THE PHENOLOGY OF SELECTED MEDITERRANEAN-TYPE CLIMATE BRYOPHYTES IN RELATION TO TEMPERATURE AND RAINFALL

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Being a thesis submitted in partial fulfilment of the requirements for the degree of B.Sc. Hons., University of Cape Town.

He kneels at morn, and noon, and eve-
He hath a cushion plump:
It is the moss that wholly hides
The rotted old oak-stump.

Samuel Taylor Coleridge
The Ancient Mariner

ABSTRACT

A study of the phenology of selected hepatics; Marchantia wilmsii Steph. , Riccia sorocarpa Bischoff, Targionia capensis Hub., Asterella marginata (Nees) Arnell, Anthoceros sp. and mosses; Fissidens curvatus Hornsch., Ptychomitrium crispatum (Hook & Grev.) Schimp., Bryum capillare Hedw., Hypnum cupressiforme Hedw., growing in the South-Western cape, a mediterranean- type ecosystem, was undertaken. The phenology of these bryophytes was related to both temperature and rainfall. Results were compared with those obtained from similar studies conducted on bryophytes growing in northern hemisphere, cool-temperate climates. Results showed that the appearance of hepatic thalli and the duration of the growth period,as well as the duration of the reproductive cycle of the mosses (with the exception of Fissidens curvatus), could be correlated with the onset and duration of the winter rainfall. Temperature did not appear to have a major effect on the bryophyte phenology. Drought-susceptible species were seriously effected by short periods of increased temperature and decreased moisture during the winter period.

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CHAPTER 1

INTRODUCTION

Phenological studies of Bryophyta have resulted in the knowledge that vegetative growth of gametophytes, gametangial formation, fertilization and sporophyte development and maturation are all variously affected by environmental conditions. Most experimental work, to date, has concentrated on the regulation of vegetative and sexual reproduction by microclimate factors, including humidity, temperature and photoperiod. Much of this work has been carried out _in vitro_. The importance of growth and reproductive responses to the distribution and radiation of bryophyte species necessitates understanding the relationship between phenology and seasonal macroclimate (ecosystem climate) variability (Zehr 1979). Relatively few studies of this nature exist.

Studies on the effect of photoperiod on initiation of gametangia showed that, in general, liverworts were less sensitive to photoperiod than were mosses. _Marchantia polymorpha_ was shown to be a long-day plant (Voth & Hammer 1940), while _Riccia glauca_, _Anthoceros laevis_ (Benson-Evans 1964) and _Asterella tenella_ (Bostic 1981), were shown to be short-day plants. Day-neutral plants included _R. crystallina_ (Chopra & Sood 1973), _Polytrichum aloides_ (Benson-Evans 1964) and _Bryum argentum_ (Chaptra & Bhātla 1981). Related to the photoperiod, and more important in the case of day-neutral plants, is the effect of temperature during the photoperiod. Gametangial induction in some cases was dependent on specific inductive temperatures, e.g. 21°C in M. polymorpha and P. aloides (Benson-Evans 1964) and 15°C for H. tenella. Species that became fertile under a wide temperature range included R. glauca, A. laevis (Benson-Evans 1964), R. crystallina (Chopra & Sood 1973) and B. argentum (Chopra & Bhatla 1981).

Monroe (1965) showed that temperature was a limiting factor in the initiation of sex organs in Funaria spp. and that the optimum temperature for their development was 10°C. He showed that photoperiod only became a limiting factor when its duration dropped below a critical level of 4 - 8 hrs. In the case of mosses temperature not only affects the rate of seta elongation but also the final seta length (Slade 1965).

Zehr (1977, 1979) concluded that favourable moisture conditions were more important than temperature for normal growth and reproduction of bryophytes. He showed that the selection of bryophytes studied grew normally at all temperatures above 0°C as long as moisture conditions were favourable. Water is essential for antherozoid transport during fertilization and is therefore vital for sexual reproduction. The effect of uninterrupted moisture conditions on the development of bryophytes has, however, only briefly been considered.

Clausen (1964) showed that the tolerance of hepatics to drought was related to habitat humidity. In liverworts exposed to different constant humidities and simultaneous different constant temperatures it was observed that, although intense desiccation was more destructive than heat or drought alone, resistance to extreme temperatures increased with slight desiccation. These factors could determine the habitat in which liverworts live in that they would only survive the reproductive season if conditions were favourable and no drought or temperature extremes were encountered.

An experiment on the moss Orthotrichum anomalum (Johnsen 1969) showed that, although gametangial initiation and sporophyte development could not occur during the summer drought, a dry period was necessary for the shedding of the capsule operculum. Artificial watering during the normally hot dry months proved detrimental in that spore release and subsequent germination were severely delayed. Johnson also found that temperature and photoperiod did not affect the phenology of this species of moss.

Bischler and Jovet-Ast (1981) showed that, although the morphology of hepatics could affect their growth and survival, it was the biochemical and biophysical properties, not necessarily expressed in the morphology, that determined species limitation to certain habitats. It is these properties that are affected by temperature and moisture content of the habitat. In Marchantiales, the means of direct water uptake and the protection of sex organs to maturity in the gametophyte are of no consequence if water is unavailable for fertilization. The survival of Marchantia sp. and Riccia sp. in particular can be regulated by the duraiton of the water supply. Although these hepatics possess efficient capillary and circulatory systems which enable them to make use of atmospheric water, rain and surface-soil water are basically essential for survival. Where the period of water availability is short the life-cycle of species of Riccia may be completed within an equally short period of time. Marchantiales have also been known to dry out even in a saturated atmosphere (Bischler & Jovet-Ast 1981). Conversely they are not able to withstand long periods of continuous submergence occurring in regions with high rainfall and a low vapour pressure deficit.

A completely different view of the regulation of the maturation cycle was provided by Newton (1972). Working on the phenology of Mnium hornum, she showed that the seasonal reproductive cycle was not controlled photoperiodically. It was suggested that, as the male and female inflorescences matured at approximately 12-monthly intervals, the cycle was controlled endogenously.

Most investigations of the climatic stimulation of the onset of reproductive phases in Bryophyta were conducted in the northern hemisphere in cold-temperate climates. The extremely cold winter period, characterized by snowfall and frost, necessitates the bryophytes overwintering this period in some phase of the life-cycle. Maturation cycles in such regions can therefore take up to 18 months.

Until 1963 M. wilmsii was recorded as occurring naturally only in summer-rainfall regime areas like the Transvaal (Arnell 1963), where it would encounter cold, dry winters and hot, wet summers. This could have been due to the fact that some hepatics show low resistance to simultaneous heat and drought (Clausen 1964). At about that time, however, it was found growing on the Cape Peninsula. This was surprising since it would have to contend with cold, wet winters and long, hot, dry summers. Colonies of male M. wilmsii occurred in Skeleton Gorge in 1964 (Schelpe pers. comm.) but have not been reported since. Although no colonies of male M. wilmsii plants were found, after extensive searches in the waterway in Kirstenbosch Gardens and in Skeleton Gorge, the present author found that the female colonies of M. wilmsii produced apparently normal sporophytes (young sporophyte matured and produced recognisable spores) in 1982. Unsuccessful attempts were made to grow thalli in the absence of male thalli in order to establish whether this species was apogamous.

Although much research has been conducted on the phenology of bryophytes in northern hemisphere, cold-temperate climates, no comparable studies have been found in the literature for mediterranean-type ecosystem climates which are characterized by long, dry summers and cool, wet winters. This study of the phenology of selected hepatics; Marchantia wilmsii Steph., Riccia sorocarpa Bischoff, Targonia capensis Hüb., Asterella marginata (Nees) Arnell, Anthoceros sp. and mosses; Fissidens curvatus Hornsch., Ptychomitrium crispatum

(Hook & Grev.) Schimp., Bryum capillare Hedw., Hypnum cupressiforme Hedw., provides an interesting comparison between mediterranean-type climate and cold-temperate (northern hemisphere) climate bryophyte phenology. Also, in the case of the hepatics, a comparison is made between phenological data for two years, i.e. 1982 and 1984 with different winter rainfall patterns.

CHAPTER 2

METHODS AND MATERIALS

2.1 PLANT COLLECTION AND LOCALITIES

Phenological data were obtained from natural populations of selected bryophyte species growing in the Kirstenbosch-Rondebosch (Cape Peninsula) area. Representative samples of Marchantia wilmsii Steph., Riccia sorocarpa Bischoff, Targionia capensis Hüb., Asterella marginata (Nees) Arnell, Anthoceros sp., Fissidens curvatus Hornsch., Ptychomitrium crispatum (Hook & Grev.) Schimp., Bryum capillare Hedw. and Hypnum cupressiforme Hedw. were collected at weekly or fortnightly intervals during the period March to October (autumn, winter, spring) in the two years of study, namely, 1982 and 1984.

F. curvatus and T. capensis grow along the bank of Window Stream in the Kirstenbosch National Botanic Gardens on clay soils, approximately 1 m above the water level. Populations of P. crispatum and B. capillare can be found both on the clay bank or on boulders in Window Stream. H. cupressiforme only occurs on rocky substrates in the stream. The Window Stream localities were totally or partially shaded during the winter months.

The locality of both Anthoceros sp. and M. wilmsii is a shallow waterway in Kirstenbosch Gardens. Both species grow on rocks or on the edge of the raised lawn beside the waterway. This site is only partially shaded by the lawn edge itself and otherwise it is totally exposed.

R. sorocarpa and A. marginata are found growing on the lower edge of a raised, sloping lawn outside the residences on the University of Cape Town campus. These sites are totally exposed.

All plant material collected was examined under a dissecting microscope after which sections of the fresh material were made using a freeze-microtome. Small amounts of material were pickled in F.A.A. for permanent mount preparation. Voucher specimens representative of the stages in the maturation cycle of each species were prepared and have been submitted to the Bolus Herbarium.

2.2 PHENOLOGICAL DATA

Vegetative and reproductive stages in the maturation cycle were monitored using the following stages:

Hepatics:

1. Appearance of young thlali
2. Appearance of antheridia
3. Appearance of archegonia
4. Immature sporophytes present

5. Mature sporophytes present
6. Dehisced sporophytes present

Mosses: (Capsule maturation)

1. Young sporophyte - calyptra present
2. Mature sporophyte - calyptra absent, operculum present
3. Dehisced capsule

This system is a vague representation of the systems for studying moss phenology proposed by Greene (1960), Forman (1965) and Hancock and Brassard (1974).

2.3 SLIDE PREPARATION

Temporary sections, 10 - 20 μm thick, were cut on a freeze-microtome and mounted in glycerine and aniline sulphate.

Permanent mounts were prepared, according to the schedule below, after material had been fixed in F.A.A. for several hours under reduced pressure for varying periods (1 - 7 hr).

Dehydration:	50% Ethanol	1 hr
	70% Ethanol	12 hr
	85% Ethanol	2 hr

	95% Ethanol	2 hr
	Absolute Ethanol (2x)	1 hr
	Tertiary-Butyl alcohol (T.B.A.) (2x)	1 hr
Infiltration:	T.B.A. + liquid paraffin (50:50)	12 hr
	50% liquid paraffin + 50% paraffin wax	4 hr
	Pure paraffin wax (Paraplast) (2x)	4 hr

Small, cut samples of material were transferred to solutions quickly using wooden toothpicks. After wax infiltration the material was embedded in Paraplast and microtome blocks prepared. These blocks, mounted for microtome use, were kept chilled in a deep-freeze. Sections (10 - 13 μm thick) were cut on a rotary microtome. Serial sections were mounted in formalin on clean slides prepared with Haupt adhesive and left to dry.

Staining of sections was carried out according to Johansen (1960) using the Safranin-Fast Green staining procedure. Cover-slips were fixed onto dried, stained sections with D.P.X. mountant and the slides left to dry once again.

2.4 PHOTOGRAPHY OF PERMANENT AND TEMPORARY SLIDES

Photomicroscope pictures of internal structure were taken using Ilford FP4 film (ASA 125) at objective magnifications of 10x and 40x. Film was developed using Acutol developer and photographs were printed on Ilford number 3 paper.

Photographs of external structure were taken on a M400 photomicroscope in the Electron Microscopy (E.M.) Unit (U.C.T.) using magnifications of 30 - 90x. The same film was used and pictures were printed at the E.M. unit.

2.5 TEMPERATURE AND RAINFALL DATA

Daily rainfall and temperature (maximum and minimum) data for 1982 and 1984 were obtained from the weather observer at Kirstenbosch Gardens. Total weekly rainfall and average weekly temperatures (maximum and minimum) were calculated. A comparison between environmental conditions and phenological data for the two years was made in order to relate any differences in the timing of reproductive stages of the bryophytes to differences in temperature and rainfall data for the two years.

CHAPTER 3

RESULTS

The first appearance of thalli of the hepatics studied occurred soon after the first late-summer or early-autumn rains. Production of antheridia, except in Marchantia wilmsii, of which no male thalli were found, occurred within five weeks of the appearance of thalli and generally took place slightly before the production of archegonia. Young sporophytes appeared within between one and six weeks after archegonia were formed. Except in the case of Targionia capensis and Riccia sarocarpa, young sporophytes were found occurring concurrently with mature sporophytes for varying lengths of time and were sometimes still present when the first of the mature sporophytes had dehisced. Dehiscence of mature hepatic sporophytes, except for those of Asterella marginata generally did not occur until after a dry period of, in most cases, longer than two weeks.

Capsule maturation in the four perennial species of moss studied varied greatly. Maturation of sporophytes of Fissidens curvatus appeared not to be seasonal, in contrast to sporophyte maturation in Bryum capillare, Hypnum cupressiforme and Ptychomitrium crispatum which appeared in late winter.

A few similarities and many differences were found between the bryophyte phenology of mediterranean-type ecosystem species and those found in northern hemisphere cool climates. Bryophyte phenology was found to be related to macroclimate as was shown by the difference in maturation cycles in 1982 and 1984. Without exception, the maturation cycles of the hepatics studied began earlier (in response to early rain) in 1984.

3.1 RAINFALL AND TEMPERATURE DATA FOR 1982

The first winter rain of 1982 fell during the week commencing 6 May (Fig. 1). This rain was directly preceeded by a three-week period, during which no rain fell. Five weeks of late summer-early autumn rain fell between 18 March and 22 April. However, total weekly rainfall during this period never amounted to more than 30 mm. Between 6 May and 30 September rainfall was considered as being continuous, despite weeks 15 - 18 July and 19 - 26 August, during which no rain fell, because the commencement of the weekly time scale was randomly chosen. These weeks were not considered as being dry because rainfall in the weeks directly preceeding and succeeding them was heavy (Appendix A). Rainfall greater than or equal to 50 mm was recorded for the weeks commencing 20 May (52 mm), 10 June (105 mm), 21 June (51 mm), 22 July (130 mm), 5 August (109 mm), 26 August (82,8 mm), and 9 September (82,5 mm). Maximum total weekly rainfall occurred at the end of July.

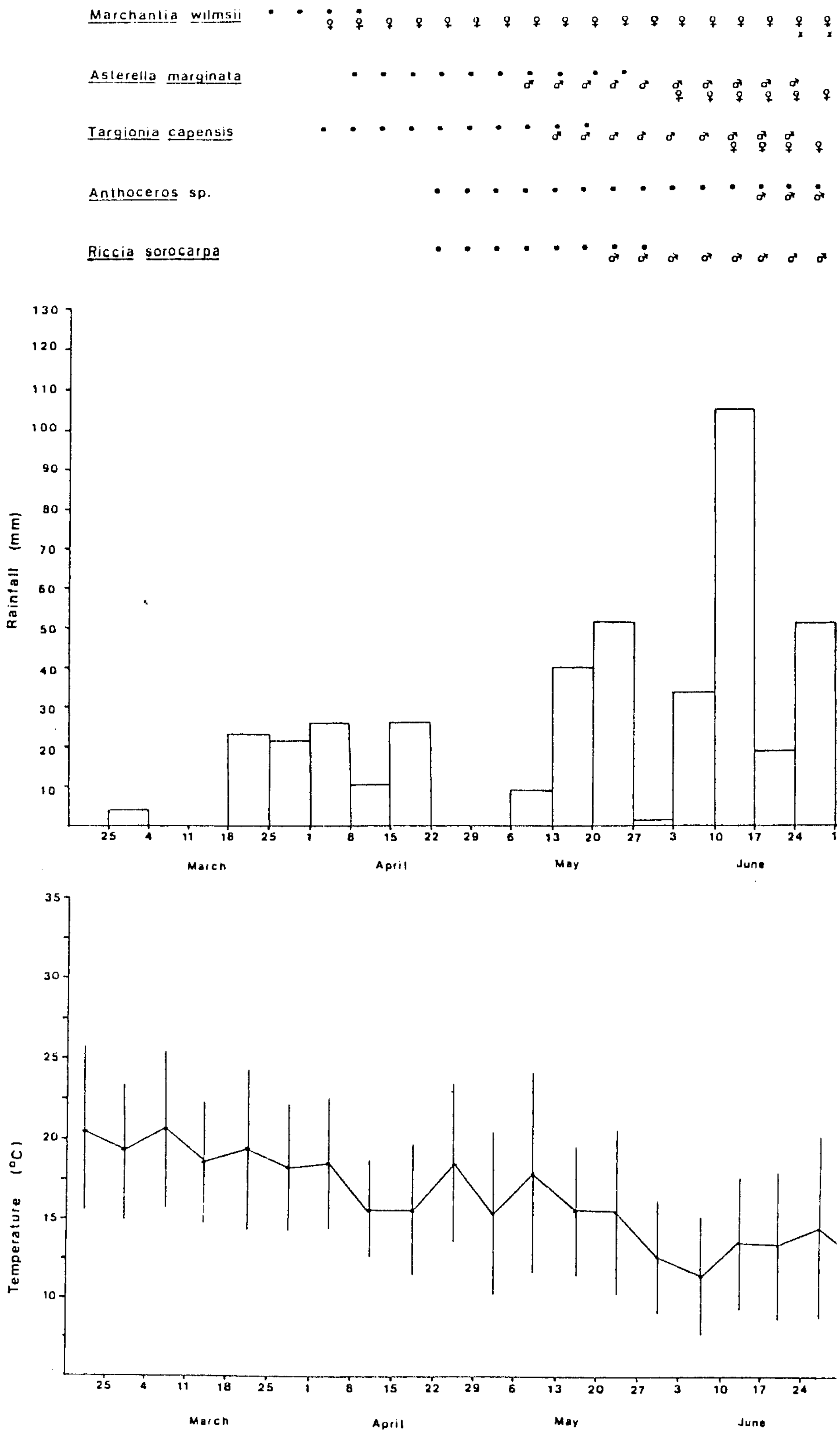

Figure 1. Representation of the maturation cycles in relation to total weekly rainfall (mn temperature (°C) in 1982.

● ● Appearance of young thalli.
♂ ♂ Appearance of antheridia.
♀ ♀ Appearance of archegonia.
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△ △ De

The maximum difference between summer and winter mean daily temperatures, averaged over a week, was 8,95°C (Fig. 1, Appendix **A**). The highest mean daily temperature was recorded for the week ending 25 February (20,87°C) and the lowest for the week ending 19 August (11,92°C). Seasonal variations in temperature resembled a sine curve (as was expected) of low amplitude.

3.2 RAINFALL AND TEMPERATURE DATA FOR 1984

Autumn rain in this year was substantial, beginning on 24 March (Fig. 2, Appendix **B**). There were 9 weeks wherein rainfall exceeded 50 mm by at least 20 mm. There were two spells, 19 May to 23 June and 11 August to 1 September, in which total weekly rainfall was continually less than 20 mm. Severe weather conditions were recorded for the week ended 19 May, including a hurrican on 15-16 May, when weekly rainfall totalled 258 mm. High rainfalls were also recorded at the beginning of July and September. During the period 24 March to 29 September rainfall was continuous.

The maximum difference between summer and winter mean daily temperatures averaged over a week, was 12,54°C (Fig. 2, Appendix **B**). The lowest mean daily temperature averaged, for the week ended 7 July, was 12,02°C, and the highest, for the week ended 7 April, was 24,56°C. A graphical plot of the seasonal temperature variations also resembled a sine curve.

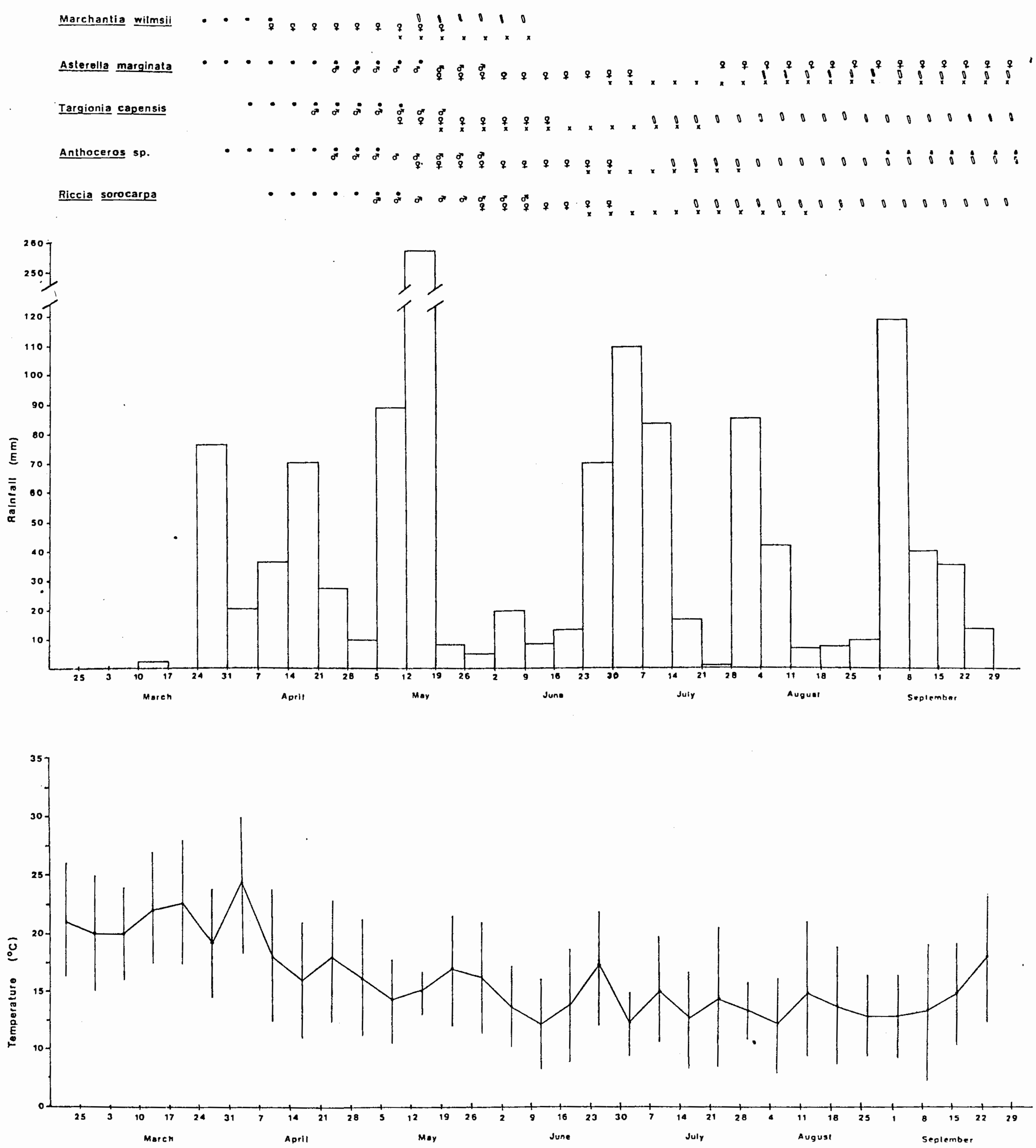

Figure **2.** Representation of the maturation cycles of the six hepatics studied in relation to total weekly rainfall (mm) and average weekly temperature (°C) in 1984.

● ● Appearance of young thalli.
♂ ♂ Appearance of antheridia.
♀ ♀ Appearance of archegonia.

x x Immature sporophytes present.
0 0 Mature sporophytes present.
Δ Δ Dehisced sporophytes present.

3.3 COMPARISON BETWEEN MACRO-CLIMATIC CONDITIONS DURING 1982 and 1984

Rainfall data for 1984 differs greatly from that recorded during 1982, the major difference being in the onset of autumn rain. In 1984 there was no break between autumn and winter rain and rainfall during the period 24 March to 19 May was extremely heavy. During this period total weekly rainfall greater than 70 mm was recorded for four weeks. During the same period in 1982 no weekly rainfall amounted to more than 40 mm. Rainfall during the period 19 May to 23 June in 1984 totalled 55,2 mm, whereas for the equivalent period in 1982 it totalled approximately 204,2 mm. The peak in rainfall at the end of July 1982 was absent in 1984, when the peak occurred mid-May.

The maximum difference between summer and winter mean daily temperatures (averaged over a week) in 1984 was 3,59°C greater than in 1982. Because the lowest average daily temperatures for the two years were comparable, i.e. 11,92°C in 1982 and 12,02°C in 1984, the difference mentioned above arose between the highest weekly temperatures, i.e. 20,87°C in 1982 and 24,56°C in 1984. This indicated that the overall temperature in 1984 was slightly warmer. The decrease in temperature between February and May in 1984 was not as gradual as in 1982. During the period 19 May to 23 June the temperature in 1984 was slightly warmer than in 1982. The slightly warmer temperatures in 1984 during this period coincided with the period of decreased rainfall.

3.4 HEPATIC PHENOLOGY: 1982

(see Figure 1)

Young thalli of Asterella marginata, a monoecious hepatic which produces antheridia in antheridial branches (Fig. 3), first appeared on about 8 April and continued to form until around 27 May. Antheridial branches, on 6 June, contained young antheridia which matured by 24 June (Fig. 4). On 6 June the archegoniophore receptacle measured 1 - 2 mm in diameter. At this stage the receptacle rim was completely folded under and the archegoniophore had not yet begun to elongate (Fig. 5) . Archegonia were present in the receptacles on 6 June (Fig. 6). The archegonia venters were slightly swollen by 14 July (Fig. 7), i.e. very immature sporophytes were present. Young sporophytes (Figs 8 & 9) persisted until shortly after 26 August. The presence of mature sporophytes (Fig. 10) was first noted on 16 August. By this time the archegoniophores had elongated to about 8 mm and the basket-like pseudoperianth was clearly visible (Fig. 11). The first sign of sporophyte dehiscence occurred on 28 August (Fig. 12). The time taken for sporophytes to reach maturity, from the archegonial stage, was approximately 9 weeks.

In Targionia capensis (monoecious or dioecious also producing antheridial branches, see Fig. 13) thalli production occurred between 1 April and 20 May. Antheridial branches contained antheridia on 13 May (Fig. 14) which matured by 23 June. On this date some antheridia had

Figure 3. Asterella marginata. Dorsal view of thallus with two antheridial branches.

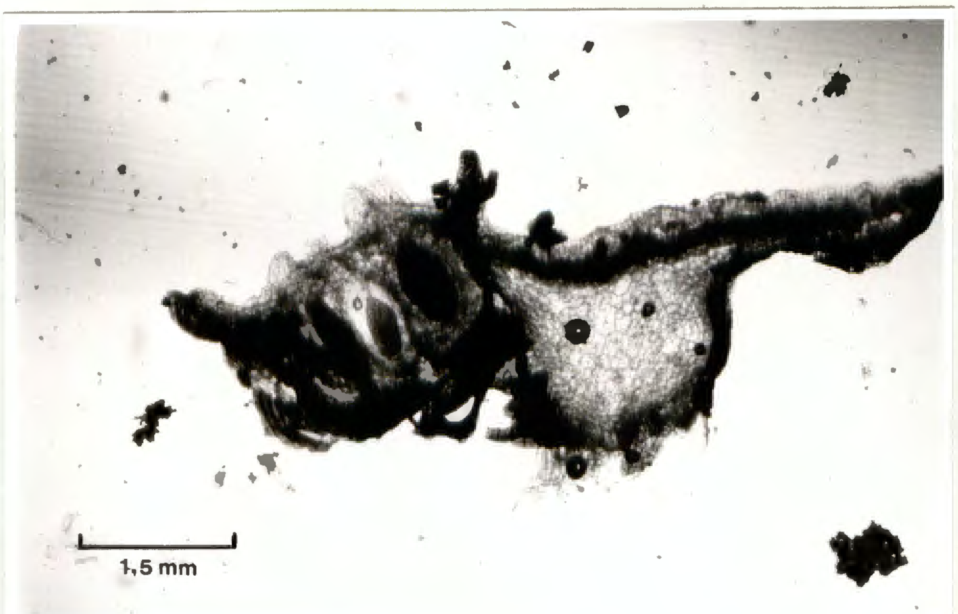

Figure 4. Asterella marginata. L/S thallus and attached antheridial branch containing mature antheridia.

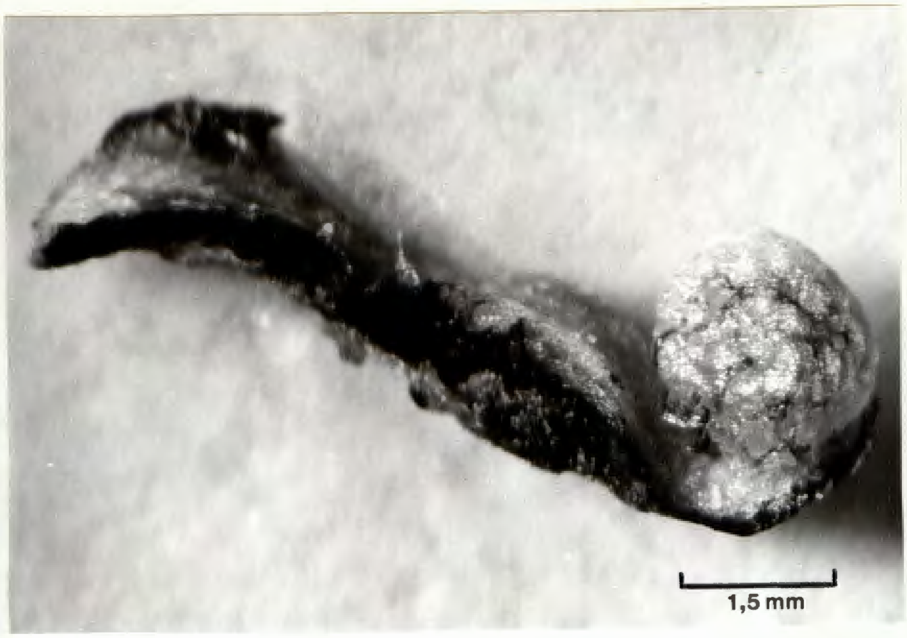

Figure 5. Asterella marginata. Lateral view of thallus showing receptacle of archegoniophore,which has not yet begun to elongate.

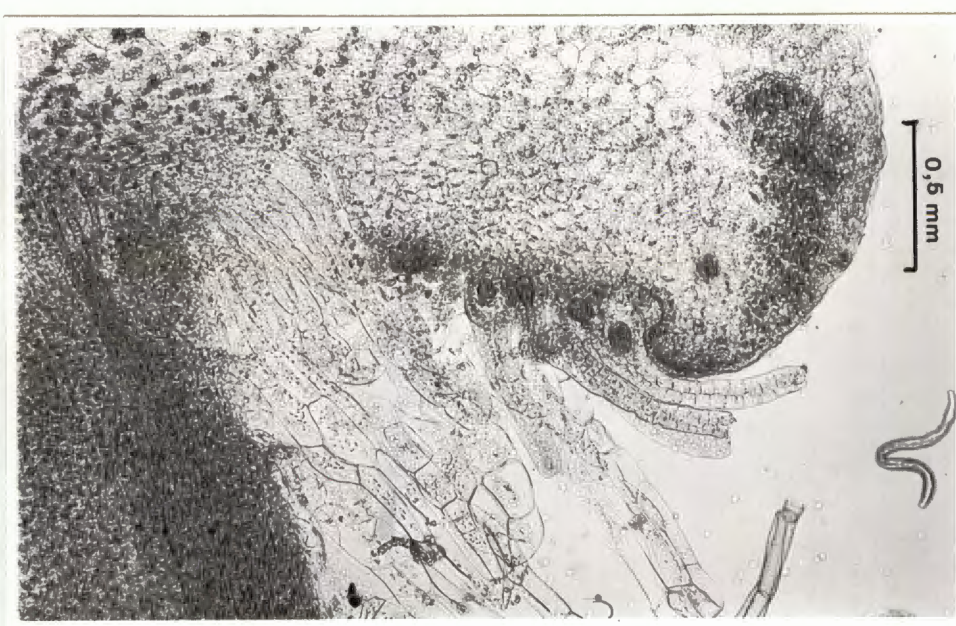

Figure 6. Asterella marginata. L/S archegoniophore showing the presence of young archegonia in the receptacle.

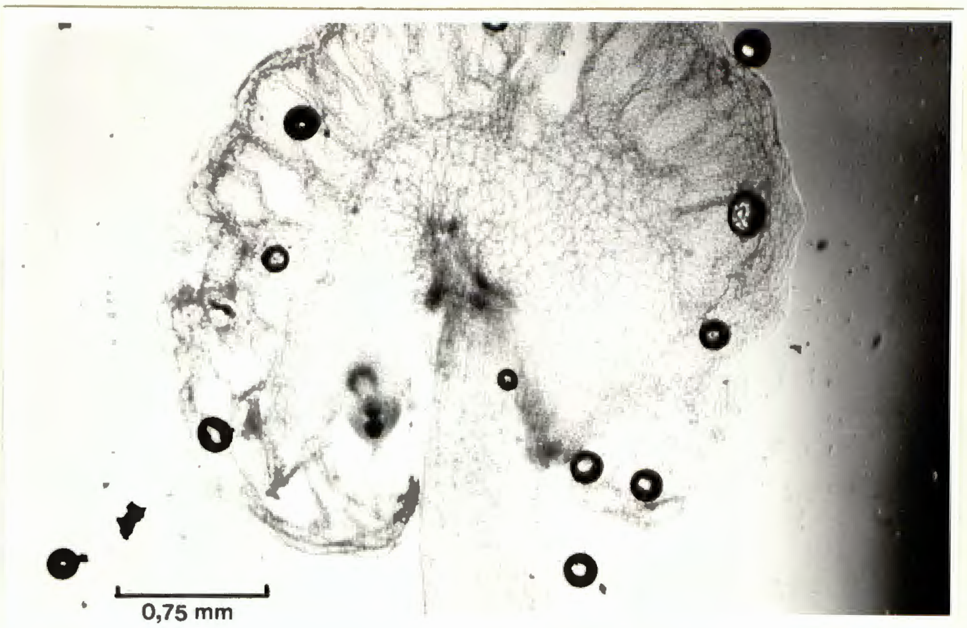

Figure 7. <u>Asterella marginata</u>. L/S archegoniophore containing a fertilized archegonium with swollen venter.

Figure 8. <u>Asterella Marginata</u>. L/S archegoniophore containing a young sporophyte.

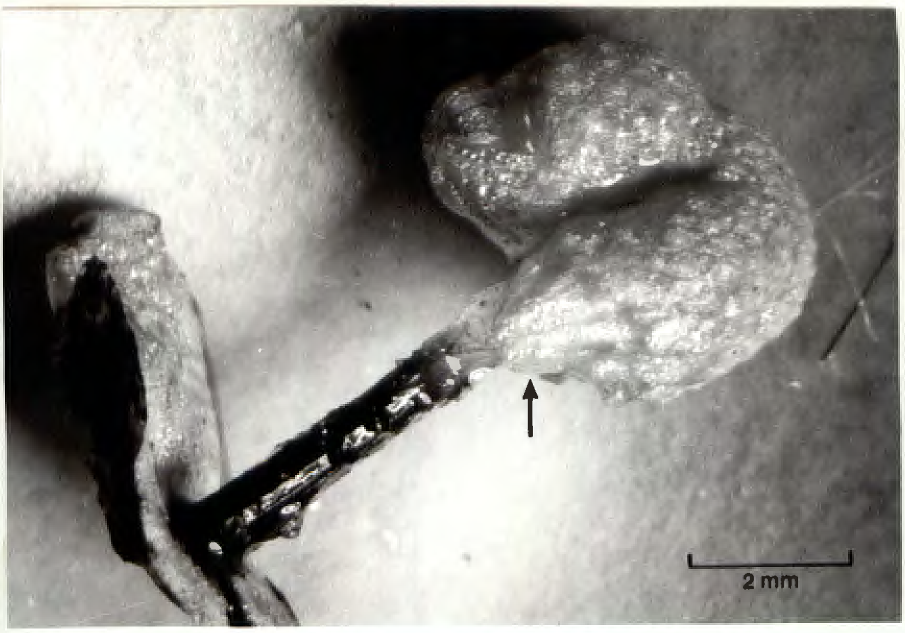

Figure 11. Asterella marginata. External view of the archegoniophore showing the basket-like pseudoperianth.

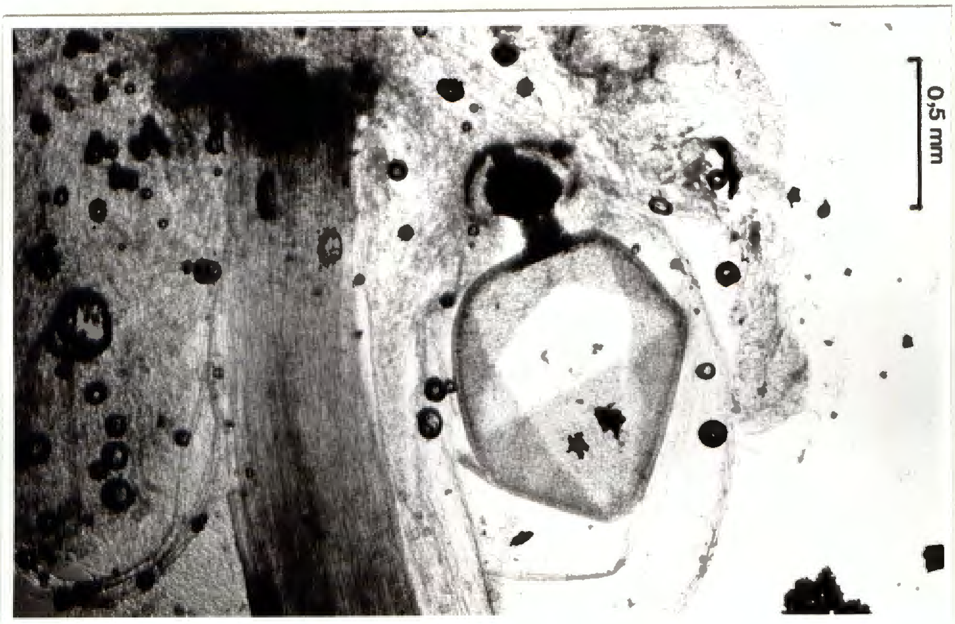

Figure 12. Asterella marginata. L/S archegoniophore containing dehisced sporophyte.

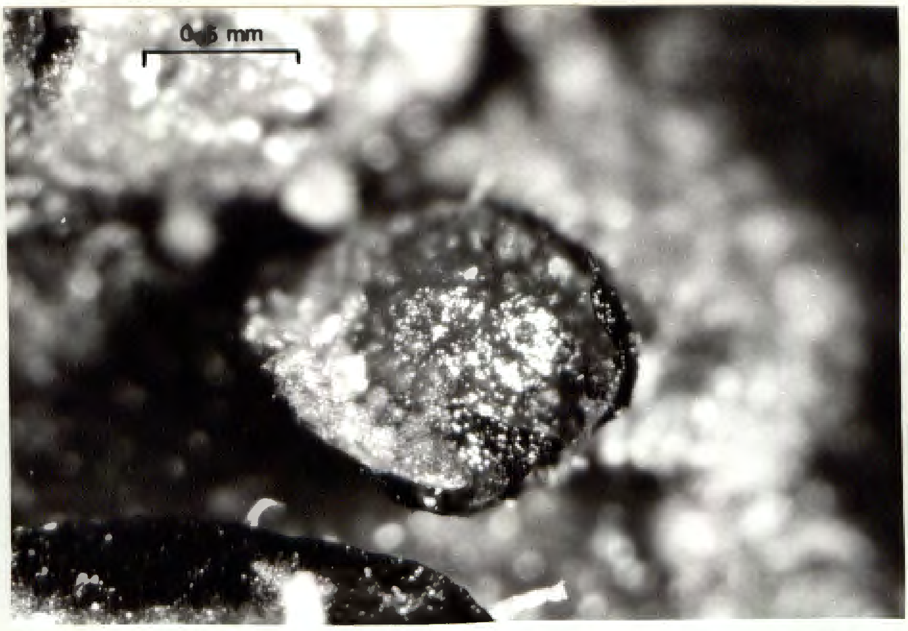

Figure 13. Targionia capensis. Dorsal view of the antheridial branch.

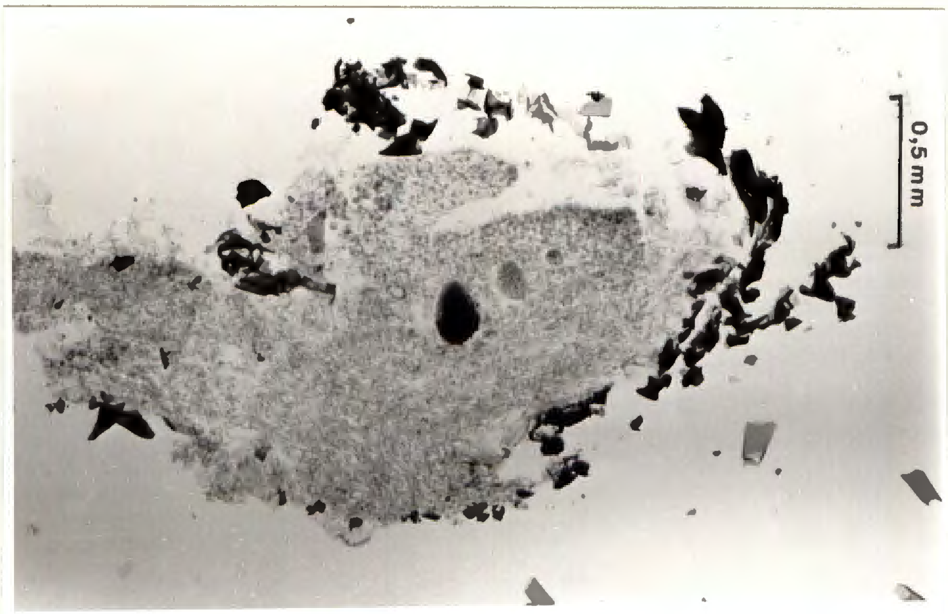

Figure 14. Targionia capensis. L/S thallus and antheridial branch. Antheridia in this section are young.

released their antheozoids (Fig. 15). Archegonia were sited between 10 June and 15 july (Fig. 16). Young sporophytes, formed by 29 June (Fig. 17), were contained in pale green involucral bracts (Fig. 18). By the time the sporophytes had matured (Fig. 19) the bracts had turned purple (Fig. 20a & b). Only very few sporangia had dehisced by 30 September. From observations made in October 1983, it was found that the thallus had to dry and pull the involucal bracts up and out before spore release occurred. In this species dehiscence occurs within closed involucral bracts. At this stage the bracts protruded quite a way from beneath the apex of the thallus (Figs 21 & 22) when viewed from above.

Appearance of thalli in Anthoceros sp. commenced on about 22 April and by 23 June thalli contained antheridia which matured by 15 July (Fig. 23). By 8 July the production of young sporophytes had begun (Fig. 24 & 25) and by 3 August these had grown to a height of 8 - 10 mm and the column was well developed (Fig. 26). The sporophytes matured, reaching a height of 14 - 20 mm by 26 August. The first signs of dehiscence only appeared towards the very end of September (Fig. 27). It is interesting to note that immature sporophytes were still present on 2 September.

Young thalli of the dioecious hepatic Riccia sorocarpa were formed between 22 April and 27 May (Fig. 28). Samples collected showed antheridia (Fig. 29a & b) to be present on 27 May and archegonia (Fig. 30) on 29 June. The presence of the latter continued until

Figure 15. Targionia capensis. L/S antheridial branch showing antheridia having already released their antherozoids.

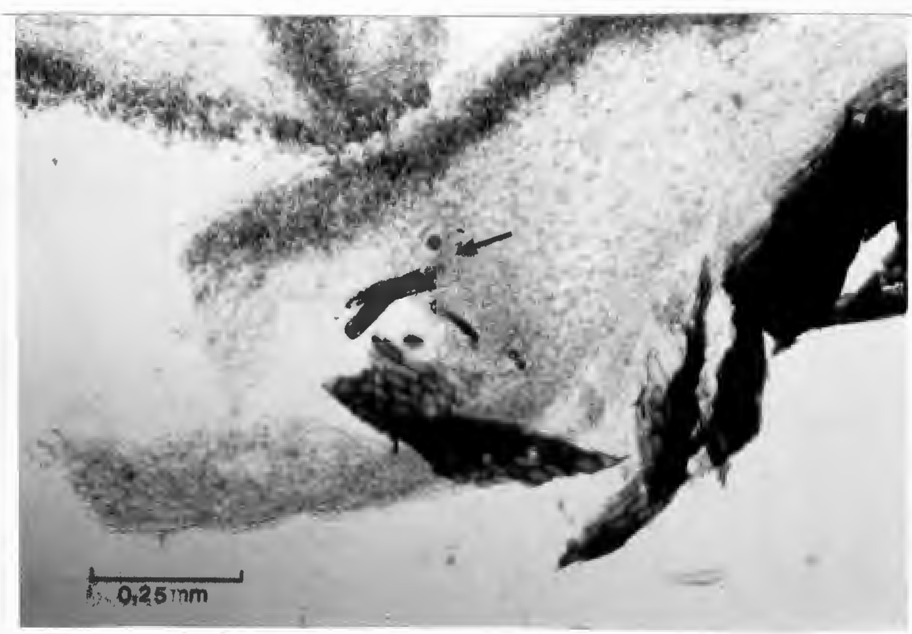

Figure 16. Targionia capensis. L/S thallus showing young archegonia contained in very immature involucral bracts.

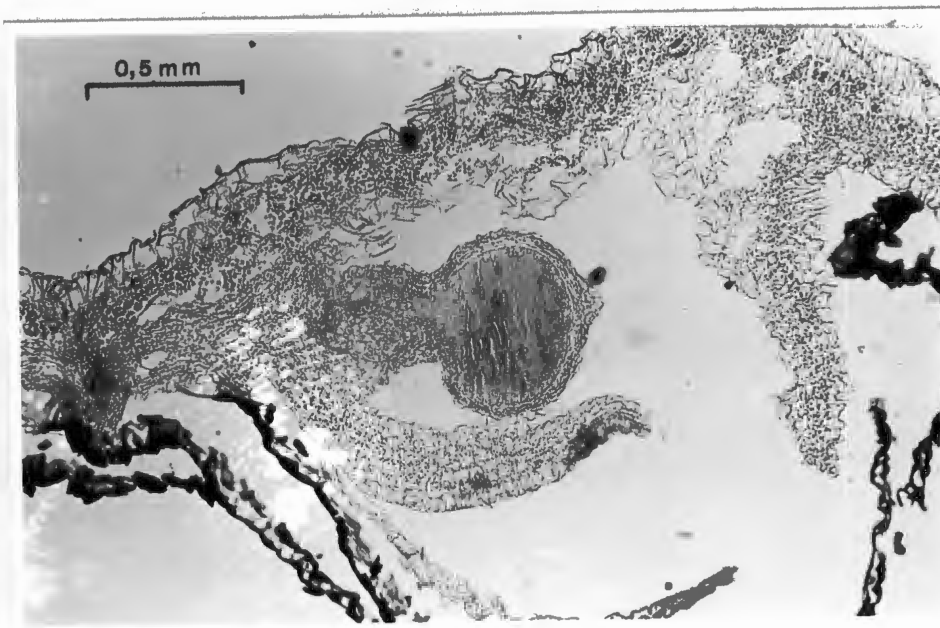

Figure 17. Targionia capensis. L/S young sporophyte contained within partially green involucral bracts.

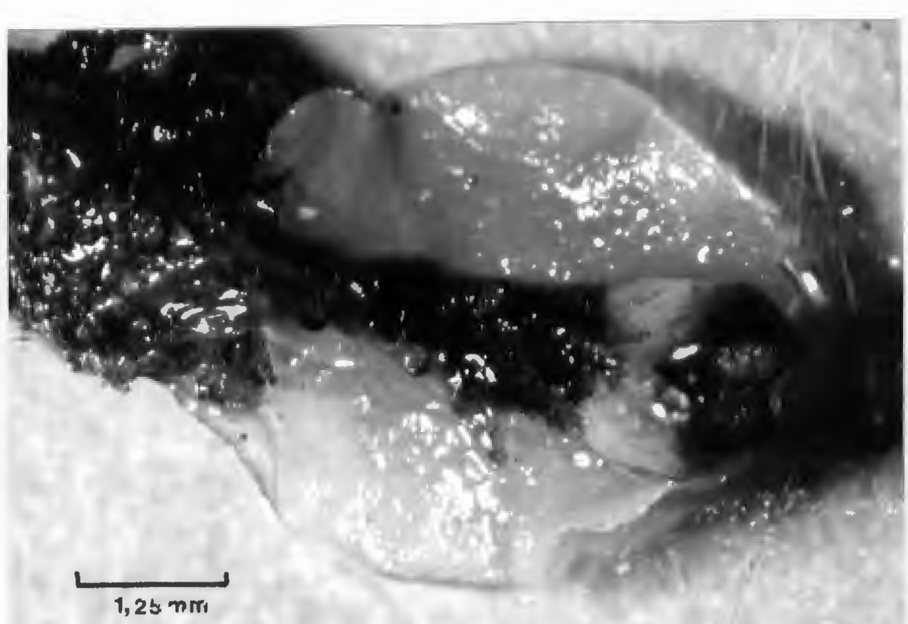

Figure 18. Targionia capensis. Ventral view of thallus showing partially green involucral bracts. At this stage the bracts were, in fact, still closed. They opened as a result of desiccation incurred during photography under strong illumination.

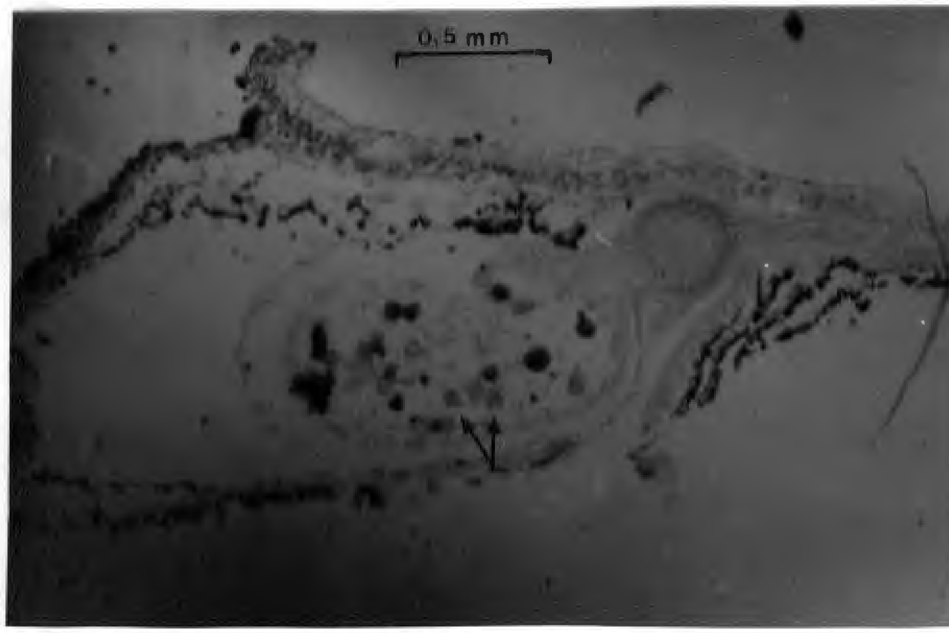

Figure 19. Targionia capensis. L/S mature sporophyte (spores clearly visible).

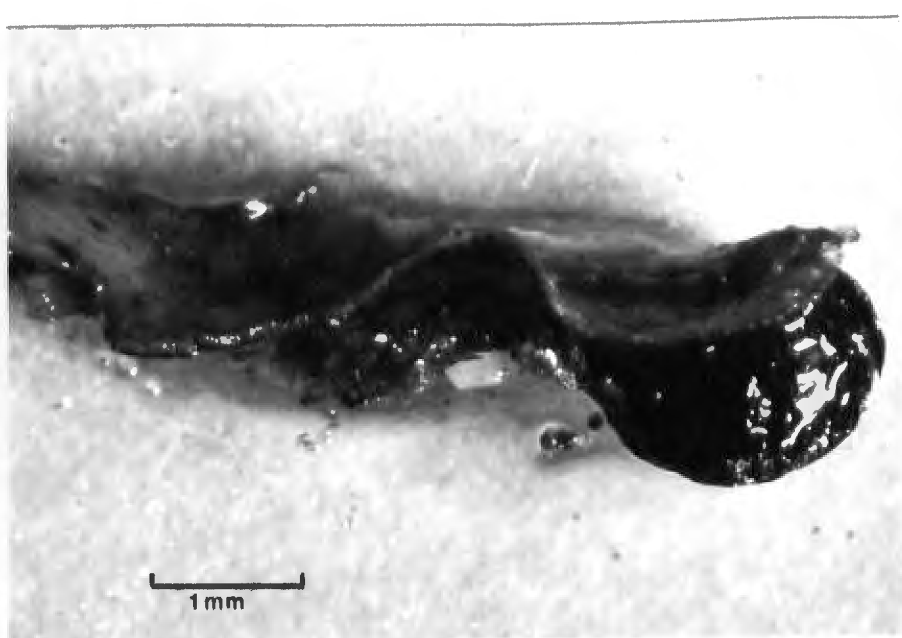

Figure 20a. Targionia capensis. Lateral view of thallus showing black involucral bracts. (Note small degree of protrusion of the bracts beyond the apex of the thallus).

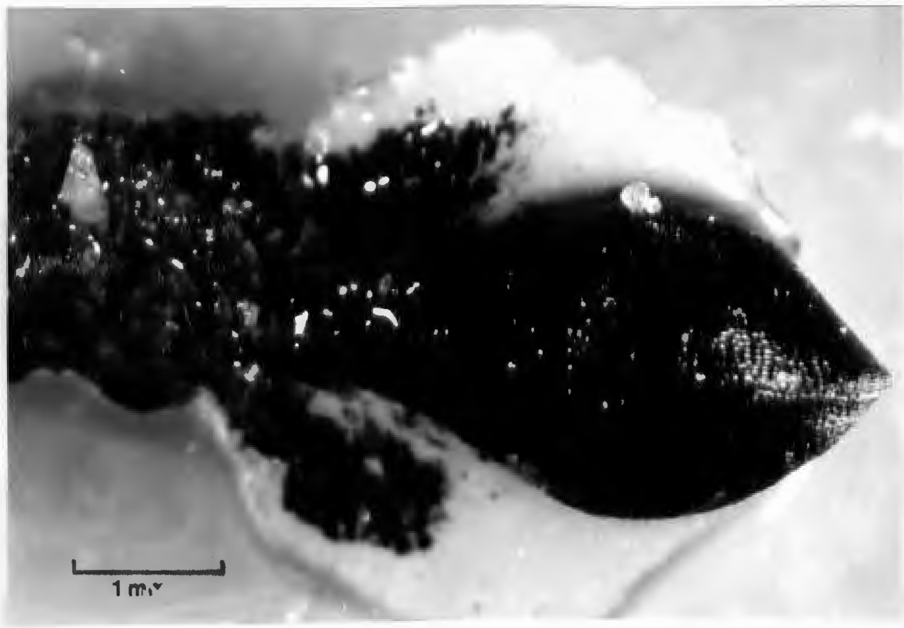

Figure 20b. Targionia capensis. Ventral view of the thallus showing black, closed involucral bracts.

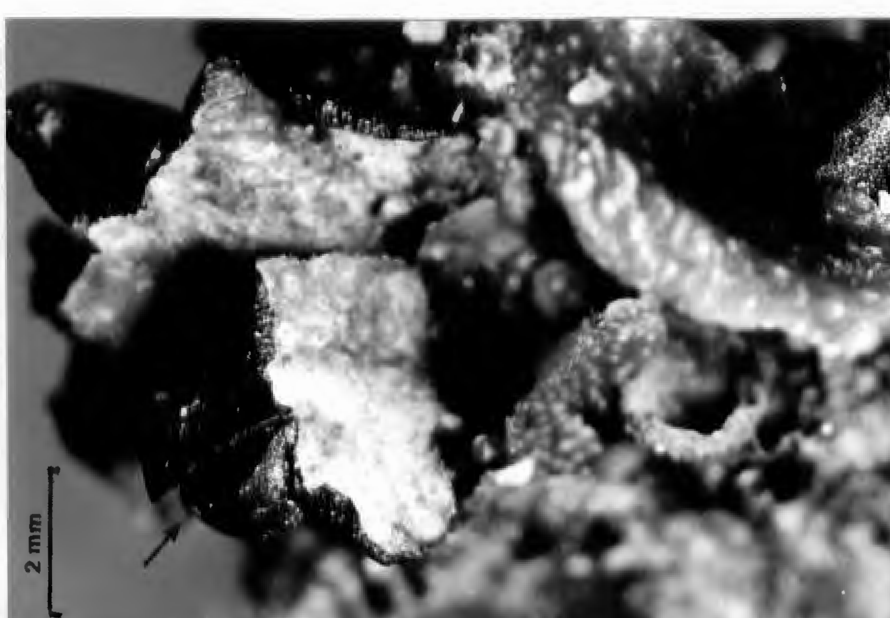

Figure 21. Targionia capensis. View of the apex of the thallus showing the bracts opened for spore release (dehiscence occurs within closed bracts).

Figure 22. Targionia capensis. Dorsal and ventral views of the thallus showing the increased degree of protrusion of the bracts beyond the thallus apex.

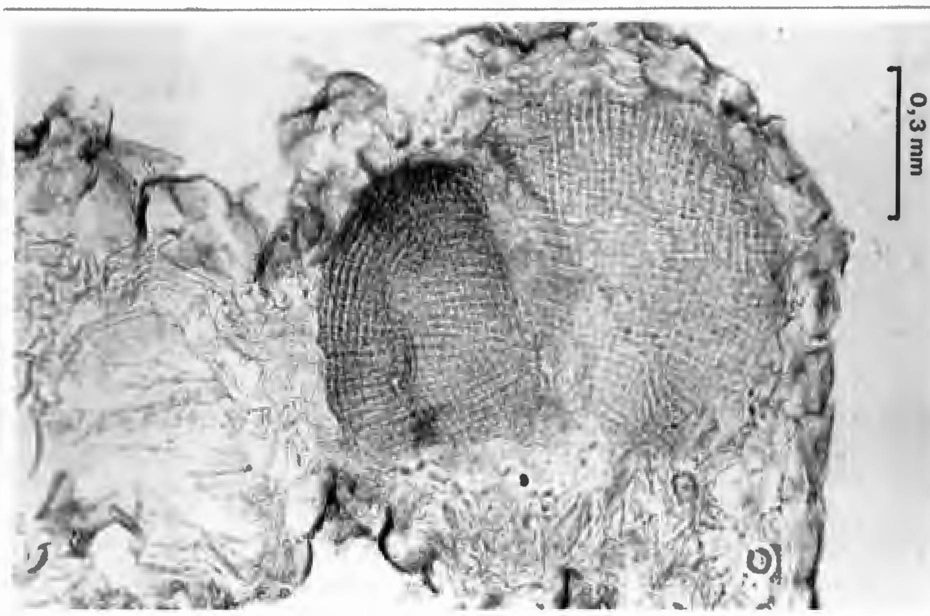

Figure 23. Anthoceros sp. L/S thallus containing two antheridia.

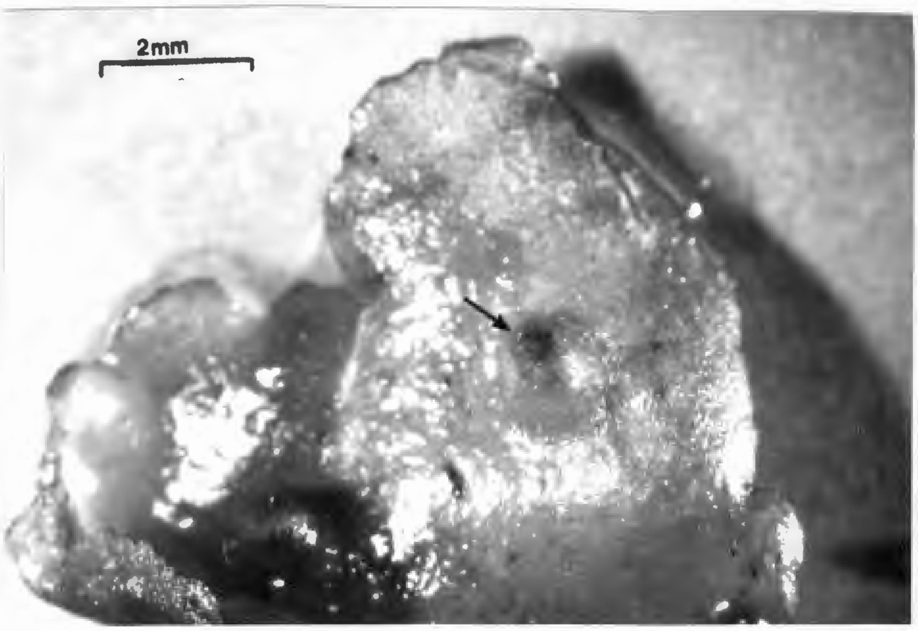

Figure 24. Anthoceros sp. Dorsal view of thallus showing very young sporophyte.

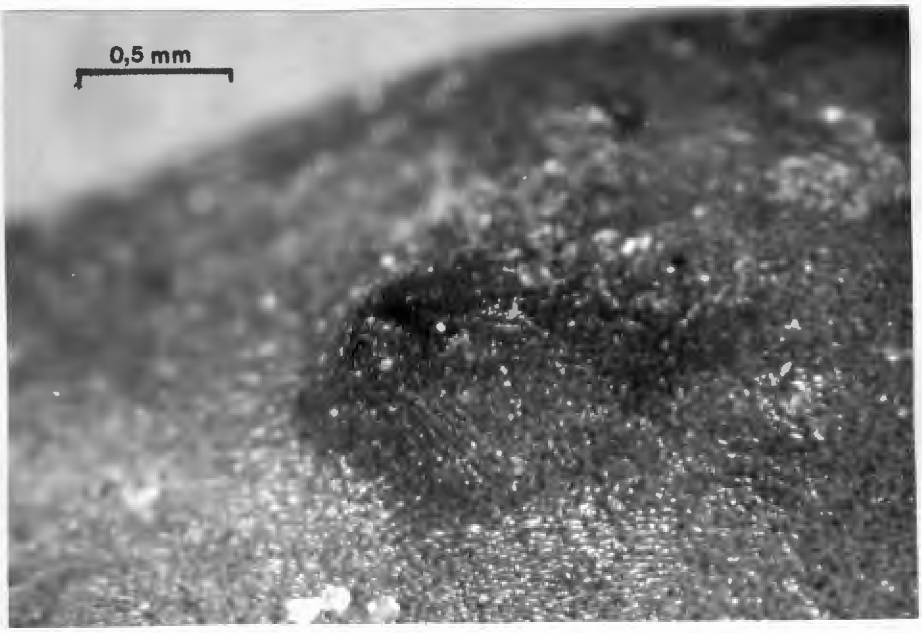

Figure 25. Anthoceros sp. Enlargement of figure 24 showing very young sporophyte protruding from the thallus.

Figure 26. Anthoceros sp. Lateral view of sporophyte showing developed column and attachment to thallus.

Figure 27. Anthoceros sp. apex of a dehiscing sporophyte.

Figure 28. Riccia sorocarpa. Dorsal view of entire colony of thalli (approximately size of colony at maturity).

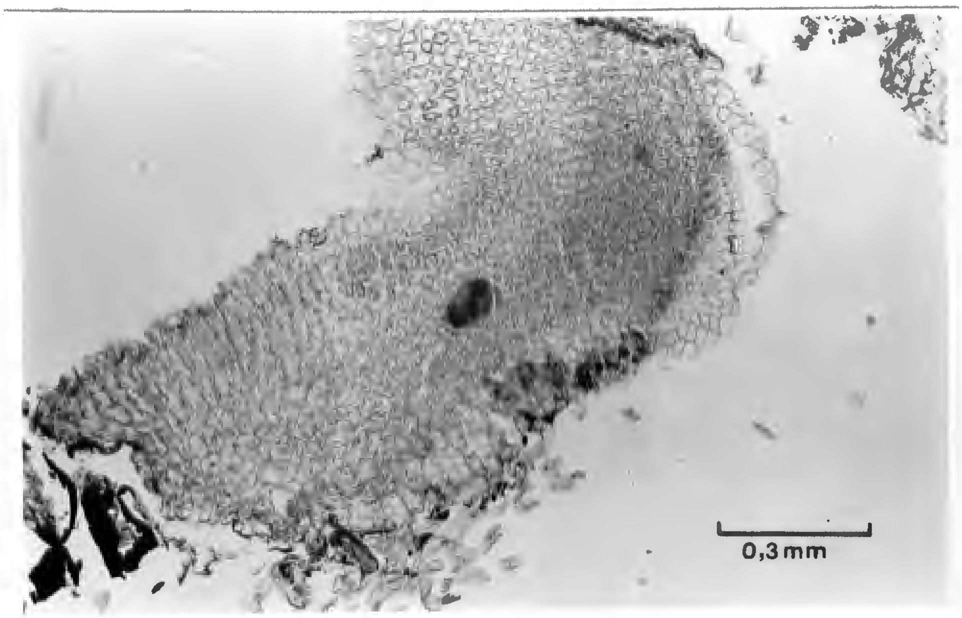

Figure 29 a. Riccia sorocarpa. L/S thallus containing very young antheridium.

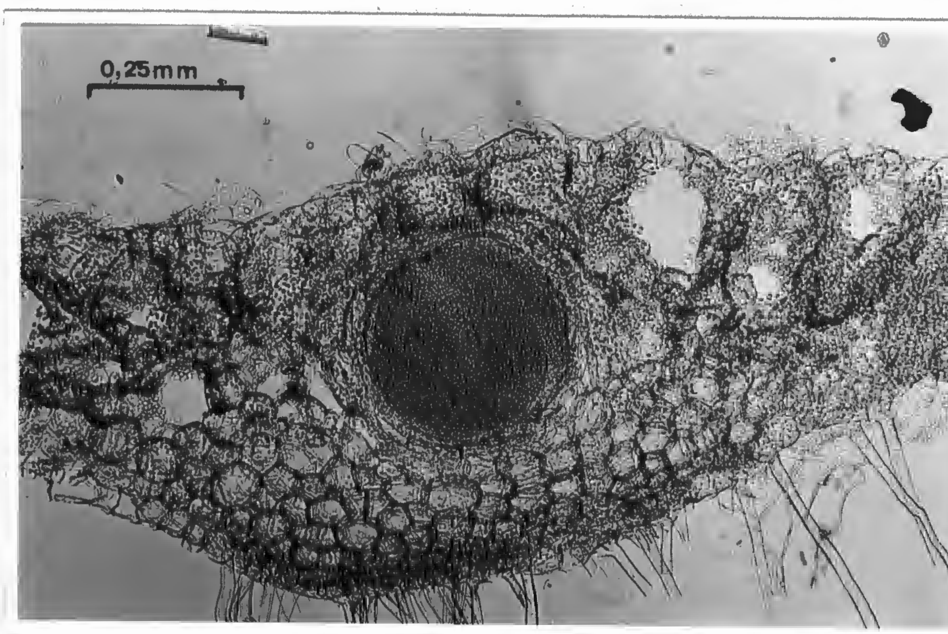

Figure 29 b. Riccia sorocarpa. L/S thallus containing a mature antheridium.

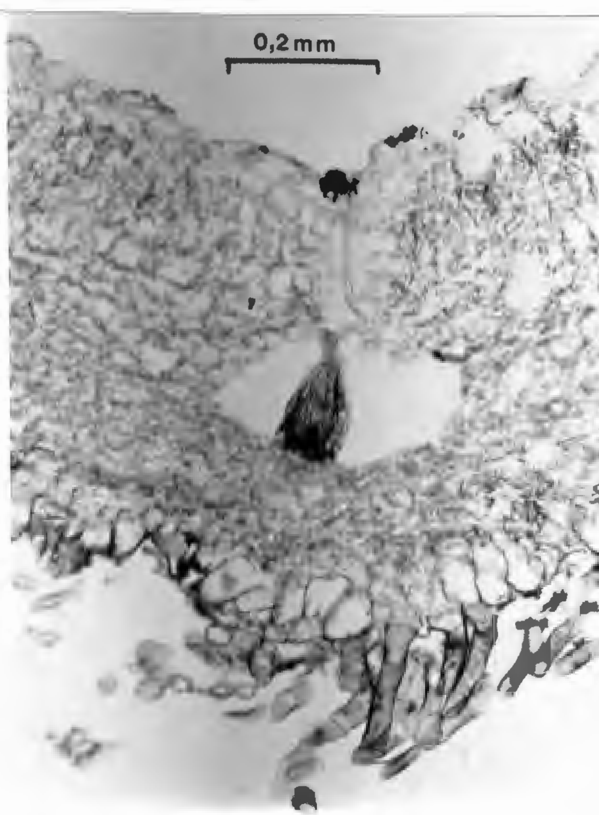

Figure 30. Riccia sorocarpa. L/S thallus containing an archegonium.

29 July, shortly after young sporophytes first developed on about 15 July. Mature sporophytes developed by 17 August containing spores clearly seen occurring in tetrads (Fig. 31). The maturation of the sporophyte from the archegonial stage took ± 7 - 8 weeks. No spore release had occurred by 30 September, although the remains of the calyptrae wich enclose the spores had begun to break down (Fig. 32a & b).

Young thalli of Marchantia wilmsii (dioecious) were observed by 4 March and archegoniophores, 8 mm tall, contained archegonia as early as 3 April (Fig. 33). By 28 April the archegoniophore lobes had opened out to expose the archegonia. At this stage the archegoniophores were 16 - 18 mm tall. By 24 June archegoniophores had grown to 25 - 30 mm in height and the archegoniophore lobes contained young sporophytes (Fig. 34). Recognisable spores had not developed by 23 July and the sporophytes only matured further after this date. Sections of the receptacles collected on 28 August showed them to be empty and tissues slightly degenerate. Archegoniophores at this stage had turned brown-red in colour.

3.4 HEPATIC PHENOLOGY: 1984

(see Figure 2)

Asterella marginata thalli first appeared on 24 March and the first

Figure 31. Riccia sorocarpa. L/S thallus (seen as two thalli because sectioning was through a dichotomous branch point) showing a mature sporophyte containing spores occurring in tetrads.

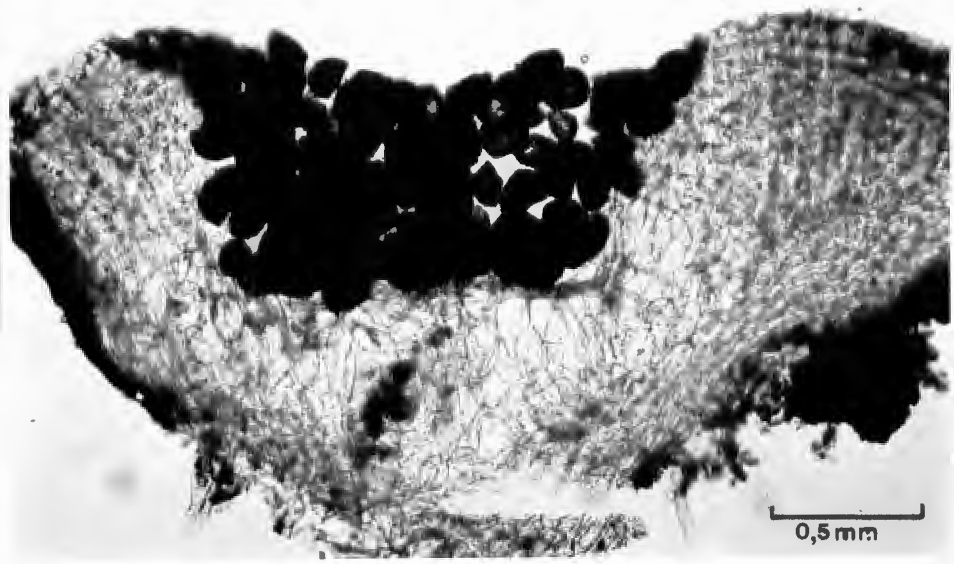

Figure 32a. Riccia sorocarpa. L/S thallus showing a mature sporophyte i.e. calyptra has broken down. No spore release has occurred.

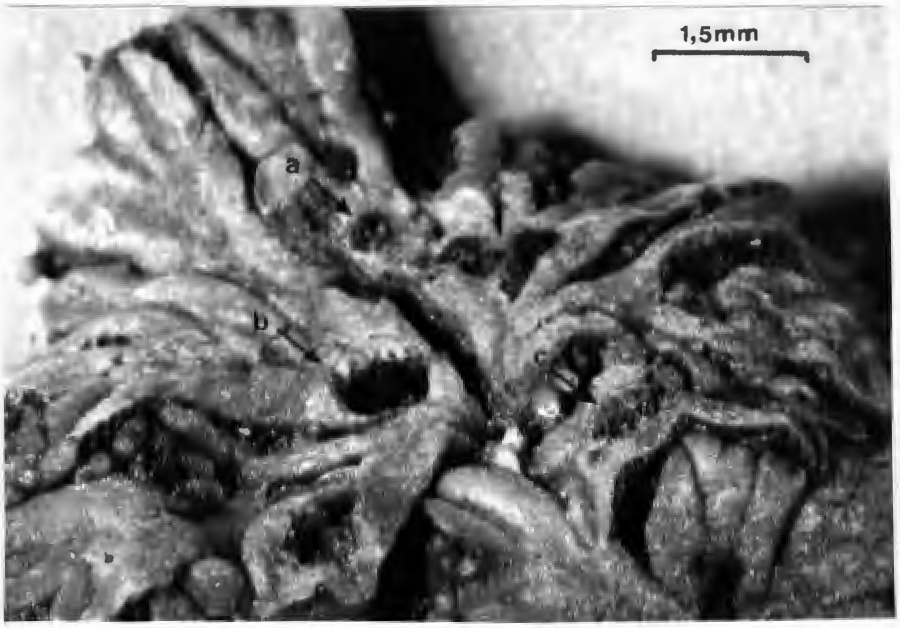

Figure 32 b. Riccia sorocarpa. Dorsal view of a colony showing (a)young sporophytes, (b) mature sporophytes and (c) sporophytes with the calyptra partially broken down.

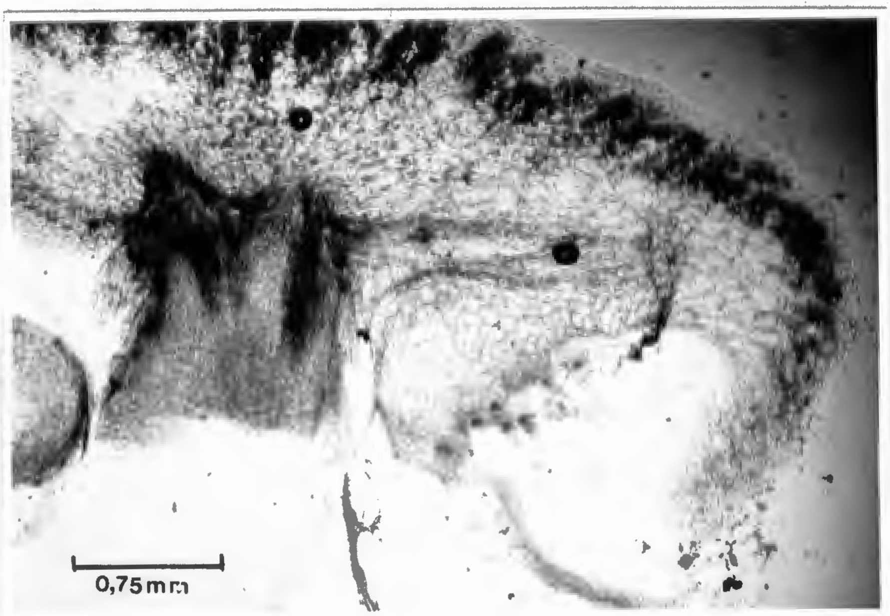

Figure 33. Marchantia wilmsii. L/S archegoniophore receptacle containing archegonia.

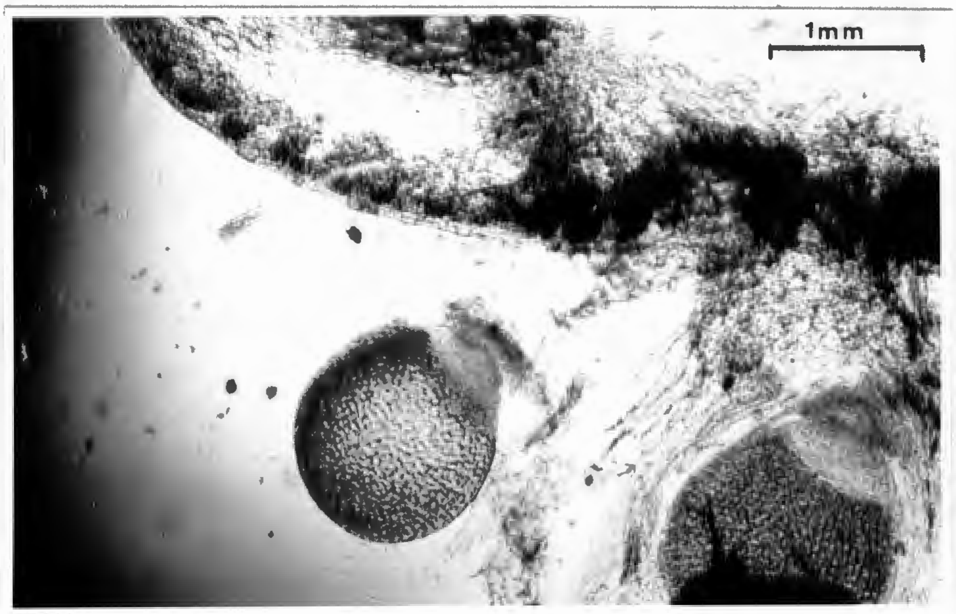

Figure 34. Marchantia wilmsii. L/S archegoniophore showing the presence of young sporophytes. The sporophytes dislodged during sectioning.

evidence of immature antheridia in the antheridial branches was found on 21 April (Fig.3+4), two weeks earlier than in 1982. Antheridia were produced until about 2 June. Archegonia were found in very young receptacles (archegoniophores not yet elongating as in Fig. 5) on 19 May, four weeks earlier than in 1982. By 30 June many archegonia had been fertilized (Fig. 7) and some immature sporophytes developed as early as 23 June (Figs 8 & 9). Young sporophytes were also found to be present in material collected at the end of September. Mature sporophytes (Fig. 10) appeared on 4 August and continued until the end of the study period. No sporophytes had dehisced by 29 September. One striking feature of Figure 2 is the fact that new archegoniophores formed after 28 July. These contained archegonia suggesting an initiation of a second maturation cycle. Unfortunately no new antheridial branches were found at this time.

The appearance of new thalli of Targonia capensis began, two weeks later than in the case of A. marginata, on about 7 April and continued until about 13 May. Male branches, containing anteridia, were first sited on 21 April (Fig. 14). The production of archegonia (Fig. 16) occurred between 13 May and 16 June. The first immature sporophytes were observed unusually early, on 19 May, only one week after the first archegonia. Mature sporophytes (Fig. 19) formed from about 7 July and, although the thalli had shrunk, lifting the involucral bracts (Fig. 22), no dehiscence had occurred by 29 September. Young sporophytes appeared 6 weeks earlier than in 1982.

Anthoceros sp. thalli appeared three weeks earlier than in 1982, on 31 March. By 21 April the thalli contained antheridia (Fig. 23) and archegonia had appeared by 13 May. The first immature sporophytes (Fig. 24a & b) developed about one week before the last archegonia appeared and had matured by 21 July, five weeks earlier than in 1982. After about 16 June many already formed sporophytes died and many colonies themselves were greatly reduced in size and distribution. The comparatively few remaining sporophytes matured until the end of September. However, a few sporophytes released their spores during the last week of that month.

Thalli of Riccia sorocarpa (Fig. 28) were present on 7 April and male thalli contained antheridia, sunken into the thallus, by 5 May (Fig. 29a & b). Archegonia appeared around 2 June and continued formation until 30 June (Fig. 30). Young sporophytes had developed by 23 June and were collected until 11 August. Mature sporophytes (Fig. 31 & 32a) were found present from 21 July until 29 September. By the latter date very little or no dehiscence had occurred as only very few portions of certain thalli had begun to decompose.

The maturaton cycle of Marchantia wilmsii during the autumn and winter of 1984 proved interesting. Archegonia appeared in the receptacles of the archegoniophores (8 - 12 mm tall) as early as 7 April (Fig. 33) and continued until 19 May. Towards the middle of May sectioning showed archegonia and mature sporophytes present in the same receptacle lobe (Fig. 35). After 9 June no further development of sex organs occurred and in most colonies the archegoniophores died completely. By 30 June some entire colonies of M. wilmsii had disappeared.

3.6 MOSS PHENOLOGY (CAPSULE MATURATION): 1984

(see Figure 36)

Capsules of Ptychomitrium crispatum were very immature on 13 May and were still almost entirely covered by the calyptra. Remains of calyptrae were present on 11 August. However, the majority had been shed leaving the operculum exposed. The first signs of capsule dehiscence appeared on 28 August (peristome teeth visible) but only very few of the capsules in the colonies studied had released their spores by 29 September. At maturity the sporophyte seta measured 7 mm and the capsules stood erect.

Bryum capillare capsules were unswollen and two-thirds covered by intact calyptrae on 28 April (Fig. 37). By 13 May the seta measured 45 mm and most capsules had lost the calyptra (some retained remains as in Fig. 38) but still had intact opercula (Fig. 39). These mature capsules persisted until 17 August, i.e. for a period of approximately

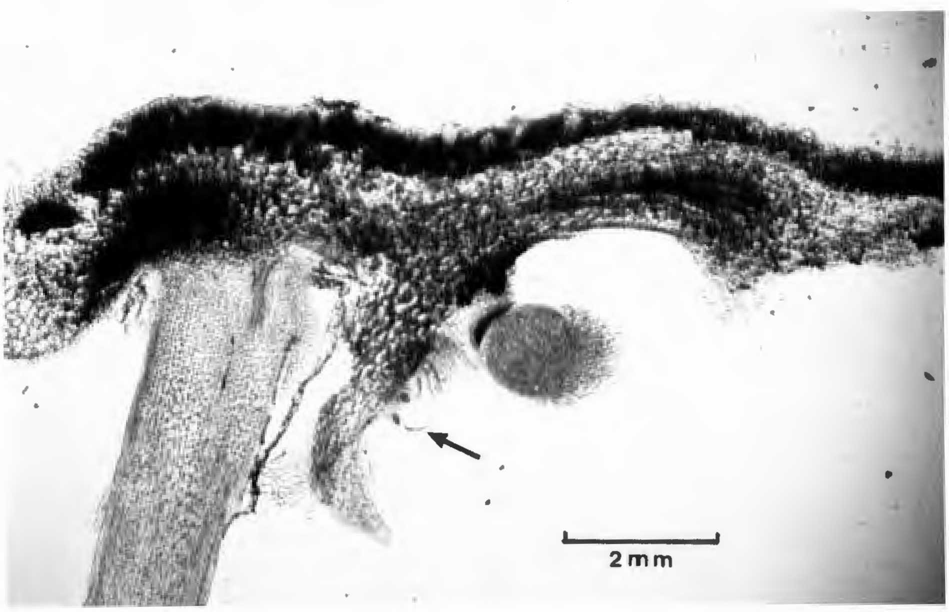

Figure 35. Marchantia wilmsii. L/S archegoniophore showing the presence of archegonia and a mature sporophyte in the same receptacle lobe. (Arrow indicates archegonia).

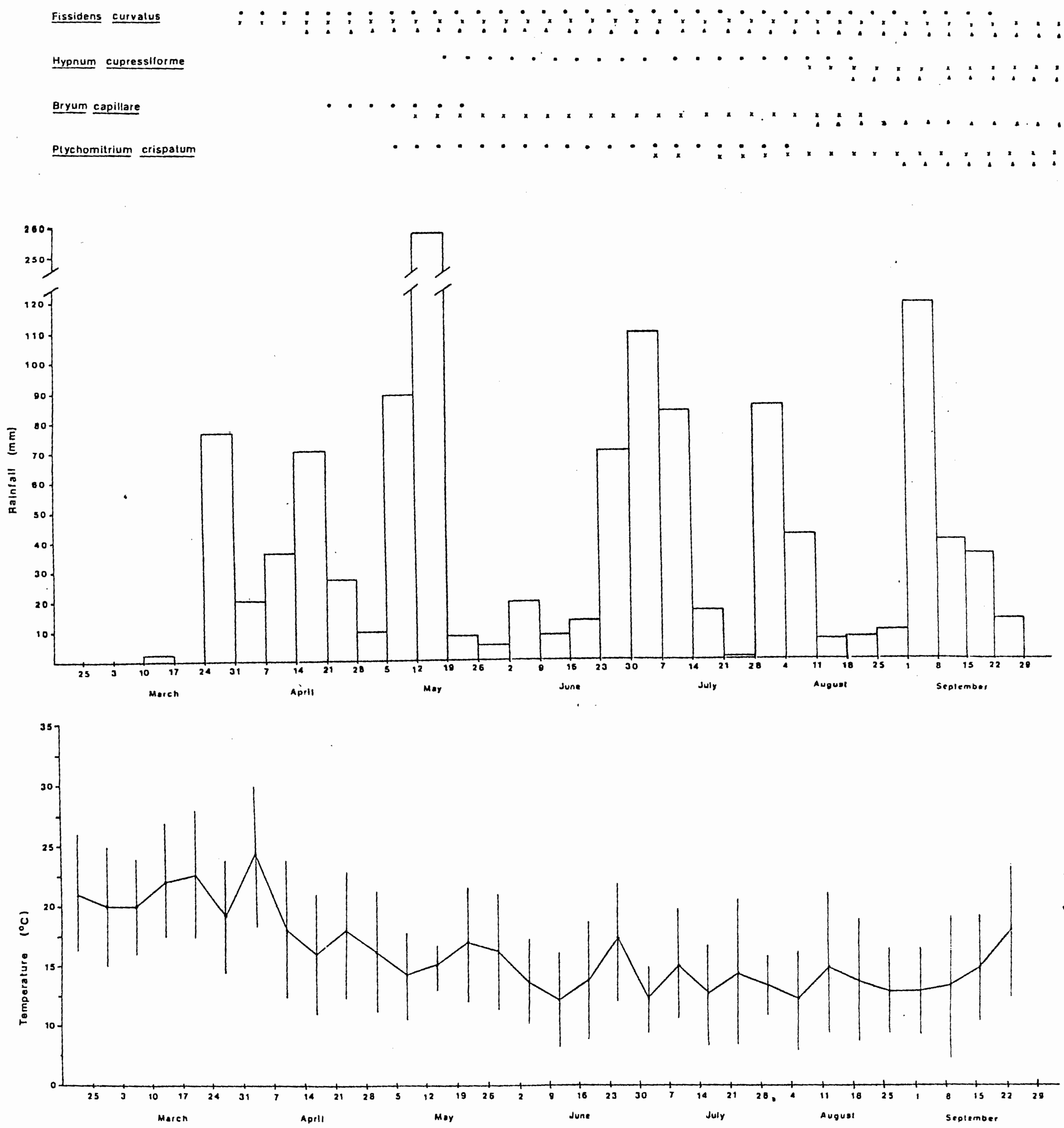

Figure 36. Representation of the sporophyte capsule maturation cycle of the four mosses studied in relation to total weekly rainfall (mm) and average weekly temperature (C) in 1984.

● ● Young sporophyte - calyptra present.
x x Mature sporophyte - calyptra absent, operculum present.
△ △ Dehisced capsule.

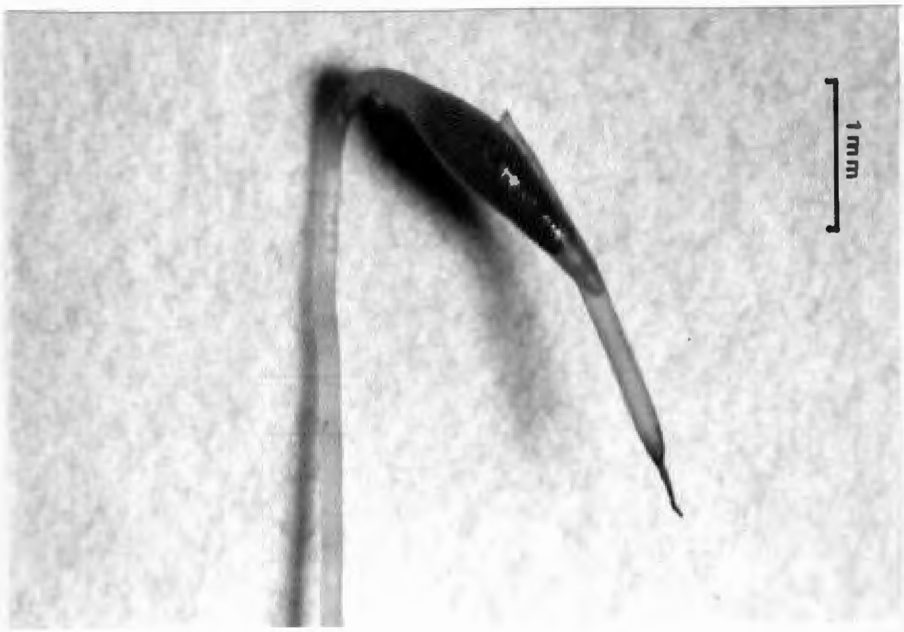

Figure 37. Bryum capillare. Young sporophyte capsule only slightly swollen and 2/3 covered by the calyptra.

Figure 38. Bryum capillare. Capsule more swollen than represented in figure 37 with only remains of the calyptra present. (Arrow indicates the partially exposed operculum).

12 weeks. The first signs of spore release were visible on 11 August and by late September some capsules had completely dried out (Fig. 40) and the capsules and setas had turned brown and had shrunk considerably.

Young capsules of Hypnum cupressiforme were still covered by a calyptra on 17 May and mature capsules, setas 15 mm in length, with the operculum exposed were only found after 11 August. Dehiscence began soon afterwards, on 20 August.

Sporophyte development and maturation in Fissidens curvatus followed no cyclical pattern during the winter as did the three mosses discussed above. During the entire period 21 April to 18 September, all of the following were found: young capsules, covered by a calyptra, still pale green in colour; mature capsules, pale brown in colour, with the operculum exposed and dehisced capsules, dark brown, with the peristome teeth exposed and opened. The only deviation from this pattern occurred during the three weeks directly preceeding and succeeding this period, when more young sporophytes and mature or dehisced capsules appeared respectively (Fig. 41).

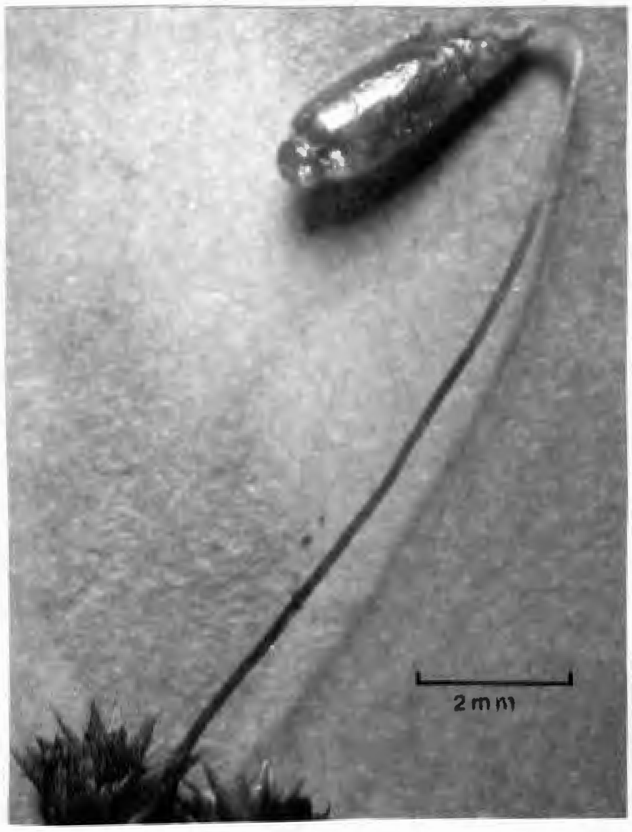

Figure 39. Bryum capillare. Mature sporophyte bearing a swollen capsule with the intact operculum exposed.

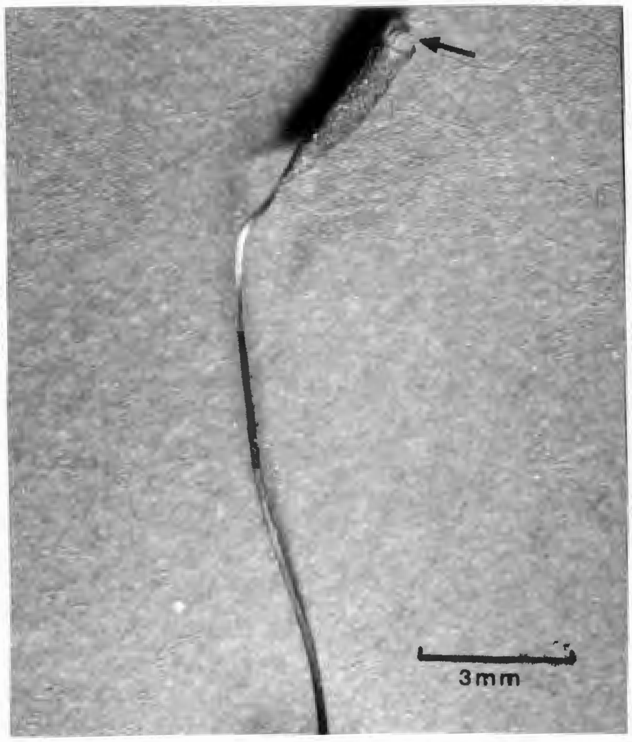

Figure 40. Bryum capillare. Old sporophyte with a dried capsule, peristome teeth are indicated by an arrow.

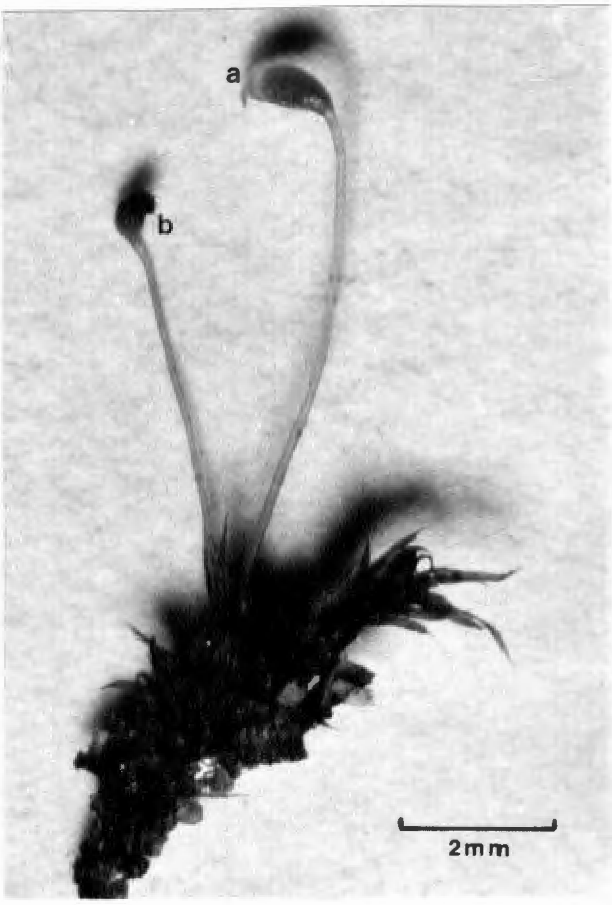

Figure 41. Fissidens curvatus. Two sporophytes, one mature with the operculum intact (a), the other with the operculum removed and the peristome teeth exposed (b).

CHAPTER 4

DISCUSSION

The observed differences between the maturation cycles of the hepatics studied in 1982 and 1984 indicated that water supply, and the duration thereof, were crucial to initiation of the gametophyte stage as well as the sporophyte stage. The observation that the five species of hepatics, including the summer-rainfall Marchantia wilmsii, completed their life cycles within a period of continuous rainfall in 1982 indicates that, not only is water necessary for fertilization, but that the moisture supply must be not interrupted by any dry period in which the habitat could dry out. This result was substantiated by the phenology of the hepatics during 1984. During this year the life cycle was also initiated by the first rain and the duration was also dependent on the duration of the rainfall (dehiscence of sporophytes occurred after the rainy season), but as a result of the very early start of the more or less continuous winter rains the sporophyte stage was reached much earlier. This resulted in most of the species, excluding Marchantia wilmsii and Anthoceros sp. having a sporophyte stage of unusually long duration.

The 'dry' period in 1984 between 19 May and 23 June when the winter temperatures were slightly higher than in 1982 had some serious effects on the phenology of the hepatics. The fact that colonies of both Anthoceros sp. and M. wilmsii were substantially reduced and that most and all, respectively, of the reproductive organs formed by 19 May died, substantiates the claim that 'dry' periods during the maturation cycle are detrimental and supports the theory (Clausen 1966) that hepatics are more tolerant to drought and increased temperature when in a slightly desiccated condition. The extremely heavy rains prior to 19 May would have prevented the beneficial desiccation occurring.

The non-appearance of Fossombronia sp. in the study area in 1984 can also be attributed to the altered rainfall conditions in 1984. Spores may have germinated and died, during the dry spell (19 May - 23 June), before the leafy gametophytes became visible. Similar observations for Fossombronia sp. were made by Schelpe (Ph.D. thesis).

Unfortunately, no comparison could be made between the phenology of the perennial mosses in 1982 and 1984 as they were not studied in 1982. It can, however, be said that the initiation of sexual reproduction (except in the case of Fissidens curvatus) only occurs after the first winter rainfall and that the termination of sporophyte maturation, i.e. dehiscence, only occurs after or at the very end of the winter rainy season.

In contrast to studies done on bryophyte phenology in north-temperate climates, the effect of temperature on the maturation cycle of bryophytes, growing in mediterranean-type ecosystems, was minimal. Although the observation that, in *M. wilmsii*, the gametangial production was initiated when temperatures were high, i.e. 21°C, agrees with observations made by Benson-Evans (1964) on *M. polymorpha*, no further correlations can be made. The maturation of moss sporophytes in 1984 occurred when temperatures were still reasonably high (19°C) in contrast to findings (Benson-Evans 1964) that some mosses, e.g. *Hypnum tenella* produced sporophytes when temperatures were low.

There is a good correlation between northern hemisphere temperature independent bryophytes, *Riccia glauca*, *Anthoceros laevis* (Benson-Evans 1964), *R. crystallina* (Chopra & Sood 1973) and *Bryum argentum* (Chopra & Bhatla 1981, 1983), and species of the same genera occurring in mediterranean-type climates, since gametangial initiation in the case of the hepatics, occurred at both cool (10 - 15°C) (1982) and warm (19 - 25°C) (1984) temperatures.

However, few comparisons between the effect of temperature on bryophyte phenology in the two climates can be made because the seasonal temperature variation in the mediterranean climate was minimal.

In 1982 it was observed that the duration of the maturation cycles of *Targronia capensis* in two localities was different. The life cycle of T. capensis growing on a steep slope of granite by a roadside took much longer than that of the species growing in Window Stream, Kirstenbosch Gardens. The fact that the first habitat depended on run-off for moisture made it considerably drier. Although the delay in the life cycle was small, it can be related to similar observations made by Arnell (1905). He showed the 'fruiting season' of species of Polytrichum to last 7 - 10 months in Uppsala, Sweden in moist habitats, whereas it lasted 16 - 18 months in drier habitats in Vermont (Trowle & Gilbert 1904).

The theory proposed by Slade (1965), that in the case of species of Funaria temperature not only affected the rate of seta elongation but also the final length of the seta, could not be applied to the mosses studied. The seta length of sporophytes of Hypnum cupressiforme and Ptychomitrium crispatum collected in 1984 was equal to that of samples collected of the same age in 1983.

The observation that a period of drought was necessary for capsule dehiscence in the moss Orthotrichum anomalum (Johnson 1969) compared well with similar observations for H. cupressiforme, B. capillare and Ptychomitrium crispatum. However, this was not the case for Fissidens curvatus as sporophytes at all three stages of maturity were observed throughout the winter. The continual production of gametangia could have been the result of the very sheltered micro-environment of the colonies of the species studied. The colonies are small and occurr in very sheltered crevices on the clay soil bank. Clay would retain moisture but, because of the steep slope of the bank, waterlogging would not occur. A high degree of humidity would have been maintained around these colonies throughout the growing season.

Spore release in the hepatics generally only occurred after a period devoid of rain. The exception to this rule was Asterella marginata which released its spores as soon as the sporophytes were mature and the pseudoperianth basket was exposed.

Environmental conditions in April, i.e. autumn in the Cape, can be compared to conditions in spring, September, in the Transvaal, as far as rainfall and temperature are concerned. In both cases temperatures are mild and rainfall is moderately light (1984 in the Cape excluded). This could be the reason why M. wilmsii, a summer-rainfall species, produced archegonia when it did, earlier than the other hepatics.

Although there must be a degree of endogenous control of sex organ production (Newton 1972), it appears that, in the case of the species of mosses and hepatics studied, moisture availability is the crucial factor affecting the development of the maturation cycle.

CHAPTER 5

CONCLUSION

As a result of this study the following conclusions can be made:

1. The appearance of thalli of annual hepatics in the Cape Peninsula can be correlated with the onset of the winter rainfall as can the initiation of the sexual reproductive cycle of perennial mosses growing in the same area.

2. The duration of both the growth period of the hepatics studied and the sexual reproductive cycle of the mosses studied is controlled by the duration of a period of uninterrupted moisture conditions, i.e. the maturation cycle can be shifted or prolonged in response to changes in moisture conditions. Fissidens curvatus is an exception because it grows in habitats which remain permanently moist through the growing season.

3. Temperature does not appear to have a major effect on the phenology of the bryophytes studied, except when slight changes in temperature are accompanied by an extreme lack of moisture.

4. Drought-susceptible species, e.g. *Anthoceros* sp. and *Fossombronia* sp. suffered reductions, total in the latter, in the number of gametophytes that matured and produced sporophytes as a result of a short period of increased temperature and decreased moisture.

5. The major difference between northern-hemisphere bryophytes and those growing in mediterranean-type ecosystems, is that the former grow and reproduce from spring to autumn and that the maturation cycle of the latter takes place from autumn to spring. The former are susceptible to summer droughts, whilst the latter are severely affected by periods of decreased moisture in the winter.

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Appendix A.

Table 1. Rainfall and Temperature data for 1982.

Date.		Rainfall (mm)		Daily Temperature (°C)		Temperature (°C) Weekly Average
Month	Day	Daily	Total Weekly	Maximum	Minimum	
Feb	19	-		20,4	14,4	
	20	-		28,0	14,0	
	21	-		28,5	13,3	
	22	-	-	26,0	17,5	20,87
	23	-		23,5	18,0	
	24	-		30,5	16,0	
	25	-		25,0	17,0	
	26	0,2		23,5	17,0	
	27	2,0		25,0	17,0	
	28	-		22,5	13,5	
Mar	01	-	4,0	23,6	12,8	19,15
	02	-		25,6	19,0	
	03	-		25,5	13,2	
	04	-		17,0	13,4	
	05	0,1		22,0	14,5	
	06	-		24,0	14,5	
	07	-		26,0	16,0	
	08	-	0,1	24,5	15,9	20,42
	09	-		28,0	17,5	
	10	-		32,5	17,0	
	11	-		19,0	14,5	
	12	-		20,1	13,7	
	13	-		21,0	14,0	
	14	-		21,5	14,5	
	15	-	-	22,6	15,3	18,72
	16	-		24,4	16,5	
	17	-		22,8	14,9	
	18	-		25,0	15,7	
	19	19,0		25,0	12,6	
	20	-		19,3	17,0	
	21	-		20,3	15,0	
	22	-	22,3	24,5	13,6	19,45
	23	-		27,5	15,5	
	24	-		31,3	14,5	
	25	3,3		24,8	11,5	
	26	20,4		22,5	12,0	
	27	0,2		20,0	13,5	
	28	-		22,0	15,0	
	29	-	20,6	22,7	15,1	18,18
	30	-		21,5	13,7	
	31	-		22,6	14,0	
Apr	01	-		24,5	15,6	

Appendix A.

Table 1. Rainfall and Temperature data for 1982.

Date.		Rainfall (mm)		Daily Temperature (°C)		Temperature (°C) Weekly Average
Month	Day	Daily	Total Weekly	Maximum	Minimum	
Apr	02	-		24,5	14,5	
	03	-		21,0	13,5	
	04	-		21,5	14,0	
	05	-	26,7	28,0	15,5	18,54
	06	-		22,0	13,0	
	07	11.7		20,5	16,0	
	08	15,0		20,5	15,0	
	09	-		18,5	15,0	
	10	4,0		20,0	13,5	
	11	4,5		19,0	13,5	
	12	3,0	11,5	18,5	10,5	16,26
	13	-		18,6	10,2	
	14	-		22,0	12,0	
	15	-		22,5	14,1	
	16	0,7		22,4	13,5	
	17	14,0		18,0	9,0	
	18	6,0		16,4	12,0	
	19	5,5	26,2	16,5	9,0	15,36
	20	-		19,6	11,2	
	21	-		20,3	12,2	
	22	-		20,5	14,4	
	23	-		23,5	15,0	
	24	-		26,5	14,8	
	25	-		30,5	15,7	
	26	-	-	26,8	13,5	18,42
	27	-		20,2	14,5	
	28	-		17,5	11,2	
	29	-		18,4	9,8	
	30	-		17,0	8,9	
May	01	-		18,0	10,5	
	02	-		20,5	9,5	
	03	-	-	22,9	9,2	15,27
	04	-		22,1	9,8	
	05	-		21,2	10,9	
	06	-		20,9	12,4	
	07	-		28,2	12,4	
	08	-		32,0	14,5	
	09	2,0		25,0	15,5	
	10	-	9,2	23,4	10,5	17,90
	11	5,5		21,2	10,8	
	12	1,0		19,2	10,4	
	13	0,7		18,5	9,0	

Appendix A.

Table 1. Rainfall and Temperature data for 1982.

Date.		Rainfall (mm)		Daily Temperature (^{o}C)		Temperature (^{o}C) Weekly Average
Month	Day	Daily	Total Weekly	Maximum	Minimum	
May	14	4,7		16,0	12,2	
	15	-		19,5	9,6	
	16	-		20,5	10,0	
	17	21,8	40,2	22,4	10,6	15,62
	18	3,0		20,0	12,6	
	19	2,5		20,5	10,9	
	20	8,2		20,4	13,5	
	21	6,5		17,3	13,4	
	22	32,2		17,0	10,2	
	23	-		18,6	8,0	
	24	12.0	52,4	20,4	11,2	13,85
	25	-		15,0	9,8	
	26	1,3		14,0	9,4	
	27	0,4		15,5	10,0	
	28	0,5		19,5	8,8	
	29	1,0		22,5	10,0	
	30	-		15,5	11,0	
	31	-	1,5	18,5	8,5	15,23
Jun	01	-		23,0	9,5	
	02	-		23,0	12,6	
	03	-		20,5	10,2	
	04	-		21,0	12,0	
	05	7,5		15,5	11,5	
	06	20,0		14,0	7,0	
	07	-	34,0	15,5	5,2	12,97
	08	-		17,5	6,5	
	09	-		23,0	9,8	
	10	6,5		21,4	11,7	
	11	33,1		13,9	7.6	
	12	1,0		14,5	6,9	
	13	-		14,8	6,3	
	14	3,4	105,8	13,8	7,5	11,20
	15	-		16,4	8,4	
	16	45.1		13,1	10,7	
	17	23,1		14,6	8,3	
	18	-		14,4	6,2	
	19	-		17,0	9,8	
	20	-		21,5	9,8	
	21	1,5	20,5	23,3	13,8	13,49
	22	19,0		14,4	7,9	
	23	-		15,0	7,2	
	24	-		20,1	8,4	

Appendix A.

Table 1. Rainfall and Temperature data for 1982.

Date.		Rainfall (mm)		Daily Temperature (°C)		Temperature (°C)
Month	Day	Daily	Total Weekly	Maximum	Minimum	Weekly Average
Jun	25	-		19,8	11,6	
	26	20,0		16,0	8,0	
	27	4,0		15,5	7,5	
	28	-	51,0	19,9	6,0	14,27
	29	-		23,5	6,5	
	30	-		25,0	12,6	
Jul	01	27,0		17,8	10,2	
	02	-		11,1	7,8	
	03	-		15,6	8,6	
	04	-		15,6	8,5	
	05	-	-	17,9	9,8	12,14
	06	-		19,8	8,6	
	07	-		16,4	8,6	
	08	-		15,2	7,8	
	09	-		22,4	8,4	
	10	-		18,4	9,6	
	11	-		22,0	7,5	
	12	3,3	11,6	18,2	9,2	14,75
	13	-		15,2	9,2	
	14	-		20,4	9,2	
	15	8,3		25,9	10,9	
	16	-		16,2	5,4	
	17	-		19,4	5,4	
	18	0,2		17,5	9,2	
	19	-	19,0	14,5	5,4	13,17
	20	-		20,6	6,5	
	21	-		22,6	9,7	
	22	18,8		16,7	9,8	
	23	91,7		14,0	9,5	
	24	7,5		13,0	6,0	
	25	-		14,0	8,0	
	26	-	130,8	16,6	7,5	12,12
	27	-		18,0	7,0	
	28	1,2		19,0	7,0	
	29	30,4		13,8	10,8	
	30	-		14,6	6,3	
	31	-		18,5	7,5	
Aug	01	9,8		18,0	10,5	
	02	0,9	26,3	15,0	6,5	12,15
	03	14,7		18,2	7,8	
	04	0,3		15,3	9,1	
	05	0,6		14,9	9,8	

Appendix A.

Table 1. Rainfall and Temperature data for 1982.

Date.		Rainfall (mm)		Daily Temperature (°C)		Temperature (°C) Weekly Average
Month	Day	Daily	Total Weekly	Maximum	Minimum	
Aug	06	-		13,4	7,0	
	07	-		16,5	7,3	
	08	1,0		15,6	9,5	
	09	25,8	109,9	13,7	9,5	12,71
	10	35,2		14,5	11,0	
	11	47,9		14,8	10,8	
	12	-		16,5	7,8	
	13	-		20,2	6,5	
	14	-		20,2	7,2	
	15	3,3		18,8	10,5	
	16	-	3,3	16,6	6,8	11,92
	17	-		18,5	7,2	
	18	-		16,8	9,2	
	19	-		19,9	7,2	
	20	8,7		18,6	9,8	
	21	12,5		14,5	7,0	
	22	-		14,0	6,0	
	23	-	21,2	18,1	7,0	13,05
	24	-		18,2	10,0	
	25	-		18,2	12,0	
	26	-		19,4	9,8	
	27	0,5		22,2	10,8	
	28	0,5		17,0	10,5	
	29	1,3		17,5	9,5	
	30	-	82,8	19,0	8,6	14,19
	31	29,5		18,5	9,5	
Sept	01	51,0		18,5	9,5	
	02	-		16,5	11,0	
	03	-		16,5	10,5	
	04	-		16,9	9,5	
	05	-		19,8	8,5	
	06	-	-	23,2	10,7	15,10
	07	-		18,4	10,5	
	08	-		20,0	10,4	
	09	-		24,5	12,0	
	10	-		29,4	14,3	
	11	35,5		23,3	12,0	
	12	45,6		15,4	10,7	
	13	0,4	82,5	13,4	10,5	14,50
	14	-		14,9	10,0	
	15	1,0		12,9	10,4	
	16	-		15,8	10,0	

Appendix A.

Table 1. Rainfall and Temperature data for 1982.

Date.		Rainfall (mm)		Daily Temperature (^oC)		Temperature (^oC)
Month	Day	Daily	Total Weekly	Maximum	Minimum	Weekly Average
Sept	17	-		24,0	6,7	
	18	-		21,5	9,5	
	19	-		23,5	11,0	
	20	17,0	17,0	17,8	12,8	15,29
	21	-		16,4	8,2	
	22	-		18,3	9,7	
	23	-		21,8	12,9	
	24	-		24,9	14,4	
	25	-		24,5	15,0	
	26	-		22,0	13,0	
	27	-	-	24,9	13,6	18,74
	28	-		20,4	13,2	
	29	-		24,7	12,4	
	30	-		25,9	13,4	

Appendix B.

Table 1. Rainfall and Temperature data for 1984.

Date.		Rainfall (mm)		Daily Temperature (^{o}C)		Temperature (^{o}C)
Month	Day	Daily	Total Weekly	Maximum	Minimum	Weekly Average
Feb	19	-	-	23,0	17,5	21,33
	20	-		22,0	17,0	
	21	-		25,2	18,6	
	22	-		32,2	15,7	
	23	-		30,5	16,1	
	24	-		23,5	15,4	
	25	-		22,5	16,8	
	26	-	-	30,0	17,5	20,28
	27	-		24,4	14,5	
	28	-		25,0	16,5	
	29	-		21,7	13,1	
Mar	01	-		30,2	13,5	
	02	-		22,7	13,7	
	03	-		25,4	15,7	
	04	-	-	24,0	13,8	19,90
	05	-		22,5	16,4	
	06	-		23,6	18,0	
	07	-		19,5	14,3	
	08	-		20,6	14,7	
	09	-		26,7	15,0	
	10	-		31,5	18,0	
	11	2,0	2,2	30,0	20,0	22,49
	12	0,2		28,4	16,2	
	13	-		24,9	15,2	
	14	-		26,0	16,1	
	15	-		30,1	16,2	
	16	-		29,2	17,6	
	17	-		31,5	18,5	
	18	-	-	34,0	16,5	22,92
	19	-		31,5	18,5	
	20	-		25,4	17,0	
	21	-		19,4	15,7	
	22	-		21,0	15,2	
	23	-		26,1	14,0	
	24	-		26,0	12,0	
	25	-	77,6	25,0	15,0	19,26
	26	77,6		19,6	12,0	
	27	-		20,0	12,5	
	28	-		20,4	13,7	
	29	-		25,2	15,0	
	30	-		28,7	16,5	
	31	-		29,0	17,0	

Appendix B.

Table 1. Rainfall and Temperature data for 1984.

Date.		Rainfall (mm)		Daily Temperature (°C)		Temperature (°C) Weekly Average
Month	Day	Daily	Total Weekly	Maximum	Minimum	
Apr	01	-		31,0	16,5	
	02	-		32,0	18,6	
	03	-		36,0	21,0	
	04	-	20,0	36,0	22,6	24,56
	05	-		31,0	21,5	
	06	-		26,5	17,5	
	07	20,0		20,5	13,5	
	08	36,0		21,0	12,7	
	09	-		19,5	12,9	
	10	-		22,6	12,6	
	11	-	36,0	26,6	12,8	18,26
	12	-		22,2	11,5	
	13	-		24,6	12,2	
	14	-		32,2	12,2	
	15	70,0		22,2	12,0	
	16	0,4		19,1	10,5	
	17	-		20,6	11,2	
	18	0,7	71,1	21,1	11,7	16,22
	19	-		22,4	11,5	
	20	-		22,5	10,9	
	21	-		20,7	10,4	
	22	-		27,7	11,7	
	23	-		22,8	13,4	
	24	-		26,7	15,9	
	25	-	27,6	34,7	18,4	18,12
	26	20,0		24,1	11,4	
	27	7,6		14,5	7,7	
	28	-		17,4	7,2	
	29	-		20,7	11,7	
	30	-		22,0	11,6	
May	01	9,7		25,1	12,2	
	02	-	9,7	20,0	12,2	16,39
	03	-		21,0	10,2	
	04	-		19,9	10,0	
	05	-		-	-	
	06	37,5		16,0	12,5	
	07	30,9		16,5	9,9	
	08	-		16,8	9,4	
	09	2,3	94,3	20,0	10,0	14,10
	10	0,4		17,5	9,2	
	11	1,2		19,8	9,5	
	12	22,0		16,5	13,8	

Appendix B.

Table 1. Rainfall and Temperature data for 1984.

Date.		Rainfall (mm)		Daily Temperature (°C)		Temperature (°C)
Month	Day	Daily	Total Weekly	Maximum	Minimum	Weekly Average
May	13	0,2		19,5	14,9	
	14	52,7		17,5	13,6	
	15	39,1		17,7	12,5	
	16	130,7	257,9	16,2	12,9	14,84
	17	8,3		14,2	7,7	
	18	25,3		14,0	10,5	
	19	1,6		16,5	7,6	
	20	-		20,0	8,9	
	21	1,1		18,9	10,5	
	22	-		17,8	9,7	
	23	-	8,4	26,0	10,9	16,83
	24	-		28,5	16,1	
	25	0,8		25,6	14,7	
	26	6,5		15,5	12,5	
	27	4,0		16,5	10,0	
	28	0,8		16,5	9,4	
	29	-		16,0	9,2	
	30	-	4,8	23,0	10,1	16,23
	31	-		24,5	10,5	
Jun	01	-		26,5	19,5	
	02	-		23,5	12,0	
	03	-		16,2	8,0	
	04	19,0		15,6	11,4	
	05	0,8		15,6	11,6	
	06	-	19,8	16,2	13,5	13,89
	07	-		17,6	7,6	
	08	-		23,2	8,0	
	09	-		20,0	10,0	
	10	4,4		17,8	10,2	
	11	2,8		17,7	8,2	
	12	1.1		14,4	8,0	
	13	0,2	8,5	13,7	7,4	12,16
	14	-		14,4	8,6	
	15	-		17,6	6,8	
	16	-		18,5	7,0	
	17	-		24,0	8,0	
	18	0,3		23,0	10,5	
	19	11,2		14,2	7,6	
	20	2,2	13,7	13,3	7,7	13,65
	21	-		17,7	9,0	
	22	-		20,1	8,7	
	23	-		17,8	9,4	

Appendix B.

Table 1. Rainfall and Temperature data for 1984.

Date.		Rainfall (mm)		Daily Temperature (°C)		Temperature (°C) Weekly Average
[illegible]	Day	Daily	Total Weekly	Maximum	Minimum	
Jun	24	-		25,0	16,0	
	25	-		20,0	9,2	
	26	-		21,7	9,5	
	27	-	70,0	25,4	9,7	16,39
	28	-		26,5	15,0	
	29	38,5		16,4	12,6	
	30	31,5		15,5	13,0	
Jul	01	82,5		17,0	13,0	
	02	16,5		16,7	7,5	
	03	3,0		14,5	7,7	
	04	0,7	110,5	12,7	8,7	12,02
	05	2,0		13,7	10,7	
	06	5,8		13,4	9,5	
	07	-		16,0	7,1	
	08	-		18,5	7,7	
	09	-		16,7	7,7	
	10	-		20,9	8,0	
	11	-	17,3	25,4	11,2	14,93
	12	0.9		25,0	14,0	
	13	26,4		15,0	12,7	
	14	56,5		14,2	12,0	
	15	5,0		14,9	9,9	
	16	-		17,6	7,4	
	17	-		22,2	7,5	
	18	7,8	0,2	18,0	9,6	12,65
	19	3,5		15,7	8,7	
	20	1,0		15,0	8,7	
	21	-		13,9	8,0	
	22	-		16,6	6,5	
	23	-		19,0	8,2	
	24	-		17,2	9,0	
	25	-	86,2	23,5	9,4	14,02
	26	-		25,4	8,2	
	27	0,1		19,5	8,2	
	28	0,1		14,5	11,0	
	29	-		13,5	10,5	
	30	-		17,7	10,2	
	31	-		18,4	9,5	
Aug	01	2,4		21,5	10,5	13,68
	02	-		15,7	12,0	
	03	58,3		14,5	11,0	
	04	25,5		15,0	11,5	

Appendix B.

Table 1. Rainfall and Temperature data for 1984.

Date.	Rainfall (mm)		Daily Temperature (°C)		Temperature (°C)
Month day	Daily	Total Weekly	Maximum	Minimum	Weekly Average
Aug 05	38,0		15,0	7,0	
06	4,2		13,5	8,6	
07	-		15,4	5,7	
08	-	42,2	17,1	5,9	12,10
09	-		17,4	7,2	
10	-		17,0	7,0	
11	-		22,5	7,5	
12	-		22,5	11,7	
13	7,3		13,7	8,5	
14	-		17,7	9,6	
15	-	7,3	19,7	8,7	14,79
16	-		17,8	8,5	
17	-		25,1	9,2	
18	-		25,2	8,2	
19	-		19,0	9,0	
20	-		19,5	10,6	
21	-		17,0	7,0	
22	-	7,9	16,5	7,7	13,49
23	1,2		17,2	11,7	
24	2,2		14,5	5,4	
25	4,5		12,0	6,5	
26	-		15,4	6,5	
27	1,0		15,0	9,4	
28	-		14,7	8,7	
29	-	9,5	20,6	11,0	12,50
30	-		19,1	9,6	
31	-		19,5	11,0	
Sept 01	8,5		15,6	11,0	
02	-		16,8	9,0	
03	31,3		16,0	9,5	
04	13,5		15,0	8,4	
05	21,0	119,6	15,7	9,4	12,43
06	14,8		15,8	6,3	
07	19,7		15,7	9,7	
08	19,3		16,6	10,0	
09	23,5		18,2	5,6	
10	3,3		21,2	7,1	
11	-		17,6	8,1	
12	7,4	41,2	14,3	10,7	12,83
13	7,0		19,6	3,6	
14	-		22,2	4,9	
15	-		16,9	7,2	

Appendix B.

Table 1. Rainfall and Temperature data for 1984.

Date.	Rainfall (mm)		Daily Temperature (^{o}C)		Temperature (^{o}C)
Month Day	Daily	Total Weekly	Maximum	Minimum	Weekly Average
Sept 16	-		18,5	8,5	
17	26,8		16,5	12,9	
18	-		18,1	12,0	
19	7,1	35,7	19,6	12,4	14,46
20	1,8		18,5	9,5	
21	-		19,5	7,5	
22	-		20,5	8,5	
23	-		23,3	11,7	
24	-		32,6	12,3	
25	5,0		21,0	14,5	
26	7,0	13,7	21,7	14,5	17,77
27	1,7		21,0	9,9	
28	-		22,0	13,8	
29	-		20,0	10,6	