

A STUDY OF THE FRUCTIFICATION OF *MILLERIA* (*PROTOPTERIDIUM*) *THOMSONII* LANG FROM THE MIDDLE DEVONIAN OF BELGIUM

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With plates 31—40 and 4 figures in the text

Abstract

Well preserved compressions from the Middle Devonian of Belgium allow a detailed study of the fructification of *Protopteridium* KREJČI 1880 here recognized as a *nomen nudum* and transferred to *Milleria* LANG 1926. New information is given on the fertile branching system, the construction of the fertile organ, the insertion of the sporangia and their spores, the type of leaf and the assumed vegetative branching system. The validity of the species of *Milleria* is reconsidered and the taxonomic position of the genus discussed.

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I. Introduction

The object of this study is to give a fuller account than has hitherto been possible of the external morphology and organization of the complex fertile branching system of *Milleria* (*Protopteridium*), to review the validity of the seven species previously ascribed to *Protopteridium*, and to discuss the affinities of the genus.

We acknowledge the financial support given to S. LECLERCQ by the "Fonds National de la Recherche Scientifique de Belgique" which made possible the two field trips (1949 and 1952) during which the specimens of *Milleria* were collected.

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We express our gratitude to the technical staff of the "Laboratoire de Paléontologie Végétale" of the University of Liège: Mr. MAURICE DISCRY, chief preparator and Mr. MARCEL LHODE, chief preparator for their valuable assistance in all phases of techniques and photography, and to Mr. JULES JACQUET, preparator, for his help with the spore preparations.

II. Stratigraphy, Material and Techniques

The plant material was collected by S. LECLERCQ from the well-known Middle Devonian (Givetian) locality at Goé, Belgium. The quarry "Carrières Brandt", is located about 50 kilometers east of Liège and 20 kilometers from Germany (see LECLERCQ & ANDREWS, 1960; LECLERCQ & BANKS, 1962). The fossiliferous outcrop consists of shaly lenses 45 cm to 1.10 m in thickness, interstratified with beds of arkose. It is abundantly fossiliferous, but the quality of preservation varies with different lenses. In the case of *Milleria* large specimens predominate in some of the lenses where several long axes parallel to each other reach 22 cm in length, though the ultimate and basal parts are missing. Numerous fertile organs are still in organic connection with the axes and closely appressed to them (fig. 23, 49). In this type of preservation the positions of the axes and their fructified organs seem to indicate a prevailing direction of a water current in a subautochthonous deposition. In other layers the specimens are more fragmentary and consist either of short axes bearing a few fructified organs (fig. 16) or of isolated fertile organs detached from the parent axis (figs. 7, 13, 20, 34, 35). Both states of preservation indicate that the plant fragments have drifted. However in both cases it is noticeable that the linear, delicate sporangia are still in organic connection. In one fortunate instance a much better preserved specimen shows a remarkably intact, widely spread branching system that indicates a subautochthonous deposition in quiet water (fig. 1, 2).

The material studied is a suite of 44 fructified compression specimens from which 14 were chosen for detailed study. Three vegetative specimens thought to belong to *Milleria* were studied with some detail. All consisted of

part and counterpart. The specimens are catalogued in the paleobotanical collection of the Laboratoire de Paléontologie Végétale of the University of Liège.

The bulk of the information in this study was obtained by means of intensive application of the technique of dégagement or uncovering. Although the uncovering method has been fully described (LECLERCQ, 1960) and successfully employed in previous works (LECLERCQ, 1951; LECLERCQ & ANDREWS, 1960; BONAMO & BANKS, 1966 and LECLERCQ, 1969), its value as a means of understanding compression fossils cannot be overemphasized.

The compressions of *Milleria* are three-dimensional. The distal portions of some branches are deeply embedded in the sediment, sometimes to a depth of about 2 cm, while their proximal portion is exposed at the rock surface (see fig. 1). The embedded branches often bear lesser, upwardly directed branches which are oriented more or less perpendicularly to the branch bearing them. Consequently, in the course of uncovering a larger branch, it is not unusual to encounter the distal region of the erect organ before reaching its real point of attachment. Thus the uncovering must be pursued with extreme care and attention to avoid removing or breaking finer ramifications while attempting to follow a plunging axis.

The first split of a fossiliferous rock cannot expose all parts of a three dimensional branch system. This is well demonstrated by the comparison of our figs. 1 and 2. Before uncovering, the part and counterpart of the specimen were almost the exact reflection of each other. After dégagement one can see (fig. 1) the following additional structures not seen on fig. 2:

a) On the ultimate fertile organ of major axis II (M.A. II), part of a second first order pinna lies 6 mm beneath the upper one (fig. 5). See Description, page 94, for terminology.

b) On the same major axis, and a little below, a complex lateral branch has appeared, bearing at least three smaller lateral branches that are themselves divided. The whole branch was embedded under 4.6 to 7 mm of sediment. Note that on fig. 2, the point of insertion of this whole lateral branch is seen.

c) On the basal portion of major axis I (M.A. I), two lateral branches have become evident. On the left side of the lowermost, two tiny, twice bifurcated and leaf-like organs have been discovered. They were covered by 19 mm of sediment.

The uncovering of the counterpart represented in figure 2 has added the following information:

a) on the lowermost right branch of M.A. I, a small lateral divided branch to the left;

b) above this, also on the left, a small bifurcated axis, which represents the base of a pair of first order pinnae;

c) the whole length of M.A. I that was covered by fertile organs (compare with fig. 1).

Despite the fact that further uncovering of this specimen (fig. 1 and 2) may have yielded more information, it was not undertaken because the block has become too fragile to allow more excavation. For that reason some connections of fertile organs that could possibly have been proven have not been uncovered (see fig. 1 on the middle part of M.A. I). In any case at the present state of dégagement the part and counterpart of the specimen have become fruitfully complementary to each other.

All the Belgian specimens studied in this work have been uncovered, as were some of the specimens formerly described by LANG (1925 and 1926). New information given by dégagement is incorporated in the description.

The transfer technique (WALTON, 1923; BONAMO & BANKS, 1967) proved complementary to the technique of dégagement. The specimen was embedded in the translucent plastic, Palatal (LECLERCQ & DISCRY, 1950). Often in the case of the Goé specimens, after 12 to 24 hours in hydrofluoric acid, a soft, colloid-like substance covered the exposed sediment surface of the transfer. This effectively stopped the acid attack. After washing and placing the transfers for 12 or more hours in concentrated hydrochloric acid (pers. comm. JOHN RICHARDSON) the colloidal substance was removed. In some cases a further attack of 6 to 24 hours with hydrofluoric acid was necessary to complete the transfers.

Some of the transfers were subsequently cleared by placing the entire transfer in SCHULTZE's solution (1 part concentrated fuming nitric acid: 1 part concentrated solution of potassium chlorate) for a period of 2 to 4 days. An illustration of the information given by this method is shown by figures 14 and 15 which come from the same fertile organ. Fig. 14 represents the compression as it appeared on the surface of the sediment, and shows numerous thick groups of linear sporangia that cover and hide the underlying three-pinnate organization of the fertile organ. This tri-pinnate organization is only revealed on the reverse side after the transfer has been made in fig. 15.

The preservation of the fertile organs of *Milleria* is often such that transfers of part and counterpart yield strikingly different results. Apparently in the course of fossilization, when the fertile organs were deposited in water or mud, the lighter sporangia floated toward the upper surface of the water. Thus, when a specimen of a fertile organ is split, one often sees a mass of sporangia on the surface of both part and counterpart. However, only one of these contains the branches which bear the sporangia. Thus if both halves are transferred, one yields nothing more than masses of sporangia (fig. 11) while the other will show the morphology of the supporting branching structure as in fig. 12, 13, and 15.

Spores and sporangial fragments were cleared in small watch glasses in SCHULTZE's solution for a period of 2 to 4 days depending on the state of carbonization of the spores. The spore material was washed by pipetting it into several changes of water and mounted to a coverslip in hydroxyethyl cellulose (H.E.C.). The mixture was allowed to dry on the coverslip and the coverslip was then mounted on a slide in Euparal.

Photomicrographs of the spores were taken with a Zeiss photomicroscope equipped for phase contrast microscopy; photographs of the compressions were obtained by means of a Linhof camera (18 x 24 cm) and certain of the transfer photographs by a Nikon camera (24 x 36 mm). Scanning electron photomicrographs were taken with the Cambridge Stereoscan microscope.

III. Previous Records and Interpretations

DAWSON in 1871 mentioned briefly a specimen from Caithness, Scotland, which consisted of circinately coiled stems bearing long, linear leaflets, and to which he gave no name. He observed: "It seems to be a plant in veneration, and the parts are too much crowded and pressed together to admit of being figured or accurately described . . ." Despite the apparently circinate veneration, DAWSON believed the fossil was related to *Lycopodites*.

CARRUTHERS in 1873 described and figured (tab. 137, fig. 2) the counterpart of the specimen reported by DAWSON in 1871. It was not apparent until later, however (see DAWSON, 1878), that DAWSON and CARRUTHERS were considering part and counterpart of the same fossil. CARRUTHERS' specimen, is preserved in the British Museum of Natural History, London (No. V9425) and is reproduced here in fig. 47. It was collected from the Caithness Flagstones (= Middle Old Red Sandstone) of Skail, Orkney, Scotland, and seems to be the remains of a plant of which only the terminal portion was preserved. CARRUTHERS thought it to be lycopodiaceous but he did not name it. His description however, is instructive for the essential characteristics of a plant, later named *Protopteridium* by KREJČI (1880) were described for the first time. CARRUTHERS noted: "The body itself looks like a compound spike. From the opposite sides of the stalk spring several erecto-patent, at length incurved, leaf-like bodies. They were obviously arranged spirally on the main axis, their opposite appearance being due to the manner in which the fossil is preserved. Scattered among them are a large quantity of linear organisms, about a quarter of an inch long, which are all arranged round special centres . . ." (These equal our pinnae of second order.) "These centres are short thickened processes on the main axis, or on the curved leaf-like bodies. About half-way up the inner curve of the lowest of these such a process is shown with the linear bodies radiating from it."

CARRUTHERS was impressed by "this interesting specimen" for which he could see "no intelligent interpretation" and stated further: "The linear bodies are too unlike the leaves to suppose this to be a mass of undeveloped leaf buds. Nor are they like organs of reproduction, although it is more probable this may be their nature." CARRUTHERS had almost grasped the correct interpretation of the fossil. He had recognized the spiral arrangement of the erect, incurved organs, the existence of second order pinnae (his centres), the masses of linear bodies connected to them and the probable reproductive nature of the linear bodies. It is amazing that this description was unnoticed by later authors except LANG who mentioned it briefly in 1926 (p. 786).

DAWSON in 1878 recognized that he (1871) and CARRUTHERS (1873) were dealing with the same specimen and gave it the name *Ptilophyton thomsoni*. He emphasized that the specimen was "not a spike of fructification but a young stem or branch in veneration . . . on the whole related to Lycopods rather than to Ferns."

KREJČI (1880) reported part and counterpart of a specimen from the argillaceous, graywacke shales of Stage H(h) of Barrande near Hostin, Bohemia. He interpreted the stem, bearing upcurved twigs with small unilateral

pinnules, as the vegetative, terminal portion of a fern frond. After a brief description, without illustration, he gave it the provisional name *Protopteridium hostinense*. In 1881 KREJČI mentioned fertile specimens of *P. hostinense* but gave no description.

STUR (1881) recognized the fructified nature of some of KREJČI's specimens but placed them and some non-fertile axes in the algae, as closely related to *Gigartina* of the Florideae and designated them *Hostinella hostinensis*.

DAWSON (1882) reconsidered the affinities of his *Ptilophyton* (1878). His belief that the pinnules were cylindrical, hollow structures which served as floats, in addition to a series of other characteristics, led him to the idea that these were aquatic plants "perhaps allied to Lycopods and Pillworts." In 1888 he reported the occurrence of small rounded sporocarps on the stems or petioles of *Ptilophyton*. Thus, for DAWSON, the specimens grouped as *Ptilophyton* were aquatic plants "more likely to have been allied to Rhizocarps than to any other group."

J. L. PIEDBOEUF (1887) in a paper on the fossil plants found at Gräfrath near Düsseldorf, described a plant that bore fertile organs like those of *Protopteridium* associated with vegetative axes. The author interpreted the plant as a marine alga close to *Sargassum dechenianum* or *Anthophycus dechenianus*. The interest of his finding is that one block of rock 40 cm long and 2 cm thick revealed abundant remains that could belong to different regions of the same plant.

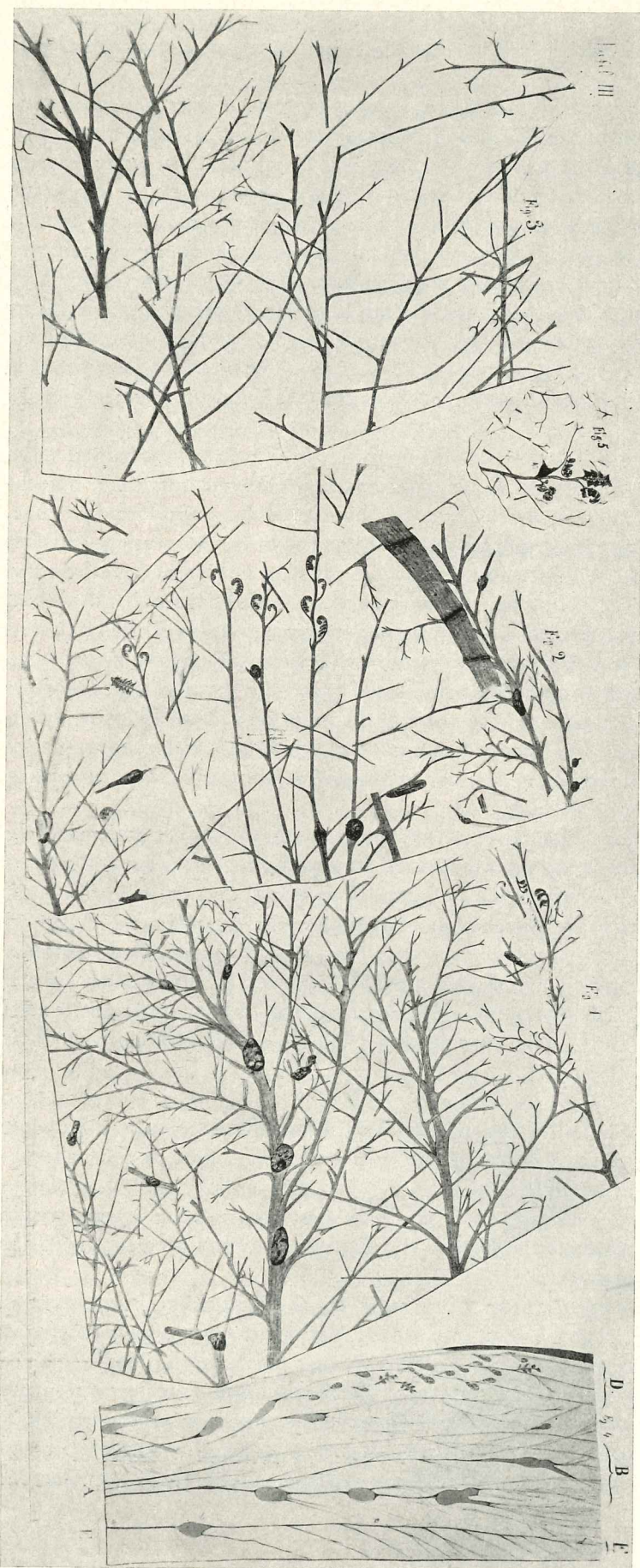
PIEDBOEUF's plate III (fig. 1—5) is reproduced in this work in text-figure 1. His fig. 2 shows the usual erect, curved fertile organs of *Protopteridium* inserted alternately on slender naked axes, which were irregularly branched. On his fig. 1, are two large parallel axes of about 1 cm in width. They are abundantly and irregularly branched. PIEDBOEUF noted that he drew the branching as it appeared successively in the course of his uncovering, and that he reproduced it as seen in one plane. He pointed out that the branches were oriented in several directions and plunged deeply in the sediment. Consequently he considered that the axes were embedded "in situ" and stressed for the first time that the whole plant had a bushy habit. In his fig. 4 PIEDBOEUF gave a sketch of the block that showed the relative positions of the different organs as they were interred in the sediment. He intentionally placed his fig. 2 immediately above fig. 1 to emphasize that he thought the fertile axes were the continuation of the strong axes seen in fig. 1 though he could not prove their connection. Later the point of view of PIEDBOEUF concerning the vigor and abundant branching of the axis was discussed and acknowledged for *P. thomsoni* by KRÄUSEL & WEYLAND, 1938. These authors had the good fortune to examine in Düsseldorf some of PIEDBOEUF's drawings and specimens which are no longer available since World War II.

KIDSTON (1903) questioned the validity of *Ptilophyton* DAWSON (1878) because the systematic position of the genus was not clearly defined. It included five species among which some were probably not plants. Moreover KIDSTON expressed the opinion that the large stem described as *Caulopteris ? peachii* by SALTER (1859) was the trunk which bore the branches he identified as *Psilophyton dechenianus* and whose terminal portion was *Ptilophyton thomsoni*. *Caulopteris ? peachii* (SALTER, 1859, fig. 14) was created for a large stem 31 cm long and about 6 to 8 cm in width that supported several large rectangular scars, disposed spirally, on some of which short (15 cm/2 cm) lateral branches were inserted. A sub-epidermal longitudinal striation occurred on some areas of the stem and lateral branches. We see no evidence that this type of stem was related to the fertile organ later called *Milleria thomsoni* LANG (1926).

POTONIE & BERNARD (1904) reexamined the specimens previously described by KREJČI and STUR. Contrary to these authors, they did not believe the remains were fertile but thought them to be young, vegetative, circinate fern fronds of doubtful affinity. For this reason they placed them in *Spiropteris*, generally used to designate croziers of ferns and made the new combination *Spiropteris hostimensis*.

ARBER (1921) though considering the genus very obscure, grouped all the above described specimens within *Ptilophyton*. The specimens of Bohemia were designated *Ptilophyton ? hostimense* (KREJČI) ARBER and the Scottish material was called *Ptilophyton thomsoni* DAWSON.

LANG (1925) shared KIDSTON's belief that the name *Ptilophyton thomsoni* for the Scottish specimen described by DAWSON in 1878 was erroneous. He transferred it to the new combination *Hostimella (Ptilophyton) thomsoni* (DAWSON) LANG. LANG selected the genus name because it did not imply systematic affinities which still remained doubtful. At the same time he described as *Hostimella pinnata* some new Middle Old Red Sandstone specimens collected at Cromarty, Scotland. The new material consisted of small disconnected specimens of thrice pinnate branch systems which he interpreted as vegetative pinnae (see our fig. 18), despite his recognition that their claw-like extremities "give the impression of being somewhat flattened and often widened, though this hardly amounts



Text-fig. 1. *Milleria (Protopteridium) thomsonii* LANG.
From J. L. PIEDBOEUF (1887, Taf. III, Abt. 1—5). Schematic reconstruction of different regions of the specimen as they appeared in the course of dégagement. $\times 1/2$

to the differentiation of a definite lamina". In association were a few fertile specimens, similar in construction to the sterile pinnae, bearing linear sporangia attached to slender subdivisions. Cleared sporangia yielded winged spores over 100μ in diameter. He considered that the Scottish material showed "striking similarity" to the Bohemian specimens, and believed that *H. pinnata* was closely related to *Hostimella (Ptilophyton) thomsoni* on which he suggested that the leaf-like bodies previously interpreted as lycopod leaves (DAWSON, 1878), were sporangia.

LANG (1926) described some well preserved new Scottish specimens of *Hostimella (Ptilophyton) thomsoni* found in the Middle Old Red Sandstone. The most spectacular specimen was 42 cm long. It consisted of a basal region, 31 cm long, which supported terminally a fertile region of 11 cm in length (LANG's fig. 6 and 7). From the broken base of the basal region up to the first fertile organ, there were five obvious fragments of lateral branches considered to be vegetative. The four basal were regularly alternate while the fifth was given off on the same side as the fourth. According to LANG, the fertile region "in construction appears to continue the alternate branching of the lower part, though all the branches are not to be recognized". The fertile pinnae, about 3 cm long, were erect and gradually inwardly curved to the tip (our fig. 50). They supported lateral short projecting branches in double series that bore, on their tips, groups of inwardly directed linear sporangia. LANG observed that the exact position in which these latter were attached was not clearly shown. The length of the sporangia was said to be about 4 or 5 mm and the breadth 0.5 mm. LANG demonstrated that the linear bodies were in fact sporangia and contained his spore type B (1925). The specimen above described was the first to show attachment of a fertile portion to a sterile region consisting of *Hostimella*-like axis. It was not known whether the basal lateral broken branches bore fructifications or vegetative leaves.

In the same paper LANG described a second fertile specimen (his fig. 1 and 2 reproduced in our fig. 46). The fertile portion of the two specimens reproduced the characters of the detached terminal regions to which the name *Ptilophyton thomsoni* was given. LANG (p. 790) correctly considered it desirable to separate the specimens he described in a distinct genus for they had well defined characters; thus he created the new genus *Milleria*. For the first time a clear diagnosis and illustration of this type of fertile organ was given: "Dorsiventral, alternately branched, frond-like branch systems, sometimes with subpinnate ultimate, vegetative divisions, and bearing elongated, linear sporangia in relation to other ultimate ramifications". The type of the genus was *Milleria thomsoni* (DAWSON) LANG. The genus also included *Milleria pinnata* LANG (*Hostimella pinnata* of LANG, 1925). LANG believed that Bohemian *Spiropteris* (POTONIE & BERNARD, 1904) belonged to *Milleria* but he did not include them.

SEWARD (1931) in his book, "Plant Life Through the Ages" gave a view of a Middle Devonian landscape. He reproduced *Milleria* with an arborescent habit on the basis of the large stem known as *Caulopteris peachii* SALTER to which he attached the fertile axis of *Milleria thomsoni*. However he recognized that there was no proof of the nature of the stem supporting the fertile branches.

KRÄUSEL & WEYLAND (1932), upon discovery of new material from the Middle Devonian of Germany, proposed that Scottish *Milleria thomsoni* (DAWSON) LANG, Bohemian *Spiropteris hostimensis* POTONIE & BERNARD, and *Hostimella hostimensis* (POTONIE & BERNARD) be united as species of the genus *Protopteridium*. In addition, they called attention to PIEDBOEUF's concept (1887) of the habit of a new species of *Protopteridium*: *P. piedboeufi* (later put in synonymy with *P. thomsoni*, in 1938). The distinct characters of the species and the analysis of PIEDBOEUF's work were not discussed until 1933 and 1938.

KRÄUSEL & WEYLAND (1933), in a study of the Middle Devonian Flora of Bohemia defined their concept of *Protopteridium hostimense*. The slender axes showed six orders of branching (see their text-fig. 1). All the subdivisions were terete. The alternate second order branches bore a system which was first dichotomously, then pinnately subdivided; it was described as vegetative in its basal portion and fertile at its apex. The sterile pinnae were like those of *P. pinnatum*. According to their reconstruction based on associated detached organs (see their text-fig. 8) the lower part of the first order or main axis bore simple lateral, dichotomizing *Hostimella*-like axes. The poorly preserved anatomy came from the detached axes. In transverse sections, three areas were visible: a primary xylem strand, more or less aliform in shape, in which the protoxylem could not be recognized; a crushed middle zone without preserved anatomy and an external zone with sclerenchyma-like tissue arranged in radial lines with occasional lateral fusion of the lines giving a net-like appearance (see their text-fig. 7). KRÄUSEL & WEYLAND included in *P. hostimense* new material from the Middle Devonian of Germany as well as Bohemian *Spiropteris hostimensis* (= *Hostimella hostimensis*), and *Hostimella hostimensis* of POTONIE & BERNARD (1904). They also showed in 1933 that *Spiropteris* was in fact fertile as STUR had believed.

HALLE (1936) described a new species, *Protopteridium minutum* from the upper Lower or lower Middle Devonian of Yunnan, China. The main axis of this species bore alternately arranged lateral branches spread out in one plane. On the main and lateral branches were borne alternately disposed, twice dichotomized segmented organs. These pinnule-like appendages were sterile on the lower portion of the axis, and bore clusters of two to four oval sporangia on the terminal portion. HALLE himself doubted the affinity of his new species with *Protopteridium*. We believe that the differences between *P. minutum* and other *Protopteridium* are too great to warrant retention of *P. minutum* within the genus, therefore we agree with OBRHEL (1966) who separated it as a new genus: *Cathaiopteridium minutum* (HALLE) OBRHEL.

KRÄUSEL & WEYLAND in 1938 finished the revision of the genus they had begun in 1932 with a definition of the remaining species, *Protopteridium pinnatum* and *P. thomsoni*.

Protopteridium pinnatum consisted of thick vegetative and fertile branches not found in organic connection. The vegetative branches, 3 cm in length, divided once dichotomously and each half bore three orders of branches in a pinnate arrangement. These vegetative branches bore a large, basal catadromic pinnule of second order. Fertile pinnae, very similar in construction to the vegetative pinnae, bore tufts of sporangia up to 7 mm long. A very poorly preserved anatomy found on associated naked axes was interpreted as consisting of a 3 to 4 lobed solid vascular strand in one axis, while in another one a transversally curved central primary xylem strand was surrounded by an outer cortical zone (p. 181, fig. 7—9, pl. XXIV). Though *P. pinnatum* possessed distinct vegetative and fertile fronds, and *P. hostinense* bore only one type of frond with fertile distal and vegetative proximal regions, the two species were very similar. KRÄUSEL & WEYLAND themselves questioned whether two separate species existed. They included in *P. pinnatum* the new material from the Middle Devonian of Germany as well as *Milleria pinnata* of Scotland.

Protopteridium thomsoni differed from the two species discussed above because it lacked vegetative fronds. On slender, naked main axes, up to 20 cm long, were borne alternate fertile branches. These varied from 3 to 8 in number according to the preserved length of the main axis. The lateral fertile branches were erect, curved toward the main axis and 2.5 cm in length. On the inner side were short, pinnately arranged protuberances, more or less parallelly disposed, bearing numerous linear sporangia 0.5 cm long. Anatomically *P. thomsoni* was the best known of the three species. Yet in that paper it was not positively stated that the anatomy was found in axes connected with the fructified organs¹). The cross section of an axis about 5 to 4.5 mm wide showed a crushed and irregular three lobed primary xylem strand surrounded by compact secondary xylem (see fig. 52, 53 and text fig. 4, p. 101). The latter consisted of radial series of tracheids some of which were square and of large size: 120 μ in diameter. They were sculptured on all walls. Varied sculpture was observed: scalariform, reticulate and doubtful circular bordered pits. The rays were uniseriate and numerous. Rows of tracheids showed a converging orientation towards the best developed arm of primary xylem. A poorly preserved cortical zone surrounded the vascular tissue. It consisted of rows of large cells more or less radially disposed. KRÄUSEL & WEYLAND drew attention to the points of resemblance and differences between the anatomy of *P. thomsoni* and *Aneurophyton germanicum* KRÄUSEL & WEYLAND (1923, 1926, 1929). On the basis of material formerly studied by PIEDBOEUF (1887) they agreed that *P. thomsoni* could have had a vigorous habit. These considerations will be developed in detail in our discussion. KRÄUSEL & WEYLAND included in *P. thomsoni* new material from the Middle Devonian of Germany and *Milleria thomsoni* (= *Hostinella [Ptilophyton] thomsoni*) of Scotland.

LECLERCQ (1940) described a few specimens of *Protopteridium* cf. *thomsoni* from a Givetian outcrop, at Mousset, Belgium. The material was entirely fertile. The best specimen was 3.5 cm long, consisting of a main axis that bore two alternate, erect, fertile fronds. The first order pinna of the fertile frond was incurved and bore in turn, 5 to 8 pair of short second order pinnae. These latter were attached in two rows on the inner side of the first order pinna towards the main axis. The second order pinnae were 1.5 to 2.5 mm long and widened at the distal portion which divided several times giving rise to short bifurcate pedicels bearing two to four slender sporangia 3.5 to 5 mm long (her text fig. 10). LECLERCQ's material was like that of *P. thomsoni* of Germany and Scotland

¹) Prof. Dr. HERMANN WEYLAND has recently clarified, in a letter of August 10, 1970, that in his paper with KRÄUSEL published in 1938, the anatomy of *Protopteridium thomsoni* was based on the study of a connected petrified axis of PIEDBOEUF's specimen (1887). At that time part of PIEDBOEUF's material was still available. The petrified areas came from one of the axes on which an oval nodule of pyrite had preserved the organic structure (our text-fig. 1). Consequently, it is now ascertained that the described anatomy belongs to *P. thomsoni*. We express our thanks to Professor Dr. WEYLAND for this kind and valuable assistance.

except that the width of the sporangia of the Belgian material (0.2 to 0.3 mm) was half that of previously described sporangia. On the compression the surface of several sporangia showed a kind of closely disposed, circular granulation giving the appearance of spores. Attempts to obtain spores indicated that the sporangia may have contained very small spores (5—7 μ) suggesting heterospory for *Protopteridium*. LECLERCQ chose to call her material *P. cf. thomsoni* until more material could confirm conclusively the existence of the unusually small "spores".

HØEG (1942) described a single, fertile specimen of *Protopteridium* from the Middle Devonian of Mimerdalen, Spitzbergen, Norway. The whole axis is 2.9 cm long; the lower stalk is naked, 2 cm long and terminated by an upcurved distal portion bearing several short, dichotomously subdivided secondary branches which end in numerous sporangia 2.5 mm long and 0.5 mm wide. HØEG considered this specimen too fragmentary for specific determination, and thought it was probably a *Protopteridium* (see his pl. 27, fig. 6, 7).

CHIRKOVA-ZALESSKAJA (1957) described three new species of *Protopteridium*: *P. rossicum*, *P. jigulense* and *P. ajense* from a different series of the Givetian in the Volga-Ural region of Russia. *P. ajense* was based on one non-fertile axis and can hardly be considered a *Protopteridium*. *P. jigulense* found at the Zolny Ravine was also based on one specimen. It consisted of a repeatedly dichotomized system of short axes resulting in a palmate-disposition of the branches (see her text-fig. 61). The axes were covered with sparse point-like tubercles. Four of the branches bore terminal clusters of sporangia consisting of three sori on each tip. Each sorus included a group of five sessile sporangia about 1 mm long. The striking differences between *P. jigulense* and *Protopteridium*, as now known, are the palmate branching, and the sporangia grouped in "sori". Consequently, in our opinion, *P. jigulense* cannot be placed in the genus *Protopteridium*.

Protopteridium rossicum bore fertile appendages which were very similar to *P. thomsoni* (see her fig. 166) except for the oval shape and size of the sporangia. It consisted of fragmentary twice dichotomized axes that bore terminally erect and inwardly curved appendages with pedicellate sporangia. The sporangia were 1 mm wide and 2 mm long and hung by fours or fives on each pedicel. Both megaspores and microspores were mentioned for this species but no description or illustration was given. The spores were observed on the compression through the carbonized walls of the sporangia. The megaspores, were about 0.5 mm in diameter and six in number within the sporangia, other sporangia had smaller spores. Apparently no maceration nor oxidation was made, therefore we cannot accept this information without reservation.

OBRHEL (1959—1961) reviewed the state of knowledge of *Protopteridium hostinense*. He corrected the orthography of the species name to *hostinense* instead of *hostimense*. He especially stressed the necessity of having fertile material in order to name a specimen *Protopteridium hostinense* because sterile material placed formerly in the taxon could belong to several fossil genera as they showed no specific characters. In the same paper OBRHEL described new specimens of *P. hostinense* from several localities of the Srbsko strata in the Middle Devonian of Bohemia. He noted that in association with a branch 6 cm long and 1.2 cm wide (his pl. 9, 10) were a few smaller broken dichotomized branches, one of these bearing sporangia. He interpreted this association as an indication that *P. hostinense*, like *P. thomsoni*, had a low arborescent habit. He also illustrated the spores of *P. hostinense* which are morphologically like those figured by LANG for *Milleria thomsoni*. A detailed description of the spores was not given nor was there any discussion of their affinities with any of the *sporae dispersae*.

OBRHEL (1966) contested the validity of the reconstruction of *Protopteridium hostinense* made by KRÄUSEL & WEYLAND (1933, text fig. 8) from the specimen represented by STUR (1881, Taf. 4, Fig. 7). For OBRHEL the "sterile pinnules" represented by KRÄUSEL & WEYLAND were, in fact, fertile pinnules seen from their dorsal surface with the tips of their ultimate divisions, that bore the sporangia, probably, still embedded in the matrix. However, he did not give evidence for this belief.

In the same paper OBRHEL reviewed the validity of the three new species described by CHIRKOVA-ZALESSKAJA (1959): *Protopteridium rossicum*; *P. jigulense*; *P. ajense*. Having re-examined the Russian material, he concluded that *P. rossicum* was the only one of the three that had any validity. We agree with his judgment. In the same publication he erected a distinct genus and made the new combination *Cathaiopteridium minutum* (HALLE) for the Chinese specimen (Province Yunnan) described and named *Protopteridium minutum* by HALLE (1936).

OBRHEL gave further description (1968A) and a new reconstruction of *Protopteridium hostinense* on the basis of the Bohemian specimens he described in 1959—1961. He omitted the basal vegetative *Hostinella*-like branches of the reconstruction by KRÄUSEL & WEYLAND (1933) because they were not found in organic connection. How-

ever his new proposed reconstruction is also made from an assemblage ("Kombination" p. 712) of detached organs. The "trunk" is nothing more than the 6 cm long, 1.2 cm wide axis that he figured in 1959—1961, pl. 9 and 10, that he enlarged up to the size of a short trunk. Consequently we see no evidence for this new reconstruction. On the other hand OBRHEL once again rejected the interpretation given by KRÄUSEL & WEYLAND (1933) concerning the vegetative pinnules inserted on the frond of *P. hostinense*. He repeated his opinion as to their fertility which he gave in 1966, page 441 (see above).

OBRHEL (1968B) in a paper on the Barrandium allochthonous and autochthonous formations, mentioned the finding of limestone concretions including plants, found in the Robbin Schichter of Devonian age. Slides made through the concretions showed transverse and longitudinal sections of sporangia and spores. The sporangia were spindle-shaped; some of them were filled with small spores, others with large spores. OBRHEL considered that the form of the sporangia, the size and the trilete mark of the megaspores recalled the spores of *Protopteridium hostinense*. Since the spores were not identifiable, the determination cannot be accepted without reservation (we know that the same spore type was produced by different plants; i.e. *Milleria* [*Protopteridium*] *thomsonii* of the present work and *Tetraxylopteris schmidtii*, in BONAMO & BANKS, 1967).

STOCKMANS (1968) described *Protopteridium thomsoni* from the Middle Devonian of Belgium. His material corresponded exactly to Scottish specimens of *Protopteridium* (*Milleria*) *thomsoni* as described previously by LANG (1926).

JURINA (1969) reported a new species, *Protopteridium* (?) *ramulosum* from the Middle Devonian of Kazakhstan, Russia. Since the specimens were naked vegetative axes only, lacking the characteristic fertile fronds, their inclusion within the genus *Protopteridium* remains open to doubt.

The above review of the genus *Protopteridium* emphasizes that little convincing is known about the following points:

1. the habit of the plant,
2. the presence or absence of vegetative pinnules on the fertile system,
3. the type of the vegetative pinnule,
4. the detailed mode of insertion of the sporangia, except that they are grouped in tufts, on the other hand;
5. the branching is described as a dorsiventral system of alternately disposed branches,
6. three types of anatomy have been described only one of which is proved to be in connection.

The new results developed in the course of this paper, give an answer to the above points 2, 3, 4, 5, allow the expression of some probable suggestions on points 1 and 6, cast a new light on the complex organization of the fertile organ, and place the plant in its taxonomic position.

IV. Synonymy

In preparing the synonymy, we have chosen the name *Milleria* because it is the earliest name, given to fertile material characteristic of the taxon, which was validly published in accordance with the International Code of Botanical Nomenclature (LANJOUW et al, 1961). Our reasons for this choice are explained briefly below; for specific details of the history of the genus see the Previous Records and Interpretations of this paper.

CARRUTHERS (1873) gave the earliest sufficient description and figure of the first recognizable *Milleria* but he did not name it.

DAWSON (1878) named it *Ptilophyton thomsoni*. Although the name was established in accordance with the rules, the genus *Ptilophyton* included at that time, a heterogeneous assemblage of forms to which *P. thomsoni* did not conform. The genus name *Ptilophyton* must be rejected but the specific epithet is valid and remains with the specimen.

Chronologically, the next possible choice of genus is *Protopteridium* KREJČI, 1880. This must be rejected as a *nomen nudum* in accordance with articles 12, 34, 41 and 42 of the International Code of Nomenclature (1961) because:

- 1) Krejčí did not give a generic or specific description,
- 2) there was no illustration,
- 3) he specifically assigned the name only provisionally.

Continuing chronologically; *Hostinella* (STUR, 1881) is a form genus for vegetative remains unlike the fertile material characteristic of the genus in question; *Spiropteris* (POTONIE & BERNARD, 1904) is a form genus for croziers of vegetative portions of ferns also unlike our material; and *Hostimella* (LANG, 1925) again is a form genus for vegetative axes and was used only temporarily by LANG.

Milleria LANG 1926, on the other hand, was established specifically for material like that described in this paper. LANG created the genus by giving full illustrations, detailed description, and both generic and specific diagnoses. He correctly used the specific epithet *M. thomsoni* as the type of the genus and designated the CARRUTHERS (1873) — DAWSON (1878) specimen as the holotype.

We have also corrected the orthographic error of the specific epithet by changing *thomsoni* to *thomsonii* in accordance with article 73 of the code.

We have omitted from the synonymy all the non-fertile, unattached "*Hostinella*-like" axes ascribed to *Protopteridium* by KRÄUSEL & WEYLAND as well as anatomy obtained therefrom.

Milleria LANG 1926. Trans. Roy. Soc. Edinburgh. 54:785—790.

Protopteridium KREJČI ex KRÄUSEL & WEYLAND 1932. Senckenbergiana 14:185—190;

Milleria thomsonii (DAWSON) LANG 1926. Trans. Roy. Soc. Edinburgh 54:785—790, pl. 1, fig. 1—5.
emend. LECLERCQ & BONAMO.

Ptilophyton thomsonii DAWSON 1878. Canadian Nat. & Quart. J. Sci. 8:379—389, pl. IVa ("*thomsoni*");
DAWSON, 1871. Quart. J. Geol. Soc. London 27:269—275, (p. 274, no illustration) as *Lycopodites* sp.;
CARRUTHERS, 1873. J. Bot. N.S. 2:321—327, tab. 137, fig. 2, unnamed;
DAWSON, 1882. Geol. Surv. Canada (p. 120, 121, no illustration);
DAWSON, 1888. Kegan Paul, Trench & Co., London, 290 p. fig. 18a;
KIDSTON, 1903. Trans. Roy. Soc. Edinburgh 40:741—833 (p. 759—760, no illustration);
ARBER, 1921. Cambridge Univ. Press 100 p., fig. 13, upper right only.

Hostinella hostinensis STUR 1881. pro parte. Sitz. Ber. K. Akad. Wiss. 84:330—391, quoad, Taf. IV, fig. 7, 8;
KREJČI, 1880. Sitz. Ber. K. Böhm. Ges. Wiss. Prague, 201—204, (p. 203, no illustration), as *Protopteridium hostinense* nom. nud.;
KREJČI, 1881. Ibid. p. 68, 69, as *Protopteridium hostinense* nom. nud., (no illustration).

Spiropteris hostimensis POTONIE & BERNARD 1904. Leipzig, 68 p., fig. 1—6.

Ptilophyton (?) *hostinense* ARBER 1921. Cambridge Univ. Press, 100 p., fig. 14.

Hostimella pinnata LANG 1925. Trans. Roy. Soc. Edinburgh 54:253—272, fig. 54—65.

Hostimella thomsonii LANG 1925. Ibid. (p. 266, no illustration, "*thomsoni*").

Milleria pinnata LANG 1926. Ibid. 54:785—790 (p. 789—790, no illustration).

Aneurophyton germanicum KRÄUSEL & WEYLAND 1926. pro parte. Abb. Senckenberg. Naturforsch. Ges. 40:115—155, quoad. Taf. 6, Abb. 6, 7.

Protopteridium piedboeufii KRÄUSEL & WEYLAND 1932. Senckenbergiana 14:185—190 (p. 187, no illustration, "*piedboeufi*");
PIEDBOEUF, 1887. Mitt. Naturwiss. Ver. Düsseldorf 1:9—57, fig. 1—5, unnamed.

Protopteridium pinnatum KRÄUSEL & WEYLAND 1932. Senckenbergiana 14:185—190 (p. 187, no illustration);
KRÄUSEL & WEYLAND, 1938. Palaeontographica 83B:172—195, Taf. 24, Abb. 10, Taf. 25, Abb. 1—5, Taf. 26, Abb. 1—6, Taf. 27, Abb. 1, text fig. 4, 6, 7.

- Protopteridium thomsonii* KRÄUSEL & WEYLAND 1932. Senckenbergiana 14:185—190 (p. 187, no illustration, "thomsoni");
 KRÄUSEL & WEYLAND, 1938. Palaeontographica 83B:172—195, Taf. 24, Abb. 1—6, text fig. 1—3 ("thomsoni");
 LECLERCQ, 1940. Acad. Roy. Belgique, Mém. in 4°, 12:3—65, fig. 34—41, text fig. 10, as *Protopteridium* cf. *thomsoni*;
 fig. 20, 21, 23, text fig. 8, as *Incertae Sedis*;
 STOCKMANS, 1968. Inst. Roy. Hist. Natur. Belgique Mém. 159:1—49, pl. IV, fig. 3—5, pl. VI, fig. 2, 2a, pl. XIV, fig. 2, ("thomsoni").
- Protopteridium hostinense* KRÄUSEL & WEYLAND 1932. Senckenbergiana 14:185—190 (p. 187, no illustration, "hostinense");
 KRÄUSEL & WEYLAND, 1933. Palaeontographica 78B:1—46, Taf. 1, Abb. 6—11, text fig. 1—4, 8, ("hostinense");
 OBRHEL, 1961. Sborník Ústředního Ústavu Geologického 26:7—46, Tab. IX, fig. 1, Tab. X, fig. 1, 2, Tab. XI, fig. 1—5;
 OBRHEL, 1966. Casopsis pro mineralogii a geologii 4:441—443 (no illustration);
 OBRHEL, 1968A. Paläontol. Abhandl. Paläobotanik 11B:709—715, text fig. 2.

Milleria cf. *thomsonii* (DAWSON) LANG 1926. Trans. Roy. Soc. Edinburgh 54:785—790, pl. 1, fig. 6, 7.
Milleria thomsonii (DAWSON) LANG 1926. Trans. Roy. Soc. Edinburgh 54:785—790, pl. 1, fig. 6, 7.

V. Description

The best preserved fertile branch here described (figs. 1 and 2) represents a portion of a more complex branching system whose main axis ($n+1$), stem or trunk is still unknown. Therefore in the description of our material, we use the following terminology:

fertile branching system: a highly branched major axis ($n+2$) on which fertile organs predominate and to which are also attached a few sterile organs;
fertile organ: erect pinnae of first order curved upward bearing two to three orders of pinnate subdivisions; the second order pinnae, the third order and the fourth order pinnae when these latter occur.

Among the specimens studied, the most complete is represented by a compression and its counterpart reproduced in figures 1 and 2. The order of its detailed description is as follows: the mode of branching of the axes, the fundamental structure of the fertile organ, and the morphology of the leaf.

1. Mode of branching

The specimen, reproduced natural size, shows two main branches designated major axis I and II (M.A. I, M.A. II). They are the largest preserved branches of the fertile system but we assume them to be part of a more extensive branching system. Both are repeatedly divided and lie closely parallel to one another. Neither their apex nor base is preserved. Their length is 12.2 cm and 7.8 cm respectively. The width of the spreading branching system is 6.8 to 7 cm. Each major axis ($n+2$) supports lateral branches given off at wide angles varying from 38° to 80° ; the proximal branches showing the widest angles. At first sight the third and fourth order branches appear to be flattened in one plane, but the uncovering shows that they depart in several planes from the axis. Some of these dip deeply (to 19 mm) into the sediment indicating that the branches were rigid structures.

The arrangement of lateral organs, of fourth order, can be illustrated by examining their points of attachment to the lowermost third order branch on the right of major axis I, figure 2.

At 10 mm from the point of insertion of the third order branch and on its left side, a small bifurcated branch of fourth order is attached. It is inserted on the lower left side of the third order branch and dips deeply into the sediment. On the complementary figure 1, the existence of this fourth order branch is indicated only by a little marginal knot (arrow).

Eight millimeters further on (fig. 2), there is a tiny oval "scar" in a slight depression, and a narrowing of the diameter of the branch. Correspondingly, on figure 1 the same depression and contraction of the branch can be

seen. We interpret the scar and the irregularity in diameter of the axis as an indication of a fourth order branch inserted on the reverse side of the third order branch, and still embedded in the matrix.

After another 8 mm the remains of a small bifurcated branch is seen on the right in fig. 2. Its base is apparent in figure 1.

Continuing up on fig. 2, 8 mm further up and to the left, a bifurcate stalk with its fertile organ is apparent. It is inserted on the lower left surface of the branch of third order. Consequently, its stalk is missing in figure 1 but the counterpart of the sporangial complex is well preserved.

About 10 mm above is a lateral branch clearly seen on the right on figure 2 and to left in fig. 1. After another 9 mm, a sudden narrowing of the third order branch (fig. 2) calls attention to the probable presence of a buried branch. Precisely at that same point, on figure 1 (see also fig. 6, arrow), the base of the branch has been uncovered. Here however, this lateral branch deeply penetrates the sediment under the third order branch and is all but hidden by it. Beyond this is a cluster of fertile organs which represents the terminal region of the third order branch. In construction the terminal cluster continues the same branching pattern as the lower part (see fig. 6).

From the above description it is apparent that the fourth order branches are spirally arranged.

For the same purpose and in like manner, it is instructive to follow the ramification of major axis I on fig. 2. The two lower third order branches are separated by a distance of 11 mm. One is inserted laterally and is to the right, the next is to the left but attached on the upper left side. The next branching point appears to be 22 mm further on, but in between, at 11 mm, is a slight narrowing of the main axis (arrow) similar to those observed on the branch of third order described above. We consider it to be the indication of a branch inserted beneath the axis and still embedded.

The next branch, buried beneath a sporangial mass (compare fig. 1 and 2), becomes clearly seen on figure 1, after uncovering, while only its base and point of attachment to major axis I are seen in figure 2. This third order branch was therefore inserted on the upper surface of major axis I seen in fig. 2. It has been followed (fig. 1) for 8 mm up to its widening where the base of a fourth order branch appears.

In order to follow major axis I on figure 2, a portion of the fertile organ that covered it has been removed. (The fertile organ is shown in fig. 10 as it appeared before dégagement.) Following major axis I on figure 2, a slight deviation is seen at about 9 mm which could suggest a point of attachment of a third order branch located below the axis (arrow).

About 8 mm further up there is a branch that hugs the lower right side of the major axis (fig. 2). Ten millimeters further on, a stout fertile organ is visible to the left. It is entirely preserved (fig. 2, 3) and is inserted on the upper lateral surface of the major axis. Again, 11 mm above, major axis I shows a distinct narrowing of the diameter that, as already pointed out, indicates the existence of a buried or detached third order branch (arrow).

From this point, major axis I decreases in width, the branching is closer, and the third order branches attached to it apparently smaller (fig. 1). These could represent some of the last branches inserted distally on major axis I.

As a result of the foregoing analysis, it is obvious that to the major axes ($n+2$) a branch of third order ($n+3$) was attached at about every 8 to 11 mm while on the third order branches, the branches of fourth order were borne about every 8 or 9 mm. In both cases the arrangement was spiral. Although neither the base nor apex of major axes I and II are preserved, it seems evident that both were attached to the same major branch ($n+1$) or stem. Moreover, from the spiral arrangement predominating on the $n+2$ and $n+3$ axes, and the parallel arrangement in the sediment of major axes I and II it may be logical to presume that they also were spirally disposed on the stem (or $n+1$). This point of view will be discussed later after a vegetative system of branches has been described (see fig. 37, 39, 40).

2. Fertile organ

The lateral, spirally arranged appendages on the third order branches are mostly fertile organs with numerous sporangia in connection.

The fertile organ varies in height from 1 to 4 cm (fig. 1,2,3,5,6,9,10,16) according to its age and degree of curvature; all show the same general structure. When preserved as compressions they appear almost pressed flat on the sediment. The erect curved line of the first order pinna represents its abaxial boundary which tapers gradually upward to the incurved tip.

Several second order pinnae are usually visible attached at right angles to the first order pinna. They are inwardly directed (fig. 3,5,9,14,16,34,46,47,50) and disposed in a double series of 6 to 16 in number. Though this arrangement in double series is not visible on every fertile organ, it is well seen in figures 21, 34 and 35 and becomes obvious on transfers (fig. 12,13,15,48 and text-fig. 2). Sometimes the second order pinnae appear to be short lateral processes widened at the distal end on which the linear sporangia are directly attached (fig. 3,5, left side, 6,14,23,35,46,47). Often, however, they can be followed to a much longer extent. In this case they are indicated by a strong, elongated, slightly curved ridge or depression emerging from the tufts of sporangia (see fig. 5 on the right, 9,19,34,35). Removal of the sporangia by *dégagement* and transfers of fertile organs have revealed the complex organization. Elongated second order pinnae (s.o.) are borne in two rows on a first order pinna (f.o.) more or less perpendicular to it and in pinnate arrangement (fig. 3,9,12,13,15,16). They decrease in size and complexity in distal progression. The most basal is usually considerably larger and more highly divided than the subsequent second order pinnae (fig. 5,9,15,21,34,48). Each second order pinna supports two to eight small third order pinnae (t.o.) also in a double series (fig. 3,5,9,12,15). These show too a decrease in complexity in relation to their position on the second order pinna. Generally the third order pinnae support the sporangia (except on a very strong basal third order pinna on which fourth order pinnae may occur; fig. 9,34 and text fig. 2).

Figs. 20 and 21 show two stages in the *dégagement* of a portion of one fertile organ. On fig. 20, a thick mass of linear sporangia completely obscures the second order pinnae. On fig. 21, all the sporangia have been removed revealing five second order pinnae of which the basal most is much more vigorous than the others. Fig. 34 and 35, part and counterpart of another fertile organ, after uncovering, show a similar aspect.

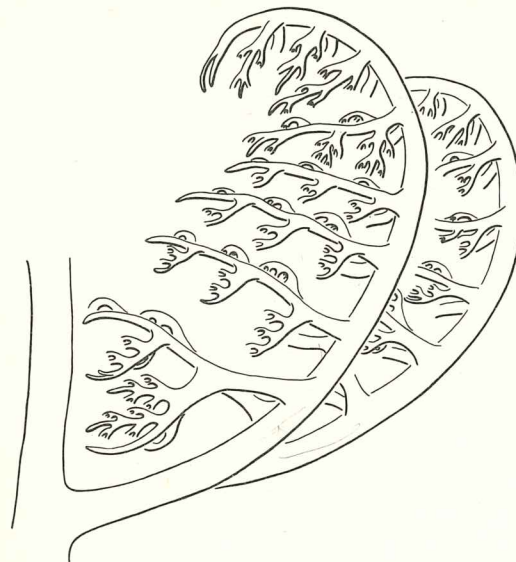
The transfer technique gives additional information. Fig. 14 represents a compression of fertile organs as they are seen on the face of the rock. On the left one can see the erect first order pinna and its mass of linear sporangia which appear to project directly from short processes (s.o.) on the first order pinna. Fig. 15 represents its transfer, thus the reverse side of the fertile organs. One can see in full length, six pinnae of second order on which a few third order pinnae (t.o.) are seen. The decrease in size and complexity of the second order pinnae in apical progression is evident. The sporangia which are so obvious on fig. 14 are scarcely discernible as they are beneath the pinnate branching structure on this surface (fig. 15).

The transfer in fig. 13 shows young second order pinnae which are sharply circinate and appear as croziers disposed in a double series (a similar state of preservation is figured in OBRHEL, 1959—1961, Pl. XI, fig. 3).

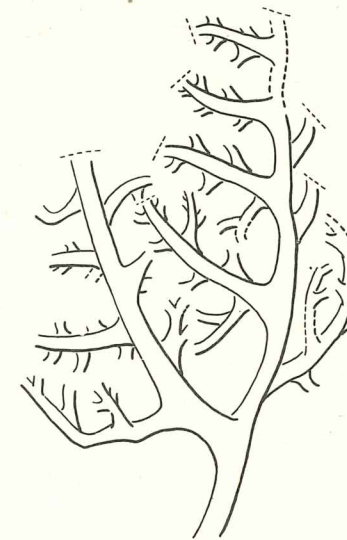
Another transfer (fig. 12) shows a portion of a stout first order pinna (f.o.) seen from its convex side. It supports six curved secondary pinnae (s.o.), disposed in a double series, that taper gradually and support, in double series, the third order pinnae (t.o.). No sporangia are clearly seen for they are held by the plastic of the lower face of the transfer. Third order pinnae vary from two to four in number and may occasionally be further subdivided. Their claw-like terminations are well seen.

3. Pair of first order pinnae

Prior to describing the exact position in which the sporangia are inserted, it is important to stress the fact that each fertile organ bifurcates into two first order pinnae, identical in organization and size. The paired pinnae are erect and parallel to each other in their distal extremities. The pair yields different aspects depending on its orientation when buried in the matrix. Sometimes the second first order pinna is seen in profile extending beside and beneath the first (p.f.o., fig. 1,5,6,35 and text-fig. 2). In other cases both pinnae are preserved and viewed from the concave side or the convex side. In the first position, the erect curved first order pinnae are deeply buried in the matrix and are not seen. However, from each member of the pair, parallel tufts of sporangia project upwards through the sediment. They converge towards the tufts of the other member resulting in an entangled mass between the two pinnae (fig. 10,1,6,46,47). When observed from the convex side, the dorsal surface of each diverging first order pinna is well exposed as are their second and third order pinnae (fig. 15, left side, 12,18,42 lower right side, 43,48, text-fig. 3). On fig. 16, the upper two first order pinnae have been twisted in the course of fossilization. The right pinna is seen partially in dorsal view and shows its dorsal boundary, its second order pinnae oriented upwards and the ends of its tufts of entangled sporangia. The left pinna is seen in ventral view and repeats a similar appearance to that described above for figure 10.



Text-fig. 2. *Milleria (Protopteridium) thomsonii* LANG. Schematic reconstruction of the successive orders of pinnae of a fertile organ on which, intentionally, no sporangia have been drawn. $\times 3$



Text-fig. 3. *Milleria (Protopteridium) thomsonii* LANG (1925, Pl. III, fig. 54-55). Drawn from specimen that LANG considered as a vegetative pinna of *Hostimella pinnata* (= *Milleria thomsonii*). $\times 3$

As demonstrated from the above examples, the common pattern of a fertile organ consists of a pair of erect, curved first order pinnae, to which are attached a complex system of pinnately arranged second, third, sometimes fourth order pinnae.

4. Sporangia and spores

The sporangia are slender, linear shortly pedicellate structures that may vary slightly in size according to their maturity and the vigor of the fertile organ which bears them. They widen from the basal region and then narrow gently to a short, apiculate tip (fig. 8,11). The largest reach 3.5 mm in length and a width of 0.5 mm. They are usually borne in pairs, but can also be found singly, in threes or fours (fig. 7,8). The sporangia are attached to the pinnae of third or fourth order (fig. 3,5,7,9) which are inserted at three to four levels along the length of the preceding order of pinnae (fig. 3,9,12,17, text-fig. 3). Undoubtedly this has a direct relation to the understanding of the true length of the sporangium, which may appear longer or shorter than it really is if the exact point of insertion of the sporangium is misunderstood. The sporangia inserted on the first level, overlap the bases of the sporangia attached to the second level and so on successively. In addition the superposition of the successive imbricated groups of sporangia reached a maximum thickness or concentration at approximately the middle of the length of the second order pinnae (fig. 3,5,9,14,46,47,50), that is to say, midway between the erect first order pinna and the axis. This overlapping of sporangia may also explain the resistance of the compressed mass to being washed away, even from a detached fertile organ (fig. 7,20,34,35,42 upper right side).

When preserved as compressions, the sporangia may show a longitudinally striated outer wall. This appearance corresponds to the elongated pattern of the cells, in which the longitudinal walls seem to be thicker than the transverse walls. This is demonstrated in macerated sporangia (fig. 33). In the same figure, two spores remain attached on the inner side of a tiny fragment of the wall. No line or point of dehiscence has been observed, though after oxidation a few sporangia showed a longitudinal line darker than the others that could have acted as a hinge. This structure recalls a similar one mentioned for sporangia of *Tetraxylopteris* (BONAMO & BANKS, 1967, p. 759, fig. 31).

Spores and spore masses (see fig. 30) were obtained repeatedly by maceration of numerous sporangia of different specimens (no. 5077/420, 5082/321, and 5047/498). Figure 23 shows a portion of a specimen which yielded spores in great abundance. Mature spores are spherical, pseudosaccate (RICHARDSON, 1960, 1965) and trilete (fig. 24, 25, 27—33). They are essentially spherical, with a distinct central body attached to the bladder only at the proximal face (fig. 27). The trilete mark, clearly seen because the rays are accompanied by distinct lips about 2 to 3 μ wide (fig. 24, 27), extends from one-third to one-half the spore radius. The bladder shows pronounced folding (fig. 25, 28, 31, 32) and a densely packed, granular ornament, while the wall of the body is smooth. The intensity of the distal folding as well as the density of the ornament is especially well illustrated in photographs made with the scanning electron microscope in figures 26, 29, 31 and 32. The ornament consists predominantly of short (less than 1 μ long) parallel rods with truncated or rounded tips (fig. 26, 29, 31). The worn truncated appearance of the ornament may be a result of corrosion factors due in part to fossilization, in part to the corrosive action of the SCHULTZE solution.

Milleria spores fall within the parameters of the dispersed spore taxon *Rhabdosporites langii* RICHARDSON (1960) and range in size from 77.5 to 130 μ ; the body from 55 to 87 μ . This corresponds to the lower limits of the size range of *R. langii* (95—190 μ). The smaller size of the spores of *Milleria* approach the upper limits of the size range of *R. parvulus* RICHARDSON (1965). However, in the latter the central body is indistinct and thin-walled and the bladder lacks the distinct folding observed in the two other taxa. We interpret the smaller size of the spores of *Milleria* to be correlated with the fact that they were immature spores obtained from sporangia, while *Rhabdosporites langii* represents mature dispersed spores. Furthermore it is comprehensible that spores which were not mature would have a thinner exoxine on which the ornament was not yet fully developed. Therefore it is unastonishing that comparisons with the sporae dispersae will yield developmental differences (compare with the developmental sequence of similar spores of *Tetraxylopteris* in BONAMO & BANKS, 1967).

5. Sterile organ

The fertile branching system of specimen 5066/497A (fig. 1) bears two kinds of sterile organs. One is a pinnate structure lacking sporangia, the other is a dichotomizing leaf-like appendage.

The best of the two pinnate structures lacking sporangia is represented in fig. 22. It is attached to a lateral third order branch, itself inserted in the middle (left side) of the length of major axis II (fig. 1). In organization it is almost identical to a fertile organ. It consists of a first order pinna (f.o.) broken at its apex, that bears about six pinnae of second order (s.o.) closely inserted in a double series. On the largest of these, five straight tiny pinnae of third order (t.o.) are seen in alternating double series. Though much reduced in size (compare fig. 22 enlarged five times to fig. 3, 5, 9 enlarged three times) the pinna shows the same general pattern as a fertile organ. However none of the pinnae of third order bears sporangia. We call attention to the fertile organ located on the same lateral branch and immediately above the sterile organ in question; it shows normal tufts of sporangia oriented obliquely upwards (fig. 1). The complete lack of sporangia on the sterile organ is perplexing. This structure might be interpreted in different ways: 1) as a fertile organ that has lost all its sporangia; 2) as an aborted fertile pinna; 3) as a vegetative pinna.

A fertile organ which has produced and subsequently lost its sporangia, resembles a small, ramified system of "axes" in which the various orders of branching are generally still recognizable and are normally spaced apart from each other (fig. 21, text-fig. 2). This state of preservation is observed on detached specimens that have been carried away from the parent branch (fig. 18, 43). An ultimate state of such a bare organ is represented in figure 19, in which all but its first and second order pinnae have been stripped away.

In contrast, the sterile organ (fig. 1 st., 22) is found in organic connection and in the midst of connected fertile organs. Its small size cannot suggest that it represents a young, not fully mature fertile organ for even smaller fertile organs occur on major axis I (see young shoot in fig. 6) and they bear abundant sporangia. Therefore we do not believe that the sterile organ, illustrated in figure 22, has lost its sporangia nor do we think it ever bore sporangia. Moreover, a second similar structure is inserted on a lateral third order branch of main axis I just below a normal fertile organ (designated st. on fig. 1, 2, 6). It consists of a very short upcurved first order pinna that bears directed inward and in a double series at least four lateral processes. These could represent partially

developed second order pinnae, on which third order pinnae and sporangia were not produced. In other words, the whole structure could represent a "dwarf" fertile organ, reduced in size and organization while the structure in figure 22 could be interpreted as an intermediate stage of maturation towards a fully developed fertile organ. We are inclined to interpret both structures as aborted fertile organs.

The sterile organ (fig. 22) cannot be interpreted as a leaf because we have found attached to the lowest lateral branch of the Goé specimen (fig. 1, left side) small bifurcate leaf-like structures. The best of these is shown in figure 4, enlarged three times. It is 5 mm long and twice bifurcated. The first dichotomy is wide, the second reduced to an apical notch. It is inserted upright on the upper surface of the base of a fourth order branch and was covered by 19 mm of sediment (fig. 1). Its upright position, maintained despite the compression, suggest that the foliar structure was a rigid probably terete organ, except in its ultimate part which is flattened and more or less limb-like. It is obvious that the leafy appendage here described in no way resembles either the aborted organ of fig. 22 or the pinnate vegetative organs described by Lang in 1925 (reproduced here fig. 18 and text-fig. 3), or KRÄUSEL & WEYLAND in 1933 (our fig. 42) and in 1938 (our fig. 43). In the discussion (p. 104) we develop our arguments for interpreting these specimens as fertile organs having lost their sporangia. On the other hand, the foliar structure in figure 4 strikingly resembles the small dichotomized leaves attached to ultimate axes of vegetative branching systems, frequently found associated with fructified axes of *Milleria*, that will be described below. Thus, we cannot retain the hypothesis of the vegetative nature of the sterile organ in fig. 22.

It is of additional importance that the leaf reproduced in figure 4 is attached on the most basal branch of the fertile branching system (fig. 1); for it brings the proof that the fertile branching system consisted of a fertile upper portion and a vegetative basal region.

6. Assumed vegetative branching system

Very often in close association with fertile *Milleria* are vegetative branching systems, the main axis of which may reach 2 cm in width. They are abundantly branched and support ultimately, crowded, dichotomizing leaves, similar in morphology to those attached to the fructified specimen in figure 1. On the grounds of their common association and the similarity of the leaves, we believe it worth mentioning them in a brief description though the purpose of this paper is the study of the fructified system of *Milleria*.

The vegetative axes, preserved as compressions, support three orders of branches all spirally arranged (fig. 37, 40). One of the longest specimens (fig. 37), measuring 15.1 cm in length and 8 to 10 mm in width, could be interpreted as either a stem or as a large axis ($n+1$). It crosses the whole extent of the slab and shows no decrease in diameter that could indicate a close terminal region. At first glance it seems to support 7 or 8 lateral, $n+2$ branches. However, several circular scars (see fig. 38 sc, 37 small arrow) found correspondingly on the part and counterpart can be interpreted as points of attachment of broken branches. These suggest that the branching was more dense than is apparent on the surface of the specimen. Some evidence of the density of the branching is given by broken bases of $n+2$ branches. One of these is located 5.1 cm up from the base of the $n+1$ axis (at arrow) and is prolonged on the counterpart where it plunges into the sediment. Another five centimeters above, a branch is represented by its base which is still attached on the middle of the $n+1$ axis. Were these axes completely detached only small scars, similar to those discussed above (fig. 38, sc) would remain as evidence of their existence. At this particular level, the close insertion of several $n+2$ branches gives a rather good aspect of the real intensity of the branching.

The longest $n+2$ axis, though incomplete, measures 14 cm long and 3 to 4 mm wide (fig. 37). It supports short branches of third order ($n+3$) spirally disposed and particularly closely spaced, about 9 mm from each other. Their observable length reaches approximately 5 cm and their width 2.5 to 3 mm (fig. 37, 39, 40). $N+3$ axes bear in turn $n+4$ axes; the longest is 7 mm long and 1 to 5 mm wide.

The $n+4$ axes bear the ultimate divisions or leaves. These decurrent, spirally arranged appendages are emitted so closely that they almost entirely cover the axis (fig. 39, 40). They are twice to three times bifurcated; the third bifurcation being sometimes reduced to a notch (fig. 41). It has proved very difficult to obtain the tips of the foliage as it is flexible and twisted through the sediment. The specimens in figures 39, 40 and 41 illustrate the sinuous aspect of the leaves, some of which however show straight ultimate segments parallel to each other. We

do not think they were terete because their sinuous course indicates instead an extreme litheness inconsistent with a terete, leathery structure. On the contrary, their faded impressions (fig. 38,40) contrast with the well-marked dark impressions of the rigid axes. Sometimes a central, fine carbonaceous line bifurcates simultaneously with the division of the appendage (fig. 41), recalling the behavior of a vein. These appendages could be considered as leaves with incipient lamina.

These leaves are similar to those found connected to the fertile system: both are small, dichotomized appendages with flattened and notched tips (compare fig. 4 with fig. 39, 41). The leaves on the vegetative system are flexible and more highly divided but it is not unusual for basal foliage leaves of a fertile system to be somewhat reduced. In the light of the above information: the similar leaves, the spiral mode of branching and the close association, we believe that these branching systems could have been part of the same plant which bore the fertile organs.

7. Anatomy

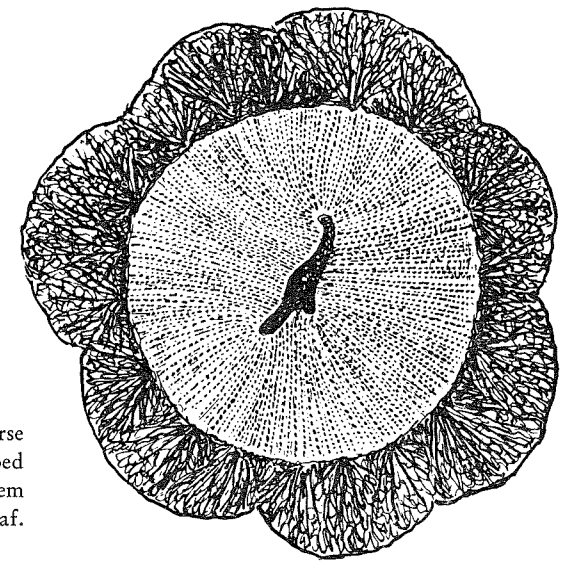
Some vestiges of anatomy still remain on the compressions. Often in the middle of the axis, a longitudinal carbonaceous band runs over its whole length (fig. 37,38,49 left side). The band is about 3.5 to 9 mm wide. We suspect it to represent remains of a stout vascular strand. Under reflected light longitudinal striations appear which could be due to tracheids. Yet attempts to macerate the "tracheids" and to photograph them with the scanning electron microscope yielded no further information. Often on the compressions the cortex displays sinuous, parallelly disposed longitudinal bands observed in tangential and radial view which are sometimes connected to each other to form a loose network of elongated meshes (fig. 38). They probably represent a fibrous or sclerenchymatous hypodermal tissue acting as a mechanical construction of importance in supporting the crowded and heavy branching. This "sparganum"-like tissue is better developed in the larger axes than in the smaller where the cortex appears more uniform.

No petrified axis that could be positively attributed to *Milleria* has been found in the Goé material. Yet we can compare information from the external morphology of our specimens with anatomy known to come from axes connected with fertile Rhenish *Protopteridium thomsonii* described by KRÄUSEL & WEYLAND, 1938 (p. 174, 175) from PIEDBOEUF's specimens, 1887 (personal communication of WEYLAND, see footnote p. 90). The petrified area that the German authors described, came from axes of $n+2$ order judging from the width of 5 to 7.5 mm of the axis studied. In transverse section the structure consisted of a stretched irregular trilobed protostele with the protoxylem located at the arms. It is surrounded by a compact secondary xylem and a strong cortex (figures 52,53 and text fig. 4 reproduced from KRÄUSEL & WEYLAND, 1938). The secondary xylem consists of tracheids and rays. The rows of tracheids corresponding to the lobes of the primary xylem converge toward it. The tracheids are square, truncated at the angles, rectangular or irregular in shape with a diameter up to 120 μ . The sculpture on all walls is scalariform or reticulate with transition between the two types; circular bordered pits are uncertain. The rays are numerous, uniseriate and high. The well developed cortex is ill preserved due to an impregnation of FeS. It shows, however, radial bands of large more or less quadrangular cells.

The triangular shape of the primary xylem is more in agreement with a spiral branching pattern as it is now known in *Milleria* than with alternate, dorsiventral branching as was formerly described. Likewise the unequal development of the three arms is in conformity with the close arrangement of $n+3$ order branches to which vascular traces would be supplied in close succession. Figure 52 and text-figure 4 can be interpreted in the following way: the smallest arm, which is hardly distinguishable, has just given off a bundle; the next emission is being prepared by the arm intermediate in length; while the longest arm is ready to give off a trace. The compact secondary xylem, is responsible for the terete external appearance of the axis. No furrows or crests corresponding to the bays and extremities of the triangular protostele were observed.

The cortical zone of the German *Protopteridium thomsonii* had radially arranged cells (KRÄUSEL & WEYLAND, p. 174, 175) that could correspond to the mechanical tissue found in the cortex of the Goé compressions.

On the grounds of specimens preserved as compressions alone, it is hazardous to assume that all axes of the branching system repeated the same type of anatomy. However, if narrow axes of $n+2$ order, 5 to 7.5 mm in width have retained a stem-like anatomy, it is reasonable to suppose that the $n+1$ order of branching had the same anatomy, because they showed an identical branching pattern. On the other hand, a change of shape must



Text-fig. 4. *Milleria (Protopteridium) thomsonii* LANG. Schematic transverse section of an $n+2$ axis of *Milleria thomsonii*; irregular trilobed primary xylem surrounded by well developed secondary xylem and cortical tissue. (From KRÄUSEL & WEYLAND 1938, Taf. XXIV, Abt. 5). $\times 10$

have occurred in the vascular supply of the fertile organs. These are pinnately constructed and show bilateral symmetry. In their case one may expect to find a vascular bundle with bilateral symmetry; slightly elongate, or crescentic in form, with the concave side facing the bearing axis and emitting traces alternately to the various orders of pinnae.

8. Habit

The facts presently at our disposal are insufficient to allow an accurate reconstruction of a large part of the plant. However, by combining information from several pieces we can propose a picture of a section of the plant that seems more plausible than the reconstructions formerly given by SEWARD (1931), KRÄUSEL & WEYLAND (1933) and OBRHEL (1968A) that have been mentioned in the Previous Records and Interpretations. On the other hand it confirms PIEDBOEUF's interpretation (1887) of the gross habit of the plant (text-fig. 1). Information such as the radial symmetry, the fundamental spiral branching pattern in all axes ($n+2$ up to $n+4$ except the subdivisions of the ultimate organs), the angle of insertion of the branches (see fig. 36,37), the stoutness of the axis and the bifurcate type of the leaf, are features common to the fertile and vegetative specimens that speak in favor of a relationship between them. As already noted, the two first order branches seen in figure 1 and 2 are disposed in parallel. If one compares fertile organs at equivalent levels on both branches, those on major axis I are smaller (younger?) than those on major axis II. This suggests that major axis I and II were borne spirally on a larger branch or stem. That is why, by way of reconstruction in figures 36 and 37, we have disposed the fertile branches ($n+2$ order) as the prolongation of vegetative axes of the same order ($n+2$) to clarify our conception of the branching system as it could have existed in *Milleria*. We do not mean that the fertile branches were necessarily inserted at this particular level, for they could have been borne directly on the $n+1$ axis at a higher level. The vegetative main axis ($n+1$), of which a length of 15 cm only is preserved, was undoubtedly longer. On figure 37, 36 the complementary information preserved on the part and counterpart of both specimens (fertile and vegetative) has been put together in order to restore each in a more complete appearance.

The spreading out of the fertile branch system (fig. 1,2) and the vegetative axes (fig. 37) indicates that the remains have sustained little transport if any and were embedded under quiet conditions. A continuous current of water would have displaced the branches from their original position, pulling them toward the parent axis as occurred on the specimens represented in figures 23 and 49. In the former, seven fructified axes situated at three levels in the sediment are parallelly disposed on a length of 20 cm. This arrangement probably indicates their insertion on the same axis ($n+1$ or a stem). Such a state of preservation, the most commonly encountered, where the fertile organs are closely appressed to their parent axis, can be held responsible for the misunderstanding of the spiral branching.

Another point on which we wish to focus attention is the incorrect usage of the term "*Hostinella*-like" axis to designate the axes that support the pinnate fertile organs. They are neither *Hostinella*-like nor have they primitive anatomy. On the contrary they are highly specialized in function and in organization as they give off lateral complex fructified organs in spiral disposition.

So far, at Goé, no specimen believed to be trunk has been found in organic connection. However often associated with *Milleria thomsonii* remains, LECLERCQ has collected large axes of 30 to 50 cm long and 10 to 20 cm wide that show at least the peculiar feature of the largest vegetative $n+1$ axis, the "sparganum"-like hypodermal structure. The longitudinal bands are from 2 to 5 mm wide and more or less sinuous in course, with irregular lateral anastomoses that form elongated meshes. Yet the available information so far gathered does not support the view that *Milleria thomsonii* had reached a tree habit, but points to the view that it was a bushy, woody plant of rather large size.

9. Summary of the description

The above observations can be summarized as follows:

- 1) The compressions studied consist of fertile and vegetative branching systems found repeatedly in close association.
- 2) The fertile branch is fertile in its upper portion and leafy in its lower region.
- 3) The fertile branching, formerly thought to be alternate and dorsiventral, consists of branches of three orders spirally arranged and radially symmetrical the fourth order of which is the fertile organ.
- 4) The fertile organ formerly believed to be single is dichotomized into two first order pinnae. It yields varied aspects when preserved in different positions; ventral, dorsal and profile.
- 5) The first order pinna is an erect adaxially curved organ that bears second and third order pinnae in alternate pinnate arrangement.
- 6) The most basal second order pinna is stronger than the others and could be misinterpreted as another first order pinna.
- 7) The third (or fourth) pinnae bear the sporangia. The linear sporangia are inwardly oriented and inserted at three to four levels along the pinnae, resulting in overlapping masses. This organization has a direct relation to the understanding of the true length of the sporangia which may appear longer or shorter than they really are.
- 8) Apiculate sporangia 3.5 mm in length, 0.5 mm in width are borne on short pedicels, mostly in pairs. They yielded one kind of spore assignable to *Rhabdosporites langii* RICHARDSON of the sporae dispersae.
- 9) Occasionally, aborted fertile organs may occur in the midst of a normal fertile branch.
- 10) Twice bifurcated leaves with incipient laminae are attached on the lowest branch of the preserved fertile branch system.
- 11) The spiral branching of the Belgian compressions is in accord with the trilobed protostele found in the Rhenish *Protopteridium thomsonii* (see footnote p. 90).
- 12) The associated vegetative system of branches consists of crowded decurrent branches of four orders all spirally arranged and radially symmetrical. The ultimate divisions, the leaves, are two to three times bifurcated, 5 to 7 mm in length, have flat apices with incipient lamina and a trace of a vein. Stem (or $n+1$ axis) up to 2 cm wide, shows a central band (vascular strand?) up to 7 mm wide and a well developed cortex with hypodermal "sparganum"-like structure.
- 13) The plant is suggested to have attained a shrubby or low arborescent habit with a crowded spirally arranged branching system of four orders; the ultimate divisions being either fertile organs or leaves. The compound fertile branching system may have been connected either with the terminal portion of the vegetative $n+1$ axis or directly inserted on the stem ($n+1$ axis).

VI. Discussion

1. Analysis of the species

Milleria (Protopteridium) has been found in Bohemia, Scotland, Germany, Belgium and Russia and has been the object of many discussions and interpretations. We have presented detailed comments on the subject in the Previous Records and Interpretations, but three of the species warrant more extensive comparison because of their great similarity to the Belgian *Milleria*. These are *M. thomsonii* LANG, *M. pinnata* LANG and *Protopteridium hostinense* KREJČI. As a consequence of our work, important differences seem to exist between the Belgian specimens and the above mentioned species. However, as we will point out below, the differences are more apparent than real.

The material of *Milleria* described by LANG in 1925 and 1926 still exists (housed at the British Museum of Natural History, London) and was available to us for reinvestigation. His *M. thomsonii* is reproduced here in figs. 17, 46, 50, 51 and the holotype (DAWSON, 1878; CARRUTHERS, 1873) in fig. 47. Our interpretation of these specimens differs from LANG's (see Previous Records and Interpretations) in three points: the fertile organs are not single, they consist of a pair of pinnae; the construction of the fertile region is not alternate and dorsiventral, it is spiral; and the second order pinnae are not short processes bearing tufts of sporangia, they are elongate, pinnately subdivided pinnae. In short, they are identical to Belgian *Milleria*.

a. Paired organization of the fertile organ: — The specimen shown in figure 50 is especially demonstrative, and for a better understanding, we begin with the description of the second fertile organ on the left. A slight uncovering, of the upper part of its stalk has clearly revealed a bifurcation (fig. 50 and 51). This bifurcation could be predicted before uncovering because some distance below it, the rows of cortical cells diverge from each other, increasing their angle of divergence simultaneously with the increasing width of the stalk. The left branch of the stalk supports the left member of the fertile organ while the right branch passes under the axis and very likely bears the member that is located on the right side of the main axis. Because of the compression of the overlying main axis, the second member of the pair has been displaced and pushed to the right. It is our opinion that in this case there is no doubt of the existence of an erect pair of pinnae.

At first glance it is more difficult to understand the basal fertile organ of this branch. Here one erect first order pinna seen in profile is connected to the axis. But its stalk (4 mm wide) is broken at approximately 1 cm from its point of insertion and shows an abrupt narrowing (to 2.5 mm). Careful examination of the rows of cortical cells shows a diverging orientation as observed on the fertile organ described above announcing a bifurcation of the stalk. The second member of the fertile organ is seen displaced on the right and a narrow band of its stalk overlies the main axis.

The fourth fertile organ is again on the left and seen for its entire height. The width of its mass of sporangia is greater than the width of the sporangial masses of the first and second fertile organ. This can be due to the sporangia of a second first order pinna lying behind the first and whose curved apical extremity is seen (see arrows fig. 50, p.f.o.). We interpret this complex as a pair of juxtaposed first order pinnae seen in profile.

On the evidence hitherto presented, we believe that the successive fertile organs of this specimen are each composed of a pair of pinnae.

On some other Scottish specimens represented in our figures 46 (LANG, 1926) and 47 (CARRUTHERS, 1873) the structure of a pair of first order pinnae seen in face view (fig. 46, p.f.o., fig. 47, m.p.) is recognizable. They present the same aspect as the specimens of Goé seen in figures 10 and 16: two groups of tufts of sporangia facing each other at exactly the same level (see description p. 96).

Milleria thomsonii from Thurso, Scotland (LANG, 1926) represented in our figure 17 (x2), gives further evidence of the paired organization of the fertile organ. The strong basal stalk on the left bifurcates into two short stalks at about 11 mm from its point of insertion (fig. 17, arrow p.f.o.). The best preserved of the two first order pinnae, on the left, is seen in side view; the second is slightly displaced to the right and is almost buried in the sediment. It is seen from the concave side with some sporangia oriented towards those of the other member of the pair to which it belongs.

b. The spiral construction of the fertile region: — Returning to figure 50; the lowest fertile organ on the left is attached laterally above the main axis which passes below the stalk of the fertile organ. The second fertile organ is also on the left side, but is inserted laterally below the main axis that overlies its stalk. The third fertile organ is to the right and inserted laterally above the main axis. Its erect first order pinna is partially cut by the margin of the slab, but the organ can be followed for almost its full length to the recurved tip. The sporangia, directed toward the main axis, cover it almost entirely. The fourth fertile organ is seen on the left side in a position similar to the first and is very likely attached above the main axis though the point of insertion of its stalk is not seen. The arrangement of the subsequent fertile organs cannot be followed. We do not think the upper portion of the specimen represents a terminal region for the main axis obviously runs obliquely to the edge of the slab, and there is no indication of a diminution in size of fertile organs. We conclude that this specimen represents a three dimensional, spirally arranged branching system. The four fertile organs can be interpreted as arranged in a 1/3 phyllotaxy with the first and fourth fertile organs corresponding in position.

The spiral branching pattern can be deduced in like manner on the specimens in figs. 17, 46 and 47. In fig. 17, starting basally, the remains of a stalk is inserted above the main axis on the right. Then on the left a bifurcated stalk (p.f.o.) is given off laterally. The next fertile organ on the right, though poorly preserved, is inserted under the main axis. In figs. 46 and 47 the two lower successive fertile organs are seen in profile while the third organ appears in face view. The whole arrangement is indicative of a three dimensional, spiral branching pattern rather than a bilateral, dorsiventral organization.

Likewise on the Rhenish specimens described by PIEDBOEUF (1887) the spiral arrangement of the branches is easily recognized on the drawings carefully executed by the author in the course of his uncovering (see our text-fig. 1).

c. Pinnate organization of the second order pinnae: — In all the Scottish specimens he studied, Lang considered that the erect first order pinnae bore only short, inwardly directed pinnae of second order supporting pedicellate sporangia on their tips. The Goé compressions too, often give this erroneous impression (see fig. 14). Yet LANG himself recognized that the sporangial position in *Milleria* was not fully elucidated. A slight uncovering on LANG's Thurso specimen (fig. 17) of some second order pinnae of the upper left fertile organ revealed a pinnate organization of the second order pinnae identical to that of the Goé specimens (compare fig. 17 arrows, f.o., s.o., t.o. with figs. 12, 15, 21).

We have particularly dwelt on the detailed description of the organization of LANG's material of *Milleria thomsonii* because it is of fundamental importance to understand the full identity of fertile regions of the Scottish and Belgian specimens. It is for this same reason, to stress the similarity of morphological organization, that we have referred to figures of Scottish as well as Bohemian and German specimens throughout the description of the Belgian material.

Milleria pinnata, LANG (LANG, 1925, KRÄUSEL & WEYLAND, 1933, 1938) differed significantly from *M. thomsonii* in the supposed possession of bifurcated, thrice pinnate vegetative leaves. Among the remains called *Hostimella pinnata*, LANG (1925, p. 268) described three pinnate structures on which no sporangia were found at their flattened and widened "claw-like terminations". One of this specimens is reproduced in our figure 18 (and textfig. 3). Though he recognized that the widening and flattening of these extremities "hardly amounts to the differentiation of a lamina", he considered them to be vegetative pinnae. Note that all the Scottish specimens are fragmentary, disconnected organs. The "vegetative leaf" in figure 18 is viewed from its dorsal surface. Uncovering of that specimen has revealed, on some of its third and fourth pinnae, traces of tiny appendages that could only be pedicels that had borne sporangia. We believe that the so called vegetative pinna was a fertile pinna which has lost its sporangia. Transfers of fertile organs of Goé, seen dorsally, show a similar configuration (fig. 12, 15) but in addition, on their ventral face, have sporangia in connection (fig. 14). When all the numerous sporangia were still attached, the three pinnate structure of the fertile organ could not be noticed. Lang who did not see the specimen in that state of preservation thought it to be vegetative and different from fertile pinnae of *M. thomsonii*.

The material described by KRÄUSEL & WEYLAND in 1933 and 1938 can be interpreted similarly. The Rhenish ex. *Protopteridium pinnatum* (KRÄUSEL & WEYLAND, 1938) in our figure 43 represents a nice example of a dorsal view of a fertile organ devoid of its sporangia (compare with fig. 21). It is a detached specimen found in an allocthonous outcrop yet the robust fertile organ shows clearly its fundamental construction: the pair of erect first order pinnae (f.o.), the second and third order pinnae (s.o., t.o.) alternately disposed and a particularly

vigorous basal second order pinna which represents their catadromic pinnule. This is equivalent to the strong basal pinnae of second order shown in Goé specimens in figs. 3, 5, 9 (b.t.o.), 21, 34 in a Scottish specimen in fig. 18 and a Bohemian specimen in fig. 42 (second fertile organ, on the left).

The organization of the fertile and sterile pinnae of Bohemian ex. *Protopteridium hostinense* (KRÄUSEL & WEYLAND, 1933) was identical to that of *P. pinnatum*, except that both pinnae were inserted on the same frond. This character, which in KRÄUSEL & WEYLAND's opinion justified the retention of a separate species, has become groundless since we have demonstrated above that the so-called sterile pinnae (= "leaf") are naked fertile pinnae. Fig. 42 shows an axis with fertile organs that have lost all their sporangia except a tuft on the uppermost organ to the right. In this condition, the naked fertile organs have acquired a false appearance of pinnate leaves. A similar interpretation is given by OBRHEL (1966, 1968A) who considers the sterile pinnules of *P. hostinense* described by KRÄUSEL & WEYLAND (1933) to be fertile pinnules seen from their dorsal surface. Up to date then, no vegetative leaves have been described for *Milleria*, except for the bifurcated leaf inserted on the basal lateral branch of the Goé specimen reproduced in fig. 1.

Like the Scottish specimens described above a careful examination of fig. 42 permits the observation of the exact insertion of the fertile organs. The lowest naked organ on the right shows the two members of a pair seen in dorsal view. It is attached laterally above the axis. Further up, the naked fertile organ on the left is inserted laterally and seen in profile. The next fertile organ on the right is obviously attached beneath the axis (see KRÄUSEL & WEYLAND 1933, fig. 9) that passed partly over the tufts of remaining sporangia. The base of the stalk of the second member of the pair appears for a short distance as a narrow line (1933, fig. 8) passing along the main axis that hides it.

We have demonstrated that the spiral arrangement of the fertile region, the organization by pairs of the first order pinnae and the pinnate construction of the second and third orders of pinnae can be considered characters of generic standing as they occur in the reviewed specimens of Scotland, Bohemia, Germany and Belgium. Consequently, the three species *Protopteridium thomsonii*, *P. hostinense* and *P. pinnatum* were based merely on different states of preservation of the same complex fertile branch system embedded in different ways under different conditions in different countries. BONAMO & BANKS (1967) also questioned the validity of the three species and felt that they could represent different states of preservation of one single species.

Thus on the basis of the construction of the fructification, the three species are not distinguishable and can be placed in the one species *Milleria thomsonii*, despite the fact that sterile portions sometimes show irregularity in their phyllotaxy. While Goé specimens show regularity in the fundamentally spiral arrangement on the stem, vegetative and fertile portions, such is not the case in the Scottish specimen described by LANG in 1926 (our fig. 50). This author noted that the fifth lateral branch just below the fertile region was out of sequence with the alternate arrangement below. The consequence of this irregularity is to place the fifth branch in conformity with the spiral construction which we have demonstrated for the fructification. A change of phyllotaxy at different levels of a plant is not unusual, but it generally occurs between different orders of branching not often in the prolongation of the same axis. Because of the above observations we suggest the name *M. cf. thomsonii* for this specimen.

2. Diagnoses

Genus *Milleria* LANG 1926 — Emended diagnosis.

Plant consisting of fertile and vegetative branch systems.

Fertile branch system vegetative proximally, fertile distally. Fertile region consisting of radially arranged axes bearing erect, adaxially curved dichotomized fertile organs divided into first order pinnae. Each first order pinna thrice pinnate in opposite, subopposite or alternate double series, the ultimate divisions bearing the sporangia. Basal second order pinna often strongly developed. Sporangia pedicellate, numerous, oblong-oval or linear in shape, with acute apices; inwardly attached at different successive levels on the pinnae of third or fourth order. Spores spherical, trilete, pseudosaccate. Central body distinct; bladder much folded distally, attached to the body at the proximal face. Rays of trilete mark accompanied by lips to 3 μ wide with a length from one-third to one-half the spore radius, never exceeding the diameter of the body. Size ratio of body to bladder varying with spore

maturity. Ornament of exoexine densely packed with truncated or rounded rods under 1μ long. Assignable to *Rhabdosporites* of the *Sporae dispersae*. Apparently homosporous.

Stem ($n+1$ axis) up to 2.5 cm in diameter or more, sympodially branched, bearing spirally arranged branch systems of three to four orders, the ultimate divisions (leaves) dichotomous. Sterile lateral branch systems monopodial, bearing either spiral or alternate lateral axes. Lobed primary xylem strand in all axes except ultimate divisions (leaves or fertile organs); protoxylem mesarch. Secondary xylem pycnoxylic with high narrow rays, scalariform and bordered pitted tracheids sculptured on all walls.

Milleria thomsonii (DAWSON) LANG — Emended diagnosis

Fertile branch system consisting of major axis $n+2$ up to 4 mm wide bearing, at about every 11 mm, spirally disposed $n+3$ axes. Fertile organs distal, inserted spirally at a distance of 9 mm on the $n+3$ axes, once dichotomized resulting in two thrice pinnate first order pinnae, the ultimate divisions bearing the sporangia. Young fertile organ tightly circinate 1 cm in height; mature organ slightly curved 4 cm in height. Sporangia linear, average 3.5 mm long and 0.5 mm wide. Spores 77.5 to 130μ in diameter, characters as in generic diagnosis. Lowest lateral branches ($n+3$) bearing tiny leaves 5 mm long, twice bifurcated, rigid, and limb-like in their upper parts. Primary xylem strand of $n+2$ axes irregularly trilobed, protoxylem mesarch located at the end of the arms. Pycnoxylic secondary xylem consisting of small tracheids, square, rectangular or irregular in shape, to 120μ in diameter. Dominant ornamentation scalariform and reticulate, circular bordered pits uncertain. Rays numerous, uniseriate and high. Cortex well developed with radial rows of large cells.

Assumed vegetative stem or $n+1$ axis as described in generic diagnosis. Sterile branch systems ($n+2$) monopodial bearing crowded, decurrent, spirally arranged, lateral axes of two orders. $N+2$ axis 3 to 4 mm wide; $n+3$ axes, 2.5 to 3 mm in width; $n+4$ axes, 1 to 1.5 mm wide. Leaves supple, thrice bifurcate about 5 to 7 mm long. Apices flattened with median, bifurcate vein-like trace. $N+1$ and $n+2$ axes with a central band (vascular strand?) up to 7 mm wide and a well developed "sparganum"-like cortex.

Holotype: No. V9425 British Museum of Natural History, London, England and counterpart No. 3268 McGill University, Montreal, Canada

Paratypes: B.M.N.H. V54160, V 54159

Locality: Stromness Beds, Skail, Orkney, Scotland (Middle Old Red Sandstone)

Age: Middle Devonian

Milleria cf. thomsonii (DAWSON) LANG

Fertile region like the specific diagnosis of *Milleria thomsonii* supported by a long axis more than 31 cm in length bearing lateral branches, the nature of which (sterile or fertile) is unknown. The four lowest of these alternately disposed while the fifth is in spiral sequence with the fertile organs above.

Specimen: V1419 British Museum of Natural History

Locality: Stonegun Quarry, near Thurso, Caithness Scotland

Age: Middle Devonian

Some additional specimens of diagnostic value are indicated below. Although these specimens were not studied until after the original species description (thus are neither holotype nor paratype) they are essential to a comprehension of the species as it is presently circumscribed.

Milleria thomsonii. "Diagnostic type".

Specimen: 5066/497A and B, and 5077/420B, Laboratoire de Paléontologie Végétale, Université de Liège, Liège, Belgium

Locality: Goé Belgium

Age: Givetian

3. Comparison with other genera

Many features of the fructification of *Milleria* correspond closely to *Tetraxylopteris schmidtii* Beck 1957 from the Upper Devonian of the United States. The two genera have the same general construction of the sporangial complex, the same type of spore, gross anatomical features and habit. They are alike in having a three-dimensional, compound fertile branching system, fertile distally and vegetative proximally, which, together with a similar vegetative system, produced an abundantly branched, bushy habit. Fertile organs in both bifurcate into erect, three-pinnate adaxially curved structures of equivalent size that bear numerous inwardly directed pedicellate sporangia.

The sporangial complexes of *Tetraxylopteris* sometimes are preserved in such a position that they reproduce patterns similar to those of fertile organs of *Milleria*. Compare BONAMO & BANKS', 1967, figures 5,6,11,12 with our figures 3,50,10,42,12,18,43,44,45. Likewise both genera have bifurcated leaf-like ultimate divisions and lobed protosteles surrounded by pycnoxylic secondary xylem. It is well demonstrated in *Tetraxylopteris* that the shape of the primary xylem strand was repeated in several succeeding orders of branches. We have suggested (p. 100) that in all probability a trilobed organization prevailed in successive orders of branches in *Milleria*.

Nevertheless there are distinct differences between the two genera. The fertile organ of *Tetraxylopteris* is twice dichotomized resulting in four first order pinnae (fig. 44,45) instead of two in *Milleria* (fig. 5,15,16,42,43,50). Lateral branching in *Tetraxylopteris* is spiral on the stem and becomes opposite and decussate in all the distal vegetative and fertile branches; in *Milleria* all orders of branches are spiral, in *M. cf. thomsonii* they are alternate, then spiral. Each node of fertile *Tetraxylopteris* bears two fertile organs (8 first order pinnae/node; fig. 45) while fertile nodes of *Milleria* bear only one fertile organ (2 first order pinnae/node). The shape of the stele is cruciform in *Tetraxylopteris*, trilobed in *Milleria*.

Another point of disagreement was the heterospory of *Milleria* formerly suggested by LECLERCQ (1940) on the grounds of very small (5 to 7μ) spore-like bodies found in a specimen from Mousset, another outcrop of the Middle Devonian of Belgium. New macerations of fertile organs from Mousset have been unsuccessful while the Goé specimens have repeatedly given LANG's spore type B (1925): *Rhabdosporites langii* RICHARDSON. It appears, in the present state of our knowledge, that no evidence exists to support heterospory in *Milleria thomsonii*. Thus the analogy of *Tetraxylopteris* and *Milleria* is now strengthened by their apparent homospority and production of identical spores, *Rhabdosporites langii*.

As information about *Milleria* increases, the differences between it and *Tetraxylopteris* dwindle. It is of interest to consider whether or not sufficient basis for generic distinction still exists.

In 1967 BONAMO & BANKS were impressed by the similarity that appeared to exist between *Tetraxylopteris* and *Milleria* (*Protopteridium*) and questioned the advisability of keeping the two genera apart. They maintained the generic distinction on the basis of the single unforked sporangial complexes, the lack of ultimate lateral (leaf-like) appendages and the poor knowledge of the anatomy in *Milleria*.

Thus *Milleria* and *Tetraxylopteris* have remained separate taxa because *Milleria* was based on fragmentary specimens mostly limited to fructified portions whose morphology was not accurately understood. Neither the type of leaf nor its arrangement on the axes were known. The described anatomy was believed to belong to associated axes, while now it has been ascertained that it came from connected branches.

Today generic distinction rests merely on spiral versus decussate phyllotaxy, 3 or 4 lobed primary xylem and once versus twice bifurcated fertile organs. Decussate phyllotaxy of branching and leaves is commonly recognized as a phylogenetically advanced character which, of course, is reflected in the anatomy: 4 lobed xylem in the case of *Tetraxylopteris* where it is associated with a more specialized fructification. Taken together these characteristics may well indicate a later stage of evolution reached by one species of a single genus during the time available between the appearance of *Milleria* in Middle Old Red Sandstone strata and that of *Tetraxylopteris* in the Upper Devonian.

However because of the poor knowledge of the anatomy in *Milleria* as compared with its extremely well documented counterpart in *Tetraxylopteris* it seems wise at present to retain two distinct genera.

Milleria also shares characteristics with *Aneurophyton*. The type species, *A. germanicum* was described by KRÄUSEL & WEYLAND in several works (1923, 1926, 1929). The plant consisted of sterile and fertile branch systems

of several orders similar in construction (1929). The ultimate divisions of the sterile fronds were linear, decurrent, one to three times bifurcated, rigid leaf-like organs, vascularized (in our opinion), though no vein was observable on the compressions. The ultimate divisions of the fertile fronds were small clusters of sporangia 5 to 6 mm in length bearing one or two rows of shortly pedicellate sporangia 1.5 to 2 mm long. KRÄUSEL & WEYLAND (1929) suggested that sporangia were of different sizes and described spores with hook-shaped appendages. However, POTONÉ (1967) upon reexamination of the spore preparations of KRÄUSEL & WEYLAND, found them to have no such forked appendages; rather the spore characteristics were barely discernible and the ornament consisted of tiny, closely spaced coni and pilae. This is more in agreement with the description of *Aneurospora goensis* STREEL (1964) found "in situ" in *Aneurophyton germanicum* from the Givetian of Belgium.

The internal structure consists of a triangular protostele surrounded, in large axes, by a pycnoxylic secondary xylem with reticulate to bordered pitted sculpture on all walls of the tracheids, and high narrow rays. KRÄUSEL & WEYLAND, on their text-fig. 9 (p. 127, 1926) represented the leaf-like organs and the clusters of sporangia as alternately disposed. Similarly STOCKMANS (1948, p. 45) described the branch system and the sporangiophores (sic) of another species *A. olnense*, as inserted in an alternate disposition.

Other species of *Aneurophyton* have been erected but none is as completely known as *A. germanicum*. *A. furcatum* (STOCKMANS, 1948) and ? *A. bohemicum* (KRÄUSEL & WEYLAND, 1933) are based on single fragments of vegetative axes whose identity is most questionable. *A. hallii* (DAWSON) ARNOLD (1940) is based on anatomical criteria alone. They confirm the internal structure described by KRÄUSEL & WEYLAND for *A. germanicum*. *A. olnense* (STOCKMANS, 1948) is an Upper Devonian species, based on compressions of fertile fronds. It consists of axes, 2 mm in width, showing a faint, median longitudinal band. The author described the lateral branches as alternately disposed and reaching a length of at least 7 cm. These axes bore sporangiophores (sic) a few millimeters in length, several times divided and alternately inserted less than one centimeter from each other. (This disposition appears in contradiction with the triangular protostele found in narrow axes by LECLERCQ, 1940.) The sporangiophore, generally dichotomized 1 mm from the insertion into two symmetrically disposed segments. The sporangia were sessile or sub-sessile, oval, narrow apiculate and 2 mm in length. Their mode of insertion is unknown due to their intricate superposition. Clusters which have lost their sporangia give some information of their mode of branching. It is described as a dichotomized system of segments not always symmetrically nor similarly subdivided. KRÄUSEL & WEYLAND (1926, 1929) mentioned for *A. germanicum* segmented leaf-like organs inserted, here and there on the fertile frond, in the position of a cluster of sporangia. STOCKMANS made similar observations in *A. olnense*. We assume those "leaf-like" organs to be fertile clusters from which the sporangia have fallen revealing the construction of the cluster which appears merely as successive bifurcated segments. However a complete understanding of the complexity and morphology of the branch system and the fertile organs of *Aneurophyton* awaits a detailed investigation with careful application of the proper techniques.

In the present state of our knowledge, striking differences exist between the fructifications of the two genera. In *Milleria* the fertile organ consists of a pair of erect (3 to 4 cm) three pinnate inwardly curved first order pinnae that support a compact mass of linear sporangia attached at different levels. In *Aneurophyton* the sporangial cluster appears to consist of two small bifurcate systems of segments (5 to 6 mm) that seem to bear one to two rows of tiny pedicellate sporangia directly inserted on their inner side. Hitherto, no complex pinnate organization of the fertile organ has been demonstrated to exist in *Aneurophyton*. Another point of dissimilarity is that branching in *Aneurophyton* is described as alternate. But this arrangement is not in agreement with the triangular construction of the vascular system which rather implies a spiral organization (LECLERCQ, 1940). It is questionable whether the alternate, planated construction of branches was natural or rather an effect due to a secondary twisting of the branches which were actually spirally inserted. *Aneurophyton* is thought to be truly arborescent (= *Eospermatopteris*, GOLDRING, 1924; KRÄUSEL & WEYLAND, 1935; ARNOLD, 1947; BECK, 1964) while so far *Milleria* is assumed to be a strong, tufted, shrubby or low arborescent plant (OBRHEL 1959—61). As a result of the above considerations, we believe *Aneurophyton* and *Milleria* can be retained as separate genera.

Milleria can also be compared with *Protopitys scotica* (WALTON, 1957). It is a Mississippian plant whose fructification and internal structure are known. The fertile organs, borne in a distichous manner, consisted of a pair of first order pinnae (= sporophyll of Walton) erect, adaxially curved, showing a tendency toward pinnate subdivisions (may be our second and third order pinnae). Pedicellate sporangia were inserted on the inner side but their mode of insertion is unknown. The sporangia (3 mm in length) were elongate, fusiform and thick-walled

(two to three cells in thickness). Dehiscence was longitudinal. Spores of different sizes were found in the sporangia; the smallest of 82 μ , the largest of 163 μ in diameter. The wide range of size between these limits led Walton to consider it as a possible incipient heterospory. The anatomy of the fertile organ consisted of a crescent shaped bundle which dichotomized in the proximal portion of the first order pinnae and then gave off traces more or less circular in shape, towards the second order divisions. We have assumed a similar vascular system in the fertile organ of *Milleria* (p. 101).

The resemblance of the sporangial complexes of *Protopitys* with the fertile organ of *Milleria* is striking. Yet the anatomy of the main axis was so peculiar that it sharply differentiates the two genera. In *Milleria* the vascular system consisted of a trilobed protostele surrounded by a well developed secondary xylem. In *Protopitys* a large pith existed, tangentially elongated, elliptical in shape with, at the two extremities, the primary xylem reduced to a pair of strands from which leaf traces originated though no foliage has been discovered. The whole structure was surrounded by a thick secondary xylem. The tracheids of the primary xylem were predominantly scalariform while those of the secondary xylem had elongated pitting intermediate in shape between scalariform and bordered pits. Thus the construction of the plant was fundamentally distichous and its vascular system was highly evolved.

WALTON on the basis of the fructification, to which he accorded priority placed *Protopitys* among the pteridophytes. BECK on the other hand (1960, p. 364) included it in the Progymnospermopsida, though no leaves are known for the genus, because he considered that the combination of pteridophytic fructification and well developed secondary xylem with bordered pits on the tracheids indicated a sufficient relationship between plants to group them within the same new class.

4. Systematic position

Fertile *Milleria* has been interpreted in many different ways (see Previous Records and Interpretations) and various authors have suggested diverse affinities: lycopods (DAWSON, 1871; CARRUTHERS, 1873), fern (KREJČI, 1880, 1881; DAWSON, 1882; POTONÉ & BERNARD, 1904), alga (STUR, 1881; PIEDBOEUF, 1887), psilophyte (KIDSTON, 1903), Pteridosperm then fern (KRÄUSEL & WEYLAND, 1933, 1938), Pteridophyte (LECLERCQ, 1940), it was considered as a member of the order Protoperidiales (HØEG, 1942; BECK, 1960). That order was erected by HØEG (1942) to include the genera *Svalbardia*, *Protopteridium*, *Aneurophyton*, *Eospermatopteris* and *Rhacophyton*. On the basis of new studies these genera have been subsequently assigned to other orders and consequently Protoperidiales becomes groundless (see for full details BECK, 1960; LECLERCQ, 1962). Finally *Milleria* was regarded as a member of the Progymnospermopsida and included in the Aneurophytales (BONAMO & BANKS, 1967).

Recently, *Rhacophyton* has been included within the Aneurophytales (BECK, 1970; BIERHORST, 1971) as a result of ANDREWS & PHILLIPS' work on *R. ceratangium* from the Upper Devonian of West Virginia (1968). We do not consider *Rhacophyton* as closely related to the Progymnosperms but as a fern allied to the Coenopteridales. In their paper on *Rhacophyton* ANDREWS & PHILLIPS wrote p. 61: "In summary *Rhacophyton* exhibits the following characters of some progymnosperms: three-dimensional branch systems terminating in dichotomized ultimate appendages, mesarch protostele, repetition of the same primary strand along with secondary xylem in one or two orders of branching, and terminally born fusiform sporangia on a highly divided branch system. The differences between *Rhacophyton* and genera of the Aneurophytales are largely limited to the clepsydroid primary strand with peripheral loops; these are characters that occur in the Coenopteridales and Cladoxylales."

In 1951, LECLERCQ described in detail the anatomy of *Rhacophyton zygopteroides* (Upper Devonian of Belgium) from connected portions of stem, sterile and fertile fronds, and their primary and secondary order of branches up to the pinnules. Her study demonstrated the following characters for *R. zygopteroides*:

The form of the stem stele is approximately stellate according to the mode of emission of the leaf traces. It consists of a peripheral zone of metaxylem around a central zone of delicate tissue (pith or mixed pith) which was generally destroyed in her material. No peripheral loop occurs. The symmetry is radial: the spiral emission of the vascular strands to the rachides conforming with the spiral insertion of the vegetative fronds on the stem impressions.

The vascular bundle of the vegetative and fertile fronds is clepsydroid in cross section containing a peripheral loop at either end. It is bilateral in symmetry. In the fertile rachis well developed radially aligned tracheids sur-

round the clepsydroid bundle. The clepsydroid xylem strand is repeated in the secondary order of branching of the fertile frond. The pinna-trace is given off according to an etapteroid mode of emission. The pinnules are laminate and deeply dissected with dichotomized ultimate recurved tips. They receive at the base a crescentic bundle with the concavity oriented toward the rachis. The tracheids are scalariform. The highly dichotomously divided cluster of sporangia hangs abaxially, in a catadromic position, from the coalescent basal part of each pinna pair. The exannulate sporangia are fusiform, have a beak and are pedicellate. They are usually born by pairs. Six of the seven points above realize a combination of characters found into two groups, the Clepsydridae and Etapteridae. They relate the genus *Rhacophyton* to the Zygopteridaceae, a fern family included within the Coenopteridales.

ANDREWS & PHILLIPS' *Rhacophyton ceratangium* consists mostly of impressions of fertile fronds, a few vegetative fronds and stems. All the petrified specimens they illustrate are bilaterally symmetrical and have peripheral loops. The authors interpret their specimens of figs. 45, 47, 48, 51 as stems in spite of the spiral arrangement of the fronds on their stem impressions (their fig. 1,2,3,6). They write, p. 59 "All of our petrified specimens of *R. ceratangium* are bilaterally symmetrical: several of these are stems by our own interpretation and homologous with the axis described for *R. zygopteroides* as a stem. It does not seem to be possible to resolve this apparent difference without having better preserved material of the Belgian plant." In our opinion petrified stems are missing in their material. We interpret all the "stem" anatomy of *R. ceratangium* as representing transverse sections of the vascular strand of robust fertile fronds. In the present state of our knowledge no secondary xylem occurs in the stem.

The abundant "secondary xylem" developed on the fertile rachides of *Rhacophyton ceratangium* is considered by ANDREWS & PHILLIPS as strikingly different from that of *R. zygopteroides*. The validity of the interpretation of an extensive production of true secondary xylem may be questioned. In *R. zygopteroides* lax radially aligned tracheids are slightly developed at the base of the vegetative frond, distally decrease then vanish completely. They accompany the clepsydroid leaf trace only for a certain distance. In the rachis of the fertile frond radial rows of tracheids are much more developed and compact. They abut on the reduced primary xylem but disappear higher up concomitantly with the decrease in diameter of the rachis and the decrease in vigor of the pairs of fertile pinnae (LECLERCQ 1951, p. 29, fig. 49—50). It is here suggested that the radially aligned tracheids could represent an oriented metaxylem, a kind of xylary mechanical tissue developed in relation to the weight of the heavy pairs of fertile pinnae. Radial disposition of tracheids is not in itself a valid criterion to establish the existence of cambial activity. Although ANDREWS & PHILLIPS briefly mention the presence of narrow rays in their *R. ceratangium* (p. 59) they do not document their presence in the description, illustrations or the diagnosis.

It is true that *Rhacophyton* shares some characters with primitive progymnosperms. The Progymnospermopsida was established (BECK, 1960) to contain plants which were anatomically gymnospermous and morphologically pteridophytic. These plants showed a combination of characteristics which prevented their inclusion in preexisting taxa. *Rhacophyton* shows no such combination of characters, on the contrary its clepsydroid anatomy and the complex morphology of its fertile frond indicate a close affinity with the Zygopteridaceae. It is noteworthy that *Rhacophyton* is placed in the Zygopteridaceae of the Coenopteridopsida by ANDREWS with BOUREAU (1970), and by BECK (1957).

Our descriptions and comparisons of *Milleria* (= *Protopteridium*) confirm the inclusion of the genus in the order Aneurophytales. Erected by KRÄUSEL & WEYLAND in 1941 (p. 365) the order was emended by BECK (1957) when he debated the systematic position of *Tetraxylopteris*, then slightly emended again by BONAMO & BANKS (1967) on the basis of new information of the fertile system. The Aneurophytales are defined as follows (BECK, 1957; BONAMO & BANKS, 1967): Plants with major axes which bear complex, three-dimensional branch systems usually terminating in dichotomized ultimate appendages. The primary xylem is a lobed protostelic strand, the form of which is repeated in all orders of branching except the ultimate divisions; protoxylem areas, several, mesarch. Plants thought to be homosporous, sporangia terminal on sparsely to highly divided branching systems. Actually the order Aneurophytales contains the following genera: *Aneurophyton*/*Eospermatopteris*, *Tetraxylopteris*, *Milleria* (= former *Protopteridium*) and possibly *Sphenoxylon* (MATTEN & BANKS, 1968) a form genus based on petrifications now thought to be mature axes of *Tetraxylopteris*.

Milleria has become a fairly well known member of the Aneurophytales. The compressions of its very distinct fructification, and its typical spores (*Rhabdosporites langii* RICHARDSON) are among the more abundant remains found in the Middle and Upper Devonian. Its geographic extension covers a large area in Europe; i.e. Bohemia,

Scotland, Germany, Belgium, Russia. It may be represented in New York State of U.S.A. where a closely related plant *Tetraxylopteris schmidtii* could represent one of its more evolved species in the Upper Devonian.

VII. Summary

1. According to the International Rules of Botanical Nomenclature, the genus name *Milleria* LANG is adopted instead of *Protopteridium* KREJČI which is a *nomen nudum*.
2. On the basis of new compressions from the Middle Devonian of Belgium, a detailed study of the fertile branching system of *Milleria* is given. The whole system is spirally arranged and bears once dichotomized fertile organs that are thrice-pinnate. The sporangia are inserted at three to four levels. Bifurcated leaves are found in connection. These are considered to be generic characters.
3. *Protopteridium hostinense* and *P. pinnata* are proved to be different states of preservation of the same complex fertile branch system and are placed in synonymy with *Milleria thomsonii* that becomes the type species.
4. The pinnate leaf-like organ formerly interpreted as a leaf is a fertile organ or part of it from which the sporangia have been detached.
5. Associated sterile systems of branches of four orders are assumed to represent the vegetative part of *Milleria thomsonii*. They are all spirally arranged and bear ultimately two to three times bifurcated leaves.
6. The plant is suggested to have attained a shrubby or a low arborescent habit.
7. Emended diagnoses of the genus *Milleria* and its species are given.
8. *Milleria* is placed in the Aneurophytales with *Aneurophyton* (*Eospermatopteris*), *Tetraxylopteris* and *Sphenoxylon*.
9. The genus *Rhacophyton* is not considered as closely related with the progymnosperms but as representing a member of the Coenopteridales.

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IX. Plate Legends

Specimens have two numbers, the first is the catalogue number, the second is the field number.

Plate 31

- Fig. 1 General view after dégagement. Two major axes, M.A. I and M.A. II, bear fertile organs, two sterile organs (st.) and two leafy appendages (1.a.). [5066/497A] × 1.
- Fig. 2 Counterpart of fig. 1 after dégagement. [5067/497B] × 1.
- Fig. 3 Most complete fertile organ of fig. 2 showing apex of first order pinna (f.o.), bases of second order pinnae (s.o.) and a few third order pinnae (t.o.). [5067/497B] × 3.
- Fig. 4 Attached leaf-like appendage of M.A. I, fig. 1, with limb-like apices. [5066/497A] × 3.
- Fig. 5 Two fertile organs enlarged from fig. 1. One (upper left) shows a pair of first order pinnae (p.f.o.), second order pinnae (s.o.) and third pinnae (t.o.). The other fertile organ shows only one of its first order pinnae (f.o.) and some of its second and third order pinnae. [5066/497A] × 3.

Plate 32

- Fig. 6 Enlargement of part of M.A. I, fig. 1 shows on the left, a young branch composed of a cluster of 8 circinate fertile organs; in the center, ventral view of a pair of first order pinnae (p.f.o.); lower right a small pair of first order pinnae (p.f.o.) and a sterile organ (st.). [5066/497A] × 3.

Plate 33

- Fig. 7 Detached fertile organ with well preserved sporangia. [5068/132A] × 3.
- Fig. 8 Detail of fig. 7 showing attachment and dimensions of sporangia. [5068/132A] × 6.
- Fig. 9 Fertile organ of fig. 2. Second order pinnae (s.o.) appear as ridges among the sporangia. Three third order pinnae are clearly visible (t.o.), the most basal of which (b.t.o.) is particularly strong and bears fourth order pinnae (fth. o.) which support the sporangia. [5067/497B] × 3.
- Fig. 10 Fertile organ seen from the concave side (counterpart of fig. 6, center). Parallel tufts of sporangia arranged in opposite groups indicate the presence of a pair of first order pinnae. [5067/497B] × 3.
- Fig. 11 Transfer of sporangial mass showing shape and acute, often curved apex of sporangia. [5082/321C] × 10. →
- Fig. 12 Transfer of a portion of a fertile organ seen from the dorsal side. The first order pinna (f.o.) bears six second order pinnae (s.o.) in a double series. Note the third order pinnae (t.o.) also borne in a double series and the claw-like terminations. [5077/420B] × 6.
- Fig. 13 Transfer of a fertile organ. A double series of sharply circinate second order pinnae (s.o.) are attached to and recurved under the first order pinna (f.o.). [5078/536] × 5.
- Fig. 14 Fertile organs prior to transfer. On the left only one second order pinna (s.o.) is seen. Sporangia seem to be attached directly to the first order pinna by slender stalks. On the right is an entangled mass of sporangia. [5077/420B] × 5.
- Fig. 15 Same fertile organs as fig. 14 after transfer. On the right, six second order pinnae are seen in full length; to the left the dorsal side of a pair of first order pinnae (p.f.o.) with their attached second (s.o.) and third (t.o.) order pinnae has become apparent. [5077/420B] × 5.

Plate 34

- Fig. 16 Fertile branch showing the spiral insertion of three lateral branches: the lowermost (l.b.), broken apically, is beneath the main branch; the next is lateral and to the left; the most distal is attached on the upper surface of the main branch (N+3) which continues into the sediment. Fertile organs consist of a pair of first order pinnae. [5070/148A] × 2.
- Fig. 17 *Milleria thomsonii*, reported by LANG (1926). The tripinnate structure (f.o., s.o., t.o.) of the fertile organ has become apparent by the loss of sporangia. The most basal organ consists of a pair of first order pinnae (p.f.o.). [British Museum of Natural History (B.M.N.H.). V54159] × 2.
- Fig. 18 *Milleria thomsonii* figured by LANG 1925, fig. 55 as a vegetative organ of *Milleria pinnata*. Note the pinnate pattern and large size of the lowest second order pinna (s.o.). [B.M.N.H., V54154] × 3.
- Fig. 19 First order pinna with naked second order pinnae; the sporangia have been completely washed away. [5079/6] × 3.
- Fig. 20 Stage 1. Fertile organ before dégagement. [5072/2B] × 3.
- Fig. 21 Stage 2. All sporangia are removed; third (t.o.) and fourth (fth.o.) order pinnae are seen. [5072/2B] × 3.
- Fig. 22 Aborted fertile organ with pinnule-like appendages equivalent in organization to the first (f.o.), second (s.o.) and third order pinnae (t.o.) of a fertile organ. [5066/497A] × 5.

Plate 35

- Fig. 23 Portion of specimen which yielded many spores. Parallel disposition of fertile branch system and type of preservation is of common occurrence. Arrows indicate different planes of deposition of the axes. [5074/498A] × 1.

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Plate 36

- Fig. 24 Spore, proximal view with trilete mark. [5077/420B-5] $\times 500$.
 Fig. 25 Spore, distal view with folds. [5077/420B-1] $\times 500$.
 Fig. 26 Detail of fig. 31. Note granules of less than $1\ \mu$. [5077/420A] Scan $\times 5400$.
 Fig. 27 Spore, distal view. [5077/420A] Scan $\times 500$.
 Fig. 28 Spore, distal view. [5077/420A] Scan $\times 500$.
 Fig. 29 Detail of fig. 28. Scan $\times 2000$.
 Fig. 30 Fragment of a sporangium with some of its spores. [5077/420B-7] $\times 100$.
 Fig. 31 Spore distal view with folds. [5077/420A] Scan $\times 1100$.
 Fig. 32 Same as 31. $\times 500$.
 Fig. 33 Small portion of sporangial wall showing dark and light parallel lines and two spores. [5077/420B-6] $\times 500$.
 Fig. 34—35 Part and counterpart of a first order pinna after dégagement showing the second order pinnae inserted on the upper series (fig. 34 [5072/2B]) and on the lower series (fig. 35 [5071/2A]) $\times 3$.

Plate 37

- Fig. 36—37 Fertile and vegetative branching system as it could have existed in *Milleria thomsonii*. $\times 1$.
 Fig. 36 Same as fig. 1 Plate 31 [5066/497A] $\times 1$.
 Fig. 37 Vegetative specimen showing spiral construction, 4 orders of branching ($N+1$, $N+2$, $N+3$, $N+4$), and leaves. [5083/73A] $\times 1$.
 Fig. 38 Detail of the counter part of the $N+1$ branch of fig. 37 showing scar (sc) of broken $N+2$ and "sparganum" like cortex. [5084/73B] $\times 3$.
 Fig. 39 Detail of fig. 40. Note the spiral arrangement of the dichotomized leaves (1) with lamina and rounded apices. [5073/577A] $\times 5$.
 Fig. 40 Small leafy stem with 3 orders of branches ($N+2$, $N+3$, $N+4$) and leaves, all spirally arranged. [5073/577A] $\times 2$.
 Fig. 41 Transfer of leaf showing dichotomies, limb-like apices and venation. [5085/493B] $\times 6$.

Plate 38

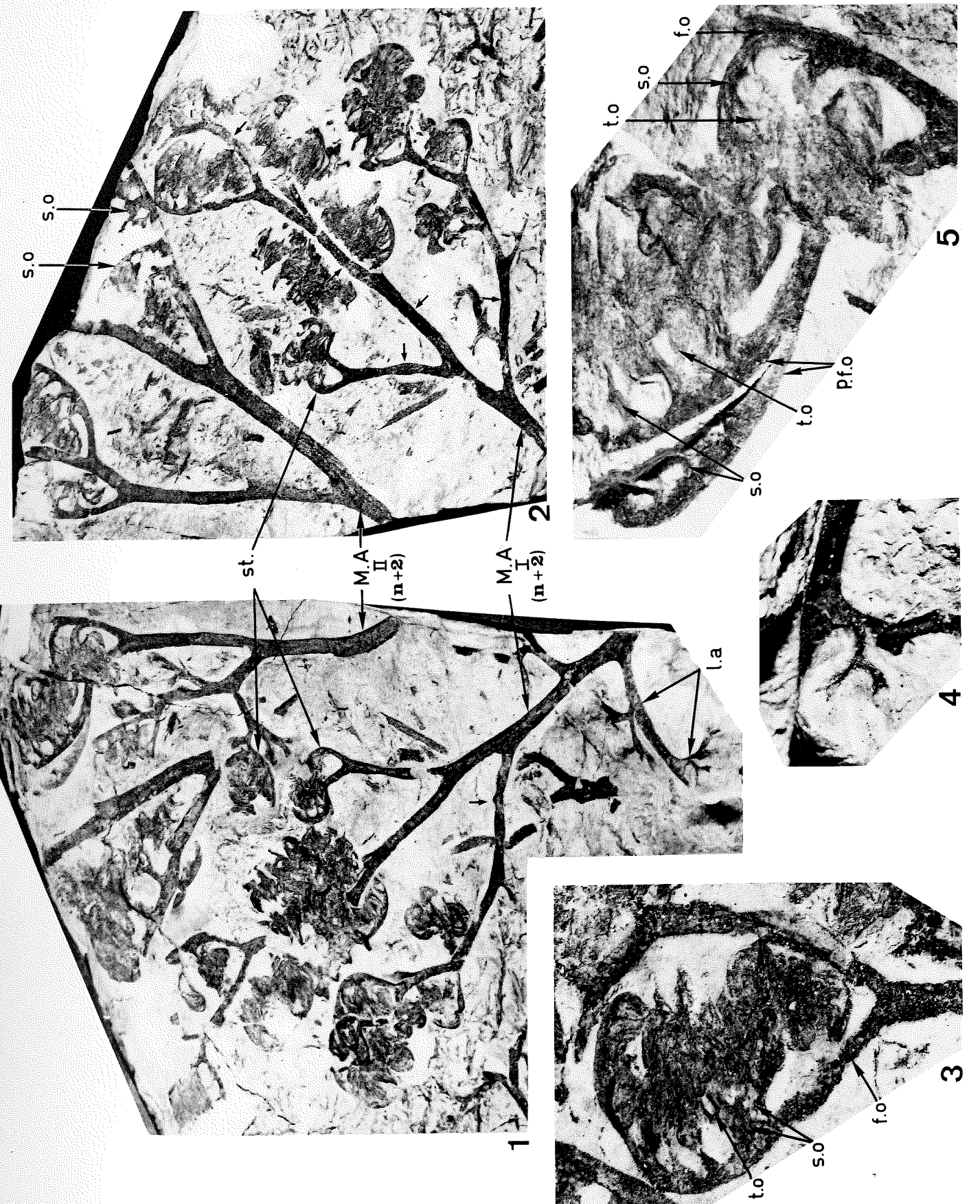
- Fig. 42 Rhenish *Milleria thomsonii* (*Protopteridium hostimense* of KRÄUSEL & WEYLAND 1933, Pl. 1, fig. 8) shows spiral arrangement of fertile organs, tri-pinnate organization and strong basal second order pinna (see text p. 105). The lowest fertile organ shows a pair of first order pinnae. $\times 1$.
 Fig. 43 One fertile organ of Rhenish *Milleria thomsonii* (*Protopteridium pinnatum* from KRÄUSEL & WEYLAND 1938, Pl. 26, fig. 4) consists of two first order pinnae (f.o.) which are four times pinnate (s.o., t.o., fth.o.). Note the strong basalmost third order pinna. $\times 2$.
 Fig. 44 *Tetraxylopteris schmidtii* (from BONAMO & BANKS 1967, fig. 17). Transfer of a fertile organ showing the four times pinnate nature of first order pinnae. Arrows indicate second dichotomy of stalk of fertile organ which results in four first order pinnae. [Cornell University Palaeontological Collection (C.U.P.C.) 1812—32] $\times 3.1$.
 Fig. 45 *Tetraxylopteris schmidtii* (from BONAMO & BANKS 1967, fig. 2). One node showing eight first order pinnae. [C.U.P.C. 1859] $\times 1$.
 Fig. 46 *Milleria thomsonii* figured by LANG, 1926, fig. 1,2. First order pinnae are arranged spirally (see text p. 104). The bases of second order pinnae (s.o.) and a face view of a pair (p.f.o.) of first order pinnae are seen. [B.M.N.H., V 54160] $\times 2$.
 Fig. 47 *Milleria thomsonii*, the holotype. (CARRUTHERS specimen, pl. 137, fig. 2.) The members of a pair of first order pinnae seen in face view are indicated by the arrows (m.p.). [B.M.N.H., V 9425] $\times 2$.
 Fig. 48 Transfer of a fertile organ showing one first order pinna (m.p.) and the base of the second (s = stalk of the fertile organ). The basal second order pinna is very well developed here (s.o., t.o., b.t.o.). [5086/518₂] $\times 3$.

Plate 39

- Fig. 49 Large specimen with close association of axes ($N+2$) bearing typical fertile organs (sp.c. = sporangial complex) and vegetative axes some of which show obvious surface scars (sc) indicating close emission of lesser axes and their spiral insertion. [5081/290A] $\times 1$.

Plate 40

- Fig. 50 *Milleria cf. thomsonii* figured by LANG, 1926, Pl. 1, fig. 7, shows spiral arrangement of four fertile organs (numbered from base to apex), three of which consist of a pair of first order pinnae (p.f.o.) see text p. 103 [B.M.N.H., V 1419] $\times 2$.
 Fig. 51 Detail of fig. 50. The second fertile organ in fig. 50 after dégagement reveals its bifurcated stalk. $\times 8$.
 Fig. 52 Transverse section of the stele of an $n+2$ axis, consisting of irregularly trilobed primary xylem surrounded by pycnoxylic secondary xylem (from KRÄUSEL & WEYLAND 1938 Pl. XXIV, fig. 5) $\times 10$.
 Fig. 53 Detail of fig. 52. Secondary xylem contiguous with the distal part of a primary xylem arm. (from KRÄUSEL & WEYLAND 1938 Pl. XXIV, fig. 6) $\times 40$.

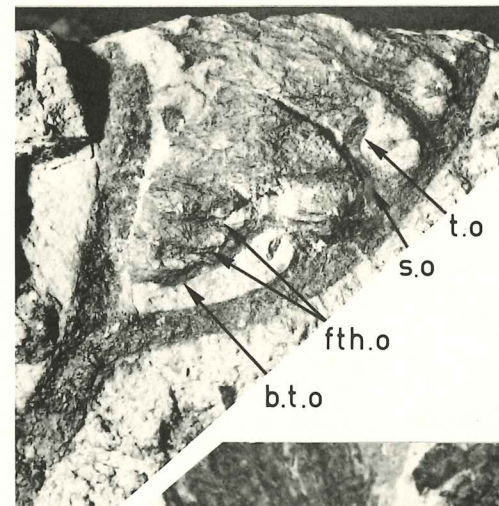
S. Leclercq & P. M. Bonamo: Study of the fructification of *Milleria thomsonii* LANG.



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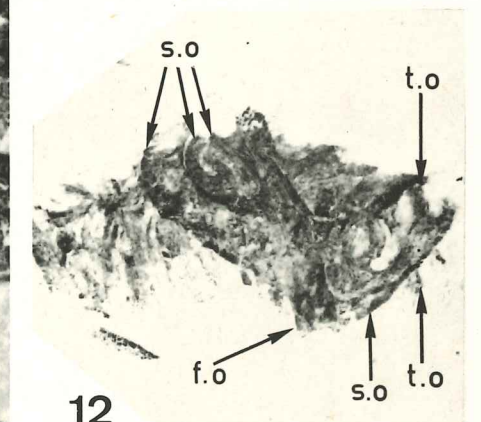
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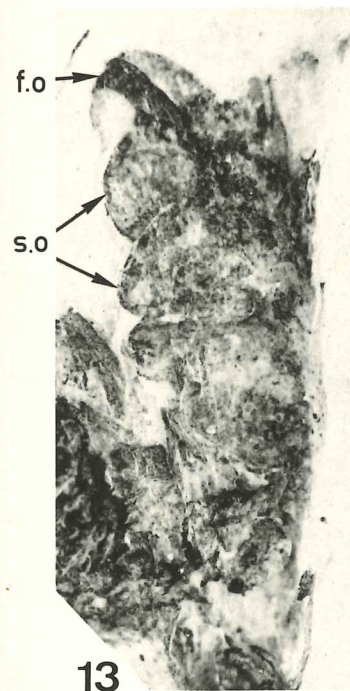
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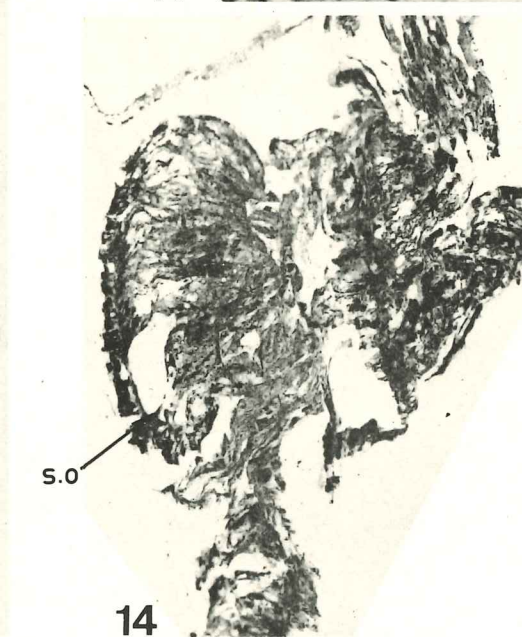
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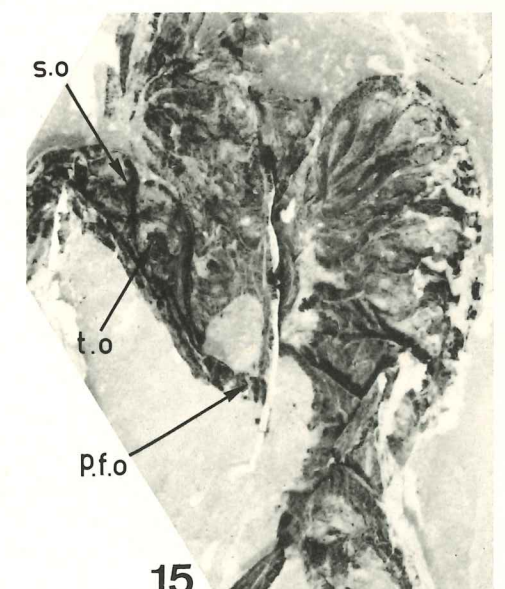
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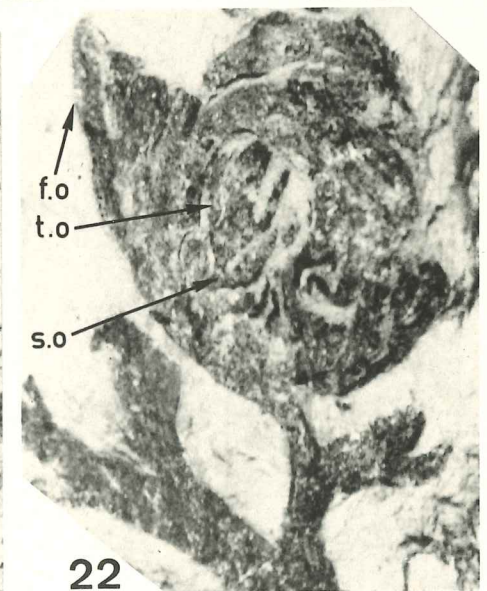
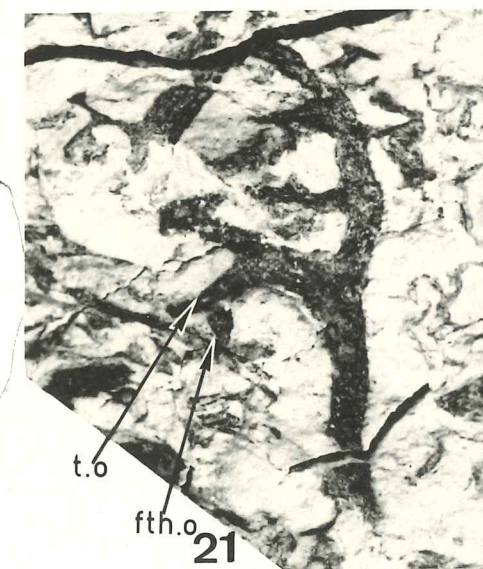
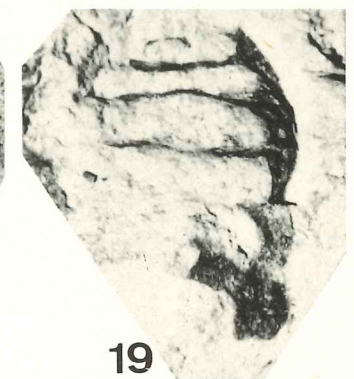
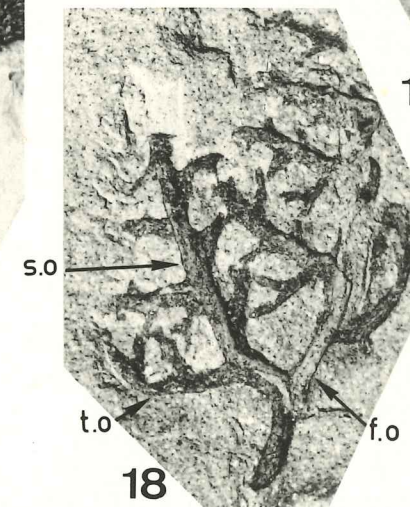
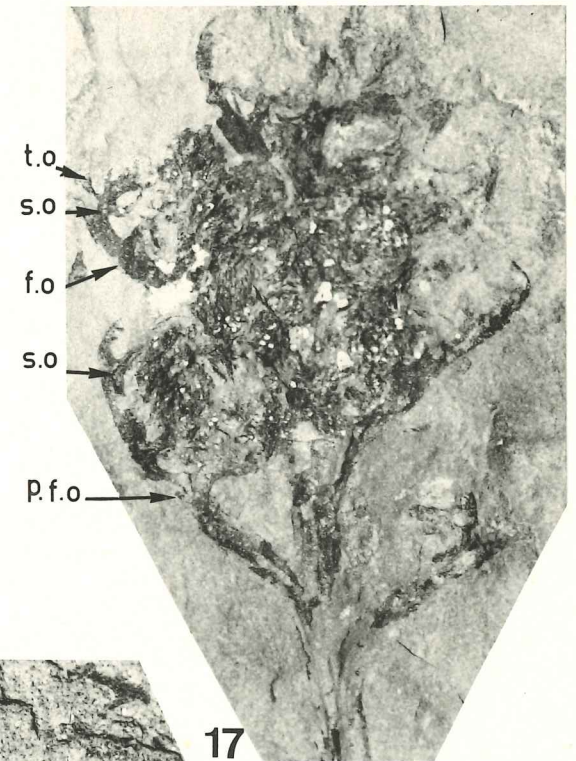
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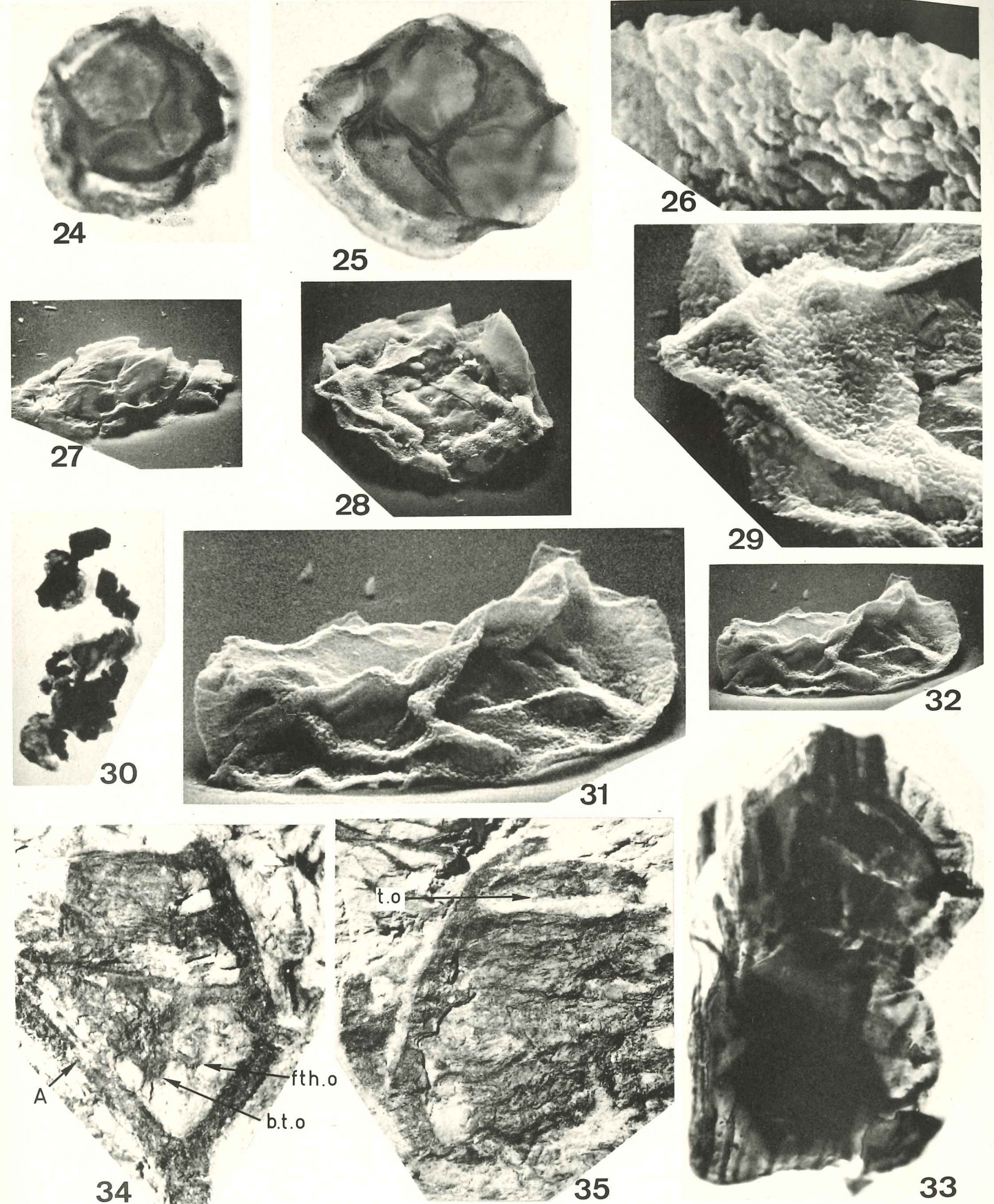


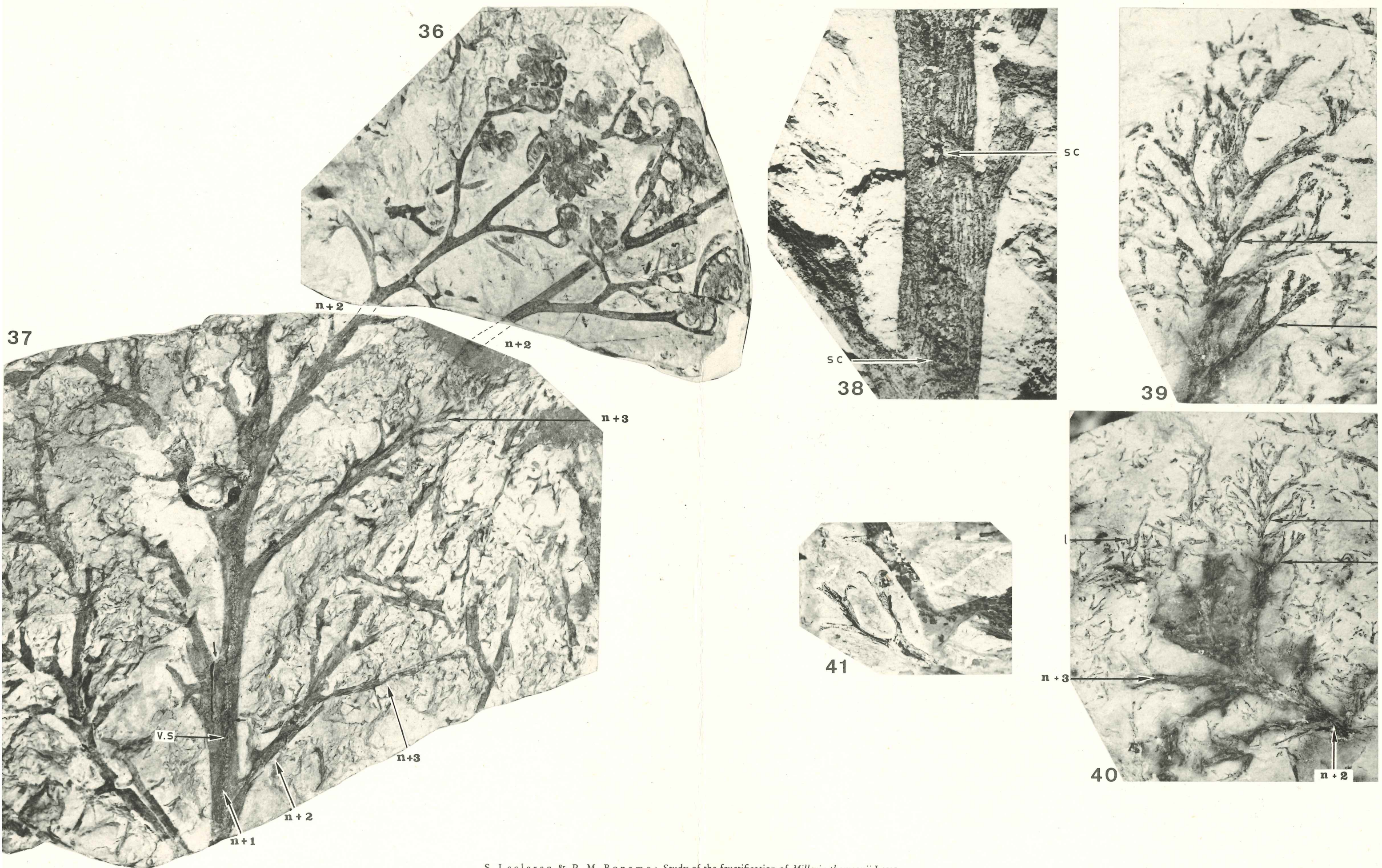
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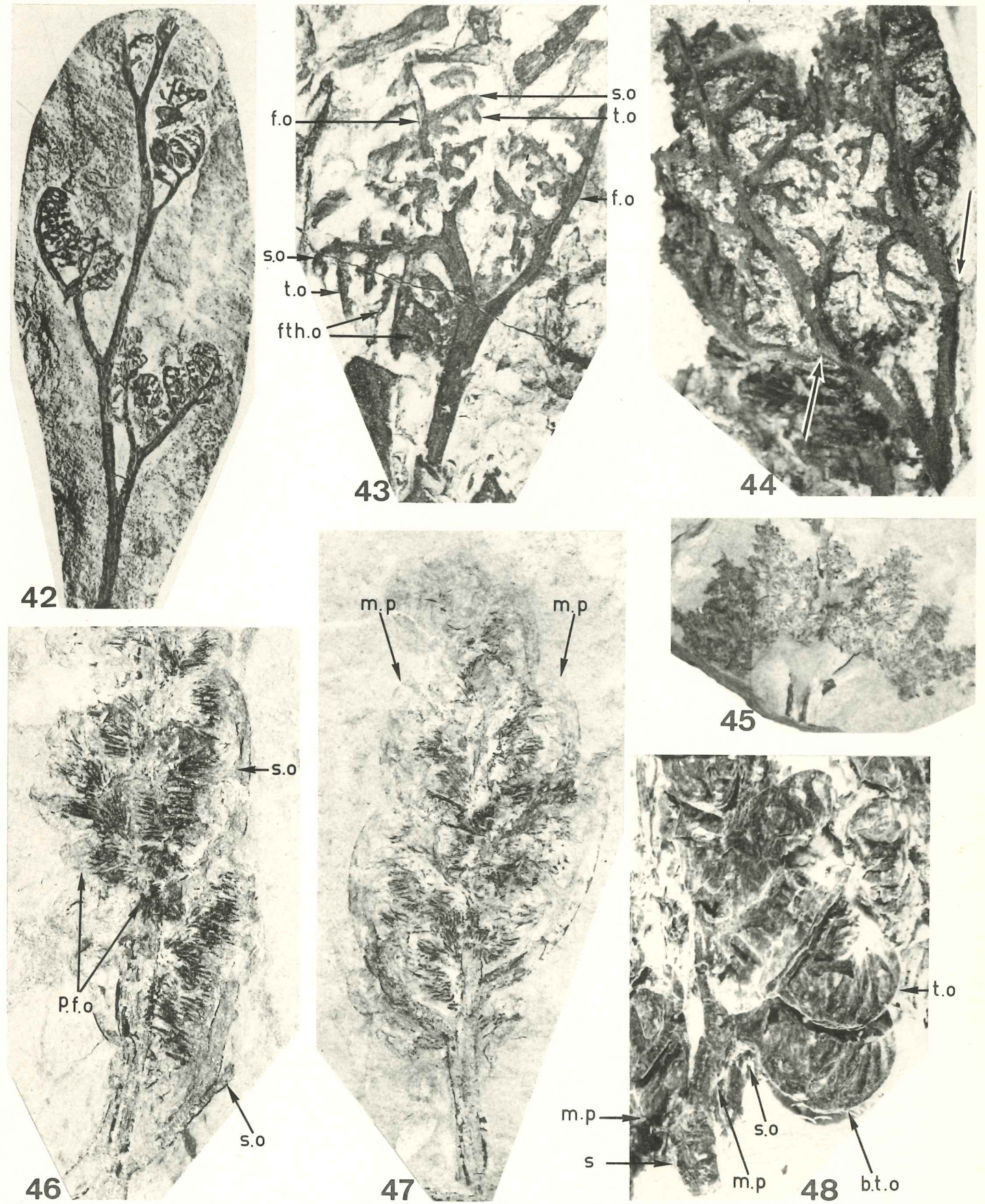




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