SEASONAL VARIATIONS IN THE SKELETON AND SPICULE DIMENSIONS OF *HALICLONA ELEGANS* (BOWERBANK) sensu TOPSENT (1887) FROM TWO SITES IN NORTH WALES

by W. Clifford Jones
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ABSTRACT

Haliclona elegans is particularly useful for a study of skeletal variation, because it is easily identified by the 'slime strand' test. Spicule samples of specimens collected at low water spring tides throughout the year have been measured and subjected to statistical analysis. Monthly changes in the mean lengths and widths of the spicules were found, and in their standard deviations and coefficients of variation (C.V.). There was a marked drop in the C.V. for width and length in June, explicable by a cessation in spicule production. Vertical and surface sections of the sponges in February were strikingly different from those in August. The taxonomy of the species and causes of skeletal variation are discussed.

INTRODUCTION

Spicule dimensions are extensively used in the diagnosis and identification of sponge species, but relatively little is known about the causes of variation in spicule lengths and widths. Information is needed on the range of genotypic and phenotypic variation and on the environmental factors responsible for the latter. However, difficulty can at times be experienced in determining the extent of the variation even for a species in a particular locality. For example, some haplosclerid species are poorly defined and have only oxeote spicules whose size range tends to overlap those of other haplosclerids in the same locality (Jones, 1984). However, *Haliclona elegans* is a haplosclerid that can easily be identified in the field, thanks to a property first used diagnostically by Topsent (1887, 1925): when pieces of the living sponge are pulled apart, interconnecting slime strands appear between them. The slime strands result from the presence of segmented organic fibres in the mesohyle, which are readily discernible in alcohol-fixed hand sections of the sponge after mounting in balsam. Each fibrous segment is contained within a single cuboidal spherulous cell, so that the fibres appear like long strings of beads. A number of such strings may be associated together in parallel, along with sclerocytes and other cells, to form 'bundles' or 'cellular tracts', the thickness of which can vary. According to Herlant-Meewis (1948), in specimens exhibiting hollow digitations there are more strings per bundle at the base of the digitations and in the centre of their walls than elsewhere, whereas beneath the subdermal cavities or near the atrium. or at the free ends of branches, the strings occur singly or in groups of merely 2 or 3. Whatever their size, the bundles tend to follow the longitudinal axes of branches of the sponge. The segmented fibres are not composed of spongin (Herland-Meewis, 1948; Lévi, 1967), which is at times abundantly present in *H. elegans*, enveloping the oxeote spicules composing the main skeletal framework. This consists of a roughly orthogonal arrangement of primary and secondary fibres of spicules and spongin. Usually the fibres are unispicular, with only the ends of the spicules overlapping those of their neighbours, but in deeper regions of the sponge multispicular bundles can occur, with two or more spicules side by side (Herlant-Meewis, 1948). The segmented organic fibres are fibrillar under the electron microscope (Lévi, 1967) and elastic, but their chemical composition is as yet unknown (Garrone & Pottu, 1973).

Other diagnostic features of *H. elegans* are: the presence of a dermal reticulation, usually exhibiting a triangular mesh with unispicular sides (Bowerbank, 1866); a smooth surface, with relatively little protrusion of spicules at the distal ends of the primary bundles; oscula usually raised, at times on the tops of large, hollow mounds, or situated at the distal ends of branches, or simple, i.e. flush with the general surface; sponge soft to touch; colour when alive, grey, yellow, rose (Greissinger, 1971), or deep lilac (Topsent, 1925); spicules curved, typically short, stout and abruptly tapering, and variable in size (see later); sponge of variable form, encrusting on rock or epiphytic on seaweeds and zoophytes.

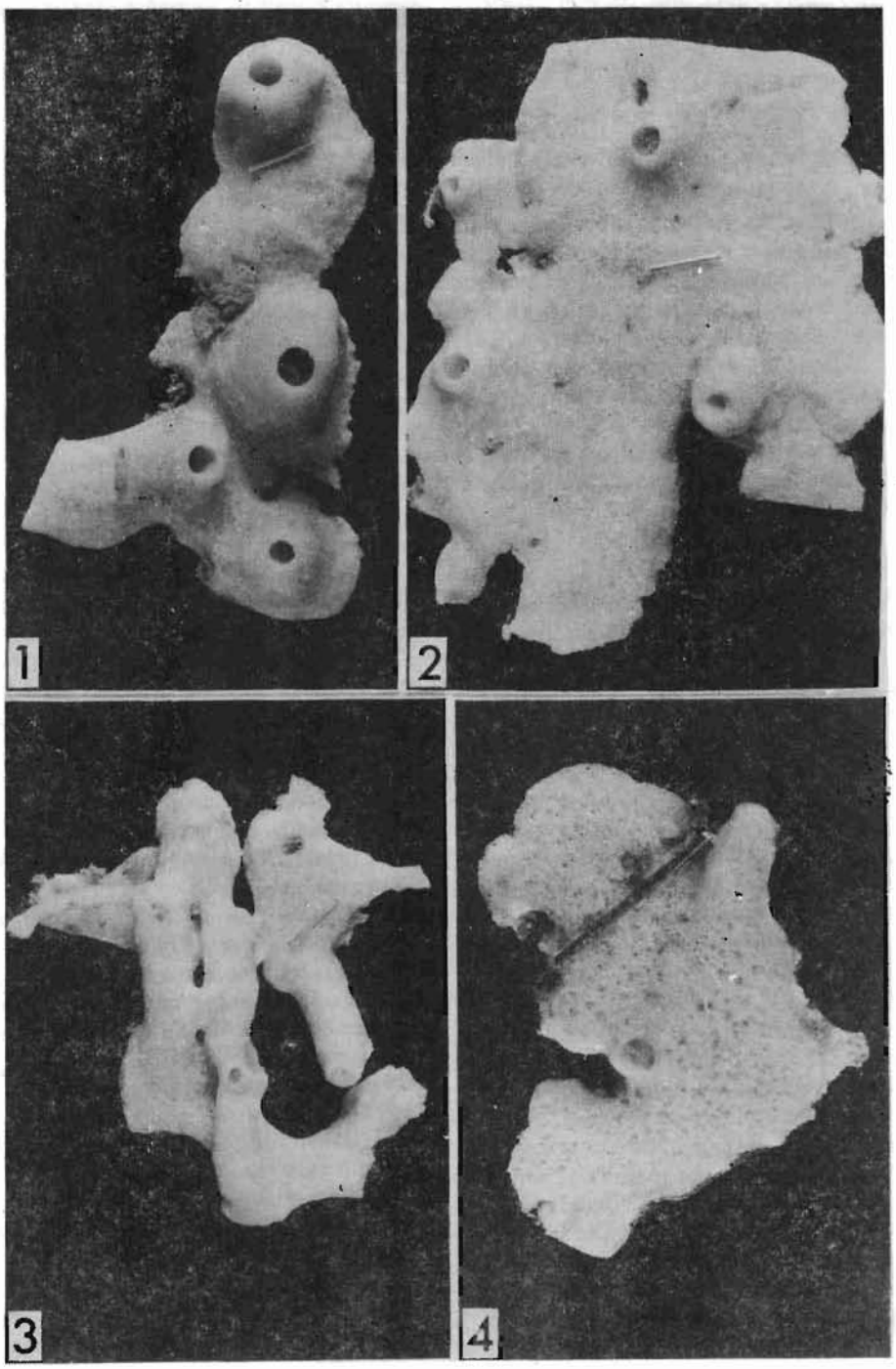

Plate 1. Alcohol fixed specimens of *Haliclona elegans*. The rod is 1cm long.
Fig. 1-3. Rhosneigr specimens collected on 16th May 1980 (figs. 1 and 2) and 27th August 1980 (fig. 3). Fig. 4. Church Island specimen collected on 1st August 1984. Note the lacework of tracts visible through the general surface, but not obvious on the sides of the oscular chimneys. In fig. 1 the oscula are large and situated at the summits of mammillate mounds. In fig. 3 the specimen is only partially encrusting, the remainder having the form of anastomosing, cylindrical branches.

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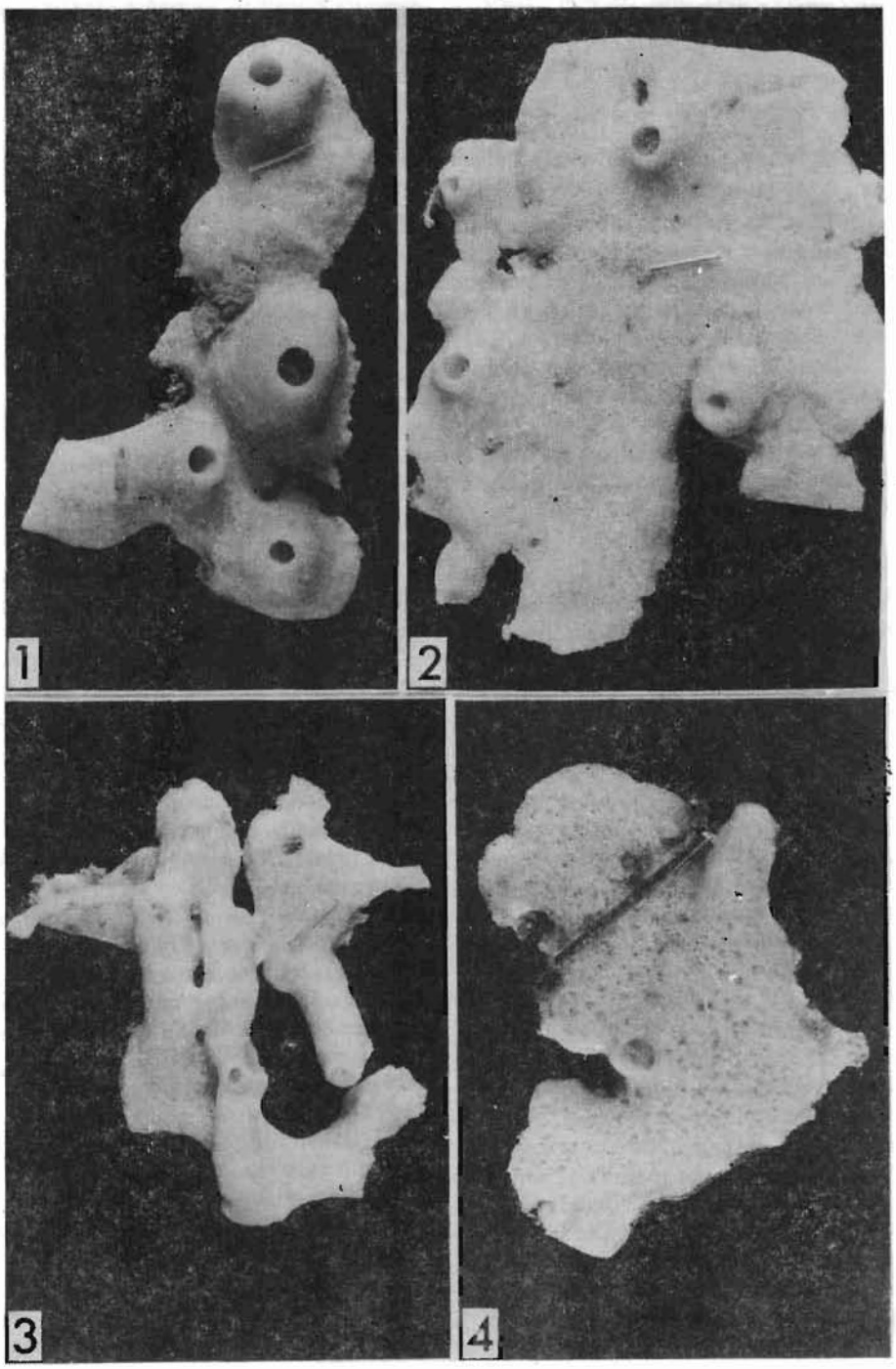

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To these characters one can add that, when observed in alcohol, a delicate tracery is visible over much of the surface of the sponge (figs. 1 - 4), representing the cellular tracts containing embedded spicules and segmented organic fibres mentioned above. Such tracts tend to radiate from the bases of the oscular mounds (fig. 2), but anastomosing and intercrossing tracts are also present in the lacework. The sides of the oscular mounds often appear to be homogeneous in texture (figs. 1, 2 and 3). With this range of specific characters to ensure accurate identification, *Haliclona elegans* is a particularly useful species for investigating spicule variation.

Recently it was shown that the coefficients of variation (standard deviation/mean) of spicule length and width of haplosclerid sponges from North Wales are not constant throughout the year (Jones, 1984). Following W.D. Hartman (1958) and A.R. Stone (1970) it was suggested that the variation was caused by a tendency for newly forming spicules to achieve thinner widths during Summer months, possibly in response to an increase in temperature or to reduction in the seawater silicon concentration resulting from the growth of plankton.

MATERIALS AND METHODS

Specimens of *H. elegans* were collected at low water spring tides from two sites, Church Island and Rhosneigr, on the shores of Anglesey, North Wales. All were identified initially in the field by the 'slime-strand' test. Spicule preparations were prepared by boiling pieces in fuming nitric acid. Vertical and tangential surface sections were hand-cut and mounted in balsam, enabling the identification to be confirmed. A random sample of 100 spicules was measured using a digitizer connected to a PDP11 computer. Statistical analysis of the stored data was carried out by means of a DEC10 main-frame computer. Further details are given by Jones (1984).

RESULTS

Coefficients of variation for spicule lengths and widths

The graph in fig. 5 shows the coefficients of variation for length (open circles) and width (closed circles) for the aggregated data from each group of specimens from the two sites collected over several years (1980-1984) on the same, or very nearly the same, dates. Both graphs exhibit two peaks, one in May and the other at the beginning of August, with a striking minimum in June and another in December. Graphs obtained by plotting the average of the coefficients of variation of the 100-spicule samples in each group, instead of the coefficient calculated from the pooled data for each group, showed similar, but less marked, fluctuations. The average coefficients and their standard deviations (in brackets) for spicule lengths and widths respectively were: 9.41 (1.43), 25.78 (4.13) (May); 5.24 (1.06), 11.49 (1.87) (June); and 7.34 (1.12), 19.15 (2.25) (July). The differences are significant ($P<0.5\%$) when the means are compared in turn successively. When the coefficients (aggregated data) for Church Island were compared with those for Rhosneigr,no essential difference in the shapes of the graphs was evident; the same marked fall in coefficients of variation in June was again obvious (Table 1). It appears therefore that the seasonal fluctuations in C.V. are real; the same trends are evident regardless of collecting site. This justifies combining the data for the two sites. Five specimens of *H. elegans* collected from the Rapids near Lough Ine (or Hyne), County Cork, Ireland on September 12th 1983 also gave, when the samples were aggregated, a C.V. (length) of 11.33 and a C.V. (width) of 44.68, agreeing more or less with the values for Rhosneigr and Church Island at the end of August.

The question arises: Are the montly changes in coefficients of variation caused by variations in the means, or the standard deviations, or both?

Average widths and lengths of the spicules

The graphs in figs. 6 and 7 show the changes in the mean width and mean length respectively throughout the year. Also shown in fig. 6 are the numbers of specimens, the standard deviations and the maximum and minimum sizes per group. The medians for each group gave graphs which were almost identical to those for the means. It can be seen that the mean values for both width and length steadily fell from February (7.5; 127.5μm) to May (5.6; 107.5μm), then peaked in June (8.0; 118.8μm). Thereafter the mean length declined to a minimum in September (99.7μm), whereas the mean width reached minima in both August (5.3μm) and October (4.8μm). The differences between the graphs for length and width are of interest, considering that the two dimensions were measured on the same 100 spicules in each sample. A strict correlation between length and width is clearly not maintained. The standard deviations did not change much from February to May, but were smaller in June and larger in August, thus contributing to the changes in coefficients.

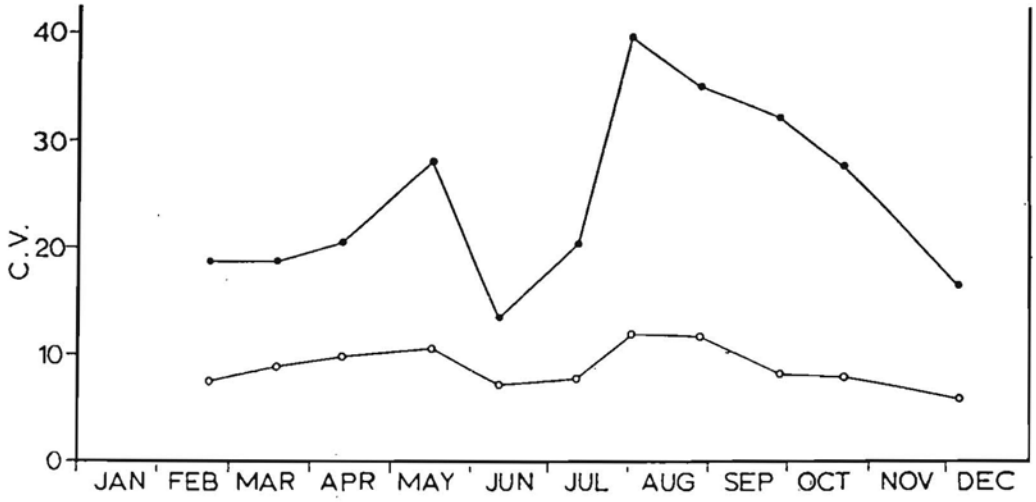


Fig. 5 Monthly changes in the coefficient of variation for width (closed circles) and length (open circles) of the spicules. The coefficients were calculated using the pooled data for specimens collected on the same or very nearly the same dates from 1980 to 1984 from Rhosneigr and Church Island. The dates coincided with the occurrence of low-water spring tides.

Table I

Monthly values for the mean coefficient of variation (C.V.) and its standard deviation (s.d.) for Rhosneigr (Rh.) and Church Island (C.I.) specimens of *H. elegans*.

Date	Number of Specimens		C.V. Length		C.V. Width	
	Rh.	C.I.	Rh.	C.I.	Rh.	C.I.
Feb. 21st	–	1		7.74	–	18.73
Mar. 17 - 19th	3	1	8.69	7.07	18.13	15.73
Apr. 1st	1	–	7.23	–	24.57	–
Apr. 8th	–	1	–	5.54	–	12.98
May 15 - 16th	4	1	10.19	11.66	27.66	28.98
Jun. 3 - 8th	–	2	–	7.21	–	13.56
Jun. 11th	8	–	6.70	–	12.98	–
Jul. 11 - 12th	6	–	7.68	–	20.38	–
Aug. 1st	–	7	–	11.81	–	39.75
Aug. 28 - 30th	6	1	11.04	11.81	33.81	44.80
Sep. 27th	5	–	8.16	–	32.15	–
Oct. 22nd	–	7	–	7.94	–	27.60
Dec. 5th	–	3	–	5.70	–	16.60

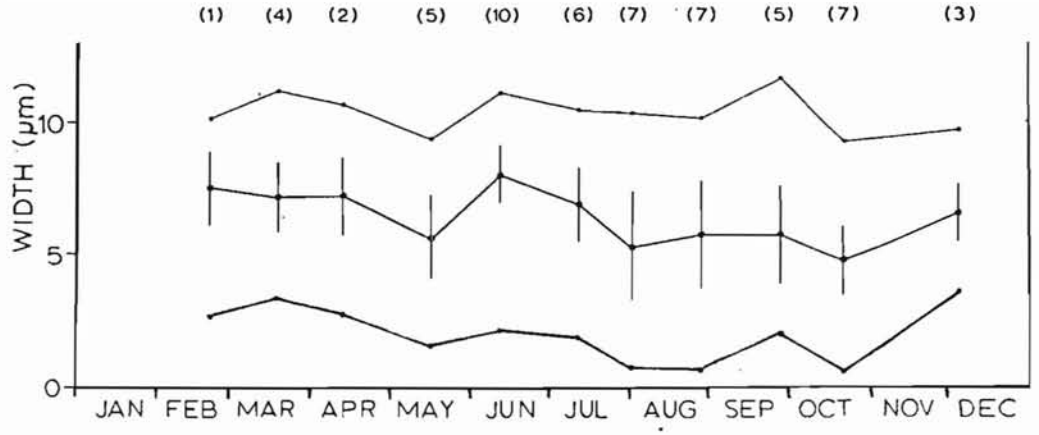


Fig. 6 The monthly variation in the mean width, standard deviation, minimum width and maximum width of spicules in the aggregated samples used for the calculations of coefficient of variation in fig. 5. The number of 100-spicule samples in each aggregate is given in brackets above the corresponding date.

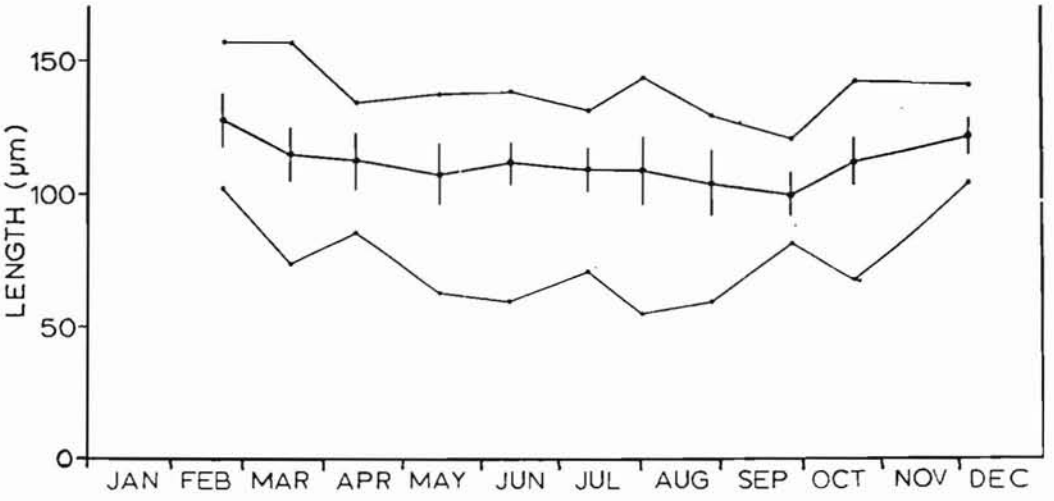


Fig. 7 The monthly variation in mean length, standard deviation, minimum length and maximum length of spicules from the same specimens as in figs. 5 and 6.

For the 5 Lough Ine specimens collected on 12th September 1983 the mean length was 87.1μm (S.D. = 9.86) and the mean width 4.04μm (S.D. = 1.81). The 5 Rhosneigr specimens (27th September 1984) gave corresponding means and standard deviations of 99.7μm (S.D. = 8.1) and 5.8μm (S.D. = 1.9). The differences are not significant (P>5<10% for length; p>10<25% for width).

Frequency distributions of spicule lengths and widths.

Histograms showing the frequency distributions of widths and lengths for each group are given in Fig. 8. From February to April, spicule production was maintained and there was little change in the frequency patterns, apart from a progressive shift to the left in the mode for length. In May there was a striking increase in relative numbers of spicules with widths of 3 - 4μm, possibly resulting from an increase in spicule production. However, the histogram for length does not reflect the same pattern, so that the newly forming spicules were probably thinner than normal in relation to length. Spicule production had ceased by June, causing a shift in the means and modes to the right. By July it had resumed and the histograms approximate to those for April. However, in August there seems to have been a considerable production of thin spicules and again there is a tendency for the histogram for width, but not for the length, to be bimodal. From September to December the histograms tend to change towards those for February, presumably as spicule production declined and thicker, longer spicules were achieved.

Correlation of spicule width with length

Linear regression analysis revealed great variation in the degree of correlation between lengths and widths. Correlation coefficients ("r") varied from 0.8998 for a specimen collected on 30th August 1984 to 0.0019 for one collected on 11th June 1984. One would have expected poor correlation for June specimens in view of the paucity of developing spicules in the samples for that month. Of the 62 samples analysed, 18 had linear correlation coefficients in the range of 0.7 to 0.8 and 6 had coefficients of 0.85 - 0.9. The mean value for "r" was 0.61(standard deviation, 0.20). No improvement in "r" value was obtained by combining the samples with the highest value in each group.

The equation of the regression line of width (dependent variable) on length (independent variable) for the sample with the best correlation coefficient is:-

$$\text{Width} = 0.16901 \times \text{length} - 13.008$$

In this sample the maximum spicule length was 129.8μm and the maximum width 9.9μm. The minimum values were respectively 77.8μm and 1.8μm. The specimen was collected at Church Island.

The overall maximum and minimum spicule lengths occurring in the 62 samples were respectively 156.7μm (17th March 1984) and 54.9μm (1st August 1984). The maximum and minimum widths were respectively 12.2μm (27th August 1980) and 0.6μm (22nd October 1984). The smallest maximum length in a sample was 93.0μm and the smallest maximum width, 4.4μm (both Lough Ine specimens collected on 12th September 1983). The smallest maximum lengths and widths for specimens from North Wales were respectively 102.2μm (28th August 1984) and 4.8μm (1st August 1984).

% frequency distribution of lengths and widths using pooled data.

Aggregating the spicule measurements for the 57 specimens collected at Rhosneigr and Church Island gave % frequency distributions which were skewed positively due to the presence of juvenile spicules in the samples. The two distributions also exhibited a 'shoulder' to the left of the mode, probably because of the production of thin, short, fully grown spicules in Summer months. The commonest size range for width was 7 - 8μm (20%) and for length, 110 - 120μm (35%). However, the number of specimens collected were not the same in each month of the year, but calculating the average % frequency distributions per month and including the average of the distributions on either side for months for which no data were available, gave an overall % frequency distribution which did not differ essentially from that obtained from the pooled data. The commonest ranges were still 7 - 8μm (25%) for width and 110 - 120μm (33%) for length.

Anatomical features revealed by hand-sections of the sponges

The skeletal arrangements in 47 of the Rhosneigr and Church Island specimens were ascertained by examination of vertical and surface sections mounted in balsam. Considerable variation was found, as would perhaps be expected for littoral sponges encrusting on boulders of various, sizes, some situated in rock pools, while others were being exposed to the air for varying periods depending on the tidal conditions. In addition to the effects of tidal and temperature rhythms, the supply of nutrients could be affec-

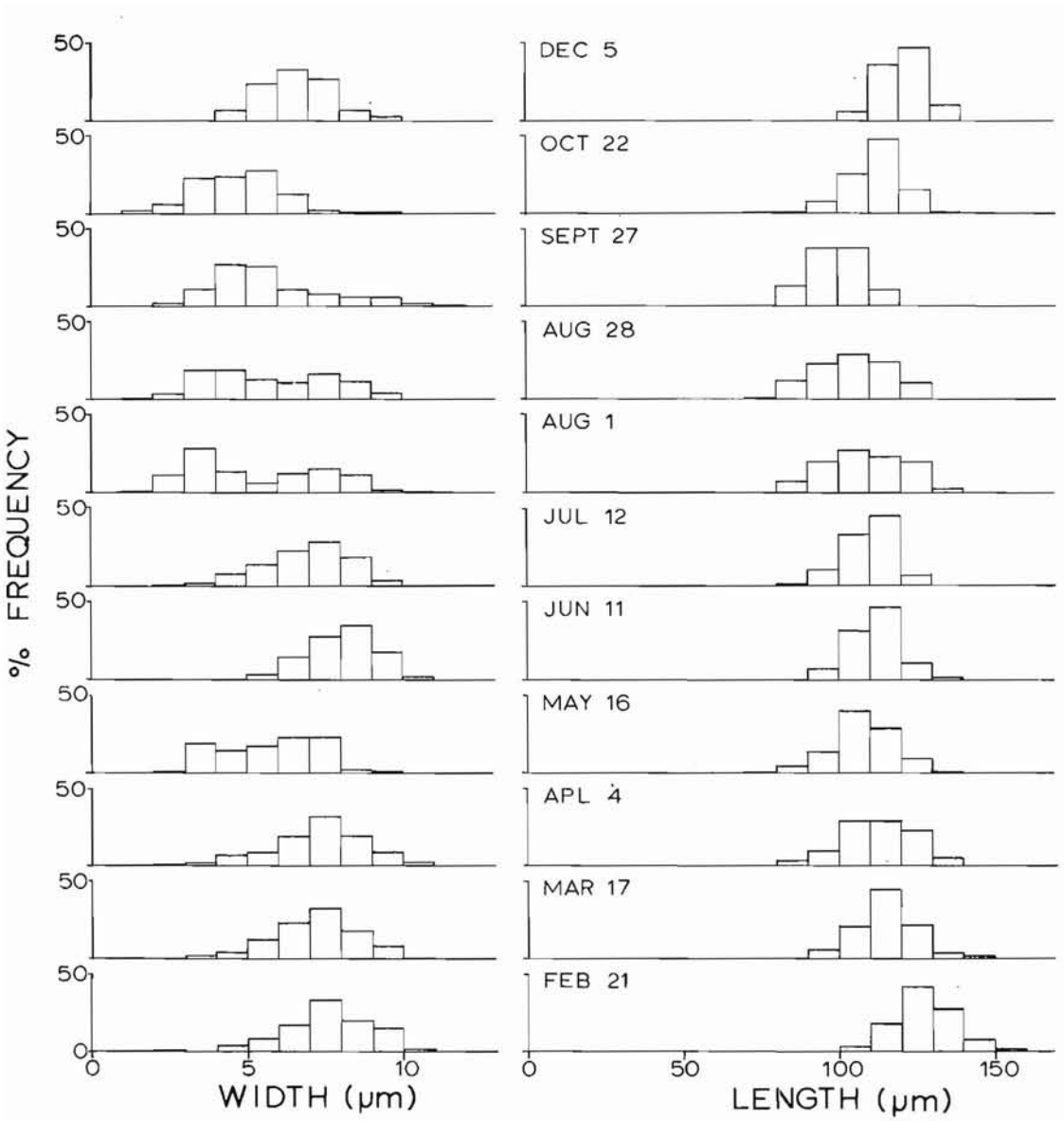


Fig. 8. Monthly percentage frequency distributions for spicule lengths and widths in the 100-spicule samples of the Rhosneigr and Church Island specimens.

LEGENDS FOR PLATES 2, 3, 4 and 5

Plate 2. Vertical sections and slime strands of *Haliclona elegans.* The magnification is the same in figs. 9 — 11. The scale lines in figs. 10 and 12 equal 100μm.

Fig. 9 Vertical section through the surface of a specimen collected at Church Island on 21st February 1984. The spicules are thick. Sections of cellular tracts containing spicules are visible on the right.

Fig. 10. Corresponding section of a Church Island specimen collected on 1st August 1984. The spicules are thin. Cellular tracts containing segmented fibres in parallel and relatively few, thin spicules are present. Note the superficial dermal membrane; segmented fibres are associated with this in places.

Fig. 11 Corresponding section of a Rhosneigr specimen collected on 11th June 1984. The spicules in the main framework are mostly thick. The cellular tracts have segmented fibres, but lack spicules. As in figs. 9 and 10, the surface is minutely hispid on account of the projecting primary spicule bundles.

Fig. 12 Segmented intracellular fibres seen at higher magnification through the surface of a balsam-mounted specimen collected at Rhosneigr on 11th June 1984.

Plate 3. The dermal reticulation and underlying lacework of cellular tracts of *Haliclona elegans.* The scale lines indicate 100μm in figs. 14 and 15. The magnification is the same in figs. 13 - 15.

Fig. 13. The dermal reticulation of a specimen collected at Rhosneigr on 11th June 1984. In the centre 5 spicules radiate to form a very imperfect hexagonal pattern of triangles, but most of the meshwork is basically polygonal.

Fig. 14. The dermal reticulation of a Church Island specimen collected on 1st August 1984. Note the thin spicules and more open meshwork.

Fig. 15 The dermal reticulation of another Church Island specimen collected on 1st August 1984. The reticulation is hardly present, being composed of relatively few spicules and exhibiting at the most only incomplete polygons.

Fig. 16. Lacework of cellular tracts beneath the dermal reticulation of a specimen collected at Rhosneigr on 27th August 1980.

Plate 4. Further sections of *Haliclona elegans.* The magnification is the same in all 4 figs. The scale line in fig. 18 indicates 100μm.

Fig. 17. Section of the Church Island specimen collected on 21st February 1984 showing densely spiculated cellular tracts running mainly along the cylindrical branch. Part of the section of a large canal can be seen in the bottom right corner.

Fig. 18. Section of a Rhosneigr specimen collected on 17th March 1984. The cellular tracts here intercross and run in a variety of directions some ascending towards the surface. A subdermal cavity is visible just beneath the surface on the left while bottom right can be seen a section of a canal.

Fig. 19. Vertical section of the basal part of an encrusting specimen collected at Rhosneigr on 12th July 1983, showing a tendency for the primary spicule bundles to branch and diverge upwards and outwards from the base. The upper surface can be seen in the bottom left corner.

Fig. 20. Vertical section of another part of the same specimen as in fig. 19, exhibiting conspicuous growth bands.

Plate 5. Sections, embryos and spicules of *Haliclona elegans.* The scale lines in figs. 22 and 26 indicate 100μm. Figs. 21 - 25 are all at the same magnification, as are figs. 26 and 27.

Fig. 21. Vertical section of a Church Island specimen collected on 15th May 1980. The oxea are thick distally and thin proximally. Segmented fibres are visible near the bottom right corner, but relatively little living tissue appears to have been present.

Fig. 22. Vertical section of a Church Island specimen collected on 1st August 1984. The oxea are thin distally and thick proximally. A delicate dermal membrance occurs at the surface.

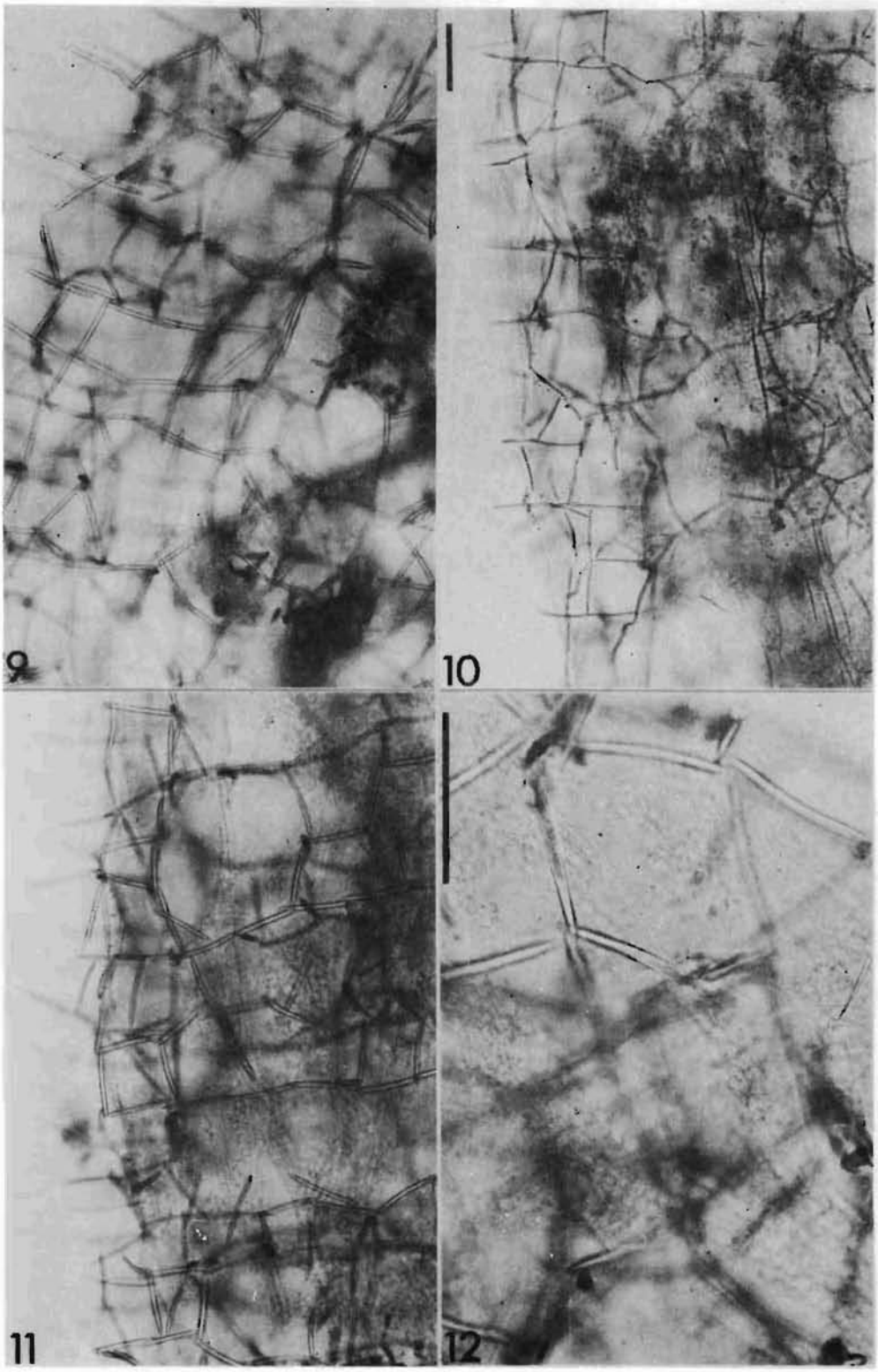
Fig. 23. Spicule-less embryo in a Rhosneigr specimen collected on 12th July 1983.

Fig. 24. Ovoid embryo containing some very thin spicules in a Church Island specimen collected on 1st August 1984.

Fig. 25. Ovoid embryo containing spicules in abundance and exhibiting a cap at one end, from a Rhosneigr specimen collected on 27th August 1980.

Fig. 26. Spicules from a Rhosneigr specimen collected on 27th August 1980.

Fig. 27. Spicules from a Church Island specimen collected on 19th March 1981.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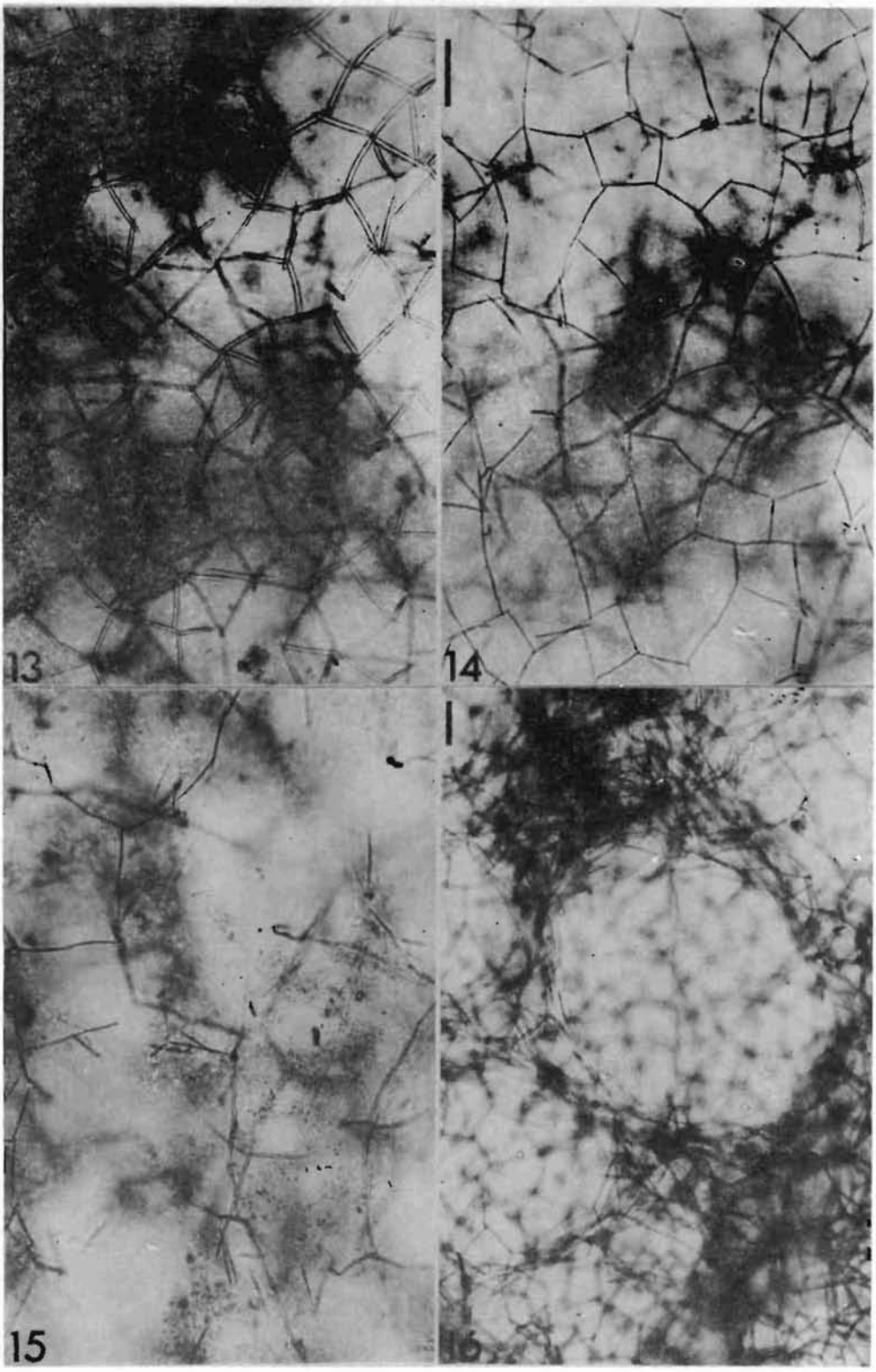
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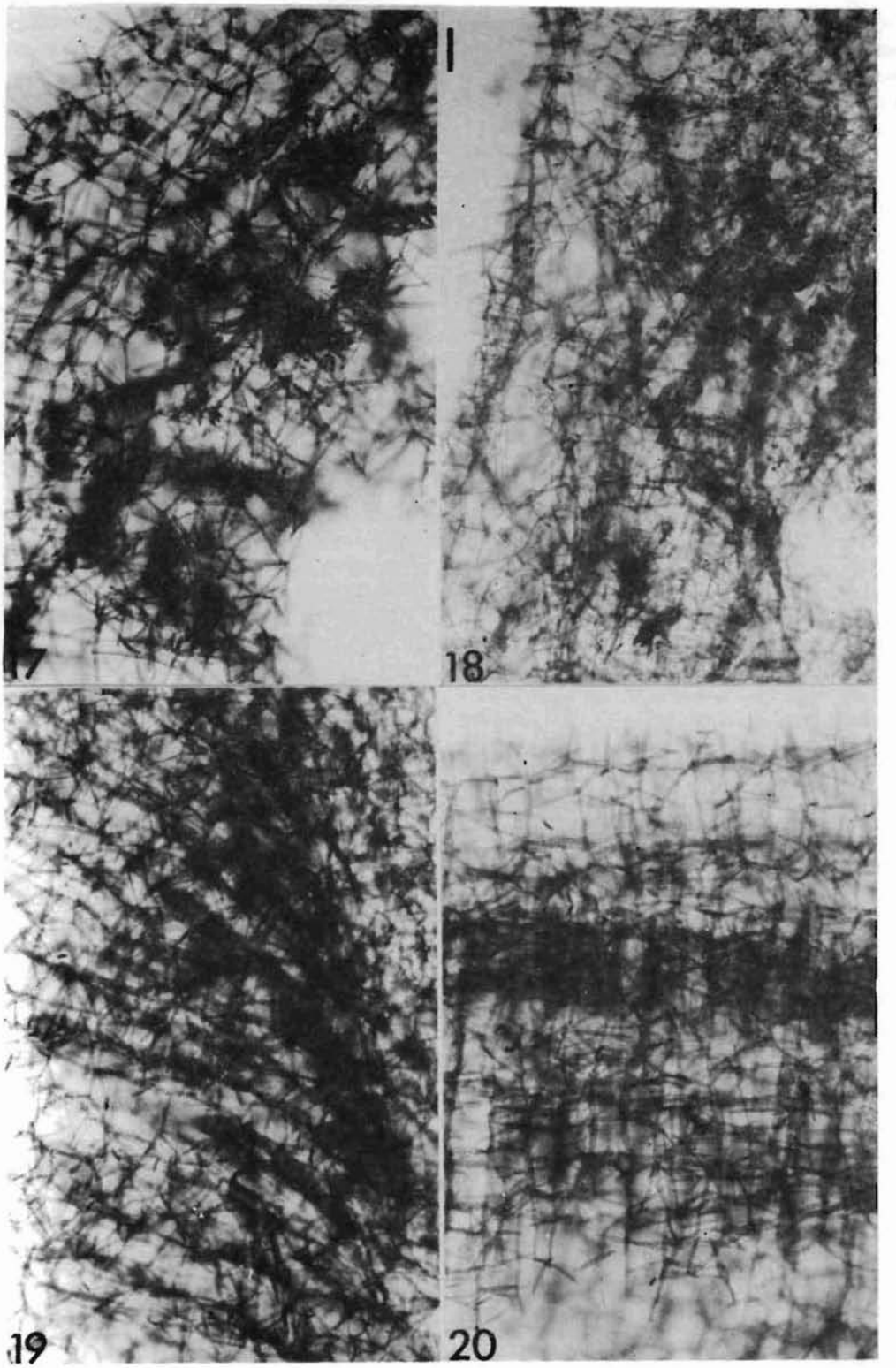
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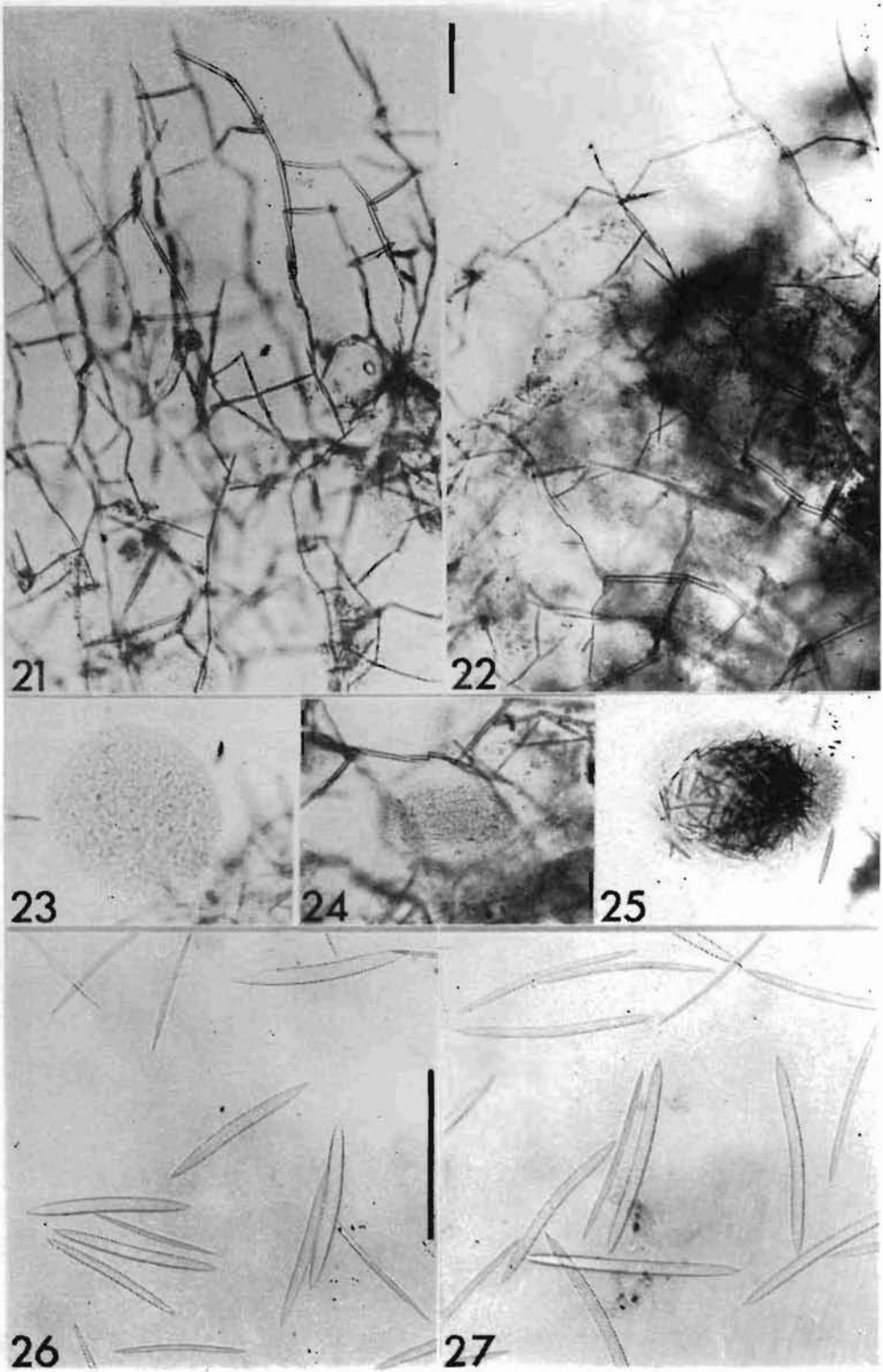
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ted by displacement or overturning of the boulders. Thus some sponges might have been quiescent or undergoing retrogression, while others elsewhere were actively growing, or engaged in sexual reproduction. Quiescence, or absence of growth, is implied when the sponge surface is littered by detritus. Distinctive growth bands (fig. 20) also are exhibited by some of the vertical sections of sponges, each dark band indicating where denser spiculation, presumably encouraged by a temporary lack of upward growth of the sponge surface, has later been overlain by a more delicate spicule framework. Such growth bands were observed in sections of some sponges collected in May, July and September. Renewal of growth need not involve the whole surface, because at times one sees a denser zone inclining upwards and curving to form the surface at the boundary of an area of more recent growth.

Where healthy growth conditions prevail the surface is minutely hispid to varying extents (fig. 9 - 11), thanks to some projecting primary spicule bundles. Beneath the dermal membrane, which tends to arch inwards between the projecting spicules, one can usually distinguish a horizontally-extending subdermal cavity, traversed by spicule bundles (fig. 10 and 11). The most distal horizontal spicules that interconnect the primary bundles make up the so-called dermal reticulation, visible in the surface sections as a spicule framework, with links of usually no more than one spicule's width in thickness bounding polygonal spaces (figs. 13 - 15). Where the surface is hispid, the primary bundles usually do not project more than one spicule's length above the level of this reticulation.

Near the surface there is a lacework of cellular tracts, which is visible through the surface at low magnification in alcohol-fixed specimens (fig. 16). The tracts are composed largely of intracellular segmented fibres (figs. 10 - 12), arranged in parallel. Spicules are frequently embedded in these tracts. Their abundance varies, as will be explained below. As many as 17 spicules have been counted in the cross-section of a tract of about 100 x 50μm in a specimen collected in February. When relatively few are present, they can be seen to be distinctly separated from one another, not contacting other spicules as in the spongin-enveloped spicule bundles of the main skeletal framework. The spicules may also vary in thickness and length and thus probably include growing and fully grown spicules which are either being transported to sites of incorporation in the main spicule framework, or being stored until a time when the sponge will resume growth. They would thus be intracellular within sclerocytes, or associated with transporting cells. The cellular tracts branch and anastomose (fig. 16) and lie at different horizontal levels (fig. 17). They can ascend towards the surface obliquely and curve into the horizontal direction (fig. 18).

The primary spicule bundles, running perpendicular to the surface, consist of usually a single row of spicules, their ends overlapping and cemented together by spongin. Typically the primary bundles are crossed by, and united with, rows of secondary bundles, more or less at right angles, in the parts nearer the free surface of the sponge. However, basally the framework tends to be more disorderly, owing to the abundance of cellular tracts, choanosomal tissue and sometimes developing embryos or larvae. The primary bundles may be more than one spicule thick in places, and they can diverge and branch upwards and outwards from the base of the encrusting sponge (fig. 19).

Rounded embryos with clearly demarcated surface and without spicules were found in generally the basal parts of some specimens collected in July and August. In late August one specimen exhibited, in addition to rounded embryos with no spicules (fig. 23), others with very fine, short oxeote spicules arranged around the periphery (fig. 24), and ovoid larvae containing an abundance of internal, short, thin spicules (fig. 25). The larvae have a distinct cap at one pole.

Seasonal variations in the skeletal arrangement.

Two extreme types of skeletons can be recognised. The arrangement in February and March is characterized by an abundance of stout spicules forming a framework of unispicular primary and secondary bundles near the surface of the sponge (fig. 9), with a more confused arrangement at the base. The dermal reticulation is composed of single spicules joined together at their ends to form irregular polygons, which approximate to squares or rectangles, occasionally triangles or pentagons. Here and there triangles are combined to form pentagonal or hexagonal patterns (fig. 13). The sponge surface can be largely smooth, or finely hirsute throughout, thanks to the projecting ends of primary bundles. A striking feature of the vertical sections, however, is the concentration of cellular tracts containing an abundance of spicules of various sizes (figs. 17 and 18).

The other extreme is best seen in specimens collected early in August. The spicules then are

very thin, forming a delicate skeleton of primary bundles with some intercrossing secondary bundles. The arrangement tends to be irregular and wide-meshed (fig. 10), with the primary bundles not completely in parallel and the secondary not crossing at regular intervals. The thin spicules tend to be completely enveloped by spongin, which seems more abundant than in the February form; spongin can even project from the surface in the form of tiny mounds enveloping the distal ends of the terminal primary spicules. The dermal reticulation is sparsely spiculated, with thin spicules forming an open tangential meshwork, in which the polygonal spaces can have sides of more than on spicule's length (fig. 14 and 15). In vertical sections the primary bundles may project some 2 or 3 spicule lengths beyond the interconnecting secondary spicules nearest to the surface (fig. 22). The cellular tracts beneath the dermal reticulation are practically free from spicules, and spicules which are present are all very thin (fig. 10). The tracts tend to be more widely dispersed in vertical sections than in the February form.

So different is the appearance between the two extreme forms that one might suppose that different species were involved were it not for the fact that most of the August specimens exhibit a thick-spicule framework in some, usually basal, regions (fig. 22). Conversely, the May specimen in fig. 21 has a framework of thick spicules overlying one of thin spicules. The primary bundles of the two zones are in continuity in both cases. Another specimen collected on 28th August 1984 had a patchy dermal reticulation, some areas exhibiting a thick- and others a thin-spicule meshwork. In the vertical sections the thin spicules formed a narrow zone above the older thick-spicule framework. Thin spicules were abundant in the interstices of the framework and in the cellular tracts in the basal regions, but distally the tracts contained relatively few spicules, if any. Rounded embryos were present in this specimen.

The specimens collected in April and May show transitional stages in that thin spicules are to be seen amongst the thick in the dermal reticulation and at the ends of some primary bundles, while the cellular tracts exhibit fewer spicules. The dermal reticulation can at times exhibit spicules in some abundance, some of the sides of the polygonal spaces being formed by two spicules, side by side. Presumably these April/May sponges were growing and spicules were being transferred from the tracts for incorporation into the newly-forming spicule framework.

The specimens collected in June are of particular interest in view of the marked decrease in coefficient of variation of the spicule dimensions reported above. The vertical sections in 4 out of the 9 specimens revealed an abundance of cellular tissue in the interstices of the spicule framework beneath the level of the subdermal cavity, but as the sponges had not been fixed for histological examination, the precise significance of this could not be established. The presence of gametes or embryos was not obvious. Some of the specimens had detritus on their surfaces, which were either smooth or minutely hirsute in places. Three specimens exhibited some very thin spicules in the tissue of the interstices in random orientation. They were not abundant and spicules of size intermediate between them and the skeletal spicules appeared to be lacking. The cellular tracts were abundantly supplied with spicules in 4 specimens, but contained no spicules in one specimen (fig. 11), and only thin spicules in another. One additional specimen had spicules in the basally-situated tracts, but not in the tracts nearer the surface. As with the May specimens, some of the links in the dermal reticulation comprised two spicules, side by side. With so much variation between the specimens, it is not easy to explain the marked fall in coefficient of variation, but probably juvenile spicules were only represented by the very thin interstitial examples, which were not abundant. While the evidence is not conclusive, it is likely that the June sponges in general had not been growing much, possibly because they had moved into a reproductive phase of activity (embryos are distinct in some July specimens).

The July specimens had cellular tracts which were free of spicules, excepting those in the basal regions of the sponges, some of which contained many thin spicules. Consequently the tracts were not so distinctly visible in surface sections when focussing beneath the dermal reticulation. Embryos were present in the sections of about half of the specimens. The embryos were distinctly rounded and did not contain any spicules (fig.23). Some very thin spicules occurred in the skeletal interstices in places. Embryos were also found in 5 out of 13 of the August specimens (figs. 24 and 25).

The September specimens exhibited basal skeletons of thick spicules overlain by spicule frameworks composed of thin, or medium-thick spicules, or frameworks with thin spicules in places and thicker spicules elsewhere. The cellular tracts

were either sparsely or moderately well spiculated. Some specimens had a zone of thin spicules united to form a delicate, somewhat irregular framework beneath the superficial, better constructed skeleton. In general the dermal reticulation had the arrangement seen in the February specimen. Spongin mounds at the distal ends of primary bundles were still in evidence in some specimens.

In October some specimens were showing thicker spicules in the cellular tracts, which appeared more numerous and crowded together. The dermal reticulation was like that of the February specimen, with a meshwork of single spicule links, but the spicules were not as thick. The lacework of cellular tracts was conspicuous beneath. The primary bundles hardly protruded above the reticulation and the spicules of the superficial framework were generally thicker than those of the underlying skeletal framework.

Finally, the December specimens had numerous tracts containing many spicules, some of which were thicker than those in the dermal reticulation. The latter, apart from its somewhat thinner spicules, resembled that of the February form. In vertical sections the superficial framework exhibited thicker spicules than the framework beneath, but their thickness was not as great as in the February specimen.

One cannot be precise about the seasonal trends in view of the considerable variation often found between specimens collected in the same month. One would need to take samples from one and the same specimen at monthly intervals throughout the year, and to make histological preparations, to be certain of understanding the changes taking place. However, in broad outline it would appear that in the Winter months the specimens are generally healthy. Spicule tracts are numerous and contain an abundance of developing and fully grown spicules, the spicule framework is well developed, with a neat orthogonal arrangement and the dermal reticulation exhibits a polygonal meshwork with singe spicule sides to the polygons. From April to May the sponge grows rapidly and spicules previously stored in, or moving along, the tracts become incorporated in the superficial skeletal framework. In June growth appears to cease and energy is probably diverted to the formation of gametes. Spicule production is at an end and the tracts become clear of spicules. Then towards the end of June and in July spicule production resumes, while embryo development is in process. The spicules formed, however, are very thin and not sufficiently numerous to enable a regular skeletal framework to be constructed, so that in August the superficial spicule framework and dermal reticulation appear delicate, wide-meshed and imperfect. From late August through to December the newly forming spicules progressively achieve greater and greater thickness and the superficial skeletal framework becomes more regular.

One specimen, collected in May, 1980, was largely composed of a clean skeleton, with clumps of detritus in some of the interstices of the distal framework and relatively little that could be regarded as representing living tissue. Slime strands were recognizable in places, however and clearly the sponge had not been completely dead at the time of collection. Most of the skeleton resembled that of a sponge collected in late Summer, while in places at the surface the spicule framework was reminiscent of the skeleton of a Spring specimen. Presumably this sponge had been living in conditions of near starvation throughout the Autumn and Winter months.

Skeletons even more extreme than the August specimens from North Wales were exhibited by most of the 5 Lough Ine specimens, collected on 12th September, 1983. The dermal reticulations were mostly composed of extremely short and thin spicules enveloped by spongin, and the mesh was wide, with sides of up to 4 spicules in series. Sometimes single spicules in isolation occurred within the spongin at the side of a polygon. Thin spicules were present in parts of the cellular tracts seen beneath the dermal reticulation, but slime strands unaccompanied by spicules were also visible. The skeletal framework superficially in vertical sections was quite irregular, the primary bundles protruding by generally 2 spicules lengths beyond the dermal reticulation. The primary bundles distally were enveloped by spongin. However, on one specimen an extensive framework of thick spicules was present just beneath the thin spicule framework at the surface. Another specimen had a dense, thick-spicule framework at the surface, from which few spicules protruded, many of which were broken. Presumably the surface here had not been growing, although in the cellular tracts and interstices of the framework there were thin spicules. Vertical sections of this specimen exhibited growth bands. Clearly it had come from a site which had not favoured continuous growth. To conclude, the Lough Ine specimens show similar varation to the specimens from North Wales, but 4 of the specimens represented a more extreme form of 'Summer' skeleton; the spicules were thinner and

shorter, the dermal reticulation wider-meshed and spongin appeared to be more in evidence. The seawater in Lough Ine reaches quite high temperatures in Summer months (Renouf, 1931; Kitching et al., 1952; Lilly et al., 1953) and at low water it cascades down the rapids, where the specimens were collected, to the sea. Probably the warmer conditions were responsible for the characteristic skeleton shown by the 4 specimens.

DISCUSSION

Taxonomy

There can be little doubt that the species identified as *Reniera elegans* (Bwk) by Topsent (1887, 1891, 1925) is the same as the *Isodictya elegans* of Bowerbank (1866, 1874). While Bowerbank was unaware of the existence of the segmented fibrils, which were first observed by O. Schmidt (1864) in a so-called variety of *Reniera aqueductus,* the characters described by Bowerbank for *I. elegans* are not incompatible with those of the species exhibiting slime strands. There is no record, to my knowledge, of Topsent having confirmed the presence of slime strands in Bowerbank's type specimen of *H. elegans* in the British Museum of Natural History. However, I have myself examined a preparation of Bowerbank's type, prepared by M. Burton in 1932 (32.11.5.9a: Herm Island), thanks to the courtesy of Miss Shirley Stone, and am convinced that the type is identical with the species containing slime strands. The preparation comprises two vertical sections and one surface section. The surface section is upside down and one of the vertical sections lies beneath it. Nevertheless one can see the characteristic dermal reticulation of the Winter-Spring specimens reported above, with a lacework of amber-brown strands beneath, possibly representing the cellular tracts (the original type was examined by Bowerbank in the dried state, so that slime strands would hardly be expected to be preserved in histologically recognizable form). The vertical sections reveal the typical, predominantly unispicular primary bundles, and the form and size (ca 105μm maximum in length) of the spicules also confirm the identity. Both thin- and thick-spicule frameworks occur in different parts of the sections.

I have also examined the slide (Bk 685) prepared by Bowerbank of a specimen identified by him as *I. elegans* that was collected from the North West coast of Ireland by the Rev. A.M. Norman and Mr. D. Robertson in 1874 (three years before Bowerbank died at the age of 80). This specimen is not *H. elegans.* The spicules are too long (up to about 180μm) and the characteristic dermal reticulation and lacework of cellular tracts are lacking. The Rev. A.M. Norman (Bowerbank, Vol. IV, 1882, p. X) writes: 'to his certain knowledge subsequently found specimens, during the latter years of Dr. Bowerbank's life when his powers of observation were not so keen as they had been, were frequently erroneously referred to already named types with which they had no connection'.

Characters given by Bowerbank for *H. elegans* are: (1) the presence of a dermal reticulation and its pattern (N.B. he over-emphasized the tendency for a triangular mesh and was unaware of the August form described above in which the reticulation seems incomplete; (2) the smooth surface (N.B. often minutely hispid under the microscope in some areas, or all over, as a result of the projection of the distal ends of the primary bundles); (3) the unispiculated primary and secondary bundles (N.B. the primary bundles may at times be more than one spicule thick in basal regions of the sponge); (4) the fistulous branches; (5) the simple or slightly raised oscula (N.B. oscula can also occur at the summits of well-developed mounds (fig. 1), the sides of which have a uniform texture and do not exhibit the characteristic lacework seen over much of the general surface of the sponge (figs. 1 - 4); (6) the short, stout spicules, 102 x 10μm and 80 x 1μm in figs. 4 and 5 of Plate XLIX in Bowerbank, 1874; and (7) the habitat (epiphytic on fucoid algae or zoophytes (Bowerbank, 1866), or encrusting under stones and on shells (Bowerbank, 1882). The short, very slender, so-called tension spicules of the "interstitial membranes", occurring in patches of 3 or 4 only, were possibly developing spicules, corresponding to the slender spicules seen in the interstices of the skeletal framework in some of the North Wales specimens. They seem of little diagnostic value.

Burton (1926), who seems to have been unaware of the existence of segmented fibrils in some haplosclerid sponges, or of Topsent's interpretation of *I. elegans,* considered this species to be no different from *I. cinerea* (Grant), apart perhaps from the colour (not recorded) of *elegans* when alive. For this identity to be valid one would need confirmation that both so-called species either have or do not have, slime strands. However, this can never be achieved, because Grant's original type specimen of *Spongia cinerea* (1827), later named *Isodictya cinerea* by Bowerbank (1866), has been lost. Instead one only

has Bowerbank's neotype. This was one of four dried specimens labelled *Halichondria cinerea* in Johnston's collection at the British Museum of Natural History. The other three were given separate species status by Bowerbank and named respectively *I. permollis, I. peachii* and *I. varians.* The neotype of cinerea was identified by Bowerbank by comparison with a portion of *Spongia cinerea* obtained from Grant (Bowerbank, 1866, p. 275). Later, however, Bowerbank stated (1874, p. 121) that the type specimen could not be found by Grant when it was required for the purpose of making an illustration. It is thus impossible to confirm that Bowerbank was correct in identifying the specimen as *cinerea,* and Johnston before him must have been uncertain because his four specimens of *cinerea* were sufficiently different to be ascribed to four different species by Bowerbank. Even if Bowerbank had been correct, one would still have to admit that he considered *I. cinerea* and *I. elegans* to be distinct species, the former, according to him, having an aspiculous dermal membrane and the latter, one that is spiculo-reticulated. This distinction cannot now be maintained, however, because the dermal reticulation of *elegans* often lies beneath the dermal membrane (see figs. 10 and 11), and having examined the sections of Bowerbank's neotype for *cinerea* I agree with Burton that there is no essential difference from those of *elegans.* The characteristic dermal reticulation is present in the former neotype, which seems better preserved than the *elegans* type; a brown granular network is visible, suggestive of slime strand tracts, also transparent spongin uniting spicules together, and the oxea attain about 110μm in length. However, while Bowerbank's *cinerea* does seem identical with his *elegans,* there is still the problem of deciding whether he was correct in applying the name *cinerea* to the specimen he selected as its neotype.

The original *Spongia cinerea* Grant (1827) was found in the Firth of Forth and was a blackish-grey specimen resembling a dark putrescent sponge even though healthy. It had a smooth, convex, fleshy, transparent surface and its oscula ('fecal orifices') were few, very large, circular and lying deeper than the general surface. The spicules were remarkably uniform in size, curved and suddenly coming to a point at both ends. They were 150μm long, judging from the illustration (fig. 3, Plate II, Grant 1826). This description is reminiscent of the plaque form of *Adocia simulans* Johnston, in regard to the smooth surface, the oscula and the uniform skeleton of short, stout, sharply pointed oxea. Moreover, I have seen healthy, blackish, putrescent-looking specimens of this species at Carriganorana, Southern Ireland and cannot full agree with Topsent's statement (1938) that exteriorly Grant's specimen scarcely resembled a plaque of *simulans.* Certainly Johnston (1842) regarded the two as distinct species, but in his description of *Halichondria cinerea* he altered somewhat the characters given by Grant, *cinerea* now being of uniform hair-brown or ash-grey colour, soft and friable when dry, of very fine sponge-like texture and with indistinctly marked oscula. There is no indication that Johnston actually saw the unique specimen of *S. cinerea* collected by Grant, which as stated above, I believe could have been what is now called *simulans.* Thus, of the two names, *elegans* and *cinerea,* there is much less doubt about the taxonomic meaning of the former and for this reason I prefer to retain the name *elegans* for the species discussed in this paper.

De Laubenfels (1936) proposed that the wide-spread lavender species customarily referred to as *cinerea* should be called *Haliclona permollis,* on the grounds that (a) Burton (1934) had stated that Bowerbank's specimens of *I. cinerea* and *I. simulans* were congeneric, whereas de Laubenfel's own studies of living specimens of *cinerea* had convinced him that the two were definitely not, (b) the name *I. ramuscula* (Bwk), which seemed closest in description to his concept of *cinerea,* was 'very unwieldy and difficult to use', and (c) the name *permollis* had been given by Bowerbank to one of the specimens labelled by Grant (sic) (? Johnston) as *H. cinerea.* However, de Laubenfels had not himself studied the specimens in the British Museum at that time, so that his proposal, to say the least, was premature. He appears to have neglected the possibility that Burton may not have been fully justified in regarding *cinerea* and *simulans* as congeneric.

For the present I shall retain the generic name *Haliclona* for the species discussed in this paper. *Haliclona* Grant 1835-1841 was first used for the species *H. occulata* (sic, 1841, p.5: *oculata* 1841, p.312) and so includes species having an isodictyal unispicular framework, with spicules tending to be short and uniform and well embedded in spongin. Certainly the species is not reniform in the sense of Griessinger (1971) and Lévi (1973) and in any case there are difficulties over using the name *Reniera* (Burton, 1934; Wiedenmayer, 1977a). Likewise the genus *Adocia* Gray (1867) would be inappropriate, because the dermal reticulation is not always in evidence

and is not sufficiently distinct to constitute a true tangential ectosomal skeleton. Wiedenmayer (1977b) and Bergquist & Warne (1980) have recently emphasized the difficulty in distinguishing *Reniera* and *Haliclona,* the characters used to separate them being relative rather than absolute. While Wiedenmayer prefers to retain *Reniera,* Bergquist & Warne unite *Reniera* and *Haliclona* under the same genus *Haliclona,* thus following de Laubenfels (1936). A recent review and revision of the taxonomy of the Haplosclerida is provided by de Weerdt (1985).

Skeletal variation

The spicule dimensions recorded here show some degree of variation from specimen to specimen, presumably due to seasonal factors operating during periods of growth of the sponges. The overall range of spicule size exceeds the 80 - 110 (+/-2.5) – 150; 2.0 - 5.0 - 8.0μm given by Griessinger (1971) for Mediterranean *H. elegans,* as would be expected from the difference in latitude (cf. *H. oculata*; Hartman, 1958). According to Topsent (1925), however, Mediterranean specimens of *H. elegans* can have spicules attaining 160 x 8 - 170 x 10μm (at Banyuls), and Channel specimens can even reach 185 - 200μm in length and 16μm in thickness (at Luc, 49°18'N 0°21'W). It remains to be seen whether these extremes result from phenotypic variation or whether distinct sub-species are concerned.

Interpretation of the changes in frequency of the spicule size categories is not completely reliable when aggregated data are concerned. Ideally the samples should have been taken from one and the same sponge at monthly intervals, to avoid the possibility of variation between specimens. However, one would have expected thinner spicules to be produced during the period from May to September, because this is the period when the dissolved silicate concentration in the seawater would have been expected to be minimal (Ewins & Spencer, 1967; Slinn & Chapman, 1965); A.R. Stone (1970) has demonstrated that the lengths and widths of styles and subtylostyles of *Hymeniacidon perleve* are correlated with the dissolved silicate concentration. Also other observations, notably by Jørgensen (1944), Pé (1973) and Simpson *et al.* (1985), leave no doubt that spicule width at least is dependent on the silicic acid concentration. The rise in the means for width and length in June, and the decrease in the corresponding standard deviations and coefficients of variation, were, however, unexpected and too great to be accounted for by the minor fluctuations in silicate concentration during the Summer. They appear to have been caused by a cessation of spicule production, possibly associated with the formation of gametes, because larvae were found in specimens collected in late July and August. Embryos or larvae have also been recorded by Topsent (1925) and Lévi (1956) for July-August specimens collected from the N.W. shores of France. It is unlikely that spicule production in June ceases because the dissolved silicate concentration has fallen below a threshhold value, because the silicate concentration tends to be a little higher in June than May. Also the evidence indicates that the number of megascleres produced in juvenile freshwater sponges is greater at lower silicate concentration (Pé, 1973; Jørgensen, 1944) than at higher, excepting subthreshold values.

The graphs showing the fluctuations in the coefficients of variation do not conform with the data given by Stone (1970) for spicules of *Hymeniacidon perleve;* the coefficients for spicules of this species were maximal in June. Also the coefficients for *Gellius angulatus* were minimal in May rather than June (Jones, 1984). Clearly there are more factors controlling the coefficients of variation than the silicate concentration of the seawater. Apart from cessation of spicule production during embryo formation, nourishment may be a factor. Weissenfels & Landschoff (1977) have stated that undernourishment can cause spicules to become thinner, even when the silicate concentration is adequate for normal growth.

Temperature also has an effect on mean spicule dimensions (Stone, 1970), particularly on width (Simpson, 1978), thicker megascleres forming at lower temperatures. The monthly mean temperatures of the seawater in the Menai Straits were minimal in March, 1984 (5.2° C) and February, 1985 (3.9°C) and maximal (17.5°C) in August, 1984 (Walker, 1985). Surface temperatures in the Irish Sea generally are minimal in February or March and maximal in August or September (Slinn, 1957-62, 1966; Slinn & Chapman, 1963-5). The rise in temperature from March to August could help to explain the general fall in mean width of the *H. elegans* spicules during the Summer, but not the apparent increase in June.

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