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## **DOCTOR OF PHILOSOPHY**

### **Calcareous algae of the silurian of the Welsh border**

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CALCAREOUS ALGAE OF THE SILURIAN  
OF THE WELSH BORDER

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A thesis  
presented to the University of Wales  
for the degree of  
Philosophiae Doctor.

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Hazel M. Green.

April, 1959.

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## A C K N O W L E D G M E N T S

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## P R E F A C E

This thesis is a continuation of the work commenced at the University of Manchester which led to an M.Sc. thesis being presented to that University in May 1955 on "The Calcareous Algae of Woolhope and Wenlock Limestones from certain localities in the Welsh Borderland." For the present thesis, the result of work carried out whilst at the University College of North Wales, the original investigation has been much extended in all directions and details of which are given in the Introduction.

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## S U M M A R Y

A general survey of the calcareous algae of the Silurian of the Welsh Border has been undertaken. The genera discovered during this investigation, and so under consideration, are those of Girvanella, Rothpletzella, Solenopora and Rhabdoporella. Systematic descriptions are given for each, and their variation shown.

Girvanella has been subdivided here into form-species, mostly new types, on the basis of character differences, combined with chronological, geographical and ecological factors. Both species of Rothpletzella together with a fine-tubed form and three species of Solenopora are recorded. Only one species of Solenopora was originally known from this area and a second just outside. Rhabdoporella has been obtained from the Wenlockian, but was only previously recorded from the Llandovery of Meifod.

The lateral and vertical distribution of each alga has been studied and as far as possible quantitative methods have also been used. These investigations have been in relation to the limestone facies and associated fauna. It is shown that algae, especially the filamentous forms, are much more abundant and are far more widespread than has been

previously recorded. In some instances, their distribution appears to change less according to horizon level than to differences of limestone facies but others still appear to be of stratigraphical value. The abundant distribution of Solenopora and Rothpletzella species is mostly correlated with reef or reef-like conditions which existed during most of the limestone formation periods, but the distribution of the other genera is not thus correlated. The apparent preferences for different types of conditions by the various algae are indicated, and comparisons are made with the ecology of present day reefs.

## I N T R O D U C T I O N

One of the main purposes of this investigation was to ascertain the calcareous algal types present in the Silurian limestones of the Welsh Border. It was hoped, that from a study of their fossil remains, their structures, vegetative and reproductive, might be further elucidated. The distribution and occurrence of the algae found could then be used to determine their geographical and chronological occurrence, hence any stratigraphical or ecological significance. Any ecological variations could be further partially established by the algal-faunal associations and the relationship, if any, between differing algae and their faunal associates to the sediments.

As the genus Girvanella was known to be present fairly abundantly in these Silurian limestones, from the preliminary investigations recorded in an M.Sc. thesis (University of Manchester), another aim was to make a systematic study of the forms present so as to be able to find if any subdivisions were possible, in preference to regarding all as forms of the Ordovician type, G. problematica.



or to retaining all specimens obtained as unclassified at generic level.

During the whole of the investigation, many localities were visited and specimens collected from the Silurian limestones from Wenlock Edge (Shropshire) in the north to May Hill (Glos.) to the south. The west-east limits were approximately demarked by Old Radnor (Radnorshire) and Dudley (Worcestershire). Some of these localities were chosen because of contrasting types of sediment present both bedded and unbedded and others just to make the contrasts over a wider area. A few localities were investigated because of known previous algal records. These were in the Woolhope limestones, Old Radnor and Nash Scar (Herefordshire) which Garwood and Goodyear (1918) described chiefly as algal limestones; also Woolhope where Garwood (1931) had found an undescribed Solenopora specimen. For the Wenlock Limestone, the only specific records of algae are at Dudley (Chapman 1907 and Crosfield and Johnston 1914) and Purley (W. Malverns) and May Hill (Wethered 1893). Several authors indicated the presence of algal limestones (no details), as opposed to the other crinoidal, brachiopodal and other facies in Wenlock Edge, and have also stated beliefs that it seemed probable

that masses of algae were engaged together with corals and stromatoporoids in the building of the Ballstones (Hill et al 1936, Whittard 1952). Likewise, the Crogballs of Dudley were the result of algal decomposition. There have been no published algal records for this area from the Aymestry Limestone. Algae have also been recorded by Whittard in 1944 from the Tortworth inlier further south and not investigated here.

The field relationships between different facies of limestone were examined in greatest detail along the lengths of Wenlock Edge where limited lateral and vertical changes were partially established. Stratigraphical sequences for the other localities were taken from Butler (1939 Dudley) and Garwood and Goodyear (1918 Old Radnor and Nash Scar), Lawson (1956 May Hill) and Gardiner (1927) and Pocock (1930, Woolhope Inlier).

As only Solenopora of the algae investigated was visible in the field, apart from rare growth forms, and even it was liable to be confused with other organic structures, especially stromatoporoids, thin sections were made and examined from the chief rock types of each locality. It was soon found that the algae were far more abundant in these localities than had previously been assumed; any of them

were liable to be found in any suitable limestone facies.

Although this investigation was commenced in the University of Manchester and led to an M.Sc. thesis being presented on the "Calcareous Algae from the Woolhope and Wenlock Limestones from selected localities in the Welsh Border", the work on these limestones has been much extended, and the Aymestry Limestone and calcareous facies of the Upper Ludlow also included. Further details have also been discovered from those earlier localities, so that the whole has been rewritten, both greatly modified and amplified and, as with the section on Girvanella, has undergone a complete change with the addition of species descriptions. Also completely new sections have been added, for example the Dasycladaceae and general distribution surveys.

Thus, the reviews of previous literature have been altered and much enlarged and hence there is now a more comprehensive bibliography. The section on the materials and methods is far more detailed on the methods of examination etc. and the systematic descriptions of each group include quantitative methods for separation into species (hence many more tables, histograms and graphs),

further characteristics including ecological factors and extended vertical and lateral ranges.

Also now, the table of algal forms found during the investigation is both increased in number of algae and in their distribution.

The new localities visited and investigated since this more detailed account was commenced include for the Woolhope Limestone, Mordiford (Herefordshire); for the Wenlock Limestone, Fownhope, Sollers' Hope (Herefordshire), Woolhope, Ledbury, May Hill (Glos.) and the southwestern quarries of Wenlock Edge; and for the Aymestry Limestone and Ludlow group, all localities cited, i.e. Whitcliffe Beds, Ludlow, Marcle Hill (Hereford), Norton Camp, Aymestry and Ledbury,

Some micro and field photographs have been repeated from the M.Sc. thesis, so as to give a more comprehensive photographic survey. The plates repeated are figs.

7-11, 17, 14, 25, 27, 29-32, 34, 35, 37, 38, 40, 42, 43, 47-50, 53-57, 80, 84.

## GENERAL REVIEW OF PREVIOUS LITERATURE.

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### I. THE RECOGNITION OF FOSSIL ALGAE

Forchhammer in 1844 concluded that as the quantity of "fucoid growth" produced annually was enormous and the mineral content of "fucoids" was higher than that of land plants, these plants must have influenced the form and change of sea deposits. Thus he suggested that minerals derived from them were important in the accumulation of Palaeozoic sediments.

In 1858, Unger, Rosanoff and Gumbel (cited by Garwood 1913a) demonstrated the presence of Nullipores in several Cretaceous and Tertiary limestones of Europe, an especial development being the Leithakalk of the Vienna Basin (Unger). It was not until 1837 that the calcareous deposits formed by Nullipores were realised by Phillipi to be directly due to growth of living lime secreting algae and 1894 (Brown) before Solenopora was recognised as a fossil coralline alga.

Munier Chalmas in 1877 recognised fossil Dasycladaceae to be algal as he transferred the group from Foraminifera to the Siphoneae Verticillatae. Dasycladacean fossils had been recorded by Eichwald (1840, 1860) and de Koninck (1842, 1872) as animal remains.

Rothpletz in 1891, gave a description of filamentous fossil algal forms (Sphaerocodium) which he ascribed to the Codiaceae and gave evidence to support his algal claims. Previous to Rothpletz, Duncan (1876) described what he regarded as parasitic filamentous algae in fossil corals allied to water moulds Saprolegnia and Achlya, and Bornemann (1887, and review of Bornemann by Hinde 1887) regarded his erected genus Siphonema as of algal origin.

Previous to 1894, there were very few references to the occurrence of fossil calcareous algae in British deposits (Garwood 1913a) as those fossil algae which were found were referred to as corals (Nicholson & Etheridge 1877), Monticuliporoids (Dybowski 1877, Dawson 1879), Hydractinae (allied to Stromatoporoids) (Wethered 1886, 1887), Rhizopods (Wethered 1889a, 1890, Nicholson & Etheridge 1878), Protozoa (Dawson 1897), Serpulae tubes (Hinde in discussion of Wethered 1890), Foraminifera (Nicholson and Lydekker 1889, Wethered 1890, Eichwald 1840, 1860, de Koninck 1842, 1872), Calcareous sponge (Sealy 1885, 1887) and inorganic concretionary structures, (Calloway 1900 on Solenopora gracilis).

Other fossil algae such as Pachythea were regarded

variously as having zoological affinities (crustacean eggs and parts of the palate of fishes) or Lycopod spore, gymnosperm seeds, etc. (Lang 1945), whereas very many inorganically formed structures were termed 'algal' or 'fucoidal'.

In 1894 Brown described various new forms of Solenopora ascribing them, as did Rothpletz, to the coralline algae and in 1898 Seward gave a general survey of the groups of algae then known including those of doubtful affinity.

IIa. THE RECOGNITION OF THE IMPORTANCE OF ALGAE AS LIMESTONE BUILDERS and their stratigraphical value as index fossils.

Wethered (1889, 1890, 1891) was of the opinion that oolites, from Silurian and Carboniferous limestone to Jurassic pisolites, were formed by Girvanella, although Cayeux (1910) thought that Girvanella was parasitic on them but that algae were important during the Palaeozoic (1930). Nicholson (1888) realised that certain anomalous organisms such as Mitcheldeania were concerned in actual limestone formation.

Various authors had expressed the abundance of algal

forms, but it was really not until the organic forms were actually recognised as fossil algae, that their part as actual limestone builders was realised. Thus Seward (1894, 1898) indicated the relations of algae to various limestones but Geikie (1903) recognised that massive limestones had been formed by algal agencies, especially in the Trias of Bavaria and the Tertiary limestones in Europe. He also became aware that the organic structures forming these limestones may have been totally destroyed.

Then Garwood (1913 a.b., 1914, 1916, 1924, 1931 a.b.) indicated that not only were some limestones formed mainly by algae, but also the stratigraphical value of these forms. He emphasised the great potential value of these fossils as index fossils especially with their wide geographical range and the distinct restrictions to definite geological periods. His examples included the following forms, Rhabdoporella, Mitcheldeania, Ortonella, Sphaerocodium, Solenopora and Girvanella (in the Girvanella Nodular band).

Since then, algae have become increasingly recognised as important rock builders (Glock 1923, Pia 1926, Maslov 1935, Johnson 1936, 1937 b, 1940, 1945, 1951, 1952, 1954, Anderson 1952), even where the organic structures have



broken down and only the fine calcite precipitation, from their life activities, remains (the 'algal dust' of Wood 1941 a). Thus various widespread calcite mudstones in the Carboniferous have been regarded by George (1954, 1956) as algal muds of the finest grades.

The value of fossil algae also in stratigraphy has been stressed amongst others by Pia (1935), Howell (1952) and Johnson (1943, 1945), the last mentioned indicating those groups of algae valueless in this respect except as indicators of environment, as they have persisted for long periods of time without any significant structural change.

Glock (1923, 1946) and Fenton and Fenton (1938) indicate that algae may be used as climatic indicators from the types found and the amount of reef consolidation undertaken by them.

#### IIb. LIMESTONE FORMATION AND CHEMICAL COMPOSITION

Skeats (1903) in a determination of the chemical compositions of limestones, found that Halimeda was an aragonite-former whereas calcite was formed by the activities of Corallines. He also realised that

Lithothamnium loses its structure comparatively easily so disintegrating into a fine calcite mud. This was followed by further work by Cullis (1904) on Funafuti atoll. Then Chapman and Mawson (1906) also emphasised the disintegration of Halimeda and other algae at depths in the rock and thallus breakdown has also been commented on by Geikie (1903), Howe (1932), Fenton and Fenton (1937), Hatch et al (1938), Johnson (1945) and Howell (1952).

Charke and Wheeler (1922) further showed that Lithothamnium had a high magnesium content, whereas in Halimeda it was almost absent. They also found that the magnesium content was highest in algae from warm regions and decreased in amount in those from cooler waters. These relationships have led several authors to comment on the possible significance of algae to dolomite formation (Blackwelder 1913, Jourdy 1914).

Fine grained limestones are regarded by some as having been formed by inorganic means, for example by the action of colloids on swamp water with a high calcium carbonate content (Boswell 1930), Carter and Beadle (1930), by evaporation and concentration (Vaughan 1917), by others, organic means (Bavendamm 1932, Black 1933 b, Hatch Rastall and Black 1938), the action of ammonifying bacteria in mangrove swamp regions

and aragonite mud formations in shoal regions later becoming lithified to calcite mudstones. Some of these mudstones though, are those in which George (1954, 1956) demonstrated the presence of large quantities of algal fragments and which he regarded as original algal muds.

Reis (1923) supposes that the ammonia from the algal decay would precipitate the calcium carbonate in the interspaces of spongy mass of the living algae. Bucher (1918) though, favoured an inorganic origin for oolites and spherulites, which in some cases is true (Kalkowsky 1908), but in others it would seem more probable that they resulted from the life activities of some organism (Wethered 1889, 1890 and algal 'ooids' of Kalkowsky 1908), even though Cayeux (1910) regarded oolites as being destroyed by parasitic forms of Girvanella, and Vaughan (1917) states that filamentous algae will bore into any calcium carbonate structure, such as an oolite, lying on the sea bottom. Jones (1925) indicates a method by which algal filaments become coated with minutely crystalline calcite. This he postulates is by the algae utilising the carbon dioxide in solution, so causing a local deficiency. This again lowers the solubility of the calcium carbonate in solution and causes a deposition around the filaments.

IIC. AIGAL PEBBLE FORMATION AND OTHER GROWTH FORMS

Barclay (1836) recognised algoid balls (aegrophila balls) forming in a lake in South Uist, and Clarke (1900) described in detail the conditions under which 'water biscuits' were being formed by a felted mass of fresh water algae influencing the lime precipitation. He also cites the then known examples.

Roddy in 1915, stressed the importance of the blue green algae in the formation of concretions. More detailed work on fresh water algal pebbles, oolites and reefs has been described by Bradley (1926, 1928) on different types of pebbles found in relation to various conditions in the Green River Formation, and Pollock (1918), Mawson (1929) on water biscuits formed in Australian lakes and their environment and marine algal balls by Dickinson (1933).

Wells (1942) however describes pseudo algal nodules occurring in the Greenfield dolomite which he considers in minute structure only to be lacking in algal characteristics.

Various other algal growth forms have been described by Rutherford (1929), Johnson (1937 a, 1946), Fenton and Fenton (1931, 1937, 1939) and Anderson (1950).

### IIId. FOSSIL ALGAL LIMESTONE DEPOSITS

The widespread occurrence throughout the geological periods since, and including the Precambrian, of the algal limestones has become increasingly recognised. Thus, these limestones are recorded from Precambrian of areas such as North America, (Rutherford 1929, Fenton 1931, Fenton and Fenton 1931, 1933, 1937), India (Rao 1949), Australia (Fairbridge 1950 b), Palaeozoic and Mesozoic deposits (Esturian series of Skye-Anderson 1948), to Tertiary and recent formations including the Eocene beds of the Salt Range, India (Rao and Rao 1939) and Oligocene of the Colorado (Johnson 1937a) the Permian of New Mexico (Johnson 1942) and the Cretaceous of South India (Rao 1942).

### III. THE RECOGNITION OF ALGAE AS REEF BUILDERS AND THEIR ECOLOGY.

Lister in 1891 found that calcareous algae together with corals to a lesser extent composed the main part of the terraces each side of Tonga Island. He assumed, however, that as corals were practically absent on the East side, the limestones were formed at the base of the coral reef.

Agassiz (1903) quoted Gardiner (1898) on Pacific Coral Reefs where Nullipores are prominent in reef building. Also Sherlock and Skeats (1903) found that in Fiji Lithothamnium and Polytrema ( a foraminifera) constituted the bulk of the rock, corals being subordinate to them. Lithothamnium was also known often in enormous quantities from Spitzbergen in the north to South Victoria Land in the south, and in the Indian Ocean they were important reef builders according to Foslie and Gardiner (1907), but in 1911 Vaughan defined a coral reef as a ridge predominantly composed of calcium carbonate mostly secreted by corals. In the same year however, Baumann described algae reefs from Bodensee.

The following year Howe (1912) gave a general resumé on reef builders and showed that previously corals had been over-estimated in their importance in reef building and suggested that the lime secreting plants might eventually be regarded as the most important type of reef builder.

Since 1917, the general ecology of reefs has been studied more as it was then realised that the constitution of reefs varied greatly in different zones (Vaughan 1917, Mayer 1918, 1924, Setchell 1926, Bramlette 1926, Pollock 1928 on fringing and fossil reefs of Oahu).

A later and more comprehensive definition of a reef structure has been given by Cumings (1932), who also gave examples of different kinds of algal rocks, this having since been modified by Wilson (1950), Ladd (1950), Ladd et al (1950), Lowenstam (1950),

IIIb.        THE ECOLOGY OF RECENT REEFS

Observations made by Howe in 1912 on the reefs of South Florida and the West Indies showed that some banks were made completely of calcareous plants, others completely of coral growths and yet others where the two intermingled. He also found that in the latter case the plants often overgrew and smothered the corals, also that these calcareous plants in Florida appeared to have a wider distribution both horizontally and vertically than corals. He realised though that their relative rates of growth must be known before their lime depositing activities could be compared.

Since 1930 there have been more detailed studies made on the ecology of recent reefs, Black (1930, 1933 a.b.), Hatch et al (1938) and Field (1928, 1931) also began a series of studies on the sedimentation and ecology of the Great Bahama Bank with its shelf lagoon.

In 1931 in observations on the structure and ecology of the reefs, Stephenson et al showed the Low Isles to have a ribbon reef, the outermost being algal. Pacific studies of the 'coral' reef ecology were increased by Umbgrove (1947) who noted the importance of Lithothamnium in coral reefs of the East Indies; the enormous oxygen consumption in reefs hence the need for well aerated waters, Yonge (1940) on coral and algal symbiosis in the Great Barrier Reef and Fairbridge (1950) on a survey of Recent and Pleistocene reefs of Australia.

The relationships between organic growths and sedimentation on Bikini Atoll and other Marshall Islands has attracted attention and various ecological papers have been published relating the function of calcareous algae to other organic growths and to sedimentation in or near reefs. (Ladd 1944, 1948, 1950; Tracey 1948, 1950; Tracey et al 1948; Emery 1948; Wilson 1950; Lowenstam 1950; Emery et al 1954; Johnson 1954 and Bryan, Emery and Wells 1953).

These have shown the very distinct zonation parallel to the reef front and the importance of algae in reef protection building and extension and have also given an



indication of the areas of most and least active sedimentation. Both Wilson (1950) and Ladd (1950) in their definitions of reefs stated that protection from wave action is often partly supplied by a Lithothamnium ridge in most Present reefs and that loose clastic material generally becomes bound together by algae, corals or foraminifera.

More general botanical problems have been discussed by Taylor (1950), Feldmann (1951), Drew (1951), and general palaeoecological problems by Fenton and Fenton (1928, 1935) amongst many others.

### IIIc. FOSSIL REEFS

The occurrence of reefs throughout the geological column from different regions of the World have been given by several authors, for example Twenhofel (1950), Vaughan (1911, 1917), Cumings (1932), Goldring (1938), Anderson (1950). Twenhofel presumes that where a reef contained few traceable fossils, it was probably of algal construction as these readily break down to show no evidence of organic structures. Thus, the Precambrian and Cambrian reefs of North America

(Wieland 1914, Fenton and Fenton 1933 et seq, Goldring 1938), many of which appear to have been algal, are indicated by various 'growth forms' (Anderson 1950); Fenton and Fenton 1939; Rutherford 1929; Walcott 1914; Fairbridge 1950 a.b).

Comparisons of fossil reefs with those in process of formation have been made on the Capitan Barrier Reef of Texas and New Mexico (Adams and Frenzel 1950) where the reef wall and fore reef have been built mainly by calcareous algae. In various other Palaeozoic upper reefs of North America (Johnson 1937, 1940, 1942, Fenton and Fenton 1939, Shrock and Twenhofel 1953) and of Russia (Levet 1950), the importance of algae is recognised in reef building and the associated lagoonal phase.

Bond (1950), suggested that the mudstones present in the Carboniferous Reef Limestone of Northern England are the lagoonal facies behind the reef proper and were precipitated either by algae or by direct chemical action. Pringle (1946) demonstrated the presence of Ortonella in probable reefs of S<sub>1</sub> age, and Prentice (1951) found that algae were present in at least some of the reef knolls.

George (1954, 1956) in an investigation of the calcite mudstones of PreSeminular age in South Wales found that they

were mostly algal in origin, thus lending support to the hypothesis of algal precipitation in some of the reef lagoonal facies.

### IIIId. SILURIAN REEFS

These have been recorded from most parts of the World (Twenhofel 1950) but in many cases there has been doubt as to the actual reef builders. In North America many are problematical reef structures (Fenton and Fenton 1931, Shrock 1939, Lowenstam 1950, Twenhofel 1950), Shrock recognised algae to be amongst the chief builders of the Wisconsin reefs, and Lowenstam (1950) described a frame building Stromactis network from the Niagaran Reefs of the Great Lake Area which he ascribes to algal activity. He contrasted Silurian reefs from Present ones by an absence of boulders, due to a lack of reef borers during the Silurian, and the absence of a Lithothamnium type of ridge also characteristic of Recent reefs.

Rock forming Solenopora is recorded from Japan (Yabe 1952).

In the great Baltic development of reefs, Kiaer (1908) in his description of them in South Norway does not mention any algae at all in the Wenlock stage, but Silurian algae

were not recognised there until Rothpletz (1891, 1908, 1913) and M $\ddot{u}$ nthe (1910) described various types of Solenopora and Sphaerocodium from Gotland and mentioned by H $\ddot{b}$ eg (1932) Kiaer (1932) and H $\ddot{o}$ ltedahl (1934) for Norway. Twenhofel (1916 a.b) recorded Sphaerocodium in Gotland reefs but did not mention algae in the Silurian of Esthonia. Hadding (1941, 1950), made various detailed studies of reefs in Sweden, their palaeoecology included, and recognised the importance of calcareous algae in certain areas, and composition of limestones near reefs and their variation away from them.

In Britain, much doubt has been placed in the past upon Silurian deposits here containing any true reefs. Before Garwood and Goodyear (1918 and Garwood in Evans and Stubblefield 1929) recognised the Woolhope Limestone of Old Radnor and Nash Scar to be an algal limestone, possibly a reef limestone, the algal nodules were regarded either as the result of metamorphism (Murchison 1854) or inorganic concretions (Calloway 1900).

North (1930) regarded the nodular 'Ballstones' of Wenlock Edge to be due to colloidal effects and not reef material and previously Lyell (1878) thought them

concretionary, but Hill, Butler, Oakley and Arkell (1936) realised Wenlock Edge limestone had been influenced by algal growths, although there appear to have been no ~~algal~~ distinct/<sup>algal</sup> records made. They described the 'ballstones' as "a reef rock formed in situ at a focus of intense activity of coral, stromatoporoid and algal growth". The Crog Balls found at Dudley were regarded by them as similar in nature to the Ballstones, their matrix possibly forming by the decomposition of masses of soft algae resulting in a chemical precipitate. Stamp (1918) suggests that the nodular concretionary stones in the Temeside shales were sometimes regarded as algal in origin.

Whittard (1952) recognises an algal limestone present as one of the different lithologies in the Wenlock Limestone of South Shropshire. May Hill is also known to contain algal limestones from Wethered's (1893, 1890) classic work, but reefs are not recorded.

#### IV. PALAEOZOIC ALGAL GENERA

Since about 1900 when fossil algae became more widely recognised, there has been a gradual discovery of

additional types in the Palaeozoic rocks. Descriptions of these types given by Pia (1927, 1937), Derville (1931, Johnson (1951 b). As well as Girvanella, Sphaerocodium (vide Rothpletzella Wood 1948), among the filamentous there are also forms such as Ortonella Bevocastria, etc. (Garwood 1914, 1931 a.b), Garwoodia (Wood 1941 b), Calcifolium (Johnson (1958).

The Corallines in Britain are mostly represented by Solenopora spp., whereas the Dasycladaceae are represented by Rhabdoporella. (Lewis 1937), Koninckopora, Coelosporella (Wood 1940, 1942), Spongiostromids, palaeozoic algal growths described by Garwood (1914), Anderson (1950).

Other algae and probable algae of more doubtful affinities, some non-calcareous, are Nematothallus (Lang (1936), Mastopora (Curry and Edwards 1942) and Pachythea (Salter 1851, Kidston and Lang 1924, Lang 1937).

Many inorganic and doubtful specimens have been labelled as fucoids but no reliance is placed on most of these identifications.

#### V. BRITISH SILURIAN ALGAL RECORDS

Wethered (1890, 1893) was the first to find Girvanella

in British Silurian rocks when he described G. problematica from the Wenlock Limestone of May Hill, Gloucestershire, Purley, W. Malvern and Ledbury. He found that there was more variety of algal material at May Hill and Purley than at Ledbury. Crosfield and Johnson (1914) noted the presence of Girvanella as small fragments in the Crog Balls of Wren's Nest, Dudley. "Girvanella" conferta had been recorded by Chapman from there in 1907. There appear to be no records for Wenlock Edge and no further information is in Butler(1939) paper on Dudley. Garwood (1931) asserts the Girvanella described by Wethered from May Hill to be 'Sphaerocodium' munthei. He also records Sphaerocodium gotlandica from Old Radnor and Nash Scar with the genus Solenopora gracilis. Solenopora gotlandica was found as fully preserved specimens by Whittard and Smith (1944) from the Wenlock Limestone of the Tortworth inlier of Gloucestershire, although Reid and Reynolds (1908) do not mention them.

No algae have been mentioned in the fossil lists of Gardiner (1927) and Pocock (1930) for the Woolhope Limestone of the Woolhope area, although Garwood (1931 a) mentions than unidentified Solenopora sp. have been found in this

district, but does not specify the actual limestone.

No algae are mentioned from the Aymestry of the main outcrop (Alexander 1936).

Parka and Mastopora have been found in the Llandoverly beds as well as the Ordovician of the Girvan district (Salter 1851), and also in Shelve district, Shropshire.

Another doubtful form, usually in carbonised or silicified state, Pachythea; (Hooker 1889, Barber 1889, 1891, 1892), has been recorded rarely in Wenlock beds but fairly common in Aymestry and Downtonian beds in various localities in the Welsh Border District. (Strickland 1853, Kidston and Lang 1924, Robertson 1927), Lang 1937, 1945).

Nematothallus has been recorded from the Wenlock of Tymawr Quarry, Cardiff (Barber 1889, 1891; Sollers 1879; Strahan 1910) and Corwen, North Wales, the Pen-y-glog Grits, and Prototaxites, another doubtful form has also been found in the Wenlockian and Ludlovian, as well as higher horizons ('Nematophycus' Barber 1892, Lang 1945).



## MATERIALS AND METHODS

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Specimens were collected from various quarries and other exposures of Silurian beds of the Welsh Border. The various facies were examined, noting the general fauna present in each, and the relationship to them of the algae, if any and if visible in the field. Thin specimens were then prepared from the rock specimens and these were examined as most of the algae found during this investigation could not be detected in hand specimens.

The investigation extended over an area to include material collected from Shropshire, Herefordshire, Radnorshire, Worcestershire and Gloucestershire. The Woolhope Limestone material was obtained from Radnorshire, Herefordshire and Gloucestershire. The Wenlock Limestone from Shropshire, Herefordshire, Gloucestershire and Worcestershire and the Aymestry Limestone from Shropshire and Herefordshire.

Grateful acknowledgment is here due to Dr. S.H.Straw who, at the beginning of the investigation, provided some bryozoan reef specimens from Old Radnor, which thus led to further collecting and investigating of this district, and to Professor P. Allen, who gave specimens of freshwater algal nodules taken from the R. Pang near Pangbourne,

Berkshire, which assisted in the comparisons made with present day forms of filamentous algae. Comparisons made with specimens from Gotland were those kindly given by Dr. Straw and V.S. Colter. Other living and fossil algae were collected and examined from various sources, including Lithothamnion from Douglas/<sup>Bay</sup> Isle of Man.

### Methods of Sampling

Specimens were collected from the different facies present in each exposure. Specimens were also taken at different levels vertically from the same facies to find if there was any noticeable change over a known vertical distance. Likewise, rock specimens were collected from the same bedding plane, wherever possible, at measured distances laterally. Particular attention was directed to those beds in the neighbourhood of reef or reef-like material where changes were likely to be rapid.

### Methods of Examination

It was found that thin ground sections were essential for the study and examination of the algae. During the investigation 265 slides were examined, of which 140 were prepared by J. Fowler (Sheffield) and the rest by the writer.

Cellulose peels were tried as a substitute for the

thin ground sections, but acids used in etching were often observed to attack the algal parts before the matrix and the algae were found to be completely calcareous.

For comparative work, living forms of calcareous algae were wholly or partially decalcified by either the use of dilute hydrochloric acid or immersion in Pérényi's solution (Mason 1953). The filaments or thallus remaining were then examined microscopically.

#### Microscopic Examination

Measurements were made on the algae by using camera lucida drawings mostly at magnifications of x330, x350 and x600. The accuracy of these drawings by this method was checked by direct measurements from photographs mostly x215 and x150, and also by direct measurement using an eyepiece with a micrometer scale. The camera lucida drawings were found to be more satisfactory than this last method.

With direct measurements from photographs only one focal plane is observed, but with the camera lucida there is no such restriction, so the best focus for each determination can be made.

The method used during the investigation to allow for the standard error in measurement, was to measure at least

five tubes per algal group so as to give the range of variation within each group including the standard error. The probable mean was estimated for each group by calculations based on frequency of each size. Graphs and/or histograms were drawn for the results of each group, for different species, localities, etc. to give comparisons of means and allow for complete variation in size, including error. With the more indistinct groups, the variation is greater, as the error is increased, hence on a histogram or graph the range would appear larger than that for many distinct groups (of even size). For a group with all the tubes identical in width, only one measurement was recorded on the graph and not five (or more) as the size comparisons are regarded as between different groups and not between every tube in every group, etc.

Wood (1957) indicates the large discrepancies in the quoted tube diameters for the type species of Girvanella and so restricts measurements to transverse sections of tubes as both the wall thickness of tube is variable and the thickness of slide is often greater than the tube diameter. During this investigation however, longitudinal sections were measured as with careful focussing the true

diameter can be ascertained. The results of these measurements were also compared with measurements made of those tubes seen in cross section. With fine filaments however, it was found almost impossible to distinguish a true transverse section from an oblique view especially where the calcite wall was thick.

Again, Wood (1957) demonstrates the variability of the thickness of the outer diameter of these algal tubes due to varying amounts of calcite dust and so uses the internal diameter measurements as seen in cross section as being more reliable. The question then arises as to whether the measured internal diameter does represent the true diameter of the algal filament. In "transverse" views often the tubes are curved into the plane of section so that the fine granular calcite in "algal dust" (Wood 1941a) appears to smudge over the "lumen" of clear calcite so that the apparent width of clear calcite is less than the true width of the original filament. The reverse is also true when the section taken is slightly oblique and/or the filament curves away. Thus a fairly high magnification is needed to ascertain whether a tube has a perfectly circular cross section and below 5  $\mu$  in diameter this method is much too inaccurate. Hence, transverse measurements become

increasingly inaccurate with decrease in tube size.

By using high magnifications, the longitudinal sections can yield more accurate results than transverse ones especially with the fine diameter groups, as here it is possible to determine a true longitudinal view by the length of tube in focus, hence error by obliqueness of section is eradicated. The true circumference of the alga is regarded to be where the calcite dust is most dense, i.e. darkest, as it is considered likeliest that as the calcite dust was formed as a life process of the living alga, then the most concentrated area of dust would lie against the living cell wall, and the concentration decreasing with distance away from the living wall. Hence a clear section of tube should show clear calcite 'lumen' where the original alga was present, then the darkest algal dust gradually becoming lighter, and then often grading into the surrounding calcite matrix. (fig. 1)

In those instances where the algal tubes are seen lengthwise, but not in section, as in the very fine filamentous groups or more often in a thicker slide, this method can still be used. The darkest limits are again measured although here there is the added difficulty of the dust obscuring the centre of the tube. (fig. 1) The

algal dust should appear darkest at the side limits of the original wall because here the focussing is on the greatest thickness of dust, whereas elsewhere it is only wall thickness of dust (or double thickness in a very fine diameter of tube where the complete tube is seen in one focus).

It was found during the investigation that often longitudinal sections could not be measured from a thallus formation, such as Solenopora with any accuracy, especially from either a photograph or a section thinner than the tube diameter. If thicker, careful focussing was needed to find the widest extent of the tube rendered difficult by the overlap of the tubes. If other measurements are taken, variation cannot be stated but maximum diameter measured will be within the variation limits for a "true" diameter. (fig. 1).

Crushing of an algal tube would not be likely to occur before the death of the alga, due to its internal pressure and then flattening appears to occur only when tubes are adherent to each other and nearly always in encrusting forms where the filaments are in a felted mass. When crushing has occurred, the clarity of the wall disappears thus giving an indication that any measurements taken are of doubtful value.

Secondary diagenesis of the calcite leads to annihilation

of wall structure over localised areas, so that the apparent width of filament may be at least double that of its real width. This may also lead to connections being observed between tubes where there were none. For example, connections seen between Wetheredella and Rothpletzella in the "Sphaerocodium" of Rothpletz. Again there is the possibility that one form may be a perforating alga (Drew 1954), so Rothpletzella under certain conditions may have been this type of alga boring into the tubes of Wetheredella, thus making it appear to be one organism.

All instances of the joining of different sized tubes cannot be easily referred to secondary recrystallisation, for example, the two main sizes of beaded filaments occurring in the Reef Limestone of Gotland. Here a number of fine threads apparently coalesce at their ends, first into pairs, then all fuse together, thus suggesting a primary origin. No end walls are visible which suggests a possible intimate association between them and the wider beaded tubes. (fig. 39).



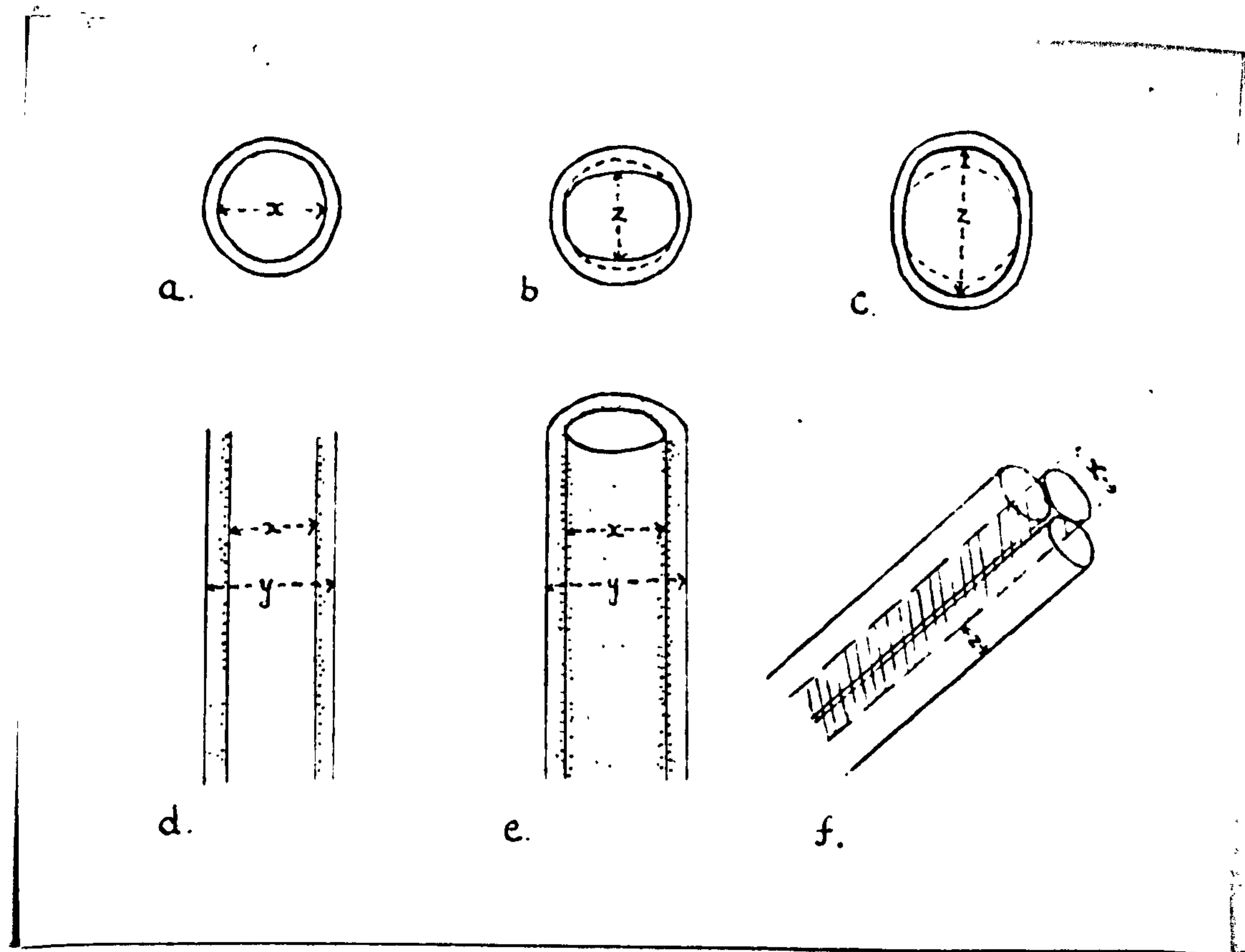


Fig. 1.

a = T.S.  
 b = tube curving towards view  
 c = tube bending away from view  
 d = L.S. showing concentration of algal dust against position of original wall and clear calcite of tube  
 f = Thallus formation - e.g. Solenopora - a few tubes to show difficulty of measurement.

x = real internal diameter  
 y = external diameter  
 z = apparent diameter.

ALGAL FORMS FOUND DURING INVESTIGATION

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Table I

Localities from which material has been collected  
and investigated for Silurian calcareous algae

A. WOOLHOPE LIMESTONE

Old Radnor	(O.R.)	Radnorshire
Nash Scar	(N.S.)	Herefordshire
Woolhope	(W.H.)	"
Mordiford	(M.F.)	"

B. WENLOCK LIMESTONE

Wenlock Edge (W.E.) Shropshire  
Wren's Nest, Dudley (D.U.) Worcestershire  
Woolhope (W.H.) Herefordshire  
Sollers' Hope (S.H.) "  
Fownhope (F.H.) "  
Ledbury (L.B.) "  
Longhope (May Hill inlier) (M.H.)  
Gloucestershire  
Park Wood, W.Malverns (M.V.) Worcestershire

C. AYMESTRY LIMESTONE AND LUDLOVIAN DEPOSITS

Aymestrey  
Norton Camp and View Edge, Craven Arms (C.A.)  
Shropshire  
Marcle Hill, Woolhope (W.H.)  
Ledbury (L.B.) Herefordshire  
Ludlow (L.U.)

Table II

Previous records of calcareous algae known to be present in the Silurian of the Welsh Border

A. WOOLHOPE LIMESTONE

<u>alga</u>	<u>Localities</u>	<u>Author and date</u>
<u>Rothpletzella gotlandica</u> Rothpletz sp.	Old Radnor	Garwood and Goodyear 1918
(Specimens in Geol. Survey Museum, from Whitfield, Glos.)	'England'	Wood 1948
<u>Solenopora gracilis</u> Garwood	Old Radnor Nash Scar	Garwood and Goodyear 1918

B. WENLOCK LIMESTONE

<u>Girvanella problematica</u> Nicholson and Etheridge	May Hill	Etheridge 1890
<u>Girvanella fragments</u>	Dudley	Crosfield & Johnston 1914
<u>Rothpletzella gotlandica</u>	England and May Hill	Wood 1948
(Specimens deposited in Geol. Survey Museum, May Hill, Wethered 1893 redescribed Wood 1948).		
<u>Rothpletzella conferta</u> Chapman sp. ) as G. conferta )	Dudley	Chapman 1907
<u>Solenopora gotlandica</u> Rothpletz	Tortworth	Whittard 1944

C. AYMESTRY LIMESTONE AND LUDLOVIAN

? Chaetocladus - unpublished records Aymestrey Lawson  
(specimens deposited in British Museum (N.H.))

D. GENERAL

Algal limestone present as a lithological group Wen.Lst.	S. Shropshire	Whittard 1952
Postulation that Ballstone and Crog Balls were influenced by algal activity	Wenlock Edge Dudley	Hill et al 1936
<u>Ortonella rigida</u> and <u>Rhabdoporella intermedia</u>	Meiford Montgomery	Lewis 1937

Table III

Types of calcareous algae found during the present investigation

A. WOOLHOPE LIMESTONE

<u>Alga</u>	<u>Localities</u> <sup>3</sup>			
	<u>O.R</u>	<u>N.S</u>	<u>W.H</u>	<u>M.F</u>
Girvanella problematica	x <sup>2</sup>		x <sup>2</sup>	x
G. fragila n.sp.				x
G. pusilla n.sp.	x		x	x
G. proluxa n.sp.				x
G. media n.sp.			x	x
G. ramosa n.sp.				x
G. effusa n.sp.				x
Rothpletzella gotlandica (large var.)	x <sup>1</sup>	x		
R. conferta	x <sup>1</sup>			
Rhabdoporella sp.			x	x
Solenopora gracilis	x	x		
S. compacta	x			
Incertae sedis	x			

KEY x = recorded

1 Recorded previously in M.Sc thesis (1955)

2 ditto ditto as Girvanella but no specific forms.

3 See table I.

Table III continued.

B. WENLOCK LIMESTONE

<u>Alga</u>	<u>Localities</u>							
	W.E	D.U	F.H	S.H + W.H	M.H	L.B	M.V	
Girvanella								
problematica	x2	x2	x	x	x	x	x	
G?problematica								
var lumbricalis		x						
G. pusilla	x	x	x	x	x	x	x	
G. proluxa	x		x					
G. sarmenta n.sp.	x		x					
G. media	x		x		x			
G. incompta n.sp.	x	x	x					
G. ramosa	x		x					
G. effusa	x	x						
Rothpletzella								
gotlandica and								
large var.	x1	x1	x	x	x		x	
R. conferta	x1	x1	x					
R. sp.		x1	x			(x)4		
Rhabdoporella sp.			x					
Obscure								
? dasycladaceae	x			x	x			
S. cf. gracilis	x1							
S. compacta	x1							
S. gotlandica	x1							
Incertae sedis	x1							

4 - Ledbury probably derived Wenlock Limestone specimen.

C. AYMESTRY LIMESTONE AND THE MORE CALCAREOUS FACIES  
OF THE LUDLOVIAN.

<u>Alga</u>	<u>Localities</u>				
	C.A.	AY.	LU.	WH.	L.B
Girvanella problematica	x		x		
G. pusilla	x				
G. ramosa			x		
G. cf ramosa	x				
Girvanella sp. indet.		x			x
Obscure dasycladaceous fragments	x				
Incertae sedis	x				

The range of each algal species is shown in the following table (IV), the localities again being represented by initials (table I). New horizons and new British records are also indicated.

Table IV.

Stratigraphical range of Algal Species

<u>Alga</u>	<u>Woolhope</u>	<u>Wenlock</u>	<u>Aymestry- Ludlovian</u>
Girvanella problematica and large var 1.2		most districts investigated	
G. fragila 3	M.F.	-	-
G. pusilla 3		most districts investigated	
G. proluxa 3	M.F	W.E F.H	-
G. sarmenta 3	-	W.E F.H	-
G. media 3	W.H M.F	W.E F.H	-
G. incompta 3	-	W.E DU F.H	-
G. ramosa 3	M.F	W.E F.H	LU
G. effusa 3	M.F	W.E DU	-
Girvanella indet.			C.A W.H
Rothpletzella gotland- ica 1 (and var)	O.R W.S	Most except L.B	-
R. conferta 1 2	O.R	W.E DU F.H	-
R. sp. 3	-	DU F.H (L.B)	-
Rhabdoporella sp. 1 2	W.H M.F	F.H S.H	-
Dasycladaceous frag- ments indet. 1		W.E	? C.A
Solenopora gracilis 1	O.R N.S	poss W.E	
S. compacta 1 4	O.R	W.E	-
S. gotlandica 1	-	W.E	
'? Chaetocladus' 5	-	-	AY.
Incertae sedis	O.R	W.E DU	C.A

KEY

1. Known horizontal range extended
2. Known vertical range extended
3. New species
4. New horizon in Britain
5. Not found during investigation.

## SYSTEMATIC DESCRIPTIONS

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### I. FILAMENTOUS FORMS

GIRVANELLA Nicholson and Etheridge (1878)

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Figs. 2-16, 18-23.

#### Establishment of genus

Nicholson and Etheridge (1878) first described the genus from the Ordovician of Girvan and as they regarded it as an anomalous organism, possibly an arenaceous foraminifera, they ascribed the name Girvanella problematica to their type species. In his redescription of the species, Nicholson (1888) compared it with the recent foraminifera Syringamina fragillissima.

In 1885, Seely ascribed several species of Strephochetus to calcareous sponges from North America, but in 1887 Hinde indicated that the Strephochetus of Seely was the same as Girvanella, as was also Siphonema described by Bornemann also in 1887, as of possible algal origin from the Cambrian of the Island of Sardinia.

Wethered (1889, 1890, 1891, 1893) recorded several different forms of Girvanella in Silurian, Devonian and

Jurassic rocks from various British localities, and assigned them to rhizopods. Hicks (discussion in Wethered 1892) suggested that the tubules might be related to Serpulae, but Hinde (discussion in Wethered 1890) had previously rejected this view on the basis that the tube size of Girvanella was too small for serpulae to inhabit.

In 1891, Rothpletz noticed dichotomous branching was a character of some of his specimens of Girvanella, hence he removed the genus from rhizopods to the calcareous algae and provisionally placed it in the Codiaceae. Wethered by 1893, also concluded that the Girvanellas were of plant origin.

Dawson 1897, still referred Girvanella to protozoa and Seward 1898 assumed its position as still uncertain although quite possibly algal. Since then Girvanella has been regarded as algal, Chapman (1907), Rothpletz (1908, 1913), Cayeux (1910, 1930), Garwood (1913 a.b, 1914, 1924, 1931), Pia (1927, 1937), and is now generally accepted as such. Many authors place it in the Myxophyceae (Cyanophyceae), stating that it might have belonged to Chlorophyceae and group it under the uncertain Porostromata (Johnson 1946 b and Fenton 1946). This requires some



modification in view of septation of some filaments (see later). Wood (1957) in his redescription of the type species does not classify the genus and Fritsch (1948) also regards its position as uncertain.

Description of genus (Historical)

Type species Girvanella problematica Nicholson and Etheridge 1878.

Nicholson and Etheridge (1878) in the description of the type species Girvanella problematica stated that the nodules were composed of "microscopic tubuli with arenaceous or calcareous walls, flexuous or contorted, circular in section, forming loosely compacted masses. The tubes are apparently simple cylinders, without perforations in their sides and destitute of internal partitions or other structures of similar kind". The tube diameters were 10 $\mu$  and 18 $\mu$ .

*Handwritten note:*  
K. ...  
... ..

Later descriptions (Wethered 1889, 1890, 1891), Cayeux (1910), have shown the frequent association of Girvanella with oolites, and new species have been formed depending on whether it was an encrusting and a non-encrusting form. Other divisions have been made on diameter, arrangement, amount of branching, convolutions and length of the tubes. The wall diameter has also been

studied, but this like the other features is variable.

The genus has also been shown to have participated in composite growths as in Mitcheldeania gregaria found by Wood (1941 b), to consist of three separate algal genera. This can be paralleled with composite associations found in present day algae.

Chapman (1907) has recorded only very doubtful young stages of Girvanella, and there appear to be no published records of any reproductive organs. This apparent rarity can be explained on the basis that the walls of fine calcite are the result of precipitation outside the original walls of the Girvanella. This also accounts for the rarity of observations on the presence of cross walls as these appear to occur only in the better preserved specimens. Published records of these are from Jurassic (G. symplocoidea (Frèmy and Dangeard 1935), Carboniferous G. ducii (Maslov 1935) and the type species from the Ordovician G. problematica Wood (1957).

Septation in the tubes, is one of the features not observed by the original authors of the genus, and certainly it does not tally with "destitute of internal partitions", hence the genus description requires some modification, as septation of tubes is not due to the presence of another genus, but a case of better preservation in at least the

Silurian specimens found during this investigation, and appears to be also in the published accounts of the Girvanella. The presence of septa does not necessarily remove Girvanella from the Myxophyceae, of which it has often been regarded as a probable member, usually on the basis that blue-green algae are the most frequent types forming present day calcareous algal pebbles. As however, members of the Chlorophyceae also form algal balls and participate together with several genera of blue-greens to form algal pebbles, some Girvanellas could equally well be the ancestors of this class. On the other hand, as the classification of algae rests on characters not seen in fossil state, Girvanella and other closely similar forms might not belong to any order in existence today.

Cayeux (1910) expressed a belief that Girvanella was a boring organism, but generally this view has not been held (Wood 1957), except the latter author found a Girvanella thread apparently boring a Saccaminopsis test. This is paralleled by a red algae by the Conchoelis-stage of Porphyra boring into shells (Drew 1954).

Thus, Girvanella could quite possibly be a fossil member of the Myxophyceae (at least), but it was not necessarily such.

## Horizons and Localities

Previous Silurian records and new records for this genus are appended in an earlier table. Specimens of this genus have now been found during this investigation from the Woolhope, Wenlock and Aymestry Limestones and Whitcliffe Beds, thus both increasing the range of localities from which it was found and the number of beds: especial mention are those of the Aymestry group.

## General Remarks

From observations made on the Silurian specimens of Girvanella, it was found that they could only be detected in thin section, and were not visible in hand specimens. Nothing was found in the field comparable to the Girvanella Nodular Band in the Carboniferous Limestone.

All filaments examined had the dark finely granular calcite 'dust' wall, which was occasionally iron stained and usually enclosed (when visible) the inner tube of clear calcite crystals. Iron ore aggregations (some of pyrite) were found in some tubes of some of the groups. (fig. 21).

The mode of growth was found to be very variable (see later section on division into species), and the groups investigated varied from parallel bunches of filaments

through to highly curved irregular types; from a loose arrangement to adherent form; from no branching to highly branched type, etc.; from free-living, possibly floating to the attached forms, encrusting forms and those types associating in composite growth forms with other genera of algae.

The size range for the Silurian members of the genus was observed to be from 2 $\mu$  to 31 $\mu$ .

Both at Fownhope and Mordiford, Girvanella was found showing septation of the filaments of different diameter size groups (see figs. 3,4,18,20). Also it was found in one group from Wenlock Edge (W.E.3). These appear to be the first Silurian records of septation. In the clearest examples, i.e. usually the wide-tube forms which were easier to examine, the inner part of the granular wall was found to curve inwards at the line of septation of the tube, the 'outer' diameter remaining unaffected, thus showing the 'inner' diameter to be a more accurate indication of the original size of the organism. The evenness of the spacing of septa, where present, further indicates cell lengths, and this is enhanced by the fact that the cross walls are of the

same fine granular calcite as the walls surrounding the tubes, and are not artefacts due to calcite cleavages, etc.

As the tubes with septa, perhaps exhibited regularly over part of their length only, or most often in patches, are found in the same slides as other groups without any, but identical in all other respects, it is regarded as an indication of better preservation, and absence of them does not mean the tubes were coenocytic in the first place.

The absence in published records of any definite reproductive organs may also be a result of indifferent preservation. Another feature leading to the noted absence may be that the main method was by fragmentation of a filament.

A possible mode of reproduction may have been by the formation of heterocysts - a possible enlargement of the walls and a general rounding in one part of a septate filament (as shown in fig. 4). This did not appear to be a branch cut across by the plane of sectioning, as this would show fracturing of the clear calcite inside. It was oval and appeared to be a composite part of the filament, rather than a protruberance emerging from it.

No merging of tubes of one size into another was

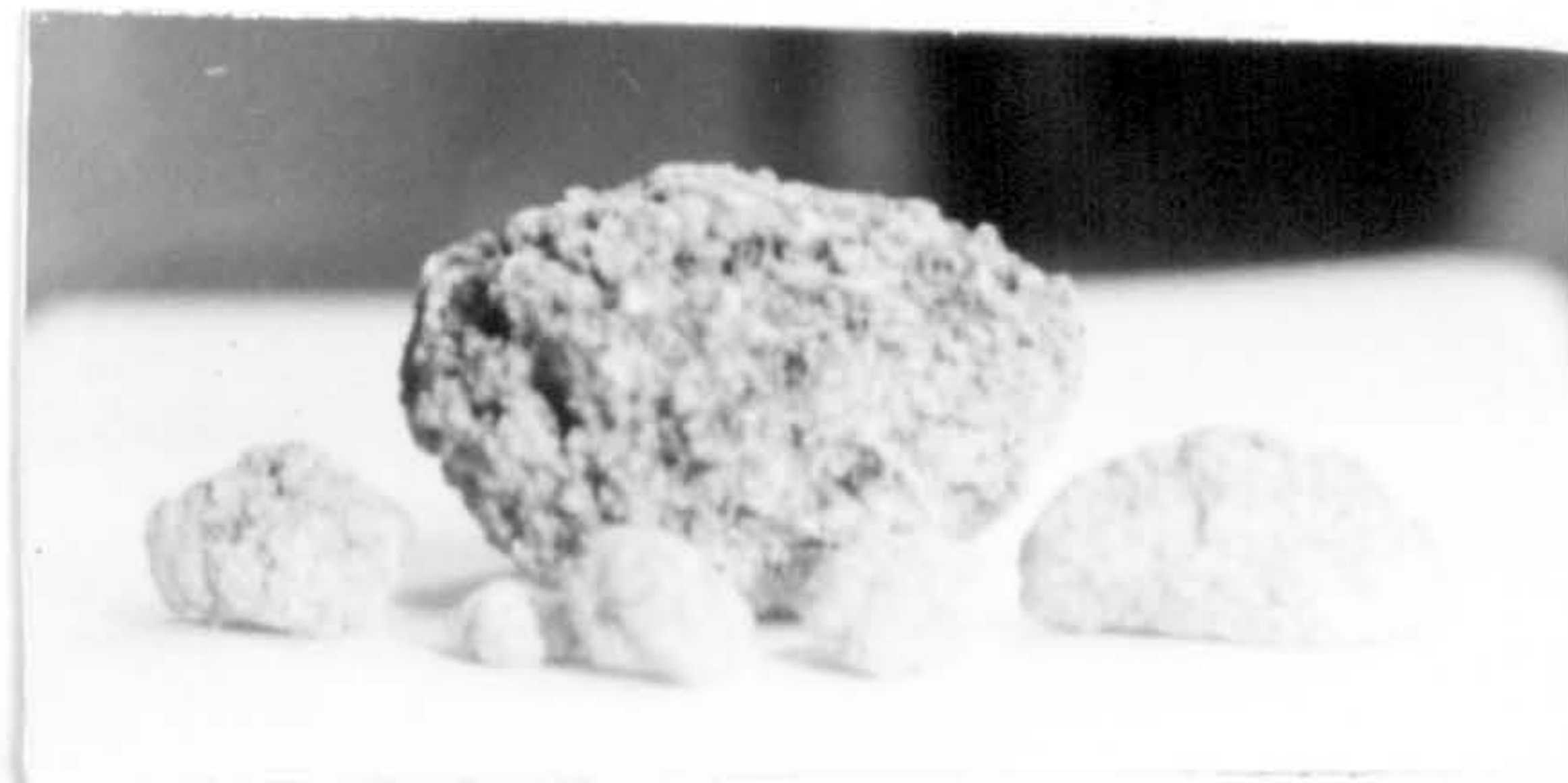


Fig.2. Present day calcareous algal balls from R. Pang.  
x c.  $\frac{1}{4}$ .

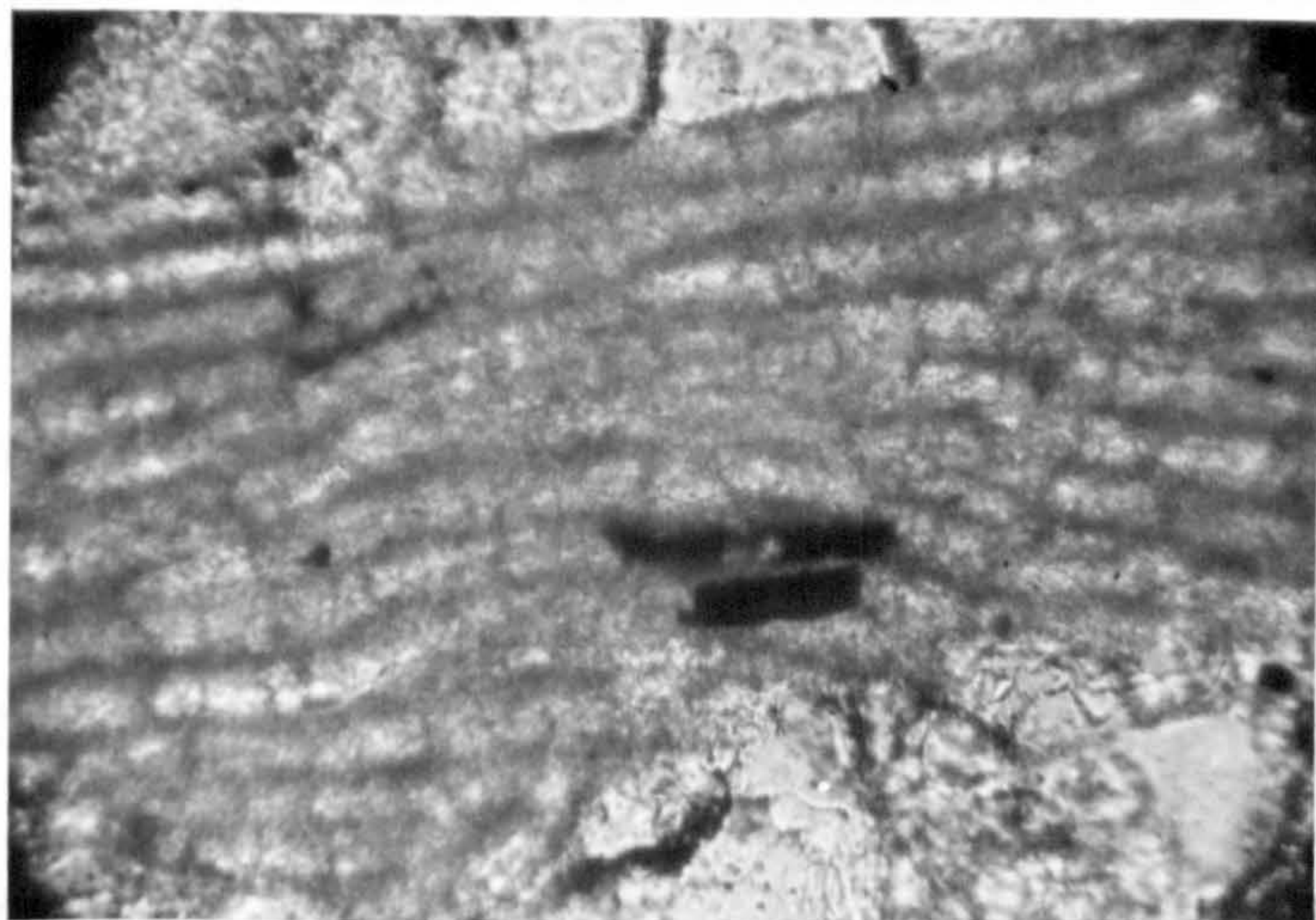


Fig.3. Girvanella proluxa, Woolhope Limestone, Mordiford,  
showing septation of tubes. x 215.

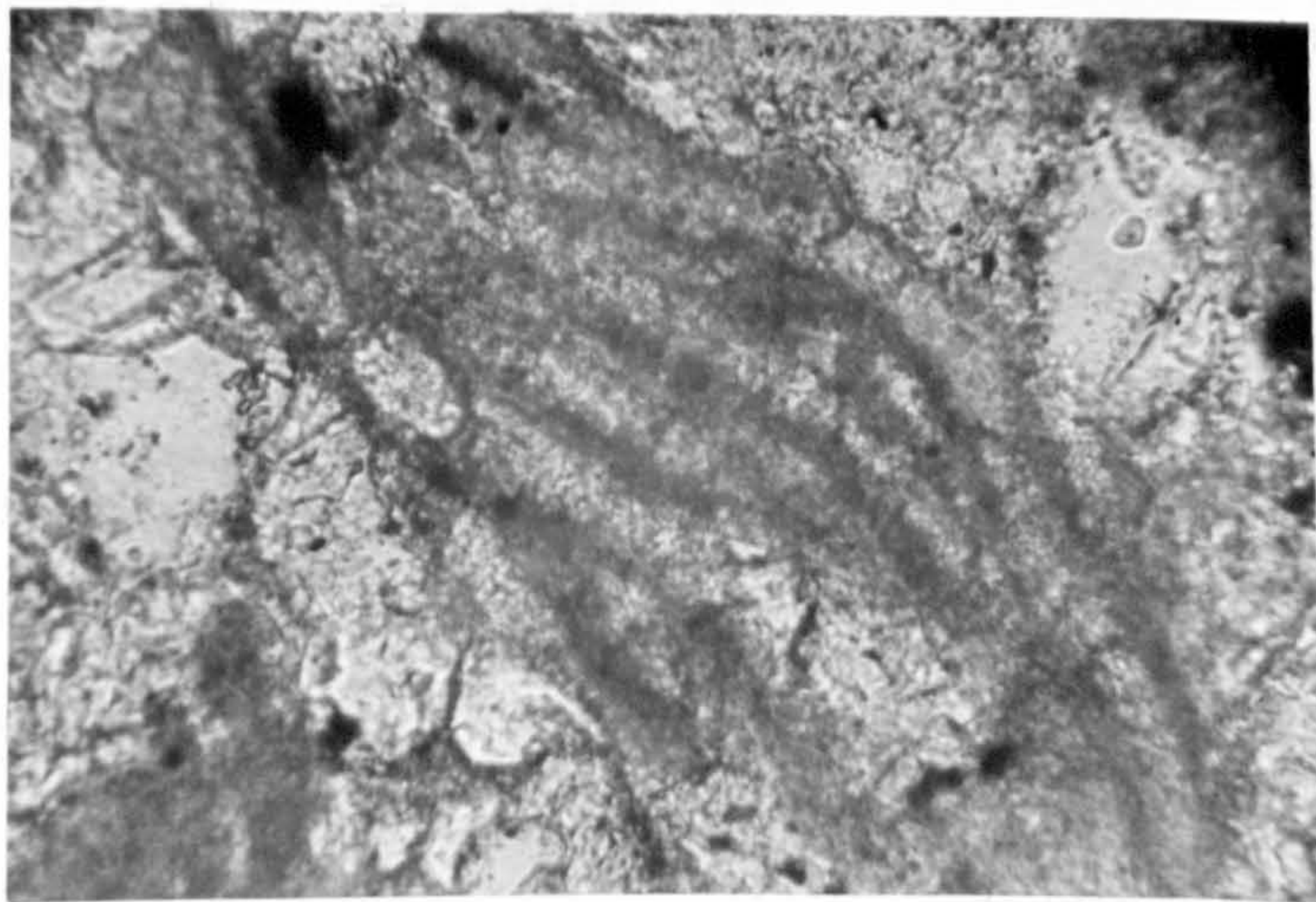


Fig.4. Girvanella, showing septation and possible  
heterocyst. Woolhope Limestone, Mordiford.  
x 215.

observed except in a few very obscure cases where the apparent merging was due to indistinctness of the wall.

The close filaments along the growth lines of stromatoporoids and corals is probably indicative of first more abundant growth of one form, then the other smothering it, etc. (fig. 17).

Growth forms indicate the close association of several algae, in which Girvanella spp. occasionally participate (see section on Rothpletzella). Small growth forms were found mostly at Dudley (figs. 84, 85), these being composed of Rothpletzella sp. and a fine filamentous type of Girvanella. These on a small scale can be compared with the associations of algae forming calcareous algal pebbles in streams and lakes at the present day (fig. 2). The loose interweaving of filaments and similar shape of colonies is very similar.

Quantitative Methods used for the separation of the  
Silurian Girvanella into species and varieties.

The most obvious method of dividing all the groups of Girvanella investigated was found to be by the measurement of their filament diameters (see materials and



method). In the majority of cases, at least five measurements were made from each group, all obviously crushed, partly hidden or obscured filaments being rejected. The aim was to give the range in diameter of filaments of a particular group, to reduce any error made in measurement, and to give a better indication of the most frequent size occurring within the diameter range of a group.

The results of these group measurements, slides made from specimens obtained mostly from the Woolhope, Wenlock and Aymestry limestones, taken from various localities, at differing horizons at each locality, and at the same horizon at different points laterally, were then either plotted on graphs or histograms. From these the most frequent diameter range and mean value for the filaments was obtained.

Some histograms (see end) and graphs showed one peak, which could mean a single "natural" population or it could mean a heterogenous assemblage with somewhat similar diameter ranges. Other histograms showed more than one peak, each indicating two or more species present. In

others the mean value as shown by the peak was more or less than the mean value from results tabulated for other localities, etc.

Each of these results was worked out to give the average mean, standard deviation, variance and population range (Mayr et al 1953, Ager 1956), even though the population may have been of several species collected together and not just one species, and may also be a thanatocoenose not a biocoenose community.

These factors were calculated as follows:-

The mean ( $m$ ), obtained by calculation and not from the graph is equal to the sum of the measurements ( $Sx$ ) divided by the total number of specimens ( $n$ )

$$m = \frac{Sx}{n}.$$

This when compared with the histogram has shown similarity in practically all cases investigated. hence the accuracy of the histogram method.

The variance is known as the square of the standard deviation and is obtained from

$$V = \frac{Sx^2 - \frac{(Sx)^2}{n}}{n - 1}$$

(or  $n$  where  $n$  is a larger number).

The standard deviation (S.D) determines the limits of variation either side of the calculated mean value for a

population. 99.14% of the population will occur within 3 S.D either side of the mean.

Therefore, the population range for a biological species is usually taken as three times the standard deviation on either side of the mean value, and is a useful means of comparing results from two localities, especially where the mean values are different, and it also gives an indication if the difference in value is significant or otherwise (Ager 1956).

Division into size groups was the first method used in the investigation to discern any speciation in the Silurian Girvanella, and later methods used embody these results with other factors in the mode of growth of members of this genus.

Thus, free-living forms were compared with attached or encrusting forms of Girvanella, and relative size relationships found.

The free-living, non-attached groups were then tabulated in relation to (a) the branching habit; the presence or absence of branches; the frequency of branching, highly branched or spasmodic; regular or irregular branching.

(b) The amount of adherence and compactness between tubes of a single group as opposed to the loose clusters where in extreme cases the filaments do not come into contact with each other.

(c) The curvature of the filaments; either a strong curvature over a short length, or just a normal amount due to loose coiling or branching or a fairly straight tube over a certain distance.

(d) The evenness or otherwise of the diameter of filament. This was found to be correlated usually with the amount of branching; highly branched forms being of a more irregular sized diameter.

(e) The length of tube; either significantly long in some forms or short in others, with all intermediate types between. The free-living forms were tabulated also as far as possible on any distinctive general form of growth, comparisons drawn from the varieties formed by Høeg (1932) and Lewis (1942).

Thus the general types of growth form considered were (a) loose coiling of filaments either as a cluster as in G. problematica redefined by Wood (1957), or more

specifically in a coil (as in G. problematica var typicalis Høeg 1932). Branching here is absent, or often infrequent or in limited portions only.

(b) sets of parallel filaments of apparently unlimited growth in length, usually at least partly adhering to each other, as in the variety Moniliformis erected by Høeg (1932).

(c) tight coiling of filaments of a group. Usually the result of adhering, often branching, curving filaments.

(d) short curved, usually loose filaments, sparsely branched, corresponding to the form of the variety lumbricalis of G. problematica (Høeg).

(e) a spiral development usually of a single filament (or few filaments) - variety spiralis (Lewis).

(f) a 'raft' like development, probably form of the parallel-tubes type, but where the filaments are of approximately equal length and appear to be of limited growth, and all are adherent.

(g) highly branched, curved, uneven diameter, filaments not strictly in a coil, but matting together.

These growth forms were then compared with their relative sizes, and the above process was repeated also

for encrusting or attached forms, and comparisons made.

The Sub-division of the genus Girvanella in the Lower Palaeozoic

Historical Høeg in 1932, describing the Ordovician algae from the Trondheim area, subdivided Girvanella problematica into three varieties on differences in size and habit, viz. vars typicalis, moniliformis and lumbricalis.

Then Lewis in 1942 reviewed the various Ordovician Girvanella and came to the conclusion that they were all varieties of G. problematica including his new variety G. spiralis from the Lèvis Group, Quebec and G. ocellata described by Seely in 1885 as a sponge Strephocetus.

No similar divisions appear to have been made on the microstructures of the Silurian Girvanella, and it has been found that these appear to show a wider range of form than their Ordovician counterparts and as a result require further division.

As a result of this investigation, the Girvanella from the Silurian have been here divided into a number of specific forms. These varying forms have not been

left as varieties of G. problematica, the type species from the Ordovician, as this would indicate a definite relationship between them and the type species where it is very possible that none existed, and so this relationship cannot be presumed. Hence, if the various forms are established of a form genus, it is regarded that they should be kept separate, and so be of more use, until any inter-relationships are established.

The characters and other features used in the separation of Girvanella into form species may be regarded as sometimes of less conclusive evidence than from any other palaeontological genera, but Girvanella is of necessity only a form genus and so divisions, while apparently slight in the fossil remains, may well reflect even greater differences than is normally the case. Thus, a slight difference, in for example, the amount of branching, would very conceivably be the result of the two groups in question not differing in species but in classes! It is also possible, that a distinction may not be a true one, and no division should have been made in this case, but note is made of the extremely numerous numbers of filamentous species of the present day, the frequent

association together of several similar forms and the nearness of some species geographically to each other in only slightly dissimilar conditions, which is not reflected easily in fossil deposits. Hence the likelihood of quite a few species being present in the Silurian, if they were abundant, as appears to be, and prolific as the present day algae, there is no justification in presuming that they were all varieties of one species. These forms are placed as species until either their removal to other genera or interrelationships can be satisfactorily proved.

The division of this genus into form species is with a regard of the variation of present ideas on the species concept in relation to fossils (Mayr 1942, Simpson 1944, Jepsen et al 1949, Sylvester Bradley and others 1956, amongst others).

#### The Division of Silurian forms of Girvanella into species

The first clear indication of the existence of more than one species of the form genus Girvanella in the Silurian calcareous deposits of the Welsh Border, is the marked difference in size (diameter of each filament) of the majority of filamentous groups in slides taken from the



Woolhope Limestone of the Mordiford District, when they are compared with those found in thin sections made from the Wenlock Limestone, as for example, even with those obtained from Fownhope, only three miles away from Mordiford, where in the first case the majority of filaments investigated have an average diameter of between  $5\mu$  and  $7\mu$ , and in the later development, most of the filaments have an average of more than  $14\mu$  wide. (vide tables)

The basis of division primarily on size was made firstly by comparison of tables and histograms which shows that in the Woolhope Limestone there are two size peaks (at least) of development (see histograms on Mordiford (M.F.) at end). From 50 separate groups measured from M.F.(1) most show a narrower type of filament range ( $2\mu$ - $8\mu$  for all groups), the remaining groups a wider filament diameter range ( $11\mu$ - $18\mu$ ). The average diameter for each group plotted further shows the two size peaks (a) between  $4\mu$  and  $8\mu$ , (b)  $13\mu$  to  $15\mu$ . Examination of the forms shows that group (a) is made up of "faggot" groups and loose coils and (b) is of branching adhering forms.

Set (a), when analysed for mean, standard deviation

and population range for M.F.1(1), gave a mean value of  $6\mu$ , a standard deviation of 1, thus showing the population range (3 S.D) to be from  $3\mu$ - $9\mu$  (as estimated from the mean value of each algal group). Other horizons and quarries in the Woolhope Limestone of Mordiford gave similar results, e.g. M.F.1(2) and M.F.2(7) both show mean value  $6\mu$ , standard deviation of 1.5 and 1.3 respectively and therefore both have a population range of  $2\mu$ - $10\mu$ .

The opposite extreme to the Woolhope Limestone of Mordiford is met by size analysis of the Wenlock Limestone of the Southwest end of Wenlock Edge (e.g. W.E.11). In W.E.11(1) out of 69 groups measured none was found with filaments beneath a diameter value of  $10\mu$  and the largest  $31\mu$ , and the peak mean (from tables and graphs) was found to be  $20\mu$  for all forms present. The range of mean values (which included several species) was between  $16\mu$  and  $25\mu$ . Similarly for W.E.11(2) (95 groups) no filament was less than the above minimum and the mean was  $20\mu$  for the several forms present and for each group the mean values were 1 specimen at  $14\mu$  then values  $17\mu$ - $25\mu$ . These results, when analysed, gave a higher value for the straight "faggot" groups and loose coiling and branching types (i.e. value

21 $\mu$ -22 $\mu$ ) than for any other types present.

When other localities were analysed in this way, intermediate size groups were found dominant in some (as in W.E.3, W.E.8, where a "faggot" group of mean 15 $\mu$ -16 $\mu$  is dominant. Others, e.g. Fownhope (vide tables and histograms; F.H.2(3), F.H.2(4), F.H.2(5)) have the fine range types and larger. (Geographical and stratigraphical distribution of the following form species is dealt with later).

The grouping of species was constructed as follows (omitting most of the geographical, stratigraphical and other details):

A. Sarmenta group

Groups of filaments mostly adherent to each other and parallel to each other. In longitudinal section therefore seen as lengthy tubes, the majority lying in contact and with scarcely any or no branching. In T.S. group appears as circular sections of tubes clustering together. No visible attachment to the substratum, unless conceivably in a few cases the group was attached at one end. Woolhope Limestone, raft-like forms when seen in L.S. are included at present as smaller specimens of this group.

Divisions of group:

- a) Filaments of internal diameter  $2\mu$ - $9\mu$ , exceptionally  $10\mu$  (Woolhope Limestone)
- b) Filaments of diameter  $12\mu$ - $18\mu$  (Wenlock Limestone)
- c) Filaments of tube diameter  $18\mu$ - $25\mu$ , peak  $19\mu$ - $21\mu$ , (Wenlock Limestone).

B. Clusters

Loosely coiling or tangled groups. Tubes not in contact with each other. In the type species there is not much branching, if any. The tubes are not parallel to each other, and if they do attain a sub-parallel direction they are not adhering and are unattached.

Branching occurs more frequently in the largest form included under this group, but here also there are long lengths of tubes, with an even diameter throughout and no indication of branching. A tendency of this larger form is to become more adherent to itself than the fine diameter species. Variation of this, is the occurrence of even diameter of filaments not adhering and coiled over each other. The extreme variety of this is the production, by usually one filament, of a spiral form, G. problematica Lewis (var Spiralis). This has only been seen in very few instances and in each case was probably a variety of

tight coiling, so is also included here.

Divisions into:

- a) G. problematica species 10 $\mu$ -18 $\mu$  diameter (mostly Wenlock Limestone)
- b) Clusters with filaments 2 $\mu$ -10 $\mu$  (Woolhope and Wenlock Limestones)
- c) Larger tubed clusters of diameter above 18 $\mu$ .

C. Adherent branching coils and clusters

This group is of those groups of filaments where tube diameters are between 8 $\mu$ -18 $\mu$ . They consist of either tightly coiling tubes or of adhering branching clusters with fairly frequent branching, but both tubes are regular in appearance having no constrictions.

D. Irregular Group

The forms are characterised by their highly branched tubes which are adherent. Branching is irregular, hence distinguishing these from the regular dichotomy of a Rothpletzella. Length between branches is short and tubes become uneven as a result. Also often visible are constrictions - hence tube diameter is not constant over any distance of tube. Most frequently these forms occur in clusters, and by virtue of this mode of branching could

not possess parallel tubes. Encrusting and other attached branching forms also included here.

a) Tubes of groups of diameters between  $11\mu$ - $20\mu$ .

b) Groups with larger tubes  $20\mu$ - $27\mu$  diameter.

E. "Lumbricalis" group corresponding to Høeg's

G. problematica var lumbricalis.

Short curved tubes, usually not adhering, not much branched, may be encrusting. Only occasional specimens found so its designation as a separate species is doubtful.

a) Tubes  $11\mu$ - $17\mu$  diameter.



Fig.5. Girvanella fragila (part of group shown)  
Woolhope Limestone, Mordiford. x 215.

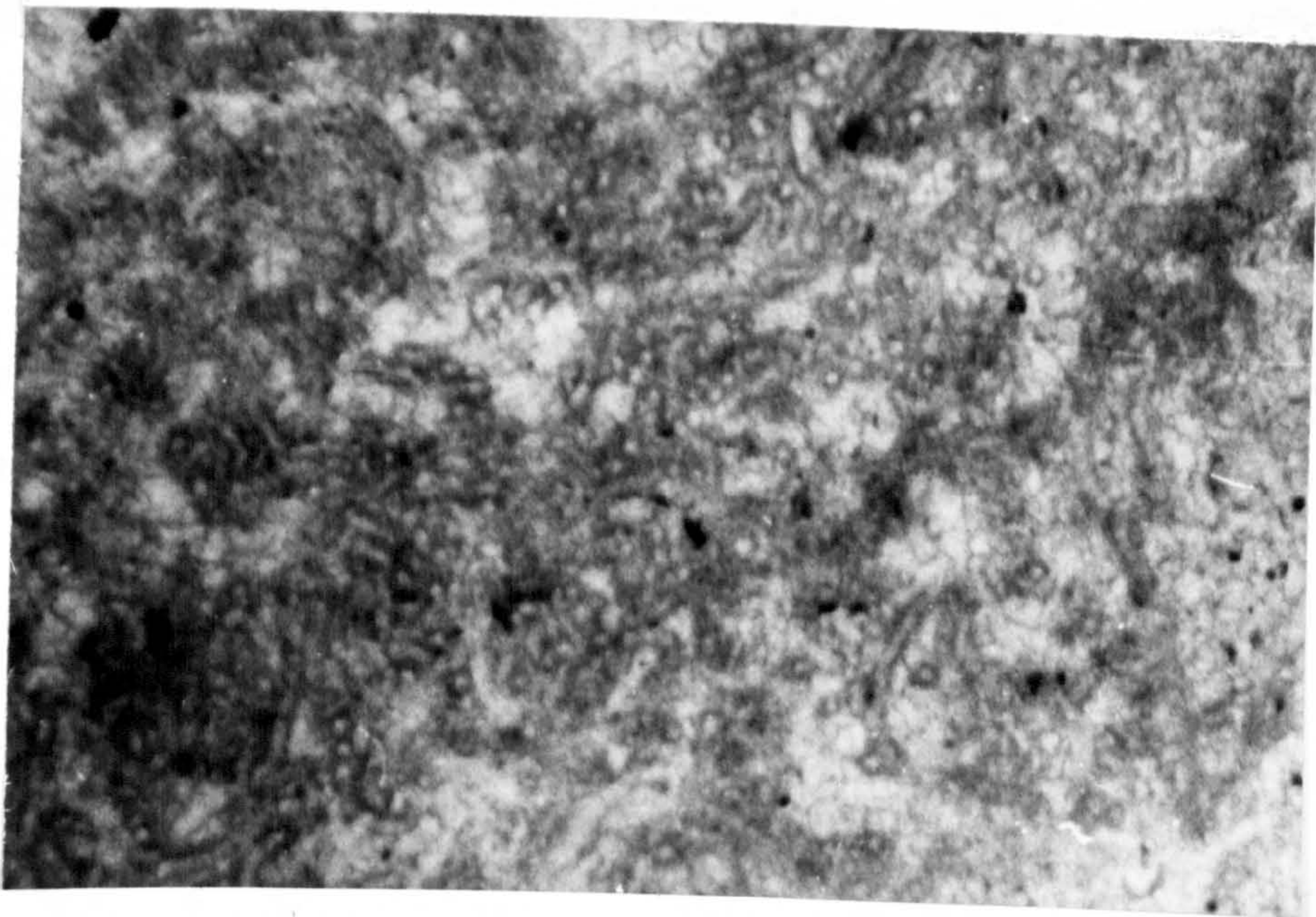


Fig.6. G. pusilla (part of group shown)  
Wenlock Limestone, Fownhope F.H.2(5) x 145.

## DESCRIPTIONS OF SPECIES

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### GIRVANELLA FRAGILA n.sp.

figs. 5, 18.

#### Description

This form occurs as bundles of filaments lying parallel to each other, mostly adherent but sometimes partly free. In longitudinal view the filaments are long, either straight or slightly undulating. Rarely branching, often no branches visible. In transverse section appear as circular cross sections of tubes in clusters mostly.

Internal diameter of the filaments ranges from  $2\mu$ - $9\mu$ , very occasionally extend to  $10\mu$  and  $11\mu$ . Majority of measurements are within  $5\mu$ - $7\mu$ .

Type specimens for this and the other species have not yet been designated.

#### Horizons and localities

This form has been found in the Woolhope Limestone of the Mordiford district. It has been found abundantly



at various horizons from just above the level of the *Petalocrinus* limestone, i.e. the base of the Woolhope limestone through to nearly the top of the limestone and in some slides it is the dominant fossil. No Girvanella has yet been found in any Silurian shales.

In the Wenlock Limestone only one specimen was found from Fownhope composed of tubes of 2 $\mu$ -4 $\mu$  diameter.

It has not been found in the Aymestry Limestone.

#### Remarks

No attachments have been seen hence it was probably a free-floating form. The tubes were mostly of a dark grey fine granular calcite which when thick obscured details.

Septation was observed in a few tubes in several groups but owing to fineness of material, it is usually somewhat indistinct. Here it is also regarded as an indication of better preservation.

GIRVANELLA PROLIXA n.sp.

figs. 3, 10, 11, 18.

Description

Bundles of filaments lying closely in contact and parallel, sometimes separate. In longitudinal view filaments long and nearly straight. In transverse section, occur in clusters. This second form differs from the previous species mainly in size and the horizons in which it was found.

Filament diameter  $12\mu$ - $18\mu$ , occasionally more, mainly  $14\mu$ - $16\mu$  wide.

Horizon and localities

Woolhope and Wenlock Limestones.

This form has been found occasionally in the Woolhope Limestones of Mordiford when the frequency is compared with the abundance of the finer species.

It occurs in the Wenlock Limestone of Fownhope and has also been obtained in most of the quarries examined in Wenlock Edge. It appears to be most abundant in the Grey Measure type of sediment (W.E.3, W.E.8).

## Remarks

The specimens obtained from Fownhope, appear to be slightly larger than the average, their diameter being between  $13\mu$  and  $20\mu$  with the majority  $17\mu$ - $18\mu$ . This is not quite large enough to be included with the next form species, and as the Fownhope district appears to have been a favourable environment for algae, it is possible that algal growths of some (at least) of the forms may have been slightly larger than the average elsewhere. This intermediate form in size is not distinct enough to be separated off in any way.

Also a few specimens from Wenlock Edge (W.E.11) appear to belong to this intermediate size but in this case the majority of algal groups are of the larger diameter type (tubes average  $21\mu$ - $22\mu$ ) but overlapping usually accounts for some apparent finer tubes which grade into the larger size.

The clearest method of deciphering the group in this case is to compare the mean value obtained for each group measured with the group sizes stated. (See histograms and figs).

Septation has been seen in only a few specimens and only from one locality (W.E.3) from Wenlock Edge, where

preservation of algae does not appear to be so good as at Fownhope. In a few cases, the ends of the filaments appear to arise from a point which suggests that possibly this form grew in length while attached to some substrate at one end.

Another pointer suggesting an attachment is that shorter length groups termed 'rafts', either broken off from the branches of a larger group or a young stage, quite often show the adherent tubes converging to a narrowed region at one end either by branches joining or more overlap; on the other hand, breakage would most likely occur at a narrower region.

GIRVANELLA SARMENTA n.sp.

figs. 15, 21.

Description

A wider tubed form than the previous two species. Distinguished by its filaments lying in a parallel position, mostly adherent to each other, seldom branching, and each with a diameter  $18\mu$ - $25\mu$  or to  $31\mu$ . The majority of filaments being of diameter  $19\mu$ - $22\mu$ .

Although this form corresponds to Høeg's Ordovician form G. problematica var moniliformis in size and approximately in longitudinal section, it differs in transverse section by being composed of a cluster of cross sections of tubes and not arranged in a single adherent row. Thus it may well have been a development from this form, but it is not identical with it.

Horizon and localities

Woolhope and Wenlock Limestones.

Three branching specimens of probably this form have been obtained from the Woolhope Limestone of Mordiford.

The majority of specimens have been obtained from the south-west end of Wenlock Edge, where they appear to be the

dominant form, and are also present at Fownhope (Wenlock Limestone). This form appears to be more infrequent in the other localities investigated on Wenlock Edge.

Remarks

Only in a few specimens is there a suggestion of tapering at one end, so this form may or may not have been attached. It seems possible, that if unattached, any bundles of this shape would not be lying on the bottom, as a coiled form might (but not necessarily) have been but have floated on the surface.

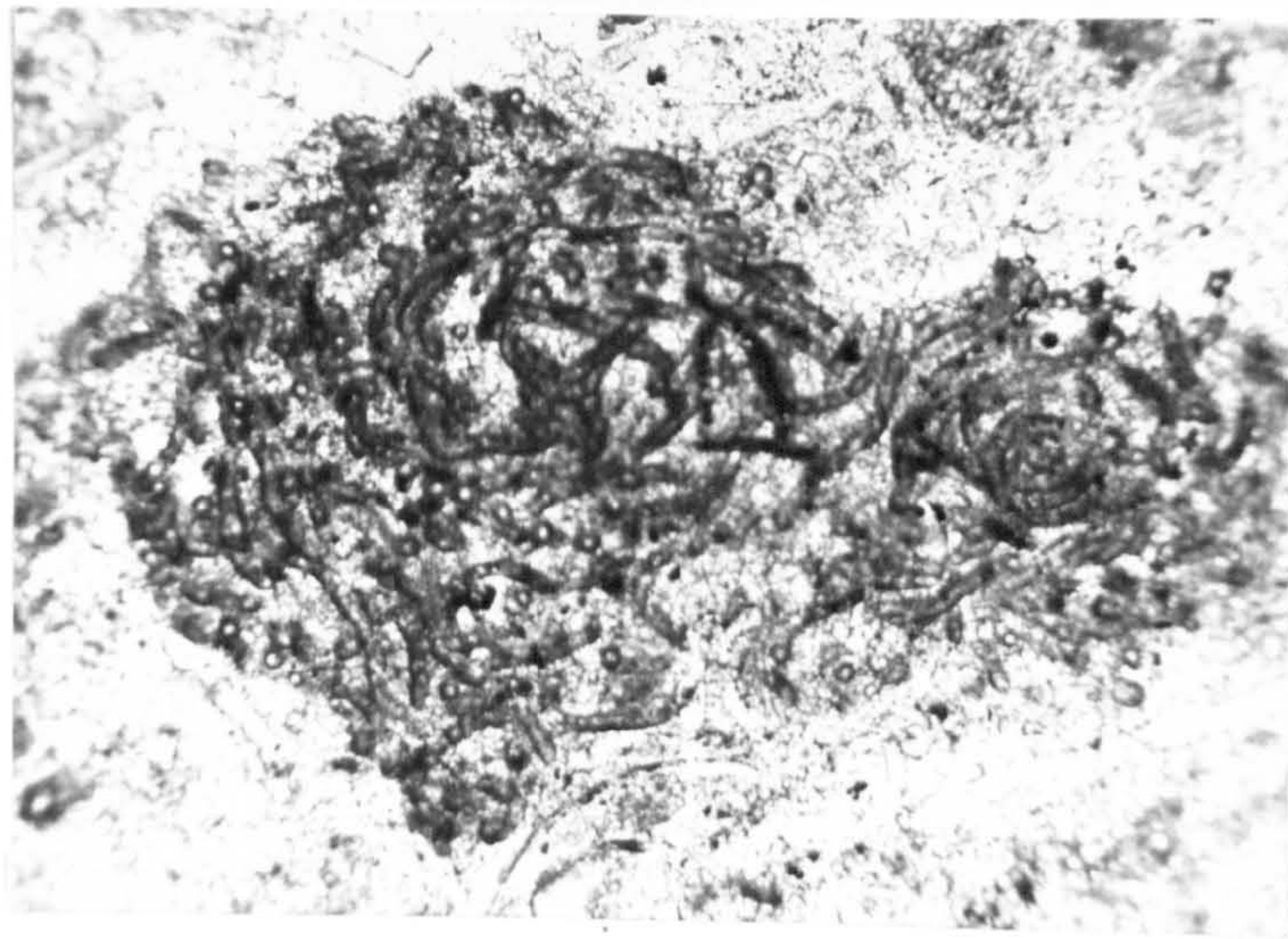


Fig.7. Girvanella problematica, loosely coiling cluster.  
Nodular Beds, Wenlock Limestone, Dudley. x 75.

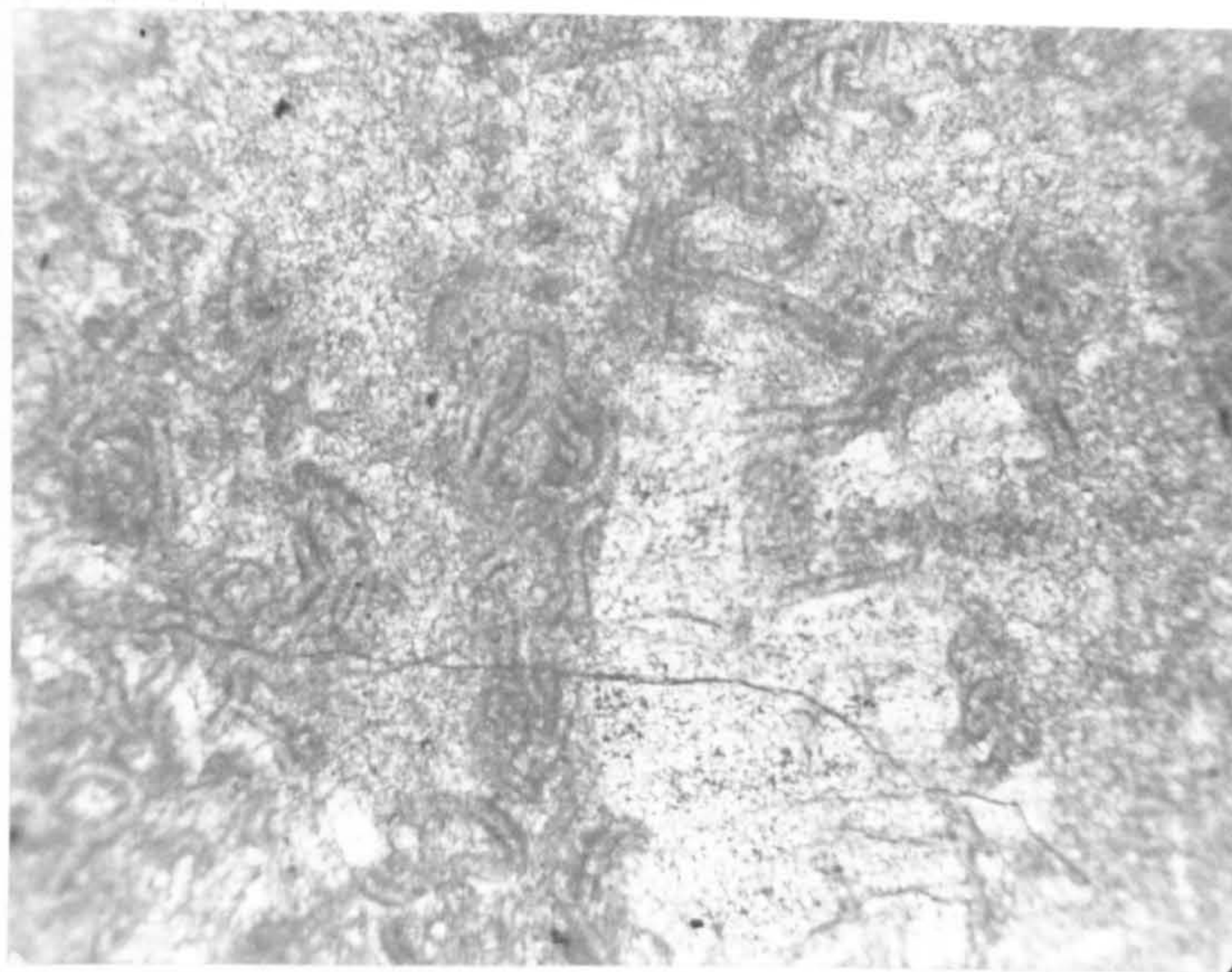


Fig.8. G. problematica, part of loose cluster encrusting  
Halysites colony. Ballstone, Wenlock Edge,  
W.E.3(11) x 100.

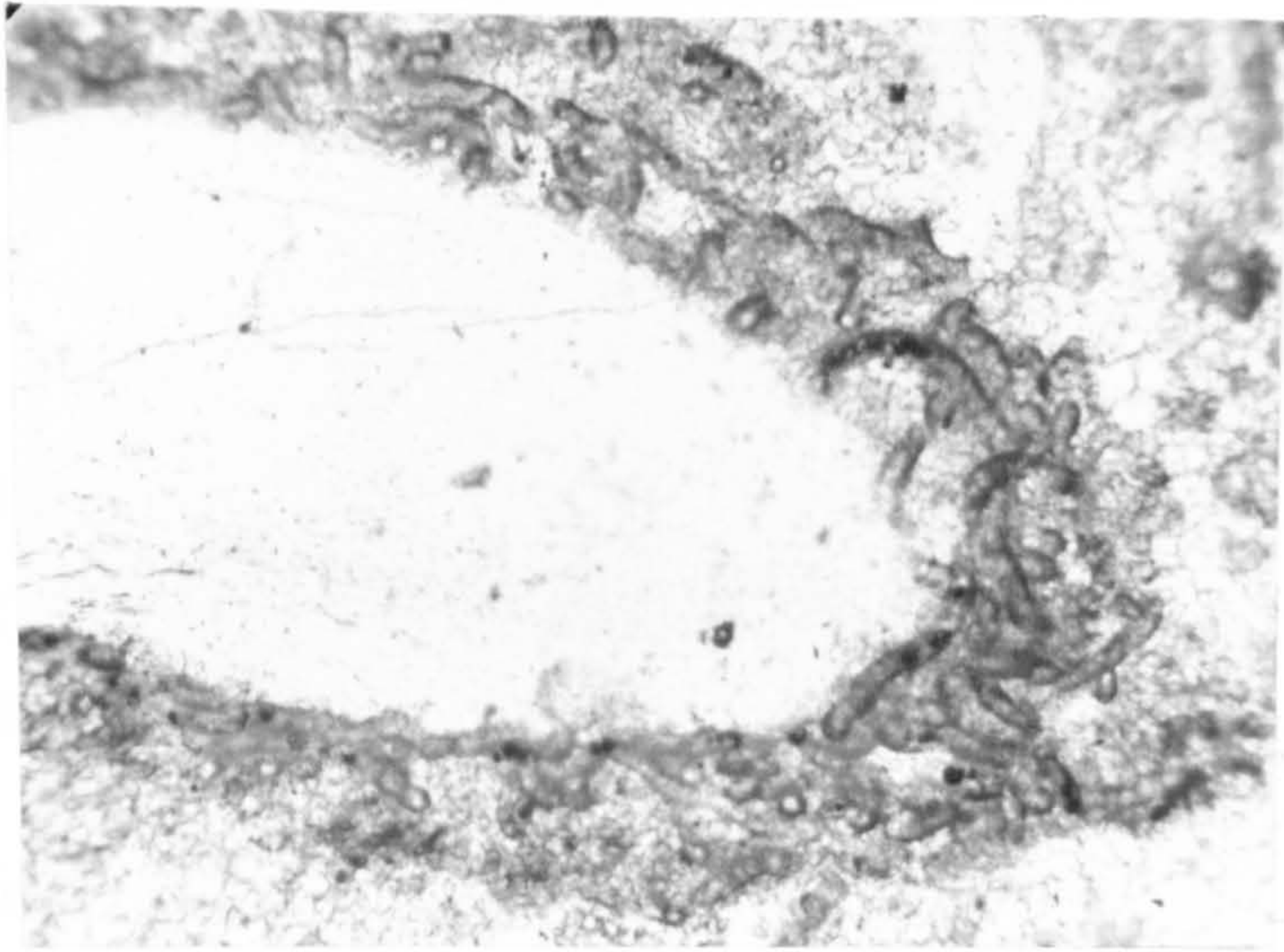


Fig.9. Girvanella problematica var lumbricalis (Høeg)  
 encrusting pleura of trilobite.  
 Nodular Beds, Dudley. x 100.



Fig.10. G. proluxa, non-  
 encrusting. Grey Measures  
 Wenlock Edge. (W.E.3(7))  
 x 150.

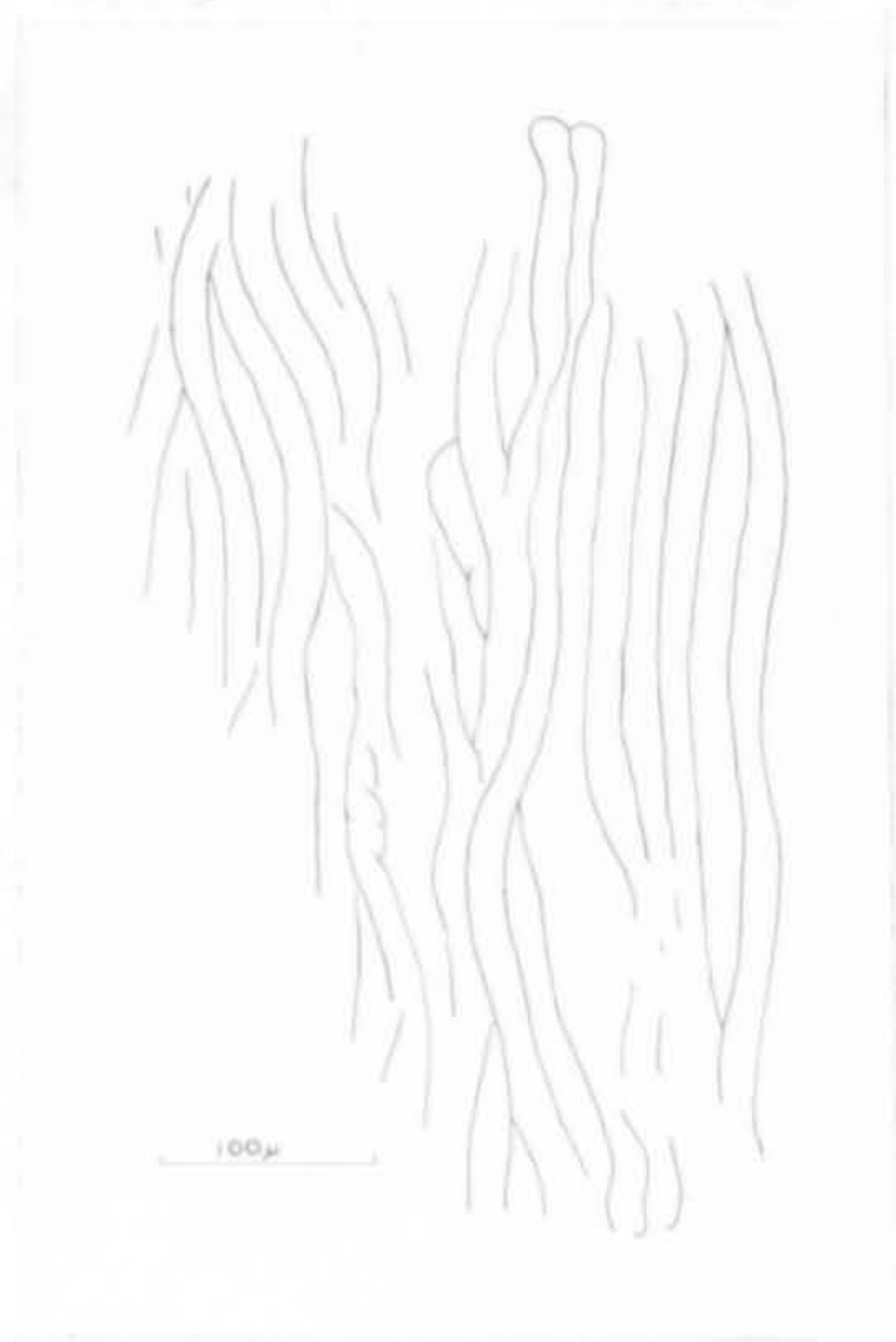


Fig.11 G. proluxa  
 diagram of group.  
 Same locality W.E.(3)7  
 x 110.



## GIRVANELLA PROBLEMATICA

figs. 7, 8, 20.

G. problematica Nicholson and Etheridge 1878

G. problematica re-description Wood 1957

Palaeontology I. pp. 22-28, pl. 5.6.

### Description

Wood (1957) in a re-description of the type species from the Ordovician Stinchar Limestone gave the diagnosis as "tubes flexuous, not observed to taper, rarely branching, twisted together in loosely aggregated mass, less commonly closely packed. Average external diameter of tubes  $21\mu$ - $22\mu$ , ranging from  $18\mu$ - $25\mu$  (rarely  $30\mu$ ), usual average internal diameter of tubes  $15\mu$ - $16\mu$ , ranging from  $13\mu$ - $20\mu$  (rarely  $22\mu$ )".

All loosely coiling groups and other loose clusters from the Silurian limestones with internal diameters  $12\mu$ - $18\mu$  (occasionally slightly more) and mostly ranging  $15\mu$ - $16\mu$  have been included in this species. This includes all forms except tight branching coils and other adherent branching groups, the groups like faggots and the form Høeg termed var lumbricalis.

### Horizon and localities

A few specimens obtained from Woolhope limestone of

Old Radnor and Mordiford, Wenlock Limestone of Dudley, Fownhope, Sollers' Hope and May Hill and also from Wenlock Edge near Much Wenlock. Also present in the Aymestry Limestone of Ledbury and View Edge and Whitcliffe Beds, Ludlow.

Slightly larger tubed coiling clusters, of usual average 17 $\mu$ -18 $\mu$  were found from further south-west quarries (W.E.15).

Remarks

Forms of this size have been found encrusting brachiopod, crinoid ossicles, bryozoa, corals, e.g. Halysites, Heliolites and Favosites.

GIRVANELLA PROBLEMATICA var LUMBRICALIS Høeg

G. problematica var lumbricalis Høeg 1932

fig. 9.

Description

Short strongly curving tubes, sometimes encrusting, but if so, not all of each tube in contact with the substrate. Tubes separate and not adherent to each other. Rarely branching. Diameter of filaments 12 $\mu$ -18 $\mu$  and occasionally to 20 $\mu$ , average diameter 14 $\mu$ -17 $\mu$ .

Horizon and Localities

This form has been found occasionally in the Wenlock Limestone of Dudley, Fownhope and Wenlock Edge.

Remarks

This form may well be only a variety of G. problematica and as it has been found only occasionally during this investigation, it is probably best left as such.

This form is often found encrusting different organisms such as seen in the photo of section of the trilobite pleura with algae around it.

GIRVANELLA PUSILLA n.sp.

figs. 6, 18, 19.

Description

Loosely coiling groups of fine thread-like filaments diameter  $2\mu$ - $9\mu$ , very occasionally to  $10\mu$ - $11\mu$ , average  $4\mu$ - $7\mu$ . Threads long, from almost completely unbranched to branching frequently and usually not in contact with each other. Frequently found encrusting other organisms.

Horizon and localities

Woolhope and Wenlock Limestones of the Woolhope District, Mordiford and Fownhope and the Woolhope Limestone of Old Radnor and the Wenlock Limestone of Wenlock Edge, Dudley, Ledbury, May Hill and the west flank of the Malverns.

It is more widespread than the straight bundle form of similar diameter range in the Wenlock Limestone, but less abundant than in the Woolhope Limestone.

Remarks

Specimens obtained from the Woolhope Limestone appear to have a slightly larger tube width than those from the

Wenlock, the majority of tube measurements falling between  $5\mu$ - $7\mu$ . In the Wenlock Limestone most groups of specimens were between  $2\mu$  and  $7\mu$ , with the majority between  $4\mu$  and  $5\mu$ .

Septation has been found in a few specimens from Mordiford and Fownhope.

Fine filamentous algal groups have been found fairly frequently in Fownhope encrusting different organisms including Coenites, crinoid ossicles and also with Wetheredella and participating in growth forms with Rothpletzella and Girvanella problematica (Dudley fig. 84).

One specimen appeared to be a growth form.

GIRVANELLA INCOMPTA n.sp.

figs. 14, 21, 23.

Description

More variable than last two species.

The groups may occur in loosely coiling cluster, often slightly adherent and usually with some branching. Other groups are completely adherent, with some or no branching, some are in tight coils, and occasionally one or more tubes may participate in spiral formation (as in var spiralis of Lewis).

Diameter of filaments 18 $\mu$ -28 $\mu$ , average type 19 $\mu$ -21 $\mu$ .

Horizon and localities

A few specimens from the Woolhope Limestone of Woolhope, Wenlock Limestone of Fownhope, and the southwest end of Wenlock Edge (W.E.11, W.E.15), and occasionally Dudley, especially D.U.1(5) and the Aymestry Limestone of View Edge.

Remarks

The size of tube, the more frequent occurrence branching and the tendency of filaments to adhere to each

other, are the main features which separate this form from the type species. Also, in connection with this, is its abundance in different localities to the type.

Occasionally found encrusting organisms such as brachiopods and bryozoa.

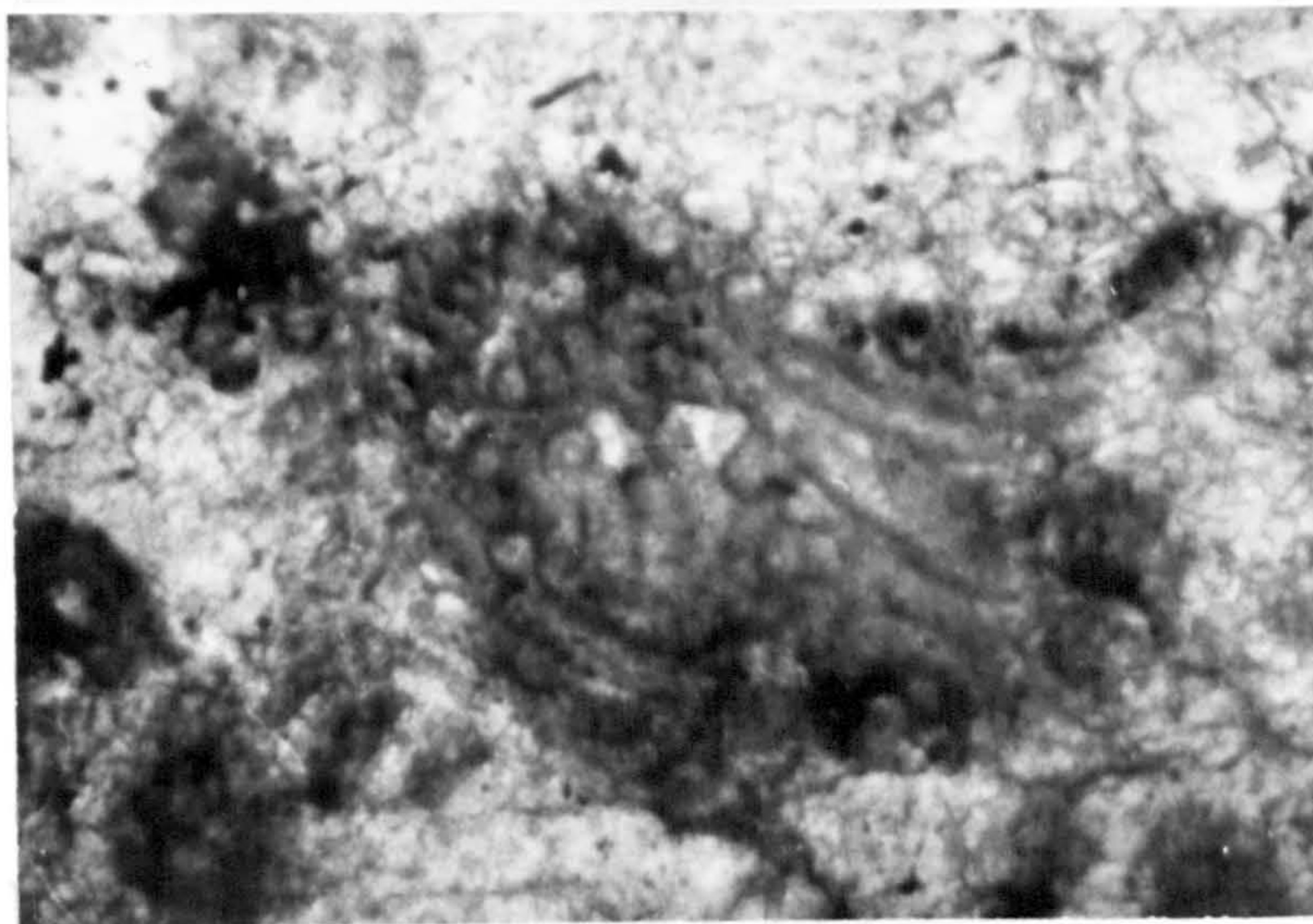


Fig.12. G. media, even diameter tubes, adhering and much branching. Wenlock Limestone, Fownhope, F.H.2(4). x 145.

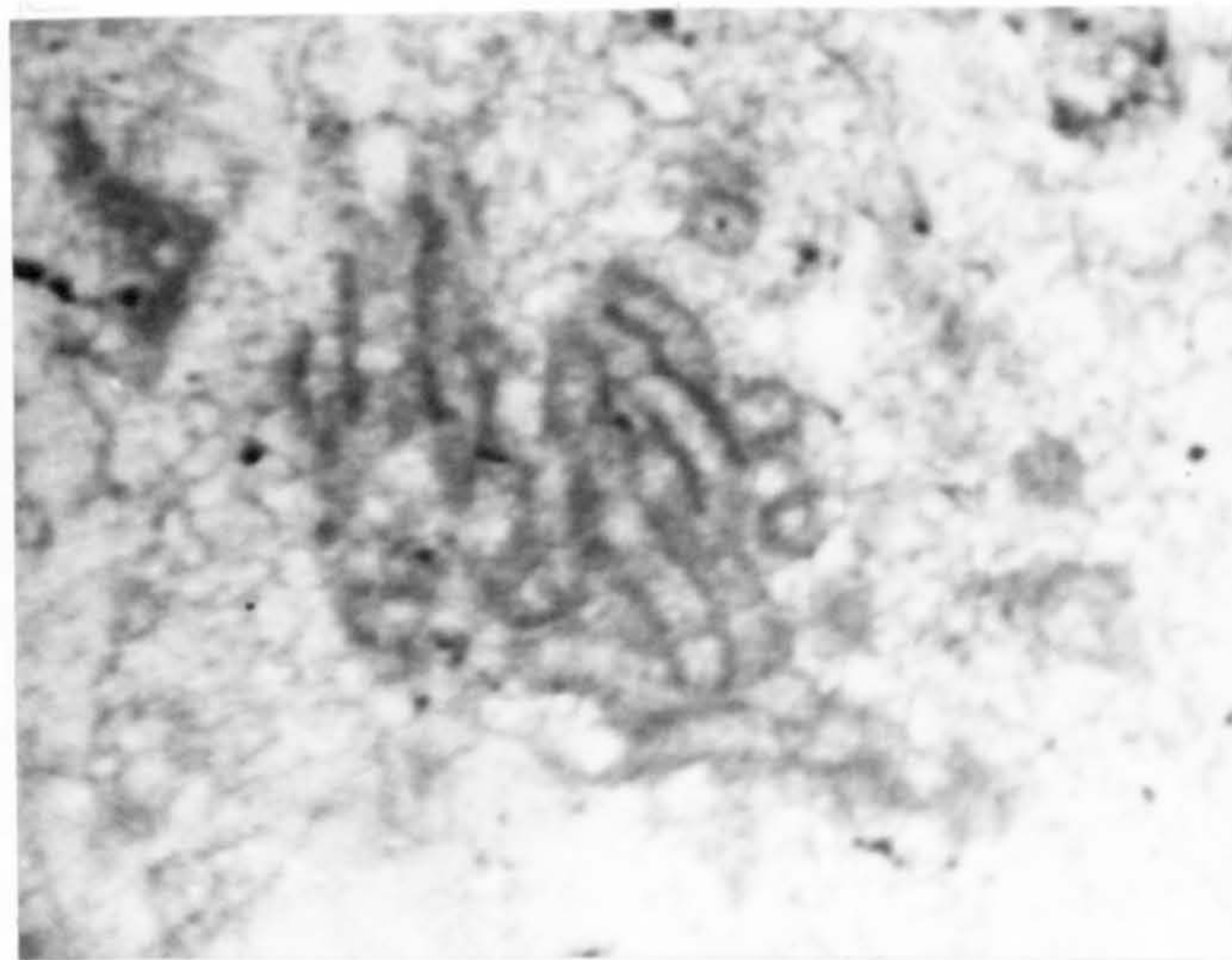


Fig.13. G. ramosa, diameter of tubes slightly larger than in G. media, irregular branching, adhering. Wenlock Limestone, Fownhope. F.H.2(3). x 145.



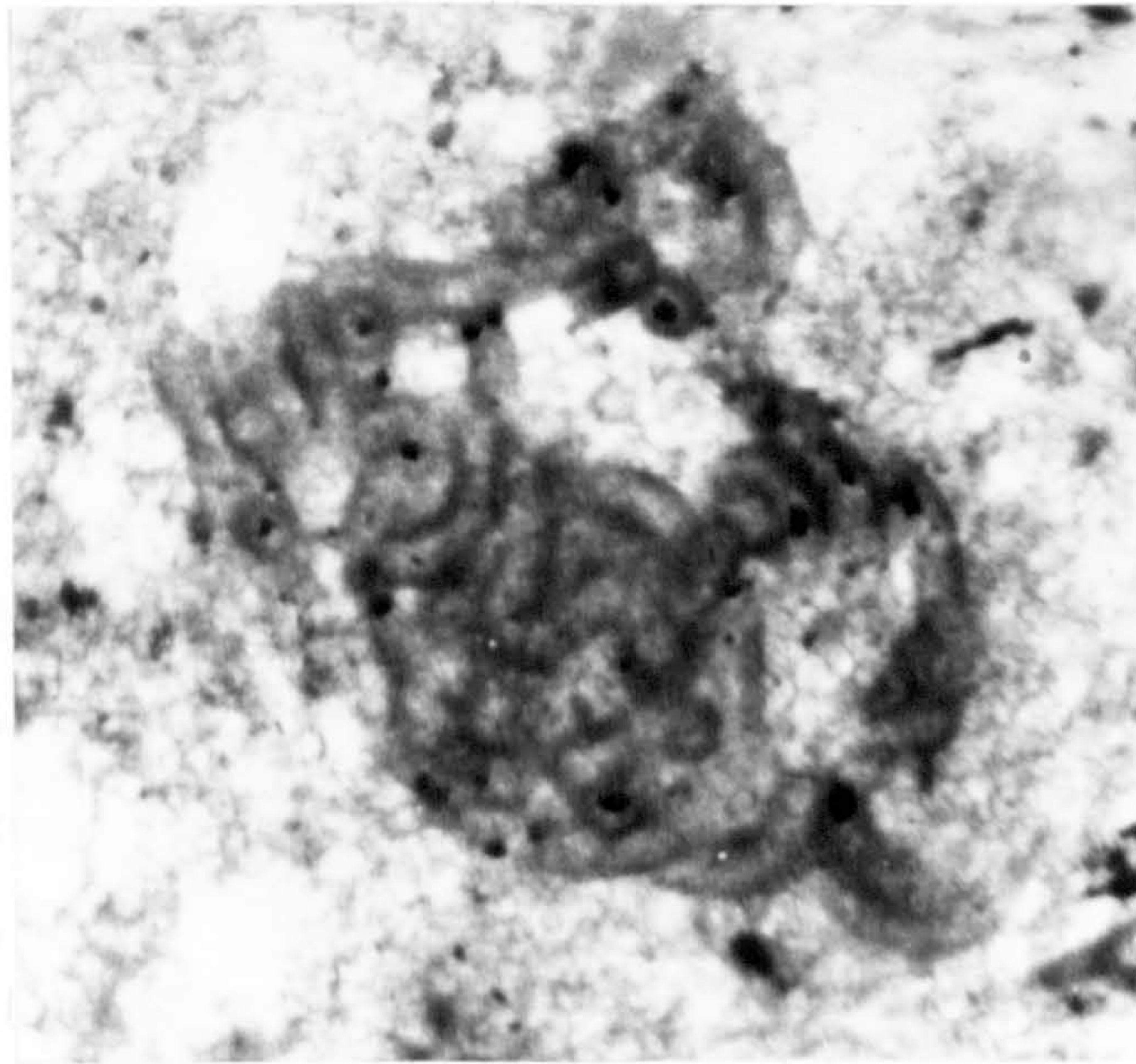


Fig.14. Girvanella incompta, coiling branching cluster,  
larger tubes than G. media.  
Wenlock Edge W.E.11(1), x 145.

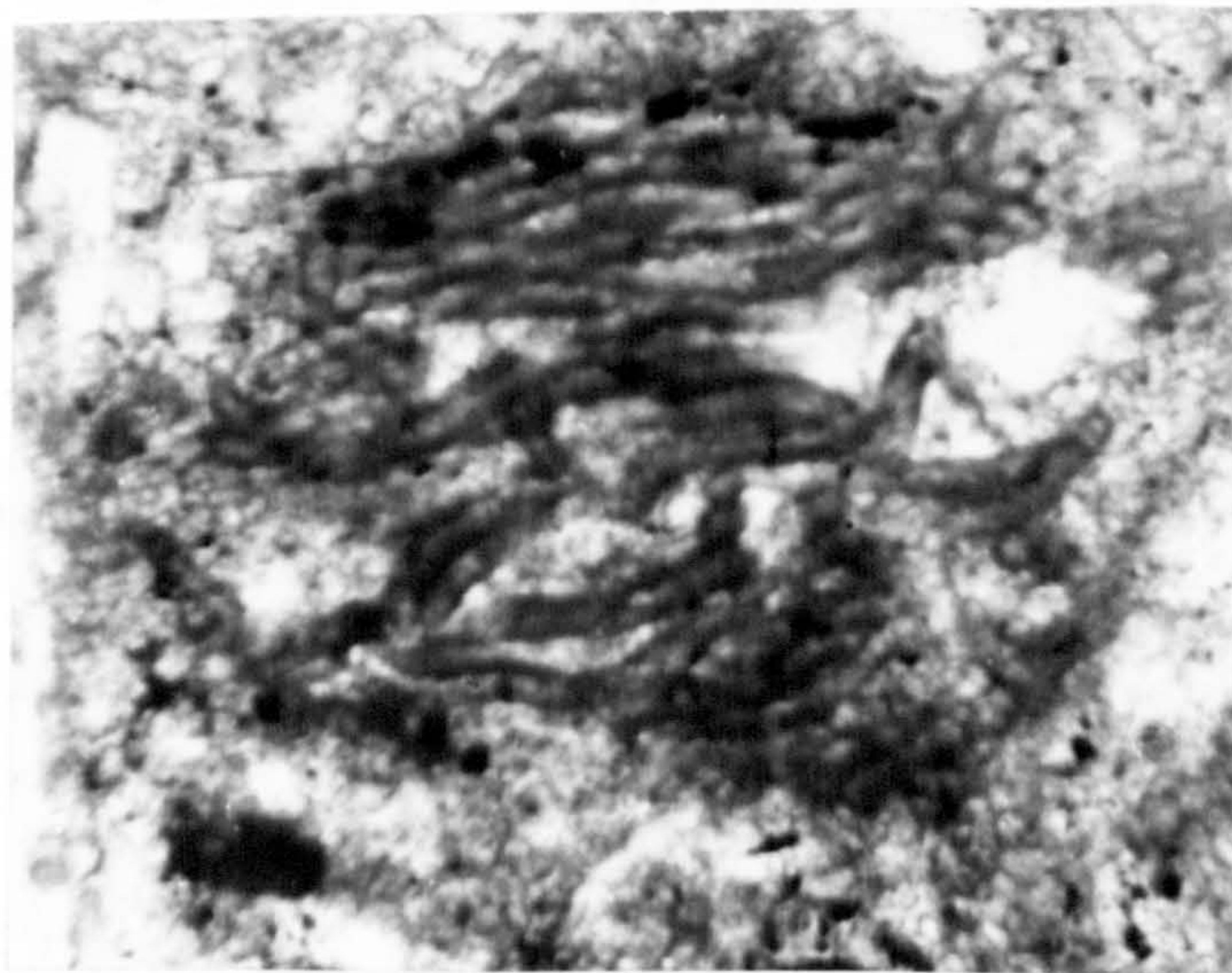


Fig.15. G. sarmentata. Tubes lie in one direction, larger  
than G. proluxa. Wenlock Edge W.E.11(1) x 145.

GIRVANELLA MEDIA n.sp.

Figs. 12, 19, 20.

Description

Tightly coiling and branching forms, or other even diameter tubes adhering together and branching fairly frequently. Diameter range  $8\mu$ - $18\mu$ , rarely more, average  $13\mu$ - $14\mu$ .

Differs from the type and previous species by the adherent nature and branching to the former and size and more frequent branching from the latter.

Horizon and localities

This has been found in Wenlock Limestone of Fownhope where it appears to be fairly profuse, Wenlock Edge, May Hill and one specimen found at Dudley. It has also been recorded from the Aymestry Limestone of View Edge.

Remarks

Occasionally found to encrust other organisms such as brachiopods and ostracods, but was mostly found in small compact adhering branching groups.

GIRVANELLA RAMOSA n.sp.

figs. 13. 19, 20, 22.

Description

Highly branching groups of filaments, diameter at internodes 11 $\mu$ -20 $\mu$  average 15 $\mu$ -16 $\mu$ . Filaments are adherent to each other and branching is irregular. The tubes are uneven in diameter due to branching and constrictions.

Horizon and localities

Woolhope and Wenlock Limestones

This form has been found from the Wenlock Limestone of Fownhope and Wenlock Edge and appears to be commonest in the former locality, where it occurs with the abundant G. media and G. problematica.

Remarks

This form has mostly been found in small groups possibly due to easy breakage of the uneven tubes.

In this and the following species, the apparent constrictions of the tube may be related to the cell length, or if not, to the branching. Both species are distinguished from Rothpletzella spp. by the mode of branching and lack of the characteristic beading of Rothpletzella.

GIRVANELLA EFFUSA n.sp.

fig. 14, 21.

Description

A wider-tubed group, with highly branched, adherent uneven tubes and some constrictions. Diameter of filaments (internode)  $18\mu$ - $27\mu$ , mostly  $22\mu$ - $23\mu$  wide.

High frequency of branching is reflected in curvature and short internodal length of filaments.

Horizon and localities

This larger tubed form has been found from <sup>Wenlock Edge</sup> (W.E.3, W.E.11, W.E.15) and occasionally at Fownhope, and was commoner than G. ramosa where the latter was less frequent in occurrence.

Remarks

This and the previous form species may on measuring show a slightly lower limit than stated above for filament diameter. This is because of the increased difficulty in finding 'true' diameters (see method) with a high branching frequency, constrictions and adhering tubes. Thus, this is where graphs which show the range of filament for each group have their especial value, as the peak figures

obtained will then give a truer result than a random measurement of odd algal filaments.

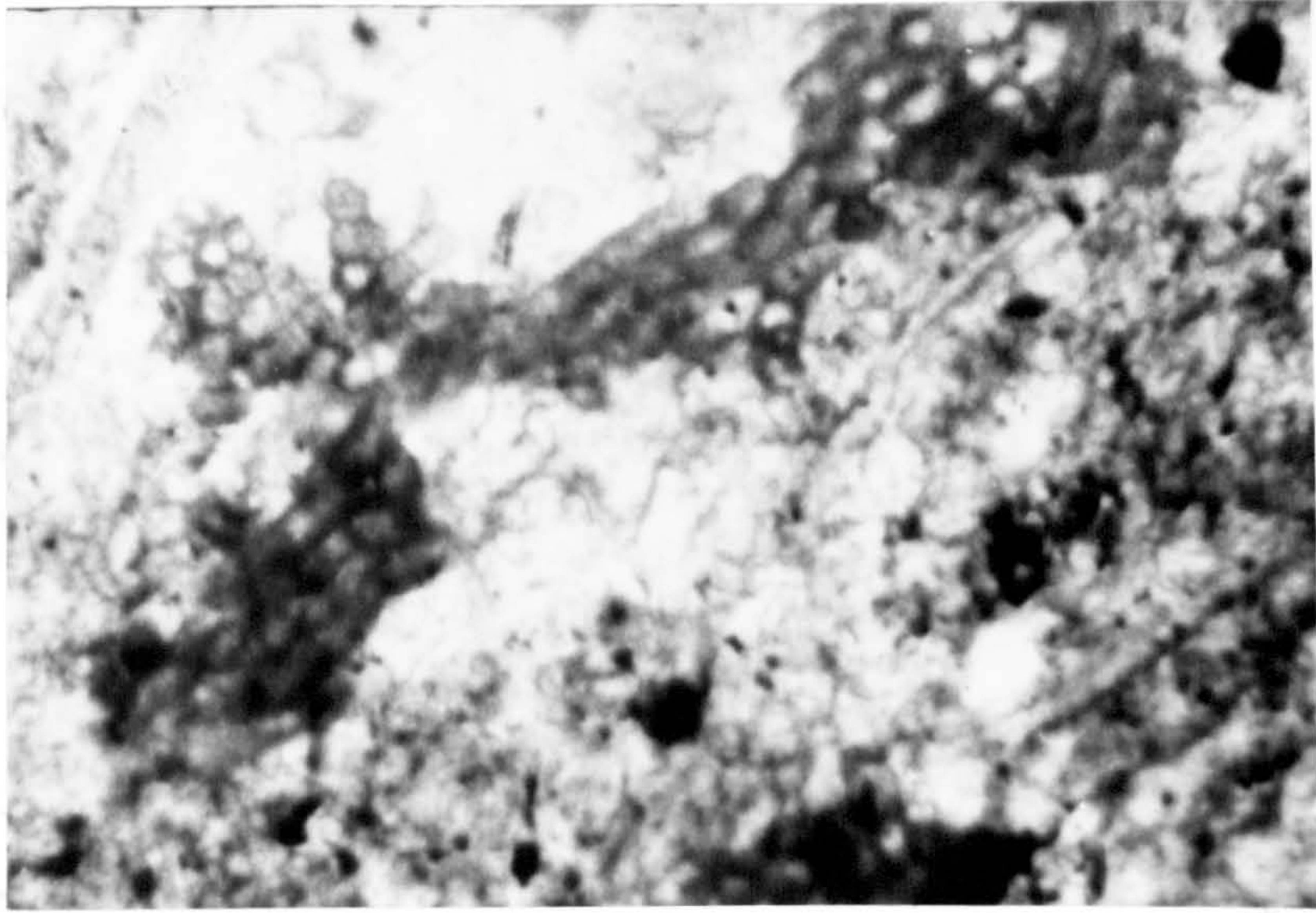


Fig.16. G. effusa. Irregular diameter to tubes, apparently encrusting. Wenlock Edge(W.E.11(1)). x 145.

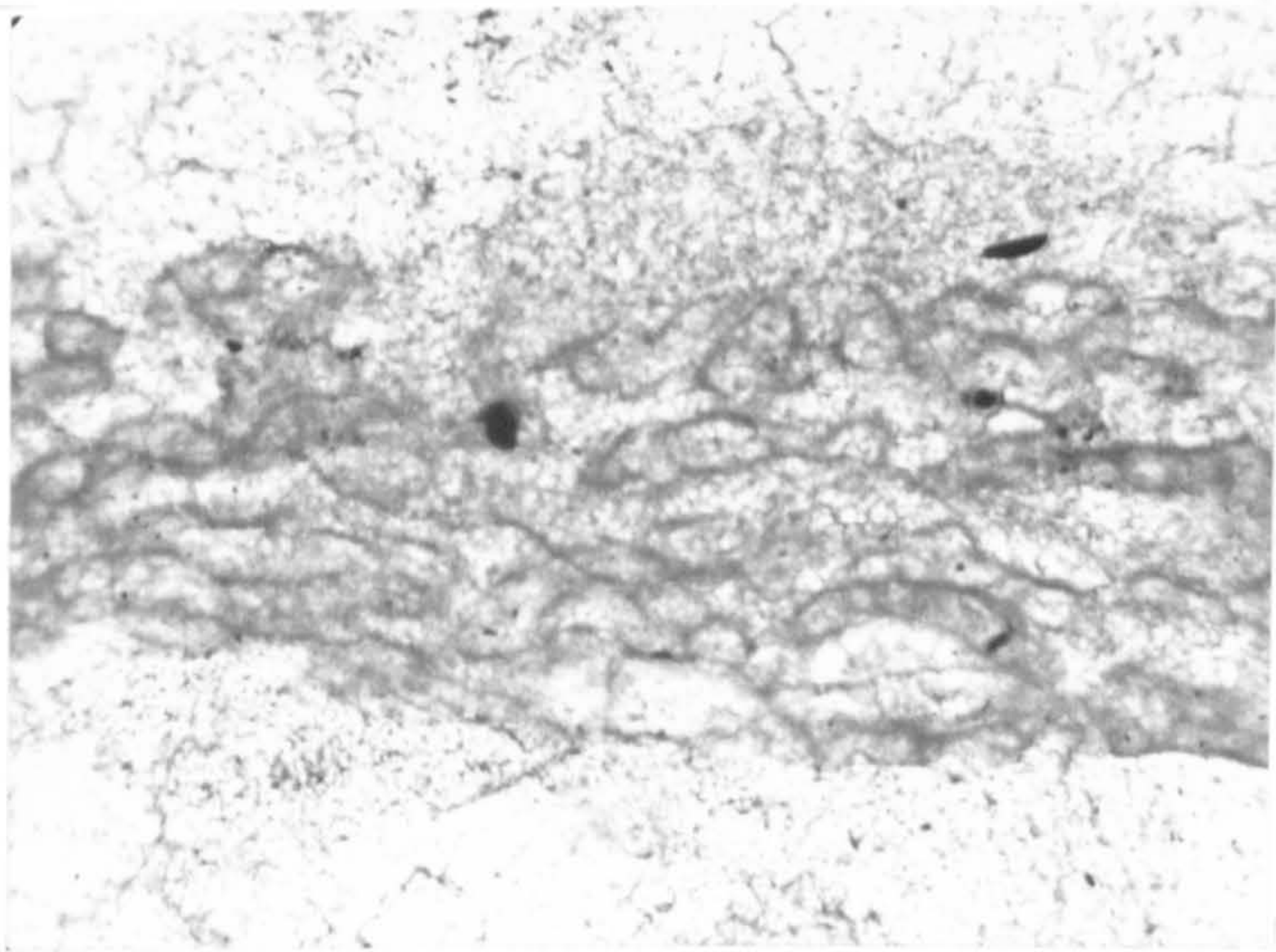


Fig.17. Algal filaments (R. conferta in photo) along growth line of stromatoporoid. Algae found along 8 lines in this instance including Girvanella strands.

Fig. 18

Diagrams, magnification x 600

Specimens from Woolhope Limestone, Mordiford,  
a, c, M.F.1(1), b, M.F.1(2).

- a - Girvanella fragila showing septation of tubes
- b - G. c.f. pusilla, branching specimen.
- c - G. proluxa, septate group. In this instance areas of algal dust have been stippled.

Fig. 19

Diagrams, magnification x 350 except b x 600.

a, b, c from Woolhope Limestone, a.b Mordiford  
(a, M.F.2(7), b, M.F.1(1)), c, Woolhope  
(W.H.9(1)).

d, e, f from Wenlock Limestone of Fownhope  
(d.f. F.H.2(3), e F.H.2(5)).

- a - Girvanella pusilla, part of group showing septation of tubes.
- b - Spiral tube of Girvanella c.f. var spiralis Lewis.
- c - G. media, branching, tubes adhering and some septation.
- d - G. ramosa, uneven diameter of tubes, branching, mostly adhering.
- e - G. c.f. ramosa, part of group showing short curved tubes, branching encrusting form.
- f - G. media, showing some septation of tubes.

Fig. 20

Diagrams, magnification x 350.

a-f from Wenlock Limestone, Fownhope  
(a.d.f. F.H.2(5), b.c.e. F.H.2(4)).

- a - Girvanella problematica, part of loose cluster shown.
- b - G. ramosa, a few tubes in a small group.
- c - G. ramosa, another small group with tubes apparently arising from the base.
- d - G. problematica, part of group showing some septation of tubes.
- e - G. media, adhering group, branching.
- f - Surface view of branching Girvanella.  
Note irregularity and long unbranched tube.

Fig. 21

Diagrams, magnification x 350

a-d from Wenlock Edge, Quarry 11.  
a, c, d, W.E.11(2), b, W.E.11(1).

- a - Girvanella effusa, part of group showing irregular tubes, adhering.
- b - G. sarmenta, part of elongated group.
- c - G. sarmenta, transverse section (nearly) through tubes.
- d - G. incompta, part of group showing looped tube with opaque iron ore infilling.

Fig. 22

Diagrams, magnification x 350

a-d from Wenlock Limestone, Wenlock Edge Quarry 11(1).

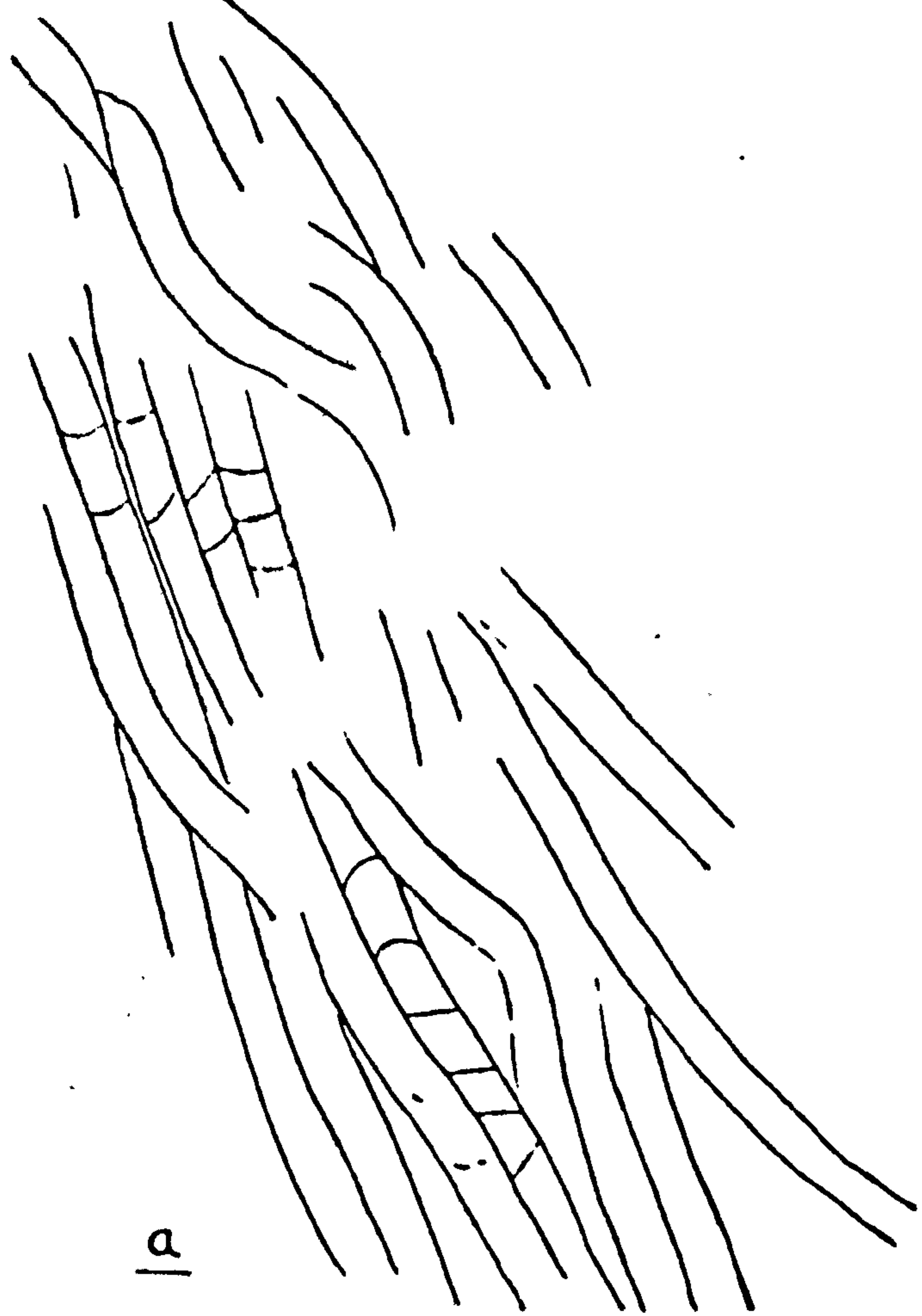
- a - G. ramosa, branching irregular cluster.
- b - G. ramosa, branching irregular form, both a, b. are large forms nearly intermediate with the smaller forms of G. effusa.
- c - G. ramosa encrusting ostracod.
- d - Coiled branching cluster of G. incompta.

Fig. 23

Diagrams, magnification x 350.

- a. b specimens from Wenlock Limestone of Wenlock Edge, a, W.E.11(1), b, W.E.11(2).
- a - G. incompta, the more usual type of loose branching cluster.
- b - G. incompta, a few tubes in a spiral - (as in var spiralis, Lewis).

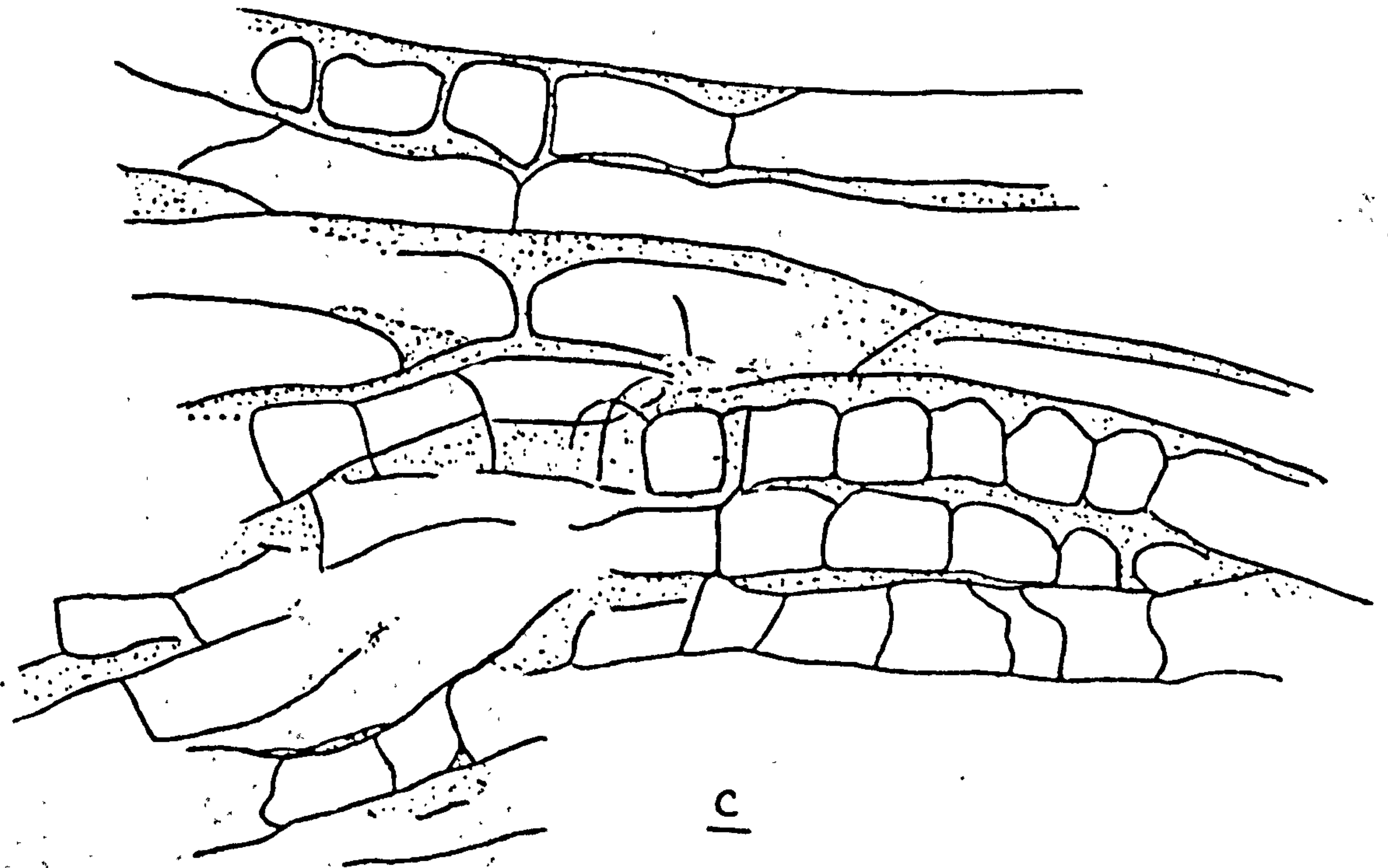




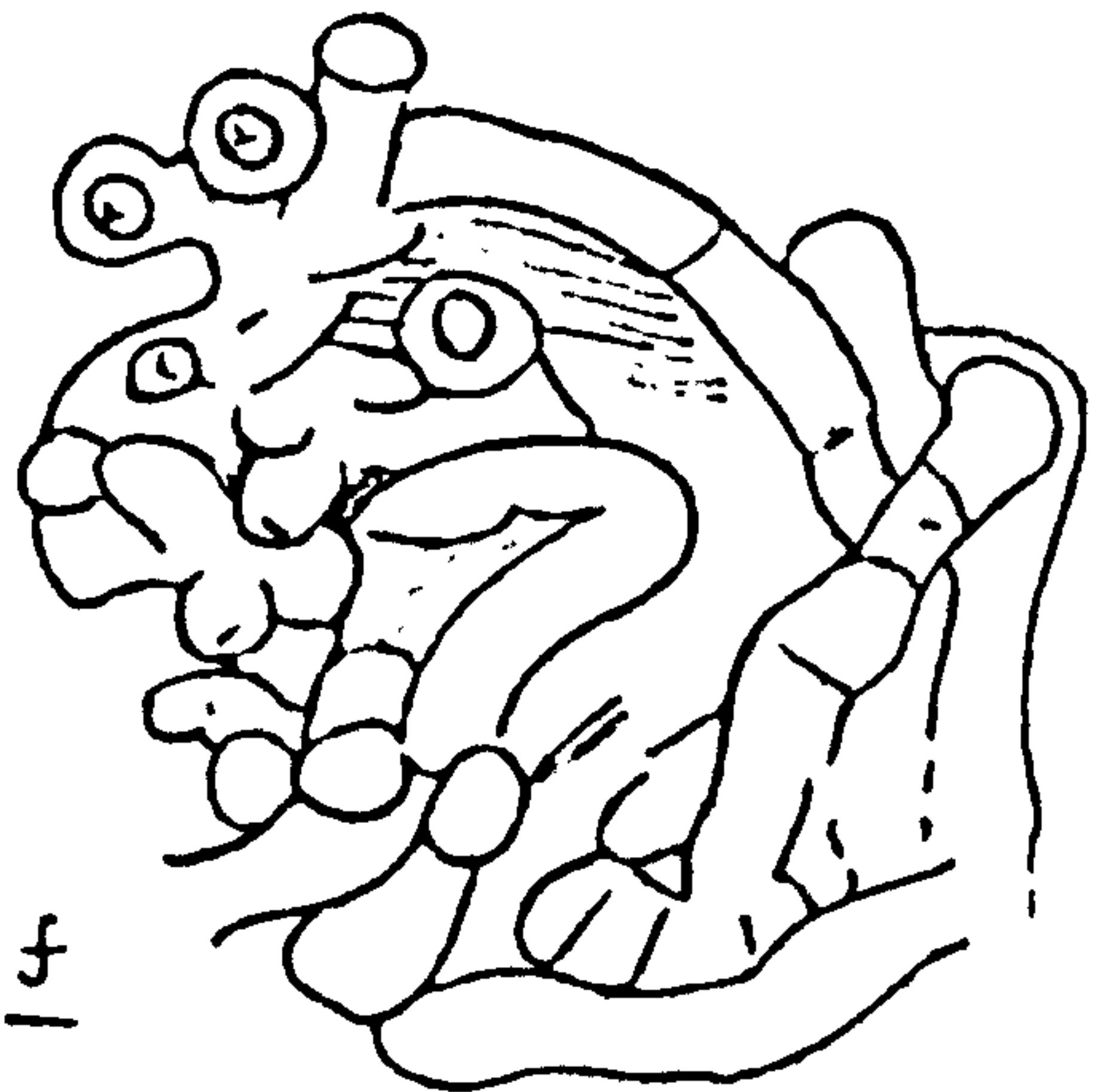
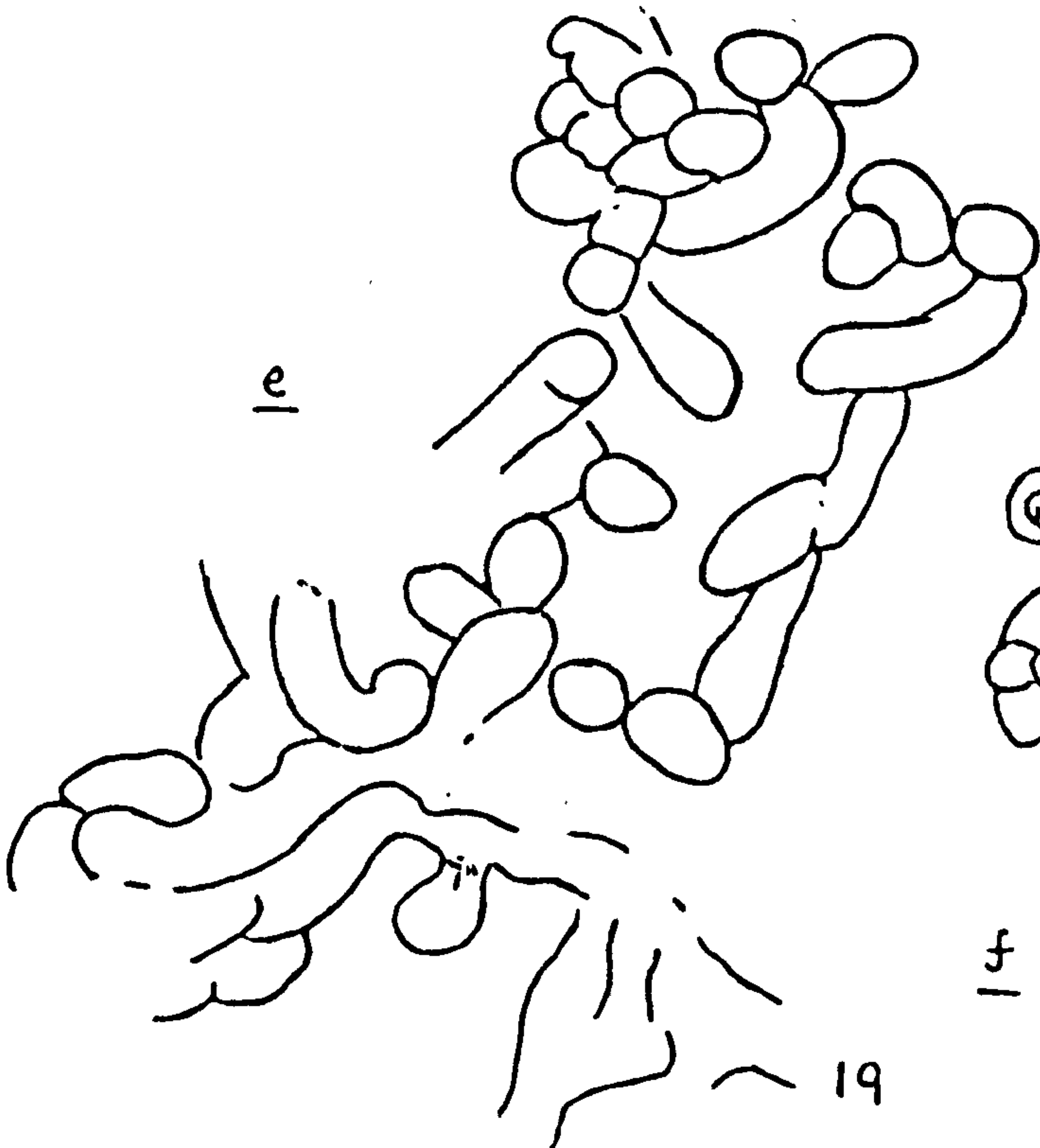
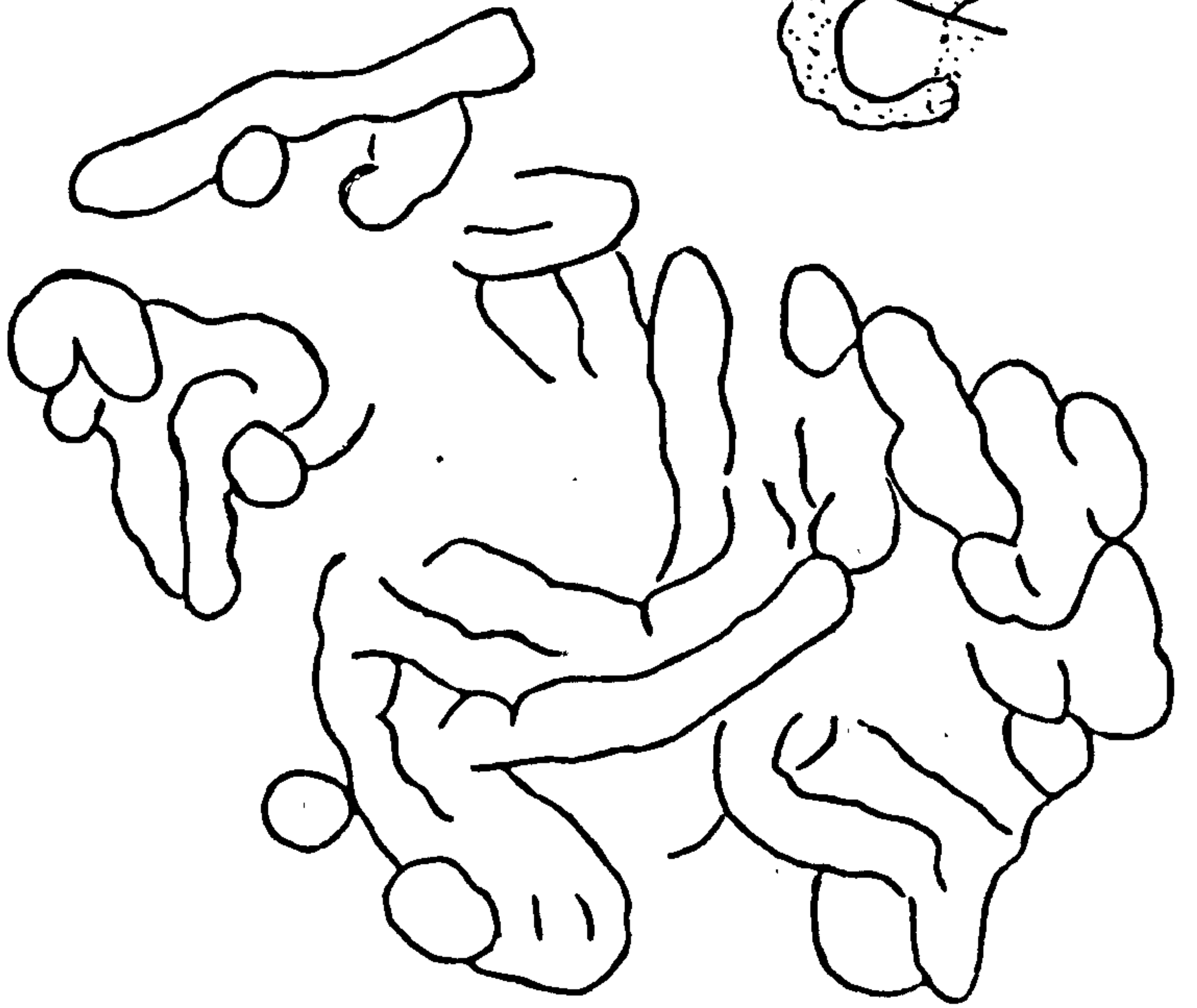
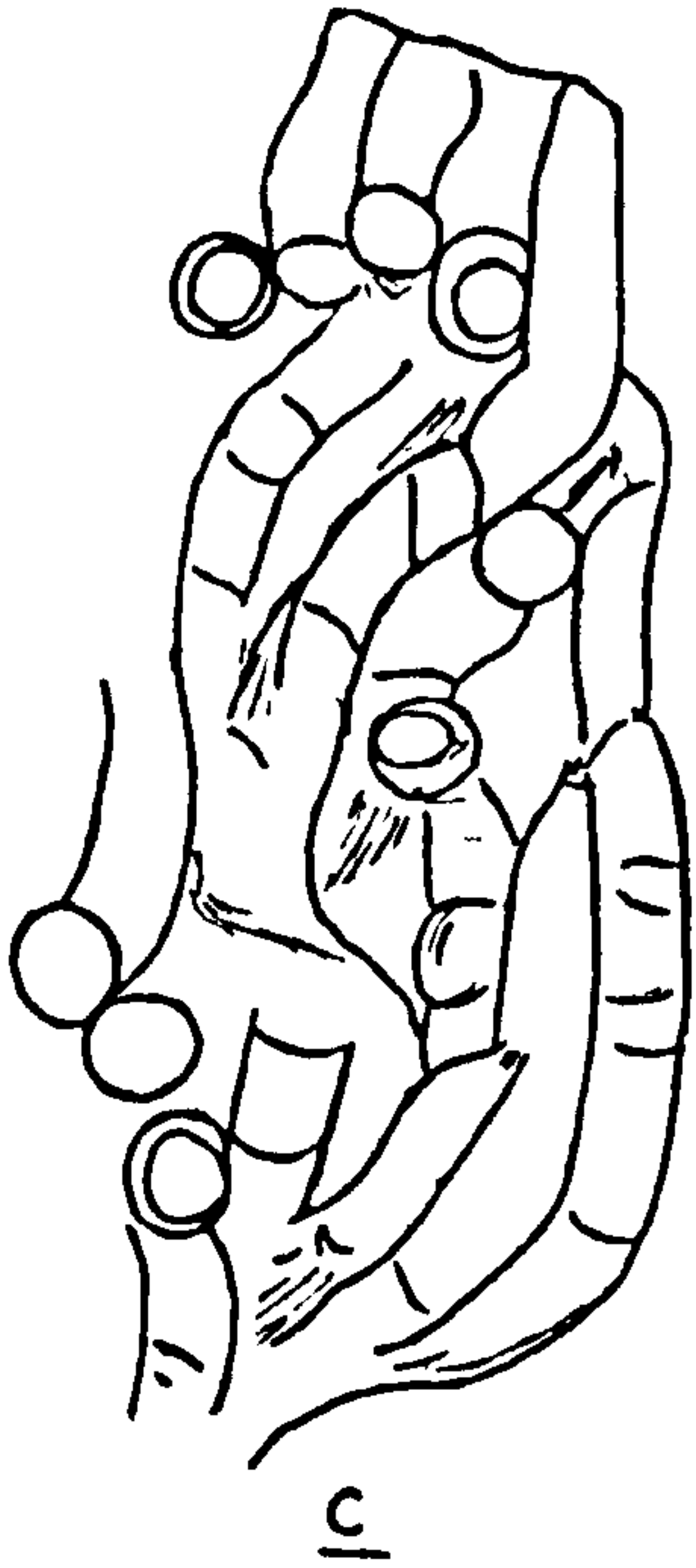
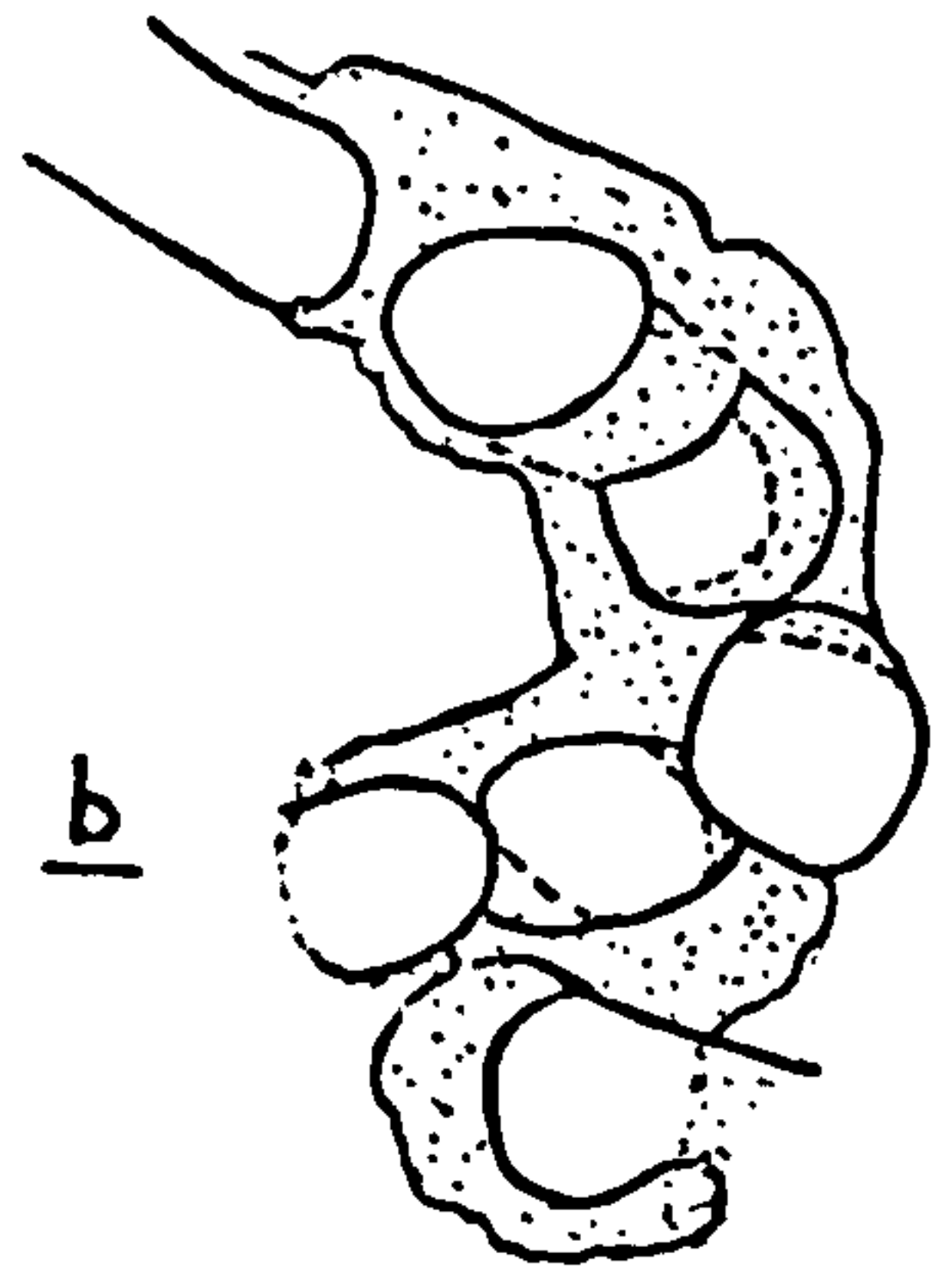
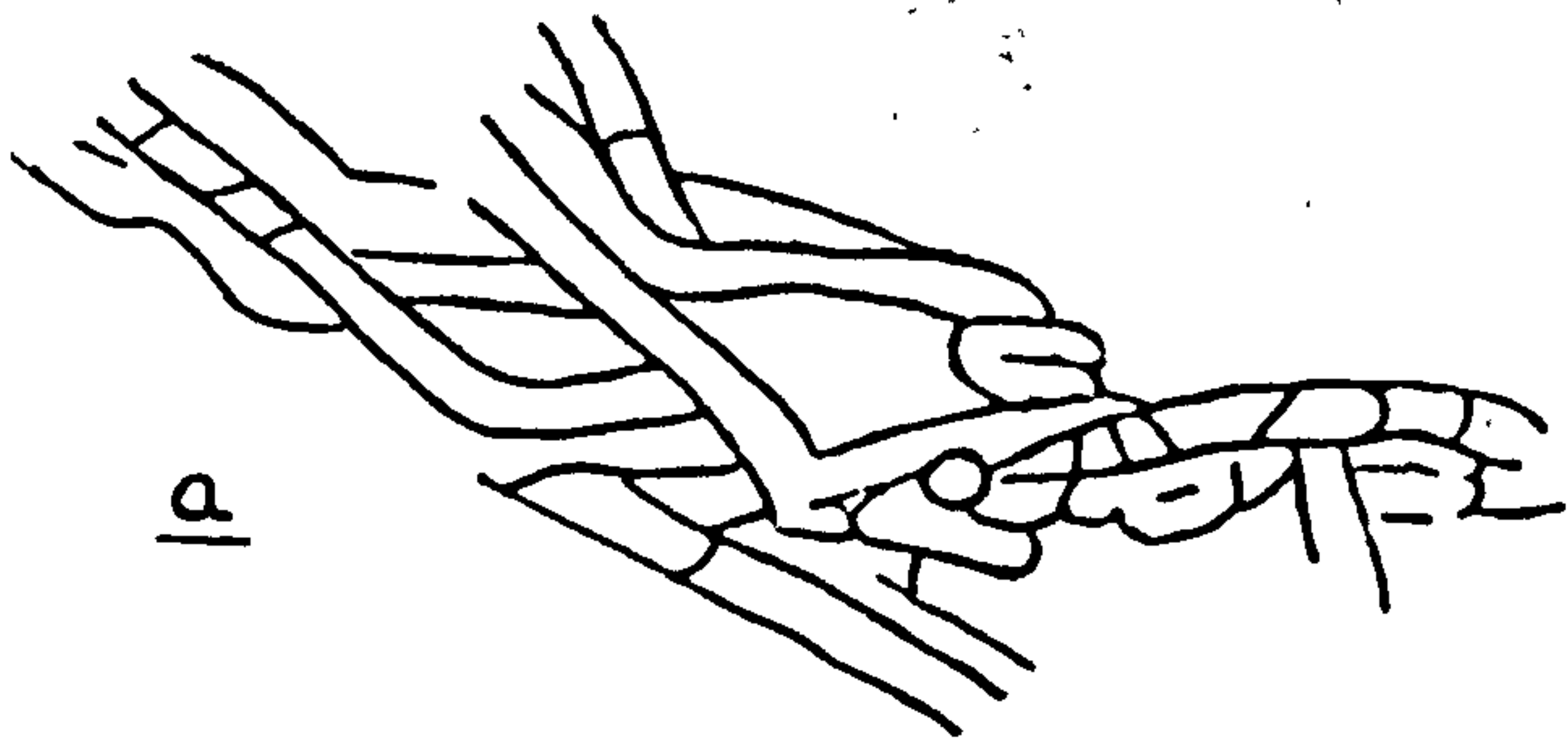
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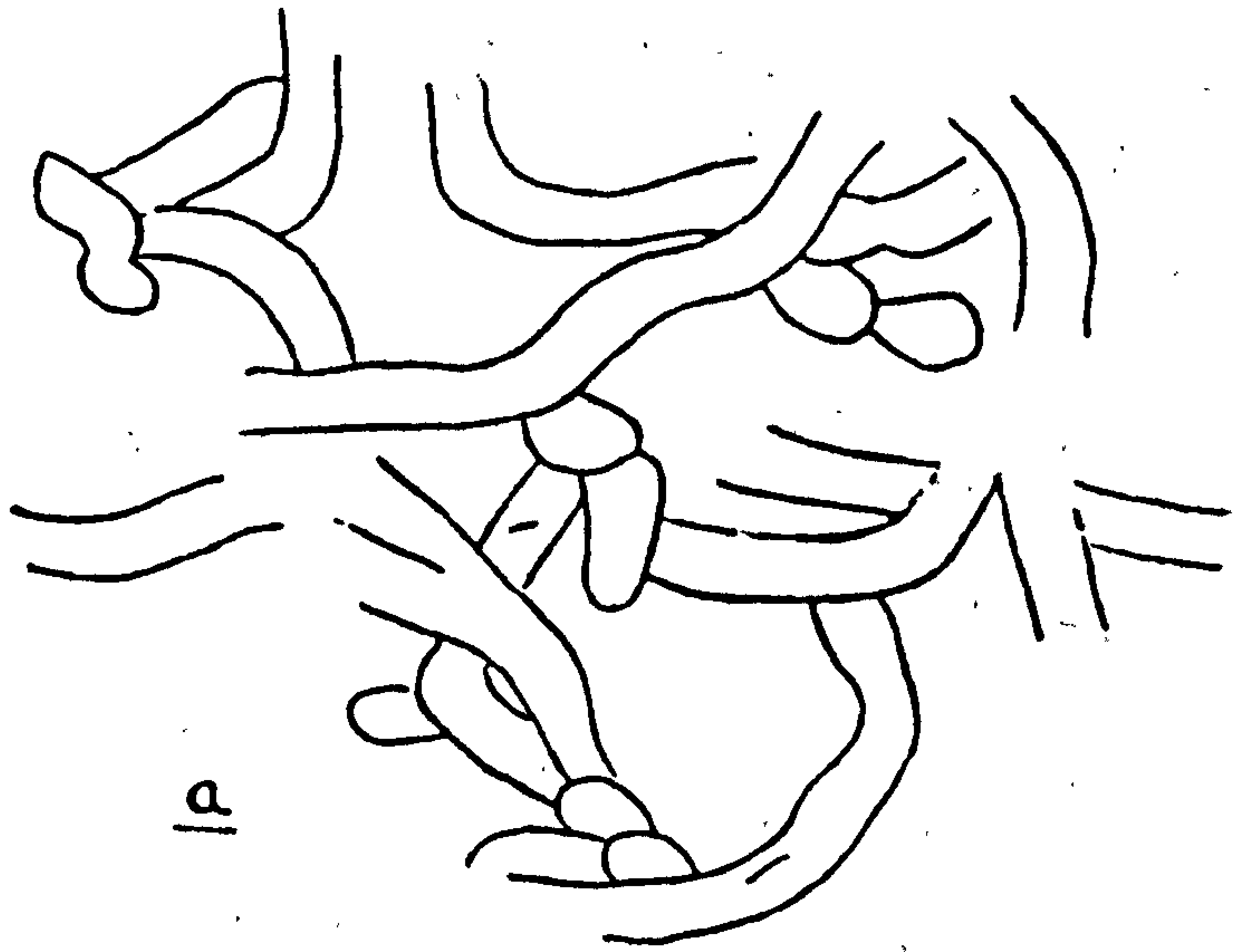


b

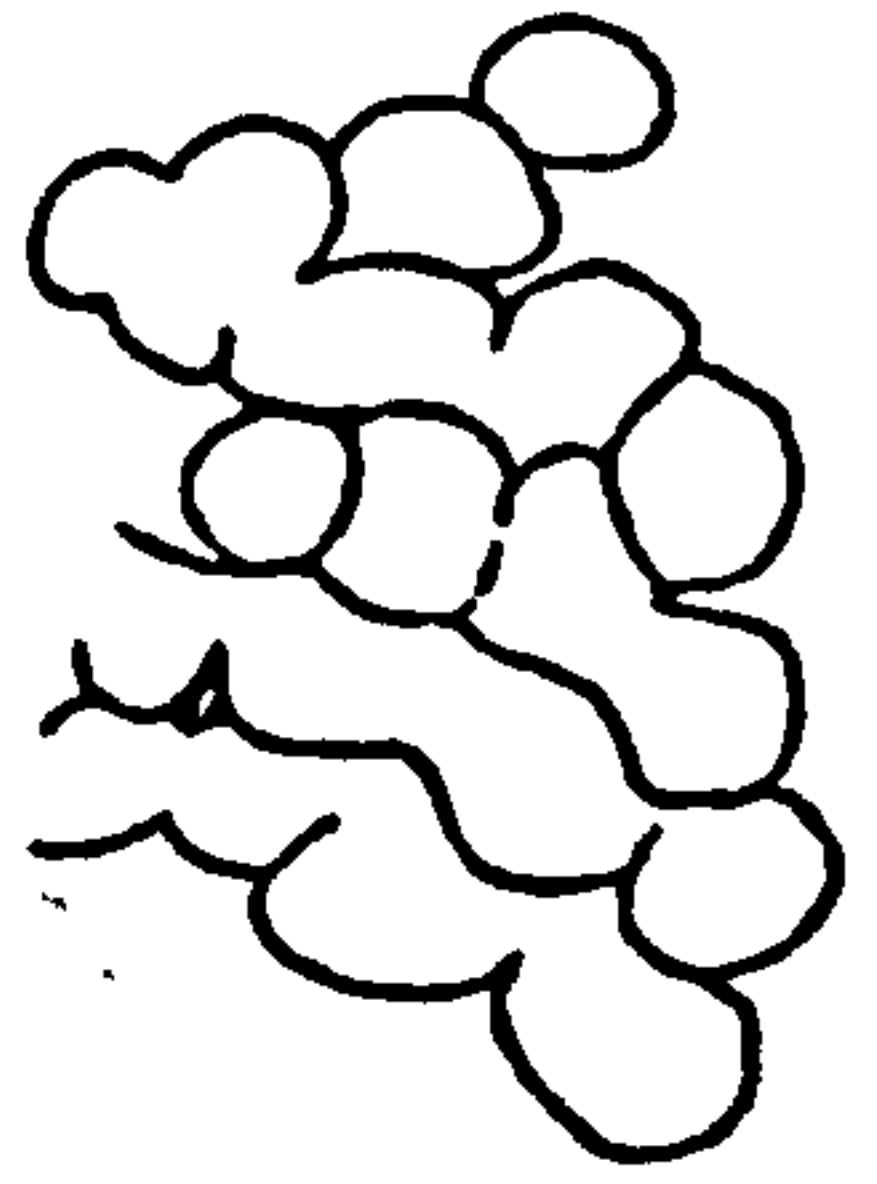


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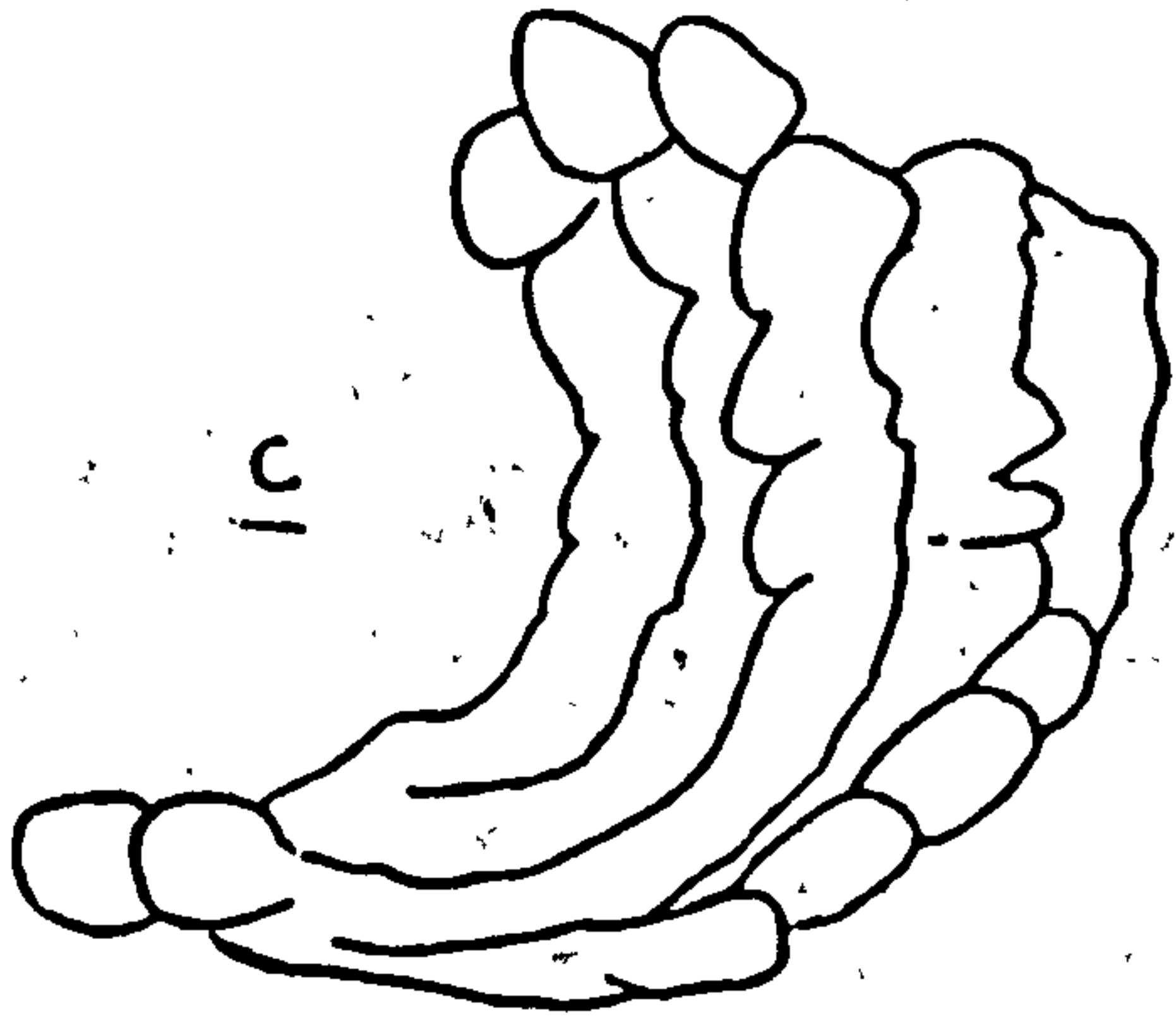




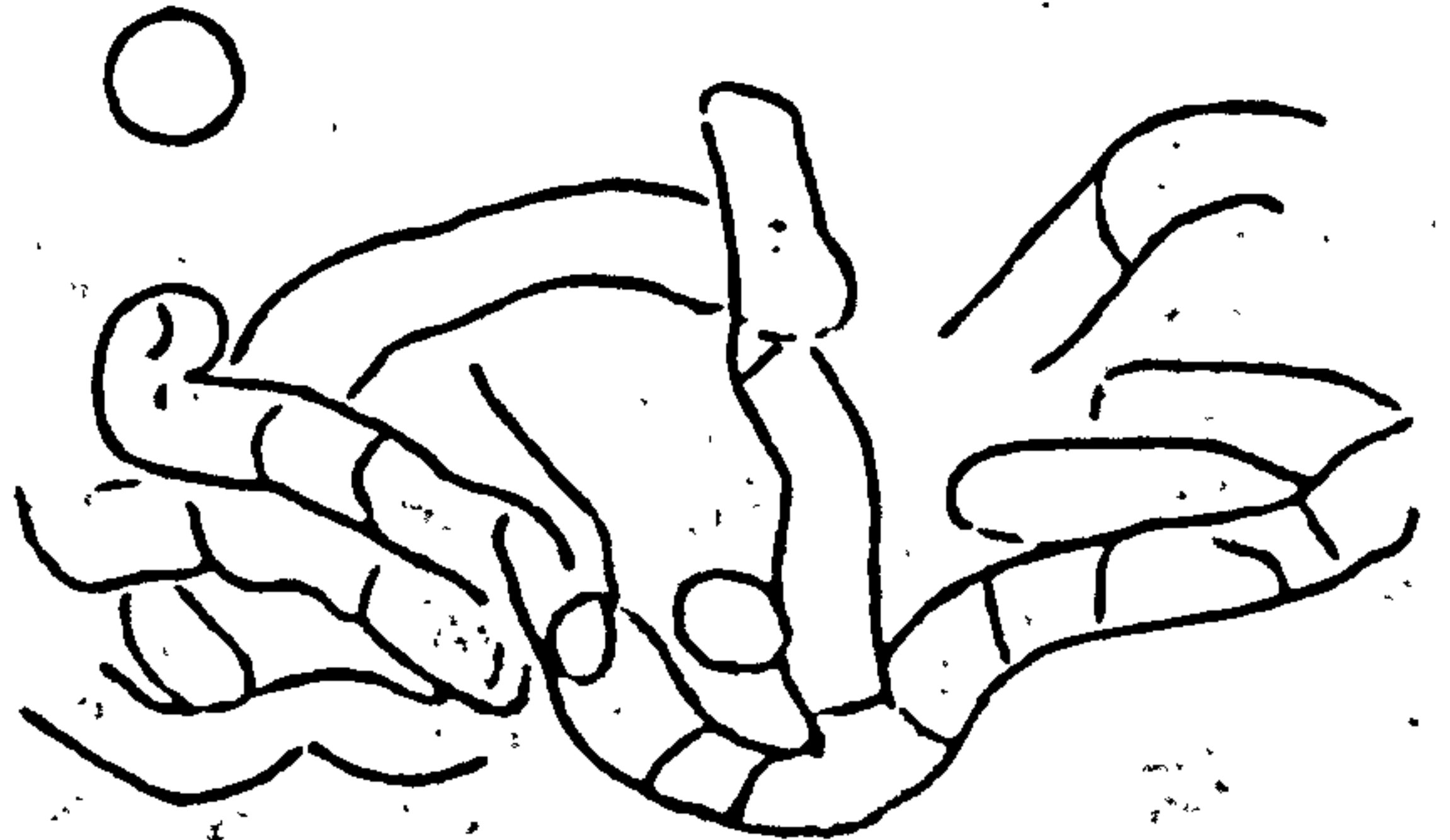
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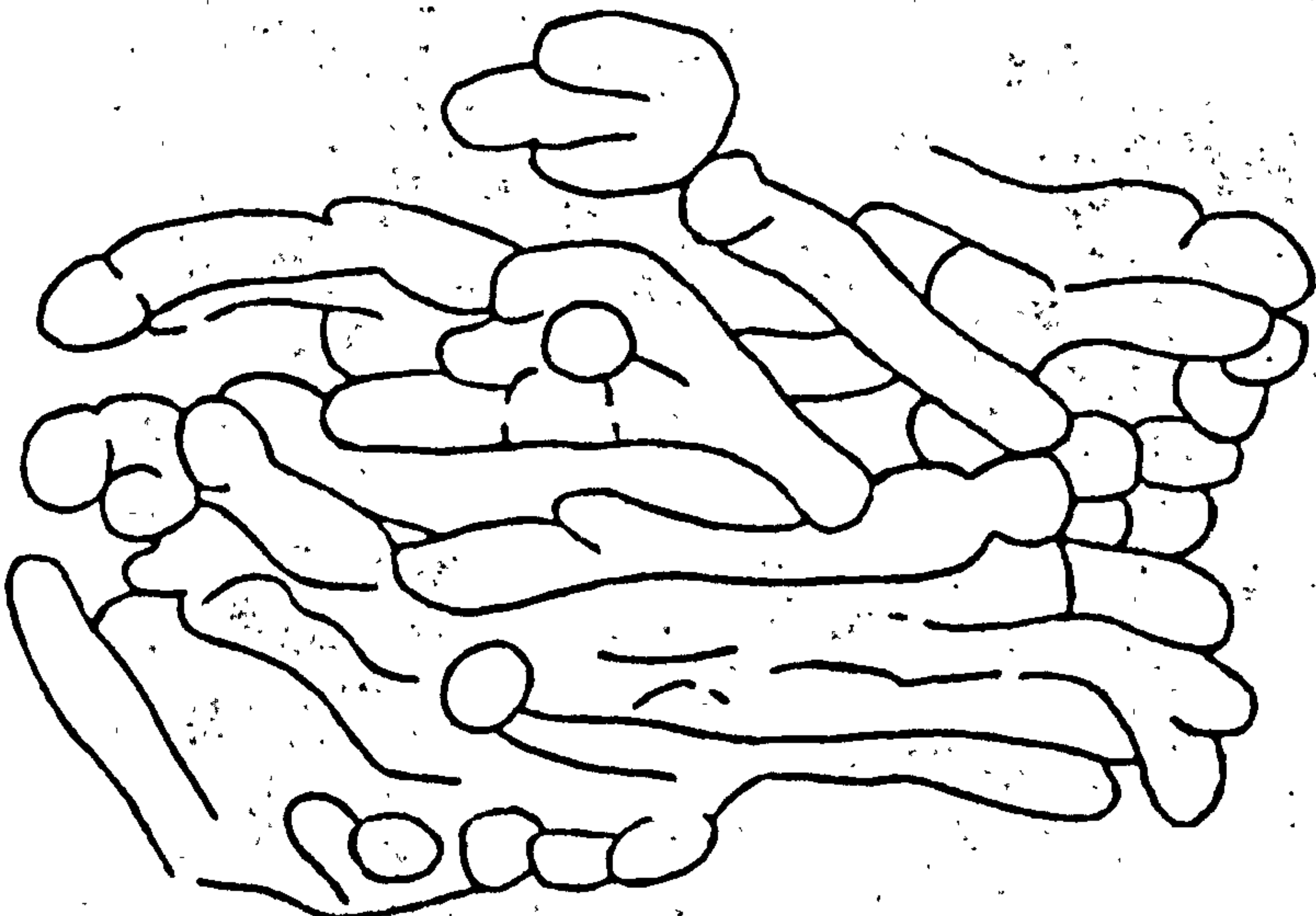
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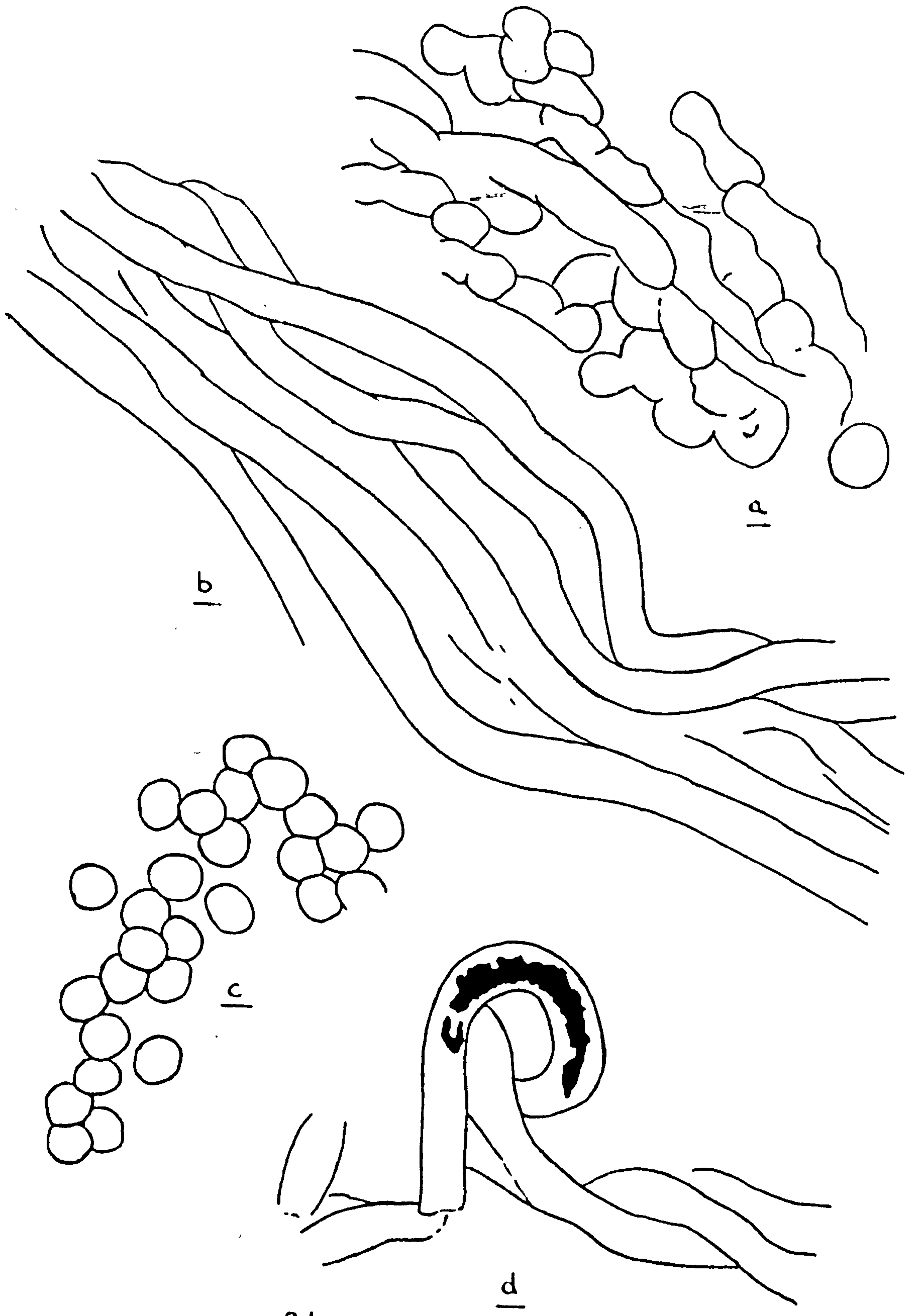
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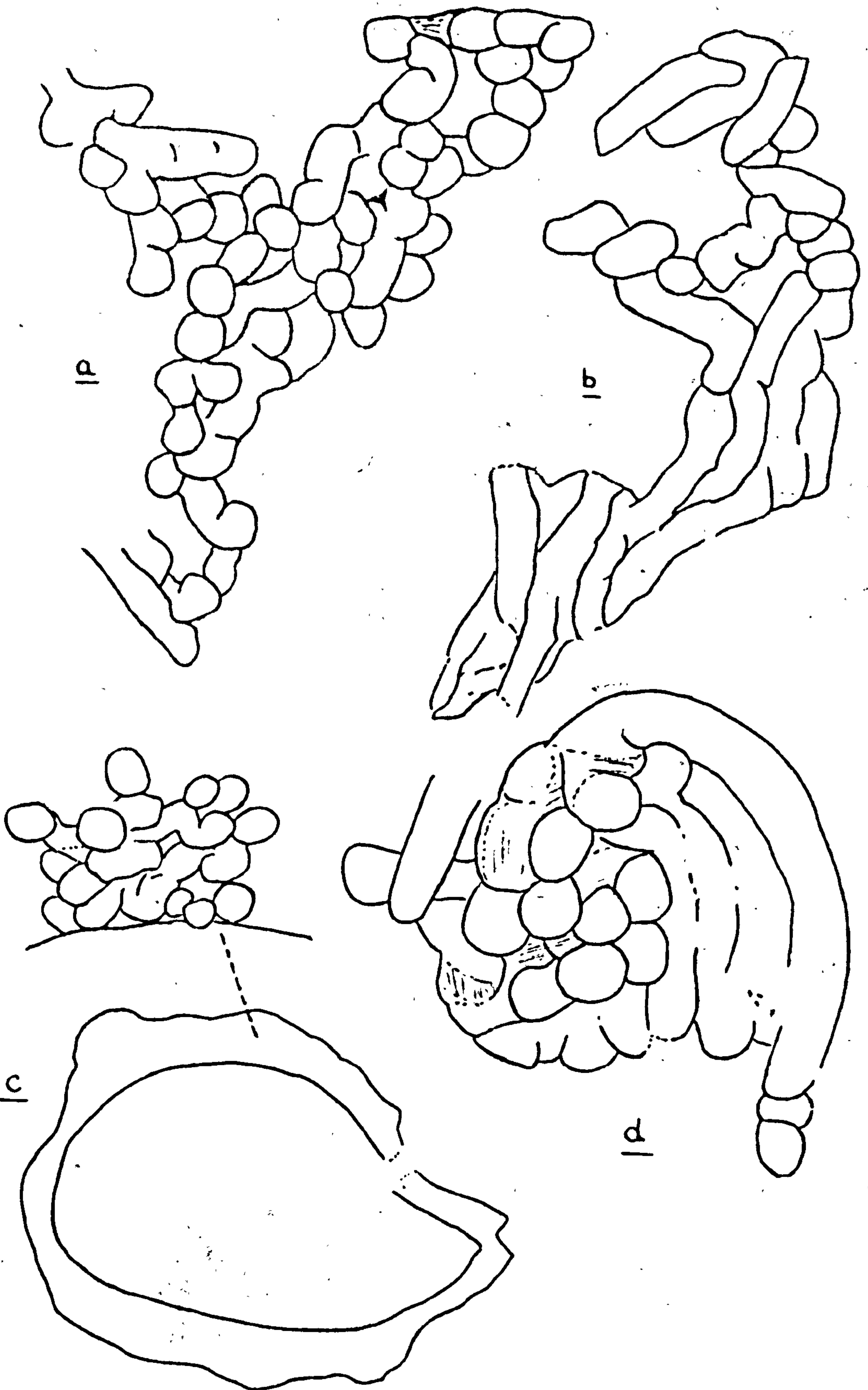
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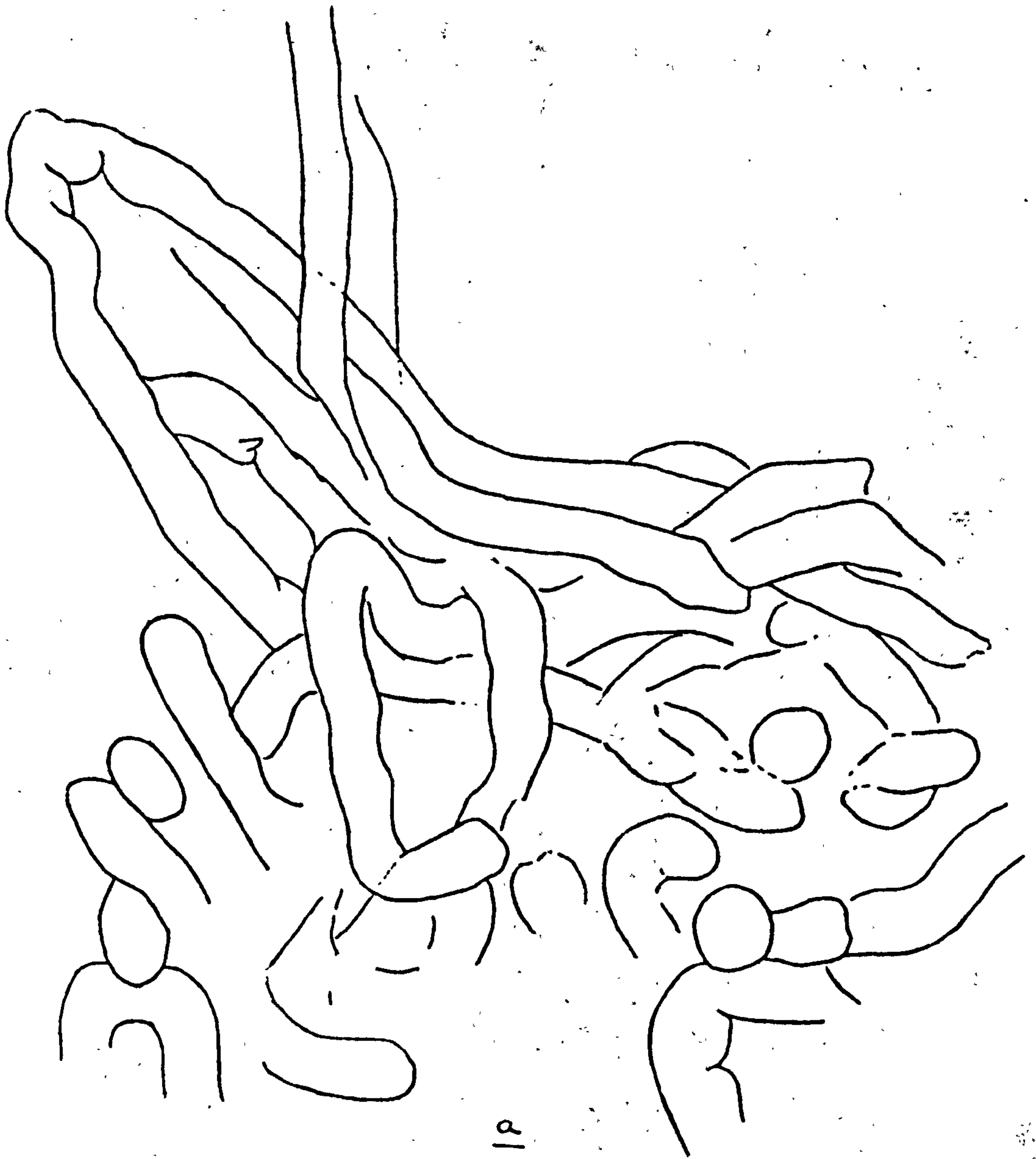


1f

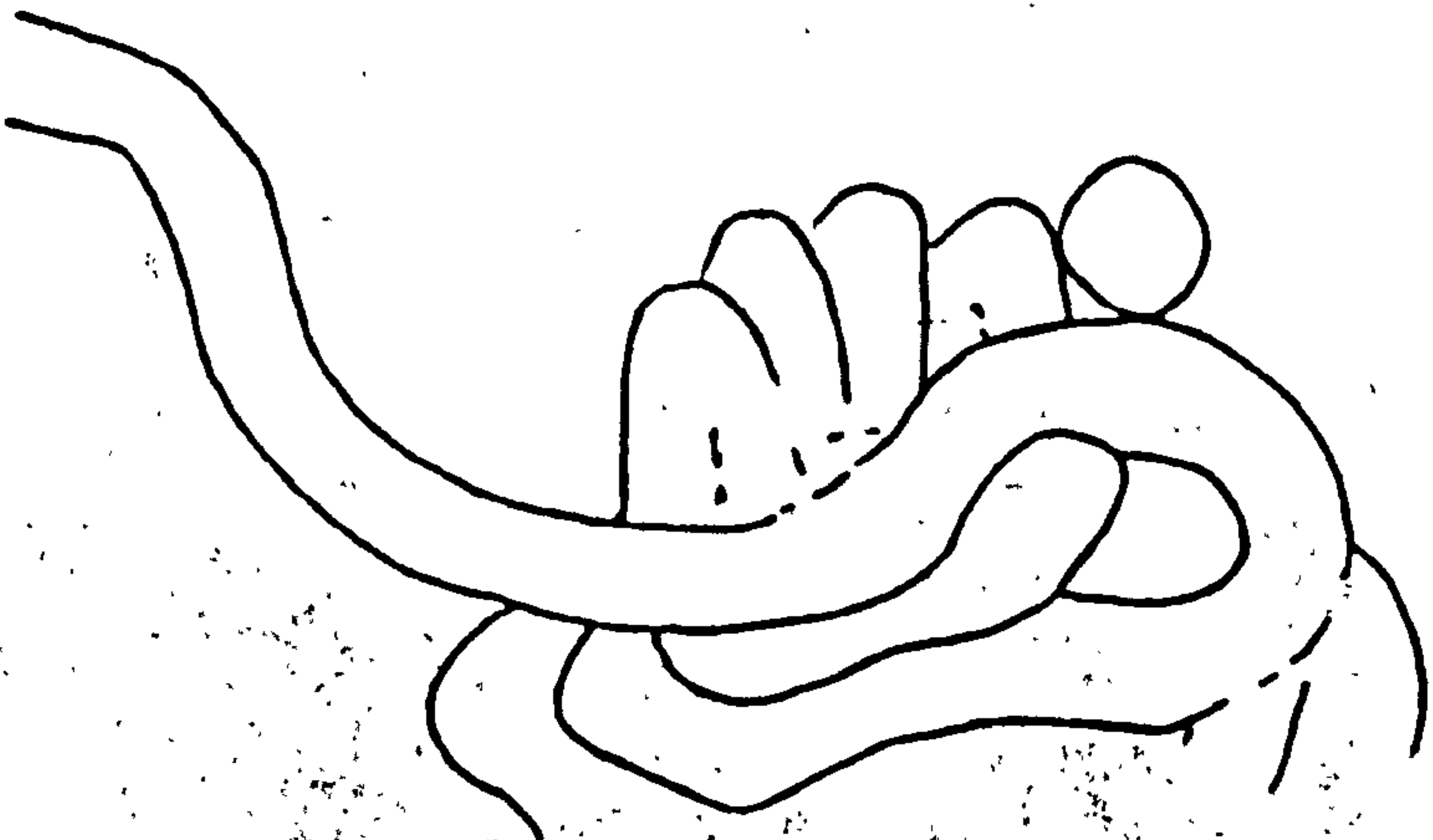


21.





19



23

b



Description of genus

(Rothpletzella) 1891

Type species is Rothpletzella gotlandica, Wood 1948.

Wood described Rothpletzella typically as an encrusting organism, only occasionally forming a tight tangled coil without any visible nucleus. The dichotomously branching filaments are in contact with each other and are arranged concentrically around a nodule, thus distinguishing it from Cayeuxia, Garwoodia and Hedstromia. The threads when cut transversely give a 'beaded' appearance. The filaments possess the same fine granular calcite wall as Girvanella, but differ from it in the mode of branching. Wood described it also as possessing no cross walls and disclaimed all records of previously postulated reproductive organs. Because of lack of septation he classified Rothpletzella with Myxophyceae or the Siphonales.

The following species descriptions are of those collected from various Woolhope and Wenlock limestone localities.

Remarks

During this investigation no sign of reproductive organs has been found in any member of the genus. This, as there are also no published records, indicates either lack of preservation of these structures, or infrequency of production of these organs, or just a lack of any visible



structure being preserved in fossil state.

In one case (fig.26) a specimen, the type species, is so preserved that a possible cellular structure is indicated rather than a coenocytic mode of life. If septation occurred, as in Girvanella, the placing of Rothpletzella need not be restricted to the Myxophyceae (Cyanophyceae) or Siphonales.

The specimens obtained were compared in their form and habit with those from the Silurian of the Högklint Series, Gotland. The most conspicuous difference found was that the Gotland specimens formed massive growth forms (fig.86) of two or three species of Rothpletzella together with Girvanella and Wetheredella, whereas the specimens were more isolated from the Welsh Border, and only in a few cases contributed to small growth forms as at May Hill and Dudley (figs. 84, 85). All showed the same beading and fan-like branching of the filaments.

Gotland specimens were measured for a ratio of width of bead against length of bead, so as to make a wider comparison with other members of the genus. The results were plotted as a histogram, and generally the ratio was 1:2.

Each bead length as measured along the length of a  
tube

When compared with the tube width should give an indication of the angle of emergence of the branch from the original tube if the tube forming the bead is equal in diameter to the tube from which it originated, this remaining in the same direction.

$$\text{Angle of emergence } B = \text{angle of divergence of branching}$$

$$\text{Sin } B = \frac{\text{tube width}}{\text{bead length}}$$

$$\text{Av. Sin } B = \frac{\text{average tube width}}{\text{average bead length}}$$

$$\text{Sin } B = (1/2) = (0.5) = \underline{30^\circ}$$

$$\underline{\text{Angle of emergence} = 30^\circ}$$

If, however, the branching is dichotomous, the angle between the fork branches would still be expected to be approximately  $30^\circ$ , each  $15^\circ$  from the original direction of growth, for if the forks were at right angles to each other the bead so formed would be very approximately the width of a tube.

'Face' views, showing dichotomous branching, were then measured from the Welsh Border specimens, and the angle of divergence between branches was usually slight and about  $30^\circ$  wide. (fig. 34).

This small divergence (approx.  $30^\circ$ ) of branches therefore seems fairly characteristic of the genus.

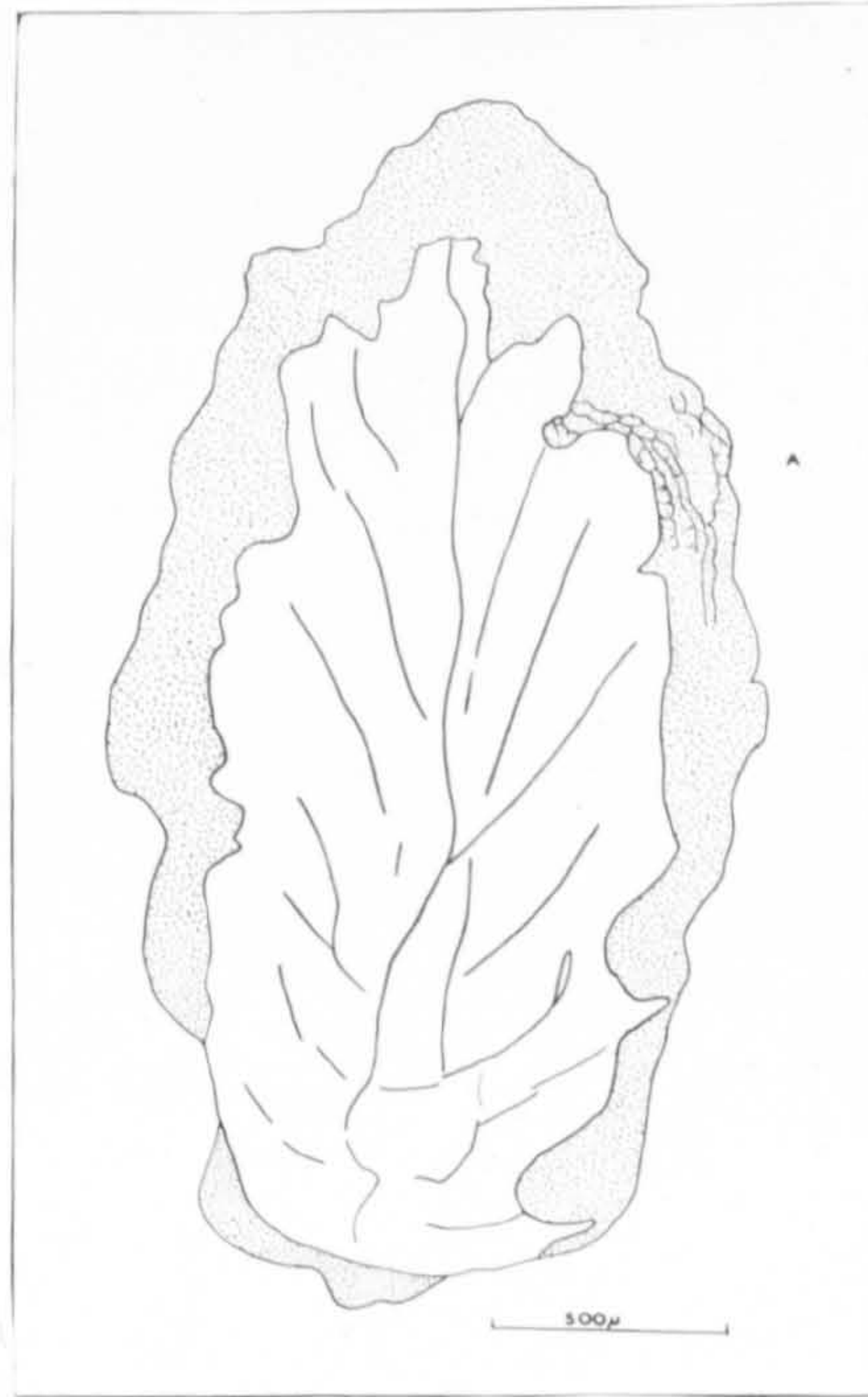


Fig.24. Rothpletzella gotlandica encrusting Coenites.  
 Diagram stippled areas is extent of alga remnants. At A, direction of filament growth is shown. Bryozoan Beds, Wenlock Edge, (W.E.2(4)) x 30.

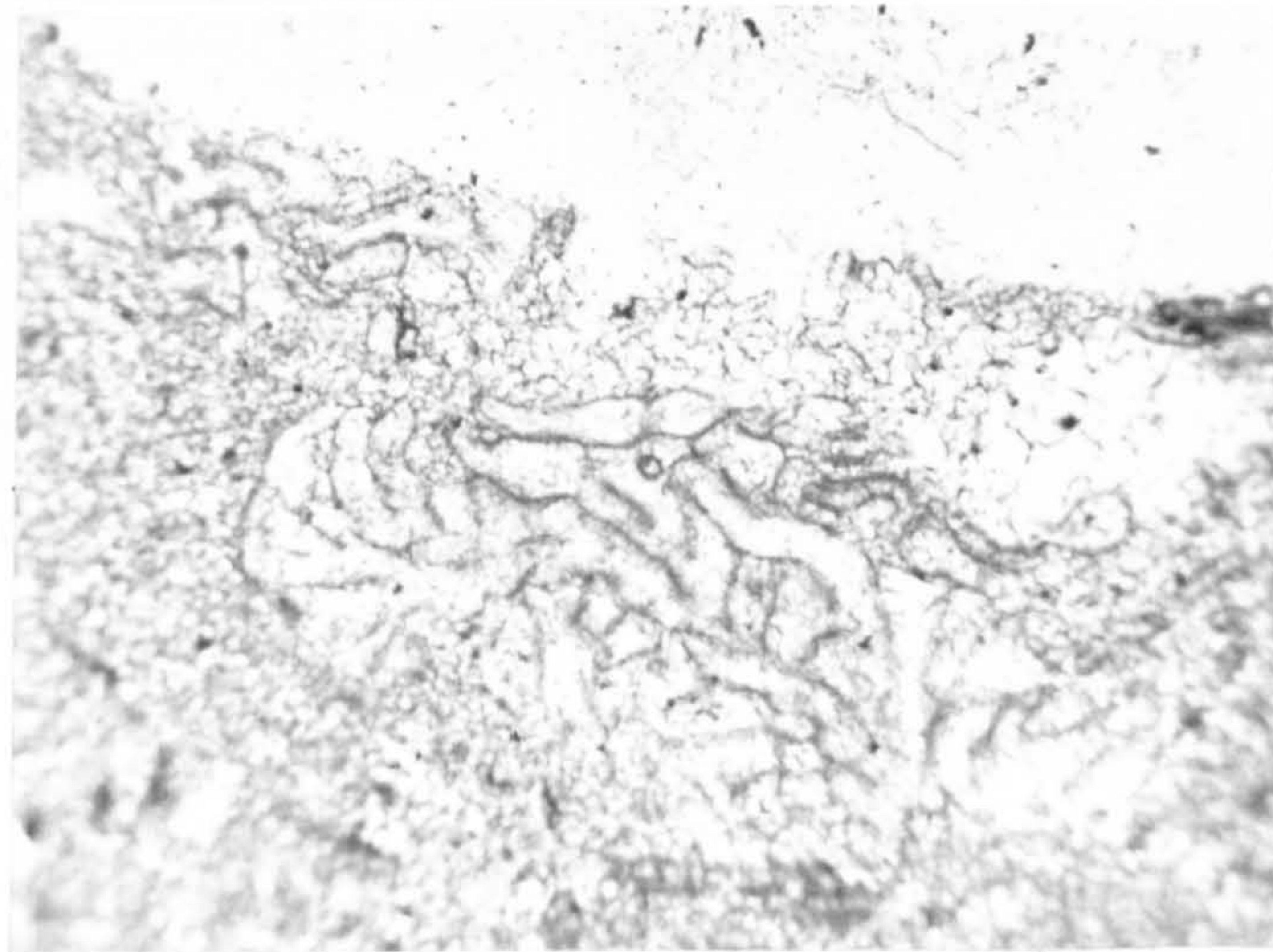


Fig.25. R. gotlandica together with a few Girvanella filaments encrusting a bryozoan. Both beading and dichotomous branching visible in Rothpletzella. Nodular Beds, Dudley. x 100.

ROTHPLETZELLA GOTLANDICA (Rothpletz)

figs. 24-27, 39.

Girvanella, Wethered 1893 p.236, pl.VI.fig.4 a.b.

Sphaerocodium gotlandicum, Rothpletz 1908, pl.II. fig.2.

Rothpletz 1913, pl.VII, fig.3.

Rothpletzella gotlandica, Wood 1948, p.19. pl.II, figs.A.B.

Description

Wood described the filaments to be of a diameter usually 30-35 $\mu$ , occasionally to 40 $\mu$  and with walls 5-6 $\mu$  thick. The filaments branch rapidly to give the fanlike form characteristic of this genus.

Horizon and localities

This form was recorded from the Silurian limestones of Gotland by Rothpletz (1908, 1913) as Sphaerocodium gotlandicum and from the Woolhope Limestone of Old Radnor district by Garwood and Goodyear (1918). Wethered also found this form at May Hill (Glos.) and Purley (W. Malverns) but regarded it as a Girvanella. Wood (1948) records this species from both Woolhope and Wenlock Limestones of the Baltic, but no localities are cited.

Rothpletzella gotlandica has been found during this investigation in the Woolhope Limestone of Old Radnor and

the Wenlock Limestone of Wenlock Edge, Dudley, Fownhope, Woolhope, May Hill and West Malverns.

### Remarks

Most filaments of this form, when measured were found to have a diameter varying between  $30\mu$  and  $36\mu$ , but occasionally a coarser variety was found with diameter  $36-40\mu$  and rarely more in their broadest parts. The more abnormal measurements may be where branching had occurred. The usual wall thickness, where tubes were in contact, was found to be between  $3\mu$  and  $6\mu$  wide.

The dichotomously branched filaments are usually adherent to each other. Where the branches have been cut through in sectioning, the 'beaded' effect is obtained, due to the unevenness of the diameter at the point of bifurcation. (figs.26,27). It is possible that beading may not always mean branching but may only mean the length of a cell (if originally septate). However, those filaments seen in face view showing the fanlike branching do not also show beading between these branches, only nodal swellings, but only show it either at the edge of a group with fan-branching or independent of it, i.e. the filaments are not seen in face view.

The possible original existence of cell walls to the filaments of this form may be indicated by the specimen obtained from Fownhope (fig.26) which shows the fine granular calcite over the walls, tending to cut off portions of the filaments. If this does indicate septation, it is another example of the results of better preservation.

R. gotlandica was found to occur either as apparently non-encrusting small clusters or encrusting other organisms such as bryozoa, stromatoporoids, Wetheredella, corals particularly Halysites. Occasionally it has been found encrusting other organisms in association with other algal filaments, such as Girvanella. Usually it completely intermingles with these other filaments, but sometimes forms distinct patches. (fig. 25).

No structures resembling reproductive organs have been found.

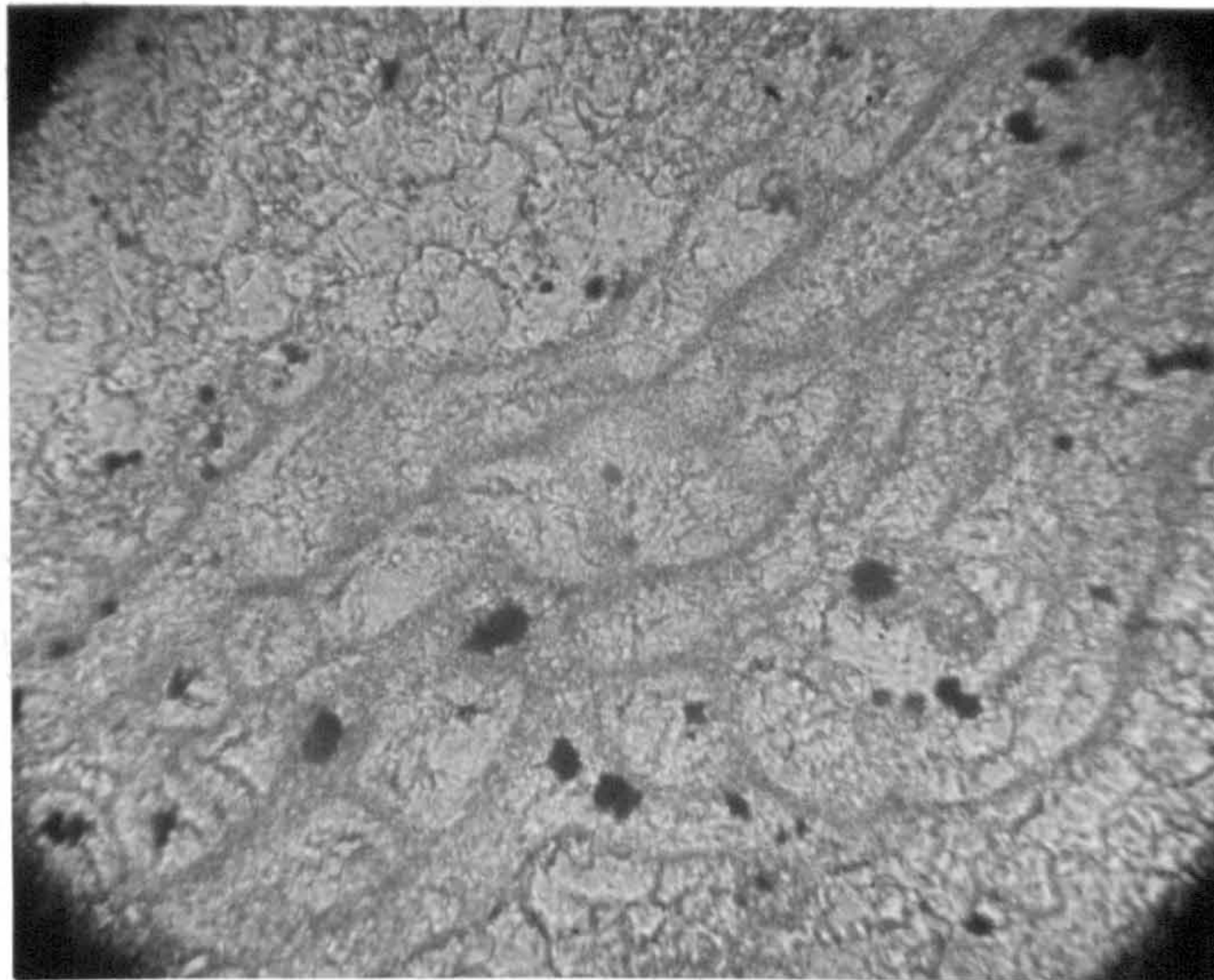


Fig.26. R. gotlandica. A small group showing beading and the finer calcite dust possibly demarking cells. Wenlock Limestone, Fownhope. x 215.

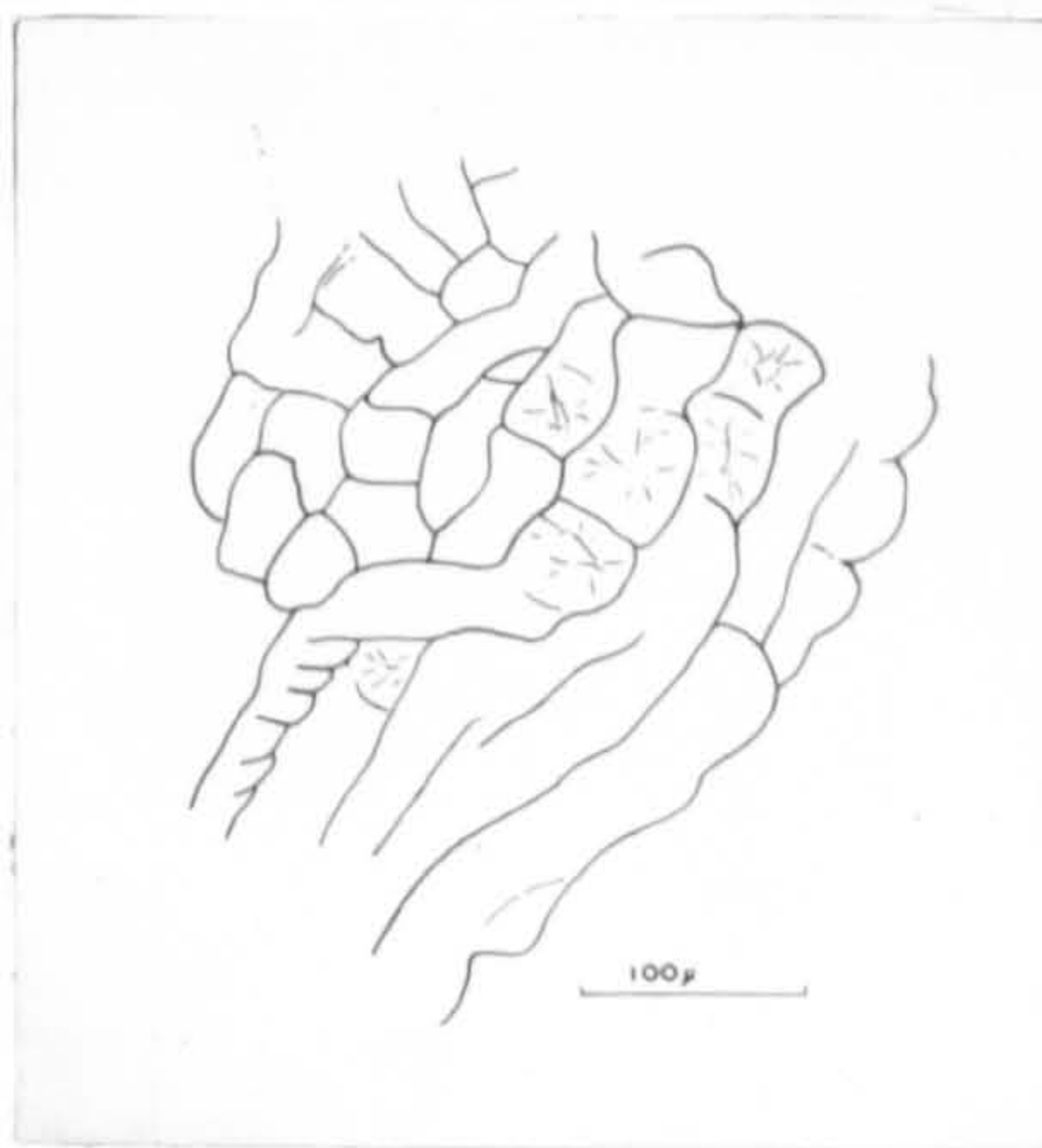


Fig.27. Diagram of branching R. gotlandica group. Cracks in calcite indicate branches cut across in section. Grey Measures, near Ballstones, Wenlock Edge, W.E.3. x 110.

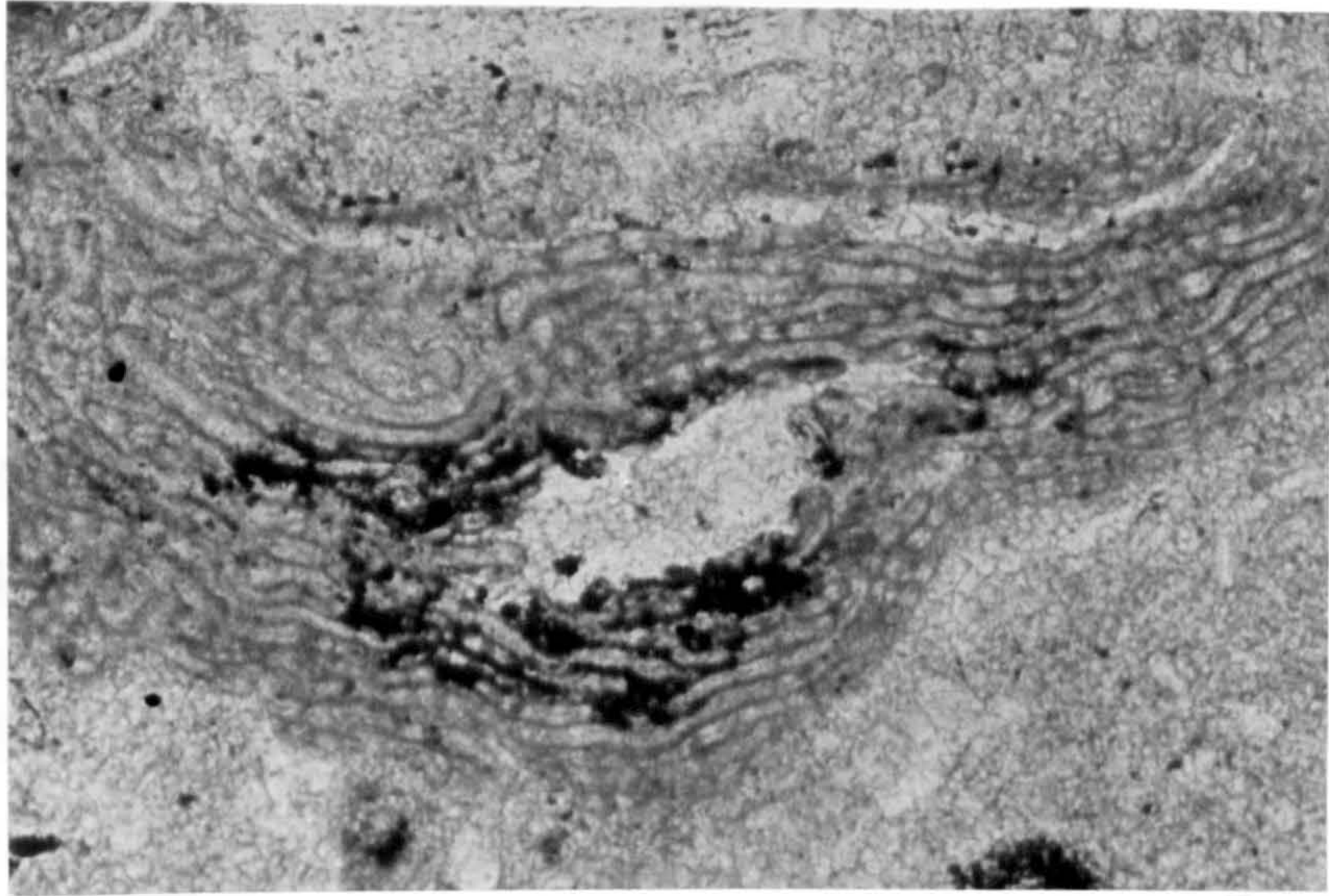


Fig.28. Rothpletzella conferta encrusting organism.  
Note beading of filaments.  
L. Limestone Group, Dudley (D.U.1(3)). x 90.

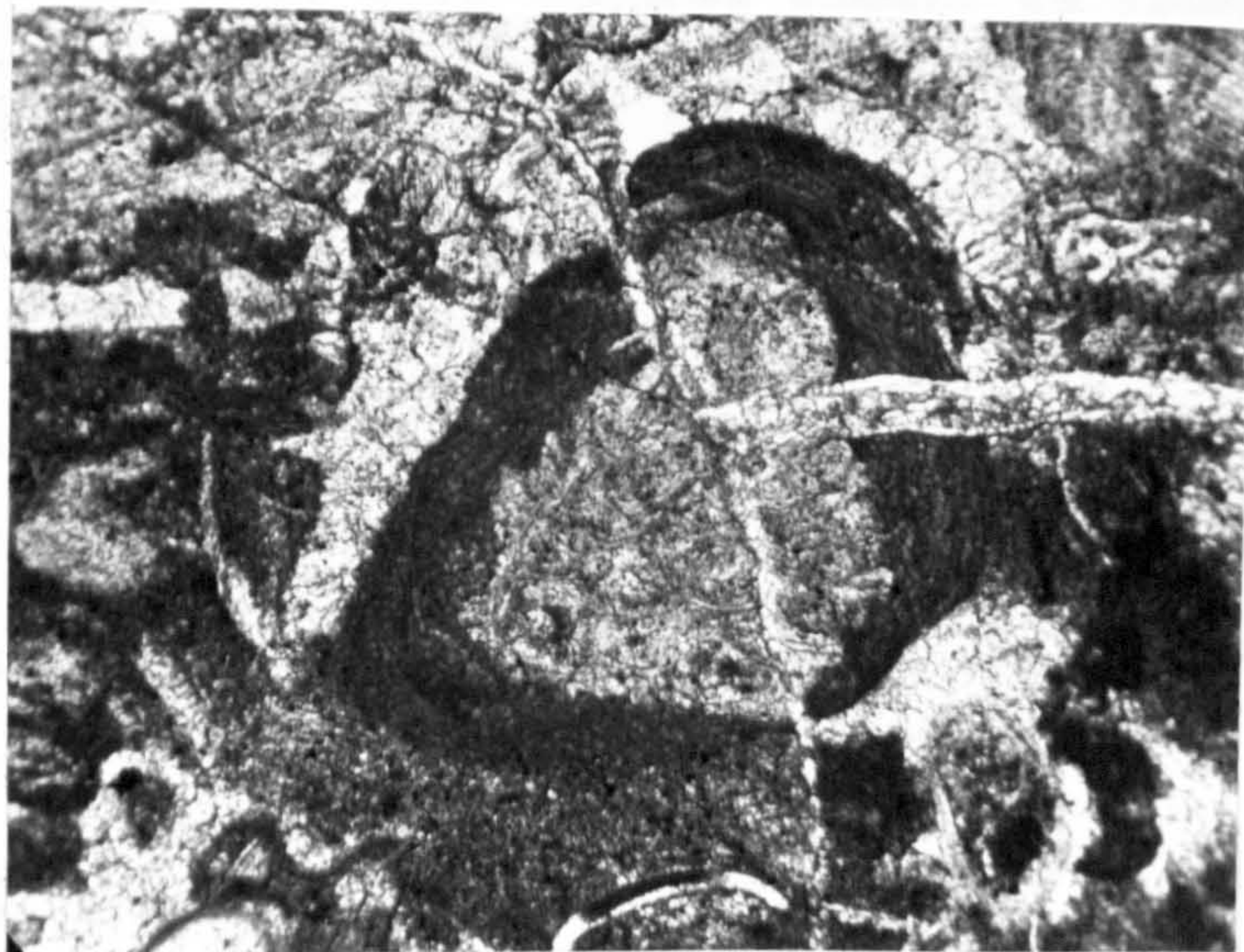


Fig.29. R. conferta filaments (dark in photo) surrounding Coenites as seen in transverse section.  
Woolhope Limestone, Yat Farm, Old Radnor  
(O.R.2(7)). x 25.



ROTHPLETZELLA CONFERTA (Chapman)

figs. 28-37

Girvanella conferta Chapman 1907, p.383, pl.2,3.

Sphaerocodium munthei Rothpletz 1913, pl.4, fig.3.

Rothpletzella munthei Wood 1948, pl.19,20 pl.4. fig.c.b.

Description

Rothpletzella is the algal constituent of Sphaerocodium (Wood 1948), and as this form species was described first by Chapman (1907) as a Girvanella from Dudley and Australia, but showed the matted filaments with tortuous outlines, and beading and branching typical of the genus Rothpletzella, it would appear that this species should be renamed <sup>replaced as</sup> R. conferta and not R. munthei, though the type specimen of G. conferta has not been seen.

Wood describes R. munthei as having tube diameters 20-25 $\mu$  but Chapman stated G. conferta had diameters of average 17 $\mu$ , but if the magnifications stated for the photographs are correct, the diameter range measured for these appears to be of the order 20-25 $\mu$ .

Wood also gives the wall thickness of 2-3 $\mu$ , so that this species differs only in the finer threads and their walls from the type species, except that possibly the filaments are

more variable in size possibly due to easier crushing than in R. gotlandica.

#### Horizons and localities

Wood recorded R. munthei from the Wenlock Limestone of Gotland only. Chapman (1907) had however recorded his Girvanella conferta from the Wenlock Limestone of Dudley and also in Australia.

During this investigation this form was discovered in both Woolhope and Wenlock Limestones, thus extending both the vertical and lateral ranges of the form. It has been collected from the Woolhope Limestone of Old Radnor and the Wenlock Limestone of Dudley, Wenlock Edge and Fownhope. In some localities it was found to be more abundant than the type species.

#### Remarks

Filament measurements taken from the specimens obtained gave a minimum to maximum diameter range of 18-27 $\mu$ , the majority occurring between 20-26 $\mu$  diameter. Crushing and overlap appear to account for slightly lesser values in a group where the normal values are as above. The calcite wall diameter, where tubes are adjacent and in clear contact, usually measured 3 $\mu$ .

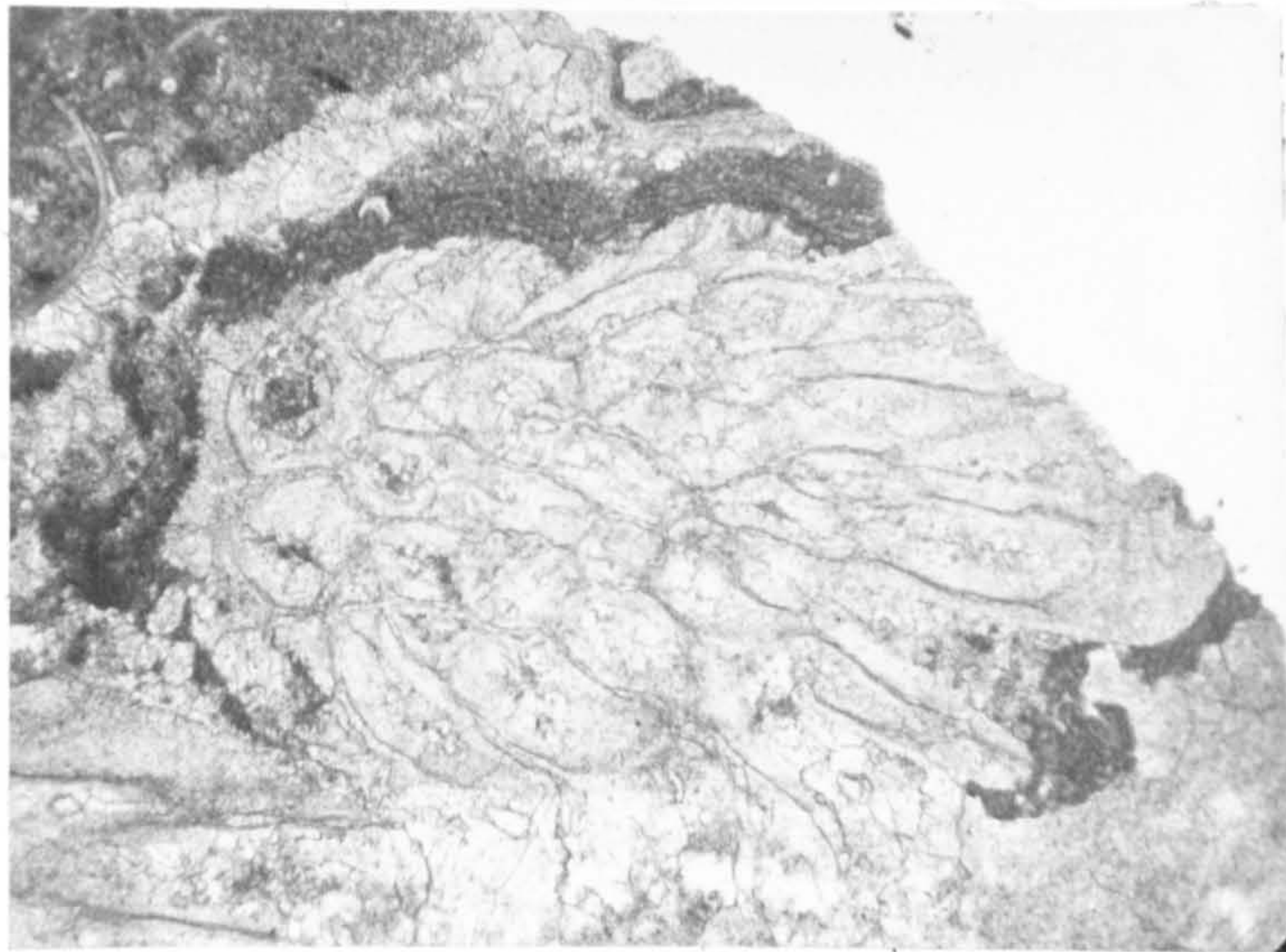


Fig.30. R. conferta encrusting Coenites. Bryozoan Band, Dolyhir Quarries, Old Radnor. x 25.

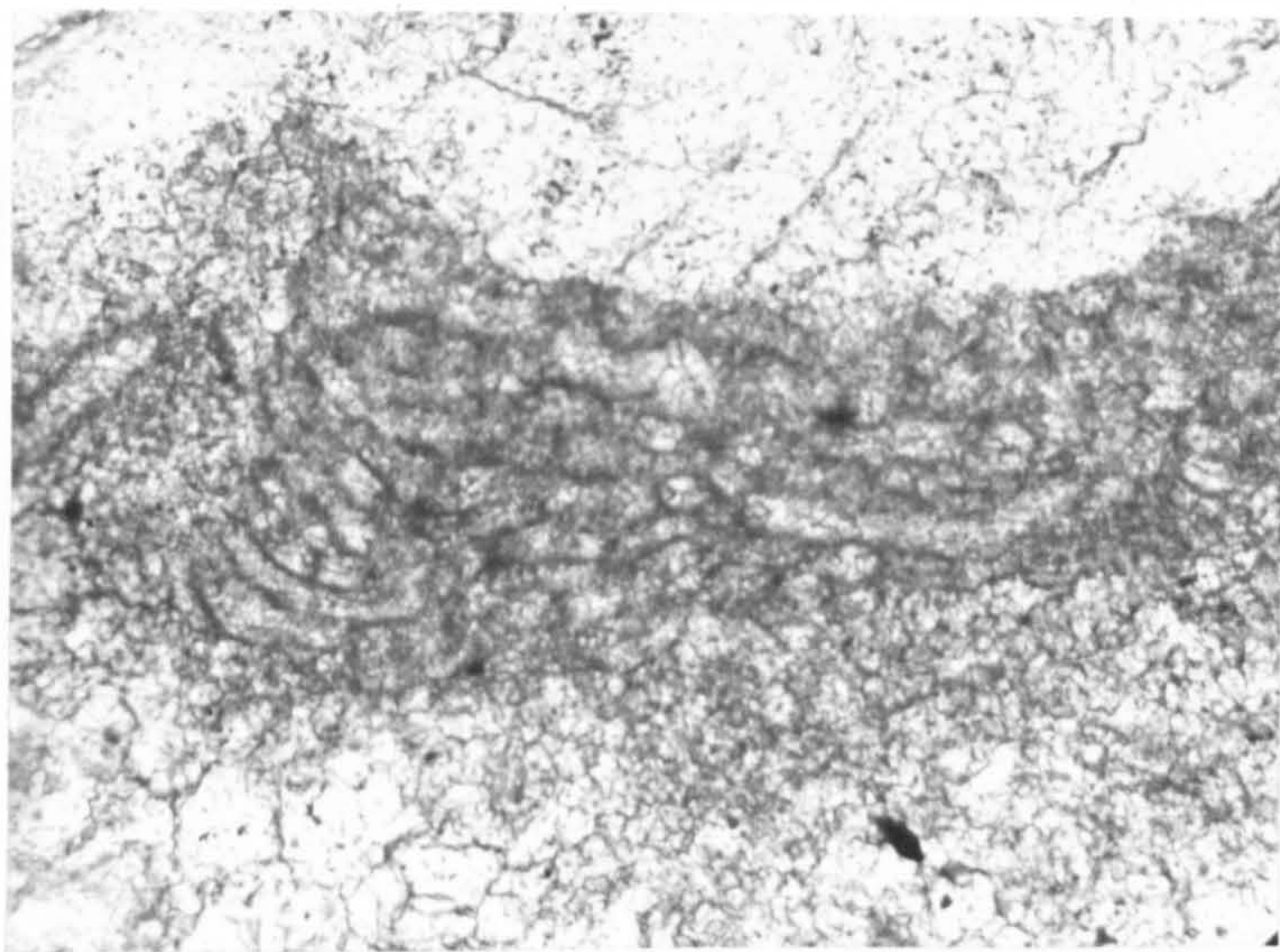


Fig.31. R. conferta, enlarged view of part of fig. 30. Shows rapid branching of filaments and noticeable beading and a gradation through algal dust to the clear calcite outside the cluster (upper part). Coenites occupies lower portion. x 150.

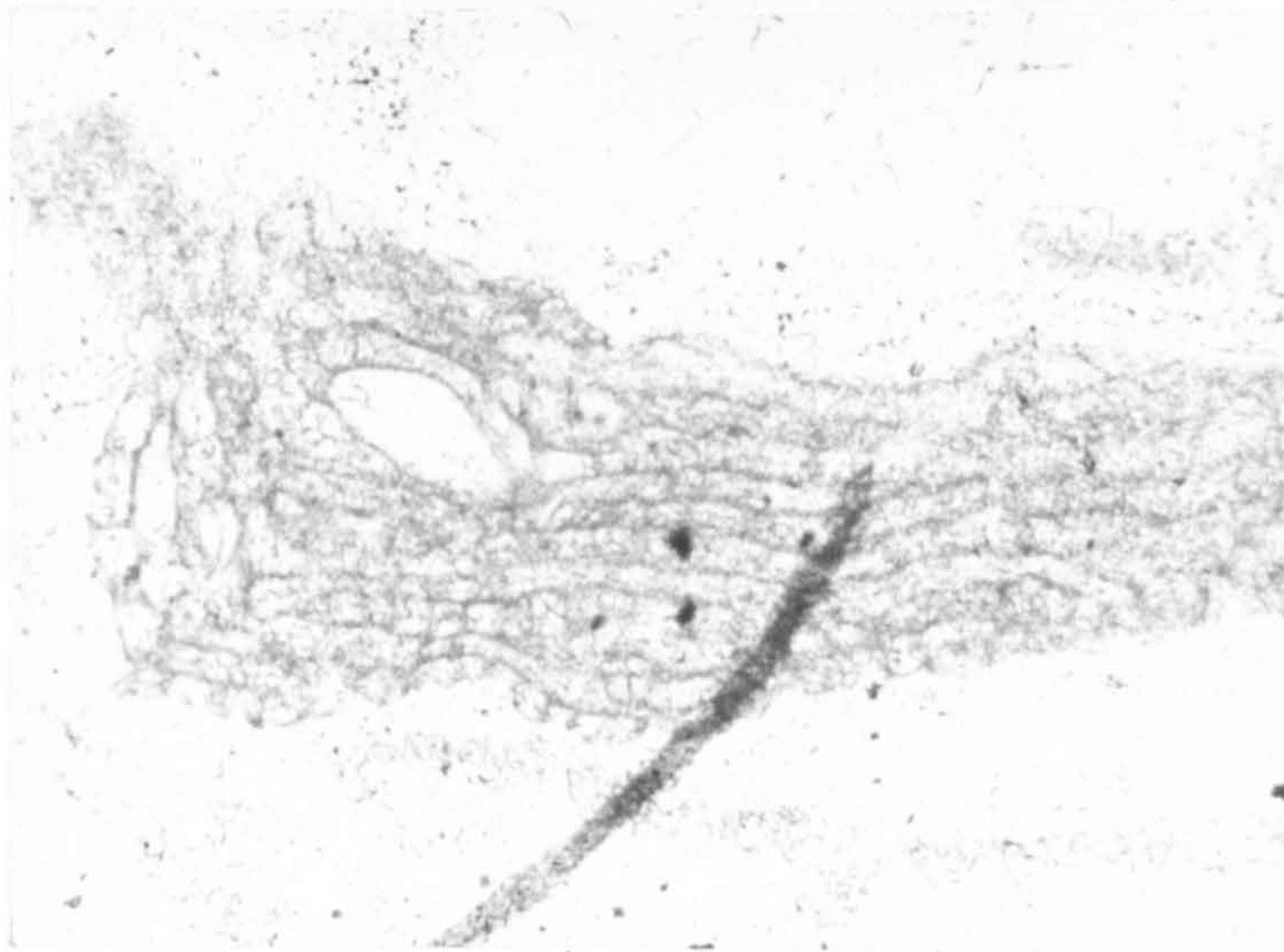


Fig.32. R. conferta. Some of the filaments encrusting Coenites (seen in L.S.). Characteristic beading. Ballstone W.E.2(3) Wenlock Edge x 150.

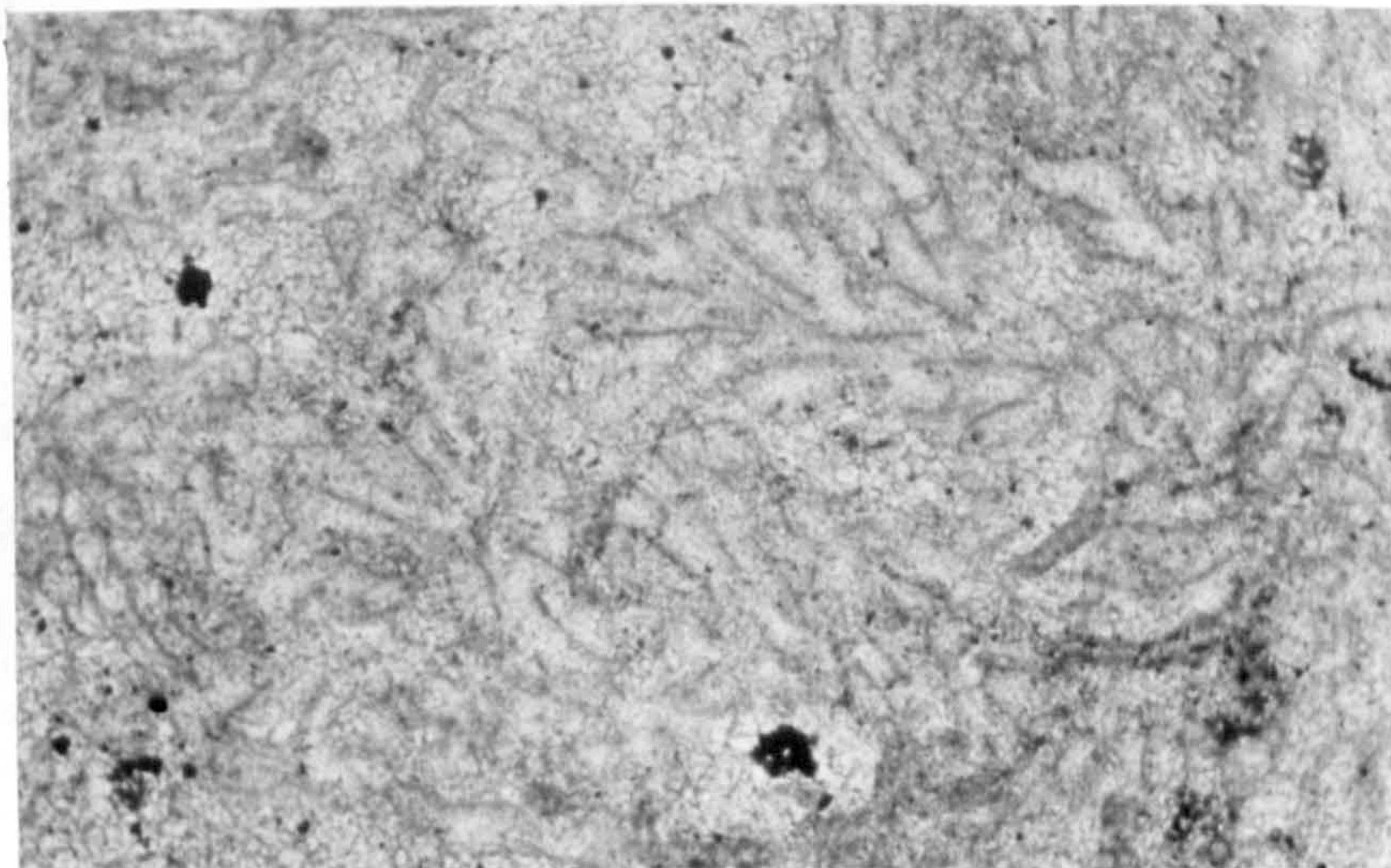


Fig.33. R. conferta. Tangential section to surface showing part of group with dichotomous branching and a little beading of a few filaments seen longitudinally. L. Limestone Group, Dudley. x 90.

In surface view, the dichotomous branching is very marked, with the tubes remaining in contact with each other (fig.33,34). The characteristic of the genus is 'beading' and the possession of long undulating threads is also seen in this form (figs. 30-32, 36).

No reproductive structures have been found.

The majority of specimens found were of filaments matted together and encrusting some other organism. These growths were found surrounding crinoid ossicles, bryozoa, stromatoporoids, corals including Halysites, Heliolites and Favosites. In a few examples, the association between the alga and the other organisms appeared to have been close. Thus one slide examined showed 8 algal bands apparently along the growth lines of a stromatoporoid. Another was in a tabulate coral.

R. conferta has also been found in small algal growth forms, together with Girvanella spp. and has also occasionally been found with R. gotlandica.

This form species is not regarded here as a depauperate form of R. gotlandica growing under unfavourable conditions as Wood (1948) gave as a possible suggestion, for if it had been the case, the diameter range would not be so constant in

specimens taken from different horizons and localities.  
Also, as it is commonest in the Ballstones, where the  
fauna is richest, in apparently more favourable conditions  
is frequently more abundant than R. gotlandica.

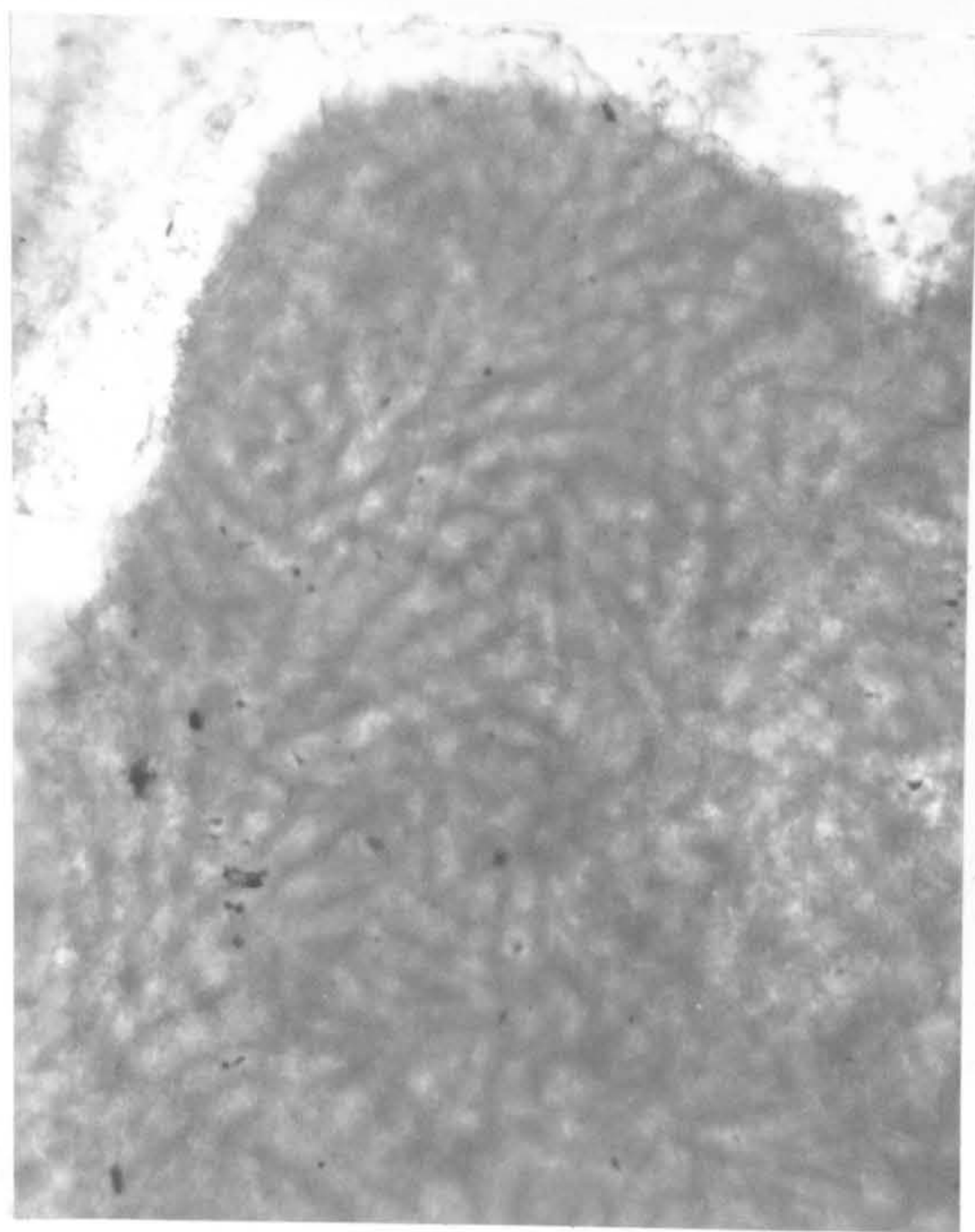


Fig. 34. Small part of group of R. conferta in surface view with dichotomous adherent branches. Wenlock Edge W.E.1. x 150.

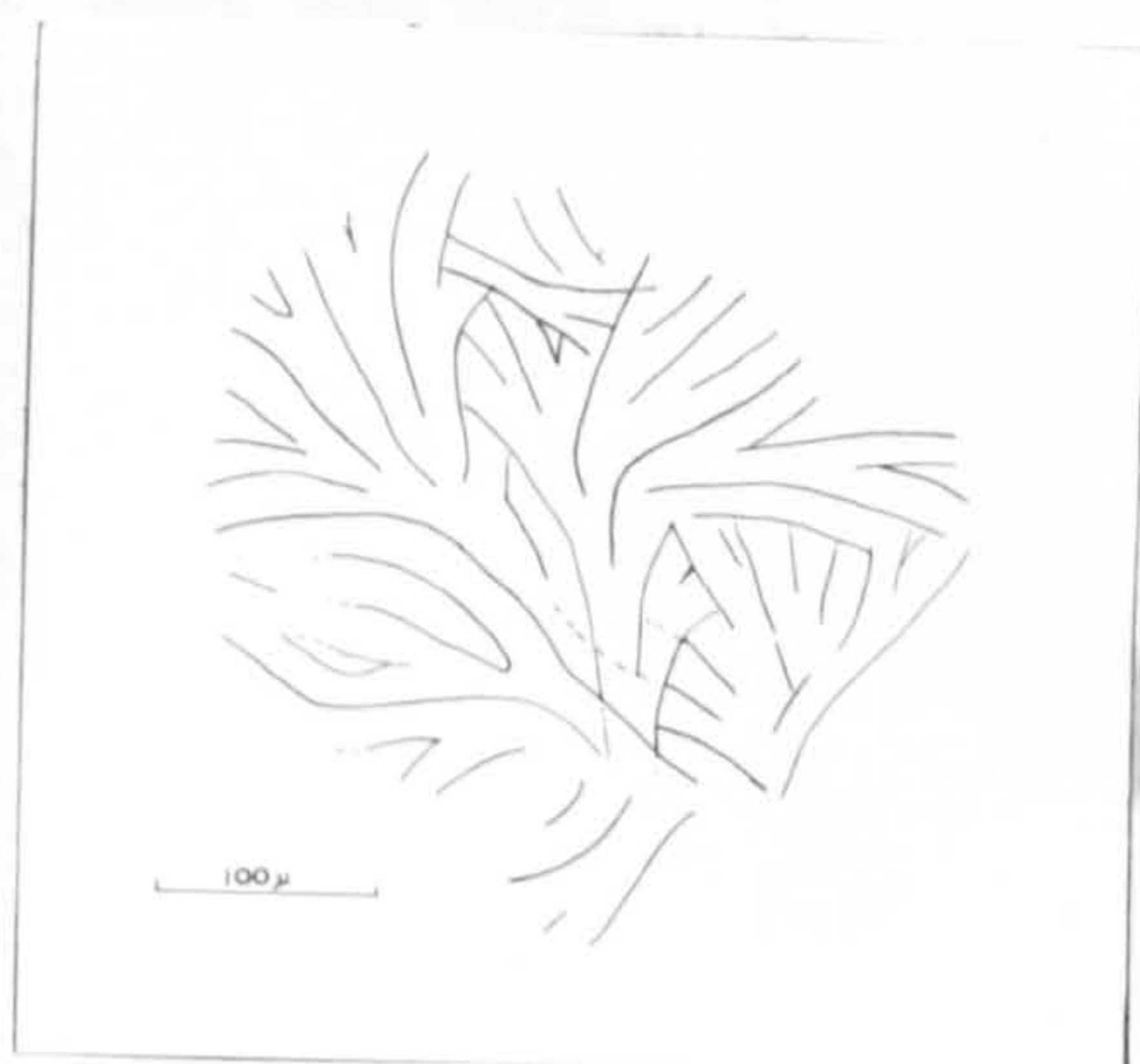


Fig. 35. Diagram of part of Fig. 34 to show dichotomies of branches. x 110.

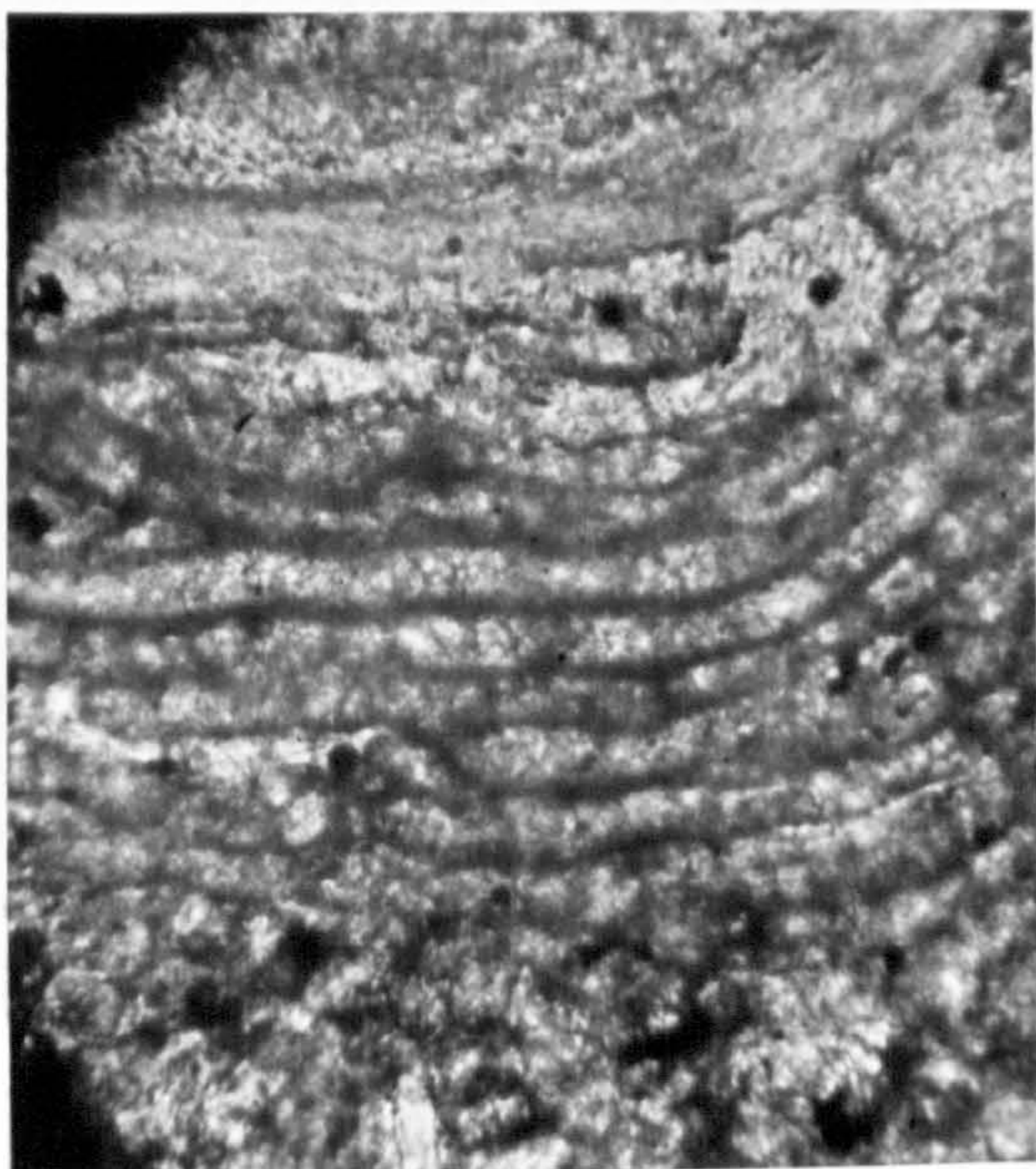


Fig. 36. R. conferta encrusting organism. Some beading visible. L. Limestone Group, Dudley. x 215.

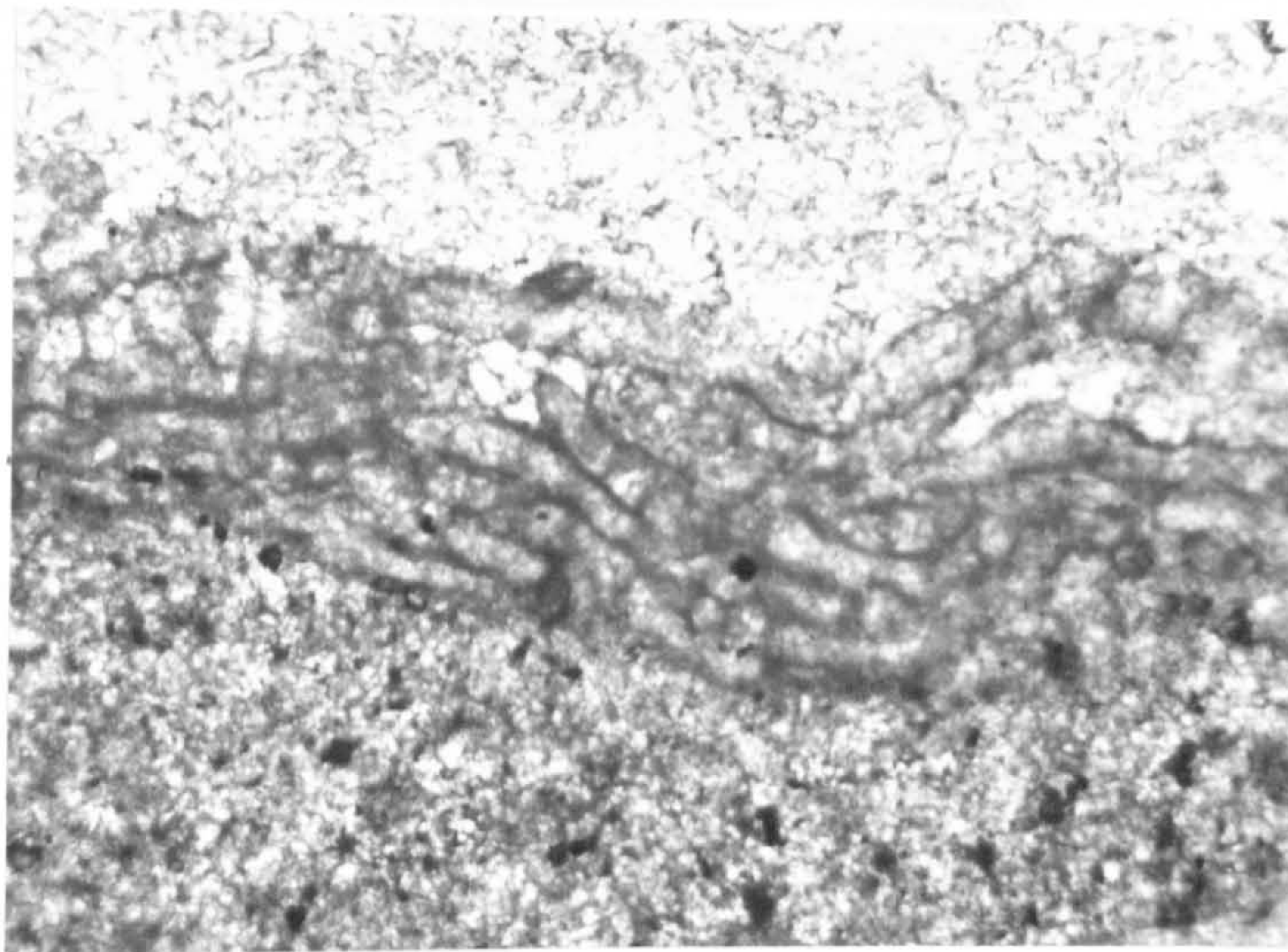


Fig. 37. R. conferta filaments encrusting crinoid ossicle (above); only part of group visible in photograph. Nodular Beds, Dudley. x 150.

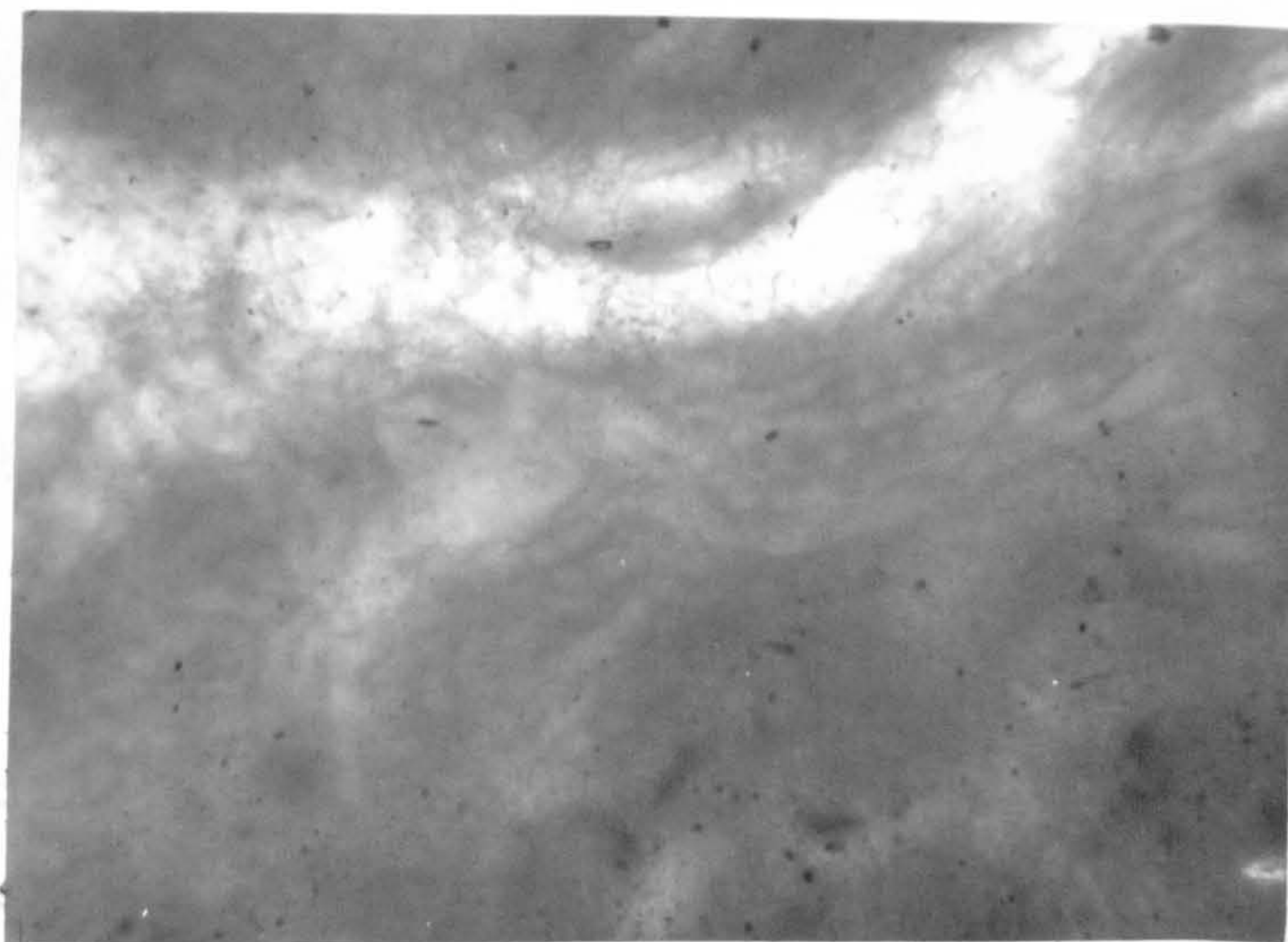


Fig. 38. Rothpletzella sp. encrusting Halysites (not seen in photo). Thick section with fine filaments just visible. Branching and beading. L. Limestone Group, Dudley. x 150.



ROTHPLETZELLA sp.

figs. 38, 39.

Description

Typical forms of the genus with finer threads than in the previous species. The diameter of filaments range from  $9\mu$  to  $18\mu$ .

The filamentous groups are matted in appearance. In longitudinal section, some filaments are very beaded, and others straight over some distance (as is also exhibited by the two previous species). In surface view, the filaments dichotomise rapidly, the walls of branches remaining in contact. Sometimes forms are encrusting.

Horizon and localities

This finer Rothpletzella was first found in material collected from the Lower Limestone Group of the Wenlock Limestone of Wren's Nest, Dudley. It has since been found from probable Wenlock Limestone material collected from drift deposits at Ledbury.

Remarks

This finer form does not appear to be a depauperate

form of R. conferta and was found in material containing Girvanella spp. which showed no signs of dwarfing.

Especially the narrowest example (diameter  $9\mu$ - $12\mu$ ) from Ledbury (fig. 39 ), shows no indication of grading into R. conferta. The lack of sufficient material, however, does not allow specific limits to be made here as one or more species may be involved.

The narrowness of tube diameter also does not appear to correspond with the Gotland specimen (fig. 39) where much overlap of tubes in the growth forms has led to crushing of tubes, hence narrowing of tube diameters. Also, obliteration of walls has led to the apparent observations being made on the fusing of tubes of one diameter into that of another. This feature has not been observed in any of the Welsh Border specimens of any species.

The filaments have been found both encrusting and in free groups. The encrusting groups have been found on the surface of Halysites and a crinoid ossicle (fig. 39).

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Wide tubed forms above the limits assigned to

Rothpletzella gotlandica large var. by Wood are included temporarily in this form, but may really constitute a separate form. Specimens of this type have been found from the Wenlock Limestone of the Woolhope area.

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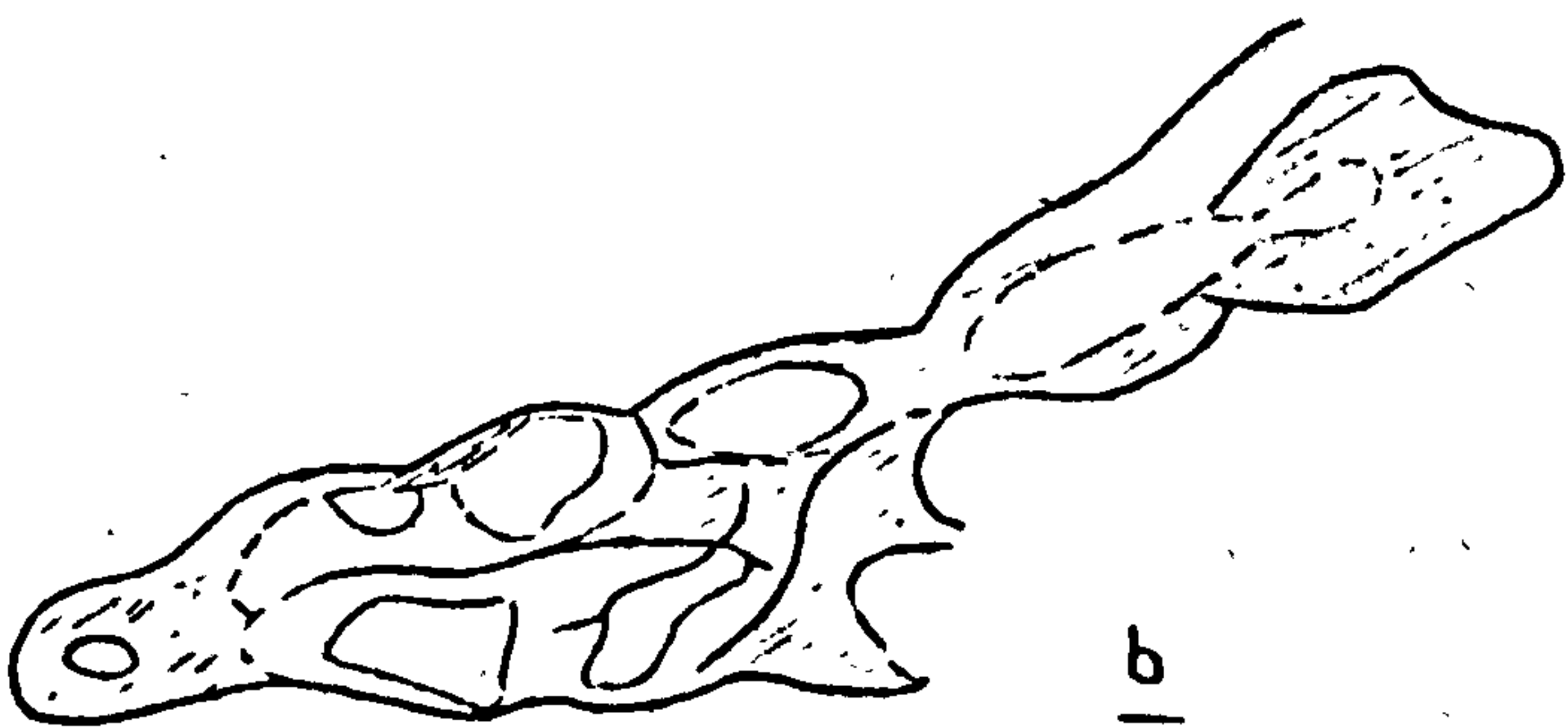
Fig. 39.

Rothpletzella various - diagrams x 350.

- a. Rothpletzella sp. filaments  $9\mu-12\mu$   
encrusting crinoid ossicle (above).  
Shows fan branching and beading.  
Ledbury (L.B.3(1)), probable  
Wenlock Limestone.
- b. Rothpletzella gotlandica branching.  
Full width of filament partly obscured  
by overlap; shows beading and possible  
cell length if not coenocytic.  
Wenlock Limestone, Fownhope (F.H.2(5)).
- c, d. Gotland specimens, Högklint Series.
  - c. Apparent merging of fine tubes into  
larger (possibly by obliteration of  
thin walls of calcite dust).
  - d. Beaded Rothpletzella filaments along  
one of the growth lines of algal growth  
form.



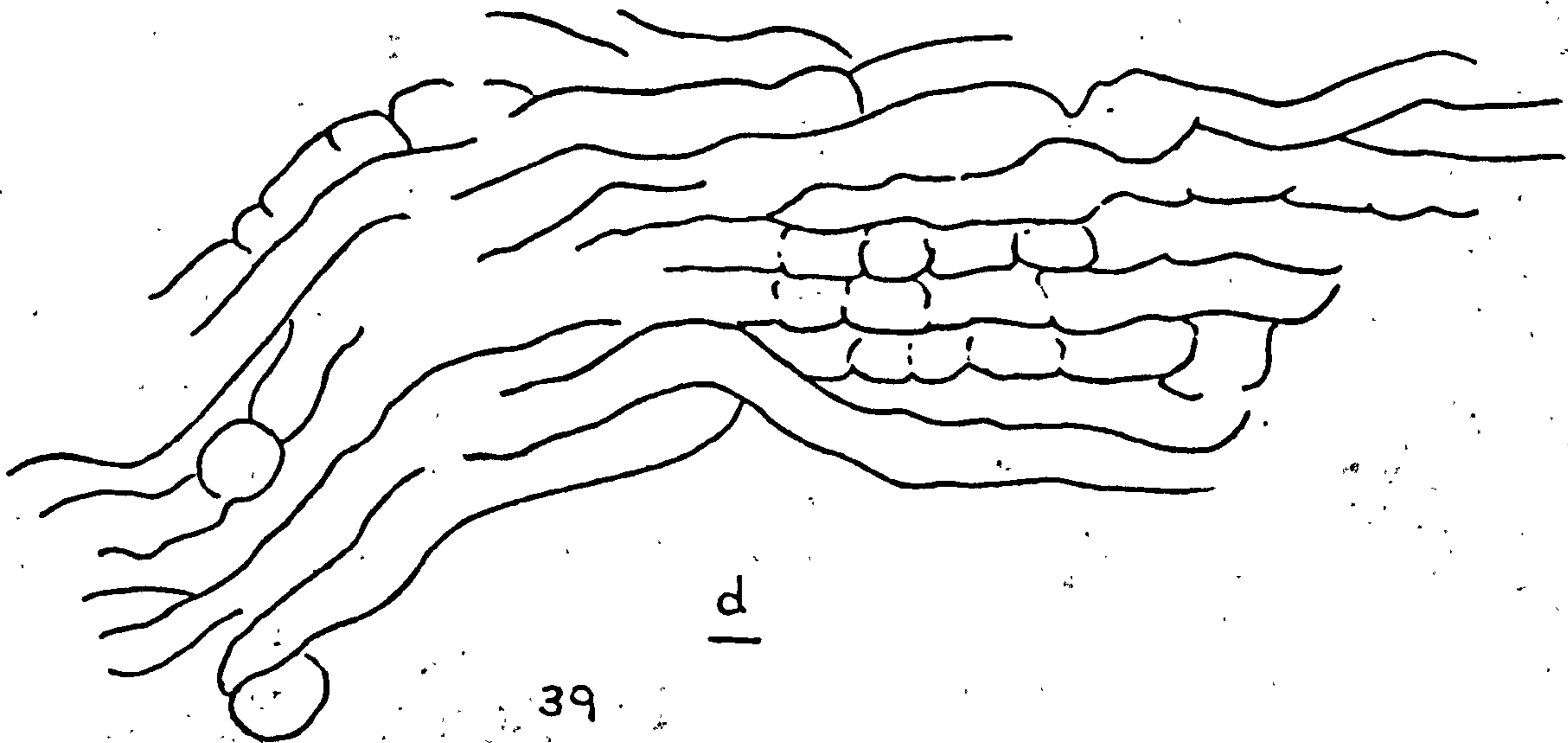
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16



17



18

II Class RHODOPHYCEAE  
Sub-class FLORIDEAE  
CORALLINACEAE  
Solenoporaceae

SOLENOPORA Dybowski

figs. 40-57

Establishment of genus

Billings in 1865 described a form 'Stromatopora compacta' from the Black River Limestone of North America which was referred to the Stromatoporoids.

In 1877, Dybowski gave a definition of an Ordovician fossil from Esthonia, Solenopora spongioides which had a "corallum spheroidal, corallites irregularly prismatical, of very small diameter, coenenchyma wanting and tabulae absent", and referred it as a monticuliporoid.

Also, in 1877, Nicholson and Etheridge gave a description of a form which they named 'Tetradium peachii' from the Ordovician rocks of Girvan and which they regarded as a hydrozoan.

Dawson in 1879 regarded Billings Stromatopora as a monticuliporoid and renamed it Stenopora compacta. Then in

1835 Nicholson and Etheridge realised that the genus described by Billings was equivalent to the Solenopora found by Dybowski and further that their Tetradium peachii was probably a variety of Billings' species.

Nicholson in 1838, still regarded Solenopora as an extinct hydrozoan, and named another new species S. filiformis, also from Girvan.

The genus Solenopora was first placed amongst the Coralline Algae by Brown (1894), who gave a redescription of all the then known forms and defined several new species from the Ordovician and Jurassic. Seward (1898) supported Brown's classification and suggested that eventually new species would be found to close the gap between the Ordovician and Jurassic species. The interval was lessened by the discovery of the Silurian species, Solenopora gotlandica, from the Faröe Isles of Gotland by Rothpletz 1908, and S. gracilis (Garwood and Goodyear 1918) from the Woolhope Limestone of Old Radnor and Nash Scar, and also by a Carboniferous species S. garwoodi from the Shap dolomite of Westmorland by Hinde in 1913.

In 1913, Rothpletz showed that four species erected by Brown, could be referred to the other already described

genera, the discrepancies mostly being due to non-recognition of a different view in thin section. Thus oblique sections through a thallus tended to produce tapering ends to cells in longitudinal view, etc. He also gave the stratigraphical range then known for the Ordovician and Silurian Algae of Gotland.

Detailed work on Lithothamnia and their relationships with Solenopora has been done by Lemoine (1918), in which close comparisons can be drawn from their vegetative mode of growth and their position in with the Coralline Algae strengthened. Also, since the discovery of narrow celled forms such as Solenopora gracilis, the discrepancy in cell width between the Lithothamnia and Solenopora has been removed. Lemoine (1918) showed the gradation from Lithothamnion through Archaeolithothamnion to Solenopora from fine (e.g. S. filiformis) to large-tubed forms (e.g. S. compacta).

Johnson(1956 a.b) described a new form Archaeolithophyllum which he postulates as having arisen from the Solenopora compacta, S. lithothamnioides type of ancestor, with their concentric layers of cells and in turn giving rise to Lithophyllum and allied genera, the other



species of Solenopora were he suggests the ancestors of Archaeolithothamnion and thence Lithothamnion. Thus he considers the division into the two main groups of present day crustose coralline algae came about during the Ordovician within the family Solenopora and not both as offshoots from the Archaeolithothamnion stock.

The present classification is according to Fenton 1946 and Fritsch 1948.

#### Description of genus

Type species Solenopora spongioides Dybowski 1877.

Nicholson (1888) in a redefinition of the genus Solenopora included organisms in it which were of an irregular-shaped calcareous mass and consisting wholly of fine radiating tubes arranged in concentric strata. The tubes are in contact so no interstitial tissue is present, and are thin walled, irregular in form, frequently with undulating walls and with some transverse partitions but no usual pores or radiating septa.

From the various descriptions of the genus macroscopically, Solenopora is shown to vary in size from less than 0.1cm to 17cm or more in diameter. In the field it is recognised mainly from its nodular shape, and possessing a conchoidal fracture which usually reveals a porcellanous

texture and often concentric layering. Thin sections are required to show any detailed structures.

Brown in 1894, supported his claims for placing the genus with Coralline Algae by indicating the importance of the tube diameter which ranges well below the known lower limit of those in the animal kingdom. He also indicated the close similarity with Lithothamnion in the longitudinal fission of the tubes.

Several authors, particularly Brown (1894), Rothpletz (1908, 1913), Lemoine (1918) and quoted by Maslov (1935) etc. have indicated the size range in this genus. The width of tube in the genus has been found to range from 17 $\mu$  (S. gracilis Garwood and Goodyear 1918) to 85 $\mu$  or more in the wide tubed forms (S. compacta etc.)

The length of tube also was found extremely variable. Garwood (1918) indicates 25 $\mu$  for the fine tubed form of S. gracilis, but other authors give figures for some species of up to 200-300 $\mu$ . It seems possible that in some cases, it may not be the length of just one cell but several due to the complete absence of the original wall structure. Hinde (1913) on the other hand, in describing a Carboniferous form S. garwoodi mentions a median septum, 1-2 $\mu$  thick, being

present within the granular calcite walls of thickness 6-8 $\mu$  which separated the filaments.

Lemoine (1918) distinguished different sized filaments into perithallium and hypothallium as is the case in some of the other coralline algae, but all authors have not followed her lead in this, being unable to distinguish the parts in most species.

Various authors have postulated the presence of reproductive organs, mostly on very slender evidence. Brown (1894) was the first to suggest possible sporangia in Solenopora, when he described larger cells in star-shaped arrangement. Seward (1898) and later writers have doubted any evidence that these were sporangial cavities, except Maslov (1935) who considered them to be female conceptacles.

Rothpletz (1908) on S. gotlandica and Garwood and Goodyear (1918) on S. gracilis, described similar elongated clear spaces the former assigning them as sporangia, and the latter as pseudosporangia, for they seemed to have arisen by solution of part of the cell walls. Lemoine (1918) considered them sporangial comparing them with Archaeolithothamnion, as did Wood (1944) reviewing the different structures assigned for reproduction.

Opik and Thomson (1933) postulated that conceptacles might have formed where there had been a local cessation of growth and a space formed with filaments growing over, but both Garwood and Goodyear (1918) and Wood (1944) presumed the space was because of some foreign body present there (and not now preserved).

Pia (1926) and Johnson and Ferris (1948) have postulated organs above the thallus, which would easily become knocked off and Pia therefore classifies on this basis.

The following descriptions of species are of those collected during the investigation from several Woolhope and Wenlock Limestone localities.

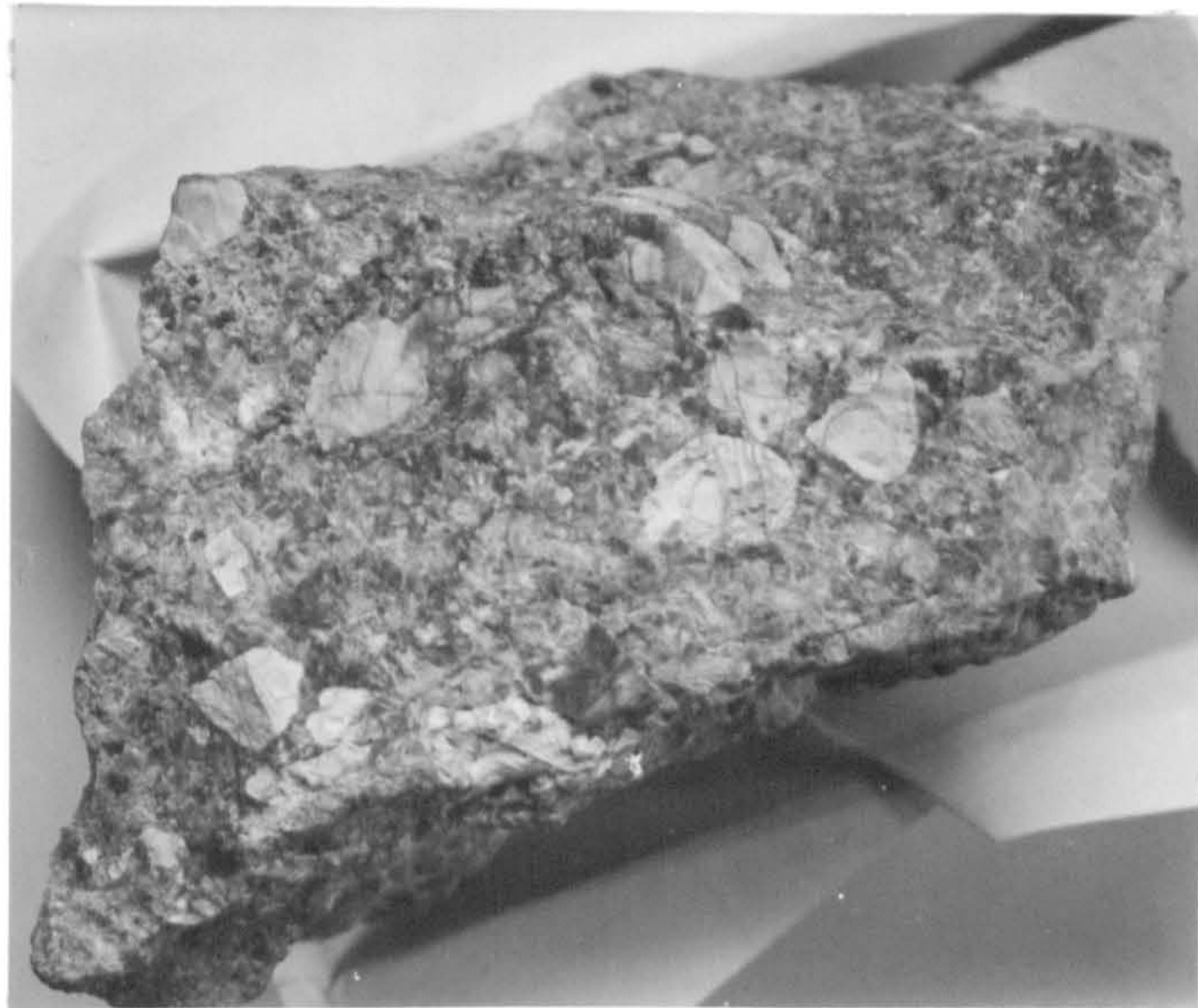


Fig.40 Solenopora gracilis thalli (light coloured, porcellanous, weathered) in rock specimen. Woolhope Limestone, Old Radnor (O.R.1). Nat. size.

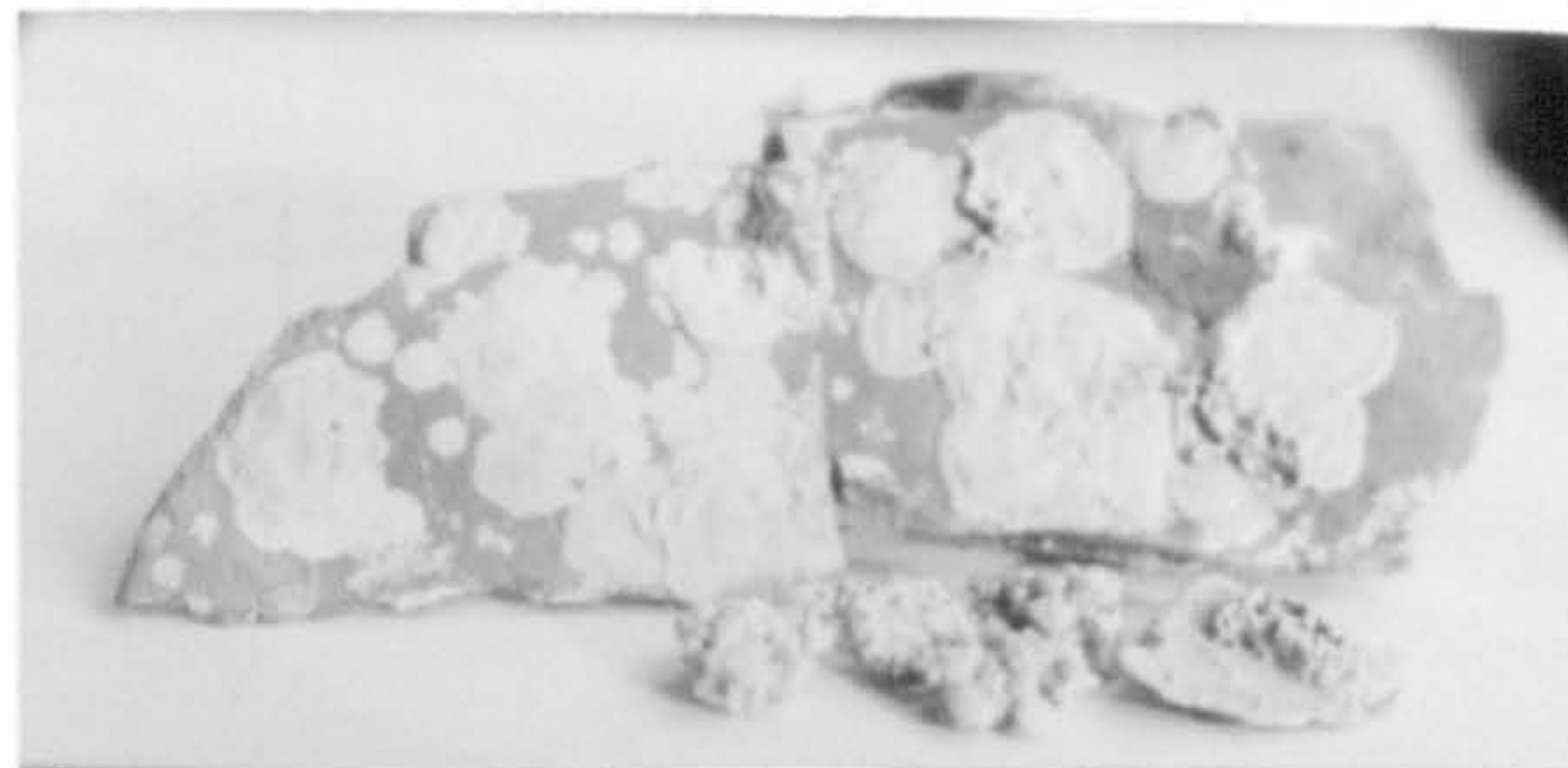


Fig.41 Lithothamnion fragments growing on Manx Slate, Douglas Bay, Isle of Man, x approx.  $\frac{1}{4}$ .

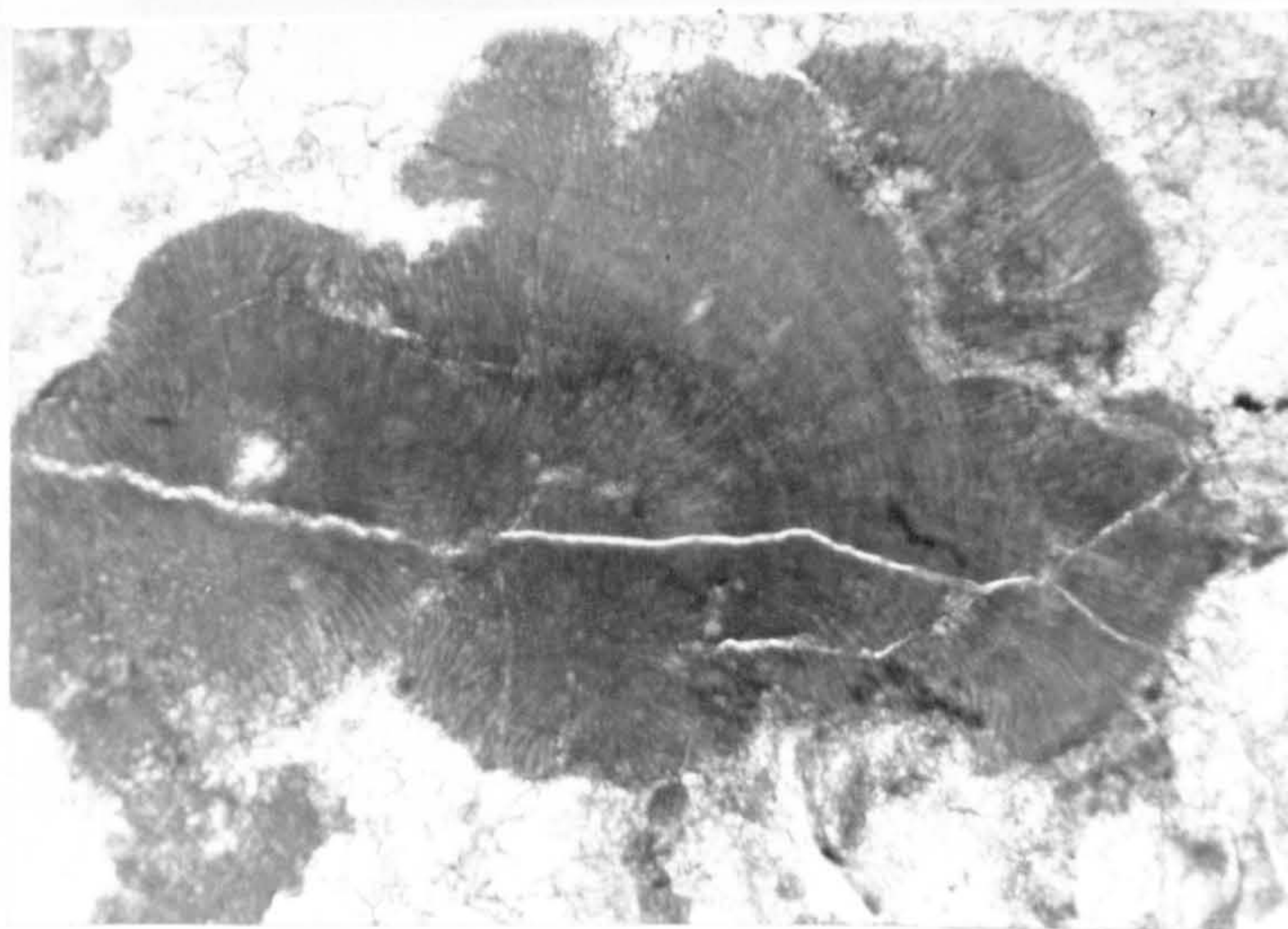


Fig.42 S. gracilis. Thin section through thallus. Filaments apparently radiate out from several epicentres. Dolyhir Quarries, Old Radnor (O.R.1) x 25.

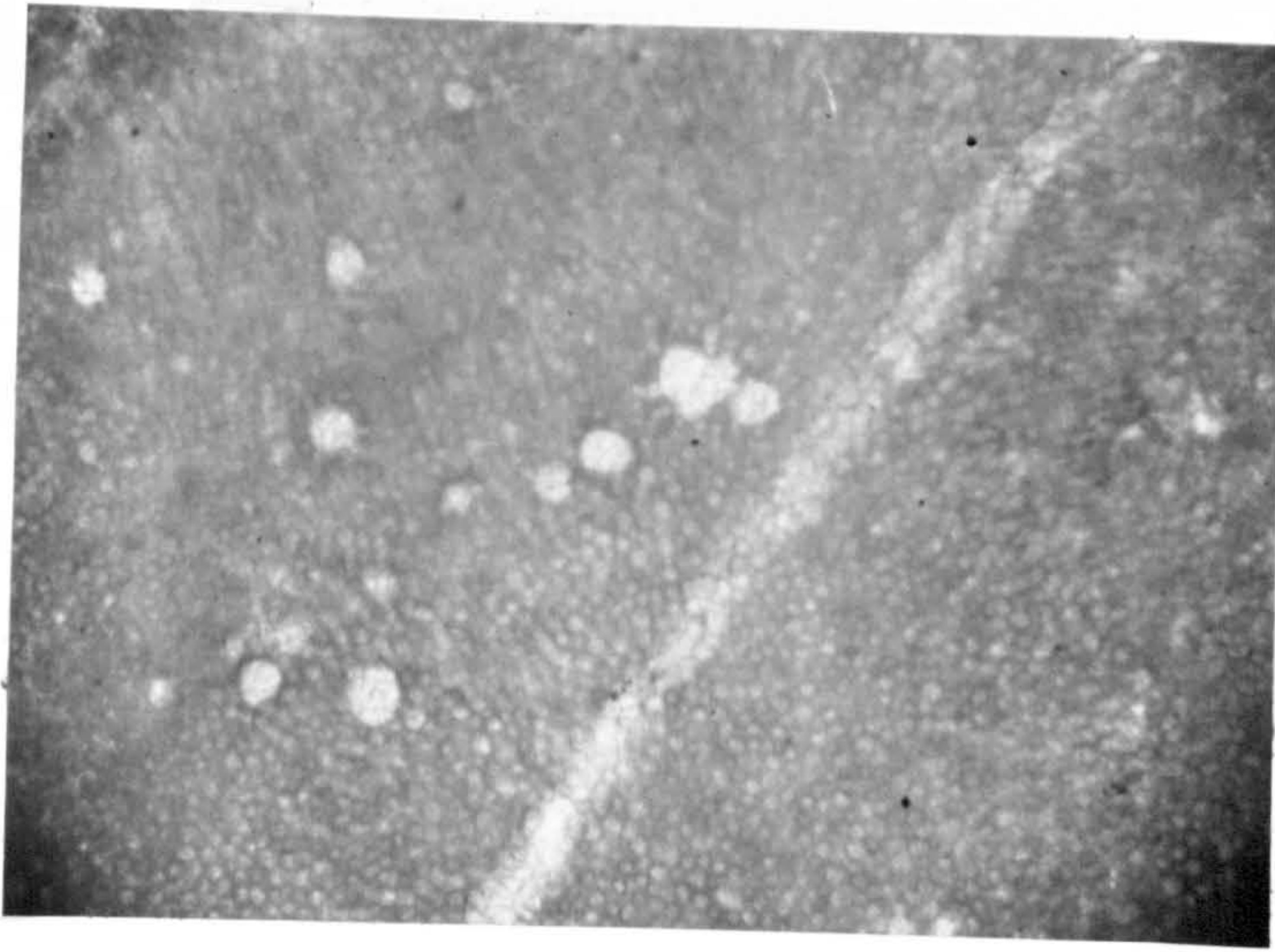


Fig.43 S. gracilis. Transverse section through filaments. Enlarged calcite spaces correspond to the elongated spaces in Fig. 48. Specimen from Dolyhir Quarries x 100.

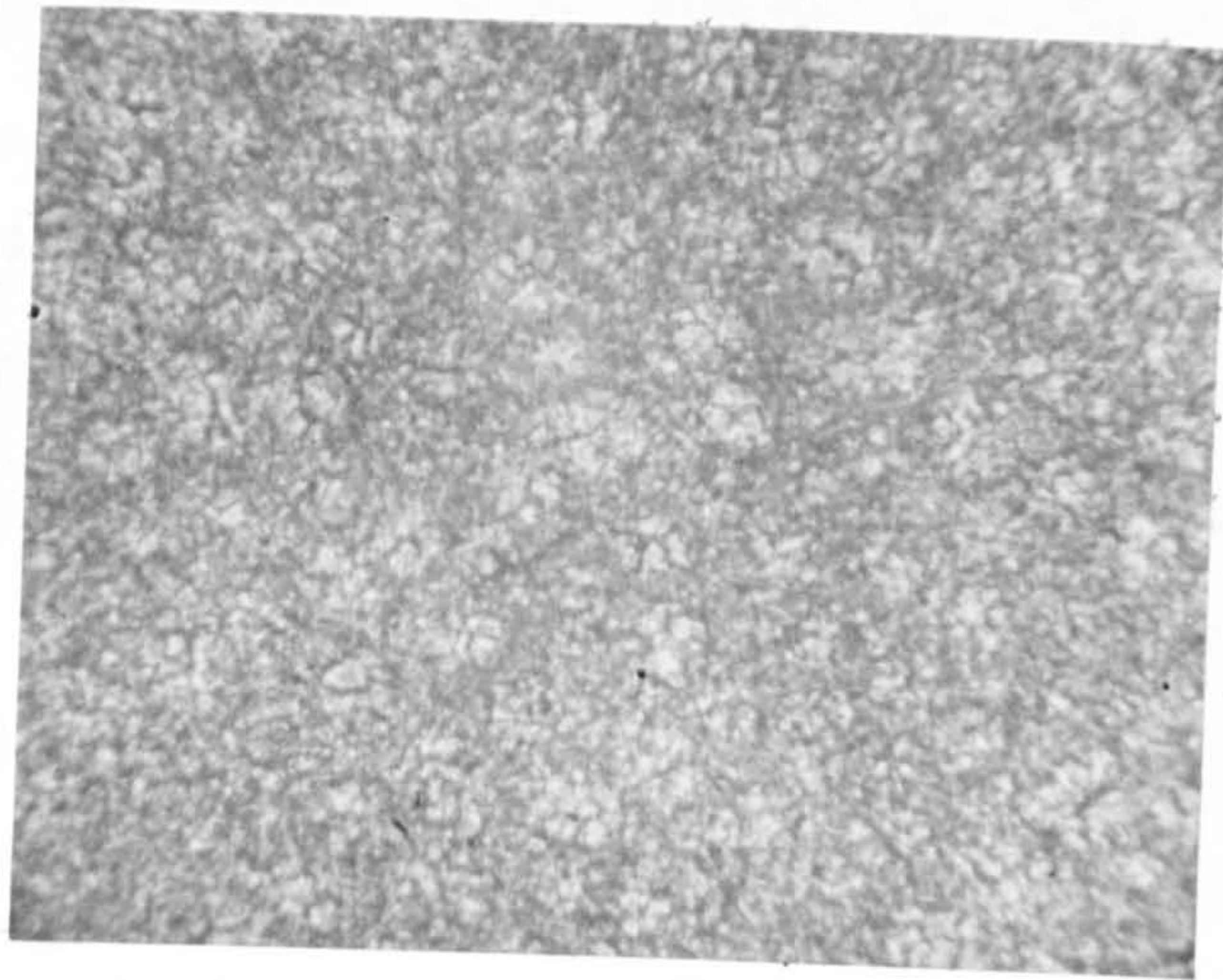


Fig.44 S. gracilis. Enlarged view of transverse section through filaments. Clear calcite of centre of filaments fractured due to cut across. Nash Scar. x 215.

SOLENOPORA GRACILIS Garwood and Goodyear

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figs. 48-54

Solenopora gracilis Garwood and Goodyear 1918 p27, plVI,  
figs. 1,2.

Description

Garwood and Goodyear recognised this species by its massive thallus but minute cell size. The diameter of the nodular thallus they found would often extend to over 17cm. Hand specimens showed a porcellanous texture with concentric lines of growth occasionally visible. When freshly exposed, these specimens were indigo or purple and when weathered, white.

With the use of thin sections, they stated the diameter of the tubes in longitudinal section to average  $17\mu$ , but up to  $25\mu$  when in contact with any foreign body, length of cell averaging  $25\mu$ . In transverse section, the diameter also averaged  $17\mu$ , the tubes appearing as polygons. They did not distinguish between a perithallium and hypothallium.

Garwood and Goodyear recorded S. gracilis as being very abundant at Old Radnor and Nash Scar.

Remarks

From the examination of specimens collected and seen in

the field, the thallus was seen to vary in colour from white to nearly black. On fracturing the porcellanous texture is characteristic, and concentric banding is sometimes visible in hand specimens (fig. 40). Although most of the specimens were nodular in shape, some showed lobing, when examined in thin section these apparently derived from several 'epicentres' of growth. (fig. 42).

In longitudinal section, the tubes are straight and even in diameter having no undulations (fig. 42 and 45 Garwood and Goodyear 1918) and a series of measurements in this plane the mean average diameter, as ascertained from the resultant graphs, was found to be  $20\mu$ . As the tubes overlap in a thallus, and sometimes the walls are not very distinct, the minimum and maximum values measured for each tube are much less reliable than if separate, or, as in this case, in transverse section. Thus, in some of the graphs determining the tube diameter by means of longitudinal sections, there are two peaks for the minimum values (see end tables and graphs). This is because of the thickness of section, overlap of tubes has sometimes resulted additional narrower measurements being made of walls between tubes and not their diameter (see section on methods). Also, the maximum values, due to the overlap obscuring the



walls, may even become apparently enlarged. However, it may be seen that some indication of tube diameter can be ascertained from measurement of the longitudinal sections in Solenopora, especially when these results are compared with those seen in transverse section.

When Solenopora is viewed in transverse section, it usually appears circular to polygonal, as the adjoining walls are in contact. (figs. 43, 44). From measurement of 450 tubes taken from different thalli of Solenopora gracilis found in different quarries in Old Radnor, the mean average diameter had an optimum value, by graph, of  $21\mu$ , nearly the same therefore as for longitudinal sections. However, the minimum and maximum curves (measured for each tube) showed a simpler curve than those of the longitudinal view, and had peaks of  $c.19\mu$  and  $23\mu$  respectively (see table V. and graphs at end).

A further check on the constancy of measurement was made by comparing different sets of measurements from the same thallus, and comparing these also with samples taken from a different thallus at a different horizon (and obtained from a different quarry). In the first case (ORI(3)b) the mean average diameter optimum for each group of 100 sets of measurements was found to be  $20\mu$ - $21\mu$  with a minimum diameter peak in each case at  $20\mu$ , and the maximum in one at  $20\mu$ - $21\mu$

and the other about  $27\mu$ . The discrepancies due to not being certain of a true transverse section apply here.

With a second group of sample measurements (OR2(7)b), one set of 100 tubes measured, the optimum of the mean average diameter ascertained from the graph was  $20\mu$ , but with the other samples it was more ( $c21\mu-22\mu$ ) in one case of 50 tubes measured, and less in two others ( $17\mu$  and  $18\mu-19\mu$ ). The minimum peak, in three out of four groups, for the graphs was found to be  $17\mu$  (and  $20\mu$  in the fourth), and the maximum in two was  $20\mu$ ,  $23\mu$  in the third, and the fourth group again was larger with a maximum peak of  $c.26\mu$ . Thus it can be seen that within a single thallus, measurements taken are apt to be variable. The larger-sized set of measurements may have been due to the original cells being larger, or it may be partially the plane of section taken.

By a calculation of the Standard deviation, which ascertains the limits between which a known percentage of the population will occur either side of the mean (i.e. the peak value of frequency obtained on a normal curve,) the population range can be estimated. (Mayr et al 1953, Ager 1956).

Here, the mean (m) used, is that of the mean average diameter at maximum frequency for the combined graph of

450 samples, (2nd graph at end, table V following).

From the combined graph and tables, it can be seen that

Mean measurement = 7 units (c.21 $\mu$ ) and  
by calculation of the mean by

$$Sx = \frac{\text{Sum of measurements}}{N \text{ (total number of specimens)}}$$

$$m = \frac{3343}{450}$$

$$= 7.4 \text{ units (magnification } \times 350)$$

$$\text{Mean} = 21\mu$$

$$\text{Variance} = \frac{Sx^2 - \frac{(Sx)^2}{N}}{N - 1 \text{ (or } N \text{ where } N \text{ is a large number)}}$$

From the table V following:-

$$Sx = 3,343$$

$$Sx^2 = 25,994$$

$$N = 450$$

$$Sx^2 = 24,721$$

$$\text{Variance} = \frac{25,994 - 24,721}{450} = 2.83$$

$$\text{Standard deviation S.D.} =$$

$$\sqrt{2.83}$$

$$= \underline{1.68 \text{ units}}$$

and as the mean = 21 $\mu$ , the S.D. = 17-25 $\mu$

$$\text{Population range} = 3 \text{ S.D.} = 4.$$

$\therefore$  is between 10 $\mu$  and 32 $\mu$  diameter tube.

TABLE V.

Measurements of transverse sections of 450 samples of tubes of S. gracilis. Magnification x 350.

Measurements (in units)	Frequency (Av. mean diameter)	$Sx^2$	$Sx$
2	0	0	0
3	2	18	6
4	5	80	20
5	38.5	962.5	192
6	83	2988	498
7	121.5	5929	850.5
8	96	6144	768
9	53.5	4334	481.5
10	34.5	3450	345
11	11	1331	121
12	3.5	504	42
13	1.5	253.5	19.5
14	0	0	0
	Total	25,994	3,343.5

Increase in width of thallus

This occurs by the occasional longitudinal division of filaments, and this as well as the division gives the original direction of growth of the thallus. Some areas of the thallus do not show much division, and in other parts it is more noticeable, hence it is presumed that divisions occurred more frequently in some parts of the thallus than in others.

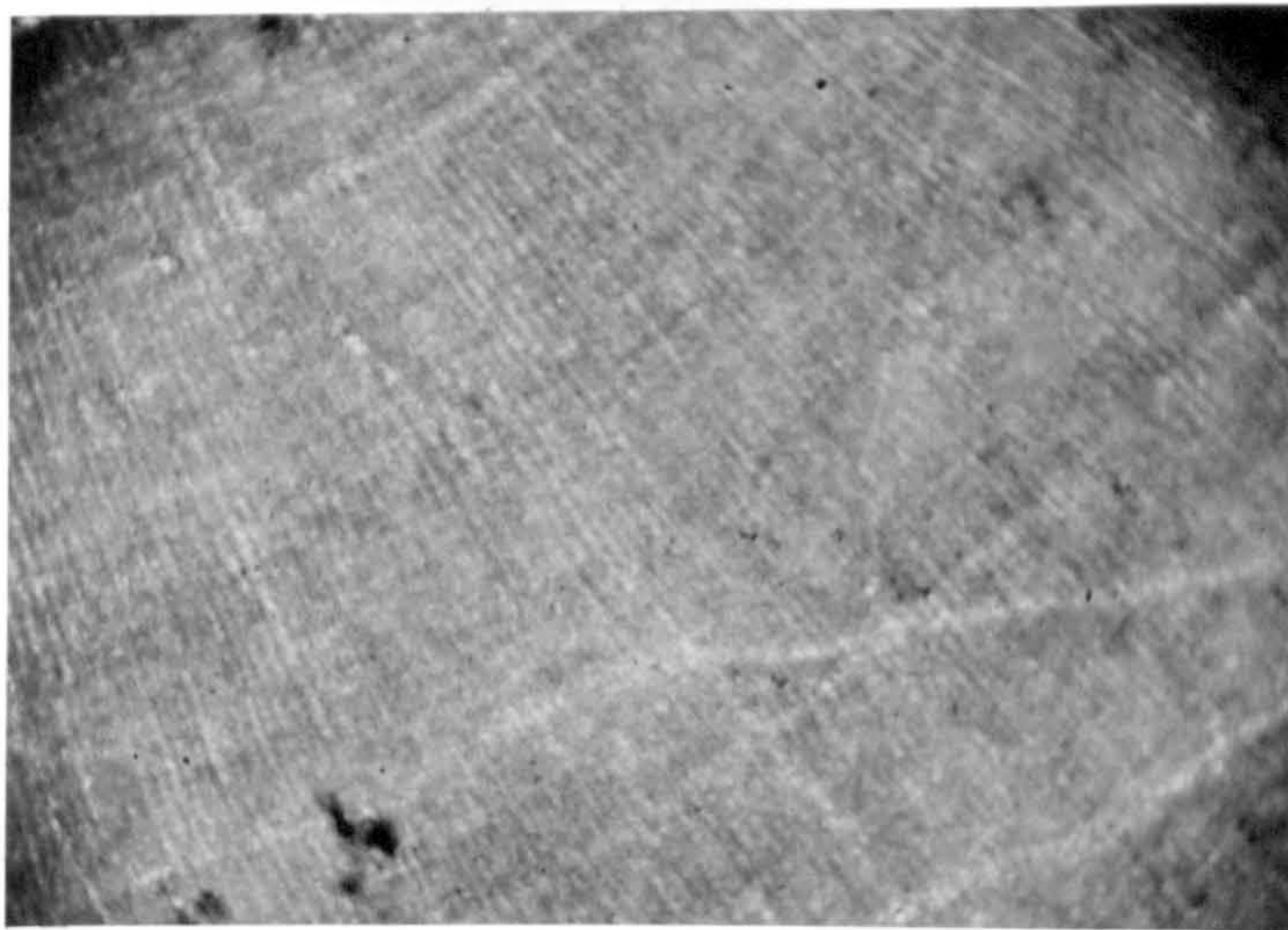


Fig.45 S. gracilis. Longitudinal section through thallus shows filaments and general round banding. Dolyhir Quarries. x 45.

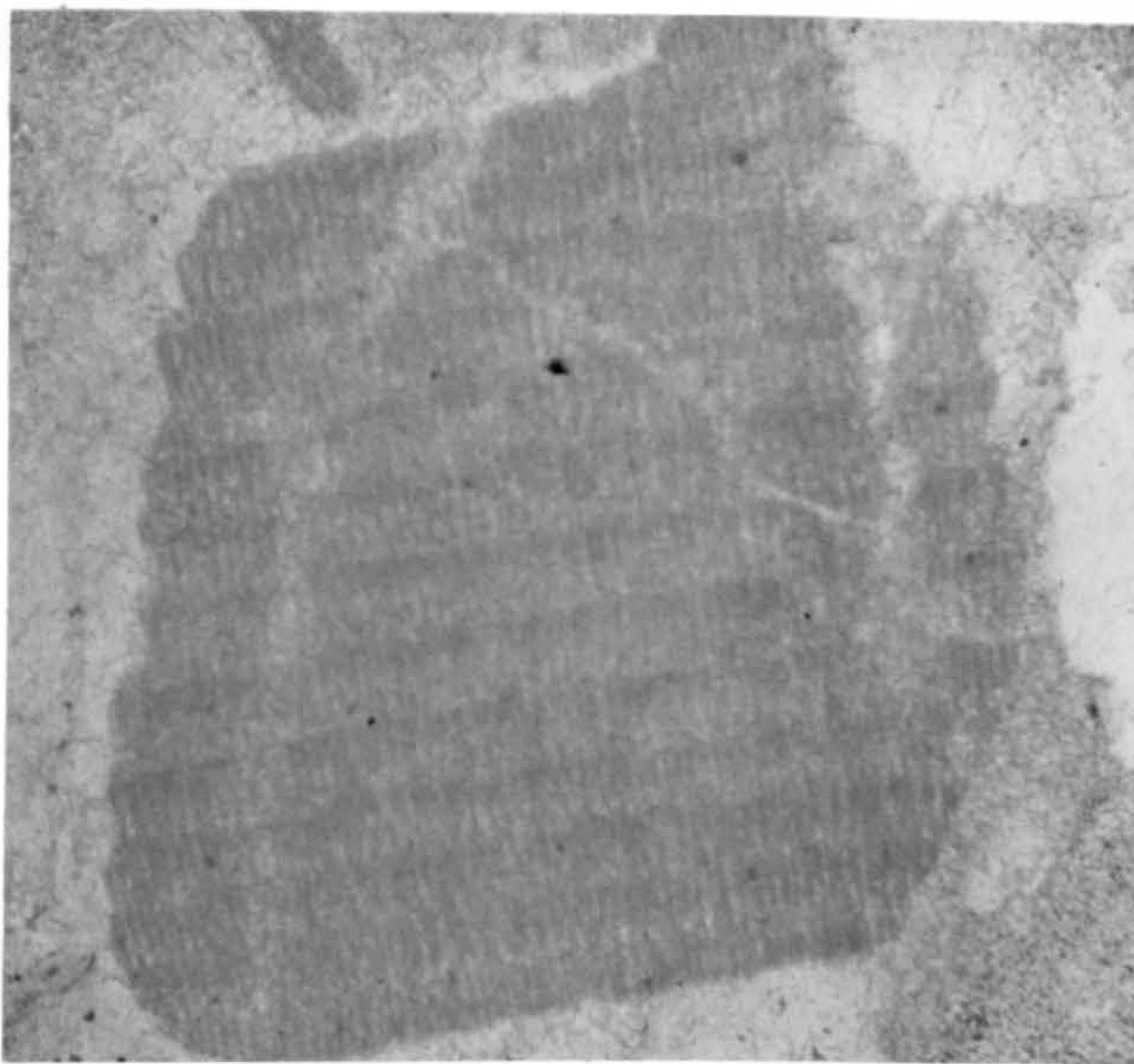


Fig.46 S. gracilis. Rythmic fine banding on small fragment of thallus. Yat Farm Quarry (O.R.2(2)). x 45.

In one instance the growth increase per cm, width for 1 cm. length of thallus calculated (new width C.D minus original width A.B) showed that it is highly probable that divisions are not even, and also that the measurements taken are in two dimensions and not in solid.

The growth increase per 6 cm. CD-AB  
= 15.4 - 13 = 2.4 cm.  
Growth increase per cm. width = 0.632 cm.  
for each cm. in length

---

### Banding

This appears to be of fairly general occurrence and may be broad or narrow in width. The bands follow direction of growth, so that where the thallus is expanding in width, the banding is convex in the direction of growth. In both types of banding there is no interruption of the filaments and these continue irrespective of the banding. Banding can only be seen in longitudinal section and an apparent impression of it is sometimes gained from oblique sections which show 'banding' at changes of filaments.

The wider type of bands (fig. 45) often appear to be an alternating of darker and lighter bands, which sometimes appear more obscurely as an occasional narrower lighter band bending round in the direction of growth. These bands may have been derived from the narrower type of banding, (fig.46)

and they are presumed to have arisen from the same cause.

The narrower dark and light coloured bands are frequent in occurrence, and mostly of uneven lateral thickness. Exceptionally the banding is more prominent than the filaments which it crosses, these sometimes being extremely obscure. The filaments are not interrupted by the presence of the bands, only appearing so in oblique sections. Garwood (1918) found frequent discontinuity of growth at a line and so described them as lines of growth, but it was not found so for this type of band during the investigation. Comparisons are drawn with the presence of banding, including the marked fine bands shown for Archaeolithothamnion and Lithophyllum zonatum and the coarser bands of L. zonatum, which Johnson and Ferris (1948) regarded as periods or zones of growth and not periodic growth lines implying a definite growth cessation.

Occasional septation across the filaments, with calcite granular walls of the same type as those in the longitudinal walls, narrower than the fine bands indicate cell lengths of  $25\mu-30\mu$ .

#### Interrupted growth

In section, when a line demarcates the limits of

filament growth, and the tubes either side of the line are not continuous through it, then the line is here regarded not as a periodic line of growth but either a local cessation of growth or a form of growth which is characteristic of many present day Corallines, (fig. 41) where there is an apparent discontinuity of growth across the thallus independent of any periodic effect (Suneson 1937, 1943, Hamel et al 1953). It seems probable that where lines of discontinuous growth are not local cessations, both lines and banding are related to the same type of growth of present day Corallines.

A local cessation of growth of a thallus appears to be indicated by interrupted growth with an enlargement of the filaments (to 25 $\mu$  or more in diameter, fig. 49). An increase in the diameter of the filaments is mentioned by Garwood et al (1918) where these are in contact with a clear calcite area which probably represented an area where a foreign body, not now traceable, was in contact.

The direction of growth was determined by various features, and from this it can be shown that usually the filaments enlarged before growth ceased, as indicated by the line, then growth was renewed by smaller filaments which





Fig.47 S. gracilis. Diagram of effects of organism boring into thallus. Dolyhir Quarries. x 9.



Fig.48 S. gracilis. Longitudinal section shows filaments and elongated calcite spaces, 'pseudosporangia' of Garwood, parallel to them. Dolyhir Quarries. x 100.

were discontinuous with the previous set (fig. 49).

The features considered were

- a) A widening of the thallus in the direction of growth
- b) Any longitudinal divisions visible in the filaments
- c) Convexity of banding in relation to the line of interrupted growth
- d) Comparison of growth with present day Corallines.

### Spaces and Reproduction

Since its formation, there has been quite a considerable amount of shattering of the algal limestone of Old Radnor and Nash Scar districts. The shattering is reflected in thin section by the numerous calcite veins and also by areas of secondary recrystallisation of the calcite. Thus, very few sections of Solenopora thallus are without any calcite veins, and some sections have clear calcite spaces due only to the diagenesis of the granular calcite.

The "conceptacles" of Opik and Thomson (1933) found for the type species Solenopora spongioides have also been figured for S. gracilis by Garwood and Goodyear (1918) and Wood (1944), the latter writer regarding these calcite spaces in thallus where the filaments exhibit a curvature into them, as the result of an animal on the surface of the thallus or similar disturbances. The spaces were found

fairly frequently in the sections examined (figs. 50-52) and the similarity of the filaments bending towards the space was noted with the condition where the thallus is dividing into two lobes.

The only spaces which do appear to have been possible conceptacles are those which occur as elongated spaces (up to 300 $\mu$  long by 50 $\mu$  wide and lie parallel to the filaments. (figs. 43,48). These "sporangial" spaces first described by Rothpletz (1908) for S. gotlandica, and regarded by Garwood and Goodyear (1918) as pseudosporangia in S. gracilis, but the sporangial nature of the space again supported by Wood (1944) by comparisons with Archaeolithothamnion where he describes solution effects as occurring in the neighbouring cell walls of both algal forms.

During the present investigation, these elongated cavities were examined, both in transverse and in longitudinal section for any solution effects. Firstly, specimens examined in longitudinal section showed the filaments apparently grading into the enlarged space both at the top and the base of the 'cavity' as noted by Wood, but in the specimens examined it was thought highly likely

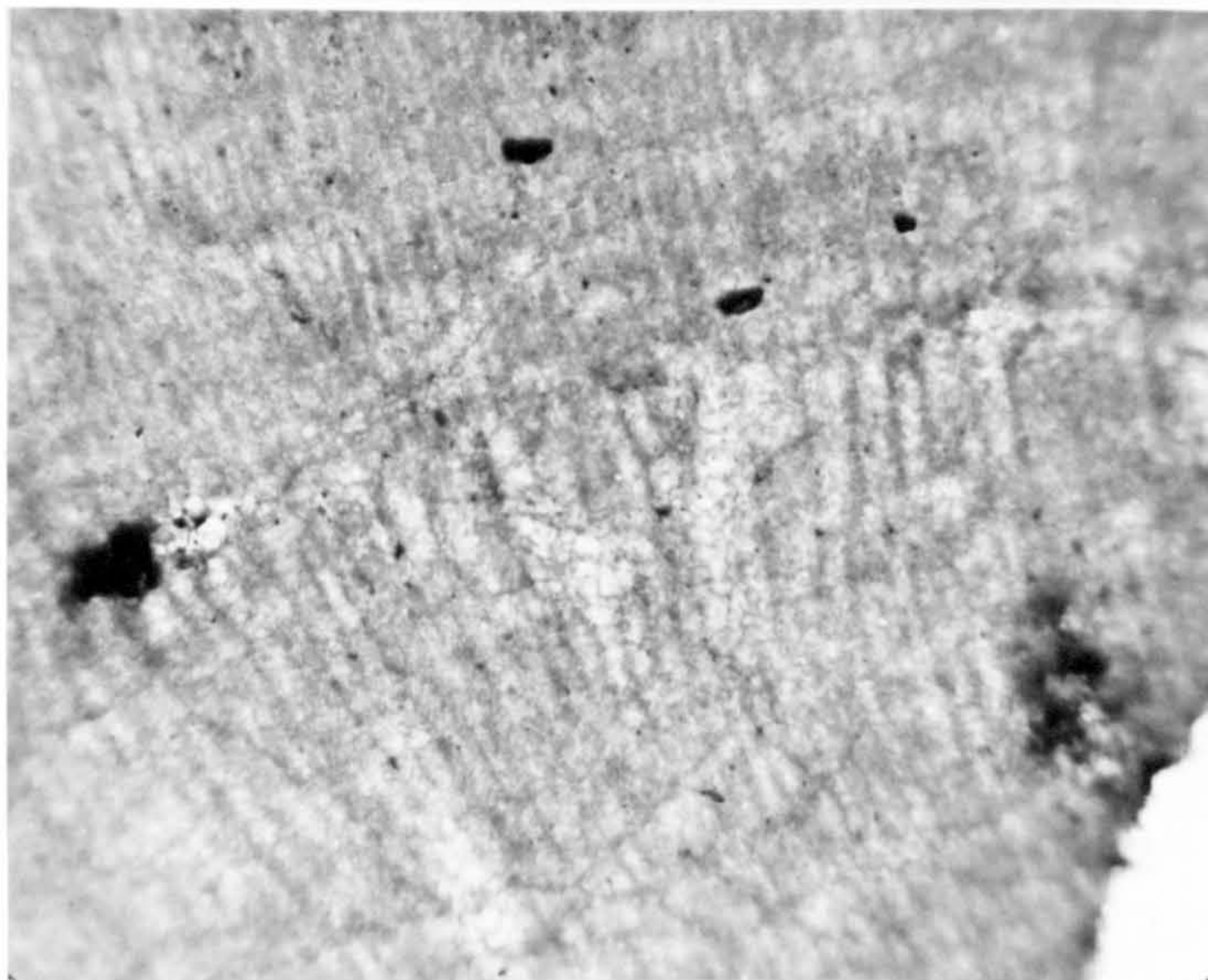


Fig.49 S. gracilis. Enlargement of filaments prior to interrupted growth as shown by line. Smaller filaments renewed growth, and show traces of banding at top of photograph. Dolyhir Quarries. x 100.

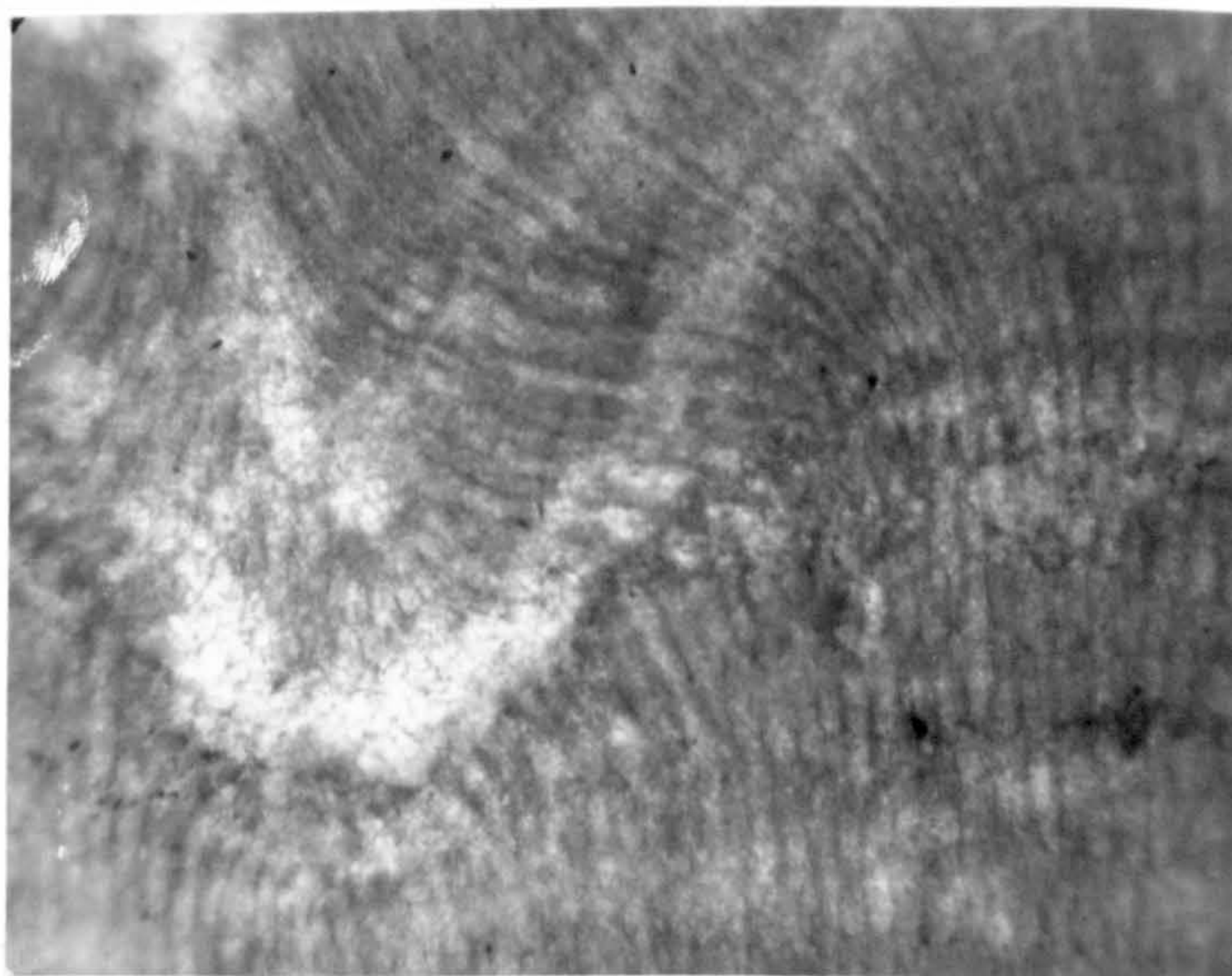


Fig. 50 S. gracilis shows line of interrupted growth, and clear space with filaments bending into it. Dolyhir Quarries. x 100.

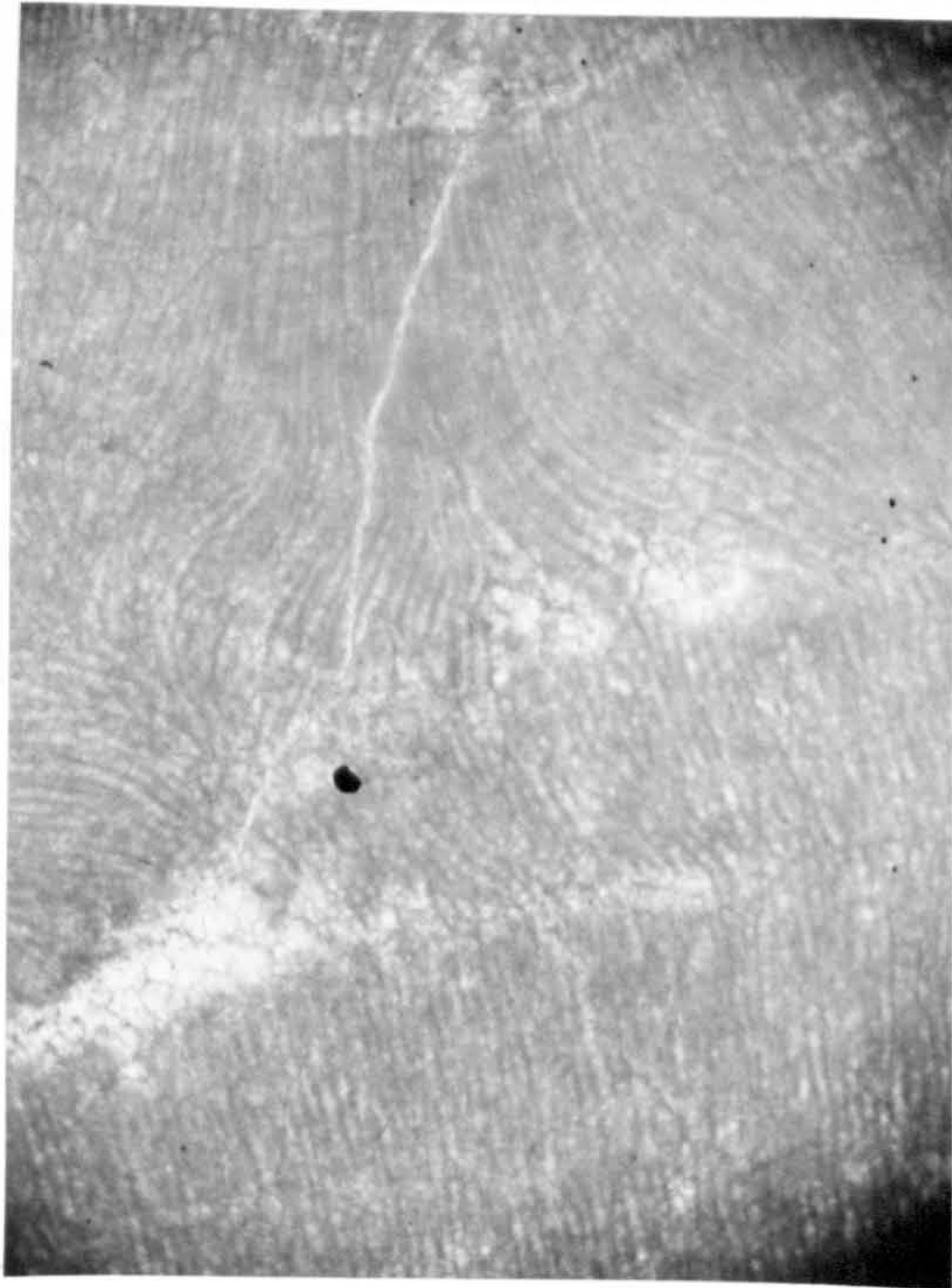


Fig.51 S. gracilis, lines of interrupted growth, and clear spaces. Yat Farm Quarries O.R.2(7). x 45.

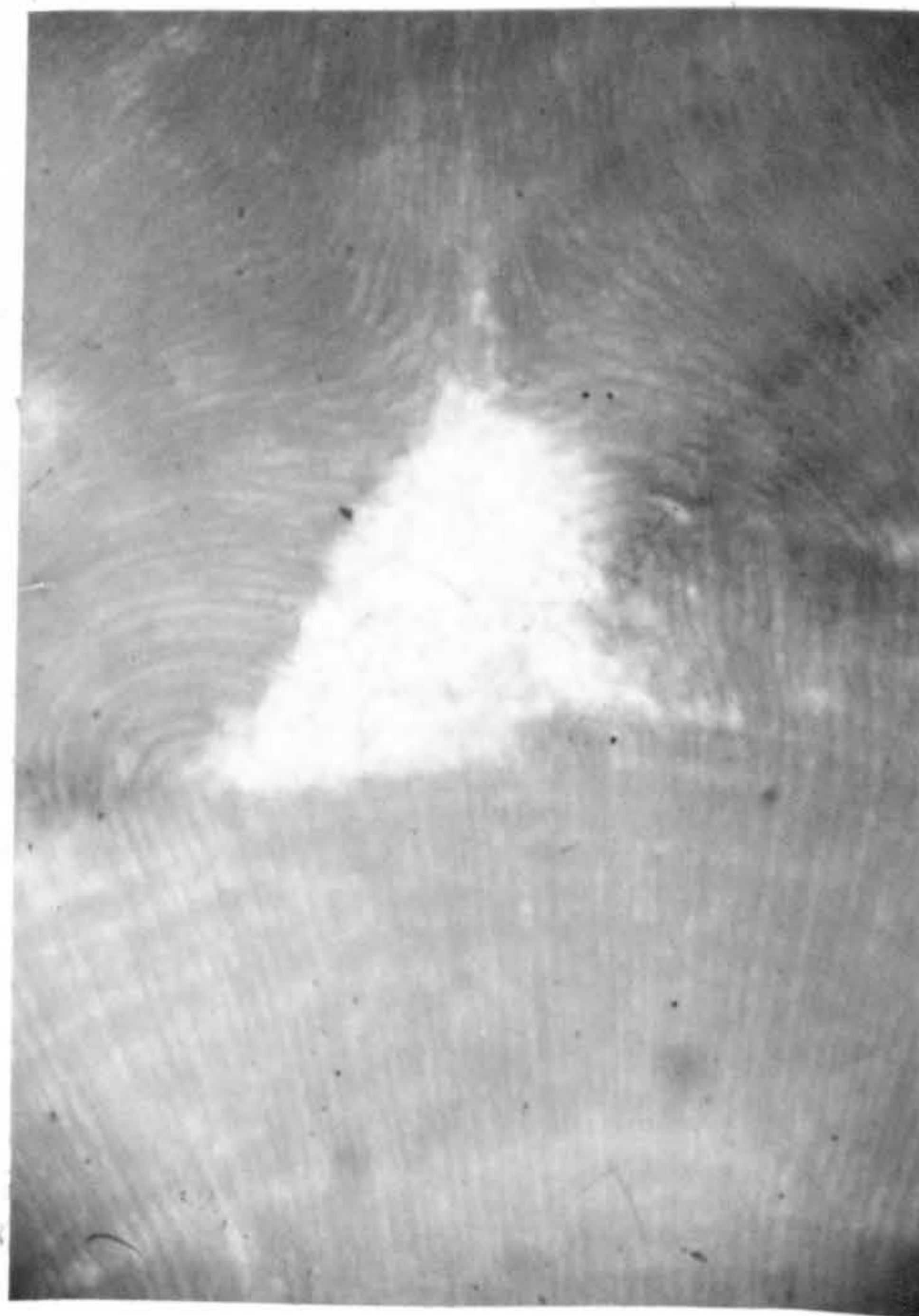


Fig.52 S. gracilis, interrupted growth, and clear space with filaments bending into it. Yat Farm Qu. (O.R.2(7)). x 45.

that the filaments in these positions were only passing out of the plane of section (above or below the thin section viewed), due to the disturbance of an enlarged cavity. No distinct wall would be seen on this change of planes, as the effect is gradual. Wood also stated that the side walls are frequently taken into solution. This may well be so in some cases, but the apparently same effect is obtained from viewing sections where the section cuts through two or three filament levels. Here the filaments appear to pass into the larger space, (as they are seen in one plane only), without any distinct wall separating them. The reason for this latter case is the same as the top and base of the enlarged area.

When examined in transverse section (fig. 43) walls of granular calcite were found around most of the enlarged cavities. The wall becomes less distinct in thicker and somewhat oblique sections, as it does with the normal filaments. In one cavity there appeared to be a possible connection between it and two of the adjacent filaments, the wall between not distinct as in the rest. This could have been a solution effect, but not necessarily, as if the calcite wall was missing as it appeared, it might mean just

no deposition, or only a little, of calcite on the original cell walls.

By comparisons with the present day Corallines. these cavities appear to resemble developing sporangial conceptacles of Lithothamnion lichenoides (Suneson 1937), L. lenormandi, L. polymorphum (Suneson 1943) and possibly some resemblance to the spaces which would be left by heterocysts as found in Porolithon etc. (Taylor 1950, Mason 1953).

Thus, although it is uncertain of the exact function of these enlarged cavities, whether or not they contained sexual or asexual reproductive organs, in the specimens examined it appears that they were surrounded by a definite cell wall in the early stages at least, even though this wall may have undergone breakdown into solution to allow for an increase in diameter of the 'sporangium' as it became more mature.

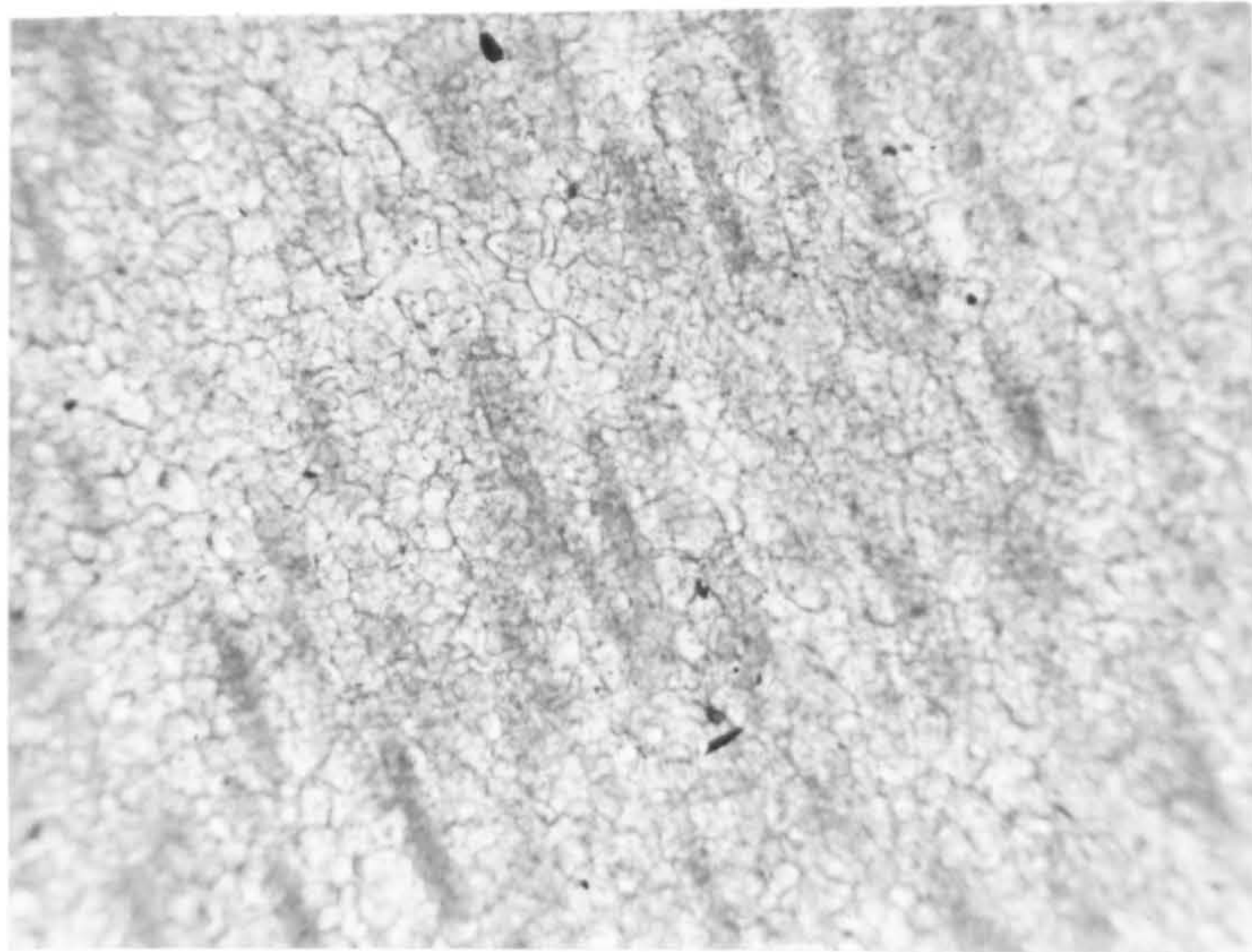
#### Horizon and localities

Solenopora gracilis was found to be very abundant in the Woolhope Limestone of Old Radnor and Nash Scar.

A single specimen 8cm. diameter, from Wenlock Edge was found, considerably recrystallised, but with typical

conchoidal fracture and banding. In thin section (figs. 53. 54) traces of filaments were found to radiate outwards from a centre. The filaments, diameter c.15 $\mu$ . were only seen adjacent to each other occasionally, due to much recrystallisation. It is placed tentatively with S. gracilis with which it agrees on thallus size and nearly so on tube diameter. This would extend this species range into the Wenlock Limestone. However, with further material, it might be regarded as a new form.





Figs.53, 54. Solenopora Wenlock Form, Wenlock Edge, W.E.4.  
53. Thin section of small portion of thallus showing banding.  
54. Enlarged longitudinal view, considerable recrystallisation. Diameter of filaments as in S. gracilis. x 100.

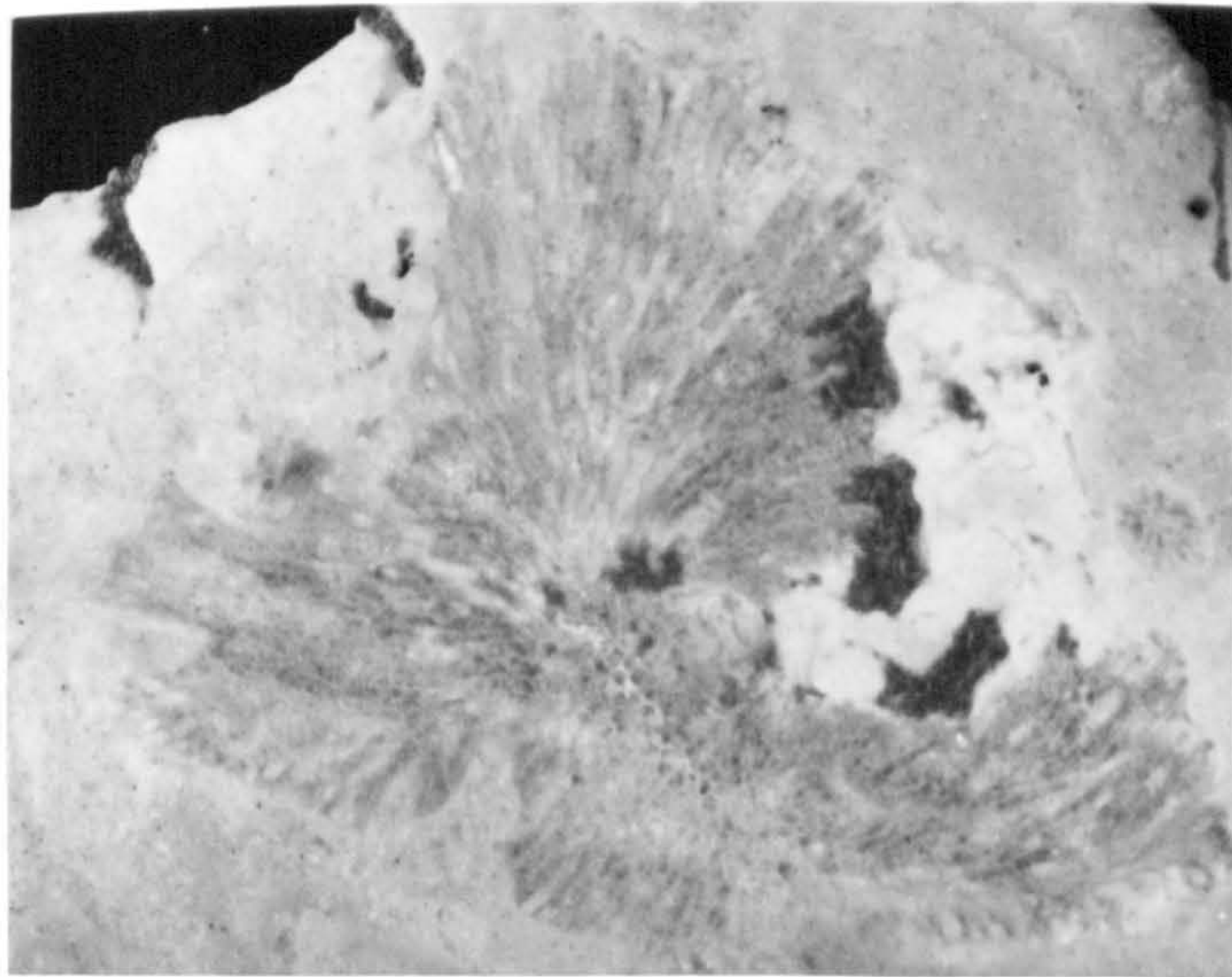


Fig.55 S. compacta. Thin section through thallus to show lobing. Filaments seen in transverse and longitudinal views. Ballstone, Wenlock Edge W.E.2(3). x 10.

## SOLENOPORA COMPACTA (Billings)

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figs. 55, 56.

Stromatopora compacta Billings 1865 p.53.

Tetradium peachii Nicholson and Etheridge 1877 p.166

Stenopora compacta Dawson 1879 p.53

Solenopora compacta (including var peachii)

Nicholson and Etheridge 1885 p.529-533

Brown 1894 p.11 pl.1 figs.3-6

Rothpletz 1908 p.12 pl.III, figs.1-6

Rothpletz 1913 p.11, pl.I, figs.5-6

### Description

Typically the thallus is subspherical usually porcellanous and varies in size "from a hempseed to an orange", (Nicholson and Etheridge 1885), and the species is distinguished by large diameter of the filaments, usual range 70 $\mu$ -130 $\mu$ . Smaller cells about 40 $\mu$  diameter, seen in transverse section are the result of divisions (Rothpletz 1913 and see also Lemoine 1918).

### Horizon and Localities

Solenopora compacta has been recorded from the Ordovician of the Trenton and Black River Limestone, N. America; the Craighead Limestone, Girvan; The Hoar Edge Limestone,

Shropshire: Esthonia and Norway, and the Silurian of Gotland, but not apparently from Britain.

During the investigation, this species (as far as can be determined) has been found in the Woolhope Limestone of Old Radnor, from two quarries Dolyher and Yat Farm, and at about the same horizon and as somewhat recrystallised specimens.

Better preserved specimens were also found in the Wenlock Limestone of Wenlock Edge in the Ballstones.

#### Remarks

Specimens found in the Ballstones of Wenlock Edge were of a massive type with some lobing (fig. 55).

The diameter of the filaments was  $60\mu$ - $120\mu$  when measured from longitudinal sections and c.  $60\mu$  for transverse sections. These measurements are above the upper limit for other species of Solenopora but below the normal lower limit for tubes of animals. The absence of pores and septa also indicates the algal nature of these specimens. In oblique section the cells appear to be fusiform and taper into each other (fig. 56), also Rothpletz 1913 on 'S. fusiformis').

In one example only there was found a line of

discontinuity of growth (fig. 56) , and no spaces indicating possible reproductive parts were found.

The somewhat recrystallised specimens found in the Woolhope Limestone of Old Radnor are also assigned tentatively to this species, as in longitudinal section, the diameter of the filaments (60 $\mu$ -70 $\mu$ ) corresponds to the size range. No traces of reproductive organs were found.

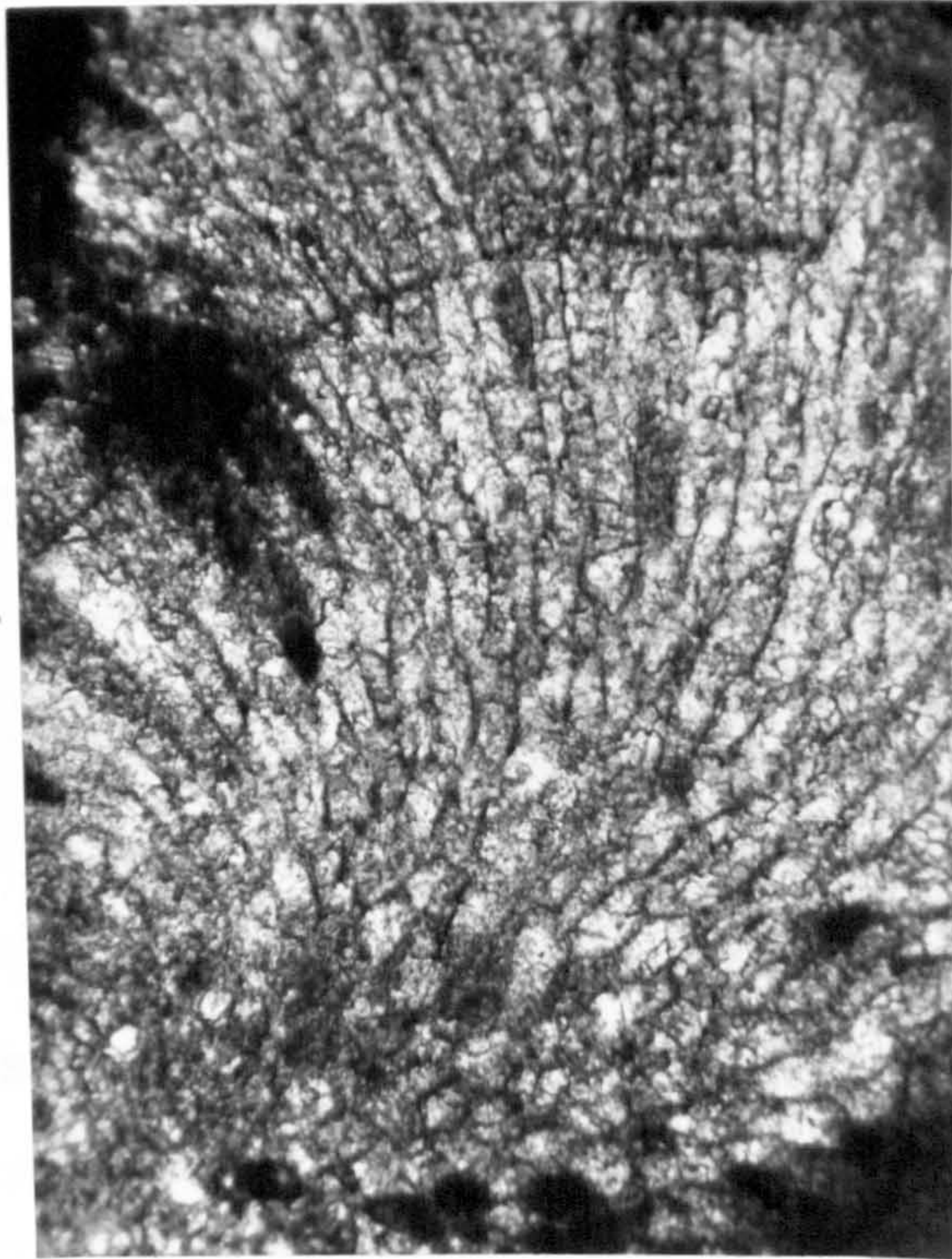


Fig.56 S. compacta. Oblique section showing band of interrupted growth, and plane of section shows tapering filaments. Ballstone, Wenlock Edge W.E.2(3). x 25.

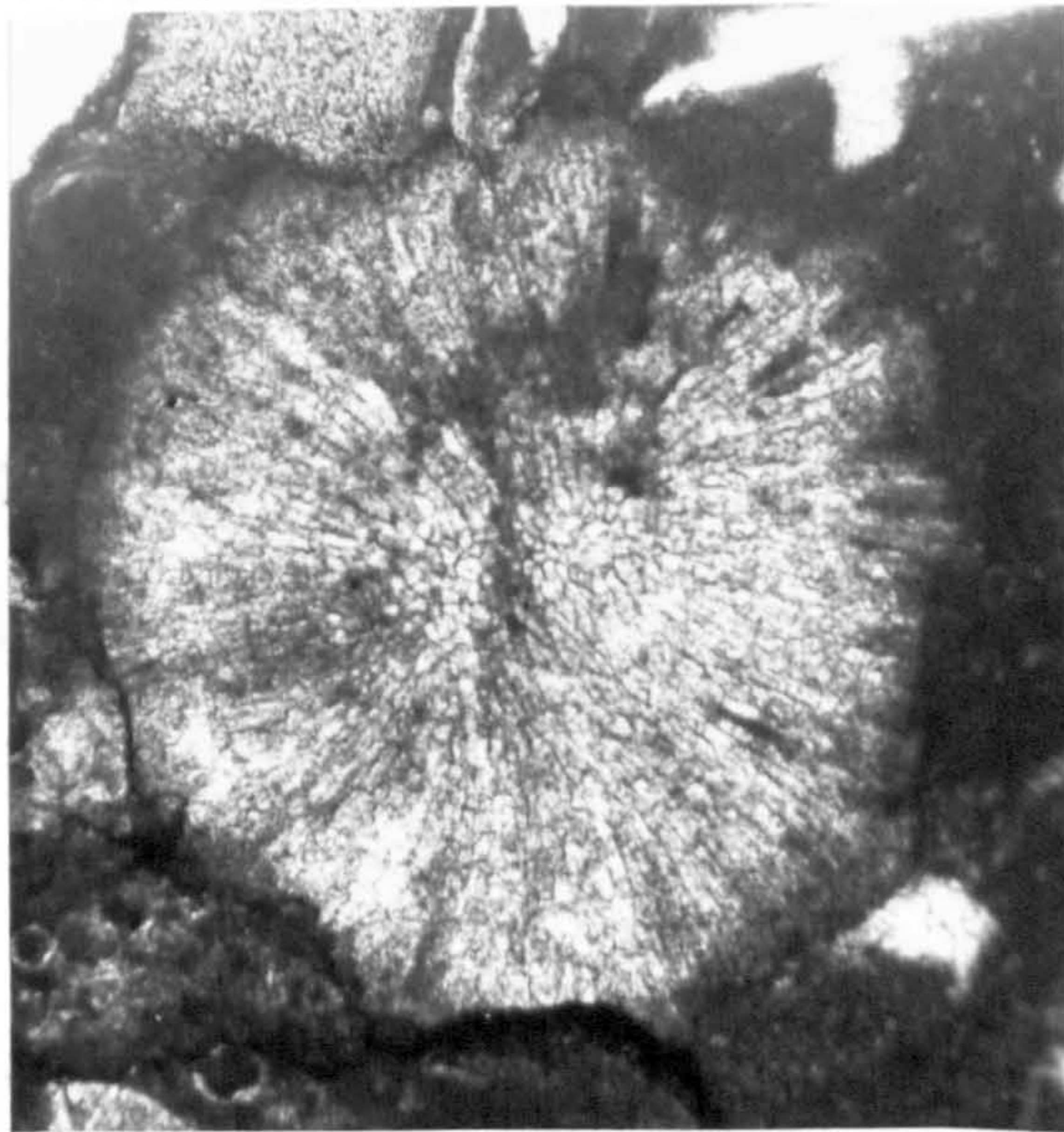


Fig.57 S. gotlandica. Section through thallus. Filaments radiate out from centre. Ballstone, Wenlock Edge (W.E.2(3)) x 25.

SOLENOPORA GOTLANDICA Rothpletz

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fig. 57

S. gotlandica Rothpletz 1908 p.14. pl.IV, figs.1-3  
Rothpletz 1913 p.15, pl.I 1-4, VII 3.

Description

Rothpletz (1908, 1913 and Lemoine 1918) records this form as occurring in the Gotlandian of the Baltic Sea region. Its characteristics are those of the genus, and it is distinguished from S. gracilis by the large diameter of its filaments, which range from 25 $\mu$ -35 $\mu$  and a small thallus, the maximum diameter of 3cm.

Horizon and Localities

A Silurian species in Gotland found mostly in the Sphaerocodium limestone (5-7 South Gotland) and often present with Solenopora compacta, but not with it in the Ordovician. Known localities include Faröe Isles, North and South Gotland, and in Britain the only previous record appears to be for the Wenlock Limestone of the Tortworth inlier (Whittard et al 1944).

During this investigation only one specimen has been collected from the Wenlock Limestone of Wenlock Edge.

Remarks

The thin section of the specimen approximately circular in outline showed a close comparison of cell size with the type. The central region shows polygonal cells cut transversely, and radiating from them the cells in longitudinal filaments. No discontinuity of growth and no 'sporangial' spaces were observed.

SOLENOPORA SPP.

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Remarks

Occasional specimens, either recrystallised or very fragmentary have been found from Old Radnor and Wenlock Edge which are referable to Solenopora, but are too indistinct to assign to any species. In these specimens, the filaments lie parallel and in contact and do not possess mural pores and septa.

From the Woolhope Limestone, a large diameter type, recrystallised, has now been assigned to S. compacta, after examination of various sections containing it, but a smaller form of 35 $\mu$ -40 $\mu$  or 35 $\mu$ -50 $\mu$  (seen from longitudinal sections) is of doubtful affinity.

Other specimens from this and the Wenlock Limestone were found to be too indistinct for measurement, except for the Wenlock form temporarily included under S. gracilis.



Class Chlorophyceae

Order Siphonales

DASYCLADACEAE - various

(Siphoneae Verticillatae)

figs. 58-62

Establishment of fossil forms of the family

The first fossils found from this group were included amongst the foraminifera (Eichwald 1840, 1860, de Koninck 1842, 1872) until Munier-Chalmas (1877) transferred the then known specimens, Dasycladus, Aestabularia Neomeris etc. to the Siphoneae Verticillatae. By 1927, Pia described as many as 58 fossil genera found from Ordovician to present, as belonging to this family, more than the present day forms (Fritsch 1948). Since then more fossil genera have been added to this group (as in Wood 1940).

Descriptions of the Lower Palaeozoic forms are given by Stolley, Rothpletz (1913) and a general survey of their distribution then known was given by Garwood (1913 a, b)

Pia includes all Lower Palaeozoic forms in 3 tribes, Dasyporalleae, Cyclocrineae and Primacorallineae.

Description

Fritsch (1948) indicates the characters of this family, apart from whorled branching etc. is the development of specially differentiated reproductive organs and a "tendency

to a more or less complete incrustation with carbonate of lime". Hence, it is this last feature which has resulted in the preservation of many fossil forms.

Occasional uncalcified fossil forms have been found which appear referable to this family, as for example Callisphenus from the Wenlock of Oslo region (Høeg 1937) and possibly also Chaetocladus which Høeg described in 1932 as an uncalcified siphonous alga.

Apart from Chaetocladus, and forms such as Mastopora (viz. Currie and Edwards 1942) which Pia also assigns to this family, the Welsh Border Silurian specimens are limited to his first tribe Dasy<sup>p</sup>relleae. A new species of Rhabdoporella was described by Lewis (1937) from the Llandovery of Meifod, and apart from the mention of obscure dasycladaceous fragments, this appears to be the only published record for Silurian deposits anywhere in or near the investigated area. Rhabdoporella itself is characterised by an unbranched elongated main axis on which the unbranched laterals were irregularly disposed and did not fit closely together. In Vermiporella the main axis branches, and in others the laterals divide, or branch only from a globular apex.

Remarks

Specimens of the type species (including holotype) of Rhabdoporella intermedia Lewis were examined (fig. 60) (by courtesy of the British Museum (Natural History)) and under high power examination appeared to show a fibrous calcite structure, as mentioned as sometimes occurring in this genus by Rothpletz (1913), but this does not appear to occur in most of the other members of the group. The structure was not found in the larger dasycladaceous types collected in the area, but only in a few smaller ones (found in the Wenlock Limestone) appearing similar to the type specimens. There is a similarity between this fibrous calcite wall and that formed by the foraminifera, Wetheredella, (Wood).

Specimens examined of 'Chaetocladus' originally collected by Lawson from the Aymestry Limestone, are mentioned here, even though uncalcified, as they have affinities with the more branching types of dasycladaceous alga and as on examination of hand specimens (also by courtesy of the British Museum (N.H.)) they appeared to be referable to this genus, the general morphology is more easily ascertainable than just by thin sections through calcified remains. The organisation is higher than in

Rhabdoporella as the branched laterals arise in whorls from nodes on the main axis, and appear to be generally more prolific nearer the apex than lower.

This form seems to be more highly organised in mode and position of branching than the members of the 3 tribes of Pia (mentioned earlier).

The specimens examined were up to 3cm or more in length and to 4mm wide.

Specimens of Mastopora have not been found calcified in the area, but are recorded from the Llandovery sandstones of the Bog Mines Outlier, Shropshire.

RHABDOPORELLA sp.            figs. 58-62

Description

This form is at present assigned to Rhabdoporella on its irregular arrangement of lateral branches (pores) on a main unbranched axis, together with lack of further branching of laterals, and complete calcification and has not yet been given specific rank as further comparisons are required between it and other members of this genus. It compares in size to R. bacillum (up to 2mm long) and in wall thickness, most specimens measured about 50 $\mu$  thick. The pores (i.e. branches) appear to be

about 15 $\mu$ -30 $\mu$ , mostly 20 $\mu$  in diameter, (in *R. intermedia* >16 $\mu$ ).

A calculation of  $d/D \times 100$  (viz. Lewis 1937), if this is valid, yielded a result of 80 in one instance, whereas in *R. bacillum* it is stated as 62.5-70 (and in *R. pachyderma* 24-60, *R. stolleyi* being a smaller form).

#### Horizon and localities

Specimens were found in thin section abundantly in the Woolhope Limestone of Mordiford and were also found in the Wenlock Limestone of this area, including Fownhope.

#### Remarks

The wall did not show any fibrous structure and the stippling shown on the figs. ( 61 and 62 ) indicates some of the granular impurities and slight iron staining present on same. This probably indicates the position of pores just out of the plane of section.

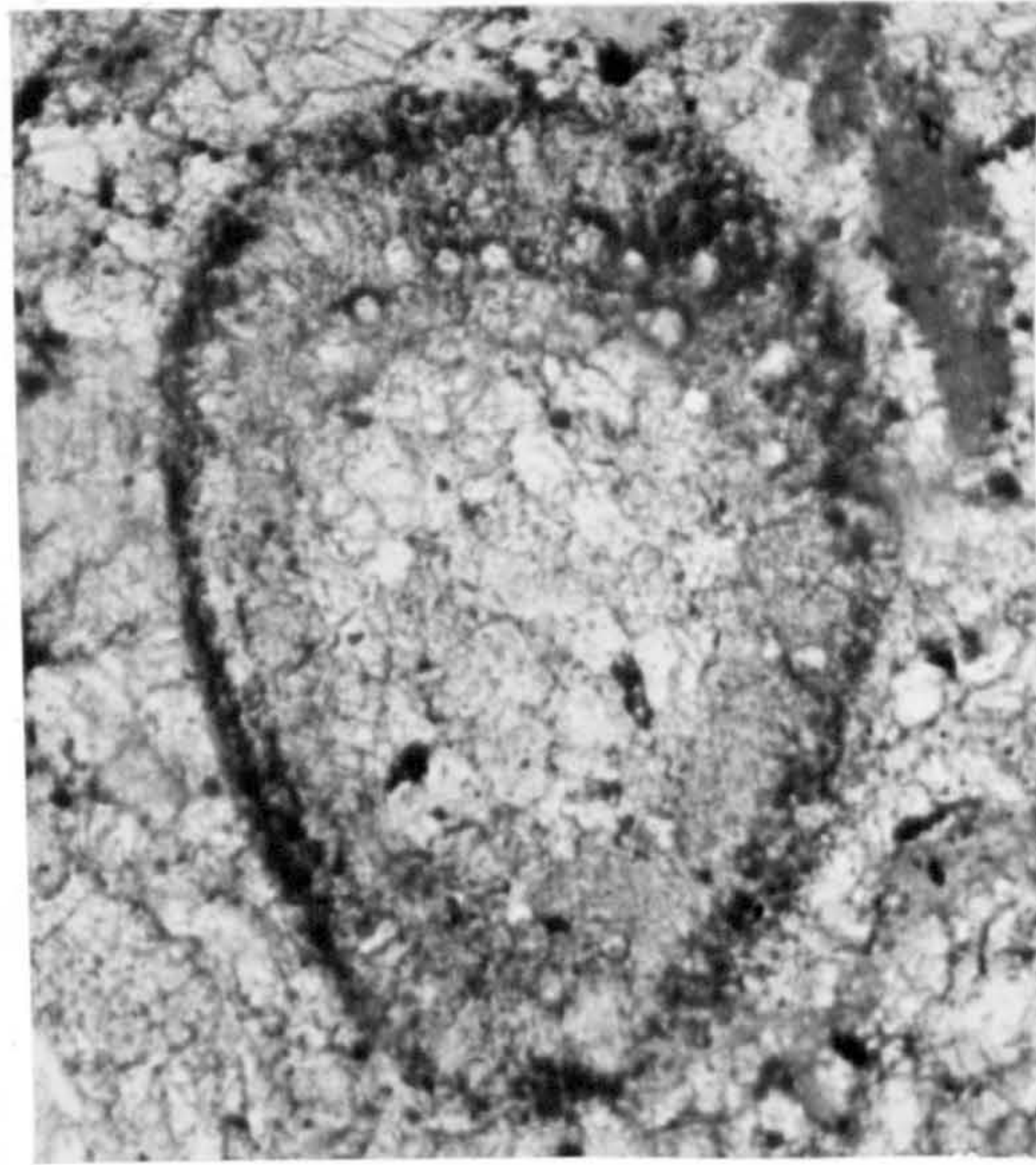


Fig.58 Rhabdoporella sp. Oblique section shows 'pores', central cavity and iron stained calcite wall. Woolhope Limestone, Mordiford M.F.1(2), x 90.

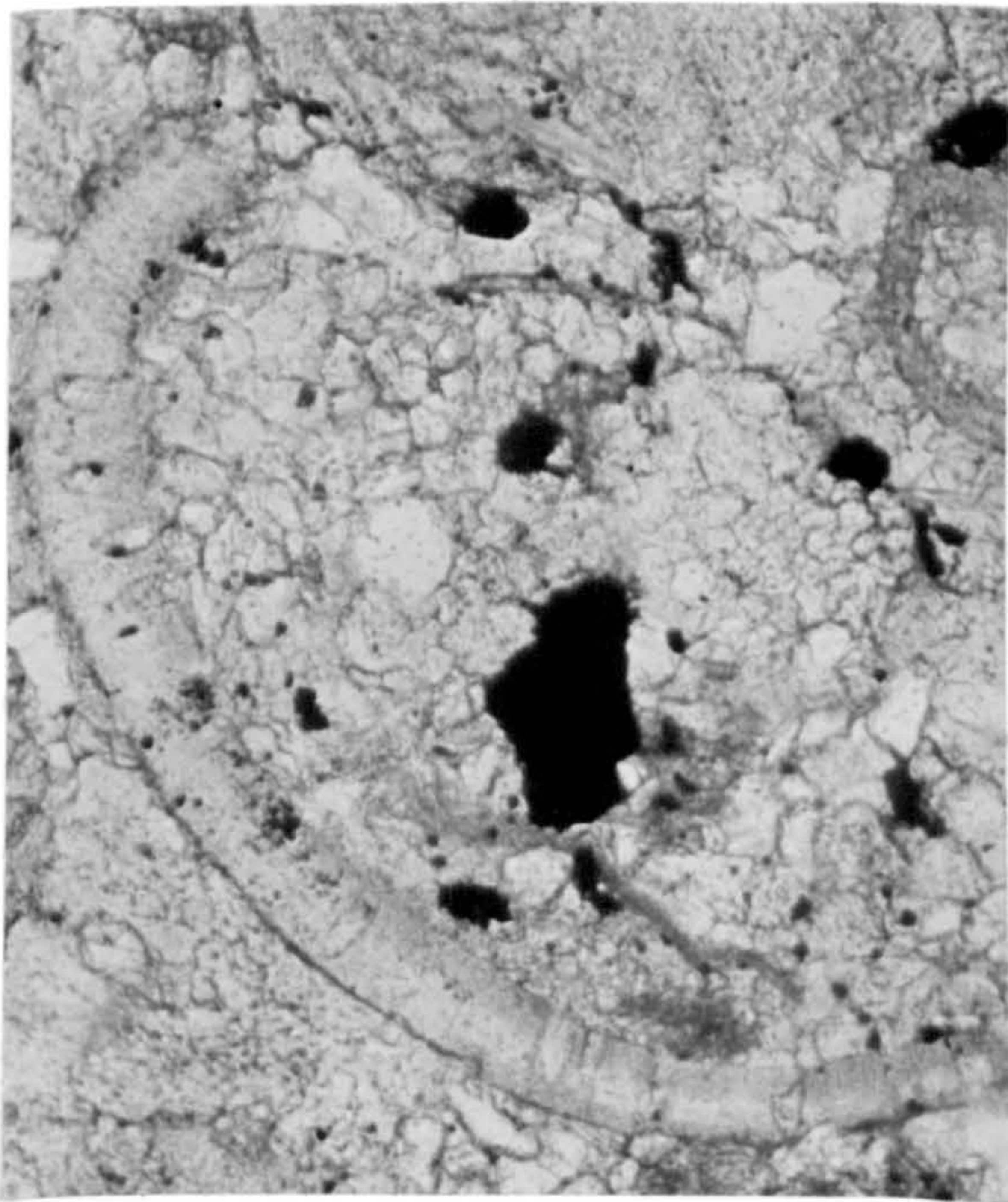


Fig.59 Rhabdoporella sp. Longitudinal section through pores. Locality as above M.F.1(2), x 90.



Fig.60 Type specimen of R. intermedia Lewis for comparison x 145.

Fig. 61.

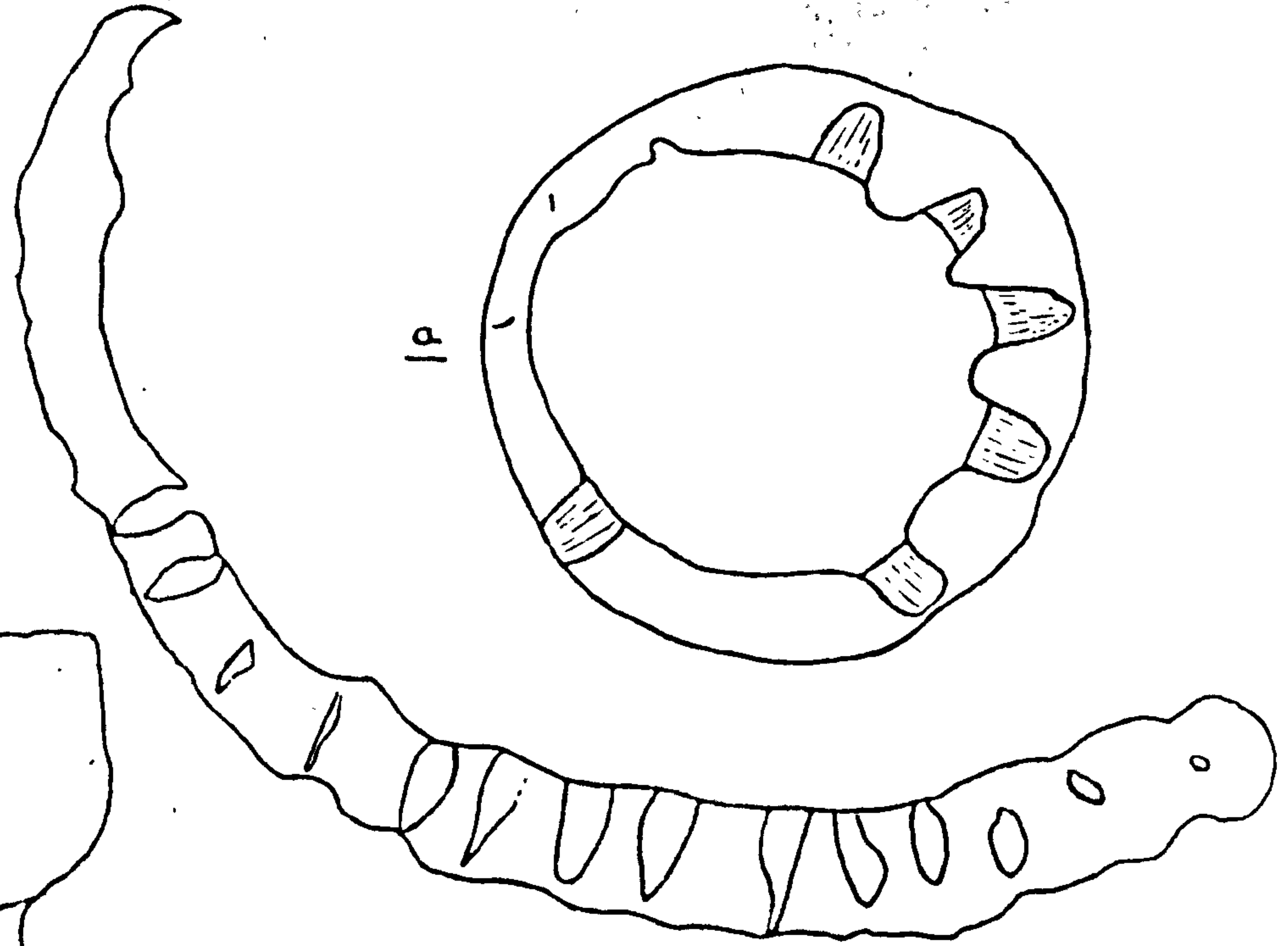
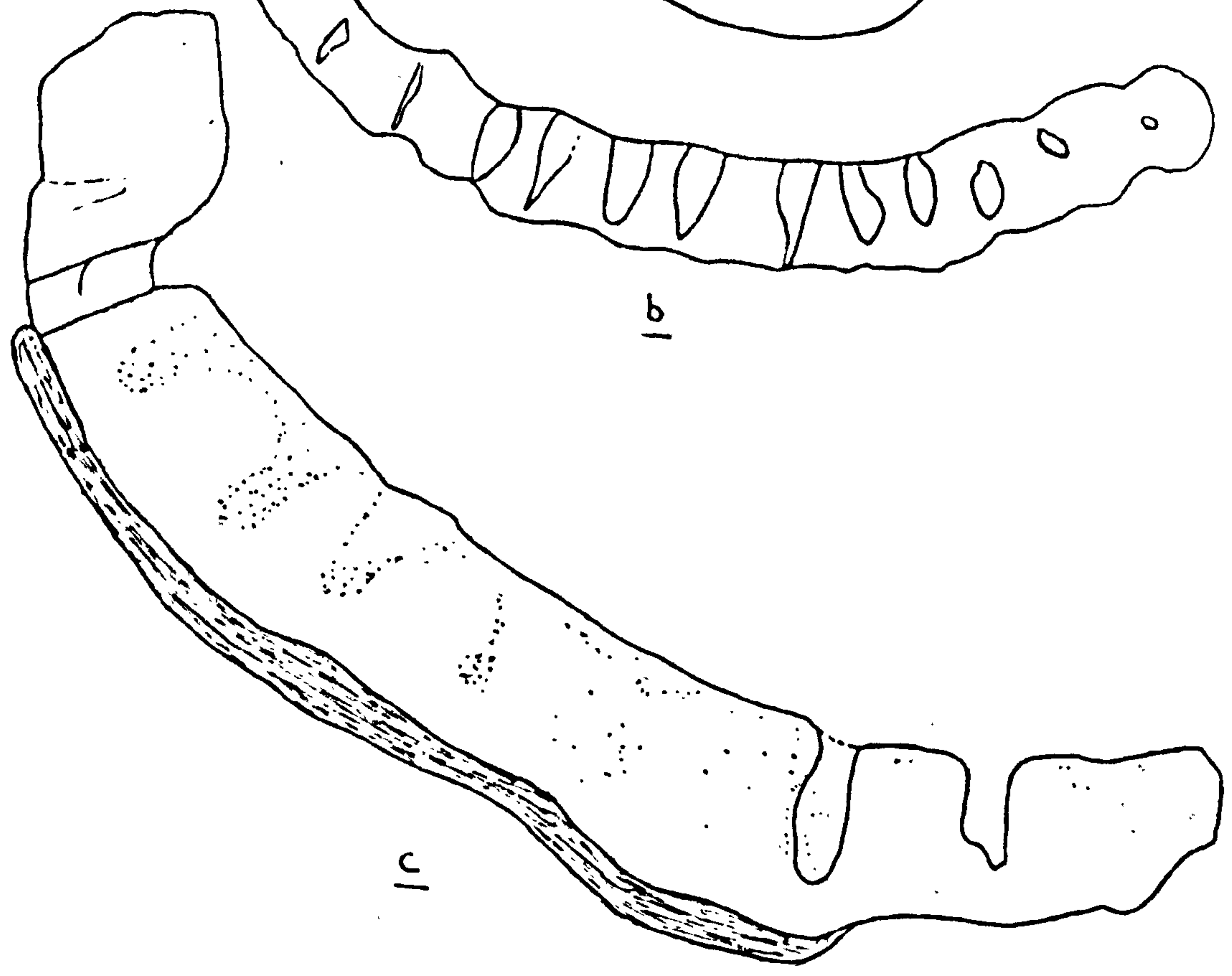
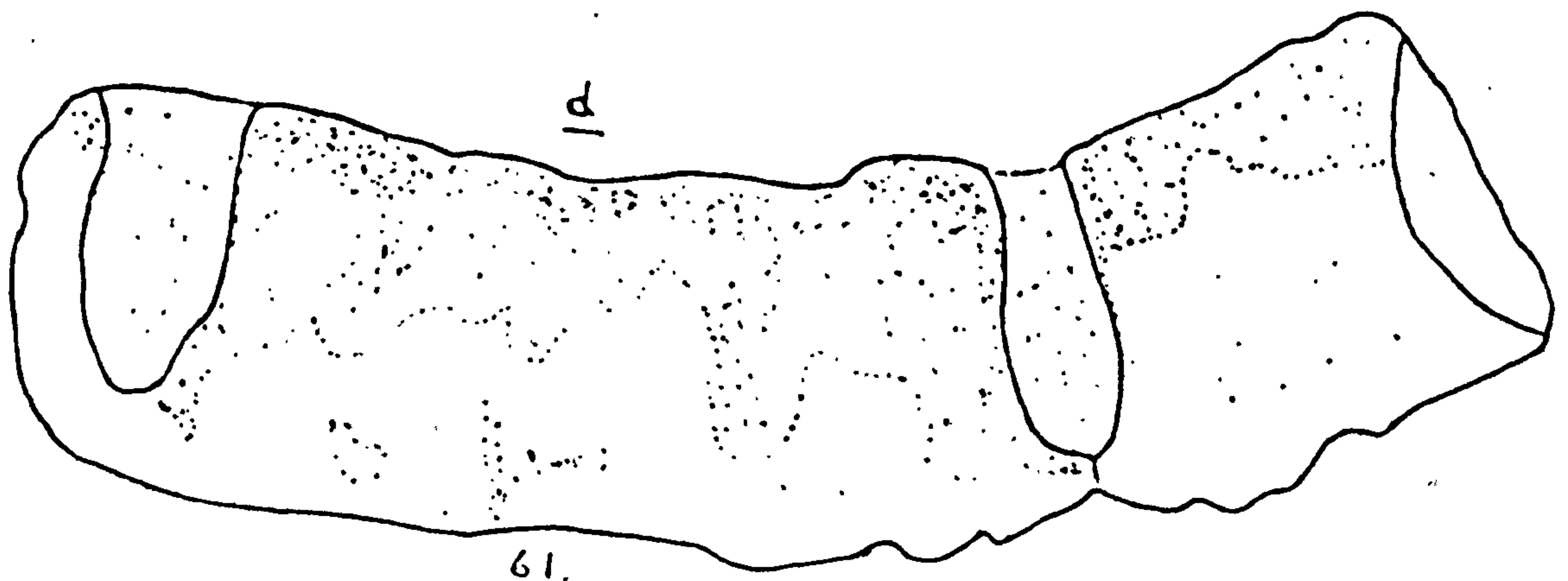
Diagrams of Rhabdoporella from Woolhope  
Limestone, Mordiford

- a. R. intermedia ? showing pores.  
M.F.4(1) x 600.
- b. Rhabdoporella Longitudinal section  
M.F.1(2) x 260
- c. Rhabdoporella Longitudinal section  
M.F.1(1) x 350
- d. Rhabdoporella Longitudinal section  
M.F.1(1) x 600

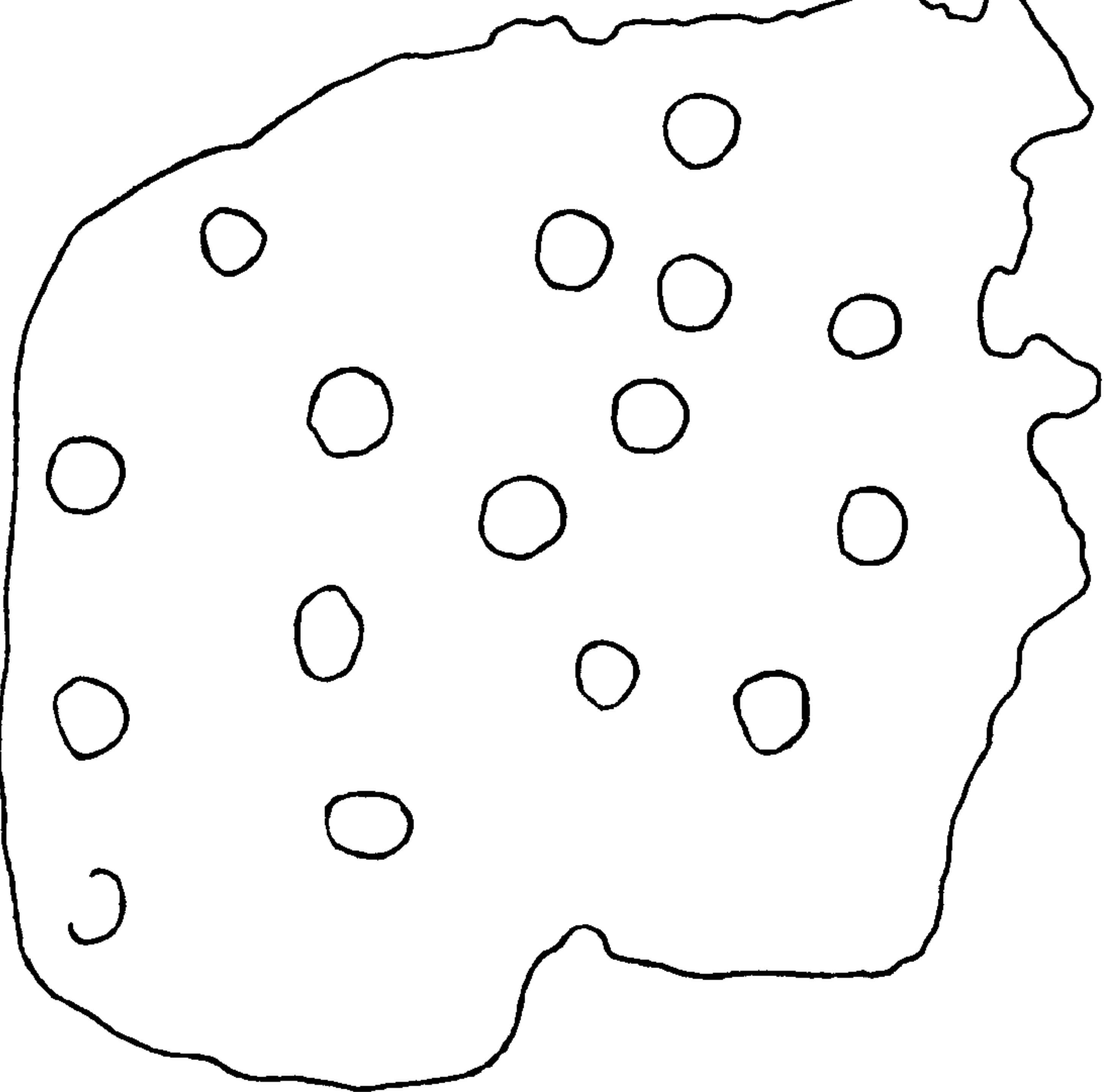
Fig. 62.

Diagrams of Rhabdoporella from Mordiford

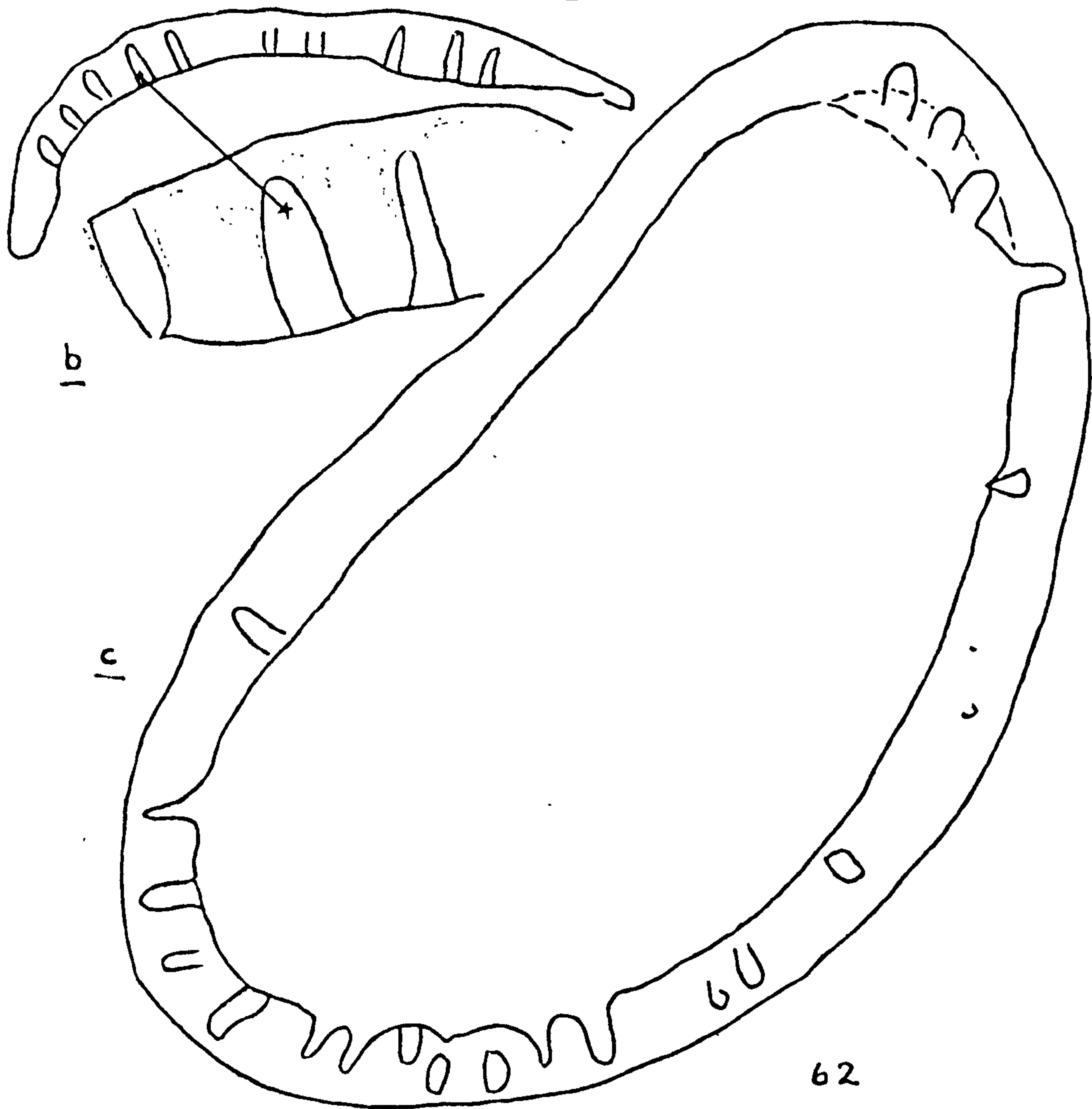
- a. Surface view of pores approx. x 300.  
M.F.1(2)
- b. Longitudinal view x 100 and x 350.  
M.F.1(1)
- c. Longitudinal section, slightly oblique.  
M.F.1(2) x 260.







18



18

19

20

21

DISTRIBUTION OF THE CALCAREOUS ALGAE IN RELATION  
TO THE DIFFERENT FAUNAS AND SEDIMENTS

General

Calcareous algae were found in the limestones and highly calcareous facies, but not in the intervening shales. Random thin sections of specimens from the Silurian shales were examined, but as no algae were found in them the investigation was practically limited to the more calcareous facies.

Records of algae in Silurian beds other than the limestones are scarce. Llandovery beds include a record of 'fucoids' from the Rubery Sandstone of Rubery (Butler 1937). The problematical structures examined in hand specimens are silicified and Mastopora from the Bog Mine Outliers (Shropshire) is also silicified. There appear to be no other records of Llandovery algae (even in the Geological Survey Museum and British Museum (Natural History)) in the Welsh Border.

A calcareous alga Ortonella rigida described by Lewis from the basal Llandovery of Meifod (Montgomeryshire) does not appear to be recorded elsewhere, and as it has not been found from any of the localities visited, its description

is omitted here. Lewis also described a member of the Dasycladaceae Rhabdoporella intermedia from this locality in his paper, comparing it with other Lower Palaeozoic forms.

Pachythea has been recorded once from the Wenlock limestones of the W. Malverns (specimen now lost), but the majority of specimens on record from the Upper Silurian are either in a carbonized or silicified state (Lang 1924, 1945), so it probably was not a calcareous alga. As also none were found during the investigation of the limestones, its description has been omitted here.

The following sections, grouped under each limestone unit, are the localities visited, the types of limestone facies investigated from each, both field and microscopically, thus relating as far as possible types of facies found with the fauna and algae present. Further, the algal-faunal relationship and also the relative abundance of algae in different environments (biocoenose and thanatocoenose), or geographical situations was worked upon. The relative abundance of different algae were also determined as far as possible.



Fig.63 Dolyhir Quarry I. Main algal limestone facies. Woolhope Limestone, Old Radnor.



Fig.64  
Algae weathered white  
in algal limestone.  
Yat Farm Quarries  
(O.R.2) Old Radnor.

## I. WOOLHOPE LIMESTONE

### A. OLD RADNOR AND NASH SCAR

#### Localities

Material was collected from the Dolyhir Quarries (Quarries C. D.), Yat Farm Quarries (J.K.) (figs. 63-66) and grid. ref. 582242 and 585246, 1" O.S. Map No. 128), and Nash Scar, Nr. Presteign (figs. 67, 68 ) and grid. ref. 623300, 1" O.S. Map No. 129) which are shown on the 6" map of the Old Radnor district by Garwood and Goodyear 1918.

#### Types of limestone investigated

The Woolhope Limestone from the district was found to consist of several lithological facies including basement beds, bryozoan and crinoidal facies and the main algal limestone.

In the field, the basement beds were seen to be conglomeratic, very crystalline and containing numerous colonies of Favosites, with fewer bryozoa and algae (Solenopora). The best exposures were found in the Yat Farm Quarries.

A facies, distinguished by numerous crinoid ossicles,

many pink-stained, is present just above the basement beds at Yat Farm. It was also located at Dolyhir. Numerous small pea-sized Solenopora and bryozoa were present.

The main facies, the massive algal limestone, is referred to as a reef facies by Garwood. The limestone has undergone considerable recrystallization, faulting and crushing, and so it is hard to ascertain whether these were originally true reefs. Solenopora gracilis was found throughout this limestone and the fauna, of Coenites, Halysites, Favosites, occasional brachiopods and few trilobites and other forms of widely scattered distribution, were subordinate to it. The matrix is coarsely crystalline, and the limestone was present in all localities visited in this district.

Garwood described a distinct facies as a bryozoan reef development with absence of bedding and occurring at two horizons. It was found in the three localities (figs. 67, 68) The "bryozoa" (mostly Coenites repens) are predominant over the other forms, and Solenopora was smaller in size and fewer in number than elsewhere. A few solitary corals and small brachiopods were also found.



Fig.65

Main algal limestone

Yat Farm, (O.R.2.)

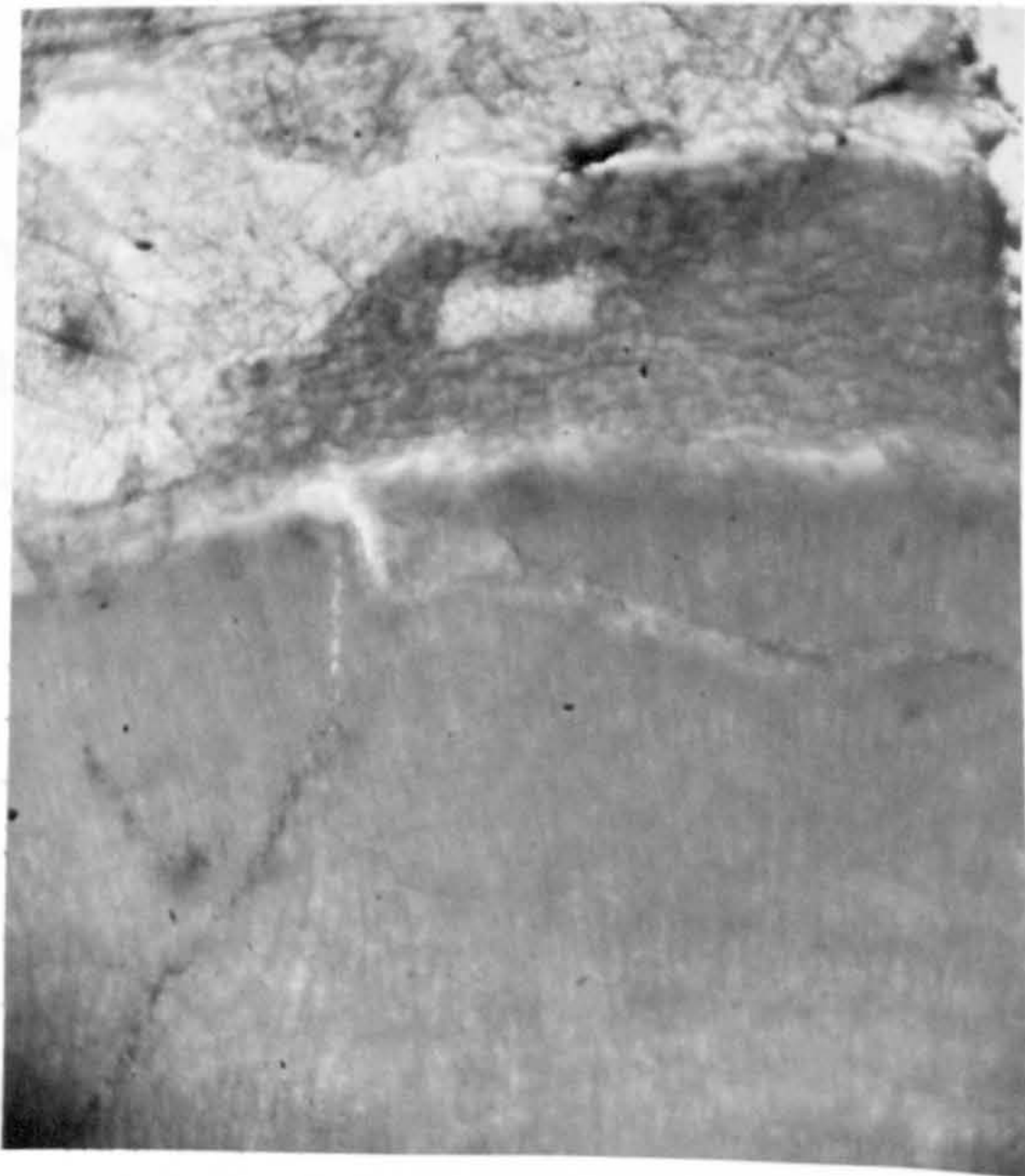


Fig.66 Rothpletzella excrusting Solenopora thallus.

This section from rock specimen, Yat Farm.

The matrix was still coarsely crystalline.

A dark limestone, where unweathered, possibly of the 'bryozoa' facies, which in thin section yielded Solenopora of larger filament diameter than S. gracilis, was found at both the Old Radnor localities.

No algae were found in the shale band described by Garwood.

#### Algal-faunal relationships

Correlations between algae and fauna are difficult to establish in this district as the limestone has been subjected to much alteration and veining and shattering of the rock is extremely common throughout, but the effects appear to have been greatest in the region of the Dolyhir Quarries. Most of the ground mass consists of coarse calcite crystals. These alterations in the rock must therefore be reflected in the algal preservations. For example, the Solenopora thalli are frequently veined with calcite and many encrusting forms are nearly obscured or appear as large areas of 'algal dust'. It would seem possible, that as this 'algal dust' often gradually grades into the crystalline calcite of the matrix, that this



latter is at least partly the result of diagenesis of organic remains, in particular of calcareous algae.

Solenopora gracilis, the most conspicuous form, is present throughout the Woolhope limestone of this district, and in most specimens examined the thallus was nodular and did not appear to be encrusting. The filamentous forms however, were mostly found encrusting other organisms, though occasionally were found as free clusters.

The Basement Beds, with the abundant Favosites, were found to contain smaller specimens of Solenopora gracilis together with occasional brachiopod, crinoid ossicle, solitary coral and Wetheredella silurica. Algal filaments, Rothpletzella gotlandica, R. conferta and Girvanella sp. (indeterminate) were also sporadically found usually encrusting Coenites repens or in association with small clusters of Wetheredella.

The crinoidal bed, occurring above the basal rocks, was distinguished by the numerous small examples of Solenopora gracilis, the abundance of crinoid ossicles together with the presence of Rothpletzella gotlandica, R. conferta, Wetheredella, Coenites, sponge spicules and obscure dasycladaceous fragments.

The 'bryozoa' beds, mostly of Coenites repens also



Fig.67 Nash Scar. Bryozoan and algal beds.  
Woolhope Limestone.



Fig.68 Bryozoan band, Nash Scar.

B. WOOLHOPE, Herefordshire

Locality

Woolhope Village (road S. of Church 1" O.S. map 142, grid. ref. 367613, also 1" Geol. Survey map No. 43 Hereford and Gardiner 1927). Exposure by roadside.

Limestone type and algal relationships

The Woolhope Limestone here is a nodular bedded limestone. Most organic remains found were small but a tabulate coral was found together with crinoid ossicles, ostracods, bryozoan fragments, Wetheredella and other spicular elements, also angular quartz fragments were abundant. Only filamentous algae were found and these were infrequent and the groups often small in size or odd scattered filaments. The algae found were Girvanella spp. including G. pusilla, G. problematica and G. media and algal dust. Quite a few specimens were found encrusting other organisms including Coenites and crinoid ossicles.

The more fragmental nature of most of these specimens would possibly indicate conditions different from those which prevailed in nearby localities during the limestone formation.



Fig.69 Mordiford Scutterdine Quarry 2. Woolhope Limestone. Middle to Upper Beds.



Fig.70.  
Mordiford Scutterdine  
Quarry 3. Upper Beds.  
Woolhope Limestone,

C. MORDIFORD, Herefordshire

Localities

Mordiford Quarry 1. is situated in Haugh Wood at the junction of the Littlehope Lane with the road (grid. ref. 373578, O.S. Map No. 142, also 1" Geol. Survey Map No. 43 and Pocock 1930). An old disused quarry mostly filled in and overgrown - exposure small.

Quarries 2 and 3 are both disused quarries at Littlehope. Quarry 2, Scutterdine Quarry, well exposed (grid. ref. 361581) and Quarry 3, by farm duckpond partly overgrown (grid. ref. 361581). Quarry 4, Haugh Wood, main road to Woolhope, c. 100 yds. from Quarry 1 (grid. ref. 373578). Exposure in Wood, rather overgrown. Quarry 5, about 30 yds. nearer Mordiford, upper beds of Woolhope limestone. Roadside exposure.

The localities were partly chosen from references including Pocock 1930, Gardiner 1927 and various older references from the journals of the Woolhope Naturalists' Field Club.

Types of limestone investigated

All the limestone seen here was bedded and appeared

to include no reef structures. The limestone in Quarry 1 situated just above (and supposed to include) the *Petalocrinus* horizon, i.e. the basal beds of the Woolhope Limestone, was a compact limestone (with crinoid ossicles visible) in the lower part exposed, but more rubbly above (as far as was seen) and which may be due to weathering.

The middle beds exposed at the base of Quarry 2, are very hard dark blue limestones, and above these is blue-hearted compact limestone above which limestone bands alternate with a few thin shaly limestones, which are more frequent at the top of the section. The exposure therefore also shows the upper beds of the Woolhope limestone.

Quarry 3 is also in the upper beds and consists of alternating bands of hard limestone beds with shale. The remaining exposures, small, are also of the compact limestone of the upper beds. (figs. 69 and 70).

#### Algae and their relationships

Filamentous and <sup>other</sup>algae (*Dasycladaceae*) but no massive forms such as Solenopora were found from this district. The algae were very abundant in the thin sections of limestone examined, especially those of Girvanella spp.

In the lowest beds (M.F.1) representative counts of different algal counts yielded the following: From the lowest horizon obtainable (M.F.1(2)) counts on sections yielded 36 distinct Girvanella groups out of 48 measured had average filaments under 10 $\mu$  in diameter (see histograms and tables). Of these, 22 were of the straight bundle type (G. fragila) and 14 were in the form of large loosely coiling clusters (G. pusilla). Of the remainder, 5 were the larger type of straight bundle (G. proluxa), and the others larger clusters of wide tubes G. problematica and frequent branching (G. media), 1 spiral form and 1 encrusting. This sample measurement gives an indication of the dominant form present (G. fragila) and the other types present in the limestone.

Several Rhabdoporella were also seen in section occurring sporadically throughout. There was no orientation to the bundles of Girvanella in this or any other slide from Mordiford district. This would in G. fragila be readily observable if either they lay in flat on bedding planes or were affected by a current (i.e. lying lengthwise in the direction of current). As the groups also show no signs of any abrasion, except one

which was rolled with feruginous staining on the outside, and separate broken algal filaments are uncommon, it seems likely that the majority of groups could not have drifted very far from their place of origin. The loose tangled groups of G. pusilla were probably unattached, and may have been floating near the surface of the water, when living, because of their minute size. The bundles of fine filaments of G. fragila also show no signs of any attachments and do not taper to a point, nor appear to be adhering to any substrate or growing on its surface, so it is possible that these also were floating algal groups. On death, or even seasonal effects, these algal groups with no current, would fall to the bottom with no definite orientation, and if plenty of debris was present already they would not all lie flat in the direction parallel to that indicated by bedding planes.

Results of counts taken from a higher horizon (M.F.1(1))  $1\frac{1}{2}$  ft. higher and immediately above the first show a strong similarity. Dasycladaceae were seen in section occasionally, but were not as common as the Girvanella. Out of 49 separate Girvanella groups 43 had a diameter range of 9 $\mu$  and less and of these 30 were G. fragila and the remainder (13) were coiling G. pusilla. Of the few larger groups



measured one is possibly spiral in form and the other mostly cluster (G. problematica) or in transverse section.

Calculations based on the 43 specimens in the smaller diameter filament group (see histogram), (that is the aggregate of both forms) gave a standard deviation of 1, the average mean being  $6\mu$ , so that the population range (3 S.D) was found to be between  $3\mu$  and  $9\mu$ . This is comparable with the results from the first count. The smaller diameter filament group being taken (see histogram) the average mean calculated from the means of each group was again  $6\mu$ . The standard deviation was slightly larger so that 3 S.D. = 4, therefore the population range was between  $2\mu$  and  $10\mu$ .

As these results are very consistent - a high proportion of the form G. fragila; a lesser of G. pusilla; and a few larger form species of Girvanella, which in size do not overlap the population ranges for the lesser groups and so are definitely distinct from them; it would seem that for this locality even at different horizons (in the lower beds) the finer species were the dominant algae. Further as the fauna consists of crinoid ossicles, occasional brachiopods, ostracods, spicules, (some sponge.)

scattered bryozoa, etc. and rarely any corals. these algae appear to have been some of the most important organisms present. It is uncertain how much they contributed to the formation of this limestone, but it is apparent that they are possibly the most important organic contributor.

Septation was observed in some specimens of G. fragila, G. pusilla and in G. media and is regarded as the better preservation of these algae.

Examination of specimens obtained from the other quarries showed many similar features, even though these were in much higher beds in the limestone. For example, out of a count of 51 distinct Girvanella groups (from M.F.2(7)) just above the main limestone 100'ft. of Pocock), 44 had a filament diameter of 10 $\mu$ . These were G. fragila and G. pusilla as before. The remaining 7 groups were the highly branched Girvanella ramosa and G. effusa with 1 G. media. Calculations based on the narrower filamentous groups, gave an average mean of 6 $\mu$  and a population range of 2 $\mu$ -10 $\mu$  (3 S.D. = 4 $\mu$ ). Out of all the groups measured from M.F.2(7), only 1 was encrusting an organism with a possibility of one other - both included under G. pusilla. All the other finer groups at least appeared to be unattached forms.

Septation occurred in some specimens of both fine and

wide filaments. At this horizon, thin sections indicated more debris in relation to the still abundant algal groups than in the thin sections examined from M.F.1.

The different species of Girvanella could either mean the increasing abundance of these forms-as they are common in the succeeding Wenlock of this district - or just absence of records of them from the lower beds.

The usual faunal assemblage was found: crinoid ossicles, ostracods and spicular elements, various bryozoa, brachiopods including rhynchonellids, atrypids, spirifers and occasional trilobite, together with Rhabdoporella. Sections from other beds and quarries were very similar.

The absence of the reef building organisms including the algae Solenopora spp. and Rothpletzella spp. and the presence of so many non-encrusting algal groups, is indicative of the absence of any nearby reef structures. This is further verified by the absence of any such structures seen in the field.

A SUMMARY OF THE COMPARATIVE OBSERVATIONS ON THE  
ALGAL DISTRIBUTION, VERTICAL AND LATERAL, THROUGHOUT THE  
WOOLHOPE LIMESTONE OF THE WELSH BORDER

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The massive reef forming Solenopora have only been found in the Old Radnor, Nash Scar district, where S. gracilis appear to have been the dominant organism in the limestone formation. It was found at all horizons investigated and in all the facies. The other species were only found at one horizon from Dolyhir and Yat Farm. Thus they appear to have, at least, a limited lateral extent even if not vertically.

The filamentous encrusting algae were mainly in the 'reef-forming' areas. Thus, all the specimens of Rothpletzella found were from the same district as Solenopora. Both R. gotlandica and R. conferta were found in all the different facies examined although R. gotlandica occurred less frequently than R. conferta in the main algal limestone, and the latter has not been found yet from the bryozoan facies of Nash Scar. No Rothpletzella or Solenopora have yet been found from the eastern Woolhope Limestone exposures.

Girvanella has only been found very sporadically in the Old Radnor quarries and usually encrusting the organisms.

The species, where determinable, were G. problematica and G. pusilla.

In the Woolhope area, Girvanella instead of sporadic occurrence becomes one of the dominant organisms, in some beds appears to be the most important genus. This is not striking at Woolhope itself where Girvanella is common and several groups are found in each slide, but at Mordiford where the counts are much higher. The nodular beds at Woolhope may well reflect a less stable environment for algal fossil preservation than the even limestone bands of Mordiford and district.

The most abundant species, and hence the dominant for this area is G. fragila, the other fine species G. pusilla being sub-dominant. As a group the bigger types are fairly common but not as common as G. pusilla. Of these types, G. problematica and G. media are most frequent and G. prolixa, G. ramosa and G. effusa have been recorded.

Rhabdoporella sp. was found in moderate numbers in the Mordiford, Woolhope district, but it has not been definitely recorded from Old Radnor district, and if present there it seems unlikely that it would be so abundant as at Mordiford.

Thus, in the Woolhope Limestone at least, Solenopora and Rothpletzella are commonly found in the same association preferring one type of environment, whereas

Girvanella is most likely prolific away from the reef-like areas, flourishing where corals and bryozoa do not abound. Evidence indicated that Rhabdoporella also prefers the latter type, but being usually associated with reef building organisms.

TABLE VI.

DISTRIBUTION TABLE FOR ALGAE OF THE WOOLHOPE LIMESTONE

	<u>OLD RADNOR</u>		<u>NASH</u>	<u>WOOLHOPE</u>	<u>MORDIFORD</u>		
	Qu.1.	Qu.2.	<u>SCAR</u>		Qu.1.	Qu.2.	Qu.3-5.
<i>Solenopora gracilis</i>	x	x	x	-	-	-	-
<i>S. compacta</i>	x	x	-	-	-	-	-
<i>Rothpletzella gotlandica</i>	x	x	x	-	-	-	-
<i>R. gotlandica</i> large var.	x	x	-	-	-	-	-
<i>R. conferta</i>	x	x	-	-	-	-	-
<i>Girvanella fragilae</i>	-	-	-	-	x	x	x
<i>G. pusilla</i>	x	x	-	x	x	x	x
<i>G. ramosa</i>	-	-	-	-	-	x	-
<i>G. effusa</i>	-	-	-	-	-	x	-
<i>G. problematica</i>	x	x	-	x	x	-	x
<i>G. media</i>	-	-	-	x	x	x	-
<i>G. proluxa</i>	-	-	-	-	x	-	-
<i>Rhabdoporella</i>	-	-	-	x	x	x	x
Algal dust	x	x	x	x	x	x	x



Fig.71 Wenlock Edge, Quarry 6, Wenlock Limestone. Shows Ballstone and related bedded sediments. In background are the Gingerbread facies.



Fig.72 Side view of Ballstone (see in Fig71). On right of photograph are sediments contemporaneous with Ballstone, containing abundant fossils.



## II. WENLOCK LIMESTONE

### A. WENLOCK EDGE

#### Localities

Material was collected from various localities along the length of Wenlock Edge (1" O.S. maps 118, 129, and 6" maps 50, 57 and Geol. Survey Map O.ser.61 S.E. S.W.) in order to find the extent of lateral variation in a district where good exposures are fairly plentiful.

The limestone exposures (shown on sketch map fig. 83) were as follows:

Qu. 1	grid ref.	996613	Qu. 8	grid ref.	003610
Qu. 2	" "	997612	Qu. 9	" "	002611
Qu. 3	Farley grid ref.	015629	Qu.10	" "	006627
Qu. 4	" "	995605	Qu.11	" "	844447
Qu. 5	" "	968575	Exp.12	Wenlock shale grid ref.	849445
Qu. 6	" "	986597	Exp.13	Wenlock limestone grid ref.	856455
Qu. 7	" "	985597	Exp.14	(1) grid ref.	856455
			Exp.15	" "	856455

#### The limestone facies of Wenlock Edge

The most distinctive division made is between the unbedded Ballstones and the bedded sediments. The latter can be further divided into various facies of which the most

noticeable are the 'Grey Measures' and 'Gingerbread' (quarrying terminology). The other bedded facies are more restricted in distribution both vertically and laterally.

The Ballstones are regarded here as true reefs in origin. Various sizes were found from a few feet to 20 or 30 ft. at least in height, from different localities and different horizons in the limestone. None however have been found or are known on the Edge to the south-west of the large ones at Major's Leap. Also beyond Major's Leap the exposures are few as quarrying was less extensive. The edges of the Ballstones often interfinger with the bedded sediments indicating that the Ballstones' growth was contemporaneous with the deposition of the surrounding bedded sediments. In one case, at least, the upper bedded sediments were seen to arch up and over the top of the Ballstone (figs. 71, 72). In the field, the Ballstones were usually found to be light grey, unbedded, very compact limestones. They are very fossiliferous and contain corals, stromatoporoids, bryozoa, brachiopods and crinoids as a high proportion of their fauna and a large percentage of the fossils appear to be in positions of growth. Much of the remaining percentage occur as debris

in the interstices between growth colonies.

The 'Grey Measures' as their local name implies, consist of grey massive bedded compact limestones and when examined away from relatively unfossiliferous crinoid ossicle, gastropod. Nearer to a Ballstone, if contemporaneous, these Measures appear more fossiliferous. The 'Gingerbread', also a local name, are the brown rubbly limestones, the colour of which is due to weathering. The main constituents are the crinoid ossicles which give the limestone a high calcite content. Other common fossils throughout include brachiopods, corals, bryozoa and occasionally there are seams richer in these or other organic forms. All these fossils are mostly not in positions of growth.

The Gingerbread was found mostly at the top of the Wenlock Limestone of the Edge where it is widespread. It occurs above the Ballstones, often immediately, as if cutting off any further development of that facies, but also a crinoidal facies has been found as a lateral development apparently contemporaneous with the Ballstones. This facies is of more limited extent and does not detract from the widespread formation of the Gingerbread beds as such.



Fig.73 Larger Ballstone Quarry 5 (18-20 ft. seen)  
with 6 ft. Gingerbread beds above.



Fig.74 Quarry 4. Sediments near a Ballstone and  
merging into it.



Fig.75 Quarry 4. Close up of part of Fig.74, showing sediments constituting reef flank of Ballstone and containing nodular stromatoporoids, etc.

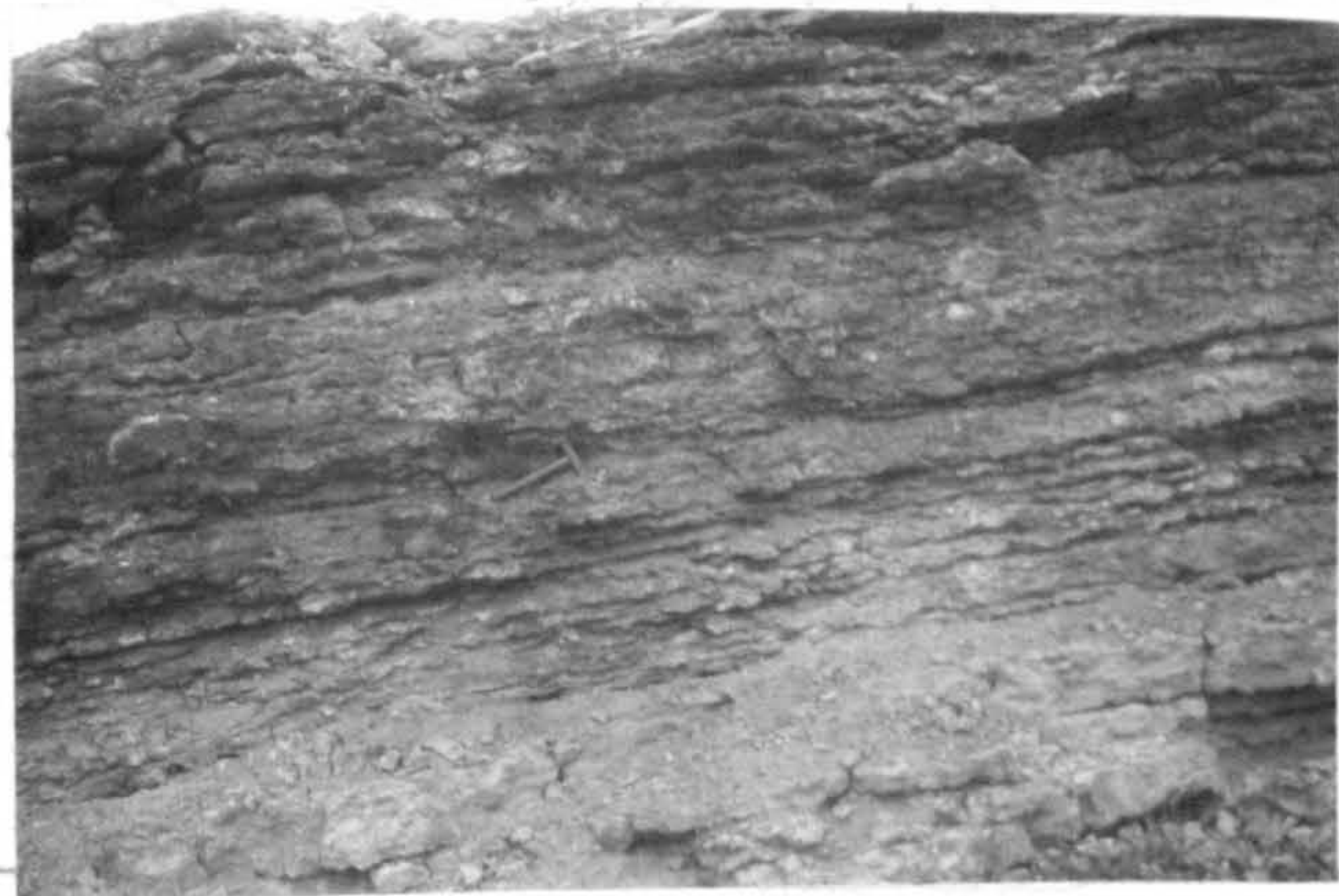


Fig.76 Quarry 6. Beds contemporaneous with the Ballstone, fewer fossils as traced away from it and grade into Grey Measures.

Other types of facies occur locally especially near the Ballstones. In vertical thickness they may vary from a few inches to many feet, but they mostly do not appear to have a wide lateral extension. These other facies include bryozoan, brachiopodal, coralliferous and other limestones with abundance of other forms. The bryozoan facies has been found where the Ballstones merge into crudely bedded limestones and this when traced laterally gradually changes into the surrounding limestone types. The other limited facies usually also grade out into the Grey Measures. The variety and abundance of forms diminish as the limestones are traced outwards and tabulate corals, where present, as well as becoming less frequent also diminish in size. These relationships were best observed in Quarry 6 (see figs. 71, 72, 76, 77).

As both the fauna and facies show a close relationship to the Ballstones, it seems probable that the greatest variety of algae might also be related in similar manner, and from a microscopical examination of each facies it appears that this is the case.

#### Algal-Faunal relationships

##### (1) In the Ballstones

Solenopora has been found so far only in the Ballstones

and not in the bedded sediments. Specimens were found near the edges of and not the centre of the Ballstones. In one instance Solenopora was found with rounded stromatoporoids at the edge of a Ballstone, which suggests a reef flank, possibly the fore-reef (fig. 75) and Hadding 1950). Both forms, with their compact nodules, would be more resistant and so comparable with the present day Lithothamnion ridge.

The filamentous algae were important as sediment binders in the Ballstone, and their debris has also added to the amount of bioclastic debris. Most algae examined from this type of material were encrusting forms of Rothpletzella and Girvanella (See Table VII) and these coated a large percentage of the tabulate corals (especially Favosites, Heliolites and Halysites, Coenites, also stromatoporoids, bryozoa, crinoid ossicles, etc. In some cases it is apparent that growth was simultaneous in algae and its 'substrate', as occasionally algal filaments have been found inside a coral (such as Heliolites) and more strikingly an example was seen of 8 lines of algal filaments, and in another 2 lines were observed along the 'growth lines' of a stromatoporoid. This shows that the association must

have been close, and first one form and then the other was dominant in growth. These last examples were found in material from the reef flank area (figs. 74, 75.)

TABLE VII

QUARRY 2, WENLOCK EDGE

BALISTONES AT DIFFERENT HORIZONS

	<u>W.E.2(3)</u>	<u>W.E.2(5)</u>
Number of thin sections examined	15	11
Alga	Number of slides in which algae were found	
Solenopora gotlandica	1	-
S. compacta	2	-
Rothpletzella gotlandica	3 (incl. 1 large var.)	4 (incl. 1 large var.)
R. conferta	1	3
Girvanella problematica	3	5
G. incompta	-	2
G. pusilla	2	1
G. proluxa	1	-
Mixed associations	1	4
a) G. problematica R. conferta	-	1
b) G. " R. gotlandica	1	-
c) R. conferta R. gotlandica	-	1
d) G. problematica G. pusilla and R. gotlandica	-	2
e) G. problematica R. conferta R. gotlandica and its large var.	-	1
Algal dust and obscure filaments	7	11





Fig.77 Quarry 6. Compact fossiliferous limestone near Ballstone.



Fig.78 Quarry 7. Grey Measure sediments below (with hammer) and above Gingerbread facies.



Fig.79 Farley Quarry 3. Typical Grey Measure sediments, fairly near Ballstone (W.E.3(5))

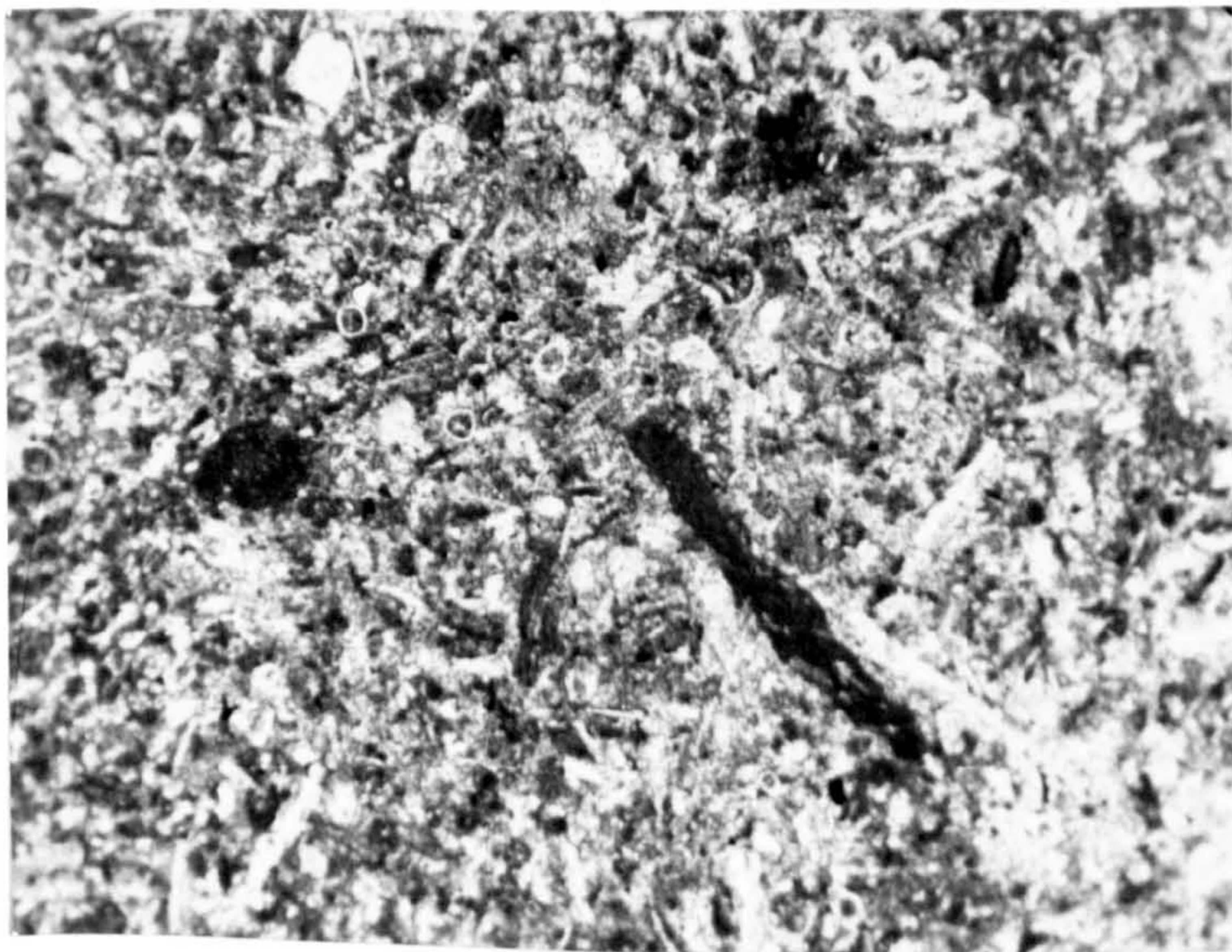


Fig.80 Thin section, Grey Measures, Quarry 8. Shows scattered algal clusters, many odd filaments and algal dust. Also scattered sponge spicules. x 25.

## (II) Bedded Sediments

### (a) Relationships in the Grey Measures

These sediments, examined at a distance from any Ballstone appear, in the field, to be rather unfossiliferous, with only crinoid ossicles scattered throughout and the very occasional other fossils being found. Nearer the Ballstones both crinoid ossicles and brachiopods, bryozoa, corals and others increase in quantity, thus indicating derivation from or connection with the latter sedimentary structure. Material from the 'Grey Measures' was examined from quarries 1-4 and 6-10. In general, most Grey Measure sediments were found in the area behind the Ballstones, that is on the more northern side of the Ballstones.

In thin section, algae were found to be the commonest fossil, numerous groups of them being found together with separate sponge spicules. The limestone does appear, from these numerous groups of mostly Girvanella to be algal in origin. The matrix apart from algae and sponge spicules appears to be either algal dust or recrystallised calcite, possibly coming from this source. Practically all the groups are of Girvanella spp. (of the forms shown in Table VIII and IX), and are non-encrusting, free clusters with no central nucleus.

The occasional encrusting alga and the majority of crinoids and other forms are regarded as derived, as when these limestones are traced nearer the Ballstones both these algae and the fauna increase. The algal groups still remain abundant even near the Ballstones (45 or more distinct groups counted on an average thin section 1" x  $\frac{3}{4}$ " ) but owing to the amount of bioclastic debris are no longer the dominant form.

Out of 43 groups measured and investigated on a thin section taken from the Grey Measures a few feet from a Ballstone, (Farley Quarry W.E.3(5) see photo, histogram and table below), only 3 were Rothpletzella gotlandica and R. conferta, the remaining 40 were Girvanella spp.

These were as follows:

TABLE VIII.      GIRVANELLA FROM W.E.3.(5) HORIZON.

Girvanella problematica	15	groups
G. proluxa	12	"
G. pusilla	3	"
G. incompta	4	"
G. media	5	"
G. sarmenta	1	"
	<hr/>	
	40	"
	<hr/> <hr/>	

Specimens were examined from different horizons in the Grey Measures from a single quarry (Qu. 8) north of

Much Wenlock, vertical range about 20', and no change was found throughout, either in flora or fauna. Out of 72 filamentous groups measured in detail, only 2 were found to be Rothpletzella gotlandica, the remainder were Girvanella spp. (see histogram WES and table IX). Of these only one was encrusting a small bryozoan, the remainder were apparently non-adherent. A noted feature from both this and the previous quarry was the increase in number of G. proluxa, as compared with the specimens from other facies and the Ballstones.

TABLE IX.

The Algae found present in thin sections taken from Quarry 8.

Rothpletzella gotlandica	2	groups
Girvanella pusilla	3	"
G. problematica	13	"
G. proluxa	16	"
G. incompta	12	"
G. media	5	"
G. effusa and G. ramosa	6	"
G. sarmenta	4	"
Indeterminate groups (fragments of either G. problematica or G. proluxa)	9	"
	<hr/>	
	72	"
	<hr/>	



Fig.81 Quarry 6. Gingerbread Facies. More weathered right of photograph.



Fig.82 Weathered Gingerbread, Farley, Quarry 3. (W.E.3(11)) Extremely fossiliferous - brachiopods, etc.

(b) Relationships in the 'Gingerbread' facies

This facies occurs mostly above the horizons containing the Ballstones and was examined in quarries 1-7. In a few exposures an abrupt change can be seen from the lower sediments and especially the Ballstones to the overlying Gingerbread (fig. 73), the main constituent of which is the abundance of loose crinoid ossicles. Within the Gingerbread certain other fossils increase noticeably in some layers, especially brachiopods, small coral colonies both tabulate and solitary and occasionally trilobites and others. The brachiopods show their greatest number and variety at the north-west end of the Edge especially Gleedon Hill and Farley. The matrix is of clear calcite, and fossils are not found in the position of growth. No algae have yet been found in this facies, which would indicate either a sparse distribution, or absence either in this localised district or over a wider area during this period of limestone formation, or that they were not preserved as fossils or have since been destroyed.

(c) Relationships in the Bryozoan Beds

These fairly compact limestones appear to be restricted

in range and were found in the neighbourhood of, and usually adjacent to, the Ballstones. It thus seems probable that there was a direct connection with them. Branching bryozoa and Coenites are the dominant types. Other common fossils include crinoid ossicles, fairly frequent corals, stromatoporoids and brachiopods. In this section, Wetheredella, sponge spicules and algal filaments were also found to be quite common. Many algal groups were found encrusting Coenites and odd crinoid ossicles, but occasionally the filaments were in nodule form having the appearance of rolled detrital matter. This contrasts markedly with the free clusters and unrolled groups in the Grey Measures.

Rothpletzella gotlandica also its large variety, R. conferta and Girvanella problematica, G. incompta, G. proluxa, G. pusilla and an obscure dasycladaceous remains have been found in these beds (see table below). Of these, G. problematica was the commonest, the other species of Girvanella being limited to one or two examples.



TABLE X.

BRYOZOAN BEDS

Example Quarry 2, bed 4.

Number of slides examined = 8.

<u>Filamentous alga</u>	<u>No. of slides in which algae were found.</u>
Rothpletzella gotlandica	3
"          " large var.	2
R. conferta	1
Girvanella spp.	6
G. problematica	6
G. incompta	2
G. proluxa	1
G. pusilla	1
Mixed association	
Rothpletzella gotlandica	1
Algal dust	2

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(d) Other limestones

These include the more restricted limestone facies in the north-eastern half of Wenlock Edge and also those limestones found in the south-western end of the Edge where the limestone has no reef structures and does not show the considerable variation exhibited in the other half of the Edge.

Quarries 11, 12, 13 and 15 were taken from exposures in the south-western part of the Edge. Quarry 11 in the lower or middle beds of the limestone contained compact rubbly dark grey limestones with occasional thin shaly partings. 20' high, not very fossiliferous but with a few bryozoa, brachiopods, trilobites and crinoid ossicles. In thin section, various spicular elements including sponge spicules, ostracods and Girvanella spp. as well as other forms. The abundance of Girvanella may be realised that in one count from a single slide there were about 250 separate groups.

Comparisons made between thin sections examined from specimens taken from the same horizon at different points laterally in the quarry W.E.11(1) and W.E.11(2) showed the following:

TABLE XI.

<u>Quarry 11.</u>	<u>No. of algal groups examined</u>	<u>W.E.11(1)</u> 69	<u>W.E.11(2)</u> 95
		<u>No. of each alga</u>	
	G. incompta	18	37
	G. sarmenta	22	30
	G. ramosa	10	4
	G. effusa	7	13
	G. problematica	6	6
	G. proluxa	4	-
	G. media	2	5

See also tables XX and XXI.  
and histograms WE11 at end.

Calculations involving the average means of these two samples showed that the standard error of difference was less than one, so that these samples were drawn from the same population even though their means showed a slight variation.

These results, when compared with a horizon several feet lower in the same quarry W.E.11(3) showed that the forms present were similar and algae were still abundant but the count per slide was not so high.

Exposures 13, 14 and 15 were taken from the top of the Edge. The limestone in these appeared platy to nodular and was in places weathered (especially exposure 13). Generally, brachiopods (especially atrypids, Parmorthis, Leptaena, strophomenids) were common and the specimens of good size, and these with scattered crinoid ossicles appeared to be the main constituents of the organic part. In thin section, <sup>small</sup> bryozoa, ostracods, algal groups and spicular elements were commonly found, and also haematite appeared to have been deposited in these beds, as it was found present in a bryozoan, in the lumina of some of the sponge spicules and some was free.

The algae were present mostly as small groups and out of 95 groups measured the following types were found.

Girvanella sarmenta (31 groups), G. incompta (27),  
G. problematica (17), G. effusa (9), G. media (4),  
G. proluxa (5), G. pusilla and G. ramosa (2). (For  
diagnosis of groups see table XX and histogram WE 14,15  
at end).

The presence of many free clusters from these various  
exposures appears to be related to the absence of the reef  
environment. The absence of Rothpletzella also is an  
indication that this form required the reef-like habitat.

Other compact limestones were found in the other half  
of the Edge. These were restricted in range and near the  
Ballstones. The limestones usually had one dominant  
faunal group with a scarcity of fragments of other forms.  
When traced laterally they appear to merge into the Grey  
Measures.

A common type is a facies in which crinoids are abundant.  
This type is not included with the Gingerbread as the  
limestone in it is more compact and it is contemporaneous  
with and not formed after the Ballstones (fig. 77.) Fossil  
fragments include sponge spicules, brachiopods, Wetheredella,  
bryozoa and occasional algal clusters of Girvanella pusilla  
and G. problematica, a few encrusting some crinoid ossicles,  
stromatoporoid and Wetheredella and others occurring free.

Other facies are also fragmentary, and although they

usually occur near Ballstones they are often almost devoid of algal remains or have a few scattered groups or odd filaments. Included in this group are those limestones with a clear crystalline calcite matrix and those with rolled detrital and not well defined contents, as these are also poor in algal remains,

These and other facies indicate the variable conditions which would have existed in the neighbourhood of a reef and hence would be localised in nature.

TABLE XII.

WENLOCK EDGE

Localities and distribution of the filamentous algae found during the present investigation

<u>Alga</u>	<u>Quarry or exposure number</u>														
	1	2	3	4	5	6	7	8	9	10	11	13	14	15	
Rothpletzella															
gotlandica	1	3	3	3	-	1	-	2	-	1	-	-	-	-	
" large var.	1	3	1	1	-	1	-	-	-	1	-	-	-	-	
R. conferta	1	2	4	2	-	4	-	1	-	-	-	-	-	-	
Girvanella															
pysilla	1	1	3	-	-	-	1	2	-	-	-	-	-	1	
G. problematica	2	3	5	3	-	2	-	2	-	1	1	-	1	3	
G. sarmenta	-	-	1	-	-	-	-	1	-	-	2	-	-	3	
G. incompta	-	2	1	-	-	-	-	2	-	-	2	-	1	3	
G. ramosa	-	-	2	-	-	-	-	1	-	-	2	-	-	1	
G. effusa	-	1	1	1	-	-	-	1	-	1	2	-	-	1	
G. proluxa	1	2	2	2	-	-	-	3	-	-	1	-	-	1	
G. media	2	-	3	1	-	-	-	2	-	-	2	-	1	2	
Mixed associations															
G. pusilla and G. problematica	-	-	-	-	-	-	-	1	-	-	-	-	-	-	
G. problematica and R. gotlandica	-	2	1	1	-	-	-	-	-	-	-	-	-	-	
do. do. and Wetheredella	-	-	1	-	-	-	-	-	-	-	-	-	-	-	
G. incompta and Wetheredella	-	-	-	1	-	-	-	-	-	-	-	-	-	-	
G. problematica and R. gotlandica and G. incompta and Wetheredella	-	-	-	-	-	1	-	-	-	-	-	-	-	-	
Algal dust and obscure remains	2	5	7	4	2	4	1	4	1	1	2	1	1	3	

Numbers in table indicate number of different beds in which the algae were found in each quarry and are in no ways related to frequency.

## WENLOCK EDGE - SUMMARY

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Along the length of the outcrop, the facies changes are numerous, but the most striking are those of the Ballstone formation between Farley and Major's Leap. South of this area, the facies become more uniform and are not exposed so well by quarrying due to their greater impurity and to the north the limestone becomes less prominent.

The massive algal thalli appear to be restricted to Ballstone areas, and the filamentous forms usually found encrusting other organisms also have a definite association with them. The free clusters are mostly found in the bedded sediments and were not apparently derived from the Ballstone material. Those clusters from the southern half of the Edge were of different dominant types to the others. At the oncoming of the 'Gingerbread' facies, the algae either ceased to flourish or their preservation was affected, so that the same quantity has not been found. Only in the upper beds of the limestone in the southern half were algal filaments found plentiful and here the facies is not 'Gingerbread'.

Thus it can be seen that algae are directly related to type of sedimentation and may possibly be used as indicators of environment.

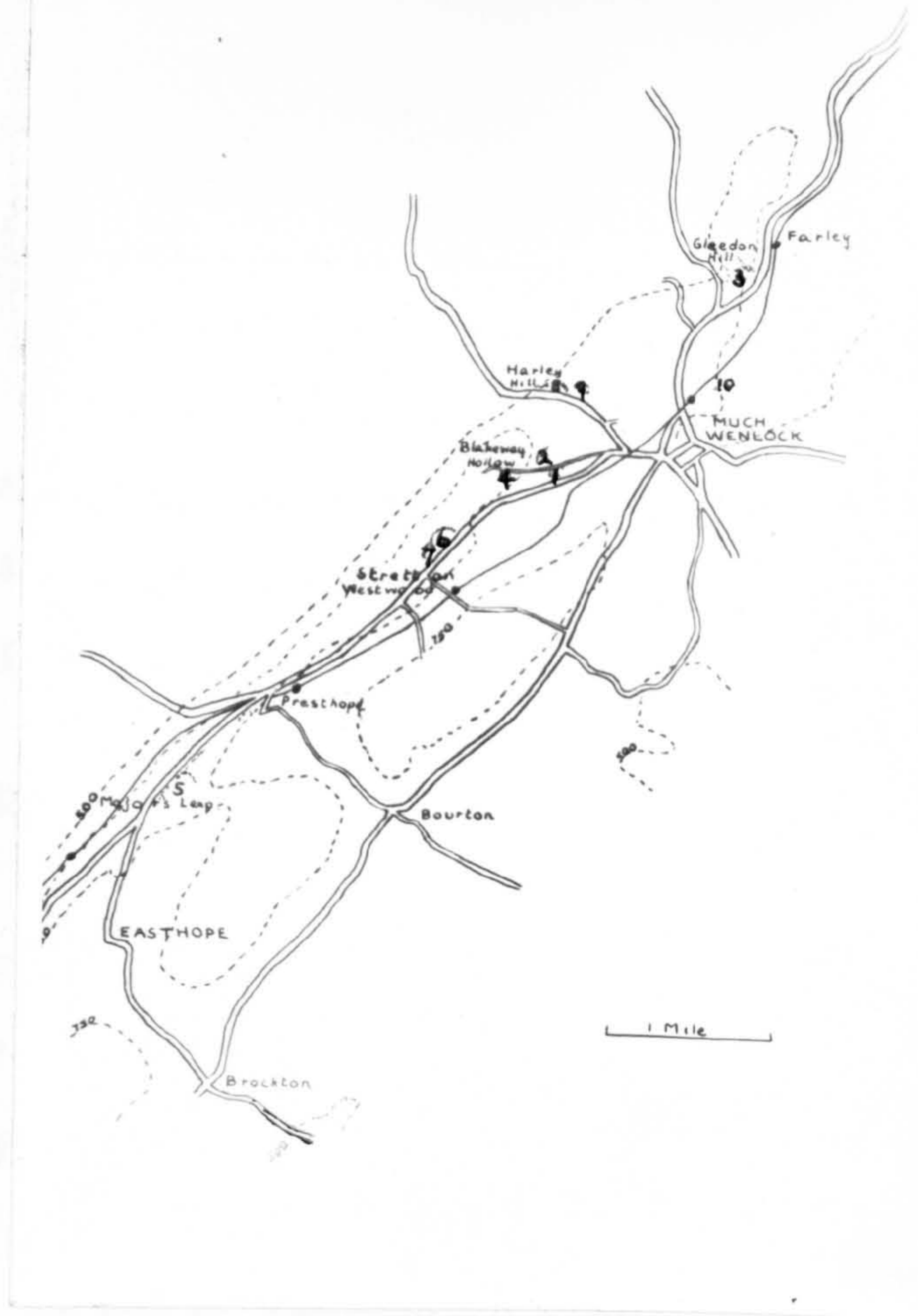


Fig.83 Sketch map of localities of quarries investigated in Wenlock Edge at north-eastern end.

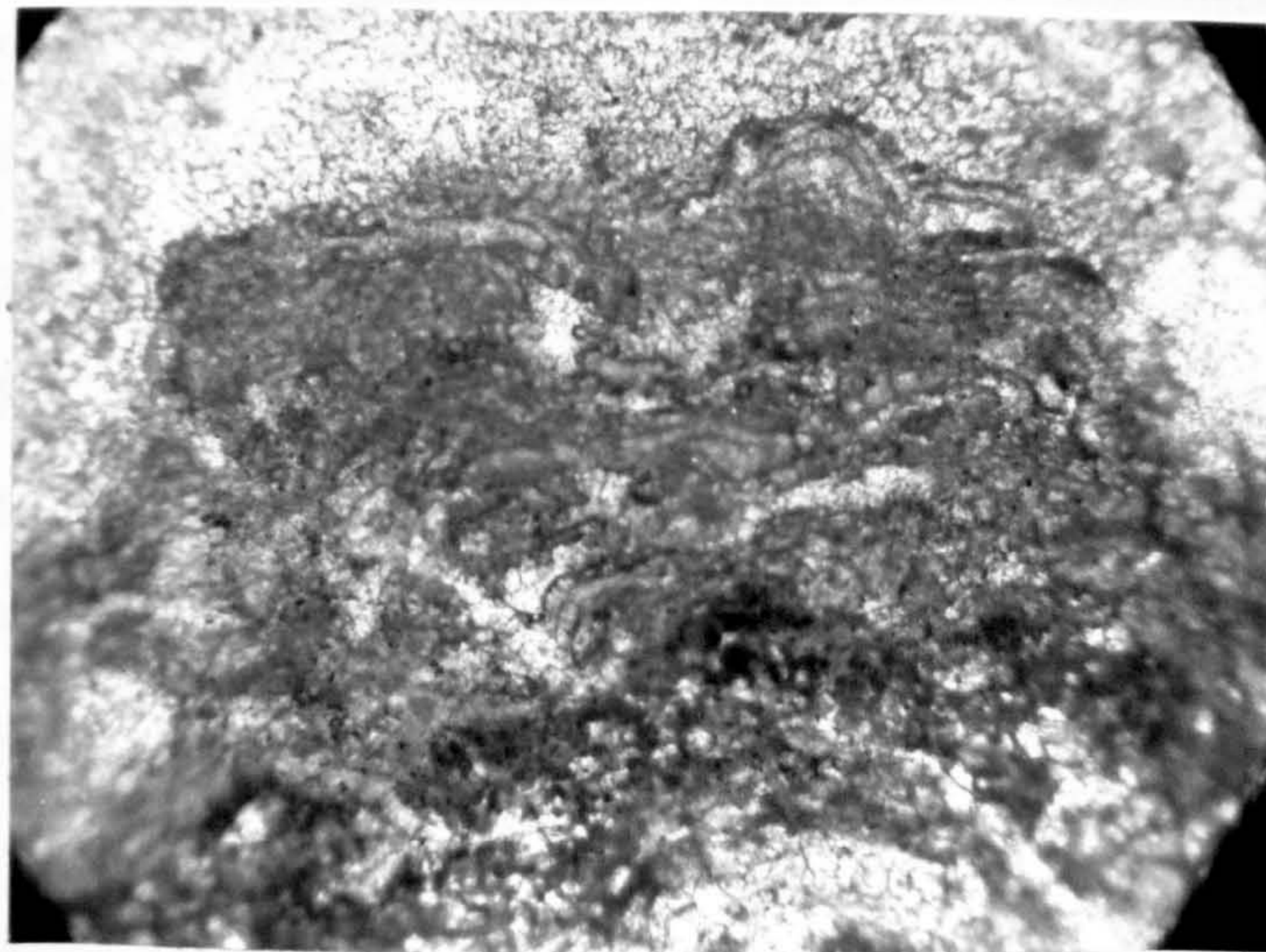


Fig.84 Algal growth from Dudley, (D.U.1(1)), 4 zones.  
 1. Below base of photo, algal. 2. Clear calcite with few filaments. 3. Girvanella pusilla, dark zone.  
 4. Rothpletzella conferta outside.

x 60.



(B) THE WREN'S NEST, DUDLEY

Locality

Material was collected from exposures around and on the Wren's Nest, Dudley, Nr, Birmingham (grid, ref, 917935, O.S.1" map No. 131).

Types of limestone facies investigated

Butler (1939) divided the Wenlock Limestone of Dudley into three main groups. Lower and Upper Limestone groups separated by three Nodular Beds. 'Crog Balls', unstratified masses of limestone, occur in the two lower groups.

All beds are very fossiliferous but especially the Nodular Beds in which numerous types of brachiopods, bryozoa, corals, trilobites, crinoids and others occur. The Upper Limestone group was not investigated.

The Lower Limestone is more platy than the Nodular Beds. The fauna was best extracted from the shaly partings but was well seen on the bedding planes.

The Crog Balls were of extremely hard limestone and do not superficially appear very fossiliferous. Also, they have been quarried away in preference to the surrounding stratified layers, thus leading to caverns in the rock.

## Algal-Faunal relationships in the limestone

As only filamentous algae have been found, the relationships between algae and fauna have been examined only from thin sections.

Different forms of Girvanella (G. problematica, G. pusilla, G. incompta) were frequently found encrusting Halysites and bryozoan colonies and occasionally also on crinoid ossicles and Wetheredella, and rarely on brachiopod shells and trilobite pleura. Non-encrusting groups of G. problematica and G. pusilla are also fairly common either in coiled groups or in small clusters or scattered filaments.

Rothpletzella conferta has been found encrusting similar organisms to the Girvanella spp., except brachiopod and trilobite remains. Rothpletzella gotlandica was found throughout both as encrusting and apparently free clusters. Rothpletzella sp. was found from the Lower Limestone group encrusting with Wetheredella on Halysites.

The filamentous algae were found in various mixed associations as at the present day several genera or species may be found intermingled. Thus, for example Rothpletzella gotlandica has been found encrusting a bryozoan in a loose association with Girvanella problematica; in addition, sometimes also with G. pusilla, and R. conferta has

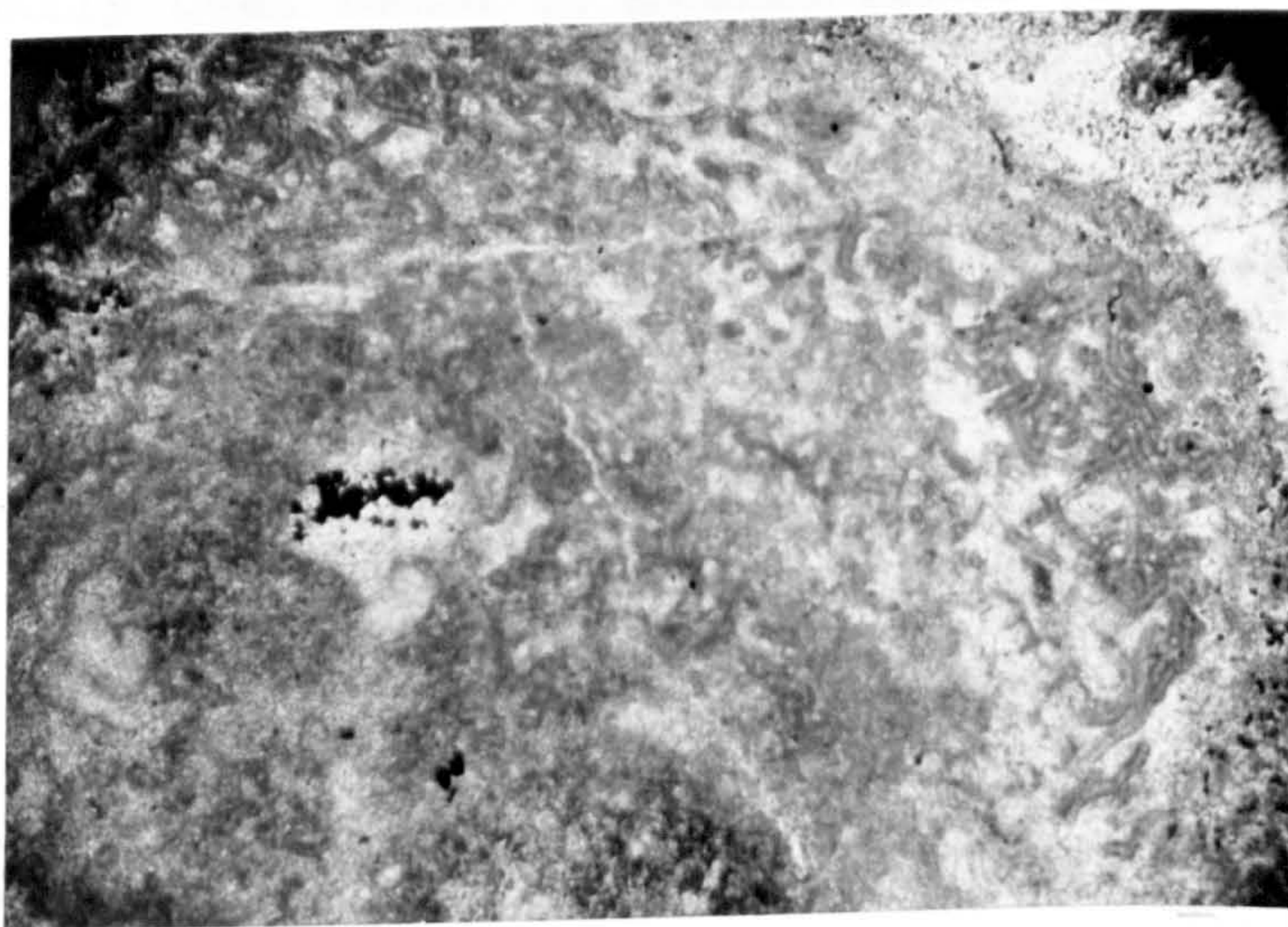


Fig.85 Part of algal growth form, L. Limestone Group, Dudley (D.U.1(3)). Girvanella problematica and Rothpletzella visible in photograph(in zones) x 45.

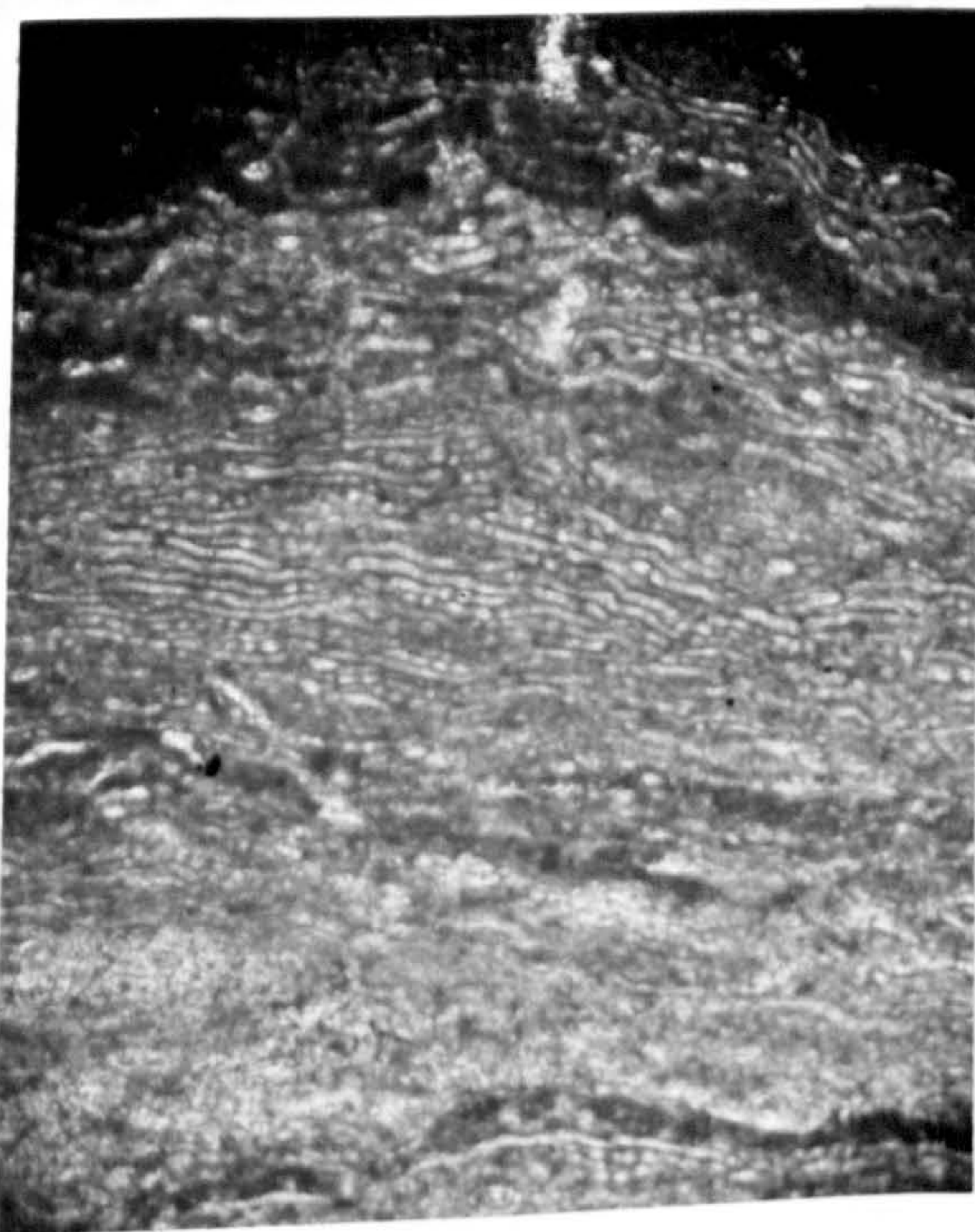


Fig.86 Comparison with part of a Gotland growth form (Högklint Series). Rothpletzella various and dark areas of Girvanella constitute main mass of the form. x 45.

occasionally been found in growth forms consisting of it and Girvanella filaments (usually G. pusilla). These growth forms (figs. 84, 85) are in zones of differing algal growths, thus in fig. 84 of a small growth form zone 1 at the base is a loose tangled coil of R. conferta filaments (not visible in photograph) which is surrounded by a clear calcite area with only a few filaments visible (zone 2 at base of photograph). This is followed by a dark zone (3) consisting of the fine G. pusilla filaments and the outer zone (4) is lighter of loose undulating filaments of R. conferta which lie apparently parallel to outer edges of group.

Other growth forms seen are similar in basic plan and may be compared with the Gotland specimens (see photograph) where development of growth forms is much greater. A thin section of part of one will yield many fluctuations or zones (see fig. 86) showing a few layers of algal filaments).

Algal dust was found to be common in the limestones and may be indicative of algae being comparatively important for the formation of the Dudley limestones.

See Table. XIII.

TABLE XIV

TABLE SHOWING DISTRIBUTION OF ALGAE IN DIFFERENT FACIES AT THE WREN'S NEST, DUDLEY.

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Alga	L.Lst.Gp. S.E.side of anticline.	Nodular Beds S.E. side.	Nodular Beds N.W.- W. side.	Crog- balls W.side.
Rothpletzella gotlandica	x	x	x	-
do. large var.	-	-	x	-
R. conferta	x	-	x	-
R. sp.	x	-	-	-
Girvanella problematica	x	x	x	x
var. lumbricalis	-	-	x	-
G. pusilla	x	x	-	x
G. incompta	x	-	x	-
G. effusa	x	-	-	-
Mixed associations				
Rothpletzella gotlandica and G. problematica	-	x	-	-
R. conferta and G. pusilla	x	-	-	-
R. gotlandica and G.problematica and G. pusilla	-	x	-	-
G. problematica and G. pusilla	-	x	-	-
Growth Form	x	x	-	-
Algal dust	x	x	x	x

x = found in limestone during investigation  
 - = not recorded.



Fig. 87 Fownhope Quarry 2. View of blocky limestone alternating with shale in the higher horizons.



Fig. 88 View of bedding plane. Fownhope Quarry 2.

Fig. 89 Thin section showing high proportion of algal groups (encrusting and free - dark and medium grey areas). Also crinoid ossicles, spicules and other organisms present. x 45.

(C) FOWNHOPE

Locality

The Old Quarries, Common Hill, Fownhope (Herefordshire), (grid ref. 348586, 1" O.S. map No.142 and Geol. Survey map No. 43).

Limestone facies description

In the field, the limestone in these quarries appeared to vary from a rather massive nodular limestone (as seen from the face of a bedding plane) full of stromatoporoids and corals to hard limestone bands, many nodular and including a coral layer, alternating with shales near the top of the Wenlock series. Specimens were collected from the upper part of the Wenlock Limestone (Exp. F.H.2) as exposures in the lower part appeared to be mostly considerably overgrown.

Algal and Faunal relationships in the limestone

The fauna, when investigated in the field, is rich, especially in corals, stromatoporoids and brachiopods (atrypids, etc.) in all those forms which in Wenlock Edge appeared to have some relationship to either Ballstones or possibly the Gingerbread beds. The presence of reef structures in the Wenlock Limestone of the Woolhope inlier (viz. including Fownhope) is mentioned by Tucker (1958) in

an abstract of a paper (read but not published) on this district, but these reef structures were not found during this investigation and the majority of the numerous algal groups examined were as free clusters not encrusting other organisms, a feature which was common in the Ballstones. This does not exclude the high possibility that these bedded limestones were very near reefs or were formed near a reef-like environment.

Only a few Rothpletzella specimens were found in the thin sections examined as opposed to Girvanella which was prolific. This also supports the non-reef origin of these particular beds examined from this quarry. On the other hand, filamentous forms were mostly highly branched, which according to Wood (1958) may indicate a favourable environment, and with this form it appears that many must have grown on a substrate (see fig. 89) although not of organic material.

Most of the algal groups were of Girvanella media and G. problematica.

A fairly common form was G. pusilla which appears to have persisted in this area from the Woolhope Limestone (viz. Mordiford district only 2-3 miles away). G. ramosa is also fairly common. The other Woolhope form G. fragila



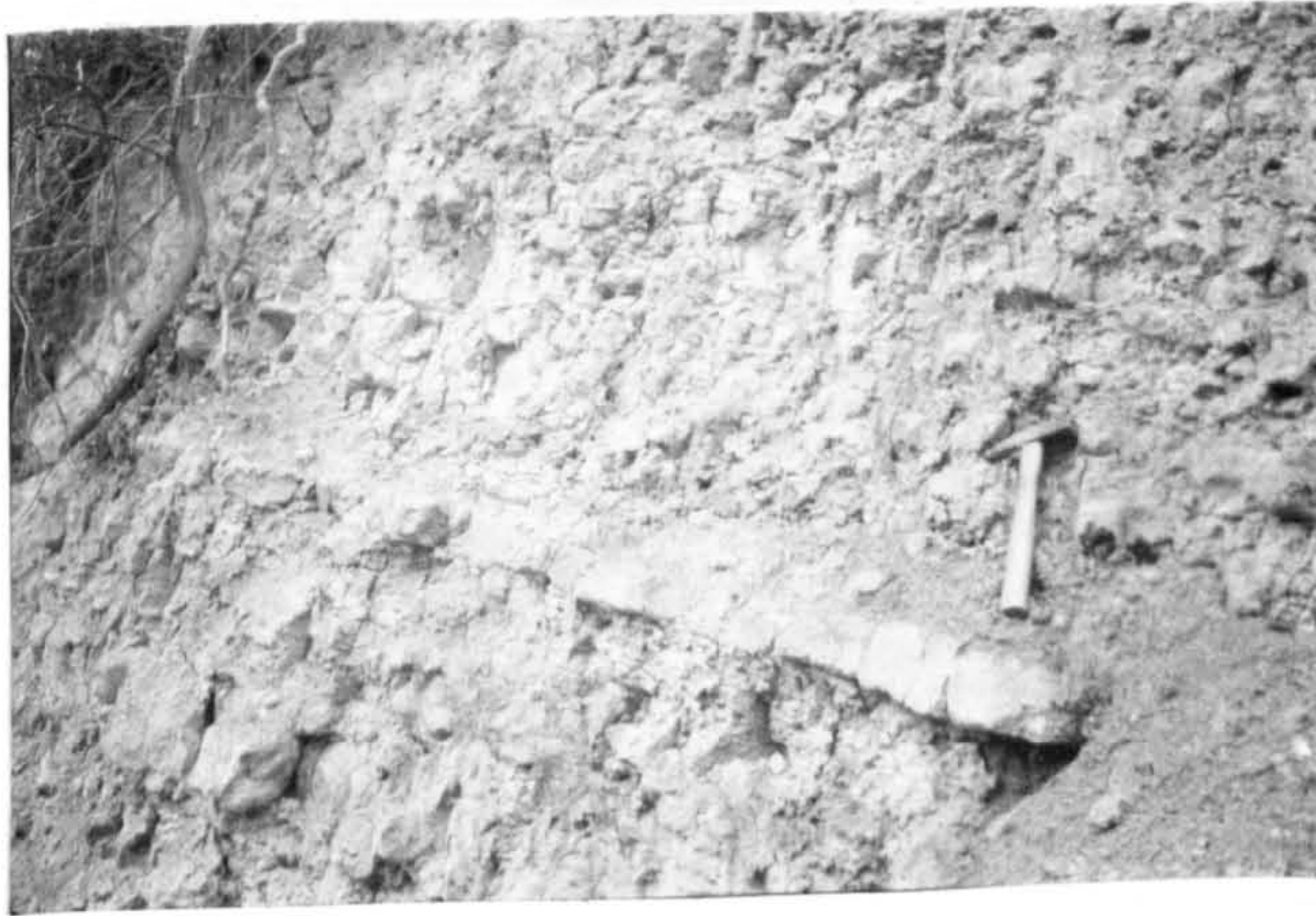


Fig.90 Upper Beds Wenlock Limestone, Sollers' Hope,  
note blocky limestone.



Fig.91 Wenlock Limestone, Ledbury. Quarry 1.

was only found very spasmodically. G. media is appears is a strong development occurring in the Wenlock Limestone of this district, as it is only recorded as being present in the Woolhope Limestone in this area. 49 out of 162 Girvanella groups measured were of G. problematica and 47 were G. media. A somewhat smaller number of G. pusilla (22) and also of G. ramosa (24), and a few G. incompta (8), G. sarmenta (5) and G. proluxa (4) (See tables and histograms at end).

A few sections of Rhabdoporella sp. were found in the thin sections, as well as Rothpletzella gotlandica, R. conferta and Rothpletzella sp.

#### D. SOLLER'S HOPE AND WOOLHOPE

##### Localities

A small roadside exposure was examined south of Woolhope Village (grid ref, 340662 1" O.S. map no. 142 and 1" Geol. Survey map No. 43), and this revealed a hard crystalline limestone.

The Wenlock Limestone of Soller's Hope was examined in order to try and find the oolitic limestone as mentioned in the annals of the Woolhope Naturalists' Club.

Exposure S.H.1 was by Lindels farm about 1 ft. in

height and was weathered limestone with shale band (grid ref. 330622 1" O.S. map no. 142).

Exposure S.H.2 was an overgrown quarry 500 yards above Lindels farm of track to south.

#### Limestone facies investigated

The limestone appeared to be the upper beds with shale predominating over the limestone bands at the top. Limestone bands blocky, highly nodular, 2-3" thick (fig. 90) In some layers the fauna was plentiful, especially in brachiopods. A few weathered specimens of limestone appeared oolitic (confirmed by thin section). The main limestone bands were of fine grained grey limestone, blue-hearted.

#### Algal-Faunal relationships to the limestone

This limestone was found to be very rich, in certain layers, in strophomenids and strophonellids, as well as various other brachiopods. A noted feature was the abundance of very small forms as well as the large specimens. This could indicate either young specimens or dwarfing of forms due to unfavourable environment either in this area or elsewhere, and as both small and large were found on the same bedding plane, this could be either a thanatocoenose or biocoenose community. Various corals including

Favosites, Stenopora and Cyathophyllum, bryozoa, stromatoporoids and crinoid ossicles were found in the fauna. In thin section it generally appears to be a thanatocoenose community.

Wetheredella and algal filaments occur in small groups sparsely in thin sections, including Girvanella problematica. G. pusilla (also encrusting), various spicular elements and crinoids were abundant. The algae did not appear to be associated with the oolitic structures of clear calcite. A few specimens apparently similar to the Rhabdoporella intermedia of Lewis were also found in thin section.

The Woolhope specimens yielded Rothpletzella gotlandica and its large var. showing the fan-branching in surface in one specimen, algal dust and obscure remains,

(E) MAY HILL

Locality

Hobb's Quarry in the Upper Group of the Wenlock Limestones of the May Hill inlier above Longhope Village (Glos.) (Lawson 1955 and grid ref. 195695 1" O.S. map no. 143 and 1" Geol. Survey map no. 43).

Limestone facies

Hobb's quarry is itself almost completely overgrown

Favosites, Stenopora and Cyathophyllum, bryozoa, stromatoporoids and crinoid ossicles were found in the fauna. In thin section it generally appears to be a thanatocoenose community.

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Limestone facies

Hobb's quarry is itself almost completely overgrown

with not very much rock remaining visible and in situ. The weathered specimens examined were irregularly nodular and it was hoped that these would correspond with Wethered's description (1893) of the limestone weathering to nodular shapes around the algal masses. In thin section however the shape did not correspond with any prolific well preserved algal growth as Wethered had found.

Exposures in the roadside just by the side of the quarry revealed mostly a crinoidal limestone with large crinoid ossicles.

#### Algal and faunal relationships

The fauna included the usual brachiopods, bryozoa, coral, crinoids, ostracods, Wetheredella and spicules. The filamentous algae were found quite numerous both as free and encrusting groups. Organisms encrusted included ostracods and brachiopods. Algae present were Rothpletzella gotlandica and G. problematica (see also Wood 1948), G. pusilla and G. media and Rhabdoporella intermedia (Lewis). The matrix was mostly of recrystallised calcite.

(F) LEDBURY

Locality

Exposures 1 and 2 in the old quarries of the main Ledbury-Worcester road (grid ref. 376715 1" O.S. map No. 143 and Geol. Survey map No. 43).

Limestone facies and algal fauna relationships

The limestone was found to be a fairly compact blue limestone with abundant crinoid ossicles and with some beds more nodular.

The nodular beds were found to contain in one section at least fairly frequent trilobites as well as small brachiopods including Parmothis, rhynchonellids, Leptaena, and Halysites was amongst the forms from the more compact limestone.

In thin section, other faunal elements were more easily seen including bryozoa, Coenites, ostracods, Wetheredella and various spicules. Some algal groups were also found including Girvanella pusilla encrusting a trilobite, and otherwise, G. problematica groups apparently non-encrusting and one group was found on a favosites. Pyrite was seen in one group of algal tubes.

(G) OTHER LOCALITIES

Specimens of Wenlock Limestone were obtained from a disused quarry at Park Wood on the west side of the Malverns (grid ref. 445763 1" O.S. map No. 143). Other specimens of probable Wenlock algae were obtained from drift on the main Ledbury-Worcester road (grid ref. 383718 1" O.S. map No. 143 and 1" Geol. Survey map No. 43).

Limestone facies

The Malvern specimens were richly fossiliferous in the fauna, including some brachiopods, bryozoa, corals, etc. In thin section Rothpletzella gotlandica encrusting a tabulate coral, G. problematica and G. pusilla were found as encrusting groups.

The Ledbury specimens were probably derived Wenlock Limestone and specimens of Girvanella problematica and a fine species of Rothpletzella (diameter of filamenys 9u - 12u) encrusting a crinoid ossicle (see fig. 39).



A SUMMARY OF THE GEOLOGICAL DISTRIBUTION OF  
ALGAE IN THE WENLOCK LIMESTONE

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Solenopora has only been found from Wenlock Edge during this investigation. Solenopora gotlandica has been recorded by Whittard (1944) from the Tortworth inlier, otherwise it is unknown in the area from this limestone. So far, it has only been found in reef material from the Edge and so is generally probably the commonest in such.

Rothpletzella has been found from most districts although its frequency is variable. The genus appears to be commonest in conditions favourable for encrusting other organisms, such as Coenites, thus is more frequently nearer reef structures than otherwise. Most specimens were found from Wenlock Edge (reef district) and Dudley, although R. gotlandica appeared to be the most widespread apart from these areas being found also at Fownhope, Woolhope, Ledbury, W. Malverns and May Hill. Rothpletzella conferta appears to be more frequent than R. gotlandica in favourable sites. The other species were restricted.

The genus Girvanella is the most ubiquitous being found in most thin sections examined, with a few exceptions such as the Gingerbread. Prolific developments occurred at the south end of Wenlock Edge with the large G. sarmenta and

G. incompta being the dominant species with G. effusa a common species here. Fownhope with the highly branching G. media as a dominant, with several other common species including G. pusilla, obviously persisting in the district from Woolhope limestone depositions. G. media although so abundant here was only occasionally found from southern<sup>end</sup> Wenlock Edge. Girvanella problematica and G. pusilla appeared relatively more common than the others from Dudley, Ledbury, Malvern, May Hill and some exposures in Wenlock Edge, but the latter appears to be virtually absent, like G. fragila from the southern end of the Edge. G. proluxa was commonest, sometimes dominant in the Grey Measure sediments of Wenlock Edge and more noticeable away from reef structures when the other types apparently decrease. It is also uncommon at the southern end of the Edge. G. ramosa was commonest at Fownhope and was also found as well as G. effusa occasionally from Wenlock Edge. G. fragila just occurs at Fownhope and is very rare here compared with the other species and also was not found elsewhere, so at present it is regarded rather as a survivor from the Woolhope limestone of this district (viz. Mordiford).

Dasycladaceous remains were found from various

localities, including Wenlock Edge, Fownhope and Soller's Hope. These were identified as similar to Rhabdoporella intermedia of Lewis (1937) from Soller's Hope and May Hill and Rhabdoporella sp. from Fownhope. The forms were not found in reef material but in bedded sediments.

## AYMESTRY LIMESTONE AND LUDLOVIAN DEPOSITS

### I. AYMESTRY LIMESTONE

(a) Craven Arms District and

(b) Aymestrey

#### Localities

The smaller exposures (C.A.1-3) were examined at Norton Camp (grid ref. 821446 1" O.S. map No. 129 and also Geol. Survey map no. 61 S.E. S.W.)

Specimens C.A.4 were taken from the quarries at View Edge (grid ref. 806426) (Alexander 1936).

Rock specimens were also collected from the type quarries of the Aymestry Limestone at Aymestrey (grid ref. 655422 1" O.S. map no. 129).

#### Limestone facies and algal relationships

The limestone, mostly massive or platy, was fairly coarsely crystalline in the specimens obtained from Norton Camp, hence well preserved algae could not be expected. The specimens from View Edge were of finer granular calcite.

Algae were found from the View Edge specimens, but not in any great abundance. The forms include Girvanella

problematica and G. cf ramosa and obscure dasycladaceous remains.

The fossil assemblage from the Norton Camp specimens definitely appears to be thanatocoenose and only a few algal fragments and groups have been G. pusilla and G. problematica with possibly obscure dasycladaceous fragments.

The only algae previously known from Aymestrey are those found by Lawson and deposited in the British Museum (Natural History). These dasycladaceous algae (Chaetocladus, about 30 specimens) were found in a shale band in the limestone in a small exposure north of the type quarries (grid ref. 655422). These are uncalcified algae and were found as carbonaceous impressions in the shale seam.

From limited material collected from the type quarries, only a very small amount of algal dust and odd Girvanella fragments were found.

## II. LUDLOVIAN

### (a) Ludlow

#### Locality

Whitcliffe (Ludlow) by the River Teme (grid ref. 742509)



Fig.92 Upper Aymestry Group, Marcle Hill.  
Nodular Beds (W.H.5)



Fig.93 Upper Aymestry Group, Sleeve Common, Marcle Hill.  
W.H.(7).

1" O.S. map No. 129).

The old quarry face by the footpath along the river.

Facies and the algae present

Specimens were obtained from the calcareous facies of the Whitcliffe beds and in thin section yielded filamentous algal groups of G. problematica and G. ramosa as well as more indeterminate clusters. These groups therefore occur in the brachiopodal facies (Camarotoechia nucula and Chonetes striatellus).

(b) Marcle Hill and Sleeve Common

Localities

Several outcrops of the Upper Aymestry Groups were investigated along the scarp of Marcle Hill including Sleeve Common 'grid ref. 347632 1" O.S. map No. 142 and 1" Geol. Survey map No. 43).

Facies type

The group is a very calcareous mudstone, highly nodular in parts, the nodules containing Camarotoechia nucula and numerous bryozoa. Small corals were included in the fauna collected in the quarry in Sleeve Common from a narrow coral bed.

No algae were found at all in most of the slides examined from this district and only in one was a small Girvanella group found (possibly G. media) indicating that conditions were not favourable for either algal growth or preservation.

(c) Ledbury District

Localities and facies types

The Aymestry Group was investigated near Bradlow (grid ref. 385715 1" O.S. map No. 143 and 1" Geol. Survey map No. 43 and Groom 1910) and consisted of a calcareous mudstone, nodular with some shale partings. Orthoeras was among the fossils recorded. No algae were found in thin section.

Several exposures on the Ledbury-Malvern and Tewkesbury road, near the divide (grid ref. 385722) were examined in Ludlow rocks. Mostly of the shales, sometimes concretionary, fossils recorded include mostly brachiopods. No algae were found in thin sections examined.



A SUMMARY OF THE ALGAL DISTRIBUTION IN THE  
AYMESTRY LIMESTONE AND LUDLOVIAN DEPOSITS

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The algae discovered so far from these deposits have only been scattered in distribution and have shown no indication of a former widespread abundance of growth. Those algal groups found were from the purer limestones and hardly any from the impure mudstones and shale deposits. (No calcareous algae were found in thin sections taken of Wenlock shale (W.E.12)). In the case of the uncalcified Chaetocladus specimens discovered by Lawson from Aymestry, the shale parting from which they were obtained was small and impersistent, the algae themselves probably grew in the clearer water of the limestone formation, and the shale represented a sudden local change of conditions, which fairly quickly reverted to the prevailing limestone formation.

The filamentous algae were mostly in small fragmental groups so that identification of species was not always possible. These higher Silurian beds so far compare very unfavourably for algae with the Woolhope and the Wenlock limestones, but it is quite possible that some facies within them not yet examined may contain prolific specimens.

## DISCUSSION

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From the results of this investigation it has been shown that calcareous algae were both abundant and widespread throughout the Welsh Border during the formation of the more calcareous facies of the Silurian. The filamentous algae were found to be especially widespread, and their known range, lateral and vertical, has been extended. Hence, algae have been found from the majority of limestone exposures examined, although they generally appear to be scarcest in the Upper Aymestry Group and in this limestone in the southern half of the area.

Septation of algal filaments where it occurs appears to be a feature of better preservation than an indication of a different genus or species, as it has been found in algal filaments of widely different sizes, but is not found completely throughout the whole of any single algal group.

Descriptions and general remarks on each alga encountered during this survey have been given, so that comparisons can be made on frequency and range of occurrence, their associations, variation and overlapping of specific forms, etc. As it was wished to include Girvanella

in these comparative studies, it necessitated the division of the Silurian representatives of this genus into form-species.<sup>x</sup> Also, it is considered that as present day filamentous algae are both extremely numerous in number and in genera, it is fairly unlikely that even during the Silurian the filamentous forms of algae were restricted to only a few genera. Hence, it seemed probable that Girvanella as such could well represent several totally unrelated genera, as the diagnostic characters are not preserved in these fossils; any slight differences in the fossils might represent a major difference in the living plant. To facilitate any palaeoecological or stratigraphical decisions, these Silurian representatives of Girvanella are grouped into nine form species (including G. problematica). If these were placed at the level of varieties of the type species, it would imply a close relationship which it is felt could not be upheld. Thus, it is more satisfactory to give them specific rank and to recognise their differences, even if eventually these form-species become either further subdivided or amalgamated.

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<sup>x</sup> A form-genus as defined by Lanjouw (1952 quoted by Sylvester Bradley 1954) which for fossil plants is "a form-genus is one that is maintained for classifying fossil specimens that lack diagnostic characteristics indicative of natural affinity but which for practical reasons need to be provided with binary names. Form-genera are artificial in varying degree".

The Silurian Girvanella are seen to have a wide distribution in these rocks. Girvanella fragila n.sp. has been found abundantly in the bedded Woolhope limestones of Mordiford and surrounding districts, and only a minute proportion have been found in the overlying Wenlock limestones of this district as at Fownhope. It has not been found in this latter limestone elsewhere so at present it appears to be a characteristic form of the Woolhope Limestone.

The common associate of G. fragila, G. pusilla n.sp. is found fairly abundantly in the Wenlock limestone, not only from the Woolhope Inlier and May Hill, but is also present in the limestones of Wenlock Edge and Dudley as well as the Woolhope Limestone of Old Radnor. As both loosely coiling and encrusting types have been included in this form species, it cannot be regarded as so specific in its environment, etc. as G. fragila and has been found in both reef-like and bedded sediments.

Girvanella proluxa n.sp. a larger form similar in some ways to G. fragila is most abundant in the Grey Measures of Wenlock Edge. It is recorded from several localities including one from the Woolhope Limestone of Mordiford but

none from the Aymestry Limestone. Unless it is found from the Woolhope Limestone in a much larger proportion in relation to the other forms, G. proluxa may be regarded as apparently having a hiatus of development during the formation of the Grey Measures. This appears more striking in an examination of sediments taken at some distance from the Ballstones.

Girvanella sarmenta n.sp. the widest tubed form of the 'sarmenta' group, occurs very abundantly in the Wenlock Limestone at the south western end of the Edge, and sometimes appears to be the dominant form here. A few specimens have been found from other localities along the Edge but they are mostly sparsely scattered and a small percentage occur at Fownhope, but it is not recorded from Dudley or from the other limestones.

Girvanella incompta n.sp. another larger form is also very common in the same sediments as G. sarmenta, but is more widespread in distribution in the Wenlock Limestone to which it is limited so far from the records made. It has been found from more localities than G. sarmenta from the Edge and it is also present at Dudley as well as Fownhope.

Girvanella problematica appears to be a common species.

especially so in the Wenlock Limestone. It is recorded as present from most exposures investigated along Wenlock Edge, but commonest at the north eastern end. It appears plentiful at Dudley, and also occurs at Fownhope, Sollers' Hope, May Hill and Ledbury. Specimens of it have also been obtained from West Malvern. Although recorded at Fownhope this species only formed a small percentage of the filamentous groups present. It was also found in the Woolhope and Aymestry Limestones of several localities.

Girvanella media n.sp. occurs most abundantly where G. proluxa and G. sarmenta are scarce. It is most frequent in the apparently more favourable environment for branching algal growths. A prolific development of this species is found at Fownhope where it is apparently co-dominant with G. problematica, and it occurred frequently in different exposures along Wenlock Edge, although not prolific. It was not recorded from Dudley, but was recorded from the Woolhope Limestone, Mordiford.

Girvanella ramosa n.sp. and Girvanella effusa n.sp. are recorded from the Woolhope Limestone, but were best observed from the Wenlock Limestone especially some from the bedded limestones of Wenlock Edge. G. ramosa was found also at Fownhope where it was commonest although only forming a fairly small percentage of the total number of

algal groups, and G. effusa at the south-western end of Wenlock Edge.

Rothpletzella has been found in both Woolhope and Wenlock Limestones but has not been found so far from the Aymestry Limestone. R. conferta has only been found from Old Radnor in the Woolhope Limestone, but fairly abundantly. The larger form, R. gotlandica is also recorded from Nash Scar, but no Rothpletzella has yet been found in the bedded Woolhope Limestone sediments of Woolhope and Mordiford.

In the Wenlock Limestone, the genus Rothpletzella appears to be more widespread. R. gotlandica and its large variety (Wood 1948) were found in most sediments examined from May Hill, Sollers' Hope, Fownhope, Woolhope, Ledbury, Dudley and Wenlock Edge, although when compared with the algae generally present in these localities, it only formed a small proportion of the algal constituent. Previous records of this species are restricted to the Old Radnor district for the Woolhope Limestone (Garwood 1918), and for the Wenlock Limestone, May Hill (Wood 1948) and specimens deposited by Wood in the Geological Survey Museum from the Tortworth Inlier (Glos.) south of the area investigated.

R. conferta, found by Chapman 1907 in Dudley ((as

Girvanella conferta) otherwise no previous records for the Welsh Border or for the Woolhope Limestone) was found here during this investigation at Wenlock Edge and Fownhope, thus extending its known range. It appeared more common than R. gotlandica in some of these localities, especially in or near reef structures, and was virtually absent in sediments well away from conditions favouring reef formation.

Rothpletzella spp. indet. were found from Dudley, Fownhope and the derived Ledbury specimens, but more material is required to define their specific limits precisely.

Solenopora is similar to the genus Rothpletzella in that it has only been found in the Woolhope and Wenlock Limestones and not the Aymestry of this district. In the Woolhope Limestone, Solenopora gracilis was the main reef builder of the Old Radnor and Nash Scar districts, but it appears to be absent from the other localities. Also present at one horizon in the limestone at Old Radnor are what appear to be rather recrystallised specimens of S. cf. compacta.

S. compacta and S. gotlandica, S. cf. gracilis and Solenopora sp. indet. have been found rarely in or near



the Ballstones of Wenlock Edge. The only previous record of Wenlock Limestone specimens for the area is at Tortworth (Whittard 1944). Thus the Silurian Solenopora of this area definitely appear related to a reef-like environment.

Various dasycladaceous fragments were found in thin section from Woolhope, Wenlock and Aymestry groups from different localities. The best Woolhope Limestone specimens were found from Mordiford and these were similar to those of the Wenlock Limestone of Fownhope and May Hill and consisted of Rhabdoporella sp. Most specimens were found from this district. Only a few either indeterminate or very scattered forms were found elsewhere including a few specimens apparently similar to Rhabdoporella intermedia of Lewis. Chaetocladus is the only member of the Dasycladaceae previously recorded from the Aymestry Limestone of Aymestrey and visible in the field (Collected by Lawson and deposited in the British Museum (Natural History)).

From these investigations it has been evident that some calcareous algae are limited to certain facies types. Thus, the massive Solenopora has been found in reef or reef-like environments, and associated with this environment, though possibly not quite so restricted, are the forms of Rothpletzella. These forms of highly branching Girvanella, requiring a substrate are found where the fauna is rich and

variable, sometimes at least near reefs. However, it would appear at least that they thrived in a favourable shallow water, with no strong currents affecting them. Other forms of Girvanella give no indication of the substrate as they were possibly free floating, either in a small loosely coiling cluster or as a long bundle of filaments, parallel or sub-parallel to each other. The latter type may have been attached at one end, or have broken away at one point, but no organs of attachment have been found. These forms occur mainly in sediments away from any reef structures.

The algal limestone of Old Radnor and Nash Scar is presumed to have been formed under reef-like conditions with Solenopora as the main limestone former. The amount of sediment binding by various organisms is uncertain as the limestone in this district has been much recrystallised and altered, and although Solenopora thalli would be wave-resistant, the matrix with its organic remnants in between may not have been so. It is quite possible though that the wave-resistant fore-reef is not exposed in the quarries examined.

The Ballstones of Wenlock Edge are regarded as being true reef structures as they appear to fulfil all the conditions which are characteristic of present day reefs

(Ladd 1950, Lowenstam 1950, Wilson 1950). The Crog Balls of Dudley were probably also of reef origin, but further investigations are needed, both in the field and microscopically. The fore-reef zone in the Ballstones appears to be the area of rounded stromatoporoids, corals, with Solenopora occurring here, and behind the filamentous algae can be included amongst the main sediment binding agents in the Ballstones where the majority of them are encrusting. Although the algal filaments may in some cases be closely associated with the organic substrate, they have not been found to partake in a completely symbiotic growth (Condra and Elias 1944, Elias 1946).

Only small algal growth forms have been found and nothing comparable in size with the Gotland deposits (Hadding 1950).

Comparisons may be drawn with the predominantly algal nature of some of the bedded sediments, especially the Grey Measures, and possibly also the Mordiford deposits, with those of the Carboniferous (Bond 1950, George 1954). It has been suggested that the Carboniferous calcite mudstones may be a lagoonal facies behind the reef limestones or a very quiet shallow water deposit with restricted access to the open sea. It seems quite possible that the

Silurian deposits may be their earlier equivalents.

The foregoing observations indicate that calcareous algae are of significance in the Silurian limestone of the Welsh Border, and that their study in relation to fauna and sediment can give evidence of the conditions prevailing during the limestone deposition in some of the facies where they occur. General observations on differing facies in relation to algae are more evident when the latter are divided into species or form-species. Hence, it is obvious that further studies in this direction would probably yield valuable results of both systematics of algae and algal environment and specific forms could then become firmly established especially in regard to the filamentous algae. Also studies on other calcareous deposits from other formations could be valuable.

## ADDITIONAL TABLES

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### A. KEY TO THE GIRVANELLA SPECIES

#### Algal groups

- a) Filaments less than 10 $\mu$  or 11 $\mu$  wide
  - 1) Brushwood or parallel cluster often partly adhering sometimes may branch occasionally  
G. fragila
  - 2) Loose or adhering coil, cluster or group  
G. prolixa
- b) Filaments 11 $\mu$  to 18 $\mu$  or 20 $\mu$  wide
  - 1) Loose coil, filaments usually not in contact, occasionally encrusting, branching.  
G. problematica
  - 2) Branching frequent, tubes adhering, even diameter  
G. media
  - 3) Branching very frequent, tubes appear irregular or constricted  
G. ramosa
- c) Filaments 18 $\mu$  or 20 $\mu$  and more in width
  - 1) Brushwood type, usually filaments more than 20 $\mu$  wide  
G. sarmenta
  - 2) Loose coil, cluster, some branching to branching fairly frequent  
G. incompta
  - 3) Branching very frequent, adherent form, diameter irregular with constrictions  
G. effusa

ADDITIONAL TABLES

I. GIRVANELLA

To show distribution of the various species Girvanella from different localities and horizons in the limestones. The numbers investigated, abundance and characters are shown in the following Tables (XIV - XXII)

Table XIV M.F.1(1)

<u>Type of Girvanella</u>	<u>Nos.</u> 49:	<u>Form</u>	<u>Br.</u>	<u>Adh.</u>	<u>Both</u>	<u>Length</u>	<u>Curv.</u>	<u>Sept.</u>
G. fragila	30	30	3x 2 occ. 21- 2 ind.	4x 2 occ. 21- 3 ind.	1	28x 2 ind. (T.S.)	30-	3
G. pusilla	13	13x incl. 2 encr.	5x 2 occ. 2- 4 ind.	2x 2 pt. 9-	3	3x 6 med. 4-	5x (3 (both 5ø	1
G. problematica	4	4x	4 ind.	2x 1- 2 ind.		1x 1- 2 ind. (incl. T.S?)	2x 1- 1 T.S	1
G. spp. inc. G. media	2	2x	2x	2x	2	1 med. 1-	2x	1

49

KEY

- |  |  |
|--|--|
| <u>Form</u> - Coil, Cluster or group x<br>Parallel group of tubes -          | <u>Length</u> - Long x short -   |
| <u>Br.</u> - Branching x (neg. -)  | <u>Curv.</u> - Curvature, strongly<br>curved tubes x,<br>curving or coiling ø<br>straight or nearly so - |
| <u>Adh.</u> - tubes adherent to each<br>other or partly (pt.) x<br>(neg. -)  | <u>Sept.</u> - Some tubes in group<br>septate.   |
| <u>Both</u> - adherent and branching x<br>(includes partly or<br>occasional) | <u>Encr.</u> - encrusting.   |
| <u>Ind.</u> - indeterminate  | <u>T.S.</u> - transverse section   |
| <u>Occ.</u> - occasional curvature   | <u>Med.</u> - medium   |

Table XV.

M.F.1(2)

<u>Type of</u> <u>Girvanella</u>	<u>Nos.</u> <u>48</u>	<u>Form</u>	<u>Br.</u>	<u>Adh.</u>	<u>Both</u>	<u>Length</u>	<u>Curv.</u>	<u>Sept</u>
G. fragillia	22	22-	6x 5 occ. 11-	2x 6 pt. 14-	3x (inc. occ.)	22x	22-	2
G. pusilla	14	14x	11x 1 occ. 2-	2x 3pt. 9-	4x (inc.)	10x 3 med. and 1 ind.	3x 3 ind. 8ø	
G. proluxa	5	5-	5x	5x	5x	5x	5-	4
G. problem- atica	4	*4x	3x 1-	3 pt. 1-	3 (inc.)	2x 2 med.	1 med. 3ø	
G. media	3	3x	3x	3x	3x	1 med. 2-	3x	

\* 1 G. problematica encrusting a brachiopod.

Table XVI

M.F.2(7)

<u>Type of</u> <u>Girvanella</u>	<u>Nos.</u> <u>51</u>	<u>Form</u>	<u>Br.</u>	<u>Adh.</u>	<u>Both</u>	<u>Length</u>	<u>Curv.</u>	<u>Sept.</u>
G. fragila	17	17-	2x 14- 1 ind.	3x 2pt. 12-	2	15x 2 med.	17-	
G. pusilla	27	27x inc.2 encl.	7x 3occ. 14- 3 ind.	1pt. 26-	1 pt.	20x 4 med. 2- 1 ind.	2x 2 med. 22♂	1
G. ramosa	4	4x	4x	4x	4	4-	4x	1
G. effusa	2	2x	2x	1x 1-	1	2-	2x	
G. media	1	1x	1x	1x	1	1x	1♂	1

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Table XVII

F.H.2(3)b

<u>Type of Girvanella</u>	<u>Nos.</u> <u>67</u>	<u>Form</u>	<u>Br.</u>	<u>Adh.</u>	<u>Both</u>	<u>Length</u>	<u>Curv.</u>	<u>Sept.</u>
G. pusilla	4	4x	2x 2 ind.	4-	-	3x 1-	3 $\phi$ 1 ind.	
G. media	25	25x	25x	17x 3pt. 3-	22	18x 3 med. 2- 2 ind.	4x 1 med. 17 $\phi$ 2 ind.	2
G. problem- atica	12	12x incl. 2 encl.	6x 2 poss. 4-	6x 6-	3	10x 2-	13 $\phi$	
G. ramosa	13	13x	13	10x 3pt.	13	4x 3 med. 5- 1 ind.	6x 1 med. 4 $\phi$ 2 ind.	
G. incompta	8	8x	7x 1 ind.	4x 2pt. 2-	6	5x 2- 1 ind.	2x 1 med. 3 $\phi$ 1 ind.	
G. proluxa	1	1-	1x	1x	1	1x	1-	
G. sarmenta	2	2-	2x	2x	2	2x	2-	

Table XVIII

F.H.2(4)

<u>Type of</u> <u>Girvanella</u>	<u>Nos.</u> <u>50</u>	<u>Form</u>	<u>Br.</u>	<u>Adh.</u>	<u>Both</u>	<u>Length</u>	<u>Curv.</u>	<u>Sept.</u>
G. pusilla	2	2x	1x 1 ind.	2-		2x	2-	
G. media	16	16x (inc. 1 encr.)	13x 1 poss. 2 ind.	10x 1 pt. 3- 2 ind.	10	14x 1 med. 1-	3x 13ø	
G. problem- atica	21	21x	12x 3 poss. 4- 2 ind.	2x 1 pt. 18-	2	20x 1 ind.	21ø	1
G. ramosa	5	5x	5x	5x	5	1x 1 med. 2- 1 ind.	3x 1ø 1 ind.	
G. proluxa	3	3-	2x 1-	3x	2	2x 1 med.	3-	
G. sarmenta	3	3-	3	2x 1-	2	3x	2-	

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Table XIX

F.H.2(5)

<u>Type of</u> <u>Girvanella</u>	<u>Nos.</u> <u>45</u>	<u>Form</u>	<u>Br.</u>	<u>Adh.</u>	<u>Both</u>	<u>Length</u>	<u>Curv.</u>	<u>Sept</u>
G. fragila	1	1-	1-	1-		1x	1-	
G. pusilla	16	16x (inc. 1 encr.)	10x 5 poss. 1 ind.	16-		9x 3 med. 3- 1 ind.	1x 15-	1
G. media	6	6x (inc. 1 encr.)	6x	3x 3-	3	2x 2 med. 2-	1x 2 med. 3♂	1
G. problem- atica	15	15x (inc. 1 encr.)	11x 2 poss. 1- 1 ind.	15-		10x 2 med. 3-	4x 2 med. 9♂	2
G. ramosa	6	6x (inc. 2 encr.)	6x	4x 1 pt. 1-		2x 1 med. 1- 1 ind.	5x 1 ind.	1 poss
G. proluxa	1	1-	1-	1x		1x	1-	

Table XX

W.E.11(1)

<u>Type of</u> <u>Girvanella</u>	<u>Nos.</u> <u>69</u>	<u>Form</u>	<u>Br.</u>	<u>Adh.</u>	<u>Both</u>	<u>Length</u>	<u>Curv.</u>	<u>Sept</u>
G. sarmenta	22	22-	14x 2 poss. 4- 2 ind.	19x 3 pt.	16	20x 1- 1 T.S	21- 1 T.S	
G. incompta	18	18x	11x 1 poss. 1- 5 ind.	10x 4 pt. 4-	9	11x 1 med. 1- 5 ind. (inc. 4 T.S)	4x 3 med. 7♂ 4 T.S	
G. ramosa	10	10x	10x	8x 2 pt.	10	1 med. 8- 1nT.S	9x 1 T.S	
G. effusa	7	7x	7x	7x	7	1 med. 6-	6x 1♂	
G. problem- atica	6	6x	2x 2- 2 ind.	1x 5-	-	1x 2 med. 3 ind.	1x 1 med. 2♂ 2 ind.	
G. proluxa	4	4-	3x 1 ind.	4x	3	3x 1 T.S	3- 1 T.S	
G. media	2	2x	2x	1x 1 pt.	2	1x 1-	1x 1 med.	

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Table XXI

W.E.11(2)

<u>Type of</u> <u>Girvanella</u>	<u>Nos.</u> <u>95</u>	<u>Form</u>	<u>Br.</u>	<u>Adh.</u>	<u>Both</u>	<u>Length</u>	<u>Curv.</u>	<u>Sept.</u>
G. sarmenta	30	30-	16x 4 poss. 10-	20x 2 pt. 8-	13	25x 1 med. 3- 1 T.S	29- 1 T.S	
G. incompta	37	37x	31x 1- 5 ind.	15x 2 pt. 20-	12	26x 7 med. 3- 1 T.S	1x 8 med. 27♂ 1 T.S	
G. ramosa	4	4x	4x	4x	4	4-	4x	
G. effusa	13	13x	13x	9x 4-	9	4x 2 med. 7-	11x 2♂	
G. problem- atica	6	6x	2x 4 ind.	5- 1 ind.		2x 4 med.	1x 5♂	
G. media	5	5x	4x 1 ind.	5x	4	1x 3 med. 1-	4x 1♂	

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Table XXIIW.E.14/15

Type of <u>Girvanella</u>	Nos. <u>95</u>	<u>Form</u>	<u>Br.</u>	<u>Adh.</u>	<u>Both</u>	<u>Length</u>	<u>Curv.</u>	<u>Sept.</u>
G. sarmenta	31	31-	12x 5 poss. 11- 3 ind.	27x 4-	12	21x 9 med. 1 T.S	30- 1 T.S	
G. incompta	27	27x	18x 2 poss. 7-	9x 2 pt. 16-	9	15x 7 med. 5-	3x 5 med. 19♂	
G. problem- atica	17	17x (inc. 1 enor)	8x 5- 4 ind. (inc.1 T.S)	4x 13-	3	6x 3 med. 7- 1 T.S	2x 1 med. 13♂ 1 T.S	
G. effusa	9	9x	9x	7x 2-	7	1 med. 8-	8x 1 med.	
G. proluxa	5	5-	2x 1- 2 ind.	2x 1 pt. 2-	1	1x 1 med. 3 T.S	2- 3 T.S	
G. media	4	4x	4x	4x	4	1 med. 3-	3x 1♂	
G. ramosa	1	1x	1x	1-		1-	1x	
G. pusilla	1	1x	1 ind.	1-		1x	1♂	

II SOLENOPORA

Measurements made to 0.5 unit. Magnification x 350 except  
1 unit = 2.85u where otherwise stated.

Graphs made only to nearest whole figure (in units) to  
 overcome standard error.

TABLE XXIII

SOLENOPORA GRACILIS

Diameter measurements of transverse sections of tubes

(a) Slide ORI(3)b - Group A 100 samples

Size of diameter in units	No. of minimum diameter tubes (d)	No. of maximum diameter tubes (D)	Mean average diameter $\frac{d+D}{2}$	% d	% D
3	0	0	0	0	0
4	0	0	0	0	0
5	5	0	2.5	5	0
6	17	2	9.5	17	2
7	39	5	22	39	5
8	30	15	22.5	30	15
9	7	27	17	7	27
10	2	26	14	2	26
11	0	17	8.5	0	17
12	0	6	3	0	6
13	0	2	1	0	2
14	0	0	0	0	0
TOTAL	100	100	100	100	100

(b) Slide ORI(3)b - Group B 100 samples

3	0	0	0	0	0
4	1	0	0.5	1	0
5	11	1	6	11	1
6	19	5	12	19	5
7	41	31	36	41	31
8	24	29	26.5	24	29
9	2	19	10.5	2	19
10	2	11	6.5	2	11
11	0	3	1.5	0	3
12	0	1	0.5	0	1
13	0	0	0	0	0
14	0	0	0	0	0
TOTAL	100	100	100	100	100

(c) Slide OR2(7)b - Group A 100 samples.

Size in units.	No. of d	No. of D	$\frac{d + D}{2}$	%d	%D	$\frac{d + D}{2}$
3	2	0	1	2	0	1
4	2	0	1	2	0	1
5	25	4	14.5	25	4	14.5
6	36	9	22.5	36	9	22.5
7	28	18	23	28	18	23
8	7	29	18	7	29	18
9	0	24	12	0	24	12
10	0	14	7	0	14	7
11	0	1	0.5	0	1	0.5
12	0	0	0	0	0	0
13	0	1	0.5	0	1	0.5
14	0	0	0	0	0	0
<b>TOTAL</b>	<b>100</b>	<b>100</b>	<b>100</b>	<b>100</b>	<b>100</b>	<b>100</b>

(d) Slide OR2(7)b - Group B 50 sample measurements.

3	0	0	0	0	0	0
4	3	0	1.5	6	0	3
5	8	0	4	16	0	8
6	23	10	16.5	46	20	33
7	10	16	13	20	32	26
8	6	15	10.5	12	30	21
9	0	8	4	0	16	8
10	0	1	0.5	0	2	1
11	0	0	0	0	0	0
12	0	0	0	0	0	0
<b>TOTAL</b>	<b>50</b>	<b>50</b>	<b>50</b>	<b>100</b>	<b>100</b>	<b>100</b>



(e) Slide OR2(7)b - Group C 50 samples

Size in units	No. of d	No. of D	$\frac{d}{2}$	$\frac{D}{2}$	$\frac{d}{D}$	$\frac{D}{d}$	$\frac{\%d}{\%D}$
3	0	0	0	0	0	0	0
4	2	0	1	0	4	0	2
5	3	0	1.5	0	6	0	3
6	8	1	4.5	0.5	16	2	9
7	19	8	13.5	4	38	16	27
8	14	13	13.5	6.5	28	26	27
9	3	15	9	7.5	6	30	18
10	1	12	6.5	6	2	24	13
11	0	1	0.5	0.5	0	2	1
12	0	0	0	0	0	0	0
Total	50	50	50	50	100	100	100

(f) Slide OR2(7)d - Group D 50 samples

3	2	0	1	0	4	0	2
4	2	0	1	0	4	0	2
5	15	5	10	2.5	30	10	20
6	21	15	18	7.5	42	30	36
7	10	18	14	9	20	36	28
8	0	10	5	12	0	20	10
9	0	2	1	15	0	4	2
10	0	0	0	18	0	0	0
11	0	0	0	21	0	0	0
12	0	0	0	24	0	0	0
Total	50	50	50	50	100	100	100

TABLE XXIV

SOLENOPORA GRACILIS

Composite Table (450 samples) of transverse measurements  
of tube diameters

Size	d	D	Mean	%d	%D
2	0	0	0	0	0
3	4	0	2	0.8	0
4	10	0	5	2.2	0
5	67	10	38.5	14.8	2.2
6	124	42	83	16.4	9.1
7	147	96	121.5	32.6	21.3
8	81	111	96	18	24.6
9	12	95	53.5	2.6	20.1
10	5	64	34.5	1.1	14.2
11	0	22	11	0	4.8
12	0	7	3.5	0	1.5
13	0	3	1.5	0	0.6
14	0	0	0	0	0
Total	450	450	450		

## H I S T O G R A M S

for comparative purposes in the study of Girvanella groups, and are in conjunction with the Tables.

Each Girvanella group, the result of 5 or more measurements, is indicated by 1 unit on the vertical scale, and the range of diameter of tubes within a group is marked on the horizontal scale (units in  $\mu$ ). Thus a group with wide variation in diameter, (usually due to indistinctness of specimen) will show a wider horizontal range than one with scarcely any variation. This method includes any error for any type but has the disadvantage of producing a greater overlap between forms. This is partly overcome by also plotting mean values for each group measured.

Throughout the set of histograms:-

Locality is indicated by initials.

Vertical scale indicates number of distinct groups containing tubes of definite diameter, as shown by horizontal scale.

The top histogram for each locality indicates size range of groups and their relevant abundance, and for comparison black areas are the mean values for each group.

The lowest histogram for each locality completed for

all groups indicates general features. Black areas indicate groups with any branching and tubes adhering to each other. Stippled areas indicate groups possessing any branching, but tubes mostly not in contact with each other. Areas with short dashes indicate groups which do not show branching, but with most (or all) tubes adhering to each other. Blank areas, loose and non-branching groups.

The smaller histograms indicate constituent form species forming the measured groups -

- a. *Girvanella fragila*
- b. *G. pusilla*
- c. *G. problematica*
- d. *G. media*
- e. *G. proluxa*
- f. *G. sarmenta*
- g. *G. incompta*
- h. *G. ramosa*
- i. *G. effusa*

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### Histograms

#### 1. Comparative studies of Girvanella from

Mordiford M.F. (Quarries 1 and 2)	148 groups
Fownhope F.H. (Quarry 2)	162 "
Wenlock Edge W.E. (Quarry 11)	164 "

(continued next page)

- |     |                             |            |   |
|-----|-----------------------------|------------|---|
| 2.  | Mordiford M.F.1(1)          | 49 groups. |   |
| 3.  | Mordiford M.F.1(2)          | 48 "       |   |
| 4.  | Mordiford M.F.2(7)          | 51 "       |   |
| 5.  | Fownhope F.H.2(3)           | 67 "       |   |
| 6.  | Fownhope F.H.2(3)           | 50 "       |   |
| 7.  | Fownhope F.H.2(5)           | 45 "       |   |
| 8.  | Wenlock Edge W.E.11(1)      | 69 "       |   |
| 9.  | Wenlock Edge W.E.11(2)      | 95 "       | (Branching etc. not indicated; similar to W.E.11(1)).                               |
| 10. | Wenlock Edge W.E. 14 and 15 | 95 groups. | Shaded areas correspond to the form species. (Mean values and branching not shown). |
- W.E.3(5) and 8      Stippled areas W.E.3(5) (40 groups), blank areas W.E.(8) (72 groups). No composite histogram, only form species shown.

### G R A P H S

To determine the normal variation in tube diameter measured in Solenopora gracilis by both T.S. and L.S. and to find the mean average diameter.

Samples taken from the same and different thalli from different localities were as follows:-

#### Set A      Transverse sections

Graphs a and b (upper 2) Locality O.R.1(3)b.  
each the result of 100 sets of measurements.

Graphs c and d (next 2) Locality O.R.2(7)b.  
c - 100 sets, d - 50 sets.

Graphs e and f. Locality O.R.2(7)b.  
50 sets of measurements each.

Graph g. Composite graph of O.R.1(3)b - Result of  
a and b = 200 sets of measurements.

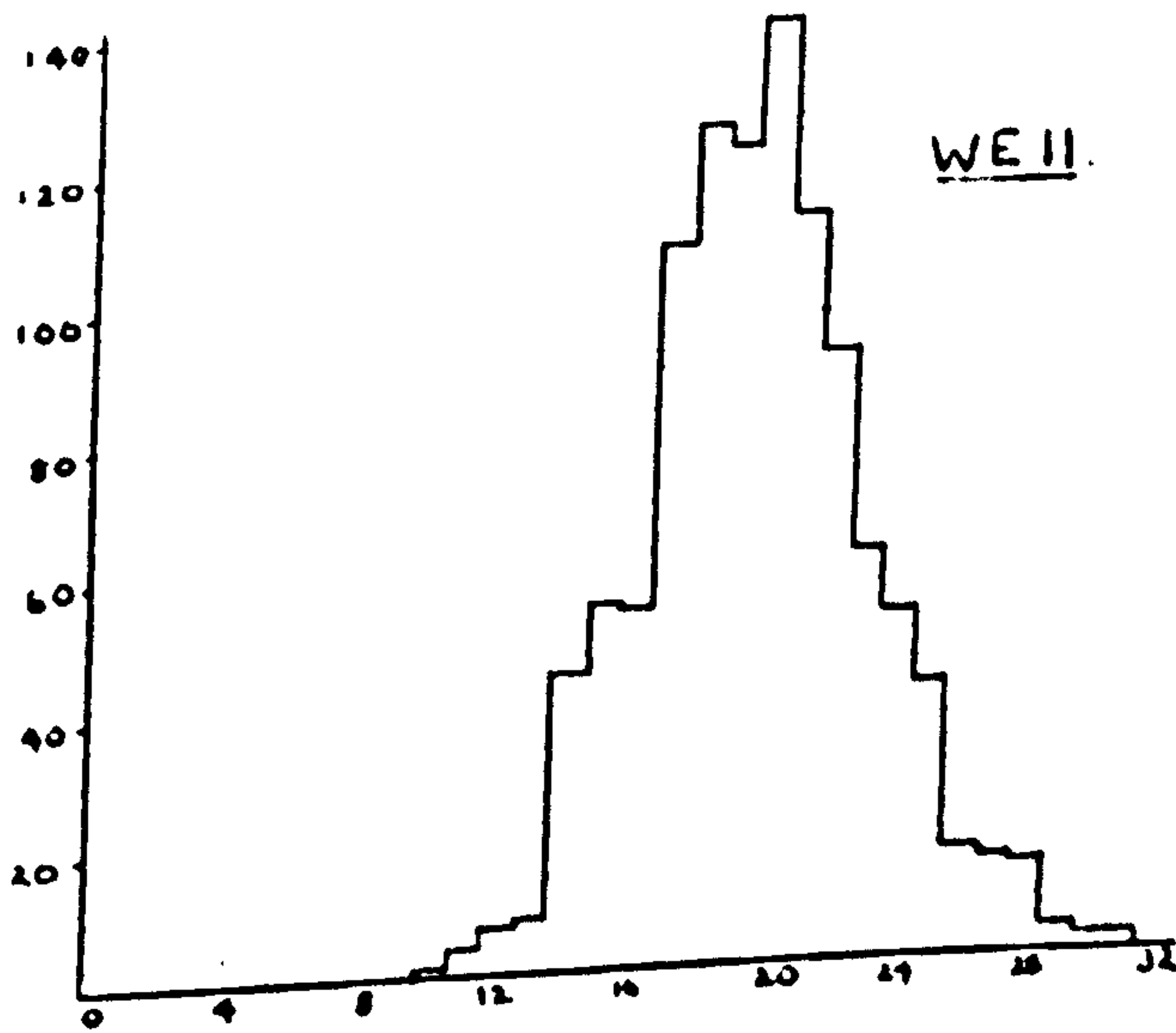
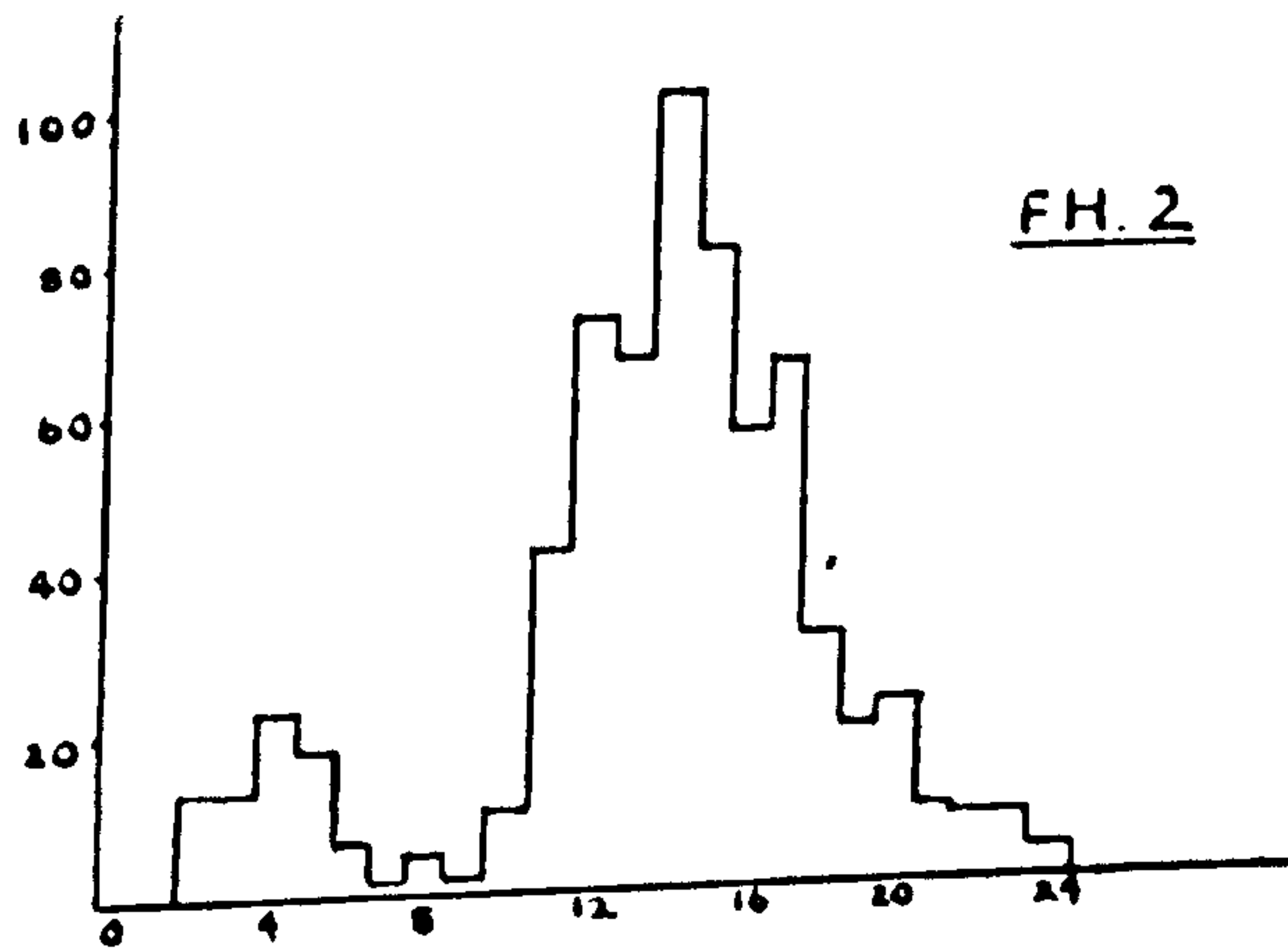
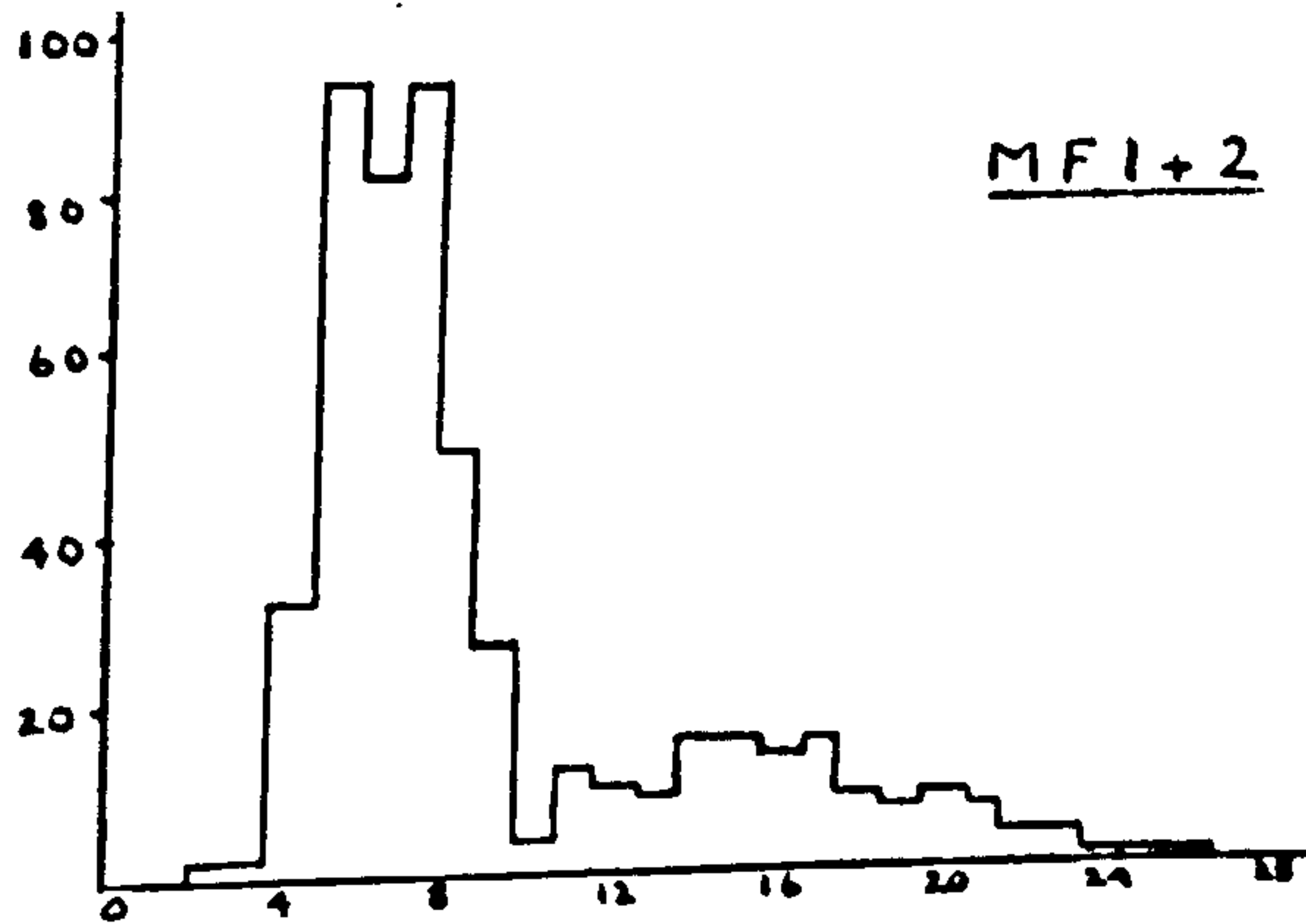
Set B. Longitudinal sections a, b, c, composite d.

Graphs a, b, c. O.R.1(3)b.

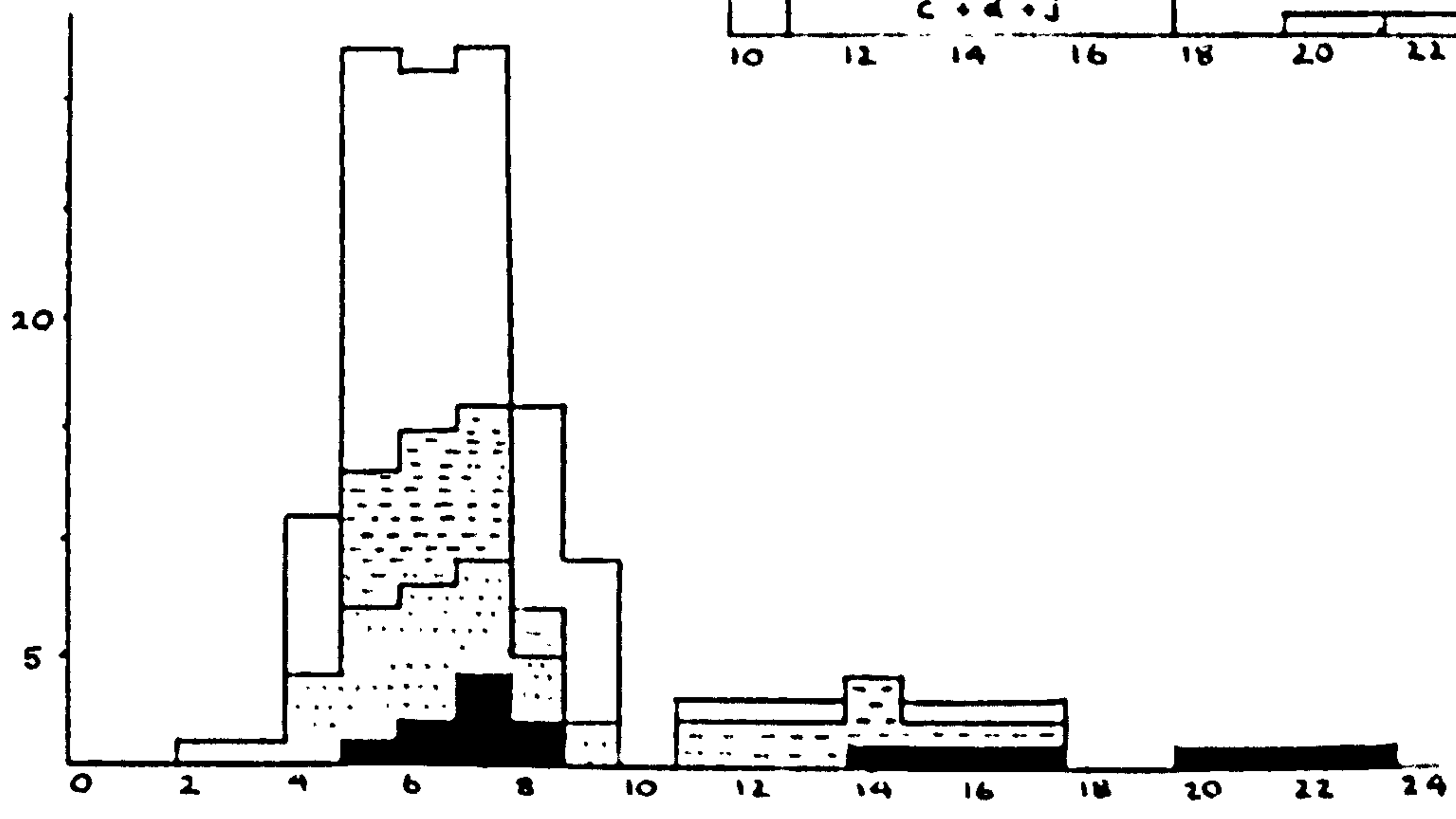
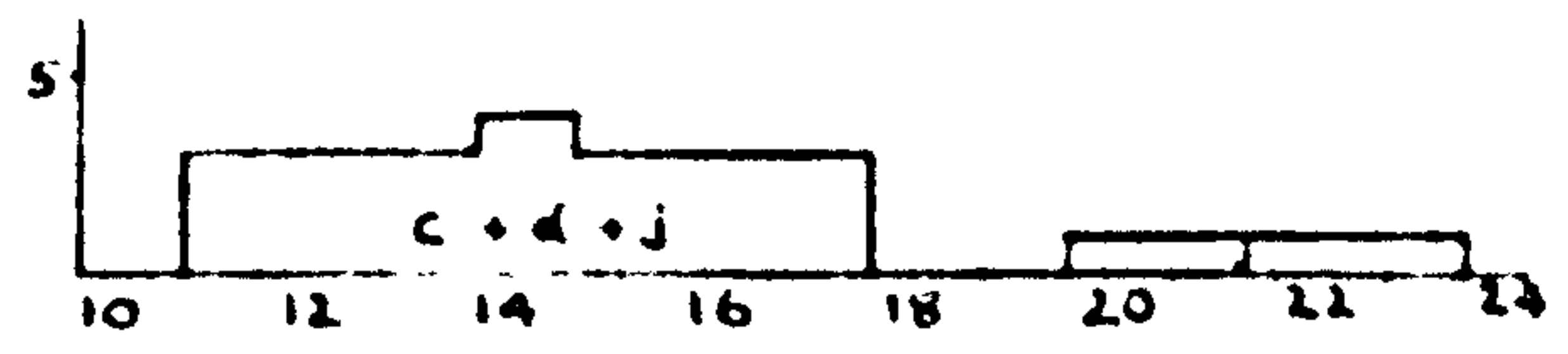
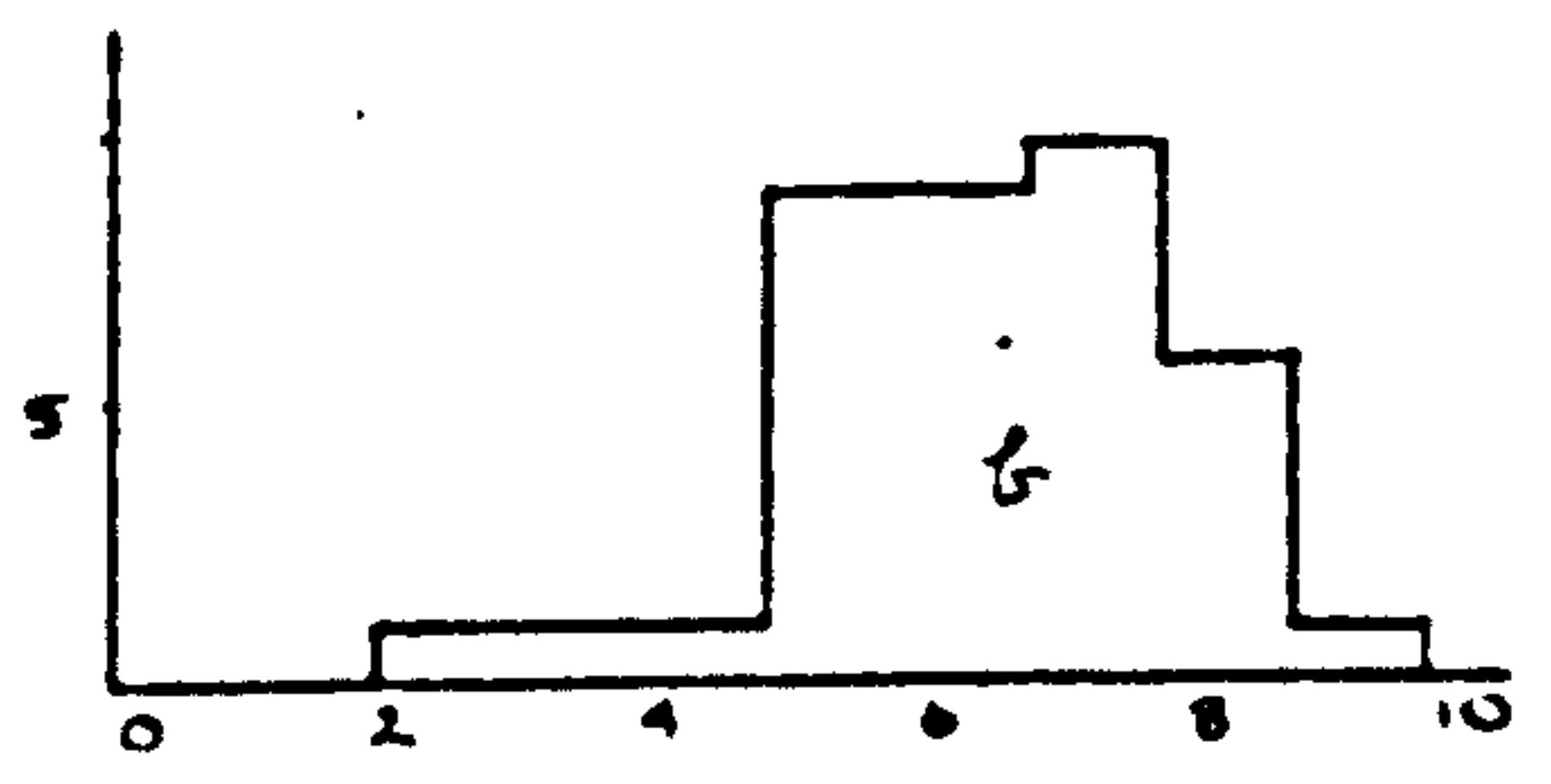
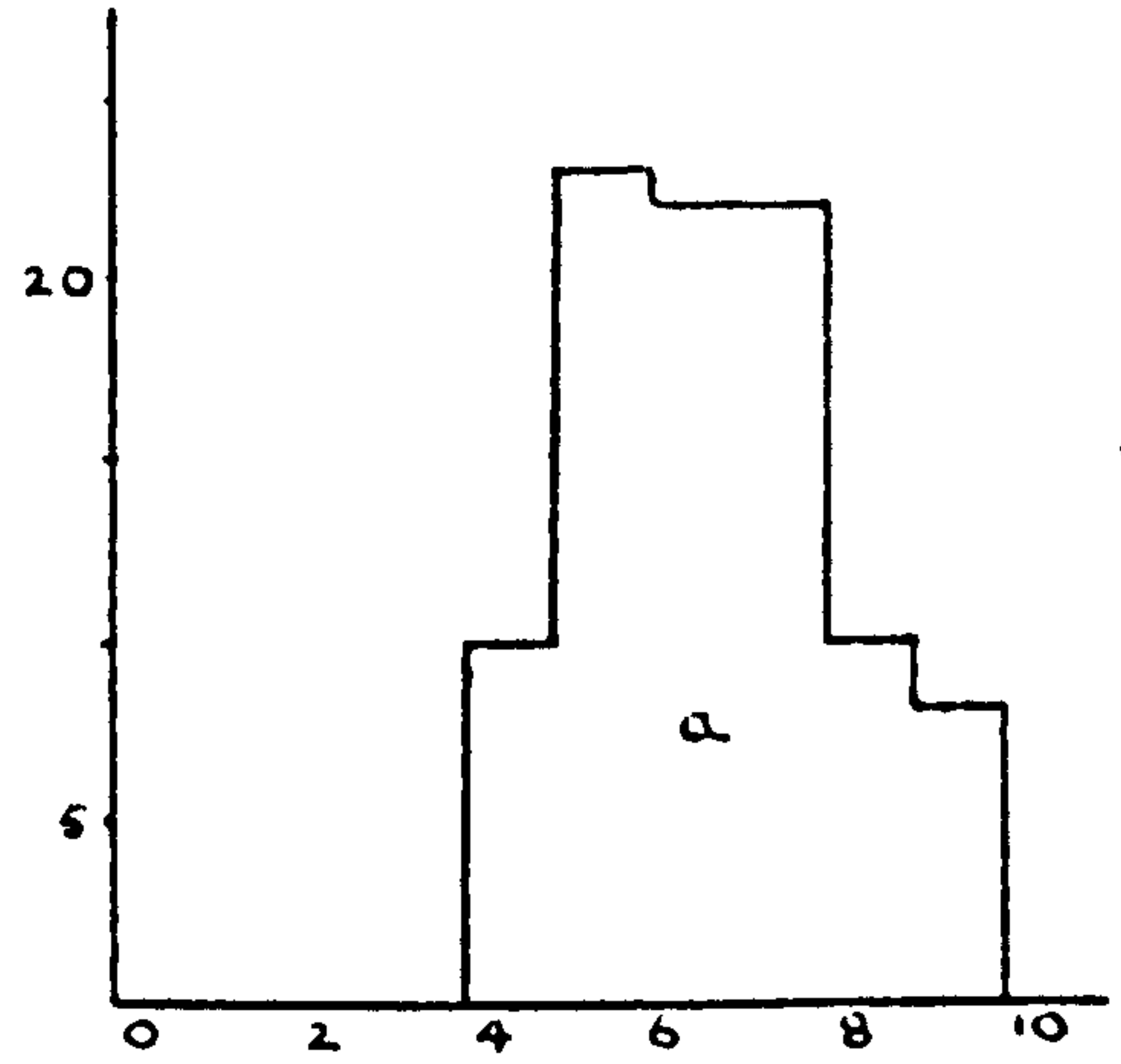
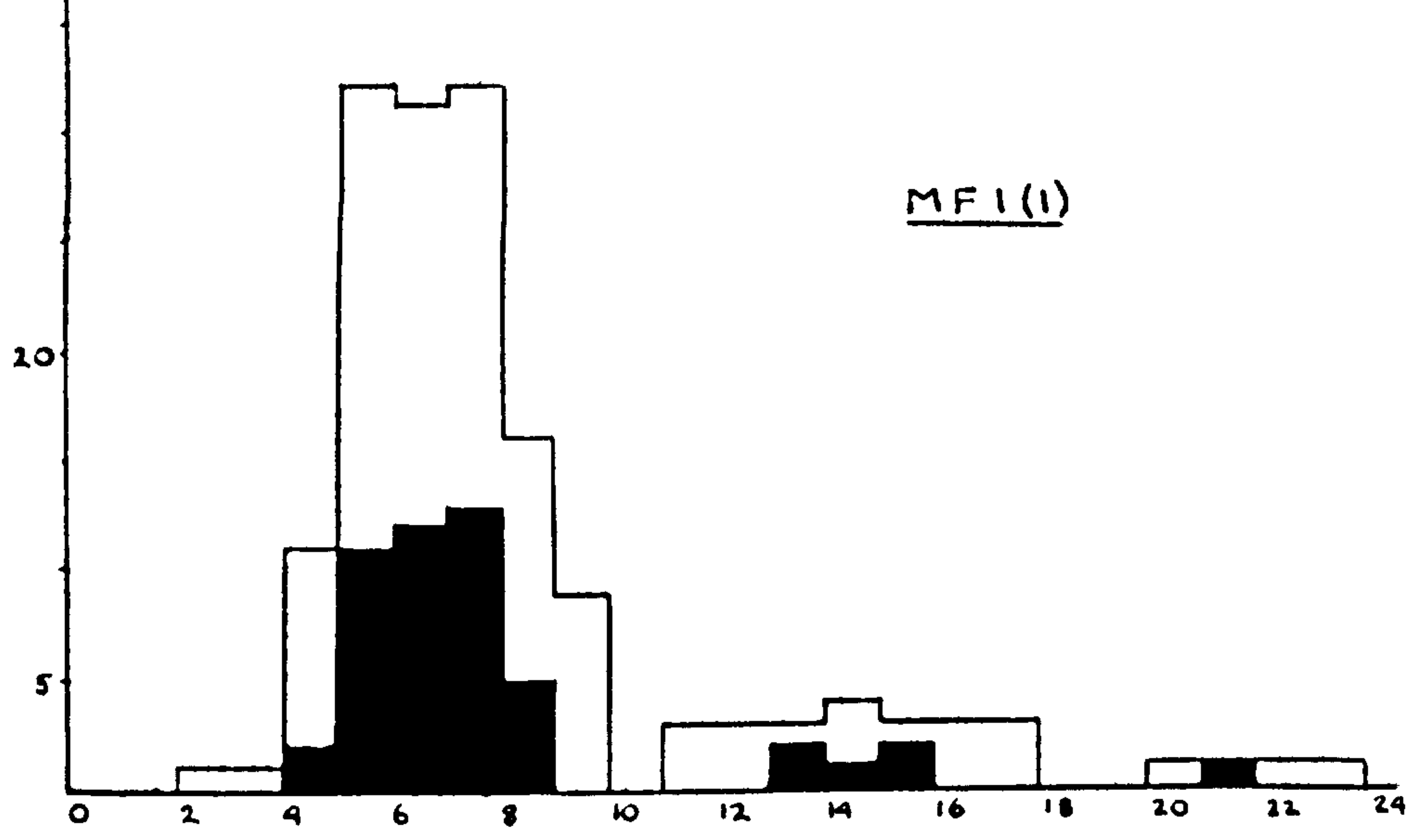
Graph c - composite of a and b - 30 sets of measurements.

Graph d - composite graph of all transverse measurements  
450 samples.

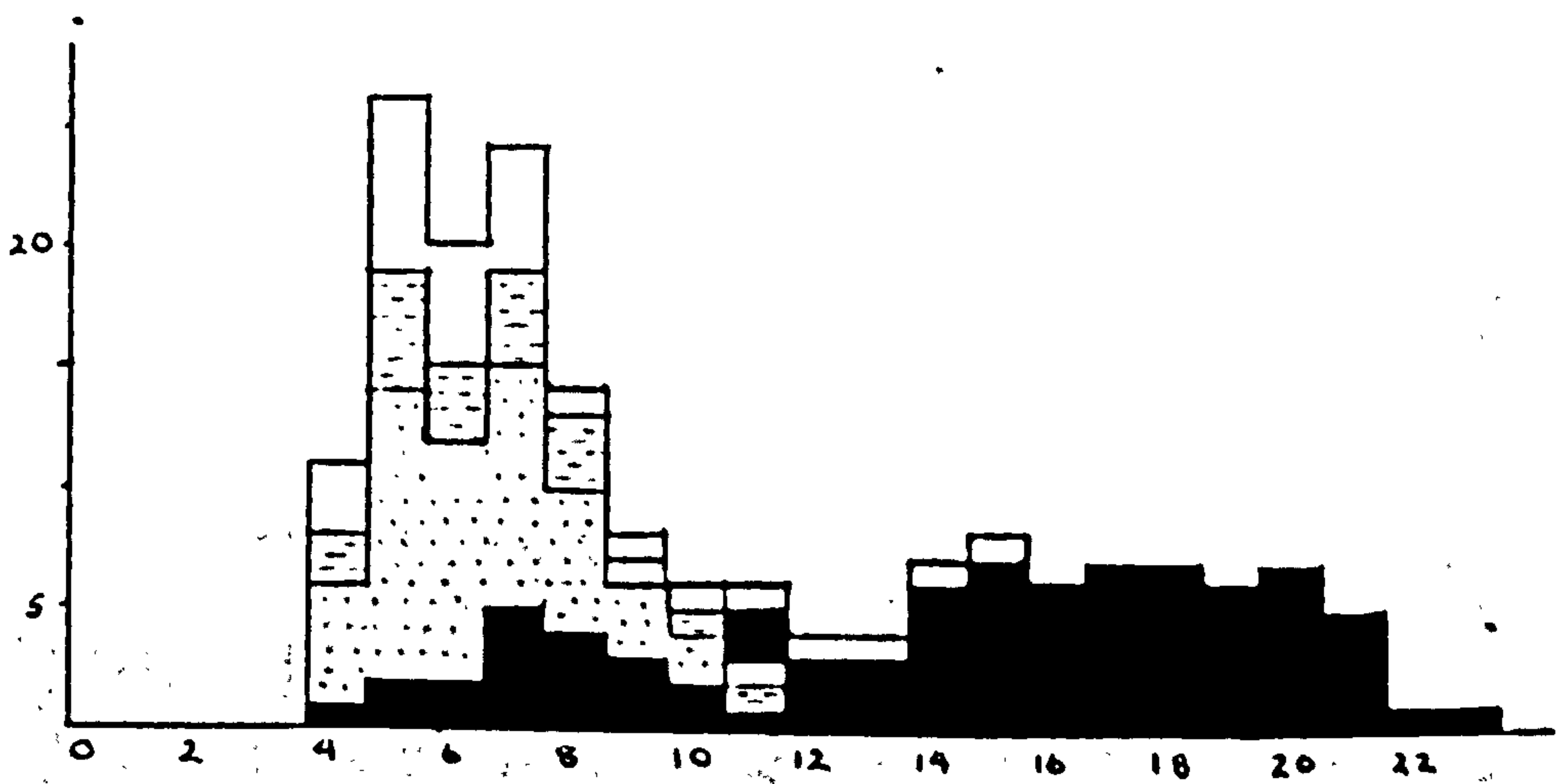
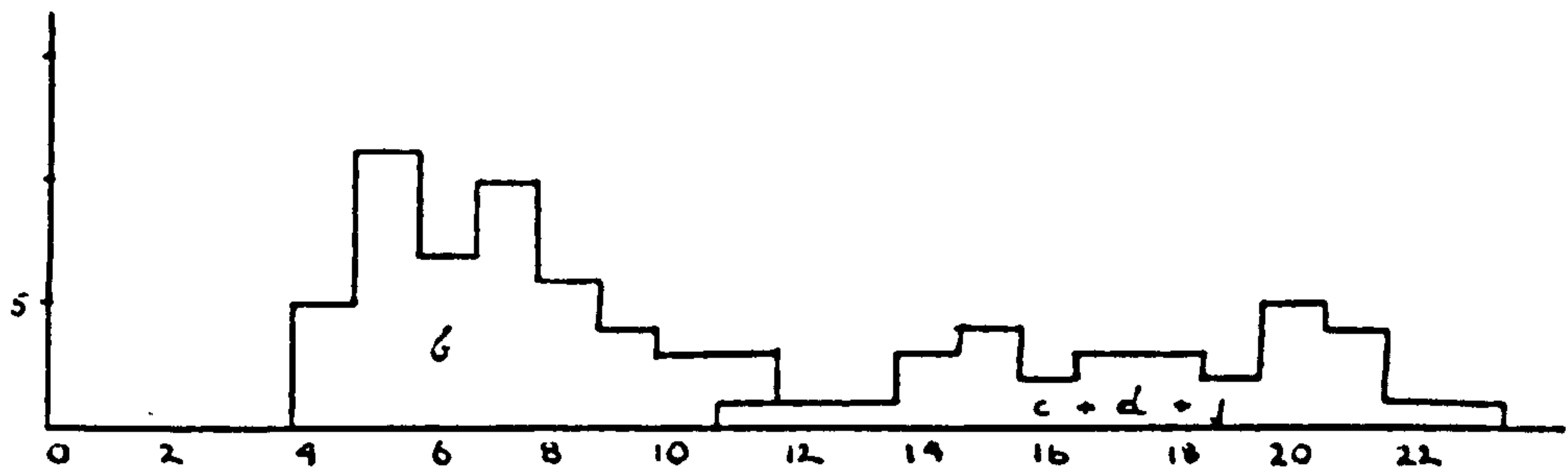
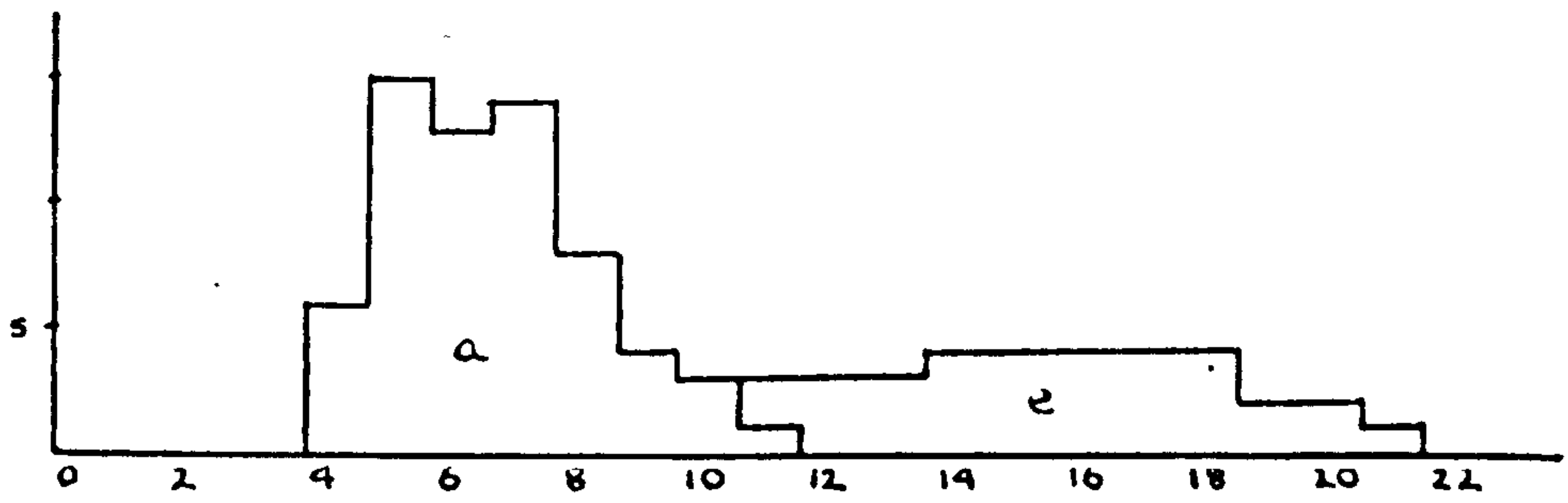
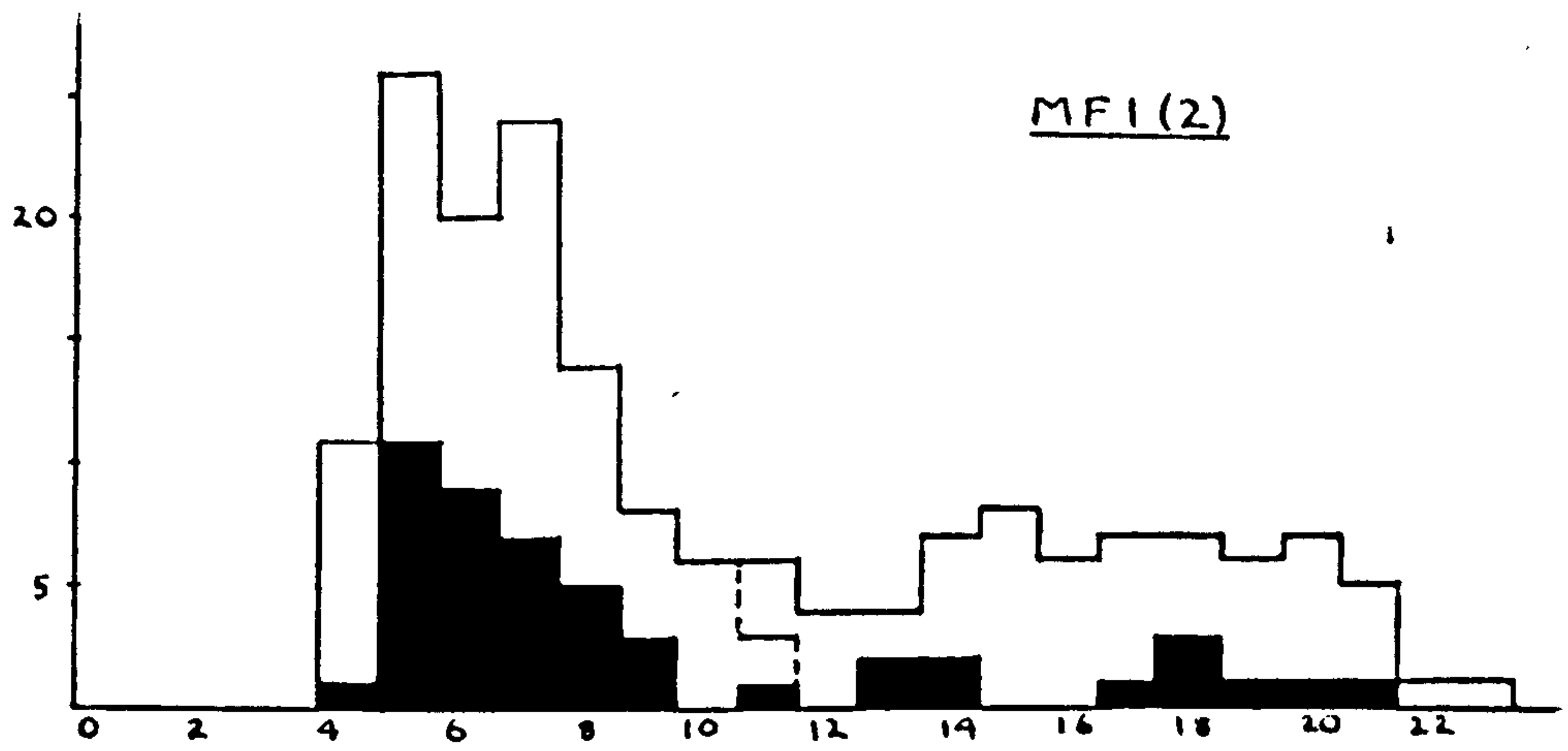
⊙	-	minimum diameter measured for a tube
+	-	maximum diameter measured
x	-	average mean diameter

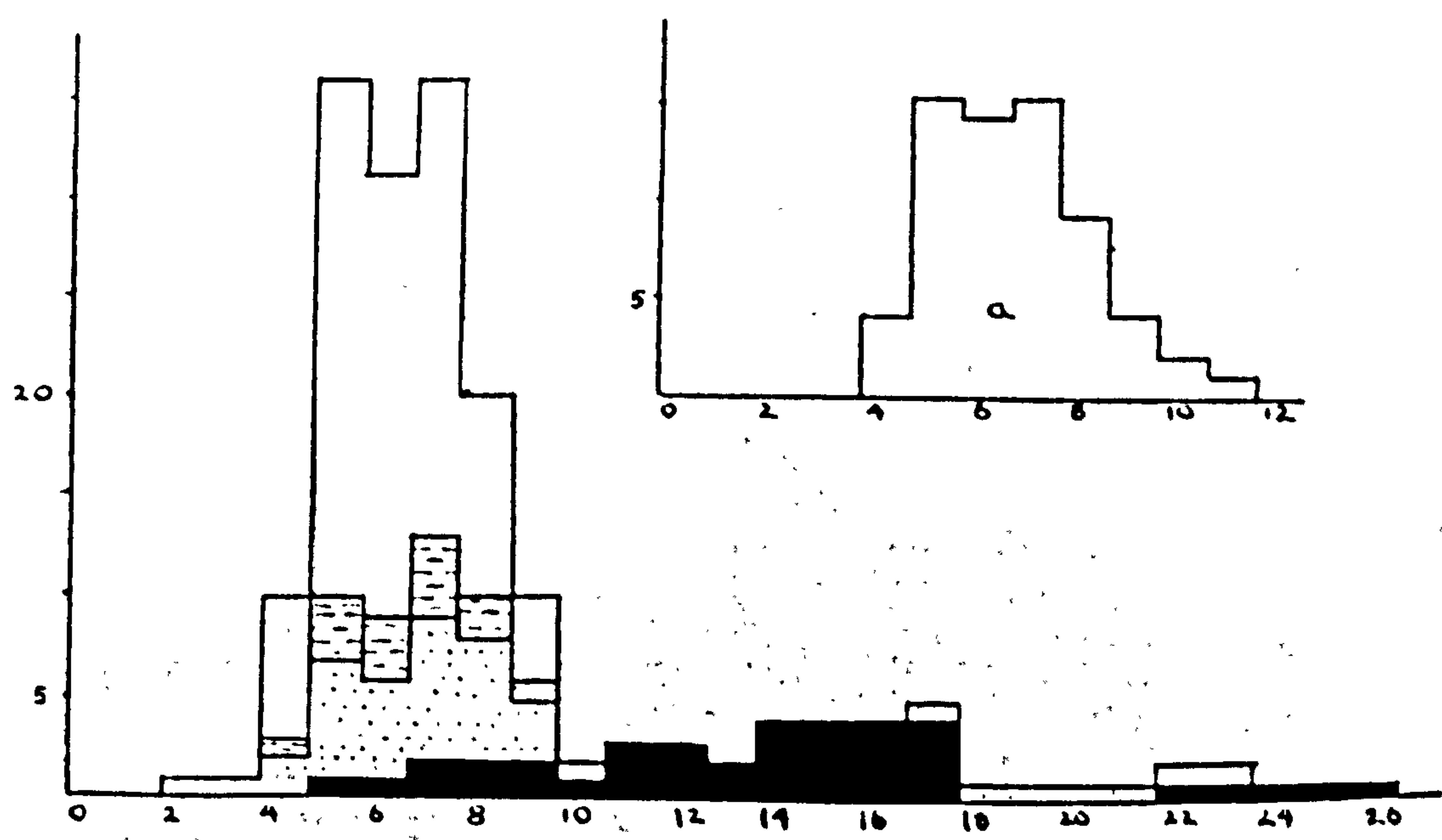
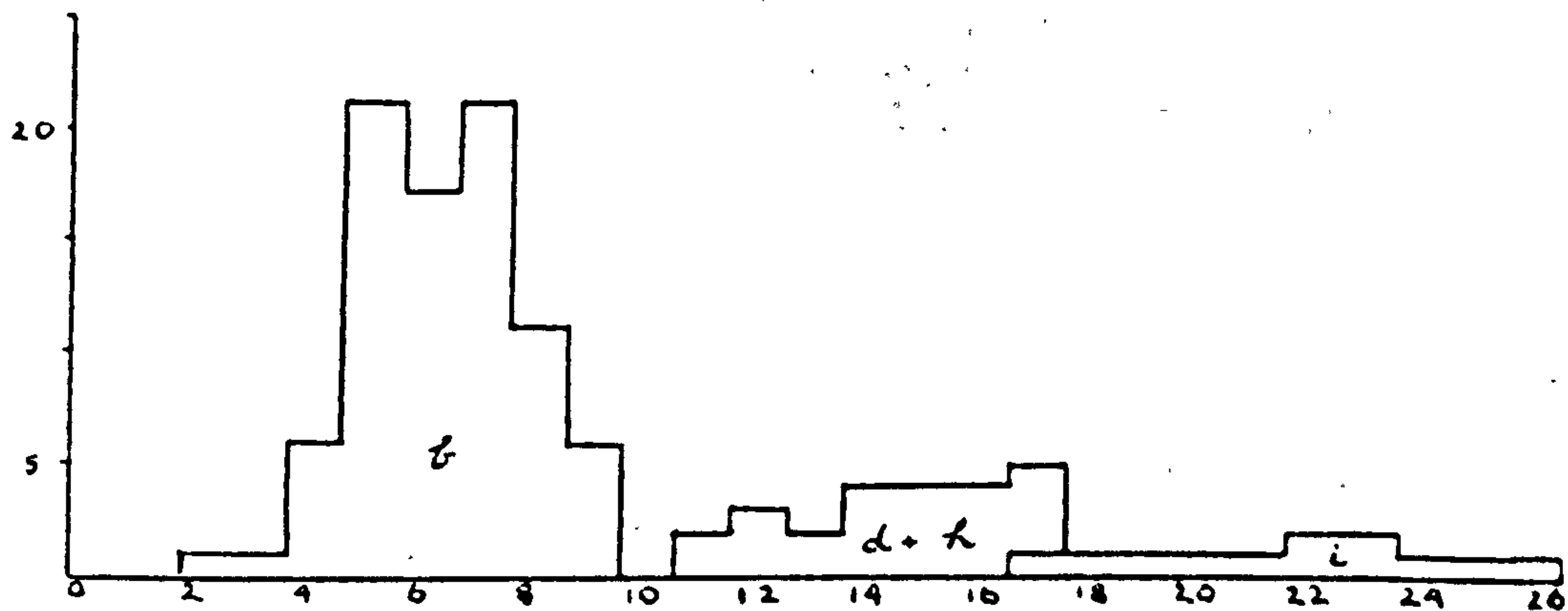
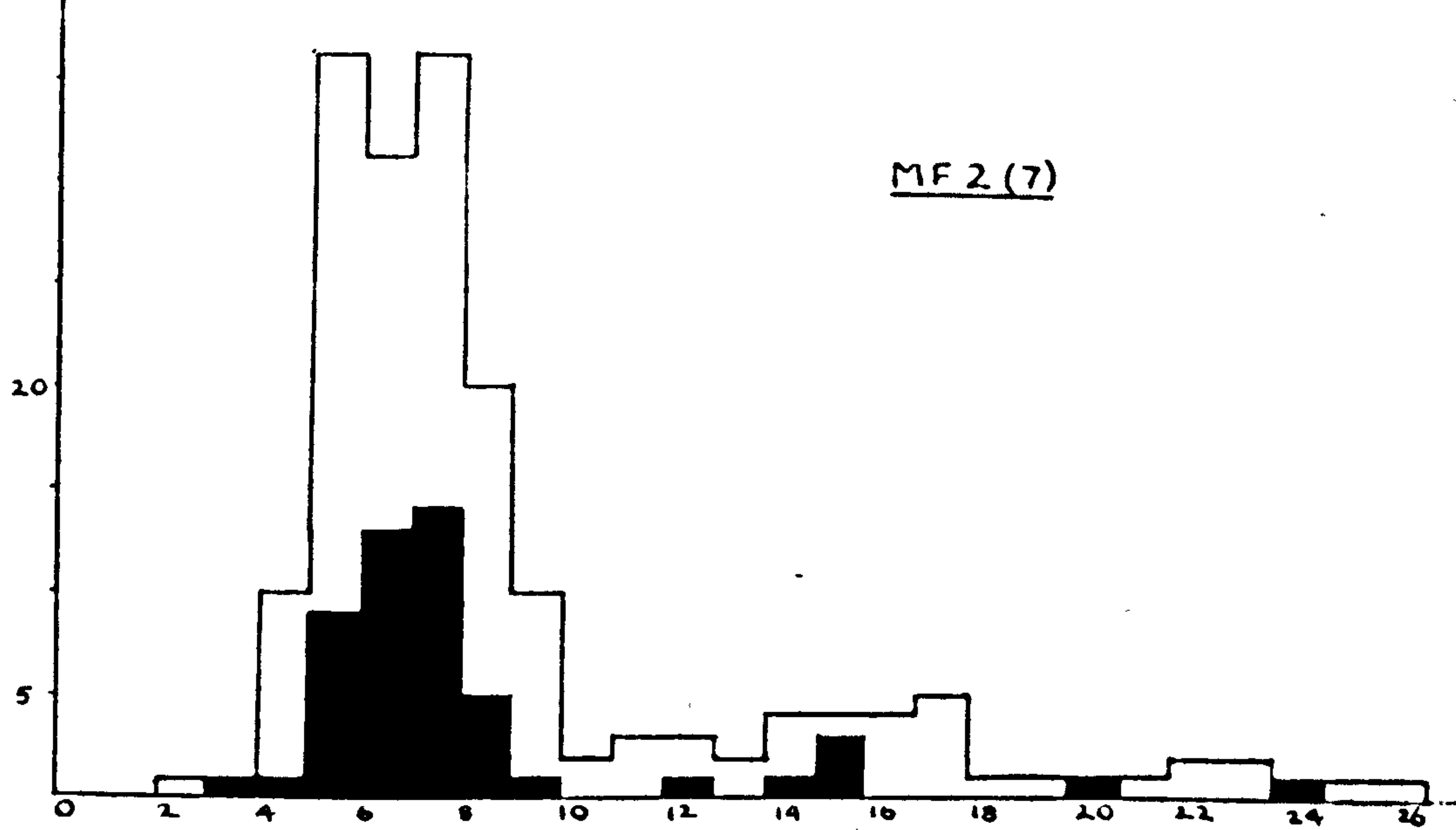


MFI(I)

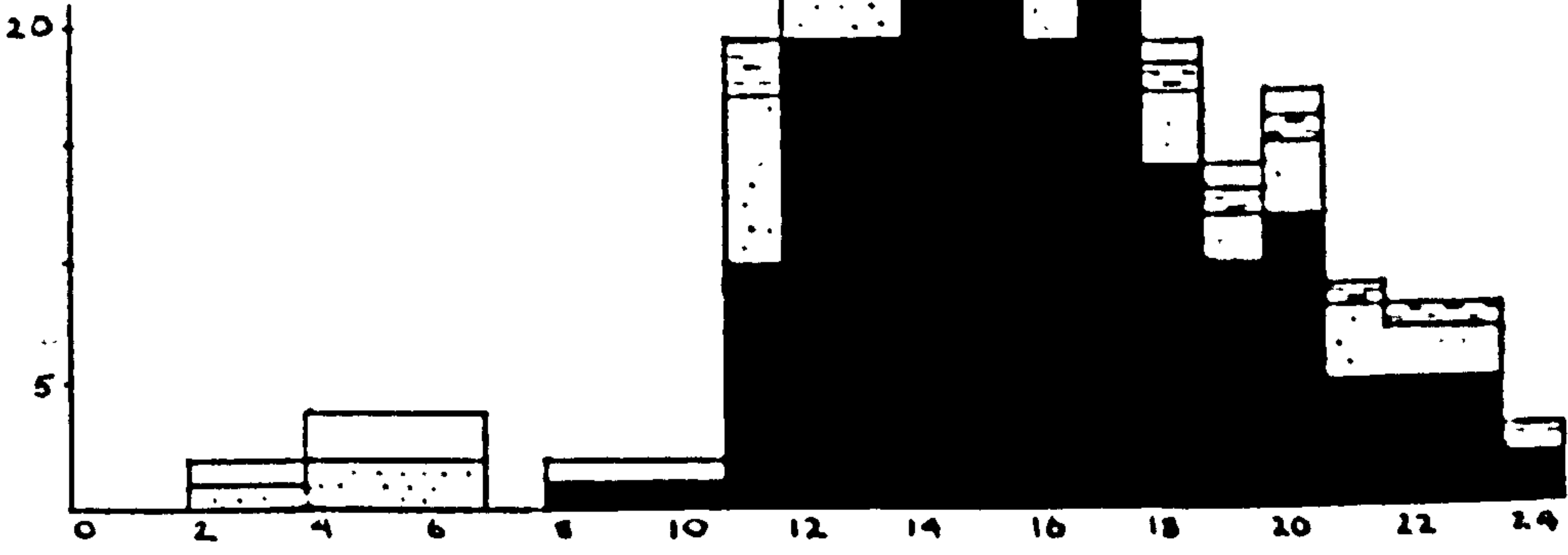
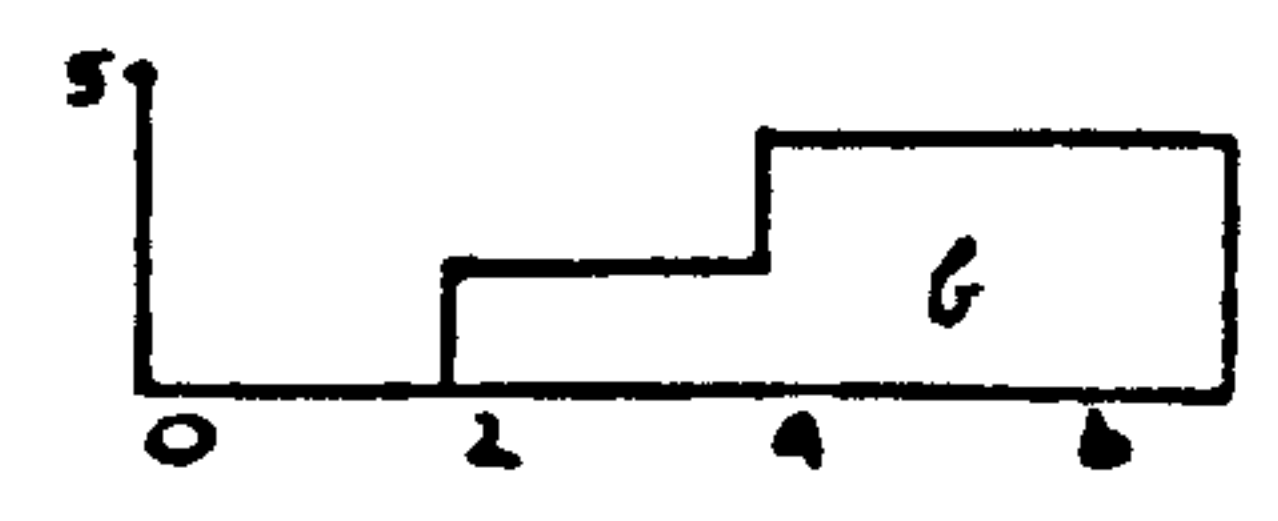
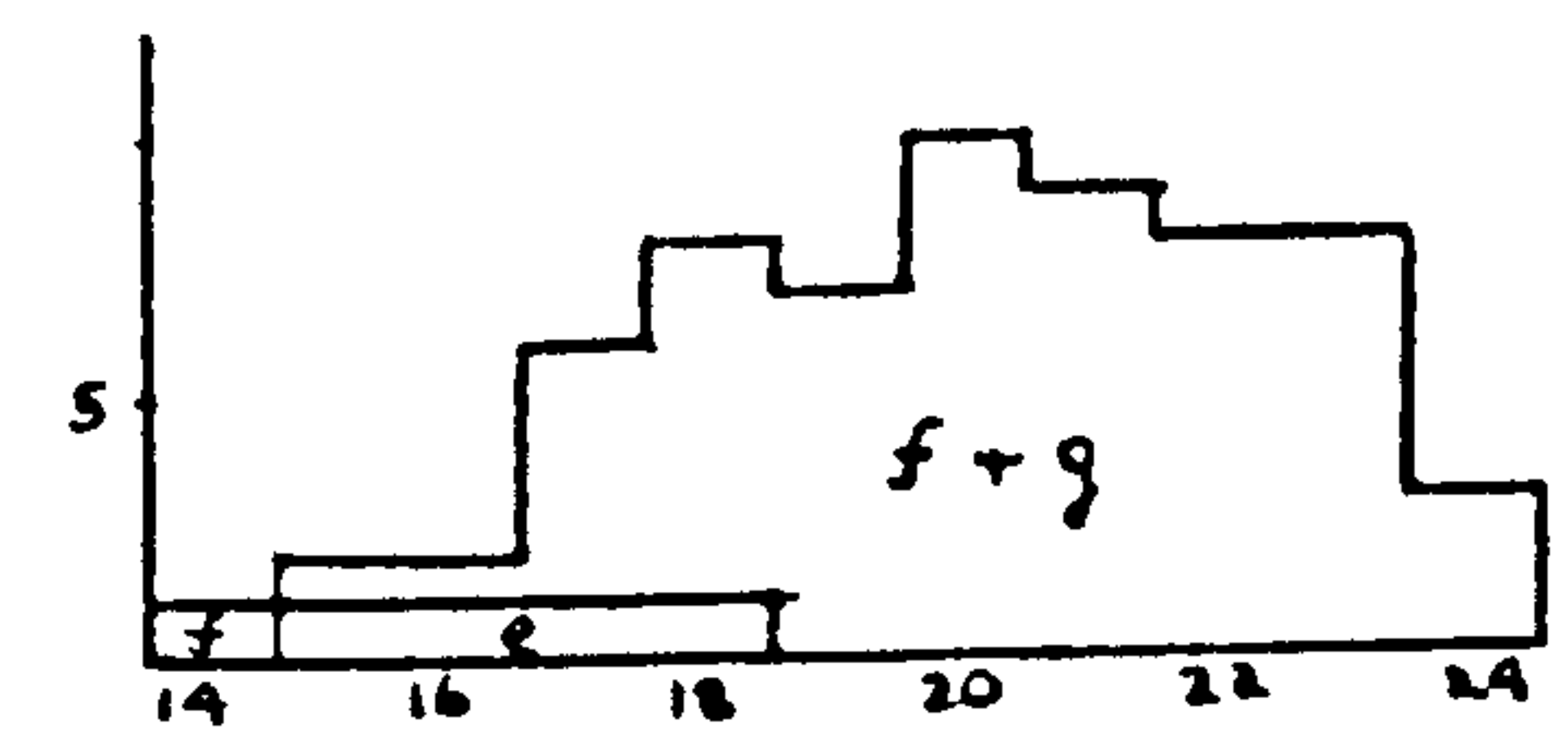
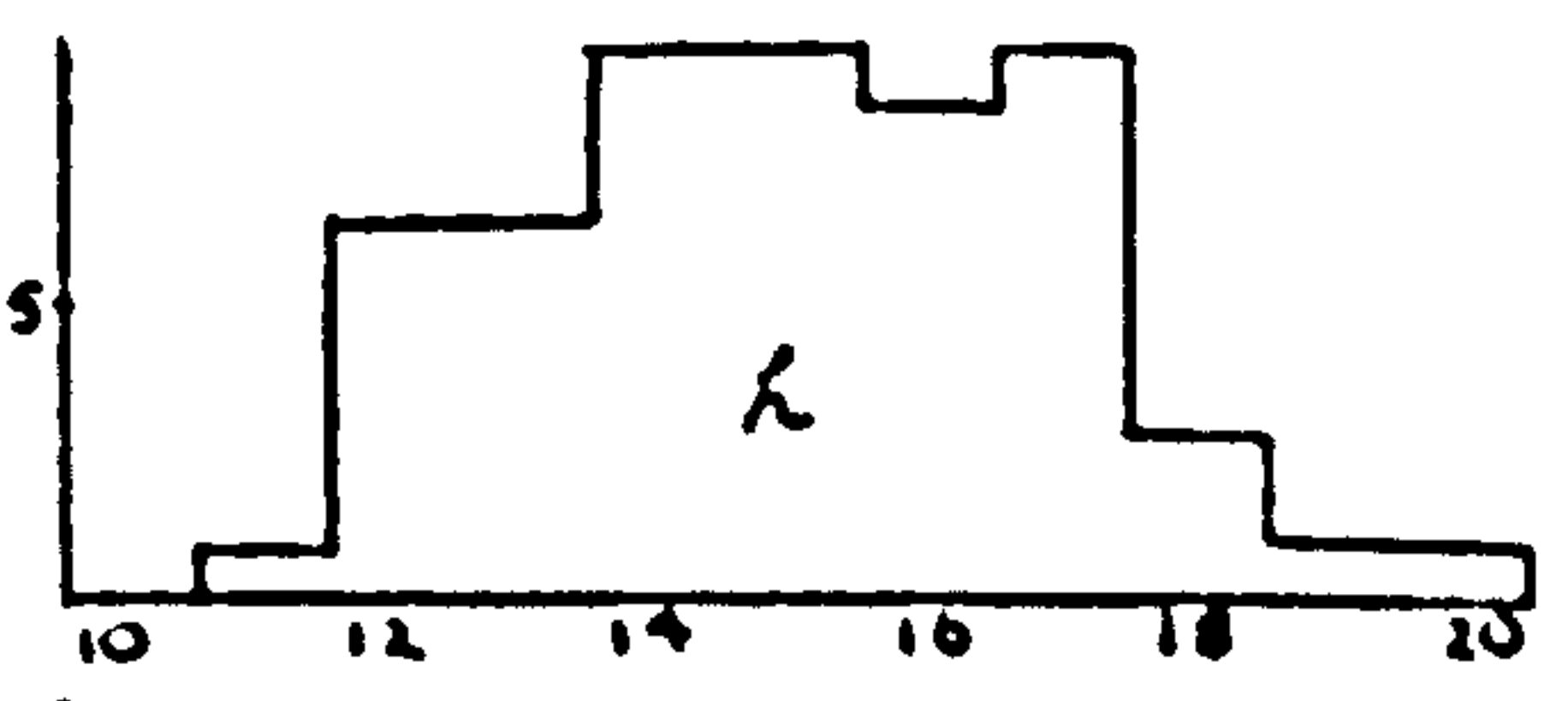
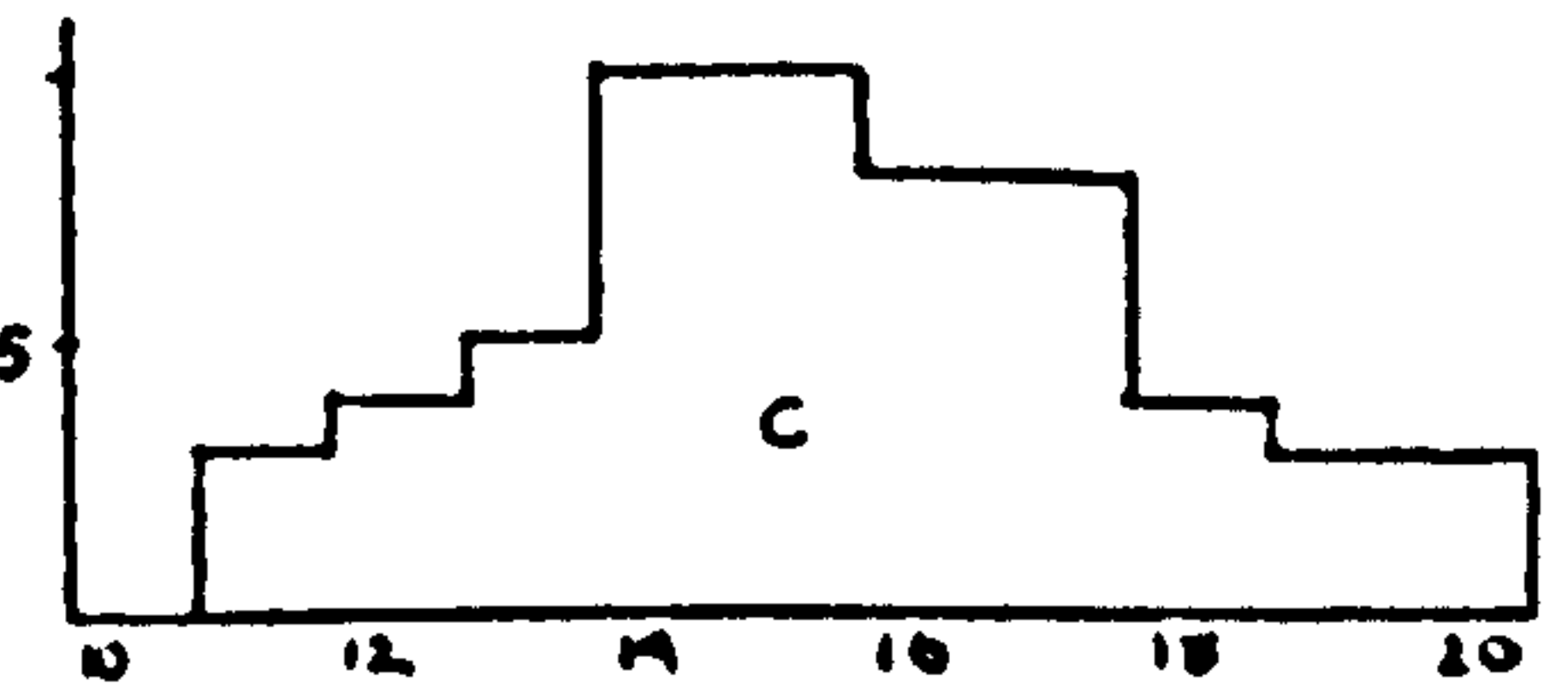
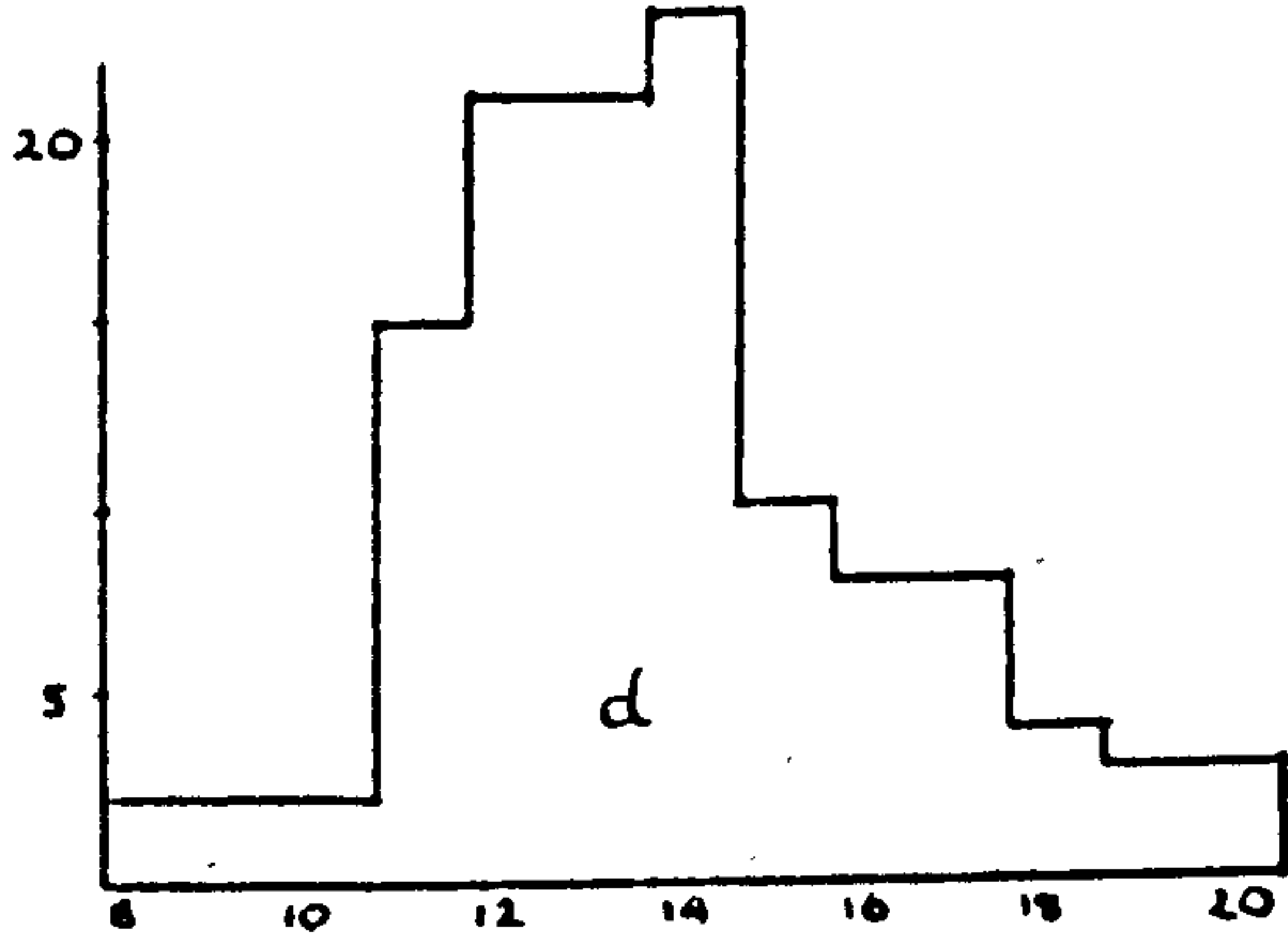
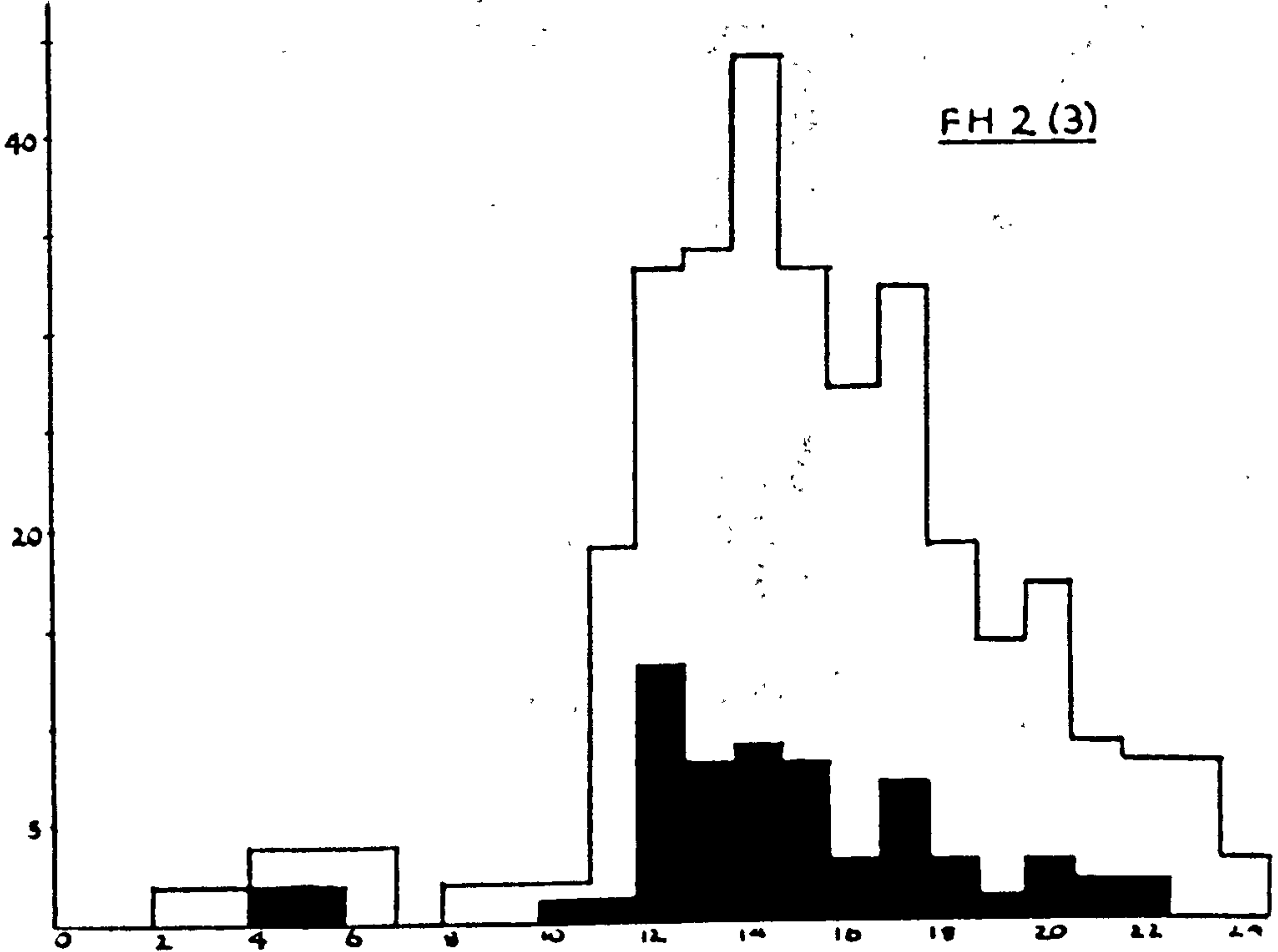




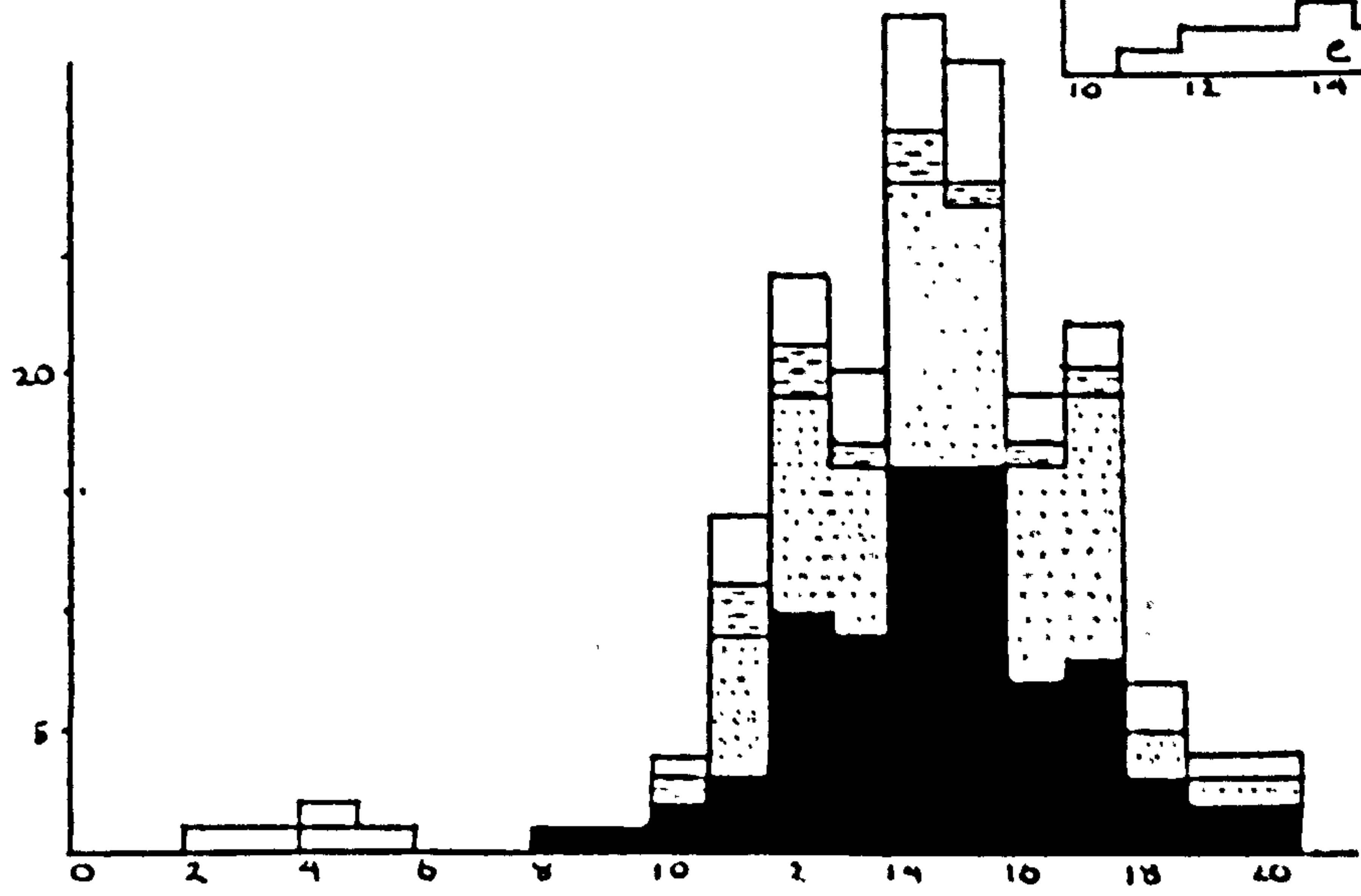
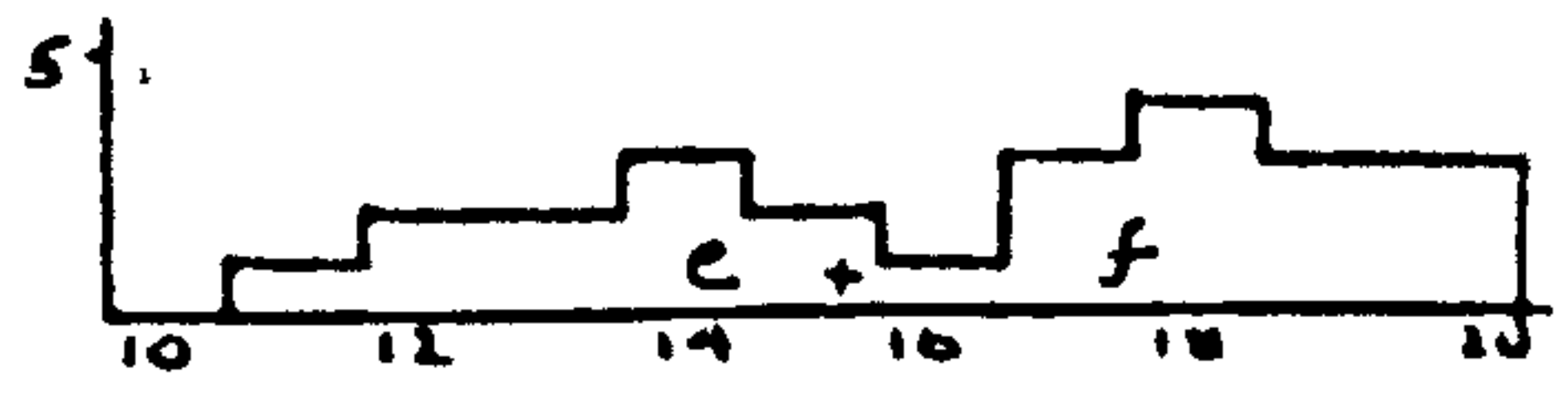
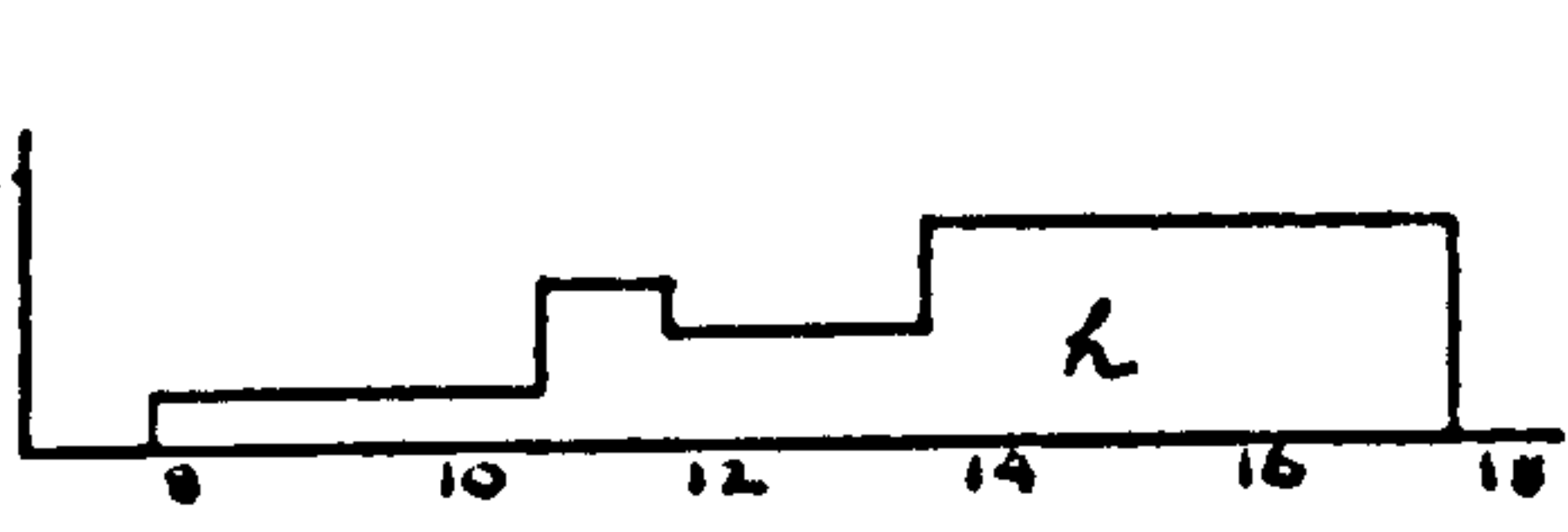
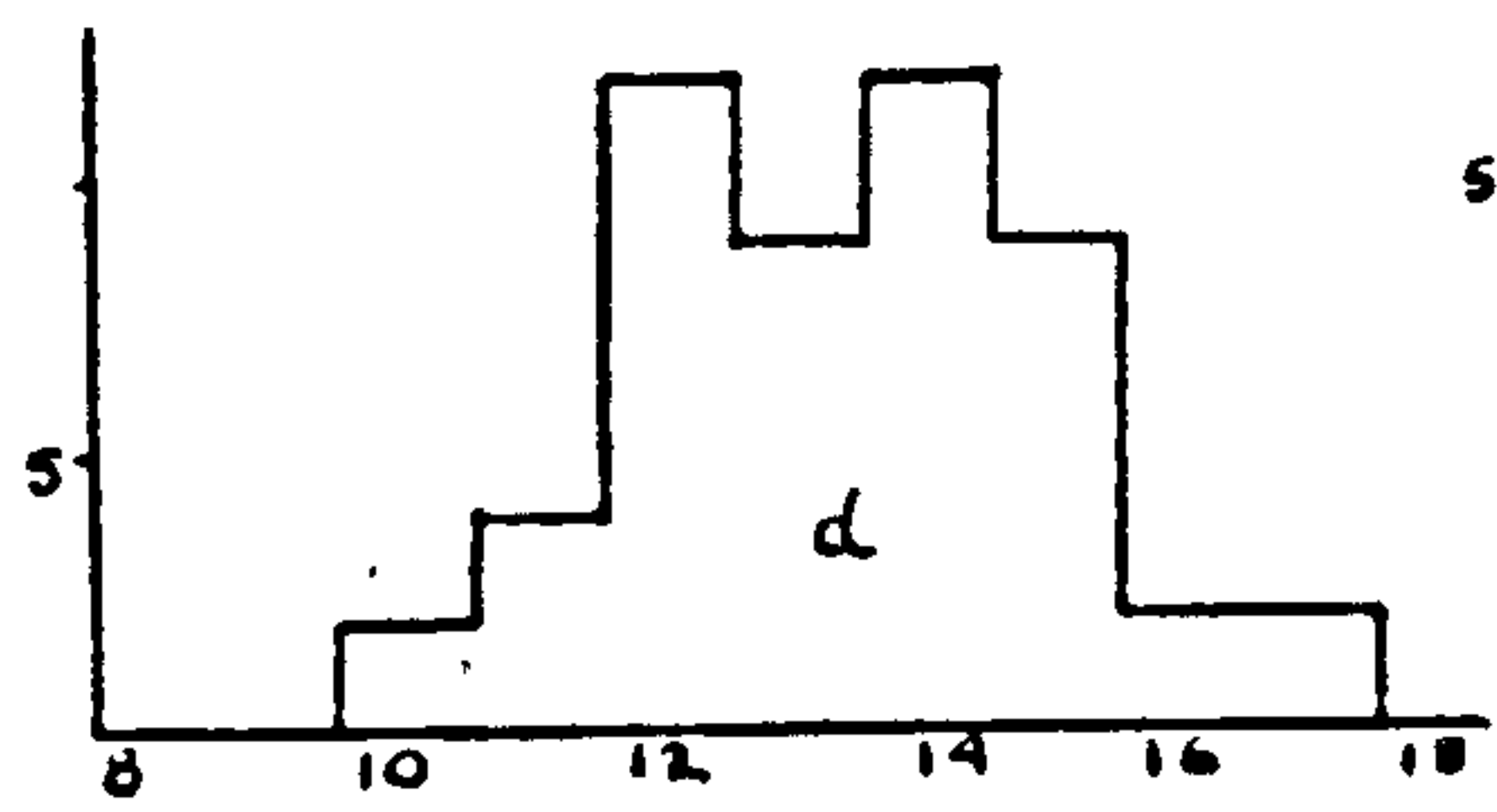
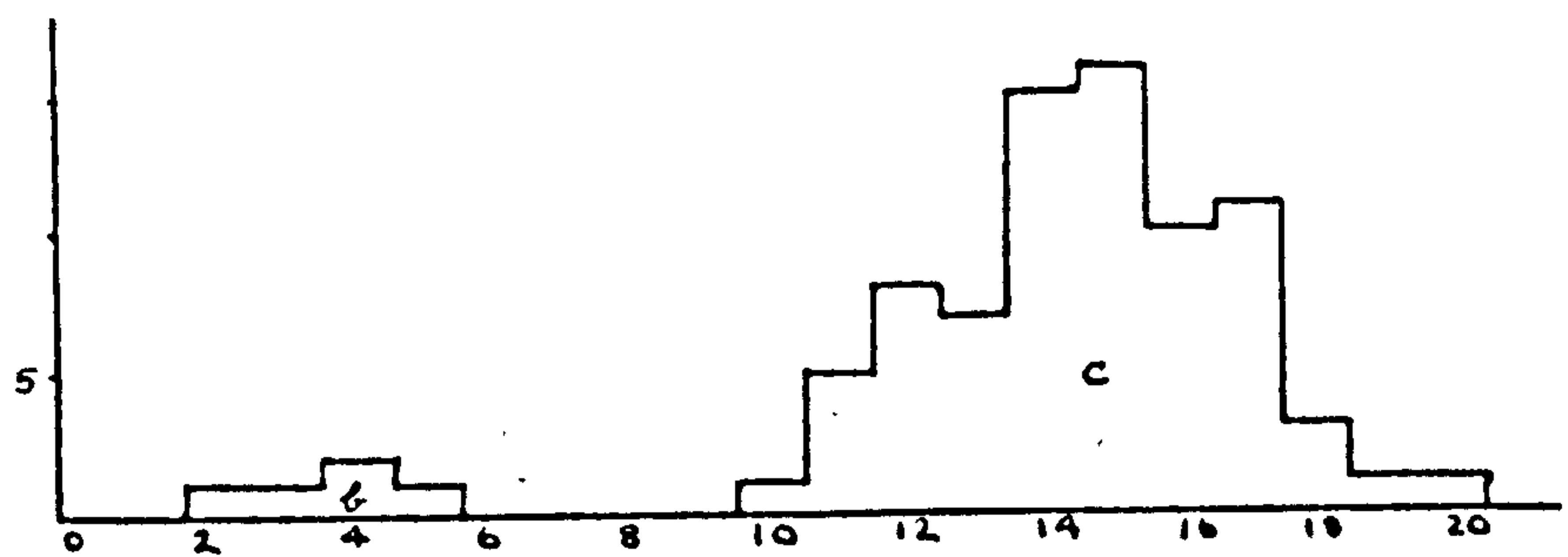
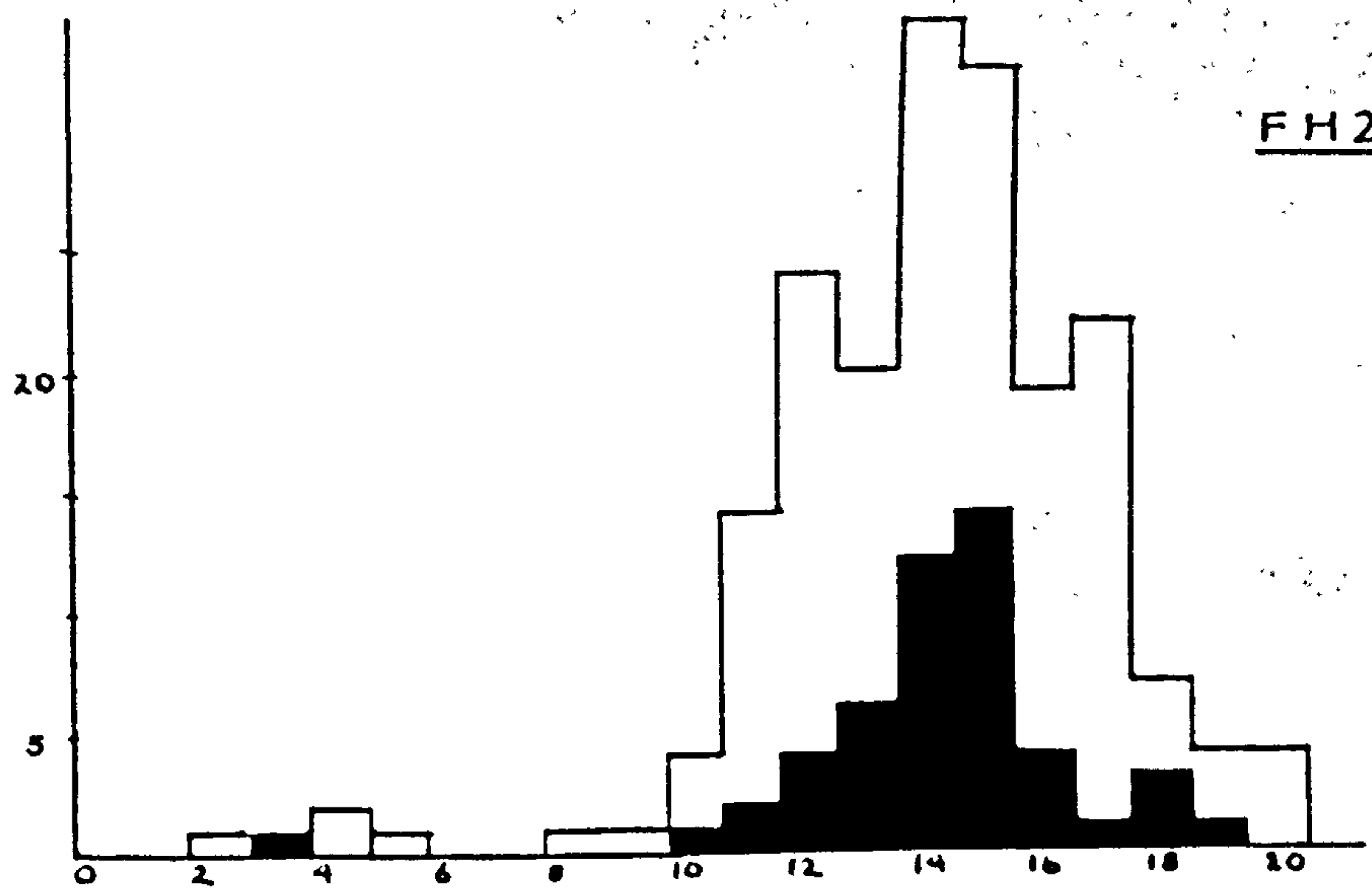


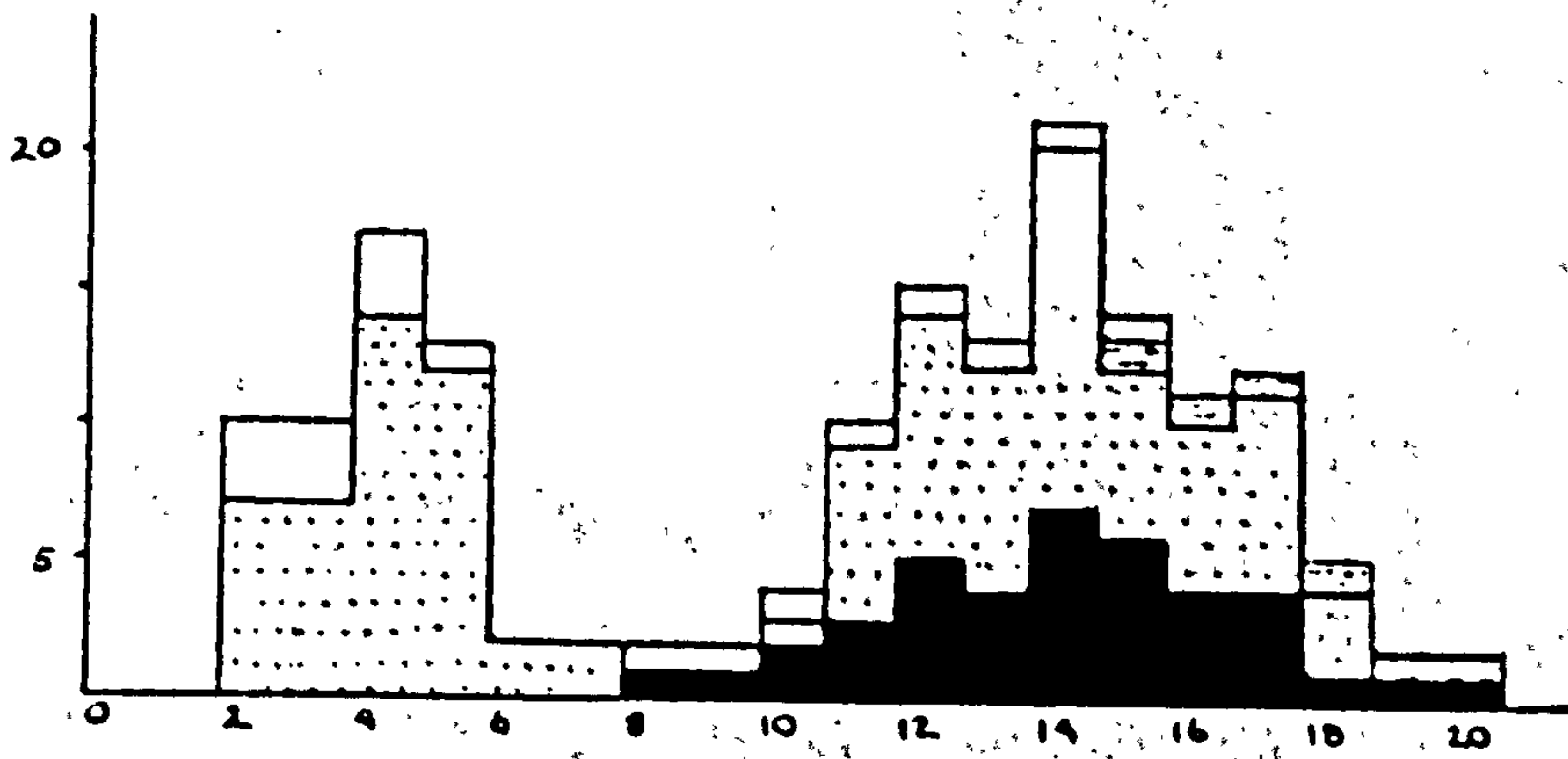
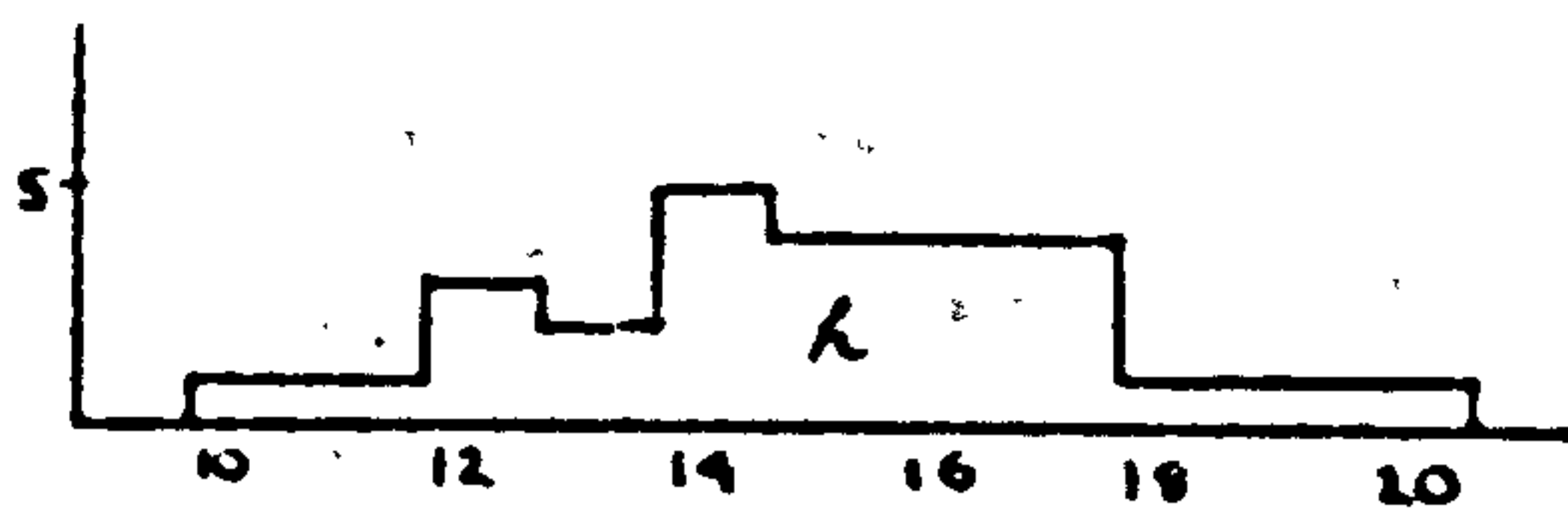
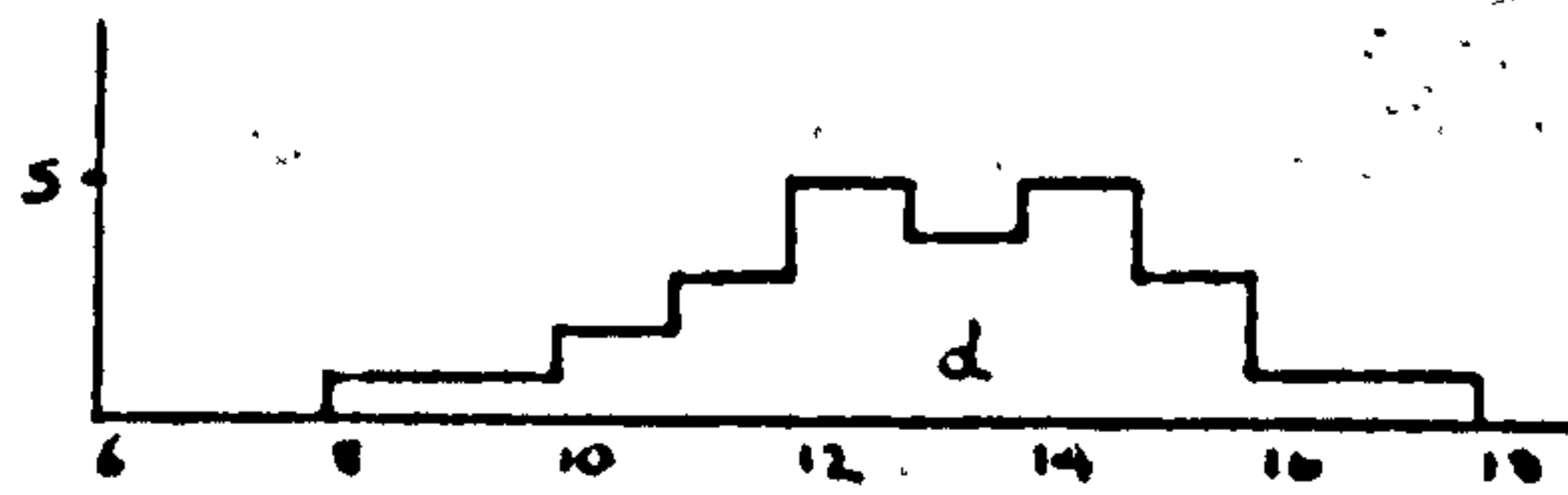
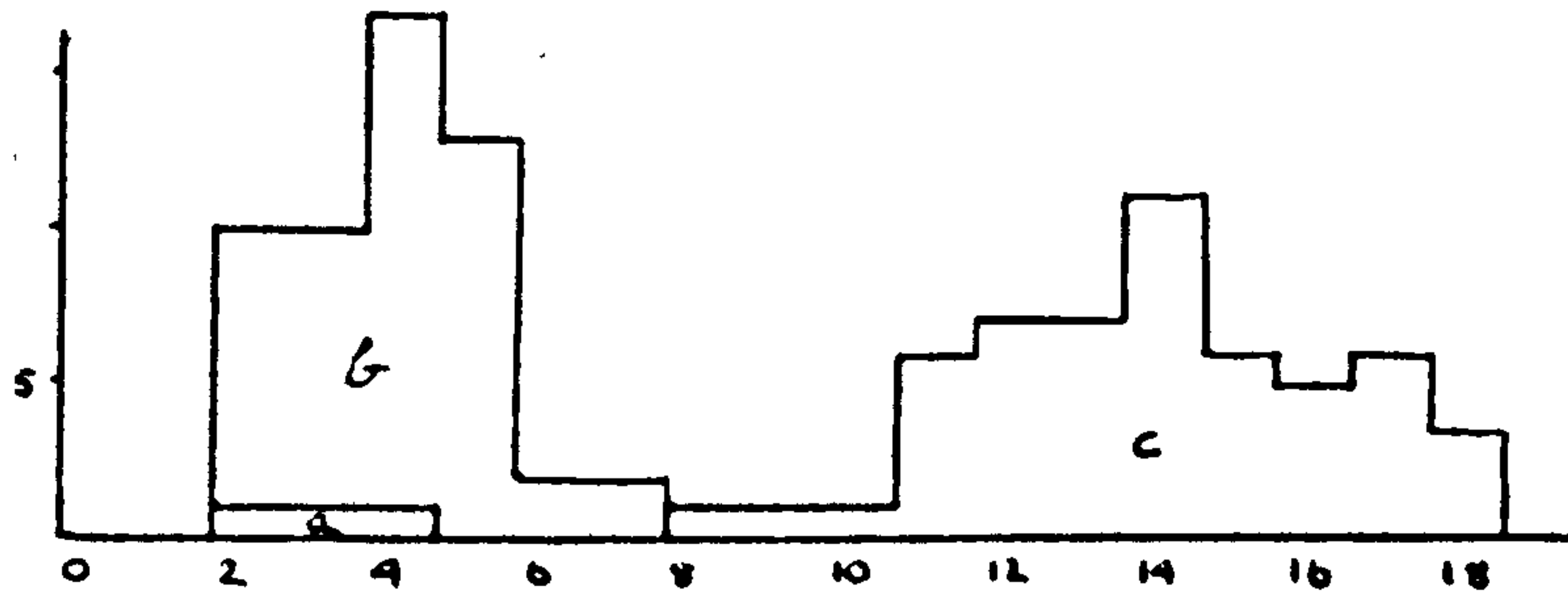


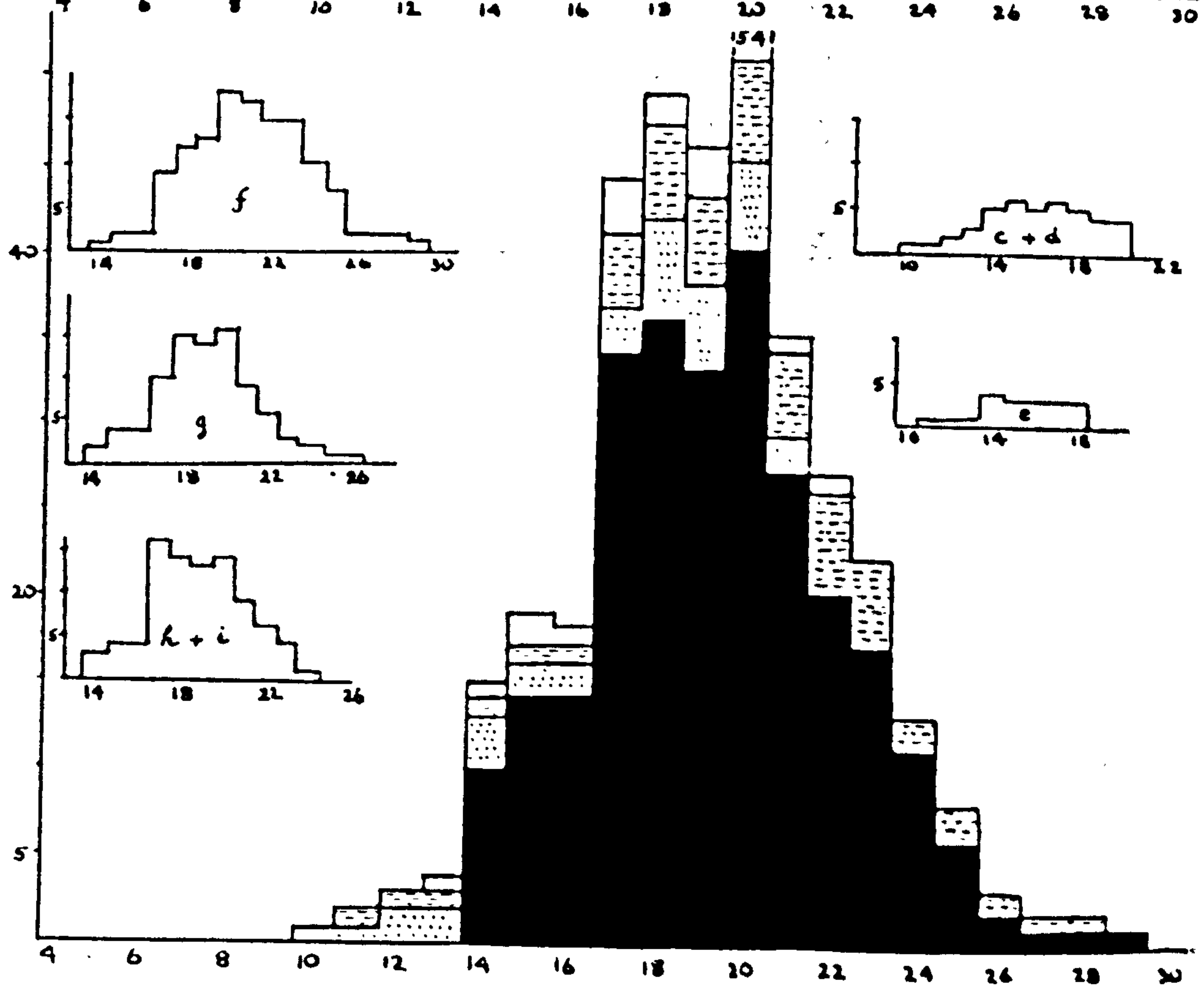
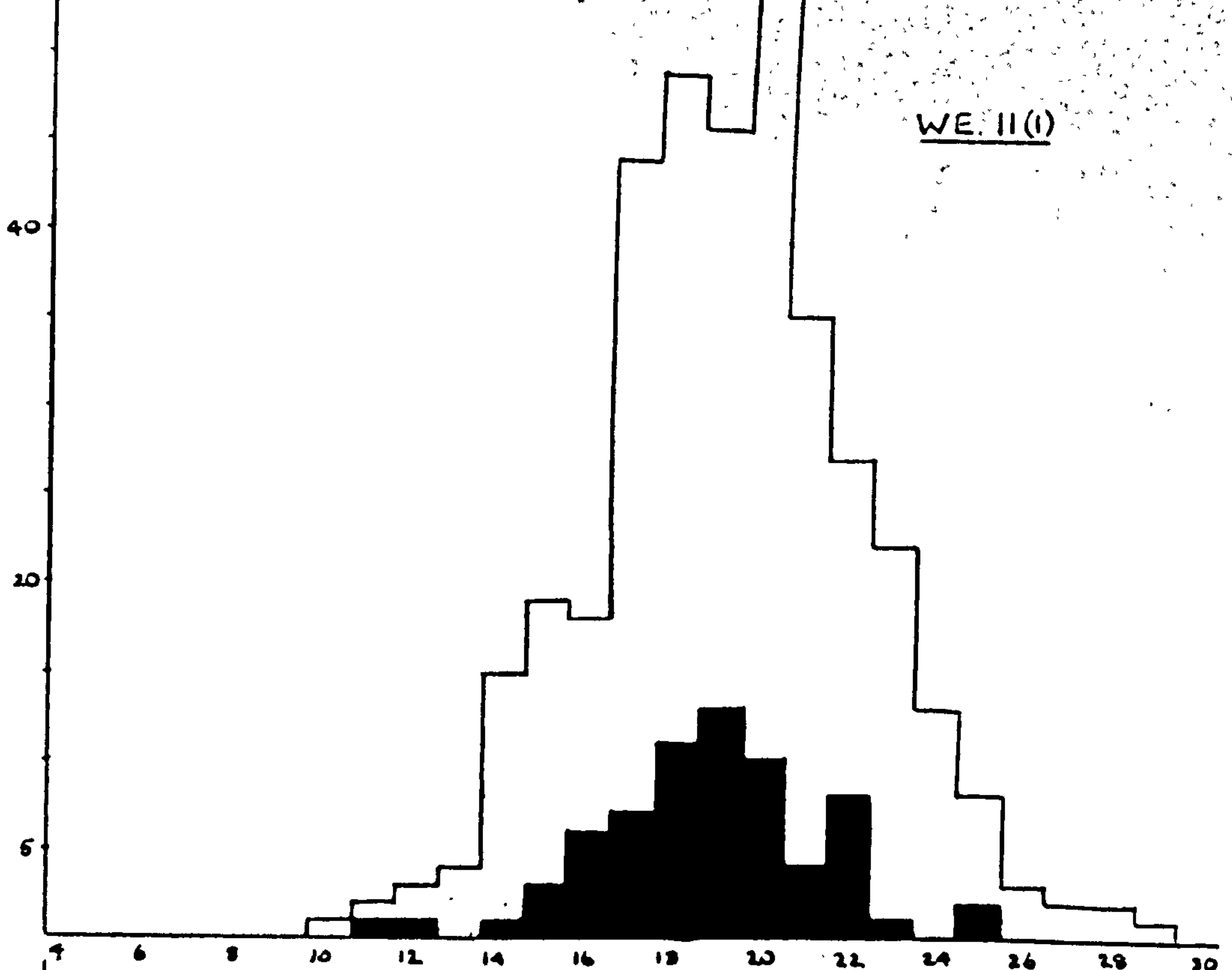
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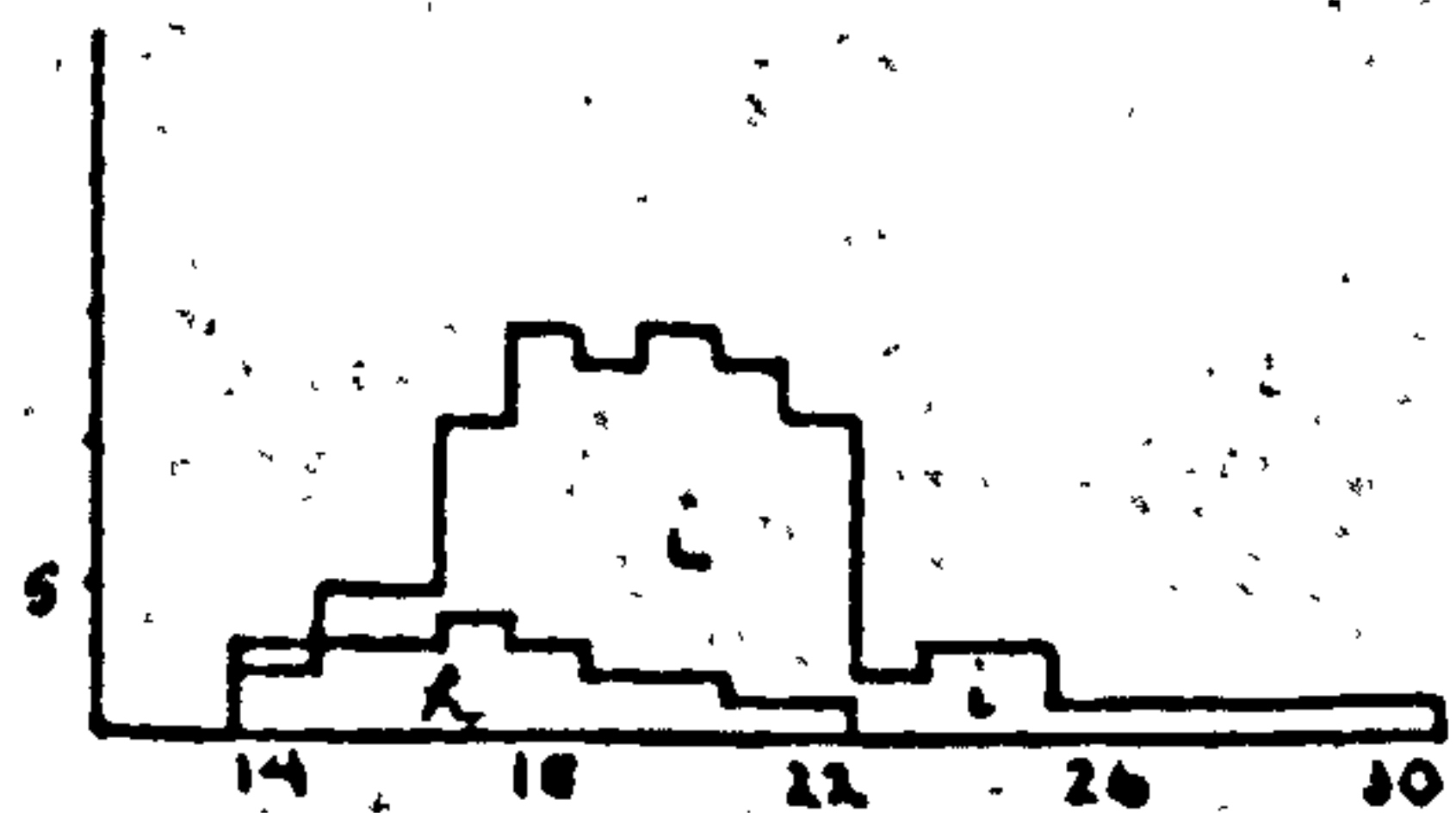
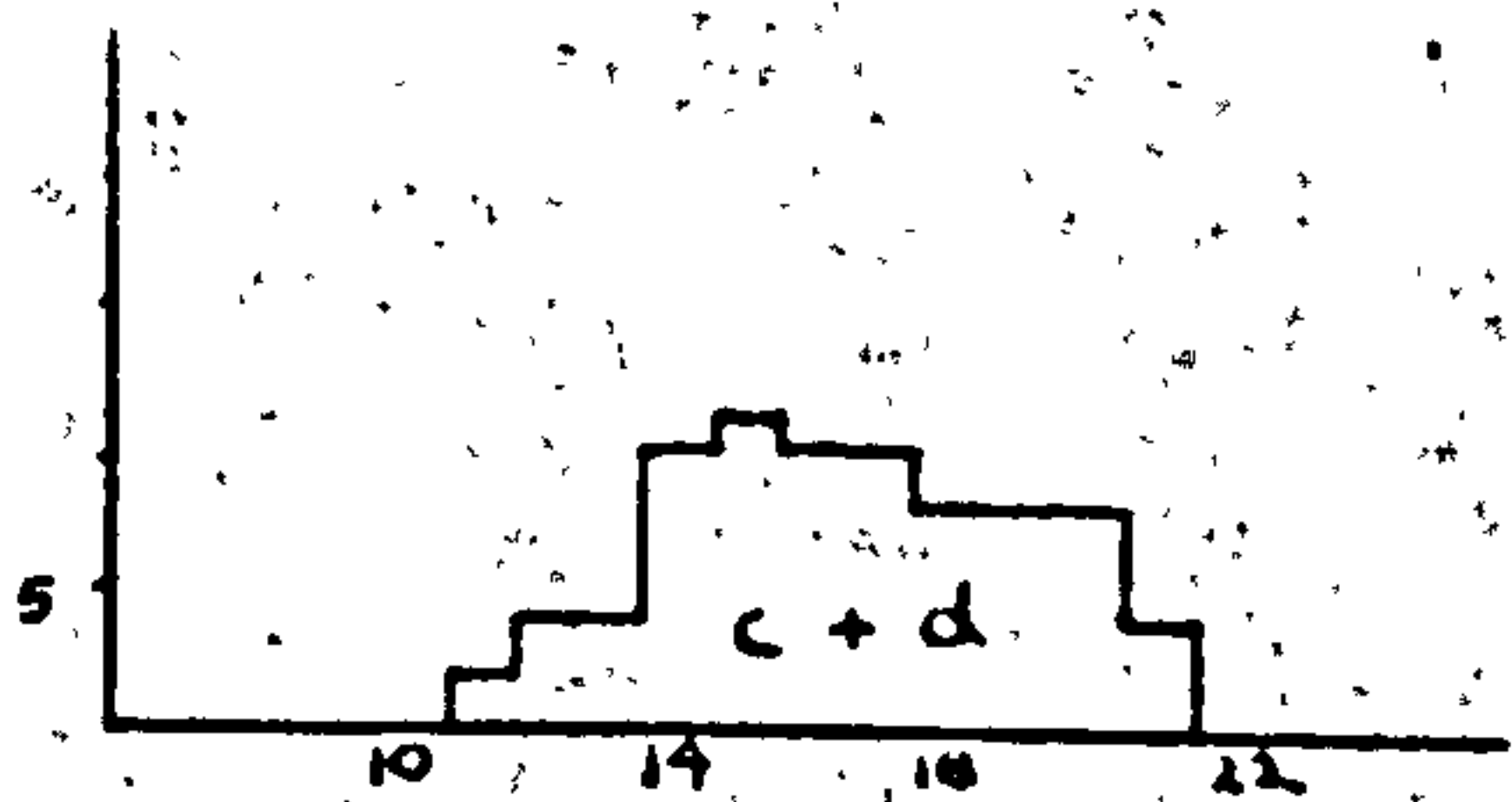
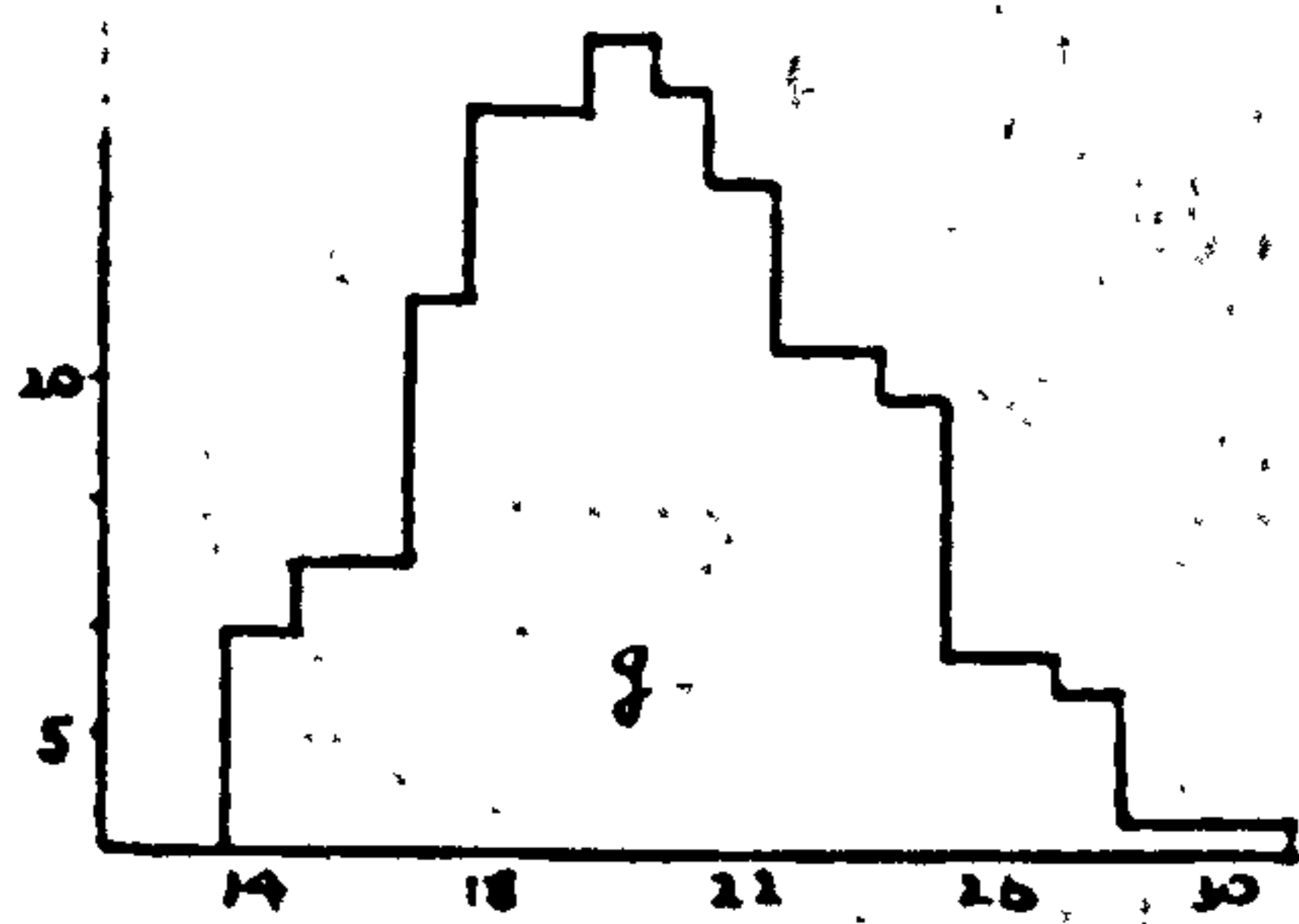
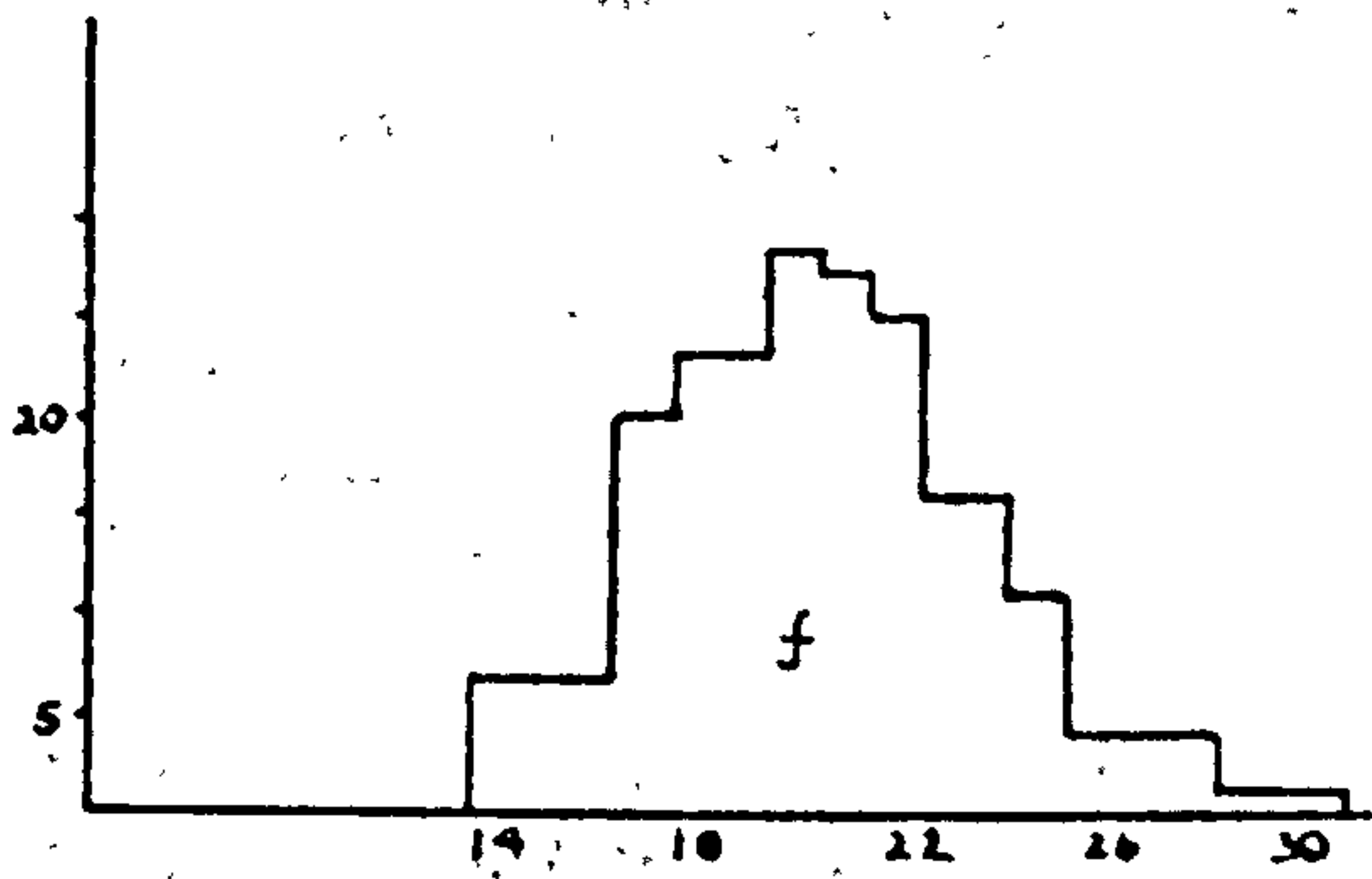
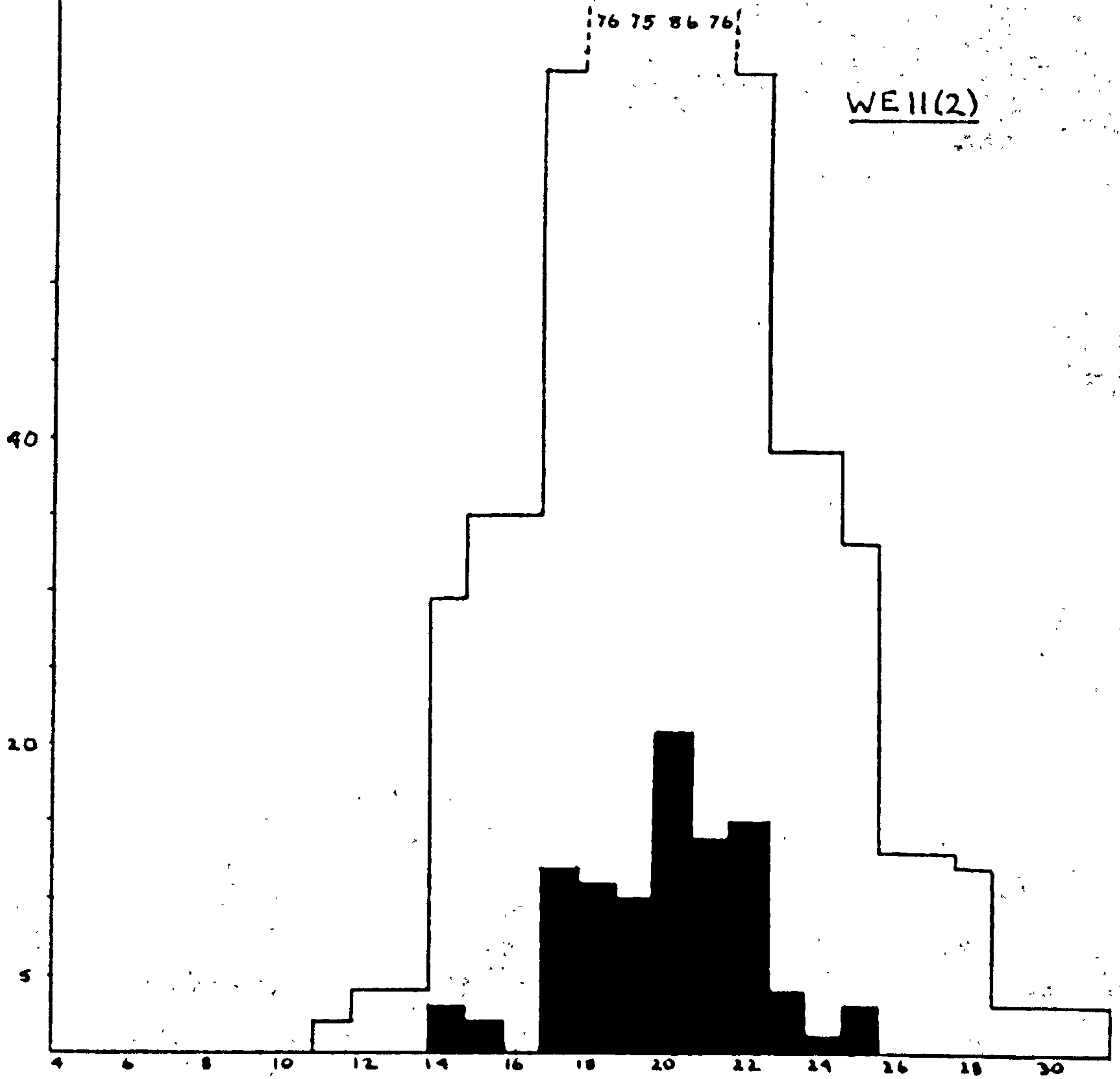


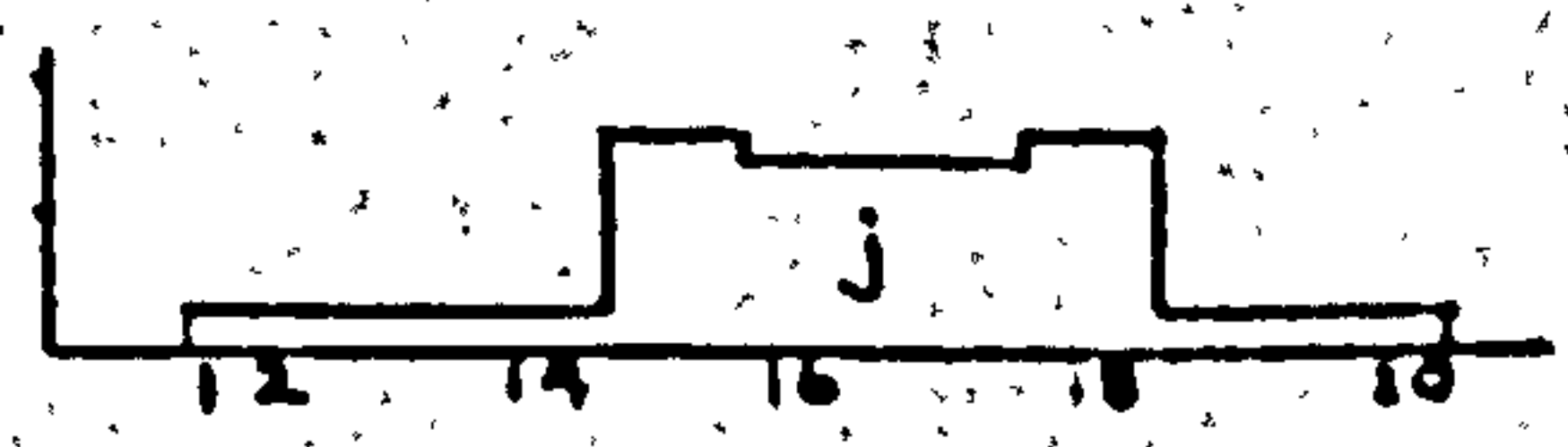
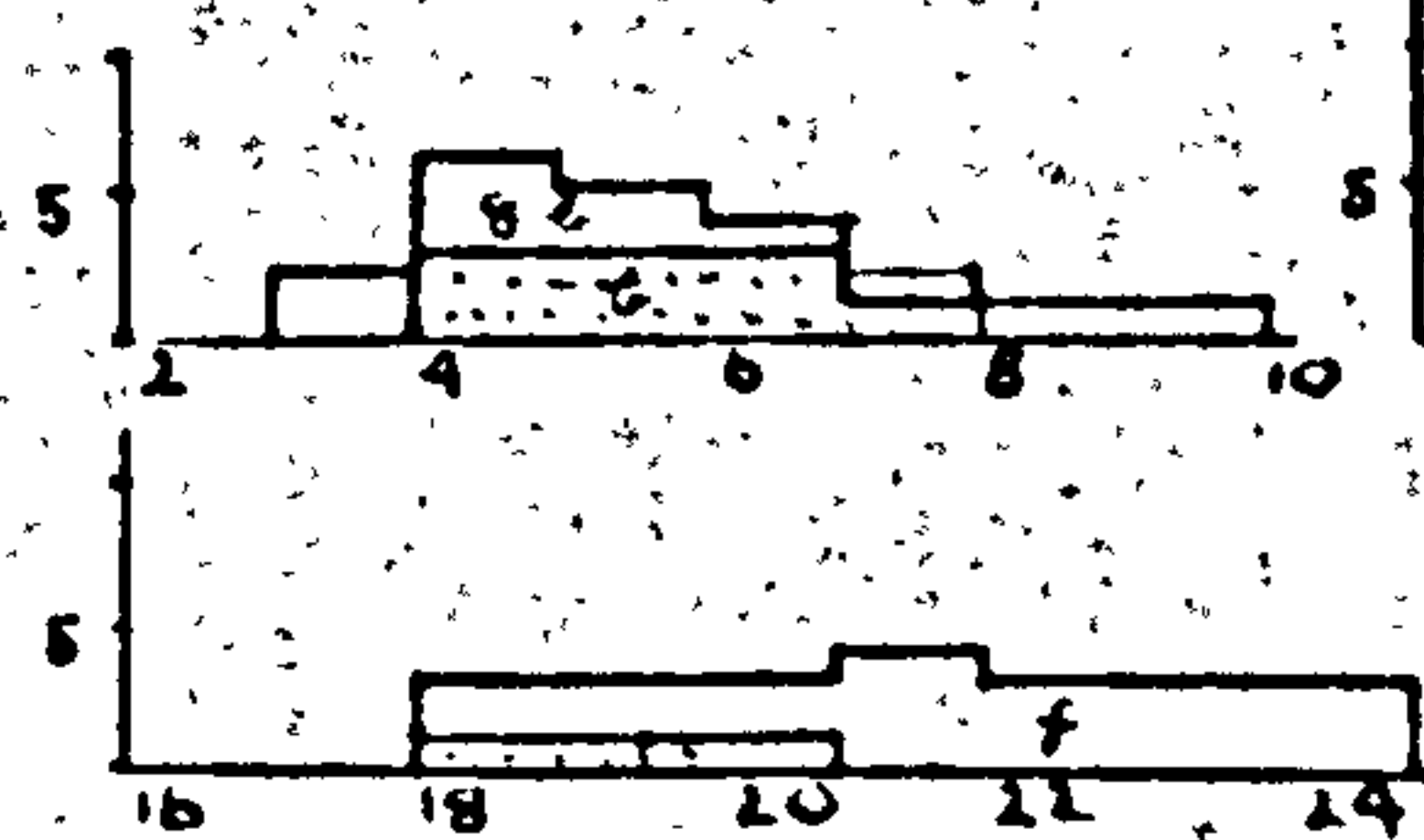
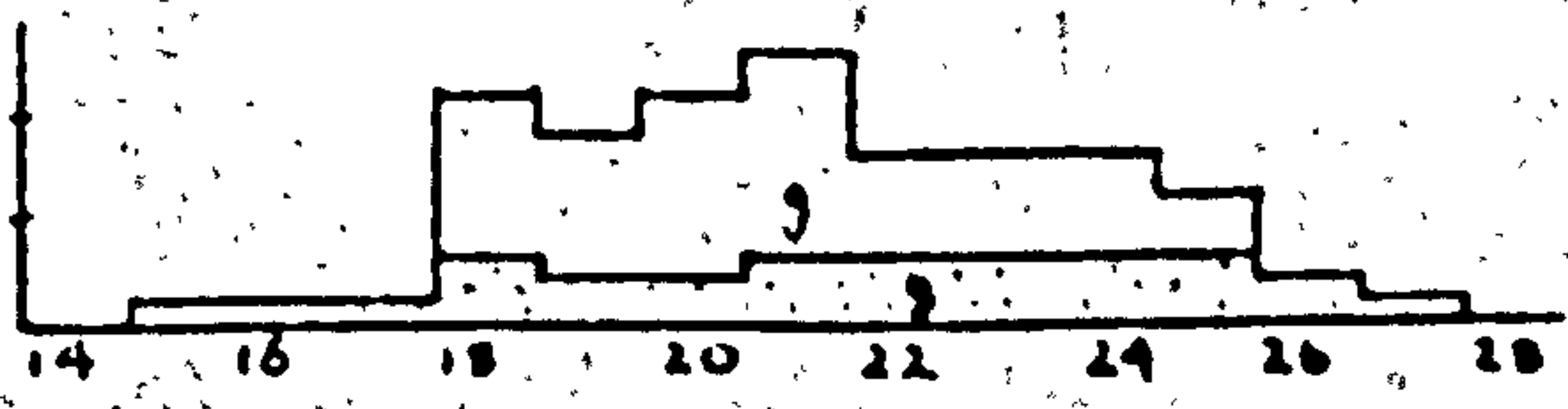
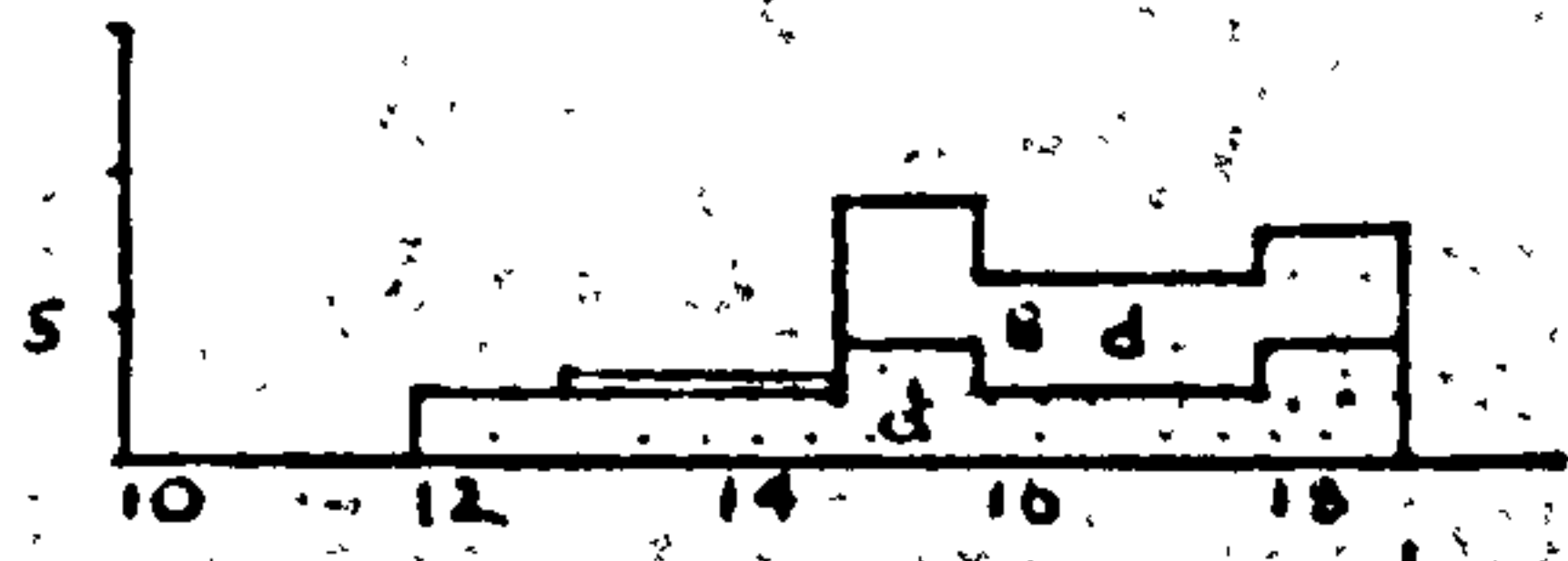
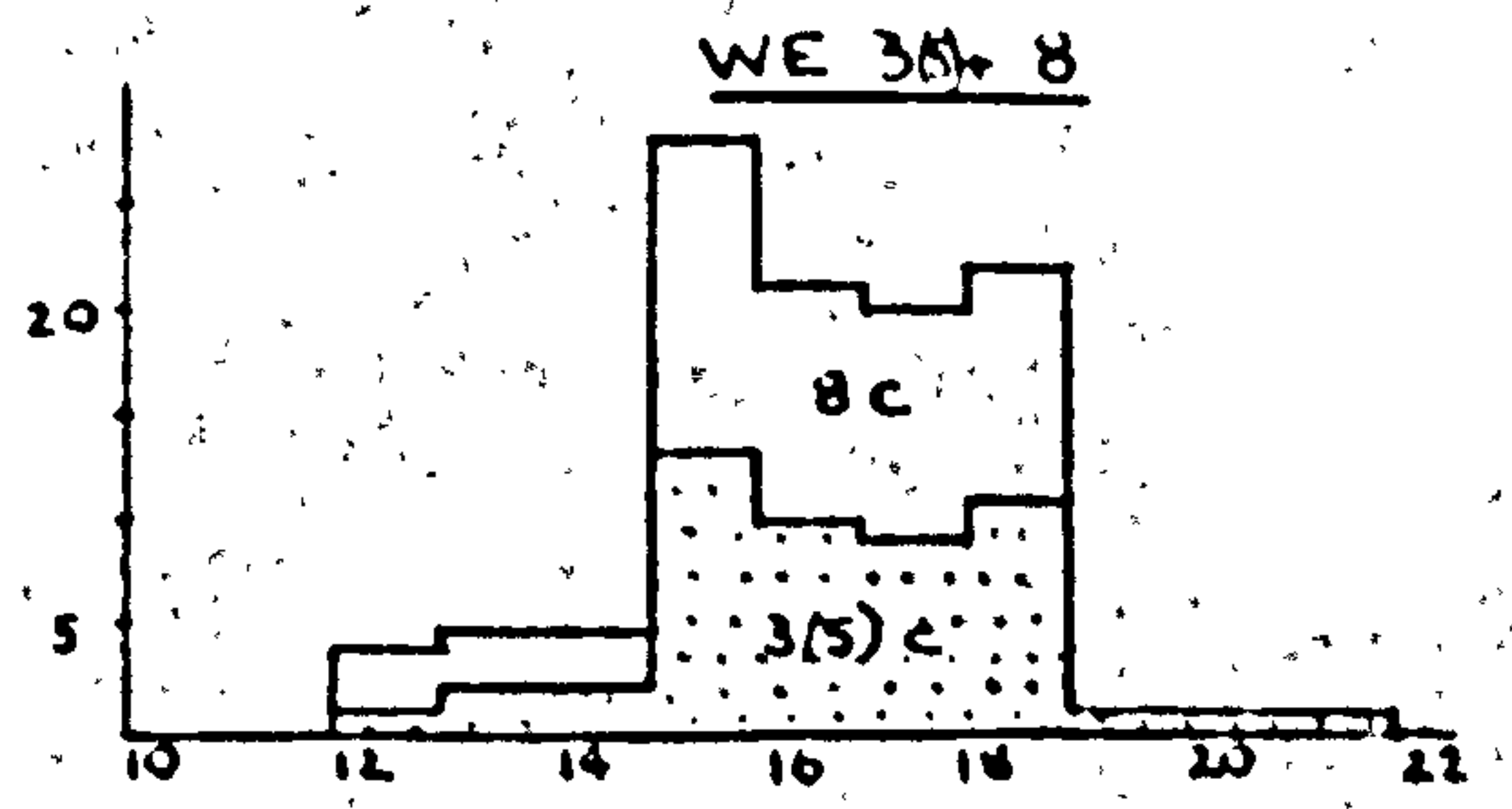
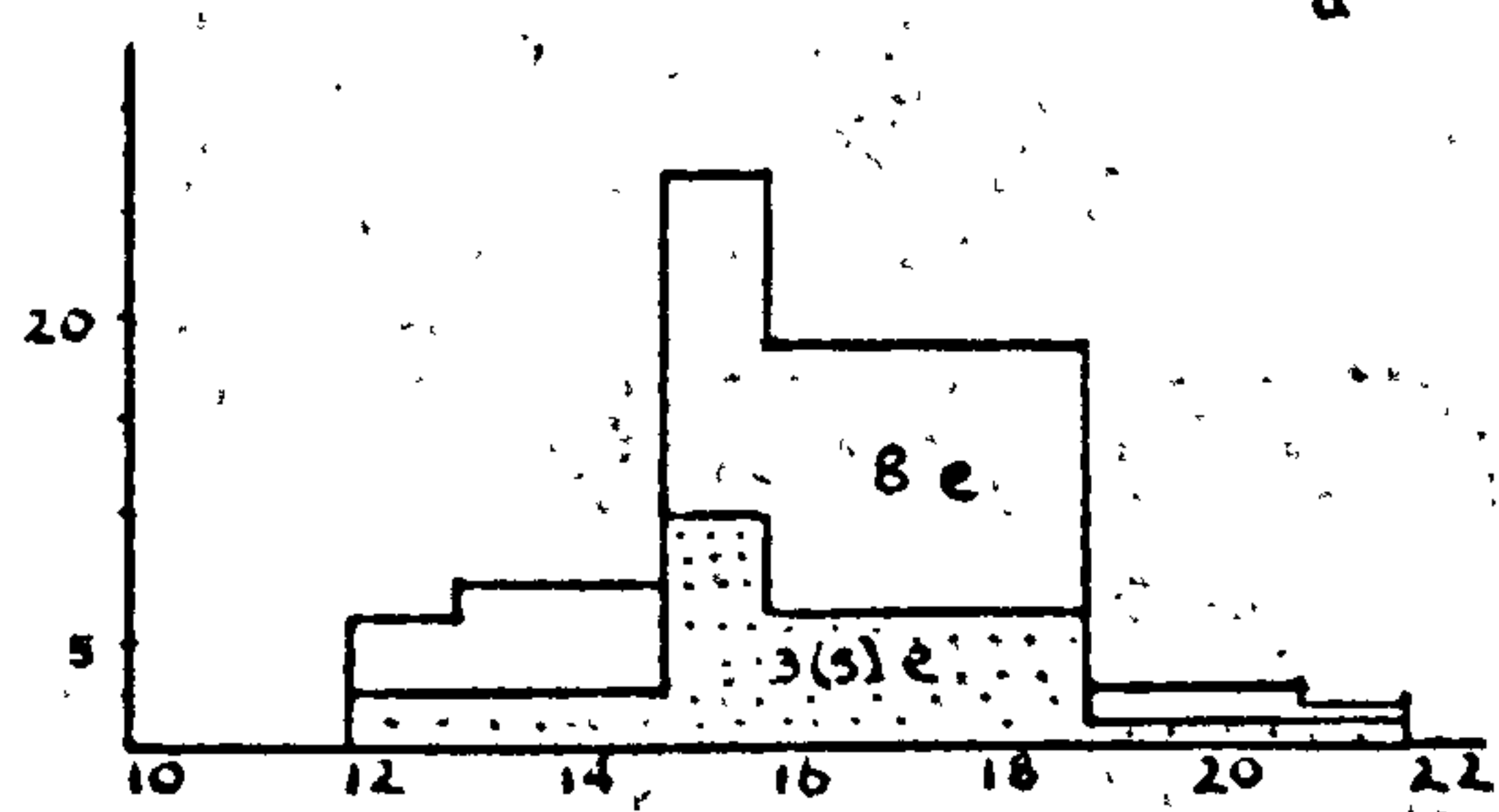
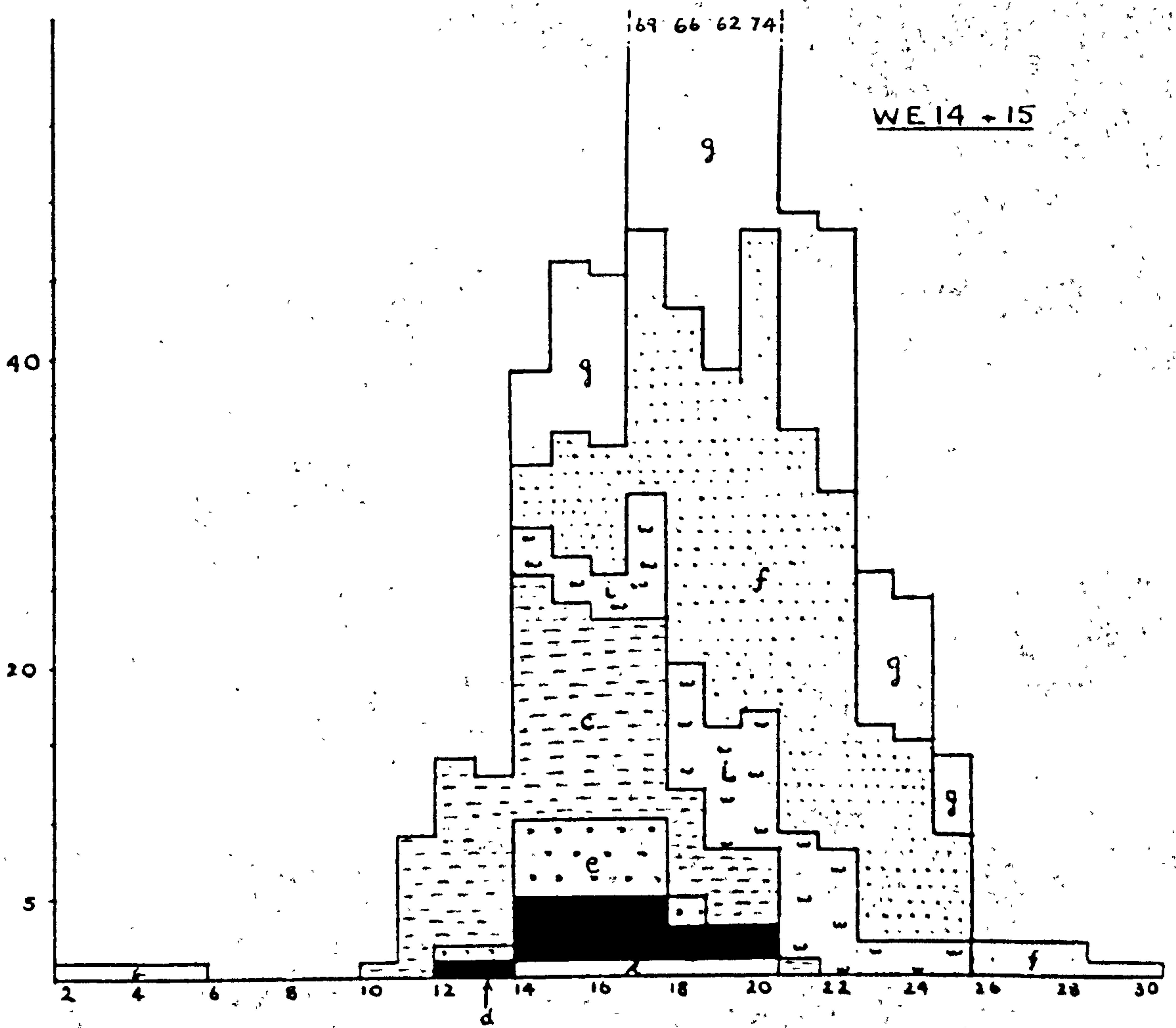
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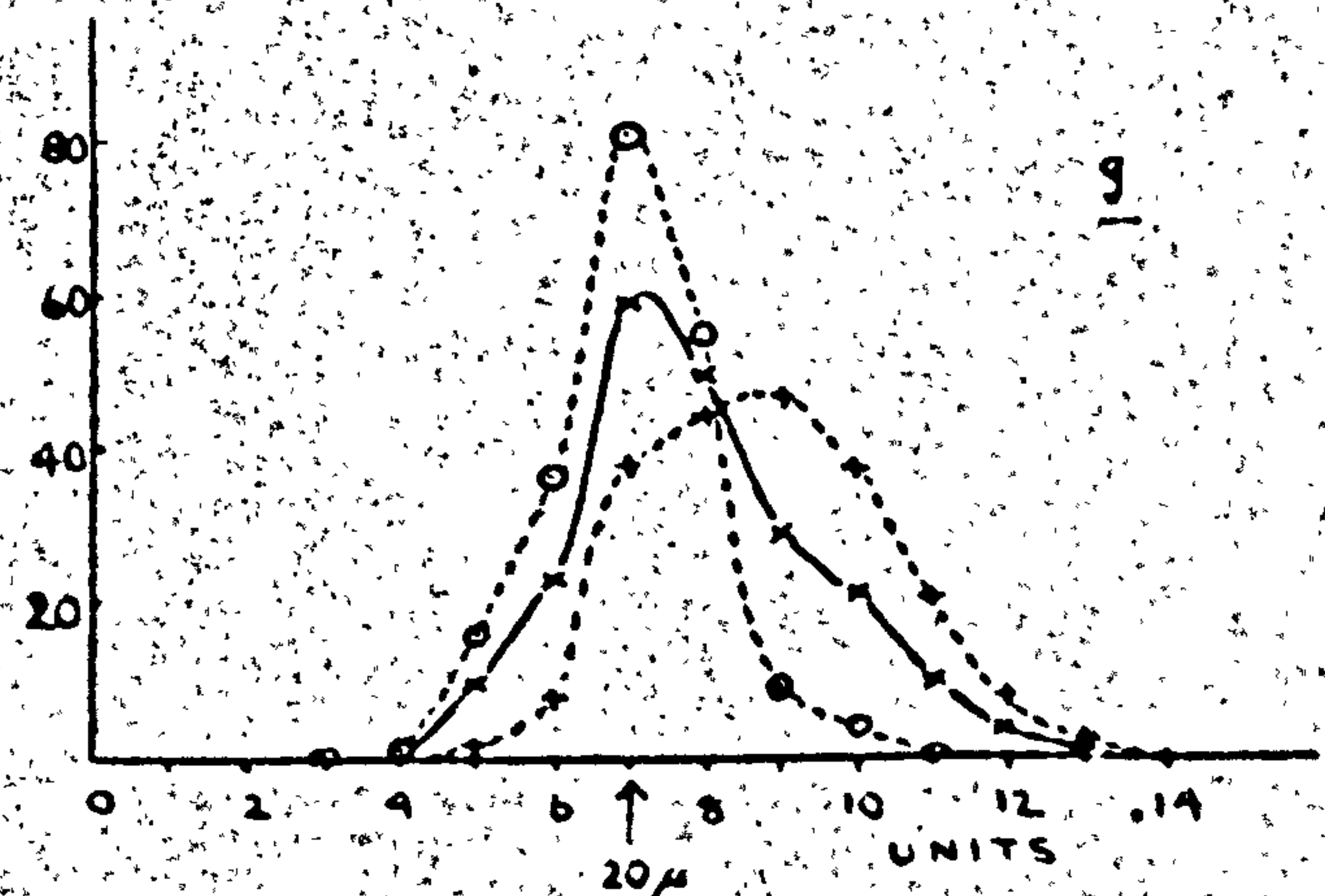
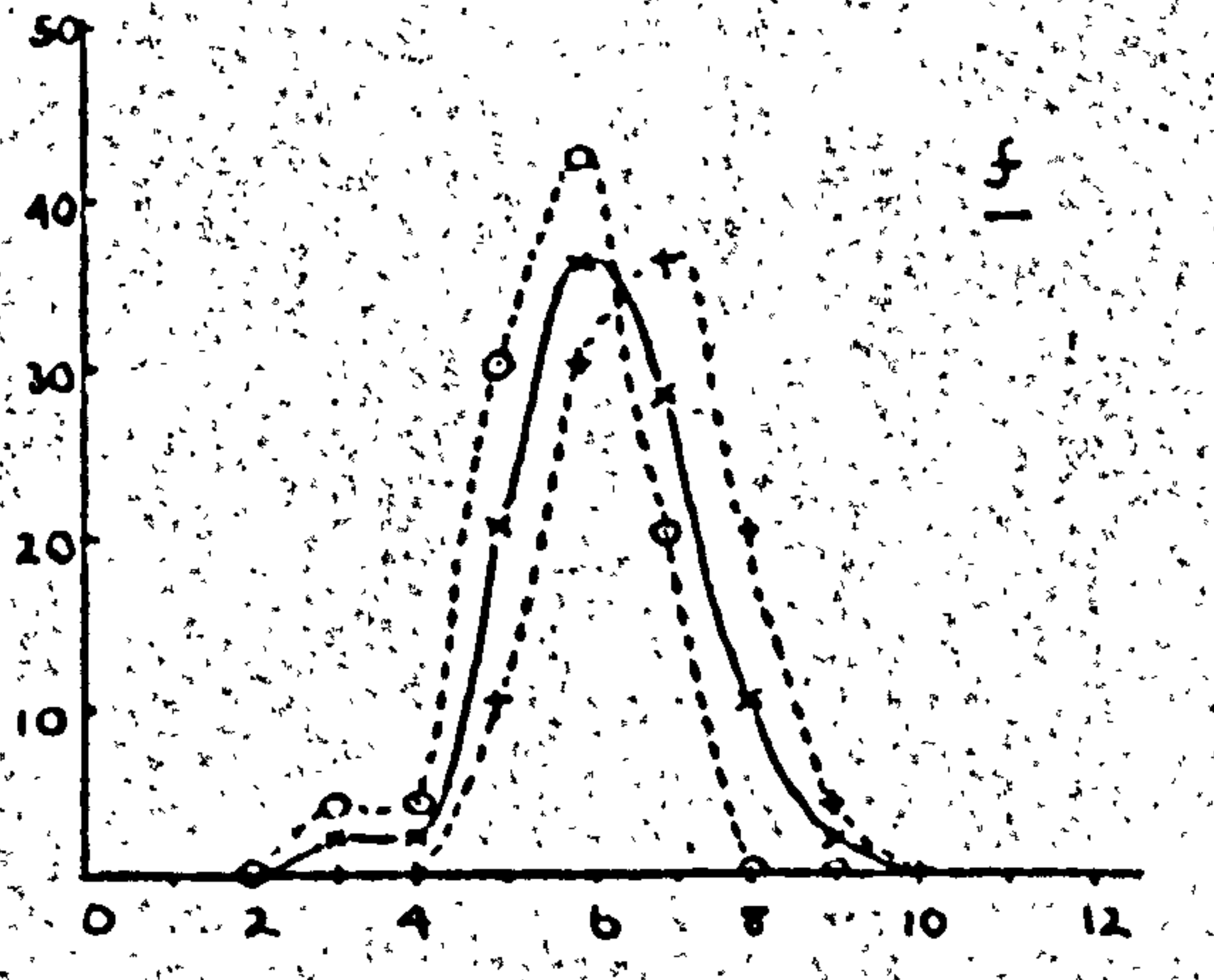
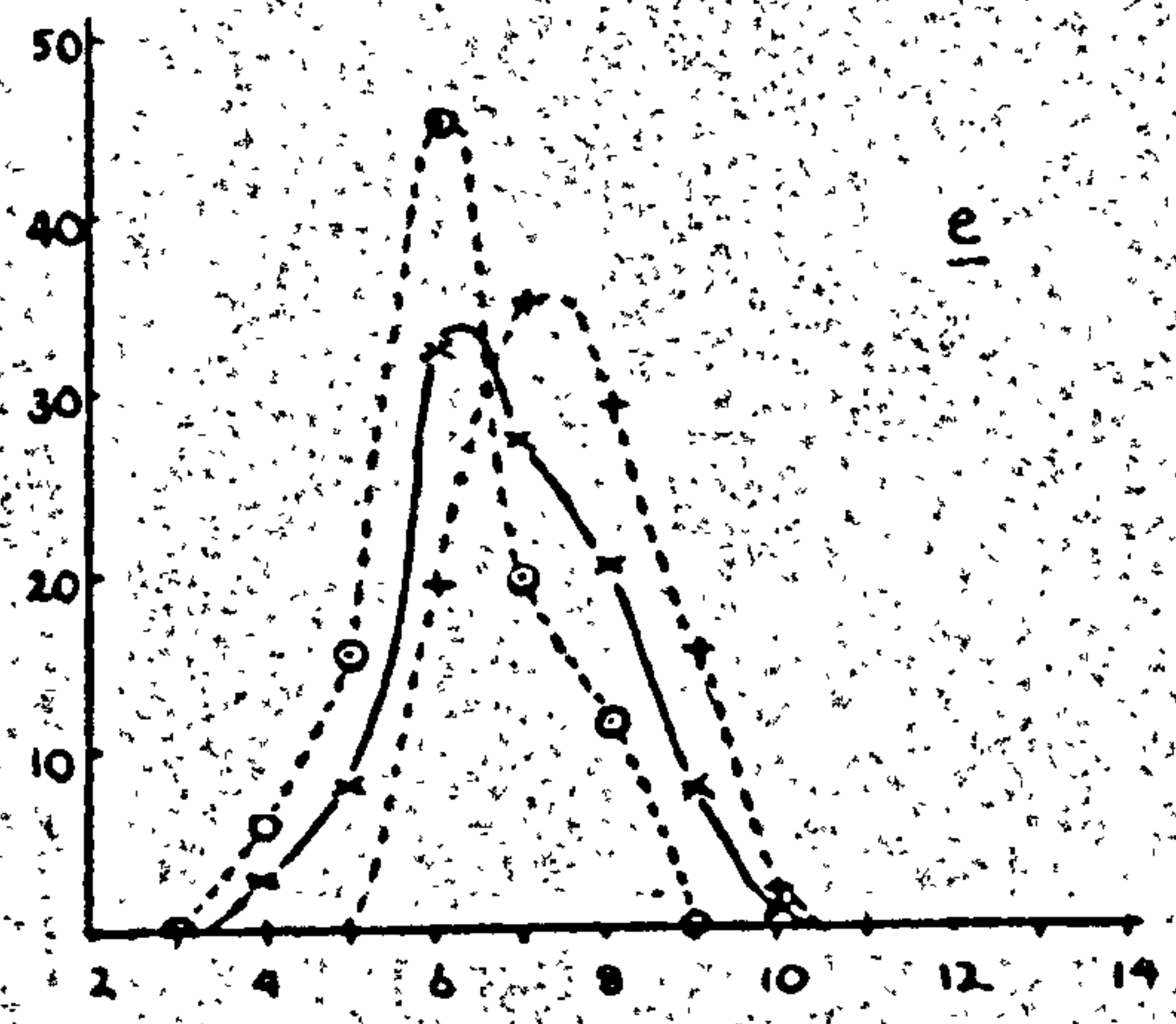
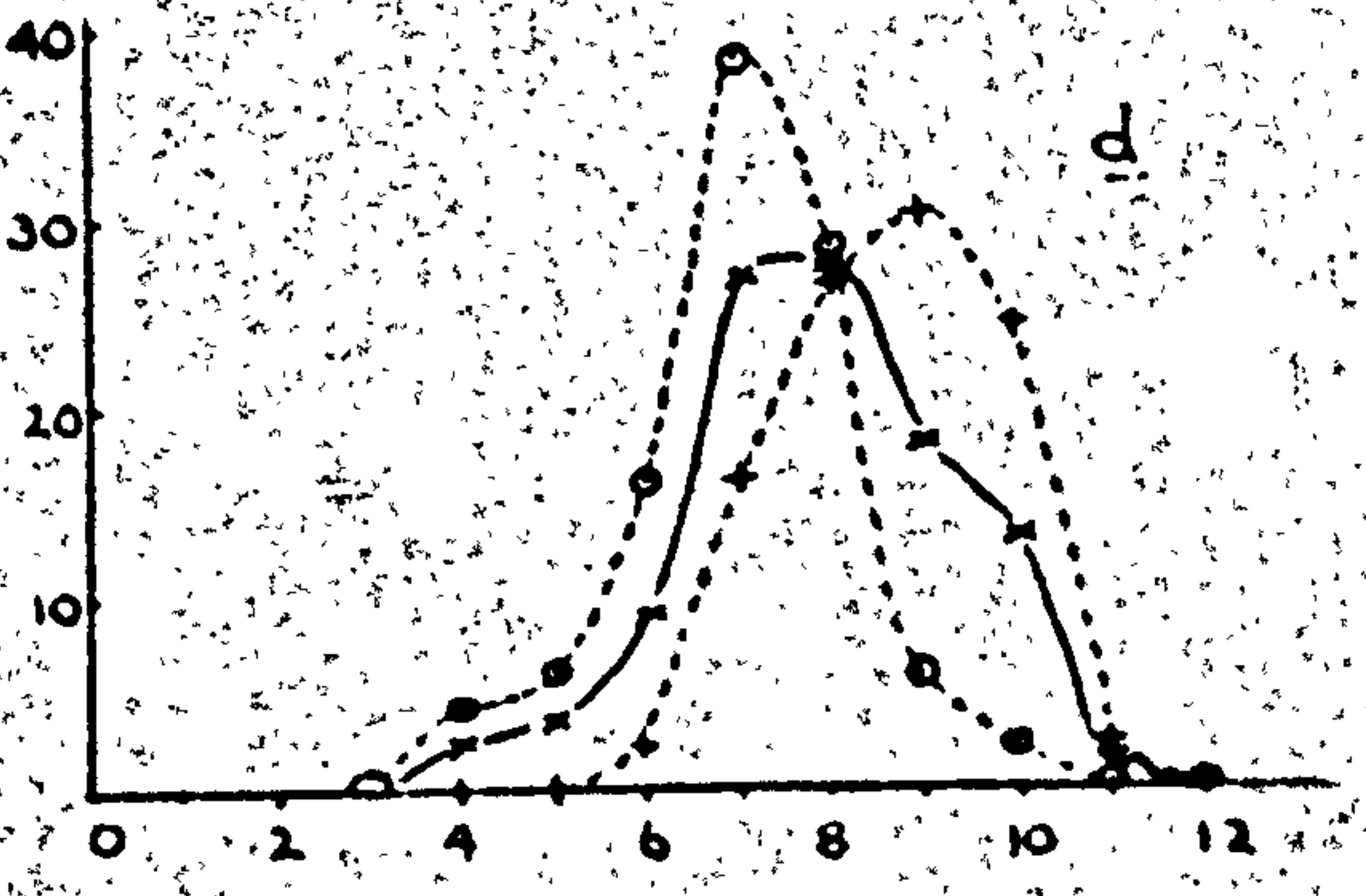
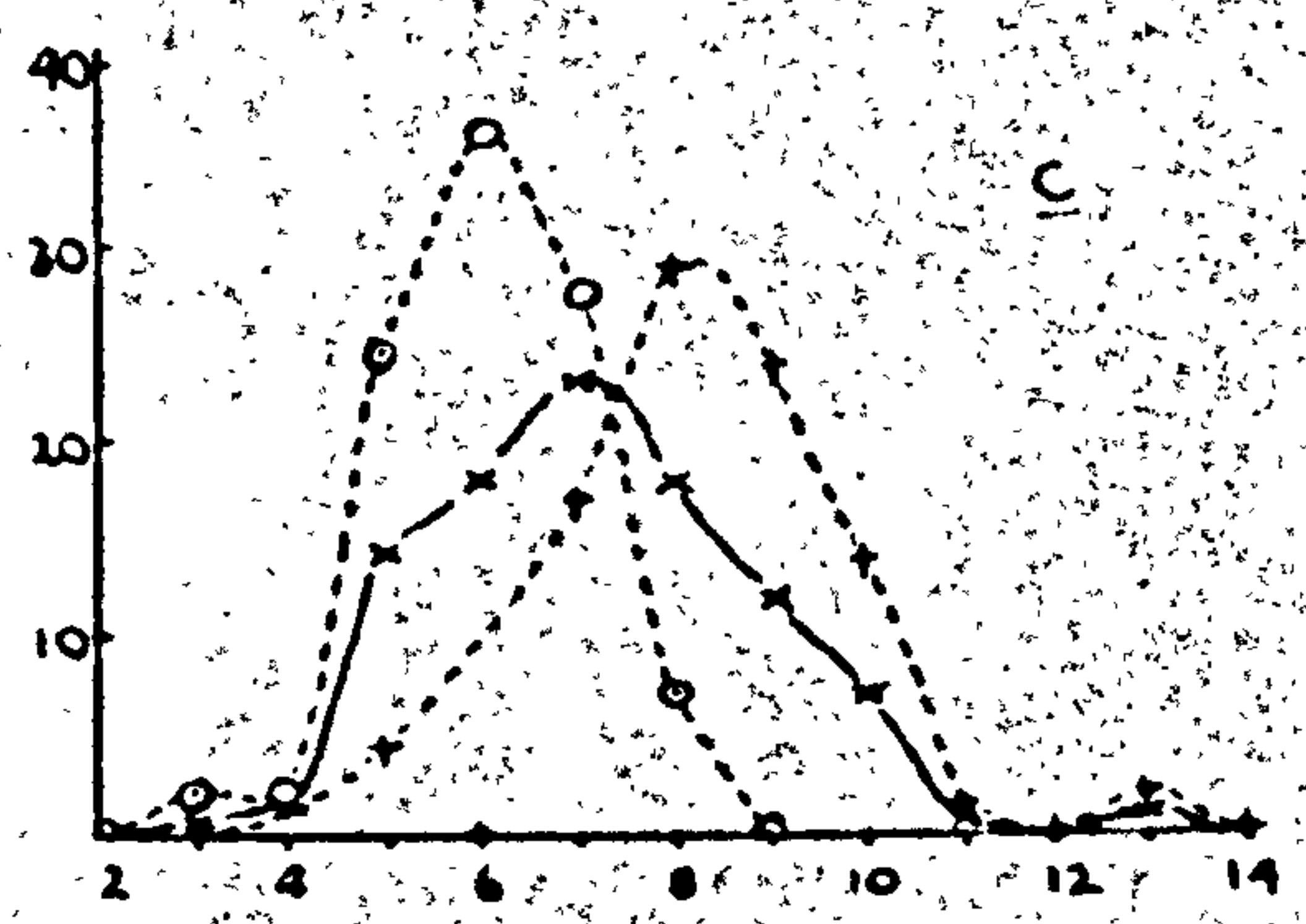
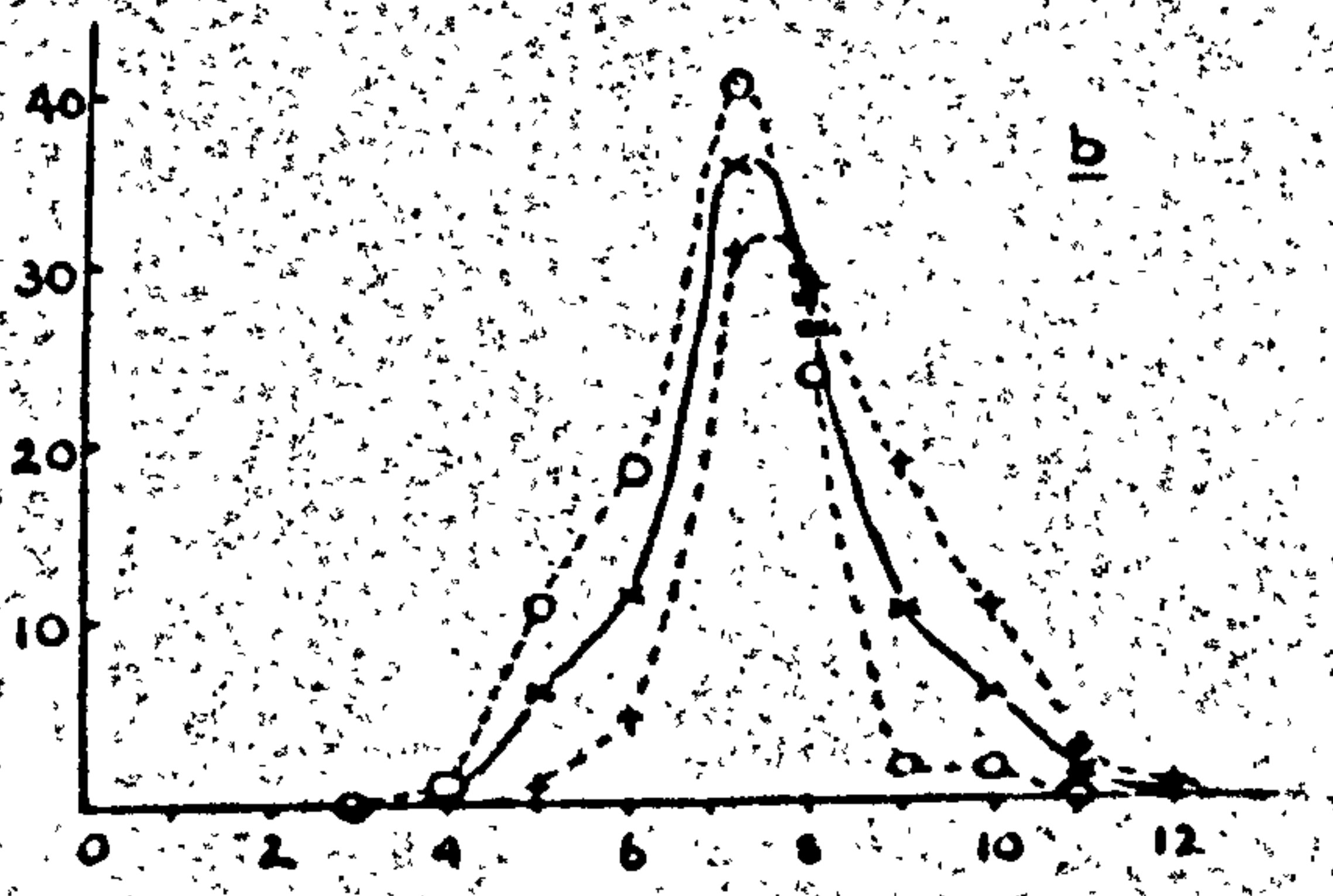
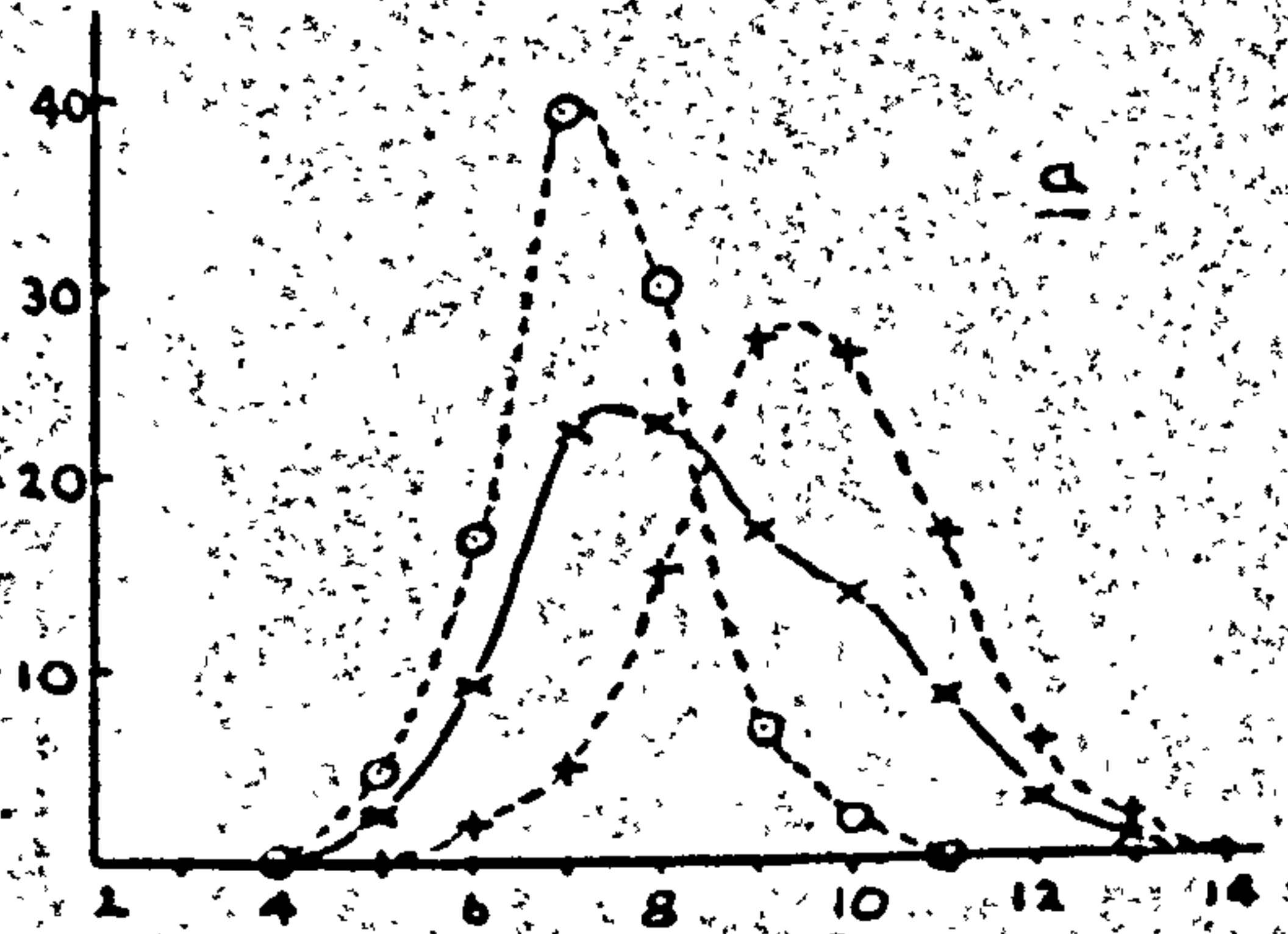




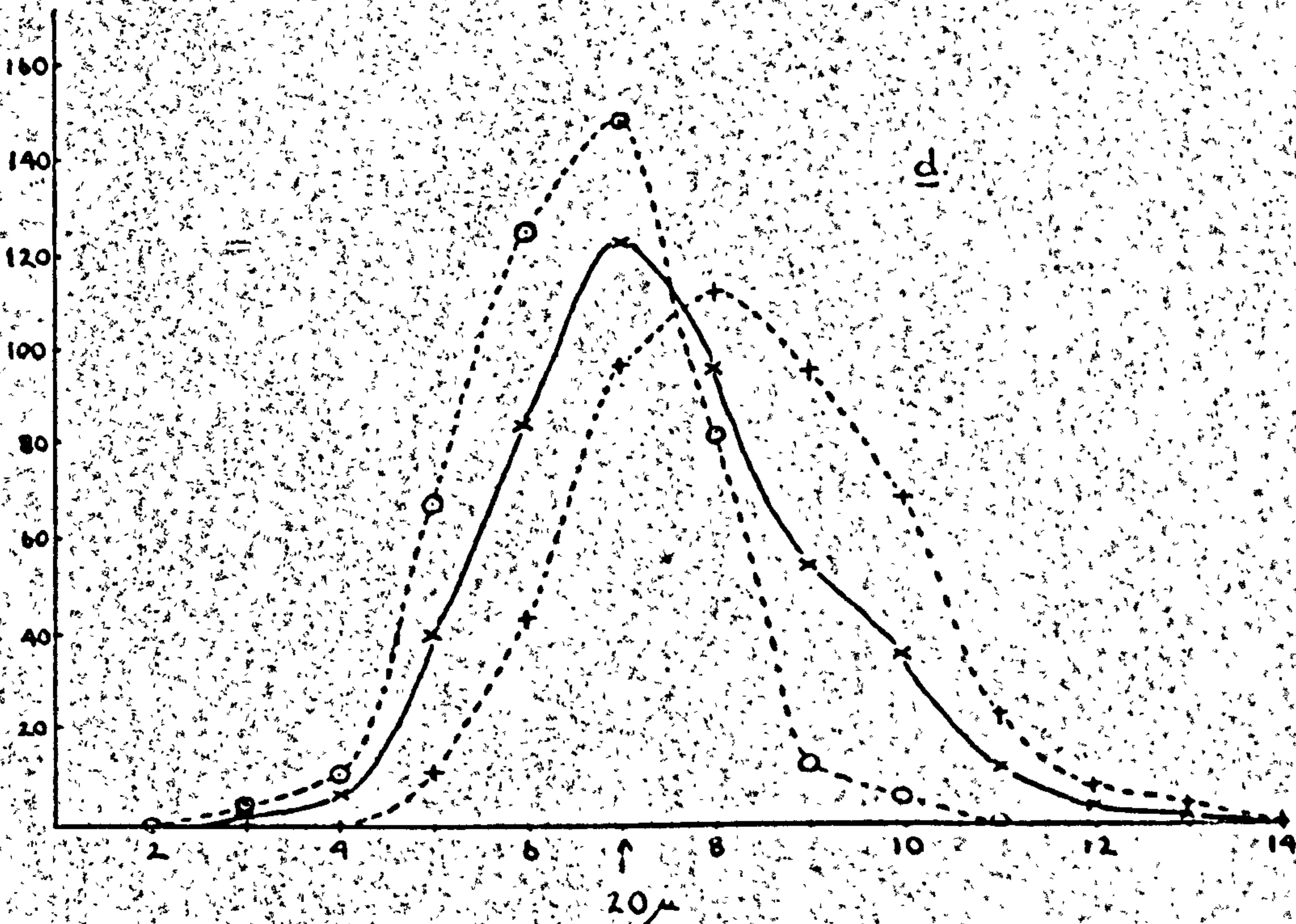
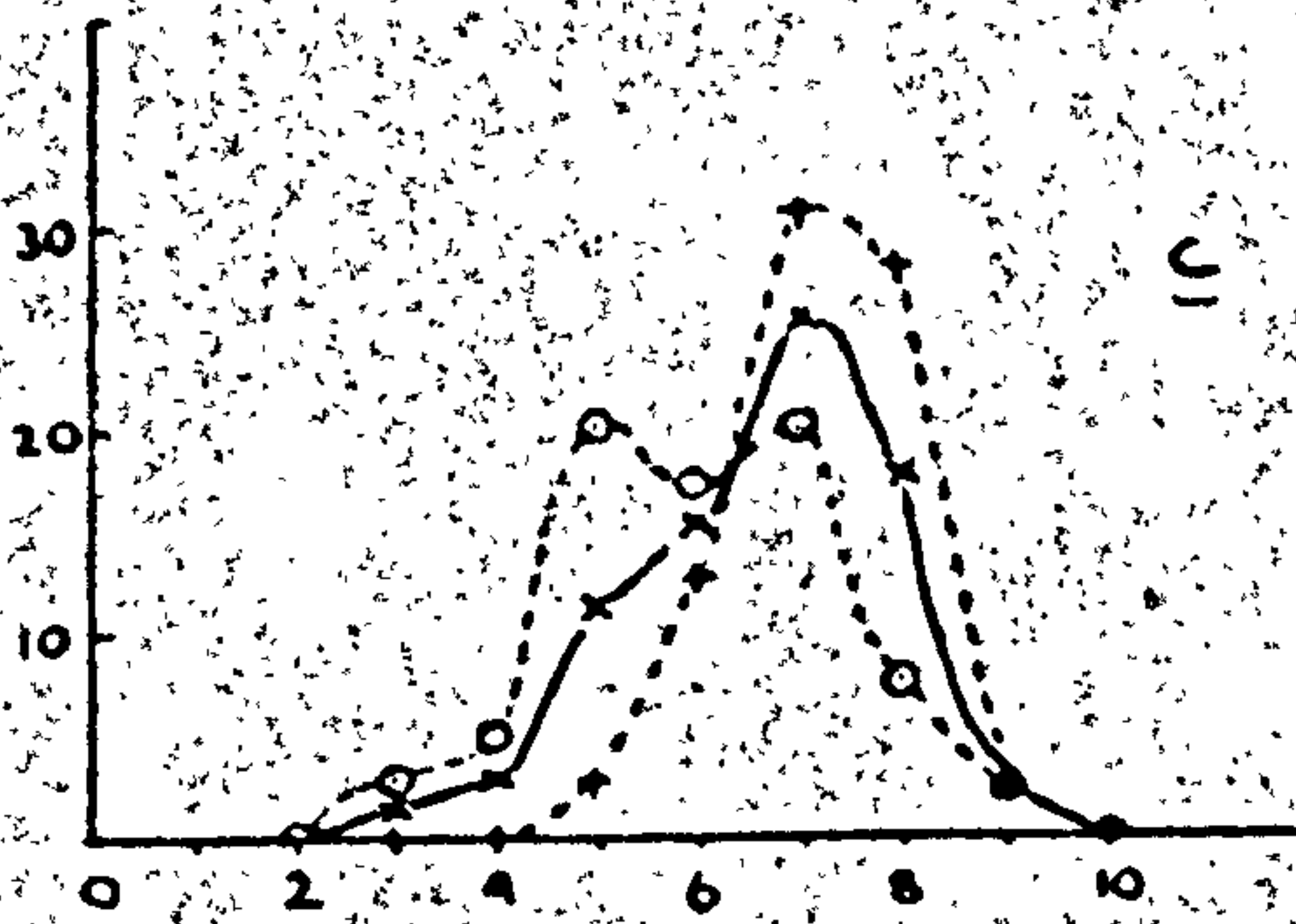
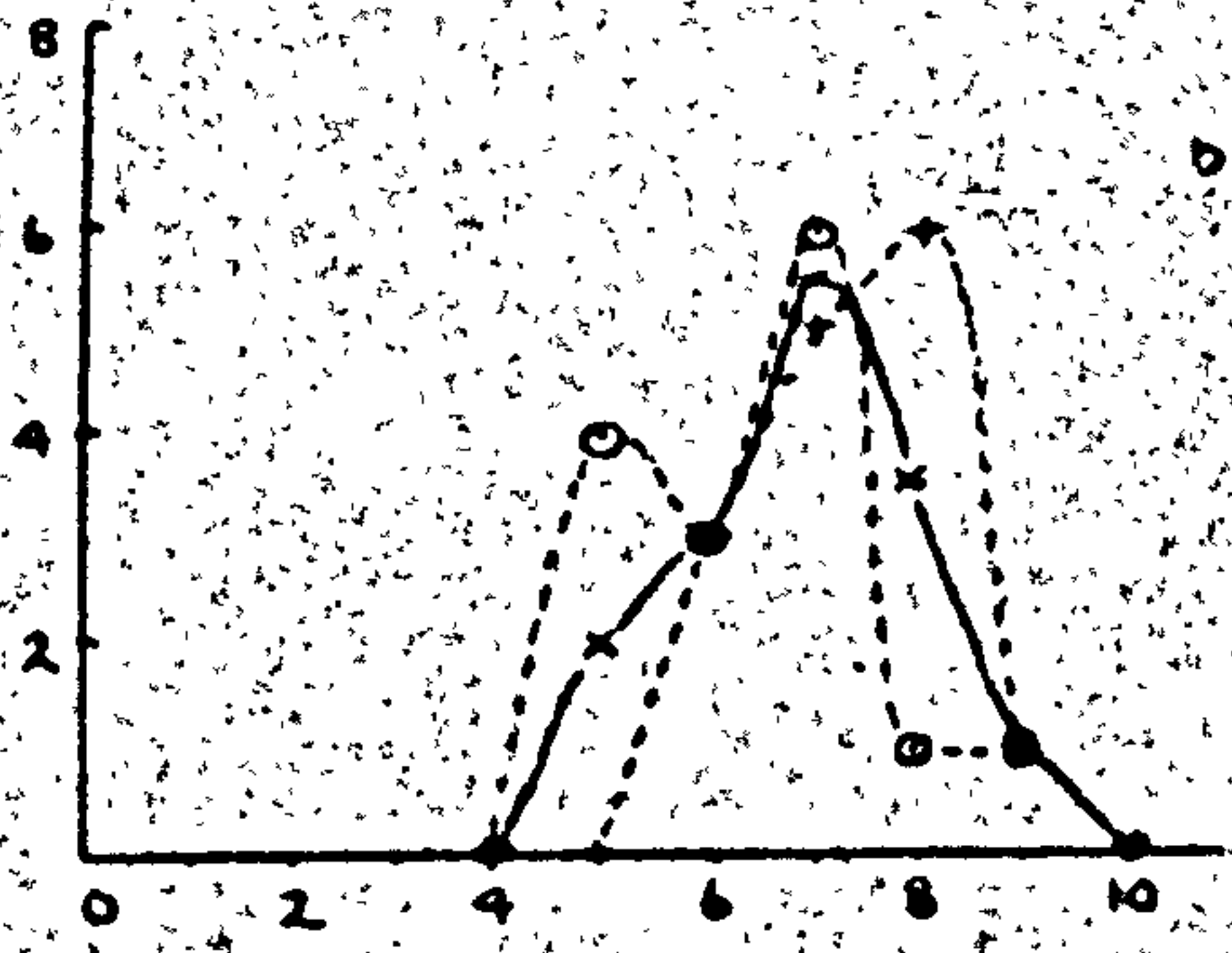
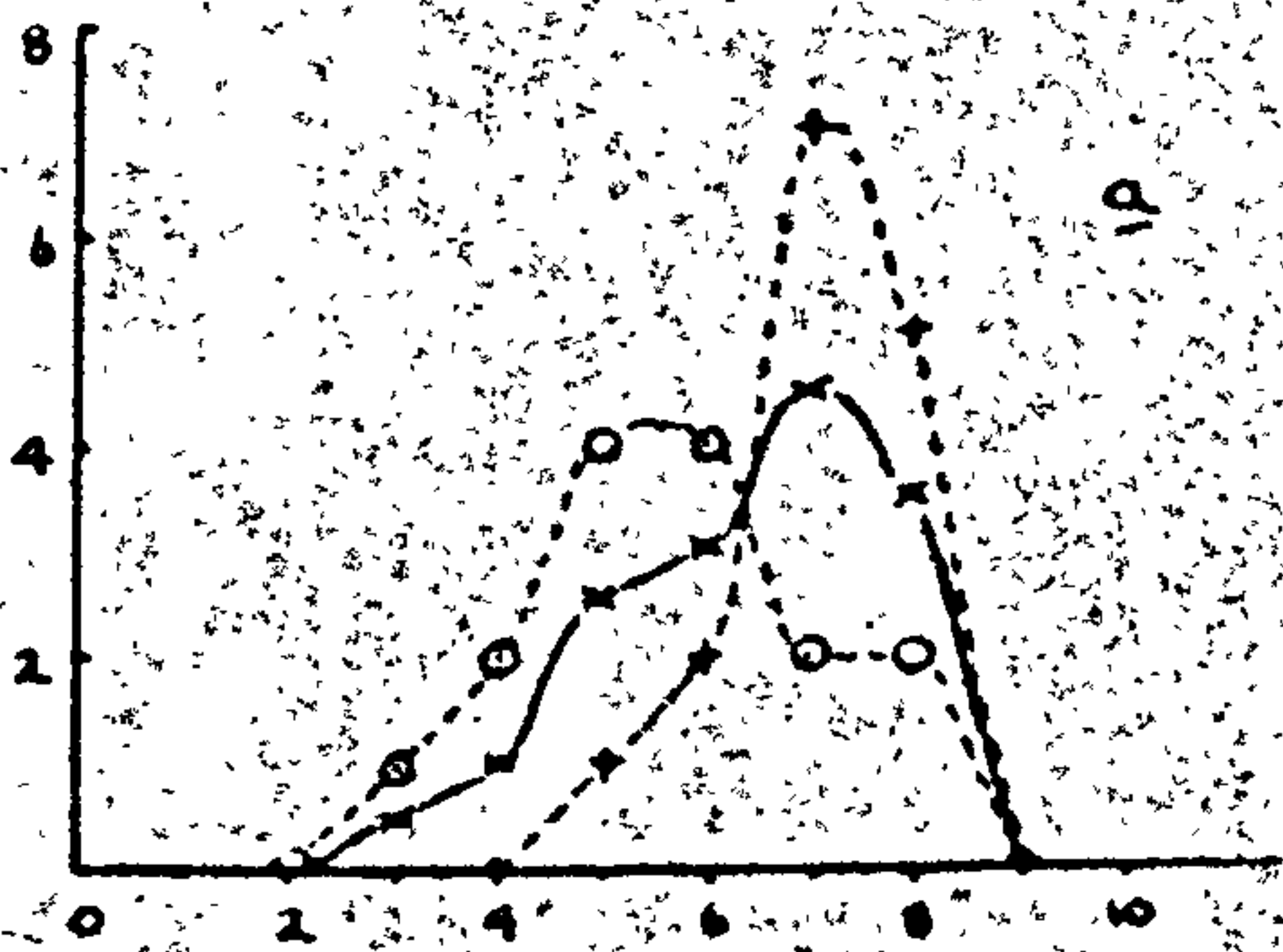








SET A



SET B

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