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ON THE GENERA ECHINAXIA AND RHABDOSIGMA [PORIFERA].

By E. F. Hallmann, B.Sc., Linnean Macleay Fellow of the Society in Zoology.

(Plates xxi.-xxii.; and two Text-figures.)

The genera *Echinaxia* and *Rhabdosigma* were proposed, without definition, in my "Revision of the Genera with microscleres included, or provisionally included, in the Family Axinellidæ," for two species wrongly referred to the genera *Axinella* and *Sigmaxinella* respectively. I now publish definitions of these genera, together with remarks on their probable relationships, and re-descriptions of their type-species; and for the reception of certain species, apparently related to *Echinaxia*, I propose two new genera, *Axinectya* and *Hetercetya*.

Genus Echinaxia.

Definition.—Desmacidonidæ of erect, lamellar or ramose habit, with a skeleton consisting axially of a reticulation of spiculospongin fibres cored by comparatively small, smooth styli and echinated by vestigially spined acanthostyli, and extra-axially of (typically non-connected) fibres radiating outwards to the surface, composed partly of the same two kinds of styli, and partly of obliquely directed (*i.e.*, plumosely disposed) long, smooth styli—the last-mentioned spicules typically occurring only towards the outer extremities of the fibres, and forming terminal tufts which project beyond the dermal membrane; the extra-axial fibres, however, may be so reduced as to be represented by scarcely more than their terminal tufts of long styli. The acanthostyli are of characteristic form, having their basal moiety free from spines and more or less curved. Microscleres are absent.

Type, *E. frondula* Whitelegge.

Two species with a spiculation closely analogous to that of *Echinaxia frondula* have been described by Thiele(5) under the

names of *Raspailia hirsuta* and *R. folium*; but whether these also agree therewith (or with one another) sufficiently to necessitate their inclusion in the same genus is not quite certain, owing to the inadequacy of their descriptions. As, however, they certainly do not belong to *Raspailia*, and the establishment of a separate genus for their reception would be premature, I propose that they be referred (provisionally, at least) to *Echinaxia*, and have attempted to define the genus accordingly. With respect to certain features of the skeleton, the differences between the three species are rather considerable. In *E. hirsuta*, according to Thiele's description, the skeleton consists axially of a network of horny fibres cored by the smaller smooth styli and echinated by more abundant acanthostyli, and the extra-axial fibres are provided with projecting long styli apparently throughout their entire length. On the other hand, in *E. frondula* the axial skeleton is a dense and nearly subrenieroid reticulation composed almost entirely of the smaller smooth styli (spongin being present only in very minute quantity, and the acanthostyli scarce), while the extra-axial fibres are provided with projecting long styli only towards their outer extremities. Regarding the arrangement of the skeleton in *E. folium*, no definite information is available, but apparently it is reticulate throughout; in this species also, however, long smooth styli project far beyond the surface of the sponge, and it is presumable that these are the terminal spicules of fibres corresponding to the extra-axial fibres of the other species. In *E. frondula* more especially, the intrafibral smooth styli approximate rather closely both in size and shape to the acanthostyli, conveying the suggestion of their original derivation therefrom; and this view of their origin is further supported by the fact that, in *E. hirsuta*, they occasionally exhibit a slight roughness of the surface, suggestive of a vestigial spination.

Acanthostyli similar to those of *Echinaxia* are characteristic also of the genus *Raspaxilla*, lately proposed by Topsent(**10**) for a new species from the Antarctic; and this genus (as exemplified by its single known species) further resembles *Echinaxia* in the possession of a skeleton condensed axially and consisting extra-axially of radiating fibres terminating at the surface in a tuft of

long projecting styli. But, in *Raspaxilla*, it is these long styli also which are the coring spicules of the fibres, both axial and extra-axial (the only spicules projecting therefrom being the acanthostyli), whilst spicules corresponding to the small intra-fibral styli of *Echinaxia* are wanting; and, furthermore, there are present in *Raspaxilla* special dermal styli, disposed as in the genus *Raspailia*. On the reasonable assumption of a near relationship between the genera *Echinaxia* and *Raspaxilla*, it accordingly appears probable that the long smooth styli of the former are homologous with those coring the fibres of the latter, and hence, almost certainly, with the principal megascleres of normal Myxillinæ.

Under the name of *Axinella mariana*, Ridley and Dendy* have described a species, of ramose habit, with a skeleton consisting axially of "a fairly dense core of irregularly arranged, short, bent, stylote spicules," and extra-axially of very large styli or tylostyli (up to 2200 by 30μ in size) having their bases imbedded in the confused central mass and their apices projecting far beyond the surface of the sponge. Only these two forms of spicules are present. The short styli (size about 300 by 13μ, but variable) are sharply bent near the base, finely and gradually pointed at the apex, and *rarely slightly spined*. It is probable, therefore, that this species is closely related to *Echinaxia*; though the differences distinguishing it therefrom appear too considerable to be regarded as of less than generic value. As the species certainly cannot be permitted to remain in the genus *Axinella*, nor yet in the genus *Syringella*, to which Topsent(9b) would assign it, I propose for its reception the new genus *Axinectya*.

Another species possessing acanthostyli similar to those of *Echinaxia* is that which Thiele(5) has described as *Raspailia*(?) *villosa*. This species, however, is of massive habit, without an

* Report on the Monaxonida collected by H.M.S. "Challenger." In the same report, there is also assigned to the genus *Axinella* a second species with acanthostyli, viz., *A. monticularis*. There can scarcely be any doubt that the correct position of this species is in the genus *Aulospongus* Norman, hitherto regarded as being represented only by the single species, *A. tubulatus* Bowerbank.

axially condensed skeleton, and also differs from *Echinaxia*, *Axinectya*, and *Raspaxilla* in the absence of megascleres corresponding to the long (principal) styli, and from *Raspaxilla*, furthermore, in the non-possession of special dermal megascleres. For the reception of this species, accordingly, a new genus appears also to be required, and for this I propose the name *Heterectya*.

Echinaxia frondula Whitelegge.

(Plate xxi., figs.3, 4; Plate xxii., figs. 1, 2; and Text-fig.1).

1907. *Axinella frondula* Whitelegge, Mem. Austr. Mus., iv., Pt. 10, p.509, Pl. xlvi., fig.32.

1916. *Echinaxia frondula* Hallmann, Proc. Linn. Soc. N. S. Wales, xli., Pt. 3, p.543.

External features.—The single example of the species which has so far been obtained consists of a very thin, flabelliform lamina, gradually narrowed proximally into a (likewise much compressed) stalk-like prolongation, and divided marginally, by very wide and deep notches, into four sub-spathulate lobes. A figure illustrating the external form accompanies the original description. The specimen appears to be complete with the exception of the basal extremity of the stalk; but possibly it represents only portion of a much larger specimen, of very deeply partite, or foliose, habit. It measures 75 mm. in total height, 50 mm. in greatest width, 7 mm. in width at the lower extremity of the stalk, and only from 1 to $1\frac{1}{2}$ mm. in thickness (except towards the base, where it ultimately attains a thickness slightly exceeding 2 mm.). The surface is even, and presents a densely hispid, or, rather, finely pilose appearance, due to the projection beyond the dermal membrane of the terminal spicules of the skeletal fibres; the dermal membrane, which is excessively thin, is thereby rendered quite indistinct. Oscula are not discernible. The consistency of the sponge in alcohol is moderately firm and tough, flexible and elastic; the colour, light brownish-grey.

Skeleton.—The skeleton (Plate xxii., figs.1, 2) consists (i.) of a dense and sharply delimited axial region, of reticulate pattern, composed chiefly or almost entirely of small, smooth styli, and

(ii.) of strongly developed, single fibres radiating therefrom outwards to the surface, at an average distance apart of about 200μ. Also participating in the formation of the axial skeleton, but occurring only interstitially, are from scarce to fairly numerous, singly dispersed, long slender styli, directed longitudinally; these spicules appear to be more abundant in the older portions of the sponge. The spaces between the extra-axial fibres are entirely free from spicules. The axial reticulation, as seen in longitudinal transverse section, presents an irregularly subrenieroid pattern, not altogether unlike that characteristic of the genus *Petrosia*; examined, however, in section parallel to and in the mid-plane of the sponge (Plate xxi., figs. 3, 4) it is seen to be formed (*i.e.*, in its most central region) of somewhat ill-defined, plurispicular strands (of the already mentioned small styli) running longitudinally in close subparallelism, and interconnected by a paucispicular, plexus-like network of the same spicules, as well as by occasional single spicules directed transversely. The longitudinal spicule-strands are echinated by scarce acanthostyli, which usually project almost perpendicularly; and echinating acanthostyli also occur (sometimes rather abundantly) on the outward side of the outermost fibres of the axial reticulation. In the youngest portions of the skeleton, spongin is present only in the least possible quantity requisite to hold the spicules together: even in the oldest parts of the sponge, it seldom forms a distinct sheath to the spicule-strands, and (owing to its colourlessness) is clearly discernible only when stained.

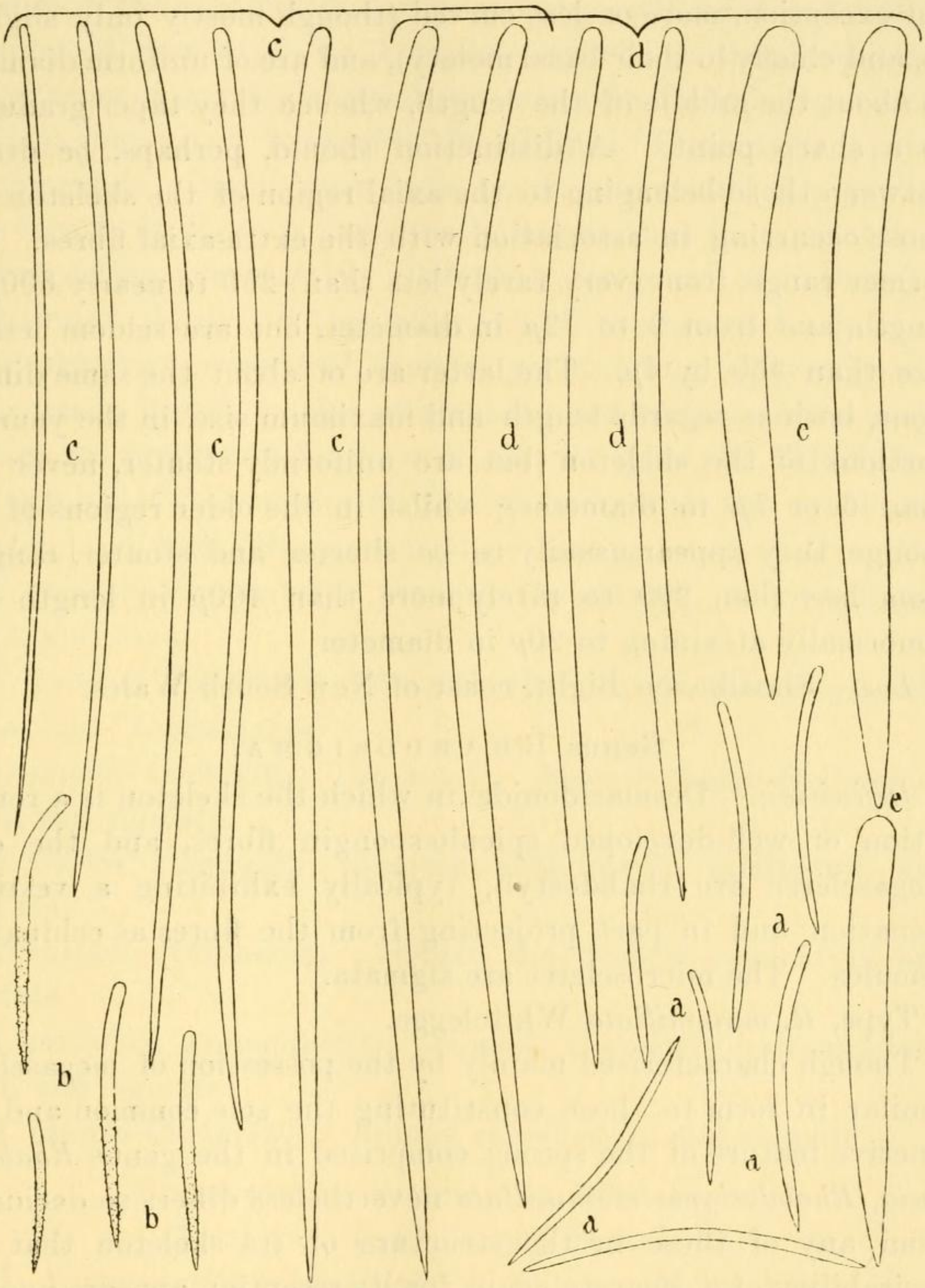
The extra-axial fibres,—which vary in stoutness from 25 to 90μ,—are composed, throughout the greater part of their length, almost entirely of small smooth styli (similar to those of the axial skeleton) closely packed together side by side; accompanying these spicules there are also acanthostyli, mostly located at the surface of the fibre, and in part projecting therefrom at a small angle of inclination as echinating spicules. The latter spicules (the acanthostyli) are at first relatively very few, but towards the outer extremity of the fibre (though still at some considerable distance below the dermal surface) they increase in number at the expense of the former, sometimes almost entirely

replacing them; and at the same time, also, there enter into the formation of the fibre, long, slender, smooth styli, which are directed at a greater or less angle of inclination to the fibre, projecting therefrom in plumose fashion. With the advent of the last-mentioned spicules, the others rapidly diminish in number and soon cease. Usually the total length of fibre from which the long styli project is relatively so short that they may appear to form scarcely more than a divergent tuft at the extremity of the fibre; occasionally, however, one or a few such spicules are to be found projecting from other parts of the fibre also. The terminal spicules project almost their whole length beyond the dermal membrane. These long styli of the fibres are generally not distinguishable from those occurring singly dispersed in the axial skeleton; but in some portions of the skeleton examined, taken from near the base of the sponge, a large proportion of them were found to be much stouter and relatively shorter. The mode of origin of the extra-axial fibres from the axial skeleton is most unusual; from the longitudinal spicule-strands of the axial skeleton, short lateral branches arise, which, several together, converge and become confluent. As already indicated, the extra-axial fibres are entirely unconnected by transverse fibres.

Spicules.—(i.) The small smooth styli (Text-fig.1, *a*) are of nearly uniform diameter throughout their length to within a short distance of their apical extremity, tapering thence gradually to a sharp point, and are, without exception, more or less curved, often rather strongly so, with the point of maximum curvature situated not far below their centre. They range from 75 to 150μ in length and up to 6·5μ in diameter; but individuals below 90μ in length or above 5μ in stoutness are extremely rare except in the older portions of the sponge. Of frequent occurence among the styli are modifications thereof in the form of oxea; these are symmetrically curved, and slightly fusiform. Transitional forms between the styli and oxea are rare or absent.

(ii.) The acanthostyli (Text-fig.1, *b*) are likewise invariably curved, but have the curvature restricted to their basal moiety, or often even to their basal third, the remainder of the shaft being straight and gradually tapered, *i.e.*, somewhat conical; the

apical extremity is acutely pointed, and the basal end evenly rounded off. The spines are confined to the distal moiety of the



Text-fig. 1.

Echinaxia frondula.—*a*, coring styli of the fibres; *b*, acanthostyli; *c*, interstitial styli of the axial skeleton; *d*, styli projecting from the extra-axial fibres and hispidating the surface of the sponge; *e*, abnormally stout, projecting styli of the extra-axial fibres in the older portions of the sponge.

spicule, and are of minute size and closely set. The acanthostyli

range from 80 to 120μ in length and from 4·5 to 8μ in stoutness.

(iii.) The long smooth styli (Text-fig. 1, *c*, *d*, *e*) are, almost without exception, more or less curved (though mostly only slightly so, and chiefly in their basal moiety), and are of uniform diameter to about the middle of the length, whence they taper gradually to a sharp point. A distinction should, perhaps, be drawn between those belonging to the axial region of the skeleton and those occurring in association with the extra-axial fibres. The former range from (very rarely less than) 250 to nearly 600μ in length, and from 2 to 12μ in diameter, but are seldom less in size than 350 by 4μ. The latter are of about the same dimensions, both as regards length and maximum size, in the younger portions of the skeleton (but are uniformly stouter, never less than 6 or 7μ in diameter); whilst in the older regions of the sponge they appear usually to be shorter and stouter, ranging from less than 200 to rarely more than 400μ in length and abnormally attaining to 20μ in diameter.

Loc. – Shoalhaven Bight, coast of New South Wales.

Genus Rhabdosigma.

Definition.— Desmacidonidæ in which the skeleton is a reticulation of well-developed spiculo-spongin fibres, and the only megascleres are rhabdostyli, typically exhibiting a vestigial spination, and in part projecting from the fibres as echinating spicules. The microscleres are sigmata.

Type, *R. mammillata* Whitelegge.

Though characterised mainly by the possession of megascleres similar in form to those constituting the sole common and distinctive feature of the species comprised in the genus *Rhabderemia*, *Rhabdosigma mammillata* nevertheless differs so decidedly from any of these in the structure of its skeleton that the desirability of a separate genus for its reception appears unquestionable. An adequate description of the skeleton in most of the species of *Rhabderemia* has not been given; but all of them are of encrusting or semi-encrusting habit, and apparently only in one of them, *R. indica*, are the megascleres at all aggregated into definite fibres or strands; even in this species, only a proportion of the megascleres are so arranged, and, according to

Dendy, no spongin cementing them together is detectible. Furthermore, in the typical species of *Rhabderemia*, including *R. indica*, the spiculation includes very small scattered styli,—designated microstyli by Topsent,—which, as they sometimes show traces of a vestigial spination, are probably homologous with the acanthostyli of "ectyonine" Myxillinæ. The only two species of the genus without microstyli are *R. intexta* and *R. prolifera*. The former of these is imperfectly known, but it appears to be an encrusting species with a skeleton composed of rhabdostyli distributed singly; in the latter, which is also encrusting, the main skeleton consists of rhabdostyli standing separately with their heads based on the substratum, and special dermal megascleres are present in the form of slender tylostyli. The following is a list of the species of *Rhabderemia*, with the spiculation of each, and with references to their descriptions:—

R. toxigera Topsent(**7**). Smooth rhabdostyli, microstyli, sigmata, and toxa.

R. guernei Topsent(**6**). Smooth rhabdostyli, microstyli, sigmata, and "thraustoxes."

R. pusilla Carter(**2**a); Topsent(**9**). Smooth rhabdostyli, microstyli, and sigmata.

R. indica Dendy(**3**). Smooth rhabdostyli, microstyli, and sigmata.

R. spinosa Topsent(**8**). Spined rhabdostyli, microstyli, and sigmata

R. prolifera Annandale(**1**). Smooth rhabdostyli, dermal tylostyli, and sigmata.

R. intexta Carter(**2**b). Spined rhabdostyli, and sigmata.

Rhabdosigma mammillata Whitelegge.

(Plate xxi., figs.1, 2; and Text-fig.2).

1907. *Sigmaxinella mammillata* Whitelegge, Mem. Austr. Mus., iv., Part 10, p.512.

1916. *Rhabdosigma mammillata* Hallmann, Proc Linn. Soc. N. S. Wales, xli., Part 3, p.520.

External features.—The type-specimen (which is the only example of the species so far obtained) may be described as possessing the form of a broad and low, moderately thick, erect

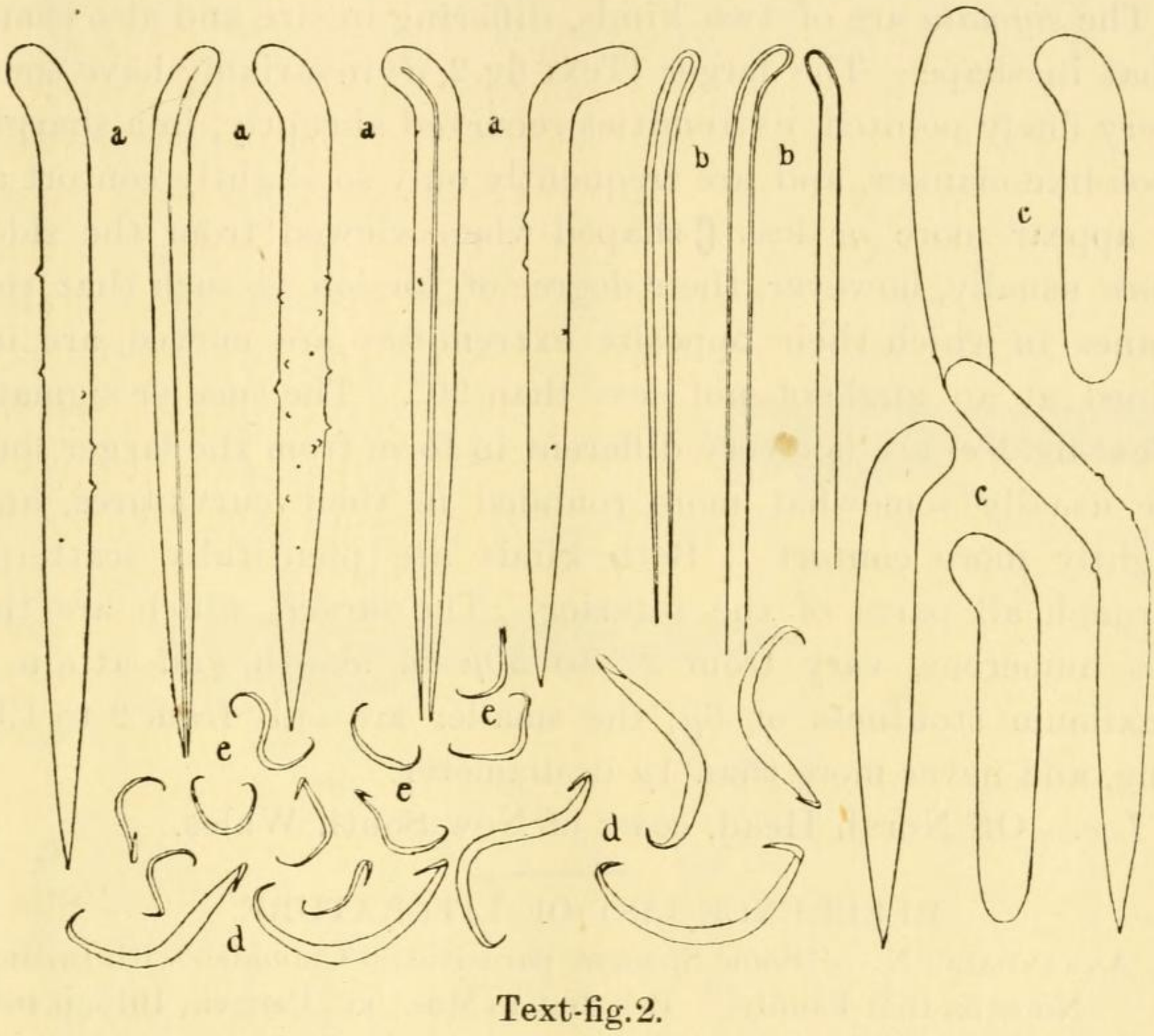
plate, proximally contracted into a short and stout stalk, and subdivided marginally into a series of short digitiform, or mammiform lobes, and provided also with (a few) additional similar lobes arising adventitiously from its sides. Probably the habit of the species is often simply flabellate, or, more precisely, digitoflabellate; but in the present instance the lamina is vertically folded, and partially concrescent with itself along one edge, so that its shape in horizontal cross-section is roughly that of the figure 6. In consequence of this, and of the laterally-arising lobes, the essentially lamellar form of the sponge is considerably obscured (Plate xxi., fig.2). The specimen, which is imperfectly preserved in alcohol, measures 70mm. in height, 65mm. in width, and about 40mm. in total thickness; the thickness of the lamina (as also the diameter of the lobes) varies from 10 to 15mm.; and the length of the longest lobe is 25 mm. On the summit of each lobe are from two to seven small, circular oscula, from 1 to (rarely) 2 mm. in diameter, arranged usually in one or two straight rows; and traversing the lobe longitudinally throughout its entire length are a corresponding number of main excurrent canals. On some of the lobes there is observable, radiating towards the oscula, a series of faintly marked grooves or shallow fissures; but these are probably only accidentally-caused cracks. Owing to its abrasion, the dermal membrane is almost entirely wanting; but from traces of it remaining here and there on the less exposed portions of the surface, it would appear to have formed, when intact, a very thin and closely adherent layer, non-separable from the underlying tissues, and finely granular on the surface. Subdermal spaces are indiscernible. Where the dermal membrane is wanting, the surface presents a somewhat velvety aspect,—due to the numerous slightly projecting points of the terminal spicules of the main skeletal fibres,—and is dotted (at distances apart of about 1 mm.) with small pinhole-like "pores;" these latter are, of course, not the dermal pores (as the original description would suggest), but the (subdermally situated) orifices of the main incurrent canals. The consistency of the sponge is firm and tough, compressible and resilient; the texture, dense. The colour in alcohol is light brown.

Skeleton.—The skeleton (Plate xxi., fig.1) is composed of well-developed spiculo-spongin fibres, echinated, as well as cored, by the characteristic megascleres, the rhabdostyli; megascleres scattered between the fibres are rare or absent. With respect to its arrangement, it presents, in keeping with the lamellar form of the sponge, a somewhat denser central, or *axial* region, of usually fairly considerable width, within which the direction of the main fibres is longitudinal or nearly so, and connecting fibres between them are numerous; and exteriorly to this (on either side of it, in the main body of the sponge), extending therefrom to the surface, an *extra-axial* region, in which the direction of the main fibres is more or less obliquely transverse (occasionally, in the lobes, nearly perpendicular to the longitudinal direction), and connecting fibres between them (excepting in the older portions of the sponge) are relatively few. The demarcation between the two regions, however, is generally by no means pronounced. In the extra-axial region, particularly, the skeleton is of very regular and simple pattern (Plate xxi., fig 1), with the main fibres running in nearly straight courses, approximately parallel to one another, at a distance apart of about a spicule's length, and chiefly connected together by their echinating spicules in the manner presently to be described, eventually, however, in the older portions of the sponge, these connecting spicules become invested each with an ensheathing layer of spongin, thus giving rise to connecting fibres, and the pattern of the extra-axial skeleton is then rectangularly reticulate. In the axial region the main fibres are much less regularly disposed, and the pattern of the skeleton is distinctly reticulate throughout, with (except in the youngest portions of the sponge) meshes of more or less rounded shape; in the oldest portions of the sponge the meshes become reduced in size, often almost to the point of obliteration. The spicules coring the main fibres (both axial and extra-axial) are disposed, somewhat loosely, in a slightly plumose fashion, frequently with the points of some of them projecting a little beyond the spongin-sheath, and vary in number, in a cross-section of the fibre at any point, from 3 to about 8; they are generally somewhat the more numerous, and

their plumose arrangement is generally the more pronounced, towards the outermost extremities of the extra-axial fibres (*i.e.*, near the surface of the sponge). The connecting fibres contain only one or two spicules. A most unusual (possibly abnormal) circumstance in connection with the coring spicules of the axial main fibres,—apparently, however, only in the older portions of the skeleton,—is the fact that a variable (often a very considerable) proportion of them fail to grow much beyond their very earliest developmental stages,—their immaturity in many cases being such that nothing more of them can be discerned than the faint outline of their axial canal. The echinating spicules are usually directed almost or quite perpendicularly to the fibres, and stand, on the average, at a distance apart of (at the most) not more than one-half their own length. A considerable proportion, if not the majority, of the echinating spicules project from their supporting fibres in such directions as apically to impinge upon and become inserted into adjoining fibres, and thus come to play the part of connecting spicules; in the axial region of the skeleton, and also (as already mentioned) in the older portions of the extra-axial region, these connecting spicules usually become entirely ensheathed in spongin, and thus give rise to additional connecting fibres. The extra-axial main fibres are usually between 60 and 80μ, rarely as much as 100μ, in stoutness; the axial main fibres, owing to the greater development of their spongin-sheath, occasionally attain to over 250μ in stoutness in the stalk of the sponge, but in the lobes seldom exceed 150μ. The terminal spicules of the extra-axial main fibres are free from spongin except basally, and form, at the extremity of each fibre, a slightly divergent penicillate tuft, projecting into the dermal membrane. There is no dermal skeleton.

Spicules.—The rhabdostyli (Text-fig.2) range from 160 to 280μ in length and attain a maximum stoutness of 18μ; in their very earliest developmental stages they already measure 5 or 6μ in stoutness, and the diameter of their axial canal is only slightly less. They have the shaft bent, as a rule rather sharply and angulately, at a distance of from 20 to very seldom more than 30μ from the base, and at an angle usually much less than

(though occasionally exceeding) 45°. The basal extremity is evenly rounded off, not tylote; the portion of the shaft between it and the point of flexure is usually straight or very nearly so; the remainder of the shaft is, almost without exception, perfectly straight, and tapers gradually to a sharp point. Basally, for at



Text-fig.2.

Rhabdosigma mammillata—*a*, fully-grown rhabdostyli; *b*, immature rhabdostyli; *c*, abnormal forms of rhabdostyli; *d*, larger sigmata; *e*, smaller sigmata.

least one-fourth of the entire length of the spicule, and also apically, for about the same distance, the shaft is invariably quite smooth; but not infrequently, over some portion of its intermediate region, there occur a few small, perpendicularly directed spines, the largest not exceeding 2μ in height. In the case of an unusually large number (at least 25%) of the (otherwise fully-grown) spicules, the axial canal remains unclosed apically, and is then frequently very conspicuous, occasionally attaining a diameter of as much as $4{\cdot}5\mu$. Also of rather frequent occurrence are abnormal forms (Text-fig.2, *c*), generally with the

apical (as well as the basal) extremity rounded off, and nearly always stouter and much shorter than the normally developed spicules; the extreme forms of these are short straight strongyla, ranging up to 25μ in stoutness, and occasionally down to less than 100μ in length.

The *sigmata* are of two kinds, differing in size and also somewhat in shape. The larger (Text fig.2, *d*) invariably have their (very finely pointed) extremities recurved abruptly, in a sharply hook-like manner, and are frequently only so slightly contort as to appear more or less C-shaped when viewed from the side; more usually, however, their degree of torsion is such that the planes in which their opposite extremities are curved, are inclined at an angle of not less than 90°. The smaller sigmata (Text-fig.2, *e*) are not very different in form from the larger, but are usually somewhat more rounded in their curvatures, and slightly more contort. Both kinds are plentifully scattered through all parts of the interior. The larger, which are the less numerous, vary from 22 to 30μ in length, and attain a maximum stoutness of 3μ; the smaller are only from 9 to 13μ long, and never more than 1μ in diameter.

Loc.—Off Norah Head, coast of New South Wales.

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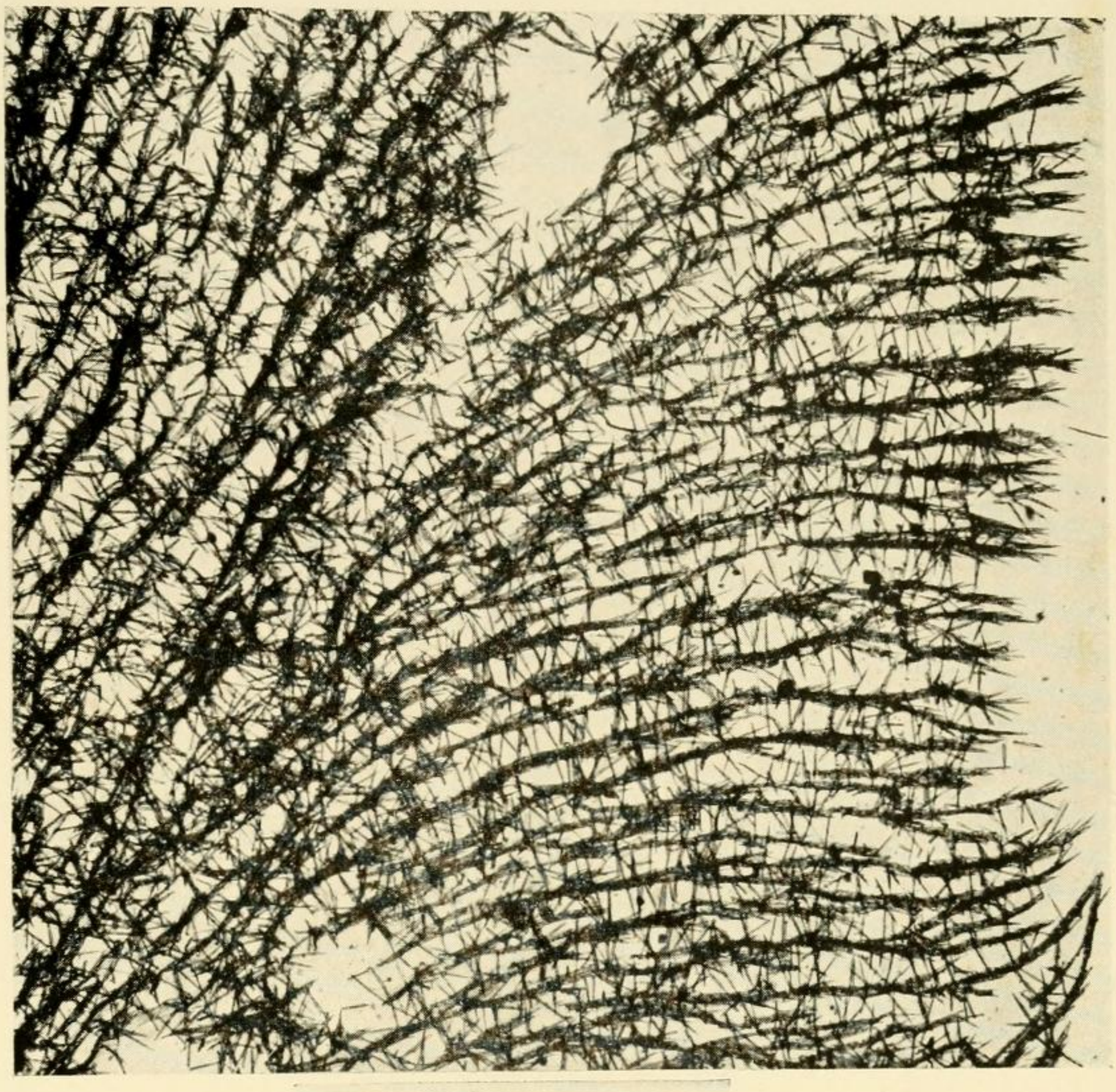

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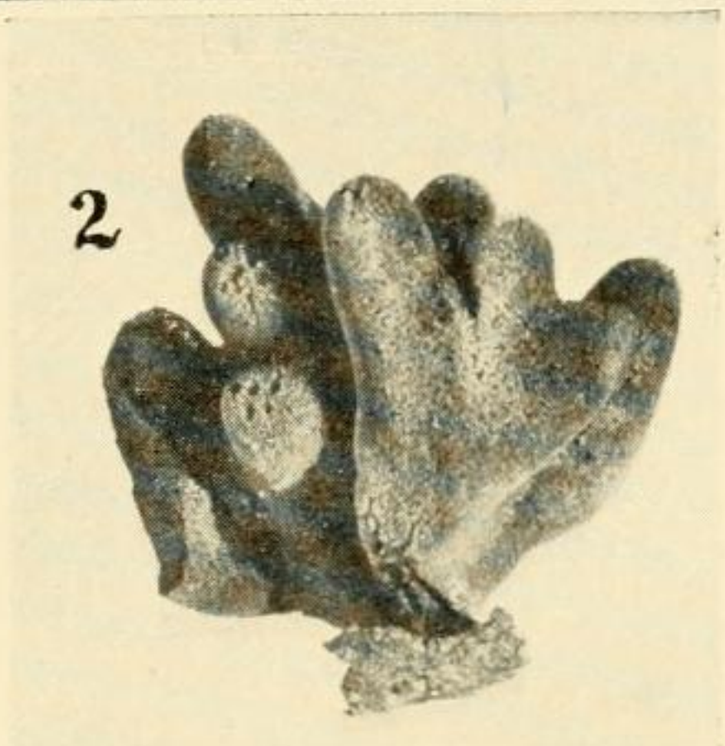

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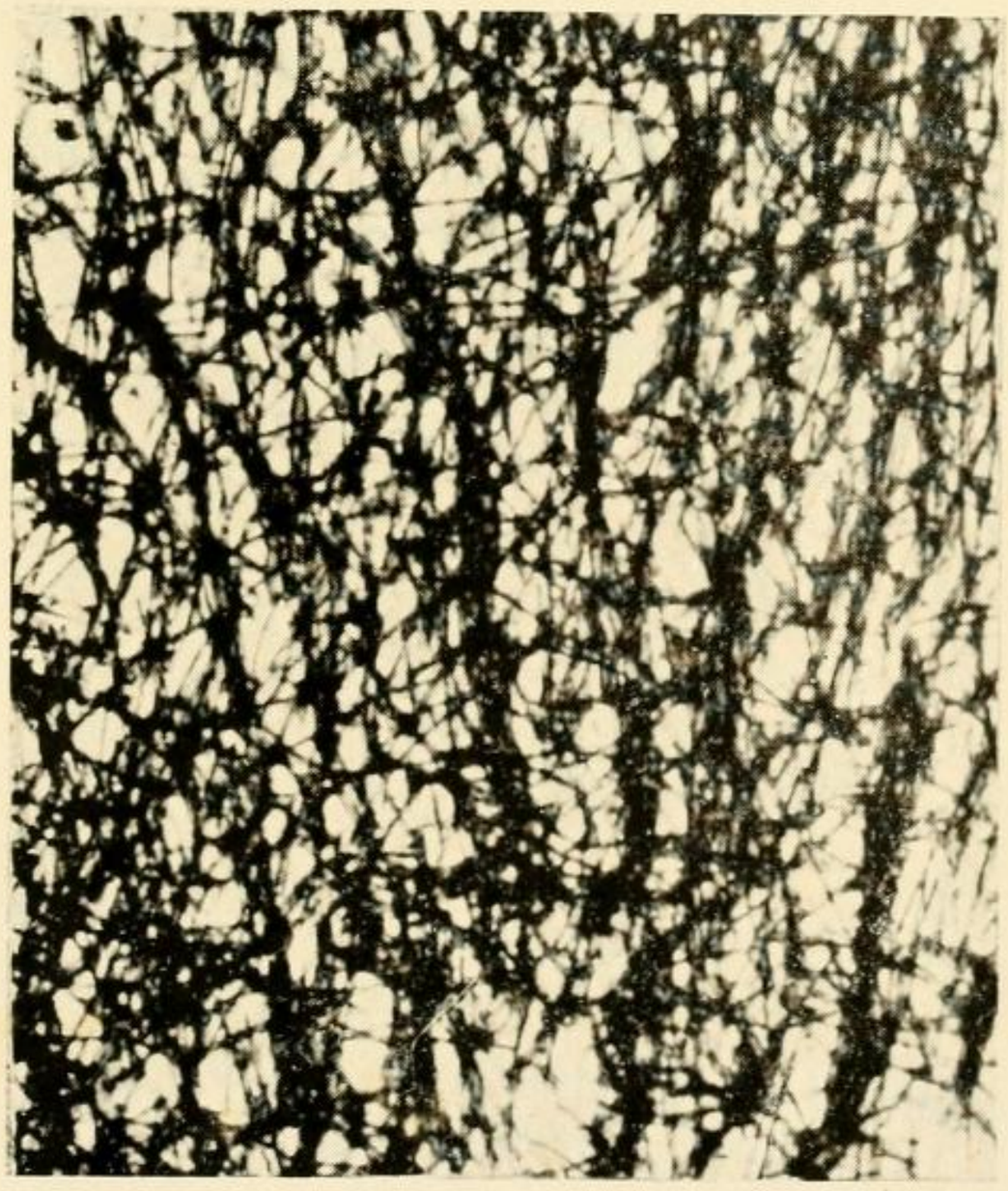

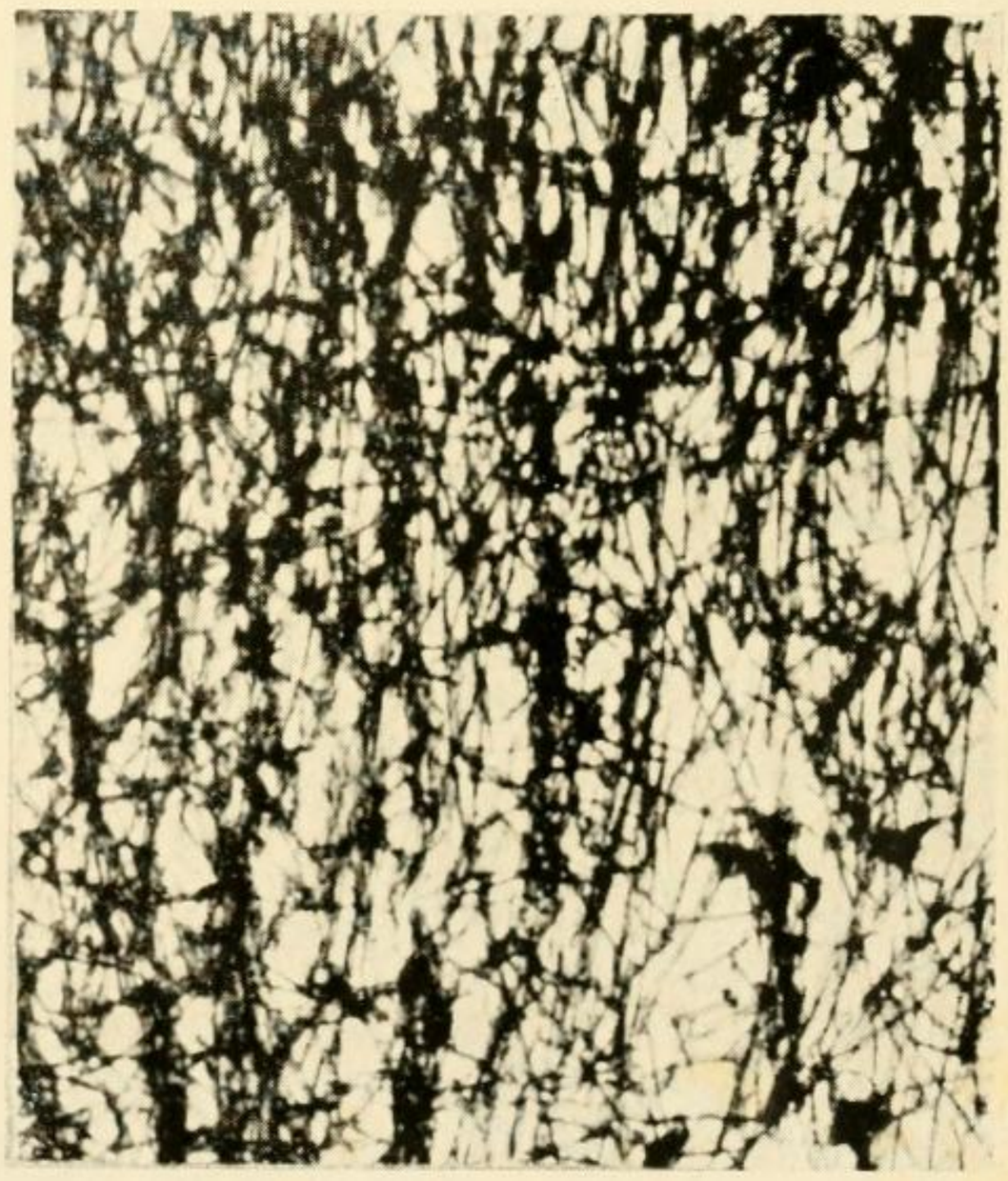

Figs. 1-2. *Rhabdosigma mammillata.*

Figs. 3-4. *Echinaxia frondula.*

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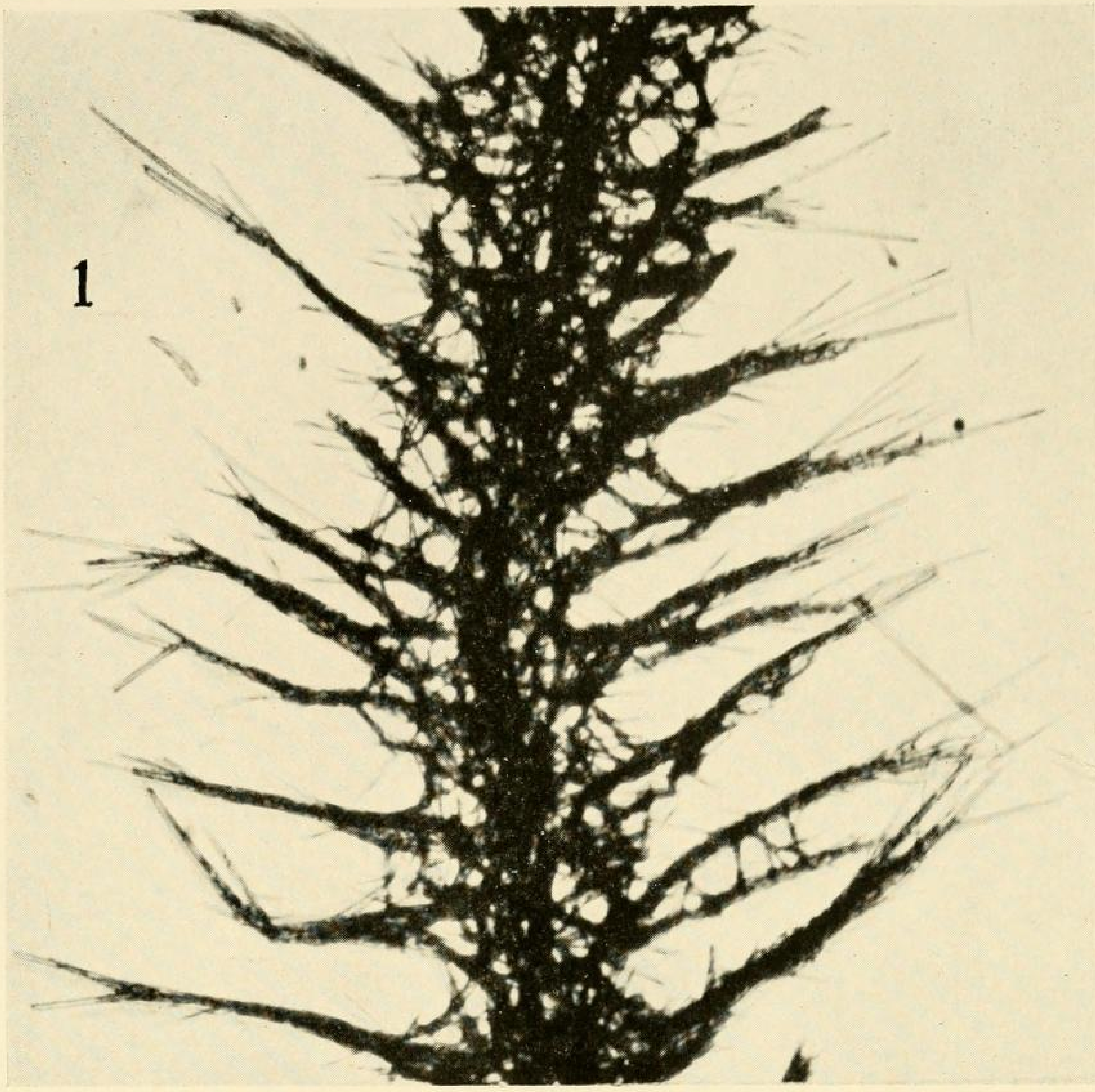

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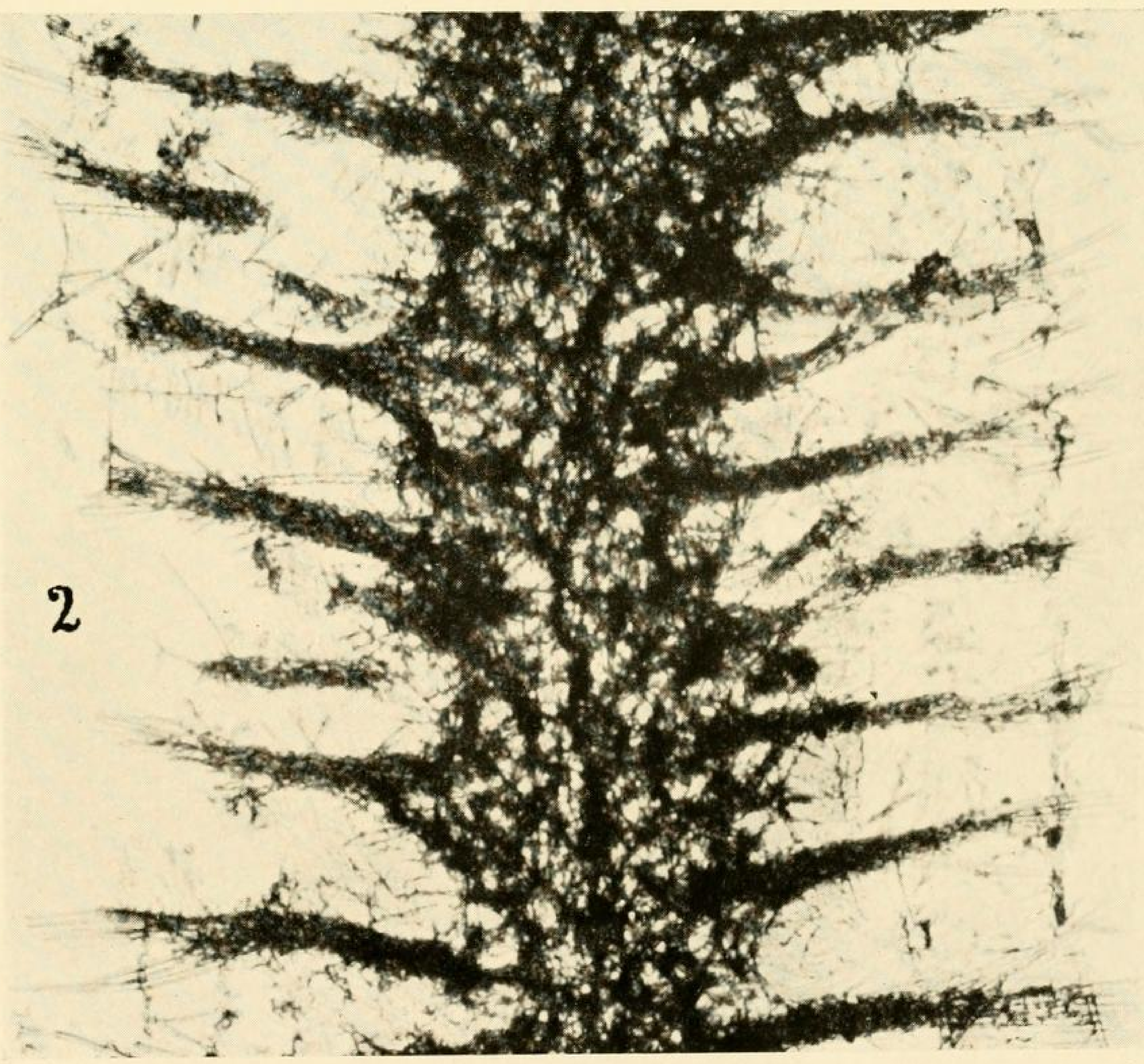

Echinaxia frondula Whitelegge.

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EXPLANATION OF PLATES XXI.-XXII.

Plate xxi.

Rhabdosigma mammillata Whitelegge.

Fig.1.—Longitudinal (desarcodised) section of the skeleton (of a digitiform lobe), showing extra-axial region thereof and also portion of the axial region; (× 15).

Fig.2.—Entire specimen; (× $\frac{3}{7}$).

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Figs.3, 4.—Pattern of the skeleton as shown in longitudinal section parallel to and in the mid-plane of the (lamelliform) sponge. Fig.3 shows more distinctly the longitudinal spicule-strands; in Fig.4, which is from a thinner section, many long interstitial megascleres are also to be seen; (× 50).

Plate xxii.

Echinaxia frondula Whitelegge.

Figs.1, 2.—Skeleton as seen in longitudinal section perpendicular to the surface of the (lamelliform) sponge. The desarcodised section (shown in Fig.1) is from near the upper margin of the sponge; the other (undesarcodised) is from near its base; (× 50).

CORRIGENDUM.

Page 391, line 14—for *Hetercetya*, read *Heterectya*.