

# DEVELOPMENT OF RHABDOSOMES WITH FOUR PRIMARY BRANCHES IN THE GROUP *DICTYONEMA FLABELLIFORME* (EICHWALD)

by PH. LEGRAND

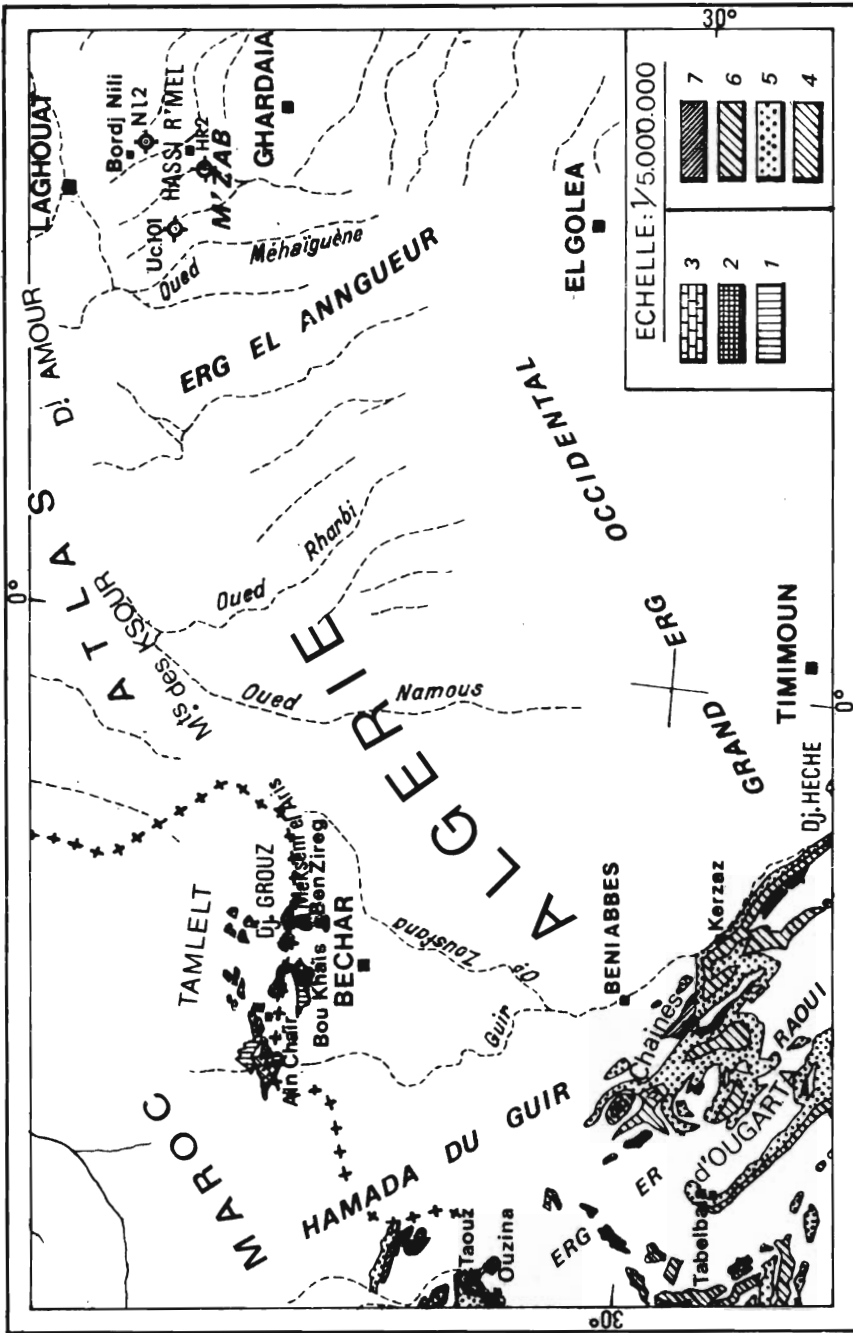
ABSTRACT. The existence of rhabdosomes with four true primary branches is shown, and their mode of development explained, in a population occupying an intermediate position between *Dictyonema sociale mehaigueni* Legrand and *Dictyonema sociale praeafricanum* Legrand.

THE discovery of the Zone of *Dictyonema flabelliforme* in the lower Ordovician of the northern Algerian Sahara (Bordj Nili Region: borehole NI 2; Hassi R'Mel Region: borehole HR 2) is due to M. Blain who described the first specimens collected (1963). Subsequently this zone was recognized in the neighbouring region of the Oued Mehaiguene (borehole UC 101) and in the Ougarta Range (Legrand 1966) (text-fig. 1). The succession of different subspecies, in particular for the lower beds, was later stated precisely (Legrand 1973).

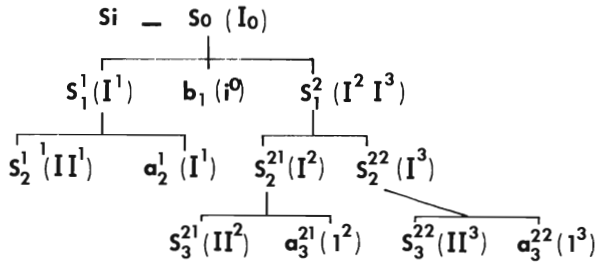
The state of preservation of the material is generally mediocre, the carbonization being relatively advanced and the flattening almost total. However, in certain cases study of the structure of the rhabdosome could be undertaken, and it was possible to observe in transparencies the different stages of development of the rhabdosome in a population of individuals occupying an intermediate position between *Dictyonema sociale mehaigueni* Legrand and *Dictyonema sociale praeafricanum* Legrand. The existence in these individuals of four true primary branches led to a revision of the development diagram for this type of rhabdosome.

## HISTORY

Although the disposition of the thecae constituting the stipes in the *Dictyonema flabelliforme* group has already drawn the attention of research workers (Eichwald 1855, 1860; Salter 1858, 1866, 1881; Nicholson 1872; Matthew 1895; Wiman 1895; Ruedemann 1904; Hahn 1912) it was Bulman (1925, 1927) who took the credit for having clearly demonstrated the structure of these stipes in successive triads, each of the triads being composed of three types of individual initially referred to as hydrothecal, bithecal, and budding individuals; subsequently as autothecal, bithecal, and stolothecal; the stolothecal tube giving rise to the succeeding triad. Further, Bulman (1925, 1927) gave the first detailed description of the development of the rhabdosome in the *Dictyonema flabelliforme* group. The material used only allowed the direct observation of the generating bud of the colony and the crossing canal (1927, p. 21, pl. 1, fig. 5), and it was, therefore, essentially from a study of microtome sections of specimens of *Dictyonema flabelliforme anglica* Bulman that a development



TEXT-FIG. 1. Location map showing the Pre-Cambrian and Lower Palaeozoic rocks. 1, Pre-Cambrian of Morocco (excluding the Adoudounien); 2, Pre-Cambrian of the Ougarta Range; 3, Cambrian of Morocco (including the Adoudounien); 4, Cambrian of the Ougarta Range; 5, Cambro-Ordovician undefined; 6, Ordovician; 7, Silurian.

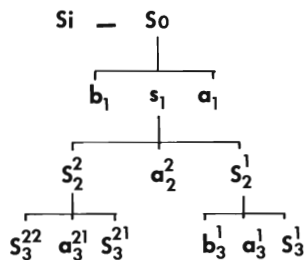


TEXT-FIG. 2. Diagram of the development of a rhabdosome of *Dictyonema flabelliforme anglica* Bulman (1925, 1927) with current notation. Bulman's notation is given in brackets.

diagram was proposed; a diagram that in current notation can be summarized as in text-fig. 2.

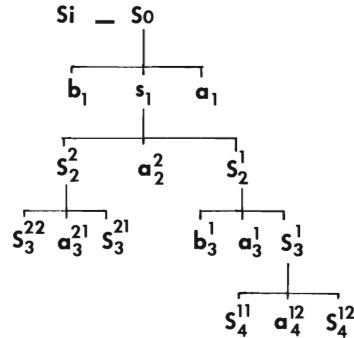
Kozłowski (1949) revealed by direct observation of particularly well-preserved material a different scheme of development for *Dendrograptus communis* Kozłowski, and the problem arose of deciding if two different modes of development existed for the early dendroids, as suggested by Kozłowski, or if the interpretation of the microtome sections by Bulman should be reinterpreted. Also in 1949 Bulman himself proposed a reinterpretation in which the scheme of development for *Dictyonema flabelliforme* became analogous to that of *Dendrograptus communis*. The new scheme in the current notation would be set out as in text-fig. 3. In this, the appearance of a completely new branch was made by replacement in the triad pattern of a bitheca by a stolothea. Since then, this interpretation has not been modified (Bulman 1955, 1970).

This history would be incomplete if one did not recall an observation by Hahn (1912) who, dealing with the development of *D. flabelliforme*, considered that four primary branches existed, this being a contradiction, at least to a certain extent, of what had been described by his predecessors and in particular by Ruedemann (1904). This difficulty did not escape Bulman (1927) who explained it (certainly with justification in a good number of cases) by the existence, apart from the three true primary



TEXT-FIG. 3. Diagram of the development of a rhabdosome of *Dictyonema flabelliforme anglica* Bulman according to the interpretation of Bulman (1949) with current notation.

branches, of an apparent fourth primary branch resulting from the precocious division of one of the three primary branches (not always the same one), this division intervening just beyond the first triad. This interpretation was retained by Bulman in his later works in accordance with text-fig. 4.



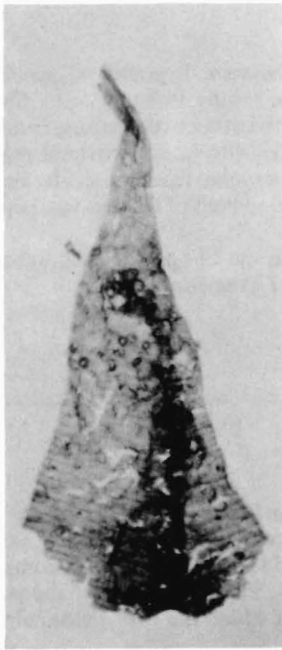
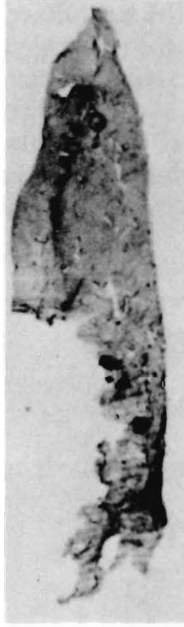
TEXT-FIG. 4. Diagram of the development of a rhabdosome of *Dictyonema flabelliforme anglica* Bulman with precocious dichotomy of a primary branch according to the interpretation of Bulman (1927, 1949) with current notation.

It should be added that it appears, when reading the descriptions since given by Bulman that the existence of a fourth primary branch appeared to him as appropriate to certain classifications and consequently able to serve as a systematic character. Thus, apart from *Dictyonema flabelliforme flabelliforme* Eichwald *sensu* Bulman, one can probably cite *Dictyonema flabelliforme anglica* Bulman, *Dictyonema flabelliforme parabola* Bulman (1954), and more recently *Dictyonema flabelliforme belgica* Bulman (1972).

On several occasions, however, when studying the material from the Algerian Sahara, the impression was gained that some rhabdosomes of *Dictyonema* appeared to have had four branches from the origin. The possibility of studying complete speci-

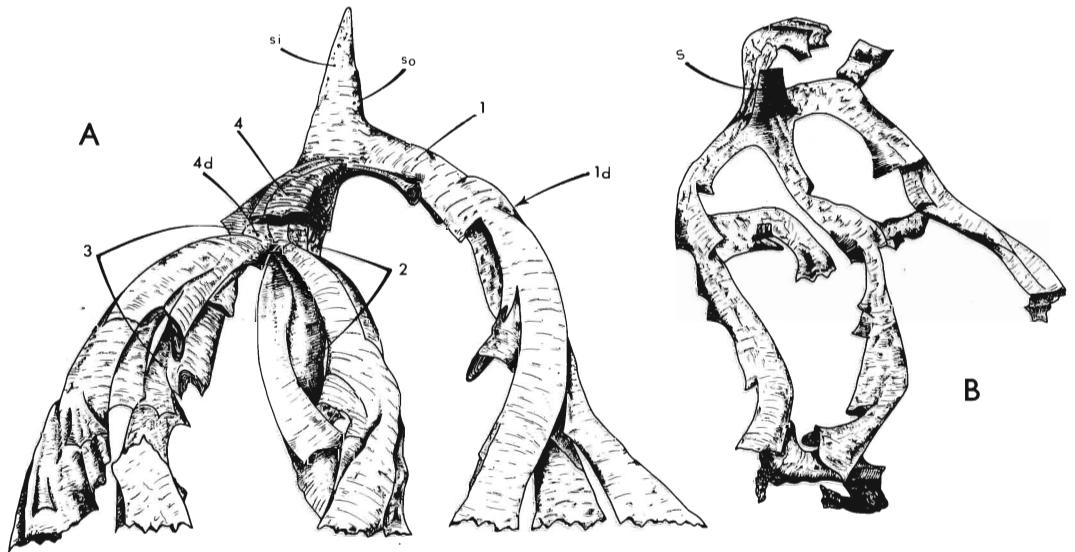
#### EXPLANATION OF PLATE I

Figs. 1-6. *Dictyonema sociale mehaigueni*-*Dictyonema sociale praeaffricanum* Legrand. From the borehole NI 2 of SN. Repal, Cote 3016.62, from the El Gassi shales, Subzone of *Dictyonema* ex gr. *sociale*. Association  $v_1a_1$ , regional substage  $n_1a_1$ . Lower Tremadoc. 1, preparation NI 2 C53 3016.62 XLVIII  $a_1$ . Sicula and generating bud of the colony, front view. 2, preparation NI 2 C53 3016.62 XL  $a_1$ . Sicula and generating bud of the colony, side view. 3, preparation NI 2 C53 3016.62 CLI  $a_1$ . Sicula and generating bud just before the formation of the first triad. 4, preparation NI 2 C53 3016.62 XXIX  $a_1$ . Sicula, generating bud, and differentiation of the first triad. Note the dark outline across the sicula corresponding very probably to the internal outline of the stolon. 5, preparation NI 2 C53 3016.62 CLXI  $a_1$ . Sicula, generating bud, and differentiation of the first triad. 6, preparation NI 2 C53 3016.62 CLXXII  $a_1$ . Sicula, generating bud, and differentiation of the first triad with the stolotheca  $s_1$  beginning to divide to give the second triad. All  $\times 80$ .



LEGRAND, *Dictyonema*

mens from boreholes NI 2 and UC 101 has allowed the confirmation of this, at least in the case of a population occupying an intermediate position between *Dictyonema sociale mehaigueni* Legrand and *Dictyonema sociale praeaffricanum* Legrand. Further, the chance isolation of a perfect rhabdosome (text-fig. 5A; Pl. 2, fig. 1) as well as of a proximal part compressed parallel to the axis of the rhabdosome (text-fig. 5B) afforded exceptional conditions for observation. But to understand better the different stages of this development it was necessary to look at detailed structures, which was not achieved without problems.

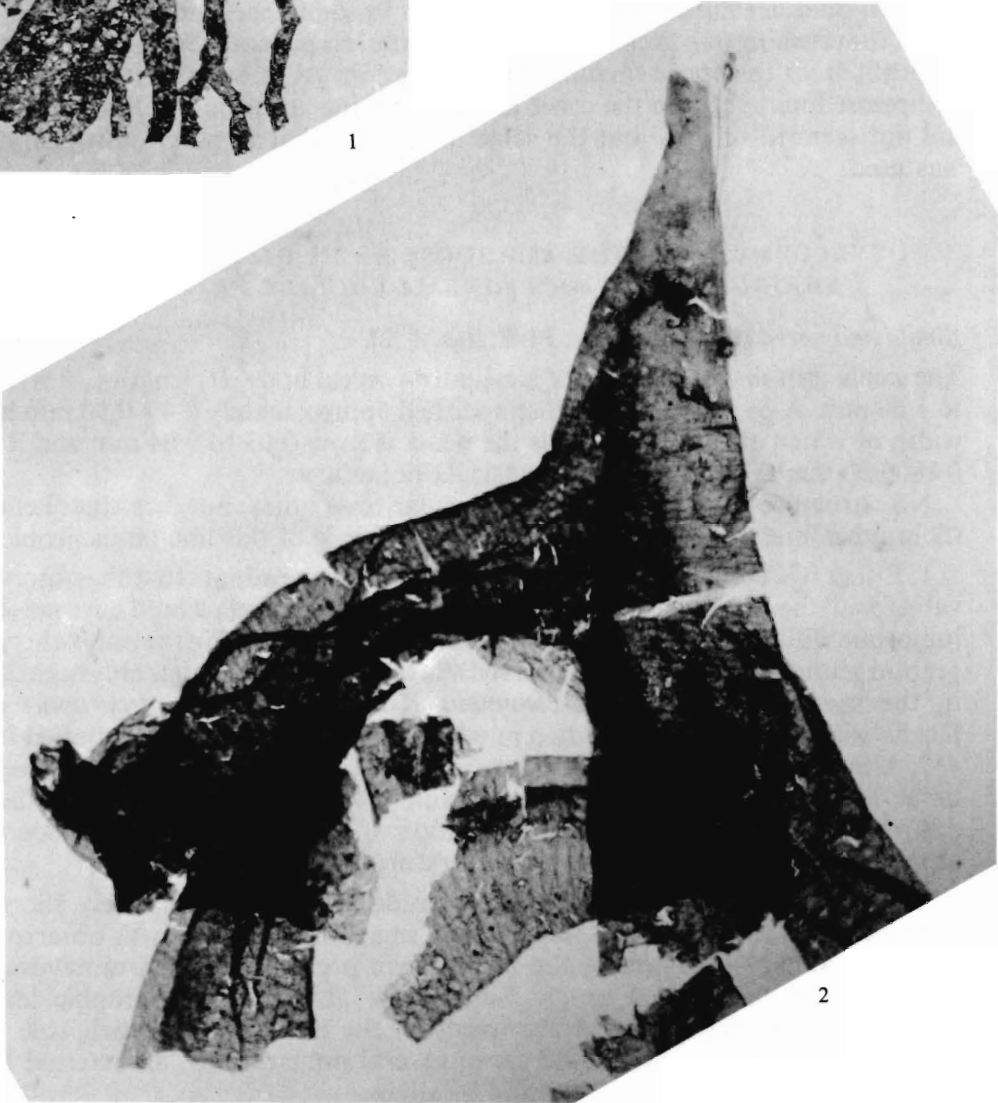
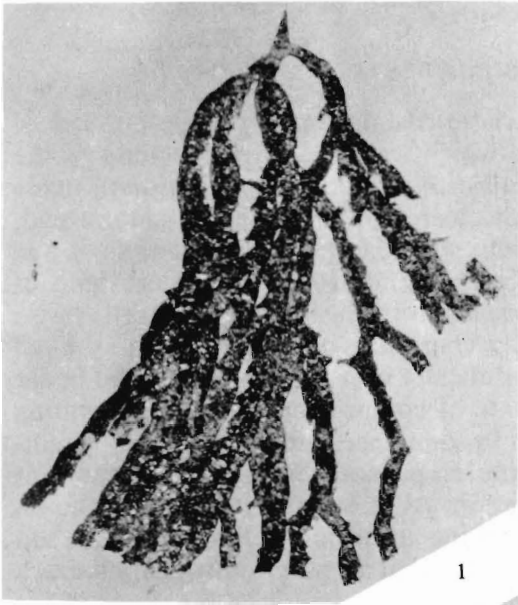


TEXT-FIG. 5. *Dictyonema sociale mehaigueni*-*Dictyonema sociale praeaffricanum* Legrand. A, specimen NI 2 C53 3016.62 a<sub>6</sub>. Proximal part of an almost complete rhabdosome totally isolated,  $\times 25$ . Shows apparently six primary branches, but only four are true primary branches, the other two resulting from the precocious division of the first and fourth branches. B, specimen NI 2 C53 3016.62 a<sub>7</sub>. Proximal part of a totally isolated rhabdosome,  $\times 13$ . Shows the differentiation of the four branches from the sicular region as well as the differentiation of an 'apparent' primary branch after the development of the first triad on the first primary branch (on the right).

Both specimens from borehole NI 2 of SN. Repal, Cote 3016.62. From the El Gassi shales, Subzone *Dictyonema* ex gr. *sociale*. Association  $\nu_1a_1$ . Regional substage  $n_1a_1$ . Lower Tremadoc.

#### EXPLANATION OF PLATE 2

Figs. 1, 2. *Dictyonema sociale mehaigueni*-*Dictyonema sociale praeaffricanum* Legrand. From borehole NI 2 of SN. Repal, Cote 3016.62. From the El Gassi shales, Subzone of *Dictyonema* ex gr. *sociale*. Association  $\nu_1a_1$ , regional substage  $n_1a_1$ . Lower Tremadoc. 1, specimen NI 2 C53 3016.62 a<sub>6</sub>. Almost complete rhabdosome totally isolated,  $\times 7$ . 2, preparation NI 2 C53 3016.62 CV a<sub>2</sub>. Proximal part of rhabdosome figured Plate 3, fig. 1. Sicular view. Note the four primary branches of which the first divides almost immediately,  $\times 80$ .



LEGRAND, *Dictyonema*

## PREPARATION OF MATERIAL

When the matrix was dissolved to obtain whole rhabdosomes, a large number of fragments were recovered, and it was these which were used for the study of the detailed structures. The high level of carbonization of the original periderm made this a delicate study. Mounting of the material, cleared by nascent hydrochloric acid, could not be achieved using the usual products; finally, after many attempts, it was a method advocated by Brideaux (1966), but modified to avoid the crushing of specimens already very compressed, which proved to be the least harmful. However, in spite of all these precautions, only about 40 preparations of the 200 possible proved suitable for further detailed study. The great difficulty in studying the material under examination was caused by its advanced state of compression, the corresponding position of each element being difficult to fix. In some cases, thanks to filling by sediment, the crushing due to compaction was a little less pronounced and it was important to profit from this more favourable preservation. All measurements were made on compressed material; on the other hand, mounting according to Brideaux's method did not seem to bring about the same dilation as that in which anti-oxide varnish was used.

DEVELOPMENT OF THE RHABDOSOME IN *DICTYONEMA SOCIALE*  
*MEHAIGUENI* AND *DICTYONEMA SOCIALE PRAEAFRICANUM*

*Sicula and nema* (text-fig. 6A, B; Pl. 2, figs. 1, 2).

The sicula is in the classic form of a cylindro-conical body. Its length varies from 1.40 to 1.60 mm. A prosicula can be distinguished approximately 0.40–0.50 mm long, the width of which at the level it joins the nema is from 0.03 to 0.04 mm and it reaches 0.18–0.20 mm at the prosicula–metasicula boundary.

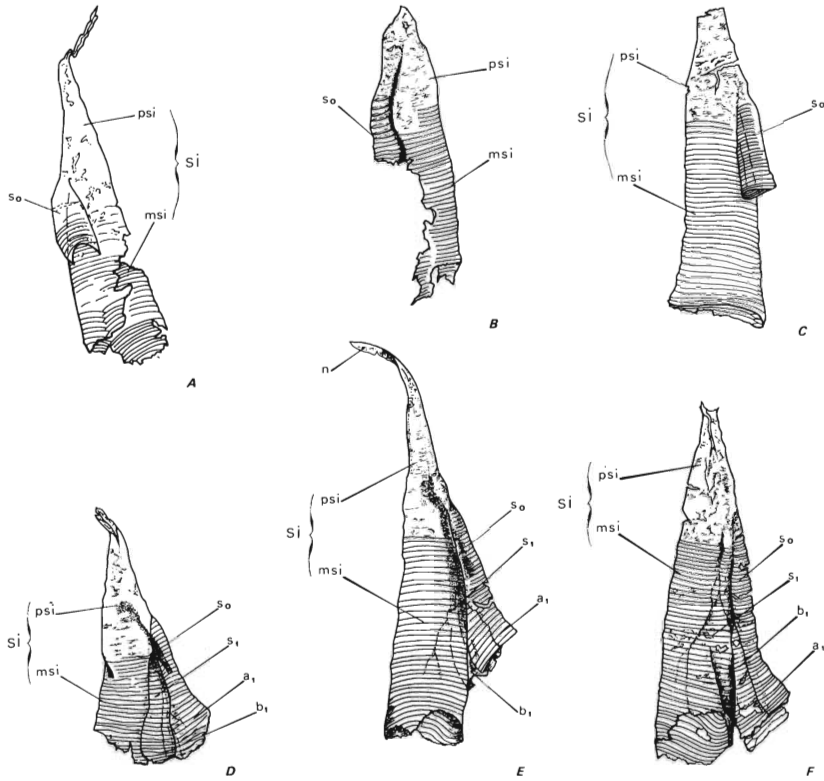
No structure is disclosed, in particular one does not see the helical line (Schraubenlinie in the sense of Kraft). The absence of this line poses problems:

1. Either it is actually lacking and, in this case, if one admits that the observation is valid for all the *Dictyonema flabelliforme* group, the prosicula would have presented an important difference from the genus *Dendrograptus* (this being the only other dendrograptid genus where it had been observed). In fact the helical line has only been described in the species *Dendrograptus communis* Kozłowski and *Dendrograptus cofeatus* Kozłowski which are the only two in which the prosicula has been studied in detail.

2. Alternatively lack of this structure is due to the fact that it belongs to the cortical tissue as Kozłowski suggested was possible (1949, p. 53) and that this tissue was destroyed due to the advanced carbonization of the material under consideration or at the time of its preparation in the laboratory.

The nema in the subspecies under consideration seems relatively short and is a structureless tube 0.03–0.04 mm wide. A small lateral tongue was observed in one specimen along the length of the nema; such organs are much more frequent in specimens of *Dictyonema* ex gr. *flabelliforme* at higher stratigraphic levels. No mention of this has appeared previously in the literature and their role remains enigmatic. At the base of the nema, in several preparations, an external film was





TEXT-FIG. 6. *Dictyonema sociale mehaigueni*-*Dictyonema sociale praeafricanum* Legrand. A, preparation NI 2 C253 3016.62 XLVIII a<sub>1</sub>. Sicula and generating bud of the colony, front view. B, preparation NI 2 C53 3016.62 XL a<sub>1</sub>. Sicula and generating bud of the colony, side view. C, preparation NI 2 C53 3016.62 CLI a<sub>1</sub>. Sicula and generating bud of the colony just before the formation of the first triad. D, preparation NI 2 C53 3016.62 XXIX a<sub>1</sub>. Sicula, generating bud, and differentiation of the first triad. Note the dark trace across the sicula corresponding very probably to the internal outline of the stolon. E, preparation NI 2 C53 3016.62 CLXI a<sub>1</sub>. Sicula, generating bud, and differentiation of the first triad. F, preparation NI 2 C53 3016.62 CLXXII a<sub>1</sub>. Sicula, generating bud, and differentiation of the first triad; the stolothecca s<sub>1</sub> has begun to divide to give the second triad, × 40.

All specimens from borehole NI 2 of SN. Repal, Cote 3016.62. From the El Gassi shales. Subzone *Dictyonema* ex gr. *sociale*. Association v<sub>1</sub>a<sub>1</sub>. Regional sub-stage n<sub>1</sub>a<sub>1</sub>. Lower Tremadoc.

observed which seemed to encase the nema and prosicula but it is probably an artefact due to crushing of the fossil through unsticking of layers of cortical tissue; an analogous phenomena, but due to mounting in Canada Balsam, has been remarked upon by Kozłowski (1949, p. 15).

*Differentiation of the generating bud* (text-fig. 6A, B, C; Pl. 2, figs. 1-3).

The generating bud s<sub>0</sub> emerges from the sicula a little above the prosicula-metasicula boundary (0.16-0.18 mm). It appears as a little tube of clearly visible fusellar structure of 0.10 mm diameter. In some cases (text-fig. 6D, E; Pl. 2, figs. 4, 5) a dark band

can be seen inside the prosicula. It seems reasonable to interpret this as the internal outline of the generating bud before the point of perforation, in the manner observed by Kozłowski (1949, text-fig. 1) in *D. communis*.

One discerns, moreover, on several preparations, a dark line or band below the point of emergence of  $s_0$ . In at least one case this band appears in the inside of the generating bud. It is probably, therefore, the outline of the middle stolon which will emerge in the future autotheca  $a_1$  or the internal part of one of the lateral tubes which will widen out later to give either the stolothecca  $s_1$  or the bithecca  $b_1$ , this arrangement having been described in *D. communis* (Kozłowski 1949, p. 23, text-fig. 1). This band seems also to divide at about 0.02 mm below the prosicular pore. However, the flattening of the preparations does not allow more precision on this point.

*First stages of development* (text-fig. 6D-F; text-fig. 7A-C; Pl. 1, figs. 4-6; Pl. 2, fig. 2; Pl. 3, figs. 1, 2; Pl. 4, fig. 1)

The generating bud  $s_0$  grows along the sicula for about 0.25 mm before widening out to give birth externally to the autotheca  $a_1$ , the bithecca  $b_1$ , and the stolothecca  $s_1$ . The autotheca  $a_1$  develops from the sicula at an angle of  $70^\circ$ , directing the development of the first branch of the rhabdosome: the length of  $a_1$  is about 1.0 mm and its width at the aperture 0.30 mm. The bithecca  $b_1$  accompanies it. The length of the sicula is rarely seen correctly, either because it is more fragile and commonly destroyed, or more likely, it has been hidden by the proximal parts of the rhabdosome, in particular at the level of its aperture where the autotheca  $a_1$  leaves the sicula and the development of autotheca  $a_2^2$  takes place. In fact, the stolothecca  $s_1$  immediately divides to generate a stolothecca  $s_2^1$  which will develop along  $a_1$ , one autotheca  $a_2^2$  and one stolothecca  $s_2^2$ .

The autotheca  $a_2^2$  commonly appears along the sicula in an anti-sicular position but is found just as commonly compressed in a position on the same side or the opposite side to  $a_1$ . This autotheca  $a_2^2$  will give direction to the development of the second primary branch of the rhabdosome. The stolothecca  $s_2^2$  in its turn almost immediately gives birth to an autotheca  $a_3^{21}$ , a stolothecca  $s_3^{22}$  which will develop along  $a_2^2$  and will generate the second primary branch of the rhabdosome, and a stolothecca  $s_3^{21}$ .

At this stage, according to the classical scheme, one should no longer observe the division until after at least the development of a normal triad. It is true that what one sees most often along the first primary branch is  $s_2^1$  resulting in a classical triad  $a_3^1$ ,  $s_3^1$ ,  $b_3^1$ , the stolothecca  $s_3^1$  dividing immediately to give a bifurcation by the emission of an autotheca  $a_{21}^{12}$ , and the two stolothecae  $s_4^{12}$  and  $s_4^{11}$ . The bithecca  $b_3^1$  has never been

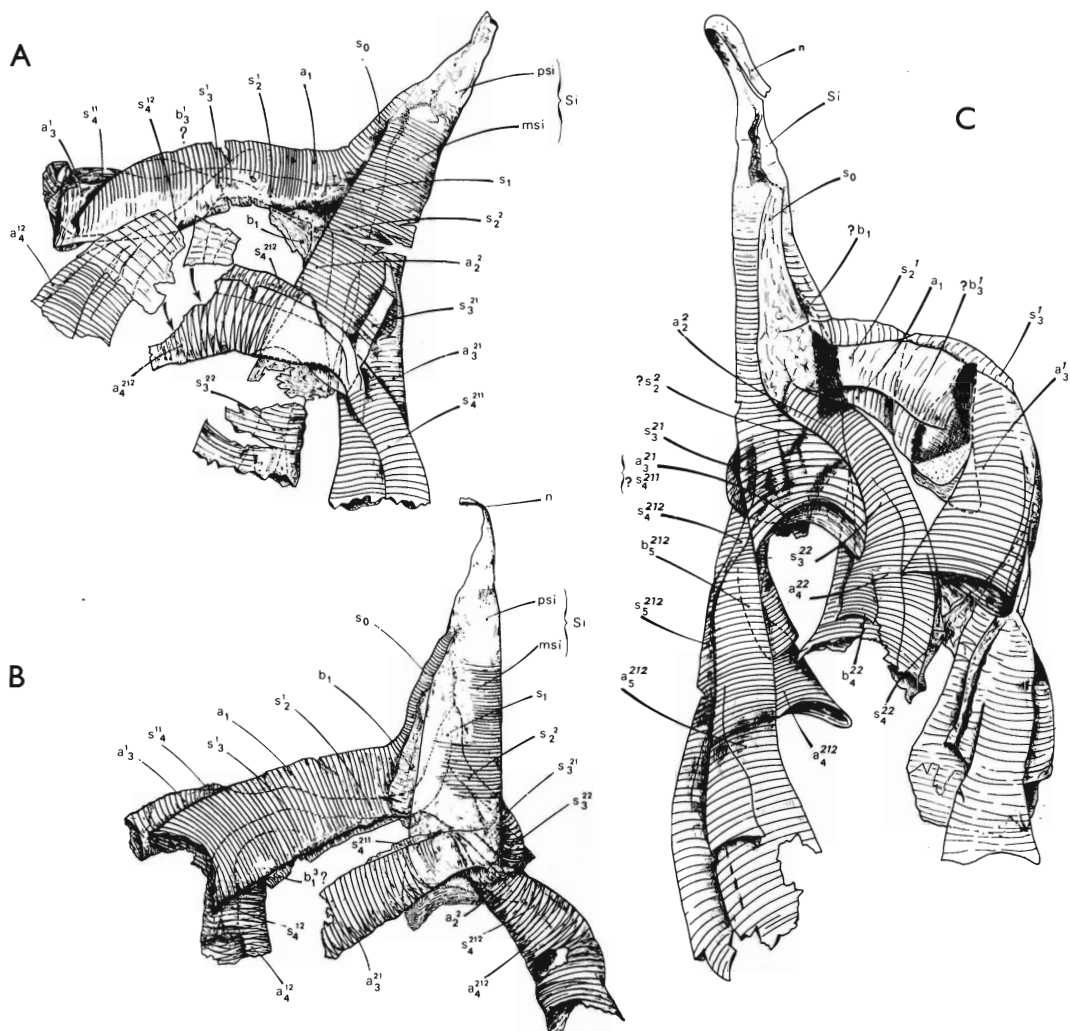
---

EXPLANATION OF PLATE 3

Figs. 1, 2. *Dictyonema sociale mehaigueni*-*Dictyonema sociale praeaffricanum* Legrand. From borehole NI 2 of SN. Repal, Cote 3016.62. From the El Gassi shales, Subzone of *Dictyonema* ex gr. *sociale*. Association  $\nu_1 a_1$ , regional substage  $n_1 a_1$ . Lower Tremadoc. 1, preparation NI 2 C53 3016.62 CV  $a_1$ , c.  $\times 30$ . 2, preparation NI 2 C53 3016.62 XXXI  $a_1$ , c.  $\times 50$ . Proximal part of laterally compressed specimen.



LEGRAND, *Dictyonema*

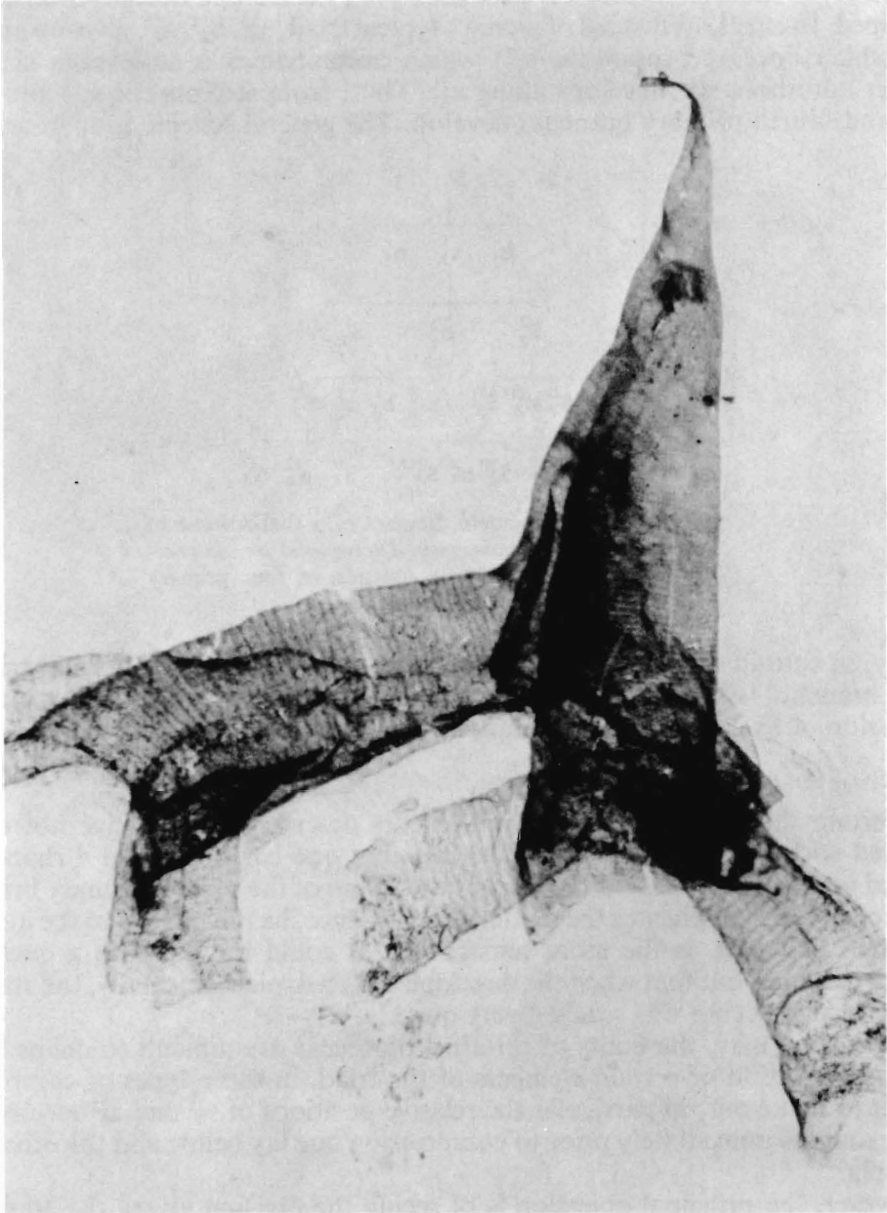


TEXT-FIG. 7. *Dictyonema sociale mehaigueni*-*Dictyonema sociale praeaffricanum* Legrand. A, preparation NI 2 C53 3016.62 CV a<sub>1</sub>. Proximal part of the rhabdosome figured in Plate 3, fig. 1. Sicular view. Showing the precocious division of the first primary branch, in addition to the four primary branches,  $\times 40$ . B, preparation NI 2 C53 3016.62 CLXXIII a<sub>1</sub>. Proximal part of rhabdosome. Sicular view. The precocious division of the first primary branch is perfectly seen with the second primary branch occupying an external position while the third and fourth branches are compressed on the sicula,  $\times 40$ . C, preparation NI 2 C53 3016.62 XXXI a<sub>1</sub>. Proximal part of rhabdosome, showing the individuality of the first branches while the base of the fourth is distinguishable beside the base of the third. Specimen is compressed from the side,  $\times 40$ .

All specimens from borehole NI 2 of SN. Repal, Cote 3016.62. From the El Gassi shales. Subzone of *Dictyonema* ex gr. *sociale*. Association  $v_1a_1$ . Regional substage  $n_1a_1$ . Lower Tremadoc.

#### EXPLANATION OF PLATE 4

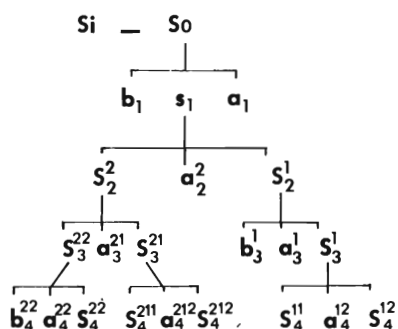
Fig. 1. *Dictyonema sociale mehaigueni*-*Dictyonema sociale praeaffricanum* Legrand. From borehole NI 2 of SN. Repal, Cote 3016.62. From the El Gassi shales, Subzone of *Dictyonema* ex gr. *sociale*. Association  $v_1a_1$ , regional substage  $n_1a_1$ . Lower Tremadoc.



1

LEGRAND, *Dictyonema*

observed in a perfectly clear form on the prepared specimens. It can be seen, however, very clearly on a totally isolated rhabdosome (text-fig. 5A). Its existence, therefore, is certain. But one ascertains at the level of the third primary branch that a division yet more precocious is produced even before one normal triad had fully developed. In effect,  $s_3^{21}$  instead of giving a typical triad,  $a_4^{21}$ ,  $b_4^{21}$ ,  $s_4^{21}$ , gives an autotheca  $a_4^{212}$  (which develops opposite  $a_3^{21}$ ) which accompanies a stolotheca  $s_4^{212}$ , while another autotheca  $s_4^{211}$  develops along  $a_3^{21}$ . Thus, from stolothecae  $s_4^{211}$  and  $s_4^{212}$  the third and fourth primary branches develop. The general scheme is as in text-fig. 8.



TEXT-FIG. 8. Development diagram of a rhabdosome of *Dictyonema sociale mahaigueni*-*Dictyonema sociale prae-africanum* Legrand with an emission of four primary branches.

Finally, in certain cases (text-fig. 5A) after the development of a normal triad, one of the branches issuing from  $s_4^{211}$  and from  $s_4^{212}$  can bifurcate again, thus giving the impression of five or six primary branches.

#### *Validity of the preceding observations*

It is certain that the successive developments described above have not all been observed with the same precision. The fact that one has not found a rhabdosome arrested in its development at the level of the origin of the second primary branch, or those following, complicates the matter. This absence, having regard to the numerous specimens collected, is the more remarkable. It could be that it is a question of aborted colonies, but that when the development took place normally, the stage with four defined branches was reached very quickly.

Be that as it may, the limits of certain stolothecae are difficult to define and the reciprocal position of certain elements of the triad, in some types of compression, difficult to make out; in particular the relative positions of  $s_3^{21}$  and  $a_3^{21}$  means that in some instances immediately prior to compression one lay below and the other above the sicula.

However, the principal objection is of seeing the division giving rise to what we call the third and fourth primary branches, a normal dichotomy not intervening until after the development of a normal triad. The aspect of four primary branches would have resulted in the precocious bifurcation of two out of three primary branches instead of on one only as had been observed by Bulman.

This interpretation cannot be retained here, although it is not to be excluded in other cases, for the following reasons:

1, direct observation does not show the existence of a normal triad at the base of the third primary branch;

2, the distance which separates the dichotomy of the first primary branch from its origin on the sicula is much bigger than that separating the point of differentiation of branches 3 and 4 and there is no room for a normal triad in the latter;

3, the precocious bifurcation of the third and fourth branches can be effectively observed in certain cases and what one sees, therefore, is the existence of five or six apparent primary branches.

Thus the reality of the existence of four primary branches does not seem in doubt and the conclusion to which this study comes is very natural. Moreover, in numerous specimens thought to have a proximal part with three primary branches, a more detailed examination made it clear that a branch had been broken and that one was, in fact, dealing with a proximal part of a specimen having *four* primary branches.

#### CONCLUSION

The existence of a *Dictyonema* of the group *Dictyonema flabelliforme* (Eichwald) *sensu lato* with four primary branches is considered demonstrated, and their mode of generation satisfactorily explained. This naturally does not preclude the existence of other *Dictyonema* of the same group with three primary branches. In the light of the present observations the mode of development proposed by Bulman following upon the works of Kozłowski is found to be confirmed. It remains to be seen whether the presence of four true primary branches can be considered of classificatory value. This appears to be the case for the population studied, but should be confirmed by other observations of the same nature. In what is yet only a hypothesis, it should, however, be possible to see the origin at least, of certain Anisograptidae with a symmetry of the order 2 such as the genus *Staurograptus*.

*Acknowledgements.* The author thanks the managements of the Compagnie Française des Pétroles (Algérie) CFP(A) and the Société Nationale de Recherche et d'Exploitation des Pétroles en Algérie (S.N. Repal) who afforded him the opportunity of studying this fauna.

#### REFERENCES

- BLAIN, M. 1963. Découverte de la zone à *Dictyonema flabelliforme* Eichwald dans l'Ordovicien inférieur du Sahara algérien septentrional. *Bull. Soc. géol. Fr. ser. 7*, **5**, 1105-1112.
- BRIDEAUX, W. W. 1966. A double layer mounting technique for aqueous palynological residues. *J. Paleont.* **40**, 224.
- BULMAN, O. M. B. 1925. Notes on the structure of an early *Dictyonema*. *Geol. Mag.* **67**, 50-67.
- 1927. British Dendroid graptolites, Part I. *Palaeontogr. Soc. [Monogr.]*, 1-28.
- 1949. A re-interpretation of the structure of *Dictyonema flabelliforme* Eichwald. *Geol. För. Stockh. Förh.* **71**, 33-40.
- 1954. The Graptolite fauna of the *Dictyonema* Shales of the Oslo region. *Norsk geol. Tidsskr.* **33**, 1-40.
- 1955. Graptolithina. In MOORE, R. C. (ed.). *Treatise on Invertebrate Paleontology. Part V.* 101 pp. Geological Society of America and University of Kansas Press.

- BULMAN, O. M. B. 1970. Graptolithina with sections on Enteropneusta and Pterobranchia. In TEICHERT, C. (ed.). *Ibid.* (2nd edition). 163 pp. Geological Society of America and University of Kansas Press.
- 1972. A new *Dictyonema* fauna from the Salmien of the Stavelot Massif. *Bull. Soc. belge Géol. Paléont. Hydrol.* **79**, 213–224.
- EICHWALD, E. 1855. Beitrag zur geographischen Verbreitung der fossilen Thiere Russlands. *Bull. Soc. Imper. Nat. Moscow*, **28**, 433–466.
- 1860. *Lethaea Rossica. Période ancienne*. Stuttgart.
- HAHN, F. F. 1912. On the *Dictyonema* fauna of Navy Island, New Brunswick. *Ann. N.Y. Acad. Sci.* **22**, 135–160.
- KOZŁOWSKI, R. 1949. Les graptolites et quelques nouveaux groupes d'animaux du Tremadoc de la Pologne. *Palaeont. pol.* **3**, (1948), 1–235.
- LEGRAND, PH. 1966. Précisions biostratigraphiques sur l'Ordovicien inférieur et le Silurien des chaînes d'Ougarta (Sahara algérien). *C.r. Somm. Séanc. Soc. géol. Fr.* **7**, 243–244.
- 1973. Résultats récents sur le problème de la limite Cambrien–Ordovicien au Sahara algérien septentrional. *Bull. Soc. Hist. nat. Alg.* **64**, 159–187.
- MATTHEW, G. F. 1895. Two new Cambrian graptolites with notes on other species of Graptolitidae of that age. *Trans. N.Y. Acad. Sci.* **14**, 262–273.
- NICHOLSON, H. A. 1872. Monograph of the British Graptolitidae. 133 pp. Blackwood, Edinburgh & London.
- RUEDEMANN, R. 1904. Graptolites of New York. Part I. *Mem. N.Y. St. Mus. nat. Hist.* **7**, 457–803.
- SALTER, J. W. 1858. On *Graptopora*, a new genus of Polyzoa, allied to the graptolites. *Proc. Am. Ass. Advmt Sci.* **11** (for 1857), 63–66.
- 1866. On the Fossils of North Wales. In RAMSAY, A. C. Geology of North Wales. *Mem. geol. Surv. Gt Br.* **III**. Appendix 239–381.
- 1881. *Ibid.* (2nd edition).
- WIMAN, C. 1895. Über die Graptolithen. *Bull. Instn geol. Univ. Upsala*, **2**, 239–316.

PH. LEGRAND  
 Total Algérie  
 7 Place el Qouds  
 Hydra  
 Algeria