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THE STRUCTURE AND MODE OF REPRODUCTION OF SIPHULA TABULARIS NYL.

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(With Plate I and 4 Text-figures.)

There are some genera and species of lichens of which little or nothing is known about the spore-producing organs. In such, the systematic position cannot, as a rule, be determined with certainty, as the evidence indicating affinity must be derived entirely from the structure of the vegetative organs.

The genera *Thamnolia*, *Endocena* and *Siphula* have been included in the Usneaceae because of the structure of the vegetative thallus.

In *Thamnolia vermicularis* (Sw.) Ach., a widely distributed arctic and alpine lichen, pycnoconidia have been discovered, but apothecia are extremely rare, and the two descriptions of them which have been published differ in important respects.

In *Endocena* (one species, *E. informis* Cromb. in Patagonia) and *Siphula* (about fourteen species, widely distributed) the spore-producing organs are still unknown.

In all three genera, vegetative reproduction is probably the efficient means of dispersal, portions of the thallus becoming detached and distributed by the wind, on the feet of birds, or in other ways.

I have had an opportunity of studying in the field the three South African species of *Siphula* which occur frequently on the

Cape Peninsula and on the neighbouring mainland. In one of these, *Siphula tabularis* Nyl., there is a highly specialised mode of vegetative reproduction of a kind which has no parallel, as far as at present known, in any other genus of lichens.

Siphula tabularis Nyl. was first collected at the Cape by Thunberg, who obtained it from Table Mountain, between 1772 and 1779. After his return to Europe, Thunberg delayed publication of his lists and descriptions of Cape plants, and his list of Cape lichens appeared only in 1800 in the *Prodromus Plantarum Capensium.*

Long before this date, however, descriptions of *Siphula tabularis* were published, the first being in 1781, in the *Supplementum Plantarum* of Carl von Linné, as *Lichen verrucosus* Linn. fil. (p. 451).

Through the kindness of the late Dr B. Daydon Jackson, I examined the specimens of *Lichen verrucosus* in the Linnean Herbarium. The writing upon the herbarium sheet is that of the elder Linnaeus, and is *Lichen verrucosus* with the letter "T," which means Thunberg. There is also a small ticket with the number 519, probably in Thunberg's writing. There are two specimens, one about 10 cm., the other about 5 cm. in diameter. The letter "T" has been written under the smaller specimen.

The works of Acharius published between 1798 and 1814 contain brief descriptions of the plant: the first published figure appears in *Methodus Lichenum*, Tab. VII, fig. 3 as *Stereocaulon tabulare* Ach. Acharius noticed that the ends of certain branches are terminated by numerous wart-like granules; but he did not consider them as equivalent to fruit-bodies.

Nylander (*Synopsis Lichenum*, 1, p. 263, 1858) placed the plant in the genus *Siphula*. He thought that it might be a deformed condition of some other lichen.

It is unnecessary to cite subsequent references in detail, as they contain nothing of importance; there was no critical examination of the plant until a new collection was made at the Cape in 1857–58, by Dr Wawra, the material being placed in the hands of Massalongo (1) (1861), who gave the first detailed description accompanied by a large, but somewhat inaccurate coloured plate.

Massalongo states that the plant is always sterile. He describes the general habit, the ashy grey colour of the young horizontal thallus, with its brownish lower surface, and in older thalli the formation of upright podetia, the ends of which become constricted and produce numerous spherical bodies containing gonidia. He regards these structures as soredia. He compares the structure of the thallus of *Siphula ceratites* and "*Stereocaulon tabulare*," as the lichen was called by Acharius, and decides that the latter lichen must be placed in the genus *Siphula*.

A few additional collections of the lichen were made by Ecklon, Zeyher, Drège, Eaton, Wilms and MacOwan, but no detailed account has been published.

Habitat.

None of the earlier collectors mentions the curious habitat of *Siphula tabularis*.

The lichen occurs as large whitish or greyish patches upon the surface of sandstone rocks in the numerous small streams which drain the summit of Table Mountain and the mountain ranges of the Cape Peninsula and the adjoining mainland. Exact localities where collections have been made are cited at the conclusion of this account; the localities are almost all upon the Cape Peninsula, and more records from the mainland will be required before we can estimate the probable distribution of the lichen in South Africa as a whole.

In winter (April to September), the plant is frequently submerged for weeks; in summer, the streams dry up, and the plant is in a state of extreme desiccation. There is as yet no record of its occurrence in rivers where there is a constant water supply, and it does not thrive in the shade, though shade forms have been found. Almost all the localities recorded have been watercourses open to full sunlight. No doubt this preference for a seasonally fluctuating water supply and intense insolation restricts the distribution to comparatively high altitudes; on the lower slopes, the streamside vegetation will shade the watercourse to a considerable extent.

Most of the material studied was collected at altitudes of from 2000 to 3000 ft., the rarity of the plant at much lower (150 ft.) or much higher altitudes (above 3000 ft.) is probably correlated with the absence of a suitable environment at these altitudes.

The structure of the horizontal thallus.

The primary, or horizontal thallus (Pl. I, fig. 1) forms irregular patches up to 10 cm., in diameter, ashy grey above, reddish-brown or yellowish below. It is attached to the rock surface by a few stout rhizines of a blackish colour, which are irregularly distributed over the lower surface (Pl. I, fig. 4). The rhizines are massive bundles of hyphae arising in the medulla, and passing outwards through the lower cortex. Their dark colour is due to the included fragments of rock, rather than to the colour of the constituent hyphae (Text-fig. 2). They force themselves into cracks in the rock surface, and they are no doubt subjected to considerable strain when water is rushing over the thallus during the period of the winter rains. Their function is probably entirely that of attachment; hence their stout solid structure, reminiscent of the haptera of many seaweeds.

The horizontal thallus (Text-fig. 1) has a bifacial structure. Towards the upper surface there is a well-defined, compact, paraplectenchymatous cortex, situated beneath which is the

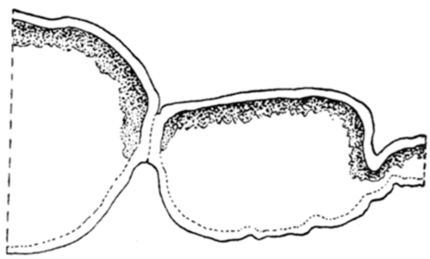


Fig. 1. Transverse section of a portion of the horizontal thallus, passing through two adjacent thallus lobes, which have united by their cortices. Gonidial zone shaded. × 25.

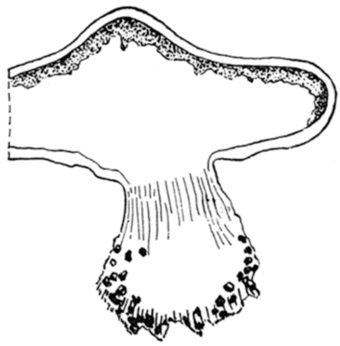


Fig. 2. Transverse section of a horizontal thallus, passing through a rhizine. × 25.

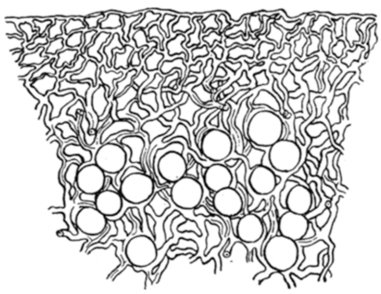


Fig. 3. Transverse section of thallus, showing cortex and portion of gonidial zone. × 620.

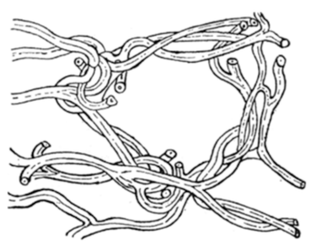


Fig. 4. Transverse section, hyphae of the medulla. × 620.

broad gonidial zone. The bright green algal cells are "chlorococcoid" but as the plants studied did not show actively dividing gonidia, their mode of division and reproduction was not determined.

The gonidia are from 7–10 μ in diameter, with an average diameter of 8 μ. They are surrounded by closely interwoven hyphae (Text-fig. 3), though penetration of gonidia by haustoria was not observed. Towards the centre of the thallus, the hyphae are more loosely arranged to form the medulla (Text-fig. 4), and a considerable amount of air is normally included between the hyphae, and is exceedingly difficult to displace.

After soaking portions of the thallus in water for two days, the air remained, even though cut surfaces unprotected by cortex were in direct contact with the water. This property of the cortex may be of considerable importance, as it enables the lichen to retain an internal supply of gases during its period of submersion. It is, however, unusual to find an aerating system in plants of rapid streams, such plants (as *e.g.* in Podostemaceae) usually deriving their supply of the necessary gases from solution in water. However, as the cortex imbibes water freely, the gonidia may make use of gases which diffuse through it.

The lower surface of the thallus follows closely the irregularities of the substratum, and is bounded by a paraplectenchymatous cortex which is a little less well defined in its limits than the cortex of the upper surface. There is no gonidial zone towards the ventral surface.

Owing to repeated branching of the thallus in the horizontal plane, the branches are often closely crowded, and fusion may occur between the cortices of adjacent branches (Text-fig. 1), thus uniting most of these into a compact mass.

In favourable circumstances, when the thallus has attained a moderate size, the tips of the horizontal thallus-branches change their direction of growth, and become more or less vertical; this reaction however, does not occur in plants which have grown in deep shade, where the thallus continues its growth, but its branches remain of the horizontal type throughout and the special organs of reproduction about to be described are not readily formed.

Examples of the shade form of the thallus were found by Mr N. S. Pillans near Somerset West (Pillans, No. 4842). These were growing upon wet rocks in deep shade at the foot of a waterfall. The rocks would be wet by the spray from the waterfall for the greater part of the year, but never actually under water.

The thallus branches of these plants are elongated, much flattened, the lower surface yellowish, with a few massive rhizines. Probably the lichens had reached this unsuitable habitat owing to detached isidia derived from plants growing in full sunlight at a higher altitude, having been washed down by the stream.

Formation of Podetia and Isidia.

In a favourable habitat, one which receives full sunshine, growth takes a very different course. Even in quite young thalli, the tips of many of the thallus-branches assume a vertical direction, forming short "podetia," as they may conveniently be termed (Pl. I, figs. 1 and 6). These vertical thallus-branches have a radial structure, a central medulla of loose hyphae being surrounded by a peripheral gonidial zone immediately below the cortex, which has the structure already described for the upper surface of the horizontal thallus.

A remarkable change now occurs at the flattened apex of each podetium. The end becomes verrucose, and small warts appear, from ten to fifty on each podetium. These verrucae enlarge considerably, and finally most of them become detached as minute spheres, each about 0·25 mm. in diameter. Each sphere leaves a small pit where it separates from the parent plant, the bottom of which is greenish, as the pit penetrates to the gonidial layer of the thallus. Each sphere, in section, is seen to consist of a mass of medullary hyphae with numerous groups of the normal gonidia, completely enclosed by a well-developed cortex of the type found in the thallus.

Thus these structures, which, like soredia, take their origin in the gonidial layer, have a more specialised structure than soredia. In being corticated, they approximate in structure to isidia, and here we shall consider them as such, though being of endogenous origin they differ from any isidium so far described.

The sequence of changes leading to the formation of isidia usually occurs at the apex of a podetium. Around a group of gonidia in the gonidial zone of this region, the hyphae become more compact and more closely interwoven, so as finally to produce in the gonidial layer a paraplectenchymatous cortex-like zone completely surrounding and enclosing the groups of gonidia. This new cortex is first differentiated on the side of the gonidial group towards the periphery of the podetium, and differentiation proceeds inwards until the gonidial group is completely enclosed (Pl. I, fig. 3 *a*). A number of groups of gonidia may become corticated in this way. Later, the cortex covering the end of the podetium is broken through by the enlarging isidia below it, which ultimately become detached, each leaving a small concavity marking the spot where it separated from the medulla (Pl. I, fig. 5 *a*).

As the isidia have their origin entirely within the gonidial zone, thus differing markedly from the usual exogenous production of isidia, it is suggested that the term *endisidia* might be applied to them.

After a number of isidia have been detached, the hyphae of the medulla are exposed directly at the end of the podetium, the normal gonidial layer having been more or less used up in the formation of isidia. Some gonidia may remain, and it is probable that after further division of the algal cells, these gonidial groups may again form centres of origin of additional isidia.

There is every indication that, following the destruction of the cortex at the apex of a podetium, and the formation of isidia, further normal growth of the podetium ceases, though, as will be seen later, the length of a podetium can be increased by the germination of one or more gonidia *in situ*.

Germination of the Isidium.

There is a remarkable difference in the behaviour of the isidium according to the nature of the substratum upon which it germinates.

If the isidium falls upon a rock surface or upon the leaves of small aquatic mosses, in a situation favourable for germination, it attaches itself by means of short hyphae growing out from the cortex at its point of contact with the substratum. The isidium, at first spherical, rapidly enlarges, and when about 0·5 to 1 mm. in diameter, becomes dorsiventrally flattened. A gonidial zone is organised towards the upper, or illuminated surface, gonidia disappearing from the lower, attached surface (Pl. I, fig. 2 *a*). The young thallus thus organised is at first almost circular in outline, but its margin becomes lobed when it has attained a diameter of about 1·5 mm. (Pl. I, fig. 2 *b*), and later, when the young thallus is about 3 or 4 mm. in diameter, the tips of some of the thallus-lobes may leave the substratum, and take on a vertical direction of growth, to form podetia (Pl. I, fig. 2 *c*). Germination of isidia upon rocks occurs at the beginning of the dry season, when the stream bed is still wet enough to afford sufficient moisture. Obviously, isidia detached when the stream is in flood may be carried away to a considerable distance, thus affording a means of distribution of the plant, but in a downstream direction only.

An isidium, or group of isidia may, however, germinate *in situ*. Here, the isidium grows out at once to form a thallus of radial structure, which is essentially a continuation of the parent podetium. The tip of the new cylindrical thallus again forms isidia, and if germination *in situ* is repeated, a long thallus-branch may be built up, each segment of which is the product of an isidium (Pl. I, fig. 7). Frequently, branches of six or seven segments are produced, the extent of the thallus formed by each isidium being marked by constrictions.

A very remarkable feature of this method of thallus formation is that the growth of one isidium more or less completely inhibits the growth of the remaining isidia which have been formed at the apex of the podetium. It is rare to find two or three isidia germinating at the end of a podetium (Pl. I, fig. 7 *a*).

Finally, if an isidium which has become completely detached from the podetium falls upon the cortex of the parent plant, or upon that of a neighbouring plant, it attaches itself, and grows to form a thallus of radial structure (Pl. I, fig. 7 *b*).

Thus, when germination takes place upon a foreign substra tum (rock, moss etc.) a dorsiventral thallus is formed; when upon the *Siphula* thallus, the young plant has a radial structure from the first. When thallus-branches (whatever their origin) come into contact, they tend to become firmly united by intermingling hyphae from the cortices at the point of contact. In this way, the branches of a thallus are firmly held together to form fruticose coral-like masses, and rigidity is thus ensured to old plants in which considerable branching has occurred.

Function of the Isidia.

The function of isidia in the biology of lichens has given rise to considerable discussion.

The older view is that they are organs of vegetative reproduction, minute but complete lichen thalli, carrying the necessary gonidia, and endowed with the power of germination upon suitable substrata. Many lichens are known, however, in which the isidia are not readily detached.

More recently it has been contended that their main function is to increase the assimilating surface of the thallus. Thus Darbishire has shown for *Peltigera praetextata* Zopf (2) that the isidia have the structure of small dorsiventral thalli attached to the parent.

A third explanation is that they are somewhat abnormal growths, appearing as the result of damage to the cortex of the parent plants, and though this explanation may be true for some lichens, it obviously does not cover those where we have parallel forms or strains, one more or less isidiose under almost all conditions of environment, the other entirely lacking the power to produce isidia (Du Rietz (3)). Probably no one explanation will cover all cases.

In *Siphula*, although the isidia differ from typical isidia in being endogenous, they combine very effectively both the functions of vegetative reproduction and increase of the assimilatory surface of the parent thallus; the first if they become detached and germinate on foreign substratum, the second if they germinate *in situ*, or upon the cortex of the parent.

Mode of distribution of Isidia.

As far as is known at present, the isidia constitute the only method of reproduction of *Siphula tabularis*. They are comparatively large bodies, visible to the naked eye, and probably much too large to be carried long distances by the wind. As already indicated, the curious habitat (in watercourses) will provide for their distribution in a downstream direction; the problem being the ascent of the plant to the fairly high altitudes sometimes reached.

Mr Pillans, who has examined a large number of habitats suggests the following possibilities.

Very strong winds may, in the dry season, carry isidia to slightly higher altitudes, thus gradually colonising the upper parts of the stream bed. In the summer, cattle frequently follow a watercourse when feeding, as in the dry season more succulent herbage is to be found on the stream bank than on the open hillside. This habit was no doubt followed by the many species of antelope formerly found in the Cape Peninsula. Finally, birds are attracted to the watercourses in the summer, and may carry the isidia attached to their feet, in the manner known to occur with some seeds, a method which would account for distribution over a wide area.

Records.

The material studied has been obtained from the following localities, all on rocks in stream beds:

Cape Peninsula.

Farmer Peck's Valley, Muizenberg. February 14th, 1920. 760 ft. Garside.

Summit of Table Mountain. May 31st, 1922. Pillans, 4211.

Saddle between Devil's Peak and Table Mountain. 2850 ft. Pillans, 3252.

Head of Kasteel's Poort, Table Mountain. 2450 ft. Pillans, 3550.

Between Wynberg upper reservoir and Disa Gorge. 2420 ft. Pillans, 3969.

Middle part of Silvermine Valley. 500 ft. Pillans, 3831.

Plateau on the Muizenberg. 900 ft. Pillans, 3168.

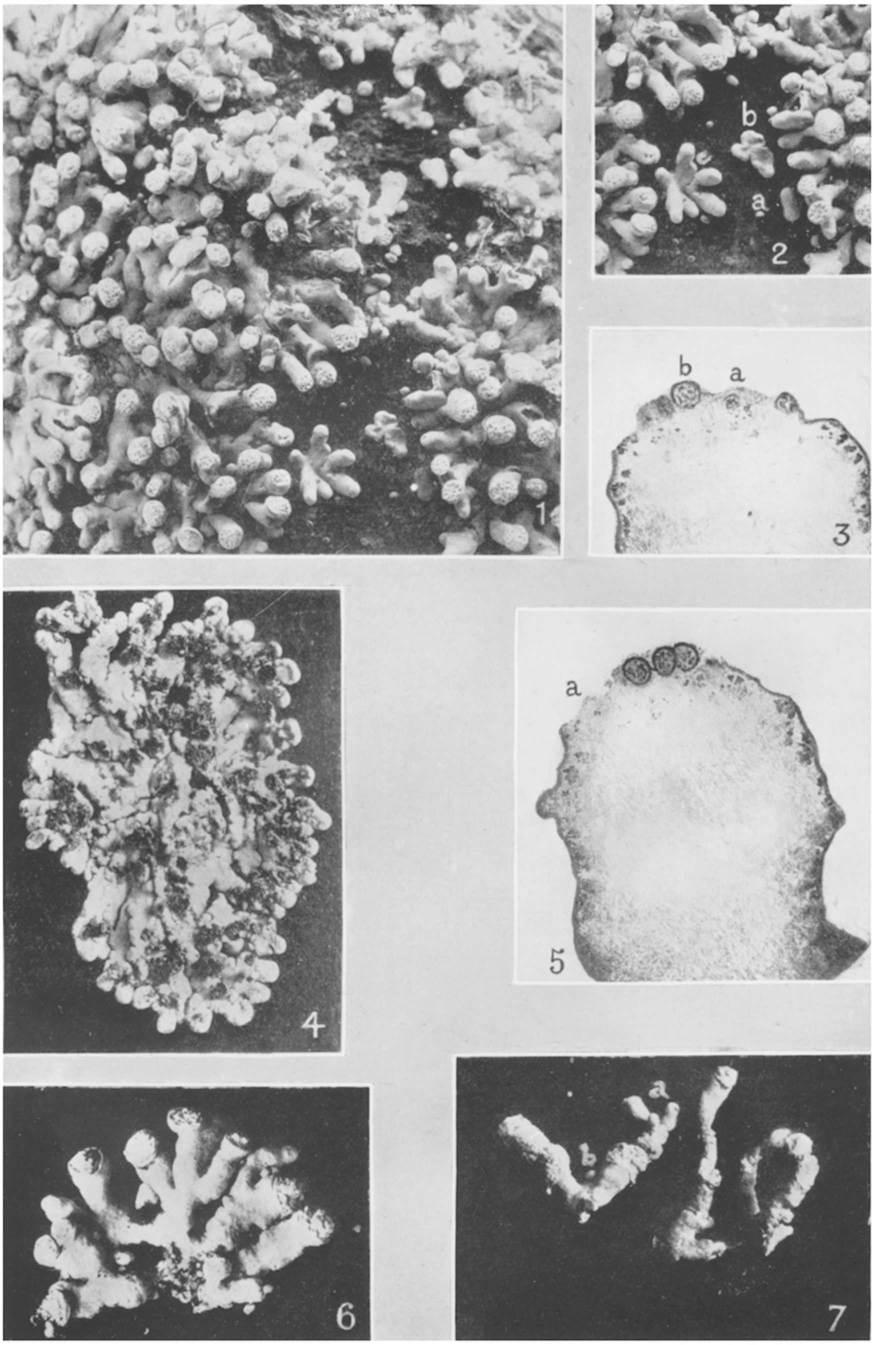
West of Paul's Berg, South West Coast. 150 ft. Pillans.

Abundant on north side of summit of Noord Hoek Mountain, near a small spring. January 1922. Pillans.

Mainland.

Rare on moist shaded rock in ravine off Staircase Ravine, Diep Gat Kloof, above Somerset West, Cape Province. April, 1925. Pillans, 4842.

On rocks, waterfall on the Swartberg near Swellendam. March, 1887. P. MacOwan.



SIPHULA TABULARIS NYL.

Bushman's Country, Cape of Good Hope. "On the ground." Zeyher.

Cape of Good Hope, Drège. Ex. Herb. Hampe. 1877.

Tulbagh Waterfall. Garside.

EXPLANATION OF PLATE I.

Siphula tabularis Nyl.

Fig. 1. Horizontal thallus growing upon sandstone rock, Farmer Peck's Valley, Muizenberg. The numerous pits at the ends of the vertical podetia are points at which isidia have been detached. Between the older plants, isidia are germinating upon the rock surface. × 2·5.

Fig. 2. A small portion of Fig. 1, showing successive stages (*a*, *b* and *c*) in the germination of isidia. × 2·5.

Fig. 3. Longitudinal section through the apex of a podetium, with developing isidia. At *a*, a cortex is forming around a gonidial group; *b*, section of an almost mature isidium. × 50.

Fig. 4. Lower surface of a small thallus, showing massive blackish rhizines. × 3. Pillans, 4211.

Fig. 5. Longitudinal section through the apex of a podetium, showing three isidia about to be liberated. At *a*, two isidia have been detached, leaving concave pits in the medulla. × 50.

Fig. 6. Small portion of a horizontal thallus, showing podetia with groups of spherical isidia at their apices. × 3. Pillans, 4211.

Fig. 7. Isidia germinating *in situ* at the ends of podetia. At *a*, three isidia from the terminal groups are germinating, forming three thalli of radial structure. At *b*, an isidium has become attached to the cortex of the old plant, and is enlarging to form a radial thallus. × 3.

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THE INVESTIGATION OF ASPERGILLI BY SEROLOGICAL METHODS.

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An extensive literature has accumulated about the serological differentiation of pathogenic bacteria, particularly animal pathogenic bacteria, but references to serological studies on pathogenic and saprophytic fungi are extremely limited. In the present paper I do not propose to discuss all the literature on this subject, but will review some of the references which seem to be more closely connected with the present investigation.

Malvoz (1901) made some serological studies on a certain