A MORPHOLOGICAL AND ANATOMICAL INVESTIGATION OF SOME OF THE THELYPTERID FERNS

Thesis submitted in accordance with the Regulations of the University of Newcastle upon Tyne for the Degree of Doctor of Philosophy

by

Christopher C. Wood

September 1971

TABLE OF CONTENTS

CHAPTER I

GENERAL INTRODUCTION

The thelypterid ferns are a large assemblage of plants belonging to the leptosporangiate family Polypodiaceae sens. lat. and are represented throughout both the Old and New Worlds by over 800 species. A comprehensive list of these, giving basinyms, authorities and approximate distribution has been compiled by Reed (1968).

There can be little doubt that this group forms a natural unit as a whole (Iwatsuki 1964a), although it has been extensively sub-divided taxonomically and the segregates given various ranks according to the views of the particular worker. Because of this very variable treatment accorded by authors (many of whom do not even agree as to the definition of a given genus) it is proposed to follow Proctor (1953), Morton (1963b), and Reed (l.c.) and, at this stage, refer to all species in the group as belonging to Thelypteris sens. lat. This is purely as a matter of convenience in that it saves confusion by eliminating the need to introduce any new nomenclatural combinations and it is not intended to restrict the use of the name Thelypteris to the relatively small group of plants to which Holttum (1968b) would assign Thelypteris Schmidel in the strict sense.

Despite the fact that the group is a natural one, it is nevertheless clear from this investigation that it is not homogeneous morphologically and several genera should be recognised within it, a system advocated by Copeland (1947a), Ching (1963), Iwatsuki (1964-5) and Holttum (1954a, 1969), although their actual divisions are not identical, as can be seen below.

Brief outline histories of the taxonomy of the thelypterids have been prepared by Iwatsuki (1963-5) and Reed (l.c.), but these are little more than catalogues of the various sub-groupings recognised by various authors without giving a clear idea of the complexity of the situation caused by the differing criteria on which these divisions were based.

For these reasons it is desirable to review the situation in rather greater detail without, at this stage, passing judgement on the merits, or otherwise, of any one particular system.

The first major detailed work on the thelypterids was carried out by Christensen (1913, 1920) on the tropical American species of the genus Dryopteris Adanson as he understood it. He divided this group into two major sections which are now referred to as Dryopteris Adans. and Thelypteris sens. lat. (although he did not refer to it as such) he formed three large divisions: Lastrea Bory, Cyclosorus Link and Goniopteris (Presl) C.Chr., each being further sub-divided.

In 1910, Nieuwland had put forward Thelypteris Schmid. as a synonym for Dryopteris Adans. and this produced confusion in the nomenclature until 1935 when Thelypteris Schmid. was overruled in favour of Dryopteris Adans. in this usage (as Fernald and Weatherby had proposed in 1929). This left Ching (1936b) free to use Thelypteris Schmid., in its modern sense, in his monograph on the Chinese and Sikkhim-Himalayan Dryopterids. He used criteria similar to those used by Christensen in delimiting his groups, although he sub-divided them to a far greater extent.

Ito (1939), working entirely with Japanese material, further sub-divided the thelypterids into seven genera, (Thelypteris Schmid., Glaphyropteris Presl, Phegopteris Fée, Gymnocarpium Newm., Cyclosorus Link, Leptogramma J.Sm. and Meniscium Schreb.). He also favoured the inclusion of Hypodematium Kunze but he excluded Dictyocline Moore.

By 1940, Ching had elevated the thelypterids from a tribe to a family, the Thelypteridaceae, which he then divided into three tribes and twelve genera. He removed Sphaerostephanos J.Sm. to a separate family solely on asexual reproductive characters, one of which (tetrahedral spores) is almost certainly due to a mis-identification (Iwatsuki 1964)

Copeland (1947) placed the thelypterids in the family Aspidiaceae (S.F. Gray) Copel. and, believing Thelypteris Schmid. to be invalid, transferred many species to Lastrea Bory. Within Lastrea he recognised seven sub-genera and gave generic rank to Cyclosorus Link, Ampelopteris Kunze, Stegnogramma Blume, Goniopteris Presl, Meniscium Schreb. and Dictyocline Moore. By basing his system on hairs, scales and venation he also reinstituted Sphaerostephanos J.Sm. which Ching had eliminated (see above) and added Currania Copel. which is now excluded from Thelypteris sens. lat. (Iwatsuki 1964a). Subsequently, his use of Lastrea Bory in favour of Thelypteris Schmid. has been supported by Pichi-Sermolli (1953), Tagawa (1959) and Fuchs (1963).

In the Flora of Malaya, Holttum (1954a) recognised only four genera in the Malayan thelypterids, these being Cyclosorus Link, Thelypteris Schmid., Abacopteris Fée emend. Ching and Ampelopteris Kunze.

More than twenty years after his original monograph in 1940, Ching (1963) produced a revision of the Asian thelypterids in which his original three tribes were maintained, but he acknowledged the views of Ito (1939) that these should be further sub-divided, and he raised Ito's sections to generic status, resulting in eighteen genera in all.

In the same year, Morton (1963b) recognised the fundamental unity of the group but did not consider that differences in venation and hairs were sufficient to accord generic status to the segregates

within the group. Therefore he placed all the species within a single genus which contained three sub-genera, each of which was further sub-divided into sections.

Iwatsuki (1963, 1964a, 1964b, 1965), working in Japan, followed Ching in recognising the Thelypteridaceae as a family but transferred the taxonomic emphasis from venation to soral characters. Thus he removed the three sub-genera with exindusiate, linear sori, (Stegnogramma, Leptogramma and Dictyocline) to Stegnogramma Bl., regardless of venation and regrouped the remaining sub-genera into Thelypteris Schmid. and Meniscium Shreb. The distinction between the latter two is based primarily, though not exclusively, on the presence or absence of branched or stellate hairs on the trichomes.

In the most recent taxonomic monograph, Holttum (1969) initiated a study of Old World thelypterids, and reviewed the three genera Phegopteris Fée emend. Ching, Pseudophegopteris Ching and Macrothelypteris (H. Ito) Ching. He produced an artificial key dependent entirely on scales, hairs and indusia whilst at the same time recognising that chromosome base numbers and spore types were important additional characters. In this connection it is interesting to note that as early as 1947 (p.132) and again in 1949 (p.284) and 1954 (p.236) he had recognised that a study of venation in isolation from other characters would not lead to a natural division of the group and he considered that "anastomosis of veins must have developed on more than one evolutionary line".

A summary of the major systems of classification will be found in Appendix III.

It can readily be seen that over the past fifty years taxonomists have been attempting to produce a natural classification of the thelypterids by using those characters which are on the whole readily

discernable in the field. Whilst these characters are without doubt useful in identifying species in the field or in the laboratory, there is little evidence to support their being of prime importance when attempting to construct a natural phylogeny. This is more especially the case now that it is thought that parallel development has occured in several instances (Holttum 1947). Hence the modern taxonomist favours the use of more basic criteria such as anatomy, gametophytic characters, cytology, biochemistry and spore architecture when considering phylogenetic relationships.

Both Presl (1836) and Thomae (1886) studied the anatomy of fern stipes and concluded that it was not possible to establish a classification of the ferns based entirely on the anatomy of the stipe.

Very little has been written concerning the detailed anatomy of the thelypterids, although many workers have made passing mention of the double "Hippocampus" (=seahorse) type of stipe vascular bundle or the dictyostelic rhizome, (Colomb 1888, Pelourde 1906, 1909, Ogura 1921, 1938, Iwatsuki 1963, 1964b, Holttum 1969) but without including further details. Ogura (1921) used purely vegetative characters in his classification of the Polypodiaceae. He attempted to form taxonomic conclusions based on an extremely narrow range of characters of the stelar gaps in the rhizome. He included thelypterids in this work but as he only studied six species which were locally common around Tokyo, his conclusions were strictly limited and of little significance when considering phylogeny within the thelypterids.

Momose, in a long series of papers (1937-42) employed what was then a novel approach by considering the features of the gametophyte in isolation. He based his classification on a relatively small number of criteria but was able to enumerate eight gametophytic features by which Thelypteridoideae could be distinguished from the

Dryopteridae. He also concluded that the diversity of features within the group was too great to give it monogeneric rank and divided the sub-family Thelypteridoideae into fourteen genera, including Dryoathyrium Ching, Gymnocarpium Newm. and Currania Copel., all of which have been excluded from Thelypteris sens. lat. by Iwatsuki (1964a) and others.

Many of the thelypterids have been investigated cytologically, but almost exclusively from a geographical standpoint, for example Manton (1950) in Britain and (1954) in Malaya, Manton and Sledge (1954) in Ceylon, Loyal (1961a) in the Himalayas, Walker (1964-5) in Jamaica, Mitui (1968) in Japan, Brownlie (1954, 1958, 1961, 1965) in New Zealand, Manton (1959) in West Tropical Africa and Wagner (1963) in the U.S.A. (A comprehensive summary of the cytological data reported up to the present time can be found in Appendix I).

In the past, cytological data has not been extensively used in the taxonomy of Thelypteris sens. lat. because the number of available chromosome counts has been comparatively small. However, as counts have now been recorded for more than 110 species of Thelypteris sens. lat. from many parts of the world, the possible importance of chromosome base numbers in this context is becoming more apparent. Thus, whilst it has long been recognised that Thelypteris sens. lat. may be separated from Dryopteris Adans. by their respective base chromosome numbers (Manton 1950, Morton 1963b, Iwatsuki 1963) more recently, workers have been using cytological data to a much greater extent to add weight to their theories regarding taxonomic groupings within the thelypterids (Manton 1953, Iwatsuki 1963, Holttum 1969, Holub 1969). However, Iwatsuki (l.c.) concluded that "a difference in chromosome (base) numbers will suggest certain taxonomic differences between the plants, but the identity in the chromosome numbers cannot indicate any

taxonomic identity between the plants." This is especially so in a group such as Thelypteris sens. lat. where parallellism is thought to have occured.

Palynology has frequently been used in the taxonomy of higher plants (Wodehouse 1926a, 1926b, 1928a, 1928b, Erdtman 1947, 1952, 1959, 1961, Kuprianova 1948, Skvarla and Larson 1955, Chanda 1966 and many others).

In the ferns there have been numerous papers concerning the morphology of the spores of the fern flora of a particular geographic region, (Tardieu-Blot 1932, in Tonkin; Selling 1946, in Hawaii; Makino 1949, in Japan; Lawralée 1950, in Belgium; Knox 1951, in Great Britain; Madalski 1954, in Poland; Harris 1955, in New Zealand; Karpowicz 1960, in Poland; Erdtman et al. 1961, in Scandinavia; Lugarden 1963, in France; Nayar and Devi 1963, in Japan; Nayar and Kaur 1963, in India; Tardieu-Blot 1963a, 1963b, in Madagascar and the Mascareigns; Bir 1966-7b, in the Himalayas and many other lesser works). Although the majority of these are purely descriptive and in some cases beautifully illustrated they contain few taxonomic conclusions based on spore morphology.

However, within the thelypterids spore morphology has been used to a limited extent as a taxonomic character by a number of workers, for instance Momose (1942), Holttum (1947), Reed (1950), Crane (1953), Harris (1955), Alston (1959), Morton (1963a), Blasdell (1963), Nayar and Devi (1963, 1964), Sorsa (1964), Davlianidze (1965), Wagner (1966), Bir (1966a), Shivas (1969) and Holub (1969). (Further details of these are given in the Chapter on Palynology, Chapter VII.)

From this survey of the available literature it can be seen that although the thelypterids have already been studied in varying degrees of detail, by many workers, the information presented has always been

of a fragmentary nature. This has been a consequence either of the restricted geographical knowledge of the worker or of the restricted lines of research along which he has worked. Thus the present situation is that at one end of the scale the taxonomy and morphology of the thelypterids have been intensively studied (although in various strictly delimited geographical areas only) whilst at the other end of the scale anatomy and palynology have been studied in only a very small number of species which, moreover, have been chosen in a somewhat arbitrary manner.

The present situation regarding the thelypterids is therefore that although there has been a large volume of work carried out, much of this has been of an incidental nature in works whose emphasis was not on the thelypterids alone. Because of this the available information is scattered throughout numerous works and an overall picture has not been constructed previously.

CHAPTER II

MATERIALS AND METHODS

GENERAL INTRODUCTION TO PROCEDURE

As can be seen from Chapter I, the majority of studies on the thelypterid ferns, which have been published up to the present time, have been based almost exclusively on gross morphology. The taxonomic conclusions have been formulated as a result of particular emphasis being placed on either single characters or a very limited number of characters. Furthermore such studies have been markedly restricted from a geographical point of view and there has been little attempt at an overall synthesis on a world-wide basis.

These present studies were undertaken with the object of attempting to rectify the above situation by studying the characters (previously considered in a restricted area) over a wide geographical range and in conjunction with alternative characters whose possible taxonomic importance had not yet been assessed.

The headings under which this present investigation was carried out are summarised below.

1) Comparative Anatomy
2) Cytology
3) Palynology
4) Morphology
5) Gametophytic Studies

Further details are given below under each heading, of the methods employed and the sources from which material was obtained.

1) COMPARATIVE ANATOMY

a) Sources of Material

The material used for anatomical studies was derived from several sources:

i) Plants collected and preserved in the field by T.G. Walker and A.C. Jermy, from Jamaica, Trinidad, New Guinea, New Britain, Sulawesi (Celebes) and Java.

ii) Plants grown in cultivation at the Royal Botanic Gardens, Kew.

iii) Material grown on from living rhizomes sent to the Moor Bank Experimental Grounds of the Botany Department in the University of Newcastle Upon Tyne. The original sources of these plants with their collectors were as follows: Japan (Dr. A. Sleep), Mauritius and Australia (Dr. C.N. Page), Trinidad, Jamaica, New Guinea, New Britain, Sulawesi and Java (Dr. T.G. Walker and Mr. A.C. Jermy).

In addition these specimens were supplemented by plants raised from spores, also obtained from the sources listed above. These plants were only used to supplement inadequate material from other sources. The reason for this being that some of the larger specimens fail to attain their full development when raised from spores in cultivation.

b) Methods

The material was either sectioned by hand or embedded in paraffin wax (congealing point 55°C) and sectioning carried out using a Reichert Om S rotary microtome at thicknesses varying between 12um and 25um according to the material.

Staining was in safranin and either light green or fast green according to standard techniques.

For studies of venation and distribution of sori and epidermal appendages (hairs and scales) whole pinnae, where feasible, were

cleared in 6% potassium hydroxide solution, stained in basic fuchsin (1%) and differentiated in alcohol acidified with concentrated hydrochloric acid (C. Fuchs, 1963).

All preparations were dehydrated and preserved in Kleermount or Xam mountants.

Plan diagrams and cell drawings were prepared by using either a projecting microscope or photographic enlarger to produce images on a sheet of card, which were then traced. These drawings were photographed (using Kodak N5.50 Line film) and reduced to standard size.

2) CYTOLOGY

a) Sources of Material

The material used for cytological studies was derived from two sources:

i) Fixings of sporangial material made in the field in the West Indies, Indonesia and New Guinea by Dr. T.G. Walker.

ii) Fixings made by myself from specimens grown in cultivation at Newcastle (the sources were as listed above for anatomical studies).

b) Methods

In most cases the sporangial material was fixed in Acetic Alcohol (one part glacial acetic acid to three parts absolute alcohol) and stored at -25°C. Other material was fixed in a 2% aqueous solution of hydroxy quinoline potassium hydrogen sulphate and stored at room temperature.

The squashing, staining in aceto-carmine and recording techniques are standard (Manton 1950).

Where sporangial material was not available preparations were made from growing root tips or young growing fronds, pre-treated with para-dichlor benzene (P.D.B.) and partially digested with cytase before squashing and staining in aceto-carmine.

3) PALYNOLOGY

a) Sources of Material

The material used in the electron microscope studies of spores was obtained from several sources:

i) Herbarium specimens from the British Museum of Natural History, South Kensington.

ii) Herbarium specimens from the Royal Botanic Gardens, Kew, given by Professor R.E. Holttum.

iii) Herbarium specimens from the herbarium in the Botany Department at Newcastle University.

iv) Field collections from the West Indies, Indonesia and New Guinea (Dr. T.G. Walker and A.C. Jermy) Mauritius and Australia (Dr. C.N. Page).

v) Living material growing at Kew and Newcastle University.

b) Methods

i) External Morphology

For studies of their external morphology, spores were prepared as follows: In cases where the specimen frond was producing spores freely, the surface of a pinna was lightly brushed with a fine paint brush to collect the spores, which were then transferred, by means of a palette knife to a quarter of an inch square piece of double-sided sellotape, fixed to the centre of a labelled glass slide. These slides were then stored until they could be examined. This technique ensures that a large quantity of spores are available for examination and hence the possibility of contaminant spores being present could be minimised by the overwhelming numbers of authentic spores.

Where the specimen was not producing spores freely, alternative methods were employed; either a quantity of sporangial material was lightly scraped from a pinnule, with the chance of transfer of a few spores, or the sori were searched using a binocular microscope and,

if possible, a few whole mature sporangia were removed and placed on the sellotape, as above. By using mounted needles and a binocular microscope the sporangia were then split open to release the spores. This technique had the advantage of ensuring that authentic spores of the specimen were gathered, instead of possible contaminants which may occur when a herbarium specimen has already liberated most of its spores.

When required for study these squares of tape were stripped from the slide and stuck onto the microscope stub before being evenly coated, under vacuum, with a very thin layer of gold.

The instrument used for viewing was a Cambridge Instrument Co. Ltd. Scanning Electron Microscope Mk. IIa, housed in the Electron Microscopy Laboratory at the University of Newcastle Upon Tyne.

ii) Thin Sections

Thin sections for study under the transmission electron microscope were prepared in the following manner: dry spores were either acetolysed by the revised Erdtman method (Erdtman 1960) or left untreated. Separate samples of each were then stained in osmium tetroxide, embedded in araldite resin (after Skvarla and Larson 1964) and sectioned using an L.K.B. ultra-microtome at a thickness of between 50nm and 100nm. The specific section stains used in each case are noted in the text.

The sections obtained were mounted on grids and examined using an A.E.I. E.M.6B electron microscope, in the Botany Departments of Newcastle University and Liverpool University.

4) MORPHOLOGY

Morphological investigations were carried out using the specimens listed in section 1) a) above.

5) GAMETOPHYTIC STUDIES

For these studies, spores, obtained from the sources named above,

were germinated on either nutrient agar under artificial light or on sterilised soil in the greenhouse. Whole mounts were prepared of various stages using lacto-phenol.

CHAPTER III

ANATOMY

Introduction

In the introductory chapter it was stated that little had been written concerning the detailed internal anatomy of the thelypterids. The most comprehensive approach to this subject was that of Iwatsuki (1963-5), but even his descriptions were brief, no illustrations were included and he entirely confined his studies to Japanese material.

Although in the past numerous workers have described (and in many cases illustrated) most of the anatomical features, their studies have largely been confined to one or two characters in isolated species and no attempt appears to have been made to assess their importance in the taxonomy of the group. The attitude of many taxonomists, to the study of anatomy, still seems to be that held by Presl (1836) namely, that anatomical data alone has only a strictly limited place in taxonomy. While this may well be true in some instances, it is important that its validity should be tested in any group that is being studied taxonomically, with due regard to Bailey's words that "Each morphological character studied in a whole range of different plants proves to be relatively stable in certain plants and highly variable in others. It is evident that anatomical characters are inherently no more reliable than exomorphic ones but are susceptible to equivalent and equally valid uses. The employment of such characters merely adds more strings to the investigator's bow."

These anatomical studies were carried out on this premise and on the basis of Iwatsuki's suggestion (l.c. P.31) so that an assessment

might be made of the contribution of anatomy to the taxonomy of the thelypterids as a whole.

In the course of a preliminary survey it was noticed that whilst the basic pattern of the internal anatomy appeared to be very similar throughout the group, certain anatomical features do show a range of variations. This initial impression has been confirmed by more extensive comparative studies, the results of which are set out in the remainder of this chapter.

RHIZOME

Within the thelypterids, the rhizome shows considerable variation in size, habit and distribution of leaf bases, the most frequently occuring forms being:

a) massive and erect with crowded stipe bases,
   e.g. T.balbisii (Spreng.) Ching,
b) more slender and erect with crowded stipe bases,
   e.g. T.patens (Sw.) Small,
c) of medium thickness and ascending,
   e.g. T.asplenioides (Sw.) Proctor,
d) slender and creeping with crowded stipe bases,
   e.g. T.kunthii (Desv.) Morton = T.normalis (C.Chr.) Moxley,
e) slender and creeping with distant stipe bases,
   e.g. T.glanduligera (Kze.) Ching.

The rhizome usually has an average diameter of between 0.5 cm and 1.0 cm although the variation may be as great as fifty-fold from the smallest to the largest. Iwatsuki (1963), working entirely with Japanese material quotes the maximum diameter as 1.5 cm in T.esquirolii (Christ) Ching and the minimum as 0.04 - 0.07 cm in T.cystopteroides (D.C. Eaton) Ching. In these present studies the maximum measured was 3.0 cm. in a specimen of T.xylodes (Kunze) Ching from New Guinea and

the minimum was 0.15 cm in a specimen of T.glanduligera from Japan.

Typically the rhizome is covered with numerous brown papery scales, especially in the vicinity of the growing point. These scales may or may not persist on the older parts and their continued presence or absence is probably largely dependent upon the nature of the organ. Thus the scales are persistent on the aerial parts of erect, ascending or epigenous rhizomes, i.e. those in which the major part is above ground level, but absent from those which are either genuinely subterranean in habit or, although creeping on the soil-surface, are normally covered by a layer of humus. It is therefore probable that the functions of such scales are to protect the young growing point and aid water conservation.

As an introduction to the anatomical studies of the rhizome, it is convenient to describe the series of events along a creeping rhizome with well-spaced stipe bases, and then to apply these events to the more erect and crowded types where, due to the proximity of adjacent stipe bases, the pattern is less easily described.

The rhizome of the thelypterids is dictyostelic* and usually consists of from three to five meristeles arranged concentrically. However up to eight meristeles may be seen in the exceptionally large erect rhizomes found in some specimens from the tropics, e.g. T.balbisii (= T.sprengelii (Kaulf.) Proctor) from Trinidad. Ogura (1921) quotes the number of meristeles as three or four in the relatively small Japanese plants that he studied.

At distances along the rhizome, corresponding to the distance between adjacent stipe bases, commissures join a pair of neighbouring

---

* Brebner 1902 "A dictyostele consists of a vascular tube with large overlapping leaf gaps, so that the whole structure becomes a network of vascular strands or meristeles. The meristeles are concentric".

meristeles and then, at a distance from the commissure which is dependent upon the species (Ogura 1921) a stipe bundle branches off from each of these two meristeles and the two bundles enter the base of the stipe together. This may be seen in cross-section as the two adjacent meristeles lengthening at their proximal ends, until finally the stipe bundles are budded off (see figs. 1 & 3). At a further constant distance along the rhizome another commissure is formed between one of the meristeles previously involved and the next adjacent one in either a clockwise or an anti-clockwise rotation, and the process is repeated. At the same time the meristeles as a unit follow a spiral pathway in the same direction as the phyllotaxis of the stipe bases. Hence in long-creeping rhizomes, adjacent stipes tend to be produced in two ranks on alternate sides of the rhizome (see fig. 2).

A basically similar series of events can be recorded for all types of rhizome, although the actual details differ somewhat according to the habit of the rhizome and the spacing of the stipe bases. In erect rhizomes with closely packed stipe bases, for example, the stipes are not produced on alternating sides because the degree of rotation of the meristeles, between adjacent stipe bases, is by no means as great as that found in creeping rhizomes. Instead, therefore, parallel spiral rows of stipes are formed ascending the rhizome, the number of rows necessarily corresponding with the number of meristeles in the rhizome. Plants showing intermediate habits show characters which are correspondingly intermediate between the two extreme types outlined above.

As a result of the structure of the dictyostele, especially in long-creeping rhizomes with distant stipe bases, the term "leaf-gap" becomes rather a misnomer. For example Ogura l.c. quotes a specimen*

---

* Dryopteris sophoroides (Thunb.) O.Ktze. = T.acuminata (Houtt.) Morton.

where adjacent stipe bases are as much as 10 cm apart. The form of the dictyostele would therefore dictate that in such a rhizome, containing only three meristeles, the "leaf-gap" would have a length of approaching 30 cm with the stipe traces branching off at some position along this length. It is therefore probably less confusing to consider the vascular system, not as a solenostele with long overlapping leaf gaps, but as a tube of separate meristeles with interconnecting commissures and stipe traces at fixed positions along its length.

Gwynne-Vaughan (1903) suggested that the dictyostele had evolved from the solenostele from either the crowding together of the leaves or the elongation of the leaf gaps. However, in the thelypterids which are comparatively uniform in many ways, it would seem that both types of development have occurred simultaneously in erect and creeping rhizomes. It is possible that there is an alternative line of development: from a protostele to a ring of protosteles which then join by commissures to form the dictyostele as found in the thelypterids. The only evidence that I can put forward to support this hypothesis is the fact that even in long-creeping rhizomes, where "leaf-gaps" are at their greatest development, there is no evidence of solenostelic origins except for a commissure joining two adjacent meristeles.

From the results of a preliminary survey it was thought that the dictyostele of any one species contained an identical number of meristeles and that this number remained constant throughout the life of the plant. It was also thought that the size of a mature rhizome was dependent upon the number of meristeles, in both the same species and in different species. Hence by measuring the diameter of the rhizome the approximate number of meristeles present could be determined.

On a more detailed examination, however, it was discovered that

in fact the number of meristeles frequently varies in a given plant as well as between plants of the same species. Furthermore the final size of the rhizome did not appear to be directly correlated with the number of meristeles except in so far as the minimum number of meristeles in a mature rhizome was three and there were invariably three meristeles in the narrowest rhizomes measured (i.e. those with a diameter of less than 0.5 cm, see table no. 1 below and fig. 3). However, one of the larger rhizomes measured, also contained only three meristeles.

It is frequently found that where a rhizome branches there is a reduction in the number of meristeles in the branches as compared with the main axis. Hence in a specimen of T.bangii (C.Chr.) Tryon, where there were four meristeles in the older portion, each of the branches formed by the dichotomy of the main axis contained only three meristeles.

It was therefore concluded that neither the diameter nor the number of meristeles in the rhizome would be of use taxonomically as they showed such a degree of variation.

The basic anatomy of the rhizome in all the species studied is remarkably uniform, whether it is massive and erect or slender and creeping. Each meristele consists of a central region of large metaxylem tracheids, interspersed with comparatively few parenchymatous cells. A relatively narrow band of metaphloem surrounds the xylem with groups of collapsed protophloem cells around its periphery. There is a continuous cylinder of thin-walled pericycle cells and a typical filicinean secondary endodermis (Priestley and Radcliffe 1924). The cortical region frequently contains large reserves of starch.

Except in the very young rhizome there is a hypodermis of sclerenchymatous tissue of variable thickness. In some erect rhizomes, e.g. T.paucijuga (Kl.) Proctor, and in the older parts of all creeping

SPECIES	No.	MEAN DIAMETER cm	NUMBER OF BUNDLES	HABIT OF RHIZOME
T.glanduligera	W5	0.15	3	Creeping
T.womersleyi	T7468	0.20	3	Creeping
T.griffithii	W26	0.40	3	Creeping
T.interrupta	T12546	0.40	3	-
T.balbisii	T6142	0.50	4	Ascending
T.sp. indet.	ACJ4683	0.50	5	Ascending
T.dentata	T10564	0.58	4	Creeping
T.unita	T10708/4	0.60	3	Creeping
T.dentata	T6184	0.60	4	Creeping
T.patens	T10311/1	0.60	5	Erect
T.patens	T10311/2	0.65	5	Erect
T.unita	T10708/5	0.80	3	Creeping
T.paucijuga	T6240	0.80	4	-
T.sp. indet.	T6198	0.80	4	-
T.heterocarpa	T12663	0.80	5	Erect
T.unita	T10708/3	0.83	3	Creeping
T.unita	T10708/1	0.90	4	Creeping
T.gongylodes	W3	0.90	4	Creeping
T.unita	T10708/2	0.93	3	Creeping
T.sp. indet.	T12759	1.00	3	Ascending
T.serra	W6	1.00	4	-
T.longipes	T12803	1.00	4	Ascending
T.setigera	T6950	1.10	4	Ascending
T.serrata	ACJ2362	1.50	5	-
T.balbisii	T7211	1.50	8	Ascending
T.xylodes	T12326	3.00	6	Erect

TABLE 1

To show the relationship between the mean of two diameter measurements at right angles, and the number of bundles within the rhizome. The measurements were taken from portions of the rhizome near the growing point, which were producing mature fronds. The specimens represent a random sample some of which were grown in cultivation and the rest from material pickled in the field.

rhizomes that have been examined (e.g. T.glanduligera) the whole of the organ becomes completely sclerenchymatous except for the vascular tissue itself and a small band of parenchymatous cortex surrounding each meristele. In other erect rhizomes and creeping rhizomes the sclerenchyma is less well developed, but frequently cells in which a black or dark brown substance "vagin" (Bäsecke 1908, Priestley and Radcliffe 1924) or 'phlobaphene" (Sporne 1962) is deposited are common in the cortical regions e.g. T.dentata (Forssk.) E. St. John and T.serra (Sw.) R.P. St. John in Small. In some species these cells form a complete sheath around the vascular tissues, e.g. T.balbisii, although in this species, at least, its deposit varies with age. Rhizomes with poorly developed sclerenchyma and no vagin also occur, these are usually creeping and more fleshy in nature e.g. T.gongylodes (Sch.) Link.

Adventitious roots branch off from all parts of the rhizome except for the commissures and stipe bases, unlike the stipe traces which branch off from the rhizome in a regular pattern. In an erect crowded rhizome this may lead to more than one root and the stipe trace branching off from one meristele simultaneously. The xylem of the root trace is circular or lens shaped in transverse section (see below) and branches off from the outer centrifugal margins of the meristele. These root traces therefore contrast with the stipe traces which are elongated in transverse section, take their origin from the sides of the meristele and enter the stipe in pairs.

The nature of the rhizome appears to have little correlation with any other taxonomic characters e.g. in the well defined group of Pseudophegopteris Ching rhizomes varying from erect to long-creeping are found. It would seem that from the taxonomist's point of view the main use to which information regarding the type of rhizome can be put

is in delimiting of species rather than of genera or sub-genera. The form of the rhizome would appear in part to be a reflection of the normal habit of the plant, a species living in stable conditions might be expected to possess an erect rhizome while one living in unstable or very wet conditions might be expected to possess a long-creeping rhizome.

Thus there is considerable variation in the range of both the habitats occupied by the thelypterids and the habit of the rhizome. Despite this there are no marked anatomical differences to be found in rhizomes of species living in very different habitats as there are in, for example, the blechnoid or acrostichoid ferns. The acrostichoid ferns which exist in very marshy habitats possess extensive aerenchyma throughout the plant and Blechnum indicum Burm. possesses extensive aerenchyma in both its rhizome and stipe whilst other closely related species do not (Walker unpub.). In the thelypterids on the other hand there are no such adaptations, thus T.gongylodes (fig. 4) which lives in very marshy habitats has a rhizome which is virtually indistinguishable from that of T.dentata which is often to be found in essentially dry habitats.

ROOT

The apical region of young roots, which extends for approximately 0.2 cm in an actively growing root, is white and translucent in colour often with a slight greenish-yellow appearance. Beyond this point, sclerenchyma is laid down as a hypodermis and imparts a brown coloration and wiry texture to the older roots. Immediately behind the apex, root hairs are found in great numbers while their frequency over the rest of the root system is sparse. The roots vary considerably in thickness, the finest being very thin and thread-like while the larger ones may be up to 0.2 cm in diameter.

Branching is very irregular and occurs in all directions, often forming a very dense tuft. In large erect rhizomes the roots intermingle with the stipe bases and together these produce a massive structure of which the rhizome itself occupies only a small proportion. In long-creeping rhizomes the roots tend to form along a spiral pathway between the stipe bases. This is a consequence of the underlying spiral structure of the meristeles from which the roots originate. The same is also true for crowded and erect rhizomes but in this case the root origins are obscured by the crowding of the stipe bases.

Root traces branch off from all parts of the meristele (except for the commissures and stipe traces) and are first visible in transverse sections of the rhizome as small protuberances on the outer edges of the meristeles, a single trace entering each root. In section (see fig. 6) the vascular tissue occupies only a small area of the root, typically being about a quarter of the diameter of the whole. As in the majority of leptosporangiate ferns, the xylem is diarch with a few large metaxylem tracheids flanked by two small groups of protoxylem cells. A layer of phloem surrounds the xylem, varying in thickness from one to five cells. There is a pericycle of 1-2 layers of thin walled cells and a clearly defined endodermis which develops secondary characters in larger roots.

The cortex often contains starch grains and in older roots the outer four or five layers of cells become sclerised and tannin is deposited giving rise to a typical brown coloration.

The only observed variation in structure is that which can be directly associated with size. Thus the extent of the conducting tissue in the root decreases with size until in the smallest there are only one or two tracheids and four or five phloem units. Hence the roots show no characters that might be of use taxonomically and are only remarkable in their uniformity.

STIPE

The term "stipe" is normally used to refer to that part of the axis of a frond below the junction of the lamina (Holttum 1954a). In the thelypterids however, this definition can cause some confusion due to the variety of frond types that are found. Some produce a definite lamina, some possess numerous reduced pinnae along the majority of the axis, while others possess auricles, or even small wart-like projections along the sides of the axis. The distinction between stipe and rachis thus becomes confused and this is discussed in greater detail below, under the section on the rachis. It is therefore proposed to use the term "stipe" in a rather loose sense here, to refer to the lower portion of the axis, which in general is that portion below the first true pinna.

For this study transverse sections of the stipe were cut at various levels, those referred to under this section occuring below the junction of the two stipe traces (see below).

The internal anatomy of the stipe is remarkably uniform in its basic layout, consisting of two independent vascular strands which branch off from adjacent meristeles in the rhizome (see above p. 18) and pass into the stipe base. Each of these traces exhibits the typical "hippocampus-form" (=seahorse-shaped) metaxylem. The tracheids are interspersed with an approximately equal number of parenchymatous cells (see fig. 7).

The xylem is circumscribed by typical metaphloem, uniformly four to six cells in width, which in turn is surrounded by a narrow layer of compressed protophloem cells. Around the phloem there is a layer of thin-walled pericycle cells which varies in thickness from one to four or five cells around each vascular bundle. The degree of development of the pericycle varies from species to species.

As in the rhizome (see above) the endodermis is of the typical filicinean type in which all but the outer wall becomes thickened by suberin and in addition a vagin is also often laid down around the traces, (Priestley & Radcliffe 1924, p. 163). This "bundle-sheath" often forms a complete cylinder around the vascular trace, although its extent varies greatly from species to species and even within one species it may vary from plant to plant (see table 2). It is however, at its most advanced state in older fronds and any conclusions that may be drawn from this table must take into account the fact that the age of the particular fronds studied is not known. The exact chemical composition and function of this layer are obscure at the present time.

Within each trace of a mature stipe there are what at first sight appear to be mucilage canals towards the inside of the bends in the narrow arms of metaxylem (see fig. 7). On closer examination, these "mucilage canals" are found to mark the position of the protoxylem cells which frequently become abortive in mature stipes (=protoxylemhöhle, Ogura l.c.). In those species which possess an elongated vascular trace the number of groups of protoxylem cells is equal to the number of "bends" or convolutions in the xylem, e.g. T.decussata (L.) Proctor, T.megaphylla (Mett.) K. Iwats. (see table 2).

As the two traces ascend the stipe, they converge and finally join to form a typical 'U' shaped trace which enters the rachis. The position of this junction is very variable and will be discussed more fully in the section dealing with the anatomy of the rachis (see figs. 34 to 36).

The periphery of the stipe, in all but the youngest fronds, has an extensive hypodermal layer of sclerenchyma, usually from six to ten cells wide, but in some extreme examples of older stipes the whole of

SPECIES	No. OF GROUPS OF PROTOXYLEM CELLS/BUNDLE	EXTENT OF BUNDLE SHEATH	MEAN DIAMETER OF STIPE (cm)	TYPE OF RHIZOME
T.glanduligera	2	0	0.10	Creeping
T.griffithii	2	Complete	0.125	Creeping
T.prolifera	2	2-3 cells	0.125	Creeping
T.palustris	2	Complete	0.16	Creeping
T.triphylla	2	0	0.175	Creeping
T.setigera	2	Complete	0.19	Creeping
T.paucijuga	2	0	0.19	Ascending
T.pyrimidata	2	0	0.22	-
T.dentata	2	0	0.30	Ascending
T.serra	2	0	0.30	Erect
T.brachyodus	3	0	0.30	-
T.resinifera	2	Approx. $\frac{1}{2}$	0.31	-
T.obliterata	2	0	0.39	Creeping
T.decussata	6-7	0	0.39	Erect
T.gongylodes	2	0	0.41	Creeping
T.megalodus	2	Complete	0.43	-
T.limbosperma	2	0	0.46	Ascending
T.balbisii	2	2-6 cells	0.51	Ascending
T.megaphylla	4	Many single cells	0.53	Erect
T.serrata	3	0	0.55	-
T.reticulata	2	0	0.56	Creeping
T.extensa	3	0	0.64	Erect
T.truncata -				
Crozier	5-6	0	-	Erect
Mature stipe	5-6	10-12 cells	0.67	
T.xylodes -				
Crozier	4-5	0	1.00	Erect

TABLE 2

To show the relationship between the number of protoxylem cells in each vascular bundle of the stipe and the extent of the bundle sheath around each bundle compared with the mean diameter (two measurements at right angles) of the mid stipe. The type of rhizome is given to show the relationship between it and the diameter of the stipe.

the cortex and central region becomes lignified, with the exception of a single layer of cells surrounding the vascular traces. In many species, this sclerenchymatous hypodermis is interrupted along each side of the stipe by a "streak" or pneumathode which is usually visible externally as a lighter green or yellowish stripe along an otherwise darker green or red-brown stipe (a similar structure is found in Cyathea Holttum 1954a p. 69). In transverse section it is found that at this position the sclerenchymatous tissue is replaced by a plug of loosely packed cortical cells which do not become thickened until the frond is near maturity. The epidermis at this stage is normally somewhat domed (see fig. 15) and is particularly prominent in the young circinate frond where it consists of large numbers of closely packed stomata which are absent from the rest of the stipe* (see fig. 16). This fact was noted by Hennipman in 1968, but it was found that the stomata were particularly difficult to observe as they were obscured by the density of the underlying tissues. A satisfactory method was eventually employed whereby shavings from the epidermis of the stipe were decolourised in Eau de Javelle at 60°C for 30 minutes and then stained in aqueous Ruthenium red for 20 minutes, before being mounted in glycerine. After this treatment the cells become completely transparent, whilst the middle lamellae stain a bright magenta. Thus the stomata become distinguishable from the underlying tissues and can be viewed by careful focusing of the microscope.

In the crozier and young frond of certain species it would appear therefore that gaseous exchange takes place, primarily or exclusively through stomata arranged linearly in the form of a pneumathode along each side of the stipe.

---

* A similar massing of stomata is found on the swollen leaf bases of Plagiogyria matsumureana Makino (Ogura 1938 p. 92).

As the stipe elongates from the crozier stage, the stomata become considerably less crowded and it is likely that, along with the underlying tissues of the cortex, they become sclerised and possibly non-functional. In the herbarium and preserved specimens this pneumathode usually provides a line of weakness, which splits due to the unthickened cells, making its morphology difficult to study in all but fresh or recently preserved material.

In a number of species, especially those from very damp habitats and tropical rain forests, the stipes (and in exceptional cases the rachises and laminae also) are found in the natural state to be covered with a layer of mucilage originating from mucilage-secreting hairs on the epidermis (see below) hence in such species gaseous exchange through the stomata must be severely impeded. These species often possess prominent, spine-like aerophores which project above the surface of the mucilage (see fig. 60) and are thought to assist in the water relations and possibly the gaseous exchange of the plant.

In species such as T.truncata (Poir.) Iwats. a vascular trace branches off from the main trace and enters the aerophore where the xylem body terminates in a hydathode according to Hennipman (l.c.). He also reports on the presence of a peculiar structure at the base of the hydathode in T.xylodes (see below Chapter IV p. 55).

In T.decussata small spine-like outgrowths are found abaxially at the base of the pinnae and also along the line of the pneumathode on the stipe. These outgrowths have been termed aerophores and their presence or absence has been used as a taxonomic character by many authors (Christensen, Ching, Iwatsuki etc.). However, there is no vascular connection, hence the term aerophore in such cases is a misnomer, although they may possibly act as such in very young croziers. In older fronds the aerophores become obsolete when the mucilage

covering disappears and they become sclerised and probably cease to function. Further details of the anatomy and morphology of these structures will be found later (Chapter IV p. 53).

The term "hippocampus" (=seahorse) was first used by Colomb in 1888 and very aptly describes the shape of the xylem, seen in transverse section (see fig. 7). Several later authors, for instance Pelourde (1906 and 1909) and Iwatsuki (1963), have used this term to describe the vascular traces of various thelypterids.

Ogura (1938) on the other hand, used the term "Onoclea-type" to describe the double trace in the thelypterids.* He recognised many types of stipe traces in his classification, amongst which were the Loxsoma-type and the Aspidium-type. In his evolutionary scheme, he placed the Onoclea-type between the Loxsoma-type and the Aspidium-type trace (see fig. 14). The weakness of his classification however is that the form of the trace is not fixed throughout the length of any one stipe and hence frequently the type of trace found depends entirely upon the level at which sections are cut. For example, at the base of the stipe of Diplazium latifolium Moore the trace consists of five bundles of the Aspidium-type, at a higher level these fuse to form two bundles of the Onoclea-type, while near the top of the stipe these in turn fuse to form a Loxsoma-type trace (Bir 1969). Similarly with thelypterids the base of the stipe exhibits the Onoclea-type while the higher regions are of the Loxsoma-type. Ogura took sections near the centre of the stipe and therefore designated both Diplazium and Dryopteris (including the thelypterids) as Onoclea-type. However had he sectioned Diplazium latifolium nearer its base or chosen one of the thelypterids in which the junction occurs near the base of the stipe

---

* Other genera included as being of the "Onoclea-type" are Peranemia, Cystopteris, Matteucia, Onoclea, Woodwardia, Athyrium, Diplazium, Gymnogramme, Ceratopteris, Trismeria, Pellaea, Microlepia, (Ogura 1938 p. 384).

he would have designated Diplazium as Aspidium-type and Thelypteris sens. lat. as Loxsoma-type.

Therefore, if evolutionary or taxonomic conclusions are to be drawn from studies of the vasculature of the stipe, great care must be taken to ensure that all parts of the stipe are considered, as no part of the stipe can be shown to be either more or less susceptible to evolutionary development.

Thomae (1886) studied many fern stipes and classified them into groups but he concluded that the anatomical features of the stipe, by themselves, were insufficient to form the basis of a classification of the ferns. Within a well defined group, studies of the vasculature of the stipe, in correlation with other characters, may however prove useful in taxonomic studies. In the thelypterids the basic pattern of anatomy is extremely similar in all the specimens studied whilst those features which do vary appear to vary throughout the group as a whole, so that there are no definite features in the anatomy of the stipe that can be singled out as being of taxonomic significance.

RACHIS

It is usual to define the rachis as that portion of the main axis of the frond between the junction of the lowest pinna and the apex. In the thelypterids, however, this definition leads to confusion in many species because of the range of frond types that are found (see figs. 17 to 36). Although in some species, e.g. T.dentata the lowest pinna is well defined, in other species the frond is narrowed downwards so that the lowest pinnae are very much reduced in size and often extend almost to the base of the axis e.g. T.sumatrana (v.A.v.R.) Reed and T.resinifera (Desv.) Proctor. Other species have their basal pinnae reduced to small auricles e.g. T.deltoidea (Sw.) Proctor although the basal true pinnae may be well defined. However, a fourth type exists

in which the basal appendages are reduced to warts along the side of the axis, e.g. T.decussata, which may or may not represent reduced pinnae (see below). Because of the confusion ensuing from the variety of frond types, the term 'rachis' is used in this study in a very loose sense to refer to that part of the axis bearing true pinnae i.e. where the two stipe traces are truly united to form a typical 'U' shaped trace.

The point at which the two hippocampus-form traces unite, after entering the base of the stipe separately, varies greatly from species to species. Certain generalisations can be made, however, for instance, when there is a discrete lamina (i.e. no reduced pinnae or auricles), the two stipe traces invariably join below the junction of the basal pinnae with the axis. Although the exact position of this junction varies from species to species it appears to be more or less constant within a species.

In those species where there is only a very small distance between the base of the stipe and the lowest reduced pinnae, e.g. T.resinifera, the junction occurs above several of the latter, but nevertheless relatively close to the base. In species such as T.deltoidea the junction occurs higher up the stipe, in the position that might be expected were there no auricles present. (see fig. 35).

The basic anatomy of the rachis is very similar to that of the stipe (see above p. 25) except that the two bundles are united at their abaxial (dorsal) ends. Where a bundle-sheath is present in the stipe it is also manifest in the rachis, though often less extensive nearer the apex.

In most species, pinnae branch off from the rachis alternately to left and right. Some species, e.g. T.opposita (Vahl) Ching and T.oppositipinna (v.A.v.R.) Ching appear to have their pinnae inserted

in pairs but on anatomical investigation even these are found to be truly alternate. The situation is often rather confused by the pinnae on one side of the rachis being slightly wider spaced than those on the other. This leads to the pinnae at the tip of the frond often being truly alternate while those at the base appear more or less opposite (see fig. 29).

The pinna traces branch off from the adaxial, free ends of the rachis trace, (Davie, 1914, = Extra-marginal development) in a typical fashion. They run parallel with the rachis trace for some way towards the apex before entering the pinnae (see fig. 37).

Where they are present, pneumathodes continue their path along the sides of the rachis, gradually decreasing in width towards the apex, and being interrupted by the stalks of the pinnae. They are not, however, found along the axes of the pinnae (=costae).

PINNA

In this section on the pinna it is proposed to limit the discussion to the anatomical features of the lamina and costa together with the morphology of the epidermis and stomata. Other features connected with the pinnae are discussed in later chapters; the venation patterns and sori in Chapter V and trichomes in Chapter IV.

The midrib of the pinna, or costa, is typically rounded in shape, although there is usually a more or less prominent groove along its upper, adaxial surface. Unlike the groove found in Dryopteris sens. strict. it does not open into the groove along the adaxial side of the stipe and rachis and thus provides a convenient morphological character for distinguishing between Dryopteris and Thelypteris (Holttum 1954).

When viewed in transverse section, the vascular tissue occupies a central position within the costa. The xylem is typically lens-shaped or slightly U-shaped in outline and the tracheids which enter the

costules branch from the outer free margin in a similar manner to that by which the pinna traces branch from the rachis (see above = extra-marginal). The tracheids of the veins are typical protoxylem cells, having lignified spiral thickening which can be readily seen after clearing and staining in basic fuchsin and concentrated hydrochloric acid (see Chapter II for method).

A small number of phloem cells and a pericycle are also found in the costa bundle, but the endodermis, which surrounds these tissues is of the primary type (Priestley and Radcliffe 1924). There is usually a hypodermis of sclerenchyma around the periphery of the costa although this is interrupted where the lamina wing is attached (see fig. 38).

The lamina in transverse section shows little or no differentiation internally although there is frequently a band of sclerenchymatous tissue around the periphery. The cells are rather loosely packed together and there is no organised pallisade tissue as is found in a few ferns e.g. Polybotrya cervina (L.) Kaulf. and many higher plants. The laminae are invariably hypostomatal and in no case have stomata been seen or reported on the adaxial surface.

In recent years considerable importance has been attached to epidermal cell and stomatal types with regard to phylogeny in the ferns. Kondo (1962) published an extensive paper on the stomata of Japanese ferns in which he favoured an ontogenetic approach. The details of his study and his conclusions are very sketchy, but it appears that having studied the development in only one or two species he assumed a similar type of development in all other ferns. He therefore produced a classification dependent upon the number of divisions of the stomatal initial cell before the final division which produces the paired guard cells. Thus he deploys the thelypterids that he studied among four stomatal types (viz. 2A, 2B, 3A, 3B, see

fig. 39), on the basis of what appear to be very subjective criteria, depending upon the particular orientations of the surrounding cells.

Van Cotthem (1970) on the other hand, used a completely topographic approach to his thorough study of stomatal types in the Filicopsida. He placed the majority of the thelypterids that he studied under one type, "polocytic", although in Dictyocline and Goniopteris he also recognised the "anomocytic-type" (see fig. 40). He defined the polocytic type as having "guard cells connected to the distal marginipolar side of the single subsidiary cell; hence the subsidiary cell generally has a U or horseshoe-shape", whilst he defined the anomocytic type as "stoma surrounded by a limited number of cells that are indistinguishable in size, shape or form from those of the remainder of the epidermis". Van Cotthem also used the term "anomomorphic" to describe the irregular shaped epidermal cell.

In addition to making a general study of stomatal types, Van Cotthem (l.c.) studied in considerable detail the constancy of stomatal and epidermal type within individuals of Pteridium aquilinum (L.) Kuhn. from throughout its geographical range. He concludes that although the basic type, structure and orientation of the stomata plus the anomomorphic nature of the epidermal cells remains constant, the undulation of the anticlinal walls and the dimension of the epidermal cells and stomata vary to such an extent that it may be possible to use these characters to distinguish between the various geographical forms of the bracken. If this is so, then a wider survey of the variation within members of a well-defined group, like the thelypterids, may be of use in their taxonomy. Such a survey has unfortunately not been possible in these present studies due to an insufficiency of material.

In this study a survey was made of stomatal types among all those

species which had been studied anatomically (see Appendix II), by investigating slides of cleared pinnae using a phase contrast microscope. All of the species studied (representing all the major sub-groups) were found to possess stomata corresponding most closely to Van Cotthem's (l.c.) polocytic-type. In neither Dictyocline (T.griffithii) nor Goniopteris (T.prolifera) were any anomocytic-type stomata found, as he had reported (l.c. p. 122).

On the other hand the majority of species possessed stomata which could be classified under all of ~~Ogura~~ Kondo's types (see fig. 39). Depending upon the relative positions of the surrounding cells it was possible to interpret them in various ways. In most species the stomata were of mixed types 2A or 3A (see fig. 39) and only in a very few species, e.g. T.obliterata, were only type 2 (A or B) present.

It would therefore appear that, as in the case of the previous anatomical studies, those of the lamina and epidermis show no variable characters upon which a division of the group might be based.

CHAPTER IV

MORPHOLOGY 1. HAIRS, SCALES AND AEROPHORES

INTRODUCTION

The major works on the taxonomy of the thelypterids by Christensen (1913 & 1920), Ching (1963), Ito (1939) and Iwatsuki (1963-5) have been based on morphological characters alone. They have used only those characters which are readily observed by the use of a simple hand-lens either in the field or in the herbarium. As mentioned in Chapter I, such characters are of great importance in identifying and distinguishing between species, by the use of artificial keys, providing that the characters can be shown to be relatively constant. It is this constancy of characters within a species, or group of species, which is very often debatable as many species are described with reference to a single specimen only.

In the vast majority of species the descriptions are drawn up from herbarium specimens without reference to their living state and as it is frequently not the collector himself who draws up the descriptions a number of characters may be entirely overlooked or misconstrued, in the absence of copious field notes made by the collector. Confusion may therefore arise with reference to such characters as deciduous hairs and scales, the age of the plant, the texture of the lamina, the habit of the plant or the presence of mucilage. Furthermore the type specimen is often incomplete or immature leading to confusion over relative sizes of species, this is especially prevalent in large species such as Cyathea.

Due to the extensive use of herbarium specimens for species descriptions it is not possible to demonstrate by experimentation the constancy of many characters which could be affected by the environment. On the other hand when material is available for study care must be taken in reproducing the natural environment thus a specimen of T.decussata which possessed slightly mucilagious croziers in the wild produced copious mucilage over the whole of the expanded frond when grown in a closed humid frame at Kew.

The morphologist must therefore attempt to decide which characters of the plant remain constant independent of external conditions by reference to a large number of specimens, or when this is not possible by drawing upon his own experience.

Unfortunately in the past the vegetative characters that have so frequently been used in producing classifications of the thelypterids are those which observations have shown to be likely to vary under different conditions. Thus in T.obliterata (Sw.) Proctor the "typical" venation is goniopteroid but it may range from this state to almost free-veined, even in the same pinna, (see fig. 68) whilst in other species e.g. T.phegopteris (L.) Slosson the indusium, which is well marked in very young fertile fronds may be lacking at maturity.

The modern taxonomist, however, is not primarily attempting to produce a neat and ordered classification but rather to relate the characters of the plant to its phylogeny. He must therefore search the information provided by the morphologist for any possible evolutionary trends and then attempt to show that any one feature has been more highly evolved than another. In some instances this can be achieved by an examination of the fossil record. Ching (1963), quoted a Tertiary fossil of Polypodites striacus Unger as one of the earliest examples of goniopteroid venation but, although he stated that free

veined species are more ancient, he quoted no examples to support this.

Before phylogenetic relationship can be discussed therefore, as complete a conspectus of morphological data as possible must be obtained from herbarium and living material. This chapter and the following one are devoted to a discussion of those morphological characters which have been used in the past for taxonomic evaluations, such as trichomes, paraphyses, aerophores and venation.

1) HAIRS AND SCALES

One of the most constant features of the thelypteroid ferns is the presence of scales and unicellular acicular hairs on many parts of the plant. These appendages have been discussed with respect to the thelypterids and other genera by many workers, for example Troll(1933), Pirard (1947), Stokey (1960), Iwatsuki (1962c), Wagner Jr. (1964, 1965), Tryon, R. (1965), Tryon A. (1965), Hennipman (1968) and Holttum (1969).

A certain amount of confusion exists in the nomenclature of such appendages (c.f. Wagner 1964 and 1965: Tryon R. 1965 and Tryon A. 1965). It is proposed, for the sake of clarity, to adapt Wagner's 1964 definition and refer to those hairs which occur as an integral part of the sorus, on the sporangial capsule or stalk, and arising directly from the receptacle, as paraphyses, and all other appendages, having their origin elsewhere, as trichomes, whether they be glandular hairs, acicular hairs or scales.

a) Trichomes:

A very thorough study of the trichomes of the thelypterids has been prepared by Iwatsuki (1962c), although he confines his work to the Far Eastern species. Nevertheless, as a result of the uniformity of the group in this respect, my own observations indicate that his comments are just as valid for species occuring elsewhere. He describes four types of trichome: scales, unicellular hairs, multicellular hairs

and capitate hairs. To this list can be added a fifth type, namely multicellular mucilaginous hairs.

i) Unicellular straight hairs (see fig. 45) occur in one form or another on all thelypteroid ferns on both the sporophyte and gametophyte generations and are one of the most stable diagnostic characters of the group as a whole. Straight, unbranched acicular hairs occur in all of the sections of the thelypterids as enumerated by Iwatsuki in 1964. These may vary in size by a large factor, from as long as 0.4 cm in T.phegopteris to 0.02 mm in T.auriculata (J.Sm.) Iwats. (Iwatsuki 1964), although in most species the long hairs do not usually exceed 0.15 cm.

These hairs, whether long or short can occur on all parts of the plant except the roots, i.e. the lamina, costules, costa, rachis, stipe, scales, rhizome and prothallus and their distribution over the plant is often used as a specific diagnostic character, although two points must be borne in mind. Firstly a divergence from the type specimen in the density of hairs on any one plant should be viewed with caution as it is distinctly possible that such changes could be brought about by differences in the environment, hence it may be more useful to accord varietal status to such forms unless additional characters suggest otherwise. Iwatsuki (1962c p. 107-8), nevertheless contends that a difference in density of hairs is not sufficient to award varietal status without additional variations in other characters, he illustrates this by reference to T.japonica (Bak.) Copel. and var. glabrata Ching. Secondly although all thelypterids are thought to possess unicellular hairs in their juvenile stages these can be deciduous and are probably shed in older plants, giving rise to the so-called "glabrous" varieties e.g. T.gongylodes var. glaber Mett., T.esquirolii var glabrata (Christ) K. Iwats. although I have not seen any of these varieties.

ii) Unicellular hooked hairs, unlike straight hairs, are much more restricted in their occurrence although in those species in which they are found they are frequently widespread on most parts of both the gametophyte and sporophyte. They are typically found in Leptogramma (J.Sm.) Iwats., Stegnogramma Blume and Dictyocline (Moore) Iwats., i.e. three of the four sections of the genus Stegnogramma Blume as delimited by Iwatsuki (1964b). They are also a common feature of Abacopteris Fée. Iwatsuki (l.c.) also mentions their presence in Phegopteris (Presl) Ching, although I have been unable to record a single hooked hair on T.decursive-pinnata (Van Hall.) Fée while in T.phegopteris the hairs are very thin and the rare hooked tips that can be found could easily be due to damage. Holttum (1969) does not record their presence in any species of Phegopteris.

Hooked hairs (see fig. 43) occur as the sole form of hairs on the lamina and axes of T.triphylla (Sw.) Iwats., any apparently unhooked hairs on closer examination are found to be hooked hairs whose tips have broken off. In this species genuinely straight-tipped hairs however do occur on scales at the base of the stipe. In other species hooked hairs occur intermingled with straight needle-like hairs on the axes and lamina.

The significance of these hooks at the tips of hairs is obscure and it is difficult to suggest any "advantage" that they might have over straight hairs. Nevertheless their restriction to a few groups which are well-defined by other characters and the constancy of their occurrence within species, does provide a useful key character.

iii) Forked or branched unicellular hairs (see fig. 44) are similarly found in only a comparatively few species of sub-genera Glaphyropteris Presl. and Meniscium Schreb. and sections Goniopteris (Presl) Iwats. and Ampelopteris (Kze.) Iwats. It is difficult to see what their

function, if any, could be although it could be construed that in sufficient numbers they might aid water conservation. In fact they are frequently too sparsely distributed to have very much effect on this and as far as protection is concerned they are rather too small to be effective against all but the most minute of creatures as they are usually only 0.1 to 0.2 mm in height.

All three types of unicellular hairs mentioned above appear to be produced by the division of a single epidermal cell, in a similar manner to that studied in T.griffithii (Moore) Reed by Momose (Vol 17, No. XVIII 1941 p. 154) (see fig. 41). The walls are strengthened by lignin or similar substance, which stains purple in basic fuchsin and hydrochloric acid (see Chapter II for details of procedure). The hairs widen to produce a "foot" at the base which is in contact with a single epidermal cell (see figs. 43 & 44). Where a pneumathode is present along the sides of the stipe and rachis, trichomes are found attached to the epidermal cells overlying the pneumathode as well as on the other parts of the stipe.

iv) Multicellular or multiseptate hairs have only a very limited occurrence, when compared with unicellular hairs. They are found in sub-genus Steiropteris (C.Chr.) Iwats. (e.g. T.decussata), Sphaerostephanos (J.Sm.) Iwats., Macrothelypteris (H.Ito) Ching (e.g. T.setigera) and Haplogramma Iwats. (by which means it is separated from Stegnogramma Blume in Iwatsuki's classification of 1964b).

These hairs are typically long and soft in texture with numerous cross-walls or septae within them (see fig. 46). Iwatsuki (1962c) reports seemingly articulated hairs from T.(Stegnogramma) cyrtomioides (C.Chr.), but these differ from the true articulated hairs of Ctenitis C.Chr. illustrated by Christensen (1913 fig. 3.1.) and he suggests that they have developed from unicellular needle-like hairs by the addition of

septae (Iwatsuki 1962c p. 109 and figs. 19 & 21).

v) Ciliate scales represent a further type of apparently multicellular hair, and are found in Phegopteris Fée emend. Ching (Iwatsuki l.c. p. 105). These form part of a complete series from unicellular straight hairs to scales and are therefore considered as reduced scales (see below p. 68).

vi) Scales, like unicellular hairs, are a constant feature of the thelypterids, and are probably found on all parts of the juvenile axis and crozier, although they do not persist in all species (Iwatsuki l.c.). Nevertheless the majority of species possess scales at maturity, at least on the base of the stipe and covering the growing point of the rhizome. Both the size and the form of the scales can vary greatly between species but in general the scales are proportional in size to the size of the organ bearing them thus large-fronded plants tend to bear large scales and vice-versa.

The smallest scales are the setiferous scales found on all axes of members of Phegopteris Fée. These consist of a variable number of scale cells with numerous long "setae" attached (see fig. 48b), they vary greatly in size, the smallest being approximately 0.2 mm and the largest in excess of 1.0 cm. Typical scales show a range of sizes even on a single stipe but nevertheless show a certain consistency, for instance the scales from the stipe of a specimen of T.resinifera varied between 1.0 mm and 4.0 mm in length and were approximately 0.5 mm in width. The scales from the stipe of a specimen of T.extensa (Bl.) Ching were found to vary between 10 and 5 mm in length and were approximately 1 mm in width at the base, whilst those from a very large specimen of T.ferox (Bl.) Reed ranged between 31 and 15 mm in length and by 2 to 3 mm in width. A few species, e.g. T.patens, are found with very broad papery scales covering their large erect rhizome

and the bases of stipes. In young croziers these completely invest the developing frond and are translucent, becoming opaque as the frond uncurls. Mature scales of this species may be as large as 26 mm long and 15 mm in width (see fig. 47).

The presence or absence of hairs on the surface of scales was thought to be of considerable taxonomic importance by Holttum (1969) and he used this feature as a key character for separating Phegopteris from Pseudophegopteris and Macrothelypteris.

The scales of the thelypterids typically bear acicular, unbranched hairs around their margins (unlike Dryopteris sens. strict. in which the scales possess entire margins). Hairs are also frequently found over one or both of the surfaces of the scales and these are usually identical with those found on the main axes of that species. For example T.serra which has only unicellular straight hairs on the main axes of the plant possesses only straight hairs on its scales. T.tetragona (Sw.) Small has typical branched hairs on both its axes and scales and both T.decussata and T.xylodes possess both multicellular straight hairs and multicellular capitate glandular hairs on their main axes and on the surface of their scales, especially near the point of attachment.

This is not an invariable rule however and T.triphylla, for example, which possesses only hooked hairs on its lamina and axes has some straight hairs on the scales from the stipe. (See Table 3).

A peculiar type of "hair" has been observed on the margins of the scales of T.limbosperma (see fig. 42). These are produced by two marginal cells running together to form small hair-like structures along the margins. These "hairs" do not appear to have a homologue in any other species of thelypterid fern or even in unrelated genera. I have been unable to find any other reference to these hairs and their

SPECIES	HAIRS ON FROND			HAIRS ON RACHIS SCALES		
T.balbisii	Med.	St.	Sim.	Sht.	St.	Sim.
T.thomsonii	Med.	St.	Sim.	Sht.	St.	Sim.
T.resinifera	Lg.	Cv.	Sim.	Sm.		Stel.
T.phegopteris	Lg.	St.	Sim.	Med.	St.	Sim.
T.setigera	Lg.	Cv.	M.sep.	Sht. Lg.	St.	Sim. M.sep.
T.limbosperma	Sht.	St.	Sim.	Sht.		Dble.
T.erubescens	Sht.	St.	Sim.	Sht.	St.	Sim.
T.decussata	Lg.	Cv.	M.sep.	Lg.	Cv.	M.sep.
T.glanduligera	Lg.	Cv.	Sim.	Sht.	St.	Sim.
T.xylodes	Lg.	Cv.	M.sep.	Sht.	St.	Sim.
T.serra	Med.	St.	Sim.	Med.	St.	Sim.
T.megaphylla	Med/Sht.	St.	Sim.	Sht.	St.	Sim.
T.extensa	Lg/Sht.	St.	Sim.	Med.	St.	Sim.
T.bangii	Med.	St.	Sim.	Sht.	St.	Sim.
T.dentata	Med/Sht.	St.	Sim.	Sht.	St.	Sim.
T.truncata	Lg/Sht.	St.	Sim.	Lg.	St.	Sim.
T.triphylla	Med.	Hk.	Sim.	Med.	St.	Sim.
T.prolifera	Med.	St.	Sim.	Sht.	St.	Sim.
T.reticulata	Med.	St.	Sim.	Med.	St.	Sim.
T.griffithii	Med.	St.	Sim.	Sht.	St.	Sim.
T.obliterata	Sht.	St.	Sim.	Sm. Sht.	St.	Stel. Sim.
T.megalodus	Lg. Sm.	St.	Sim. Stel.	Sm.		Stel.
T.paucijuga	Med. Sm.	St.	Sim. Stel.	Med. Sm.	St.	Sim. Stel.
T.asplenioides	Med. Sm.	St.	Sim. Stel.	Sm.		Stel.
T.pyrimidata	Sht.	St.	Sim.	Sm.		Stel.
T.tetragona	Sm.		Stel.	Sm.		Stel.

ABBREVIATIONS:

Lg.	-	Long	Cv.	-	Curved	Sim.	- Simple
Med.	-	Medium	St.	-	Straight	Stel.	- Stellate
Sht.	-	Short	Hk.	-	Hooked	M.sep.	- Multiseptate
Sm.	-	Small				Dble.	- Double

TABLE 3

Summary of hair types on the frond and rachis scales of various species.

presence adds additional support to the placing of T.limbosperma in a distinct group, Oreopteris, by Holub (1969).

The majority of scales are only one cell thick throughout but in some of the larger Macrothelypterids e.g. T.setigera (Bl.) Ching the basal parts of the long lanceolate scales are more than one cell thick.

Scales are always basifixed, never peltate. Although Holttum (1954 p.299) describes T.(Ampelopteris) prolifera (Retz.) Reed as having "a few peltate ciliate scales on the costa beneath", these in fact are basifixed but with a deeply lobed base (see fig. 48a) giving the scales a peltate appearance at a cursory glance.

The function of such scales in general would seem to be protection. The apical growing region of the rhizome is invariably covered by scales and in some of the larger erect species may form a layer up to 1.0 cm thick (e.g. T.patens). By covering the growing point they can protect the apex from both mechanical damage and desiccation by providing a transpiration barrier, as they are themselves dead tissue.

Bower (1910a) and Holttum (1949) regard scales as being more highly evolved than hairs, from which they are thought to have evolved, unicellular hairs giving rise to multiseptate hairs from which evolve basifixed scales; whereas forked hairs, they consider, give rise to peltate scales by "webbing" between the branches. It would therefore seem that, as in many other characters, e.g. the rhizome, the degree of dissection of lamina and the nature of the sorus, the trichomes of the thelypterids show both higher and lesser evolved characters, although these features do not appear to be correlated with each other to produce a unidirectional evolutionary pattern but rather a reticulate one.

vii) Unicellular capitate hairs (see fig. 49) are a widespread feature on all parts of the sporophyte and gametophyte. Despite Iwatsuki's

misleading statements* my own observations (see below p. 48) indicate that in fact they are found on many parts i.e. lamina, axes, indusia, scales, and gametophyte of many species. The misconception may have arisen because their presence is often difficult to detect in herbarium specimens as they tend to be deciduous, but in most species it is easiest to observe them on young unexpanded croziers.

The majority of the thelypterids whose gametophytes were studied by Momose (1937-42) have capitate hairs at least around the margin of their prothalli, the only notable exceptions he found being T.laxa var. typica (Fr. et Sav.) Ching, T.(Leptogramma) totta, (Thunb.) Schelpe and possibly T.(Dictyocline) griffithii although his diagrams are not very clear and the text is in Japanese. Holttum et al. (1970) stated that capitate hairs were absent from the prothalli of T.obliterata, but I have confirmed their presence on the prothalli of this species grown on artificial agar medium in the laboratory. The remaining species from the major sub-genera (Thelypteris, Cyclosorus, Meniscium, Phegopteris and Glaphyropteris) all have capitate hairs. However, this is not a feature which is restricted to the thelypterids, many other genera** also have capitate hairs on the margins of their prothalli. It is interesting to note that all the genera that Momose studied whose prothalli do possess capitate hairs on their margins are in either the Aspidiaceae or the Aspleniaceae of Copeland's classification (1947).

Momose (see fig. 41) has studied the method by which acicular

---

* Iwatsuki (1962c p. 109) states at the beginning of his section on glands "The species having the glandular under surface of fronds are not so rare in the thelypteroid ferns.", whilst in the second paragraph he states "The glandular hairs are rather rare in the species of thelypteroid ferns."

** for example Rumohra, Cyrtomium, Dryopteris, Camptosorus, Athyrium, Polystichum, Currania and Ctenitis.

cells are developed and it is likely that these unicellular capitate hairs are produced in a similar manner, that is from the division of a single epidermal cell.

Capitate hairs consist of a short erect stalk with a broader rounded head (see fig. 49). On young fronds they appear under the microscope to be shining, usually with a yellow or red-brown sheen, whilst on herbarium material they appear as brown or orange in colour.

The function of these hairs is not known although they are frequently referred to as glandular hairs. The only evidence for their glandular nature is provided by the golden or orange sheen which is often visible, especially on young croziers and young fronds and the stickiness of the surface to the touch. Fresh material frequently glistens with moisture, suggesting that the hairs have a secretory function but the chemical nature of this secretion has not been investigated.

Three important factors must be borne in mind when considering the presence or nature of capitate hairs. Firstly, in many species the hairs are more conspicuous on younger fronds, secondly the appearance and colouring of the hairs differs considerably between young fresh material and dried herbarium material e.g. T.patens and thirdly in many cases the dried hairs are deciduous. Hence it is important that if such hairs are to be considered as taxonomic key characters their nature and distribution must be studied in both young and mature living plants as well as in dried herbarium specimens. The vast majority of specific descriptions available give little indication as to whether the plant described was living or dead. In the case of capitate hairs therefore it might be of importance to know whether the original description was drawn up purely on herbarium material or also taking into account field notes and living specimens.

viii) Multicellular mucilage-secreting hairs are also found in the thelypterid ferns. Their presence has been recorded in T.(Cyclosorus) aff. T.truncata (Poir.) Tard. and T.(Pseudocyclosorus) xylodes by Hennipman 1968 and in T.sumatrana by Troll (1933). Kuhn (1889), Goebel (1926) and Guttenberg (1935) have also described glandular hairs from a few thelypterids. Their presence is also now recorded here in T.decussata (see fig. 50).

In all these species the plants inhabit very damp habitats and the mucilage which is apparently secreted by the hairs forms a dense layer over the whole of the crozier and the basal parts of the stipe, such species are found to possess functional aerophores (see below) to aid gaseous exchange.

The actual amount of mucilage varies to a great extent with the environment. For example, within a small area (El Tucuche, Trinidad) where T.decussata was abundant it was found secreting copious amounts of mucilage in a narrow sheltered area of genuine mist forest whereas on the windward side of a slope just below a peak in low scrub, the same species was found to be almost devoid of mucilage. In cultivation at Kew specimens from both areas produced copious mucilage when kept in a warm still humid atmosphere (T.G. Walker pers. comm.).

There are two different forms of multicellular mucilaginous hairs, firstly the unbranched form, found in T.truncata and T.decussata, which is particularly frequent on the stipe scales (see fig. 51) and secondly the much branched, many-headed hairs which are found in T.xylodes and T.decussata, predominately at the base of the stipe (see fig. 50).

Most of the mucilage appears to be produced by the very young circinate frond which may be completely enveloped except for the aerophores which project through (see fig. 60). The mucilage in some

species is carried up onto the frond as it expands from the crozier stage. The function of the mucilage is unknown, as is its chemical composition (Hennipman l.c.) but as these plants are typically found in very damp habitats it is conceivable that it plays some part in their water relations, or possibly has a purely excretory function. This view is supported by the observation that in very still humid conditions the amount of mucilage produced is greatly enhanced as compared with plants growing in less favourable conditions.

It is significant to note here that although certain of the thelypterids secrete copious amounts of mucilage their internal anatomy does not differ from those which do not. This contrasts markedly with adaptations observed in the mucilaginous members of the Marattiaceae, Osmundaceae and Blechnaceae (c.f. Gardiner and Ito 1887, Ito and Gardiner 1887, Brebner 1894, 1895, Lutz 1898 and West 1915) in which complex and highly organised systems of internal canals are found and the mucilage only escapes when the plant is damaged. In the thelypterids on the other hand the mucilage is a purely external phenomenon.

Mucilage secreting hairs of this type are too rare within the thelypterids to enable any evolutionary or taxonomic significance to be placed on their occurrence. They should therefore be regarded as rare adaptations to particular ecological niches which may, incidentally, be of use in the identification of certain species.

b) <u>Paraphyses</u>:

In the thelypterids the distinction between paraphyses and trichomes would appear to be a purely arbitrary one based on the particular location of the structure involved. All forms of "trichome", apart from scales, described above are also found closely associated with the asexual reproductive organs and can therefore be described as "paraphyses".

i) Unicellular hairs occur in intimate association with the sporangia of certain species of Thelypteris, especially the exindusiate members of Stegnogramma, Phegopteris, Cyclogramma and Abacopteris. These hairs arise occasionally from the stalk cells of the sporangium but much more frequently from the capsule cells themselves, although not from the annulus (see fig. 52 to 59). As with the hairs found on the scales (see above) the paraphyses associated with the capsule are typically the same as those on the main axis of the plant.

ii) Multiseptate hairs, on the other hand, are not found arising directly from either the sporangial capsule or the stalk cells. However in certain species e.g. T.decursive-pinnata it has been reported that the indusium is replaced by a dense tuft of multiseptate hairs (Iwatsuki 1964 p.138) which were presumed to be a remnent of a setiferous indusium. Elsewhere (see p.68) I have shown that in the above species at least these hairs arise from a small setiferous scale and are themselves unicellular.

iii) Capitate hairs are also found quite frequently in close association with the sporangia but occur in a variety of forms and positions according to the particular species.

For instance T.novoguineensis (Brause) Reed possesses unicellular capitate hairs attached to the stalk or capsule cells; T.keysseriana (Rosenst.) Reed possesses multicellular capitate hairs arising from the stalk cell and in T.jermyi (Holttum ined.) these are frequently branched. There is frequently more than one glandular hair on a single stalk but the number appears to be limited to three because this is the number of stalk cells. In addition capitate hairs may occur on both the capsule and the stalk of the same sporangium e.g. T.callosa (Bl.) K. Iwats.

The capitate hairs are most conspicuous and probably only

functional on the very young, immature sporangia. As the sporangia mature the hairs cease to function and either shrivel and become inconspicuous or drop off completely, hence in herbarium specimens they are frequently difficult to locate. A rather incidental source is provided by sporangial fixings prepared for cytological studies which are of necessity fixed while the sporangia are immature.

Because of the limited range of fresh material available a truly comprehensive survey of the distribution of capitate hairs on the sporangia of the thelypterids as a whole has not been possible. Nevertheless the studies which have been possible have emphasised those areas which would be worthy of further study:

a) Capitate hairs are frequently found associated with young and developing sporangia of certain species, but their function is unknown.

b) In mature sori, capitate hairs are rarely found because they shrivel as the sporangia matures, and drop off, leaving no "stumps" in evidence.

c) Capitate hairs appear to be more frequently associated with indusiate species, possibly because they play some part in maintaining a damp micro-climate beneath the indusium.

Further studies in these fields may well be able to reveal whether, unlike the trichomes, the paraphyses possess a definite function. Setose sporangia are only found in exindusiate species and would therefore appear to be similar in function to the indusium, in having a protective function. It should be noted however that not all exindusiate species possess setose sporangia, for example those species belonging to the sub-genera Glaphyropteridopsis and Meniscium are exindusiate but have glabrous sporangia. It would appear that in these species some alternative method of protection for the developing

spore mother cells must have been evolved. As mentioned above it seems probable that the capitate glandular cells are secretory and aid in maintaining the turgor of developing spore mother cells.

2) AEROPHORES

An aerophore is defined by J.H. Kenneth (1960) as being "An aerating outgrowth or pneumatophore, found in certain ferns." Strictly speaking, therefore, there are four types of structure in the thelypterids which can be described as aerophores:

i) The pneumathode along the side of the stipe,

ii) the small spine-like outgrowths beneath the pinnules, pinnae and auricles, especially in Glaphyropteris,

iii) the larger outgrowths along the side of the stipe below the lamina e.g. in T.truncata,

iv) the structures (=excrescences, Hennipman 1968) on the stipe of T.xylodes and T.callosa (Bl.) Iwats.

i) Pneumathodes. These are dealt with in Chapter III (p. 28).

ii) The small non-vascular aerophore is found at its greatest extent in Glaphyropteris where small projections are found at the bases of the pinnae and pinnules (see fig. 61a). In the young fronds this consists of loosely packed parenchymatous cells, continuous with the cortex and a layer of epidermal cells completely covering the tip of the projection. In older fronds the epidermal cells appear to rupture and the underlying tissues become somewhat sclerised to produce a structure reminiscent of the lenticels of some higher plants.

These aerophores are frequently found in plants which produce large amounts of mucilage on their young croziers (see above p. 49). They protrude through the mucilage thus producing an alternative route for gaseous exchange since the stomata of the pneumathode and lamina are either non-functional or occluded by mucilage. This was noted by

Bower (1910) and later by Christensen (1913 p. 157) who stated that the "Function of 'aerophores" ... appears to be during the development of the leaf, while the growing parts of this are covered by mucilage. Very likely they are provisions for the aeration of the young parts: in the developed leaf they are shrivelled".

iii) The larger aerophores with a vascular connection are usually found in those species with their lower pinnae reduced to auricles e.g. T.truncata. The aerophores are found on the lower parts of the stipe in similar positions to those taken by the auricles on the upper part of the stipe, and are visible externally as rather hard projections. On sectioning, these are found to possess a vascular trace which divides from the double stipe trace in typical extra-marginal manner (see above p. 33) and passes nearly to the tip of the aerophore; the surrounding tissues are rather loosely packed and aerenchymatous, (see fig. 61b).

Hennipman (l.c.) reports that in young specimens the epidermis completely covers the aerophore and therefore, strictly speaking this is not a hydathode, which by definition is an open pore for the discharge of water to the exterior (Kramer 1945, Esau 1965). However as the xylem tracheids approach very near to the surface and appear to be open-ended, this structure probably does function as a hydathode.

The thelypterids which do possess these structures are usually those which live in shady habitats where there is a saturated atmosphere and a plentiful supply of ground water. Eames and MacDaniels (1947) stated that in such habitats plants often possess hydathodes in order to excrete excess water. In addition, when the lamina has not expanded from the crozier, normal transpiration routes via the stomata are blocked, especially if the pneumathode is also covered with mucilage. Hence the aerophores are functional in the young

crozier and excrete excess water from the developing frond.

As the frond ages the epidermis ruptures at the tip of the projection and the underlying tissues become suberised very rapidly. Even while the frond is still at the crozier stage, the aerophores on the lowest portions of the stipe become suberised. This development probably curtails the useful life of the aerophore which is primarily a structure of the young developing crozier.

iv) The large specialised aerophore has only been reported in two species, T.callosa (Goebel 1926) and T.xylodes, and is found along the lower portions of the stipe in similar positions to those of the above type. Each consists of a small outgrowth approximately 0.5 cm in length with a semi-circular "frill" around the lower side (see fig. 62a). These organs are vascularised and the vascular tissue arises from the stipe bundle in the usual manner. Once the vascular bundle has entered the base of the organ, instead of continuing towards the tip it is deflected downwards and branches irregularly into the semi-circular frill. The xylem branches run to a position immediately below the epidermis but do not break through it to form a true hydathode (see fig. 62b). The extended projection is non-vascular and consists of sclerised aerenchyma similar to that which constitutes the remainder of the ground tissue of the organ. This structure would appear to function as a connection between the vascular system and the surroundings in this highly mucilaginous species.

A point of interest regarding this organ is its basic similarity with a leafy auricle (see fig. 62c) which possesses a similar simple, irregularly branching vascular system. These auricles are also found along the basal portions of the stipe, however they lie in the same plane as the pinnae and are not deflected downwards.

These observations agree in general outline with those of

Hennipman (1968) using the same species although he does not describe their morphology or anatomy in any great detail. He reports that "each xylem branch ends in what is obviously a hydathode".

The differences in morphology and anatomy of the four different types of aerophore suggest that there is a division of physiological function between them. The pneumathode and small spine-like projections of Glaphyropteris have no vascular connection and probably only permit the free passage of air between the surroundings and the cortex. The remaining two types however possess a vascular supply and therefore offer a direct connection between the vascular tissue and the exterior. The excrescence of T.xylodes possesses a branched vascular trace which is very similar in form to that found in the leafy auricles of this and other species. It would therefore appear to represent a very greatly reduced pinna. This theory is further enhanced by the fact that where there is a leafy member present, there is no vascular connection with any projection beneath the pinna, (but on the other hand, no projection has been observed below a vascularised aerophore) and also where a vascularised aerophore is present no leafy member has been observed in close association.

CHAPTER V

MORPHOLOGY 2. VENATION, FROND FORM AND SORI

1) VENATION

Bower (Vol. I 1923 p. 96) stated that the "detailed study (of venation) cannot be used as a consistent or trustworthy basis for the phyletic seriation of the Filicales at large ..... (in many isolated genera,) closed venation has originated repeatedly in distinct stocks, it is in fact a widely homoplastic character, determined in great measure by physiological necessity or convenience."

During the first half of this century great emphasis was placed on the importance of venation in the taxonomy of the thelypterids as it provided a convenient key character which possesses obvious implications with regard to phylogenetic relationships.

Christensen (1913, 1919) used venation, together with the presence or absence of a sinus membrane and aerophores, in deliminating his major groups. Thus he separated Cyclosorus, Goniopteris and Meniscium (having anastomosing veins of various types) from Lastrea and Glaphyropteris (with free veins), Steiropteris occuping a somewhat intermediate position.

Ito (1939), Copeland (1947) and Ching (1963) also followed Christensen and used venation as a major criterion in their classifications. In 1947, Holttum recognised the basic relationship that exists between Thelypteris and Cyclosorus but he decided to maintain this rather artificial division for reasons of convenience. In 1948 he again discussed the problem with regard to the anastomosis of veins and pointed out the differences between Athyrium-type and

goniopteroid-type of venation. He considered that the presence and degree of anastomosis of veins was dependent upon the nature of the pinnae and that this produced an unnatural division of the group. He concluded that anastomosis of veins had occurred along several different evolutionary lines, without discussing further what these lines were. He therefore suggested that natural divisions of the thelypterids might be based primarily on characters other than venation and suggested that the aerophore might provide a useful subject for study in this connection.

In 1960 Holttum once again expressed the need to re-define the groups within the thelypterids, and pointed to cytological evidence which indicates that certain species with free veins are more closely related to Cyclosorus than they are to other free-veined species. Moreover he again emphasised the need to use other characters to establish a more natural classification, but was unable to put forward any alternative to venation for this purpose.

Iwatsuki (1962c) made a brief survey of the venation in the thelypterids in which he criticised recent classifications which were dependent entirely upon this character. In 1963-5 he published his papers on the taxonomy of the thelypterids in which he defined his genera on soral characters whilst differences in venation were merely used to de-limit sub-genera and sections. Nevertheless he discussed the differences in the nature of the anastomoses of veins in Meniscium and Dictyocline and suggested that these two groups were not monophyletic in origin (see below). Iwatsuki also discussed the differences between the type of venation found in Dictyocline on the one hand and in Tectaria and the Polypodiaceae, on the other. He pointed out that the major difference is the potentiality of Dictyocline to produce sori along its veins from all parts of the lamina, whereas

Tectaria and members of the Polypodiaceae produce discrete sori.

In 1969, Holttum, investigating three groups containing only free-veined members (Phegopteris, Pseudophegopteris and Macrothelypteris) emphasised the importance of scales and hairs but he has still to publish his studies on those groups containing species with anastomosing veins.

The present situation is therefore that, whilst it is thought that the degree of anastomosis of the venation might indicate some phyletic lines, this must not be considered in isolation but in conjunction with other characters as there is evidence to suggest a polyphyletic origin of those groups having anastomosing veins.

One of the reasons for not considering venation in isolation is that whilst at one end of the scale there are species which are invariably free-veined and at the other end there are those which have pleocnemioid venation there are many species groups which occupy an intermediate position. These show a considerable variation in the degree of anastomosis whilst at the same time being relatively constant in other characters. This can be taken to extremes in certain species e.g. T.extensa and T.obliterata which can show considerable variability in the degree of anastomosis even within a single pinna (see fig. 68).

It is therefore proposed to describe the variation that does occur in the venation of the thelypterids and to use this to elucidate some possible phylogenetic relationships.

a) Free venation:

Species in which no anastomosis of veins occurs are found in Phegopteris, Cyclogramma, Thelypteris, Glaphyropteris, Glaphyropteridopsis, Steiropteris and Leptogramma (Iwatsuki 1964b) (see figs. 63 & 64).

The veinlets are either unbranched or branched, dependent upon the species, although some species possess branched veinlets in large

segments and unbranched ones in smaller segments e.g. T.(Stegnogramma) pozoi (Lagasca) Morton and T.gracilescens (Bl.) Ching. Sori are always produced on the smallest branches of the veins (see below p. 66). In certain sub-genera the veinlets reach to the margin itself e.g. Phegopteris although in others they stop some way short of this e.g. Pseudophegopteris (Lastrella) Iwatsuki (l.c.) considers this character as sufficiently constant to circumscribe these species groups.

In those species which have both free venation and a sinus membrane (see below) the basal veinlets run to the membrane within the lamina e.g. sub-genus Cyclogramma and the T.erubescens (Wall.) Ching group (Iwatsuki l.c.)

b) Goniopteroid or Meniscioid Venation:

It is now generally held that the only major difference between these two types of venation is the degree of fusion of the pinna segments. The veinlets either join at the sinus itself or unite within the lamina and produce an excurrent veinlet which behaves in a variety of ways dependent upon the presence or absence of a sinus membrane.

Where there is no sinus membrane the excurrent veinlet may:

i) terminate within the leaf tissue e.g. T.triphylla,

ii) join with others and run to the sinus

e.g. T.asterothrix (Fée) Proctor (see fig. 66), or

iii) run directly to the sinus e.g. T.paucijuga (see fig. 65).

Where there is a sinus membrane the excurrent veinlet may:

i) terminate at its base with the veinlets above running to the membrane e.g. T.ferox (see fig. 67),

ii) terminate at its base with the veinlets above running to the margin above e.g. T.gongylodes, or

iii) run alongside it to the sinus and then form a commissural vein around the periphery of the pinna e.g. T.obliterata (see fig. 68).

The most noteable feature of these species is the regularity in the manner of these vein fusions, although the number of fusions may vary from plant to plant or even within a specimen or a single frond or pinna (see fig. 68).

This type of fusion is only found elsewhere in ferns in some species of Athyrium, e.g. A.esculentum (Retz.) Copel., which is basically very similar to some thelypteroid species. In these species, although the basal veinlets fuse within the lamina, the excurrent veinlet stops short of the sinus, divides and each branch then runs to the edge of the lamina above the sinus (Holttum 1954a p. 556). A very similar form of venation is found in certain goniopteroid species e.g. T.obliterata where the excurrent veinlet runs to the base of the sinus membrane and runs alongside this to the edge of the lamina at or just above the sinus. In this species at least, there is then a commissural veinlet running around the periphery of the lamina. Hence there is a basic difference between this type of venation and that of athyrioid species and true goniopteroid venation is found in the thelypterids alone.

During the early stages of development of these species, free venation is found in the smallest pinnae, but as the size of the lamina increases, so does the complexity of the anastomosis, until it reaches its full development in fully expanded fronds. This increase in complexity with development, within a single specimen, forms the basis of the theory that goniopteroid venation is more highly evolved than free venation.

Sori are typically found between the main veins and the point of anastomosis of their laterals (see for example fig. 65) although in some exindusiate species the sorus may elongate along the veinlets and join with that of the neighbouring veinlet e.g. T.(Abacopteris) salicifolia (Wall.) Reed (see fig. 69).

c) Pleocnemioid Venation:

Two forms of pleocnemioid venation are found in the thelypterids. The first is formed where anastomosis occurs in species with branched veinlets, each veinlet branch unites with the corresponding branch from the adjacent segment and the abcostal fusion sends an excurrent veinlet to the next fusion above (see fig. 71). Three lines of aereoles are thus formed between each vein, as opposed to two in normal goniopteroid-types. This type is found only in Haplodictyum (Presl) Iwats. and differs markedly from the form of pleocnemioid venation found in Dictyocline (see below) by virtue of its regularity and the discrete, round non-confluent sori. Although the development of the former type of venation has not been studied in the young stages, it would seem likely that it follows the expected path, via simple free veins to branched free veins and finally to the adult form.

In dictyoclinioid venation the pattern of areoles is also built up in a similar manner to that in Haplodictyum although this may not be as obvious. The pattern is based upon branching veinlets but the branching and re-anastomosis continues to a greater degree. In the widest segments there may therefore be five or more rows of areoles and in addition an increase in complexity towards the edge of the lamina (see fig. 70).

The developmental stages in the venation of Dictyocline however, have been studied by Iwatsuki (l.c.) and he concluded that the venation "developed without any natural rule. The areoles are formed on the fronds at an early developmental stage when the laminar surfaces are wide enough to allow the existence of the areoles". However, in these present studies it has been noted that there is in fact some degree of natural rule found in these developmental stages. In very small fronds, in the narrowest segments, goniopteroid or meniscioid venation is found

(see fig. 70). As the frond widens so the venation becomes haplodictyoid and finally reaches its full development in older and wider fronds. Thus there would seem to be a logical sequence relating the haplodictyoid type to the dictyoclinioid type.

It is something of a misnomer to refer to these types of venation as pleocnemioid as there is a fundamental difference in structure to that found in Pleocnemia, as illustrated by P.hemiteliiformis (Racib.) Holtt., where anastomoses and areoles are formed in the free segments as well as between the costa and the sinus (see fig. 72). In the thelypterids on the other hand anastomoses only occur below the sinus. The true pleocnemioid type would appear to be more similar to that of Woodwardia or Tectaria where anastomoses occur throughout the pinnae.

The main differences between Haplodictyum and Dictyocline lie not only in the venation patterns described above but also in the fact that in Haplodictyum the sori are discrete, round and indusiate, whilst in Dictyocline they are confluent and linear, the sporangia being formed on veins in all parts of the lamina.

d) Sinus Membrane:

A membrane, often described as "cartilaginous", due to its forming a hardened ridge especially in herbarium specimens, is found running between the sinus and the costa. Species belonging to Cyclosorus, Stegnogramma, Thelypteris, Cyclogramma and Steiropteris frequently show this character.

The sinus membrane is interesting in its structure because it appears to represent an intermediate stage in the expansion of the lamina from a dissected to an entire condition. It shows laminar characters in being continuous with the tissue on either side and in bearing typical hairs but differs by being non-photosynthetic, lacking stomata and being slightly thinner than the adjacent tissues of the

true lamina. In addition it is not traversed by veinlets (see figs. 67-69).

Unfortunately there is no evidence regarding developmental stages of species possessing sinus membranes, but it is probable that the membrane is not present in the youngest leaflets, which would suggest that it might represent a later evolutionary development, and an intermediate stage in the expansion of the lamina.

2) FROND FORM

As has been stated above, the elaboration of the anastomosis of veins within the pinna appears to run parallel with the degree of dissection of the frond. Species with simple venation always have a very deeply cleft sinus, and as the number of anastomoses increases so the depth of the sinus is reduced until in meniscioid or dictyoclinioid species the lamina is slightly toothed e.g. T.poiteana (Bory) Proctor (see fig. 32) or entire e.g. T.salicifolia (see fig. 30). The only slight deviation from this rule is found in those species which possess a sinus membrane where the veins anastomose as if the membrane were the sinus gap itself and do not form any connections across it, e.g. T.megalodus (Sch.) Proctor. Therefore if the sinus membrane is not considered as an integral part of the lamina, the sinus proper is at the adcostal end of the membrane and the veins anastomose accordingly. It is probable that the sinus membrane represents an intermediate evolutionary stage between pinnate and entire pinnae.

A problem therefore arises that there are two lines of development apparently taking place simultaneously, either of which might conceivably have affected the other, i.e. an increase in anastomosis might bring about the shortening of the sinus or an increase in laminar surface might promote the anastomosis of veins. It is the sinus membrane which might provide the answer to this for if it were vein

anastomoses which caused the expansion of the lamina we should expect anastomoses to occur across the sinus membrane, but in no case is this found. On the other hand if it is the expansion of the lamina which permits extra anastomoses then observed facts are more readily explained. For instance, during the development of a pinnate frond or near the tip of an entire pinna, anastomoses only occur when the lamina has achieved a certain width and free veins are never found in species with entire pinnae, except in its earliest development or narrowest segments.

We can probably therefore consider those groups of species with entire pinnae, e.g. Meniscium, or in some examples bipinnatifid fronds, e.g. Cyclosorus, as being more highly evolved than the species with typically bipinnate fronds, e.g. Phegopteris and Thelypteris sens. strict. or even tripinnate fronds, e.g. Macrothelypteris. If this is so then it would be expected that those species with entire fronds and a greater degree of anastomosis of veins would exhibit some other more highly evolved characters, this is to some extent borne out by cytological evidence, spore morphology and soral characters (see below).

Associated with this increase in the degree of anastomosis there is often a corresponding decrease in the overall size of the plant. As a general rule, the larger species are found in groups such as Macrothelypteris which have lower chromosome numbers and non-anastomosing veins (there are exceptions to this e.g. T.extensa and T.patens, both in Cyclosorus with n=36). The converse is more usually true, i.e. species belonging to Meniscium e.g. T.prolifera and Dictyocline e.g. T.griffithii, are small in size. Large numbers of field measurements would need to be carried out on a wide range of species to verify this. Nevertheless this generalisation might indicate the direction of evolution within the group as a whole.

3) SORI

As in other morphological characters the sori of the thelypterids exhibit a great range of form:

i) Round with persistent indusium e.g. T.megaphylla

ii) Round with deciduous indusium e.g. T.extensa

iii) Round with "tufts of hairs" at centre e.g. T.decursive-pinnata

iv) Round exindusiate e.g. T.megalodus

v) Elongate along vein, discrete, exindusiate e.g. T.pozoi

vi) Elongate, confluent with that from adjacent vein e.g. T.salicifolia

vii) Linear along all veins e.g. T.(Dictyocline) griffithii.

The form of the sorus is, to a certain extent, dependent upon venation, for instance confluent sori can only occur in species in which anastomoses occurs, although round sori could be formed regardless of anastomosis.

Bower (Vol. I 1923) put forward a number of views regarding the nature of the sorus in the ferns. He states that where the individuality of the sorus is established, "it is liable to be lost in many (evolutionary) sequences." This can be brought about either by fusions or by fission, both leading to the obliteration of the individuality of the sorus, with the result that the sporangia spreads over the whole surface of the sporophyll (=Acrostichoid condition).

Secondly he believed that in the primitive condition, protection is afforded to the developing sporangia by menas such as the curling of the leaf edge but more recently a specialised protective organ, the indusium, has developed. He points out however that many of the more advanced types of fern are without indusia at all and indicates that in some groups the gradual abortion of the indusium can be followed,

whilst at the same time the nature of the sorus advances towards Acrostichoid conditions. In these ferns "hairs grow up together with massed sporangia, this helping to protect them while young."

He puts forward three possible functions of the indusium or paraphyses. Firstly, protection from alien creatures seeking shelter amongst the sporangia, secondly the paraphyses might have a cushioning effect between neighbouring sporangia whilst they are growing or thirdly to help maintain a moist atmosphere around the sporangia. Neither of the first two appear very plausible, for if a creature was small enough to be able to shelter among the sporangia the paraphyses would not prove a great barrier and the second suggestion would not explain why only exindusiate species possess acicular hairs on their sporangia. The third suggestion is by far the most reasonable, for the developing sporangia contain actively dividing spore mother cells in close proximity to their walls and would therefore readily be affected by sudden changes in temperature or humidity. The paraphyses or indusium, often with the aid of glandular hairs, help maintain a stable state around the sporangia during meiosis. This would explain several observed facts, namely that the capitate glandular hairs shrivel in mature sporangia, that indusia are often deciduous or at least become inconspicuous in mature sporangia and that acicular hairs are not normally present on the sporangia of indusiate species.

The curling inwards of the edges of the segments of fertile pinnae forms an additional protection in certain species e.g. T.palustris, Schott. but this does not necessarily make the indusium obsolete for in this species at least, there is also an indusium present. Hence the curling of the edges could be a remnant of the pre-indusial state or merely a peculiar adaptation found in isolated species in response to a specific requirement. However, no detailed

survey on those species which exhibit this phenomenon has been carried out. This might prove of interest, especially with due regard to edaphic and climatic conditions.

a) Indusium:

The indusium of the thelypterids appears to have evolved directly from a basifixed setiferous scale, rather than by the fusion of a tuft of hairs at the centre of the sorus.

Evidence for this is provided by members of Phegopteris in which setiferous or rudimentary scales are present on most axes of the plant (see above p. 43). In T.phegopteris (=Phegopteris connectilis (Michx.) Watt.) these scales are present over the surface of the plant but the sori are exindusiate. In T.decursive-pinnata however there is present at the centre of the sorus, a structure which has been variously regarded and described by numerous authors. John Smith first described it as an indusium (Holttum 1951 p. 11) when he formulated the type-description of Lastrea decurrens J.Sm. in 1846 (this is now considered as a synomyn for T.decursive-pinnata). Kunze on the other hand considered that there was a tuft of hairs arising from a small scale or imperfect involucre (Iwatsuki 1965). Ching (1936b) considered the sori as exindusiate but having "a stalked and branched hair at the centre". Ito (1939) and Tagawa (1959) however described the species as having a small deciduous indusium but Iwatsuki (l.c.) believed that there is a small tuft of hairs "at the posterior base of a little lengthened receptacles", these hairs, he said, are "unicellular and have no direct connection with their neighbourings".

On treating a pinna of T.decursive-pinnata from Japan* with potassium hydroxide and staining in basic fuchsin and concentrated

---

* Kindly provided by Prof. R.E. Holttum of Kew.

hydrochloric acid the lignified portion of the pinna take up the magenta coloured stain. The cell walls of trichomes are thickened by lignin and are therefore stained. By this treatment the nature of the appendage at the centre of the sorus could be clearly defined after careful removal of a few of the clustered sporangia. In the pinna investigated, a setiferous scale (see fig. 48b) was found in each sorus, identical with those found on the other axes of the plant. Unfortunately it has not been possible to investigate the nature of this appendage from any other specimens.

Two alternative factors might be responsible for the confusion and possible mis-identification of this appendage mentioned above:

1) This is the structure variously described by many authors and the divergence of opinion as to its form stems from its true nature being obscured by the fully developed sporangia. The different appearances might be due to differences in the maturity of the specimens described.

2) Alternatively the actual size of this scale may vary from specimen to specimen so that in fact the authors mentioned above did describe what they had seen in particular species or possibly in those species from a particular area.

Which ever of these alternatives is in fact the case, the setiferous scale studied in this investigation would appear to represent an intermediate stage in either the evolution or the abortion of the indusium. It seems to be more likely that it is a precusor of the indusium and would explain several of its structural peculiarities. If the indusium were evolved from the "webbing" of a tuft of hairs then a peltate indusium would be expected but the development from a scale would explain its uniform shape (c.f. the deeply lobed scale of T.prolifera , see fig. 48a). Also the presence of hairs on the edges

and surface of both scales and indusia could be explained by this theory.

b) Sporangia:

The thelypterids possess a common form of sporangia with a vertical annulus running from near the point of attachment of the stalk to the stomium. The stalk always consists of three cells in cross-section and is typically two or three cells in length. The number of sporangia in a sorus is highly variable, depending primarily upon the size of the frond and its position upon it. In those species with exindusiate, linear or confluent sori the individuality of the sorus has been lost and hence the size of a sorus cannot be calculated. The spore production is typically 64 per sporangium, i.e. there are sixteen spore mother cells.

Reed (1952-3) discussed the significance of differences in the number of indurated cells in the annulus of various thelypterid species from North America (see Table 4a). He discovered that in T.hexagonoptera there was a marked difference in the numbers of annular cells between plants from Northern (10-13 cells) and Southern (13-16 cells) areas. In this instance there were also other morphological differences which might lead to giving varietal status to the two types. In T.palustris he also noted a discrepancy in the numbers of annular cells between two established varieties (var. pubescens and var. haleana). He also measured the spores and found a difference in spore size between the varieties which he considered might be responsible for an increase in the size of the sporangia and hence an increase in the number of annular cells. Unfortunately he did not study the cytology of the varieties in question and it seems probable that the specimens he studied were of different ploidies having a corresponding difference in spore size (see also Blasdell 1963 and Bir 1966-7b). Apart from

SPECIES	NUMBER OF ANNULAR CELLS/SPORANGIUM
T.hexagonoptera - Northern Plant	10-13
Southern Plant	13-16
T.palustris var. pubescens	19-23
T.palustris var. haleana	13-17
T.noveboracensis	13-15
T.phegopteris	13 (rarely 14)
T.simulata	15-16
T.resinifera	13
T.patens	15-17 (rarely 14)
T.augescens var. puberula	15-17 (rarely 14)
T.normalis (=T.kunthii)	15-17 (rarely 14)
T.dentata	15-17 (rarely 14)
T.limbosperma	13-14
T.reptans	17-19
T.sub-tetragona	14
T.nevadensis	14-16

- - - - -

Gymnocarpium robertianum	11-12
G.disjuncta	10-11
G.lineana (=Dryopteris) f. glandulosum	11-13

TABLE 4a

To show the numbers of annular cells per sporangium in various North American species (after Reed 1952-3).

* * * * *

SPECIES	NUMBER OF ANNULAR CELLS/SPORANGIUM
T.serra	13-16
T.dentata	12-15
T.brachyodus	11-15
T.serrata	12-17
T.reticulata	13-18
T.resinifera	11-14 (rarely 16)

(50 sporangia from the same specimen were studied)

TABLE 4b

To show the numbers of annular cells per sporangium in various West Indian species.

these results his records indicate that whilst in some species there is a remarkable uniformity in the number of annular cells, in others there is considerable variety.

My own investigation shows that this variation in numbers of annular cells is a general phenomenon throughout the group (see Table 4b) although the particular range does vary from species to species. For example in T.brachyodus (Kunze) Ching the number varied between 11 and 15, whilst in T.reticulata (L.) Proctor it varied between 13 and 18.

It is felt that in the absence of cytological or geographical evidence too much emphasis should not be placed on this character. Reed (l.c.) recorded only 13 annular cells from T.resinifera whereas my own count of this same species revealed a variation between 11 and 14 (rarely, as many as 16) although a majority of sporangia (58%) did possess 13.

On the other hand the noteable divergence in the reports for T.dentata by Reed (15-17, rarely 14) and myself (12-15 with 68% having 14) indicate that there might be some differences between the specimens studied. Caution must be exercised however, before placing too much weight on this single character in the absence of such basic information as the effects that edaphic and climatic factors might have on the physical size of the frond, sori and the individual sporangia.

Apart from the spores whose morphology is considered below (Chapter VII) the only morphological character of the sporangia that appears worthy of study is the presence or absence of glandular and acicular hairs and their numbers and distribution on the capsule and stalk. This has been considered above (page 51) under the section referring to hairs and scales.

CHAPTER VI

CYTOLOGY

The use of chromosome numbers in the study of the taxonomy of ferns is comparatively recent, having been initiated in an extremely coherent way by Manton (1950). In the past twenty years many workers have followed Manton's example and have counted and recorded the chromosome numbers of species representing the majority of fern genera. These have been studied from many parts of the world, although there are certain notable deficiencies such as South America and Australia where much more work is needed in this field. Typically these studies have been either on a strict geographical basis or as a passing mention in papers relating primarily to anatomy or taxonomy.

As a result, chromosome counts have been made on more than one hundred species of the thelypterids by more than forty separate workers (a summary of these can be found in Appendix I). The reliability of these counts and the identification of the material used has in most cases not been checked, hence a certain degree of mis-identification may be expected from the less experienced workers. Despite this there are few discrepancies between counts for the same species carried out by different workers. In addition there is a good correlation between counts for specimens formerly identified as distinct but more recently assigned to the same species. (For example those counts given under T.pyrrhorhachis were originally given under T.brunnea and Pseudophegopteris pyrrhorhachis but these have been shown by Holttum (1969) to be but variants of the same species.) It has therefore been necessary to accept the author's identification since the scope of this

investigation would not permit otherwise. On the other hand the count of n=36 for T.palustris by Mitui (1968) from Japan is anomalous; this could be due to a mis-identification, a mis-count or alternatively to a difference in the species in Japan. In the absence of further details it is advisable to ignore this result.

Many of these results have been catalogued by Chiarugi (1960) and Fabbri (1963, 1965) and these papers have been a useful guide in correlating the data. Their information as it stands, however, is rather confusing since they varied the system of classification used, they did not include the countries of origin, which are particularly useful in many cases, and the latest supplement was published in 1965. Appendix I is an attempt to illustrate the range of chromosome counts in the thelypterids, placing prime importance on the base number of chromosomes. These chromosome numbers have also been correlated with other characters, such as venation and spore morphology and the lists have been further divided to illustrate these points more fully.

In compiling the Appendix, the level of ploidy has been disregarded as there is little evidence at the present time to suggest any morphological differences between specimens with differing levels of ploidy in the thelypterids. In some instances the distribution of diploids and tetraploids may be of significance, for instance in the determination of migratory pathways, but except in a few isolated cases these considerations are outside the scope of this study. The base number of chromosomes has therefore been considered as being of prime importance. Where identical base numbers are found it is reasonable to assume and search for, some similarities between the species concerned. Where different numbers are found then investigations have been carried out to determine whether, as might be expected, this is reflected in the morphology of the species concerned. Caution must

be exercised, however, in assuming that identity of chromosome number will necessarily be reflected in a similarity in morphology. Among those species with a base number of 31 there are at least two groups (Pseudophegopteris and Macrothelypteris) which are readily distinguishable by a number of different morphological characters which nevertheless remain constant within each group. In addition there is a small group of species which have also been counted as having 31 chromosome pairs but which cannot be ascribed to either of the two groups.

Manton (l.c.) differentiated between Dryopteris and Thelypteris by the difference in their chromosome complement, 41 in Dryopteris and 30-36 in Thelypteris, (there are numerous further differences as enumerated by Wagner, 1963). More recently many species have been cytologically studied and it is now probable, in the light of the morphological and anatomical studies carried out (see above, Chapters III, IV and V) that the thelypterids are a distinctive group in which the species form an aneuploid series, with base numbers ranging between 27 and 36 (with the exception of 33). The table below indicates the number of species with exact base numbers that have so far been reported:

TABLE 5

Base No. of Chromosomes	No. of species counted			
	Total	Free Veined	Some Veins Anastomosing	All Veins Anastomosing
27	2	2	-	-
28	1	1	-	-
29	8	8	-	-
30	3	3	-	-
31	16	16	-	-
32	2	2	-	-
33	-	-	-	-
34	3	3	-	-
35	6	5	1	-
36	75	16	55	4
Total	116	56	56	4

For these figures to bear any significance it must be assumed that the choice of material has been purely random. This would seem to be a reasonable assumption because of the large number of sources from which this data was obtained.

In Chapter V it was concluded that the available evidence supported the theory that the more anastomosing veins, as opposed to free veins, a species possessed the more highly evolved and therefore the more recent in origin it was. If this is the case, and there seems little evidence to the contrary, then in general those species with the larger chromosome complement are more recent than those with the lower numbers.

Of the species counted approximately 98% of those with anastomosing veins have a base number of 36 (the sole exception is T.singalanensis (Bak.) Ching). Among the free veined species, approximately 70% have a base number less than 36. Out of the total 116 species counted approximately 65% have a base number of 36, the remainder having less. All those species with completely anastomosing (meniscioid or dictyoclinioid) veins have a base number of 36.

If we therefore assume that anastomosis has been facilitated by the expansion of the lamina (see Chapter V) then it appears that as the lamina has expanded the base number of chromosomes has increased. Branched non-anastomosing veins are found in Macrothelypteris and Phegopteris though not Amauropelta and are very uncommon in species with a base number of 36. It therefore seems likely that the primitive thelypterids possessed between 30 and 32 pairs of chromosomes and the aneuploid series has developed from this number by the addition or loss of pairs of chromosomes. For some reason this series has been blocked at 36 pairs and any further divergence in morphology (such as the loss of indusium, loss of the individuality of the sorus, increase

in anastomosis and possibly a decrease in overall size) has not been reflected in the chromosome complement.

As only one example has been counted where anastomosis occurs and the base number is not 36 then the criterion of base number is of no importance when attempts are made to sub-divide these species. Similarly it would be wrong to lay too much emphasis on the fact that all of those species with meniscioid or dictyoclinioid venation have a base number of 36, since the number of such species which have been counted is very small. It is of more significance to note that those species which Iwatsuki (1965) placed in Stegnogramma Blume, because of their linear confluent, exindusiate sori, possess a base number of 36 regardless of the type of venation. This suggests that there may be further characters to distinguish these species (see below under spore morphology p. 98) which may therefore represent a separate evolutionary line. Along this line, although the individuality of the sorus has been lost in all cases, anastomosis occurs to differing degrees whilst the base number remains constant at 36. These species therefore represent the stages in the series of events which it seems likely that the thelypterids in general have undergone. The loss of the individuality of the sorus and peculiar spore morphology has separated them from the general mass of species based on 36 at an early stage. This makes them a readily distinguishable group and an interesting subject for further study.

In those species having a base number of fewer than 36 pairs of chromosomes there is a more significant correlation between morphology and chromosome number, hence there is a greater agreement with those classification systems based exclusively on morphology.

Iwatsuki (1963-5) included a large group of species in the sections Thelypteris and Metathelypteris of his sub-genus Thelypteris with base

numbers ranging from 29 to 36. He took little notice of chromosome number, thus in section Thelypteris there are found T.palustris (n=35), T.oreopteris (=T.limbosperma (All.) Fuchs) (n=34), T.glanduligera (n=36) and T.japonica (n=31) while in section Metathelypteris, T.gracilescens (n=36) and T.uraiensis (Ros.) Ching (n=35) are found in the same group, and T.laxa (n=36) and T.flaccida (Bl.) Ching (n=35) together in another. The final group of this section does however correspond to the genus Macrothelypteris of Holttum's treatment with n=31 in all those for which counts are available.

In Iwatsuki's sub-genus Thelypteris are found species which have been ascribed to the sub-genus Lastrea Bory by Christensen (1913) with T.limbosperma as the type species. Holub (1969) has proposed this species as the type of a separate genus - Oreopteris. This group also includes the small but uniform group of species from the West Indies having a base number of 29 (Walker 1963-4). All of these species have been ascribed to Lastrea by Christensen and possess other features in common (see below p. 111) which set them aside from the other members of this group.

I do not propose to produce an additional re-grouping of these species but emphasise that a system in which there is no uniformity of base numbers of chromosomes even in the groups of a section within a sub-genus, should be viewed with some caution. A search must be made for alternative characters which might produce a correlation with the cytological data available.

Setting aside, for the present, the problems of classification and nomenclature there are several groups of species that have been clearly defined on morphological grounds which exhibit a uniformity of chromosome base number.

Phegopteris Fée emend. Ching is remarkable in this context, all

three species possessing a base number of 30 a fact which Holttum (l.c.) indicates in defence of the inclusion of T.decursive-pinnata in this group.

Pseudophegopteris Ching, also circumscribed by Holttum (l.c.), comprises the remaining members of Iwatsuki's (l.c.) sub-genus Phegopteris, after the removal of the species in Holttum's genus Phegopteris. Within this group the nine species which have been counted, out of a total of twenty recognised by Holttum, have a base number of 31. This factor alone certainly supports Iwatsuki's view of the limits of these two genera.

A further group of species having a base number of 31, is recognised by Holttum as the genus Macrothelypteris, but by Iwatsuki as a group of the section Macrothelypteris. Holttum has circumscribed the group on morphological grounds re-inforced by cytological data. (It should be noted that only two out of the nine species have been counted).

While these two groups are recognisable on morphological grounds there is a further group of five species which have a base number of 31. Of these T.resinifera shows affinities with the group having a base number of 29 and the remainder have, at present, a rather indefinite position, though Iwatsuki (l.c.) places them together in the same group of section Thelypteris.

The species with a base number of 32 to 35 are too few for further comment although it is significant that such species do exist and form a "bridge" between the two major groups (n=29-31 and n=36). As stated above, with the exception of T.singalanensis, these species are all free veined.

Hence it can be seen that whilst in certain instances cytological data can be taken as conclusive evidence for taxonomic groupings it is

by no means absolute. Nevertheless if it is accepted that the thelypterids do form an aneuploid series then obviously cytology must play a major part in any consideration of phylogeny within the group.

During the course of this investigation a small number of species were examined cytologically the results are given in the table below and the vouchers are in my possession.

TABLE 6

Species	No.	n	Ploidy	Origin
T.asplenioides	T4601	72	4x	Jamaica
T.asplenioides	s.n.	72	4x	Jamaica
T.megalodus	T10557	36	2x	Trinidad
T.oligocarpa	T10674	29	2x	Trinidad
T.oligocarpa	T10688	c29	2x	Trinidad
T.tetragona	T11029	70-2	4x	Trinidad
T.torresiana	s.n.	c90	6x	Trinidad
T.sp. indet.	T10312	70-2	4x	Trinidad
T.sp. indet.	T10555	35-6	2x	Trinidad
T.dentata	Jermy 2158	35-6	2x	Trinidad
T.dentata	Page 2198	70-2	4x	Mauritius
T.archboldii	T7743	35-6	2x	New Guinea
T.glabriuscula	T7744	36	2x	New Guinea
T.sumatrana	T8367	70-2	4x	New Guinea
T.cavitensis	T8431	36	2x	New Guinea
T.sp. indet.	T8529	36	2x	New Guinea
T.sp. indet.	T8880	70±2	4x	New Guinea

T.megalodus has been counted previously as 36 on Jamaica (Walker 1964-5), this is a new count for Trinidad.

T.oligocarpa (Maxon) Proctor has been previously counted as 29 from Jamaica (Walker l.c.), this is a new count for Trinidad and the first record of a species with 29 pairs of chromosomes outside Jamaica.

T.tetragona has been recorded as a diploid from Jamaica (Walker l.c.), this tetraploid is a new record for Trinidad.

T.dentata has been recorded several times (see Appendix I) however

the only previous diploid record was from India (Ghatak 1962) these two records are new counts for Mauritius and Trinidad.

T.torresiana has been counted as a tetraploid from Jamaica, this is the first hexaploid count from Trinidad, the only previous hexaploid being from Malaya (Manton 1954).

T.glabriuscula (Holttum ined.) is a new and as yet undescribed species from New Guinea.

CHAPTER VII

PALYNOLOGY

INTRODUCTION

Malpighi is reported as having stated in 1687 that pollen grains have different forms in different plants (Wodehouse 1926b). Today it is recognised that the pollen of higher plants and the spores of certain fungi, bryophytes and many pteridophytes possess a certain variety of characters which makes them particularly useful material for taxonomic studies.

Spores are the organs of dispersal and as such are frequently invested with a protective layer or perispore which may be extremely resilient, as demonstrated by its presence in Boreal peat deposits. At the present time, apart from chromosomal studies, the spore and the nature of its protective covering presents a unique basis for study. It is a single cell which, as far as can be ascertained, shows very little appreciable variation throughout a given species.* The resilience of the outer layer at least, enables it to be preserved entire on herbarium specimens which may be more than one hundred years old. Hence when spore morphology can be shown to be of taxonomic value there is the additional advantage that if the type specimen is available and fertile, spores may be taken for reference without undue harm to the specimen itself. The problem of the availability of the type material for study arises when other recently developed methods of approach such as chromosome number, chromosome morphology, chemotaxonomy and to a

---

* This fact is supposed to have been first appreciated by Geoffroy in 1711 (Wodehouse l.c.)

certain extent anatomy are used. Although a certain amount of anatomical detail can be obtained from the reconstitution of herbarium specimens, the information is limited and the process is obviously to the detriment of the specimen itself.

As was stated in the introductory chapter (p. 7) palynological data has been widely employed in the taxonomy of many groups of species, expecially amongst the flowering plants. The spores of ferns in general have also been studied fairly extensively but largely upon a geographical basis. Many of these studies contain descriptions and drawings or photographs of the thelypteroid spores, prepared from light microscope preparations. It has long been recognised that spores of a given species, and to a more limited extent, those of closely related species, exhibit uniformity of type, shape, size and perispore architecture, which makes them particularly useful material for taxonomic and phylogenetic studies (Reed 1950, Brown 1960). Thus we find that spore morphology has been used in a variety of ways by many different workers. Reed (1942, 1950) and Momose (1942, Nos. 24-26) used spore morphology to demonstrate the similarity between related species whereas Crane (1953), Harris (1955), Alston (1959), Morton (1963a), Nayar and Devi (1963 & 1964), Sorsa (1964), Davlianidze (1965) and Holub (1969) have used differences in the morphology to elucidate differences between similar species. Harris, for example, produced a key for the identification of all New Zealand ferns by their spores, including the five species of Thelypteris found there, and was able to distinguish clearly between them. He, nevertheless, agreed with Holttum (1948) that spore morphology presented insufficient evidence for the separation of Thelypteris sens. strict. from Cyclosorus.

Wagner (1966) has used a difference in spore size to distinguish between species and hybrids of Gymnocarpium and Shivas (1969) used

scanning electron micrography to good effect in defining a new species of Asplenium. This method has also been employed by Crabbe et al. (1969) in studying the Dryopteris assimilis complex.

There has been some confusion with regard to the relationship that may exist between the size of spores and the polyploid level of the plant. Hagenah (1961) demonstrated a distinct correlation between spore size and the level of polyploids in the Cystopteris fragilis complex and his results appear conclusive although he only measured ten spores from each cytotype. Some degree of overlap between the groups was found but this was eliminated by considering the average figures. Blasdell (1963) extended these findings to include all species of Cystopteris and claimed that from spore measurements he could determine accurately the polyploid level of herbarium specimens. He made rather sweeping assumptions based on a minimal amount of cytological data and his conclusions must be considered as unreliable in the light of Bir's report (1966-7a) that he could find no correlation between the polyploid level and the spore size in the Himalayan cystopterids. In his studies of Himalayan asplenioid and athyrioid ferns, however, he was able to show the existence of such a relationship within a species complex but not between even the closest of related species.

In her paper briefly surveying the role of fern spores in taxonomy, Brown (1960) pointed out that little is known regarding the effect of varying techniques of mounting, on the size of spores nor whether or not differences in size or shape might be induced by different nutrition or other external factors. In general she felt that small differences in spore size might be of little importance and that although the role of the spore in fern taxonomy is increasing, spore data was in fact of little use in distinguishing between species within certain groups.

Since Brown wrote her paper, several workers have attempted to assess the effect of different mountants on the shape and size of pollen grains (Erdtman and Praglowski 1959, Manten 1959, Faegri and Devse 1960, Cushing 1961, Punt 1962, Praglowski 1970) and have shown that there is a significant change in size attributable to certain mounting techniques. One of these is that pollen grains mounted in glycerine jelly are liable to swell over a period of time (Praglowski 1970). To my knowledge there has been no similar work carried out on fern spores, but because of their similarity to pollen grains in many other respects, it would appear likely that similar phenomena might occur. Nevertheless spore size is still used as a taxonomic criterion, e.g. Shivas (1969), but as this is usually employed to demonstrate a difference between closely related species or sub-species it is probable that so long as the pre-treatment and mountants used are identical there will be an equal effect on all of the spores.

There has been no attempt to carry out a world-wide investigation of a large but well defined group of ferns, such as the thelypterids, with regard to the possible role that the morphology of spores might play in taxonomic and phylogenetic studies. This present chapter outlines my attempt to produce such a survey using modern techniques of electron microscopy in order to investigate any possible correlation between spore morphology, cytology, anatomy and morphology.

Until comparatively recently several methods of studying spore morphology have been available to the palynologist. Certain workers favoured the use of drawings which can be prepared freehand or with the aid of a camera lucida. (e.g. Knox, 1951, Harris 1955, Nayar and Devi 1963, 1964, Bir 1966-7a & b). The specimen can be focussed under the microscope at various levels and a three dimensional diagram produced. In many cases the excellent draughtsmanship and

interpretation of the artist have produced very good results. The usefullness of such drawings depends to a great extent upon the extrapolation of a series of two-dimensional fields of view into a three-dimensional figure because the depth of field of an optical microscope at high magnifications is very small.

Alternatively it is possible to record spore morphology using photography, Nayar and Devi (1963), or more usefully, a series of photographs at successive depths of focus, e.g. Reed (1942), Hires (1969), but these tend to leave the extrapolation into a three dimensional figure to the viewer and hence differences in interpretation can easily occur.

Another method available is the utilisation of optical thin sections e.g. Nayar and Devi (1963, 1964), but little detail, apart from the number of primary layers and their relative thicknesses, can be obtained. More detailed information regarding the morphology and anatomy of the spore wall can be obtained from ultra-thin sections viewed under the transmission electron microscope, e.g. Pettitt (1966a). The necessary rigorous processing and the uncertainty of the exact position of the section can lead to difficulties and differences of interpretation when attempts are made to relate these sections to a three-dimensional whole.

Once it was realised that spore morphology might provide some correlations with other characters all of the above methods were assessed for suitability, using thelypterid spores. Whilst it was possible to see differences between the morphology of certain spore types, the problem of displaying these in a manner which could be readily understood and reproduced had not yet been adequately resolved. In addition it appeared that there were minute differences between some of the spores which could not be seen in sufficient detail to evaluate

them using light microscopy. After a few preliminary experiments it was decided to employ the scanning electron microscope for this purpose. These experiments proved highly successful and significant differences were readily discernable. A large programme of investigation into the relation between spore morphology and other characters was therefore initiated (for methods employed in this study see Chapter II).

1) PRELIMINARY SURVEY

The preliminary feasibility survey was carried out using the following five West Indian species and one Malayan species.*

T.dentata

T.balbisii

T.megalodus

T.rudis

T.obliterata

T.extensa (Malaya)

Two of these species, T.balbisii and T.rudis were found to possess nearly identical spores, with a highly complex reticulate perispore (see fig. 81 and fig. 74). These two species both belong to the sub-genus Lastrea of Christensen's classification (1913). T.rudis had been cytologically investigated and found to have a base chromosome number of 29 (Walker 1964-5). Of the rest T.obliterata and T.megalodus both belonged to sub-genus Goniopteris and their spores possessed a perispore with prominent ridges arranged in an irregular fashion over its surface (see figs. 168 and 181). T.extensa has been placed in Cyclosorus (e.g. Holttum 1954) and differed considerably from the former pair by having numerous thickened ridges over the whole of its surface,

---

* These species were used purely because a plentiful supply of their spores was readily available at the time.

for example there was no plane region between the ridges (see fig. 171). On the other hand the perispore of T.dentata showed a somewhat intermediate structure having slightly thickened ridges with flatter areas between them in which small pits were visible.

The latter four spores were thus significantly different in structure from the first pair, yet each exhibited an individual structure which would enable it to be readily distinguished from the remainder. It was then realised that the chromosome counts for all four had been recorded as 36 (see Appendix I for authorities etc.). Hence it was concluded, somewhat prematurely as it later proved, that there might be a positive correlation between spore morphology and chromosome number on the one hand and morphology on the other (the genera Lastrea, Cyclosorus and Goniopteris had all been delimited by morphological characters).

Upon this premise a large collection of spores was collected (see Chapter II for sources) and photographed under the Scanning Electron Microscope (S.E.M.). The basis for the selection of species covered by this survey was four-fold:-

1) Species for which chromosome counts were available (see Appendix I).

2) Species which have been taken as the type of the numerous sub-genera which have been described in Thelypteris (see Iwatsuki 1964 pages 11-12).

3) Jamaican species of Thelypteris (because of the high percentage of these species for which chromosome counts are available).

4) Any other species which were of obvious interest, for instance T.ciliata which has been quoted as having trilete spores (Holttum 1954).

Unfortunately the short time available meant that the identification

of each specimen cited could not be checked. Duplicates were therefore taken whenever possible either from the collections of different workers or from different localities. A list of those specimens used will be found in Appendix II. In addition, to ensure the greatest possible accuracy, either large numbers of spores or single undehisced sporangia were used as described in detail in Chapter II (page 12).

In all cases the whole of the microscope stub was thoroughly searched to ensure the uniformity of the specimen and a spore was chosen which showed any distinctive features to their best advantage. Dirty or cracked spores were rejected in favour of clean whole spores. For each spore a photograph was taken at magnifications of approximately 2000x and 5000x. In some cases lower or higher magnifications were used to study various points of interest.

Harris (1955) stated that using the light microscope "Sculpture elements less than 1μ (1μm) in diameter may be too small for precise classification (of spores) and even if determined at higher magnification may be untrustworthy for the purposes of a key". Whilst it is recognised that features which can only be recognised under the electron microscope are of little use for the production of a field key it is proposed to show that these greater magnifications do indicate an underlying similarity in the structure of the perispore of many of the thelypterids. This might indicate something about their phylogenetic relationships which could not have been appreciated using the light microscope alone, Harris's statement would mean, for example that the bars which form the raised reticulum of T.balbisii (see fig. 208) are an unreliable character, as they are approximately 0.5 μm in diameter.

It has been assumed that if coating with a gold film, evacuation of the viewing chamber or bombardment with electrons has any effect

upon the perispore then this effect would be the same on all the specimens. If there are any changes in size, as have been shown to exist with other techniques (Praglowski 1970), they would therefore be similar in all the samples. Little importance has been placed upon spore size in this survey as the three-dimensional effect produced on the S.E.M. screen makes the length of spores difficult to measure. Measurements of the height of the sculpture elements however are possible, especially on slightly angled views of the spore.

2) SPECIES FOR WHICH CHROMOSOME COUNTS WERE AVAILABLE

The counts listed in Appendix I represent chromosome counts of over 100 species and it has been possible to obtain spores from 80 of these. It would naturally have been desirable to study spores from the actual voucher specimens which represent the counts but several factors prevented this. Firstly many authors have not stated where such vouchers have been deposited or even if voucher material is available. Secondly, a great deal of time would be necessary to collect such specimens together. Thirdly, and probably most relevant, specimens which are used for cytological studies are, of necessity, immature and therefore in many cases mature spores are not to be found on the voucher material. Hence a list of priorities was drawn up to attempt to minimise the effects of misidentification.

Collections from the author by whom the counts were reported were used whenever possible. Secondly collections from the same region or country were given precedence over those which originated elsewhere. If none of these were available then collections by known authors were given precedence over those of lesser known or unknown authors. For many of the species, in fact, only one or two specimens were available which satisfied any of the above criteria. Whenever possible duplicates were taken, from different areas or different collectors and those

indicated that the majority of species had been correctly identificd.

The spores which were studied are grouped below for convenience under various headings.

a) Base Chromosome Number Less Than 29:

T.noveboracensis (fig. 112)

T.nevadensis (fig. 113)

The spores which were obtained from T.noveboracensis collapsed readily and showed an irregularity of patterning which suggests that they were immature, nevertheless a crude raised reticulate pattern is visible over most of the surface. T.nevadensis on the other hand was found to be producing good spores with a rather spiny appearance, on closer examination these are seen to consist of rod-like projections frequently joining together to present a reticulate effect. This basically reticulate pattern suggests affinities with group b) described below but as yet I have been unable to compare their morphological data.

b) Base Chromosome Number Usually 29:

These species are found in the West Indian Islands, especially Jamaica, but spreading into Central America.

T.thomsonii (fig. 73)

T.rudis (fig. 74)

T.oligocarpa (fig. 75)

T.nockiana (fig. 76)

T.heteroclita (fig. 77)

T.sancta (fig. 78)

T.sancta var. magna (fig. 79)

T.concinna (fig. 80)

T.navarrensis (fig. 82)

T.resinifera (n=31) (fig. 83)

T.linkiana (figs. 84 & 209)

These species form a very well defined group. The basic architectural pattern of the perispore consists of a reticulate layer supported above the lower layer of the perispore by short "pillars" (see also figs. 207 and 208). Transmission electron micrographs (see figs. 225 and 226) show that this outer reticulate layer is continuous with the rest of the perispore below.* At certain irregular positions on the spore what appear as plane areas can be seen (see figs. 82 and 83). Sectioning shows that this is due to the imperfect formation of the columella, with the fussion of the tectum and the foot layer. The position of such plane areas would appear to be an inconsistent character and many spores can be found without such areas.

These species are apparently unique among the thelypterids in having a base number of 29 chromosomes (see Chapter VI). The other noteworthy factor is that the species possess a remarkable morphological similarity and can all be referred to under Christensen's (1913) sub-genus Lastrea. All of the representatives of this sub-genus found on the island of Jamaica, that have been cytologically studied, have a base number of 29. The only exception to this is T.resinifera a tetraploid species based on 31 (Walker 1964-5). I have seen the original voucher preparations of this count and have been unable to revise the figures reported by Walker although there certainly appear to be more than 58 pairs at first metaphase which would be expected were the species based on 29. Further discussion on the importance of this group will be found below. (page 111).

c) Base Chromosome Number Of 30:

These three species form the group of Phegopteris (Presl) Fée.

---

* The terminology applied to pollen grains by Larson, Skvarla and Lewis (1962) can be applied to these layers, i.e. the reticulate layer is the tectum, the pillar is a columella and the underlying layer, the foot layer.

T.hexagonoptera (fig. 92)

T.phegopteris (figs. 93 & 211)

T.decursive-pinnata (fig. 94)

Morphologically these species form a well defined group (Holttum 1969). The British member, T.phegopteris is a classical example of an apogamous triploid, hence it is not surprising to discover that its spores are very irregular in size, shape and architecture. There is nevertheless a certain degree of regularity and the spores of this species can be readily recognised from all others by the rugate ridges which are often reticulate in construction (see fig. 211) with the foot layer between possessing a somewhat warty appearance.

The remaining two species are less widespread consisting of fertile diploids, tetraploids or hexaploids. Their spores are rather similar (see figs. 93 and 94) but I believe that those illustrated may be immature, although they do possess a warty appearance very similar to the underlying "foot-layer" of T.phegopteris.

d) Base Chromosome Number of 31:

Morphologically there are three groups of species having a base chromosome number of 31, Pseudophegopteris and Macrothelypteris, which have been clearly defined by Holttum (1959) and the remaining species e.g. T.japonica, T.beddomei which have been placed together for convenience (see Appendix I). Only the spores of T.japonica* were available and so no conclusions can be reached regarding the position of these species.

i) Pseudophegopteris. This group has been delimited by Holttum (l.c.)

T.aurita (fig. 95)

T.sub-aurita (fig. 96)

---

* Also T.resinifera which has been included in section b) above.

T.cruciata (fig. 98)

T.cyclocarpa (figs. 99 & 210)

T.levingei (fig. 100)

T.bukoensis (fig. 101)

This group was recognised only comparatively recently by Ching (1963) and since then a number of similarities between the members have been noted in their morphology and cytology. This study has provided another constant character, spore morphology. All of the species (figs. 95 to 105) possess spores with a perispore architecture which is unique among the thelypterids and, as far as they have been studied,* among the ferns as a whole. The sculpture consists of a basic foot layer with a reticulate tectum superimposed over it, more robust than that found in group b) above and with no columella. It is not known, at present, whether this tectum is hollow or solid. In some species, e.g. T.cyclocarpa (see fig. 99) the tectum appears to be overlying the foot layer whereas in other species, e.g. T.levingei (see fig. 100), it has the appearance of an integral part of the foot layer. Some straight-forward sectioning would soon resolve its nature but at the present time insufficient quantities of the spores have been available to accomplish this. In some species the sculpturing does not appear to cover the whole of the surface e.g. T.sub-aurita, T.cruciata whilst in others it appears to be more or less even over the whole surface, e.g. T.levingei. No significance has been attached to this apart from the observation that the sculpturing is more prominent upon the surface of the tetrad from which the spores originated.

ii) Macrothelypteris. This group has been clearly delimited by Holttum (l.c.) and possesses uniform vegetative characters.

T.ornata (fig. 107)

---

* With one possible exception see T.elwesii, section f).

The only species for which both a chromosome count and spore micrograph are available is T.ornata which possesses a reticulate perispore apparently identical to that described for group b), above. At this point I shall make no additional comment except to note that this structure is common throughout Macrothelypteris, among those species for which counts are not available.

iii) Group of T.japonica. This group, represented by one species here, possesses a base number of 31 and yet does not fall within either of the preceeding sub-genera.

T.japonica (fig. 114)

The spores of this species are very ornate, having a series of raised ridges with dentate crests and reticulate bases arising from a regularly warty foot layer.

e) Base Chromosome Number of 32:

The type of spore found in T.japonica is also found in the two species of Thelypteris in this group.

T.pectiniformis (fig. 117)

T.simulata (fig. 116)

The morphology of the spores of T.pectiniformis is almost identical with that of T.japonica (see fig. 114) whereas that of T.simulata is of a similar structure but the crests of the ridges are considerably less dentate. No morphological study has been carried out on these two species to determine their affinities but, like the vast majority of species with base numbers less than 36, they both have free veins.

f) Base Chromosome Number of 34:

This group possesses free venation yet there is little correlation between the spores as was shown in the group above.

T.limbosperma (fig. 118)

T.quelpaertensis (fig. 119)

T.elwesii (fig. 120)

The spores of T.limbosperma show a definite similarity with those with base number 36 (see below section h). The perispore bears dentate ridges over most of its surface with a rather wrinkled foot layer between. This structure rarely shows any affinities with the reticulate type although sectioning indicates that these ridges are hollow (Nayar and Devi 1964).

The spores of T.quelpaertensis conversely show definite affinities with the reticulate type, having small spine-like projections over their surface. Each of these arises from two or three processes from the foot layer which is otherwise comparatively smooth and featureless.

The specimen of T.elwesii that has been studied bore spores remarkably similar to the members of Pseudophegopteris (section d)i) above). I have been unable to obtain a further specimen of this species and because of this shall not draw any further conclusions from this apparent anomaly.

g) Base Chromosome Number of 35:

T.flaccida (fig. 121)

T.singalanensis (figs. 122 &212)

T.esquirolii (fig. 123)

T.palustris (figs. 124 & 213)

None of these spores resemble each other in their architecture, and it has only been possible to obtain duplicate material of T.palustris.

The spores obtained from the specimen of T.flaccida were unique among all those studied, having a nearly smooth, apparently folded, perispore. These ridges are however perforated in a few places,

possibly indicating a relationship between this type and the reticulate type (sections b and d. ii).

T.singalanensis also produces a peculiar form of spores* which possess a "folded" perispore which is reticulate along the ridges and extremely warty between. These ridges are never sharp and dentate and the general appearance is rather granular (see fig. 122). The interest in this particular species is that it is the only thelypteroid so far studied which has a chromosome base number of less than 36 and yet possesses conjugating veinlets. Further study is obviously needed into the affinities of this species.

T.esquirolii possesses spores with a structure which is very similar to many species with a base number of 36 and in fact there are no other species with similar spores with less than 36. As there is only one count available for this species and only one specimen was available to me, I shall make no further comment on this species.

T.palustris on the other hand is extremely well known and documented. It occurs throughout the northern hemisphere and spore specimens studied from many parts of the world indicate little appreciable difference in structure. The basic construction is of a smooth foot layer, overlaid with a raised reticulum, similar but more complex than that of Pseudophegopteris (see above, section d.ii.) and the tectum is raised up to form pointed projections (see figs. 124 and 213). This structure is sufficient to distinguish this species from the majority of the thelypterids with the exception of some of the members of Stegnogramma (see below section h.i. e.g. T.gymnocarpa fig. 128).

---

* I have no doubt as to the authority of this material as it was kindly sent to me by Professor R.E. Holttum.

h) Base Chromosome Number of 36:

Within this large mass of species, two relatively small groups can be separated from the remainder on gross morphological grounds. When the spores of these species are compared it is found that they also possess a remarkable uniformity of sculpturing.

i) Stegnogramma Blume. This group has been delimited by Iwatsuki (1964b).

T.griffithii	(figs. 125 &215)
T.gymnocarpa ssp. amabilis	(fig. 128)
T.pozoi	(fig. 127)

The spores of all three species of this group which have been counted were available and exhibit a remarkable similarity of structure. Basically the perispore possesses a superficial layer consisting of spiny projections which often exhibit a base consisting of a number of radiating ridges (see fig. 215). This basic structure is by no means unique in the thelypterids but it is remarkably uniform in all the members of this group which were available for study.

ii) Meniscium Schreber. This readily defined group displays the greatest development of goniopteroid venation.

T.reticulata	(fig. 201)
T.prolifera	(figs. 202 & 214)
T.serrata	(fig. 203)

The perispore consists of a basic foot layer with frequent spiny projections and also a ridged tectum with a basically reticulate pattern and numerous spines. The resulting spore possesses a perispore in which reticulate, spiny and ridged elements can all be recognised (see fig. 214).

The remaining species with a base number of 36 have been divided on the basis of venation, largely for convenience, into those with some

anastomosing veins (Cyclosorus) and those without (Thelypteris). Evidence has already been put forward in the chapters on Morphology and Cytology (Chapters V and VI) supporting the more primitive nature of free venation and hence it might be expected that there would be some degree of gradation in spore architecture.

iii) Thelypteris Schmid. (free veined species). It can readily be seen (see figs. 129 to 139) that there are four more or less distinct patterns of spore morphology in this group.

a) Spores with small spine-like projections over the whole of their surface:

T.ciliata (figs. 129 & 218)

T.crassifolia (fig. 130)

Despite their superficial similarity the structures of these spores are quite different. T.ciliata is remarkable among the thelypterids in its possession of trilete spores. I have been unable to study the anatomy of this species but morphologically and cytologically there is little doubt that it is a true thelypterid. I have studied the spores from several specimens (see Appendix II) and have found the same type of spores in each.

The projections over the surface of the spores of T.crassifolia are very much smaller than those of T.ciliata and a higher power view reveals an underlying reticulate pattern to the projections.

It would appear therefore that although there is some basic similarity between these species, it is not possible to postulate any interrelationships elucidated by their spore morphology.

b) Spores with architecture based upon a reticulate pattern:

T.erubescens (fig. 134)

T.gracilescens (fig. 132)

T.laxa (fig. 133)

As was shown in the previous group, these species show certain apparent superficial similarities and yet differ considerably from each other.

In T.gracilescens there is a basic reticulate pattern forming, in places, a raised tectum which in other areas is closely adherent with the foot layer. There are small projections over most of the surface and the whole of the architecture is on a minute scale.

In T.laxa however, there is also a basic reticulate pattern but considerably more massive. The architecture consists of a ridged reticulate tectum with a rather featureless foot layer between.

The spores of T.erubescens are unlike any other thelypterids in their appearance although they do show a basic reticulate pattern. The tectum is thrown up into bold arches arising from all over the surface of the foot layer. Two or three of these arches may join together to form a rudimentary reticulum. It is hard to visualise the exact relationship that this might have with any of the other spore types.

The remaining five species possess a more standard type of architecture based on ridges and spines.

c) Spores with a ridged perispore:

T.decussata (fig. 135)

T.deltoidea (fig. 137)

T.paleata (figs. 136 & 222)

As with the above species, these three species show considerable similarities, nevertheless the differences are readily appreciated by a study of electron micrographs of the spores (see figs. 135 to 137). The basic pattern is one of narrow ridges arising perpendicularly from a nearly featureless foot layer. In T.decussata these ridges have a rather rounded appearance with quite massive spines irregularly spaced

along their length. In T.paleata there are fewer ridges, the crests are deeply toothed and in addition the foot layer between the ridges possesses small spines clustered in the centre of the plane areas.

The foot layer in T.deltoidea is remarkably smooth and featureless. The ridges though somewhat toothed are rather narrow and are frequently found lying on their sides (c.f. also T.megalodus fig. 181).

d) Species with a spiny perispore:

T.subochthodes (fig. 139)

T.xylodes (fig. 138)

These two species show the two different types of spiny construction that are found in the thelypterids. In T.xylodes the spines appear to be formed from very protracted ridges, (alternatively these may be thought of as a series of joined spines), with a featureless foot layer between. In T.subochthodes however the spines are more rounded and possess ridged bases which indicate a similarity to the species of Stegnogramma (page 98 above and figs. 125 to 128).

The conclusions from these studies must obviously be viewed in the light of the small number of species which have both a base number of 36 chromosomes and free venation. If a complement of 36 chromosome pairs does represent an advanced status within the phylogeny of the group and if anastomosis of veins is an advanced character (as has been discussed above, Chapters V and VI) then it might reasonably be expected that the spores of this group would show intermediate stages between those of species having free veins and fewer than 36 chromosomes and those of species having 36 chromosomes and anastomosing veins. Nevertheless it must be remembered that there is no evidence to suggest that spore morphology evolves at the same rate and in the same direction as other morphological and cytological characters.

iv) Cyclosorus Link (Species having at least one pair of veins anastomosing). In this group there are also apparently four sub-groups which can be separated on similar criterea to those used in the above group.

a) Species with small projections over the whole of their surface:

T.kunthii (fig. 148)

T.megaphylla (fig. 149)

T.serra (figs. 131 & 223)

These species possess spores which show definite affinities in architecture to T.crassifolia (see above page 99) and little more need be said regarding these patterns.

b) Spores with a reticulate perispore. Only two species can be placed in this group:

T.patens (fig. 154)

T.pennigera (fig. 153)

Both spore types show a pattern based on spiny and reticulate ridges. T.pennigera spores bear certain similarities to those of T.erubescens (see fig. 134) whereas T.patens spores are more similar to those of T.laxa (see fig. 133).

c) Species with a more or less spiny perispore:

T.multilineata (fig. 150)

T.rubicunda (fig. 151)

T.gongylodes (fig. 152)

T.papilio (fig. 155)

T.truncata (figs. 156 & 220)

T.crinipes (fig. 157)

T.triphylla (fig. 158)

T.dentata (figs. 159 & 219)

T.multilineata, T.rubicunda and T.gongylodes appear to form a group in which the spines are rounded (c.f. T.subochthodes fig. 139) and arise from a reticulate base layer. In the latter two species the perispore is also ridged but the ridges are not as massive as those of T.kunthii (see fig. 148).

In the remaining five species the projections appear to be rather short ridges giving a spiny effect (c.f. T.xylodes fig. 138).

d) Spores having a ridged perispore:

T.afra	(fig. 155)
T.asplenioides	(fig. 166)
T.asterothrix	(fig. 172)
T.biolleyi	(fig. 163)
T.extensa	(fig. 171)
T.guadeloupensis	(fig. 170)
T.interrupta	(fig. 160)
T.invisa	(fig. 173)
T.megalodus	(fig. 181)
T.molliuscula	(fig. 177)
T.obliterata	(fig. 168)
T.parasitica	(fig. 178)
T.poiteana	(fig. 165)
T.quadrangularis	(fig. 174)
T.reptans	(fig. 169)
T.rubra	(fig. 180)
T.sclerophylla	(fig. 167)
T.serrulata	(fig. 162)
T.subpubescens	(fig. 176)
T.tetragona	(fig. 179)
T.urophylla	(fig. 182)

T.venusta (fig. 161)

T.venusta var. usitata (fig. 164)

In all of these species the basic spore pattern is one consisting of ridges, usually with more or less dentate crests. The width of the ridges varies from very thick (T.extensa fig. 171, T.asterothrix fig. 172) to very thin and easily damaged (T.megalodus fig. 181) with a whole range of thicknesses and complexity between. In some species the foot layer between the ridges is relatively smooth (T.asplenioides fig. 166) while in others there are numerous smaller ridges (T.reptans fig. 169, T.guadeloupensis fig. 170) or spines (T.afra fig. 155, T.rubra fig. 180). I believe however that there is insufficient evidence to place any greater emphasis on characters of this type other than in demonstrating differences between species. It is probably better to consider the whole group as a single unit.

It would appear at first sight that the perispore architecture in these species was very different from that of the preceeding groups. However many of the spores illustrated show that the ridges are hollow and produced in a similar fashion to those of the reticulate species, the lacunae in the reticulum being largely filled in. In some species perforations are apparent in the overlying tectum e.g. T.extensa (fig. 171), T.quadrangularis (fig. 174) and T.invisa (fig. 173). Similarly many spores have spines arising from between the ridges indicating an affinity with both the spiny types and the reticulate types (in which they would represent the baculae of the tectum). Examples of these spines can be seen on T.venusta (fig. 161), T.interrupta (fig. 160), T.serrulata (fig. 162) and T.biolleyi (fig. 163).

3) STUDY OF TYPE SPECIES OF THELYPTERIS

In order to cover as wide a range of species as possible it was decided to compare the spore morphology of the type species of each of

the numerous genera and sub-genera which have been proposed from time to time over the past hundred years. It has been possible to obtain material from 28 of the 36 and these are listed below, grouped, for convenience in accordance with Iwatsuki's scheme (1964b).

TABLE 7

List of the various sub-genera which have been delimited, and their type species arranged in accordance with Iwatsuki (1964b).

	Type of Genus	
STEGNOGRAMMA		
Leptogramma	T.pozoi	(fig. 127)
Stegnogramma	T.aspidioides	(fig. 126)
Haplogramma	T.cyrtomioides	
Dictyocline	T.griffithii	(fig. 125)
THELYPTERIS		
Thelypteris ≡ Hemestheum	T.palustris	(fig. 124)
Lastrea	T.limbosperma	(fig. 118)
Amauropelta	T.limbata	(fig. 88)
Oochlamys	T.opposita	(fig. 91)
Parathelypteris	T.glanduligera	
Metathelypteris	T.gracilescens	(fig. 132)
Macrothelypteris	T.torresiana	(fig. 106)
Steiropteris	T.deltoidea	(fig. 137)
Glaphyropteridopsis	T.erubescens	(fig. 134)
Neocyclosorus	T.heterocarpa	
Pseudocyclosorus	T.xylodes	(fig. 138)
Mesoneuron	T.crassifolia	(fig. 130)
Phegopteris	T.phegopteris	(fig. 93)
Toppingia	T.keraudreniana	(fig. 105)
Lastrella	T.decursive-pinnata	(fig. 94)
Pseudophegopteris	T.pyrrhorhachis	(fig. 97)
Glaphyropteris	T.decussata	(fig. 135)
Cyclogramma	T.squamaestipes	(fig. 146)
Haplodictyum	T.canescens	
Sphaerostephanos ≡ Mesochlaena	T.polycarpa	(fig. 187)
Abacopteris ≡ Pronephrium	T.urophylla	(fig. 182)
Menisorus	T.pauciflora	

THELYPTERIS (Cont.)	Type of Genus
Cyclosoriopsis	T.dentata (fig. 159)
Cyclosorus	T.gongylodes (fig. 152)
Pneumatopteris	T.callosa
Macrocyclosorus	T.megaphylla (fig. 149)
Cyrtomiopsis	T.boydiae
Dimorphopteris	T.moniliformis
MENISCIUM	
Meniscium	T.reticulata (fig. 201)
Ampelopteris	T.prolifera (fig. 202)
Asterochlaena	T.reptans (fig. 169)
Goniopteris	T.vivipara (fig. 193)

When these type species are considered there appears to be a certain amount of correlation between the morphological characters, upon which this system was drawn up, and the spore morphology.

Among the free veined species in Iwatsuki's scheme (his sub-genera Thelypteris, Steiropteris, Glaphyropteridopsis, Phegopteris, Glaphyropteris and Cyclogramma) there appear to be only two basic patterns one reticulate and the other winged. The latter are found only in the types of the genera Lastrea, Steiropteris, Glaphyropteris and Cyclogramma. The reticulate forms may be the simple reticulum found in Oochlamys, Amauropelta and Macrothelypteris or the smooth pattern of Pseudophegopteris and Toppingia or alternatively a structure consisting of reticulate ridges in Parathelypteris, Metathelypteris, Phegopteris and Lastrella or a complex arrangement of reticulate spiny projections in Thelypteris, Glaphyropteridopsis, Pseudocyclosorus and Mesoneuron.

It can readily be seen that those groups which Iwatsuki has placed together in his sub-genus Thelypteris possess as wide a variation in spore morphology as they do in chromosome base number. The significance of this will be discussed below. Similarly his sub-genus

Phegopteris can be divided both by chromosome base number and spore type into two distinct groups. However the type species under Glaphyropteridopsis show a considerable degree of similarity.

In the remaining groups of Thelypteris where there are anastomosing veins (Sphaerostephanos, Abacopteris, Cyclosoriopsis, Cyclosorus and Pneumatopteris) there are also two basic spore types. Winged spores are found in Abacopteris and Cyclosoriopsis whilst the types of the other genera have spores with either very small wings or spines.

Spores from the groups Parathelypteris, Neocyclosorus, Menisorus, Pneumatopteris, Cyrtomiopsis and Dimorphopteris were not available for this study.

The spores from the type species of the genus Stegnogramma all possess a spiny tectum based on a reticulate pattern.

In Iwatsuki's genus Meniscium two types of spore are found. In Asterochlaena and Goniopteris the spores are winged, while in Meniscium and Ampelopteris they are of a complex ridged, reticulate and spiny form. The similarity between the New World species of Meniscium and the Old World specimen of Ampelopteris is significant evidence confuting Morton's (1963) statement that he did not believe that the Old and New World species of Meniscium were closely related.

4) JAMAICAN SPECIES OF THELYPTERIS

The thelypterids of Jamaica are a geographically distinct group of species which have been thoroughly studied both morphologically (Christensen 1913, 1919) and cytologically (Walker 1964-5) and have been efficiently enmumerated by Proctor (1953). Because of the relatively advanced state of knowledge of these species and the accessibility of a considerable volume of the material used by Walker and whose identity has been endorsed by Proctor, it was felt that this

group provided a useful basis for a comparative study involving spore morphology. It was hoped that in such a distinct group it would be possible to determine whether the spore morphology could be usefully correlated with gross morphology and cytology as has been proposed in the previous two sections of this work.

Given below is a list of those species recorded for the Jamaican flora by Proctor (l.c.) together with their base chromosome number and spore type. Out of the total of fifty species (and three varieties) listed as being present on the island, all but T.tenebrica and T.patens var. dependens were obtained for study. The photomicrographs of the spores of T.angustifolia were of insufficient quality to print but sufficiently clear to determine the spore type. Thirty six of these species have been cytologically studied, mainly by Walker (l.c.) and all are included in Christensen's works (l.c.).

TABLE 8

Jamaican species of Thelypteris sens. lat. grouped according to Christensen (1913).

	x	Spore Type	Figure
LASTREA			
T.balbisii	-	Reticulate	81
T.cheilanthoides	-	Reticulate	86
T.concinna	29	Reticulate	80
T.germaniana	-	Reticulate	90
T.gracilis	-	Reticulate	85
T.heteroclita	29	Reticulate	77
T.limbata	-	Reticulate	88
T.linkiana	29	Reticulate	84
T.navarrensis	28	Reticulate	82
T.nockiana	29	Reticulate	76
T.oligocarpa	29	Reticulate	75
T.pachyrachis	-	Reticulate	89
T.resinifera	c31	Reticulate	83
T.rudis	29	Reticulate	74

LASTREA (Cont.)	⁂	Spore Type	Figure
T.sancta	29	Reticulate	78
T.sancta var. magna	29	Reticulate	79
T.underwoodiana	-	Reticulate	87
GLAPHYROPTERIS			
T.decussata	36	Ridged	135
T.thomsonii	29	Reticulate	73
STEIROPTERIS			
T.deltoidea	36	Ridged	137
CYCLOSORUS			
T.dentata	36	Spiny ridges	159
T.gongylodes	36	Spino-reticulate	152
T.invisa	36	Ridged	173
T.patens	36	Spino-reticulate ridges	154
T.patens var. dependens	-	-	-
T.serra	36	Small spines on thick ridges	131
MACROTHELYPTERIS			
T.setigera	31	Reticulate	111
GONIOPTERIS			
T.asplenioides	36	Ridged	166
T.asterothrix	36	Thick ridges	172
T.biolleyi	36	Short ridges	163
T.cordata	-	Smooth ridges	199
T.guadeloupensis	36	Ridged	170
T.hastata	-	Ridged	194
T.kunthii	36	Small spines on thick ridges	148
T.leptocladia	-	Smooth ridges	198
T.megalodus	36	Ridged	181
T.nephrodioides	-	Short ridges	190
T.obliterata	36	Ridged	168
T.poiteana	36	Ridged	165
T.reptans	36	Smooth ridges	169
T.sagittata	36	Ridged	196

GONIOPTERIS (Cont.)	x	Spore Type	Figure
T.sclerophylla	36	Ridged	167
T.scolopendrioides	-	Spiny ridges	189
T.serrulata	36	Short ridges	162
T.tenebrica	-	-	-
T.tetragona	36	Ridged	179
T.venusta	36	Ridged	161
T.venusta var. usitata	36	Ridged	164
T.wrightii	-	Spiny ridges	147
MENISCIUM			
T.angustifolia	-	Spino-reticulate ridges	-
T.reticulata	36	Spino-reticulate ridges	201
T.serrata	36	Spino-reticulate ridges	203

From this list it can readily be appreciated that in some of Christensen's sub-genera there is a remarkable degree of correlation between morphology, cytology and spore morphology.

Christensen (l.c.) defined his sub-genus Lastrea on purely morphological grounds of venation and hair type; the validity of using these structures is shown clearly by the members of Lastrea found on the island. Of those species which have been counted, with the exception of T.resinifera and possibly T.navarrensis, the only chromosome base number is 29 which is in itself peculiar among the thelypterids (see page 78). In addition all members of Lastrea (plus T.thomsonii and T.setigera) possess identical spore morphology, a raised reticulum.

Christensen admitted that the distinction between Lastrea and Glaphyropteris was a very tenuous one and so it would seem reasonable to include T.thomsonii in this group. This does not exclude T.decussata which appears to show greater affinites with anastomosing vein types of Cyclosorus and Goniopteris.

The type of Lastrea in T.palustris (see fig. 124) which possesses both a distinct chromosome number (n=35) and distinct spores from these species which Christensen included in Lastrea. If this group is to be delimited therefore it must be achieved by considering an alternative type. This group of species is not restricted to Jamaica and species with similar gross morphology and spore morphology are found on neighbouring islands (e.g. Cuba, Costa Rica and Trinidad) and also the mainland of Central America (e.g. Mexico, Equador). Although it has not been reported, some of these species are now being found to have a complement of 29 chromosome pairs (Holttum pers. comm.) and also have an identical spore morphology. One of these species is T.limbata (Sw.) Proctor (see fig. 88) which Kunze used* as the type of his genus Amauropelta (his specimen was named Amauropelta breutelii Kunze which is now recognised as a synonym for T.limbata). Unfortunately at the present time this species has not been cytologically studied and hence this cannot be taken as a delimiting character of this species. However I believe it will be possible to resurrect the epithet Amauropelta Kunze in an amended form to include the spore morphology and chromosome base number, with T.limbata as the type of the genus.

The remaining groups are more straightforward. The three species of Meniscium all possess typical ridged tecta with numerous spines and reticulae upon them (e.g. figs. 201 and 203) and the species of Goniopteris (with the exception of T.kunthii) all possess a ridged or winged tectum. Although there are obvious differences by which it might be possible to distinguish groups or even species.

T.setigera is the only species of the sub-genus Macrothelypteris and possesses the typical characteristics of this group.

T.deltoidea like T.decussata was closely allied to the remainder

---

* Farnkr. 1: 86, p. 109, 1843.

of Christensen's Lastrea but shows closer affinities with Cyclosorus by virtue of chromosome number and spore morphology.

The members of Cyclosorus although uniform in chromosome complement and morphology show considerable variation in their spore morphology. The five species studied all show different variations in their morphology with no general pattern at all.

From this survey it would therefore appear that in certain groups there is a considerable degree of correlation between gross morphology, spore morphology and cytology and in the absence of cytological data, spore data could possibly play a major part in delimiting certain groups of the thelypterids.

5) THIN SECTIONS

In order to supplement the observations made using the scanning electron microscope, spores were prepared and secioned for viewing with the transmission electron microscope. The main object of this investigation was to ascertain whether the raised reticulate layer found in species belonging to Amauropelta and Macrothelypteris was an additional layer, laid down around the true foot layer or was an extension of the foot layer and hence analagous with the ridges and spines found in many other species (Nayar and Devi 1964).

The hollow structure of the ridged perispores of fern spores and higher plant pollen has been well documented by Pettitt (1966) and many others. A reticulate pattern, apparently identical with that found in some thelypterids has been illustrated by Echlin (1968) in higher plant pollen but I have found no reference to a similar structure in any other genus of ferns.

Spores of T.balbisii were used for this study and it was assumed that their structure would be typical of spores with a raised reticulate pattern. When viewed with the transmission electron microscope these

sections revealed that the raised bacculi and tectum are in fact continuous with the foot layer (see figs. 225 & 226).

From these sections it is obvious that, at least in acetolysed spores, there is a space (or a non-electron dense layer) between the inner and outer layers of the spore coat. The inner layer possesses small projections which apparently correspond with small projections along the inner surface of the outer layer (marked with an arrow in fig. 226). This "layer" provides a line of weakness and in treated spores, the inner layer frequently parts from the outer layer along this line. The exact significance of this structure is uncertain at the present time.

The study of spore-wall stratification is a very detailed one and many tests need to be carried out using a variety of fixing and staining techniques before any further conclusions can be drawn from the structures found in this group. The study of the structure of the spore wall of Pseudophegopteris would also be of interest as it would be expected to show a somewhat medium position between the reticulate and the ridged types.

Thin sectioning has therefore revealed that the underlying patterns of stratification of the spore wall are very similar in ridged and reticulate type spores. A considerable amount of further study is, however, obviously required.

6) THE USE OF SPORE MORPHOLOGY IN THE TAXONOMY OF THE THELYPTERIDS

It was pointed out in Chapter VI (page 74) that identical chromosome numbers did not necessarily indicate a close relationship between species, but if, as has been shown several times in this study, the base chromosome number can be shown to be correlated with either or both gross morphology and spore morphology then we have a useful tool for determining possible phylogenetic relationships. The

possibility of three such diverse features being correlated by chance is remote. In addition, if we can show a positive relationship between chromosome number and spore type and, in some strictly limited instances spore size, then it may be feasible to postulate the chromosome numbers (and possibly the ploidy levels) of herbarium specimens.

From these present studies it would appear that spore morphology can be used to elucidate certain relationships between species and groups of species of the thelypterid ferns. The conclusions from this study are outlined below:

It has been possible to demonstrate the uniformity of chromosome base number, spore morphology and gross anatomy in a group of species from the Carribbean and Central America. These species have previously been classified under the sub-genus Lastrea by Christensen (1913) and section Thelypteris by Iwatsuki, typified by T.limbosperma (=L.oreopteris) and T.palustris respectively. These typifications were based solely on gross morphology. The spore morphology of these species, reinforced by their chromosome numbers, indicates that these typifications might not be natural. Considering those species studied in this work it would therefore seem reasonable to re-arrange the divisions within the group.

The Central American species having a base chromosome number of 29, free venation and uniformly reticulate spores have been placed in Amauropelta typified by T.limbata (q.v.)

Holub (1969) has put forward sound arguments for removing to its own group, T.limbosperma, he has called this group Oreopteris. This species had been studied in detail by myself before the publication of Holub's paper. My findings are wholly in agreement with his and hence no further description is necessary here. As mentioned above (page 44)

I have added additional support to the separateness of this species by virtue of the peculiar double hairs along the margins of the scales. Therefore there seems to be good morphological, cytological and palynological grounds for accepting this proposal.

Holttum (1969) elucidated the group Macrothelypteris and his mainly morphological conclusions are wholly substantiated by a uniformity of base chromosome number (31) and uniformly reticulate spores.

Of the free-veined species remaining after the separation of the above three groups, Phegopteris and Pseudophegopteris have been well defined by Holttum (l.c.) on morphological grounds, again these are substantiated by cytological and palynological data (q.v.).

The group of Thelypteris typified by T.palustris can be distinguished on cytological and palynological grounds and I proposed here to consider this as an unispecific group. In the present studies the spore morphology is unique and coupled with a base chromosome number of 35 sets this species apart from any other species considered.

The remaining recognised groups fall into two sections, Metathelypteris and Parathelypteris having spores with reticulate ridges on them and Cyclogramma, Steiropteris and Glaphyropteris having ridged spores.

The situation among those groups of species with anastomosing veins is somewhat simpler and the only group in which there appears to be a major conflict is that which Iwatsuki considered as the sub-genus Abacopteris. In this sub-genus Menisorus is distinct in having spino-reticulate spores while those of Abacopteris are ridged.

Considering the spore morphology of the type species alone, therefore, two groups can be considered; those with ridged spores, Abacopteris and Cyclosoriopsis and those with more or less spiny spores,

Cyclosorus, Sphaerostephanos, Haplodictyum, Pneumatopteris and Menisorus. The position of Dimorphopteris is uncertain as I have not been able to examine any specimens.

As has been mentioned several times there seems little doubt regarding the separateness of Stegnogramma on morphological, cytological and palynological grounds.

The position regarding Meniscium is however less clear. Iwatsuki included Goniopteris with Meniscium in his genus on rather indefinite grounds of a sum of characters involving hairs, sori and venation. When spore morphology is considered it is seen that there is a very large rift between the spino-reticulate type found in Meniscium from both the Old and New Worlds and the ridged type found in Goniopteris and Asterochlaena. Coupled with the geographic distinctness of the two latter groups the spore morphology would suggest that these groups should not be included under Meniscium but show much greater affinities with Abacopteris and Cyclosoriopsis.

Whilst the shortcomings of a method involving mainly the generic types is recognised it is felt that some useful information might be gained from a classificatory system based primarily on spore morphology. Where this has been supplemented by studying larger numbers of apparently related species (as in Amauropelta and Pseudophegopteris) the correlation has been shown to be good and hence a system involving the definition of groups involving spore morphology is felt to be justified.

The scheme which I have prepared, based mainly upon spore morphology but also considering the features of gross morphology and in certain cases, geographical distinctness will be found in the final Chapter (page 133).

CHAPTER VIII

GAMETOPHYTE

The literature relating to the gametophyte in general is very dispersed and that regarding the thelypterids is particularly so. Since the gametophyte and its position in the life cycle was established by Hofmeister as long ago as 1851 it is surprising that very little is in fact known about its anatomy, physiology and ontogeny. Some attempts to rectify this are reported in Verdoorn (1938).

Orth (1936) was one of the earliest workers to attempt to assess the importance of the gametophyte and in a translation by Verdoorn (l.c. p. 149) he "criticises the 'artificial' taxonomic systems of ferns based exclusively on the differences in the annuli, the construction of the sporangia and the indusia and on sorus distribution; he wants these systems to be replaced by a 'natural' system based on the developmental history and the morphology of the gametophyte". Verdoorn commented that "probably most taxonomists will not yet be inclined to go to that length". Waldermain (1938) made a brief comparison of the gametophytes of the genera Thelypteris and Dryopteris.

One of the earliest major works was by Momose (1937-42) who, in a long series of papers, described the gametophytes of Japanese ferns in great detail and with clear illustrations. A concise summary of his findings was given by Iwatsuki (1964b), who considered that the three most significant points arising from Momose's work were:

1) The thelypterids can be classified by features of the gametophyte and the resulting classification is very similar to that produced by considering the morphology of the sporophyte alone.

2) Using Momose's criteria it is feasible to include Currania, Dryoathyrium and Gymnocarpium with the thelypterids. Iwatsuki considered these genera to be more closely related to the athyrioid ferns.

3) Conversely to the first statement above, the features available from the gametophyte are so very few in number and simple in structure that a system of classification cannot be established considering gametophytic characters in isolation from those of the sporophyte.

Stokey has made numerous contributions to the study of the gametophyte (e.g. Stokey, 1951, 1960, Stokey and Atkinson, 1954, Atkinson and Stokey, 1964). In her paper of 1960 she described the hairs which are found on the gametophytes of certain ferns including some thelypterids. She noted that Cyclosorus was unusual in having acicular hairs on the gametophytes of several species, these were mostly unicellular but occasionally two-celled, e.g. T.(Cyclosorus) parasitica* or stellate, e.g. T.(Goniopteris) biolleyi. In this latter example the hairs are similar to those found on the sporophyte and developed on the gametophyte after approximately three months, before the plant reached maturity. By the time the plant was producing sex organs (around nine months) these stellate hairs were found around the margins and all over the surface of the prothallus.

Nayar and Chandra (1961) studied the gametophytes of eight species of Cyclosorus Link from India with special reference to the development of the prothallus. The typical stages of differentiation into its mature state with a cordate outline, thickened midrib, rhizoids and gametangia, usually takes from eight to ten weeks. They also discussed the peculiar property of some of the gametophytes to

---

* Although both Schmelzeisen, 1933 and Nayar and Chandra, 1961, only reported acicular hairs on this species.

proliferate themselves under cultural conditions. They do not note whether this has been found in natural populations nor put forward any possible reasons for its existence. The usefulness of this paper is greatly decreased by a muddled presentation and the failure to describe the complete series of events in the development of a single prothallus.

Holttum, Sen and Mittra (1970) describe the gametophytes of some type species within Thelypteris sens. lat. and mention that "Nothing is known about the gametophyte of this species (T.obliterata), but the reported formation of stellate hairs on the gametophytes of T.biolleyi (Atkinson and Stokey 1964) is certainly significant". I have studied at least the immature gametophyte of T.obliterata and have found capitate hairs around the margin, but few, if any, on the surface. I was not able to discover any hairs, either acicular or stellate, on any of the specimens although it must be noted that none of these were mature.

In this present work a brief study of the gametophyte was undertaken. A few spores from recently gathered fronds were sown very thinly onto a nutrient agar in glass petri dishes. These were placed under artificial light and viewed from time to time using a binocular microscope. The spores very quickly germinated under these conditions and developed in a similar manner to those studied by Nayar and Chandra (1961). Unfortunately, due to invasion by fungi these experiments were concluded prematurely.

At this stage a decision had to be made as to whether further studies on the gametophyte were feasible, considering the fact that although gametophytes can be readily grown under artificial conditions little is known about the prevention of fungal attack or the physiological requirements of the spore and young gametophyte. There is a minimal amount of physiological information regarding the effect

of light, temperature, water and nutrients upon the time taken to germinate or indeed upon the actual morphology of the gametophyte. It is known that in certain species the position of the sex organs can be affected by light and that their production can to a certain extent be controlled by the environment (Verdoorn 1938). It was therefore apparent that before any morphological data could be considered as relevant an extensive study of the physiological factors, which might and do act upon the gametophyte, must be carried out. Such a study was deemed outside the limits of this present work.

As a result of such studies that have been completed however, I tend to agree with Iwatsuki (l.c.) rather than Orth (l.c.) that the features of the gametophyte are likely to be affected by the environment to a great extent and in any event are too few and too little understood to prove significant in present taxonomic systems.

CHAPTER IX

GYMNOCARPIUM

The taxonomic position of the small group of species normally referred to under the generic name Gymnocarpium Newman* has caused much confusion to taxonomists in the past. The genus was established by Newman who included three species: G.robertianum, G.dryopteris and G.phegopteris. Early workers believed these species to be related to Thelypteris sens. lat. by virtue of anatomical features and frond form. Copeland (1929, 1947) placed them in his genus Lastrea while Christensen (1921, 1938) included them in his genus Dryopteris, recognising their difference by placing them in the Dryopteris sens. strict. section of his classification.

This has led other workers to refer these species to the genus Thelypteris e.g. Clapham et al (1964). Manton (1950) however, considered them under the heading of Dryopteris but pointed out the obvious genetic differences between Gymnocarpium and Thelypteris and believed that G.robertianum and G.dryopteris were more closely related to Dryopteris sens. strict. while G.phegopteris was more closely related to the thelypterids T.limbosperma and T.palustris.

Holttum (1959) followed Manton and disagreed with Copeland by placing Gymnocarpium in the Dryopteroid series. He agreed that G.phegopteris showed very much closer relationships with his group

---

* It is proposed to adhere to the name Gymnocarpium here to avoid confusion although there would appear to be sound evidence that this name is illegitimate (Ross 1966) and the name Carpogymnia has been proposed to replace it (Löve and Löve 1966, 1967).

Thelypteris by virtue of hairs and rachis characters and he considered that Copeland had overlooked these. Holttum believed these characters to be more basic in nature than frond form and stipe anatomy which he concluded could be attributed to parallellism in their evolutionary lines.

The detailed reasoning for the exclusion of Gymnocarpium from Thelypteris sens. lat. has been clearly set out by Iwatsuki (1964a p. 5). He points out that although Ching (1933) allied Gymnocarpium to both the thelypteroid series and the athyrioid series the distinctness of these two groups is now clearly defined and any similarities can be attributed to parallel evolution. He believes that an intermediate phyletic position therefore makes little sense and favours an alliance between Gymnocarpium and Woodsia in the athyriod series rather than with the thelypteroid series.

There is little doubt now that G.phegopteris should be referred to the thelypteroid series and all modern classifications include it there. Iwatsuki (1963-5) uses it as the type of his sub-genus Phegopteris of the genus Thelypteris whereas Holttum (1969) uses it as the type of his genus Phegopteris in the family Thelypteridaceae.

By features of the gametophyte, Momose (1937-42) included Gymnocarpium in his sub-family Thelypteridoideae, but Iwatsuki (l.c.) believes that Gymnocarpium, Currania and Dryoathyrium should be removed to the sub-family Athyrioideae.

In this present work a particular study was made of the morphology and anatomy of the two British species of Gymnocarpium so that a comparison might be made with the thelypteroid ferns. The results of this are set out below.

1) GROSS MORPHOLOGY

The fronds of Gymnocarpium are small, typically about 25 cm tall

with a tripartite, tripinnate frond arising from a long, slender, creeping rhizome. The rhizome is much branched so that the fronds may often form dense clumps. The frond itself is thin in texture and the veinlets are branched with not more than one sorus on the terminal veinlet. The sori are exindusiate but unlike most exindusiate thelypteroids the sporangia are glabrous and do not possess glandular hairs on either the stalk or capsule. Glandular hairs of a very similar nature to those found on many thelypterids (see fig. 231) are however found on the lamina and stipe of G.robertianum. A few scales are usually found scattered sparsely on the lower region of the stipe and around the growing point of the rhizome. Scales are absent from the older parts of the rhizome, probably due to its sub-terranean habit (see above p. 17).

The scales of both G.robertianum and G.dryopteris possess capitate hairs around their margins although they are more frequent in the former where nearly every marginal cell possesses a capitate hair, very similar in appearance to those found in the true thelypterids. There are, however, no acicular hairs found associated with the scales, nor are capitate hairs found on the surface of the scale (see fig. 232). It is of interest to note that one of the most readily discernable differences between the two species of Gymnocarpium is the absence of capitate hairs on the frond and rachis of G.dryopteris: as stated here, my observations indicate that they are not absent from the whole plant. If scales are present on the very young crozier and lamina then they are extremely ephemeral and I have been unable to detect any on the species studied.

One conspicuous feature of the Gymnocarpium frond is the groove which runs along the ventral surface of the axes. The groove is open to accept those grooves from the smaller segments. This contrasts

markedly with the thelypterids in which the grooves are non-confluent and the two ridges along the ventral surface of the axis are continuous throughout its length.

At the junction of the two basal pinnae there is a swollen region consisting of rather thinner-walled cells. This appears to act as a point of articulation for the two basal pinnae and the remainder of the frond with the main axis, but the exact function is unknown. No such articulation at the base of the frond is found in any thelypterids although the pinnae frequently have swollen bases, often associated with aerophores. In Gymnocarpium these structures may permit a slight re-orientation in the position of the pinnae relative to the rachis and do not appear to act as a abcision layer.

2) ANATOMY

The anatomy of Gymnocarpium species has been one of the major arguments for their inclusion in Thelypteris sens. lat. The vascular tissue in the rhizome is a dictyostele, usually with three bundles, (see fig. 233) very similar in form to those of Thelypteris. There is very little mechanical tissue and if a bundle sheath is present then it is incomplete. The vascular supply to the stipe branches in a similar manner to that described above for Thelypteris (see figs. 1-3), two hippocampus-type bundles entering the base of the stipe and uniting below the lamina to form a typical U-shaped bundle. Unlike the situation found in the rhizome there is a well developed bundle sheath in both the stipe and rachis. This is probably associated with the slenderness of the stipe but in contrast to the rhizome which, although slender, does not need mechanical tissues for support.

Pinna branches are produced in the typical extra-marginal manner (see fig. 37) and run into all the pinnae including the large basal pair. When a pinna is cleared with potassium hydroxide solution and

stained with basic fuchsin and concentrated hydrochloric acid, the ultimate branches of the vascular system of the frond can be readily observed. These consist of a small number of xylem tracheids which terminate in a more or less swollen region at a short distance from the margin of the lamina, this is usually termed a hydathode (Priestley and Radcliffe 1924). Such hydathodes are also a common feature of the thelypterids.

The sori are produced approximately half-way along the terminal veinlet and are exindusiate. Unlike the exindusiate members of Thelypteris the sporangia do not possess any glandular or acicular hairs associated with the sorus nor is there any tendency for the sorus to elongate along the vein. The sporangia are of the typical Polypodium-type with three stalk cells bearing the capsule which has a vertical band of 10-16 indurated cells and a horizontal stomium.

The lamina is hypostomatal, in common with the majority of ferns, and the epidermal cells are of the typical tesselated type. The stomata are usually of types 2A and 2B as proposed by Kondo (1962), but stomata of types 3A and 3B are also frequently present. In this feature the species of Gymnocarpium are similar to those of Thelypteris (see above p. 34).

3) SPORE MORPHOLOGY

The morphology of the spores of the species of Gymnocarpium is very different from any of the thelypterids so far studied. The spores themselves, in common with the rest of the plant, are comparatively small and monolete with the outer spore wall thrown into large bulbous protuberances (see figs. 204 to 206). From the consideration of similar spore types (Nayar and Devi 1963) it is presumed that these protuberances are hollow and the whole outer layer is lightly attached to the underlying spore coat. The surface of this outer layer is

comparatively smooth and shows no warts, spines or reticulate structures as are typical of the thelypterids. Hence spore morphology gives a clear indication of the basic differences which exist between Gymnocarpium and Thelypteris sens. lat. and indicates the possible closer alliance with other aspidiaceous ferns such as Dryopteris and Polystichopsis.

4) CYTOLOGY

The cytology of the species of Gymnocarpium has been studied using plants from many parts of its geographic range, these form a polyploid series based on a chromosome number of 40 (see Appendix I). I have been unable to carry out any confirmatory counts but it is obvious from the several sources quoted that this is a reliable feature. This gives another clear-cut character which separates Thelypteris, in which the base number never exceeds 36, from Gymnocarpium and indicates its possible allegiance with Dryopteris which has a base number of 41 chromosomes.

It can, therefore, be readily seen that those species commonly placed in Gymnocarpium show several marked differences from the species of Thelypteris sens. lat. Three differences occurring in those features by which the thelypterids are generally classified, namely the presence of typical acicular hairs, the spore type and the basic chromosome number.

CHAPTER X

CONCLUSIONS

The aim of this investigation has been to study anatomical and morphological variation within the thelypterids. This has necessarily involved some evaluation of the ways in which such variations have been used in the past or might now be used in the taxonomy of the group, especially in the light of recent advances in the techniques for studying such variations.

The investigation has fallen naturally under the headings of Anatomy (Chapter III), Morphology (Chapters IV and V), Cytology (Chapter VI), Palynology (Chapter VII) and Gametophytic Studies (Chapter VIII). An evaluation of the role of each of these in the taxonomy of the group as a whole has been included at the conclusion of each section.

With continued study it becomes apparent that although the basic anatomy is remarkably constant throughout the whole of the group, the cytology, palynology and morphology show considerable variations and these variations are frequently interrelated. A brief summary of these findings is given below followed by a scheme of classification which has been worked out on the basis of these interrelationships.

Anatomical studies on a large number of specimens from a wide geographical range and also a wide range of habitats have shown that the basic pattern varies very little between species whether from temperate or tropical climates from the New or Old Worlds or Australasia. By virtue of their anatomical distinctness the group shows both its unity and its distinctness from other groups. Such

variation as does occur, for example in the number of rhizome bundles or number of groups of protoxylem in the stipe, can be attributed to the habitat, size or habit of the species and tend to obscure rather than elucidate any interrelationships. The conclusions from anatomical studies on the thelypterids must therefore be that there is no correlation between anatomical variations and any other characters, except those which can be said to have caused them (for example long-creeping rhizomes can be correlated with fewer vascular bundles and widely spaced stipe bases).

Features of the gross morphology have been used extensively in the taxonomy of the group during the past fifty years. It has been assumed that morphological characters alone are sufficient to delimit the major sub-groups as well as smaller divisions and species. This has inevitably involved placing a greater weight on certain characters, usually the more easily recognisable ones, possibly with the exclusion of other characters which have been either less convenient to study in the field or have just not been considered of sufficient importance. Hence venation has constantly been used as a major factor, despite evidence of its varability, even within a single plant, whereas the distribution of glandular hairs for example has been largely ignored, possibly because of the difficulties involved in distinguishing them on both live and herbarium specimens. Thus the tendency has been to employ those characters which will be most useful in preparing an artificial key and then assuming that these characters can produce a natural classification.

Hairs and scales provide a convenient diagnostic character for the group as a whole, and are a useful key character. They are almost certainly of a constant form, or nearly so, within a species and often also within groups of species having other features in common. Holttum

has delimited Phegopteris, Macrothelypteris and Pseudophegopteris primarily on features of their trichomes. In these species there is a correlation between the type of scale, other morphological characters, spore morphology and cytology but similar relationships have not been worked out in other groups.

Pneumathodes and aerophores are found on many diverse species. No conclusion has been reached on either their function or possible taxonomic merits although the small non-vascular aerophores which are common in Christensen's groups of Glaphyropteris and Steiropteris might prove a good character. It seems likely however that these, like the more prominent vascularised aerophores have developed as a response to the environment rather than being phylogenetically determined. The vascularised aerophores are more specialised and much less widespread and appear to represent very greatly reduced pinnae and occur in only highly mucilaginous species. Because these structures are found in extremely few species they are only of passing interest and of little use for any phylogenetic studies. However, from the view of comparative morphology there is an interesting possible reduction series from pinna to auricle to vascular aerophores of the T.xylodes type and finally to the spine-like aerophore. The non-vascular aerophores below the pinnae appear to represent an alternative adaptation to the problems of water relations within the plant.

The form of the frond runs parallel with the nature of the venation. Species having greatly dissected fronds e.g. Macrothelypteris possesses branching veins and no anastomoses while at the other end of the scale Meniscium possesses entire pinnae and all veins anastomose and in Dictyocline the frond is further reduced to a single unit with a complex arrangement of branching and anastomosing veins. Evidence for the more primitive nature of simple venation is given by

developmental studies and backed up by cytological evidence.

Features of the sorus are frequently used as evidence in phylogenetic studies. In the thelypterids there is a great range of structures from discrete, round, indusiate sori to acrostichoid, linear, exindusiate sori. At a cursory glance it would seem reasonable to assume that the evolutionary trend was simply a line between these two extremes, the discrete round sori being more primitive, this being partially dictated by the venation and frond form as mentioned above. However it appears that those species which have been shown to be primitive in other characters e.g. cytology, frond form and venation in fact are often exindusiate (Macrothelypteris) or possess only a rudimentary indusium (Phegopteris). Hence the situation appears to be that the indusium has been lost and the sori elongated in certain groups of species e.g. Stegnogramma while in others the indusium has been retained despite anastomosis of veins e.g. T.urophylla.

The development of paraphyses on the stalk cells and capsule of the sporangia appears to represent a reaction to the loss of the indusium and the necessity to protect the developing sporangia. The presence or absence of capitate hairs intimately associated with the sporangia is a subject on which little work has been done and their function is unknown although it may be presumed that they are in some way protective and concerned with the maintenance of turgidity in the developing spore mother cells.

The sporangia themselves are all basically very similar in form but show a considerable variation in the number of indurated cells. This variation has been shown to be too great within even single species to be of use in the taxonomy of the group. The number of cells may be an indication of the size of the sporangium and hence possibly of ploidy level.

Although one of the major arguments in favour of separating Thelypteris sens. lat. from Dryopteris sens. strict. has been the basic difference in chromosome number, this same feature has been very little used within the group as a whole. There is now sufficient evidence for considering the chromosome number to be of prime importance in recognising relationships within the group. Morphological studies have indicated that there may have been a trend towards the anastomosis of veins and the simplification of the frond. This evidence becomes more convincing in the light of cytological data which indicates that the species form an aneuploid series, radiating from a base chromosome number of 30-31 pairs. Species with lower chromosome numbers very rarely have any vein anastomoses in their pinnae whilst the species having 36 chromosome pairs are highly likely to show some vein anastomoses.

Until the present time palynology has played only a minor part in the taxonomy of the group, and it has been used merely as a descriptive character rather than as a useful key character. This investigation has shown that there is considerable variation in the architecture of spore exines within the group and that clear electron micrographs can readily be obtained, by the use of the scanning electron microscope, from either fresh, pickled or herbarium specimens. By considering a large number of species it is apparent in many instances that there is an excellent correlation between the spore morphology, the cytology and the gross morphology of the species and that it is possible to use such characters as key characters to form taxonomic groupings. It is believed that there is sufficient evidence to link spore morphology with cytology, however no attempt has been made to postulate relationships between the types of spore architecture which have been found. It is felt that a considerable amount of information

must be obtained from experimental cross-breeding before any comments can be made about interrelationships or evolutionary pathways elucidated by spore morphology alone.

When more information is to hand regarding the physiology and ecology of the gametophyte it may well be possible to utilise its morphology in the taxonomy of the group. At present however there is insufficient evidence for any conclusions in this matter. Because of the limited size and range of associated structures of the gametophyte the information content of the gametophyte will always be considerably less than that of the sporophyte and hence its use in taxonomy must be limited.

By considering the anatomy, morphology, cytology and palynology of species of Gymnocarpium it has been possible to further indicate the separateness of this group from Thelypteris.

As a result of the investigations into the cytology and palynology it has been possible to draw up a system for the classification of the thelypterids on a world wide basis using primarily these two characters plus in certain instances geographical and morphological data. Whilst it is not intended that such a system should be definitive it is hoped that it may form the basis of further studies on the group as a whole. Because of this no new nomenclatural epithets have been proposed, but where an already existing group coincides exactly with the group that is proposed here it is given in capitals (e.g. STEGNOGRAMMA).

Proposed System Of Classification Of The Thelypterids Based On Spore Morphology, Cytology And Gross Morphology

A Venation free to dictyoclinioid; sori exindusiate, elongate along veins, sometimes reticulate; spores spino-reticulate; base chromosome number 36; tropical and temperate species; (e.g. fig. 125):

STEGNOGRAMMA

T.aspidioides	(fig. 126)
T.griffithii	(fig. 125)
T.gymnocarpa	(fig. 128)
T.pozoi	(fig. 127)

B Veins all free, running to sinus membrane, sinus or margin above the sinus; sori indusiate or exindusiate, round or elongate along veins; spores variously ornamented; base chromosome number 27-36:

1) Spores with raised reticulate tectum:

a) Spores with a rather imperfect reticulate tectum; base chromosome number 27; North American species:

T.nevadensis	(fig. 113)
T.noveboracensis	(fig. 112)

b) Spores with a uniform, usually perforated, raised, reticulate tectum; (e.g. fig. 207):

i) Base chromosome number 29, Central American and Carribbean species; (e.g. fig. 73):

Oochlamys, AMAUROPELTA

T.balbisii	(fig. 81)
T.cheilanthoides	(fig. 86)
T.concinna	(fig. 80)
T.germaniana	(fig. 90)
T.gracilis	(fig. 85)
T.heteroclita	(fig. 77)
T.limbata	(fig. 88)

AMAUROPELTA (Cont.) T.linkiana (fig. 84)
T.navarrensis (fig. 82)
T.nockiana (fig. 76)
T.oligocarpa (fig. 75)
T.opposita (fig. 91)
T.pachyrachis (fig. 89)
T.resinifera (fig. 83)
T.rudis (fig. 74)
T.sancta (fig. 78)
T.sancta var. magna (fig. 79)
T.thomsonii (fig. 73)
T.underwoodiana (fig. 87)

ii) Base chromosome number 31, pan-tropical species; (e.g. fig. 106):

MACROTHELYPTERIS

T.multiseta (fig. 110)
T.ornata (fig 107)
T.polypodioides (fig. 109)
T.setigera (fig. 111)
T.torresiana var. calvata (fig. 106)
T.viridifrons (fig. 108)

c) Spores with a smooth tectum with slightly raised reticulate patterning; (e.g. fig. 210):

i) Base chromosome number 31, species from India and S.E. Asia; (e.g. fig. 95):

Toppingia, PSEUDOPHEGOPTERIS

T.aurita (fig. 95)
T.brunnea (fig. 104)
T.bukoensis (fig. 101)
T.cruciata (fig. 98)
T.cyclocarpa (fig. 99)
T.hirtirachis (fig. 103)
T.keraudreniana (fig. 105)
T.levingei (fig. 100)

PSEUDOPHEGOPTERIS (Cont.) T.pyrrhorhachis (fig. 97)
T.subaurita (fig. 96)
T.yunkweiensis (fig. 102)

ii) Base chromosome number 34, one species from Sikkhim:

T.elwesii (fig. 120)

iii) Base chromosome number 35, one species from Malaya:

T.flaccida (fig. 121)

d) Spores with irregular ridges with reticulate bases; base chromosome number 30; Northern hemisphere species; (e.g. fig. 92):

Lastrella, PHEGOPTERIS

T.decursive-pinnata (fig. 94)
T.hexagonoptera (fig. 92)
T.phegopteris (fig. 93)

e) Tectum of spores formed from reticulate ridges; (e.g. fig. 217):

i) Base chromosome number 32, one species from Malasia:

T.pectiniformis (fig. 117)

ii) Base chromosome number 36, species from Asia:

T.gracilescens (fig. 132)
T.hattorii (fig. 142)
T.laxa (fig. 133)
T.uraiensis (fig. 140)

iii) Base chromosome number 36, one species from Jamaica:

T.firma (fig. 143)

f) Spores with spino-reticulate ridges; (e.g. fig. 194):

i) Base chromosome number 31; one species from the Far East:

T.japonica (fig. 114)

ii) Base chromosome number 32; one species from the U.S.A.:

T.simulata (fig. 116)

iii) Base chromosome number 34; one species from Korea to Japan:

T.quelpaertensis (fig. 119)

g) Tectum of spores formed from raised, reticulate arches; base chromosome number 36; one S.E. Asian species:

T.erubescens (fig. 134)

h) Spores with spino-reticulate tectum;

i) Large reticulate spines; base chromosome number 35; one species with a world wide distribution:

THELYPTERIS

T.palustris (fig. 124)

ii) Minute reticulate spines; base chromosome number 36; species from S.E. Asia:

T.calcareta (fig. 141)

T.crassifolia (fig. 130)

2) Spores with a ridged (winged) tectum:

a) Base chromosome number 34; scales with double hairs on margins; one species from the Northern hemisphere:

OREOPTERIS

T.limbosperma (fig. 118)

b) Base chromosome number 35; one species from the Far East:

T.esquirolii (fig. 123)

c) Base chromosome number 36:

i) Species from West Indies and Tropical America:

T.decussata (fig. 135)
T.deltoidea (fig. 137)
T.wrightii (fig. 147)

ii) Asian species:

T.duclouxii (fig. 144)
T.nipponica (fig. 145)
T.paleata (fig. 136)
T.squamaestipes (fig. 146)

3) Spores with a spiny tectum; base chromosome number 36:

a) Spores trilete; small projections over whole of surface; one species from S.E. Asia:

T.ciliata (fig. 129)

b) Spores with rounded spines without a ridged or reticulate base; Asian species:

T.subochthodes (fig. 139)
T.xylodes (fig. 138)

C Venation goniopteroid (some veins anastomosing):

1) Spores reticulate:

a) Reticulate ridges; one species from the West Indies:

T.patens (fig. 154)

b) Arched-reticulate; one species from Australasia:

T.pennigera (fig. 153)

c) Spino-reticulate; one pan tropical species:

T.gongylodes (fig. 152)

d) Tectum undulating and reticulate; one species from Malasia:

T.singalanensis (fig. 122)

2) Spores winged:

a) Species from the New World:

i) Narrow crenate ridges; species having stellate hairs at least on scales:

Asterochlaena, GONIOPTERIS

T.asplenioides (fig. 166)
T.biolleyi (fig. 163)
T.guadeloupensis (fig. 170)
T.hastata (fig. 194)
T.leptocladia (fig. 198)
T.megalodus (fig. 181)
T.nephrodioides (fig. 190)
T.obliterata (fig. 168)
T.paucijuga (fig. 192)
T.poiteana (fig. 165)
T.reptans (fig. 169)
T.sclerophylla (fig. 167)
T.serrulata (fig. 162)
T.tetragona (fig. 179)
T.venusta (fig. 161)
T.venusta var. usitata (fig. 164)

ii) Smooth thickened ridges; some stellate hairs:

T.asterothrix (fig. 172)
T.cordata (fig. 199)

iii) Thick ridges with very small spines; no stellate hairs:

T.kunthii (fig. 148)

iv) Spores with narrow crenate ridges; no stellate hairs:

T.bangii (fig. 191)
T.dentata (fig. 159)
T.invisa (fig. 173)
T.parasitica (fig. 178)
T.sagittata (fig. 196)
T.serra (fig. 131)
T.vivipara (fig. 193)

b) Species from Asia, Africa and Australasia:

i) Spores with narrow crenate ridges:

T.afra (fig. 175)
T.crinipes (fig. 157)
T.insularis (fig. 197)
T.interrupta (fig. 160)
T.molliuscula (fig. 177)
T.quadrangularis (fig. 174)
T.rubra (fig. 180)
T.sub-pubescens (fig. 176)
T.tonkinensis (fig. 195)
T.triphylla (fig. 158)
T.truncata (fig. 156)
T.urophylla (fig. 182)

ii) Thick crenate ridges:

T.extensa (fig. 171)

3) Spores with spiny tectum:

a) Rounded spines arranged in ridges:

T.ferox (fig. 184)
T.glanduligera (fig. 185)

b) Ridged tectum with very small spines:

T.kunthii (fig. 148)
T.megaphyllus (fig. 149)
T.multilineata (fig. 150)
T.penangiana (fig. 183)
T.rubicunda (fig. 151)

c) Large rough spined tectum:

T.accuminata (fig. 188)
T.papilio (fig. 155)
T.polycarpa (fig. 187)
T.taiwanensis (fig. 186)

D Venation meniscioid; pinnae more or less entire; base chromosome number 36; pan tropical; spores with minutely spino-reticulate ridges (e.g. fig. 214):

a) New World species:

MENISCIUM

T.angustifolia

T.reticulata (fig. 201)

T.salicifolia (fig. 200)

T.serrata (fig. 203)

b) Old World species:

AMPELOPTERIS

T.prolifera (fig. 202)

ACKNOWLEDGEMENTS

I should like to extend my thanks to the following:

All donors of specimens (as noted in the text) and especially Professor R.E. Holttum of the Royal Botanic Gardens, Kew.

Professors J.H. Burnett, S.L. Ransome and A.D. Bradshaw for the use of facilities in their respective departments.

The Keeper of Botany of the British Museum (Natural History) for permission to use the Cryptogamic Herbarium and Mr. Clive Jermy and his staff for their assistance and advice.

Mr. J. Kent for assistance with the Transmission Electron Micrography.

Mr. Eric Boult and Mrs. Margaret Iley of the Electron Microscope Unit in the Chemistry Department of the University of Newcastle upon Tyne for advice and assistance with the Scanning Electron Micrography.

My wife who has willingly, and frequently, given up numerous hours to assist by working in the dark room, checking the manuscript and typing both the draft and final copies.

My Supervisor, Dr. Trevor Walker, who provided both the original idea and many of the specimens cited and has been a constant source of advice and encouragement.

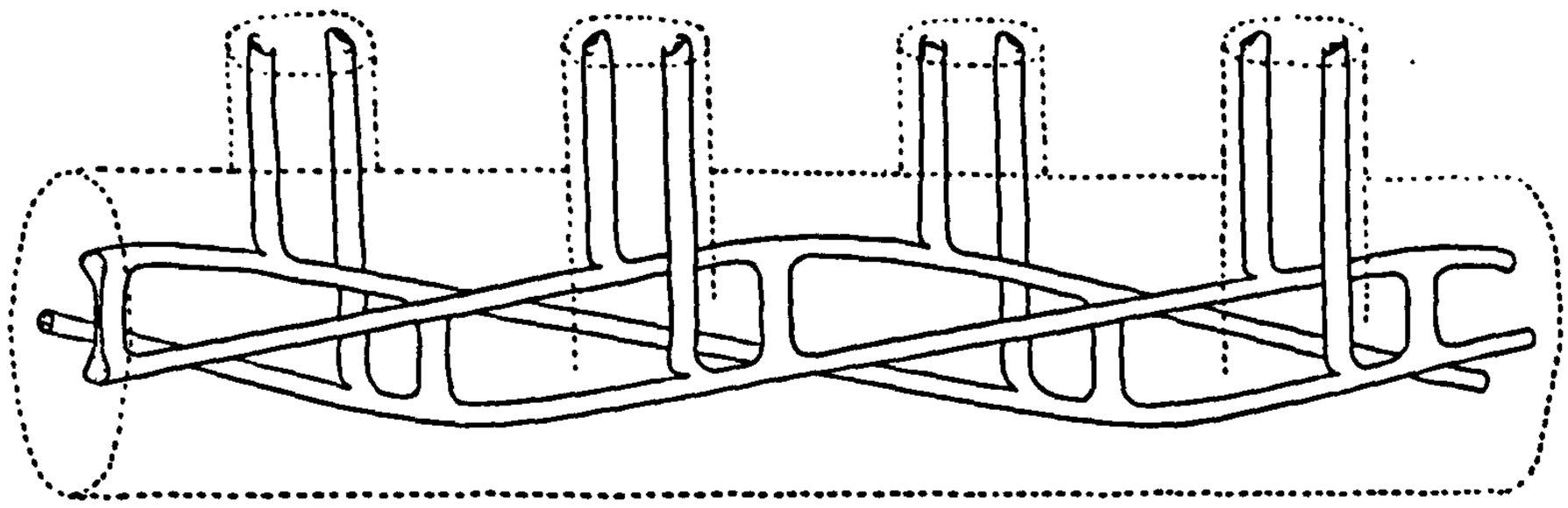
Finally to the Science Research Council who provided the necessary financial support.

PLATE 1

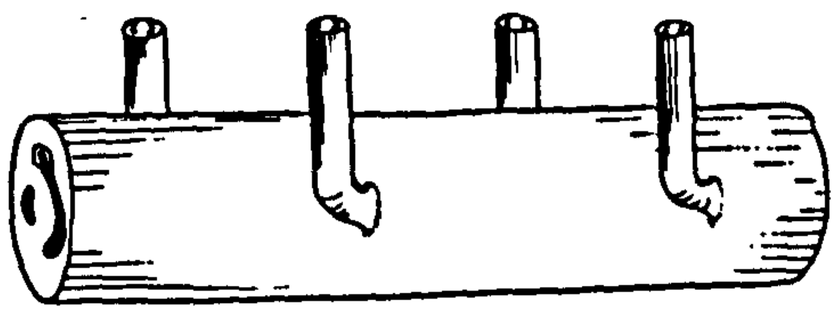
Fig. 1 Diagram of vascularisation of a typical creeping rhizome.

Fig. 2 Diagram of the arrangement of stipe bases on a typical creeping rhizome.

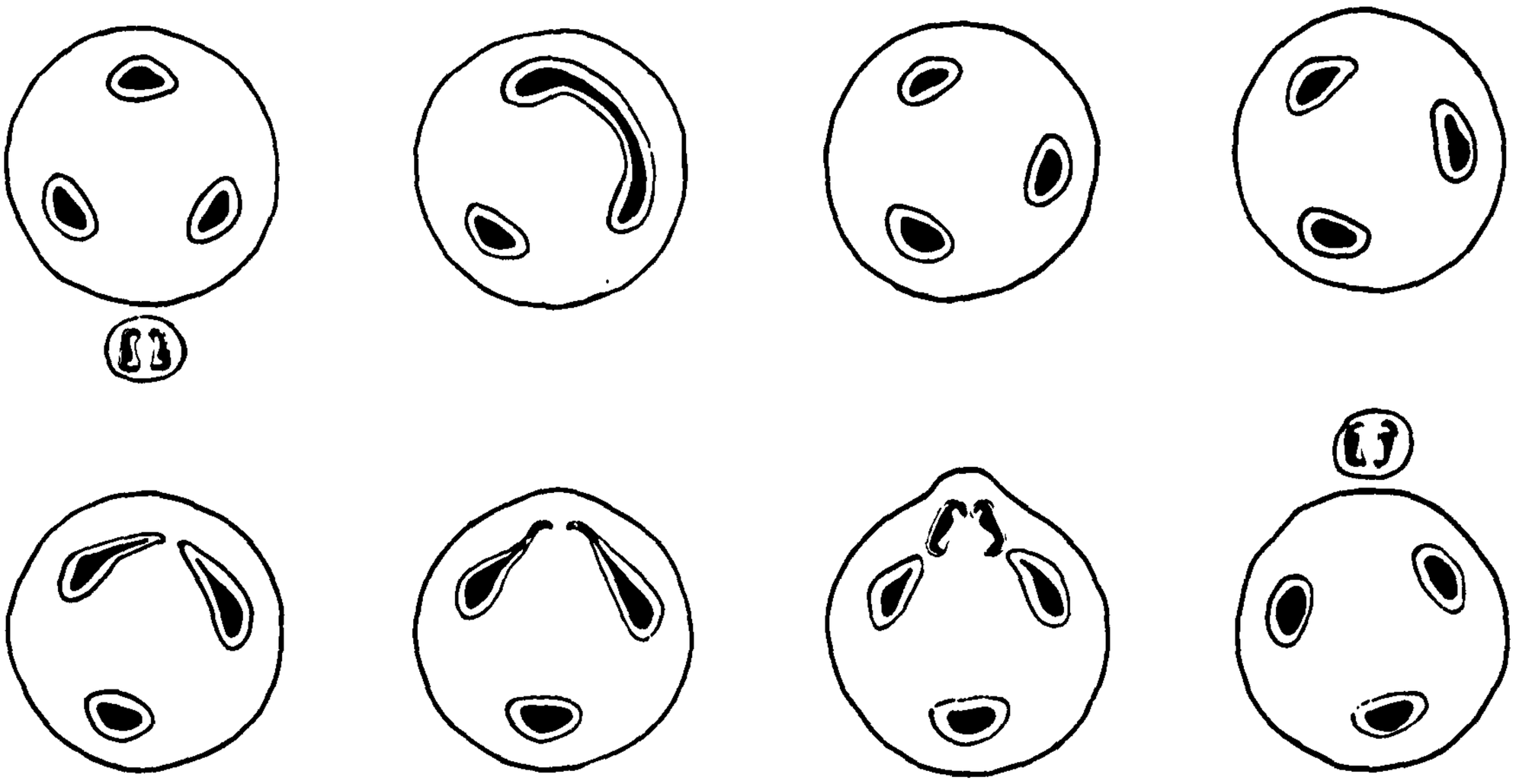
Fig. 3 Serial sections along a typical creeping rhizome, numbered 1-8.



1



2



3

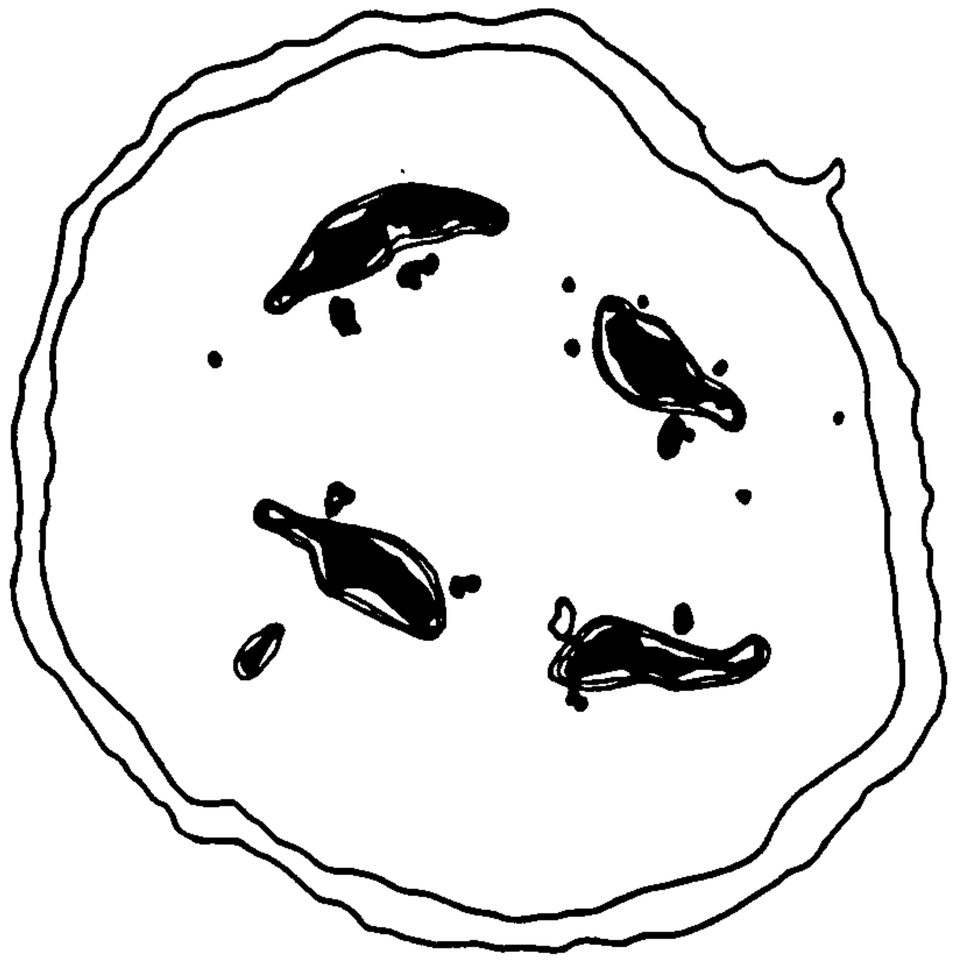
PLATE 2

Fig. 4 Transverse section of creeping rhizome of T.gongylodes.

Fig. 5 Transverse section of creeping rhizome of T.serra (shaded areas represent groups of sclerised cells).

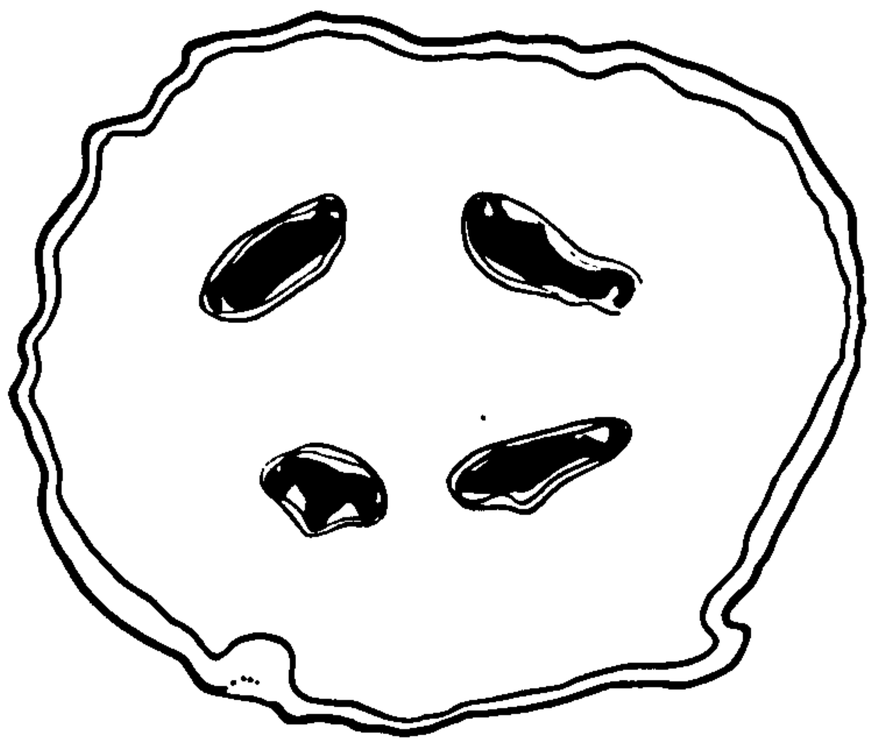
Fig. 6 Transverse section of old root of T.gongylodes.

Fig. 7 Transverse section of vascular bundle of T.obliterata from the mid-stipe region.

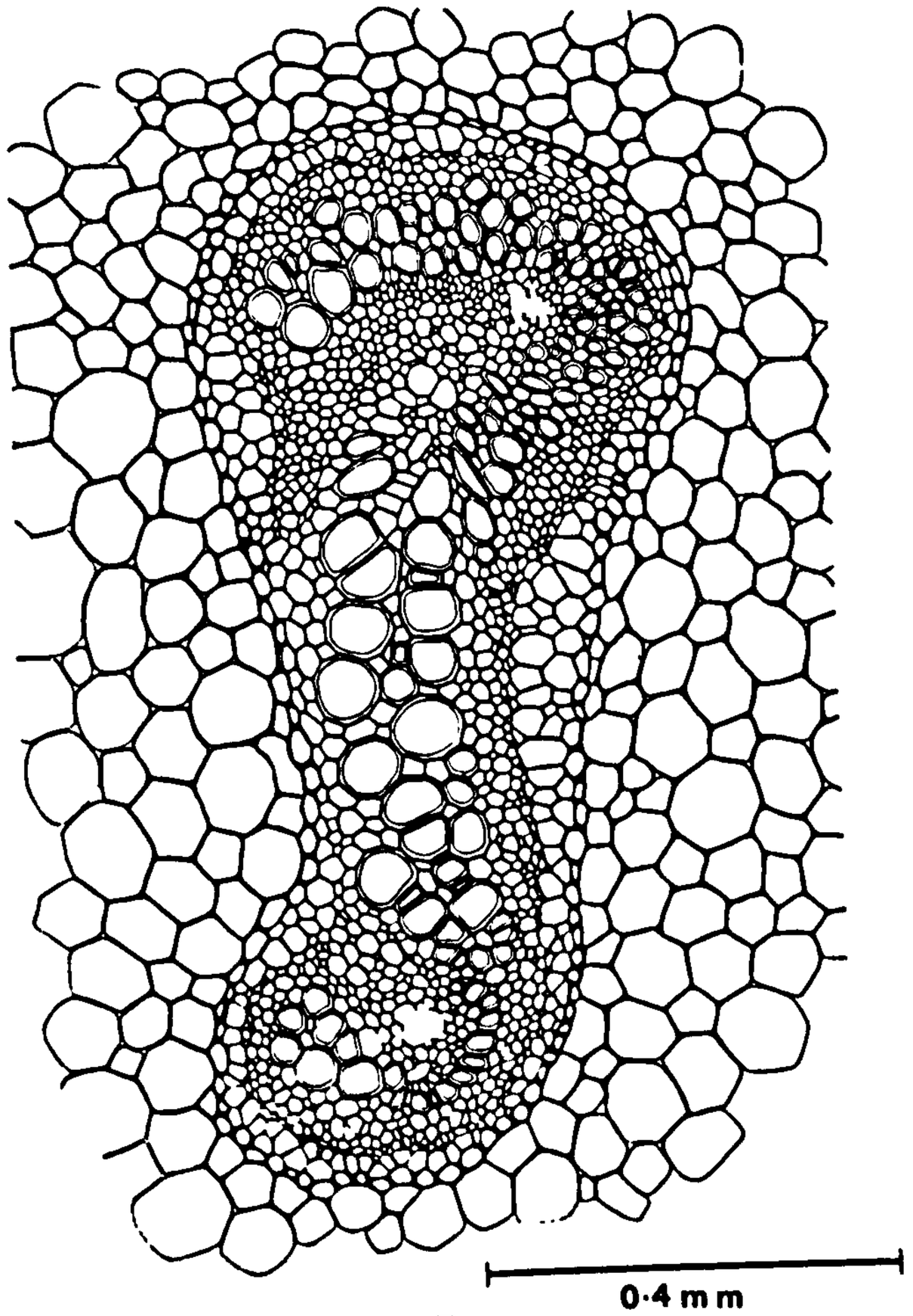


5·0 mm

5

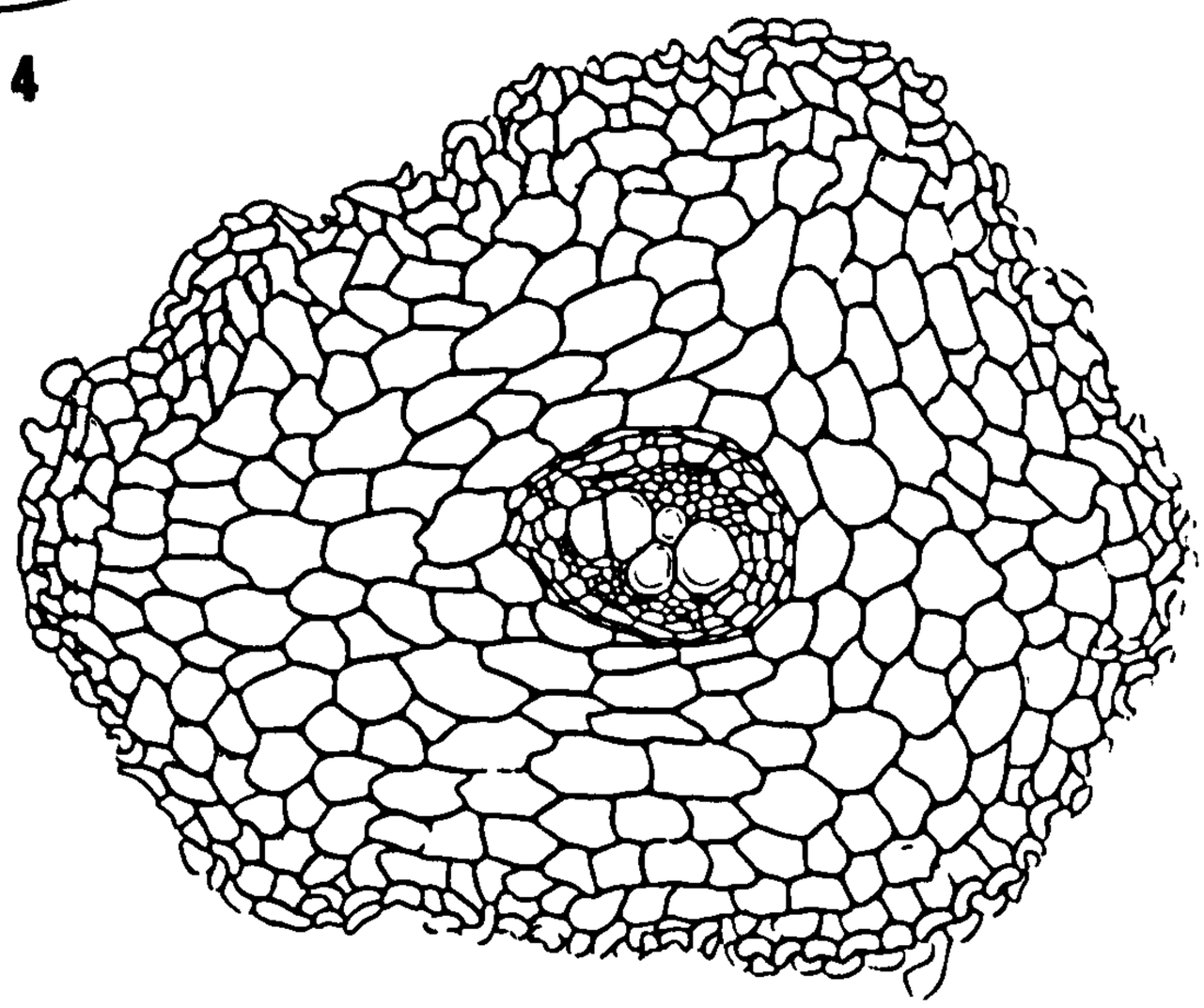


4



0·4 mm

7



6

0·4 mm

PLATE 3

Diagrams to illustrate the variety of size and form of the trace from the mid-stipe of various thelypterids. The protoxylem region and bundle sheath are represented by dotted lines and the sclerenchymatous regions are dotted.

Fig. 8 T.megalodus

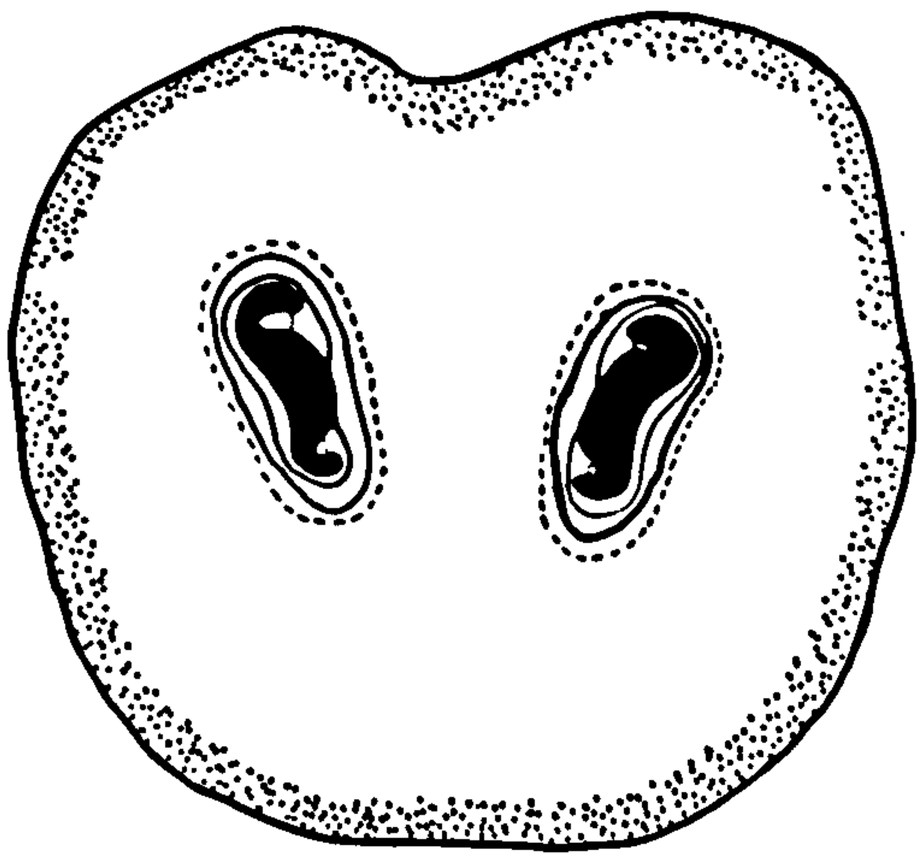
Fig. 9 T.decussata

Fig. 10 T.brachyodus

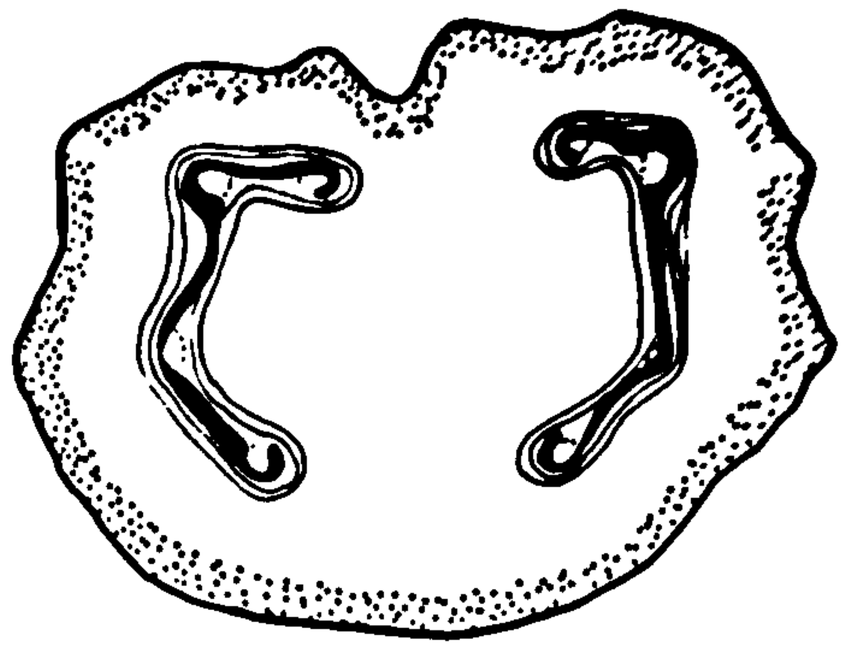
Fig. 11 T.megaphylla

Fig. 12 T.truncata

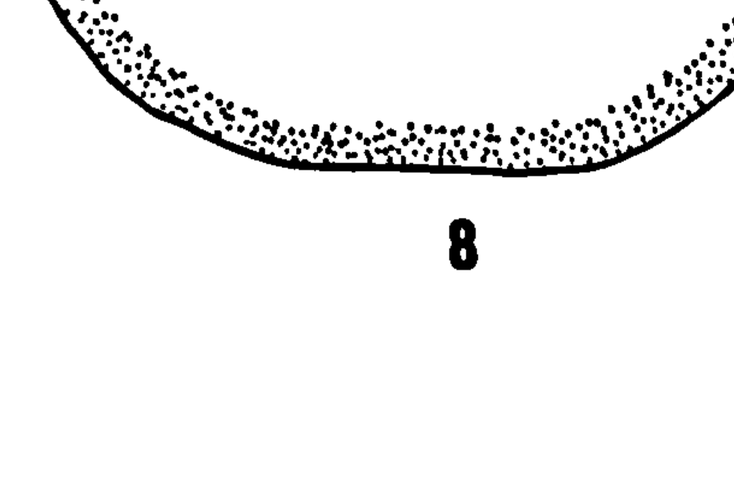
Fig. 13 T.triphylla



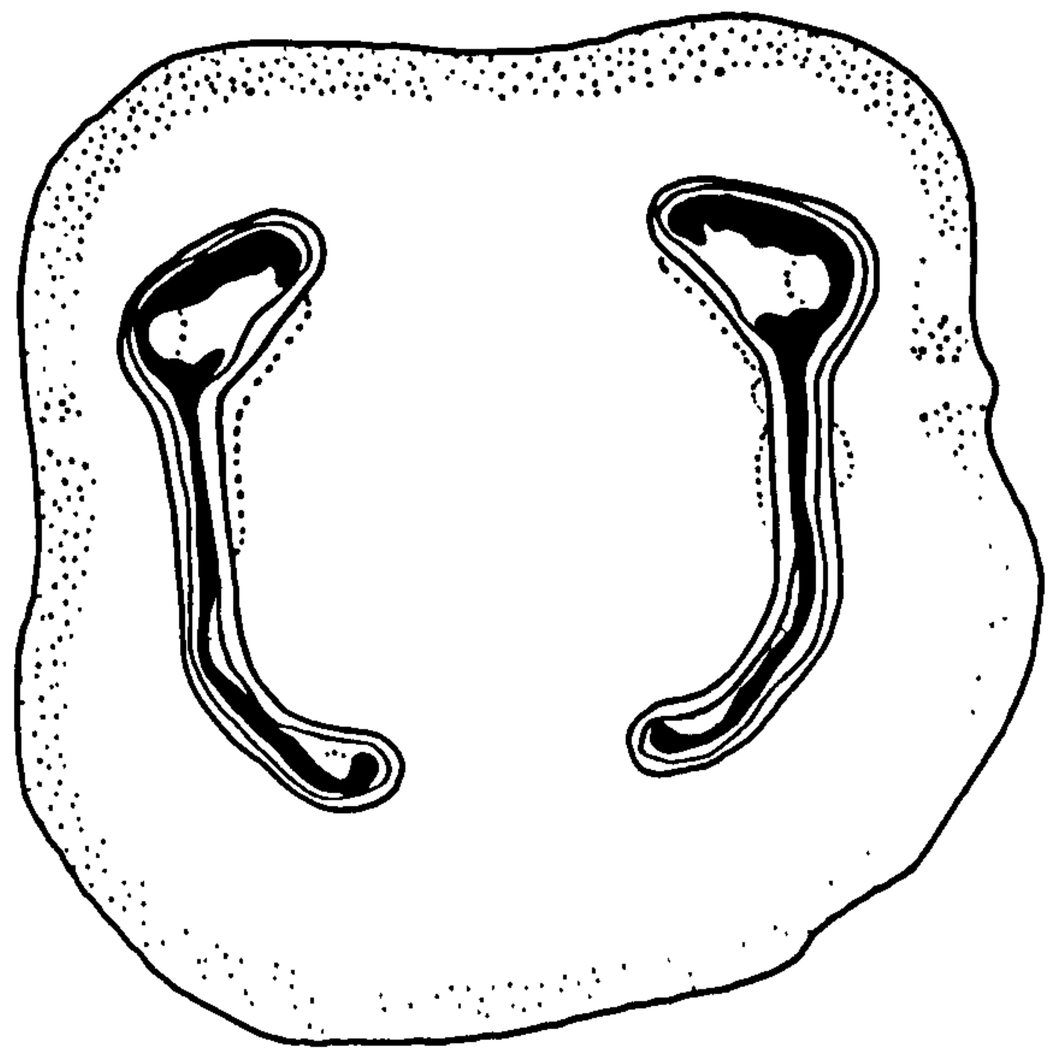
8



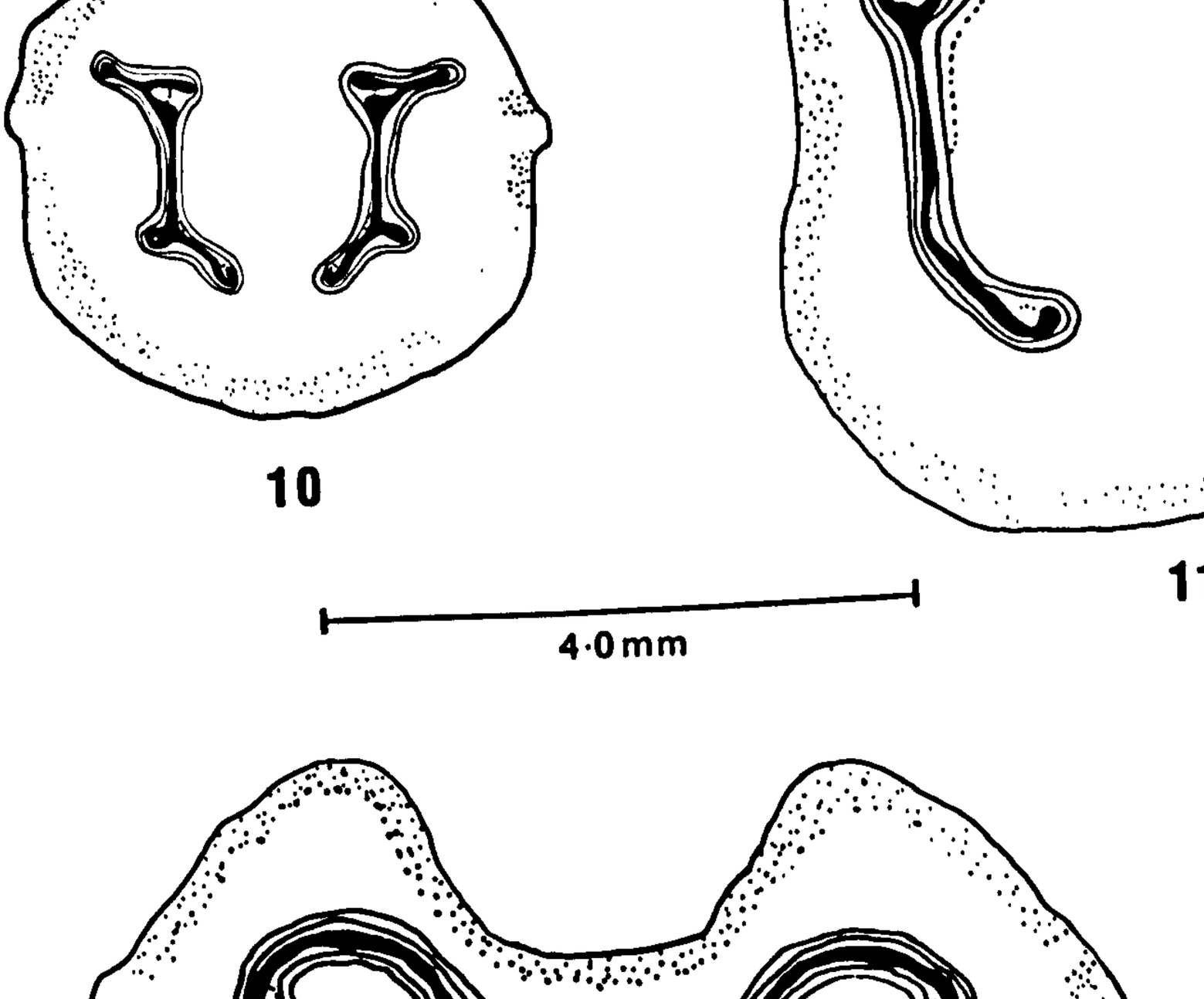
9



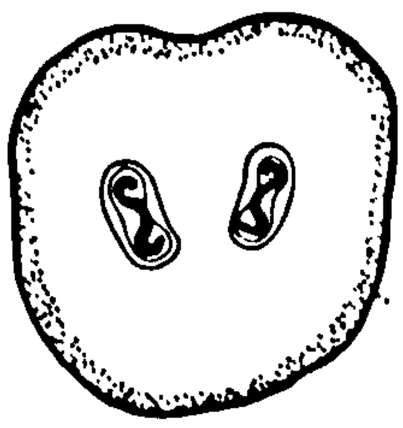
10



11



12



13

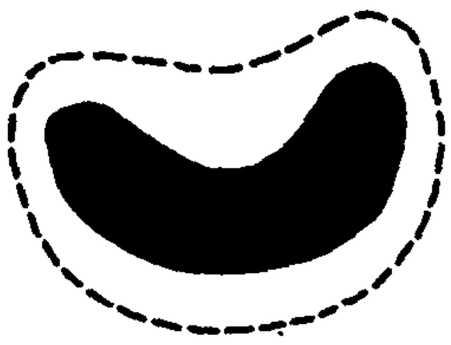
PLATE 4

Fig. 14 Ogura's scheme for the evolution of stipe traces in various ferns.

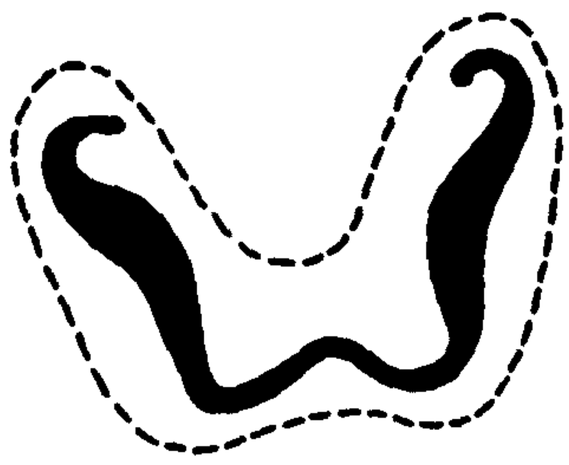
a) "Basic fern" type
b) Loxsoma-type
c) Onoclea-type
d) Aspidium-type

Fig. 15 Transverse section of a pneumathode of T.brachyodus, showing how partially sclerised cortical cells are found in a position immediately underlying the epidermis along the line of the pneumathode.

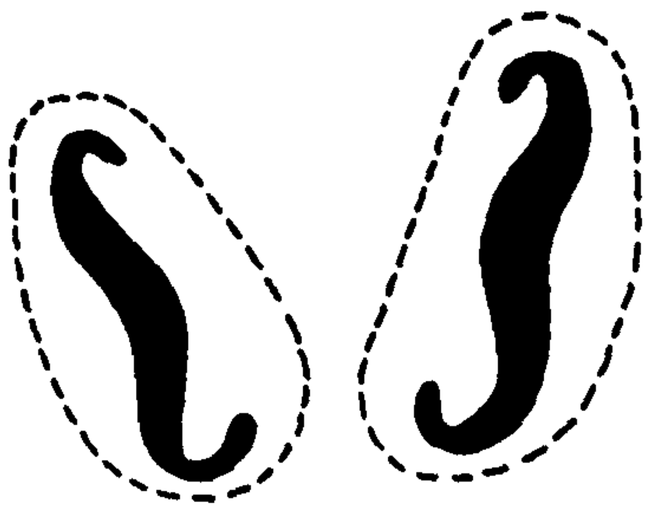
Fig. 16 Diagram of stomata on pneumathode of T.truncata. Note the non-tesselated epidermal cells and the irregular, "anomocytic" type of stomata.



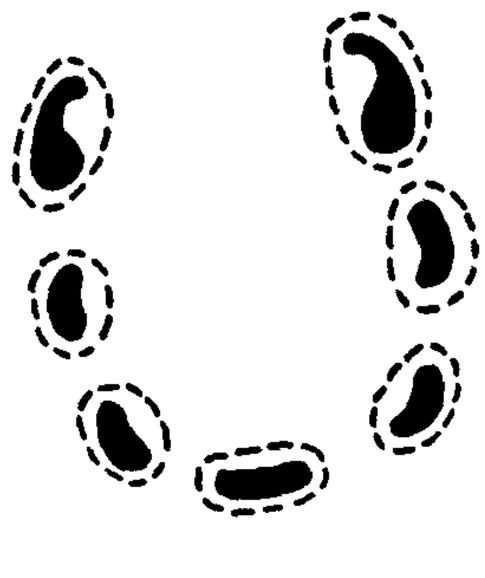
a



b

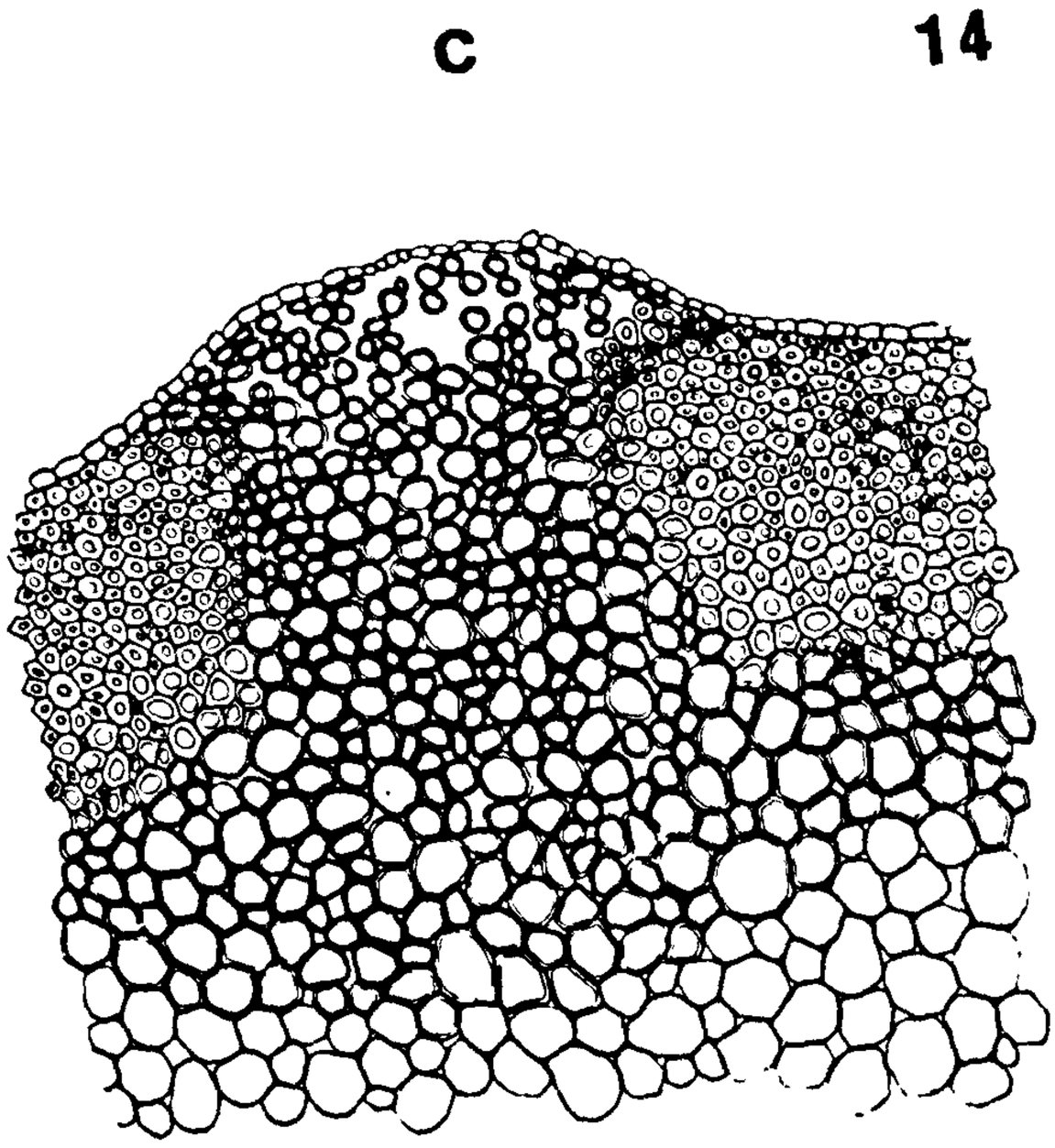


c



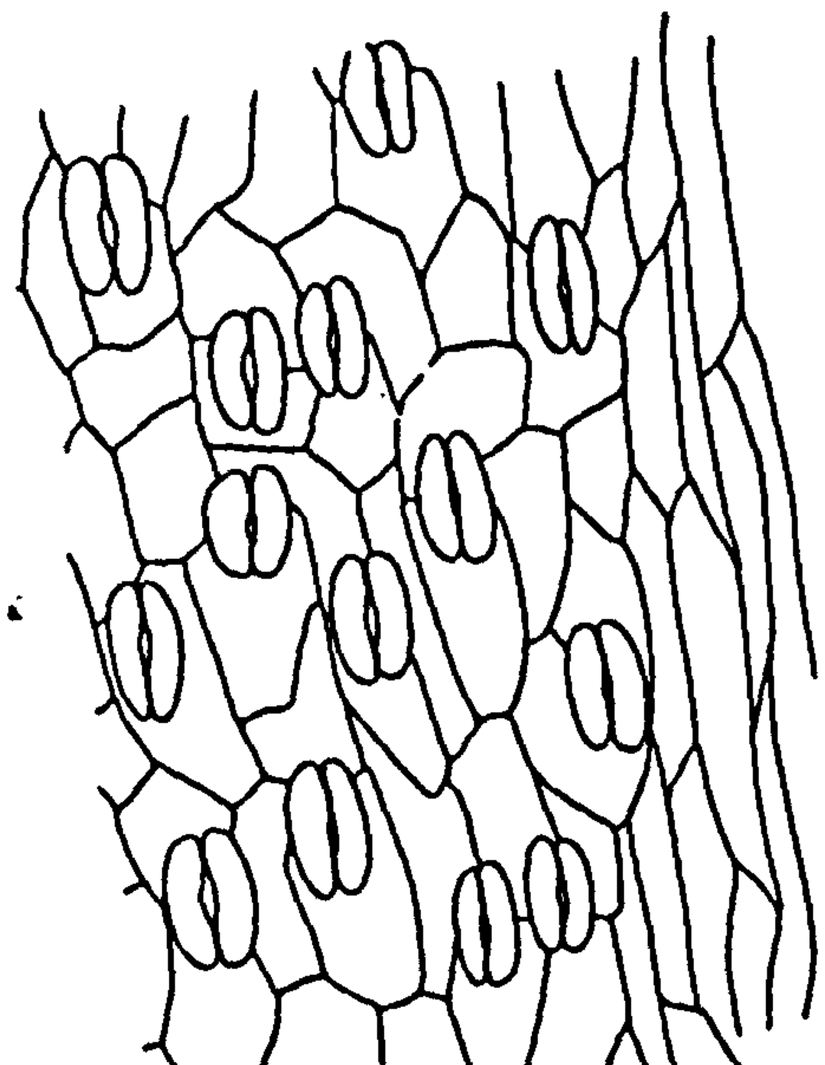
d

14



15

0·5 mm



16

0·1 mm

PLATE 5

Silhouettes (x 1/6) Of Various Thelypterids To Show The Range Of Frond Form

Fig. 17 T.heteroclita

Fig. 18 T.concinna

Fig. 19 T.triphylla

Fig. 20 T.deltoidea

Fig. 21 T.extensa (approx. x 1/12)

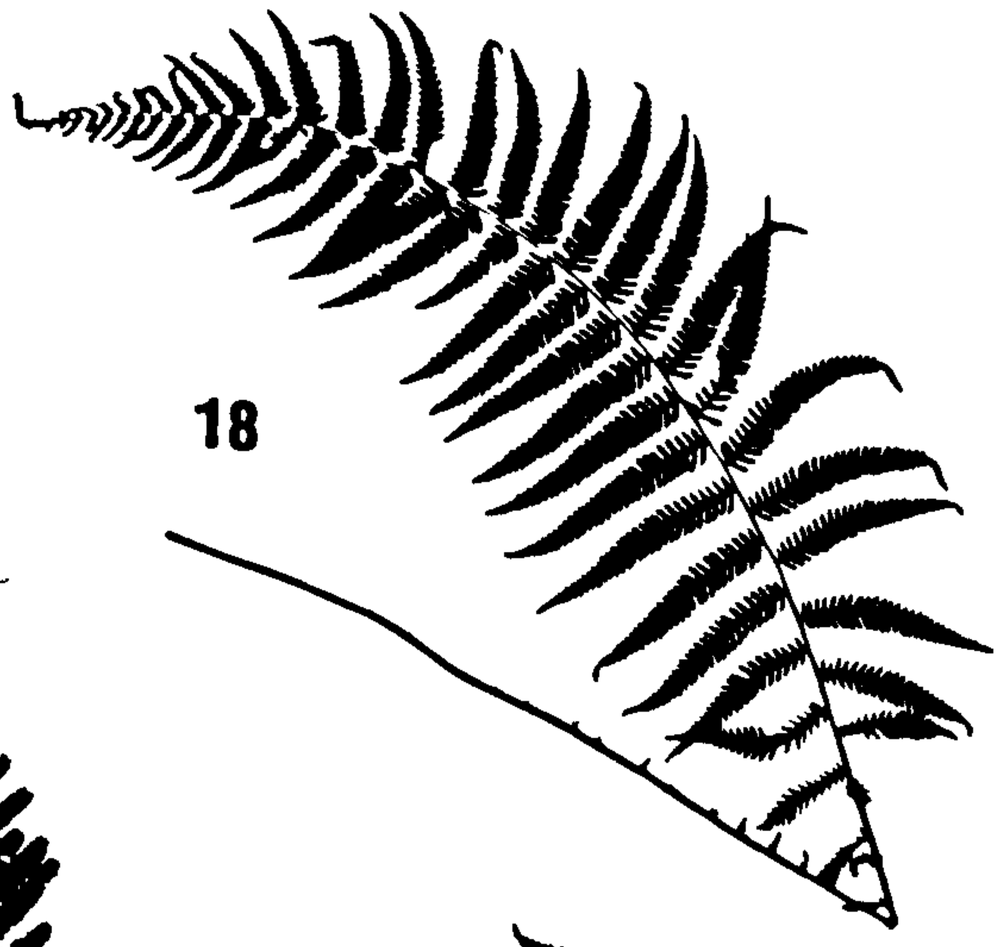
Fig. 22 T.oligocarpa

Fig. 23 T.obliterata

Fig. 24 T.reptans

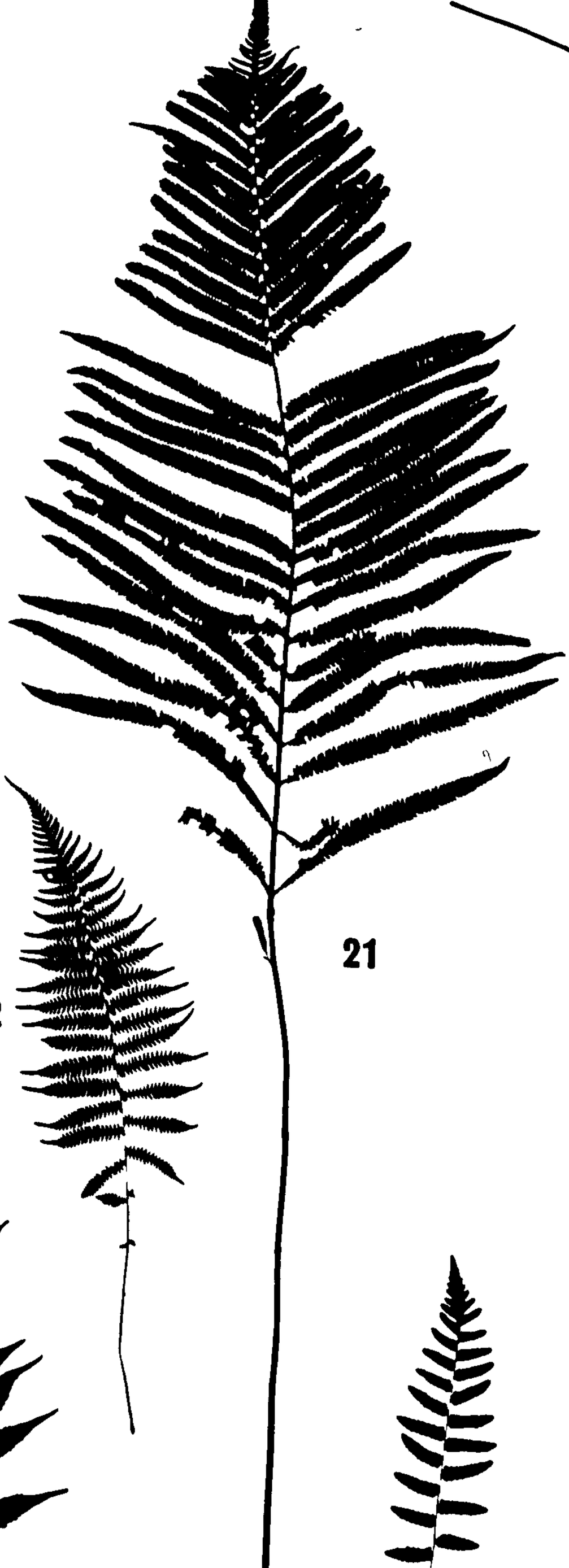
Fig. 25 T.kunthii

17



18

19



20

22

21

23

24

25

PLATE 6

Silhouettes (x 1/6) Of Various Thelypterids To Show The Range Of Frond Form

Fig. 26 T. ~~asplenioides~~ quadeloupensis

Fig. 27 T.nockiana

Fig. 28 T.linkiana

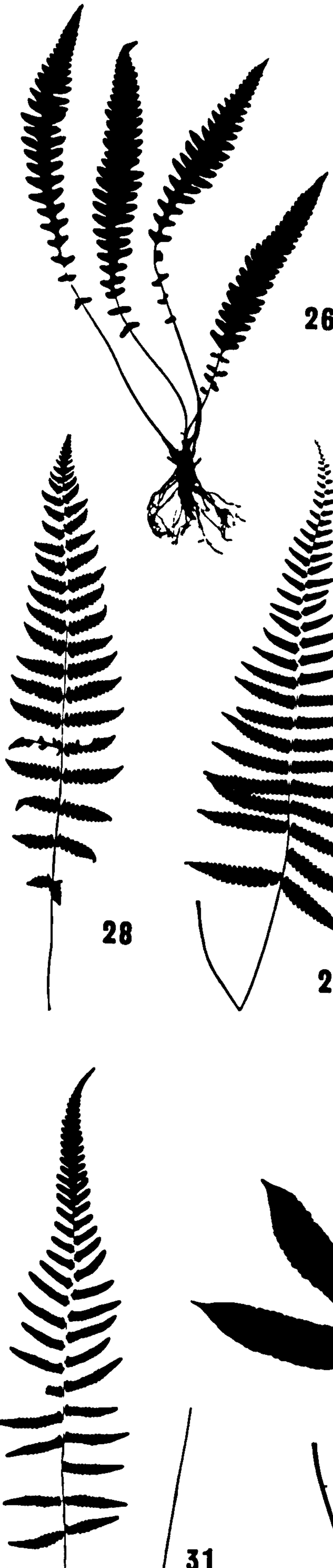
Fig. 29, T.leptocladia

Fig. 30 T.angustifolia

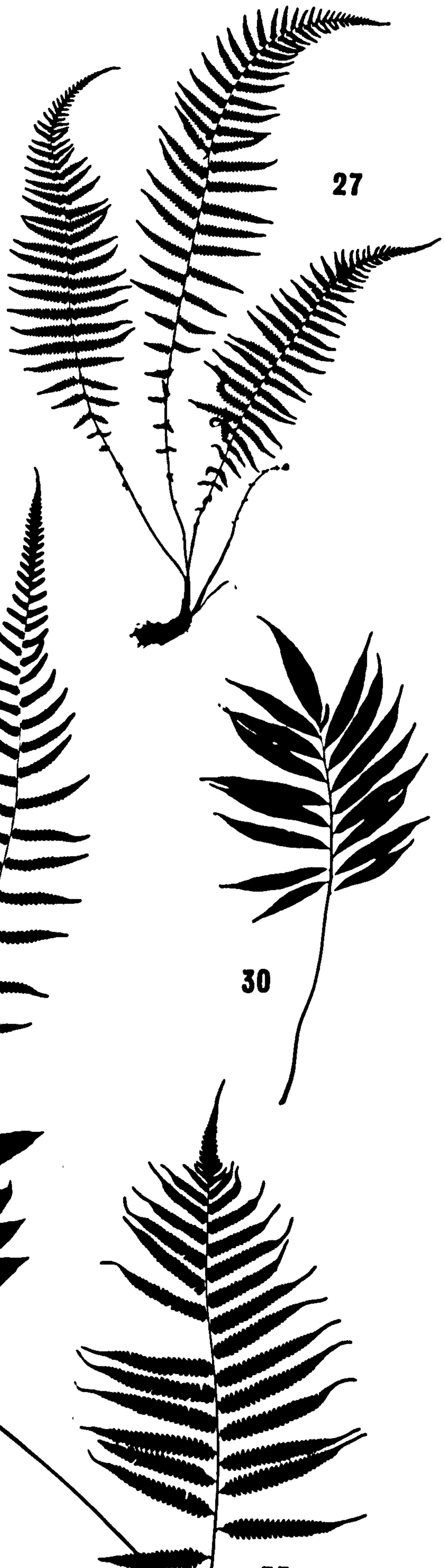
Fig. 31 T.hybrid (probably leptocladia x reptans)

Fig. 32 T.poiteana

Fig. 33 T.biolleyi



26



27

28

29

30

31

32

33

PLATE 7

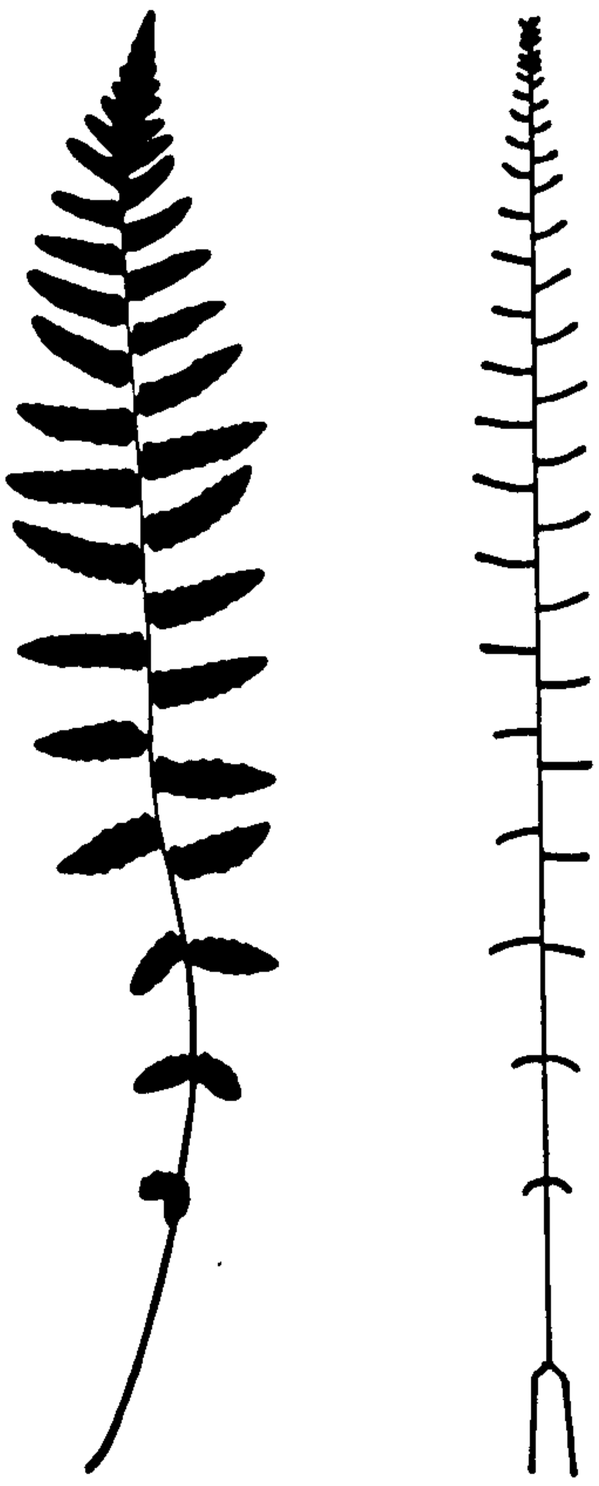
Diagrams to show differences in the relationship between the frond type and the position of the fusion of the vascular bundles in the stipe of various thelypterids.

Fig. 34 T.resinifera

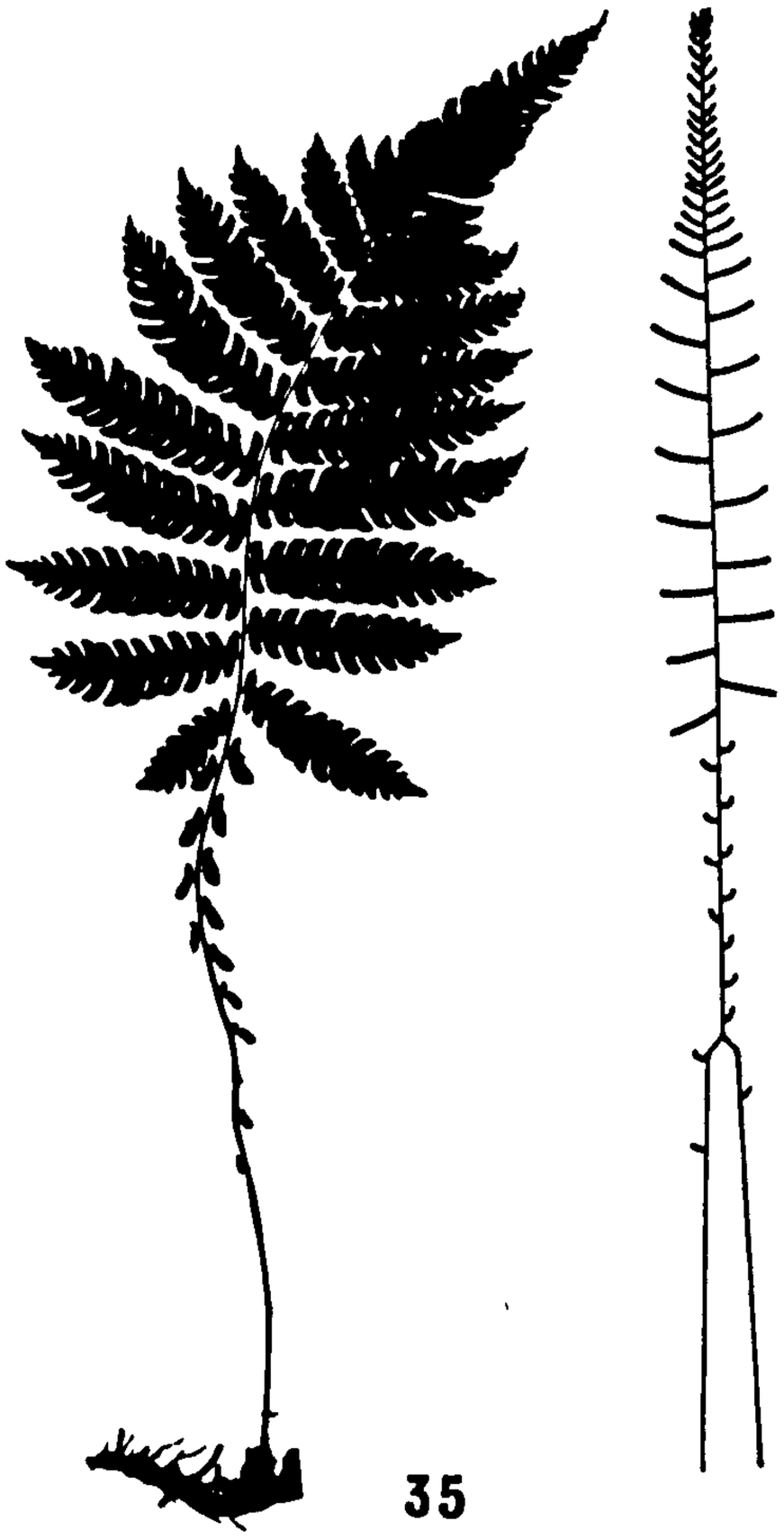
Fig. 35 T.deltoidea

Fig. 36 T.kunthii

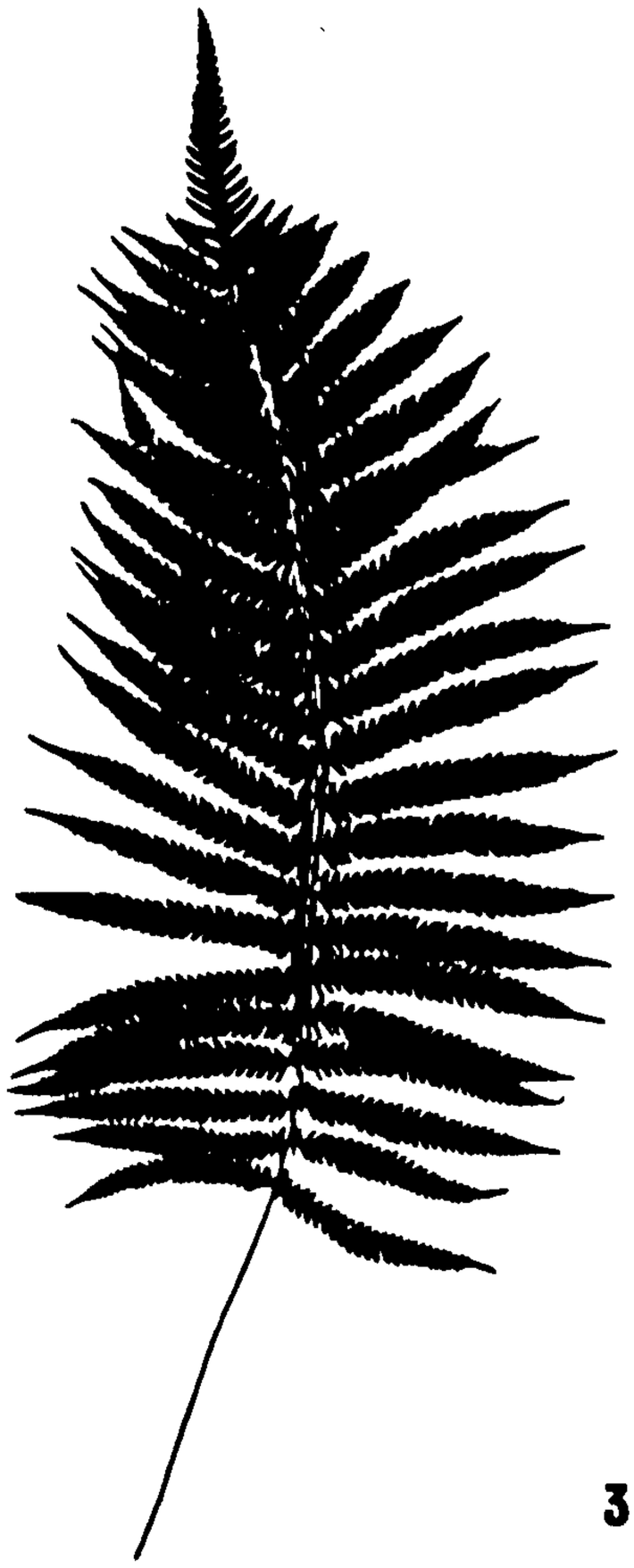
N.B. Not to the same scale.

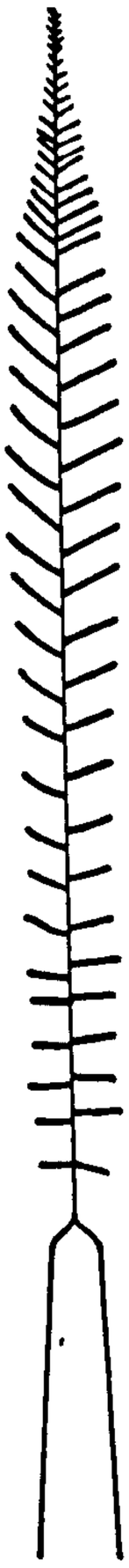


34



35





36

PLATE 8

Fig. 37 Serial sections to illustrate the typical extra-marginal type of branching of the main rachis trace into a pinna (T.resinifera)

Fig. 38 Transverse section of the costa of T.resinifera.

a

b

c

d

e

f

g

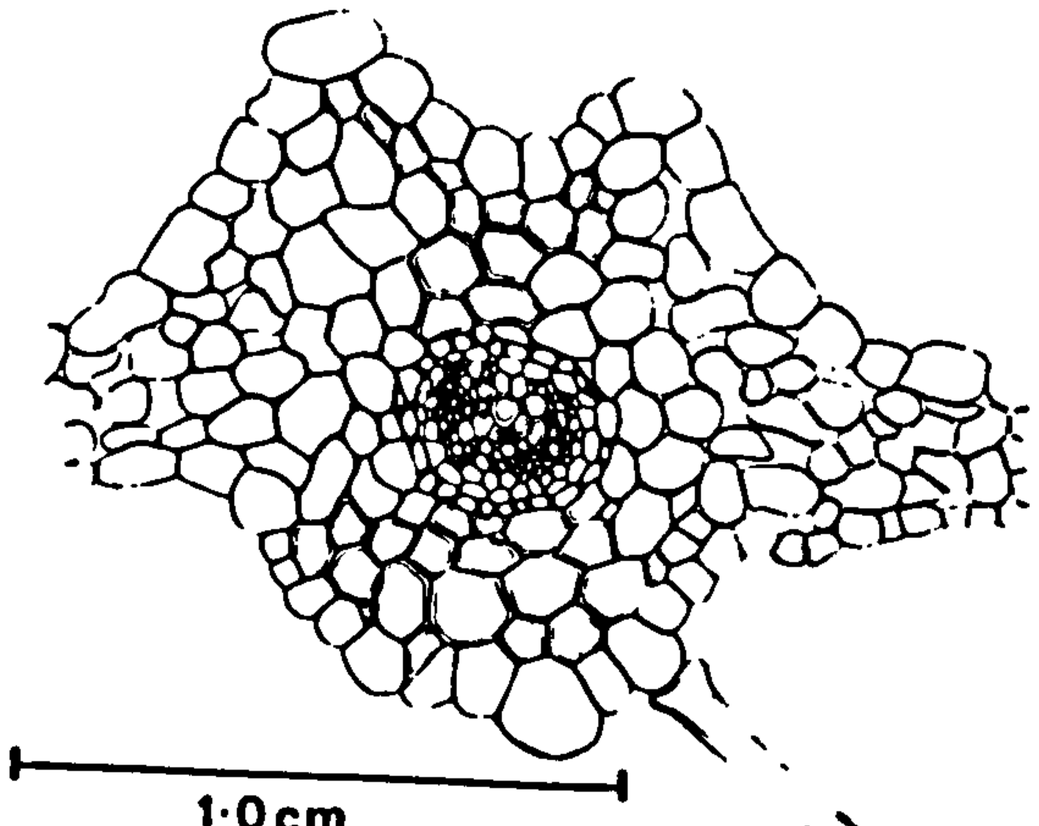
h

i

j

37

2·0 mm



1·0 cm

38

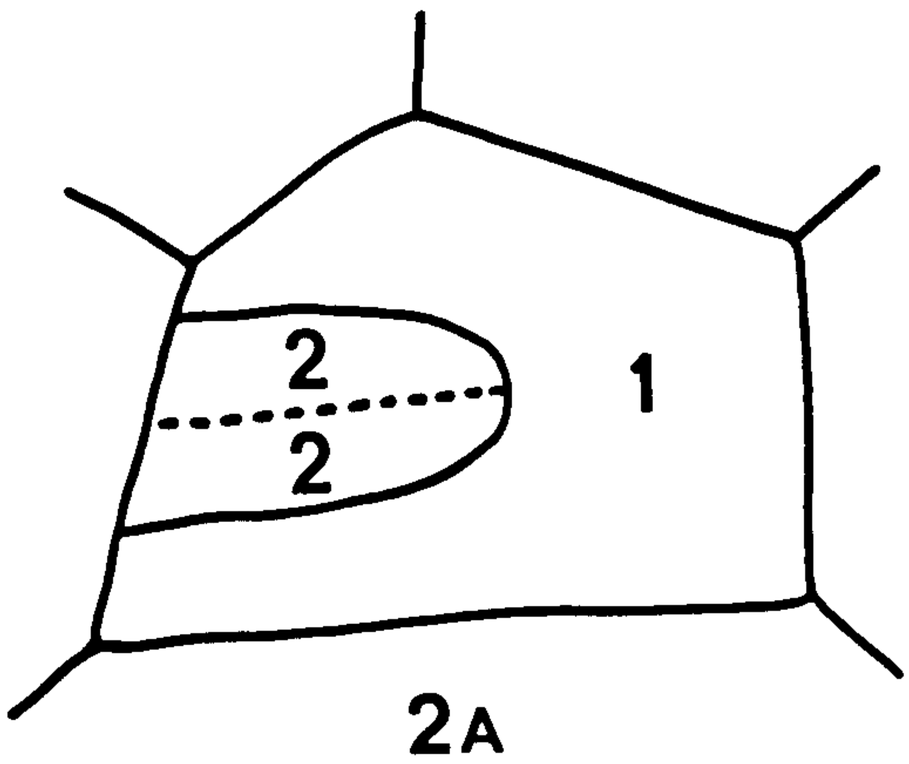
PLATE 9

Fig. 39 The four types of stomatal arrangement found in the thelypterids (after Kondo 1962) Types 2A, 2B, 3A, 3B.

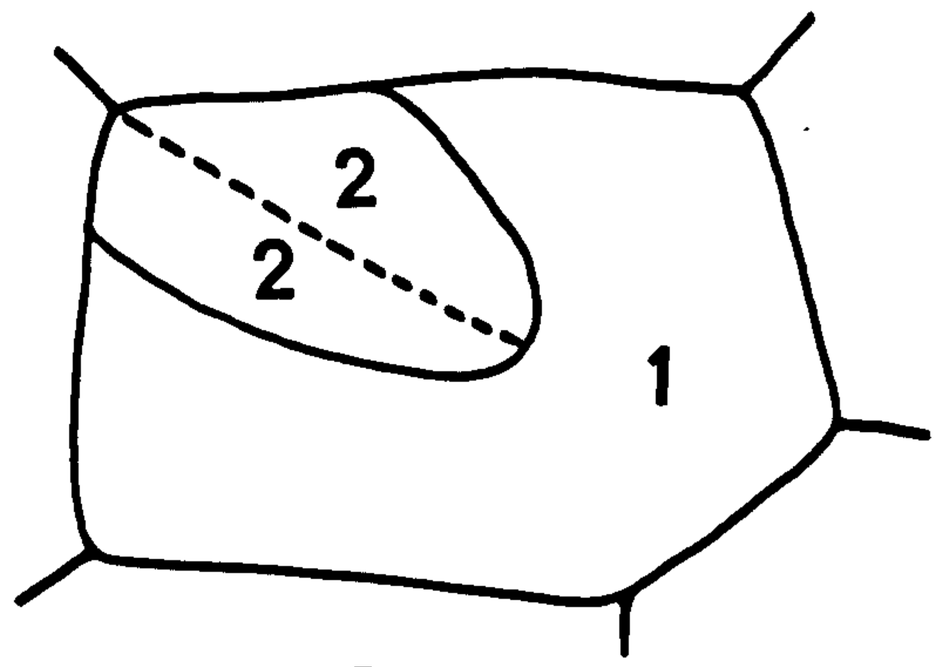
Fig. 40 The two basic types of stomatal arrangement found in the thelypterids (after Van Cotthem 1970).

a - Anomocytic

b - Polocytic

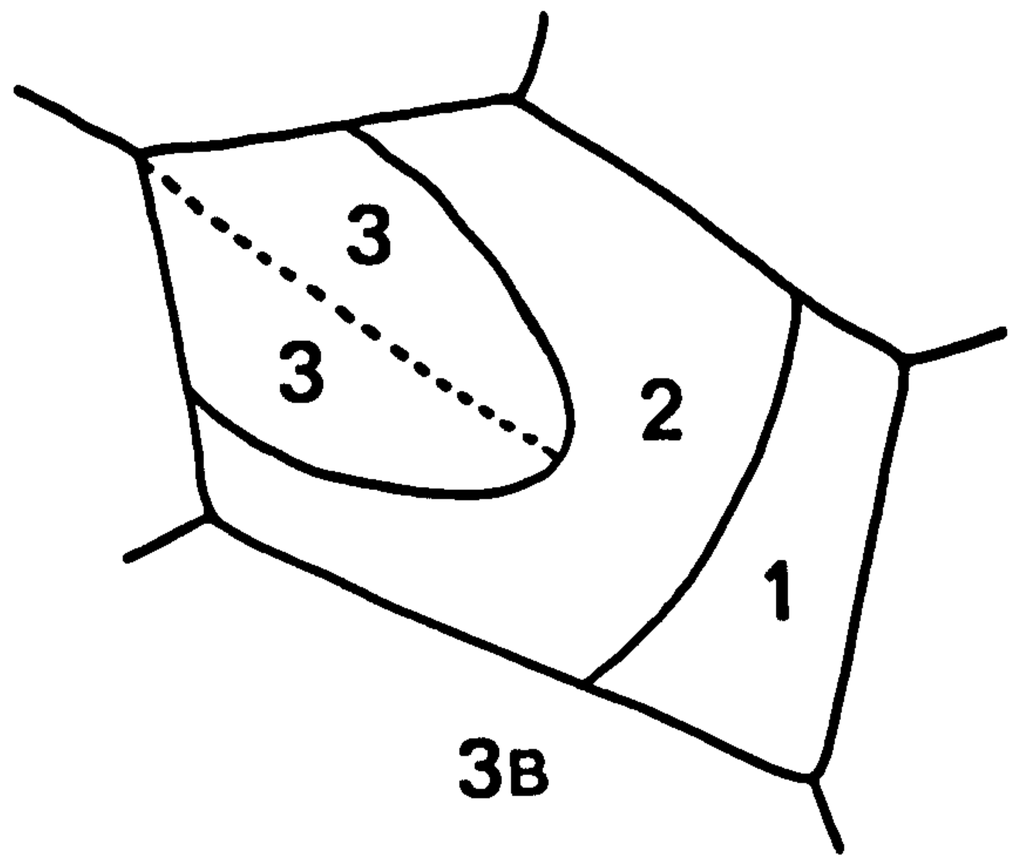


2A



2B

3A



3B

39

a

b

40

PLATE 10

Drawings Of Hairs From Various Thelypterids

Fig. 41 Development of unicellular hair after Momose 1937-42.

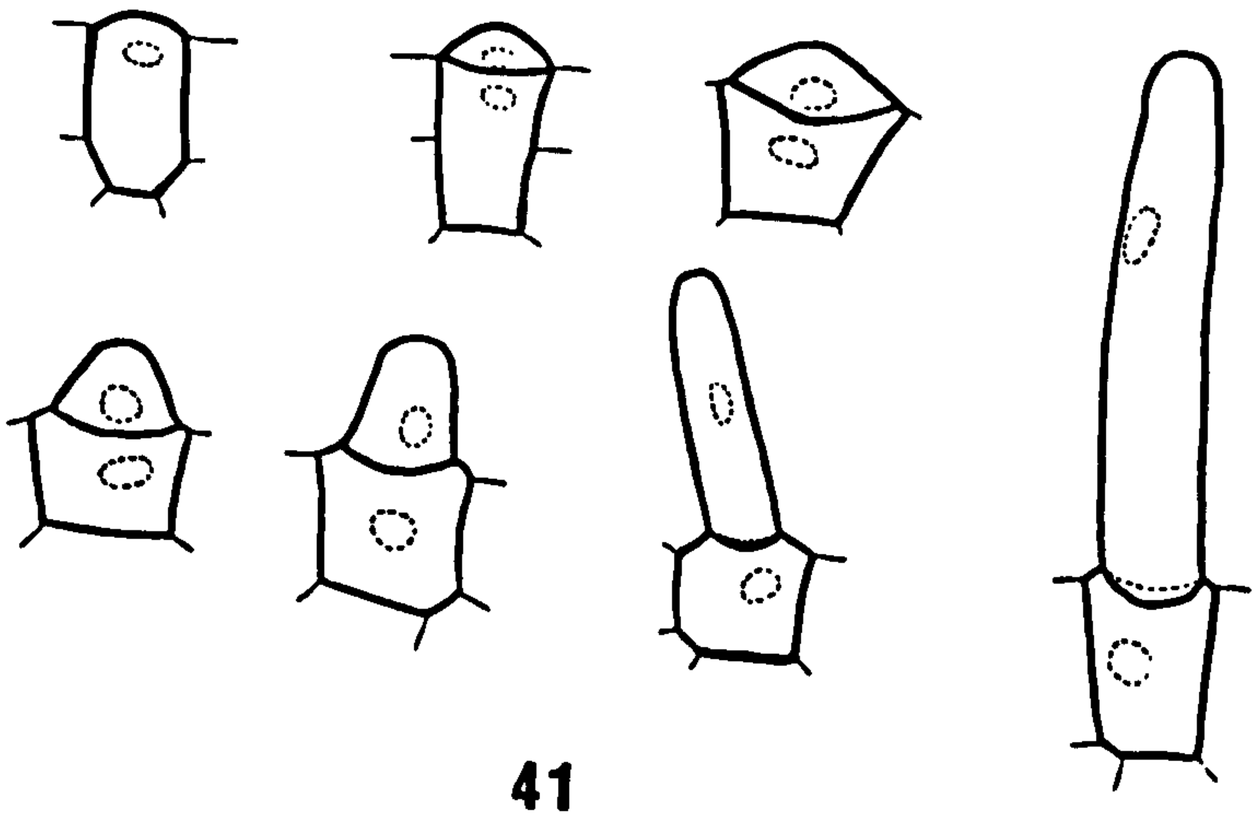
Fig. 42 Double "hair" from the margin of the stipe scale of T.limbosperma.

Fig. 43 Unicellular hooked hair from stipe of T.triphylla.

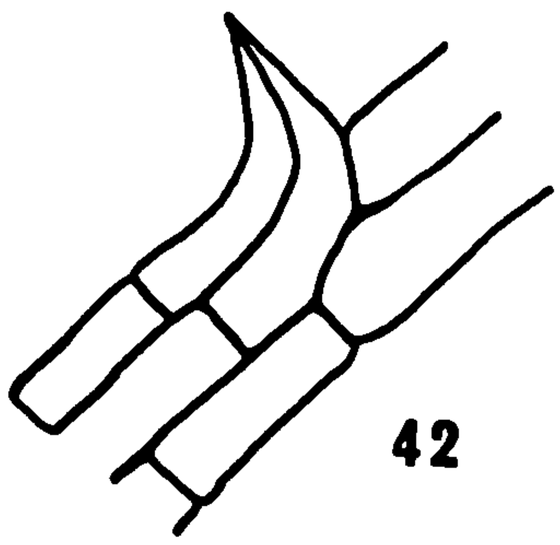
Fig. 44 Stellate hairs from stipe of T.obliterata.

Fig. 45 Unicellular straight hairs from the stipe and scales of various species.

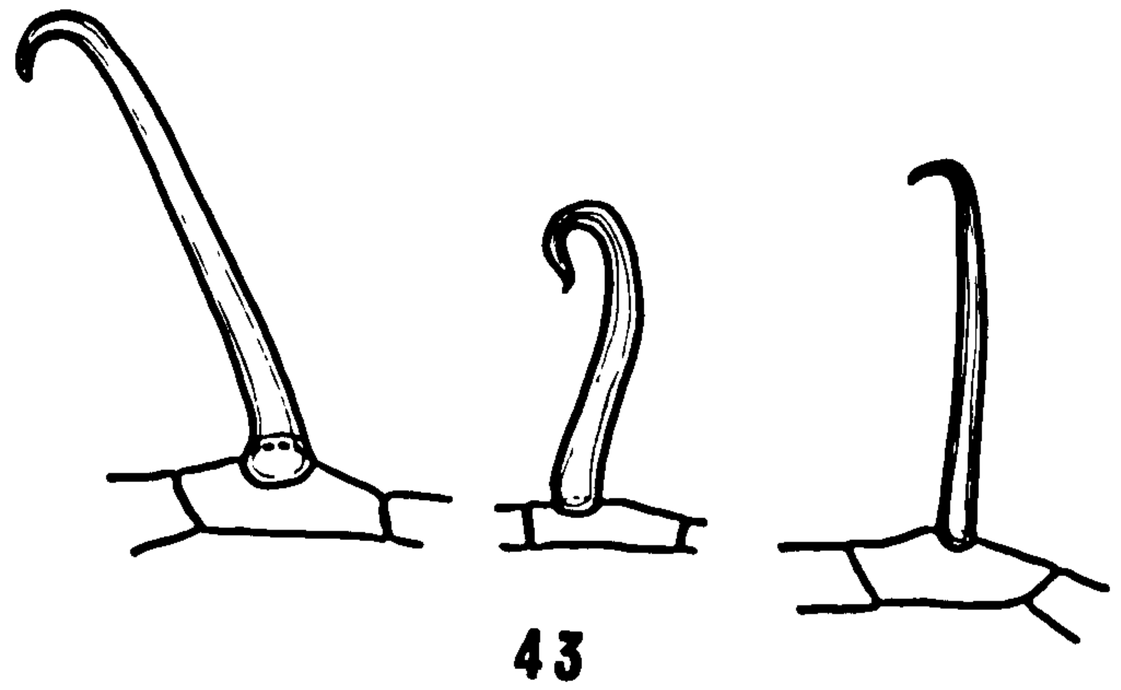
Fig. 46 Multiseptate hairs from stipe of T.decussata.



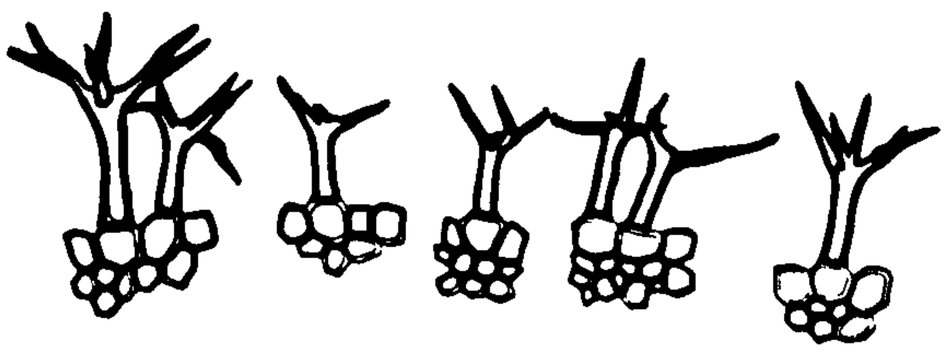
41



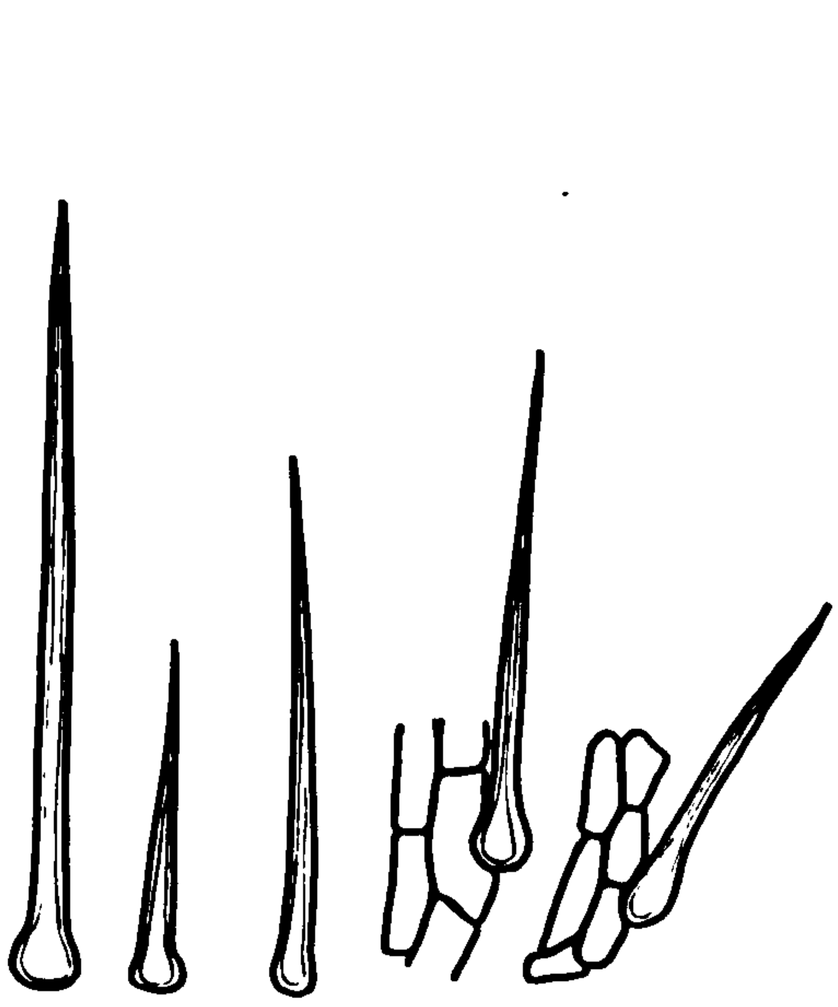
42



43

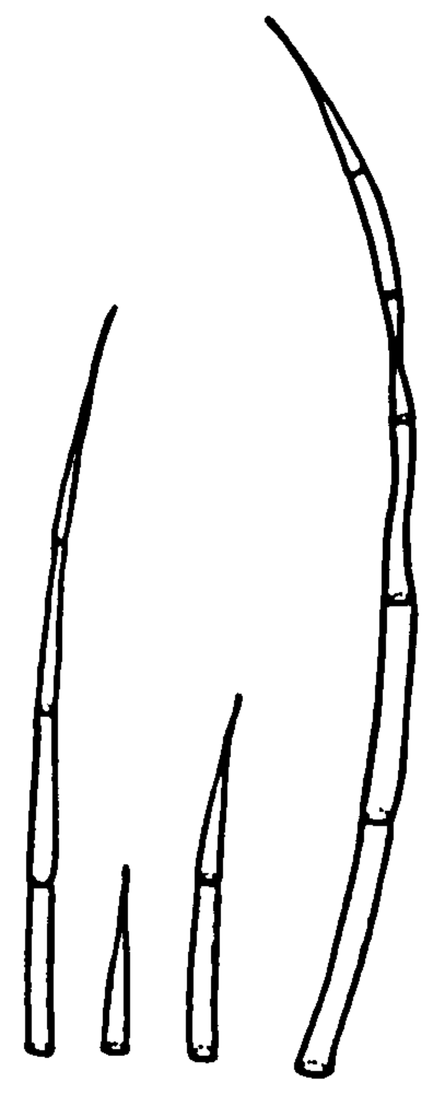


44



45

0·5cm



46

PLATE 11

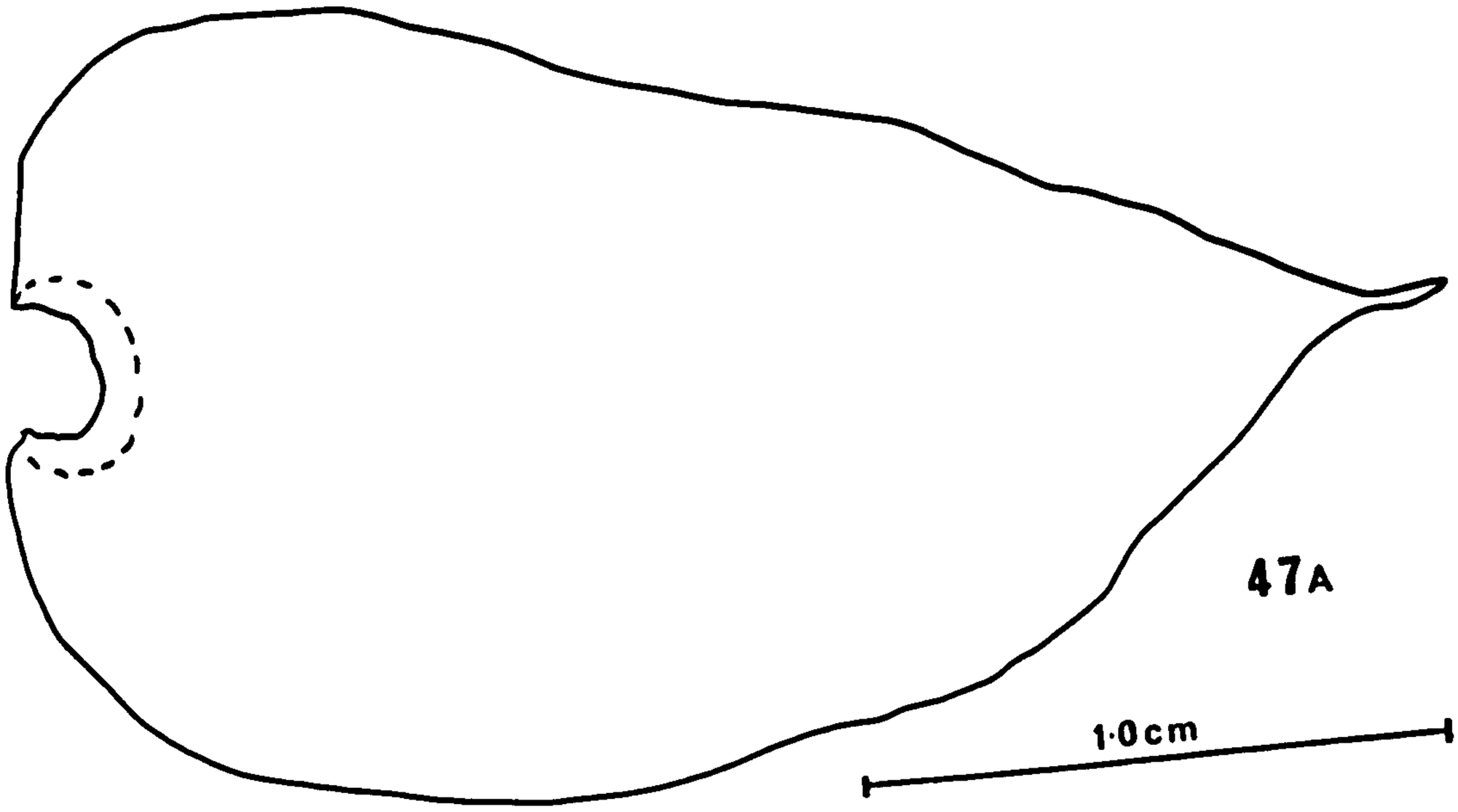
The Variation Of Scales Within The Thelypterids

Fig. 47a Large, broad scale from stipe of T.patens.

Fig. 47b Large, narrow scale from stipe of T.extensa.

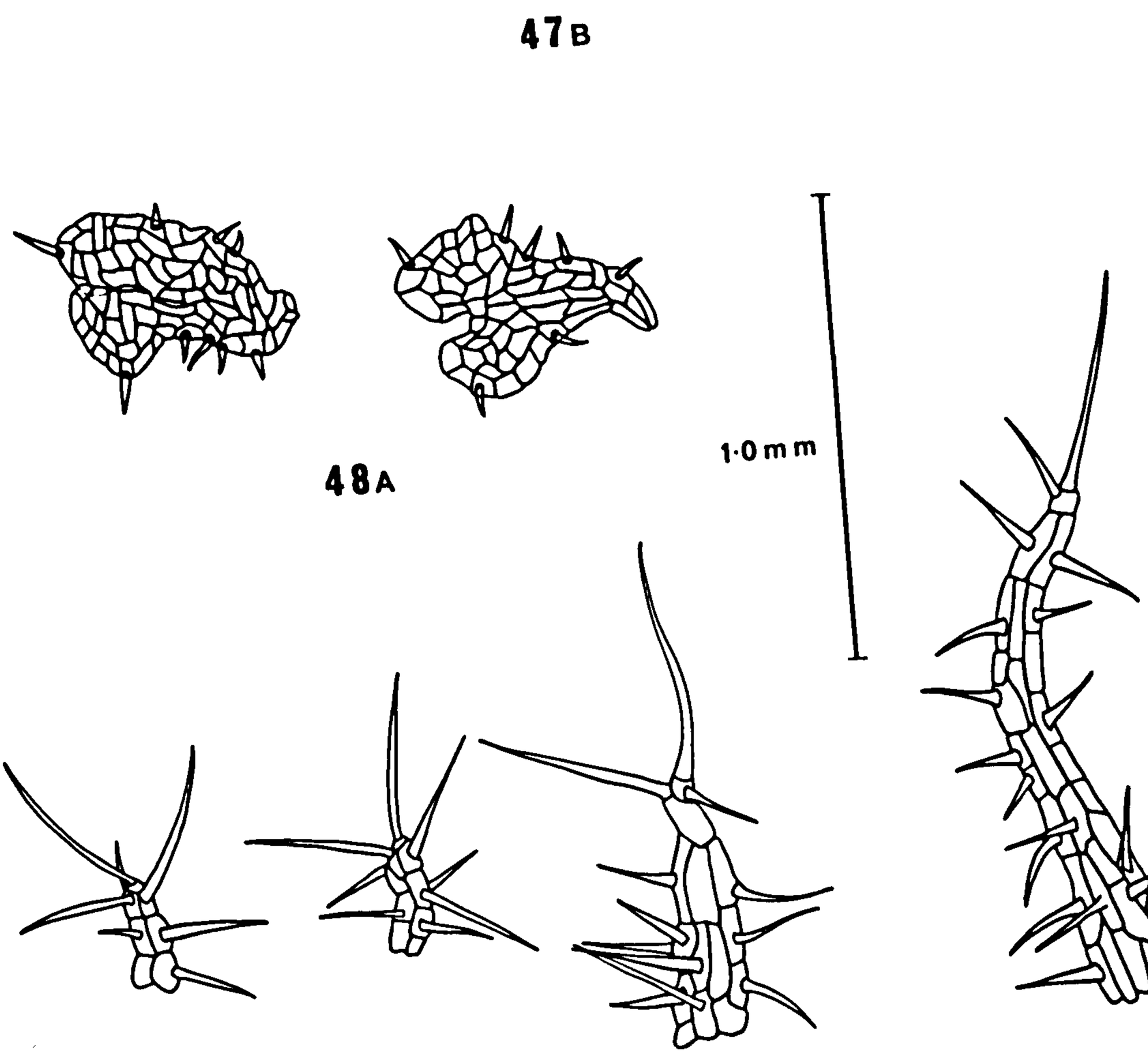
Fig. 48a Scale from rachis of T.prolifera showing deeply lobed base giving a "peltate" appearance.

Fig. 48b Small ciliate scales from lamina of T.decursive-pinnata



47A

47B



48A

48B

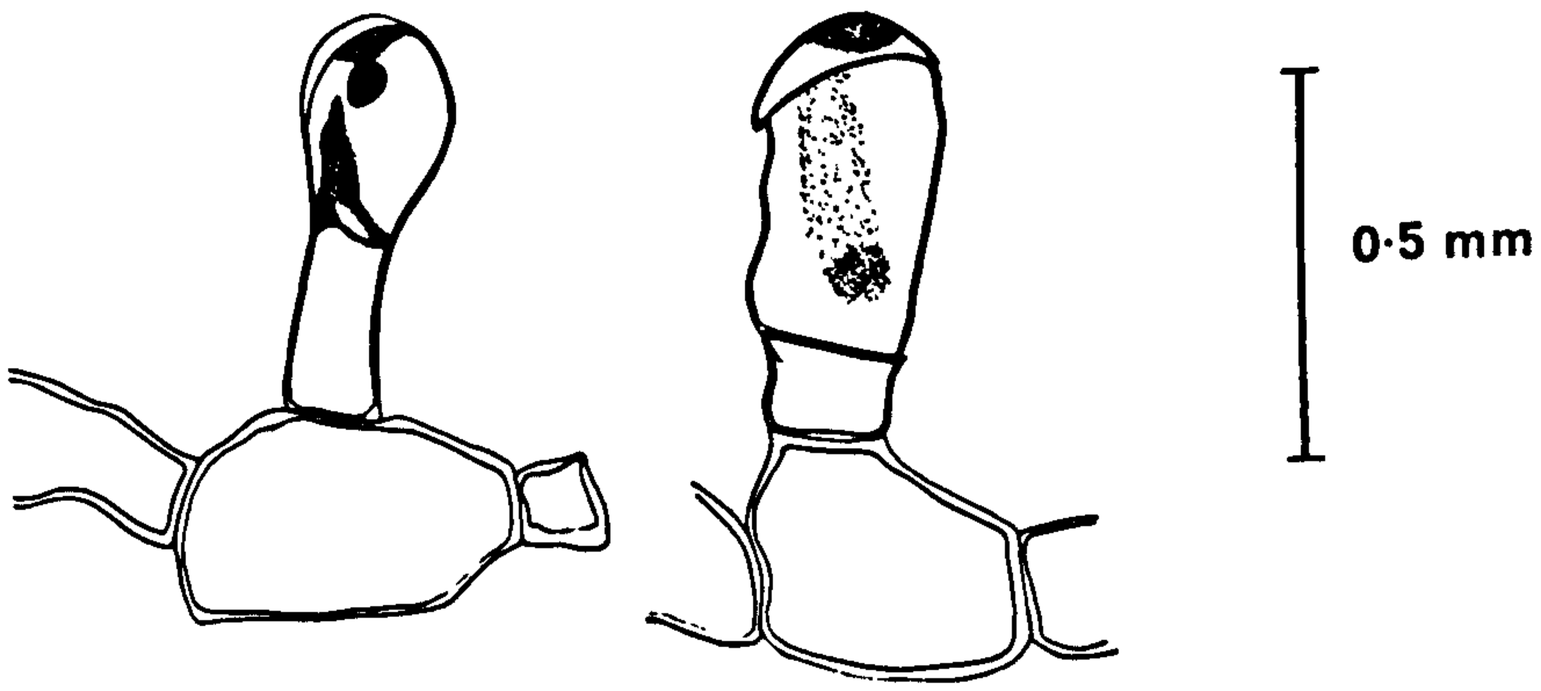
PLATE 12

Drawings Of Glandular Hairs From Various Thelypterids

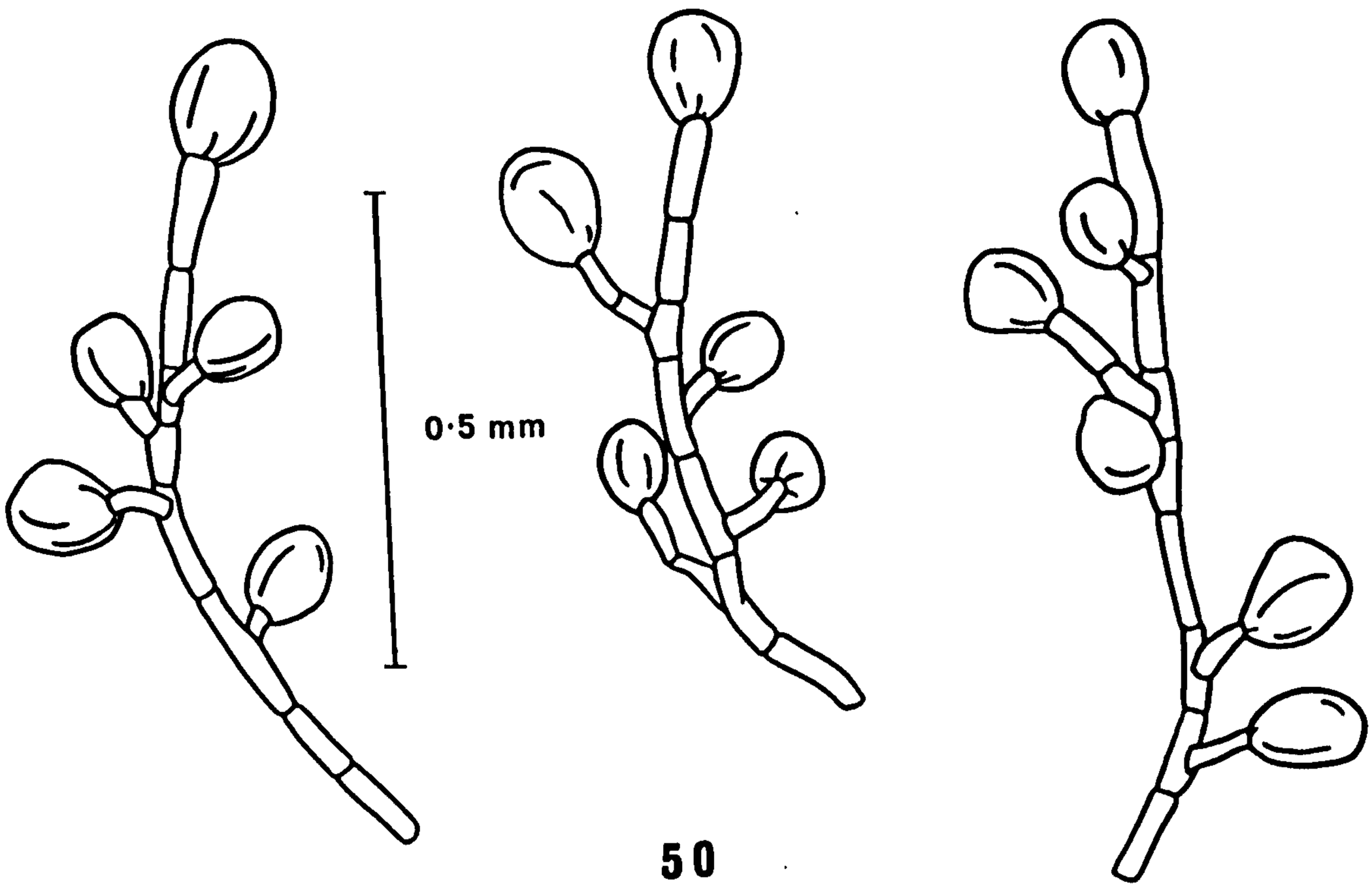
Fig. 49 Simple capitate hairs from stipe of T.extensa.

Fig. 50 Multicellular capitate hairs from base of stipe of T.callosa.

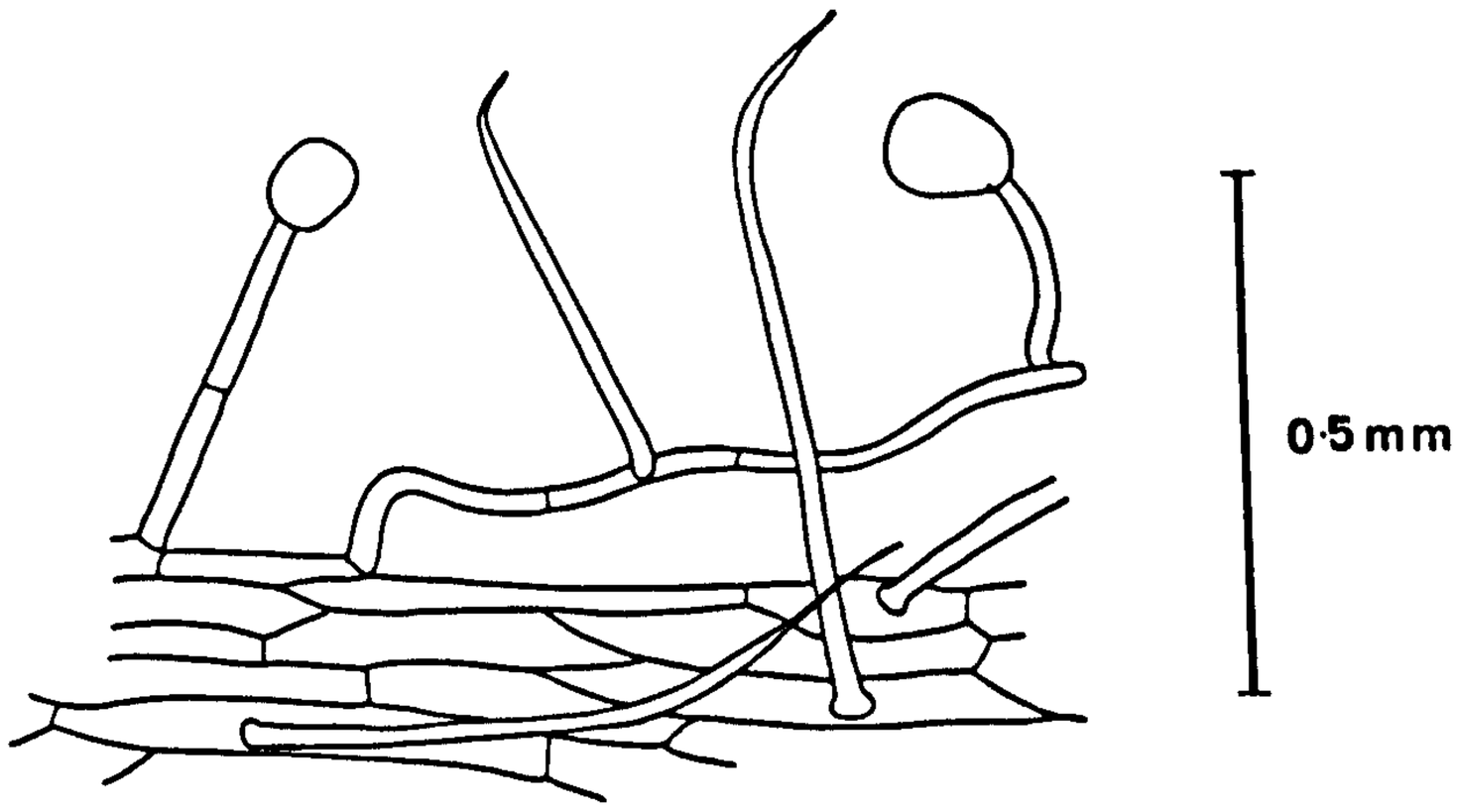
Fig. 51 Capitate hairs on scale of T.xylodes (Hennipman 1968).



49



50



51

PLATE 13A

Scanning Electron Photomicrographs Of Paraphyses (x 500)

Fig. 52 Hooked paraphyses on sporangia of T.triphylla.

Fig. 53 Hooked paraphyses on sporangia of T.triphylla.

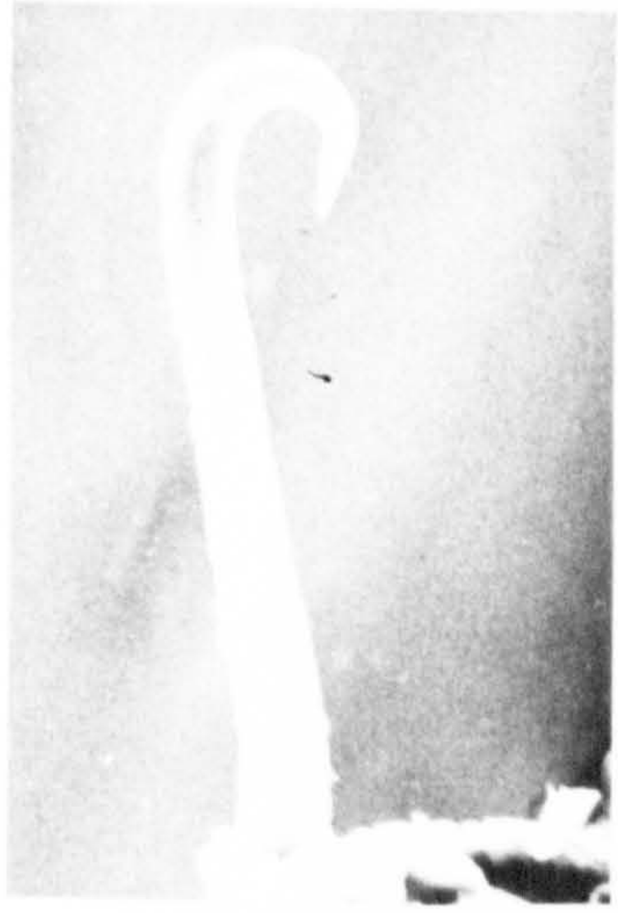
Fig. 54 Hooked paraphyses on sporangia of T.triphylla.

Fig. 55 Unbranched paraphyses on sporangia of T.gymnocarpa.

Fig. 56 Unbranched paraphyses on sporangia of T.gymnocarpa.

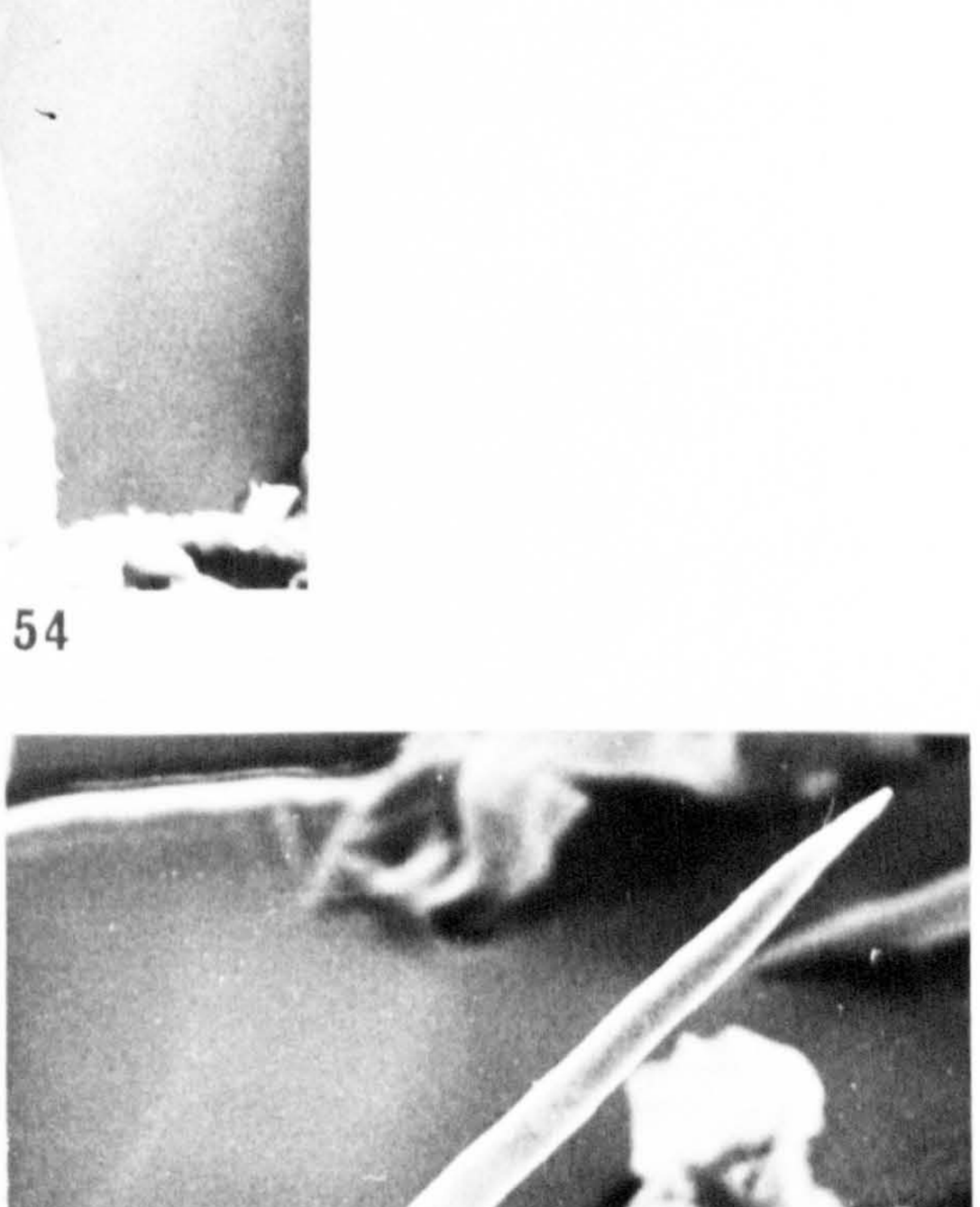
52

53



54

55



56

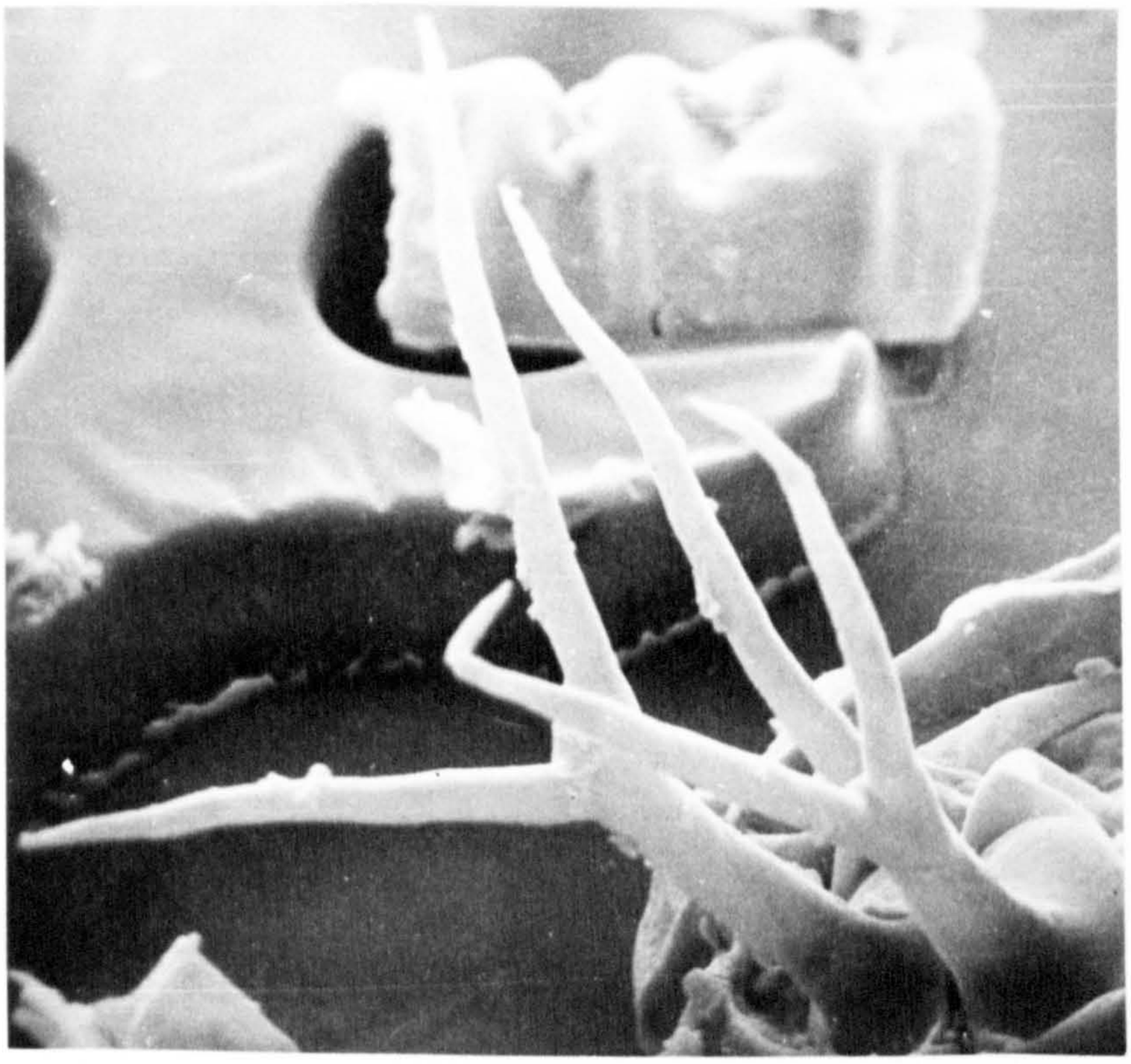
PLATE 13B

Scanning Electron Photomicrographs Of Paraphyses (x 500)

Fig. 57 Forked paraphyses from T.reptans.

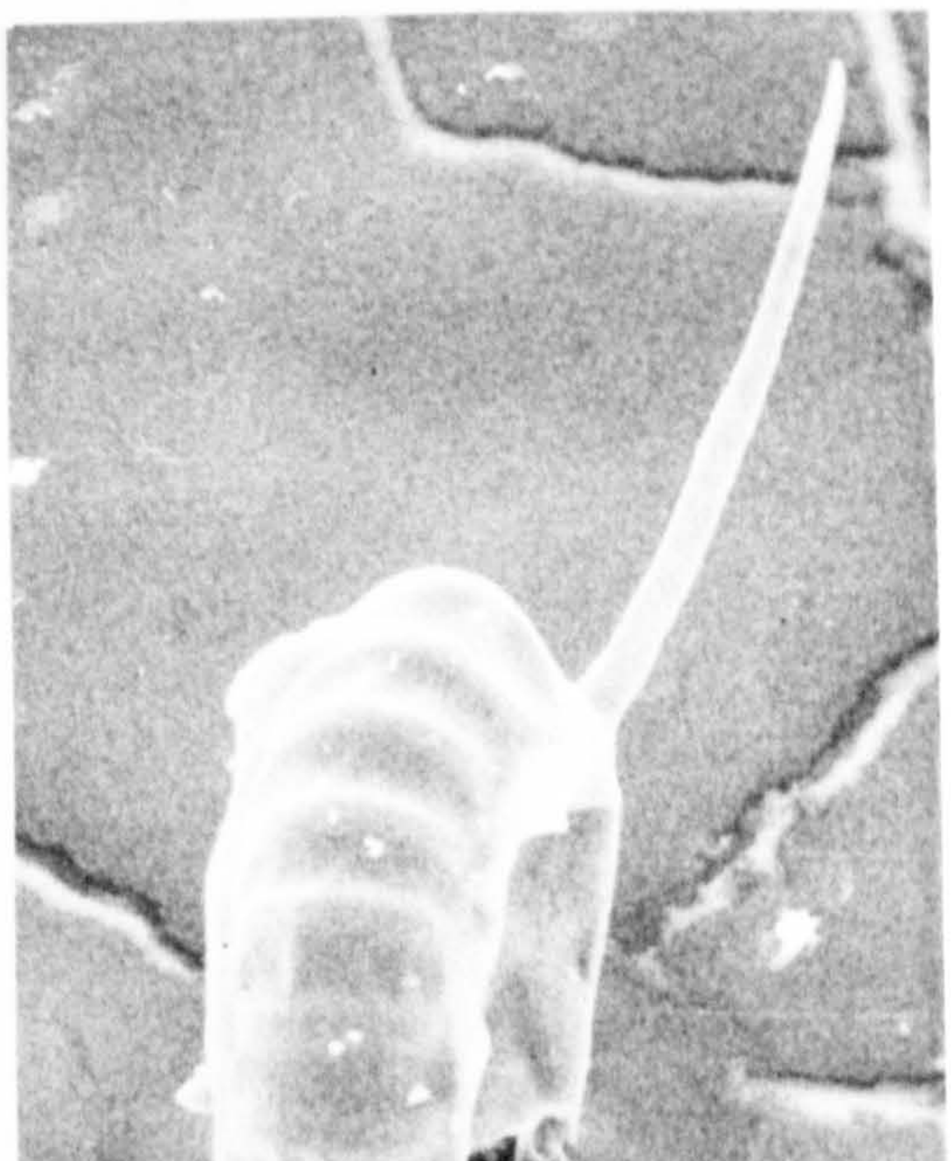
Fig. 58 Forked paraphyses from T.reptans.

Fig. 59 Whole sporangium of T.gymnocarpa with unbranched paraphysis (x 100).



57

58



59

PLATE 14

Fig. 60 Crozier of T.callosa showing long aerophores protruding through the thick layer of mucilage (reproduced from colour slide of T.G. Walker's).

Fig. 61a Transverse section of small non-vascular aerophore from frond of T.decussata.

Fig. 61b Transverse section of vascular aerophore from base of stipe of T.truncata.

Fig. 62a Large specialised aerophore from base of stipe of T.xylodes (After Hennipman 1968).

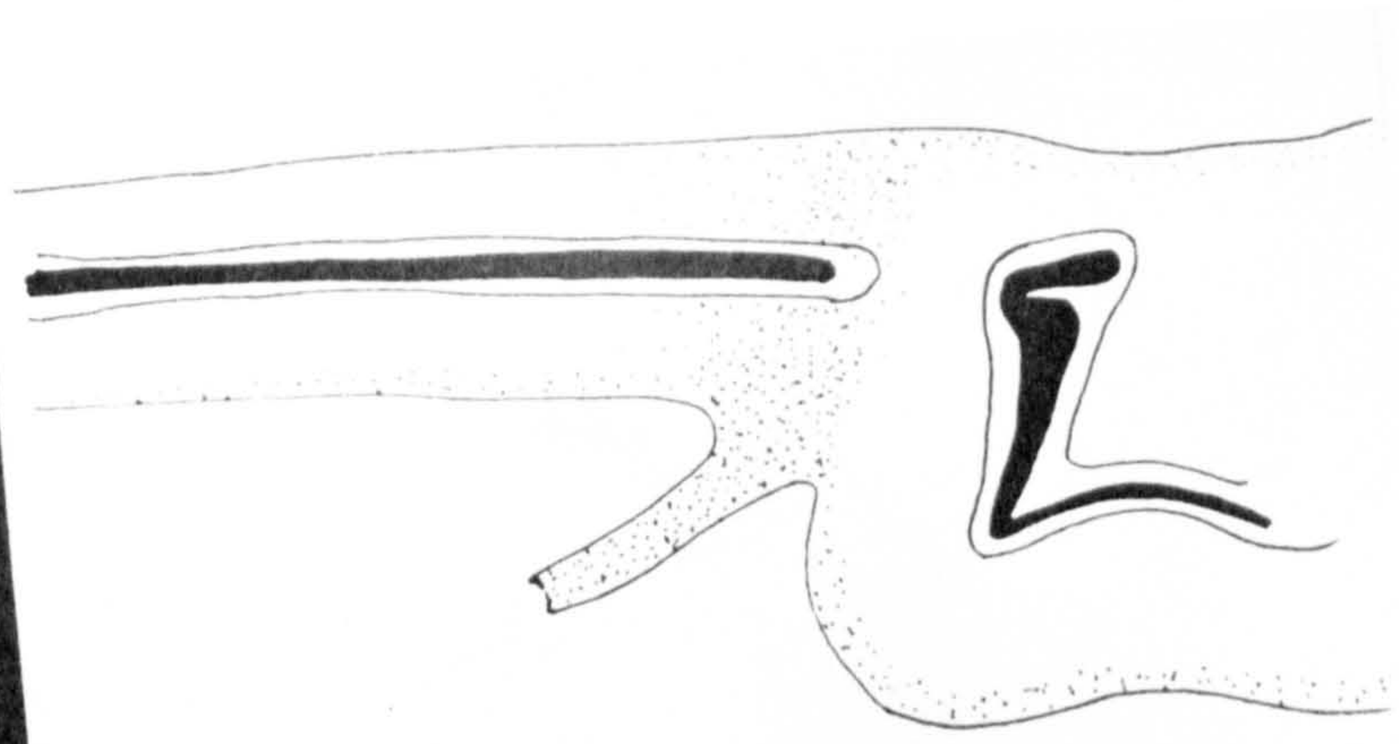
Fig. 62b Section of aerophore of T.callosa taken parallel with the axis of the frond.

V = vascular tissue

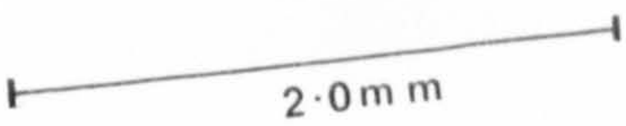
A = sclerised aerenchyma

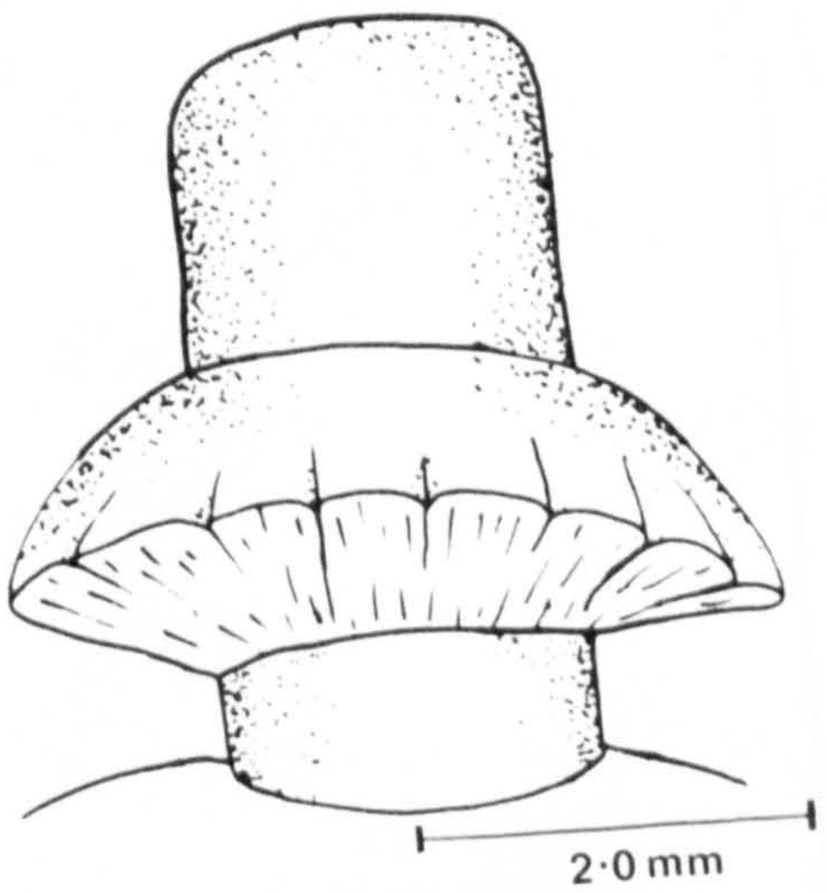
Fig. 62c Leafy auricle from lower stipe of T.truncata (for comparison with Fig. 62b).

60

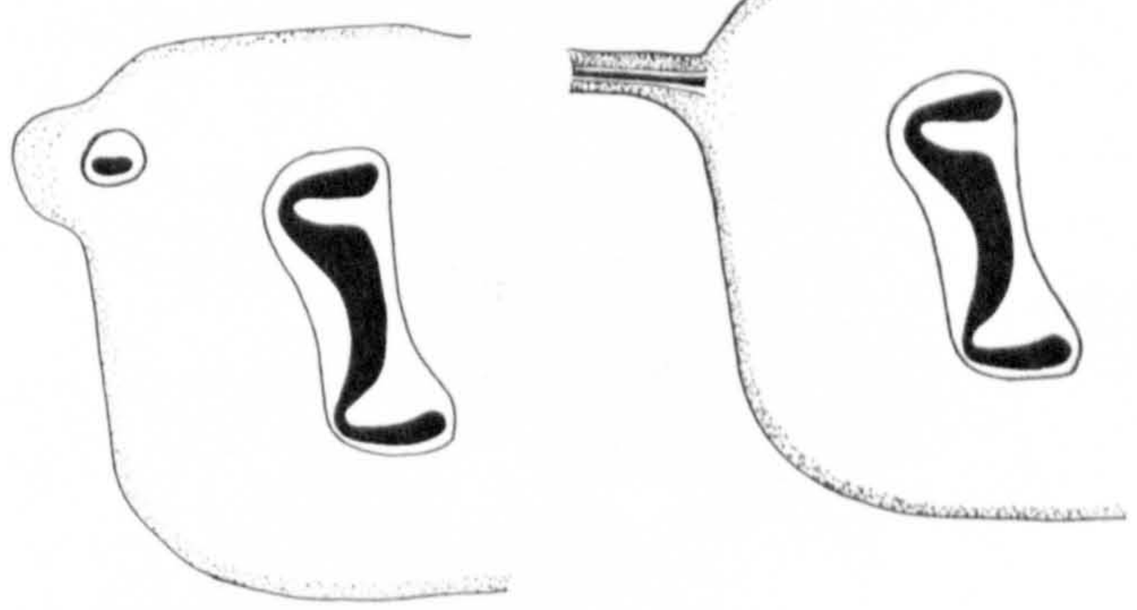


61 a

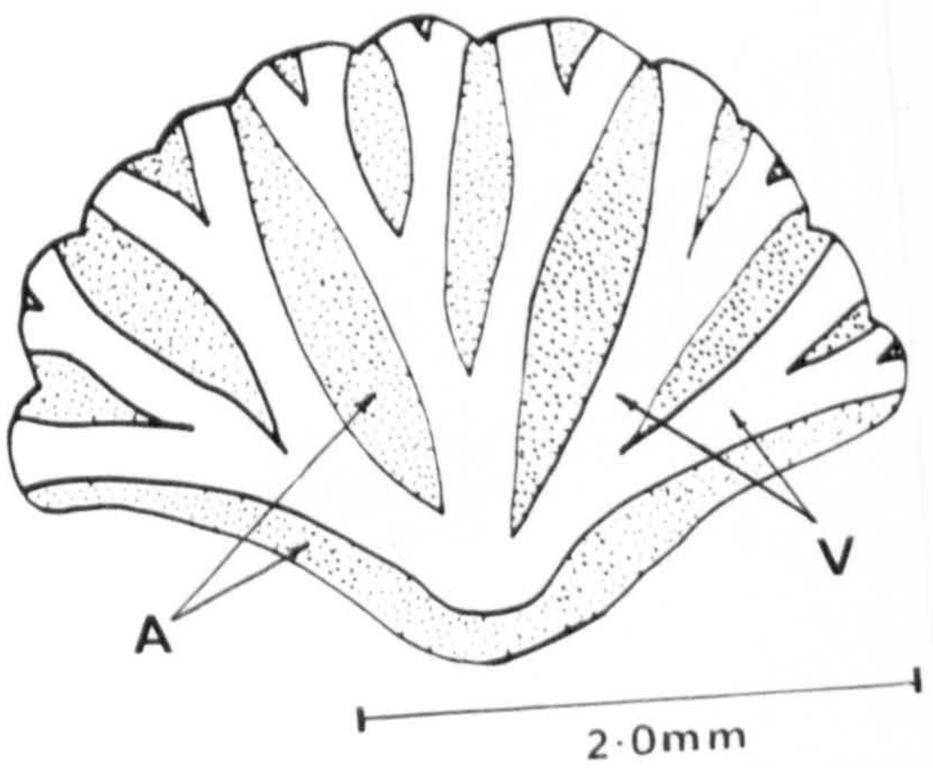




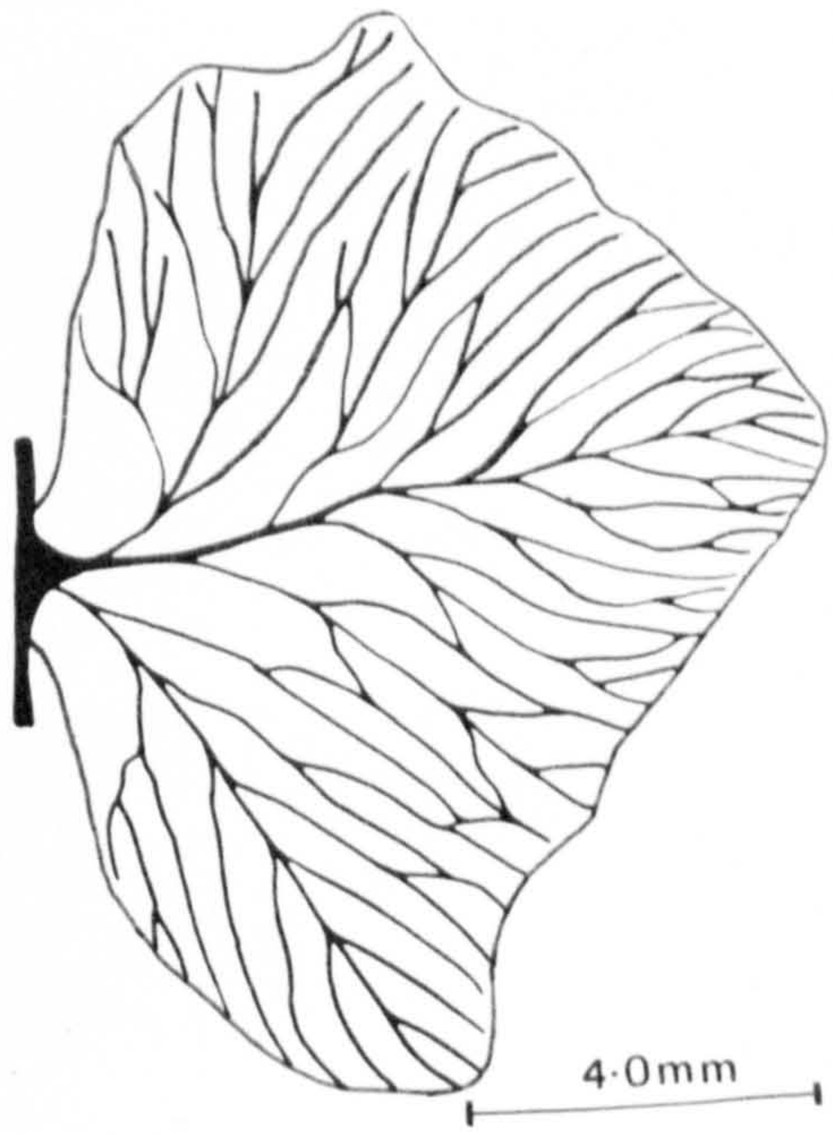
62 a



61 b



62 b



62 c

PLATE 15

Major Types Of Venation Found In The Thelypterids

Fig. 63 Branching and non-anastomosing venation.

Fig. 64 Simple non-anastomosing venation.

Fig. 65 One pair of veins meeting at the sinus.

Fig. 66 Goniopteroid venation.

Fig. 67 One pair of veins unite at base of sinus membrane.

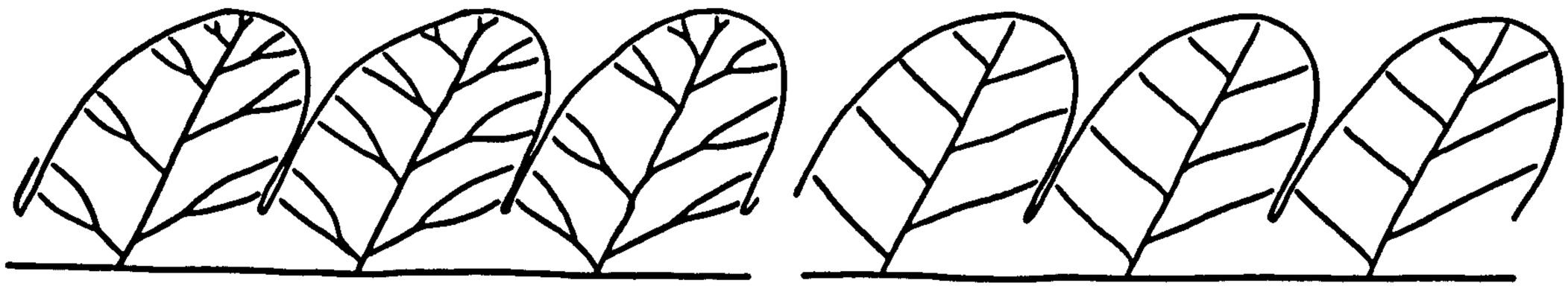
Fig. 68 Veins unite and run alongside membrane to true sinus then form a commissural vein.

Fig. 69 Menisciioid venation

Fig. 70 Dictyoclinioid venation

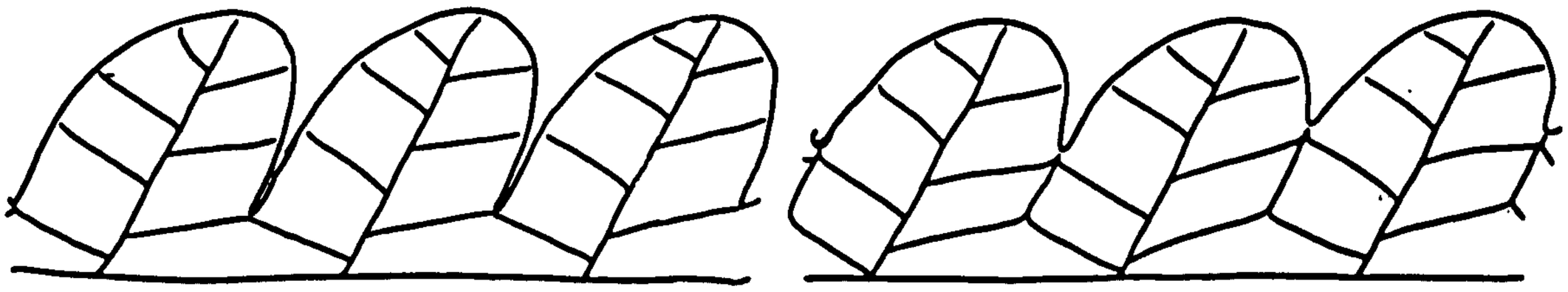
Fig. 71 Haplodictyoid venation

Fig. 72 Pleocnemioid venation



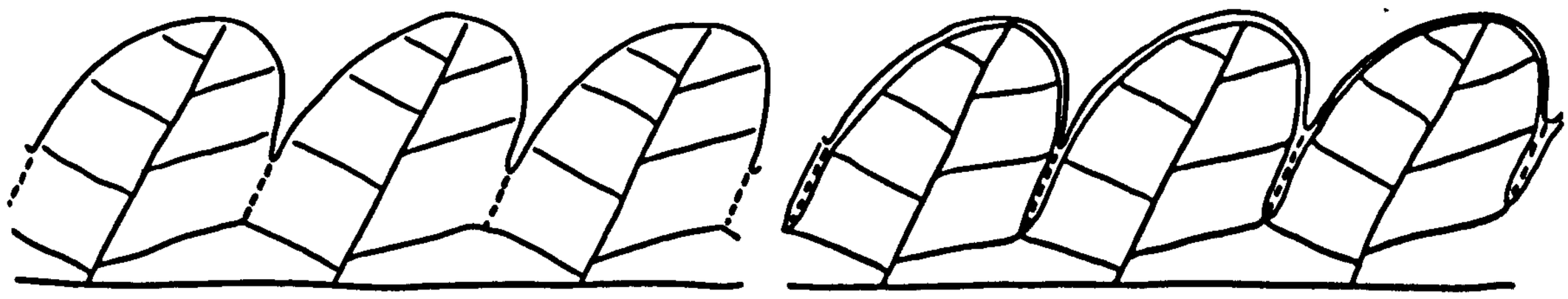
63

64



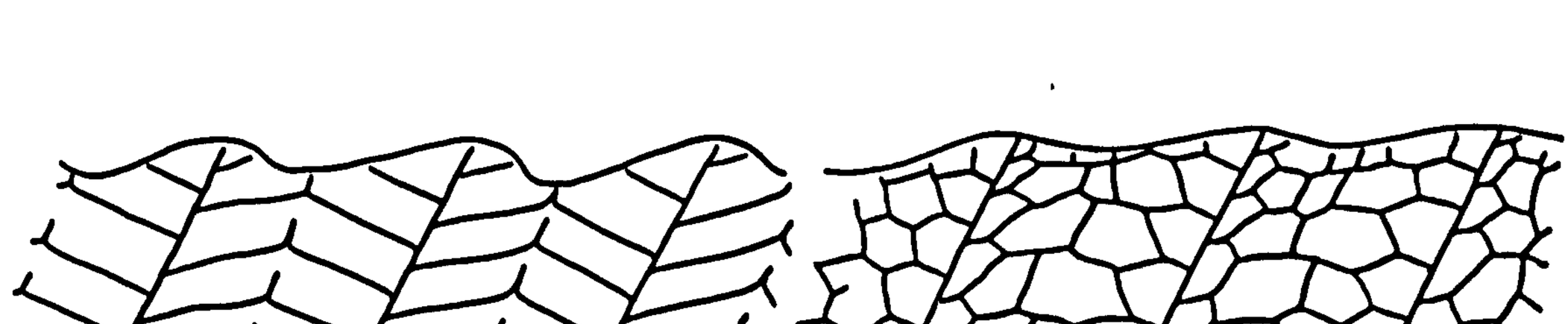
65

66



67

68



69

70

71

72

PLATE 16

Scanning Electron Photomicrographs Of Spores : X1000

Fig. 73 *T.thomsonii*

Fig. 74 *T.rudis*

Fig. 75 *T.oligocarpa*

Fig. 76 *T.nockiana*

Fig. 77 *T.heteroclita*

Fig. 78 *T.sancta*

Fig. 79 *T.sancta* var. *magna*

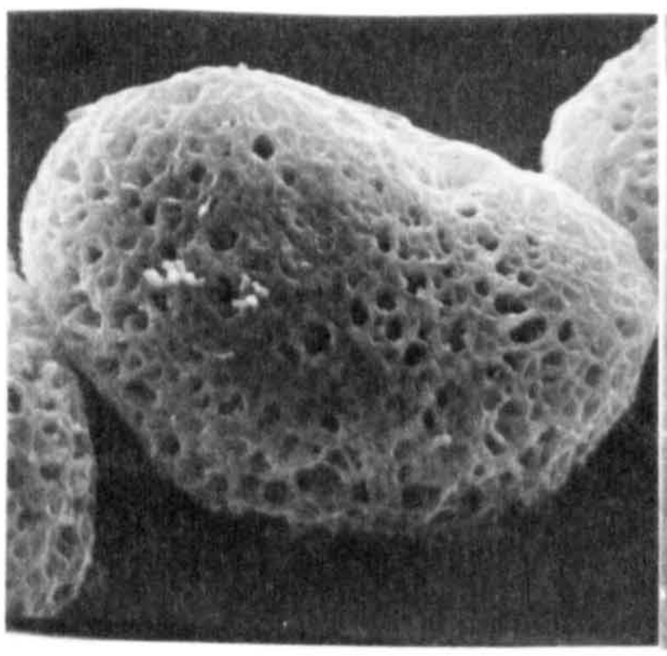
Fig. 80 *T.concinna*

Fig. 81 *T.balbisii*

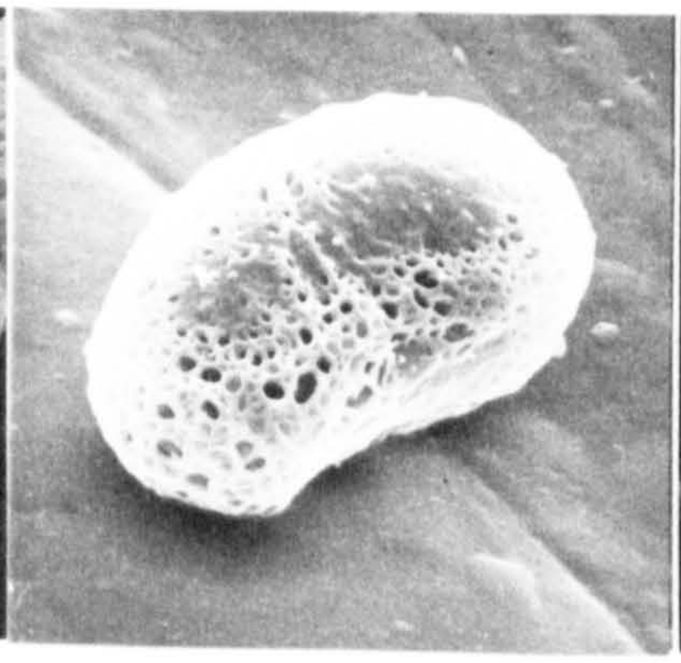
Fig. 82 *T.navarrensis*

Fig. 83 *T.resinifera*

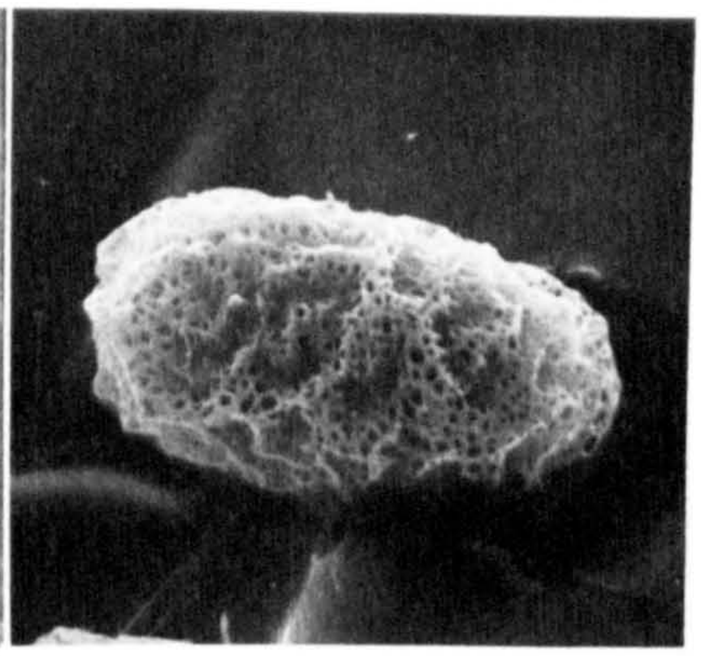
Fig. 84 *T.linkiana*



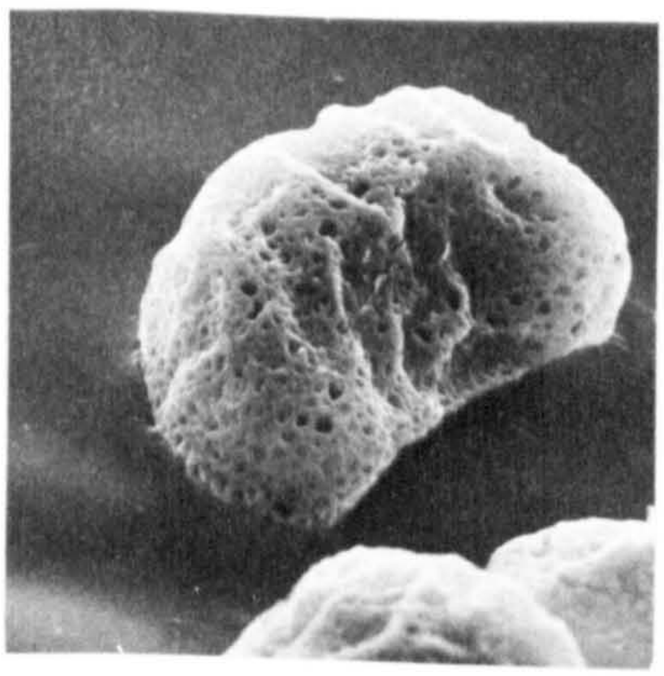
73



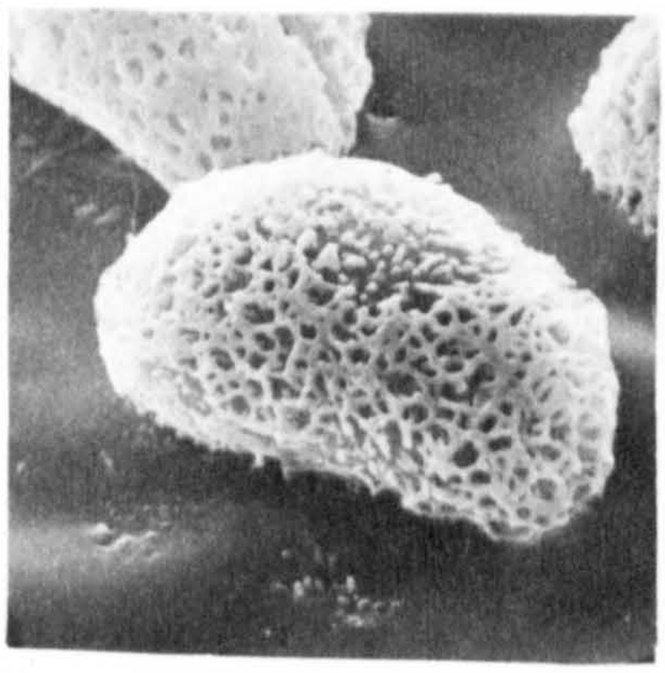
74



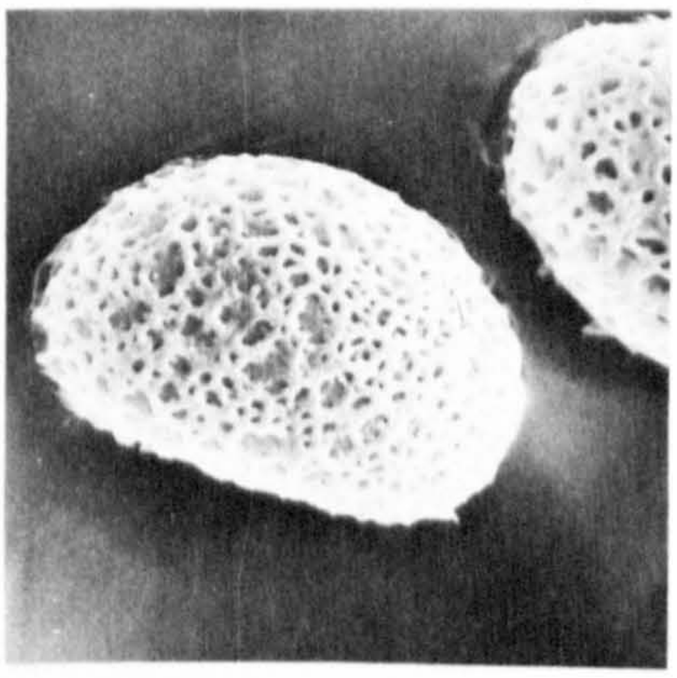
75



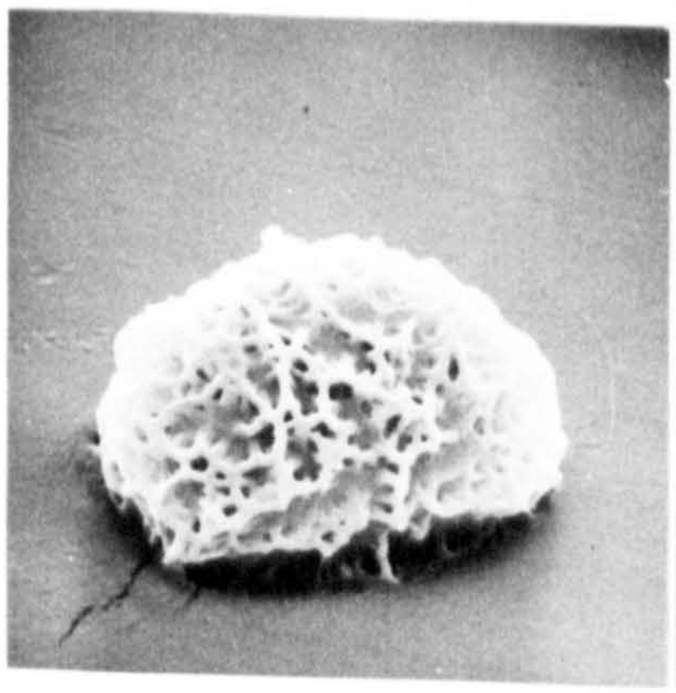
76



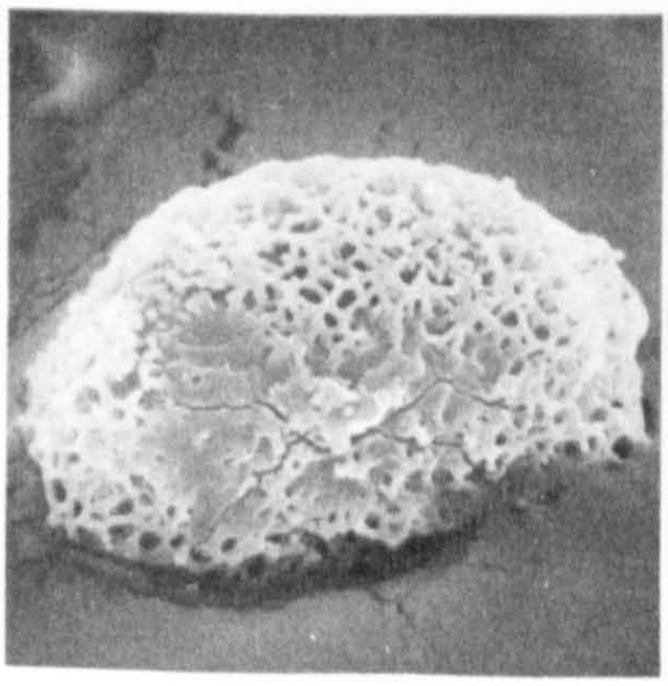
77



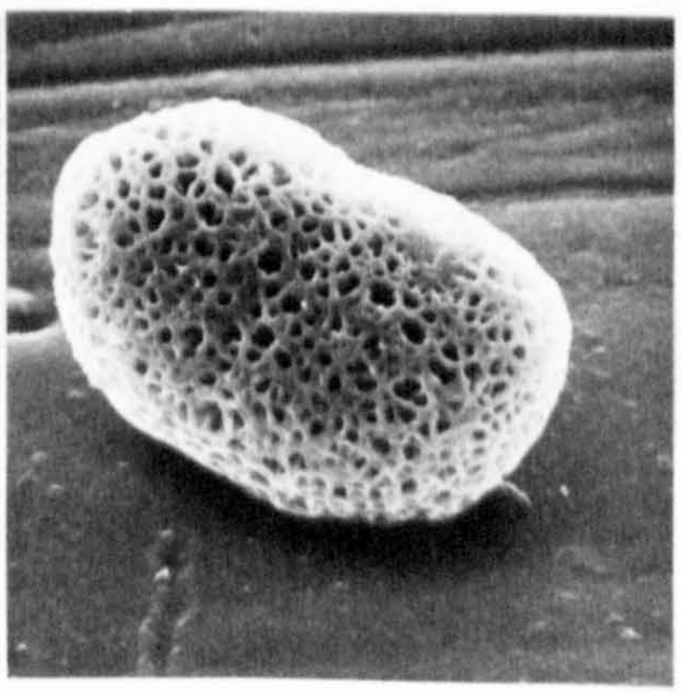
78



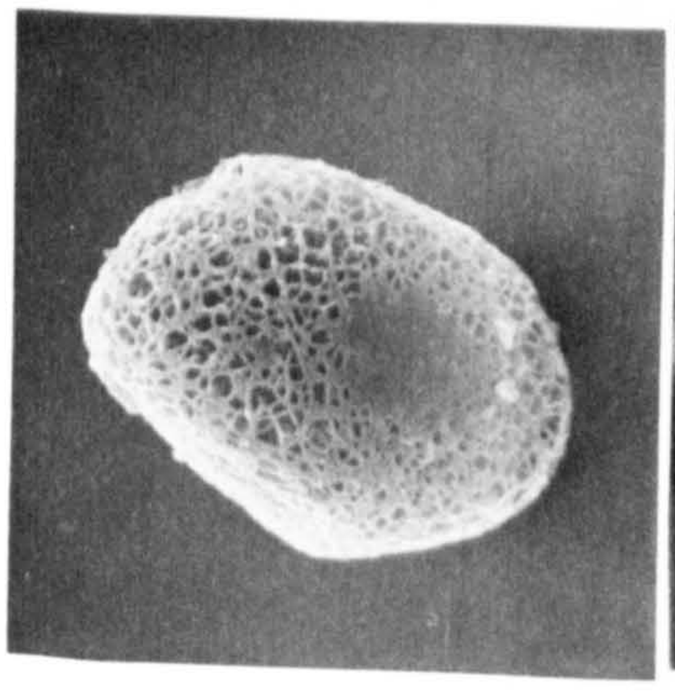
79



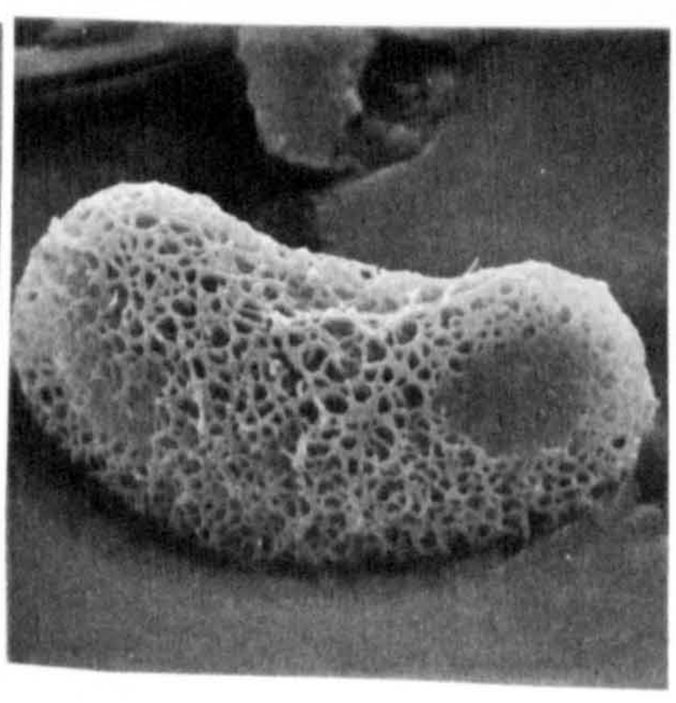
80



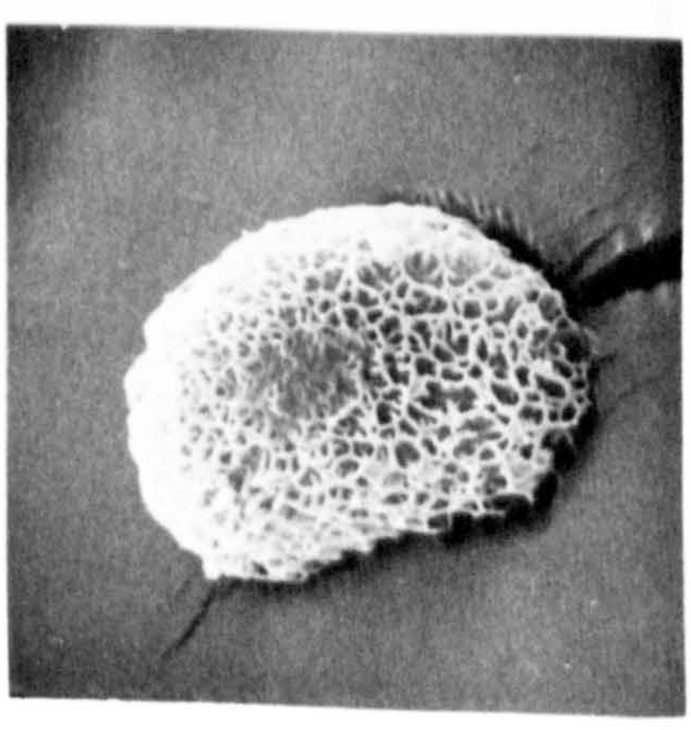
81



82



83



84

PLATE 17

Scanning Electron Photomicrographs of Spores : X1000

Fig. 85 T.gracilis

Fig. 86 T.cheilanthoides

Fig. 87 T.underwoodiana

Fig. 88 T.limbata

Fig. 89 T.pachyrachis

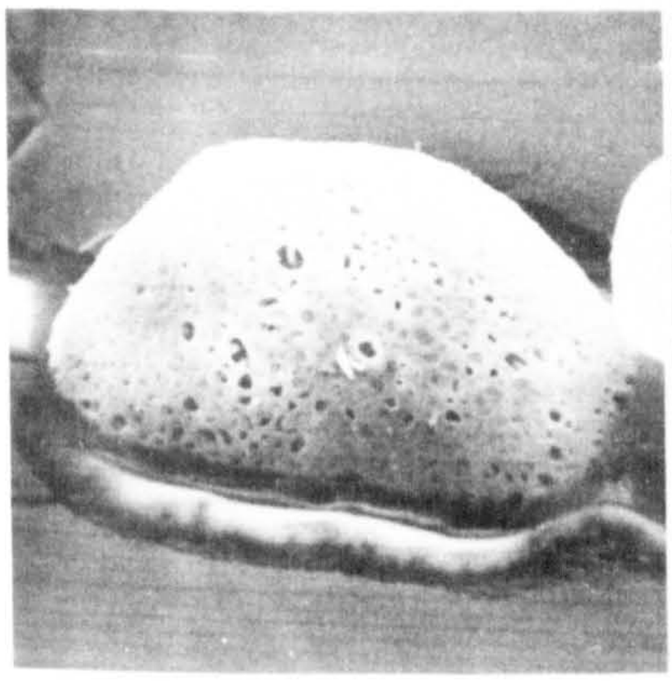
Fig. 90 T.germaniana

Fig. 91 T.opposita

Fig. 92 T.hexagonoptera

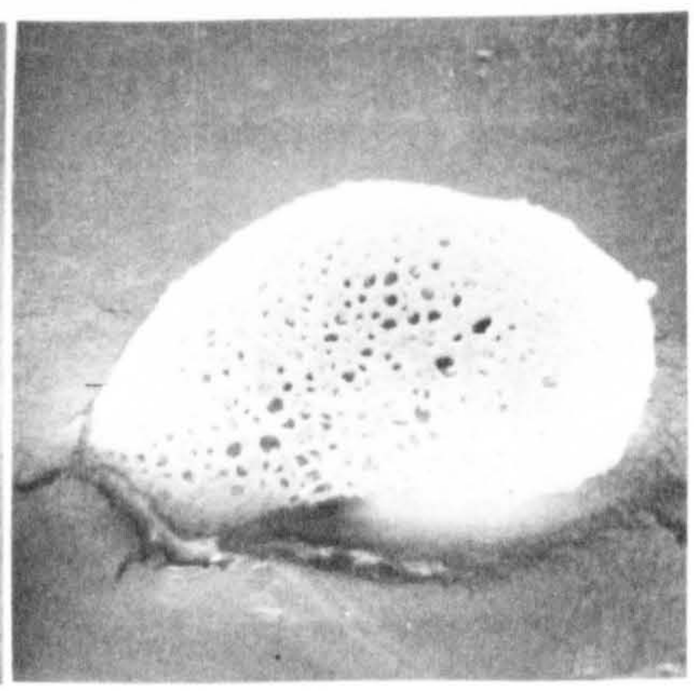
Fig. 93 T.phegopteris

Fig. 94 T.decursive-pinnata

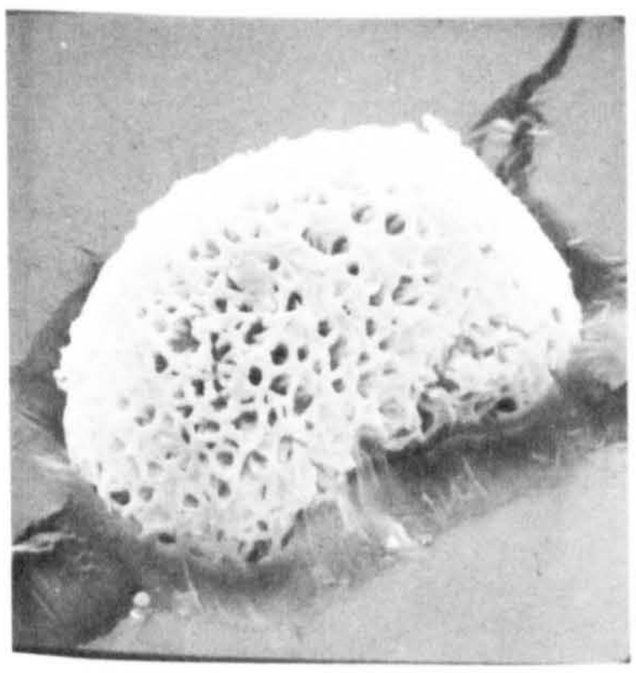


85

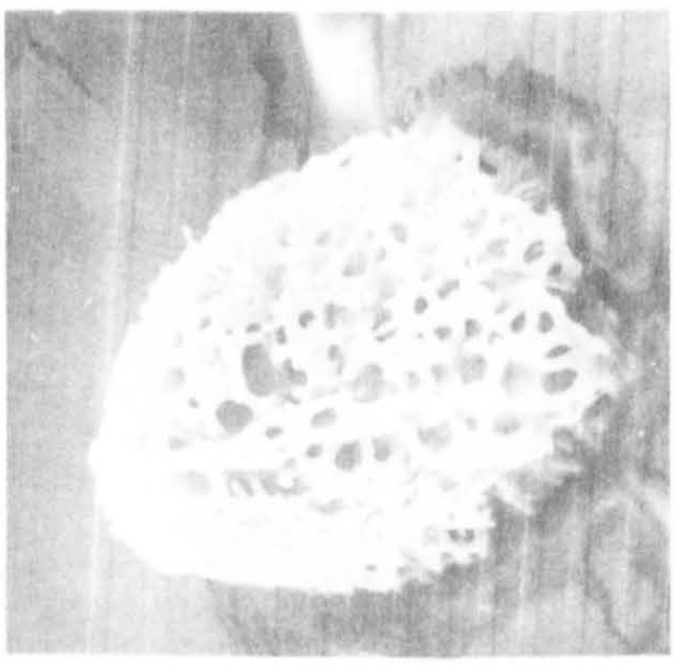
86



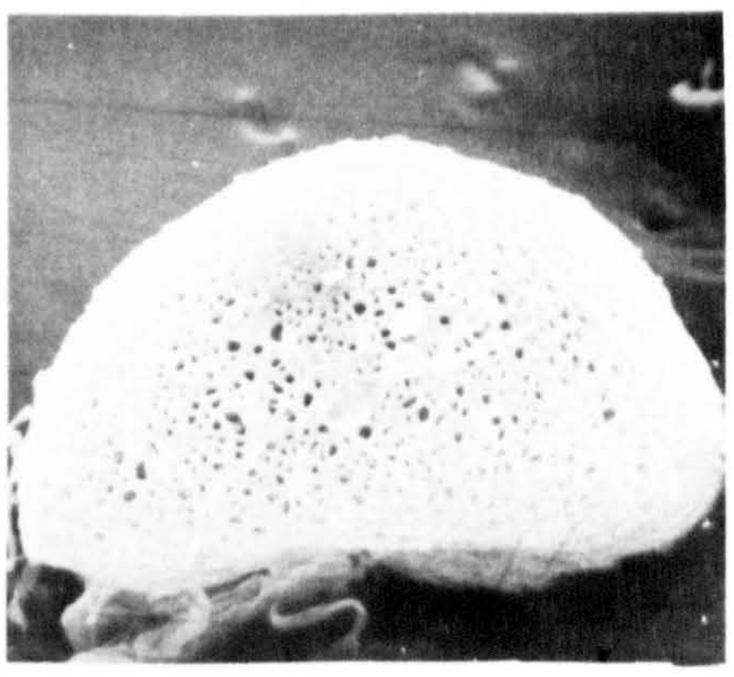
87



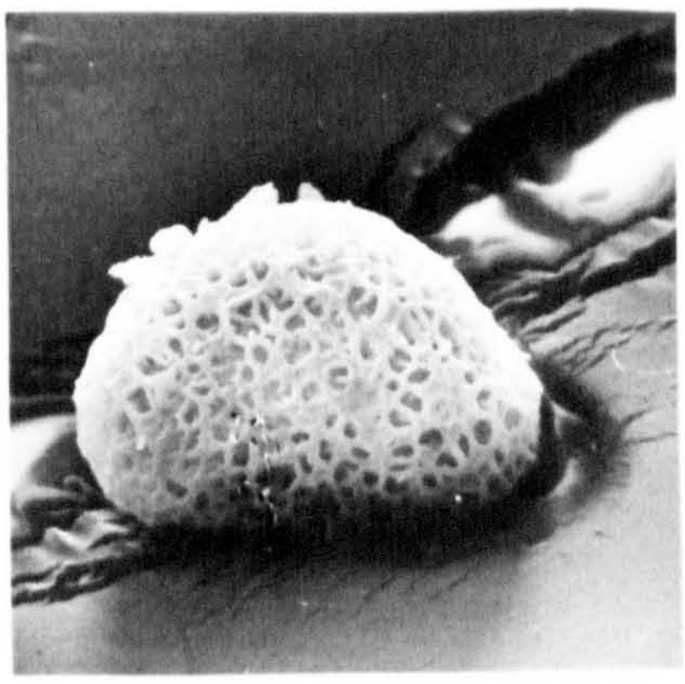
88



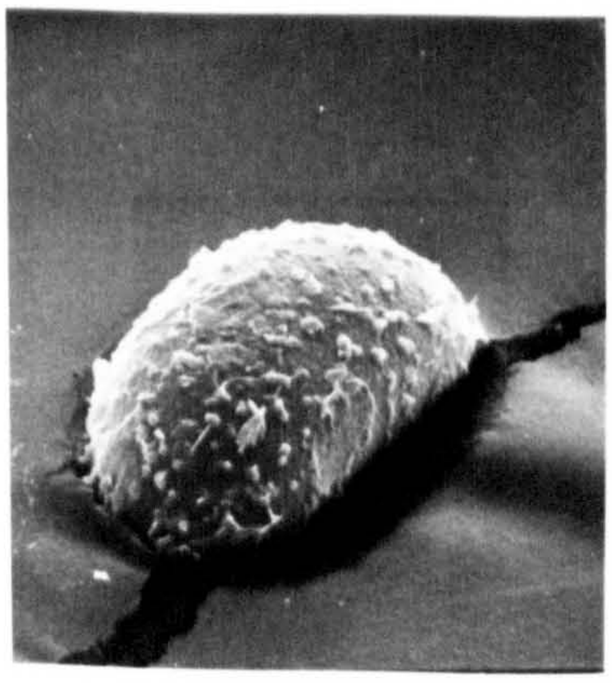
89



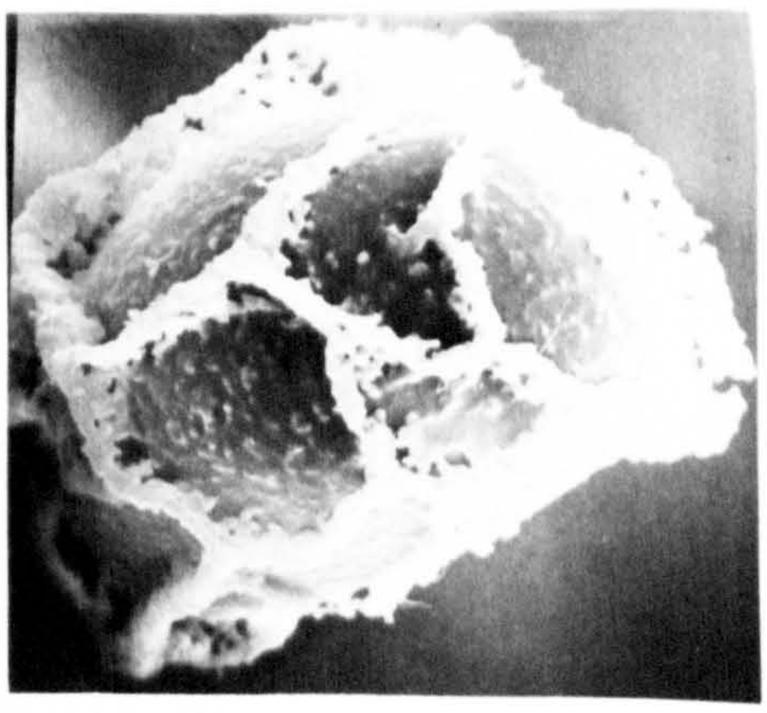
90



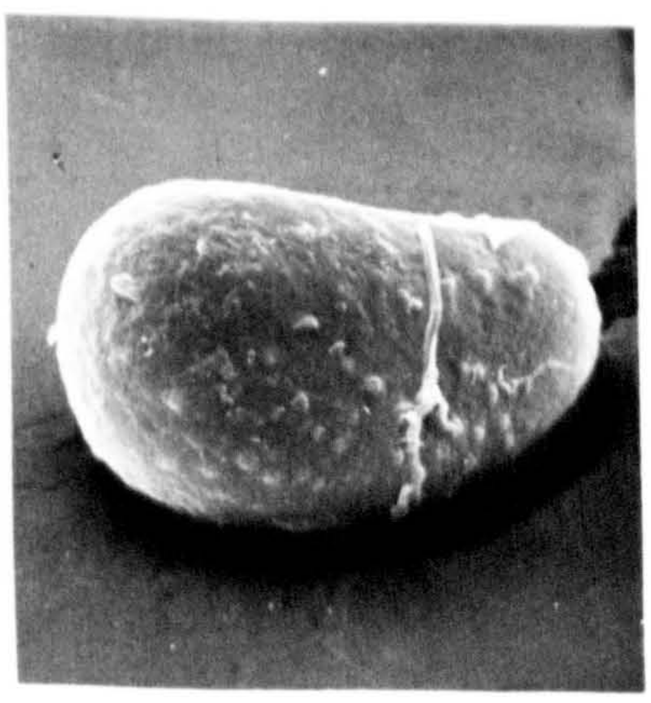
91



92



93



94

PLATE 18

Scanning Electron Photomicrographs Of Spores : X1000

Fig. 95 T.aurita

Fig. 96 T.subaurita

Fig. 97 T.pyrrhorhachis

Fig. 98 T.cruciata

Fig. 99 T.cyclocarpa

Fig. 100 T.levingei

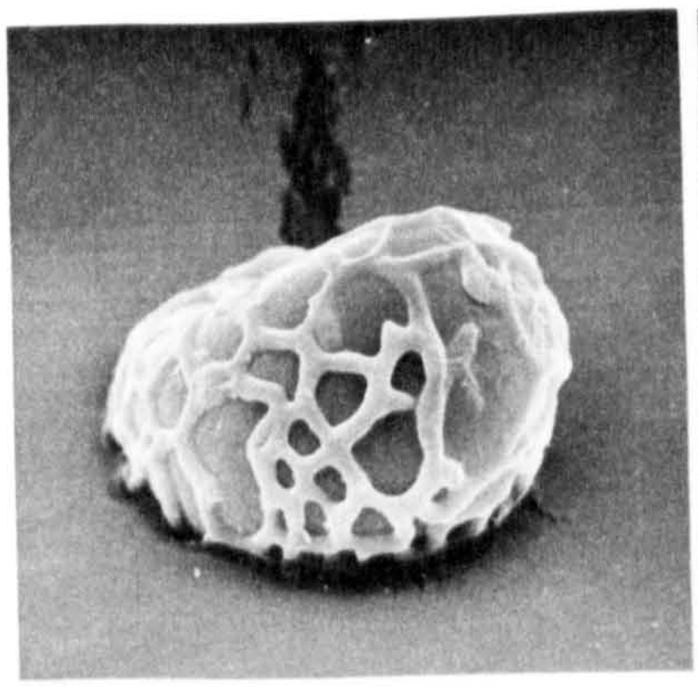
Fig. 101 T.bukoensis

Fig. 102 T.yunkweiensis

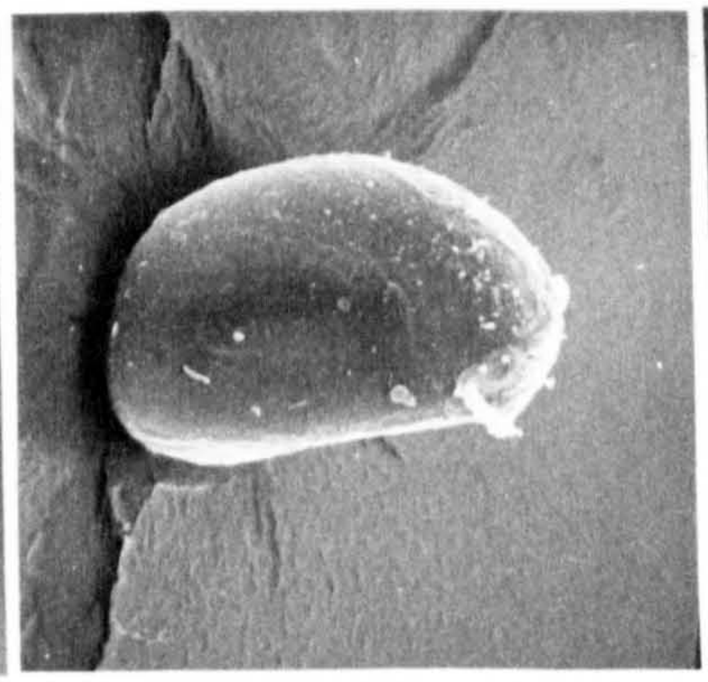
Fig. 103 T.hirtirachis

Fig. 104 T.brunnea

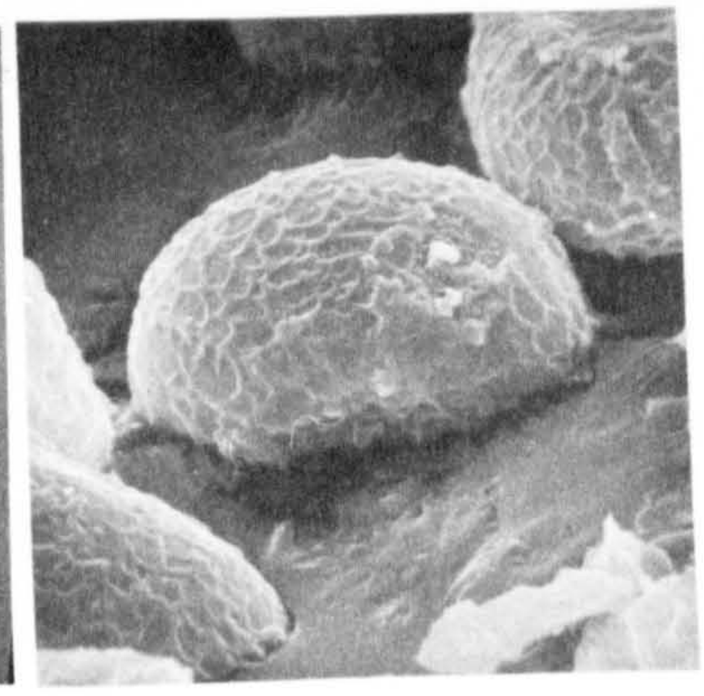
Fig. 105 T.keraudreniana



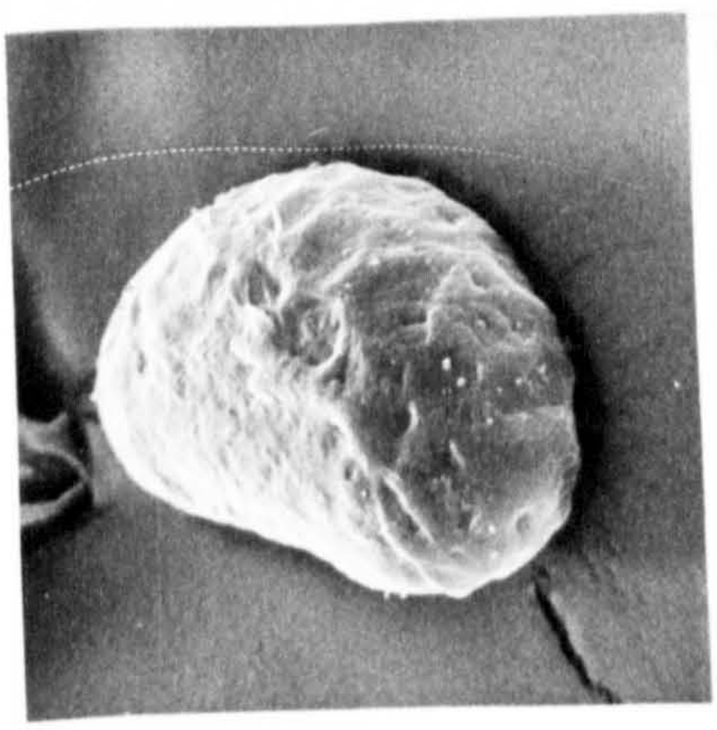
95



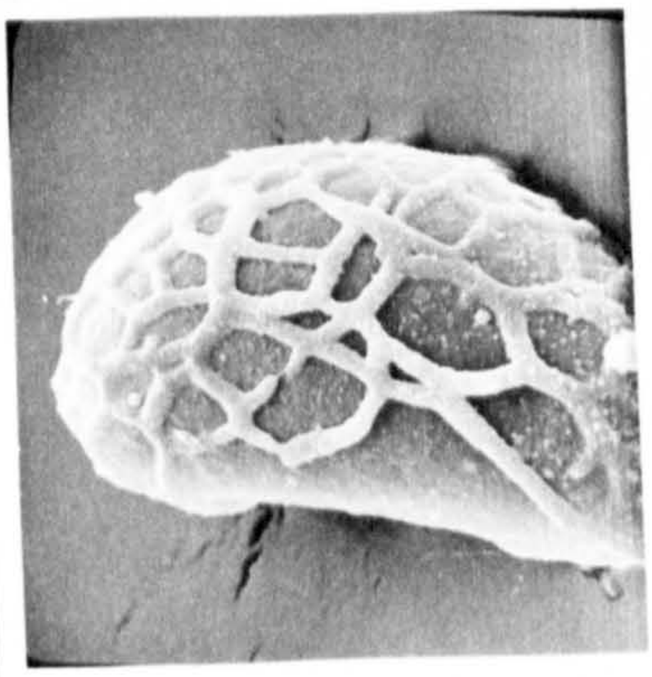
96



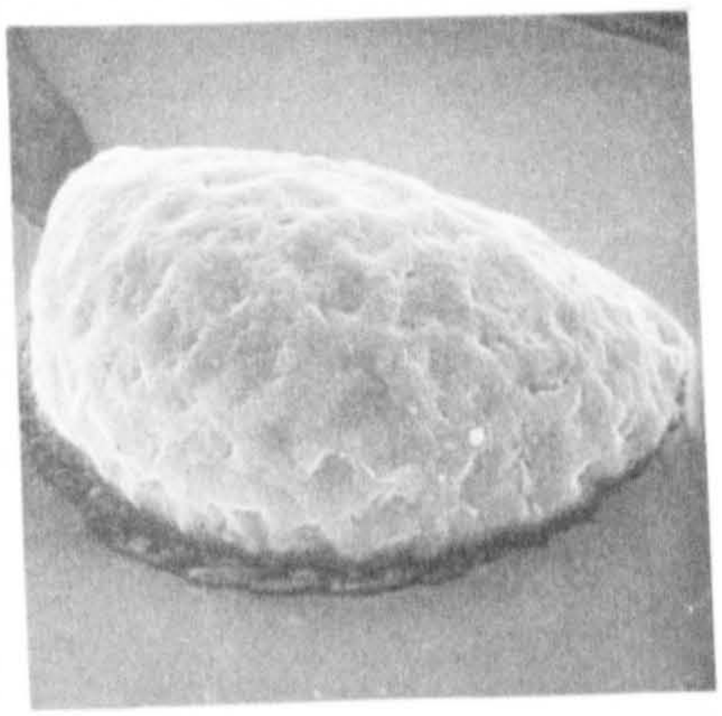
97



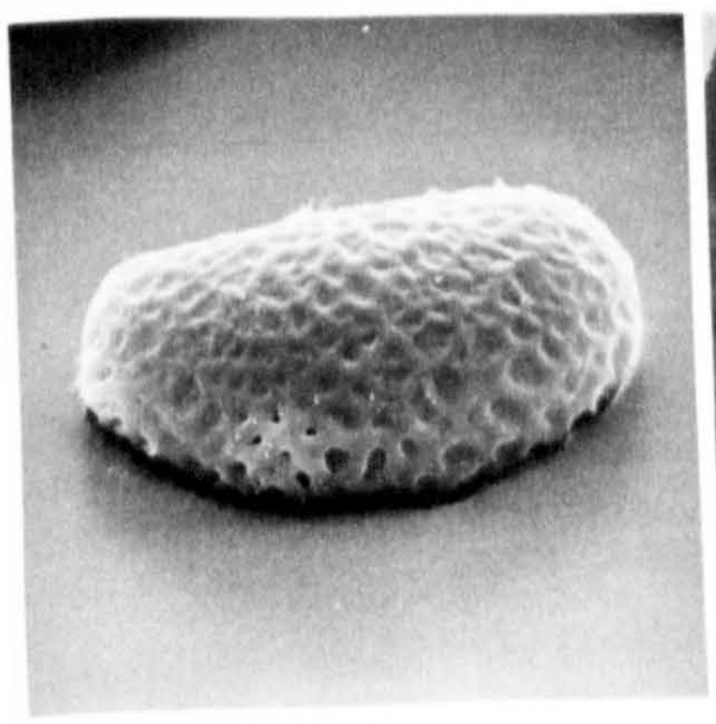
98



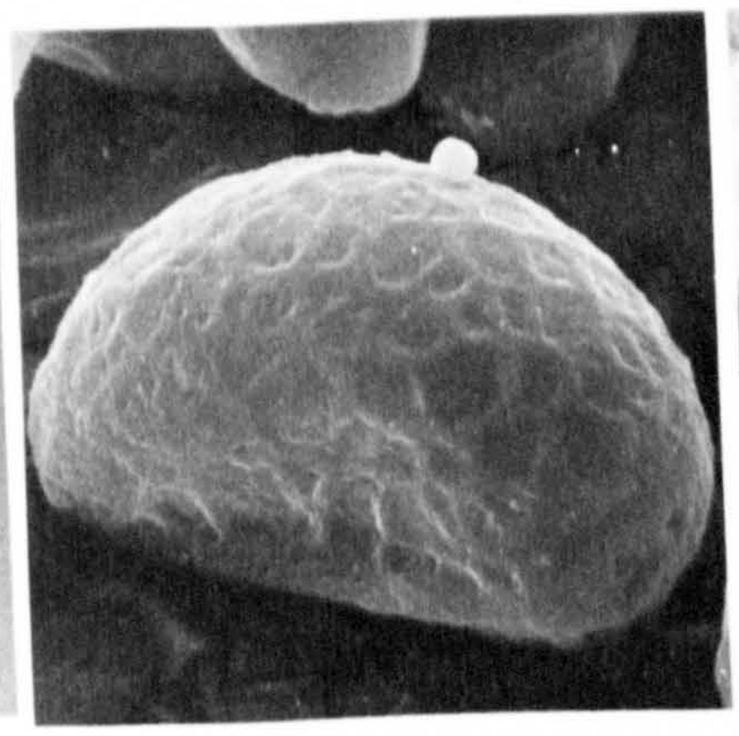
99



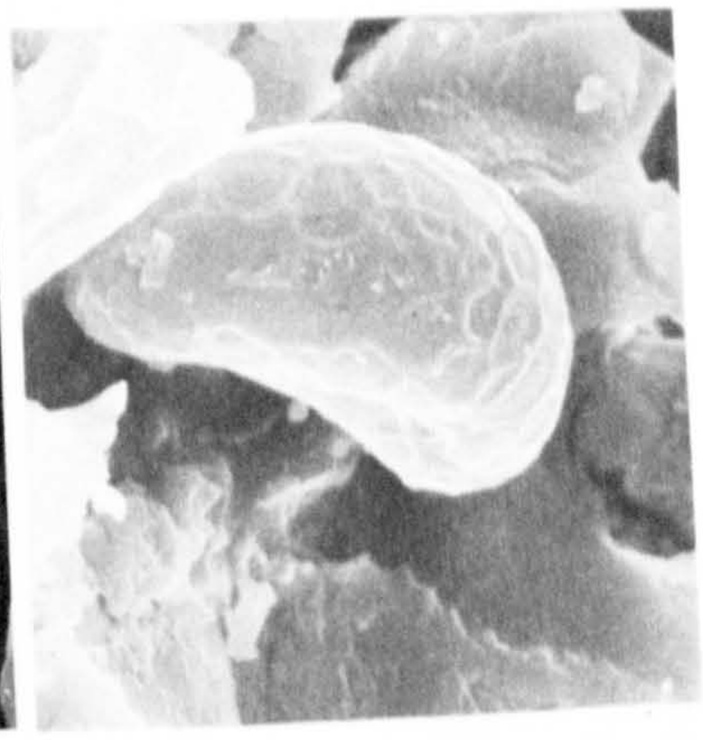
100



101

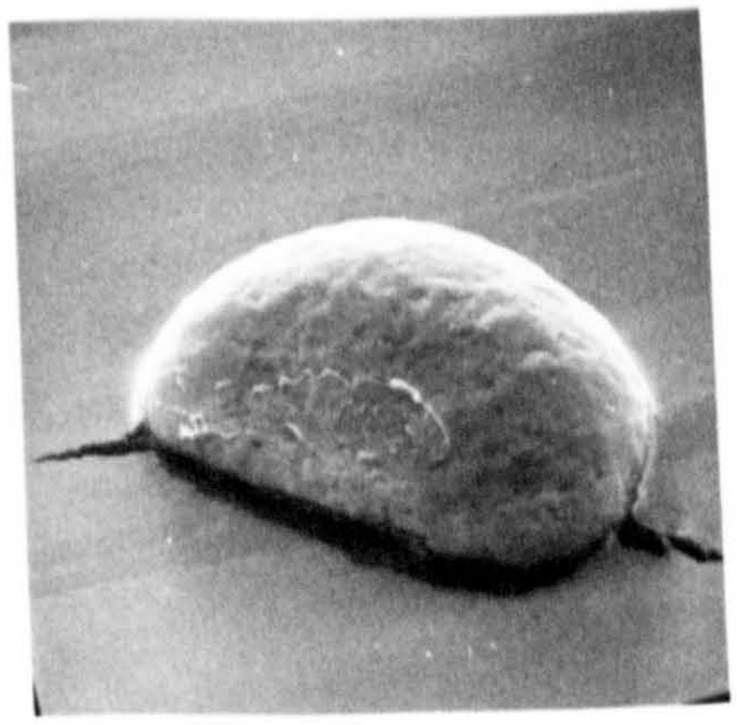


102



103

104



105

PLATE 19

Scanning Electron Photomicrographs Of Spores : X1000

Fig. 106 T.torresiana var. calvata

Fig. 107 T.ornata

Fig. 108 T.viridifrons

Fig. 109 T.polypodioides

Fig. 110 T.multiseta

Fig. 111 T.setigera

Fig. 112 T.noveboracensis

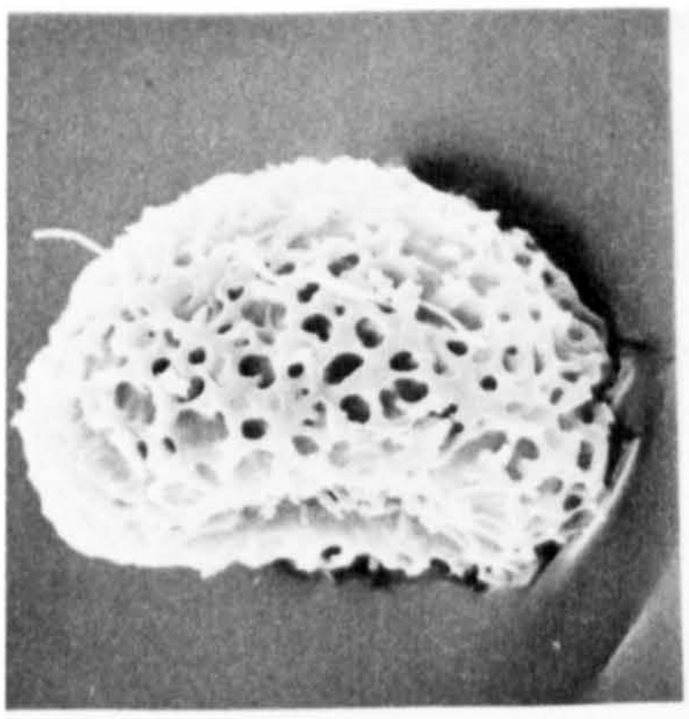
Fig. 113 T.nevadensis

Fig. 114 T.japonica

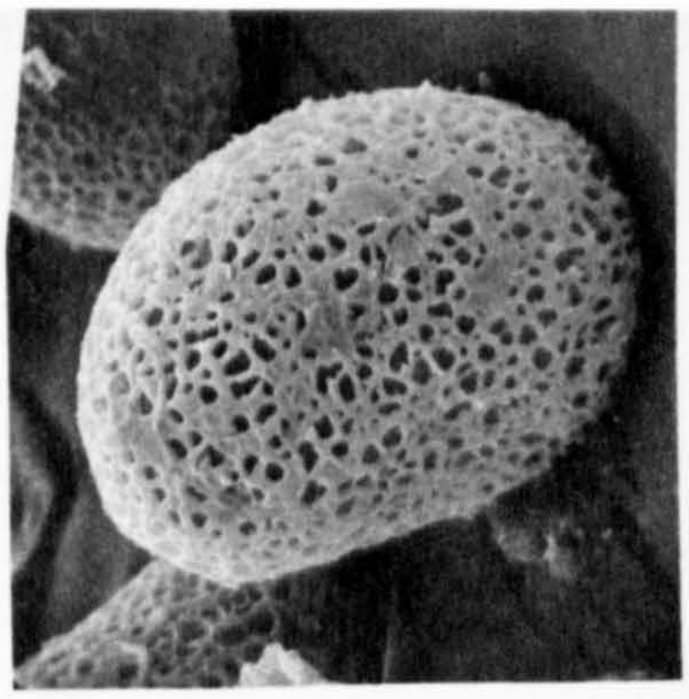
Fig. 115 T.resinifera

Fig. 116 T.similata

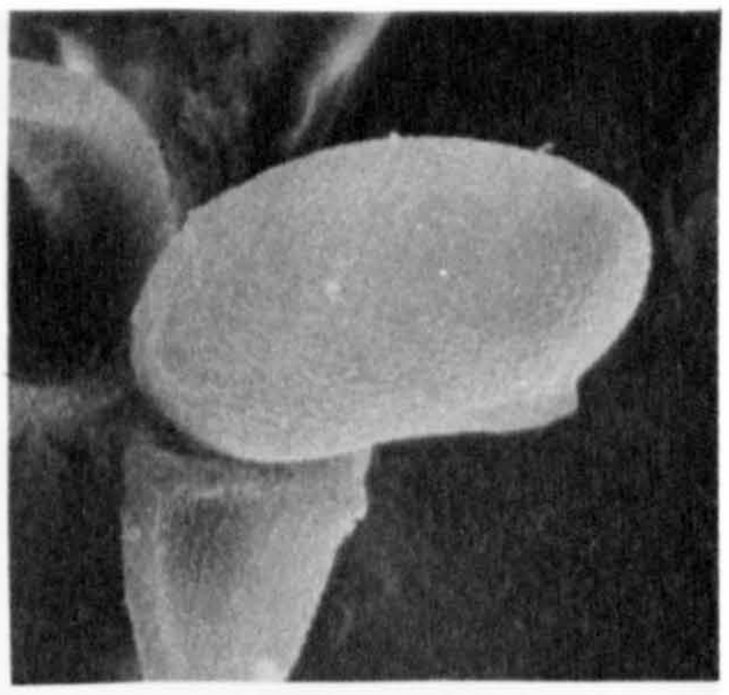
Fig. 117 T.pectiniformis



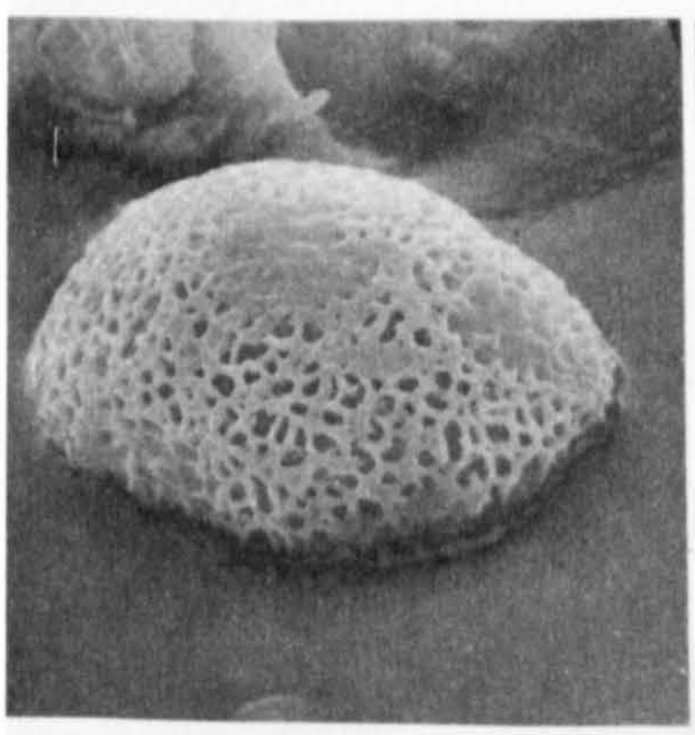
106



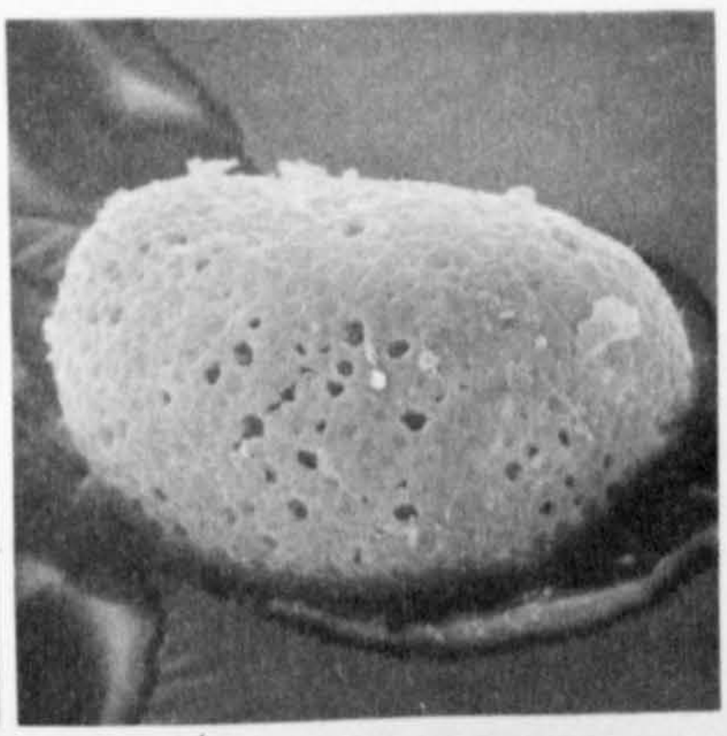
107



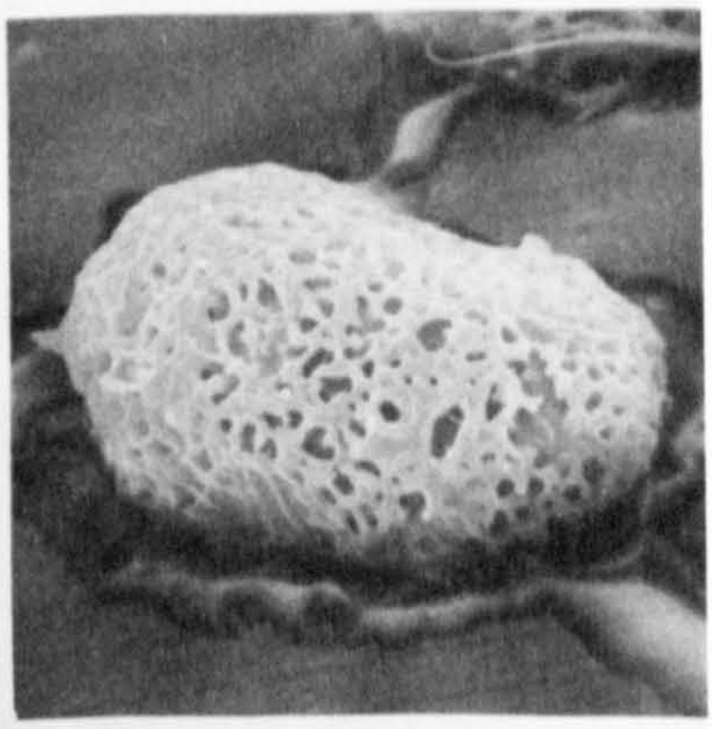
108



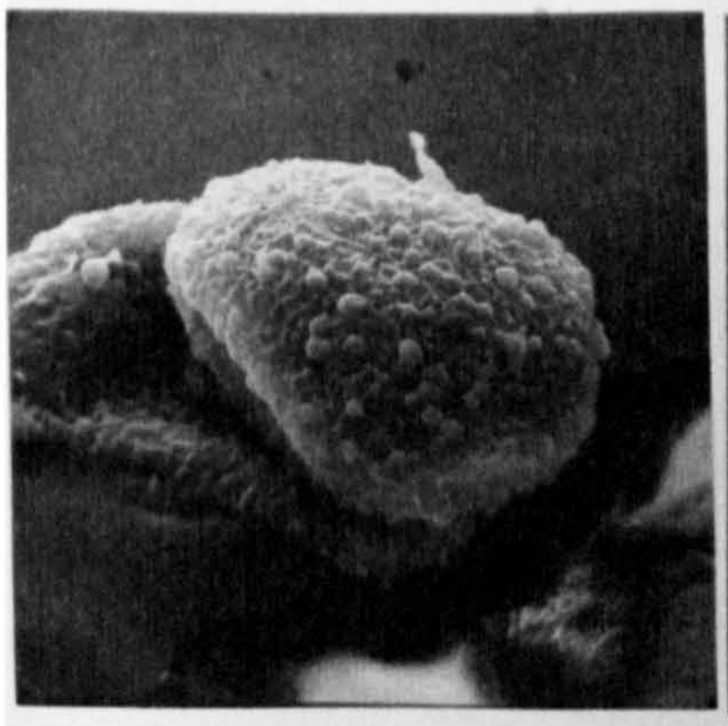
109



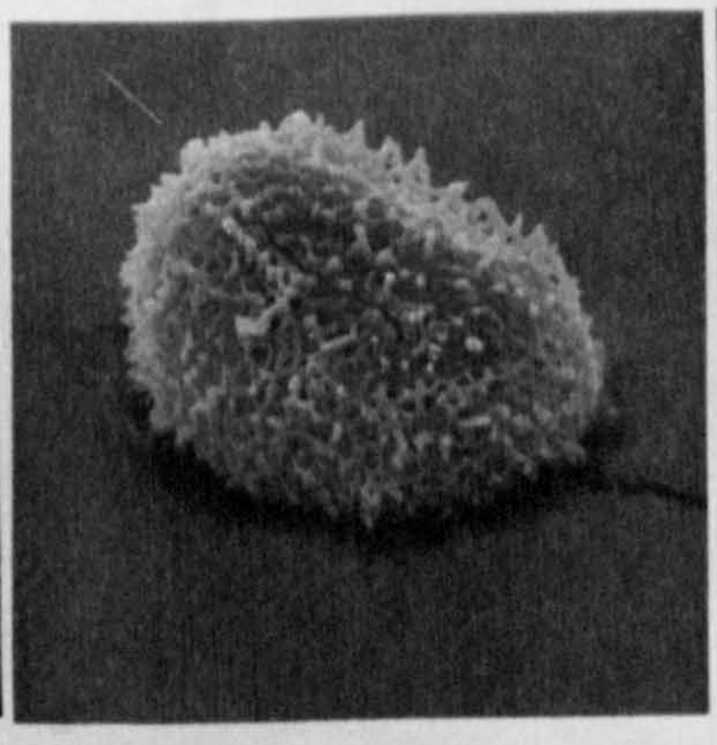
110



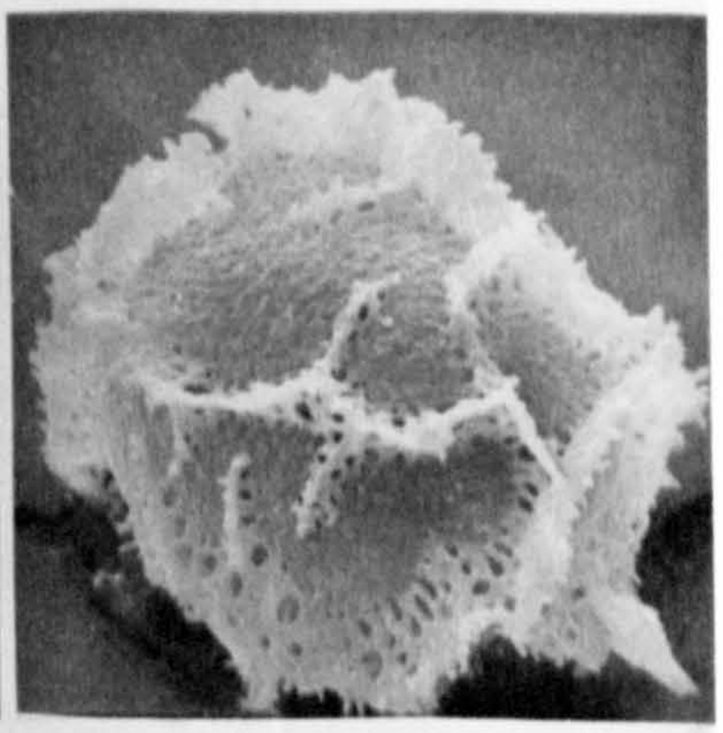
111



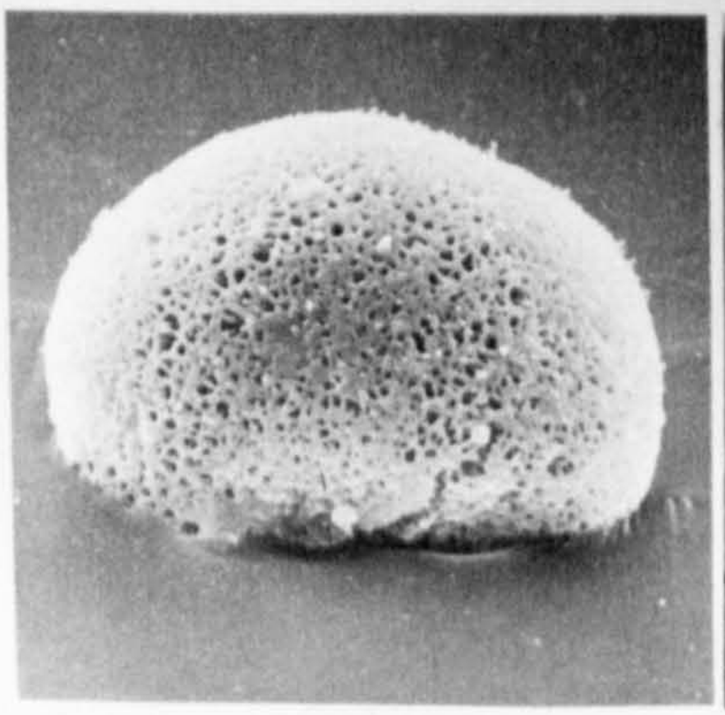
112



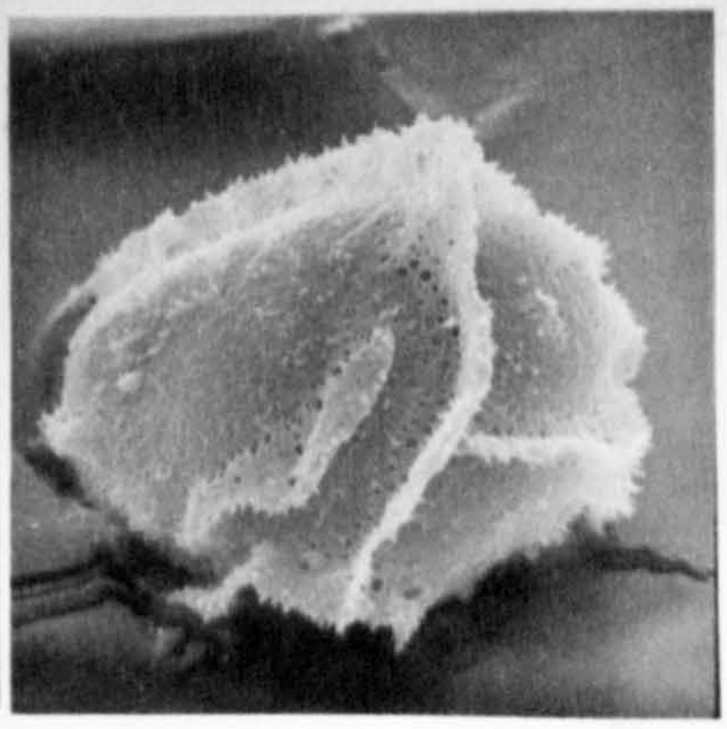
113



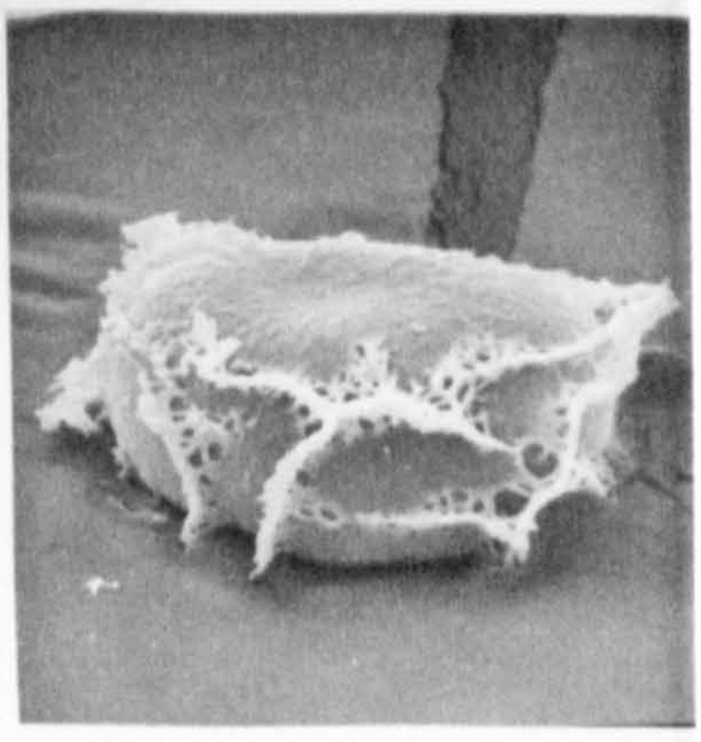
114



115



116



117

PLATE 20

Scanning Electron Photomicrographs Of Spores : X1000

Fig. 118 T.limbosperma

Fig. 119 T.quelpaertensis

Fig. 120 T.elwesii

Fig. 121 T.flaccida

Fig. 122 T.singalanensis

Fig. 123 T.esquirolii

Fig. 124 T.palustris

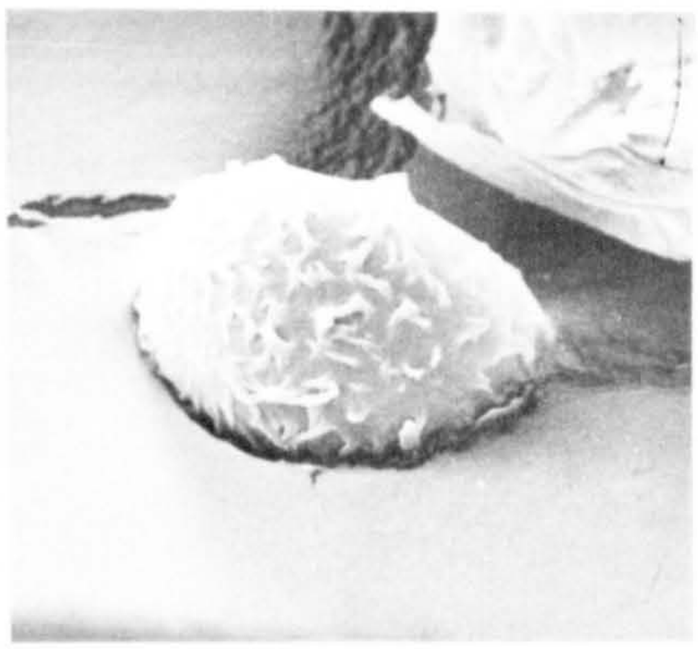
Fig. 125 T.griffithii

Fig. 126 T.aspidioides

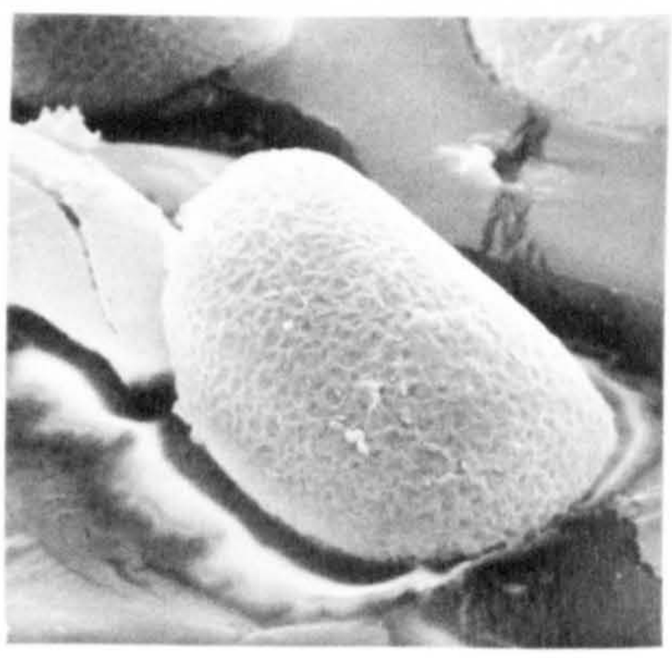
Fig. 127 T.pozoi

Fig. 128 T.gymnocarpa

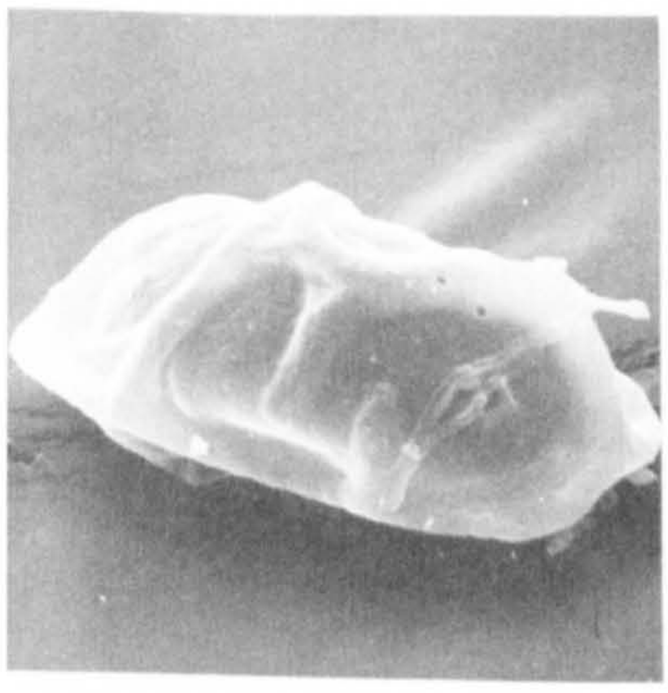
118



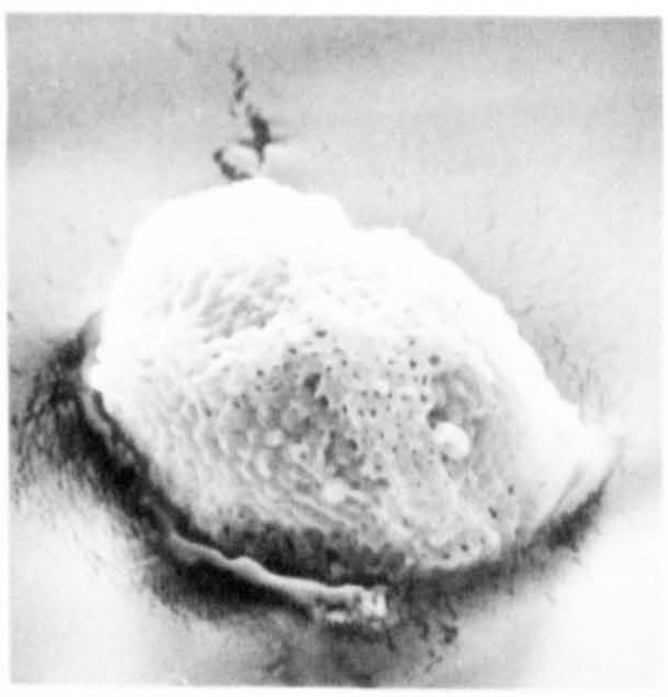
119



120



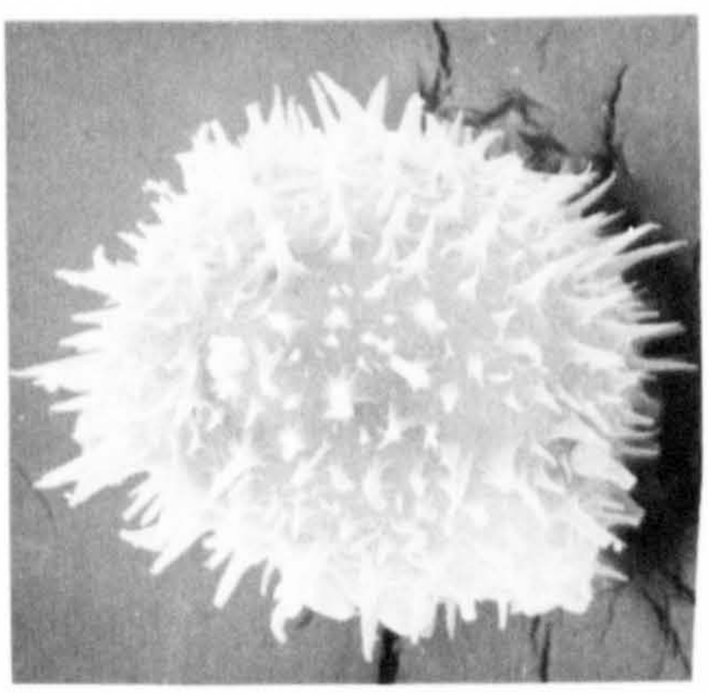
121



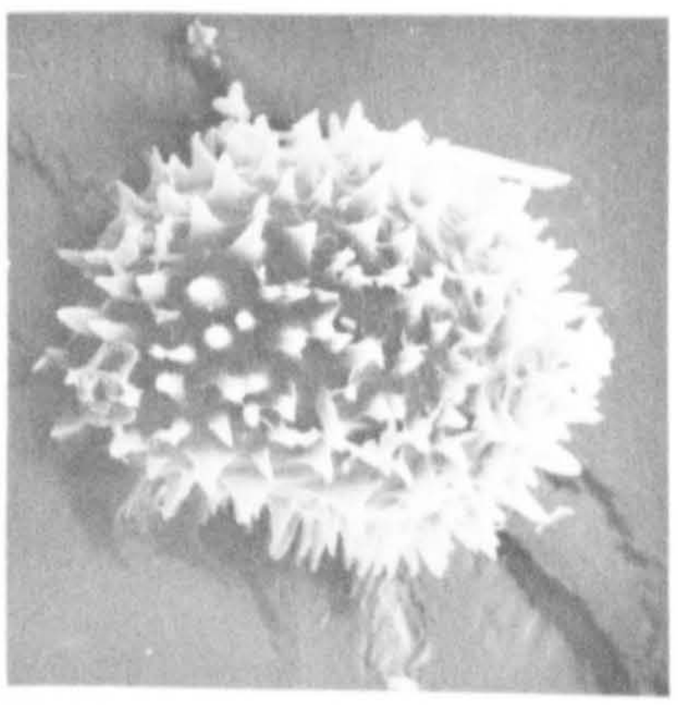
122

123

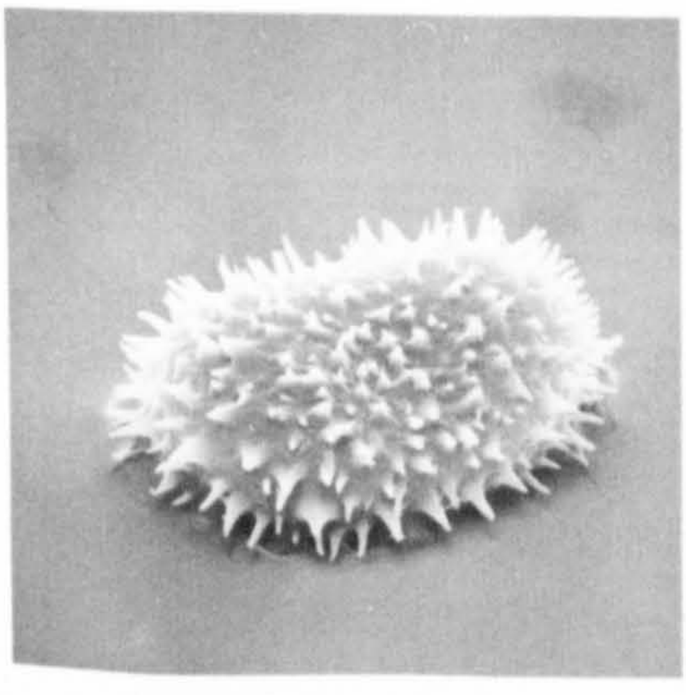
124



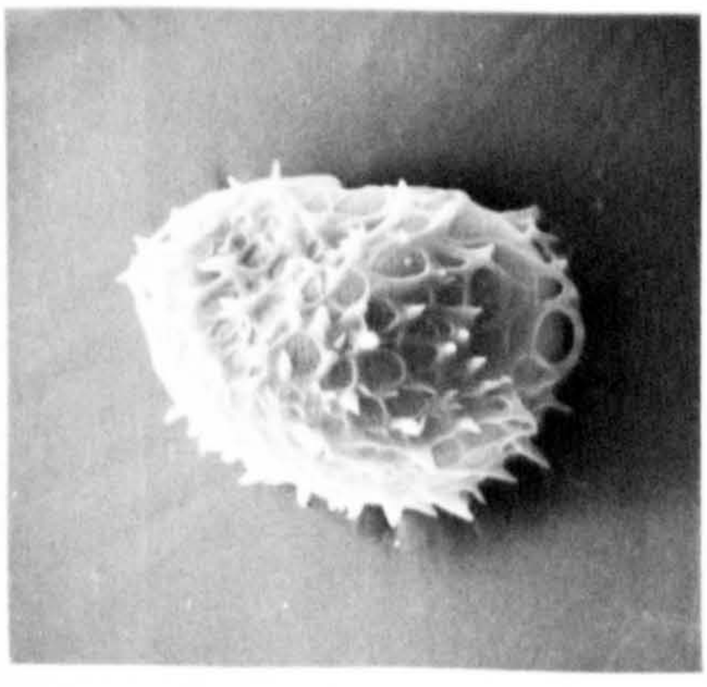
125



126



127



128

PLATE 21

Scanning Electron Photomicrographs Of Spores : X1000

Fig. 129 T.ciliata

Fig. 130 T.crassifolia

Fig. 131 T.serra

Fig. 132 T.gracilescens

Fig. 133 T.laxa

Fig. 134 T.erubescens

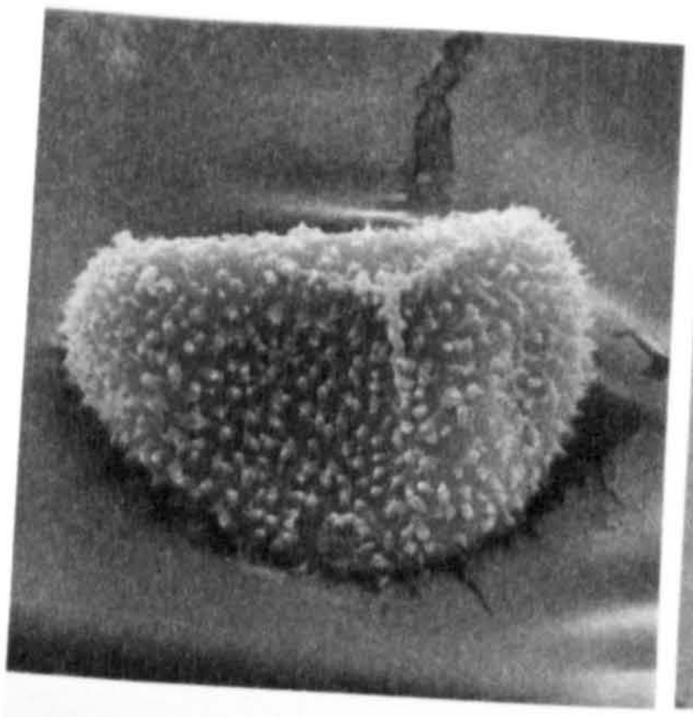
Fig. 135 T.decussata

Fig. 136 T.paleata

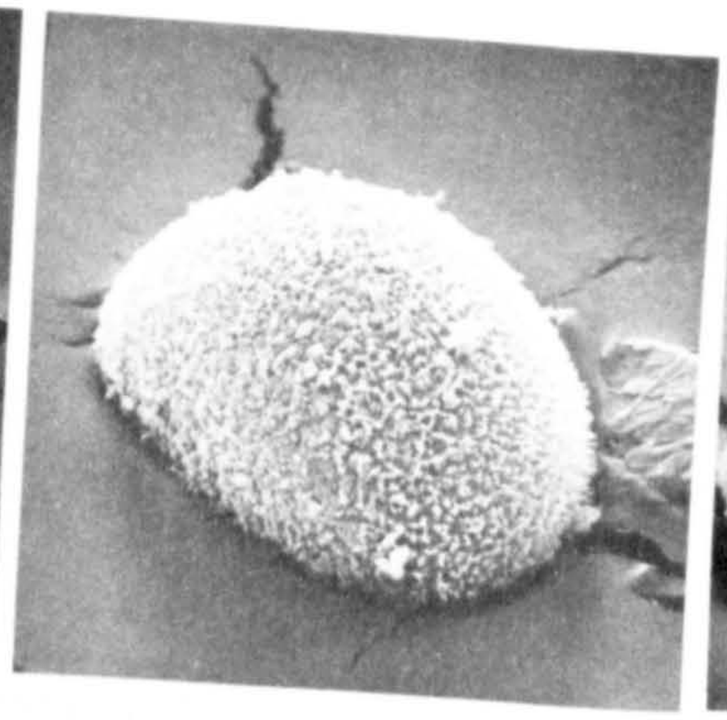
Fig. 137 T.deltoidea

Fig. 138 T.xylodes

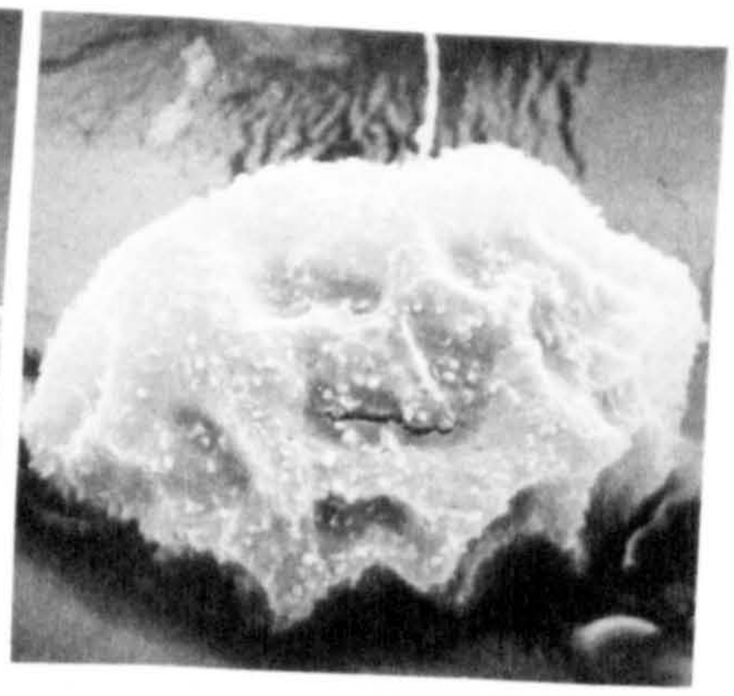
Fig. 139 T.subochthodes



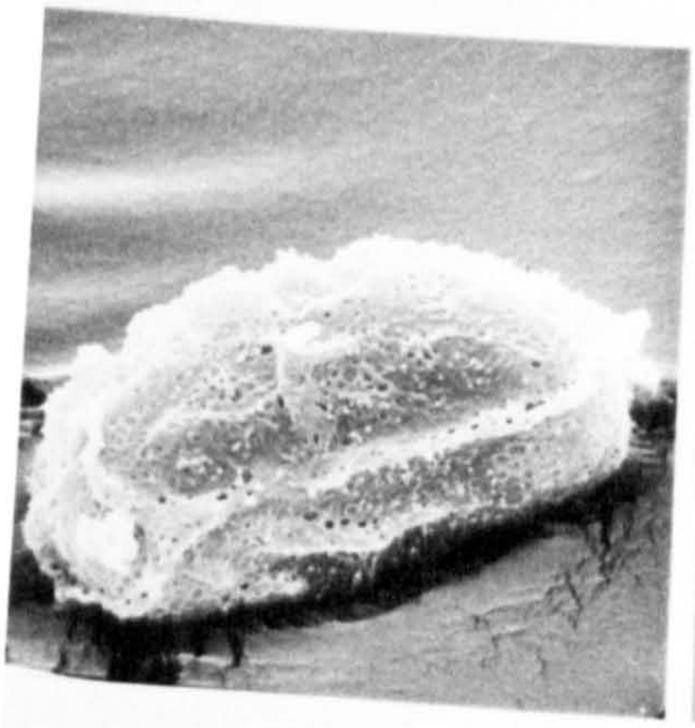
129



130



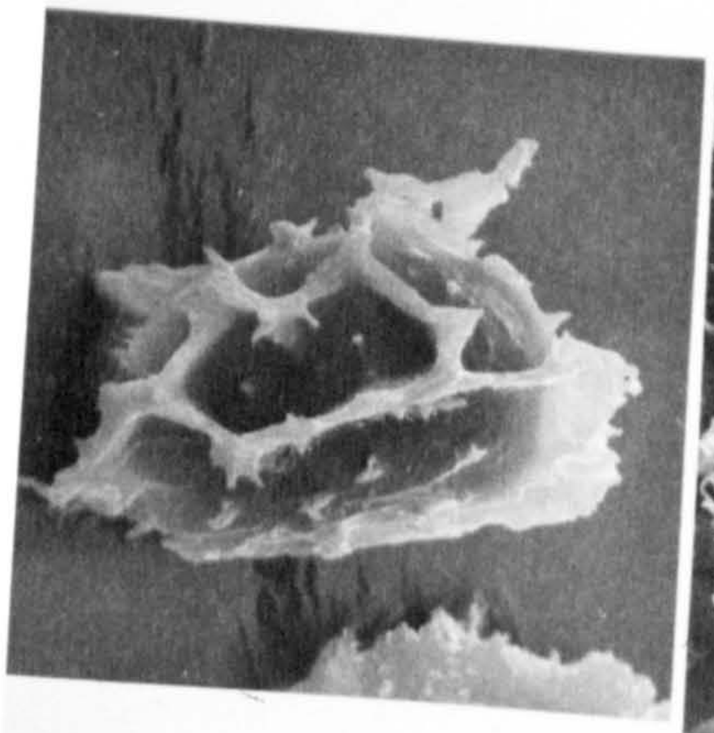
131



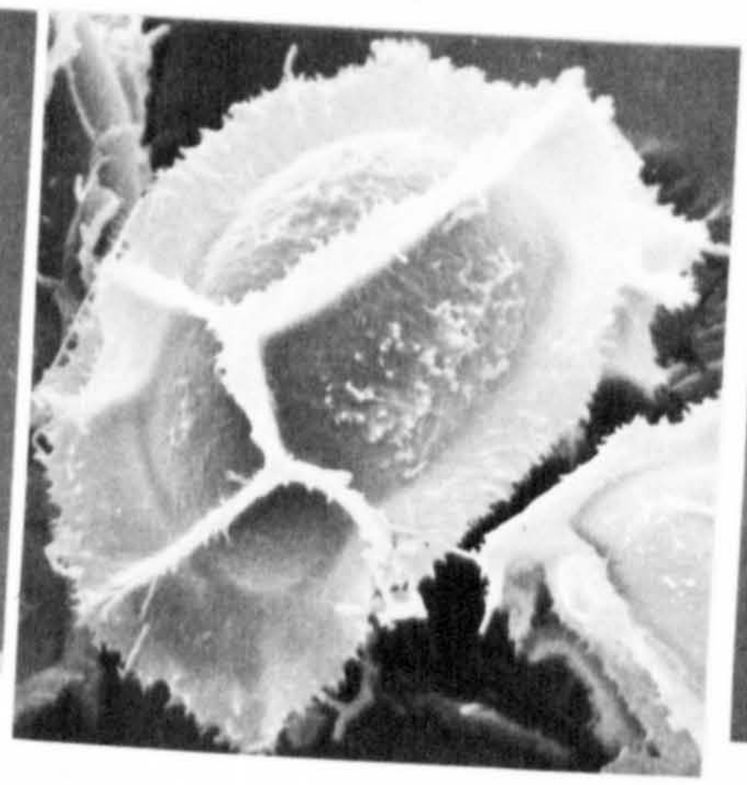
132

133

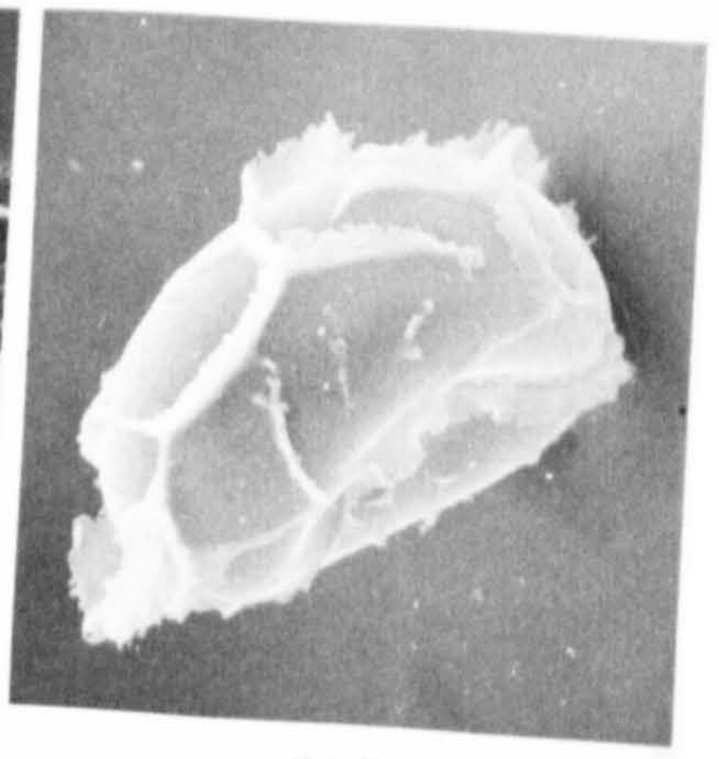
134



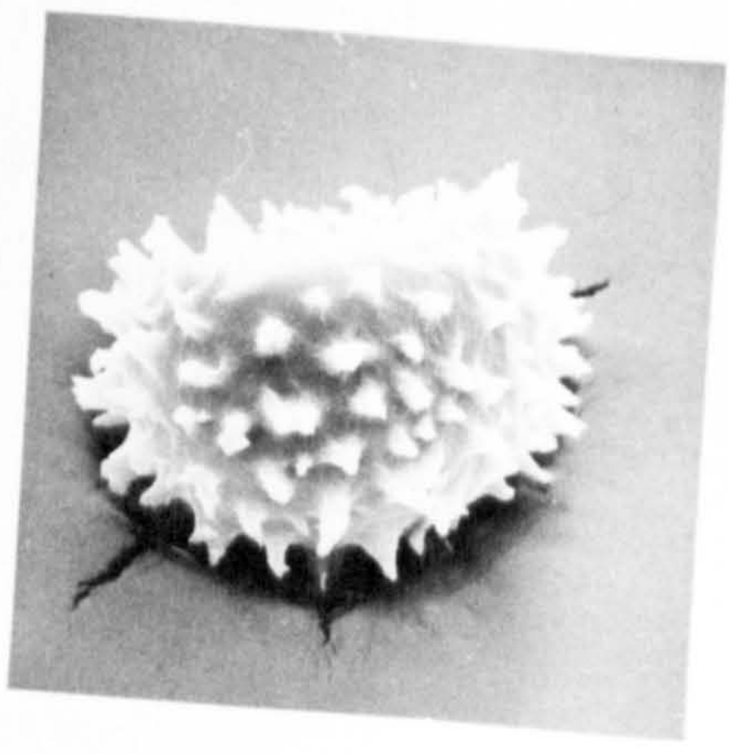
135



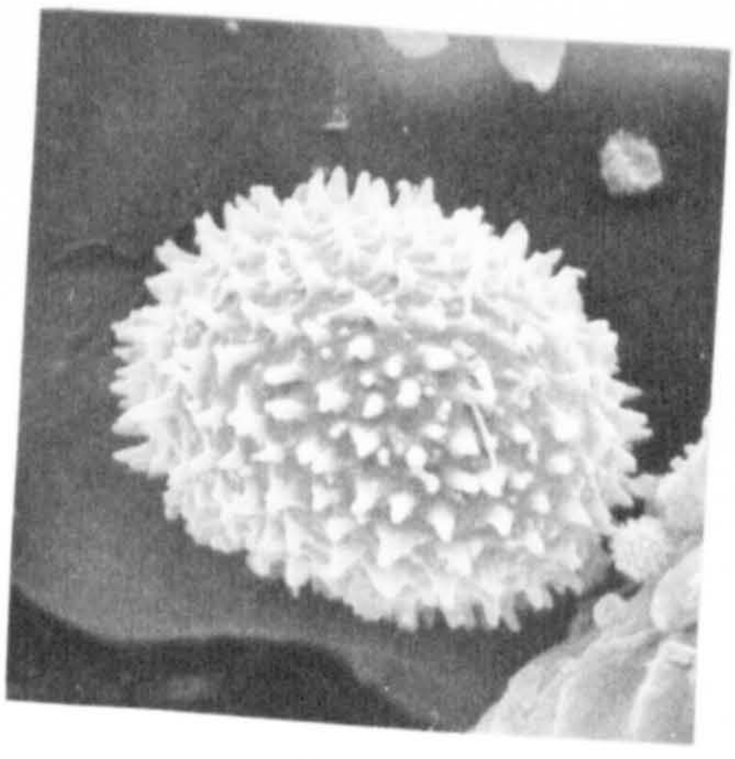
136



137



138



139

PLATE 22

Scanning Electron Photomicrographs Of Spores : X1000

Fig. 140 T.uraiensis

Fig. 141 T.calcareta

Fig. 142 T.hattorii

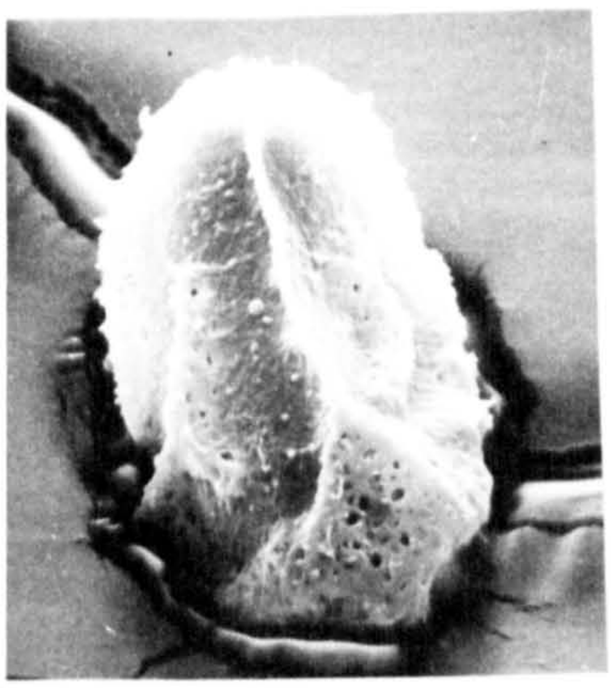
Fig. 143 T.firma

Fig. 144 T.duclouxii

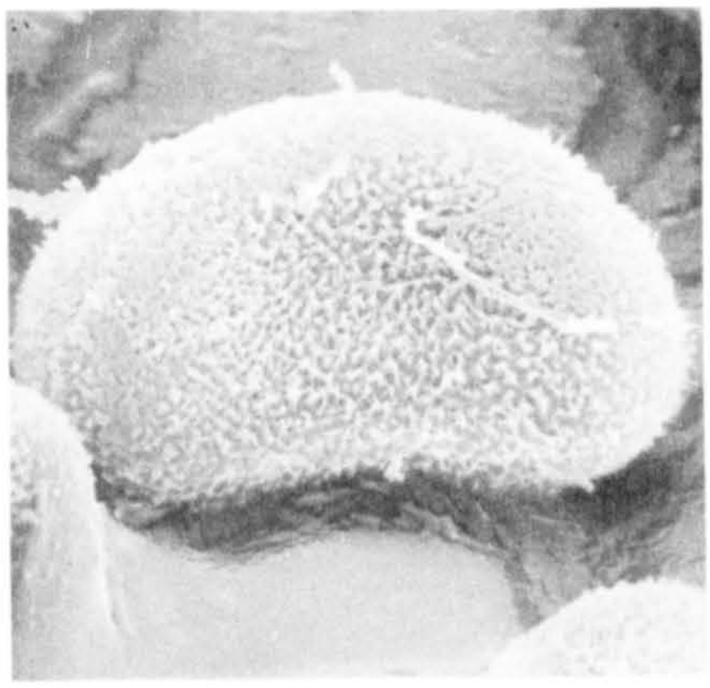
Fig. 145 T.nipponica

Fig. 146 T.squamaestipes

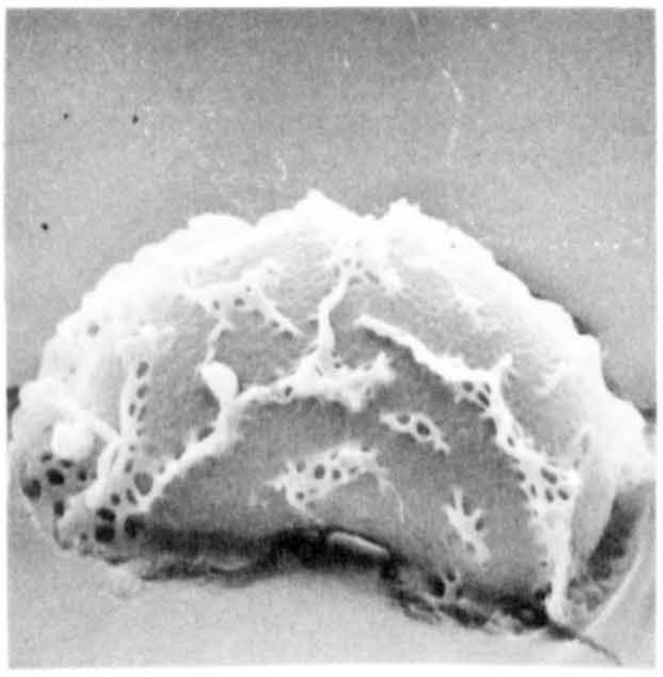
Fig. 147 T.wrightii



140

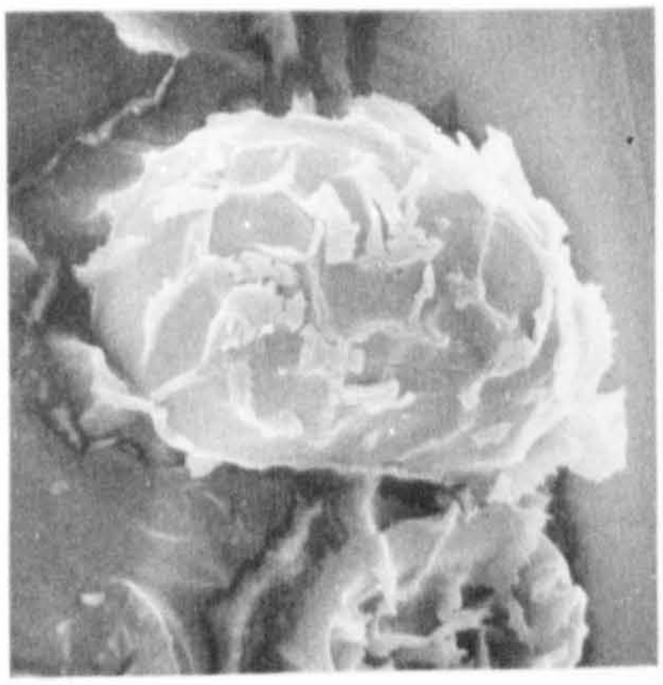


141

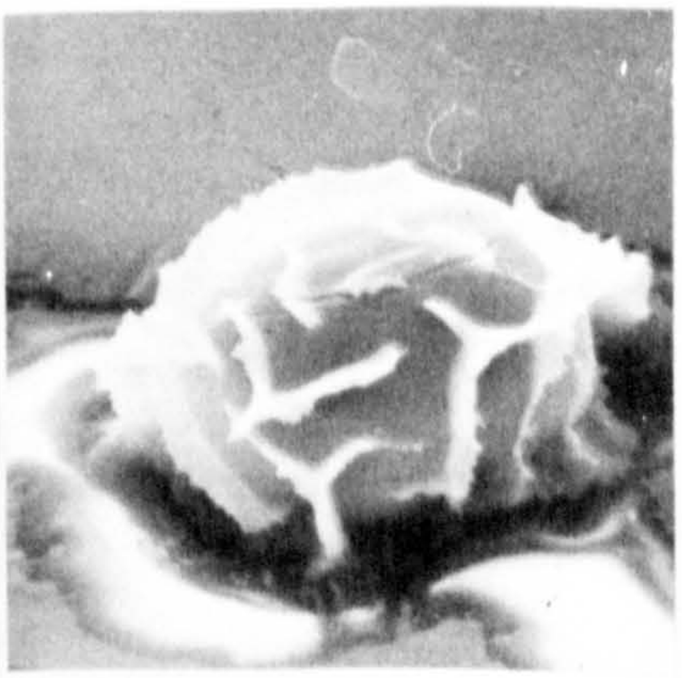


142

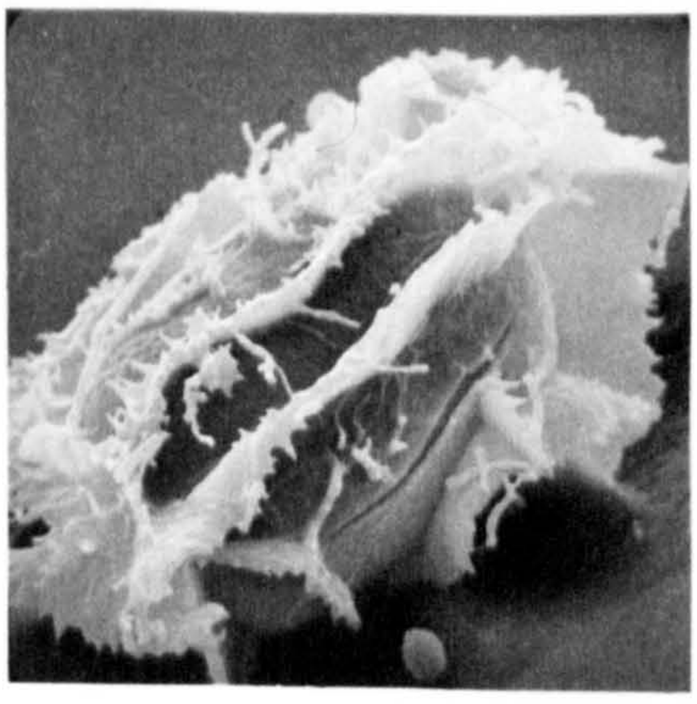
143



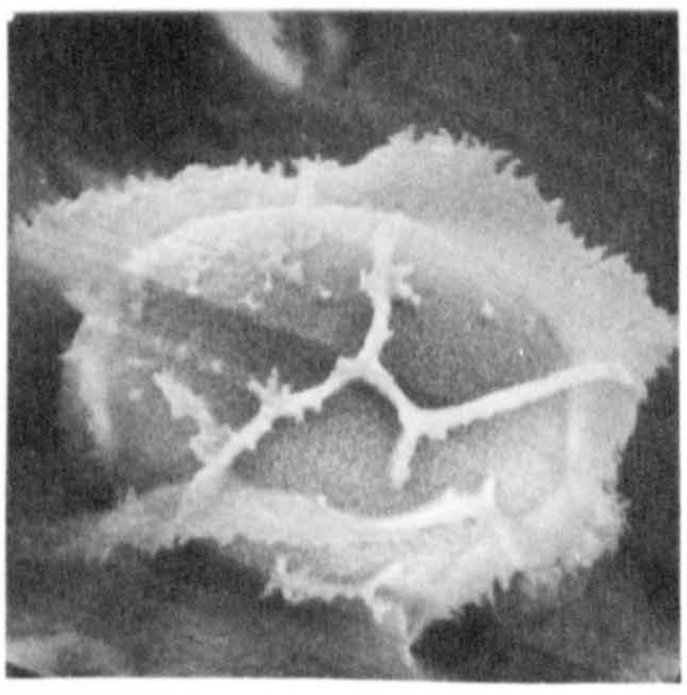
144



145



146



147

PLATE 23

Scanning Electron Photomicrographs Of Spores : X1000

Fig. 148 T.kunthii

Fig. 149 T.megaphylla

Fig. 150 T.multilineata

Fig. 151 T.rubicunda

Fig. 152 T.gongylodes

Fig. 153 T.pennigera

Fig. 154 T.patens

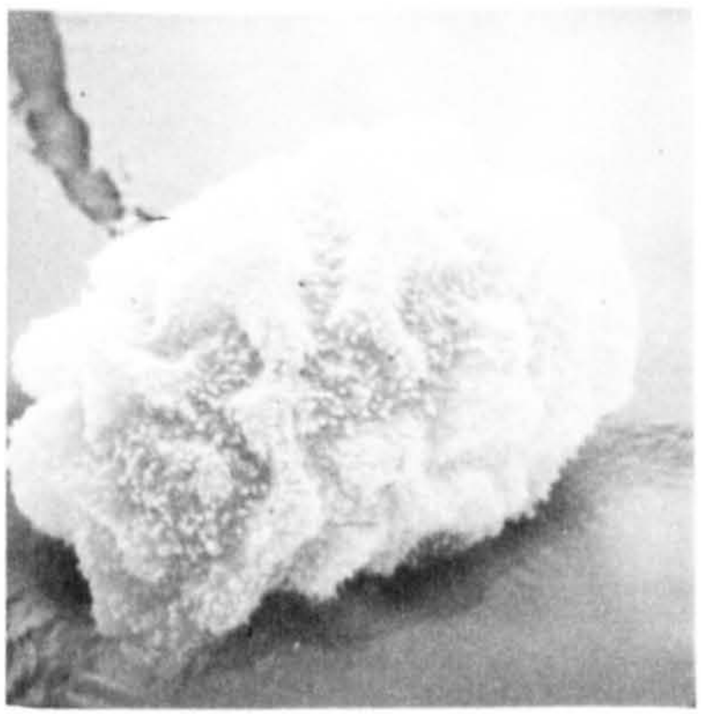
Fig. 155 T.papilio

Fig. 156 T.truncata

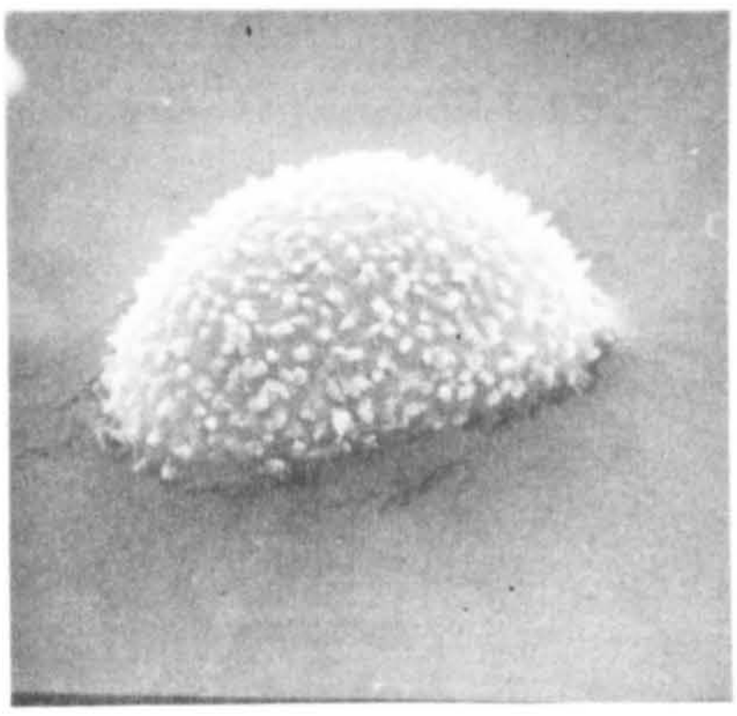
Fig. 157 T.crinipes

Fig. 158 T.triphylla

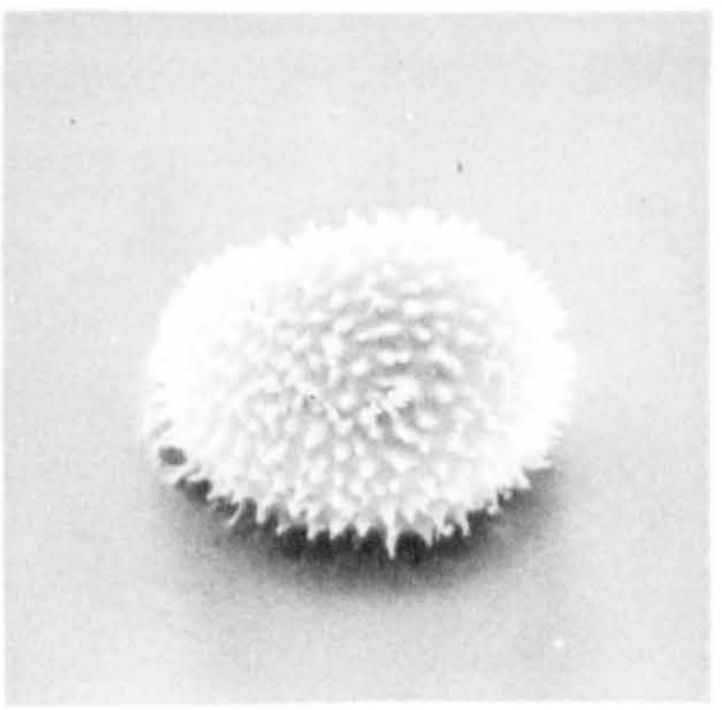
Fig. 159 T.dentata



148

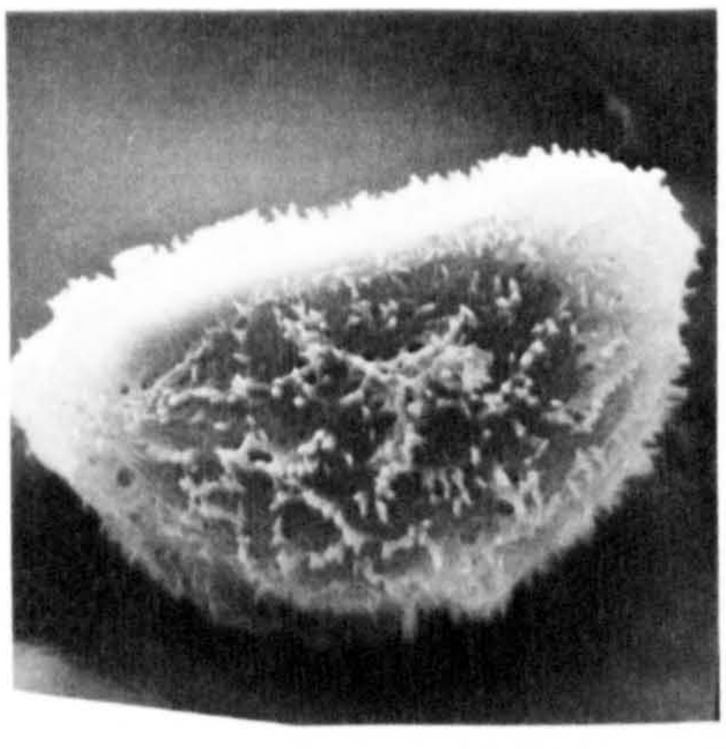


149

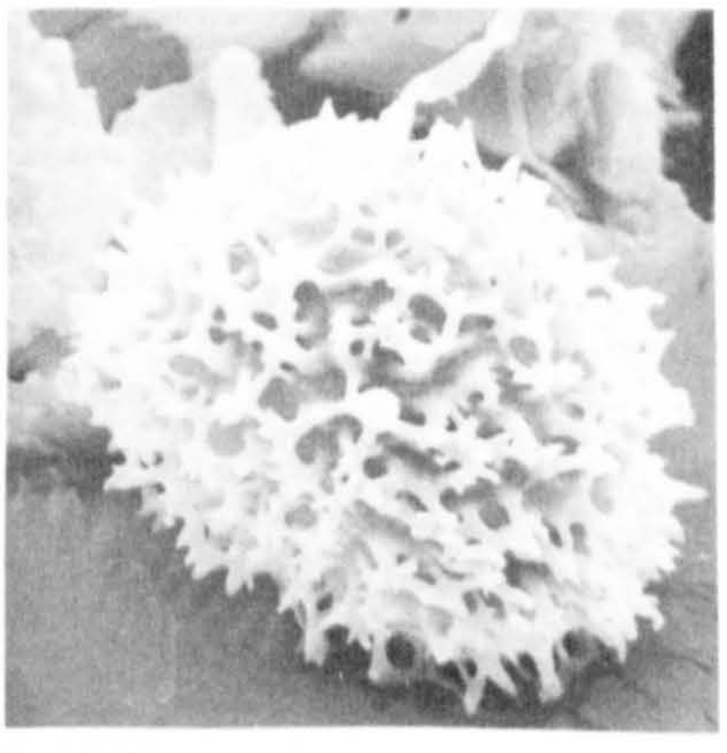


150

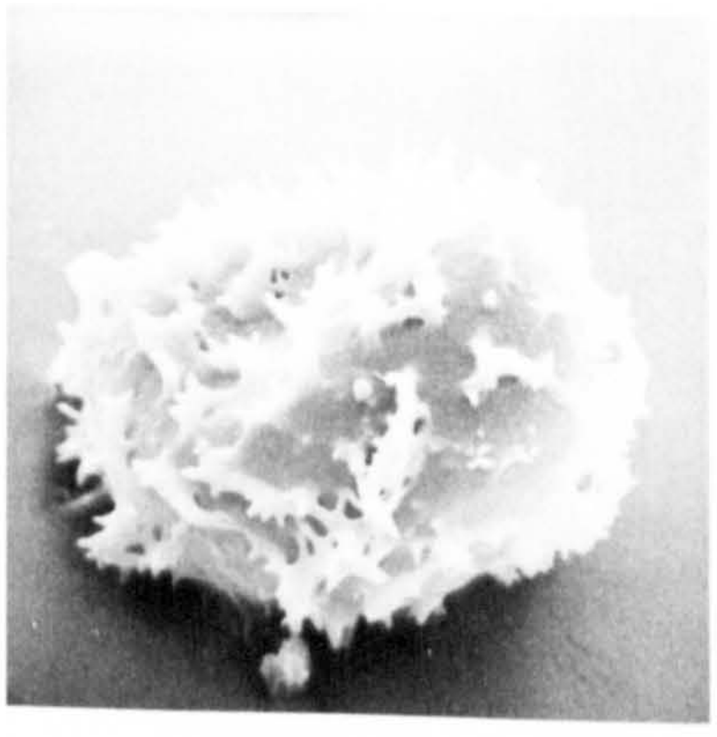
151



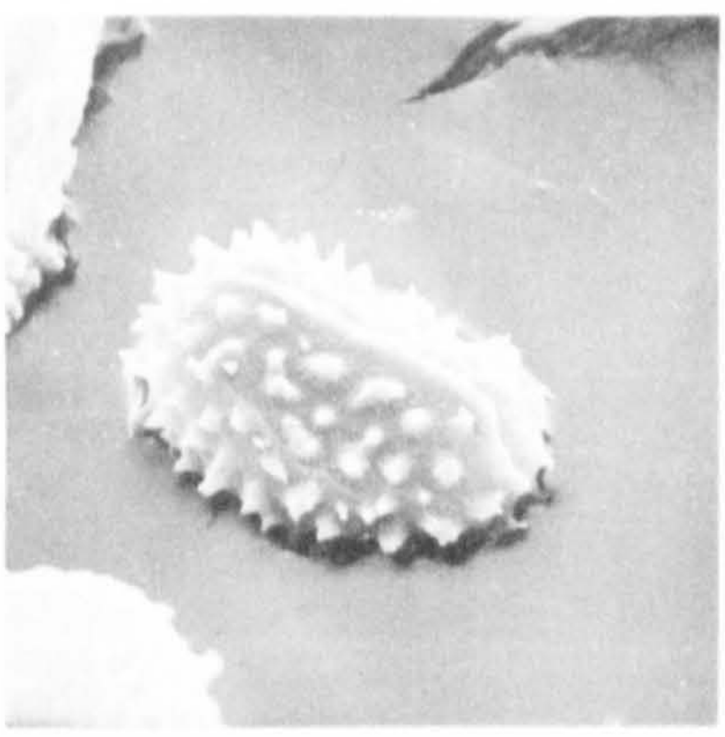
152



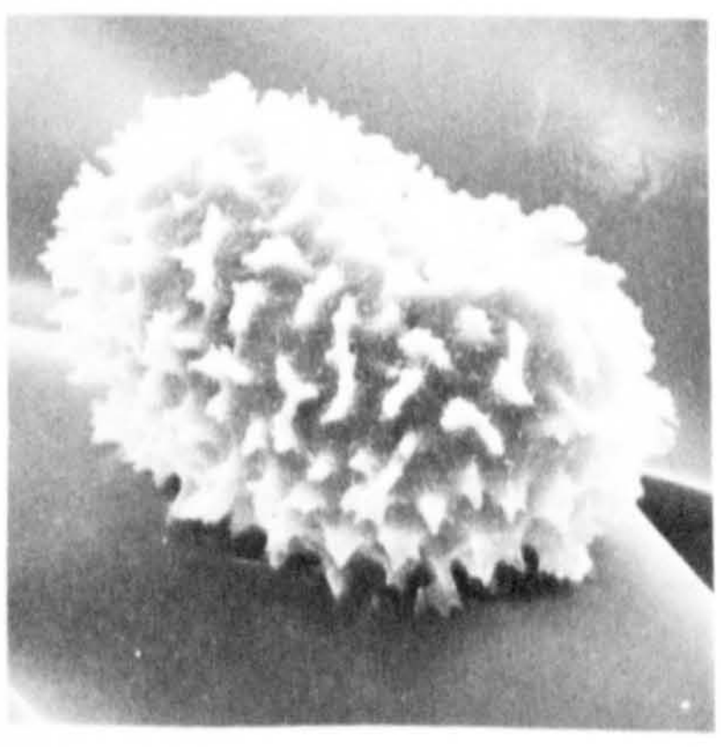
153



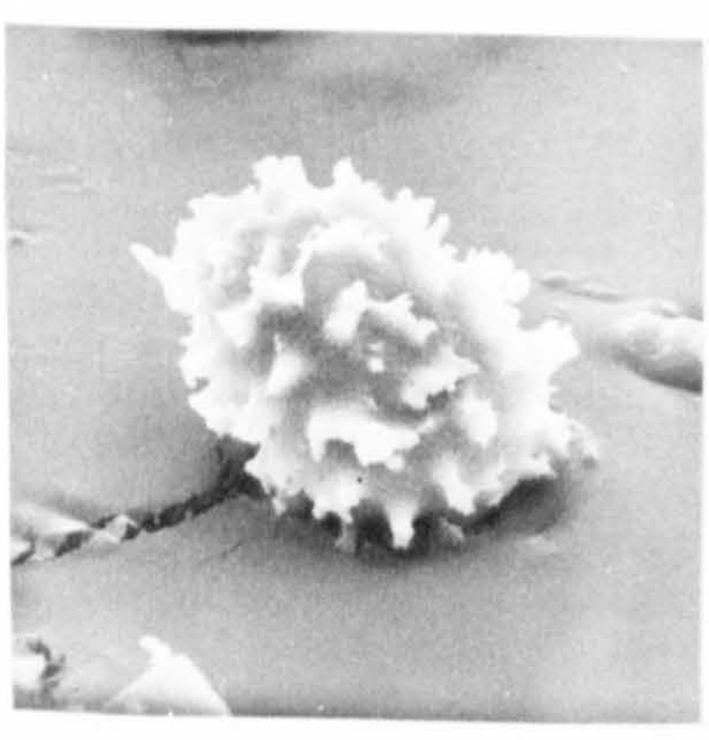
154



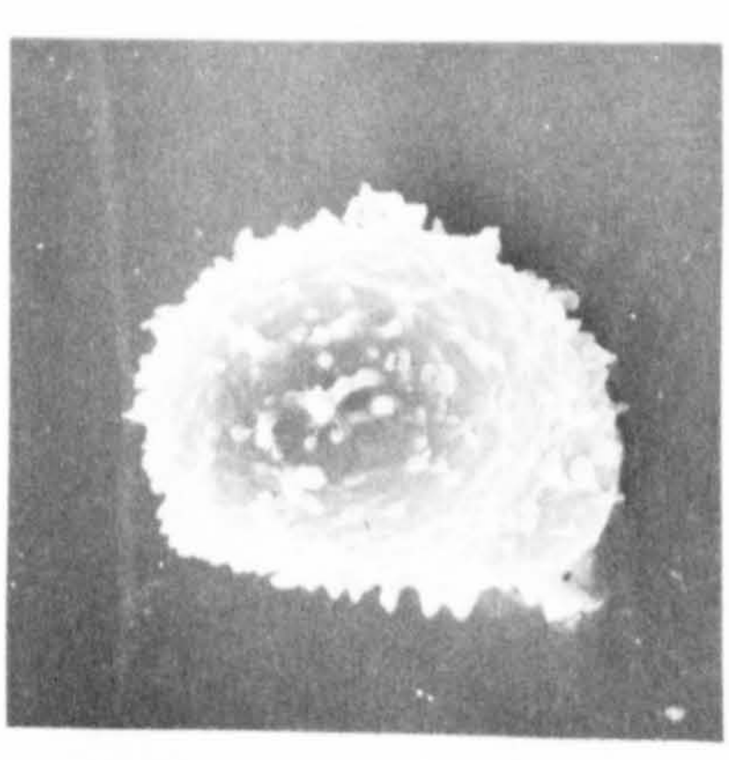
155



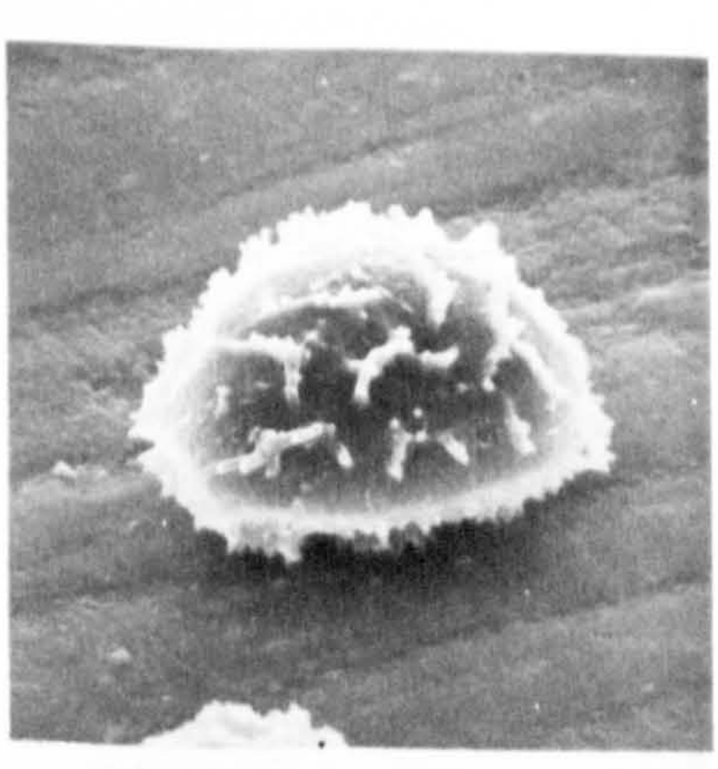
156



157



158



159

PLATE 24

Scanning Electron Photomicrographs Of Spores : X1000

Fig. 160 T.interrupta

Fig. 161 T.venusta

Fig. 162 T.serrulata

Fig. 163 T.biolleyi

Fig. 164 T.venusta var. usitata

Fig. 165 T.poiteana

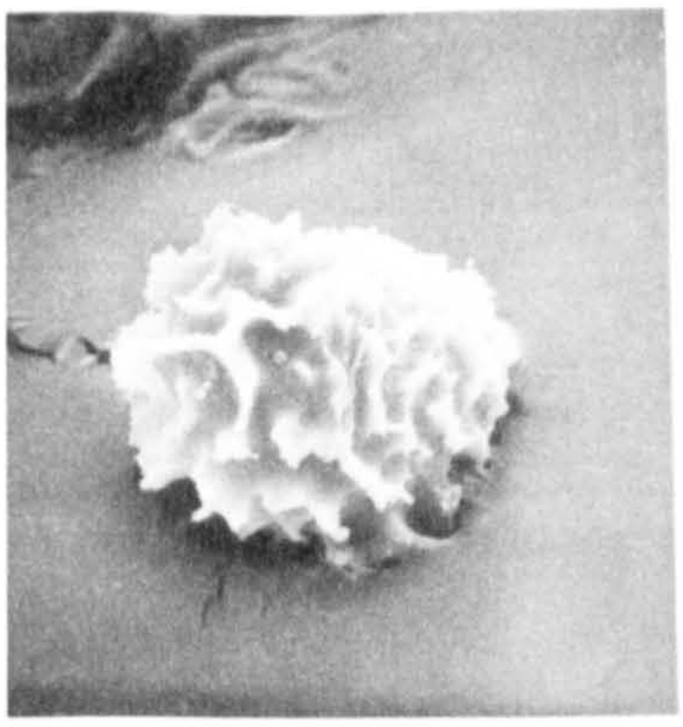
Fig. 166 T.asplenioides (=T.polycarpa)

Fig. 167 T.sclerophylla

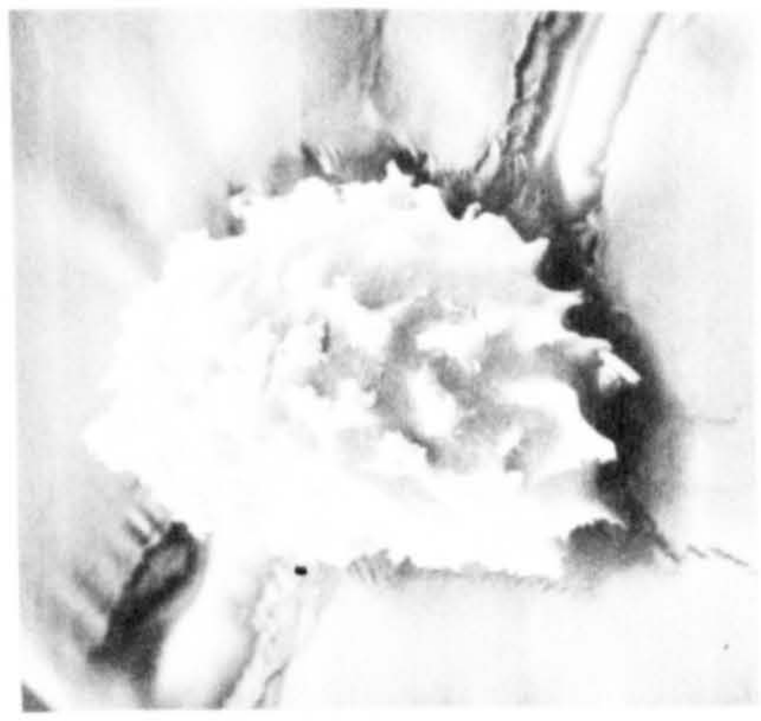
Fig. 168 T.obliterata

Fig. 169 T.reptans

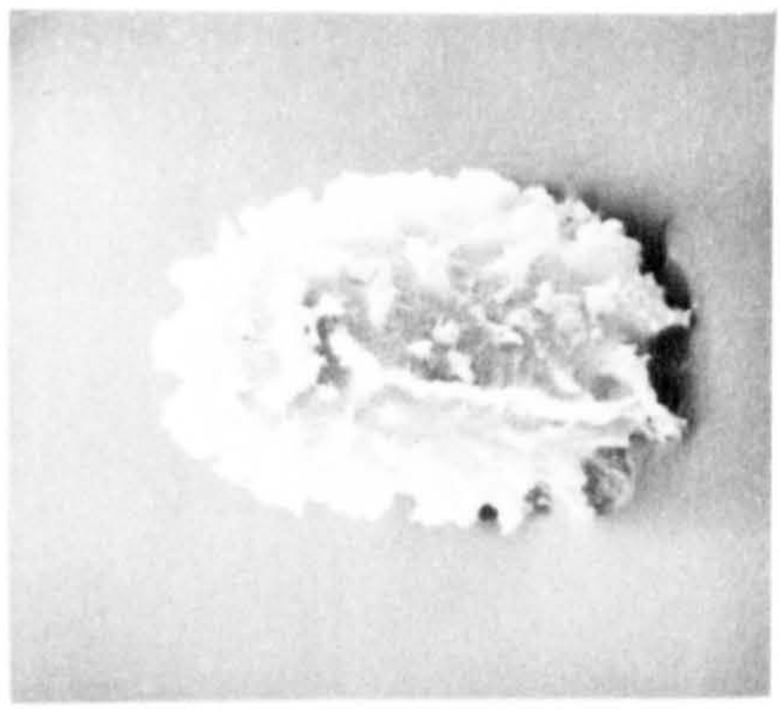
Fig. 170 T.guadeloupensis



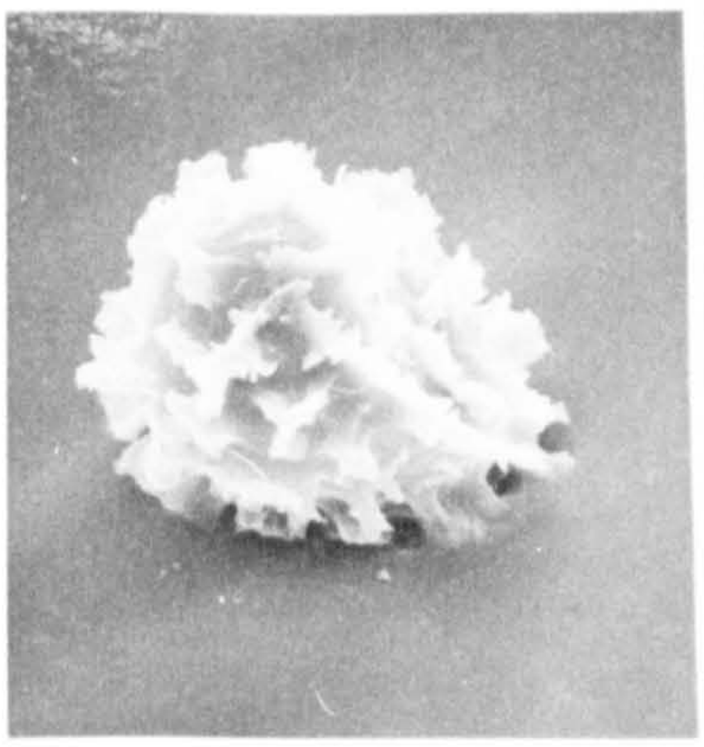
160



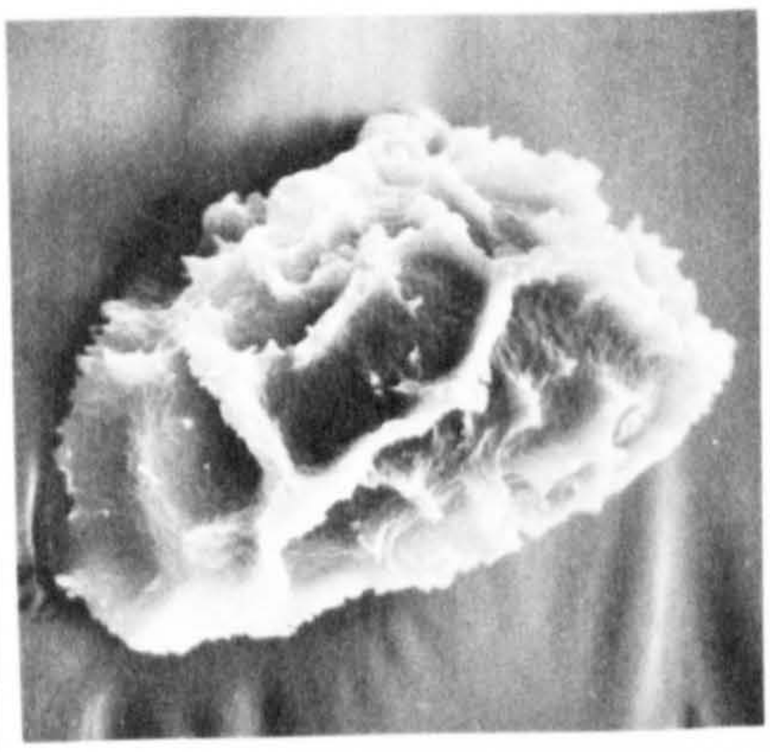
161



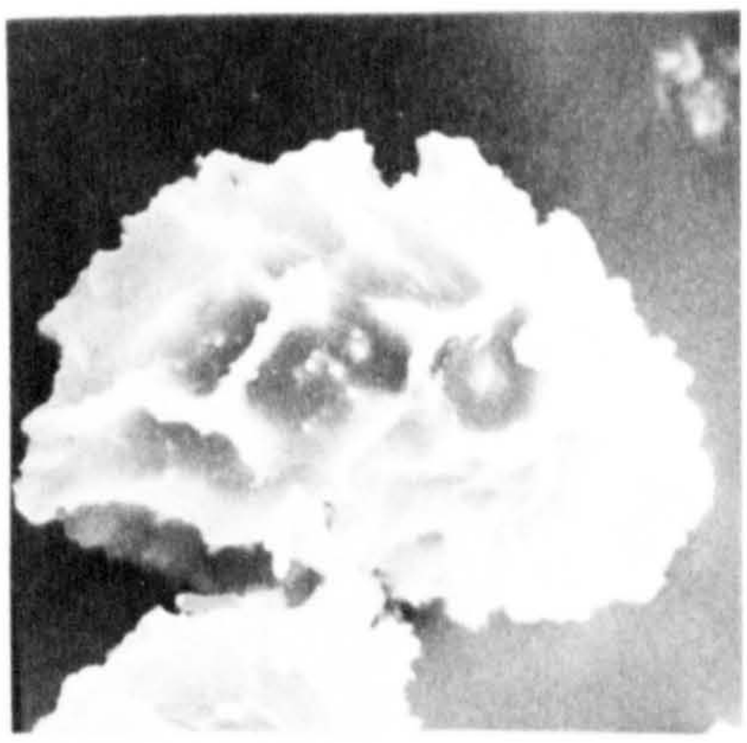
162



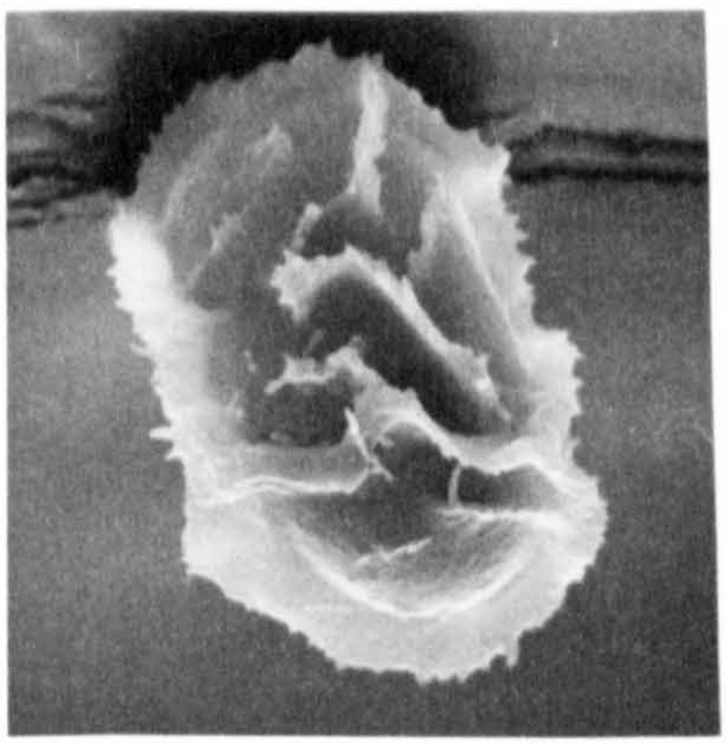
163



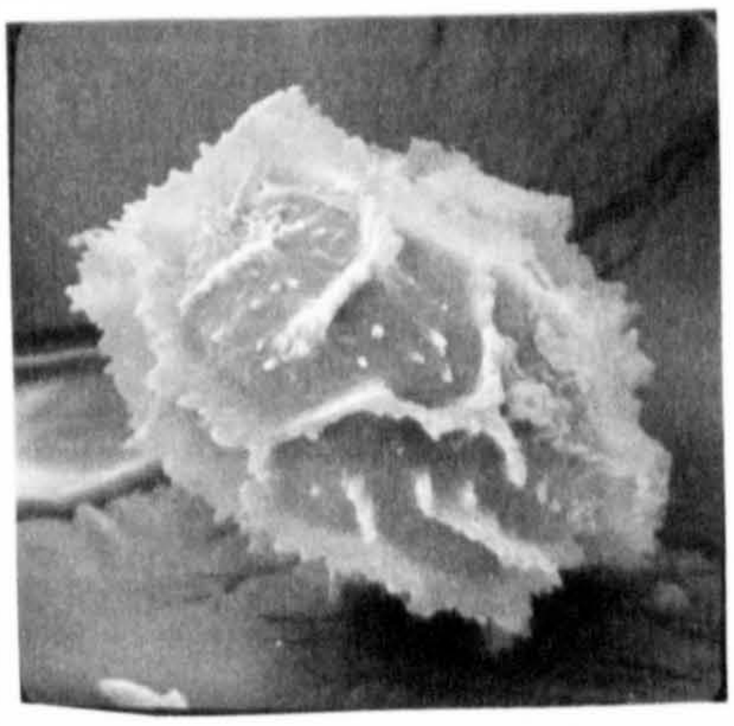
164



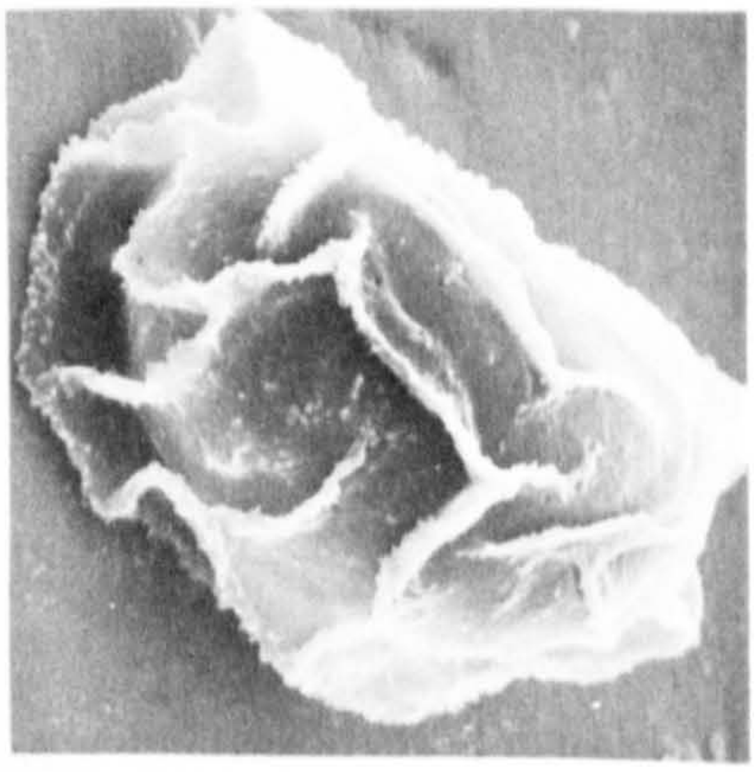
165



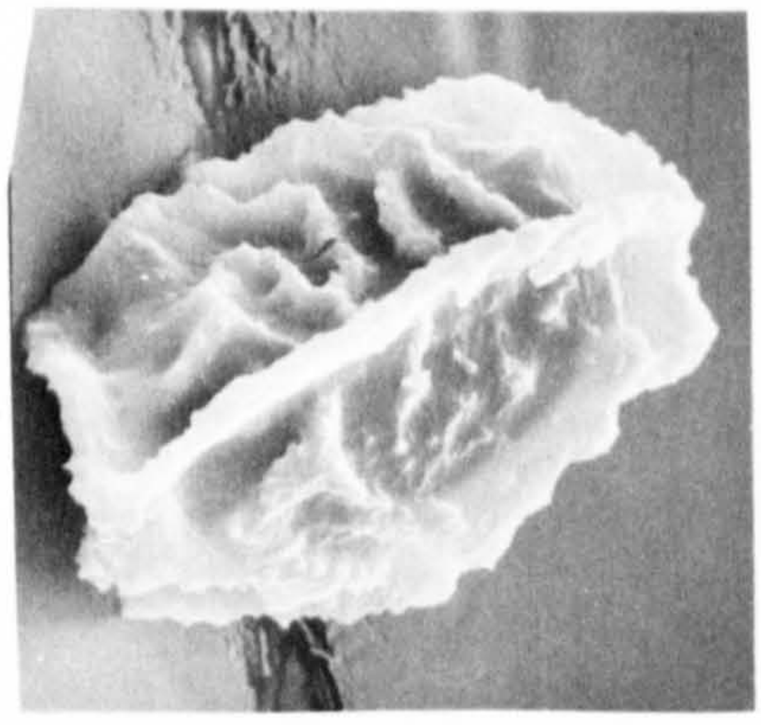
166



167



168



169

170

PLATE 25

Scanning Electron Photomicrographs Of Spores : X1000

Fig. 171 T.extensa

Fig. 172 T.asterothrix

Fig. 173 T.invisa

Fig. 174 T.quadrangularis

Fig. 175 T.afra

Fig. 176 T.sub-pubescens

Fig. 177 T.molliuscula

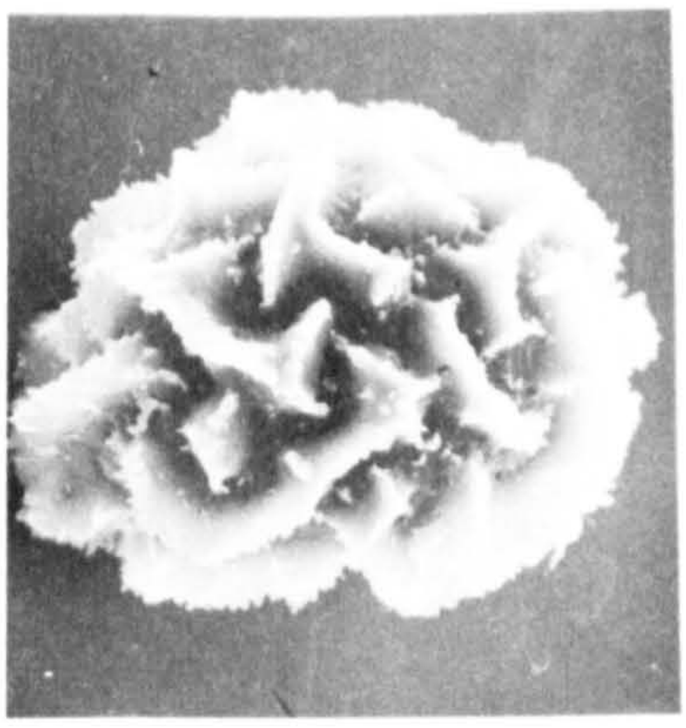
Fig. 178 T.parasitica

Fig. 179 T.tetragona

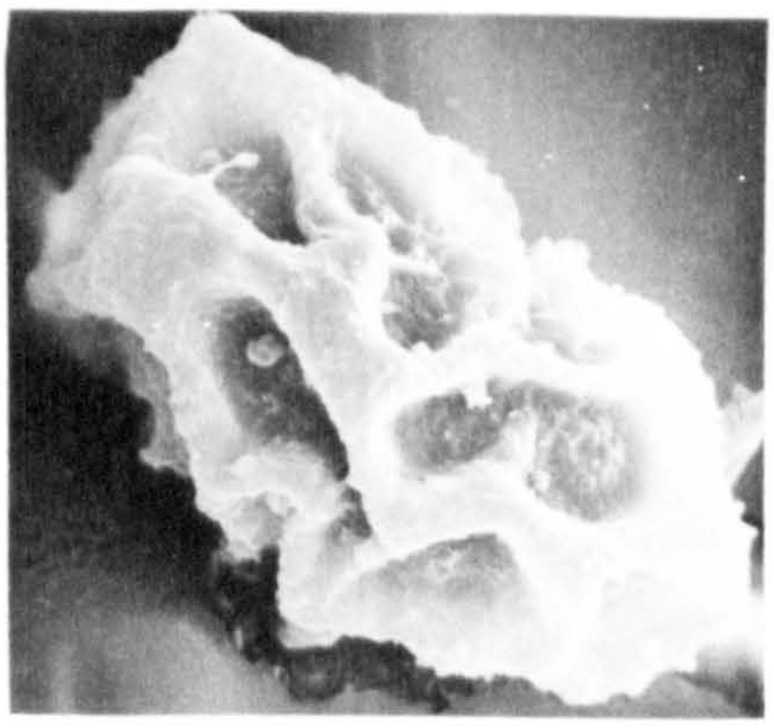
Fig. 180 T.rubra

Fig. 181 T.megalodus

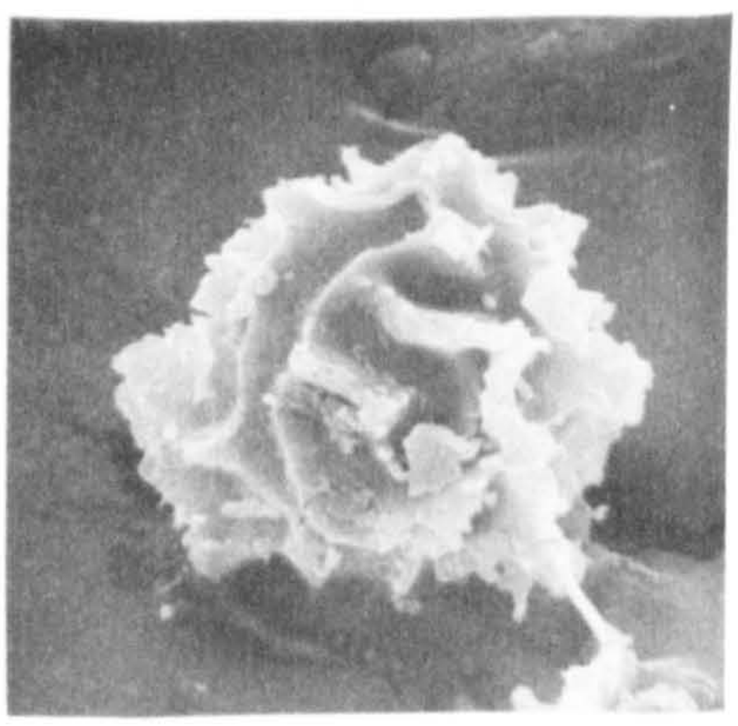
Fig. 182 T.urophylla



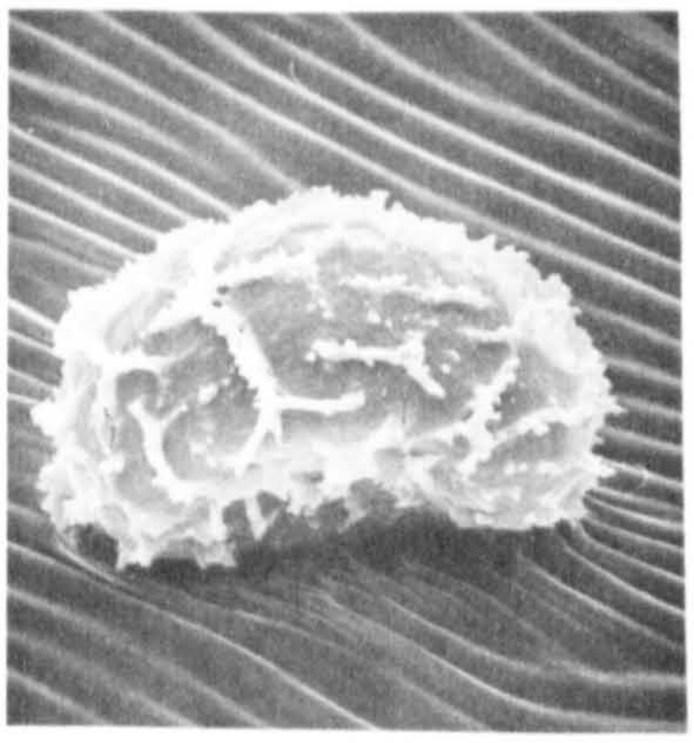
171



172



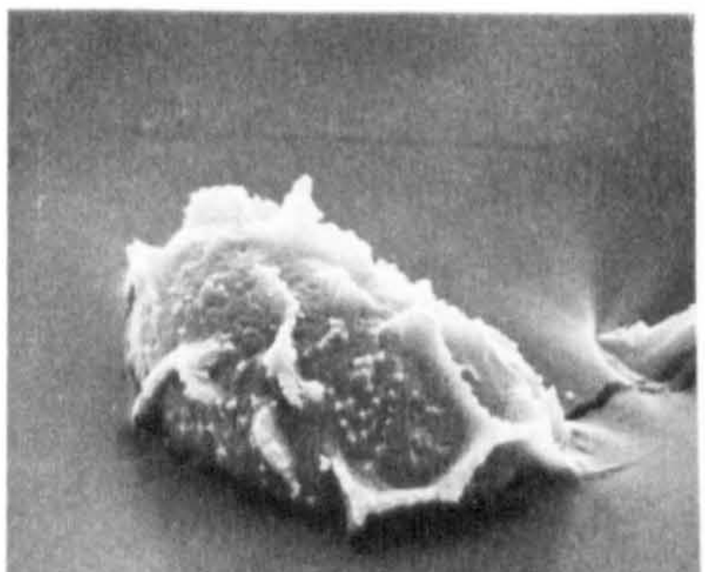
173



174

175

176



177

178

179

180

181

182

PLATE 26

Scanning Electron Photomicrographs Of Spores : X1000

Fig. 183 T.penangiana

Fig. 184 T.ferox

Fig. 185 T.glandulosa

Fig. 186 T.taiwanensis

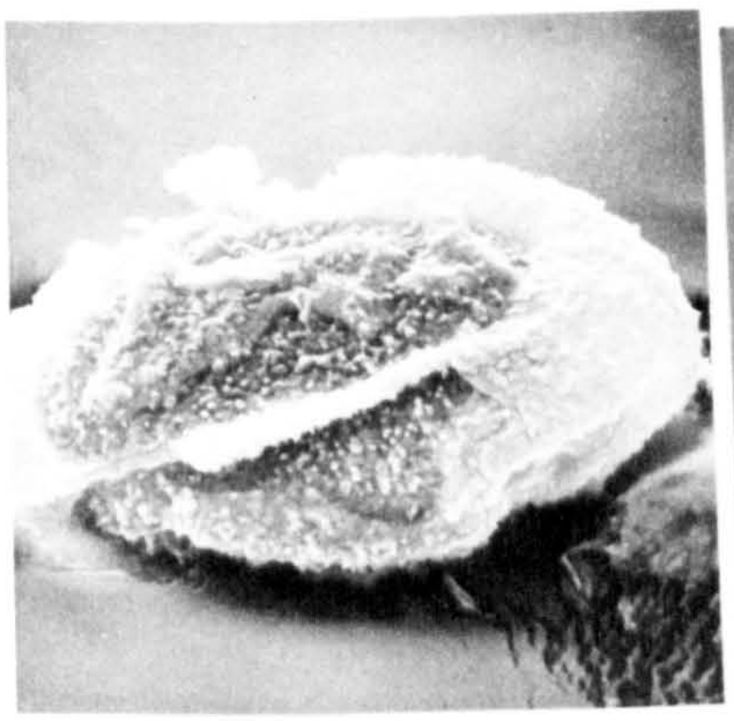
Fig. 187 T.polycarpa

Fig. 188 T.acuminata

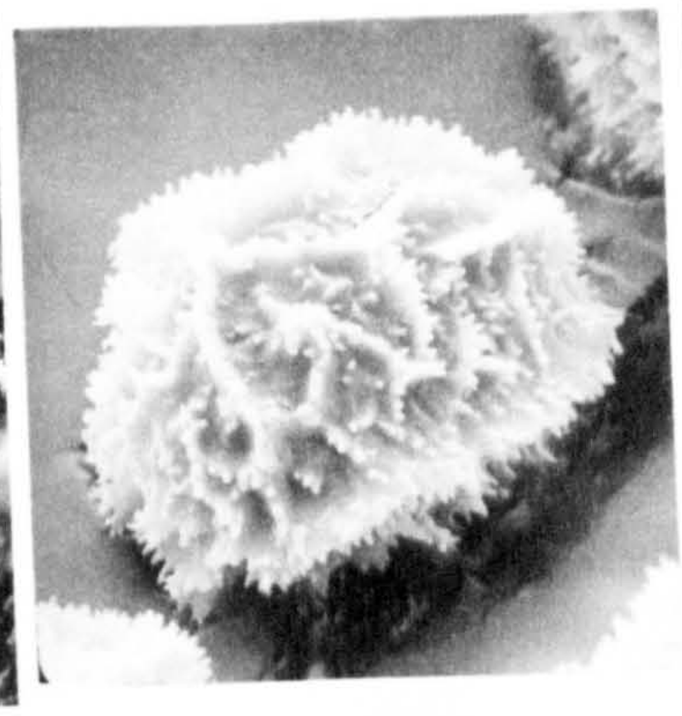
Fig. 189 T.scolopendrioides

Fig. 190 T.nephrodioides

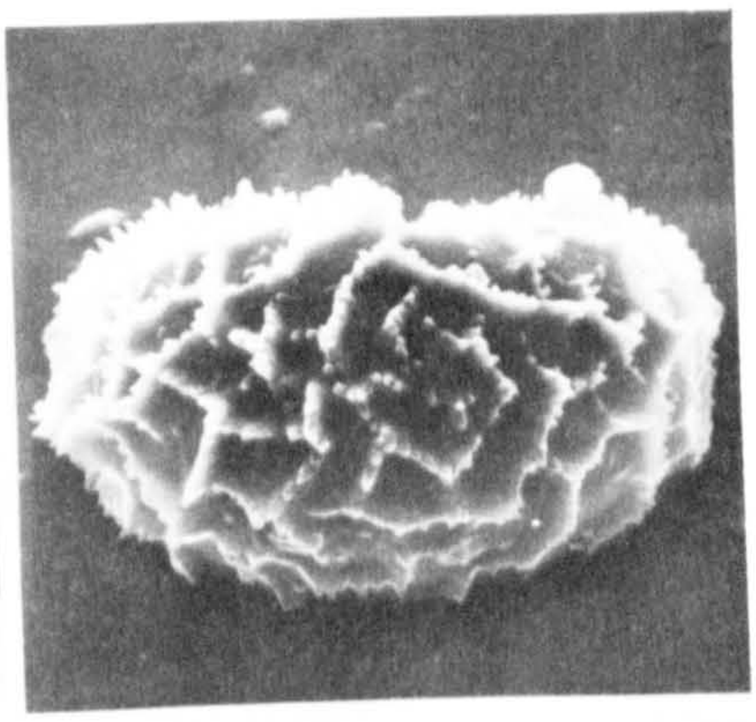
Fig. 191 T.bangii



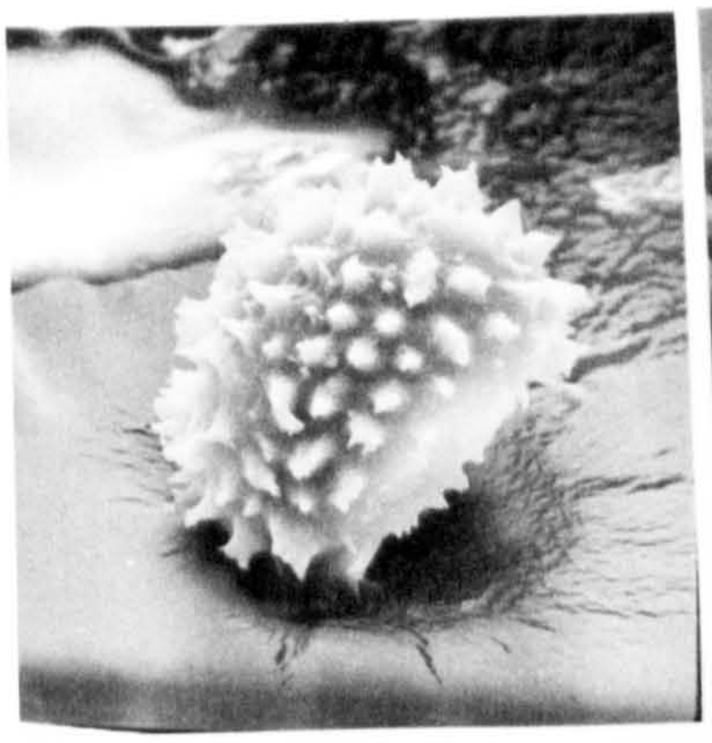
183



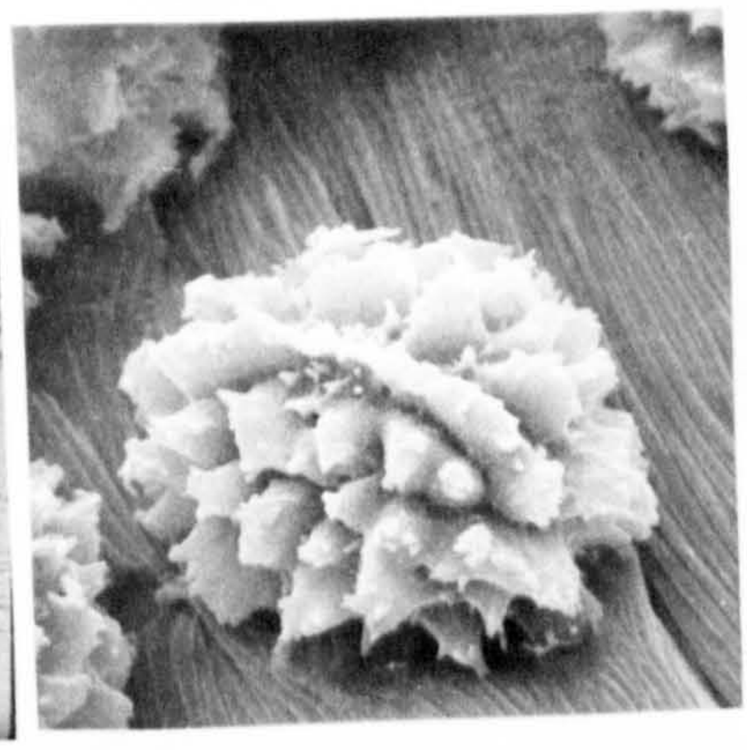
182



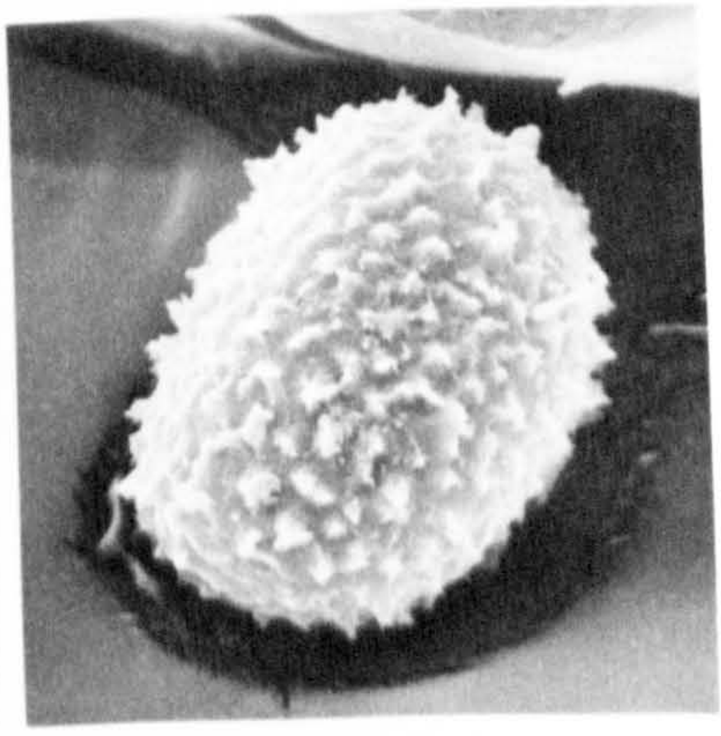
185



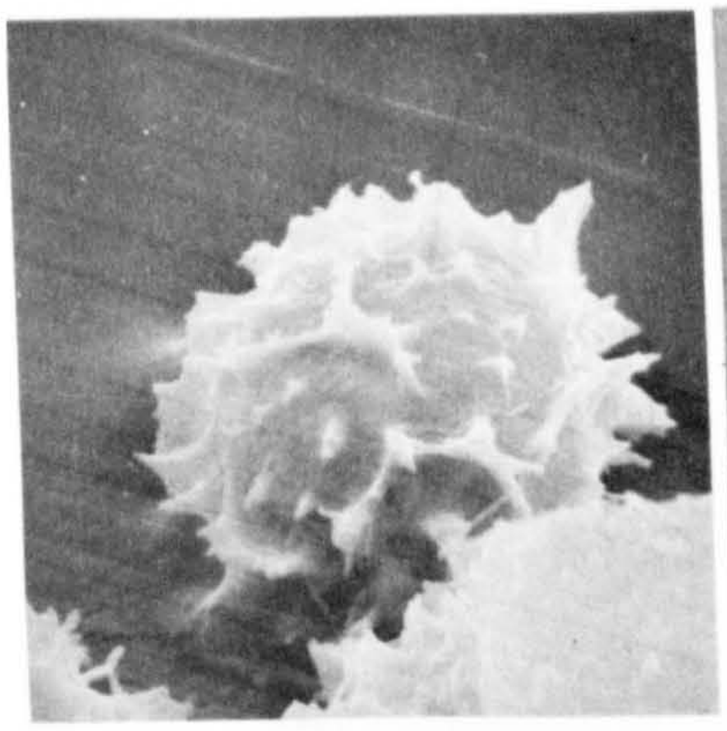
186



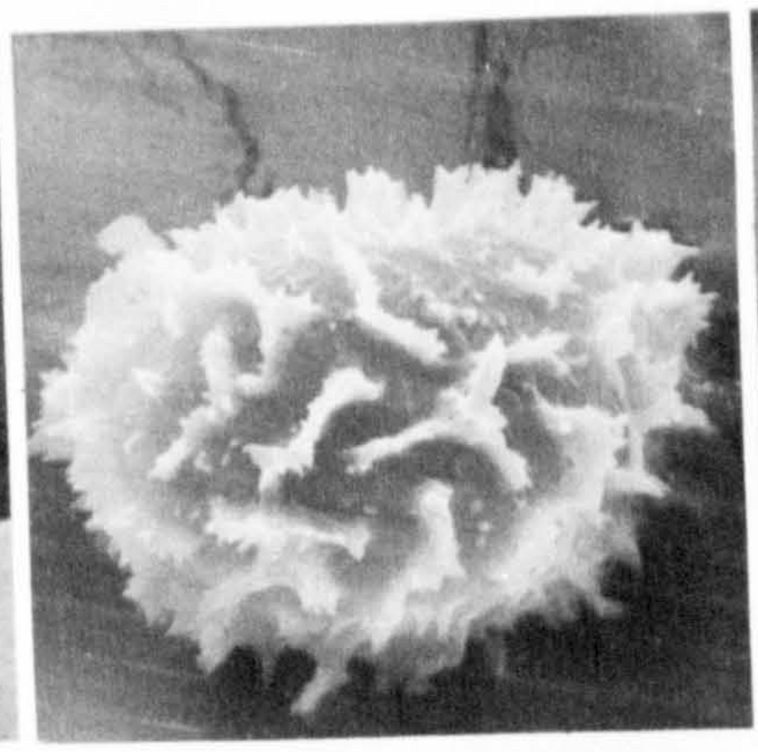
187



188



189



190

191

PLATE 27

Scanning Electron Photomicrographs Of Spores : X1000

Fig. 192 T.paucijuga

Fig. 193 T.vivipara

Fig. 194 T.hastata

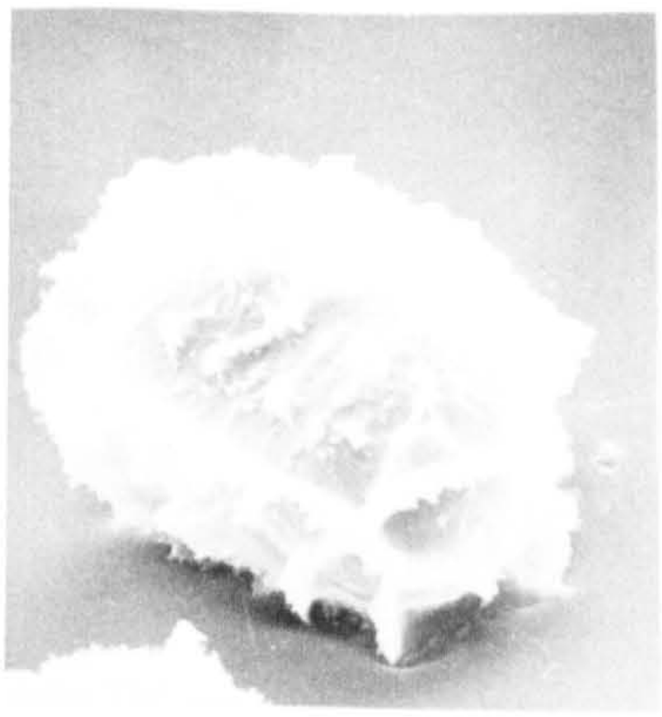
Fig. 195 T.tonkinensis

Fig. 196 T.sagittata

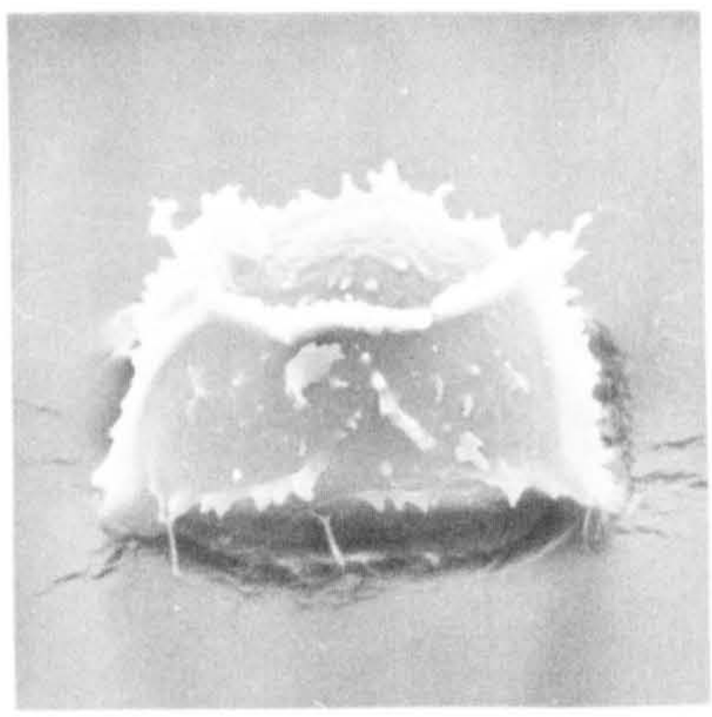
Fig. 197 T.insularis

Fig. 198 T.leptocladia

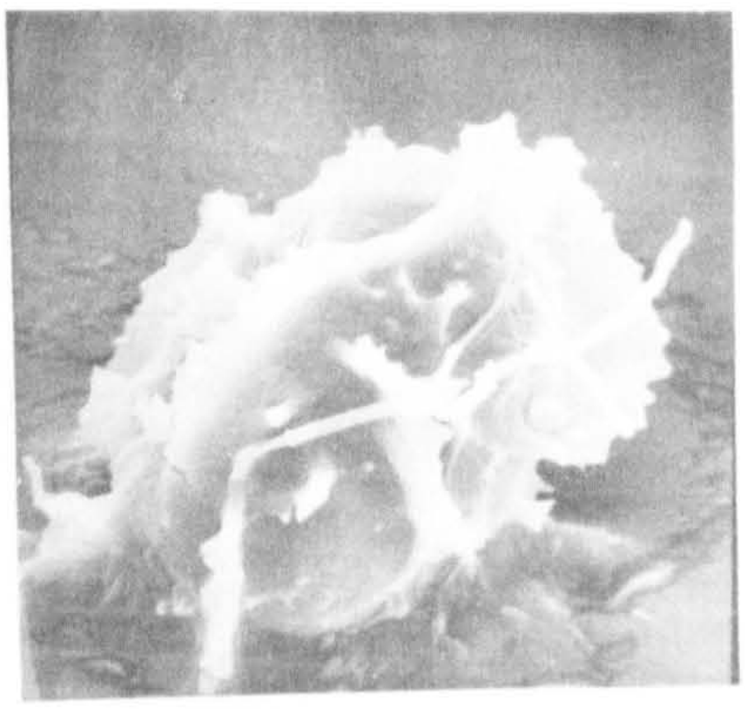
Fig. 199 T.cordata



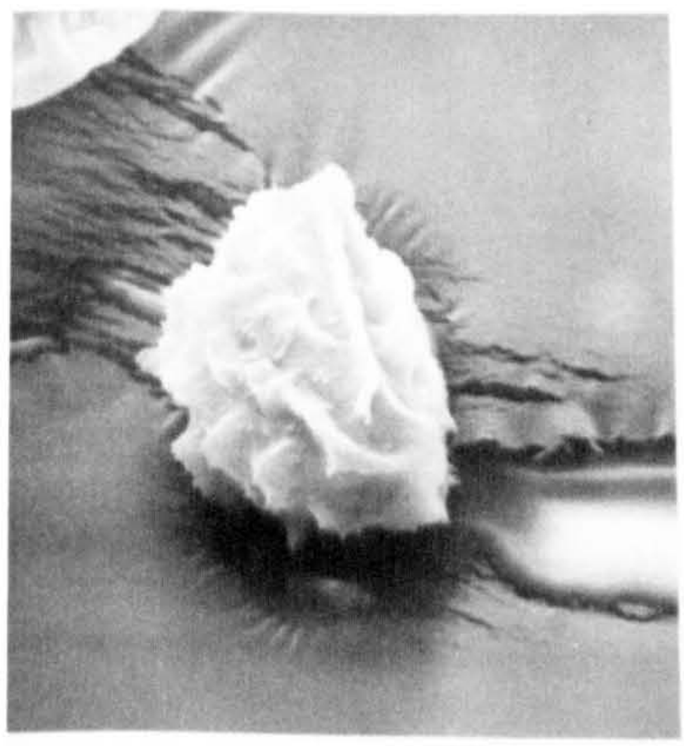
192



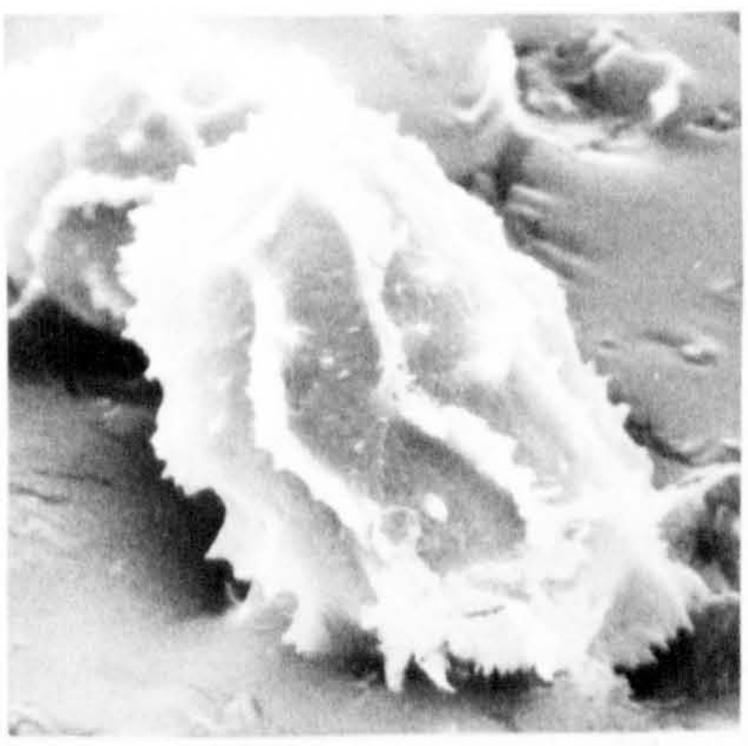
193



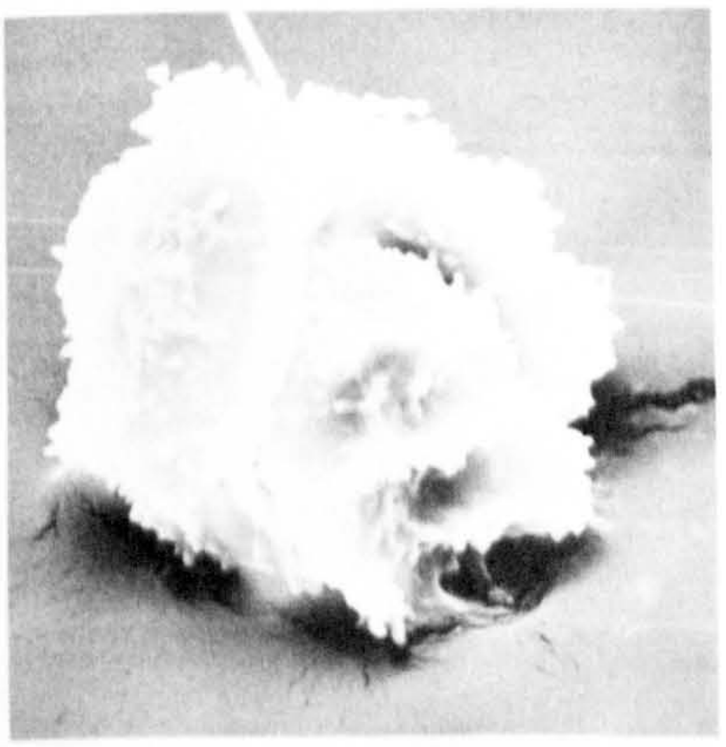
194



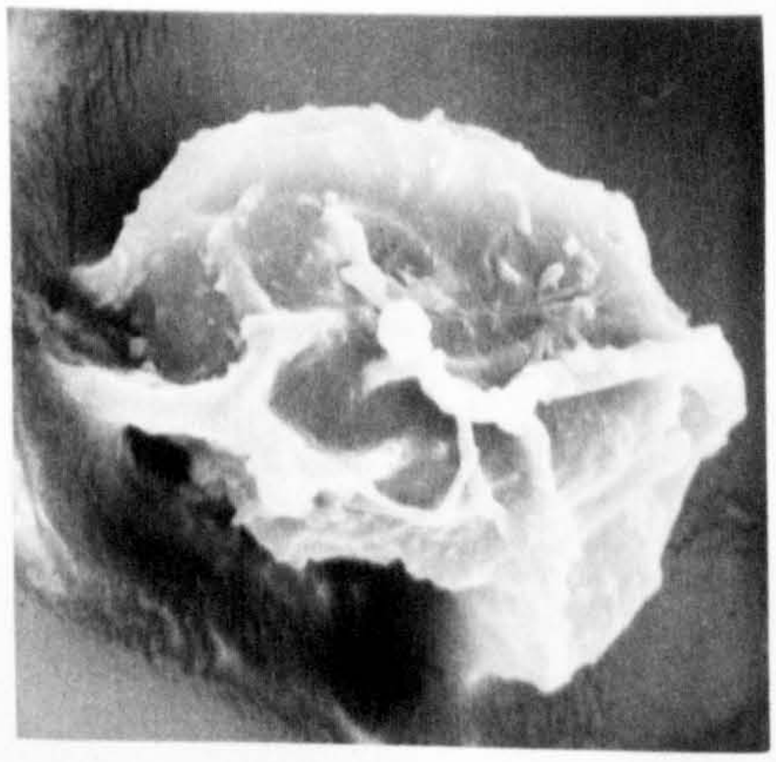
195



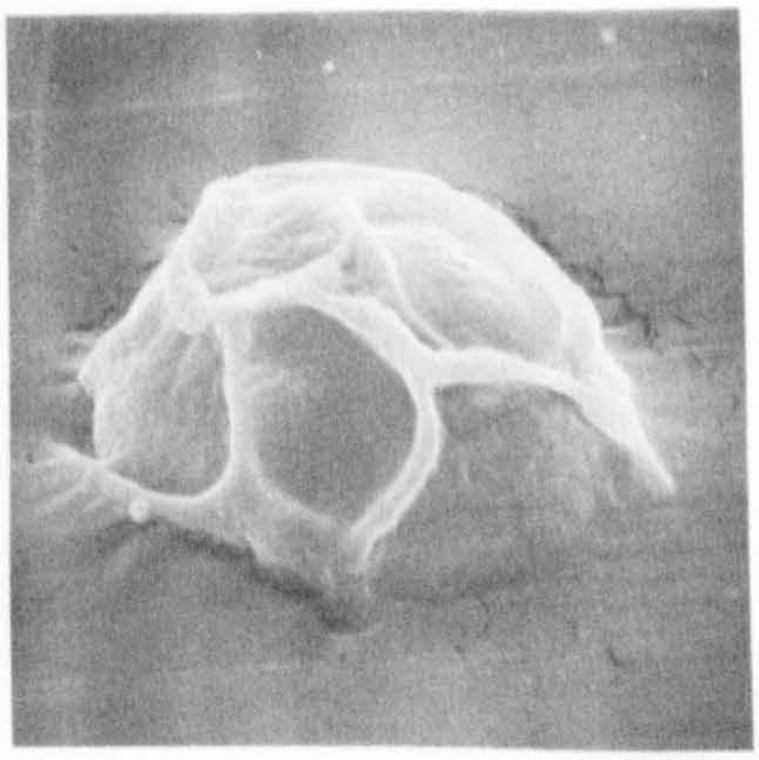
196



197



198



199

PLATE 28

Scanning Electron Photomicrographs Of Spores : X1000

Fig. 200 T.salicifolia

Fig. 201 T.reticulata

Fig. 202 T.prolifera

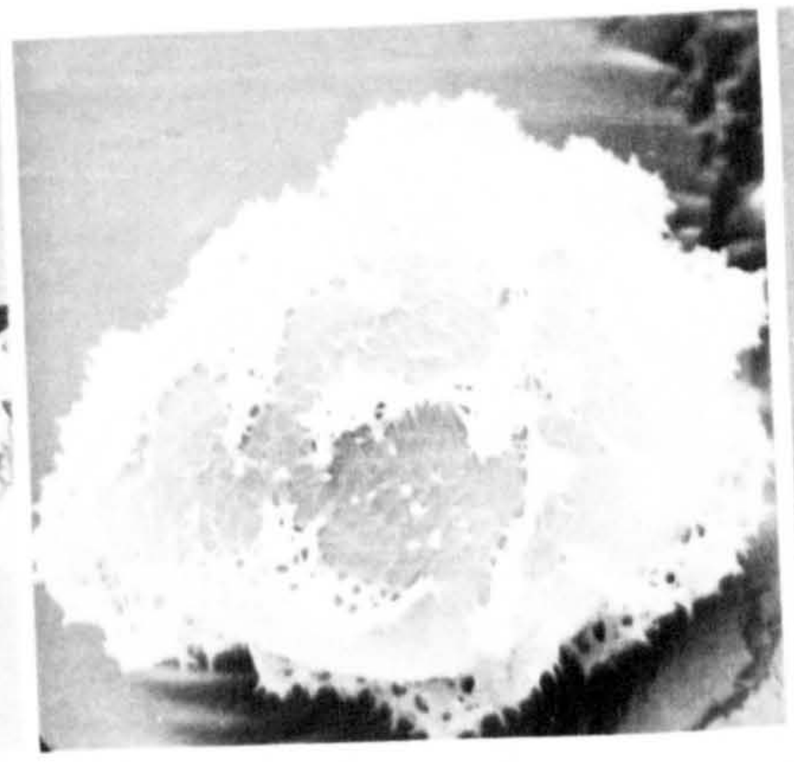
Fig. 203 T.serrata

Fig. 204 Gymnocarpium dryopteris

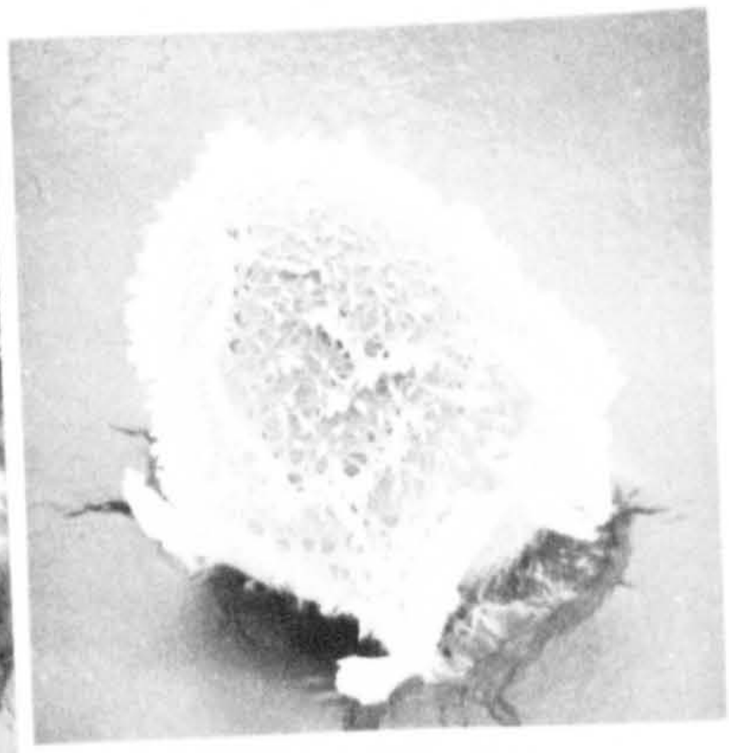
Fig. 205 G.robertianum

Fig. 206 G.jessoensis

200

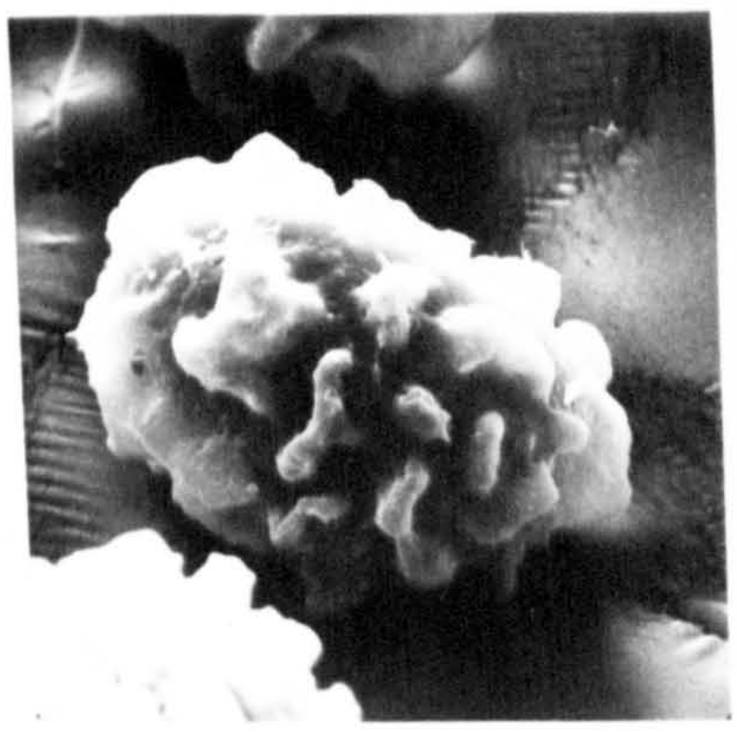


201



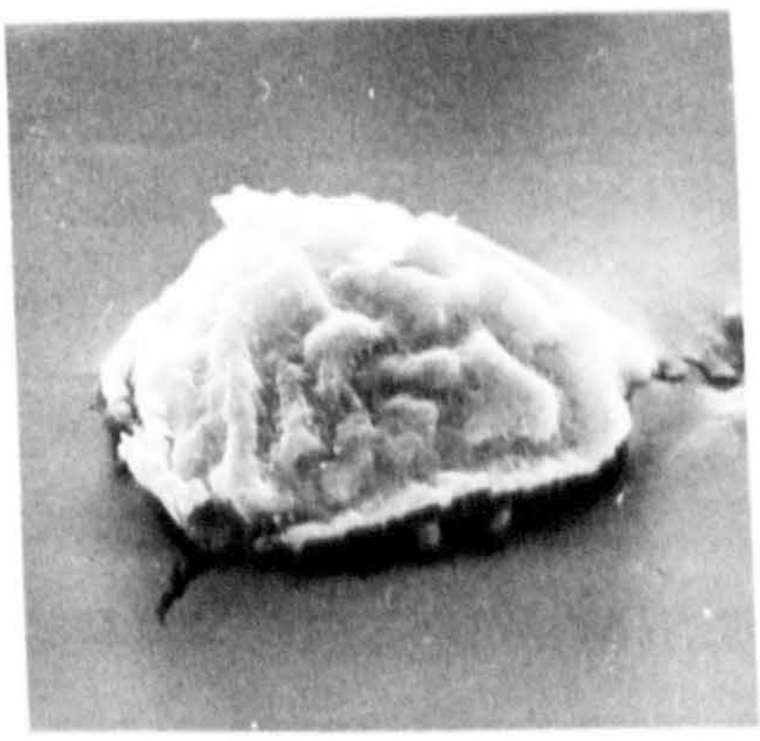
202

203



204

205



206

PLATE 29

Scanning Electron Photomicrographs Of Spores : X2500

Fig. 207 T.balbisii

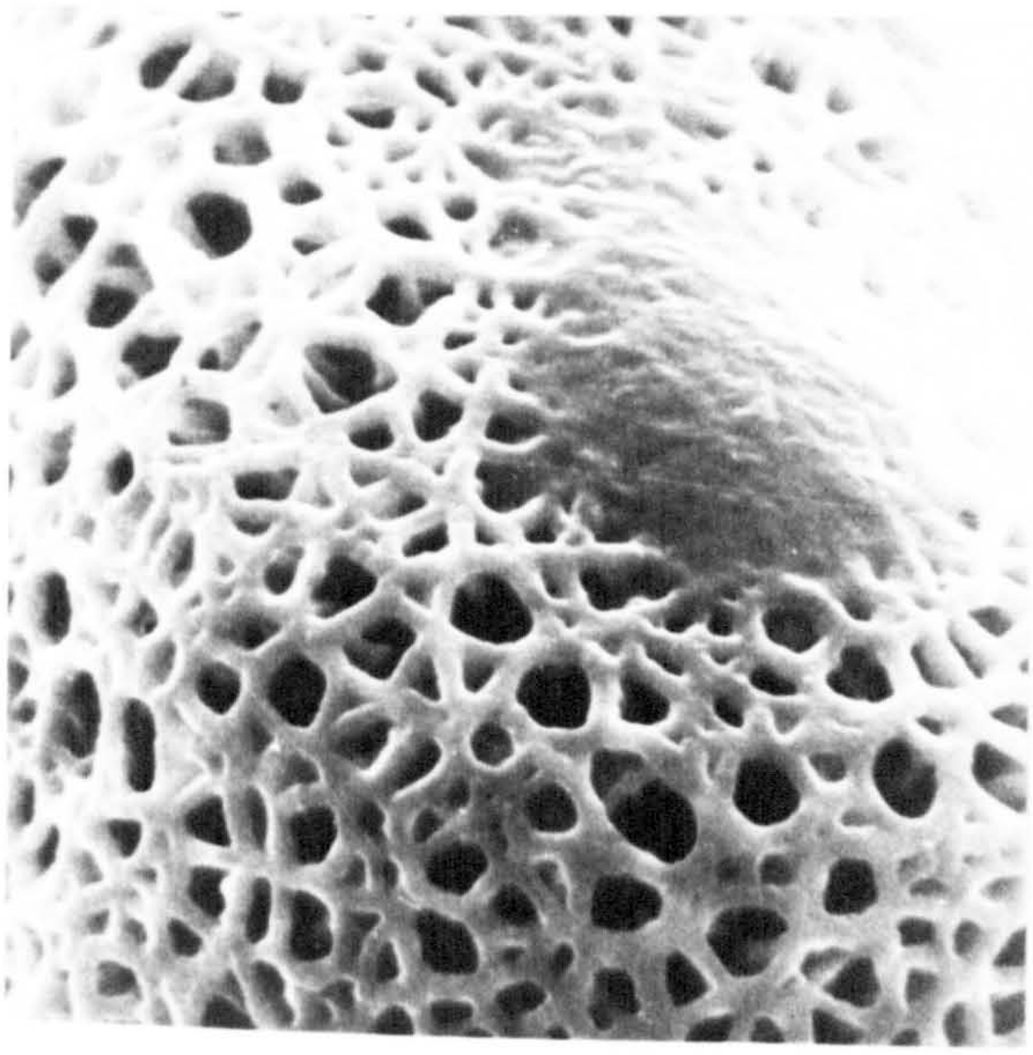
Fig. 208 T.balbisii (x 10,000)

Fig. 209 T.linkiana

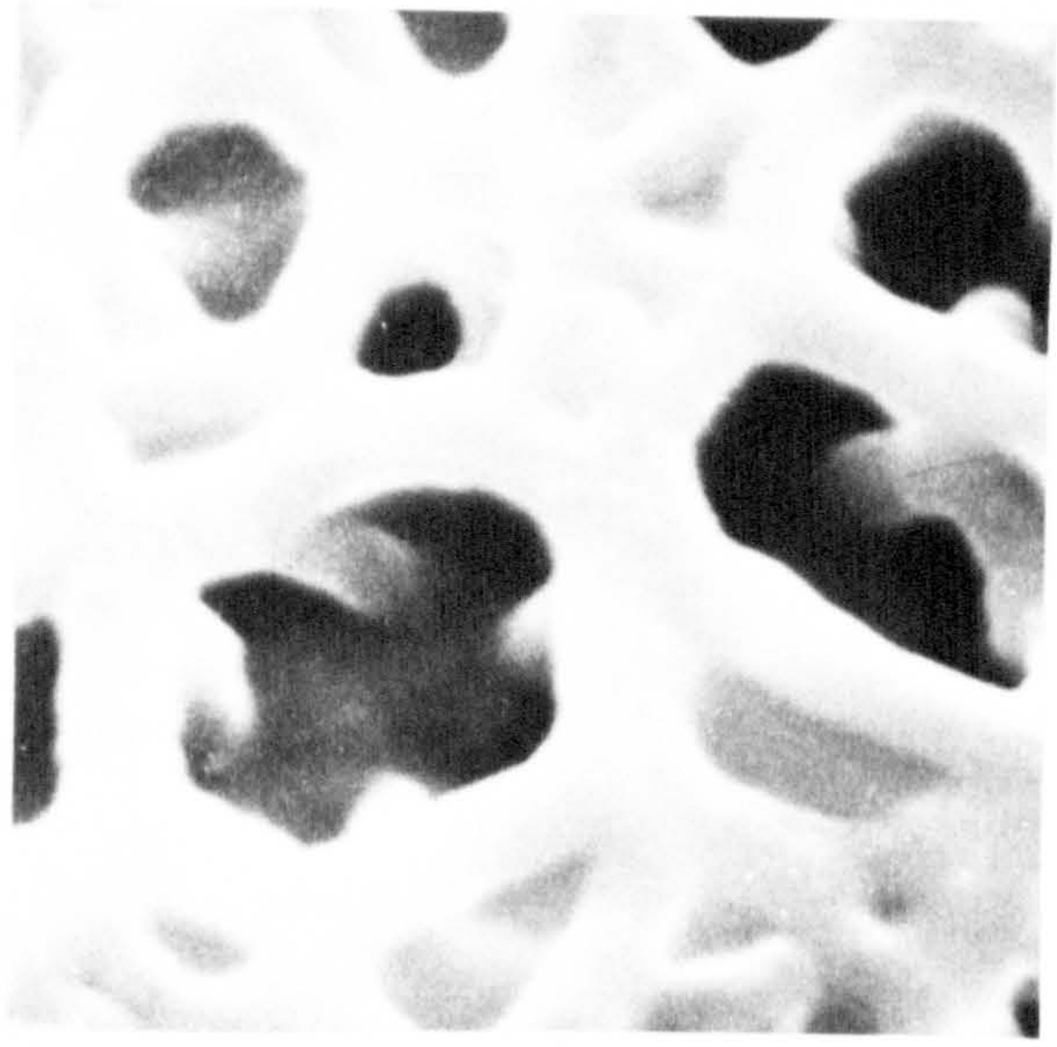
Fig. 210 T.cyclocarpa

Fig. 211 T.phegopteris

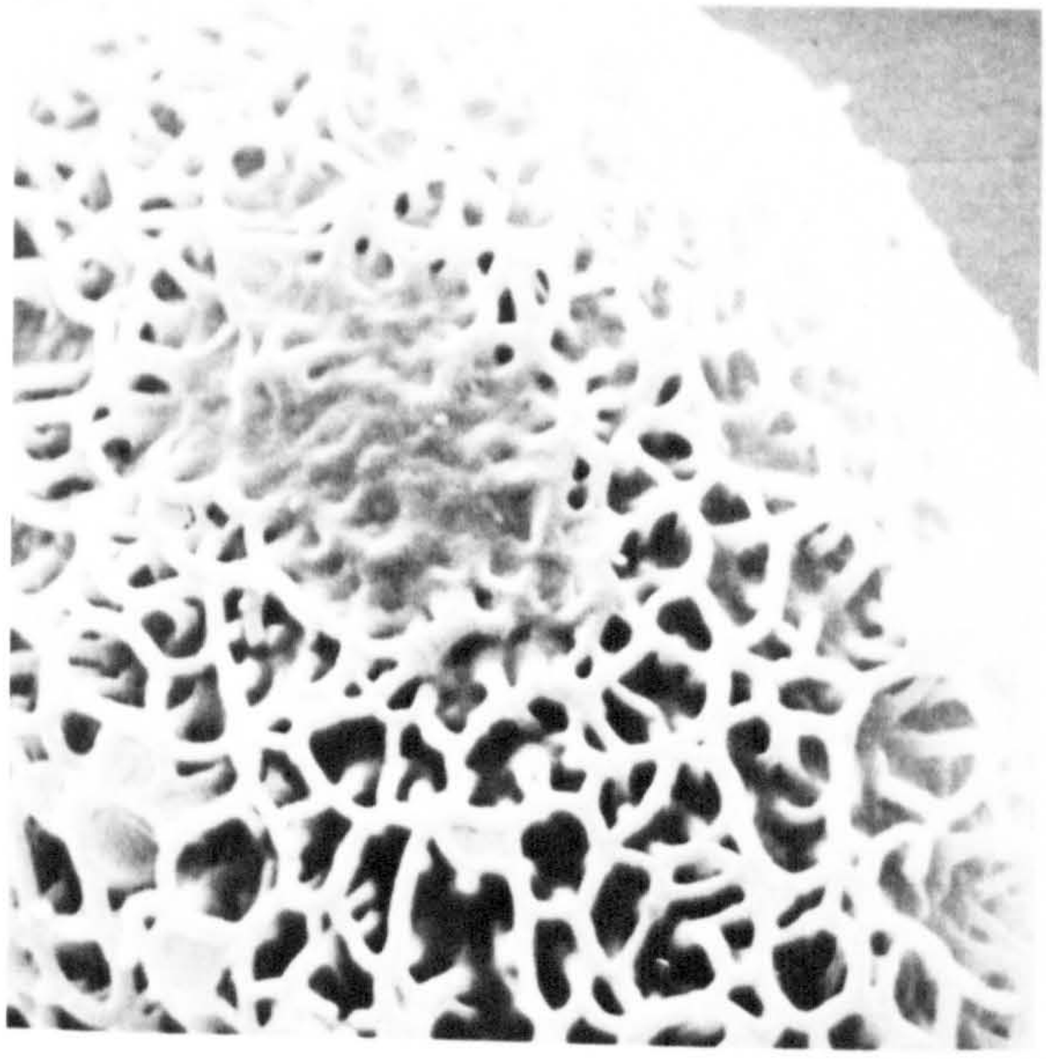
Fig. 212 T.singalanensis



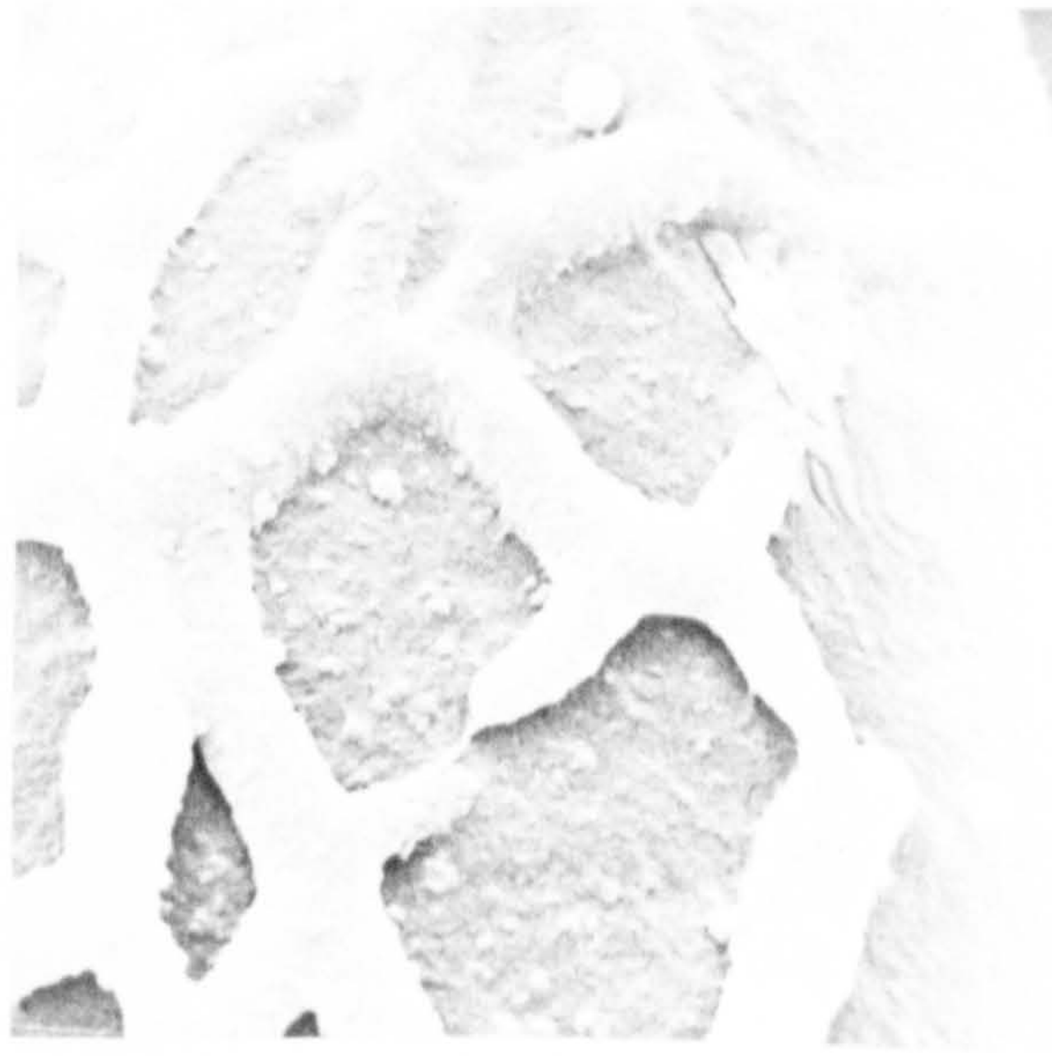
207



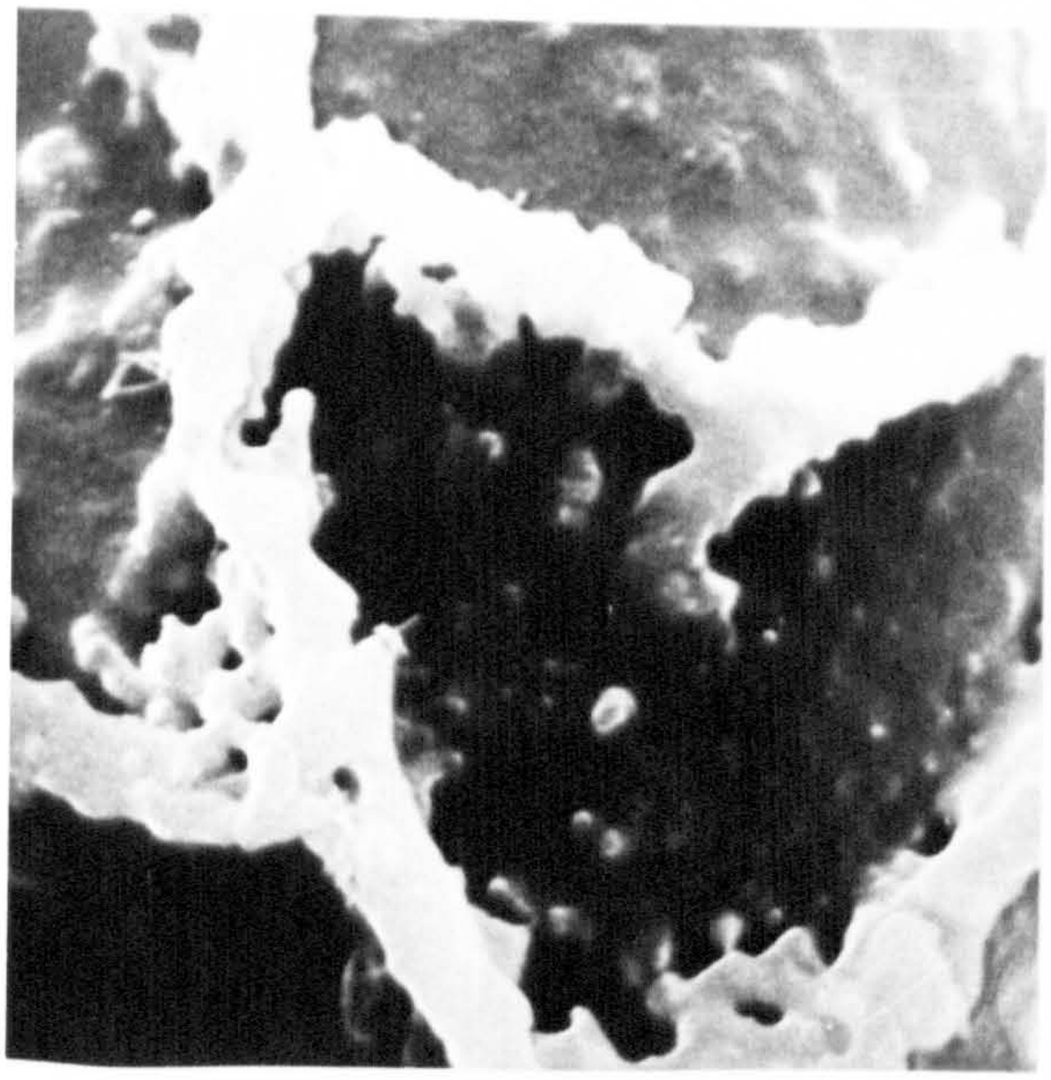
208



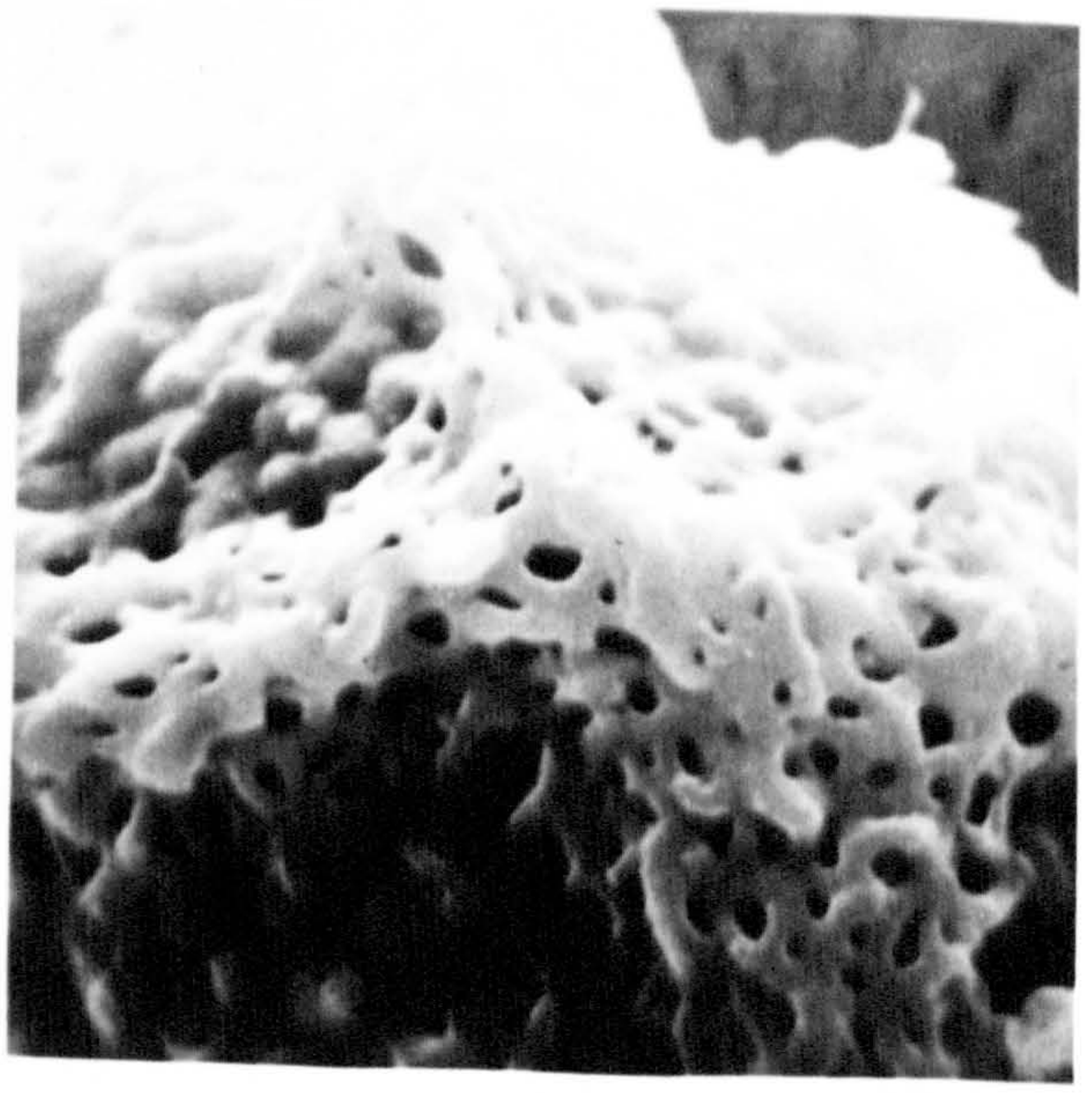
209



210



211



212

PLATE 30

Scanning Electron Photomicrographs Of Spores : X2500

Fig. 213 T.palustris

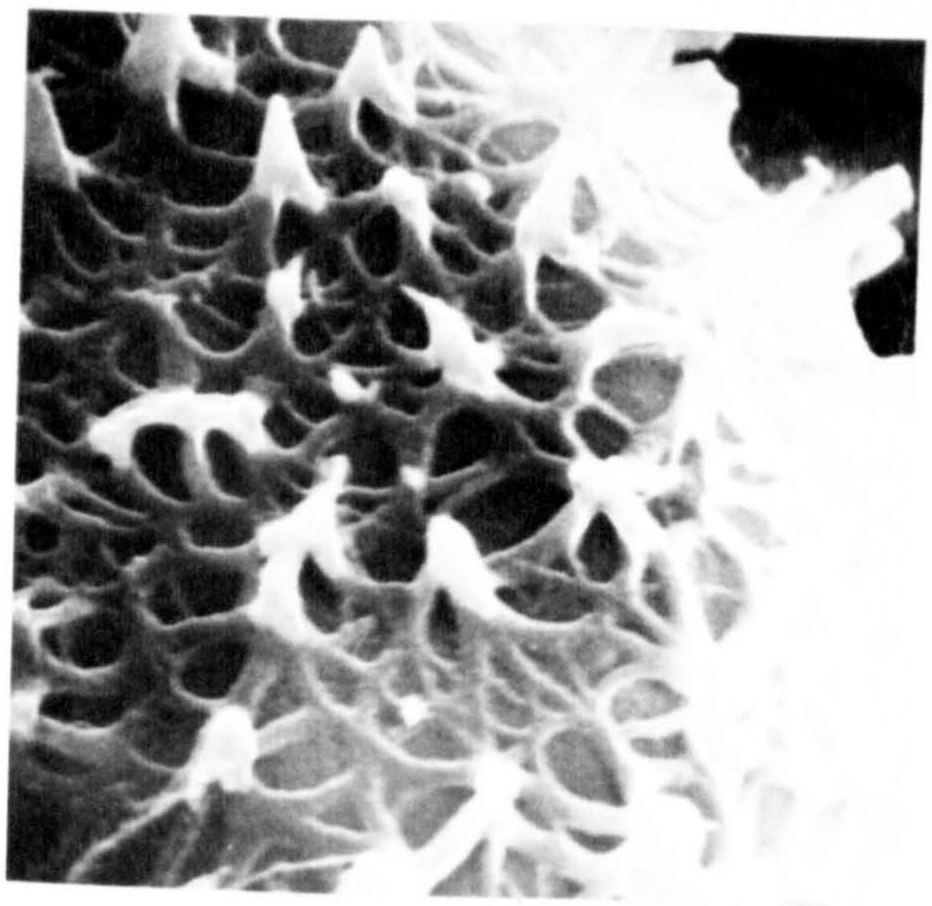
Fig. 214 T.prolifera

Fig. 215 T.griffithii

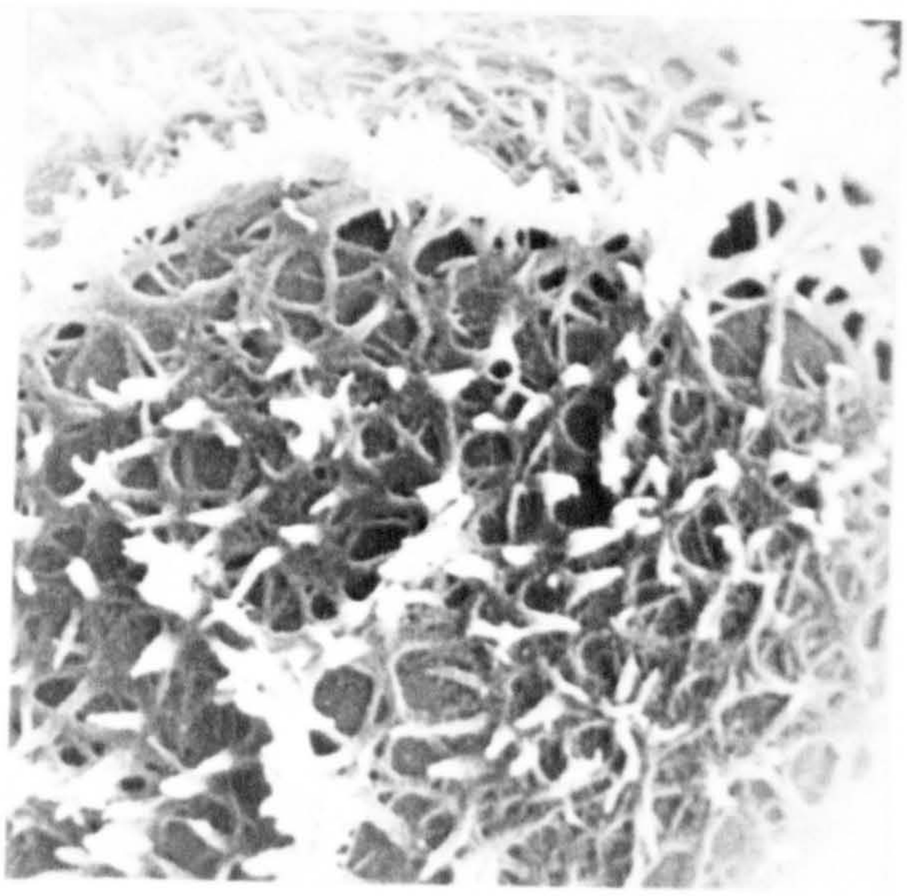
Fig. 216 T.callosa

Fig. 217 T.patens

Fig. 218 T.ciliata

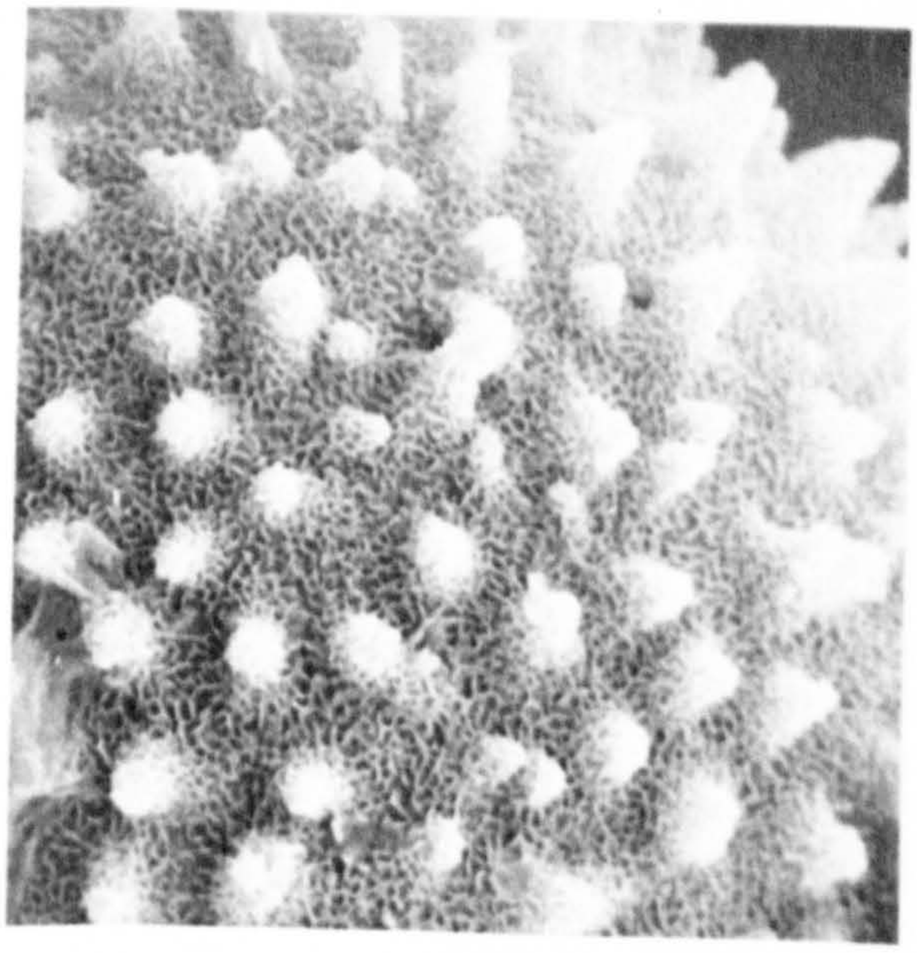


213

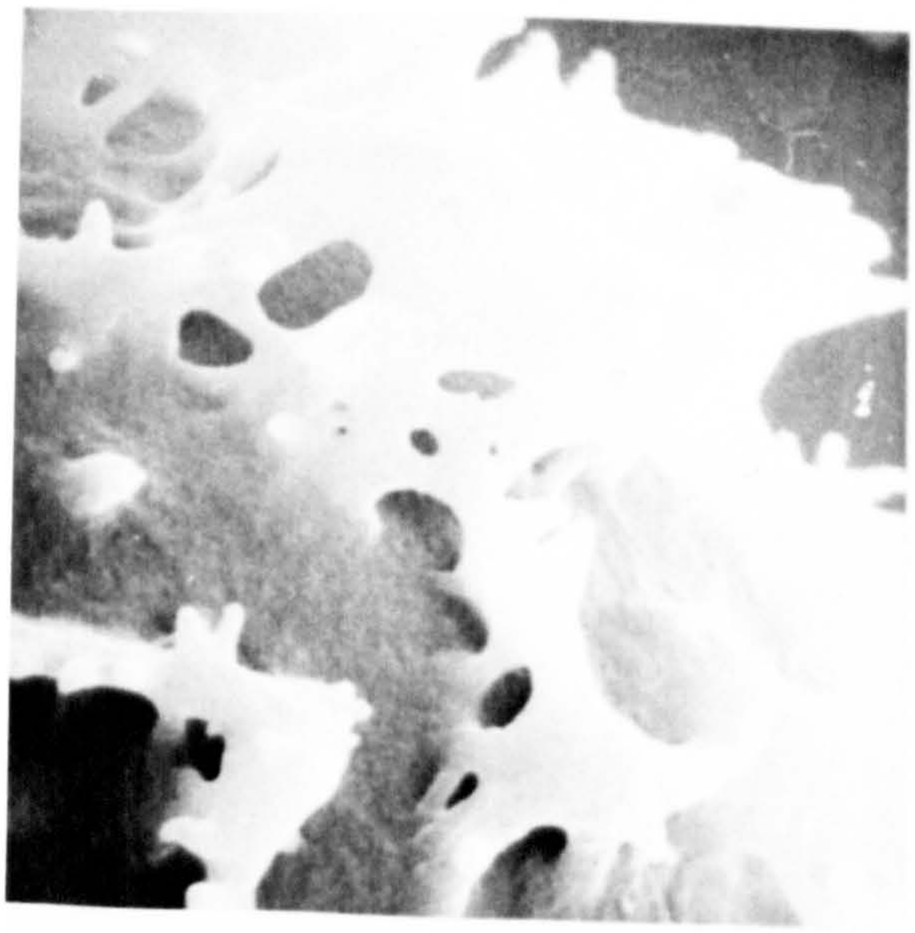


214

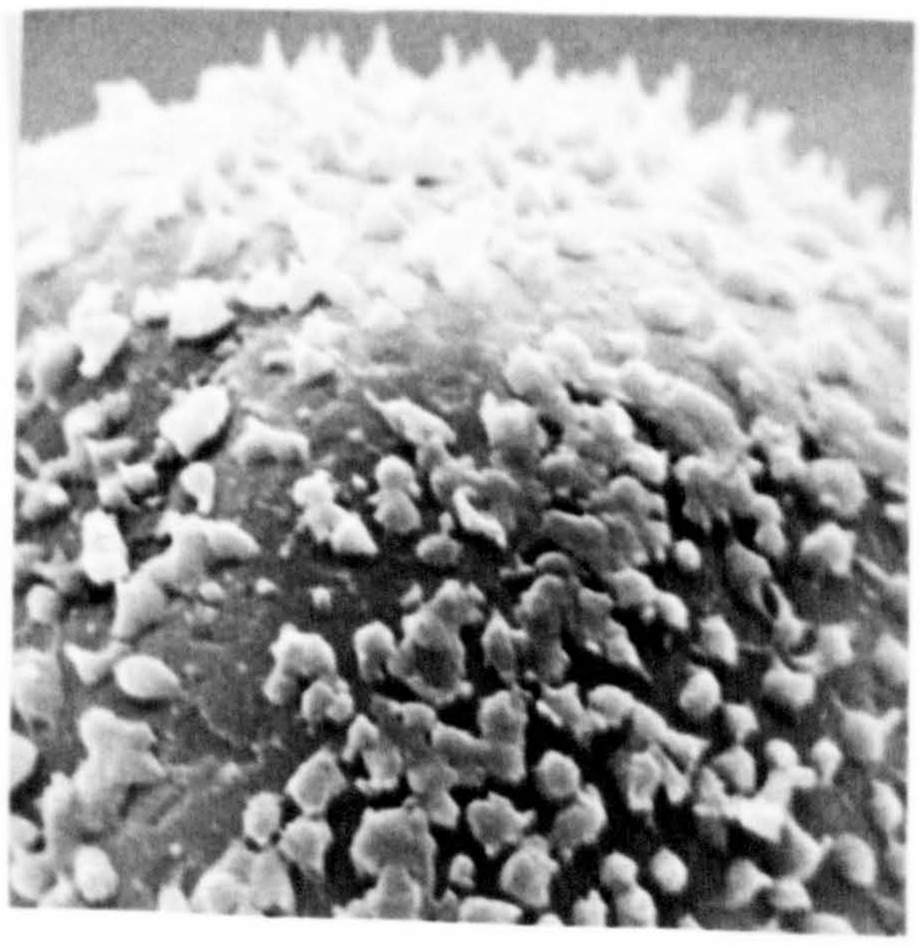
215



216



217



218

PLATE 31

Scanning Electron Photomicrographs Of Spores : X2500

Fig. 219 T.dentata

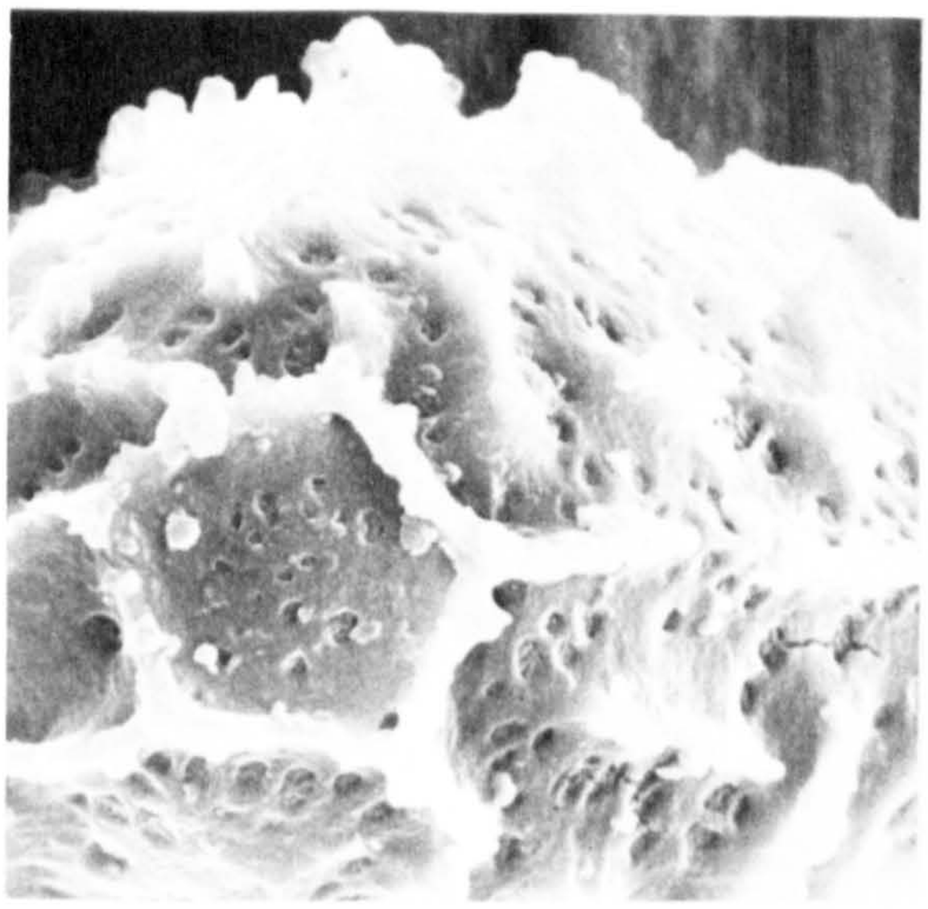
Fig. 220 T.truncata

Fig. 221 T.squamaestipes

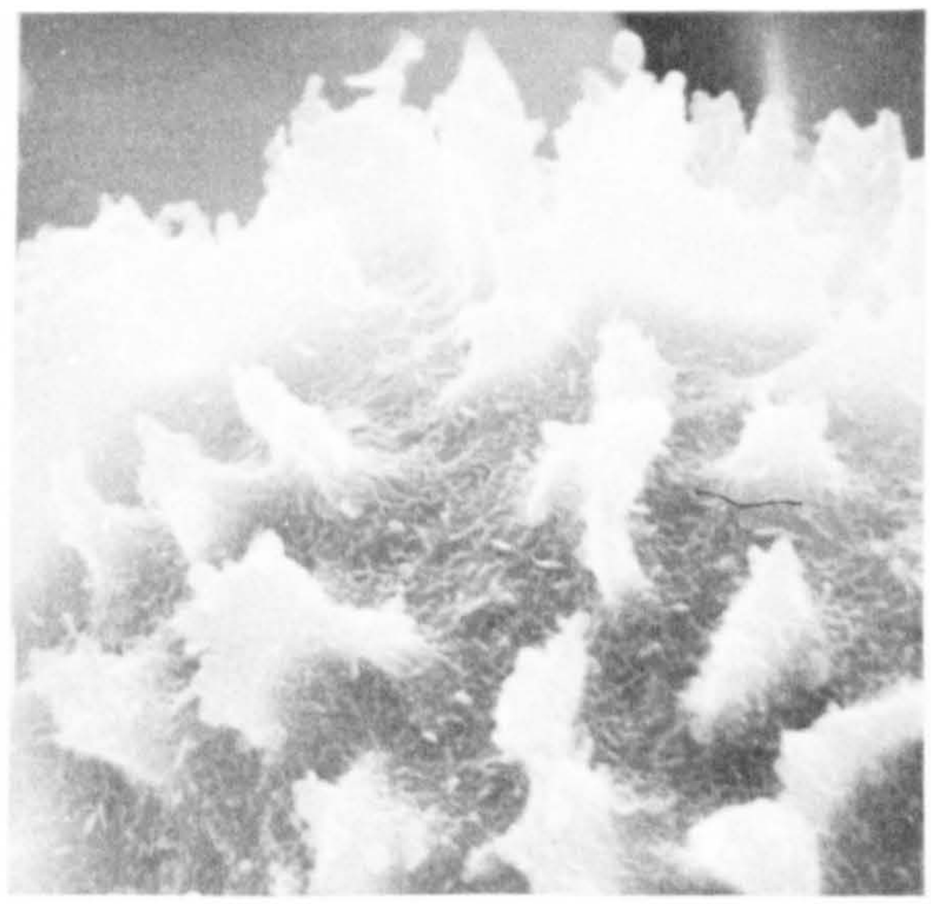
Fig. 222 T.paleata

Fig. 223 T.serra

Fig. 224 T.xylodes

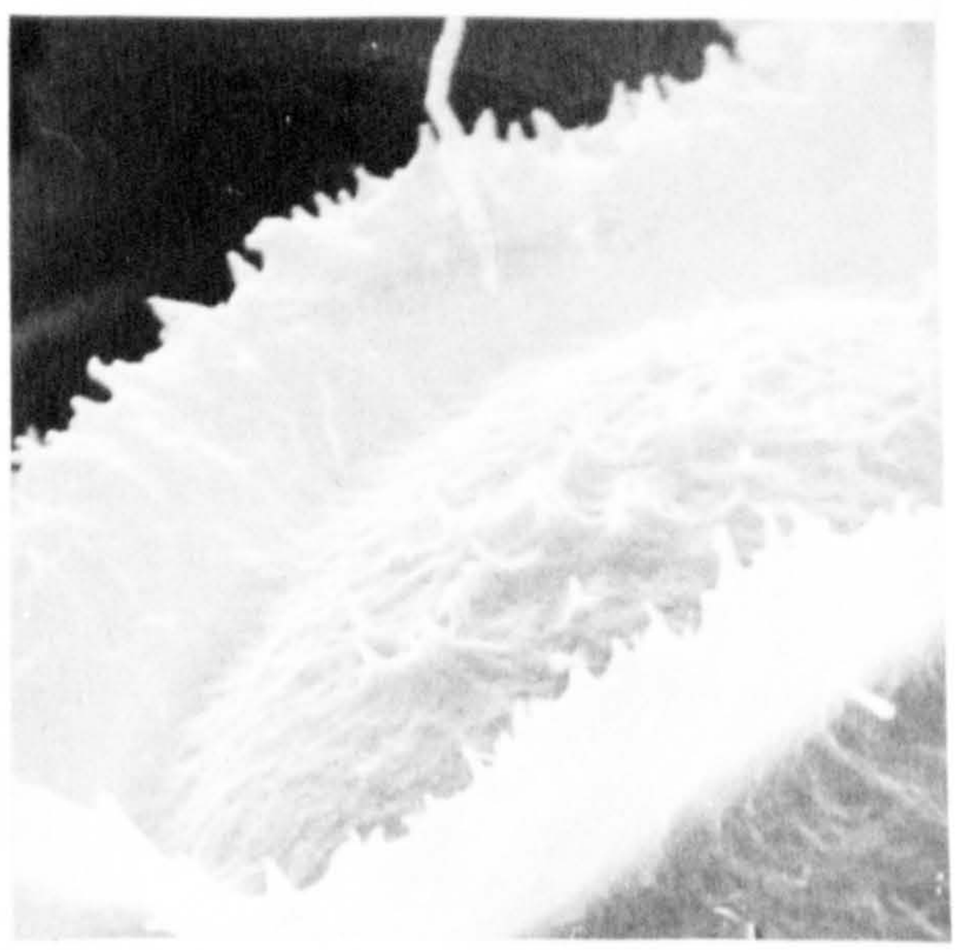


219

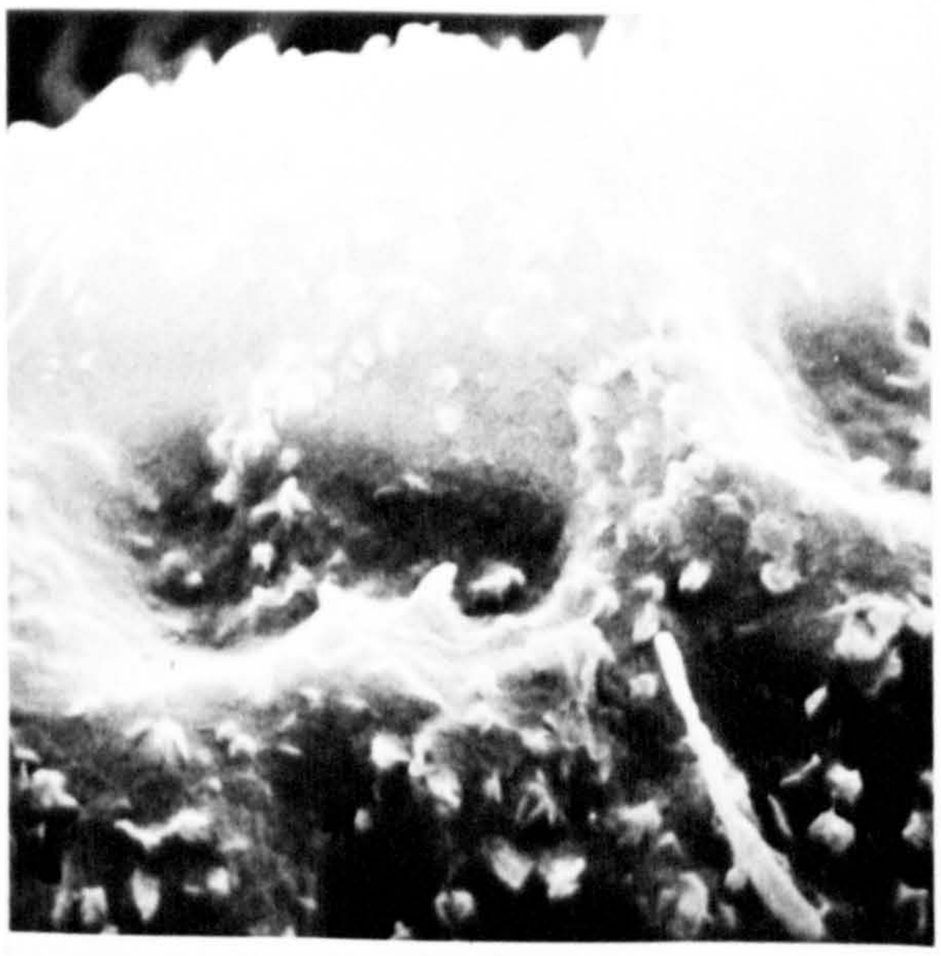


220

221



222



223

224

PLATE 32

Transmission Electron Photomicrographs Of Sections Of Spore Wall Of T.balbisii

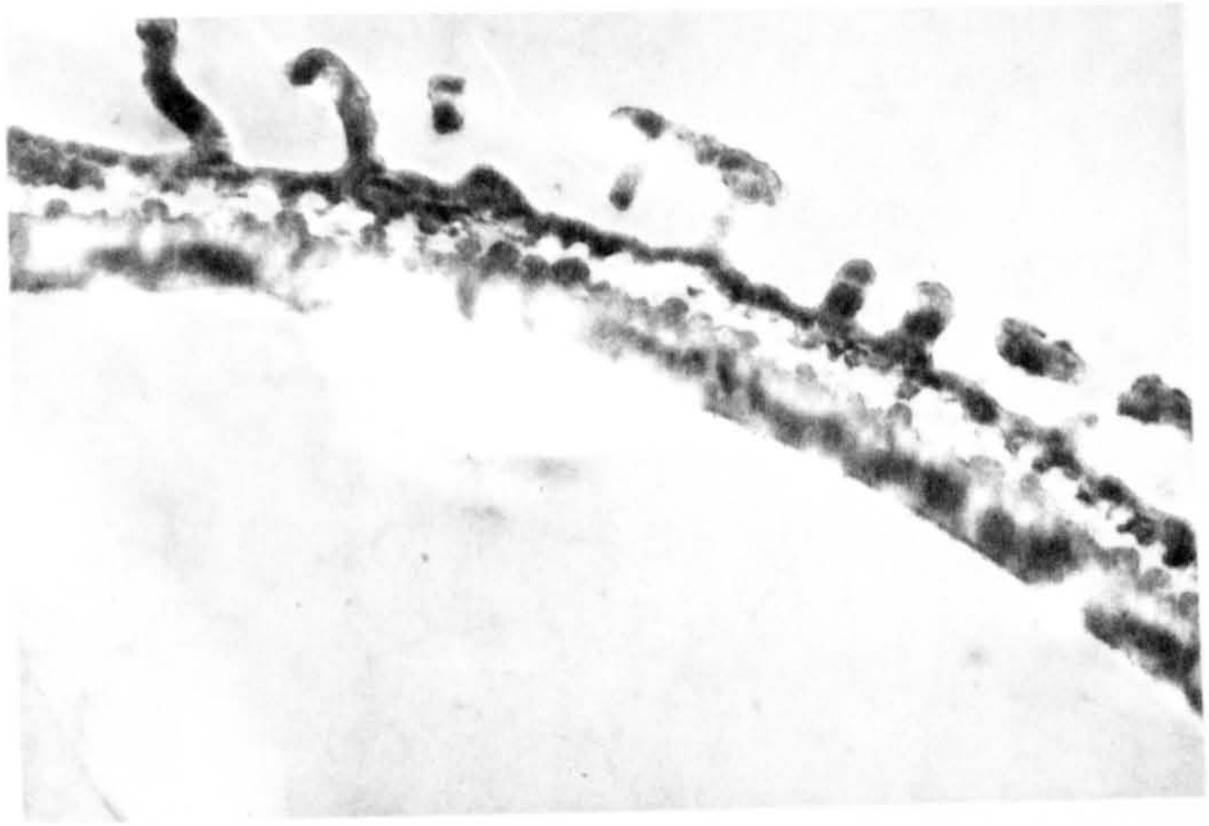
Fig. 225 Transverse section through wall of acetolysed spore (approx. x 10,000).

Fig. 226 Transverse section through spore wall showing inner wall separated from outer wall after acetolysis (approx. x 10,000).

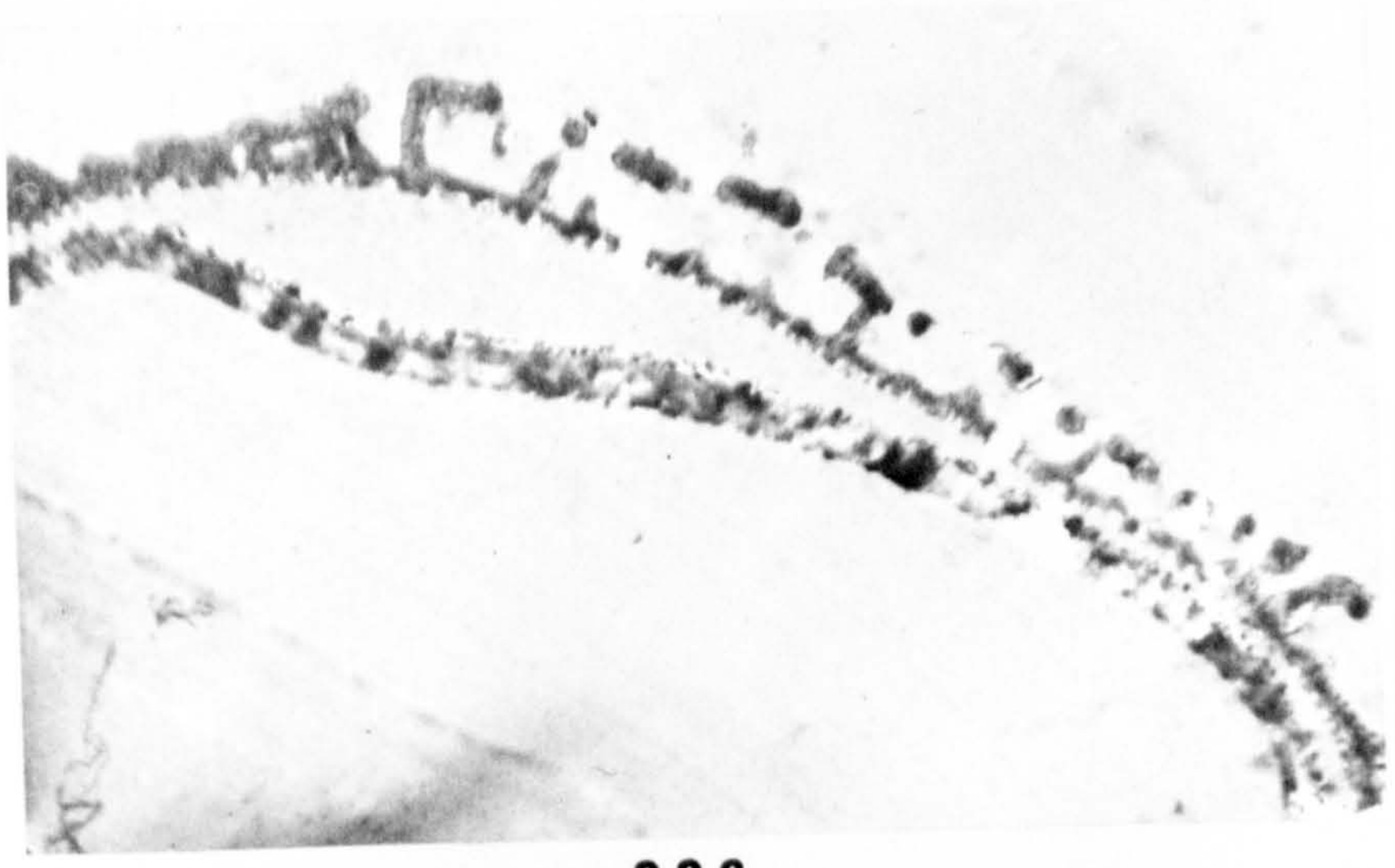
Fig. 227 Tangential section to show reticulate surface pattern (approx. x 10,000).

Fig. 228 High Power transverse section through spore wall showing juxtaposition of processes on inner and outer walls (approx. x 25,000).

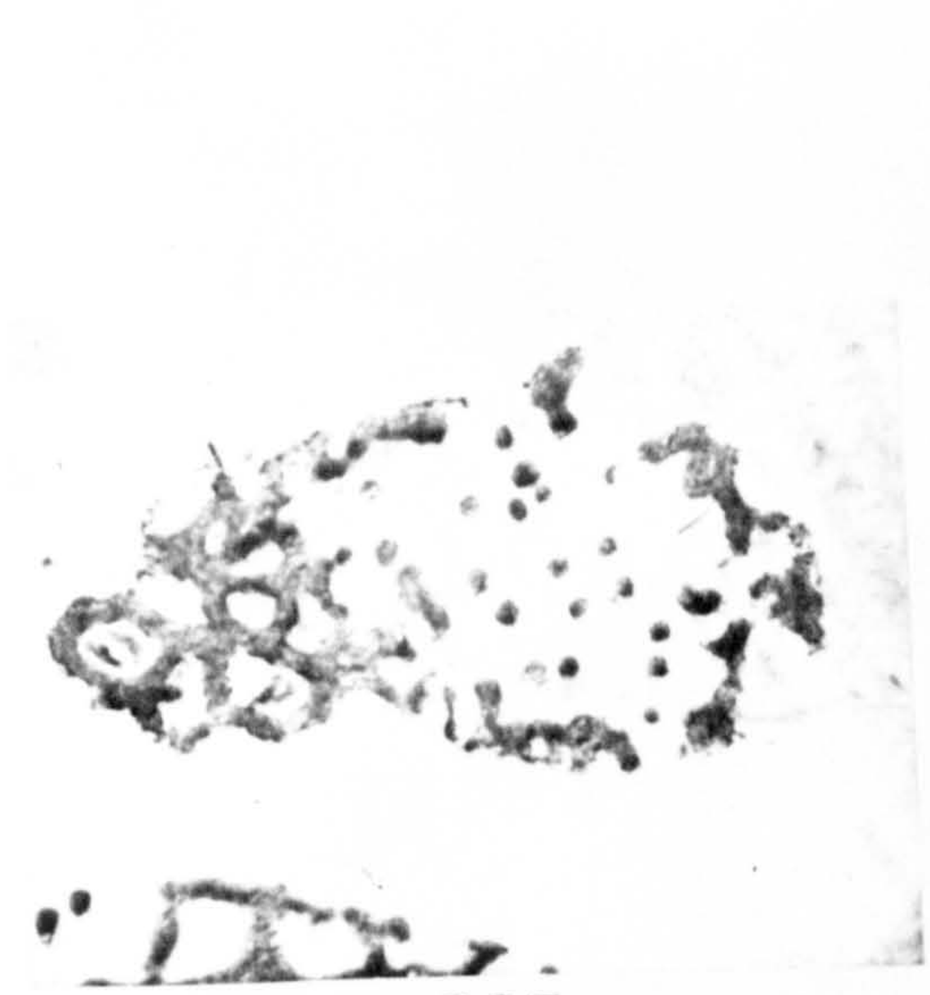
Stain : osmium/uranyl acetate.



225



226



227

228

PLATE 33

Anatomy And Morphology Of Gymnocarpium robertianum

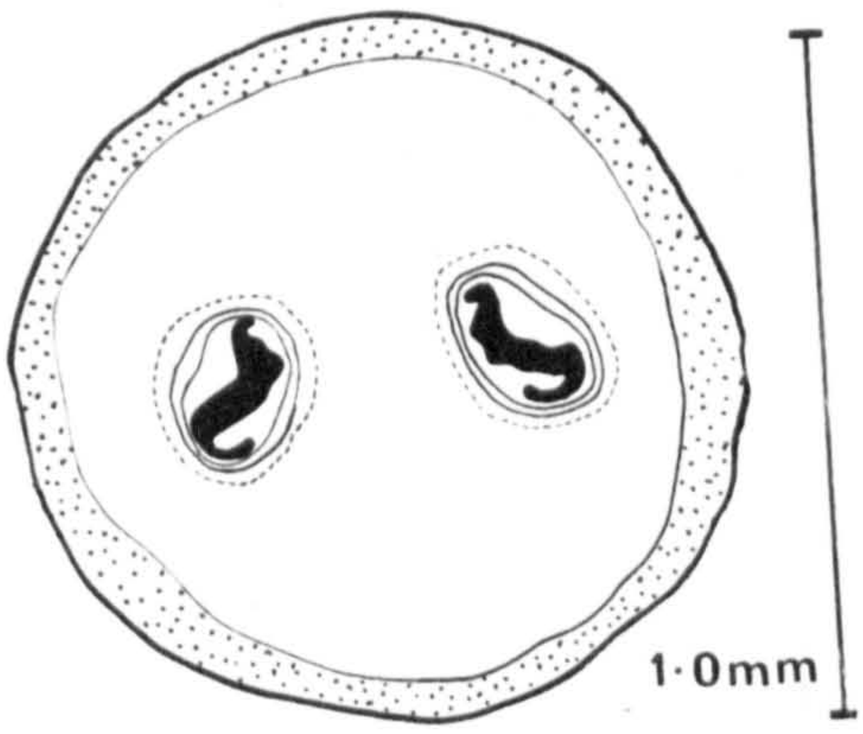
Fig. 229 Plan of vascularisation of stipe.

Fig. 230 Silhouette of frond.

Fig. 231 Capitate hairs from frond.

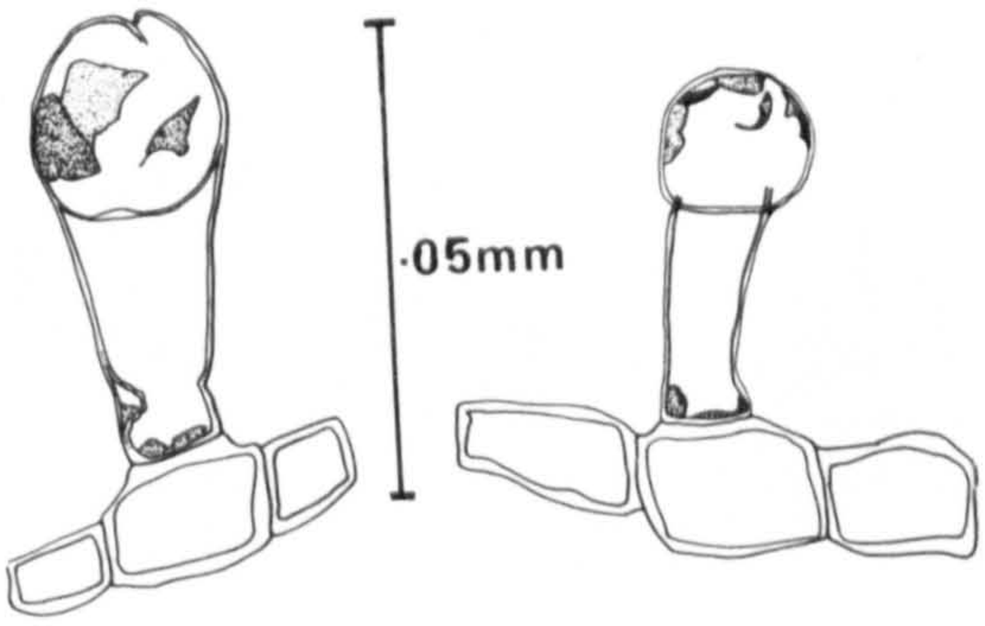
Fig. 232 Stipe scales.

Fig. 233 Plan of section through rhizome.

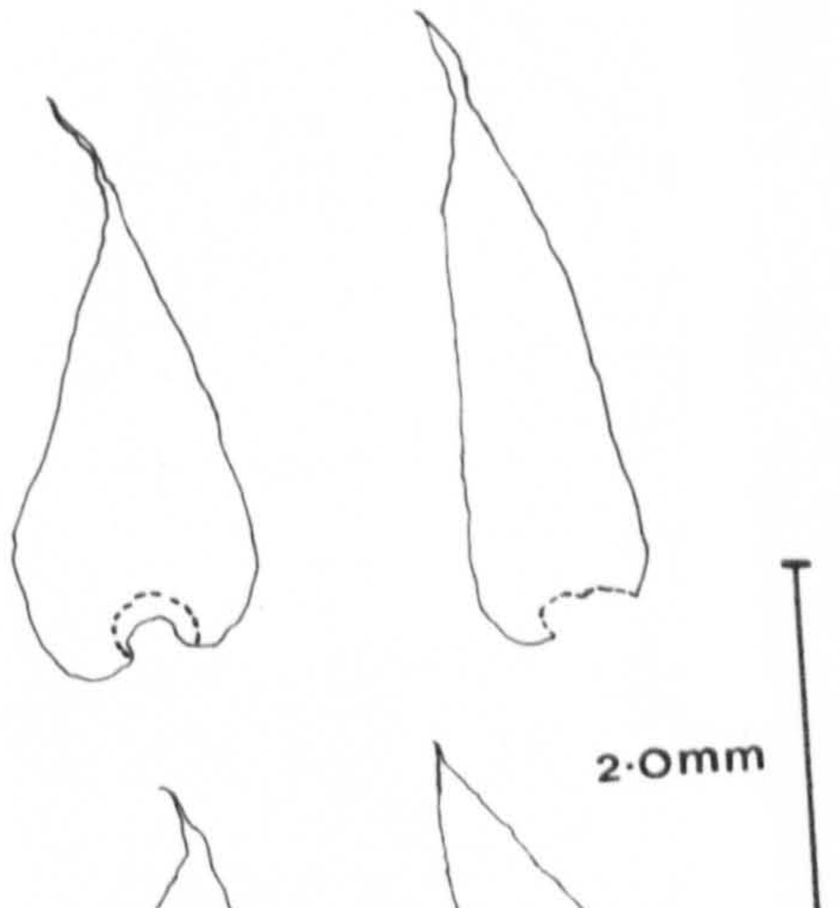


229

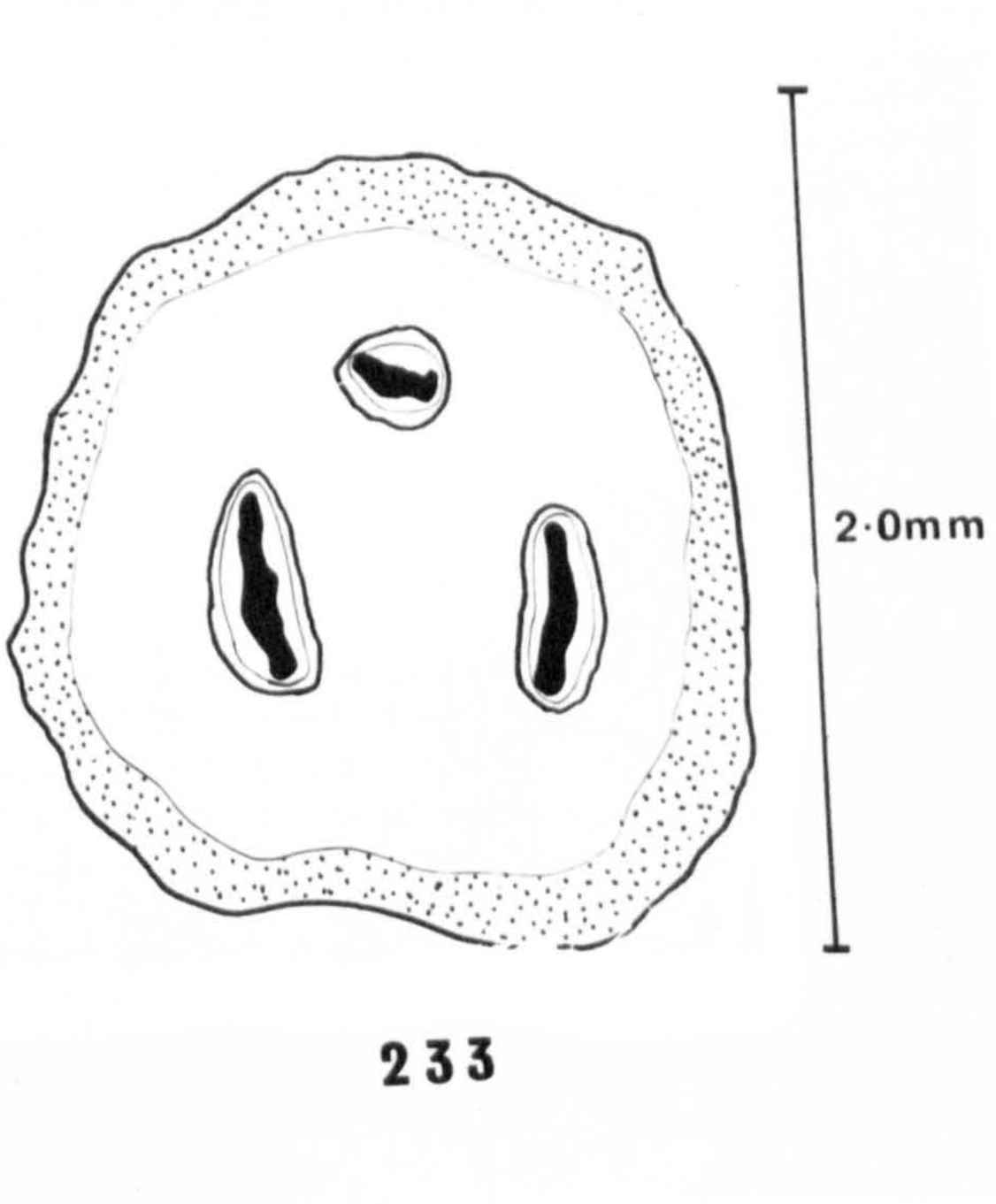
230



231



232



233

PLATE 34

Permanent aceto-carmine Preparations Of Chromosomes At Metaphase Of First Meiotic Division

(magnification approx. x 1000)

Fig. 234a *T.megalodus*, T10557, n=36.

Fig. 234b Explanatory diagram for above.

Fig. 235a *T.oligocarpa*, T10674, n=29.

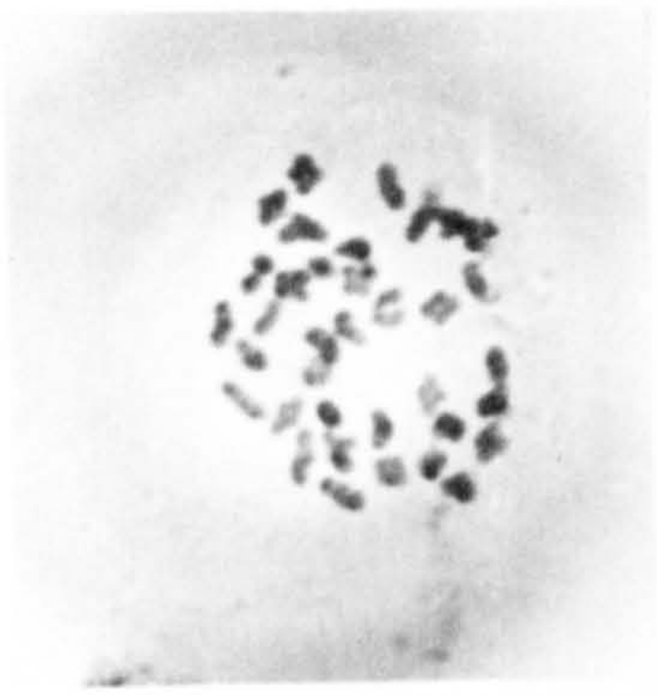
Fig. 235b Explanatory diagram for above.

Fig. 236a *T.glabriuscula*, T7744, n=36.

Fig. 236b Explanatory diagram for above.

Fig. 237a *Thelypteris* sp. indet., T8529, n=36.

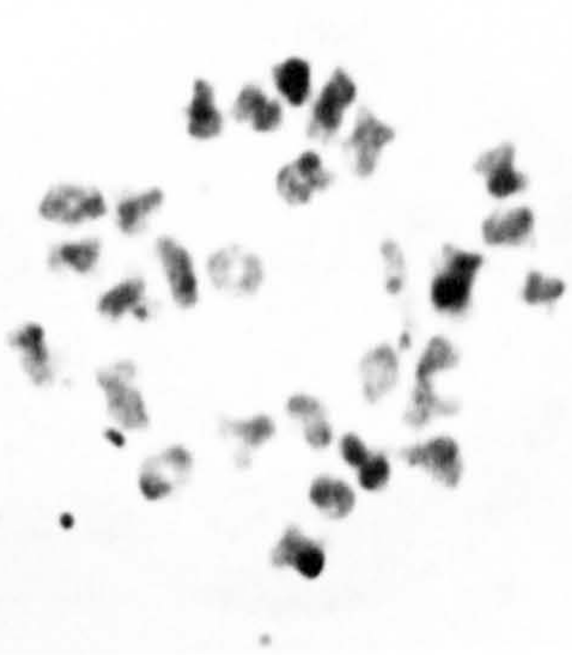
Fig. 237b Explanatory diagram for above.



a

b

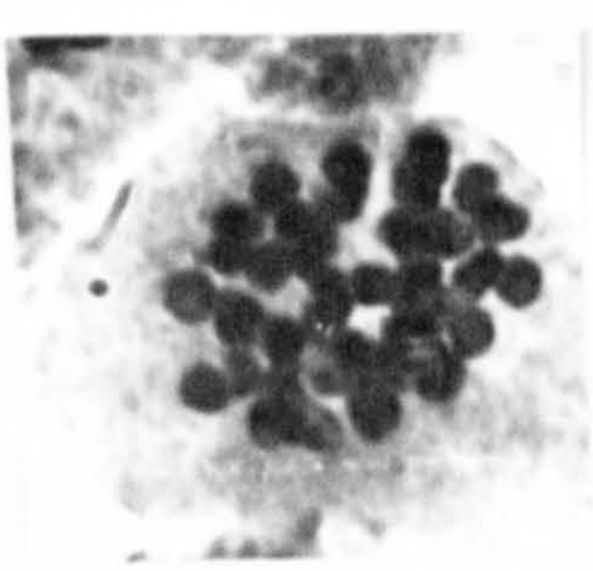
234



a

b

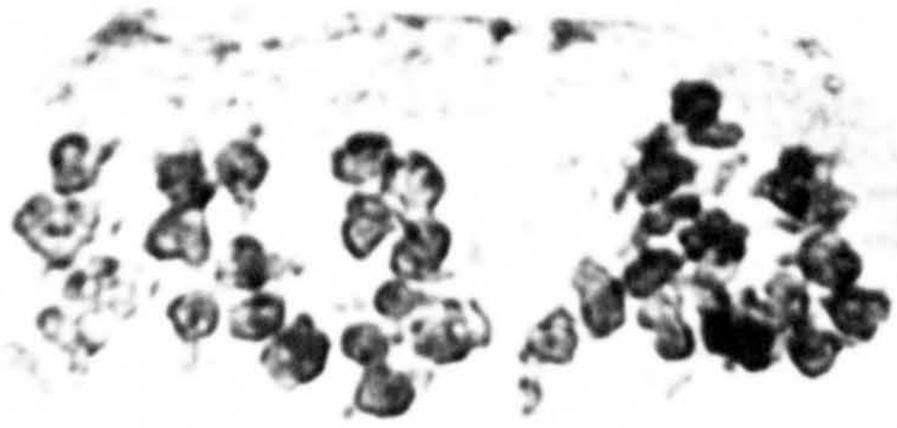
235



a

b

236



a

b

237

APPENDIX I

CYTOLOGICAL DATA

Species	n	Ploidy	Country of Origin	Source
n=27				
T.nevadensis (Bak.) Clute	26-7	2x	B. Columbia	46
T.noveboracensis (L.) Nieuwl.	c29	2x	-	4
	27	2x	N. America	49
	27	2x	Canada	5
	27	2x	Canada	6
n=28				
T.navarrensis (Christ) Proctor	28	2x	Costa Rica	45
AMAUROPELTA (n=29)				
T.concinna (Willd.) Proctor	29	2x	Jamaica	52
T.heteroclita (Desv.) Proctor	29	2x	Jamaica	52
T.linkiana (Presl) Tryon	29	2x	Jamaica	52
T.nockiana (Jenm.) Proctor	29	2x	Jamaica	52
T.oligocarpa (Maxon) Proctor	29	2x	Jamaica	52
T.rudis (Kze.) Proctor	29	2x	Jamaica	52
T.sancta (L.) Proctor	29	2x	Jamaica	52
T.sancta var. magna (Jenm.) Proctor	29	2x	Jamaica	52
T.thomsonii (Jenm.) Proctor	58	4x	Jamaica	52
PHEGOPTERIS (n=30)				
T.decursive-pinnata (Van Hall) Ching	30	2x	Japan	37
	c60	4x	Japan	16
	30	2x	Japan	38
	60	4x	Japan	38
	90-2	6x	Japan	38

Species	n	Ploidy	Country of Origin	Source
PHEGOPTERIS (n=30) (Cont.)				
T.hexagonoptera (Michx.) Weatherby	30	2x	N. America	49
T.phegopteris (L.) Slosson in Rydb.	90	3x	U.S.A.	23
	90	3x	Iceland	21
	90	3x	Europe	22
	90	3x	Britain	27
	90	3x	U.S.A.	4
	90	3x	Finland	43
	90	3x	-	48
	90	3x	Finland	44
	90	3x	Japan	39
PSEUDOPHEGOPTERIS (n=31)				
T.aurita (Hook.) Ching	62	4x	N. Guinea	13
	31	2x	Himalayas	24
T.bukoensis (Tag.) Ching	c30	2x	Japan	16
T.cruciata (Willd.) Tard.	62	4x	W. Africa	30
	62	4x	Ghana	2
T.cyclocarpa (Holttum)	124	4x	N. Guinea	13
T.levingei (Clarke) Ching	93	3x	Himalayas	24
T.oppositipinna (v.A.v.R.) Ching	62	4x	Himalayas	24
T.cf.panamensis (Presl) E.P. St. John	31	2x	Mexico	35
T.pyrrhorhachis (Kze.) Ching	62	4x	Ceylon	28
	93	6x	Ceylon	28
	62	4x	Ceylon	32
	93	6x	Ceylon	32
	31	2x	India	47
	31	2x	Himalayas	24
T.subaurita (Tag.) Ching	31	2x	Japan	19
	31	2x	Japan	38
MACROTHELYPTERIS (n=31)				
T.ornata (Wall.) Ching	31	2x	Himalayas	24
T.torresiana (Gaud.) Alston	62	4x	Malaya	29
	62	4x	Ceylon	32
	93	6x	Malaya	29
	62	4x	Himalayas	24
	62	4x	India	1

Species	n	Ploidy	Country of Origin	Source
MACROTHELYPTERIS (n=31) (Cont.)				
T.torresiana (Cont.)	62	4x	India	11
	62	4x	Jamaica	52
	62	4x	India	10
T.torresiana var. calvata (Bak.) Holttum	62	4x	Japan	38
n=31				
T.angulariloba Ching	c62	4x	Japan	38
T.beddomei (Bak.) Ching	31	2x	Ceylon	32
T.japonica (Bak.) Ching	c62	4x	Japan	19
	62	4x	Japan	38
	92-3	6x	Japan	38
	31	2x	Japan	38
T.resinifera (Desv.) Proctor	31	2x	Mexico	35
	62	4x	Jamaica	52
T.sumatrana (v.A.v.R.) Reed	62	4x	-	40
n=32				
T.pectiniformis (C.Chr.) Ching	32	2x	Malaya	29
T.simulata (Davenp.) Nieuwl.	64	4x	U.S.A.	50
n=34				
T.elwesii (Bak.) Ching	34	2x	Himalayas	24
T.limbosperma (All.) H.P. Fuchs	34	2x	Eruope	48
	34	2x	B. Colombia	46
	34	2x	England	27
	68	4x	Poland	14
T.quelpaertensis (Christ) Ching	34	2x	Japan	39
n=35				
T.esquirolii (Christ) Ching	35	2x	Himalayas	24
T.flaccida (Bl.) Ching	35	2x	Ceylon	32
	70	4x	Ceylon	32
	70	4x	Himalayas	24

Species	n	Ploidy	Country of Origin	Source
n=35 (Cont.)				
T.palustris Schott.	35	2x	Finland	43
	35	2x	England	27
	35	2x	Europe	48
	35	2x	U.S.A.	12
	36	2x	Japan	38
	70	4x	Poland	14
	35	2x	Finland	44
T.palustris var. pubescens (Lawson) Fernald	35	2x	-	4
	35	2x	N. America	49
T.repens (Hope) Ching	35	2x	India	47
	35	2x	Himalayas	24
	35	2x	S. India	1
	105	3x	Himalayas	24
T.singalanensis (Bak.) Ching	70	4x	Malaya	29
T.viscosa (Bak.) Ching	c70	4x	Malaya	29
STEGNOGRAMMA (n=36)				
T.griffithii var. wilfordii (Hook.) Reed	144	8x	Formosa	38
T.gymnocarpa ssp. amabilis (Tag.) Morton	36	2x	Japan	38
T.pozoi (Lagasca) Morton	36	2x	Ceylon	32
	36	2x	Japan	15
	36	2x	Japan	38
FREE VEINED SPECIES (n=36)				
T.ciliata (Wall.) Ching	36	2x	Ceylon	32
	72	4x	Malaya	29
T.crassifolia (Bl.) Ching	72	4x	Malaya	29
T.decussata (L.) Proctor	72	4x	Puerto Rica	45
	36	2x	Jamaica	53
T.deltoidea (Sw.) Proctor	c36	2x	Jamaica	52
T.erubescens (Wall.) Ching	36	2x	India	47
	36	2x	Himalayas	24
	36	2x	Nepal	42
	72	4x	Japan	38
T.glanduligera (Kunze) Ching	c72	4x	Japan	38

Species	n	Ploidy	Country of Origin	Source
FREE VEINED SPECIES (n=36) (Cont.)				
T.laxa (Fr. et Sav.) Ching	72	4x	Japan	19
T.microbasis (Bak.) Ching	72	4x	W. Africa	31
T.omiensis (Bak.) Ching	c136	8x	Japan	20
T.paleata (Copel.) Holtt.	72	4x	Malaya	29
T.serra (Sw.) R.P. St. John in Small	36	2x	Jamaica	52
	72	4x	Jamaica	52
	72	4x	Himalayas	24
T.sub-ochthodes Ching	36	2x	Japan	17
	36	2x	India	11
	36	2x	Japan	38
	36	2x	-	10
T.sub-villosa Ching	72	4x	Himalayas	24
T.wantotensis (Copel.) Reed	36	2x	New Guinea	13
T.xylodes (Kze.) Ching	36	2x	Ceylon	32
	36	2x	Himalayas	24
SPECIES WITH SOME VEINS ANASTOMOSING (n=36)				
T.acuminata (Panz.) Morton	36	2x	Japan	16
	36	2x	Japan	38
T.afra (Christ) Reed	72	4x	W. Africa	30
T.arbuscula (Willd.) Iwats.	36	2x	Ceylon	32
	36	2x	S. India	1
T.arida (D.Don) Manton	36	2x	Himalayas	26
T.asplenioides (Sw.) Proctor	36	2x	Jamaica	52
	72	4x	Jamaica	52
T.asterothrix (Fée) Proctor	72	4x	Jamaica	52
T.asterothrix var. bibrachiata (Jenm.) Proctor	72	4x	Jamaica	52
T.beccariana (Ces.) Reed	77	4x	New Guinea	13
T.biolleyi (Christ) Proctor	36	2x	Jamaica	52
T.caudata (Ching) Holttum	72	4x	New Guinea	13
T.conferta (Brause) Reed	72	4x	New Guinea	13
T.crinipes (Hook.) Reed	36	2x	Himalayas	26

Species	n	Ploidy	Country of Origin	Source
SPECIES WITH SOME VEINS ANASTOMOSING (n=36) (Cont.)				
T.cylindrothrix (Ros.) Iwats.	36	2x	Himalayas	26
T.dentata (Forsk.) E.P. St. John	36	2x	India	10
	56-8	3x	Costa Rica	45
	72	4x	Malaya	32
	-	4x	-	40
	72	4x	W. Africa	30
	72	4x	Himalayas	47
	72	4x	Himalayas	26
	72	4x	India	11
	72	4x	New Guinea	13
	72	4x	Jamaica	52
	72	4x	-	10
T.extensa (Bl.) Morton	70-2	4x	Malaya	29
T.forsteri Morton	36	2x	New Zealand	9
T.gongylodes (Schkuhr) Small	36	2x	Malaya	32
	c72	4x	Ceylon	29
	36	2x	New Zealand	8
	36	2x	Japan	37
	72	4x	Jamaica	52
	36	2x	Japan	38
	72	4x	Japan	38
T.guadalupensis (Wikstr.) Proctor	72	4x	Jamaica	52
T.heterocarpa (Bl.) Morton	36	2x	W. Africa	30
	72	4x	New Guinea	13
T.interrupta (Willd.) B.C. Stone	72	4x	Ceylon	28
T.invisa (Sw.) Proctor	36	2x	Jamaica	52
T.kunthii (Desv.) Morton	72	4x	Jamaica	52
	36	2x	U.S.A.	50
	36 IIs 36 Is	3x	Mexico	35
	43 IIs 21 Is	3x	Mexico	35
T.lineata (Bl.) Iwats.	c72	4x	Malaya	29
	c72	4x	Ceylon	32
T.megalodus (Schkuhr) Proctor	72	4x	Japan	19
	36	2x	Jamaica	52
T.megaphylla (Mett.) Iwats.	36	2x	Malaya	29
T.mollis (Mett.) Tryon	-	2x	Ceylon	28
	-	4x	Ceylon	28
T.molliuscula (Kuhn) Iwats.	36	2x	Himalayas	26

Species	n	Ploidy	Country of Origin	Source
SPECIES WITH SOME VEINS ANASTOMOSING (n=36) (Cont.)				
T.multilineata (Wall.) Ching	36	2x	Malaya	29
	36	2x	Ceylon	32
	36	2x	Ceylon	34
	36	2x	Himalayas	33
	36	2x	Himalayas	26
	36	2x	India	41
T.nymphalis (Forst.) Ching	72	4x	New Zealand	8
	72	4x	Australia	3
T.obliterata (Sw.) Proctor	c108 Is & IIs	3x	Jamaica	52
T.papilio (Hope) Ching	72	4x	Ceylon	32
	36	2x	Himalayas	26
	36	2x	Himalayas	24
T.parasitica (L.) Tard. in Tard. et C. Chr.	72	4x	Malaya	29
	72	4x	Ceylon	32
	-	4x	-	40
	72	4x	S. India	1
T.patens (Sw.) Small	c36	2x	W. Africa	30
	72	4x	Jamaica	52
	72	4x	Trinidad	53
T.pennigera (G.Forst.) Allan	72	4x	New Zealand	7
T.petrophila (Copel.) Reed	36	2x	New Guinea	13
T.poiteana (Bory) Proctor	72	4x	Jamaica	52
T.quadrangularis (Fée) Schelpe	36	2x	W. Africa	30
T.repandula (v.A.v.R.) Reed	36	2x	Ceylon	32
T.reptans (J.F.Gmel.) Morton	72	4x	U.S.A.	50
	36	2x	Jamaica	52
T.rubicunda (v.A.v.R.) Iwats.	c36	2x	Malaya	29
	c36	2x	Ceylon	32
T.rubra (Ching) Iwats.	36	2x	Himalayas	26
T.sagittata (Sw.) Proctor	36	2x	Jamaica	52
T.salicifolia (Wall.) Reed	36	2x	Malaya	29
	36	2x	Ceylon	32
T.sclerophylla (Poepp. ex Spreng.) Morton	72	4x	U.S.A.	50
T.serrulata (Sw.) Proctor	36	2x	Jamaica	52

Species	n	Ploidy	Country of Origin	Source
SPECIES WITH SOME VEINS ANASTOMOSING (n=36) (Cont.)				
T.striatus (Schum.) Schelpe	36	2x	W. Africa	30
T.sub-pubescens (Bl.) Ching	72	4x	Malaya	29
	72	4x	Ceylon	32
	36	2x	Japan	38
	-	4x	-	40
T.sumatrana (v.A.v.R.) Ching	72	4x	Malaya	29
	72	4x	Ceylon	32
T.tetragona (Sw.) Small	c72	4x	Jamaica	52
	72	4x	Mexico	35
	c35	2x	Mexico	35
T.triphylla (Sw.) Iwats.	72	4x	Malaya	29
	72	4x	Ceylon	32
	72	4x	Japan	18
	72	4x	Japan	38
T.truncata (Poir.) Farwell	c72	4x	Ceylon	32
	36	2x	Himalayas	26
	36	2x	Formosa	38
T.unita (L.) Morton	36	2x	Ceylon	32
T.urophylla (Wall.) Iwats.	36	2x	Malaya	29
	36	2x	Ceylon	32
T.venusta (Hew.) Proctor	72	4x	Jamaica	52
T.venusta var. usitata (Jenm.) Proctor	72	4x	Jamaica	52
MENISCIUM (n=36)				
T.prolifera (Retz.) Reed	72	4x	W. Africa	30
	36	2x	W. Africa	34
	36	2x	Himalayas	33
	36	2x	Himalayas	26
	36	2x	S. India	1
T.reticulata (L.) Proctor	72	4x	Puerto Rica	44
	72	4x	Jamaica	52
T.serrata (Cav.) Alston	36	2x	U.S.A.	50

Species	n	Ploidy	Country of Origin	Source
GYMNOCARPIUM (n=40)				
G.dryopteris (L.) Newm.	80	4x	U.S.A.	23
	80	4x	Britain	27
	80	4x	Finland	43
	40	2x	U.S.A.	51
	80	4x	Iceland	21
	80	4x	Cen/N.W.Europe	22
	c80	4x	U.S.A.	50
	40	2x	U.S.A.	45
	80	4x	-	48
	80	4x	Finland	44
G.jessoensis (Koidz.) Koidz.	40	2x	Japan	39
G.oyamense (Bak.) Ching	80	4x	Japan	18
	40	2x	Japan	38
G.robertiana (Hoff.) Newm.	c80	4x	Britain	27
	c80	4x	U.S.A.	50
	80	4x	Europe	48

Many of the references listed below were in fact reported in the following three papers;

CHIARUGI, A., (1960) "Tavole chromosomicle delle Pteridophyta". Caryologia, 13: 27-150.

FABBRI, F., (1963) "Primo supplemento alle 'Tavole chromosomiche delle Pteridophyta' de Alberto Chiarugi". Caryologia, 16: 327-335.

FABBRI, F., (1965) "Secundo supplemento alle 'Tavole chromosomiche delle Pteridophyta' de Alberto Chiarugi". Caryologia, 18: 675-731.

The following is the key to the numbers given as the source of the individual counts.

1. ABRAHAM, A., NINAN, C.A. and MATHEW, P.M., (1962) "Studies on the cytology and phylogeny of the pteridophytes VII. Observations on 100 species of South Indian ferns". J.Indian bot. Soc., 41: 339-412.

2. ALSTON, A.H.G., (1959) "The ferns and fern allies of West Tropical Africa". In the Flora of West Tropical Africa. 2nd. Edition, London.

3. BRIGGS, in BEADLE, N.C.W., EVANS, O.D. and CAROLIN, R.C., (1962) Handbook of the vascular plants of the Sydney district and Blue Mountains.

4. BRITTON, D.M., (1953) "Chromosome studies on ferns". Am. J. Bot., 40: 575-583.

5. BRITTON, D.M., (1963) in FABBRI, F., (1963).

6. BRITTON, D.M., (1964) "Chromosome numbers of ferns in Ontario". Can. J. Bot., 42: 1349-1354.

7. BROWNLIE, G., (1954) "Introductory note to cytotaxonomic studies of New Zealand ferns". Trans. R. Soc. N.Z., 82: 665-666.

8. BROWNLIE, G., (1961) "Additional chromosome numbers of studies of New Zealand ferns". Trans. R. Soc. N.Z., 1: 1-14.

9. BROWNLIE, G., (1965) "Chromosome numbers in some Pacific pteridophyta". Pacific Science, 19: 493-497.

10. GHATAK, J., (1962) "Observations on the cytology and taxonomy of some ferns from India". Nucleus, Calcutta, 5: 95-114.

11. GHATAK, J., (1963) "Observations on the cytology and taxonomy of some ferns from India". Proc. Indian Sci. Congr. Assoc. 50th Sess., 3: 371-2.

12. HARTLEY, T.G., (1965) in FABBRI, F., (1965)

13. HOLTTUM, R.E., and ROY, S.K., (1965) "Cytological observations on ferns from New Guinea with descriptions of new species". Blumea, 13: 129-139.

14. KARPOWITCZ, W., (1960) "A comparative study on the species of the genera Dryopteris and Thelypteris occurring in Poland". Acta Soc. Bot. Pol., 29: 175-189.

15. KURATA, S., (1960) "Notes on Japanese ferns, (20)" J.Geobot., 8: 80-86.

16. KURITA, S., (1960) "Some chromosome numbers of some Japanese ferns I". J. Jap. Bot., 35: 269-272.

17. KURITA, S., (1961) "Some chromosome numbers of some Japanese ferns II". Bot. Mag. Tokyo, 74: 395-401.

18. KURITA, S., (1962) "Chromosome numbers of some Japanese ferns III". J.Coll. Arts Sci. Chiba Univ., Nat. Sci. Ser., 3: 463-468.

19. KURITA, S., (1963) "Cytotaxonomic studies on some leptosporangiate ferns". J. Coll. Arts Sci. Chiba Univ., Nat. Sci. Ser., 4: 43-52.

20. KURITA, S., (1965) "Chromosome numbers of some Japanese ferns IV". J.Jap. Bot., 40: 234-244.

21. LÖVE, A., and LÖVE, D., (1961a) "Some chromosome numbers of Icelandic ferns and fern allies". Am. Fern J. 51: 127-128.

22. LÖVE, A., and LÖVE, D., (1961b) "Chromosome numbers of Central and Northwest European plant species". Opera Botanica (Suppl. Bot. Notiser) 5: Almqvist and Wicksell, Stockholm.

23. LÖVE, A., and LÖVE, D., (1966) "Cytotaxonomy of the Alpine vascular plants of Mount Washington." Univ. Colo. Stud. Ser. Biol., No. 24.

24. LOYAL, D.S., (1961a) "Cytological studies on Himalayan Thelypteridaceae, I. Cytology of Thelypteris Schmid." Proc. 48th Indian Sci. Congr., Pt. III, 265-266.

25. LOYAL, D.S., (1961b) "Ibid. II, Cytology of Cyclosorus Link and Abacopteris Fée and Ampelopteris Kunze". Proc. 48th Indian Sci. Congr., Pt. III, 266-277.

26. LOYAL, D.S., (1961c) in MEHRA, P.N., (1961).

27. MANTON, I., (1950) Problems of cytology and evolution in the pteridophyta. Camb. Univ. Press, London.

28. MANTON, I., (1953) "The cytological evolution of the fern flora of Ceylon". Symp. Soc. exp. Biol., 7 (Evolution): 174-185.

29. MANTON, I., (1954) "Cytological notes on one hundred species of Malayan ferns". in HOLTTUM (1954), Flora of Malaya, Vol. 2, Ferns of Malaya. Singapore: 623-627.

30. MANTON, I., (1959a) "Cytological information on the ferns of West Tropical Africa". in ALSTON, A.H.G., (1959).

31. MANTON, I., (1959b) "Cytological information on the ferns of West Tropical Africa". in ALSTON, A.H.G., (1959).

32. MANTON, I., and SLEDGE, W.A., (1954) "Observations on the cytology and taxonomy of the pteridophyte flora of Ceylon". Phil. Trans. R. Soc. (London), 238B: 127-185.

33. MEHRA, P.N., (1961) "Chromosome numbers in Himalayan ferns". Res. Bull. Panjab Univ., n.s. 12: 139-164.

34. MEHRA, P.N., and LOYAL, D.S., (1956) "Colchicine effect on the prothalli of Goniopteris multilineata (Wall.) Bedd. and G.prolifera (Retz.) Presl with emphasis on abnormal spermatogenesis in polyploid prothalli". Ann. Bot., n.s. 20: 545-552.

35. MICKEL, J.T., WAGNER, W.H.Jr., and LIM CHEN, K., (1966) "Chromosome observations on the ferns of Mexico". Caryologia, 19: 95-102.

36. MITUI, K., (1965a) "Chromosome studies in Japanese ferns I". J. Jap. Bot., 40: 117-124.

37. MITUI, K., (1965b) in FABBRI, F., (1965)

38. MITUI, K., (1968) "Chromosomes and speciation in ferns". Sci. Rep. Tokyo Kyoiku Daig., Sec. B., 13: 285-333.

39. MITUI, K., (1970) "Chromosome studies on Japanese ferns (4)". J. Jap. Bot., 45: 84-90.

40. PANIGRAHI, G., and MANTON, I., (1958) "Cytological and taxonomic observations on some members of the Cyclosorus parasiticus complex". J. Linn. Soc. (Bot.), 55: 729-743.

41. ROY, R.P., and PANDEY, S.N., (1963) "Cytotaxonomical studies of the fern flora of the Parasnath Hills". Proc. Indian Sci. Congr., 50.

42. ROY, R.P., and SAKYA, A.R., (1963) in FABBRI, F., (1963).

43. SORSA, V., (1958) "Chromosome studies on Finnish pteridophytes". Hereditas 44: 541-546

44. SORSA, V., (1962) "Chromosomenzahlen Finnischer kormophyten". Ann. Acad Sci. Fenn., Ser. A IV, Biol., 58: 1-14.

45. SORSA, V., (1965) in FABBRI, F., (1965).

46. TAYLOR, T.M.C., and LANG, F., (1963) "Chromosome counts on some British Columbian ferns". Am. Fern J., 53: 123-126.

47. VERMA, S.C., and LOYAL, D.S., (1960) "Chromosome counts on some ferns from Naini Tal". Curr. Sci., 29: 69-70.

48. VIDA, G., (1963) "A Dryopteris remzetség (sens. lat.) sziszlematikja". Bot. Közl., 50: 125-133

49. WAGNER, W.H.Jr., (1955) "Cytotaxonomic observations on North American ferns". Rhodora, 57: 219-240.

50. WAGNER, W.H.Jr., (1955) "A biosystematic survey of U.S. ferns. Preliminary abstract". Am. Fern J., 53: 1-16.

51. WAGNER, W.H.Jr., (1963) in FABBRI, F., (1963).

52. WALKER, T.G., (1964-5) "A cytotaxonomic survey of the pteridophytes of Jamaica". Trans. R. Soc. Edinb., 64: 169-237.

53. WALKER, T.G., Commun. pers.

APPENDIX II

The following is a list of those specimens which have been consulted during the course of this investigation.

KEY:

Location of Specimens:

BM - Herbarium of the British Museum of Natural History, South Kensington.

K - Herbarium or collection of the Royal Botanic Gardens at Kew.

N - Herbarium of the Department of Botany in the University of Newcastle Upon Tyne.

Studies In Which The Specimens Have Been Utilised:

A - Anatomical Studies

S - Spore Morphology

C - Cytological Studies

The brackets following the location of the specimen refer to the label on the herbarium sheet.

The figure numbers refer to the spore photo/micrographs in this work.

Collecting numbers prefixed by a T (e.g. T1579) indicate that the specimens were collected by Dr. T. G. Walker.

THELYPTERIS

T.acuminata (Panz.) Morton:

Oti 15118 Japan BM (Cyclosorus) (fig. 188) S

T.afra (Christ) Reed:

Exell 259 Saô Tomé W. Trop. Africa BM (Dryopteris) (fig. 175) S

T.angulariloba Ching:

Iwatsuki 5010 Japan BM S

T.angustifolia (Willd.) Proctor:

T1579 Jamaica N. S

T.arbusculus (Willd.) K. Iwats:

Schmid 1036 Ceylan, Cashmire BM (Cyclosorus) S

T.archboldii (C.Chr.) Reed:

T7743 New Guinea BM (Cyclosorus) C
T8817 New Guinea BM (Cyclosorus) A

T.aspidioides (Willd.) Tryon:

Hooker and Thompson s.n. Khasya, India BM (Dryopteris) (fig. 126) S

T.asplenioides (Sw.) Proctor:

T4601 Jamaica N (fig. 166) S C
T5285 Jamaica N S
S.n. Walker, Jamaica N C

T.asterothrix (Fée) Proctor:

T4545 Jamaica N (fig. 172) S

T.atasripii (Rosenst.) Reed:

T8005 New Guinea BM (Cyclosorus) A
T8970 New Guinea BM (Cyclosorus) A
T9053 New Guinea BM (Cyclosorus) A

T.aurita (Hk.) Ching:

Petelot 3144 Formosa BM (Dryopteris) (fig. 95) S

T.balbisii (Spreng.) Ching:

T6142 Trinidad N (T.sprengelii) A
T7208 Jamaica N (T.sprengelii) (figs. 81, 207, 208, & 225-8) S
T7211 Trinidad N (T.sprengelii) A

T.bangii (C.Chr.) Tryon:

W18 Kew (cult.) South America K (fig. 191) S A

T.beccariana (Ces.) Reed:

T9369 New Guinea BM (Cyclosorus) A

T.beddomei (Bak.) Ching:

Java s.n. BM (Nephrodium macilentum) S
T7763 New Guinea BM A
T8435 New Guinea BM A

T.biolleyi (Christ) Proctor:

T4822 Jamaica N (Dryopteris) (fig. 163) S

T.brachyodus (Kunze) Ching:

T3088 Jamaica N S
T6741 Trinidad N A
T7213 Trinidad N A
Jermy 2250 Trinidad N S
Fay 246 West Indies N S

T.brunnea (Wall.) Ching

Molesworth-Allen 2511 Pahang BM (Pseudophegopteris paludosa) (fig. 104) S

Hooker and Thompson 15 Nilgheri, India BM (Dryopteris) S

T.bukoensis H.Ito:

Tagasi 1216 Japan BM (fig. 101) S

T.calcareta (Bl.) Ching:

Burbridge s.n. 6/98 Borneo BM (Nephrodium) (fig. 141) S

T.callosa (Bl.) K. Iwats.:

Rosenstock 187 Sumatra BM (Dryopteris) (fig. 216) S
T11,951 Sulawesi BM (Cyclosorus) A
T12,283 Sulawesi BM (Cyclosorus) A

T.canescens (Bl.) K. Iwats.:

Brass 22992 Papua, New Guinea BM (Dryopteris) S

T.cavitensis (Copel.) Reed:

T8431 New Guinea BM (Lastrea) C

T.cheilanthoides (Kunze) Proctor:

Spruce 5302 Equador BM (Nephrodium resino-foetidum) (fig. 86) S

T.ciliata (Wall.) Ching:

Kingdom-Ward s.n. N.Burma BM S

Molesworth-Allen 2158 Siam BM S

Schmid 1070 Kashmir BM (figs. 129 & 218) S

Beccari 430 Sumatra BM S

No. 58 15/8/81 Sumatra/Java BM S

T.concinna (Willd.) Proctor:

T4714 Jamaica N S

Ynes Mexica 8184 Peru BM (Dryopteris) (fig. 80) S

T.cordata (Fée) Proctor:

C. Wright 1014 Cuba BM (Aspidium reptans var. cordatum) (fig. 199) S

T.crassifolia (Bl.) Ching:

Cummings 390 Malacca BM (Lastrea) (fig. 130) S

Mrs. E. Smith 3061 Siam BM (Dryopteris) S

Freeman 284a Ceylon BM (Nephrodium) S

T.crinipes (Hook.) Reed:

Hooker and Thompson 238 India BM (Nephrodium) (fig. 157) S

T.cruciata (Willd.) Ching:

Bruce 56 Tanganyika BM (Dryopteris) S

Deans-Cowan 16 Madagascar BM (Dryopteris) (fig. 98) S

Adams 1092 Gold Coast BM (Dryopteris) S

T.cyclocarpa Holttum:

Clemens 6917 New Guinea BM (Pseudophegopteris) (figs. 99 & 210) S

T.cyrtomiodes (C.Chr.)

H.Smith 13499 Szechuan, China BM (Dryopteris) S

T.decursive-pinnata (Van Hall.) Fée:

V.V.Hart s.n. (1848) China BM (Nephrodium) (fig. 94) S
W22 Kew (cult.) Japan K S A

T.decussata (L.) Proctor:

Husnot 389 Martinique BM (Phegopteris) (fig. 135) S
T4977 Jamaica N A

T.deltoidea (Sw.) Proctor:

Wilson 1861 Jamaica BM S
T2873 Jamaica N (fig. 137) S A

T.dentata (Forssk.) Ching:

T6184 Trinidad N (Cyclosorus) A
T10662 Trinidad N (figs. 159 & 219) S
Jermy 2158 Trinidad N C
Fay 222 West Indies N
Page 2198 Mauritius C
Hynes 31444 New Zealand BM (Cyclosorus) S

T.dimorpha (Brause) Reed:

T8121 New Guinea BM (Cyclosorus) A

T.duclouxii (Christ) Ching:

Hara et al. s.n. 1963 E.Nepal BM (fig. 144) S

T.elwesii (Bak.) Ching:

Varma 101 Sikkhim BM (fig. 120) S

T.erubescens (Wall.) Ching:

Wilson 5390 W.China BM (Polypodium) (fig. 134) S
W21 Kew (cult.) Nepal K S

T.esquirolii (Christ) Ching:

Tsiang 4734 Ching BM (Dryopteris) (fig. 123) S

T.extensa (Bl.) Ching:

W7 Kew (cult.) Malaya N (Cyclosorus) (fig. 171) S A

T.falcatipinnula (Copel.) Reed:

T7742 New Guinea BM A

T.ferox (Bl.) Reed:

Rosenstock 1304 Malaya BM (Nephrodium) (fig. 184) S
Brooks s.n. 1908, Sarawak BM (Nephrodium) S

T.firma (Bak.) Proctor:

T2367 Jamaica N (fig. 143) S

T.flaccida (Bl.) Ching:

Gardner 1152 Ceylon BM (fig. 121) S
T11373 Java BM A

T.germaniana (Fée) Proctor:

L'Hoerminier s.n. (1886) Guadeloupe BM (Phegopteris) S
Rosenstock n48 Puerto Rica BM (Dryopteris) (fig. 90) S

T.glabriuscula (Holttum ined.):

T7744 New Guinea BM (Pneumatopteris) C

T.glanduligera (Kunze) Ching:

M.Ogata 276 Kyusyu BM S
W5 Kew (cult.) Japan N A

T.glanduligera var. elatior (Eat.) Kurata:

Kidó 2203 Japan BM S
Kido 2987 Japan BM S

T.glandulosa (Desv.) Proctor:

Lellinger 353 Dominica K (fig. 185) S

T.gongylodes (Sch.) Link:

R.E. Holttum 6/69 Kew (cult.) New Zealand N (Cyclosorus) S
Kodamoy 6378 Japan BM S
K 545/56 Kew (cult.) Florida N (Cyclosorus) (fig. 152) S A
Hooker and Thompson 235 Madras BM (Nephrodium propinquum) S
Kido 2204 Japan BM (Cyclosorus) S

T.gracilescens (Bl.) Ching:

M.Ogata 278 Formosa BM (fig. 132) S
Forbes 743 Kiu Kiang, China BM (Nephrodium) S

T.gracilis (Hew.) Proctor:

Maxon and Killip 220 Jamaica BM (T.consimilis) (fig. 85) S

T.griffithii (Moore) Reed:

Fl. of Brit. India 155 Khasya, India BM (Dictyocline) (figs. 125 & 215) S

A.Sleap s.n. Japan N (Dictyocline) A

T.guadeloupensis (Wikstr.) Proctor:

T2240 Jamaica N (fig. 170) S

T.gymnocarpa (Copel.) Morton:

Iwatsuki 4732 Japan BM (Leptogramma amabilis) (fig. 128) S

T.hastata (Fée) Proctor:

Christensen 1875 s.n. Puerto Rica BM (Dryopteris) (fig. 194) S

T.hattorii (H.Ito) Tagawa:

Kido 1892 Japan BM (T.nemoralis) (fig. 142) S

Iwatsuki 5010 Japan BM S

T.heterocarpa (Bl.) Ching:

T12663 Java BM (Cyclosorus) A

T.heteroclita (Desv.) Proctor:

T2343 Jamaica N (fig. 77) S

T.hexagonoptera (Michx.) Weatherby:

C.A. Davis s.n. Michegan BM (fig. 92) S

T.hirtirachis (C.Chr.) Ching:

Ching 5895 N.Luchen, China BM (Dryopteris) (fig. 103) S

T.insularis (K.Iwats.) K.Iwats.:

Tagawa and Iwatsuki 2248 Japan BM (Abacopteris) (fig. 197) S

T.interrupta (Willd.) Ching:

Randall 124 Ceylon BM (Nephrodium terminans) (fig. 160) S

T12546 Java BM (Cyclosorus) A

T.invisa (Sw.) Proctor:

Wilkes 1834 Jamaica BM (Lastrea) (fig. 173) S

T1155 Jamaica N (T.oligophylla) S

T.japonica (Bak.) Copel.:

Tagawa 383 Japan BM (Dryopteris) (fig. 114) S
Tagawa 7157 Kyoto, Japan BM (Lastrea) S

T.keraudreniana (Gaud.) Holttum:

Skottsburg 41 Aanan BM (Dryopteris) (fig. 105) S

T.keysseriana (Rosenst.) Reed:

T8154 New Guinea BM A
T9020 New Guinea BM A
Jermy 4991 New Guinea BM A

T.kunthii (Desv.) Morton:

T1417 Jamaica N (T.normalis) S
T1739 Jamaica N (T.normalis) (fig. 148) S

T.laxa (Franch. et Sav.) Ching:

Ogata 280 Japan BM (fig. 133) S
Oti 15572 Japan BM S

T.leptocladia (Fée) Proctor:

T1260 Jamaica N (fig. 198) S

T.levingei (Clarke) Ching:

Schelpe 3603 Punjab BM S
Stewart 24526 N,W. India BM (Dryopteris) S
Bonnez 1686 Nepal BM (Dryopteris) (fig. 100) S

T.limbata (Sw.) Proctor:

L'Hoerminier p50 Guadeloupe BM (Dryopteris) (fig. 88) S

T.limbosperma (All.) H.P. Fuchs:

The Sneap s.n.n. N S
Davies 21291 Japan BM (T.oreopteris) S
A.W.B. 2287 Raasay Is. Scotland N (L.montana)(fig. 118) S
S.n. McAllister Scotland N A

T.linkiana (Presl.) Tryon:

T1095 Jamaica N (T.diplazioides) (figs. 84 & 209) S

T.longipes (Bl.) Reed:

T12803 Java BM (Cyclosorus) A

T.megalodus (Sch.) Proctor:

T6265 Trinidad N A

T10557 Trinidad N C

T10564 Trinidad N (fig. 181) S

T.megaphylla (Mett.) Ching:

Allen 1448 Pahang BM (Cyclosorus) (fig. 149) S

R.E. Holttum 15/58 Kew (cult.) Malaya N A

T.millarae (Holttum ined.):

T8083 New Guinea BM (Pronephrium) A

T.molliuscula (Kuhn) K.Iwats.:

Stainton, Sykes and Williams 8715 Nepal BM (Cyclosorus) (fig. 177) S

T.multilineata (Wall.) Morton:

Polunin, Sykes and Williams 5713 Nepal BM (Abacopteris) (fig. 150) S

T.multiseta (Bak.) Ching:

Brooks 275.s. Sumatra BM (Macrothelypteris)(fig. 110) S

T.navarrensis (Christ) Proctor:

Holdridge 909 Haiti BM (Dryopteris) (fig. 82) S

T.nephrodioides (Klotsch.) Proctor:

Spruce 4659 Puerto Rica BM (Dryopteris) S

Hart 172 Jamaica BM (fig. 190) S

T.nevadensis (Eaton) Clute:

Mrs. Austin s.n. California BM (Nephrodium) (fig. 113) S

T.nipponica (Fr. et Sav.) Ching:

Ogata 281 Japan BM S

Hutoh 18181 Honshu, Japan BM (fig. 145) S

T.nockiana (Jenm.) Proctor:

T4584 Jamaica N (fig. 76) S

T.nothofageti (Holttum ined.):

T7486 New Guinea BM (Pronephrium) A (TYPE)
T8670 New Guinea BM (Pronephrium) A
T8786 New Guinea BM (Pronephrium) A
Jermy 4043 New Guinea BM (Pronephrium) A

T.noveboracencis (L.) Nieuwl.:

Maré-Klorian and Rolland-Gormaine 55282 Quebec BM (Dryopteris) (fig. 112) S

T.novoguineensis (Brause) Reed:

T8247 New Guinea BM A

T.nudisora (Holttum ined.):

T12269 Sulawesi BM (Sphaerostephanos) A (TYPE)

T.obliterata (Sw.) Proctor:

W2 Kew (cult.) West Indies N (fig. 168) S A

T.ochropteroides (Bak.) Proctor:

Spruce 4661 Puerto Rica BM (Dryopteris) S

T.oligocarpa (Maxon) Proctor:

T1462 Jamaica N A
T5286 Jamaica N (fig. 75) S
T10674 Trinidad N C
T10688 Trinidad N C

T.omiensis (Bak.) Ching:

Petelot 5207 Tonkin BM (Cyclosorus levellei) S

T.opposita (Vahl) Ching:

Broadway 5997 Trinidad BM (Dryopteris) (fig. 91) S

T.ornata (Wall.) Ching:

S.S. plants s.n. (ex herb. Hooker 1840) 'South Seas' BM (Dryopteris)(fig. 107) S

T.pachyrachis (Kunze) Ching:

J.Sm s.n. (1886) Jamaica BM (Lastrea horizontalis)(fig. 89) S

T.paleata (Copel.) Holtt.:

Brooks 68.S Sumatra BM (Dryopteris) (figs. 136 & 222) S

T.paludosa (Bl.) K.Iwats.:

Jermy 5232 New Guinea BM A

T.palustris Schott:

Horning s.n. N (Lastrea) (figs. 124 & 213) S
M.Hutoh 17943 Honshu, Japan BM (Phegopteris) S
Forbes 17 Japan BM (D.thelypteris) S
Tagawa and Iwatsuki 1995 Japan BM S
S.n. Kew (cult.) N A

T.papilio (Hope) K.Iwats.:

Angus, Campbell and Hope s.n. N.W. India BM (Nephrodium) (fig. 155) S

T.parasitica (L.) K.Iwats.:

Iwatsuki 4926 Japan BM (Cyclosorus) (fig. 178) S

T.patens (Sw.) Small:

T1076 Jamaica N (figs. 154 & 217) S

T.patentipinna (Holttum ined.) :

T8476 New Guinea BM (Pneumatopteris) A

T.pauciflora (Hook.) Reed:

Germaine 5296 Belgian Congo BM (Dryopteris) S

T.paucijuga (Kl.) Proctor:

T6240 Trinidad N A
T10626 Trinidad N (fig. 192) S
Jermy 2457 Trinidad N A
Fay 370a West Indies N

T.pectiniformis (C.Chr.) Ching:

Scortechium s.n. Perak BM (Nephrodium gracilescens var. glanduligera) (fig. 117) S

T.penangiana (Hook.) Reed:

Zimmerman 2056 Nepal BM (Dryopteris) (fig. 183) S

T.pennigera (G,Forst.) Allan:

K.Wood s.n. North Is. New Zealand BM (Cyclosorus) (fig. 153) S

T.pentaphylla (Rosenst.) Reed:

T7482 New Guinea BM (Cyclosorus) A
T9351 New Guinea BM (Cyclosorus) A
T9355 New Guinea BM (Cyclosorus) A

T.petelotii Ching:

Viellard 534 Indo-China BM (Dryopteris petiolata) S

T.phegopteris (L.) Slosson:

B.King s.n. (4.9.82.) Merionith N (Polypodium) S
Komarow 11 Manchuria BM (Polypodium) S
S.n. Tanfield N (Polypodium) (figs. 93 & 211) S
Lister 187 Newfoundland BM (Dryopteris) S
Rainsford-Hanning 32 Finnish-Lapland BM (Dryopteris) S

T.poiteana (Bory) Proctor:

T1798 Jamaica N
T1799 Jamaica N S
T10892 Trinidad N (fig. 165) S

T.polycarpa (Bl.) K.Iwats.:

Brooks 3828 Sumatra BM (Mesochlaena) (fig. 187) S

T.polypodioides (Hook.) Holttum:

Elmer 9889 Phillippines BM (Macrothelypteris) (fig. 109) S

T.pozoi (Lagasca) Morton:

Schelpe 5114 Natal BM (Dryopteris africana) (fig. 127) S
Kido 1859 Japan BM (Leptogramma mollissima) S
Oti 15510 Japan BM (Leptogramma mollissima) S

T.prolifera (Retz.) Reed:

Forbes 2257 N.India BM (Dryopteris) S
Stainton, Sykes and Williams 4184 Nepal BM (Ampelopteris) (figs. 202 & 214) S
105/65 Kew (cult.) New Guinea N A

T.pubescens (L.) Proctor:

Maxon and Killip 1352 Japan BM S

T.pyrimidata (Fée) —

T6198 Trinidad N (Cyclosorus) A

T.pyrrhorhachis (Kze.)-:

Schelpe 3605 Punjab, India BM (Pseudophegopteris late-repens) (fig. 97) S

T.quadrangularis (Fée) Schelpe:

Johnston 1323 San Jose Is. Panama BM (Dryopteris) (fig. 174) S

Adams 317 Ghana BM (Dryopteris) S

T.quelpaertensis (Christ) Ching:

Ogata 284 Japan BM (fig. 119) S

T.rectangularis (Zoll.) Holttum:

Molesworth-Allen 2239 Pahang BM S

T.reptans (Gmel.) Morton:

T1204P Jamaica N

T1536 Jamaica N (fig. 169) S

T.resinifera (Gmel.) Morton:

T2707 Jamaica N (fig. 83) S

545/58 Kew (cult.) Jamaica N (fig. 115) S A

T.reticulata (L.) Proctor:

Harris 7420 Japan BM (Meniscium) (fig. 201) S

Lellinger 353 Dominica K

T1806 Jamaica N A

T7011 Jamaica N S A

Box 263 St. Kitts BM (Dryopteris) S

T.rodrigasiana (T.Moore) Reed:

T10165 New Guinea BM (Cyclosorus) A

T.rotundata

Fay 427 West Indies N

T.rubicunda (v.A.v.R.) K.Iwats.:

Brooks 232S Sumatra BM (Dryopteris) (fig. 151) S

T.rubra (Ching) K.Iwats.:

Linsley-Gressitt 1388 S.E. China BM (Dryopteris cuspidata) (fig. 180) S

T.rudis (Kunze) Proctor:

T5271 Jamaica N (fig. 74) S

Pringle 8920 Mexico BM (Phegopteris) S

T.sagittata (Sw.) Proctor:

T2259 Jamaica N (fig. 196) S

T.salicifolia (Wall. ex Hook.) Reed:

Wallisch 63 Penang BM (Meniscium) (fig. 200) S

T.sancta (L.) Proctor:

T2501 Jamaica N (fig. 78) S

T.sancta var. magna (Jenm.) Proctor:

T1286 Jamaica N (fig. 79) S

T.sclerophylla (Poepp.) Morton:

Curtiss 592 Cuba BM (Dryopteris) (fig. 167) S

T.scolopendrioides (L.) Proctor:

Palmer and Riley 393 Cuba BM (Dryopteris stenopteris) (fig. 189) S

T.sepikensis (Brause) —

T7980 New Guinea BM (Cyclosorus) A

T.serra (Sw.) R.P. St. John:

Maxon 4130 Cuba BM (Dryopteris) S

T4219 Jamaica N (figs. 131 & 223) S

T1201 Jamaica N S

T5083 Kew (cult.) Jamaica N A

T.serrata (Cav.) Alston:

T2033/1 Jamaica N (fig. 203) S

T1077/2 Jamaica N S

Jermy 2362 Trinidad N A

T.serrulata (Sw.) Proctor:

T1274 Jamaica N (fig. 162) S

T.setigera (Bl.) O.Ktze.:

Bisset 823 Japan BM (Nephrodium) (fig. 111) S

S.n. Newcastle (cult.) West Indies N A C

T.simplex (Hook.) K.Iwats.:

Tagawa and Iwatsuki 2119 Ryukyu, Japan BM (Abacopteris) S

T.simulata (Davenp.) Nieuwl.:

Maxon 427 Maryland BM (Dryopteris) (fig. 116) S

T.singalanensis (Bak.) Ching:

Sirdair and Kiah 38614 Perak K (Metathelypteris) (figs. 122 & 212) S

T.squamaestipes (Clarke) Ching:

F.M.B.I. f256 Himalayas BM (Polypodium appendiculatum) (figs. 146 & 221) S

Fauri 179 Arisan BM (Dryopteris) S

T.striata (Schum.) Schelpe:

Andrews A1448 Sudan BM (Dryopteris stricta ?) S

T.sub-aurita (Tagawa) Tagawa:

Ogata 220 Formosa BM (Phegopteris) (fig. 96) S

T.sub-nigra (Brause) Ching:

T9822 New Guinea BM A

T.sub-ochthodes Ching:

Arao 30/3/59 s.n. Japan BM (Dryopteris) S

Rosenstock 60 China BM (Dryopteris) (fig. 139) S

T.sub-pubescens (Bl.) K.Iwats.:

S.n. No 65 Sarawak BM (Dryopteris) (fig. 176) S

T.sumatrana (Holttum) —

T8367 New Guinea BM (Pseudophegopteris) A C

T9978 New Guinea BM (Pseudophegopteris) A

T.superba (Brause) Reed:

Jermy 4154 New Guinea BM (Cyclosorus) A

T.taiwanensis (C.Chr.) K.Iwats.:

McClune 9664 Hainan BM (Dryopteris) (fig. 186) S

T.tetragona (Sw.) Small:

T1515 Jamaica N (fig. 179) S
T11029 Trinidad N C
Fay 233 West Indies N

T.thomsonii (Jenm.) Proctor:

T1176 Jamaica N A
T5272 Jamaica N (fig. 73) S
T5283 Jamaica N S
Proctor 23415 Jamaica BM (Dryopteris) S

T.tonkinensis (C.Chr.) Ching:

S.n. No. 3715 Japan BM (Dryopteris) (fig. 195) S

T.torresiana (Gaud.) Ching:

Elmer 9893 Phillippines BM S

T.torresiana var. calvata (Bak.) Holttum:

Kido 1873 Japan BM (T.oligophlebia var. elegans) S
M.Ogata 107b Linkiu BM (Dryopteris oligophlebia) (fig. 106) S

T.totta (Thunb.) Schelpe:

Lakela 30672 Florida BM S

T.triphylla (Sw.) K.Iwats.:

722/54 Kew (cult.) Ceylon N (Cyclosorus) (fig. 158) S A
Iwatsuki 4920 Japan BM (Abacopteris) S

T.truncata (Poir.) K.Iwats.:

Giles 498/65 N.Borneo K (Cyclosorus) (figs. 156 & 220) S A

T.underwoodiana (Maxon) Proctor:

T4415 Jamaica N (fig. 87) S

T.unita (L.) Morton:

T8430 New Guinea BM (Cyclosorus) A

T.unita var. papillifera Holttum:

T8430 New Guinea BM (Cyclosorus) A

T.uraiensis (Ros.) Ching:

Tagawa and Iwatsuki 3245 Japan BM (fig. 140) S

T.urophylla (Wall.) K.Iwats.:

Robinson and Kloss 195 Sumatra BM (Polypodium) (fig. 182) S

T.varievestita (C.Chr.) Reed:

T8810 New Guinea BM A

Jermy 4146 New Guinea BM A

T.venusta (Hew.) Proctor:

T1936 Jamaica N (fig. 161) S

T.venusta var. usitata (Jenm.) Proctor:

T2469 Jamaica N (fig. 164) S

T.vestigiata (Copel.) Reed:

Jermy 4987 BM (Cyclosorus) A

T.viridifrons Tagawa:

Tagawa 7912 Kyoto, Japan BM (fig. 108) S

T.vivipara (Raddi) Reed:

Hochne 646 Brazil BM (Dryopteris) (fig. 193) S

T.walkeri (Holttum ined.):

T9980 New Guinea BM (Pneumatopteris) A (TYPE)

T.womersleyi (Copel.)

T7468 New Guinea BM (Cyclosorus) A

T.wrightii (Mett.) Reed:

C.Wright 824 Cuba BM (Aspidium) (fig. 147) S

T.xylodes (Kunze) Ching:

Hooker and Thompson 248 Madras BM (figs. 138 & 224) S

T12326 Sulawesi N A

T.yunkweiensis (Ching) Ching:

Petelot 3642 Indo-China BM (Dryopteris) (fig. 102) S

The following as yet unidentified Thelypterids were also examined:

T6130 Trinidad BM A

T6198 Trinidad BM A

T8277 New Guinea BM A

T8527 New Guinea BM C

T8529 New Guinea BM C

T8689 New Guinea BM A

T8880 New Guinea BM C

T10272 New Guinea BM C

T10312 New Guinea BM C

T10555 New Guinea BM C

T11483 Java BM A

T12185 Sulawesi BM A

T12326 Sulawesi BM A

T12374 Sulawesi BM A

T12759 Java BM A

Jermy 2235 New Guinea BM C

Jermy 4041 New Guinea BM A

Jermy 4683 New Guinea BM A

Jermy 4990 New Guinea BM A

Jermy 5255 New Guinea BM A

Page 2243 Mauritius N A S

Page 2475 Mauritius N A S

Page 3641 Australia N A

GYMNOCARPIUM

G.dryopteris (L.) Newm.:

Gt. Britain s.n. N (Polypodium) (fig. 204) S

Brignal Banks, Yorks. s.n. N (Polypodium) S

s.n. Moor Bank, Newcastle (cult.) Teesdale N A

G.robertianum (Hoffm.) Newm.:

R.B.B. 28/7/33 Arncliffe, Yorks, N (Polypodium calcaretum) (fig. 205) S

O.L. Gilbert s.n. Yorkshire (1968) N A

G.jessoensis (Koidz.) Koidz.:

Hutoh 19411 Japan BM (fig. 206) S

OTHER GENERA

Dryopteris nothochlaena Maxon:

T2619 Jamaica N S

D.lurida (Underw. and Maxon) Proctor:

Maxon and Killip 455 Jamaica BM S

T2221 Jamaica N (Polystichopsis) S

D.funesta

T6431 Trinidad N A

Polystichopsis rudis

T5434 Jamaica N A

Hypodematium crenatum (Forssk.) Kuhn:

M.Ogata 182 Formosa BM (H.onustum) S

Monachosorium sub-digitatum (Bl.) Kuhn:

Colani 2737 Indo-China BM S

APPENDIX III

SYNOPSIS OF THE MAJOR SYSTEMS OF CLASSIFICATION OF THELYPTERIS SENS. LAT.

C. Christensen 1913

FAMILY: Polypodiaceae

GENUS: Dryopteris

SUB-GENUS

1. Eudryopteris C. Chr.
2. Stigmatopteris C. Chr.

SECTION

i. Eustigmatopteris

ii. Peltochlaena

---

3. Ctenitis C. Chr.
4. Lastrea Bory.
5. Glaphyropteris (Presl) C. Chr.
6. Steiropteris C. Chr.
7. Cyclosorus Link
8. Leptogramma J.Sm. emend C. Chr.
9. Goniopteris (Presl) C. Chr.

i. Asterochlaena

---

ii. Eugoniopteris

10. Meniscium Schreb.

H.Ito 1939

FAMILY: Polypodiaceae

SUB-FAMILY: Dryopteroideae

GENUS:
1. Hypodematium Kuhn
2. Thelypteris Schmid.

SECTION
i. Euthelypteris
ii. Parathelypteris H.Ito
iii. Metathelypteris H.Ito
iv. Macrothelypteris H.Ito

3. Glaphyropteris Presl
i. Euglaphyropteris
ii. Cyclogramma (Tagawa) H.Ito

4. Phegopteris (Presl) Fée
i. Euphegopteris
ii. Lastrella H.Ito

5. Gymnocarpium Newm.
i. Eugymnocarpium
ii. Currania (Copel.) H.Ito

6. Leptogramma J.Sm.

7. Cyclosorus Link

8. Meniscium Schreb.
i. Eumeniscium
ii. Goniopteridopsis H.Ito

R.C. Ching 1940

FAMILY: Thelypteridaceae

TRIBE I: Thelypterideae

GENUS 1. Thelypteris Schmid.

2. Lastreopsis Ching

3. Hypodematium Kunze

4. Glaphyropteris Presl

5. Parapolystichum (Key.) Ching

6. Leptogramma J.Sm.

TRIBE II: Goniopterideae

1. Cyclosorus Link

2. Stegnogramma Bl.

3. Goniopteris Presl

4. Abacopteris Fée

5. Meniscium Schreb.

TRIBE III: Dictyoclineae

1. Dictyocline Moore

FAMILY: Sphaerostephanaceae

1. Sphaerostephanos J.Sm.

S. Momose 1942

SUB-FAMILY: Thelypteridoideae

GENUS

1. Dryoathyrium Ching
2. Gymnocarpium Newm.
3. Currania Copel.
4. Phegopteris (Presl) Fée

SUB-GENUS

i. Euphegopteris-type
ii. P.bukoensis-type

5. Macrothelypteris H.Ito
6. Metathelypteris H.Ito
7. Parathelypteris H.Ito
8. Thelypteris Schmid.

i. Euthelypteris
ii. T.beddomei-type

9. Glaphyropteris Presl sensu H.Ito
10. Lastreopsis Nakai nom. nud., non Ching 1938
11. Leptogramma J.Sm.
12. Cyclosorus Link
13. Meniscium Schreb. sensu H.Ito
14. Dictyocline Moore

R.C. Ching 1963

FAMILY: Thelypteridaceae

TRIBE A: Thelypterideae

SUB-TRIBE I Thelypteridineae

GENUS 1. Thelypteris Schmid.

2. Lastrea Bory

3. Parathelypteris (H,Ito) Ching

SECTION i. Parathelypteris

SERIES a) Nipponicae Ching

b) Glanduligerae Ching

ii. Melanostipes Ching

a) Japonicae Ching

SUB-SERIES x) Hirsutipedes Ching

y) Japonicae Ching

b) Castaneae Ching

4. Metathelypteris (H.Ito) Ching

5. Hypodematium Kunze

SUB-TRIBE II Phegopteridineae Ching

6. Macrothelypteris (H.Ito) Ching

7. Phegopteris (Presl) Fée

8. Pseudophegopteris Ching

9. Cyclogramma Tagawa

10. Leptogramma J.Sm.

TRIBE B: Goniopterideae Ching

SUB-TRIBE I Pseudocyclosorineae Ching

11. Glaphyropteridopsis Ching

12. Pseudocyclosorus Ching

13. Mesoneuron Ching

SUB-TRIBE II Cyclosorineae Ching

14. Cyclosorus Link

15. Stegnogramma Bl.

SUB-TRIBE III Goniopteridineae Ching

16. Ampelopteris Kunze

SUB-TRIBE IV Meniscineae Ching

17. Abacopteris Fée

TRIBE C: Dictyoclineae Ching

18. Dictyocline Moore

K. Iwatsuki 1964

FAMILY: Thelypteridaceae

GENUS I: Stegnogramma Bl.

SECTION i. Leptogramma (J.Sm.) K.Iwats.

ii. Haplogramma K.Iwats.

iii. Stegnogramma Bl.

iv. Dictyocline (Moore) K.Iwats.

GENUS II: Thelypteris Schmid.

SUB-GENUS 1. Phegopteris Presl

SECTION i. Phegopteris

ii. Lastrella (H.Ito) K.Iwats.

2. Cyclogramma (Tagawa) K.Iwats.

3. Thelypteris Schmid.

i. Thelypteris

ii. Metathelypteris H.Ito

4. Cyclosoriopsis K.Iwats.

5. Glaphyropteris (Presl) Alston

6. Glaphyropteridopsis (Ching) K.Iwats.

i. Glaphyropteridopsis

ii. Mesoneuron (Ching) K.Iwats.

iii. Neocyclosorus K.Iwats.

7. Steiropteris (C.Chr.) K.Iwats.

8. Cyclosorus (Link) Morton

9. Sphaerostephanos (J.Sm.) K.Iwats.

10. Haplodictyum (Presl) K.Iwats.

11. Pneumatopteris (Nakai) K.Iwats.

i. Pneumatopteris

ii. Macrocyclosorus K.Iwats.

—

SUB-GENUS 12. Abacopteris (Fée) K.Iwats.

13. Dimorphopteris (Tagawa and K.Iwats.) K.Iwats.

14. Cyrtomiopsis K.Iwats.

GENUS III: Meniscium Schreb.

i. Asterochlaena (C.Chr.) K.Iwats.

ii. Goniopteris (Presl) K.Iwats.

iii. Ampelopteris (Kunze) K.Iwats.

iv. Meniscium Schreb.

BIBLIOGRAPHY

ALSTON, A.H.G., (1959) "The ferns and fern allies of West Tropical Africa" in The Flora of West Tropical Africa, 2nd Ed., London.

ANDERSEN, S.T., (1960) "Silicone oil as a mounting medium for pollen grains". Danm. geol. Unders. Ser. 4, 4 (1): 24.

ATKINSON, L.R., and STOKEY, A.G., (1964) "Comparative morphology of the gametophyte of homosporous ferns". Phytomorphology, 14: 51-70.

BASECKE, P., (1908) "Beiträge zur Kenntuis der Physiologischen Scheiden der Achsel und Wedel der Filicineen sowie über den Ersatz des Korkes bei dieser Pflanzengruppe". Bot. Ztg., 66: 25-87.

BIR, S.S., (1966-7a) "The role of spore morphology in the taxonomy of the family 'Aspleniaceae'." Palynological Bulletin, 2: 3-11

BIR, S.S., (1966-7b) "Correlation between spore size and polyploid level in the Himalayan Asplenioid and Athyrioid ferns". J. Palynol., 2-3: 41-48.

BIR, S.S., (1969) "The stelar anatomy of Diplazium latifolium Moore". Am. Fern J., 59 (1): 23-26.

BLASDELL, R.F., (1963) "A monographic study of the fern genus Cystopteris". Mem. Torrey bot. Club, 21 (4): 1-102.

BOWER, F.O., (1910) "Studies in the phylogeny of the Filicales I. Plagiogyria". Ann. Bot., 24: 427 (footnote).

BOWER, F.O., (1923) The Ferns Vol. I. Cambridge University Press.

BREBNER, G., (1895) "On the mucilage canals of the Marattiaceae". J. Linn. Soc. (Bot.), 30: 444-451.

BREBNER, G., (1902) "On the anatomy of Danaea and other Marattiaceae". Ann. Bot., 16: 523.

BROWN, C.A., (1960) "What is the role of spores in fern taxonomy?" Am. Fern J., 50 (1): 6-14.

BROWNLIE, G., (1954) "Introductory note to cytotaxonomic studies of New Zealand ferns". Trans. R. Soc. N.Z., 82: 665-666.

BROWNLIE, G., (1958) "Chromosome numbers in New Zealand ferns". Trans. R. Soc. N.Z., 85: 213-216.

BROWNLIE, G., (1961) "Additional chromosome numbers of New Zealand ferns". Trans. R. Soc. N.Z. (Bot.), 1:1-14.

BROWNLIE, G., (1965) "Chromosome numbers in some Pacific Pteridophyta" Pacific Science, 19: 493-497.

BUSCALIONI, L., (1917) "Sui trichoma della Felci con particolare riguando alle parafisi". Malphigia, 28: 163-178; 545-554; pls. 3-4.

CHANDA, S., (1966) "On the pollen morphology of the Centrolepidaceae, Restionaceae and Flagellariaceae with special reference to taxonomy". Grana palynol., 6 (3): 355-415.

CHIARUGI, A., (1960) "Tavole chromosomiche delle Pteridophyta". Caryologia, 13: 27-150.

CHING, R.C., (1936) "A revision of the Chinese and Sikkim-Himalayan Dryopteris with reference to some species from neighbouring regions". Bull. Fan. Mem. Inst. Biol. (Bot.), 6: 237-352.

CHING, R.C., (1938) "A revision of the Chinese and Sikkim-Himalayan Dryopteris with reference to some species from neighbouring regions". Bull. Fan. Mem. Inst. Biol. (Bot.), 8: 157-268.

CHING, R.C., (1940) "On the natural classification of the family 'Polypodiaceae'." Sunyatsenia, 5: 201-268.

CHING, R.C., (1963) "A reclassification of the family Thelypteridaceae from the mainland of Asia". Acta Phytotax. Sinica, 8: 289-335.

CHRISTENSEN, C., (1913) "A monograph of the genus Dryopteris, Part I - The Tropical American pinnatifid-bipinnatifid species". K. danske Vidensk. Selsk. Skr. 7 (10): 55-282.

CHRISTENSEN, C., (1919) "A monograph of the genus Dryopteris, Part II - The Tropical American bipinnate-decompound species". K. danske Vidensk. Selsk. Skr., 8 (6): 1-123.

CHRISTENSEN, C., (1938) in VERDOORN, F., (1938) Ch. 20 p. 522-550.

CLAPHAM, A.R., TUTIN, T.G., and WARBURG, E.F., (1962) Flora of the British Isles, 2nd. Ed., Cambridge.

COLOMB, (1888) "Essai d'une classification des Fougères de France basée sur leur étude anatomique et morphologique". Bull. Soc. bot. Fr., 35: 102.

COPELAND, E.B., (1929) "The oriental genera of Polypodiaceae" Univ. Calif. Publs. Bot., 16: 44-128.

COPELAND, E.B., (1947) Genera Filicium Waltham, Mass, U.S.A.

CRABBE, J.A., JERMY, A.C., and WALKER, S., (1970) "The distribution of Dryopteris assimilis S. Walker, in Britain". Watsonia, 8: 3-15.

CRANE, F.W., (1953) "Spore studies in Dryopteris, I". Am. Fern J., 43 (No. 4): 159-169.

CRANE, F.W., (1960) "A key to American Dryopteris species based on characters of the perispore". Am. Fern J., 50(No 4): 270-274.

CUSHING, E., (1961) "Size increase in pollen grains mounted in thin slides". Pollen Spores, 3: 265-274.

DAVIE, R.C., (1914) "The pinna-traces in the ferns". Trans. R. Soc. Edinb. 50(2): 348-378.

DAVIE, R.C., (1918) "A comparative list of fern pinna-traces with some notes on the leaf-trace in the ferns". Ann. Bot., 32: 223-245.

DAVLIANIDZE, N., (1965) "Morfologija spor Kavkazskich predslavilelej roda Dryopteris Adans." Zametski Sist. Geogr. Rost., 24: 35-40.

EAMES, A.J., and MACDANIELS, L.H., (1947) An introduction to plant anatomy, 2nd. Ed., New York.

ECHLIN, P., (1968) "Pollen" Scient. Am., 218(4): 81-90.

ERDTMAN, G., (1947) "Suggestions for the classification of fossil and recent pollen grains and spores". Svensk bot. Tidskr., 41: 104-114.

ERDTMAN, G., (1952) "Pollen morphology and plant taxonomy - Angiosperms". Chronica bot., 1: 3.

ERDTMAN, G., (1959) Pollen and spore morphology/plant taxonomy Gymnospermae, Pteridophyta, Bryophyta. (An introduction to Palynology II) p. 1-151, Almqvist and Wiksell, Stockholm.

ERDTMAN, G., (1960) "The acetolysis method - A revised description". Svensk bot. Tidskr., 51: 561-564.

ERDTMAN, G., BERGLUND, B., and PRAGLOWSKI, J., (1961) "Introduction to a Scandinavian pollen flora". Grana Palynol., 2(3): 1-92.

ERDTMAN, G., and PRAGLOWSKI, J., (1959) "Six notes on pollen morphological technique". Notiser Lunds Botan. Foren, 112: 175-184.

ESAU, K., (1965) Plant Anatomy, 2nd. Edit., New York.

FABBRI, F., Ed. (1963) "Primo supplemento alle 'Tavole chromosomiche delle Pteridophyta' de Alberto Chiarugi". Caryologia 16: 237-335.

FABBRI, F., Ed. (1965) "Secundo supplemento alle 'Tavole chromosomiche delle Pteridophyta' de Alberto Chiarugi". Caryologia, 18: 675-731.

FAEGRI, K., and DEVSE, P., (1960) "Size variation in pollen grains with different treatments". Pollen Spores, 2: 239-304.

FERNALD, M.L., and WEATHERBY, C.A., (1929) "Schmidel's publication of Thelypteris". Rhodora, 31: 21-26.

FUCHS, C., (1963) "Fuchsin staining with Sodium Hydroxide clearing for lignified elements of whole plants or plant organs". Stain Technol., 38(3): 141-144.

FUCHS, H.P., (1963) "Nomenklatorische Liste der in Ungaren vorkommenden Gefäss Kryptogamen". Acta bot. hung., 9: 11-20.

GARDINER, W., and ITO, T., (1887) "On the structure of the mucilage-secreting cells of Blechnum occidentale L. and Osmunda regalis L.". Ann. Bot., 1: 27-54.

GHATAK, J., (1962) "Observations on the cytology and taxonomy of some ferns from India". Nucleus, Calcutta, 5: 95-114.

GOEBEL, K., (1926) "Morphologische und biologische studien VIII Ueber Schleinfarne und Aërophore". Ann. J. bot. Btzg., 36: 84-106 (not seen).

GUTTENBERG, H. von., (1935) "Studien an Pflanzen der Sunda-Insel III. Histologische - Cytologische studien an Tropenfarnen". Ann. J. bot. Btzg., 44: 42-58. (not seen).

GWYNNE-VAUGHAN, D.T., (1903) "Observations on the anatomy of solenostelic ferns". Ann. Bot., 17: 694.

HAGENAH, D.G., (1961) "Spore studies in the genus Cystopteris I: The distribution of Cystopteris with non-spiny spores in North America". Rhodora, 63: 181-193.

HANKS, S., and FAIRBROTHERS, E., (1970) "Effects of preparation technique on pollen prepared for scanning electron microscope observations". Taxon, 19(6): 879-886.

HARRIS, W.F., (1955) "A manual on the spores of New Zealand pteridophyta". Bull. N.Z. Dept. sci. ind. Res., 116: 1-186.

HENNIPMAN, E., (1968) "The mucilage secreting hairs on the young fronds of some leptosporangiate ferns". Blumea, 16: 97-103.

HIRES, E.S., (1965) Spores, Ferns, Microscopic illusions analysed, Vol. I, Millburn, New Jersey; Mistaire Laboratories.

HOFMEISTER, W., (1851) Vergleichende Untersuchungen der Keimung Entfaltung und Fruchtbildung höherer Kryptogamen und der Samenbildung der Coniferen. Leipsig. (not seen).

HOLTTUM, R.E., (1947) "A revised classification of the Leptosporangiate ferns". J. Linn. Soc. (Bot.), 53: 123-158.

HOLTTUM, R.E., (1949) "The classification of ferns". Biol. Rev., 24: 267-296.

HOLTTUM, R.E., (1951) "The fern genus Pleocnemia". Reinwardtia, 1: 171-189.

HOLTTUM, R.E., (1954) Flora of Malaya, Vol. II Ferns of Malaya, Singapore.

HOLTTUM, R.E., (1960) "Vegetative characters distinguishing the various groups of ferns included in Dryopteris of Christensen's Index Filicum and other ferns of similar habit and sori". Gdns' Bull., Singapore, 18: 361-367.

HOLTTUM, R.E., (1968) "Nomina conservanda proposita 229: Thelypteris". Taxon, 17: 330-331.

HOLTTUM, R.E., (1969) "Studies in the family Thelypteridaceae. The genera Phegopteris, Pseudophegopteris and Macrothelypteris". Blumea, 17: 5-32.

HOLTTUM, R.E., SEN, U., and MITTRA, D., (1970) "Studies in the family Thelypteridaceae II. A comparative study of the type species of Thelypteris Schmidel, Cyclosorus Link and Ampelopteris Kunze". Blumea, 18(No 1): 195-215.

HOLUB, J., (1969) "Oreopteris, a new genus of the family Thelypteridaceae" Folia geobot. phytotax., Praha, 4: 33-53.

ITO, H., (1939) "Polypodiaceae, Dryopteridoideae I" in Nakae and Honda 1939. Nova Flora Japonica, 4.

ITO, T., and GARDINER, W., (1887) "On the structure of the mucilage cells of Blechnum occidentale and Osmunda regalis". Proc. R. Soc., 42: 353-355.

IWATSUKI, K., (1962a) "On the venation of the thelypterid ferns". Acta Phytotax. Geobot., 20: 219-227. (in japanese)

IWATSUKI, K., (1962b) "The trichomes of the thelypterid ferns". Mem. Coll. Sci. Kyoto Univ. Ser. B, 29: 103-111.

IWATSUKI, K., (1963a) "Taxonomic studies of Pteridophyta VII". Acta Phytotax. Geobot., 19: 112-126. (in japanese)

IWATSUKI, K., (1963b) "Taxonomy of the thelypterid ferns, with special reference to the species of Japan and adjacent regions. I General considerations". Mem. Coll. Sci. Kyoto Univ. Ser. B, 30(3B): 21-50.

IWATSUKI, K., (1964a) ibid. "II Circumscription of the group". Mem. Coll. Sci. Kyoto Univ. Ser. B, 31(1B): 1-10.

IWATSUKI, K., (1964b) ibid. "III Classification". Mem. Coll. Sci. Kyoto Univ. Ser. B, 31(1B): 11-40.

IWATSUKI, K., (1964c) "Taxonomic studies of pteridophyta VIII. 10 classification of the genus Thelypteris s.l.". Acta. Phytotax. Geobot., 21: 35-42.

IWATSUKI, K., (1965) "Taxonomy of the thelypterid ferns, with special reference to the species of Japan and adjacent regions. IV Enumeration of the species of Japan and adjacent regions". Mem. Coll. Sci. Kyoto Univ. Ser. B, 31(3B): 125-197.

JOHANSEN, D.A., (1940) Plant Microtechnique. McGraw Hill Book Co. Inc. New York and London.

KACHROO, P., (1957) "Gametophytes of Cyclosorus molliusculus (Wall.) Ching and C.moulmeinensis (Bedd.) Copel.". Sci. Cult., 23.

KACHROO, P., (1963) "Morphology of the gametophyte of Cyclosorus moulmeinensis". J. Indian bot. Soc., 42(2): 190-194.

KARPOWICZ, W., (1960) "A comparative study on the species of the genera Dryopteris and Thelypteris occuring in Poland". Acta. Soc. Bot. Pol., 29(2): 175-189.

KENNETH, J.H., (1960) A Dictionary of Scientific Terms. Ed. HENDERSON I.F. and HENDERSON J.H. 7th Ed. London.

KLEKOWSKI Jr., E.J., (1967) "Observations on Pteridophyte life cycles: Relative lengths under cultural conditions". Am. Fern J., 57(2): 49-51.

KNOX, E.M., (1951) "Spore morphology in British ferns". Trans. Proc. bot. Soc. Edinb., 35: 437-448.

KONDO, T., (1962) "A contribution to the study of fern stomata". Fac. Educ. Shizuoka Univ. Bull., 13: 239-267.

KRAMER, P.J., (1945) "Absorption of water by plants". Bot. Rev., 11: 310-355.

KUHN, R., (1889) "Arbeiten aus dem botanischen Institut zu Marburg, V. Untersuchungen über die Anatomie der Marattiaceen und anderer Gefässkryptogamen". Flora, 72: 457-504. (not seen)

KUPRIANOVA, L.A., (1948) "Pollen morphology and the phylogeny of the Monocotyledons". Comm. Komarov Inst. Acad. Sci.1:7 (not seen) (in russian).

LARSON, D.A., (1964) "Processing pollen and spore walls for electron microscopy". Stain Tech., 39: 237-243.

LAWRALÉE, A., (1950) Floré Generale de Belgique "Pteridophytes" IV, 1-95. Ministèr d'agriculture, Jardin Botanique de l'Etat, Bruxelles.

LÖVE, A., and LÖVE, D., (1966) "Cytotaxonomy of the alpine vascular plants of Mount Washington". Univ. Colo. Stud. Ser. Biol., 24.

LÖVE, A., and LÖVE, D., (1967) "New combinations in Carpogymnia" Taxon, 16: 191-192.

LOYAL, D.S., (1961) "Cytological studies on Himalayan Thelypteridaceae, I. Cytology of Thelypteris Schmid." Proc. 48th Indian Sci. Congr. Pt. III: 265-266.

LUGARDON, B., (1963) "Les spores des Pteridacées de France". Pollen Spores, 5: 325-336.

LUTZ, L., (1898) "Sur l'origine des canaux gommifères des Marattiacées". J. Bot., 12: 33-35.

McVAUGH, R., (1935) "Spores of some North-Eastern ferns" Am. Fern J., 25: 73-85.

MADALSKI, J., (1954) Atlas Flory Polskiej I Ziem Ościennych, 1(1). Polska Akademia Nank. Warszawa. (not seen)

MAKINO, T., (1949) An Illustrated Flora of Japan, Rev. Ed. Tokyo.

MANTEN, A.A., (1959) "Pollen grains size and its value in palynology". Acta. bot. neerl., 8(3): 369-371.

MANTON, I., (1950) Problems of cytology and evolution in the Pteridophyta. Cambridge Univ. Press. London.

MANTON, I., (1953) "The cytological evolution of the fern flora of Ceylon". Symp. Soc. exp. Bot. (Evolution), 7: 174-185.

MANTON, I., (1954) "Cytological notes on one hundred species of Malayan ferns" in HOLTTUM, R.E., (1954).

MANTON, I., (1959) "Cytological information on the ferns of West Tropical Africa" in ALSTON, A.H.G., (1959).

MANTON, I., and SLEDGE, W.A., (1954) "Observations on the cytology and taxonomy of the pteridophyte flora of Ceylon". Phil. Trans. Roy. Soc. (London), 238(B): 127-185.

MITUI, K., (1968) "Chromosomes and speciation in ferns" Sci. Rep. Tokyo Kyoiku Daig., Sec. B, 13: 285-333.

MOHL, H., VON, (1835) "Sur la structure et les fermes des grains de pollen". Ann. Aci. Nat. Bot. II, 3: 148.

MOMOSE, S., (1937-42) "Studies on the gametophyte of ferns I - XXIX". J. Jap. Bot., 13-18.

MORTON, C.V., (1963a) "Some West Indian species of Thelypteris". Am. Fern J., 53(2): 57-70.

MORTON, C.V., (1963b) "The classification of Thelypteris" Am. Fern J., 53(4): 149-154.

MORTON, C.V., (1966) "Some new combinations in Thelypteris". Am. Fern J., 56(4): 177-179.

MORTON, C.V., (1967) "Studies of fern types I". Bull. U.S. Nat. Mus., Cont. from U.S. Nat. Herbarium, 38(2): 29-83.

NAGAI, I., (1915) "On the influence of nutrition upon the development of sexual organs in the fern prothalli". J. Coll. Agric. imp. Univ. Tokyo, 6: 121-164.

NAGAI, I., (1919) "The correlation in the differentiation of sex in fern prothallia". Bot. Mag., Tokyo, 33: 157-170.

NAYAR, B.K., (1960) "The gametophyte and young sporophyte of Athyrium esculentum". Am. Fern J., 50: 194-203.

NAYAR, B.K., and CHANDA, P., (1963) "Observations on the morphology of the gametophyte of Cyclosorus". J. Indian Bot. Soc., 42: 392-400.

NAYAR, B.K., and DEVI, S., (1963) "Spore morphology of some Japanese Aspidiaceae". Pollen Spores, 5(2): 355-372.

NAYAR, B.K,, and DEVI, S., (1964) "Spore morphology of Indian ferns I. Aspidiaceae". Grana Palynol., 5(1): 80-120.

NAYAR, B.K., and KAUR, S., (1963) "Spore morphology of some Indian members of the Lomariopsidaceae". Pollen Spores, 5: 87-89.

NEWMAN, E., (1851) "Genus Gymnocarpium". Phytologist, 4: 371. (not seen)

NIEUWLAND, J.A., (1910) "Dryopteris - a synonym". Am. Midl. Nat., 1: 224-226. (not seen)

OGURA, Y., (1921) "On the gaps in the stele of some Polypodiaceae". Bot. Mag., Tokyo, 35: 113-125.

OGURA, Y., (1927) "On the structure of Diplazium esculentum (Retz.) Sw." Bot. Mag., Tokyo, 41: 172-180.

OGURA, Y., (1938) "Anatomie der Vegetationsorganie der Pteridophyten" in LINSBAUR, K., ed. Handbuch der Pflanzenanatomie, II Abt. Band. VII, 2 Tiel B. Berlin.

OLIVER, J.C., (1968) "A study of spore characteristics of the ferns of Indiana". Am. Fern J., 58(1): 5-11.

ORTH, R., (1936) "Morphologie und physiologische Untersuchungen an Farn prothallien". Planta, 25: 104.

PELOURDE, F., (1906) "Recherches anatomiques sur la classification des Fougères de France". Ann. Sci. nat. (Bot.), Ser. IX, 4: 281-372.

PELOURDE, F., (1909) "Recherches comparatives sur la structure des Fougères fossiles et vivantes". Ann. Sci. nat. (Bot.), Ser. IX, 10: 115-147.

PETTITT, J.M., (1966) "A new interpretation of the structure of the megaspore membranes in some Gymnospermous ovules". J. Linn. Soc. (Bot.), 59: 253-263 and pls. 1-4.

PICHI-SERMOLLI, E.G., (1953) "The nomenclature of some fern genera". Webbia, 9(2): 387-454.

PIRARD, N., (1947) "Sporanges, paraphyses et organes connexes chez les Fougères". Cellule, 51: 155-184 and pls. 2-3.

PRAGLOWSKI, J., (1970) "The effects of pre-treatment and the embedding media on the shape of pollen grains". Rev. Palaeobotan. Palynol., 10: 203-208.

PRESL, C.B., (1836) Tentamen Pteridographiae. Prague (not seen)

PRIESTLEY, J.H., and RADCLIFFE, F.M., (1924) "A study of the endodermis in the Filicinae". New Phytol., 23(4): 161-193.

PROCTOR, G.R., (1953) "A preliminary check-list of Jamaican Pteridophytes" Bull. Inst. Jamaica, 5: 1-89.

PROCTOR, G.R., (1961) "Notes on Lesser Antillean ferns I". Rhodora, 63: 31-35.

PROCTOR, G.R., (1966) "Notes on Lesser Antillean ferns II". Rhodora, 68: 464-469.

PUNT, W., (1962) Pollen morphology of the Euphorbiaceae with special reference to taxonomy. North Holland, Amsterdam. 116 p.

REED, C.F., (1942) "Comparative morphology of spores in ferns and its relationship to taxonomy". PhD Thesis, Harvard. Unpub.

REED, C.F., (1950) "Morphology of fern spores and its relation to taxonomy". Am. J. Bot., 37: 673-674.

REED, C.F., (1954) "Spores, sporangia and indusia of the genus Dryopteris in North America, north of Mexico". Bartonia, 27: 47-56.

REED, C.F., (1968) "Index Thelypteridis". Phytologia, 17: 249-328.

ROSS, R., (1966) "General Committee, 1964-1969. Report No. 1". Taxon, 15: 286-287.

SCHMELZEISEN, W., (1933) "Beitrage zur Entwicklungsgeschichte der prothallien einiger Marattiaceen, Cyatheen und Polypodiaceen". Flora, 127: 46-80.

SELLING, O.H., (1946) "Studies in Hawaiian pollen statistics part 1. The spores of Hawaiian pteridophytes". B.P. Bishop Mus. spec. Pub., 37: 1-87.

SHIVAS, M.G., (1969) "A cytotaxonomic study of the Asplenium adiantum-nigrum complex". Br. Fern Gaz., 10(2): 68-80.

SKVARLA, J.J., and LARSON, D.A., (1964) "An electron microscope study of pollen morphology in the Compositae, with special reference to the Ambrosiniiae". Grana Palynol., 6(2): 210-269.

SORSA, P., (1964) "Studies of the spore morphology of Fennoscandian fern species". Ann. Bot. Fenn., Helsinki, 1: 179-201.

SPORNE, K.R., (1962) The morphology of Pteridophytes. Hutchinson, London.

STOKEY, A.G., (1951) "The contribution by the gametophyte to classification of the homosporous ferns". Phytomorphology, 1: 39-58.

STOKEY, A.G., (1960) "Multicellular and branched hairs on the fern gametophyte". Am. Fern J., 50: 78-87.

TAGAWA, M., (1959) Index Pteridophytorum Japanicorum. Tokyo.

TANSLEY, A.G., (1907-8) "Lectures on the evolution of the Filicinean vascular system". New Phytol., 7(1): 1-16; 7(2): 29-40.

TARDIEU-BLOT, M-L., (1932) "Les Aspleniées du Tonkin". Bull. Soc. Hist. nat. Toulouse, 64: 193-384.

TARDIEU-BLOT, M-L., (1954) Cryptogamia - Pteridophytes. p. 1-107. Paris.

TARDIEU-BLOT, M-L., (1963a) "Sur les spores de Lindsaeaceae and Dennstadtiaceae de Madagascar et des Mascareignes, étude de palynologie apliquée à la systématique". Pollen Spores, 5: 69-86.

TARDIEU-BLOT, M-L., (1963b) "Sur les spores de Pterideae malgaches". Pollen Spores, 5: 337-354.

THOMAE, K., (1886) "Die Blattstiele der Farne. Ein Beitrag zur vergleichenden Anatomie". Jb. wiss. Bot., 17: 99-161. (not seen)

TROLL, W., (1933) "Botanische Mitteilungen aus den Tropen, IX. Dryopteris sumatrana v.A.v.R., ein neur Schleinform aus dem ostindischen Archipel". Flora, 128: 329-337.

TRYON, A.F., (1965) "Trichomes and Paraphyses in ferns". Taxon, 14(7): 213-214.

TRYON, R.M., (1965) "Paraphyses in the ferns". Taxon, 14(7): 215-218.

VAN COTTHEM, W., (1970) "Comparative morphological study of the stomata in the Filicopsida". Bull. Jard. bot. Nat. Belg., 40: 81-239.

VERDOORN, F., Ed., (1938) Manual of Pteridology. Martinus Nighoff, The Hague.

WAGNER Jr., W.H., (1954) "The evidences used in recent classifications of ferns". Proc. int. Bot. Cong. VIII, Paris, 4: 9-15.

WAGNER Jr., W.H., (1961) "Problems in the classification of ferns". in Recent advances in Botany, 1: 841-844.

WAGNER Jr., W.H., (1963) "A biosystemmatic survey of U.S. ferns. Preliminary abstract". Am. Fern J., 53: 1-16.

WAGNER Jr., W.H., (1964) "Paraphyses : Filicineae". Taxon, 13(2): 56-64.

WAGNER Jr., W.H., (1965) "Fern paraphyses : Comments on recent papers". Taxon, 14(9): 299-302.

WAGNER Jr., W.H., (1966) "New data on North American Oak Ferns : Gymnocarpium". Rhodora, 68: 121-138.

WALKER, T.G., (1964-5) "A cytotaxonomic survey of the pteridophytes of Jamaica". Trans. R. Soc. Edinb., 66(9): 169-237.

WEST, C., (1915) "On the structure and development of secreting tissue in the Marattiaceae". Ann. Bot., 29: 409-422.

WODEHOUSE, R.P., (1926a) "Pollen grain morphology in the classification of the Anthemideae". Bull. Torrey bot. Club, 53: 479-485.

WODEHOUSE, R.P., (1926b) "Morphology of pollen grains in relation to plant classification". J. N.Y. bot. Gdn., 27: 145-154.

WODEHOUSE, R.P., (1928a) "Pollen grains in the identification and classification of plants, I. The Ambrosiaceae". Bull. Torrey bot. Club, 55: 181-198.

WODEHOUSE, R.P., (1928b) "The phylogenetic value of pollen grain characters". Ann. Bot., 42: 891-934.