ON THE DICTYONEMA-FAUNA OF NAVY ISLAND, NEW BRUNSWICK

BY F. F. HAHN

(Presented by title before the Academy, 13 May, 1912)

	Page
Introduction.....	135
Given faunula.....	136
Astogeny of <i>Dictyonema flabelliforme</i> in comparison with that of <i>Staurograptus</i>	144
On the structure of <i>Dictyonema flabelliforme</i>	146
Mode of life of <i>Dictyonema flabelliforme</i>	148
On the occurrence of stratigraphical range of the varieties of <i>Dictyonema flabelliforme</i>	151
Significance of the varietal range and its phylogenetic value.....	153

INTRODUCTION

One of the older modes of paleontological investigation, the study of the range and significance of variability, seems now to be somewhat overtaken by and neglected on account of the excellent results obtained in the study of the stages of earliest youth, growth and senescence. My own studies on Jurassic invertebrates, which made me familiar with a vast number of individuals of many species, brought me to the conviction that a combination of these two modes of treatment would, in every case where the given material is sufficient, lead to an advance greater than would be possible by either method alone. Thus, when I worked over in the Museum of Columbia University the wonderful collections from the Dictyonema-shales made by G. van Ingen and W. D. Matthew at Navy Island, N. B., from Division III, b, c, commonly regarded as Upper Cambrian,¹ of course my first thought was to see whether I could find any relationship between the range of variability and the history of the races among the Dictyonemas. And this animal association seemed well adapted to this kind of study, for though the Dictyonema-shales contain a vast number of individuals, there are only four species common, two of which are graptolites.

¹ According to the trilobites found in Sweden and England, it must apparently be placed at the base of Ordovician.

G. F. Matthew, it is true, presented in 1891-2² a detailed description of this fauna, to which in 1895³ he added some important remarks; but R. Ruedemann, the masterly monographer of the graptolites of New York,⁴ reached such a different result concerning the questionable graptolites, that from this standpoint, too, a careful revision seemed to me somewhat desirable.

I hold it a pleasant duty to give my full thanks to those who have so kindly aided me in the preparation of this paper, in the first place to Prof. A. W. Grabau, to whom I owe many a reference and suggestion, then to Dr. R. Ruedemann, who took part in the discussion of the preliminary paper, presented at the Washington meeting of the Paleontological Society in 1911.

It is the task of this paper to give

1. A detailed faunal redescription;
2. some general remarks on the early stages, structure, basal organs, occurrence and preservation;
3. the significance of the varietal range and its supposed phylogenetic value.

THE GIVEN FAUNULA

Dictyonema flabelliforme Eichw. (sp.)

- (1) 1904. R. RUEDEMANN, Graptolites of New York, I, p. 599, Pl. 1 (with references to the earlier descriptions).
- (2) 1906. J. CHR. MOBERG and C. O. SEGERBERG, Bidrag till Kaennedomens om Ceratopyge-regionen. Meddelande från Lunds Geologiska fäbtklubb, Ser. B, No. 2 (and Lunds Universitets Årskrift, N. F. Afdeln, 2. Vol. 2, No. 7).
- (3) 1907. W. G. FEARNSIDES, The lower Ordovician Rocks of Scandinavia. Geol. Mag., Dec. V, Vol. 4, N. S., p. 257.
- (4) 1909. A. H. WESTERGAARD, Studier æfver Dictyonema-skiffern, Meddelande från Lunds Geologiska fäbtklubb, Ser. B, No. 4, p. 60 (Lunds Univ. Årskrift, N. F. Afdeln, 2. Vol. 5, No. 3).

I consider the following to be the best apotypical⁵ figures:

- (5) 1882. W. C. BRÜGGER, Sil. Etagen, pl. 12, figs. 17, 18.
- (2) 1906. J. CHR. MOBERG, Ceratopyge regionen, pl. 1, fig. 6.
- (4) 1909. A. H. WESTERGAARD, Dictyonema-skiffern, pl. 3, figs. 3-5.*

² Trans. Roy. Soc. Canada, Sect. IV, No. VI, p. 33, and No. VII, p. 45.

³ Two New Cambrian Graptolites, Trans. N. Y. Acad. Sci., Vol. 14, p. 262.

⁴ New York State Mus., Mem. 7. 1904 (1).

⁵ Buckman, Yorkshire Type Ammonites, Terminology, p. VI. 1909.

* Of all long-known index fossils like *Dictyonema flabelliforme*, the best figured types ought to be mentioned, in order to get correct reproductions into the textbooks.

The former investigators of this species had very diverse ideas regarding the question of the significance of the modifications occurring in these forms. While most of the writers remained quite doubtful as to the possibility of separating even earlier varieties on account of the abundance of crossing forms, [*e. g.*, S. A. Tullberg (1882),⁷ who thought such separations "erroneous," R. Ruedemann (1904), who called them "questionable"], Th. Kjerulf (1865),⁸ listed *D. norwegicum* and *D. graptolithinum* (= *flabelliforme*) as being different species and he was followed by W. C. Brögger (1882 (5),⁹ p. 35), who distinguished and described carefully *D. flabelliforme forma typica*, var. *conferta* and var. *norvegica*. Among the *D. flabelliforme* of Navy Island, G. F. Matthew¹⁰ regarded his variety "*acadica*" as the normal type and he was quite able to identify two more varieties with those described by Brögger. Finally Moberg (1906, (2), p. 60) separated *D. flabelliforme* and *D. norwegicum*, but did not furnish sufficient proof of his contention. In the guide books of the International Geological Congress in Sweden in 1910 (compare No. 40, Scania), the same author again uses, as did A. H. Westergård a year before, the names *typica*, *conferta*, *norvegica*, as varieties of *D. flabelliforme*.

Indeed, one glance over the descriptions and figures of the protographers, in comparison, *e. g.*, with Ruedemann's pl. 1, fig. 20, Westergård's pl. 3, fig. 7, or Brögger's pl. 12, fig. 17, shows such a distinct aspect of the forms mentioned that at least a varietal subdivision seems a quite natural one.

My own abundant material, among which I have examined carefully about 500 individuals, soon compelled me to keep apart the five variations: *acadica*, *conferta*, *ruedemanni*, *desmograptoidea* and *norvegica*, as did Matthew to a certain extent before me.

Dictyonema flabelliforme Eichw. var. *acadica* Matthew

Apotypes. Besides the figures of BRÖGGER, MOBERG, WESTERGÅRD, mentioned above.

- (6) 1859. GÖPPER, Fossile Flora d. sthr. dev. und unt. Kohlenform. Acta Leop., 27: 31, pl. 36, fig. 6.
- (7) 1865. TH. KJERULF, Veiviser, Christiania, p. 3, fig. 5, 4a.
- (8) 1882. S. A. TULLBERG, in Helsingers graptollites. Bihang till kgl. Sven. Vet. Ak. Handl., Vol. 6, pl. 3, fig. 4.
- (1) 1904. R. RUEDEMANN, pl. 1, fig. 21.

⁷ Helsingers Graptollites. Bihang till kgl. Sven. Vet. Ak. Handl., Vol. 6.

⁸ Veiviser, Christiania.

⁹ The numbers in parentheses refer to the literature citations as the basis of the divisions of the text.

¹⁰ *Loc. cit.*

Description: Generally infundibuliform, branches more or less parallel, frequently dividing, width of tissue 9-10 mm., cross-threads somewhat irregular, of medium number; open rectangular meshes; thecae 15 to 17, projecting, of medium size.

Notes: Slight changes of the characters are fully shown on the diagram. Plate XX. Greatest length observed about 200 mm., width 190 mm.; approximately 2 x 150 branches.

The variation of the number of thecae is marked, 16 being present on the American examples, but only 10-15 in 10 mm. on the European examples. This fails to be of general value, as G. F. Matthew has pointed out, since the figures of Brögger (5) and Tullberg (8) also exhibited 16 thecae and Westergård states recently a usual number of 15-16 thecae on the Swedish examples ((4), p. 58). When comparing the form, collected by Prof. A. W. Grabau from Skåne (region of Fogelsång), with the American specimens, a more delicate character of the whole tissue of the European type is apparently the one observable difference on which a separation of var. *acadica* Matth. and "forma *typica*" of the Swedish authors can be based.

Var. *conferta* Linns (ms.)¹¹

Apotypes:

- (6) 1860. GÖPPERT, pl. 36, fig. 11, 4.
- (9) 1861. SALTER, Geol. Survey Gr. Brit., Mem. 3, pl. 4, fig. 1.
- 1881. SALTER, Geol. Survey Gr. Brit., sec. ed., p. 535, pl. 41, figs. 1, 1a, 1b.
- (8) 1882. TULLBERG, p. 20, pl. 3, fig. 3 (1, 2?).
- (4) 1909. WESTERGÅRD, pl. 3, fig. 7.

Description: Characterized by Brögger (5), p. 36) as having very fine and close network and cross-threads of the same kind.

Matthew¹² added "commonly vasiform, cross-threads more frequent than in *acadica* (5-7). 15-17 thecae are usually met with in 10 mm."

I have observed even 18 on a typical specimen; young specimens often show only 14-15 thecae. The rigid aspect of the branches and their regular branching, which commonly takes place in the same level, seem rather important additional features. Here, too, a little more delicate structure of the whole tissue distinguishes the Swedish specimens, so that Westergård found 13 branches in 10 mm. of width, while 8-10 branches may be usually numbered on the American variety. The largest observed colony measures 22 mm. in width, occupied by 19 branches, and 82 mm. in length.

¹¹ Brögger (5) furnished as long ago as 1882 an undoubted description of this form, while Poeta created his species "*conferta*" not earlier than 1894 (Système allurien, Bryozoaires, etc., Vol. VIII, t. 1er, p. 194). The last ought to be renamed, if this is necessary at all.

¹² *Loc. cit.*

Var. *norwegica* Kjerulf.

Apotypes:

- (7) 1865. KJERULF, p. 2, fig. 4 (1-3).
 (2) 1906. MOBERG, pl. 1, fig. 7.
 (4) 1909. WESTERGÅRD, pl. 30, figs. 8, 9.

Description: After Brögger (5), p. 36), thick cross-threads, close network; small, short, rounded meshes.

I observed only 15 thecæ. Young stages like var. *acadica*. Crossings of all kinds into true *acadica* occur. A slight distinction between my specimens and the Swedish ones is in so far recognizable as the first are furnished with a little more elongated meshes, but they can be precisely compared with Westergård's figures. My largest colony is 40 by 40 mm., while Westergård cited a specimen 115 by 30 mm. in size.

Var. *ruedemanni* nom. nov.

Typical figures:

- (1) 1904. R. RUEDEMANN, pl. 1, figs. 16-20, 22 (12-15, non fig. 21).

Apotypes:

- (10) 1895. G. F. MATTHEW, Trans. N. Y. Acad. Sci., Vol. 14, pl. 49, figs. 1, 2.
 (The figures are not quite correct, showing a too open tissue.)

Compare

- (5) 1882. BRÖGGER, pl. 12, fig. 19.

Description: In neplastic stage strongly branching at an almost acute angle. Full-grown specimens with crowded, more or less parallel branches up to 14 in 10 mm. width. Dissepiments appearing early, but afterwards irregularly scattered. Thecæ small, not much projecting. Adhesion organs relatively common.

Notes: Generally funnelform, sometimes of intermediate shape (pyriform) towards the vasisform variety "*conferta*." Measurement of a typical pyriform specimen:

Length	Width in mm.
10	10
20	25
25	35
48	65

The specimens obtained from Navy Island (N. B.) fully agree with Ruedemann's figures, but several specimens considerably surpass the given characters in the same direction. In Europe it is rare, but abundant in America, at Navy Island as well as at Schaghticoke. Largest measured colony 165 mm. in length and 140 mm. in width.

Var. *desmograptoides* var. nov.

Description: Infundibullform. Open meshwork of irregular, mostly sub-oval fenestrules. Branches undulating and sometimes confescent. Infundib.

ments quite irregular, partly thickened. Thecae 15 in 10 mm., not much projecting, rarely visible.

Note: Sometimes an old stage of var. *acadica* has these characters.

J. Hall's¹³ *Dictyonema irregularis* resembles most this variety, but has a closer arrangement of the branches (25-28 in 1 inch) and occurs in higher Ordovician of Canada and Great Britain. *Dictyonema homfrayi*, described by T. Hopkinson and Ch. Lapworth,¹⁴ seems to be a closely related species. *Desmograptus intricatus*, as shown in fig. 30, p. 609, by Ruedemann (1), exhibits exactly the same type in early stages, though belonging to the Chazy and having appressed thecae. No well-preserved, large specimens are known, but several pieces are found indicating a width of the colony of more than 60 mm.

***Staurograptus dichotomus* Emmons var. *apertus* Rued.**

- (1) 1904. R. RUEDEMANN, pp. 612-614, pl. 2.
- (11) 1891. G. F. MATTHEW, "*Bryograptus kjerulfii*," Trans. Roy. Soc. Canada, Sect. IV, No. VI, p. 35.
- 1892. G. F. MATTHEW, "*Bryograptus patens* Matth.," No. VII, p. 95, figs. 1a, 1d (excl. lower figure of 1b).
- (10) 1895. G. F. MATTHEW, *id.*, p. 268, pl. 48, fig. 4 (?).
- 1895. G. F. MATTHEW, "*Bryograptus lentus* Matth.," *id.*, p. 270, pl. 48, fig. 2.
- 1895. G. F. MATTHEW, "*Clonograptus proximatus* Matth.," *id.*, p. 265, pl. 48, fig. 1.

In 1895, G. F. Matthew tried to keep separate five species of *Clonograptus* and *Bryograptus*, occurring in Division 3, band c on Navy Island, N. B. In 1903, Ruedemann¹⁵ followed him, believing that four of Matthew's species were again recognizable, but a year later, in his Monograph on the Graptolites, he came to the conclusion that practically all these species and even genera present only definite stages of growth and preservation of *Staurograptus dichotomus*, a species established by Emmons in 1855, but rather dubious up to 1904. Ruedemann, indeed, furnished such a description and figures of this species, especially of the variety "*aperta*," that complete identity with the species of Matthew enumerated above becomes apparent, if we look over the types of Matthew, which fortunately were in part accessible to me.

¹³ Canadian Organic Remains. Geol. Surv. Can., Dec. 2, p. 136, pl. 20, figs. 1, 2, 1868.

¹⁴ Graptolites of the Arenig and Llandello rocks of St. David's. Quart. Journ. Geol. Soc. London, Vol. 31, p. 608, pl. 36, fig. 13. 1875.

¹⁵ "The Cambic *Dictyonema* fauna in the Slate Belt of Eastern New York." N. Y. St. Pal. Ann. Rep., Bull. 69, p. 938.

The type specimen of *Clonograptus proximatus* (1895, pl. 48, Figs. 1a, 1d) proves to be almost identical with Ruedemann's figure 23 on plate 2, besides a slightly greater elongation of the thecae. Of these, I have found distinctly 8 in 8 mm. of length of the branches, the latter not surpassing 25 in number. The fork-like mode of branching seems highly characteristic.

On the same slab, the type of *Bryograptus lentus* Matth. (1895, pl. 48, fig. 2) is found, appearing at first glance very distinct from that of "*Clonograptus proximatus*," but here, too, 9 to 10 thecae of a breadth up to .75 mm. are seen, showing the same aspect as Ruedemann's figs. 19 and 21. Moreover, this slab exhibits another crowd of branches which in part are completely identical with "*Clonograptus proximatus*," while a few branches turned to side view show the real aspect of "*Bryograptus lentus*." Here again, 9 thecae are recognizable in 10 mm. of length of a branch which is 1.6 mm. thick and of the same shape as Ruedemann's fig. 15. This group of *Staurograptus* has still greater importance, since three individuals of medium size have their siculae preserved and present the characteristic side view of Ruedemann's fig. 6. As a great many other specimens of the collection which formerly were determined as "*Bryograptus patens*," and indeed readily conform to Matthew's fig. 4, on plate 48, really belong to nepiastic stages of *Dictyonema*,¹⁰ a similar reference of the type of Matthew seems quite possible, but I have not seen the type specimen, and thus this explanation may still be questionable.

A few additional notes can be added to the description by Matthew and Ruedemann.

The preservation showing the thecae in full size and the sicula is rare on examples surpassing a diameter of 5 mm. The thecae, scarcely more or less than 9 in 10 mm. length of the branch, are sometimes irregularly exposed, 6 smaller ones being visible in 4 mm. of the distal end and 4 a little coarser ones in 4 mm. of the proximal part of the same branch. Young stages, especially when crowded together, are almost inseparable from those of *Dictyonema flabelliforme* var. *ruedemanni*, while the bryograptoid neanastic stages of *D. flabelliforme* var. *aradica* and *conferta* are easily mistaken for the "*Bryograptus lentus*" aspect of laterally compressed *Staurograptus*. The great thinness of the periderm of *Staurograptus*, which never shows such a tubulose structure or wrinkling as in the case of *Dictyonema* (compare the above), is a very remarkable fact and helpful in distinguishing these two genera. In the same respect, the

¹⁰ Compare Westergård (4), pl. 3, figs 5 and 6

more rigid characters of the mucronate apertural margin of the thecae in *Staurograptus* may be noticeable.

Unfortunately, I was not successful in finding any remains which can be compared with "*Bryograptus spinosus* Matth." ((10), p. 269, pl. 48, fig. 3) and "*Clonograptus spinosus* Matth." ((11), p. 97, pl. 7, fig. 2), which is said to present only 8 thecae in 10 mm. of length of the branch and a distinct "axis or virgula." Nevertheless, here, too, the identity with *Staurograptus dichotomus* seems to me not quite impossible. Nor could I observe any specimens belonging to "*Bryograptus ? retroflexus*" (Matthew (10), p. 271) or to *Callograptus* (l. c., pl. 48, fig. 5), which therefore must be at least extremely rare.

On the contrary, with an abundance of individuals there is found

***Monobolina refulgens* Matthew**

(11) 1891. G. F. MATTHEW, p. 44, pl. 12, fig. 6.

(12) 1903. G. F. MATTHEW, Report on the Cambrian Rocks of Cape Breton. Geol. Surv. of Canada, Ottawa, p. 210, pl. 11, fig. 4, pl. 16, fig. 2.

Since generally separated valves and even broken pieces occur, nothing can be added to the careful description of the author, besides the observation that this species is seen on the same surface associated with all varieties of *Dictyonema flabelliforme* and with *Staurograptus dichotomus*.

***Lingulella nicholsoni* (?)**

Almost the same is true of a linguloid shell, cited by Matthew in 1895 (p. 273) as *Lingulella nicholsoni* (?) and in 1903 ((12), p. 204) doubtfully called *Lingulella "lepis* Salter." The specimens of the Columbia collection usually have a length of 4 to 5.5 mm., a width of 3 to 4.8 mm. and exhibit a distinct ridge on the interior of the pedicle valve. They differ from the English type as described by Salter ((9), second ed., p. 538, fig. 11) in a relatively greater feebleness and scarcity of the lines of growth. It may be of interest to note that a very similar "*Lingulella*" of Scandinavia is referred by Brögger ((5), p. 44, pl. 10, fig. 5, from the Tremadoc shales) and by Moberg ((2), from the *Bryograptus* zone) to *L. lepis* Salter.

In addition to this detailed discussion of the *Dictyonema* fauna, a callograptoid graptolite of the upper Beekmantownian may be described, because of its interesting phyletic relationships.

***Callograptus grabaui* sp. nov.**

Flabelliformis or shrub-like, not more than 15 mm. in length and 10 mm. in width of the dendromes observed. Short, non-celluliferous, basal stem (1 mm.

long, .5 mm. wide) with terminal expansion to an adhesive bulb (of .8 mm. in width). Branches 10 to 13 in 10 mm. width, 3-4 mm. wide, closely arranged, sub-parallel, sometimes slightly flexuose. Scula of one specimen 7 mm. long, determinable as being a very thin tube about 1 mm. in length, with a minute basal disk .7 mm. in width. Within the first 5 mm. of the length of the dendrome, a very frequent branching, sometimes of monopodial aspect, with a common angle of 50-60° takes place. Branches of the third and fourth order are usual, those of the sixth still observable. The interspaces between the branches vary from .3 mm. to 1 mm. in width. Most of the specimens are dorsally depressed and therefore, as commonly found in sandy shales, they do not exhibit the thecae. Only a few branches, laterally compressed, show 19 to 21 thecae in 10 mm. of length of the branch, as sharp spinelike prolongations, quite similar to those of *Dictyonema tabelliforme* (cf. Ruedemann (1), p. 601, fig. 26). Very seldom one or the other of these apertural processes reaches the neighboring branch, joining it like a dissepiment. The periderm seems to be composed of two layers, of which the greenish external one adheres to one side of a split slab, while the black interior layer remains on the other side, distinguished by a wrinkled surface. Aside from this no striation is visible.

FIG. 1.—*Callograptus grabauti*
sp. nov. (3/1)

Stratigraphic Position and Mode of Occurrence: The type specimen was sent to the Columbia Collection by Victor Ziegler, who obtained the fossil from Center County, Pa., "2000 feet from the bottom of the limestone series which are referred by Collie to the Beekmantown."¹⁷ The animal mass is profusely scattered on the sandy surface of the thin-bedded, impure limestone.

The close relationship of this species to *Callograptus salteri* Hall and *C. compactus* Walcott is proved by the following table: it is contrasted only by the distinction of the thecae.

	<i>C. salteri</i>	<i>C. compactus</i>	<i>C. grabauti</i>
Max. observed size	17 mm.	40 mm.	15 mm.
Number of branches in 10 mm. width	12	13	10-15
Thickness of branches	2 mm.	3-4 mm.	3-4 mm.
Number of thecae in 10 mm.	14-18	12-14	19-21
Interspaces	thickness of branches	thickness of branches	average thickness of branches

¹⁷ This zone may belong to Ulrich's Stoughsike limestone

J. Hall, who first described *Callograptus*, laid special emphasis on the characters of the whole dendrome and as in this respect the new species, *C. grabau* fully agrees, it must be for the present referred to this genus, even though the deviation in the aspect of the thecae shows two divergent lines of evolution among this "genus," similar to those in *Dendrograptus*, *Ptilograptus* etc. The striation of the rhabdomes, which some authors regard as an important feature of the genus, is not mentioned in the early description of *Callograptus salteri* by J. Hall, while Ruedemann observed such longitudinal striations "when the thecal tubes have been pressed through the periderm." This is also entirely the case in the new species.

There are three other genera of the Dendroidea which hold a median position between *Dictyonema* and *Dendrograptus* and to which *C. grabau* could be considered to belong. *Odontocaulis* is of quite the same shape, but occurs a little later in Ordovician and Silurian time and differs in its celluliferous stem. *Calyptragraptus*, a Niagaran genus, shows independence of the main rhabdomes down to the root as an essential feature. *Rhizograptus*, in its genotype (the Niagaran "*bulbosus*"), has branches, more or less reticulated, joined or overlain by others. The dissepiments of *C. grabau* are extremely rare, so that a position among the true *Dictyonema* would be erroneous, likewise, a union with *Dendrograptus* seems to transgress the natural and originally assumed limits of this genus, considering the presence of cross-bars and the shrub-like, or perhaps even funnel-form growth of the polyparium.

ASTOGENY OF DICTYONEMA FLABELLIFORME IN COMPARISON WITH THAT OF STAUROGRAPTUS

The collection of Columbia University contains such a number of the earlier stages of the two genera that I was easily able to select a complete series beginning with the sicula and closing with the full-grown colony and this series is now preserved in the paleontological museum. Still, only a few remarks can be added to the illuminating description of Ruedemann so far as the later stages of *D. flabelliforme*, as described by this author, deviate in some respects from the normal ones presented by "*forma typica*." All essential features, however, fully harmonize with Ruedemann's observations.

After the formation of the sicula, marked by a short, stout initial part on *Dictyonema*, by a slender, curved one on *Staurograptus*, the katembryastic¹⁸ series begins with the budding of the first, second and third

¹⁸E. R. CUMINGS, "Development of some Paleozoic Bryozoa," Am. Journ. Science, Vol. XVII p. 50, 1894.

thecæ. These nepiastic stages of *Dictyonema* are characterized by the large angle of divergence of the first theca, the next following tripod aspect, particularly by the 4-branch-stage fairly symmetrical and basket-like (compare figures on plate XXI), while *Staurograptus* has the first bud apically derived and mostly appressed and passes afterwards through a characteristic stage with six branchlets resting in a plane vertical to the axis of the sicula. It further exhibits a slight asymmetry because of accelerated divisions of one of the primary branches. The following neanastic stage develops not only wholly the specific features, but even some of varietal value, while nemas become rare. In *D. flabelliforme* var. *acadica*, a subsequent dividing of the co-equal four primary branches happens after this, though on one or the other retarded branch 3, 4 or even 6 thecæ may form a uniserial twig before its division. (Compare figure 2 on Plate XXI.)

The first dissepiment, being the last appearing generic feature, is developed as a rule when branches of the third or fourth order are present. Thus very often a lateral compression of the movable branches will furnish a striking bryograptoid view. The same is true in var. *conferta*, besides the fact that with the latter a monopodial dividing frequently occurs. The neanastic stages of var. *ruedemanni*, however, are characterized by irregularly crowded branching and early appearance of cross-threads, as fully described and figured ((1), plate 1, figs. 13 to 19) by Ruedemann. Beyond that, several of the neanastic specimens of this variety prove to be so much accelerated, that immediately from the sicula a thick scarcely resolvable bush of rhabdomes appears to arise in a real dendrograptoid manner of growth. Neanastic stages of var. *norwegica* and var. *desmograptoides* do not deviate from those of the forma *typica* except in one specimen of the latter variety, which has the irregular division of the branches at a remarkably large angle somewhat accelerated.

Staurograptus dichotomus generally runs through a 5- or 7-branch-stage and the individuals of this collection turn into var. *aperta* by slow or retarded dividing of an angle of 70° to 90° .

The ephebastic stage of *Dictyonema flabelliforme* chiefly establishes the characteristic outline of the colony which is infundibutiform in var. *acadica*, *norwegica*, *ruedemanni* and *desmograptoides*, pyriform in *ruedemanni* m. f. *conferta* and vasiform in *conferta*. It is in this stage that the essential features of variety *desmograptoides* and *norwegica* are fully developed. Basal expansions are now more commonly found. The ephebastic stage of *Staurograptus*, relatively rare, regarding the surplus of younger individuals, shows a diminution of the angle of divergence, en-

largement of the theca and an oblique tendency of the unsupported rhabdomes, which leads to a bryograptoid exterior.

Gerontastic features are noticeable in some specimens of *Dictyonema flabelliforme* var. *conferta*, in which the development of the main varietal feature is carried to an extreme as exhibiting a reduction of the diameter of the synhabdome on its posterior end. Very large individuals of var. *acadica* indicate an undulating shape of the rhabdome, while this is telescoped in other specimens into ephebastic and even neanastic stages.

As to the possibility of keeping distinct the young stages of *Dictyonema* and *Staurograptus*, the 4-branch-stages of the first one, which does not go beyond the declined¹⁹ position, and the 6-branch-stage of *Staurograptus*, which gets into a deflexed or even horizontal position of the branches, are of greatest importance. A similar difference holds true in regard to *Bryograptus*, of which Westergård has recently described beautiful specimens of *B. hunnebergensis* (4), pl. 5, figs. 10-23).

I may call attention to the fact that the *Dictyonemas* here found exhibit all features of a true epacmic genus, since this increasing period of evolution is indicated by (1) the relatively long duration and the clear distinction of the early stages, because of non-existence or at least only the beginning of acceleration of the characters; (2) the appearance of new "postspecific" features in the metephebastic age, which may become inherent ones and may be pushed back by acceleration in the descendants; (3) the fact that senile features make their appearance late and are rare, if we confine them to those which doubtless manifest a decline of the individual or the colony; (4) the fact that the genus in question maintains its position at the base of a more or less widely branching evolutionary series. All these features are shown in *Dictyonema flabelliforme* from Navy Island, N. B.

ON THE STRUCTURE OF *Dictyonema flabelliforme*

Though the specimens available for study were compressed upon the shale and so do not permit investigations similar to those made by Wiman, I have nevertheless been compelled to direct my attention to the points raised by these investigations, since several recent writers have spoken rather slightly of them or have considered them open to question.

At first glance, a striking difference seems to exist between the graptolitic mass, one rhabdome exhibiting a reflecting silvery surface while others show a matt blackish one. By cautiously scraping on the best-

¹⁹ See Ruedemann (1), p. 485.

preserved specimens, the reflecting layer is found beneath the matt exterior, which usually adheres to one side of the split slab, the reflecting layer remaining on the counter side. If we shave the reflecting mass away, again a matt black skin can be recognized. This is apparently the same type of observation made by Frech on the graptolites of Sadewitz.²⁰ He states that a dark horny cover is separable from a brilliant interior layer and that the latter consists of calcite crystals. I could not get, it is true, any reaction on touching the mass with hydrochloric acid. Nevertheless, I believe that the two sheets described may represent the epidermal and mesodermal tissues of these ancient hydroid zoaria.

As to the composite character of the rhabdomes, on all better preserved branches, the wrinkled structure long ago recognized by a great many authors can easily be seen in var. *acadica* and *conferta*, while rarely observable in the other varieties. After much search, I succeeded in finding a few dendromes on which pyritization had partly taken place, so that several minute tubes about .10 mm. in width are shown in relief running along the thecæ in a slight curve (compare Ruedemann (1), p. 607, text figure 28) toward the aperture.

The terminal pores of these little tubes, however, were to be found only on one flanking branch of a rhabdome belonging to var. *acadica*, which closely resembled Wiman's *Dictyonema rarum*²¹ (pl. 12, fig. 10). I was able to trace back this composite structure up to the second theca, but it was by no means recognizable either on the sicula or on any adhesive organ. That, furthermore, the wrinkling of the surface has nothing to do with any stress, is proved by the fact that a true cleavage sometimes does exist, cutting the widely scattered rhabdomes on a slab in one and only one direction. It produces a very fine cross striation which, in the beginning, I was inclined to regard as a true ornamentation; but when R. Ruedemann kindly called my attention to the possibility of the other explanation, a renewed study soon brought me to accept it.

Another old observation, that below the fan-like tissue of a *Dictyonema*, the counter wall of the funnel can be obtained by careful preparation, which I always found true among my material, was elucidated in another way, because I got several specimens which had been quickly buried and compressed in such a manner that the apertural spines of the thecæ of one wall make their appearance in regular, pointed rows between the meshes of the covering side of the funnel. Very often, too, the variety *ruedemanni* has its rhabdomes so badly pressed together that it

²⁰ F. FRECH and F. ROEMER, *Lethæa geognostica*, part 1, p. 510, 1880-91.

²¹ CARL WIMAN: "Ueber die Graptoliten," *Bull. Geol. Inst. Univ. Ups.*, Vol. 2, p. 12, fig. 10, 1895.

becomes rather difficult to keep those of the two sides distinct, on account of the shape and density of the branches.

MODE OF LIFE OF *Dictyonema flabelliforme*

Writers differ greatly in their opinion regarding the mode of life of *Dictyonema flabelliforme*, one considering it planctonic, another benthonic, but in recent years the idea of an epiplanctonic²² life, i. e., by adhesion to floating seaweed, has been introduced with success by Walther and Lapworth. Even, however, in the case of *Dictyonema*, where among the Dendroidea the epiplanctonic theory might possibly have applied, an earnest objection was raised by Wiman when he showed that *D. cavernosum* had branching stolons, partly strengthened by radial ribs, leading him, as it did Jaekel before him, to the conclusion that this species, like the "sessile denizens of the deeper regions," must have formed meadows on the bottom. Matthew found at Navy Island two mature forms, each with a distinct rootlet, and yet he made the suggestion that "possibly these processes may have had some other office than that of anchoring." Ruedemann, agreeing with him, lays special stress on the fact that all well-preserved specimens from Schaghticoke, whenever retaining more than the sicula, were provided with long thin nemas. Thus he is inclined to assume a suspended life for *Dictyonema flabelliforme*, with fixation in old stages, as unimportant exceptions. Recently, Westergård, to whom we owe the best work on the Swedish material, completely disregards the indications of what was called a "rootlet," stating that among one hundred specimens no nema and no disk has been observed in spite of distinct proximal parts exhibiting free siculae.

With these contradictory facts in mind, when studying the Columbia collection, which fortunately preserves the two known examples of rootlets, I proceeded to investigate all the available material with the following results: Of 500 specimens part way through the first stages of growth, only 20 per cent have a well-preserved sicula, which even in ephibastic stages ends, as a rule, in a sharp point; a few specimens, most of which are not quite ephibastic, are provided with a nema as in Ruedemann's examples and I observed only three nemas up to 20 mm. in length; the younger the stages, the more individuals possess nemas; 78 per cent have a more or less broken or concealed end, about 2 per cent other basal organs.

In order to present a fair account of the last, I have tried to draw all the examples in question with most careful accuracy. (Plate XXI.)

²² Walther used the term pseudoplancton; the term epiplancton has been introduced by Grabau to cover organisms living on or attached to pseudoplancton.

In this connection several observations seem noteworthy.

1. Number of basal organs: var. *conferta* 2, var. *ruedemanni* and *ruedemanni* m. f. *acadica* 6, *acadica* juv. 2.

2. At least one neanastic specimen of var. *ruedemanni*, 10 mm. long, shows clearly a perfect stipe with a fringed, attaching expansion at the base.

3. Nema and stolon-like stem have the same structure. They gradually increase from .1 to .6 mm. in width and are traversed by a central canal.

4. Disks may be expanded from the nema, the stolon-like stem or immediately from the sicula.

5. When basal stipes are present, the siculae are rarely kept distinct.

6. Budding from stolons is not an unlikely occurrence.

A few detailed observations may give confirmatory evidence. As to point 6, a young individual of var. *conferta* (11 mm. in length) has attached to the top of its sicula a small body .5 mm. in length, from which an irregularly fringed stem rises in the opposite direction, while to the left denticulated processes depart. I consider it quite possible that these denticles mark newly appearing thecae which budded from the stolon-like stipe, as in the case of Wiman's *Dictyonema cavernosum*; but the unfavorable kind of preservation as well as the singularity of the specimen fail to furnish sufficient certainty of this explanation (see plate XXI, 1b).

Figs. 3b and 4d on plate XXI are the types of Matthew (1895) which belong to the variety *ruedemanni* and are crowded on the same surface with 16 other *Dictyonemas*. Only four of them have distinct proximal parts, one a simple sicula, one (see fig. 4a) exhibits a relatively thick stem distally broken off, the other "rootlets," the distal portions of which are not quite evident. Siculae are lacking, apparently from being overgrown by the mass of the stem.

The individuals of figs. 3a, 4b can be explained as provided with true floating organs. The specimen of figure 4c is excellently preserved, therefore of particular importance.

Now, Ruedemann, though fully discussing the great probability or, as I think, necessity of the suggestion of a true sessile life in the later Dendroidea, objects ((1), p. 579) that "no cases of actual attachment and fixation have yet been recorded." Hence, I searched among modern benthonic forms provided with similar organs for attachment and believed I had succeeded, when I visited the excellent collection of the Smithsonian Institution at Washington. On the Gorgonias there exhibited, exactly the same kind of stems, partly stout and short, partly

elongated and relatively thin are observable and they rise from the same terminal expansions characterized by irregular shape, fringed margins, corroborating ribs and rootlike filaments, all that as changeable as required by the nature of the point of fixation. I mention, especially, *Paramuricea borealis* (from 200 fathoms) and *Acanthogorgia armata* (from 160 fathoms), from the Gloucester fisheries. The last, a large, dendroid form, is furnished with a basal stem extending distally into a rather thin, irregularly shaped expansion which adheres by means of two dependent lobes to the rounded edge of a boulder about four inches long. The similarity of this attaching instrument to that of the *Dictyonema* figured plate XXI, 3b, is of great significance. According to my opinion, the only reason that we have not yet succeeded in finding actual fixation of the Dendroidea lies in the fact that the sediments of those places on which the dendroids actually flourished were not favorable for preserving the delicate graptolites, while in the common "graptolite shales" we do not have the sediments on which the Dendroidea actually grew, an assumption strengthened by the mode of embedment discussed in the next chapter.

To get the significance of the foregoing statements, I may explain them in the following manner: Of all distinct varieties from Navy Island, those which tend to a callograptoid and dendrograptoid aspect also present the greater part of adhesive organs; these are not confined to the gerontastic stage and not separable from the nemas; the great variation of basal organs imply a similar variation of habitat.

Here, too, we must bear in mind the results of the last fifty years' work, as follows:

Supposed Cambrian ancestors of *Dictyonema*, with sicula, planetic.

Earliest Ordovician, *Dictyonema flabelliforme*; young stages with long flexible nema and thin adhesive disk, ephebastic stages generally with free sicula, one variety sometimes sessile and that possibly beginning in neanastic stage.

Later Beekmantown, *Callograpti*²³; free siculae sometimes observed, particularly in young stages, later robust stems or hydrorhiza commonly occur.

Later Ordovician and Silurian, *Dictyonemas*; no nema and almost no trace of a free sicula observed; on *D. cavernosum* branching stolons with buds; on the whole, 12 species²⁴ are known provided with organs adapted for constant fixation. *Odontocaulis*; robust main stem, from which new thecae arise. On almost all other genera of the Dendroidea, especially *Dendrograptus* no free sicula known, an abundance of organs of attachment described.

²³ Compare *C. saltet*, *grabant*, *elegans*, *radicans*.

²⁴ *Dictyonema arept*, *bohemicum*, *cavernosum*, *crassithalate*, *dendroidea teropense*, *paraticum*, *percrassum*, *polymorphum*, *subretiforme*, *stenactinatum*, *tenellum*.

I cannot help feeling that all these facts urge the conclusion that in the history of one large part of the ancient hydroids, there was one route of evolution prescribed, namely: The change of habitat starting from a holoplanctonic and passing through a partly epiplanctonic to a definitely sessile mode of existence.

ON THE OCCURRENCE AND STRATIGRAPHICAL RANGE OF THE VARIETIES OF *DICTYONEMA* FLABELLIFORME

Because, fortunately, large slabs up to a size of 2 square feet were collected, I was enabled to attend to the association of the *Dictyonema* faunula. This is imbedded in an extremely homogeneous, highly carbonaceous black shale of finest grain. Small concretions of iron pyrites are frequently scattered over the surface, though infiltration of the fossil material is rarely to be found. The more profusely the animal mass lies buried in the slates, the thinner they split. Cleavage of any considerable amount rarely appears, though often recognizable in minute pseudo-striation running in the same direction over all rhabdomes of a slab. The slates are exactly of the same character as those of the *Diplograptus geminus*-zone (Llandeilo) from Fogelsång (Skåne, Loc. E 5 of No. 40 of the Guide of the International Geol. Congress, 1910), those of the Upper Graptolite-shale (Tarannon) from Stommen (Westergoetland) or those of the upper Hartfell-shale (Caradoc) from the Moffat district (zone No. 8, South Scotland), except that most of the European occurrences have been a little more affected by stress.

Two different kinds of embedment can be noticed. Slabs on the surface of which single specimens with remarkably fine preservation are found, accompanied by clusters of early stages, alternate with others which are completely covered with a pell-mell of fragments and individuals, often almost indeterminable and lacking any favored direction. Here the variety *ruedemanni* and *Staurograptus* are extremely common. On a single slab 1.5 feet square, I numbered more than one hundred neanastic and ephebastic dendromes, omitting the rhabdomes pieced. As a rule, both sides of the colony are closely pressed together without any interbedded layer of mud, a strong evidence of rapid sedimentation, caused by rough and sudden events. On the contrary, the slabs of the first-described mode frequently show a rather thick sheet of mud inserted between the walls of the dendrom. Sometimes this is imbedded at a distinct angle of up to 5 degrees, found between the axis of the colony and the surface of the split shale which is likely to be caused by the weighing down of the heavier, distal end of the body. A rather slow deposition has to be assumed in these cases.

As a matter of special interest, but also of insufficient evidence, the strange arrangement of several specimens around a common center demands careful attention. It was originally figured by Salter and Goeppert. Afterward, however, it was questioned by the majority of authors, but was recently again mentioned by Fearnside (3), p. 307) and I likewise have observed some examples, particularly of early stages which can be classed herewith. Fig. 1a on plate XXI presents two *Dictyonemas* opposite each other, each of them attached to a minute common disk. Fig. 2c shows two young individuals joined to each other by means of their proximal parts. I observed also four full-grown specimens of the variety *acadica* m. f. *ruedemanni*, uniting as appears in the text-figure 2. In all the examples studied, no nema and only once a

FIG. 2.—*Dictyonema flabelliforme*
var. *acadica* m. f. *ruedemanni*
(1/1)

common disk is present, so that an immediate fixation by the basal parts of the colonies must be assumed. If this is the fact, which I am rather inclined to hold on account of the specimen discussed, a colonial arrangement of the third order possibly existed comparable with that of *Diplograptus pristis*.

The statements thus far made about the association of the faunula with *Dictyonema flabelliforme* do not vary to any considerable extent, provided that we will except the fossils gathered from interbedded limy nodules ("orstensbollarne"). G. F. Matthew²⁵ pointed out that in the *Dictyonema*-shales of New Brunswick, two bands (b, c) are distinguishable, namely, a lower one with var. *conferta* as the predominant type besides var. *acadica* and a higher one containing an abundance of the var. *acadica* and also var. *norwegica*. At Navy Island, both zones furnish the "Bryograpti" and a few brachiopods, the latter being better represented on the section of McLeod brook. In the slate belt of Eastern New York, Ruedemann,²⁶ though not able to fix the relative position, again recognized the *Dictyonema* bed separated from the *Staurograptus* bed, which also contains *Dictyonema flabelliforme* var. *acadica*, together with several species of brachiopods, identical with those of Matthew. As to the European occurrence, the best recent explorations were made by Moberg (2) and Westergård (4), who generally agree with each other

²⁵ See references (10), (11), (12) and "On a New Horizon in the St. John Group," Can. Rec. Science, Vol. 4, No. 7, p. 339, 1891.

²⁶ Cf. footnote No. 15.

in keeping distinct the lower level of *Dictyonema flabelliforme forma typica* which is accompanied by *Obolus salteri* and *appolinis* and a large *Lingula* ? *corrugata*, and the higher zone of *Bryograptus kjerulfi*, which has associated with it *Clonograptus tenellus*, *Dictyonema norvegicum* and *Lingulella* cf. *lepis*. It is Westergård who interpolates between them a separate zone of *Clonograptus tenellus* and *Bryograptus hunnebergensis*. My own observations harmonize with these statements in a quite satisfactory manner, for I found that occasionally individuals of all described species and varieties were met with on the same slab; that, however, in one part of the collection studied, *Dictyonema flabelliforme* var. *acadica* and var. *conferta* prevailed, associated with *Monobolina refulgens*, while, in another part, *Dictyonema flabelliforme* var. *ruedemanni* was mixed with var. *acadica*, *norvegica*, *desmograptoides* and *Lingulella* ? cf. *lepis*, but that in both cases *Staurograptus* occurs frequently. Although, of course, I am not able to make any statements about the relative age of these two beds, the close conformity of the facies on both sides of the Atlantic, when considered in a general manner, seems to me to urge the assumption of homotaxial relationship, provided we are willing to hold to the slight faunal differences due to the geographical separation, for the supposed evolution of the *Dictyonema* follows exactly in the same order as the historical succession. Hence, the identification of Matthew's zones with the two lower beds of Westergård seems, according to my opinion, to be correct.

SIGNIFICANCE OF THE VARIETAL RANGE AND ITS PHYLOGENETIC VALUE

Before balancing the observations on the Navy Island faunula, some general questions bearing on the zoölogical point of view must be discussed. The first one has to deal with the term "variety," applied to the observed changes of *Dictyonema flabelliforme*. The following points come into consideration: The features in change are not only confined to one or the other character of *Dictyonema flabelliforme*, but, as shown by the diagram and textfigure 3, every feature of specific, even of generic value is subjected to a more or less extended change. While a small part of the observed varieties are mostly restricted to later stages of *Dictyonema flabelliforme*, in some cases, e. g., var. *ruedemanni*, and *desmograptoides*, a considerable telescoping of the varietal features appears, which thus have already become inherent. Furthermore, not all of these varietal features are interchangeable; for instance, links between var. *ruedemanni* and var. *norvegica* never occur. On those links, however, that are found, even new crossing features are observable (pyriform

shape of var. *ruedemanni* m. f. *conferta*). That this variability is of rather important value is illustrated by the fact that the same features which characterize the varieties are to be met again, somewhat further developed and more distinctly separated, in later genera, e. g., *Callograptus*, *Dendrograptus*, so that these features have true orthogenetic significance.²⁷

Considering only this point of view, we could come to the conclusion, as did Moberg in 1906, that these modifications are useful for specific separation. We must bear in mind, however, that all the varieties start from a common center, i. e., var. *acadica* = forma *typica* of the European localities; that, therefore, an unbroken chain of bridging types exists which embrace all the different forms which elsewhere, when isolated, were scarcely regarded as being in any way related one to another.

FIG. 3.—Range of variability of *Dictyonema flabelliforme*

Finally, any separation by time is significant only between the var. *conferta* and most of the other varieties, which all have apparently grown together. For the separation of types, I regard the foregoing as of varietal, but not of specific or mutational value. For this last, we may regard either the saltative character or the interval of time as the essential point.

As to the cause of those changes, we may find it by starting from a mechanical point of view. How do sessile organisms react to a more or less continuous pull? If the pull is small, there results elongation of

²⁷ The constantly increasing number of Dendroidea, found in the Ordovician of North America, as compared with their sporadic appearance in European localities, makes it probable that the continuous evolution was more likely confined to the American seas.

the organs combined with elasticity and flexibility; if the pull is too great, only concentrated forms may exist. Near the boundary line of the trees of Alpine regions, we find species with slender, movable branches (*Betula*, *Larix*), while in places relatively protected from storms, we find dwarf trees and bushes, low and closely clinging (*Pinus*, *Picea*) or extremely thickened stems on the slopes of hills exposed to windy squalls. Water-plants lengthen their stalks or build a concentrated mass according to their standing places. And the same reaction must be true in benthonic animal life. The whole dendrome of *Dictyonema* was subjected to the pull in water, *i. e.*, the mechanical stress exerted against the fixed body by the action of currents, waves and breakers and thus the animal mass proves to be influenced.

As a result of this we have:

I. Var. *acadica*. This middle type of all the varieties shows very great progress over the small bryograptoid ancestors of *Dictyonema*, as is proved by the neanastic and nepiastic stages, for the elastic cross-threads enable single branches to grow to such an extent that, for example, a colony 160 mm. long could have 20,000 theca and yet have sufficient firmness for existence.

The varieties given here show the complete possibility of improvement, but that *acadica* has not reached the highest place is proved by the fact that of all perfectly preserved examples of later ephebaestic stages, *acadica* has less than 10 per cent, the pyriform paratype up to 50 per cent, *ruedemanni* up to 50 per cent, *conferta* 70-80 per cent, *norwegica* less than 10 per cent, *desmograptoides* less than 10 per cent.

Forms like *acadica* take the middle line of all true *Dictyonemas* through the Silurian, Devonian into the Carboniferous (compare *retiforme*, *scalariforme*, *stenactinotum*, *spenceri*, *leroyense*, *brairi*).

II. Var. *norwegica* endeavors to progress by a heavy thickening of the rhabdome net, but it causes great weighting down of the body and much profusion of organic matter, so that this mode of building up will be possible only when food is abundant. Compare *D. quadrangulare*, *murrayi*, *crassum*, *arayi*.

Result: A few sporadic species up to Devonian time; no generic evolution; one-half of one per cent of our forms, more or less broken in pieces.²⁸

III. Var. *desmograptoides* has closer and even elastic branches joining with fewer cross-threads.

²⁸ Also Westergård mentions the scarcity of unbroken specimens of this variety (1) p. 60.

Result: Through forms like *irregulare*, *homphrayi*, generic evolution into *Desmograptus* up to Devonian; one-half per cent of our forms, because of somewhat later starting of evolution.

Good stolon in later species, sessile; finally, thinning of rhabdomes (*tenuiramosus*, a sessile pseudo-*Dendrograptus*).

IV. Var. *ruedemanni*. Heavy branching and a successive diminution of the elastic cross-threads produce a thick brush and dense crowding of nourishing thecæ, while still allowing movement of the rhabdomes.

Result: 35 per cent of whole fauna; 50 per cent perfectly preserved.

Half of the observed attaching organs belong to this variety. Evolution: (a) persistence of type in a few Ordovician and Silurian species; stolons and roots common. Compare *delicatulum*, *perezile*, *rectilineatum*, *subretiforme*, *tenellum*, *filiramus*. (b) Further reduction of cross-threads, enforced reduction in size. Intermediate forms: *Callograptus*, *Rhizograptus*, *Odontocaulis*, *Callyptograptus*; sessile, in early stages vagrant; then *Dendrograptus*; stolons and roots. Further evolution of *Dendrograptus* leads to thin flexuose types (i. e., under slight pull) or to succulent types (i. e., under heavy pull); latter forms sometimes with central axis. End of this evolution: *Ptilograptus*, *Acanthograptus*, etc.

V. Var. *conferta*, cylindrical growth and close network, giving mechanically the best type.

Result: On one side 6 per cent of our forms and 70-80 per cent perfectly preserved; on the other no specific evolution at all, probably on account of very unfavorable conditions of food supply.

VI. Last type of change by thickening and dividing of the cross-threads (groups of *pellatum*, *cervicorne*, *cavernosum*, *tuberosum*) not represented in our fauna. Appears first in American Ordovician. Stolons and roots well developed.

Considering this mechanical starting point, it becomes of interest that the Gorgonias of equivalent habitat (disregarding the funnel shape of the *Dictyonema* colony) present the same lines of changes as those sketched in the foregoing for *Dictyonema flabelliforme*. Thus we find among the *Leptogorgias*, *L. eximia* and *media* with a network like that of var. *acadica*, *Leptogorgia agassizi* with close fine meshes comparable to those of var. *conferta*, while *Leptogorgia rigida* looks like a callograptoid type and *Eugorgia multifida* like a *Dendrograptus* with beginning central axis. The latter, still further developed, gives *Pterogorgia acerosa*, while *Gorgonia flabellum* has a typical desmograptoid appearance and *Gorgonia quercifolia* resembles closely the *norwegica-murrayi* line. I cannot help thinking such a conformity indicative of parallelism in

evolution and that it represents one of the usual lines of development of such benthonic forms under a given environment.

Now, with all the foregoing statements, we may touch upon the final question of the *phylogeny* of the dendroids as indicated by the range of variation in the earliest *Dictyonema*. A certain branch of the planctonic ancestors common to both Graptolites and Dendroidea was evidently pushed forward in the lines of directed evolution by the formation of dissepiments as a supporting mechanism of the elongating rhabdomes. This represents the *Dictyonema* stage, beyond which a group of retarded species and genera (*e. g.*, *Desmograptus*) never passed to any considerable extent. While in the *Dictyonemas* of the early days, fixation was realized only by means of a thin, fragile nema, the adhesive organs were now brought into vital and ever increasing significance. For gradually thickened stems with basal expansions, with stolonial ramifications, with ability of independent budding of thecae and of colonies, were built, while the original planctonic period of life becomes shortened to its final disappearance (*Dendrograptus*-stage). From this point on, an extreme widening of the main stipe, on one side, gave rise to the *Galeograptus*, *Discograptus*, *Cyclograptus*, *Rodanograptus*-group, while a thickening of the central axis led to forms like *Inocaulis*, *Acanthograptus*, *Cactograptus*, *Palædictyota*, to which even *Chaunograptus*, *Corynoides* and *Thamnograptus* may be related, as held by Ruedemann. Finally, in types like *Mastigograptus*, a striking approach to the present hydroids has been revealed. When considering the various races of Dendroidea on such a broad basis, the various genera do not of course mean anything else than stages in development; and every line of separation seems an arbitrary one, as is shown in a comparison of the species thus far assigned to "one genus" by the different authors (*e. g.*, the *Callograpti* and *Dendrograpti*). Nor is the difference between the forms in the early Ordovician with free siculae and those with unknown siculae a reliable one upon which alone to base the natural classification.

Within the last five years, two papers of such importance regarding the differentiation and evolution of the *Dictyonemas* have been published that they must be considered with great care. In 1907, W. S. Fearnside (3) made some striking suggestions. He believes that

"in the earliest *Dictyonema*, the cells are very indistinct and rarely project more than about a quarter of the diameter of the common canal, cross threads thin and numerous; stipes close together, parallel, branching at all levels; elongated rectangles of meshes. This supposed *Dictyonema* diverges in two distinct families, one approaching the true graptolites (*Dictyograptus*) the other seems more nearly related to the Dendroids (*Dictyonema, sensu stricto*)

Dictyograptus

"Cells: Well-marked; tend to become uniserial.

"Shape: Like a fisherman's net from a sicula of no great length with primary branches, diverging at an angle rarely greater than 90°.

"Dissepiments: Their development ever more and more delayed until they become practically abortive.

"Type: var. *acadica forma typica*."

Dictyonema

"Cells: Small, generally disposed at angles of about 120°. Crinkly longitudinal ornament appears.

"Shape: Basketlike, starting from a long narrow tube or nema and diverging at angles which in the later forms approach 160°.

"Dissepiments: Their importance, increase and the general aspect of the later forms is that of a square or rhomboidal mesh in which cross bars and stipes are of approximately equal importance.

"Type: var. *norvegica*."

There is one point in which I completely agree with this author, viz: the importance of the differentiation among *Dictyonema flabelliforme*. We both believe in this as the point of generic divergence; but in detail, I cannot help stating that all my observations run along the opposite direction. I merely recur to the facts that

Var. *conferta*, restricted to a lower horizon, according to the suggestions of Matthew, Fearnside and the majority of the Scandinavian authors, shows clearly the tubulose structure and mode of growth and dissepiments of "*Dictyonema*" and the projecting cells of "*Dictyograptus*."

Var. *desmograptoides* has cells, mode of growth like "*Dictyonema*," cross-threads like "*Dictyograptus*."

Var. *acadica* has cells, sicula, like "*Dictyograptus*," tubulose structure like "*Dictyonema*."

Var. *norvegica* has cells like "*Dictyograptus*," dissepiments like "*Dictyonema*."

Var. *ruedemanni* has sicula, dissepiments, structure like "*Dictyograptus*," cells and growth like "*Dictyonema*."

Hence, as all the known varieties are in part distinguished by the features of "*Dictyonema*" and in part by those of "*Dictyograptus*," such a separation, of course, seems impossible. Furthermore, the ancestors were doubtless bryograptoid with very distinct cells, without numerous dissepiments. Nor did Westergård agree with Fearnside's assumption, so that against this hypothesis there appears to be no further objection necessary.

On the other hand, Westergård, from whose detailed work my own observations do not differ widely, starts with the following suggestions:

Among a hundred examples of *Dictyonema flabelliforme* examined, he failed to observe nemas or disks or any adhesive organs in spite of distinct proximal parts with free siculæ. He regards the wrinkling of the rhabdomes as produced merely by pressure, and the early appearing divisions of the nepiastic thecæ as due to rapid budding of nourishing thecæ. He holds it probable that the early Dendroidea like *Dictyonema flabelliforme* when derived from graptolites must have possessed thecæ like those of *Bryograptus kjerulfi*. From this point on, he considers that there existed a great difference between the *Dictyonema flabelliforme* and the "*Dictyonemas*" of the later Ordovician and Silurian, as described partly from sections by Wiman and others, and he introduces "*Dictyodendron*" for the later forms.

The following objections, however, must be made after careful consideration: 1. Young individuals of *Callograptus (salteri* in Ruedemann's monograph, *grabaui* as described in this paper) exhibit distinct siculæ and even nemas. 2. True adhesive expansions occur among the *Dictyonemas* of Navy Island. 3. The tubulose structure is by no means referable to any kind of stress, because this, when exerted, produces a fine striation, running in parallel fashion over all specimens of one slab, but cutting, of course, the tubes at quite different angles. The associated *Staurograptus*, moreover, never show a similar structure. 4. The young stages of *Dictyonema flabelliforme*, as fully discussed in the foregoing, are found to be clearly distinct from all stages of *Bryograptus*, as they exhibit a more primitive character (dependent growth) than *Bryograptus* (declined or horizontal growth of the first branchlets). Hence the ancestors of *Dictyonema flabelliforme* were not at all true *Bryograpti*, but simpler types with features bridging over those of *Dictyonema* and *Bryograptus*.

Thus I feel quite certain that the progress of evolution which Westergård believes to have existed between the early *Dictyonema flabelliforme* and the so-called "*Dictyodendron*," did really take place among the varietal series of the *Dictyonema flabelliforme*.

Finally, there is one point left which thus far I have deliberately disregarded in order to simplify its consideration, for it adds merely some complications without modifying the preceding conclusion. There is no doubt of the fact that most of the dendroid genera have the characters not only of stadial, but also of collective groups. Of this James Hall was partly convinced even in the '60's, but it has only been recently fully substantiated by the masterly works of Wiman and Ruedemann. Among the *Dictyonemas*, one part has thecæ with sharply prominent

lips, another possesses obscure pits and grooves in place of thecal apertures; one group is distinguished by an uniserial, the other by a biserial arrangement of the thecae; a few species belonging to widely separated divisions are proved to be heterothecal, while others are strongly suspected to be homœothecal.

We find similar differences among the genera of Callograptoid appearance, particularly among the *Dendrograpti*, the *Ptilograpti* and in the *Galeo-Disco-Cyclograptus* group. Those differences are not confined to a certain geological age. Early as well as later species may show the same kind and arrangement of the thecae, while congeners reveal the difference as great as possible in this respect, *e. g.*, the highly variegated Niagaran dendroids of America. This difficulty of a heterogeneric but parallel evolution seems still further increased in complexity by the repeated development of features either retrogressive or intermingled. For we observe the strongly differentiated genus *Dendrograptus* already at the base of the Ordovician (if not earlier) and yet we see that the path of varietal evolution is in the same direction in much later strata. We observe true *Dictyonemas*, the neanastic stages of which suggest certain ancestral relationship to members of the *Desmograptus* or the *norvegica-murrayi* group. That the same is true among the Callograpti is proved by a comparison of Počta's, Bassler's and Ruedemann's species herein referred to. Even the characteristic bifurcation of the apertural margins and dissepiments has now been found in quite different species and genera, *e. g.*, *Ptilograptus*, a very doubtful and not unlikely retrogressive genus, to which some *Callograpti* described by Počta bear an undeniable similarity.

However complicated the paths of evolution of the Dendroidea may be, paths which can be traced back only after the manner of Wiman's and Ruedemann's keen-eyed and careful investigations, I am convinced that, generally speaking, they followed directions similar to those manifested pre-figuratively in a small but equivalent ratio by the range of variation in *Dictyonema flabelliforme*.

PLATE XX

RANGE OF VARIABILITY IN DICTYONEMA FLABELLIFORME AND ITS EVOLUTIONAL SIGNIFICANCE

Varieties of *Dictyonema flabelliforme* and *Callograptus grabau* n. sp. correctly drawn after actual specimens in the collection of Columbia University; other species and genera sketched after Hall, Ruedemann and Wiman.
(Reduce all given magnifications by three-fourths.)

crassum
x5

quadrangularis
x4

areyl
x5

DICTYONEMA

var norwegica
x4

DICTYOI

var. desmograptoides
x4

intricatus
x10

cancellatus
x4

DESMOGRAPTUS

YOUNG STAGES

x20

PLATE XXI

BASAL ORGANS OF DICTYONEMA FLABELLIFORME

1 *a, b, var. conferta*

2 *a, b, c, acadica (b, c, juv.)*

3 *a, b, acadica in. f. ruedemanni*

4 *a-d, ruedemanni*

All specimens are preserved in the collection of Columbia University and are enlarged five times in the figures. The measurements given refer to the length of the entire colony, which is not always represented.

PLATE XXII

**TABULAR COMPARISON OF THE SPECIES OF DICTYONEMA, DESMOGRAPTUS AND
CALLOGRAPTUS**

Names	Shape and size	Length to width	Per cent of individual	Number in 10 mm.	
<i>Dictyonema flabelliforme</i> <i>v. acedica</i>	infundibuliform and pyriform large—very large	1.6:1 .9:1	60%	9-10 (8-12)	
<i>brairi</i>	infundibuliform medium size	.8:1 (?)		8-10	
<i>leroyense</i>	infundibuliform large ?	1:1		8-10	
<i>v. conferta</i>	vasiform--cylindrical medium size (large)	2.5:1 (3.7:1) (1.5:1)	6%	8.5-10	
<i>v. norwegica</i>	infundibuliform large	.9:1	$\frac{1}{4}\%$	8-10	
<i>murrayi</i>	? large	?		4	
<i>crassum</i>	infundibuliform large	1:1 (?)		9	
<i>v. desmograptoides</i>	infundibuliform medium size	1:1	$\frac{1}{4}\%$	8 (7-9)	
<i>intricatus</i>	Desmograptus infundibuliform medium size	1:1		15-20	
<i>cancellatus</i>		2:1 (?)		12-14	un
<i>v. ruedemanni</i>	infundibuliform—pyriform large—very large	.7:1 (.63:1) (1.1:1)	33%	12 (10-15)	
	?				

Diverg. of branches	Number in 10 mm.	Character	Meshes	Number	Character	Basal organs
45° 80°	4-5 (3-8)	thin .2 mm.	quadrang. (elongated)	16 (15-17)	projecting	sicula, nema ? 1 stolon (young s
± 45°	4-5	.25 mm.	quadrang.			
45° 80°	2-4	.25 mm.	subquadrang.			basal adhesive disk
45° 70°	7 (6-8)	thin .1-.2 mm. regular	quadrang. (regular)	17 (16-18)	delicate projecting	sicula, 1 basal disk ? 1 branching sto
50° 90°	6 (4-8)	thick— irregular (.1)–.6 mm.	rectang. subcircular	15	robust acute	
50° 90°	4	rigid .4–.9 mm.	rectang.	9-10	acute	
50– (90°)	4-5	irregular .4–.9 mm.	rounded subquadrang.			
± 90 (45°–90°)	3-4 (1-5)	very irregular .1–.4 mm.	irregular subovate	15	delicate less projecting	
45°–90°	(0-1)	very rare irregular	elongated subovate		appressed circular	sicula ?
± 90°	(0-1)	very rare irregular	elongated subovate	frequent	appressed circular	chitinous basal expansion, short stem
± 45°	3 (1-5)	thin—irregular .1 mm.	quadrang. elongated	15-16	delicate	sicula, nema or stolon with branching stolon neanastic stage
		irregular				