ON THE MORPHOLOGY OF *NOTOTHYLAS INDICA* Kashyap

BY

S. K. PANDE, M.Sc.,

Demonstrator in Botany, University of Lucknow

(With five plates)

Contents.

Introduction.

Notothylas is an interesting member of the Anthocerotales. The genus was founded by Sullivant (see Müller (11)). Schiffner (15) recognizes nine species, but remarks that some of these may not be specifically different. Stephani (16) has described eleven species.

In India two species are found and one of these, which forms the subject of the present paper, was described by Kashyap and Dutt (7).

A review of the available literature on *Notothylas* shows that although several species have been investigated, especially with a view to study the origin and development of the archesporium and the columella, conflicting statements have been made by different authors.

According to Gottsche and Milde, as quoted by Cavers (4), the columella may be present or absent in the sporophytes of different plants of the same species and its structure is also very variable.

Sometimes it is well developed and permanent, at others it is represented by a short outgrowth at the base of the sporogonium; while at still other times it breaks up into its constituent parts at maturity.

Leitgeb (see Cavers (4)) confirmed the above observations and further added that the absence of the columella is not due to disintegration of the cells as was suggested by Gottsche (*loc. cit.*). In *N. Breutelii* he found that some sporogonia had a columella, while others had none. The endothecium he regards as potentially fertile and the columella, when present, arises as a secondary differentiation within it.

Mottier (10) investigated *N. orbicularis* and states that the columella and the archesporium are produced in the same manner as in other Anthocerotaceæ.

Lang (8) states that in *N. Breutelii* the endothecium, instead of forming the columella, produces the archesporium for the greater part of the intercalary growth of the sporogonium; but in many cases it forms the sterile tissue towards the end of development.

Campbell (2) supports Lang from his study of *N. javanicus*.

Goebel (5) found that in *N. flabellata* the columella is absent and only the endothecium produces the archesporium, while the whole of the amphithecium gives rise to the wall.

Kashyap and Dutt (7) from a study of the meristematic zone concluded that in *N. Levieri*, a species which also lacks a columella, both the entire endothecium and the inner layer of the amphithecium produce the archesporium while in *N. indica* the inner layer of the amphithecium alone gives rise to the archesporium and the endothecium forms the columella. The embryogeny which is very important has not been followed in either of the two species.

In view of the above facts, and also because *Notothylas* is a convenient type for teaching in Indian Universities, an attempt has been made to follow in detail the life-history of both the Indian species. As a result three preliminary papers have been contributed (12, 13, 14).

The present paper deals with *N. indica*, a species which has a well developed columella, and in a subsequent paper it is intended to publish an account of *N. Levieri* which has no columella in the mature sporophytes. *Theoretical considerations and conclusions will be taken at the end of the second paper.*

Occurrence.

N. indica is a common liverwort growing in shady places during the rains in several parts of the United Provinces. It often grows on

the walls and floors of old buildings and on gravelly foot-paths; it is sometimes associated with *Cyathodium sp.*, *Riccia discolor* L. et L. *(R. himalayensis Kash.)* and a moss. It also occurs at Bombay (6) and Rangoon. The Rangoon material was obtained through the courtesy of Dr. S. L. Ghose, to whom the author's thanks are due. In September 1928 and October 1931 *N. indica* was also collected from the Municipal Gardens, Mussoorie (about 7,000 ft. above sea-level) where it was growing within a few yards from *N. Levieri* and more or less under identical conditions. The fact that these two species of *Notothylas*, one with a definite columella *(N. indica)*, and the other without it *(N. Levieri)*, grow side by side, shows that the difference cannot be due to climatic causes.

Material and Methods.

The material was mostly obtained from a number of localities in Lucknow and collected for several years at different times throughout the period of growth. A fairly large number of fixatives, including several modifications of chromo-acetic acid, both with and without osmic acid, has been used. The washing and dehydration was done as usual. It is very desirable to pass quickly through the grades of alcohol and xylol as otherwise the material becomes brittle. Sections were cut 4–10 microns thick and stained in safranin, safranin and gentian violet and in Haidenhain's iron haematoxylin. In some cases Flemming's triple combination was also used.

Thallus.

The thallus of *N. indica* is generally orbicular or sub-orbicular (fig. 1) and light-green. The thickness of the thallus in the middle varies from 6 to 8 cells, thinning out to 3 layers of cells towards the margins. The internal cells are much larger and some of these contain mucilage. Each epidermal cell has a large chloroplast. *Nostoc* colonies are frequently found, resulting in the hypertrophy of the neighbouring tissue (fig. 4). The rhizoids are only smooth-walled. Scales are absent.

Sex Organs.

My experience is that *N. indica* is not dioecious as described by Kashyap and Dutt (7) and by Kashyap (6) but strictly monoecious and protrandrous (figs. 1, 5). The antheridia and archegonia may occur on the same or on different lobes of the thallus.

Antheridium.—The antheridia arise endogenously, as elsewhere in the group Anthocerotales, and as a rule four of these occur in each chamber; but sometimes as many as six may be met with. Fig. 7

shows an antheridial initial. A comparison of this with other stages observed (figs. 8, 9) shows that the sequence of development is the same as in other species of *Notothylas*.

The mature antheridia are orange-coloured bodies, becoming brick-red as they grow older. The roof of the antheridial cavity is two-layered (fig. 9).

Archegonium.—The details of the development of the archegonium have not been followed, but from the stages obtained (figs. 10–12) it is evident that these are formed in the normal way, with slight variations in detail. The neck canal of the archegonium is often very wide. The ventral canal-cell is large, in some cases being practically of the same size as the egg. The mature archegonium generally has four neck-canal-cells (fig. 11) but occasionally there may be six (fig. 12). In *N. orbicularis* Mottier (10) found only three neck-canal-cells, but according to Campbell (1) there are five. In *N. javanicus* Campbell (1) records three neck-canal-cells but remarks that exceptionally there may be more.

Abnormal archegonia.—Two anomalous archegonia were observed (figs. 13, 14). In one of these both the egg and the topmost neck-canal-cell have divided by a vertical wall (fig. 14). In the other case the ventral canal-cell has divided (fig. 13). Abnormal sexual organs are of common occurrence in the other groups of Hepaticae; but in the Anthocerotales the author has not come across any such anomaly apart from the one recorded by Campbell in *N. javanicus* (1), where he figures an archegonium in which the egg has divided in the same way as in our fig. 14.

Embryo.

The first division in the oospore is transverse, producing two equal segments (fig. 15). Mottier (10) found the same condition in *N. orbicularis*. In *N. Breutelii* (8) this wall is longitudinal.

The second wall is at right angles to the first, resulting in a four-celled embryo (fig. 16) and presumably there is a third wall at right angles to both of these. In the next stage observed the embryo consists of three tiers (fig. 17). One of the cells of the lowest tier has already divided. A comparison with the previous figure suggests that probably the second transverse wall is laid down in the upper segment. Of the three tiers the lower two produce the foot, while the capsule and the seta arise from the uppermost tier alone, as in *N. Breutelii* (8) and in *Anthoceros* (9).

The embryo has now become pear-shaped (fig. 17). Periclinal walls arise in the uppermost tier and cut off the endothecium from the

amphithecium (fig. 18). Fig. 19 shows a median longitudinal section through an embryo where the differentiation of the amphithecium into the inner archesporial cells, and the outer cells which give rise to the wall, has commenced. As development proceeds further this differentiation also progresses (fig. 20).

Towards the apex of the embryo the archesporial cells divide more actively and the archesporium becomes massive in this region (figs. 21, 22).

A careful study of the different stages observed shows that in this species the whole of the endothecium produces the columella; while the inner layer of the amphithecium alone produce the archesporium, its outer layer giving rise to the wall of the sporogonium.

The foot is bulbous and root-like processes are evident at very early stages. The cells of the thallus in the region of the foot are much smaller.

At the base of the capsule is the meristematic seta and through its activity intercalary growth takes place. In a vertical longitudinal section of the sporophyte a regular alternation of horizontal layers of the fertile and sterile cells is seen; the former can be recognized by their larger size (fig. 25).

Mature Sporophyte.

The ripe sporogonia are cylindrical, though sometimes slightly curved bodies, tapering at both ends, and are borne horizontally along the margins of the thallus. Each sporogonium may be completely enclosed within the involucre or project beyond it. The capsule is two-valved and the margins of each valve have a row of very thick brown cells (fig. 35). Kashyap and Dutt (7), who described the marginal cells of the valves in both the Indian species, remark that the capsules remain enclosed within the involucre and do not open under natural conditions. The author has observed that frequently the sporogonia open like a follicle (*i.e.* the dehiscence takes place along one suture only) after which the valves spread out and expose the spores (figs. 36, 37). Later on the valves may sometimes separate along the other suture as well, but even in such cases the separation is generally incomplete along this suture. Acting on a suggestion of Dr. B. Sahni I placed some dried dehisced capsules inside a moist chamber when, as expected, the valves became closed.*

* The author has observed that in *N. Levieri* the mode of dehiscence is the same as in *N. indica* and the valves are hygroscopic.

In a few cases capsules were observed even with three or four lines of dehiscence (figs. 33, 34). A sporogonium was also seen in which one of the additional lines of dehiscence was free, the other, while free below was confluent towards the apex with one of the normal ones. In all such cases the cells along these lines were similar to those found along the normal valves. Probably these additional lines represent margins of accessory valves. Amongst previous investigators Muller (11) noticed indications of four lines of dehiscence in *Notothylas*.

The columella is well developed and in the mature sporophyte runs through more than three-fourths of its length (figs. 24, 31). Even in dehisced capsules it often stands out as a firm column. This may be seen from figs. 36 and 37, drawn from specimens collected in September 1927. It will be observed that in most cases even after a lapse of over four years the columella has remained intact.

In fully mature sporogonia the cells of the columella, especially towards the apex show some band-like structures (fig. 30 c), looking very much like the thickenings found on the sterile cells (fig. 30 b). Campbell (3) has recorded thickenings of this type in another species; but Kashyap and Dutt (7) observe that these are absent from the cells of the columella in *N. indica*, the species in question.

The capsule wall is about four layers in thickness and has no stomata.

The ripe spores are almost black and finely granulose, and the sterile cells show bands of thickenings (fig. 30 b). It is probable that the sterile cells and the columella may aid in scattering the spores.

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Department of Botany,
Lucknow University,
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Summary.

1. *Notothylas indica* is mainly a species found in the plains: but sometimes it occurs in the hills (e.g. Municipal Gardens at Mussoorie in the North Western Himalayas).
2. The species is monoecious and protandrous.
3. The sequence of development of the sex organs is of the normal type.

4. The number of neck-canal-cells in generally four, sometimes six.
5. Two anomalous archegonia have been observed.
6. The first division in the oospore is transverse.
7. The capsule and the seta arise from the uppermost tier, while the foot is produced from the lower two tiers.
8. The columella arises from the endothecium and the archesporium from the inner layer of the amphithecium.
9. The sporogonium normally has two valves; but sometimes there are indications of three or four valves.
10. The valves are hygroscopic and the dehiscence of the sporogonium generally takes place along one suture.
11. The walls of the marginal cells of the normal as well as of the accessory valves are very thick and brown.

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Explanation of Figures.

PLATE I.

sp. Sporophyte ; *in.* involucre ; *nt.* Nostoc : *th.* thallus.

Fig. 1. *Notothylas indica*. A single plant. × 1½.

Fig. 2. A portion of the thallus. × 10.

Fig. 3. A mature sporophyte (one of the largest observed) with the adjoining portion of the thallus. × 10.

Fig. 4. L. S. of the thallus. × 150.

Fig. 5. Horizontal section of thallus. × 58.

PLATE II.

w. wall ; *n.c.* neck-canal-cell ; *v.c.* ventral-canal-cell ; *e.* egg.

Fig. 6. Horizontal section through growing point. × 390.

Fig. 7. Antheridial initial. × 600.

Fig. 8. Horizontal section of thallus with antheridial chamber containing antheridia of different ages. × 450.

Fig. 9. T. S. of thallus with antheridia. × 300.

Fig. 10. Young archegonium. × 600.

Figs. 11–12. Mature archegonia. × 600.

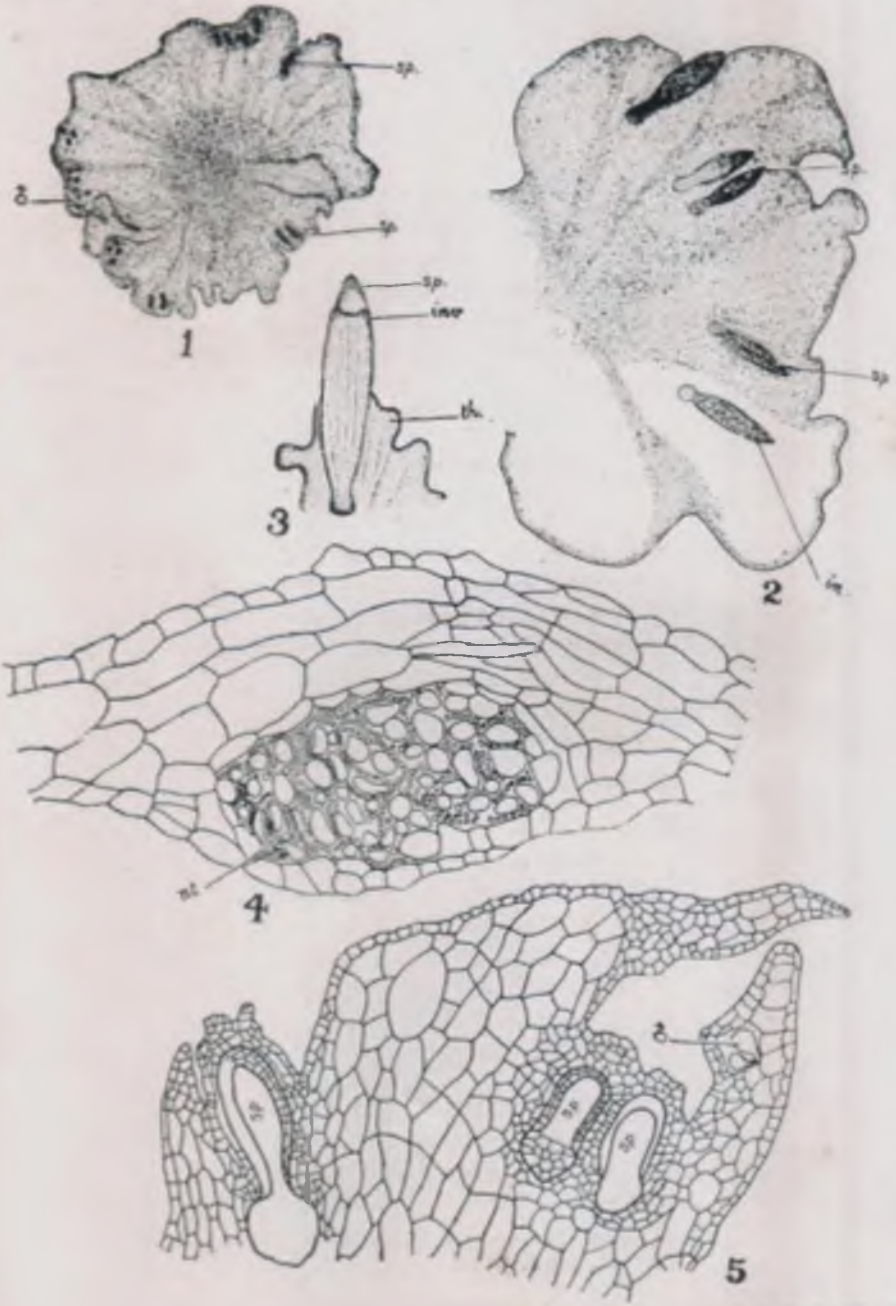
PLATE III.

n.c. neck-canal-cell ; *v.c.* ventral-canal-cell ; *e.* egg ; *end.* endothecium ; *amph.* amphithecium ; *f.* foot ; *col.* columella ; *arch.* archesporium ; *w.* wall.

Figs. 13–14. Two abnormal archegonia. × 600.

Fig. 15. Two-celled embryo. × 285.

Fig. 16. Embryo after the second wall. × 330.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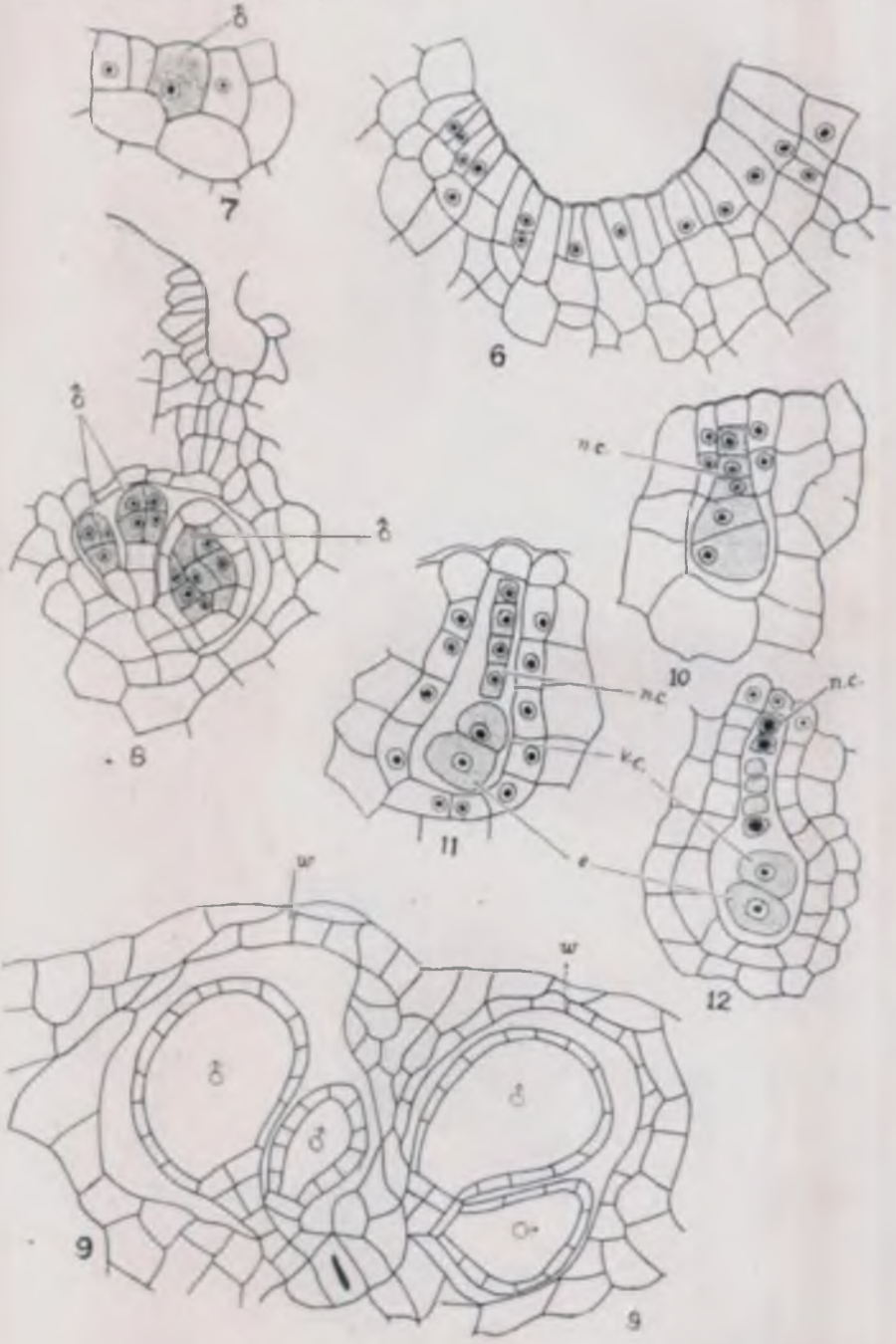
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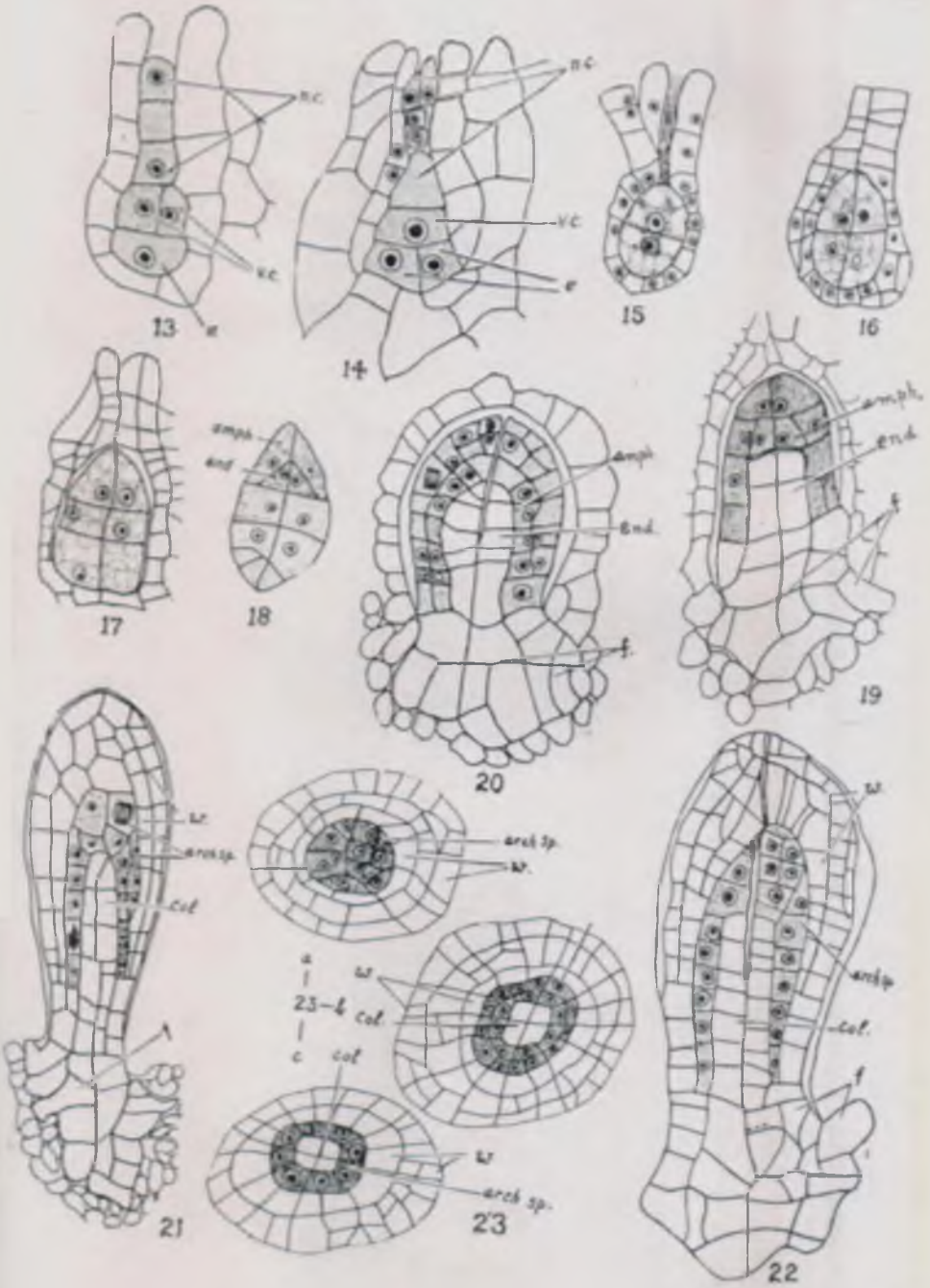
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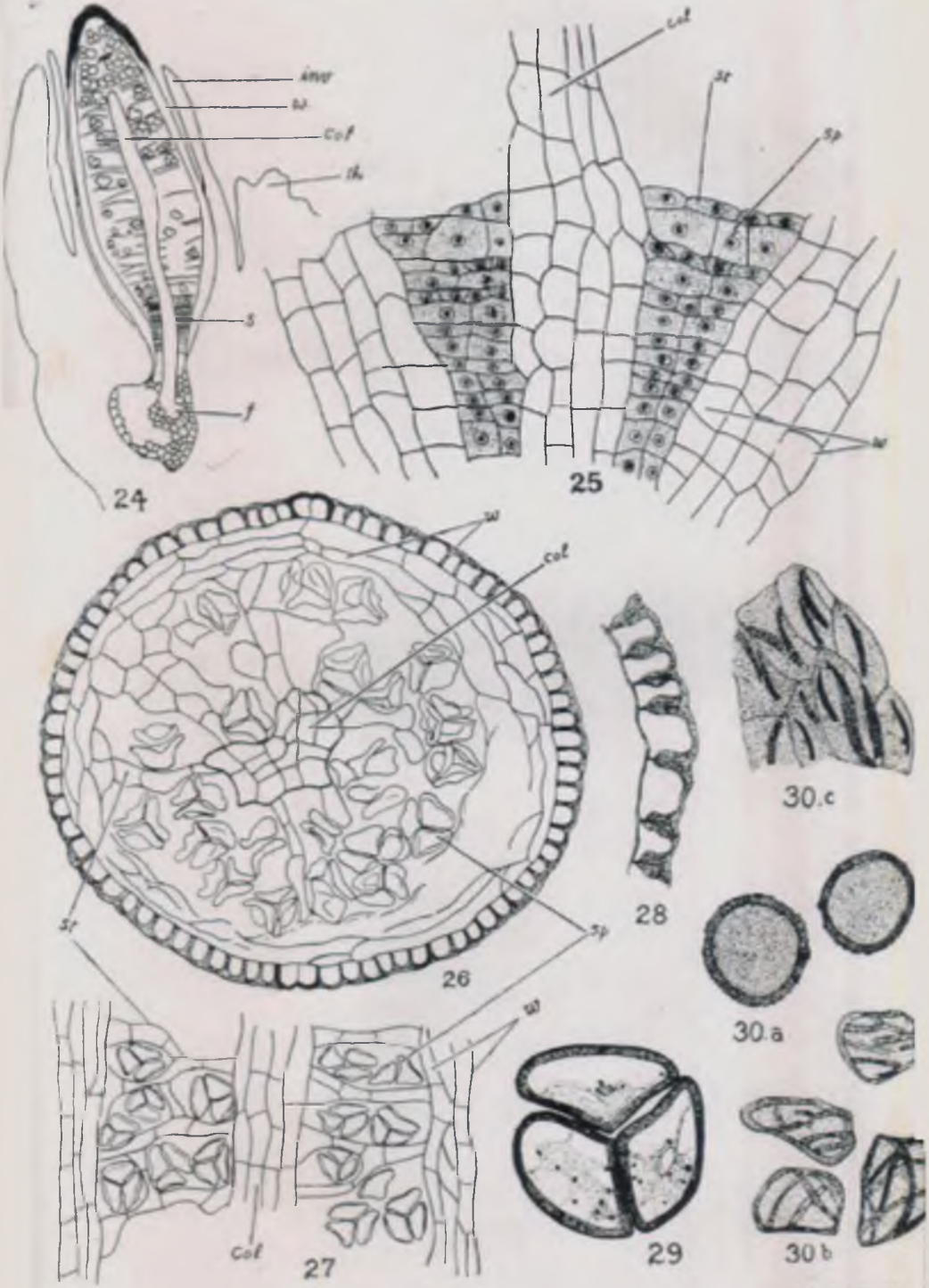
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Fig. 17. Embryo after three tiers have been established. (One of the cells of the lowest tier has already divided). × 285.

Fig. 18. Embryo after the periclinal walls in the upper tier. × 330.

Fig. 19. L. S. of embryo. Note commencement of differentiation in amphithecium. × 425.

Fig. 20. L. S. of embryo at a later stage. × 475.

Figs. 21, 22. L. S. of young sporophytes. × 285.

Fig. 23. T. S. of young sporophyte. (*a* apex, *b* middle, *c* base) × 285.

Plate IV.

in. involucre; *col.* columella; *s.* seta; *f.* foot; *st.* sterile-cells; *sp.* spores; *w.* wall; *th.* thallus.

Fig. 24. L. S. of mature sporophyte. × 40.

Fig. 25. Median longitudinal section from near base of sporophyte. × 300.

Fig. 26. T. S. of mature sporophyte. Note distribution of sterile and fertile cells. × 195.

Fig. 27. L. S. of mature sporophyte. Note distribution of sterile and fertile cells. × 150.

Fig. 28. Outer portion of wall of sporogonium. × 390.

Fig. 29. Spore tetrad as seen in a section. × 600.

Fig. 30 *a*. Spores. × 295.

Fig. 30 *b*. Sterile cells (note the bands of thickenings). × 295.

Fig. 30 *c*. A few cells from the apex of a columella. × 245.

Plate V.

col. columella, *sp.* spores.

Fig. 31. Sporophyte separated in two valves. × 25.

Fig. 32. Entire columella. × 58.

Fig. 33. Wall of sporophyte with three valves. × 40.

Fig. 34. Sporophyte with four valves. × 55.

Fig. 35. Wall of sporophyte in surface view. × 150.

Fig. 36. A portion of thallus with sporophytes showing mode of dehiscence. × 10.

Fig. 37. A single sporophyte showing mode of dehiscence. × 16.