ON THE MORPHOLOGY OF *NOTOTHYLAS LEVIERI* SCHIFF. MS.

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Introduction.

ALTHOUGH it has generally been accepted that of all the Anthocerotales *Notothylas* shows the nearest approach to other groups of Liverworts in the structure of its sporophyte, the only instance where any direct relationship has been suggested is to be found in the classical researches of Leitgeb. From an examination of *N. breutelii* and *N. fertilis* he concluded that the sporogenous tissue is derived from the endothecium as in other Liverworts and that the columella, when present, is due to secondary differentiation within the archesporium like the elaterophore of *Pellia*. In view of this similarity, he regarded *Notothylas* as a connecting type between the Jungermanniales and the other Anthocerotales.

This view found little support from the subsequent investigators, who, on the contrary, have claimed that in *Notothylas* also, the primary sporogenous tissue arises precisely in the same way as in *Anthoceros*. The amphithecial archesporium has therefore generally been regarded as a characteristic feature of the Anthocerotales and a fundamental point of difference from other Liverworts.

In the light of these observations which had all the facilities of the modern technique and which are based on a study of the embryogeny of several species by different investigators, doubts have been raised on the conclusions of Leitgeb, which were made more than fifty years ago and which were based mostly on an examination of herbarium material. The only fresh material at his disposal was that of *N. fertilis*.

It has thus generally been felt that, so long as we do not definitely ascertain, that in some species of *Notothylas* at least, the endothecium alone forms the sporogenous tissue, there is little justification for Leitgeb's view of the close relationship between the Anthocerotales and other Liverworts. That we have not been able to settle this question so far is largely due to a lack of knowledge of those species of the genus that have no columella.
The only contributions to our knowledge that took into account the origin of the sporogenous tissue in such species, as far as I know, are those of the late Prof. Goebel on *N. flabellata* and of Kashyap and Dutt on *N. levieri.* Unfortunately, the authors in both the cases were handicapped by a want of suitable material and though they observed that there is no columella their views are not in agreement among themselves with regard to the origin of the sporogenous tissue. Thus, while for *N. flabellata* Goebel could not definitely ascertain if any part of the sporogenous tissue is derived from the amphitheciurn, Kashyap and Dutt thought that in *N. levieri* this tissue is partly derived from the amphitheciurn and partly from the endothecium.

An investigation of the two Indian species was therefore undertaken by me in 1926 as it appeared that questions such as the above could only be settled from a detailed and comparative study of the embryogeny of a columellate and a non-columellate species of the genus.

My observations on *N. indica* have been published elsewhere and some preliminary papers have been contributed on *N. levieri* also. The object of the present communication is to describe in detail the results of my investigations on *N. levieri*, to discuss the relationships of the two Indian species and finally, if possible, to say a few words on the relationships of the genus.

It is my pleasant duty to record here my most sincere thanks to Professor B. Sahni for his very kind guidance, helpful criticism and very keen interest and advice throughout the progress of this work. I am also deeply indebted to him for various other facilities which he has always generously provided. To Rai Bahadur Professor S. R. Kashyap I am thankful for many helpful suggestions and kindly criticism.

**Historical.**

The genus *Notothylas* was established by Sullivant (see Lang). According to him the sporogonia have a columella. In 1856 Milde found another plant in Germany and as this plant had no columella he made it the type of a new genus *Chamæceros.* Two years later Gottsche (see Lang) examined carefully all the species known at that time and discovered that in many cases Milde's plant had a columella and hence he referred it back to *Notothylas*. The apparent absence of a columella, he thought, was due to disorganisation of this structure. Milde, on a reinvestigation of the genus in 1859, concluded that in every case the columella ultimately breaks down into its component cells. These cells are similar to the sterile cells.
The obvious result of these observations was that the columella in *Notothylas* was regarded as an unstable structure which might break up into its constituent cells in the mature sporogonia and hence may be demonstrated in some cases but not in others.

An important work and the earliest one that took into account the development of the sporogonium is that of Leitgeb. The observations recorded in his monograph published in 1879 are based on a study of herbarium material of *N. valvata*, *N. melanospora*, *N. breutelii* and on fresh material of *N. fertilis*. Like the earlier investigators he also thought that the columella may be present in some capsules but absent from others in the same species, but he held that in those cases where the columella was absent it was not due to the breaking down of its cells as was previously thought, but in such cases no columella was ever formed. By examining some young sporogonia of *N. fertilis* and *N. breutelii* he further concluded that the central tissue (endotheciuni), which in other Anthocerotales forms the columella, in *Notothylas* produces the archesporium; and that the columella, when present, arises only as a secondary structure within this. In those cases where a well-developed columella was present he thought that it might have possibly (but not probably) arisen in the same way as in *Anthoceros*, but doubted if such an important act as the laying down of the sporogenous tissue should take place in two different ways in the same genus.

In 1894 appeared the results of Mottier's investigations on *N. orbicularis*. He made a detailed and careful study of the embryogeny and concluded that the sporogenous tissue is produced from the amphithecium and that the endothecium produces the columella precisely in the same way as in *Anthoceros*. These observations were later confirmed by Campbell, who questioned the correctness of Leitgeb's view in this connection. Prof. Campbell remarks (*Mosses and Ferns*, p. 155) "That this is not true for *N. orbicularis* is shown beyond question from sections of both the older and younger sporogonium, and it would be extremely strange if the other species should differ so radically from this one as would be the case were Leitgeb's surmise correct."

Lang's observations on *N. breutelii* were published in 1907. He concluded (*Ann. Bot.*, 1907, p. 207) that "the embryogeny conforms to the usual type for the Anthocerotaceae, but that the endothecium instead of being devoted to the formation of a sterile columella, forms sporogenous tissue for the greater part of the intercalary growth of the sporogonium. In a considerable proportion of cases, however, it produces sterile tissue towards the close of development." A year later Campbell described a somewhat similar condition in *N. javanicus*. 2, 3
The first account of a non-columellate species of *Notothylas*, apart from Leitgeb's work, is that of *N. flabellata* by Goebel, but his observations regarding the origin of the sporogenous tissue are not quite conclusive.\(^8\)

In 1925 Kashyap and Dutt published an account of *N. levieri* Schiff. and *N. indica* Kashyap.\(^11\) In the case of *N. levieri* they recorded the opinion that there was no columella and that both the endothecium and the inner layers of amphithecium contributed to the formation of the sporogenous tissue, while in *N. indica* they believed that while the endothecium formed the columella, the sporogenous tissue was produced from the amphithecium alone. These conclusions were based on a study of the meristematic zone in the mature sporogonium.

In the same year appeared a paper by Campbell on the relationships of the Anthocerotaceae\(^4\) and a few years later was published the 3rd edition of his book on Mosses and Ferns. In both of these publications Campbell maintained his previous views with regard to the origin of the sporogenous tissue and the nature of the columella in *Notothylas*. It appears that he still doubted the existence of a non-columellate species of *Notothylas*. While speaking of the differences between the Anthocerotaceae and the other Liverworts (*Flora*, 1925, p. 66), he says, "The most marked feature of the embryo is the origin of the archesporium, or primary sporogenous tissue, which differs from that of all other Bryophytes, so far as is known, except *Sphagnum*.

"The central tissue (endothecium), which in other Liverworts and most Mosses gives rise to the sporogenous cells, in the Anthocerotaceae forms a sterile columella, while the sporogenous tissue is derived from the outer tissue (amphithecium) (Fig. 3, A, B)."

At another place (*Flora*, 1925, p. 67) he observes, "The writer has examined carefully the development in two species, *N. orbicularis* and *N. javanicus*. In both of these the sporogenous tissue was cut off, as usual, from the amphithecium and a columella was present. In *N. javanicus* the smaller capsules showed a decided reduction in the size of the columella, and it is possible that in this species a complete suppression of the columella might occur; but no cases of this kind were seen, and we doubt if such is ever the case."

Quite recently the author investigated *N. indica*\(^9\) and his observations regarding the origin of the sporogenous tissue in this species are quite in harmony with those of Kashyap and Dutt.\(^11\)

**Occurrence and Distribution.**

*Notothylas levieri* Schiff. is a common liverwort that grows abundantly during the rains in the outer and the middle Kumaon Himalayas generally
between the heights of 6,000 and 7,000 feet. The plant is very common at Mussoorie and Nainital where, often on moist and shady northern slopes, it forms beautiful light green patches.

**Material and Methods.**

The material for this study was chiefly collected from Mussoorie in the Western Himalayas. Some material was also obtained from Nainital in the same region. Collections were made from time to time between the months of August and October, the growing season of the plant. Sex organs are formed early in August and hence the material collected at this time is good for the study of the development of these and the early stages in embryogeny. Plants collected at the end of the season show only the mature sporogonia. The material was mostly fixed in various strengths of chromacetic acid and Flemming's solutions but a part of it was also fixed in Bouin's and Benda's solutions. In every case the fixation was done in the field. Dehydration was carried out by gradual degrees (5-10-15-20-30-40-50% at intervals of 6 hours and 60-70-80% at intervals of about 10 hours) and the material brought to 90% alcohol; then it was gradually transferred to a mixture of equal parts of glycerine and 90% alcohol. The corks of the tubes containing the material were replaced by cotton-wool and the tubes were kept in stoppered jars of alcohol-glycerine. From these jars the material was taken out when required and carefully dehydrated with absolute alcohol. It was then cleared with xylol and embedded in the usual way. Sections were cut 4-10 microns thick and stained with Haidenhain's iron hæmatoxylin. In some cases safranin alone or in combination with gentian violet was also used.

**Thallus.**

The form and structure of the thallus of *N. levieri* have been accurately described by Kashyap\(^{10}\) and Stephani\(^{23}\) and most of the facts presented here conform to their observations. The plants are rather thin and delicate and light green in colour. Very often they grow crowded together in small thick patches and are then generally obovate. Sometimes, however, they form complete circular rosettes. The margins are finally dissected and the lobes are narrow and toothed. The structure of the thallus is essentially similar to that of *N. indica*. The greatest thickness in the middle is up to 6 cells. The epidermal cells are much smaller and each contains a single large chloroplast. There is a single large initial and the growth of the thallus takes place exactly as in other species (Fig. 1). The familiar mucilage cavities containing *Nostoc* colonies are quite common. There are no scales and only smooth walled rhizoids are present. The latter sometimes become irregularly lobed near their free ends.
Sex Organs.

*N. levieri* is monoeious and not dioecious as has sometimes been supposed. The sex organs are formed early in the season and both the antheridia and archegonia may be borne on the same lobe of the thallus. Usually the antheridia make their appearance first. In all these respects *N. levieri* closely resembles *N. indica*. Plants collected late in the season contain only the mature sporogonia and this is probably the reason that the species has previously been regarded as dioecious.

Antheridium. The antheridia are formed near the growing point but with the growth of the thallus they are shifted further back. Usually 3 or 4 antheridia occur inside each antheridial cavity but in some cases there may be more. The details of development have not been followed, but an examination of stages like those shown in Figs. 2–3, indicates that the process is probably the same as in other members of the group. The sperm mother cells are very small and difficult to fix and the details of spermato-ogenesis are not easily followed. The roof of the antheridial chamber is two layered (Figs. 2–3).

Archegonium. Like the antheridia the archegonia are also produced near the growing region of the thallus. They are sunken and inconspicuous. The sequence of development is of the usual type and is illustrated in Figs. 1, 4-10. The mature archegonium has four neck canal cells but sometimes there may be more. This is true for *N. indica* also but occasionally as many as six were seen in that species. Mottier records only three neck canal cells for *N. orbicularis* but Campbell gives the number as five in the same species. In *N. javanicus*, Campbell observed only three neck canal cells but added that exceptionally there may be more.

As in *N. indica* the neck of the archegonium is generally quite wide and the ventral canal cell is practically of the same size as the egg. In one case unusually large neck canal cells were observed and the canal was almost as wide as the venter (Fig. 11). The cover cells are four in number and in a mature archegonium these are quite above the general level of the thallus and much distended (Fig. 9).

Abnormal archegonia. Two cases of anomalous archegonia were observed. In one of these (Figs. 12, 13) two archegonia were noticed lying side by side without any intervening tissue. A longitudinal septum was seen between the two venters both of which had an egg and a ventral canal cell. An examination of the succeeding sections of the series showed that in the region of the neck also there was no tissue between the canal cells of the two archegonia.
In another case the lowermost neck canal cell has divided by a longitudinal wall. A somewhat similar condition has previously been described by the author in *N. indica*.\(^{19}\)

**Embryo.**

The fertilised egg almost completely fills the entire cavity of the venter (Fig. 14). Only a very few two-celled embryos were sectioned. In all these cases the division wall was longitudinal (Fig. 15) as in *N. javanicus*\(^{2}\) and *Anthoceros*.\(^{14}\) In *N. indica*\(^{19}\) and *N. orbicularis*\(^{18}\) this wall is transverse. Evidently, in some species of *Notothylas* the first division in the oospore is transverse, while in others it is longitudinal. The next divisions are transverse and divide the embryo into four cells. The upper two cells are somewhat larger than the lower ones. Presumably vertical walls are now laid down in these cells and give rise to an eight-celled embryo (Fig. 16). Later on by further transverse divisions in the upper cells the three tiers of the embryo are established (Fig. 17). Of these tiers the uppermost is the largest. Probably the lower two tiers produce the foot, while both the capsule and seta are derived from the uppermost tier alone as in *N. indica*.\(^{19}\)

Periclinal walls now separate the central tissue (endothecium) from the peripheral tissue (amphithecium) (Figs. 18-20). These walls are more or less concentric with the outer walls and are laid down in the uppermost tier of the embryo (Fig. 18). In some cases the embryo at this stage consists of four tiers (Fig. 19). So far the process is practically the same as in other Anthocerotales, but an essential difference is seen in the formation of the sporogenous tissue.

The central tissue (endothecium) which in all other genera of Anthocerotales forms the columella in *N. levieri* produces the sporogenous tissue alone; while the entire peripheral tissue produces only the wall (Figs. 18-25). In this respect the species in question differs from all other members of the Anthocerotales for which the structure is definitely known and corresponds closely to the condition found in other Liverworts.

As on this point my conclusion was opposed to that of previous workers, I had at first some hesitation in making a definite statement. But from an examination of more than three hundred serial preparations of almost all the stages of the sporophyte I am now able to say with confidence that in this species the endothecium alone is fertile, while the entire amphithecium forms only the wall (see Figs. 18-25 and microphotographs 28-30, 34 and 36-38). In young sporogonia often the inner cells of the amphithecium have dense granular contents similar to those of the endothelial (archesporial) cells and occasionally the distinction between the
endothecium and amphithecium is not sharp (Fig. 22). If we had only such sporogonia at our disposal, it would be difficult to decide the limits of the sporogenous tissue. Prof. Goebel noticed a somewhat similar condition in *N. flabellata* but he could not say whether these cells were of archesporial nature or not. In *N. levieri* the author has studied this question very thoroughly and a comparison of the embryos of different ages (Figs. 18-25 and microphotographs 28-30, 34 and 36-38) establishes beyond all doubt that the amphithecium never contributes to the sporogenous tissue. The archesporium can be clearly traced downwards to four rows of cells in the stalk (only two such rows can be seen in a longitudinal section) (Figs. 23-25 and microphotographs 29-30, 34 and 36-38).

Gradually the dense granular contents of the inner amphithecial cells disappear and ultimately as the sporogonium reaches maturity these are the first layers of the wall that get disorganised and probably serve to nourish the developing spores.

In *N. indica* which has a definite columella the cells of the endothecium in immature sporogonia often have dense granular contents like the cells of the inner layer of the amphithecium from which the sporogenous tissue is produced. In fact there is hardly any difference between these cells and those of the archesporium and if conclusions were to be drawn from such cases it would be impossible to say if a part of the sporogenous tissue is produced from the endothecium or not. But in the mature sporogonia a well-developed columella like the one shown in Fig. 33 (microphotograph) is found in every case. It can be distinctly traced downwards to four rows of cells in the stalk (Fig. 35). If, however, a part of the sporogenous tissue were produced from the endothecium, in some cases at least we would be able to trace the origin of this tissue from the endothecium in the mature sporogonia. This was never observed by me although I have examined no less than three hundred serial microtome sections of various ages. The obvious conclusion, therefore, is that in *N. indica* the entire endothecium produces the columella, while the sporogenous tissue is derived from the inner layer of the amphithecium alone. A comparison of Figs. 28-30 with Figs. 31-33 which are the microphotographs of the longitudinal sections of *N. levieri* and *N. indica* respectively at the corresponding stages of development also suggests the same conclusion. It will be seen from these figures that the region of the sporogonium which in *N. levieri* forms the sporogenous tissue, in *N. indica* gives rise to the columella (compare also Figs. 34, 35).
Mature Sporophyte.

The ripe sporogonia in *N. levieri* are cylindrical bodies about 2 or 3 mm. in length. They taper at both ends and are always horizontal. Very often they are borne in pairs. The thin and membranous involucre completely encloses the sporogonium. The seta is short and slender and there is very little meristematic growth. An examination of a vertical longitudinal section of a mature sporogonium shows a gradual differentiation of the spores and elaters from the meristematic zone (Figs. 24-26). The wall is about four cells thick and the cells contain chloroplasts, but there are no stomata. As the capsule reaches maturity the inner layers of the wall are disorganised. The sporogonia are bivalved and the sutures are very distinct. Almost invariably the sporogonia open along one suture only (Fig. 28 a) as in *N. indica* but in some cases they may dehisce along both the sutures. The mode of dehiscence in the two species under consideration is strikingly similar to what has been described and figured by Bartlett for *Anthoceros Hallii.*

There is no columnella; the axis of the sporogonium is occupied by spores and elaters (Figs. 24-25), the latter have spiral bands on their walls.

Discussion.

The relationship of the two Indian species may now be briefly discussed. The gametophyte and sex organs need no special comment as these show on the whole the same structure and plan of development throughout the genus.

The structure of the sporophyte and its development has been a subject of repeated investigations and much discussion in the past.

According to Leitgeb, as pointed out elsewhere, the sporogenous tissue arose from the endothecium and the columnella when present was a secondary structure within it. Campbell and some others on the contrary have maintained that these structures are formed in the same way as in *Anthoceros.*

The observations recorded here for the two Indian species show some interesting variations which easily explain these contradictory statements. We have established beyond all doubt that in *N. levieri* only the endothecium is fertile, while in *N. indica* the sporogenous tissue is produced from the inner amphithecium, the entire endothecium forming the columnella.

The significance of this will at once be realised if it is borne in mind that one of the main arguments for separating the Anthocerotales from the rest of the Liverworts has been the difference in the origin of the archesporium in these two groups.
The idea to separate the Anthocerotales from the rest of the Liverworts was originally put forth by Gayet\textsuperscript{7} and subsequently supported by Howe\textsuperscript{9}. This view has been greatly emphasised by Campbell\textsuperscript{3,4,5} from time to time. In the course of his discussion of the inter-relationships of the Hepaticae (\textit{Mosses and Ferns}, p. 621) he says, "While there are certain similarities between the young sporophyte of the Anthocerotaceae and such Liverworts as \textit{Sphaerocarpus}, \textit{Cyathodium} and especially \textit{Fossombronia}, the fact that the primary sporogenous tissue in the Anthocerotales always arises from the amphithecium, while in all other Liverworts it is developed from the endothecium, would seem to be a radical difference."

We have seen that in some species of \textit{Notothylas} the sporogenous tissue arises from the endothecium, while in others it is derived from the amphithecium. Evidently in the origin of the archesporium, \textit{Notothylas} forms a perfect connecting link between the remaining Anthocerotales on the one hand and the rest of the Liverworts on the other.

Observations by Lang\textsuperscript{12} and Campbell\textsuperscript{2} have shown that in some species of \textit{Notothylas} the sporogenous tissue is derived partly from the endothecium and partly from the amphithecium. In the light of all these observations, it is now possible to arrange the different species of \textit{Notothylas} in a perfectly graded series, one end of which would be occupied by such species as \textit{N. indica}, while at the other end we would have non-columellate species like \textit{N. levieri}.

Two interpretations of this are possible: either the non-columellate species are primitive and columellate ones have been derived from these by a gradual sterilisation of the central tissue and the concomitant shifting of the sporogenous tissue to the outer region, or else the columellate species are primitive and those that lack a columella are reduced.

Lang\textsuperscript{12} has been inclined to the view that \textit{Notothylas} is a reduced genus. He observed that the origin of the sporogenous tissue from the amphithecium even when the endothecium is fertile points to its origin from such forms in which the amphithecium was originally fertile. Goebel\textsuperscript{8} and Bartlett\textsuperscript{1} are also of the opinion that the species of \textit{Notothylas} examined by them are reduced. Dr. Kashyap\textsuperscript{10} has also held the same view. Cavers\textsuperscript{6} has, however, left this an open question. "The organisation of the \textit{Notothylas} sporogonium," says he (\textit{Inter-relationships of the Bryophyta}, p.147), "need not necessarily be interpreted as due to reduction from \textit{Anthoceros} type; the reverse interpretation does not appear to be excluded by the fact that both the endothelial and the inner amphithecial tissues produce spores."

According to Campbell\textsuperscript{4} the sporophyte of \textit{Notothylas} is the most primitive among the Anthocerotaceae and shows the nearest approach to the
sporophyte of other Liverworts, but he does not think that the relationship is anything but a very remote one.

Both the species examined by me show signs of reduction in the organisation of their capsules. The small sporogonia which are ensheathed within the involucres, the presence of photosynthetic tissue on the wall of the sporogonium even when there are no stomata and the hygroscopic valves with an efficient arrangement for dehiscence which is generally incomplete and sometimes even ineffective, are characters which undoubtedly suggest that the species are reduced. It is further believed that *N. levieri* with its capsules devoid of columella and in which the sporogenous tissue arises only from the endothecium, represents the last stage in the reduction series.

**Summary.**

1. *Notothylas levieri* Schiff. is generally found in the West Himalayas at altitudes between 6,000 and 7,000 ft.
2. The species is monoeccious and protandrous.
3. The development of the sex organs is of the usual type found among the Anthocerotales.
4. The number of neck canal cells in the archegonium is generally four, sometimes more.
5. Some abnormal archegonia have been described.
6. The first division in the oospore is longitudinal.
7. There is no columella and the entire endothecium forms the sporogenous tissue, while the whole of the amphithecium produces the wall.
8. The sporogonium generally remains enclosed within the involucre.
9. The capsule generally opens like a follicle that is along one suture.
10. The valves are hygroscopic.
11. The elaters have spiral bands on their walls.

**Conclusions.**

The facts presented here for the two Indian species appear to suggest that :

1. The columella is a definite specific character and when present (at least in the Indian species) arises from the entire endothecium.
2. In the columellate species of the genus (*N. indica*) the sporogenous tissue is formed from the inner amphithecium, while in the non-columellate species (*N. levieri*) it is formed from the entire endothecium.
3. The genus *Notothylas* is reduced and the species which have no columella represent the last stage in the reduction series.
4. In the structure of its sporogonium, *Notothylas* forms a perfect connecting link between the Anthocerotales and other Liverworts. This fact suggests a close relationship between the two groups and favours the retention of the Anthocerotales within the Hepaticae.

LITERATURE.

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