THE TYPE-SPECIES OF THE GENUS *GIRVANELLA* (CALCAREOUS ALGAE)

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ABSTRACT. Topotype Ordovician material containing *Girvanella problematica* Nicholson and Etheridge has been studied, several species being found to occur together. The genus is redefined and the limits of variation of the type species indicated.

INTRODUCTION

THE genus *Girvanella* was founded by Nicholson and Etheridge (1878) to include aggregations of tiny tubes with granular walls occurring in the 'Craighead Limestone' (later called the Stinchar Limestone) of Tramitchell, near Girvan, south Scotland. These beds are of Upper Ordovician age. One small illustration was given, reproduced as Pl. 5, fig. 1, of the present paper. The original generic diagnosis runs: 'Microscopic tubuli, with arenaceous or calcareous (?) walls, flexuous or contorted, circular in section, forming loosely compacted masses. The tubes apparently simple cylinders, without perforations in their sides, and destitute of internal partitions or other structures of a similar kind.' One species, *G. problematica*, was established 'for convenience' sake'. The authors, after seeking the advice of H. B. Brady, ascribed the genus to the Foraminifera.

It was soon found that similar forms occurred at other horizons. Wethered (1889, 1890) described new species from the Silurian, Carboniferous, and Jurassic. Seely (1885) and Bornemann (1886) erected the genera *Stephochetus* and *Siphonema*, considered to be a calcareous sponge and a calcareous alga respectively, which were shown by Hinde (1887) to be synonyms of *Girvanella*. The genus is now known to be world-wide in distribution and has been recorded from rocks of all ages from Cambrian to Cretaceous (Pia 1927).

Concerning the systematic position of this fossil, Brady (1884) stated that the generic and specific characters cited for *Girvanella problematica* agreed so well with those of the recent foraminifer *Hyperammina vagans* Brady, except for the diameter of the tubes, that 'it seems scarcely worth while to recognize these trifling differences as a basis of generic distinction'. Rhumbler (1895) likewise regarded this genus as a foraminifer; he was inclined to consider *Girvanella* as the basic type, from which *Ammodiscus* was derived, and he erected a new subfamily Girvanellinae to include *Girvanella*, *Tolypammina*, and *Syringammina*.

Already Bornemann (1886) had described his new genus *Siphonema* as a calcareous alga, and in 1891 Rothpletz considered *Girvanella* to belong to this group, a view followed by Brown (1894) and Seward (1898). There can be little doubt that this position is correct (subject to the reservation made on p. 27). The genus occurs in nodules similar to those of other calcareous algae, and in the same facies. Furthermore, the walls of the tubes are composed of typical 'algal dust'. When compared with the tubes constructed by agglutinating foraminifera, there is a contrast in mode of growth. The foraminiferal tubes are irregularly constricted at intervals, probably at periods when the food supply

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was restricted, while the tubes of *Girvanella* maintain a more even diameter, quite possibly due to uniform assimilation over the whole surface.

As such the genus has considerable value as a facies indicator, the nodules and pisoliths formed by its growth indicating shallow clear water. By comparison with modern algal balls these forms cannot have flourished below depths of about 30 fathoms. Often, as in the case of the well-known *Girvanella* Band in the Lower Carboniferous of northern England, these fossils show the sea to have been shallow and of uniform depth over an area of hundreds of square miles.

THE TYPE OF *GIRVANELLA*

The original description of *G. problematica*, the type species by monotypy, runs: 'Tubes from $\frac{1}{600}$th to $\frac{1}{700}$th of an inch in diameter, not observed to taper, twisted together in loosely reticulate or vermiculate aggregations of a rounded or irregular shape, which seem to be mostly from $\frac{1}{20}$th to $\frac{1}{10}$th of an inch across'. In the discussion which followed this diagnosis, which was mainly concerned with the zoological affinities of the fossil, the important statement was made that the tubes were always so loosely reticulated that the interstices of the mass were filled up with transparent calcite 'readily distinguishable from the more opaque and granular matrix which surrounds them'. The genus was later redescribed by Nicholson (1888) and by Wethered (1890) in much more accessible publications, and in 1891 Rothpletz, who had received specimens from Nicholson himself, stated that the tubes of the typical *Girvanella* showed dichotomous branching, and that there were two sets of tubes visible, distinguished by their different size. One group measured 6–9, the other 9–15μ in diameter, and he considered that there was a direct connexion ('unmittelbarer Zusammenhang') between the two. Already there was a considerable discrepancy between the quoted diameters for the tubes of this species; Nicholson and Etheridge's figures correspond to 35–42μ, Nicholson in 1888 gave a range between $\frac{1}{25}$ and $\frac{1}{60}$ mm. with a most common size of $\frac{1}{45}$ mm. (17–40μ, commonly 22μ), and Rothpletz's figures were smaller again.

Later authors passed over this discrepancy. Høeg (1932), for instance, describing forms of *G. problematica* from the Trondheim area, laid emphasis on the aggregation and mode of preservation of the filaments. He distinguished three groups, *typicalis*, occurring in crowded masses of threads, often with diffuse outlines, with a diameter of 16–20μ, *lumbricalis* occurring sparsely scattered or loosely aggregated, with a diameter of 14–17μ, exceptionally 20μ, and *moniliformis* which occurred dispersedly in a calcareous matrix, and often showed a prevailing direction of tubes in the colony, with a diameter of 20–26μ, sometimes larger. A further discussion of *G. problematica* was given by Lewis (1942) who concluded that all the forms, ranging in diameter from 11 to 26μ (rarely 30μ), were varieties of one species, within which American Ordovician *Girvanella* spp., for instance *G. ocellata* (Seely), could be accommodated.

Part of the discrepancy between the various descriptions may be due to the fact that most specimens from Girvan studied by later authors, including those figured by Nicholson in 1888, did not come from Tramitchell, but from the much more accessible Craighead Quarry near the town. To clear up the confusion search has been made for the original slides of 1878. Unfortunately Nicholson's collection was destroyed by fire in Aberdeen, and the only slide in the British Museum (N.H.) collections from Tramitchell (reg. no. V. 20734), though presented by Nicholson, does not contain the type specimen. Nineteen different aggregations of algae are seen in the slide, and they can be divided into three or four species on size of tube and mode of aggregation. The slide is thick and the boundaries between the species are uncertain and difficult to draw. Accordingly a fresh collection has been made from Tramitchell (now Tormitchell) Quarry and through the whole section exposed of the Stinchar Limestone at the typical locality, Benan Burn, south of Girvan. Over 100 thin sections were made containing very many algae. Camera lucida drawings were found to be unsuitable and finally 375 quarter-plate photographs of different aggregates at a uniform magnification of 200 diameters were taken as negatives on bromide paper, and these made a comparative study possible.

RESULTS OF STUDY OF NEW SPECIMENS FROM GIRVAN

Mode of aggregation of the tubes. Very considerable variation exists. Many specimens show tubuli freely twisting about within areas of clear crystalline calcite. Others are preserved in dark algal dust, and their boundaries are difficult to discern. Among the largest tubuli are many whose mode of aggregation recalls that of the type figure (Pl. 5, fig. 1), vermiform tubes, gently curving and rarely in contact. Other tubuli are more strongly curved and closely aggregated. Occasionally tubes run subparallel, being in every other feature identical with the more flexuous type. On the whole, however, those specimens having the widest tube diameter are less twisted and contorted than the slimmer tubes, though a few specimens of the large species were found showing the closely adpressed and twisted tubes hitherto considered typical of *Girvanella* (Pl. 5, fig. 4). Branching has been seen several times and in the large species is never of symmetrical dichotomous type (Pl. 6 , figs. 1, 2). No passage between tubes of one diameter and one of another has been seen, and the tubes of one aggregation are generally of uniform diameter, though there are exceptions.

Diameter of the tubes. Careful measurement of the diameter of the tubes showed that tubes of all sizes intermediate between the largest and smallest occurred. Though it was possible to recognize 'species' by observation alone, their boundaries were extraordinarily difficult to draw. Measurement of several hundred tubes from different aggregations was of no avail; eventually it was realized that measurements of longitudinal sections of tubes whose diameter was less than the thickness of the slide must lead to inaccurate results. Furthermore, if these algae are actually preserved as moulds in a fine granular calcareous matrix precipitated by their own life-processes, the 'wall' may well vary in thickness according to local conditions. Accordingly measurement was restricted to cross-sections, and all the well-preserved cross-sections in the photographs

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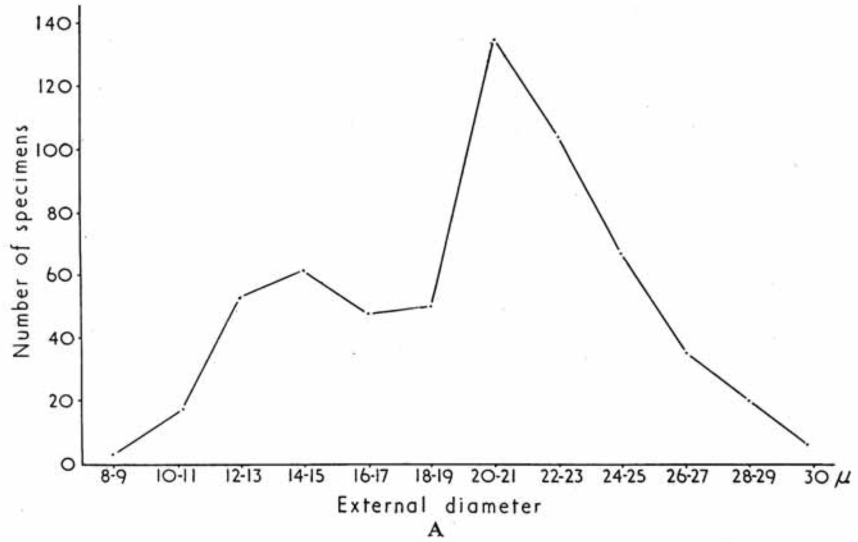
EXPLANATION OF PLATE 5

Figs. 1–5. *Girvanella problematica* Nicholson and Etheridge. 1, Reproduction of Nicholson and Etheridge's original figure, 'Portion of a slice of limestone showing the tubes of *G. problematica.* Tramitchell. ×50 (Coll. H. A. Nicholson).' 2, Neotype, B.M. (N.H.) reg. no. V. 34566, ×120, Stinchar Limestone, Tormitchell Quarry, Girvan. 3, Small aggregation showing cross-sections and possible cell walls, ×87. Stinchar Limestone, Benan Burn, Girvan. 4, Aggregation closely packed with meandering tubes, ×87½. Stinchar Limestone, Benan Burn, Girvan. 5, Subparallel tubes with possible repeated branching at top, ×87½. Stinchar Limestone, Benan Burn, Girvan.



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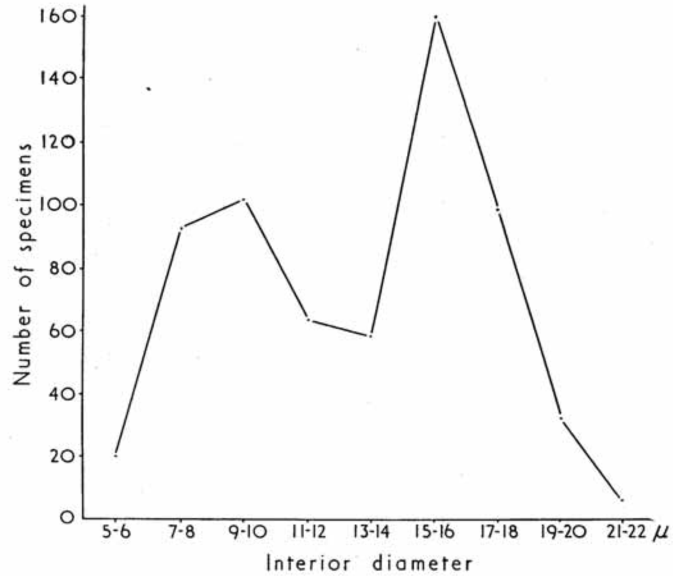

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TEXT-FIG. 1. A. Graph of external diameter of circular cross-sections of tubuli of *Girvanella*. Stinchar Limestone, Tramitchell and Benan Burn. B. Graph of internal diameter of circular cross-sections of *Girvanella* tubuli. Stinchar Limestone, Tramitchell and Benan Burn.

were measured, their diameter being estimated to $\frac{1}{5}$th of a millimetre, representing 1μ. Often a single tube did not show both exterior and interior clearly, so that the number of readings in the two graphs (text-fig. 1) is different. Inspection of these graphs shows that tubes of every internal diameter from 5 to 22μ, and every external diameter from 8 to 30μ, occur in these slides. Maxima occur at an external diameter of 20–21μ (internal diameter 15–16μ) and 14–15μ (internal diameter 9–10μ). By inspection it can be seen that the graph of internal diameters is more compact than that of external diameters, and that its maxima are more clearly marked, and more symmetrical. The graph of external diameters is skewed towards the right, as can be seen especially in the range from 20 to 30μ. This is presumably due to variation in the amount of precipitation of calcium carbonate on the exterior of the thread. The operation of the same factor has caused the gap between the smaller and larger group to be partially filled. It is clear that readings of the internal diameter of the tubes are more reliable.

Even when the internal diameters are measured, however, there is a considerable number of specimens intermediate in diameter between the two peaks on the graph. To account for the continuity of the graph, we must assume that either the two species are highly variable, in response perhaps to outward conditions, or there are five or six, or even more, species present which are being confounded. Though the evidence is not good enough to decide between these possibilities it is clear that at least two species occur, with the average diameters previously cited. The larger of these corresponds to Nicholson and Etheridge's original description, and is redefined below.

SYSTEMATIC DESCRIPTION

Girvanella problematica Nicholson and Etheridge 1878

Plates 5 and 6

Diagnosis. Tubes flexuous, not observed to taper, rarely branching, twisted together in loosely aggregated masses, less commonly closely packed. Average external diameter of tubes 21–22μ, ranging from 18 to 25 (rarely 30)μ, average internal diameter of tubes 15–16μ, ranging from 13 to 20 (rarely 22)μ.

Observations. Branching has been observed on several occasions. A single branch at a wide angle is shown in Pl. 6, fig. 2, while repeated branching occurs in the specimen figured on Pl. 6, fig. 1. Here the whole *Girvanella* is lying more or less parallel to a shell fragment (seen in the lower left-hand corner) and is branching away from it. The repeated branching strongly suggests growth out into a favourable environment. All the branches end at the same level. Cross walls appear to occur in some well-preserved specimens, a feature already observed by Frémy and Dangeard (1935) in *G. symplocoidea* of the Jurassic. In the specimen figured in Pl. 5, fig. 3 the possible cell walls are clearly seen in the upper part of the photograph. The circular cross-section of the tubes, the thickness of their walls, and their uniformity in size can also be appreciated.

EXPLANATION OF PLATE 6

Figs. 1–4. *Girvanella problematica* Nicholson and Etheridge. 1, Repeated branching, $\times 87\frac{1}{2}$. Stinchar Limestone, Benan Burn, Girvan. 2, Single branch in a lax aggregation, $\times 200$. Top bed of Stinchar Limestone, Benan Burn, Girvan. 3, *G. problematica* inside a *Saccamminopsis* test, $\times 87\frac{1}{2}$. Stinchar Limestone, Benan Burn, Girvan.

The specimen figured on Pl. 6, fig. 3 is unusual in that the *Girvanella* threads occur inside the middle chamber of a three-chambered *Saccamminopsis* test. The tubular connexions with the chambers in front and behind are complete, and the initial chamber is filled with clear crystalline calcite. The lower part of the chamber in which the *Girvanella* occurs is filled with finer grained rather murky calcite partially shown in the figure, the *Girvanella* threads occurring in the upper, more crystalline portion. The last chamber is broken, its contents merging with the matrix. If *Girvanella* was a green or blue-green alga it would seem to be impossible for it to flourish in the dark, inside the chamber of a foraminifer. The tubular connexion between the two last chambers is just large enough to allow the *Girvanella* to slip through, so that it may be a detrital fragment. However, one piece of evidence points the other way. A single thread of *Girvanella*, seen on the right of the photograph, appears to traverse the wall of the foraminiferal test. This is the only fact observed that supports the view of Cayeux (1909) that *Girvanella* was a boring organism, all other observations being in accord with a free mode of life. However, if other specimens are found in a similar situation the systematic position of *Girvanella* will have to be reviewed.

The loose packing of the threads is a point of difference from *Girvanella* spp. described from other horizons, as is the fact that the threads quite commonly grow subparallel (Pl. 5, fig. 5). Occasional closely packed specimens with contorted tubes do occur (Pl. 5, fig. 4). These may be cut parallel to the surface on which the algae were growing. The sharp boundaries of many aggregations may be interpreted as detrital rounding, which suggests that they were soon lithified.

It is unfortunate that Høeg (1932) gave the name *typicalis* to one of his forms of *G. problematica*, since this does not correspond exactly to the original description and figure. The form he termed *moniliformis* is, however, very close to and probably identical with the true *G. problematica*. However, the alga is so protean that many other forms might be distinguished, probably related to micro-environments.

Neotype (here chosen). The specimen shown on Pl. 5, fig. 2, now in the British Museum (N.H.) collection, reg. number V. 34566.

Horizon and locality. Stinchar Limestone (Ordovician, Llandeilo), Tormitchell, Girvan, Ayrshire.

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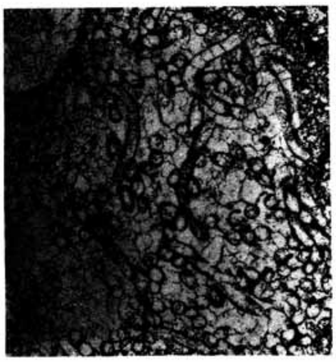

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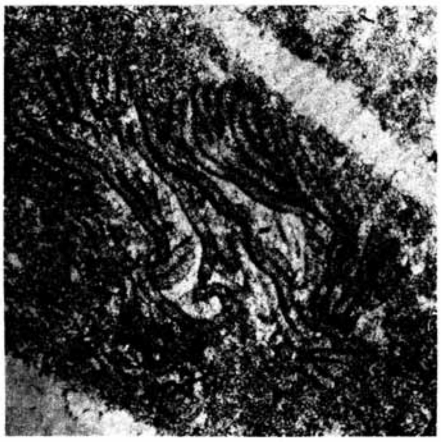
WOOD, *Girvanella*



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