A NEW VARIETY OF ORTHORETIOLITES HAMI WHITTINGTON

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Abstract. A variety of *Orthoretiolites hami* Whittington is recorded from two levels in the Viola limestone of Oklahoma. The varietal distinction is based on the more robust nature of the clathria and the presence of a structureless periderm. Early growth stages recovered illustrate the initial development of the species *O. hami* whilst adult stages are represented in several rhabdosomes. It is concluded that, in spite of its mode of development, the genus *Orthoretiolites* could be most conveniently placed in the family Retiolitidae.

INTRODUCTION

NUMEROUS specimens of a variety of *O. hami* were recovered from fragments of Ordovician Viola limestone collected by Dr. P. K. Sutherland from a horizon 50 feet above the base in the Criner Hills at Rock Crossing, 6 miles south-west of Ardmore, Oklahoma. These include growth stages both earlier and later than those which Whittington obtained of his species, *O. hami*; though differing in certain structural features, to be described later, the actual mode of development of the two forms is identical. The purpose of this note is to clarify one or two points, concerning early development, which Whittington had, of necessity, to leave undecided; to justify the creation of a variety of the species *O. hami*; and to comment on the affinities of the genus *Orthoretiolites*.

The fragments of limestone were left to decalcify in strong HCl for about three weeks; they were then washed and transferred to HF for from four to five hours, by which time the limestone was usually completely broken down and the graptolites set free; the specimens ranged from immature siculae to seemingly adult rhabdosomes. The early growth stages were cleared in a solution of concentrated nitric acid and potassium chlorate, dehydrated in alcohol, and mounted in euparal. No attempt was made to clear the larger specimens, which were also mounted in euparal.

The author is indebted to Professor O. M. B. Bulman for his supervision throughout the preparation of this paper. Thanks are due also to Dr. P. K. Sutherland who collected the material. The originals of all figured specimens are in the Sedgwick Museum. Cambridge, and numbered A24581–600.

Orthoretiolites hami Whittington var. robustus nov.

Plates 34 and 35

- 1934 Lasiograptus (Thysanograptus) eucharis Ruedemann and Decker (non Hall), pp. 324–6, pl. 43, figs. 18–20.
- 1945 (?) Lasiograptus (Thysanograptus) eucharis Decker and Coleman, Bull. Amer. Ass. Petrol. Geol. 29, p. 457, pl. 1, fig. 1.
- 1947 Lasiograptus (Thysanograptus) eucharis Ruedemann, pl. 82, figs. 23-26.
- 1950 (non) Lasiograptus (Thysanograptus) eucharis Decker. Bull. Amer. Ass. Petrol. Geol. 34, pp. 1904, 1908-9, pl. 1, fig. 19.

Diagnosis. Rhabdosome 1 mm. in width at first thecal pair (excluding apertural spines), increasing to 2.2 mm. at fifth pair, thereafter increase slight. Greatest length preserved [Palaeontology, Vol. 2, Part 2, 1960, pp. 226–35, pl. 34–35]

7.7 mm. Sicula and proximal parts of th1¹, th1², and th2¹ provided with complete periderm, remainder of rhabdosome represented by clathria with covering of structureless periderm (presumably cortical tissue alone). Virgula straight, central, and confined to obverse wall; reverse wall has zigzag 'virgula'. Paired lateral spines developed infrequently on true virgula. Development non-septate diplograptid, thecae alternating and of orthograptid type with straight ventral walls and provided with long, single, apertural spines. Thecae numbering 15 in 10 mm. at proximal end; probably about 12 in 10 mm. distally.

Description. In a comparison of Whittington's holotype (Specimen MCZ 511—see Whittington 1954, p. 615, fig. 4) with the specimens collected from the 50-foot level in the limestone, two differences are at once apparent: (a) the stouter clathrial lists and more pronounced lateral spines of the latter; and (b) the presence, in some of the latter, of a periderm throughout the rhabdosome of the larger growth stages and adult specimens.

Every specimen of Orthoretiolites collected from the 50-foot horizon possesses lists which are much stouter than those of Whittington's species. The fact that this feature is shown by even the earliest growth stages which possess lists indicates that it is not developed only with the onset of maturity. The lateral spines are similarly more strongly developed. Furthermore, their arrangement shows a marked tendency towards regularity; thus, a pair of such spines—one obverse and one reverse—is present on the sicula, about one-third of the distance down from the base of the nema (Pl. 34, fig. 3). Both spines are directed outwards approximately normal to the axis of the rhabdosome. The obverse spine is unrelated to the skeletal framework, but the reverse spine, on the other hand, is linked with the rods of the clathria. In specimen A24592 (Pl. 34, fig. 3) it passes through the mid-point of the dorsal list of th22, whilst in specimen A24594 (Pl. 35, fig. 2) it cuts across the junction of the dorsal lists of th21 and th22 and the parietal list between th21 and th31. Thus, in its initial part, between the sicula and the clathrial lists, the reverse spine functions as an additional, transverse list, strengthening the clathria. A similar pair of spines may be present at the level of the fourth or fifth thecal pairs (Pl. 35, fig. 2). These spines are again obverse and reverse and both originate at the same level on the virgula proper; in consequence, the reverse spine, in its early part, again acts as a transverse list, in this case linking the obverse and reverse walls of the clathria in the mid-line.

In Orthoretiolites hami, continuous periderm is present only in the sicula and the proximal parts of th1¹, th1², and th2¹, though Whittington (1954) states that shreds of this material are occasionally found in more distal thecae, in the angles between the lists of the clathria. On the other hand, with a single exception (Pl. 34, fig. 2), all the adult and later growth stage specimens from the 50-foot level—together with examples from a horizon 3 feet above the base at the same locality—show a damaged, though apparently once continuous, periderm throughout (Pl. 34, fig. 3; Pl. 35, figs. 1–4). This periderm is quite structureless and presumably represents only cortical tissue. Several growth stages, younger than Whittington's holotype, show this periderm, which again is therefore not a feature acquired only at a late stage in development.

In spite of the features noted above, the mode of development, the extent of fusellar tissue, and the arrangement of the clathrial lists correspond in the specimens from the two levels. The differences which exist are a matter only of degree and do not merit the erection of a new species. They represent, at the most, a variety of *O. hami*—an ancestral

form in which the reduction of the skeleton had not progressed so far as in the typical *O. hami*—for which the name *robustus* is proposed.

Additional material, collected 3 feet above the base of the limestone, possesses features identical with those of specimens from the 50-foot horizon and it can be concluded that this material also belongs to the new variety of Whittington's species (Pl. 35, figs. 3, 4).

Development. The prosicula is typically subcylindrical in shape. At its proximal end it merges into the base of the nema and shortly below this point it attains a width which is retained, with little increase, to its distal margin. In the original of text-fig. 1b the prosicula is 0·31 mm. in length and 0·10 mm. in width at the margin; in text-fig. 2b the respective dimensions are 0·31 mm. and 0·11 mm. In one specimen, text-fig. 1e, there is, however, a slight contraction towards the apertural margin, the maximum width being at a level about two-thirds of the way down the prosicula. In the original of text-fig. 1a the prosicula is missing and the 'bifurcating virgula' is attached directly to the metasicula. The longitudinal rods are four or five in number and extend the length of the prosicula; the intervening, short, secondary rods, growing up from the margin, total eight or more.

The slight increase in diameter of the prosicula towards its distal margin is followed by a much more definite increase in the proximal part of the metasicula. The growth lines in this initial part of the metasicula are closely spaced and meet, on both the virgellar and anti-virgellar sides, along a zigzag suture. On the anti-virgellar side, as noted by Whittington, the margins of the chitinous growth bands are straight, but on the virgellar side they bend downwards to a progressively increasing degree as the origin of the virgella is approached, becoming asymptotic to the long axis of the sicula as they pass into the virgella (text-figs, 1c, d, e). This latter originates usually between 0·20 and 0·30 mm, below the prosicular margin, but in one specimen this distance is only 0·15 mm. (text-fig, 1d). At about the level of the virgella origin there is typically a marked increase in the width of the metasicula; the diameter thus attained remains more or less constant to the aperture.

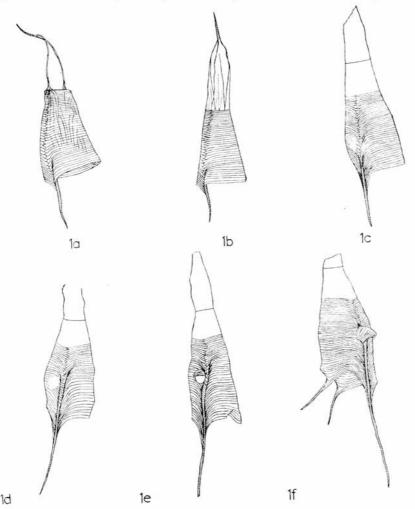
Variation in the shape of the sicula was a feature commented upon by Whittington and can be verified by a consideration of the accompanying text-figures, the originals of which were preserved in full relief. Despite the variety of shapes possible, however, there is a form typical of the species having a subcylindrical prosicula and showing expansion of the proximal part of the metasicula down to the level of the virgella origin, where a swelling occurs giving an increase in diameter which is more or less retained to the aperture.

In the earliest growth stages of the metasicula, before the appearance of the virgella proper, the position of that feature on the growing edge is marked by a blunt tubercle. In later stages, however, the virgella forms a prominent part of the metasicula and in the fully developed sicula it projects as a spine below the aperture, only slightly less than the length of the metasicula itself; thus, in the original of text-fig. 1*f*, the metasicula measures 0.55 mm, and the virgella extends a further 0.42 mm, beyond the level of the aperture.

EXPLANATION OF PLATE 34

Figs. 1-3. Orthoretiolites hami Whittington var. robustus nov. Viola limestone, 50 feet above the base, at Rock Crossing, 6 miles south-west of Ardmore, Criner Hills, Oklahoma. 1, Reverse view, th1¹ incomplete, flange representing proximal part of th1², × 86. A24590. 2, Obverse view, growth stage with four thecae complete, total absence of structureless periderm, × 20. A24591, 3, Reverse view, growth stage with six thecae complete, note patches of periderm. ls—lateral spine. × 20. A24592.

On the anti-virgellar side of the metasicular aperture are two diverging spines directed outwards and downwards and making an angle of 45° with the axis of the sicula. In fully mature siculae the spines may attain a length of 0.25 mm. The two spines are



TEXT-FIG. 1. Orthoretiolites hami Whittington var. robustus nov. Stages of growth up to the appearance of the initial bud, × 35. a, Malformed immature sicula A24581. b, Prosicula complete, beginning of metasicula and appearance of virgella. A24582. c, Appearance of resorption foramen; specimen slightly damaged. A24583. d, Foramen complete, virgella prominent. A24584. e, Initial bud, development of apertural spines on sicula. A24585. f, Initial bud, sicula complete. A24586.

separated by a section of the apertural margin along which growth has been checked, resulting in an embayment which may extend proximally for as much as 0·11 mm. above the general level of the aperture. In addition, the apertural margin of the sicula commonly exhibits a noticeable thickening.

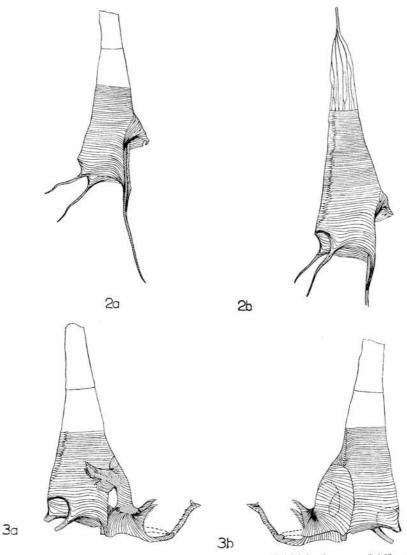
The foramen, marking the point at which the initial bud—the proximal part of th1¹—originates, is produced by the resorption of periderm (text-figs. 1c, d). It is situated just distally to the virgellar origin, and to the left of that feature. The foramen is formed at or about the stage when the apertural spines are beginning to develop; it lies below the mid-point of the metasicula and typically three-fifths of the distance from the prosicular aperture. The initial bud originates as a hood at the top of the foramen (text-fig. 1e). In the very early stages of formation growth is directed outwards from the sicula and downwards towards the sicular aperture; by the time the bud has grown to the level of the lower rim of the foramen the sicular is normally fully developed. The direction of growth of the bud soon changes so that the right-hand edge crosses the virgella to the obverse side of the sicula; the left-hand edge of the bud grows towards the virgella, and may pass on to it, but does not cross it.

At approximately the stage of growth represented by the original of text-fig. 2a, growth is checked along the left-hand, or reverse, growing edge of the initial bud-thus producing an embayment which becomes the upper rim of the foramen of th12. This latter, therefore, takes the form of a primary notch, as distinct from the resorption foramen of thl1. Further growth of thl2 is by the addition of periderm to the outer margin of the foramen, producing a flap or flange (text-fig. 2b), and this is contemporaneous with the continued development of th11. In its earliest stage, therefore, th12 is elongated parallel to the axis of the sicula, and at the same time its outer margin is extended round the reverse wall of the sicula, and generally towards the anti-virgellar side. When complete, the margin of the foramen is oval in shape. Text-fig. 2b shows an early stage in the development of the flange, and the growth lines of this feature indicate that the direction of growth is downwards (towards the metasicular aperture), across (towards the antivirgellar side of the sicula), and outwards so as to form a sheath-like structure about the sicula. The right-hand, or obverse, wall of the initial bud is unaffected by flange development and continues to grow downwards until the level of the metasicular aperture is reached.

In the original of text-fig. 3 the flange has extended across the metasicula, half-way to the anti-virgellar side, and downwards, partly obscuring the foramen of th1². The flange is in contact with the sicula along its upper edge, and with the outer margin of the foramen; the inner margin of this latter is coincident with the virgella. The growing edge of the flange is affected by folding, but it is probable that this is mostly a preservational

EXPLANATION OF PLATE 35

Figs. 1–4. Orthoretiolites hami Whittington var. robustus nov. 1, 2, Viola limestone, 50 feet above the base, at Rock Crossing, 6 miles south-west of Ardmore, Criner Hills, Oklahoma. 1, Obverse view, adult rhabdosome extending to seventh thecal pair, structureless periderm strongly in evidence. × 10. A24593. 2a, Reverse view, damaged adult rhabdosome, note pair of lateral spines (/s) developed at fifth thecal pair. × 10, A24594. 2b, Obverse view of same. 3, 4, Viola limestone, 3 feet above the base, at Rock Crossing. 3, Part of surface of fragment of Viola limestone. Obverse view with fourteen thecae visible; darker patches within the thecae represent the structureless periderm. × 15. A24599. 4, Ditto. Several specimens crushed together, periderm clearly developed. × 15. A24600.



TEXT-FIGS. 2, 3. Orthoretiolites hami Whittington var. robustus nov. Initial development of th1², × 35. 2a. Reverse view, appearance of the foramen of h1² in reverse wall of the initial bud. A24587. 2b. Reverse view, appearance of the flange. A24588. 3a. Reverse view, th1³ incomplete, flange representing proximal part of th1². A24589. 3b. Obverse view of same.

feature. The growth lines on the flange are quite indistinct, except in one part where the flange lies above the virgella; elsewhere, only vaguely defined striations are evident, very closely set, but parallel to the directions in which one would have expected the growth lines to trend.

Down to approximately the level of the lower rim of the foramen of th12, th11 grows as a hood which is interrupted only on its reverse side by the formation of that foramen. Below this level, however, striking developments occur (text-fig. 3; Pl. 34, fig. 1). At the level of the metasicular aperture the obverse side of thl1 recrosses the virgella and the growth of this theca as a whole is then directed outwards normal to the sicula axis. At a short distance from the sicula the growth of thl1 becomes concentrated along its obverse and reverse edges, both dorsally and ventrally. The dorsal obverse and reverse edges become respectively the obverse and reverse parietal lists of thl1; in their subsequent growth these lists diverge and are directed upwards and away from the sicula. The obverse and reverse ventral lists develop from the respective ventral edges and their direction of growth is such that they extend outwards, away from the sicula, and also towards each other, so that eventually they meet and fuse. The single ventral list so produced continues to grow, but in a different direction: upwards and outwards, away from the sicula. When this single list has reached the level of the base of the foramen of th12, a second change in growth direction is begun, and it is at this point that the single ventral list becomes the apertural spine of th11. The method of formation of the lists is best illustrated by reference to text-fig. 3, which shows the detailed courses of the growth lines.

It is highly probable that, at the stage represented by the original of text-fig. 3, the lateral walls of the free part of th1¹, between the parietal and ventral lists, were present, being formed of a periderm so thin as to defy preservation. This is suggested by the course of the growth lines of the parietal lists which project beyond the intervening preserved periderm and are directed towards the ventral lists and their fused representative (text-fig. 3). This may be true also of the dorsal and ventral walls of the free part of th1¹, but there is no similar evidence to support this contention.

Specimen A24595—which is too poorly preserved to be figured—is a slightly later stage than the original of Pl. 34, fig. 1, and it shows the beginnings of the two pleural lists necessary to complete th11. These lists originate at the base of the apertural spine and they grow towards the terminal points of the respective parietal lists, which have turned slightly out and down to meet the pleural lists. These two lists—obverse and reverse—are essentially backward projections of the apertural spine, with which they are in alignment.

In the latest early growth stage recovered—Pl. 34, fig. 1—apart from the damaged specimen A24595, the flange has extended down to the level of the base of the foramen of th12 and across almost to the anti-virgellar side of the sicula. The growth is still, in general, across the sicula, but now there is an upward tendency as distinct from the earlier downward one. The detailed form of the upper edge of the flange is uncertain, but there appears to be incipient development of a spine which is directed upwards and across the sicula—this will become the reverse parietal list of th12. The blunt tubercle on the anti-virgellar side of the sicula is the initial part of the obverse pleural list of th12.

Growth lines on the flange are discernible only in the vicinity of its growing edge, and the remaining part is either composed of a structureless film or is missing altogether, presumably having been too thin to be preserved and thus paralleling the case of the distal lateral walls of thl¹, as noted above. Several of the adult specimens show the flange incompletely developed—just as the distal part of thl¹ shows no trace of fusellar material; yet, in both features, the early growth stages provide evidence that fusellar tissue was present. Thus, it may have existed during the life of the graptolite colony, but was too delicate to be preserved.

THE VALIDITY OF WHITTINGTON'S PARIETAL LIST

Holm defined the parietal list as the outer line of contact with the theca immediately above or below; that is, it would represent the trace of the interthecal septum on the lateral wall of the rhabdosome, if such a septum were present.

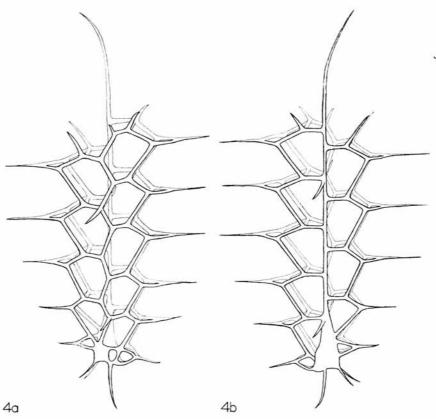
The list which Whittington defines as parietal is, in Orthoretiolites, inclined at a remarkably high angle to the ventral list with which it is in contact. It might be expected that the interthecal septum, if present, would lie approximately parallel to the free ventral wall of which it is the internal continuation-especially as Whittington claims the thecae to be of 'orthograptid type with straight ventral wall' (1954, p. 614). Bearing this in mind, two possibilities exist regarding the mutual relationship of the thecae in Orthoretiolites. If it is assumed that the interthecal septa were present but not preserved, nor their margins indicated by lists on the walls of the rhabdosome, then adjacent thecae overlapped to an unknown extent, and the parietal list of Whittington is, in reality, a connecting rod (Bouček and Münch 1952). On the other hand, if Whittington's parietal list is correctly identified, it may very well correspond to that small section of the parietal list which, in Holm's diagram of a retiolitid (reproduced in Elles and Wood 1908, p. 337, fig. 220f), is separated from the main part of the list by a geniculate bend. Admittedly, the orientation of the lists in the two cases is different, but Holm's diagram is of a retiolitid with completely overlapping thecae. If this should be the correct interpretation then, in Orthoretiolites, the thecae overlap for approximately one-quarter of their length.

AFFINITIES OF THE GENUS

The incorporation of the virgula into one of the lateral walls of the rhabdosome (text-fig. 4) gives *Orthoretiolites* a superficial resemblance to certain retiolitids, in particular *Paraplectograptus* Bouček and Münch 1948 and *Retiolites* Barrande 1850. In addition, Whittington has noted the features which distinguish his genus from two other retiolitid genera: *Plegmatograptus* Elles and Wood 1908 and *Archiretiolites* Eisenack 1935. A detailed comparison of *Paraplectograptus* and *Retiolites* with *Orthoretiolites* likewise reveals important differences. *Paraplectograptus* lacks both dorsal and parietal lists and possesses instead diagonal lists; whereas, in this genus, the zigzag 'virgula' is formed of diagonal lists, in *Orthoretiolites* it is the dorsal lists which are responsible for that feature (text-fig. 4). Neither lateral nor apertural spines have been recorded, and the corona takes the place of the chitinized sicula; the shape and course of the thecae in *Paraplectograptus* are unknown and a comparison cannot, therefore, be attempted.

In *Retiolites* the thecae are completely overlapping and, in consequence, ventral lists cannot be present. On the other hand, *Orthoretiolites* has nothing to compare with the aboral (or interior) list of *Retiolites*. Furthermore, the deficient chitinization of the sicula of the latter serves also to distinguish it from Whittington's genus.

The discovery of adult rhabdosomes further justifies the erection of the genus *Orthoretiolites* Whittington, which cannot be associated with any genus at present included in the family Retiolitidae. It is provisionally placed in the sub-family Archiretiolitinae, although a superficial resemblance to such genera as *Paraplectograptus* and *Retiolites*



TEXT-FIG. 4. Orthoretiolites hami Whittington var. robustus nov. Diagrammatical reconstruction of the clathria, \times 20. Dimensions are based on measurements of specimens A24593 and A24594 but, apart from the width of the lists, this reconstruction may be regarded as typical of the genus. a, Reverse side, b, Obverse side.

suggests that it may be a parallel development to later retiolitids. Whittington preferred to regard the genus as a diplograptid; certainly the development is of diplograptid type, but so also is that of *Archiretiolites*, *Plegmatograptus* and *?Retiograptus* Hall 1859, all of which are at present grouped in the sub-family Archiretiolitinae of the family Retiolitidae.

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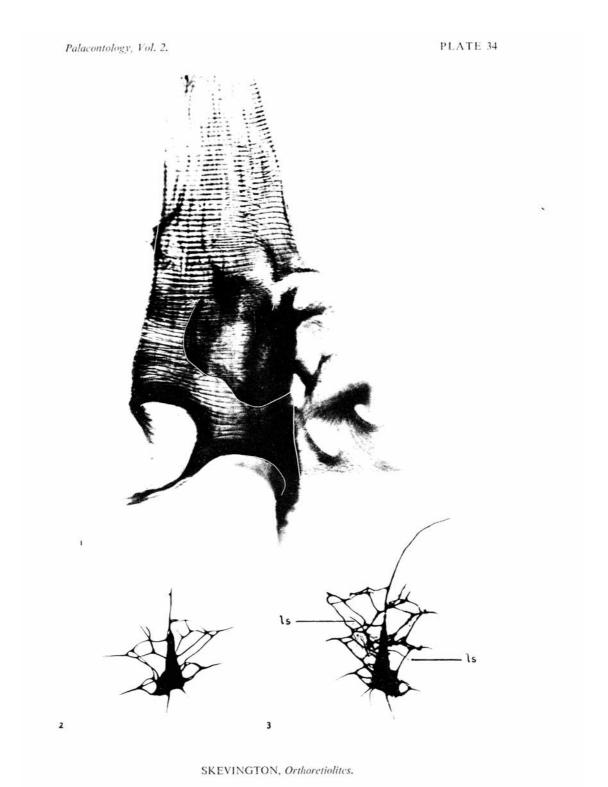
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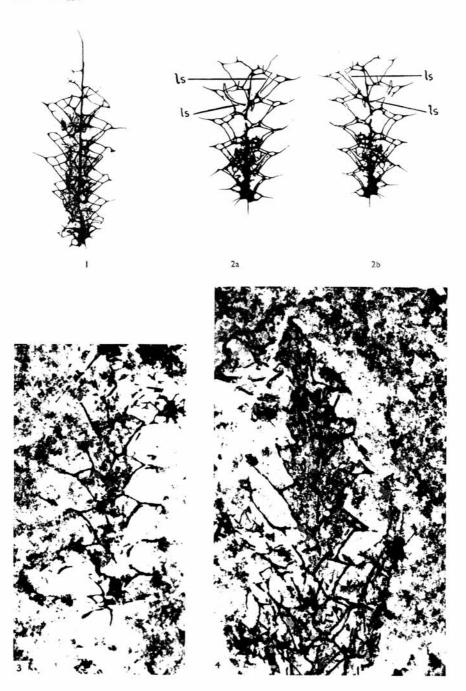
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Manuscript received 12 February 1959





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