IX.—*On the Nature and Zoological Position of the* Graptolitidæ. By Henry Alleyne Nicholson, D.Sc., M.B., F.G.S.

[Plate III.]

The Graptolitidæ constitute a group of extinct organisms which may be considered characteristically Silurian, though one genus (*Dictyonema*) passes up as high as the Middle Old Red in America. Their zoological position has always been a matter of doubt; and they have been referred by different palæontologists to the Cephalopoda, the Hydrozoa, the Actinozoa, the Polyzoa, and recently to the Foraminifera. The first and last of these views require no further notice; but the remaining three are still maintained by different competent authorities, and the question must be looked upon as still undecided. In the following brief description of the morphology, development, and reproduction of the Graptolitidæ I purpose to draw attention to the facts which appear to favour the view, originally put forth by Prof. M'Coy, that the group should be referred to the Hydrozoa.

Morphology.—As to the morphology of the Graptolitidæ, the simplest form of Graptolite is composed of three factors, structurally and developmentally distinct, but united into a single linear stipe. These three elements (Pl. III. fig. 2) are known as the "solid axis," the "common canal," and the "cellules;" and when combined together the solid axis is found as a cylindrical filament, or laminar plate, having on one side of it the common canal, from which, as a common connecting substance, arise the denticulated cellules. In this way are formed those simple forms of Graptolites (Pl. III. fig. 1) to which alone the genus *Graptolites* or *Graptolithus* ought to be restricted; and by the combination of such in various different modes are formed all the remaining generic types of the Graptolitidæ. The simple uniserrate Graptolites thus composed, such as *G. Sedgwickii*, *G. sagittarius*, &c., have certainly no direct representatives amongst either the Hydrozoa or the Polyzoa; but the corneous nature of the entire polypary and the presence of a "common canal" would seem to refer them to the former, since the latter have, as a rule, a more or less calcareous test, and the individuals forming the compound organism are not united by any organized connecting substance. There is, besides, an obvious resemblance between the monoprionidian stipes and the separate branchlets of some of the Plumulariæ, such as *Plumularia pennatula* and *P. cristata*; whilst the diprionidian forms constituting the genus *Diplograpsus* have an equally obvious analogy to the ramuscles of some of the Sertularians, such as *Sertularia abietina* and *S. filicula*.

The "solid axis" is one of the primitive elements in the formation of every Graptolite. In the simple monoprionidian species it seems to be a solid cylindrical rod (Pl. III. fig. 2); but in the biserrate forms it is certainly a corneous plate, dividing the frond into two vertical compartments (Pl. III. fig. 3), apparently composed of two laminæ, with a median cylindrical rod and perhaps including a central canal. The axis may be prolonged beyond one or both extremities of the celluliferous stipe; and for convenience I shall term these respectively the basal or "proximal" and the terminal or "distal" extensions of the axis. These prolongations (Pl. III. fig. 4) are little understood; but they require especial attention, as throwing great light upon the true nature of the Graptolitidæ. The proximal extension of the axis is present in probably all the true Graptolites, and constitutes the "radicle" or "initial point" of Hall. The radicle varies greatly in length, and it may consist of the solid axis alone, as in *Diplograpsus teretiusculus* &c.; or it may be bordered by the common canal prolonged upwards into the first cellule or cellules, as in *G. sagittarius*, Linn., *Diplograpsus cometa*, Gein., and *D. acuminatus*, Nich.

Again, in most of the branching and complex Graptolites the solid axes of the various simple stipes composing the frond, together probably with the common canal, are prolonged proximally and are united into a connecting process, which is always destitute of cellules and is termed the "funicle" by Hall, as is seen in the genera *Dichograpsus* and *Tetragrapsus* (Pl. III. figs. 5, 6, 15, 16, and 20).

Lastly, the subdivisions of the funicle may be embraced by a central corneous disk or cup, which is apparently composed of two laminæ, and probably enclosed a central cavity. This corneous cup (fig. 6) is best seen in several species of *Dichograpsus* and *Tetragrapsus*; but it also exists in some specimens of *Diplograpsus bicornis*, Hall (figs. 8, 9, 10), and in a new species of *Diplograpsus* from the Upper Llandeilo rocks of Dumfriesshire, which I have named *D. physophora* (fig. 7). The distal extension of the solid axis is only seen in the *Diplograpsi*, and possibly in *Retiograpsus*, Hall, and *Retiolites*, Barr., seeming to be merely accidental when seen in the adult monoprionidian forms, as it rarely is. This distal extension of the axis usually consists of the solid axis alone, as in all the common *Diplograpsi*; but it may consist of a bladder-like body, more or less elliptical in form, with a distinct filiform margin and of uncertain function. This vesicular dilatation seems always to be a direct expansion of the axis, which would thus appear to be tubular. It is seen to a very moderate extent in some specimens of *D. pristis*, His., and *D. palmeus*,

Barr., but it is very largely developed in a new species of *Diplograpsus* from the Dumfriesshire Shales, which I have named *D. vesiculosus* (Pl. III. fig. 11).

The homologies of the solid axis, with its extensions and appendages, are by no means clear. There is no known structure, either amongst the Hydrozoa or Polyzoa, which could be looked upon as its exact equivalent; and it is probably related (but by analogy only) with the horny or calcareous "sclerobasis" of the Gorgonidæ and Pennatulidæ amongst the Actinozoa. Its chief function certainly seems to have been to give due support to the cœnosarc, and to prevent injurious flexion of the pliable polypary; but it probably subserved other purposes of even greater importance. No close parallel can be drawn between the "radicle" of the Graptolitidæ and the foot-stalk of the Sertularidæ, since the former structure beyond doubt did not serve as an organ of attachment. The central disk or cup of some *Dichograpsi*, *Tetragrapsi*, and *Diplograpsi* was compared by Prof. Huxley with the basal plate of *Defrancia*, a Bryozoon; but I think a more probable homologue is to be found in the "float," or "pneumatocyst," of the Physophoridæ, an order of the oceanic Hydrozoa. The distal extension of the axis is entirely without a parallel; and when dilated, as in *Diplograpsus vesiculosus*, Nich., it is difficult to conceive of any function which it can have subserved. It cannot be of the nature of a float, since it occupies the distal and not the proximal extremity of the organism; and the most probable view would perhaps be to consider it in some way connected with the reproductive process. The second element, namely the "common canal," is structurally a tube extending along more or less of the axis, and giving origin to the cellules. Ordinarily it appears as a flattened space between the cellules and the solid axis (Pl. III. fig. 2); and it seems certainly to be a distinct structure even in those forms in which the cell-partitions are attached to the axis. As to the intimate nature of the common canal, there seems to be no doubt that it conveyed a soft connecting substance uniting the various polypites into an organic whole; and it is therefore homologous with the "cœnosarc" of the Hydrozoa. Its existence consequently forms one of the strongest grounds for eliminating the Graptolitidæ from the Polyzoa, since no analogous structure is known to occur in any of the latter.

Of the cellules there is little to be said. They vary much in shape; but they usually constitute more or less cylindrical or quadrangular tubes, the bases of which are attached to the common canal, whilst the opposite extremities terminate in open mouths—the "cell-apertures." They thus come to re-

semble somewhat the "hydrothecæ" of the Sertularidæ; but they are invariably in contact for a greater or less portion of their length, and they do not seem ever to be cut off from the common canal by any partition or diaphragm.

Development.—The ordinary germs or embryonic forms of Graptolites (Pl. III. figs. 12, 13), in the youngest condition in which they are preserved to us, are minute corneous bodies, consisting of a small radicle or mucro, which is in fact the commencement of the solid axis. This, the primitive structure of the embryo, is widened out distally by the presence of the common canal on one or both sides, according as the germ belongs to a mono- or to a diprionidian species; and finally one or two primordial cellules are superadded. Even at this stage the solid axis projects beyond the primitive cellules as a naked rod; and its growth was probably carried on to a certain extent independently of the rest of the organism. These germs are various in size, and differ in minor details; but they all possessed a corneous envelope, and they cannot safely be compared to any of the embryonic forms of the existing Hydrozoa or Bryozoa. It must, in fact, be considered very probable that these germs, as we see them, are considerably advanced in growth, and that the earliest form of the embryo was devoid of any corneous test.

As to the further development of the stipe, it must suffice to state that in the simpler genera the secondary cellules appear to be intercalated between the initial point or radicle and the primordial cellule or cellules, so that the youngest cellules are proximal, the oldest distal in position. This mode of development corresponds with that observed in the Calycophoridæ and Physophoridæ amongst the Hydrozoa.

Reproduction.—Until quite of late years, the reproductive process in the Graptolitidæ was quite unknown; and even now our knowledge is partial and to a great extent inferential. In 1858 Prof. Hall gave a description of some specimens of *Diplograpsus Whitfieldii* bearing bodies which he regarded as ovarian vesicles. According to Hall, these appear as small ovate buds attached to the stipe on both sides, enlarging to form elongated sacs, and finally dehiscing. These sacs are limited along their margins by a filiform border like the solid axis of a Graptolite; and it appears inconceivable that their function can have been other than reproductive.

At the meeting of the British Association in 1866, I drew attention to the occurrence in the Graptolitic rocks of Dumfriesshire of bodies essentially similar to those described by Hall; and I have since described them more fully and have adduced instances in which they are seen attached to

the stipe of *Graptolites Sedgwickii*. These bodies differ from those noticed by Hall in being free in the later stages of their growth, instead of remaining permanently attached. They are oval or bell-shaped, provided with a mucro or spine at one extremity, and surrounded by a strong filiform border, which ultimately ruptures. In many instances these bodies may be seen, when small, to be attached to the cellules of *Graptolites Sedgwickii*; and they appear sometimes to spring from the common canal, though this is rare and is perhaps accidental.

That these bodies are connected in some way with reproduction appears to me to be beyond doubt. They resemble the "gonophores" of the recent Hydrozoa in being external processes, in some cases permanently attached, in others ultimately detached; the likeness in form is also striking. They differ, however, in possessing a corneous envelope, so that, when detached, they were either simple free-floating organisms, or, if they possessed any independent locomotive power of their own, this must have been obtained by means of cilia or by some soft apparatus which would leave no traces of its existence. It is probable that the capsules did not contain the germs of Graptolites as we now find them in a fossil condition, as thought by Hall, but that their contents were the ova in their earliest stages. The ova would probably be liberated, on the dehiscence of the capsule, as minute ciliated free-swimming organisms, which subsequently and as a later development acquired a corneous envelope. With regard to other species of Graptolites, it may be looked upon as probable that the gonophores, if corneous, were attached to the sides of the polypites or to "gonoblastidia," whilst in other species, again, the gonophores were probably without any corneous test; so that the great majority of species will perhaps never be found in conjunction with ovarian capsules, either free or in connexion with the parent stipe. Judging, however, from analogy, there seem to be good grounds for the belief that the reproductive process in all the Graptolitidæ was in all essential points identical with that of the Hydrozoa.

Mode of Existence. — As to the mode of existence of the Graptolitidæ, there can be no question that by far the greater number were free-floating or free-swimming organisms. In some species of *Dichograpsus*, *Tetragrapsus*, and *Diplograpsus*, there are the remains of a body (the "disk") which, as I have aleady said, probably acted as a float, and finds its best homologue in the "pneumatocyst" of the Physophoridæ. Other genera, as *Graptolites*, *Phyllograpsus*, *Pleurograpsus*, *Retiolites*, &c., were very possibly provided with "nectocalyces" or "swimming-bells;" but these, of course, could

never be preserved in a fossil condition. With regard to *Dendrograpsus* (Pl. III. figs. 16, 17) and *Callograpsus* (two genera which more closely resemble the Sertularidæ than any other), the probabilities are, perhaps, in favour of their having been fixed, though there is no decided evidence in support of this view; and the same may be said of *Dictyonema*.

Allied forms.—The affinities of *Graptolites* as regards other extinct organisms are few and uncertain. There exists, however, one allied form (Pl. III. fig. 19), which I described last year from the Dumfriesshire Shales under the name of *Corynoides calicularis*. In this the polypidom is in the form of a simple elongated tube, without any central axis, furnished at the base with two spines, and expanding distally into a toothed cup or "hydrotheca." In general form *Corynoides* closely resembles some of the Corynidæ or Tubularidæ; but the "hydrosoma has certainly been free, and was never fixed by a hydrorhiza." Whether *Corynoides* should be included amongst the Graptolitidæ, or should be regarded as the type of a new order, is doubtful; but it is certainly allied to the Graptolites, and greatly strengthens the belief that the latter belong to the Hydrozoa.

Conclusion.—I have now endeavoured to show that the position of the Graptolitidæ amongst the Hydrozoa is supported by the phenomena observed in their morphology, development, and reproduction, in their mode of existence, and by the determination of allied forms. As to their exact place, it is certain that they cannot be referred to any existing order or even subclass of the Hydrozoa, and it is probable that they stand in the same relation to the recent Hydrozoa that the Trilobites do to the Crustacea. In the arrangement of their parts and in their mode of growth, as well as in the nature of their structural elements, they more or less resemble the Hydroid polypes; but they are widely separated by their free hydrosoma. On the other hand, they approximate to the oceanic Hydrozoa in the fact that they were free-floating organisms, and in the possession, by some forms, of an organ resembling a "float." In the present state of our knowledge it seems, therefore, most advisable that the Graptolitidæ should be held to constitute a new subclass, which will hold an intermediate position between the fixed and oceanic Hydrozoa, and which might possibly, on the derivative theory of development, be considered the primitive stock from which the above existing sections of our living Hydrozoa have originally diverged.

EXPLANATION OF PLATE III.

Fig. 1. *Graptolites sagittarius*, Linn., nat. size: showing the radicle (*a*).

Fig. 2. Portion of the same, enlarged: showing the solid axis, the common canal, and the cellules.

Fig. 3. Transverse section of *Diplograpsus teretiusculus*, His.: showing the axis as a transverse plate or partition.

Fig. 4. *Diplograpsus teretiusculus*, His., nat. size: showing the proximal extension of the axis, or radicle (*a*), and the distal extension (*b*).

Fig. 5. Central portion of *Dichograpsus Logani*, Hall, sp., from a specimen collected by the author from the Skiddaw Slates: showing the branched funicle and the celluliferous stipes.

Fig. 6. Central disk and funicle of *Dichograpsus octobrachiatus*, Hall, sp. One of the divisions of the funicle (*a*) is shown prolonged into a celluliferous style (*b*).

Fig. 7. *Diplograpsus*, n. sp.: showing a disk at the proximal extremity. Collected by the author at Garple Linn, near Moffat.

Figs. 8, 9, 10. Varieties of *Diplograpsus bicornis*, Hall. Fig. 8. Normal form. Fig. 9. Variety with a rudimentary disk or cup; collected by Prof. Harkness at Glenkiln Burn, Dumfriesshire. Fig. 10. Variety with a fully developed disk, after Hall.

Fig. 11. *Diplograpsus vesiculosus*, n. sp.: showing the distal extremity of the axis expanded into a pointed vesicle. Collected by the author at Dobb's Linn, near Moffat.

Fig. 12. Germ of a monoprionidian Graptolite, enlarged.

Fig. 13. Germ of a diprionidian Graptolite, enlarged.

Fig. 14. *Didymograpsus flaccidus*, Hall, nat. size (recently described by Mr. W. Carruthers under the name of *D. elegans*). This form could obviously never have been attached, but must have been free.

Fig. 15. *Helicograpsus* (*Graptolithus*) *gracilis*, Hall, sp., nat. size: *a*, funicle: *b*, *b*, celluliferous stipes. From a specimen collected by the author at Glenkiln Burn, Dumfriesshire.

Fig. 16. Non-celluliferous stem, or funicle, of *Dendrograpsus Hallianus*, Prout, after Hall. This species may perhaps have been attached.

Fig. 17. Portion of the celluliferous branches of the same.

Fig. 18. *Diplograpsus* resembling *D. teretiusculus*, His., but furnished with two lateral spines in addition to the central radicle.

Fig. 19. *Corynoides calicularis*, Nich., enlarged. This form is allied to the Graptolites, but probably represents a different order.

Fig. 20. *Tetragrapsus quadribrachiatus*, Hall, sp.: showing the funicle, radicle, and celluliferous stipes.

X.—*On the Miocene Flora of the Polar Regions.*

By Professor O. Heer *.

The numerous expeditions sent some years ago into the arctic regions have been, in every respect, productive in a scientific point of view. The bold navigators who explored the polar regions, surmounting the greatest difficulties, used every effort to bring back whatever they supposed might possess interest. Geology has had its share in the results of these researches. A considerable number of fossil plants

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