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Parmelia hueana Gyeln*., a vagrant lichen from the Namib Desert, SWA/Namibia. I Anatomical and reproductive adaptations

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ABSTRACT

The anatomy of *Parmelia hueana* Gyeln. showed specializations distinctive to the vagrant habit of the species. These include specializations in terms of the anatomy of the upper cortex, algal layer and medulla as well as mode of reproduction. The manner in which rolling and unrolling of the thallus during successive wet and dry cycles is brought about is shown. Possible ecological implications of the specializations are discussed.

KEY WORDS

Anatomy, Lichens, Namib Desert, *Parmelia hueana* Anatomical adaptations, Reproduction

INTRODUCTION

Unattached lichen species, also known as vagrant or vagant lichens, have been reported from every continent of the world. These so called "Wanderflechten" (German) appear to be characteristic of arid and semi-arid areas. Rogers (1977) discussed vagrant and erratic growth forms in his review on the ecology of lichens in hot-arid and semi-arid lands. Two types of unattached forms can be distinguished; those that are simply detached forms of normally attached species (Smith, 1921) and obligatory unattached lichens, devoid of all organs of attachment. The last mentioned lichen

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* = *Xanthomaculina convoluta* (Hue)Hale;
Hale 1985, Lichenologist 17 p. 263.

forms are only found on soil surfaces. As the origin, normal habit and original habitat of these two types of unattached lichens are totally different it seems essential that a distinct, descriptive difference should be made between non-obligatory and obligatory unattached forms. It is suggested that obligatory unattached forms be referred to as vagrant lichen species and non-obligatory unattached forms as erratic thalli.

The study was undertaken to determine the mechanisms by means of which thalli of *P. hueana* undergo their transformation from a dry to a wet state and to investigate the possible adaptations the species has undergone to survive in the inhospitable habitat of the Namib desert.

MATERIALS AND METHODS

Material

Thalli of *P. hueana* were collected on the gravel plain east of Swakopmund during February 1980.

Specimens are kept in the private herbarium of B. Büdel, no. 15003 and herbarium of the University of the North (no. 8021).

Macro Photographs

Macro photographs were taken by means of a Nikon camera using either a 55 mm Micro-Nikkor or a 40 mm Zeiss Luminar lens.

Light Microscopy

The internal morphology of thalli of the lichen was studied by means of freeze microtome sections embedded in Lactophenol cotton-blue (Henssen 1963).

Scanning Electron Microscopy (SEM)

In order to show the anatomy during the wet state, wet pieces of the lichen thallus were fixed in FEE for c. 6 h and thereafter washed in three changes of tap water. The thalli were thereafter dehydrated according to Samson *et al.* (1979). Critical point dried specimens were mounted on stubs and coated with gold. To show the anatomy of thalli in the dry state, air dry thalli were mounted and covered with gold. The specimens were studied by means of a Leitz AMR 1200 B SEM.

RESULTS AND DISCUSSION

1. Habitat and environment

Parmelia hueana is one of numerous lichen species which occur in the mist oases of the Namib Desert. Fog (mist) is a regular phenomenon along this coast and may occur up to 200 days per year. The yearly average precipitation from fog amounts to 40—50 mm yr^{-1} (Walter, 1962). Lichen thalli are wetted during such occurrences and thrive mainly on water obtained in this way. During these wet periods thalli of

P. hueana unroll quickly to expose the algal layer to sunlight. The first signs of movement are visible soon after thalli have come into contact with water. (The whole unrolling process is usually completed within 20 min. after being placed into a moist chamber.)

Parmelia hueana is a hygrochasic, vagrant lichen species and seems to be confined in its distribution to the wind blown gravel plains of the Namib Desert, South West Africa/Namibia. The presently known localities are shown in Fig. 1. The species occurs in abundance on the gravel plain east of Swakopmund in a lichen community composed of mainly saxicolous and especially terricolous lichens such as *Caloplaca volkii* and *Lecidella cristallina*. Thalli of *P. hueana* are frequently found along the periphery of this community where they occur on sandy patches.

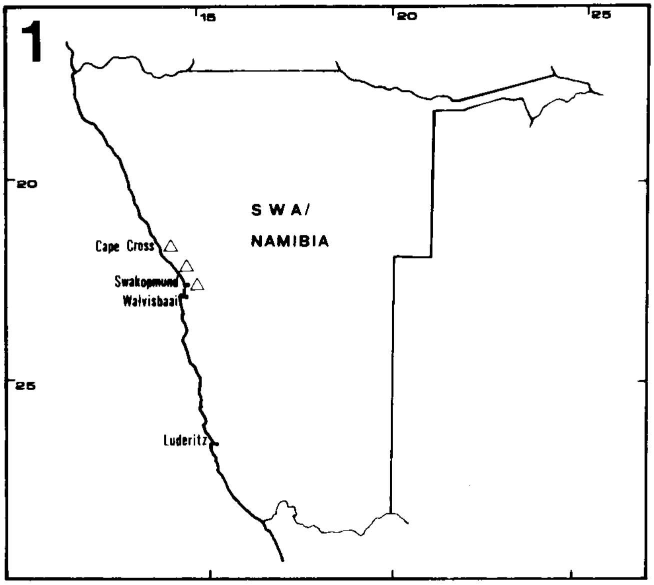


Figure 1: The distribution of *Parmelia hueana* in the central Namib Desert, SWA/Namibia.

In the second locality, north-east of Wlotzkasbaken, *P. hueana* grows in a mainly foliose/fruticose lichen community in which *Teloschistes capensis* is the dominant species. The third locality north-east of Cape Cross, is a mainly foliose/fruticose lichen community in which species such as *Parmelia hottentotta* and *Teloschistes capensis* dominate.

The occurrence of *P. hueana* fits well with the following general characteristics associated with a vagrant habit; (i) such life forms tend to be concentrated in areas of high and persistent winds which implies wind as the prime mover in the production of vagrant modifications (Weber, 1977), (ii) wind is an important agent of natural selection in the evolution of vagrant taxa and (iii) a vagrant or erratic life form is significant in that it allows the colonization of soil surfaces which are too unstable to support attached forms (Rogers, 1977).

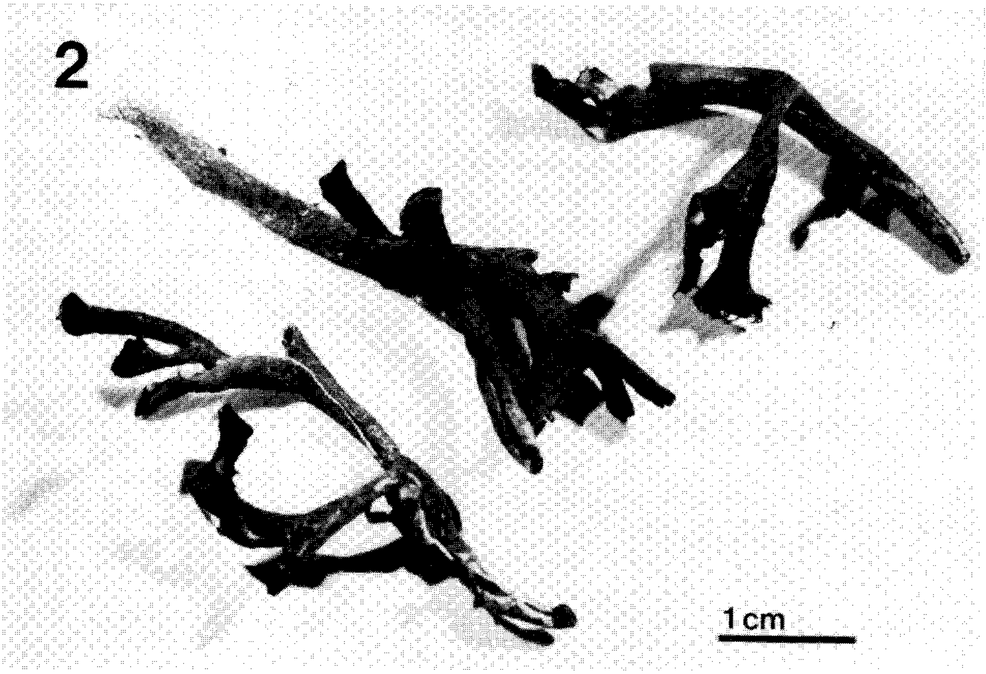


Figure 2: External morphology of *P. hueana* during the dry state.

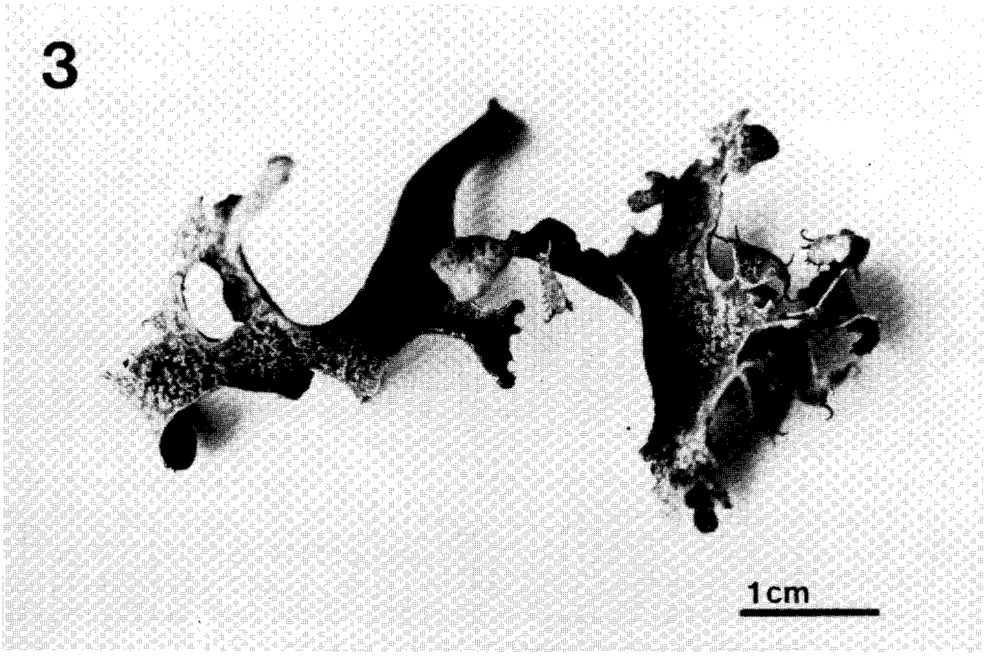


Figure 3: Thalli of *P. hueana* during the wet state.

As pointed out by Weber (1977), a vagrant habit represents a contradiction in that on the one hand it is an adaptation providing mobility and enhanced dispersal of the lichen. On the other hand this mobility can also lead to a deathtrap in that such thalli may accumulate in depressions sheltered from the wind. Accumulations of *P. hueana* thalli are often found in sandy washes. They are, however, especially abundant along the sides of dirt roads which cut across the plains on which *P. hueana* occurs. Such accumulations can form mats a few meters long and a few centimeters thick.

Thalli at the bottom of these mats eventually die. This phenomenon underlines the ecological susceptibility of the species and especially its susceptibility to unnatural disturbances in its habitat.

2. External morphology

Thalli of *P. hueana* show considerable variation in their external morphology and vary from streamlined forms to branched thalli shown in Fig. 2. Thalli differ in size from 1 – 15 cm. Despite differences in length and external morphology, thalli of *P. hueana* always have a main axis. A main axis may give off side branches which may be richly subdivided. The point of origin, external morphology and length of side branches differ appreciably. This variation in side branches is responsible for the

Figure 4: Phyllidia (arrows) along the thallus margin of *P. hueana*.

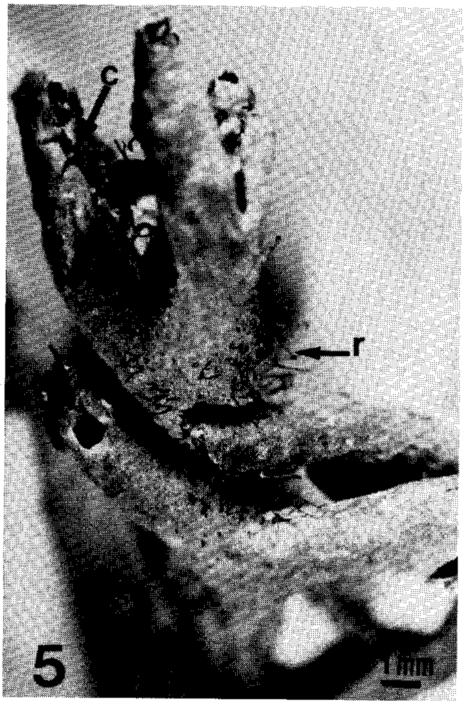


Figure 5: Rhizines (r) and cilia (c) on side branches of *P. hueana*.

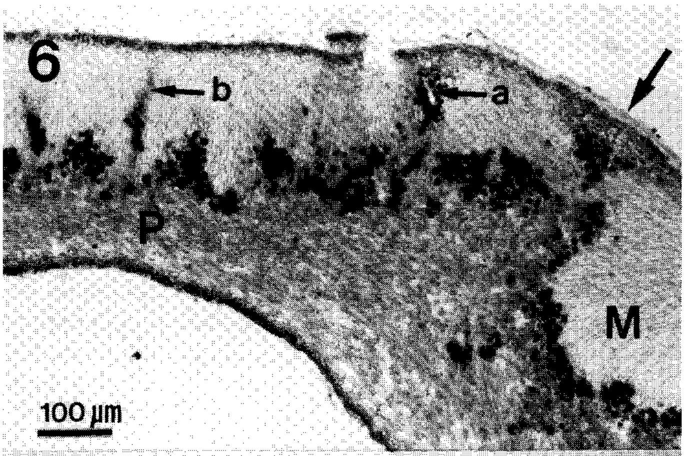


Figure 6: Cross section through a thallus of *P. hueana* showing the transitionary region between a phillidium (P) and the main axis (M). Arrow indicates the possible rupture zone. Intrusion which ends underneath the epicortex (a). Intrusion which ends blind in the lower layer of the upper cortex (b).

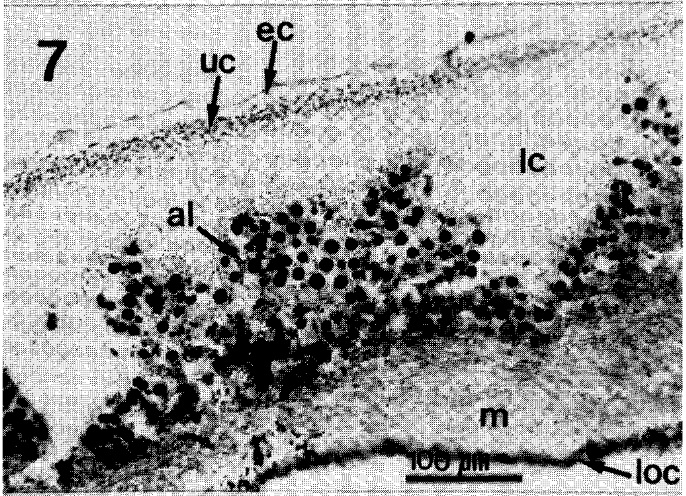


Figure 7: Longitudinal section through a thallus of *P. hueana* showing the internal morphology of the thallus. Epicortex (ec), upper layer of the upper cortex (uc), lower layer of the upper cortex (lc); algal layer (al) medulla (m); and lower cortex (loc).

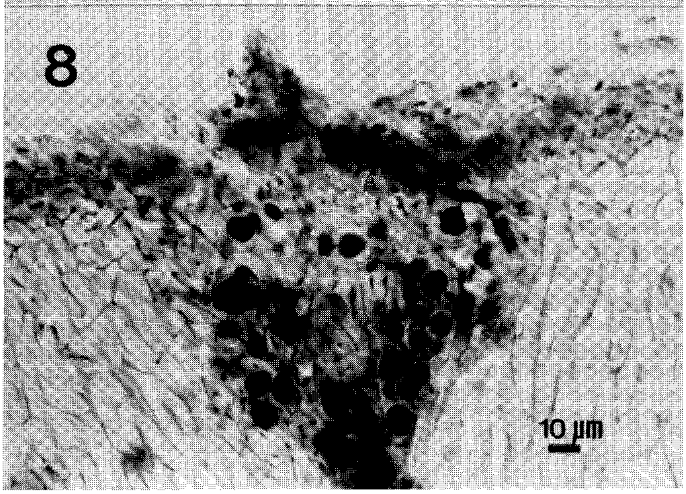


Figure 8: Intrusion of medullary hyphae and algal cells into the upper cortex which end in the epicortex.

multiformity present in mature thalli of *P. hueana*. Side branches usually have a constricted base and may act as vegetative diaspores.

During the wet (unrolled) state of the thallus, the upper cortex is visible and has a yellowish-green colour and a patchy appearance (Fig. 3). The upper cortex is exposed to sunlight only during wet stages of the thallus (Fig. 3). The lower sides of dry, inrolled thalli of *P. hueana* vary in colour from grey-black to black. The upper cortex is rarely visible during the dry state of a thallus as it is tightly rolled in upon itself. Such rolled up thalli expose the minimum surface area to the natural elements.

Rhizines are sparsely present on the lower side of thalli of *P. hueana*, are black in colour, smooth, unbranched and taper towards their tips. The tips can be either straight or bent in different ways and degrees. Rhizines are usually concentrated towards the upper portions of side branches. These parts represent more protected

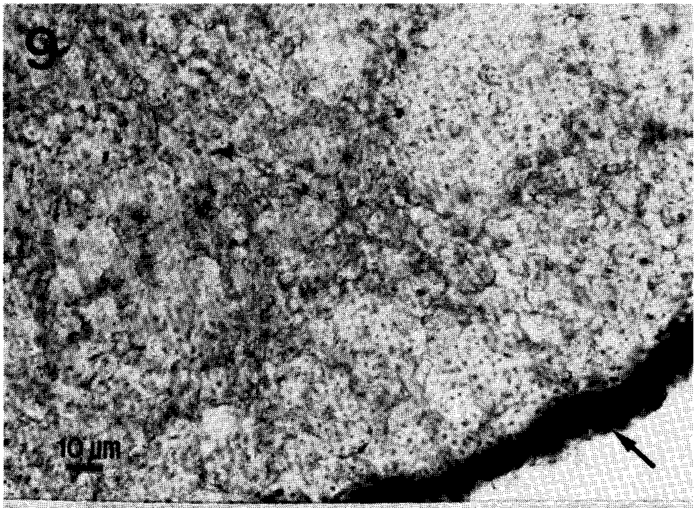


Figure 9: The medulla of *P. hueana* as seen in a cross section (arrow = darkly pigmented lower cortex).

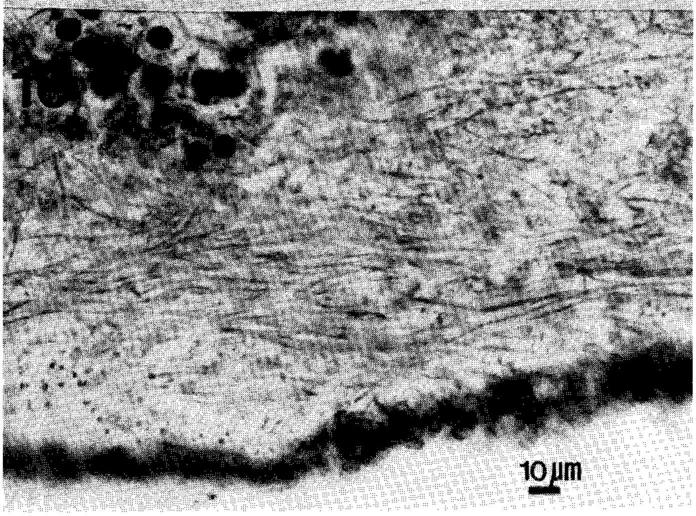
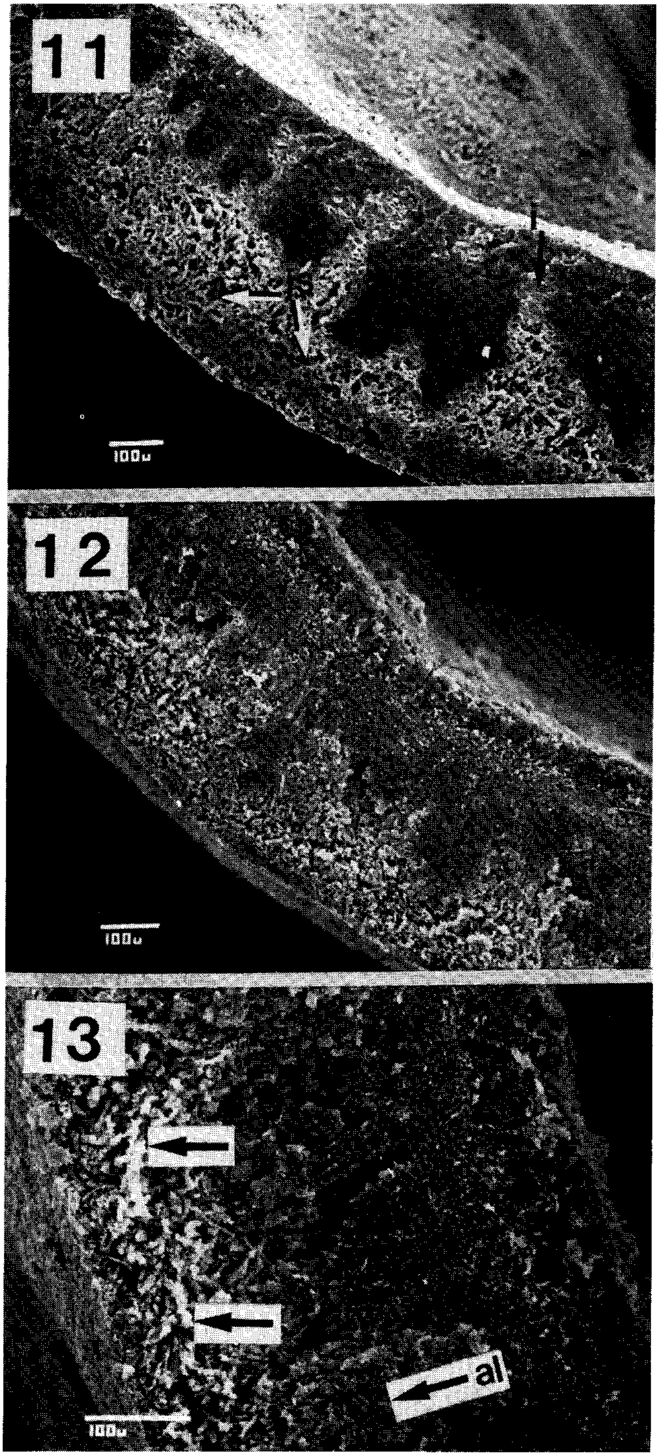


Figure 10: The medulla and part of the algal layer of thalli of *P. hueana* as seen in a longitudinal section.



Figures 11, 12 & 13: Cross section of thalli of *P. hueana* as viewed by means of a scanning electron microscope. Fig. 11 Thallus during the dry state showing the size and occurrence of interspaces in the medullary layer and intrusions into the upper cortex. Intrusions (i); Interspaces (is).

Fig. 12 Thallus during the wet state. The upper cortex shows considerable swelling, the intrusions into the upper cortex are much smaller and interspaces in the medulla are smaller in size and number.

Fig. 13 Thallus section showing the swollen cortex, compacted medulla and intrusions into the upper cortex. Numerous lichen acid cristals can be seen on the medullary hyphae (arrows). During the wet stage lumina of cortical hyphae are clearly visible. Clusters of algal cells (al).

areas as rhizines on other parts of the thallus easily brake off when a thallus is blown over the soil surface. Scars are sometimes visible where rhizines have broken off. Rhizines may make contact with the soil surface only during the wet unrolled state of a thallus. As they obviously do not play a role in the ecology of *P. hueana*, rhizines of this species may be regarded as evolutionary relics.

Cilia are frequently found along the margins of side branches (Figures 3 + 5), along the main axis they occur less frequently. Cilia along the margins of the main axis might be damaged or broken off more often than those occurring on the inrolled lobe tips where they receive a degree of protection during movement of the thallus over the soil surface. In a cross section cilia are ellipsoidal at their bases but become spherical as they taper of towards their tips. Cilia of *P. hueana* are mostly single, unbranched, smooth and black in colour. The cilial tips can be either straight or bent in various ways and degrees.

3. Anatomical features

Thalli of *P. hueana* are heteromerous and contain *Trebouxia* as a phycobiont. An epicortex covers the thick upper cortex which can be subdivided into an upper and lower cortical layer. The medulla is composed of loosely interwoven hyphae. A thin, sometimes rudimentary lower cortex is present (Figures 6—13).

An epicortex, 7—15 μm thick covers the upper cortex (Figures 6 + 7). The upper layer of the upper cortex varies in thickness from 15 μm — 25 μm. Hyphae within this layer are periclinally arranged, tightly packed and have thickly gelatinized walls (Figures 7, 8 + 11).

The lower layer of the upper cortex is prosoplectenchymateous, devoid of interspaces, varies in thickness from 200 — 500 μm and has a scalloped lower margin. Hyphae within this layer have thickly gelatinized walls (Figures 7, 8 + 11).

The algal layer forms an irregular pattern within the thallus (Fig. 7). The majority of algal cells are found between the lower side of the lower layer of the upper cortex and the medulla where they form clusters interconnected by a thin layer of individual cells (Figures 6 + 7). The remainder of the algal layers is found as two types of intrusions into the upper cortex; those that end blind in the inner parts of the lower layer of the upper cortex (Figures 6 + 7) and those that end in the epicortical layer, the second type (Figures 6 + 8).

A medullary layer of loosely interwoven hyphae (Figures 9 + 10) is characteristic of *P. hueana*. Numerous lichen acid crystals are present in the medulla. The following lichen substances could be distinguished; Usnic acid, unknown substance, a Triterpenoid, Norstictic acid, Stictic acid, Cryptostictic acid and Constictic acid.

Thalli of *P. hueana* have a thin, sometimes rudimentary lower cortex. Hyphae within this layer exhibit a network arrangement, similar to those in the medulla, but are more tightly packed and sometimes gelatinized. The hyphae within this layer are short celled and darkly pigmented. The lower surface of the thallus is always covered by a dense layer of crystals and pieces of substrate are often attached to it.

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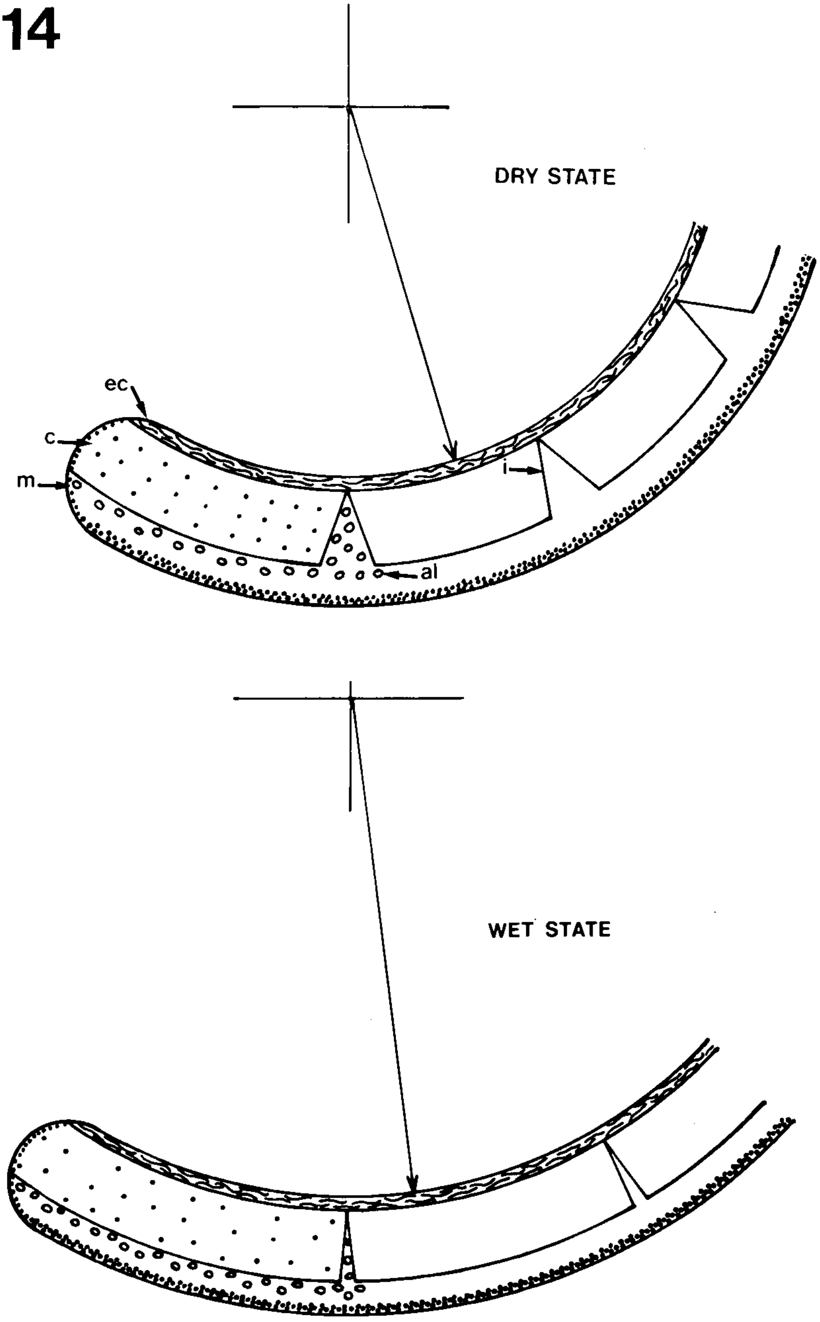

Figure 14: Diagrammatic representation of the unrolling action of thalli of *Parmelia hueana.*

4. Mechanism of movement

Water uptake and unrolling of the thallus is primarily the function of the upper cortex. During imbibition of water the hyphal walls of the upper cortex expand. Due to the absence of interspaces between hyphae in the upper cortex the entire upper cortex expands. Pressure exerted during movement of the upper cortex is partly absorbed by the interspaces present in the medulla (Fig. 11) and both types of intrusions of the medulla and algal layer into the upper and lower layers of the upper cortex. These intrusions act as hinges and allow free movement of the rigid, gelatinized sections of the upper cortex between the intrusions (Figures 11 — 14). Hyphae within these regions are resultingly more densely packed during the wet state (Figures 12 + 13). The size of the medulla (bound by its lower layer) stays more or less constant during rolling actions of the thallus and counteracts the movement of the upper cortex (Fig. 14). The necessary flexibility of the thallus during unrolling is brought about by the arrangement of the medullary hyphae. The loosely interwoven hyphae of the medulla allows stretching and limited rearrangement of the medullary hyphae. The lower cortex exerts a certain degree of restraint on the free movement of the upper cortex. The degree of restraint is governed by the amount of free movement present in the lower cortex (Fig. 14). Upon drying of the thallus, the whole process is reversed.

5. Physiological implications of thallus anatomy

The patchy appearance of the upper cortex is caused by the presence of the second type of intrusion into the epicortex (Fig. 8). Such intrusions may play an important role in the rapid absorption of water during wetting cycles and may also enhance the exchange of gasses. Exactly the opposite might also be true in that water loss through these intrusions might increase as the thallus becomes drier, with a subsequent increase in the size of these intrusions within the upper layer of the upper cortex. Increased gas exchange might also be hampered during the physiologically active wet state of the thallus as the intrusions become progressively smaller during unrolling of the thallus.

The thick upper cortex becomes opaque as it dries out and may thus protect the algal layer against harmful light intensities during the drying out and initial rolling up stages of the thallus (Kappen, 1973; Vogel, 1955).

During the wet state of a thallus the upper cortex has a screening effect and may thus protect the algal layer against harmful light intensities. The upper cortex might also play a role in the retention of water within wet thalli (Vogel, 1955; Barkman, 1958). The degree to which water is retained in the thallus will however be governed by the amount of water lost through the intrusions in the upper layer of the upper cortex. Because of the structure of their upper cortexes, thalli of *P. hueana* might be able to absorb water vapour more efficiently from the air. The upper cortex might also provide the necessary strength for the thallus to be blown about by the wind (Poelt & Romauch, 1977).

The darkly coloured lower cortex might also play an important role in the physiology of the thallus. Black coloured thalli or areas of thalli might be heated up at a faster rate than thalli coloured otherwise Rogers (1977). This phenomenon might play an important role during both the physiologically active and inactive stages of thalli of *P. hueana*. The lower cortex might also provide the necessary protection against the sandblasting effect of sandstorms which frequently occur in the Namib Desert. When the thalli are rolled up the lower cortex may furthermore play a role in the protection of the algal layer against damaging light intensities during the dry state of the thallus (Kappen, 1973).

6. Reproduction

It seems as if *Parmelia hueana* reproduces solely by vegetative diaspores. Sexual and asexual reproductive structures normally associated with lichens have as yet not been observed. Reproduction can also be faciliated by means of phyllidia which are foliose, flattened protuberances (Poelt, 1973 & 1980). Phyllidia are usually attached to the margin of a thallus by means of a constricted base (Fig. 4). The production of phyllidia seems to be genetically fixed (Lindahl, 1960) and is known from *Parmelia, Collema* and other genera (Poelt, 1973 & 1980). During transport of thalli of *Parmelia hueana* over the soil surface phyllidia may brake off to act as diaspores. Such diaspores can either remain in the vicinity where they have fallen or can be blown to other localities. Scars remain where phyllidia have fallen off. It is also interesting to note that these phyllidia may act as "vanes" which will consequently enhance the movement of thalli of *P. hueana* by the wind (Fig. 4). The transitionary region between a phyllidium and the remainder of the thallus is shown in Fig. 6. The region where the phyllidium is joined to the main axis represents a weak zone (rupture zone) due to an underdeveloped upper cortical layer.

The presence of phyllidia as reproductive mechanism underscores the importance of wind as an agent of natural selection in the evolution of *P. hueana*.

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