VI.—The Morphology and Development of the Free-swimming Sporosacs of the Hydroid Genus *Dicoryne* (including *Heterocordyle*). By J. H. Ashworth, D.Sc., University of Edinburgh, and James Ritchie, M.A., D.Sc., Royal Scottish Museum, Edinburgh.

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[Plates VI–VIII.*]

CONTENTS.

	PAGE		PAGE
Introduction	257	A Discussion of the Homology of the Sporosacs of <i>Dicoryne</i>	271
<i>Dicoryne conybearei</i> , General Description of Colonies	258	Abnormal Sporosacs of <i>Dicoryne conybearei</i>	277
Stolon: Regenerative Capacity of the Stolon	259	Early Developmental Stages of <i>Dicoryne conybearei</i>	278
Hydrocaulus and Hydranth	260	Distinctive Characters of the Species of <i>Dicoryne</i>	280
Blastostyles	261	Specific Characters of <i>Dicoryne conybearei</i> (Allman), emend.	282
Development of the Sporosacs	263	<i>Dicoryne</i> , Allman, char. emend.	282
The Sporosacs of <i>Dicoryne conferta</i>	266	List of Works Quoted	283
Affinities of the Free-swimming Sporosacs of <i>Dicoryne conybearei</i>	269	Description of Figures	284

INTRODUCTION.

Hitherto there has been described only a single species—*Dicoryne conferta* (Alder)—amongst the Hydrozoa in which the reproductive body is a sporosac which becomes ciliated and free-swimming. We have found that another species which, as we shall show (pp. 269–271), must be named *Dicoryne conybearei* gives rise to reproductive bodies of this type, which, however, differ from those of *Dicoryne conferta* in several important respects. The free-swimming type of sporosac has not been the subject of close observation since 1872; we have therefore made as complete a study of the structure and development of the sporosacs, especially of *D. conybearei*, as material gathered from several sources would permit.

The material of *D. conybearei* at our disposal consists of colonies on seven gastropod shells,† dredged off the island of Nisida, in the Bay of Naples, in April

* The cost of the blocks for text-figs. 2 and 3 and of reproduction of the plates has been defrayed by a grant from the Carnegie Trust for the Universities of Scotland, and we are further indebted to the Trust for a grant for artistic assistance in connection with Plate VI.

† The specimens were brought to the Naples Zoological Station, and handed, along with other hydroid material, to Mr T. J. ANDERSON, who was at that time studying the Hydrozoa while holding a Carnegie Scholarship. I was working in the Naples Station at the same time, and, on seeing these colonies and their sporosacs, realised, as did Mr ANDERSON, that they presented several new and interesting features. Mr ANDERSON left Naples shortly afterwards, and, before he had been able to work further at the material, went to Nairobi to take up the appointment he now holds. On his departure he kindly placed the specimens in my hands. Unfortunately, Mr ANDERSON did not make any notes on the colours of the colonies, or on the movements of the sporosacs, so that on these points I have merely impressions derived from glimpses of the specimens in the brief intervals of my own work on other subjects.—[J. H. A.]

1906, and of two slides containing a considerable number of sporosacs of both sexes, from the same source, mounted in formalin. The eruption of Vesuvius of that year had just concluded, and the showers of fine dust had produced great mortality among the marine organisms. To this cause we attribute the fact that, of the seven shells, one bore a dead colony, and five others bore colonies from which the ordinary polyps had almost wholly disappeared. In these five colonies, however, living substance in the form of *cœnosarc* in the stolon was present, and a number of blastostyles—though on two of the colonies there were very few—had managed to survive. The remaining shell bore a colony in good condition, and it is on this that most of our observations have been made.

GENERAL DESCRIPTION OF THE COLONIES OF *DICORYNE CONYBEAREI*.*
(See Pl. VI.)

The colonies are in each case on small, gastropod shells of the genus *Nassa*, and those which are well established spread over the entire shell, showing no preference for any particular portion, though, as a rule, the individuals in the neighbourhood of the mouth of the shell are more luxuriantly developed.

In young examples the stolon can be easily seen forming an irregular meshwork on the surface of the shell, but in older examples the interspaces between the strands of the stolon become filled with diatoms and debris so that a uniform rusty-grey covering is formed, obscuring the stolon and obliterating the finer marking of the shell.

From the stolon, at irregular intervals, arises either a short stalk terminated by a single hydranth, or a longer branched stem bearing two, three, or four (rarely more) hydranths. The stems are rusty grey in colour, due, as in the case of the stolons, to a covering of foreign bodies (in this case chiefly volcanic dust) adherent to the chitin. The perisarc of the stem is irregularly corrugated or wrinkled, and at its distal end widens slightly, forming a small, transversely wrinkled cup, which bears a dense coating of foreign particles. This elementary hydrotheca covers, in the full-grown polyps, only a very small proximal portion of the hydranth body. The hydranths are ovoid or fusiform according to the state of expansion. Each has a prominent conical hypostome surrounded by a whorl of filiform tentacles. The number of tentacles varies from six in the youngest specimens observed to sixteen in the largest adults.

The sporosacs are borne on blastostyles which arise either directly from the stolon or from the stems of polyps. The blastostyle varies in form according to its phase of development. It is at first almost cylindrical or slightly dilated at its distal end, which is armed with numerous nematocysts, but soon becomes swollen about the middle of its length and is henceforward more or less vase-shaped.

* For the diagnostic characters of this species see p. 282.

The fully developed blastostyle has a narrow base of attachment to the stolon or to a hydranth stem, a wide middle region on which the sporosacs are borne, and a narrower, dome-shaped distal region bearing plentiful nematocysts. The blastostyle, which has neither mouth nor tentacles, is enveloped at its base by a simple hydrotheca similar to that of a hydranth.

A full-grown blastostyle bears usually from eighteen to twenty-four sporosacs, but occasionally more are present; the largest number observed was thirty-four. All the sporosacs on a blastostyle are of the same sex, and throughout any one colony the sex of the blastostyles is uniform.

The free-swimming sporosac is provided with a single tentacle* and is ciliated all over. The female sporosac is sub-spherical and bears in every case only a single oocyte, at one side of which a well-developed spadix is present. The male sporosac is usually rather smaller, and more oval in form, and the mass of spermatozoa is arranged round an axial spadix.

Further details of the various portions of the colony may now be given.

STOLON (Pl. VI, fig. 1; Pl. VIII, figs. 14, 15).

The external surface of the stolon or hydrorhiza is moderately smooth, *i.e.* without corrugations, and there are no internal chitinous projections of the perisarc such as are found supporting the walls in several gymnoblastic and calyptoblastic hydroids, *e.g.* *Podocoryne anechinata*, Ritchie; *Sertularia heterodonta*, Ritchie; *Plumularia lagenifera*, var. *septifera*, Torrey. Branches are produced from the stolon strands (fig. 1), and for a time their ends are free and rounded, but later they anastomose with neighbouring strands of the stolon, and thus the meshwork becomes complex. The perisarc of the stolon is about 6μ thick and of a brown colour. The histology of the cœnosarc does not present any unusual feature.

Regenerative Capacity of the Stolon.—A point of considerable biological interest may be noted here. It has already been remarked that on all the colonised shells, except one, almost all the larger hydranths are disintegrated and their stems empty of cœnosarc. One colony was evidently dead when preserved, but even in the least promising of the others a few very small hydranths, with only six tentacles (fig. 1, H 1), can be seen growing out directly from the stolon, thus giving evidence that, in spite of the destruction of the more visible portions of the colony, a residue of living cells still remains within the stolon ready to start into being a new series of individuals. Probably these young hydranths had developed during the few days the colonies had been living under favourable conditions in an aquarium in the Zoological Station. Microscopic examination of the stolons from these colonies shows that although many parts are empty, other portions contain a plentiful amount of normal cœnosarc. This living cœnosarc had been protected and shut off from the influence of deleterious

* One abnormal sporosac with a bifid tentacle and two others each with two tentacles have been observed (see p. 277).

conditions by the formation of thin transverse partitions of chitin barring the lumen of the stolon at certain points. In several cases barrier after barrier had been successively formed by the cœnosarc, which had been forced to retreat stage by stage within the stolon (Pl. VIII, fig. 14). Such chitinoid barriers are formed by a plug of cœnosarc (fig. 15), composed of a circular plate of thick ectoderm and of solid endoderm, similar in general form and structure to the "Deckenplatte," which secretes the operculum in many species of calyptoblastic hydroids. It is clear, therefore, that, in addition to serving as a hold-fast for the colony, the stolon performs an important function during time of stress in retaining and protecting from harmful environmental influences sufficient cœnosarc to give rise, when conditions have again become favourable for normal existence, to new series of nutritive and reproductive individuals.

HYDROCAULUS AND HYDRANTH (Pl. VI).

The smallest hydranths observed on the stolon are sessile, are about 2–3 mm. in length, and have already developed six slender tentacles (fig. 1). The stem of the polyp gradually elongates, and not long after the polyp has attained a length of about a millimetre a branch usually appears, others being formed later. The largest living stems observed are 2·8 mm. long and bear four individuals. There are, however, on two of the colonies dead stems 4–5 mm. long, which bore seven to eight individuals. The branches arise at intervals along the stem and lie at acute angles to the main stem, to which they are more or less parallel. It is rare to find the branches subdivided; this occurs only in a very few of the basal branches of the largest stems. Such branches bore two, and in one case three, hydranths, one of which was small—a blastostyle-bud or a very young hydranth. Examination of hydranths of various ages gives the impression that there are longer and shorter tentacles alternating, and that the longer ones in life pointed distally while the shorter ones were directed more or less horizontally. It is, however, difficult to make certain of this in preserved specimens in which the tentacles exhibit various phases of contraction. When well extended the longer tentacles slightly exceed 5 mm. in length.

Towards the base of the stem or hydrocaulus the perisarc, which as usual is laminate, is 3–4 μ thick, and of a brownish-yellow colour. Here the covering of extraneous debris is often meagre, in strong contrast to the dense coating present at the distal end of the stem at the base of the hydranth body. In its distal portion the perisarc is less definite in outline, its laminæ more feebly marked, and its colour gradually pales until the portion surrounding the base of the hydranth is represented by a thin hyaline substance the outline of which is merely indicated by the presence of adherent foreign particles.

The hydrocaulus and hydranth have been examined in several series of longitudinal sections. As the two cell-layers do not appear to present special features, we do not describe their histology in detail. The ectoderm of the hydrocaulus lies in

close contact with the perisarc, especially in the distal region. At the level of the distal edge of the hydrotheca the cells of the ectoderm are generally more columnar, elsewhere they are less regular. Among the ectoderm cells of the stem may be noticed a few large nematocysts. The bases of the ectoderm cells are prolonged into very thin contractile processes which run longitudinally. The ectoderm is separated from the endoderm by a well-defined lamella of mesogloea. The endoderm of the stem is a layer of flattened epithelial cells with granular protoplasm and large vesicular nuclei in most of which a large nucleolus is present. Here and there are large oval cells crowded with deeply staining spherules, probably of excretory nature.

In the greater part of the hydranth the mesogloal lamella is more strongly developed than in the stem, but diminishes in thickness towards the mouth and also on entering the tentacles. The ectoderm at the apex of the hypostome contains numerous oval nematocysts. The largest of these are about 6μ long and 3μ broad, but many others are only about two-thirds this size. The endoderm, which in the stem is thin, becomes in the hydranth a very thick layer. Among the ordinary elongate, vacuolated endoderm cells are many clavate cells packed with spherules of secretion. The wide lumen of the hydranth narrows rapidly proximally, *i.e.* on approaching the stem, to a canal about $25-30\mu$ in width which is continuous through the similar lumen in the stolon with the cavities of the neighbouring individuals of the colony.

The tentacles are solid, the endoderm of each being composed of a single column of discoidal cells with stout walls. Each cell is much vacuolated, the protoplasm being aggregated into a small mass around the central nucleus, from which a few strands radiate. The nematocysts of the tentacles are small and oval, about 4μ long and 2μ broad.

BLASTOSTYLES (Pl. VI).

The blastostyles arise either directly from the stolon or from the hydrocaulus, but most of them are borne on the stolon. Those arising from polyps (fig. 1, B v) are more recently formed than the majority of those on the stolon; possibly they are formed in seasonal succession, first on the stolon and later on the hydrocaulus. A blastostyle arising from a hydrocaulus is at first difficult to distinguish from a polyp-bud of the same size, but the latter soon develops tentacles and a mouth, structures which are not present in blastostyles. The basal portion of each blastostyle is protected by an envelope of perisarc the distal region of which is sometimes moderately thick, widened into a shallow cup-shape, and easily seen; but more often the perisarc is thin and almost transparent. Invariably, however, the distal margin of the perisarc is marked by a coating of extraneous matter.

The blastostyles vary in form according to their phases of development, and there are also considerable individual variations. Young blastostyles are, for the most part, nearly cylindrical or slightly dilated at their distal ends, where numerous

nematocysts are present (fig. 1, B I). In some cases, however, the blastostyle is more clavate, and in others is even more dilated, being almost ovate distally owing to the great development of the ectoderm of the region bearing the nematocysts (fig. 1, B III). The nematocysts are of two kinds: those at the tip of the blastostyle are large and elongate oval in form (Pl. VII, fig. 7), their length being about $15-16\mu$ and their breadth $4-5\mu$; the nematocysts on the sides of the distal portion of the blastostyle are smaller and of more rounded oval form, their length and breadth being about $6-7\mu$ and 4μ respectively.

In young blastostyles the endoderm consists of high columnar cells, filled with finely granular protoplasm, so that the coelenteron is represented by a narrow axial slit, but in mature blastostyles a large coelenteron is present, though in the distal portion—corresponding to the hypostome of a hydranth—the cavity is smaller. The greater part of the endoderm of such a mature blastostyle is composed of elongate, thin-walled cells which are highly vacuolated, but the endoderm of the hypostomal region consists of smaller columnar cells similar to those of the young blastostyle, and their granular protoplasm is but little vacuolated. Among the ordinary endoderm-cells are globular cells—numerous in some blastostyles, more scanty in others—containing masses of granules, probably excretory, which stain deeply with iron-haematoxylin.

The ectoderm of the column of the blastostyle is similar to that of a hydranth, and its cells are provided with muscle-processes which run longitudinally, but at the distal end of the blastostyle the ectoderm is thicker and heavily charged with nematocysts of two kinds (see above). The external surface of the ectoderm is covered by a thin cuticle.

The mesogloea of the middle region of the blastostyle attains a great development, often reaching a thickness of 6μ , and on the endodermal side is raised into many irregular folds. In the hypostomal area the mesogloea is much thinner, and at the tip of the blastostyle is a film of extreme tenuity.

Oocytes about 6μ in diameter are distinguishable in the ectoderm of the blastostyles by the time the latter have attained a length of little more than $\cdot 2$ mm. They are situated in a zone around the blastostyle near the middle of its length. By the time the blastostyle is about $\cdot 5$ mm. long the oocytes become so large as to cause ectodermal elevations*—the beginnings of the sporosacs—on the surface of the blastostyle. About this time the blastostyle generally becomes swollen in its middle region and is henceforward vase-shaped, the sporosacs being borne on this wider portion (fig. 1, B IV). The distal region, which throughout the life of the blastostyle is armed with the two varieties of nematocysts described above, remains narrower and somewhat dome-shaped. The longest blastostyles observed are about $\cdot 7$ mm. in length (see fig. 1, B IV).

* Occasionally such elevations are present in smaller blastostyles, in one case when the blastostyle was only $\cdot 25$ mm. long (see fig. 1, B II), but this is exceptional.

DEVELOPMENT OF THE SPOROSACS.

A. *The Female Sporosacs* (Pl. VII).

The oocytes are differentiated and grow in the ectoderm of a blastostyle in the positions which the sporosacs will subsequently occupy; there is no migration of oocytes from endoderm to ectoderm, nor does there appear to be any movement of oocytes in the ectoderm. The differentiation and early phases of growth of an oocyte precede the formation of the sporosac which is to contain it. Oocytes of apparently very different ages are present in the reproductive zone of a single blastostyle, and there seems to be no definite rule as to the period of growth or size of oocyte governing the first appearance of the sporosac. For instance, small oocytes $7-10\mu$ in diameter have been observed within distinct ectodermal swellings, but two others, each about 18μ in diameter, lie in ectoderm the surface of which is not elevated.

The first stage of formation of the sporosac is due directly to the growth in volume of the oocyte. As the bulk of the latter increases the overlying ectoderm is raised into a dome-shaped mound, and the ectoderm cells surrounding the oocyte become considerably elongated. At this stage (fig. 2) the sporosac-elevation is entirely ectodermal, no changes having taken place in the neighbouring endoderm and mesogloea.

Further increase in the size of the oocyte soon involves the formation of a more definite ovoid outgrowth (fig. 3). The ectoderm cells covering the rapidly growing oocyte multiply and form a single layer of moderately regular cells; at the same time the subjacent endoderm increases and the mesogloea becomes arched outwards and diminishes in thickness to a mere film. The base of the sporosac thus becomes occupied by a mass of endoderm—the spadix—connected with the endoderm of the blastostyle by a narrow neck. The cells of the spadix are arranged radially and with considerable regularity, and there is a small axial cavity (frequently filled with granular matter as indicated in the figure) continuous with the coelenteron of the blastostyle. The base of the oocyte applied to the endoderm lies obliquely with regard to the axis of the gonophore, and this obliquity is still further increased as growth proceeds, the spadix eventually being pushed to one side of the oocyte.

In the older sporosac, shown in fig. 4, the spadix has a large central cavity and its cells contain brownish granules which apparently increase in number with the age of the sporosac. Some time prior to the stage figured there appears, immediately proximal to the sporosac proper, a constriction which is of great importance in the subsequent history of the sporosac. For convenience of description we shall refer to the region proximal to the constriction as the sporosac-stalk, to the distal region as the sporosac, and to the connection between the two at the zone of constriction as the sporosac-neck. In the sporosac-stalk the ectoderm retains its original character and resembles that of the blastostyle, being composed of relatively large cells with

correspondingly large oval nuclei. The ectoderm cells of the sporosac are smaller and of a different type; they have undergone rapid division, resulting in the formation of a thin layer of uniform squarish or oblong cells with small, spherical, deeply staining nuclei. Occasional small oval nematocysts are present in the ectoderm of the sporosac and the cells are finally ciliated. A thin continuous cuticle envelops the whole ectoderm both proximal and distal to the constriction. In the sporosac-stalk the mesogloea is of moderate thickness, but at the constriction it rapidly diminishes in amount and in the sporosac is very thin. At an early stage in the differentiation of the neck-region of the sporosac an outgrowth—consisting of ectoderm and endoderm—appears at the base of the sporosac. This outgrowth undergoes rapid development and becomes a finger-like process—the future tentacle of the sporosac—with ectoderm like that of the sporosac and with solid endoderm in a single column of cells. The tentacle is confined between the ectoderm and cuticle of the sporosac, its tip being directed distally.

With the further development of the sporosac the constriction at the neck becomes more and more pronounced. The ectoderm of the sporosac and that of the stalk no longer maintain continuity, with the result that in its final stage the neck consists only of a narrow tube of mesogloea with a slender central core of vacuolated endoderm (fig. 4).

During the later phases of growth of the sporosac and oocyte a narrow peripheral zone of the latter becomes differentiated; it is more finely granular than the remainder of the yolk cytoplasm and reacts differently to stain (p. 278). Several of the larger oocytes examined in sections are enveloped by a thin pellicle about 1μ in thickness—the vitelline membrane.

By the time the oocyte has attained a diameter of about $80-90\mu$ the tentacle of the sporosac is fully developed, the neck has been reduced to its minimum, and the sporosac is ready to break away from the blastostyle and become free-swimming. The process of release appears to be purely mechanical, and to be due to the action of currents in the surrounding medium playing upon the relatively large bulk of the sporosac and breaking its slender attachments. At any rate, no histological change could be observed in sporosac-stalks from which the sporosacs had recently escaped. The escape is evidently due simply to the rupture of the loose cuticle in the neighbourhood of the neck and then of the thin neck itself. In a few cases where the cuticle had failed to rupture, the sporosacs have remained attached to their stalks, and their respective oocytes have undergone degeneration.

On the sporosac becoming free the loose cuticle which covers it is usually soon discarded. The tentacle, now released from its confined position, becomes extended so as to lie more or less in line with the long axis of the sporosac, in the position shown in fig. 5. The numerous cilia of the general ectoderm and of the tentacle come into play and the sporosac swims, at the same time rotating on its own axis, probably with the tentacle directed anteriorly, though the observations on the

living specimens in captivity were not sufficient to establish this point with certainty.

The subsequent life of the sporosac is probably of short duration. The ectoderm is ruptured (fig. 6), the oocyte escapes, and maturation and fertilisation no doubt soon take place. We have, however, seen three examples in which fertilisation and egg-cleavage had occurred while the egg was still contained in the remains of the sporosac, but these are probably exceptional cases and may have been determined by the abnormal conditions of captivity. All the other developing eggs were found free from the sporosacs. Whether the eggs, when liberated, float or sink to the bottom we are unable to say.

The blastostyles apparently produce successive series of sporosacs, for on a blastostyle which bears almost fully formed sporosacs are oocytes only about 15μ in diameter in small elevations of the ectoderm, forming incipient sporosacs of a new series.

B. *The Male Sporosacs* (Pl. VIII, figs. 8, 9, 10).

The material at our disposal for the study of the male sporosacs, while not so complete as for the females, is sufficient to enable us to give an account of the main features of their development. Several blastostyles bearing male sporosacs in their early and middle stages of development were present on three of the colonies; these have been studied entire and in longitudinal serial sections, and about a score of free male sporosacs have also been examined.

The male sporosacs are confined to a narrow zone about the middle of the blastostyle. The first indication of their appearance is the differentiation in the base of the ectoderm of one or more cells (usually there seem to be two or three). These are ovoid in form, their protoplasm stains more deeply than that of the neighbouring cells, and their nuclei are larger and of a more vesicular type, with peripheral granules of chromatin and a large nucleolus (fig. 8).

The elevation which eventually becomes the sporosac seems to be due to the almost simultaneous activity of both cell-layers. The ordinary ectoderm cells of such an incipient sporosac multiply *pari passu* with the spermatogonia, and the subjacent endoderm, judging from the special character of the cells, is also in a state of considerable activity, so that the condition seen in fig. 9 soon results.

The thick ectoderm of the distal end of the sporosac is composed chiefly of a mass of deeply staining cells—the spermatogonia—on the periphery of which are scattered cells which stain more faintly, these being the ordinary cells which will later form the ectodermic envelope of the sperm mass. The endoderm cells below the spermatogonia are more granular and stain rather more deeply than the cells proximal to them. This endodermal spadix is either solid or has a narrow central lumen continuous with the coelenteron of the blastostyle. The mesogloea of the sporosac is thin and grades into that of the blastostyle. Such a sporosac, having

an axial spadix, is radially symmetrical, a symmetry which it retains until the formation of the tentacle.

We have no examples intermediate between that just described and the free sporosac (fig. 10), but no doubt the male sporosac becomes detached from the blastostyle in the same manner as the female. Like the latter, it is clothed with long cilia, as also is the tentacle, which comes to lie in line with the long axis of the sporosac; and probably the male sporosac, like the female, swims with the tentacle directed anteriorly.

In shape the male sporosac is readily distinguishable from the female, since it is elongate oval—the female being sub-spherical,—and is usually a little smaller. The average length (excluding the tentacle) and breadth of twenty male sporosacs are .096 mm. and .064 mm. respectively, the largest being .12 mm. long and .07 mm. broad. The tentacle, when extended, is .04–.06 mm. long. The average length and breadth of twenty female sporosacs are .115 mm. and .1 mm. respectively, the largest being .135 mm. long and .115 mm. broad, and the tentacle is .05–.07 mm. in length when extended.

The free male sporosac is of simple structure (fig. 10). Externally it is covered with ectoderm composed of regular ciliated cells. The endodermal spadix, which has a central cavity, runs axially from one pole to the other, passing at one end into the solid endoderm of the tentacle and at the other abutting against the ectoderm. The cells of the spadix of most free sporosacs exhibit a degenerate appearance. Between the ectoderm and the spadix lies the cylindrical mass of spermatozoa. We have no observations on the mode of escape of the sperms from the sporosac.

THE SPOROSACS OF *DICORYNE CONFERTA* (ALDER).

The characters of the reproductive bodies described in the preceding pages clearly place them in close relationship with the free-swimming sporosac of *Dicoryne conferta* described by ALLMAN (1861 and 1872). The most marked differences lie in the single tentacle of the Neapolitan examples as contrasted with a pair in *D. conferta*, and in the single oocyte of the former as against the normal pair* in the latter. ALLMAN was content merely to mention the “defined line” along which the sporosac of *D. conferta* becomes detached, without indicating its origin or nature, and, owing to lack of mature material, the detailed descriptions of later writers have stopped short of the stage at which the tentacles develop. In the hope of correlating more definitely the developmental stages of these remarkable and closely related sporosacs, we have re-examined their development in *D. conferta*.

The material examined consists of colonies from (a) Kristineberg, Sweden, lent by Professor HJALMAR THÉEL from the collections of the Stockholm Museum; (b)

* GOETTE (1907, p. 67) has stated that in young sporosacs of *D. conferta* there are occasionally three or four oocytes, and sometimes only one; and HARTLAUB (1897, p. 480) has recorded the finding of free-swimming sporosacs of this species, in plankton collections off Heligoland, which possessed three oocytes and the normal two tentacles.

Blacksod Bay, Plymouth, lent by Dr E. J. ALLEN, F.R.S., from the collections in the Laboratory of the Marine Biological Association, Plymouth; and (c) North Sea, lat. $57^{\circ} 43' N.$, long. $0^{\circ} 38' E.$, in a collection received for identification by one of us from the North Sea Investigation Committee of the Scottish Fishery Board.

It is a matter for regret that the specimens from each of these localities bear male sporosacs only. As in the Neapolitan examples these are clustered upon blastostyles borne upon the hydrorhiza or upon the hydrocaulus, but in *D. conferta* they are relatively more frequent on the latter.

The spermatogonia are first to be distinguished in the ectoderm of the blastostyle on account of the deeper stain absorbed by their nuclei. They do not migrate: their situation already indicates the position of the future sporosacs. In all the blastostyles of *D. conferta* which we have sectioned the mesogloea is of unusual thickness, averaging 6μ and reaching even 13μ , and this induces a slight modification in the early development of the gonophore. For whereas in the Neapolitan examples of *D. conybearei* the mesogloea, even at the earliest stage, was bent outwards into the sporosac-mound, in *D. conferta* the abrupt edges of mesogloea at the junction between blastostyle and gonophore show that a disc of the mesogloea has been almost completely resorbed, the thin film remaining being then pushed outwards by the growing endoderm taking part in the formation of the sporosac.

The early development of the sporosac follows the course described for the Neapolitan examples (see pp. 265, 266). There is a large endodermal spadix which either has a narrow central lumen or is solid, a thin film of mesogloea, and a thick cap of ectoderm consisting of a mass of spermatogonia with more peripherally placed covering cells. The sporosac is invested with a cuticle considerably thicker and usually developing at an earlier stage than that present in the Neapolitan ones, and foreign particles are adherent to it.

The subsequent development is marked by a constriction in the proximal portion of the sporosac. This proceeds to such an extent that finally a neck is formed containing only a narrow cylinder of endoderm invested by a thin film of mesogloea which is separated by a considerable interval from the cuticle still strengthening the connection between the newly developed sporosac-stalk (see p. 263) and the sporosac proper (Pl. VIII, fig. 16). The blastostyle type of ectoderm is retained in the sporosac-stalk, but in the sporosac a thin ectoderm of almost uniform cells, with relatively large nuclei, is formed by rapid division. With the appearance of two tentacles, the origin of which dates from the beginning of the constriction at the sporosac-neck, the sporosac assumes bilateral in place of radial symmetry. The tentacles originate as a couple of buds which arise opposite each other from the wall of the sporosac immediately distal to the narrow neck. Pushing distalwards they are retained alongside the sporosac by the cuticle. With the maturing of the reproductive products the cells of the spadix undergo regenerative changes, and in most cases the spadix exhibits a distinct central cavity. The cuticle enveloping the

sporosac appears to become gradually thicker and of deeper colour, and its coat of debris also increases in amount. The length of a mature male sporosac is .17-.19 mm., and its maximum diameter .1-.13 mm.

Although we have been unable to follow the development further and to study the actual release of the sporosacs, it is evident that, as in the Neapolitan examples, the cuticle, probably under mechanical tension, becomes ruptured in the neighbourhood of the sporosac-neck, that the neck itself, being unable to bear the whole strain put upon it, breaks, and thus the sporosac is liberated. The tentacles, on being released from confinement, come to lie more or less parallel to the long axis of the body.

ALLMAN, in 1861 (p. 169), gave a description of the adult male sporosac, and this he repeated in substance in his monograph (1872, p. 226). He gives no information regarding the development of the sporosac, nor does he mention the peculiar constriction which ultimately leads to its release; indeed his figure (1871, pl. viii, fig. 5) is defective in showing no trace of a constriction nor of the "defined line" to which he refers as forming the breaking plane proximal to the tentacle bases. It seems to us also that ALLMAN has distorted his description and obscured the issues by impressing on this unique type of sporosac a terminology derived from and depending on medusoid homologies. Thus, as applied to the male sporosac of *D. conferta*, ALLMAN's "internal sac" or "endotheca" is no more than the ectoderm, a direct derivative, slightly modified, of the ectoderm of the blastostyle; and the "external sac" or "ectotheca" is simply the cuticle secreted by the ectoderm, homologous and continuous with the cuticle which covers the ectoderm of the blastostyle and of the colony in general. The assumption that the sporosac is a medusoid has led ALLMAN into a further error; for assuming the usual construction of a medusoid to be followed in this case, he described and figured a distinct space between the "ectotheca" and the "endotheca" (1871, pl. viii, fig. 5). So far as we have observed, the cuticle, except for such small distortion and displacement as are unavoidable in preservation and mounting, lies close upon the ectoderm, and there is no determinate space between the two as represented in ALLMAN's figure. The tentacle in its growth forces apart the cuticle from the ectoderm, but there is not an already pre-existing space. In his description of the release of the sporosac an obvious slip occurs, for the sporosac could not break through the "endotheca," as he states, but escapes from the so-called "ectotheca."

Female sporosacs were not discovered on any of the mature colonies of *D. conferta* examined by us. In this respect our experience agrees with that of GOETTE (1897, p. 67), who found that colonies with female sporosacs were entirely unisexual. ALLMAN, however, states that he "occasionally met with both male and female stems in the same colony" (1872, p. 226). The earliest stages in the development of the female sporosacs have been described by GOETTE (1897, pp. 67, 68, Taf. vi, figs. 122-127). They closely resemble those of our Neapolitan material, except that in place of the single oocyte of the latter the sporosac of the former includes two. In

the Neapolitan sporosacs the spadix lies to one side of the enlarged oocyte, in *D. conferta* the spadix is situated between the two oocytes and, notwithstanding considerable compression in the later stages, retains its original axial position throughout development. GOETTE's observations on the development of the female sporosac cease at a stage long before the appearance of the tentacles, but ALLMAN has given a moderately full description of the free, tentacled sporosac (1861, 1872).

From direct observation we can add nothing to ALLMAN's account, but the closeness of the developmental and structural relations between the male sporosacs of *D. conferta* and *D. conybearei*, together with the similarity in the general lines of development of the earlier stages of the female sporosac in these species, suggest that the adult female gonophores of the two species will present similar structure. We may, therefore, indicate probable additions to and slight emendations in the description given by ALLMAN. Some of the remarks made on his description of the male gonophore (p. 268) apply also to the female, *e.g.* in regard to the "ectotheca" and "endotheca" and their supposed homology with the layers of a medusoid gonophore. ALLMAN does not mention the formation of a constriction at which the sporosac breaks away from the sporosac stalk, although such a neck is no doubt formed in the female as in the male. Further, he states that "each ovum is invested by a proper membrane, which presents the remarkable and unique character of possessing considerable thickness and being richly set with thread-cell-like bodies" (1872, p. 227). In connection with this statement we draw attention to the fact that the oocyte of *D. conybearei* exhibits a differentiated peripheral zone of cytoplasm and not infrequently also a thin vitelline membrane, but these are not cellular layers and they do not contain nematocysts. Probably the condition is similar in *D. conferta*.

AFFINITIES OF THE FREE-SWIMMING SPOROSACS OF DICORYNE CONYBEAREI.

The free-swimming sporosacs from Naples are evidently closely related to those of *Dicoryne conferta*, and the former should undoubtedly be referred to the genus *Dicoryne*. The origin and development of the gonads and of their investment agree in the two cases almost to the smallest details, the main point of difference being that the Neapolitan sporosacs possess only one tentacle and the female bears one oocyte, while the sporosacs of *D. conferta* have two tentacles and the female contains as a rule a pair of oocytes.

A close relationship also exists between the sporosacs from Naples and those of *Heterocordyle conybearei*, Allman, described by ALLMAN (1872, pp. 307, 308; pl. x, figs. 4-7) from material collected in Glengariff Harbour, Co. Cork, and by WEISMANN (1883, p. 84, Taf. xi, figs. 7, 8) from Neapolitan specimens. ALLMAN names the parts of the sporosac of *H. conybearei* in accordance with his view of their medusoid homologies, but from WEISMANN's account it appears that in every respect the

development of the male and female sporosacs, as far as it was traced, agrees with that of our Neapolitan sporosacs. The female sporosac of *H. conybearei* bears a single oocyte. According to the accounts of ALLMAN and WEISMANN, the development of the sporosacs in *H. conybearei* stops a long way short of the stage reached by our Neapolitan sporosacs, for in the former no free-swimming stage was observed and no trace of tentacle detected, so that the sporosac was considered by both authors to belong to the fixed type.

Evidence we have accumulated indicates that the sporosacs of *Heterocordyle conybearei* examined by ALLMAN and WEISMANN were not fully mature, and that consequently these authors (whose accounts have been followed by later writers) were misled as to the final structure and essential nature of the sporosacs. The identity of the early stages of the sporosacs of *H. conybearei* with those of our material has already been pointed out, but it was desirable to ascertain definitely whether or not the later phases were identical, which could only be determined by examining a well-preserved, mature colony indubitably belonging to *H. conybearei*, and preferably obtained from some source other than Naples. We were unable to obtain such a colony until this paper was standing in proof, when Mr E. T. BROWNE kindly lent to us a colony, collected near Plymouth in 1895, and identified by him as *H. conybearei**—an identification with which we fully agree. This colony covers an area of about 9×4 mm. on a portion of a shell, and is probably younger than those from Naples examined by us, since nearly all the stems bear a single hydranth, only a few having two. The characters of the trophosome of Mr BROWNE's colony are in agreement with those of our Neapolitan examples, but the largest polyps of his colony are distinctly larger than any of ours. Further, the mature blastostyles of his colony are longer than ours (his longest being about 1.3 mm. and ours .7 mm. in length respectively), but have approximately the same width. We do not attach any significance to these differences, as they may both be due to the exceptional conditions under which the Neapolitan examples passed their last days in the sea† (see p. 258).

The blastostyles of Mr BROWNE's colony are, with one exception, confined to the stolon, and are for the most part young, only five bearing sporosacs. One blastostyle, which was removed for detailed examination, bears a dozen large sporosacs—evidently its first series—in a cluster slightly distal to its middle. More distal, and extending to the base of the hypostomal area, is a broad zone the ectoderm of which exhibits numerous small elevations (incipient sporosacs) each containing a single oocyte. Had these sporosacs become mature, the blastostyle would have been similar (except in length) to that shown in fig. 1, B iv. The large sporosacs on this blastostyle are about .13 mm. long and .1 mm. broad; each has a single tentacle and a

* Recorded from Plymouth on shells of *Nassa* (cf. p. 258) and *Buccinum*, particularly the former. See *Journ. Marine Biol. Assoc.*, vol. vii (N.S.), p. 190, 1904.

† It is possible that the Neapolitan and British specimens belong to distinct geographical sub-species or races, but this can only be determined by examination of a longer series of mature examples.

single oocyte, and exhibits a distinct neck or constriction near its base, indicating clearly that the sporosacs would soon have broken loose and become free-swimming.

The sporosacs borne upon this specimen of *Heterocordyle conybearei* from Plymouth have approximately the same form and size, and present exactly the same morphological features, as our Neapolitan sporosacs; and the trophosomes of the two specimens being also in agreement, there can no longer be any doubt that the specimens are specifically identical. Hence *Heterocordyle conybearei*, Allman, is really a *Dicoryne*, and should therefore be known as *Dicoryne conybearei* (Allman). To this species belong the British examples described by ALLMAN, and the Neapolitan examples * described by WEISMANN, and by ourselves in the earlier part of this paper.†

A DISCUSSION OF THE HOMOLGY OF THE SPOROSACS OF DICORYNE.

Several views have been advanced as to the homology of the sporosac of *Dicoryne conferta*. The discovery in another species of a closely related sporosac, of which we have been able to trace the complete development, and the re-examination of the male sporosac of *D. conferta*, have provided new facts on which to base a reconsideration of the homology of the sporosacs.

The views hitherto advanced may be grouped into two classes:—

- (1) The medusoid homology.
- (2) The polyp-homology.

To take them in the order of their appearance:

1. *The Medusoid Homology.*

In 1861 (p. 170) ALLMAN stated his opinion that the sporosac of *D. conferta* corresponded to a normal medusiform gonophore in which certain parts were much reduced. This theory he retained, and restated in somewhat greater detail in his classical monograph (1872, p. 227). The significant points in his statement are as follows:—"The planoblast [=free sporosac] admits of a very instructive comparison with an ordinary medusiform gonophore. It is, in fact, a medusa in which the place of the umbrella and its canals is taken by two tentacles, the manubrium of the medusa being represented by the rest of the planoblast. It will be recollected

* The species apparently extends over the northern portion of the western Mediterranean, for MME. MOTZ-KOSSOWSKA has recorded specimens from the Mediterranean coast of France (Banyuls) and Spain (Blanes), and from the Balearic Islands (Cabrera, Mahon), in *Arch. Zool. Expér.*, sér. 4, tome iii, p. 76, 1905.

† Owing to the lack of mature material indubitably belonging to *H. conybearei* for comparison with our Neapolitan specimens, and being faced with the definite and accepted statements of ALLMAN and WEISMANN that the sporosacs of this species did not become free, we considered that we were not fully justified, on the evidence available when our paper was read to the Society, in regarding our Neapolitan examples as identical with *H. conybearei*, and as the former clearly belonged to the genus *Dicoryne* we designated them as a new species—*D. parthenopeia*. (This name, which has appeared only in the brief report of the meeting given in *Nature*, vol. xcv, p. 552, now lapses.) We suggested, however, that further study of the sporosacs of *H. conybearei* might reveal their identity with those described by us from Naples. Conclusive evidence now available has shown this to be so, and accordingly the name *parthenopeia* has been deleted from the proof.

that the two tentacles are turned forward, while the sporosac is still invested by its ectotheca, and that they then hold exactly the place of an umbrella (mesotheca) between endotheca and ectotheca. They are, in fact, the radiating canals of the medusa reduced to two and developed as free tubes, instead of being immersed in the walls of an umbrella. . . . The free sporosac of *Dicoryne* is thus a medusa reduced to the condition of a manubrium and two opposite radiating canals. In order, indeed, to convert it into an ordinary medusa, little more is necessary than to suppose the number of tentacles increased to four by the symmetrical development of two others, their extremities connected by a circular canal, and their sides by a continuous muscular membrane (umbrella) inflected at its fore margin so as to form a velum."

ALLMAN was led to this view by the interpretation he put upon the parts of the sporosac. He regards the external cuticular envelope as homologous with the "ectotheca" of an ordinary medusiform gonophore, and the ectoderm layer in which the oocytes or spermatogonia are differentiated is, in his view, the "endotheca." Consequently the tentacles of *D. conferta*, lying as they do between the supposed "ectotheca" and "endotheca," occupy exactly the position of the umbrella or "mesotheca" and its canals, in a normal medusoid gonophore.

But this view appears to us to be untenable and to have been supported by false homologies. The typical medusoid gonophore exhibits, according to ALLMAN's terminology (1860, p. 3), an "ectotheca," a "mesotheca," and an "endotheca." "The ectotheca is a simple extension of the ectoderm of that part of the zoophyte from which the gonophore arises, and it encloses either a sporosac or a medusoid" (*loc. cit.*). Of the other layers "the inner (endotheca) is the equivalent of the ectoderm layer of the manubrium of the medusa; the middle layer (mesotheca) corresponds to the umbrella, and like it may have a system of canals more or less completely developed in it" (1871, pp. 39, 40).

If these terms are to be employed in support of any homology, their application must be uniform. The "ectotheca," for instance, must be understood in its original significance as applied by ALLMAN in the case of a medusiform gonophore, where it is represented by the external investment—an ectodermal layer which arises, along with the ectoderm of the ex-umbrella, from the ectoderm of the blastostyle. The "ectotheca" may secrete on its outer surface a delicate cuticular film, as, for instance, in *Bougainvillea*. This ectoderm is totally distinct in origin from that covering the manubrium, for the latter arises from the thick mass of ectoderm cells—the "Glockenkern"—at the distal end of the medusa, in which, by the development of the future umbrella cavity, the manubrium becomes differentiated from the ectoderm of the sub-umbrella. In a fully differentiated medusa ("phanerocodonic gonophore") there are four layers of ectoderm from without inwards, namely, the "ectotheca," the ectoderm of the ex-umbrella, that of the sub-umbrella, and that covering the manubrium. A similar condition exists in a medusoid gonophore ("adelocodonic

TEXT-FIG. 1.—Diagrammatic sections of A, phaneroconic, and B, adeloconic gonophores. *a*, ectotheca; *b*, mesotheca or umbrella; *c*, endotheca or ectodermal layer of manubrium; *d*, spadix; *e*, ova; *f*, radial canals; *g*, circular canal seen in transverse section; *h*, marginal tentacle; *i*, ocellus; *k*, velum; *l*, peduncle of gonophore; *m*, general cavity of coenosarc; *n*, mouth of medusa. The endoderm is distinguished from the ectoderm by its darker tint.

[From ALLMAN, 1871, fig. 13, p. 39. Printed from the original wood-block, kindly lent by the Council of the Ray Society.]

TEXT-FIG. 2.—Diagrammatic sections of female sporosacs of *Dicoryne conybearei*. A, a mature sporosac on the point of liberation; B, a younger stage which shows more clearly the essential simplicity of the sporosac. COEL., coelenteron (general cavity of coenosarc); ECT., ectoderm; END., endoderm; O., oocyte; S.N., neck of sporosac; S.S., stalk of sporosac; T., tentacle. The ectoderm is indicated by a pale tint, the endoderm is darker, and the cavity of the spadix and coenosarc is black.

gonophore"), except that the two ectoderm layers of the reduced umbrella have become conjoined (text-fig. 1).

But a very different condition is presented by the sporosacs of *Dicoryne conferta* and *D. conybearei* (text-fig. 2), for in these the only layer of ectoderm is that in which the reproductive products have been differentiated. This forms the external ectodermal layer of the sporosac and secretes a thin cuticle over its free surface. The tentacle or tentacles lie between this cuticle and the layer which formed it. The tentacles therefore do not lie in the position of a "mesotheca," *i.e.* between an "ectotheca" and "endotheca," as in a medusoid gonophore, and ALLMAN's attempt to interpret them as homologous with the canals of a medusa, which lie in the "mesotheca," therefore falls to the ground. The tentacles have nothing to do with a "mesotheca"; there is, in fact, no "mesotheca" in the full-grown sporosac of *Dicoryne*, nor is there any trace of it during the entire course of development of the sporosac.

Further, the single ectodermic layer of the sporosac of *Dicoryne* does not agree in mode of origin, and is clearly not homologous, with that covering the manubrium of a medusiform gonophore, *i.e.* is not homologous with the "endotheca." If the enveloping ectoderm of the sporosac can be regarded as a homologue of any layer in a medusoid gonophore, it is with the external layer of the early stage of the latter, which subsequently gives rise to the "ectotheca" and to the ex-umbrellar ectoderm.

Consequently the gonophore of *Dicoryne* cannot be regarded as a manubrium, and we have already seen that the tentacles are not the homologues of radial canals. It may be noted that the tentacles of the sporosacs of *Dicoryne* are solid, and not "free tubes," as ALLMAN stated.

Several authors have followed the view propounded by ALLMAN, that the sporosac represents a degenerate medusa which has lost its umbrella but retained two radial canals. HINCKS (1868 [1869], p. 106) considered that it consisted "of a sexual polypite (manubrium) furnished with two tentacles, which represent the more usual natatory organ, while simple ciliary action replaces the propulsive movement of the swimming bell." DELAGE and HÉROUARD (1901, p. 64) and KEMNA (1908, p. 280) give a general adherence to ALLMAN's "ingénieuse conception," reserving final judgment to such time as the development shall be completely known.

CHUN has suggested an alternative view. He regards the sporosac as representing a much-compressed medusa in which the sub-umbrellar cavity has become entirely closed and filled with sexual products. Regarding the tentacles he offers no suggestion. "Bei ihnen [the sporosacs] ist die Glockenhöhle vollständig geschlossen und von den Geschlechtsproducten erfüllt. In der Nähe des aboralen Poles des Medusoids entspringen zwei lange opponirte Tentakel, die ebenso wie der dünnwandige Glockenmantel mit Cilien besetzt sind" (CHUN, 1896, p. 264). Both DELAGE and HÉROUARD (1901, p. 64) and KEMNA (1908, p. 280) allege that CHUN regards the tentacles as true marginal tentacles, and on this account readily demolish

his theory. But CHUN's statement in the passage quoted above will not bear this interpretation. Indeed, the fact that he described the tentacles as occurring at the aboral pole shows that he did not regard them as marginal. Unfortunately, CHUN does not show how his "complete medusoid" homology is to be applied in detail to the sporosac, nor can we, after examination of his view, offer any interpretation which will bear even the semblance of probability. If the sub-umbrellar cavity is closed and has become filled with sexual products, then the ova and sperms should lie between ectodermal layers, the inner one representing the ectoderm of the manubrium, and the outer one either the ectoderm of the whole umbrella or that of its inner surface. But there is no such complication in the sporosac of *Dicoryne*, nor in the development is there any trace of a medusa rudiment (Glockenkern). Apart from the impossibility of applying CHUN's theory in detail to the cell-layers, there remain the tentacles to be accounted for. With complacency CHUN leaves them arising from the roof of the supposed umbrella, offering no explanation of so unlikely a condition.

CARLGREN (1909, p. 11) adopts CHUN's view of the relationship of the sporosac without adding to our knowledge of its interpretation.

A third suggestion as to the possible medusoid homology of the sporosac of *Dicoryne* has been made by DELAGE and HÉROUARD: "On pourrait plutôt admettre que le corps n'est formé que par un manubrium nu, que l'ombrelle n'existe pas et que les tentacules ont été reportés à la base du manubrium par la regression de l'ombrelle. . . . Dès lors, le corps reproducteur serait non un simple sporosac, mais un gonophore, puisqu'il aurait un rudiment d'endoderme ombrellaire" (1901, pp. 64, 65).

As we have seen above, however, the ectoderm of the sporosac of *Dicoryne* does not correspond in mode of origin to the ectoderm of the manubrium of a medusa, and there is no rudiment of umbrellar endoderm, nor, indeed, of any portion of an umbrella. The view of DELAGE and HÉROUARD is therefore entirely unsupported by the facts of development and the structure of the fully formed sporosac of *Dicoryne*.*

The sporosac of *Dicoryne* (taking the female as an example) is not a preformed structure into which migrate comparatively small oocytes, but is an elevation first of ectoderm, later of both layers, following upon and seemingly called forth by the presence at that point of a large and growing oocyte.

Even in gonophores so reduced as those of *Clava squamata* (HARM, 1902) a "Glockenkern" is present for some time, and subsequent to its disappearance a primary endoderm lamella is found between the oocyte and the ectoderm enveloping the gonophore. Such an endoderm layer is not visible in our preparations of the early sporosacs of *Dicoryne*. Further, it may be noted that the ectoderm of the

* Another argument of general bearing may be adduced against the homology of the sporosac of *Dicoryne* with a manubrium. In the regression of medusae and medusoid gonophores the marginal tentacles are first lost, then the manubrium suffers reduction or disappears, and only a hint of the medusoid rudiment is apparent. It is therefore directly contrary to the general course of events to suppose that the manubrium should survive the umbrella, and still more difficult to imagine that a marginal tentacle should remain after loss of the umbrella.

distal end of the young female sporosac is thinner than that present elsewhere, there being no attempt at the formation of a "Glockenkern," and although young male sporosacs exhibit distally a thickened ectoderm, the increased thickness is due to the presence there of the spermatogonia.

To summarise the evidence regarding medusoid homologies of the sporosac of *Dicoryne*. This view derives no support from the facts of development, for there is not at any stage a "Glockenkern," and therefore there cannot be a manubrium,* nor is there any trace of umbrella or canals. The single or paired tentacles of the sporosac of *Dicoryne* do not arise at the free end, where marginal tentacles are formed in medusæ, but at the proximal end, and the tentacles are therefore not equivalent in the two cases. There is no evidence that the sporosacs of *Dicoryne* have undergone regression from the condition of medusæ or medusoid gonophores. If they have undergone such regression, it is so far-reaching as to have completely suppressed all trace of the ancestral condition and to have brought the tentacles into an anomalous position.

2. The Polyp-Homology.

GOETTE has suggested the polyp-homology of the sporosac of *Dicoryne* in place of the earlier medusoid homologies. Having traced the earlier stages of formation of the female sporosacs of *D. conferta* (although he failed to obtain the tentacle-bearing stage), GOETTE came to the conclusion that there could be no question of medusoid likeness, and that the resemblance to a degenerate polyp was much more evident: "Von einer medusoiden Bildung kann also bei den Gonanthen von *Dicoryne* gar nicht Rede sein; und mit viel grösserem Recht kann man behaupten, dass die basalen Tentakel dieser Gonanthen deren Polypen-ähnlichkeit unzweideutig hervortreten lassen; es fehlt nur noch der Mund, um ein Hydranthenköpfchen vollständig zu machen" (1907, p. 68). According to this view, the body of the sporosac is equivalent to the mouthless hypostome of a hydranth, the tentacles are normal in position, but the proximal portion of the hydranth is wanting.

Of the various theories advanced, GOETTE's polyp-homology appears to agree most closely with the actual condition of the sporosac. But owing to the essential simplicity of the structure and development of a polyp, resemblances between any two-layered bud and a polyp may be taken for granted, and on this account the polyp-homology is as difficult to prove as it is to refute.

WEISMANN (1883, p. 245) has suggested that the fact that hydranths never spring from the heads of other hydranths militates against the possibility that blastostyle-

* This statement refers only to the development of medusæ in the Anthomedusæ, Leptomedusæ, and perhaps the Siphonophora. An interesting comparison might be made between the sporosac of *Dicoryne*, regarded as a manubrium, and the larva of certain Narcomedusæ in which the manubrium first appears and two tentacles arise subsequently near its aboral end. There is a general external resemblance between the free-swimming, two-tentacled, ciliated sporosac of *Dicoryne conferta* and the free-swimming, two-tentacled, ciliated larva of *Egginopsis mediterranea*, four days old. But in its mode of origin and its subsequent history this larva differs entirely from the sporosac of *Dicoryne*, and the general resemblance in external form is not to be taken as evidence of homology, but is probably an instance of "convergence."

borne sporosacs can be regarded as degenerate hydranths. Although there are exceptions to this postulate, the general criticism advanced by WEISMANN seems to be valid.

Further, the suggestion that the sporosacs of *Dicoryne* are degenerate hydranths which have become secondarily the bearers of sexual products seems to be at variance with the actual order of development observed in *D. conybearei*. For there, in the case of both male and female sporosacs, the first indication was the differentiation of the germ cell or cells, the stimulus of the presence of which apparently brought about the origin and growth of the sporosacs. On the hydranth-hypothesis we should have expected that the hydranth-bud or hydranth-sporosac would have first been indicated, and that secondarily the germ cells would have been differentiated therein or migrated thereto. KÜHN (1910, p. 103) favours GOETTE's view, but the theory that the sporosac of *Dicoryne* is a modified hydranth is unsatisfactory in a general way, because in asserting it a far-reaching assumption of homology is made which, owing to the simplicity of the structures concerned, seems incapable of being either proved or definitely disproved.

A close examination of the anatomy, and especially of the development of the sporosacs of two species of *Dicoryne*, has left us with the impression that too great efforts have been made to bring these essentially simple structures into line with theories necessitating detailed and not infrequently obscure homologies. It seems to us that the sporosac of *Dicoryne* is essentially an outgrowth of almost the simplest possible form, produced apparently by the stimulus due to the presence of the germ cells. The ectoderm in which these lie grows *pari passu* with them and forms the envelope for them, the subjacent endoderm—which soon grows out as a “spadix”—is applied to the germ cells and carries the supply of nutrient material necessary for their growth. This bud-like outgrowth, like other simple buds in the Hydrozoa, produces one or two tentacles, similar in structure to those of a polyp, and eventually becomes free. The most striking difference between such a bud and any other known in the Hydrozoa is its ciliation, which is probably an adaptive development. The free-swimming sporosacs of *Dicoryne* are the only ciliated reproductive members known in the Hydrozoa.

ABNORMAL SPOROSACS OF *DICORYNE CONYBEAREI*.

Amongst the many free sporosacs examined three only show any departure from the normal, and in each case the variation relates to the tentacle. Both sexes are represented in this short abnormal series, which exhibits two types of variation.

In one of the male sporosacs, otherwise normal, the tentacle is bifurcated near the tip (text-fig. 3, A), both branches possessing ectoderm and endoderm cells of the usual type and arrangement.

The second type of variation consists in the development of two tentacles. In another male sporosac (text-fig. 3, B) one of the tentacles is of normal length, while the other is little more than a bud. The remainder of the sporosac is normal, so that the abnormality may be regarded as a sport tending towards the condition represented in the two-tentacled sporosac of *Dicoryne conferta*.

In the solitary abnormal female sporosac two well-developed tentacles, each of normal length, are present (text-fig. 3, C). These arise contiguously, and resemble in

TEXT-FIG. 3.—Three abnormal sporosacs of *Dicoryne conybearei*, from Naples. $\times 250$.

their arrangement and divergence the tentacles of the sporosac of *D. conferta*. In our specimen, however, the spadix appears to be double, a branch embracing either side of the single oocyte. The simplest interpretation of this condition is probably that here the phenomenon of duplication of parts, moderately common in other groups of animals, is exhibited.

EARLY DEVELOPMENTAL STAGES OF *DICORYNE CONYBEAREI*.

(Pl. VIII, figs. 11, 12, 13.)

A considerable number of free-swimming sporosacs of *D. conybearei* of both sexes—but males predominating—were kept alive in small vessels for a day or two, and many of them shed their genital products. About sixteen of the eggs had been fertilised and had passed through the cleavage phases before the material was preserved.

The earliest stage of development represented is a blastula (fig. 11), slightly oval in form, about $100\ \mu$ long and $90\ \mu$ broad, and consisting of about 120 similar cells which surround the large central cleavage-cavity or blastocoele. Cleavage of the egg was total, and apparently equal or nearly so. Cell-outlines are present though not easily seen, as the cells are loaded with yolk-spherules of different sizes. In each blastomere is a peripheral zone of minute granules of uniform size, which differ from the yolk-spherules in their reactions to stains. These granules—the presence of which in the oocyte has been already noted (p. 264)—remain peripheral throughout development and are found, though in diminished number, in the ectoderm cells of

the latest stage examined. Their ultimate fate cannot be ascertained in our material, but it is probable that they will later form the thin, cuticular covering of the young polyp. The nucleus of each blastomere lies near the peripheral margin, is vesicular, and usually exhibits two or three deeply staining nucleoli. Ten of the nuclei of this blastula are in karyokinetic division, and the axes of the spindles are all placed tangentially (see fig. 11); the planes of division of the blastomeres are therefore radial, and by such divisions the cells increase rapidly in number, with the result that they become less in size, for five blastulæ in this later stage, with about 400 blastomeres, are no larger than the blastula first described.

The next phase of development, represented in our material by four specimens, shows the cleavage-cavity containing numerous cells—the endoderm—with here and there small spaces between them (fig. 12). A few nuclei in karyokinesis are visible in the ectoderm; the spindles of some of these lie tangentially, but others are at right angles to the periphery, so that the divisions of these cells result in the formation of inner (endodermic) and outer (ectodermic) elements. The appearances presented by sections of these specimens suggest that the endoderm has been produced at several or many places (multipolar immigration), though here and there are blastomeres which have apparently not yet taken part in this process. Some of the endoderm cells are of considerable size, but by division of the central cells, and the accession to the endodermic mass of other cells from the wall of the blastula, the cleavage-cavity becomes tightly packed with cells, in a few of which karyokinetic divisions are present. The surrounding ectoderm is composed for the most part of cells of almost uniform size, and the nuclei are situated fairly regularly near the periphery.

In the latest phase (fig. 13), represented by a single complete and two damaged specimens, there is a central cavity—the coelenteron,—which has been formed by the breaking down of some of the endoderm cells, the debris of which lies in the cavity. Cell-outlines are scarcely distinguishable in the ectoderm, except at the extreme periphery of the cells, and are apparent only in a few places in the endoderm. The nuclei of ectoderm and endoderm are similar in size and structure. There is no indication of the mesogloæal lamella at this stage.

The general development of the egg most closely resembles that of *Bougainvillea superciliaris* as described by GERD (1892), a point of some interest, since on other grounds, *e.g.* resemblances in the trophosomes, *Dicoryne* and *Bougainvillea* are placed in the family Bougainvillidæ.

The egg is usually completely detached from the sporosac. We have three examples of *D. conybearei* in which the sporosac has ruptured and the egg, having escaped from the now wrinkled body of the sporosac, has, however, remained attached near the point of union of the spadix and the tentacle. Here it has undergone normal cleavage: in one case a blastula and in the others morula stages had been reached.

DISTINCTIVE CHARACTERS OF

	MATURE TROPHOSOME.				
	Hydrocaulus.			Polyp.	
	Height.	Branches.	Wrinkling of Perisarc.	Maximum No. of Polyps on Hydrocaulus.	No. of Tentacles on Polyp.
<i>Dicoryne conybearei</i> (Allman), char. emend.	Up to 4-8 mm.	Few or none, seldom subdivided, arising from a main stem which resembles them in thickness	Generally distributed, but irregular and indistinct	8	6 on youngest to 16 on largest specimen
<i>Dicoryne conferta</i> (Alder)	Up to 13 mm.	Many, usually subdivided, arising from a weak main stem, which scarcely exceeds them in diameter	Base of stem indistinctly wrinkled	[About 12]	6 on youngest to about 16
<i>Dicoryne flexuosa</i> , Sars	7 mm.	Few, occasionally subdivided, arising from a thin, flexible stem which is often dichotomously divided	Hardly any wrinkles	[About 3]	12
<i>Dicoryne annulata</i> , v. Lendenfeld	About 10 mm.	Few, not subdivided, arising from a stout stem	Wrinkled throughout, "terminal cup-shaped expansions a little larger than in <i>D. conferta</i> "	[2]	[About 10 or 11]

Note.—Square parentheses [] indicate that in view of the incomplete descriptions of authors the

SPECIES OF DICORYNE.

GONOSOME.				DISTRIBUTION.	
Blastostyle.		Sporosacs.		Locality.	Depth.
Position of Blastostyles.	Shape of Blastostyles.	No. of Sporosacs on Blastostyle.	Character of Sporosacs.		
On stolon and hydrocaulus	Long, spindle- or vase-shaped, projecting above and below mass of sporosacs	18 to 24 as a rule, exceptionally as many as 34 to 40, in globular or elongate clusters	Free-swimming, ciliated, with 1 tentacle, and female with 1 ovum	West coast of Scotland, and Ireland, and south coast of England; Gulf of Naples and Western Mediterranean	Down to about 10 fathoms
On stolon and hydrocaulus. [7 on a single hydrocaulus]	Long, spindle-shaped, projecting above and below mass of sporosacs	17 to 33, in globular clusters	Free-swimming, ciliated, with 2 tentacles, and female with 2 ova (exceptionally with 1 or 3 ova)	Iceland, Norway, Sweden, Scotland, England, Ireland, Denmark, North Sea, Heligoland, Mediterranean Sea	14 to 200 fathoms
On hydrocaulus only	Very short, almost or entirely covered by mass of sporosacs	[24 to 30], in globular clusters	[Free sporosacs not observed Female with 2 ova]	Norway; north-west of Shetland Islands; Gulf of Maine, Nova Scotia	50 to 150 fathoms
[On stolon]	Long, spindle-shaped, projecting far above and below mass of sporosacs	[About 12], in elongated clusters	"Generative zooids similar to those of the European species" [i.e. <i>D. conferta</i>]	South coast of Australia	

information has necessarily been derived from the figures illustrating the original accounts.

SPECIFIC CHARACTERS OF *Dicoryne conybearei* (ALLMAN), emend.Syn., *Heterocordyle conybearei* of ALLMAN and later authors.

Trophosome.—The hydrocaulus springs from a network of creeping hydrorhizal tubes, reaches a height of 4–8 mm., and is either simple or furnished with a few branches which arise acutely from the stem and are seldom subdivided. A well-developed perisarc is present, slightly and irregularly wrinkled throughout its length. It is covered with a dense coat of foreign particles and widens at the base of each polyp into a shallow, cup-like expansion. Up to four to eight polyps are borne on a single hydrocaulus, and these are furnished according to age with from six to sixteen tentacles in a single whorl.*

Gonosome.—Blastostyles arise on the stolon and on the hydrocaulus; their basal portion is covered with perisarc which terminates in a cup-like expansion similar to that beneath the polyps. Around the blastostyle the sporosacs, in general eighteen to twenty-four and exceptionally as many as thirty-four to forty, are grouped in a spherical or elongate cluster. The sporosacs arise from a zone encircling the middle region of the blastostyle, the tip and base of which project beyond the mature cluster. In the adult state the sporosacs are free-swimming, are furnished with one tentacle, and are covered with cilia. Female sporosacs bear a solitary oocyte. The structure of the sporosacs is of the simplest nature, as they consist of a single layer of ectoderm between which and the endodermal spadix lies the oocyte or the mass of spermatozoa.

The inclusion of this species within the genus *Dicoryne* necessitates a slight alteration in the generic characters as given by ALLMAN and accepted by subsequent writers. The new definition is as follows:—

Dicoryne, ALLMAN, char. emend. (including *Heterocordyle*, ALLMAN).

Trophosome.—Hydrocaulus consisting of simple or more frequently, in mature colonies, of branched stems arising at intervals from a creeping filiform stolon, which forms a close network. Hydranths fusiform, merging gradually into the hydrocaulus, with a single whorl* of filiform solid tentacles (with a single series of endoderm cells) surrounding the base of a conical hypostome.

Gonosome.—Simple sporosacs, consisting of a single layer of ectoderm and an endodermal spadix, between which the sexual products lie. The sporosacs are borne in clusters on blastostyles which arise from the stolon or the hydrocaulus or from both. At maturity the sporosacs, which are furnished with one or two tentacles with solid endoderm and are entirely covered with cilia, break away from their stalks and are free-swimming.

* In many hydranths there are longer and shorter tentacles alternating; in life the longer ones probably pointed distally, while the shorter ones were directed more or less horizontally (see p. 260).

For the convenience of systematic workers we have inserted a table summarising the distinctive characters of species of *Dicoryne*, pp. 280, 281. In this table an endeavour has been made to indicate as far as possible the points in which authors themselves regarded their new species as differing from species previously known. These characters are in some cases highly unsatisfactory.

Dicoryne conferta and *D. flexuosa*.—As regards the sporosacs themselves no difference has been observed, but unfortunately the free-swimming stage of *D. flexuosa* is not known. The "immersion" or otherwise of the blastostyle in the sporosac-cluster seems to us to depend more on the state of contraction of the blastostyle and on the maturity, and therefore size, of the sporosacs, than upon any constant difference in shape. Further, the characters upon which Sars especially relied—the deficiency of wrinkling on the perisarc and the flexible and often dichotomously branched stem in *D. flexuosa*—are characters upon which little weight can be placed, since on occasion they are exhibited by *D. conferta*. In *D. conybearei* the number of tentacles has been found to vary from six to sixteen; a similar range of variation has been observed in *D. conferta*, and it is possible that twelve is not a fixed number for *D. flexuosa*. It seems to us that on the whole these two species approach suspiciously close to one another, but since we have not seen specimens attributed to Sars' species we hesitate to state definitely that *D. flexuosa* is a synonym of *D. conferta*.

Dicoryne annulata.—The description of this species given by VON LENDENFELD is entirely unsatisfactory. There is no evidence that free sporosacs were seen, and the statement that the generative zooids are "similar to those of the European species" is so vague as to be valueless. Nor is the statement that the "terminal cup-shaped expansions [are] a little larger than in *D. conferta*" of any significance, for comparison of VON LENDENFELD'S figure with North Sea specimens of *D. conferta* shows that his contrast is inaccurate. The probability is that VON LENDENFELD has misinterpreted the structure of *D. conferta* in this respect from ALLMAN'S figure (1871, pl. viii), in which the terminal expansions are scarcely indicated.

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DESCRIPTION OF FIGURES.

LIST OF REFERENCE LETTERS.

BI, BII, BIII, BIV, BV, blastostyles.	P., partition formed across lumen of stolon.
C., cuticle.	PE., perisarc.
C.C., covering cell.	P.Z., peripheral zone of oocyte containing fine granules.
CEL., coelenteron.	S.N., sporosac-neok.
D., debris adherent to perisarc.	SP., spermatogonia.
ECT., ectoderm.	SPD., spadix.
END., endoderm.	SPZ., spermatozoa.
EX.C., excretory cell.	S.S., sporosac-stalk.
HI, youngest hydranth of colony.	ST., stolon.
M., mesogloea.	T., tentacle.
N., nematocyst.	

PLATE VI.

Dicoryne conybearei (Allman), from Naples.

Fig. 1. A portion of a colony showing a recently formed hydranth (HI) with six tentacles, and three larger hydranths, one bearing a blastostyle-bud (BV) in the ectoderm of which several oocytes are seen. Arising from the stolon are three young blastostyles (BI, BII, BIII) and one full grown (BIV), the latter bearing twenty-two sporosacs, fifteen of which are seen. It is exceptional for a blastostyle so small as BII to exhibit such large oocytes and elevations of the ectoderm (*i.e.* incipient sporosacs). Two free female sporosacs (SI, SII) and one free male (SIII) are also shown; the male was produced on another colony. The stolon was covered with debris (omitted, except in a small area on the left), and there was also a considerable amount of debris on the perisarc, shown only on the large central hydrocaulus. $\times 75$.

PLATE VII.

All the figures relate to *Dicoryne conybearei* (Allman), from Naples.

Fig. 2. Longitudinal section through the wall of a blastostyle, showing a large oocyte in the ectoderm. The space around the oocyte is an artefact. For further description see p. 263. $\times 1000$.

Fig. 3. Longitudinal section of a young sporosac and the adjacent wall of the blastostyle which bears it. See p. 263. $\times 1000$.

Fig. 4. Longitudinal section of an older and almost full-grown sporosac. For description see p. 263. $\times 1000$

Fig. 5. Free-swimming, ciliated female sporosac. See p. 264. $\times 500$.

Fig. 6. Female sporosac after escape of the egg by rupture of the ectoderm. $\times 500$.

Fig. 7. Section of a portion of the ectoderm at the distal end of a blastostyle, showing a discharged nematocyst of the large, elongate oval type. See p. 262. $\times 1400$.

PLATE VIII.

All the figures except fig. 16 relate to *Dicoryne conybearei* (Allman), from Naples.

Fig. 8. Longitudinal section of the ectoderm and mesogloea of a male blastostyle, showing the first differentiation of the male sexual cells. In addition to the two spermatogonia represented there was a third lying immediately underneath them (*i.e.* at a deeper level). See p. 265. $\times 1000$.

Fig. 9. Longitudinal section of the wall of a male blastostyle showing two stages in the formation of sporosacs. On the left of the figure note the spermatogonia in the ectoderm; the mesogloea is already bending outwards. In the later stage shown on the right of the figure numerous spermatogonia are seen in the ectoderm at the distal end of the sporosac, and peripheral to them are, here and there, cells with paler protoplasm and smaller nuclei which will later form the covering cells. There is a small central cavity in the endodermal spadix, but it is filled with granular matter. See p. 265. $\times 1000$.

Fig. 10. Longitudinal section of a free-swimming male sporosac. See p. 266. $\times 500$.

Fig. 11. Section of a blastula consisting of about 120 to 130 cells. See p. 277. $\times 500$.

Fig. 12. Section of a later stage of development; the cleavage cavity is now filled with a mass of endoderm cells. See p. 278. $\times 500$.

Fig. 13. Section of a still later stage in which the coelenteron has been formed by breaking down of some of the endoderm cells, the debris of which lies in the cavity. See p. 278. $\times 500$.

Fig. 14. Horizontal section of a portion of the stolon, showing the thick perisarc, the adherent debris, and the internal partitions (P I-P IV) formed successively by the coenosarc as it retreated under the influence of deleterious conditions. See p. 260. $\times 250$.

Fig. 15. Horizontal section of another portion of the stolon, showing the coenosarc, here composed of ectoderm with a solid mass of endoderm, secreting a chitinous barrier across the lumen of the stolon. The coenosarc has contracted away from the perisarc. $\times 500$.

Fig. 16. *Dicoryne conferta* (Alder). Median section, in the plane of the tentacles, of a mature male sporosac ready to be released from its stalk. In most spadices of this species there is at maturity a central cavity. Note the great thickness of the mesogloea in the wall of the blastostyle. Compare with figs. 4 and 10. For further description see p. 267. $\times 500$.

Ashworth and Ritchie: Dicoryne.

Fig. 1.

Ashworth and Ritchie: Dicoryne.

Ashworth and Ritchie: Dicoryne.