

2.4 Pathways of Water Movement in Relation to Structure and Micromorphology in Antarctic Mosses*

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Summary: Experimental observations on pathways of water movement are discussed in relation to anatomical and micromorphological features of five moss species from Signy Island, South Orkney Islands. Significant internal uptake of water was recorded only in the mesic species *Polytrichum alpinum* (internal = >60% of total) and *Bartramia patens* (internal = c. 30% of total), in experiments in which uptake by cut shoots was compared in individuals with the external pathway blocked, and others with both external and internal pathways open. Internal uptake maintained shoot water content close to full turgor in *P. alpinum* and at 30% of full turgor in *B. patens*, whereas water content fell to 12—15% dry wt. in the lithophytes *Andreaea gamii* and *Schistidium antarctici* and in the mesic/hydric species *Drepanocladus uncinatus*, with the external pathway blocked. Where both pathways were open water uptake from below maintained water content at or above full turgor in shoots of all five species. External water uptake by capillarity occurred most rapidly in the lithophytes, and was slower in initially air-dry than in hydrated shoots of the other species. The spreading limbs of leaves in *B. patens* and *P. alpinum* are water-repellent, as are the bright green leaves in the apical 1—2 mm of dry shoots of the lithophytes. A central strand of hydroids is well-developed only in *B. patens* and *P. alpinum*. These two species have deposits of surface wax on parts of the leaves, and surface wax also occurs on the green apical leaves in some specimens of *S. antarcticum* and other lithophytes from Signy Island.

Zusammenfassung: Bei 5 Moosarten von Signy Island, Süd Orkney Inseln, wurden die Beziehungen zwischen gemessenen Wasserbewegungen und anatomischen und histologischen Eigenschaften untersucht. Die mesischen Arten *Polytrichum alpinum* und *Bartramia patens* nahmen auf internem Weg Wasser auf: *P. alpinum* zu 60%, *B. patens* zu 30%. Dies ergab sich in Experimenten mit abgeschnittenen Sprossen, bei denen der externe Weg blockiert war bzw. bei solchen mit blockiertem internem und offenem externem Weg. Durch interne Wasseraufnahme konnte der Wassergehalt von *P. alpinum* im Bereich der Sättigung gehalten werden, der von *B. patens* bei etwa 30%. Bei den Lithophyten *Andreaea gamii* und *Schistidium antarctici* und der mesisch-hydricen *Drepanocladus uncinatus* fiel er bei blockierter externer Aufnahme auf 12—15% des Trockengewichtes ab. Hatte das Wasser Zugang auf beiden Wegen, dann konnten sich 20 mm lange Sproßchen voll aufsättigen. Lithophyten nehmen kapillar sehr rasch Wasser auf, allerdings war die Wasseraufnahme bei lufttrockenen gegenüber feuchten Sproßchen verzögert. Die Flächen der Blättchen von *B. patens* und *P. alpinum* sowie die hellgrünen apikalen Sproßteile von trockenen hophyten sind wasserabstoßend. Nur *B. patens* und *P. alpinum* haben einen wohlentwickelten zentralen Hydroidstrang. Sie, einige Exemplare von *S. antarctici* und andere Lithophyten tragen auch Wachsablagerungen auf den Blättchen.

1. INTRODUCTION

This work forms part of a broader study of water relations in mosses on Signy Island, South Orkney Islands (NOAKES & LONGTON 1988). Signy Island lies in the cold-Antarctic (= maritime Antarctic: LONGTON 1988), and has a cold-oceanic climate. Mean monthly air temperatures range from 1.3° C in summer to -9° C in winter. Precipitation is light but frequent, averaging some 400 mm water equivalent per year, and relative humidity is generally high with a mean annual value of 86% (COLLINS et al. 1975). There is snow cover for up to 6—7 months per year except in exposed habitats, with frequent rain in summer.

Signy Island supports extensive, often luxuriant vegetation dominated by mosses and lichens (LONGTON 1967, SMITH 1972). The principal bryophyte communities range from loose carpets of pleurocarpous mosses such as *Calliergon* and *Drepanocladus* spp. on ground saturated by melt-water seepage, through tall turfs of acrocarpous mosses, to assemblages of *Andreaea* and *Schistidium* spp. and other small acrocarps occurring as dense short turfs and small cushions on rocks, or on soil in exposed upland habitats.

Mosses have traditionally been regarded as ranging from ectohydric to endohydric in terms of pathways for water movement (BUCH 1945). Ectohydric species lack specialized, internal water-conducting tissue, and possess at most a thin cuticle. They are believed to rely on water absorbed directly into photosynthetic cells of the leaves from precipitation retained in external capillary spaces, or from soil moisture drawn upwards by external capillary movement. Endohydric mosses have a central strand of hydroids in the stem and Buch considered them to have a well developed cuticle on aerial surfaces, with upward water movement occurring internally in the central strand as well as by external capillarity. Surface features such as papillae and deposits of wax may also be significant

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in terms of water relations (PROCTOR 1982). The objective of the work described here was to relate anatomical and micromorphological features to pathways of water movement in selected moss species from Signy Island.

2. MATERIAL AND METHODS

2.1 Plant Material

Observations were conducted on the species listed in Table 1. *Adreaea gainii* Card. and *Schistidium antarctici* (Card.) Savicz. et Smirn. grow in habitats subject to periodic desiccation, often occurring as lithophytes. *Drepanocladus uncinatus* (Hedw.) Warnst. is typically reported from Signy Island as a form with smooth leaves growing in permanently waterlogged habitats, but the plicate-leaved form used here tends to form mats in more mesic situations. Both *Bartramia patens* Card. and *Polytrichum alpinum* Hedw. are found in a range of habitats as regards water availability.

Species	Habitat
<i>Adreaea gainii</i>	Boulders, dry stones and coarse gravel on quartz mica-schist, in exposed situations
<i>Bartramia patens</i>	Moist, sheltered and shaded rock crevices and overhangs, on quartz mica-schist
<i>Drepanocladus uncinatus</i>	Moist, calcareous soil among marble outcrops
<i>Polytrichum alpinum</i>	Sandy and gravelly soil on mesic but exposed slope
<i>Schistidium antarctici</i>	Fine, calcareous clay soil among marble outcrops

Table 1: Study species and habitats from which experimental material was collected on Signy Island

Experimental plants were collected on Signy Island during February. They were kept outside until late March or early April when they were transported to the UK by ship, arriving during May. On board, the plants were kept at ca 4° C in the dark. In Reading, they were maintained as stock cultures in a growth room at 10° C with a 16 hour photoperiod at 50—100 $\mu\text{M m}^{-2} \text{sec}^{-1}$. The plants were grown on sand under transparent plastic propagators, and were sprayed lightly with water three times each week. Plants from the stock cultures were used in transpiration experiments and anatomical studies, the latter considering both young material that had grown in culture and older parts that had developed in the field. Leaf surface features were investigated in a range of dried herbarium specimens from Signy Island.

2.2 Structural Studies

Stem anatomy was investigated by means of hand-cut transverse and longitudinal sections examined by light microscopy, supplemented by SEM studies. For the latter, the material was cut transversely with a sharp scalpel while immersed in 4% glutaraldehyde buffered to pH 7.0. After dehydration in an acetone series, the material was critical-point dried (MAGILL et al. 1974), mounted on aluminium stubs with the cut surface facing upwards, and gold-coated. Observations were made with a JOEL JSM 35R scanning microscope at an accelerating voltage of 15 KV. In studies of surface features, whole leaves were mounted on stubs, gold-plated and examined as before, using air-dry and critical-point dried material. The latter technique reveals surface features with less distortion than the former (MAGILL et al. 1974), but the acetone treatment is likely to remove surface wax.

2.3 Experimental Studies on Water Movement

The relative importance of internal and external water movement in cut shoots was compared at two vapour pressure deficits (VPD) using a modification of MAGDEFRAU's (1935) method. Shoot water contents sustained by internal, and by internal plus external uptake were also assessed.

In each experiment 40 shoots were cut to an initial length of 30 mm and soaked in deionized water for several hours. The shoots were divided into four groups, those in the "internal" (I) group having the leaves, including sheathing bases, removed from a region 12—15 mm below the shoot apex. The shoots were then blotted lightly with paper towel and treated as indicated in Figure 1. In the "internal", "total" (T) and "control 1" (C1) groups the cut bases were pushed through holes in squares of parafilm so that the shoots were held loosely in position by the film, with a 10 mm length projecting above. The shoots were then cut just below the parafilm (C1), or 10 mm below the parafilm with the newly-cut bases immediately immersed in deionized water in plastic vials (I and T). In the "internal" treatment a layer of liquid parafin was pipetted onto the surface of the water in the vials. Finally the parafilm was fastened in position by a rubber band around the mouth of each vial. Shoots in the "control

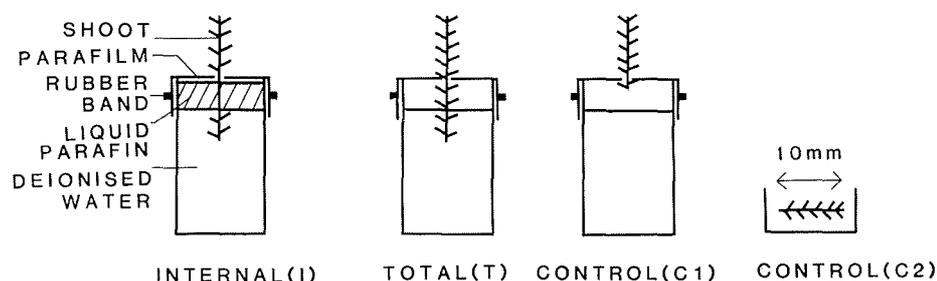


Fig. 1: Arrangement of shoots in experimental comparisons of internal and total water uptake.

2" (C2) group were cut to 10 mm in length, lightly blotted, and allowed to dry during the experiments. Additional samples of lightly-blotted shoots were weighed wet (FW) and after oven-drying at 80° C (DW) to determine initial water content (100 FW — DW/DW), and mean values (n = 3—4) were calculated.

During the experiments all plants were enclosed in a 20 cm diameter desiccator in the 10° C growth room. Relative humidity (RH) was controlled by circulating air at 1.0 l min⁻¹ from the top of the desiccator, over a saturated salt solution, and back to the base of the desiccator. This procedure normally maintained RH at 80±5% (VPD = 245 Pa) over NH₄NO₃ and at 40±5% (VPD = 736 Pa) over MgCl₂, as indicated by a hygrometer in the desiccator. However, it was sometimes necessary to place silica gel in the base of the desiccator to maintain the lower RH.

Each vial and its contents were weighed to ±0.01 mg initially and after 24 and 48 hours, and water loss during each 24-hour period was calculated. After 48 hours the apical 10 mm of each shoot was cut off level with the parafilm, weighed fresh and after oven-drying, and the final water content calculated. Water loss by internal conduction (I) and by internal plus external movement (T) were corrected by reference to C1 and C2 as indicated in Tables 2 and 3. Using the corrected values, external water movement was calculated as T — I. In Tables 2 and 3 water loss is expressed on the basis of shoot length and dry weight, in both cases with reference to the 10 mm length of shoot projecting above the parafilm.

	<i>Andreaea gainii</i>	<i>Drepanocladus uncinatus</i>	<i>Schistidium antarctici</i>	<i>Polytrichum alpinum (1)</i>	<i>Polytrichum alpinum (2)</i>	<i>Bartramia patens</i>
Water loss (mg cm ⁻¹)						
Internal (I)	1.1 (1.1)	1.4 (1.0)	1.4 (0.7)	31.7 (7.3)	29.0 (12.3)	21.9 (8.6)
Total (T)	29.3 (22.5)	105.1 (17.3)	87.2 (8.6)	33.8 (6.6)	48.3 (21.1)	80.6 (13.0)
Control 1 (C1)	2.0 (0.3)	2.8 (0.7)	3.8 (0.6)	3.3 (0.5)	2.9 (0.9)	5.0 (0.9)
Control 2 (C2)	0.0	0.1	0.0	0.0	0.5	0.0 (0.9)
Internal corrected (I-C2)	1.1 (4%)	1.3 (1%)	1.4 (2%)	31.7 (104%)	28.5 (63%)	21.9 (29%)
Total corrected (T-C1)	27.3	102.3	83.4	30.5	45.4	75.6
External	26.2	101.0	82.0	-1.2	16.9	53.7
Water loss (mg mg ⁻¹ dry wt)						
Internal (I)	1.1 (1.0)	1.0 (0.6)	0.8 (0.4)	28.1 (5.7)	8.5 (2.8)	26.5 (19.8)
Total (T)	39.4 (32.2)	117.8 (28.5)	91.8 (12.0)	29.5 (7.8)	12.3 (3.4)	77.7 (9.2)
Control 1 (C1)	2.4 (0.5)	3.5 (1.1)	4.7 (1.4)	3.5 (1.2)	0.7 (0.2)	6.5 (2.1)
Control 2 (C2)	0.0	0.1	0.0	0.0	0.4	0.0
Internal corrected (I-C2)	1.1 (3%)	0.9 (1%)	0.8 (1%)	28.1 (108%)	8.1 (70%)	26.5 (37%)
Total corrected (T-C1)	37.0	114.3	87.1	26.0	11.6	71.2
External	35.9	113.4	86.3	-2.1	3.5	44.7
Water content (% dry wt)						
Initial	144	411	167	407	345	500
By internal movement	15 (3.4)	12 (8.3)	15.1 (6.0)	285 (81.6)	173 (33.5)	101 (69.3)
By total movement	86 (106.9)	1022 (197.3)	480 (59.8)	264 (33.8)	216 (34.5)	512 (193.4)
At full turgor	205	288	183	159	228	359

Table 2: (n = 8 — 10) evaporation from individual shoots of antarctic mosses during 24 h at 10° C and 80% RH (VPD = 245 Pa). Figures in brackets are sample standard deviations. Percentages show internal movement as a proportion of total.

	<i>Andreaea gainii</i>	<i>Drepanocladus uncinatus</i>	<i>Schistidium antarctici</i>	<i>Polytrichum alpinum</i>
Water loss (mg cm ⁻¹)				
Internal (I)	2.0 (1.3)	3.4 (1.8)	6.1 (5.7)	56.9 (16.1)
Total (T)	94.1 (44.4)	130.2 (32.4)	130.9 (13.2)	87.8 (23.9)
Control 1 (C1)	5.0 (1.1)	4.7 (0.4)	6.1 (2.6)	3.4 (1.6)
Control 2 (C2)	0	0	0	0
Internal corrected (I-C2)	2.0 (2%)	3.4 (3.0)	6.1 (5%)	56.9 (67%)
Total corrected (T-C1)	89.1	125.5	124.8	84.4
External	87.1	122.1	118.7	27.5
Water loss (mg mg ⁻¹ dry wt)				
Internal (I)	1.1 (0.8)	2.3 (1.3)	3.6 (3.6)	20.3 (3.7)
Total (T)	77.7 (35.5)	227.5 (48.2)	106.9 (22.9)	25.9 (5.0)
Control 1 (C1)	4.5 (1.2)	7.6 (1.5)	4.8 (2.0)	1.1 (0.4)
Control 2 (C2)	0	0	0	0.1
Internal corrected (I-C2)	1.1 (1%)	2.3 (2%)	3.6 (4%)	20.2 (81%)
Total corrected (T-C1)	73.2	219.9	102.1	24.9
External	72.1	217.6	98.5	4.7
Water content (% dry wt)				
Initial	230	528	212	385
By internal movement	8 (5.8)	24 (14.7)	29 (10.2)	211 (30.8)
By total movement	260 (146.8)	640 (220.2)	396 (199.5)	220 (32.5)
At full turgor	205	288	199	228

Table 3: Mean (n = 7 - 10) evaporation from individual shoots of Antarctic mosses during 24 h at 10° C and 40% RH (VPD = 736 Pa). Figures in brackets are sample standard deviations. Percentages show internal movement as a proportion of total.

Water content at full turgor in samples of the experimental material was determined by binding replicate groups of shoots into loose bundles with fine (5 amp) fuse wire, soaking them overnight in deionized water, allowing them to drain briefly, and centrifuging them for 5 minutes at 1500 g (3,000 rpm on a 14.5 cm rotor). The centrifuge tubes had a cotton-wool plug at the base overlain with a layer of glass beads. The shoots were inserted above the beads, their apices pointing downwards, and the mouths of the tubes were sealed with plastic film. After centrifugation the bundles of shoots were weighed immediately and after oven-drying at 80° C. Mean (n = 4-8) water content at full turgor was calculated from the formula above. The technique is based on the assumption that centrifugation removes externally-held water without causing a loss of internal water. A similar approach was adopted by DILKS and PROCTOR (1979) and GIMINGHAM & SMITH (1971).

2.4 Microscopic Observations on External Water Movement

Moss shoots, either air-dried or soaked in water and lightly blotted, were cut to lengths of 20-30 mm depending on the species. The lower ends of the shoots were inserted into short (ca. 10 mm) lengths of 2.0 mm internal diameter glass tubing, sealed at one end, and previously filled with water or with aqueous aniline blue stain. The tubes were mounted horizontally, and capillary movement of the liquid along parts of the shoots projecting from the tubes was observed under a dissecting microscope. The tests were carried out at laboratory temperature (ca. 20° C) and RH (ca. 40%), giving a VPD of ca. 1400 Pa. Evaporation of water from the shoots is likely to have been increased by heat from the microscope lamp.

3. RESULTS

3.1 Plant Structure

3.1.1 *Polytrichum alpinum*

Stem structure in *P. alpinum* conformed in essential respects to that described and illustrated in *Polytrichum* spp. by HEBANT (1977), showing a prominent central strand of hydroids surrounded by a hydrom sheath and leptom, with leaf traces running through the cortex. Hydroids are narrow, elongate cells with tapering, overlapping end walls and other features which suggest that they provide a preferential pathway for water conduction: they lack a living protoplast when mature (HEBANT 1977).

Leaves in *Polytrichum* spp. comprise a broad base tightly clasping the stem, and a spreading, multistratose limb bearing longitudinally-oriented plates of cells, the lamellae, which form the principal site of photosynthesis. Low papillae are present on cells forming the distal edge of the lamella in the Signy Island material. These cells, cells

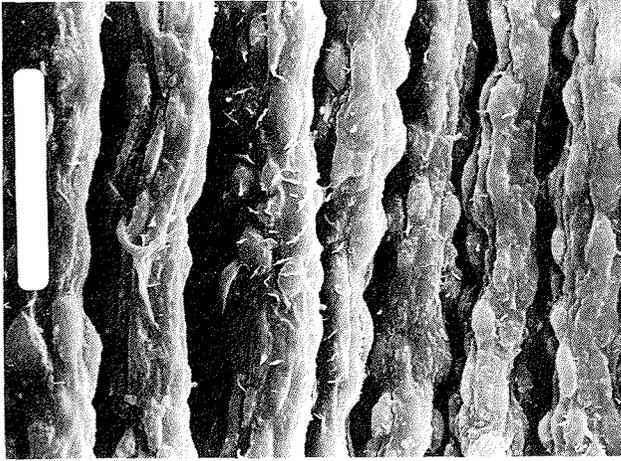


Fig. 2: Apices of lamellae on the adaxial surface of the limb in a leaf of *P. alpinum*. SEM photograph of air-dry material: magnification 1000. The white bar indicates the long axis of the leaf.

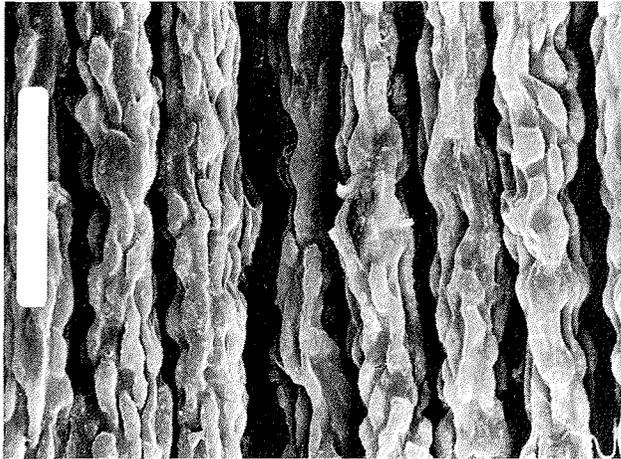


Fig. 3: Apices of lamellae on the adaxial surface of the limb in a leaf of *P. alpinum*. SEM photograph of air-dry, chloroform-washed material: magnification 1000. White bar as in Fig. 2.

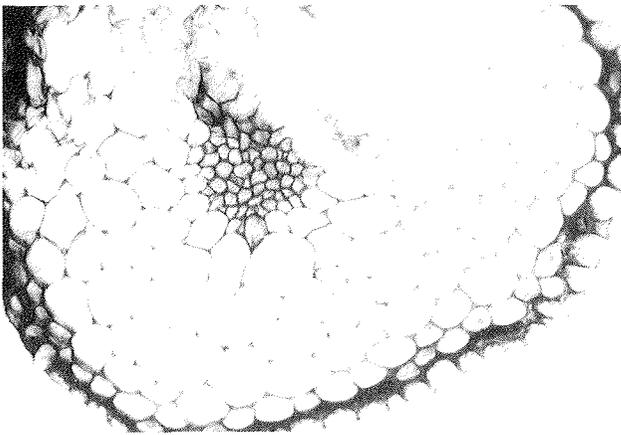


Fig. 4: Transverse section of the stem in *B. patens*. Light micrograph: magnification 250.

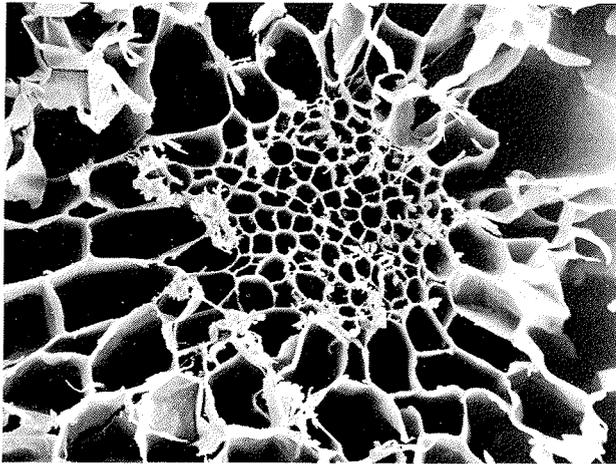


Fig. 5: Transversely-cut stem of *B. patens*. SEM photograph of critical-point dried material; magnification 500.

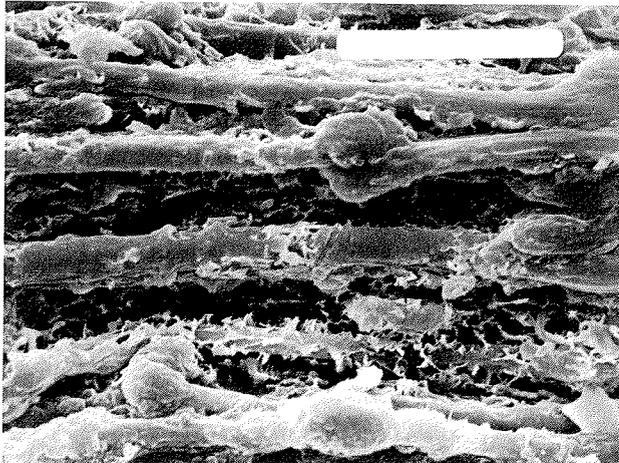


Fig. 6: Abaxial surface of the limb in a leaf of *B. patens*. SEM photograph of air-dry material; magnification 1000. White bar as in Fig. 2.

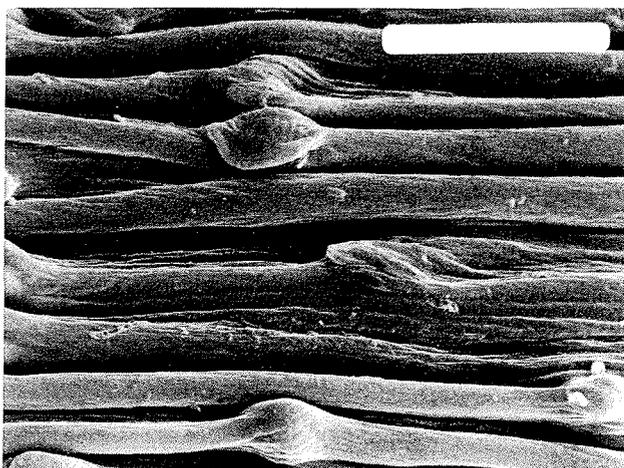


Fig. 7: Adaxial surface of the limb in a leaf of *B. patens*. SEM photograph of air-dry, chloroform-washed material; magnification 1000. White bar as in Fig. 2.

on the abaxial surface of the limb, and those on both surfaces of the base, are thinly coated with small rods of a chloroform-soluble material interpreted as surface wax (Figs. 2 and 3).

3.1.2 *Bartramia patens*

The stem cortex comprises broad, elongate, thin-walled cells surrounded by a narrow band of smaller cells with thicker walls. There is also a prominent central strand of hydroids, but no leaf traces (Figs. 4 and 5). The leaves comprise a broad, hyaline, sheathing base, and a tapering, photosynthetic limb, with a narrow midrib. No leptom or lamellae are present in this, or the succeeding species. Lamina cells are elongate parallel with the long axis of the leaf. In the limb there is a prominent, commonly bilobed papilla at the junction between adjacent cells on both adaxial and abaxial surfaces, apparently caused by projections from the ends of the cells. SEM observations showed that the surface of the lamina comprises alternating ridges and furrows in both air-dry and critical-point dried material, due to the cells being rounded in transverse section. Surface wax is abundant as large, irregular plates and ribbons on both surfaces of the lamina (Figs. 6 and 7). Cells of the sheathing leaf base lack both papillae (Fig. 8) and wax. The lower parts of the shoots are tomentose.

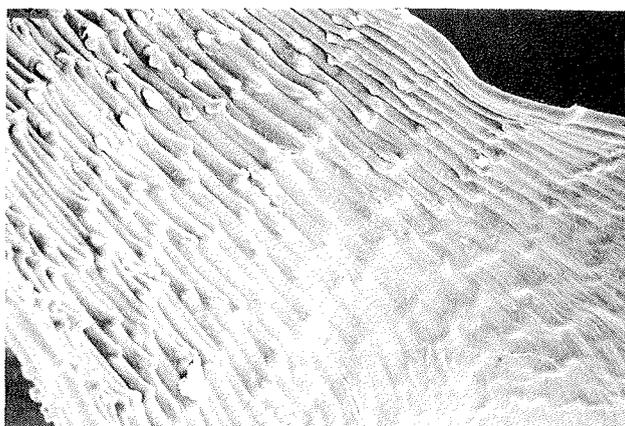


Fig. 8: Junction between the limb (top left) and sheathing base (bottom right) on the adaxial surface of a leaf of *B. patens*. SEM photograph of critical-point dried material: magnification 500.

3.1.3 *Schistidium antarctici*

Stem structure resembles that in *B. patens*, but the cortical cells are smaller, with thicker walls, and the central strand is only 2—3 cells wide. The ovate-lanceolate leaves have a midrib running to near the apex or excurrent as a short, hyaline hair point. Lamina cells range from irregularly quadrate above to rectangular below and have very thick walls. The leaf margin is recurved, and the leaf is folded along the midrib so that the adaxial surface

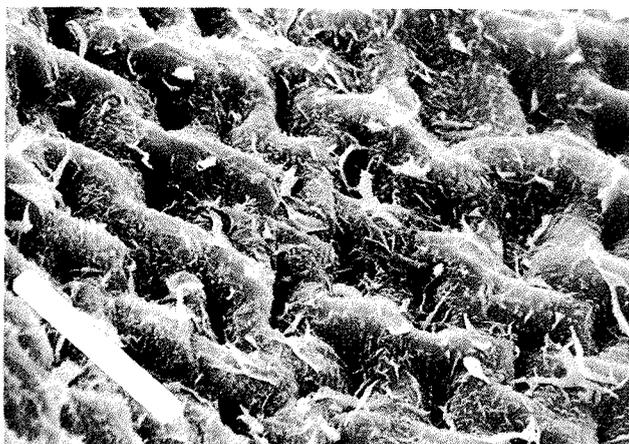


Fig. 9: Adaxial surface in the upper part of a green, apical leaf of *S. antarctici*. SEM photo-

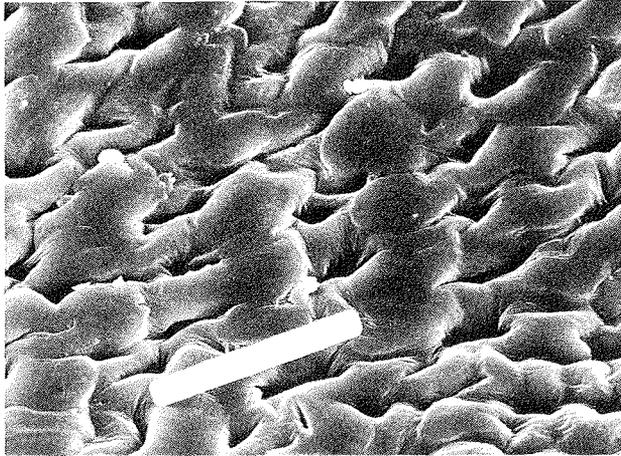


Fig. 10: Adaxial surface in the upper part of a green, apical leaf of *S. antarctici*. SEM photograph of air-dry, chloroform-washed material; magnification 2000. White bar as in Fig. 2.

forms a V-shaped channel. There is no distinct, sheathing base, but the basal cells have few chloroplasts. Leaves in the apical 1—2 mm of the shoots are bright green, with abundant chloroplasts in the upper cells, but the lower leaves are brownish in colour. The walls of the lamina cells are sinuose, but papillae are lacking. Needles and platelets of wax are sometimes present on both leaf surfaces of the uppermost, bright green leaves (Figs. 9 and 10). No wax was observed on the lower, brownish leaves, and its presence on the upper leaves varied between specimens.

3.1.4 *Andreaea gainii*

The stem is composed of elongate cells that increase in both length and breadth towards the centre. There is no central strand of hydroids. The cells have uniformly thick longitudinal walls (Fig. 11), but the transverse walls are thinner. The leaves are triangular and have no midrib. They are typically brown in colour, being green only at the shoot apex. The margins are plane and the leaves only slightly concave. The leaf cells have thick walls, particularly those running longitudinally, and range from shortly rectangular below to isodiametric above. A single, rounded papilla is present on each cell towards the leaf apex on the abaxial surface (Figs. 12 and 13), the adaxial surface being smooth. No surface wax was observed in *A. gainii*, but wax in various forms was seen on the adaxial surface, and on the abaxial papillae, in the uppermost, green leaves in some specimens of the related species *A. depressinervis* and *A. regularis* (Fig. 14).

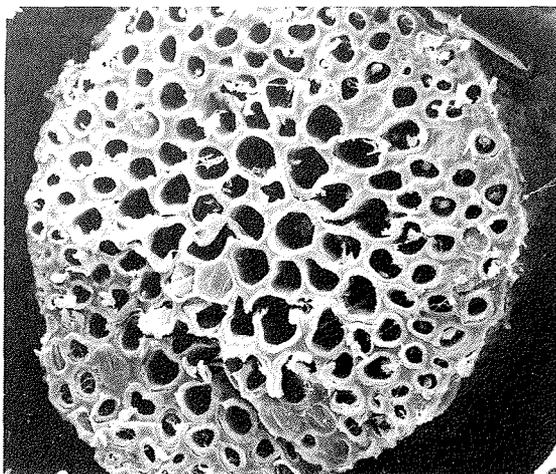


Fig. 11: Transversely-cut stem of *A. gainii*. SEM photograph of critical-point dried material; magnification 350.

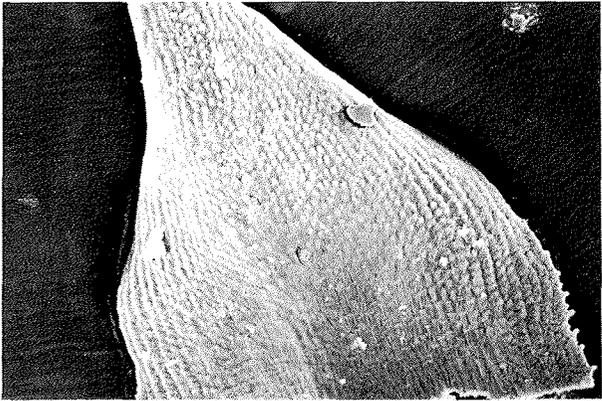


Fig. 12: Adaxial surface of a leaf of *A. gainii*. SEM photograph of critical-point dried material: magnification 500.

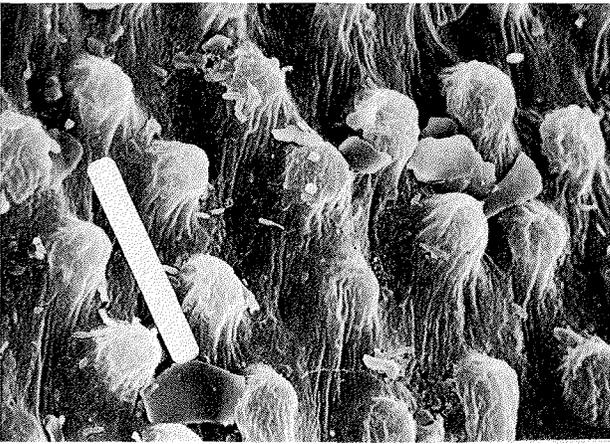


Fig. 13: Adaxial surface in the upper part of a leaf in *A. gainii*. SEM photograph of critical-point dried material: magnification 2000. White bar as in Fig. 2.

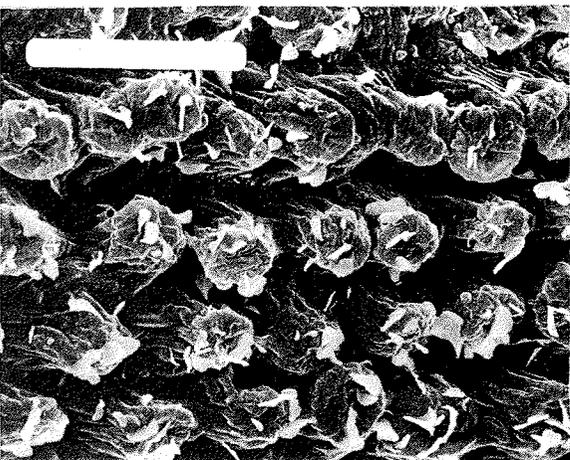


Fig. 14: Adaxial surface in the upper part of a green, apical leaf of *Andreaea depressinervis* from Signy Island. SEM photograph of air-dry material: magnification 2000. White bar as in Fig. 2.

3.1.5 *Drepanocladus uncinatus*

Stem structure resembles that in *S. antarcticum*. The leaves are lanceolate to ovate-lanceolate, long-acuminate and falcate-secund. They are concave, and plicate in the material examined here. There is a long, single midrib, the lamina cells being linear above and shorter and broader below with moderately thick walls. No papillae or surface wax were observed (Fig. 15).

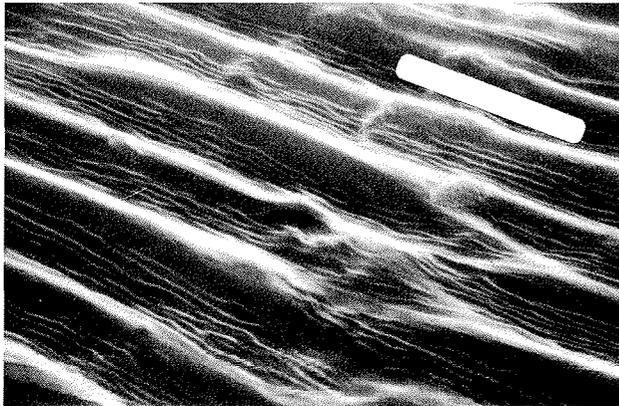


Fig. 15: Adaxial surface of a leaf of *D. uncinatus*. SEM photograph of air-dry material: magnification 1750. White bar as in Fig. 2.

3.2 Pathways of Water Movement

3.2.1 Experiment Studies

In the experiments on pathways of water movement, water loss from the C2 shoots was negligible during the second 24 hours, indicating that little of the water lost during this period could be attributed to water initially present in the shoots. The results for the second 24-hour period are shown in Tables 2 and 3. The data are means of ten shoots less any shoots, generally in the "internal" treatment, where the experimental system broke down.

In *P. alpinum*, water movement was almost entirely internal in the initial experiment, at VPD = 245 Pa (1 in Tab. 2). Indeed, application of the correction factor C1 resulted in estimates of internal movement slightly exceeding those for total movement. C1 was intended to correct for losses from the vials in the "total" water movement series by diffusion of water vapour through spaces between the parafilm and the shoot (Fig. 1), this correction being unnecessary in the "internal" series as the liquid parafin prevented evaporation. It is possible that the magnitude of the correction was exaggerated by the "total" shoots being more turgid than those in C1, thus reducing the space between the shoots and the parafilm. However, it is clear that water movement was predominantly internal in this experiment, and as C1 was generally small in relation to total movement the present uncertainty represents only a minor error.

In a subsequent experiment, conducted several months later at a VPD = 736 Pa, estimates of internal water movement in *P. alpinum* represented 67% or 81% of the total, depending on the form in which the results were expressed (Tab. 3). The experiment at the lower VPD was therefore repeated, the results then indicating internal movement to represent 63—70% of the total (2 in Tab. 2). The data thus suggest that internal conduction accounted for over half the total movement in *P. alpinum*, and sometimes almost 100%, under the conditions tested. Internal water movement consistently accounted for less than 5% of the total in *A. gainii*, *D. uncinatus* and *S. antarctici*, at both VPDs, but internal movement represented 29—37% of the total in a single experiment on *B. patens* (Tab. 3).

Tables 2 and 3 indicate that for a given species total water movement was consistently higher at VPD = 736 Pa than at VPD = 245 with the highest rates generally recorded in the ectohydric species, particularly *D. uncinatus* and *S. antarctici*. Total water movement was relatively low in *Andreaea gainii* at VPD = 245 Pa, and in this case it was inadequate to maintain the shoots at full turgor. In other experiments total water movement maintained shoot water content at or considerably above full turgor, indicating the presence of externally held water. In *P. alpinum*, internal water movement gave shoot water contents near to or rather above full turgor and the leaves

remained in a spreading position characteristic of turgid shoots. Internal water movement maintained a water content of only ca. 30% of the rather high value recorded for full turgor in *B. patens*, and in the other species lack of external water movement resulted in shoot desiccation.

3.2.2 Microscopic Observations on External Water Movement

In microscopic observations of capillary water movement, the most consistently rapid uptake occurred in *S. antarctici*. With 10 mm of the air-dry shoot projecting from the tube, water reached the apical region within 60 seconds. Its movement was marked by equally rapid spreading of the leaves. Water moved principally in the spaces between overlapping leaf bases and the stem. Water could also be seen moving rapidly up the V-shaped channel formed by the adaxial leaf surfaces, spreading over the midrib and part of the lamina, and spreading also under the recurved leaf margin. The behaviour of *A. gainii* was more variable. Some shoots became irrigated as rapidly as those of *S. antarctici*; in others both leaf-spreading and visible water movement were slower, with the upper part of the shoot not irrigated after five minutes. The difference appeared to be associated with leaf size, movement being most rapid in shoots with relatively large leaves, and this might account for the different rates of total water movement recorded in experiments on *A. gainii* (Tables 2 and 3).

In *S. antarctici*, capillary water movement resulted in the adaxial leaf surfaces becoming covered by water, while the distal part of the abaxial surfaces remained dry. This effect was less pronounced in the relatively broad leaves of *A. gainii* than in those of *S. antarctici* with their longer, spreading apices, and in *A. gainii* the abaxial leaf surfaces commonly became partially wet. It was noted that in both these species upward capillary water movement normally stopped abruptly at the base of the apical, bright green region of the shoots, which did not become visibly irrigated within 10 minutes. Similarly, no evident capillary uptake occurred when shoots were held with their extreme apices touching a small pool of water, whereas water rapidly moved down the shoots when brought in contact with the uppermost brown leaves. Thus the youngest, presumably most photosynthetically active leaves appear to have water-repellent surfaces. This was confirmed by the observation that when air-dry shoots 1—2 cm long were immersed in water they commonly floated in a vertical position, with the apices upwards, for several hours: air bubbles could then be seen on the surfaces of the uppermost leaves through a dissecting microscope.

The behaviour of air-dry *D. uncinatus* differed from that described above in that rapid capillary uptake of water (within 5 minutes) normally extended only ca. 5 mm from the water source. However, when air-dry shoots were arranged as for "total" movement in Figure 1, the apices, 10 mm above the parafilm, became visibly wet overnight, even under laboratory conditions of rapid evaporation. Capillary movement again occurred primarily in spaces between the stem and overlapping leaf bases. Rapid movement was also visible along the concave, adaxial leaf surfaces. In experiments with aniline blue, the results for air-dry material were similar to those using water, but with hydrated shoots the stain spread up to 20 mm and reached the shoot apices with 20 minutes, replacing water lost by evaporation. In contrast to *A. gainii* and *S. antarctici*, dry shoot apices of *D. uncinatus* were readily wetted.

In *B. patens* and *P. alpinum* no capillary movement of either water or aniline blue was detected within 60 minutes along parts of air-dry shoots bearing foliage leaves with spreading limbs, despite the presence of sheathing leaf bases. In several cases, water movement was observed to occur among the sheathing bases of scale leaves near the shoot base in *P. alpinum*, but to cease when the level of the foliage leaves was reached. Aniline blue spread slowly along mature regions of hydrated shoots in both species, extending 2—8 mm within 60 minutes but failing to reach the apical region of the shoots.

4. DISCUSSION

The data on rates of water uptake (Tables 2 and 3) suggest that *B. patens* and *P. alpinum* are partially endohydric, while the other species considered here appear to be essentially ectohydric. These results agree with the anatomical observations which indicate a well developed central strand only in *B. patens* and *P. alpinum*. Moreover, when dried shoots of *P. alpinum* were immersed in water the leaves spread to assume their form in fully-hydrated material more slowly than in the ectohydric species, suggesting the presence of a stronger resistance to water movement into, and presumably also out of the cells. The experimental material had been in cultivation for several months, but no important structural differences were recorded between plants grown in the field or in cultivation.

Previous experiments with tracers, reviewed by PROCTOR (1982), have demonstrated upward conduction of water in the central strand of *Polytrichum* spp. and other endohydric mosses, and we have confirmed these findings for *B. patens* and *P. alpinum* using the fluorescent tracer Tinopal in similar experiments. Other experiments have suggested that, as here, internal conduction may account for ca. 30—70% of total uptake in endohydric mosses (MAGDEFRAU 1935). In *Polytrichum commune* the proportion of internal water uptake increased at high evaporative stress, a result attributed to drying out of the external capillary system (BAYFIELD 1973). No comparable effect was seen in *P. alpinum* at the rather low VPDs employed here, and indeed in one experiment at the lower VPD internal conduction accounted for almost all the water uptake recorded. The differences between the results of the two experiments on *P. alpinum* in Table 2 could have resulted from subtle morphological differences between the shoots, as the experiments were performed at different times.

Comparison of the water contents maintained by internal water movement with those recorded at full turgor (Tables 2 and 3) suggest that internal movement alone would be sufficient to permit significant metabolic activity in *P. alpinum*, and possibly in *B. patens*, under the experimental conditions. In contrast, the ectohydric species are likely to be dependent on uptake of precipitation or of water drawn from the substratum by external capillary flow. It is possible that the use of cut shoots in these, and in most previous experiments influenced the results by, for example, reducing the resistance to water movement from outside the plant into the central strand.

Except for the experiment with *A. gainii* at VPD = 245 Pa, shoot water content in the three ectohydric species generally increased during the experiments in plants allowed to conduct both internally and externally (Tables 2 and 3), a result attributable to external uptake and storage of water. In *B. patens*, total water movement resulted in little change in water content, but in *P. alpinum* water content declined during the experiments in both the internal and total treatments, although remaining close to or above full turgor. These differences, and also the variation between species in external water movement (Tables 2 and 3), are generally in agreement with the visual observations of external water conduction. Rapid uptake occurred even in air-dry shoots of *S. antarctici* and *A. gainii*. In *D. uncinatus*, *B. patens* and *P. alpinum* capillary movement appears to be retarded if the capillary spaces dry out, but in the two endohydric species movement of an aqueous stain along fully hydrated shoots was substantially less rapid than in *D. uncinatus*. The tightly sheathing leaf bases of *B. patens* and *P. alpinum* thus appear to form less effective capillary pathways than the loosely-overlapping leaf bases of the ectohydric species.

Surface wax on leaf surfaces in *P. alpinum* and *B. patens* could act to restrict evaporation from within the leaf, or to limit surface wetting and its consequent restriction of CO₂ uptake. PROCTOR (1979) regards the latter as more generally applicable in mosses, noting that wax is most prevalent in endohydric species such as *Bartramia* and *Polytrichum* spp. in which it is not necessary for water to be absorbed over much of the leaf surface. CLAYTON-GREENE et al. (1985) suggested that wax on the surface of lamellae in leaves of polytrichaceous mosses may enhance photosynthesis by preventing flooding of the inter-lamellar channels. The occurrence of wax on both surfaces of the sheathing leaf base in *P. alpinum* may explain in part the restricted external water movement in this species, and is consistent with the report that uptake through the leaf bases is relatively small in British plants of *P. commune* (BAYFIELD 1973).

If these interpretations are correct, then *P. alpinum* appears to derive most of its internal water by upward conduction in the central strand. The position in *B. patens* may differ, for here internal conduction formed a lower proportion of total water movement than in *P. alpinum* (Tables 2 and 3), it maintained a water content substantially below full turgor, and no wax was observed on the leaf base. As in *P. alpinum*, the wax-covered limbs of *B. patens* are clearly water-repellent since water accumulates as large droplets when the plants are sprayed, but uptake through the leaf base remains a possibility.

The observation that capillary water movement ceased at the base of the green, apical region of dry shoots in *A. gainii* and *S. antarcticum* suggests that the youngest, potentially most photosynthetically active leaves also have water repellent properties that might favour efficient CO₂ uptake. This would imply that water moves internally over a short distance from stem tissue immediately below the apical region into the young leaves. The free space system of the thick cell walls appears to be the most likely pathway for such movement (PROCTOR 1982). The surface wax observed in *S. antarctici* and *Andreaea* spp., occurring only on the youngest, uppermost leaves, could contribute towards this water repellence. No wax was observed in *A. gainii*, or in some specimens of *S. antarctici*. However, surface wax as revealed by the SEM is known to be variable in occurrence in some species, and it is

possible that a smooth coating of wax is sometimes present but not detectable by the present methods.

Papillae on moss leaves may serve to form capillary channels encouraging rapid water movement over the leaf surface or, particularly where hollow, to facilitate gaseous exchange when intervening parts of the surface are wet. Indeed, they may conceivably serve both functions simultaneously, as in *Tortula* spp. where the papillae are both closely packed, hollow, and appear to contain extensions of the cell protoplast (LIGHTOWLERS 1983). It is not yet clear whether papillae on the leaves of *A. gainii* and *B. patens* are hollow or solid. Those in *A. gainii* seem most likely to function in gaseous exchange as they occur on the upper, abaxial surface which, in the older leaves, appears to attract a thinner film of water than the concave adaxial surface. The function of the papillae on the highly water-repellent surface of *B. patens* leaves remains obscure.

Finally, the differences in water relations demonstrated by the present study should be considered in relation to the habitats occupied by the species concerned. As lithophytes, *A. gainii* and *S. antarctici* may be expected to experience desiccation more frequently than the other three species. Their capacity to rehydrate rapidly from an air-dry condition, as demonstrated by the present observations on isolated shoots, could thus be a considerable advantage. This effect may be enhanced by their compact colony structure, which also appears to favour retention of externally stored water under drying conditions (GIMINGHAM & SMITH 1971). It is of great interest that even in these species the youngest leaves show water-repellent properties.

D. uncinatus, the other ectohydric species considered, occurs from mesic to hydric habitats. Ability to rehydrate rapidly may of less importance here but, when moist, individual shoots are clearly able to support upward, external water movement at a rate adequate to maintain turgor under normal field conditions. Indeed, maintenance of gaseous exchange through predominantly wet leaf surfaces may be a more significant problem. It is possible that the rather loose colony structure of this species is advantageous in creating a situation where the concave, adaxial leaf surfaces may commonly be wet while distal parts of the abaxial surfaces are dry.

The two endohydric species are characteristic of mesic habitats, and *P. alpinum* commonly has a well-developed rhizome system embedded in the soil. *B. patens* appears to be less reliant on internal water conduction than *P. alpinum*, a feature consistent with its more compact colony structure, with tomentum below, which may be expected to provide more effective uptake and storage of external water.

Variation in anatomical and morphological features thus appears to be significant in equipping the study species to operate in habitats that differ profoundly in their water-availability regimes. More information is required, however, for example on patterns of variation in field water content and its influence on water potential and rates of physiological activity, before the water relations of these mosses are properly understood. The present studies have revealed no features that can be regarded as specific adaptations to the rather humid cold-Antarctic environment. Plants in the frigid-Antarctic (= continental Antarctic: LONGTON 1988) are likely to experience considerably more severe stress, and would merit investigation.

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