1) The conjugation hypothesis of von Koch.

(2) The parasitic theory of Strethill Wright and Robin.

(3) The developmental theory of Claparède and Lachmann, Fraipont, and Sand.

(4) The dimorphic theory of Hincks and Bütschli.

(1) The Conjugation Theory of von Koch.—Von Koch, as has already been shown in the historical introduction, put forward the view that the various stages of the connection between the vermiform and the proboscidiform individual are not to be regarded as stages of budding, but rather in the inverse order as stages in a conjugation which results in the complete fusion of the copulating individuals. This theory is excluded by the observations above made upon living forms in which it has been found that the vermiform individual is actually budded off from the proboscidiform, the whole process from the first appearance of the bud to the setting free of the vermiform individual having been observed to occupy about twenty-four hours.

(2) The Parasitic Theory of Strethill Wright and Robin.—It is interesting to note that both the upholders of this view were working on the species of *Ophryodendron sertulariæ*, in which the vermiform and proboscidiform individuals are so different in appearance that it is almost impossible to imagine transitional stages between them; and the very fact that this theory has been put forward must, I think, be regarded as an indication that Claparède and Lachmann's view of the identity of the two individuals is, to say the least of it, strained.

Robin's belief that the vermiform individual is a young nematode, is of course quite untenable, and Strethill Wright's view that the vermiform individual is a parasite protozoan is contradicted by:—

- (a) The fact that the nucleus of the vermiform is during the process of budding in continuity with the nucleus of the probosciform individual.
- (b) The identity of the ciliate embryos in the two forms.
- (3) The Developmental Theory.—This theory must be examined from two points of view:—

- (a) From that of the original belief of Claparède and Lachmann, that the vermiform individual possessed a retracted proboscis and was identical with the probosciform individual.
- (b) From that of its later development in the hands of Fraipont and Sand according to which the vermiform individual must be regarded as a developmental stage of the probosciform individual, this development consisting in a change in shape, the resorption of the characteristic rod-like stalk, and the formation of the proboscis.

(A) Claparède and Lachmann's view is, I think, explained by the fact that in morbid vermiform individuals which have been kept some time under a coverslip, the cytoplasm towards the anterior end can contract away from the pellicule to fill the central cavity, and thus give the appearance of a dark central mass which might be taken for a retracted proboscis. Their fig. 2, Pl. 5, which is said to represent an "*Ophryodendron abietinum* avec la trompe retractée" is quite clearly a young vermiform individual which has not yet formed its stalk.

(B) There are no observations on the living *Ophryodendron* showing the development of the vermiform individual into the probosciform individual, and though I have frequently observed the same vermiform individual at intervals for periods of over forty-eight hours, I have never been able to see any indication of such a transformation.

The figures on which Fraipont bases this view are quite unconvincing:—Fig. 31, Pl. I, which is said to represent a “Lagèníforme ayant perdu son pédicule et dont la forme du corps se rapproche de celle d’un Proboscídien,” is quite clearly again a young vermiform individual which has not yet developed its stalk, while fig. 10, which is said to represent a “Lagèníforme dont l’extrémité antérieure se différencie en trompe pour passer à la forme Proboscídien,” is probably a proboscídiform individual in a morbid condition in which, as is frequently found, the proboscis is the first portion of the body to break down.

In the case of Sand the evidence is of the same kind, but, as has been shown in the special part, even less satisfactory.

Sand states on p. 200 of his monograph:—“Lorsque la trompe et rétractée l’individu s’appelle lagèníforme, vermiforme ou individu B, il diffère quelquefois des proboscídiens ou individus A. par la forme extérieure. Cependant toutes les transitions ont été observées pour plusieurs espèces.”

The only evidence of this transition which Sand brings forward rests on a single specimen of *Ophryodendron abietinum*, which (p. 206) “a été fixé dans nos préparations au moment où ses 14 tentacules commençaient à proéminer sur un petit cercle du corps.” The specimen is again referred to on p. 74. “Or, sur un exemplaire d’*Ophryodendron belgicum* nous avons pu observer un phénomène, qu’aucun auteur n’a vu jusqu’ici: le premier stade de l’expansion de la trompe (Pl. 14, fig. 2, probably Pl. 16, fig. 2). L’animalcule en question affectait cette forme ovalaire et trapue qui est décrite comme caractéristique des *Ophryodendron belgicum* pourvus d’une trompe. Sur une petite zone circulaire de l’extrémité distale du corps, proéminaient 14 tentacules courts cylindriques, capités en tout semblables à ceux des autres Suceurs.

“Ce petit cercle forme, à n’en pas douter, l’extrémité distale de la trompe lorsque la partie environnante du corps s’étire pour former cet organe.”

The figure is rather a puzzling one, as the tentacles are

represented end on, and it is only safe to say that it certainly does not furnish the required evidence of the transformation of the vermiform into the proboscidian individual.

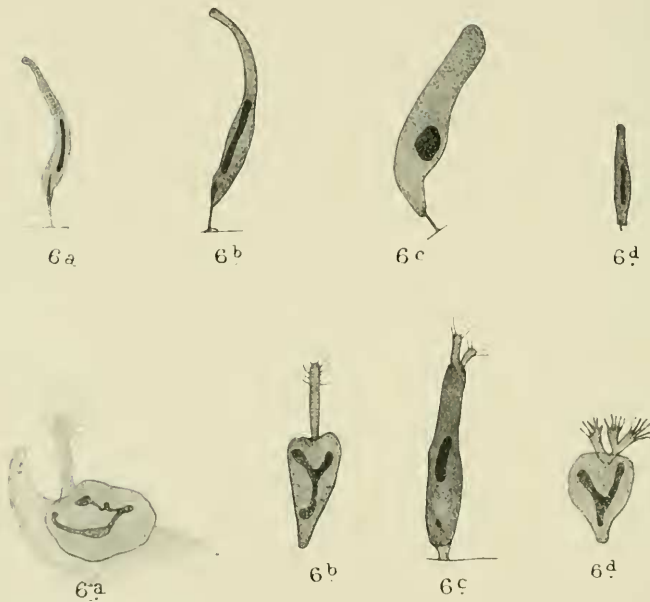
It will thus be seen that there are two main sources of error in attempting the proof of this theory from a mere examination of fixed specimens—(1) The presence of young vermiform individuals which have broken loose from the proboscidian individual, but have not yet developed their stalk; (2) the presence of degenerating proboscidian forms seen in a horizontal plane.

Finally the presence of active ciliated embryos in the vermiform individuals show that they can hardly be regarded as immature forms, and it will be evident, from what has been said above as to the structure of the two individuals, that the change from the vermiform individual to the proboscidian individual would need to be of a far more radical nature than Fraipont and Sand have imagined.

(4) Hincks' Theory of Dimorphism.—Of the various theories put forward to explain the appearance of the two individuals in *Ophryodendron*, I think that the observations given above show clearly that Hincks' theory of dimorphism is alone in accordance with the facts. The proboscidian individual gives rise by a process of external budding to the vermiform individual; both the proboscidian and the vermiform individual can give rise to ciliated buds, which are already ciliated before the process of division is complete. This last fact gives the explanation of the two sizes of ciliated embryo found by Claparède and Lachmann. I have never been able to follow the history of the ciliated buds from the vermiform individual, but from the fact that the smallest free vermiform individual that I have been able to find, after looking over many hundreds, was far larger than the largest free ciliate embryo found, I believe the ciliate embryos of both forms always develop into proboscidian individuals.

From an evolutionary standpoint, it would seem that the dimorphism of *Ophryodendron* presents a case which is

full of difficulties. It has always been assumed that the proboscoidform individual represents more closely the ancestral acinetarian form, and that the vermiform individual is a more recent development. If this point of view is accepted, it is rather remarkable that in the various species of *Ophry-*



TEXT-FIGURE 6.—Diagrams of the Proboscoidform and Vermiform individuals of *Ophryodendron sertulariæ* (A.), *O. abietinum* (B.), *O. trinaeria* (C.), and *O. multicapitatum* (D.), to show the similarity of the Vermiform individuals and the diversity of the Proboscoidform individuals. (2 Searcher, comp. oc. + 4 mm., apochromat.).

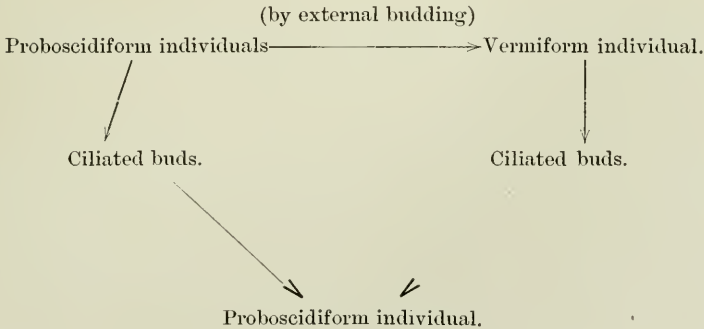
odendron the vermiform individuals are almost indistinguishable in shape, whereas the proboscoidform individuals are absolutely different from one another (text-fig. 6). In this case, apparently, the more primitive proboscoidform individual has undergone far more extensive changes than the more recently developed vermiform individual. It might be suggested that the vermiform individual, once it had been

produced, was in such perfect accordance with the environment, that no further change would be necessary.

It is very difficult to regard this explanation as being in any way adequate when it is remembered how different the environment of a vermiform individual of *Ophryodendron trinacria*, which is attached to a free swimming copepod, must be from that of the vermiform individual of *Ophryodendron abietinum*, which is to a large extent a true external parasite of a hydroid. On the other hand, if the number of embryos of the same type produced by these two forms is to be regarded as some measure of their success in the struggle for existence, there is distinct evidence that the vermiform type cannot be regarded as so successful a form as the proboscidiform type.

Diagram of the life cycle.

The stages actually followed in living specimens are indicated by black arrows. The probable development of the ciliate buds of the vermiform individual is shown by a dotted line.



10. SUMMARY OF RESULTS.

- (1) *Ophryodendron abietinum* is a true ectoparasite of the hydroid to which it is attached, and its contained nematocysts are derived from its host.

This conclusion holds good for *Ophryodendron sertulariæ*.

- (2) *Ophryodendron* is a true dimorphic form, the proboscidiform individual (A) giving rise by a process of external budding to a vermiform individual (B) of quite different structure.
- (3) Both the proboscidiform and the vermiform individual can give rise to ciliate embryos.
- (4) The ciliate embryos of the proboscidiform develop on fixation into young proboscidiform individuals. It is probable that the ciliate embryos of the vermiform individuals also develop into proboscidiform individuals.

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EXPLANATION OF PLATE 15,

Illustrating Mr. C. H. Martin’s “Observations on Acinetaria.”
 Part 3.—“The Dimorphism of Ophryodendron.”

ABBREVIATIONS.

C. e. Ciliate embryo. *E. M.* Embryonic mass. *Ma.* Macronucleus.
Mi. Micronucleus. *Ne.* Nematoblast. *Ob. t.* Obelia tentacle. *Pr.* Proboscis.
Pr. I. Probosciform individual. *Te.* Tentacle. *Ti.* Tinctinkörper. *V. B.* Vermiform bud. *V. I.* Vermiform individual.

PLATE 15.

Ophryodendron abietinum.

FIG. 1.—Diagram showing probosciform with extended proboscis, some of the tentacles being attached to the tentacle of an Obelia. (4 comp. oc. + 4 mm. apochr. Zeiss.)

FIG. 2.—Details of the proboscis shown above; one nematocyst (*Ne.*) has just been dragged out of its position in the ectoderm. (6 comp. oc. + 2 mm. apochr.)

FIG. 3.—Later stage of the feeding of a probosciform individual; the proboscis is now retracted. *Ne.* = nematoblasts at the end of the tentacles. *Ne*¹ = a nematoblast on its way down the proboscis into the cytoplasm. *Ne*², *Ne*³ = stages in the digestion of the nucleus of the nematoblast. (6 comp. oc. + 2 mm. apochr.)

FIG. 4.—Probosciform which has just budded a vermiform individual on one side, and shows the beginning of a second vermiform bud on the other. (2 [Searcher] comp. oc. + 2 mm. apochr.)

FIG. 5.—The last stage in the division of the macronucleus between a proboscidiform and a vermiform bud. (4 comp. oc. + 2 mm. apochr.)

FIG. 6.—Early stage in the development of the ciliated embryos in a proboscidiform individual. The rounding-off of the embryonic mass. The proboscis is not retracted. (2 [Searcher] comp. oc. + 2 mm. apochr.)

FIG. 7.—Two proboscidiform individuals showing the later stages in the development of the ciliated embryos. The proboscides are retracted. (2 [Searcher] comp. oc. + 2 mm. apochr.)

FIG. 8.—Dividing ciliate embryo from the brood-pouch of a proboscidiform individual. (6 comp. oc. + 2 mm. apochr.)

FIG. 9.—Part of the brood-pouch of a proboscidiform individual showing the two stages of the ciliate embryo. (2 [Searcher] comp. oc., + 2 mm. apochr.)

FIG. 10.—A vermiform individual containing ciliate embryos. (2 [Searcher] comp. oc. + 2 mm. apochr.)

FIG. 11.—A free ciliate embryo. (6 comp. oc. + 2 mm. apochr.)

FIG. 12.—A young proboscidiform individual. The whole of the proboscis is not drawn. (6 comp. oc. + 2 mm. apochr.)