2. Carl Wiman's Work on the Structure of the Graptoloidea.

By

O. M. B. Bulman.

Sedgwick Museum, Cambridge.

By 1880, the graptolites were becoming accepted by most geologists as accurate horizonal indices and their correlative value had been established. During the decade preceding, graptolite literature had been enriched by a steady flow of papers, particularly in Sweden and Great Britain, all tending to this end, which may be regarded as culminating in LAPWORTH's paper on the Geological Distribution of the Rhabdophora.[1] Yet it is not too much to say that at that time, with the foundations of the stratigraphical palaeontology of the group securely laid, our knowledge of the morphology of these organisms was still in its infancy. Graptolite morphology was, in fact, awaiting the discovery of special material and the development of special technique, and it is not to belittle the work of the pioneers, from BARRANDE and HALL to LAPWORTH and TÖRNQUIST, to claim that our present knowledge of the organisation of the graptolites rests principally upon the discoveries of WIMAN and HOLM and the methods they exploited.

In 1890, HOLM published the first of his papers on graptolite morphology[2], famous for its demonstration of the polymorphic nature of the Dendroidea (exemplified by *Dictyonema cervicorne*) and containing also figures and descriptions of some Monograptids and Retiolitids more or less freed from their calcareous matrix by acid (though many of HOLM's early preparations retain an undissolved filling of matrix). Then, in 1893, appeared WIMAN's papers, »Ueber *Diplograptus*» and »Ueber *Monograptus*». Priority for the methods followed by these workers must be given to GÜMBEL, who as far back as 1878[3] had described both the isolation

[1] *Ann. Mag. Nat. Hist.*, Ser. 5, vols. iii-vi, 1879—80.

[2] »Gotlands Graptoliter», *Bihang till K. Svenska Vet.-Akad. Handl.*, 16, 1890, Afd. iv, No. 7.

[3] »Einige Bemerkungen über Graptolithen». *Neues Jahrb.*, Jahrg. 1878, p. 292.

treatment and the »clearing» of graptolites, but processes which yielded comparatively little result to GÜMBEL became in the hands of WIMAN and HOLM a means of the most penetrating investigation. Two years later, WIMAN published his Inaugural Dissertation »Über die Graptolithen», and followed this with four more papers between 1896 and 1901 dealing wholly or in part with graptolites. While his more prolific and spectacular work was on the Dendroidea, this series of papers contains an extremely important body of fact regarding the Graptoloidea, and much suggestive, though cautious, speculation.

In 1895 also, HOLM published his account of the detailed structure of certain species of *Didymograptus, Tetragraptus* and *Phyllograptus.*[1] For over twenty years he continued to collect and prepare material and accumulated for the Riksmuseum, Stockholm, the finest collection of »isolated» graptolites in the world; but he never lived to describe much of this collection, and the morphological studies of WIMAN and HOLM were not followed by any kindred work until the last decade.[2]

It was LAPWORTH who first recognised[3] the true significance of the *sicula,* designating thus the minute conical body from which the graptolite rhabdosome originates, and discussing its relation to the vague and now obsolete term *radicle* of HALL. He further appreciated and discussed the orientation of the rest of the rhabdosome in relation to the sicula, and subsequently[4], with a remarkable combination of observation, inference and prophecy, suggested that most probably »the sicula in *all* the *Graptoloidea* throws off a single bud only, and thus theoretically invariably originates a single coenosarcal tube». Nevertheless he thought it desirable to qualify this as a theory which might »appear at first sight totally irreconcilable with the successive phases of the budding polypary in some forms of the *Diplograpti*» and it does not seem to have gained any very wide recognition.

WIMAN, in his first paper, showed that the sicula is composed of an apical and an apertural portion, which differ in ornamentation though they are continuous with one another and not separated by any transverse septum. KRAFT[5] has more recently furnished still more exact details of

[1] *Geol. Fören. Förh.*, 17, 1895, p. 319.

[2] I am not unmindful of the careful investigations and progress made by many workers during this period, particularly TÖRNQUIST in Sweden and ELLES and WOOD in Great Britain; but shale material, even when pyritised, imposes severe limitations for palaeozoological work and the results can never be strictly comparable with those obtained from limestone material.

[3] *Geol. Mag.*, x, 1873; also *Quart. Journ. Geol. Soc.*, xxxi, 1875.

[4] *Geol. Mag.*, xiii, 1876, p. 546.

[5] *Paläont. Zeitschr.*, 7, 1926, 207—49.

these two divisions which he has named Prosicula and Metasicula respectively, and with more modern facilities and technique the prosicula is shown to possess not such irregular and anastomosing striae as WIMAN depicts, but comparatively few longitudinal strengthening rods and a peculiar spiral band. These, however, are details only. Secondly, WIMAN was able to show that the virgula is not continuous with what is now known (TÖRNQUIST, 1897)[1] as the virgella, but that the virgula proper »durch das Vereinigen der longitudinalen Streifen des distalen Teils der Sicula entstanden ist», while the virgella is a structure which arises during the course of development of the metasicula. More detailed observations on the origin of the virgella may be found in KRAFT (*op. cit.*) and COX.[2] Thirdly, WIMAN's earliest paper provided a clear demonstration of the development of a biserial rhabdosome by a single bud from the sicula, and rendered extremely probable the general application of LAPWORTH's prediction. In this, he was forestalled by a few weeks by TÖRNQUIST[3], who investigated several biserial graptolites by means of longitudinal and transverse sections of pyritised specimens, concluding that »the sicula sends out a connecting canal which on the other hand opens into the common cavity of the rhabdosoma».

Some of the »conclusions» in WIMAN's paper on *Diplograptus* were based on the special conditions existing in *Orthograptus gracilis* (the species investigated) — for instance, that there is no longitudinal septum — and were evidently not intended as generalisations. Others, — the general characters of the sicula and its relation to the virgula and virgella — were speedily confirmed by his work on *Monograptus,* and certain other facts there noted are of interest to recall. Thus, it was remarked that the initial bud in *Monograptus dubius* appears on the same side of the virgella as in the *Diplograptus*, but lies nearer the apertural end and produces very marked interference with the growth-lines of the sicula; it now seems a fairly safe generalisation that there *is* a definite side for the normal development of the initial bud, that it is typically nearer the apex of the sicula in earlier graptolites and closer to the aperture in later forms, and that the origin of its foramen may either be by resorption (having no effect on the growth-lines) or by the formation of a »hood» which leaves very distinct traces on the course of the growth-lines. Another of WIMAN's observations, that in distinction to the downward growth of the initial part of the first theca in *Diplograptus*, the first theca in *Monograptus* »wächst von Anfang nur gegen das distale Ende» practically

[1] »Diplograptidae and Heteroprionidae . . . .», *Fysiogr. sällsk. Handl.*, Lund, 1897, viii, p. 4.

[2] *Geol. Mag.* lxx, 1933 and *Ann. Mag. Nat. Hist.,* 10, xiv, 1934.

[3] »Observations on the Structure of some Diprionidae», *Fysiogr. sällsk. Handl.*, Lund, 1892—3.

constitutes the definition of what is now known as the Monograptid type of development.

Of the other matters raised in this paper on *Diplograptus,* none had more influence on the development of later ideas than WIMAN's conclusions regarding the *common canal* in graptolites. LAPWORTH had accepted from earlier investigators the idea of a common canal lodging a coenosarc from which the thecal individuals were budded off. He thus speaks[1] of a »longitudinal tube or canal for the conveyance of the common body», while the term theca is restricted to »the exterior and separable portion of the chamber, — in other words, to that which is capable of being broken off from the common portion» (*op. cit.*, p. 503). Similarly, TÖRNQUIST regarded the rhabdosome as consisting of a common canal together with and distinct from hydrothecae. WIMAN, on the other hand, stated categorically »ein eigentlicher gemeinsamer Kanal als Urheber der Thecen existirt nicht» and »jede Theca geht von der nächsten mehr proximalen . . . aus, nicht von einen gemeinsamen Kanal» and this conception appears in almost identical words in most modern writings. To what extent is this change in view justified?

A few weeks prior to the appearance of WIMAN's paper on *Diplograptus,* TÖRNQUIST had published the results of his work on the structure of biserial graptolites (1893, *op. cit.*) in which he concluded: — »The sicula sends out a connecting canal which on the other hand opens into the common cavity of the rhabdosoma. This consists either of two uniserial canals separated by a complete median septum, and originating from a short biserial chamber, which occupies the proximal portion of the rhabdosoma, or of one single biserial canal extending throughout the whole rhabdosoma, in some cases provided with an incomplete septum, in others destitute of any septum whatever.» These terms are illustrated (diagrammatically) in the accompanying Text-fig. 1 A. WIMAN commented briefly on this paper in a postscript to his own, claiming that the »connecting canal» of TÖRNQUIST is precisely the initial part of the first theca, and that the subsequent development of *Climacogr. scalaris, Cl. internexus, Diplogr. palmeus* and *Cephalogr. cometa* is capable of interpretation on the lines he had already indicated for *Orthogr. gracilis* (Text-fig. 1 B). TÖRNQUIST, in his reply to WIMAN's views[2], reiterated his earlier conclusions, stressing the significance of the median septum, variable in length, and wholly absent in some forms; since this septum never extends to the most proximal part of the rhabdosome, he considered it justifiable to designate the biserial chamber by a special name, and he defended his retention of the term common canal by reference to the original definition of the term theca (see LAPWORTH, above). WIMAN's use of the word

[1] *Geol. Mag.* x, 1873, p. 502.

[2] *Geol. Fören. Förh.,* 16, 1894, 375—9.

theca had, according to TÖRNQUIST, acquired a new meaning gathered from an idea of the living animal content. Of this, one might conceive three possibilities, *viz.*,

(1) that the periderm enclosed an undifferentiated protoplasm without other individualisation than the apparent one of division into thecae;
(2) that each theca enclosed an individual connected with its neighbours by coenosarcal content of the common canal; or
(3) that the colony was composed entirely of individuals, developed from one another and remaining in contact.

It is this last view which may be attributed to WIMAN and which has become so generally accepted at the present time.

Approaching the question by the consideration of an internal cast of the rhabdosome, it is easy to see how TÖRNQUIST would be led to regard the common canal as a morphological unit bounded by the dorsal wall of the stipe (or the median septum of a biserial graptolite) and the inner limit of the interthecal septa; and particularly how he would be impressed with the existence of a proximal biserial chamber. But the conception of these as definite rhabdosomal units conflicts with the evidence of the growth-lines of the periderm. It was this evidence which WIMAN had for the first time brought to bear on the problem, and by which he was clearly influenced. There is no sharp break in the regular succession of growth-lines as we pass from the common-canal region of the periderm or the region of the biserial chamber to the thecal area *sensu stricto*. Accordingly, in 1895, WIMAN defined his interpretation of *theca* as »ein Teil der Haut eines bilateral symmetrischen tierischen Individuums»; claimed that »den Thecen entsprechenden Personen aus Thecen entsprechenden Personen, nicht aus einem einen gemeinsamen Kanal erfüllenden Strang gesprosst»; pointed to the analogy of the Dendroidea in which there is no common canal, but a series of budding individuals; and defined the expression common canal as the sum of the proximal parts of the thecae — parts lying dorsal to the interthecal septa.

When, however, we examine with a high power of the microscope a transparent preparation of the periderm of a graptolite (and it is for this purpose desirable to use the periderm of one side only, since the superposition of the two sides may cause confusion) we find that there are certain irregularities in the disposition of the growth-bands, as indeed WIMAN himself observed.[1] In the more distal portions of *Orthograptus gracilis*, this irregularity leads to the formation of a narrow axial zone, rather more slender than the common canal as conceived by LAPWORTH

[1] In *Monograptus,* »wie auch bei *Diplograptus,* kleinere Unregelmässigkeiten in der Anordnung der Streifen entstehen.»

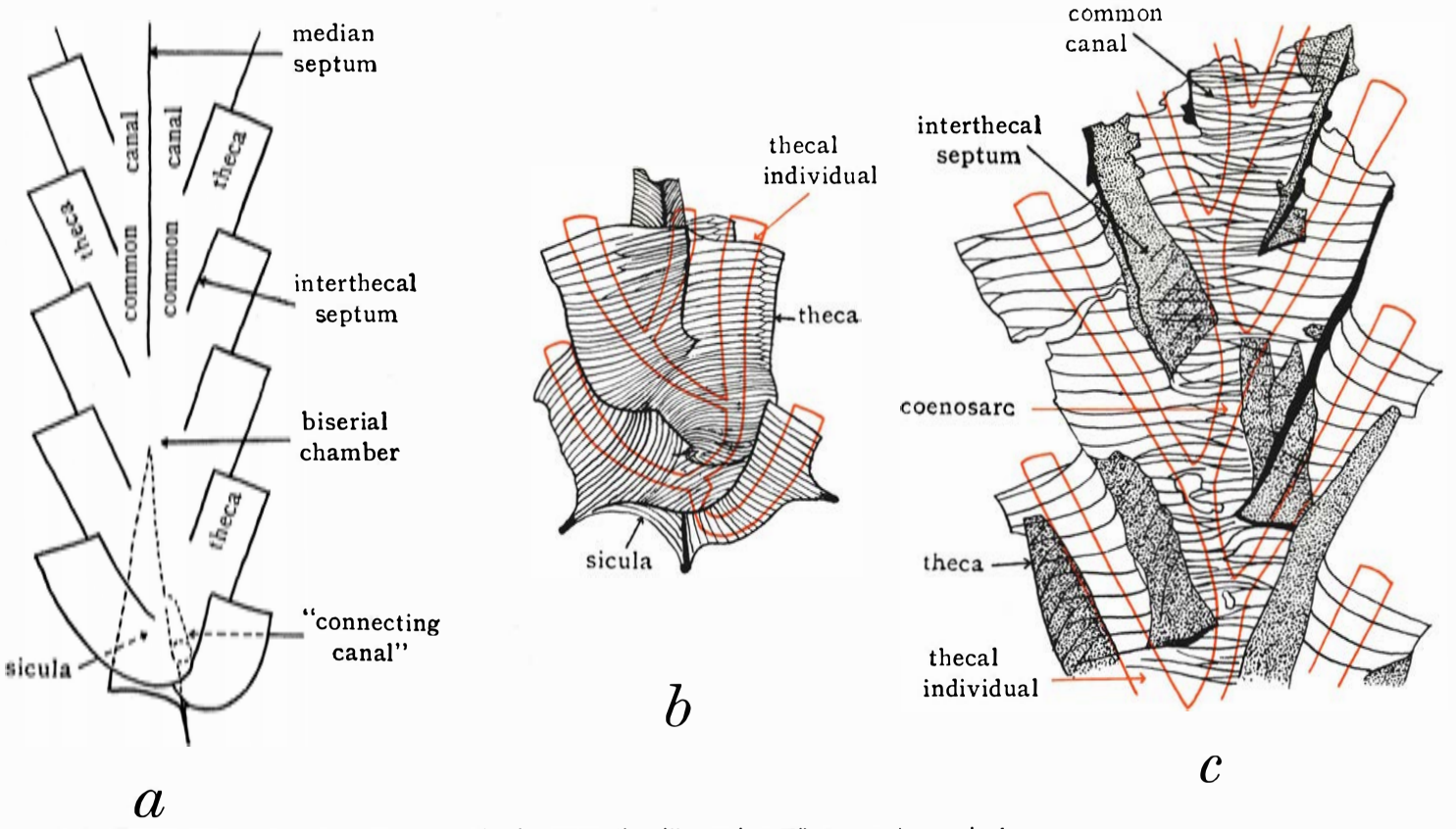

Fig. 1 A. Diagrammatic proximal end of a biserial graptolite, illustrating TÖRNQUIST's terminology.
B. Proximal end of *Orthograptus gracilis*, after WIMAN, with organic content of the periderm inserted diagramatically, illustrating the development of each thecal individual from the preceding individual.
C. Distal portion of rhabdosome of *Orthograptus gracilis* (HOLM collection, Riksmuseum, Stockholm, No. 635) with organic content of the periderm inserted diagramatically to show postulated coenosarc.

and TÖRNQUIST, formed of short lenticular growth-bands interspersed among the thinning-out growth-bands of the thecae on either side. It must be admitted that this does not seem to be distinguishable at the extreme proximal end, where the evidence of the growth-lines would lead one to infer that each of the first few thecae develops from the preceding opposite theca. Again in *Monograptus*, however, there is a comparable structure distally in the region of the virgula, and moreover »the free ventral wall of the theca shows a wedging-out of growth-bands down the median line, but when these are traced down to the interthecal septum of the ventral wall, of which it is a continuation, a change in their disposition is apparent».[1] Are such structures as these merely irregularities due to the growth of one theca from another, as WIMAN supposed, or may they not be taken to imply the presence of some living content of this part of the rhabdosome distinct from the individuals occupying and secreting the hydrothecae? It may be noted at this point that, on this evidence, the coenosarc would not have quite the same extent as it was formerly thought to possess, and probably would not fill the entire »common canal».

This evidence alone is far from conclusive, but I have elsewhere[2] summarised indirect evidence, much of it later than WIMAN's work, bearing on the question. WIMAN recognised that the matter could not be adequately considered without reference to the Dendroidea. Details of the structure of *D. flabelliforme, Clonogr. tenellus* and *Bryogr. hunnebergensis* have been made known since WIMAN's work and we now seem justified in concluding provisionally that the Graptoloidea are descended from the Dendroidea. This involves the disappearance of the bithecae and some modification of the budding individuals. We still cannot altogether exclude the possibility of WIMAN's suggestion (1895, p. 35 [273]) that perhaps the graptolite rhabdosome represents only the superficial periderm of the Dendroidea, i. e. »den gemeinsamen Kanal mit mehreren zarten Röhren füllenden, proximalen Fortsetzung der Thecen bei den *Dendroideen,* welche auch bei diesen nur selten beibehalten sind, waren bei den *Graptoloideen* noch dünner und weniger haltbar, so dass sie fast immer verschwunden sind.» The rhabdosome of the graptoloidea, however, is typically completely bilaterally symmetrical, scarcely suggesting that the thecal walls enclosed both thecal and bithecal individuals, and what little direct evidence we have favours more the actual loss of bithecae. If the bithecal individuals are lost, what has become of the budding individuals? It is apparent that the budding individual of the Dendroidea corresponds functionally to the coenosarc, whatever view may be taken of its morphological equivalence, and I believe that with the loss of a separate

[1] I. H. COX: *Ann. Mag. Nat. Hist.*, 10, xiv, 1934, p. 432.

[2] *Arkiv för Zool.*, 24 A. No. 13, 1932, p. 26.

chitinous covering (together apparently with the suppression of bithecal individuals) the graptoloid condition has resulted, retaining a slender thread of coenosarc which often leaves a somewhat indefinite trace in the growth-lines of the rhabdosome.

Of the remainder of WIMAN's descriptive work on graptolite morphology, it is impossible to deal adequately in the space available. HOLM had, in his earlier paper (1890) described the structure of the distal part of *Retiolites geinitzianus*, *Stomatograptus törnquisti* and *Gothograptus nassa*. WIMAN furnished another and still more complete account of *Retiolites (Gothograptus) nassa,* giving full details of the whole rhabdosome including the proximal end; but even with the recent work of MÜNCH[1] on a nearly related species, and EISENACK's remarkable *Archiretiolites*[2], we can still do little more than express the opinion that although highly modified, the Retiolitids are probably based on the *Diplograptus* type, so far as concerns the structure and development of the rhabdosome.

On the origin of *Monograptus,* WIMAN held highly unorthodox views, since he considered this to have arisen by a merging of the two rather than by the actual failure of one thecal series of a *Diplograptus*-like form, — »nicht durch irgend eine Reduction etwa eines *Didymograptus* oder *Diplograptus* entstanden, sondern so zu sagen hervorgegangen durch die Erfindung seine Thecen in bloss eine Reihe zu stellen» (1895, p. 31 [269]) — possibly through an intermediate *Diplograptus*-like form »bei denen die beiden Thecenreihen Winkel mit einander bildeten» (1893, p. 117). *Dimorphograptus* he would relegate to the status of an atavistic form. There seems *a priori* much reason to regard *Dimorphograptus* as a true intermediate between *Diplograptus* and *Monograptus,* but it may still perhaps be questioned whether this was the only line of descent. The genus *Diversograptus*[3] occupies an anomalous position which may possibly be shown to have some relation to *Monograptus;* similarly WIMAN's suggestion cannot be dismissed until more is known of this critical stage in graptolite evolution.

Had WIMAN written no more than his early papers *Diplograptus* and *Monograptus,* his work would rank very high in graptolite literature, for they set a magnificent standard in technique, description and interpretation. Followed as they were by his later papers describing further types and adding his brilliant investigation of the Dendroidea, it is a truly remarkable achievement. He never strained his evidence nor forced his

[1] A. MÜNCH: »Retiolites Mancki», xxiii *Bericht Naturw. Gesellsch. Chemnitz,* 1930, 1—8.

[2] A. EISENACK, *Pal. Zeitschr.,* 17, 1935, 73—90.

[3] E. MANCK: »Untersilurische Graptolithenarten». *Natur,* XIV Jahrg., 1923, 282—9.

theoretical conclusions. Speculation is still active concerning the interrelations of the Graptoloidea, their connection with the Dendroidea, and the zoological affinities of both groups, but WIMAN's views, though they may well be modified in the light of later discoveries, will always command the respect due to a highly gifted investigator.

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