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THE DEVELOPMENT OF THE RYE SPIKE UNTIL EMERGENCE

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1. Introduction

In the course of investigations into the influence of herbicidal compounds on growth and development in winter rye (*Secale cereale* L.), a scale was needed for the accurate measurement of the early stages of reproductive development (Bruinsma, 1962, 1963a). Feekes (1941) published a scale for determining the developmental stages of wheat, which can also be used for other cereals (Large, 1954), but which is based on external morphological features only and does not include the development of the spike until after emergence. Bremer–Reinders (1958) presented a detailed description of eight stages in the early development of the rye spike. This division is, however, too wide for a close determination and, moreover, the stages are of inequal durations, which excludes arithmetical compilation of the results. In the latter respect, the scales given by Andersen (1952a, 1954a) for the generative development in barley, oats and wheat, meet the needs. Again, however, since the average duration of the stages is three to six days, the graduation is still rather coarse. In addition, the scales cannot be applied to rye without certain precautions being taken.

Purvis and Gregory (1937) described stages in the development of the growing point of winter rye, which were afterwards (Gregory and Purvis, 1938) converted into numerical values to render them suitable for computations. These values correspond approximately with the number of days required by spring rye to reach the stage in question when grown in 17 hour days (Purvis, 1961). The twelve values given are: 10, 15, 21, 24, 26, 28, 30, 33, 35, 37, 39 and 49, ranging from the vegetative state of the growing point to anthesis. Afterwards Hänsel (1953) extended the scale by distinguishing nine morphological stages from value 35 on. Since, however, these nine stages correspond with the values 35 up to and including 39 of the scale of Gregory and Purvis, the progress in score is no longer proportional with time.

It is the intention of the present paper to give a further differentiation of the scale of Gregory and Purvis, by describing the developmental stages of the rye spike for each of the values from 23 up to 37, that is from the first generative stages until just before emergence.

2. Material and method

Samples of growing points were collected from two field trials with Petkus winter rye (*Secale cereale* L.). One of these experiments was performed on a humous sandy soil, which was seeded with a row drill at 25 cm and at 7 seed rates, ranging from 5 to 180 kg/ha, in the middle of November. Samples were taken at the end of March (Bruinsma, 1962). The other experiment was laid out on a former heath field. At the end of October, 100 kg/ha was seeded with a row drill at 25 cm. Four nitrogen treatments, from 0 to 120 kg/ha, were applied. In the middle of April spike primordia were sampled (Bruinsma, 1963a). The vegetative growing point shown in Plate I was obtained from an unvernalized winter rye plant, cultivated in the greenhouse.

The primordia of main axes, together with the surrounding unexpanded leaves, were stored in 96 % ethanol. Before dissection they were transferred into 48 % ethanol, in which the tissues were tough and flexible and, by that, easy to handle. The growing points were stained in a strong solution of iodine in potassium iodide just before examination, to facilitate the distinction of details (Khalil, 1956). The primordia were examined under water with a Zeiss stereomicroscope II. Photographs were made with a Contarex camera provided with a bellows and a Zeiss Luminar microscope objective, 16 mm or 25 mm, allowing for magnifications up to 12 times (Bruinsma, 1963b).

3. Brief morphology of the rye spike

The flowers are strongly reduced and adapted to wind pollination (Fig. 1). The gynaeceum consists of a single-seeded ovary bearing two long feathery styles. Only one whirl of three stamens is present, the large anthers being protruded from the flower by long filaments. The perianth is reduced to two small scales, the *lodicules*, and has

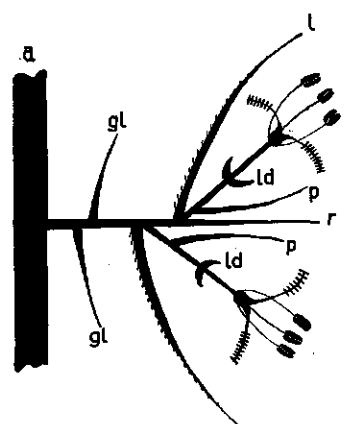

Fig. 1. Schematic view of the rye spikelet (modified after Gill and Vear, 1958). a = spike axis; gl = glume; l = lemma; ld = lodicule; p = palea; r = rachilla.

lost its protective function. At anthesis the lodicules swell and thereby open up the really protecting structure formed by the subtending bract, the *lemma*, and the bracteole on the flower axis, the *palea*. The awned lemma partially encloses the membranous palea; together with the flower proper the whole structure is called the *floret*.

Generally, two sessile florets are borne on a very short axis, the *rachilla*, one floret on each side. Under favourable nutritive conditions a third floret may develop but this one seldom produces a grain. At the base of the rachilla is a pair of empty bracts, the *glumes*. The rachilla with its florets and glumes is called the *spikelet*.

The rye ear consists of an unbranched spike of spikelets, the number of which varies from a few to about forty, depending mainly on the nutritive state of the culm.

4. The development of the spike until emergence

When still in the vegetative state, the growing point shows alternating hemicircular ridges representing the leaf primordia. Such a vegetative growing point is shown in the first photograph of Plate I.

The first signs of the transition into the generative state are a rapid elongation of the growing point and the initiation of swellings between the leaf primordia, being the beginnings of spikelet primordia in the axil of the subtending leaf primordia. This feature was termed "double ridge" by Purvis and Gregory (1937). It begins in the middle part of the growing point and extends down- and upwards. The tip remains undifferentiated, which means that it grows at about the same rate as that at which the formation of double ridges proceeds. According to Gott *et al.* (1955), double ridges show up when the growing point is about 1.6 mm long, although shortage of nitrogen may considerably reduce this length. A Figure given by Purvis (1934) shows growing points in the double-ridge state of about 1 mm only. Bremer–Reinders (1958) states that 5 or 6 spikelet primordia can be seen on each side at a spike length of slightly more than 1 mm and 9 or 10 at a length of 1.5 mm, further differentiation occurring only at a spike length of about 2 mm.

Our data are in accordance with the view that the formation of double ridges, without any further differentiation, takes place when the length of the growing point is between about 1 and about 2 mm. These data apply, however, to the lengths of ethanol-stored primordia; the amount of shrinkage taking place during storage has not been examined by us. Since Gregory and Purvis (1938), in the description of their scale units, connect the emergence of double ridges with score value 21, and the swelling of these ridges with value 24, the spike shown in the second photograph of Plate I, 1.3 mm long and with already 9 pairs of double ridges, must be in between, about value 22 or **23**.

In each double ridge, but again showing up first in the middle part of the growing point, the spikelet primordium extends and the subtending leaf primordium disappears. This "swelling of the ridges", as it is termed by Gregory and Purvis, is connected by them with score **24**, a spike of 1.7 mm in the photograph. On the spike to which value **25** is attached, 2.1 mm long, this process of swelling proceeds and especially the ends of the spikelet primordia expand, the spikelets becoming cone-shaped. In a later stage, the swollen ends of the spikelet primordia begin to round off and show the first signs of superficial inequalities: value **26.** This "branching of lateral initials", as it is referred to by Gregory and Purvis, advances in stage **27.** From the growing point, now 2.4 mm long, 18 spikelet initials on a side are borne, which is already nearly the ultimate number (BREMER–REINDERS, 1958). The most advanced ones clearly show the lateral ridges from which the glumes originate.

The glume is separated by a constriction from the floret initial, which appears in stage **28.** This initial hardly arises as a single swelling under the rachilla tip before it divides into two parts, separated by a furrow. The lower fold is the lemma primordium, while from the upper one the rest of the floret develops. Stage **29** shows the extension of this development down- and upwards over the spike; unfortunately a specimen with an imperfect top was photographed. Above the glume, the lemma partially enclosing the undifferentiated flower primordium proper can be clearly distinguished. The palea cannot be seen without dissection of the spikelet primordium since it remains hidden between the flower primordium and the rachilla throughout the development of the spike.

The developmental stage in which the stamen initials appear was rated **30** by Gregory and Purvis. From the main axis outward, the following structures can be distinguished on a far developed spikelet: a conical glume, bearing a dish-shaped lemma; this partly surrounds the flower primordium, which differentiates into three lobes, the stamen initials, round an undifferentiated centre; above this first floret, a lemma and flower primordium of a second floret; finally the rachilla tip.

The same details, but spread over a larger part of the spike, are shown in stage **31**; in particular the differentiation of stamens is to be seen in quite a number of pairs of florets. On the photograph, the spikelet axis is about perpendicular to the plane of the paper.

Stage **32** shows that the structures formed in earlier stages become more distinct without new differentiations arising. In the picture, from left to right are to be distinguished: the spike axis, the glume, the lemma whose tip bends already somewhat over one of the three clearly separated stamens; these stamens enclose the ovary; diagonally above the first floret the second flower and its lemma; the rachilla tip.

In accordance with the scale of Gregory and Purvis, the stage in which the stamen lobes develop, is termed **33.** Florets in the upper half of the photograph show stamens becoming knucklebone-shaped. In the mean time, in some second flower primordia stamen initials are already apparent.

Stage **34** is one of transition between the foregoing and the subsequent, value 35, in which, according to Gregory and Purvis, the awns grow out. This growing of the awns begins already at the time that the stamens differentiate their anthers. In stage 34 the awns lie clearly at right angles to the lemmas from which they originate. In stage **35** the awns are definitely pointed and already longer than the lemmas; the anthers are plainly recognizable as such and have overgrown the gynaeceum. In the upper half of the photograph, above the primordium of the second floret, a third one is already arising in some cases. Although the differentiation of these second and third florets proceeds for some time, the first florets grow much quicker and will soon overgrow the more distal ones, so that normally the spikelets develop only one fertile floret on each side. This can be seen in stage **36**, in which the spikelet tips seem to sink down between the florets of the first order. Anthers, awns and glumes of these florets grow rapidly, the last ones forming hooked tips.

In stage **37**, finally, the glumes become rough and touch the awns. These meet those of the opposite floret on the same spikelet. Glumes and awned lemmas overgrow and cover the more fragile structures of the flowers proper, and the ear now is almost ready to emerge.

5. Discussion

The practically self-sterile, protandrous rye plants constitute heterogeneous populations, the members of which develop at different rates. In order to judge how far the average development of such a population is advanced, the stage of development of individual specimens of a sample must be evaluated, and the resulting values arithmetically treated. For this purpose features expressing the growth rate are little suited, the more since growth proceeds exponentially with time (Purvis, 1934). Leaf numbers, too, are less appropriate, since this characteristic is only a vegetative one and, moreover, leaves of winter varieties wither away in spring, while it is often difficult to distinguish between leaves of the first order and those of higher orders (Andersen, 1952a, 1954a).

The stage of development of the growing point, on the other hand, provides a good measure of the developmental rate, especially because in cereals the transition into the generative state occurs at a rather early stage. Therefore, the scale of units, given by Gregory and Purvis (1938), with values progressing approximately lineally with time under standard conditions, meets the requirements for the determination of the stage of development in a sample of rye plants. The description of the scale by these authors is, however, very concise and without any illustrations. Moreover, their scale shows gaps since its units do not constitute an uninterrupted series of successive numbers.

In the present paper an attempt has been made to produce such an uninterrupted series of scores for that part of the scale concerning the generative development of the growing point until emergence. The very first stage, valued 21 by Gregory and Purvis, is omitted, since according to Bremer–Reinders (1958) growing points can be found with only 5 and 6 double ridges on each side; such primordia were not recognized among the specimens examined. The primordia definitely belonging to the units mentioned by Gregory and Purvis were selected first, and then the gaps in the scale were filled in with primordia showing transitions from one of the given units to the next. To these intermediate primordia the missing values were attached so that a continuous series was obtained. The distances between the units are now equal, in other words the stages must be of about equal duration under constant conditions. This was not experimentally verified, however, owing to the large number of rye plants to be grown under constant conditions, required for the daily sampling of at least 50 spike primordia.

With the aid of the photographs the stages of the scoring scale are all readily distinguishable after some training. If in samples plants are found which are still in the vegetative state or whose ears have already emerged, they can be rated according to the more extensive scale of Gregory and Purvis and their values can be added to those obtained with the present scale. In practice two persons, rating the same samples independently, obtained average values which agreed generally to within 0.1 unit (Bruinsma, 1962, 1963a).

Calculation of standard deviations of arithmetic means presupposes a symmetrical frequency distribution of the scores. From vernalisation experiments samples of partially vernalised plants may be drawn in which this condition is not fulfilled (Purvis, 1948).

Apart from this type of experiment, the proposed scale can possibly be applied in other physiological investigations, *e.g.* in studying the effects on development of physical conditions, nutrients, growth regulators (Andersen, 1952b, 1954b) and other chemical compounds (Bruinsma, 1962, 1963a), as well as in agricultural studies on cultivation techniques, breeding (Bremer–Reinders, 1958) and pathology (Large, 1954).

ACKNOWLEDGEMENT

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SUMMARY

In 1938, Gregory and Purvis proposed a scale of units to evaluate the stage of development in rye plants. This scale, based upon morphological features of the growing point, has now been refined for that part concerning the generative development of the growing point until emergence. After a survey of the spike morphology, a scale of 15 stages, each of about equal duration, is described and its use discussed.

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Plates I, II, III and IV.

A vegetative growing point, and the development of the rye spike in 15 stages, from the beginning of the generative state until emergence.
The white bar corresponds with 1 mm.
The numbers indicate the values of the scoring scale.

Plate I.

Vegetative growing point.

23. About 10 pairs of double ridges, length $\pm 1\frac{1}{2}$ mm.

24. Ridges swelling, length $\pm 1\frac{3}{4}$ mm.

25. Ridges cone-shaped, length ± 2 mm.

Plate II.

26. Lateral initials branching.

27. Glume initials appear.

28. Floret initials appear.

29. Lemma initials appear.

Plate III.

30. First stamen initials appear, together with floret initials of the second order.

31. Many florets show stamen initials.

32. Lemma tip bends.

33. Stamen lobes appear.

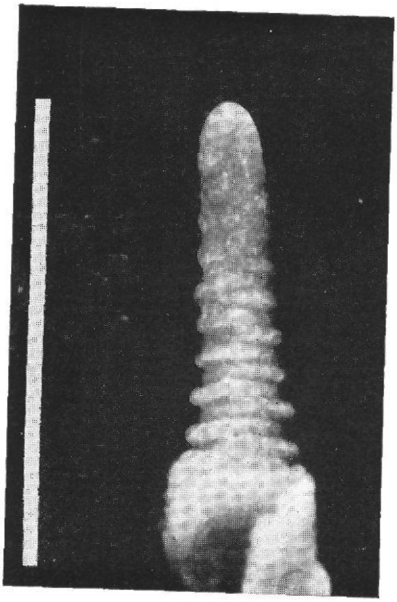
Plate IV.

34. Lemma tip at right angle with its base; in second florets stamen initials appear.

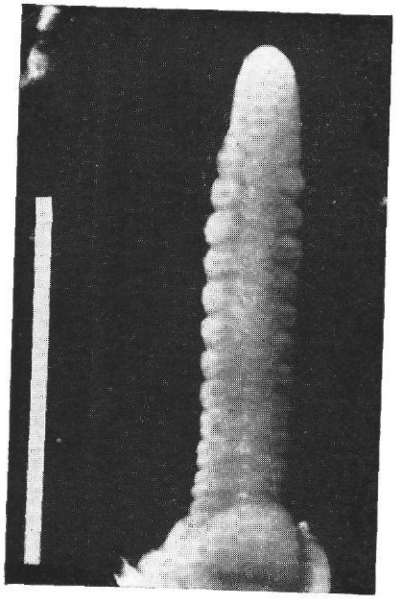
35. Awns growing; gynaeceum disappears between anthers.

36. Glumes with hooked tip; second florets being overgrown by first florets.

37. Spike elongating; glumes and awned lemmas overgrow flower proper.



Vegetative apex



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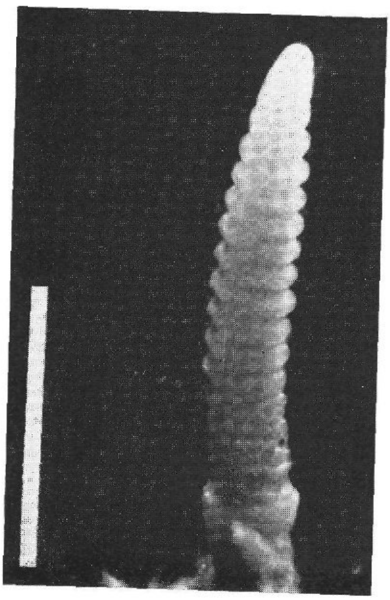

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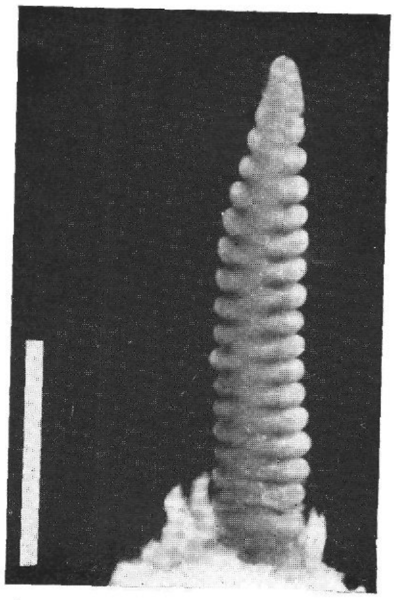

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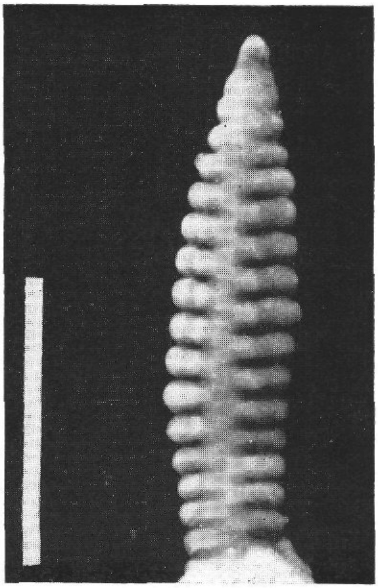
PLATE I



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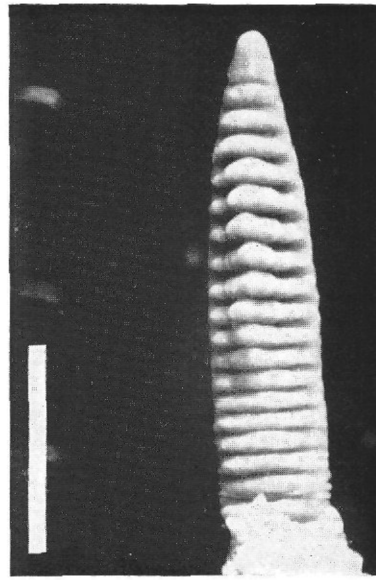

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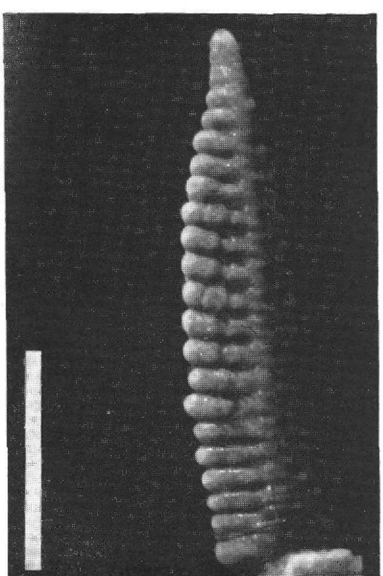

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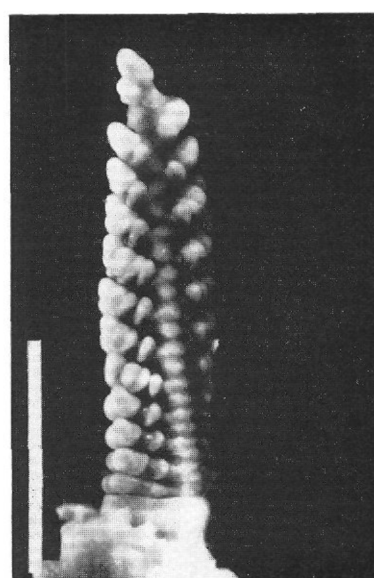

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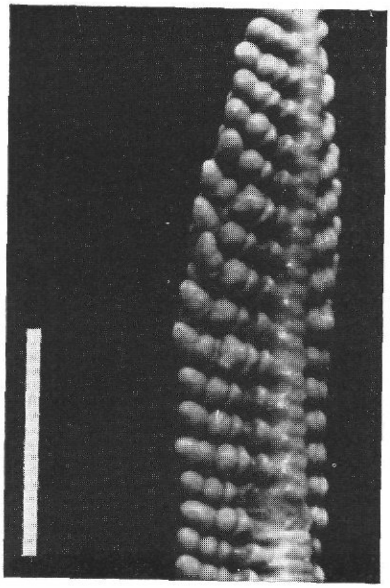

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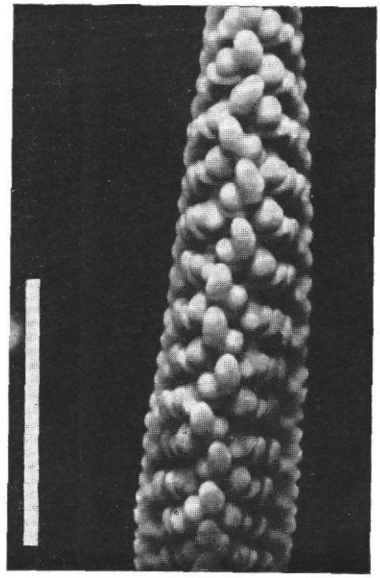

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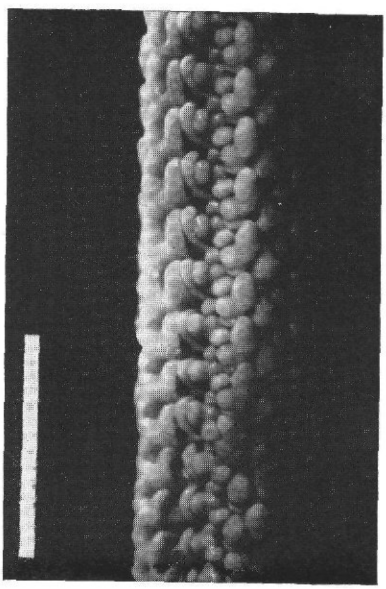

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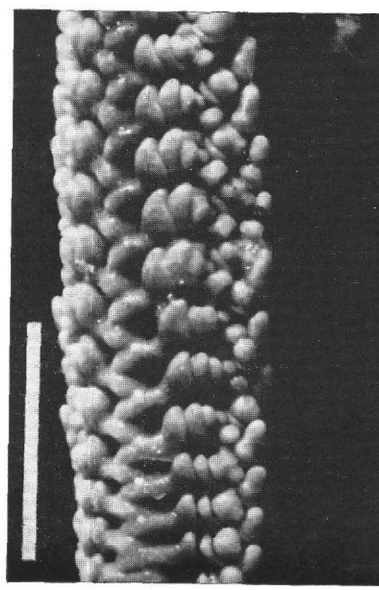

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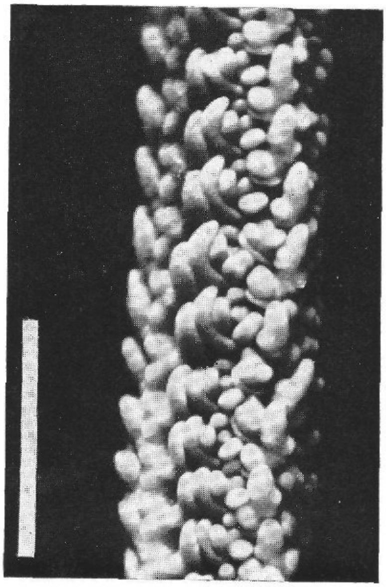
PLATE III



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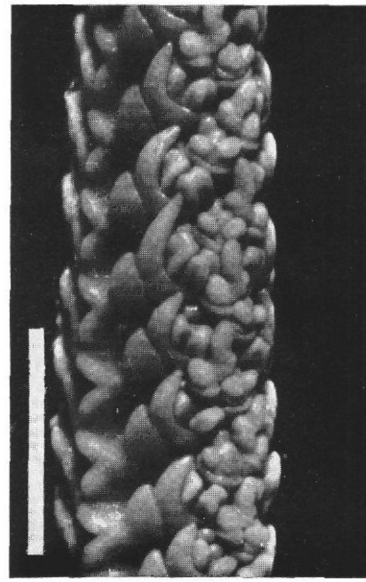

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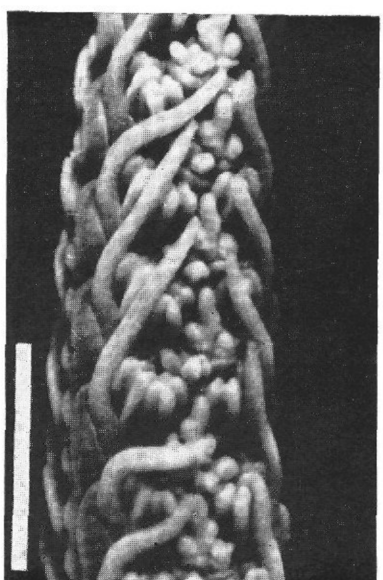

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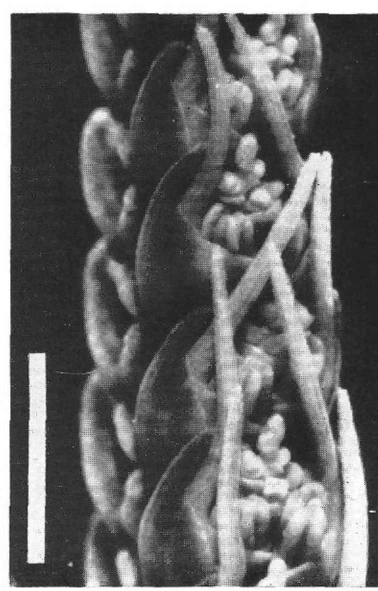

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PLATE IV