The Journal of the Indian Botanical Society.

(Formerly "The Journal of Indian Botany".)

Vol. X. JULY, 1931. No. 3

ON *SAUCHIA SPONGIOSA* Kashyap

BY

M. L. Sethi,

Lecturer in Biology, Multan College, Multan.

Professor Kashyap collected this plant for the first time in 1914 from the neighbourhood of the Sauch pass in the Middle Himalayas along the Chamba-Pangie road. He described it as a new genus under the name of *Sauchia spongiosa* in 1916 (10). Prof. Kashyap visited the Chamba-Pangie road again in 1928. The present writer was with him during that trip. *Sauchia* was found and collected again after 14 years from its original haunts. Because of the rarity and several interesting features of the plant, Prof. Kashyap suggested to the writer to work it out in detail. The material was accordingly fixed in Bouin's fixative, Farmer's fixative and absolute alcohol and preserved for study in July 1928. Microtome sections between 5 and 12 microns were cut and stained with iron-alum haematoxylin.

While the present work was in progress Prof. Kashyap published a detailed description of *Sauchia spongiosa* (12) in 1929.

Sauchia spongiosa has so far been collected above 10,000 ft. growing on rocks which are continually washed by very cold water or it is found growing very near snow where air cooled by the snow is blowing against it. Plants growing near snow are small and they do not form large patches. It is only near very cold running water that *S. spongiosa* forms its beautiful light green luxuriant patches.

The gametophyte plant body of *S. spongiosa* is a yellow green, once or twice dichotomously divided thallus. The margins of the thallus in old plants are bent inwards. Both the kinds of rhizoids and scales arise from the under surface. The scales are hyaline, small and triangular. The scales are unappendaged. The plants may be

1.6 cm. in length and about .6 cm. in breadth. The male shoots are small and slender. They arise as ventral outgrowths from the larger plants. A single large plant may bear as many as half a dozen male shoots on the two sides.

When seen with the naked eye a reticulate pattern is visible on the dorsal surface of the thallus. This is due to the air-chambers in the thallus. The roofs of older air-chambers disappear and so shallow pits are to be seen on the dorsal surface.

The anatomy of the thallus has been studied from serial vertical longitudinal and transverse sections. Some thick microtome sections were specially cut to obtain a comprehensive view of the internal structure of the thallus. Some plants were dissected under a binocular dissecting microscope to see the entire air-chambers.

In sections the thallus can at once be distinguished into two regions, the upper spongy and the lower compact region. In thin vertical longitudinal and transverse sections the spongy region of the thallus shows from two to four layers of empty air-chambers (Pl. I, Fig. 1). Such thin longitudinal sections are altogether misleading in regard to the anatomy of the thallus as was found by dissecting the plants under a binocular dissecting microscope and by cutting thick longitudinal sections. By studying such thick sections along with the thin ones it was found that in the young thallus there is a single layer of very oblique air-chambers. As the thallus goes on growing in length the air-chambers go on elongating lengthwise obliquely till they become almost horizontal. The older the thallus the greater the obliquity of the air-chambers. Thus every air-chamber begins to overlap the air-chambers in front of it (Pl. I, Fig. 2). Each air-chamber runs along the thallus for a considerable distance before it touches its roof and opens on the dorsal surface. Due to some lateral enlargement a chamber begins to cover the chambers towards its right and left also. A thin longitudinal section appears as represented in Figs. 1 and 3, Pl. I. Three to four layers of superposed empty air-chambers are seen. If a pin is thrust vertically into the thallus at any place a little behind the growing point it passes through three or four superposed air-chambers. The pin will not touch the floor of any except the lowermost air-chamber while it would pass through the very much oblique or horizontal sides of two or three air-chambers. The air-chambers in *Plagiochasma*, *Reboulia*, and *Grimaldia* are found in several layers. The layers are formed by secondary partitions and plates. There is some overlapping of air-chambers in *Athalamia*, *Stephensoniella*, etc., but not to the extent in which it is met with in *Sauchia spongiosa*.

The epidermis and all the cells of the upper spongy region of the thallus contain large sized chloroplasts. In the lower compact region plastids smaller than the chloroplasts are seen. The lower compact region may consist of nine layers of cells. All the cells of the thallus are thin-walled and parenchymatous. The small amount of rigidity met with in the thallus of *Marchantia* spp. is wanting.

The Growing-point and the Origin of Air-chambers.

The growing-point of the thallus is occupied by a single large wedge-shaped apical cell (Pl. I, Figs. 4, 5). This apical cell cuts off 4 series of segments. It seems that far more segments are cut off posteriorly and laterally than anteriorly. The anterior segments of the apical cell by further growth and division give rise to the scales. Behind the apical cell schizogenous splits appear in between the young cells. The first indications of these splits are internal in origin. Figure 4, Pl. I represents a vertical longitudinal section through a growing point. The first split is deep-laid and is seen between the third and the fourth cells behind the apical cell. The next older split is between the fourth and the fifth cells and is opening on the outside. The first split may appear between the second and the third cells behind the apical cell (Pl. I, Fig. 5). As a result of these splits the cells become arranged in piles or filaments. The splits grow into cavities which grow into larger spaces which we call the air-chambers. In the meantime the filaments grow into plates of cells separating these chambers. The topmost cells of the filaments bounding a split bend inwards and surround the opening of an air-pore.

Beginning with the investigations of Barnes and Land (2) on the air-chambers and the scrutiny to which Leitgeb's (13) statements were subjected, a number of papers have appeared on the origin of the air-chambers in the liverworts. Barnes and Land (2) state that 'the air-chambers of *Marchantiales* arise invariably by the splitting of internal cellwalls usually at the junction of the outermost and the first internal layer of cells. Thence in one type splitting proceeds inwardly and outwardly more extensively than laterally and lateral enlargement of the chambers follows growth, while in the other type expansion of the chambers is due to extensive inward splitting accompanied by growth.' Deutsch (5) describes that the cracking apart of two epidermal cells marks the beginning of an air-chamber in *Targionia.* Evans (7) reviews and criticises the papers of Hirsh, Pietsch, Deutsch, O'Keeffe, and Black dealing with the origin of air-chambers in liverworts. Haupt (9) has described the schizogenous origin of the air-chambers in *Preissia.* Haupt confirms the observations of Barnes and Land (2) and supports their conclusions. Sealey (14) has recently described the schizogenous origin of the air-chambers in *Oxymitra*. *Sauchia spongiosa* is another liverwort in which the air-chambers arise schizogenously.

From the above brief review it is clear that data has gradually accumulated in regard to the schizogenous origin of air-chambers in the *Marchantiales* and the conclusions of Barnes and Land (2) have been fully borne out by later researches. Leitzeb's view (13) is therefore untenable in the light of recent work.

The Sex-organs

Sauchia spongiosa is monoecious. The antheridia are borne on short adventitious shoots. The slender male shoot consists of a cylindrical basal portion and an expanded distal part as in *Targionia*. The expanded distal part bears the antheridia in acropetal order. Any number of antheridia up to a dozen may be borne on a male shoot.

The archegonia arise from a sessile cushion-like receptacle which is solid in the earliest stages. The young receptacle is enclosed in a series of scales which spring up from below the archegonia. The scales protect the archegonia very efficiently. Only the apices of the necks of the archegonia are allowed to project beyond the scales. The growing-point of the thallus forks very often after forming the female receptacle so that the receptacle comes to lie in the fork as in *Exormotheca*. The mature female receptacle is raised on a long stalk.

Writing about the female receptacle of *Sauchia spongiosa* Kashyap (12) states that the receptacle is four-lobed. In the writer's material there was no dearth of five-lobed receptacles.

The Antheridium

The apex of the male shoot is also occupied by a single large apical cell. The antheridial initial is a segment of this apical cell. It is therefore superficial in origin. It is very difficult to distinguish it from the other young cells behind the apical cell. The antheridial initial grows and divides by a periclinical wall into two daughter cells (Pl. I, Fig. 6). The proximal cell forms the pedicel or the stalk of the antheridium. In the meantime the cells lying in front and behind the antheridial initial begin to project above the growing antheridium (Pl. I, Fig. 6). These projecting cells grow and divide. By their continued growth and division the long papilla of the antheridial chamber is formed. The developing antheridium sinks to some extent and gets enclosed in the antheridial chamber. The first wall in the stalk cell may be periclinal or anticlinal. It ultimately forms a multicellular stalk. The cells of the stalk are large and empty. The distal cell which forms the antheridium proper divides by a periclinal wall into two cells. After this the two cells divide by anticlinal walls (Pl. I, Fig. 7). Thus the vertical walls in the developing antheridium of *S. spongiosa* are laid down pretty early. A long filament of four or five cells is not formed before the formation of the vertical walls as in most other Marchantiales. The four cells formed in this way divide by periclinal and anticlinal walls till the body of the antheridium shows about 25 cells. After this cells are cut off peripherially which go to form the single-layered wall of the antheridium (Pl. I, Fig. 8). The wall cells soon grow and use up much of their protoplasm. They become large and empty. Thus the wall of the antheridium becomes distinct from the spermatogenous cells. All the spermatogenous cells undergo divisions and so a very large number of sperm mother cells is formed. Fig. 9 Pl. II, shows a very old antheridium. It has a multicellular stalk, a single-layered wall and numerous sperm mother cells.

The sequence of the development of the antheridium as given above corresponds to the regular *Marchantiales* type as stated by Campbell (3) and Cavers (4). There is, however, this very important difference that a long filament of four or five cells is not formed in *S. spongiosa.* Vertical walls are formed after a short filament of two cells is formed.

It has been seen that the body-cell of the antheridium may not divide by a periclinal wall. On the other hand, it may divide by oblique walls which are laid down right and left. Two young antheridia of this type are shown in Figs. 10 and 11, Pl. I. There seems to be a single large apical cell with two cutting faces in these antheridia. This kind of antheridium is rather unusual for the liverworts while it is common among the mosses. Dupler (6) mentions some occasional variations of this kind in the development of the antheridium in *Reboulia hemispherica.* The occasional presence of this apical cell in the young antheridia of *Reboulia* and *Sauchia* shows that too much stress should not be laid on this point of difference between the liverworts and the mosses.

The development of the spermatozoids was not investigated in detail but it has been seen that every sperm mother cell undergoes two divisions to form a group of four spermatids. The second division takes place soon after the first and the cellwalls do not get time enough to thicken. The spermatids are cubical and not triangular because the last division is not diagonal as described by Ikeno (10) for *Marchantia.* The four cubical spermatids can be easily recognised by the thin walls which separate them.

The Archegonium.

In the material at the disposal of the present writer the female receptacles were pretty well advanced and the development of the archegonium could not be followed. The youngest female receptacle seen by the present writer was a solid globular cushion enclosed by scales (Pl. II, Fig. 12). Archegonia are seen arising from the underside of this cushion. The growing-point of the thallus forks after forming the female receptacle. A fully ripe archegonium shows a two-layered wall of the venter.

Fertilisation.

In Fig. 13, Pl. II the egg of an archegonium is represented. There are two nuclei enclosed in the cytoplasm. The larger one is the female nucleus and the smaller one is the male nucleus. From this it may be concluded that the spermatozoid transforms itself into a rounded nucleus after entering the egg cytoplasm. The diameter of the female nucleus is to that of the male nucleus as 3 is to 2. The chromatin of the male nucleus is aggregated around the nucleolus while the female nucleus shows a fine reticulum (Fig. 13).

The Embryo and the Sporogonium.

The nucleus of the oospore divides. The wall which is laid down between the two nuclei is somewhat obliquely transverse (Pl. II, Fig. 14). The wall of the venter is three layers of cells in thickness at this time. Both the cells of the embryo divide and form four cells. The walls which are laid down after this division are not exactly at right angles to the previous wall. The wall of the venter is four layers of cells in thickness at this time. The octant stage was not observed but later stages which were seen indicate that the octant stage does obtain in the development of the embryo of *S. spongiosa*. Fig. 15, Pl. II represents an older embryo surrounded by a four-layered venter. Not only the wall cells of the venter divide to accommodate the growing embryo but the cells of the basal part of the neck also divide by tangential walls.

In describing the embryogeny of *Marchantia domingensis* Anderson (1) states that 'in the very early stage the fertilised egg is surrounded by a venter which consists of a single layer of cells'. He further states that 'the venter may not begin tangential divisions till after the octant stage'. *Marchantia domingensis* is very peculiar in this respect because in several genera of the liverworts many-layered venters have been reported by different writers during very early embryogeny. In reviewing the early embryogeny of liverworts Haupt (8) distinguishes two kinds of embryos: the filamentous type and the octant type. Evidently the embryo of *S. spongiosa* belongs to the latter type.

Fig. 16, Pl. II shows an older embryo in which elongation has taken place. The future foot and the capsule are apparent in this figure, while a few cells between the two represent the seta. Moreover, the sporogenous cells of the capsule are marked off from the wall cells. Later on the sporogenous cells become dense and stain very deeply. After this the cells of the seta also undergo some elongation (Pl. II, Fig. 17). At this stage there is no distinction between the spore mother cells and the elater forming cells. The many-layered calyptra completely encloses the young sporogonium (Pl. II, Fig. 17). The writer has not been able to trace the development of the foot, seta and the capsule from the epibasal and the hypobasal cells of the embryo.

It has been seen that when spore tetrads are formed in the capsule the elater forming cells are only elongated and have not developed the characteristic thickenings.

The ripe sporogonium has a spherical foot, a short seta and a globular capsule (Pl. II, Fig. 18). The cells of the foot show dense contents and stain very deeply. Presumably these contents are the food supplies which the foot absorbs from the receptacle. The spores show certain markings on their walls (Pl. II, Fig. 19). The elaters are long and curved. Each elater shows two thickening bands (Pl. II, Fig. 19). Just below the apex and just above the bottom of the capsule there are a few sterile cells within the capsule wall. The wall cells of the capsule bear annular and spiral thickenings. There appears to be no special mechanism for the dispersal of the spores.

Summary.

The thallus of *Sauchia spongiosa* shows a single layer of very oblique air-chambers which due to extensive elongation and overlapping appear in 3 or 4 superposed layers in transverse and longitudinal sections.

The growing-point of the thallus is occupied by a single large wedge-shaped apical cell.

The air-chambers of the thallus arise schizogenously.

S. spongiosa is monoecious. The short slender male shoots arise as ventral outgrowths from the sides of the larger plants which bear the female receptacles. The antheridia develop as in the other *Marchantiales* with this difference that vertical wall-formation sets in after a short filament of two cells has been formed.

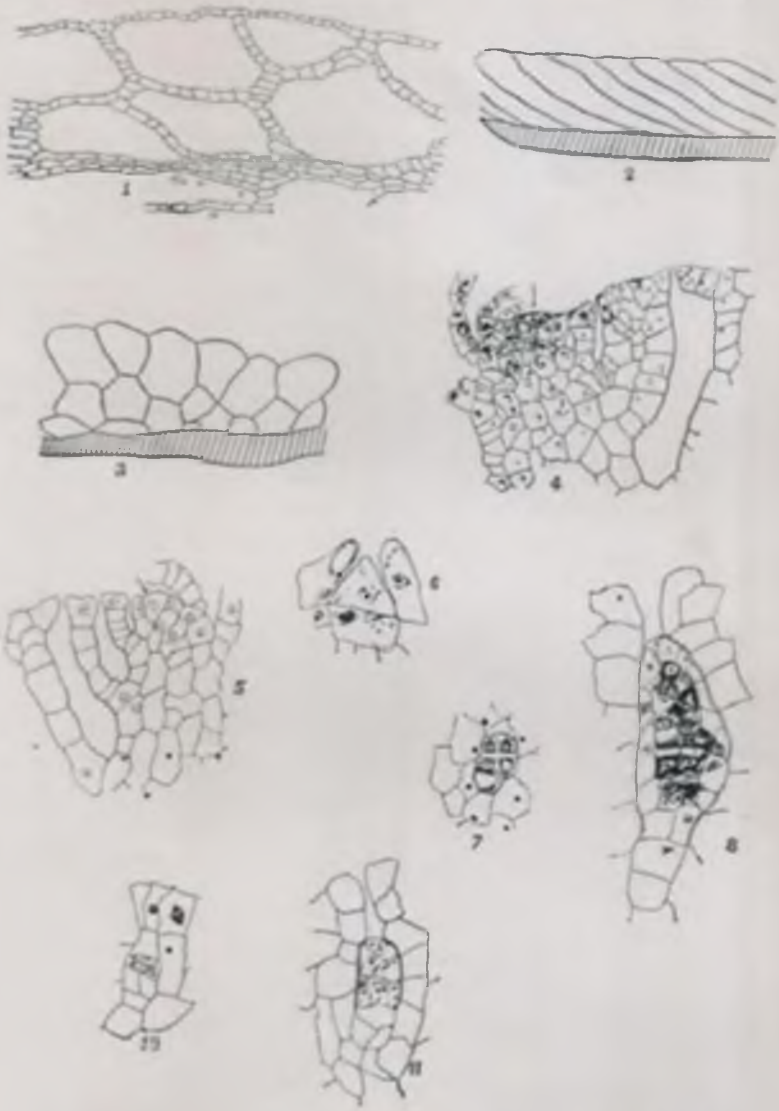
Two antheridia with apical cells like those met with in the antheridia of mosses were found.

The wall of the venter forms a very thick calyptra around the young sporogonium. The sporogonium is of the usual type.

In the end the writer takes this opportunity to thank Prof. Kashyap for much helpful criticism and encouragement.

Literature cited

1. ANDERSON, E. N.: Morphology of sporophyte of *Marchantia domingensis*. Bot. Gaz. LXXXVIII: 150–166, 1929.
2. BARNES, C. R. AND LAND, J. G.: Bryological Papers I. The origin of air-chambers. Bot. Gaz. XLIV: P 197, 1907.
3. CAMPBELL, D. H.: Mosses and Ferns. 1918.
4. CAVERS, F.: The Inter relationships of the Bryophyta. New Phy. Reprint. 1910.
5. DEUTSCH,: A study of *Targionia hypophylla*. Bot. Gaz. LIII: 492–503, 1912.
6. DUPLER, A. W.: The male receptacle and antheridia of *Reboulia hemispherica*. Amr. Jour. Bot. IX; 285–295. 1922.
7. EVANS, A. W.: The air-chambers of *Grimaldia fragrans*. Bull. Tor. Bot. Club.: XLV: 235–251, 1918.
8. HAUPT, A. W.: Embryogeny and sporogenesis in *Reboulia hemispherica*. Bot. Gaz. LXXI: 446–453, 1921.
9. HAUPT, A. W.: Morphology of *Pressia quadrata*. Bot Gaz LXXXII: 30–54. 1926.
10. IKENO, S.: Die spermatogenese von *Marchantia polymorpha*. Beiheft. 3. Bot. Centralblat. XV: 58–88, 1903.
11. KASHYAP, S. R.: Liverworts of the Western Himalayas and the Panjab, with notes on known species and descriptions of new species. Jour. Bom. Nat. Hist. Soc. XXIV: P. 347, 1916.
12. KASHYAP, S. R.: Liverworts of the Western Himalayas and the Panjab plain. Panjab University, 1929.
13. LEITGEB, H.: Atemofnungen der Marchantiaceen, Sitzungsber d. Kais. Akad. Wiss, Wien. Vol. 81, 1880.
14. SEALEY, J Q.: The morphology of *Oxymitra androgyna*. Amr. Jour. Bot. XVII; 19–28, 1930.


1
2
3
4
5
6
7
8
10
11

9

12

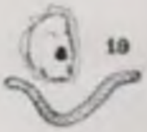
13

14

15

16

17



19

18

Explanation of Figures.

All the figures were drawn with a camera lucida except Fig. 2 which was partly drawn freehand.

Fig. 1. Longitudinal section of the thallus showing two superposed layers of air-chambers. × 250.

Fig. 2. Thick longitudinal section of the thallus showing the overlapping air-chambers. × 30.

Fig. 3. Transverse section of the thallus showing three layers of superposed air-chambers. × 85.

Fig 4. Longitudinal section of the growing-point of the thallus. × 610.

Fig. 5. Another longitudinal section of the growing point of the thallus. × 610.

Fig. 6. Two-celled antheridium with the two surrounding cells projecting upwards. × 1500.

Fig. 7. Young antheridium showing vertical walls. × 890.

Fig. 8. An older antheridium than the one shown in Fig. 7 showing wall cells marked off from the spermatogenous cells. × 890.

Fig. 9. A very old antheridium showing a multicellular stalk, single-layered wall and the long papilla. × 230.

Fig. 10. A young antheridium showing an oblique wall in the body cell which results in the formation of an apical cell. × 890.

Fig. 11. Another young antheridium showing an apical cell × 890.

Fig. 12. L. S. of a female receptacle, showing an archegonium on the right. The section passes through the periphery of another archegonium on the left. × 610.

Fig. 13. Venter of an archegonium with the male nucleus lying close to the female nucleus. × 2200.

Fig. 14. A two-celled embryo. × 890.

Fig. 15. An old embryo. × 610.

Fig 16. A still older embryo in which elongation has taken place. The foot, seta and the capsule can be distinguished. × 610.

Fig. 17. A young sporogonium enclosed in the calyptra. × 185.

Fig. 18. L. S. sporogonium showing foot, seta and capsule. × 120.

Fig. 19. A spore and an elater. × 600.