

A MONOGRAPH OF THE  
FERN GENUS BOLBITIS  
(Lomariopsidaceae)

E. HENNIPMAN

Rijksherbarium, Leiden



1977  
LEIDEN UNIVERSITY PRESS

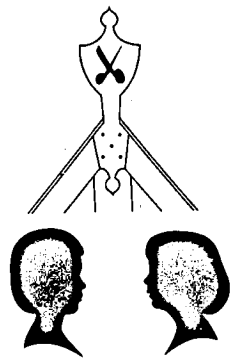
*Published with financial support from the Netherlands Organization for the Advancement of Pure Research (Z.W.O.).*

ISBN 90.6021.405.6.

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Printed in the Netherlands by Intercontinental Graphics.

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*Aan Alexander en Annemieke*

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## **General Part**

## 1. INTRODUCTION AND SUMMARY

The present study deals with systematic and taxonomic problems in the acrostichoid fern genus *Bolbitis* (*Lomariopsidaceae*). The idea came from Prof. Holttum, Kew, in view of his intended revision of the lomariopsidoid ferns for Flora Malesiana.

Originally the study was confined to the Asian representatives. However, various problems remained unsolved after the study of these taxa alone, and it was decided to monograph the genus.

The taxonomy of the genus *Bolbitis* was seriously misunderstood in the past—parallel evolution obscuring true relationships—and a rather intricate synonymy has resulted. A brief historical sketch of its taxonomic adventures is worked out.

The gross-morphological criteria used for the discrimination of the species by Copeland (who revised the Asian representatives in 1928) and Ching (who revised ser. *Egenolfianae* in 1931) could not be applied satisfactorily to the ample material at hand. Therefore, several features of the sporophyte were analyzed in detail, including rhizome- and petiole-anatomy, venation pattern and spore-morphology. The results are described and discussed.

Further, the possible occurrence of hybridization and polyploidization was investigated. For this purpose a collection of different species was taken into cultivation and their mitotic and/or meiotic chromosome number and behaviour recorded. A limited number of species could also be studied in the field. From several species significant information on the morphology of the juvenile leaf stages could be obtained.

As could be demonstrated the delimitation of the genus as given especially by Ching (in Christensen, 1934) is largely correct, though he included the species with anastomosing veins only. A number of Ching's species, however, are excluded and referred to non-lomariopsidoid genera. Also, in a few cases, species from other genera are here included in the genus for the first time. As most of the taxa under discussion were formerly included in *Leptochilus*, this genus was critically investigated as well. The results will be published separately. The genus *Bolbitis* as here defined and emended includes the genera *Egenolfia* and *Edanyoa*.

Fourty-four species (one of which new) and 13 hybrids (12 of which new) are recognized, based on morphological criteria. The venation pattern and the spores provide important characters. In some species infraspecific categories are listed. Identification keys to all taxa are included. The genus is subdivided into 10 series which accommodate a total of 34 species; another ten species are separately listed mostly in view of their suspected hybrid origin.

Hybrids could be detected because of structural irregularities, especially in spores, but usually also as to other features. Putative hybrids between cytotypes of one species are not separately listed. Generic and/or specific delimitation differs considerably from that given by Ching (in Christensen, 1934), Christensen (1934), Holttum (1954), and Copeland (1960); the latter eventually recognized 97 different species in four different genera (*Stenosemia dimorpha* included).

Notes are given on specific delimitation. Data are supplied which stress the evo-

lutionary importance of polyploidization, hybridization, vegetative propagation, and the retention of juvenile characters, factors that may explain the often fascinating diversity found within many species.

The study of ontogenetic leaf stages (which may be very different from adult ones) has received great attention after it was understood that at least part of the variation as found in the adult sterile leaves recalls features found in the juvenile leaves. The relation between ontogeny and phylogeny is shortly discussed. Some facts are given which support my impression that the retention of juvenile characters may have played an important role during the diversification within the genus.

Some general considerations about the probably great general significance of the retention of juvenile characters for the past diversification of the leptosporangiate ferns are included. It is postulated that the recognition of this neglected phenomenon may add considerably to our understanding also of the larger groups of leptosporangiate ferns.

## 2. ACKNOWLEDGEMENTS

It is a pleasure to express my gratitude to Prof. Dr. C. G. G. J. van Steenis, who appointed me as a pteridologist at the Rijksherbarium, and under whose stimulating directorship the present study was largely completed. I had the privilege that Prof. Dr. R. E. Holttum took an interest in my work; he has been (and still is!) very helpful in various ways.

Specific subjects were discussed with staff members at Leiden, which include Dr. R. C. Bakhuizen van den Brink (nomenclature) who also prepared the Latin diagnoses, Dr. Ding Hou (karyology), Dr. P. W. Leenhouts (general), Mr. J. Muller (spore-morphology), and Dr. W. Vink (editing).

Technical assistance was received from Miss Ruth van Crevel (illustrations), Mr. A. K. Groenewegen and staff (loans of specimens), Mr. B. N. Kieft (photography), Mr. D. N. F. Kiehl (proof-reading), Miss A. M. Kuenen (microtechnique, photography), Mr. A. Mulder (cultivation), Miss E. E. van Nieuwkoop (typing), Mr. E. Vijsma (drawings; lay-out of plates), and Mr. L. Vogelzang and staff (bibliography). S.E.M.-photographs could be made due to the valued co-operation with the Netherlands Organization for Applied Scientific Research TNO (Miss R. N. Hooftman), and the Geological Institute, Leiden (Mr. H. Kammeraat).

Several correspondents from overseas sent living plants of quite a few species. Amongst them is Mr. M. G. Price who sent all the Philippine plants recorded here, and to whom I am especially indebted.

Prof. Dr. I. Manton (Leeds) and Dr. T. G. Walker (Newcastle-upon-Tyne) permitted me to include a few unpublished records on chromosome numbers.

Dr. L. R. Atkinson (Amherst, Mass.) kindly put at my disposal the notes on gametophytes of *Bolbitis* species prepared by the late Dr. A. G. Stokey and herself.

Although several European herbaria (Berlin, Brussels, Kew, London, and Paris) could be visited personally, a considerable number of specimens were received on loan from these and other herbaria for quite a period, due to the kind co-operation of their Directors. My stay at Berlin was financed by the Netherlands Organization for the Advancement of Pure Research (Z.W.O.).

Constructive criticism on (parts of) the manuscript was received from Mr. G. J. de Joncheere, Prof. Dr. C. Kalkman, Prof. Dr. K. U. Kramer (Zürich), and Prof. Dr. C. G. G. J. van Steenis.

I tender my sincere thanks to these persons and to all others who took an active interest in my work.

## 3. MATERIAL AND METHODS

### Material

The far greater part of the specimens studied is located in the following herbaria (the abbreviations refer to the standard abbreviations of the Index Herbariorum):



A	The Arnold Arboretum of Harvard University, Cambridge, Mass.
B	Botanisches Museum, Berlin-Dahlem.
BKF	The Forest Herbarium, Bangkok.
BM	British Museum (Natural History), London.
BO	Herbarium Bogoriense, Bogor.
BR	Jardin Botanique de l'Etat, Bruxelles.
C	Botanical Museum and Herbarium, Copenhagen.
F	Chicago Natural History Museum, Chicago, Ill.
G	Conservatoire et Jardin botaniques, Genève.
GH	Gray Herbarium of Harvard University, Cambridge, Mass.
K	The Herbarium and Library, Royal Botanic Gardens, Kew.
L	Rijksherbarium, Leiden.
M	Botanische Staatssammlung, München.
MICH	University Herbarium, University of Michigan, Ann Arbor, Mich.
MO	Missouri Botanical Garden, Saint Louis, Mo.
NY	The New York Botanical Garden, New York, N.Y.
P	Muséum National d'Histoire Naturelle, Laboratoire de Phanérogamie, Paris.
PNH	Philippine National Herbarium, National Museum, Manila.
S	Botanical Department, Naturhistoriska Riksmuseet, Stockholm.
SING	Herbarium of the Botanic Gardens, Singapore.
S-PA	Palaeobotanical Department, Swedish Museum of Natural History, Stockholm.
UC	Herbarium of the University of California, Berkeley, Cal.
US	United States National Museum, Department of Botany, Washington, D.C.
W	Naturhistorisches Museum, Wien.

In addition, smaller quantities of specimens were studied from:

BISH	Bernice P. Bishop Museum, Honolulu, Hawaii.
BLAT	Blatter Herbarium, St. Xavier's College, Bombay.
BRI	Botanic Museum and Herbarium, Brisbane.
CAHUP	College of Agriculture, University of the Philippines, Laguna.
CAL	Central National Herbarium, Calcutta.
DS	Dudley Herbarium, Stanford University, Stanford, Cal.
GL	Department of Botany, University of Glasgow, Glasgow.
IJ	Science Museum, Institute of Jamaica, Kingston, Jamaica.
—	Private herbarium Mr. G. J. de Joncheere, Wassenaar.
LAE	Division of Botany, Department of Forest, Lae, Papua New Guinea.
LDS	Botany Department, The University, Leeds.
LP	Museo de la Plata, División de Plantas Vasculares, La Plata.
LWG	National Botanical Gardens, Lucknow.
NSW	National Herbarium of New South Wales, Sydney.
TI	Botanical Institute, Tokyo.
TO	Instituto Botanico della Università, Torino.
U	Botanical Museum and Herbarium, Utrecht.
WAG	Laboratory for Plant Taxonomy and Plant Geography, Wageningen.
Z	Botanischer Garten und Institut für Systematische Botanik der Universität Zürich.

Some taxa were studied in the field during a botanical expedition to Thailand, 1965/1966; living material of several species was cultivated at the Botanic Garden, Leiden.

A considerable part of the specimens studied comprise so-called duplicates. Phanerogamists sometimes object to studying duplicates as they are said not to provide anything new. This may sound sensible when large Angiosperms (trees!) are concerned. However, when studying *Bolbitis* specimens, it was found very informative to see duplicates as they give often a better idea of the usually large variation between

specimens from a particular site. They further afford a better chance for studying characters not always present on all sheets (e.g. rhizome, mature spores).

## Methods

### Scales

Scales were brushed with a strong solution of a detergent (Kodak, Photo-Flo 200) in water (Kramer, 1957), and after washing in water embedded in glycerine jelly.

### Rhizome and petiole

To obtain sections of the rhizome and petiole from herbarium material, pieces of petiole and rhizome were softened in polyvinyl lactophenol (Edward Gurr, Ltd.; for details see Van Brummelen, 1967) for 24 hours at 60°C. After washing in distilled water the material was sectioned with a slide microtome (Reichert) using razor blades. Sections were embedded in glycerine jelly. By these methods the (presumed) natural condition of the material could be reconstructed rather easily.

For anatomical studies of living material, small pieces of material were preserved in F.A.P.A. (formaline 40%: 5; glacial acetic acid: 2.5; propionic acid: 2.5; alcohol 50%: 90), for 24 hours or longer. A routine histological paraffine procedure was followed. Sections were stained with saffranine followed by fast green.

### Venation pattern

For the present study it became necessary to develop a method which made it possible to obtain a large number of magnified illustrations of the venation pattern in a short time. The method applied was based on the idea that liquid-stored cleared parts of the leaves show sufficient contrast between the veins and the tissues in between, for using these parts as negatives (without grains!) in an enlarger. For this purpose a special jar of similar size as the negative holder of an enlarger, holding the material in a flat position, was devised. The method used did not make it necessary to stain the xylem elements for contrast (as is usually done). Besides, many patterns of any magnification could be recorded on photographic paper in a short time.

#### *a. Clearing of (parts of) the leaves*

1. Boil the herbarium material during 5 minutes in water to which a few drops of a detergent are added.
2. Fix in F.A.P.A. during 24 hours at room temperature.
3. Replace F.A.P.A. by chloro-lactophenol (chloralhydrate: 1, lactophenol: 1) to which a small amount of hydroxyperoxide ( $H_2O_2$ ) is added. Store for 2 or 3 days at 60°C. The amount of hydroxyperoxide depends on the quality of the herbarium

material. In well-dried specimens it can be omitted. When too much hydroxyperoxide is added the cleared material can suffer from air bubbles which then have to be evacuated.

4. Replace by pure chloro-lactophenol. Store for 1 to 3 days at 60°C.
5. Rinse in several changes of distilled water.
6. Proceed through graded alcohol to alcohol 50% in which it can be stored until used for photography.

The material may be still of a light brown colour after this treatment. This does not affect its use, provided there is reasonable contrast between the veins and the remaining parts.

7. Dry the material and remount it on the herbarium sheet.

#### *b. Projection photography of cleared parts*

The cleared parts were put into a jar made of plexiglass of similar sizes as the negative holder of a Liesegang 'Raja' enlarger. Representative areas up to 9 cm long were recorded on photographic paper (Agfa-Gevaert BH 1).

The square jar (see fig. 1) consists of a basal part with supports situated at the inside corners, apart from a cover which is resting upon the supports and is provided with vertical flanges somewhat remote from the margin. The supports of the basal part are hook-shaped (following the corners) and composed of two 'steps', each 3 mm tall and 6 mm broad, the lowest one of which faces the jar's interior. The cover rests on the lowest step of the supports at each corner, thus leaving a narrow slit along the margin between the supports and between the outside margin of the cover and the inside wall of the basal part. Addition or removal of liquid through these slits is easy as the flanges on the cover prevent possible excessive liquid to spread over the cover. The slits also allow long materials to project through the slits beyond the jar. The actual jar which contains the liquid (evacuated alcohol 50%) is thus only 3 mm tall.

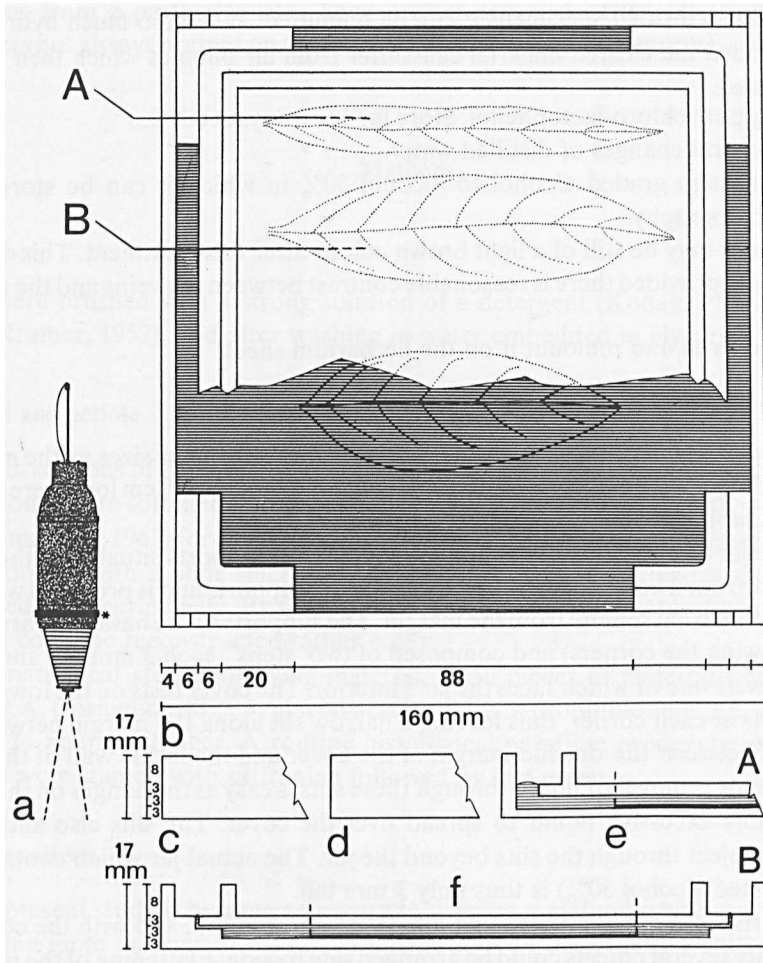
Cleared parts were arranged in the jar filled with some liquid, and with the cover removed. Usually several objects could be arranged side by side. Flattening of the material was readily obtained using thin pieces of glass of different sizes (the different kinds of object slides do well). When fixing the cover one has to avoid the inclusion of large air bubbles. After the adjustment of the right amount of liquid the jar is ready for use in the enlarger. The equipment of the enlarger devised for frames of 6 × 9 cm was applied. To prevent too much spreading of light through the jar during magnification, the jar's outside were painted black.

Good prints showing (details of) the venation pattern could then be readily obtained. Representative photographs are given in plate 1. For the present study the standard magnification of the venation pattern was four times.

In spite of its liquid contents the jar appeared to be quite handy in use.

#### *c. Drawings*

For publication in the Taxonomic Part, a selection of the photographs were exposed to transmitted light, and the venation pattern copied on translucent paper. Afterwards the drawings were reduced five times.



*Fig. 1.* Schematic drawings of the jar used for projection photography of cleared pinnae or laminas.—a. enlarger, the asterisk indicates the location of the jar in the enlarger; b–d. different views of the jar; b. view from above; c. part of frontal view; d. part of lateral view; e, f. cross-sections at A and B resp. of fig. b. For further information see text.

## Spores

Spores of herbarium material were transferred to glycerine jelly after wetting with alcohol 96%. A representative selection of the material of each species was studied. In addition, some samples of different species were weakly acetolyzed following routine procedures.

The different types of spores as seen with the light microscope were also studied with a Cambridge S.E.M. (scanning electron microscope). For this purpose spores were directly taken from the herbarium material, fixed to a standard aluminium specimen

stub with double-stick Scotch tape, and coated with evaporated gold shortly before examination at 10 or 20 kV.

Cross-sections of sporangia and spores were obtained from F.A.P.A.-fixed (sporangia) or from dried material (spores) after sectioning in ice in a kryostate at  $-30^{\circ}\text{C}$ . The sections, mounted on a specimen stub of the S.E.M., were dried at room temperature prior to coating.

### Chromosomes

Manton (1950) gives an ample discussion about the techniques that can be applied to record the mitotic and meiotic chromosome number. The following technique is basically similar:

1. Pretreat with alpha-bromonaphtalen in distilled water (ABN) during 24 hours at  $5^{\circ}\text{C}$ ; only applied when necessary.
2. Fix in Carnoy's solution (alcohol 100%: 3, glacial acetic acid: 1) for at least 5–10 minutes at room temperature. In this solution it can stay for one or two days at room temperature, or much longer at  $-20^{\circ}\text{C}$ .
3. Hydrolyze in a solution of equal parts of absolute hydrochloric acid and absolute alcohol for one to several minutes at room temperature.
4. Wash in two changes of Carnoy's solution.
5. Stain in acetocarmine for at least 10 minutes at room temperature.
6. Squash a selected piece of material under a cover slip. Remove excessive dye and seal with paraffine. A sufficient spreading of the chromosomes was sometimes difficult to achieve. The application of a mixture of pectinase and cellulase (Kawano, 1965) did not improve the results markedly.
7. Photograph the suitable plates using phase contrast microscopy when necessary.

Vouchers of the author's counts are at Leiden, those of Manton and Walker—which are published here for the first time—at K and the BM, respectively. The subsequent numbers of Walker's collections of *B. quoyana* have all been included. The morphological heterogeneity of the vouchers excludes the possibility of their being parts of one clone.

### Microscopy

The preparations were studied with a binocular microscope (Leitz, 'Greenough') and/or a light microscope (Leitz, 'Laborlux'). Photographs of microscopic preparations were made with a photomicroscope (Leitz, 'Ortholux').

### Drawings of outlines of the leaves

The outline drawings in the Taxonomic Part were all made at natural size from dried specimens, then reduced five times.

## Cultivation

The cultivation of tropical lowland ferns in a greenhouse with only limited facilities in a temperate area is a matter of trial and error. I have persisted in my attempts to grow living material in view of the presumed contribution of cytological, morphological, and anatomical studies to the taxonomy of the present genus.

The best results with the cultivation of sporophytes were obtained when the plants were grown in large terraria or in small houses of polyethylen within the greenhouses.

The specimens were potted in rocky soil composed of variously large pieces of lava-rock, apart from a mixture of about equal parts of chopped *Sphagnum*, coarse sand, and black peat.

During the winter period growth was slow or even absent. Sometimes the temperature in the greenhouses did not rise above 17°C for several weeks. Then measures had to be taken to prevent the atmosphere from becoming saturated which causes rapid moulding and rotting. Considerable changes in temperature between day-time and night-time, as well as between sunny and cloudy outside weather conditions, are regarded the most important factors causing untimely death of the specimens.

The majority of the specimens showed good or excellent growth during the summer period. Then most of the specimens could be vegetatively propagated in order to get sufficient material for carrying the species through the winter.

The Leiden greenhouses suffer from American cockroaches which were reasonably controlled by inundating the terraria at intervals during periods of good growth, or by trapping specimens in brown flasks with a narrow neck containing old fruit.

Spores of only a few species could be sown on sterilized soil, following routine procedures. Growth of the gametophytes is very slow; the cultures are easily affected by growth of bryophytes and fungi.

It is noted that in cultivation the plants may show aberrances which are not formed in the wild. A specimen of *Bolbitis crispatula* var. *copelandii* formed bipinnatifid and bipinnate leaves in cultivation, whereas the leaves of all the wild specimens of this taxon are simply pinnate.

## 4. TAXONOMIC HISTORY OF THE GENUS

The genus *Bolbitis* comprises acrostichoid ferns, i.e. ferns with separate fertile leaves the underside of which is fully covered with sporangia possessing a vertical annulus. The earliest authors, who used the shape of the sporangium, the shape of the sorus, and the presence or absence of an indusium as the main principles for classification, included the acrostichoid ferns all into the genus *Acrostichum* (e.g. Swartz, 1806; Willdenow, 1810). Kaulfuss (1824) placed two species with free veins in the genus *Gymnogramma*, a genus he created to accommodate the ferns with sporangia mainly or exclusively on the veins, and lacking an indusium.

The genus *Bolbitis* was established by Schott (1834) for a part of *Acrostichum* with a

creeping rhizome and anastomosing veins. He included '*B. serratifolia, virens, diversifolia, flagellifera, repanda, etc.*'. At the same time Schott accommodated a free-veined species in the genus *Egenolfia* (here united with *Bolbitis*) which included *Polybotrya sensu* Blume (1828). The genus *Polybotrya* was restricted by Schott to its present circumscription. The recognition of the Asian genus *Egenolfia*, separate from the American genus *Polybotrya*, is illustrative for the quality of his work. It was not until Ching (1931; in Christensen, 1934) that this classification was accepted.

Presl (1836) who used mainly anatomical characters and especially the venation pattern, merged *Egenolfia* with *Polybotrya*, both having free veins. The other species were placed in the genera *Poecilopteris*, *Campium*, and the two subgenera of *Gymnopteris*.

Smith (1841: 150) too listed the species with free veins under *Polybotrya*, the others composed the genus *Cyrtogonium* (a homotypic synonym of *Bolbitis*) and the minor part of *Gymnopteris*.

Fée (1845) was the first to monograph the acrostichoids. He based his work on the material present in the large herbaria in continental Europe; some of Wallich's species were not taken into consideration. Using the venation pattern and the leaf architecture as the more important characters, he divided the acrostichoids into 18 genera. The species of the genus *Bolbitis* in its present construction were classed in the genera *Polybotrya*, *Heteroneuron* (which included Presl's genera *Campium* and *Poecilopteris*, as well as *H. raddianum* = *Lomagrum guianensis*), *Gymnopteris*, and *Leptochilus* (one species). Later Fée (1850–1852) recognized the genus *Egenolfia*. Presl (1851), giving additions and emendations to the Tentamen (1836), placed the species in *Anapausia* (which was a subgenus of *Gymnopteris* in the Tentamen), *Poecilopteris*, *Campium*, and *Heteroneuron* (in a much narrower sense than Fée, 1845). Presl inferred that the features of the venation pattern would add much to the understanding of the classification: '... , darf man der Hoffnung Raum geben, dass man endlich in das geheimnisvolle Dunkel dieser wundervoll organisierten Gewächse eindringen wird.'

The systems proposed by Fée and Presl were in part artificial, and not convincing to Hooker (1861, opp. pl. 88): 'Notwithstanding the valuable labours of M. Fée and his excellent writings and figures of the *Acrostichaceae*, no group of Ferns requires more careful study and revision than this does. Species are, assuredly, too much multiplied, I fear on very slight grounds: and the multitude of Genera only serve to puzzle and perplex the student as well as the practical Pteridologist himself.'

Hooker (1864: 194) (and also Baker, in Hooker & Baker, 1865–1868) reverted to the classical conception and massed all acrostichoids into the genus *Acrostichum* which he subdivided into the subgenera *Egenolfia*, *Heteroneuron*, *Gymnopteris*, and *Leptochilus*; of these the three last also contained representatives of one or more other genera. Baker accommodated the species in the subgenera *Egenolfia*, *Gymnopteris* (in part), and *Chrysodium* (species which Hooker included in *Gymnopteris* and *Heteroneuron*).

J. Smith (1875) reinstated *Egenolfia* as a genus. The species with anastomosing veins were placed in the genera *Poecilopteris* and *Gymnopteris* (in part).

Classical authors used to place all or most of the acrostichoids as a separate group either at the beginning (J. Smith, 1875) or at the end of their classification (e.g. Hooker,

1864) of the '*Polypodiaceae*' (leptosporangiate ferns with a vertical annulus). Christ (1897) and Diels (in Engler & Prantl, 1899), however, referred all the acrostichoids with free veins again to *Polybotrya*, those with anastomosing veins to the genus *Gymnopteris* which included quite a variety of unrelated ferns as well, and both these unnatural genera were placed in the *Aspidiinae (Polypodiaceae-Aspidieae)* also comprising dryopteroid and tectarioid ferns. Underwood (1903) accommodated the present species of *Bolbitis* in *Egenolfia* and a heterogeneous *Anapausia*, including both in the *Polypodiaceae-Dryopterideae*, a group containing dryopteroid, thelypteroid and tectarioid ferns. Christensen (1904) followed Underwood, but correctly used the generic name *Leptochilus* for the assemblage named *Anapausia* by Underwood. He thought the genus *Leptochilus* to include mainly Old World species. Only a dozen species were said to occur in America which he referred to sect. *Bolbitis*, at the same time supplying a revision; the others he assembled later (1906) in sect. *Anapausia* and were regarded as 'essentially different'. *Leptochilus guianensis* (= *Lomagamma guianensis*) was included in sect. *Bolbitis* with misgivings; it possibly should be regarded 'a peculiar subgenus or even genus'. In the Index (Christensen, 1906) the species were placed in *Leptochilus* sect. *Bolbitis* and sect. *Anapausia*, and in sect. *Egenolfia* of *Polybotrya*. Both genera were included in the *Polypodiaceae-Aspidieae*.

Schumann (1915) followed Christensen, but regarded the *Leptochilus* species with pinnate leaves, such as *Leptochilus heteroclitus* (= *B. heteroclita*), as ex-indusiate derivatives of thelypteroid ('dryopteroid') ferns, whereas the species with simple leaves were thought to represent derivatives of *Polypodium* species. Although she based herself on but little material, her key is of interest as it also mentions features of the spores. Bower (1917, 1928) largely agreed with Schumann.

Copeland (1928) attempted to clear up the heterogeneous assemblage called *Leptochilus* by Christensen and *Gymnopteris* by Diels. He referred the American species of *Leptochilus sensu* Christensen to the genus *Bolbitis* which he thought to be derived from *Phlebodium* (polypodioid). These were not included in his revision. The greater part of the Old World species of *Leptochilus* were, together with representatives of other genera, transferred to the genus *Campium*, and thought to have evolved from Old World polypodioid ancestors with 'definite sori'. *Campium linnaeanum* (a dwarf of *B. heteroclita*) was regarded as the most primitive element of the genus. Other Old World species of *Leptochilus sensu* Christensen were classified in the genera *Leptochilus*, *Christiopteris*, *Lomagamma*, *Hemigramma*, and *Quercifilix*, a view now generally accepted.

Christensen (1931) agreed with Copeland to keep the American and the Old World species generically separate. He retained *Leptochilus* sect. *Anapausia* for the American species and accepted the genus *Campium* though in a somewhat different circumscription as he suggested to exclude from *Campium* the simple-leaved species that Schumann considered of polypodioid origin. According to Christensen the genus so construed was of thelypteroid affinity, and closely related to, or even congeneric with the genus *Egenolfia*. As regards the American species, Christensen thought *Leptochilus alienus* (= *B. aliena*), the type species of *Leptochilus* sect. *Anapausia*, to be derived from *Tectaria*, 'and it is also possible that certain Asiatic species, such as *L. [Leptochilus] diversifolius* [= *B.*



*sinuata*], have their nearest relatives among the species of *Tectaria*.' This shows Christensen's doubts as to the systematic position of these acrostichoids as dealt with by Copeland (the pinnate fern *Leptochilus diversifolius* being included by Copeland in the genus *Campium*).

Ching (1931) monographed the genus *Egenolfia*. He recognized nine species and added one variety. The genus was divided into two sections. Later (in Christensen, 1934), he referred Christensen's *Leptochilus* sect. *Anapausia* and part of Copeland's genus *Campium* to *Bolbitis*, thus largely delimiting the genus as circumscribed here. This I regard as an important advance. Christensen himself, in the same paper, also added several new combinations in *Bolbitis*, which shows his interest in the acrostichoids. He also stimulated Ching to make further studies in this group, as is suggested by Ching's later publication (1932). Ching apparently also attempted to monograph the genus *Bolbitis*; I found Ching's annotations on sheets present in the herbaria at Paris and Kew (including type sheets of several unpublished species).

Christensen (1938) regarded the genera *Bolbitis* and *Egenolfia* as probably related to the *Polypodiaceae-Dryopterideae* (i.e. to the dryopteroid and thelypteroid ferns).

Copeland (1947) qualified his earlier treatment of the acrostichoids (Copeland, 1928) as 'inexcusably bad' (which may be true as far as the genus *Campium* is concerned) and further agreed with Christensen (1938) as to the relationship of the genus *Bolbitis*.

Kramer (1954), following a suggestion of Holttum (1937), transferred *Lomagrumma guianensis*, a paraphysate species, to *Bolbitis*; it is here excluded.

Manton & Sledge (1954) identified *B. singaporensis* Holttum as a hybrid between *Egenolfia appendiculata* (= *B. appendiculata*) and *B. diversifolia* (= *B. sinuata*).

Iwatsuki (1959) revised the Japanese species and, following a suggestion of Christensen (1931), united the genera *Egenolfia* and *Bolbitis*. He divided the genus into four sections.

Nayar & Kaur (1964a, 1964b) published an elaborate but uncritical paper on the taxonomy of the species occurring in India based on but a few collections. In addition, they published a number of papers dealing with the morphology of these acrostichoids (for references see Kaur, 1974). They kept the genera *Bolbitis* and *Egenolfia* separate, also because of supposed differences in the shape of the perispore of the spores which was refuted by the present author (Hennipman, 1970). Kaur (1974) thought the genus *Bolbitis* (excluding *Egenolfia*) the most primitive member of the *Lomariopsidaceae* (including *Elaphoglossum*) which she regarded related to the tectarioid ferns.

Earlier studies on the acrostichoids (Hennipman, 1965, 1976) revealed the proper taxonomic alliance of *Leptochilus neglectus* (F. M. Bailey) C. Chr. (= *Pteridoblechnum neglectum* (F. M. Bailey) Hennipman), and *Leptochilus acuminatus* White & Goy (= *Pteridoblechnum acuminatum* (White & Goy) Hennipman). Detailed information on *Bolbitis macrophylla* (Kunze) Maxon & Morton (= *Thelypteris macrophylla* (Kunze) Morton) was made known to Mr. Morton, who accordingly transferred the species to its proper place (Morton, 1971).

As a result of floristic work by Christ, Copeland, Maxon & Morton, and Holttum (for references see the Taxonomic Part), a considerable number of new species were

described during this century. Copeland described 18 new species and one new genus which belong to the present genus; of these only one species is here retained.

## 5. MORPHOLOGY AND ANATOMY

### Introduction

Representatives of the present genus have been studied in detail by Schumann (1915), Bower (1917), and Nayar and collaborators (for references see Kaur, 1974).

Schumann studied *Leptochilus heteroclitus* (= *B. heteroclita*) and *Leptochilus cuspidatus* (= *B. repanda*) from living material at Munich. Bower studied the vascular organisation in the rhizome of *B.* ('*Leptochilus*') *nicotianifolia* and *B. repanda* ('*Leptochilus cuspidatus*'). The Indian representatives have been dealt with by Nayar *et al.* The works of the Indian authors contain much interesting and in part new information as was confirmed during the present study. However, their material represents only three of the ten series recognized. The names of the taxa used in their morphological studies are those as given in a kind of elaborate checklist of the Indian members (Nayar & Kaur, 1964a, 1964b). The latter publications are based on but very few collections, whereas the nomenclature of part of the species listed is incorrect; their taxonomic concepts differ much from those presented here.

It is further much regretted that their works include some distinctly erroneous observations such as those on the spores of *Bolbitis*, which consequently led them to recognize the genus *Egenolfia* as distinct (see Hennipman, 1970). The value of their publications is also marred by the fact that part of the material attributed by them to *Bolbitis* belongs to other genera. For instance, the bipinnate juvenile leaves reported to occur in certain *Bolbitis* species (of which I studied the juvenile leaves myself) do not belong to the present genus but presumably to *Microlepia* species (Nayar & Kaur, 1965b: pl. 2 facing p. 155). Further, a special kind of venation pattern, generally called diplodesmic, reported by them (Nayar & Kaur, 1966) to be found in the fertile leaf of *B. heteroclita* ('*B. subsimplex*'), actually does not occur in the reference sheet cited (kindly sent on loan), nor for that matter in the genus. They also described certain species as 'high-climbing' whereas in reality true Asian *Bolbitis* species do not conform to this mode of life. These erroneous observations play an important role in their ideas regarding the phylogeny of the lomariopsidoid ferns: 'From the evolutionary point of view, *Bolbitis* possibly is the more primitive genus in the family. It exhibits a tendency towards evolution of high climbing forms with special venation to supply sporangia in the fertile leaves (*B. subsimplex*); this might lead on to the high-climbing genera, as well as towards forms with a short, creeping, dorsiventral rhizome with simplification of venation pattern, leading to genera like *Egenolfia*.'

Speaking about classification in general, Holttum (1967) stated that there is still much confusion 'because the right kind of morphological knowledge is not all available, and because no one has yet discerned which kinds of such knowledge are most signifi-

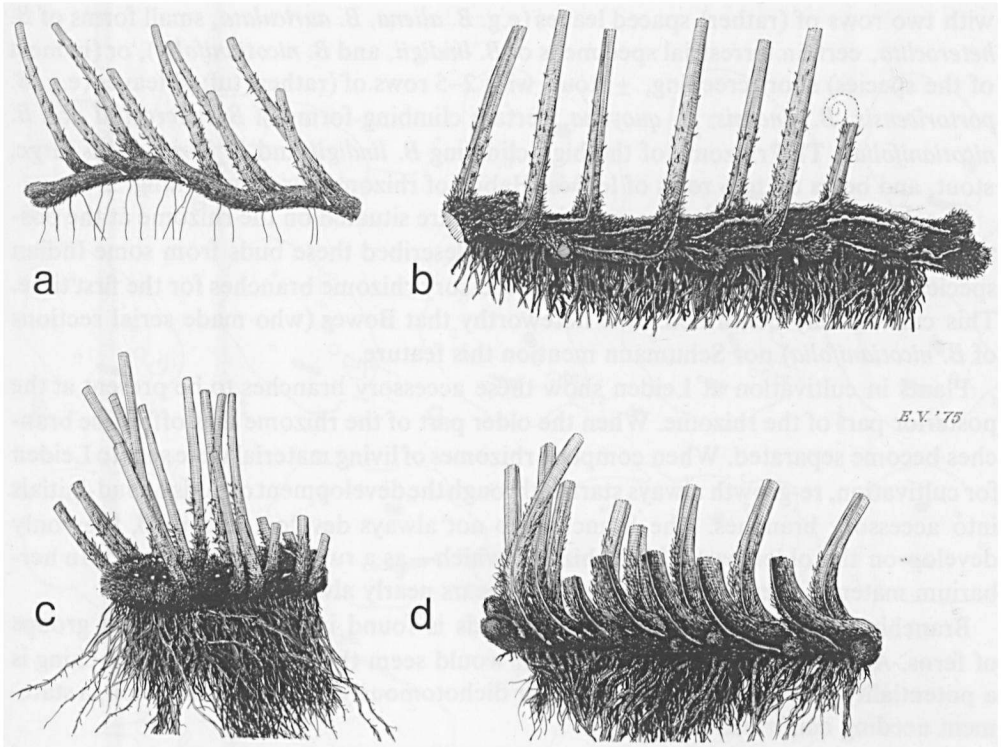


Fig. 2. Habits of rhizomes drawn from living material showing amongst other things aerophores and (in fig. b and d) accessory buds,  $\times 3/5$ .—a. *Bolbitis heteroclita*; b. *B. heudelotii*; c. *B. sinensis*; d. *B. sinuata* (a. *Hennipman* 4085; b. *H.* 4118; c. *H.* 4046; d. *H.* 4052).

cant in particular cases . . .'. The present chapter has been written in view of my agreement with that statement.

My observations on the rhizome and petiole have been taken from cross-sections of herbarium material of all the species of which adequate material was at hand, as well as from cross-sections of living material pickled in the field or cultivated. In several species from different series (except ser. *Lindigianae*) serial sections were studied in order to obtain information on the spatial arrangement of the vascular system. Indument, spores, and venation patterns were studied from all the species. Of only a few species gametophytes were obtained in cultivation.

### Rhizome

In most of the species the rhizome is creeping, usually on rocks or in rocky soil; in a few species it is either low- or—in some American species—high-climbing. The shape of the rhizome shows variation. The creeping rhizome may be long-creeping, slender,

with two rows of (rather) spaced leaves (e.g. *B. aliena*, *B. auriculata*, small forms of *B. heteroclita*, certain terrestrial specimens of *B. lindigii*, and *B. nicotianifolia*), or (in most of the species) short-creeping,  $\pm$  stout, with 2–5 rows of (rather) tufted leaves (e.g. *B. portoricensis*, *B. sinensis*, *B. quoyana*, certain climbing forms of *B. heteroclita* and *B. nicotianifolia*). The rhizome of the high-climbing *B. lindigii* and *B. bernoullii* is large, stout, and bears up to 6 rows of leaves. Habits of rhizomes are given in fig. 2.

In some species conspicuous spherical buds are situated on the rhizome at the posterior side of the leaf-bases. Nayar & Kaur described these buds from some Indian species, and reported development into accessory rhizome branches for the first time. This can be fully confirmed. It is noteworthy that Bower (who made serial sections of *B. nicotianifolia*) nor Schumann mention this feature.

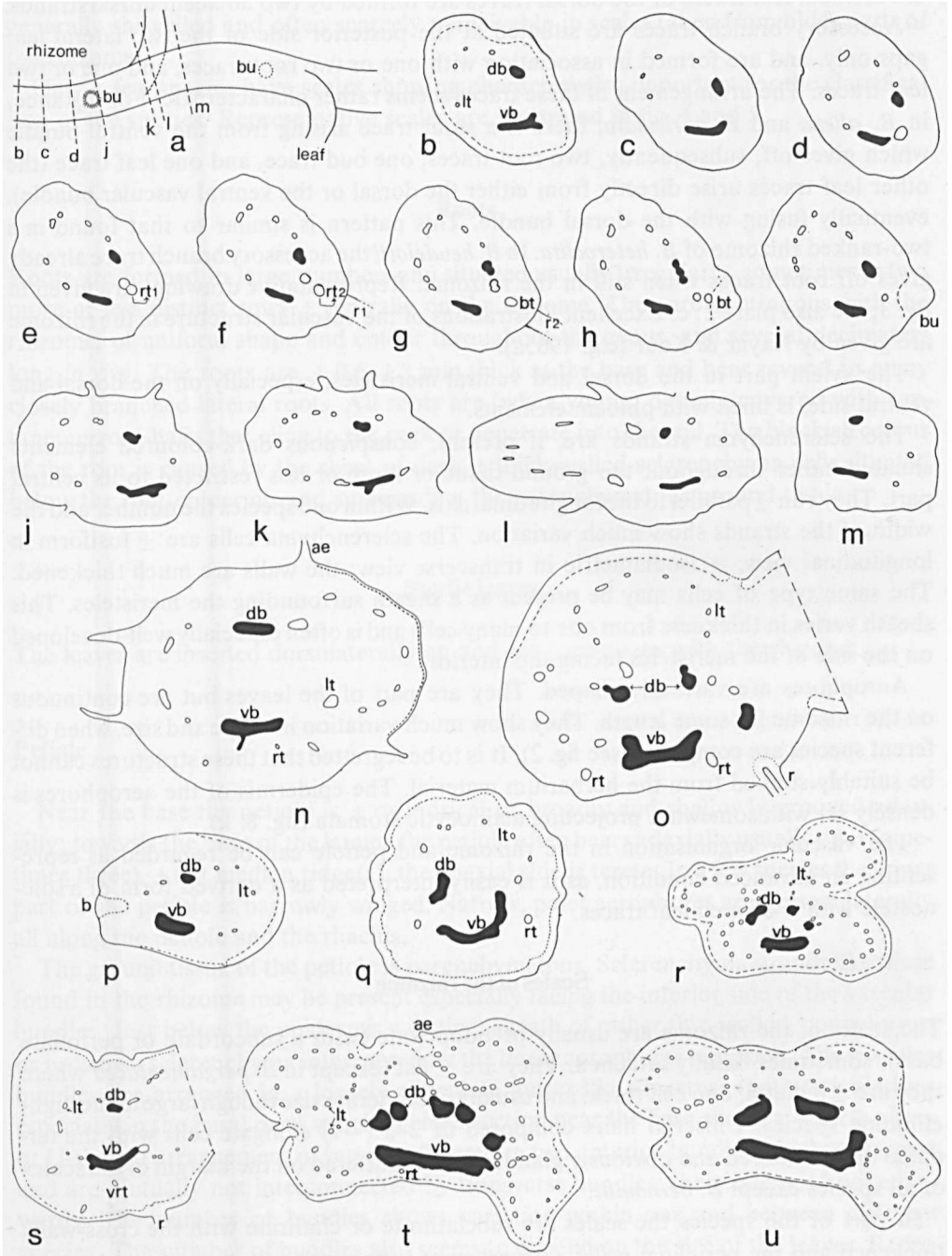
Plants in cultivation at Leiden show these accessory branches to be present at the posterior part of the rhizome. When the older part of the rhizome dies off, these branches become separated. When complete rhizomes of living material were sent to Leiden for cultivation, re-growth always started through the development of buds or bud-initials into accessory branches. The branches do not always develop, and if so, they only develop on the older part of the rhizome which—as a rule—is not collected. In herbarium material, therefore, the rhizome appears nearly always unbranched.

Branching due to the development of buds is found in several unrelated groups of ferns. According to Dickason (1946) it would seem that this mode of branching is a potentiality added to the unbranched or dichotomously branched condition, a statement needing confirmation.

The rhizome consists of parenchymatous ground-tissue in which the vascular and in many species also sclerenchyma strands are situated. In association with the leaves, a sheath of relatively thin-walled, often dark-coloured sclerenchyma cells may occur a few cells below the epidermis. Aerophores also associated with the leaves are present dorsally and laterally; in these places the sheath of sclerenchyma is interrupted.

The stele is a dorsiventral dictyostele (incorrectly called solenostele by Nayar & Kaur, 1965a), a characteristic of all lomariopsidoid ferns (Holtum, 1946), with dorsally (and laterally) very wide overlapping leaf-gaps. The ventral part consists of a (rather) broad, entire, gutter- or ribbon-shaped strand. Root traces arise from this ventral strand (either in two irregular rows, or irregularly from all over the strand)  $\pm$  laterally and ventrally. The dorsal part consists of one to five cylindrical or strap-like strands. In case the rhizome bears two rows of leaves, leaf traces originate from the lateral sides

Fig. 3. Rhizome anatomy. a–m. *Bolbitis auriculata*; a. schematic habit of rhizome,  $\times 1$ ; b–m. cross-sections as indicated in fig. a,  $\times 4$ .—n–u. cross-sections of rhizomes,  $\times 4$  (except for fig. r–u, which are  $\times 2$ ); n. *Bolbitis heudelotii*; o. *B. heteroclita*; p. *B. heteroclita* (triploid); q. *B. oligarchica*; r. *B. lindigii*; s. *B. portoricensis*; t, u. *B. bernoullii*.—ae = aerophore, bt = bud trace, bu = rhizome bud, db = dorsal bundle, lt = lateral bundle, r = root; r<sub>1</sub>, r<sub>2</sub> = subsequent roots; rt<sub>1</sub>, rt<sub>2</sub> = subsequent root traces, vb = ventral bundle; for further explanation see text (a–m. *Louis 12196*, BM; n. *Hennipman 4118*, L; o. *Mann s.n.*, US 329566; p. *Hennipman 4069*, L; q. *Scamman 7683*, GH; r. *Alston 7836*, BM; s. *Alston 5826*, BM; t, u. *Philipson & Idrobo 1796*, BM).



of both the ventral and the single dorsal strand. When more than two rows of leaves are formed, leaf traces of the dorsal leaves are formed by two adjacent dorsal strands.

Accessory branch traces are situated at the posterior side of the two lateral leaf gaps only, and are formed in association with one or two root traces, and one or two leaf traces. The arrangement of these traces seems rather characteristic. For instance, in *B. aliena* and *B. auriculata*, there is a stout trace arising from the ventral bundle which gives off, subsequently, two root traces, one bud trace, and one leaf trace (the other leaf traces arise directly from either the dorsal or the ventral vascular bundle), eventually fusing with the dorsal bundle. This pattern is similar to that found in a two-ranked rhizome of *B. heteroclita*. In *B. heudelotii* the accessory branch trace already gives off root traces when still in the rhizome. Representative drawings are given in fig. 3; see also plate 2: c. Excellent illustrations of the vascular structure in the rhizome are given by Nayar & Kaur (e.g. 1965a).

The xylem part in the dorsal and ventral meristeles, especially on the dorsal and ventral side, is lined with phloem elements.

The sclerenchyma strands are, if present, conspicuous dark-coloured elements situated either throughout the ground tissue or more or less restricted to its central part. They run  $\pm$  parallel to the longitudinal axis. Within one species the number and the width of the strands show much variation. The sclerenchyma cells are  $\pm$  fusiform in longitudinal view,  $\pm$  isodiametric in transverse view; the walls are much thickened. The same type of cells may be present as a sheath surrounding the meristeles. This sheath varies in thickness from one to many cells and is often especially well-developed on the side of the meristeles facing the interior.

Aerophores are variously shaped. They are part of the leaves but are continuous on the rhizome for some length. They show much variation in shape and size, when different species are compared (see fig. 2). It is to be regretted that these structures cannot be suitably studied from the herbarium material. The epidermis of the aerophores is densely set with somewhat projecting actinocytic stomata (fig. 8: k).

The vascular organisation in the rhizome and petiole can be regarded as representing an advanced condition, as it is easily interpreted as a derived form of a solenostele with U-shaped leaf traces.

### Scales of the rhizome

The scales of the rhizome are usually pseudopeltate (with a subcordate or perfoliate base), sometimes basally attached. They are  $\pm$  flat (except in *B. pergamentacea* where they are  $\pm$  bullate), one cell thick, and usually of moderate size though large in the high-climbing species. Uniserial hairs composed of 2–3 (–7) elongate cells with the terminal dark-coloured and obviously glandular, are scattered on the margin of the scales of all species except *B. bernoullii*.

In part of the species the scales are subclathrate or clathrate with the cross-walls thickened and the periclinal walls  $\pm$  translucent (often with a mother-of-pearl shine), in other species the scales are opaque throughout.

Scales are best studied from the apical region of the rhizome. They grow from a basal meristem. Mature glandular hairs are best studied from developing scales, as they are generally shrivelled and often scarcely perceivable in scales taken from older parts of the rhizome.

Only a few species have scales showing characteristics important for the classification of the species. Representative scales are illustrated in fig. 4 and 5.

### Roots

Roots are formed in large numbers and situated usually irregularly, sometimes in two more or less distinct rows  $\pm$  ventrally on the rhizome. They are continuous with the rhizome, of uniform shape and colour throughout the genus, and several decimeters long *in vivo*. The roots are  $\pm$  0.5–1.5 mm thick at the base and bear several to many closely branched lateral roots. All roots are (when young) densely covered with castaneous root-hairs that cling to the rock or penetrate into the soil. The blackish colour of the root is caused by the sheet of dark  $\pm$  thick-walled sclerenchyma cells situated below the root-epidermis and surrounding the parenchymatous ground tissue.

### Sterile leaves

The leaves are inserted dorsolaterally on and are continuous with the rhizome.

### Petiole

Near the base the petiole is  $\pm$  cylindrical or broadly and shallowly grooved adaxially; towards the base of the lamina the petiole often bears adaxially usually one (sometimes three)  $\pm$  flat median ridge(s); the abaxial side is terete. In a few species the upper part of the petiole is narrowly winged. Narrow, paler aerophores are present laterally all along the petiole and the rachis.

The ground tissue of the petiole is parenchymatous. Sclerenchyma strands like those found in the rhizome may be present especially facing the interior side of the vascular bundles. Just below the epidermis a distinct sheath of rather thin-walled, concolorous or brownish sclerenchyma interrupted by the linear aerophores is present. The vascular bundles are arranged in a loosely reticulate gutter-like structure (with reticulations especially in the basal part) which in cross-section near the base shows a  $\pm$  horse-shoe- or U-shaped arrangement of bundles. There are two anterior bundles which are largest and are mutually not interconnected by transverse bundles; their xylem is hooked inwards. The number of bundles shows variation within one and between different species. The number of bundles also seems to depend on the size of the leaves. Representative illustrations are given in fig. 6.

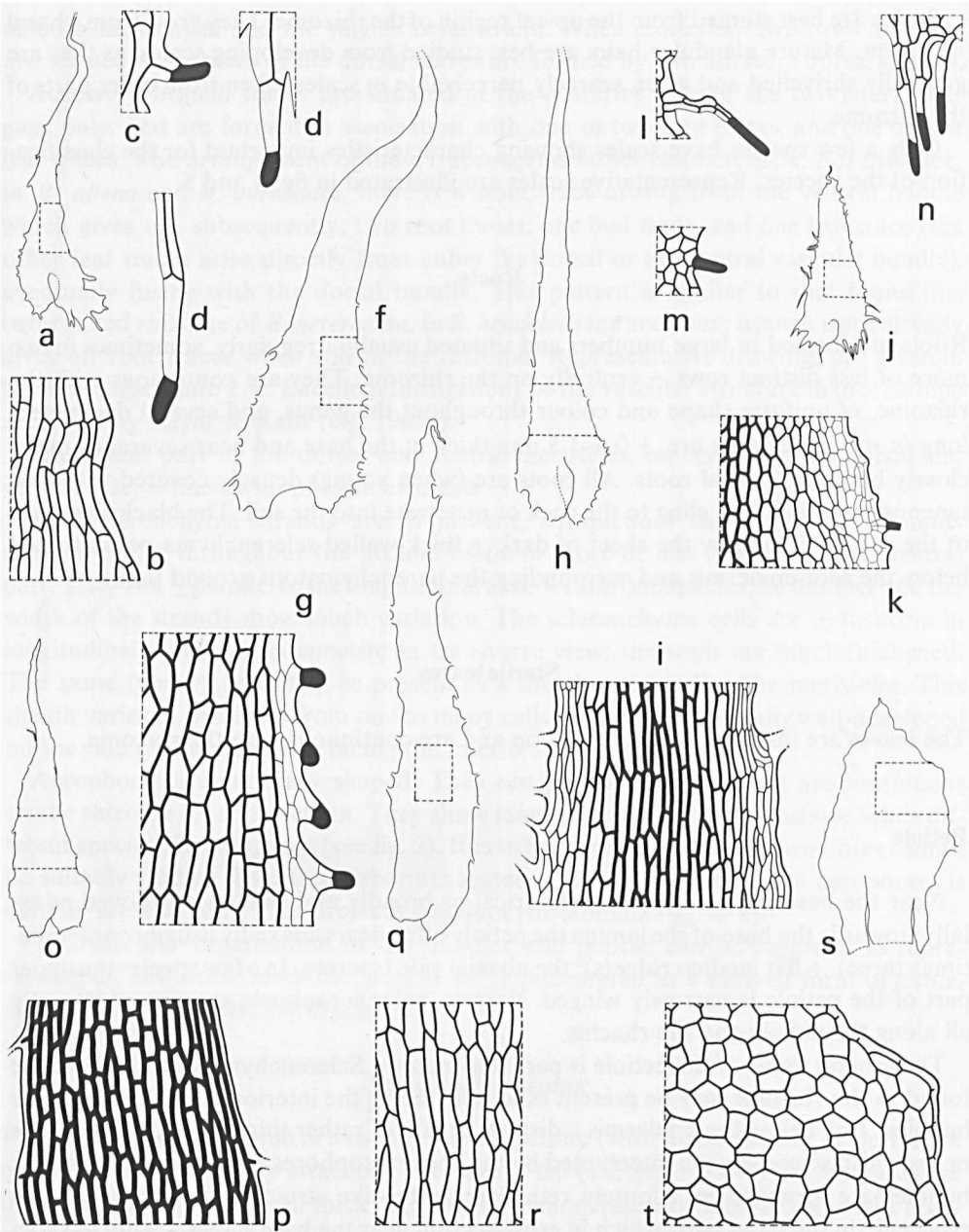


Fig. 4. Scales; outlines  $\times 10$ , details  $\times 40$ , marginal hairs  $\times 45$ .—a–e. *Bolbitis aliena*; f, g. *B. bipinnatifida*; h, i. *B. acrostichoides*; j–n. *B. rhizophylla*; o, p. *B. gaboonensis*; q, r. *B. nicotianifolia*; s, t. *B. pergamentacea* (a–e. Valeur 535, K; f, g. Jeffrey 759, K; h, i. Hepper 1476, K; j–n. Hennisman 4066, L, from living material ex Price s.n., L; o, p. Zenker 2456, S-PA; q, r. Maxon 9316, US; s, t. Tonduz 13353, G).



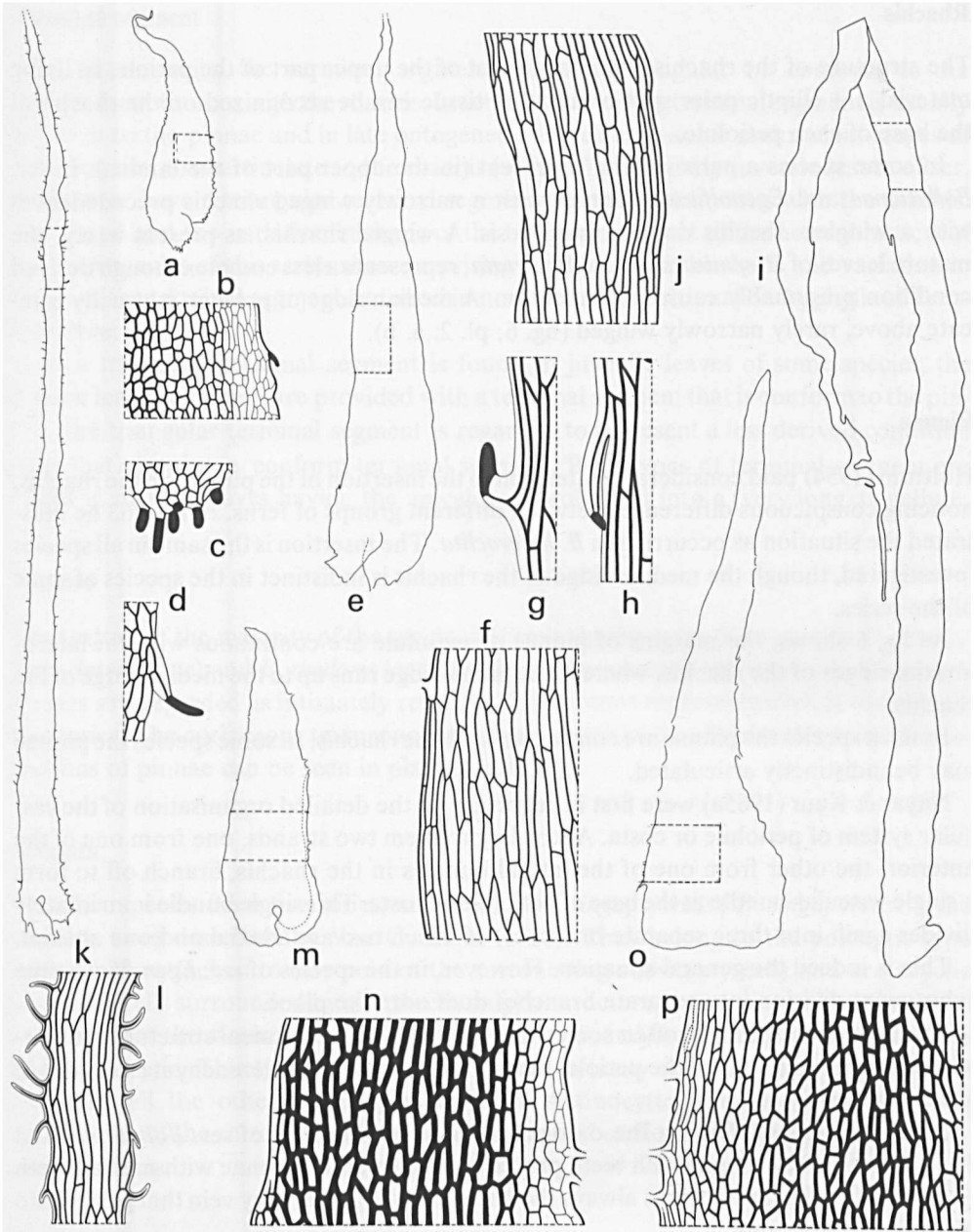


Fig. 5. Scales; outlines  $\times 10$ , details  $\times 40$ , marginal hairs  $\times 45$ .—a–d. *Bolbitis heteroclita*; e–h. *B. heudelotii*; i, j. *B. lindigii*; k, l. *B. bernoullii*; m, n. *B. quoyana*; o, p. *B. portoricensis* (a–d. Hennipman 4085, L, from living material ex Price 303, L; e–h. H. 4118, L, from living material ex Van Bruggen; i, j. Brade 371, BM; k, l. Philipson & Idrobo 1796, BM; m, n. Pleyte 452, BO; o, p. Salvin & Goodman 280, K).

## Rhachis

The structure of the rhachis is similar to that of the upper part of the petiole. In living material a  $\pm$  elliptic paler spot of aerating tissue can be recognized on the rhachis at the base of each petiolule.

In some species a narrow wing is present (in the upper part of the lamina). In ser. *Bolbitianae* and *Egenolfianae* leaves with a narrowly winged rhachis precede leaves with a wingless rhachis during ontogenesis. A winged rhachis, as present in e.g. the mature leaves of *B. semicordata* and *B. serrata*, represents a less complex though derived condition presumably caused by retention. A median ridge, if present, is usually truncate above, rarely narrowly winged (fig. 6; pl. 2: a, b).

## Pinnae

Holtum (1954) paid considerable attention to the insertion of the pinnae on the rhachis, noticing conspicuous differences between different groups of ferns. In fig. 263 he illustrated the situation as occurring in *B. heteroclita*. The insertion is the same in all species investigated, though the median ridge of the rhachis is indistinct in the species of some of the series.

As fig. 6 shows, the margins of pinnae or petiolule are continuous with the latero-abaxial ridges of the rhachis, whereas the pinna-ridge runs up to the median ridge of the rhachis.

In most species the pinnae are continuous with the rhachis. In some species the pinnae may be indistinctly articulated.

Nayar & Kaur (1965a) were first in reporting on the detailed organisation of the vascular system of petiolule or costa. According to them two strands, one from one of the anterior, the other from one of the lateral bundles in the rhachis, branch off to form a single vascular bundle at the base of petiolule or costa. This single bundle immediately divides again into three separate branches, of which two are adaxial and one abaxial.

This is indeed the general situation. However, in the species of ser. *Egenolfianae* the subsequent division into separate branches does not take place.

The base of the pinna is often somewhat swollen. The anatomical structure is otherwise identical with that of the petiole, though aerophores and sclerenchyma strands are absent.

Teeth and spines. During the ontogenesis of several species of ser. *Bolbitianae* and *Egenolfianae* lobed pinnae with teeth precede lobed or entire pinnae with narrow teeth or spines. In these species it is always the basal acroscopic tertiary vein that passes into the tooth or the spine.

Teeth are found in the sinuses of the pinnae of several species outside the genus, for instance in *Pleocnemia* (tectarioid). As during ontogenesis leaves with teeth in the sinuses precede leaves with spines (e.g. *B. appendiculata*), the margin with spines therefore may represent a more complex condition than the margin with teeth.

## Terminal segment

In most species the terminal segment, whether triangular or conform to the pinnae, is continuous with the rhachis. In ser. *Bolbitianae* the terminal segment is usually conform to the pinnae and in late ontogenetic as well as in some mature leaf-stages of some species  $\pm$  subarticulate to the rhachis (see fig. 7). The early juvenile leaves of ser. *Bolbitianae* have a triangular terminal segment which is continuous with the rhachis. The shape and the variation in shape of the terminal segment of the heteroblastic leaf series of species of this series show surprising similarities to the shape and variation in shape of the terminal segment as found in normal and transitional bathyphylls of *Teratophyllum*.

As a triangular terminal segment is found in juvenile leaves of some species, the mature leaves of which are provided with a terminal segment that is conform to the pinnae, the triangular terminal segment is regarded to represent a less derived condition than that showing a conform terminal segment. Both types of terminal segment are found in mature leaves having the apical part prolonged into a (very long) flagellum.

## Texture

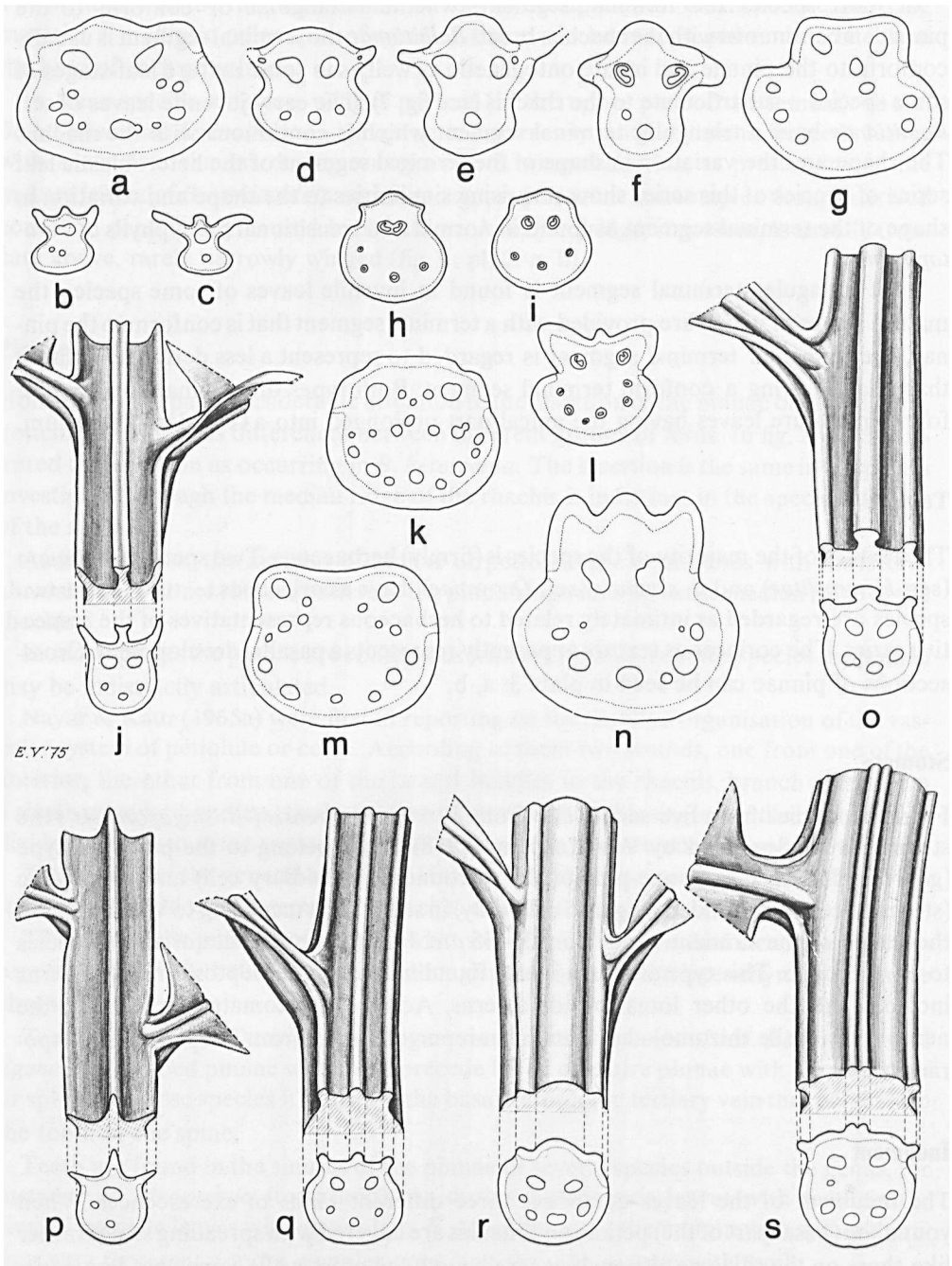
The texture of the majority of the species is (firmly) herbaceous. Two species, *B. sinuata* (ser. *Heteroclitae*) and *B. rivularis* (ser. *Quoyanae*), have a coriaceous texture. These two species are regarded as intimately related to herbaceous representatives of the respective series. The coriaceous texture apparently represents a parallel development. Cross-sections of pinnae can be seen in plate 3: a, b.

## Stomata

From six species from five series, and from *B. \times singaporensis* ('*B. singaporensis*') the stomata were described by Van Cotthem (1968). They belong to the polocytic type (guard cells attached to one pole of the surrounding subsidiary cell) and are acyclic (stomatal cells surrounded by guard cells only) in structure. According to Van Cotthem, the length of the stomata varies from 35–65  $\mu\text{m}$ . I found the stomata of all the species to be polocytic. This type of stoma is also found in many other leptosporangiate ferns including all the other lomariopsidoid ferns. Actinocytic stomata—present on the aerophores of the rhizome—have not been reported earlier from isosporous leptosporangiate ferns.

## Indument

The indument of the leaves comprises three different kinds of excrescences. When young the (basal part of the) petiole and rhachis are covered with spreading scales rather like those on the rhizome although generally with the cross-walls somewhat less thick-



ened. Smaller, almost orbicular appressed scales of the same structure or with a fimbriate margin occur throughout on the (young) petiole and rhachis. The laminar parts of the circinnate leaves of all species are usually densely covered with 2–5-celled uniseriate glandular hairs. See fig. 8. Old leaves may have lost all or most of their indument.

### Leaf shape

Within the genus various types of leaf shapes occur. The leaf shape (including that of juvenile leaves) shows much plasticity. On the other hand similar types of leaf shape may occur in series which are otherwise very different, for instance as regards features of the rhizome and venation pattern. Thus a pinnatipartite leaf is found in *B. fluviatilis* (ser. *Alienae*) and in *B. hastata* (ser. *Portoricenses*).

The variation in leaf shape as found in some series is schematically illustrated (fig. 9) and shortly discussed. In the illustration the solid-line arrows indicate the sequence of the leaves during ontogenesis, the broken-line arrows point to shapes that are here regarded as more derived in a semophyletic sense. The shape of juvenile leaves is indicated if known and/or relevant. The shape of the mature leaves should be evaluated preferably in relation to that of the juvenile leaves. See therefore also chapter 12.

Ser. *Alienae* and *Lindigianae*.—Apart from leaf shape ser. *Alienae* is very homogeneous; the monotypic ser. *Lindigianae* is possibly closely related to the first series. The different types of leaf shape found in these two series can be easily related to those as found in *B. aliena* with deltoid basal pinnae. Apart from other considerations this idea is based on the similarities of part of the juvenile leaves of *B. auriculata* and *B. lindigii* with those as presumed for *B. aliena*.

As regards *B. fluviatilis* there seems to be little doubt that it sprung from *B. auriculata*. The restricted distribution of *B. fluviatilis* supports its derived character. The  $\pm$  entire mature leaves of part of the material of *B. fluviatilis* (origin: Congo Basin) resembles that of certain juvenile leaves of *B. auriculata*. Such plants are obviously derived from *B. auriculata*. However, in an other part of *B. fluviatilis* (origin: islands in the Gulf of Guinea) the plants may have pinnatipartite leaves that are generally also larger than those of the plants discussed above. An ample collection of mature plants from Fernando Poo with pinnatipartite leaves shows that entire juvenile leaves precede the

Fig. 6. a–s. Cross-sections through the upper part of petioles (fig. a, d, h, k) and the lower part of rhachises (all others),  $\times 7$ .—j, o–s. Adaxial views on rhachises and on junction of rhachis with pinnae,  $\times 7$ .—a. *Bolbitis auriculata*; b, c. *B. aliena*; d. *B. gaboonensis*; e, f. *B. oligarchica*; g. *B. hemiotis*; h, i. *B. rhizophylla*; j. *B. sinensis*; k. *B. bernoullii*; l. *B. sinuata*; m. *B. lindigii*; n. *B. portoricensis*; o. *B. virens*; p. *B. appendiculata* ssp. *appendiculata*; q. *B. heteroclita*; r. *B. heudelotii*; s. *B. quoyana*. Fig. h–j, l, o–s drawn from living material (a. Hallé 4231, L; b, c. Proctor & Mullings 21999, U; d. Zenker 2456, L; e, f. Standley 33952, US; g. Jermy 2639, L; h, i. Hennipman 4066, L; j. H. 4046, L; k. Purpus s.n., vi-1913, M; l. Hennipman 4052, L; m. Buchtien 2220, G; n. Donnell Smith 2721, US; o. Hennipman 4047, L; p. H. 4048, L; q. H. 4085, L; r. H. 4118, L; s. H. 4147, L).

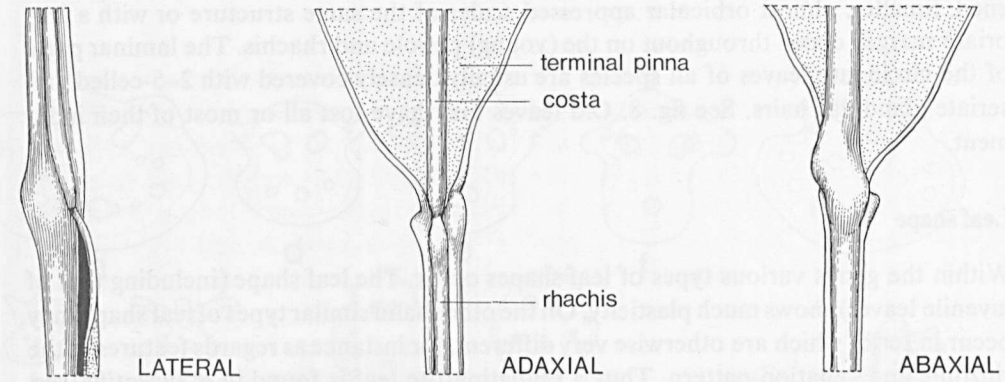


Fig. 7. Different views on the junction between rhachis and terminal segment (terminal pinna) in *Bolbitis virens*,  $\times 4$  (Hennipman 4047, L, drawn from living material ex Van Beusekom 2606, L).

pinnatipartite ones during ontogenesis. Therefore, it seems probable that plants with pinnatipartite leaves are derivatives of plants with entire leaves.

*B. lindigii* starts life as a terrestrial fern. As such its rhizome structure and leaf shape are much like those of *B. aliena*. The mature condition as shown in high-climbing forms with a coarse rhizome bearing several rows of leaves with many pinnae is habitually much different. The leaf shape (with many pinnae) as found in the latter form is regarded as more complicated and is presumably also more derived.

Ser. *Euryostichae*.—Most of the species have usually pinnate leaves; the number of pinnae per leaf varying from 2–10. A simple leaf is found in *B. gaboონensis*, and in part of the material of *B. nicotianifolia*, *B. pergamentacea*, and *B. hemiotis*. Characteristics of the shape of the pinnae of *B. hemiotis* (asymmetrical pinna base), *B. oligarchica* (ternate leaves), and *B. pergamentacea* (rhomboid terminal segment) are derived if compared with those of *B. nicotianifolia*.

Ser. *Heteroclitae*.—The shape of the juvenile leaves of *B. heteroclita* indicates how the derived condition of a pinnate leaf with a terminal segment that is conform to the lateral pinnae is related to a condition, where a pinnate leaf has a triangular terminal segment. In the Taxonomic Part the wealth of variations in leaf shape of *B. heteroclita* is amply discussed. See also fig. 13, 20, 60: a–s.

*B. sinuata*. The various types of leaf shape as found in this species are similar to (part of the) mature leaf shapes found in *B. heteroclita*. The available material shows that variation may be determined by differences in ploidy as well. The leaf shapes of the diploid specimens from the Philippines (fig. 61: e, g) may well be regarded as more derived if compared with those found in specimens from outside the Philippines, as the sinuata margin of the segments of the Philippine diploid is likely to represent a retentive condition. The (auto)triploid specimen from the Philippines (fig. 61: c, d)

forms entire leaves much different from the simple and pinnate leaves of the Philippine diploid, but on the other hand agreeing in detail with the simple leaves formed by the diploid and (auto)triploid specimen from Singapore. The only difference between the latter two specimens and the triploid Philippine specimen is to be found in the pinnate leaves. Those of the Philippine triploid are often irregularly lobed in the basal part of the terminal segment and have more or less adnate pinnae, whereas the leaves of the specimens from Singapore are perfectly regular with sessile or shortly petiolulate pinnae.

Ser. *Portoricenses*.—*B. portoricensis* is obviously the central species. This widely distributed fern varies much in leaf shape. The leaf shape of *B. hastata*, a Mexican endemic, is related to that of *B. portoricensis*; both have a similar venation pattern. The shape (and size) of its leaves is similar to that of certain forms of the not closely related *B. fluviatilis*. *B. pandurifolia* is found at the southern limit of the distribution of *B. portoricensis*. Its leaves are entire or ternate. A leaf shape with only two pinnae can be regarded to be simpler than that found in mature *B. portoricensis*. On the other hand, other aspects determining the shape (for instance, the shape of the terminal segment which is conform to the pinnae) can be interpreted as more complex. Juvenile leaves could not be investigated in either *B. hastata* or *B. pandurifolia*. This is regretted as one should like to know for instance if entire juvenile leaves precede the pinnatifid ones during development of the mature leaf of *B. hastata* (as is the case in *B. fluviatilis*).

Ser. *Quoyanae*.—In *B. quoyana* the leaf shape shows considerable variation (fig. 69: a–f). The small forms of this species are certainly derived. The leaf of *B. taylorii* comprises a proportionally large terminal segment and a winged rhachis (in the upper part). Some juvenile leaves of *B. quoyana* (for instance those of Price 2255, L) match some mature leaves of *B. taylorii* in detail.

*B. rivularis*, which has a  $\pm$  coriaceous leaf texture, is polymorphic (see fig. 71). The shape of its terminal segment of pinnate leaves is not always easy to describe in terms of 'triangular' or 'conform' to the pinnae'.

*Discussion*.—The variation in leaf shape as shown by (the ontogenetic stages of the) species of this genus is very striking. The drawings illustrate that the mature entire leaf can be regarded as representing a derived condition. This shape is found as a parallel development in different, unrelated series. Obviously such a leaf shape was acquired rather easily during diversification of species with pinnate leaves, a conclusion which was also reached by Tryon (1966). An entire leaf is a dominant feature in several other groups of unrelated ferns (e.g. *Vittariaceae* and to a lesser extent *Polypodiaceae*). A pinnatipartite leaf as found e.g. in *B. fluviatilis* (ser. *Alienae*) possibly represents an even more derived condition than does the entire leaf. It remains to be demonstrated if plants with this kind of leaf shape can revert, by divergent evolution, to a plant, of which the mature leaves are similar to the entire leaf except for being pinnate.

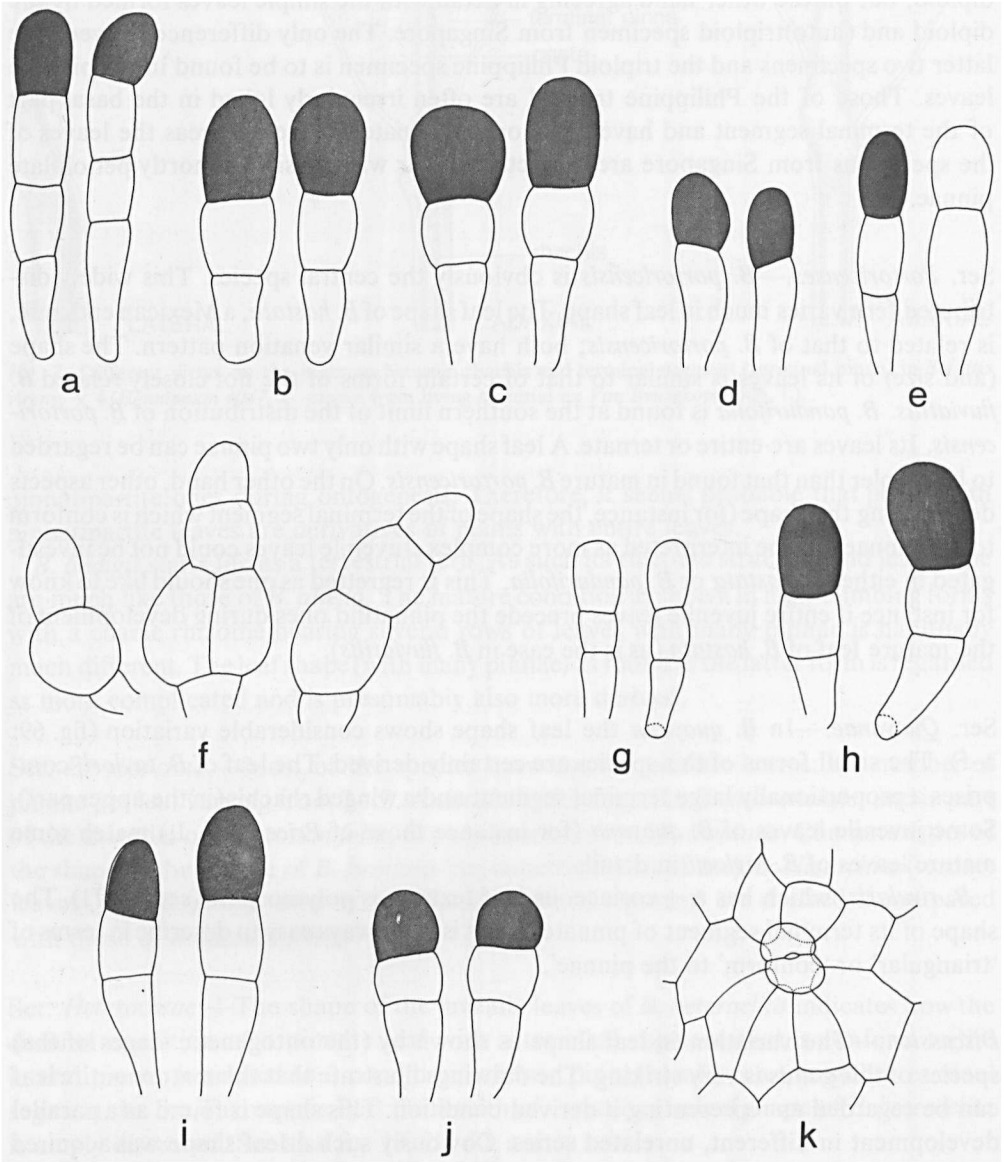


Fig. 8. a-j. Leaf epidermal hairs,  $\times 180$ ; all except fig. d and g drawn from living material or material preserved in F.A.P.A. a. *Bolbitis bipinnatifida*; b. *B. subcrenata*; c. *B. rhizophylla*; d. *B. nicotianifolia*; e. *B. heteroclita*; f. *B. heudelotii*; g. *B. lindigii*; h. *B. portoricensis*; i. *B. quoyana*; j. *B. repanda*, tetraploid (a. Kew 301-73, 04045 ex Whitehead 45, K; b. Hennipman 4142, L, ex Jarrett 600, K; c. H. 4068, L; d. LePrieur 17, P; e. Hennipman 4085, L; f. H. 4118, L; g. Gascoyne-Cecil 88, L; h. Kew 407-74, 03190 ex Jermy 10987, BM; i. Hennipman 4147, L; j. H. 4023, L).—k. *Bolbitis heudelotii*, actinocyctic stoma from the aerophores at the petiole base,  $\times 180$  (Hennipman 4118, L).



From the study of the juvenile and mature leaves in *Bolbitis* it is postulated that the ancestral form had a (bi-?)pinnate non-flagellate leaf with a triangular terminal segment, and triangular basal pinnae.

### Venation pattern

The venation pattern of the fern leaf has been studied in detail by many pteridologists, including Von Ettingshausen (1865), Mettenius in his 'FarnGattungen' (for references see Christensen, 1906), and Goebel (1922). Presl (1851) used this feature extensively in his classification of the genera, a system now generally regarded obsolete in many instances.

The venation pattern, like some other features such as the soral arrangement and the leaf shape, is subject to parallel evolution. Thus the venation pattern of *B. crenata* is about similar to that of the meniscioid thelypteroid ferns. Schumann (1915: fig. 36) who was much praised by Bower (1928), illustrated a progressive series of venation patterns comprising a meniscioid *Thelypteris* species and some *Bolbitis* species which she thought closely related. Another fine example of parallelism is displayed by the venation patterns of *B. (Leptochilus) heteroclita* and *Pteridoblechnum (Leptochilus) acuminatum* (White & Goy) Hennipman.

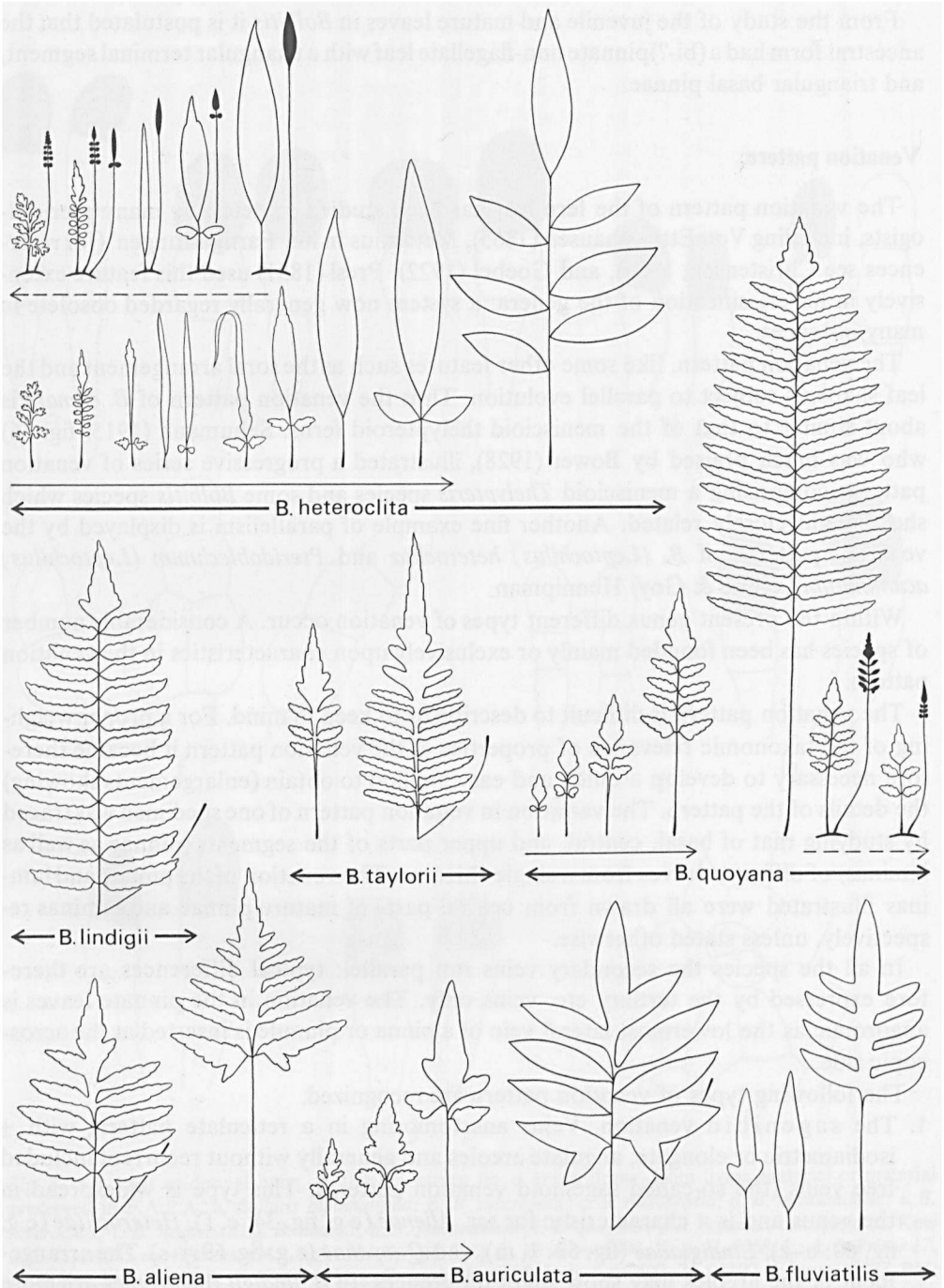
Within the present genus different types of venation occur. A considerable number of species has been founded mainly or exclusively upon characteristics in the venation pattern.

The venation pattern is difficult to describe or to keep in mind. For a proper weighing of the taxonomic relevance of properties of the venation pattern it became therefore necessary to develop a quick and easy method to obtain (enlargements showing) the details of the pattern. The variation in venation pattern of one specimen was traced by studying that of basal, central, and upper parts of the segments (pinnae as well as laminas) of different leaves from a single rhizome. The venation of the pinnae and laminas illustrated were all drawn from central parts of mature pinnae and laminas respectively, unless stated otherwise.

In all the species the secondary veins run parallel; typical differences are therefore expressed by the tertiary etc. veins only. The venation in the pinnate leaves is anadromic as the lowermost lateral vein of a pinna or pinnule is inserted at the acroscopic side.

The following types of venation pattern are recognized:

1. The sagenioid venation. Veins anastomosing in a reticulate pattern, with  $\pm$  isodiametric or elongate, angulate areoles and generally without recurrent included free veins (the so-called sagenioid venation pattern). This type is widespread in the genus and is a characteristic for ser. *Alienae* (e.g. fig. 34: e, f), *Heteroclitae* (e.g. fig. 60: u-z), *Lindigianae* (fig. 63: l, m), and *Quoyanae* (e.g. fig. 69: j-s). The arrangement of the areoles may show slight differences. In *B. lindigii* the areoles are more uniform than is usual in ser. *Heteroclitae*; the pattern does not change when going from the costa towards the margin of the pinna. In *B. fluviatilis* (with simple leaves)



**Fig. 9.** Leaf shapes in some taxa of *Bolbitis*. The solid-line arrow indicates the sequence of the leaves during ontogenesis; the broken-line arrow indicates plants with increasingly more derived leaf shapes.

the areoles gradually decrease in size towards the margin (fig. 36: h, i); it is the only species where the secondary veins are difficult to perceive.

In ser. *Bipinnatifidae* included free excurrent veins are present in part of the areoles (fig. 37: e–g).

2. The *Bolbitianae* type of venation. Veins anastomosing to form at least a costal areole, otherwise without or with, usually excurrent, included free veins. This type of venation shows much variation; it is found in ser. *Bolbitianae*. The occurrence of excurrent included free veins in the areoles of several species is regarded as indicating a derived condition if compared with a reticulate pattern. In a few specimens of *B. acrostichoides* (see fig. 38: f) and *B. serratifolia* (see fig. 45: d, c) the venation pattern is (locally) sagenioid (type 1). In *B. angustipinna* the venation pattern as seen between two adjacent secondary veins may be asymmetrical (see fig. 40: e, f).

Within the Asian species of ser. *Bolbitianae* a considerable variation in the venation pattern is found. A simple type is present in *B. crispatula* (fig. 40: h, i) and *B. semicordata* (fig. 43: g–i) whereas a very intricate regular network showing excurrent included free veins is found in other species, for instance in *B. costata* (fig. 41: d–f). The latter type of pattern is not at all reminiscent of the sagenioid pattern sometimes displayed by others. All these types can, however, be interpreted as variations of an ancestral one if the ontogenesis of the patterns as shown by different juvenile leaves is considered. See chapter 12.

3. The pattern with free veins. This is found in ser. *Egenolfianae*. The evidence from the study of juvenile and mature leaves of different species of ser. *Bolbitianae*, in combination with characteristics of ser. *Egenolfianae*, indicates that the pattern probably represents a derived condition.
4. The reticulate venation with recurrent (and excurrent) included free veins. This type is found in ser. *Euryostichae*, *Heudelotianae*, and *Portoricenses*. The venation of *B. portoricensis* is essentially regular and it probably evolved from divergent evolution and not by (recent) hybridization. This is not necessarily true for the type of venation shown by ser. *Euryostichae*; it was found that presumed hybridization between different cytotypes of one species (*B. sinuata*) or between two species with a (slightly different) reticulate venation may produce an almost identical condition; see fig. 10, and the venation pattern of *Leptochilus* × *trifidus* in fig. 85: v, w.
5. The irregular venation. Detailed analysis of the venation of a specimen nearly always results in finding incidental irregularities. These are regarded as analogous to for instance the occurrence of incidental aborted spores in the spore output of a sexual diploid, and have therefore not been given much attention. On the other hand it was found that in known or suspected hybrids or allopolyploids the venation may be structurally irregular, e.g. in *B. lonchophora* (fig. 76: c–g), *B. repanda* (–3n and –4n; fig. 78: c–i), *B. × singaporensis* (fig. 85: a–d), etc. Besides, a number of taxa which were thought to be of hybrid origin because of other properties like the presence of aborted spores and the irregular leaf shape (*B. × boivinii*, *B. angustipinna* × *sinensis*), often show a very irregular type of venation pattern as well. By ‘irregular’ is meant here the condition in a sterile leaf, where marked differences exist between

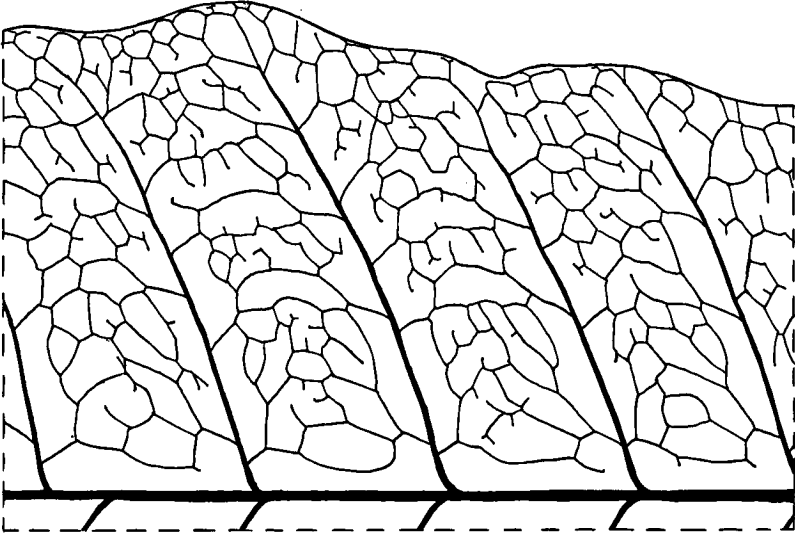


Fig. 10. *Bolbitis sinuata*, irregular venation pattern,  $\times 2$  (Williams 2055, UC; drawn from dried material).

the venation of the various areas included by the secondary veins (or parts of that area in case an intricate type is involved). Irregularities in the venation are here regarded as an important indication for the hybrid status of a certain plant. On the other hand hybrids do not necessarily have an irregular type of venation. In some (*B.*  $\times$  *sinuosa*; fig. 85: f, h, j, l, n, p) it may be perfectly regular.

In a number of cases a very irregular pattern was found in specimens which were typical as to other features. Thus one of the autotriploid specimens of *B. heteroclita* in cultivation shows many irregularities in its pattern. And so does the venation of many collections belonging to species with an intricate network. Examples are included in the patterns illustrated for the species.

In some irregular intricate patterns pieces of veins not connected with other veins may be found within an areole. See the asterisks in fig. 85: v, w.

*Discussion.*—The ferns with the types of venation patterns as listed above can be regarded as derivatives of a hypothetical predecessor with a free venation. Juvenile leaves of such an ancestral fern would all show an open venation.

The venation pattern of the contracted laminae (i.e. laminae which are less divided and often also smaller than those found in related taxa) as present in many a modern fern shows much variation. The contraction of the leaf obviously resulted in a vast array of venation patterns. These patterns may have free veins (e.g. the type with closely placed parallel veins) or may comprise variously intricate networks. All these different types, whether simple or intricate, are derived in a semophyletic sense. The pattern of juvenile leaves of ser. *Bolbitianae*—as well as that of many other leptospor-

angiate ferns having mature leaves with a complex venation pattern—may have existed in the juvenile leaves of the ancestral fern.

The same kind of processes that led to the contraction of parts of the leaf, may also cause the retention of certain leaf stages in ferns which acquired a complex venation and a (more or less) contracted lamina. The resulting neotenic fern may then have leaves with a venation that might be very similar to that of the juvenile leaves of the ancestral fern. But in spite of this, the neotenic fern is more derived than the fern showing the more complex type of venation from which it originated. The open types of venation found in small or moderately sized ferns (*Polypodiaceae*, *Grammitidaceae*, *Hymenophyllaceae*, etc.) should be interpreted also in view of this hypothesis.

Bower (1923) regarded the ferns with an open type of venation pattern as primitive, as the study of fossil ferns showed that ferns with an open type of venation preceded those with a more intricate type. Bower (p. 96) also applied this to the modern ferns: 'Instances might be multiplied which indicate that among living Ferns there has been frequent progression within narrow circles of affinity from the more primitive open to the more advanced reticulate venation.' This idea which is still generally accepted seems, however, not necessarily correct in view of both the differences in the venation pattern of heteroblastic leaf stages and the general occurrence of retentive stages.

The idea that ferns with a simple morphological expression are also primitive is reflected in classifications. The present genus represents a good example, as the species with an open type of venation (ser. *Egenolfianae*) have been formerly (and still are) given generic recognition, whereas the species showing a more complex venation were assembled in another genus which was considered more derived.

As regards the types of complex venation patterns Bower (p. 96) remarked: 'Beyond the fact that these complex venations are characteristic for the most part of relatively late and advanced types of Ferns, their detailed study cannot be used as a consistent or trustworthy basis for the phyletic seriation of the *Filicales* at large. This conclusion, which robs the subject of much of its interest, naturally follows from the fact now demonstrated in so many isolated genera that a 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.'

I agree with Bower as regards the homoplastic nature of the intricate types of venation. But the same may be true for patterns showing free veins only. Better than to disregard the venation one should first attempt to understand the different types of venation as occurring in juvenile and mature leaves of species forming a natural group.

The study of the venation patterns as shown by a particular sporophytic phase is here considered of great importance, as such data known for ser. *Bolbitianae* have added to the understanding of the diversification of this group. Another result from such a study might be a better knowledge of the intricate venation patterns as present in modern isosporous ferns.

As regards the ancestral type of venation in the genus *Bolbitis* (which is presumably also the ancestral type of venation of the lomariopsidoid ferns), ser. *Bolbitianae*—a coherent group of species—furnishes significant information. From the variation in the

venation of *B. acrostichoides* and *B. serratifolia* it is inferred that the sagenioid type of venation represents the original type within ser. *Bolbitianae*. The species of this series with mainly free excurrent veins (*B. crispatula*) as well as the species showing a venation consisting of an intricate network with excurrent included free veins, can easily be derived from the species with a more sagenioid type of venation; these different species obviously resulted from divergent evolution, and, accordingly, represent a derived element within this series. In view of the interpretation of the simple type of venation within ser. *Bolbitianae*, it seems possible that the free venation as shown by ser. *Egenolfianae* represents a derived condition as well.

The two other types of venation are the 'true' sagenioid venation and that with recurrent (and excurrent) included free veins. A sagenioid venation is found in series from all over the tropics, including tropical America, tropical Africa eastward to Madagascar and the Mascarenes, northeast India to eastern Malesia and the Pacific, and the Bonin Islands, but excluding southern India and Ceylon. Groups with a venation showing recurrent included free veins are restricted to Africa and America.

In *B. portoricensis* included free veins are found only in the late juvenile leaf stages with a reticulate venation and in the adults. As earlier leaf stages show a  $\pm$  reticulate venation only, and as such a pattern is found in mature specimens of the related ser. *Bipinnatifidae*, it seems likely that the mature pattern of *B. portoricensis* (with included free veins) represents a derived condition.

Morphological evidence suggests that divergent evolution in ferns with a sagenioid venation pattern may lead to species having a free venation or a venation with several types of included free, ex- and/or recurrent veins.

The venation pattern as found in ser. *Euryostichae* could have resulted also from hybridization between species, one of which has a sagenioid venation.

## Bulbils

Three quarters of the species have bulbil(s) on the sterile (and fertile) laminae. The bulbils in the genus *Bolbitis* are usually  $\pm$  globular, sometimes elongate, persistent structures, situated adaxially on the lamina.

Bulbils are covered with scales like those on the rhizome though smaller. Cross-sections of the subterminal bulbil of *B. repanda* and *B. sinuata* show a  $\pm$  orbicular structure with mostly parenchyma and vascular tissue (plate 3: a, b). The vascular system comprises a single strand which is continuous with a (the) rachis bundle. In large bulbils this strand gives off lateral bundles that serve the (primordia of) roots and leaves. In most species leaves and roots are formed already on the globular bulbil. In *B. auriculata* and *B. gaboonensis* the development of the bulbil into a short rhizome occurs prior to the formation of leaves and roots.

The different localisations of the bulbil:

1. The subterminal bulbil is situated subterminally (and sublaterally) on an entire lamina, or subterminally on the terminal (and lateral) segments of a (bi)pinnate leaf. Thus on an entire lamina a conspicuous subterminal bulbil which is inserted later-

ally on the rhachis at the junction with a secondary vein, as well as (primordia of) bulbils which are inserted subterminally on a secondary vein at a junction with a tertiary vein, usually can be recognized. In pinnate leaves, primordia of bulbils are usually present subterminally on the pinnae as well. They are likewise inserted where the costa and one of the secondary veins of the pinna meet. Certain leaf stages with but few pinnae and a relatively large terminal segment may show subterminal bulbils on the pinnae and the terminal segment, apart from several bulbils situated sublaterally on the terminal segment. The illustration in the original publication of *Cyrtogonium rivulare* (= *B. rivularis*) is a good example.

In most of the species only one subterminal bulbil is found on the terminal segment, whereas several remotely placed bulbils occur on the long-flagelloid terminal part of the terminal segment of *B. portoricensis* (fig. 68: c). Some leaves of a normally triploid specimen of *B. heteroclita* kept in cultivation formed a multitude of closely set bulbils on the flagelloid terminal part of the terminal segment. Wild specimens invariably bear one subterminal bulbil only.

The subterminal bulbils of the leaves of certain plants grown in cultivation in terraria, for instance those of *B. repanda* and *B. heteroclita* × *sinensis*, all developed into small plants. These plants, situated subterminally on pinnae and terminal segment, reach the ground only after senescence of the leaf on which they are formed.

2. The terminal bulbil. In *B. rhizophylla* (see fig. 52: d, e) and *B. novoguineensis* (see fig. 74: k, l) the bulbil is always situated terminally, or almost so, as in *B. rhizophylla* an inconspicuous portion of the lamina is incidentally present distally from the bulbil. A (primordium of a) terminal bulbil is present on the pinnae of *B. novoguineensis* (fig. 74: m) but generally absent on those of *B. rhizophylla*.

Part of the material attributed to *B. crispatula* var. *copelandii* has the bulbil situated at the pseudo-articulation of the rhachis just below the lamina of the terminal segment. In another part of this material the terminal segment is scarcely developed (obviously aborted). Incidentally the terminal segment is not developed at all; as a result the situation of the bulbil is terminal (*Hennipman 3632*, L; *Tagawa et al. T 1910*, L).

3. The axillary bulbil. Distinct, almost spherical or elongate structures are present in the axils of (part of) the pinnae (rarely on the petiolule somewhat away from the rhachis) of *B. hemiotis* (fig. 56: a) and *B. oligarchica* (fig. 56: e, f). Axillary bulbils occur incidentally in *B. auriculata*. In one specimen of the latter species (*Ledermann 689*, B) the bulbils of the lowermost axils had developed into elongate structures up to 7 mm long, still devoid of roots or leaves, a condition reminiscent of that of *B. gabooneensis*.
4. The bulbil of *B. gemmifera* is situated on the rhachis in the basal part of the terminal segment and generally opposite the laminar part of the usually unequal base. The shape of the terminal segment as well as the exact place where the bulbil is inserted varies, as illustrated in fig. 74; a, c, and d. In relation to this unique position of the bulbil it should be noted that morphological characteristics afford evidence that *B. gemmifera* probably has originated from hybridization between *B.*

*acrostichoides* and *B. auriculata*. The first species always has a distinct subterminal bulbil on a terminal segment which is conform to the pinnae; the second is generally devoid of bulbils, though axillary bulbils are incidentally present. The shape of the leaves of these species and *B. gemmifera* are illustrated in the Taxonomic Part.

The distribution of the types of bulbils throughout the genus.—Bulbils are absent from ser. *Heudelotianae* and *Lindigianae*. In ser. *Alienae* (axillary) bulbils are incidentally present in *B. auriculata* only. In ser. *Euryostichae* axillary bulbils are present in two species, a subterminal bulbil in one, whereas bulbils are lacking in the other two species. In all other series the subterminal (or terminal) bulbil is present in (nearly) all of the species (and its specimens).

Marchal (1965) studied a considerable number of bulbiferous ferns including some *Bolbitis* species. She recognized apical, axillary, subapical, and laminar bulbils. From my observations it seems impractical to discriminate between the latter two types of bulbils. The bulbil of *B. gemmifera* was not included in her studies.

### Fertile leaves

The fertile leaves are erect, generally of the same architecture, anatomy, and of similar size as the sterile ones occurring in conjunction. They stand more erect, have a longer petiole, a smaller lamina which is often proportionally shorter, and a more coriaceous texture. The shape of the fertile segments is usually about the same (though much contracted) as in the sterile ones, but sometimes different. The margin of the fertile segments often lacks the prominent marginal projections found in the sterile ones; bulbils are less prominent or even absent.

Shape of the pinnae.—In many species the shape of the fertile pinnae is the contracted version of the sterile one. Some deviating shapes are found as well.

The fertile pinnae of *B. appendiculata* ssp. *appendiculata* are mostly contracted; the sporangia are inserted exclusively on the veins (in specimens from mainland Asia) or all over the lower surface (e.g. in specimens from the Philippines). However, within a restricted area in the borderland of Burma and Thailand plants with the contracted type of fertile pinna are found next to plants with typical sterile leaves but with (bi) pinnate fertile ones. The fertile pinnae of these are moniliform with the sporangia restricted to the lower surface of semicircular patches of lamina. Between this type (on which *Polybotrya helferiana* was based) and the typical one all intermediates are found (fig. 49: k–p). In ssp. *vivipara* var. *vivipara* the fertile leaves lack laminar tissue; the sporangia are inserted on the costa (and costules) and exposed in all directions (plate 3: e). In var. *neglecta* a narrow strip of laminar tissue is present along the costa on which the sporangia are inserted; they are exposed to both the upper and lower sides.

Within ser. *Bolbitianae* the shape of the fertile pinnae shows much variation. Some taxa have contracted fertile pinnae, those of others are either linear, or not fully acrostichoid and so-called intermediate.

The shape of the fertile leaf is usually similar to that of the preceding sterile one.



It is not rare in cultivation that a sterile leaf of a shape as found in juvenile ones, occurs in association with a fertile leaf of similar shape, whereas the sterile and fertile leaves formed on the full-grown plant are quite different. This, and the common occurrence of so-called intermediate leaves point to the important part physiological factors may play in the determination of the fertility.

**Intermediate leaves.**—Leaves that are in part fertile and in part sterile are here called 'intermediate' leaves. They do not rarely occur and show much variation as to the sporangial arrangement, also in one species (see fig. 11). A few examples will illustrate this.

In *B. portoricensis*, the specimen *Linden 1751* (P) has a fertile leaf with its lowermost pinnae, the basal part of its central pinnae, and the lowermost lobes of its terminal segment sterile, otherwise being completely acrostichoid; in *l'Herminier s.n.* (P) the leaf shows irregularly shaped areas with sporangia between the secondary veins of the pinnae in the basal part of the lamina, the leaf being more regularly acrostichoid towards the apex; in *Rivoire s.n.* (P) one of the fertile leaves displays a pteridoid arrangement of sporangia.

In *B. heteroclita* one of the several intermediate leaves found has large fertile pinnae all showing a perfectly regular distribution of the sporangia exclusively on the veins (E. Smith 1696, K). This hemionitoid arrangement of the sporangia is rather obligate in *B. acrostichoides*, an old species in ser. *Bolbitianae*, as well as in some other taxa of this series. In several species of other series the sporangia are also inserted on the veins.

In *B. quoyana* one out of several different intermediate leaves shows the sporangia situated towards the margin of the pinna only. The linear 'sorus' is in some places interrupted. As a result irregularly shaped 'sori' can be distinguished which are in part 'protected' by the marginal lobes the lateral margins of which face each other. See fig. 11: j.

**The venation pattern.**—The venation largely recalls that of the sterile leaves, although free included veins and small areoles are less frequent or (largely) lacking. The fertile leaves of *B. semipinnatifida*, *B. heudelotii*, and *B. portoricensis* are as a rule almost devoid of free included veins which are always present in the sterile leaves. The fertile pinnae of *B. rhizophylla* sometimes have locally some costal areoles which are always lacking in the sterile ones.

Incorrectly, Nayar *et al.* (see Kaur, 1974) reported a special kind of venation pattern (diplodesmic venation) occurring in the fertile segments of the present genus.

**Sporangia.**—Insertion of the sporangia is variable. In some groups the sporangia are situated all over the lower surface (e.g. ser. *Alienae*, plate 1: a), in other taxa they are present on the tertiary veins only (e.g. *B. acrostichoides*, plate 1: c; *B. sinensis*) or both conditions occur within one taxon (e.g. *B. appendiculata* ssp. *appendiculata*).

Sporangia are formed in dense masses. During maturation of the fertile leaf sporangia of different age occur together without definite sequence (the so-called 'mixed sorus' of Bower, 1928). In a cross-section of a mature pinna (plate 3: c–e) the sporangia are nearly all of the same developmental stage and irregularly piled together, often three above each other. In spite of the basipetal development of the fertile leaf, the

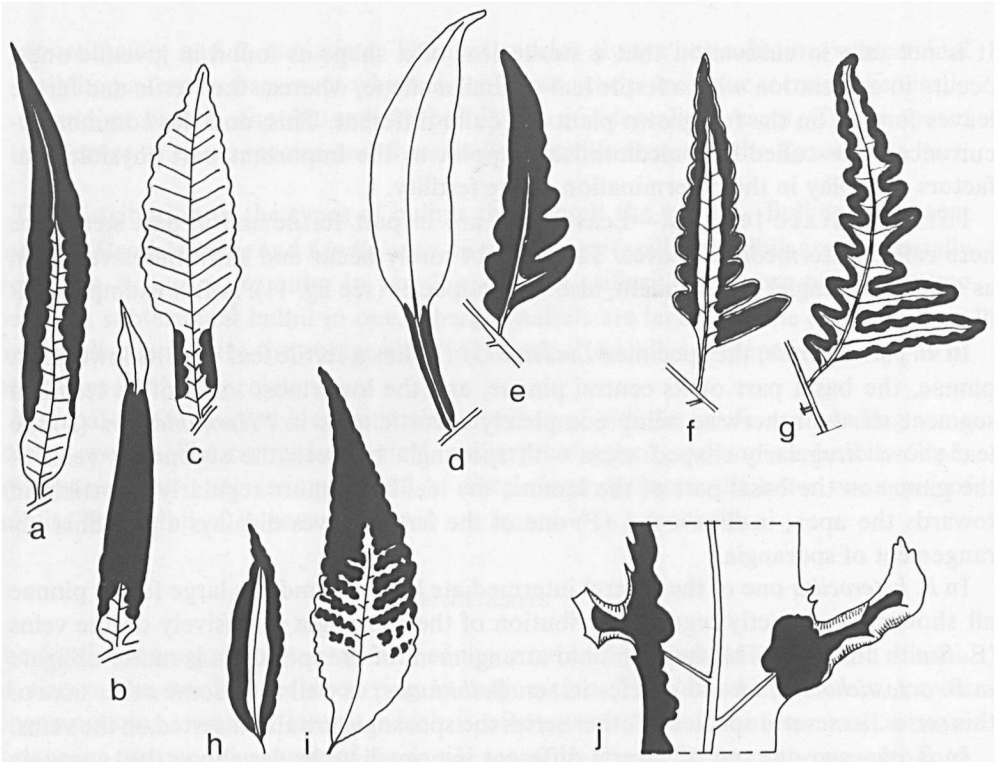


Fig. 11. Abaxial view of (parts of) so-called intermediate pinnae, all  $\times 1/2$  except for fig. j which is  $\times 6$ .— a–c. *Bolbitis serratifolia*, pinnae from the lower (fig. a), central (fig. b) and upper (fig. c) part of the same side of a leaf of which all pinnae from the other side are completely sterile. d–g. *B. portoricensis*; d. central pinnae; e–g. lowermost pinnae; fig. f has been drawn from a leaf of which all other pinnae including the other lowermost pinna are completely fertile. h, i. *B. heteroclita*, central pinnae. j. *B. quoyana*, central part of central pinna (a–c. Stübel 690, B; d. Skinner s.n., K; e. Proctor 19262, U; f. Anonymus 6477 bis, US; g. Rivoire s.n., P; h. Levinge s.n., G; i. Clarke 11964 A, BO; j. Herb. Filic. Luerssen no. D, P).

sporangia of all parts are all mature at about the same time. When in cultivation two or three fertile leaves were formed in succession it was not rarely found that all leaves reach maturity at about the same time.

Sporangia are long-staked, broadly elliptic when seen from the flat side, 1–1.5 times as long as wide, provided with a vertical annulus which is interrupted at the insertion of the stalk (plate 3: d). For further details see Nayar & Kaur (1965a). The sporangia were not studied in detail. From incidental observations it was found that within one species the stalk may vary much as to its length and colour (*B. appendiculata*), and the head as to its size (*B. sinensis*).

**The ancestral condition.**—In the genus *Bolbitis* a considerable range of different intermediate leaves is found, and some of these are characteristic for certain taxa. Part of these have misled the systematists, e.g. those of *Jenkinsia undulata* (= *B. virens* f. *virens*) and *Meniscium deltigerum* (= *B. virens* var. *deltigera*).

Intermediate leaves do not give uniform evidence regarding a supposed ancestral soral condition. Some show a pteridoid arrangement of sporangia, which represents a derived condition. In others the sporangia may be situated exclusively or mainly on the veins. Schumann (1915), who cultivated a few species at Munich, studied the ontogeny of the fertile leaves of *Leptochilus cuspidatus* (= *B. repanda*) and *Leptochilus heteroclitus* (= *B. heteroclita*). As generally the sporangia develop first on the veins, and as sporangia are situated mainly on the veins in intermediate leaves ('Mittelformen') of these species she concluded that the species investigated were derivatives from ferns 'bei denen die Sporangien dem Verlauf der Adern folgen', which may be correct for the present genus. Incidentally marginal 'sori' are found. Such a condition as present in the specimen of *B. quoyana* illustrated can be easily interpreted as an incomplete pteridoid arrangement. Indusiate sori have never been found in the ample material of different intermediate leaves.

When trying to reconstruct the original condition of the sporangial arrangement in *Bolbitis*, we note that distinct submarginal sori are a generic characteristic of the monotypic lomariopsidoid genus *Thysanosoria* from New Guinea. This genus is based on two collections (from adjacent localities) agreeing in detail with those of *Lomariopsis kingii* (Copel.) Holttum (Holttum, in preparation) except for having round sori on small marginal lobes of the fertile pinnae. Their sporangia are situated on a narrow cone-shaped receptacle placed at right angles to the pinna-lamina, somewhat apart from the marginal lobe. Because of this sporangial arrangement, Holttum postulates that an indusiate (!) sorus at a vein-ending might be the original fertile state of the group of lomariopsidoid ferns. This seems a far-fetched conclusion and to me *Thysanosoria* should be regarded as a deparioid derivative (Christensen, 1938: 'peculiar derivative') of *Lomariopsis*.

Within the non-acrostichoid fertile leaves found in *Bolbitis* the hemionitidoid arrangement of the sporangia is best represented. Such an arrangement is also found in such 'old' species as *B. acrostichoides*. However, the non-indusiate hemionitidoid arrangement might represent a secondary development as well. If so, it is postulated that the acrostichoid condition was already present prior to the differentiation of the ancestral group into the modern genera of *Lomariopsidaceae*.

Notes on the acrostichoid condition.—It is now generally understood that the acrostichoid condition has developed in quite different lines independently. Further, that the tendency to become acrostichoid (or pteridoid) can be perceived in the major groups of isosporous ferns.

Copeland (1929: 381) and Ching (1958) have pointed out advantages of an erect disposition of the fertile leaves of dimorphic ferns. '... the fertile fronds, on longer stipes than the sterile stand quite erect and high in the middle of the plant to insure better light and consequently a better chance of dispersal of its spores in the dry air ...' (Ching, 1958: 133).

The acrostichoid condition is not always 'complete'; and so-called intermediate leaves, which are in part fertile, in part sterile, may occur. On the other hand, the acrostichoid condition may be characteristically 'intermediate' or unstable in other ferns.

Sledge (1972) noted that in the acrostichoid fern *Quercifilix zeilanica* (Houtt.) Copel. round sori may occur on the basal lobes of the fertile lamina. This, and the fact that this fern hybridizes easily with *Tectaria decurrens* (Presl) Copel. induced him to sink *Quercifilix* in *Tectaria*.

As species of the present genus have been formerly included in the genus *Leptochilus*, I have checked all of its species as conceived by Ching (1933). It will be demonstrated (Hennipman, in preparation) that the acrostichoid arrangement in *Leptochilus* shows (a characteristic) instability in several species. Thus in *Leptochilus minor* Fée one can sometimes recognize individual elongate sori situated parallel to the rachis of the narrow fertile leaf, a situation similar to that found in *Colysis poilanei* C. Chr. & Tardieu-Blot. Further, I traced a specimen of *Colysis hemionitidea* (Wall.) Presl which consisted of a ± acrostichoid fertile leaf of a type as found in *Leptochilus* species, apart from a typical monomorphic fertile leaf (with round and elongate sori between the secondary veins), occurring together on a single rhizome! I agree with Ching (1933) that the genera *Leptochilus* and *Colysis* are otherwise similar, and there seems no objection to unite these genera formally.

The true affinity of acrostichoids is sometimes difficult to ascertain. In *Leptochilus acuminatus* White & Goy the linear arrangement of sori may be 'broken' showing two rows of variously elongate sori parallel to the costa. The identity of this fern became manifest only after an intermediate leaf became available showing a woodwardioid arrangement of sori in an atavistic part of this leaf. The species is transferred to the genus *Pteridoblechnum* (Hennipman, 1976).

The facts indicate that the acrostichoid condition may become manifest in any group at any time. The observations on the fertile leaves of *Leptochilus* and *Colysis* reveal that such a condition might not necessarily be the result of a gradual change in leaf shape and soral insertion as is generally believed. The acrostichoid condition is sometimes difficult to weigh taxonomically, as potentially important features like those pertaining to the sori are lacking, whereas the vegetative features of the non-acrostichoid potential relatives are not (yet) always fully known.

## 6. SPORES

### Introduction

Although spores as seen with the light microscope were described as early as the last century (e.g. Fée, 1845), the study of the morphology of the spores has been rather neglected until recently. For a survey see Lugardon (1972, 1974) and Wagner (1974).

As regards the spores of the genus *Bolbitis*, Erdtman (1957) supplied a brief description and an illustration of the spores of *B. turrialbae* (= *B. pergamentacea*) and *Polybotrya appendiculata* (= *B. appendiculata*). Nayar & Kaur (1965c) described the spores of mainly the Indian species. These authors included features of the perispore ('perine') to keep the genera *Bolbitis* and *Egenolfia* (here united) separate. This, and my interest in the structural properties of the spore walls, induced me to study the spores of several

species with both the light and the electron microscope (Hennipman, 1970). It was shown that the spores do not provide evidence justifying the treatment of *Egenolfia* as a separate genus. Erdtman & Sorsa (1971) reported the light microscopical observations on 21 species of the genus (including the species formerly referred to *Egenolfia*). Their data were largely taken from the publications of Nayar & Kaur.

The structure of the spores of the ferns as seen with the electron microscope was first described by Lugardon (1965) for *Blechnum spicant*, by Pettitt (1966) for *Asplenium adiantum-nigrum*, by myself (op. cit.) for four species of *Bolbitis*, and by Lugardon (1972, 1974) for a considerable number of ferns including also eusporangiate ferns. Lugardon's excellent work is of general interest.

As regards the detailed structure of the spores of *Bolbitis* I demonstrated that the exospore ('exine') of several species does not show noteworthy structural differentiation. Further, that the perispore ('perine') is not a simple but a much differentiated structure. Besides, the perispore of closely related species may be markedly different, whereas the spatial distribution of the perispore in almost mature sporangia of different species shows surprising variation. During the present study spores of all taxa were studied with the light microscope. Representatives of the different spore types recognized were studied with the scanning electron microscope (S. E. M.). In the descriptions of the spores I have usually mentioned the general characteristics only. For the detailed structure the reader is referred to the S. E. M. photographs.

The present chapter includes some observations on certain aspects of the sporogenesis, including those obtained from material in which abnormal spores are formed.

The term 'spores' stands for the eventual shape of the divisional products of the spore-mother-cell (S. M. C.) and includes the perispore. I now prefer to use the terms exospore and perispore instead of exine and perine, respectively. These terms are applied as defined by Lugardon (1972).

## Results

### Types of spores

Spores as seen with the light microscope are monolete, biconvex, and provided with a variously shaped brown perispore. The exospore is thin, structurally not differentiated, and shows a short, straight laesura which is rarely forked at one end. The perispore as seen from cross-sections studied with the S. E. M. is composed of two more or less distinct elements which have been named 'inner' and 'outer' perispore. The types of spores as set out below are primarily based on differences in the shape of the outer perispore, which can also be recognized with the light microscope.

**TYPE A.**—Spores with the outer perispore reticulate and cristate, the inner perispore closed and the crests of adjacent spores in a  $\pm$  mature sporangium continuous. The inner surface of the inner perispore is smooth and does not show connections with the exospore; the outer surface of the inner perispore is  $\pm$  smooth, though its fine sculpture is somewhat scabrous because of the occurrence of minute, irregular,

wart-like excrescences. The crests of the outer perispore are continuous with the plasmodial remains on the inner wall of the almost mature sporangium. This reticulate cristate perispore occurs in *B. appendiculata*.

Within this species two main subtypes of perispore can be distinguished. In the first subtype the outer perispore consists of crests only. The crests are generally  $\pm$  perpendicular to the inner part of the perispore, and are reticulately arranged, showing in the meshes included crests which end free and gradually decrease in height distally (ssp. *appendiculata*; plate 4: a, b; 5). In the other subtype the outer part of the perispore covers the inner part completely (ssp. *vivipara*). Between its crests the outer part of the perispore is apparently either adnate to the inner part of the perispore (var. *vivipara*; plate 4: c, d) or continuous with it (var. *neglecta*; plate 4: e, f).

Atypical specimens of ssp. *appendiculata* from southern India (autopolyploids?) show large spherical spores with a low-cristate perispore the outer surface of which shows thread-like irregularities (plate 10: a, b).

**TYPE B.**—Spores with the outer part of the perispore closed, cristate or cristate-undulate, the inner part closed, and adjacent spores in an almost mature sporangium not connected, or connected by a few thread-like structures, or with partly continuous crests (plate 6–8).

In a cristate-undulate perispore, the inner perispore is of the same shape as the exospore; its inner surface is smooth, whereas the outer surface  $\pm$  densely set with spine- or wart-like excrescences and scattered threads (not septae as communicated earlier by me) which connect the outer surface of the inner perispore with the inner surface of the outer perispore. The outer part of the outer perispore is cristate-undulate and the proximal folds may be adnate to the inner part of the perispore. The inner surface of the outer perispore is smooth except for thread-like structures usually running to the inner perispore or rarely connecting the lateral sides of a particular fold. The outer surface of the outer perispore is either about smooth or densely or sparsely beset with minute, spine- or wart-like excrescences (plate 6, 7).

A cristate perispore is similar but lacks folds in its outer perispore. The crests of the outer perispore are  $\pm$  perpendicular to the inner one (plate 8).

Although some species are characterized by either a cristate or a cristate-undulate perispore, the spores of several other species display both types of perispore as well as the intermediates.

This type is very common in the genus. It is found in a few variants relating to the density of folds or crests.

**TYPE C.**—Spores with the outer part of the perispore undulate, the inner part of the perispore closed, membrane-like, and adjacent spores in an almost mature sporangium not connected.

The inner part of the perispore adheres closely to the exospore. Its outer surface is smooth and in a few places, as it seems, connected with the proximal sinuses of the undulations of the other perispore.

The inner surface of the outer perispore is smooth; its outer surface is also smooth or minutely scabrous. The perispore of adjacent spores are not interconnected in mature sporangia.

This type is found in all species of ser. *Bolbitianae* (plate 9). The shape of the outer part of the perispore varies from shallowly to densely undulate; in one species (*B. semicordata*; plate 9: d, e) it may be verrucate.

**TYPE D.**—Spores with the outer part of the perispore closed and undulate, the inner part of the perispore present as a multitude of small, irregular, solitary or aggregated warts or pustules on the exospore; adjacent spores in an almost mature sporangium not connected. Outer perispore similar to that described above, generally situated at a considerable distance from the exospore.

This type is found in the monotypic ser. *Heudelotianae* only (plate 10: C).

With the light microscope it is not possible to discriminate between the types C and D. It should be noticed that ser. *Bolbitianae* and ser. *Heudelotianae* are not closely related.

Erdtman & Sorsa (1971) erroneously reported the absence of a perispore in the type material of *Bolbitis longiflagellata* (= *B. spec. dub.*). The sporangia of the type specimen are immature. A perispore was found in another collection of this taxon (see the Taxonomic Part), which is in accordance with Tardieu-Blot (1966). Stratification of the spore wall as published by Erdtman (1957) for *Bolbitis turrialbae* (= *B. pergamentacea*) could not be confirmed.

The variation in the perispore of the present genus as demonstrated earlier by me with the electron microscope (Hennipman, 1970) is not unique. For instance, Wood (1973) demonstrated a similar variation in *Thelypteris s.l.*, and Tryon & Tryon (1973) in cheilanthoid ferns, both with the use of the S.E.M. A.F. Tryon (1971) in a very interesting study found even exceptional variation in the shape of the spores of *Thelypteris palustris s.l.*, which she thought to indicate a more complex relationship than that supposed till now.

The differences between the perispores of different species in *Bolbitis* provide important taxonomic characters. For instance, the presence of a distinct type of perispore in ser. *Bolbitianae* adds significant weight to its taxonomic recognition.

#### Notes on variations in shape of the perispore

The shape of the perispore in a plant with normal spores shows but little variation. This variation mainly applies to the density of the crests or folds, the height of the crests, etc. A more surprising heterogeneity was occasionally also observed.

- a. The spiny perispore. In some species with a cristate-undulate perispore plants were found with part of their spores with a densely spiny perispore as seen with the light microscope. When studied with the S.E.M. the outer perispore appeared not to be smooth but perforated and to consist of low spines and narrow crests. In one collection sporangia with all of its spores with a spiny perispore occurred next to sporangia

with typical spores. Occasionally sporangia are found with both types of spores and including the intermediate condition (see plate 6: c).

Occasionally a spiny perispore was found in a tetraploid specimen of *B. repanda* and in a specimen of *B. sinensis* (Rock 2913, US; see *B. sinensis* note 2a).

- b. In a few specimens of species with a cristate perispore (e.g. *B. fluviatilis*), spores with an undulate or cristate-undulate perispore were traced.
- c. An observation which seems worth mentioning regards the differences between the spore output of different specimens belonging to one gathering, collected at the same site. I had the privilege to study all specimens of a considerable number of collections prior to the distribution of duplicates. Not rarely the quality of the spores of different specimens was very different. In some cases autopolyploidy is inferred.
- d. Nayar & Kaur (1963: 94) concluded that a branched or trilete laesura, as occasionally found by them in the spores of *B. costata*, *B. presliana*, *Egenolfia helferiana* (= *B. appendiculata* ssp. *appendiculata*), and *Egenolfia sinensis* (= *B. sinensis*), might indicate a comparatively primitive nature of these species. Although I have not paid attention to the abnormal laesuras, I suffice to say that my studies are not in support of their conclusion.

### Size

The spores of a certain plant, and of different collections of one species, show variation in size. Examples are given in the Taxonomic Part.

Differences in the average size of the spores of different species are slight. For details see Erdtman & Sorsa (1971). The average spore size is hard to ascertain from herbarium specimens. Proportionally few sheets have mature spores. Exact measuring is made difficult by the presence of a perispore. In some species noteworthy differences were found in the size of the spores of individual plants. These anomalies are discussed in the notes on the species, when necessary.

In some cases conspicuous variation was found in the size of the spores of the same or different collections. This may reflect, though not necessarily so (Britton, 1972), genetical differences (Manton, 1950). On the other hand, A. F. Tryon (1971) found that mature spores of *Thelypteris palustris* var. *pubescens* could vary up to one-third in length in a single sporangium.

### Number of spores per sporangium

The number of spores in a sporangium of pickled or cultivated material was invariably found to be 64. Sporangia of herbarium material were only investigated when apogamy was suspected (in which case the sporangia should regularly contain 32 spores only).

### Abnormal spores (including aborted S.M.C.'s)

For a taxonomist it is important to know the appearance of abnormal spores and to what extent this kind of spores contributes to the total spore production of a certain leaf.



Therefore, different types of abnormal spores are described. In case the spore output of a plant shows a mixture of normal and abnormal spores, as was frequently found in the *Bolbitis* specimens investigated, it is often impossible, and when possible it may be time-consuming, to find out if this mixture has possibly resulted from e.g. apogamous reproduction.

Abnormal spores are formed as a result of certain genetic and metabolic conditions of the plant.

- a. The genetic condition.—The fertile leaves of the cultivated material were as a rule first studied during meiosis of the S.M.C.'s, and later again as the remaining part of the leaf showed mature sporangia. The shape of the mature spores largely reflects the pairing behaviour of the chromosomes during meiosis. When there is no pairing at all, as found in primary hybrids (e.g. *B. heteroclita* × *rhizophylla*) and sometimes also in autotriploids of both *B. heteroclita* and *B. sinuata*, spore-formation is already prevented early during sporogenesis. As a result the sporangia are eventually filled with 16 or so (mostly) shrivelled bodies enveloped by perisporeal substances, usually located in the central part of the sporangium. When almost complete pairing takes place during sporogenesis (e.g. *B. sinensis*), the sporangium is eventually filled with 64 shrivelled or normally-shaped spores (the latter with a ± typical perispore), which are equally distributed throughout the sporangium. All intermediate types of abnormal spores, and of spore-distribution in the sporangium, are represented. For instance, the abnormal spores were not rarely found to be clustered in the central part of the sporangium and enveloped by a (sometimes very regularly shaped) 'perispore' (plate 10: d-f).

Part of the spores formed by a certain leaf may be small, the size being obviously related to the amount of cytoplasm that becomes associated with the different nuclear parts resulting from an abnormal meiosis. In some primary hybrids minute spherical hyaline bodies were found in the mature sporangium.

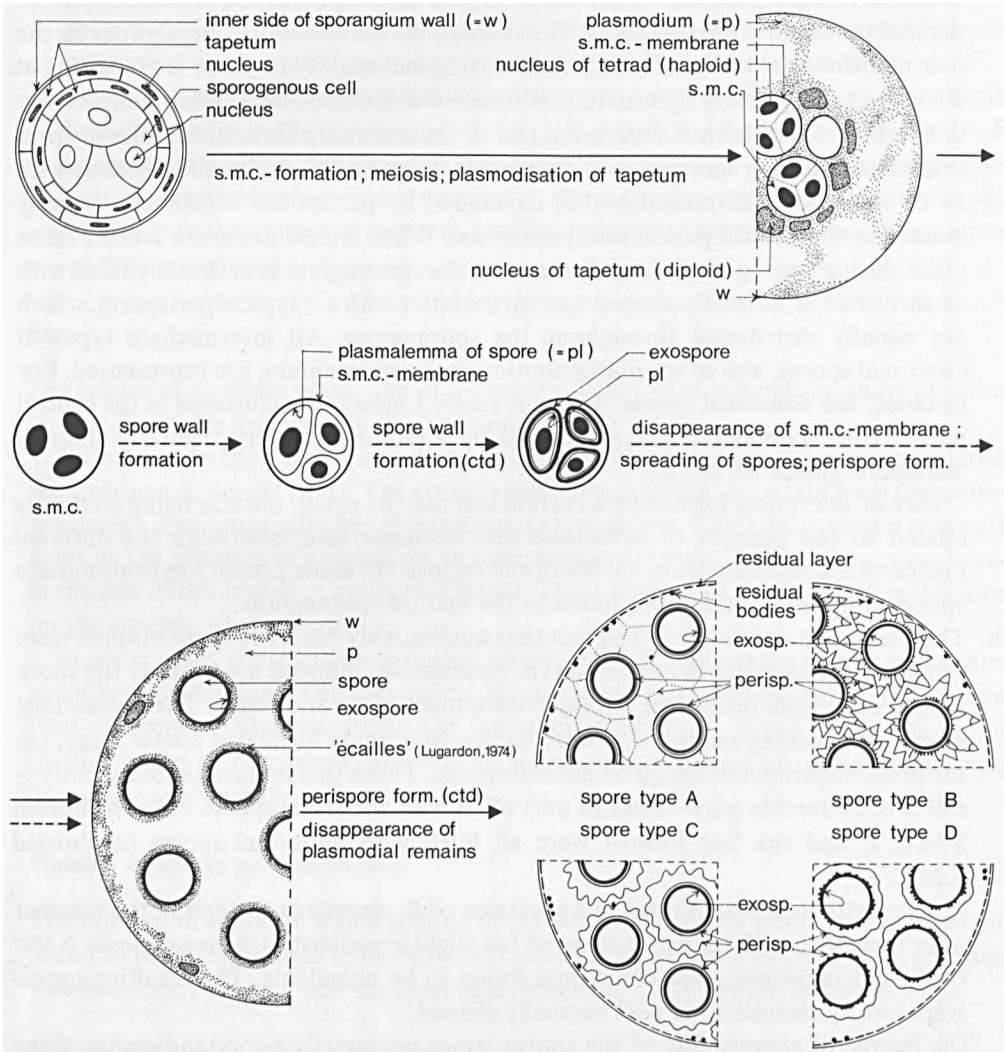
- b. The metabolic condition.—The fact that qualitatively different spore outputs were found in a single plant in cultivation (*B. repanda*, 4n) induced me to study the spore output of a single fertile leaf during development of the sporangia. The few earliest sporangia reaching mature size were empty. Sporangia formed at a later stage, i.e. the great majority, contained 64 normal spores. Those that matured subsequently—still a considerable part—were in part filled with abnormal spores or even aborted S.M.C.'s, and the last formed were all filled with abnormal spores or aborted S.M.C.'s.

The fertile leaf first formed in a specimen of *B. sinensis* at the end of the summer after three years of cultivation showed but slight irregularities during meiosis. A few of the chromosomes were sometimes found to be univalents. The resulting spores were mostly shrivelled, in part normally shaped.

The degree of abnormality of the spores is not necessarily a good indication of the degree of relationship. The spore output of an autotriploid specimen may show (mostly) aborted S.M.C.'s only, whereas the diploid hybrid between two different species may show shrivelled spores.

External factors have an influence on the metabolic condition of the plant (Manton & Sledge, 1954) and thus also on the processes involving sporogenesis.

The 'Fehlschlag' of spores caused by a sudden change in the weather conditions in temperate areas is well known. Braithwaite (1964: 301) reported the complete abortion of almost all sporangia in an *Asplenium* polyploid in South Africa, which in the previous year had produced an abundance of good spores. Manton & Sledge found that a high proportion of newly transplanted adult plants from other latitudes failed to pair their chromosomes successfully when sporangia were first produced in cultivation. A varia-



**Fig. 12.** Schematic illustration of supposed sporogenesis in *Bolbitis*. The diagram illustrating the start of the perispore formation (left hand bottom figure) is based on data from Lugardon (1974) and the present author (unpublished). See also text and Plate 12: a, b.

tion in spores as found in cultivated specimens of *B. repanda* and *B. sinensis* may be caused by the suboptimal conditions in the greenhouses where they were cultivated.

In some cases it was found that the spores of a single sporangium looked in part perfectly normal, in part abnormal. Such a condition can only be explained in view of the genetical differences between meio-spores.

### Notes on sporogenesis

Some aspects of sporogenesis could be studied with the light microscope from the cultivated material that was primarily used for chromosome counts.

During sporogenesis in plants producing normal spores a developmental stage occurs in which the spores are arranged in 16 cross-tetrads (Erdtman, 1945) in the central part of the sporangium within the tapetal plasmodium. At this stage the exospore of the spores looks already mature, and each tetrad is enveloped by a thin hyaline membrane (called here the S.M.C.-membrane) which is best demonstrated using phase-contrast microscopy. In a slightly older sporangium the spores are distributed regularly throughout the sporangium, whereas their exospores show inconspicuous hyaline deposits; an S.M.C.-membrane cannot be recognized anymore. In the oldest stages of the sporangium, the spores are similarly distributed in the sporangium and are enveloped by a perispore. Intermediate stages as regards the earliest stages of perispore formation were only rarely found.

The significance of the S.M.C.-membrane during sporogenesis is also inferred from the study of abnormal spores. The sporogenesis in plants eventually producing shrivelled spores is similar to that of normal spores until the stage in which the S.M.C.-membrane cannot be perceived anymore. This means that abnormal spores with abnormal nuclear contents and often with conspicuous rounded lagging chromosomes show a typical shape and structure when still in a cross-tetrad arrangement and enveloped by a S.M.C.-membrane. See pl. 11: b; fig. 31: b. Shrivelled spores (pl. 11: a; fig. 31: a), however, were never found surrounded by a S.M.C.-membrane; they always do show (inconspicuous) perisporial deposits. These data suggest that the disappearance of the S.M.C.-membrane coincides with the end of exospore formation, with the start of perispore formation, and with the spreading of the spores throughout the tapetal plasmodium in the maturing sporangium. The formation of the perispore after the formation of the exospore during sporogenesis has also been suggested by others (for instance Erdtman, 1969, Lugardon, 1974).

A perispore or perisporial deposit was always found whether the spores are haploid, diploid, or abnormal, clustered, etc. The shape of the perisporial deposit that eventually envelopes a cluster of abnormal spores, or a S.M.C. which retained its spherical shape, might even be rather regular as is typical for a true perispore. Perispore formation does not seem to be exclusively correlated with the production of normal spores.

The structure of the perispore or perisporial material does not show structural differences when studied with the light microscope.

In my previous publication on the spores I demonstrated  $\pm$  spherical, small, acetolysis-resistant so-called 'residue bodies' in the residual material inside the mature sporangium of *B. contaminans* (= *B. angustipinna*). Residual bodies which were also found by Lugardon (1974, 'globules') have been found frequently by me during the study of the perispore (also of other genera) with the S.E.M., and their presence may be related to the formation of the outer perispore (Hennipman, in preparation).

The tapetal origin of the perispore is also inferred from the S.E.M. observations that the perispore of the spores in sporangia of *B. appendiculata* and *B. sinensis* is continuous with the residual material on the inner wall of a mature sporangium and including these residual bodies.

The exospore and the perispore, two apparently quite different structures, are both involved in the construction of the (dia)spore.

In fig. 12 supposed sporogenesis is schematically presented.

### The fine structure of the spores and its significance for classification

From the results of my previous work on the fine structure of *Bolbitis* spores I anticipated that this kind of data about the structure of the spore-walls might provide evidence leading to a better delimitation of especially the higher taxa of *Pteridophytes* (Hennipman, 1970).

Lugardon's (1972, 1974) studies on the spores with the electron microscope fully confirm this. His studies are of particular interest as they provide basic general knowledge about the structure of the spores in different groups of both eu- and leptosporangiate ferns. Lugardon was able to demonstrate a perispore in all the different types of spores he studied. Formerly a perispore was supposed to be lacking in several groups of ferns. In case the perispore—which is always structurally different from the exospore when studied with the transmission electron microscope—is adherent to the exospore, it cannot be perceived with the light microscope, also as the optical qualities of both the exospore and the perispore might be identical. Within the ferns Lugardon recognized three main types of perispore to which I do not assign much systematic weight because of the differences of the perispore as found in otherwise related groups. I am convinced, however, that the eventual significance for classification of the differences within the often heterogeneous and complex structures, called 'perispore', can only be known when more information about its genesis within the different groups has become available.

Because of differences in the complexity of the exospore Lugardon recognized five different types which in the present author's view are easily reduced to three: that found in the eusporangiate ferns (the most complex), that found in the *Osmundaceae* and the *Gleicheniaceae*, and that found in the remaining leptosporangiate ferns (the simplest).

Lugardon (1974: 222) further emphasized the limitations of the light microscope for the recognition of the structure of the exospore '... les couches que la plupart des auteurs ont distingué dans cette paroi n'ont qu'un très lointain rapport avec sa structure réelle'. And this largely holds for the descriptions and drawings of *Bolbitis* spores by Erdtman (1957) and Nayar *et al.*

## 7. KARYOLOGY

The existing knowledge of the chromosome number of *Bolbitis* species is scanty. There is, for instance, not a single record in literature of the chromosome number of the commonest Asian (*B. heteroclita*) and American (*B. portoricensis*) species. The haploid number as far as reported is based on  $n = 41$ . This number is also found in the other genera of lomariopsidoid ferns whereas in *Lomariopsis* also an aneuploid number lower than 41 is known (Roy & Manton, 1966).

I have attempted to study a fair number of different plants of several species of the present genus to find out to what extent polyploidy and hybridization might contribute to the often surprising heterogeneity of the (vegetatively propagating) species. Therefore, material was assembled of Asian representatives. A good start to cultivation was given by Prof. Holttum, who had brought several specimens of the present genus to Kew, collected by him during his trips to Asia, and material of which he kindly sent to Leiden. Additional material was received from several correspondents, especially from Mr. M. G. Price.

Table 1 includes all plants successfully grown in cultivation in Leiden, as well as a number of unpublished records kindly made available to me by Dr. T. G. Walker (Newcastle-upon-Tyne) and Dr. I. Manton (Leeds). Different morphological forms of one species have been given fancy names (added between quotation marks to the specific name) which have no status according to the Code. When the study of the chromosomes at meiosis was completed, the fertile leaf was as a rule not removed until maturation of the greater part of the sporangia. Then the spores were studied and a voucher prepared. Literature records have been included when reliable evidence regarding the identity of the material was available. Species are cited in the same sequence as in the Taxonomic Part. All voucher specimens are in Leiden. Living duplicate specimens obtained by vegetative multiplication can be forwarded on request.

### Notes

#### Ser. *Alienae*.

*B. aliena*. Tetraploid. The specimen investigated by Dr. Walker was taken from a very shady place on limestone.

*B. auriculata*. Tetraploid. This count is not at all a surprise in view of the notorious variation found in herbarium specimens.

#### Ser. *Bolbitianae*.

*B. crispatula* var. *copelandii*. Diploid. Fertile leaves were formed following a period of good growth. The spores of the fertile leaf from which the meiotic chromosome number was obtained were for the greater part shrivelled.

*B. virens* f. *virens*. Diploid. Pl. 12: b. In spite of excellent vegetative growth of both plants, fertile leaves were only occasionally formed during cultivation. Although both collections originate from the same mountain (Doi Suthep), the shape of their fertile leaves is somewhat different. The fertile pinnae formed by the specimen of Van

Table 1. Chromosome counts in *Bolbitis*

No.	Taxon no.	Taxon	Chromosome number		Ploidy
			mitotic	meiotic	
1.	1.	<i>Ser. Alienae</i> <i>B. aliena</i>		n = 82	tetraploid
2.	2.	<i>B. auriculata</i>		n = c.82	tetraploid
3.	5.	<i>Ser. Bolbitianae</i> <i>B. acrostichoides</i>		n = 41	diploid
4.	8.b.	<i>B. crispatula</i> var. <i>copelandii</i>		n = 41	diploid
5.	11.	<i>B. semicordata</i>		n = 41	diploid
6.	14.a.	<i>B. subcrenata</i>	2n = c.82	n = 41	diploid
7.	15.a.	<i>B. virens</i> f. <i>virens</i> 'Van Beusekom'		n = 41	diploid
8.	"	" 'Hennipman'	2n = 82	*	diploid
9.	16.a.	<i>Ser. Egenolfianae</i> <i>B. appendiculata</i> asp. <i>appendiculata</i>		n = 41	diploid
10.	"	"	2n = 82	*	diploid
11.	"	"		n = 41	diploid
12.	"	"		n = 41	diploid
13.	"	"		n = 41	diploid
14.	16.b.1.	<i>B. appendiculata</i> asp. <i>vivipera</i> var. <i>vivipera</i>		n = 41	diploid
15.	18.	<i>B. rhizophylle</i>		n = 41	diploid
16.	"	"		n = 41	diploid
17.	19.	<i>B. sinensis</i> 'Van Beusekom'	2n = 82		diploid
18.	"	" 'Hennipman'		n = 41	diploid
19.	"	" 'Nooteboom'	2n = 82	*	diploid
20.	24.	<i>Ser. Euryostichae</i> <i>B. pergamentacea</i>	2n = 82		diploid
21.	25.	<i>Ser. Heterooclitae</i> <i>B. heterooclita</i> 'cuspidata 2n'		n = 41	diploid
22.	"	" 'cuspidata 3n'		41II+41I or irregular	triploid
23.	"	" 'edenyos difformis'	2n = 82		diploid
24.	"	" 'flagellifera'		n = 41	diploid
25.	"	" 'india'	2n = c.123	**	triploid
26.	"	" 'linneana'		**	triploid
27.	"	" 'melaccensis'		n = 41 or *	diploid
28.	"	" 'tenuissima'		n = 41 or *	diploid
29.	"	" 'typical'		n = 41 or *	diploid
30.	26.	<i>B. sinuata</i>	2n = 82		diploid
31.	"	" 'gigas'	2n = 123	**	triploid
32.	"	" 'sinuata'		n = 41	diploid
33.	"	" 'typical'	2n = 122 + fragm.	**	triploid
34.	27.	<i>Ser. Heudelotianae</i> <i>B. heudelotii</i>	2n = 82	*	diploid
35.	32.	<i>Ser. Quoyanae</i> <i>B. quoyana</i>	2n = 82		diploid
36.	"	"		n = 41	diploid
37.	"	"		n = 41	diploid
38.	"	"		**	triploid
39.	"	"		**	triploid
40.	"	"		**	triploid
41.	33.	<i>B. rivularis</i>		n = 41	diploid
42.	38.	<i>Species incertae sedis</i> <i>B. lonchophora</i>		n = 82	tetraploid
43.	41.	<i>B. repanda</i> 'Holttum'		n = 82	tetraploid
44.	"	" 'München'	2n = c.120	**	triploid
45.	43.	<i>B. subcordata</i>	2n = 82	**	diploid
46.	"	"		n = 41	diploid
47.	H.7.	<i>Hybrids</i> <i>B. heterooclita</i> x <i>rhizophylle</i>	2n = 82	**	diploid
48.	H.11.	<i>B. x singaporensis</i>	2n = 82	**	diploid
49.	H.12.b.	<i>B. x sinuosa</i> nm. <i>foxii</i>	2n = c.80		diploid

\* meiosis slightly irregular, i.e. with but few chromosomes unpaired.  
\*\* meiosis irregular.

Table 1. Chromosome counts in *Bolbitis*

No.	Source	Wild fix / Cultivated	Voucher (H=Hennipman, in L)
1.	Jamaica. Walker (1966: 178, 211)	wild fix	
2.	Ghana. Manton (1959: 80)	not indic.	
3.	Ghana. Walker ex Manton (1959: 80)	not indic.	
4.	SE.Thailand. Van Beusekom 3204 (L)	cultivated	H. 4040, 4050
5.	S.India. Abraham et al. (1962: 364)	wild fix	
6.	Ceylon. Manton & Sledge (1954: 137, 157)	cultivated	
7.	N.Thailand. Van Beusekom 2606 (L)	cultivated	H. 4047, 4120
8.	N.Thailand. Hennipman 3136 (L)	cultivated	H. 4067
9.	Ceylon. Manton & Sledge (1954: 137, 158, pl.8; fig. 82; ' <i>Egenolfia appendiculata</i> ')	wild fix	
10.	SE.Thailand. Van Beusekom s.n.	cultivated	H. 4048
11.	Singapore. Manton in Holttum (1954: 626; ' <i>Egenolfia appendiculata</i> ')	cultivated	
12.	S.India. Abraham et al. (1962: 364, pl.24: fig. 58; ' <i>Egenolfia appendiculata</i> ')	wild fix	
13.	S.India. Abraham et al. (1962: 364, pl.24: fig. 59; ' <i>Egenolfia asplenifolia</i> ')	wild fix	
14.	S.Thailand (doubted, see the Taxonomic Part) Manton & Sledge (1954: 137, 158; ' <i>Egenolfia nodiflora</i> ')	cultivated	
15.	Philippines, Luzon. Price 531 (L)	cultivated	H. 4068
16.	Philippines, Luzon. Price s.n. (L)	cultivated	H. 4066, 4113
17.	N.Thailand. Van Beusekom 2602 (L)	cultivated	H. 4096
18.	N.Thailand. Hennipman 3229 (L)	cultivated	H. 4046, 4060
19.	N.Thailand. Nootboom s.n.	cultivated	H. 4037, 4045
20.	Jamaica. Walker (1966: 178, 210)	wild fix	
21.	Philippines, Luzon. Price 351 (L)	cultivated	H. 4108
22.	Philippines, Luzon. Price 351 (L)	cultivated	H. 4110
23.	Philippines, Negros I. Price 2518A (L)	cultivated	H. 4136
24.	Philippines, Luzon. Price 303 (L)	cultivated	H. 4085
25.	Unknown; in cultivation at B. GRON, L, U	cultivated	H. 4069
26.	Malaysia, Pahang. Holttum s.n. (K)	cultivated	Holttum s.n.
27.	Philippines, Luzon. Price 462 (L)	cultivated	H. 4027
28.	Philippines, Luzon. Price 1073 (L)	cultivated	H. 4106
29.	Philippines, Luzon. Price 1078 (L)	cultivated	H. 4051, 4098
30.	Singapore. Manton in Holttum (1954: 626; ' <i>B. diversifolia</i> ')	cultivated	
31.	Philippines, Luzon. Price 604 (L)	cultivated	H. 4047, 4116
32.	Philippines, Luzon. Price 305 (L)	cultivated	H. 4117
33.	Singapore. Johnson s.n. (L)	cultivated	H. 4052, 4084
34.	Upper-Volta. Arnoult s.n. (ex Van Bruggen)	cultivated	H. 4118
35.	New Guinea. Roy & Manton (1966: 344; ' <i>B. naumannii</i> ')	cultivated	
36.	New Guinea. Walker T 9603 (BM)	wild fix	Walker T 9603
37.	New Guinea. Walker T 9604 (BM)	wild fix	Walker T 9604
38.	New Guinea. Walker T 9615 (BM)	wild fix	Walker T 9615
39.	New Guinea. Walker T 9616 (BM) = Jermy 4945 (BM)	wild fix	Walker T 9616, Jermy 4945
40.	Bismarck Arch., New Britain. Walker T 10052 (BM)	wild fix	Walker T 10052
41.	New Guinea. Walker T 9128 (BM)	wild fix	Walker T 9128
42.	Not indicated. Fabbrri (1963: 308)	not indic.	
43.	Java. Holttum s.n.	cultivated	H. 4023
44.	Unknown; in cultivation (ex M)	cultivated	H. 4022
45.	China, Canton. Roy & Holttum (1965: 155). Holttum s.n.	cultivated	H. 4087
46.	Japan. Kurita (1965: 236)	cultivated	
47.	Philippines, Luzon. Price s.n.	cultivated	H. 4093
48.	Singapore. Manton in Holttum (1954: 626, pl.2: fig.13; p.spec.). Holttum s.n.	cultivated	H. 4077, 4088
49.	Philippines, Luzon. Price 763 (L)	cultivated	H. 4119

Beusekom are narrow and fully acrostichoid (sporangia all over the lower surface) whereas those of Hennipman's are much wider and  $\pm$  hemionitoid (sporangia restricted to the veins). The spores formed by the fertile leaves from which the meiotic counts were obtained are for the greater part abnormal.

Ser. *Egenolfianae*.

*B. appendiculata* ssp. *appendiculata*. Diploid. Although meiosis was seemingly regular, the greater part of the spores that were eventually formed appeared shrivelled.

*B. rhizophylla*. Diploid. Pl. 11: f; fig. 31: f. Vegetative growth was excellent in cultivation. Only few fertile leaves were formed the spores of which were for the greater part abnormal.

*B. sinensis*. Diploid. Pl. 12: d. Growth was very slow in cultivation. In both plants a fertile leaf was formed only once. Spores of both for the greater part abnormal.

Ser. *Euryostichae*.

*B. pergamentacea*. Diploid. Ser. *Euryostichae* comprises plants similar to certain species of *Tectaria* ( $n = 40$ ). The chromosome number given by Dr. Walker further justifies its inclusion in the present genus.

Ser. *Heteroclitae*.

*B. heteroclita*. Diploid and triploid. The plants enumerated below are all 'distinct' as regards the shape of the mature leaves formed when the plants show good growth. Many of such plants have been formerly described as separate species. The similarities in the shape of the juvenile leaves and the leaves formed on bulbils of these plants is manifest.

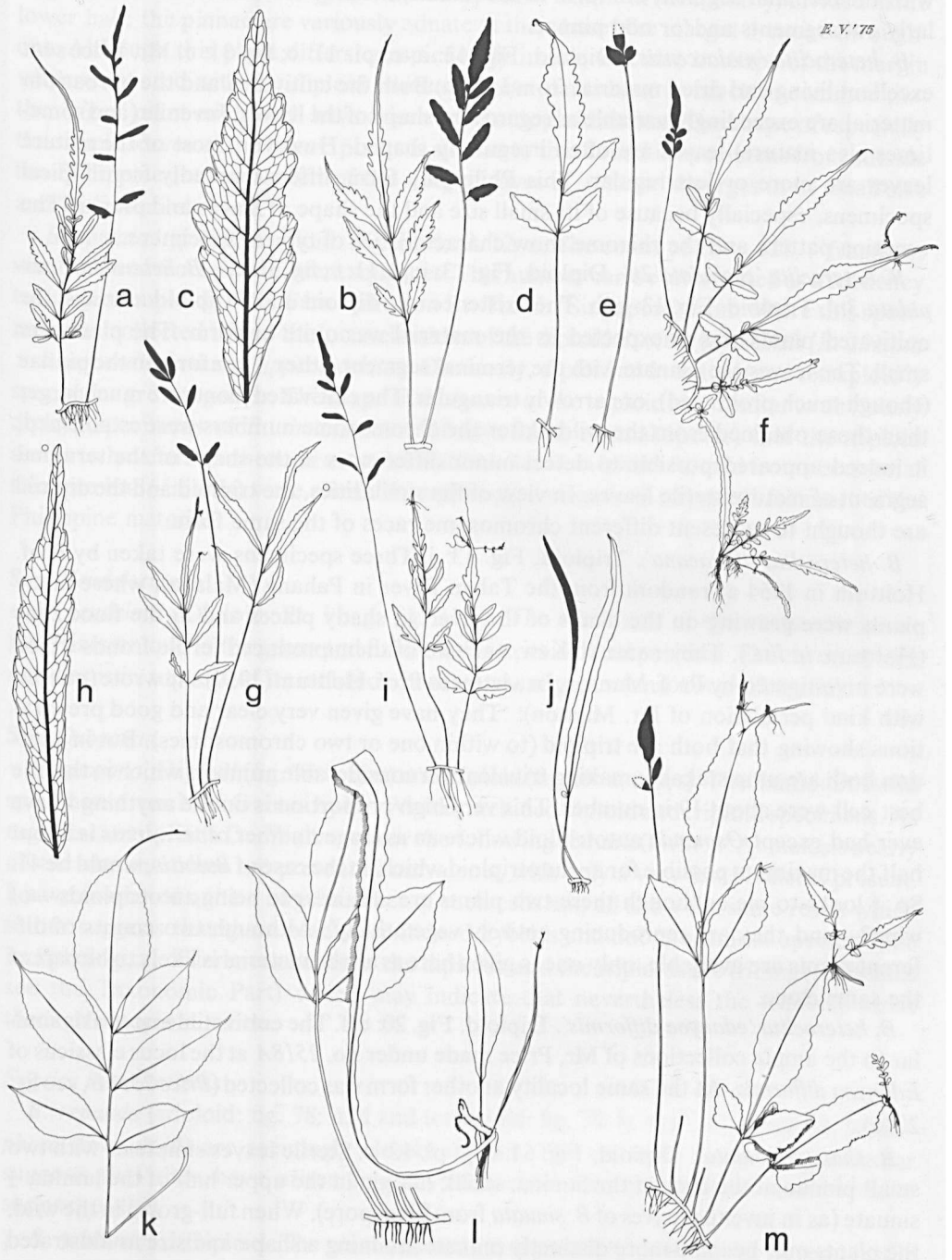
*B. heteroclita* 'typical'. Diploid. Fig. 13: k. A large number of variously shaped juvenile leaves preceded typical leaves during cultivation.

*B. heteroclita* 'flagellifera'. Diploid. Fig. 13: m. The leaf is typical except for its potentiality to form a very long flagellum provided with usually irregularly spaced bulbils. Fertile leaves were only occasionally formed.

*B. heteroclita* 'india'. Triploid. Fig. 13: l. Plants in cultivation at the Botanic Gardens of Berlin, Groningen, and Utrecht are all similar and obviously have the same origin. They are coarse plants the leaves of which form distinct flagella with conspicuous buds. This form occurs in the wild in northeastern India. As the cultivated plant is similar to typical specimens of *B. heteroclita*, it is presumably an autotriploid.

Fig. 13. Cultivated material of *Bolbitis heteroclita*. a, b. *B. heteroclita* 'malaccensis', plants,  $\times 1/5$ ; c. *ibid.*, venation pattern of sterile pinna,  $\times 4/5$ ; d-f. *B. heteroclita* 'tenuissima', sterile and fertile leaves,  $\times 1/5$ ; g. *B. heteroclita* 'cuspidata 3n', plant,  $\times 1/5$ ; h. *ibid.*, venation pattern of sterile pinna,  $\times 4/5$ ; i. *B. heteroclita* 'cuspidata 2n', plant,  $\times 1/5$ ; j. *B. heteroclita* 'linnaeana', plant,  $\times 1/5$ ; k. *B. heteroclita* 'typical', leaf,  $\times 1/5$ ; l. *B. heteroclita* 'india', plant,  $\times 1/5$ ; m. *B. heteroclita* 'flagellifera', plant,  $\times 1/5$  (a. Hennipman 4027, L; b, c. H. 4092, L; d, e. H. 4106, L; f. H. 4090, L; g, h. H. 4110, L; i. H. 4039, L; j. *Holttum s.n.*, K; k. Hennipman 4098, L; l. H. 4069, L; m. H. 4085, L; for chromosome numbers see table 1).





*B. heteroclita 'tenuissima'*. Diploid. Fig. 13: d–f. Rather small plants. Leaves pinnate with the terminal segment conform to the pinnae, the largest leaves often with irregularly cut segments and/or odd pinnae.

*B. heteroclita 'malaccensis'*. Diploid. Fig. 13: a–c; pl. 11: c; fig. 31: c. Mr. Price sent excellent living and dried material from Luzon. Both the cultivated and the herbarium material are exceedingly variable as regards the shape of the leaves. Juvenile (and sometimes also mature) leaves are often irregularly shaped. However, most of the mature leaves are more or less regular. This Philippine form differs markedly from typical specimens, especially because of its small size and the shape of leaves and pinnae. The venation pattern and the rhizome show characteristics of typical specimens.

*B. heteroclita 'cuspidata 2n'*. Diploid. Fig. 13: i; pl. 11: e; fig. 31: e.—*B. heteroclita 'cuspidata 3n'*. Triploid. Fig. 13: g, h. The existence of a diploid and a triploid amongst the cultivated plants was unexpected as the material was quite uniform. The plants are small. The leaves are pinnate with the terminal segment either  $\pm$  conform to the pinnae (though much prolonged), or narrowly triangular. The cultivated plants are much larger than those obtained from the wild. After the chromosome numbers were established, it indeed appeared possible to detect minor differences in the shape of the terminal segment of mature sterile leaves. In view of the similarities, the triploid and the diploid are thought to represent different chromosome races of the same form.

*B. heteroclita 'linnaeana'*. Triploid. Fig. 13: j. Three specimens were taken by Prof. Holttum in 1954 at random from the Tahan River in Pahang (Malaya), where many plants were growing on the banks of the river, in shady places and in the flood zone (Holttum, *in litt.*). They came to Kew, and two of them produced fertile fronds which were investigated by Prof. Manton. In a letter to Prof. Holttum (1957) she wrote (quoted with kind permission of Dr. Manton): 'They have given very clear and good preparations showing that both are triploid (to within one or two chromosomes). But in addition both are unmistakably making trivalents in considerable numbers which in the one best cell were about 19 in number. This very high proportion is unlike anything I have ever had except *Osmunda* autotriploid where an average number of trivalents is about half the maximum possible for an autotriploid which, in the case of *Bolbitis*, would be 41. So it looks to me as though these two plants are very near to being autotriploids—of what?—and they are reproducing entirely vegetatively'. Although two counts of different plants are available, only one is given here as all the material is likely to be part of the same clone.

*B. heteroclita 'edanyoa difformis'*. Diploid. Fig. 20: e, f. The cultivated material is similar to the ample collections of Mr. Price made under no. 2518A at the locus classicus of *Edanyoa difformis*. At the same locality another form was collected (Price 2518B, see fig. 20: o).

*B. sinuata 'sinuata'*. Diploid, Fig. 61: e, g; pl. 12: c. Sterile leaves simple or with two small pinnae at the base of the lamina, small; margin in the upper half of the lamina  $\pm$  sinuate (as in juvenile leaves of *B. sinuata* from Singapore). When full-grown in the wild, the plants may become more distinctly pinnate attaining a shape and size as illustrated in fig. 61: a.

*B. sinuata* 'gigas'. Triploid. Pl. 11: d; fig. 31: d. The cultivated and the wild material (fig. 61; c, d) are similar. The sterile leaves are either simple or (irregularly) divided in the lower half; the pinnae are variously adnate at their base; the margin  $\pm$  entire throughout. Although this plant differs conspicuously in size and also in shape of the margin when compared with the diploid 'sinuata', these plants have so much in common that the 'gigas' plant might well have arisen from autopoloidization. The shape of especially the simple leaves of the 'gigas' plants is similar to that found in specimens from outside the Philippines, whereas that of the simple leaves of 'sinuata' diverges in its small size and its 'juvenile' shape.

*B. sinuata* 'typical'. Triploid. Fig. 61: l; pl. 12: a. The count of  $2n = 122 +$  fragment was obtained from five different squashes. This number can be interpreted as a tendency towards aneuploidy. The Fern Valley on Bt. Timah (Singapore) from where this specimen was collected is also the locus classicus of the diploid *B. × singaporensis* (*B. sinuata*  $\times$  *B. appendiculata* ssp. *appendiculata*). Obviously, diploid and triploid (and tetraploid?) specimens grow together. The shape of the leaves of the triploid is so similar to obviously diploid specimens of *B. sinuata* from Malaya (with normal spores) that the triploid seems to have arisen through autopoloidization. The first leaves formed from accessory rhizome bud (-initials) were small, the upper part sinuate as is typical for most of the Philippine material.

#### Ser. *Heudelotianae*.

*B. heudelotii*. Diploid. Pl. 11: g; fig. 31: g. The small size of the chromosomes at meiosis is unique in the genus and further adds to its isolated position. The chromosome number is in support of its inclusion in the present genus (and not in *Tectaria*).

#### Ser. *Quoyanae*.

*B. quoyana*. Diploid (fig. 69: b, f, m) and triploid (fig. 69: a, e, p, s). The fixations of wild specimens from New Guinea by Dr. Walker included diploid and triploid specimens. As regards the triploids Dr. Walker made the following remark (*in litt.*): 'At meiosis nearly all the chromosomes are present as univalents, with only a very few bivalents present. I have examined quite a large number of such cells and all show the same result which rather suggests that these plants are indeed hybrids and not apogamous species.' The morphological differences between the diploids and the triploids are trifling (for details see the Taxonomic Part) which may indicate that nevertheless the triploids arose through autopoloidization.

#### *Species incertae sedis*

*B. repanda* (triploid: fig. 78: a, d and tetraploid: fig. 78: b, c; pl. 12: e) and *B. lonchophora* (tetraploid) are seemingly closely related. The venation pattern in particular suggests that they have arisen from hybridization. The chromosome number is in support of this.

*B. subcordata*. Diploid. The plant showed good growth in cultivation. Several fertile leaves were formed. They all showed irregular pairing of chromosomes at meiosis and

mature sporangia of all were filled with mainly aborted S.M.C.'s. Possibly a hybrid. The shape of the pinnae of the voucher includes a distinct basal acroscopic lobe and is strongly reminiscent of cultivated material of *B. × singaporensis*. The morphology of the former hybrid gives some indication that *B. subcordata* arose through hybridization. The regular meiosis ( $n = 41$ ) reported by Kurita (1965) is not in support of this.

### Hybrids

*B. × sinuosa* nm. *foxii*. Diploid. Growth slow; up to the present (1976) only sterile leaves have been formed.

*B. heteroclita × rhizophylla*. Diploid. Growth excellent. For a considerable time the plants remained rather small and sterile showing abundant vegetative propagation (also subterminally on the pinnae). After a considerable period of sunny weather in early summer of 1971, much larger sterile leaves as well as two large fertile ones were formed rather suddenly. There was no pairing of chromosomes at meiosis, sporangia showing aborted S.M.C.'s only.

*B. × singaporensis*. Diploid. Growth good. Fertile leaves were formed regularly. There was no pairing of chromosomes at meiosis, sporangia containing aborted S.M.C.'s only. The morphology of this hybrid is of a kind that a relationship with *B. sinuata* does not seem obvious even should it be known that *Bolbitis* species are involved.

### Discussion and conclusions

Chromosome numbers are given for 49 plants: 41 belong to 16 species from 7 series, 5 to 3 species of the group *Species incertae sedis*, and 3 to 3 hybrids. Out of 46 plants belonging to 19 species, 33 (72%) were diploids, 9 (19%) were triploids, and 4 (9%) were tetraploids. These data confirm the idea of the common occurrence of hybridisation and polyploidisation as obtained from the study of herbarium material.

From table 2 it can be seen that the majority of the polyploid specimens are from ser. *Heteroclitae* and ser. *Quoyanae*. The taxonomy of the species of these series is notoriously difficult.

All the triploids are supposed to be autotriploids, as their morphology shows but trifling differences if compared with the diploids. The diploids (and triploids) of especially *B. heteroclita* are strikingly different from each other and include also several distinct dwarfs. During the cultivation of these forms similarities in their juvenile leaves became manifest. There is no correlation between the ploidy and the shape of the plants of *B. heteroclita* investigated. Many of such distinct forms have formerly been described as separate species. See also chapter 17.

Although quite a number of counts are available for series *Bolbitianae* and *Egenolfianae*, only diploids were found.

The present investigation confirms the haploid chromosome number of *Bolbitis* species to be 41 or 82. In one species (*B. sinuata*) a weak indication of aneuploidy was found. Within the lomariopsidoid ferns aneuploidy was earlier demonstrated, as said before, by Roy & Manton (1966) in *Lomariopsis*.

Table 2. Distribution of presently known chromosome numbers according to series, species incertae sedis, and hybrids.					
	total of counts	number of species	2n	3n	4n
<b>SERIES</b>					
Alienae	2	2	-	-	2
Bolbitianae	6	5	6	-	-
Egenolfianae	11	3	11	-	-
Euryostichae	1	1	1	-	-
Heteroclitae	13	2	8	5	-
Heudelotianae	1	1	1	-	-
Quoyanae	7	2	4	3	-
<b>SPECIES</b>					
<i>B. repanda</i>	2	1	-	1	2
<i>B. lonchophora</i>	1	1	-	-	-
<i>B. subcordata</i>	2	1	2	-	-
	<u>46</u>	<u>19</u>	<u>33</u>	<u>9</u>	<u>4</u>
<b>HYBRIDS</b>					
	<u>3</u>	<u>-</u>	<u>3</u>	<u>-</u>	<u>-</u>
	<u>49</u>	<u>19</u>	<u>36</u>	<u>9</u>	<u>4</u>

The chromosomes are rod-shaped and well discernable with the light microscope. They show variation in size, place of the centromere, and occurrence of satellites.

Several plants showed considerable variation in the pairing behaviour of the chromosomes belonging to different S.M.C.'s in different sporangia. Some S.M.C.'s showed bivalents only, whereas others showed a various number of univalents.

Apogamy was not found in any of the specimens. Manton & Sledge (1954) estimated that *c.* 10% of the ferns of Ceylon were apogamous. Abraham *et al.* (1962) stated 8% for pteridophytes in southern India.

Several observations were made implying that, though meiosis was (largely) regular, the greater part of the spores eventually formed was abnormal and mostly shrivelled

(*B. crispatula*, *B. appendiculata* ssp. *appendiculata*, *B. rhizophylla* (both plants), *B. sinensis* (both plants), *B. heteroclita* 'typical', 'flagellifera', 'tenuissima', and 'malaccensis'). Whether this is (solely) caused by external factors remains to be demonstrated.

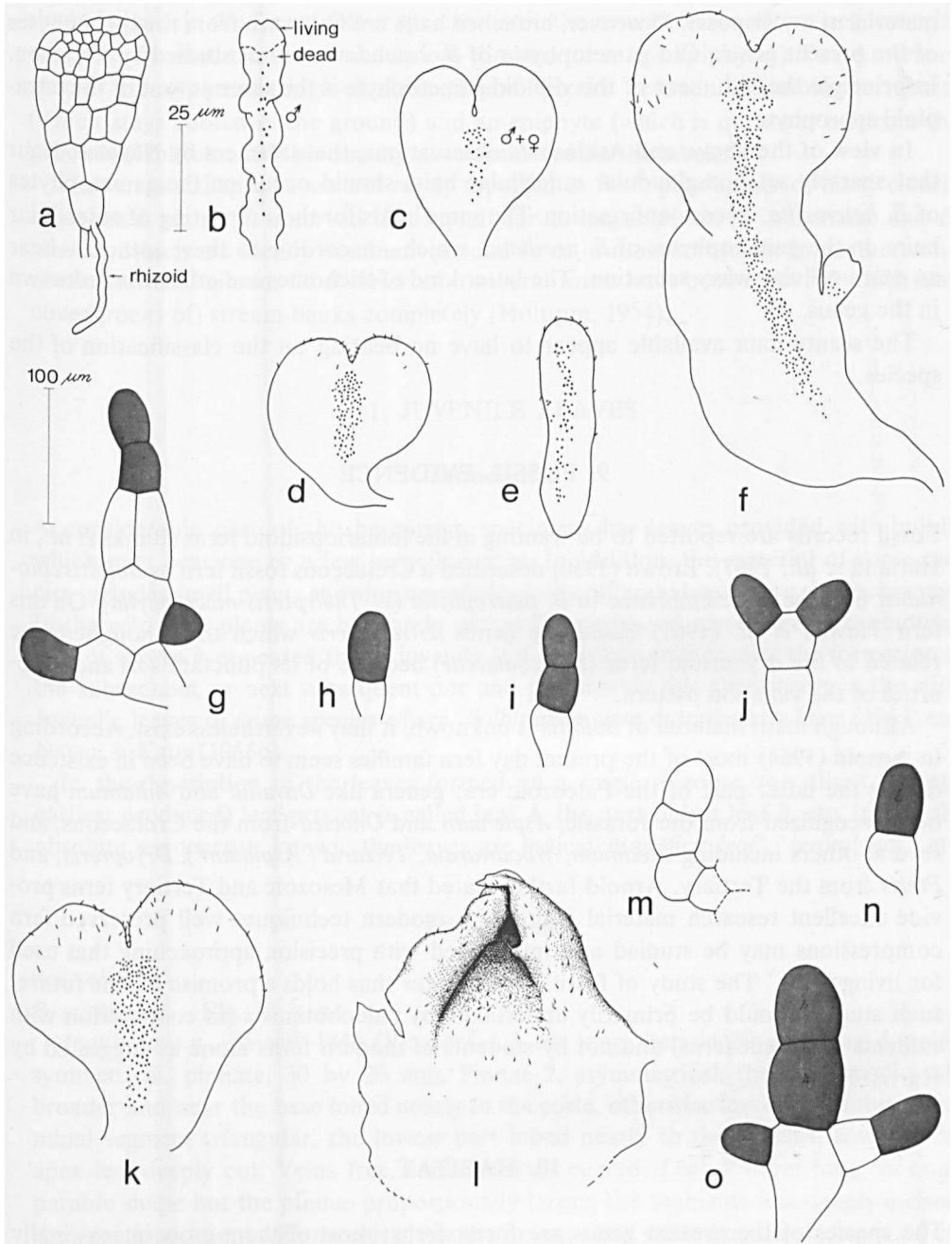
## 8. GAMETOPHYTES

Gametophytes of the present genus have been described by Nayar & Kaur (for references see Nayar & Kaur, 1971) and Atkinson (1973). These authors studied a few species from several series and described the gametophytes as cordate or strap-like, consisting of a relatively thick and wide midrib and two (overlapping) wings of one layer of cells; the (ill-defined) meristem being present in the anterior sinus. Hairs were reported to be generally absent (Nayar & Kaur, 1965b), although in some species marginal hairs were said to occur. Atkinson reported that the sex organs of all lomariopsidoid gametophytes belong to the so-called advanced type. She further compared the gametophyte of *B. repanda* which is subcordate with (un)branched marginal glandular hairs, with that of *B. portoricensis* ('*B. cladorrhizans*') which is strap-like with an ill-defined meristem and devoid of hairs.

Gametophytes of three species were at my disposal; they are here briefly described. Atkinson's material of *B. repanda* proved to have the same origin as mine.

1. The mature gametophytes of *B. angustipinna* are cordate or elongate, measuring up to 5 by 4 mm. The sinus is narrow and the wings somewhat overlap apically. Hairs are absent. Material: *Hennipman 3637* (L). See fig. 14: a-c.
2. Mature gametophytes of *B. heteroclita* are usually elongate with a (sub)cordate apex measuring up to 10 by 4 mm. The apical part bears 2-5-celled glandular hairs especially on the margin, but also scattered on both the upper and the lower surfaces. The hairs are either similar to those occurring on the young sporophytic leaves (which have only one terminal glandular cell) or consist of 2-3 cells all of which are glandular. Small glandular scales occur on the larger gametophytes. Material: *Price 1277* (L), kindly cultivated for the present study by Mr. M. G. Price at Laguna, Philippines. See fig. 14: d-j.
3. Mature diploid gametophytes of the allotetraploid *B. repanda* are cordate or rather elongate with a cordate apex. Cordate gametophytes are up to 10 by 6 mm with non-overlapping wings and a narrow sinus. Few-celled glandular hairs are present on the anterior margin and on the upper and the lower surfaces. Gametophytes that are 9 months old are elongate and measure up to 15 by 10 mm, the meristem firmly appressed to the substratum and the adjacent part of the non-overlapping wings spreading. Glandular hairs like those described for the gametophytes of *B. heteroclita* as well as few-celled scales are present in the apical part, both on the margin as well as on upper and lower surfaces. See fig. 14: k-o.

My observations largely agree with those of Nayar & Kaur and Atkinson. The latter also reported the occurrence of branched hairs on the gametophytes of *B. repanda*. This observation is likely to be erroneous as such hairs were not found in the ample



**Fig. 14.** Gametophytes. a–c. *Bolbitis angustipinna*; cultivated from spores of *Hennipman 3637*, L; b, c,  $\times 6$ .—d–j. *B. heteroclita*, cultivated in the Philippines by Mr. Price from spores of *Price 1277*, L; d–f, habits,  $\times 6$ ; g–j, glandular indument.—k–o. *B. repanda*, tetraploid, cultivated from spores of *Hennipman 4023*, L; k, habit of a 3 months old gametophyte,  $\times 6$ ; l–o, a 9 months old gametophyte; l, habit,  $\times 3$ ; m–o, glandular indument.

material at my disposal. Moreover, branched hairs are unknown from the sporophytes of the present genus. Old gametophytes of *B. repanda* were not studied by Atkinson. In principle the indument of this diploid gametophyte is the same as that of the tetraploid sporophyte.

In view of the above and Atkinson's observations, the statement by Nayar & Kaur that sparsely set non-glandular unicellular hairs should occur on the gametophytes of *B. heteroclita*, needs confirmation. The same holds for their reporting of unicellular hairs on the gametophytes of *B. presliana*, which—according to these authors—bear an extra-cellular waxy secretion. The latter kind of trichomes are otherwise unknown in the genus.

The scanty data available appear to have no bearing on the classification of the species.

## 9. FOSSIL EVIDENCE

Fossil records are reported to be wanting in the lomariopsidoid ferns (Banks *et al.*, in Harland *et al.*, 1967). Brown (1950) described a Cretaceous fossil fern as *Bolbitis coloradica* because of resemblance to *B. macrophylla* (= *Thelypteris macrophylla*). On this fern Tidwell *et al.* (1967) based the genus *Astralopteris* which they thought to be related to the drynarioid ferns (*Polypodiaceae*) because of its punctate sori and properties of the venation pattern.

Although fossil material of *Bolbitis* is unknown, it may nevertheless exist. According to Arnold (1964) most of the present day fern families seem to have been in existence during the latter part of the Paleozoic era; genera like *Davallia* and *Adiantum* have been recognized from the Jurassic, *Asplenium* and *Onoclea* from the Cretaceous, and several others including *Blechnum*, *Woodwardia*, *Tectaria* ('*Aspidium*'), *Dryopteris*, and *Pteris* from the Tertiary. Arnold further stated that Mesozoic and Tertiary ferns provide excellent research material and: 'With modern techniques well preserved fern compressions may be studied and interpreted with precision approaching that used for living ferns.' The study of fossil *Pteridophytes* thus holds a promise for the future; such studies should be primarily undertaken by paleobotanists (in cooperation with students of recent ferns) and not by students of modern ferns alone as suggested by Harris (1973).

## 10. HABITAT

The species of the present genus are forest ferns; most of them grow in seasonally dry forest, others in everwet habitats. One species (*B. heudelotii*) is aquatic and grows also outside the forest belt. They mostly occur at low altitudes; a few species are found above 1500 m.

The greater part of the species prefer rocks, especially near rivers in more or less



shaded places in the forest. Other species root in the ground. Some otherwise terrestrial species are sometimes also found as low-climbers (or as low-epiphytes). Two American species are apparently high-climbers. The difference between a climbing terrestrial (which stays rooted in the ground) and an epiphyte (which is quite cut off from the ground) (Holttum, 1954) is usually not considered on the labels.

The terrestrial species are not rarely reported to form pure stands of many closely aggregated plants. I observed this myself for *B. angustipinna*, *B. crispatula*, and *B. sinensis*, which are locally dominant ground ferns in monsoon forest in northern and northeastern Thailand. Of *B. heteroclita* several forms have been reported which may cover (rocks of) stream-banks completely (Holttum, 1954).

## 11. JUVENILE LEAVES

### Introduction

A considerable part of the herbarium specimens has leaves provided with bulbils which may bear one or a few juvenile leaves. In addition, the material of some species includes small plants showing morphologically different leaves on a single rhizome. In the wild such plants are but rarely met as I experienced myself. From the cultivation of spores it appeared that a juvenile leaf may soon wither after the formation of the subsequent or next subsequent one and presumably this also occurs in the wild. Juvenile leaves of some species of ser. *Bolbitianae* were described by Devi (1963) and Nayar & Kaur (1965b).

In the description of the leaves formed on a single rhizome, the oldest (i.e. the earliest produced) leaf present is called leaf *A*, the next oldest leaf *B*, etc. In case the absolute sequence is known, the leaves are indicated as 'first leaf', 'second leaf', etc.

### Observations

Ser. *Alienae*.

*B. auriculata*.—Fig. 15: a–e.

*Anonymus s.n.*, 25–viii–1846 (P). *Leaf A* 5 cm long. Petiole 20 mm long. Lamina symmetrical, pinnate, 30 by 20 mm. Pinnae 2, asymmetrical, their basicopic side broader and near the base lobed nearly to the costa, otherwise less deeply lobed. Terminal segment triangular, the lowest part lobed nearly to the rhachis, towards the apex less deeply cut. Veins free, some endings curved. *Leaf B* 6 cm long, of comparable shape but the pinnae proportionally larger, the segments less deeply incised, the venation pattern with areoles along the primary and secondary veins. *Leaf C* 10 cm long. Petiole 45 mm long. Lamina 55 by 30 mm, of about the same shape as leaf *B*, but the segments less deeply cut, the veins anastomosing as in the adult stage. Bulbils absent.

*Anonymus s.n.*, 29–viii–1846 (P). *Leaves A* (7 cm long) and *B* (10 cm long) otherwise

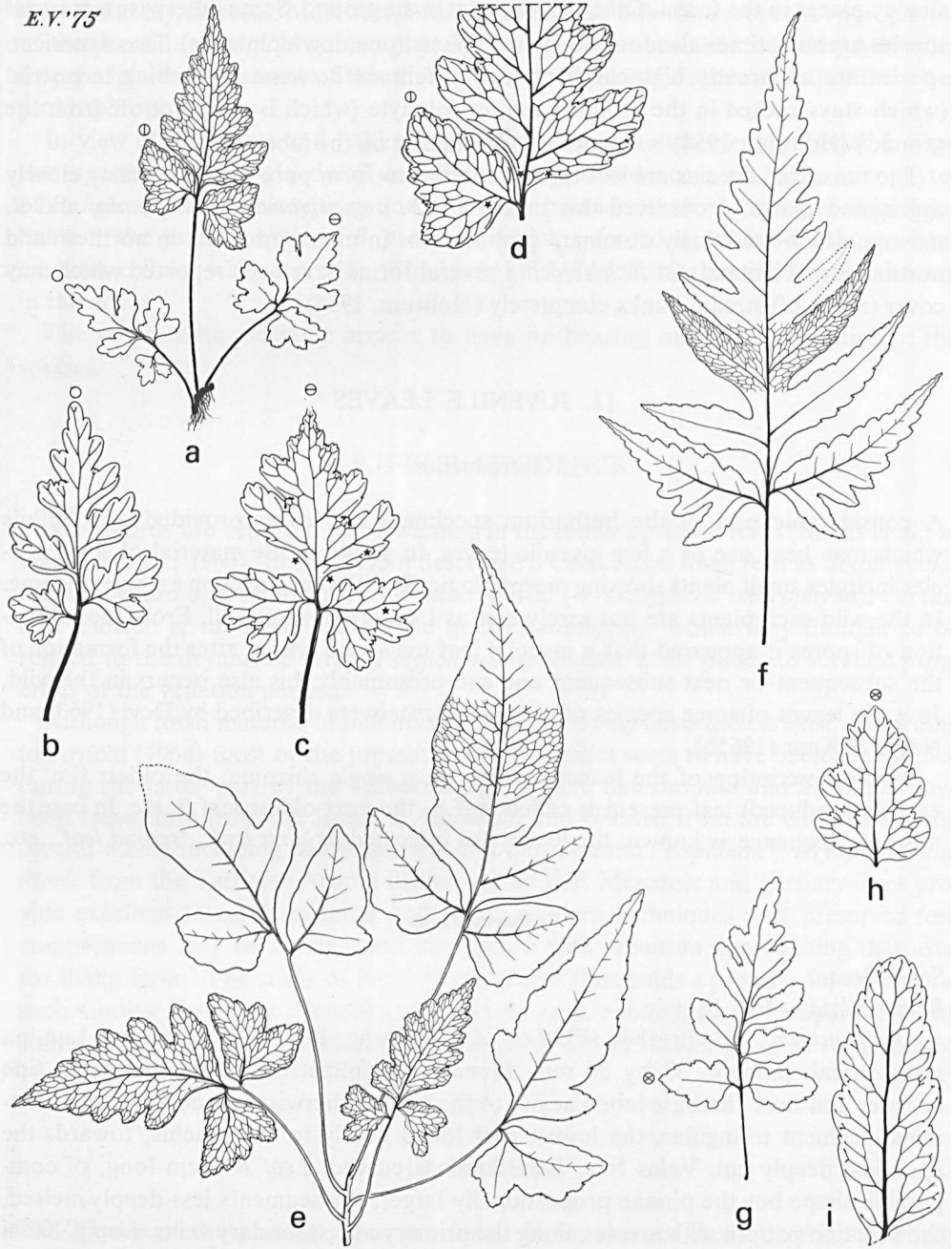


Fig. 15. Juvenile leaves. a-e. *Bolbitis auriculata*. a. plant with 3 leaves,  $\times 1/2$ ; b-d. details of fig. a,  $\times 1$ ; e. plant with 5 leaves,  $\times 1/2$ ; asterisks indicate recurrent veins (a-d. *Anonymus s.n.*, 28-viii-1946, P; e. *Anonymus s.n.*, 25-viii-1946, P).—f. *Bolbitis aliena*,  $\times 1/2$  (Proctor & Mullings 21999, U).—g-i. *Bolbitis bipinnatifida*. g,  $\times 1/2$ ; h, i. pinnae,  $\times 1$  (g, h. Hennisman 4144, L; i. Brauer 12, B).

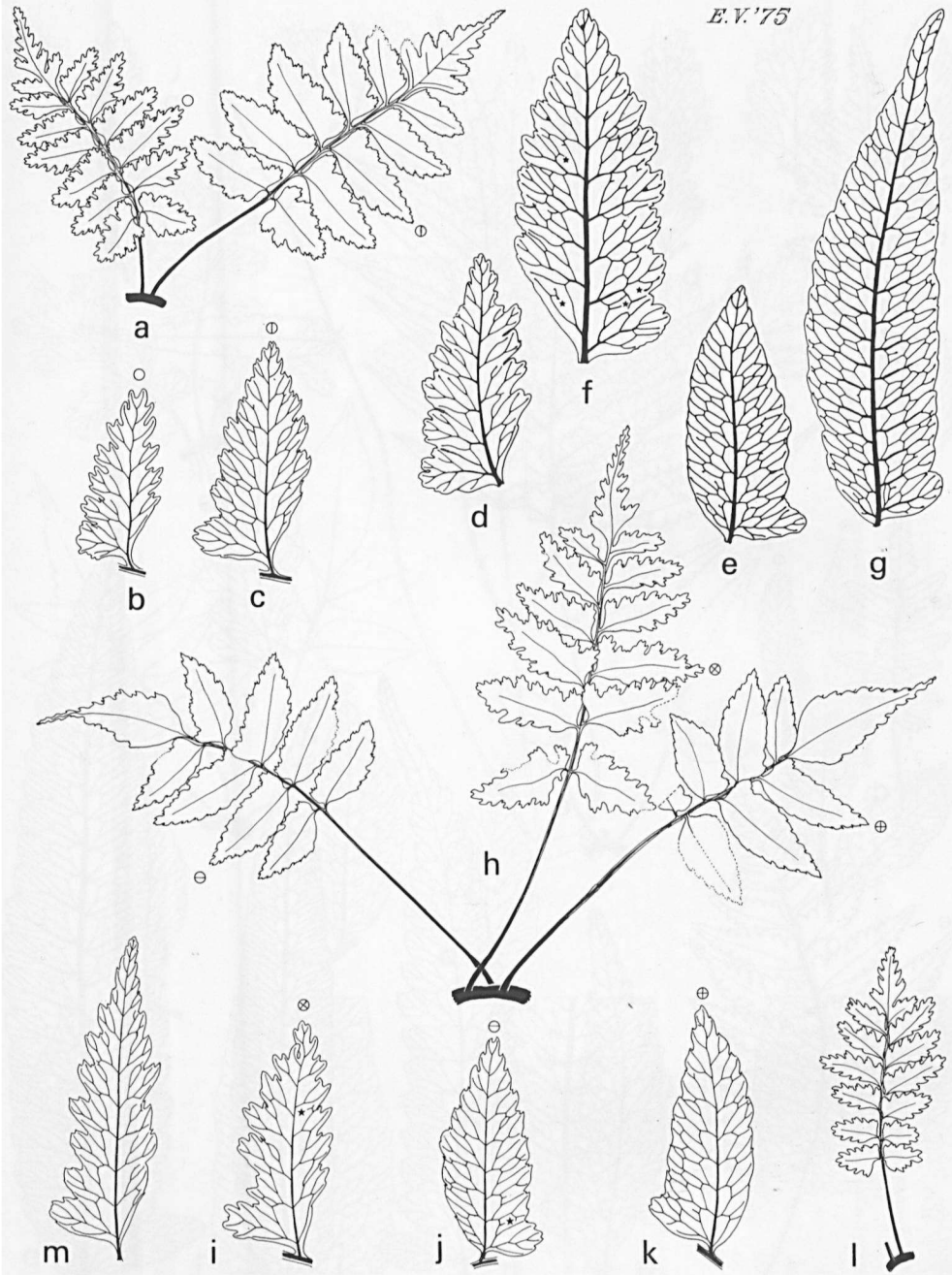
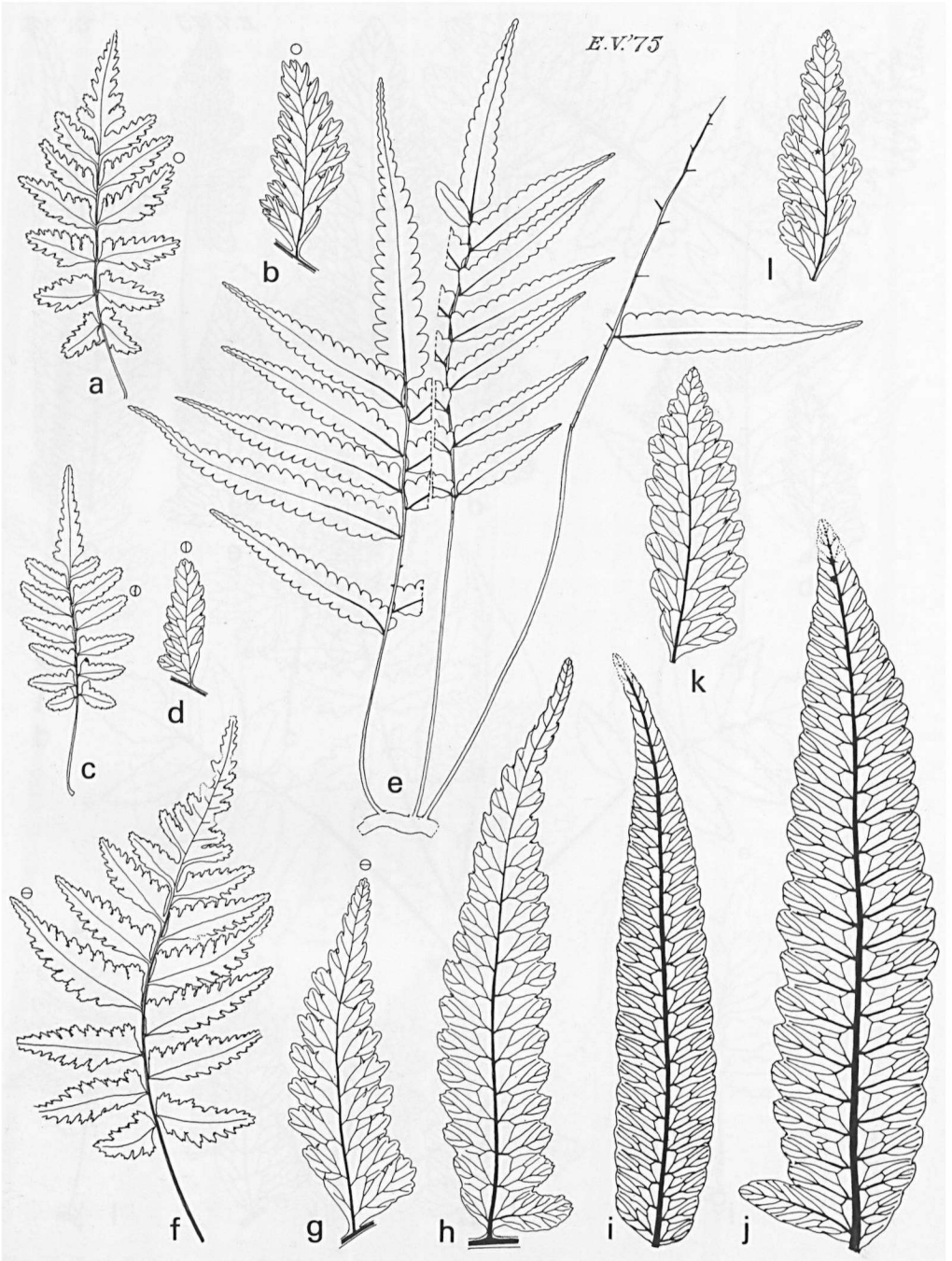
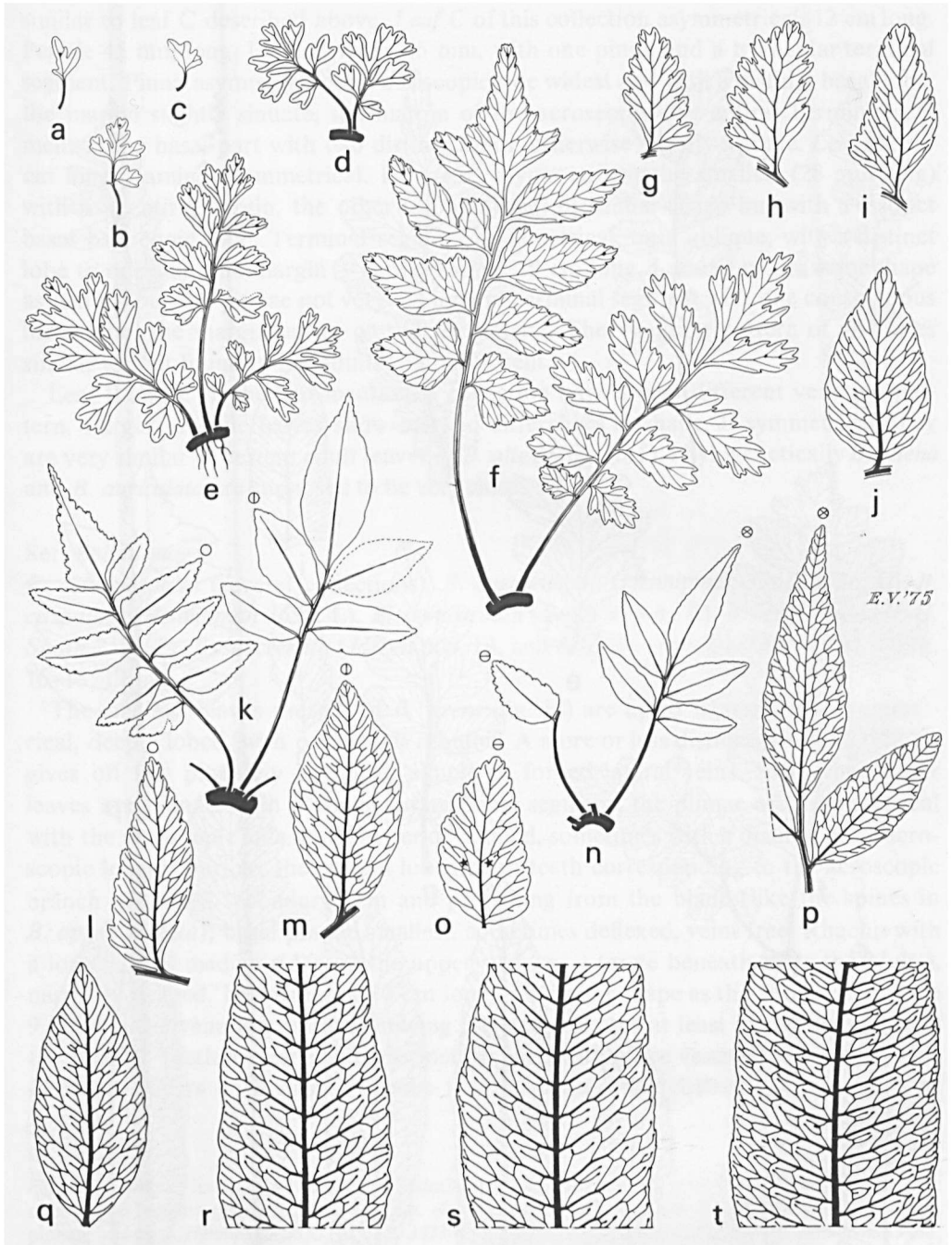


Fig. 16. Juvenile leaves of *Bolbitis acrostichoides*. a. plant with 2 leaves,  $\times 1/2$ ; b, c. pinnae of fig. a,  $\times 1$ ; d. pinna of plant 1 leaf n,  $\times 1$ ; e. ibid. of leaf n + 1,  $\times 1$ ; f, g. pinnae of different leaves of plant 2,  $\times 1$ ; h. plant with 3 leaves,  $\times 1/2$ ; i-k. pinnae of fig. h,  $\times 1$ ; l.  $\times 1/2$ ; m. pinna,  $\times 1$ ; asterisks indicate recurrent veins (a-g. Mugnier Sérand s.n., P; h-k. Mugnier Sérand 3, P; l. Cremers 307, P; m. Schweinfurth 2235, P).

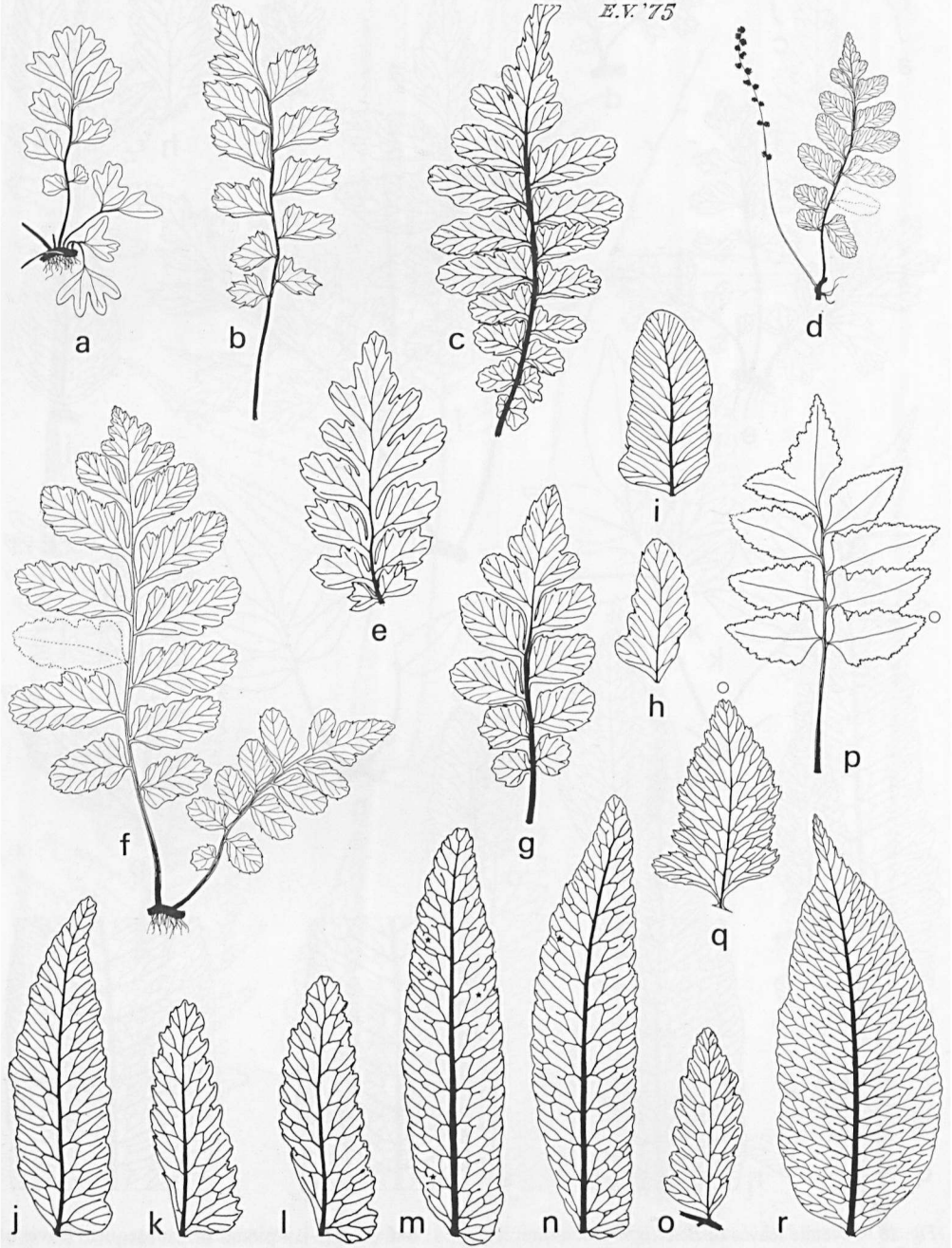


**Fig. 17.** Juvenile leaves of *Bolbitis angustipinna*. a.  $\times 1/2$ ; b. pinna of fig. a,  $\times 1$ ; c.  $\times 1$ ; d. pinna of fig. c,  $\times 1$ ; e. plant with 3 leaves,  $\times 1/2$ ; f.  $\times 1/2$ ; g. pinna of fig. f,  $\times 1$ ; h. pinna,  $\times 1$ ; i. pinna of leaf  $n + 1$  of plant 1,  $\times 1$ ; j. pinna of leaf  $n$  of plant 1,  $\times 1$ ; k, l. pinnae of different leaves of a single plant,  $\times 1$  (a-j. *Hennipman 3361*, L.; k, l. *H. 4146*, L).



**Fig. 18.** Juvenile leaves of *Bolbitis virens*. a. first leaf,  $\times 1$ ; b-f.  $\times 1$ ; g-j. 4 pinnae of 4 subsequent leaves of a single plant,  $\times 1$ ; k. plant with 2 leaves,  $\times 1/2$ ; l, m. pinnae of fig. k,  $\times 1$ ; n. plant with 2 leaves,  $\times 1/2$ ; o, p. pinnae of fig. n,  $\times 1$ ; q-t. pinnae,  $\times 1$ ; asterisks indicate recurrent veins (a-c, g-j, n-p, r-t. *Hennipman 3159*, L; d-f, k-m, q. *H. 3320*, L).

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similar to leaf C described above. *Leaf C* of this collection asymmetrical, 12 cm long. Petiole 45 mm long. Lamina 75 by 45 mm, with one pinna and a triangular terminal segment. Pinna asymmetrical, its basiscopic side widest and with a distinct basal lobe, the margin slightly sinuate, the margin of the acroscopic side entire. Terminal segment in the basal part with two distinct lobes, otherwise slightly sinuate. *Leaf D* c. 13 cm long. Lamina asymmetrical. Pinnae 2, asymmetrical, the smallest (28 mm long) with a  $\pm$  entire margin, the other (38 mm long) of similar shape but with a distinct basal basiscopic lobe. Terminal segment asymmetrical, base oblique, with a distinct lobe to one side, the margin  $\pm$  entire. *Leaf E* 19 cm long. Lamina of the same shape as leaf D, but the pinnae not very dissimilar. Terminal segment with one conspicuous basal lobe, the margin entire or slightly sinuate. The venation pattern of all leaves similar to that found in the adults; bulbils absent.

Leaf B and C of the first-mentioned collection have a very different venation pattern. Larger juvenile leaves show marked differences in shape. If symmetrical, they are very similar to certain adult leaves of *B. aliena* (fig. 15: f). Phylogenetically *B. aliena* and *B. auriculata* are supposed to be very close.

#### Ser. *Bolbitianae*

*B. acrostichoides* (several collections), *B. angustipinna* (Hennipman 3361, 3536, L), *B. crispatula* (Hennipman 3632, L), *B. semicordata* (Perrottet s.n., L), *B. serratifolia* (H. H. Smith 2522, ?), *B. subcrenata* (Jarrett 600, L), and *B. virens* (several collections).—Fig. 16–18; 19: j–r.

The smallest leaves present of *B. virens* (fig. 18) are up to 10 mm long, asymmetrical, deeply lobed, with or without a bulbil. A more or less distinct, flexuous rhachis gives off few pinnately arranged, simple or forked lateral veins. Somewhat larger leaves are pinnate with a triangular terminal segment; the pinnae are asymmetrical with the acroscopic side much better developed, sometimes with a distinct basal acroscopic lobe or auricle, the margin lobed, with teeth corresponding to the acroscopic branch of forked secondary vein and projecting from the blade (like the spines in *B. appendiculata*); basal pinnae smallest, sometimes deflexed, veins free. Rhachis with a longitudinal median ridge on the upper surface,  $\pm$  terete beneath (as in the adults), narrowly winged. Leaves up to 10 cm long of a similar shape as the above, with up to 9 pinnae; the venation pattern showing few anastomoses at least in the basal part of the pinnae. Teeth are especially distinct on parts with a free venation. The latter type of leaves occurs on a single rhizome together with  $\pm$  equal-sized pinnate leaves of

Fig. 19. (Juvenile) leaves. a–d. *Bolbitis appendiculata* ssp. *appendiculata*. a. plant with 4 leaves,  $\times 1$ ; b.  $\times 1$ ; c.  $\times 1/2$ ; d. mature plant,  $\times 1/2$ .—e–i. ssp. *vivipara*. e.  $\times 1$ ; f. plant with 2 leaves,  $\times 1/2$ ; g.  $\times 1$ ; h, i. pinnae,  $\times 1$  (a, b. Hennipman 3855, L; c. H. 3527, L; d. Hansen & Smitinand 12205, C; e–h. Hennipman 3488, L; i. H. 3320, L).—j. *Bolbitis crispatula*, pinna,  $\times 1$  (Hennipman 3632, L).—k–n. *Bolbitis semicordata*, pinnae,  $\times 1$ ; asterisks indicate recurrent veins (Anonymus, L 908.316–446, L).—o. *Bolbitis serratifolia*, pinna,  $\times 1$  (Smith s.n.?).—p–r. *Bolbitis subcrenata*. p.  $\times 1/2$ ; q. pinna of fig. p,  $\times 1$ ; r. pinna of the same plant,  $\times 1$  (p–r. Hennipman 4142, ex Jarrett 600).

quite different shape. These different leaves resemble the adults by having a relatively longer petiole, a firmer texture, far less (3 or 4)  $\pm$  symmetrical pinnae with an entire or crenate margin, a conform terminal segment which is  $\pm$  articulated to the rhachis, and a more intricate venation pattern (with thicker veins) having costal areoles with included excurrent free veins.

A single rhizome of a specimen of *B. virens* sometimes also bears a leaf which is morphologically intermediate between these two types. Such leaves show much variation. For instance, they may have asymmetrical pinnae (as found in the preceding leaf) with an entire margin (as found in the next subsequent leaf), or may have symmetrical pinnae (as found in the next subsequent leaf) with a venation pattern as simple as that of the preceding leaf. It is interesting to see that the degree of complexity demonstrated by a certain feature on a certain juvenile leaf, is not strictly correlated with that as displayed by another feature on the same leaf.

Marked differences between subsequent or next-subsequent leaves also occur in single plants of *B. acrostichoides* (fig. 16) and *B. subcrenata* (in which the number of pinnae per leaf is not significantly different in subsequent or next subsequent dissimilar leaves), and *B. angustipinna* (in which this kind of juvenile leaves may be up to 45 cm long); see fig. 19: p-r and fig. 17, respectively. The adult leaf of the latter species generally bears a large number of pinnae. Separate juvenile leaves of *B. semicordata* and *B. serratifolia* show similar morphological differences. The little material available of *B. crispatula* var. *copelandii* indicates that two successive leaves may be conspicuously different as regards the shape of the pinnae and the size of the leaves. All young juvenile leaves of the species of this series have many, mostly 3-celled, glandular hairs like those found in young adults. Bulbils are present in all juvenile leaves except the smallest, but not in those of *B. crispatula*.

#### Ser. *Egenolfianae*.

*B. appendiculata* ssp. *appendiculata*.—Fig. 19: a-d.

*Hennipman 3835* (L). *Leaf A* (= first leaf?) 8 mm long. Petiole 3 mm long. Lamina simple, asymmetrical, 5 by 6 mm, with three lobes of unequal size. Veins pinnately arranged. *Leaf B* 12 mm long. Petiole 6 mm long. Lamina symmetrical, 6 by 9 mm, with 4 c. 3 mm long lobes. *Leaf C* incomplete, the terminal part lacking. Petiole 7 mm long. Lamina with two alternately placed,  $\pm$  symmetrical pinnae, the lowermost 7 by 6 mm, distinctly lobed, the other smaller. *Leaf D* 20 mm long. Petiole 5 mm long. Lamina symmetrical, widest about the middle, 15 by 12 mm, pinnate with a deeply lobed triangular terminal segment. Pinnae 4, asymmetrical, the two lowest the smallest. *Leaf E* 30 mm long. Petiole 8 mm long. Lamina 22 by 13 mm, otherwise similar to that of leaf D but with a less deeply cut terminal segment and with small basal pinnae. Larger juvenile leaves of the same architecture, but the lamina with more pinnae, the pinna-margin with teeth, the venation pattern more elaborate. Bulbils absent in the earliest juvenile leaves. The smallest leaf is slightly asymmetrical and entire. The basal pinnae of the smallest pinnate leaf are larger than those present on the later formed juvenile leaves which are very similar to the adults.

The pinnate juvenile leaves have teeth on the pinna-margin which project from the



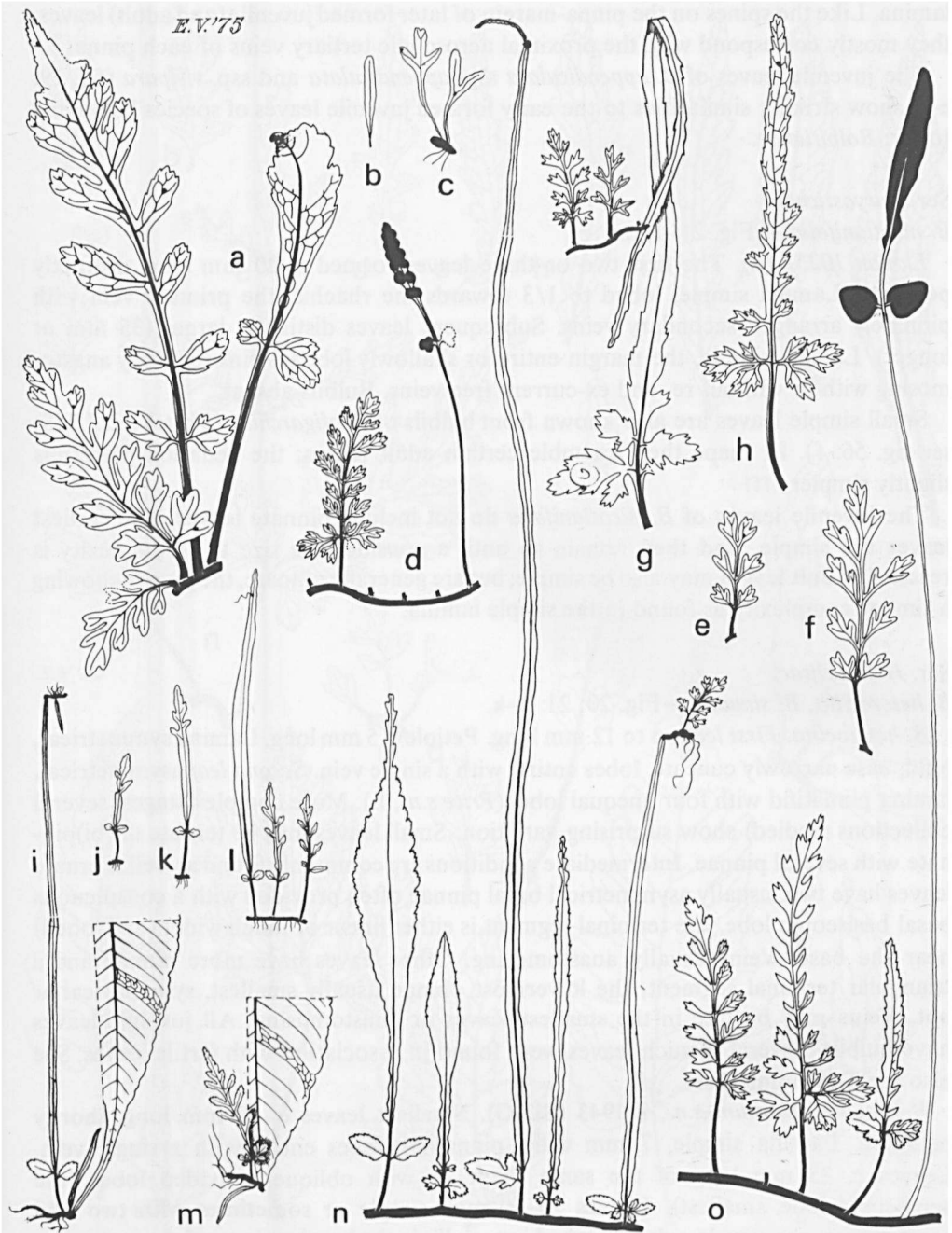


Fig. 20. (Juvenile) leaves of *Bolbitis heteroclita*.—a. plant with 4 leaves,  $\times 1$ ; b. first leaf,  $\times 1$ ; c. second and third leaf,  $\times 1$ ; d. mature plant,  $\times 1$  ('*Edanyoa difformis*'); e, f.  $\times 1$  (ibid.); g, h.  $\times 1$ ; i–n.  $\times 1/2$ ; o. mature plant,  $\times 1$  (aff. '*Edanyoa difformis*') (a. Hennipman 4085, culta, L; b, c. Price 1277, culta, L; d. Price 2518A, L; e, f. Hennipman 4143, L (= Price 2518A, culta); g, h. Edaño PNH 21374, MICH; i. LeRoy Topping 718, US; j, k. LeRoy Topping 444, US; k. ibid., GH; m. Elmer 18068, L; n. Jacobs 7950, L; o. Price 2518B, L, loc. class. of '*Edanyoa difformis*').

lamina. Like the spines on the pinna-margin of later formed juvenile (and adult) leaves, they mostly correspond with the proximal acroscopic tertiary veins of each pinna.

The juvenile leaves of *B. appendiculata* ssp. *appendiculata* and ssp. *vivipara* (fig. 19: e-i) show striking similarities to the early formed juvenile leaves of species belonging to ser. *Bolbitianae*.

Ser. *Euryostichae*.

*B. nicotianifolia*.—Fig. 21: 1, m.

*Ekman 10257* (S). The first two or three leaves formed *c.* 20 mm long, distinctly petiolate. Lamina simple, lobed to 1/3 towards the rhachis, the primary vein with pinnately arranged secondary veins. Subsequent leaves distinctly larger (35 mm or longer). Lamina simple, the margin entire or shallowly lobed. Veins regularly anastomosing with or without re- and ex-current free veins. Bulbils absent.

Small simple leaves are also known from bulbils of *B. oligarchica* (*Skutch 2927*, US; see fig. 56: f). In shape they resemble certain adult leaves; the venation pattern is slightly simpler.

The juvenile leaves of *B. nicotianifolia* do not include pinnate leaves. The earliest leaves are simple, and they remain so until a considerable size and complexity is reached. Adult leaves may also be simple, but are generally pinnate, the pinnae showing a similar complexity as found in the simple lamina.

Ser. *Heteroclitae*.

*B. heteroclita*, *B. sinuata*.—Fig. 20; 21: a-k.

*B. heteroclita*. *First leaf* up to 12 mm long. Petiole *c.* 5 mm long. Lamina symmetrical, bifid, base narrowly cuneate, lobes entire, with a single vein. *Second leaf* asymmetrical, lamina pinnatifid with four unequal lobes (*Price s.n.*, L). More complex stages (several collections studied) show surprising variation. Small leaves may be ternate or (bi)pinnate with several pinnae. Intermediate conditions are commonly found as well. Ternate leaves have two, usually asymmetrical basal pinnae often provided with a conspicuous basal basisopic lobe, the terminal segment is either linear or much wider (and lobed) near the base. Veins usually anastomosing. Other leaves have more pinnae and a triangular terminal segment, the lowermost pinnae usually smallest, symmetrical or not. Veins may be free in the smallest leaves or anastomosing. All juvenile leaves have bulbils. Several of such leaves were found in association with fertile leaves. See also the Taxonomic Part.

*B. sinuata*. *Holtum s.n.*, ii-1943 (SING). Smallest leaves *c.* 20 mm long, shortly petiolate. Lamina simple, 7 mm wide, pinnatifid, lobes entire with a single vein. Leaves *c.* 25 mm long of the same shape or with obliquely divided lobes (the acroscopic lobe smallest). Leaves 25–50 mm, simple or sometimes with two odd basal pinnae, more or less deeply lobed especially in the basal region; veins anastomosing. Larger leaves agreeing with the adult simple leaf though with a less complex venation pattern. All leaves are  $\pm$  coriaceous short-petiolate or sessile. The large juvenile leaves have bulbil initials. The smallest leaf of *B. sinuata* agrees in shape with

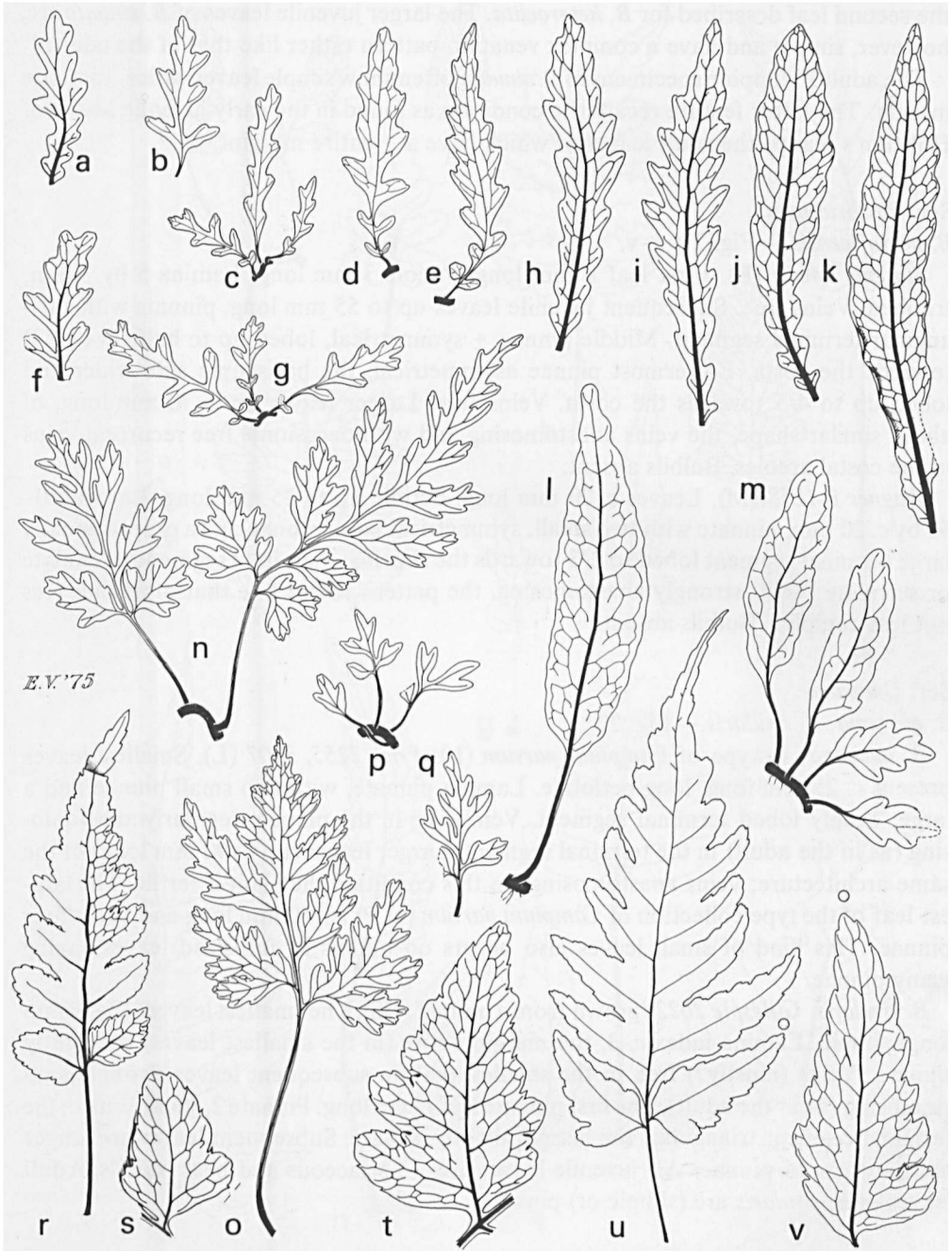


Fig. 21. Juvenile leaves. a-k. *Bolbitis sinuata*,  $\times 1$  (Holtum s.n., SING 20804).—l, m. *Bolbitis nicotianifolia*,  $\times 1$  (Ekman 10257b, S).—n-v. *Bolbitis portoricensis*. n-r.  $\times 1$ ; s. basal pinna of a leaf subsequent to the leaf of fig. r,  $\times 1$ ; t.  $\times 1$ ; u.  $\times 1/2$ ; v. basal pinna of fig. u,  $\times 1$  (n-q. Sintenis 5464b, B; r, s. M. Wagner s.n., M; t-v. Fournier s.n., 1885, P).

the second leaf described for *B. heteroclita*. The larger juvenile leaves of *B. sinuata* are, however, simple and have a complex venation pattern rather like that of the adult.

The adult Philippine specimens of *B. sinuata* often show simple leaves with a  $\pm$  sinuate margin. The latter feature recalls the condition as found in the early juvenile leaves of Holttum's plants, the adult leaves of which have a  $\pm$  entire margin.

Ser. *Portoricenses*.

*B. portoricensis*.—Fig. 21: n–v.

*Sintenis 5464b* (B). First leaf 8 mm long. Petiole 3 mm long. Lamina 5 by 3 mm, trilobed. Veins free. Subsequent juvenile leaves up to 55 mm long, pinnate with a triangular terminal segment. Middle pinnae  $\pm$  symmetrical, lobed up to halfway ( $-2/3$ ) towards the costa. Lowermost pinnae asymmetrical, the basiscopic side wider and lobed up to  $4/5$  towards the costa. Veins free. Larger leaves up to 70 mm long, of about similar shape, the veins anastomosing and with occasional free recurrent veins in the costal areoles. Bulbils absent.

*Wagner i-1858* (M). Leaves *c.* 70 mm long. Petiole up to 25 mm long. Lamina 50–60 by *c.* 20 mm, pinnate with two small, symmetrical basal pinnae and a proportionally large terminal segment lobed to  $2/3$  towards the rhachis; margin of segments crenulate or serrulate. Veins strongly anastomosing, the pattern rather like that of adult leaves but less complex. Bulbils absent.

Ser. *Quoyanae*.

*B. quoyana*, *B. rivularis*.—Fig. 22.

*B. quoyana*; isotype of *Campium parvum* (L); *Price 2255, 3007* (L). Smallest leaves present *c.* 25 mm long, long-petiolate. Lamina pinnate, with two small pinnae and a large, deeply lobed terminal segment. Veins free in the pinnae, regularly anastomosing (as in the adult) in the terminal segment. Larger leaves (up to 90 mm long) of the same architecture; veins anastomosing. In this condition the plant is fertile. The largest leaf of the type collection of *Campium parvum* (at P) is 150 mm long and bears four pinnae. This kind of small leaves also occurs on bulbils of full-sized leaves having many pinnae.

*B. rivularis*. *Gillespie 2622* (grown from a bulbil?, US). The smallest leaves (12–70 mm long) simple. Lamina index *c.* 3, the margin entire (in the smallest leaves) or slightly sinuate. Veins (mostly?) free in the smallest leaf, in subsequent leaves strongly anastomosing (as in the adult). The first pinnate leaf 12 cm long. Pinnate 2, small, entire; the terminal segment triangular, the margin slightly sinuate. Subsequent leaves are longer and have more pinnae. All juvenile leaves are  $\pm$  coriaceous and bear bulbils. Adult leaves of *B. rivularis* are (simple or) pinnate.

*Species incertae sedis*.

*B. repanda*.—Fig. 23: a–f.

*Hennipman 4139* (L), a tetraploid specimen in cultivation. *First leaf* up to 15 mm long. Petiole 5–7 mm long. Lamina simple, as long as wide, the base broadly acute, otherwise

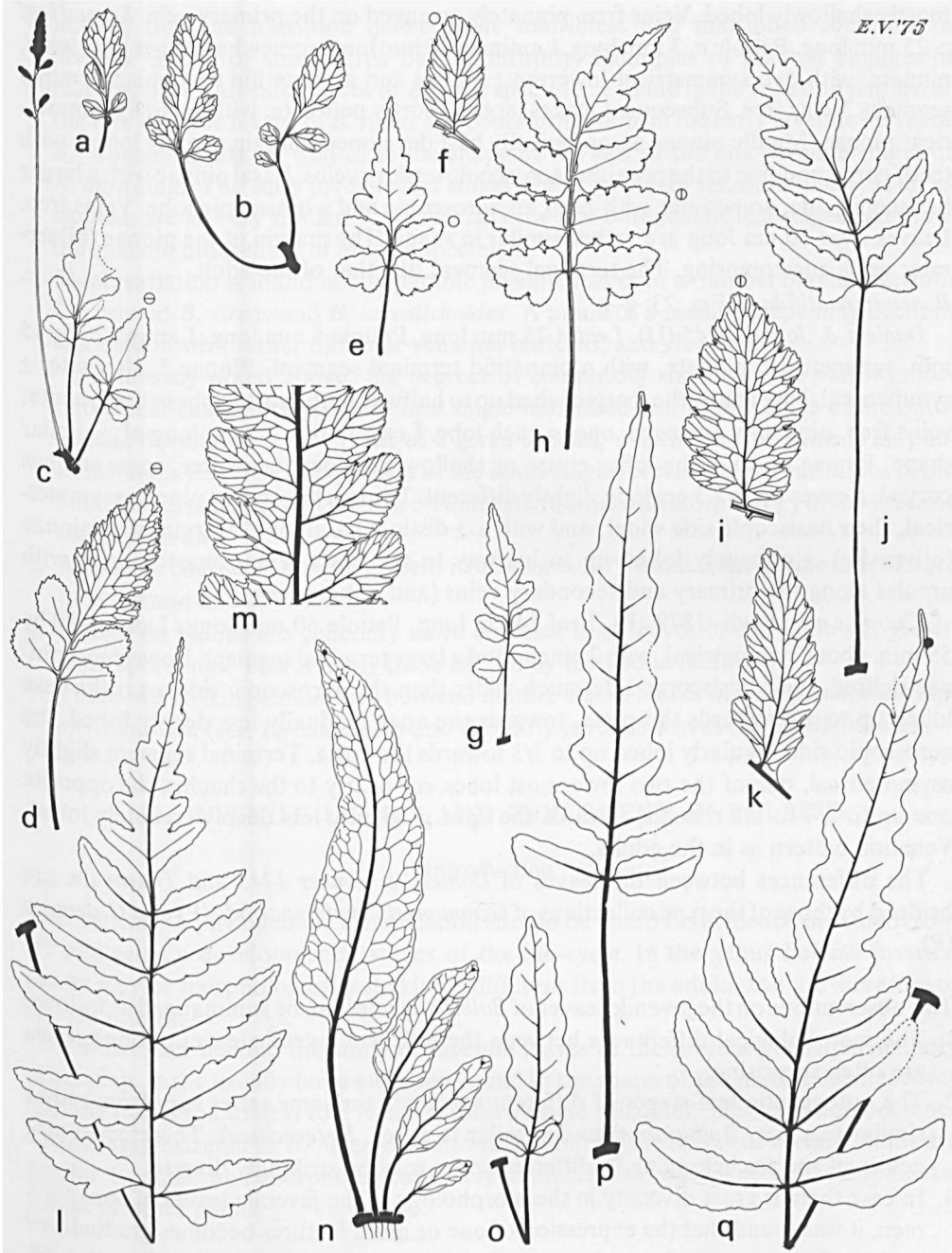


Fig. 22. (Juvenile) leaves. a-m. *Bolbitis quoyana*. a.  $\times 1$ ; b. plant with 2 leaves,  $\times 1$ ; c. mature plant,  $\times 1/2$  ('*Campium parvum*'); d. sterile leaf of fig. c,  $\times 1$ ; e.  $\times 1/2$ ; f. pinna of fig. e,  $\times 1$ ; g, h.  $\times 1/2$ ; i. pinna of fig. h,  $\times 1$ ; j.  $\times 1/2$ ; k. pinna of fig. j,  $\times 1$ ; l.  $\times 1/2$ ; m. venation pattern of central part of a central pinna,  $\times 1$  (a-d. *Schlechter 16163*, L, isotype of *Campium parvum*; e, f, h, i. *Price 3007*, L; g, j-m. *Price 2255*, L).— n-q. *Bolbitis rivularis*. n. plant,  $\times 1$ ; o-q.  $\times 1/2$  (*Gillespie 2622*, UC).

mostly shallowly lobed. Veins free, pinnately arranged on the primary vein. *Second leaf* c. 25 mm long. Petiole c. 7 mm long. Lamina c. 20 mm long, somewhat longer than wide, pinnate, with two symmetrical lowermost pinnae and a pinnatifid triangular terminal segment. Veins free. Subsequent leaves larger, shortly petiolate, with up to 8 asymmetrical pinnae. Middle pinnae acroscopically best developed, margin acutely lobed, with teeth corresponding to the proximal acroscopic tertiary veins. Basal pinnae with a larger basiscopic side, sometimes with both an acroscopic and a basiscopic lobe. Veins free. Leaves over 10 cm long are rather similar in shape. The margin of the pinnae (bi)serate; veins anastomosing. The terminal segment like that of the adult.

*B. semipinnatifida*.—Fig. 23: g–p.

*Daniëls & Jonker 1245* (U). *Leaf A* 25 mm long. Petiole 5 mm long. Lamina 20 by 15 mm, symmetrical, pinnate, with a pinnatifid terminal segment. Pinnae 3, alternate, ± symmetrical, base acute, the margin lobed up to halfway to the costa, lobes entire, acute; veins free, pinnately arranged, one to each lobe. Leaves up to 3.5 cm long of ± similar shape. Pinnae up to 4, the lobes entire or shallowly divided; veins free, some endings curved. Leaves up to 8.5 cm long slightly different. The two lowermost pinnae asymmetrical, their basiscopic side wider, and with a ± distinct basal lobe. Margin of all pinnae (otherwise) ± crenately lobed up to halfway to the costa. Veins anastomosing with areoles along the primary and secondary veins (and in between).

*Thurm s.n.*, 31–vii–1879 (P). Leaf 14 cm long. Petiole 60 mm long. Lamina 80 by 55 mm, about symmetrical, with 2 pinnae and a large terminal segment. Lowermost pinnae deltoid, their basiscopic side much wider than the acroscopic side, near the base lobed up to 3/4 towards the costa, towards the apex gradually less deeply lobed, the acroscopic side regularly lobed up to 1/3 towards the costa. Terminal segment slightly asymmetrical, one of the two lowermost lobes cut nearly to the rhachis, the opposite one up to 3/4 to the rhachis, towards the apex gradually less deeply crenately lobed. Venation pattern as in the adults.

The differences between the leaves of *Daniëls & Jonker 1245* and *Thurm s.n.* are bridged by those of the type collections of *Gymnopteris semipinnatifida* (P) and *G. dentata* (P).

The observations on the juvenile leaves of *Bolbitis* species can be summarized as follows:

1. The morphological differences between the different juvenile leaves of one species are often surprising.
2. The ontogenetic leaf stages of different species in the same series vary from rather similar (e.g. ser. *Bolbitianae*) to dissimilar (e.g. ser. *Heteroclitae*). Therefore, ontogenies of species belonging to different series may be strikingly diverse.
3. In case there is great diversity in the morphology of the juvenile leaves of one specimen, it was found that the expression of one or more features becomes gradually or ± abruptly more complex; subsequent leaves on a single rhizome may be quite different in various respects. Abrupt changes may be observed e.g. in the shape of the terminal segment and the pinnae of juvenile leaves of *B. virens* and *B. acrostichoides*, and in the venation pattern of early juvenile leaves of *B. auriculata*. Wagner (1952)

noticed that the transition between the midribless and midribbed condition in juvenile leaves of some ferns occurs abruptly. Examples of gradual changes in features of the juvenile leaves of *Bolbitis* species are found in the venation pattern of the late juvenile leaves of *B. virens* and *B. acrostichoides*, in the early juvenile leaves of *B. semipinnatifida*, as well as in the shape of the leaf of the late juvenile stages of *B. auriculata*. The early juvenile leaf stages of the species of ser. *Bolbitianae*, as far as studied, are all very similar. It is especially the late ontogenetic leaf stages that show the specific differences of mature specimens.

4. Much variation is found in comparable juvenile leaves of a number of plants in both the related *B. virens* and *B. acrostichoides*. A pinna of a certain shape may occur in association with rather different venation patterns, and vice versa.

As already noted above, the degrees of complexity shown by the various morphological characters as found in a single individual leaf at any stage of the ontogenetic development in a plant of a given species, may not be the same. This phenomenon is less clearly expressed in the adult stages. Nevertheless, variations in the adult leaves can be predicted to a certain extent, when the morphology of the juvenile stages is known.

5. A specific character may be present in all stages, for instance, the coriaceous texture in *B. sinuata* and *B. rivularis*.
6. Leaves on bulbils are generally more complex than leaves of the same size grown from sporelings. This is likely to be caused by metabolic factors.
7. There are striking similarities between mature sterile leaves of *B. appendiculata* ssp. *appendiculata* (ser. *Egenolfianae*) and the early juvenile leaves of ser. *Bolbitianae*.

## 12. JUVENILE LEAVES AND PHYLOGENY IN BOLBITIS

### Introduction

Theoretically a phylogenetic classification should be based on evidence obtained from all ontogenetic developmental stages of the life-cycle. In the genus *Bolbitis* juvenile plants may be morphologically strikingly different from the adults and are therefore of special interest.

Another fact making the study of juvenile leaves of the present genus particularly promising, is the usually large variation found in the shape of the mature sterile leaves (i.e. the leaves found next to a fertile leaf on a single rhizome). This variation becomes surprisingly extreme in *B. heteroclita* in which adult sterile leaves of certain plants are similar to small and morphologically very characteristic ontogenetic developmental stages of other plants.

The fact that subsequent stages of a certain life-cycle may be morphologically strikingly different has fascinated especially zoologists. It inspired Haeckel (1866) to state that ontogeny is the recapitulation of phylogeny. Thus phylogeny is the mechanical cause of ontogeny. Haeckel's law has received great attention. However, several authors have

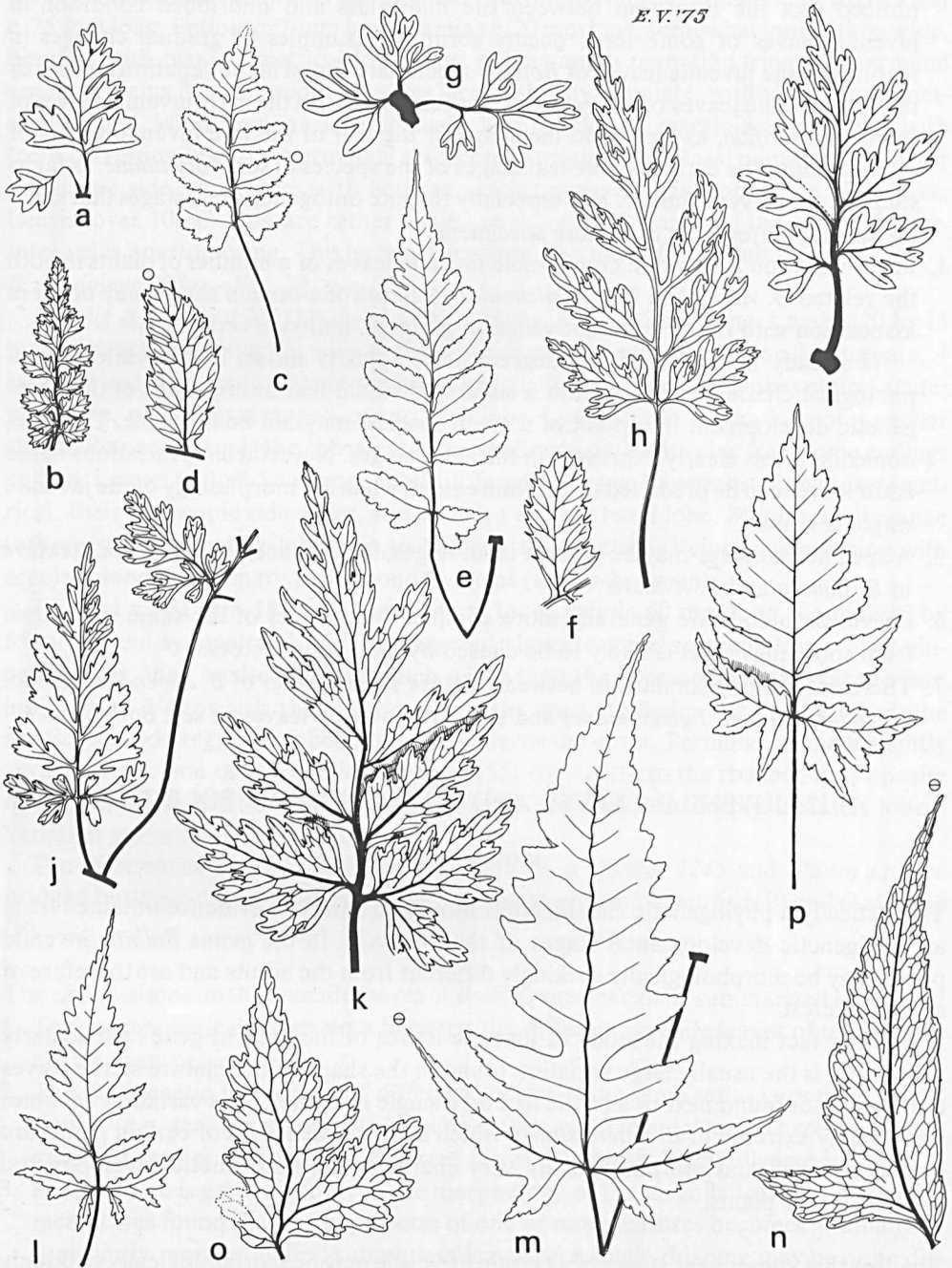


Fig. 23. Juvenile leaves. a-f. *Bolbitis repanda*. a. first and second leaf,  $\times 1$ ; b, c.  $\times 1/2$ ; d. pinna of fig. c,  $\times 1$ ; e.  $\times 1/2$ ; f. pinna of fig. e,  $\times 1$  (*Hennipman 4139*, tetraploid, drawn from cultivated material ex *Holtum*, Java).—g-p. *Bolbitis semipinnatifida*. g. plant with 3 leaves,  $\times 1$ ; h, i, k.  $\times 1$ ; j. plant with 2 leaves,  $\times 1$ ; l, m.  $\times 1/2$ ; n. basal pinna of fig. m,  $\times 1$ ; o. basal pinna,  $\times 1$ ; p.  $\times 1/2$  (g-i, k. *Daniëls & Jonker 1245*, U; j, l-n. *Le Prieur s.n.*, P, type of *Gymnopteris semipinnatifida*; o. *ibid.*, P, type of *Gymnopteris dentata*; p. *Thurm s.n.*, P).



—often independently—objected to this theory by stating just the reverse. They include the zoologists Boas (1881, cited by Diels, 1906), Garstang (1922), Koltzoff (1936, cited by Takhtajan, 1959), Hardy (1954), and De Beer (1951), and the botanists Diels (1906) and Takhtajan (1959).

Diels's interesting book on precocious fructification was written following a trip to Australia. He adhered to the view that fructification is the result of quantitative changes in the physiology and not connected with a certain developmental stage. 'Aus allem geht mit Bestimmtheit hervor, dass in den tropischen und subtropischen Ländern bei vielen Arten das Verhältnis zwischen vegetativer Entfaltung und generativer Reife unbeständig ist, d.h. dass irgend welche Abhängigkeit des Blühens von einer bestimmten Phase des vegetativen Wachstums nicht besteht' (p. 19). He accepted Boas's idea of neoteny to indicate the situation by which 'das Tier auf einer Entwicklungsstufe geschlechtsreif wird, auf welcher seine übrigen Organe—alle oder wenige—nicht die volle Ausbildung erreicht haben und dann überhaupt diese Ausbildung nicht erreichen' (p. 115), and pointed out that certain retentive ontogenetic stages, when fertile, might become the roots ('Phylembryonen', p. 110) of a new phylogeny. Garstang said it more concisely: 'Ontogeny does not recapitulate Phylogeny: it creates it.' He and De Beer stressed the fact that the real phylogeny (of *Metazoa*) has never been a direct succession of the adult forms, but a succession of ontogenies or life-cycles. Thus, new characters may appear at all stages of ontogeny.

Zimmermann (e.g., 1959) paid considerable attention to the significance of the ontogeny of a plant for the understanding of its phylogeny. He used the term 'Hologenese' to indicate the history of a plant in terms of its past life-cycles. As regards Haeckel's law, he is of the opinion that the juvenile stages of a plant often recapitulate the ancestor. In his first edition of 'Die Phylogenie der Pflanzen' (1930) he roughly estimated that Haeckel's law would be true for 80%. Neoteny is mentioned in the second edition of his book (1959) as an (obviously rare) case of heterochrony. Neoteny as circumscribed by Diels affords a means by which an organism is able 'to escape from specialization' (Hardy) or to 'despecialize' (Takhtajan). According to Takhtajan (who took the idea of neoteny from Koltzoff) it is very probable that the neotenic forms with their simpler phenotype but with their complex genotype, retain evolutionary plasticity, as they have lost the burden of specialization.

Little is known about the significance of neoteny (*s.l.*) for the phylogeny of the *Pteridophytes*. Diels gave examples of how neoteny might have played a role in the creation of some ferns, including *Phylloglossum* and some *Bolbitis* (*Gymnopteris*) species. Unfortunately, the plants that Diels thought to represent different neotenic forms of a single *Bolbitis* species, belong to different species. Williams (1927) pointed out that the stele of *Antrophyum* cannot be properly explained by reduction; he convincingly demonstrated that it can be regarded much better as an arrested development, the arrest having come into operation at an early stage. Van Steenis (1948) communicated Dr. Donk's view on the identity of *Holttumiella* Copeland, which was originally assigned to the lindsaeoid ferns. Donk regarded *Holttumiella* simply as a neotenic *Taenitis* to which it was formally reduced by Holttum (1968). Kramer (1957: 128) noticed that Haeckel's law cannot be well applied to the different leaf shapes occurring in certain *Lindsaea* species: 'simply

pinnate leaves appear in the development of a single plant before the bipinnate ones, but in a phylogenetic sense they are very probably more derived.' Devi (1963) and Nayar & Kaur (1965b) reported an indument exclusively confined to the juvenile leaves of ser. *Bolbitianae*. Devi discussed the possible phylogenetic significance of this finding accepting Haeckel's ideas. In the stimulating book 'The Phylogeny and Classification of the Ferns' (Jermy *et al.*, eds., 1973), based on papers read at the International Symposium on Ferns at London, neoteny is only mentioned by De la Sota as a 'rare phenomenon' (p. 231) to explain the foliar dichotomy of *Dipteris*; Wagner (*ibid.*, p. 249) still listed recapitulation as one of the criteria for the determination of primitive states.

### General observations and results

How genetic changes may affect the ontogenetic developmental stages of the predecessor is theoretically figured in fig. 24. In this model the ontogenetic developmental stages of adult sporophytic generations are indicated by horizontal lines. The most primitive fern illustrated is the one whose adult stage is the sum total of  $n$  different ontogenetic stages (i.e. the whole of its ontogeny). Mutations in this fern may result in a progeny with a slightly different ontogenesis. The latter's ontogeny may show, if compared with that of its parent, a loss or an increase of development(al stages). The adult progenitors are of course capable of radiating in all directions. The scheme illustrates schematically only some of the numerous theoretical possibilities. The real ontogenies of related ferns are of course much more complicated. The scheme just aims to provide one possible mechanism to understand the complex diversity found in the genus.

Although the term *neoteny* can be restricted to the phenomenon of a sexual maturity in a juvenile phase (in the axolotl, the classical example, neoteny is even facultative (!): De Beer, 1951), it is often also used in a broader sense (Diels, 1906; De Beer, 1951; Takhtajan, 1959) in which it covers the retention of every juvenile character by the adult. The difference between neoteny as thus defined and De Beer's gerontomorphosis (i.e. the phylogenetic change as a result of modifications affecting 'characters already adult') is a gradual one in view of the scheme presented above.

The probable significance of neoteny for the past diversification in the genus *Bolbitis* as seen from the juvenile leaves:

Ser. *Alienae*.

*B. auriculata* and *B. aliena*.

The similarities between the late juvenile leaves of *B. auriculata* and mature leaves of *B. aliena* can be interpreted differently. Gerontomorphosis in a fern like *B. aliena* may have resulted in a fern like *B. auriculata* with a more complex leaf shape. Theoretically, however, the reverse may be true in case of a genetic change in a fern like *B. auriculata* causing the retention of a juvenile stage with a symmetrical leaf but with already a reticulate venation.

Ser. *Bolbitianae* and *Egenolfianae*.

The species of series *Bolbitianae* show marked differences between subsequent or next-subsequent juvenile leaves of a certain stage of development of the juvenile plants. Possibly part of the ontogenesis of the ancestor has disappeared. The diversity of the juvenile leaves shows great resemblances in the different species. The differences in the ontogeny of the species investigated become manifest in the more complex juvenile leaves. Especially, with particular reference to the shape and the number of the pinnae, and the venation pattern. The first leaves grown from bulbils resemble late juvenile leaves of sporelings.

The early formed juvenile leaves are morphologically very similar to adult leaves of *B. appendiculata* ssp. *appendiculata*. However, they lack spines on the margin of the pinnae. This difference does not seem to be important, as the teeth present in the juvenile leaves can be regarded as homologous with the teeth as found in the juvenile leaves of *B. appendiculata* ssp. *appendiculata*.

The surprising similarities between the leaves of *B. appendiculata* ssp. *appendiculata* and the juvenile leaves found in some species of ser. *Bolbitianae* can be explained by assuming that the shape of the leaves of the former taxon resulted from retention of juvenile characters as found in ser. *Bolbitianae*. It is noteworthy that presumably ser. *Bolbitianae* and *Egenolfianae* are genetically closely related in view of the occurrence of hybrids between these series. The simple type of (juvenile) leaf shape found in *B. appendiculata* ssp. *appendiculata* may well have been formed by retention. The shape of the spores and the complex anatomy found in the base of the pinnae are in favour of the supposition that ssp. *appendiculata* has a derived genome in spite of its simple leaf shape.

From the study of the ample material of juvenile and mature specimens of ser. *Bolbitianae* it seems justified to present the following hypothesis regarding the past speciation in this series. For this purpose some characteristics of the series are recapitulated.

As far as known from the study of mature specimens, ser. *Bolbitianae* is homogeneous. For instance, all its members have a characteristic type of spores. Cytologically they appear uniform. All species are (largely) confined to seasonally dry forests. The pantropical distribution of the series is the widest in the genus.

Leaving two critical species out of further consideration (i.e. *B. salicina* which is African, and *B. serrata* which is American), this series consists of eleven species. The one American representative is very similar to the one African species. The other nine species are confined to Asia (from S. India and Ceylon eastwards to Formosa, the Philippines, and Celebes; see fig. 28). The species with a venation pattern best matching that as found in the American and African species is *B. angustipinna*, the most widespread species in Asia. The venation pattern of *B. scalpturata*, a somewhat critical species, is usually only slightly different. A markedly deviating venation is found in the other Asian representatives. In the small-sized *B. semicordata* (endemic to S. India) and *B. crispatula* (with two local varieties) it is much simpler, in *B. virens*, *B. subscrenata*, and especially *B. costata* it is much more complicated than that of *B. angustipinna*.

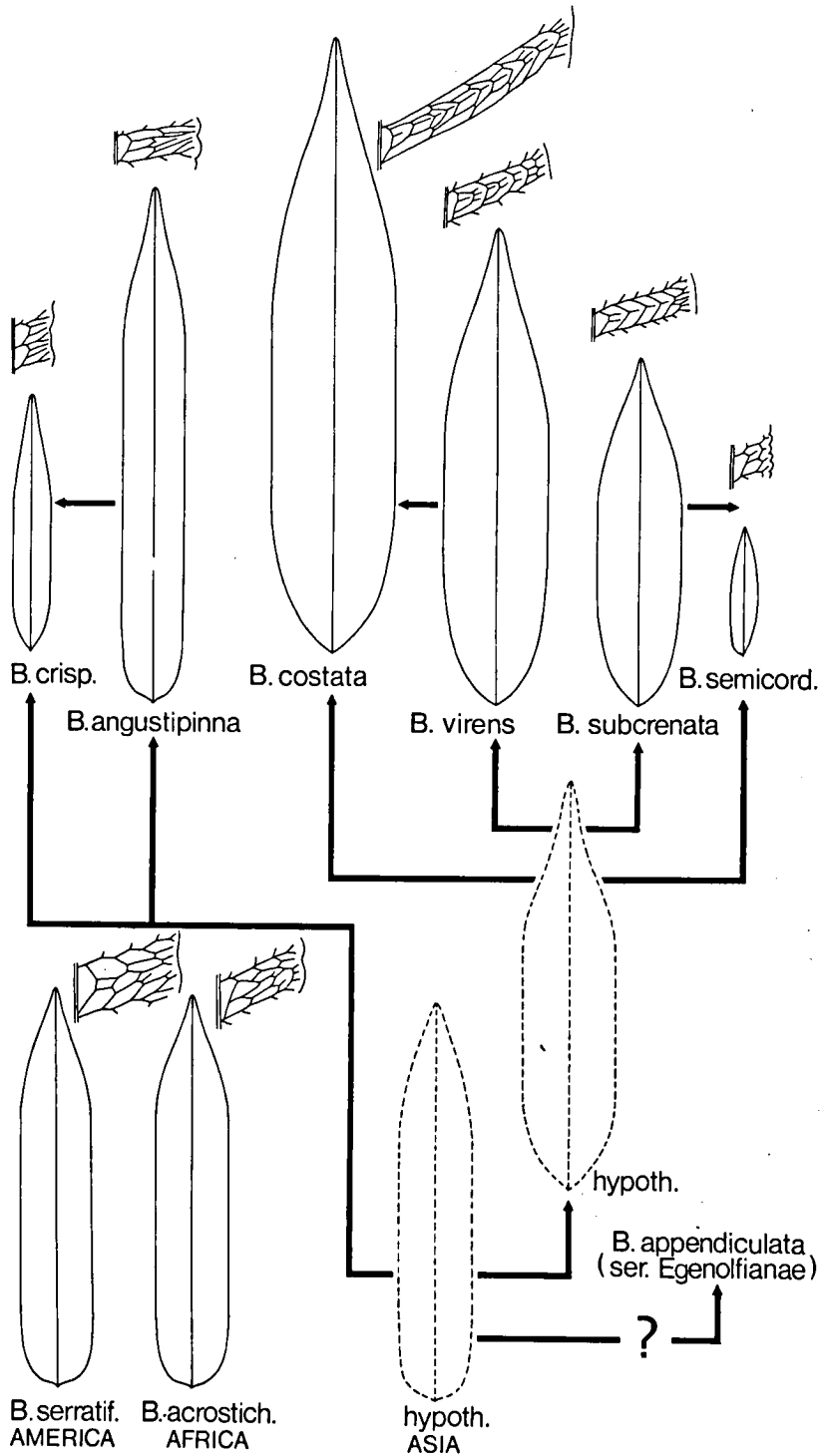
The venation patterns of *B. semicordata* and *B. crispatula* should be regarded to represent a primitive condition when following Haeckel, as this kind of patterns precedes the more complex types as found in the adults of other species. The other species with a more complex network should then be derived. This supposition, however, seems unlikely as it would mean that a fern like *B. semicordata* should have spread as far as Africa and America giving rise to ± similar plants much different from their ancestor. Further, it so happens that the spores of *B. semicordata* (and *B. costata*) are slightly but conspicuously different from those of all other species of the group, which have very uniform spores.

Another possible explanation presented here starts with the assumption that a species with a venation pattern as found in *B. acrostichoides* and *B. serratifolia* once also inhabited (parts of) Asia. This seems realistic as some of the species, including the widespread *B. angustipinna*, have a venation agreeing with that of these species. The Ceylonese plants of *B. angustipinna* in particular show a pattern reminiscent of the patterns as found in specimens of *B. acrostichoides* from eastern Africa. A hypothetical scheme of the evolution of the venation patterns in this series is given in fig. 24 (*B. scalpturata* is not included). *B. semicordata* has small asymmetrical pinnae and a narrowly winged rachis, features also found in the early juvenile leaves. The venation shows included excurrent free veins resembling certain late juvenile stages as found in *B. virens*. The venation of *B. semicordata* is likely to be the result of the retention of such a pattern in species like *B. angustipinna*, *B. virens*, *B. subcrenata*, or *B. costata*. If so, the (somewhat atypical) spores of *B. semicordata* may represent a derived condition as well. *B. crispatula*, with small symmetrical pinnae, is very near to *B. angustipinna*, and this type obviously arose by retention from a late juvenile stage of *B. angustipinna*.

The venation of *B. virens* shows resemblances to that of *B. angustipinna*, and it seems possible that *B. virens* arose from the latter species because of a genetic change causing a different venation pattern already in rather early ontogenetic stages. The venation patterns of *B. subcrenata* and *B. costata* have much in common with that of *B. virens*. *B. costata* has the most complex type of venation of the series, and has slightly deviating spores in addition.

The various types of venations as found in early and mature leaves of the species in this series can be easily understood when it is accepted that all the Asian species of ser. *Bolbitianae* are derivatives of a species with a venation as found in *B. acrostichoides* and *B. serratifolia*. Presumably, the genetic changes leading to speciation have been only slight, as the early juvenile leaves are hardly affected; only the later juvenile stages show differences in venation, number and shape of the pinnae. The species showing the extreme conditions in the venation patterns are also divergent in other features (spores, size, etc.). If this hypothesis is correct, one may even boldly suggest that a considerable

*Fig. 24.* Schematic illustration of probable past evolution of the Asian representatives of ser. *Bolbitianae*. The length and width of the pinnae represent the average length and width of sterile central pinnae of the respective species, based on 30 or more (*Bolbitis semicordata*: 15) leaves of each species. The venation pattern as far as given is schematic. Broken-line illustrations are hypothetical. For further explanation see the text.



genetic change in a representative of ser. *Bolbitianae* may cause the retention of still earlier stages resulting in an adult with free veins and pinnate leaves, the pinnae of which are asymmetrical. Such a fern may be very similar to *B. appendiculata* ssp. *appendiculata* (ser. *Egenolfianae*)! On the other hand, gerontomorphosis in a fern like *B. serratifolia* or *B. acrostichoides* may result in a fern with an intricate venation pattern (as realized in *B. costata*). It is fascinating to see that in this series both the morphologically simple and complex species can be regarded as representing derived conditions.

A comparative analysis of all the different juvenile leaves of all the species is of importance as it may give additional evidence regarding the significance of retention of juvenile characters when trying to unravel the evolution in this group in the past.

#### Ser. *Euryostichae*.

##### *B. nicotianifolia*.

Only the smallest leaf stages show  $\pm$  marked differences. Obviously part of the juvenile stages as present in the ancestral fern has been 'lost' during evolution. The venation pattern—basically similar in all representatives of this group—is very complex.

Adults of ser. *Euryostichae* are usually pinnate, but adults with simple leaves are known from all species but one. The latter adults are likely to represent a derived condition, as their sterile leaves are similar to the simple sterile juvenile leaves that precede the adult pinnate ones.

#### Ser. *Heteroclitae*.

The ontogenies of *B. heteroclita* and *B. sinuata* are different. They only share the shape (not the texture) of the smallest juvenile leaves. The juvenile leaves of *B. sinuata* show but slight morphological variation. Obviously, the genetic changes leading to the origin of *B. sinuata* caused a loss of juvenile stages. This, and the coriaceous texture of the juvenile leaves is here regarded to represent a derived condition. A parallel development is seen in ser. *Quoyanae* (*B. rivularis*).

The astonishing variation in the morphology of the leaves as found in *B. heteroclita* (see fig. 9, 13, 20, and the Taxonomic Part) indicates that when (slight) genetic differences cause retention of characters, morphologically very different populations (or species) may be formed. It is supposed that the pinnate condition as found in large mature specimens was present prior to the other types of leaves found in mature specimens of this species.

#### Ser. *Portoricenses*.

##### *B. portoricensis*.

The two collections studied show considerable differences which are of a kind also found in the juvenile leaves of *B. auriculata* and *B. semipinnatifida*. It is noteworthy that free included veins occur rather late during ontogenesis.

The leaf shape and the venation pattern of certain stages are also similar to the juvenile leaves, as far as known, from *B. bipinnatifida* (fig. 15: g-i). The juvenile leaves of the latter species have a reticulate venation pattern except for the incidental occur-

rence of short re-(!) and excurrent free veins. The mature leaves of *B. bipinnatifida* have a characteristic pattern with short included excurrent veins. The similarities observed in the juvenile leaves of that species and *B. portoricensis* have parallels in the adult leaves which have, however, a different type of venation (without and with many included free veins, respectively). The study of the juvenile leaves has been a considerable help in properly weighing these differences for taxonomic purposes.

Ser. *Quoyanae*.

*B. quoyana* and *B. rivularis*.

The ontogeny of *B. rivularis* shows simple leaves in all juvenile stages; the venation is like that as found in adults (except in the smallest leaf). This, and the coriaceous texture are regarded to represent derived conditions.

Part of the juvenile leaves of *B. quoyana* are similar in size, shape, and, almost so, in venation, to certain mature leaves of *B. taylorii*, and the latter may well have come into existence by the retention of a juvenile condition.

*Species incertae sedis*.

*B. repanda*.

The adult condition of the tetraploid studied is established through gradual changes occurring in the (successive) leaves. The first leaf formed shows greater complexity than that in *B. heteroclita*, one of its putative parents.

*B. semipinnatifida*.

The collections studied have very diverse juvenile leaves. The differences between the juvenile leaves are of a kind also seen in *B. auriculata*. The adult condition of the venation results from gradual changes.

## Discussion

From the observations on the juvenile leaves in the genus it has become likely that retention of juvenile characters might have been a factor of importance in creating the present diversification. According to Stebbins (1950) it is probable that genetic changes acting relatively late in ontogeny are less likely to disorganise the whole process of development than those which alter the earlier stages. 'The mutations established will therefore usually be those which affect development at the latest possible stage for the modification of the mature structure in the direction of a selectively advantageous shape. That part of the ontogeny which is less modified by the sum total of these late-acting genes will show embryonic similarity' (p. 492).

As becomes clear also from the juvenile leaves studied in ser. *Bolbitianae*, it is especially the late stages and not exclusively the latest stage, that are affected (for instance in leaf shape). This and other observations suggest that Haeckel's law is only of limited value for the determination of phylogenetic relationships. A theory about fern diversification taking into consideration all stages of ontogeny, therefore, constitutes a better approach to the understanding of fern phylogeny.

In spite of the fact that Zimmermann (e.g. 1959) largely adhered to the Biogenetical Law, he also mentioned facts which I regard as strong arguments against the validity of this theory. Firstly, in Haeckel's law the juvenile stages of the modern organisms are compared with the adult stage of the ancestor. There is little in this context that justifies a comparison between different elements of two ontogenies. Besides, if true, all of the ancestors of modern leptosporangiate ferns would be of very limited size. Secondly, only a part of the morphological features show special characteristics in their juvenile leaves. Thus, in ser. *Bolbitianae* the juvenile leaves, if compared with adult ones have, for instance, a deviating leaf shape and texture, but are similar as regards other features (e.g. the rhizome scales). Therefore, the features of a juvenile leaf or stage may be often better studied semophyletically and not phylogenetically.

If retention of juvenile characters commonly takes place, one has to reconsider the morphological features in terms of primitive and derived. For instance, a free venation is generally regarded to represent the more primitive condition if compared with an anastomosing venation. One should realize, however, that the latter pattern is that as found in the adults; the juvenile stages of such ferns may have a venation that is less, if at all, anastomosing. In case the juvenile condition is retained during diversification, a simple morphology is not necessarily an indication for a primitive genome.

The interpretation of the morphology of a fern is further complicated by the fact that a similar leaf shape, e.g. the pinnate condition, may be found in different ontogenetic developmental stages of a particular plant as already noticed by Holttum (1954) for leaves of *B. heteroclita*. Pinnate leaves from different parts of the ontogeny may have a different complexity as regards venation pattern, texture, etc. In principle both pinnate conditions are liable to retention.

The observations on the juvenile leaves have a great bearing also on classification. They not only confirmed the classification as based on the study of adults but also suggested the relationship of several other taxa.

Finally it can be pointed out that within the lomariopsidoid ferns as defined by Holttum (1946) morphologically very different expressions in a single plant are also found in mature *Teratophyllum* (with bathyphylls and acrophylls). Also, the similarities between mature *Elaphoglossum* and *Lomariopsis palustris* (Hook.) Mett. are striking. It seems of interest to study their juvenile leaves as the systematic position of *Elaphoglossum* is ambiguous. The relationship of the derivatives of *Elaphoglossum* (Copeland, 1947), *Microstaphyla*, and *Peltapteris* to each other and to *Elaphoglossum*, may become better known when the juvenile leaves of *Elaphoglossum* species, e.g. *E. dimorphum* (Hook. & Grev.) Moore are studied. As far as studied, *Microstaphyla* and *Peltapteris* easily fit in *Elaphoglossum* (as already advocated by Christensen, 1906) and the recognition of these dwarfs as separate genera seems just a matter of convenience.

### 13. RETENTION OF JUVENILE CHARACTERS AND PAST DIVERSIFICATION OF FERNS

Amongst the modern isosporous leptosporangiate ferns great differences in morphological complexity exist, not only between the various groups (families) of a higher



order, but also between species of e.g. the same genus. In this connection one may mention the morphologically simple structure of small dichotomously branched leaves as found in a number of hymenophyllaceous ferns, as against the complex architecture of the large fronds as displayed by the *Cyatheaceae*.

Though the phenomenon of reduction is widely known and accepted, and therefore generally referred to, it is nevertheless not uncommon to find that modern research is still afflicted with the idea that leaves with a dichotomous venation or branching system (as known from fossils) are in principle primitive.

The preceding chapter contains arguments that make it plausible to postulate that a simple morphology of the leaf as found in some representatives of the genus *Bolbitis*, does not necessarily mean that the taxa bearing such leaves, are primitive as well. It is therefore tempting to ascertain whether a more general and wider interpretation may be attributed to this finding.

In order to circumscribe more precisely the arguments that should be used for defining the identity of a fern in terms of primitive and derived, it seems useful to recapitulate the following two phenomena encountered when studying the ontogeny of the pteridophytes:

1. The adult sporangiferous leaf is often preceded by a series of juvenile sterile leaves that have—especially in the early developmental stages—a completely different morphology, not only if compared with the full-grown stage, but also when a comparison is made of such leaves inter se. Such observations are not limited to leaf shape, but may also apply to e.g. venation, relative size of a single organ, and glandularity.
2. Fertility of the individual may be reached at various stages in the ontogeny. Dwarfing is known from many groups (incl. *Cyatheaceae!*). Diels (1906) already observed that there exists no strict correlation between the morphological development of a plant and its capacity to become fertile.

The results of the present study make it possible to connect the above two phenomena. In *Bolbitis* we know dwarfed specimens that in the sterile stage show a leaf morphology strikingly similar to that of the juvenile stages of other full-grown plants. It looks as if such different forms may be found even within one population of a certain species.

What does this observation mean to the question as to how evolution progressed in ferns generally? In this connection it is interesting to notice that it is now generally believed that the leptosporangiate ferns evolved under influence of and during the evolution of seed plants (A. R. Smith, 1972). The pteridophytes must have been crowded out to a large extent during the development of these plants. However, at the same time the seed plants themselves created numerous new habitats several of which with only limited conditions for growth. Also because of properties of the spores (which are generally produced in large quantities and easily dispersed) and the genome (high chromosome numbers allow pre-adaptation to many environments, see Klekowski & Baker, 1966) it is not surprising to find that many ferns are epiphytes or terrestrials in rain forest. The habitat of the first mentioned has good conditions for light but the 'soil' conditions are poor, whereas the situation is just the reverse in the

second. Ferns are also found commonly in rock crevices, and even on (*Bolbitis*!) and below rocks.

In so-called 'poor' habitats there might have been a strong selection for ferns being able to complete their life-cycle. And it seems likely that under these circumstances mutations that caused (also) a retention of the juvenile stages had better chances to become established than those affecting the adult stage. Such 'juvenile-looking' progenitors may show a very simple morphological development as to one or more features which are nevertheless expressions of a derived genome.

Although I agree with Wagner (1952) that the small ferns showing foliar dichotomy are derived, foliar dichotomy itself did not necessarily arise *de novo* as Wagner stated. In my opinion it may be also possible that foliar dichotomy is caused by the retention of juvenile properties. The idea that the simply built small ferns represent either an evolutionary end-point (Wagner) or a primitive condition (what is the classical conception) is unlikely. These simple ferns are the result of a derived genome and may represent starting points for further divergent evolution; in a genus like *Platyserium* divergent evolution is evident.

It is likely that retention of juvenile characters has played a part in the development of, for instance, *Hymenophyllaceae* and *Polypodiaceae*. In view of Williams's work (1927) on the vittarioid ferns it seems further of interest to find out in how far the so-called primitive characters, e.g. the simple type of vascular organisation in part of the lindsaeoid ferns, the free venation of small ferns, and the simple leaf shape, cannot be better regarded as representing a derived condition caused by the retention of characteristics of the juvenile leaves. Kramer (1957) already suggested that the simple type of vascular organisation in the lindsaeoid ferns should represent a derived stage. It must be added here that if retention affects one organ only, it may be difficult to recognize.

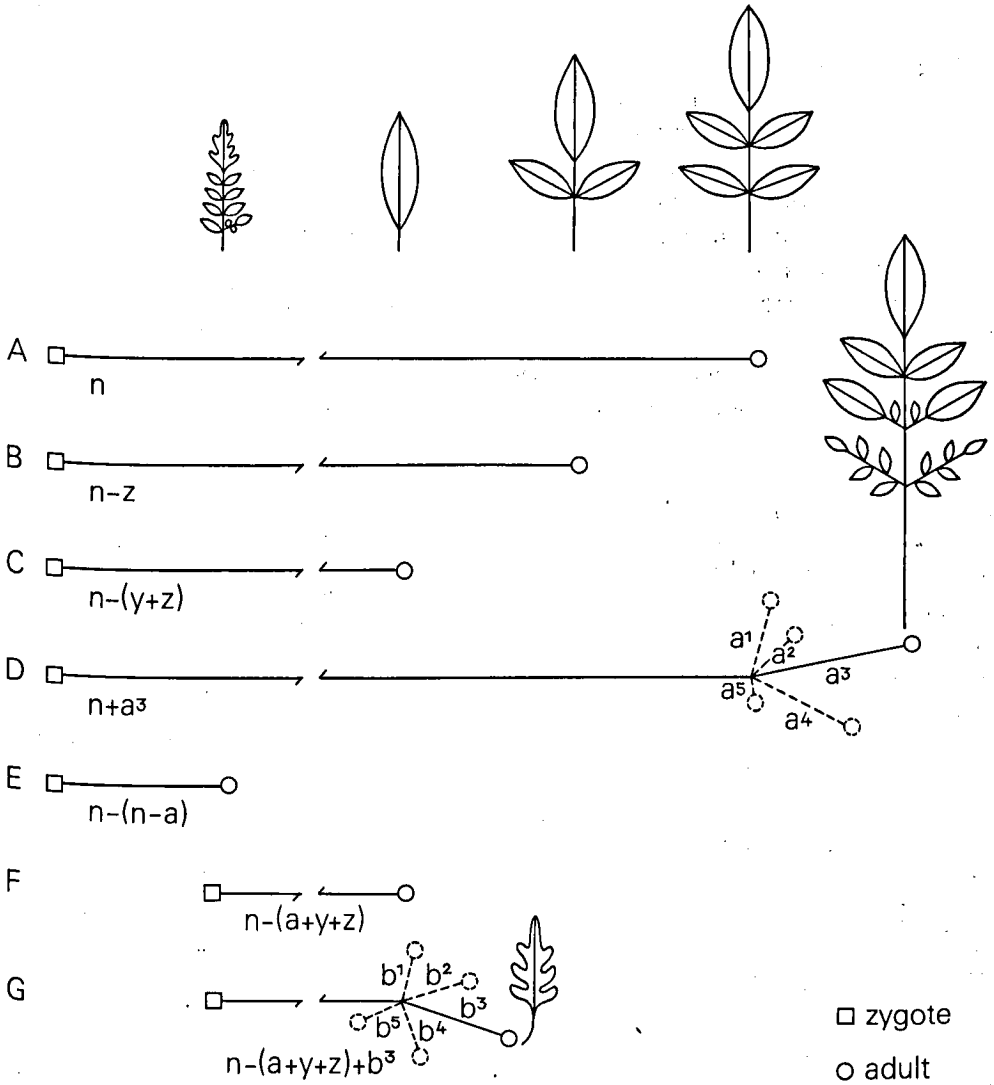
The remarks given in this chapter should be regarded as a plea for a comparative study of the juvenile leaves of the isosporous leptosporangiate ferns as well; it is the present author's opinion that such studies may reveal the vital importance of retention of juvenile characters as one of the phenomena that induced the present-day morphological diversity. See also fig. 25.

#### 14. NOTES ON THE DELIMITATION OF THE GENUS

'But the point upon which pteridologists appear to differ most, and upon which the only agreement seems to be an agreement to differ, is the definition of genera and their limits.'

J. Smith, *Genera Filicum*, 1875, p. 5.

*Bolbitis*, an acrostichoid genus in the old sense, has not escaped that most serious problem that confronts systematists when studying the ferns in general. Convergent evolution or parallelism, 'the tendency of separate evolutionary lines to produce similar characteristics' (Wagner, 1966: 165) is particularly well-expressed, not only in



**Fig. 25.** Schematic illustration of supposed relation between ontogenesis and diversification. A represents a fern the ontogenesis of which comprises  $n$  different stages. Genetic changes in a population with ferns like A may on one hand affect the latest ontogenetic stages of fern A (ferns B and C) or on the other hand (also) early ontogenetic stages of fern A (fern E). Ferns B and C are retarded, i.e. their adult shape is reminiscent of ontogenetic developmental stages of their supposed predecessor. Progressed evolution of ferns like A may result in a heterogeneity including fern D. Fern F arose after the loss of both early and late developmental stages in populations of ferns like A. Ferns like G resulted from progressive evolution of ferns like F.

In this diagram  $a^1$ - $a^5$  and  $b^1$ - $b^5$  of ferns D and G resp., represent evolutionary potentialities leading to more complex ferns.

the shape of the leaves and the venation pattern, but also in the soral location and arrangement. The acrostichoid condition has clearly evolved in definite lines not otherwise related. As a result of the classical tendency to lay great stress on soral conditions for classification, the '*Acrosticheae*' of most classical authors were heterogeneous, and the resulting confusion has been an obstacle to the proper delimitation and classification of the genus *Bolbitis* in the past (see chapter 4). It is hoped that the present study will be conducive to a better understanding of the genus.

My work on the genus shows Ching's and Christensen's concept of it (though in a narrower sense, excluding ser. *Egenolfianae*) as given by these authors in Christensen's Third Supplement (1934) to be largely correct. As far as the delineation of the genus is concerned, Ching's and Christensen's work is therefore considered of great importance.

Nevertheless, several more or less recent publications are illustrative of the difficulty to evaluate morphological features in view of the decision if a taxon properly belongs to *Bolbitis*.

*Meniscium macrophyllum* Kunze is an American fern of which ample material was studied in detail by Maxon & Morton (1938). They concluded that the species did not fit into *Dryopteris* (*s.l.*; including the thelypteroid ferns), and that it must be included in *Bolbitis* (*B. macrophylla* (Kunze) Maxon & Morton) because of characteristics of the venation pattern and the fertile parts. My studies of the leaf indument, petiole anatomy, and the spores indicated, however, that it represents a genuine thelypteroid fern, to which it was transferred later by Morton (1971).

Soon after starting the study of the acrostichoids, it was shown that an insufficiently known acrostichoid fern attributed to the present alliance was a blechnoid fern for which the genus *Pteridoblechnum* was created (Hennipman, 1965).

Recently, it became clear (Hennipman, 1976) that *Leptochilus acuminatus* White & Goy, which was thought to be related to species of the present genus, also fits in *Pteridoblechnum*. Its proper systematic position became known largely by surprise: a so-called intermediate leaf showed indusiate blechnoid sori atavistically. The venation pattern of this fern falls within the range of that found in *B. heteroclita* (to which White & Goy thought their species related), and represents a fine example of parallel development.

Some other ferns, referred to the present genus by experienced pteridologists, are here identified as representatives of the genera *Cyclodium*, *Colysis*, and *Lomagrumma* (for details see the excluded species in the Taxonomic Part).

On the other hand, following a hint given by Prof. Holttum, it became clear that *Stenosemia dimorpha* (Copeland, 1955; = *B. quoyana*) fits the genus as presently construed.

From the above it will not surprise the reader that species of *Bolbitis* have been assigned to 23 different genera in the past, resulting in a somewhat intricate synonymy.

Studies of other Asian acrostichoid ferns now in progress give strong indication that some significant changes in the taxonomy of part of this group can be anticipated.

## 15. THE SYSTEMATIC POSITION OF THE GENUS

The genus *Bolbitis* is nowadays generally referred to the lomariopsidoid ferns for which the family name *Lomariopsidaceae*, given by Alston (1956), is available. In the sense of Holttum (1946, and onwards), the genus *Elaphoglossum* should be included in this alliance, whereas Ching (1940) and Pichi Sermolli (1968) accommodated this genus in the monotypic family *Elaphoglossaceae*. The great resemblance of *Elaphoglossum* to (juvenile leaves of) *Lomariopsis* is in support of Holttum's classification. The inclusion of the genus *Lomagramma* in this group has never been questioned, also as the venation pattern is very much like that found in part of *Bolbitis*. The former genus deviates from all others because of the presence of paraphyses amongst the sporangia. Whether this feature has a bearing on its taxonomic position cannot be ascertained until these organs are better understood. *Thysanosoria* is here regarded as an atavistic *Lomariopsis*, as serious doubts can be expressed whether a characteristic of the fertile leaf alone in this group of ferns is sufficient for recognizing a separate genus.

Holttum (1946, 1949) first recognized this group following excellent work on most of its genera (unfortunately not of the present genus). The 'dorsiventral rhizome with its broad root-bearing ventral vascular strand, the acrostichoid condition, in most cases the simply pinnate fronds with free veins, and the perispore' (1949: 290) were regarded by him as distinctive common characters. He later (1954) also paid some attention to the shape of the rhachis and the way of insertion of the pinnae, which can be considered important characteristics as well.

There are several opinions about the interrelationship within the lomariopsidoid ferns and the relationship of the lomariopsidoid ferns to the other groups of leptosporangiate ferns.

With reference to the relationship of *Bolbitis* to the other lomariopsidoid ferns, Holttum (1946, 1949) considered *Lomariopsis* the 'central' genus. From his elegant observations on the bathyphylls (a kind of juvenile leaves) of *Teratophyllum* he concluded that a rhizome bearing two rows of leaves, and leaves with a free venation should be interpreted as representing the primitive condition. As regards the venation pattern it is elucidated elsewhere that the free venation in *Bolbitis* can also be considered as representing a derived condition. The leaves of ser. *Egenolfianae* and ser. *Bolbitianae* show conspicuous similarities to the bathyphylls and acrophylls of *Teratophyllum*, which might be an indication of the relationship between these taxa (and the related genera *Arthrobotrya*, *Lomariopsis*, and *Elaphoglossum*). The affinity of the other groups in *Bolbitis* to these genera is far less obvious. The position of *Lomagramma* needs further study. Pichi Sermolli (1969) thought *Egenolfia*, *Edanyoa*, and *Bolbitis* (here united) as not very closely related to the other genera of his *Lomariopsidaceae* (*Elaphoglossum* excluded) and assigned these two groups to two different tribes. The interrelationships between the lomariopsidoid ferns are still insufficiently understood. The respective genera show conspicuous biological differences (for details, see Holttum, 1946).

There is little agreement regarding the relationship of the lomariopsidoid ferns to other groups of ferns. Some of the different opinions of rather recent years are the

following. Christensen (1938) thought the genus an acrostichoid representative of probably the tectarioid derivative of his *Polyodiaceae-Dryopteridoidae*. Copeland (1941) was still quite pertinent as to the relationship of *Bolbitis* (in a very artificial conception comprising the American representatives only) to *Phlebodium* (a genus of polypodioid ferns of quite different affinity): 'As to the real *Bolbitis*, I merely repeat myself, that it is derived from *Phlebodium*, and I have yet to see any refutation of the evidence by those who ignore it. Its resemblance to *Campium* [which comprises in Copeland's conception exclusively Old World species of mainly *Bolbitis*], however complete, is none the less casual, the result of divergent evolution' (p. 168). He later (1947) corrected his view and agreed with Christensen. Holttum related the lomariopsidoid ferns to the dennstaedtiaceous ferns (a very large assemblage of non-polypodioid ferns) 'probably on a line near *Davallia*' (1946: 146). Nayar & Kaur (1965b) thought the genus systematically rather isolated, possibly 'remotely related to the '*Rumohra-Polystichum* line of evolution in Copeland's *Aspidiaceae*' (p. 152). In another publication (Nayar & Kaur, 1965c) they favoured a tectarioid ancestry of the group, which was elaborately set forth again by Kaur (1974). These authors based themselves mainly on similarities between certain lomariopsidoid ferns and *Tectaria* species which are, however, quite different as to the indument of the young leaves and the chromosome number. At present I cannot give any positive indication as to the systematic position of the lomariopsidoid ferns. Absence of a detailed study of *Bolbitis bernoullii*, which possibly originated from intergeneric hybridization with a non-lomariopsidoid genus (*Polybotrya*?), as well as of *Leptochilus* × *trifidus* (possibly a cross between *B. sinuata* and *Leptochilus decurrens*) precludes further speculation at present.

## 16. SUBDIVISION OF THE GENUS

Iwatsuki (1959), basing himself almost exclusively on Japanese species, was the first to unite *Egenolfia* and *Bolbitis*. He divided the emended genus into four sections; two are based on species here referred to *B. appendiculata*, one is based on *B. laxireticulata* (a dubious species from Japan), whereas all other species are included in sect. *Bolbitis*.

When using characters from the venation pattern, the perispore, and the rhizome, it is easy to fit the majority of the species into ten series. The remaining species, nearly all regarded as of hybrid origin, have been kept separate as *species incertae sedis*. Distribution maps of the series are given in fig. 27–30.

The series are mainly defined on characters as present in the adult stages. The often scarce and incomplete data available on juvenile forms or even the complete absence of such information concerning quite a number of species in the genus made it not always possible to compare the ontogeny of the constituent species in a series, or of the series mutually.

Group 1. Ser. *Alienae*, *Lindigianae*, *Quoyanae*, and *Heteroclitae*. The venation pattern generally shows a regular network of ± isodiametric or elongate, angulate areoles without included (ex- and/or) recurrent free veins.

Ser. *Alienae* is a very natural group. It occurs terrestrially in America and throughout tropical Africa to Madagascar and the Mascarenes. It seems intimately related to the monotypic American ser. *Lindigianae*, a high-climber. The leaf architecture and the venation pattern of ser. *Alienae* show marked resemblances to that of ser. *Quoyanae* which occurs in eastern Malesia, the Pacific, and the Bonin Islands.

The venation pattern and leaf architecture of the species of ser. *Heteroclitae* differ from those of the other members of Group 1. The mature pinnate leaves of *B. heteroclita* and *B. sinuata* have a terminal segment that is conform to the pinnae (triangular in the others). Such a difference is not necessarily of much significance; both types of leaves are found, for instance, in ser. *Portoricenses*.

Group 2. Ser. *Portoricenses*, *Heudelotianae*, and *Euryostichae*. The venation generally shows a part of the areoles to have re- and excurrent included free veins.

Ser. *Portoricenses* (America) is characterized also by its scales of the rhizome. The group appears a natural one in spite of differences in shape of the leaves of its members. Ser. *Heudelotianae* (Africa) is unique because of its habitat requirements and the shape of the perispore. Both are likely to represent a derived condition.

Ser. *Euryostichae* (America and Africa). The American species are very homogeneous. The only African species deviates, amongst other things, in the localisation of the bulbil. This group puzzled me for some time as it shows several features (venation pattern, leaf shape, petiole anatomy, spores) which show similarities to some species of *Tectaria*. However, the chromosome number as found in this series ( $n = 41$ ) differs from that of *Tectaria* ( $n = 40$ ), and so does the indument as found on (young) leaves.

The systematic position of ser. *Bipinnatifidae* is of interest. Its venation pattern is very close to that of the series listed in Group 1. On the other hand, the adult plants of *B. bipinnatifida* have a number of characteristics in common with *B. portoricensis* (ser. *Portoricenses*) including rather large basally attached scales, a leaf with a proportionally large terminal segment, and teeth in the sinuses of the pinnae. Further, the scanty material of the juvenile leaves of these species shows conspicuous and surprising similarities. Apart from a similar outline, the juvenile leaves may have an almost identical venation pattern (reticulate without or with but few included free veins). The relationship of ser. *Bipinnatifidae* to ser. *Portoricenses* seems a reality in spite of its type of venation. To this alliance may also belong *B. umbrosa* (*Species incertae sedis*) which has leaves with a reticulate venation without free included veins. The proper position of this species will become better known after complete material of the rhizome has become available.

The remaining series *Bolbitianae* and *Egenolfianae* do not fit the two groups mentioned above.

Ser. *Bolbitianae*. This pantropical series is conspicuous because of the shape of the perispore and the venation pattern. One species (*B. crispatula*) shows costal areoles only. The group is especially characterized by its undulate perispore. The undulate condition of the perispore possibly represents a derived condition in ser. *Heudelotianae*,

and almost certainly so in a few specimens of *B. fluviatilis* (a derivative of *B. auriculata*), normally with a cristate perispore. Therefore, the undulate perispore as found in ser. *Bolbitianae* may likewise represent a derived condition.

*B. acrostichoides* and *B. serratifolia* are regarded to represent the most primitive species. Amongst specimens of both species a similar type of venation pattern may be found as is typical of the series of Group 1. This seems in favour of a relationship between ser. *Bolbitianae* and this group.

Ser. *Egenolfianae* is unique because of its free venation. Therefore, this Asian group of species has been generally regarded as primitive. Its species show variation as to the localisation of the bulbil, features of the rhizome, petiole anatomy, spores, etc. The venation pattern is superficially nearest to that of *B. crispatula* (ser. *Bolbitianae*). Besides, certain mature leaves of *B. appendiculata* ssp. *appendiculata* are surprisingly similar to the juvenile leaves of species in ser. *Bolbitianae*, which may indicate relationship.

In view of earlier publications it was unexpected to find that these two groups, formerly given generic rank, may be closely related.

Further research will show in how far the idea is justified to treat the series of Group 1, those of Group 2 (including ser. *Bipinnatifidae*), and ser. *Bolbitianae* and *Egenolfianae*, as the three sections of the present genus. See also table 3.

Table 3. The series of *Bolbitis* arranged according to properties of their spores and venation patterns. Squares indicate groups of probably related series.

PERINE VENATION	smooth undulate (spore type D)	smooth cristate-undulate (spore type B)	reticulate cristate (spore type A)	smooth undulate (spore type C)
veins free bolbitianae type		Egenolfianae	Egenolfianae	Bolbitianae
reticulate without recurrent veins		Alienae Quoyanae Heteroclitae Lindigianae		
with recurrent veins	Heudelotianae	Bipinnatifidae Portoricenses Euryostichae		

### Hybrids and infrageneric classification

It is generally believed that hybrids between taxa are an expression of the genetic relationship between the parents. On the other hand, one should not give much weight to the absence of hybrids between taxa prior to experimental proof. During the present study I came across a considerable number of hybrids or hybrid derivatives.



Those of which the parents can be postulated with reasonable certainty and of which the parents belong to different series are:

<i>B. angustipinna</i> × <i>sinensis</i> :	<i>Bolbitianae</i> × <i>Egenolfianae</i>
<i>B. appendiculata</i> × <i>virens</i> :	<i>Egenolfianae</i> × <i>Bolbitianae</i>
<i>B.</i> × <i>boivinii</i> :	<i>Alienae</i> × <i>Euryostichae</i>
<i>B. cadieri</i> :	<i>Bolbitianae</i> × <i>Heteroclitae</i>
<i>B. fluviatilis</i> × <i>heudelotii</i> :	<i>Alienae</i> × <i>Heudelotianae</i>
<i>B. heteroclita</i> × <i>rhizophylla</i> :	<i>Heteroclitae</i> × <i>Egenolfianae</i>
<i>B. interlineata</i> :	<i>Bolbitianae</i> × <i>Heteroclitae</i>
<i>B. lonchophora</i> :	<i>Egenolfianae</i> × <i>Heteroclitae</i>
<i>B. nicotianifolia</i> × <i>portoricensis</i> :	<i>Euryostichae</i> × <i>Portoricenses</i>
<i>B. presliana</i> :	<i>Bolbitianae</i> × <i>Egenolfianae</i>
<i>B. repanda</i> :	<i>Egenolfianae</i> × <i>Heteroclitae</i>
<i>B. semipinnatifida</i> :	<i>Alienae</i> × <i>Euryostichae</i>
<i>B.</i> × <i>singaporensis</i> :	<i>Egenolfianae</i> × <i>Heteroclitae</i>

This list shows that seven of the ten series are involved in this kind of hybridization. Hybridization occurs most (9 out of a total of 13 cases) between species of ser. *Bolbitianae*, *Egenolfianae*, and *Heteroclitae*. This indicates a relationship between ser. *Bolbitianae* and *Egenolfianae*, and of both to ser. *Heteroclitae*, which is in accordance with the remarks given above. There are no hybrids listed between species of these series and other series. See, however, also below.

Three other hybrids have parents belonging to species of which the series are classified in Group 1 and 2. There are hybrids between species of ser. *Alienae* with both ser. *Euryostichae* (2 ×) and ser. *Heudelotianae* (1 ×).

The first two hybrids and the hybrid between species of ser. *Portoricenses* and *Euryostichae* further confirm the inclusion of the latter series in the present genus. See also above.

Several other hybrids or hybrid derivatives are worth mentioning:

1. *B. gemmifera* probably arose from hybridization between *B. auriculata* (ser. *Alienae*) and a representative of either ser. *Bolbitianae* or ser. *Euryostichae*.
2. Because of properties of the venation pattern *B. humblotii* seems to have been derived from hybridization between species here referred to series listed in Group 1 and Group 2 respectively.
3. *B. longiflagellata* may have originated through hybridization between a species of ser. *Alienae* and *B. humblotii* (see 2).
4. *B. subcordata* could be the result of hybridization between species here referred to ser. *Bolbitianae* and ser. *Quoyanae*.
5. Probably *B. laxireticulata* is a hybrid between a species from ser. *Egenolfianae* and *B. subcordata* (see 4).

These hybrids further indicate the genetic relationship between the respective series.

6. *B. bernoullii* arose from a cross between *B. lindigii* (ser. *Lindigianae*) and a species belonging to a different genus (*Polybotrya?*).

7. *Leptochilus* × *trifidus* probably is a hybrid between *B. sinuata* (ser. *Heteroclitae*) and *Leptochilus decurrens*.

The study of the latter two taxa seems promising in so far that it may be the key to trace the proper systematic position of the present genus (and of the *Lomariopsidaceae*).

## 17. NOTES ON SPECIFIC DELIMITATION

### Introductory remarks

Manton's (1950) publication on the cytology and evolution of the pteridophytes initiated a new era of taxonomic research. She convincingly demonstrated, further elaborated by herself and later (co-)workers in this field (for references see Lovis, 1973), the common occurrence of hybridity, auto- and allopolyploidy, apospory, and apogamy, as well as the consequential importance of these phenomena for phylogeny and taxonomy.

Formerly, when hybridization was considered to be non-existent, or extremely rare in ferns, hybrids were not recognized as such in the vast majority of cases. They were described as species, and being intermediate, thought to be 'links' in the (gradual) course of evolution. Manton and others elucidated the origin of new species by the process of hybridization, auto- and allopolyploidization. So-called reticulate relationships were found to exist in many groups of ferns. The Appalachian *Aspleniums* are a famous example (for details see Wagner, 1954).

Generally hybrids, allopolyploids and also autopolyploids (as was only more recently shown) are apparently so commonly formed that they may constitute a dominant element amongst the ferns of a certain area. Walker (1966) estimated the amount of polyploids in tropical ferns at 60%; 53% of the British ferns are polyploids (Manton, 1953).

As to apogamy, several hybrids and also a considerable number of 'good' species are known to reproduce in that way and it is thought to be widespread in ferns (Manton, 1950). Evans (1969) boldly suggested that many, if not all taxa that are considered 'sterile hybrids', have the capacity of apogamous reproduction, albeit on a (very) low level; also that in principle the same possibility exists in sexually reproducing species.

Last but not least, modern cytogenetic research made clear that certain recognized morphological characters are correlated with karyological differences, whereas others, although frequently used for specific taxonomic differentiation in the past, are not. The latter characteristics are now regarded as the obvious result of divergent evolution and/or habitat conditions, and are taxonomically treated accordingly.

Cytogenetic research has mainly advanced in the ferns of North-temperate regions; Manton originally based her studies on mainly North-European taxa. However, ample information has been published more recently on tropical ferns (for references see Walker, 1973) indicating clearly that the same phenomena as recognized in temperate ferns are also found in tropical ones. As a consequence the difficulties experienced in taxonomy when investigating the limited number of ferns of Europe or the U.S.A. is not an isolated case.

In the present study attention has been given to apply these methods of research to the various taxa of the genus *Bolbitis*. Although these investigations were—perforce—relatively limited, sufficient data were obtained to state with confidence that hybridization, allo- and autopoloidization are common phenomena in this group too. An indication of apogamy could not be detected.

The impossibility of further research in this field and the absence of karyological data on quite a few species in the genus, is regretted. However, it must not be forgotten that, when even in e.g. Europe difficulties are experienced to come to satisfactory and final conclusions in cytogenetic research, such difficulties become tenfold when working with tropical groups. The number of species is of quite a different order, live material can only be obtained to any extent by organizing (costly) expeditions and provided that sophisticated methods of cultivation can be applied. The attempt made to obtain significant information regarding the karyology of the ferns under study was an important reason why the present study took as long as it did. The data submitted, although far from complete, must be regarded as the best obtainable under the circumstances.

One may wonder whether there is any sense in starting a systematic study of a group of tropical acrostichoid ferns which are notoriously plastic in their leaf shape, if mainly herbarium material is at hand. The answer is related to the extent in which such factors as hybridization and polyploidization, precocious fructification, etc. can be reliably recognized from herbarium material.

*The detection of hybrids and polyploids in herbarium material.*—Hybrids and allopolyploids may be traced because of the following properties:

1. *Spores.* Hybrids generally have aborted spores. However, hybrids may be able to reproduce apogamously by normally shaped mitospores. In that case the number of sporangia that produce 32 normally shaped spores may vary in different taxa from all to merely an incidental sporangium.

The number of spores per sporangium is usually difficult to estimate in herbarium material (Kramer, 1957), as I experienced also myself.

On the other hand, normal species may have at least some abortive spores (Wagner & Lim Chen, 1965), or may produce abnormal spores only, for reasons set forth elsewhere (see chapter 6). Allopolyploids produce normal spores. Spores of autopolyploids are either normal or abnormal, the frequency of abnormal spores being dependent on the ploidy level (Wagner & Lim Chen, 1965).

2. *Instability.* When the herbarium taxonomist traces extreme variation in shape of different plants thought to belong together, he should try to find out by studying the spores if such plasticity might be the result of hybridization. Some hybrids may reach a mature stage which resembles ontogenetic stage (s) of the parents involved, resulting in an excessive variation.

3. *Intermediacy.* Hybrids generally tend to bridge the differences between their parents. The hybrid is a 'compromise' (Wagner, 1968: 118). Few exceptions are known from this rule. However, I found it very difficult or even impossible to identify a certain expression of a hybrid as representing the exact intermediate condition. What is the intermediate

condition of the venation pattern when that of the two parent species is very different? I doubt if anyone would have been able to predict that the venation pattern as found in *B. × singaporensis* (fig. 85: a–d) is intermediate between that of *B. appendiculata* ssp. *appendiculata* (fig. 49: q–d') and *B. sinuata* (fig. 61: k–m)! The same holds for the localisation of the bulbil in *B. gemmifera* ( $\pm$  at the base of the terminal segment of the sterile leaf) (fig. 74; a, c, d), a presumed hybrid derivative of either *B. acrostichoides* or *B. gaboonensis* (both with subterminal bulbils) and *B. auriculata* (usually without, rarely with axillary bulbils).

4. *Structural irregularity.* Wagner (1962) brought together the 'sporadic observations' (p. 87) on ferns in which there is deviation from normal symmetry, either morphologically or anatomically. Wagner found that these irregularities were associated with known or suspected hybridity and called them structural irregularities. The feature that is irregularly expressed is generally one in which the parents are highly different. It is best known from the irregularly shaped leaves as found in some hybrids. Von Giesenhagen (1918) related the irregular leaves of *Pteris otaria* Beddome, a hybrid between *Pteris biaurita* and *Pteris multiaurita* (Walker, 1958), with suboptimal nutrient conditions; this explanation is rejected by Wagner with good reasons.

Wagner suggested that structural irregularities might be more common than actually observed by him, which is confirmed by the present investigations.

In conclusion, it is my opinion that the herbarium taxonomist has good possibilities to trace reticulate relationship especially when he has ample, preferably including some live material at his disposal.

*Hybridization and evolution.*—There is some difference of opinion regarding the role of hybridization in evolution. Wagner (1968: 122) concluded after perusing numerous monographs 'that the majority of species in most groups are allopatric and divergent, i.e. "normal" species produced by ordinary processes of mutation, recombination, selection and isolation'. Wagner (1970), admitting that tetraploids have the capacity for evolution, regarded the main pillars for plant evolution to be populations of 'normal' species, i.e. diploid, sexual, and outbreeding. The fact that 'normal' species with normal life cycles still prevail today should according to him be a strong indication for such plants to be responsible for 'the primary thrust of evolution'. Apogamous ferns and allopolyploids are regarded by him as 'evolutionary noise' that vanishes while the diploid continues to evolve. This idea is not quite shared by others. For instance, Walker (1973) included hybridization and polyploidization as mechanisms in his hypothesis on the evolution of the different chromosome numbers as found in *Dennstaedtia* and the tree ferns. Stebbins (1971) speaking about Angiosperms thought it likely that polyploidization has been important in the diversification of genera and species within families (but not in the origin of families and orders themselves). De Wet & Stalker (1974: 695) commented on Wagner (1970): 'In fact, "normal" species may be diploid or polyploid, annual or perennial, sexual or facultatively apomictic, and inbreeding or outbreeding. What makes a species normal is its ability to strike a balance between releasing variability and maintaining adaptive gene combinations.' In the present paper a distinct

minority of the species is regarded to be of hybrid origin. In view of the opinions mentioned above their significance for evolution is as yet not ascertainable.

### Concluding remarks

Apart from reticulate relationship I have also paid attention to the shape of the juvenile leaves (see chapter 11). Knowledge of the juvenile leaves enabled me to properly identify material in spite of precocious fructification.

Different plants belonging to one species were found to behave differently when in cultivation. This is not only true for plants with different cytotypes. For instance, the plant of *B. sinensis* which was collected by Dr. H. P. Nootboom on Doi Chieng Dao (diploid; Thailand) developed into a rather small plant which regularly formed fertile leaves. The specimens collected by myself from Doi Inthanon (diploid; Thailand) grew out into large plants which but seldom formed a fertile leaf. On the other hand certain diploid and triploid dwarfs of *B. heteroclita* are morphologically almost indistinguishable. Habitat conditions may further determine the shape of the plant considerably.

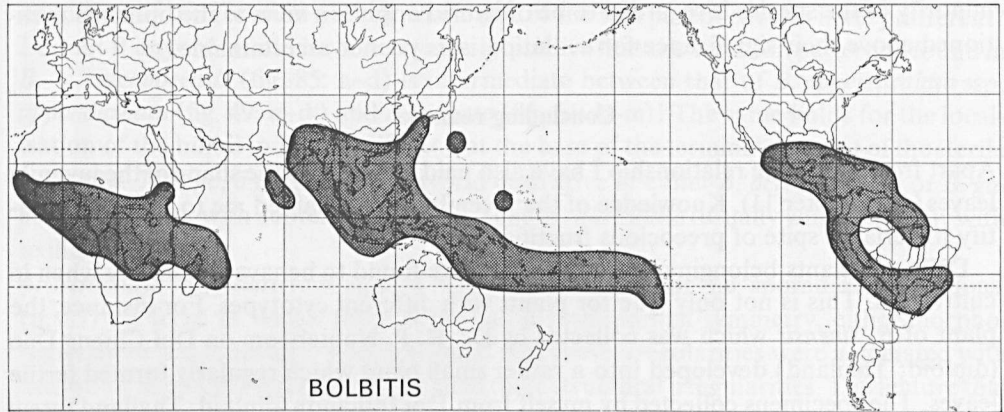
I have tried to classify the material in categories that can be morphologically recognized. Sometimes it appeared easy to draw lines in material showing continuous variation when studied superficially, also as important new characters became available after my detailed studies of some features. Most of the common species are, however, extremely variable, and could, moreover, not be divided into infraspecific categories. This variation is also illustrated by the characteristics of a number of spores studied from each of the species (see the Taxonomic Part). Species that could be subdivided into lower categories happened to belong to series in which polyploids are not (yet?) known. It also became clear that many of the morphologically distinct plants described during the last decades as new species could be interpreted as undoubted representatives of long-standing species when taking full account of the phenomena mentioned in this chapter.

## 18. NOTES ON GEOGRAPHY

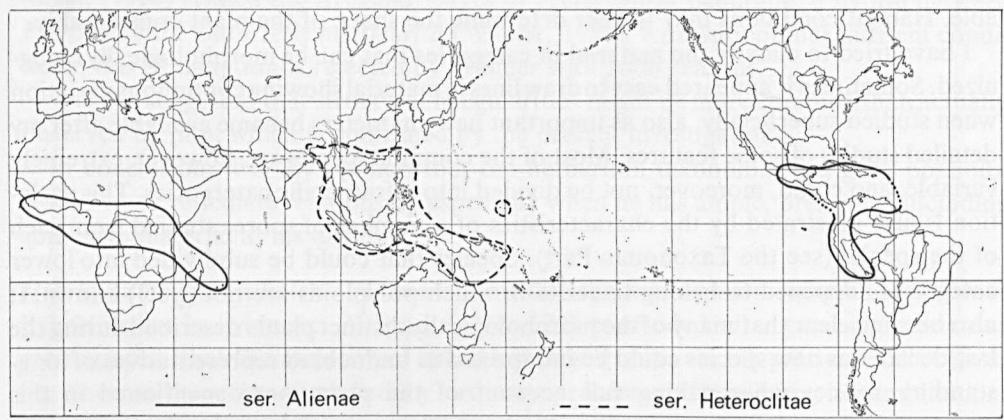
Distribution maps have been compiled for most of the taxa recognized. They represent a historical element which might help in understanding the present diversity. As I do not feel qualified to weigh properly the present theories which deal with the origin and fate of the continents, I confine myself to mentioning a few characteristics of the distribution patterns of the series which seem to be of interest for plant geographers. See table 4 and fig. 26–30.

In the genus ser. *Bolbitianae* has the largest number of species; it is the only series that is pantropical. The majority of its species are confined to Asia. *B. serratifolia* is the most widespread American species, also occurring on the so-called Brazilian shield. The African *B. acrostichoides* is a close relative, but also resembles *B. angustipinna*, the most widespread Asian species of this series.

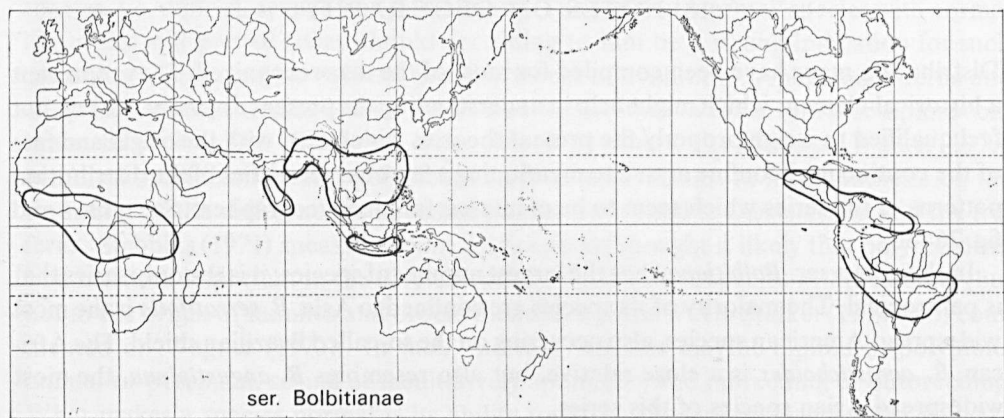
Ser. *Euryostichae* and *Alienae* inhabit both Africa and America. The only African rep-



**Fig. 26.** Distribution of *Bolbitis*.



**Fig. 27.** Distribution of *ser. Alianae* and *ser. Heteroclitae*.



**Fig. 28.** Distribution of *ser. Bolbitianae*.

Table 4. Geographical distribution of series and species incertae sedis

Series	Number of species				Notes
	Total	Africa	America	Asia & Pacific	
<i>Bolbitianae</i>	11	2	2	7	Including southern India and Ceylon; not in New Guinea and the Pacific
<i>Alienae</i>	3	2	1	-	Also in Madagascar and the Mascarenes
<i>Euryostichae</i>	5	1	4	-	The African species confined to the Congo Basin
<i>Bipinnatifidae</i>	1	1	-	-	Seychelles only
<i>Heudelotianae</i>	1	1	-	-	Not in Madagascar and the Mascarenes
<i>Lindigianae</i>	1	-	1	-	Andean
<i>Portoricenses</i>	3	-	3	-	
<i>Egenolfianae</i>	4	-	-	4	
<i>Heteroclitae</i>	2	-	-	2	Not in southern India and Ceylon
<i>Quoyanae</i>	3	-	-	3	Eastern Malesia to the Pacific; Bonin Is.
Species incertae sedis	10	3	2	5	
Total no. of species	44	10	13	21	
Total no. of series	10	5	5	4	

representative of ser. *Euryostichae* is confined to the Congo Basin. As regards ser. *Alienae*, *B. auriculata* is of interest as it occupies a large area in Africa, also occurring in Madagascar and the Mascarenes. Phylogenetically this species seems very close to the American *B. aliena*, differing mainly in leaf architecture (a feature liable to variation in other groups), indicating that speciation in this group is possibly very slow indeed.

Endemic to America are ser. *Lindigianae* and ser. *Portoricenses*. Ser. *Lindigianae* is possibly related to ser. *Alienae*; the only species—presumably a high-climber—is restricted to the Andes. One of the three species of ser. *Portoricenses* is widely distributed, the two other species are restricted to rather small areas in Mexico and South America respectively.

Two monotypic series are strictly African. Ser. *Bipinnatifidae* is confined to the Seychelles, whereas ser. *Heudelotianae* is the most widespread African taxon, obviously due to habitat tolerance. These two series are possibly related to the American ser. *Portoricenses*.

As to the Asian elements of the genus it is of interest to note that ser. *Egenolfianae*—like the Asian part of ser. *Bolbitianae*—covers a large area including southern India and Ceylon but not New Guinea and the Pacific. On the other hand, ser. *Heteroclitae* and *Quoyanae* are absent from southern India and Ceylon, but do occur in eastern Malesia and the Pacific. Ser. *Quoyanae* is restricted to eastern Malesia, the Pacific, and the Bonin Is., whereas the distribution of ser. *Heteroclitae* includes mainland Asia from north-eastern India to Japan, the whole of Malesia, and the western part of the Pacific. (A dis-

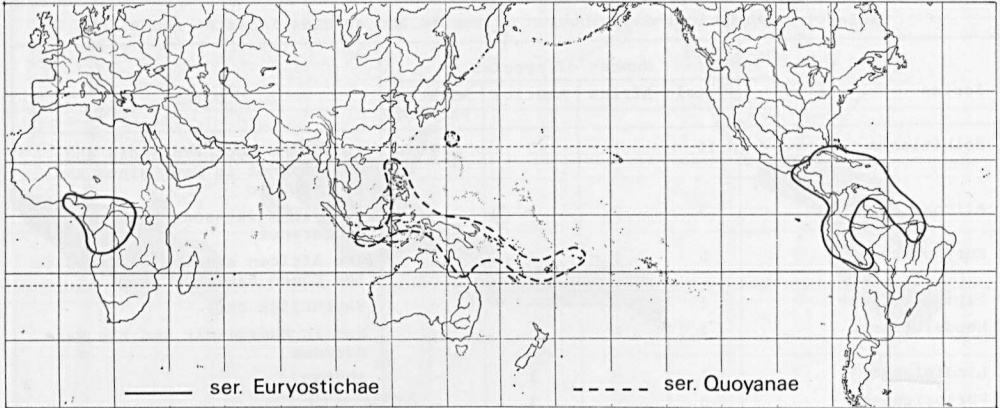


Fig. 29. Distribution of *ser. Euryostichae* and *ser. Quoyanae*.

tribution pattern like that found in *ser. Quoyanae* is also known for *Santalum* (*Santalaceae*) and *Metrosideros* (*Myrtaceae*)—Pers. common. Dr. M. M. J. van Balgooy).

A pantropical distribution is displayed by the group (Group 1 as described in chapter 16) representing the species with a reticulate venation pattern, i.e. those of *ser. Alianae*, *Heteroclita*, *Lindigiana*, and *Quoyanae*. If we consider *ser. Bolbitiana* to represent (possibly together with *ser. Egenolfiana*) another group, there are two groups in the genus with a pantropical distribution (which may be regarded as an indication of age). It is difficult to find out which of these two groups is the oldest. It is, however, of interest to notice that the venation pattern of *ser. Bolbitiana* can be regarded as derived from a reticulate pattern. Besides, the distribution of the first group in Asia is much more widespread than that of the other.

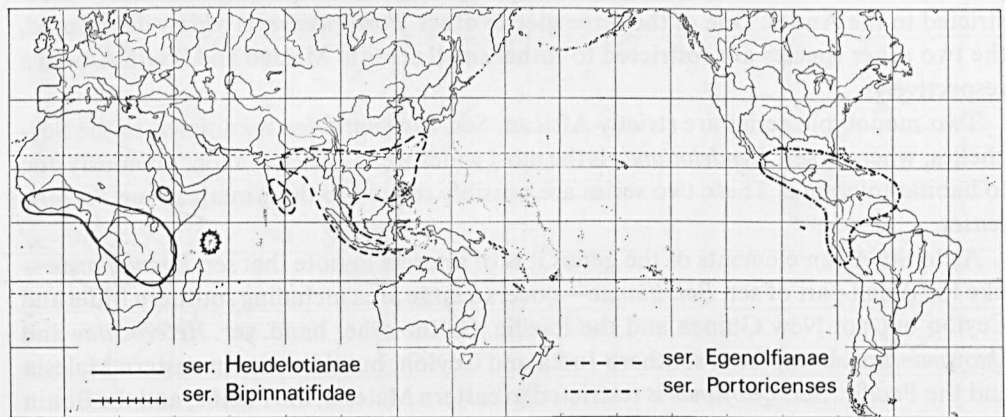


Fig. 30. Distribution of *ser. Bipinnatifidae*, *ser. Egenolfiana*, *ser. Heudelotiana*, and *ser. Portoricenses*.



The morphological distinctness of both the ser. *Heteroclitae* and ser. *Quoyanae* from their nearest relatives (ser. *Alienae* and ser. *Lindigianae*) may suggest that these Asian series arose earlier than did the Asian part of ser. *Bolbitianae* from the African element. Whether the 'western' distribution of ser. *Bolbitianae* in Asia is indeed in support of this idea remains unsolved; besides, we do not know how possible differences in habitat preferences (ser. *Heteroclitae* and ser. *Quoyanae* presumably prefer a wetter habitat than does ser. *Bolbitianae*) could also determine the present distribution.

Ser. *Euryostichae*, *Alienae*, and *Bolbitianae* have closely related American and African species. This allows the assumption of a possible relationship between ser. *Heudelotianae* and ser. *Bipinnatifidae* (African) and ser. *Portoricenses* (American). Except for the pantropical ser. *Bolbitianae*, all Asian series are endemic.

Series with reticulate venation pattern occur throughout the distribution area of the genus, whereas the one series with free veins is exclusively Asian (ser. *Egenolfianae*). As stated elsewhere the great number of species of ser. *Bolbitianae* in Asia is possibly the product of relatively recent speciation. Also because of certain similarities in the ontogenies of ser. *Bolbitianae* and *Egenolfianae* it seems possible, although contrary to the commonly accepted idea that a free venation is more primitive than an anastomosing pattern, that ser. *Egenolfianae* is the result of recent speciation likewise.

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## **Plates**

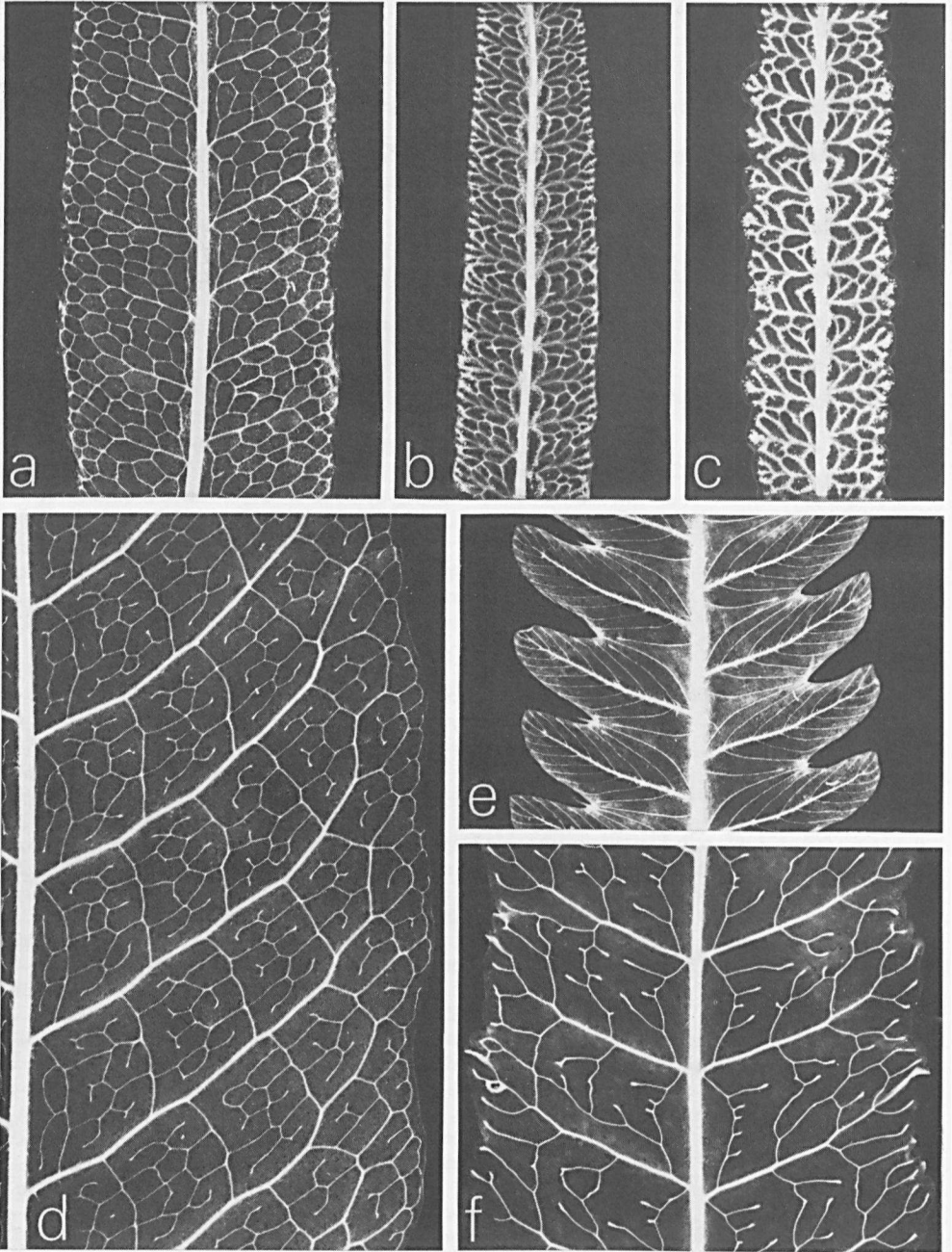


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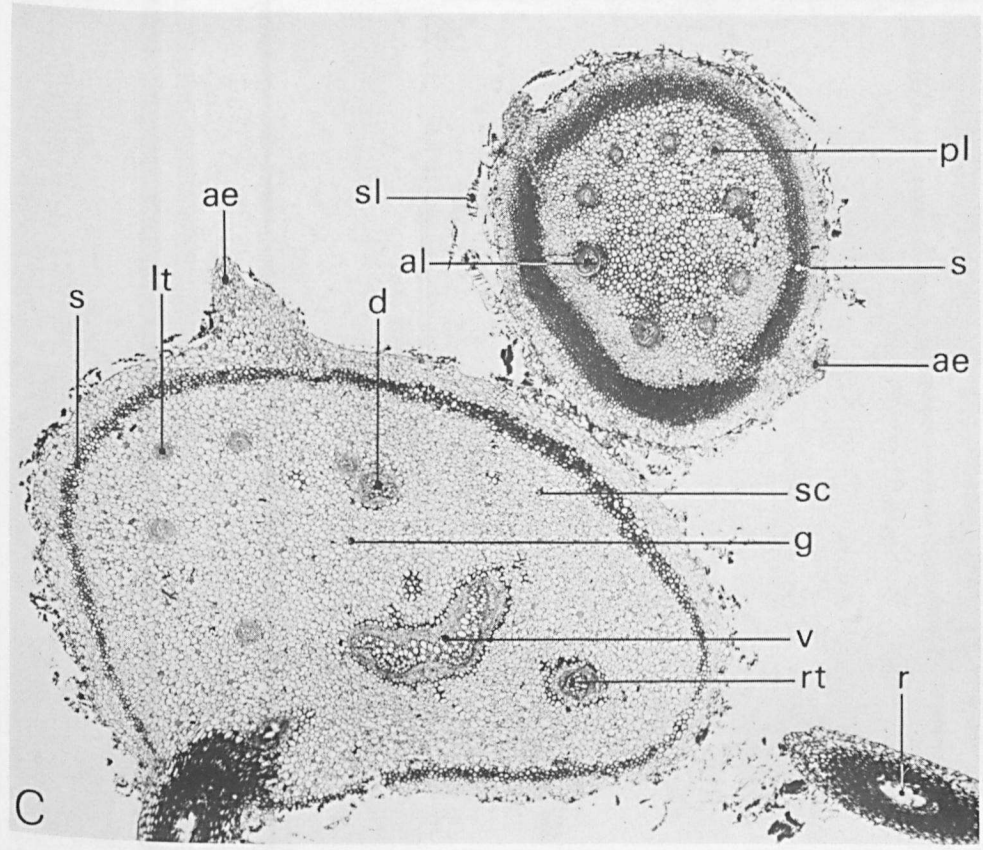
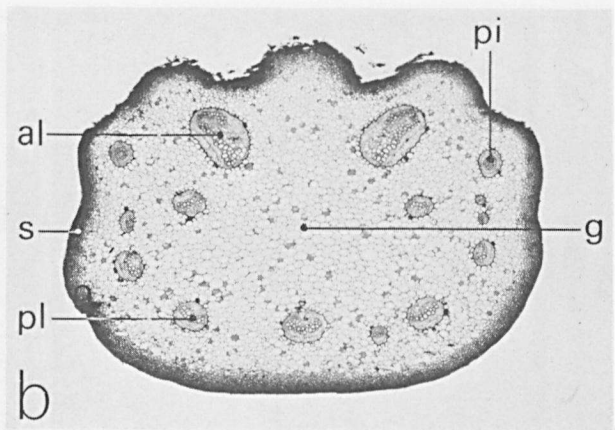
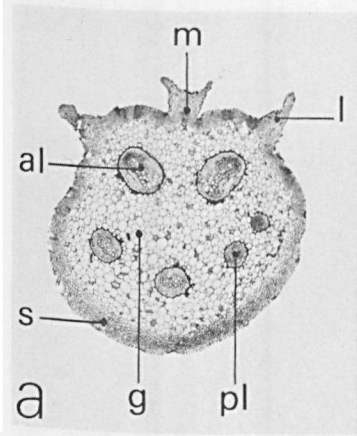


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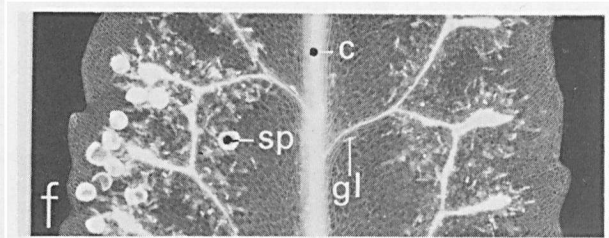
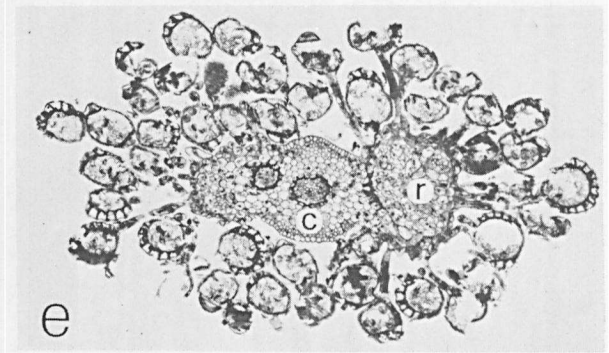
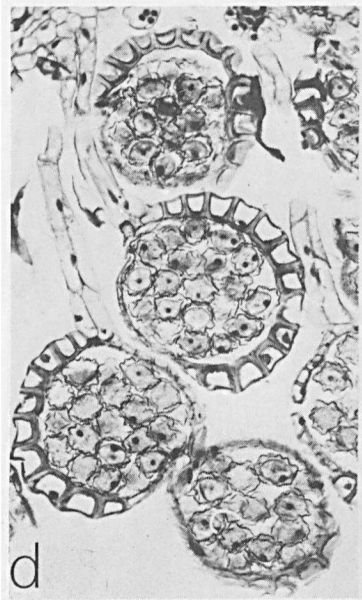
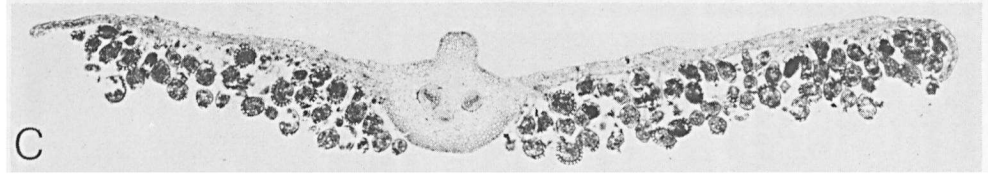
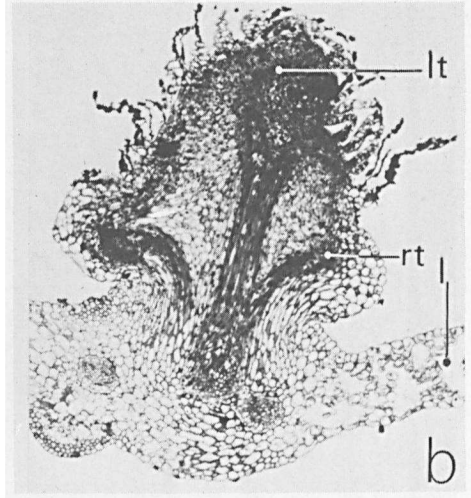
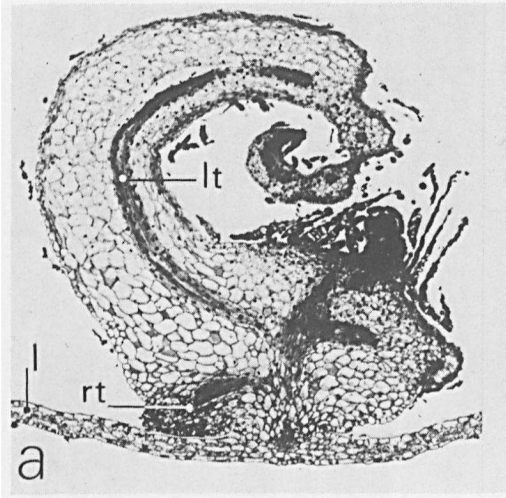


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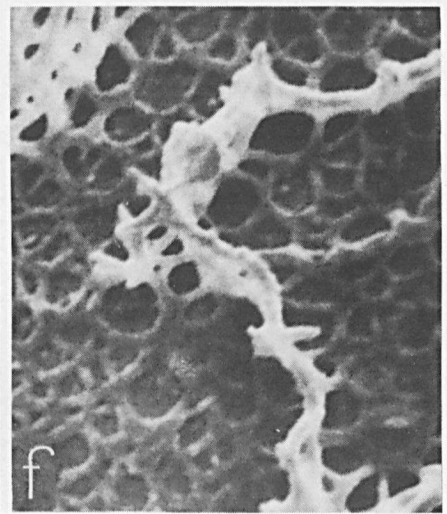
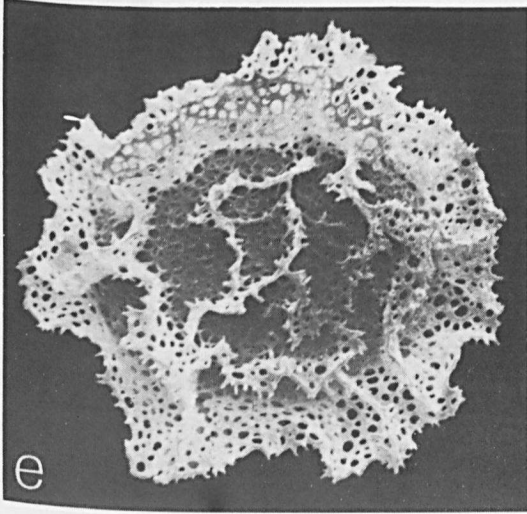
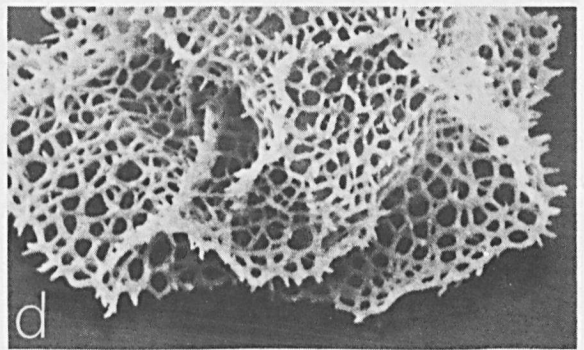
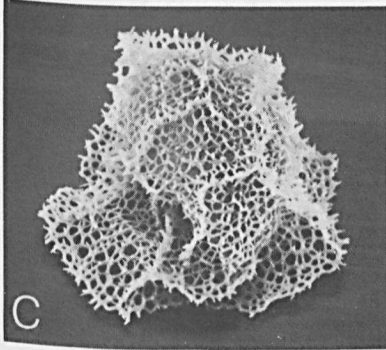
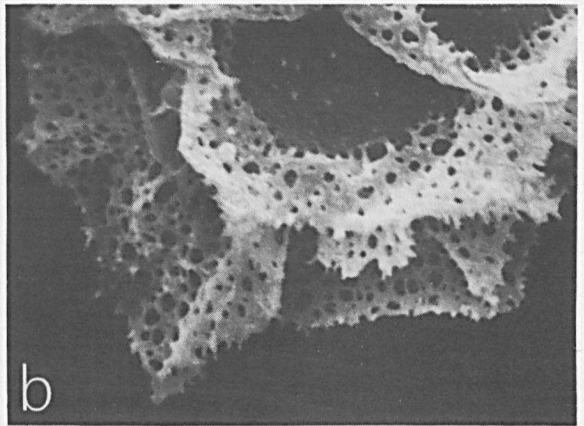
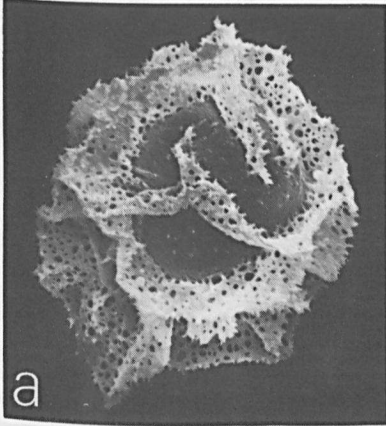


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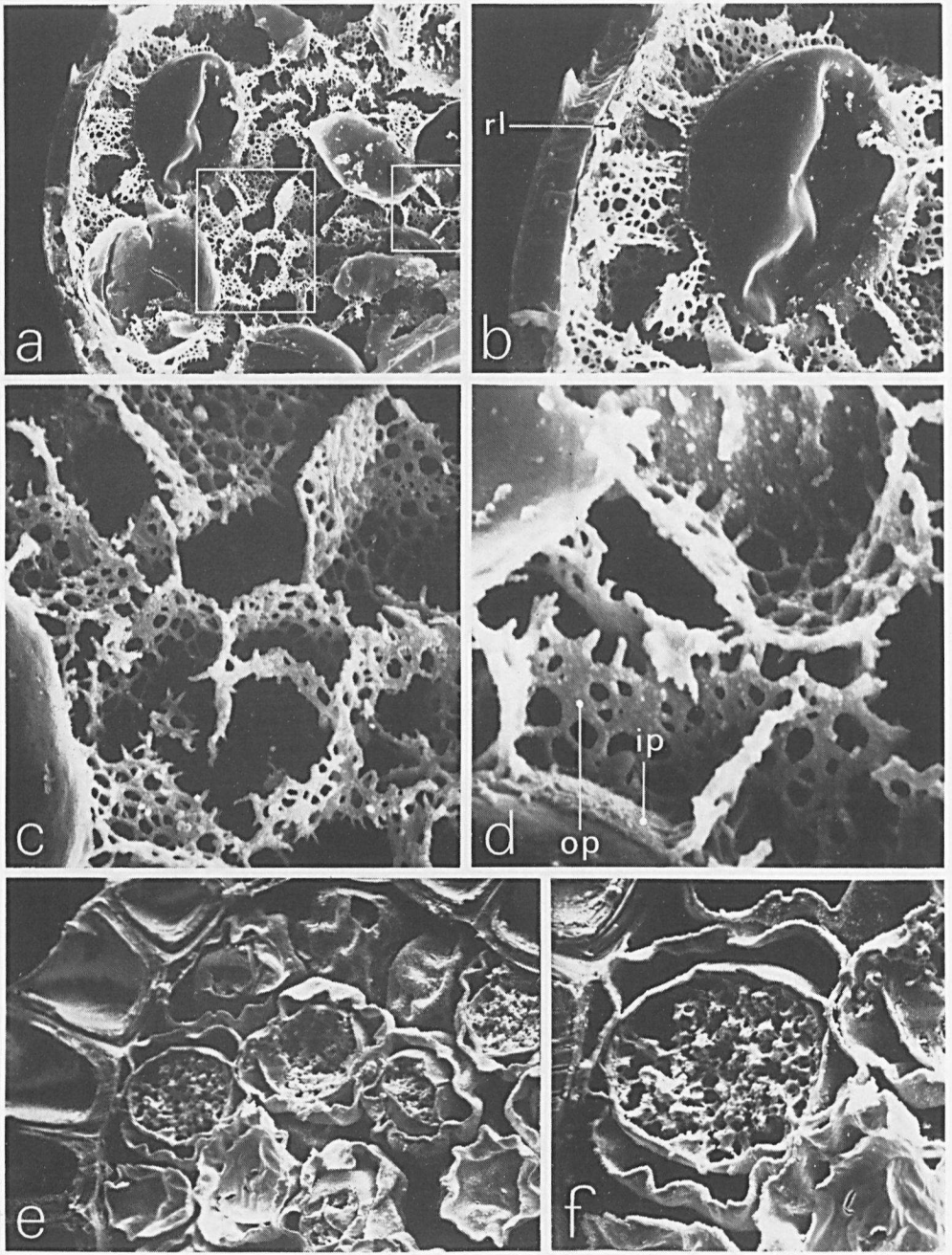


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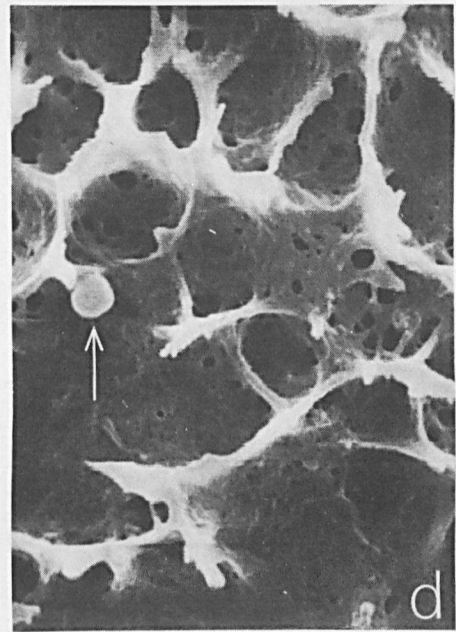
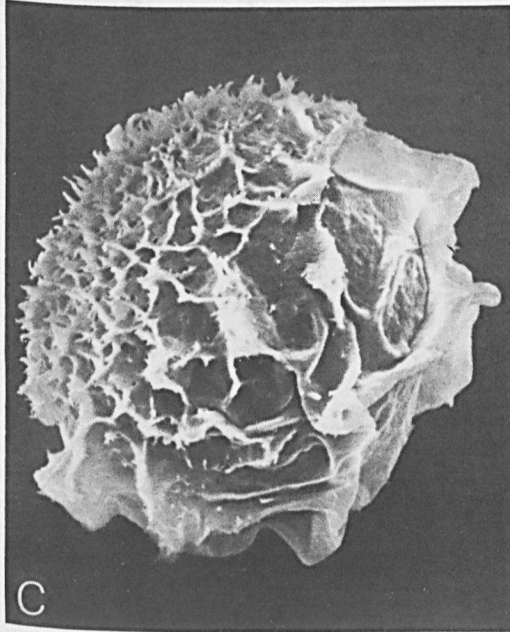
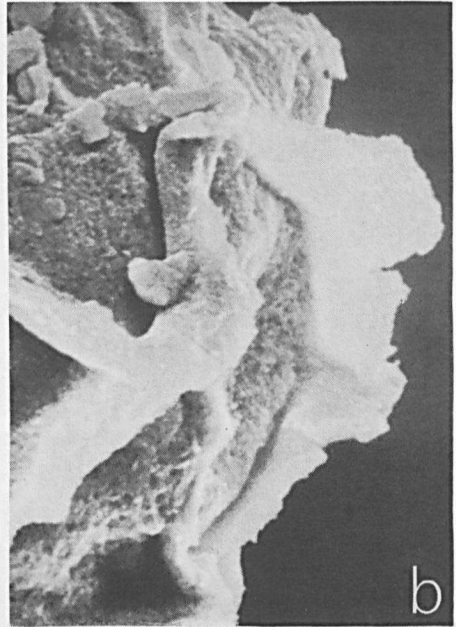
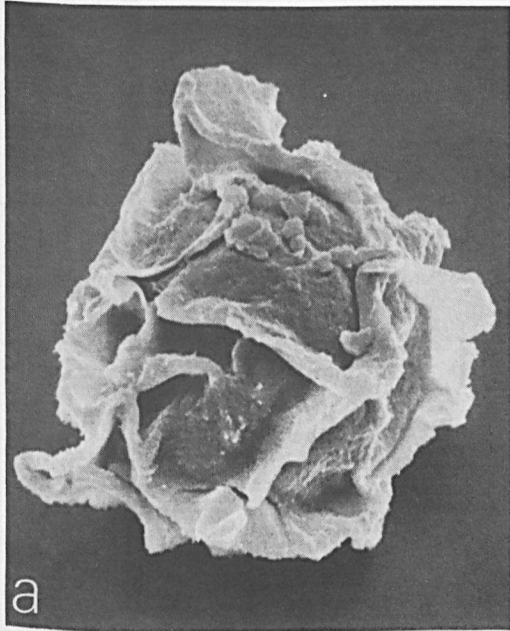


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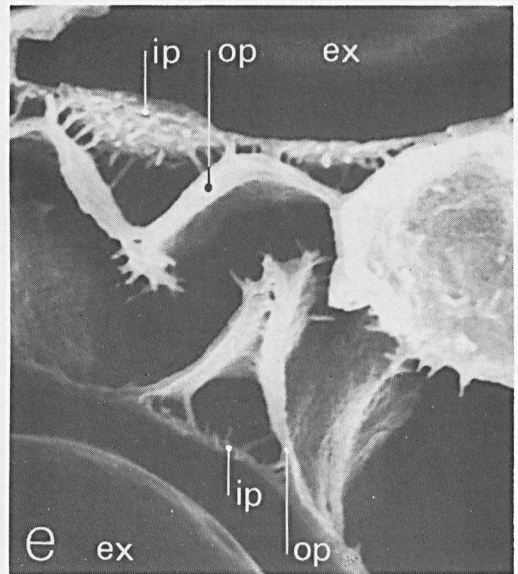
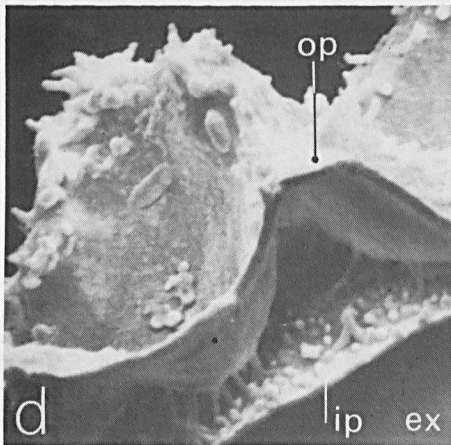
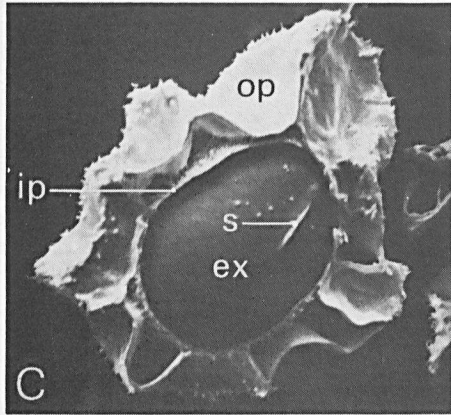
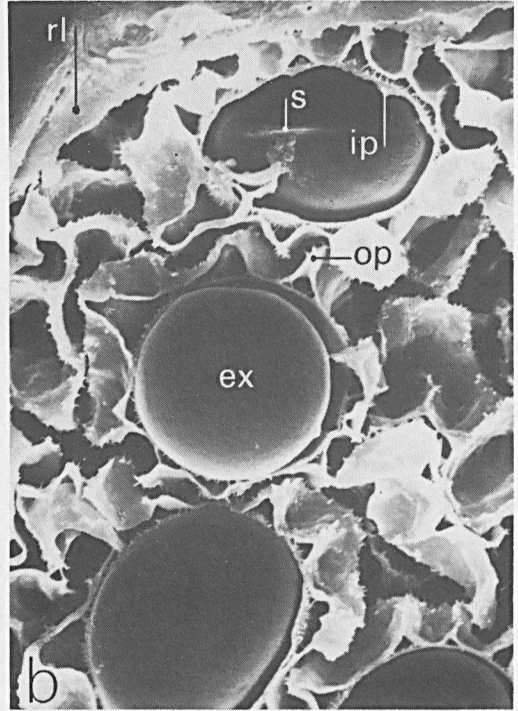
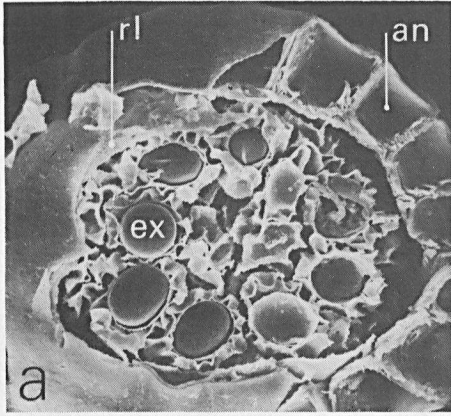


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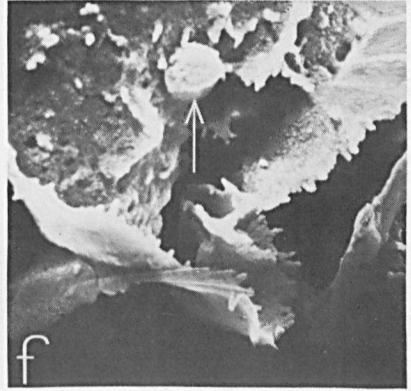
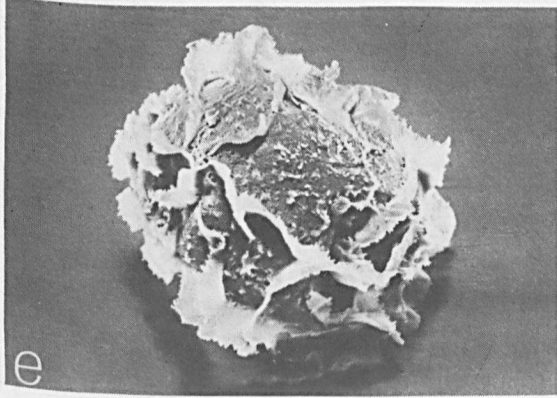
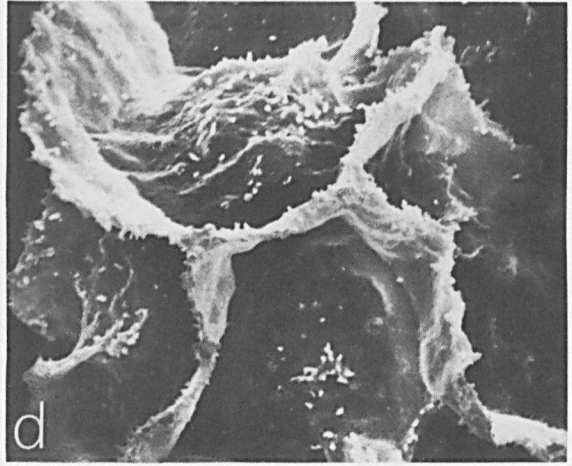
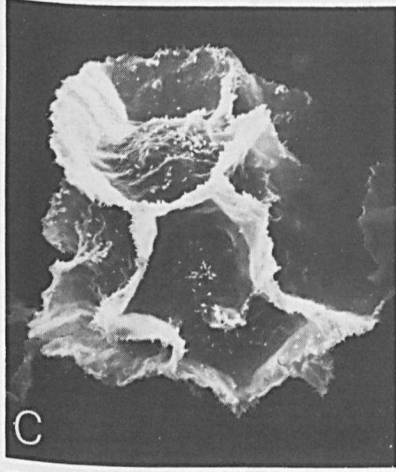
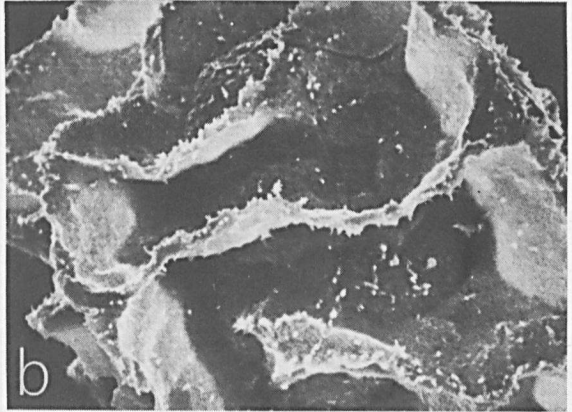
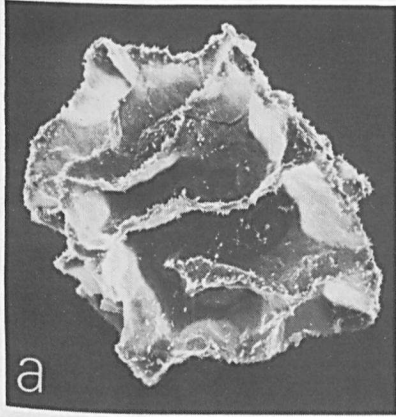


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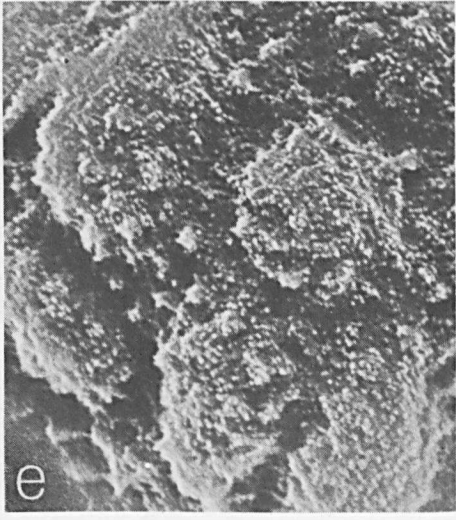
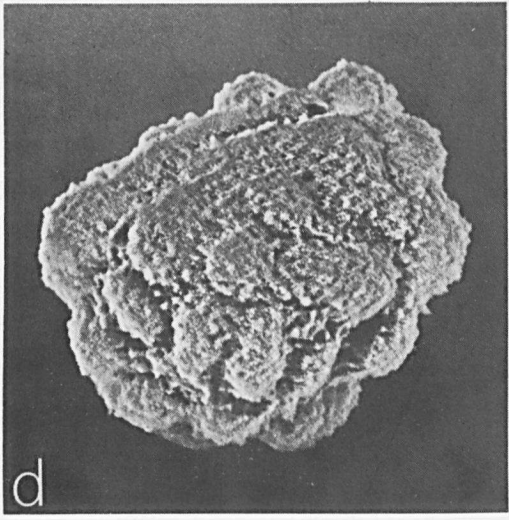
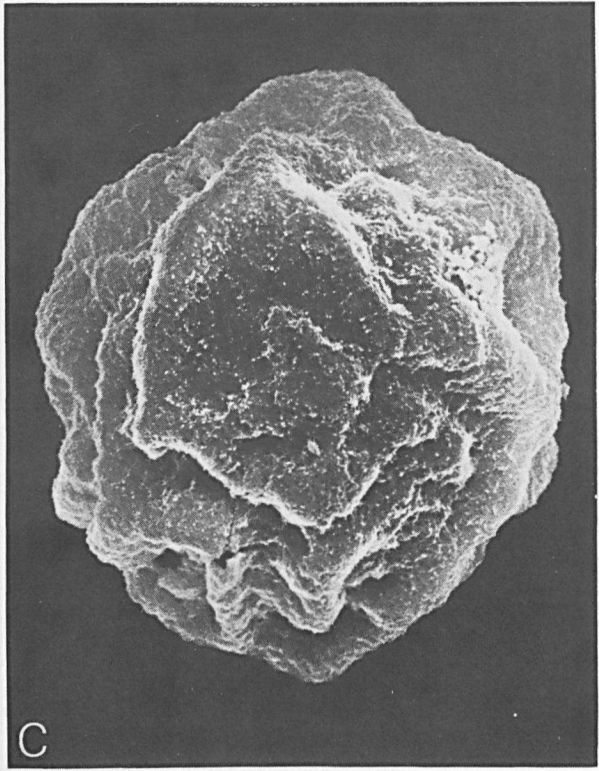
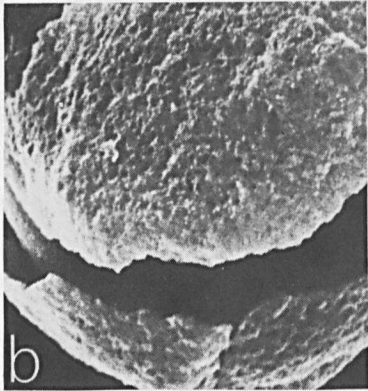
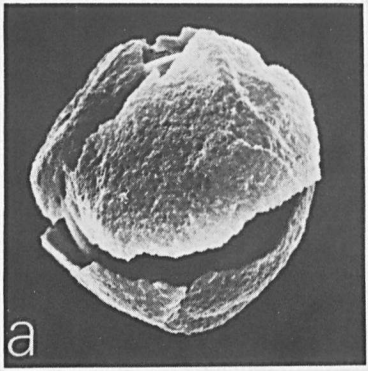


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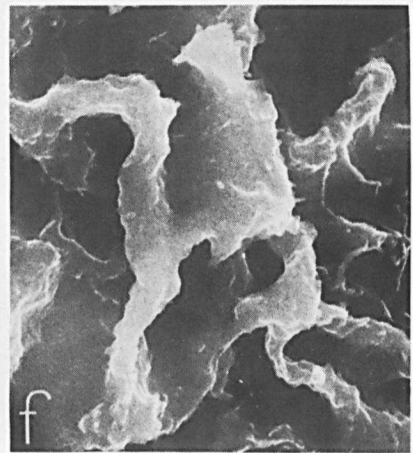
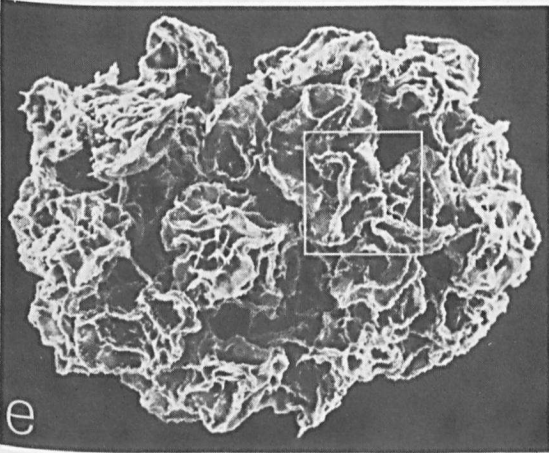
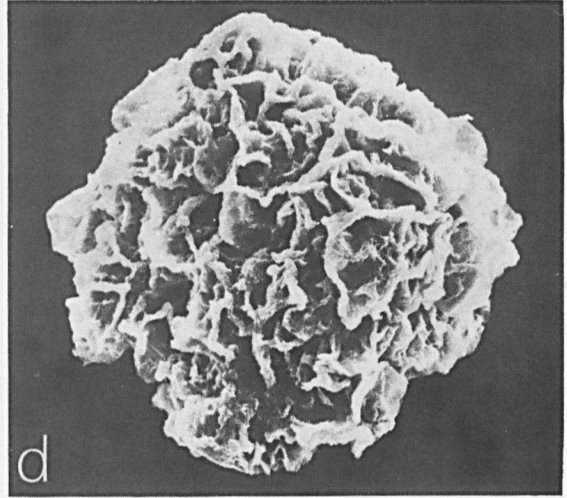
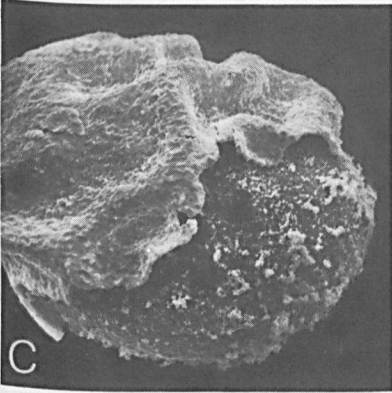
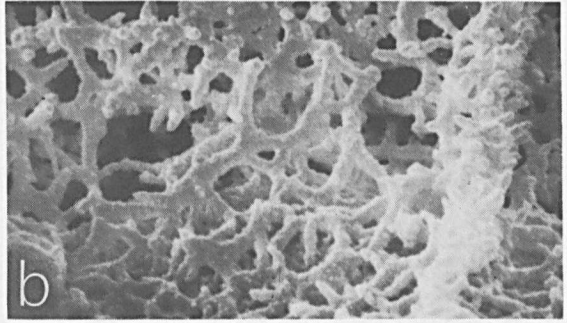
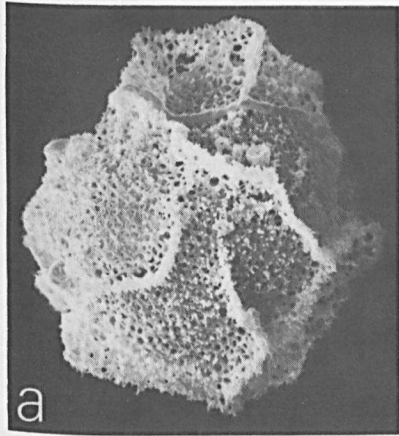


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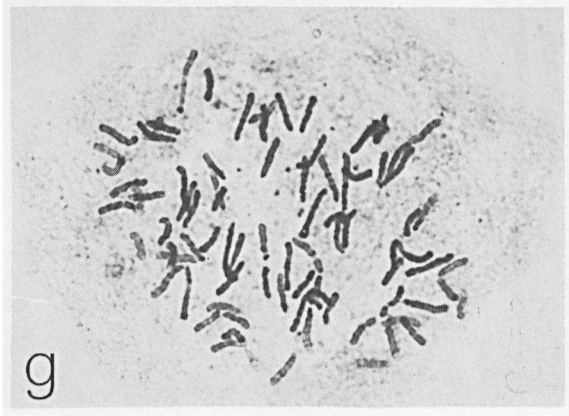
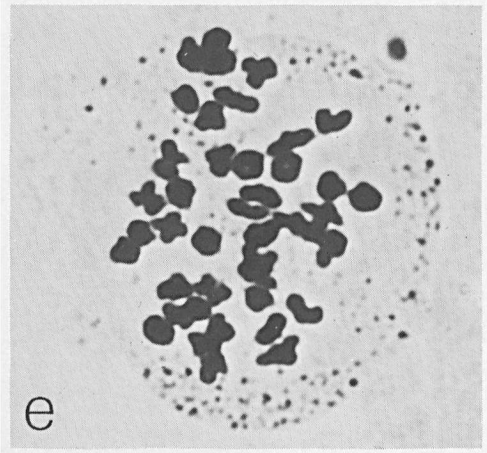
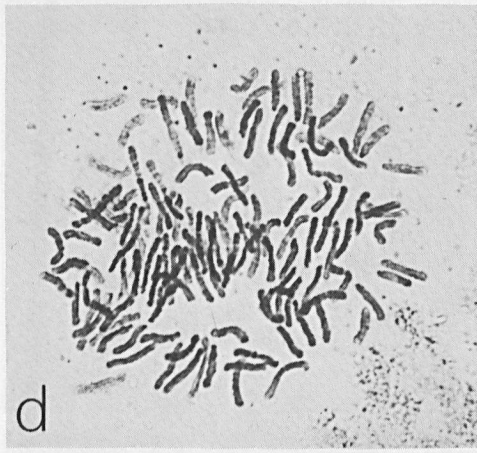
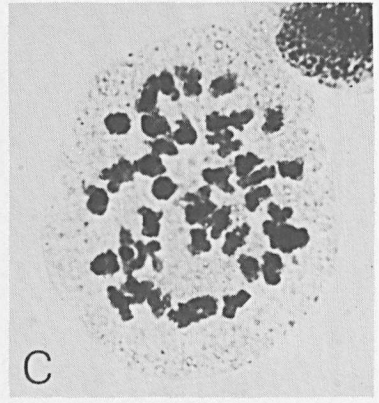
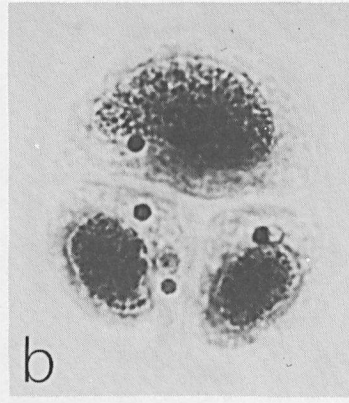
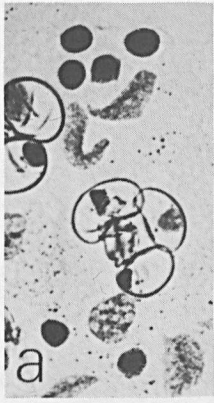


Plate 11



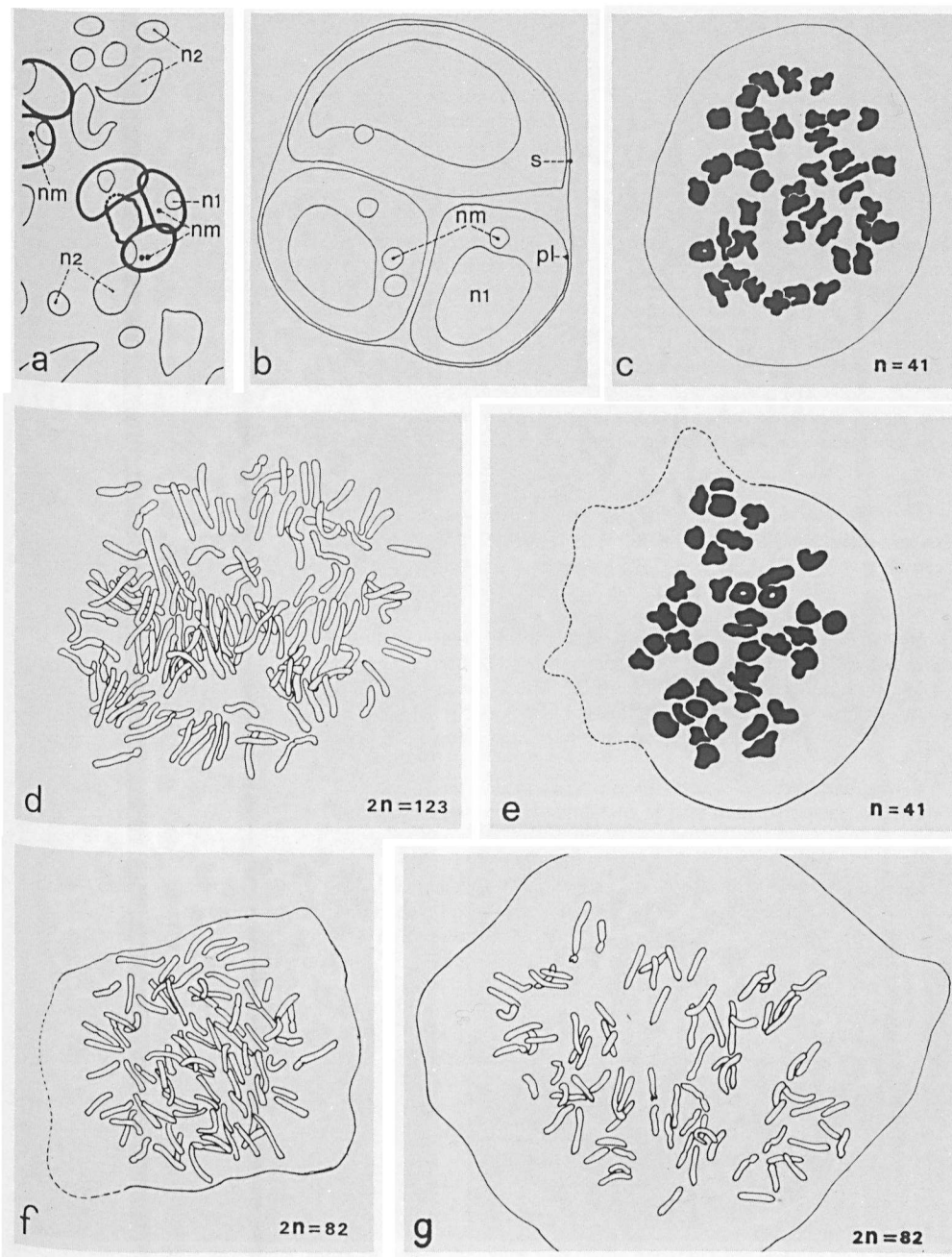


Fig. 31

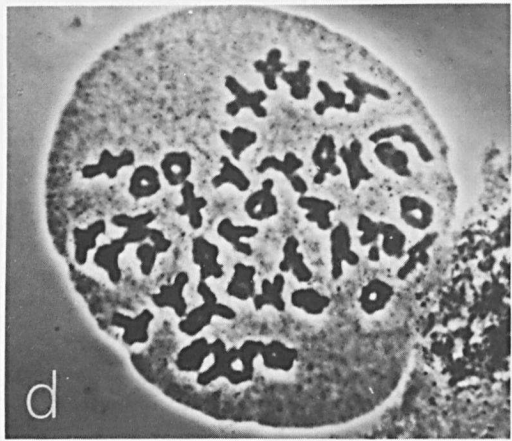
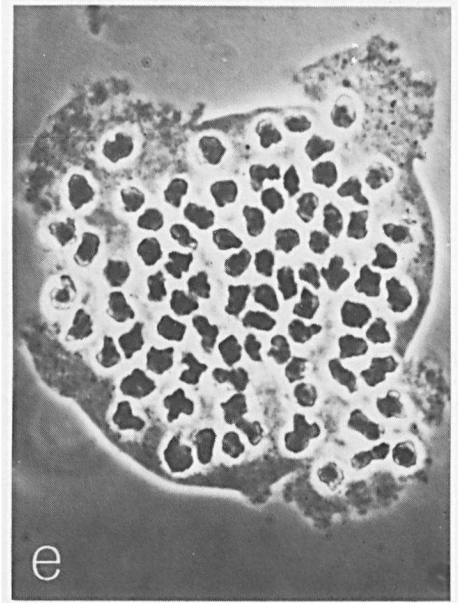
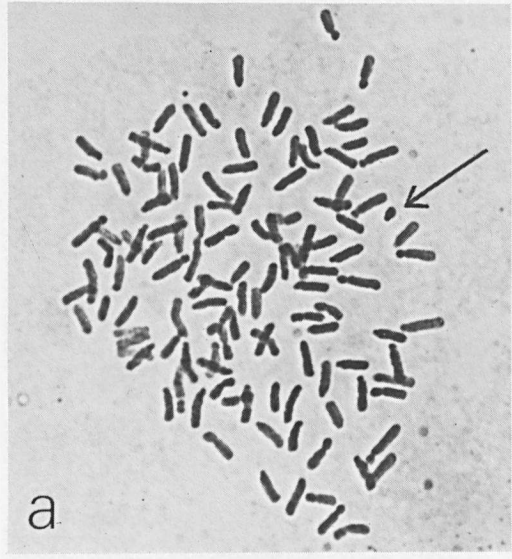


Plate 12

## EXPLANATION OF PLATES

**Plate 1.** a–c. Venation patterns and sporangial insertion of central parts of fertile pinnae,  $\times 2$ . a. *Bolbitis auriculata*; b. *B. serratifolia*; c. *B. acrostichoides* (a. *Kew Distr. no. 1175*, L; b. *Balansa 2852*, L; c. *Young 547*, L);—d–f. Venation patterns of central parts of sterile pinnae,  $\times 2$ . d. *B. nicotianifolia*; e. *B. major*; f. *B. bernoullii* (d. *Maxon 9316*, US; e. *Levinge s.n.*, P; f. *Greeves & Ray 490*, U).

**Plate 2.** Cross-sections showing anatomy,  $\times 12$ .—a. *Bolbitis sinensis*, rhachis—b. *B. angustipinna*, rhachis—c. *B. sinuata*, rhizome and petiole near rhizome apex (a. *Hennipman 3229*, L; b. *H. 3536*, L; c. *H. 4052*, L). ae = aerenchym, al = anterior leaf trace, d = dorsal bundle, g = ground tissue, l = lateral ridge, lt = leaf trace, m = median ridge, pi = pinna trace, pl = posterior leaf trace, r = root, rt = root trace, s = sclerenchyma sheath, sc = sclerenchyma strands of ground tissue, sl = scale, v = ventral bundle.

**Plate 3.** a, b. Cross-sections of laminar bulbils,  $\times 24$ . a. *Bolbitis repanda*; b. *B. sinuata* (a. *Hennipman 4023*, L; b. *H. 4052*, L). l = lamina, lt = leaf trace, rt = root trace.—c–f. Fertile pinnae. c, d. *Bolbitis angustipinna*. c. cross-section of pinna,  $\times 16$ ; d. *ibid.* of sporangia,  $\times 125$ .—e. *Bolbitis appendiculata* var. *vivipara*, cross-section of fertile pinna,  $\times 30$ .—f. *Bolbitis crispatula*, projection photograph of part of cleared pinna,  $\times 14$  (c, d. *Hennipman 3536*, L; e. *H. 3488*, L; f. *H. 3632*, L). c = costa, gl = glandular hair, r = receptacle, sp = sporangium.

**Plate 4.** Spores.—a, b. *Bolbitis appendiculata* ssp. *appendiculata*. a.  $\times 1000$ ; b. detail of a,  $\times 2000$ .—c, d. *B. appendiculata* ssp. *vivipara* var. *vivipara*. c.  $\times 500$ ; d. detail of c,  $\times 1000$ .—e, f. *B. appendiculata* ssp. *vivipara* var. *neglecta*. e.  $\times 1000$ ; f. detail of e,  $\times 4000$  (a, b. *Hennipman 3527*; c, d. *H. 3119*; e, f. *Van Borssum Waalkes 603*, L).

**Plate 5.** Cross-sections of mature sporangia.—a–d. *Bolbitis appendiculata* ssp. *appendiculata*. a. part of sporangium,  $\times 500$ ; b. detail of a, showing the residual layer connected with crests of the perispore,  $\times 1000$ ; c. detail of (interconnecting) crests of different spores,  $\times 2000$ ; d. *ibid.*,  $\times 4000$ .—e, f. *Bolbitis angustipinna*. e. arrangement of spores within the sporangium,  $\times 500$ ; f. detail of e, near annulus,  $\times 1000$  (a–d. *Hennipman 3527*; e, f. *H. 3536*). ip = inner perispore, op = outer perispore, rl = residual layer.

**Plate 6.** Spores of *Bolbitis sinensis*. a, b. spore with a normally shaped, cristate-undulate perispore. a.  $\times 2000$ ; b.  $\times 4000$ . c. spore with an abnormal, in part cristate-undulate, in part spiny perispore,  $\times 2000$ ; d. detail of a spiny perispore (with perforations), also showing a residual body (arrow),  $\times 8000$  (*Rock 2913*, US).

**Plate 7.** Cross-section of a mature sporangium of *Bolbitis sinensis*. a. sporangium,  $\times 500$ ; b. detail of a,  $\times 1000$ ; c. cross-section of spore,  $\times 1000$ ; d. detail of the perispore,  $\times 4000$ ; e. detail of the arrangement of the perispore of adjacent spores,  $\times 4000$  (*Hennipman 3229*, L). ex = exospore, ip = inner perispore, op = outer perispore, rl = residual layer, s = scar of spore.

**Plate 8.** Spores.—a, b. *Bolbitis bipinnatifida*. a.  $\times 1000$ ; b. detail of a,  $\times 2000$ .—c, d. *Bolbitis quoyana*. c.  $\times 1000$ ; d.  $\times 2000$ .—e, f. *Bolbitis nicotianifolia*. e. general view,  $\times 1000$ ; f. detail of e showing also a residual body (arrow),  $\times 2000$  (a, b. *Jeffrey 759*, L; c, d. *Millar & Holtum NGF 15887*, K; e, f. *Herminier s.n.*, L).

**Plate 9.** Spores.—a–c. *Bolbitis angustipinna*. a.  $\times 1000$ ; b, c.  $\times 2000$ .—d, e. *Bolbitis semicordata*. d.  $\times 2000$ ; e.  $\times 5000$  (a–c. *Hennipman 3229*, L; d, e. *Van Hardeveld & Van der Werff 323A*, L).

**Plate 10.** a, b, d–f. Aberrant spores. a, b. *Bolbitis appendiculata* ssp. *appendiculata*. a.  $\times 1000$ ; b.  $\times 5000$ . d–f. clustered spores (the total output of one sporangium) of triploid *B. repanda*. d, e.  $\times 500$ ; f. detail of the 'perispore' of the cluster,  $\times 2000$  (a, b. *Anonymus* in herb. *Hooker & Thomson*, BM; d–f. *Hennipman 4028*, L).—c. *Bolbitis heudelotii*, spore of which the outer part of the perispore has been in part removed,  $\times 1000$  (*Hepper 1826*, K).

Plate 11. a, b. Spore tetrads. a. *Bolbitis heteroclita* 'flagellifera', contents of young sporangium (tetrad already without S.M.C.-membrane),  $\times 250$ ; b. *B. repanda* 'München' (triploid), spore tetrad with S.M.C.-membrane,  $\times 1250$  (a. Hennipman 4027, L; b. H. 4022, L.).—c–g. Chromosome portraits,  $\times 1000$ . c. *Bolbitis heteroclita* 'malaccensis'; d. *B. sinuata* 'gigas'; e. *B. heteroclita* 'cuspidata 2n'; f. *B. rhizophylla* (Price 351, L); g. *B. heudelotii*. See also table 1 and fig. 31.

Fig. 31. Explanatory diagrams of plate 11.  $n_1$  = nucleus of spore,  $n_2$  = nucleus of tapetum, nm = nuclear material originating from lagging chromosomes, pl = plasmalemma of spore, s = S.M.C.-membrane.

Plate 12. Chromosome portraits,  $\times 1000$ . a. *Bolbitis sinuata* 'typical',  $2n = 122 +$  fragment (arrow); b. *B. virens* f. *virens* 'Hennipman',  $2n = 82$ ; c. *B. sinuata* 'sinuata',  $n = 41$ ; d. *B. sinensis* 'Nooteboom',  $n = 41$ ; e. *B. repanda* 'Holtum',  $n = 82$ . See also table 1.

## **Taxonomic Part**

## 1. NOTES ON THE PRESENTATION OF DATA

The presentation of the taxa is alphabetical within the alphabetically arranged series and within the *Species incertae sedis*. The synonymy of the taxa is listed in full. Basionyms and the homotypic synonyms of each basionym are listed chronologically. Relevant literature is included. The names of the authors have been abbreviated as much as possible according to the Kew Index of Author Abbreviations. Nearly all the type collections have been studied; those for which I searched in vain are designated by 'n.v.' (*non vidi*). Herbaria are abbreviated according to the Index Herbariorum. Lectotypes have generally been indicated only for taxa accepted in this paper. The additions 'fert.' (= fertile) and 'ster.' (= sterile) to type collections are given to indicate that the type material consists only of fertile and sterile material respectively. These additions are also added when but little material of a certain taxon was available.

The *material* studied represents almost exclusively adult plants. It is often incomplete. Only part of the collections consists of plants with a rhizome. When leaves are available only, they often lack part of the petiole or the apex of the lamina. Incomplete leaves have been included in the description when parts of it provided relevant information. Fertile leaves not rarely have immature sporangia and spores. Mature fertile leaves often do not show mature spores for the obvious reason that when fertile leaves are collected with mature sporangia and spores, the sporangia open during the drying process, and the mature spores generally disappear together with the drying paper. So-called intermediate leaves, dwarfs, and aberrant specimens are generally not considered in the descriptions. They are discussed in the notes when necessary. A survey of the identity of all the numbered collections studied is given in the Index of collections; the numbers following the collection numbers refer to the numbers assigned to the taxa.

Descriptions are prepared from adult plants. The term segment is used for a portion of the lamina that has an axis (R. M. Tryon Jr, *Taxon* 9, 1960, 104–109).

The *shape of the lamina and the pinnae* is indicated by the index (length/width ratio) and the place where the segment is widest. The number of pinnae given refers to the total number of pinnae to a leaf. Caudate apices of pinnae are not included in the measures given for the length of the pinnae. The width of the fertile pinnae and laminas (in case the leaf is entire) is sometimes difficult to ascertain from herbarium material as the margin of the pinnae is not rarely rolled up.

Primordia of *bulbils* can be traced when the sterile leaves are examined in transmitted light. If present, they appear as small knobs terminally, or subterminally either in the axil of a primary and a secondary vein (in pinnate leaves) or in the axil of a secondary and a tertiary vein (in simple leaves).

*Venation pattern.* The costa of the pinna and the simple lamina are regarded to represent the primary vein. The pinnately arranged lateral veins arising from these primary veins are designated as the secondary veins. Tertiary veins are the veins between adjacent secondary veins. The venation pattern as found between two adjacent secondary veins is usually described in general terms only. Both the descriptions and the illustrations of the venation patterns are as a rule taken from central parts of either central

pinnae (in pinnate leaves), or central lobes (in pinnatifid leaves), or the lamina (in entire leaves). The venation pattern is illustrated for all species. The drawings (4/5 natural size) were taken from projection photographs showing the venation pattern four times magnified, and were afterwards reduced. Elements of the description that are similar in the sterile and the fertile leaves are not repeated in the description of the fertile leaves. Some of the terms relating to the fern leaf and used in this paper are schematically set forth in fig. 32.

The information on the *spores* as given in the separate heading is generally taken from collections randomly selected from the available appropriate material.

*Chromosome numbers* are taken from the list supplied in chapter 7; this list also includes references. S.M.C. stands for Spore Mother Cell.

The *distribution* is given following political boundaries. Large countries have been subdivided. In order to supply also an indication of the frequency of a certain taxon throughout its geographical range, both the countries (or its administrative units) and the number of collections studied from each of them, is indicated. If there are more than 25 collections available from a certain area, they have been generally denoted as 'many collections'.

Distribution maps have been compiled for most of the species from the collections studied. As a precise indication of the locality especially of the older collections has often been neglected, I was unable to spot all the localities, in spite of the fact that different atlases, indices, as well as miscellaneous information regarding localities and itineraries were consulted.

Data regarding the *habitat* conditions and the altitude of the taxa are compiled from the usually scanty information on the labels and summarized under separate headings. Some species were studied in the field.

*Vernacular names* are only rarely recorded on the labels. They have not been taken into consideration.

*Notes* are added to most of the species. They contain amongst other things remarks on the taxonomic position and the relationship of the respective species, and should therefore be regarded as an important element.

*Illustrations* of specimens in outline were generally prepared from dried material and on translucent paper, natural size. These drawings were reduced afterwards. Fertile parts are given in solid black.

*Keys.* The keys to the species are based on characters of the sterile leaves, and sometimes on those of the spores. The fertile leaves generally do not provide important additional characters. Identification will be possible for most of the material using a good hand lens and preferably also a source of transmitted light to study the venation pattern. For a limited part of the material examination of the spores may be necessary. The keys also include hybrids and doubtful species in case these are known from more than one locality. Several species are inconsistent in the characters employed; they appear on more than one place in the key. Keys to infraspecific taxa are given under the species.

It seems more practical to provide keys for each of the continents and including also

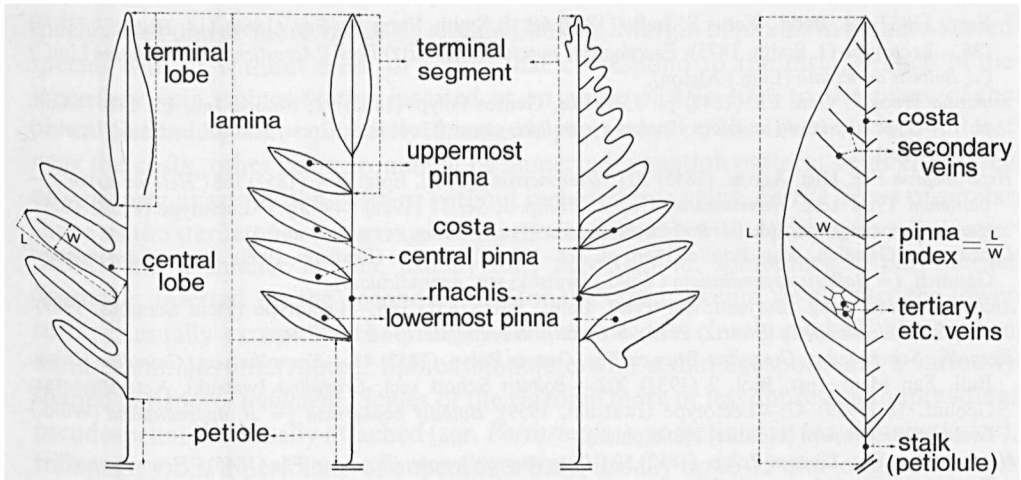


Fig. 32. Schematic illustration explaining the terms used in the Taxonomic Part.

doubtful species and hybrids, than to provide a key to all the recognized species only. The relationships between species of different regions is—where necessary—elucidated in the notes to the species.

*Hybrids, dubious species and excluded species* are separately listed.

## 2. BOLBITIS

- Bolbitis* Schott, Gen. Fil. (1835) *ad tab.* (13) (excellent); C. Chr., Ind. Fil., Suppl. 3 (1934) 102; Tardieu-Blot & C. Chr., Not. Syst. 7 (1938) 99; Backer & Posthumus, Varenfl. Java (1939) 80; Tardieu-Blot & C. Chr. in Lecomte, Fl. Gén. I.-C. 7 (1941) 431; Copel., Gen. Fil. (1947) 115; Holttum, Ferns Malaya (1954) 461; Iwatsuki, Acta Phytotax. Geobot. 18 (1959) 44; Copel., Fern Fl. Philip. (1960) 254; Nayar & Kaur, Bull. Nat. Bot. Gard. Lucknow 88 (1964) 1; Pichi Sermolli, Webbia 23 (1969) 383; DeVol & Kuo in Fl. Taiwan 1 (1975) 347—*Cyrtogonium* J. Smith, in Hook., J. Bot (1841) 154, *nom. illeg.* (art. 63).—*Leptochilus* Kaulf. sect. *Bolbitis* C. Chr., Bot. Tidsskr. 26 (1904) 283—*Leptochilus* subg. *Bolbitis* C. Chr., Ind. Fil. (1906) xxvi.—Lectotype (C. Chr., 1906): *Bolbitis serratifolia* (Kaulf.) Schott.
- Egenolfia* Schott, Gen. Fil. (1835 or 1836) *ad tab.* (16) (excellent); Fée, Genres Polyp. (1852) 48, 358; J. Smith, Hist. Fil. (1875) 131; Copel., Univ. Cal. Publ. Bot. 16 (1928) 64 (= Or. Gen. Polyp.); C. Chr., Contr. U.S. Nat. Herb. 26 (1931) 290; Ching, Bull. Fan Mem. Inst. Biol. 2 (1931) 297; Backer & Posthumus, Nat. Tijds. N. I. 93 (1933) 152; Tardieu-Blot & C. Chr., Not. Syst. 7 (1938) 98; Backer & Posthumus, Varenfl. Java (1939) 84; Tardieu-Blot & C. Chr. in Lecomte, Fl. Gén. I.-C. 7 (1941) 423; Copel., Gen. Fil. (1947) 116; Holttum, Ferns Malaya (1954) 459; Copel., Fern Fl. Philip. (1960) 265; Nayar & Kaur, Bull. Nat. Bot. Gard. Lucknow 100 (1964) 1; DeVol & Kuo in Fl. Taiwan 1 (1957) 350.—*Polybotrya* Humb. & Bonpl. ex Willd. subg. *Egenolfia* Fée, Hist. Acrost. (1845) 14.—*Polybotrya* subg. *Ectoneura* Fée, Hist. Acrost. (1845) 75 ('*Ectoneura*'), *nom. illeg.*, see note 4.—*Acrostichum* L. subg. *Egenolfia* Hooker, Spec. Fil. 5 (1864) 251; Baker in Hooker & Baker, Syn. Fil. (1868) 415.—*Polybotrya* Humb. & Bonpl. ex Willd. sect. *Egenolfia* Diels in E. & P., Nat. Pfl. Fam. 1 (1900) 195, fig. 102; v.A.v.R., Handb. Mal. Ferns (1908) 722.—Type: *Egenolfia hamiltoniana* Schott (= *Bolbitis appendiculata* (Willd.) Iwatsuki ssp. *appendiculata*).
- Campium* Presl, Tent. Pterid. (1836) 238, pl. X: 22, 23; Epim. Bot. (1851) 169; Copel., Philip. J. Sc. 37 (1928) 341, *p.p.*; Backer & Posthumus, Nat. Tijds. N. I. 93 (1933) 157, *p.p.*—Lectotype (C. Chr., 1906): *Campium virens* (Hooker & Grev.) Presl (= *Bolbitis virens* (Hooker & Grev.) Schott var. *virens*, see note 5).
- Poecilopteris* [Eschweiler, Linnaea 2 (1827) 117, *nom. nud.* ('*Poikilopteris*')] Presl, Tent. Pterid. (1836) 241, pl. X: 18, 19, pl. XI: 1, 2; Epim. Bot. (1851) 171; Moore, Ind. Fil. (1857) xx, pl. 7; J. Smith, Cat. Cult.



- Ferns (1857) 23; Bedd., Ferns S. India (1864) 68; J. Smith, Ferns Br. For. (1866) 117; Hist. Fil. (1875) 136.—Lectotype (J. Smith, 1875): *Poecilopteris punctulata* (Swartz) Presl ('*Acrostichum punctulatum* Linn.') (= *Bolbitis auriculata* (Lam.) Alston).
- Jenkinsia* Hooker, Gen. Fil. (1842) pl. 75B; Fée, Genres Polyp. (1852) 92; Moore, Ind. Fil. (1857) xxiii, pl. 10—Type: *Jenkinsia undulata* Hooker (= *Bolbitis virens* (Hooker & Grev.) Schott f. *undulata* (Hooker) Hennipman).
- Heteroneuron* Fée, Hist. Acrost. (1845) 20 ('*Heteroneuron*'); Presl, Epim. Bot. (1851) 168 ('*Heteroneuron*').—*Campium* Presl sect. *Heteroneuron* Copel., Philip. J. Sc. 37 (1928) 349, p.p.—Lectotype (Presl, 1851): *Heteroneuron argutum* Fée (= *Bolbitis heteroclita* (Presl) Ching, see note 2 and 3).
- Lacaussadea* Gaudich., Voy. Bonite (1846) pl. 118–120.—Lectotype (Iwatsuki, 1959): *Lacaussadea montana* Gaudich. (= *Bolbitis appendiculata* (Willd.) Iwatsuki ssp. *appendiculata*).
- Anapausia* Presl subg. *Euryostichum* Presl, Epim. Bot. (1851) 188.—Lectotype (Pichi Sermolli, 1969): *Anapausia nicotianifolia* (Swartz) Presl (= *Bolbitis nicotianifolia* (Swartz) Alston).
- Egenolfia* Schott subg. *Granulina* Bory ex Fée, Genres Polyp. (1852) 48.—*Egenolfia* sect. *Granulina* Ching, Bull. Fan Mem. Inst. Biol. 2 (1931) 302.—*Bolbitis* Schott sect. *Granulina* Iwatsuki, Acta Phytotax. Geobot. 18 (1959) 47.—Lectotype (Iwatsuki, 1959): *Bolbitis hookeriana* (= *B. appendiculata* (Willd.) Iwatsuki ssp. *vivipara* (Hooker) Hennipman).
- Heteroneuron* Fée, Genres Polyp. (1852) 59 ('*Heteroneuron*'), *nom. illeg., non* Fée (1845) ('*Heteroneuron*').—Type: not indicated, see note 2.
- Edanyoa* Copel., Philip. J. Sc. 81 (1952) 22, pl. 17.—Type: *Edanyoa difformis* Copel. (= *Bolbitis heteroclita* (Presl) Ching).
- Bolbitis* Schott sect. *Lysidictyon* Iwatsuki, Acta Phytotax. Geobot. 18 (1959) 47.—Type: *Bolbitis laxireticulata* Iwatsuki (= *Bolbitis spec. dub.*).

Small to medium-sized, terrestrial, low-epiphytic, or usually low-climbing ferns. *Rhizome* short- to long-creeping, unbranched or with accessory branches, slender or stout, almost terete to dorsiventrally flattened, dorsally and/or laterally with 2–6 rows of leaves and in the apical part with variously shaped aerophores occurring in a line with those on the petiole (distinct in living rhizomes only), roots usually ventral, sometimes also lateral, either in two longitudinal rows or irregularly arranged; anatomy: ground tissue parenchymatous, when living light green, longitudinal sclerenchyma strands, if present, scattered in the ground tissue,  $\pm$  cylindrical, with a sheet of sclerenchyma of varying thickness situated just below the epidermis and interrupted by aerophores, vascularization dictyostelic, markedly dorsiventral, with a broad gutter-shaped ventral bundle giving off root and leaf traces, and 1–5 narrower to almost cylindrical dorsal ones giving off leaf traces. *Leaves* spaced to aggregate, dimorphic, simple, pinnate, or rarely bipinnate. *Sterile leaves*: *petioles* usually short-decurrent on the rhizome, sometimes either almost perpendicular to the rhizome or (in epiphytes) long-decurrent on the rhizome, near the base dark brown or blackish, otherwise light brown or stramineous, near the base adaxially flattened or convex, abaxially terete, near the apex adaxially usually  $\pm$  flat with one or three median, longitudinal ridges and on either side 1 (2) lateral ones, sometimes adaxially round or convex, aerophores linear, pale, present laterally on either side and especially conspicuous in the basal part of young leaves; anatomy: ground tissue parenchymatous, in the basal region with or without sclerenchyma strands similar to those in the rhizome, with a firm sheet of sclerenchyma situated just below the epidermis and interrupted by aerophores, with a more or less U-shaped arrangement of vascular bundles of which the two anterior ones are largest; *lamina* green, above somewhat shining, texture mostly more or less herbaceous, sometimes coriaceous or pergamentaceous, in most

species with one or more variously situated bulbils. Margin of pinnae in pinnate-leaved species with or without teeth or spines that correspond to the distal branch of the secondary vein, spines *in vivo* inserted at an angle of 150–100° to the plane of the pinna. Secondary veins pinnately arranged, prominent on the lower surface at least near the costa, other veins prominent or immersed; venation pattern: veins either free or variously anastomosed, with or without included free veins. *Fertile leaves* of similar shape as the sterile ones occurring in conjunction, though with a proportionally longer petiole and a smaller lamina, usually fully acrostichoid, sometimes in part sterile. *Sporangia* inserted on the secondary and/or the tertiary veins, or all over the lower surface, usually except for the primary vein, numerous, closely packed, black when mature, annulus interrupted. Spores monolete with a thin exospore and a variously shaped perispore. *Indument*. Scales of the rhizome more or less appressed to spreading, pseudo-peltate or basally attached (ser. *Portoricenses*, sometimes in ser. *Bipinnatifidae*), triangular from a perfoliate or subcordate base, usually up to 15 mm long, sometimes up to 25 (–40) mm long, membranaceous to firmly herbaceous, light brown to blackish, opaque to almost clathrate, of the same colour throughout or with a paler marginal strip, margin almost entire, in one species (*B. bernoullii*) conspicuously denticulate, when mature sparsely set with slender, uniseriate, usually few-celled, thin-walled glandular hairs. Scales of the petiole in part ± similar to those on the rhizome, usually on the basal part only, rarely on petiole and rhachis throughout, in part appressed, of smaller size and ± orbicular. Scales of the lamina scattered on the lower face, especially on the rhachis at the junction with the pinnae, ± similar to the appressed type of scales of the petiole. Leaves usually glabrescent. The crozier on either side densely covered with 2- or 3(–5)-celled uniseriate hairs, the terminal and sometimes also the subterminal cell of which are glandular.

Chromosomes.  $n = 41, 82; 2n = (c.) 82, (c.) 123, \text{ and } 164.$

Gametophyte. Cordate or elongate.

Distribution. Pantropic. See fig. 26.

Habitat. Mostly creeping on rocks, sometimes creeping in soil or epiphytic, in moist places—often nearby and even in streams—in monsoon and evergreen forest. Altitude: 0–1500(–2000) m.

Notes. 1. There is disagreement about the sequence of the plates in Schott's *Genera Filicum*, due to the fact that the plates have not been numbered. The 20 plates and descriptions were issued between 1834–1836 as 4 fascicles containing five plates each (Staffeu, *Taxonomic Literature*, 1967). At the British Museum I found Fée's copy of this book in which the plates are bound alphabetically. The number of the fascicles and the plates are indicated on the cover of that book in Fée's characteristic handwriting, except for the plates of *Nephrodium* and *Taenitis*. The copy at the Rijksherbarium shows *Nephrodium* to represent the fifth plate of fascicle 2 (plate 10), which makes the plate of *Taenitis* the fifth plate of fascicle 4 (plate 20). In conclusion, the following sequence is proposed: Fascicle 1 (1834): *Anaxetum* (1), *Aspidium* (2), *Nephrolepis* (3), *Sphaeropteris* (4), *Trichopteris* (5)—Fascicle 2 (1834): *Olfersia* (6), *Polybotrya* (7), *Cystopteris* (8), *Polystichum* (9), *Nephrodium* (10)—Fascicle 3 (1835): *Lonchitis* (11), *Meniscium* (12),

*Bolbitis* (13), *Hemionitis* (14), *Marattia* (15)—Fascicle 4 (1835 or 1836): *Egenolfia* (16), *Cochlidium* (17), *Monogramma* (18), *Aglaomorpha* (19), *Taenitis* (20).

2. The genus *Heteroneuron* Fée (1845) included 16 species. It was typified by Presl (1851) who excluded all but one of Fée's species (*H. argutum*) and added a second. The remaining 15 species which Fée attributed to *Heteroneuron* were transferred by Presl to the genera *Campium* and *Poecilopteris* at the same time. Presl's spelling '*Heteroneurum*' should be regarded as an orthographic variant. The effort of Pichi Sermolli (1969) to recognize a genus *Heteroneurum* Presl beside a genus *Heteroneuron* Fée, is contrary to the Code. The same holds for the selection of another type for *Heteroneuron* Fée, as was done by Iwatsuki (1959; *H. diversifolium*) and Pichi Sermolli (1969; *H. scalpturatum*). *Heteroneuron* Fée (1852) is a different genus, as Fée excluded *H. argutum*.

3. *Heteroneuron*, the original spelling also adopted by Pichi Sermolli (1969), has according to the Code (art. 73) to be replaced by *Heteroneuron*.

4. When dealing with the genera of acrostichoid ferns, Fée (1845: 14) divided the genus *Polybotrya* into two subgenera, '1. *Egenolfia*, Schott; Gen. Filic.' and '2. *Eupolybotrya*'. In the part where the species are described (op. cit.: 72 and 75, resp.) he divided it into the subgenera 'I. *Eupolybotrya*' and 'II. *Ectonevra*' (*Egenolfia*, Schott). Therefore, the subgenera *Egenolfia* and *Ectoneura* are homotypic synonyms.

5. Iwatsuki (1959) overlooked Christensen's publication (1906) and selected *Campium punctulatum* Presl (= *Bolbitis spec. dub.*) as the type of *Campium*.

6. Synonyms have been listed only when their type species are part of this genus. Other genera to which species of the present genus have been referred include *Acrostichum*, *Aspidium*, *Asplenium*, *Chrysodium*, *Diplazium*, *Gymnogramma*, *Gymnopteris*, *Hypoderris*, *Leptochilus*, *Lomariopsis*, *Meniscium*, *Nephrodium*, *Neurocallis*, *Notholaena*, *Polybotrya*, *Polystichum*, and *Stenosemia*.

7. Etymology. As fully explained by Pichi Sermolli (Webbia 12, 1969, 386) the genus was probably so named on account of a bulbil on its leaves.

### 3. KEYS TO SPECIES AND HYBRIDS

H: Hybrids (p. 284 onwards). D: Species dubiae (p. 302 onwards)

#### KEY TO THE SPECIES AND HYBRIDS OF AFRICA AND MADAGASCAR

- |  |                          |
|--|--------------------------|
| 1. Leaves simple . . . . .   | 2                        |
| 1. Leaves pinnate . . . . .  | 3                        |
| 2. Lamina with a subterminal bulbil. Venation pattern intricate, part of the areoles with re- and/or excurrent included free veins . . . . . | <b>20. B. gaboensis</b>  |
| 2. Lamina without a bulbil. Veins forming a regular network of angulate areoles without included free veins . . . . .                        | <b>3. B. fluviatilis</b> |

- 3. Terminal segment with a bulbil in the basal part; veins forming an intricate network which is locally irregular, part of the areoles with usually few ex- or recurrent included free veins . . . . . 36. **B. gemmifera**
- 3. Terminal segment without bulbils or with a subterminal bulbil . . . . . 4
- 4. Venation pattern with ex- and recurrent included free veins . . . . . 5
- 4. Venation pattern without or with only excurrent included free veins . . . . . 7
- 5. Bulbils absent. Usually in streams . . . . . 27. **B. heudelotii**
- 5. Bulbils present . . . . . 6
- 6. Upper half of lamina almost entire, not prolonged. Scales up to 5 mm long. *Congo Basin* . . . . . H.5. **B. × boivinii**
- 6. Upper half of lamina deltoid, regularly lobed, tapering towards the acute or flagelloid apex. Scales up to 12 mm long. *Madagascar* . . . . . 37. **B. humblotii**
- 7. Terminal segment triangular, as long as to longer than the remaining part of the lamina . . . . . 8
- 7. Terminal segment usually either conform to the pinnae or flagelloid, sometimes narrowly triangular and much shorter than the remaining part of the lamina . . . . . 9
- 8. Margin of pinnae ± entire. Terminal segment usually asymmetrical, consisting of few (2–5) lobes, not flagelloid. Veins regularly reticulate, without included free veins . . . . . 2. **B. auriculata**
- 8. Margin of pinnae lobed 3/7–5/7 towards the costa; a tooth present in the sinuses. Terminal segment symmetrical, composed of many lobes, sometimes flagelloid. Veins regularly reticulate, at least the costal arch with few short excurrent included free veins . . . . . 4. **B. bipinnatifida**
- 9. Terminal segment flagelloid. Perispore cristate. *Madagascar*. . . . . D. 5. **B. longiflagellata**
- 9. Terminal segment conform to the pinnae or somewhat prolonged. Perispore undulate. *Mainland Africa* . . . . . 10
- 10. Pinnae 8–20 mm wide. Venation pattern without or with only one or a few excurrent included free veins. Terminal segment not prolonged. Fertile pinnae fully acrostichoid, the sporangia inserted all over the lower surface . . . . . 9. **B. salicina**
- 10. Pinnae 15–45 mm wide. Venation pattern usually with several excurrent included free veins. Terminal segment usually somewhat prolonged. Fertile pinnae usually hemionitoid, sometimes acrostichoid, the sporangia inserted exclusively or mainly on the veins . . . . . 5. **B. acrostichoides**

KEY TO THE SPECIES OF AMERICA

- 1. Scales of the rhizome 10–20 mm long or longer. Tertiary veins prominent throughout. Leaves in 2–6 rows. High-climbing plants . . . . . 2

1. Scales of the rhizome up to 10(–15) mm long. Tertiary veins prominent near the costa or near the secondary veins only. Leaves in 2(–5) rows. Terrestrial, sometimes on the bases of trees . . . . . 3
2. Margin of the scales entire. Veins forming a regular network of  $\pm$  isodiametric or elongate areolae . . . . . 28. *B. lindigii*
2. Margin of the scales denticulate. Veins forming an irregular network, part of the areoles with mostly excurrent included free veins . . . . . 35. *B. bernoullii*
3. Leaves either simple, or pinnate with the terminal segment usually conform to the pinnae, rarely narrowly triangular and much shorter than the remaining lamina . . . . . 4
3. Leaves pinnate with the terminal segment triangular and longer than the remaining lamina . . . . . 15
4. Leaves pinnatifid . . . . . 5
4. Leaves entire or pinnate . . . . . 6
5. Leaves with a subterminal bulbil. The majority of the areoles along the leaf margin with usually one recurrent included free vein. *Mexico* . . . . . 29. *B. hastata*
5. Leaves without a bulbil. The majority of the areoles along the margin without included free veins. *South America* . . . . . 42. *B. semipinnatifida*
6. Leaves entire and with a subterminal bulbil, or pinnate . . . . . 7
6. Leaves entire, without a subterminal bulbil (uncommon forms of generally pinnate species) . . . . . 13
7. Venation pattern without recurrent included free veins; excurrent free veins present or not. Perispore undulate . . . . . 8
7. Venation pattern with both re- and excurrent included free veins. Perispore cristate . . . . . 9
8. Rhachis with a narrow wing. Lamina with 4–8 pinnae, without bulbils. . . . . 12. *B. serrata*
8. Rhachis not winged. Lamina with 9–30 or more pinnae and (a primordium of) a subterminal bulbil . . . . . 13. *B. serratifolia*
9. Bulbils absent . . . . . 10
9. Bulbils present, either axillary or subterminal . . . . . 11
10. Scales of the rhizome soft, rusty brown, bullate. Texture of leaves pergamentaceous; terminal segment if present  $\pm$  rhomboid; secondary veins prominent nearly to the margin . . . . . 24. *B. pergamentacea*
10. Scales of the rhizome firm, dark brown or blackish, flat, appressed. Texture of leaves thin-herbaceous; terminal segment if present biconvex; secondary veins slightly prominent and only to some distance from the margin. . . . . 22. *B. nicotianifolia*
11. Bulbil subterminal . . . . . 30. *B. pandurifolia*
11. Bulbils axillary . . . . . 12
12. Leaves ternate; pinnae (sub) opposite; base of terminal segment (almost) symmetrical. *The Andes* . . . . . 23. *B. oligarchica*

- 12. Leaves with 3–9 usually alternate pinnae; base of terminal segment (strongly) asymmetrical . . . . . **21. B. hemiotis**
- 13. Scales of the rhizome bullate, rusty brown. Secondary veins prominent nearly to the margin . . . . . **24. B. pergamentacea**
- 13. Scales of the rhizome flat, blackish. Secondary veins towards the margin either prominent or inconspicuous . . . . . 14
- 14. Base of the lamina truncate to subcordate, sometimes asymmetrical. *Trinidad, Venezuela* . . . . . **21. B. hemiotis**
- 14. Base of the lamina  $\pm$  acute, symmetrical . . . . . **22. B. nicotianifolia**
- 15. Venation pattern without included free veins or with only an incidental short, simple, included free vein . . . . . 16
- 15. Venation pattern with many recurrent (and excurrent) included free veins some of which are once forked . . . . . 17
- 16. Leaves tufted. Margin of pinnae with teeth in the sinuses. Leaves green when dried. *Mexico* . . . . . **44. B. umbrosa**
- 16. Leaves spaced. Margin of pinnae without teeth in the sinuses (if present). Leaves usually dark green or blackish when dried . . . . . **1. B. aliena**
- 17. Bulbils present. Terminal segment regularly triangular, composed of many lobes, apex often flagelloid. Scales of the rhizome up to 10 mm long, basally attached. Venation pattern: see fig. 68: e–j . . . . . **31. B. portoricensis**
- 17. Bulbils absent. Terminal segment either asymmetrical or symmetrical, composed of but few (up to 6) lobes, apex acute. Scales of the rhizome up to 4 mm long, pseudo-peltate. Venation pattern: see fig. 79: g, h . . . . . **42. B. semipinnatifida**

KEY TO THE SPECIES AND HYBRIDS OF ASIA AND THE PACIFIC

- 1. Plants small (dwarfed) and/or leaves simple . . . . . 35
- 1. Plants not dwarfed. Leaves pinnate . . . . . 2
- 2. Veins free . . . . . 3
- 2. Veins anastomosing . . . . . 7
- 3. Bulbil  $\pm$  terminal on the lamina. Spines on the margin of the pinnae  $\pm$  flattened at their bases. Base of pinnae symmetrical. Margin entire or shallowly lobed. *Taiwan, Philippines* . . . . . **18. B. rhizophylla**
- 3. Bulbil subterminal on the lamina. Spines on the margin not flattened at their bases. Base of pinnae symmetrical or asymmetrical. Margin entire or lobed . . . 4
- 4. Rhizome long-creeping. Petiole with  $>10$  vascular bundles . . . . . **17. B. major**
- 4. Rhizome short-creeping. Petiole with  $<10$  vascular bundles . . . . . 5
- 5. Perispore smooth. Base of pinnae symmetrical, margin lobed  $1/3$ – $2/3$  ( $-3/4$ ) towards the costa . . . . . 6
- 5. Perispore reticulate. Base of pinnae either symmetrical or asymmetrical; if symmetrical the margin of the pinna  $\pm$  entire or lobed to  $1/3$  ( $-1/2$ ) towards the costa. **16. B. appendiculata**

6. Perispore cristate-undulate. Petiole and rhachis glabrescent . . . **19. B. sinensis**
6. Perispore cristate. Petiole and rhachis scaly throughout . . . **D. 7. B. tonkinensis**
7. Leaves  $\pm$  coriaceous . . . . . **8**
7. Leaves  $\pm$  herbaceous . . . . . **9**
8. Terminal segment conform to the pinnae, though usually larger . . . **26. B. sinuata**
8. Terminal segment triangular . . . . . **33. B. rivularis**
9. Central pinnae asymmetrical. Rhachis narrowly winged, at least in the upper part. Venation pattern regular, without or with but one short excurrent included free vein. Pinnae 25–100 by 7–25 mm . . . . . **10**
9. Central pinnae  $\pm$  symmetrical. Rhachis not winged and lamina with a  $\pm$  regular venation pattern, or rhachis with a narrow wing in the upper part and lamina with a very irregular venation pattern. Venation pattern and size of the pinnae various . . . . . **11**
10. Terminal segment conform to the pinnae. *S. India* . . . . . **11. B. semicordata**
10. Terminal segment triangular. *S. Japan* . . . . . **D. 4. B. laxireticulata**
11. Venation pattern without excurrent included free veins, or with both ex- and re-current included free veins . . . . . **12**
11. Venation pattern with excurrent included free veins . . . . . **25**
12. Terminal segment  $\pm$  conform to the pinnae . . . . . **13**
12. Terminal segment triangular . . . . . **16**
13. Veins forming a costal areole, otherwise free . . . . . **8. B. crispatula**
13. Veins more intricately anastomosing . . . . . **14**
14. Dried leaves purplish. Pinnae 4–24 to a leaf . . . . . **10. B. scalpturata**
14. Dried leaves greenish. Pinnae 2–50 to a leaf . . . . . **15**
15. Pinnae 2–10(–15) to a leaf . . . . . **25. B. heteroclita**
15. Pinnae 20–50 to a leaf . . . . . **6. B. angustipinna**
16. Bulbil  $\pm$  terminal. Small plants . . . . . **39. B. novoguineensis**
16. Bulbil subterminal or absent . . . . . **17**
17. Leaves purplish when dried. Perispore undulate . . . . . **10. B. scalpturata**
17. Leaves greenish when dried. Perispore cristate or undulate . . . . . **18**
18. Terminal segment narrowly triangular, much shorter than the remaining lamina. Perispore undulate . . . . . **6. B. angustipinna**
18. Terminal segment triangular. Perispore cristate or cristate-undulate . . . . . **19**
19. Venation pattern irregular. See fig. 76: c–g; 78: c–i . . . . . **24**
19. Venation pattern regular . . . . . **20**
20. Base of pinnae narrow-acute or -cuneate. Pinnae 75–120 by 11–18 mm. *Philippines* . . . . . **H. 12. B.  $\times$  sinuosa**
20. Base of pinnae wider. Pinnae larger or not . . . . . **21**
21. Terminal segment shorter than the remaining part of the lamina . . . . . **22**
21. Terminal segment longer than to about as long as the remaining part of the lamina . . . . . **23**
22. Venation pattern symmetrical. Margin usually with distinct spines. *E. Malesia to the Pacific, Bonin Is.* . . . . . **32. B. quoyana**

22. Venation pattern asymmetrical (see fig. 86: f). Margin with inconspicuous teeth in the sinuses. *Tonkin, S. China* . . . . . **D. 2. B. christensenii**
23. Veins forming a costal areole, without or with but few smaller distal areoles. *Queensland* . . . . . **34. B. taylorii**
23. Veins forming a costal areole and many smaller distal areoles. *Pacific*.  
**D. 6. B. sagenioides**
24. Venation pattern as in fig. 76: c-g. *E. Malesia* . . . . . **41. B. repanda**
24. Venation pattern as in fig. 78: c-i. *Pacific* . . . . . **38. B. lonchophora**
25. Terminal segment conform to the pinnae or somewhat prolonged (or flagelloid)  
. . . . . **27**
25. Terminal segment triangular, not flagelloid . . . . . **26**
26. Pinnae 4-28 to a leaf. Margin of pinnae usually lobed, with spines or teeth. Venation pattern as in fig. 81: b-d. Perispore cristate or cristate-undulate.  
**43. B. subcordata**
26. Pinnae 20-50 to a leaf. Margin of pinnae usually  $\pm$  entire, usually without spines or teeth. Venation pattern as in fig. 40: d-f. Perispore undulate.  
**6. B. angustipinna**
27. Leaves purplish when dried . . . . . **28**
27. Leaves greenish when dried . . . . . **29**
28. Pinnae 20-40 mm wide. Venation pattern as in fig. 43: c, d . . . **10. B. sculpturata**
28. Pinnae 40-90 mm wide. Venation pattern as in fig. 42: d-f . . . . **7. B. costata**
29. Pinnae up to 15 mm wide. Without bulbil(s). *S. India* . . . . . **40. B. presliana**
29. Pinnae wider. Bulbil(s) present or not . . . . . **30**
30. Venation pattern  $\pm$  regular . . . . . **31**
30. Venation pattern very irregular. *S. India* . . . . . **34**
31. Venation pattern asymmetrical; included free veins few. Pinnae 20-50 to a leaf.  
**6. B. angustipinna**
31. Venation pattern  $\pm$  symmetrical; included free veins several to many. Pinnae 3-22 to a leaf . . . . . **32**
32. Venation pattern as in fig. 86: b-d. Perispore cristate or spiny. *Tonkin, S. China*.  
**D. 1. B. cadieri**
32. Venation pattern as in fig. 46: b, c, f; 48: d, e, m . . . . . **33**
33. Venation pattern as in fig. 46: b, c, f. *S. India and Ceylon* . . . **14. B. subcrenata**
33. Venation pattern as in fig. 48: d, e, m . . . . . **15. B. virens**
34. Terminal segment narrowly triangular, rhachis not winged: Pinna index usually 5-12, pinnae generally more than 10 cm long. Venation patterns as illustrated in fig. 84: b-g . . . . . **H. 8. B.  $\times$  lancea**
34. Terminal segment usually conform to the pinnae, rhachis narrowly winged. Pinnae index usually 3-6, pinnae generally shorter than 15 cm. Venation patterns as illustrated in fig. 84: j-m . . . . . **H. 10. B.  $\times$  prolifera**
35. Bulbil  $\pm$  terminal. Pinnae > 16-30. *New Guinea* . . . . . **39. B. novoguineensis**
35. Bulbil subterminal (or absent). Pinnae less . . . . . **36**
36. Veins anastomosing, without free veins or with few ex- and recurrent free veins.



Leaves entire . . . . .	37
36. Veins anastomosing, usually with many ex- and recurrent free veins. Leaves entire or (bi-)trifid . . . . .	<b>H. 13. <i>Leptochilus</i> × <i>trifidus</i></b>
37. Leaves herbaceous . . . . .	39
37. Leaves coriaceous . . . . .	38
38. Areoles (except the costal areole) all of about the same shape, decreasing in size towards the margin . . . . .	<b>33. <i>B. rivularis</i></b>
38. Areoles of differing size and shape, not decreasing in size towards the margin.	<b>26. <i>B. sinuata</i></b>
39. Leaves pinnate. Terminal segment triangular, venation as in fig. 22: d.	<b>32. <i>B. quoyana</i></b>
39. Leaves entire or, if pinnate, with a venation as in fig. 20: a	<b>25. <i>B. heteroclita</i></b>

#### 4. DESCRIPTIONS

##### 1. Series *Alienae* Hennipman, *ser. nov.*

Rhizoma longe repens gracile, sine fasciculis sclerenchymatorum. Folia dispersa biseriata. Lamina simplex, vel pinnata segmento terminali triangulari, bulbillis axillaribus raris. Pinnae 0–11, marginibus sine spinis vel dentibus. Ordinatio venularum: venulae regulariter reticulatae, areolis angulatis isodiametris vel elongatis. Sporae perisporio laevi cristato.

Typus: *Bolbitis aliena* (Swartz) Alston.

Terrestrial. *Rhizome* usually long-creeping, up to 20(–30) cm long, slender, with 2 rows of leaves, without sclerenchyma strands. Scales of the rhizome up to 15 mm long. *Leaves* spaced, up to 40 mm apart. Sterile leaves simple or pinnate; petiole with 5–7 vascular bundles; lamina sometimes with usually ± spherical, sometimes elongate, axillary bulbils; pinnae 0–11, the margin without teeth or spines; terminal segment triangular; *venation pattern*: veins regularly reticulate, areoles angulate, ± isodiametric or somewhat elongate, decreasing in size towards the margin. *Sporae* with a smooth cristate perisporium.

Chromosomes.  $n = (c.) 82$  (*B. aliena*, *B. auriculata*).

Distribution. Tropical America, tropical Africa, Madagascar, and the Mascarenes. See fig. 27.

##### 1. *Bolbitis aliena* (Swartz) Alston—Fig. 33.

*B. aliena* (Swartz) Alston, Kew Bull. (1932) 310; Vareschi in Lasser, Fl. Venezuela 1 (1969) 375, *p.p.*—*Acrostichum alienum* Swartz, Schrader J. Bot. 1800, 2 (1801) 13; Syn. Fil. (1806) 13; Willd., Spec. Pl. 5 (1810) 119, *p.p.*; Poiret in Lam., Enc., Suppl. 1 (1810) 123; Sprengel, Syst. Veg. 4 (1827) 37, *p.p.*; Hooker, Spec. Fil. 5 (1864) 272, *p.p.*; Baker in Martius, Fl. Brasil. 1, 2 (1870) 589, *p.p.*, pl. 51; fig. iii; Jenman, Bull. Bot. Dept. Jamaica (Kingston) n.s. 5 (1898) 153, *p.p.*—*Gymnopteris aliena* Presl, Tent. Pterid. (1836) 244; Hooker & Bauer, Gen. Fil. (1842) pl. 85, *quoad nomen solum*; Fée, Hist. Acrost. (1845) 84, *ibid.*—*Anapausia aliena* Presl, Epim. Bot. (1851) 187, *p.p.*—*Chrysodium alienum* Mettenius, Fil. Lips. (1856) 21, pl. 10: fig. 5, *quoad nomen solum*.—*Leptochilus alienus* C. Chr., Bot. Tidsskr. 26 (1904) 285, *p.p.*; Ark. Bot. 9 (1910) 35,

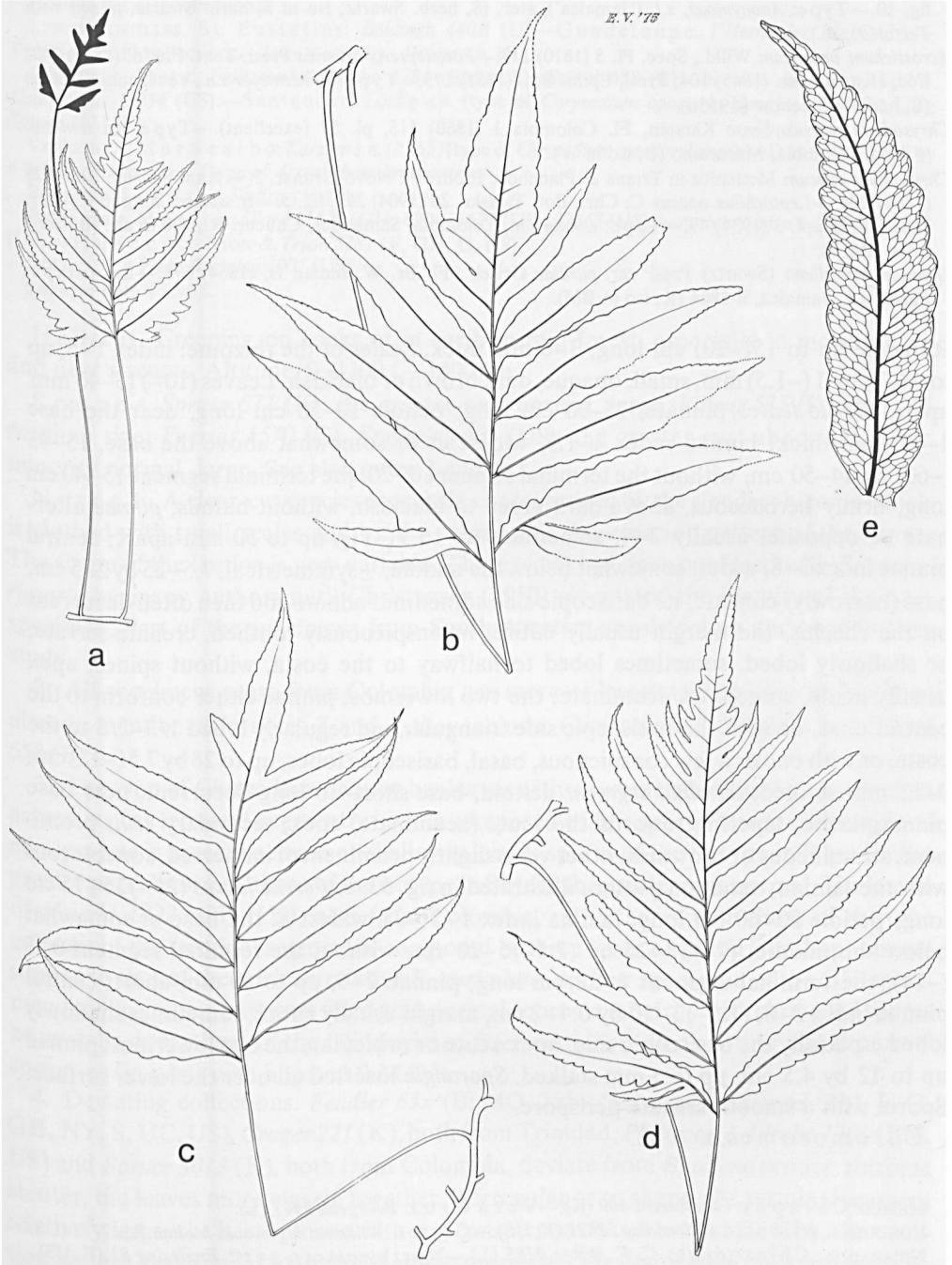


Fig. 33. *Bolbitis aliena*.—a–d. sterile leaves,  $\times 1/5$ ; e. venation pattern of sterile pinna,  $\times 4/5$  (a. *Sintenis* 5166, B; b. *Spruce* 577, K; c. *Lindig s.n.*, P, a possible isotype of *Chrysodium opacum*; d. *Valeur* 535, K; e. *Proctor & Mullings* 21999, U).

fig. 10.—Type: *Anonymous, s.l.* ('Jamaica'), ster. (S, herb. Swartz; iso in S, herb. Swartz, mixed with *Tectaria spec.*).  
*Acrostichum brunneum* Willd., Spec. Pl. 5 (1810) 113.—*Poecilopteris brunnea* Presl, Tent. Pterid. (1836) 242; Féé, Hist. Acrost. (1845) 104; Presl, Epim. Bot. (1851) 173.—Type: *Bredemeyer s.n.*, Venezuela, Caracas (B, herb. Willdenow (19536)).  
*Chrysodium maracaybense* Karsten, Fl. Colombia 1 (1860) 115, pl. 57 (excellent).—Type: *Karsten s.n.* (? 165), Colombia, Maracaibo (B; iso in W).  
*Chrysodium opacum* Mettenius in Triana & Planchon, Prodr. Fl. Novo-Granat. 2 (= Ann. Sc. Nat. Bot. V.2) (1864) 204.—*Leptochilus opacus* C. Chr., Bot. Tidsskr. 26 (1904) 292, fig. 5.—*B. opaca* Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 49.—Type: *Lindig s.n.*, Colombia, Santander, Chucuri R., 900 m alt. (B, ster.; iso in BM, P).  
*Gymnopteris aliena* (Swartz) Presl var. *purdieae* Griseb., Fl. Br. W. Indian Is. (1864) 674.—Lectotype: *Purdie s.n.*, Jamaica, ii-1864 (K; iso in BM).

Rhizome up to 15(–20) cm long, 3–6 mm thick. Scales of the rhizome: index 1–5, up to 4(–7) by 1(–1.5) mm, small, opaque, dark brown or blackish. Leaves (10–)15–40 mm apart. *Sterile leaves* pinnate, 25–90 cm long; petiole 10–50 cm long, near the base 1–4.5 mm thick; lamina index 1–1.5, widest at or somewhat above the base, 15–45 (–60) by 14–50 cm, without the terminal segment 0–20, the terminal segment 15–40 cm long, firmly herbaceous, above dark green to blackish, without bulbils; *pinnae* alternate or opposite, usually 2–4, sometimes up to 9(–11), up to 50 mm apart; central pinnae index 3–8, widest somewhat below the middle, ± symmetrical, 7.5–25 by 2–5 cm, base (narrowly) cuneate, its basisopic side sometimes adnate and then often decurrent on the rachis, the margin usually entire, inconspicuously toothed, crenate-serrate, or shallowly lobed, sometimes lobed to halfway to the costa, without spines, apex usually acute, sometimes acuminate; the two lowermost pinnae either conform to the central ones, or with the basisopic side triangular and regularly lobed 1/3–2/3 to the costa, or with one or a few conspicuous, basal, basisopic lobes, up to 28 by 7.5(–11) cm, 0–12 mm stalked; *terminal segment* deltoid, base short- to long-decurrent, near base pinnatipartite, tapering towards the acute (acuminate) apex; secondary *veins* prominent, stramineous or brownish, other veins slightly prominent or immersed, concolorous with the lamina; venation pattern illustrated in fig. 33: e. *Fertile leaves* (25–)35–75 cm long; petiole 20–60 cm long; lamina index 1–2(–3), widest at the base or somewhat below the middle, (7–)13–25 by (2.5–)5–20 cm, without the terminal segment 0–8 (–14), the terminal segment 6–22 cm long; pinnae 2–6, up to 50 mm apart; central pinnae index 2–8, (1.5–)3–10 by 0.4–2 cm, margin usually entire, sometimes shallowly lobed especially the basisopic side, apex acute or orbicular; the two lowermost pinnae up to 12 by 4.5 cm, up to 5 mm stalked. *Sporangia* inserted all over the lower surface. Spores with a smooth cristate perispore.

Chromosomes.  $n = 82$ .

MEXICO. Chiapas: *Ghiesbrecht 409* (K).—Vera Cruz: *Bourgeau 2147* (L).  
HONDURAS. Atlantida: *Standley 52821* (F, US).—Cortes: *Williams & Antonia Molina R. 17771* (US).  
NICARAGUA. Chinandega: *C. F. Baker 2185* (L).—Northwestern part: *Englesing 83* (F, US).  
CUBA. 11 collections.  
JAMAICA. 8 collections.  
DOMINICAN REPUBLIC. 10 collections.

PUERTO RICO. 9 collections.

LESSER ANTILLES. St. Eustatius: *Boldingh 440B* (U).—Guadeloupe: *l'Herminier 21* (CAL).—Trinidad: 10 collections.—Leeward Is.: *Holme s.n.* (K).

COLOMBIA. Meta: *Philipson & Idrobo 1781* (BM, US); *Stübel 658* (B).—Norte de Santander: *Cuatrecasas 13254* (US).—Santander: *Lindig s.n.* (type of *Chrysodium opacum*); *Haught 1322* (GH, US); *Spruce 3013* (K).

VENEZUELA. Maracaibo: *Karsten s.n. (? 165)* (type of *Chrysodium maracaybense*).—Distrito Federal: *Bredemeyer s.n.* (type of *Acrostichum brunneum*).

ECUADOR. Los Rios: *Sodiro s.n.* (B).

PERU. San Martín: *Allard 21558* (GH, US), *21672* (US), *22367* (US).—Amazonas: *Wurdack 2033* (US).—Huanuco: *Tryon & Tryon 5281* (F, GH, U, US).

BOLIVIA. La Paz: *Buchtien 1002* (US).

See also note 4 and 6.

Habitat. Creeping on rocks or in earth in rain forest, especially in moist places and near streams. Altitude: 0–1100 (—1400) m.

Spores. *Spruce 577* (K): the greater part normal, large. *Valeur 535* (K): *ibid.*, of medium size. *Fuertes 1570* (G), *Englesing 83* (US): the greater part abnormal, a fair minority normal, large. See also notes 3 and 4.

Notes. 1. A clear-cut species especially characterized by the slender rhizome which is clothed with small scales and by the colour and the venation pattern of the leaves. The shape of the lamina is very variable. This species has been confused with *B. portoricensis* by many authors until Christensen (1910) elucidated the identity of the type specimen. Part of the specimens from South America are deviating and need further study.

2. All specimens seem from Colombia are more or less deviating. Except for those already mentioned in notes 3 and 4, they include: *Cuatrecasas 13254* (US) and *Stübel 658* (B).

3. The type of *Chrysodium opacum* has leaves with  $\pm$  symmetrical basal pinnae and an asymmetrical terminal segment which is composed of few spaced lobes; the margin of all segments is crenate-serrate or shallowly lobed; spores of the isotype in P are for the greater part abnormal, those of the isotype in BM for the greater part normal. The leaves of *Haught 1322* (GH, US), also from Colombia, rather agree with those of the type collection; the terminal segment is composed of three lobes only and is in shape almost similar to that of the African relative *B. auriculata*; spores: sporangia of the GH-specimen for the greater part filled with normal spores, a minority with shrivelled spores or juvenile ones; those of the US-specimen filled with shrivelled or otherwise abnormal spores or (in part) with aborted S.M.C.'s.

4. Deviating collections. *Fendler 63x* (B; MO, 2 sh., '63'; not *Fendler 63*, BM, F, G, GH, NY, S, UC, US), *Cruger 221* (K), both from Trinidad, *Philipson & Idrobo 1781* (BM, US) and *Spruce 3013* (K), both from Colombia, deviate from *B. aliena* proper: rhizome stouter, the leaves more closely together,  $\pm$  irregular as to shape, the terminal segment relatively large, the basal pinnae with a  $\pm$  conspicuous basal basicopic lobe, the venation pattern very similar to that of *B. aliena* proper but the size of adjacent areolae sometimes very different, some areolae with an unbranched, ex- or recurrent, included free vein. Spores: *Philipson & Idrobo 1781* (BM): the majority of the sporangia filled with

normal spores, a minority with aborted spores; *ibid.* (US): nearly all sporangia filled with aborted S.M.C.'s and/or shrivelled spores, an incidental normal spore also present in the preparation; *Fendler 63x* (MO, a separately mounted fertile leaf): sporangia filled with clusters of aborted spores or with aborted S.M.C.'s.

The outline of these plants is strongly reminiscent of that described for *B. semipinnatifida*. However, the venation pattern is different, showing far fewer free included veins than is generally found in *B. semipinnatifida*. These collections need further study; they are not plotted on the distribution map.

5. Christensen (1904) excluded *Leptochilus alienus* ('essentially different') from *Leptochilus* sect. *Bolbitis*. In this section he included *Leptochilus opacus* (= *B. aliena*), the venation pattern of which he judged 'very irregular' and to resemble that of *Leptochilus contaminoides* (= *B. serratifolia*).

6. The species is absent from eastern Nicaragua towards western Colombia. Lack of exploration seems not to be the obvious reason to explain this disjunction as much field work has been performed at least in Costa Rica. A.F. Tryon (Contr. Gray Herb. 200, 1970, 104, 110) reported an almost similar disjunction for *Eriosorus hirtus* and *E. hispidulus*, which she thought more widely distributed in the past.

7. I suppose that a species like *B. aliena* has given rise to *B. semipinnatifida* through hybridization with a species of ser. *Euryostichae*. See also under *B. semipinnatifida*.

## 2. *Bolbitis auriculata* (Lam.) Alston—Fig. 34, 35.

- B. auriculata* (Lam.) Alston, J. Bot. 72, Suppl. 2 (1934) 3; C. Chr., Ind. Fil., Suppl. 3 (1934) 47, 197; Alston, J. Bot. 77 (1939) 284; in Exell, Cat. Vasc. Pl. S. Tomé (1944) 68; Tardieu-Blot, Mém. I.F.A.N. 28 (1953) 112, pl. 18: fig. 6–8; Alston in Hutch. & Dalziel, Fl. West Trop. Afr. ed. 2, Suppl. (1959) 68; Tardieu-Blot in Humbert, Fl. Madag. 2 (1960) 60, fig. 16: 3–4, *p.p.*; Harley, Handb. Liberian Ferns (1963) 42, fig.; Tardieu-Blot in Aubrév., Fl. Gabon 8 (1964) 187; in Aubrév., Fl. Cameroun 3 (1964) 318.—*Acrostichum punctatum* L. f., Spec. Pl., Suppl. (1781) 444, *nom. illeg., non L.*; Carruth., Cat. Afr. Pl. Welwitsch 2, 2 (1901) 277.—*A. auriculatum* Lam., Enc. 1 (1783) 36; Poiret in Lam., Enc., Suppl. 1 (1810) 122 ('auritum').—*A. punctatum* Swartz, Schrader J. Bot. 1800, 2 (1801) 12; Syn. Fil. (1806) 13; Willd., Spec. Pl. 5 (1810) 118; Hooker, Spec. Fil. 5 (1864) 258; Baker in Hooker & Baker, Syn. Fil. (1868) 419.—*Poecilopteris punctulata* Presl, Tent. Pterid. (1836) 242; Epim. Bot. (1851) 173; J. Smith, Ferns Br. For. (1866) 117.—*Cyrtogonium punctulatum* J. Smith, Hook. J. Bot. 4 (1841) 154.—*Heteroneuron punctulatum* Fée, Hist. Acrost. (1845) 91, pl. 54 ('Heteroneuron').—*Chrysodium punctulatum* Mettenius, Fil. Lips. (1856) 21; Ettingsh., Denkschr. K. Ak. Wiss. M.-N. Kl. Wien 22 (1854) 58, pl. 7: fig. 8, pl. 8: fig. 2 ('punctata').—*C. punctatum* Mettenius ex Kuhn, Fil. Afric. (1868) 51.—*Gymnopteris punctata* Christ, Farnkr. Erde (1897) 50.—*Leptochilus punctatus* C. Chr., Bot. Tidsskr. 26 (1904) 292.—*L. auriculatus* C. Chr., Ind. Fil. (1906) 384; Henriques, Bol. Soc. Brot. 27 (1917) 178.—*Gymnopteris auriculata* Engler, Veg. Erde 9, 2 (1908) 16, fig. 11.—*Campium auriculatum* Copel., Philip. J. Sc. 37 (1928) 398, fig. 49; C. Chr., Dansk Bot. Ark. 7 (1932) 70.—Type: *Sonnerat per Thouin s.n.*, Mascarenes, Réunion (Isle de Bourbon) (iso in C. herb. Vahl, fert., S-PA, herb. Swartz, fert.).
- Acrostichum mascarenense* Sprengel, Syst. Veg. 4 (1827) 37.—Type: *Sieber s.n. (?24)*. (*n.v.*); see note 3.
- Leptochilus auriculatus* (Lam.) C. Chr. var. *undulati-crenatus* Hieron., Bot. Jahrb. 46 (1911) 345; Bonap., Notes Ptérid. 1 (1915) 51; *ibid.* 10 (1920) 85.—*B. auriculata* (Lam.) Alston var. *undulato-crenata* Kunkel, Ber. Schweiz. Bot. Ges. 73 (1963) 187, *comb. invalid.* (art. 33).—Lectotype: *Zenker 1598*, Cameroun, Epossintonga near Bipindi, 500 m alt. (B, 2 sh.).
- B. fluviatilis* (Hooker) C. Chr. var. *crenatis* Kunkel, Ber. Schweiz. Bot. Ges. 73 (1963) 188.—Type: *Kunkel F-200*, Liberia, Western Prov., Gola Forest, 300–400 m alt. (private herb. Dr. Kunkel).
- B. fluviatilis auct. non* (Hooker) C. Chr.: Harley, Handb. Liberian Ferns (1963) 43, fig.; Kunkel, Ber. Schweiz. Bot. Ges. 73 (1963) 187, *pp.*

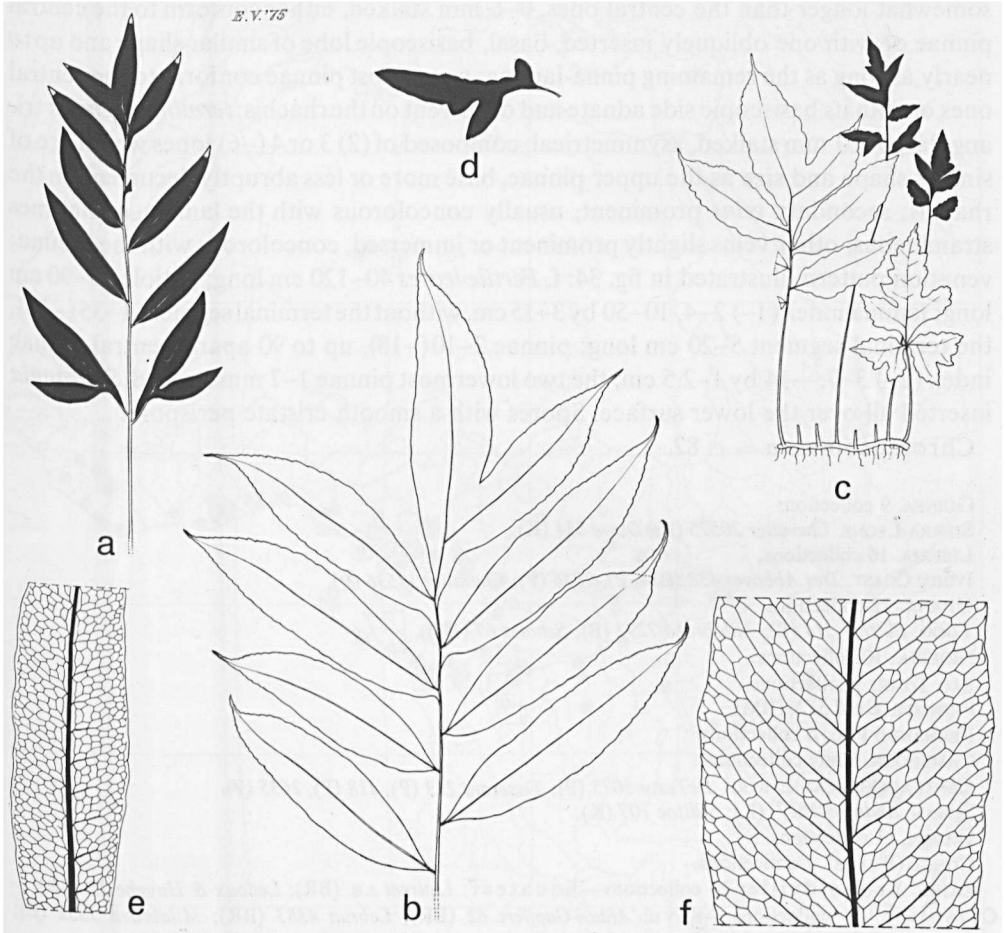


Fig. 34. *Bolbitis auriculata*.—a–c. sterile and fertile leaves,  $\times 1/5$ ; d. basal pinna of fertile leaf,  $\times 1/5$ ; e. venation pattern of fertile pinna,  $\times 4/5$ ; f. ibid. of sterile pinna (a. *Sonnerat per Thouin s.n.*, S-PA, holotype of *B. auriculata*; b. *Hildebrandt 1803*, L; c. *Zenker 2751*, B; d. *Barter 1170*, K; e. *Kew Distr. no. 1175*, L; f. *Boivin 2847*, L).

Rhizome up to a few dm long, 3–7 mm thick. Scales of the rhizome: index 2–5, up to 7 by 0.5–1(–1.5) mm, opaque, brown or blackish. Leaves 15–40 mm apart. *Sterile leaves* pinnate, 30–115 cm long; petiole 15–65 cm long, near the base 2–4(–6) mm thick; lamina index 1–2, widest about or below the middle, 15–55(–70) by 15–40(–50) cm, without the terminal segment 0–35, the terminal segment 15–40 cm long, usually herbaceous, sometimes papyraceous, olivaceous, rarely with a spherical or elongate axillary bulbil; *pinnae* (2–) 4–10, up to 60 mm apart; central pinnae index 2–6, widest about or below the middle, symmetrical, 8.5–30 by 2.5–7.5 cm, base cuneate, margin usually entire, sometimes finely serrate-crenate or unevenly and shallowly lobed, without spines or distinct teeth, apex acute or acuminate; the two lowermost pinnae somewhat shorter to

somewhat longer than the central ones, 0–6 mm stalked, either conform to the central pinnae or with one obliquely inserted, basal, basiscopic lobe of similar shape and up to nearly as long as the remaining pinna-lamina; uppermost pinnae conform to the central ones or with its basiscopic side adnate and decurrent on the rhachis; *terminal segment* triangular, 0–20 mm stalked, asymmetrical, composed of (2) 3 or 4 (–6) lobes which are of similar shape and size as the upper pinnae, base more or less abruptly decurrent on the rhachis; secondary *veins* prominent, usually concolorous with the lamina, sometimes stramineous, other veins slightly prominent or immersed, concolorous with the lamina; venation pattern illustrated in fig. 34: f. *Fertile leaves* 40–120 cm long; petiole 35–90 cm long; lamina index (1–) 2–4, 10–50 by 3–15 cm, without the terminal segment 1–35 (–50), the terminal segment 5–20 cm long; pinnae 2–10 (–18), up to 90 apart; central pinnae index (2–) 3–7, —14 by 1–2.5 cm; the two lowermost pinnae 1–7 mm stalked. *Sporangia* inserted all over the lower surface. Spores with a smooth cristate perispore.

Chromosomes.  $n = c. 82$ .

GUINEA. 9 collections.

SIERRA LEONE. *Chevalier 20575* (P); *Dawe 534* (K).

LIBERIA. 16 collections.

IVORY COAST. *Des Abbayes 438* (BM, P), *2146* (P); *Chevalier 17536* (P).

GHANA. 22 collections.

TOGO. *Büttner 514* (B); *Mildbraed 7292* (B); *Scholes 67* (BM).

NIGERIA. 10 collections.

SÃO TOMÉ. 5 collections.

PRINCIPE. *Exell 572* (BM).

FERNANDO POO. 6 collections.

CAMEROUN. many collections.

CENTRAL AFRICAN EMPIRE. *LeTestu 3075* (P); *Tisserant 223* (P), *418* (P), *2635* (P).

SUDAN. *Andrews 1627* (K); *Sillitoe 107* (K).

GABON. 11 collections.

CONGO (BRAZZ). 7 collections.

ZAIRE. Leopoldville: 29 collections—Equateur: *Laurent s.n.* (BR); *Ledoux & Huyghe 23* (BR).—Orientale: 14 collections.—Kivu: *Antun-Gupfert 62* (BR); *Lebrun 4383* (BR); *Mildbraed 2332* (B); *Troupin 2995* (BR).—Kasai: *Flamigni 35* (BR); *Laurent 446* (BR); *Vanderijst 22409* (BR).

ANGOLA. Cabinda: *Gossweiler 6591* (BM).—Cuanza Norte: *Welwitsch 153* (BM, K).

UGANDA. Western: *Kassner 3132b* (P); *Sangster S 87 p.p.* (BM), *192* (BM), *292* (BM).—Buganda: *Longfield 13* (BM); *Maitland 667* (K); *Thomas 1390* (K).—Mulange: *Dümmer 4471* (K).

TANGANYIKA. Tanga: 7 collections.—Southern Highland: *Schweinfurth 3102* (B).—Eastern: *Schlieben 2875* (B, BR). 'Ruwenzori Exp.': *Scott Elliot 7096* (BM, K).

COMORES. Grande Comore: *Humblot s.n.* (P).—Anjouan (= Johanna Is.): *Hildebrandt 1803* (B, K, L, P).—Mohelli: *Benson 135A* (BM).—Mayotte: *Boivin 2847* (B, BM, L, P), *Marie 151* (P), *188* (G).

MADAGASCAR. 7 collections.

MASCARENES. Réunion: 6 collections.—Mauritius: 8 collections.

**Habitat.** On rocks or in earth in humid or swampy places (frequently in and near streams) in primary and secondary forest. Altitude: 0–1200 m.

**Spores.** *Félix 41* (S-PA), *Harley F 111* (K), *F 180* (GH), *De Jussieu s.n.* (S-PA): the majority normal; the sporangia of *De Jussieu s.n.* and *Harley F 111* filled with over 50 spores of varying size. *Peter 18921* (C): in part (the majority ?) normal. Baldwin 6709 (GH), *Harley F 76A* (GH), *Sonnerat per Thouin s.n.* (type of *Acrostichum punctulatum*): the greater part abnormal.

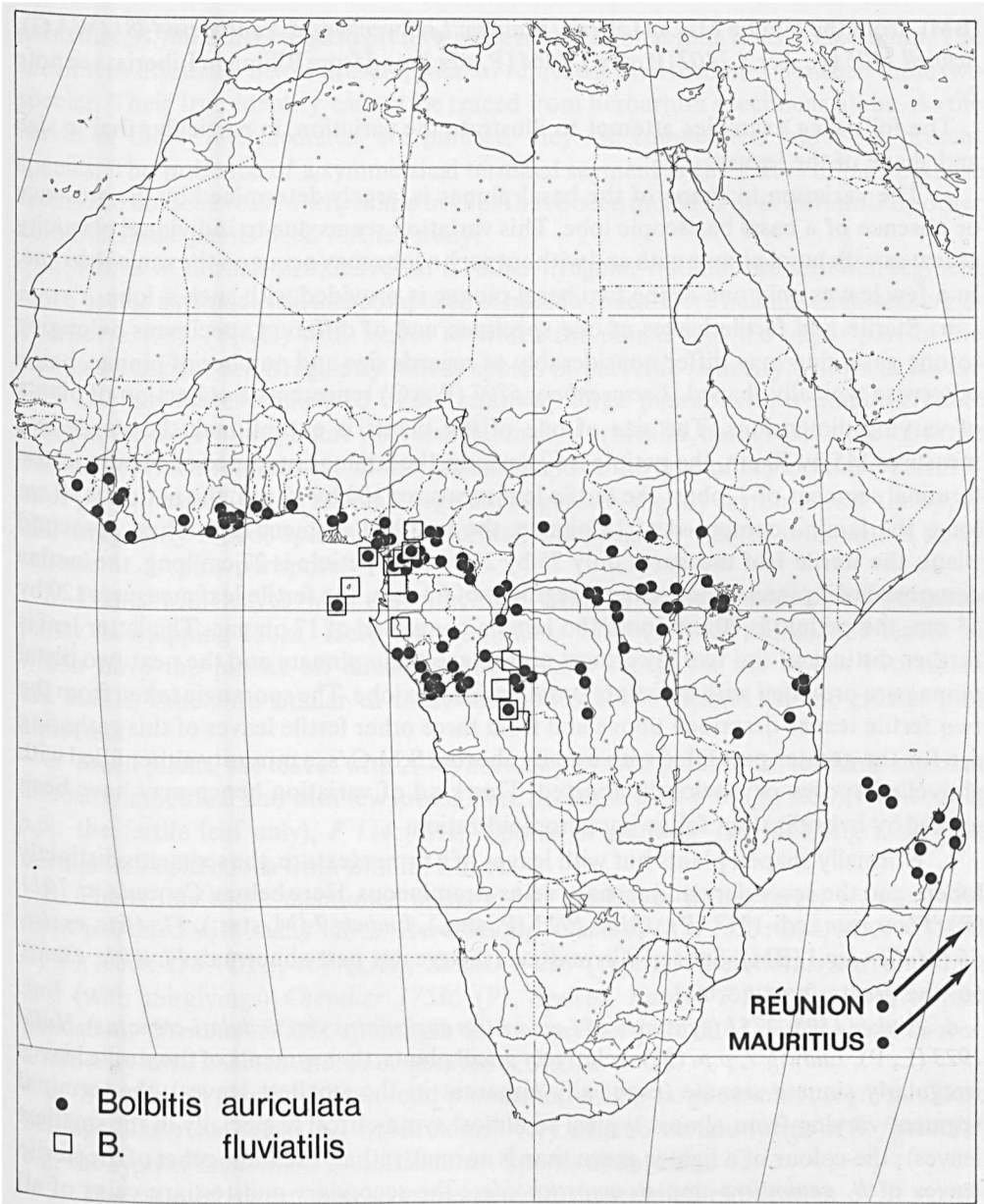


Fig. 35. Distribution of *Bolbitis auriculata* and *B. fluviatilis*.

Notes. 1. Although normally shaped specimens of the present species are obviously common throughout its geographical range, a considerable number of more or less atypical collections was found as well. Part of these collections have been gathered from but few localities. Such local outbursts of different forms are for instance known from the Puso Puso Ravine in Ghana: *Adams* 331 (BM; M, ster.), 415 (BM, K, P, all ster), 1892



(BM), from the Nimba Mts. in Liberia/ Guinea: *Leeuwenberg & Voorhoeve 4781* (WAG), *Schnell 1105* (P, ster.), *1402* (P, ster.), *1464* (P, ster.), and from Bilimu in Liberia: see note 2c.

The following examples attempt to illustrate the variation, in particular that in size and shape of the leaves.

a. The variation in shape of the basal pinnae is largely determined by the presence or absence of a basal basispic lobe. This variation seems due to individual plasticity as leaves with basal pinnae with and without such a lobe may occur on the same rhizome. In a few leaves only one of the two basal pinnae is provided with such a lobe.

b. Sterile and fertile leaves of one specimen and of different specimens belonging to one gathering may differ considerably as regards size and number of pinnae, being otherwise typically shaped. *Leeuwenberg 6797* (WAG) represents a collection of plants of varying dimensions. The size of one of the plants is exceptional: the sterile leaf measures 145 by 50 cm, the petiole is 67 cm long, the lamina composed of 14 pinnae, the terminal segment of 7 lobes; the fertile leaf measures 160 by 19 cm, the petiole is 90 cm long, the lamina composed of 18 pinnae, the terminal segment of 6 lobes. A second plant: the sterile leaf measures only 75 by 26 cm, the petiole is 27 cm long, the lamina composed of 7 pinnae, the terminal segment of 6 lobes; the fertile leaf measures 120 by 13 cm, the petiole is 80 cm long, the lamina composed of 17 pinnae. The latter leaf is further distinct as the two lowermost pinnae are again pinnate and the next two distal pinnae are provided with a distinct basal basispic lobe. The sporangia taken from the two fertile leaves described above and from three other fertile leaves of this gathering are for the greater part filled with usually aborted S.M.C.'s, a minority either filled with shrivelled spores or obviously aborted. This kind of variation hence may have been caused by hybridization following autopoloidization.

c. Normally shaped plants but with leaves of a firmer texture, the segments distinctly lobed, and the secondary and tertiary veins stramineous. Here belong *Cervoni s.n.*, 1911 (P), *Fleury s.n.*, vii-1917 (P), *Hallé 1923* (P, ster.), *Ludwig 7* (M, ster.), *Fl. Afric. exsicc. 66* (*Moller leg.*) (BM). Spores: *Cervoni s.n.*: the greater part abnormal. *Fl. Afric. exsicc. 66*: the greater part normal.

d. *Zenker 1598, 2751* (syntypes of *Leptochilus auriculatus* var. *undulati-crenatus*), *Hallé 1923* (L, P), *Ludwig 7, p.p.* (M): relatively small plants, the segments of the sterile leaves irregularly sinuate-crenate (especially apparent in the smallest leaves), the terminal segment varying from almost typical to almost symmetrical (especially in the smallest leaves); the colour of a lighter green than is normal, rather resembling that of the sterile leaves of *B. gemmifera* and *B. acrostichoides*; the secondary and tertiary veins of all except *Zenker 2751* stramineous. Spores: *Zenker 2751* (B): in part normal. The question arises if these collections result from hybridization between the present species and *B. acrostichoides*.

2. Plants with leaves intermediate between those of *B. auriculata* and *B. fluviatilis*. Generally, *B. auriculata* and *B. fluviatilis* are easily distinguished because of differences in leaf architecture, in the prominence of the secondary veins, and also more or less

in texture. *B. fluviatilis* seems to prefer a more humid habitat than does *B. auriculata*. The specimens discussed below are supposed to represent intermediates between these two species. Their true identity cannot be traced from herbarium specimens alone. As the leaves of these 'intermediates' are pinnate, they are enumerated under the present species. The presence of a symmetrical terminal segment in the leaves of part of these seems the obvious reason why some of them have been included in *B. fluviatilis* by other authors. These plants need further study.

a. Plants of normal size; leaves of a rather irregular outline; the terminal segment more or less asymmetrical and composed of but few lobes. Here belongs *Leeuwenberg & Voorhoeve 4781* (WAG) with leaves of which the pinnae and the upper part of the terminal segment are irregularly lobed; spores in part (the minority?) normal. *Barker 1170* (K) has leaves composed of six relatively large pinnae with a sinuate-crenate margin, the lowermost pinnae with several small,  $\pm$ orbicular, basal basispic lobes the outline of which reminiscent of the lamina shape of the type of *Leptochilus grossedentatus* (= *B. fluviatilis*), the terminal segment large, only slightly asymmetrical, the upper half irregularly lobed; spores: all abnormal, the normally shaped ones with a finely cristate or  $\pm$  spiny perispore.

b. Plants with leaves with a symmetrical terminal segment provided with many partly overlapping lobes. Here belongs *Adams 1892* (= 3851; BM), the leaves of which have the pinnae all adnate to the rachis except for the lowest two which are sessile, otherwise similar to those mentioned above. Spores for the greater part abnormal.

c. Small plants, the leaves with 2(-4) normally shaped pinnae, the terminal segment almost symmetrical and with few lobes. Here belong *Harley F 76* (K, ster.), *F 76A* (GH, p.p.: the fertile leaf only), *F 114* (GH). Spores of *Harley F 114* for the greater part normal. All collections from Bilimu, Liberia.

d. Plants like those mentioned under c. but the leaves with a larger terminal segment provided with many lobes. Here belong *Adams 331* (= 2635; BM, M), *415* (BM, K, P), *Cook 138* (GH), *167* (GH), *Kunkel F-200* (type of *B. fluviatilis* var. *crenatis*), and (with misgivings) *Chevalier 17536* (P). Spores: *Kunkel F-200*: the greater part abnormal; *Chevalier 17536*: sporangia for the greater part filled with normal spores, a minority with aborted spores or aborted S.M.C.'s.

e. Small-sized plants with two odd pinnae and a very large terminal segment. Here belongs *Linder s.n.*, 1926 (K) which comes very near to certain forms of *B. fluviatilis*, e.g. the type of *Leptochilus grossedentatus*. Spores abnormal.

3. The type of *Acrostichum mascarenense*. In the original publication of *A. mascarenense* a type specimen was not indicated. Sprengel referred to a plant named '*A. punctulatum* Sieb.', a MS name. The type is presumably *Sieber* (Syn. Fil. no.) 24 from Mauritius (B, BR, G, K, L, MO, P, UC, W) or *Sieber s.n.* from the same place which may both belong to the same collection.

4. It is supposed that a *B. auriculata*-like fern may be one of the parents of *B. gemmifera*, *B. longiflagellata* (see: *spec. dub.*), *Leptochilus gemmifer* var. *latipinnata* (see: *B. acrostichoides*), and hybridized with *B. heudelotii* (see: hybrids).

### 3. *Bolbitis fluviatilis* (Hooker) Ching—Fig. 35, 36.

- B. fluviatilis* (Hooker) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 48; Alston, J. Bot. 77 (1939) 284; in Exell, Cat. Vasc. Pl. S. Tomé (1944) 69; Tardieu-Blot, Mém. I.F.A.N. 28 (1953) 110, pl. 18: fig. 4 & 5; Adams & Alston, Bull. Br. Mus. Nat. Hist. 1 (1955) 172; Alston, Bull. I.F.A.N. ser. A, 21 (1959) 447; in Hutch. & Dalziel, Fl. West Trop. Afr. ed. 2, Suppl. (1959) 68; Kunkel, Ber. Schweiz. Bot. Ges. 73 (1963) 187, p.p.; Tardieu-Blot in Aubrév., Fl. Gabon 8 (1964) 186, pl. 33: fig. 1–3; in Aubrév., Fl. Cameroun 3 (1964) 316.—*Acrostichum fluviatile* Hooker, Spec. Fil. 5 (1864) 274; Baker in Hooker & Baker, Syn. Fil. (1868) 422.—*Chrysodium fluviatile* Kuhn, Fil. Afric. (1868) 51.—*Poecilopteris fluviatilis* J. Smith, Hist. Fil. (1875) 137.—*Leptochilus fluviatilis* C. Chr., Ind. Fil. (1906) 385.—*Gymnopteris fluviatilis* Engler, Veg. Erde 9, 2 (1908) 16.—*Campium fluviatile* Copel., Philip. J. Sc. 37 (1928) 399, fig. 50, pl. 32.—Lectotype: Mann 442, Fernando Poo (K, 2 sh.; iso in GH, Kew Distr. no. 1181).
- Acrostichum phanerodictyon* Baker in Henriq., Bol. Soc. Brot. 4 (1886) 156, pl. 4: fig. C; Copel., Philip. J. Sc. 37 (1928) 401.—*Leptochilus phanerodictyus* C. Chr., Ind. Fil. (1906) 387.—*Gymnopteris phanerodictya* Engler, Veg. Erde 9, 2 (1908) 16.—*B. phanerodictya* Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 49.—Type: Fl. Afric. exsicc. 68 (Moller, not Quintas leg.), São Tomé, 200 m alt. (K; iso in B, BM, BR, C, G, K, MO, P). See note 7.
- Leptochilus grossedentatus* Bonap., Notes Ptérid. 14 (1923) 217.—*B. grossedentata* C. Chr., Ind. Fil., Suppl. 3 (1934) 48.—Type: LeTestu 1570, Gabon, Mayombe Bayaka, Djengila, Ravine of Dougouatzi (P).
- B. fluviatilis* (Hooker) Ching var. *crenatis* auct. non Kunkel: Kunkel, Ber. Schweiz. Bot. Ges. 73 (1963) 188.

Rhizome up to 20 cm long, up to 7 mm thick. Scales of the rhizome: index 1–6, up to 15 by 2.5 mm, large, opaque, castaneous. Leaves up to 15(–25) mm apart. *Sterile leaves* either entire or pinnatipartite, 15–85 cm long. *Entire leaves*: petiole 4–20 cm long, near the base 1–3.5(–5) mm thick; lamina index 3–7, widest about the middle, 10–60 by 2–12 cm, (thin-)herbaceous, usually olivaceous or blackish, without bulbils, base short- to long-decurrent, margin usually entire, sometimes in the basal half shallowly and irregularly lobed, without teeth or spines, apex acute to acuminate; costa prominent on either side, other veins immersed or the secondary veins near the costa slightly prominent; venation pattern: see fig. 36: h, i. *Pinnatipartite leaves*: petiole 4–35(–45) cm long; lamina index 1–4, widest below the middle, 20–50 by 5–25(–35) cm; lobes 2–8, usually opposite, those of one side usually spaced, sometimes overlapping, straight or the upper half somewhat falcate, those of one leaf rather varying in size, up to 20(–24) by 6.5(–8) cm, margin usually entire, sometimes shallowly and irregularly lobed, apex usually acute or acuminate, sometimes orbicular; the lamina at the sinuses above the two lowermost lobes 1–3.5 cm wide; terminal segment relatively long, 2.5–10 cm wide, usually entire, sometimes pinnatifid near the base; otherwise similar to the entire leaves.—*Fertile leaves* 15–90 cm long. Entire leaves: petiole 10–30 cm long, near the base 1–4 mm thick; lamina index 5–10(–18), usually widest about (to below) the middle, 4–40 by 1–3 cm. Pinnatipartite leaves: petiole 10–55 cm long; lamina index 2–8, 9–40 by 1–10(–20) cm; lobes 2–8, up to 9(–13) by 2(–3) cm, the lamina at the sinuses above the two lowermost lobes 0.5–1.5 cm wide; terminal segment 1.5–3.5 cm wide. *Sporangia* inserted usually all over the lower surface; sometimes a narrow strip along the costa in the basal half and along the secondary veins of pinnatipartite leaves devoid of sporangia. Spores usually with a smooth cristate perispore.

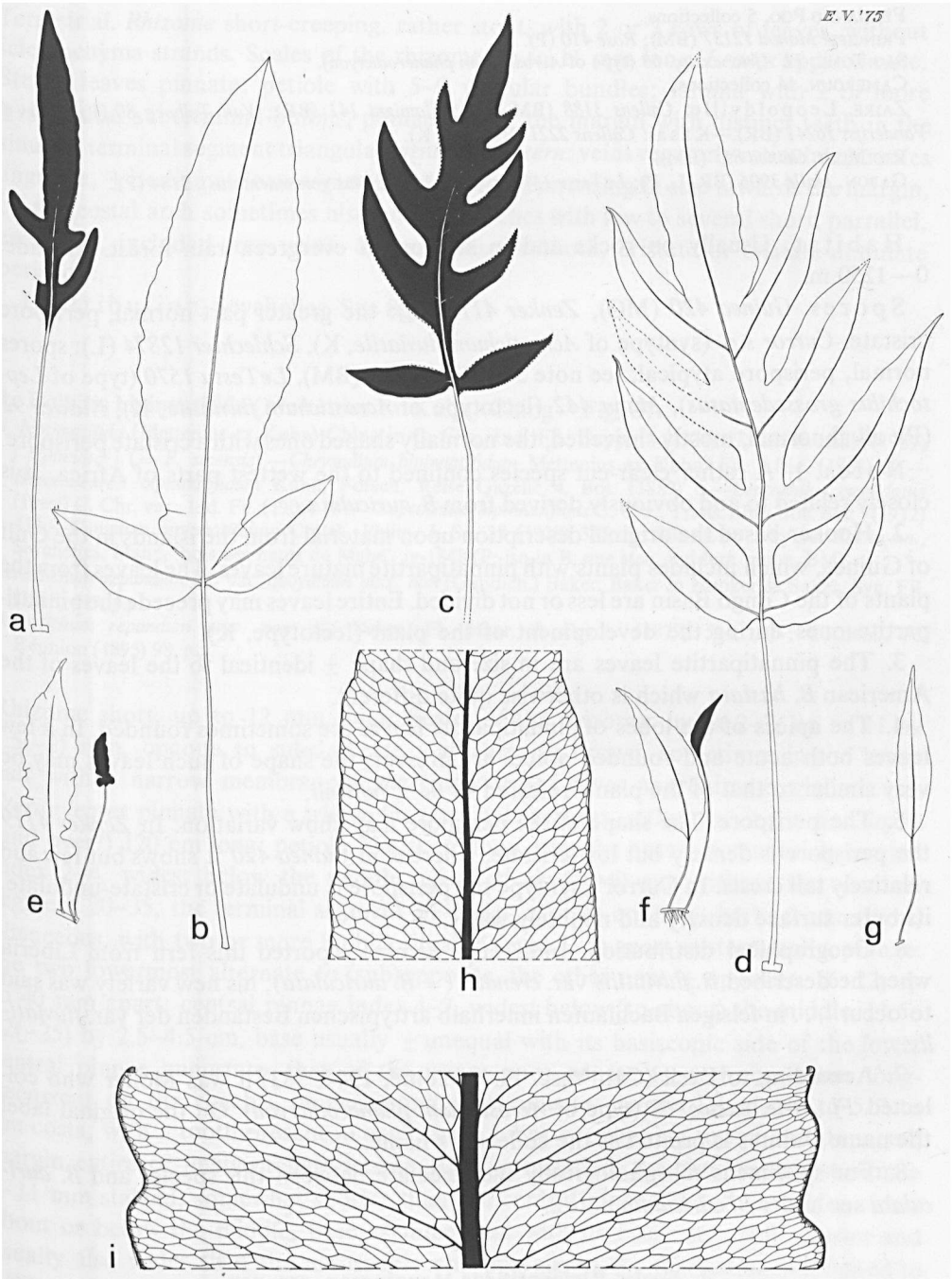


Fig. 36. *Bolbitis fluviatilis*.—a–g. sterile and fertile leaves,  $\times 1/5$ ; h, i. venation pattern of sterile laminae,  $\times 4/5$  (a. Zenker 4119, G; b, i. Raynal 10705, P; c, d. Curror s.n., K, paratype of *B. fluviatilis*; e. Linder s.n., 1926, K; f, g. *Fl. Afric. exsicc.* 68, K, holotype of *Acrostichum phanerodictyon*; h. Schlechter 12874, L).

FERNANDO POO. 5 collections.

PRINCIPE. *Monod* 12137 (BM); *Rose* 410 (P).

SÃO TOMÉ. *Fl. Afric. exsicc.* 68 (type of *Acrostichum phanerodictyon*).

CAMEROUN. 14 collections.

ZAIRE. Leopoldville: *Callens* 3188 (BM, BR); *Flamigni* 141 (BR); *Van Telborg* 80 (P).—Kivu: *Vanderijst* 16241 (BR).—Kasai: *Callens* 2221 (BM, BR, K).

RIO MUNI. *Guinea* 855 (BM).

GABON. *Hallé* 3906 (BR, L, P); *LeTestu* 1570 (type of *Leptochilus grossedentatus*), 2184 (P).

**Habitat.** Usually on rocks and in streams in evergreen rain forest. Altitude: 0—1250 m.

**Spores.** *Guinea* 420 (MO), *Zenker* 4119 (G): the greater part normal, perispore cristate. *Curror s.n.* (syntype of *Acrostichum fluviatile*, K), *Schlechter* 12874 (L): spores normal, perispore atypical, see note 5. *Callens* 3188 (BM), *LeTestu* 1570 (type of *Leptochilus grossedentatus*), *Mann* 442 (lectotype of *Acrostichum fluviatile*, K), *Nickles* 92 (P): all abnormal, mostly shrivelled, the normally shaped ones with a cristate perispore.

**Notes.** 1. A rather clear-cut species confined to the wettest parts of Africa. It is closely related to and obviously derived from *B. auriculata*.

2. Hooker based the original description upon material from the islands in the Gulf of Guinea, which includes plants with pinnatifid mature leaves. The leaves from the plants of the Congo Basin are less or not divided. Entire leaves may precede the pinnatifid ones during the development of the plant (lectotype, K).

3. The pinnatifid leaves are in size and shape  $\pm$  identical to the leaves of the American *B. hastata* which is otherwise quite different.

4. The apices of the lobes of pinnatifid leaves are sometimes rounded. In a few leaves both acute and rounded apices are present; the shape of such leaves may be very similar to that of the plants referred to *B.  $\times$  boivinii*.

5. The perispore. The shape of the perispore may show variation. In *Zenker* 4119 the perispore is densely but low-cristate, whereas in *Guinea* 420 it shows but few and relatively tall crests. In *Curror*'s syntype the perispore is undulate or cristate-undulate, its outer surface densely and minutely warty.

6. Geographical distribution. Indirectly, Kunkel reported this fern from Liberia when he described *B. fluviatilis* var. *crenatis* (= *B. auriculata*); his new variety was said to occur '... in felsigen Bachläufen innerhalb arttypischen Beständen der var. *fluviatilis* ...'.

7. According to Exell (*Cat. Vasc. Pl. S. Tomé*, 1944, 383) it was Moller who collected *Fl. Afric. exsicc.* 68 (type of *Acrostichum phanerodictyon*). On the original label the name Quintas is printed as the collector's name.

8. For specimens morphologically intermediate between this species and *B. auriculata* see under *B. auriculata* note 2.

## 2. Series Bipinnatifidae Hennipman, *ser. nov.*

Seriei Quoyanae similis, differt marginibus pinnarum dentibus in sinibus munitis, ordinatione venularum venulis liberis paucis ad pluribus brevibus excurrentibus, positis in arcu costali, interdum etiam in arcu distali.

**Typus:** *Bolbitis bipinnatifida* (Mettenius ex Kuhn) Ching.

Terrestrial. *Rhizome* short-creeping, rather stout, with 2 or 3 rows of leaves, without sclerenchyma strands. Scales of the rhizome up to 11 mm long. *Leaves* approximate. Sterile leaves pinnate; petiole with 5–9 vascular bundles; lamina with 2 or more  $\pm$  spherical subterminal bulbils, pinnae 16–22, the margin with distinct teeth in the sinuses; terminal segment triangular; *venation pattern*: veins regularly reticulate, areoles angulate,  $\pm$  isodiametric or somewhat elongate, decreasing in size towards the margin, on the costal arch sometimes also on distal arches with few to several short, parallel, excurrent, included free veins. *Spores* with a smooth, cristate or cristate-undulate perispore.

Distribution. Seychelles. See fig. 30.

#### 4. *Bolbitis bipinnatifida* (Mettenius ex Kuhn) Ching—Fig. 37.

*B. bipinnatifida* (Mettenius ex Kuhn) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 47, non Iwatsuki (1959) ('*bipinnata*') (= *B. sinensis*).—*Chrysodium bipinnatifidum* Mettenius ex Kuhn, Fil. Afric. (1868) 50.—*Heteroneuron bipinnatifidum* Kuhn, Forsch. Reise Gazelle 4, Bot. (1889) 6.—*Leptochilus cuspidatus* (Presl) C. Chr. var., Ind. Fil. (1906) 181.—*Leptochilus bipinnatifidus* C. Chr., Trans. Linn. Soc. Bot. 7 (1912) 414.—*Campium bipinnatifidum* Copel., Philip. J. Sc. 37 (1928) 377, fig. 30.—Lectotype: *Boivin s.n.*, Seychelles, Mahé, 'bois des hauts de Mahé', iv-1848 (P; iso in B, one ster. and fert. pinna, BM).

*Acrostichum repandum* Bl. var. *quoyanum* auct. non (Gaudich.) Baker. Baker in Hooker & Baker, Syn. Fil. (1868) 419, p.p.

*acrostichum repandum* auct. non Bl.: Baker, Fl. Maur. & Seych. (1877) 514, p.p.; Cordem., Fl. Réunion (1895) 98, p.p.

Rhizome short, up to 12 mm thick. Scales of the rhizome: index 2–7, up to 11 by 1.5(–2) mm, opaque to subclathrate, dark greyish brown, sometimes in the lower half with a narrow membranous marginal strip. Leaves approximate, glabrescent. *Sterile leaves* pinnate with a triangular terminal segment, rather varying in size, up to (and over?) 120 cm long; petiole 20–30 cm long, near the base 3–6 mm thick; lamina index 2–4, widest below the middle, up to 95 by 20–40 cm, without the terminal segment 20–35, the terminal segment 30–65 (or more?) cm long, herbaceous, (light) olivaceous, with two or more bulbils situated several cm apart subterminally; pinnae: the two lowermost alternate to (sub)opposite, the other ones  $\pm$  opposite, 16–22, up to 40 mm apart; central pinnae index 4–7, widest below (to about) the middle, 11.5–22(–25) by 2.5–4.5 cm, base usually  $\pm$  unequal with its basispic side of the lower central pinnae angustate, that of the upper ones adnate to and sometimes long-decurrent on the rhachis, its acroscopic side cuneate, margin lobed 3/7 to 5/7 to the costa, with a tooth present in each sinus, lobes overlapping to somewhat spaced, margin entire or finely crenate-serrate, apex  $\pm$  rounded; the two lowermost pinnae 3–11 mm stalked, somewhat shorter than the central pinnae, 3.5–8 cm wide, widest about or below the middle, base asymmetrical with its basispic side shorter and usually also wider than the acroscopic one, margin of the basispic side lobed to 9/10 to the costa, lobes usually entire or crenate-serrate, sometimes lobed to 2/5 towards the costule; *terminal segment* relatively large, base short- to long-decurrent, margin near the base deeply pinnatifid, tapering towards the apex, apex acute (in small leaves) or flagelloid, flagellum near the base with lobes which are spaced,  $\pm$  tri-

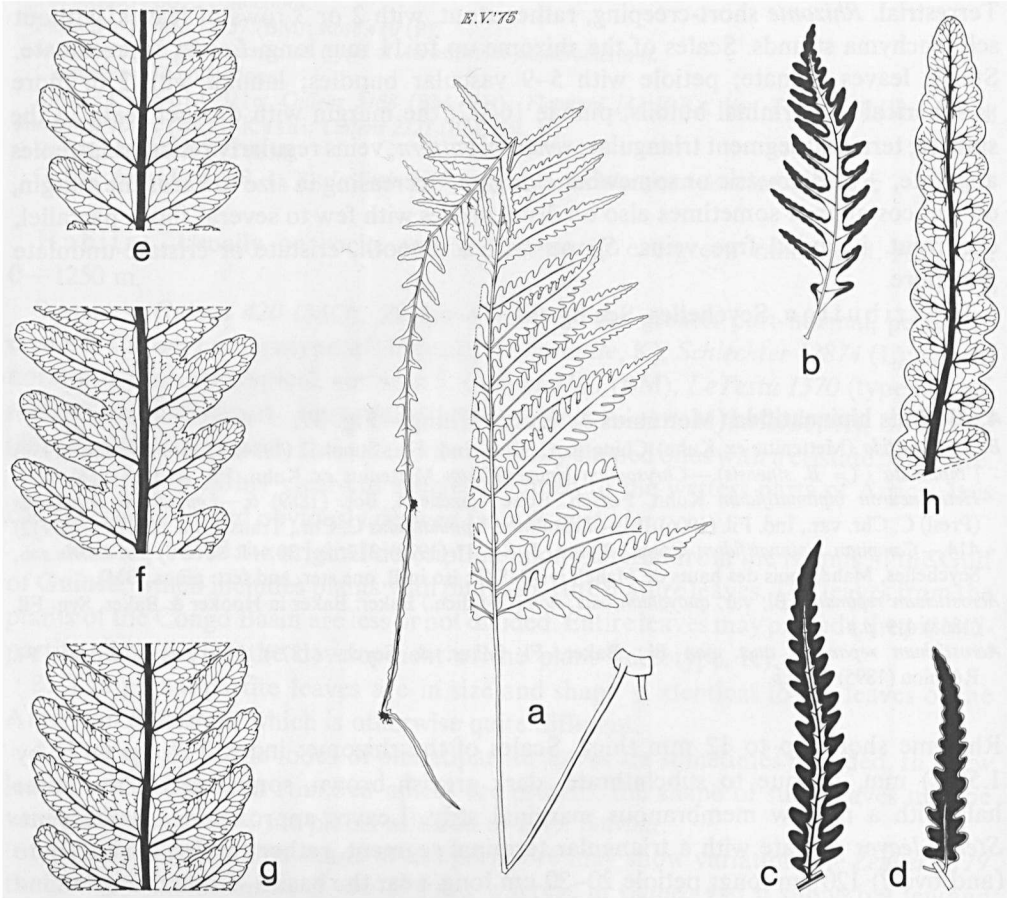


Fig. 37. *Bolbitis bipinnatifida*.—a. sterile leaf,  $\times 1/5$ ; b. basal pinna of fertile leaf,  $\times 2/5$ ; c, d. central pinnae of fertile leaf,  $\times 2/5$ ; e–g. venation pattern of sterile pinnae,  $\times 4/5$ ; h. *ibid.* of fertile pinna,  $\times 4/5$  (a, h. Jeffrey 759, L; b. Horne 166, K; c. Jeffrey 759, K; d. Horne s.n., K; e. Brauer 12, B; f, g. Horne s.n., B).

angular, unequal with the margin of the basiscopic side long-decurrent on the rachis, flagellum  $\pm$  sinuate towards the apex; costa and secondary veins stramineous, prominent on either side, other veins immersed or almost so, concolorous with the lamina; venation pattern: see fig. 37 e–g. *Fertile leaves*. Only two complete and fully acrostichoid fertile leaves available: Jeffrey 759 (L): leaf 73 cm long, petiole 35 cm long, near the base c. 5 mm thick; *ibid.* (K): leaf 108 cm long, petiole 74 cm long, near the base c. 5 mm thick. Lamina index 2–3, widest below the middle, 30–38 by 10–20 cm, without the terminal segment 18–28, the terminal segment 6–20 cm long; pinnae 14–22, up to 50 mm apart; central pinnae index 5–8, widest about the middle, 7–9.5 by 1–2 cm, margin lobed 1/5 to 4/5 towards the costa, a tooth in the sinus not always distinct; the two lowermost pinnae 5–8 mm stalked, sometimes slightly longer than the

central ones, up to 3.5 cm wide. *Sporangia* inserted all over the lower surface or on part of the lamina (see note 3).

SEYCHELLES. Mahé: *Boivin s.n.* (lectotype); *Bouton s.n.* (K); *Brauer 10, 11, 12* (all in B); *Gardiner s.n.*, 1908 (K); *Horne 166* (B, BM, K); *Kew 1174, ex coll. Rawson W. Rawson 890* (L); *Meriau s.n.*, 1903 (P); *Rawson W. Rawson 1059* (BM); *Pervillé 74* (P); slopes of Morne Blanc: *Jeffrey 584* (K); Niolo: *Jeffrey 759* (K, L, P); Cascade Estate: *Thomasset 113* (K).—Silhouette I.: *Gardiner s.n.*, 1908 (K).—Sine loc.: *Horne s.n.* (B, BM); *Kew 1174* (B, GH, P, W); *Ward s.n.* (P).

Habitat. 'one of the commonest ferns in damp woods' (*Horne 166*); 'on rocks and boulders' (*Jeffrey 759*). Altitude: 200 m (*Jeffrey 759*).

Spores. *Horne s.n.* (B), *Jeffrey 759* (L): by far the greatest part normal.

Notes. 1. A very distinct species which relationship is not obvious. Because of its venation pattern it seems related to *B. quoyana* (eastern Malesia to the Pacific) and to the American *B. umbrosa*. On the other hand it shares several features with the American *B. portoricensis* (ser. *Portoricenses*) but not with *B. quoyana* (ser. *Quoyanae*): scales (perfoliate in *B. quoyana*), the projection in the sinus (a spine in *B. quoyana*), and the shape of the terminal segment (not flagelloid and with only one bulbil in *B. quoyana*). Relationship to *B. portoricensis* seems at first sight not so likely as its venation pattern is quite different from that of the present species. The shape of the leaf and the venation patterns of the juvenile leaves of the present species and *B. portoricensis* (and also of *B. quoyana*) are, however, similar. A juvenile leaf of a cultivated specimen of *B. bipinnatifida* at Kew even showed incidental short recurrent veins (absent in mature leaves). Therefore, these two species may be related after all.

2. If the basal pinnae are not conform to the central ones, they are widest about or below the middle and not at the base as in all other species where the basal pinnae differ from the central ones.

3. Only few complete sterile and fertile leaves of this plant were available for study. Among the fertile leaves there were quite a few that were only in part acrostichoid, having a  $\pm$  conspicuous band along the main veins devoid of sporangia.

4. The locality 'Ile de Bourbon' printed on the labels of Boivin's material at P has been scratched out and was replaced by 'Iles Seychelles' in Boivin's handwriting. It is therefore very likely that the same kind of printed labels with Boivin's collections in B and L should be corrected in the same way.

5. The epithet '*bipinnata*' should not be regarded a new name in the genus *Bolbitis* as Iwatsuki (1959: 49) erroneously referred to '*Egenolfia bipinnata* J. Sm.' (= *Egenolfia bipinnatifida* J. Smith = *B. sinensis*).

### 3. Series *Bolbitianae* Hennisman, ser. nov.

*Bolbitis* Schott, Gen. Fil. (1835) pl. s.n. (13), *typo incl., pro genere*.

Terrestrial or low-epiphytic. *Rhizome* short-creeping,  $\pm$  stout, with 2—4 rows of leaves, with or without sclerenchyma strands. Scales of the rhizome up to 10 mm long. *Leaves* close together. Sterile leaves pinnate; petiole with 5—20 vascular bundles; lamina with a (primordium of a)  $\pm$  spherical, subterminal (or terminal) bulbil; pinnae 3—50, the margin sometimes with inconspicuous spines in the sinuses; terminal segment usually con-



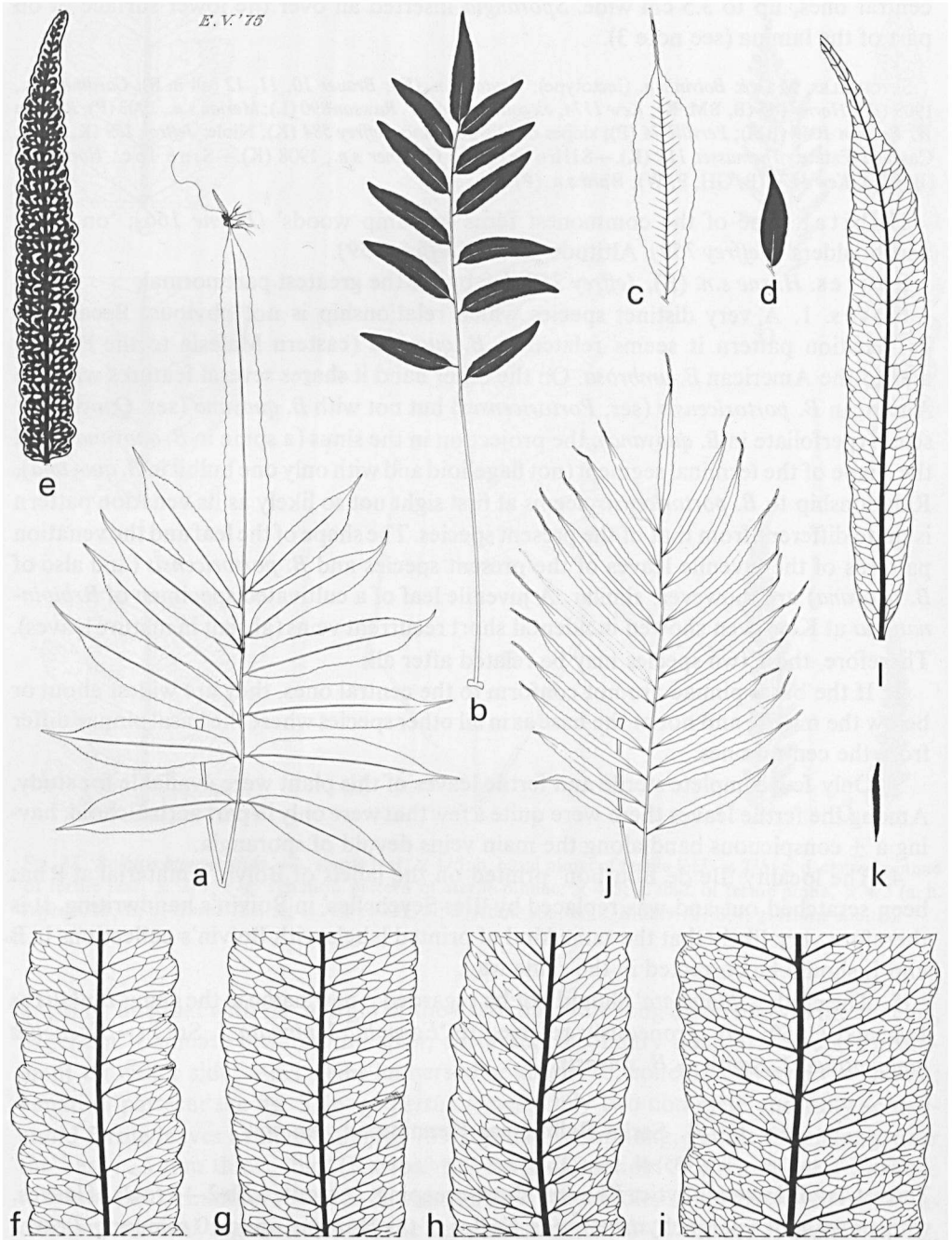


Fig. 38. a-i. *Bolbitis acrostichoides*. a, b. sterile and fertile leaf resp.,  $\times 1/5$ ; c, d. sterile and fertile pinna resp.,  $\times 1/5$ ; e. receptacles of fertile pinna,  $\times 4/5$ ; f-i. venation pattern of sterile pinnae,  $\times 4/5$  (a, b. *T. S. Jones* 321, BM; c, d. *Staudt* 463, W; e, f. *Young* 547, L; g. *W. de Wilde* c.s. 4323, WAG; h. *LeTestu* 3076, S-PA; i. *Félix* 41a, S-PA).—j-l. *Bolbitis salicina*. j. sterile leaf,  $\times 1/5$ ; k. fertile pinna,  $\times 1/5$ ; l. venation pattern of sterile pinna,  $\times 4/5$  (j, k. *Hallé* 4009, P; l. *Kew Distr.* no. 1182, *Barter* leg., GH).

form to the pinnae, sometimes narrowly triangular; secondary veins prominent on either side, stramineous or concolorous with the lamina, tertiary and other veins slightly prominent or immersed; *venation pattern*: veins variously anastomosing, always with a costal areole, with or without excurrent included free veins. *Spores* with a smooth undulate (in *B. semicordata*:  $\pm$  verrucate) perispore which is usually situated close to the exospore in one species (*B. costata*) widely spaced from the exospore.

Chromosomes.  $n = 41$  (*B. acrostichoides*, *B. crispata*, *B. semicordata*, *B. virens*);  $2n = (c.) 82$  (*B. subcrenata*, *B. virens*).

Distribution. Pantropical. See fig. 28.

Note. A very homogeneous series, the only pantropical one. The two American and the two African species are intimately related to each other. In Asia seven distinct species occur which are primarily characterized by venation pattern and leaf architecture. *B. angustipinna*, the most widespread Asian representative, is most closely related to the species from America and Africa.

### 5. *Bolbitis acrostichoides* (Swartz) Ching — Fig. 38: a—i; 39.

*B. acrostichoides* (Swartz) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 47; Alston, J. Bot. 77 (1939) 286, *p.p.*; in Exell, Cat. Vasc. Pl. S. Tomé (1944) 68, *p.p.*; in Hutch. & Dalziel, Fl. West Trop. Afr. ed. 2, Suppl. (1959) 68, *p.p.*; Tardieu-Blot, Mém. I. F. A. N. 28 (1953) 115, *p.p.*, pl. 19: fig. 4; Harley, Handb. Liberian Ferns (1963) 38, fig.; Tardieu-Blot in Aubrév., Fl. Gabon 8 (1964) 190, *p.p.*; in Aubrév., Fl. Cameroun 3 (1964) 320, *p.p.*, pl. 51: fig. 4.—*Hemionitis acrostichoides* Swartz, Schrader J. Bot. 1800, 2 (1801) 17; Syn. Fil. (1806) 21; Willd., Spec. Pl. 5 (1810) 130; Poiret in Lam., Enc., Suppl. 3 (1813) 38; J. E. Smith in Rees, Cyclop. 17 (1811) *s. pag.*—*Gymnogramma ? acrostichoides* Desvaux, Mag. Ges. Naturf. Freunde Berlin (Berl. Mag.) 5 (1811) 304; J. Bot. Soc. Ann. (not: Desv. J. Bot.) 3 (1814) 25; Kaulf., Enum. Fil. (1824) 80; Sprengel, Syst. Veg. 4 (1827) 40—*Polybotrya acrostichoides* Mettenius ex Kuhn, Fil. Afric. (1868) 52.—*Acrostichum afzelii* Carruth., Cat. Afr. Pl. Welwitsch 2, 2 (1901) 77.—*Leptochilus acrostichoides* C. Chr., Ind. Fil. (1906) 384.—*Gymnopteris acrostichoides* Engler, Veg. Erde 9, 2 (1908) 16.—*Campium acrostichoides* Copel., Philip. J. Sc. 37 (1928) 394, fig. 44, pl. 30.—*Lectotype*: *Afzelius s.n.*, *p.p.*, Sierra Leone (S-PA). See note 2.

*Leptochilus acrostichoides* (Swartz) C. Chr. var. *cuneatus* Bonap., Notes Ptérid. 7 (1918) 208; *ibid.* 15 (1924) 19, *quoad nomen solum*; Copel., Philip. J. Sc. 37 (1928) 398, *quoad nomen solum*.—*Syn types*: *Mugnier-Serand 1 C*, *2 C*, *3 C*, Guinea, Iles de Los (Conakry), 40–50 m alt. (P).

*Leptochilus diversibasis* Bonap., Notes Ptérid. 14 (1924) 216.—*B. diversibasis* Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 48.—*Type*: *LeTestu 1589*, Gabon, Mayombe Bayaka, Midouanga (P, 3 sh.).

*Acrostichum virens et syn. homot. auct. non* Hooker & Grev.: *auct. div. p.p.*

*Leptochilus gemmifer* Hieron. var. *latipinnatus auct. non* Hieron.: Hieron., Bot. Jahrb. 46 (1911) 346, *p.p.*

*Campium gemmiferum auct. non* (Hieron.) Copel.: Copel., Philip. J. Sc. 37 (1928) 397, *p.p.*

Rhizome up to 12 cm long, up to 10 mm thick, with 2 rows of leaves. Scales of the rhizome: index 3–7, up to 8 by 1–1.5 (–2) mm, opaque to subclathrate, blackish. *Sterile leaves* pinnate, 30–110 cm long; petiole 10–40 (–70) cm long, near the base 1.5–5 mm thick, with 7–11 vascular bundles; lamina index 1–3, widest about or below the middle, 20–80 by 10–35 cm, without the terminal segment 6–50, the terminal segment 7–45 cm long, herbaceous, usually light green to olivaceous, sometimes with a purple tinge, with a subterminal bulbil; rhachis not winged; pinnae alternate or opposite, 7–27 or rarely more, up to 65 mm apart; central pinnae index 3–8, widest about (to below) the middle, mostly the central part with parallel margins, 7.5–24 by 1.5–4.5 cm, base usually  $\pm$  symmetrical, sometimes its basiscopic side shorter and/or narrower, angustate to cuneate, margin  $\pm$

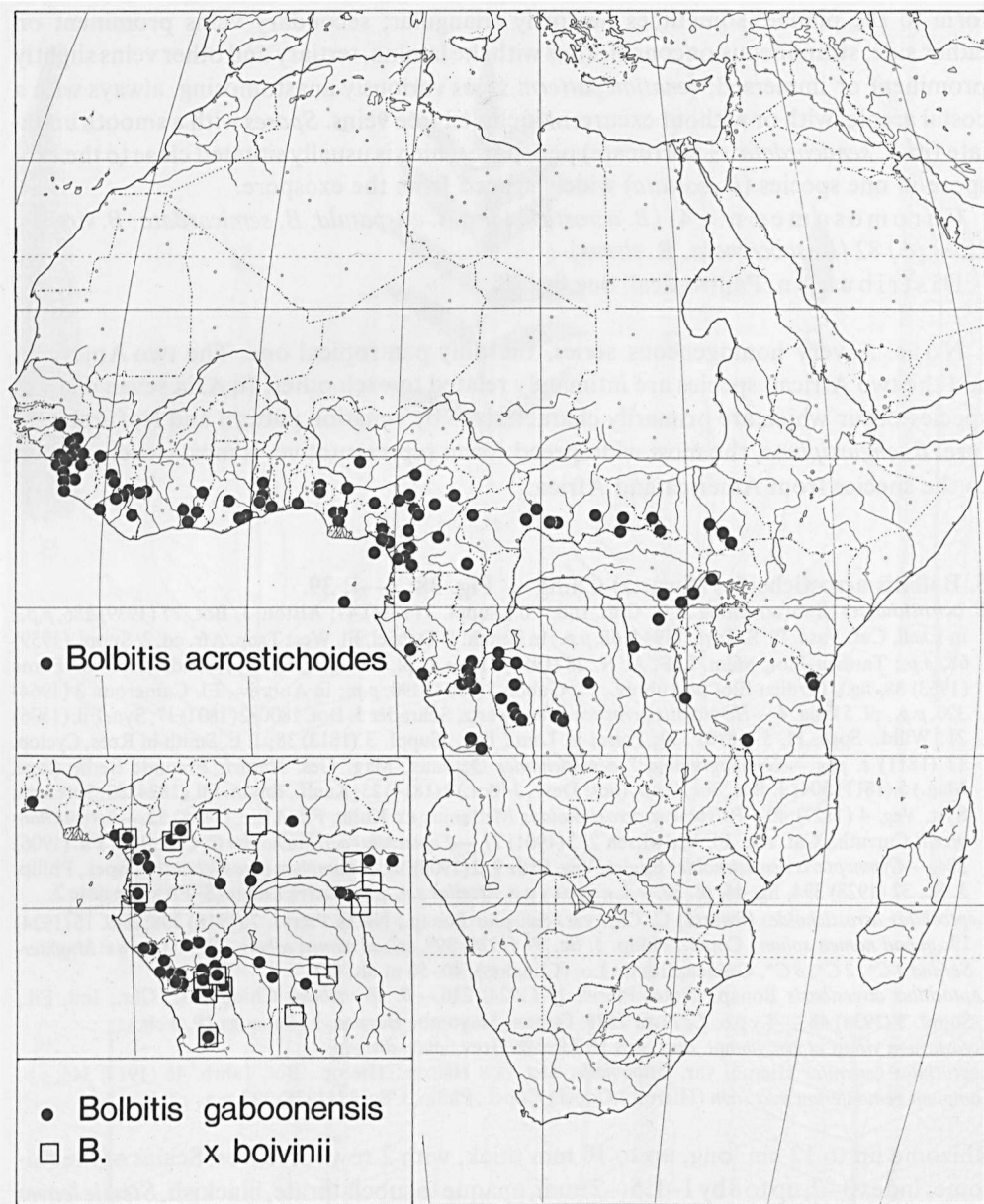


Fig. 39. Distribution of *Bolbitis acrostichoides*, *B. gaboonensis*, and *B. x boivinii*.

entire or finely (doubly-) serrate, without spines, apex acute to long-acuminate; the two lowermost pinnae ± conform to the central ones, 1–10 mm stalked; *terminal segment* usually joined to the rhachis, sometimes ± subarticulate, usually conform to the central pinnae but (much) prolonged, sometimes narrowly triangular; *venation pattern*: veins forming a costal areole and few to many smaller distal areoles, with few to many excur-

rent included free veins; see also fig. 38: f–i. *Fertile leaves* 35–140 cm long; petiole 18–70 cm long; lamina index 1–6, 10–75 by 5–30 cm, without the terminal segment 7–60, the terminal segment 5–30 cm long; pinnae 7–27, up to 80 mm apart; central pinnae index 4–15, 3–17.5 by 0.5–1.8 cm; the lowermost pinnae stalked 1–20 mm. *Sporangia* inserted usually  $\pm$  on the veins, arranged gymnoagrammoid, rarely inserted all over the lower surface, arranged acrostichoid.

**Chromosomes.**  $n = 41$ .

SENEGAL. *Heudelot 702* (B, K, P).

GUINEA. 42 collections.

SIERRA LEONE. 22 collections.

LIBERIA. 14 collections.

IVORY COAST. 13 collections.

GHANA. 11 collections.

TOGO. *Busse 3534* (B); *Büttner 57* (B); *Mildbraed 7364* (B); *Mischlich s.n.* (P).

NIGERIA. 14 collections.

SÃO TOMÉ. *Moller 63* (K); *Welwitsch 63b* (BM).

FERNANDO POO. *Henderson s.n.* (K).

CAMEROUN. 26 collections.

CENTRAL AFRICAN EMPIRE. 13 collections.

SUDAN. 10 collections.

GABON. *Hallé 2300* (P); *LeTestu 1589* (type of *Leptochilus diversibasis*).

CONGO (BRAZZ.). *Cervoni s.n.* (P); *Charvet 79* (P); *Descoing 11319* (P).

ZAIRE. Leopoldville: 18 collections.—Oriental: *Germain 4410* (BR, P).—Kivu: *Antun-Gupffert 11* (BR); *Bequaert 6593* (BR, P), *Mildbraed 2215* (B), *2330* (B).

ANGOLA. Lunda: *Gosswiler 14069* (K, P); *Young 547* (L).—Cuanza Norte: *Welwitsch 134* (K), *153* (K), *154* (BM).

UGANDA. Western: *Sangster 190* (BM), *293* (BM); *Thomas 1527* (K).

TANZANIA. Tanga: *Peter 18129* (BM, BR, K, P); *Verdcourt 90* (BM, K).—Western: *Jefford et al. 2720* (K); *Newbould & R. M. Harley 4447* (K).—Southern Highlands: *Schweinfurth 3034* (B, G, K, P, W).

**Habitat.** Usually creeping on rocks, sometimes in soil in (seasonally) humid places in primary and secondary forest. Altitude: 0–1000 (–1500) m. Locally common.

**Spores.** *Hepper 1476* (K), *LeTestu 2533* (GH), *Nielsen 1667* (C), *Schweinfurth 2235* (W): the greater part normal. *Afzelius s.n.* (lectotype of *Hemionitis acrostichoides*). *W. de Wilde c.s. 4323* (WAG): in part normal. *Jones 348* (GH): all shrivelled. See also notes 4 and 5.

**Notes.** 1. A variable species, especially regarding the venation pattern and the size of the leaves. It is intimately related to, or possibly even conspecific with, the American *B. serratifolia*. *B. salicina*, a rather critical species, is considered by me a derivative of the present species. See also *B. serratifolia*.

2. The material upon which the original description was based is a mixture of a fertile and a sterile leaf of *B. acrostichoides* and a fertile leaf belonging to *B. gemmifera*.

3. There is strong evidence that a fern like *B. acrostichoides* is one of the parents of *B. gemmifera* from which it is easily distinguished because of differences in the venation pattern, in the place of insertion of the bulbil, and in the shape of the perispore.

4. Some collections have relatively wide acrostichoid fertile pinnae rather resembling the central pinnae of *B. auriculata*. Their sporangia are inserted mainly on the veins or all

over the lower surface. Here belong *Annet 298* (P), *Ludwigs 7, p.p.* (M), *Staudt 463* (B, GH, K, W; syntype of *Leptochilus gemmifer* var. *latipinnatus*), *Zenker 4120* (G, K, L, MO, S-PA, W), all from Cameroun, and *Hallé 2300* (P) from Gabon. Spores: *Ludwigs 7, Staudt 463, Zenker 4120* (G): all abnormal. Possibly hybrids with *B. auriculata*.

5. Plants morphologically intermediate between the present species and *B. salicina* include *Callens 2233* (K), *Harley F 56* (BM, GH, K), and *Kunkel F-30* (WAG). These specimens have leaves with relatively narrow pinnae, a venation pattern with but very few included free veins and a terminal segment which is not prolonged but conform to the central pinnae; spores of all these collections are abnormal. Here may also belong *LeTestu 1589* (type of *Leptochilus diversibasis*) of which the large and relatively narrow sterile leaves are composed of a high number of pinnae (over 50) and a relatively short terminal segment; the venation pattern shows but occasionally an included free vein; sporangia inserted all over the lower surface of the fertile leaf; spores obviously for the greater part normal. Mainly because of the width of the pinnae this rather dubious specimen is included here.

## 6. *Bolbitis angustipinna* (Hayata) Ito — Fig. 40: a–f.

*B. angustipinna* (Hayata) Ito, J. Jap. Bot. 14 (1938) 443.—*Leptochilus angustipinnus* Hayata, Ic. Pl. Formos. 5 (1915) 297, fig. 119.—*Campium angustipinum* Copel., Philip. J. Sc. 37 (1928) 381, fig. 33; C. Chr., Contr. U.S. Nat. Herb. 26 (1931) 292.—Lectotype: (Iwatsuki, Acta Phytotax. Geobot. 18, 1959, 53): *Owatori s.n.*, Taiwan, near Hokkokei, 20-i-1898 (TI, n.v.; L, phot.).

*Leptochilus cuspidatus* (Presl) C. Chr. var. *crenatus* Rosenst., Hedwigia 56 (1915) 348.—Type: *Faurie 281* (= *Rosenstock, Fil. Formos. exsicc. 198*), Taiwan, Takao, Bankinsing, 800 m alt. (B; iso in BM, L, M, MICH, fragm., PNH, S-PA, UC).

[*Acrostichum contaminans* Wall., Cat. (1829) no. 22, *nom. nud.*—*Poecilopteris contaminans* Moore, Ind. Fil. (1857) 8, *nom. nud.*]—*Acrostichum crispatum* Clarke var. *contaminans* Clarke, Trans. Linn. Soc. Bot. 1 (1880) 580, pl. 84: fig. 2A, 2C.—*B. contaminans* Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 47; Iwatsuki, Acta Phytotax. Geobot. 18 (1959) 53, fig. 9; DeVol & Kuo in Fl. Taiwan 1 (1975) 348.—Type: *Wallich 22*, Nepal, between Helounda and Bhimpey, 1820 (K, herb. Wallich; iso in K, p.p.). See note 4.

*Acrostichum semicordatum* auct. non Baker: Baker, Syn. Fil. (1868) 422, p.p.

*Gymnopteris contaminans* auct. non Bedd.: Bedd., Handb. Ferns Br. India (1883) 435, p.p.; *ibid.*, Suppl. (1892) 105; Hayata, Bot. Mag. Tokyo 23 (1906) 26, p.p.

*B. sculpturata* auct. non (Fée) C. Chr.: Ito, J. Jap. Bot. 14 (1938) 439, fig.; Nayar & Kaur, Bull. Nat. Bot. Gard. Lucknow 88 (1964) 55.

Rhizome up to 10(–20) cm long, 10–20 mm thick, with 2–4 rows of leaves. Scales of the rhizome: index 3–8, 3–6(–8) by 0.5–1.5(–2.5) mm, subclathrate, dark brown or blackish throughout. *Sterile leaves* pinnate, 55–150 cm long; petiole 20–60 cm long, near the base 2.5–7 mm thick, with 7–16 vascular bundles; lamina index 1–3, widest somewhat below the middle, 30–90 by 20–45 cm, without the terminal segment 25–80, the terminal segment 8–25 cm long, (firm) herbaceous, usually light to dark green, sometimes with a purple tinge, with a subterminal bulbil on terminal segment (and pinnae); rhachis not winged; pinnae alternate or opposite, 20–50, 5–45 (–90) mm apart; central pinnae index 5–12, usually widest about (to below) the middle, the central part usually with parallel margins, 11–30 by 2–3(–5) cm, base  $\pm$  symmetrical, acute, broadly attenuate or truncate, margin usually slightly serrate-crenate, sometimes lobed to 1/3 to the costa and with a short or inconspicuous spine in each sinus, apex acute or acuminate; the two lowermost pinnae  $\pm$  conform to the central ones, 0–10 mm stalked; the pinnae in the upper

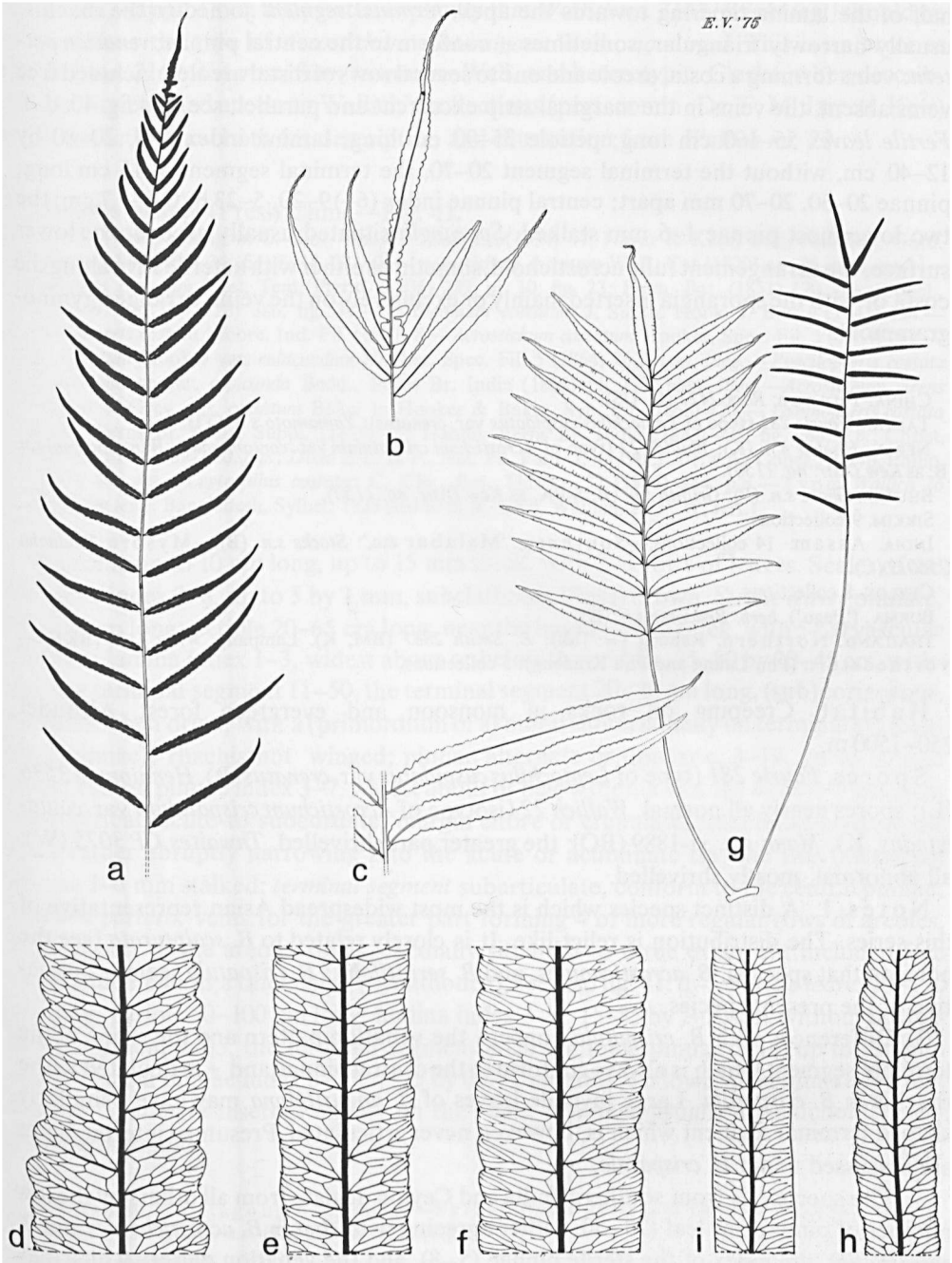


Fig. 40. a-f. *Bolbitis angustipinna*. a. fertile leaf,  $\times 1/5$ ; b. terminal part of sterile leaf,  $\times 1/5$ ; c. central pinnae,  $\times 1/5$ ; d-f. venation pattern of sterile pinnae,  $\times 4/5$  (a, d. Hennisman 3536, L; b, c, e. H. 3637, L; f. Tagawa et al. T 380, L).—g-i. *Bolbitis crispatula*.—g, h. var. *crispatula*. g. sterile and fertile leaf,  $\times 1/5$ ; h. venation pattern of sterile pinna,  $\times 4/5$ .—i. var. *copelandii*, venation pattern of sterile pinna,  $\times 4/5$  (g. Mann s.n., ix-1889, M; h. Austen s.n., US 418607; i. Van Beusekom 3204, L).

half of the lamina tapering towards the apex; *terminal segment* joined to the rhachis, usually narrowly triangular, sometimes  $\pm$  conform to the central pinnae; *venation pattern*: veins forming a costal areole and one to several rows of distal areoles, included free veins absent, the veins in the marginal strip excurrent and parallel; see also fig. 40: d–f. *Fertile leaves* 55–160 cm long; petiole 35–90 cm long; lamina index 1–4, 20–80 by 12–40 cm, without the terminal segment 20–70, the terminal segment 3–15 cm long; pinnae 20–50, 20–70 mm apart; central pinnae index (6–)9–20, 5–23 by 0.4–1.7 cm; the two lowermost pinnae 1–6 mm stalked. *Sporangia* situated usually all over the lower surface, the arrangement fully acrostichoid, sometimes either with a sterile strip along the costa or with the sporangia inserted mainly or exclusively on the veins, arranged gymno-grammoid.

CHINA. Yunnan: *Rock 2427* (C, US).

TAIWAN. *Faurie 281* (type of *Leptochilus cuspidatus* var. *crenatus*); *Yamamoto s.n.* (TI).

NEPAL. *Hooker s.n.* (K); *Wallich 22* (type of *Acrostichum crispatum* var. *contaminans*); *Winterbottom s.n.* (B, as *Kew Distr. no. 1150*).

BHUTAN. *Ghose s.n.* (P); *Griffith s.n.* (B; S-PA, as *Kew Distr. no. 1150*).

SIKKIM. 9 collections.

INDIA. Assam: 14 collections.—Southern. 'Malabar etc.': *Stocks s.n.* (B).—Mysore: *Saldanha C56012* (C).

CEYLON. 8 collections.

BURMA. ('Pegu'). *herb. Beddome s.n.* (K).

THAILAND. Northern. Raheng (= Tak): *E. Smith 2837* (BM, K). Lampang: *Winit 1126* (BKF).—Northeastern (Phu Luang and Phu Kradeng): 5 collections.

*Habitat*. Creeping on rocks in monsoon and evergreen forest. Altitude: 250–1500 m.

*Spores*. *Faurie 281* (type of *Leptochilus cuspidatus* var. *crenatus*, B), *Hennipman 3536* (L): spores nearly all normal. *Wallich 22* (isotype of *Acrostichum crispatum* var. *contaminans*, K), *Mann s.n.* xi-1889 (BO): the greater part shrivelled. *Thwaites CP 3075* (W): all abnormal, mostly shrivelled.

*Notes*. 1. A distinct species which is the most widespread Asian representative of this series. The distribution is relict-like. It is closely related to *B. scalpturata* (see the notes to that species), *B. acrostichoides*, and *B. serratifolia*: *B. crispatula* seems a derivative of the present species.

2. Differences with *B. crispatula* concern the venation pattern and the shape of the terminal segment which is always conform to the central pinnae and  $\pm$  articulated to the rhachis in *B. crispatula*. Large juvenile leaves of *B. angustipinna* may have a similarly shaped terminal segment which is, however, never articulated. Presumed intermediates are discussed under *B. crispatula*.

3. The specimens from southern India and Ceylon deviate from all others by the low number of pinnae per leaf (20–30; rather agreeing with that in *B. acrostichoides* and *B. serratifolia*), the index of the sterile pinnae (5–8), and the venation pattern which may show irregularities. Hybridization seems also involved. See also the note to *B. subcrenata* var. *subcrenata*.

4. Typification of *Acrostichum crispatum* var. *contaminans*. Beddome (Handb. Ferns

Br. India, Suppl. 1892: 105) stated explicitly that *Wallich no. 2168 (Wight leg.)* should be regarded as the type of *Acrostichum contaminans* Wall., *nom. nud.* This is an error as *Wallich no. 2168* is *Acrostichum terminans* Wall. and heterotypic. Clarke, when describing the variety, had access to Wallich's collections (pers. comm. Dr. F. M. Jarrett, Kew) and correctly drew both his description and illustration from *Wallich no. 22*.

**7. *Bolbitis costata* (Presl) Ching—Fig. 41.**

*B. costata* (Presl) Ching in C. Chr., Ind. Fil., Suppl. 3(1934) 47; Nayar & Kaur, Bull. Nat. Bot. Gard. Lucknow 88 (1964) 34; fig. 8, 16, 27, 60.—[*Acrostichum costatum* Wall., Cat (1829) no. 26, *nom. nud.*]—*Campium costatum* Presl, Tent. Pterid. (1836) 239, pl. 10: fig. 23; Epim. Bot. (1851) 170, *p.p.*; Copel., Philip. J. Sc. 37 (1928) 386, fig. 37.—*Cyrtogonium costatum* J. Smith, Hook. J. Bot. 4 (1841) 154.—*Poecilopteris costata* Moore, Ind. Fil. (1857) 8.—*Acrostichum costatum* Hooker, Spec. Fil. 5 (1864) 262.—*A. costatum* Hooker var. *rubicundum* Hooker, Spec. Fil. 5 (1864) 262, *nom. illeg.*—*Poecilopteris costata* (Presl) Moore var. *rubicunda* Bedd., Ferns Br. India (1865) pl. 113, *nom. illeg.*—*Acrostichum virens* Hooker & Grev. var. *costatum* Baker in Hooker & Baker, Syn. Fil. (1868) 420.—*Gymnopteris costata* Bedd., Ferns Br. India, Suppl. (1876) 27; Handb. Ferns Br. India (1883) 438, fig. 266, *p.p.*; Christ, Farnkr. Erde (1897) 50, *p.p.*; Diels in E. & P., Nat. Pfl. Fam. 1, 4 (1902) 201, *p.p.*; Copel., Polyp. Philip. (1905) 44, *p.p.*—*Leptochilus costatus* C. Chr., Bot. Tidsskr. 32 (1916) 344, *p.p.*—Type: *Wallich 26 (De Sylva leg.)*, Bangladesh, Sylhet, 1823 (iso in B, K, herb. Wallich, K, P, W, fert.).

Rhizome up to 10 cm long, up to 15 mm thick, with 2–4 rows of leaves. Scales of the rhizome: index 3–8, up to 5 by 1 mm, subclathrate, (light) brown. *Sterile leaves* pinnate, 55–140 cm long; petiole 20–65 cm long, near the base 2–7 mm thick, with 5–20 vascular bundles; lamina index 1–3, widest about or below the middle, 35–80 by 20–45 cm, without the terminal segment 11–50, the terminal segment 20–40 cm long, (sub)coriaceous, purplish when dried, with a (primordium of a) bulbil subterminally on terminal segment (and pinnae); rhachis not winged; pinnae alternate or opposite, 3–19, up to 80 mm apart, central pinnae index 3–7, widest about or below the middle, 16–43 by 4–9 cm, base symmetrical, acute to subcordate, margin entire or crenulate, sometimes crisped, the apex rather abruptly narrowing into the acute or acuminate tip; the two lowermost pinnae 1–6 mm stalked; *terminal segment* subarticulate, conform to the central pinnae; *venation pattern*: veins for the greater part forming 4 or more regular rows of areoles, with in part of the areoles one ( $\pm$ medially situated) to three excurrent included free veins which end in a thickening (hydathode?), see also fig. 41: d–f. *Fertile leaves* 40–170 cm long; petiole 20–100 cm long; lamina index 3–7, 15–85 by 7–30 cm, without the terminal segment 9–65, the terminal segment 8–20 cm long; pinnae 5–18, up to 130 mm apart; central pinnae index 6–15, 4–25 by 0.6–2 cm, the two lowermost pinnae 1–6 mm stalked. *Sporangia* inserted mainly on the veins, arranged usually acrostichoid, rarely gymnoagrammoid.

BANGLADESH. Chittagong: 6 collections.—Sylhet: *Wallich 26* (type of *Campium costatum*).

NEPAL. East: *Hooker s.n.* (K), *Clarke 31730* (K).

SIKKIM. 5 collections.

INDIA. Assam: 18 collections.

BURMA. Bhamo Dist. near Shwebo: *Lace 5210* (K).—Moulmein: *Parish s.n.* (B).

THAILAND. Northern. Lampang. *Winit (Wanadorn) 58* (BKF, SING), 927 = *BKF 1368* (BKF, K). Doi Inthanon: *Murata et al. T 15546* (L).



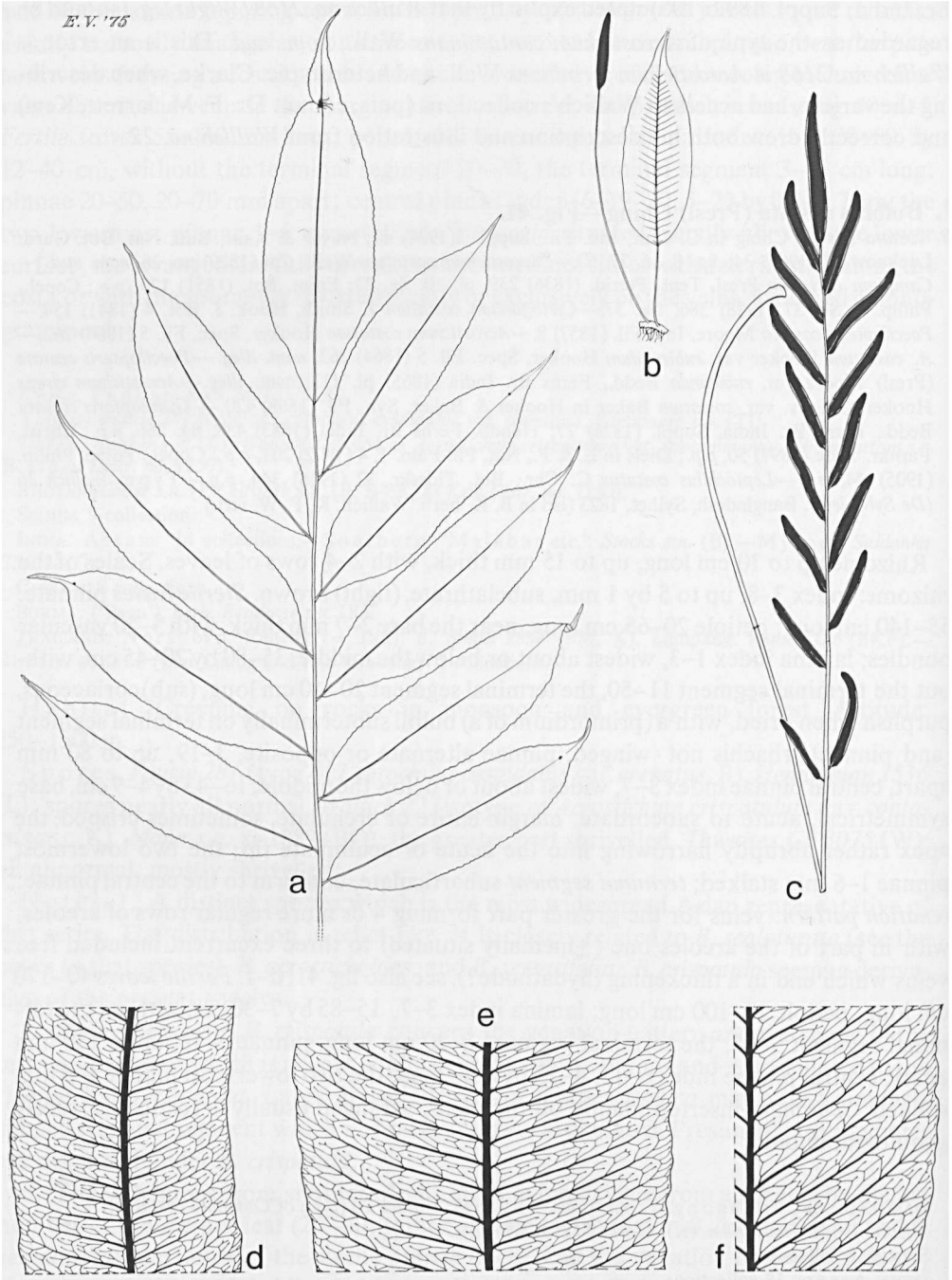


Fig. 41. *Bolbitis costata*.—a–c. sterile and fertile leaves,  $\times 1/5$ ; d–f. venation pattern of sterile pinnae,  $\times 4/5$  (a, e. *Anonymus s.n.*, W; b. *Mann s.n.*, xii-1886, M; c. *Mann s.n.*, ii-1886, S-PA; d. *Hooker & Johnson '110'*, GH; f. *Anonymus s.n.*, Assam, B).

**Habitat.** Only few data available; obviously growing in forest. Altitude: 0–1200 m. According to Nayar & Kaur (1964) specimens of this species grow closely together forming dense colonies in forests near streams; the rhizome partially covered with gravelly soil.

**Spores.** *Mann s.n.*, Ukiam, ii-1889 (M), Nambur Forest, i-1888 (S-PA), Naga Hills, iii-1883 (L, 908.206–45), *Wallich 26* (isotype of *Acrostichum costatum*, B), *Winit 58* (SING): all or the greater part normal.

**Notes.** 1. A clear-cut species which is mainly characterized by the purplish colour of the dried leaves, the number of pinnae per leaf, and the shape and venation pattern of the pinnae.

2. The present species was validly published by Presl (1836), who mentioned the number of vascular bundles (12–18) in the petiole of this species in the description of his new genus *Campium*, and also provided a drawing of the venation pattern of part of a fertile pinna. Later (1851) he included in *B. costata* all the elements which Fée (1845) listed under *Heteroneuron scalpturatum* (see *B. scalpturata*, note 6). Hooker (1864) agreed with Presl (1851) but added *Meniscium deltigerum* (= *B. virens* var. *deltigera*) and *Jenkinsia undulata* (= *B. virens* var. *virens*) as varieties of *Acrostichum costatum*. Baker (1868) united *Acrostichum costatum sensu* Hooker (1864) with *A. virens sensu* Hooker (1864). Clarke's concept (1880) is correct; he excluded from *A. costatum* the ferns described as *Meniscium deltigerum* and *Jenkinsia undulata*. Beddome (1883) largely agreed with Hooker (1864) but characterized *Meniscium deltigerum* and *Jenkinsia undulata* as 'only abnormal forms, such as occur more or less in nearly all the other species of *Gymnopteris* and cannot be recorded as varieties'; he strongly criticized the concepts of both Baker and Clarke. Christensen's concepts (1906, 1916) are discussed under *B. scalpturata*, note 6. Copeland (1928) based himself on Clarke.

3. Variation in size of the fertile leaves. Occasionally small fertile leaves are formed (e.g. *Clarke 19653*, K). One collection (*Mann s.n.*, Besisto, Khasi Hills, xii-1886, M) comprises a simple fertile leaf (spores all abnormal) occurring in conjunction with a simple sterile leaf; the shape of the simple leaf agrees with the terminal segment of leaves of typical plants.

4. *Winit 58* (BKF, 2 sh.) consists of one sterile and two fertile leaves (all separately mounted). The venation pattern of the sterile leaf looks intermediate between that of the present species and *B. virens*; the colour of the leaf is greenish. The colour of the two fertile leaves is typically purplish; the spores of one of the leaves are all shrivelled, those of the second leaf typical. *Winit 59–928* (BKF), collected from the same place, represents *B. virens*; hybridization between the latter and the present species may underly the deviations shown in the material of *Winit 58*.

5. Spores. The perispore is situated at considerable distance from the exospore.

8. ***Bolbitis crispatula* (Copel.) Ching—Fig. 40: g–i; 42.**

*B. crispatula* (Copel.) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 47; Nayar & Kaur, Bull. Nat. Bot. Gard. Lucknow 88 (1964) 36, fig. 17, 33, 61, 65, 74, 86.—*Acrostichum crispatum* [Wall., Cat. (1829) no. 24, *nom. nud.*] Clarke, Trans. Linn. Soc. Bot. 1 (1880) 580, pl. 84: fig. 2B, 2D, excl. var., *nom. illeg., non*

Fée (1852) (= *Elaphoglossum spec.*).—[*Cyrtogonium crispatum* J. Smith, Hook. J. Bot. 4 (1841) 154, *nom. nud.*]—*Campium crispatum* [Presl, Epim. Bot. (1851) 171, *nom. nud.*] Copel., Philip. J. Sc. 37 (1928) 382, fig. 34, pl. 26.—[*Poecilopteris crispata* J. Smith, Cat. Cult. Ferns (1857) 23, *nom. nud.*; Moore, Ind. Fil. (1857) 8, *nom. nud.*; J. Smith, Ferns Br. For. (1866) 117, *nom. nud.*]—*Acrostichum virens* Hooker & Grev. var. *crispatum* Hooker, Spec. Fil. 5 (1864) 261 ('var.?'); Baker in Hooker & Baker, Syn. Fil. (1868) 420.—*Gymnopteris contaminans* (Bedd.) Bedd. var. *crispata* Bedd., Handb. Ferns Br. India, Suppl. (1892) 105.—*Leptochilus virens* (Hooker & Grev.) C. Chr. var. *crispatus* C. Chr., Bot. Tidsskr. 32 (1916) 344.—Type: Wallich 24 p.p. (*Blinkworth leg.*), Bangladesh, Kumaon (Kamoun?) (K, herb. Wallich; iso in K, MICH, fragm.).

*B. copelandii* Cing ex Tardieu-Blot & C. Chr., Not. Syst. 7 (1938) 101; Tardieu-Blot & C. Chr. in Lecomte, Fl. Gén. I.-C. 7 (1941) 434, fig. 50: 1, 2.—Type: *H.M. Smith 302*, Cambodia, Angkor (BM; iso in MICH, US).

[*B. copelandii* Ching f. *viridis* Tardieu-Blot & C. Chr., Not. Syst. 7 (1938) 102, *nomen*—Type: *Pierre s.n.*, Cochinchina, Deon Ba, vii-1866 (iso in K).]

*Gymnopteris contaminans auct. non* (Bedd.) Bedd. (*nom. illeg.*): Bedd., Ferns Br. India, Suppl. (1876) 27, p.p.; Handb. Ferns Br. India (1883) 435, p.p.

Rhizome up to 10 (–15) cm long, up to 10 mm thick, with 2–4 rows of leaves. Scales of the rhizome: index 4–15, up to 8 by 1 mm, subclathrate, blackish. *Sterile leaves* pinnate, 25–90 cm long; petiole 10–40 (–50) cm long, near the base 1.5–3 mm thick, with 5–8 vascular bundles; lamina index 1–3, widest about or below the middle, 15–50 by 9–25 cm, without the terminal segment 10–35, the terminal segment 4–15 cm long, firm-herbaceous, olivaceous, purplish or purplish-brown (light to dark green when living), usually without, sometimes with a ± terminal bulbil; rhachis not winged; pinnae alternate or opposite, 10–30 (–60), 10–40 mm apart; central pinnae index 4–11, widest about or below the middle, 5–17.5 by 0.9–2 cm, base symmetrical, narrowly to broadly cuneate, margin ± entire or finely serrate or serrate-crenate, ± crisped, without spines, apex acute or acuminate; the two lowermost pinnae 0–4 mm stalked, base symmetrical or asymmetrical with the basiscopic side shorter, otherwise conform to the central pinnae; *terminal segment* subarticulate, usually conform to the central pinnae, sometimes inconspicuous (see note); *venation pattern*: veins forming a costal areole, otherwise free, excurrent, see also fig. 40: h, i. *Fertile leaves* 25–90 cm long; petiole 15–50 (–65) cm long, lamina index 1–3, 9–40 by 3–20 cm, without the terminal segment 7–35, the terminal segment 2–9 cm long; pinnae 10–30 (–45), up to 50 mm apart, index 4–35, 2–12 by 0.2–1.2 cm; the two lowermost pinnae 0–6 mm stalked. *Sporangia* either inserted all over the lower surface, arranged acrostichoid, or mainly inserted on the veins and along the margin, arranged ± pteridioid.

Chromosomes.  $n = 41$  (var. *copelandii*).

Distribution. *Assam, Thailand, Indo-China*. See fig. 42.

Habitat. Creeping on stones usually in riverbeds in monsoon forest. Altitude 0–1200 m.

Note. A distinct species which is closely related to *B. angustipinna*. For differences see under that species. For specimens with part of their features intermediate between the present species and *B. angustipinna* see var. *copelandii*, note 1. The leaves of *B. crispata* usually turn purplish upon drying, like those of *B. sculpturata* and *B. costata*. The material is easily divided into two allopatric varieties.

KEY TO THE VARIETIES

- 1a. Fertile pinnae acrostichoid; index (7-) 10-35 . . . . . a. var. *crispatula*  
b. Fertile pinnae  $\pm$  pteroid; index 4-10 (-20) . . . . . b. var. *copelandii*

**a. var. *crispatula*—Fig. 40: g, h; 42.**

*B. crispatula* (Copel.) Ching.

Scales of the rhizome: index 4-10, up to 5 by 1 mm, upper half acute. *Sterile leaf* 30-90 cm long; petiole 10-40 (-50) cm long; lamina 20-50 by 10-25 cm, without the terminal segment 15-35, the terminal segment 5-15 cm long, without bulbils; pinnae 10-26; central pinnae index (4-)7-11, usually widest about, sometimes below the middle. *Fertile leaves* 35-90 cm long; petiole 20-50 (-65) cm long; lamina 10-40 by 4-20 cm, without the terminal segment 7-35, the terminal segment 2-9 cm long; pinnae 10-25; central pinnae index (7-)10-35, 2-12 by 0.2-0.5 cm. *Sporangia* inserted all over the lower surface.

BANGLADESH. Sylhet: *Clarke 42452* (K); *Wallich 24 p.p.* (*Gomez leg.*) (K, herb. Wallich).—Not traced: Kumaon: *Wallich 24 p.p.* (*Blinkworth leg.*; type of *Acrostichum crispatulum*).

INDIA. Assam. Garo Hills, Khasya Hills, Jaintia Hills: 15 collections.

Habitat. See the species.

Spores. *Austen s.n.* (MICH), *Nayar et al. LWG 63414* (LWG): the greater part normal. *Hooker & Thomson '107'* (BM), *Mann s.n.*, ix-1889 (L): all abnormal, mostly shrivelled.

**b. var. *copelandii* (Ching) Hennipman, stat. nov.—Fig. 40: i; 42.**

*B. copelandii* Ching ex Tardieu-Blot & C.Chr., Not. Syst. 7(1938) 101.

Scales of the rhizome: index 4-15, up to 8 by 1 mm, upper half acute or hair-like. *Sterile leaf* 25-60 (-85) cm long; petiole 10-35 cm long; lamina 15-45 by 9-25 cm, without the terminal segment 11-35, the terminal segment 4-10 cm long, sometimes aborted or absent, a bulbil if present situated at the base of the terminal segment or pseudo-terminal; pinnae 15-30 (-60); central pinnae index 4-8, widest below or about the middle. *Fertile leaves* 25-60 (-90) cm long; petiole 15-35 (-50) cm long; lamina 9-25 (-40) by 3-11 cm, without the terminal segment 7-22 (-35), the terminal segment 2-6 cm long; pinnae 12-30 (-45); central pinnae index 4-10, 2-8 by 0.2-1.2 cm. *Sporangia* inserted on the veins and along the margin only.

THAILAND. Northern. Lampang: *Winit 1026* (BKF, K, SING).—Northeastern. Phu Pan: *Hansen et al. 11300* (C). Phu Luang: *Hennipman 3632* (BKF, KYO, L); *Tagawa et al. T 1910* (L, US).—Eastern. Nangrawng Waterfall: *Kerr 8218* (K); *Smitinand & Floto 6093* (= *BKF 24438*) (BKF).—Southeastern. Koh Kut (island in the Gulf of Thailand): *Van Beusekom 3204* (L).

CAMBODIA. Angkor: *Lecomte & Finet 1796* (P), 1813 (P); *H. M. Smith 298* (C, GH, US), 302 (type of *B. copelandii*). Pnom-chom: *Poilane 28825* (P).

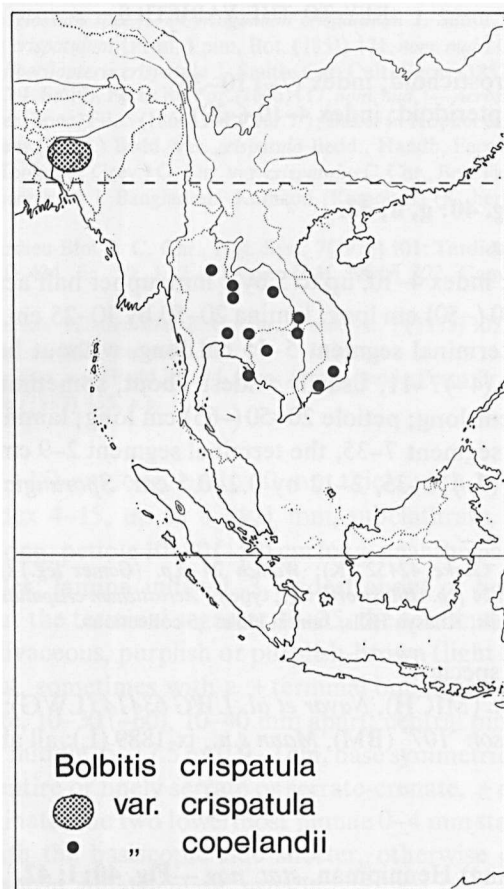


Fig. 42. Distribution of *Bolbitis crispatula*.

LAOS. Khong: *Thorel* 2480 (P). Bassac: *Thorel s.n.* (P). Oudang: *Thorel s.n.* (P).  
 VIETNAM. Cochinchina: *Chevalier* 29851 (P); *Matthew s.n.* (K); *Pierre* 1300 (BM, BO, GH, K, P), 1300bis (P), s.n., vii-1866 (K, P); *Poilane* 2564 (P).—S. Annam: *Squires* 845 (B, BO, GH, K, M, MO, SING, S-PA, W).

Habitat. See the species.

Spores. *Van Beusekom* 3204 (L, sh. no. 8), *Hennipman* 3632 (L), *Matthew s.n.* (K), *H.M. Smith* 302 (type of *B. copelandii*, US), *Squires* 845 (BO): the greater part normal. *Tagawa et al.* T 1910 (L): in part (the majority?) abnormal.

Notes. 1. This variety is heterogeneous. It includes the following elements.

a. The collections from Thailand except those from Koh Kut. Part of the sterile leaves occurring in conjunction with the fertile ones are large and consist of a great number of pinnae per leaf (the figures given between brackets in the description refer to these specimens). The shape, size, and venation pattern of these pinnae are  $\pm$  interme-

diate between those of typical plants and those of *B. angustipinna*. The shape of the pinnae of the fertile leaves is uniform throughout the material attributed to this variety. These collections from Thailand are further of great interest for two reasons. Firstly, they all have a conspicuous bulbil situated at the articulation of the terminal segment of both the sterile and the fertile leaf. Secondly, the shape of the terminal segment varies; usually the terminal segment is either conform to the central pinnae, or inconspicuous, or absent, rarely (in a few fertile leaves only) narrowly triangular. In leaves where the terminal segment is absent or inconspicuous, the localization of the bulbil is terminal or almost so. Such a terminal localization of the bulbil is characteristic for *B. rhizophylla* and *B. novoguineensis*. For a correct interpretation of these facts it seems of interest to know that the smaller-sized sterile leaves occurring on the same rhizome as the deviating ones agree in all details (including size!) with the mature sterile leaves of the non-deviating collections of this species.

b. *Lecomte & Finet 1796 and 1813, Thorel s.n.*, from Oudang, and *Pierre 1300 (p.p.)* rather agree with the collections mentioned above, but the obviously mature specimens lack a bulbil.

2. One out of eight fertile plants of *Van Beusekom 3204*. (Thailand, Koh Kut) has fertile leaves agreeing as to shape of the pinnae with those of the typical variety. The sporangia are situated on the veins (all over the lower surface in the typical variety).

3. Cultivated material. One out of three living plants sent by Van Beusekom from Koh Kut, Thailand, and belonging to the gathering *Van Beusekom 3204*, shows abnormally shaped sterile and fertile leaves in cultivation. These sterile leaves are bipinnate in the lower half of the lamina, the two lowermost pinnae again pinnate with a terminal segment conform to the central pinnules, up to 18 by 10 cm; pinnules up to 14, up to 55 by 11 mm; the terminal segment of the leaf is sometimes in the lower half either lobed to halfway towards the costa, or shows some odd free pinnules at the base of the segment. The fertile leaves are usually  $\pm$  normal, sometimes the lowest pinnae with some odd pinnules at the acroscopic side of the base (*Hennipman 4087, L*).

## 9. *Bolbitis salicina* (Hooker) Ching—Fig. 38: j-l.

*B. salicina* (Hooker) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 50; Alston, J. Bot. 77 (1939) 286; Tardieu-Blot, Mém. I.F.A.N. 28 (1953) 116, pl. 19: fig. 5; Alston in Hutch. & Dalziel, Fl. West Trop. Afr. ed. 2, Suppl. (1959) 69; Harley, Handb. Liberian Ferns (1963) 40, fig.; Tardieu-Blot in Aubrév., Fl. Gabon 8 (1964) 189.—*Acrostichum salicinum* Hooker, Spec. Fil. 5 (1864) 265; Baker in Hooker & Baker, Syn. Fil. (1868) 422.—*Chrysodium salicinum* Kuhn, Fil. Afric. (1868) 52.—*Gymnopteris salicina* J. Smith, Hist. Fil. (1875) 138.—*Leptochilus salicinus* C. Chr., Ind. Fil. (1906) 387.—*Campium salicinum* Copel., Philip. J. Sc. 37 (1928) 395, fig. 46.—Lectotype (Tardieu-Blot, op. cit., 1964, 'holotype'): *Barter s.n.* (Niger Expedition), Sierra Leone (K).

Rhizome up to 10 cm long, up to 7 mm thick, with 2(3) rows of leaves. Scales of the rhizome: index 2–6, up to 3.5 by 1(–1.5) mm, opaque to subclathrate, blackish, sometimes with a paler marginal strip. *Sterile leaves* pinnate, 30–60 cm long; petiole 5–35 cm long, near the base 1.5–3 mm thick, with 3–7 vascular bundles; lamina index 1–3, widest about or below the middle, 15–45 by 8–20 cm, without the terminal segment 10–35, the

terminal segment 5–15 cm long, firm-herbaceous, light to dark green, usually with a distinct bulbil subterminally on the terminal segment (and pinnae); rhachis not winged; pinnae alternate or opposite, 14–23, up to 45(–60) mm apart; central pinnae index 5–15, widest about (to below) the middle, 6.5–16 by 0.8–2 cm, base symmetrical, usually narrowly cuneate, margin  $\pm$  entire or finely crenate-serrate, without spines, apex acute to long-acuminate; the two lowermost pinnae up to 10 mm stalked, otherwise similar to the central pinnae; *terminal segment* joined to the rhachis or subarticulate, usually conform to the pinnae, rarely narrowly triangular; *venation pattern*: veins forming a regular network of a costal areole and usually one transverse row of smaller distal ones, sometimes the costal arch with a single excurrent included free vein, see also fig. 38: 1. *Fertile leaves* 40–90 cm long; petiole 24–55 cm long; lamina index 2–6, 15–35 by 3–10 cm, without the terminal segment 10–30, the terminal segment 4–6 cm long; pinnae 12–25, up to 60 mm apart, central pinnae index 7–13, 2.5–9 by 0.2–0.7 cm; the two lowermost pinnae up to 10 mm stalked. *Sporangia* usually inserted all over the lower surface, arranged acrostichoid, sometimes on and near the veins only.

GUINEA. 13 collections.

SIERRA LEONE. 5 collections.

LIBERIA. 10 collections.

IVORY COAST. *Chaper s.n.* (P); *Chevalier 17545* (L, P); *Portères s.n.* (P).

GHANA. *Adams 1978 (=3877)* (BM, K, P).

NIGERIA. *Baldwin Jr. 13763* (BM); *Jones & Onochie FHI 18931* (BM); *Talbot s.n.* (BM).

FERNANDO POO. *Henderson s.n.* (K); *Mann 133?* (not 1339; syntype of *Acrostichum salicinum*, K). *Portères s.n.* (P).

CAMEROUN. *De Wit 7030* (WAG).

GABON. *Hallé 3919* (P), *4009* (BR).

CONGO (BRAZZ.). 5 collections.

ZAIRE. Leopoldville: 6 collections.

**Habitat.** Usually on rocks, either in streams or in streambeds, in forest; obviously seasonally submerged. Altitude: 0–1200 m.

**Spores.** *Cook 163* (GH), *Cremers 306* (P), *Harley F 77* (K), *Leeuwenberg & Voorhoeve 4735* (WAG): all or the greater part normal. See also the notes.

**Notes.** 1. A medium-sized species from wet habitats, obviously derived from a fern like *B. acrostichoides*. Most of the collections attributed to this have a combination of characters that justifies keeping *B. salicina* and *B. acrostichoides* separate. I have strong doubts, however, whether this classification is correct, as it remains uncertain to which degree the morphological characteristics of these two species are determined by habitat conditions. Specimens  $\pm$  intermediate are discussed under *B. acrostichoides*, note 5; see also note 2 below.

2. The identification of some small-sized fertile plants is problematical. Their sterile leaves resemble juvenile leaves of *B. acrostichoides*. Here I think belong Mann's syntype (a collection consisting of 14 sterile leaves and one fertile leaf), *Henderson s.n.* (K), and *Portères s.n.* (P), all with abnormal spores, all from Fernando Poo.

3. Occasionally the terminal segment of the lamina is narrowly triangular. Both types of terminal segment may occur on the same rhizome (e.g. *Wellens 327*, BR).

4. Copeland regarded the present species (as *Campium salicinum*) and *Campium feeianum* (= *B. presliana*) as more closely related to each other than to any other known species.

**10. Bolbitis scalpturata (Fée) Ching—Fig. 43: a–d.**

*B. scalpturata* (Fée) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 50; Ito, J. Jap. Bot. 14 (1938) 439, fig., *quoad nomen solum*; Backer & Posthumus, Varenfl. Java (1939) 82, p.p.; Posthumus, Ann. Bot. Gard. Btzg vol. hors série (1944) 62; Iwatsuki, Acta Phytotax. Geobot. 18 (1959) 59, see note 5; Nayar & Kaur, Bull. Nat. Bot. Gard. Lucknow 88 (1964) 55, *quoad nomen solum*.—*Heteroneuron scalpturatum* Fée, Hist. Acrost. (1845) 95, pl. 56, p.p. ('*Heteroneuron*').—*Acrostichum scalpturatum* Kunze, Bot. Zeit. (1848) 103, p.p., non Lindman (1903) (= *B. serratifolia*, nec (Fée) Presl (1851) (= *Acrostichum aureum*).—*Chrysodium scalpturatum* Mettenius, Fil. Lips. (1856) 21, p.p., non Fée (1845) (= *Acrostichum aureum*), nec Ettingsh. (1864) (= *B. × lancea*).—*Leptochilus scalpturatus* C. Chr., Ind. Fil. (1906) 387, p.p.; v.A.v.R., Handb. Malayan Ferns (1908) 743, p.p.; C. Chr., Bot. Tidsskr. 32 (1916) 344.—*Campium scalpturatum* Copel., Philip. J. Sc. 37 (1928) 383, fig. 35; Backer & Posthumus, Nat. Tijdschr. Ned. Ind. 93 (1933) 162.—*Lectotype*: *Gaudichaud s.n.*, Philippines, Manila, xi-1836 (P; iso in B, 2 sh., BM, P, 2 sh.). See note 6. *Leptochilus reimersii* Rensch, Hedwigia 74 (1934) 249, pl. 7: fig. 2.—*Type*: *Rensch 636*, Lesser Sunda Is., Sumbawa, Batu Dulang (B). *Gymnopteris costata* (Presl) Bedd. var. *undulata* auct. non (Hooker) Christ: Christ, Bot. Tidsskr. 24 (1901) 109. *Leptochilus scalpturatus* (Fée) C. Chr. var. *undulatus* auct. non (Hooker) C. Chr.: C. Chr., Bot. Tidsskr. 32 (1916) 344. See note 3.

Rhizome up to 10 cm long, up to 10 mm thick, with 2 rows of leaves. Scales of the rhizome: index 1–10(–15), up to 7 by 1.5 mm, subclathrate, blackish. *Sterile leaves* pin-nate, 25–90 cm long; petiole 7–40 cm long, near the base 1.5–4 mm thick, with 5–9 vascular bundles; lamina index 1–3, widest below (to about) the middle, 20–55 by 7–30 cm, without the terminal segment 4–40, the terminal segment 9–20 cm long, herba-ceous to subcoriaceous, purplish or purplish-brown, with a bulbil subterminally on the terminal segment; rhachis not winged; pinnae alternate or opposite, 4–24, 15–50 mm apart; central pinnae index 3–7, widest about or below the middle, 5.5–17.5 by 1.5–4 cm, base ± symmetrical, narrowly to broadly cuneate, margin ± entire or finely serrate-crenate, without spines, apex acute to (long-)acuminate; the two lowermost pinnae 1–7 mm stalked; *terminal segment* usually subarticulate, sometimes joined to the rhachis, usually conform to the central pinnae, sometimes narrowly triangular and/or some-what prolonged; *venation pattern*: veins forming a network of a costal areole and one to few transverse rows of smaller distal ones, part of the areoles with few to several, mostly excurrent included free veins; see also fig. 43: c, d. *Fertile leaves* 30–70 cm long; petiole 15–50 cm long; lamina index 1–4, 10–40(–45) by 3–15 cm, without the terminal segment 4–35, the terminal segment 3–10 cm long; pinnae 4–26, up to 60 mm apart; central pinnae index 3–8, 3–9 by 0.6–1.5 cm, the two lowermost pinnae 0–6 mm stalked. *Sporangia* inserted mostly on and near the veins, either all over the lower surface, arranged acrostichoid, or along the margin only, arranged pteridoid.

BURMA. Moulmein: *Parish s.n.* (BM, K).

THAILAND. Northern: *Molesworth Allen 2164* (BM, SING, S-PA, US).—Northeastern: *Hennipman 3688* (L).—Southeastern: *Kerr 9751* (P); *Schmidt 891* (C).—Peninsular: *Seidenfaden 2123* (C).

VIETNAM. Cochinchina: *Pierre s.n.*, 1886 (P).



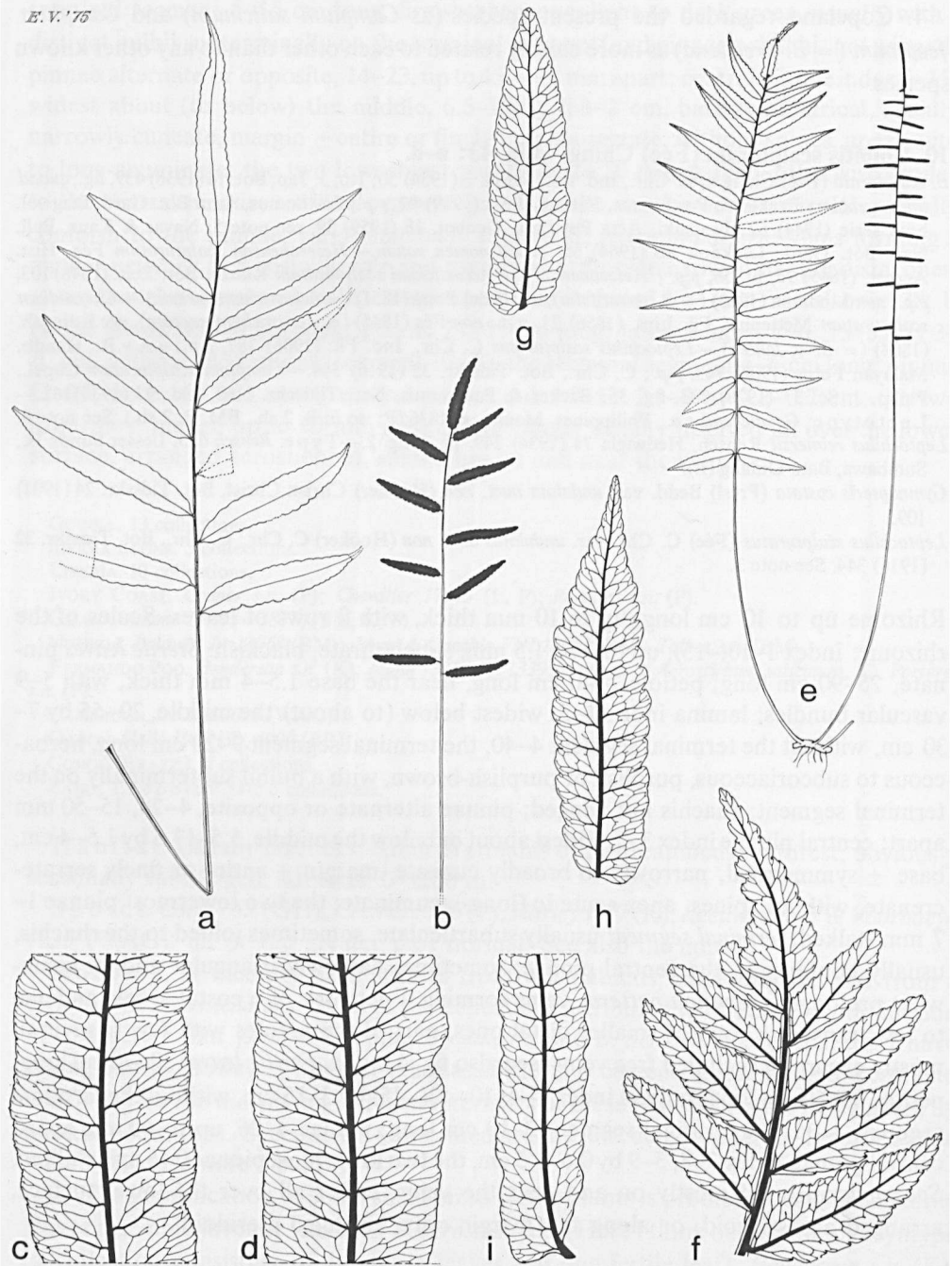


Fig. 43. a-d. *Bolbitis scalpturata*. a, b. fertile and sterile leaf resp.,  $\times 1/5$ ; c, d. venation pattern of sterile pinnae,  $\times 4/5$  (a, b. *Gaudichaud s.n.*, P, lectotype of *B. scalpturata*; c. *Mousset 562*, L; d. *Posthumus 1126*, BO).—e-j. *Bolbitis semicordata*. e. sterile and fertile leaf,  $\times 1/5$ ; f. terminal part of sterile leaf,  $\times 4/5$ ; g-i. Venation pattern of sterile pinnae,  $\times 4/5$  (e. *McIvor 4*, 's.n.', BM, paratype of *B. semicordata*; f. *Stocks & Law s.n.*, C; g. *Perrottet 1473*, L; h. *Wight 63*, B; i. *Anonymus s.n.*, iii-1838, BRI).

SUMATRA. Lampong Dist.: *Posthumus* 1103 (BO), 1126 (BO).

JAVA. East: 7 collections, presumably all from Mt. Tengger.

LESSER SUNDA Is. Bali: *Posthumus* 3708 (BO).—Sumbawa: *Rensch* 636 (type of *Leptochilus reimersii*).

Flores: *Schmutz* 3677A (L).

PHILIPPINES. Palawan: *Merrill* 7267 (MICH, P).—Luzon: 6 collections.

CELEBES. Southwest: *Sarasin* 1193 (P).—Salajar group: *Docters van Leeuwen* 1621 (BO, U).

**Habitat.** On rocks in (exclusively monsoon?) forest; twice recorded from limestone (Thailand, Celebes). Altitude: 0—1200 m.

**Spores.** *Allen* 2164 (BM), *Hennipman* 3688 (L), *Kerr* 9751 (P), *Posthumus* 1103 (BO): nearly all normal. *Allen* 2164 (S-PA), *Copeland* 249 (MICH), *Seidenfaden* 2123 (C), *Williams* 30 (US), 234 (UC), *Zollinger* 2162 (G, P): the greater part abnormal. *Gaudichaud s.n.* (lectotype of *Heteroneuron scalpturatum*) (BM, P, 2 sh.): spores (nearly?) all abnormal, mostly shrivelled, with many small, smooth, brown, accessory bodies inside each sporangium.

**Notes.** 1. A somewhat critical species which needs further study when more material is at hand. The venation pattern of the pinnae shows considerable variation and is usually locally  $\pm$  irregular; it may come near to that of *B. angustipinna* or *B. virens*. As in *B. costata* and *B. crispatula* the colour of the dried leaves is purplish. The scales of the rhizome are similar to those found in part of *B. crispatula* var. *copelandii*.

2. As regards the arrangement of the sporangia there occur two types of plants, one acrostichoid, the other  $\pm$  pteridoid. There is no distinct correlation between the arrangement of the sporangia and the geographical distribution. For instance, the specimens from Koh Chang (Thailand) and Palawan are  $\pm$  pteridoid whereas those from Luzon and Celebes are acrostichoid; both types of plants occur on Java.

3. The combination *Gymnopteris costata* var. *undulata* (Hooker) Christ was made to accommodate *Schmidt* 891. Christ referred to *Notholaena undulata* Wall. For full synonymy see *B. virens*. C. Christensen (1916) identified the same collection as follows: '*L. [eptochilus] scalpturatus* (Fée) C. Chr. Ind. [1906] 387 (excl. syn. omnibus, *Heteroneuron scalpturatum* Fée exceptum), var. *undulatus* var. nov. *Gymnopteris costata* var. *undulata* Christ, l.c. 109,—[Schmidt] (no. 891).' He thus excluded *Notholaena undulata* as a synonym of *Leptochilus scalpturatus*, at the same time recognizing it as a variety of that species; obviously an error.

4. *Allen* 2146 and *Hennipman* 3688 from northern Thailand agree with *B. virens* as regards the number of pinnae and more or less so as regards venation pattern.

5. Iwatsuki listed *B. scalpturata* as a doubtful species but obviously only had in mind to cite a certain collection from Formosa as a doubtful specimen as he reported at the same time not to have examined any specimen of *B. scalpturata* proper.

6. The lectotypification of *Heteroneuron scalpturatum* Fée. The relevant entry in Fée's original description runs as follows:

*Cyrtogonium costatum*? J. Smith, in *Journ. bot. Hook.*, IV, 1841 [nom. nud.].

*Acrostichum costatum*, Wall., *herb.*, n.<sup>o</sup> 26 [nom. nud.].—*Campium*, Presl, *Tentam. pterid.*, p. 239?

*Habitat in India occidentali* [orientali], *Nepaul, Sylhet* (Wallich); *Manilla* (Gaudichaud, *Voy. de la Bonite*, 1836).—*V.S. in herb. Bory et Mus. Par.*, ex Gaudichaud.

*Exsiccata*: Hugel, in *herb. imper. Vindob.*, n.<sup>os</sup> 2165, 2161, 4140, 4974.

The protologue consists of the following elements:

A. The material. Firstly, the specimens annotated by Fée (in his characteristic elegant handwriting) as '*Heteronevron scalpturatum*':

a. *Hügel* 2161, 2165, 4140, and 4974; all sterile (all in W). Referred to *B. × lancea*.

b. *Wallich* 26, a fertile leaf (W). The sheet bears also Wallich's original label and identification. It represents an isotype of *Acrostichum costatum* (= *B. costata*).

c. *Gaudichaud s.n.*, a sterile plant composed of three leaves (P). It is part of the lectotype of *B. scalpturata*.

Secondly, the material not annotated by Fée but also or possibly also studied by him.

a. *Wallich* 26 (P).

b. *Gaudichaud s.n.* (P, 2 sh.). At least one of these sheets, comprising both sterile and fertile material, was studied by Fée as will be elucidated below.

B. The synonyms. The addition, by Fée, of queries to the names of Wallich, J. Smith, and Presl has been variously interpreted. Presl (1851) thought that the queries indicated that Fée doubted if J. Smith and he himself had studied original material of *Wallich* 26: 'Species a me et a J. Smith enumerata ad specimina Wallichiana autographa constituta fuit, inde signa interrogationis a clar. Fée illata plane inutilia censenda sunt.' Copeland, however, concluded that the queries were added because: '... Fée was questioning the identity of *Campium costatum* and his own species. What he described and knew positively as *Heteronevron scalpturatum*, was Gaudichaud's plant from the Philippines, which must accordingly be regarded the type.' Christensen (1906) listed *Campium costatum* as a synonym of *Leptochilus scalpturatus*. Later (1916), after studying the material of both taxa at P, he ranked them as different species.

C. The illustration. The material Fée studied being known, it should be easy, accordingly, to indicate the material from which the lithograph was drawn. Christensen (1916), who studied original material at Paris, stated: 'The form illustrated by Fée is according to authentic specimens examined by me, collected near Manila by Gaudichaud; ...'. Christensen is incorrect as neither the material of Gaudichaud at Paris, nor that of other collections studied by Fée at Paris or Vienna comprise leaves matching those of the lithograph satisfactorily.

*The sterile leaf.* The drawing of the sterile leaf remained a mystery until I understood that the beautifully depicted sterile leaf is a composition of elements belonging to three different sterile leaves present on three different sheets in two different herbaria:

a. The petiole and the terminal segment are drawn from *Hügel* 4140.

b. The number of pinnae is taken from *Gaudichaud s.n.*, the specimen annotated by Fée as: '*Heteronevron scalpturatum*,—Espèce à faire figurer'.

c. The size and the venation pattern of the greater part of the pinnae are taken from a sterile leaf of *Gaudichaud s.n.*, a sheet not annotated by Fée. The length of the lamina without the terminal segment of the latter leaf is 25 cm whereas it is 19 cm in the drawing.

*The fertile leaf.* It cannot be indicated with certainty from which specimen the illustration of the fertile leaf was drawn; the fertile leaves of *B. costata* and *B. scalpturata*

may be much alike. The drawing shows a leaf with an incomplete petiole, the lamina 37 cm long (the terminal segment 9 cm long) and composed of 11 pinnae. These data neither correspond with *Gaudichaud s.n.* (P) nor with *Wallich 26* (W). The spores illustrated look normal; the outer surface shows low crests which are lacking in both *B. costata* and *B. scalpturata*. Fée described the spores as irregular.

*The rhizome.* The rhizome pictured presumably has been taken from a plant of Gaudichaud as a rhizome is lacking in all other collections cited by Fée.

D. The description. Fée (1845) used to give relevant details of the plants, such as sizes of leaves, pinnae, etc. in the entry on 'Dimensions'. In this entry the length of the sterile leaf is given as 50—60 cm. I found the length of the sterile leaves of Gaudichaud's plants to vary from 50—74 cm, whereas that of Hügel's collections is much greater. The length of the petiole of the sterile leaves is given by Fée as *c.* 15 cm. I found it to range between 17 and 32 cm in the leaves of Gaudichaud's collections, and to be 38 cm in *Hügel 4140* and in Fée's drawing. The length of the fertile leaf is given as 92 cm. The length of the fertile leaves of Gaudichaud's collections is *c.* 70 cm. The length can only have been taken from *Wallich 26* as all of Hügel's collections are sterile. It is further remarked that the measures given for the distance between two adjacent pinnae ('entre-noeuds') of the fertile and the sterile leaf have been interchanged.

Discussion. As regards the significance of the queries Fée added to the names of Wallich, J. Smith, and Presl, I share Copeland's conclusion but not his argumentation. Fée's had a very good knowledge not only of the material of Gaudichaud but also of that collected by Hügel and of *Wallich 26* (type of *Acrostichum costatum*). In Fée's description elements taken from each of these different collections can be indicated. As *Acrostichum costatum* is not included with certainty in Fée's eventual concept of *Heteroneuron scalpturatum*, the name *Heteroneuron scalpturatum* is not superfluous.

The discrepancies between the data provided in the description if compared with those of the drawing, have never been noticed before, presumably also since the quality of the text of Fée's *Histoire des Acrostichées* is much praised; the illustrations are generally regarded masterpieces, the aesthetic and scientific value of which are unquestioned. Amongst those misled in recent years is Pichi Sermolli (1969) who chose *Heteroneuron scalpturatum* as the type of *Heteroneuron* (the choice is against the Code, see the note to the genus) after careful examination of all species concerned and having taken into consideration '... the descriptions, the specimens studied and the illustrations given by Fée...'.  
.

#### 11. *Bolbitis semicordata* (Baker) Ching—Fig. 43 : e-j.

*B. semicordata* (Baker) Ching in C. Chr., Ind. Fil., Suppl. 3(1934) 50; Nayar & Kaur, Bull. Nat. Bot. Gard. Lucknow 88 (1964) 57, fig. 22, 36, 68, 71, 90.—[*Acrostichum virens* Hooker & Grev. var. *minus, fuscatum* Hooker, Sec. Cent. Ferns (1861) pl. 88, *nom. inval.* (art. 24 hence art. 32)]—*Acrostichum semicordatum* Baker in Hooker & Baker, Syn. Fil. (April 1868) 422, *p.p.*—*Poecilopteris semicordata* Bedd., Ferns Br. India (1868) pl. 270 (= Hooker, *op. cit.*, pl. 88).—*Gymnopteris semicordata* J. Smith, Hist. Fil. (1875) 138.—*Campium semicordatum* Copel., Philip. J. Sc. 37 (1928) 378, fig. 31, pl. 23, 24.—Lectotype (Copel., *op. cit.*, 'cotype'): *Law s.n.*, India, Concan (K; iso in B, C, GH, K, P, S-PA, W).

*B. semicordata* (Baker) Ching var. *incisa* Nayar & Chandra, Amer. Fern J. 54 (1964) 14, fig. 10–15; Nayar & Kaur, Bull. Nat. Bot. Gard. Lucknow 88 (1964) 61, fig. 37, 38, 91.—Type: *Chandra et al. LWG 95145*, India, Mysore, Castle Rock, Gudkewadi, 400 m alt., 9–xii–1962 (LWG; iso in LWG, 2 sh. '10–xii–1965'). *Gymnopteris contaminans* auct. non Bedd.: Bedd., Ferns Br. India, Suppl. (1876) 27, p.p.; Handb. Ferns Br. India (1883) 435, p.p., fig. 264; *ibid.*, Suppl. (1892) 105, p.p.

Rhizome up to 10 cm long, 3–5(–8) mm thick, with 2 rows of leaves. Scales of the rhizome: index 4–8, up to 6 by 1 mm, opaque to subclathrate, blackish. *Sterile leaves* pinnate, 15–70 cm long; petiole 5–40 cm long, near the base 1.5–2.5 mm thick, with 3–7 vascular bundles; lamina index 1–3, widest about or below the middle, 10–30 by 5–13 cm, without the terminal segment 8–23, the terminal segment 3–16 cm long, (firm-) herbaceous, light green to olivaceous, without or with 1(2) subterminal bulbil(s); rhachis narrowly winged; pinnae usually ± opposite, 12–29, up to 30 mm apart; central pinnae index (2–) 3–6, widest somewhat below the middle, 2.5–10 by 0.7–2.5 cm, base ± equally long-sided, oblique, its acroscopic side subcordate to broadly cuneate, its basispic side ± narrowly cuneate, margin usually ± entire or finely crenate-serrate, sometimes shallowly lobed, sometimes with teeth, apex acute or acuminate; the two lowermost pinnae deflexed, 0–3 mm stalked; *terminal segment* usually subarticulate and conform to the pinnae, sometimes joined to the rhachis and narrowly triangular; *venation pattern*: veins forming a costal areole, without or with few to several smaller distal areoles, usually with a short, excurrent, included, free vein on the distal part of the costal arch, see also fig. 43: g–i. *Fertile leaves* 20–60 cm long; petiole 10–45 cm long; lamina index 2–6, 7–30 by 2–13 cm, without the terminal segment 4–25, the terminal segment 1.5–7 cm long; pinnae 10–26, up to 30 mm apart, usually perpendicularly spreading; central pinnae index 5–30, 0.8–6.5 by 0.15–0.4 cm, the acroscopic side of the base sometimes auricled; the two lowermost pinnae 0–2 mm stalked. *Sporangia* inserted all over the lower surface or (in narrow pinnae) mainly on the costa, arranged acrostichoid.

Chromosomes.  $n = 41$ .

INDIA. Western Ghats. Mysore, Madras, and Kerala: 21 collections.

Habitat. Creeping (exclusively?) on rocks (often near streams) in forest. Presumably common. Altitude (but few records available): 400–1800 m.

Spores. *Barnes 545* (MICH), *Chandra et al. LWG 95145* (type of *B. semicordata* var. *incisa*), *Van Hardeveld & Van der Werff 323A* (L), *323B* (L), *Law s.n.* (lectot. dupl. of *Acrostichum semicordatum*, K): nearly all normal, perispore verrucate. *Hooker & Thomson s.n.* (BM), *Meebold 10905* (B), *Law s.n.* (isolectotype of *Acrostichum semicordatum*; 'Stocks, Law etc.', C): nearly all normal, large, perispore thick, usually ± spherical, sometimes with a few inconspicuous folds or verrucae.

Notes. 1. The retention of certain juvenile features has presumably played a decisive role in the origin of *B. semicordata*. See the general part.

2. Although a considerable part of the material fits the description, still a significant number of specimens is more or less divergent. Hybridization with the other members of this series, occurring in southern India, seems common. See also *B. × lancea*, *B. × prolifera*, and note 3.

3. From the study of herbarium material of the *Bolbitis* species growing in southern India, I got the impression that these may grow intermingled, that hybridization between them is common, and that vegetative propagation is markedly developed in all. This impression was confirmed by the following collections made by *Van Hardeveld & Van der Werff*, two students from Utrecht University. Their magnificent *Bolbitis* collections are all from one locality in Anaimalai Hills, State of Madras.

a. *Van Hardeveld & Van der Werff 323B* (L, 7 sh.) represents  $\pm$  typical *B. semicordata*. The shape of the terminal segment shows variation; it is either entire or near the base deeply lobed, or the base shows many odd pinnae. Both types of leaf are of comparable size and may occur on the same rhizome. Spores: the greater part normal, perispore verrucate. Referred to *B. semicordata*.

b. *Ibidem 323A* (L, 4 sh.). Leaves almost similar to those mentioned above but somewhat larger and with the terminal segment always deeply lobed and (much) prolonged, with a wing along the rachis of the upper half of the lamina only, the base of the central pinnae more or less oblique, the venation pattern rather irregular and rather resembling that pictured by Beddome for *Poecilopteris repanda* and *Gymnopteris contaminans*. Spores for the greater part normal, perispore verrucate. Referred to *B. semicordata* with misgivings.

c. *Ibidem 323* (L, 4 sh.). Plants rather agreeing with those of *323A* but larger, the rachis of the sterile leaves not winged, the venation pattern very irregular. Spores in part (the majority?) abnormal. As regards the outline of the leaves these plants agree with *Acrostichum terminans* (*Wallich 2168*). Referred to *B. × prolifera*.

4. One of the two isotypes of var. *incisa* studied has pinnae with a  $\pm$  entire margin. According to Nayar & Kaur both varieties grow intermingled.

5. The basionym was validly published during 1868 by either Baker or Beddome. As Beddome referred to '*Poecilopteris semicordata* (Baker)' I presume that Baker's publication was the earliest.

6. Posthumus (*Ann. Bot. Gard. Botz.*, vol. hors série 1944, 62) reported the present species from Sumba (Lesser Sunda Is.); I could not trace the reference collections.

## 12. *Bolbitis serrata* (Kuhn) Ching—Fig. 44.

*B. serrata* (Kuhn) Ching in *C. Chr., Ind. Fil., Suppl.* 3 (1934) 50.—*Acrostichum serratum* Baker in Hooker & Baker, *Syn. Fil.* (1868) 524, *nom. illeg., non* Lam. & Poiret (1796) (= *Grammitidaceae?*).—*Chrysodium serratum* Kuhn, *Linnaea* 36 (1869) 63.—*Leptochilus serratus* C. Chr., *Bot. Tidsskr.* 26 (1904) 289, fig. 2.—  
Type: *Spruce 4123*, Peru, San Martin, near Tarapoto, 1855–56 (K; iso in BM, GH, NY, P, US).

*Acrostichum serratifolium* auct. non Kaulf.: Hooker, *Spec. Fil.* 5 (1864) 253, *p.p.*

Rhizome up to 10(–15) cm long, 2–5 mm thick, with 2 rows of leaves. Scales of the rhizome: index 2–4, up to 2 by 1 mm, subclathrate, dark brown or blackish. *Sterile leaves* pinnate, 15–40 cm long; petiole 8–20 cm long, near the base 1–2 mm thick, with 3–5 vascular bundles; lamina index 1–3, widest about or below the middle, 8–20 by 3–12 cm, without the terminal segment 1.5–10, the terminal segment 6–12 cm long, herbaceous, light to dark green, without bulbils; rachis narrowly winged; pinnae usually alternate, 4–8, up to 25 mm apart; central pinnae index 3–6, straight, widest about the middle,

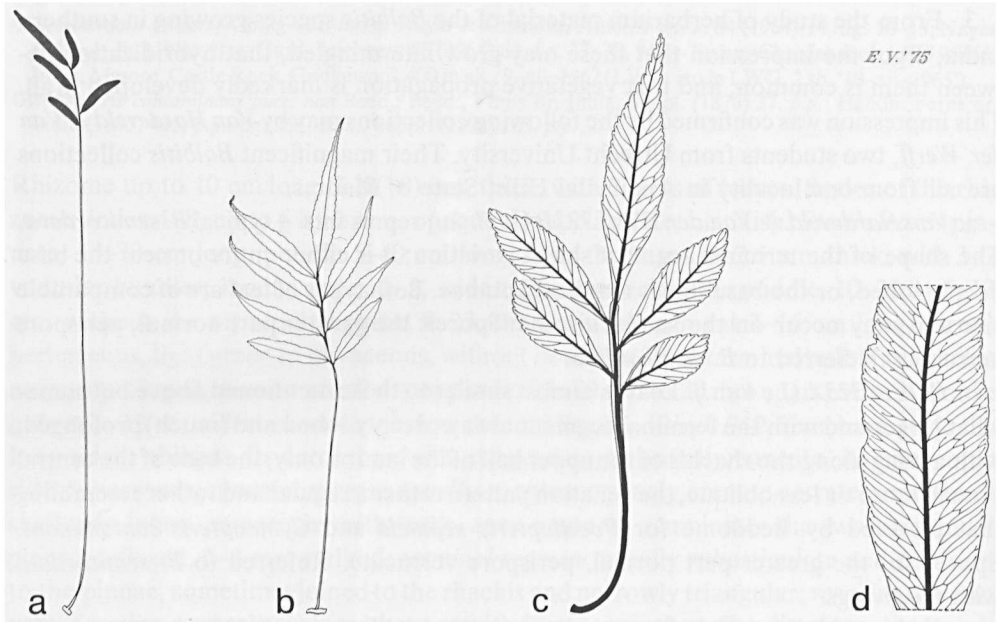


Fig. 44. *Bolbitis serrata*.—a, b. fertile and sterile leaf resp.,  $\times 1/5$ ; c. juvenile leaf,  $\times 4/5$  d. venation pattern of sterile pinna,  $\times 4/5$  (a. Spruce 4123, K; b, d. *ibid.*, P; c. Wurdack 2110, U).

3.5–12 by 0.8–2.5 cm, base symmetrical, narrowly cuneate or attenuate, margin entire or crenate-serrate (especially in the upper half), without spines, apex acute or acuminate; the two lowermost pinnae 0–1.5 mm stalked, otherwise conform to the central pinnae; *terminal segment* conform to the central pinnae, usually subarticulate, sometimes joined to the rachis; *venation pattern*: veins forming a costal areole, smaller distal areoles present or not, included free veins absent, see also fig. 44:d. *Fertile leaves* 22–50 cm long; petiole 15–35 (–40) cm long; lamina index 1–3, 7–12 by 3–6 cm, without the terminal segment 3–7, the terminal segment 3–6 cm long; pinnae 4–8, 10–25 mm apart; central pinnae index 3–8, 1.5–5.5 by 0.4–1 cm; the two lowermost pinnae 0.5–7 mm stalked. *Sporangia* mainly inserted on and near the veins, arranged acrostichoid.

COLOMBIA. Meta: Pinto & Bischler 223 (G).

ECUADOR. Antisana: Grubb *et al.* 1710A (NY, US).—Santiago-Zamora: Van der Werff 671 (L, U).

PERU. Amazonas: Wurdack 2110 (G, NY, S, U, UC, US).—Loreto: Killip & Smith 28495 (F, NY).—San Martin: Spruce 4123 (type of *Chrysodium serratum*).—Sine loc.: Godet *s.n.* (B).

**Habitat.** Creeping on rocks or in soil (in streambeds) in rain forest. Altitude: 250–700 m. Locally common (Wurdack 2110).

**Spores.** Wurdack 2110 (US): all normal, the perispore usually with few folds. Wurdack 2110 (UC): the greater part normal, the perispore usually with many folds.

*Killip & Smith 28495* (NY): in part (the majority?) abnormal, the perispore situated close to the exospore and provided with low rather sharp crests. *Spruce 4123* (GH, K): in part normal, the perispore with or without crest-like folds. See also note 2.

Notes. 1. A rather critical species closely related to and obviously derived from a fern like *B. serratifolia*. The differences between the present species and *B. serratifolia* are presumably caused by retention. A narrow wing along the rhachis is also found in *B. semicordata* which is otherwise different.

2. The collections from Colombia and Peru consist of relatively stout plants. The leaves are composed of 3–7 large pinnae, the venation pattern is intricate and resembles that found in part of *B. serratifolia*. Spores: *Pinto & Bischler 223* (G): the greater part normal, the perispore rather densely folded; *Grubb et al. 1710A* (US): sporangia filled with aborted spores and/or with aborted S. M. C.'s.

3. According to Baker, *Acrostichum serratum* should be near *Acrostichum raddianum* (= *Lomagamma guianensis*). Christensen thought *Leptochilus serratus* closely related to *Leptochilus guianensis* (= *Lomagamma guianensis*). In my opinion the juvenile leaves of *Lomagamma guianensis* and the mature leaves of *B. serrata* are good examples of parallel evolution.

### 13. *Bolbitis serratifolia* (Mertens ex Kaulf.) Schott—Fig. 45.

- B. serratifolia* (Mertens ex Kaulf.) Schott, Gen. Fil. (1835) ad tab. (13).—*Acrostichum serratifolium* Mertens ex Kaulf., Enum. Fil. (1824) 66; Hooker, Spec. Fil. 5 (1864) 263, p.p.; Baker in Hooker & Baker, Syn. Fil. (1868) 423, p.p.; in Martius, Fl. Brasil. 1, 2 (1870) 590, pl. 38: fig. 18–22; Lindman, Ark. Bot. 1 (1903) 252, fig. 8; Hedwigia 43 (1904) 311.—*Cyrtogonium serratifolium* J. Smith, Hook. J. Bot. 4 (1841) 154.—*Heteroneuron serratifolium* Fée, Hist. Acrost. (1845) 94, pl. 55: fig. iiiB ('*Heteroneuron*'); Fournier, Mex. Pl. I, 1 Crypt. (1872) 69, quoad nomen solum.—*Chrysodium serratifolium* Ettingsh., Denkschr. K. Ak. Wiss. M.-N. Kl. Wien 22 (1864) 57.—*Gymnopteris serratifolia* Diels in E. & P., Nat. Pfl. Fam. 1, 4 (1899) 201.—*Leptochilus serratifolius* C. Chr., Bot. Tidsskr. 26 (1904) 289, fig. 3.—Type: *Mertens s.n.*, Brazil, Rio de Janeiro (n.v.; B?, LE?).
- Acrostichum fraxinifolium* Presl in Presl & Presl, Deliciae Pragenses 1 (1822) 161, non R. Brown (1810) (= *Acrostichum spec.*).—*Poecilopteris fraxinifolia* Presl, Tent. Pterid. (1836) 242, pl. 11: fig. 1, 2; Hooker, Gen. Fil. (1842) pl. 81B; Presl, Epim. Bot. (1851) 173.—*Chrysodium fraxinifolium* Mettenius, Fil. Lips. (1856) 21, non Fée (1845) (= *Acrostichum speciosum* Willd.).—*Polybotrya fraxinifolia* Mettenius, Fil. Lechl. 2 (1859) 8.—Type: *Pohl s.n.*, Brazil, Guanabara, Rio de Janeiro, Corcovado Mts. (PR).
- Acrostichum triste* Vellozo in Arrabida, Fl. Fluminensis 11 (1836) pl. 90, s. descr.; Arch. Mus. Nac. Rio de Jan. 5 (1881) 453.—Type: *Vellozo s.n.*, Brazil, Guanabara, Rio de Janeiro, Mt. Nhamduaray, fert. (n.v.; R?).
- Poecilopteris crenata* Presl, Epim. Bot. (1851) 174; Underwood, Bull. Torr. Bot. Cl. 33 (1907) 603, fig. 15, 16.—*Leptochilus crenatus* C. Chr., Ind. Fil., Suppl. 1 (1913) 48.—*B. crenata* C. Chr., Ind. Fil. Suppl. 3 (1934) 47.—Type: *Mikan s.n.*, Brazil, Guanabara, near Rio de Janeiro (n.v.; PR?).
- Heteroneuron serratifolium* (Kaulf.) Fée var. *undulatum* Fée, Crypt. Vasc. Brésil 1 (1869) 18.—Syntypes (all from Brazil, Guanabara, Rio de Janeiro): *Martius s.n.* (n.v.; herb. Fée?), *Glaziou 953* (BR), 2422 (BR, P).
- Gymnopteris contaminoides* Christ, Ann. Cons. Jard. Bot. Genève 3 (1899) 32.—*Acrostichum contaminoides* Lindman, Hedwigia 43 (1904) 311.—*Leptochilus contaminoides* C. Chr., Bot. Tidsskr. 26 (1904) 294, fig. 6a–c.—Lectotype (C. Chr., op. cit.): *Balansa 2852*, Paraguay, near Paraguari, mountain ridge near Tchololo (B, BM, G, L, 3 sh., P).
- Acrostichum pervium* Lindman, Ark. Bot. 1 (1903) 254, pl. 8: fig. 7.—Type: *Mosén 75*, Brazil, Guanabara, Corcovado Mts. near Rio de Janeiro (S–PA; iso in GH, P, S, U, US).



*Acrostichum curupirae* Lindman, Hedwigia 43 (1904) 311.—*Leptochilus curupirae* C. Chr., Bot. Tidsskr. 26 (1904) 296, fig. 7.—*B. curupirae* Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 48.—Type: *Exp. 1. Regnell A 3061 Lindman leg.*, Brazil, Mato Grosso, Mato do Curupira, ster. (S-PA; iso in BM, S, US). *Leptochilus serratifolius* (Kaulf.) C. Chr. f. *caudatus* C. Chr., Bot. Tidsskr. 26 (1904) 290.—Syntypes (both from Brazil, *s. loc.*): *Langsdorff s.n.* (B), *Mendoza 1368* (B). *Leptochilus mexicanus* Christ, Bull. Herb. Boiss. II, 7 (1907) 414.—*B. mexicana* C. Chr., Ind. Fil., Suppl. 3 (1934) 49.—Type: *Munch 19*, Mexico, Chiapas, San Christobal (iso in US; no specimens traced by me at P, nor by Dr. Farron, in litt., at BAS). *Leptochilus contaminoides* (Christ) C. Chr. var. *lobulatus* Christ, Fedde Rep. 6 (1909) 351.—Type: *Hassler 10377a*, Paraguay, Sierra de Amambay (*n.v.*; *Hassler 10377, Rojas leg.*, at B, K, L, P = *B. serratifolia*). *Leptochilus serratifolius* (Kaulf.) C. Chr. var. *prolifer* Rosenst., Fedde Rep. 20 (1924) 93.—Type: *Von Luetzelburg 7180*, Brazil, Espirito Santo, Rio Doce (M). *B. maguirei* Maxon & Morton, Bull. Torr. Bot. Cl. 75 (1948) 71.—Type: *Maguire 24744*, Surinam, Table Mt., near Augustus Falls (US; iso in NY, U). *Lomaria bredemeijeriana* auct. non Klotzsch:Klotzsch, Linnaea 20 (1847) 346. *Acrostichum scalpturatum* auct. non (Féé) Kunze: Lindman, Ark. Bot. 1 (1903) 253, pl. 8: fig. 9.

Rhizome up to 10 cm long, up to 15 mm thick, with 2 rows of leaves. Scales of the rhizome: index 2–4, up to 6 by 2 mm, subclathrate, dark brown or blackish. *Sterile leaves* pinnate, (35–) 50–>135 cm long; petiole 18–50 cm long, near the base 2–5 mm thick, with 5–13 vascular bundles; lamina index 1–3, usually widest below, sometimes about the middle, (20–) 25–90 by 10–40 cm, without the terminal segment 23–65 cm, the terminal segment 10–30 cm long, herbaceous, usually light to dark green, sometimes with a purple tinge or purplish, with a (primordium of a) bulbil subterminally on the terminal segment (and the pinnae); rhachis not winged; pinnae alternate or opposite, 9–30 (–42), up to 60 mm apart; central pinnae index 3–10 (–14), widest usually about (to below) the middle, 7.5–28 by 2–4 cm, base usually equally long sided, either somewhat asymmetrical with its basiscopic side orbicular and sometimes narrower than the broadly attenuate or truncate acroscopic side, or symmetrical, (narrowly) cuneate to subcordate, margin usually entire, sometimes crenate-serrate or shallowly lobed, with or without indistinct teeth, sometimes somewhat crisped, apex acute to (long-) acuminate; *terminal segment* usually joined to the rhachis, sometimes subarticulate, usually ± conform to the central pinnae, sometimes either prolonged or with some odd pinnae at the base; *venation pattern*: veins forming a costal areole and few to many smaller distal areoles, without or with few to many, excurrent, included, free veins; see also fig. 45: d–k. *Fertile leaves* 50–100 (–140) cm long; petiole 30–60 (–80) cm long; lamina index 2–6, 17–65 by 4–15 cm, without the terminal segment 13–60, the terminal segment 2–10 cm long; pinnae 12–30 (–45), up to 70 mm apart; central pinnae index 2–9 (–12), 2–11 by 0.6–1.5 cm; the lowermost pinnae 0–11 mm stalked. *Sporangia* mainly situated on and near the veins, less so on the tissue between the veins, arranged acrostichoid.

MEXICO. Chiapas: *Ghiesbrecht 409* (GH); *Munch 19* (type of *Leptochilus mexicanus*).

COSTA RICA. San José: *Skutch 3084* (US).

PANAMA. *Pittier 5336* (US), *5608* (US); *Williams 881* (NY, US).

COLOMBIA. Magdalena: *Bennett 18* (US); *Grant 10899* (US); *H. H. Smith 2522* (BM, F, G, GH, K, MICH, MO, NY, P, S, UC, US, W).—Cundinamarca: *Grant 10463* (US); *Stübel 673* (B), *690* (B), *695* (B).—Meta: *Alston 7654* (BM); *Idrobo 478* (US); *Philipson & Idrobo s.n.* (BM).—Sin eloc.: *Joad s.n.* (K); *Moritz 129* (BM, fragm.).

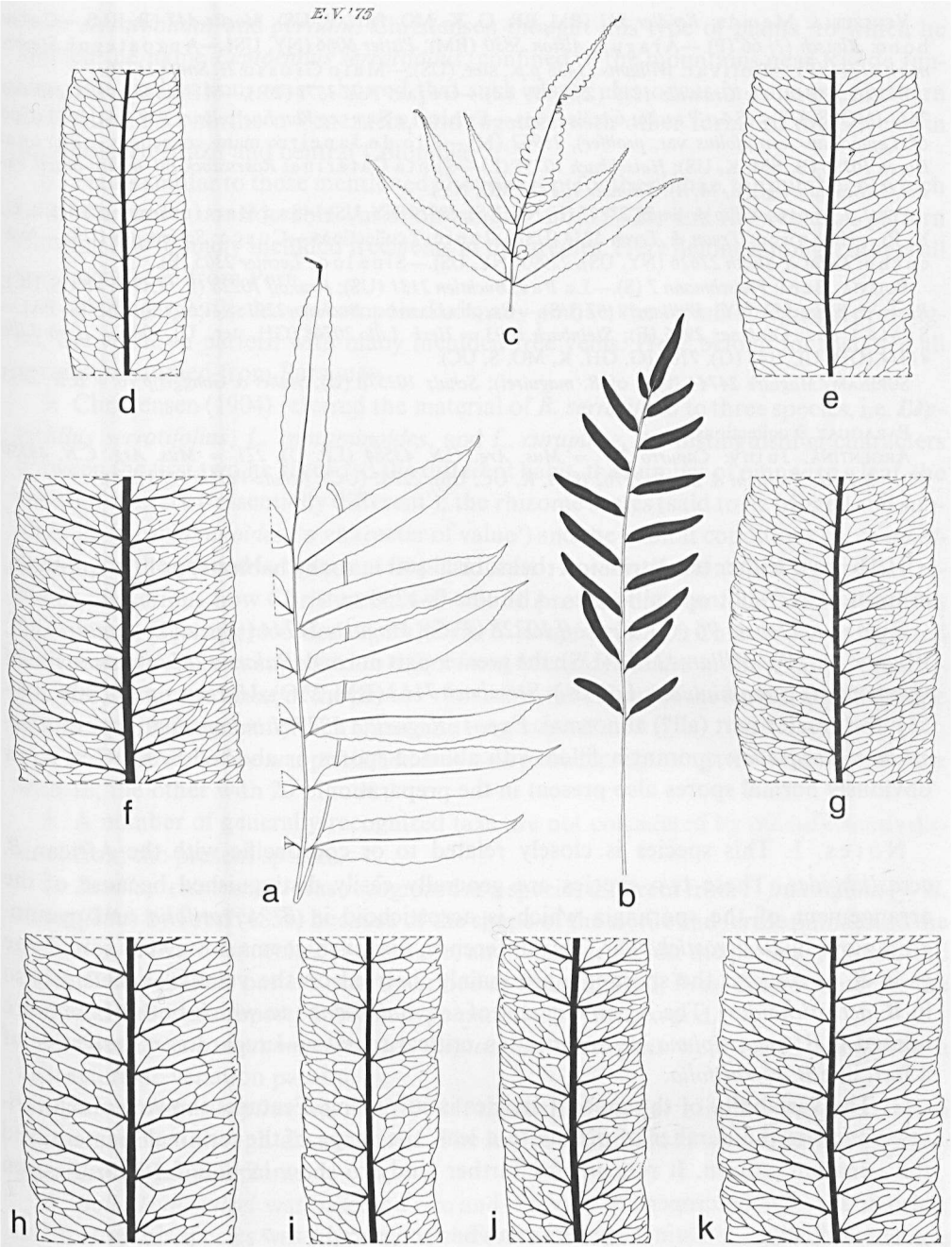


Fig. 45. *Bolbitis serratifolia*.—a, b. sterile and fertile leaf resp.,  $\times 1/5$ ; c. terminal part of sterile leaf,  $\times 1/5$ ; d–k. venation pattern of sterile pinnae,  $\times 4/5$  (a, b. Wagner 76, P; c. Skutch 3084, K; d. *Anonymus s.n.*, L; e. Pohl & Schott s.n., L; f. L. B. Smith 1214, US; g. Krukoff 10228, UC; h. Spruce 4736, P; i. Eyerdam & Beetle 22762, US; j. *ibid.*, UC; k. Schunke A 215, US).

VENEZUELA. Merida: *Fendler 311* (BM, BR, G, K, MO, fert., P, US); *Moritz 447* (B, BM).—Carabobo: *Klotsch (?) 66* (P).—Aragua: *Alston 5830* (BM); *Pittier 6066* (NY, US).—Anzoategui: *Steyermark 61144* (F).—Bolivar: *Williams 11438 p.p.*, ster. (US).—Mato Grosso: *H. Smith 16* (P).

BRAZIL. Para: *De Granville 1219* (Z), *1499* (Z).—Goiás: *Pohl 1871* (BR).—Minas Gerais: *Macedo 2437* (MO, S, US).—São Paulo: 6 collections.—Espírito Santo: *Von Luetzelburg 929* (M), *7180* (type of *Leptochilus serratifolius* var. *prolifer*), *18962* (M).—Rio de Janeiro: many collections.—Paraná: *Dusén 10136* (B, BM, K, US); *Hatschbach 10755* (L).—Santa Catarina: *Rosenstock Fil. austro-brazil. exsicc. 5* (*Schmalz leg.*) (B, M, S); *Schmalz 101* (F, MO, NY).

PERU. Loreto: *Killip & Smith 27797* (F, NY, US), *28919* (NY, US).—San Martín: *Spruce 4726* (BR, G, K, P).—Huanuco: *Tryon & Tryon 5234* (US).—Junín: 7 collections.—Cuzco: *Scolnik 877* (US).—Ayaacucho: *Killip & Smith 22626* (NY, US), *22995* (NY, US).—Sine loc.: *Lechler 2305* (B).

BOLIVIA. Beni: *Fleischmann 7* (S).—La Paz: *Buchtien 2131* (US); *Krukoff 10228* (F, G, GH, MO, S, UC); *Rusby & White 552* (NY); *Williams 1187* (US).—Cochabamba: *Buchtien 2221* (S-PA, US), *2223* (S-PA).—Santa Cruz: *Cárdenas 2996* (F); *Steinbach 1093* = *Herb. Lillo 20768* (GH, ster., U), *3003* = *Herb. Lillo 41314* (GH, U), *7143* (G), *7163* (G, GH, K, MO, S, UC).

SURINAM. *Maguire 24744* (type of *B. maguirei*); *Schulz 10257a* (U); *Stahel & Gonggrijp 76* = *B.W. 2933* (U).

PARAGUAY. 9 collections.

ARGENTINA. Jujuy: *Capurro 217* = *Mus. Arg. C.N. 43584* (LP, U), *271* = *Mus. Arg. C.N. 43580* (U).—Salta: *Eyerdam & Beetle 22762* (GH, K, UC, US), *22765* (UC); *Schulz-Varela 5179* (LP).

**Habitat.** Either terrestrial (on rocks, or in soil in rocky habitats) or low-epiphytic, in tropical and subtropical forests. Altitude: 0–1250 m.

**Spores.** *Fiebrig 96* (G), *Krukoff 10228* (F, S), *Maguire 24744* (type of *B. maguirei*, U), *Wagner s.n.* (P), *Williams 1187* (US): the greater part normal. *Balansa 2852* (lectotype of *Gymnopteris contaminoides*, L, 3 sh.), *Steinbach 7163* (BM, MO), *Martius s.n.* (L, 908.206–55): the greater part (all?) abnormal. *Exp. 1. Regnell A 2337* (*Lindman leg.*; type of *Acrostichum curupirae*): sporangia filled with aborted spores or aborted S. M. C.'s, a few obviously normal spores also present in the preparation.

**Notes.** 1. This species is closely related to or conspecific with the African *B. acrostichoides*. These two species are generally easily distinguished because of the arrangement of the sporangia which is acrostichoid in *B. serratifolia* and gymno-grammoid in *B. acrostichoides*. This difference, however, seems not a very sound one as in *B. serratifolia* the sporangia are mainly inserted on the veins (+ exclusively so in *B. acrostichoides*). The Asian element of ser. *Bolbitianae* to which both of them are related is *B. angustipinna*. *B. serrata* —a critical species—I regard as a derivative of a fern like *B. serratifolia*.

2. The variability of the present species is surprising. Features showing much variation include the number of pinnae to a leaf, the shape of the terminal segment, and the venation pattern. It remains for further study to show in how far hybridization also adds to the heterogeneity.

The following, ± distinct elements can be recognized.

a. Plants small; sterile leaves 50–90 cm long, pinnae 10–20, usually 14 to a leaf, terminal segment conform to the central pinnae, venation pattern fully anastomosed and without or with but few included excurrent free veins ('more accidentally than normally', Christensen, 1904). These plants agree with the original descriptions of *Acrosti-*

*chum serratifolium* and *pervium*. Christensen thought this type of plants, to which he applied the name *Leptochilus serratifolius*, confined to the mountains near Rio de Janeiro. But explorations since showed that such plants also occur in Panama, northern Colombia, and northern Venezuela, and together with other forms of this species in southeastern Brazil and central Colombia.

b. Plants similar to those mentioned above except for the pinnae, the number of which to a leaf shows considerable variation ranging from 9–28, and the venation pattern showing few to many included free veins in the areoles. Here belong amongst others all specimens seen from Peru.

c. Plants large; the leaves composed of many pinnae, the terminal segment prolonged, the venation pattern with many included free veins. Here belong for instance all specimens studied from Paraguay.

3. Christensen (1904) referred the material of *B. serratifolia* to three species, i.e. *Leptochilus serratifolius*, *L. contaminoides*, and *L. curupirae*. As distinguishing characters between the first two he recorded the different habit, the number of pinnae to a leaf, the venation pattern ('essentially different'), the rhizome scales (said to be fringed and subulate in *L. contaminoides*, 'a character of value') and the habitat conditions (*L. contaminoides*: 'on the ground in the dense tropical forest'; *L. serratifolius*: 'open ground'). It remains mysterious how Christensen was able to provide data on habitat conditions as such data are scantily recorded on the labels. *L. curupirae*, which Christensen recognized with some doubt, was supposed to differ from *L. contaminoides* in the shape of the lamina, the margin and base of the pinnae, the scales, the colour of the leaves, and the shape of the terminal segment which should be long-stipitate.

4. *Acrostichum triste* was published only on a plate representing two fertile leaves, one with 18, the other with 20 pinnae.

5. A number of generally recognized taxa are not considered by me sufficiently distinct from the present species.

a. *Poecilopteris crenata* was recognized as a species different from *P. fraxinifolia* (= *B. serratifolia*) by Presl (1851) because of the shape of the sterile and fertile pinnae and the presence of ovate-lanceolate, acuminate, and ciliate scales on the petiole, rhachis, and costa. The venation pattern was described as anastomosed; Presl did not describe the included free veins reported for the type material by Underwood.

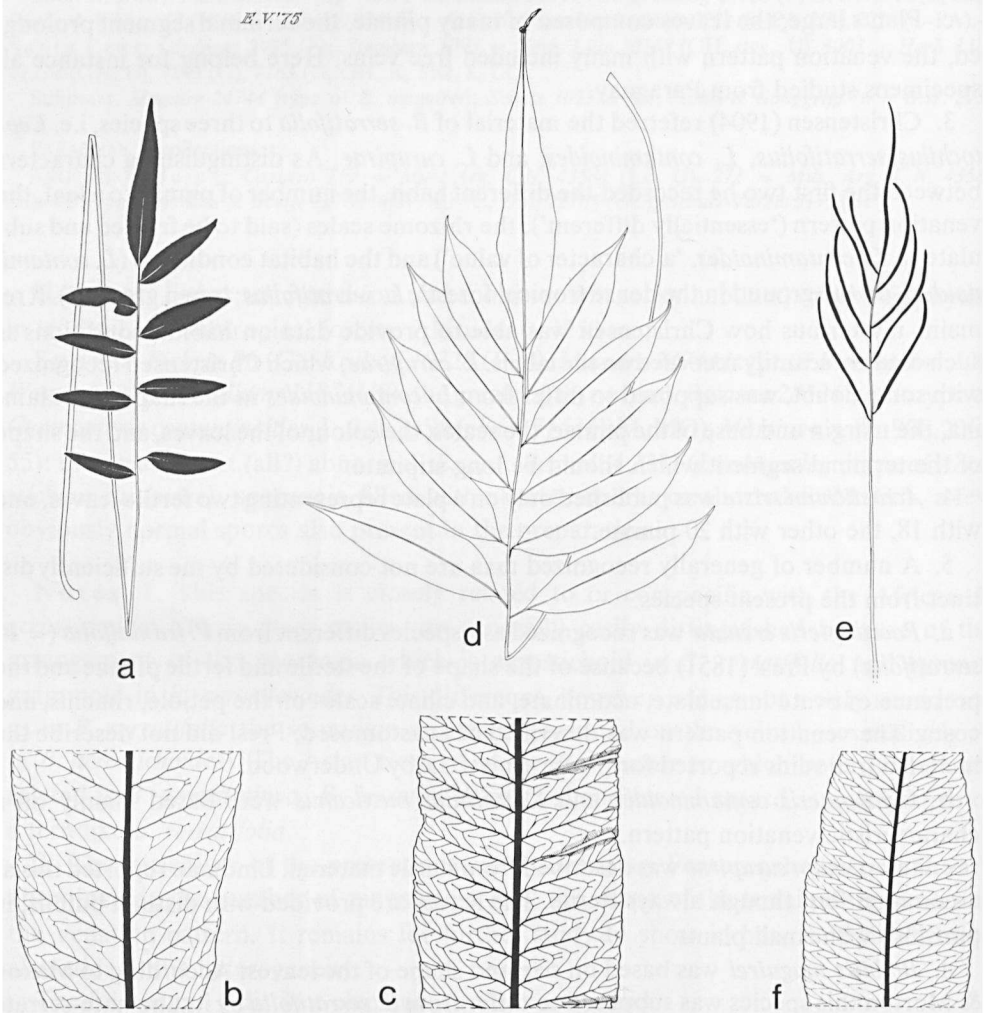
b. *Gymnopteris contaminoides* and *Leptochilus mexicanus* were based mainly on a characteristic venation pattern.

c. *Acrostichum curupirae* was described from sterile material. Lindman reported this as a common fern though always sterile. The leaves are provided with distinct bulbils, in part also with small plants.

d. *Bolbitis maguirei* was based on size and shape of the leaves. According to Maxon & Morton this species was supposed to differ from *B. serratifolia* by its uncinately-serrate rather than crenately-lobate pinnae, and from *B. crenata* (= *B. serratifolia*) by its venation pattern which should not show included free veins. Included free veins are, however, rather common in the large sterile leaf of the holotype, far less so in a small leaf of the isotype in NY.

**14. *Bolbitis subcrenata* (Hooker & Grev.) Ching—Fig. 46, 47.**

*B. subcrenata* (Hooker & Grev.) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 50; Backer & Posthumus, Varenfl. Java (1939) 80, see note 4; Nayar & Kaur, Bull. Nat. Bot. Gard. Lucknow 88 (1964) 63, fig. 2–6, 11, 14, 23, 32, 41, 43, 46, 50–52, 59, 72, 73, 76–80, 83–85, 92, 93.—*Acrostichum subcrenatum* Hooker & Grev., Ic. Fil. (1829) pl. 110 (excellent); Clarke, Trans. Linn. Soc. Bot. 1 (1880) 581, p.p.—*Campium subcrenatum* Presl, Tent. Pterid. (1836) 39; Hooker, Gen. Fil. (1842) pl. 80; Copel., Philip. J. Sc. 37 (1928) 391, fig. 42; Backer & Posthumus, Nat. Tijdschr. Ned. Ind. 93 (1933) 158, excl. specim.—*Cyrtogonium subcrenatum* J. Smith, Hook. J. Bot. 4 (1841) 154.—*Heteroneuron subcrenatum* Fée, Hist. Acrost. (1845) 93, *quoad nomen solum* ('*Heteroneuron*').—*Poecilopteris subcrenata* Moore, Ind. Fil. (1857) xx.—*Gymnopteris subcrenata* Bedd., Handb. Ferns Br. India (1883) 437, fig. 265.—*Leptochilus subcrenatus*



**Fig. 46. *Bolbitis subcrenata*.**—a–c. var. *subcrenata*. a. fertile leaf,  $\times 1/5$ , b, c. venation pattern of sterile pinnae,  $\times 4/5$ .—d–f. var. *prolifera*. d, e. sterile and fertile leaf resp.,  $\times 1/5$ ; f. venation pattern of sterile pinna,  $\times 4/5$  (a. Thwaites CP 1313, P; b. Wall '60/107', BO; c. Thwaites CP 1313, B (sh. 1); d, e. Anonymus s.n. iii-1838, BRI; f. Wight, Pen. Ind. Or. 3175, L).

C. Chr., Ind. Fil. (1906) 388.—Type: *Emerson s.n.*, eastern Ceylon, near Saffragan (n.v.; not at K, GL).  
*Acrostichum proliferum* Hooker, Ic. Pl. 7 (1844) pl. 681, 682, *nom. illeg.*, *non* Bl. (1828) (= *B. repanda*).—*Campium proliferum* Presl, Epim. Bot. (1851) 170.—*Polybotrya prolifera* Mettenius, Fil. Hort. Lips (1856) 24, pl. 2: fig. 11, *nom. illeg.*, *non* Bory (1833) (= *B. × prolifera*).—*Poecilopteris hookeriana* Moore, Ind. Fil. (1857) xx; Thwaites, Enum. Pl. Zeyl. (1864) 380.—Type: *Falconer s.n.*, southern India, Bombay (K).  
 [*Acrostichum terminans* Wall., Cat. (1830) no. 2168, *nom. nud.*, *quoad nomen solum*]—*Poecilopteris terminans* [Moore, Ind. Fil. (1857) 15, *nom. nud.*, *quoad nomen solum*] Bedd., Ferns S. India (1864) 68, pl. 203.—Le cotype: Beddome's plate drawn from a specimen from southern India.  
*Campium bradfordii* Copel., Philip. J. Sc. 37 (1928) 390, fig. 40, pl. 28.—*B. bradfordii* Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 47.—Type: *Bradford s.n. (1954?)*, s. loc. ('Ceylon') (UC, 267415).  
*Acrostichum virens auct. non* Hooker & Grev.: *auct. p.p.*

Rhizome up to 10 cm long, up to 12 mm thick, with 2 (3) rows of leaves. Scales of the rhizome: index 2–8, up to 7 by 1.5 mm, opaque to subclathrate, brownish or blackish. Sterile leaves 40–125 cm long, pinnate; petiole 10–55 cm long, near the base 2–4 mm thick, with 5–13 vascular bundles; lamina index 1–3 (–5), widest below (to about) the middle, 20–75 by 8–30 cm, without the terminal segment 3–30, the terminal segment 15–50 cm long (possibly longer), ± subcoriaceous, light to dark green, with a (primordium of a) bulbil subterminally on the terminal segment (and pinnae); rhachis usually not winged, sometimes inconspicuously winged in the upper half of the lamina; pinnae alternate or opposite, 3–19, up to 45 mm apart, central pinnae index 2–6, widest usually about, sometimes below the middle, 6–21 by 2.5–4 (–5.5) cm, base almost symmetrical, usually narrowly cuneate or attenuate, margin ± entire or finely serrate or (bi) crenate-serrate especially in the upper half, not crisped, without teeth or spines, apex acute to (long-)acuminate; the two lowermost pinnae 1–8 mm stalked; *terminal segment* joined to the rhachis or subarticulate, either conform to the pinnae, or prolonged, or flagelloid; *venation pattern*: the corresponding tertiary veins of two adjacent secondary veins fusing in pairs, the costal arch with usually one, sometimes 2 or 3 excurrent included free veins, or with a small, medially situated, distal areole, the distal arches usually with one medially situated excurrent free vein (± meniscioid), see also fig. 46: b, c, f. Fertile leaves 30–120 cm long; petiole 18–90 cm long; lamina index 1–4, 7–45 by 4–20 cm, without the terminal segment 3–30, the terminal segment 4–20 cm long; pinnae 3–17, up to 60 mm apart; central pinnae index 4–50, 2.5–16 by 0.2–1.4 cm; the two lowermost pinnae 1–8 (–13) mm stalked. *Sporangia* inserted mainly on and near the veins, arranged acrostichoid.

Chromosomes.  $2n = c. 82$  (var. *subcrenata*).

Distribution. Southern India and Ceylon. See fig. 47.

Habitat. See the varieties.

Notes. 1. A clear-cut species easily recognized because of its venation pattern reminiscent of that of the meniscioid ferns. The species is closely related to *B. virens*.

2. Hooker, in his *Species Filicum*, merged both *Acrostichum subcrenatum* and *A. proliferum* into *A. virens* which in Hooker's construction is a receptacle of different elements. See *B. virens*, note 2. Beddome had eventually (1883) a good concept of this species. Copeland (1928) included northern India in the 'sure geographical range' of *Campium subcrenatum* and described a pauci-pinnate form from Ceylon as *Campium bradfordii*.

3. Backer & Posthumus (1939) reported this fern from West Java, near Tjikoja and on Mt. Salak. Posthumus based himself on a sterile specimen which he found mixed with *Zollinger 2162* (= *B. sculpturata*), but which he thought to be part of *Zollinger 884* (= *B. repanda*; 884x = *B. heteroclita*). The herbarium material at Bogor is labelled 'Zollinger 2162, 4856 H. Bog.' and has the locality 'Modjopahit' (East Java, south of Surabaya). This specimen shows a venation pattern characteristic for the typical variety of the present species. Therefore, and also as the sheet bears a record number of the garden, I suppose that the material was cultivated at Bogor, and originated from Ceylon.

4. Beddome, who validly published *Poecilopteris terminans*, erroneously referred to *Acrostichum terminans* Wall. The latter was based on *Wallich 2168* which represents *B. × prolifera*.

#### KEY TO THE VARIETIES

- 1a. Fertile pinnae index 3–10; terminal segment of sterile leaves usually conform to the central pinnae but (much) prolonged, sometimes conform or subflagelloid.  
*Ceylon* . . . . . a. var. **subcrenata**
- b. Fertile pinnae index > 10; terminal segment of sterile leaves usually flagelloid, sometimes (mostly in small-sized leaves) conform to the central pinnae. *Southern India* . . . . . b. var. **prolifera**

**a. var. subcrenata—Fig. 46: a—c.**

*B. subcrenata* (Hooker & Grev.) Ching.—*Campium bradfordii* Copel.

Sterile leaves: lamina 20–50 cm long, without the terminal segment 3–23, the terminal segment 15–33 cm long; *venation pattern*: if two veins arise distally on the costal arch, these may fuse into a small areole with a short excurrent vein distally. *Fertile leaves*: lamina 7–45 cm long, without the terminal segment 3–30, the terminal segment 4–13 cm long; central pinnae index 4–10, 2.5–8 by 0.6–1.4 cm.

CEYLON. *Ballard 1525* (K); *Bradford s.n.* (type of *Campium bradfordii*); *Ferguson 210* (US), *s.n.* (GH); *Leschenault s.n.* (P); *Skinner s.n.* (K); *Thwaites CP 1313* (B, BM, BO, GH, K, L, P, W); *Wall 10562* (BO), '60/107' (GH).

**Habitat.** No information on the labels available. According to Manton & Sledge (op cit.) this taxon should occur 'in the wetter forests of the central and southern provinces among dense undergrowth.'

**Spores.** *Ballard 1525* (K): all normal. See also the note.

**Note.** Some of the collections show some irregularities in the venation pattern. Hybridization, presumably with *B. angustipinna*, seems to occur. Examples: *Thwaites CP 1313* (B, sh. 1); spores: all shrivelled, *ibid.* (B, sh. 2) the greater part abnormal, in part normally shaped.

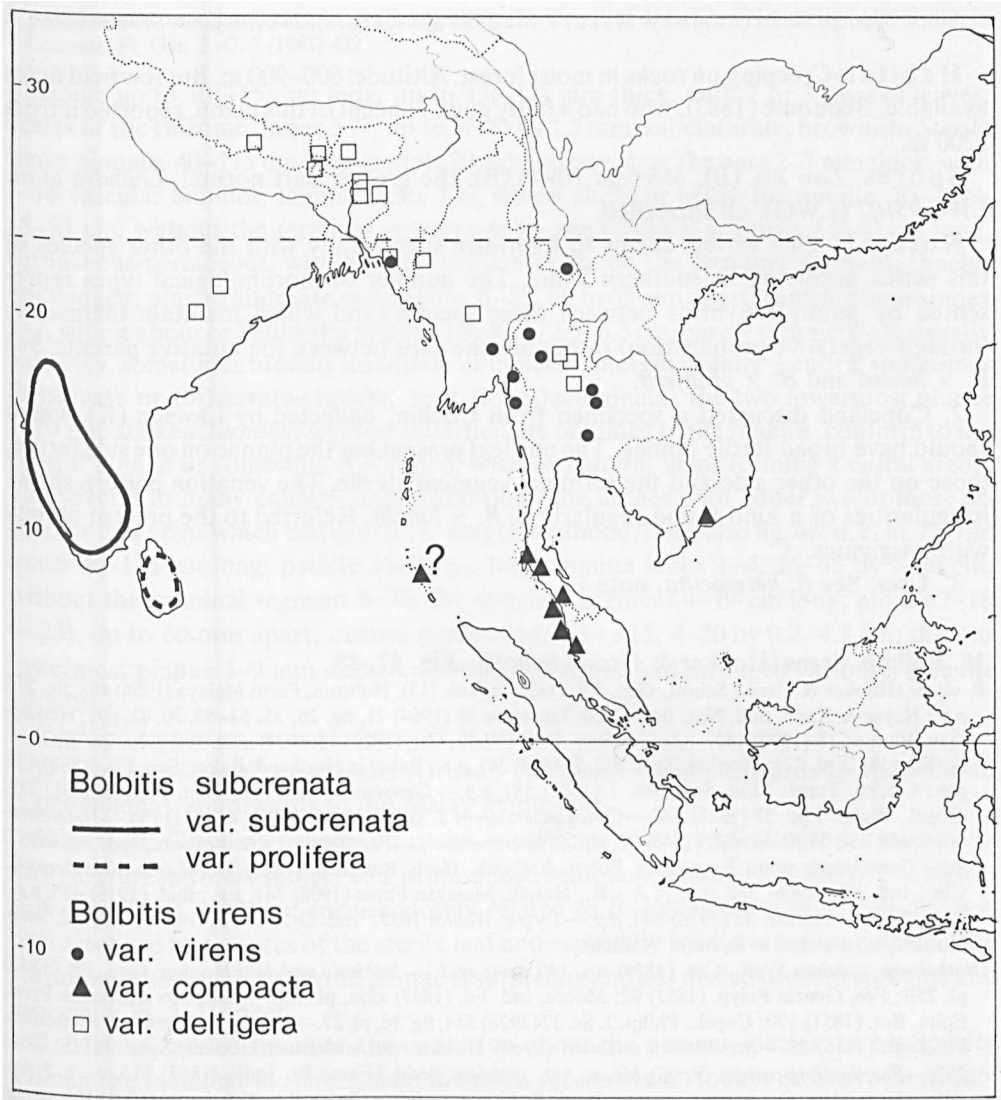


Fig. 47. Distribution of *Bolbitis subcrenata* and *B. virens*.

**b. var. prolifera** (Hooker) Hennipman, *stat. nov.*—Fig. 46: d—f.

Basionym: *Acrostichum proliferum* Hooker, Ic. Pl. 7 (1844) pl. 681, 682.—*Poecilopteris terminans* Bedd.

Sterile leaves: lamina 30–75 cm long, without the terminal segment 7–30, the terminal segment 23–50 cm long, possibly (much) longer; *venation pattern*: if two or three veins arise distally on the costal arch, these run free and excurrent. *Fertile leaves*: lamina 12–35 cm long, without the terminal segment 5–20, the terminal segment 6–20 cm long; pinnae index 10–50, 4–16 by 0.2–0.6 cm.



INDIA. Western Ghats (Bombay, Mysore, Madras and Kerala): 24 collections. See also note 2.

**Habitat.** Creeping on rocks in moist forest. Altitude: 600–900 m. But few field notes available. Beddome (1883), who had a fairly good concept of this taxon, reported it from 1200 m.

**Spores.** *Law s.n.* (B), *Meebold 10906* (B): the greater part normal. *Chandra et al. LWG 95102* (LWG): all shrivelled.

**Notes.** 1. This variety seems to hybridize successfully with the other species of this series occurring in southern India. The number of morphological types represented by putative hybrids between these species (and which maintain themselves through vegetative propagation) rather fills the gaps between the putative parents. See *B. × lancea* and *B. × prolifera*.

2. Copeland discussed a specimen from Cochin, collected by Lawson (K), which should have broad fertile pinnae. The one leaf present has the pinnae on one side fertile, those on the other side and the terminal segment sterile. The venation pattern shows irregularities of a kind found regularly in *B. × lancea*. Referred to the present variety with misgivings.

3. Uses. See *B. heteroclita*, note 11.

## 15. *Bolbitis virens* (Hooker & Grev.) Schott—Fig. 47, 48.

*B. virens* (Hooker & Grev.) Schott, Gen. Fil. (1835) *ad tab.* (13); Holttum, Ferns Malaya (1954) 468, fig. 275, *p.p.*; Nayar & Kaur, Bull. Nat. Bot. Gard. Lucknow 88 (1964) 71, fig. 26, 35, 53–58, 70, 82, *p.p.*; Hennipman, Blumea 18 (1970) 149.—*Acrostichum virens* [Wall., Cat. (1829) no. 1033, *nom. nud.*] Hooker & Grev., Ic. Fil. (1831) pl. 221; Hooker, Spec. Fil. 5 (1864) 261, *p.p.*; Baker in Hooker & Baker, Syn. Fil. (1868) 420, *p.p.*; Clarke, Trans. Linn. Soc. Bot. 1 (1880) 581, *p.p.*—*Campium virens* Presl, Tent. Pterid. (1836) 239; Copel., Philip. J.Sc. 37 (1928) 388.—*Cyrtogonium virens* J. Smith, Hook. J. Bot. 4 (1841) 154.—*Heteroneuron virens* Fée, Hist. Acrost. (1845) 93, *p.p.* ('*Heteroneuron*').—*Poecilopteris virens* Moore, Ind. Fil. (1857) xx.—*Gymnopteris virens* Keyserling, Polyp. & Cyath. Herb. Bungeani (1873) 33.—*Leptochilus virens* C. Chr., Ind. Fil. (1906) 388, *p.p.*; v.A.v.R., Handb. Malayan Ferns (1908) 741, *p.p.*; *ibid.* (1916) 435, *p.p.*; C. Chr., Bot. Tidsskr. 32 (1916) 344, *p.p.*—Type: *Wallich 1033*, 'Ind. Or.', Tovag (not traced) (K, herb. Hooker; no material in K, herb. Wallich).

[*Notholaena undulata* Wall., Cat. (1829) no. 140, *nom. nud.*]—*Jenkinsia undulata* Hooker, Gen. Fil. (1842) pl. 75B; Fée, Genres Polyp. (1852) 92; Moore, Ind. Fil. (1857) xxiii, pl. 10B.—*Campium undulatum* Presl, Epim. Bot. (1851) 170; Copel., Philip. J. Sc. 37 (1928) 384, fig. 36, pl. 27.—*Lomariopsis undulata* Mettenius, Fil. Lips. (1856) 22.—*Acrostichum costatum* (Presl) Hooker var. *undulatum* Hooker, Spec. Fil. 5 (1864) 262.—*Poecilopteris costata* (Presl) Moore var. *undulata* Bedd., Ferns Br. India (1865) 115, pl. 115, *p.p.* ('*Poecilopteris*').—*Gymnopteris costata* (Presl) Bedd. var. *undulata* Christ, Bot. Tidsskr. 24 (1901) 109, *quoad nomen solum*.—*Leptochilus scalpturatus* (Fée) C. Chr. var. *undulatus* C. Chr., Bot. Tidsskr. 32 (1916) 344, *quoad nomen solum*; Bonap., Notes Ptérid. 7 (1918) 103.—*B. undulata* Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 50.—Type *p*: *Wallich 140*, Burma, Martaban (north of Moulmein) (K, the fertile leaf only; iso in BM).—*Poecilopteris costata* (Presl) Moore var. *deltigera* Bedd., Ferns Br. India (1865) 114, pl. 114 ('*Paecilopteris*').—*Meniscium deltigerum* [Wall., Cat. (1829) no. 59, *nom. nud.*] Clarke, Trans. Linn. Soc. Bot. 1 (1880) 572.—*Campium deltigerum* Copel., Philip. J. Sc. 37 (1928) 387, fig. 38.—*B. deltigera* C. Chr., Ind. Fil., Suppl. 3 (1934) 48; Tagawa & Iwatsuki, Southeast Asian Studies 5 (1967) 91.—*B. virens* (Hook. & Grev.) Schott var. *deltigera* Hennipman, Blumea 18 (1970) 149.—Type: *Wallich 59*, Nepal, between Katmandu and Bhimpey, above Mt. Chesapang (K, herb. Wallich; iso in K).

*B. virens* (Hooker & Grev.) Schott var. *compacta* Hennipman, Blumea 18 (1970) 149.—Type: *Tagawa et al. T. 6802*, Peninsular Thailand, Nakhon Sri Thammarat, Trang, Khao Chong, 600–1100 m alt. (L; iso in KYO).

*Gymnopteris contaminans* *auct. non* Bedd.: Bedd., Ferns Br. India, Suppl. (1876) 27, *p.p.*; Handb. Ferns Br. India, Suppl. (1892) 105, *p.p.*

*Leptochilus scalpturatus* *auct. non* (Fée) C. Chr.: C. Chr., Ind. Fil. (1906) 387, *p.p.*

*B. prolifera* auct. non (Bory) C. Chr. & Tardieu-Blot: Tardieu-Blot & C. Chr., Not. Syst. 7 (1938) 102; in Lecomte, Fl. Gén. I.-C. 7 (1941) 432.

Rhizome up to 10(-15) cm long, up to 13(-17) mm thick, with 2 or 3 rows of leaves. Scales of the rhizome: index 3-7, up to 5(-8) by 1.5 mm, subclathrate, brownish. *Sterile leaves* pinnate, 40-115 cm long; petiole 20-65 cm long, near the base 2-7 mm thick, with 7-14 vascular bundles; lamina index 1-3, widest about or below the middle, 20-75 by 15-50 cm, without the terminal segment 4-50, the terminal segment 14-40 cm long, herbaceous-coriaceous, with a bulbil subterminally on the terminal segment; rhachis not winged; pinnae alternate or opposite, 6-22, up to 65 mm apart; central pinnae index 3-7, widest about or below the middle, 10-30 by 2.5-6.5 cm, base  $\pm$  symmetrical, usually narrowly, sometimes broadly attenuate or cuneate, margin usually  $\pm$  entire, sometimes (bi)serrate or (bi)serrate-crenate, apex (long-)acuminate; the two lowermost pinnae 1-10 mm stalked; *terminal segment* subarticulate or joined to the rhachis, conform to the central pinnae or somewhat prolonged; *venation pattern*: veins forming a costal areole and several to many equally large distal ones, the arches with either two or more ex-current free veins which end in a thickening (hydathode?); see also fig. 48: d, e, m. *Fertile leaves* 40-125 cm long; petiole 25-70 cm long; lamina index 1-4, 15-65 by 7-30 cm, without the terminal segment 6-55, the terminal segment 4-19 cm long; pinnae 7-18 (-23), up to 60 mm apart; central pinnae index 3->15, 4-20 by 0.2-4.5 cm; the two lowermost pinnae 1-9 mm stalked. *Sporangia* inserted and arranged variously (see the varieties).

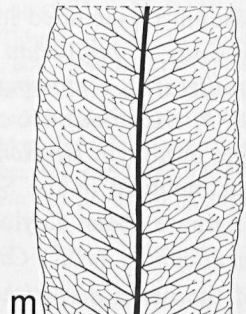
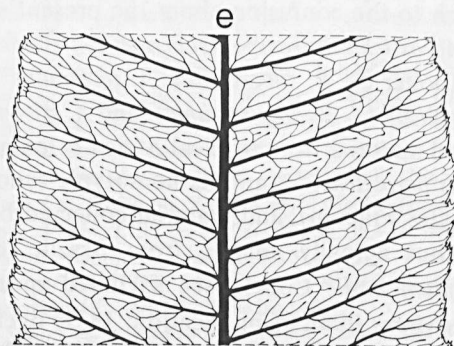
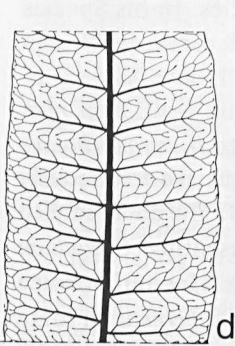
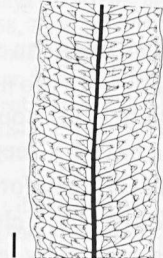
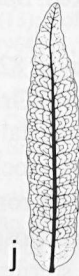
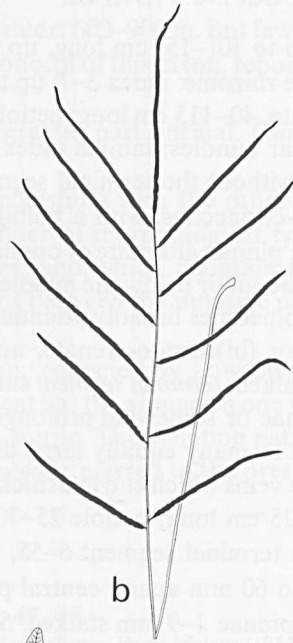
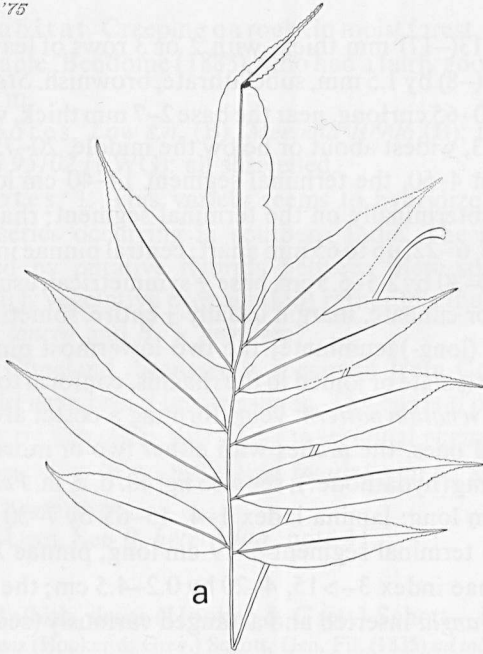
Chromosomes.  $n = 41$ ;  $2n = 82$  (f. *virens*).

Distribution. Central India (Orissa), Northeast India eastwards to Indo-China (Cochinchina), southwards to the Malay Peninsula.

Habitat. Creeping usually on rocks, sometimes in soil and often near streams in (dry) evergreen forest subject to a pronounced seasonal climate. Altitude: 200-1100 m.

Notes. 1. A clear-cut species closely related to *B. subcrenata* and *B. costata*. It is characterized by features of the sterile leaf and especially by the venation pattern. The variation in shape of the fertile pinnae is surprising and has misled the fern students and especially W. J. Hooker.

2. Hooker added much to the confusion about the present species. In his Species Filicum he included in *Acrostichum virens*: *A. subcrenatum* Hooker & Grev. (= *B. subcrenata*), *A. proliferum* Hooker (= *B. subcrenata*), *A. terminans* Wall. nom. nud. (= *B. prolifera*), *A. contaminans* Wall. (= *B. angustipinna*), and *A. crispatum* Wall., nom. nud. (= *B. crispatula*). He cited material from tropical Africa belonging to *B. acrostichoides* (the basionym *Hemionitis acrostichoides* and its homotypic synonyms are erroneously not included in the Species Filicum), and material collected by G. Gardner, said to originate from Ceylon but actually coming from Brazil, representing *Cyclodium meniscioides* (syn.: *Campium molle* Copel.; see excluded species). Hooker's choice of the name *Acrostichum virens* (date of publication: 1831) over *A. subcrenatum* (date of publication: 1829) is against the present Code. In the Species Filicum *Meniscium deltiigerum* Wall., nom. nud. (= *B. virens* var. *deltigera*) and *Jenkinsia undulata* Hooker (= *B. virens* f. *undulata*) were given varietal status under *Acrostichum costatum* (= *B. costata*).



KEY TO INFRASPECIFIC TAXA

- 1a. Fertile pinnae either  $\pm$  gymnochromoid or with irregular patches of sporangia on the veins between the secondary veins and near the margin. c. var. *deltigera*
- b. Fertile pinnae either fully acrostichoid or with sporangia along the margin only . . . . . 2
- 2a. Sporangia along the margin only . . . . . a.2. var. *virens* f. *undulata*
- b. Sporangia all over the lower surface . . . . . 3
- 3a. Central pinnae index  $> 15$  . . . . . a.1. var. *virens* f. *virens*
- b. Central pinnae index 3–8 . . . . . b. var. *compacta*

a. var. *virens*—Fig. 47; 48: a—h.

*B. virens* (Hooker & Grev.) Schott.—*Jenkinsia undulata* Hooker.

Fertile leaves: central pinnae index 4— $> 15$ , 5.5—20 by 0.2—1.5 cm. *Sporangia* inserted either all over the lower surface, or on the veins near the margin only; arranged either acrostichoid or  $\pm$  pteridoid.

Distribution. See the formae.

Habitat. See the species.

a.1. f. *virens*—Fig. 48: a—g.

*B. virens* (Hooker & Grev.) Schott.

Fertile leaves: central pinnae index  $> 15$ , 8–20 by 0.2–0.9 cm. *Sporangia* arranged acrostichoid.

CHINA. Yunnan: Wang 78807 (A).

BANGLADESH (Chittagong). Clarke 19840 (K).

BURMA. Southern. *Beddome s.n.* (K); *Dickason 6711* (BM, GH, L, MICH, US).

THAILAND. Northern: 20 collections, mainly from Doi Chieng Dao and Doi Suthep.—Northeastern: 6 collections, from Phu Luang and Phu Kradeng.—Southwestern. Khao Yai: *Van Beusekom 164* (L).

Habitat. See the species.

Spores. *Hennipman 3136* (L), *3159* (L): in part (the majority?) normal.

Fig. 48. *Bolbitis virens*.—a–h. var. *virens*.—a–g. f. *virens*. a, b. sterile and fertile leaf resp.,  $\times 1/5$ ; c. aberrant fertile pinna,  $\times 1/5$ ; d, e. venation pattern of sterile pinnae,  $\times 4/5$ ; f, g. venation pattern of fertile pinnae,  $\times 4/5$ .—h. f. *undulata*. fertile pinna,  $\times 1/5$ .—i, j. var. *compacta*. i. fertile pinna,  $\times 1/5$ ; j. venation pattern of fertile pinna,  $\times 4/5$ .—k–m. var. *deltigera*. k. fertile pinna,  $\times 1/5$ ; l. venation pattern of fertile pinna,  $\times 4/5$ ; m. venation pattern of sterile pinna,  $\times 4/5$  (a. f. *Hennipman 3159*, L; b. *Van Beusekom 164*, L; c, g. *Hennipman 3136*, L; d. *Hansen & Smitinand 11836*, C; e. *Tagawa et al. T 932*, L; h. *Dickason 7014*, US; i. *Tagawa et al. T 6802*, L; j. *Henderson SF 29084*, BO; k. *Mann s.n.*, xii-1888, US; l, m. *Dickason 7766*, US).

**Note.** One sheet of *Hennipman 3136* (L) has a fertile leaf with pinnae of intermediate shape: the basal and apical part acrostichoid, the central part  $\pm$  pteridoid.

**a.2. f. undulata** (Hooker) Hennipman, *stat. nov.*—Fig. 48: h.

*Jenkinsia undulata* Hooker.—For references see the species.

Fertile leaves: central pinnae index 4–8, 5.5–11 by 1–1.5 cm; sporangia arranged  $\pm$  pteridoid.

BURMA. Tenasserim. Moulmein: 5 collections. Thaton Dist.: *Dickason 7014* (BM, GH, US).

THAILAND. Northern: *Winit 1034* (SING).

**Habitat.** See the species.

**Spores.** *Lobb s.n.* (K): the greater part normal. *Winit 1034* (SING): abnormal, mostly shrivelled.

**Note.** *Wallich 141* (K) is presumably mislabelled; it has the identification '*Taenitis blechnoides*' and the locality Penang in Wallich's handwriting.

**b. var. compacta** Hennipman—Fig. 47; 48: i, j.

*B. virens* (Hooker & Grev.) Schott var. *compacta* Hennipman.

Fertile leaves: central pinnae index 3–8, 4–11.5 by 0.8–2 cm; sporangia inserted all over the lower surface, arranged acrostichoid.

VIETNAM, Cochinchina: *Chevalier 2544* (*Poilane leg.*) (P); *Matthew 34* (K).

THAILAND. Peninsular: *Haniff & Nur SF 3830* (SING); *Hansen & Smitinand 11836* (C); *Murton 10* (K); *Seidenfaden 2123* (BM, C); *Tagawa & Yamada T 214* (BKF); *Tagawa et al. T 6802* (type of *B. virens* var. *compacta*).

MALAY PENINSULA. Kedah: *Ridley 15707* (BM, K, SING).—Selangor: *Holtum s.n.* (BO, K); *Matthew s.n.* (K); *Ridley 1682* (SING).—Langkawi I.: *Henderson SF 29084* (BO, K); *Robinson 6358* (K).—Penang: *Curtis 628* (MICH, fragm., SING, US).

INDIA. Nicobar Is. (probably): *Helper s.n.* (B).

**Habitat.** See the species.

**Spores.** *Curtis 628* (SING), *Tagawa et al. T 6802* (holotype of *B. virens* var. *compacta*): the greater part normal. *Chevalier 2544* (P): the greater part abnormal, mostly normally shaped. *Henderson SF 29084* (BO): abnormal, mostly shrivelled.

**c. var. deltigera** (Bedd.) Hennipman—Fig. 47; 48: k–m.

*Poecilopteris costata* (Presl) Moore var. *deltigera* Bedd.

Fertile leaves: central pinnae index 3–5, 5–17 by 1.5–4.5 cm; sporangia inserted on the veins and near the margin only, arranged non-acrostichoid.

BANGLADESH. Chittagong: *Clarke 19841* (K).

NEPAL. *Wallich 59* (type of *Meniscium deltigerum*).

BHUTAN. *Griffith s.n.* (B, BM, K, S-PA).

SIKKIM. 7 collections.

INDIA. Darjeeling: *Clarke 9090* (K), 36582 (G, K, P); *Gamble s.n.* (P); *Warburg 988* (B).—Assam: 5 collections.—Orissa: *Mooney 675* (K); *Sanyal 2639* (K).

BURMA. Chin Hills: *Dickason 7766* (BM, GH, MICH, US).—Southern Burma: *Dickason 7029* (BM, GH, MICH).

THAILAND. Northern: *Tagawa & Fukuoka T 2110* (L, US); *Winit 59* (SING), 1034 (BKF).

Habitat. See the species.

Spores. *Mann s.n.* (L, 908.206–47), *Winit 59* (SING): the greater part normal. *Tagawa & Fukuoka T 2110* (L): in part (the majority?) normal.

#### 4. Series *Egenolfianae* Hennipman, *ser. nov.*

*Egenolfia* Schott, Gen. Fil. (1835 or 1836) pl. *s.n.* (16), *typo incl., pro genere.*

Terrestrial or low-epiphytic. *Rhizome* usually short-creeping and stout, in one species (*B. major*) long-creeping and slender, with 2 or 3 (4) rows of leaves, sclerenchyma strands usually present. Scales of the rhizome up to 7.5 mm long. *Leaves* usually close together, in one species (*B. major*) spaced. Sterile leaves pinnate (to bipinnate); petiole with usually 5–7, in one species (*B. major*) with 12–18 vascular bundles; lamina with one ± spherical, usually subterminal, in one species (*B. rhizophylla*) ± terminal bulbil; pinnae 14–90, the margin with spines corresponding to the most distal acroscopic tertiary vein of each secondary vein; terminal segment triangular; venation: secondary veins (slightly) prominent on either side, tertiary veins slightly prominent or immersed; *venation pattern*: veins free. Fertile leaves pinnate (to tripinnate). *Spores* with either a smooth, cristate or cristate-undulate perispore, or with a reticulate ± cristate perispore.

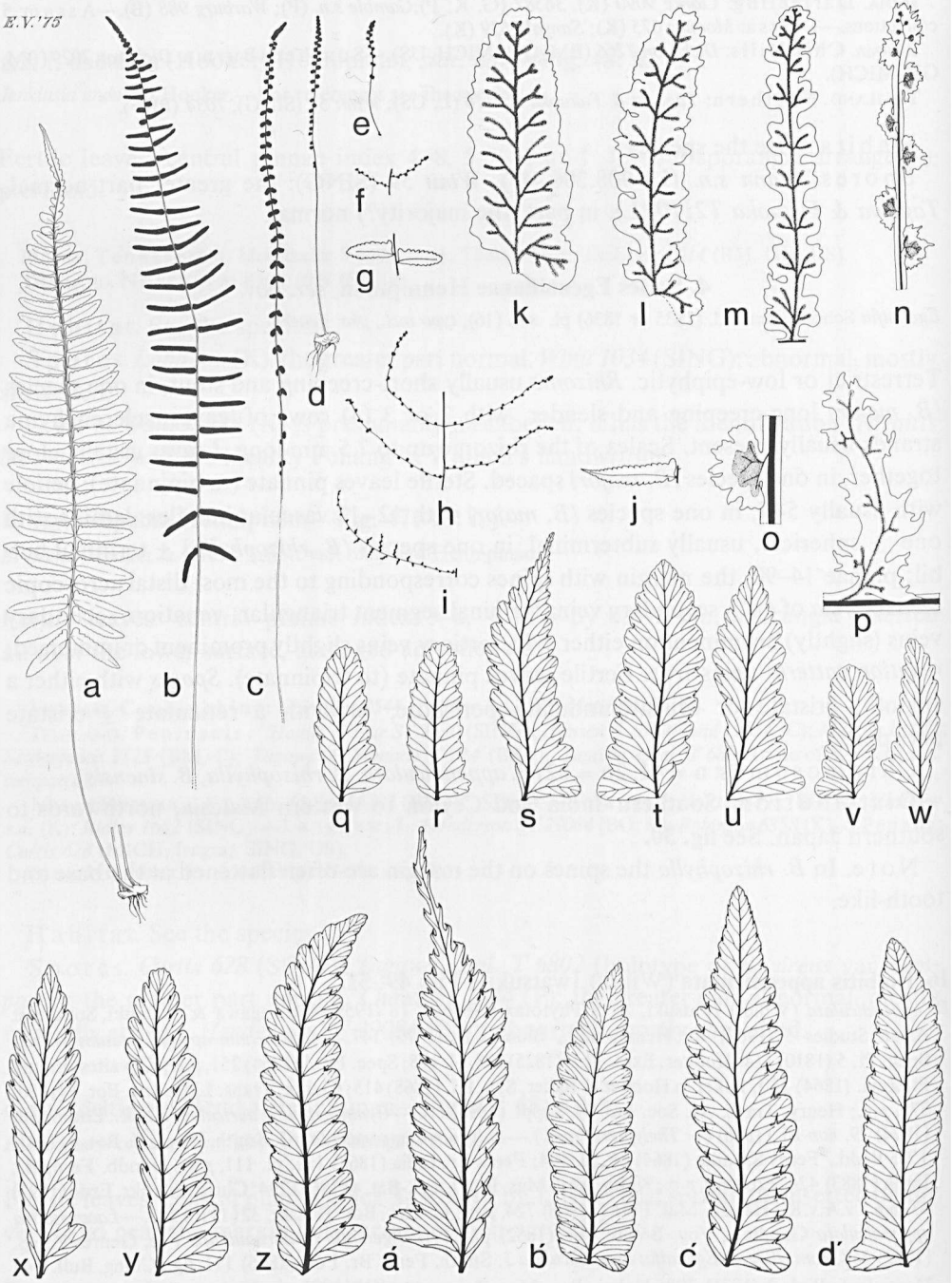
Chromosomes:  $n = 41$ ,  $2n = 82$  (*B. appendiculata*, *B. rhizophylla*, *B. sinensis*).

Distribution. Southern India and Ceylon to western Malesia, northwards to southern Japan. See fig. 30.

Note. In *B. rhizophylla* the spines on the margin are often flattened at the base and tooth-like.

#### 16. *Bolbitis appendiculata* (Willd.) Iwatsuki—Fig. 49–51.

*B. appendiculata* (Willd.) Iwatsuki, Acta Phytotax. Geobot. 18 (1959) 48; Tagawa & Iwatsuki, Southeast Asian Studies 5 (1967) 90; Hennipman., Blumea 18 (1970) 147.—*Acrostichum appendiculatum* Willd., Spec. Pl. 5 (1810) 114; Hooker, Exot. Fl. 2 (1825) 108, pl. 108; Spec. Fil. 5 (1864) 251, *p.p.*; Thwaites, Enum. Pl. Zeyl. (1864) 380; Baker in Hooker & Baker, Syn. Fil. (1868) 415; Clarke, Trans. Linn. Soc. Bot. 1 (1880) 577, *p.p.*; Henry, Trans. As. Soc. Jap. 24, Suppl. (1896) 116.—*Gymnogramma auriculata* Kaulf., Enum. Fil. (1824) 79, non Bl. (1828) (= *Thelypteris spec.*).—*Polybotrya appendiculata* J. Smith, Hook. J. Bot. 4 (1841) 150; Bedd., Ferns S. India (1864) 66, pl. 194; Ferns Br. India (1865) 111, pl. 111, *p.p.*; Handb. Ferns Br. India (1883) 424, excl. var. *p.p.*; Kuhn, Ann. Mus. Bot. Lugd.-Bat. 4 (1869) 294; Christ, Farnkr. Erde (1897) 43, *p.p.*; v.A.v.R., Handb. Mal. Ferns (1908) 724, *p.p.*; C. Chr., Bot. Tidsskr. 32 (1916) 343.—*Lacaussadea appendiculata* Gaudich., Voy. Bonite Bot. (1852) pl. 119.—*Egenolfia gaudichaudiana* Fée, Genres Polyp. (1852) 358, *nom. illeg.*—*Egenolfia appendiculata* J. Smith, Ferns Br. For. (1866) 111, fig.; Ching, Bull. Fan Mem. Inst. Biol. 2 (1931) 308; Nakai, Bot. Mag. Tokyo 47 (1933) 169, *p.p.*; Backer & Posthumus, Nat. Tijdschr. Ned. Ind. 93 (1933) 153; Tardieu-Blot & C. Chr., Not. Sys. 7 (1938) 98; Backer & Posthumus,



- Varenfl. Java (1939) 84, fig. 14; Tardieu-Blot & C. Chr. in Lecomte, Fl. Gén. I.-C. 7 (1941) 427; Holttum, Ferns Malaya (1954) 459, fig. 270; Copel., Fern Fl. Philip. (1960) 266; Nayar & Kaur, Bull. Nat. Bot. Gard. Lucknow 100 (1964) 17, fig. 9, 25; DeVol & Kuo in Fl. Taiwan 1 (1975) 350, pl. 123.—Type: *Klein 912*, 'Ind. Or.', iii—1803 (B, herb. Willdenow 19551).
- Polybotrya vivipara* Hamilton ex Hooker, Exot. Fl. 2 (1825) 107, pl. 107; Sprengel, Syst. Veg. 4 (1827) 33.—*Egenolfia vivipara* C. Chr., Ind. Fil., Suppl. 3 (1934) 102; Tardieu-Blot & C. Chr. in Lecomte, Fl. Gén. I.-C. 7 (1941) 423; Nayar & Kaur, Bull. Nat. Bot. Gard. Lucknow 100 (1964) 35, fig. 1, 2, 6, 8, 11, 12, 17, 32.—*Egenolfia appendiculata* (Willd.) J. Smith var. *vivipara* Deb, Taxon 14 (1965) 110, p.p.—*B. hookeriana* Iwatsuki, Acta Phytotax. Geobot. 18 (1959) 49.—*B. appendiculata* (Willd.) Iwatsuki ssp. *vivipara* Hennipman, Blumea 18 (1970) 147.—Type: *Wallich 29 p.p.* (*Hamilton leg.*), India, Assam, Goalpara, 1808 (K, herb. Hooker; iso in K, herb. Wallich).
- Acrostichum viviparum* Hamilton ex Sprengel, Syst. Veg. 4 (1827) 36, *nom. illeg., non L.f.* (1781) (= *Asplenium spec.*), *nec* Cav. (1802) (= *Onychium?*).—Type: *Wallich 28 p.p.* (*Hamilton leg.*), India, Assam, Kamrup, Nabovi, 1801 (K, herb. Hooker, *n.v.*; iso in K, herb. Wallich?, see note 2).
- Polybotrya marginata* Bl., Enum. Pl. Jav. (1828) 100, *nom. superfl.*, see note 3; Fl. Java Filices (1829) 18, pl. 3; Presl, Tent. Pterid. (1836) 231, *quoad nomen solum*; Fée, Hist. Acrost. (1845) 75; Hance, J. Linn. Soc. Bot. 13 (1873) 138; Hayata, Ic. Pl. Formos. 5 (1915) 306.—*Polybotrya appendiculata* (Willd.) J. Smith var. *marginata* C. Chr., Bot. Tidsskr. 32 (1916) 343.—Type: *Blume s.n.*, West Java, G. Burangrang (L, 908, 316–449).
- Acrostichum asplenifolium* Bory in Bélanger, Voy. Ind. Or. Bot. 2 (1833) 21, pl. 3.—*Polybotrya asplenifolia* Presl, Tent. Pterid. (1836) 231; Fée, Hist. Acrost. (1845) 77; Ettingsh., Denkschr. K. Ak. Wiss. M.-N. Kl. Wien 22 (1864) 65, fig. 6, pl. 1: fig. 4, 12, 13; Bedd., Ferns S. India (1964) 66, pl. 195.—*Polybotrya appendiculata* (Willd.) J. Smith var. *asplenifolia* Bedd., Handb. Ferns Br. India (1883) 424, fig. 255.—*Egenolfia asplenifolia* Fée, Genres Polyp. (1852) 358; Ching, Bull. Fan Mem. Inst. Biol. 2 (1931) 309; Tardieu-Blot & C. Chr., Not. Syst. 7 (1938) 98; in Lecomte, Fl. Gén. I.-C. 7 (1941) 427; Nayar & Kaur, Bull. Nat. Bot. Gard. Lucknow 100 (1964) 19, fig. 3–5, 14, 18, 29.—*B. asplenifolia* Iwatsuki, Acta Phytotax. Geobot. 18 (1959) 49.—Type: *Bélanger s.n.*, Southern India, Madura, Dendigal, 1831 (P, herb. Bory 26.149 or 26.549).
- Polybotrya nodiflora* Bory in Bélanger, Voy. Ind. Or. Bot. 2 (1833) 17; Fée, Hist. Acrost. (1845) 77, pl. 38: fig. 2; Ching, Bull. Fan Mem. Inst. Biol. 2 (1931) 304.—*Egenolfia nodiflora* Fée, Genres Polyp. (1852) 48.—Type: *Bélanger s.n.*, Burma, Rangoon, 1831 (P, herb. Bory 26.27 or 26.47; iso in L, '451').
- Egenolfia hamiltoniana* Schott, Gen. Fil. (1835 or 1836) pl. (16), *non* Fée (1852) (= *B. appendiculata* var. *vivipara*).—*Egenolfia schottii* Fée, Genres Polyp. (1852) 48, *nom. illeg.*—Typification: see note 4.
- Acrostichum alatum* Roxb. ex Griff., Calc. J. Nat. Hist. 4 (1844) 480, *non* Fée (1845) (= *Elaphoglossum spec.*).—Type: *Roxburgh s.n.*, 'Malay Islands' (BR; BM, phot.).
- Acrostichum seetacoconense* Roxb. ex Griff., Calc. J. Nat. Hist. 4 (1844) 480.—Type: *Roxburgh s.n.*, Bangladesh, Chittagong, Seetacoond (BR; BM, phot.).
- [*Acrostichum hamiltonianum* Wall., Cat (1829) no. 28, *nom. nud.*]—*Polybotrya hamiltoniana* [Presl, Tent. Pterid. (1836) 236, *nom. nud.*] Fée, Hist. Acrost. (1845) 78, *nom. superfl.*—*Egenolfia hamiltoniana* Fée, Genres Polyp. (1852) 48, *non* Schott (1835 or 1836) (= *B. appendiculata* ssp. *appendiculata*).—*Acrostichum appendiculatum* Willd. var. *hamiltonianum* Baker in Hooker & Baker, Syn. Fil. (1868) 415;

Fig. 49. *Bolbitis appendiculata* ssp. *appendiculata*.—a–e. sterile and fertile leaves,  $\times 1/5$ ; f–j. (parts of leaves with) sterile and fertile pinnae,  $\times 1/5$ ; k–n. venation patterns and receptacles (dotted) of fertile pinnae,  $\times 3$ ; o, p. *ibid.* of fertile pinnules,  $\times 6$ ; q–d'. shape and venation pattern of sterile pinnae,  $\times 4/5$  (a, k, l, s–w. *Hennipman 3527*, L; b–d. *H. 3721*, L; e. *Hansen & Smitinand 12205*, C; f, g. *Helfer s.n.*, holotype of *Polybotrya helferiana*, B, leaf 1; h, i. *ibid.*, leaf 2; j, p. *Rock 759*, US, isotype of *Egenolfia helferiana* var. *incisa*; m. *Winit 53b*, SING; n, o. *Kew Distr. no. 1154*, B; q. *Edaño BS 76512*, UC; r. *Loher s.n.*, UC, 229550; x *Thwaites CP 1314*, SING; y. *Bory s.n.*, P, holotype of *Acrostichum asplenifolium*; z. *Anonymus s.n.*, Ceylon, GH; a'. *Holttum SF 19307*, SING; b'. *Norris s.n.*, B; c'. *Holttum s.n.*, SING 20982; d'. *Molesworth Allen 1538*, SING).



- Clarke, Trans. Linn. Soc. Bot. 1 (1880) 578.—*Polybotrya appendiculata* (Willd.) J. Smith var. *hamiltoniana* Bedd., Handb. Ferns Br. India (1883) 426, fig. 256, p.p.; v.A.v.R., Handb. Mal. Ferns (1908) 724, *quoad nomen solum*; *ibid.* (1916) 431, *ibid.*—Type: *Wallich 29 p.p.* (*De Sylva leg.*), Bangladesh, Sylhet (iso in B, BM, G, ster., K, US).
- Polybotrya helferiana* Kunze, Farrnkr. Erde 2 (1849) 35, pl. 94 (excellent); Mettenius, Fil. Hort. Lips. (1856) 24, pl. 2: fig. 7.—*Egenolfia appendiculata* (Willd.) J. Smith var. *helferiana* Christ, Bot. Tidsskr. 24 (1901) 109, *quoad nomen solum*; Bull. Herb. Boiss. II, 4 (1904) 610, *ibid.*—*Polybotrya appendiculata* (Willd.) J. Smith var. *helferiana* Bonap., Notes Pterid. 7 (1918) 102.—*Egenolfia helferiana* C. Chr., Contr. U.S. Nat. Herb. 26 (1931) 292; Ching, Bull. Fan Mem. Inst. Biol. 2 (1931) 303, p.p.; Nayar & Kaur, Bull. Nat. Bot. Gard. Lucknow 100 (1964) 28, p.p.—*B. helferiana* Iwatsuki, Acta Phytotax. Geobot. 18 (1959) 49.—Type: *Helper s.n.*, Burma, Tenasserim (B; iso in B, BR, K, M, MICH, S-PA, UC). See also note 3.
- Lacusaadea montana* Gaudich., Voy. Bonite Bot. (1852) pl. 118.—*Egenolfia montana* Fée, Genres Polyp. (1852) 358.—*Egenolfia asplenifolia* (Bory) Fée var. *montana* Tardieu-Blot & C. Chr., Not. Syst. 7 (1938) 99.—*Egenolfia appendiculata* (Willd.) J. Smith var. *montana* Tardieu-Blot & C. Chr. in Lecomte, Fl. Gén. I.-C. 7 (1941) 427.—Type: *Gaudichaud 24*, Vietnam, Annam, Tourane (P).
- Polybotrya appendiculata* (Willd.) J. Smith 'var.' Bedd., Ferns Br. India (1865) 111, pl. 111: the 3 left-hand top figs.—*Polybotrya appendiculata* (Willd.) J. Smith var. *subintegra* Bedd., Handb. Ferns Br. India (1883) 427.—*Egenolfia appendiculata* (Willd.) J. Smith var. *subintegra* C. Chr., Contr. U.S. Nat. Herb. 26 (1931) 291.—Type: *Parish s.n.*, Burma, Moulmein (K, ster.).
- Egenolfia helferiana* (Kunze) C. Chr. var. *incisa* Ching, Bull. Fan Mem. Inst. Biol. 2 (1931) 304.—Type: *Rock 759*, Lower Burma, Oktada beyond Paung, Martaban Hills, Kalama Range (C; iso in US).
- Egenolfia asplenifolia* (Bory) Fée var. *moniliformis* Tardieu-Blot & C. Chr., Not. Syst. 7 (1938) 99.—*Egenolfia appendiculata* (Willd.) J. Smith var. *moniliformis* Tardieu-Blot & C. Chr. in Lecomte, Fl. Gén. I.-C. 7 (1941) 427.—Syntypes: *Harmand 96*, Vietnam, Cochinchina, P. Condore (P); *Poilane 18179*, Vietnam, Annam, near Kontum, 1000 m alt. (P); *Poilane 21668*, *ibid.*, near Bien Hoa (P); *Thorel s.n.*, Laos, Bassac, 1866–68 (BM, P).
- Egenolfia keralensis* Nayar & Kaur, Bull. Nat. Bot. Gard. Lucknow 94 (1964) 4, fig. 1, 2B; *ibid.* 100 (1964) 30, fig. 15, 28.—Type: *Chandra LWG 77752*, Southeast India, Kerala (LWG, n.v.).
- B. appendiculata* (Willd.) Iwatsuki var. *neglecta* Hennipman, Blumea 18 (1970) 147.—Type: *Van Borssum Waalkes 603*, Java, P. Panaitan, G. Panjaweran near Legon Kadam, 70 m alt. (L; iso in BO).
- Egenolfia appendiculata* × *helferiana*.—Holttum, Dansk Bot. Ark. 23 (1965) 237.
- See for *misidentifications* under the infraspecific taxa.

Rhizome with 2 or 3 rows of leaves. Scales of the rhizome: index 2–10, up to 7(–15) by 1(–2) mm, opaque or subclathrate, usually blackish. *Sterile leaves* pinnate, 15–100 cm long; petiole 3–25 cm long, near the base 1–4 mm thick; lamina index 2–6(–8), usually widest somewhat below the middle, 10–80 by 2.5–20 cm, without the terminal segment 10–77, the terminal segment 1–10 cm long, herbaceous, usually olivaceous; rhachis with or without a narrow wing; pinnae alternate to opposite, (20–)25–60(–85), up to 30 mm apart; central pinnae index 2–5(–7), widest about or below the middle, 1.5–10(–15) by 0.5–2.5 cm, base symmetrical to strongly oblique, margin ± entire, finely serrate, or lobed to 1/3 (–1/2) towards the costa, apex acute or acuminate; the two lowermost pinnae (strongly) deflexed, 0–2(–5) mm stalked, conform to the central pinnae; *terminal segment* triangular, apex sometimes somewhat prolonged; *venation pattern*: secondary veins on either side with 2 or 3 tertiary veins, see also fig. 49: q—d'; 50: c—g, k—m. *Fertile leaves* pinnate to tripinnate, 15–90 cm long; petiole 10–45 cm long; lamina index 1–20(–40), 3–55 by 0.7–12 cm, without the terminal segment 3–52, the terminal segment 0.5–5 cm long; pinnae 15–65(–90), up to 60 mm apart, variously shaped, 0.2–11 by 0.15–1.7 cm; the two lowermost pinnae 0–6 mm stalked. *Sporangia* inserted all over the lower surface or ± restricted to the veins. Spores with a reticulate cristate perispore.

Chromosomes.  $n = 41$  (ssp. *appendiculata*, ssp. *vivipara* var. *vivipara*);  $2n = 82$  (ssp. *appendiculata*).

Distribution. Southern India and Ceylon; northeast India eastwards to southern Japan and Luzon, southwards to Java.

Habitat. Creeping on rocks or in soil in deciduous and evergreen forest. Altitude: 0–1500 m.

Spores. See the infraspecific categories.

Notes. 1. Typification of *Polybotrya vivipara*. Wallich 29 p.p. (*Hamilton leg.*) with Hamilton's MS name in Hooker's handwriting, which agrees with Hooker's plate (Exot. Fl. 2, 1825, pl. 107) is the holotype. This sheet lacks an authentic label of Hamilton, which was obviously retained by Wallich together with a duplicate specimen (K, herb. Wallich) not studied by Hooker. Wallich 29 p.p. (*De Sylva leg.*) is the type of *Polybotrya hamiltoniana*.

2. Typification of *Acrostichum viviparum* Hamilton ex Sprengel. Sprengel listed *A. viviparum* Hamilton, which he referred to '*A. appendiculatum* Hook. [Exot. Fl. 2, 1825, pl. 108] excl. syn. W[ilddenow, 1810]'. Hooker (1825) referred *A. appendiculatum* to '*A. appendiculatum?* Willd. Sp. Pl. v. 5, p. 114.' and to '*A. viviparum* Hamilton's MSS'. As Sprengel supplied a description, *A. viviparum* Hamilton ex Sprengel is a new species, typified by Wallich 28 p.p. (*Hamilton leg.*) from which Hooker's plate was drawn; the name is a later homonym and therefore illegitimate. I failed to trace (overlooked?) the type specimen of this at K, herb. Hooker. Wallich 28 p.p. (*Hamilton leg.*), sheet C in K, herb. Wallich, and with the locality 'Nibari' (sphalm.? = Nabovi) possibly represents an isotype. Wallich 28 p.p. (*De Sylva leg.*) is *B. appendiculata* ssp. *appendiculata* proper, whereas Wallich 28 p.p. (*Anonymus leg.*) agrees with the type of *Polybotrya helferiana* (see spp. *appendiculata*, note 2B).

3. *Polybotrya marginata* Bl. is a superfluous name as in the 'Addenda et Emendanda' of the original publication Blume included in it references to *Acrostichum viviparum* Sprengel (*nom. illeg.*) and *A. appendiculatum* Willd. ('Hooker') which is legitimate.

4. The typification of *Egenolfia hamiltoniana* Schott. The relevant entry in Schott's original publication of the genus *Egenolfia* (1835 or 1836) runs as follows:

Species *E. hamiltoniana* (*Acrost. viviparum* Hamilton, *Polybotrya marginata* Blume).'

The three elements involved in the construction of *E. hamiltoniana* are: (a) the material, the plate, and the description of Schott, (b) *Acrostichum viviparum* Hamilton ex Sprengel, *nom. illeg.*, and (c) *Polybotrya marginata* Bl., *nom. illeg.*

*E. hamiltoniana* should be regarded a new species; it is not a *nom. nov.* as it is based on two heterotypic synonyms.

The material from which Schott's plate was drawn was not included in the loan I received from Vienna. If lectotypification becomes necessary I recommend to select *Acrostichum viviparum* Sprengel as lectotype, as Hamilton's material is well-described and illustrated by Hooker (1825).

5. Fée (1825) retained the name *Egenolfia hamiltoniana* (Fée) Fée (bas.: *Polybotrya hamiltoniana* [(Wallich) Presl ex] Fée, 1845) and renamed *E. hamiltoniana* Schott into *E. schottii*. This procedure is against the present Code.

6. Ching (1931) recognized *Egenolfia nodiflora* (Bory) Fée (bas.: *Polybotrya nodiflora* Bory) in which he included *Polybotrya hamiltoniana* [(Wallich) Presl ex] Fée (1845), *Polybotrya vivipara* Hooker (1925) ('*Acrostichum*'), and *P. appendiculata* var. *subintegra* Beddome (1883). The correct name for this taxon, however, in the genus *Egenolfia* is *E. vivipara* (Hooker) C. Chr., and in the genus *Bolbitis* is *B. hookeriana* Iwatsuki, as there is already a *B. vivipara* (bas.: *Campium viviparum* Kjellberg = *B. quoyana*).

7. *Koorders 119* (BO, ster.) from Karimondjawa Is. and *Palmer & Bryant 1268* (US, ster.) from West Java, Palabuan Ratu, could not be identified infraspecifically.

8. The present species is amongst others characterized by the shape of the perispore which is unique in the genus. See chapter 6.

#### KEY TO INFRASPECIFIC TAXA

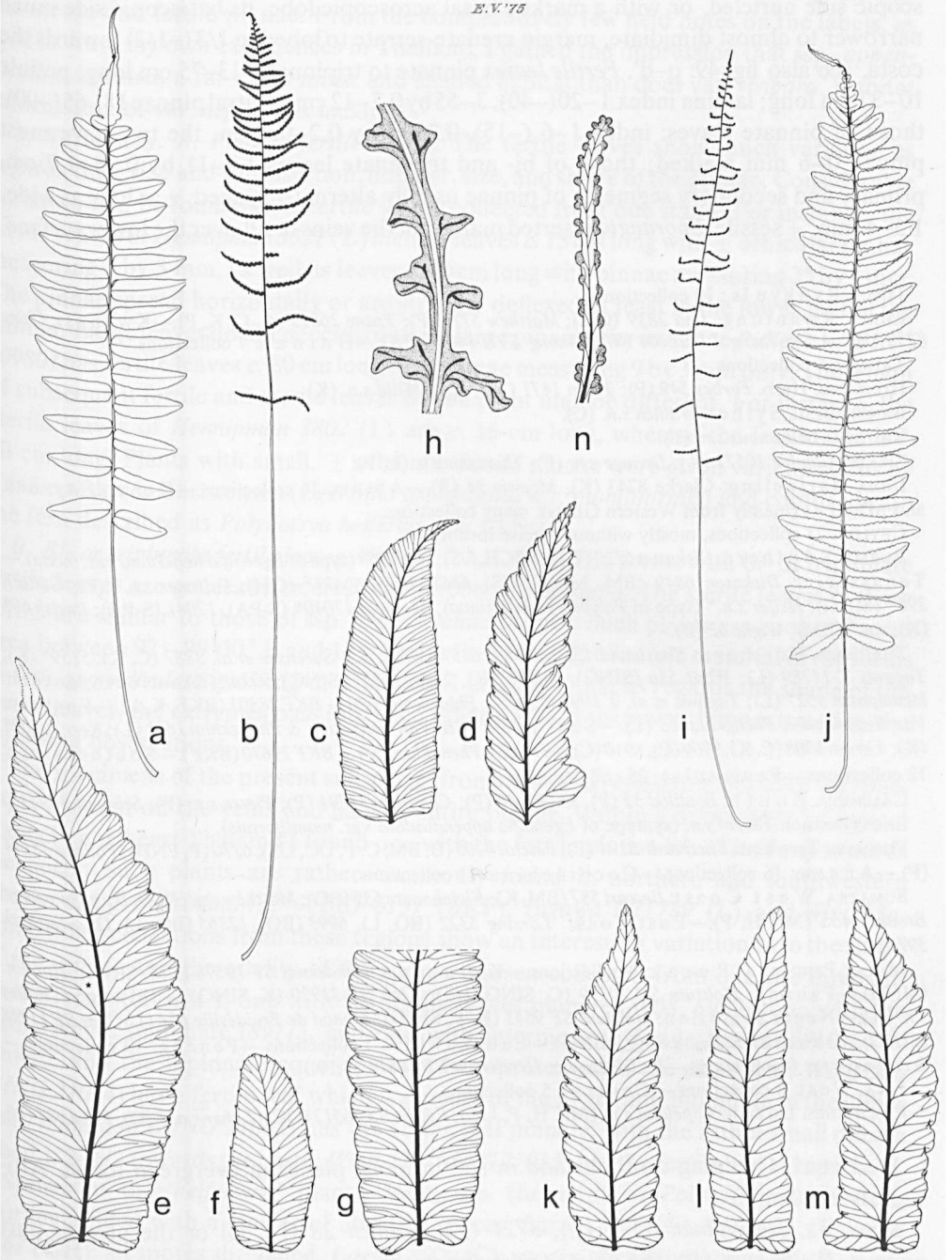
- 1a. Fertile pinnae with a lamina. Sporangia situated on the lower surface of the leaf.
  - a. ssp. *appendiculata*
- b. Fertile pinnae without a lamina or with a narrow strip of lamina present along the costa only. Sporangia facing to all directions . . . . . 2
- 2a. Fertile pinnae without a lamina, moniliform. Base of sterile pinnae symmetrical.
  - Mainland Asia* . . . . . b.1. ssp. *vivipara* var. *vivipara*
- b. Fertile pinnae with a narrow strip of lamina along the costa, ± moniliform. Base of sterile pinnae variously shaped. *Andaman and Nicobar Is., W. Java.*
  - b.2. ssp. *vivipara* var. *neglecta*

#### a. ssp. *appendiculata*—Fig. 49.

*Acrostichum appendiculatum* Willd.—*A. viviparum* Hamilton ex Sprengel.—*Polybotrya marginata* Bl.—*Acrostichum asplenifolium* Bory.—*Egenolfia hamiltoniana* Schott.—*Acrostichum alatum* Roxb. ex Griff.—*Polybotrya helferiana* Kunze.—*Lacaussadea montana* Gaudich.—*Egenolfia helferiana* (Kunze) C. Chr. var. *incisa* Ching.—*E. asplenifolia* (Bory) Fée var. *moniliformis* Tardieu-Blot & C. Chr.—*E. keralensis* Nayar & Kaur.—*E. appendiculata* × *helferiana*.  
*Polybotrya appendiculata* (Willd.) J. Smith var. *helferiana* auct. non (Kunze) Christ: Christ, Bot. Tidsskr. 24 (1901) 109; Bull. Herb. Boiss. II, 4 (1904) 610.

Rhizome 3–9 mm thick, with usually 3 rows of leaves, usually with many sclerenchyma strands. *Sterile leaves* 15–60(–80) cm long; petiole 3–25 cm long, with a narrow wing at least in the upper part either with spreading scales mainly present at the petiole base, or glabrescent; lamina 10–45(–55) by 2.5–13 cm, without the terminal segment 10–40(–50), the terminal segment 1–7 cm long; rhachis with a narrow wing; pinnae 25–60(–85);

*Fig. 50. Bolbitis appendiculata* ssp. *vivipara*.—a–h. var. *vivipara*. a, b. sterile and fertile leaf resp., × 1/5; c–g. shape and venation pattern of sterile pinnae, × 4/5; the asterisk indicates anastomosing veins; h. venation pattern and receptacle (dotted) of basal part of fertile pinna, × 3.—i–n. var. *neglecta*. i, j. fertile and sterile leaf resp., × 1/5; k–m. shape and venation pattern of sterile pinnae, × 4/5; n. venation pattern and receptacle (dotted) of fertile pinna, × 3 (a, b. *Hennipman 3119*, L; c–g. *H. 3488*, L; h. *Rock 823*, US; i, j, l, m. *Van Borssum Waalkes 603*, L, holotype of *B. appendiculata* var. *neglecta*; k. *Backer s.n.*, BO; n. *Korthals s.n.*, Java, L).



central pinnae index 2–5, 1.5–7.5 by 0.5–1.7 (–2) cm, base oblique either with its acroscopic side auricled, or with a marked basal acroscopic lobe, its basiscopic side much narrower to almost dimidiate, margin crenate-serrate to lobed to 1/3 (–1/2) towards the costa, see also fig. 49: q–d'. *Fertile leaves* pinnate to tripinnate, 13–75 cm long; petiole 10–37 cm long; lamina index 1–20 (–40), 3–55 by 0.7–12 cm; central pinnae 18–65 (–90); those of pinnate leaves: index 1–6 (–15), 0.25–4 by 0.2–0.7 cm, the two lowermost pinnae 0–6 mm stalked; those of bi- and tripinnate leaves 1.2–11 by 0.15–1.7 cm, primary and secondary segments of pinnae usually alternate, spaced, ± as long as wide, 1.5–4 mm, ± sessile. *Sporangia* inserted mainly on the veins or all over the lower surface.

JAPAN. Ryukyu Is.: 10 collections.

CHINA. Kwantung: *Lau 2839* (GH); *Matthew 5113* (P); *Tsang 26823* (A, C, K, P).—Kwangsi: *Ching 8238* (UC, US); *Tsang LU 23204* (W); *Whong SYU 140* (S-PA).—Hainan: 7 collections.

TAIWAN. 6 collections.

HONGKONG. Herb. *Forbes 549* (P); *Taam 1471* (UC, US); *Willd s.n.* (K).

BANGLADESH. Sylhet: *Wallich s.n.* (C).

BHUTAN. *Anonymous s.n.* (P).

SIKKIM. *Gamble 10571* (K); *Levinge s.n.* (P); *Thomson s.n.* (L, P).

INDIA Darjeeling: *Clarke 8743* (K), *Moewis 34* (B).—Assam: 16 collections.—Kerala, Mysore, and Madras (mainly from Western Ghats): many collections.

CEYLON. 23 collections, mostly without precise locality.

BURMA. Southern: *Dickason 6789* (GH, MICH, US); *Rock 759* (type of *Egenolfia helferiana* var. *incisa*).—Tenasserim: *Dickason 6849* (BM, MICH, US), *6867* (BM), *6867\**<sup>1)</sup> (GH); *Falconer s.n.\** (P); *Gallatly 296\** (SING); *Helfer s.n.\** (type of *Polybotrya helferiana*); *Meebold 17040\** (S-PA), *17041* (S-PA); *Parish 69\** (K), *s.n.\** (BM); *Wight 62* (B).

THAILAND. Northern: *Smitinand 132* = *BKF 6157* (BKF, K); *Sørensen et al. 3887* (C, K), *5159\** (K); *Tagawa T 11789* (L); *Winit 53a* (SING), *53b* (SING, 2 sh.), *53b\** (SING), *922a\** (K).—Northeastern: *Hennipman 3527* (L); *Tagawa et al. T 1094* (L, US); *Phloenchit 2030* = *BKF 28301* (BKF, K, L).—Eastern: *Van Beusekom & Phengkhilai 83* (L).—Southwestern: *Van Beusekom & Phengkhilai 163\** (L); *Kerr 10502\** (K); *Larsen 8908* (C, K), *8909* (C), *8910* (C) *8911\** (C); *Phengkhilai 294* = *BKF 29670* (BKF).—Southeastern: 12 collections.—Peninsular: 25 collections.

CAMBODIA. South: *Bouillod 32* (P), *33* (P), *46* (P); *Chevalier 31791* (P); *Pierre s.n.* (P); *Schmidt 349* (C). LAOS (Bassac). *Thorel s.n.* (syntype of *Egenolfia appendiculata* var. *moniliformis*).

VIETNAM. Tonkin: *Eberhardt 5194* (P); *Pételot 4205* (B, BM, C, P, UC, US), *6270* (P, PNH); *Poilane 25144* (P).—Annam: 16 collections.—Cochinchina: 11 collections.

SUMATRA. West Coast: *Beccari 587* (BM, K); *Kleinhoonte 635* (BO); *Matthew s.n.* (K).—Bencoolen: *Brooks 145S* (MICH, P).—East Coast: *Lörzing 5322* (BO, L), *6993* (BO), *12365* (BO, L); *Otto-Surbeck 397* (L).

MALAY PENINSULA. Perak: 8 collections.—Kelantan: *Henderson SF 19578* (BM, SING); *Nur s.n.* (SING).—Pahang: *Holtum SF 20799* (C, SING, US); *Kiah SF 31920* (K, SING).—Selangor: *Ridley s.n.* (K).—Negri Sembilan: *Holtum SF 9541* (K, P, SING); *Monod de Froideville 654* (L); *Nur SF 11848* (SING).—Johore: *Ridley s.n.* (P, SING).—Langkawi Is.: 7 collections.—Penang: 10 collections.—Singapore: 6 collections.—P. Tioman: *Henderson SF 18614* (SING).

JAVA. West: 8 collections.—Central: 5 collections.

PHILIPPINES. Luzon: *Copeland s.n.* (MICH, P, UC); *Edaño BS 76512* (UC); *Loher s.n.* (UC); *Price 884* (L).

Habitat. Creeping on rocks and in soil in moist places in evergreen forest. Altitude: 0–1500 m.

Spores. *Hennipman 3527* (L), *3721* (L), *Wallich 28* (L): all or the greater part normal. *Walker s.n.* (P): the greater part abnormal. See also the notes.

<sup>1)</sup>The collections with an asterisk agree with *Polybotrya helferiana*; see note 2B.

Notes. 1. A distinct taxon easily distinguished from var. *vivipara* by the shape of the sterile and fertile pinnae. From the comparatively few field notes on the labels, as well as from my own experiences in Thailand, I gained the impression that ssp. *appendiculata* requires a far more moist and shaded habitat than does var. *vivipara*. Habitat information of var. *neglecta* is lacking.

2. Variability. *A. Pinnate fertile leaves.* The fertile leaves show much variation as regards their size and the insertion, number, size, and shape of the pinnae. Considerable variation can be found in the fertile leaves collected from one stand. For instance, the fertile leaves of *Hennipman 3527* (L) include leaves *c.* 15 cm long with  $\pm$  orbicular pinnae measuring 3 by 3 mm, as well as leaves *c.* 70 cm long with pinnae measuring 35 by 4 mm. The pinnae spread horizontally or are strongly deflexed at least in the lower half of the lamina. Large leaves do not necessarily bear large pinnae. For instance *Ridley s.n.* (*SING 20980*) has fertile leaves *c.* 80 cm long with pinnae measuring 9 by 3 mm only. The length of subsequent fertile and sterile leaves of one plant may be different. For instance, the sterile leaves of *Hennipman 3802* (L) are *c.* 16 cm long, whereas the fertile one is *c.* 40 cm long. Plants with small,  $\pm$  orbicular fertile pinnae were given varietal status by Tardieu-Blot & Christensen (*Egenolfia asplenifolia* var. *moniliformis*) and confused with the fern described as *Polybotrya helferiana* by Christ.

*B. Bi- or tripinnate fertile leaves.* Fig. 49: f, h, i, n-p. The forms with bi- or tripinnate fertile leaves are generally referred to *Polybotrya helferiana*. The sterile leaves of these forms are similar to those of ssp. *appendiculata* proper. Such plants are confined to an area between 97°–99°30' E and 14°–19° N. From a study of ample material of the forms of ssp. *appendiculata* growing in Thailand, I conclude that as regards the shape of the fertile leaves, the extremes pass into each other smoothly as is also demonstrated by the following observations.

The specimens of the present subspecies from mainland Asia generally have the sporangia inserted on the veins and have  $\pm$  entire pinnae. Within a dense stand of typical plants in northeast Thailand I found one with the fertile pinnae lobed halfway towards the costa. Such plants are rather commonly found in northern and southwestern Thailand, e.g. *Smitinand 132 = BKF 6157* (BKF), *Tagawa T 11789* (L), and *Winit 53a*. Some other collections from these regions show an interesting variation as to the shape of the pinnae and the quality of the spores. Larsen collected from one site three different forms (all in C), one with the fertile leaves pinnate (*8908, 8909*), one with the fertile leaves bipinnate (*8911*), and one with intermediate fertile leaves (*8910*). The pinnate and the bipinnate condition may be represented in the same leaf: *Winit 53b* (*SING 21014*) has a fertile leaf which is pinnate in the lower and bipinnate in the upper half; *Winit 53b* (*SING 21002*) has the fertile leaf pinnate, with the rather small pinnae lobed 1/2–1/3 towards the costa; *Winit 53b* (*SING 21013*) has the fertile leaves bipinnate.

Spores of the 'helferiana' plants. *Helfer s.n.* (holotype of *Polybotrya helferiana*): sporangia filled with a cluster of abortive spores. *Larsen 8910* (C), *8911* (C), *Dickason 6867* (GH): all spores shrivelled. *Larsen 8909* (C): spores normally shaped but contents abnormal. *Van Beusekom & Phengkhilai 163A, 163B, 163C* (all from the same site, all in L): *163A*: nearly all sporangia with > 50 normal spores, a few sporangia with abortive

spores; 163B: *ibid.*, but with proportionally more sporangia with abnormal spores; 163C: all sporangia filled with usually abortive S.M.C.'s some in part also with aborted spores.

One of the sterile leaves of *Larsen 8911* (C) has a few of its central pinnae atypically shaped; these pinnae are lobed to halfway towards the costa, lack spines in the sinuses, and have a glaucous tinge (absent from all other pinnae).

The '*helferiana*' plants discussed above might be the result of divergent evolution. The observation that plants with lobed fertile pinnae (and normal spores) are found occasionally within a stand of typical specimens is in support of this. However, the information from the spores of the '*helferiana*' forms and the incidental occurrence of abnormally shaped pinnae might be indications that these plants are of hybrid origin. As var. *vivipara* is the nearest related taxon which, moreover, has moniliform fertile pinnae, it seems possible that in case '*helferiana*' has a hybrid origin, its parents are ssp. *appendiculata* and var. *vivipara*.

C. *The sterile pinnae.* The most distinct form is that described as *Acrostichum asplenifolium*. The base of the sterile pinnae is very oblique, the margin deeply lobed with conspicuous spines in the sinuses. Such plants occur in southern India and Ceylon. The majority of the specimens from southern India belongs to '*asplenifolium*'; it is rare in Ceylon, where it fully integrates with more typical forms. A specimen of '*asplenifolium*' kept in cultivation at Singapore for many years retained its shape (Holtum, 1954). Part of the specimens from Vietnam have  $\pm$  similarly shaped sterile pinnae. Spores (of specimens from southern India): *Chandra LWG 77703* (LWG): all abnormal. *Van Hardeveld & Van der Werff 322* (L), *Nayar LWG 45552* (LWG): the majority abnormal, a minority normal with a densely cristate perispore. A minority of the plants from southern India is much different from '*asplenifolium*' as to the size and shape of the pinnae. For instance *Anonymus s.n.* (in herb. Hooker & Thomson; BM, C, P, W) from Mysore has large sterile pinnae (up to 90 by 22 mm) the base of which varies from slightly asymmetrical to normal; the fertile pinnae also are large (up to 30 by 7 mm), the spores are either all shrivelled (the specimen in P) or  $\pm$  spherical, proportionally large (40–45  $\mu$ m), the perispore with few and low crests. The specimen with the latter spores presumably represents an (auto)ploid; its spores are discussed in chapter 6, and illustrated in plate 10: a, b.

3. Geographical distribution of the '*helferiana*' form. Ching (1931) erroneously located Helfer's type in Assam. Nayar & Kaur also reported this fern (as: *Egenolfia helferiana*) from Assam. The reference sheet cited, *Nayar LWG 77005* (LWG) is sterile, however! These authors also reported this fern from the Andamans; the reference sheet cited belongs to var. *neglecta*.

4. The type of *Egenolfia helferiana* var. *incisa* was said to have sterile pinnae which are deeply lobed and of a different texture. Actually, the sterile pinnae are typical, but the fertile leaves are  $\pm$  atypical being tripinnate.

5. The specimens from the Philippines are somewhat aberrant as regards the sterile pinnae which have acute or serrate lobes ( $\pm$  orbicular in ssp. *appendiculata* proper) and which are reminiscent of those of *B. rhizophylla*. Spores: *Copeland s.n.* (MICH), *Loher*

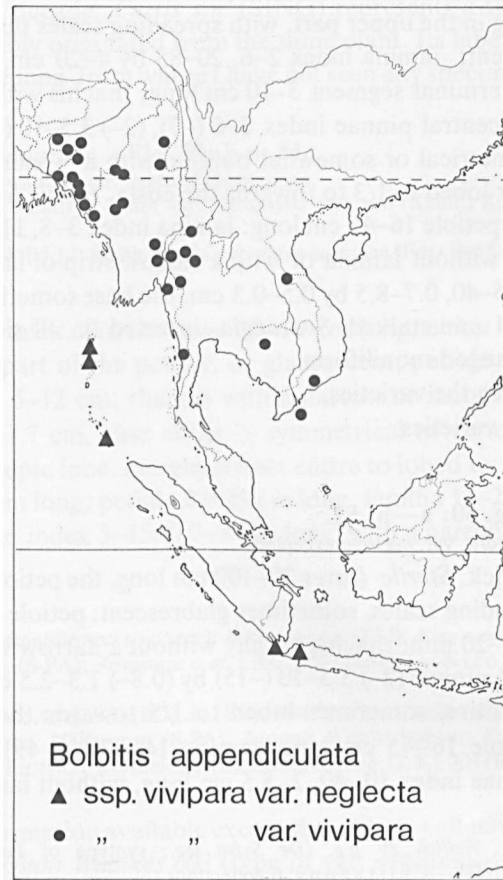


Fig. 51. Distribution of *Bolbitis appendiculata* ssp. *vivipara*.

*s.n.* (UC), Price 884 (L): normal, the perispore rather eroded. *Edaño BS 76512* (UC): normal.

6. *Pételot 4083* (*Colani leg.*) (B. MICH, P, US) from a limestone hill in Pha Vang, Laos, is abnormal as to the shape of the sterile pinnae which have a  $\pm$  symmetrical narrow base, the rather terminal position of the bulbil, and the purplish tinge present on part of the leaves. Spores: all abnormal. Possibly a hybrid with *B. crispatula* var. *copelandii*.

**b. ssp. *vivipara* (Hooker) Hennisman—Fig. 50, 51.**

*Polybotrya vivipara* Hamilton ex Hooker.—*P. nodiflora* Bory.—*Acrostichum seetacoonense* Roxb. ex Griff.—*Polybotrya hamiltoniana* Fée.—*P. appendiculata* (Willd.) J. Smith var. *subintegra* Bedd.—*B. appendiculata* (Willd.) Iwatsuki var. *neglecta* Hennisman.

Rhizome 2.5–12 mm thick, with 2 or 3 rows of leaves, without or with but few sclerenchyma strands. *Sterile leaves* 20–100 cm long; petiole 5–25 cm long, the margins acute



or with a narrow wing in the upper part, with spreading scales throughout or mainly at the base, or glabrescent; lamina index 2–6, 20–85 by 4–20 cm, without the terminal segment 12–77, the terminal segment 3–10 cm long; rhachis with or without a narrow wing; pinnae 20–60; central pinnae index 2–6 (–7), (2–) 3.5–10 (–15) by (0.8–) 1.1–2.5 cm, base either symmetrical or somewhat oblique with a ± marked basal acroscopic lobe, margin entire or lobed to 1/3 to towards the costa. *Fertile leaves* pinnate or bipinnate, 30–90 cm long; petiole 16–45 cm long; lamina index 3–8, 11–37 (–> 49) by 0.7–10 cm; pinnae 15–> 55, without lamina or with a narrow strip of lamina along the costa; central pinnae index 5–40, 0.7–8.5 by 0.5–0.3 cm, the base sometimes wider; the lowermost two pinnae 0–4 mm stalked. *Sporangia* inserted on all sides of the costa (and costules), usually arranged moniliform.

**Distribution:** See the varieties.

**Habitat:** See the varieties.

**b.1. var. *vivipara***—Fig. 50: a–h; 51.

For synonyms see ssp. *vivipara*, var. *neglecta* excepted.

Rhizome 5–12 mm thick. *Sterile leaves* 20–100 cm long, the petiole and rhachis usually throughout with spreading scales, sometimes glabrescent; petiole 5–25 cm long; lamina index 2–5, 20–85 by 4–20 mm; rhachis usually without a narrow wing in the basal part; pinnae 33–60; central pinnae (2–) 3.5–10 (–15) by (0.8–) 1.3–2.5 cm, base ± symmetrical, margin usually entire, sometimes lobed to 1/5 towards the costa. *Fertile leaves* 40–90 cm long; petiole 16–45 cm long; lamina 14–37 (–> 49) by 4–10 cm; pinnae 35–> 55; central pinnae index 10–40, 2–8.5 cm long, without lamina.

BANGLADESH. Sylhet: *Wallich 29 p.p.* (*De Sylva leg.*; syntype of *Polybotrya hamiltoniana*).—Tippera: *Biswas 5083* (PNH).—Chittagong: 6 collections.

INDIA. Assam: 12 collections.

BURMA. Arakan: *McKee 6109* (BM); *NSW P8261* (US).—Northeastern: *Belcher 610* (PNH, US); *Lace 4508* (K).—Central: *Rock 823* (US).—Southern: *Dickason 7120* (BM, GH, MICH, US); *Lace 5023* (K).—Tenasserim: 8 collections (7 from Moulmein).

THAILAND. Northern: 12 collections.

CAMBODIA. (Angkor). *Smith 306* (C, GH, MICH, UC, US).

LAOS. *Harmand s.n.* (BM, P); *Poilane 11388* (K, P).

VIETNAM. Cochinchina: *Pierre 1269* (P); *Poilane 2541* (*Chevalier leg.*) (P).—Con Son Is.: *De Lanessan s.n.* (P).

**Habitat.** Creeping on rocks or in soil in dry evergreen (or deciduous?) forest. Several times reported from limestone. Altitude: 0–900 (–1200) m.

**Spores.** *Hennipman 3488* (L), *Smith 306* (UC): nearly all normal. *Rock 823* (US): the greater part abnormal, mostly shrivelled.

**Notes.** Manton & Sledge (1954) counted the chromosome number of a plant cultivated at the Botanic Garden at Singapore. They stated that the plant is native in southern Thailand from whence it was said to have been introduced to Penang by Curtis. From Penang it apparently was passed on to Singapore. I have not seen any specimen of this taxon from southern Thailand, a region at least locally thoroughly explored for

ferns during the last decade. *Curtis s.n.* (SING) represents a specimen cultivated at Penang, and presumably originated from the same plant. Its label bears the annotation 'Wild on the hills in Penang' from where I have not seen any specimen either.

**b.2. var. neglecta** Hennipman—Fig. 50: i–n; 51.

*B. appendiculata* (Willd.) Iwatsuki var. *neglecta* Hennipman.

*Polybotrya appendiculata* (Willd.) J. Smith var. *rhizophylla* auct. non (Kaulf.) Kuhn: Kuhn, Ann. Mus. Bot. Lugd.-Bat. 4 (1869) 225.

*Polybotrya appendiculata* (Willd.) J. Smith var. *hamiltoniana* auct. non (Fée) Bedd.: v.A.v.R., Handb. Malayan Ferns (1916) 431.

Rhizome 2.5–7 mm thick. *Sterile leaves* 30–50 cm long, either with spreading scales mostly on the basal part of the petiole, or glabrescent; petiole 6–15 cm long; lamina index 3–6, 20–45 by 5–12 cm; rhachis with a narrow or inconspicuous wing; pinnae 20–54, 3.5–8 by 1.1–1.7 cm, base either  $\pm$  symmetrical or variously oblique with a  $\pm$  marked basal acroscopic lobe, margin almost entire to lobed to 1/3 towards the costa. *Fertile leaves* 30–70 cm long; petiole 22–35 cm long; lamina 11–29 by 0.7–5 cm; pinnae 15–45; central pinnae index 5–15, 0.7–3 cm long, with a narrow strip of lamina along the costa.

INDIA. Andaman Is. (middle and southern): *Buchanan s.n.* (BM); *King's coll. s.n.* (B, P, U, W); *Kurz s.n.* (P); *E.H. Man (Mau?) s.n.* (S-PA); *Srivastava et al. LWG 79581* (LWG).—Nicobar Is.: *Galathea Exp. 2858* (C), 2900 (C).

JAVA. West. P. Panaitan: *Amdjah 31* (BO), 32 (BO); *Van Borssum Waalkes 603* (type of var. *neglecta*). West Priangan, Palabuhan Ratu: *Möller s.n.* (S-PA). Around Wijnkoopsbaai: *Kuntze 5017* (P).—*Sine loc.*: *Anonymus 385* (B); *Backer s.n.* (BO); *Korthals s.n.* (L); *Lobb 200* (BM, G, K), 203 (BM).

**Habitat.** No information available except that of type collection: 'on stone', at 70 m.

**Spores.** *Van Borssum Waalkes 603* (type of var. *neglecta*): nearly all normal. *King s.n.* (W), *Lobb 200* (BM): all abnormal, mostly shrivelled.

**Note.** The moniliform shape of the fertile pinnae is sometimes obscured when the pinnae bear mature sporangia. In such cases they are easily confused with the fertile pinnae of ssp. *appendiculata* if mounted with the abaxial side up.

**17. Bolbitis major** (Bedd.) Hennipman, *stat. nov.*—Fig. 52: a–c.

*Polybotrya appendiculata* (Willd.) J. Smith var. *major* Bedd., Handb. Ferns Br. India (1883) 424.—Type: *Atkinson s.n.*, Sikkim, 1200 m alt. (K; iso in BM).

Rhizome up to c. 20 cm long, up to 7 mm thick, with 2 rows of leaves. Scales of the rhizome: index 2–5, up to 2.5 by 1 mm, opaque, brownish to blackish. *Sterile leaves* pinnate, the two complete ones 110 and 160 cm long; petioles 45–65 cm long, near the base 4–7 mm thick with more than 10 vascular bundles; lamina index 2–4, widest somewhat below the middle, 60–95 by 24–30 cm, without the terminal segment 54–80, the terminal segment 6–14 cm long, herbaceous, dark brown or blackish, the rhachis densely covered with small, appressed, dark brown,  $\pm$  permanent scales, not winged; pinnae alternate to opposite, 52–>64, up to 70 mm apart; central pinnae index 5–9, widest about the

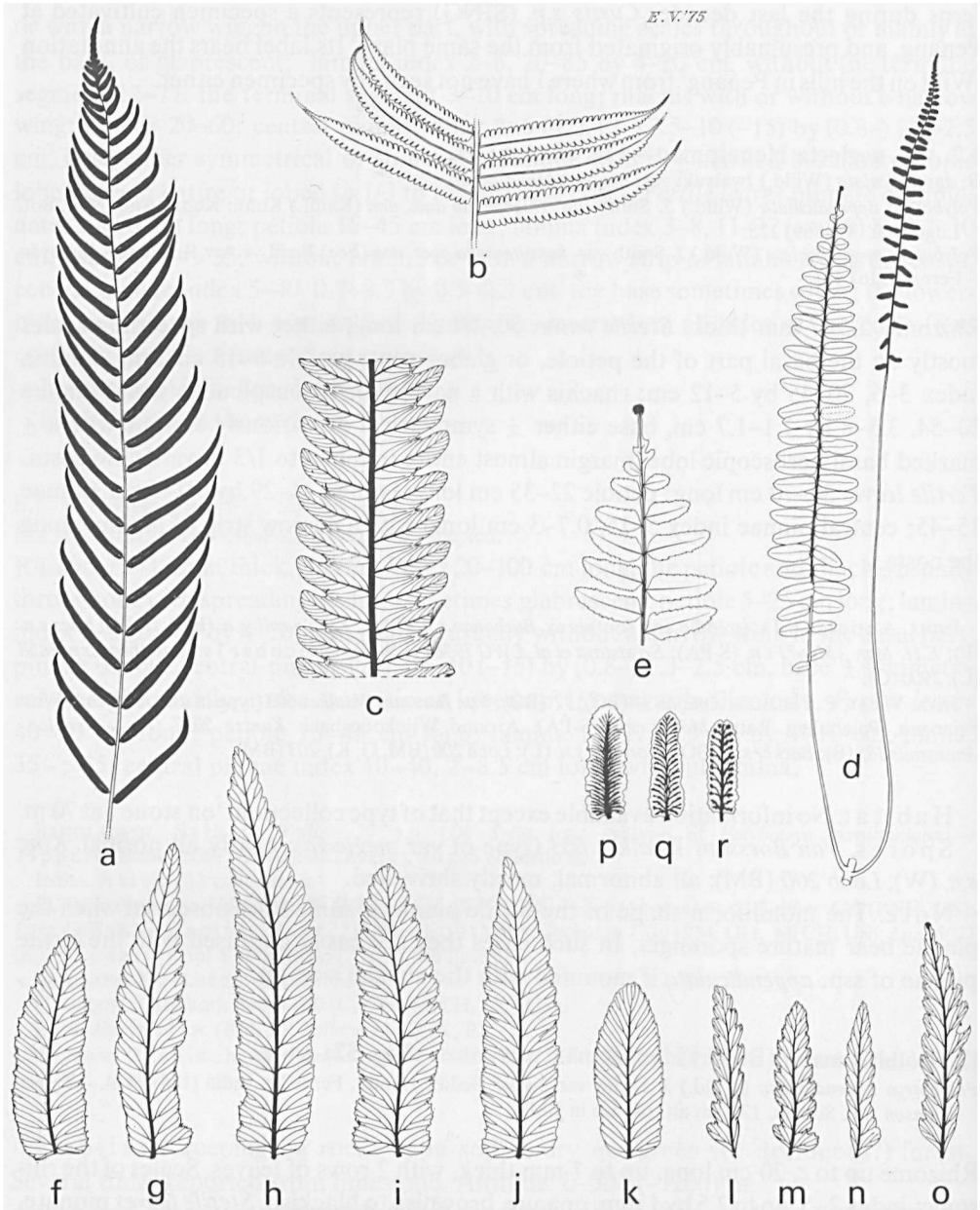


Fig. 52. a-c. *Bolbitis major*. a. fertile leaf,  $\times 1/5$ ; b. central part of sterile leaf,  $\times 1/5$ ; c. venation pattern of sterile pinna,  $\times 4/5$  (a, b. *Atkinson s.n.*, K, holotype of *B. major*; c. *Levinge s.n.*, P).—d-r. *Bolbitis rhizophylla*. d. sterile and fertile leaf,  $\times 1/5$ ; e. terminal part of sterile leaf with bulbil,  $\times 2/5$ ; f-o. shape and venation pattern of sterile pinnae,  $\times 4/5$ ; p-r. *ibid.*, fertile pinnae,  $\times 4/5$  (d. *Hallier 4218*, L; e. *Fénix BS 12984*, L; f. *Loher 1262*, US; g. *Elmer 15899*, UC; h. *Elmer 16793*, GH; i. *Sinclair & Edaño 9476*, SING; j. *LeRoy Topping 655*, US; k. *Copeland 1983*, MICH; l-n. *Ramos & Edaño BS 46986*, B, isotype of *Egenolfia fluviatilis*; o. *ibid.*, UC; p. *Ramos BS 77179*, MICH; q. *Copeland s.n.*, MICH, herb. Copel. 4343; r. *Elmer 15899*, BO).

middle, 13.5–20 by 2–3 cm, base symmetrical, broadly cuneate, attenuate or truncate, margin lobed 2/5–3/5 towards the costa, with a conspicuous spine in the sinuses, lobes somewhat falcate, *c.* 4–5 mm wide near the base, apex oblique, truncate or orbicular, the two lowermost pinnae ± sessile, otherwise conform to the central pinnae; *terminal segment* relatively small, triangular, apex acute; *venation pattern*: secondary veins on either side with > 6 tertiary veins, see fig. 52: *c.* *Fertile leaves* pinnate, the two complete ones 137 and 165 cm long; petiole 67 and 91 cm long resp.; lamina index *c.* 5, 70 by *c.* 18 cm and 74 by *c.* 15 cm resp.; pinnae 54 and 60 resp., up to 55 mm apart; central pinnae index 13–17, widest somewhat below the middle, 7.5–10 by 0.5–0.6 cm, the margin ± entire. Sporangia inserted all over the lower surface. Spores with a smooth cristate perispore.

SIKKIM. *Atkinson s.n.* (type); *Gamble 8556* (K); *Levinge s.n.*, 26–ix–1883 (P, W, ster.).

INDIA. Assam: *Mann s.n.*, i–1891 (K, UC).

BANGLADESH. Chittagong: *Clarke 19621* (BM, K). See also note 3.

**Habitat.** No information available.

**Spores.** *Atkinson s.n.* (BM, K; type): all normal. *Gamble 8556* (K), *Levinge s.n.* (P): all abnormal.

**Notes.** 1. An apparently rare fern characterized by the long-creeping rhizome with widely spaced big leaves, the large number of vascular bundles in the petiole, and the leaf architecture. The leaves have a dark colour as in those of *B. tonkinensis*. Its position within this series seems isolated.

2. Typification. Beddome did not mention a (type) collection. At the time Beddome described var. *major*, however, only Atkinson's material of this taxon was in his herbarium, which is accordingly the type.

3. *Duthie 10654* (K, P, UC, all ster.) from Madhya Pradesh (Central India) possibly belongs here.

### 18. *Bolbitis rhizophylla* (Kaulf.) Hennipman—Fig. 52: d—r; 53.

*B. rhizophylla* (Kaulf.) Hennipman, *Blumea* 18 (1970) 148.—*Gymnogramma rhizophylla* Kaulf., *Enum. Fil.* (1824) 78 ('*rhizophyllum*').—*Polybotrya rhizophylla* Presl, *Tent. Pterid.* (1836) 231; Fée, *Hist. Acrost.* (1845) 77; Mettenius, *Fil. Hort. Lips.* (1856) 24; Ettingsh., *Denkschr. K. Ak. Wiss. M.-N. Kl. Wien* 22 (1864) pl. 7: fig. 9.—*Lacaussadea rhizophylla* Gaudich., *Voy. Bonite Bot.* (1852) pl. 120, *s. descr.*—*Egenolfia rhizophylla* Fée, *Genres Polyp.* (1852) 48; Copel., *Fern Fl. Philip.* (1960) 266; DeVol & Kuo in *Fl. Taiwan* 1 (1975) 352.—*Polybotrya appendiculata* (Willd.) J. Smith var. *rhizophylla* Kuhn, *Ann. Mus. Bot. Lugd.-Bat.* 4 (1869) 295, *quoad nomen solum.*—Type: *Chamisso s.n.*, Philippines, Manila (*n.v.*, LE?; iso in B).

*Polybotrya intermedia* [J. Smith, *Hook. J. Bot.* 3 (1841) 72, *nom. nud.*] Fée, *Hist. Acrost.* (1845) 76, pl. 40: fig. 1; Ettingsh., *Denkschr. K. Ak. Wiss. M.-N. Kl. Wien* 22 (1864) 63, pl. 6: fig. 7.—*Egenolfia intermedia* Fée, *Genres Polyp.* (1852) 48; Ching, *Bull. Fan Mem. Inst. Biol.* 2 (1931) 308; Copel., *Fern Fl. Philip.* (1960) 266.—*B. intermedia* Iwatsuki, *Acta Phytotax. Geobot.* 18 (1959) 49.—Type: *Cuming 269*, Philippines, Luzon, Ilocos (G; iso in BM, GH, K, P, UC, US, W).

*Polybotrya neglecta* Fée, *Hist. Acrost.* (1845) 76, pl. 39: fig. ii.—Type: *Cuming 47*, Philippines, Luzon, Laguna (P, herb. Bory). See note 2.

*Polybotrya serrulata* [J. Smith, *Hook. J. Bot.* 3 (1841) 401, *nom. nud.*] Fée, *Hist. Acrost.* (1845) 76, pl. 39: fig. ii\*; Mettenius, *Fil. Hort. Lips.* (1856) 24; Ettingsh., *Denkschr. K. Ak. Wiss. M.-N. Kl. Wien* 22 (1864) 64, pl. 1: fig. 3.—*Egenolfia serrulata* Fée, *Genres Polyp.* (1852) 358; Ching, *Bull. Fan Mem. Inst. Biol.* 2 (1931)

307; Nakai, Bot. Mag. Tokyo 47 (1933) 170; Tagawa, Acta Phytotax. Geobot. 16 (1956) 175.—*B. serrulata* Iwatsuki, Acta Phytotax. Geobot. 18 (1959) 49.—Syn type: *Cuming 47 p.p.*, Philippines, Luzon, Laguna (BM, G, GH, K, L, P, US, W); *Hügel 4636*, Philippines, Luzon, Manila (W).  
*Polybotrya exaltata* Brackenr. in Wilkes, U.S. Expl. Exp. 16 (1854) 78.—Type: *Brackenridge s.n.*, Philippines, Luzon, Mt. Makiling (US, 62635).  
*Polybotrya duplicato-serrata* Hayata, Ic. Pl. Formos. (1915) 305, fig. 123 A. Type: *Nakahara s.n.*, Taiwan, Akocho, Tanashu, i-1905 (TI, n.v.; L. phot.).  
*Egenolfia fluviatilis* Copel., Philip. J. Sc. 38 (1929) 152, pl. 5; Fern Fl. Philip. (1960) 267.—*B. copelandii* Iwatsuki, Acta Phytotax. Geobot. 18 (1959) 49, *nom. illeg., non* Ching ex Tardieu-Blot & C. Chr. (1938) (= *B. crispatula* var. *copelandii*).—Type: *Ramos & Edaño BS 46986*, Philippines, Luzon, Isabela, San Mariano, Mt. Yalobo region, 700 m alt. (iso in B, UC, US).

Rhizome with 2 or 3 rows of leaves. Scales of the rhizome: index 2–6, up to 3(–4) by 1 mm, subclathrate, brownish or blackish, with or without a paler marginal strip. *Sterile leaves* pinnate, 20–90 cm long; petiole 8–25 cm long, near the base 1.5–3 mm thick; lamina index 3–9, widest usually below, sometimes about the middle, 18–80 by 4.5–15 cm, without the terminal segment 15–75, the terminal segment 1–6 cm long, herbaceous, green to blackish, the petiole and lower side of the basal part of the rachis (apart from the appressed scales) usually with small, blackish, spreading, ± permanent scales; rachis with a narrow wing except for the lowest part; pinnae alternate to opposite, 35–90, up to 35 mm apart; central pinnae index 2–6, widest usually below, sometimes about the middle, 2.5–8 by 0.8–2 cm, base usually symmetrical, (narrowly) cuneate to subcordate, margin finely serrate, biserrate, or serrately lobed to 1/3 towards the costa, the spines often tooth-like, apex orbicular or acuminate; the two lowermost pinnae deflexed or not, conform to the central pinnae, 0–2 mm stalked; *terminal segment* narrowly triangular, apex acute; *venation pattern*: secondary veins on either side with 1–3 tertiary veins, see also fig. 52: f–o. *Fertile leaves* 20–80 cm long; petiole 10–45 cm long; lamina index 5–20, 7–45 by 0.8–4.5 (–7) cm, without the terminal segment 6–43, the terminal segment 0.5–2.5 cm long; pinnae 22–65, up to 55 mm apart; central pinnae index 1–6, 0.4–3(–4) by 0.3–0.7 cm. *Sporangia* inserted on and near the veins. Spores with a smooth cristate-undulate perispore.

Chromosomes. n. = 41.

TAIWAN. Bankinsing: *Faurie 279* (BM, P); *Henry 81* (K, P), *81A* (B, US); *Rosenstock, Fil. Formos. exsicc. 197* (*Faurie leg.*) (B, GH, MICH, S–PA, UC).—Takao: *Ogata s.n.* (BM).—Tanashu: *Nakahara s.n.* (type of *Polybotrya duplicato-serrata*).—'Northern Formosa': *Maries s.n.* (K).

PHILIPPINES. Balabac Is.: *Mangubat 388* (B, BO, GH, P, US).—Palawan: *Merrill 1236* (B, BO, BRI, CAL, GH, L, P, SING), *9243* (GH, SING, UC, US).—Mindoro: *Ramos BS 39793* (BO, P, US); *Sulit & Conklin PNH 16693* (A, K, MICH, PNH).—Luzon: 74 collections (from all over the island but especially from the central and northern provinces).

Habitat. Usually creeping on rocks in moist forests and often near riverbanks. Altitude: 0–1000 m.

Spores. *Copeland s.n.* (MICH), *Cuming 269* (type of *Polybotrya intermedia*; US, W), *Merrill 1236* (GH), *Ramos BS 77186* (MICH), *Rosenstock, Fil. Formos. exsicc. 197* (UC): all, or the greater part normal, those of *Merrill 1236* large. *Brackenridge s.n.* (type of *Polybotrya exaltata*), *Elmer 15899* (GH), *LeRoy Topping 655* (GH), *Ramos & Edaño BS 46986* (type of *Egenolfia fluviatilis*, US): in part normal, in part abnormal. *Chamisso*

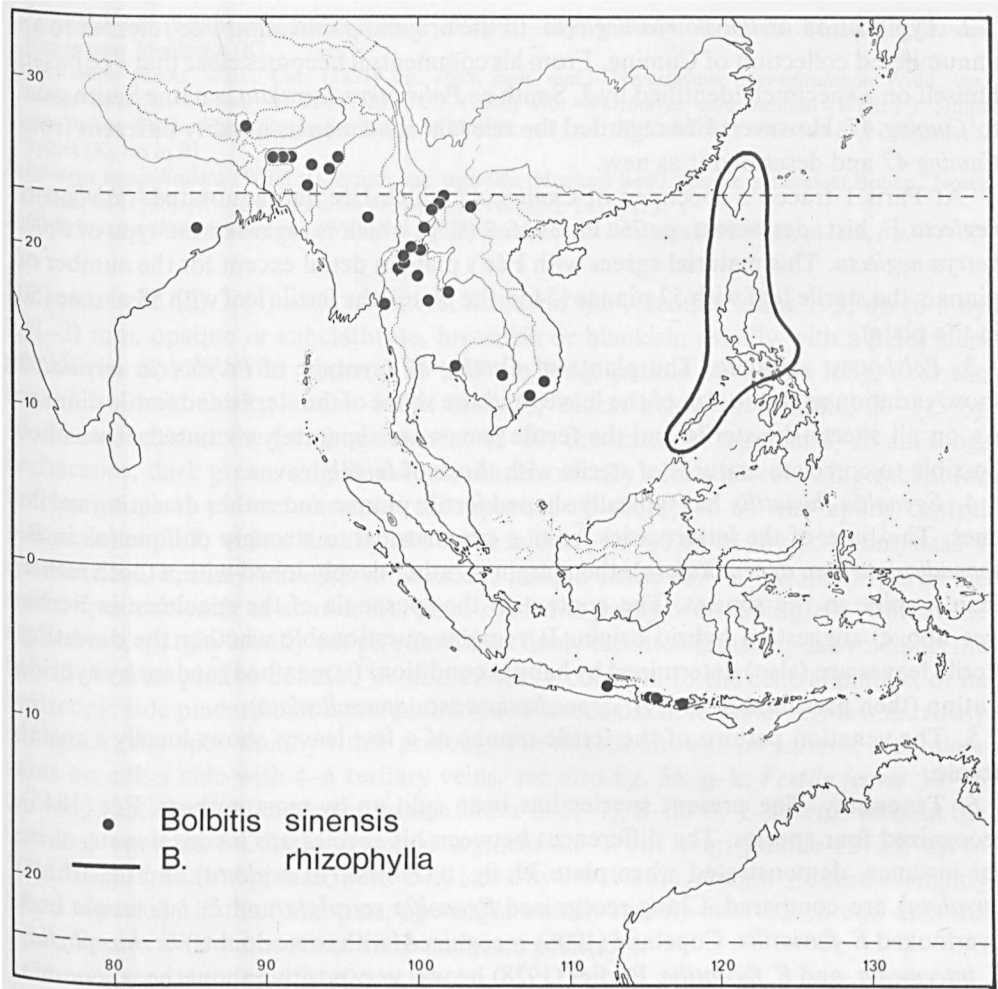


Fig. 53. Distribution of *Bolbitis rhizophylla* and *B. sinensis*.

*s.n.* (type of *Gymnogramma rhizophylla*), *Cuming 47* (syntype of *Polybotrya serrulata*, BM, both the normally shaped and the irregularly shaped fertile leaf; P, herb. Bory), *Curran 8982* (US), *Elmer 16793* (L), *Usteri s.n.* (MICH): the greater part abnormal. *Ramos & Edaño BS 46986* (type of *Egenolfia fluviatilis*, B): sporangia usually filled with aborted spores and/or aborted S.M.C.'s, a few sporangia with mostly normal rather large spores.

Notes. 1. A distinct species easily characterized by the shape of the sterile and fertile pinnae, the terminal bulbil, and the shape of the perispore. The shape of the sterile pinnae and the indument rather resemble those of *B. appendiculata* var. *vivipara*. The perispore is similar to that of *B. sinensis*.

2. Typification of *Polybotrya neglecta*. In the original publication Fée referred to an unnumbered collection of Cuming. From his comments it becomes clear that Fée based himself on a specimen identified by J. Smith as *Polybotrya serrulata*, a name Smith gave to *Cuming 47*. However, Fée regarded the relevant specimen as notably different from *Cuming 47* and described it as new.

At Paris I traced a specimen of *Cuming 47* which Fée had annotated '*Polybotrya neglecta* F. hist. des acrost. p. 76. Pl. 39, f. 2 ('1')', which is regarded the type of *Polybotrya neglecta*. This material agrees with Fée's plate in detail except for the number of pinnae: the sterile leaf with 52 pinnae (54 in the plate), the fertile leaf with 53 pinnae (50 in the plate).

3. *Polybotrya serrulata*. The plants of *Cuming 47* (syntype of *Polybotrya serrulata*) show variation as to the size of the leaves and the shape of the sterile and fertile pinnae. As on all sheets the sterile and the fertile leaves are separately mounted, it was not possible to correlate features of sterile with those of fertile leaves.

4. *Egenolfia fluviatilis* has typically shaped fertile pinnae and rather deviating sterile ones. The base of the latter varies from  $\pm$  symmetrical to strongly oblique (as in *B. appendiculata* ssp. *appendiculata*), the margin is rather deeply lobed with a tooth rather than a spine in the sinuses. The content of the sporangia of the specimen in Berlin (see above) suggests a hybrid origin. It remains questionable whether the deviating sterile leaves are (also) determined by habitat conditions (streambed) and/or by hybridization (then presumably with *B. appendiculata* ssp. *appendiculata*).

5. The venation pattern of the fertile pinnae of a few leaves shows locally a costal areole.

6. Taxonomy. The present species has been split up by most authors. Fée (1845) recognized four species. The differences between his species are inconspicuous as is, for instance, demonstrated when plate 39, fig. ii (*Polybotrya neglecta*) and fig. ii\* (*P. serrulata*) are compared. Ching recognized *Egenolfia serrulata* and *E. intermedia* and overlooked *E. fluviatilis*. Copeland (1906) recognized (with some doubts) *E. rhizophylla*, *E. intermedia*, and *E. fluviatilis*. Earlier (1928) he was very positive about the taxonomic value of less salient characters which would have been 'refused recognition as of specific value by those blinded by the common characters of the genus.'

## 19. *Bolbitis sinensis* (Baker) Iwatsuki—Fig. 53, 54.

*B. sinensis* (Baker) Iwatsuki, Acta Phytotax. Geobot. 18 (1959) 49.—*Acrostichum sinense* Baker, Kew Bull. (1906) 14.—*Egenolfia sinensis* Maxon, Proc. Biol. Soc. Wash. 36 (1923) 173; Ching, Bull. Fan Mem. Inst. Biol. 2 (1931) 305; Tardieu-Blot & C. Chr. in Lecomte, Fl. Gén. I.-C. 7 (1941) 424, fig. 48, Nayar & Kaur, Bull. Nat. Bot. Gard. Lucknow 100 (1964) 32.—*Campium sinense* C. Chr., Contr. U.S. Nat. Herb. 26 (1931) 292, excl. specim. p.p.—Type: *Henry 12494*, China, Yunnan, forest of Szemao (K; iso in B, BM, US).

*Acrostichum appendiculatum* Willd. var. *costulatum* Hooker, Spec. Fil. 5 (1864) 252 ('*costulata*').—*Polybotrya appendiculata* (Willd.) J. Smith var. *costulata* Bedd., Ferns Br. India (1865) 110, pl. 110; Handb. Ferns Br. India (1883) 426, fig. 257; Christ, Farnkr. Erde (1897) 44, fig. 102, the upper two drawings of sterile parts only.—*Egenolfia bipinnatifida* J. Smith, Hist. Fil. (1875) 132; Backer & Posthumus, Varenfl. Java (1939) 85; Nayar & Kaur, Bull. Nat. Bot. Gard. Lucknow 100 (1964) 24, fig. 30.—*B. bipinnatifida* Iwatsuki, Acta Phytotax. Geobot. 18 (1959) 49 ('*bipinnata*', sphalm.), *nom. illeg. non* (Kuhn) Ching in C. Chr., 1934.—*B. sinensis* (Baker) Iwatsuki var. *costulata* Tagawa & Iwatsuki, Acta Phytotax. Geobot.

22 (1967) 102; Southeast Asian Studies 5 (1967) 91.—Type: *Parish 60*, Burma, Tenasserim, Dawna Range near Moulmein (K).

[*Acrostichum ludens* Wall., Cat. (1831) no. 2685, *nom. nud.*]—*Acrostichum appendiculatum* Willd. var. *ludens* Baker in Hooker & Baker, Syn. Fil. (1868) 415.—*Polybotrya appendiculata* (Willd.) J. Smith var. *ludens* Bedd., Ferns Br. India, Suppl. (1876) 26.—Type: *Wallich 2685* (= *Gomez 87*), Bangladesh, Sylhet (K; iso in B).

*Polybotrya appendiculata* (Willd.) J. Smith var. *costulata* (Hooker) Bedd. subvar. *petiolulata* Bonap., Notes Ptérid. 14 (1923) 33.—Type: *Parish 69*, Burma, Nwalabo, Tavoy (P).

*Polybotrya appendiculata auct. non* (Willd.) J. Smith: Bedd., Ferns Br. India (1865) 111, pl. 111, *p.p.*

Rhizome with (2) 3 (4) rows of leaves. Scales of the rhizome: index 1–5, up to 6 by 1.5(–2) mm, opaque or subclathrate, brownish or blackish, usually with a paler marginal strip. *Sterile leaves* pinnate, 35–145 cm long; petiole 10–35 cm long, near the base 1.5–4 mm thick; lamina index 1–4(–5), widest below the middle, 20–115 by 10–35 cm, without the terminal segment 12–80, the terminal segment 8–35 cm long, herbaceous, dark green, ± glabrescent; rhachis usually with a narrow wing except for the lowest part; pinnae alternate to opposite, 14–40, up to 65 mm apart; central pinnae index 3–7, widest usually about the middle, 5.5–17.5(–21) by 1.5–5 cm, base ± symmetrical, broadly cuneate to auricled, margin lobed 1/3–2/3(–3/4) towards the costa, apex orbicular or acuminate, lobes spaced to partly overlapping, *c.* 6–8 mm wide at the base, margin usually entire, sometimes finely crenate-serrate, apex orbicular; the two lowermost pinnae deflexed or not, either ± conform to the central pinnae, or its basisopic side pinnatifid or again pinnate, 1–8 mm stalked; *terminal segment* narrowly triangular, the apex usually either prolonged or flagelloid; *venation pattern*: secondary veins on either side with 4–6 tertiary veins, see also fig. 54: *g–k*. *Fertile leaves* 18–85 cm long; petiole 8–50 cm long; lamina index 2–5(–7), 8–40 by 2–13 cm, without the terminal segment 5–35, the terminal segment 1.5–7 cm long; pinnae 12–35, up to 70 mm apart; central pinnae index 2–8, 1.3–6 by 0.4–1.2 cm, margin ± entire to slightly lobed especially in the basal part. *Sporangia* usually mainly inserted on and near the veins. Spores with a smooth cristate-undulate perispore.

Chromosomes.  $n = 41$ ;  $2n = 82$ .

CHINA. S. Yunnan: 6 collections.

BANGLADESH. Sylhet: *Wallich 2685* (type of *Acrostichum appendiculatum* var. *ludens*).

INDIA. Assam: 25 collections (13 collections from the Khasya Hills).—Orissa: *Mooney 1468* (K), 4097 (K).

BURMA. Central: *Dickason 6621* (BM, GH), 6657 (BM); *Lace 4900* (K).—Southern Shan States: *Dickason 9140* (GH).—Tenasserim: *Parish 60* (type of *Acrostichum appendiculatum* var. *costulata*).

THAILAND. Northern: many collections.—Northeastern: *Hennipman 3624* (L); *Tagawa et al. T 1100* (L, US); *Shimizu et al. T 11381* (L).—Southeastern: *Iwatsuki & Fukuoka T 7169* (L).

CAMBODIA. *Poilane 28761* (P).

VIETNAM. Cochinchina: *Matthew s.n.* (K).—Annam. South: *Poilane 23888* (P), 24408 (BM, P).

JAVA. East: *Mousset 873* (MICH).

LESSER SUNDA ISLANDS. Bali: *Holstvoogd 809* (L), 873 (L); *Posthumus 3704A* (BO, ster.).—Sumbawa: *Rensch 630* (B, ster.).

Habitat. Usually terrestrial, creeping either in soil or on rocks, sometimes low-epiphytic (up to 1 m), in (hill) evergreen (monsoon) forest. I found it in several places



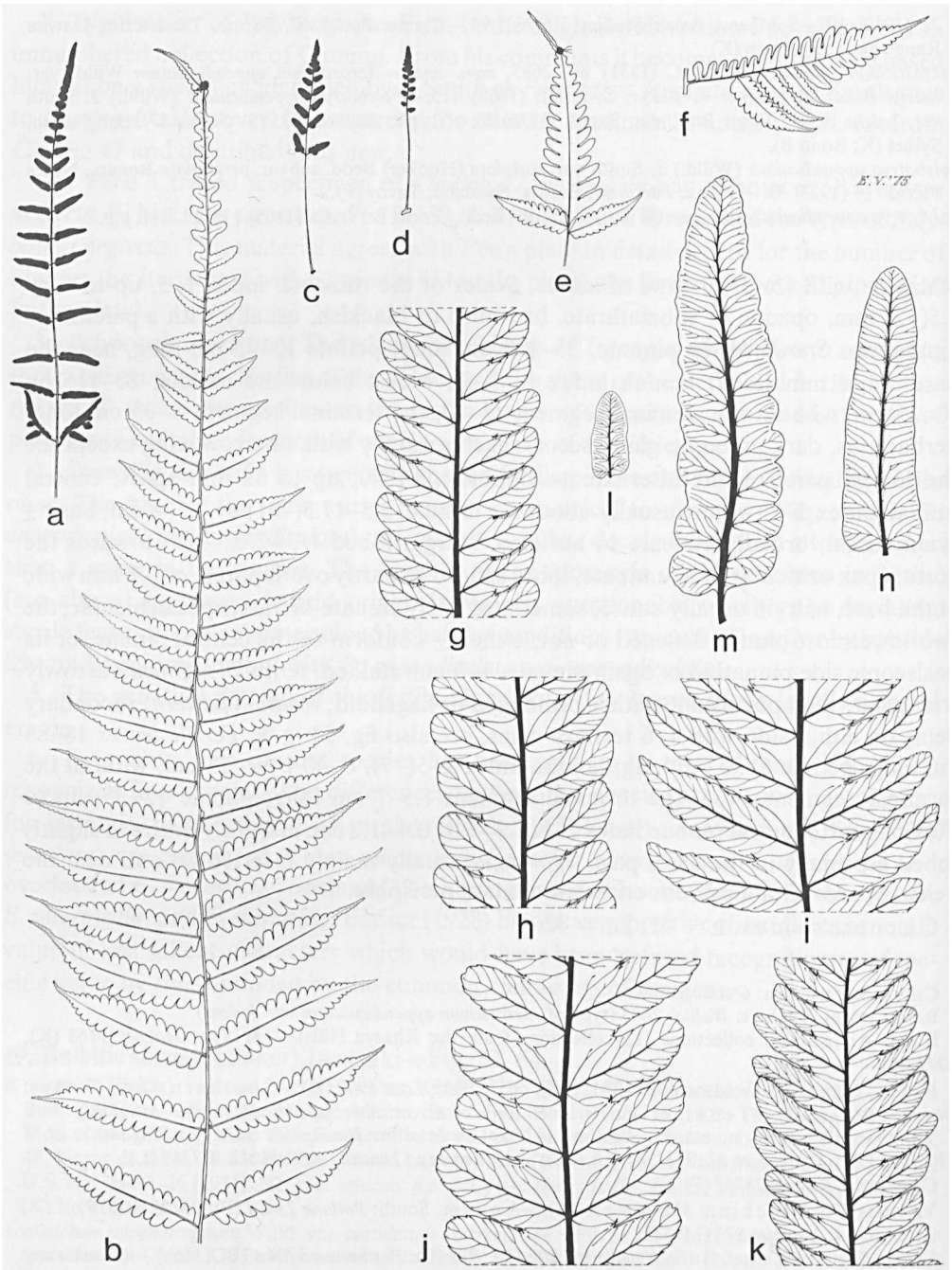


Fig. 54. *Bolbitis sinensis*.—a-d. sterile and fertile leaves,  $\times 1/5$ ; e. terminal part of sterile leaf,  $\times 1/5$ ; f. lowermost pinna of sterile leaf,  $\times 1/5$ ; g-k. venation pattern of sterile pinnae,  $\times 4/5$ ; l-n. *ibid.* of fertile pinnae (a. Parish 60, K, holotype of *Acrostichum appendiculatum* var. *costulatum*; b, e, f, j, l-n. Hennisman 3229, L; c. H. 3389, L; d. Beddome s.n., K; g. Hennisman 3229A, L; h, i. Van Beusekom 1328, L; k. Rock 2913, US).

in northern Thailand to be locally the dominant ground fern forming stands of many specimens densely growing together. Altitude: 0—1900 m.

**Spores.** *Van Beusekom 1328* (L), *Hennipman 3155* (L), *3229* (L), *Henry 12494* (type of *Acrostichum sinense*, US), *Holstvoogd 809* (L), *Rock 2657* (C, US): the greater part normal. *Cavalerie 4230* (L): in part normal. *Griffith s.n.* (BM), *Parish 60* (type of *Acrostichum appendiculatum* var. *costulatum*): the greater part (all?) abnormal.

**Notes.** 1. A clear-cut species primarily characterized by the combination of free veins, symmetrical pinnae, and an undulate-cristate perispore. It may be related to *B. appendiculata* and is certainly so to *B. tonkinensis* (= *spec. dub.*, see also note 2). The relationship to *B. major*, which has  $\pm$  similarly shaped sterile and fertile pinnae, is obscure.

The species is confined to regions in Asia with a monsoon climate in both the northern and the southern hemisphere.

Most authors recognized two species within this complex which are primarily based on differences in shape of the two lowermost pinnae (see note 4).

## 2. Variability.

a. The collections of Rock. Rock made several collections in southern Yunnan which were critically studied by Christensen. The latter author noticed the difference in venation pattern of the sheets he received: *Rock 2657* (C; = *B. sinensis*) with free veins; *Rock 2913* (BM; = *B. sinensis* s.l., see below) with a venation pattern sometimes showing a costal areole; and *Rock 2636* (= *B. angustipinna*  $\times$  *sinensis*) with the veins rather irregularly anastomosing into a pattern that Christensen thought not to be materially different from that of *Campium angustipinum* (= *B. angustipinna*). Christensen commented: 'It is without question that the specimens mentioned belong to the same species, . . . and as mentioned before, it is very probable that *Egenolfia* and *Campium* (= *Bolbitis*) should be united.' Iwatsuki (1959) largely based himself on Christensen when he formalized this view.

Except for the venation pattern, *Rock 2913* (BM) is almost typical. The venation pattern of the pinnae not only deviates by the occurrence of costal areoles (which are occasionally also present in *Rock 2657*, US) but also as the most distal tertiary vein generally springs directly from the costa and not from the secondary vein. The small fertile leaf is heavily attacked by a fungus. Still, nearly all sporangia are mature and not infected. The majority of these is filled with shrivelled spores, a minority with either aborted S.M.C.'s or with obviously normal spores.

*Rock 2913* (US) differs somewhat from the specimen in BM as regards details of colour, texture, and shape of the sterile leaf. The shape of the fertile leaf is typical. Spores: nearly all sporangia filled with 64 normal, or largely normal spores having an undulate-cristate or a spiny perispore. The spores of this specimen are described in detail in chapter 6.

b. Two plants which originated from northern Thailand were cultivated side by side in the Botanic Garden, Leiden. One has been collected by Nooteboom on Doi Suthep, the other by myself (*Hennipman 3229*) on Doi Chieng Dao. Both are diploid. During two seasons with excellent growth these two plants behaved differently. The plant of Nooteboom formed small, rather erect sterile and fertile leaves, whereas mine formed

much larger and nearly exclusively sterile, paler leaves which touched the ground, the bulbils developing into small plants.

c. Plants more or less intermediate between *B. sinensis* and *B. appendiculata* ssp. *appendiculata* are known from Tonkin and Burma. They agree fairly well with *B. tonkinensis* (see *Spec. dub.*) but are smaller and the leaves lack residual scales. These plants include *Cadière 1146* (P) and *Herb. Ec. Sup. Agric. & Sylvic. Hanoi 4078* (Colani leg.) (BM, MICH, P, UC), both from Tonkin, and *Parish 69* (type of *Polybotrya appendiculata* subvar. *petiolulata*) and *71* from Burma, Tenasserim. Beddome's figures (1865, pl. 111, the two upper right figures) were prepared from these Burmese collections.

3. A considerable part of the specimens has fertile leaves with a fungal infection. The fungus forms a variously thick whitish mycelium around all parts of the leaf. Hyphae are found between the sporangia and inside part of mostly juvenile sporangia. Occasionally sporangia of mature size were found with a number of normal spores embedded in a loose reticulum of hyphae (*Hennipman 3229*, L).

4. The present species was first recognized by Hooker (1864)—who lumped all the egenolfioid ferns into *Acrostichum appendiculatum*—as var. *costulata*. He characterized this variety by the central pinnae which are symmetrical and pinnatifid, and the two lowermost pinnae which are bipinnatifid. As Hooker already remarked, the shape of the two lowermost pinnae shows considerable variation; they may also be  $\pm$  conform to the central pinnae. Lowermost pinnae representing both extremes are found on different leaves from the same plant. The intermediate condition is frequent (for instance the type of *Acrostichum sinense*).

Tagawa & Iwatsuki (1967), in contrast with Iwatsuki (1959), agreed with the view that differences in the shape of the two lowermost pinnae have no taxonomic value. Still, they recognized a var. *costulata* of *B. sinensis* representing plants 'which are usually larger than those of the type variety'. However, the shape of the basal pinnae is not correlated with the size of the leaves: the type of var. *costulata* represents a small plant.

The differences given by Nayar & Kaur between *Egenolfia sinensis* and *E. bipinnatifida* are either trifling or not represented in the reference sheets of both studied by me (*LWG 83037* and *LWG 77006*; both in LWG).

5. The present species was reported from East Java by Backer & Posthumus and by De Joncheere (*Amer. Fern J.* 43, 1953, 45). The material upon which Backer & Posthumus based themselves was not traced, that of De Joncheere was lost during World War II (Van Steenis-Kruseman, *Fl. Mal. I*, 1, 1950, 265).

6. See also *B. bipinnatifida*, note 6.

##### 5. Series *Euryostichae* Hennipman, *ser. nov.*

*Anapausia* Presl subgen. *Euryostichum* Presl, *Epim. Bot.* (1951) 188, *typo incl., pro subgenere.*

Terrestrial or on tree bases. *Rhizome* short-creeping, slender or not, with 2, in one species (*B. nicotianifolia*) with 2—5, rows of leaves, with sclerenchyma strands. Scales

of the rhizome usually  $\pm$  appressed, in one species (*B. pergamentacea*) almost spreading, up to 10 mm long, usually flat, in one species (*B. pergamentacea*)  $\pm$  bullate. *Leaves* approximate or up to 40 mm apart. Sterile leaves usually pinnate, sometimes simple; petiole with 5—20 vascular bundles; lamina: bulbil(s) if present either elongate and subterminal on the terminal segment or  $\pm$  spherical and axillary, appressed scales

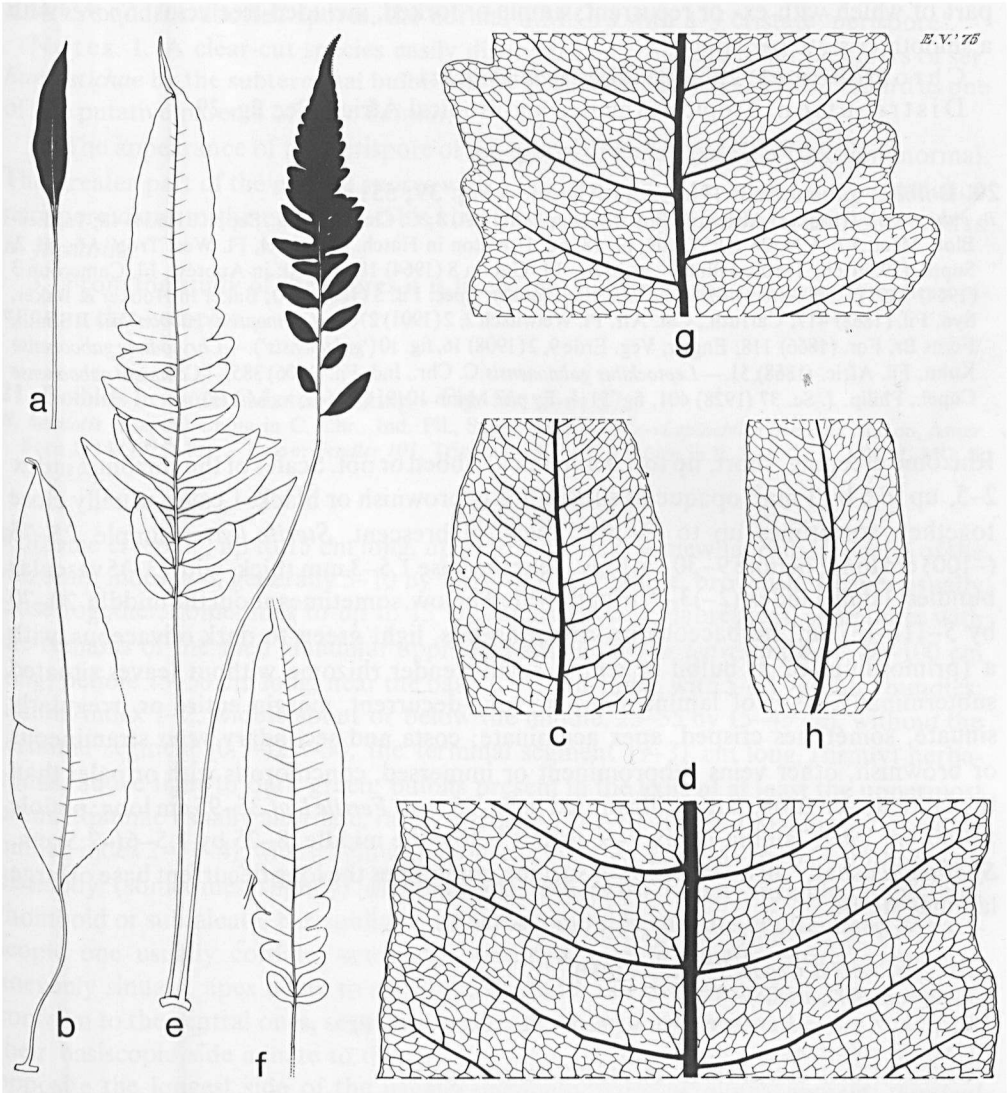


Fig. 55. a–d. *Bolbitis gaboensis*. a, b. sterile and fertile leaf resp.,  $\times 1/5$ ; c, d. venation pattern of sterile laminae,  $\times 4/5$  (a, b. Mann 1049, K, holotype of *B. gaboensis*; c, d. Zenker 2456, L).—e–h. *Bolbitis*  $\times$  *boivinii*. e, f. sterile and fertile leaves,  $\times 1/5$ ; g. venation pattern of sterile lamina,  $\times 4/5$ ; h. *ibid.* of sterile pinna (e. Welwitsch 156, K, lectotype of *B. x boivinii*; f. Anonymus s.n., 17-viii-1946, P; g. Letouzey 2925bis, L; h. Welwitsch 156, BM, see e).

on the rachis deeply cut, the ultimate divisions ending in a glandular cell; rachis not winged; pinnae 2—8, the margin without teeth or spines; terminal segment  $\pm$  conform to the pinnae though somewhat, in one species (*B. oligarchica*) much larger; venation: secondary veins prominent on either side, tertiary veins prominent or immersed; *venation pattern*: secondary veins connected by  $\pm$  curved transverse tertiary veins, the areoles including a network of smaller areoles varying in size and shape in part of which with ex- or recurrent, simple or forked, included free veins. *Spores* with a smooth cristate perispore.

Chromosomes.  $2n = 82$  (*B. pergamentacea*).

Distribution. Tropical America and tropical Africa. See fig. 29.

**20. *Bolbitis gaboonensis* (Hooker) Alston.—Fig. 39; 55: a–d.**

*B. gaboonensis* (Hooker) Alston, J. Bot. 72, Suppl. 2 (1934) 3; C. Chr., Ind. Fil., Suppl. 3 (1934) 48; Tardieu-Blot, Mém. I.F.A.N. 28 (1953) 109, pl. 18: fig. 1; Alston in Hutch. & Dalziel, Fl. West Trop. Afr. ed. 2, Suppl. (1959) 68; Tardieu-Blot in Aubrév., Fl. Gabon 8 (1964) 184, pl. 30; in Aubrév., Fl. Cameroun 3 (1964) 315, pl. 50.—*Acrostichum gaboonense* Hooker, Spec. Fil. 5 (1864) 270; Baker in Hooker & Baker, Syn. Fil. (1868) 417; Carruth., Cat. Afr. Pl. Welwitsch 2, 2 (1901) 276.—*Gymnopteris gaboonensis* J. Smith, Ferns Br. For. (1866) 118; Engler, Veg. Erde 9, 2 (1908) 16, fig. 10 ('*gabunensis*').—*Chrysodium gaboonense* Kuhn, Fil. Afric. (1868) 51.—*Leptochilus gaboonensis* C. Chr., Ind. Fil. (1906) 385.—*Campium gaboonense* Copel., Philip. J. Sc. 37 (1928) 401, fig. 51.—Type: Mann 1049, Guinea, 'coast' (K).

Rhizome creeping, short, up to 4.5 mm thick, ribbed or not. Scales of the rhizome: index 2–5, up to 5 by 1 mm, opaque to subclathrate, brownish or black. Leaves usually close together, sometimes up to 15 mm apart, glabrescent. *Sterile leaves* simple, 25–75 (–100) cm long; petiole 9–30 cm long, near the base 1.5–3 mm thick, with (3–)5 vascular bundles; lamina index (2–)3–7, usually widest below, sometimes about the middle, 20–70 by 5–11 (–13) cm, herbaceous or subcoriaceous, light green to dark olivaceous, with a (primordium of a) bulbil or with a small slender rhizome without leaves situated subterminally, base of lamina short- to long-decurrent, margin entire or irregularly sinuate, sometimes crisped, apex acuminate; costa and secondary *veins* stramineous or brownish, other veins subprominent or immersed, concolorous with or paler than the lamina; venation pattern illustrated in fig. 55: c, d. *Fertile leaf* 35–95 cm long; petiole 15–60 cm long; lamina index 2–9, widest below the middle, 8–25 by 1.5–6 (–7.5) cm. *Sporangia* usually all over the lower surface, sometimes the long decurrent base of large laminas sterile.

NIGERIA. *Jones & Onochie FHI 17514* (BM).

CAMEROUN. 10 collections.

CENTRAL AFRICAN REPUBLIC. *Cervoni s.n.* (P); *Tisserant 2716* (L, P).

GABON. 5 collections.

CONGO (BRAZZ.). *Charvet 160* (L, P), *184* (P); *Thollon 719* (P).

ZAIRE. Leopoldville: 29 collections.—Equateur: *Laurent s.n.*, 22–xii–1903 (BR); *Néré 2226* (P).—Orientale: 5 collections.—Kasai: *Laurent s.n.*, xi–1895 (BR).

ANGOLA. Cabinda: *Gosswailer 7647* (BM, P).—Cuanza Norte: *Welwitsch 155* (BM, K).

Habitat. Moist places in rain forest; reported from streambanks and from rocks in rivulets. Altitude: 0–500 m.

**Spores.** *Luja 216* (BR): the majority normal with a cristate perispore. *Vanderijst 8019* (BR): likewise but the appearance of the perispore different, see note 2. *Thollon 719* (P): in part normal. *Callens 2819* (BM), *Welwitsch 155* (BM, K): the majority of the sporangia filled with aborted spores, a minority of the sporangia with aborted S.M.C.'s: some normal spores also present in the preparations. *Mann 1049* (type of *Acrostichum gaboonense*), *Zenker 3806* (BM, K, L): sporangia filled with either (aborted and 'normal') S.M.C.'s and/or aborted spores, the normal S.M.C.'s with a  $\pm$  cristate 'perispore'.

**Notes.** 1. A clear-cut species easily distinguished from the other members of ser. *Euryostichae* by the subterminal bulbil on the sterile leaf. *B. gaboonensis* I regard as one of the putative parents of *B. × boivinii*.

2. The appearance of the perispore of the spores of *Vanderijst 8019* (BR) is abnormal. The greater part of the normal spores with a cristate-undulate, a few with an undulate perispore close to the exospore. This kind of variation in perispore is also observed in *B. fluviatilis*.

3. From the study of the spores it is likely that hybridization is a common phenomenon in this complex.

## 21. *Bolbitis hemiotis* (Maxon) Ching—Fig. 56: a–d; 57.

*B. hemiotis* (Maxon) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 48.—*Leptochilus hemiotis* Maxon, Amer. Fern J. 14 (1925) 101.—Type: *Fendler 101*, Trinidad, 1877–80 (US; iso in B, BM, G, K, MICH, MO, S, UC, US).

Rhizome creeping, up to 15 cm long, up to 10 mm thick, somewhat ribbed. Scales of the rhizome: index 2–6, generally 5–10 by 1–3 (–4) mm, opaque, brownish. Leaves usually close together, sometimes to up to 15 mm apart, usually glabrescent, sometimes with the remains of the shed glandular appressed scales. *Sterile leaves* pinnate, 40–100 cm long; petiole 15–50 cm long, near the base 2.5–7 mm thick, with 5–11 vascular bundles; lamina index 1–2, widest about or below the middle, 25–55 by 15–45 cm, without the terminal segment (0.5–)2.5–30, the terminal segment 19–31 cm long, (firmly) herbaceous, above light to dark green, bulbils present in the axils of at least the uppermost pinnae; pinnae usually alternate, rarely opposite, (2) 3–6 (–8), 40–100 mm apart; central pinnae index 2–3 (–4), widest below or about the middle, (8.5–) 15–26 by (4–)5.5–12 cm, distinctly (sometimes slightly) asymmetrical, otherwise rather variable, sometimes rhomboid or subfalcate, base oblique, its acroscopic side cuneate or attenuate, its basiscopic one usually cordate, sometimes rounded, margin usually entire, sometimes unevenly sinuate, apex acute to shortly acuminate; the two lowermost pinnae almost conform to the central ones, sessile or up to 3 mm stalked, uppermost pinnae often with their basiscopic side adnate to the rhachis, the uppermost pinna sometimes inserted opposite the longest side of the usually unequally based terminal segment; *terminal segment* 7.5–13.5 cm wide, sometimes almost symmetrical and either cuneate or decurrent; rhachis, costae, and secondary *veins* stramineous or brownish, other veins immersed or almost so, concolorous with the lamina; venation pattern illustrated in fig. 56: d. *Fertile leaf* 40–115 cm long; petiole 30–65 cm long; lamina index 1–3 (–4), widest about or below the middle, (10–)15–35 (–50) by 5–17 cm, without the terminal segment

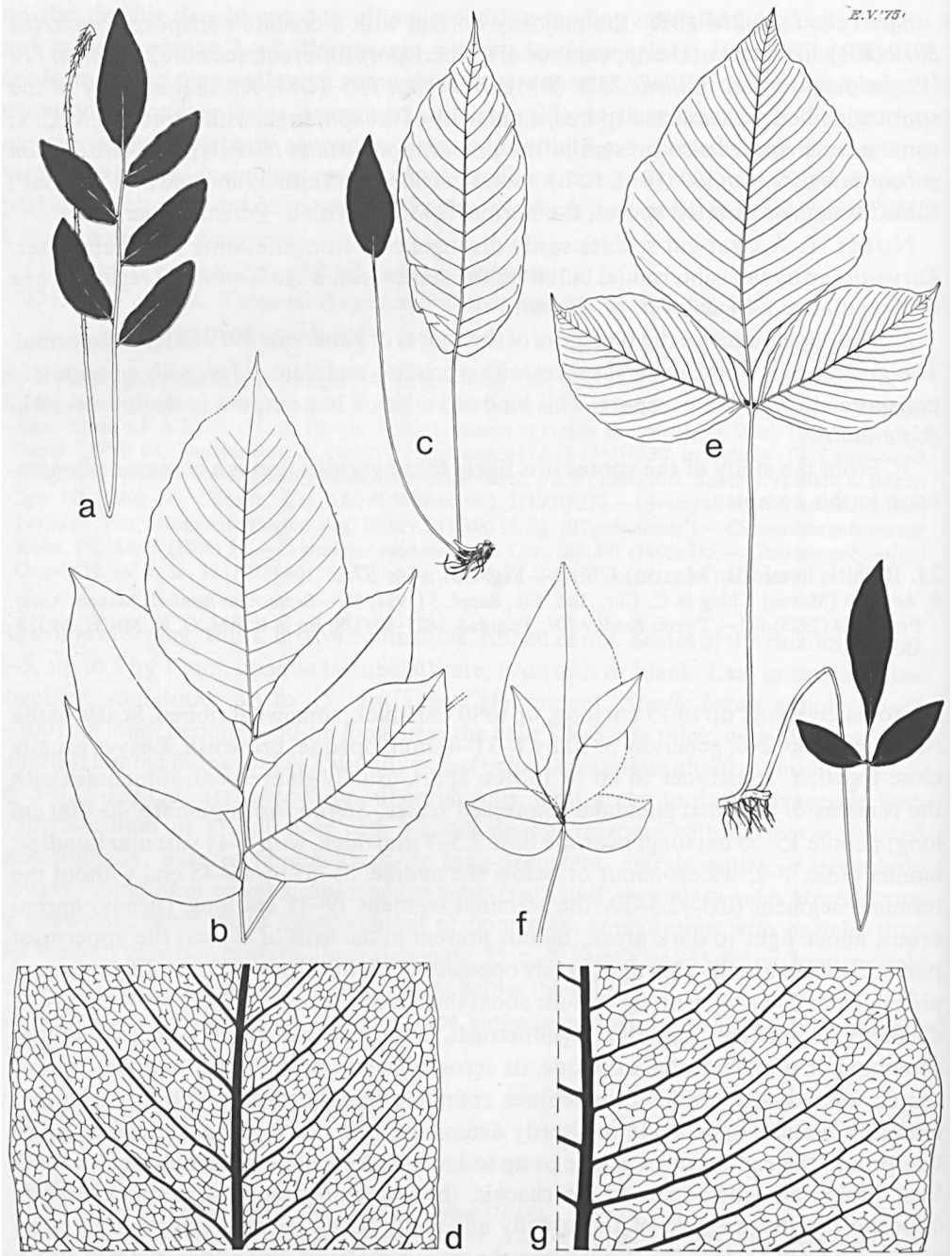


Fig. 56. a–d. *Bolbitis hemiotis*. a–c. sterile and fertile leaves,  $\times 1/5$ ; d. venation pattern of sterile pinna,  $\times 4/5$  (a. *Broadway s.n.*, BM; b. *Fendler 101*, BM, isotype of *B. hemiotis*; c. *Aldridge s.n.*, BM; d. *Jermy 2642*, BM).—e–g. *Bolbitis oligarchica*. e. sterile and fertile leaf,  $\times 1/5$ ; f. sterile leaf with developing bud,  $\times 1/5$ ; g. venation pattern of sterile pinna,  $\times 4/5$  (e. *Rojas 98*, US; f. *Skutch 2972*, US; g. *Idrobo & Schultes 1113*, US).

1.5–22(–37), the terminal segment 7–14 cm long; pinnae (2)3–9, 15–100 mm apart; central pinnae index 2–4, 4–12.5 by 1.5–5 cm, apex round; terminal segment 2.5–5.5 cm wide. *Sporangia* all over the lower surface except for a narrow marginal strip.

TRINIDAD. Northern part: 16 collections.

VENEZUELA. Sucre: *Steyermark & Agostini 91193* (US); *Steyermark & Rabe 96119* (U, ster.).—Aragua: *Oberwinkler 14678* (M, ster.).

See also note 4.

**Habitat.** On the ground or on rocks in wet forest gullies. Altitude: 200–900 m.

**Spores.** *Jermy 2638* (BM), *2640* (BM), *2906* (BM): the majority normal, a minority shrivelled. *Fendler 101* (isotype, GH):  $\pm$  equal parts normal and abnormal. *Fendler 101* (isotype, BM), *Homersley 61b* (US): the majority abnormal. *Fendler 101* (holotype): all abnormal, the greater part shrivelled, a few normally shaped but empty; a few sporangia with aborted S.M.C.'s.

**Notes.** 1. Closely related to the other species of the series, to *B. oligarchica* in particular. The latter differs amongst others in leaf architecture, in texture, and in the shape of the base of the pinnae.

2. A few plants were found with leaves composed of only two alternately placed pinnae and a markedly asymmetrical terminal segment. *Fendler 101* (MO) contains also a plant consisting of four small simple sterile leaves with a  $\pm$  symmetrical base. One simple fertile leaf was found, see fig. 56: c.

3. In the greatest part of the material the rhachis is more or less flexuous and often finely spotted by the darker scars of the scales.

4. I have my doubts about the following locality records: Jamaica (*Fielding s.n.*, BRI), and Ecuador (*Hinds s.n.*, 'brought on board', US); these are excluded from the distribution map.

## 22. *Bolbitis nicotianifolia* (Swartz) Alston—Fig. 58: a–e.

*B. nicotianifolia* (Swartz) Alston, Kew Bull. (1932) 310; C. Chr., Ind. Fil., Suppl. 3 (1934) 49, 198; Vareschi in Lasser, Fl. Venezuela 1 (1969) 373, p.p.—*Acrostichum nicotianifolium* Swartz, Syn. Fil. (1806) 13, 199 ('*nicotianaefolium*'); Poiret in Lam., Enc., Suppl. 1 (1810) 122; Willd., Spec. Pl. 5 (1810) 118; Hooker, Garden Ferns (1862) pl. 26 (excellent); Spec. Fil. 5 (1864) 275, p.p.; Baker in Hooker & Baker, Syn. Fil. (1868) 419, p.p.; in Martius, Fl. Bras. 1, 2 (1870) 589, pl. 39: fig. 9, p.p.—*Gymnopteris nicotianifolia* Presl, Tent. Pterid. (1836) 244; Fée, Hist. Acrost. (1845) 86, *quoad nomen solum*; J. Smith, Ferns Br. For. (1866) 118, p.p.; Christ, Farnkr. Erde (1897) 51, p.p.—*Anapausia nicotianifolia* Presl, Epim. Bot. (1851) 189.—*Chrysodium nicotianifolium* Mettenius, Fil. Lips. (1856) 22, *quoad nomen solum*.—*Leptochilus nicotianifolius* C. Chr., Bot. Tidsskr. 26 (1904) 285; Maxon, Sc. Surv. Porto Rico & Virgin Is. 6 (= Pterid. Porto Rico & Virgin Is.) (1926) 459.—Type: *Ventenat s.n.*, Lesser Antilles, Virgin Is., St. Thomas (S-PA). See note 5. *Acrostichum acuminatum* Willd., Spec. Pl. 5 (1810, January) 116, p.p., non Jussieu ex Poiret in Lam. (1810, September).—*Gymnopteris acuminata* Presl, Tent. Pterid. (1836) 244; Fée, Hist. Acrost. (1845) 85, p.p., pl. 46: fig. ii.—*Anapausia acuminata* Presl, Epim. Bot. (1851) 188.—*Chrysodium acuminatum* Mettenius, Fil. Lips. (1856) 22.—*Photinopteris acuminata* Morton, Contr. U.S. Nat. Herb. 38 (1967) 31.—L e c t o t y p e (Presl, 1851): Plumier, Tract. Fil. Amer. (1705) 100, pl. 115, 'Lingua cervina, scandens, Citrei foliis, major' drawn from *Plumier s.n.*, Lesser Antilles, eastern Martinique, St. Maria (P-JU). See note 6. *Gymnopteris acuminata* Presl var. *heterophylla* Fée, Hist. Acrost. (1845) 86.—Type: *Anonymous (Herminier?)*, Lesser Antilles, Guadeloupe (P, 3 sh., '*Acrostichum fallax* Bory', MS). *Acrostichum nicotianifolium* Swartz var. *saxicolum* Jenman, Bull. Bot. Dept. Jamaica (Kingston) n.s. 5 (1898) 153.—Type: *Jenman s.n.*, Greater Antilles, Jamaica (K).



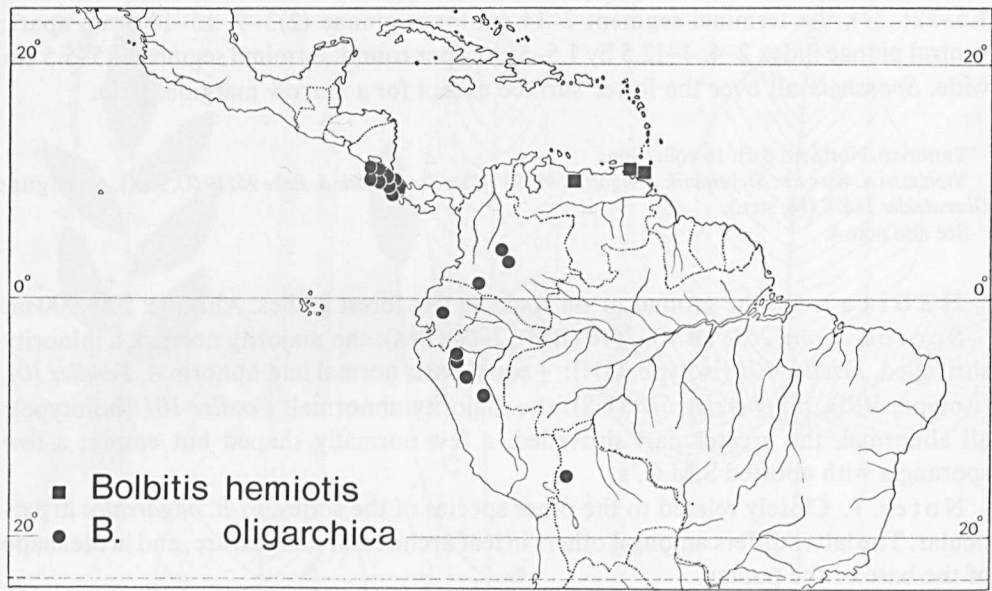


Fig. 57. Distribution of *Bolbitis hemiotis* and *B. oligarchica*.

*Leptochilus nicotianifolius* (Swartz) C. Chr. var. *simplex* Rosenst., Fedde Rep. 22 (1926) 23.—Type: *Brade* ('*Brade & Brade*') 552, Costa Rica, Llanuros de San Carlos, 200 m alt. (S-PA).  
*Leptochilus killipii* Maxon, Amer. Fern J. 21 (1931) 138.—*B. killipii* Lellinger, Fern Gaz. 11 (1975) 107.—  
 Type: *Killip* 2778, Panama, 4 miles above Juan Diaz (US; iso in B, P, S-PA).  
*B. bradeorum* auct. non (Rosenst.) Ching; Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 47, p.p.

Rhizome creeping or climbing, up to 15 cm long, up to 15 mm thick, slightly ribbed. Scales of the rhizome: index 4–9, 5–10 by 0.5–1.5 mm, opaque to subclathrate, dark brown or blackish. Leaves rather close together to up to 45 mm apart, glabrescent. *Sterile leaves* usually pinnate, rarely simple. Pinnate leaves 40–125 cm long; petiole 14–55 cm long, near the base 2.5–6 mm thick, with 7–18 vascular bundles; lamina index 1–2(–3), usually widest about, sometimes below the middle, 20–65(– > 70) by 15–40(–60) cm, without the terminal segment 0.5–25(–40), the terminal segment 20– > 45 cm long, thin-herbaceous, light to dark green, without bulbils; pinnae usually alternate, 2–10, 0–80 mm apart; central pinnae index 2–5, usually widest about or below, rarely above the middle, (5.5–)13–37 by (2–)3.5–9.5 cm, usually with a proportionally large central part with parallel margins, sometimes biconvex, the upper half slightly falcate or not, the basal half usually somewhat asymmetrical, base variously truncate, margin entire or slightly sinuate, apex attenuate or acuminate; the two lowermost pinnae usually ± conform to the central ones, sometimes with a more or less marked basal basispic lobe, sessile or up to 7 mm stalked, the uppermost pinnae usually sessile, sometimes the basispic side of the base shortly adnate to the rhachis; *terminal segment* 5–14 cm wide;

costa and secondary veins stramineous, tertiary veins slightly prominent, stramineous or concolorous, other veins immersed or almost so, usually concolorous with the lamina, sometimes stramineous, the secondary veins spreading and ending some distance from the margin; venation pattern illustrated in fig. 58: d. *Simple leaves* 29–44 cm long; petiole 7–16 cm long; lamina index 3–4, 21–30 by 6–9 cm, otherwise similar to the terminal segment of pinnate leaves.—*Fertile leaves*. Pinnate leaves 30–110 cm long; petiole 20–65 cm long; lamina index 1–3, widest somewhat below or about the middle, 12–50 by 7–25 cm, without the terminal segment 2–30, the terminal segment 8–20 cm long; pinnae 2–10, 20–85 mm apart; central pinnae index 2–6, 4–14.5 by 0.8–3 cm, base truncate to subcordate, the apex acute or orbicular; the two lowermost pinnae sessile or up to 7(–14) mm stalked, the two uppermost pinnae sessile to shortly adnate to the rachis; terminal segment 1.5–4.5 cm wide. *Simple leaves* 32–40 cm long; petiole 20–28 cm long; lamina index 4–7, 10–18 by 2–4.5 cm, otherwise similar to the terminal segment of pinnate leaves. *Sporangia* all over the lower surface, except for a usually indistinct marginal strip.

GUATEMALA. *Standley* 24202 (GH, US), 49365 (US); *Von Türckheim II* 1077 (BR), 8829 (US).

HONDURAS. *Ray* 2139 (GH); *Shank & Antonio Molina R.* 4873 (GH); *Standley* 52943 (F, US), 54164 (US).

COSTA RICA. 10 collections.

JAMAICA. 8 collections.

DOMINICAN REPUBLIC. 10 collections.

PUERTO RICO. 10 collections.

VIRGIN IS. *Ventenat s.n.* (type of *Acrostichum nicotianifolium*).

GUADELOUPE. 11 collections.

MARTINIQUE. *Bélanger s.n.* (P); *Duss* 1699 (B, US); *Hahn* 10 (BM, P).

BRITISH GUYANA. *Appun* 882 (K); *Jenman* 2142 (K, U); *Mell & Mell* 207 (US); *Schomburgk s.n.* (K).

SURINAM. *Kappler* 8 (L); *Schulz* 8922 (GH), 10252 (US).

FRENCH GUYANA. *LePrieur* 62 (G, P); *Mélinon* 364 (P); (*ex herb.?*) *Rudge s.n.* (BM).

PANAMA. 12 collections.

COLOMBIA. 10 collections.

ECUADOR. *Sodirol s.n.*, 1883 (K, UC), *s.n.*, 1891 (P); *Verleyesen s.n.* (P).

PERU. 7 collections.

See also note 8.

**Habitat.** Terrestrial or on tree bases; in rain forest. Altitude: up to 600 m.

**Spores.** *Haught* 1432 (US), *Herminier s.n.* (L, 908.328–291), *Killip & Garcia* 33530 (US); the greater part normal. *Cuatrecasas & Llano* 24199 (US), *Schunke* 372 (US); the greater part abnormal. *Haught* 2037 (GH): sporangia filled either with aborted often clustered S. M. C.'s, or with shrivelled spores. See also notes 4, 5, and 7.

**Notes.** 1. A variable species which is in particular characterized by the combination of features from rhizome scales and leaves (architecture and texture). It is very close to *B. oligarchia* which has, to mention a salient character, ternate leaves with axillary bulbils, and to *B. pergamentacea* with which it was long confused by many authors.

2. Generally the specimens from Central America and western tropical South America have more prominent and more stramineous veins which are, moreover, arranged in a more coarsely reticulated venation pattern, if compared with those from the West Indies and Guyana.

3. The terrestrial specimens usually have their leaves in two rows. Large epiphytes

(only known from Colombia and Peru) may have their leaves arranged in 4 or 5 rows. The rhizome anatomy of these epiphytes is similar to that of *B. lindigii* and *B. bernoullii*, but sclerenchyma strands are included in the ground tissue.

4. Specimens with simple sterile and fertile leaves. Simple sterile leaves precede pinnate ones during development. The following specimens have both simple fertile and sterile leaves:

*Spruce 4636* (syntype of *Acrostichum oligarchicum*). Spores nearly all shrivelled or otherwise abnormal, a few obviously normal. The sterile laminas agree in detail with the sterile pinnae of *Spruce 28* (P), which represents a large plant of which the greater part of the spores is abnormal.

*Killip 2778* (type of *Leptochilus killipii*). Spores: the US specimen: nearly all normal, a considerable number of the sporangia young; the S-PA specimen: likewise but young sporangia lacking. Except for the leaf architecture the plants agree in detail with those of *Killip 2753* (GH, US) which was collected from a similar habitat ('muddy banks of a small stream') near the site where *Killip 2778* was gathered. The GH sheet of *Killip 2753* comprises a plant with pinnate leaves as well as one with simple sterile leaves. The latter matches those of *Killip 2778* in detail.

*Brade 552* (type of *Leptochilus nicotianifolius* var. *simplex*). Spores all shrivelled or otherwise abnormal.

5. The holotype of *Acrostichum nicotianifolium*. Ventenat's collection represents an intermediate leaf composed of two fertile pinnae to one side, two sterile pinnae to the other, and a fertile terminal segment. The few scales present on the petiole base are proportionally wide, opaque, and light brown. They resemble those present on the rhizome of *Von Türckheim 2822* (L), regarded as a deviating specimen and presumably a hybrid between the present species and *B. pergamentacea* (see note 7). The shape, texture, and venation pattern of the sterile pinnae are typical. The fertile pinnae have a narrow sterile marginal strip. The strip is inconspicuous in the present species and usually  $\pm$  conspicuous in *B. pergamentacea*. A considerable number of the relatively few sporangia are juvenile, the mature ones present are for the greater part filled with mostly aborted S.M.C.'s and less so with abnormal spores. *B. pergamentacea* has not been recorded from St. Thomas.

6. Morton lectotypified *Acrostichum acuminatum* by the other syntype: *Anonymus s.n.*, Asia ('Malaspina, Peru'), ster. (B, herb. Willdenow 19539) which represents the common Malesian fern *Photinopteris speciosa* (Bl.) Presl. Consequently, he proposed the new combination *Photinopteris acuminata* (Willd.) Morton. His efforts were against the Code (Hennipman, Blumea 22, 1974, 51).

7. Deviating specimens. A considerable number of more or less atypical specimens were met. From their shape and the data of the spores it is concluded that hybridization is commonly encountered in this species.

a. Specimens with but two alternate pinnae, a rather firm texture and a rather coarse venation pattern. They are reminiscent of *B. oligarchica*. Here belong: *Allen 2132* from Panama (MO), a small specimen, the fertile leaf showing abnormal spores only; *Wendland 787*, from Costa Rica (W), a large specimen, the fertile leaf with sporangia mostly filled with a cluster of abnormal spores, some obviously normal spores also present.

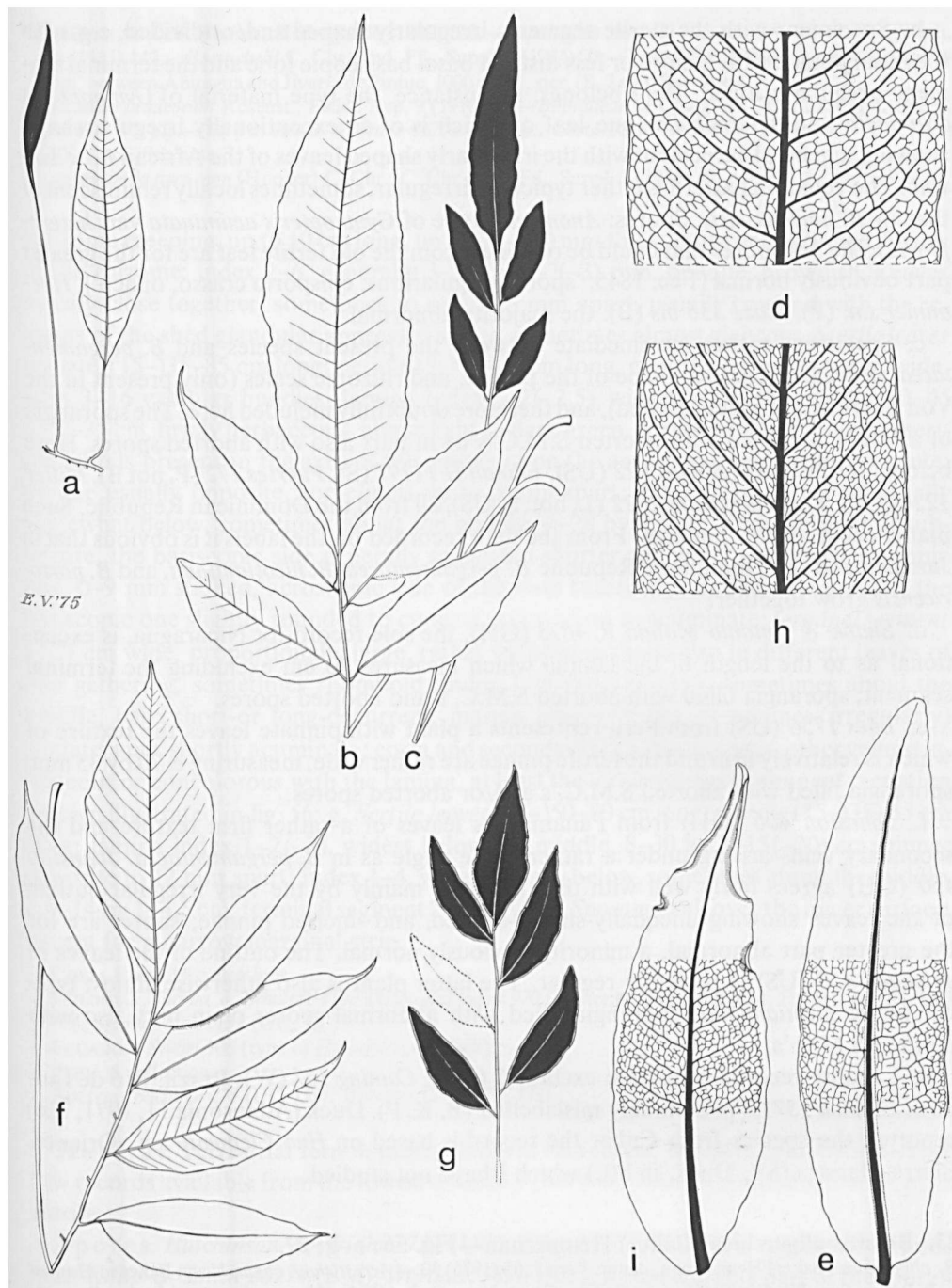


Fig. 58. a-c. *Bolbitis nicotianifolia*. a-c. sterile and fertile leaves,  $\times 1/5$ ; d. venation pattern of sterile pinna,  $\times 4/5$ ; e. ibid. of fertile pinna (a. Killip 2778, P, isotype of *Leptochilus killipii*; b, c. Herminier s.n., L 908.289-052; d. Maxon 9316, US; e. Anonymus (Wright?) 690, L).—f-i. *Bolbitis pergamentacea*. f, g. fertile and sterile leaf resp.,  $\times 1/5$ ; h. venation pattern of sterile pinna,  $\times 4/5$ ; i. ibid. of fertile pinna (f, i. Wright 788, L; g. Eggers 2755, L; h. Linden 2117, L).

b. Specimens with the sterile segments irregularly shaped and/or divided, e.g. with the basal pinnae with a more or less distinct basal basisopic lobe and the terminal segment irregularly lobed. Here belongs, for instance, the type material of *Gymnopteris acuminata* var. *heterophylla*. one leaf of which is of an exceptionally irregular shape showing a general agreement with the irregularly shaped leaves of the African *B. × boivinii*. The venation pattern is either typical or irregular, sometimes locally reminiscent of that of *B. portoricensis*. Spores: *Anonymus* (type of *Gymnopteris acuminata* var. *heterophylla*): the few spores that could be obtained from the old fertile leaf are for the greater part obviously normal (Fée, 1845: 'sporis irregularibus, episporio crasso, opaco'). *Hermannier s.n.* (P), *Mazé 336 bis* (B): the majority abnormal.

c. Specimens rather intermediate between the present species and *B. pergamentacea* as regards texture, shape of the pinnae, and rhizome scales (only present in the Von Türckheim collection cited), and therefore doubtfully included here. The sporangia of all these are filled with aborted S.M.C.'s or in part also with aborted spores. Here belong, for instance, *Abbott 822* (US), *Ekman H 11197* (S), *Fuertes 772* (P, not B), *Miller 1226* (US), *Von Türckheim 2822* (L, not: S, US), all from the Dominican Republic. Such plants occur also in Jamaica. From the data recorded on the labels it is obvious that in Jamaica and the Dominican Republic *B. pergamentacea*, *B. nicotianifolia*, and *B. portoricensis* grow together.

d. *Shank & Antonio Molino R. 4873* (GH), the sole record for Nicaragua, is exceptional as to the length of the lamina which measures 40 cm excluding the terminal segment; sporangia filled with aborted S.M.C.'s and aborted spores.

e. *Bües 1756* (US) from Peru represents a plant with pinnate leaves the texture of which is relatively firm and the fertile pinnae are rather wide, measuring *c.* 70 by 35 mm; sporangia filled with aborted S.M.C.'s and/or aborted spores.

f. *Johnston 406* (GH) from Panama has leaves of a rather firm texture and the secondary veins arising under a rather acute angle as in *B. pergamentacea*. *Johnston 450* (GH) agrees fairly well with this, differing mainly by the very irregular outline of the leaves showing unequally-sized, -shaped, and -incised pinnae; spores are for the greater part abnormal, a minority obviously normal. The outline of the leaves of *Johnston 450* (US) is perfectly regular. The latter plant is also otherwise almost typical for *B. nicotianifolia*; sporangia filled with abnormal spores or in part also with aborted S.M.C.'s.

8. Locality records which are excluded: Chile, *Cuming 157* (W); Brazil, Rio de Janeiro, *Glaziou 15715*, presumably mislabelled (B, K, P). Duek (*Adansonia* 11, 1971, 726) reported the species from Cuba; the record is based on *Hno Clemente s.n.*, Oriente, Sierra Maestra (SV, Duek, in litt.) which I have not studied.

### 23. *Bolbitis oligarchica* (Baker) Hennisman—Fig. 56: e–g; 57.

*B. oligarchica* (Baker) Hennisman, Amer. Fern J. 65 (1975) 30.—*Acrostichum oligarchicum* Baker in Hooker & Baker, Syn. Fil. (1868) 418, *p.p.*; Sodiro, Crypt. Vasc. Quit. (1893) 493, *quoad nomen solum*.—*Gymnopteris oligarchica* J. Smith, Hist. Fil. (1875) 138.—*Chrysodium oligarchicum* Salomon, Nomencl. Gefässskr. (1883) 136.—*Leptochilus oligarchicus* C. Chr., Bot. Tidsskr. 26 (1904) 285.—Lectotype (Maxon, Amer. Fern J. 21, 1931, 139): *Spruce 4737*, Peru, San Martin, Mt. Guayrapurima near Tarapoto (K). See note 1.

*Hypoderris stuebelii* Hieron., Hedwigia 46 (1907) 323.—*Leptochilus stuebelii* Maxon, Proc. Biol. Soc. Wash. 46 (1933) 142.—*B. stuebelii* C. Chr., Ind. Fil., Suppl. 3 (1934) 50.—Type: *Stübel 906*, Ecuador, Tunguragua, between Abitagua and Jivaria de Pintuc, 1000 m alt., ster. (B, 2 sh.). See note 4.  
*Leptochilus bradeorum* Rosenst., Fedde Rep. 9 (1910) 70.—*B. bradeorum* Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 47, p.p.—Type: *Brade & Brade 367* ('s.n.'), p.p., Costa Rica, La Palma, 1400 m alt. (UC; iso in NY, ster.). See note 3.  
*B. pandurifolia* auct. non (Hooker) C. Chr.: C. Chr., Ind. Fil., Suppl. 3 (1934) 49, p.p.

Rhizome creeping, up to 10 cm long, up to 10(–15) mm thick, more or less ribbed. Scales of the rhizome: index 2–6, generally 3–10 by 1–2(–3) mm, opaque, brownish. Leaves usually close together, sometimes to up to 15 mm apart, usually covered with the remains of the shed glandular appressed scales, sometimes almost glabrous. *Sterile leaves* ternate, (15–)35–85 cm long; petiole (5–)10–45 cm long, near the base 1.5–6 mm wide, with 3–16 vascular bundles; lamina index 1–2(–2.5), widest below the middle, 10–45 by 7–35 cm, firmly herbaceous, above light to dark green, (primordia of) almost spherical bulbils present in the axils of the pinnae or on the acroscopic side of the petiolule; pinnae usually opposite, sometimes up to 5 mm apart; index 1–3(–4), widest usually somewhat below, sometimes about the middle, 4–28 by 2.5–13.5 cm, straight or sub-falcate, the basiscopic side generally somewhat shorter and wider than the acroscopic one, 0–9 mm stalked, acroscopic side of the base (narrowly to) broadly cuneate, the basiscopic one slightly rounded to cuneate, apex acute to acuminate; *terminal segment* 7–20 cm wide, proportionally large, rather variable in shape also in different leaves of one gathering, sometimes rhomboid, index 1–3, widest below, sometimes about the middle, base short- or long-decurrent, margin almost entire, sometimes (irregularly) sinuate, apex shortly acuminate; costa and secondary veins stramineous, other veins stramineous or concolorous with the lamina, at least the tertiary veins prominent; venation pattern illustrated in fig. 56: *g. Fertile leaves* (25–)50–80 cm long; petiole (15–)35–65 cm long; lamina index 1–2(–3), widest below the middle, 8–30 by 3–15(–20) cm; pinnae opposite to 12 mm apart; index 1–4, widest usually below, sometimes about the middle, 2.5–14 by 1–4.5 cm; terminal segment 2–9 cm wide. *Sporangia* all over the lower surface, except for a narrow marginal strip.

COSTA RICA. 13 collections.

COLOMBIA. *Idrobo & Schultes 1113* (US); *Kalbreyer 970* (B, ster.); *Klug 1873* (BM, F, GH, MICH, MO, NY, S); *Plowman 2132* (GH, L).

ECUADOR. *Stübel 906* (type of *Hypoderris stuebelii*).

PERU. 8 collections.

BOLIVIA. *Buchtien 273* (UC, US); *Williams 1293* (GH, US).

**Habitat.** Terrestrial fern in moist places in rain forest. Altitude: 300–1600 m. Only few records available from the lowest altitudes. Obviously locally common, though often sterile.

**Spores.** *Hutchinson & Wright 3712* (UC), *Klug 1873* (MICH): the greater part normal. *Killip & Smith 26174* (BM), *Wurdack 1896* (NY): a considerable part of the sporangia aborted; a minority of the spores normal, the others, though usually normally shaped, mostly small and empty, sometimes shrivelled.

**Notes.** 1. Maxon (1931) first noted that the material upon which Baker based his

'inadequate and misleading' description of *Acrostichum oligarchicum* is a mixture of two elements. Maxon referred the other syntype, *Spruce 4636* from the same place, to *Leptochilus killipii* (= *B. nicotianifolia*). Ching, during 1931, annotated the material of the present species in Kew and Paris as *Bolbitis oligarchica* (Baker) Ching. Christensen (1934) who as a rule based himself on Ching as far as the new combinations in *Bolbitis* were concerned, obviously ignored Ching as regards the nomenclature of this species and referred Baker's species to *B. pandurifolia*.

2. Apart from *B. oligarchica* (see note 1) Ching (in C. Chr., 1934) also recognized *B. bradeorum* to which he referred *Leptochilus killipii* (= *B. nicotianifolia*) as a synonym.

3. Apart from the type collection of *Leptochilus bradeorum* I found two other collections from Costa Rica annotated by Rosenstock as '*Leptochilus Bradeorum* Ros. n. sp.' which are, however, not cited with the original description: *Brade & Brade 367*, p.p. (B, S-PA, US), gathered from the type locality on a different date (22-vi-1910) and also representing this species, and *Brade 552*, Llanuros de San Carlos, 200 m alt., v-1910 (S-PA), type of Rosenstock's *Leptochilus nicotianifolius* var. *simplex* (= *B. nicotianifolia*)!

4. The typification of *Hypoderris stuebelii*. Hieronymus reported this fern from two localities. He based himself solely on one collection composed of two sterile leaves. On the label of this sheet Stübel mentioned the second locality where he had seen (not collected!) this fern.

5. The petiole of this species is rather fleshy and has proportionally slender vascular bundles.

6. Juvenile leaves. A few, old, decaying leaves have in the axils of the two pinnae a short rhizome bearing one small simple leaf with an inconspicuous bulbil situated at the lamina base (fig. 56: f). The venation pattern of the small leaf is somewhat simpler than that of the large ones.

7. The species is closest to *B. hemiotis*. For differences see there. It occurs in part sympatric with *B. nicotianifolia*, but is apparently confined to higher altitudes.

#### 24. *Bolbitis pergamentacea* (Maxon) Ching—Fig. 58: f-i; 59.

*B. pergamentacea* (Maxon) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 49; Vareschi in Lasser, Fl. Venezuela 1 (1969) 372.—*Leptochilus pergamentaceus* Maxon, J. Wash. Acad. Sc. 14 (1924) 144; Sc. Surv. Porto Rico & Virgin Is. 6 (= Pterid. Porto Rico & Virgin Is.) (1926) 460.—Type: *Underwood 1426*, Jamaica, Green River Valley, 750 m alt. (US, 2 sh.).

*Leptochilus turrialbae* Rosenst., Fedde Rep. 22 (1925) 22.—*B. turrialbae* Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 50.—Type: *Brade & Brade 370*, Costa Rica, Turrialba, 650 m alt. (S-PA).

*Acrostichum nicotianifolium* auct., non Swartz c. syn. homot.: auct. p.p., see *B. nicotianifolia*.

Rhizome creeping, up to 15 cm long, up to 10 mm thick, slightly ribbed. Scales of the rhizome: index 1-2, up to 6(-15) by 4(-10) mm, the central and upper part (sub) clathrate, the basal part opaque, light or rusty brown. Leaves rather close together to 35 mm apart, glabrescent. *Sterile leaves* pinnate, (25-)50-140 cm long; petioles

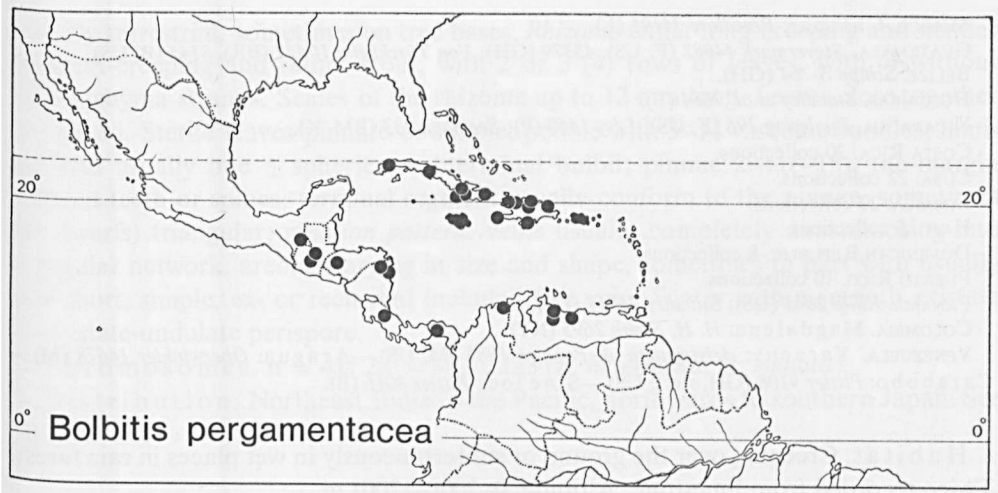


Fig. 59. Distribution of *Bolbitis pergamentacea*.

(10–)20–80 cm long, near the base 2–10 mm thick, firm, with 9–20 vascular bundles; lamina index 1–2, widest usually below, sometimes about the middle, (15–)25–60 by (9–)20–50 cm, without the terminal segment 0–20, the terminal segment 15–45 cm long, pergamentaceous, light (to dark) green, usually with a glaucous tinge, without bulbils; pinnae usually alternate, 2–6, 0–60 mm apart; central pinnae index (1–)2–4 (–5), widest usually about, sometimes below or above the middle, (8–)13–32.5 by (2.5–)4–15 cm, usually somewhat asymmetrical with the basiscopic side larger than the acroscopic one, and the basiscopic margin convex, the acroscopic one convex or sigmoid, base usually oblique with its acroscopic side narrowly cuneate, its basiscopic one (broadly) cuneate to rounded, sometimes symmetrical, cuneate, margin usually entire, sometimes especially towards the apex (irregularly) sinuate, apex acuminate; the two lowermost pinnae 0–6 mm stalked, conform to the central pinnae; uppermost pinna usually with the basiscopic side shortly adnate to the rhachis, rarely sessile; *terminal segment* usually about rhomboid, rarely biconvex, 60–200 mm wide; costa and secondary *veins* stramineous, other veins immersed or almost so, concolorous with the lamina, secondary veins arising under an acute angle, conspicuous nearly to the margin; venation pattern illustrated in fig. 58: h. *Fertile leaves* (25–)50–135 cm long; lamina index 1–4, usually widest somewhat below, sometimes about the middle, 12–45 by 5–25 cm, without the terminal segment 0–30, the terminal segment 9–20 cm long; pinnae 2–8, 0–100 mm apart; central pinnae index 3–6, (3.5–)6–15.5 (–19) by 1–5.5 cm, apex acute or rounded; the two lowermost pinnae 1–12 (–30) mm stalked; terminal segment 20–60 mm wide. *Sporangia* all over the lower surface except for a generally conspicuous sterile marginal strip.

Chromosomes.  $2n = 82$ .



MEXICO. Chiapas: *Breedlove 34191* (L).  
GUATEMALA. *Steyermark 44982* (F, US), *45379* (GH); *Von Türckheim II 422* (BR), *8145* (B, US).  
BELIZE. *Schipp S-764* (GH).  
HONDURAS. *Standley et al. 7034* (F).  
NICARAGUA. *Englesing 296* (F, US); *Lévy 1460* (P); *Seemann 233* (BM, K).  
COSTA RICA. 20 collections.  
CUBA. 22 collections.  
JAMAICA. 20 collections.  
HAITI. 5 collections.  
DOMINICAN REPUBLIC. 8 collections.  
PUERTO RICO. 10 collections.  
PANAMA. *Killip 2863* (US); *Standley 26217* (US).  
COLOMBIA. Magdalena: *H. H. Smith 2695* (NY).  
VENEZUELA. Yaracuy: *Aristeguieta & Pannier 1885* (M, US).—Aragua: *Oberwinkler 14678* (M).—  
Carabobo: *Pittier 9108* (GH, ster.; US).—Sine loc.: *Pittier 8016* (B).

**Habitat.** Creeping over the ground or subterraneously in wet places in rain forest. Twice recorded from limestone. Altitude: 0–700(–1200) m.

**Spores.** *Eggers 2755* (L), *Webster 4158* (MICH): nearly all normal. *Underwood 1426* (holotype of *Leptochilus pergamentaceus*): a considerable part (the majority?) shrivelled or otherwise abnormal. *Anonymus s.n.* (P, the specimen illustrated by Fée, 1845, 'Linden 2117'), *Aristeguieta & Pannier 1885* (US), *Hioram s.n.* (GH), *Pittier 9108* (GH), *Valeur 340* (SING): the majority of the spores shrivelled or otherwise abnormal. *Brade & Brade 370* (type of *Leptochilus turrialbae*): the mature sporangia present all filled with (a cluster of) abnormal mostly shrivelled spores.

**Notes.** 1. A clear-cut species which, however, has been combined with *B. nicotianifolia* by most authors. Fée (1845) already recognized these two species; incorrectly he used the names *Gymnopteris acuminata* and *G. nicotianifolia*. Both Fée and Maxon (1924) listed a number of differences between the two species. But the best distinguishing characters are features of the rhizome scales and the texture of the sterile leaf, not mentioned by them. *B. nicotianifolia* grows (exclusively?) on rocks and trees, whereas *B. pergamentacea* grows on or in soil.

2. A few specimens were found with all but one of the features of *B. pergamentacea*. *Blauner 303* (BM) has the outline of the segments of the sterile leaf intermediate between the present species and *B. nicotianifolia*; spores: the greater part shrivelled. *Von Türckheim 2648* (W) has one of the two lowermost pinnae with a distinct basal basiscopic lobe, the other with a free pinnule; spores: sporangia filled with aborted S.M.C.'s and/or aborted spores. The outline of the sterile leaves of the latter is reminiscent of that described for *B. nicotianifolia* in note 7.

## 6. Series *Heteroclitae* Hennipman, *ser. nov.*

Lamina simplex vel pinnata pinna terminali, bulbillo subterminali, marginibus pinnarum integris, sine spinis vel dentibus. Ordinatio venularum: venulae plerumque regulariter reticulatae, areolis statura ac forma diversis; internum venulis inclusis liberis. Sporae perispora laevi cristata vel cristato-undulata.

**Typus:** *Bolbitis heteroclita* (Presl) Ching.

Usually terrestrial, sometimes on tree bases. *Rhizome* either long-creeping and slender or short-creeping and rather stout, with 2 or 3 (4) rows of leaves, with or without sclerenchyma strands. Scales of the rhizome up to 12 mm long. *Leaves* close together to spaced. Sterile leaves pinnate or simple; petiole with 3–14 vascular bundles; lamina with usually one ± spherical subterminal bulbil; pinnae 2–11(–15), the margin without teeth or spines; terminal segment usually conform to the pinnae, sometimes (in dwarfs) triangular; *venation pattern*: veins usually completely anastomosing into a regular network, areoles varying in size and shape, sometimes in part with usually one short, simple, ex- or recurrent included free vein. *Spores* with a smooth, cristate or cristate-undulate perispore.

Chromosomes.  $n = 41$ ;  $2n = 82$ ,  $c. 123$  (*B. heteroclita*, *B. sinuata*).

Distribution. Northeast India to the Pacific, northwards to southern Japan. See fig. 27.

## 25. *Bolbitis heteroclita* (Presl) Ching—Fig. 60.

*B. heteroclita* (Presl) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 48; Tardieu-Blot & C. Chr., Not. Syst. 7 (1938) 102; Backer & Posthumus, Varenfl. Java (1939) 83, fig. 13; Tardieu-Blot & C. Chr. in Lecomte, Fl. Gén. I.-C. 7 (1941) 435; Holttum, Ferns Malaya (1954) 462, fig. 271; Iwatsuki, Acta Phytotax. Geobot. 18 (1959) 57, fig. 12; Copel., Fern Fl. Philip. (1960) 257; Ching, Fl. Hain. (1964) 165, fig. 75; DeVol & Kuo in Fl. Taiwan 1 (1975) 348, pl. 122.—*Acrostichum heteroclitum* Presl, Rel. Haenk. (1825) 15, pl. 2: fig. 2; Epim. Bot. (1851) 172.—*Heteroneuron heteroclitum* Fée, Hist. Acrost. (1845) 92 ('*Heteroneuron*').—*Chrysodium heteroclitum* Kuhn, Ann. Mus. Bot. Lugd.-Bat. 4 (1869) 294 ('*heterocliton*').—*Leptochilus heteroclitus* C. Chr., Ind. Fil. (1906) 385; Christ, Bull. Herb. Boiss. II, 6 (1906) 1005; Philip. J. Sc. 2 (1907) Bot. 159; v.A.v.R., Handb. Malayan Ferns (1908) 739.—*Campium heteroclitum* Copel., Philip. J. Sc. 37 (1928) 359, fig. 13; Backer & Posthumus, Nat. Tijdschr. Ned. Ind. 93 (1933) 163.—Type: *Haenke s.n.*, Philippines, Luzon, Sorsogon (PRC; iso in B, 2 sh., BR, W, 2 sh.; all ster.).

*Nephrodium cuspidatum* Presl, Rel. Haenk. (1825) 31 ('*Nephrodium?*').—*Polystichum cuspidatum* Presl, Tent. Pterid. (1836) 82.—*Heteroneuron cuspidatum* Presl, Epim. Bot. (1851) 169.—*Chrysodium cuspidatum* Kuhn, Ann. Mus. Bot. Lugd.-Bat. 4 (1869) 293, *p.p.*—*Leptochilus cuspidatus* C. Chr., Ind. Fil. (1906) 384, *quoad nomen solum*.—*Campium cuspidatum* Copel., Philip. J. Sc. 37 (1928) 365, fig. 19.—*B. cuspidata* Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 48; Copel., Fern Fl. Philip. (1960) 259.—Type: *Haenke s.n.*, Philippines, Luzon, Sorsogon, ster. (PRC; iso in W, '77').

*Acrostichum flagelliferum* Wall. ex Hooker & Grev., Ic. Fil. (1827) pl. 23, *p.p.*; Bl., Enum. Pl. Jav. (1828) 104; Fl. Java Fil. (1829) 37, pl. 13, *p.p.*; Kunze, Bot. Zeit. (1848) 102; Hooker, Spec. Fil. 5 (1864) 258, *p.p.*; Baker in Hooker & Baker, Syn. Fil. (1868) 418, *p.p.*; Clarke, Trans. Linn. Soc. Bot. 1 (1880) 579, *p.p.*—*B. flagellifera* Schott, Gen. Fil. (1835) *ad tab.* (13).—*Cyrtogonium flagelliferum* J. Smith, Hook. J. Bot. 4 (1841) 154.—*Chrysodium flagelliferum* Mettenius, Fil. Lips. (1856) 21, pl. 20: fig. 11; Ettingsh., Denkschr. K. Ak. Wiss. M.-N. Kl. Wien 22 (1864) 58, pl. 8: fig. 9.—*Poecilopteris flagellifera* J. Smith, Cat. Cult. Ferns (1857) 23; Bedd., Ferns Br. India (1865) pl. 112, *p.p.*; J. Smith, Ferns Br. For. (1866) 117.—*Gymnopteris flagellifera* Bedd., Ferns Br. India, Suppl. (1876) 27; Handb. Ferns Br. India (1883) 433; Christ, Farnkr. Erde (1897) 49; Copel., Polyp. Philip. (1905) 42, *p.p.*—Type: *Wallich s.n.*, a specimen of unknown origin cultivated at the Botanic Garden, Calcutta (K. herb. Hooker).

*Acrostichum proliferum* Bl., Enum. Pl. Jav. (1828) 104, *non* Hooker (1844) (= *B. subcrenata*).—Type: *Blume s.n.*, Java, Mt. Parang (*n.v.*).

*Leptochilus linnaeanus* Fée, Hist. Acrost. (1845) 87, pl. 47: fig. 2, *excl. syn.*; v.A.v.R., Handb. Malayan Ferns (1908) 735; *ibid.*, Suppl. (1917) 60.—*Dendroglossa linnaeana* Fée, Gen. Polyp. (1852) 81.—*Acrostichum linnaeanum* Hooker, Sec. Cent. Ferns (1861) pl. 26, *p.p.*; Spec. Fil. 5 (1864) 278; Baker in Hooker & Baker, Syn. Fil. (1868) 417; Christ, Bull. Herb. Boiss. 6 (1898) 206.—*Chrysodium linnaeanum* Kuhn, Ann. Mus. Bot. Lugd.-Bat. 4 (1869) 293, *p.p.*—*Chrysodium linnaeanum* Kuhn var. *sinuatum* Kuhn, Ann. Mus. Bot. Lugd.-Bat. 4 (1869) 293 ('*sinuata*'), *nom. illeg.*—*Gymnopteris linnaeana* Christ, J. de Bot. 19 (1905) 125; Copel., Polyp. Philip. (1905) 41.—*Leptochilus heteroclitus* (Presl) C. Chr.

- var. *linnaeanus* Christ, Philip. J. Sc. 2 (1907) Bot. 160.—*Campium linnaeanum* Copel., Philip. J. Sc. 37 (1928) 343, *quoad nomen solum*; Backer & Posthumus, Nat. Tijdschr. Ned. Ind. 93 (1933) 159, excl. syn.—*B. linnaeana* C. Chr., Ind. Fil., Suppl. 3 (1934) 198; Backer & Posthumus, Varenfl. Java (1939) 80.—Type: *Zollinger 1441*, West Java, Mt. Salak, Tjikoja (P; iso in BM, G).
- Cyrtogonium acuminatum* Brackenr. in Wilkes, U.S. Expl. Exp. 16 (1854) 86.—Type: *Brackenridge s.n.*, Philippines, Luzon, near Los Baños (US, 51087).
- Poecilopteris stenophylla* Kurz ex Teijsmann & Binnendijk, Nat. Tijdschr. N. I. 27 (1864) 15; Copel., Philip. J. Sc. 37 (1928) 393, *pro spec. dub.*—*B. stenophylla* Ching in C. Chr. Ind. Fil., Suppl. 3 (1934) 50.—Type: *Kurz s.n.*, West Java, Mt. Salak, 900–1200 m alt. (L, 908.289–062; iso in BM). See note 3.
- Chrysodium heteroclitum* (Presl) Kuhn var. *subcrenatum* Kuhn, Ann. Mus. Bot. Lugd.-Bat. 4 (1869) 294, p.p. ('heterocliton', 'subcrenata').—Type: *Zollinger 884x*, West Java, Mt. Salak, Tjikoja (P; iso in B, K, '884'). See note 4.
- Acrostichum modestum* Baker, J. Linn. Soc. 22 (1886) 231; C. Chr. in Copel., Philip. J. Sc. 37 (1928) 411.—*Leptochilus modestus* C. Chr., Ind. Fil. (1906) 386.—*Campium modestum* Copel., Brittonia 1 (1931) 76, fig. 1.—*B. modesta* Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 49.—Type: *C. Hose 159*, Borneo, Sarawak, Kako, Kriau (K; iso in BM, SING).
- Gymnopteris inconstans* Copel. in Perkins, Fragm. Fl. Philip. (1905) 177; Polyp. Philip. (1905) 43.—*Leptochilus inconstans* Christ, Bull. Herb. Boiss. II, 6 (1906) 1005.—*Leptochilus heteroclitus* (Presl) C. Chr. var. *inconstans* Christ, Philip. J. Sc. 2 (1907) Bot. 160.—*B. inconstans* Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 48.—Syn types: *Copeland 251*, Philippines, Luzon, Bataán, Mt. Mariveles, along Lamao R. (B, BM, P); *Merill 3128*, *ibid.* (B, K, P, US).
- Leptochilus heteroclitus* (Presl) C. Chr. var. *eurybasis* Christ, Philip. J. Sc. 2 (1907) Bot. 159.—*Campium heteroclitum* (Presl) Copel. var. *eurybasis* Copel., Philip. J. Sc. 37 (1928) 361.—Type: *Clemens 552*, Philippines, Mindanao, Lake Lanao, Camp Keithley, 660 m alt. (P; iso in MICH).
- Leptochilus heteroclitus* (Presl) C. Chr. var. *foxworthyi* Christ, Philip. J. Sc. 2 (1907) Bot. 160.—Type: *Foxworthy BS 68*, Philippines, Luzon, Prov. Rizal, Bosoboso (P; not MICH which is the type of *Campium foxworthyi* = *B. heteroclita*).
- Leptochilus sumatranus* v.A.v.R., Bull. Jard. Bot. Btzg II, 23 (1916) 15, pl. 2: fig. la—c; Handb. Malayan Ferns, Suppl. 1 (1917) 436; *ibid.*, Corrections (1917) 60.—Type: *Brooks 260.S*, South Sumatra, Bencoolen, Lebong Tandai (BO; iso in BM, P).
- Campium nigrum* Copel., Philip. J. Sc. 37 (1928) 361, fig. 14, pl. 10.—*B. nigra* Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 49.—Type: *Karigone 69*, Caroline Is., Ponape, ster., 1925 (UC, 267415).
- Campium pseudoscalpturatum* Copel., Philip. J. Sc. 37 (1928) 363, fig. 16, pl. 11.—*B. pseudoscalpturata* Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 49; Copel., Fern Fl. Philip. (1960) 261.—Type: *Ramos BS 14816*, Philippines, Mindanao, Camiguin de Mindanao (MICH).
- Campium foxworthyi* Copel., Philip. J. Sc. 37 (1928) 364, fig. 17, pl. 12.—*B. foxworthyi* Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 48; Copel., Fern Fl. Philip. (1960) 258.—Type: *Foxworthy BS 68*, Philippines, Luzon, Prov. Rizal, Bosoboso (MICH; not P which is the type of *Leptochilus heteroclitus* var. *foxworthyi*).
- Campium tenuissimum* Copel., Philip. J. Sc. 37 (1928) 364, fig. 18, pl. 13.—*B. tenuissima* Copel., Fern Fl. Philip. (1960) 259.—Type: *Copeland s.n.*, Philippines, Luzon, Laguna Prov., Los Baños, 17-iii-1906 (MICH, herb. Copeland 290).
- Leptochilus simplicifolius* Holttum, Gard. Bull. S. S. 4 (1929) 409.—*B. simplicifolia* Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 50; Holttum, Ferns Malaya (1954) 464, fig. 272.—Type: *Henderson SF 17977*, Malay Peninsula, Pahang, Cameron Highlands, Robinson's Falls, c. 1350 m alt. (K; iso in SING).
- Campium membranaceum* Copel., Philip. J. Sc. 40 (1929) 307, pl. 7.—*B. membranacea* C. Chr., Ind. Fil., Suppl. 3 (1934) 198; Fern Fl. Philip. (1960) 261.—Type: *Copeland s.n.*, Philippines, Mindanao, Mt. Matutum, v-1917 (MICH, herb. Copeland 11538; iso in UC, 352513).
- B. koidzumii* Tagawa, Acta Phytotax. Geobot. 6 (1937) 93; Ito, Fil. Liuk. (1938) 644.—Type: *Koidzumii s.n.*, Japan, Ryukyu Is., Iriomote, vii-1923 (KYO, n.v., L, phot.; iso in KYO, 2 sh., n.v., L, phot., US).
- B. annamensis* Tardieu-Blot & C. Chr., Not. Syst. 7 (1938) 100; in Lecomte, Fl. Gén. I.-C. 7 (1941) 436, fig. 50: 3 & 4.—Type: *Cadière 149*, Vietnam, Annam, Thanh Tan, 100–200 m alt. (BM; iso in P, 3 sh.).
- B. edanyoi* Copel., Philip. J. Sc. 81 (1952) 22, pl. 15; Fern Fl. Philip. (1960) 258.—Type: *Edaño PNH 8811*, Philippines, Mindanao, Davao Prov., Baguan R., 1525 m alt. (MICH; iso in PNH).
- Edanyoa difformis* Copel., Philip. J. Sc. 81 (1952) 22, pl. 17; Fern Fl. Philip. (1960) 265.—Type: *Edaño PNH 5213*, Philippines, Negros I., Oriental, Lake Balinsasayo (MICH; iso in PNH, 2 sh.).

[*Gymnopteris trilobata* J. Smith, Hook. J. Bot. (1841) 403, *nom. nud.*]

*Cyrtogonium diversifolium* auct. non (Bl.) J. Smith: J. Smith, Hook. J. Bot. 3 (1841) 403.

*Heteroneuron diversifolium* auct. non (Bl.) Fée: Fée, Hist. Acrost. (1845) 91, p.p. ('*Heteroneuron*').

*Dendroglossa lanceolata* auct. non (L.) Presl: Presl, Epim. Bot. (1851) 149, p.p.

*Leptochilus diversifolius* auct. non (Bl.) C. Chr.: Christ, Philip. J. Sc. 2 (1907) Bot. 160.

*Leptochilus cuspidatus* auct. non (Presl) C. Chr.: auct. japon. p.p. See: Tagawa, Acta Phytotax. Geobot. 6 (1937) 93

*Gymnopteris repanda* auct. non (Bl.) C. Chr.: auct. japon. p.p. See: Tagawa, Acta Phytotax. Geobot. 6 (1937) 93.

*B. interlineata* auct. non (Copel.) Ching: Ito, J. Jap. Bot. 14 (1938) 439, fig.

*B. diversifolia* auct. non (Bl.) Schott: Nayar & Kaur, Bull. Nat. Bot. Gard. Lucknow 88 (1964) 42, fig. 12, 19, 29, 62.

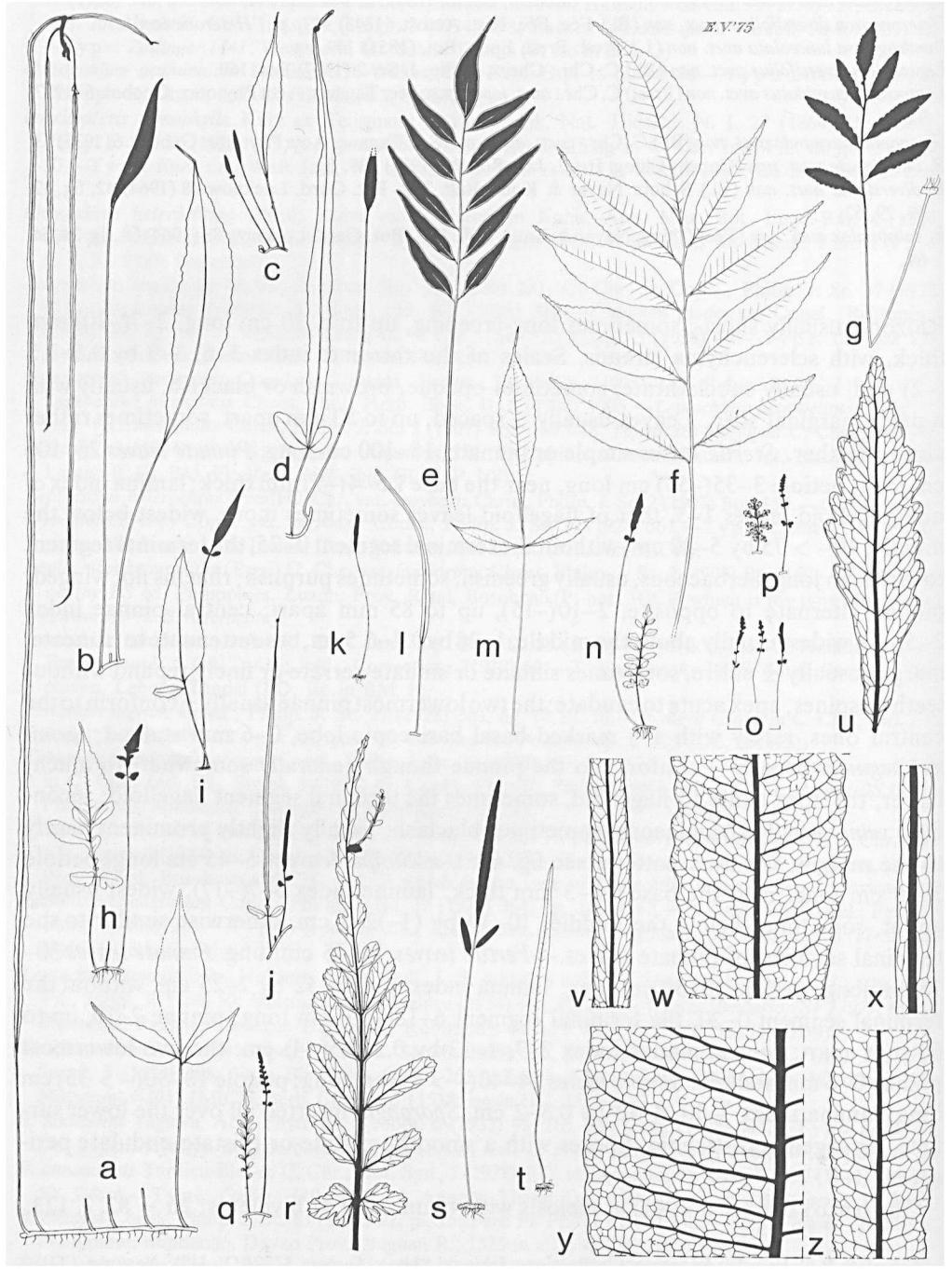
*B. subsimplex* auct. non (Fée) Ching: Nayar & Kaur, Bull. Nat. Bot. Gard. Lucknow 88 (1964) 68, fig. 24, 64, 69.

Rhizome usually short-, sometimes long-creeping, up to c. 20 cm long, 2–7(–10) mm thick, with sclerenchyma strands. Scales of the rhizome: index 3–6, 3–9 by 0.5–1.5 (–2) mm, usually subclathrate, sometimes opaque, brownish or blackish, usually with a paler marginal strip. Leaves usually  $\pm$  spaced, up to 50 mm apart, sometimes rather close together. *Sterile leaves* simple or pinnate, 15–100 cm long. *Pinnate leaves* 25–100 cm long; petiole 3–35(–55) cm long, near the base 1.5–4(–7) mm thick; lamina index of non-flagelloid leaves 1–5, that of flagelloid leaves sometimes more, widest below the middle, 10– > 75 by 5–30 cm, without the terminal segment 0–25, the terminal segment to > 75 cm long, herbaceous, usually greenish, sometimes purplish; rhachis not winged; pinnae alternate to opposite, 2–10(–15), up to 85 mm apart; central pinnae index 2–5(–7), widest usually about the middle, 1–26 by 0.7–6.5 cm, base attenuate to truncate, margin usually  $\pm$  entire, sometimes sinuate or sinuate-serrate or finely repand without teeth or spines, apex acute to caudate; the two lowermost pinnae usually  $\pm$  conform to the central ones, rarely with a  $\pm$  marked basal basisopic lobe, 0–6 mm stalked; *terminal segment* usually  $\pm$  conform to the pinnae though generally somewhat (to much) larger, the apex acute to flagelloid, sometimes the terminal segment flagelloid; secondary veins usually stramineous, sometimes blackish, usually slightly prominent nearly to the margin; venation pattern: see fig. 60: t–z. *Simple leaves* 15–45 cm long; petiole 3–18 cm long, near the base 0.5–3 mm thick; lamina index 3–7(–17), widest usually about, sometimes below the middle, 10–30 by (1–)2–7 cm, otherwise similar to the terminal segment of pinnate leaves.—*Fertile leaves* 14–75 cm long. *Pinnate leaves* 30–75 cm long; petiole 10–52 cm long; lamina index 1–4, 8–32 by 2–25 cm, without the terminal segment 0–20, the terminal segment 6–18(–30) cm long; pinnae 2–10, up to 60 mm apart; central pinnae index 2–7, 1–13 by 0.5–2.5(–4) cm; the two lowermost pinnae 0–6 mm stalked. *Simple leaves* 14–40(– > 45) cm long; petiole 10–30(– > 35) cm long; lamina index 3–10, 4–13 by 0.5–2 cm. *Sporangia* inserted all over the lower surface, arranged acrostichoid. Spores with a smooth, cristate or cristate-undulate perispore.

Chromosomes.  $n = 41$ ; at meiosis with 41 uni- and 41 bivalents;  $2n = 82$ ,  $c. 123$ .

JAPAN. S. Ryukyus, Iriomote: 6 collections. Ishigaki Shima: Fosberg 37801 (L, US); Nozu s.n. (TI).

CHINA. Kweichow: Cavalerie s.n. (BM, S-PA).—S. Yunnan: 7 collections.—Kwangtung: Mat-



thew s.n. (P); Tsoong 2842 (UC).—Kwangsi: Ko 56007 (A).—Hainan: Hancock 10 (K, US); Tsang 382 (= LU 17131) (B, BO, GH, K, UC, US).

TAIWAN. Tato, Gukutsu, Kwarenko: Matsuda s.n. (UC). Mt. Koto: Miyake s.n. (TI).

BANGLADESH. 9 collections.

NEPAL. East: Hara et al. 6305227 (US); Hooker s.n. (K).

SIKKIM. 5 collections.

INDIA. Assam: 14 collections.

BURMA. Northeast: Kaulback 250 (BM); Kingdon Ward 21615 (BM).—Southern: Meebold 17039 (S-PA).—Tenasserim: Falconer s.n. (L, M); Gallatly 64 (K); Parish s.n. (P).

MALAY PENINSULA. Kedah: Namen SF 38015 (A, BO, BRI, PNH, SING).—Perak: 7 collections.—Kelantan: Haniff & Nur SF 10354 (BM, BO, K, SING); Yapp 210 (B, K).—Trengganu: Holttum s.n. (SING).—Pahang: 13 collections.—Selangor: 5 collections.—Johore: Holttum SF 17700 (SING); Ridley 12510 (SING).—Langkawi Is.: Curtis s.n. (SING).—P. Penang: Anonymus s.n. (SING).—Singapore. Bt. Panjang (= Panjam): 5 collections.—P. Tioman: Henderson SF 18590 (BM, SING).

THAILAND. Northern: 6 collections.—Southeastern: 7 collections.—Southwestern: Van Beusekom 293 (L); Larsen 9588 (C).—Peninsula: Hennipman 3800 (L), 3835 (L); Tagawa et Yamada T 211 (BKF, L); Tagawa et al. T 5289 (L).

VIETNAM. Tonkin: 9 collections.—Annam: 12 collections.—Cochinchina: Pierre 5723 (P); Poilane 2482 (P, UC), 19467 (MICH, P).

SUMATRA. Atjeh: Asdat 54 (BO, K, L), 55 (BO, L).—Tapanuli: Rahmat si Boeea 5374 (L), 5577 (L); Surbeck 660 (L).—West Coast: Alston 13756 (BM), 14266 (BM).—East Coast: 5 collections.—Bencoolen (3 localities): Brooks 95.S (P), 99.S (BM, MICH, P), 226.S (BM, BO), 260.S (type of *Leptochilus sumatranus*), 7924 (BM); Hancock 56 (K); Van Steenis 3632 (BO).—Lamong Districts. Mt. Radjabasa: Posthumus 1106 (BO), 1112 (BO), 1128 (BO).—P. Simalur: Achmad 447 (BO, L, SING, U).—P. Engganor: Lütjeharms 3944 (BO, GH, L), 4040 (BO, GH, K, L, P).

JAVA. West: 15 collections.—Central: Docters von Leeuwen-Reijnvaan 929 (BO, L), 2007 (BO, L); Kostermans & Van Woerden 181 (BO).—East: 7 collections.—Christmas I.: 6 collections.

BORNEO. Sarawak: 10 collections.—Sabah: Allen 1631 (S-PA, SING).—Indonesian Borneo. West: Teuscher s.n. (BO, L); Teijsmann s.n. (BO). East: Kostermans 9518 (BO, L). Southeast: Hub Winkler 2225 (B). Northeast: (3 localities): Amdjah 443 (BO, L), 444 (BO), 562 (BO), 600 (BO), 670 (BO).—Anambas Is.: Van Steenis 953 (BO).

PHILIPPINES. Palawan: 7 collections.—Busuanga: Marche s.n. (P).—Mindoro: 6 collections.—Batanes Is.: Ramos BS 80160 (MICH, SING, UC), BS 80351 (BR, MICH, UC).—Babuyan Is.: Fénix BS 3912 (US).—Luzon: many collections.—Rombon: Bartsch 307 (US), 313 (US).—Samar: Wagner & Grether 4229 (MICH, UC, US).—Negros: Copeland s.n. (B, MICH, US); Edaña PNH 21374 (PNH); Elmer 9705 (BM, BO, K, L, MICH, MO, P, US, W), 10041 (G, MICH, P).—Panay: Paniza PNH 9243 (PNH).—Sulu Is. Jolo: Williams 3114 (UC, US). Tawitari: Kondo & Edaña PNH 38631 (K, PNH), PNH 38696 (K, L, PNH); Ramos & Edaña PNH 44024 (B, BO, P, SING, UC, US, W).—Mindanao: 15 collections.

CELEBES. North: 5 collections.—West Central: Posthumus 2323 (BO), 2331 (BO).—Southwest: Bünnemeijer 10914 (BO).—Southeast: Kjellberg 408 (BO, S-PA).

MOLUCCAS. Sula Is. Mangole: Bloembergen 4800 (BO, K, L, PNH, SING).

NEW GUINEA. West. Babo: Aët 93 (BO, L); Sorong: Djamhari 562 (BO); Vink (BW) 17580 (L). Bernhard Camp: Brass 13242 (GH, MICH, UC), 13902 (GH).—Northeast: 5 collections.—Papua: 6 collections.—Misoö: Teijsmann s.n. (BO, P).

Fig. 60. *Bolbitis heteroclita*.—a—s. sterile and fertile leaves,  $\times 1/5$ ; t—z. venation pattern of sterile pinnae,  $\times 4/5$  (a. Price 303, L; b. Holttum SF 31352, SING; c. Foxworthy BS 68, MICH, holotype of *Campium foxworthyi*; d. Edaña PNH 8811, MICH, holotype of *B. edanyoi*; e, f, m. Jacobs 7950, L; g, u. Price 452, L; h. Copeland 279, US; i. Holttum SF 21625, SING; j. Copeland s.n., MICH, holotype of *Campium tenuissimum*; k, v. Richards 2233, US; l. Hose s.n., SING, isotype of *Acrostichum modestum*; n. Ramos & Edaña BS 28843, P; o. Merrill 3128, L, 3 fertile leaves, syntype of *Gymnopteris inconstans*; p. Price 2518A, L, sterile and fertile leaf; q, r. Price 351, L; s, t. Backer 21291, BO; w. Tagawa & Iwatsuki 4690, L; x. Fox PNH 5060, MICH; y. Hennipman 3836, L; z. Holttum SF 24699, C).

SOLOMON IS. Bougainville: *Wakefield 1156* (BM); *Waterhouse 411 B* (K).—New Georgia. Kolombangara: *Braithwaite R.S.S. 4356* (L), *R.S.S. 4442* (L); *Whitmore & Grubb BSIP 2120* (US).—Malaita: *Templeton Crocker Exp. s.n.* (BISH).

CAROLINE IS. Ponape: 9 collections.—Kusaie: *Takamatsu 531* (BISH, BO, K, MICH).

Habitat. Creeping on rocks, in soil or on bases of trees in moist places in rain forest (often near streams), sometimes rheophytic. Altitude: 0–1500(–1750) m.

Spores. *Bamler 97* (UC), *Copeland, Pterid. Philip. exsicc. 279* (GH), *Elmer 18068* (L), *Hennipman 3836* (L), *Merrill 3128* (US, syntype of *Gymnopteris inconstans*), *Price 452* (L), *Richards 2233* (US): all or the greater part normal. *Braithwaite R.S.S. 4442* (L), *Brooks 260.S* (BO, type of *Leptochilus sumatranus*): about equal parts normal and abnormal. *Henderson SF 17977* (SING, type of *Leptochilus simplicifolius*): the majority abnormal. *Clemens 22001* (BO), *Copeland s.n.* (holotype of *Campium membranaceum*): the greater part abnormal. *Elmer 17554* (C), *Jacobs 7950* (L), *Tagawa & Iwatsuki 4732* (US): all abnormal. *Anonymus 33* (BISH), *Backer 21291* (BO), *Ledermann 13176* (B), *13279* (B), *13765* (B), *Takamatsu 953* (BISH): sporangia filled with aborted S.M.C.'s and/or aborted spores. See also the entries on variation.

Notes. 1. This species is closely related to *B. sinuata* from which it differs especially in the texture of the sterile leaves. Possible intermediates are discussed under *B. sinuata*, note 1.

Most of the material is easily recognizable. However, a considerable part represents (much) deviating facultative rheophytes and dwarfs. The latter material is not included in the description; it is discussed below. The present species takes part in the parentage of several hybrids (see there).

2. *Acrostichum proliferum* and *A. repandum* were described by Blume (1828) at the same time. *A. proliferum* was based on sterile material collected by Blume on Mt. Parang in Java. I have not found a proper type collection (obviously there has been a mixing of specimens of this species and of *B. repanda* when Blume's herbarium was remounted during 1908 and 1909) but the description is almost similar to that given by Blume for *A. flagelliferum*. Both should have ternate leaves which are typical for *B. heteroclita* and never occur in *B. repanda* to which Blume (1829) referred *A. proliferum*.

3. It remains uncertain whether Teijsmann & Binnendijk described *Poecilopteris stenophylla* from wild or from cultivated material.

4. *Zollinger 884*, the type of *Chrysodium heteroclitum* var. *subcrenatum* Kuhn, was also cited by Kuhn under *Chrysodium cuspidatum* in the same publication.

5. The geographical distribution. *B. heteroclita* is absent from the lowland plains and the proportionally dry areas in Burma, Thailand, Laos, Cambodia, and the Lesser Sunda Is.

The following collections have not been included in the distribution map:

a. *W. Smith s.n.* (M) from Anaimallai Hills, southern India; *Carruthers s.n.*, Ceylon (P, 'Kaulfuss Tauschverein'). From these areas the present species was unknown from the wild to Beddome, who knew the species of southern India particularly well, and to Blatter & d'Almeida (*Ferns of Bombay*, 1922). *B. heteroclita* was not rarely found cultivated in southern India.

b. *Dietrich s.n.*, southern Queensland, Brisbane R. (B). Possibly a mislabelled collection. This record awaits confirmation.

c. *Buchanan 118*, Fiji (B). The outline of the leaves is reminiscent of the type of *Poecilopteris stenophylla*. Presumably mislabelled. Buchanan eventually was Superintendent of the Botanic Garden at Calcutta; he made two or three voyages to eastern Malesia (not the Pacific) from which no herbarium material is known (Van Steenis-Kruseman, Fl. Mal. I, 1, 1950, 214).

6. Iwatsuki discussed the occurrence of *B. heteroclita* in Taiwan as reported in some papers by Japanese authors. According to him all these records are unreliable.

7. Ching (in C. Chr., 1934) regarded *Campium tenuissimum* and *B. inconstans* as synonymous, but kept *B. cuspidata* separate. Copeland (1960) argued about this view: 'but as I know these variable, "inconstant" little ferns in the field, *B. tenuissima* is distinguishable, but *B. inconstans* is *B. cuspidata*.'

8. Apart from *B. heteroclita* two names listed by Nayar & Kaur (1964) apply to the present species, i.e. *B. diversifolia* and *B. subsimplex* in their sense. The discriminating characters between these three species as given in their key did not hold in the reference material of *B. heteroclita* and *B. subsimplex* I received on loan. For *B. diversifolia* no reference material is cited; the description gave sufficient information.

9. Nayar & Kaur (1966) amply described the venation pattern of the fertile leaf of *B. subsimplex* in their sense, which should be diplodesmic (a term not mentioned by them). The only reference material cited is a badly preserved specimen in which I was unable to trace such a pattern. See also the general chapters.

10. As measured from cross-sections (paraffine method) of cultivated material, the thickness of the leaves of triploid *B. heteroclita* (origin: the botanic garden, Groningen) varies from 85–110  $\mu\text{m}$ , that of triploid *B. sinuata* (origin: *Johnson s.n.*, Singapore) varies from 285–315  $\mu\text{m}$ .

11. Uses. Hooker & Greville received the type of *Acrostichum flagelliferum* with Dr. Wallich's MS name and reference to Rheede's *Pannamara-maravara* (Hort. Malab. 12, 1703, 39, pl. 19). As already communicated by Hooker & Greville, Rheede ascribed great medicinal value to this plant. However, Rheede's plant cannot be properly identified; see *Species dubiae* no. 11.

12. Plants with leaves of a texture supposedly intermediate between those of the present species and of *B. sinuata* are discussed under *B. sinuata* (note 2). *Copeland 1543* (B, MICH, P, US), by Christ referred to *Leptochilus diversifolius*, has slightly thicker leaves than normal.

Variation. The morphological variation is outstanding. The following types are included:

A. Specimens with usually pinnate leaves of which the terminal segment is either conform to the pinnae or conform-flagelloid. The venation pattern shows maximum development or nearly so. These ferns include the type specimens of *Acrostichum heteroclitum*, *A. flagelliferum*, *Cyrtogonium acuminatum*, *Chrysodium heteroclitum* var. *subcrenatum*, *Campium membranaceum*, *C. nigrum*, *C. pseudoscalpturatum*, and *Bolbitis koidzumii*. *Campium nigrum* was described from a sterile leaf from Ponape. Copeland preferred to keep this collection separate from *Campium heteroclitum*: 'the combination of frond



color and opacity and of the striking scaliness of the dark stout stipe marks it off clearly enough'. I found the type material to have a somewhat thicker leaf than is usually found. The colour of the leaf does not deviate, but the light brown scales which lack a paler marginal strip and which seem more persistent than those usually found, give it a rather distinct appearance. The sporangia of several collections from Ponape studied invariably contained either aborted S.M.C.'s or aborted S.M.C.'s and/or aborted spores. Possibly all the morphologically strikingly similar plants from Ponape are part of the same clone.

The epiphytic specimens of northeastern India are stout plants. The sterile pinnae are typical as to size. The venation pattern of part of the material shows irregularly arranged excurrent free veins in a considerable part of the areoles. The fertile pinnae are large, measuring 60–130 by 17–35 mm. Spores: *Mann s.n.*, vi–1889 (UC): nearly all normal. *Ibid.* (US): a majority normal, the perispore rather densely cristate. *Jerdon s.n.* (MICH): the (apparent) majority normal, rather large (the longest axis *c.* 50–55  $\mu$ m), the perispore densely cristate. *Mann s.n.*, xi–1885 (S-PA), vii–1888 (SING), vi–1889 (L): all or the greater part of the sporangia with abnormal spores or abnormal S.M.C.'s. The triploid specimens of the present species which are in cultivation at the botanic gardens of Berlin, Groningen, Utrecht, and Leiden and which presumably originate all from the same gathering, are very similar to these Indian plants.

The type material of *Campium membranaceum* deviates as to the leaf architecture only. The basal pinnae of the sterile leaves are either entire, or provided with a small, basal, basispicopic lobe, or have a basal basispicopic pinnule. One of the fertile leaves shows three pinnae inserted at the same place of the rhachis. Spores of the holotype largely abnormal.

B. Specimens with mostly simple leaves, sometimes with leaves that have two small pinnae. The venation pattern is variously developed. The shape of the lamina or of the terminal segment (in case the leaf is pinnate) is similar to the (upper part of the) terminal segment as found in the specimens mentioned under A. The specimens with narrow leaves (leaf index 10–20(–40)) are generally rheophytic. Here belong the type specimens of *Bolbitis annamensis* from Indo-China, *B. edanyoi*, *Campium foxworthyi*, *C. tenuissimum*, all from the Philippines, *Leptochilus linnaeanus* from Java, *Acrostichum modestum* from Borneo, *Leptochilus simplifolius* from the Malay Peninsula and *L. sumatranus* from Sumatra.

*Acrostichum modestum*, with very narrow and small leaves, was regarded by Christensen (quoted by Copeland, 1928) 'a simple fronded *Tectaria*, in habit resembling *Diplazium lanceum*'.

*Leptochilus simplicifolius*, amply discussed by Holttum (1954), was regarded by him as the mountain form of *B. heteroclita*. The differences between these two species as given by Holttum appeared to be quantitative only.

*B. annamensis* was supposed by Tardieu-Blot & C. Christensen to be closely related to *Campium hydrophyllum* (= *B. sinuata*). The type rather agrees with that of *Leptochilus linnaeanus*, also in venation pattern, which these authors incorrectly regarded as being totally different.

Plants intermediate between A and B include the type of *Poecilopteris stenophylla* (from Java). The outline of this plant is reminiscent of *Leptochilus malaccensis* which is regarded as parallel variation of *B. sinuata*.

C. Small plants with pinnate leaves, with a well-developed triangular terminal segment. The venation pattern of the two lowest pinnae without or with but few areoles. Here belong the type of *Nephrodium ? cuspidatum*, part of the type of *Gymnopteris inconstans*, and part of *Cuming 161* (the type of *Heteroneuron argutum* excluded).

Plants intermediate between B and C include *Copeland 33* (GH), *Elmer 17554* (L), *Le Roy Topping 386* (US), *444* (GH, US), *Merrill 3128* (B, syntype of *Gymnopteris inconstans*), all from the Philippines. The outline of these plants not rarely shows irregularities.

D. Small plants with bipinnate leaves and a well-developed terminal segment; veins free or anastomosing. Here belongs the type material of *Edanyoa difformis*.

*Edanyoa difformis* has bipinnate sterile leaves up to 4 cm long; veins are free. The plants of the type collection recall the genera *Microstaphyla* and *Peltapteris* (derivatives of *Elaphoglossum*). In the type locality of *E. difformis* (Negros I.) Mr. Price collected ample material fully matching the type (*Price 2518A*, L), as well as slightly different plants (*Price 2518B*, L) that also show leaves of a different shape on a single rhizome. These leaves include ternate leaves of a shape as found in juvenile leaves of *B. heteroclita* proper though much smaller, as well as leaves the terminal segment of which is shaped exactly like sterile segments as found in *Heteroneuron argutum* (= *B. × arguta*); all leaves have free veins. Spores: *Edaño PNH 5213* (isotype of *Edanyoa difformis*, PNH), *Price 2518A* (CAHUP, L), *2518B* (CAHUP, L): sporangia filled with aborted S.M.C.'s and/or aborted spores.

Sterile leaves like those of the type of *Edanyoa difformis* were also met in several other collections. The leaves on the bulbils of the sterile collections of *Edaño PNH 21374* (MICH), also from Negros I., are small, and either similar to the leaves of the type of *E. difformis* or less complex. The leaves that bear the small plants are up to 20 cm long; the lamina consists of two small basal pinnae and a proportionally long, flagelloid terminal segment, and is similar to that of the larger juvenile leaves as found in well-developed specimens; veins are anastomosed. All kind of intermediate leaves are present in this collection as well. The variation in leaf shape as found in this and other collections justifies the inclusion of *E. difformis* in the present species.

The types of the fertile dwarfs included here in *B. heteroclita* have sterile leaves matching the juvenile leaves formed on the bulbils of (more) well-developed plants. The ample herbarium material of these dwarfs cannot be satisfactorily classified using herbarium methods only.

Cytology. I have attempted to add further to the understanding of the present complex by cultivating a number of specimens and including some dwarfs of conspicuously different habit. In cultivation these plants show considerable common variation as to the shape of their juvenile leaves in particular; the fertile adults are slightly, though conspicuously dissimilar.

The chromosome numbers of well-developed plants (showing the complex venation pattern) are  $2n = 82$  and  $2n = 123$ . The triploid is so similar to the diploid that the latter

may have arisen through autopoloidization. Jerdon's herbarium collection from north-eastern India, mentioned above because of its large spores, possibly represents an autotetraploid. The '*linnaeana*' dwarf collected by Prof. Holttum at Pahang, Malaya, is an autotriploid<sup>1</sup>. '*Cuspidata*' dwarfs from the Philippines have  $2n = c. 82$ , and  $2n = c. 123$ . The diploid and the triploid are so similar that they were originally collected and cultivated under a single number. I only came across the mixture when preparing a count from a meiosis after the material had become fertile. A somewhat larger specimen, also from the Philippines, shows in the wild and in cultivation an astonishing variation of the juvenile leaves; it is a diploid. (Auto)-tetraploids have not (yet) been recorded from the Philippines. They are likely to occur there.

All diploid dwarfs have a  $\pm$  irregular meiosis when in cultivation, which is reflected by the abortive spores found in the wild gatherings. The degree of chromosome pairing at metaphase 1 of the meiosis varies from sporangium to sporangium. Some karyotypes showed mainly (exclusively?) bivalents.

**D i s c u s s i o n.** Because of the shape of the leaves, both the triploid and the diploid dwarfs are likely to be the result of the same process. The abnormal spores formed by the diploids are at first sight strong evidence that these diploids originate from a cross between different species. However, these diploids showed at metaphase 1 a varying number of bivalents, and not univalents only (as seems the rule). They did not originate by simple retention from well-developed diploids as the spores are abnormal. I further fail to recognize substantial differences between the leaves of these diploids and the juvenile leaves as found in well-developed specimens. The question then arises in how far this kind of heterogeneity can be caused by autopoloidization as well. The reversal of the polyploid to the diploid condition is not otherwise known from collections occurring in the wild. However, Manton (1950) found, as a result of repeated large-scale sowings of spores of an artificially produced autotriploid of *Osmunda regalis* L., that most of the 24, sexually produced eventual sporophytes had  $\pm$  diploid somatic cells. Of the few plants that became fertile she made exact counts: two plants were exact diploids, one was a 'diploid plus 1', and two were 'diploids plus 2'. Her illustration of the chromosomes of the 'diploid plus 1' at meiosis shows, apart from one univalent, bivalents only. She did not further report on the meiosis and spores resulting from the 'exact' diploids. These  $\pm$  diploid plants of *Osmunda regalis* showed quite a diversity as to the shape of the leaves. Some plants were perfectly normal, the others were smaller and showed either irregularities in the leaves or remained permanently in the juvenile condition.

This or a comparable process as found by Manton in artificial *Osmunda regalis* autopoloids might be a possible explanation for the existence of the diploid dwarfs with aborted spores in *B. heteroclita*. The chance that a viable spore is produced by an autotriploid is exceedingly small. But when formed in *Bolbitis heteroclita* the resulting sporophyte has means for maintaining itself in the wild through vegetative propagation (bulbils and/or accessory branching). The same holds for the triploids, whether

<sup>1</sup> Manton, in a letter to Prof. Holttum, 1958; published with kind permission of Dr. Manton.

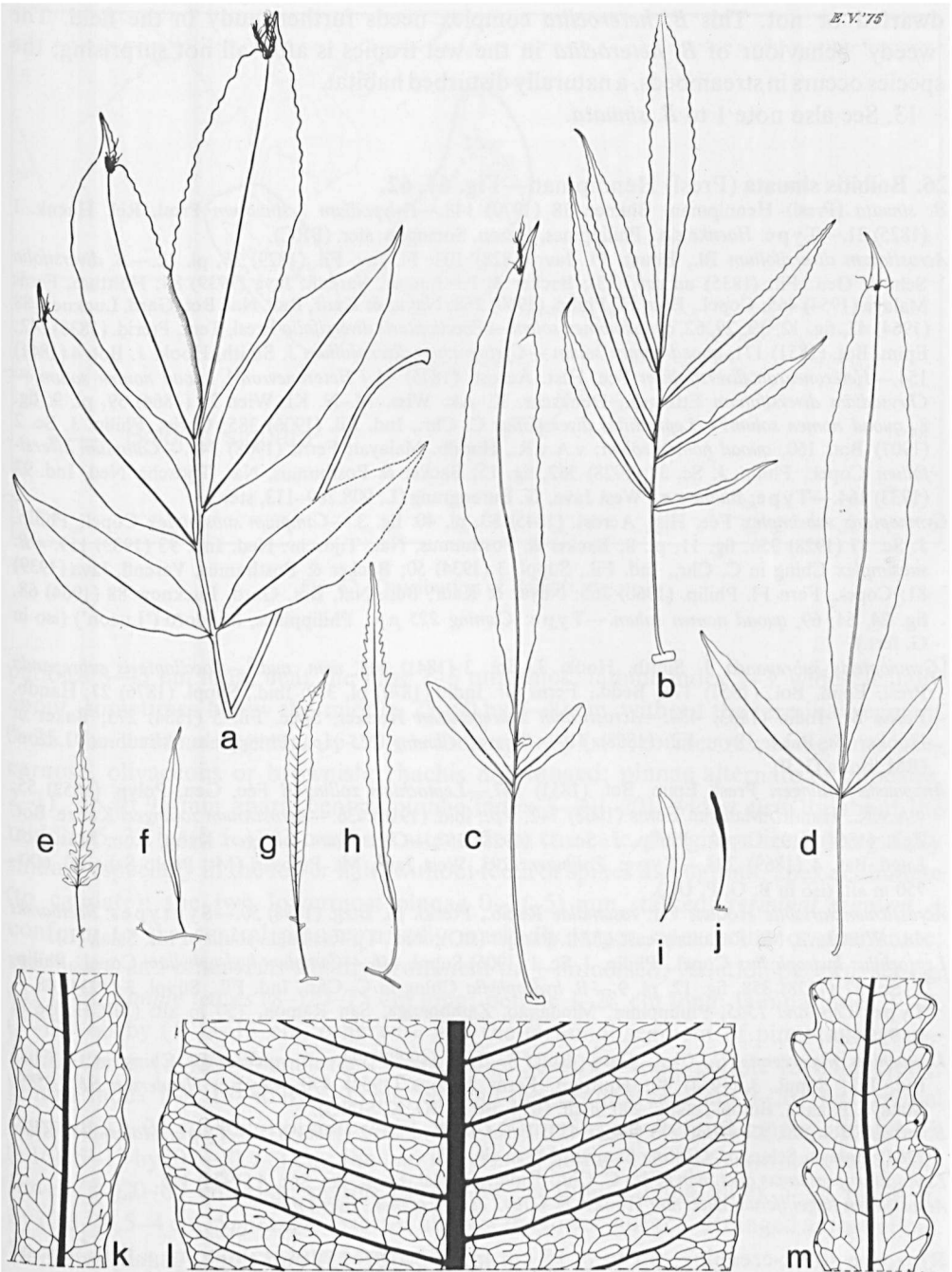


Fig. 61. *Bolbitis sinuata*.—a, b, e–j. sterile and fertile leaves,  $\times 1/5$ ; c, d. sterile leaves,  $\times 1/7$ ; k–m. venation pattern of sterile leaves,  $\times 4/5$  (a. Van Beusekom 550, L; b, k. Price 291, L; c, d. Price 604, L, triploid; e. Hennipman 4100, L, diploid; f. Alcasid & Edaño PNH 4748, MICH; g. Hennipman 4117, L, diploid; h. Edaño BS 79653, MICH; i, j. Copeland 1565, MICH, holotype of *Campium hydrophyllum*; l. Johnson s.n., L 965.110–982, L, triploid; m. Hennipman 4064, L, diploid).

dwarfed or not. This *B. heteroclita* complex needs further study in the field. The 'weedy' behaviour of *B. heteroclita* in the wet tropics is after all not surprising; the species occurs in streambeds, a naturally disturbed habitat.

13. See also note 1 to *B. sinuata*.

**26. *Bolbitis sinuata* (Presl) Hennipman—Fig. 61, 62.**

- B. sinuata* (Presl) Hennipman, Blumea 18 (1970) 148.—*Polypodium* ? *sinuatum* Presl, Rel. Haenk. 1 (1825) 21.—Type: *Haenke s.n.*, Philippines, Luzon, Sorsogon, ster. (PRC).
- Acrostichum diversifolium* Bl., Enum. Pl. Jav. (1828) 103; Fl. Jav. Fil. (1829) 36, pl. 12.—*B. diversifolia* Schott, Gen. Fil. (1835) *ad tab.* (13); Backer & Posthumus, Varenfl. Java (1939) 84; Holttum, Ferns Malaya (1954) 465; Copel., Fern Fl. Philip. (1960) 258; Nayar & Kaur, Bull. Nat. Bot. Gard. Lucknow 88 (1964) 42, fig. 12, 19, 29, 62, *quoad nomen solum*.—*Poecilopteris diversifolia* Presl, Tent. Pterid. (1836) 242; Epim. Bot. (1851) 171, *quoad nomen solum*.—*Cyrtogonium diversifolium* J. Smith, Hook. J. Bot. 4 (1841) 154.—*Heteroneuron diversifolium* Fée, Hist. Acrost. (1845) 91 ('*Heteroneuron*'), *quoad nomen solum*.—*Chrysodium diversifolium* Ettingsh., Denkschr. K. Ak. Wiss. M.-N. Kl. Wien 22 (1864) 59, pl. 9: fig. 8, *quoad nomen solum*?—*Leptochilus diversifolius* C. Chr., Ind. Fil. (1906) 385; Christ, Philip. J. Sc. 2 (1907) Bot. 160, *quoad nomen solum*; v.A.v.R., Handb. Malayan Ferns (1908) 740.—*Campium diversifolium* Copel., Philip. J. Sc. 37 (1928) 362, fig. 15; Backer & Posthumus, Nat. Tijdschr. Ned. Ind. 93 (1933) 164.—Type: *Blume s.n.*, West Java, G. Burangrang (L, 908.289–113, ster.).
- Gymnopteris subsimplex* Fée, Hist. Acrost. (1845) 83, pl. 40: fig. 3.—*Campium subsimplex* Copel., Philip. J. Sc. 37 (1928) 356, fig. 11, pl. 8; Backer & Posthumus, Nat. Tijdschr. Ned. Ind. 93 (1933) 159.—*B. subsimplex* Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 50; Backer & Posthumus, Varenfl. Java (1939) 81; Copel., Fern Fl. Philip. (1960) 265; Nayar & Kaur, Bull. Nat. Bot. Gard. Lucknow 88 (1964) 68, fig. 24, 64, 69, *quoad nomen solum*.—Type: *Cuming 225 p.p.*, Philippines, Mindoro ('Luzon') (iso in G, fert.).
- [*Gymnopteris subrepanda* J. Smith, Hook. J. Bot. 3 (1841) 403, *nom. nud.*]—*Poecilopteris subrepanda* Presl, Epim. Bot. (1851) 171; Bedd., Ferns Br. India (1870) pl. 339; *ibid.*, Suppl. (1876) 27; Handb. Ferns Br. India (1883) 434.—*Acrostichum subrepandum* Hooker, Spec. Fil. 5 (1864) 275; Baker in Hooker & Baker, Syn. Fil. (1868) 419.—Type: *Cuming 225 p.p.*, Philippines, Mindoro, 'Luzon' (BM; iso in G, P).
- Anapausia zollingeri* Presl, Epim. Bot. (1851) 187.—*Leptochilus zollingeri* Fée, Gen. Polyp. (1852) 55; v.A.v.R., Handb. Malayan Ferns (1908) 742, *p.p.*; *ibid.* (1916) 436.—*Acrostichum zollingeri* Kunze, Bot. Zeit. (1864) 419; Copel., Philip. J. Sc. 37 (1928) 357.—*Chrysodium zollingeri* Kuhn, Ann. Mus. Bot. Lugd.-Bat. 4 (1869) 293.—Type: *Zollinger 1293*, West Java, Mt. Pulosari (Mt. Poelo Saharie), 600–750 m alt. (iso in B, G, P, UC).
- Acrostichum variabile* Hooker var. *rasamalae* Racib., Pterid. Fl. Btzg. (1898) 50.—Syntypes: *Raciborski s.n.*, West Java, Mt. Rasamala east of Mt. Pantjar (BO); *ibid.*, Tji Rasamala south of Mt. Salak (L).
- Leptochilus hydrophyllus* Copel., Philip. J. Sc. 1 (1906) Suppl. 146.—*Campium hydrophyllum* Copel., Philip. J. Sc. 37 (1928) 358, fig. 12, pl. 9.—*B. hydrophylla* Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 48.—Type: *Copeland 1565*, Philippines, Mindanao, Zamboanga, San Ramon, 150 m alt. (MICH; iso in B, P, S–PA, US).
- Leptochilus malaccensis* C. Chr., Gard. Bull. S. S. 4 (1929) 394.—*B. malaccensis* Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 49; Holttum, Ferns Malaya (1954) 470.—Type: *Henderson SF 18589*, Malaya, Pahang, Buloh Telang, 240 m alt. (BM; iso in BO, K, SING).
- B. nitens* Holttum, Kew Bull. 13 (1958) 453; Ferns Malaya ed. 2 (1966) 635.—Type: *Molesworth Allen 3384*, Malaya, Selangor, Ginting Simpah, 240 m alt. (K).
- Leptochilus preslianus auct. non* (Fée) C. Chr.: Ridley, J. Mal. Br. As. Soc. 4 (1926) 115.
- Acrostichum flagelliferum auct. non* Hooker & Grev., *et syn. homot.: auct., p.p.*

Rhizome short-creeping, up to c. 15 cm long, 3–10(–15) mm thick, usually without, sometimes with few sclerenchyma strands. Scales of the rhizome: index 3–10, up to 12 by 1.5 mm, ± opaque, blackish. Leaves rather close together to 20(–30) mm apart. *Sterile leaves* simple or pinnate, (8–)20–100 cm long. *Pinnate leaves* 35–100 cm long;

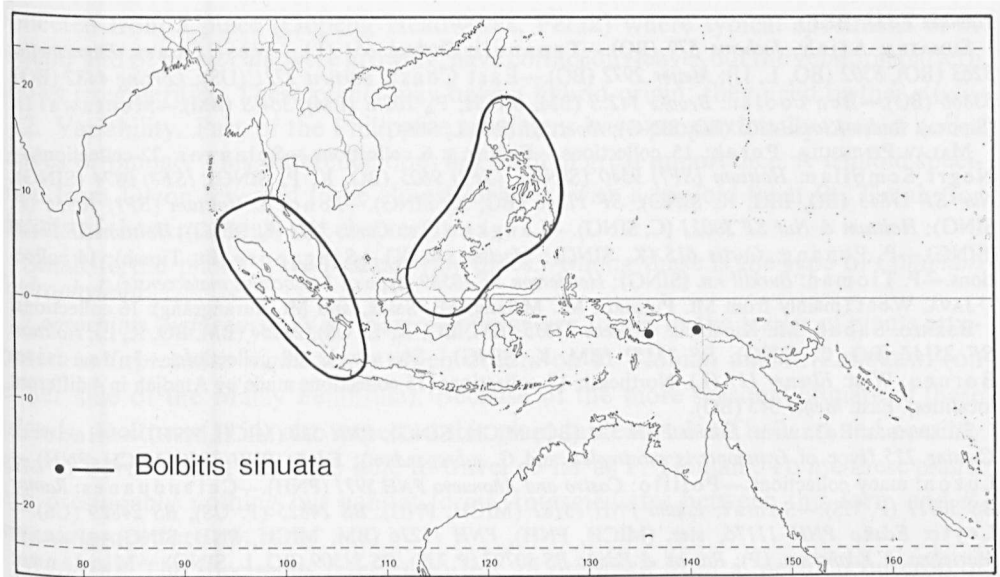


Fig. 62. Distribution of *Bolbitis sinuata*.

petioles 8–45 cm long, near the base 1–5 mm thick; lamina index 1–3, widest usually about, sometimes below the middle, 25–60 by 8–40 cm, without the terminal segment 0–25, the terminal segment 15–50 cm long, usually (sub)coriaceous, sometimes sub-carnose, olivaceous or brownish; rhachis not winged; pinnae alternate or opposite, 2–11, up to 95 mm apart; central pinnae index 3–10(–20), widest usually about the middle, 5–35 by (0.5–)1–7 cm, base attenuate to truncate, margin entire or irregularly sinuate especially in the lower half, without teeth or spines throughout, apex acuminate (to caudate); the two lowermost pinnae 0–3(–5) mm stalked; *terminal segment* ± conform to the central pinnae, usually markedly larger, apex acute or acuminate; secondary and other *veins* slightly prominent or ± immersed; venation pattern: see fig. 61: k–m. *Simple leaves* (8–)20–75 cm long; petiole 1–28 cm long; lamina index 3–10, (7–)20–60 by (1–)3–15 cm, otherwise like the terminal segment of pinnate leaves.—*Fertile leaves* (8–)20–90 cm long. *Pinnate leaves* 30–90 cm long; petiole 10–65 cm long; lamina index 1–4, 15–40 by 8–25 cm, without the terminal segment 0–20, the terminal segment 11–28 cm long; pinnae 2–10, up to 60 mm apart; central pinnae index 4–10 (–16), 5–17 by (0.5–)0.7–3 cm; the two lowermost pinnae 1.5–3(–6) mm stalked. *Simple leaves* (8–)20–60 cm long; petiole (4–)10–40 cm long; lamina index 5–18, (4–)8–35 by (0.3–)0.5–4 cm. *Sporangia* inserted all over the lower surface, arranged acrostichoid. Spores with a smooth cristate perispore.

Chromosomes.  $n = 41$ ;  $2n = 122 + \text{fragm.}$

INDIA. Nicobar Is.: *Galathea Exp.* 2691 (C), 2859 (BM, C), *s.n.* (US).

THAILAND. Peninsular: *Van Beusekom* 550 (L); *E. Smith* 541 (K), 2019 (K, SING); *Tagawa &*

*Yamada T 213* (BKF).

SUMATRA. Atjeh: *Jochems 579* (BO).—Tapanuli: *Surbeck 651* (L).—West Coast: *Bünnemeijer 3263* (BO), *8502* (BO, L, U); *Meijer 2972* (BO).—East Coast: *Bartlett 7721* (US); *Lörzing 4482* (BO), *5386b* (BO).—Ben coolen: *Brooks 142.S* (BM, MICH, P), *202.S* (BM), *364.S* (BM).—Mentawai Is. (Sipora): *Boden-Kloss 14805* (BO, SING); *Iboet 531* (BO, L, SING).

MALAY PENINSULA. Perak: 15 collections.—Pahang: 6 collections.—Selangor: 22 collections.—Negri Sembilan: *Holtum (SF?) 9540* (SING), *(SF?) 9605* (BO, K, P, SING), *(SF?) 9874* (SING); *Nur SF 11845* (BO, BRI, K, SING), *SF 11846* (BO, K, SING).—Johore: *Holtum (SF?) 10956* (P, SING); *Holtum & Nur SF 20021* (C, SING).—Langkawi Is.: *Curtis 3371* (K, SING); *Holtum SF 17440* (SING).—P. Penang: *Curtis 615* (K, SING); *Mactier s.n.* (K).—Singapore (Bt. Timah): 14 collections.—P. Tioman: *Burkill s.n.* (SING); *Henderson SF 18589* (type of *Leptochilus malaccensis*).

JAVA. West (mainly from Mt. Pulosari, Mt. Malang, Mt. Salak, and Mt. Burangrang): 16 collections.

BORNEO. Sabah. Mt. Kinabalu: *Clemens 27635* (BM, BO, K, L, US), *28234* (BM, BO, K, L); *Holtum SF 25141* (BO, C, SING), *SF 25352* (BM, K, SING).—Sarawak: 18 collections.—Indonesian Borneo. West: *Elsener 127* (L). Northeast: 17 collections (15 collections made by Amdjah in 4 different localities). East: *Meijer 545* (BO).

PHILIPPINES. Palawan: *Edaño PNH 524* (BO, MICH, SING), *PNH 532* (MICH, PNH).—Mindoro: *Cuming 225* (type of *Gymnopteris subsimplex* and *G. subrepandum*); *Edaño PNH 3876* (MICH, PNH).—Luzon: many collections.—Polillo: *Castro and Añonuevo PNH 5971* (PNH).—Catanduanes: *Ramos BS 30311* (P, US).—Samar: *Edaño PNH 15182* (MICH, PNH), *BS 24825* (P, US), *BS 24829* (US).—Leyte: *Edaño PNH 11176*, ster. (MICH, PNH), *PNH 11226* (BM, MICH, PNH, SING).—Panay: *Martelino & Edaño s.n.* (P); *Ramos & Edaño BS 30797* (P, US), *BS 31309* (BO, L, SING).—Mindanao: 8 collections.

NEW GUINEA. West. Albatros bivouac: *Docters van Leeuwen 9135* (BO, K, L). *Sine loc.*: *Beccari s.n.* (K).—Northeast. Torricelli Mts.: *Schlechter 14442* (B).

Habitat. Terrestrial and low epiphytic in evergreen forest. Altitude: 0–1200 (–1800) m.

Spores. *Allen 3405* (S–PA), *Van Beusekom 550* (L), *Copeland s.n.* (MICH, herb. Copeland 10212), *Elsener H 127* (L), *Henderson SF 18589* (type of *Leptochilus malaccensis*), *Kiah s.n.* (SING): the greater part normal. *Elmer 7629* (P): about equal parts normal and abnormal. *Copeland 1565* (MICH, type of *Leptochilus hydrophyllus*), *Cuming 225* (BM, type of *Gymnopteris subrepanda*), *Elmer 9041* (MICH), *Holtum SF 25352* (SING), *Zollinger 1293* (P, type of *Acrostichum zollingeri*): the greater part abnormal. *Backer 14467* (BO), *Brooks 364.S* (BM), *Curtis 3371* (SING, paratype of *Leptochilus malaccensis*), *Johnson s.n.* (L, a triploid), *Nur s.n.* (SING), *Ramos & Edaño BS 36971* (L), *Williams 205* (NY): only abnormal spores and aborted S.M.C.'s present.

Notes. 1. A rather heterogeneous species readily recognized through the combination of texture—markedly different from that of *B. heteroclita*, its closest relative—leaf architecture, and venation pattern. A texture similar to that of the present species is also found in *B. rivularis* which belongs to a different series. *B. sinuata* is confined to the wettest parts with evergreen forest in Malesia. *B. × singaporensis* is a hybrid between the present species and *B. appendiculata* spp. *appendiculata*. *B. sinuata* is also included in the parentage of *Leptochilus × trifidus*. Hybrids with *B. heteroclita* are likely to be formed. The texture of the leaves, which is the best differentiating character, is difficult to evaluate from herbarium material. Plants with a seemingly less coriaceous texture than normal include *Zollinger 1293* (type of *Leptochilus zollingeri*, Java) and *Elmer 7629* (BO, K, L, M, P) from the Philippines, which is also otherwise very similar to *Zollinger 1293*. *Molesworth Allen 4365* (S–PA), *4556* (S–PA), *4731* (S–PA), all

collected from a place (Gopeng Headworks, Perak) where typical specimens of *B. sinuata* and *B. heteroclita* were growing, have coriaceous leaves but the venation pattern shows irregularities. These plants may have a hybrid origin; they need further study.

2. Variability. Part of the Philippine specimens have proportionally narrow entire leaves or pinnae. This difference does not seem of great importance. A triploid specimen from Luzon revealed to be almost identical with a triploid from Bt. Timah (for details of these materials see chapter 7).

Small fertile plants were found a few times. Among these is the type of *Campium hydrophyllum*.

*Leptochilus malaccensis*. Very narrow pinnae are found in the leaves of plants attributed to *Leptochilus malaccensis* which occurs on P. Tioman and P. Langkawi (on either side of the Malay Peninsula). Because of the more seasonal climate of these islands, Holttum (1954) also expected this plant in Peninsular Thailand and possibly also in Borneo 'as it has been able to travel so far as P. Tioman'. To me these plants are presumably nothing but habitat forms. Intermediates between this form and *B. sinuata* proper are not rare.

*B. nitens*. The specimens referred to this all originate from a 'peculiar outcrop of white quartzite (?), of c. 100 × 60 feet which apparently becomes very dry' and 'which may well simulate a more seasonal climate than is experienced by the ferns in the normal rainforest a few yards away' (Holttum, 1958). The only feature by which the material from this area deviates distinctly is that of the scales on the petiole, which seem permanent or almost so. In how far such a condition is not the result of the different habitat conditions remains to be demonstrated. Mrs. Allen (in Holttum, 1958) was of opinion that *B. nitens* also occurred in a similar habitat in Sarawak. This is incorrect; the material she had in mind (e.g. *Lörzing 12405 p.p.*, L) represents *Leptochilus* × *trifidus*.

### 7. Series Heudelotianae Hennipman, ser. nov.

Terrestres, crescunt in locis temporaliter inundatis vel in fluminibus permanentibus. Lamina pinnata segmento terminali triangulari, sine bulbillis, marginibus edentatis vel espinosis. Ordinatio venularum iis series Portoricensium similis. Sporae perispora laevi undulata.

Typus: *Bolbitis heudelotii* (Bory ex Fée) Alston.

Terrestrial in seasonally flooded habitats or in permanent streams. *Rhizome* ± long-creeping, slender to rather stout, with 2 rows of leaves, without sclerenchyma strands. Scales of the rhizome up to 10 mm long. *Leaves* ± spaced. Sterile leaves pinnate; petiole with 5–11 vascular bundles; lamina without bulbils; pinnae 8–21(–26), the margin without teeth or spines; terminal segment triangular; *venation pattern*: veins forming an intricate network, areoles varying in size and shape, the majority with one or a few ex- or recurrent, simple or forked, included free veins. *Spores* with a smooth undulate perispore.

Chromosomes.  $2n = 82$ .

Distribution. Tropical Africa. See fig. 30, 64.



**27. *Bolbitis heudelotii* (Fée) Alston—Fig. 63: a–i; 64.**

*B. heudelotii* (Bory ex Fée) Alston, J. Bot. 72, Suppl. 2 (1934) 3; C. Chr., Ind. Fil., Suppl. 3 (1934) 48, 198, Alston, J. Bot. 77 (1939) 285; in Hutch. & Dalziel, Fl. West Trop. Afr. ed. 2, Suppl. (1959) 68; Harley, Handb. Liberian Ferns (1963) 41, fig.; Tardieu-Blot in Aubrév., Fl. Gabon 8 (1964) 188; in Aubrév., Fl. Cameroun 3 (1964) 319, pl. 51: fig. 1 & 2; Arnoult, Bull. Assoc. Franç. Aquariophiles n.s. 19 (1964) 4; Pichi Sermolli, Webbia 23 (1969) 388, fig. 1–3; Benl, Heine & Michel, Pisciculture Franç. 20 (1969) iv–xi, pl. 1–2, phot.; Schelpe, Contr. Bolus Herb. 1 (1969) 41.—*Gymnopteris heudelotii* Bory ex Fée, Hist. Acrost. (1845) 84, pl. 45; Christ, Farnkr. Erde (1897) 51, fig. 1–3; Engler, Veg. Erde 9, 2 (1908) 6.—*Anapausia heudelotii* Presl, Epim. Bot. (1851) 187.—*Acrostichum heudelotii* Hooker, Spec. Fil. 5 (1864) 264; Baker in Hooker & Baker, Syn. Fil. (1868) 224.—*Acrostichum heudelotii* Hooker var. *major* Hooker, Spec. Fil. 5 (1864) 264, *nom. illeg.*—*Chrysodium heudelotii* Kuhn, Fil. Afric. (1868) 51.—*Leptochilus heudelotii* C. Chr., Ind. Fil. (1906) 385.—*Campium heudelotii* Copel., Philip. J. Sc. 37 (1928) 396.—Type: *Heudelot 805* ('s.n.'), Guinea, Fouta-Djallon ('Senégambie, Foula-Dhiallon') (P; iso in B, some sterile and fertile pinnae, K, L).

*Acrostichum heudelotii* (Fée) Hooker var. *minor* Hooker, Spec. Fil. 5 (1864) 264.—Syn types: *Barter s.n.*, Sierra Leone (K); *Kirk s.n.*, Malawi, Manganja country, 90 m alt. (K).

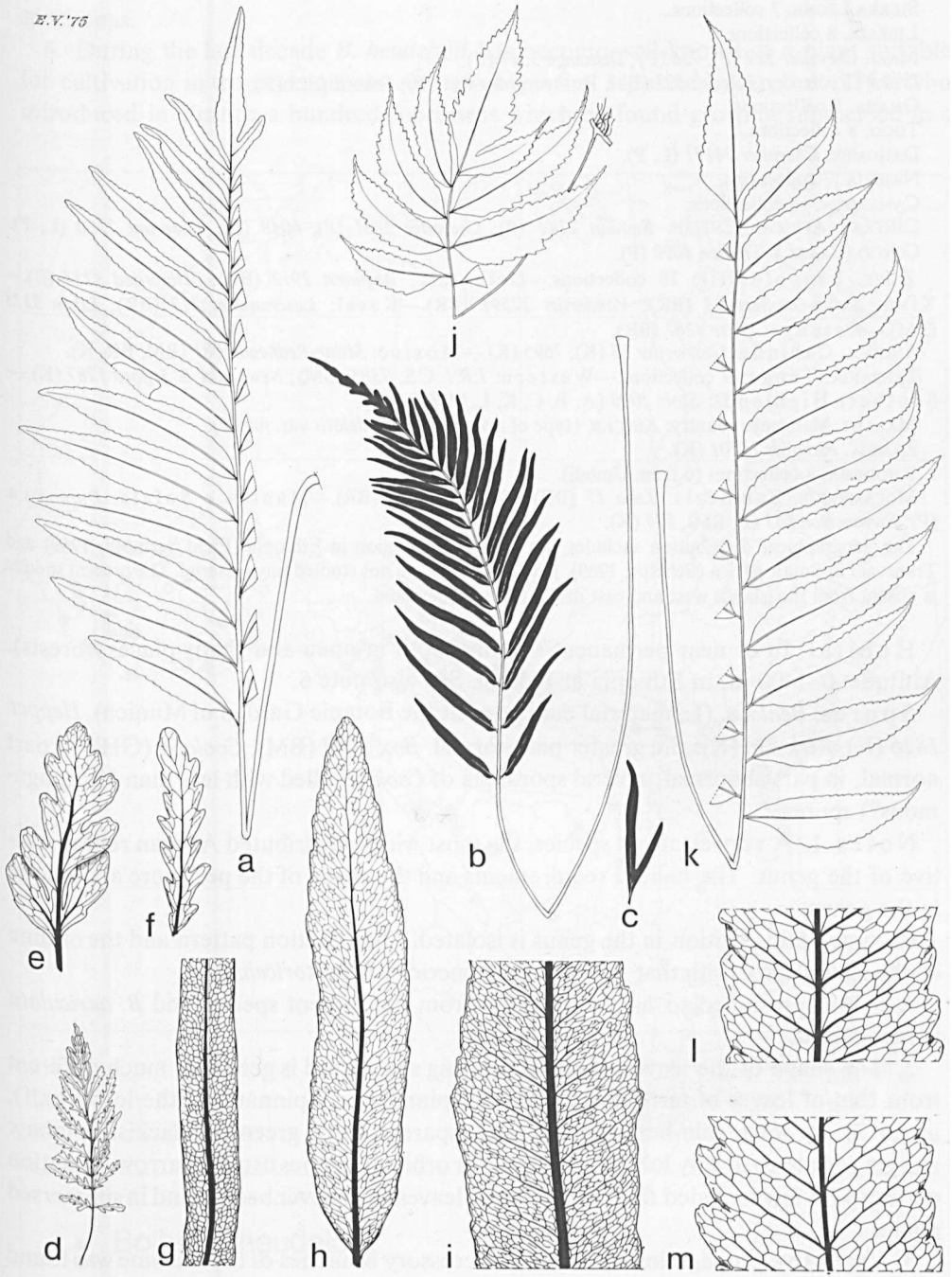
*Campium angustifolium* Copel., Philip. J. Sc. 37 (1928) 396, fig. 47, pl. 31.—*B. heudelotii* var. *angustifolia* Tardieu-Blot, Not. Syst. 14 (1953) 349.—Type: *Mildbraed 9404*, Cameroun, Buar, c. 1000 m alt. (K, 2 sh.).

*B. felixii* Tardieu-Blot, Not. Syst. 13 (1948) 169.—Type: *Félix 933*, Guinea, vicinity of Macenta (P).

Rhizome up to 20 cm long, up to 10 mm thick. Scales of the rhizome: index 2–5, up to 10 by 2 mm, opaque, light to dark brown. *Sterile leaves* 30–85 cm long; petiole 8–40 cm long, near the base 2–6 mm thick; lamina index 1–4, widest about or below the middle, 25–50 by 12–25 cm, without the terminal segment 6–35, the terminal segment 10–22 cm long, herbaceous, green to blackish; rhachis not winged; pinnae alternate or opposite, 8–21(–26), 15–30 mm apart; central pinnae index 5–14, widest about or below the middle, 5.5–17 by 1–3 cm, base  $\pm$  symmetrical, cuneate, margin usually  $\pm$  entire, sometimes serrate, without teeth or spines, apex acute, acuminate, or orbicular; the two lowermost pinnae 2–8 mm stalked, usually  $\pm$  conform to the central pinnae, sometimes asymmetrical with the basispic side wider and lobed to 3/5 towards the costa; the uppermost pinnae usually adnate at the basispic side of the base; *terminal segment* triangular, deeply lobed near the base, tapering towards the acute or acuminate apex; secondary and other *veins* slightly prominent or  $\pm$  immersed; venation pattern: see fig. 63: e, f. *Fertile leaves* 25–100 cm long; petiole 25–55 cm long; lamina index 2–5, 15–45 by 9–17 cm, without the terminal segment 10–35, the terminal segment 5–13 cm long; pinnae 11–28, 10–30 mm apart; central pinnae index 8–15(–20), widest below the middle, 4–14.5 by 0.4–1.3 cm; the two lowermost pinnae 3–8 mm stalked. *Sporangia* inserted all over the lower surface. Spores large, with a smooth undulate perispore usually situated at considerable distance from the exospore.

Chromosomes.  $2n = 82$ .

Fig. 63. a–i. *Bolbitis heudelotii*. a, b. sterile and fertile leaf resp. of a terrestrial plant,  $\times 1/5$ ; c. lowermost pinna of a fertile leaf,  $\times 1/5$ ; d. sterile leaf of an aquatic plant,  $\times 1/5$ ; e, f. shape and venation pattern of pinnae of an aquatic plant,  $\times 4/5$ ; g. venation pattern of a fertile pinna,  $\times 4/5$ ; h, i. *ibid.* of sterile pinnae (a. *Stolz 1003*, M; b. *Hepper 1826*, K; c. *Cook 66*, GH; d, f. *Linder 1154*, GH; e. *Dusén s.n.*, 1892, P; g. *Peter 10301*. S-PA; h. *Stolz 1003*. S-PA; i. *ibid.* L).—i–m. *Bolbitis lindigii*. j. juvenile leaf,  $\times 1/5$ ; k. sterile leaf,  $\times 1/5$ ; l, m. venation pattern of sterile pinnae,  $\times 4/5$  (j. *Lewy 1851*, P, isotype of *Chrysodium pellucens*; k. *Alston 7836*, BM; l. *Gascoyne-Cecil 88*, L; m. *Lancaster 588*, US).



GUINEA. 15 collections.

SIERRA LEONE. 7 collections.

LIBERIA. 8 collections.

MALI. *Chevalier* 529 (P), 756 (P); *Demange* 3547 (P).

IVORY COAST. *des Abbayes* 593 (BM, P); *Anonymus* 4 (L, P); *Schnell* 1323 (P).

GHANA. 8 collections.

TOGO. 8 collections.

DAHOMY. *Chevalier* 24171 (L, P).

NIGERIA. 7 collections.

CAMEROUN. 18 collections.

CENTRAL AFRICAN EMPIRE. *Baudon* 2244 (P); *Chevalier* 5801 (P), 6048 (P); *Tisserant* 2200 (L, P).

CONGO (BRAZZ.). *Thollon* 4099 (P).

ZAIRE. Leopoldville: 18 collections.—Oriente: *Bequaert* 2912 (BR); *Mildbraed* 3134 (B).—Kivu: *Antun-Gupfert* 33 (BR); *Vanderijst* 17591 (BR).—Kasai: *Lescrauwaet* 213 (BR); *Liben* 3223 (BM).—Katanga: *Witte* 4267 (BR).

ANGOLA. Cabinda: *Gossweiler* 58 (K), 7695 (K).—Moxico: *Milne-Redhead* 4081 (BM, BR, K).

TANZANIA. Tanga: 9 collections.—Western: *I.R.L.C.S.* 7385 (BM); *Newbould & Jefford* 1287 (K).—Southern Highlands: *Stolz* 1003 (A, B, C, K, L, M, S-PA, U).

MALAWI. Manganja country: *Kirk s.n.* (type of *Acrostichum heudelotii* var. *minor*).

ZAMBIA. *Richards* 13201 (K).

RHODESIA. 8 collections (6 from Umtali).

MOCAMBIQUE, Zambézia: *Luja* 17 (BR), 421 (BR), 456 (BR).—Manica e Sofala: *Durand s.n.* (P); *Swynnerton* 833 (B, BM), 834 (K).

The geographical distribution includes the Lake Tana region in Ethiopia (Pichi Sermolli, 1969) and Transvaal in South Africa (Schelpe, 1969), from where I have not studied any material. The present species is absent from the islands west and east of the tropical mainland.

**Habitat.** In or near permanent streams, both in open and shady places (forests). Altitude: 0–1400 m; in Ethiopia at 1850 m. See also note 6.

**Spores.** *Benl s.n.* (L, material cultivated at the Botanic Garden of Munich), *Hepper* 1826 (K), *Kirk s.n.* (K): the greater part normal. *Box* 2083 (BM), *Cook* 66 (GH): in part normal, in part abnormal; several sporangia of *Cook* 66 filled with less than 32 (apogamous?) spores.

**Notes.** 1. A very clear-cut species, the most widely distributed African representative of the genus. The habitat requirements and the shape of the perispore are unique in the genus.

Its systematic position in the genus is isolated. The venation pattern and the outline of the leaves agree with that found in the American *B. portoricensis*.

A hybrid presumed to have originated from the present species and *B. auriculata* is recognized.

2. The shape of the leaves of plants growing submersed is generally much different from that of leaves of terrestrials. They are pinnate or bipinnate (in the lower half), up to 30 cm long, thin-herbaceous,  $\pm$  transparent, dark green to blackish; pinnae: margin serrate to deeply lobed, apex acute or orbicular; lobes usually narrow. Venation pattern with few included free veins. Fertile leaves have never been found in submersed plants.

3. Vegetative propagation by means of accessory branches of the rhizome was found in all plants in cultivation whether growing submersed (when growth is slow) or terrestrial (when growth may be rapid). The accessory branches formed in association with the formation of the leaf (see fig. 2: b) are well-developed on the oldest part of

the rhizome only; this is the reason why they are generally not present in herbarium specimens.

4. During the last decade *B. heudelotii* has become well-known as a plant suitable for cultivation in tropical aquaria. As such it was first reported by Arnould (1964) who introduced in France a hundred specimens which he found growing submersed in a

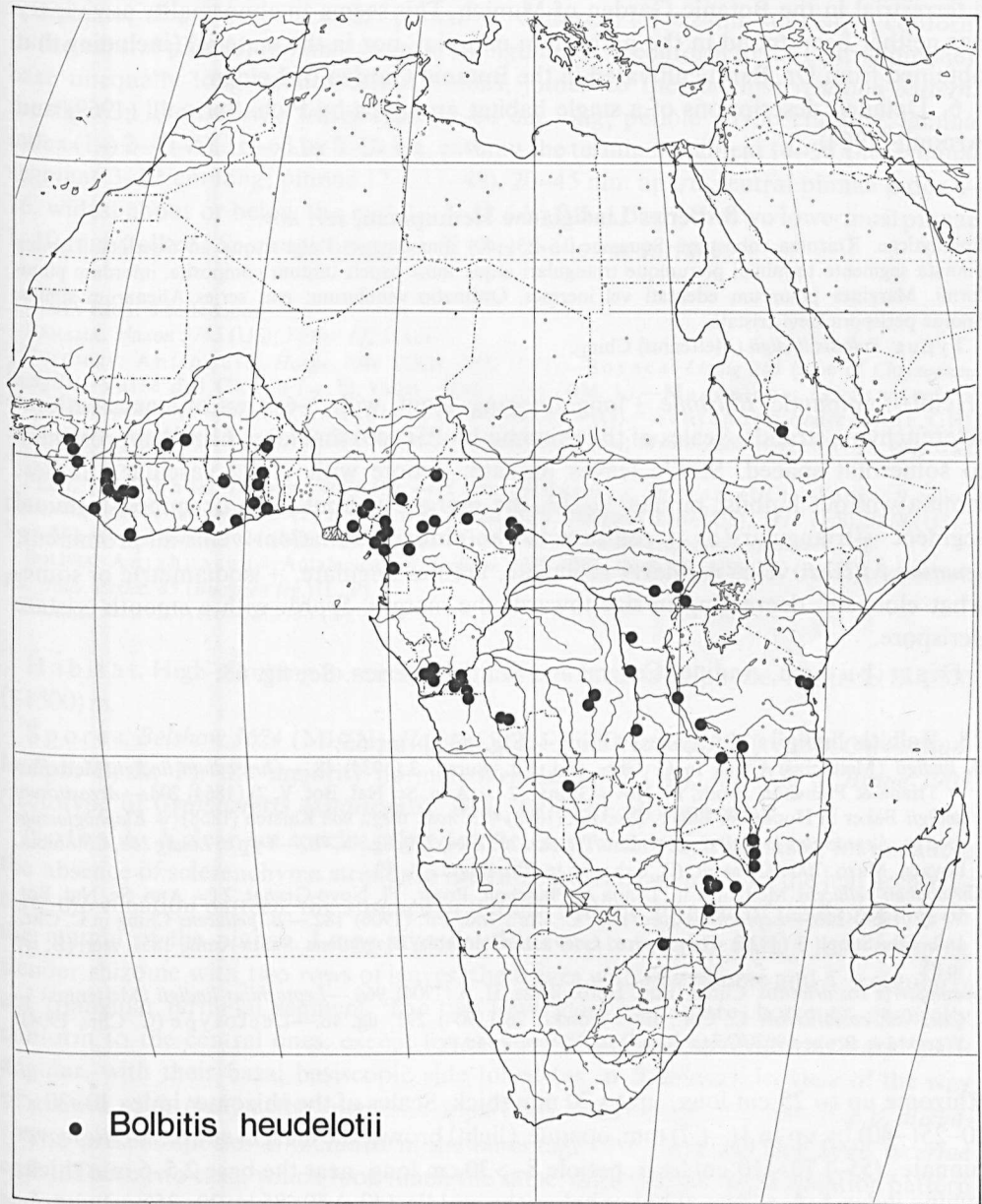


Fig. 64. Distribution of ser. *Heudelotianae* (monotypic).

river in Upper Volta. He treated these like aquatics and all but one perished. The remaining plant was multiplied by means of vegetative propagation (accessory branches of the rhizome). Later, the species was introduced from other localities as well. Benl *et al.* (1969) cultivated the material as a terrestrial and were the first to obtain fertile leaves in cultivation.

5. Benl *et al.* (1969) reported a case of vivipary on the leaves of a plant grown as a terrestrial in the Botanic Garden of Munich. This seems an abnormality as vivipary has neither been found in the herbarium material, nor in the material (including that obtained from Dr. Benl) cultivated in the Botanic Garden of Leiden.

6. Detailed descriptions of a single habitat are given by Pichi Sermolli (1969) and Arnoult (1964).

### 8. Series Lindigianae Hennipman, *ser. nov.*

Epiphyticae. Rhizoma robustum. Squamae 15–25(–40) mm longae. Folia usque ad 6-seriata. Lamina pinnata segmento terminali plerumque triangulari atque lobis paucis tantum composita, interdum pinniformi. Margines pinnarum edentati vel inermes. Ordinatio venularum: eius series Alienarum similis. Sporae perispora laevi cristata.

Typus: *Bolbitis lindigii* (Mettenius) Ching.

(Hemi-?) epiphytic. *Rhizome* ± long-creeping, stout, with 2–6 rows of leaves without sclerenchyma strands. Scales of the rhizome 10–25(–40) mm long. *Leaves* approximate to somewhat spaced. Sterile leaves pinnate; petiole with 10–22 vascular bundles; lamina without bulbils; pinnae 12–37, the margin without teeth or spines; terminal segment ± triangular (or ± conform to the pinnae); venation: veins all prominent; *venation pattern*: veins regularly reticulate, areoles angulate, ± isodiametric or somewhat elongate, decreasing in size towards the margin. *Spores* with a smooth cristate perispore.

Distribution. Andine. Central and South America. See fig. 65.

### 28. *Bolbitis lindigii* (Mettenius) Ching—Fig. 63: j–m; 65.

*B. lindigii* (Mettenius) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 48.—*Chrysodium lindigii* Mettenius in Triana & Planchon, Prodr. Fl. Novo-Granat. 2 (= Ann. Sc. Nat. Bot. V, 2) (1864) 204.—*Acrostichum lindigii* Baker in Hooker & Baker, Syn. Fil. (1868) 423, *nom. illeg., non* Karsten (1858) (= *Elaphoglossum spec.*).—*Leptochilus lindigii* C. Chr., Bot. Tidsskr. 26 (1904) 290, fig. 4a, 4b.—Type: *Lindig 258*, Colombia, Boyaca, Muzo, 700–900 m alt. (B, 2 sh.; iso in BM, fragm., K, P).

*Chrysodium pellucens* Mettenius in Triana & Planchon, Prodr. Fl. Novo-Granat. 2 (= Ann. Sc. Nat. Bot. V, 2) (1864) 205.—*Leptochilus spec. dub.* C. Chr., Ind. Fil. (1906) 182.—*B. pellucens* Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 49.—Type: *Lewy s.n.*, Colombia, Magdalena, Santa Anna, 1851, ster. (B; iso in P).

*Gymnopteris costaricensis* Christ, Bull. Herb. Boiss. II, 4 (1904) 964.—*Leptochilus lindigii* (Mettenius) C. Chr. var. *costaricensis* C. Chr., Bot. Tidsskr. 26 (1904) 291, fig. 4b.—Lectotype (C. Chr., 1904): Wercklé & Brune 1903, Costa Rica, *s. loc.* (P; iso in BM).

Rhizome up to 25 cm long, up to 20 mm thick. Scales of the rhizome: index 10–30, *c.* 10–25(–40) by up to 1(–1.7) mm, opaque, (light) brown, the margin entire. *Sterile leaves* pinnate, (55–) 70–110 cm long; petiole 8–>30 cm long, near the base 2.5–6 mm thick; lamina index 1–4, widest about or below the middle, (40–) 50–85 by 20–35 cm, without

the terminal segment (20–)35–73, the terminal segment 10–21 cm long, firmly herbaceous, light to dark green; rhachis not winged; pinnae usually alternate, 12–37, 25–60 mm apart; pseudo-articulate, straight to sigmoid; central pinnae index 3–8, widest about or below the middle, 12–26 by 2.5–5 cm, base usually  $\pm$  symmetrical, (narrowly) cuneate (to subcordate), sometimes  $\pm$  oblique, margin usually finely crenate-serrate especially towards the apex, or crenate-serrately lobed to 1/5 towards the costa, apex (long-) acuminate; the two lowermost pinnae  $\pm$  deflexed, 1.5–12 mm stalked,  $\pm$  conform to the central pinnae; *terminal segment* triangular (or  $\pm$  conform to the central pinnae), base unequally long-sided, without bulbils, joined to the rhachis; *venation pattern*: see fig. 63: 1, m. *Fertile leaves* (25–)35–80 cm long; petiole 10–30 cm long; lamina index (1–)2–4 (–5), 16–65 by 8–20 cm, without the terminal segment 14–58, the terminal segment 3–12 cm long; pinnae 12–33 (–48), 20–45 mm apart; central pinnae index 4–16, widest about or below the middle, 5–12.5 by 0.5–1.5 cm; the two lowermost pinnae 1–10 mm stalked. *Sporangia* inserted all over the lower surface.

COSTA RICA. 8 collections.

PANAMA. *Maxon* 5745 (US); *Pittier* 4225 (US).

COLOMBIA. Antioquia: *Hodge* 7044 (GH), 7072 (GH).—Boyaca: *Lindig* 258 (type of *Chrysodium lindigii*).—Valle del Cauca (= El Valle): *Alston* 7836 (BM, L).—Magdalena: *Lewy* s.n. (type of *Chrysodium pellucens*).—Norte de Santander: *Bischler* 2609 (G).—Santander: *Hodge* 6512 (F, GH).

ECUADOR. *Grubb et al.* 1651 (US); *Jvosio(?)–Morecalli* 45/8 (K); *Mexia* 7260 (GH, MICH, UC, US); *Stübel* 929 (B).

PERU. Amazonas: *Tessmann* 4001 (B), 4415 (B).—Huanuco: *Stork* s.n. (UC).—Junin: 9 collections.—Loreto: *Schunke* 333 (F, NY, S, US), 14076 (US); *Williams* 3240 (US), 3416 (US), 3418 (US).—San Martin: *Belshaw* 3624 (MICH, UC).—Sine loc.: *Matthew* 1107 (K); *Sandeman* 3446 (K).

BOLIVIA. Antahuaca (= Antahuacana): *Buchtien* 2220 (BM, G, S-PA, US), s.n. (P, US); *Rosenstock, Fil. Boliv. exsicc.* 85 (*Buchtien leg.*)(L, P).

BRAZIL. South. Acre: *Ule* 9138 (B).

**Habitat.** High-climbing in rain forest, also reported as epiphytic. Altitude: 0–1200 (–1500) m.

**Spores.** *Belshaw* 3624 (MICH), *Hodge* 6512 (F, GH), *Lindig* 258 (type of *Chrysodium lindigii*, B, K, P): the majority normal. *Wendland* 507 (W), *Wercklé & Brune* 1903 (lectotype of *Gymnopteris costaricensis*, BM), 1904 (P): all abnormal.

**Notes.** 1. A clear-cut species related to *B. aliena* with which it shares, for instance, the absence of sclerenchyma strands in the rhizome, the essentials of the leaf architecture, the venation pattern, the absence of bulbils, and the absence of teeth or spines on the margin of the pinnae. Large juvenile plants are terrestrial, with a long-creeping slender rhizome with two rows of leaves, the leaves with few pinnae and a  $\pm$  regularly cut triangular terminal segment. The two lowermost pinnae are, however, generally conform to the central ones, except for those of *Wendland* 507 (W) which are  $\pm$  triangular, with their basal basisopic side lobed (as in *B. aliena*). In view of the way of growth of *B. lindigii*, the species is apparently a derivative of a fern like *B. aliena*.

The present species is included in the parentage of *B. bernoulli* (see *Spec. incertae sedis*). These two taxa, which look much the same, differ mainly in the venation pattern and details of the scales of the rhizome.

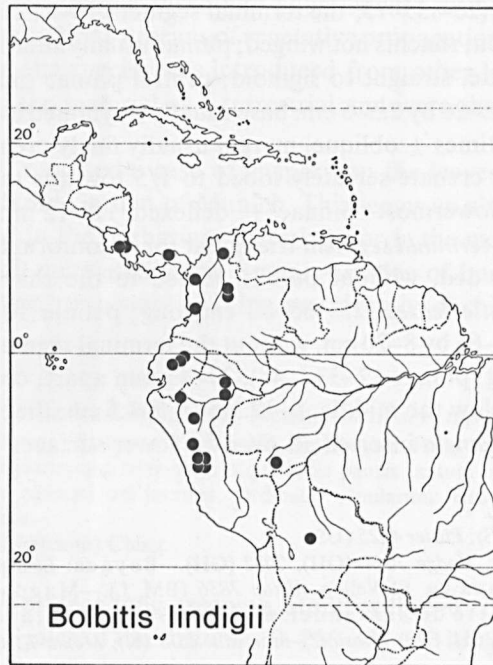


Fig. 65. Distribution of ser. *Lindigianae* (monotypic).

2. *Chrysodium pellucens* was not understood by Christensen (op. cit. 1904, 1906). The type material consists of small sterile plants, the leaves of which are composed of only six pinnae. The margin of the pinnae is lobed to 1/4 towards the costa. They represent juvenile leaves.

### 9. Series *Portoricenses* Hennipman, ser. nov.

Squamae basi affixae. Lamina simplex, vel pinnata segmento terminali pinnatifidum vel triangulare, bulbillis unico vel plerisque subterminalibus. Ordinatio venularum: venulae in reticulationem intricatam anastomosantes, areolis in parte venulis liberis plerumque recurrentibus.

Typus: *Bolbitis portoricensis* (Sprengel) Hennipman.

(Exclusively?) terrestrial. *Rhizome* ± short-creeping, ± stout or rather slender, with 2 rows of leaves, with or without sclerenchyma strands. Scales of the rhizome up to 10 mm long. *Leaves* approximate to somewhat spaced. Sterile leaves pinnate or simple; petiole with 3–11 vascular bundles; lamina with one or more ± spherical subterminal bulbi(s); pinnae up to 14(–18), the margin sometimes with teeth in the sinuses; terminal segment either triangular or conform to the pinnae; secondary veins slightly prominent at the base, others veins immersed; venation pattern: veins forming an intricate network, areoles varying in size and shape, part of which with one or more, (mostly

recurrent, simple or forked, included free veins. *Spores* with a smooth, cristate or cristate-undulate perispore.

Distribution. (Sub)tropical America. See fig. 30, 67.

**29. *Bolbitis hastata* (Fournier) Hennipman—Fig 66: a–c; 67.**

*B. hastata* (Fournier) Hennipman, Amer. Fern J. 65 (1975) 30.—*Acrostichum hastatum* Liebmann, Kong. Dansk. Vid. Selsk. Skrift. V, 1 (1849) 172, *nom. illeg.*, non Thunb. (1784) (= *Pyrrosia spec.*).—*Gymnopteris hastata* Fournier, Mex. Pl. 1 (1872) 70.—*Leptochilus liebmannii* Maxon, Proc. Biol. Soc. Wash. 43 (1930) 86, *nom. illeg.* (art. 72).—*B. liebmannii* C. Chr., Ind. Fil., Suppl. 3 (1934) 49.—Type: *Liebmann s.n.* (in part distributed as *Liebmann Pl. Mexic. 2446*), Mexico, Vera Cruz, Arroyo de Isapa, Baranca de Jovo, near St. Maria Tlapacoyo (= Tlapacoyan), 450–600 m alt. (C; iso in B, K, US).  
*Acrostichum alienum* auct. non Swartz c. *syn. homot.*: auct. p.p.

Rhizome rather slender, c. 5 mm thick (*Barrington 403*, GH). Scales of the rhizome: index 3–4, up to 4 by 1 mm, opaque, light brown. Leaves somewhat spaced. *Sterile leaves* pinnatipartite, the three complete ones available 63, 84, and 95 cm long, resp. (*Liebmann*: 45–65); petiole 23, 40, and 41 cm long, resp., near the base c. 3 mm thick, with 5–7 vascular bundles; lamina index 1–2, widest somewhat below the middle, 28–54 by 17–35 cm, herbaceous, olivaceous, sometimes with a glaucous tinge, with one subterminal bulbil on terminal (and lateral) segment(s); lateral segments usually  $\pm$  opposite, 4–8, spaced; the two lowermost segments: index 3–5, widest about the middle, 13–22 by 3–5 cm, margin  $\pm$  entire, with an inconspicuous  $\pm$  translucent membrane, apex acute or acuminate, the sinus between the segments orbicular or truncate, without teeth or spines; the lamina at the sinuses above the two lowermost lobes 8–30 mm wide; *terminal segment* conform to the lateral ones but larger; *venation pattern*: secondary veins of the segments somewhat unequally dichotomous quite near the costa, see also fig. 66: c. *Fertile leaves*: only incomplete leaves available; lamina index c. 2, 15–20 by 6–11 cm; segments 4–7, the two lowermost segments: index 3–4, 4.5–7 by c. 1.5 cm; the lamina above the two lowermost segments 0.7–1.6 cm wide. *Sporangia* inserted all over the lower surface. *Spores* with a smooth cristate or cristate-undulate perispore.

MEXICO. Chiapas: *Ghiesbrecht 370* ('Chiapas, etc.'): BM, GH, K).—Oaxaca. Dist. Choapan: *Hallberg 1597* (L, NY).—Vera Cruz: *Liebmann s.n.* (type of *Acrostichum hastatum*); *Barrington 403* (GH).

Dr. J. T. Mickel (*in litt.*) kindly communicated three other localities in the State of Oaxaca: Dist. Villa Alta: *Hallberg 1616* (NY); Dist. Tuxtpec: *Mickel 5903* (NY); Dist. Ixtlan: *Mickel 6420* (NY).

Habitat. Terrestrial in moist ravines in the subtropical forest region; on wet rock ledges or in sand. Altitude: 100–850 m.

Spores. *Ghiesbrecht 370* (BM, GH, K): the greater part normal, perispore cristate. *Liebmann s.n.* (type of *Acrostichum hastatum*, US): *ibid.*, perispore cristate-undulate.

Notes. 1. *Liebmann* regarded the present species as one of the rarest Mexican ferns. It is closely related to *B. portoricensis* which differs in the shape of the leaves and the rhizome, as well as in the relative position of the leaves on the rhizome. I



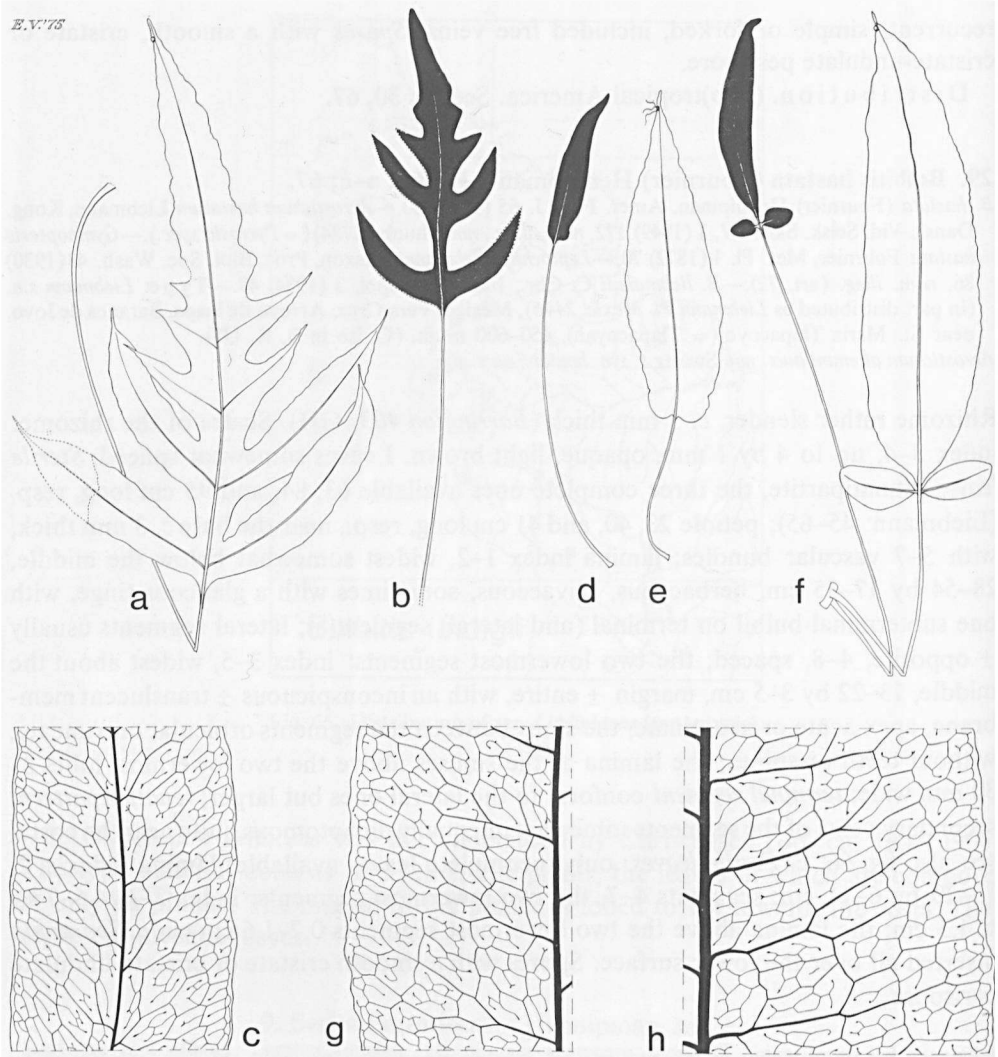


Fig. 66. a–c. *Bolbitis hastata*. a, b. sterile and fertile leaf resp.,  $\times 1/5$ ; c. venation pattern of lobe of sterile leaf,  $\times 4/5$  (a, b. Ghiesbrecht 370, K; c. Liebmann s.n., K, isotype of *B. hastata*).—d–h. *Bolbitis pandurifolia*. d–f. sterile and fertile leaves,  $\times 1/5$ ; g. venation pattern of central part of terminal segment,  $\times 4/5$ ; h. ibid. of lamina (d, e. Spruce 4741, BR, isotype of *B. pandurifolia*; f. Spruce 5684, K; g. ibid., P; h. Spruce 4741, BM, see d).

regard the present species a derivative of a fern like *B. portoricensis*. The derived shape of the leaves agrees with that of *Phymathodes scolopendria* (as was already noticed by Liebmann) and also with that found in the African *B. fluviatilis* which is otherwise quite different.

2. The altitude records on the labels of the type specimens show variation; it is given as 450 m (iso in US) and as 600 m (iso in K).

**30. *Bolbitis pandurifolia* (Hooker) C. Chr.—Fig. 66: d–h; 67.**

*B. pandurifolia* (Hooker) C. Chr., Ind. Fil., Suppl. 3 (1934) 49, p.p. (excl. syn. *Leptochilus oligarchicus*; '*oligogarchicus*').—*Gymnopteris pandurifolia* Hooker, Sec. Cent. Ferns (1861) pl. 87 (excellent).—*Acrostichum pandurifolium* Hooker, Spec. Fil. 5 (1864) 271; Baker in Hooker & Baker, Syn. Fil. (1868) 422; Sodiro, Crypt. Vasc. Quit. (1893) 497.—*Leptochilus pandurifolius* C. Chr., Bot. Tidsskr. 26 (1904) 286.—Type: *Spruce 4741*, Peru, San Martin, Mt. Guayrapurima near Tarapoto (K; iso in BM, BR, P). *Acrostichum oligarchicum* auct. non Baker: Sodiro, Crypt. Vasc. Quit. (1895) 493.

Rhizome ± stout, *c.* 4 mm thick, without sclerenchyma strands (Killip & Smith 26039, US). Scales of the rhizome: index 3–8, up to 7 by 1.5 mm, opaque, brown. Leaves ± approximate. *Sterile leaves* simple or ternate with proportionally small pinnae, 20–60 cm long. *Ternate leaves* 45–60 cm long; petiole 16–27 cm long, near the base 3–4 mm thick, with 3(–5?) vascular bundles; lamina index 2–5, widest usually below (to about) the middle, 26–36 by 6–12 cm, firm-herbaceous to subcarnose, greenish, with one sub-terminal bulbil; rhachis not winged; pinnae ± opposite, index 1–3, widest about or below the middle, 2–10 by 1.8–4 cm, 0–2 mm stalked, base ± symmetrical to slightly oblique with the basiscopic side larger, cuneate, margin usually entire, sometimes slightly repand or sinuate especially in the basal part, without teeth or spines, apex acute to acuminate; *terminal segment* not articulated to the rhachis, 6–9 cm wide, base (short-) decurrent, otherwise like the pinnae; *venation pattern*: areolae relatively large, free included veins relatively long, see also fig. 66: g. *Simple leaves* 20–50 cm long; petiole 3–17 cm long; lamina index 2–5, widest somewhat below (to about) the middle, part of the leaves also broadened near the base but never conspicuously panduriform, 15–35 by 4.5–10 cm, base (narrowly to) broadly cuneate to auriculate, otherwise like the terminal segment of pinnate leaves.—*Fertile leaves* 20–56 cm long. *Ternate leaves* (2 leaves of *Spruce 5684*) 48 and 56 cm long; petiole 32 and 42 cm long, resp.; lamina index *c.* 4, *c.* 4 cm wide; pinnae shortly stalked, resp. *c.* 2 by 1, and 1.5 and 2.5 by *c.* 0.8 cm; terminal segment *c.* 2 cm wide, base narrowly cuneate. *Simple leaves* 20–45 cm long; petiole 13–30 cm long; lamina index 4–8, 7–17 by 1.2–2.7 cm, base usually gradually decurrent, sometimes subcordate and long-decurrent. *Sporangia* inserted all over the lower surface. Spores with a smooth cristate perispore.

ECUADOR. Chimborazo: *Spruce 5684* (BM, K, NY, P).—Sine loc.: *Sodiro s.n.*, viii-1891 (B, P, UC).

PERU. Amazonas: *Wurdack 1897* (NY).—San Martin: *Spruce 4741* (type of *Gymnopteris pandurifolia*).—Junin: *Killip & Smith 26039* (NY, US).

**Habitat.** Rain forest. Terrestrial (*Wurdack 1897*) or (low?) epiphytic (*Killip & Smith 26039*). Altitude: 350–500 m (*Wurdack 1897*); 1100 m (*Killip & Smith 26039*).

**Spores.** *Spruce 4741* (type of *Gymnopteris pandurifolia*, BM, K), *5684* (K), *Wurdack 1897* (NY): the greater part normal. *Killip & Smith 26039* (NY): sporangia mostly young, the mature ones with aborted spores or aborted S.M.C.'s.

**Notes.** 1. A somewhat critical species of which the details of the venation pattern and the shape of the bulbil suggest relationship to *B. portoricensis* and *B. hastata* rather than to a representative of ser. *Euryostichae* with a similar shape of the leaves. The

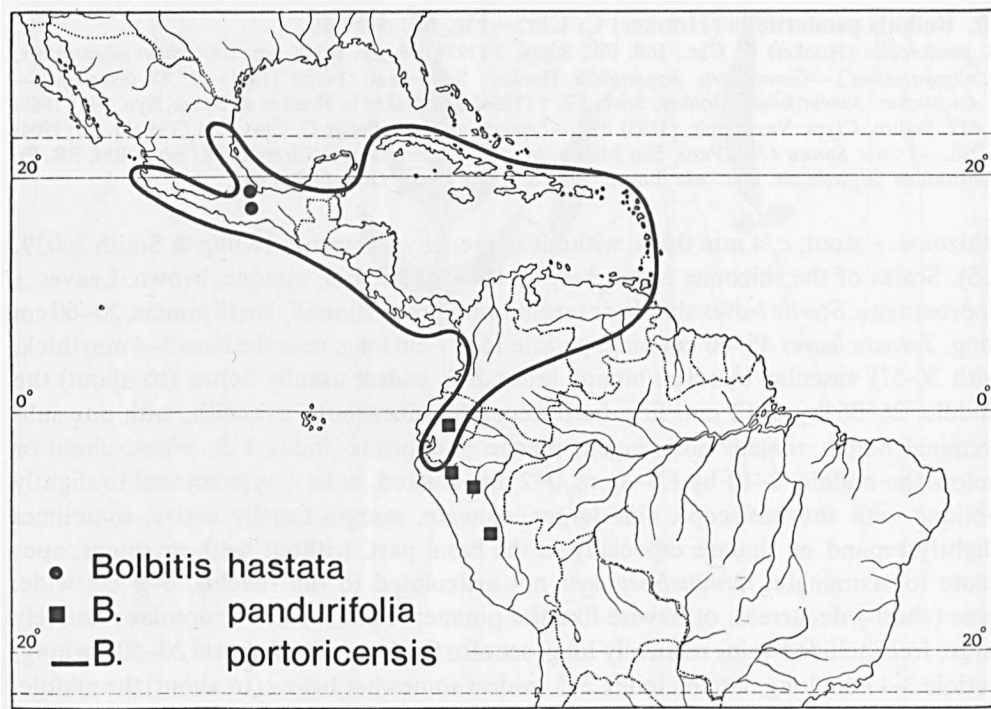


Fig. 67. Distribution of ser. *Portoricenses*: *Bolbitis hastata*, *B. pandurifolia*, and *B. portoricensis*.

configuration of the vascular strands in the one rhizome sectioned is also unlike that found in ser. *Euryostichae*. The appressed scales on the petiole could not be studied in sufficient detail.

2. Variation in the shape of the leaves. The collections from Ecuador have ternate leaves with a long and firm petiole, whereas those from Peru have simple leaves with a relatively shorter and carnosely petiole.

### 31. *Bolbitis portoricensis* (Sprengel) Hennisman—Fig. 67, 68.

*B. portoricensis* (Sprengel) Hennisman, Amer. Fern J. 65 (1975) 30.—*Acrostichum portoricense* Sprengel, Nova Acta Caes. Leop. Carol. 10 (1821) 226.—*Gymnopteris portoricensis* Fée, Hist. Acrost. (1845) 85.—*Anapausia portoricensis* Presl, Epim. Bot. (1851) 187.—Type: *Bertero s.n.*, West Indies, Puerto Rico (G; iso in P, herb. Bory, fert., TO, fert.).

*Acrostichum cladorrhizans* Sprengel, Nova Acta Caes. Leop. Carol. 10 (1821) 225; Syst. Veg. 4 (1827) 37.—*Leptochilus cladorrhizans* Maxon, Sc. Surv. Porto Rico & Virgin Is. 6 (= Pterid. Porto Rico & Virgin Is.) (1926) 460.—*B. cladorrhizans* Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 47; Vareschi in Lasser, Fl. Venezuela 1 (1969) 374, pl. 70.—Type: *Bertero s.n.*, West Indies, Puerto Rico (G; iso in P, herb. Bory, fert., TO, fert.).

*Acrostichum irregulare* Liebmann, Kong. Dansk. Vid. Selsk. Skrift. V, 1 (1849) 173.—*Gymnopteris irregularis* Fournier, Mex. Pl. 1 (1872) 70.—Type: *Liebmann s.n.*, Mexico, Vera Cruz, Baranca de St. Maria Tlatetlá, 450–540 m alt. (iso in B).

*Poecilopteris lobulosa* Presl, Epim. Bot. (1851) 174; C. Chr., Bot. Tidsskr. 26 (1904) 297; Ind. Fil. (1906) 503.—Type: *Friedrichsthal s.n.*, Guatemala, 1841, fert. (W).  
*Acrostichum alienum* Swartz var. *flagellum* Jenman, Bull. Bot. Dept. Jamaica (Kingston) n.s. 5 (= 11) (1898) 154.—*Leptochilus alienus* (Swartz) C. Chr. var. *flagellus* Bonap., Notes Ptérid. 1 (1915) 164.—Type: *Jenman s.n.*, Jamaica (*n.v.*).  
*Acrostichum alienum* Swartz var. *semipinnatifidum* auct. non (Fée) Baker: Christ, Bull. Soc. Bot. Belg. 35 (1896) 246; Jenman, Bull. Bot. Dept. Jamaica (Kingston) n.s. 5 (1898) 154.  
*Acrostichum alienum* auct. non Swartz c. syn. *homot.*: auct. p.p.  
 [*Filix latifolia laciniata*, et ad lacinias molliter aculeata, Plumier, Tract. Fil. Amer. (1705) 9, pl. 9.—Leg.: *Plumier s.n.*, Santo Domingo (P, herb. Vaillant).]  
 [*Filix latifolia*, in pinnulas obtusas, et leviter crenatas divisa, Plumier, Tract. Fil. Amer. (1705) 10, pl. 10.—Leg.: *Plumier s.n.*, Martinique (P, herb. Surian, *n.v.*).]

Rhizome stout, up to 15(–20) mm thick, with sclerenchyma strands. Scales of the rhizome: index 3–8, up to 10 by 2 mm, usually opaque, sometimes subclathrate, reddish brown. Leaves approximate. *Sterile leaves* pinnate, 20–> 200 cm long; petiole 4–60 cm long, near the base 1.5–7 mm thick, with 5–11 vascular bundles; lamina of non-flagelloid leaves: index 1–3, widest usually somewhat below the middle, sometimes at the base, 15–80 by 7–50 cm, without the terminal segment 0–35(–45), the terminal segment 15–55 cm long, herbaceous, usually light or bright green, usually without conspicuous bulbils; rhachis not winged; lamina of flagelloid leaves up to c. 200 cm long, without the terminal segment 6–50, the terminal segment up to 150 cm long, possibly even longer, the flagellum with 3–5 bulbils situated 10–30 cm apart; pinnae usually ± opposite, 2–14(–18), up to 110 mm apart; central pinnae index (2–)3–8, widest about or below the middle, 3.5–30(–35) by 1.3–7 cm, base ± symmetrical, variously shaped, margin either entire or (bi)serrate-crenate or lobed to 2/3 towards the costa, with or without ± distinct teeth (in the sinuses), apex acute or acuminate, lobes or segments of pinnae obliquely inserted, straight or subfalcate, the margin entire to (bi)serrate-crenate; the two lowermost pinnae 0–10 mm stalked, usually asymmetrical with the acroscopic side conform to that of the other pinnae, the basiscopic side triangular to about as long as wide, deeply pinnatifid near the base, segments of about similar shape as those of proximal pinnae; *terminal segment* triangular, near the base deeply pinnatifid, gradually less incised towards the apex, base narrowly cuneate, apex acute, acuminate, or (long-) flagelloid, base of segments usually abruptly long-decurrent; *venation pattern*: rather variable as to the size of the areoles, see also fig. 68: e–j. *Fertile leaves* with an acute or somewhat prolonged apex, 12–135 cm long; petiole 7–85 cm long; lamina index 1–4, 5–50 by 2.5–25 cm, without the terminal segment 0–30, the terminal segment 5–30 cm long; pinnae 2–12, 15–85 mm apart; central pinnae index 3–15, widest about the middle, 0.9–17 by 0.3–3.5 cm; the two lowermost pinnae 0–8 mm stalked. *Sporangia* inserted usually all over the lower surface, sometimes along the main veins with a narrow sterile strip. Spores with a smooth cristate or cristate-undulate perispore.

MEXICO. Central and southern states: many collections.  
 BELIZE. 6 collections.  
 GUATEMALA. Many collections.  
 HONDURAS. 13 collections.

SALVADOR. 6 collections.

NICARAGUA. 14 collections.

COSTA RICA. Many collections.

CUBA. 13 collections.

JAMAICA. *Hart* 63 (US); *Jenman* 26 (K); *Watt* 118 (P, U, US).

DOMINICAN REPUBLIC. 8 collections.

HAITI. 5 collections.

PUERTO RICO. 9 collections.

LESSER ANTILLES. (St. Eustatius, St. Kitts, Montserrat, Guadeloupe, Dominica, Martinique, St. Lucia, St. Vincent, Trinidad, and Tobago). 60 collections.

PANAMA. Many collections.

COLOMBIA. Antioquia: *Haught* 4629 (F, US).—Guajira: *Haught* 4293 (S, US).—Magdalena: *Bennett* 17 (F, US); *Purdie* s.n. (BM, K); *H. H. Smith* 1054 (B, BM, BR, F, G, GH, K, L, MO, NY, P, U, UC, US).—Meta: *Philipson et al.* 2055 (BM).—Norte de Santander: *Bischler* 2418 (G).

VENEZUELA. Aragua: 5 collections.—Anzoategui: *Steyermark* 61142 (F, US).—Bolívar: *L. Williams* 11438 (F, US).—Carabobo: *Alston* 6161 (BM); *Linden* 1573 (BR).—Merida: *Fendler* 336 (BR, G, GH, K, MO); *Vogl* s.n. (M).—Yaracuy: *Vareschi & Pannier* 2619 (US).

ECUADOR. *Seemann* 368 (K); *Sodiro* s.n. (P); *Verleysen* s.n. (P).

**Habitat.** Usually creeping on rocks (several times reported from sandstone), sometimes in soil, in usually wet places in forests. Altitude: 0–1250 (in Guatemala—1800) m.

**Spores.** *Herminier* s.n. (L), *Proctor* 19262 (U), *Schipp* 526 (K): the greater part normal, the perispore densely and low cristate. *Friedrichsthal* s.n. (type of *Poecilopteris lobulosa*, W): *ibid.*, the perispore with few inconspicuous crests, sometimes locally with minute spines. *Liebmann* s.n. (type of *Acrostichum irregulare*, B): *ibid.*, the perispore cristate-undulate. *Bertero* s.n. (type of *Acrostichum portoricense*, G), *ibid.* (type of *A. cladorrhizans*, P), *Sinten* 6261 (L), *H. M. Smith* 1054 (L): abnormal, the normally shaped ones with a cristate perispore.

**Notes.** 1. A clear-cut species which is exceedingly variable as regards the shape of both the leaves and the pinnae. *B. portoricensis* is easily recognized especially by the combination of leaf-shape and venation pattern. It is closely related to *B. hastata*. The relationship to *B. pandurifolia* is less apparent. The present species has been confused with *B. aliena* by others. It is presumably included in the parentage of *B. semipinnatifida*.

2. The type specimens of *Acrostichum portoricense* and *A. cladorrhizans*, though with leaves of a rather different outline, easily fit into the species as delimited here. Fée (1845) who first united these species under the name *A. portoricense*, used characters of the sporangia (size, shape, and number of indurated cells) to discriminate between these two and *Gymnopteris aliena sensu* Fée (= *B. portoricensis*). However, these features show considerable variation in a number of collections studied (the material studied by Fée included).

3. *Poecilopteris lobulosa*. Presl (1851) based himself on fertile material collected by Friedrichsthal and referred to a collection which Fée had earlier annotated as *Heteronevron* . . .'. As Presl did not annotate this specimen, the original material of this could be traced only thanks to Fée's annotation. The type matches completely the piece of fertile leaf present on *Friedrichsthal* 1044 (W, 3 sh.) that Presl annotated as *Anapausia aliena*.

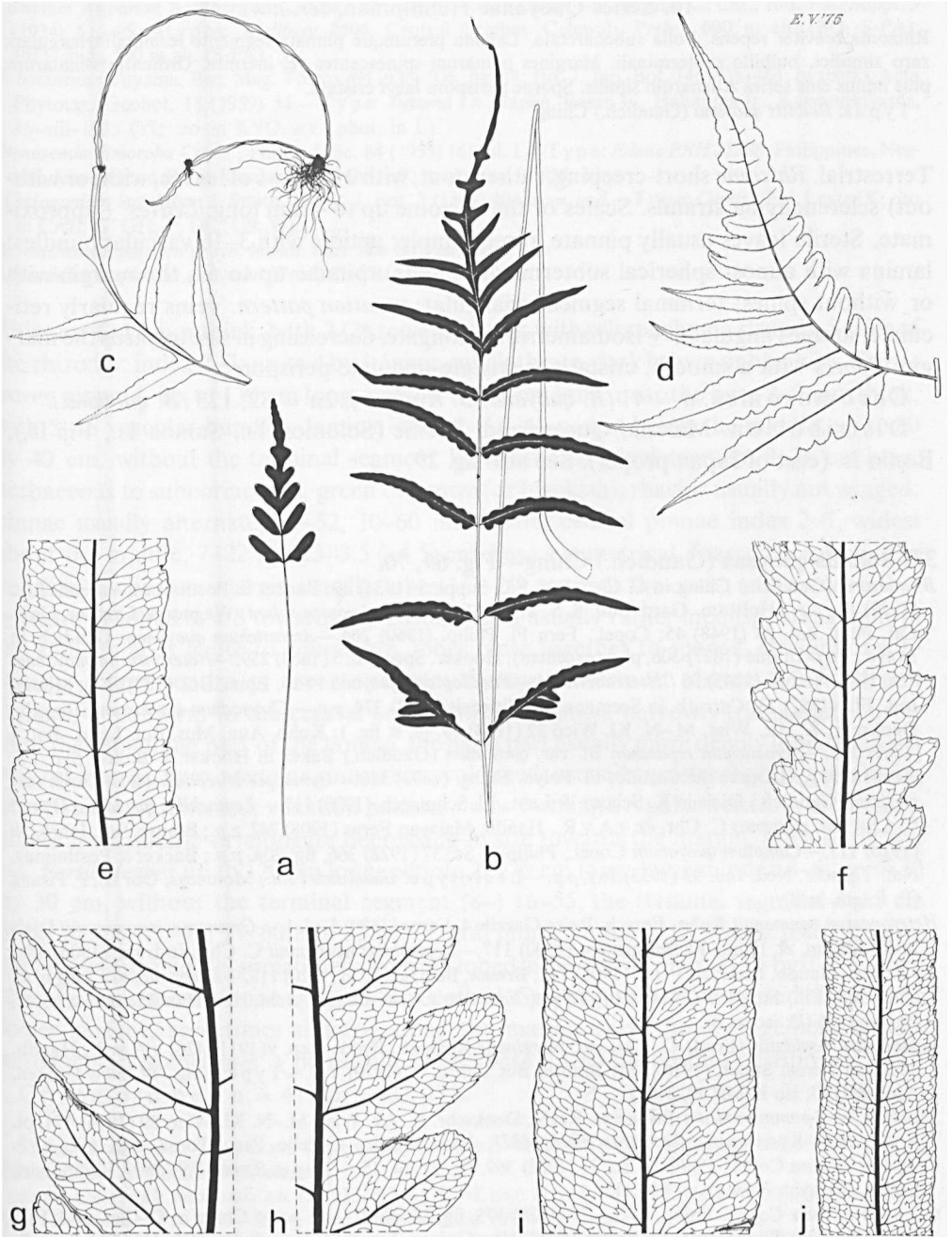


Fig. 68. *Bolbitis portoricensis*.—a, b. fertile leaves,  $\times 1/5$ ; c. terminal part of sterile leaf,  $\times 1/5$ ; d. basal pinna of a sterile leaf,  $\times 1/5$ ; e–j, venation pattern of sterile pinnae,  $\times 4/5$  (a. *Skutch 2577*, K; b. *Dodge & Allen 17329*, US; c. *H. H. Smith 1054*, K; d. *Kupper 739*, M; e. *Walker T 10495*, BM; f. *Von Türckheim 2728*, P; g. *Herminier s.n.*, L; h. *Alston 5826*, BM; i. *Alfaro 16535*, P; j. *C. F. Baker 2185*, P).

## 10. Series Quoyanae HENNIPMAN, ser. nov.

Rhizoma breviter repens. Folia subcoarctata. Lamina plerumque pinnata segmento terminali triangulari, raro simplici, bulbillo subterminali. Margines pinnarum spinescentes vel inermes. Ordinatio venularum: plus minus eius series Alienarum similis. Sporae perispora laevi cristata.

Typus: *Bolbitis quoyana* (Gaudich.) Ching.

Terrestrial. *Rhizome* short-creeping, rather stout, with 2 (3) rows of leaves, with (or without) sclerenchyma strands. Scales of the rhizome up to 4 mm long. *Leaves* ± approximate. Sterile leaves usually pinnate, rarely simple; petiole with 3–16 vascular bundles; lamina with almost spherical subterminal bulbil(s); pinnae up to 52, the margin with or without spines; terminal segment triangular; *venation pattern*: veins regularly reticulate, areoles angulate, ± isodiametric or elongate, decreasing in size towards the margin. *Sporae* with a smooth, cristate or cristate-undulate perispore.

Chromosomes.  $n = 41$  (*B. quoyana*, *B. rivularis*),  $2n = 82$ , 123 (*B. quoyana*).

Distribution. Malesia, Queensland, Pacific (Solomon Is., Samoa Is., Fiji Is.), Bonin Is. (east of Japan proper). See also fig. 29.

## 32. *Bolbitis quoyana* (Gaudich.) Ching—Fig. 69, 70.

*B. quoyana* (Gaudich.) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 49; Backer & Posthumus, Varenfl. Java (1939) 81, p.p.; Holttum, Gard. Bull. S. S. 11 (1947) 271, *quoad nomen solum*: Wagner & Grether, Univ. Cal. Publ. Bot. 23 (1948) 45; Copel., Fern Fl. Philip. (1960) 264.—*Acrostichum quoyanum* Gaudich. in Freyc., Voy. Uranie (1827) 306, pl. 3 (excellent); Hooker, Spec. Fil. 5 (1864) 259.—*Heteroneuron quoyanum* Fée, Hist. Acrost. (1845) 96 ('*Heteroneuron*').—*Poecilopteris quoyana* Presl, Epim. Bot. (1851) 173; Moore, Ind. Fil. (1857) 13; Carruth. in Seemann, Fl. Vitiensis (1873) 374, p.p.—*Chrysodium quoyanum* Ettiingsh., Denkschr. K. Ak. Wiss. M.–N. Kl. Wien 22 (1864) 59, pl. 8: fig. 1; Kuhn, Ann. Mus. Bot. Lugd.–Bat. 4 (1869) 293.—*Acrostichum repandum* Bl. var. *quoyanum* (Gaudich.) Baker in Hooker & Baker, Syn. Fil. (1868) 419, p.p.; Drake del Castillo, Fl. Polyn. Franç. (1893) 320.—*Gymnopteris repanda* (Bl.) Christ var. *quoyana* (Gaudich.) Diels in K. Schum. & Laut., Fl. Schutzgeb. (1900) 117.—*Leptochilus cuspidatus* (Presl) C. Chr. var. *quoyanus* C. Chr. ex v.A.v.R., Handb. Malayan Ferns (1908) 742, p.p.; Brause, Bot. Jahrb. 56 (1920) 117.—*Campium quoyanum* Copel., Philip. J. Sc. 37 (1928) 366, fig. 20a, p.p.; Backer & Posthumus, Nat. Tijdschr. Ned. Ind. 93 (1933) 161, p.p.—*Lectotype*: *Gaudichaud s.n.*, Moluccas, Obi Is., P. Pisang (P; fragm. in B).

*Heteroneuron naumannii* Kuhn, Forsch. Reise Gazelle 4, Farne (1889) 5, pl. 1.—*Gymnopteris naumannii* Diels in K. Schum. & Laut., Fl. Schutzgeb. (1900) 117.—*Leptochilus naumannii* C. Chr., Ind. Fil. (1906) 386; v.A.v.R., Handb. Malayan Ferns (1908) 742; Brause, Bot. Jahrb. 56 (1920) 118.—*B. naumannii* Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 49.—*Type*: *Naumann s.n.*, Bismarck Arch., New Hanover, south coast, 23–vii–1875 (B; iso in B).

*Leptochilus cuspidatus* (Presl) C. Chr. var. *marginalis* Rosenst., Fedde Rep. 9 (1911) 426; v.A.v.R., Handb. Malayan Ferns, Suppl. (1916) 435; Brause, Bot. Jahrb. 56 (1920) 117.—*Type*: *King 144*, New Guinea, Ambasi (BO; iso in MICH, 3 sh.).

*Aspidium novo-pommeranicum* Brause ex Rech., Denkschr. K. Ak. Wiss. M.–N. Kl. Wien 89 (1914) 471, pl. 3: fig. 8b.—*Syntypes*: *Rechinger 3836, 4371*, New Britain, Gazelle Pen., Toma, ster. (W, n.v.).

*Campium validum* Copel., Philip. J. Sc. 37 (1928) 369, fig. 22, pl. 15.—*Type*: *Ramos BS 13807*, Philippines, Luzon, Cagayan Prov. (n.v.; MICH?).

*Campium parvum* Copel., Philip. J. Sc. 37 (1928) 375, fig. 28, pl. 21.—*B. parva* Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 49.—*Type*: *Schlechter 16163*, New Guinea, Terr. of New Guinea, 300 m alt. (UC; iso in B, L, P).

*Campium enorme* Copel., Philip. J. Sc. 40 (1929) 307, pl. 8.—*B. enormis* C. Chr., Ind. Fil., Suppl. 3 (1934) 197; Copel., Fern Fl. Philip. (1960) 264.—*Type*: *Copeland s.n.*, Philippines, Mindanao, Mt. Matatum, 1–v–1917 (MICH, herb. Copeland 11539, 11540; iso in UC, 353983).

*Campium viviparum* Kjellberg in C. Chr., Bot. Jahrb. 66 (1933) 50.—*B. vivipara* C. Chr., Ind. Fil., Suppl. 3 (1934) 51.—Syntypes: *Kjellberg 2506*, Central Celebes, Celewab, Preho, 600 m alt. (BO, S-PA), 3635, *ibid.*, 500 m alt. (S-PA).

*B. boninensis* Tuyama, Bot. Mag. Tokyo 49(1935) 506, fig. 14; Ito, J. Jap. Bot. 14(1938) 443; Iwatsuki, Acta Phytotax. Geobot. 18 (1959) 54.—Type: *Tuyama s.n.*, Japan, Bonin Is., Hahajima Is., Kuwanokiyama, 15–viii–1933 (TI; iso in KYO, *n.v.*, phot. in L).

*Stenosemia dimorpha* Copel., Philip. J. Sc. 84 (1955) 161, pl. 1.—Type: *Edaño PNH 21388*, Philippines, Negros, Kinabkaban River, Canlaon Volcano, 650 m alt. (iso in BM, L).

[*Cyrtogonium laciniatum* J. Smith, Hook. J. Bot. 3 (1841) 403, *nom. nud.*—Type: *Cuming 294*, Leyte (K; iso in CAL, G, GH, P, UC, US, W).]

*Acrostichum repandum* et *syn. homot. auct. non B1.*: *auct. p.p.*

*Leptochilus cuspidatus* *auct. non* (Presl) C. Chr.: *auct. p.p.*

Rhizome 6–13 mm thick, with 2 (3) rows of leaves, with sclerenchyma strands. Scales of the rhizome: index 2–7, up to 4 by 1.5 mm, subclathrate, dark brown or blackish. *Sterile leaves* pinnate, up to 130 cm long; petiole 10–50 cm long, near the base 2–9 mm thick, with 5–16 vascular bundles; lamina index 1–3 (–4), widest below the middle, up to 80 by 40 cm, without the terminal segment 12–70, the terminal segment 9–26 cm long, herbaceous to subcoriaceous, green or brown (or blackish); rhachis usually not winged; pinnae usually alternate, 13–52, 10–60 mm apart; central pinnae index 2–7, widest about the middle, 7–22 by 1.3–3.5 (–4.5) cm, base symmetrical, (narrowly to) broadly cuneate to cordate, margin usually lobes 1/3–2/3 towards the costa, sometimes either ± entire or lobed to 4/5 towards the costa, with a usually rather inconspicuous spine in the sinuses, apex acute to acuminate, lobes close together to spaced, straight or sub-falcate, margin entire or crenate-serrate; the two lowermost pinnae 1–9 (–13) mm stalked, ± conform to the central ones; *terminal segment* narrowly triangular, shorter than the remaining part of the lamina, the basal part usually more deeply lobed than the central pinnae, apex acute or somewhat prolonged; secondary *veins* slightly prominent, other veins ± immersed; venation pattern: veins forming a regular network, areoles angulate isodiametric or elongate decreasing in size towards the margin, see also fig. 69: 1–s. *Fertile leaves* up to 120 cm long; petiole 25–70 cm long; lamina index 3–6, up to 70 by 30 cm, without the terminal segment (8–) 16–55, the terminal segment 4–15 cm long; pinnae 11–42, 17–60 mm apart; central pinnae index 5–15, widest usually about (to below) the middle, sometimes as deeply lobed as the sterile ones, 3–15 by 0.4–1.7 cm; the two lowermost pinnae up to 13 mm stalked. *Sporangia* usually inserted all over the lower surface, sometimes situated along the margin only, the arrangement usually acrostichoid, sometimes ± pteridoid. Spores with a smooth cristate perispore.

Chromosomes.  $n = 41$ ;  $2n = 82, 123$ .

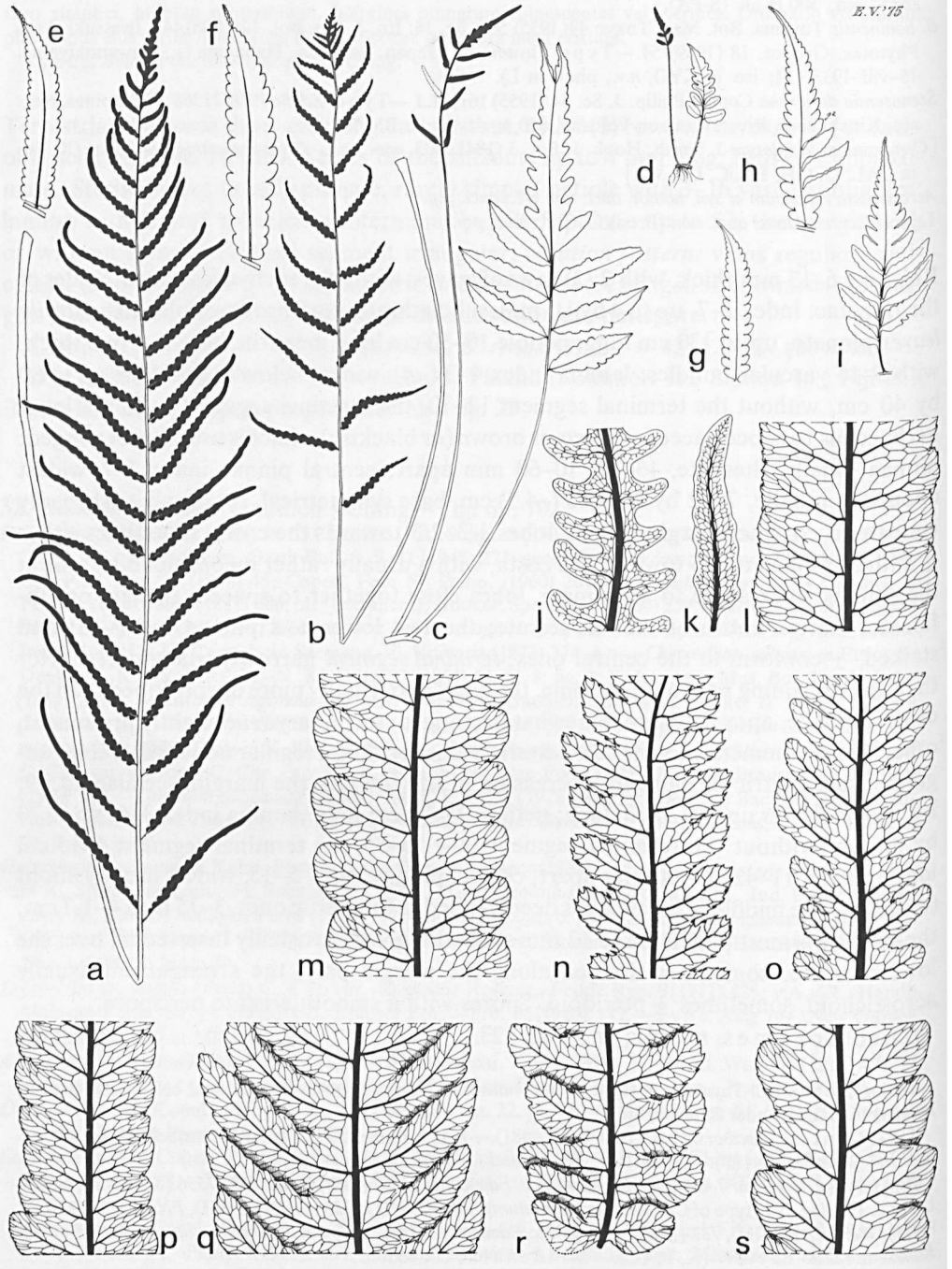
JAPAN. BONIN IS.: *Tuyama s.n.* (type of *B. boninensis*); *Warburg s.n.* (B). Additional collections cited by Iwatsuki (op. cit.) under *B. boninensis*.

JAVA. Central: *Raciborski s.n.* (L, 938.297–481).—East: *Franck 37* (C, US); *Rosenstock Fil. Jav. Or. ex-secc. 107* (*Mousset leg.*) (P).—Sine loc.: *Hildebrand s.n.* (P); *Zippel s.n.* (B).

PHILIPPINES. Luzon: 7 collections.—Samar: *Edaño BS 24868* (US); *Ramos BS 17556* (K, MICH, US).—Leyte: *Cuming 294* (type of *Cyrtogonium laciniatum*); *Edaño PNH 11238* (MICH, PNH), *PNH 11252* (MICH, PNH); *Wenzel 432* (GH), 732 (MO).—Negros: *Edaño PNH 21388* (type of *Stenosemia dimorpha*).—Panay: *Ramos & Edaño BS 30847* (K, P, US).—Mindanao: 6 collections.

CELEBES. Central: *Kjellberg 2506* (syntype of *Campium viviparum*; BO, S-PA), 3635 (*ibid.*; S-PA).—





North Peninsula: *Alston 15766* (BM); *Posthumus 2280* (BO); *Savinière s.n.* (P); *Wisse 72* (BO, WAG).

MOLUCCAS. P. Morotai: *Reimschlüssel 10* (US).—Halmaheira: *Teijsmann s.n.* (BO).—Ternate: *Alston 16656* (BM); *Beguín 1012* (BO, L); *Von Martens s.n.* (B).—P. Pisang: *Gaudichaud s.n.* (lectotype of *Acrostichum quoyanum*).—Amboin: *Rant 388* (BO); *Zippel 207* (B), *s.n.* (L).

NEW GUINEA. 70 collections from the mountainous regions all over the island.—D'Entrecasteaux Is.: *Brass 25931* (GH, L, PNH), *27162* (K, L).—Biak: *Grether & Wagner 4218* (UC).—Aru Is.: *Buwalda 5078* (BO).

BISMARCK ARCHIPELAGO. New Britain: 10 collections.—New Ireland: *Anonymus 94* (B); *Lahaie 766* (P).—New Hanover: *Naumann s.n.* (type of *Heteroneuron naumannii*).—Admiralty Is.: *Grether 4583* (UC); *Grether & Wagner 4036* (UC). *Moseley s.n.*, *Challenger exp.* (K); *Wagner 3277* (US).

SOLOMON Is. Buka: *Waterhouse 47* (K).—Bougainville: *Wakefield 1037* (BM), *1161* (BM).—Shortland I.: *Guppy 99* (BM).—Santa Ysabel: *Braithwaite R.S.S. 4527* (K).—Vella La Vella: *Wall & Nakisi BSIP 17502* (L).—Guadalcanal: *Braithwaite R.S.S. 4130* (K, L); *McKee 1612* (LAE).

SAMOA Is. Upolu: *Flohr s.n.* (S-PA); *Rechinger 626* (W), *783* (W).—Sine loc.: *Reinecke 5b* (G).

Fiji Is. Sine loc.: *Horne s.n.* (K).

AUSTRALIA. Queensland: 6 collections.

**Habitat.** Creeping on rocks and in soil in rain forest, mostly near streams. Several times reported from limestone. Altitude: 0–1200(–1700) m.

**Spores.** *Brass 5621* (BM), *Gaudichaud s.n.* (type of *Acrostichum quoyanum*), *Jermy 9604* (diploid; BM), *Kostermans 2909* (L), *Raciborski s.n.* (L, 938.297–481), *Schlechter 16163* (type of *Campium parvum*; B, L): all or the greater part normal. *Copeland s.n.* (type of *Campium enorme*; UC): part of the sporangia filled with normal spores, part with normal and abnormal spores, part with only abnormal spores. *Brass 23616* (A), *Grether 3601* (MICH), *Rechinger 3650* (W): the majority (?) normal. *Brass 12833* (GH), *Mendoza & Convocar PNH 8606* (MICH), *Ramos BS 17556* (MICH): the greater part abnormal. *Tuyama s.n.* (type of *B. boninensis*; TI), *Walker T 10053* (triploid; BM): sporangia filled with usually aborted S.M.C.'s.

**Notes.** 1. A distinct species which has been confused by most authors with *Bolbitis repanda*. It is closest to *B. rivularis*, its coriaceous counterpart (and also showing a tendency to dwarfing), to *B. taylorii* which differs especially in leaf architecture and venation pattern, and to *B. sagenioides* (see: *Spec. dub.*). *B. bipinnatifida* and *B. subcordata* are more distant relatives.

The present species is best recognized by the shape and venation of the pinnae or, when dwarfs are at hand, of the terminal segment.

The study of the spores has contributed considerably to the present classification as it allowed me to exclude an essential part of the morphological heterogeneity which I first had assembled and in which I was unable to draw lines. Amongst these excluded specimens are *B. × foxii*, *B. × sinuosa*, and the type of *Heteroneuron argutum* (= *B. heteroclita s.l.*).

**Fig. 69.** *Bolbitis quoyana*.—a–f. sterile and fertile leaves,  $\times 1/5$ ; g, h. central pinnae,  $\times 1/5$ ; i. lowermost pinna,  $\times 1/5$ ; j, k. venation pattern of fertile pinnae,  $\times 4/5$ ; l–s. *ibid.* of sterile pinnae (a, e, p. *Walker T 10052*, BM, triploid; b, f, m. *Walker T 9604*, BM, diploid; c. *Walker T 9300*, BM; d. *Schlechter 16163*, L, isotype of *Campium parvum*; g–i. *Braithwaite RSS 4527*, leaf C, K; j. *Ledermann 10487a*, BO; k. *Ramos BS 7522*, B; l. *Pleyte 452*, BO; n. *Elmer 13468a*, BO; o. *Brass 13473*, GH; q. *Grether & W. H. Wagner 4036*, UC; r. *Teijsmann s.n.*, BO; s. *Walker T 9615*, BM, triploid).

2. Variability. The features varying most markedly are the size of the leaves and the shape of the pinnae. The two extremes are represented by the type specimens of *Campium parvum* (New Guinea) and by *Braithwaite* R.S.S. nos. 4130 and 4527 (Solomon Islands).

a. *Campium parvum* is in a fertile condition only known by the type collection (10 plants) upon which the following description is based. Rhizome up to 3 mm thick with 2 rows of leaves. Scales of the rhizome up to 2 by 0.8 mm. Leaves rather spaced. Sterile leaves pinnate with a triangular terminal segment, up to 15 cm long; petiole up to 7 cm long, with 3 vascular bundles; lamina index 1–3, widest below the middle, up to 8.5 by 5.5 cm, with primordia of bulbils subterminally on the terminal (and lateral) segments; pinnae 2–5, up to 7 mm apart; central pinnae index 1–3, widest about the middle, up to 35 by 13 mm, the margin slightly crenate-serrate; the two lowermost pinnae up to 2 mm stalked; terminal segment near the base deeply lobed, with distinct spines in the sinuses; venation pattern in the basal part of the terminal segment  $\pm$  similar to that found in the central pinnae of *B. quoyana* proper; the venation pattern of the pinnae simpler. Fertile leaves up to 19 cm long; petiole up to 15 cm long; lamina index 2–3, up to 4 by 2 cm; pinnae 4. Sporangia inserted all over the lower surface.

In a sterile condition known by two other collections from New Guinea: *King 269* (MICH) and *Werner 41 = Rosenstock Fil. Novog. exsicc. 11* (S-PA, p.p., UC, p.p.). The sterile leaves agree completely with leaves grown on bulbils situated on typical specimens of *B. quoyana*.

Fertile plants intermediate between *Campium parvum* and typical *B. quoyana* are represented by *Walker T 7882* (BM) and *T 9300* (BM), both from New Guinea.

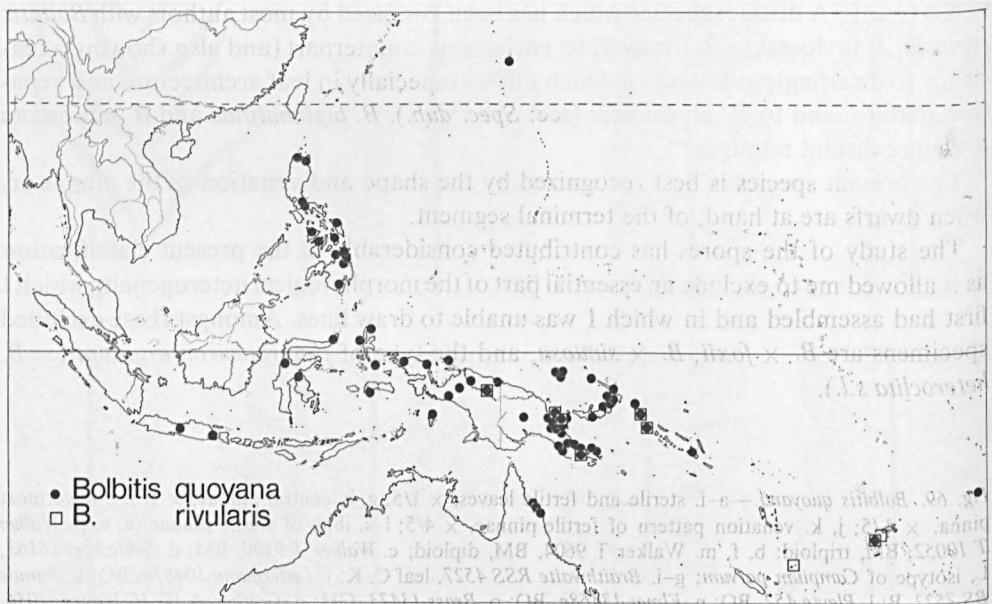


Fig. 70. Distribution of *Bolbitis quoyana* and *B. rivularis*.

b. Braithwaite's collections from the Solomon Islands. *Braithwaite R.S.S. 4130* (L). Sterile leaves pinnate, 155 cm long; petiole 80 cm long; lamina 75 by 45 cm; pinnae 32, normally shaped, the largest c. 24 by 5 cm, lobes rather spaced. Spores: sporangia with aborted S.M.C.'s only.

*Braithwaite R.S.S. 4527* of which I was kindly permitted by Dr. F. M. Jarrett, Kew, to study all the material prior to the distribution of duplicates; it was provisionally identified by Prof. Holttum as '*Bolbitis spec. nov.*'. The plants revealed features similar to typical *B. quoyana* except for the shape of the leaves. The lowest part of the leaves is bipinnate; the pinnae are composed of up to 10 pinnules. The bipinnate condition gradually passes into the pinnate one in the central and upper part of the leaf. Spores in part normal, large (the longest axis up to 50  $\mu$ m long), in part shrivelled. The bipinnate condition is not consistent; it covers a variously large part of the three sterile leaves studied. The shape of the pinnae of typical specimens from the Admiralty Is. and Solomons shows considerable variation. The plants from these regions are in need of cytological investigation.

3. The differences between the diploids and triploids collected by Walker (vouchers in BM) mainly regard the number of pinnae to a leaf. This number is 17 in *Walker T 9603*; 19–22 in *T 9604*, *T 9605* (all diploids); 26–30 in *T 9616* (= *Jermy 4945*), 40 and 46 in *T 10052* (both triploids). The fertile pinnae of the diploids are smaller than those of the triploids but otherwise not much different. As the differences between the diploid and triploid specimens are otherwise trifling, the triploids are likely to be the result of autopoloidization. However, Walker (*in litt.*) informed me that the meiosis of the triploids showed the chromosomes nearly all to be present as univalents, only very few as bi- or trivalents.

4. Copeland's classification of the specimens from the Philippines and New Guinea is confusing. As regards the specimens from the Philippines, he included *Cuming 294*, the type of *Cyrtogonium laciniatum*, in *Bolbitis quoyana*. *Cyrtogonium laciniatum* deviates in the following characters: sterile leaves bear comparatively few (13–16) pinnae lobed 1/2–4/5 towards the costa, the lobes are remote and  $\pm$  serrate. A specimen similar to the latter was described by Copeland (1951) as *Stenosemia dimorpha*! *Campium validum*, which he (1928) newly described, was regarded as synonymous with *B. sinuosa* (= *B. x sinuosa*, later (1960). Copeland thought *B. sinuosa* related to *B. presliana* which is quite different. The type specimen of *Campium validum* (as far as could be studied from the plate) and that of *Campium enorme* are strikingly similar to that of *Acrostichum quoyanum* (which was not studied by Copeland).

5. The typification of *Acrostichum quoyanum*. In the original description *Acrostichum quoyanum* was reported from several localities. Only the collection from P. Pisang, from which the plate and the original description obviously were drawn, could be traced.

### 33. *Bolbitis rivularis* (Brackenr.) Ching—Fig. 70, 71.

*B. rivularis* (Brackenr.) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 50; Backer & Posthumus, Varenfl. Java (1939) 82 ('*B. ? rivulare*').—*Cyrtogonium rivulare* Brackenr. in Wilkes, U.S. Expl. Exp. 16 (1854) 85, pl. 11:

fig. 2.—*Neurocallis rivularis* Moore, Ind. Fil. (1861) 276.—*Acrostichum rivulare* Hooker, Spec. Fil. 5 (1864) 263; Baker in Hooker & Baker, Syn. Fil., 2nd ed. (1874) 524.—*Poecilopteris rivularis* Carruth. ex Seemann, Fl. Vitiensis (1873) 374.—*Leptochilus rivularis* C. Chr., Ind. Fil. (1906) 387.—*Campium rivulare* Copel., Philip. J. Sc. 37 (1928) 373, fig. 27, pl. 20; Backer & Posthumus, Nat. Tijdschr. Ned. Ind. 93 (1933) 161 ('*C. ?rivulare*').—Type: *Brackenridge s.n.*, Fiji Is., Ovalau (US, 51090).  
*Campium kajewskii* Copel., Philip. J. Sc. 60 (1936) 112, pl. 22.—Type: *Kajewski 1763*, Solomon Is., Bougainville, Kupei Gold Field, 1000 m alt. (iso in A, one of the two sheets with this number; BRI).

Rhizome up to 6 mm thick, with 2 rows of leaves, with sclerenchyma strands. Scales of the rhizome: index 1–3, up to 4 by 1.5(–2) mm, subclathrate, dark brown or blackish. *Sterile leaves* usually pinnate, rarely simple, 10–70 cm long. *Pinnate leaves* 10–70 cm long; petiole 3–35 cm long, near the base 2–5 mm thick, with 5–12 vascular bundles; lamina index 1–3 (–5), widest usually below (to about) the middle, 7–40 by 3–25 cm, without the terminal segment 0–15, the terminal segment 5–30 cm long, fleshy-coriaceous, olivaceous to brownish; rhachis not winged; pinnae alternate to opposite, 2–11, up to 50 mm apart; central pinnae index 1–5, widest about or below the middle, 1.5–16 by 0.8–4.5 cm, straight to subfalcate, base  $\pm$  symmetrical, cuneate to subcordate, margin  $\pm$  entire to lobed to 1/5(–2/5) towards the costa, without or with but an inconspicuous tooth or spine in the sinuses, apex acute or acuminate; the two lowermost pinnae usually opposite, 0–4 mm stalked; *terminal segment* triangular, as long as to longer than the remaining part of the lamina, apex acute or acuminate; secondary and other *veins* slightly prominent or  $\pm$  immersed; venation pattern: veins forming a regular network of angulate, isodiametric or elongate areoles which decrease in size towards the margin; see also fig. 71: i–1. *Simple leaves* 15–30 cm long; petiole 3–9 cm long, near the base 1–1.5 mm thick; lamina index 4–7, widest about or somewhat below the middle, 12–23 by 2.5–4.5 cm, base cuneate to subcordate, margin  $\pm$  entire to lobed to 2/5 towards the costa, apex acute or acuminate, otherwise similar to the terminal segment of pinnate leaves.—*Fertile leaves*. *Pinnate leaves* 20–75 cm long; petiole 13–45 cm long; lamina index 1–4, 5–35 by 2–20 cm, without the terminal segment 0.5–23, the terminal segment 2.5–15 cm long; pinnae 2–12, up to 80 mm apart; central pinnae index 1–6, widest about or below the middle, 1.2–9 by 0.3–1.5 cm, the two lowermost pinnae 1–10 mm stalked; terminal segment with an acute apex. *Simple leaf* (*Graeffe 108*, P) 33 cm long; petiole 22 cm long, near the base c. 1 mm thick; lamina 11 by 2 cm, widest below the middle, base acute, margin slightly lobed in the lower half, otherwise  $\pm$  entire, apex acute. *Sporangia* inserted all over the lower surface. Spores with a smooth cristate perispore.

Chromosomes.  $n = 41$ .

NEW GUINEA. West. Bernhard Camp: *Brass 13833* (A), *13856* (A).—East. 15 collections.

SOLOMON IS. Bougainville: *Kajewski 1763* (type of *Campium kajewskii*); *Wakefield 1101* (BM).—Shortland Is.: *Guppy 98* (BM).

NEW HEBRIDES. Aneityum: *Kajewski 893* (BISH, BO, K, US).

FIJI IS. OVALAU: *Brackenridge s.n.* (type of *Cyrtogonium rivulare*); *Graeffe 108* (P).—Viti Levu: *Degener 14410* (A, MICH); *Gillespie 2622* (BISH, K, MICH, UC).—Sine loc.: *Horne 814* (K).

Habitat. Terrestrial and on rocks in moist places in rain forest; several times reported to grow near or in streams. Altitude: 0–2000 m.

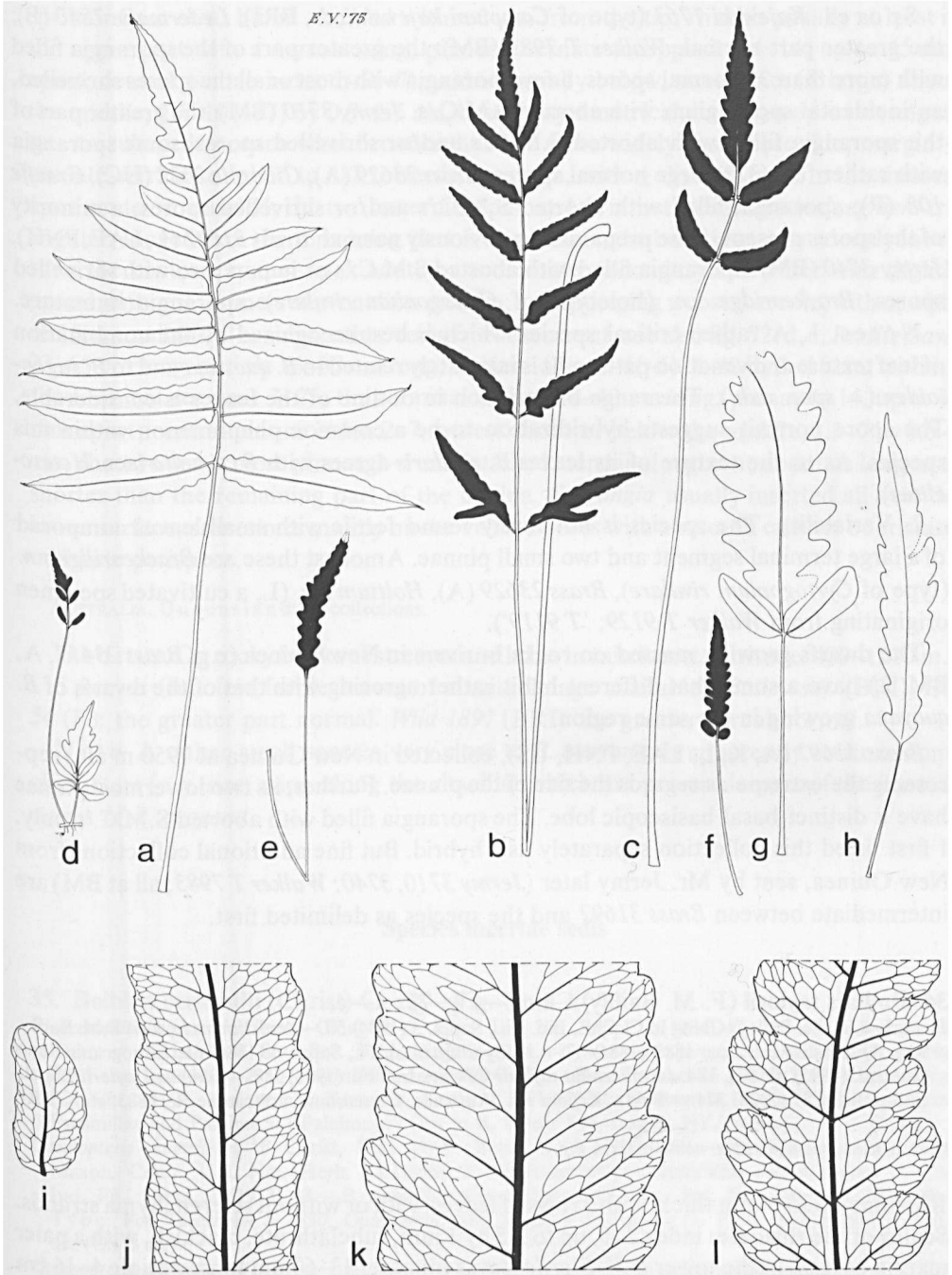


Fig. 71. *Bolbitis rivularis*.—a–h. sterile and fertile leaves,  $\times 1/5$ ; i–l. venation pattern of sterile pinnae,  $\times 4/5$  (a. Gillespie 2622, MICH; b, k. Brass 31692, L; c. Jermy 3740, BM; d. Brass 23627, L; e. Graeffe 108, P; f–h. Walker T 9127, BM; i, j. Gillespie 2622, UC; l. Kajewski 893, BO).

Spores. *Kajewski 1763* (type of *Campium kajewskii*; A, BRI), *Ledermann 7840* (B): the greater part normal. *Walker T 7983* (BM): the greater part of the sporangia filled with more than 32 normal spores, a few sporangia with most or all the spores shrivelled, an incidental sporangium with aborted S.M.C.'s. *Jermy 3710* (BM): the greater part of the sporangia filled with aborted S.M.C.'s and/or shrivelled spores, some sporangia with rather few (32?) large normal spores. *Brass 23629* (A), *Gillespie 2622* (UC), *Graeffe 108* (P): sporangia filled with aborted S.M.C.'s and/or shrivelled spores, a minority of the spores present in the preparations obviously normal. *Brass 31692* (L, LAE, PNH), *Jermy 3740* (BM): sporangia filled with aborted S.M.C.'s or in part also with shrivelled spores. *Brackenridge s.n.* (holotype of *Cyrtogonium rivulare*): sporangia immature.

Notes. 1. A rather critical species which is best recognized by the combination of leaf texture and venation pattern. It is intimately related to *B. quoyana* and to *B. sagenioides* (= *spec. dub.*). The range of variation in outline of the leaves is considerable. The spore portrait suggests hybridization to be a common phenomenon within this species. As to the texture of its leaves *B. rivularis* agrees with *B. sinuata* (ser. *Heteroclitae*).

2. Variability. The species is not rarely found fertile with small leaves composed of a large terminal segment and two small pinnae. Amongst these are *Brackenridge s.n.* (type of *Cyrtogonium rivulare*), *Brass 23629* (A), *Holtum s.n.* (L, a cultivated specimen originating from *Walker T 9129*; 'T 9119').

The dwarfs growing massed on rocks in rivers in New Guinea (e.g. *Brass 23417*, A, BM, L) have a somewhat different habit rather agreeing with that of the dwarfs of *B. quoyana* growing in the same region.

*Brass 31692* (A, K, L, LAE, PNH, US), collected in New Guinea at 1950 m alt., represents the extreme as regards the size of the pinnae. Further, its two lowermost pinnae have a distinct basal basiscopic lobe. The sporangia filled with aborted S.M.C.'s only. I first listed this collection separately as a hybrid. But fine additional collections from New Guinea, sent by Mr. Jermy later (*Jermy 3710, 3740*; *Walker T 7983*; all at BM) are intermediate between *Brass 31692* and the species as delimited first.

#### 34. *Bolbitis taylorii* (F. M. Bailey) Ching—Fig. 72: a—e.

*B. taylorii* (F. M. Bailey) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 50.—*Acrostichum taylorii* F.M. Bailey, Rep. Queensl. Accl. Soc. 1883 (1884) 11, n.v.; Syn. Queensl. Fl., Suppl. 1 (1886) 65; Lithograms Ferns Queensl. (1892) pl. 183, 184.—*Leptochilus taylorii* C. Chr., Ind. Fil. (1906) 388.—*Campium taylorii* Copel., Philip. J. Sc. 37 (1928) 374.—Type: *Kefford s.n.*, Australia, Queensland, Johnstone R., 1883, ster. (BRI, 50121).

*Acrostichum repandum* auct. non Bl.: auct. p.p.

Rhizome up to 6 mm thick, with 2 rows of leaves, with or without sclerenchyma strands. Scales of the rhizome: index 2–5, up to 3.5 by 1 mm, subclathrate, blackish, with a paler margin at least in the lower half. Sterile leaves pinnate, 13–60 cm long; petiole 4–16 cm long, near the base 0.5–2.5 mm thick, with 3–5 vascular bundles; lamina index 1.5–4, widest usually below (to about) the middle, 8–50 by 4–22 cm, without the terminal segment 1–20, the terminal segment 7–30 cm long, herbaceous, bright to dark green, the

(primordium of a) bulbil situated within 2 cm from the tip; rhachis usually at least in the upper part with a narrow wing; pinnae alternate to opposite, 4–14, up to 45 mm apart; central pinnae index 2–5(–7), widest usually below, sometimes (if large) about the middle, 2.5–10(–17) by 0.9–2.5 cm, base  $\pm$  asymmetrical, its acroscopic side angustate to subcordate, somewhat broader than the more widely basiscopic side, margin  $\pm$  crenate-serrate to lobed to 1/2 towards the costa, with  $\pm$  distinct teeth in the sinuses, apex acute or rounded; the two lowermost pinnae 1–4 mm stalked; *terminal segment* triangular, longer than the remaining part of the lamina, the basal part more deeply lobed than the central pinnae, apex acute or acuminate; secondary and other *veins* slightly prominent or  $\pm$  immersed; venation pattern: veins forming a costal areole, with or without few small distal areoles, other veins free, excurrent, see also fig. 72: d, e. *Fertile leaves* 23–65 cm long; petiole 16–37 cm long; lamina index 2–4(–6), 7–40 by 3–11 cm, without the terminal segment 3–25, the terminal segment 4–13 cm long; pinnae 6–14, up to 45 mm apart; central pinnae index 2–7, widest about or below the middle, 1.3–7 by 0.5–1 cm; the two lowermost pinnae 2–4 mm stalked; terminal segment about as long as to shorter than the remaining part of the lamina. *Sporangia* usually inserted all over the lower surface, sometimes mainly on the veins. Spores with a smooth cristate or cristate-undulate perispore.

AUSTRALIA. Queensland: 17 collections.

*Habitat*. On rocky banks of streams and lakes in rain forest. Altitude: 400–1200 m.

*Spores* (but few fertile leaves of a suitable age available). *Bailey s.n.* (BRI), *Hill 54* (K): the greater part normal. *Wild 1891* (BRI): the greater part abnormal.

*Note*. A rather small species very close to *B. quoyana*. It apparently retained some characters (e.g. size, wing along the rhachis) which are present in part of the juvenile stages of *B. quoyana*.

### Species incertae sedis

#### 35. *Bolbitis bernoullii* (Christ) Ching—Fig. 72: f–k; 73.

*B. bernoullii* (Kuhn ex Christ) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 47.—*Acrostichum bernoullii* Kuhn ex Christ, Bull. Soc. Bot. Belg. 35 (1896) 244.—*Gymnopteris bernoullii* Diels in E. & P., Nat. Pfl. Fam. 1, 4 (1899) 201.—*Leptochilus bernoullii* C. Chr., Bot. Tidsskr. 26 (1904) 296.—*Lectotype* (C. Chr., 1904, 'holotype'): *Bernoulli & Cario 382* ('282'), Guatemala, Costa Grande, between Escamillas and Palahuco ('Palahuco') (iso in B, holo?, BM, fragm., NY, fragm.).

*Gymnopteris donnell-smithii* Christ, Bull. Herb. Boiss. II, 6 (1906) 289.—*Poecilopteris donnell-smithii* Maxon, Contr. U.S. Nat. Herb. 13 (1909) 20 ('*Poikilopteris*').—*Leptochilus donnell-smithii* C. Chr., Ind. Fil., Suppl. 1 (1913) 48.—*B. donnell-smithii* Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 48.—*Type*: *Von Tuerckheim N 8830*, Guatemala, Alta Verapaz, Cubilquitz (= Finca de Cubilquitz), 350 m alt. (US, 3 sh.).

*Gymnopteris tuerckheimii* Christ, Bull. Herb. Boiss. II, 6 (1906) 290.—*Leptochilus tuerckheimii* C. Chr., Ind. Fil., Suppl. 1 (1913) 48.—*Type*: *Von Tuerckheim N 8831*, Guatemala, Alta Verapaz, Cubilquitz (= Finca de Cubilquitz), 350 m alt. (US, 2 sh.).

*Acrostichum serratifolium* auct. non Kaulf.: Baker in Hooker & Baker, Syn. Fil. (1868) 423, p.p.

*Heteroneuron serratifolium* auct. non (Kaulf.) Fournier: Fournier, Mexic. Pl. 1, 1 Crypt. (1872) 69.



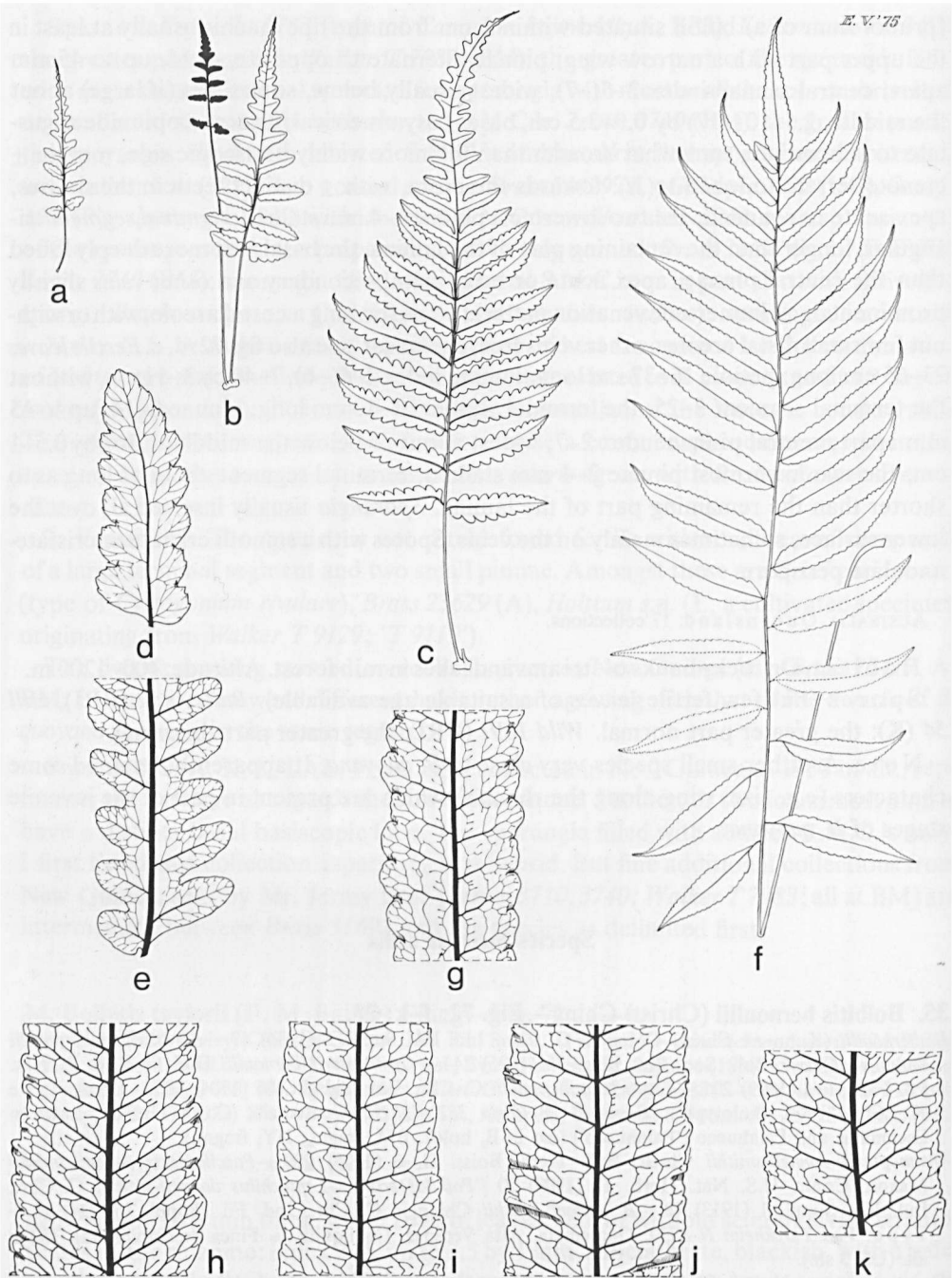


Fig. 72. a–e. *Bolbitis taylorii*. a–c. sterile and fertile leaves,  $\times 1/5$ ; d, e. venation pattern of sterile pinnae,  $\times 4/5$  (a. Kefford s.n., BRI 50121, holotype of *B. taylorii*; b. Messmer P 6854, BRI; c. Goy 436, BRI; d. Brass 20273, L; e. Messmer P 6932, NSW).—f–k. *Bolbitis bernoullii*. f. sterile leaf,  $\times 1/5$ ; g–k. venation pattern of sterile pinnae,  $\times 4/5$  (f, g. Bourgeau 2008, L; h. Stübel 929a, B; i. Von Türckheim 4034, L; j, k. Steeves & Ray 490, L).

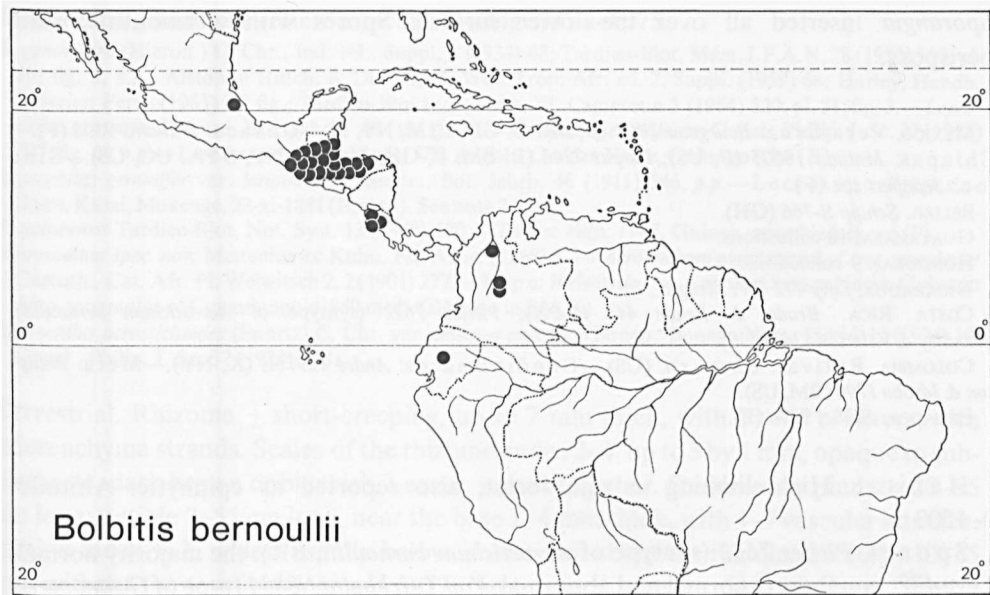


Fig. 73. Distribution of *Bolbitis bernoullii*.

Rhizome  $\pm$  long-creeping, without sclerenchyma strands, up to 20 cm long, up to 30 mm thick, with 2–6 rows of leaves. Scales of the rhizome: index (5–)20–30, *c.* 10–20 by 0.5–1.5 (–3) mm, opaque, red-brown, the margin conspicuously denticulate. Leaves approximate to somewhat spaced. *Sterile leaves* pinnate, 60–135 cm long; petiole 14–40 cm long, near the base 2.5–5 mm thick with 10–22 vascular bundles; lamina index (1–)2–4, widest usually somewhat below, sometimes about the middle, 35–110 by 15–50 cm, without the terminal segment 24–94, the terminal segment 7–16 cm long, firmly herbaceous, light to dark green, without bulbils; rhachis not winged; pinnae alternate or opposite, 16–48, 20–60 mm apart, pseudo-articulate, straight to sigmoid; central pinnae index 4–9, widest about or below the middle, 9–26 by 2–4 cm, base  $\pm$  symmetrical, narrowly to broadly cuneate, margin usually either entire or especially towards the apex crenate-serrate, sometimes lobed to 1/6 towards the costa, without spines or teeth, apex (long–) acuminate; the two lowermost pinnae usually  $\pm$  deflexed,  $\pm$  conform to the central pinnae, 1.5–12 mm stalked; *terminal segment* joined to the rhachis, usually triangular and composed of but few lobes, sometimes  $\pm$  conform to the central pinnae and with an unequally long-sided base; *veins* all prominent; venation pattern: veins forming areoles varying in shape and size, the tertiary veins with few to several mostly excurrent free veins ending in a thickening (hydathode?); see also fig. 72: g–k. *Fertile leaves* 35–90 cm long; petiole 9–23 cm long; lamina index 2–5, 20–70 by (5–)9–23 cm, without the terminal segment 18–67, the terminal segment 2–9 cm long; pinnae 16–49, (10–)25–65 mm apart; central pinnae index 5–15 (–20), widest about or below the middle, 3.5–15.5 by 0.6–1.2 (–1.7) cm; the two lowermost pinnae 2–10 mm stalked.

*Sporangia* inserted all over the lower surface. Spores with a smooth cristate perispore.

MEXICO. Vera Cruz: *Bourgeau 2008* (B, BR, G, GH, L, M, NY, P).—Oaxaca: *Williams 9508* (F).—Chiapas: *Matuda 18605* (F, US); *Purpus 7246* (B, BM, F, GH, M, MO, NY, S-PA, UC, US).—Sine loc.: *Jeanpert s.n.* (F).

BELIZE. *Schipp S-766* (GH).

GUATEMALA. 18 collections.

HONDURAS. 9 collections.

NICARAGUA. *Lévy 472* (NY, fragm., P).

COSTA RICA. *Brade & Brade 443* (S-PA); *Pittier 7632* (syntype of *Acrostichum bernoullii*); *Standley & Valerio 44743* (US).

COLOMBIA. Bolivar: *Curran s.n.* (US).—Cundinamarca: *André 1297bis* (K, NY).—Meta: *Philipson & Idrobo 1796* (BM, US).

ECUADOR. *Stübel 929a* (B).

**Habitat.** High-climbing in rain forest, also reported as epiphytic. Altitude: 0–1500 m.

**Spores.** *Pittier 7632* (syntype of *Acrostichum bernoullii*, BR): the majority normal. *Lévy 472*: equal parts normal and abnormal. *Von Tüerckheim N8831* (type of *Gymnopteris tuerckheimii*, US): a minority normal. *Contreras 2260* (US), *Von Tüerckheim N8830* (type of *Gymnopteris donnell-smithii*, US), *Bernoulli & Cario 382* (lectotype of *Acrostichum bernoullii*, B): (nearly) all abnormal.

**Notes.** 1. A clear-cut species which is of particular interest as part of its features suggests that it is closely related to *B. lindigii*, whereas other features such as the scales and the venation pattern show interesting differences with those of *B. lindigii*.

In contrast to the scales, the venation pattern shows much variation. It is superficially rather similar to that of *B. serratifolia*, and Christ regarded the venation pattern of *Gymnopteris donnell-smithii* and *G. tuerckheimii* as of the same 'type' as that of *G. contaminoides* (= *B. serratifolia*). The venation pattern of all specimens of the present species shows at least local irregularities. This I regard as a strong indication for hybridity. As the venation pattern of quite a few specimens has at least locally areoles like those typical for *B. lindigii*, and as excurrent free veins are always frequent, the venation pattern of *B. bernoullii* seems intermediate between that described for *B. lindigii* and a pattern with exclusively or mainly free excurrent veins. Acrostichoids of the New World with the latter type of venation pattern and with a presumably similar growth pattern are found in the genera *Polybotrya* (*Soromanes*) and *Lomariopsis*. Terrestrial ferns that may be involved are *B. serratifolia* and *Cyclodium meniscioides* (Willd.) Presl. The precise identity of *B. bernoullii* seems a promising field for further study.

2. *Gymnopteris donnell-smithii* and *G. tuerckheimii* were regarded by Christ to be related to the following species: *G. costaricensis* (= *B. lindigii*), *G. guianensis* (= *Lomagramma guianensis*), and *G. serratifolia* (= *B. serratifolia*). Christ did not refer to *Acrostichum bernoullii* which he himself had described ten years earlier and in which both fit easily.

**36. *Bolbitis gemmifera* (Hieron.) C. Chr.—Fig. 74: a–f; 75.**

- B. gemmifera* (Hieron.) C. Chr., Ind. Fil., Suppl. 3 (1934) 48; Tardieu-Blot, Mém. I.F.A.N. 28 (1953) 113, pl. 19; fig. 3, *p.p.*; Alston in Hutch. & Dalziel, Fl. West Trop. Afr. ed. 2, Suppl. (1959) 68; Harley, Handb. Liberian Ferns (1963) 39, fig.; Tardieu-Blot in Aubrév., Fl. Cameroun 3 (1964) 320, pl. 51: fig. 3.—*Leptochilus gemmifer* Hieron., Bot. Jahrb. 46 (1911) 345.—*Campium gemmiferum* Copel., Philip. J. Sc. 37 (1928) 387, fig. 48, *p.p.*—Lectotype: *Welwitsch 157b*, Angola, Cuanza Norte, Golungo Alto (B).  
*Leptochilus gemmifer* var. *latipinnatus* Hieron., Bot. Jahrb. 46 (1911) 346, *p.p.*—Lectotype: *Pogge s.n.*, Zaire, Kasai, Mukenge, 22-xi-1881 (B, ster.). See note 2.  
*B. guineensis* Tardieu-Blot, Not. Syst. 13 (1948) 170.—Type: *Félix 1147*, Guinea, near Nzérékoré (P).  
[*Chrysodium spec. nov.* Mettenius ex Kuhn, Fil. Afric. (1868) 52]—*Acrostichum punctatum* L. f. var. *angolense* Carruth., Cat. Afr. Pl. Welwitsch 2, 2 (1901) 277.—Type: *Welwitsch 157*, Angola, Cuanza Norte, Golungo Alto, mountains of Cungulungulo, 850 m alt. (BM; iso in BM, K).  
*Leptochilus acrostichoides* (Swartz) C. Chr. var. *cuneatus* auct. non Bonap.: Bonap., Notes Ptérid. 15 (1924) 19; Copel., Philip. J. Sc. 37 (1928) 398.

Terrestrial. Rhizome ± short-creeping, up to 7 mm thick, with 2 rows of leaves, with sclerenchyma strands. Scales of the rhizome: index 2–4, up to 3 by 1 mm, opaque to sub-clathrate, dark brown or blackish. Leaves ± close together. *Sterile leaves* pinnate, 20–95 cm long; petiole 7–55 cm long, near the base 1–4 mm thick, with 4–7 vascular bundles; lamina index 1–2, widest usually below, sometimes about the middle, 15–50 by 10–35 cm, without the terminal segment 5–37, the terminal segment 6–17 cm long, (firmly) herbaceous, green, sometimes with a purple tinge, with a distinct, usually globose (elongate) bulbil inserted laterally on the basal part of the terminal segment; rhachis not winged; pinnae alternate or opposite, 6–25, 10–50 mm apart; central pinnae index (2–) 3–6, widest usually about, sometimes below the middle, 7–21 by 2–4.5 (–6) cm, base usually ± symmetrical, ± cuneate, sometimes asymmetrical, usually its acroscopic side broader, rarely with one odd acroscopic pinnule, margin usually irregularly lobed with adjacent lobes often (much) differing in size and shape, sometimes ± entire without teeth or spines, apex acute to shortly caudate; the two lowermost pinnae ± conform to the central pinnae, 1–10 mm stalked; *terminal segment* joined to the rhachis, either ± conform to the central pinnae or with the base strongly asymmetrical with its longest side sometimes with a ± distinct lobe; secondary and other *veins* slightly prominent or ± immersed; venation pattern: veins forming a locally irregular pattern of ± isodiametric areoles varying in shape and size, few areoles with usually one, mostly simple, re- or excurrent included vein; see also fig. 74: e, f. *Fertile leaves* 30–85 cm long; petiole 20–60 cm long; lamina index 1–4, 9–40 by 5–15 cm, without the terminal segment 6–36, the terminal segment 1–8 cm long; pinnae 6–22, 15–70 mm apart; central pinnae index 3–6, widest about or below the middle, 2.5–9 by 0.8–1.6 cm; the two lowermost pinnae 1–12 mm stalked. *Sporangia* inserted all over the lower surface. Spores with a cristate perisperm.

SENEGAL. Dakar: *Anonymus 1556* (P).

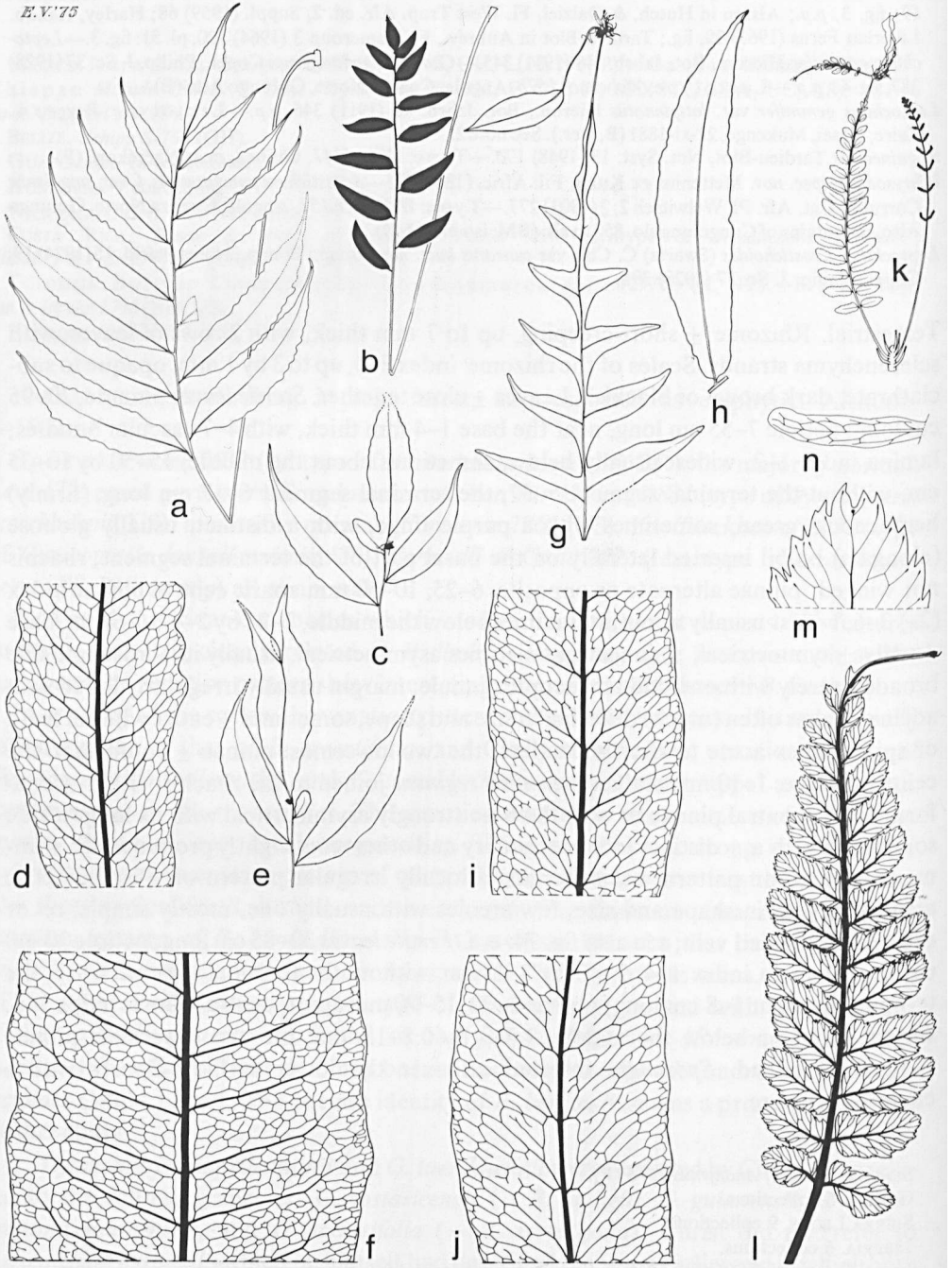
GUINEA. 5 collections.

SIERRA LEONE. 9 collections.

LIBERIA. 6 collections.

IVORY COAST. *Hallé 96* (P), 279 (P); *Leeuwenberg 3834* (WAG); *Rousseau s.n.* (P).

GHANA. 6 collections.



CAMEROUN. 8 collections.

CENTRAL AFRICAN REPUBLIC. *Anonymus* 'C' (P); *Leeuwenberg* 7091 (U, WAG).

ZAIRE. Leopoldville: 22 collections.—Equateur: *De Joncheere* BCO 23 (private herb. De Joncheere); *Kassner* 3409 (L, P).—Orientale: 14 collections.—Kivu: *Antun-Gupffert* 4 (BR); *Gillet* 2309 (BR).—Kasai: 7 collections.—Katanga: *Mullenders* 2248 (BR).

ANGOLA. Cabinda: *Gossweiler* 9037 (BM).—Cuanza Norte: *Welwitsch* 157 (type of *Acrostichum punctatum* var. *angolense*), 157b (lectotype of *Leptochilus gemmifer*).

UGANDA. Eastern: *Wood* 788 (BM, K).—Buganda: *Dümmer* 698 (BM, MICH, fragm., P, fragm.); *Longfield* 16 (BM); *Thomas* 1344 (K).

TANGANYIKA. Tanga: 9 collections.

ZAMBIA (N. RHODESIA). *Carson* s.n. (K).

**Habitat.** In primary and secondary forest. Altitude: 0–1000 (in Tanganyika: —1200) m.

**Spores.** *Holst* 2277 (K, paratype of *Leptochilus gemmifer*), *Barter* s.n. (GH): all normal, c. 60 spores in each sporangium. *Engler* 619 (B): a distinct minority abnormal. *Jensen* s.n., xii-1922 (C): all abnormal.

**Notes.** 1. A distinct species easily recognized by the localization of the bulbil, the shape of the terminal segment, and the venation pattern. The shape of the terminal segment seems intermediate between that found in *B. auriculata* and that of a fern with simple leaves or, if pinnate, with a terminal segment which is conform to the pinnae. The venation pattern seems intermediate between the pattern of *B. auriculata* and a pattern with part of its veins not anastomosing. The origin of the present species seems bifold. Apart from a fern like *B. auriculata*, a fern either like *B. gaboonensis* or like *B. acrostichoides* seems involved. The anatomy of the rhizome, the shape of the perispore, and the shape of the bulbil (which is sometimes elongate) point to a fern like *B. gaboonensis* rather than to one like *B. acrostichoides*.

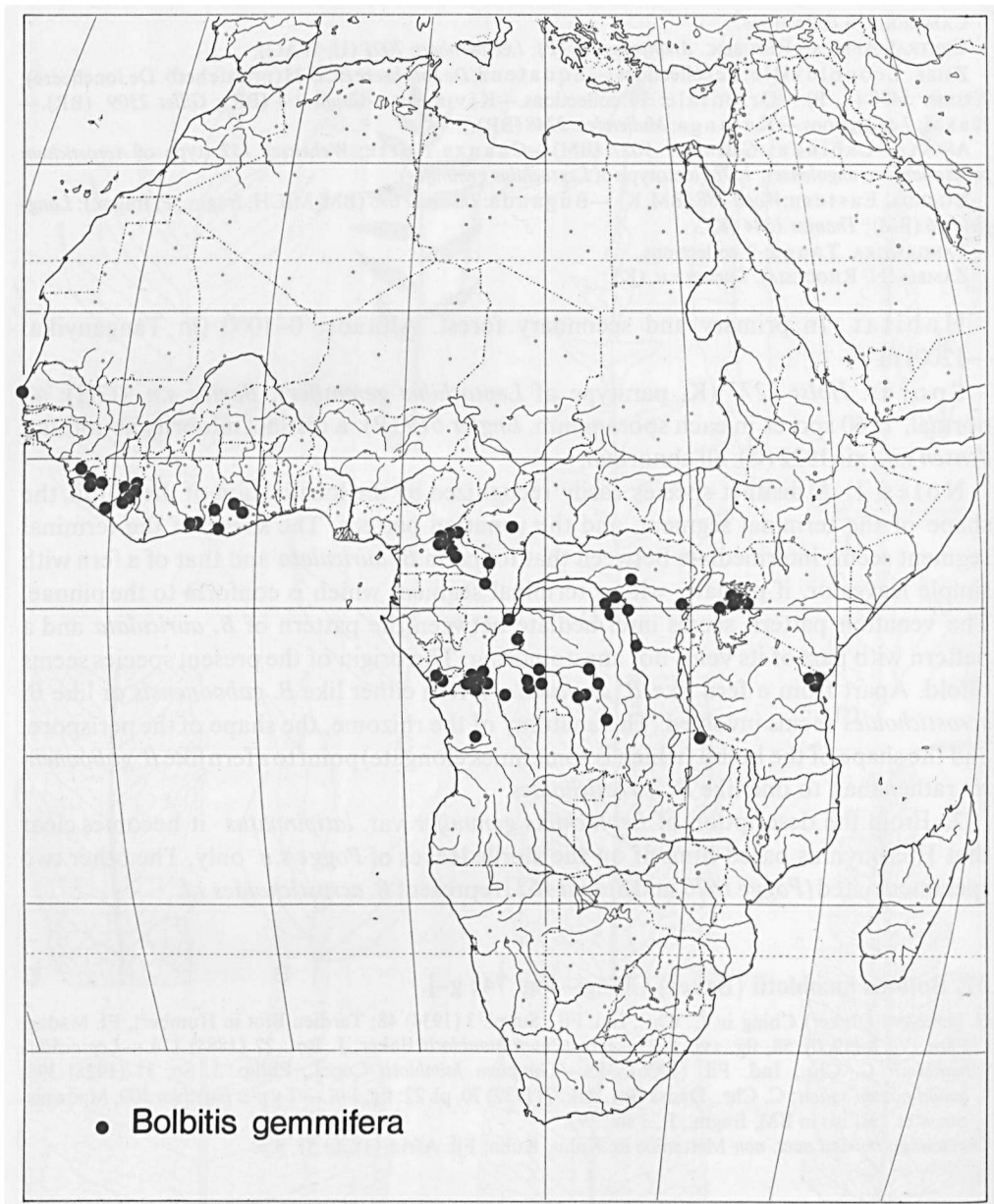
2. From the description of *Leptochilus gemmifer* var. *latipinnatus* it becomes clear that Hieronymus based himself on the sterile leaves of *Pogge* s.n. only. The other two specimens cited (*Pogge* 1620 and *Staudt* 463) represent *B. acrostichoides* s.l.

### 37. *Bolbitis humblotii* (Baker) Ching—Fig. 74: g–j.

*B. humblotii* (Baker) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 48; Tardieu-Blot in Humbert, Fl. Madag. Fam. V, 2 (1960) 58, fig. xvi: 1–2.—*Acrostichum humblotii* Baker, J. Bot. 22 (1884) 114.—*Leptochilus humblotii* C. Chr., Ind. Fil. (1906) 385.—*Campium humblotii* Copel., Philip. J. Sc. 37 (1928) 395, *quoad nomen solum*; C. Chr., Dansk Bot. Ark. 7 (1932) 70, pl. 22: fig. 1–4.—Type: *Humblot* 300, Madagascar, ster. (K; iso in BM, fragm., P, 3 sh., W).

*Chrysodium boivinii* auct. non Mettenius ex Kuhn: Kuhn, Fil. Afric. (1868) 51, p.p.

**Fig. 74.** a–f. *Bolbitis gemmifera*. a, b. sterile and fertile leaf resp.,  $\times 1/5$ ; c, d. terminal part of sterile leaves with bulbil,  $\times 1/5$ ; e, f. venation pattern of sterile pinnae,  $\times 4/5$  (a. *Peter* 21872, C; b. *De Joncheere* BCO 23, herb. De Joncheere; c. *Harley* F 120, GH; d. *Callens* s.n., 27-xi-1947, GH; e. *Peter* 16901, S-PA; f. *Pogge* s.n., B, paratype of *B. gemmifera*).—g–j. *Bolbitis humblotii*. g. terminal part of sterile leaf,  $\times 1/5$ ; h. sterile pinna,  $\times 1/5$ ; i, j. venation pattern of sterile pinnae,  $\times 4/5$  (g, h. *Humblot* 300, P, isotype of *B. humblotii*; i. *Last* s.n., 1890, BM; j. *Humblot* 300, W, see g).—k–n. *Bolbitis novoguineensis*. k. sterile and fertile leaf,  $\times 1/5$ ; l. sterile leaf,  $\times 4/5$ ; m. terminal part of sterile pinna,  $\times 3$ ; n. venation pattern of fertile pinna,  $\times 3$  (k, m, n. *Brass* 28008, L, holotype of *B. novoguineensis*; l. *Brass* 27916, L).



*Fig. 75. Distribution of Bolbitis gemmifera.*

Terrestrial. Rhizome insufficiently known, that of *Cours 3410* (P) short-creeping, 10 mm thick, with 2 rows of leaves, with sclerenchyma strands. Scales of the rhizome: index 3–4, large, up to 12 by 3 mm, subclathrate, brownish or blackish. Leaves  $\pm$  close together, the material available largely incomplete. *Sterile leaves* pinnate, the only complete one

90 cm long; petiole *c.* 40 and 50 cm long, near the base 3–5 mm thick, with 5–7 vascular bundles; lamina index 1–4, widest about or below the middle, 30–85 by 20–40 cm, without the terminal segment 6–32, the terminal segment 25–60 cm long, firm-herbaceous (rather fleshy when living?), dark olivaceous to blackish, with a spherical bulbil just below the apex; rhachis not winged; pinnae alternate or opposite, 6–14, up to 20–45 mm apart; central pinnae index 3–7, widest about the middle, 11–26.5 by 2.5–5.5 cm, base  $\pm$  asymmetrical, its basiscopic side more or less adnate, decurrent, the acroscopic side acute to subcordate, margin  $\pm$  entire, without teeth or spines, apex acute to acuminate; the two lowermost pinnae (slightly) asymmetrical, the basiscopic side somewhat shorter and narrower than the acroscopic side, 0–2 mm stalked; *terminal segment* triangular, deeply pinnatifid near base, large, apex acute to flagelloid; *venation*: secondary veins usually not well discernable; venation pattern: veins forming an irregular pattern of areoles decreasing in size towards the margin, in part of the areoles, and especially in those about halfway between margin and costa with one or few simple or branched, ex- or recurrent free included veins, see also fig. 74: i, j. *Fertile leaves* 87 and 100 cm long; petiole 56 and 59 cm long resp.; lamina index 2–4, 30–41 by *c.* 13 cm, without the terminal segment 12–23, the terminal segment 11–18 cm long; pinnae 8–12, up to 60 mm apart; central pinnae index 5–7, widest about the middle, 6.5–9 by 1.1–1.5 cm; the two lowermost pinnae 0–1 mm stalked. *Sporangia* inserted all over the lower surface except for a narrow strip along the primary veins of the segments. Spores with a smooth cristate perispore.

MADAGASCAR. Sambirano. Nossi-bé: *Boivin s.n.*, 1846/1848 (W, fert.), iii-1851 (P). Massif of Manongarivo: *Perrier de la Bâthie 7489* (P); *Last s.n.*, iv/vi-1890 ('Be kilus Mts.')(K).—E a s t. St Marie Is., Tafondro: *Boivin 1581/2* (P). Ambatosoratra: *Cours 3410* (P).—Central. Northern part, source of Sambirano R. (= Tsaratanana Mt.): *Last s.n.*, xii-1890 (K). Lokoho Valley: *Humbert & Cours 22971* (P). Central part, Tananarive: *Warpur (Warbur?) s.n.*, 19-vii-1900 (K). South of Moramanga: *Decary 18306* (P).—*Sine loc.*: *Humboldt 300* (type of *Acrostichum humblotii*).

**Habitat.** Terrestrial in forest. Altitude: 75–1000 m.

**Spores.** *Last s.n.*, iv/vi-1890 (BM): the majority normal. *Last s.n.*, xii-1890 (K): the greater part abnormal, mostly normally shaped and with a perispore with rather thick, minutely spiny crests. *Boivin s.n.*, iii-1851 (W): sporangia with mostly aborted S.M.C.'s or aborted spores.

**Notes.** The relationship of this obviously locally common and very distinct fern is not at all clear. It seems not related to species of the series *Bolbitianae*, *Egenolfianae*, *Euryostichae*, *Heteroclitae*, or *Lindigianae*.

*B. humblotii* may possibly have arisen through hybridization, and if this assumption is correct, the venation pattern of *B. humblotii* points to a fern like *B. auriculata* as one of the parents.

The present species seems to have taken part in the origin of *B. longiflagellata* (= *spec. dub.*).

2. In spite of the firm texture of the leaves, vegetative propagation by means of bulbils seems common.



3. It is doubtful whether the locality Mayotte (Comores Is.) as given on part of Boivin's collection (W, ster.) is reliable, as the species has not been collected on that island since. The label of a fertile leaf of this (W) gives Nossi-bé as the locality. Boivin visited both islands; his labels cannot always be trusted (C. Chr., 1932, viii).

**38. *Bolbitis lonchophora* (Fée) C. Chr.—Fig. 76: a–g; 77.**

*B. lonchophora* (Fée) C. Chr., Ind. Fil., Suppl. 3 (1934) 49; Bull. Bish. Mus. 177 (1943) 103, p.p.; Yuncker, Bull. Bish. Mus. 220 (1959) 41; Brownlie, Fl. Nouv.-Caléd. 3 (1969) 259, pl. 34: fig. 5, 6.—*Acrostichum lonchophorum* Kunze, Farrnkr. 1 (1840) 5, pl. 2, nom. illeg.—*Heteroneuron lonchophorum* Fée, Hist. Acrost. (1845) 94 ('*Heteroneuron*'; nom. leg., art. 72).—*Poecilopteris repandum* (Bl.) Presl var. *lonchophora* Presl, Epim. Bot. (1851) 172, p.p.—*Acrostichum repandum* Bl. var. *lonchophorum* Powell, J. Bot. 6 (1868) 341, quoad nomen solum?—*Campium lonchophorum* Copel., Bull. Bish. Mus. 93 (1932) 14, 75, p.p.—Type: *Cuming 1416*, Austral Is. (= Society Is. s.l.), Otaroha (= Rurutu) (iso in BM, K).

*Cyrtogonium palustre* Brackenr. in Wilkes, U.S. Expl. Exp. 16 (1854) 86, pl. 12.—*Acrostichum repandum* Bl. var. *palustre* Powell, J. Bot. 6 (1868) 341.—*Campium palustre* Copel., Philip. J. Sc. 37 (1928) 371; Wilder, Bull. Bish. Mus. 86 (1931) 9.—*B. palustris* Hennipman, Blumea 18 (1970) 148.—Type: *Brackenridge s.n.*, Society Is., Tahiti (US, 51085).

*Acrostichum repandum* auct. non Bl.: auct. p.p.

*Leptochilus cuspidatus* auct. non (Presl) C. Chr.: auct. p.p.

Terrestrial. Rhizome short-creeping, rather stout, up to c. 20 cm long, up to 10 mm thick, with (2) 3 rows of leaves, with few sclerenchyma strands. Scales of the rhizome: index 1–4, up to 5 by 2 mm, opaque to subclathrate, brown to blackish. Leaves  $\pm$  close together. *Sterile leaves* pinnate, 30–95 cm long; petiole 7–35 cm long, near the base 1–5 mm thick, with 5–9 vascular bundles; lamina index 1–4, widest usually below the middle, sometimes at the base, 23–65 by 8–25 cm, without the terminal segment 10–43, the terminal segment 8–28 cm long, herbaceous-chartaceous, dark green with sometimes a purple tinge, with a spherical subterminal bulbil; rhachis not winged; pinnae alternate (or opposite), 12–25, 10–45 mm apart; central pinnae index 3–6, widest usually about, sometimes either below or above the middle, 6–20 by 1.7–4.5 cm, base  $\pm$  symmetrical, angustate or narrowly cuneate, margin usually lobed 2/5 (–3/5) towards the costa, sometimes  $\pm$  entire especially in the upper part, with distinct teeth in the sinuses, apex acute to caudate, lobes of the margin narrow, c. 5 mm wide, entire or crenulate; the two lowermost pinnae 1–10 mm stalked, usually  $\pm$  asymmetrical with the acroscopic side longer and more narrowly angustate, the basisopic side sometimes with a  $\pm$  distinct basal basisopic lobe; the uppermost pinnae with the basisopic side decurrent along the rhachis; *terminal segment* triangular, deeply lobed near the base, tapering towards the usually flagelloid, sometimes acute or prolonged apex; secondary and other *veins*  $\pm$  immersed, angle between costa and secondary vein narrow; venation pattern irregular, veins in part forming areoles varying in size and shape, in part (towards the margin) free, excurrent, the areoles sometimes with usually one ex- or recurrent, included free vein, see also fig. 76: c–g. *Fertile leaves* 35–65(–75) cm long; petiole 24–45 cm long; lamina index 2–6, 11–35 by 2–12 cm, without the terminal segment 9–31, the terminal segment 2–8 cm long; pinnae 12–23, 10–50 mm apart; central pinnae index 3–6, widest below the middle, often somewhat falcate, 2.5–8 by 0.7–1.5 cm; the two

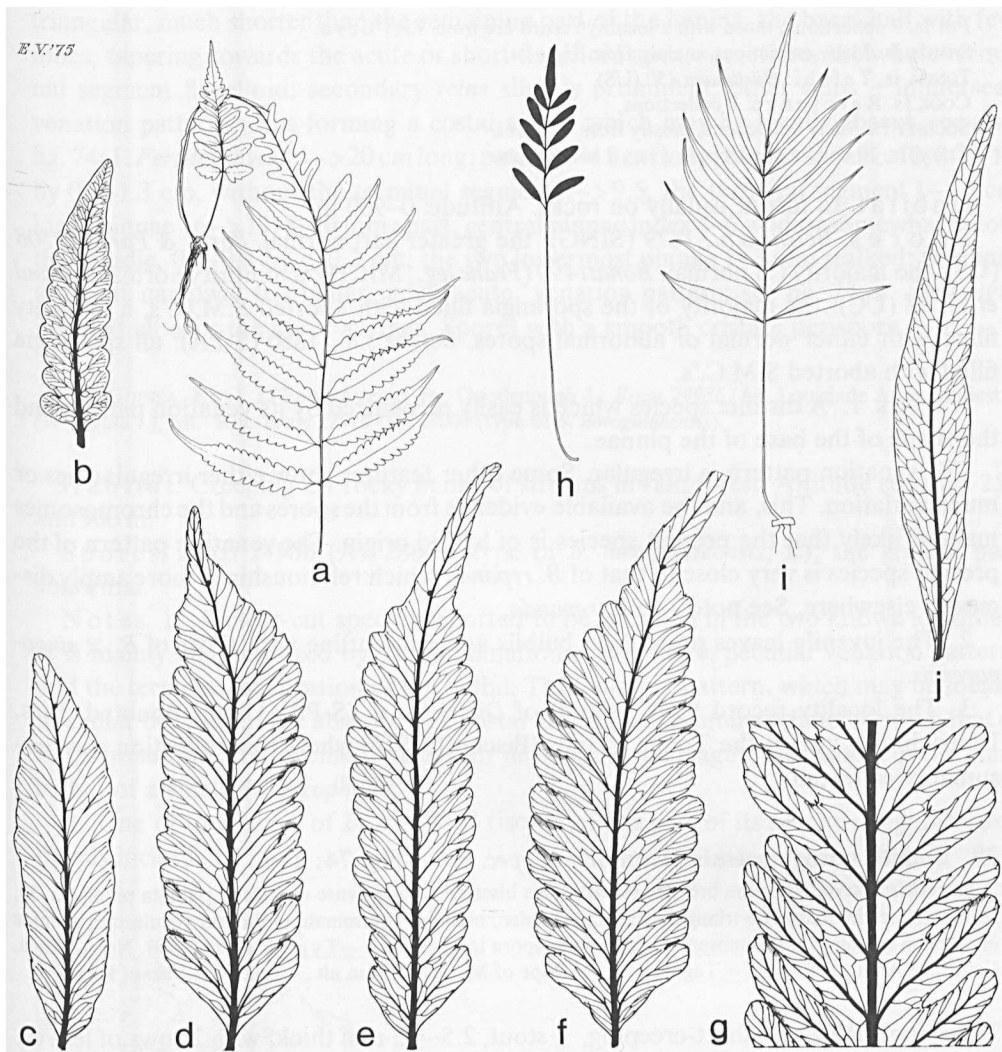


Fig. 76. a–g. *Bolbitis lonchophora*. a. sterile leaf,  $\times 1/5$ ; b. venation pattern of a fertile pinna,  $\times 4/5$ ; c–g. venation pattern of sterile pinnae,  $\times 4/5$  (a. Safford 974, GH; b. Tilden 87, Leland et al. leg., UC; c. MacDaniels 1279, UC; d. St. John 16654, BO; e. Kew Distr. no. 1173, L; f. St. John 16768, UC; g. Degener 14351, GH).—h–j. *Bolbitis presliana*. h, i. fertile and sterile leaf resp.,  $\times 1/5$ ; j. venation pattern of sterile pinna,  $\times 4/5$  (h. Hügel 3854, W, holotype of *B. presliana*; i. Beddome s.n., BM; j. Hooker & Thomson s.n., B).

lowermost pinnae 1–12 mm stalked. *Sporangia* inserted all over the lower surface. Spores with a smooth cristate-undulate perispore.

Chromosomes.  $n = 82$ .

NEW HEBRIDES. Banks Is.: Palmer 9 (K), 10 (K).

NEW CALEDONIA. 17 collections from all over the island.

FIJI Is. 9 collections; those with a locality record are from Viti Levu.

SAMOA Is. Many collections, mainly from Upolu.

TONGA Is. Tafahi: *Hürlimann 450* (US).

COOK Is. Rarotonga: 8 collections.

SOCIETY Is. Many collections, mostly from Tahiti.

TUBAI Is. 10 collections from Rurutu and Rapa.

**Habitat.** In forest; usually on rocks. Altitude: 0–900 m.

**Spores.** *Betche s.n.*, 1879 (SING): the greater part normal. *Parks & Parks 22508* (US): the majority (?) normal. *Bonati 490* (*Franc leg.*, MICH): a minority normal. *Leland et al. 87* (UC): the majority of the sporangia filled with aborted S.M.C.'s, a minority filled with either normal or abnormal spores. *Betche s.n.*, 1880 (S-PA): all sporangia filled with aborted S.M.C.'s.

**Notes.** 1. A distinct species which is easily recognized by its venation pattern and the shape of the base of the pinnae.

The venation pattern is irregular. Some other features show either irregularities or much variation. This, and the available evidence from the spores and the chromosomes make it likely that the present species is of hybrid origin. The venation pattern of the present species is very close to that of *B. repanda* which relationship is more amply discussed elsewhere. See note 1 to *B. repanda*.

2. The juvenile leaves present on bulbils agree in outline with those of *B. × singaporensis*.

3. The locality record 'Queensland' of *Dietrich s.n.* (S-PA, US) is doubted. Mrs. Dietrich also visited the Tonga Islands (Bischoff, 1916) where this collection was presumably collected.

### 39. *Bolbitis novoguineensis* Hennipman, *spec. nov.*—Fig. 74: k–n.

Terrestris, parva. Rhizoma breviter repens, foliis biseriatis. Folia dense coarctata, pinnata pinnis 20–30, segmento terminali anguste triangulari vel flagelloideo, bulbillo ± terminali. Ordinatio venularum: venulae in aerolam costalem anastomosantes. Sporae perispora laevi cristata.—**Typus:** *Brass 28098*, New Guinea, Louisiade Arch., Sudest I. (= Tagula I.), west slope of Mt. Riu, 250 m alt., 4-ix-1956 (L; iso in K, L).

Terrestrial. Rhizome short-creeping, ± stout, 2.5–4.5 mm thick, with 2 rows of leaves, without sclerenchyma strands. Scales of the rhizome: index 1–4, up to 1.5 (–2) by 0.5 mm, subclathrate, reddish brown. Leaves ± close together. *Sterile leaves* pinnate, 9–21 cm long; petiole 2–5 cm long, near the base 1–1.5 mm thick, with 3 vascular bundles; lamina index 3–5, widest somewhat below the middle, 7–17 by 2–4 cm, without the terminal segment 5–13, the terminal segment 1.5–4 cm long, firm-herbaceous (to subcarnose?), olivaceous, with a ± terminal bulbil; rhachis with a narrow wing throughout or in the upper half only; pinnae alternate to opposite, > 16 to 30, 5–10 mm apart; central pinnae index 1–3, widest about or below the middle, 1–2.4 by 0.7–0.8 cm, base usually symmetrical, cuneate, sometimes somewhat asymmetrical, its basisopic side cuneate, the acroscopic side either broadly attenuate or with a basal acroscopic lobe, margin (bi)crenate-serrate with distinct spines in the sinuses, apex acute or rounded; the two lowermost pinnae 0.5–1.5 mm stalked, ± conform to the central pinnae; *terminal segment* usually narrowly

triangular, much shorter than the remaining part of the lamina, the basal half with few lobes, tapering towards the acute or short-flagelloid apex, sometimes the whole terminal segment flagelloid; secondary veins slightly prominent, other veins  $\pm$  immersed; venation pattern: veins forming a costal areole which may be locally absent, see also fig. 74: 1. *Fertile leaves* 15–>20 cm long; petiole 6–15 cm long; lamina index c. 10, 8–> 12 by 0.8–1.3 cm, without the terminal segment 7–>9.5, the terminal segment 1–>3 cm long; pinnae 16–> 19, 8–20 mm apart; central pinnae index 4–6, widest somewhat below the middle, 0.6–0.8 by c. 0.2 cm; the two lowermost pinnae 1–3 mm stalked; terminal segment narrowly triangular, apex acute; venation pattern: see fig. 74: n. *Sporangia* inserted all over the lower surface. Spores with a smooth cristate perispore.

NEW GUINEA. East. D'Entrecasteaux Is., Goodenough I.: *Brass* 24986 (A); Louisiade Arch., Sudest I. (= Tagula I.), Mt. Riu: *Brass* 27916 (L), 28008 (type of *B. novoguineensis*).

**Habitat.** Creeping on rocky banks of streams in rain forest. Altitude records: 250 and 900 m.

**Spores.** *Brass* 24986 (A), 28008 (type of *B. novoguineensis*, L): the greater part abnormal.

**Notes.** 1. A clear-cut species reported to be common in the two known localities. It is mainly characterized by the combination of small size, peculiar venation pattern, and the terminal localization of the bulbil. The venation pattern, which may be locally irregular because of the absence of a costal areole, seems intermediate between that of *B. quoyana* and a free-veined species (or developmental stage). The aspect of the plant is that of a small *B. rhizophylla*.

2. One of the leaves of *Brass* 28008 (iso in L) has part of its pinnae irregularly and deeply incised.

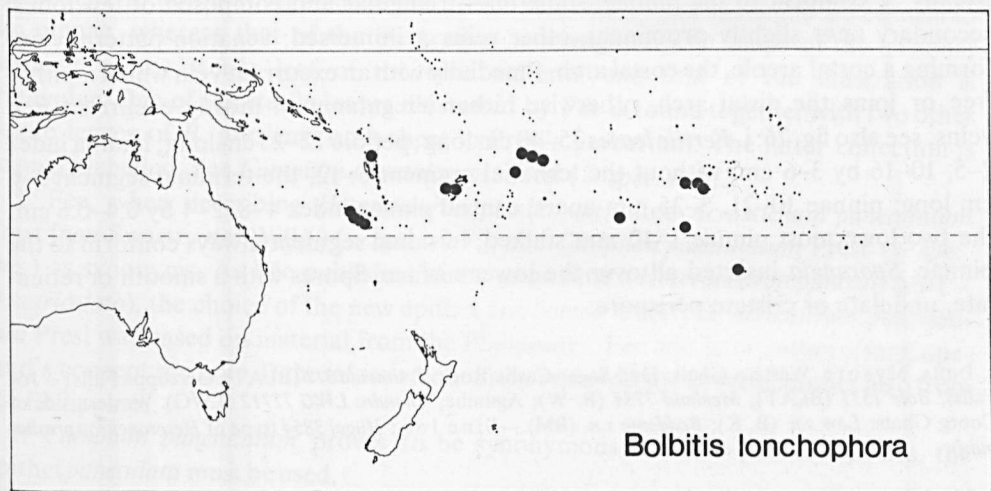


Fig. 77. Distribution of *Bolbitis lonchophora*.

3. A small thickening presumably representing a primordium of a bulbil is found terminally on the costae.

**40. *Bolbitis presliana* (Fée) Ching—Fig. 76: h–j.**

*B. presliana* (Fée) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 49, p.p.; Copel., Fern Fl. Philip. (1960) 260, p.p.; Nayar & Kaur, Bull. Bot. Gard. Lucknow 88 (1964) 53, fig. 21, 34, 67, 81, 89, p.p.—*Heteroneuron preslianum* Fée, Hist. Acrost. (1845) 92, pl. 39: fig. i, p.p. ('*Heteroneuron*').—*Poecilopteris presliana* Moore, Ind. Fil. (1857) xx, p.p.; Bedd., Ferns Br. India (1868) pl. 269, c. descr., p.p.—*Acrostichum preslianum* Hooker, Spec. Fil. 5 (1864) 265, p.p., nom. illeg., non Fée (1845) (= *Elaphoglossum spec.*).—*Gymnopteris presliana* J. Smith, Hist. Fil. (1875) 138, p.p.; Bedd., Handb. Ferns Br. India (1883) 439, fig. 267, p.p.—*Leptochilus preslianus* C. Chr., Ind. Fil. (1906) 387, p.p.; v.A.v.R., Handb. Malayan Ferns (1908) 704, p.p.; Ridley, J. Mal. Br. R. As. Soc. 4 (1916) 115, quoad nomen solum; v.A.v.R., Handb. Malayan Ferns, Suppl. 1 (1917) 435, p.p.—*Campium feeianum* Copel., Philip. J. Sc. 37 (1928) 392, fig. 43, nom. illeg.—Type: Hügel 3854, 'Asia' (W; iso in PR, ster.). See note 2.

Terrestrial. Rhizome short-creeping, up to 10 cm long, 4–6 mm thick, with 2 rows of leaves, without sclerenchyma strands. Scales of the rhizome: index 2–5, up to 3 (–4) by 1 (–1.5) mm, opaque to subclathrate, dark reddish brown or blackish. Leaves  $\pm$  close together. Sterile leaves pinnate, 20–50 cm long; petiole 5–24 cm long, near the base 1–3 mm thick, with 5–7 vascular bundles; lamina index 1–3, widest usually somewhat below (to about) the middle, 12–26 by 5–15 cm, without the terminal segment 7–18, the terminal segment 4–12 cm long,  $\pm$  herbaceous, dark green to blackish, without bulbils; rhachis sometimes with a narrow wing in the upper half of the lamina; pinnae alternate or opposite, 8–22, up to 25 mm apart; central pinnae index 4–11, widest above to below the middle, tapering towards both ends, 4–10 by 0.6–1.3 cm, base angustate, margin  $\pm$  entire or slightly and irregularly sinuate, without teeth or spines, apex acute to acuminate; the two lowermost pinnae 3–10 mm stalked, usually conform to the central pinnae, rarely with a basal acroscopic lobe; terminal segment joined to the rhachis, usually  $\pm$  conform to the pinnae, sometimes triangular and composed of few lobes; secondary veins slightly prominent, other veins  $\pm$  immersed; venation pattern: veins forming a costal areole, the costal arch  $\pm$  medially with an excurrent vein which is either free or joins the distal arch, otherwise rather irregular with mostly excurrent free veins, see also fig. 76: j. Fertile leaves 25–40 cm long; petiole 12–25 cm long; lamina index 2–5, 10–16 by 3–6 cm, without the terminal segment 6–12, the terminal segment 3–6 cm long; pinnae 10–21, 5–25 mm apart; central pinnae index 4–8, 2–4 by 0.4–0.6 cm; the two lowermost pinnae 1–10 mm stalked; terminal segment always conform to the pinnae. Sporangia inserted all over the lower surface. Spores with a smooth or reticulate, undulate or cristate perispore.

INDIA. Mysore. Western Ghats: Dnd Sagar-Castle Rock, d'Almeida 311 (BLAT); Gersoppa Falls (= Jog Falls), Bole 1531 (BLAT); Meebold 7734 (B, W); Agumbe, Chandra LWG 77712 (LWG). Western side of Coorg Ghats: Law s.n. (B, K); Beddome s.n. (BM).—Sine loc.: Hügel 3854 (type of *Heteroneuron preslianum*).

Habitat. On rocks in riverbeds in forest. Obviously (in part) submersed during the rainy season. Altitude records; 600 m (Meebold 7734); 'sea level' (Bedd., op. cit., 1883).

Spores. *Hügel 3854* (W, holo): the greater part normal, perispore usually smooth, sometimes reticulate, usually with variously tall crests, sometimes undulate. *Bole 1531*: the greater part normal, perispore smooth cristate. *Chandra LWG 77712*: in part normal, the perispore usually smooth undulate with minute spines, sometimes smooth cristate (or the crests reticulate?). *Beddome s.n.* (BM, 2 sh.): the majority normal, the perispore reticulate and low cristate.

Notes. 1. A small and presumably rare fern which is easily recognized by the colour of the dried leaves, the shape of the pinnae, the absence of bulbils, and the venation pattern. As regards its relationships Hooker (1864) thought its affinities to be 'certainly with *Acrostichum Heudelotii*' (= *B. heudelotii*), with which it seems to share the preference for wet habitats only; Copeland, however, regarded the present species (as *Campium feeianum*) as very close to *B. salicina*, also a fern of very moist places.

*B. presliana* shows characters which suggest hybrid origin. Firstly, the perispore shows much variation and seems intermediate between that of *B. appendiculata* and ser. *Bolbitianae*. Secondly, the outline of the leaves shows irregularities. Odd pinnae occur in quite a number of the leaves, and a few leaves have one or more pinnae showing a basal acroscopic lobe. The venation pattern also shows irregularities and may resemble the pattern of *B. subcrenata* and a pattern with free veins (ser. *Egenolfianae*). The absence of a bulbil is noteworthy as a bulbil is present in species of the series to which I regard *B. presliana* as possibly related (ser. *Egenolfianae* and ser. *Bolbitianae*; both also in Mysore).

2. In the original publication Fée cited *Hügel 3854* (W) from southern India as '*exsiccatum*'. Fée's excellent illustration shows two sterile leaves and a fertile one attached to a single rhizome. The type specimen at Vienna shows a sterile leaf corresponding with the largest of those illustrated, and a separately mounted fertile leaf also corresponding with that of the illustration except for the shape of the terminal segment. The terminal segment of the fertile leaf of the type specimen is conform to the pinnae, whereas that of the illustration is triangular. The shape of the terminal segment of the sterile leaf of the type material and that of the illustration is triangular. One of the sterile leaves illustrated by Fée is found together with two other sterile leaves of *B. presliana* on a sheet in Presl's herbarium. The latter collection is wrongly labelled. See *Campium punctulatum* Presl (= *spec. dub.*).

3. Fée, when describing *Heteroneuron preslianum*, cited *Acrostichum punctulatum* Presl (*non* Swartz, *nec* Willd.) (= *spec. dub.*), and *Campium punctulatum* Presl (= *spec. dub.*) as synonyms. As Fée published at the same time a *Heteroneuron punctulatum* (= *B. auriculata*), the choice of the new epithet *preslianum* is correct. *Acrostichum punctulatum* Presl was based on material from the Philippines, Fée and later authors (for Copeland's concept see note 4) therefore erroneously reported the present species also from the Philippines.

If *Campium punctulatum* proves to be synonymous with the present species, the epithet *punctulata* must be used.

4. Copeland (1928) listed the present species as *Campium feeianum*. He copied Fée's original description verbatim and only added 'This is a rare fern of southern India'. The

reason why Copeland did not use the epithet *preslianum* in the genus *Campium* is obscure. He possibly wanted to restrict that epithet to the Philippine element of Fée's species. In his Fern Flora of the Philippines (1960) he cited *Campium feeianum* as a synonym under *B. presliana*; the locality 'southern India' is given with a query.

5. Van Alderwerelt van Rosenburgh (1908) erroneously reported this fern from Madagascar, and later (1917) also from Singapore (following Ridley).

#### 41. *Bolbitis repanda* (Bl.) Schott—Fig. 78.

*B. repanda* (Bl.) Schott, Gen. Fil. (1835) *ad tab.* (13).—*Acrostichum repandum* Bl., Enum. Pl. Jav. (1828) 104; Fl. Jav. Fil. (1829) 39, pl. 14, 15, *p.p.*; Hooker, Spec. Fil. 5 (1864) 260, *p.p.*; Baker in Hooker & Baker, Syn. Fil. (1868) 419, *p.p.*—*Campium repandum* Presl, Tent. Pterid. (1836) 239.—*Cyrtogonium repandum* J. Smith, Hook. J. Bot. 3 (1841) 403.—*Heteroneuron repandum* Fée, Hist. Acrost. (1845) 96, pl. 59 ('*Heteroneuron*').—*Poecilopteris repanda* Presl, Epim. Bot. (1851) 172; Bedd., Ferns S. India (1864) 68, pl. 202, *quoad nomen solum*.—*Chrysodium repandum* Mettenius, Novara Exp. Bot. 1 (1870) 202, *p.p.*—*Gymnopteris repanda* Christ, Farnkr. Erde (1897) 50, *p.p.*; Diels in E. & P., Nat. Pfl. Fam. 1, 4 (1901) 201, *p.p.*; Copel., Publ. Bur. Gov. Lab. 28 (= Polyp. Philip.) (1905) 43, *p.p.*—Type: *Reinwardt s.n.*, E. Java, Besoeki, Banjuwangi, xii-1821 (L, 908.288-262, ster.).

*Leptochilus cuspidatus* auct. non (Presl) C. Chr.: auct. div., *p.p.*

*Campium quoyanum* auct. non (Gaudich.) Copel.: Copel., Philip. J. Sc. 37 (1928) 366, *p.p.*; C. Chr. & Holttum, Gard. Bull. S.S. 7 (1934) 262.

*B. quoyana* auct. non (Gaudich.) C. Chr.: Backer & Posthumus, Varenfl. Java (1939) 82, *p.p.*

Usually terrestrial, sometimes low-epiphytic. Rhizome short-creeping, up to 10 (-15) cm long, up to 9 mm thick, with 2 or 3 rows of leaves, with few sclerenchyma strands. Scales of the rhizome: index 2-5, up to 4 by 1.5 mm, subclathrate, brown to blackish, usually with a paler margin. Leaves  $\pm$  close together. *Sterile leaves* pinnate, 35-100 (-120) cm long; petiole 10-40 cm long, near the base 1-4 mm thick, with 5-7 vascular bundles; lamina index of non-flagelloid leaves 1-3, of flagelloid leaves up to 7, widest below the middle, 15-70 (-100) by 6-30 cm, without the terminal segment 7-40, the terminal segment 8-60 (-70) cm long, herbaceous-pergamentaceous, green to blackish, with a (primordium of a) spherical subterminal bulbil; rhachis not winged; pinnae alternate or opposite, 8-20 (-24), 20-50 mm apart; central pinnae index (2-) 3-6 (-8), widest about (to below) the middle, 4.5-22 by 1.5-4.5 cm, base  $\pm$  symmetrical, angustate to broadly cuneate, margin lobed 1/4-1/2 towards the costa, usually with a distinct tooth in each sinus, apex acute to long-acuminate, lobes usually finely serrate-crenate, sometimes entire; the two lowermost pinnae 1-11 mm stalked, either  $\pm$  conform to the pinnae, or asymmetrical with its basisopic side shorter, wider, and more deeply lobed than the acroscopic side; *terminal segment* triangular, deeply lobed near the base, tapering towards the acute to flagelloid apex; secondary veins slightly prominent, other veins  $\pm$  immersed; venation pattern irregular, veins forming areoles varying in shape and size, some of which with usually one, mostly excurrent included free vein, see also fig. 78: c-i. *Fertile leaves* 35-85 cm long; petiole 18-45 cm long; lamina index 2-5 (-7), 8-45 by 2-10 cm, without the terminal segment 5-35, the terminal segment 3-11 cm long; pinnae 9-20 (-23), 20-60 mm apart; central pinnae index 3-9, widest usually below, sometimes about the middle, 1.5-7 by 0.4-1.5 (-2) cm; the two lowermost

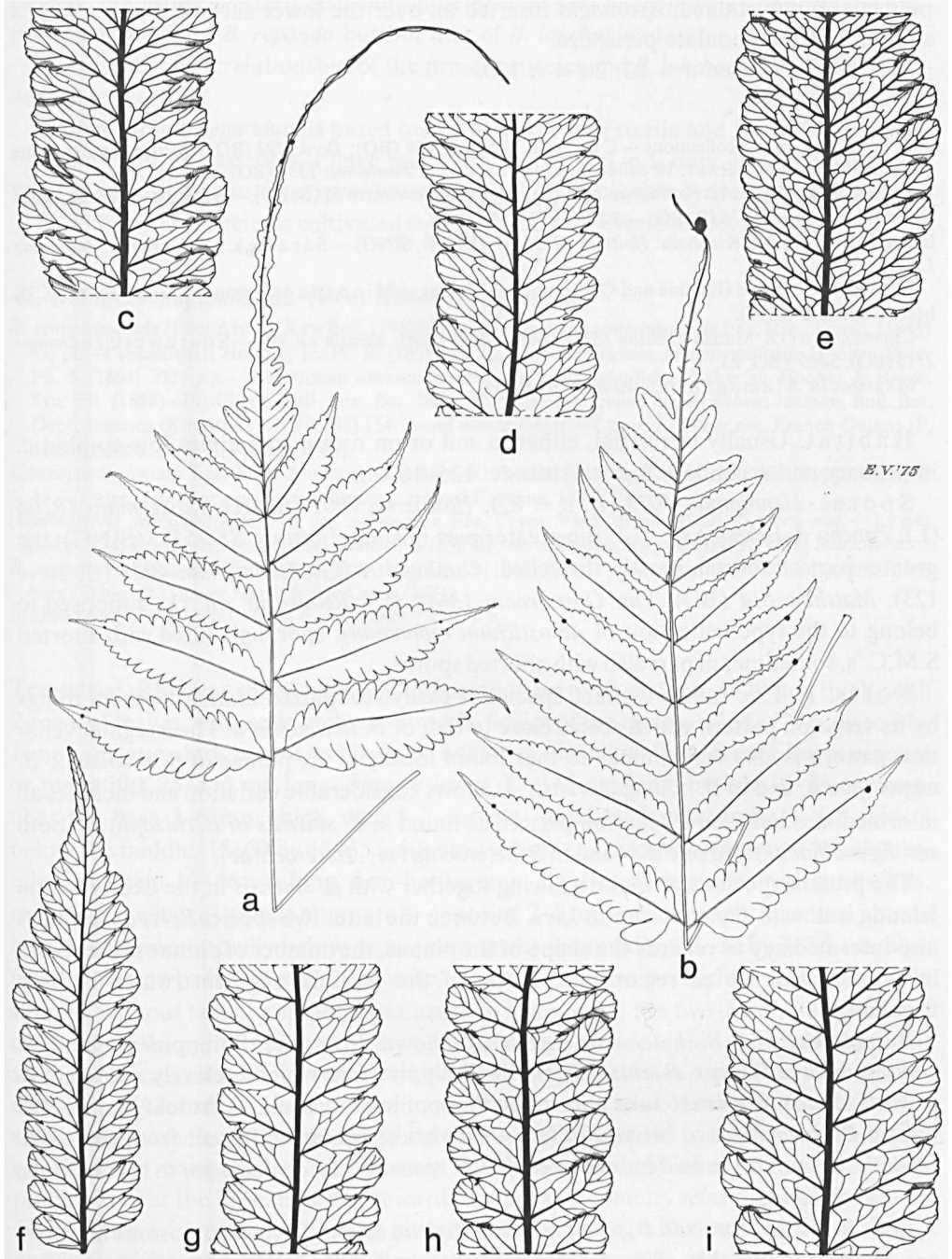


Fig. 78. *Bolbitis repanda*.—a, b. sterile leaf of a triploid and a tetraploid specimen resp.,  $\times 1/5$ ; c-i. venation pattern of sterile pinnae,  $\times 4/5$  (a. *Hennipman 4032*, L, culta, triploid; b. *H. 4026*, L, culta, tetraploid; c. *H. s.n.*, L, culta, tetraploid; d. *H. s.n.*, L, culta, triploid; e. *Van Ooststroom 13644*, L; f. *Korthals 205*, L; g. *Donk 54*, BO; h. *Holtum SF 25585*, SING; i. *Blume s.n.*, L).



pinnae 1–8 mm stalked. *Sporangia* inserted all over the lower surface. Spores with a smooth cristate-undulate perispore.

Chromosomes.  $n = 82$ ;  $2n = c. 120$ .

JAVA. West: many collections.—Central: *Beumée 1108* (BO); *Donk P92* (BO); *Docters van Leeuwen-Reijnvaan 1121* (BO).—East: 16 collections.—P. Bawaan: *Posthumus 1331* (BO), *1369* (BO).

LESSER SUNDA IS. Bali: *Posthumus 3704* (L).—Lombok: *Rensch 52* (B, BO).—Sumbawa: *Kostermans 18206* (K, L); *Rensch 576* (B, BO).—Flores: 5 collections.

BORNEO. Sabah. Mt. Kinabalu: *Holtum SF 25585* (BM, K, SING).—Sarawak. Mt. Merinjak: *Anonymus 133* (P).

PHILIPPINES. Luzon (Laguna and Quezon): 6 collections.—Mindanao. Davao: *Copeland s.n.* (MICH, herb. Copeland 10199).

CELEBES. North. Manado: *Alston 15774* (BM), *16231* (BM); *Sarasin s.n.* (P).—Southwest: *Posthumus 2715* (BO), *3440* (BO, L).

MARIANA IS. Almagana: *Hosokawa 7901* (BISH).

Habitat. Usually terrestrial, either in soil or on rocks, sometimes low-epiphytic, in primary and secondary forest. Altitude: 125–1650 m.

Spores. *Hennipman 4023* (L,  $n = 82$ ), *Hosokawa 7901* (BISH), *Kostermans 18206* (L), *Pancho & Hernaez s.n.* (L): the greater part normal. *Holtum SF 25585* (SING): the greater part abnormal, mostly shrivelled. *Cuming 104* (G), *Hennipman 4028* (L,  $2n = 123$ ), *Matthew 614* (BO), *Van Ooststroom 13644* (L), *Reinwardt s.n.* (L, supposed to belong to the type collection of *Acrostichum repandum*): sporangia filled with aborted S.M.C.'s, sometimes in part also with aborted spores.

Notes. 1. This rather distinct species is easily recognized amongst others things by its venation pattern which seems close to that of *B. lonchophora*. The irregular venation pattern is also very similar to that found locally in the pinnae of *B. sinensis*  $\times$  *B. angustipinna*, and in *B. \times singaporensis*. It shows considerable variation and includes all intermediates between a venation pattern as found in *B. sinensis* or *B. rhizophylla* (both ser. *Egenolfianae*) and one as found in *B. heteroclita* (ser. *Heteroclitae*).

The present species was found growing together with *B. sinensis* in the Lesser Sunda Islands, and with *B. heteroclita* in Java. Between the latter two species *B. repanda* shows also intermediacy as regards the shape of the pinnae, the number of pinnae present on a leaf, and rather so as regards the shape of the terminal segment (which is often flagelloid).

*B. repanda* and *B. heteroclita* are also known from the Philippines where *B. sinensis* does not occur. *B. rhizophylla*, the Philippine fern which is closely related to *B. sinensis*, does not seem to take part in the Philippine *B. repanda*, as the leaf shape of the hybrid *B. rhizophylla*  $\times$  *heteroclita* (see the hybrids) is quite different from that of *B. repanda*. It remains to be demonstrated that *B. repanda* was formed prior to speciation in ser. *Egenolfianae*.

Both *B. lonchophora* and *B. repanda* seem of hybrid origin. Their chromosome numbers are in support of this view. Because of the similarities in the venation pattern it seems likely that the parentage of *B. repanda* is in part the same as or closely related to that of *B. lonchophora*. This suggestion is only supported as far as *B. heteroclita* is con-

cerned; the rather western distribution of present ser. *Egenolfianae* supports the proposed parentage of *B. repanda* but not that of *B. lonchophora*.

There might be a relationship of the present species and *B. lonchophora* to *B. novoguineensis*.

2. *Acrostichum repandum* is based on a collection with sterile and fertile leaves made by Reinwardt in East Java. I have found sterile material in L only. Blume (1929) erroneously regarded *Acrostichum proliferum* Bl. (= *B. heteroclita*) as synonymous.

3. The present species is cultivated in greenhouses in several places in Europe.

#### 42. *Bolbitis semipinnatifida* (Fée) Alston—Fig. 79, 80.

*B. semipinnatifida* (Fée) Alston, Kew Bull. (1932) 310.—*Gymnopteris semipinnatifida* Fée, Hist. Acrost. (1845) 83, pl. 44 (excellent); Hooker, Ic. Pl. 10 (1854) pl. 71, 72.—*Acrostichum semipinnatifidum* Hooker, Spec. Fil. 5 (1864) 273, p.p.—*Acrostichum alienum* Swartz var. *semipinnatifidum* Baker in Hooker & Baker, Syn. Fil. (1868) 419; Christ, Bull. Soc. Bot. Belg. 35 (1896) 246, *quoad nomen solum*; Jenman, Bull. Bot. Dept. Jamaica (Kingston) n.s. 5 (1898) 154, *quoad nomen solum*.—Type: *LePrieur s.n.*, French Guiana (P, herb. Richard; iso in K, P, herb. Bory).

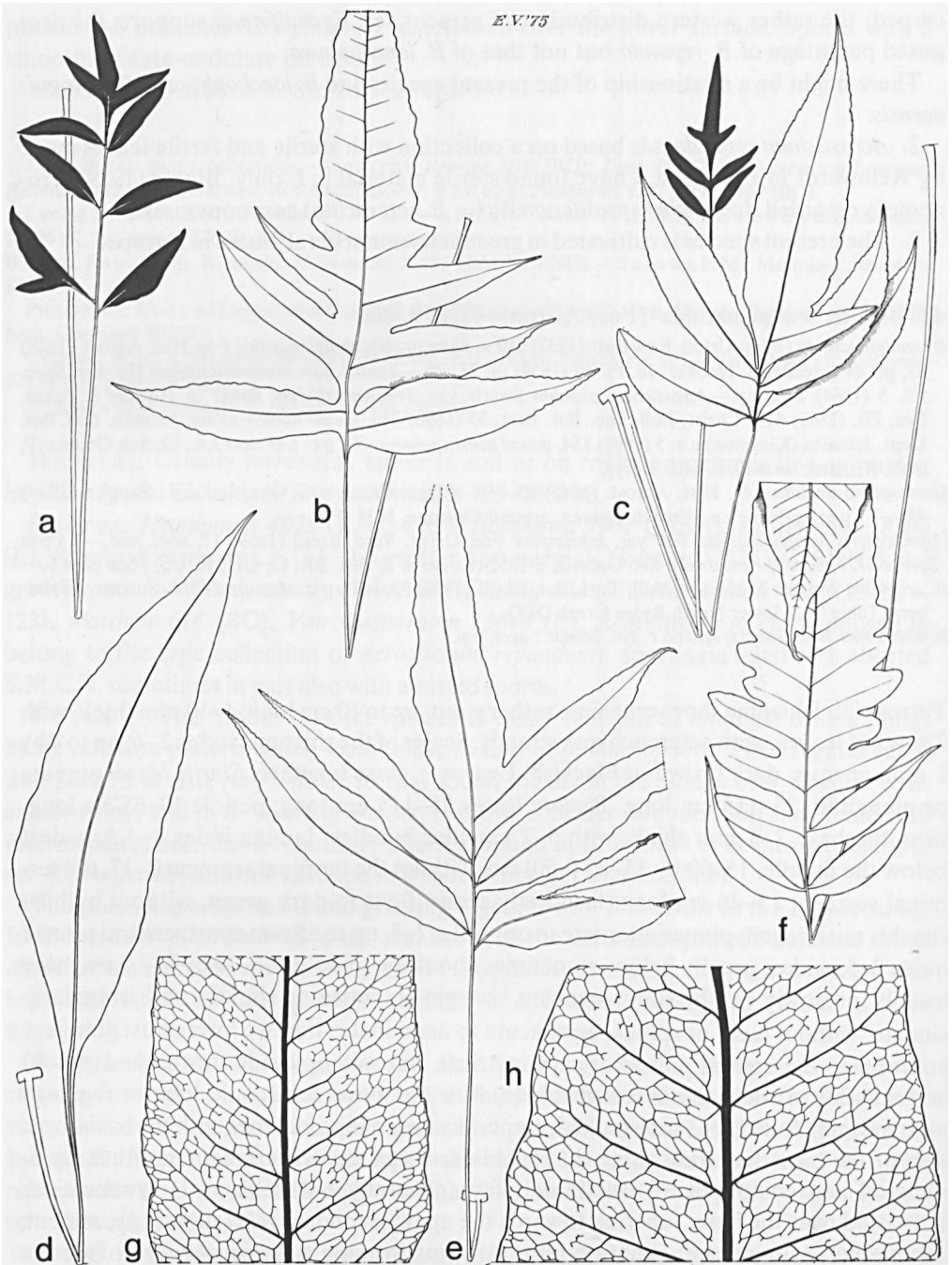
*Gymnopteris dentata* Fée, Hist. Acrost. (1845) 85.—*B. dentata* Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 48.—Type: *LePrieur s.n.*, French Guiana, around Cayenne, 1834 (P).

[*Gymnopteris semipinnatifida* Fée var. *subsimplax* Fée, Crypt. Vasc. Brésil (1869) 17, *nom. nud.*—Type: Spruce 2121, Brazil, Amazonas, Sao Gabriel, ii-1852 (K; iso in B, BM, BR, G, GH, K, US)] See note 6.

*B. scopulina* Maxon & Morton, Bull. Torr. Bot. Cl. 75 (1948) 72.—Type: *Maguire 24814*, Surinam, Tafelberg (Table Mt.), lower North Ridge Creek (NY).

*B. aliena auct. non* (Swartz) Alston *c. syn. homot.: auct. p.p.*

Terrestrial. Rhizome short-creeping, rather stout, up to 10 cm long, 4–10 mm thick, with 2 rows of leaves, with sclerenchyma strands. Scales of the rhizome: index 2–6, up to 4 by 1 mm, opaque, dark brown or blackish. Leaves  $\pm$  close together. *Sterile leaves* pinnate or pinnatifid, 25–115 cm long. *Pinnate leaves* 25–115 cm long; petiole 10–65 cm long, near the base 2–6 mm thick, with 5–7 vascular bundles; lamina index 1–1.5, widest below the middle, 15–60 by 15–35 (–50) cm, without the terminal segment 0–17, the terminal segment 15–46 cm long, firm-herbaceous, light to dark green, without bulbils; rhachis not winged; pinnae alternate to opposite, 2–8, up to 55 mm apart; central pinnae index 3–5, widest usually below, sometimes about the middle, 9.5–30 by 3–7.5 cm, base usually narrowly (to broadly) cuneate, margin  $\pm$  entire or slightly and irregularly sinuate, without teeth or spines, apex acute to acuminate; the two lowermost pinnae  $\pm$  conform to the central pinnae or asymmetrical, its basisopic side shorter and (much) wider (–20 cm) than the acrosopic side, with one basal basisopic lobe or regularly and  $\pm$  deeply lobed, 0–3 mm stalked; uppermost pinnae sometimes with the basisopic side of the base decurrent along the rhachis; *terminal segment* triangular, either asymmetrical and composed of usually only few (generally 2–4) lobes or  $\pm$  symmetrical, pinnatifid near the base, tapering towards the apex; secondary veins slightly prominent, other veins  $\pm$  immersed; venation pattern: veins forming a dense network of areoles varying in size and shape, the larger areoles with usually one mostly simple, ex- or recurrent vein, see also fig. 79: g, h. *Pinnatifid leaves* 50–105 cm long; petiole 20–50 cm long; lamina index 1–3 (–5), widest below the middle, 30–60 by 8–35 cm,



**Fig. 79. *Bolbitis semipinnatifida*.**—a–f. sterile and fertile leaves,  $\times 1/5$ ; g, h. venation pattern of sterile pinnae,  $\times 4/5$  (a, e. *Fanshawe 4822*, BM; b. *Daniëls & Jonker 820*, U; c. *Maguire 24814*, NY, holotype of *B. scopulina*; d. *Croizat 793*, U; f. *Spruce 2212*, K; g. *Geijskes 1008*, U; h. *Lemos Froés 21474*, NY).

either regularly pinnatifid throughout or with 2 conspicuous basal lobes, margin usually  $\pm$  entire, sometimes irregularly and undeeply sinuate; otherwise similar to pinnate leaves.—*Fertile leaves* (25–) 35–110 cm long. *Pinnate leaves* (25–) 35–110 cm long; petiole (20–) 30–80 cm long; lamina index 1–3, (5–) 10–30 by 2–14 cm, without the terminal segment 0–17, the terminal segment (5–) 8–18 cm long; pinnae 2–8, 0–70 mm apart; central pinnae index 3–7 (–10), 3.5–10.5 by 0.8–2 cm, the two lowermost pinnae either  $\pm$  conform to the central pinnae and 0.8–2 cm wide, or asymmetrical and up to 5.5 cm wide. *Pinnatifid leaves* 55–90 cm long; petiole 40–70 cm long; lamina index 2–5, 14–25 by 3–9 cm; the two lowermost lobes 20–70 by 9–16 mm; otherwise similar to pinnate leaves. *Sporangia* inserted all over the lower surface. Spores with a smooth, usually cristate, rarely cristate-undulate perispore.

LESSER ANTILLES. Trinidad: *Prestoe s.n.* (BM).

FRENCH GUIANA. 7 collections.

SURINAM. 9 collections.

BRITISH GUIANA. 8 collections.

BRAZIL. Amazonas: *Lemos Froés 21474* (NY); *Von Luetzelburg 21294* (M); *Spruce 2121* (type of *Gymnopteris semipinnatifida* var. *subsimplex*).—Para: *Spruce 577* (B, K).

COLOMBIA. Vaupes: *Schultes & Cabrera 12929* (US).

VENEZUELA. Bolivar: *Wurdack & Monachino 41313* (US).—Amazonas: Ugueto R.: *Croizat 793* (MO, U); *Rusby & Squires 380* (BM, F, G, GH, M, MO, NY, US).

**Habitat.** Rocky places along streams in rain forest. Altitude: 0–800 m. Jonker & Wensink (Tijdschr. Kon. Ned. Aardr. Gen. II, 77, 1960, 145–161) reported the present species as the most common fern in ‘high dryland forest’ of the Emma Range in central Surinam.

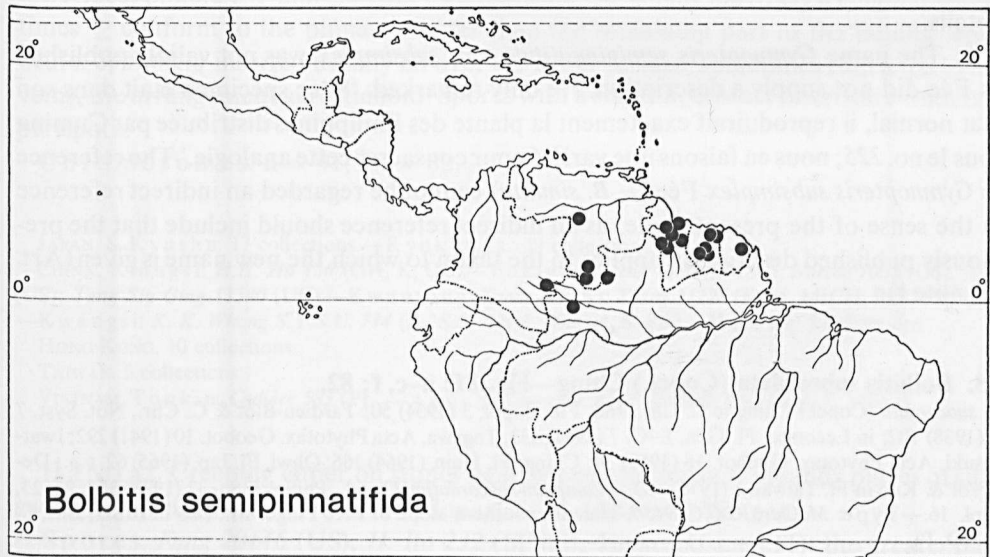


Fig. 80. Distribution of *Bolbitis semipinnatifida*.

Spores. *Jenman s.n.* (P), *Rusby & Squires 380* (MO, US), *Maguire 24814* (type of *B. scopulina* NY), *Wurdack & Monachino 41313* (US): the greater part normal. *Daniëls & Jonker 820* (U), *Fanshawe 4882* (BM): in part normal. *Lemos Froés 21474* (NY). *Von Luetzelburg 21294* (M), *Spruce 2121* (type of *Gymnopteris semipinnatifida* var. *subsimplax*, BR, G, GH): all or the greater part abnormal.

Notes. 1. Apparently a good species which was not recognized by either Ching or Christensen. For a long time it was confused with *B. portoricensis* (as *B. aliena* auct. non (Swartz) Alston). Its relationships seem bifold. On one side it seems close to *B. aliena* with which it shares the outline of the leaves of a considerable part of the specimens, features of the rhizome, and the absence of a bulbil. On the other hand it seems also related to ser. *Euryostichae* because of features of the venation pattern and the outline of the leaves of another part of the material. It may well have arisen through hybridization.

2. The outline of the pinnate leaves is very variable. The extremes may be found in one collection, e.g. *Rusby & Squires 380* (US, 2 sh.).

3. Plants with pinnatifid sterile leaves are found outside the Guianas and west of 60° W: *Lemos Froés 21474*, *Von Luetzelburg 21294*, *Schultes & Cabrera 12929*, *Spruce 2121*, *Wurdack & Monachino 41314*. The outline of these leaves rather agrees with that found in the African *B. × boivinii* which parentage includes a member of ser. *Euryostichae*. The plants with pinnatifid leaves were at first considered a different variety. Supposedly intermediately shaped leaves became available from plants collected in Surinam later, e.g. *Daniëls & Jonker 820* (IJ, U).

4. See also note 6 to *B. aliena*.

5. *Gymnopteris semipinnatifida* and *G. dentata* were described by Fée in the same part of his opus, both from collections made by *LePrieur* in French Guiana. The sterile leaves of the type specimens of both species are very similar in outline and identical in details.

6. The name *Gymnopteris semipinnatifida* var. *subsimplax* was not validly published as Fée did not supply a description. He only remarked: 'Si ce spécimen était dans son état normal, il reproduirait exactement la plante des Philippines distribuée par Cuming sous le no. 225; nous en faisons une variété pour consacrer cette analogie.' The reference to *Gymnopteris subsimplax* Fée (= *B. sinuata*) cannot be regarded an indirect reference in the sense of the present Code, as an indirect reference should include that the previously published description applies to the taxon to which the new name is given (Art. 32, note 1).

#### 43. *Bolbitis subcordata* (Copel.) Ching—Fig. 81: a–c, f; 82.

*B. subcordata* (Copel.) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 50; Tardieu-Blot & C. Chr., Not. Syst. 7 (1938) 102; in Lecomte, Fl. Gén. I.–C. 7 (1941) 433; Tagawa, Acta Phytotax. Geobot. 10 (1941) 292; Iwatsuki, Acta Phytotax. Geobot. 18 (1959) 54; Ching, Fl. Hain. (1964) 166; Ohwi, Fl. Jap. (1965) 62, p.p.; DeVol & Kuo in Fl. Taiwan 1 (1975) 350.—*Campium subcordatum* Copel., Philip. J. Sc. 37 (1928) 369, fig. 23, pl. 16.—Type: *McCure C.C.C. 9436*, Hainan, southern slope of Five Finger Mt. (iso in BISH, BM, C, MO, P).

*B. formosana* Tagawa, Acta Phytotax. Geobot. 6 (1937) 92.—Type: *Tagawa 984*, Taiwan (KYO, n.v., L, phot.; iso in TI, n.v., L, phot.).

*B. nakaii* H. Ito, J. Jap. Bot. 14 (1938) 442.—Lectotype (Iwatsuki, 1959): *H. Ito s.n.*, Japan, Ryukyu Is.,

Okinawa, Mt. Benokiyama (TI, n.v., L, phot.).  
*Gymnopteris repanda* auct. non (Bl.) Christ: auct. jap. p.p.  
*Acrostichum virens* auct. non Hooker & Grev. c. syn. homot.: auct. jap. p.p.  
*B. quoyana* auct. non (Gaudich.) Ching: auct. jap. p.p.

Terrestrial. Rhizome short-creeping,  $\pm$  stout, 4–14 mm thick, with 2 or 3 rows of leaves, with sclerenchyma strands. Scales of the rhizome: index 1–4, up to 4.5 (–7) by 1 (–1.5) mm, subclathrate, brown or blackish. Leaves  $\pm$  close together. *Sterile leaves* pinnate, 20–115 cm long; petiole 6–52 cm long, near the base 1–5.5 mm thick, with 5–9 vascular bundles; lamina index 1–3, widest below (to about) the middle, 13–70 by 7–35 cm, without the terminal segment 1.5–50, the terminal segment 10–27 cm long, herbaceous, dark green or brownish; rhachis not winged; pinnae alternate or opposite, 4–28, 15–75 mm apart; central pinnae index 2–7, widest below or about the middle, 3.5–22.5 by 1.7–4 cm, base  $\pm$  symmetrical, broadly cuneate to subcordate, margin usually lobed to 1/3 (–1/2) towards the costa, sometimes entire, crenate-serrate, with  $\pm$  distinct spines (or teeth) in the sinuses, apex acute or acuminate; the two lowermost pinnae 0–8 mm stalked,  $\pm$  conform to the central pinnae; *terminal segment* narrowly triangular, longer to shorter than the remaining part of the lamina, near the base somewhat more deeply incised than the central pinnae, apex acute to short-flagelloid; secondary veins slightly prominent, other veins  $\pm$  immersed; venation pattern: veins forming a costal areole and several to many distal areoles, the veins towards the margin free, excurrent, areoles in part with usually one simple, excurrent free vein, see also fig. 81: b,c,f. *Fertile leaves* 23–125 cm long; petiole 15–70 cm long; lamina index 2–10, 16–60 by 3–17 cm, without the terminal segment 4–47, the terminal segment 4–13 cm long; pinnae 6–25, 20–80 mm apart; central pinnae index 3–10, widest about or below the middle, 2–8 by 0.4–1.2 cm; the two lowermost pinnae 1–7 mm stalked; terminal segment usually narrowly triangular sometimes  $\pm$  conform to the pinnae, shorter than the remaining part of the lamina, apex acute. *Sporangia* inserted usually all over the lower surface, sometimes restricted to the veins, the arrangement acrostichoid. Spores with a smooth, cristate or cristate-undulate perispore.

Chromosomes.  $n = 41$ ;  $2n = 82$ .

JAPAN. S. Kyushu: 17 collections.—Ryukyu Is.: 19 collections.

CHINA. Kiangsi: H.H. Hu 156 (GH, K, UC).—Fukien: Metcalf 7380 (BM, C); Norton 1058 (US), 1059 (US); Tang Siu Ging 13580 (UC).—Kwantung: Taam 221 (A); Tsang 21228 (K, M, MICH, P, S-PA, US).—Kwangsi: K. K. Whong S.Y.S.U. 714 (B, 'S.S. Sin & Whang', S-PA).—Hainan: 5 collections.

HONG KONG. 10 collections.

TAIWAN. 5 collections.

VIETNAM. Tonkin: Cadière 583 (P). —Annam: Chevalier 4167 (*Poilane leg.*) (BM, P, SING).

Habitat. Creeping either on stones near streams in forest or in sandy places of silty swamps. Altitude: from 0–600 m in Japan, 1100–1500 m in Vietnam.

Spores. Fung 20146 (US), H. Ito 232 (SING), Yamazaki s.n. (TI): the greater part normal. McClure C.C.C.9436 (type of *Campium subcordatum*, MO): the majority (?) normal. Tagawa 7704 (US): sporangia for a considerable part filled with rather large nor-

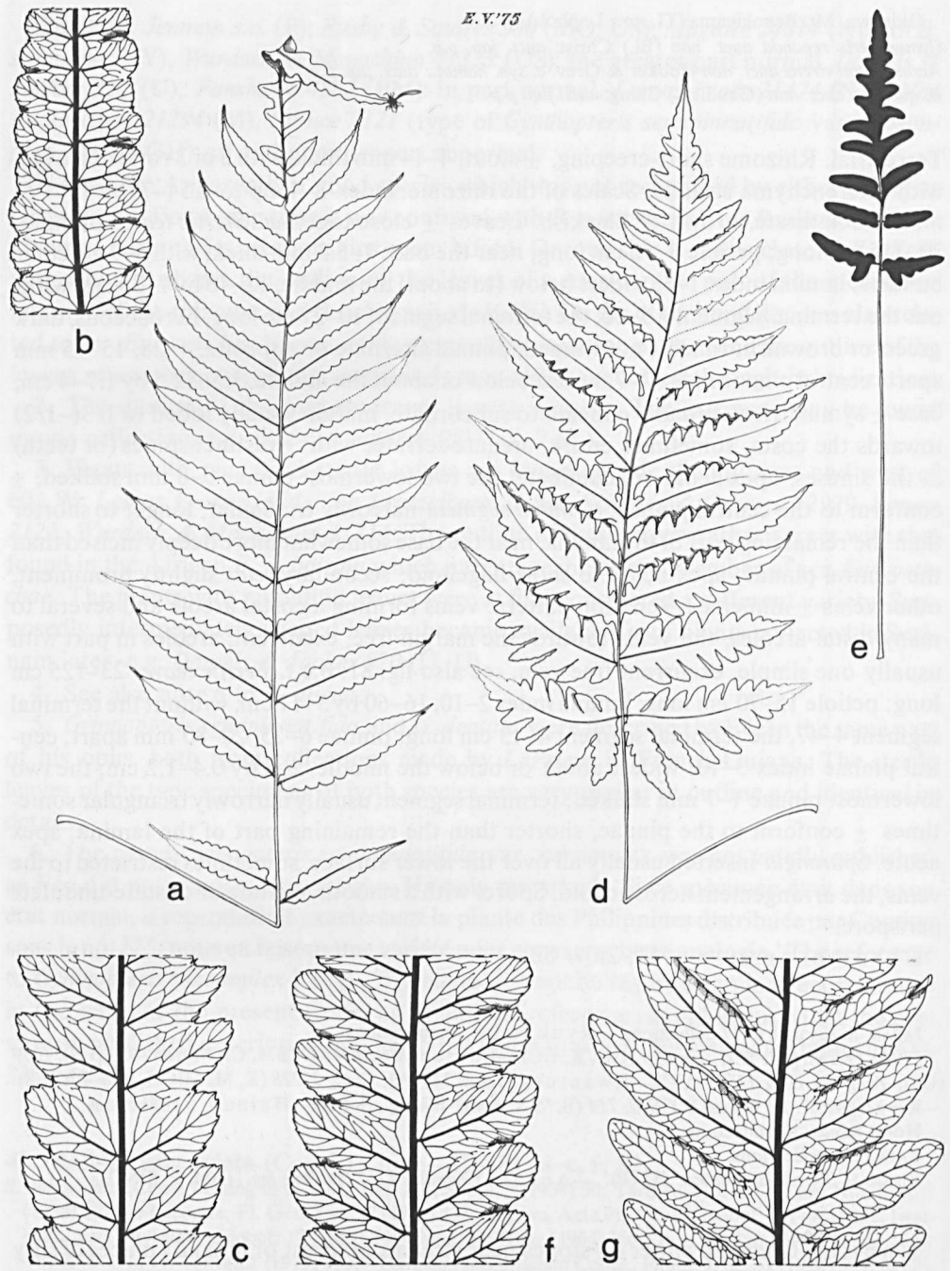


Fig. 81. a–c, f. *Bolbitis subcordata*. a. sterile leaf,  $\times 1/5$ ; b, c, f. venation pattern of sterile pinnae,  $\times 4/5$  (a. Tagawa 7704, L; b. Ohba 662254, L; c. Tagawa & Iwatsuki 1496, L; f. Fosberg 37296, US).—d, e, g. *Bolbitis umbrosa*. d, e. sterile and fertile leaf resp.,  $\times 1/5$ ; g. venation pattern of sterile pinna,  $\times 4/5$  (d, e. Purpus 4355, P; g. Liebmann s.n., L, paratype of *B. umbrosa*).

mal as well as abnormal spores, some sporangia filled with aborted spores or aborted S.M.C.'s.

Notes. 1. A distinct species especially characterized by venation pattern and leaf architecture. The venation pattern looks intermediate between that of *B. quoyana* and one with mainly or exclusively free veins (that of *B. angustipinna*?). The pattern agrees with that sometimes found in *B. sculpturata* which is conspicuously different in several other features; there is also some resemblance to that of *B. cadieri* (= *spec. dub.*). *B. laxi-reticulata* (= *spec. dub.*) seems related on other grounds.

2. The largest plants are found in southern Japan. Specimens from more southern latitudes are often small with leaves composed of proportionally few (six or more) pinnae.

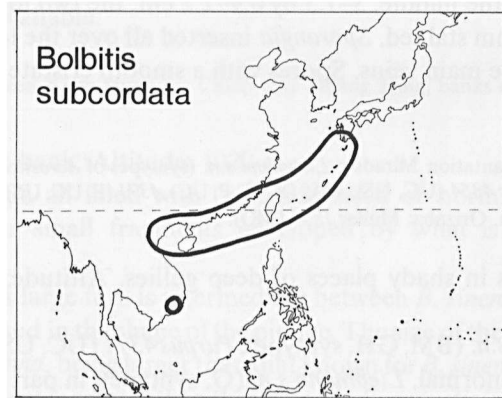


Fig. 82. Distribution of *Bolbitis subcordata*.

#### 44. *Bolbitis umbrosa* (Liebmann) Ching—Fig. 81: d, e, g.

*B. umbrosa* (Liebmann) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 50.—*Acrostichum umbrosum* Liebmann, Kong. Dansk. Vid. Selsk. Skr. V, 1 (1849) 174.—*Leptochilus umbrosus* C. Chr., Ind. Fil. (1906) 388.—Le cotype: Liebmann s.n. Mexico, Vera Cruz, near plantation Mirador, c. 60 km west of Paso de Ovejas, barranco de S. Francisco, 600–750 m alt., x-1841 (BM).

Terrestrial. Rhizome (only incomplete material available) short-creeping, c. 7 mm thick, with 2 rows of leaves, with few sclerenchyma strands. Scales of the rhizome: index 2–6, up to 5 by 2 mm, subclathrate, brownish. Leaves  $\pm$  close together. *Sterile leaves* pinnate, > 50 to 115 cm long; petiole > 19 to 63 cm long, near to the base 2–5 mm thick, with 5–7 vascular bundles; lamina index 1–2(–3), widest somewhat below the middle, 32–72 by 20–35 cm, without the terminal segment 0–16, the terminal segment 29–56 cm long, thin-herbaceous, light green to olivaceous, without bulbils; rhachis not winged; pinnae alternate or opposite, 2–6, 0–65 mm apart; central pinnae index 2–4, widest about or below the middle, 12–21 by 3.5–7 cm, base usually asymmetrical, variously shaped, its basisopic side narrower and usually decurrent along the rhachis, the acroscopic side free, margin lobed 2/5–4/5 towards the costa, with a distinct tooth in the sinuses, apex



acute to acuminate; lobes of the margin straight to falcate,  $\pm$  triangular or the basal part with parallel margins, margin crenate-serrate; the two lowermost pinnae asymmetrical, index 1-2(-4), widest somewhat below the middle or at the base, its basiscopic side broader, the margin lobed nearly to the costa, lobes up to 11 by 3 cm, margin crenate-serrate or lobed to 2/5 towards the costule; *terminal segment* proportionally long, deeply pinnatifid near the long-decurrent base, gradually narrowing towards the acute or acuminate apex; secondary and tertiary *veins* slightly prominent or immersed; venation pattern: veins forming a regular network of angulate areoles decreasing in size towards the margin, the areoles usually without, sometimes with a short, recurrent included free vein, see also fig. 81: g. *Fertile leaves* 38-65 cm long; petiole 23-47 cm long; lamina index 1-3, 14-32 by 5-14 cm, without the terminal segment 3-12, the terminal segment 10-25 cm long; pinnae 4-8, 25-50 mm apart; central pinnae index (2-)3-5(-6), widest about or below the middle, 3-7.5 by 0.9-2.2 cm; the two lowermost pinnae 3.6-10.5 by 1-4 cm, 2-7 mm stalked. *Sporangia* inserted all over the lower surface leaving a sterile zone along the main veins. Spores with a smooth cristate or cristate-undulate perispore.

MEXICO. Vera Cruz. Plantation Mirador: *Liebmann s.n.* (syntypes of *Acrostichum umbrosum*); *Ross 669* (BM, M). Zacuapam: *Purpus 4354* (UC, US), *4355* (B, G, P, UC), *4371* (P, UC, US), *4471* (P), *11142* (F, UC), *12082* (MO, US), *16723* (US). Orizaba: Müller *1854* (MO).

**Habitat.** On rocks in shady places of deep gullies. Altitude: 450-1000 m (Liebmann, 1849).

**Spores.** *Liebmann s.n.* (BM, GH, syntype), *Purpus 4371* (UC, US), *11142* (US), *12082* (MO): the greater part normal. *Liebmann s.n.* (G, syntype): in part normal. *Purpus 4355* (P): sporangia filled with (a cluster of) shrivelled spores.

**Notes.** 1. A clear-cut species of which the relationships are not clear. It seems nearest to *B. portoricensis*. The venation pattern agrees with that of ser. *Alienae*. The outline of the leaves and the shape of the pinnae agree with those of *B. bipinnatifida* (endemic to the Seychelles). Unfortunately, the material at hand does not permit to study the features of the rhizome in sufficient detail.

2. Para(syn)types with a different combination of data (if at all recorded) and/or locality are in B, G, GH, K, L, NY, fragm., P, S-PA, ster., UC, US, fragm. '*Pl. Mexic. Liebmann 2689*'.

## HYBRIDS

### H.1. *Bolbitis angustipinna* $\times$ *sinensis*—Fig. 83: a-c.

*Campium sinense* auct. non (Baker) C. Chr.: C. Chr., Contr. U.S. Nat. Herb. 26 (1931) 292, p.p.

Rhizome 9 mm thick, with 2 rows of leaves, with sclerenchyma strands. Leaves close together. *Sterile leaves* (one complete and one incomplete leaf available) pinnate, 165 cm long; petiole 58 cm long; laminas: (1) >99 by 35 cm, without the terminal segment 61 cm long; (2) 107 by 40 cm, without the terminal segment 55 cm long;

herbaceous, olivaceous, with a spherical subterminal bulbil; rhachis without a narrow wing; pinnae subopposite, 22 (in both of the leaves), 70 mm apart; central pinnae index 5–8, widest about or below the middle, 20–24 by 3.5–4 cm, base symmetrical, broadly attenuate, margin lobed to 1/3 towards the costa, with a spine in each sinus, apex acute or acuminate; the two lowermost pinnae 2 mm stalked,  $\pm$  conform to the central ones; *terminal segment* narrowly triangular, pinnatifid near the base, otherwise flagelloid; *venation pattern* rather irregular: veins forming a costal areole and one or two smaller distal ones, excurrent free veins varying in length, see also fig. 83: b, c. *Fertile leaf* (but one incomplete leaf available) >100 cm long; petiole >51 cm long; lamina 49 by 15 cm, without the terminal segment 39 cm long; pinnae 21, 75 mm apart; central pinnae index 7, the two largest ones 9.5 and 10 by 1.4 cm; the two lowermost pinnae 6 mm stalked. *Sporangia* mainly inserted on the veins. Spores: normal spores not available.

CHINA. Yunnan, between Keng Hung (= Cheli) and Muang Hing, banks of the Meh Nam Wäh: *Rock 2636* (BM, C, ster., US).

*Habitat*. A river bank. Altitude: 1020 m.

*Spores*. Sporangia all filled with (either aborted or normally shaped) S.M.C.'s, abnormal spores, or small fragments enveloped by what is supposed to be perisporial material.

*Parentage*. This large fern is intermediate between *B. sinensis* and *B. angustipinna* in venation pattern and in the shape of the pinnae. The size of the leaves agrees with that found in *B. angustipinna*, being larger than that known for *B. sinensis*. The relative length of the terminal segment is greater than that found in *B. angustipinna* and agrees with that sometimes found in *B. sinensis*. The number of pinnae to a leaf is more like that found in *B. sinensis* than in *B. angustipinna*.

*Notes*. 1. Ching, in his monograph of *Egenolfia*, did not cite this collection though he referred to Christensen (1931) who amply discussed the present fern in relation to the delimitation of the genus *Bolbitis*.

2. Rock's field-label reads: 'The long tip of this fern strikes root and produces new plants. Only one of the many seen had [a] separate fertile frond'.

## H.2. *Bolbitis appendiculata* $\times$ *sinensis*—Fig. 83: d, e.

Rhizome short-creeping, 8 mm thick, with 2 rows of leaves. Scales of the rhizome: index 3–6, up to 4 by 1 mm, dark brown, subclathrate. Leaves close together. *Sterile leaf* (only one complete leaf and two complete laminas present) pinnate with a triangular terminal segment, 104 cm long; petiole 47 cm long; laminas: (1) 57 by 20 cm, the terminal segment 5 cm long and with 38 pinnae, (2) 42 by 18 cm, the terminal segment 10 cm long and with 26 pinnae, (3) 59 by 20 cm, the terminal segment 6 cm long and with 38 pinnae, widest somewhat below the middle, herbaceous, light olivaceous, with a spherical subterminal bulbil; rhachis with a narrow wing in the upper part; pinnae alternate, up to 40 mm apart; central pinnae index 4–6, widest about the middle, the two largest ones 4–15 by

3 cm, base  $\pm$  symmetrical, narrowly to broadly truncate, margin shallowly lobed, with a distinct spine in each sinus, apex acuminate; the two lowermost pinnae conform to the central ones, *c.* 2 mm stalked; *terminal segment* triangular; *venation pattern*: veins free, see also fig. 83: e. Fertile leaf: petiole > 40 cm long; lamina 34 by 9 cm; pinnae 26, the two largest ones 5 by 0.6 and 5.5 by 0.7 cm. *Sporangia* inserted all over the lower surface. Spores: all abnormal.

HIMALAYAS. *Griffith s.n.* (B, 2 sh., one also labelled as *Kew Distr. no. 1155*; BM, ster.).

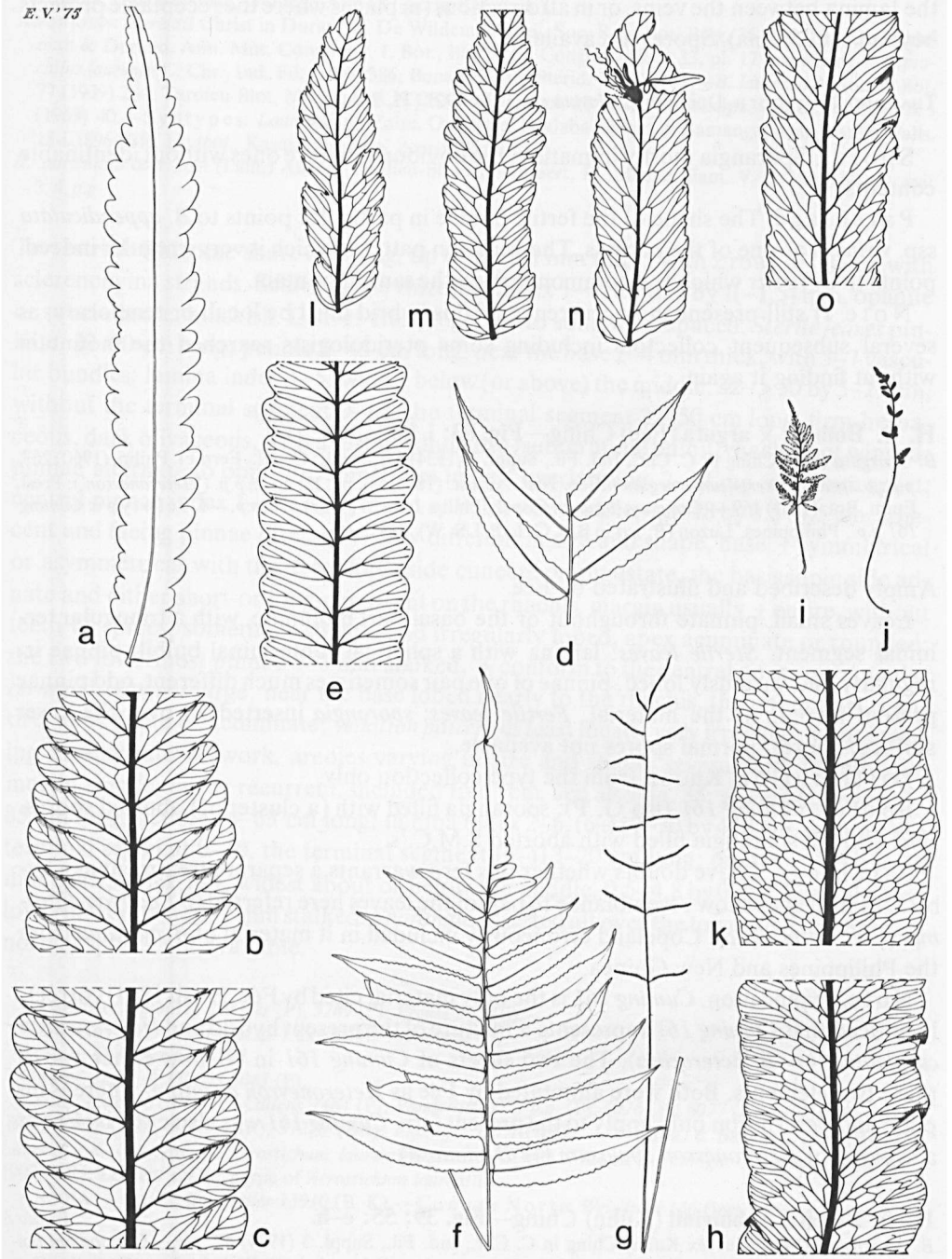
**Spores.** All abnormal, mostly shrivelled, some with a normally shaped reticulate cristate perispore, the meshes of the crests wider than in *B. appendiculata*.

**Parentage.** The size of the leaves and of the pinnae is that of *B. sinensis*. The base of the sterile pinnae agrees with that of *B. sinensis* and *B. appendiculata* ssp. *vivipara*, the margin of the pinna is slightly lobed ( $-1/5$  towards the costa) rather like that of *B. appendiculata* ssp. *appendiculata*. The shape of the fertile pinnae resembles that of *B. sinensis* and *B. appendiculata* proper. The sporangia are inserted all over the lower surface as found in part of *B. appendiculata* proper. The shape of the perispore is intermediate between that found in the putative parents.

### H. 3. *Bolbitis appendiculata* ssp. *vivipara* $\times$ *virens*—Fig. 83:f–h.

Rhizome 90 by 9 mm, with 2 rows of leaves. Scales of the rhizome up to 4.5 by 1 mm, subclathrate, blackish. Leaves rather close together. *Sterile leaves* pinnate, 62 and 65 cm long; petioles 18 and 17 cm long resp.; laminas: (1) 44 by 23 cm, the terminal segment 17 cm long, with 22 pinnae, (2) 48 by 27 cm, the terminal segment 19 cm long, with 23 pinnae, firm-herbaceous, dark purplish brown, with a spherical subterminal bulbil; rhachis not winged; pinnae alternate, *c.* 20 mm apart; central pinnae index 4–6, widest about the middle, 12.5–14 by 2.5–3.0 cm, base subcordate to cuneate, margin irregularly and shallowly lobed, locally irregularly undulate, without spines or teeth, apex  $\pm$  acute; the two lowermost pinnae 1 mm stalked,  $\pm$  conform to the central ones; *terminal segment* triangular, deeply lobed near the base, apex acute or acuminate; *venation pattern* irregular: veins anastomosing into a costal areole (rarely absent) and several smaller distal ones varying in size and shape, see also fig. 83: h. *Fertile leaf* (but one available) 53 cm long; petiole 30 cm long; lamina 23 by 4.5 cm, without the terminal segment 18 cm long; pinnae 16, the two largest ones 3 and 3.2 by *c.* 0.15 cm, margin obliquely dentate, between adjacent teeth with but little laminar tissue; terminal segment  $\pm$  conform to the

*Fig. 83.* a–c. *Bolbitis angustipinna*  $\times$  *sinensis*. a. sterile pinna,  $\times$  2/5; b, c. venation pattern of sterile pinnae,  $\times$  4/5 (a. *Rock 2636*, C; b, c. *ibid.*, US).—d, e. *Bolbitis appendiculata*  $\times$  *sinensis*. d. sterile pinna,  $\times$  1/5; e. venation pattern of sterile pinna,  $\times$  4/5 (d, e. *Kew Distr. no. 1155*, *Griffith leg.*, B).—f–h. *Bolbitis appendiculata* ssp. *vivipara*  $\times$  *virens*. f, g. sterile and fertile leaf resp.,  $\times$  1/5; h. venation pattern of sterile pinna,  $\times$  4/5 (f–h. *Hayata s.n.*, 16-x-1921, TI).—i, j. *Bolbitis*  $\times$  *arguta*, sterile and fertile leaf resp.,  $\times$  1/5 (*Cuming 161*, P).—k. *Bolbitis fluviatilis*  $\times$  *heudelotii*, venation pattern of sterile pinna (*Callens 3183*, BM).—l–o. *Bolbitis heteroclita*  $\times$  *rhizophylla*, shape and venation pattern of sterile pinnae,  $\times$  4/5 (l, m. *Copeland s.n.*, MICH, herb. Copel. 20358; n, o. *Hennipman 4091*, L, culta).



pinnae. *Sporangia* mainly near the margin, inserted either beneath on both the veins and the lamina between the veins, or in all directions (in places where the receptacle projects beyond the lamina). Spores not available.

THAILAND. Northern. Doi Suthep: *Hayata s.n.*, 16-x-1921 (TI, 2 sh.).

**Spores.** Sporangia mostly immature, the obviously mature ones without identifiable contents.

**Parentage.** The shape of the fertile pinnae in particular points to *B. appendiculata* ssp. *vivipara* as one of the parents. The venation pattern, which is very irregular indeed, points to *B. virens* which is a common fern on the same mountain.

**Note.** If still present the occurrence of this hybrid must be local, or temporary, as several subsequent collectors including some pteridologists searched the mountain without finding it again.

#### H. 4. *Bolbitis* × *arguta* (Fée) Ching—Fig. 83: i, j.

*B. × arguta* (Fée) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 47, p. spec.; Copel., Fern Fl. Philip. (1960) 263, p.p., p. spec.—*Heteroneuron argutum* Fée, Hist. Acrost. (1845) 96, pl. 25; fig. 2, p.p. ('*Heteroneuron*'); Presl, Epim. Bot. (1851) 169.—*Campium argutum* Copel., Philip. J.Sc. 37 (1928) 376, p.p.—**LECTOTYPE:** *Cuming 161 p.p.*, Philippines, Luzon (P; iso in BM, G, L, P, US, W). See note.

Amply described and illustrated by Fée.

Leaves small, pinnate throughout or the basal part bipinnate, with a triangular terminal segment. *Sterile leaves:* lamina with a spherical subterminal bulbil; pinnae irregularly and variously lobed, pinnae of one pair sometimes much different, odd pinnae present in part of the material. *Fertile leaves:* *sporangia* inserted all over the lower surface. Spores: normal spores not available.

**Distribution.** Known from the type collection only.

**Spores.** *Cuming 161* (iso G, P): sporangia filled with (a cluster of) aborted spores. *Ibid.* (iso L): sporangia filled with aborted S.M.C.'s.

**Parentage.** I have doubts whether this fern warrants a separate treatment as a hybrid, as its leaves show resemblance to part of the leaves here referred to *Edanyoa difformis* (= *B. heteroclita*). Copeland erroneously included in it material of *B. quoyana* from the Philippines and New Guinea.

**Note.** Typification. *Cuming 161* is the only material cited by Fée. Presl (1851) correctly noticed that *Cuming 161* represents a mixture of the present hybrid and *Heteroneuron cuspidatum* (= *B. heteroclita*). The two sheets of *Cuming 161* in W show either one of these two elements. Both were annotated by Fée as *Heteroneuron argutum*, whereas his plate and description only apply to the present fern. *Cuming 161* was also cited by Fée as a syntype of *Heteroneuron sinuosum* (= *B. sinuosa*).

#### H. 5. *Bolbitis* × *boivinii* (Kuhn) Ching—Fig. 39; 55: e-h.

*B. × boivinii* (Mettenius ex Kuhn) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 47, p.p.—*Chrysodium boivinii* Mettenius ex Kuhn, Fil. Afric. (1868) 51, p.p.—*Acrostichum boivinii* Welwitsch ex Carruth., Cat. Afr. Pl. Welwitsch 2, 2 (1901) 276, p.p., non Mettenius ex Kuhn (1868) (= *Elaphoglossum spec.*).—*Lep-tochilus boivinii* C. Chr., Ind. Fil. (1906) 384, p.p.—*Gymnopteris boivinii* Engler, Veg. Erde 9, 2 (1908)

16, p.p.—*Campium boivinii* Copel., Philip. J. Sc. 37 (1928) 378, p.p.—Lectotype: *Welwitsch 156*, Angola, Cuanza Norte, Golungo Alto (K; iso in BM, 2 sh.).  
*Acrostichum laurentii* Christ in Durand & De Wildeman, Bull. Soc. Roy. Bot. Belg. 36 (1897) 94; De Wildeman & Durand, Ann. Mus. Congo Ser. I. Bot., Illustr. Fl. Congo 1 (1898) 33, pl. 17 (excellent).—*Leptochilus laurentii* C. Chr., Ind. Fil. (1906) 386; Bonap., Notes Ptérid. 1 (1915) 51.—*B. laurentii* Alston, J. Bot. 77 (1939) 284; Tardieu-Blot, Mém. I.F.A.N. 28 (1953) 110, pl. 18: fig. 2, 3; Schelpe, Contr. Bolus Herb. 1 (1969) 40.—Syn types: *Laurent s.n.*, Zaire, Orientale, Lualaba-Congo at Bamanga, near Stanley Falls, 18-i-1896 (BR, L); *ibid.*, Kasai, Lusambo, 2-xii-1895 (BR, P).  
*B. auriculata* auct. non (Lam.) Alston: Tardieu-Blot in Humbert, Fl. Madag. Fam. V, 2 (1960) 60, pl. xvi: 3, 4, p.p.

Terrestrial. Rhizome short-creeping, up to 7(–10) mm thick, with 2 rows of leaves, with sclerenchyma strands. Scales of the rhizome: index 1–4, up to 5 by 1(–1.5) mm, opaque or subclathrate, blackish. Leaves close together to somewhat spaced. *Sterile leaves* pinnate, 30–90 cm long; petiole 8–45 cm long, near the base 2–4 mm thick, with 5–7 vascular bundles; lamina index 1–5, widest below (or above) the middle, 22–> 50 by 5–25 cm, without the terminal segment 0–17, the terminal segment 22–50 cm long, firm-herbaceous, dark olivaceous, with a (primordium of a) subterminal bulbil; rhachis not winged; pinnae alternate to opposite, sometimes in part overlapping, 2–14, up to 35 mm apart; central pinnae index 1–6, widest about or below the middle, 0.5–18 by 0.5–4.5 cm, adjacent and facing pinnae often markedly different in size and shape, base ± symmetrical or asymmetrical with the acroscopic side cuneate or angustate, the basispic side adnate and either short- or long-decurrent on the rhachis, margin usually ± entire, without teeth or spines, sometimes slightly and irregularly lobed, apex acuminate or rounded; the two lowermost pinnae 0–3 mm stalked, ± conform to the central ones; ± triangular *terminal segment* large, near the base lobed nearly to the rhachis, the upper part ± entire, apex acute or acuminate; *venation pattern* at least locally very irregular, veins forming an intricate network, areoles varying in size and shape, several with usually one mostly simple, ex- or recurrent, included free vein, see also fig. 55: g. *Fertile leaves* 25–85 cm long; petiole 14–63 cm long; lamina index 2–6, (6–) 17–30 by 4–8 cm, without the terminal segment 0–10, the terminal segment (6–) 13–20 cm long; pinnae 2–8, up to 35 mm apart, index 1–4, widest about or below the middle, 0.5–4.8 by 0.5–1.8 cm; the two lowermost pinnae 0–2 mm stalked. *Sporangia* inserted all over the lower surface. Spores: normal spores not available.

CAMEROON. *Letouzey 2935bis* (P), 3289 (P); *Preuss 205* (B).  
CENTRAL AFRICAN REPUBLIC. Lake Babi: *Anonymus* (P).  
TCHAD. *Chevalier 6252* (P).  
GABON. *Hallé & Villiers 5043* (P).  
ZAIRE. Leopoldville: *Callens 1484* (P); *Vanderijst 6075 p.p.* (P), 6076 (P), 6077 (BR), 8083 (P), 30587 (BR), 30902 (BR), 30923 (BR). 31229 (BR); *Flamigni 187A* (BR).—Orientale: *Bequaert 1514* (BR, L); *Laurent s.n.* (syntype of *Acrostichum laurentii*); *Seret 48* (BR).—Kasai: *Flamigni 50* (BR); *Gentil s.n.*, 1902 (BR); *Laurent s.n.* (syntype of *Acrostichum laurentii*).  
ANGOLA. Lunda: *Gossweiler 13910* (B, K).—Cuanza Norte: *Welwitsch 156* (lectotype of *Chrysodium boivinii*).

**Habitat.** Forest; several times reported from forest along streams. Altitude: 700 m (*Gossweiler 13910*).

**Spores.** *Welwitsch 156* (lectotype of *Chrysodium boivinii*; all the specimens). *Laurent s.n.*, 2–xii–1897 (syntype of *Acrostichum laurentii*, BR), *Callens 2818* (BM), *Germani 8605* (BM): sporangia filled with aborted S.M.C.'s and/or aborted spores. In all the other collections the spores were studied with the dissecting microscope; the sporangia contained aborted S.M.C.'s and/or aborted spores.

**Parentage.** In outline the leaf is intermediate between a simple and a pinnate one. The only two African species with simple leaves are *B. fluviatilis* and *B. gaboonensis*. Because of the properties of the venation pattern and the texture of the hybrid, *B. gaboonensis* seems a better choice than *B. fluviatilis*. Besides, the data on the label indicate that *B. × boivinii* is frequently found growing together with *B. gaboonensis*. There is little doubt that *B. gaboonensis* is one of the parents. The other parent is *B. auriculata*, *B. acrostichoides*, or *B. gemmifera*. Specimens of these three species have been collected from the same place as from where specimens belonging to the present hybrid were taken. The geographical distribution of the hybrid largely excludes the Congo Basin. As *B. gaboonensis* is common throughout the Basin, it seems possible that the geographical distribution of the second parent also largely excludes the Congo Basin. If so, *B. acrostichoides* seems a better choice for the other parent than both *B. auriculata* and *B. gemmifera*.

**Notes.** 1. The structural irregularities as seen in the shape of the pinnae and in the venation pattern, together with the evidence from the spores, are decisive for the hybrid status assigned by me to this form. The outline of the leaves and the venation pattern of the present hybrid are strikingly similar to these features in part of *B. semipinnatifida*.

2. Copeland (1928), without studying any specimen of this, placed it in 'the group of *B. quoyana*' (Asia and the Pacific).

3. In a few collections tufts of small scales were found in the axils of the lowermost pinnae and the rhachis. These tufts might indicate primordia of axillar bulbils (known from ser. *Alienae* and ser. *Euryostichae*).

#### **H.6. *Bolbitis fluviatilis × heudelotii*—Fig. 83: k.**

Rhizome not seen. *Sterile leaf* pinnate, 50 cm long; petiole 13 cm long; lamina 37 by 22 cm, widest somewhat below the middle, without the terminal segment 4 cm long, herbaceous, dark olivaceous, without a bulbil; pinnae alternate, 4, 15 mm apart, the largest one 16 by 3.3 cm, widest somewhat below the middle, base cuneate, margin entire, without teeth or spines, apex acuminate; the two lowermost pinnae almost sessile, conform to the two other ones; *terminal segment* triangular, large, deeply lobed nearly to the rhachis throughout, lateral lobes 12, resembling the pinnae, terminal lobe with a smaller lobe at the base; *venation pattern*: veins anastomosing into an intricate network of areoles varying in size and shape, several with one simple, ex- or recurrent included free vein. *Fertile leaf* 57 cm long; petiole 25 cm long; lamina 32 by 13 cm, without the terminal segment 10 cm long; pinnae 6, the largest one 11 by 1.5 cm; terminal segment with several small lobes near the base. *Sporangia* inserted all over the lower surface. Spores: no normal spores available.

ZAIRE. Leopoldville. Kwango, Kambangu: *Callens 3183* (BM).

**S p o r e s.** The far greater part of the sporangia immature, a minority filled with aborted S.M.C.'s and/or aborted spores.

**P a r e n t a g e.** The shape of the leaves, that of the pinnae, and the venation pattern are regarded to be intermediate between those of *B. heudelotii* and *B. fluviatilis*. The present fern grew together with *B. acrostichoides* (*Callens 3185*), *B. fluviatilis* (*Callens 3188*), and *B. heudelotii* (*Callens 3184*).

**N o t e.** The venation pattern is reminiscent of that of *B. humblotii*.

**H.7. *Bolbitis heteroclita* × *rhizophylla*—Fig. 83: 1–o.**

Rhizome short-creeping, 3.5 mm thick, with 2 rows of leaves. Scales of the rhizome: up to 3(–4) by 1(–1.5) mm, opaque to subclathrate, brownish, sometimes with a paler marginal strip. Leaves rather close together to spaced (to 15 mm). *Sterile leaves* (5 complete leaves available) pinnate, 38–43 cm long; petiole 13–16 cm long; lamina index 2–4, widest about the middle, 24–28 by 7–10 cm, without the terminal segment 16–20, the terminal segment 6–12 cm long, with a spherical subterminal bulbil; rachis with or without narrow wing; pinnae ± symmetrical, alternate to opposite, 16–24, 15–30 mm apart; central pinnae index 3–5, widest about or somewhat below the middle, 4.5–6 by 1.2–1.6 cm, base truncate to cuneate, margin usually ± entire, sometimes irregularly and finely serrate or with a few incisions about halfway towards the costa, with distinct spines, apex acute or acuminate; the two lowermost pinnae 0–1 mm stalked, conform to the central ones; *terminal segment* triangular, deeply lobed near the base, apex acute or acuminate; *venation pattern* irregular: veins forming a costal areole (rarely lacking), sometimes also one or a few smaller distal areoles, see also fig. 83: 1–o. *Fertile leaves* 41, 42, and 54 cm long; petioles 25, 28, and 29 cm long resp.; laminas: (1) 16 by 4.5, the terminal segment 3 cm long and with 16 pinnae, (2) 14 by 4 cm, the terminal segment 4 cm long and with 18 pinnae, (3) 25 by 7.5 cm, the terminal segment 4 cm long and with 19 pinnae; central pinnae index 2–5, 1.6–4 by 0.6–0.8 cm; the two lowermost pinnae c. 2 mm stalked. *Sporangia* inserted mainly on the veins. Spores: normal spores not available.

**C h r o m o s o m e s.**  $2n = 82$ ; at meiosis univalents only.

PHILIPPINES. Luzon. Mt. Maquiling: *Copeland s.n.* (MICH, herb. Copeland, 20358); *Price 163* (CAHUP, L).

**H a b i t a t.** A shady place in forest. Altitude: 350 m (*Price 163*), 400 m (*Copeland s.n.*).

**S p o r e s.** *Copeland s.n.*, *Price 163* (L): sporangia filled with aborted S.M.C.'s, sometimes also in part with aborted spores.

**P a r e n t a g e.** The venation pattern indicates that one of the parents is free-veined. Because of the shape of the sterile pinnae which is ± symmetrical, and the insertion of the sporangia which is mainly on the veins, *B. rhizophylla* almost certainly takes part.



The shape of the rhizome, the relative position of the leaves on the rhizome, the margin of the sterile pinnae, the number of pinnae to a leaf, and the venation pattern point to *B. heteroclita* rather than to *B. repanda* as the other parent. The shape of the pinnae from the largest leaves cultivated comes very near to that of those of *B. × singaporensis*. *B. heteroclita* and *B. rhizophylla* were found growing together with the present hybrid (Mr. Price, *in litt.*).

**Note.** Cultivation. The living material of this hybrid, sent by Mr. Price to me in June 1969, formed small-sized sterile leaves which became loaded with small plants grown from the bulbils on the terminal and lateral segments. After a sunny period in early summer 1971 the newly formed sterile leaves attained a much larger size (to 55 cm long); several large-sized fertile leaves were formed later in the same year.

#### **H. 8. *Bolbitis × lancea* (Copel.) Ching—Fig. 84: a–g.**

*B. × lancea* (Copel.) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 48, p. spec.—*Campium lanceum* Copel., Philip. J. Sc. 37 (1928) 380, fig. 32, pl. 25.—Type: *Gamble 15921*, India, Madras, Rumpa Hills, 900 m alt. (K).

*B. kanarensis* Nayar & Chandra, Amer. Fern J. 54 (1964) 9, fig. 1–9; Nayar & Kaur, Bull. Nat. Bot. Gard. Lucknow 88 (1964) 48, fig. 88.—Type: *Chandra LWG 95146*, India, Mysore, N. Kanara, Gudkewadi, Castle Rock, 400 m alt. (LWG, n.v.).

*Heteroneuron scalpturatum* auct. non Fée: Fée, Hist. Acrost. (1845) 95, pl. 56, p.p.

Amply described by Copeland (1928), Nayar & Chandra (1964), and Nayar & Kaur (1964).

**Sterile leaves.** Shape of the pinnae rather as in *B. angustipinna*; terminal segment ± triangular, either much prolonged or flagelloid; venation pattern irregular, see fig. 84: b–g. **Fertile leaves** with narrow pinnae. Spores: the normally shaped spores with a smooth variously shaped perispore.

INDIA. Southern part: *d'Almeida 299* (BLAT); *Anonymus (?Nuddie) 912* (G); *Beddome s.n.* (K); *Chandra LWG 77718* (LWG); *Fairbank 1501* (MO, UC); *Gamble 15921* (type of *Campium lanceum*); *Hooker & Thomson s.n.* ('105', BM); *Hügel 2161, 2165, 4140, 4974* (all at W, all paratypes of *Heteroneuron scalpturatum* Fée); *Law s.n.* (BM, P); *Saldanha 6012* (C).

**Habitat.** In forest. Altitude: 900 m (*Gamble 15921, Mooney 677*), 1140 m (*Beddome s.n.*).

**Spores.** *d'Almeida 299, Chandra LWG 77718*: the majority abnormal. *Gamble 15921*: nearly all abnormal, the normally shaped spores with a densely folded and minutely spiny perispore. *Mooney 677*: all abnormal, the perispore of the normally shaped spores verrucate-undulate.

**Parentage** of *B. × lancea* and *B. × prolifera*. Plants with part of their features very irregularly expressed, but otherwise obviously related to *B. angustipinna*, *B. subcrenata*, and *B. semicordata* (all three belonging to ser. *Bolbitianae*), are common in Peninsular India. The venation pattern of the hybrids in particular shows much variation; also when comparing that of pinnae of different parts of the same leaf, or

when comparing that of adjacent areas of one pinna. All plants are provided with distinct bulbils. Vegetative propagation seems dominant, also as the spores of the collections studied are largely abnormal.

It appeared possible to divide this heterogeneity into two rather distinct groups, one composed of plants which are as to size and venation pattern intermediate between *B. angustipinna* and *B. subcrenata* (*B. × lancea*) and one intermediate between *B. angustipinna* and *B. semicordata* (*B. × prolifera*). Plants intermediate between *B. subcrenata* and *B. semicordata* were not recognized, although hybridization between these two species is likely to occur. In the venation pattern of *B. × lancea* areoles along the distal parts of the secondary veins are few or absent; the ultimate veins usually run about parallel and are usually not connected by tertiary veins. In the venation pattern of *B. × prolifera* areoles are usually present also along the distal parts of the secondary veins, whereas the ultimate veins generally do not run parallel being often connected by tertiary veins. *B. × lancea* and *B. × prolifera* deserve detailed experimental study.

Notes. 1. Copeland (1928) regarded *Campium lanceum* 'really near' to *C. undulatum* (= *B. virens* f. *undulata*), keeping the latter separate because of differences in the shape of the fertile pinnae only.

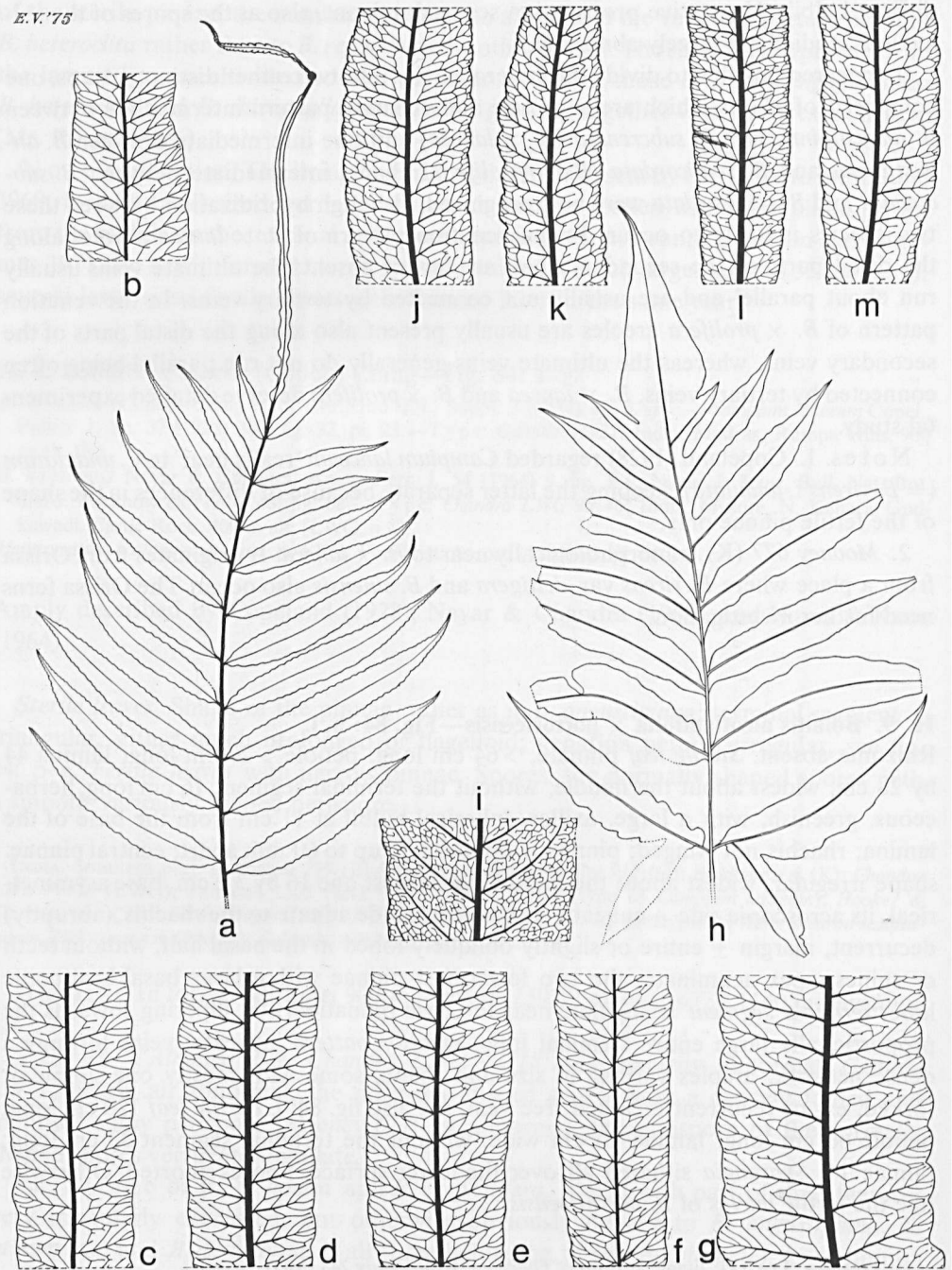
2. Mooney 677 (K) is morphologically near to *B. × lancea*. It originates from Orissa from a place where *B. virens* var. *deltigera* and *B. sinensis* also occur. The Orissa ferns need further investigation.

#### H. 9. *Bolbitis nicotianifolia* × *portoricensis*—Fig. 84: h, i.

Rhizome absent. *Sterile leaf* pinnate, > 64 cm long; petiole > 20 cm long; lamina 44 by 28 cm, widest about the middle, without the terminal segment 16 cm long, herbaceous, greenish, with a large, axillar, spherical bulbil at 11 cm from the base of the lamina; rhachis not winged; pinnae ± opposite, 8, up to 60 mm apart; central pinnae: shape irregular, widest about the middle, the largest one 16 by 3.2 cm, base asymmetrical, its acroscopic side ± cuneate, its basispic side adnate to the rhachis, (abruptly) decurrent, margin ± entire or slightly obliquely lobed in the basal half, without teeth or spines, apex acuminate; the two lowermost pinnae with a large basal basispic lobe; *terminal segment* triangular, near the base pinnatipartite, tapering towards the proportionally large entire terminal lobe; *venation pattern* intricate; veins forming a dense network, areoles varying in size and shape, some with mostly one simple or forked, ex- or recurrent included free vein, see also fig. 84: i. *Fertile leaf* 120 cm long; petiole 66 cm long; lamina 20 cm wide, without the terminal segment 33 cm long; pinnae 14. *Sporangia* situated all over the lower surface. Spores aborted. Otherwise like the fertile leaves of *B. portoricensis*.

GUATEMALA. Izabal: Jungle at ruins of Quirigua, *Weatherwax* 248 (MO).

Parentage. The shape of the sterile pinnae is irregular, but ± intermediate be-



tween that of *B. portoricensis* and *B. nicotianifolia*. The latter two species are also known from Quirigua. The presence of an axillar bulbil in the lower half of the lamina is of interest. The bulbils in *B. portoricensis* are subterminal, whereas they are not known from *B. nicotianifolia*. Bulbils are axillar in some other species of ser. *Euryostichae*. The sporangia are all filled with aborted spores. The fact that aborted S.M.C.'s were never found may be significant for the relationship between ser. *Portoricensis* and ser. *Euryostichae*.

**H. 10. *Bolbitis* × *prolifera* (Bory) C. Chr. & Tardieu-Blot—Fig. 84: j–m.**

*B. × prolifera* (Bory) C. Chr. & Tardieu-Blot in Tardieu-Blot & C. Chr., Not. Syst. 7 (1938) 102, *p. spec.*, quoad nomen solum.—*Polybotrya prolifera* Bory in Bélanger, Voy. Ind. Or. Bot. 2 (1833) 18, *p. spec.*, non (Hooker) Mettenius (1856) (= *B. subcrenata*).—*Heteroneuron proliferum* Fée, Hist. Acrost. (1845) 92, pl. 55: fig. 1 ('*Heteroneuron*').—*Poecilopteris prolifera* Presl, Epim. Bot. (1851) 172.—*Leptochilus prolifer* C. Chr., Ind. Fil. (1906) 387; v.A.v.R., Handb. Malayan Ferns (1908) 738, *p.p.*; Brause, Bot. Jahrb. 56 (1920) 119, *p.p.*—Type: *Bélanger s.n.*, India, Madras, Madura ('Madurai'), Dendigal ('Dindigul') (P).

*B. virens* auct. non (Hooker & Grev.) Ching *c. syn. homot.*: auct. *p.p.*

*Poecilopteris repanda* auct. non (Bl.) Presl: Bedd., Ferns S. Ind. (1864) 68, pl. 202.

*Gymnopteris contaminans* Bedd., Ferns Br. Ind., Suppl. (1876) 27, *p.p.*, *nom. superfl.*; Handb. Ferns Br. Ind. (1883) 435, fig. 264, *ibid.*; Handb. Ferns Br. Ind., Suppl. (1892) 105, *ibid.*—Lectotype: Beddome, Ferns S. India (1864) pl. 202 ('*Poecilopteris repanda* auct. non (Bl.) Presl').

*Acrostichum terminans* Wall., Cat. (1830) no. 2168, *nom. nud.*—Type: *Wallich 2168* (*Wight leg.*), South India, Courtallum (K, herb. Wallich; iso in K, herb. Hooker).

*Sterile leaves.* The shape of the leaves and the pinnae is usually rather as in *B. semicordata*; terminal segment usually conform to the central pinnae, sometimes triangular and mostly prolonged; rhachis generally with a narrow wing; venation pattern irregular, see also fig. 84: j–m. *Fertile leaves* usually with narrow pinnae. Spores: the normally shaped spores with a smooth, usually undulate, sometimes verrucate perispor.

INDIA. South: *Abraham 1105* (US), *1141* (US), *1143* (US); *Bates s.n.* (K); *Beddome s.n.* (K); *Bélanger* (type of *Polybotrya prolifera*); *Bole s.n.* (BLAT); *Cockburn 101* (BM); *Van Hardeveld & Van der Werff 323* (L); *Hooker & Thomson s.n.* (BM, '105', '107'; K, P, W); *Hooper & Ramaswami 39418* (CAL); *Law s.n.* (K); *Nayar & party LWG 44621* (LWG), *45058* (LWG); *Noyes s.n.* (US, 299693); *Wallich 2168/1* (K, herb. Hooker); *Wight 63* (= Pen. Ind. Or. 3178; B, K, L, W), (Pen. Ind. Or.?) *3175* (B), *s.n.* (W).

*Habitat.* Forest. Altitude: 500–1200 m.

*Spores.* *Bélanger s.n.* (type of *Polybotrya prolifera*), *Van Hardeveld & Van der Werff 323* (L), *Wallich 2168/1* (K, herb. Hooker): all abnormal.

*Parentage.* See *H. 8. Bolbitis × lancea*.

*Fig. 84.* a–g. *Bolbitis × lancea*. a. sterile leaf, × 1/5; b–g. venation pattern of sterile pinnae, × 4/5 (a, c. Hügel 4140, W, syntype of *Heteroneuron scalpturatum*; b. *Gamble 15921*, K, holotype of *B. × lancea*; d. *D'Almeida 299*, BLAT, loc. class. of *B. kanarensis*; e. *Fairbanks s.n.*, UC 811487; f. *Chandra LWG 77718*, LWG; g. *Nuddie 912*, G).—h, i. *Bolbitis nicotianifolia × portoricensis*. h. sterile leaf, × 1/5; i. venation pattern of sterile pinna, × 4/5 (h, i. *Weatherwax 248*, MO).—j–m. *Bolbitis × prolifera*, venation pattern of sterile pinnae, × 4/5 (j. *Wight Pen. Ind. Or. 3178*, B; k. *Anonymus s.n.* in herb. Hooker & Thomson, Mysore, B; l. *Hooper & Ramaswami 39418*, CAL; m. *Anonymus s.n.* in herb. Hooker & Thomson, Mysore, W).

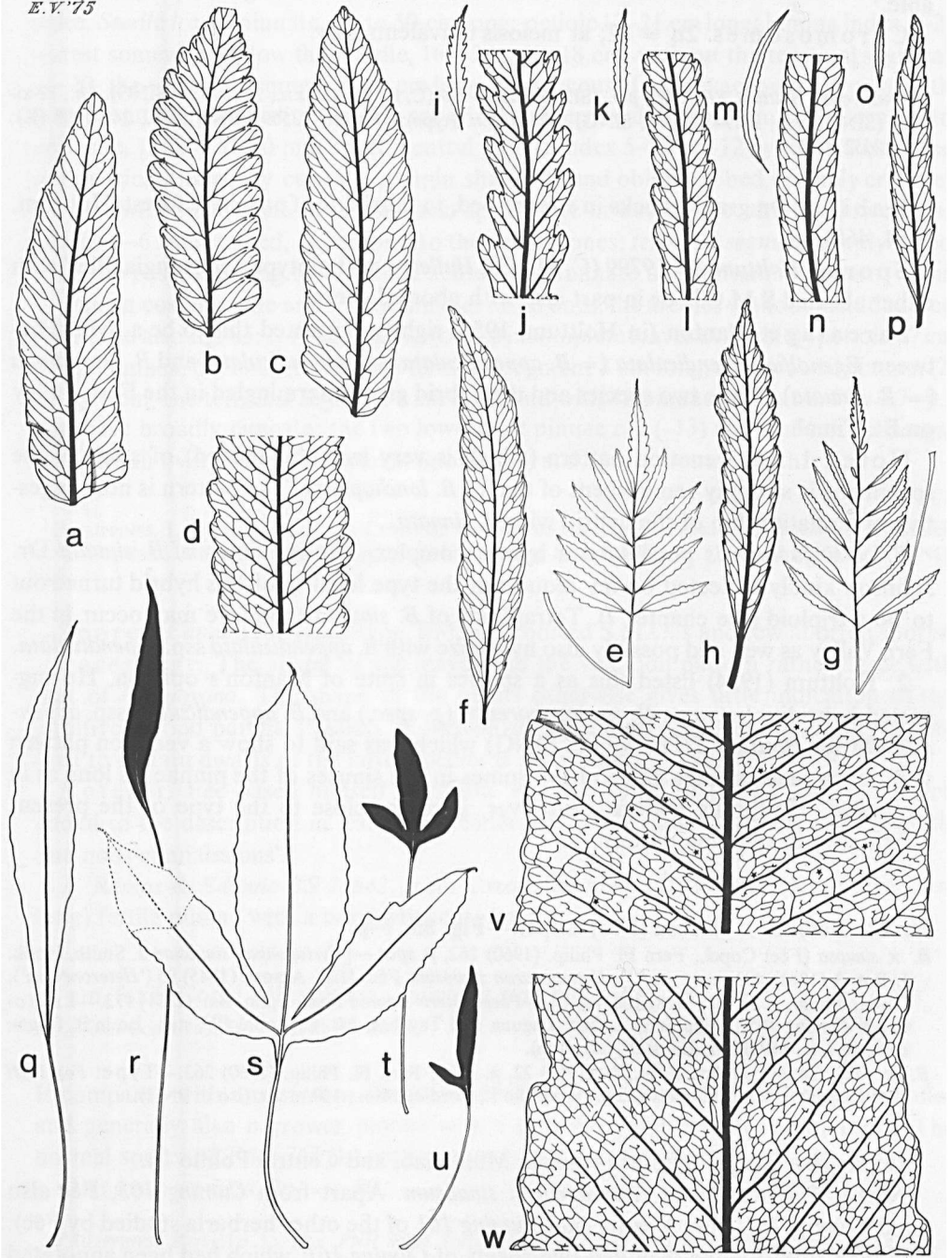
Note. Beddome (1876) described *Gymnopteris contaminans* to accommodate the material he earlier (1864, 68, pl. 202) referred to *Poecilopteris repanda* auct. non (Bl.) Presl, and (Ferns Br. India, 1868, 270, pl. 270) to *Poecilopteris semicordata* (Baker) Bedd. His species also included '*Acrostichum virens* and *crispatum*'. I have selected pl. 202 (1864) as the lectotype, as Beddome (1868, *l.c.*)—when enumerating *Poecilopteris semicordata*—expressed the opinion (though with misgivings) that the fern he (1864) named *Poecilopteris repanda* should be renamed '*Poecilopteris contaminans* (Wall.)'. The venation pattern as figured by Beddome is very irregular; his species easily fits in the hybrid as here construed.

**H. 11. *Bolbitis* × *singaporensis* Holttum—Fig. 85: a–d.**

*B. × singaporensis* Holttum, Gard. Bull. S. S. 11 (1947) 271, *p. spec.*; Ferns Malaya (1954) 467, fig. 274, *p. spec.*—Type: *Hullett s.n.*, Singapore, Bt. Timah, iii-1882 (SING, 20947; iso in BM, K, SING).  
*B. quoyana* auct. non (Gaudich.) C. Chr.: Holttum, Gard. Bull. S. S. 9 (1937) 122.

Rhizome short-creeping, 3–6 mm thick, with 2 rows of leaves. Leaves approximate to somewhat spaced. *Sterile leaves* pinnate, 35–70 cm long; petiole 16–30 cm long; lamina index 1–3, widest somewhat below the middle, 22–45 by 10–25 cm, without the terminal segment 11–29, the terminal segment 10–19 cm long, firm-herbaceous, bright green to olivaceous, with a spherical subterminal bulbil; rhachis not winged; pinnae opposite or alternate, 14–27, 15–35 mm apart; central pinnae index 3–5, widest below (to about) the middle, 5.5–12.5 by 1.5–3 cm, base varying from ± symmetrical, subcordate, cuneate or angustate, to (strongly) oblique with its acroscopic side much better developed and provided with a distinct basal acroscopic lobe (or auricle), margin entire to lobed to 1/7(–1/4) towards the costa, with a more or less distinct spine in (some of) the sinuses, apex acute or orbicular; the two lowermost pinnae 0–1 mm stalked, conform to the central pinnae; *terminal segment* triangular, deeply lobed near the base, gradually narrowing towards the acute or acuminate apex; *venation pattern* very irregular: veins forming a costal areole (rarely lacking), with or without few to several smaller distal areoles varying in size and shape, the areoles with or without usually one excurrent included free vein, see also fig. 85: a–d. *Fertile leaves* 50–70 cm long; petiole 37–> 46 cm long; lamina index 2–5, 14–34 by 3–12 cm, without the terminal segment 10–26, the terminal segment 4–8 cm long; pinnae 16–22, 25–50 mm apart; central pinnae index 4–8, 2–6.5 by 0.4–1.2 cm; the two lowermost pinnae 0–1

*Fig. 85. a–d. Bolbitis × singaporensis*, venation pattern of sterile pinnae, × 4/5 (a. *Anonymus s.n.*, SING 20950; b. *Holttum SF 19799*, C; c, d. *Holttum s.n.*, SING).—e–p. *Bolbitis × sinuosa*.—e, f. nm. *sinuosa*. e. sterile leaf, × 1/5; f. venation pattern of sterile pinna, × 4/5.—g–p. nm. *foxii*. g. sterile leaf, × 1/5; h, j, l, n, p. venation pattern of sterile pinnae, × 4/5; i, k, m, o. shape of sterile pinnae, × 1/5 (e. *Cuming 105*, W, holotype of *B. × sinuosa*; f. *ibid.*, BM, isotype; g, h. *Fox PNH 8904*, PNH, isotype of *B. × foxii*; i–p. *Price 763*, L).—q–w. *Leptochilus × trifidus*. q–u. sterile and fertile leaves, × 1/5; v, w. venation pattern of sterile laminas, × 4/5, the asterisks indicate isolated veins within areoles (q. r. *Brooks 403.S.*, BM; s, t. *Van Alderwerelt van Rosenburgh s.n.*, BO, holotype of *Leptochilus × trifidus*; u. *ibid.*, P; v. *ibid.*, L; w. *Matthew s.n.*, K).



mm stalked. *Sporangia* inserted mainly on the veins. Spores: normal spores not available.

**Chromosomes.**  $2n = 82$ ; at meiosis univalents only.

SINGAPORE. *Holttum SF 10479 p.p.* (SING), *SF 19799* (C, K, SING), *s.n.*, 27-ii-1923 (SING), *s.n.*, 12-xi-1928 (SING), *s.n.*, ii-1943 (K, L, SING); *Hullett s.n.* (type); *Matthew 12569* (SING), *s.n.*, 24-i-1908 (K); *Allen 2052* (US).

**Habitat.** On granite rocks in stream-bed, in the shade of primitive forest (Holttum, 1954, 468).

**Spores.** *Holttum SF 19799* (C, SING), *Hullett s.n.* (holotype): sporangia filled with either aborted S.M.C.'s or in part also with aborted spores.

**Parentage.** Manton (in Holttum, 1954) rightly suggested this to be a hybrid between *Egenolfia appendiculata* (= *B. appendiculata* ssp. *appendiculata*) and *B. diversifolia* (= *B. sinuata*). These two species and the hybrid grow intermingled in the Fern Valley on Bt. Timah.

**Notes.** 1. The venation pattern (which is very irregular indeed) of some of the specimens is strongly reminiscent of that of *B. lonchophora*. The pattern is not suggestive of a relationship of the hybrid with *B. sinuata*.

*B. × singaporensis* possibly is a hybrid complex. The specimen of *B. sinuata* Dr. Johnson kindly collected on my request in the type locality of this hybrid turned out to be a triploid (see chapter 7). Tetraploids of *B. sinuata* therefore may occur in the Fern Valley as well and possibly also hybridize with *B. appendiculata* ssp. *appendiculata*.

2. Holttum (1954) listed this as a species in spite of Manton's opinion. He suggested hybridity between *B. × singaporensis* (*p. spec.*) and *B. appendiculata* ssp. *appendiculata* for *Holttum SF 19799* (C, SING) which was said to show a venation pattern with fewer anastomoses and to have spines in the sinuses of the pinnae 'as long as in *Egenolfia*'. Holttum's material, however, is rather close to the type of the present hybrid also in venation pattern.

## H. 12. *Bolbitis × sinuosa* (Fée) Copel.—Fig. 85: e–p.

*B. × sinuosa* (Fée) Copel., Fern Fl. Philip. (1960) 262, *p. spec.*—[*Cyrtogonium sinuosum* J. Smith, Hook. J. Bot. 3 (1841) 403, *nom. nud.*]—*Heteroneuron sinuosum* Fée, Hist. Acrost. (1845) 95 ('*Heteroneuron*'); Copel., Philip. J. Sc. 37 (1928) 368, fig. 21.—*Poecilopteris sinuosa* Presl, Epim. Bot. (1851) 173.—**Lectotype:** *Cuming 105*, Philippines, Luzon, Laguna and Tayabas, Mt. Cristobal (W, ster.; iso in B, fragm, ster., BM, K, MICH, fragm. ster., US, ster.).

*B. × foxii* Copel., Philip. J. Sc. 81 (1952) 22, *p. spec.*; Fern Fl. Philip. (1960) 263.—**Type:** *Fox PNH 8904* (*Fieldno.* 328), Philippines, Central Polillo I., Bordios Mun., 150 m alt. (iso in PNH).

**Distribution.** Philippines (Luzon, Mindanao, and Central Polillo I.).

**Note.** Typification of *Heteroneuron sinuosum*. Apart from *Cuming 105*, Fée also cited *Cuming 161* from Vienna (not *Cuming 161* of the other herbaria studied by Fée). The loan from Vienna included two sheets of *Cuming 161*, which had been annotated by Fée as '*Heteroneuron argutum*' and which represent *B. heteroclita*.

**a. nm. sinuosa—Fig. 85: e. f.**

Rhizome (only a fragment available) 5 mm thick, with 2 rows of leaves. Leaves approximate. *Sterile leaves* pinnate, up to 50 cm long; petiole 12–21 cm long; lamina index 1–2, widest somewhat below the middle, 16–32 by 10–18 cm, without the terminal segment 11–20, the terminal segment 8–12 cm long, herbaceous, dark olivaceous or brown, with or without (a primordium of) a spherical subterminal bulbil; pinnae alternate to opposite, 13–20, 20–30 mm apart; central pinnae index 5–7, 7.5–12 by 1.1–1.8 cm, base symmetrical, narrowly cuneate, margin shallowly and oblique lobed or finely crenate-serrate, with small teeth in the sinuses, apex acute or acuminate; the two lowermost pinnae 3–6 mm stalked,  $\pm$  conform to the central ones; *terminal segment* deeply lobed near the base, tapering towards the acute or acuminate apex; *venation pattern*: veins forming a costal areole and several smaller distal ones, the areoles without included free veins, see also fig. 85: f. *Fertile leaves* (only 3 incomplete leaves available); petiole 27 cm long; laminas: (1) 19 by 16 cm, the terminal segment 8 cm long, and with 10 pinnae, (2) 21 by 6 cm, the terminal segment 7 cm long, and with 12 pinnae; pinnae c. 5 by 0.7–0.9 cm, base broadly cuneate; the two lowermost pinnae c. 2 (–13) mm stalked. *Sporangia* inserted all over the lower surface. Spores: normal spores not met with.

PHILIPPINES. Luzon. Laguna, Mt. Cristobal: *Cuming 105* (lectotype); Pagsanjan: *Copeland s.n.* (MICH, herb. Copeland 10191, *p.p.*, ster.); Tayabas, Mt. Binuang: *Ramos & Edaña BS 28842* (BO, K, L, SING, US).

**Spores.** *Cuming 105* (lectotype, BM, K): aborted S.M.C.'s and few aborted spores.

**Parentage.** The shape of the leaves and the venation pattern rather agree with that of *B. quoyana*. The shape of the plants otherwise gives little indication of the putative second parent. Possibly *B. rhizophylla* or *B. heteroclita*. The similarity of nm. *foxii* to certain dwarfs of the latter species is noteworthy.

**Notes.** 1. Fée based himself on sterile material only. In the phrases in French added to the description in Latin he erroneously spoke about fertile leaves 'les seuls que nous connoissions'.

2. *Ramos & Edaña BS 28842*, from Luzon, has markedly petiolulate (up to 13 mm long) fertile pinnae with a narrowly acute base.

**b. nm. foxii (Copel.) Hennipman, comb. et stat. nov.—Fig. 85: g–p.**

*B. × foxii* Copel., Philip. J. Sc. 81 (1952) 22.

If compared with mn. *sinuosa* the plants are of the same size or smaller, with smaller and generally also narrower pinnae with a somewhat simpler venation pattern. The normal spores of *Price 763* (L) with a smooth cristate perispore; crests low.

**Chromosomes.**  $2n = c. 80$ .

PHILIPPINES. Polillo I: *Fox PNH 8904* (type of *B. × foxii*).—Luzon. Quezon, Llavac, Univ. Philip. Land Grant, 250 m alt.: *Price 763* (L, 6 sh.).—Mindanao. Agusan del Sur Prov., Esperanza, 125° 30' E, 8° 45' N: *Price 2805* (L).



Habitat. 'On rocks in stream' (type); 'in partial shade along riverbank' (Price 763).

Spores. Fox 8904 (iso PNH), Price 763 (L, sh. 2 & 3): all abnormal. Price 763 (L, sh. 4): the greater part normal.

Parentage. See nm. *sinuosa*.

Note. Price 763 is in cultivation at Leiden since early 1970. The plants grow rather well; as yet (1976) they have not produced fertile leaves.

### Hybridae incertae sedis

#### H. 13. *Leptochilus* × *trifidus* v.A.v.R.—Fig. 85: q–w.

*L.* × *trifidus* v.A.v.R., Bull. Dép. Agr. I. N. 18 (1908) 26, p. spec.—Type: Van Alderwerelt van Rosenburgh s.n., 1907, cult. (BO; iso in L, ster., P).

*Hemigramma latifolia* auct. non Copel.: Copel., Philip. J. Sc. 37 (1928) 404, p.p.

Rhizome short-creeping, up to 10 cm long, up to 5 mm thick, with 2 rows of leaves, without sclerenchyma strands. Scales of the rhizome: index 2–6, up to 5 by 1.5 mm, pseudo-peltate, or attached with the central part of the base, triangular, opaque to subclathrate, blackish, margin entire, apex acuminate. Leaves rather close together to somewhat spaced. *Sterile leaves* simple, either entire or trifid, 30–60 cm long. *Entire leaves* 30–52 cm long; petiole 8–20 cm long, near the base 1–3 mm thick; lamina index 3–6, widest about the middle, 22–32 by 4–9 cm, firm-herbaceous to subcoriaceous, brownish, with a small but conspicuous spherical subterminal bulbil, base narrowly cuneate or angustate, gradually decurrent on the petiole, margin entire or slightly sinuate, apex acuminate. *Trifid leaves* 41–60 cm long; petiole 10–25 cm long, near the base 2–4 mm thick; lamina index 1–1.5, widest below the middle, 24–35 by 17–30 cm, base ± abruptly decurrent on the petiole; lateral lobes somewhat falcate, widest about the middle, the basiscopic side somewhat larger than the acroscopic one, 11.5–20 by 2.5–8 cm; *terminal lobe* symmetrical, widest about or below the middle, 20–30 by 5.5–12 cm, at the base 2.5–4.5 cm wide; otherwise like the entire leaves; *venation pattern* rather irregular but otherwise like that found in Ser. *Euryostichae*, see also fig. 85: v, w.—*Fertile leaves*. *Entire leaves* 27–50 cm long; petiole 18–30 cm long; lamina index 5–10, 8–20 by 1.5–3.5 cm. *Trifid leaves* 25–40 cm long; petiole 16–27 cm long; lamina index 1–2, 6–13 by 5–10 cm; lateral lobes 2–5.5 by 0.7–2 cm; terminal lobe 5–11 by 1.2–3.5 cm, at the base 0.4–1.2 cm wide. *Sporangia* inserted all over the lower surface. Spores: normally shaped spores with a smooth, (imperfectly developed) cristate-undulate or cristate perispore.

SUMATRA. West Coast. Padangpandjang, 'Anai Kloof': *Matthew* s.n. (K).—East Coast. Sibolangit Forest Reserve: *Lörzing* 12404 (BO), 12405 (BO, K, L, p.p.).—Bencoolen. Lebong Tandai: *Brooks* 44.S. (BM), 61.S. (BM), 73.S. (BM, MICH, P), 75.S. (BM), 403.S. (BM), s.n. (BM).

Habitat. Forest; reported from rocks either in streams or on stream banks. Altitude: 450–500 m (Lörzing's collections).

**Spores.** *Van Alderwerelt van Rosenburgh s.n.* (BO, holo): all abnormal, a few normally shaped with an (imperfectly developed) undulate-cristate perispore. *Brooks s.n.* (BM), *Lörzing 12405* (K): all abnormal, a few normally shaped with an imperfectly developed cristate perispore. *Lörzing 12404* (BO): sporangia filled with either (a cluster of) abnormal spores, or in part with (apogamous?) normal spores with a cristate perispore.

**Parentage.** A specimen of the present fern was once found mounted together with a specimen of *Leptochilus decurrens* (also dimorphic). Lörzing (annotations to his collections), Copeland (annotation to *Brooks 73.S.*, MICH), and Van Alderwerelt van Rosenburgh (1908) thought it related to this species. Copeland (1928) included it in *Hemigramma latifolia* Copel. which is, however, different.

**The rhizome.** The arrangement of the vascular bundles in the rhizome is  $\pm$  radially symmetric; there is one slightly larger ventral bundle; roots are given off in all directions and arise from all bundles; leaves occur in 2 rows dorsolaterally. In *Leptochilus decurrens* this arrangement is  $\pm$  radially symmetric; cross-sections show a number of  $\pm$  equally wide bundles in a  $\pm$  circular arrangement; roots are formed in 2 rows ventrolaterally; leaves occur in 2 rows dorsolaterally. The arrangement in *Bolbitis sinuata* is dorsiventral (see the general chapters). Sclerenchyma strands of the ground tissue of the rhizome are absent in *Leptochilus*  $\times$  *trifidus*, present or absent in *B. sinuata*, and present in *Leptochilus decurrens*. A sheath of sclerenchyma somewhat below the epidermis which is present in *B. sinuata* is absent in *Leptochilus*  $\times$  *trifidus* and *L. decurrens*. Aerophores are absent in *L. decurrens*, absent or not distinctly developed in *L.*  $\times$  *trifidus*, and present in *B. sinuata*.

The anatomical data of *Leptochilus*  $\times$  *trifidus* were obtained from *Lörzing 12405* (K) and *Brooks 73.S.* (P).

**The petiole.** The leaves of all three plants are joined to the rhizome. The sheath of sclerenchyma as seen from cross-sections in the basal part of the petiole: in *Leptochilus decurrens* the sheath is situated directly below the epidermis and not interrupted by aerophores. In *Leptochilus*  $\times$  *trifidus* the sheath is situated somewhat below the epidermis and not interrupted by aerophores. In *Bolbitis sinuata* the sheath is situated somewhat below the epidermis and interrupted by aerophores.

**The scales.** The shape of the scales is similar in all three. *Leptochilus decurrens* has clathrate scales without or with but few glandular cells which are situated terminally on (incisions of) the scales, or on short, stout, glandular hairs. *Leptochilus*  $\times$  *trifidus* has subclathrate or opaque scales with few, stout, glandular cells. *Bolbitis sinuata* has subclathrate scales with slender glandular hairs.

**The stomata** are polocytic in all three.

**A bulbil** is absent in *Leptochilus decurrens* and present in *L.*  $\times$  *trifidus* and *Bolbitis sinuata*.

**The spores.** The spores are monolete in all three.

**The perispore.** It is generally believed that the spores of *Leptochilus* species lack a perispore. This proved to be incorrect as a rather well developed minutely spiny perispore was found in several *Leptochilus* species (*L. axillaris*, *decurrens*, *lanceolatus*,

and *minor*). The perispore of the normally shaped spores of *Leptochilus* × *trifidus* is imperfectly cristate or cristate-undulate, that of *B. sinuata* is either cristate or cristate-undulate.

The gametophyte of *Leptochilus decurrens* is of the ribbon-like type, and bears one-celled papillate hairs (Nayar & Kaur, Bot. Rev. 37, 1971, 368), those of *L. × trifidus* and *B. sinuata* are unknown.

In conclusion, the shape, texture, and venation pattern of *Leptochilus* × *trifidus* I consider intermediate between that of *L. decurrens* and *B. sinuata*. The presence of a bulbil, the shape of the perispore, and the texture of the scales rather agree with these properties of *B. sinuata*; the absence of aerophores on the petiole and the rhizome, the absence of a sclerenchyma sheath in the rhizome, and to some extent also the vascularization in the rhizome, point towards a fern like *Leptochilus decurrens*.

In spite of this I have refrained of creating a new hybrid genus as the chromosome number of *Bolbitis* ( $n = 41$ ) differs from that of *Leptochilus* ( $n = 36$ , see Manton & Sledge, Phil. Trans. R. Soc. Lond. ser. B, 238, 1954, 171), and as the spore output does not reflect this difference (aborted S.M.C.'s are not found). This very interesting hybrid which possibly questions the relationships of the polypodioid genera *Leptochilus* and *Colysis* (which are likely to be congeneric, see Sledge, Ann. Mag. Nat. Hist. ser. 12, 9, 1956) needs to be studied for its karyology.

Notes. 1. The type collection and *Brooks s.n.* (BM) consist of sterile and fertile leaves which are either entire, or trifid, or 'bifid' (with but one lateral lobe, see the illustration).

2. The specimens with entire leaves have a similar habit as certain specimens with simple leaves of ser. *Euryostichae*.

## TAXA ATQUE NOMINA DUBIA

### Species dubiae

#### D. 1. *Bolbitis cadierei* (Christ) Ching—Fig. 86: a–d.

*B. cadierei* (Christ) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 47; Tardieu-Blot & C. Chr., Not. Syst. 7 (1938) 100; in Lecomte, Fl. Gén. I.-C. 7 (1941) 432.—*Gymnopteris cadierei* Christ, J. de Bot. 19 (1905) 126; Copel., Philip. J. Sc. 37 (1928) 358.—*Leptochilus cadierei* C. Chr., Ind. Fil. (1906) 384.—Type: *Cadière 146*, Vietnam, Annam, Thanh Tan (= Thua Thien), 100–200 m alt. (P).

Rhizome (but 2 available) short-creeping, 5 and 15 mm thick, with 2 and 3 rows of leaves resp., with sclerenchyma strands. Scales: index 3–8, up to 5 by 1 mm, subclathrate, with or without a paler margin, brownish. Leaves tufted. *Sterile leaves* pinnate, 56–>84 cm long; petiole 24–50 cm long; lamina index 1–2, widest below or about the middle, 30–>46 by 24–30 cm, without the terminal segment 10–26, the terminal segment 17–25 cm long, subcoriaceous, with a spherical subterminal bulbil on terminal (and lateral) segments; rhachis not winged; pinnae alternate or opposite, 6–10, 20–

60 mm apart; central pinnae index 4–6, widest somewhat below the middle, 12–24 by 2.7–6 cm, base symmetrical or asymmetrical with its basiscopic side rounded, the acroscopic side broadly attenuate, margin entire or sinuate, apex acute to long-acuminate; the two lowermost pinnae up to 4 mm stalked, conform to the central pinnae; *terminal segment* conform to the pinnae or with an odd lobe near the base; *venation pattern* resembling that of *B. heteroclita* but part of the areoles with mostly one simple, excurrent, included free vein ending in a hydathode, see also fig. 86: b–d. *Fertile leaves* 65–105 cm long; petiole 50–70 cm long; lamina index 2–4, 15–40 by 6–12 cm, without the terminal segment 11–31, the terminal segment 4–9 cm long; pinnae 8–12, up to 55 mm apart; central pinnae index 5–6, 4.5–10 by 0.8–2 cm; the two lowermost pinnae 6–12 mm stalked. *Sporangia* all over the lower surface. Spores with a smooth, cristate or cristate-spinose.

VIETNAM. Tonkin. Lang Met: *Pételot s.n.* (BM, P).—Annam. Thua Thien: *Cadière 123* (BM, P, both ster.), *146* (type), *169* (P, ster.), *196* (P); Mt. Bah-na (near Danang): *Cadière 91* (C, ster., P), *129* (P); *Clemens s.n.* (UC, 339924); *Sallet s.n.* (C, L, P, all ster.).

**Habitat.** Forest; terrestrial (near streams). Altitude: 100–200 m (type), 800–1500 m (Mt. Bah-na).

**Spores.** *Cadière 196* (P): the greater part normal. *Cadière 146* (type): the greater part abnormal. *Pételot s.n.* (P): sporangia filled with aborted S.M.C.'s and aborted spores.

**Notes.** 1. The venation pattern and leaf architecture are intermediate between that of *B. heteroclita* and *B. virens* (or *B. subcordata*?). *B. cadieri* is likely to be of hybrid derivation.

2. Christensen (annotations to *Campium juglandifolium* C. Chr. *ined.*, based on Pételot's collection from Lang Met) compared this fern with *Campium costatum* (= *B. costata*) which is quite different.

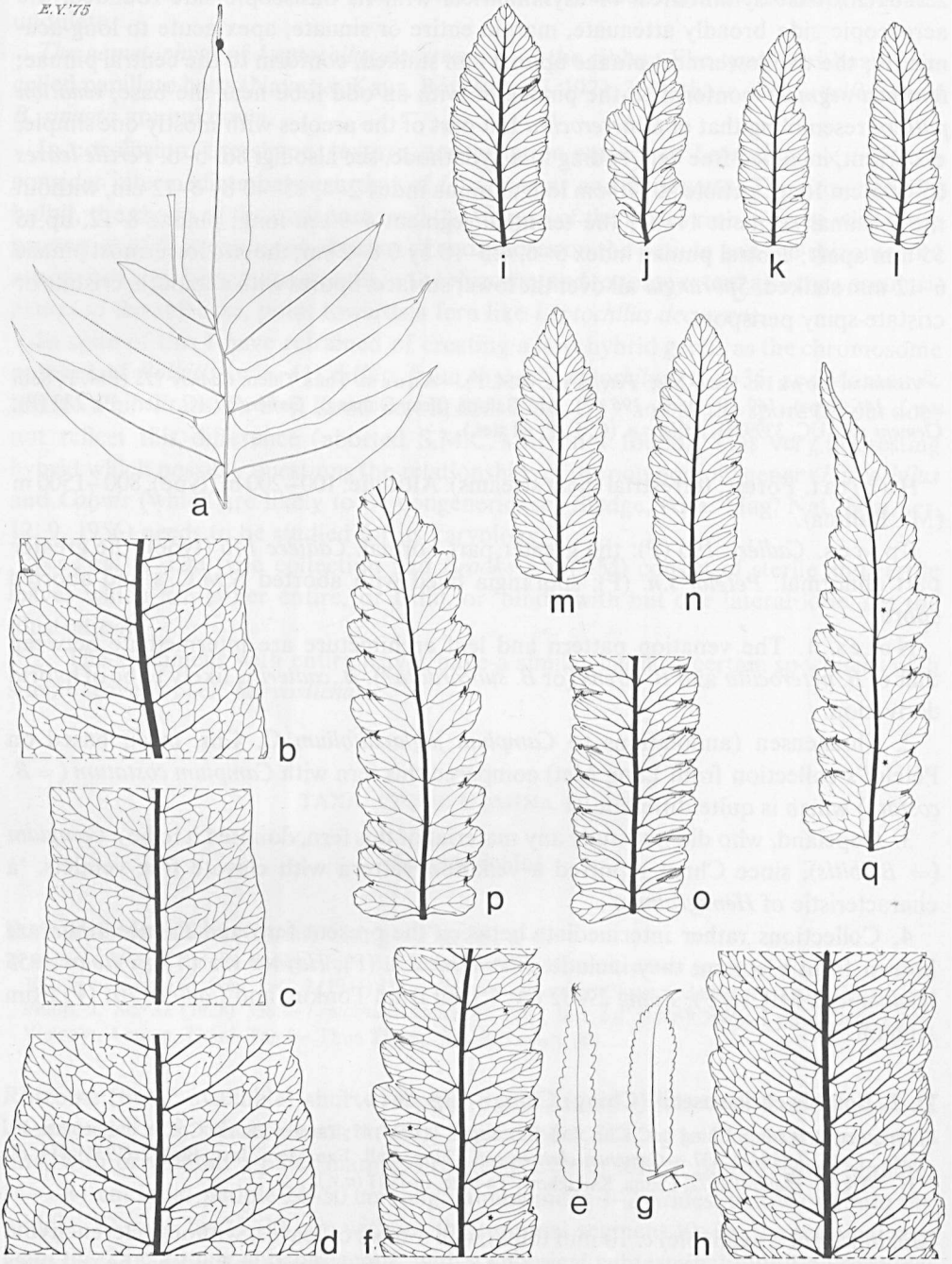
3. Copeland, who did not study any material of this fern, doubted it to be a *Campium* (= *Bolbitis*), since Christ reported a venation pattern with clavate free veinlets, 'a characteristic of *Hemigramma*'.

4. Collections rather intermediate between the present fern and *B. subcordata* are known from Vietnam; they include: *Eberhardt s.n.* (P), *Hayata s.n.* (TI), *Pételot 3955* (*Colani leg.*, MICH, P), *Tsang 29432* (A, C), all from Tonkin, and *Cadière 101* (P) from Annam.

## D. 2. *Bolbitis christensenii* (Ching) Ching—Fig. 86: e, f.

*B. christensenii* (Ching) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 47; Tardieu-Blot & C. Chr. in Lecomte, Fl. Gén. I.—C. 7 (1941) 437.—*Campium christensenii* Ching, Bull. Fan Mem. Inst. Biol. 2 (1931) 214, pl. 31.—Type: *Esquirol 2672*, China, Kweichow, Ta-iong, iii-1911 (n.v.).

Rhizome (but 2 available) c. 10 mm thick, with 3 rows of leaves, without sclerenchyma strands. Scales: index 3–6, up to 4.5 by 1.5 mm, subclathrate, blackish, the old ones with a paler margin. Leaves tufted. *Sterile leaves* pinnate, 49, 73, and 86 cm long resp.;



petiole 7, 25, and 33 cm long resp.; laminas widest about the middle, (1) 42 by 22 cm, the terminal segment 22 cm long, with 11 pinnae, (2) 48 by 22 cm, the terminal segment 21 cm long, with 18 pinnae, (3) 53 by 25 cm, the terminal segment 18 cm long, with 20 pinnae, resp.; herbaceous, olivaceous, with a spherical subterminal bulbil quite near the apex (also of pinnae); rhachis not winged; pinnae alternate or opposite, up to 60 mm apart; central pinnae index 4–7, widest about the middle, 13–15 by 2.3–3.2 cm, base  $\pm$  symmetrical,  $\pm$  truncate to subcordate, margin lobed to 1/5 towards the costa, sometimes with small teeth in the sinuses, apex acute to acuminate; the two lowermost pinnae conform to the central ones, shortly petiolulate; uppermost pinnae: their basisopic side adnate, decurrent on the rhachis; terminal segment triangular, pinnatipartite near the base, tapering towards the apex; venation pattern: veins forming a regular network similar to that sometimes found in *B. angustipinna*, aeroles without included free veins, see also fig. 86: f. *Fertile leaves* 38, 82, and >87 cm long resp.; petioles 25, 40, and 47 cm long resp.; laminas widest below the middle, (1) 13 by 9 cm, the terminal segment 5 cm long, with 12 pinnae, (2) 42 by 12 cm, the terminal segment 10 cm long, with 19 pinnae, (3) >40 by 10 cm, without the terminal segment >37 cm long with >20 pinnae; pinnae up to 70 mm apart; central pinnae index 4–7, widest about or below the middle, 4–6.5 by 0.9–1.2 cm. *Sporangia* mainly inserted on the veins. Spores with a cristate-undulate perispore.

CHINA. Kweichow. Ta-iong: *Esquirol* 2672 (type, n.v.).

VIETNAM. Tonkin. Than-moi: *Balansa* 150 (= 95); Dong-son: *Balansa* 151 (= 94); Chobo: *Balansa* 1951 (P).

**Habitat.** Forest, along streams. Once reported from limestone.

**Spores.** *Balansa* 1951: normal. *Balansa* 151: in part normal. *Balansa* 150: sporangia filled with aborted spores and/or aborted S.M.C.'s.

**Notes.** 1. A very interesting fern as the venation pattern of the sterile pinnae suggests it to be intimately related to *B. angustipinna* which has, however, quite a different leaf architecture and an undulate perine. I doubt the relationship to *B. subcordata* as suggested by Ching, as the venation pattern does not show included free veins. The sporangia are mainly inserted on the veins. This, and the habit of the fertile leaves are also found in *B. sinensis*. The venation pattern of the fertile pinnae shows many irregularities, being rather similar to that of *B. angustipinna*  $\times$  *sinensis*.

**Fig. 86.** a–d. *Bolbitis cadierei*. a. sterile leaf,  $\times$  1/5; b–d. venation pattern of sterile pinnae,  $\times$  4/5 (a, b. *Cadière* 146, P, holotype of *B. cadierei*; c. *Clemens* s.n., UC 339924; d. *Cadière* 91, C).—e, f. *Bolbitis christensenii*. e. sterile pinna,  $\times$  1/5; f. venation pattern of sterile pinna,  $\times$  4/5; asterisks indicate asymmetry in the venation pattern (e, f. *Balansa* 151, P).—g, h. *Bolbitis interlineata*. g. sterile pinna,  $\times$  1/5; h. venation pattern of sterile pinna,  $\times$  4/5 (g, h. *Brooks* 12, MICH, holotype of *B. interlineata*).—i–q. *Bolbitis laxireticulata*, venation pattern of sterile pinnae,  $\times$  4/5; asterisks indicate local differences in venation pattern (i, j. *Tagawa & Iwatsuki* 4605, L, both from one leaf; k, l. *ibid.*, L; m–o. *ibid.*, US; p, q. *Iwatsuki* 4884, L).

The fern possibly has a hybrid origin; it is likely that a fern like *B. angustipinna* takes part. The other parent is likely to have a cristate or cristate-undulate perispore; I have no well-founded suggestions.

2. The shape of the leaves and the pinnae, and the venation pattern are surprisingly similar to that of *B. quoyana*. The venation pattern of *B. quoyana* is symmetrical, whereas it is usually asymmetrical in *B. angustipinna*.

3. The bulbil of the sterile leaf of *Balansa 151* bears two small sterile leaves composed of a large triangular, shallowly lobed terminal segment and two  $\pm$  orbicular pinnae. The venation pattern of the terminal segment is similar to that found in the adults; it is free in part of the basal pinnae.

### D. 3. *Bolbitis interlineata* (Copel.) Ching—Fig. 86: g, h.

*B. interlineata* (Copel.) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 48; Ito, J. Jap. Bot. 14 (1938) 439, *quoad nomen solum*.—*Campium interlineatum* Copel., Philip. J. Sc. 37 (1928) 370, fig. 24, pl. 17.—Type: *Brooks 12*, Borneo, Sarawak, Bungo Range, iv-1909 (MICH; iso in BM).

Rhizome (only fragments available) 5 mm thick, with many sclerenchyma strands. Scales up to 4 by 1 mm, subclathrate, blackish. Leaves close together. *Sterile leaves* pinnate, 60–75 cm long; petiole 30–35 cm long; lamina index 1–2, widest about or below the middle, 30–40 by 20–24 cm, without the terminal segment 10–28, the terminal segment 12–20 cm long, herbaceous, with a spherical subterminal bulbil; rachis not winged; pinnae alternate or opposite, 8–16, 20–35 mm apart; central pinnae index 3–5, widest above or below the middle, 13.5–15 by 3–4 cm, base either  $\pm$  symmetrical, broadly cuneate to subcordate, or asymmetrical with its basiscopic side longer and/or wider than its acroscopic side, margin entire or (in part) slightly sinuate, apex acute to acuminate; the two lowermost pinnae up to 4 mm stalked, conform to the central ones; *terminal segment*  $\pm$  conform to the pinnae or triangular with 1–2 basal lobes; *venation pattern* very intricate, reminiscent of that of *B. heteroclita* but part of the areoles with usually one excurrent included free vein, see also fig. 86: h. *Fertile leaves* 60–85 cm long; petiole 44–50 cm long; lamina index 2–4, 17–35 by 8–10 cm, without the terminal segment 13–30, the terminal segment 4–9 cm long; pinnae 10–18, up to 40 mm apart; central pinnae index 5–8, 5–6 by 0.7–1 cm, the two lowermost pinnae up to 5 mm stalked. *Sporangia* all over the lower surface. Spores with a smooth cristate perispore.

BORNEO. Sarawak. Southern part. Bungo Range: *Brooks 12* (type); Mt. Matang: *Allen 3145* (K, ster.); *Matthew s.n.* (K, ster., juv.); Mt. Penrissen: *Brooks s.n.* (BM).

**Habitat.** Forest; on rocks in streams. Altitude: 300–690 m.

**Spores.** *Brooks s.n.* (BM): in part normal. *Brooks 12* (holotype of *Campium interlineatum*): the greater part abnormal. *Brooks 12* (iso in BM): all abnormal.

**Note.** A distinct fern easily characterized by leaf architecture and venation pattern which resembles that of *B. cadieri* (*spec. dub.*). Possibly of hybrid origin and related to *B. heteroclita* (venation pattern!) and to either *B. sculpturata* or *B. repanda*.

**D. 4. *Bolbitis laxireticulata* Iwatsuki—Fig. 86: i–q.**

*B. laxireticulata* Iwatsuki, Acta Phytotax. Geobot. 18 (1959) 50, fig. 7 & 8.—*Egenolfia laxireticulata* Kuo in Fl. Taiwan 1 (1975) 352.—Type: *Tagawa & Iwatsuki 2918*, Japan, Ryukyu, Amami-Ooshima, Mt. Yuwan-dake, 500 m alt. (KYO, n.v., L, phot.; iso in KYO, n.v., L, phot., L, ster., US).

Rhizome c. 4 mm thick, with 2 rows of leaves, with sclerenchyma strands. Scales up to 3(–5) by 1.5(–2) mm, subclathrate, brown-blackish. Leaves  $\pm$  approximate. *Sterile leaves* pinnate, 30–75 cm long; petiole 10–34 cm long; lamina index 2–4, widest below or about the middle, 20–42 by 10–15 cm, without the terminal segment 14–35, the terminal segment 4–11 cm long, papyraceous, with a spherical subterminal bulbil; rhachis (in the upper half) with a narrow wing; pinnae alternate or opposite, 18–31, up to 35 mm apart; central pinnae index 3–7, widest about or below the middle, 4.5–9.5 by 1.3–2.3 cm, base sometimes symmetrical, variously cuneate, usually asymmetrical, its acroscopic side broader than its basiscopic side and sometimes with a basal lobe, margin  $\pm$  entire to lobed to 2/5 towards the costa, lobes finely crenate-serrate, with a distinct spine in the sinuses, apex acute to acuminate; the two lowermost pinnae up to 1.5 mm stalked, conform to the central pinnae, base of pinnae of the upper half of the lamina asymmetrical; *terminal segment* triangular; *venation pattern* (very) irregular, veins forming a costal areole at least in part of the pinnae of one plant, otherwise varying, see also fig. 86: i–q. *Fertile leaves* (only 2 immature leaves available); pinnae 12 and 17. *Sporangia* inserted mainly on the veins. Spores not available.

JAPAN. Ryukyu Is. Amami-Ooshima: *Iwatsuki 4884* (L, US, ster.); *Serizawa 11713* (= *Pterid. Jap. exsicc. 48*) (L, U, both ster.); *Tagawa & Iwatsuki 2918* (type). Iriomote: *Tagawa & Iwatsuki 4605* (L, US, both ster.). Also reported from Okinawa (Iwatsuki, 1959).

**Habitat.** Terrestrial in moist places in forest. Altitude: 500–550 m.

**Notes.** 1. The venation pattern, the shape of the pinnae, and the presence of a very narrow wing along the rhachis may be regarded as intermediate between those of *B. appendiculata* ssp. *appendiculata* and *B. subcordata*. The venation pattern is structurally irregular: in many pinnae it does not decrease in complexity towards the apex, the venation pattern in the basal part of a certain pinna being less complex than that in the middle and apical part of the same pinna. Iwatsuki himself judged the venation pattern ‘quite indefinite’ and found it to be different in every individual. He also noted the enormous variation of other features.

Iwatsuki did not describe the spores. The sporangia available to me are all immature. *B. laxireticulata* seems to be of hybrid derivation.

Iwatsuki related the present fern to *B. sinensis* and *B. × singaporensis* (*p. spec.*). The differential characters he gave do not hold. His concept of *B. sinensis* is that of Christensen which is heterogeneous (see the notes on *B. sinensis*). He suggested hybridity between *B. laxireticulata* and *B. appendiculata* and referred to Holttum (Ferns of Malaya, 1954) who found plants intermediate between *B. × singaporensis* (*p. spec.*) and *B. appendiculata*. See also *B. × singaporensis* note 2 and sect. *Lysidictyon* Iwatsuki (= sect. *dub.*).



2. The shape of the pinnae and the venation pattern (only incidental anastomoses) of *Tagawa & Iwatsuki 4605* (ster.) resemble that of *B. rhizophylla*.

**D. 5. *Bolbitis longiflagellata* (Bonap.) Ching—Fig. 87.**

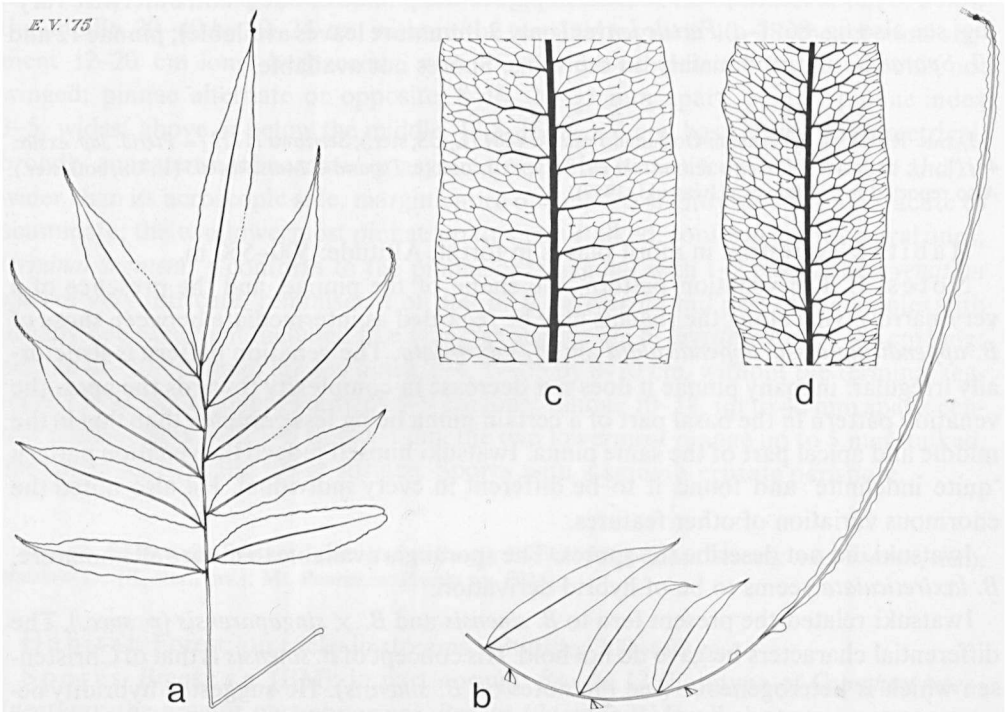
*B. longiflagellata* (Bonap.) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 49; Tardieu-Blot in Humbert, Fl. Madag. Fam. V, 2 (1960) 57, fig. xvi: 5, 6.—*Leptochilus longiflagellatus* Bonap., Notes Ptérid. 4 (1917) 68.—*Campium longiflagellatum* C. Chr. in Perrier de la Bâthie, Cat. Pl. Madag., Pterid. (1932) 32; Dansk Bot. Ark. 7 (1932) 70, pl. 22: fig. 5.—Type: *Perrier de la Bâthie 7490 p.p.*, Madagascar, Sambirano, Manongarivo Massif (P; iso in P, 6 sh., one mixed with *B. humblotii*, BM, fragm.).

*Acrostichum virens* auct. non Hooker & Grev.: auct. p.p.

*Campium humblotii* auct. non (Baker) Copel.: Copel., Philip. J. Sc. 37 (1928) 395, fig. 45.

*B. acrostichoides* auct. non (Swartz) C. Chr.: Alston, J. Bot. 77 (1939) 286, p.p.; in Exell, Cat. Vasc. Pl. S. Tomé (1944) 68, p.p.; Tardieu-Blot, Mém. I.F.A.N. 28 (1953) 115, p.p.; in Aubrév., Fl. Gabon 8 (1964) 190, p.p.; in Aubrév., Fl. Cameroun 3 (1964) 320, pl. 51: fig. 4, p.p.; Schelpe, Contr. Bolus Herb. 1 (1969) 42, p.p.

Rhizome short-creeping, up to 8 mm thick, with 2 rows of leaves, with sclerenchyma strands. Scales of the rhizome: index 1–8, up to 12 by 1.5 mm, subclathrate, rather firm, blackish or brownish, at least the basal part with a paler marginal strip. Leaves  $\pm$



**Fig. 87. *Bolbitis longiflagellata*.** a. sterile leaf,  $\times 1/5$ ; b. terminal part of a sterile leaf,  $\times 1/5$ ; c, d. venation pattern of sterile pinnae,  $\times 4/5$  (a–c. *Perrier de la Bâthie 7490*, P, type of *B. longiflagellata*; d. *Last s.n.*, K).

approximate. *Sterile leaves* pinnate, 48–>110 cm long; petiole 12–28 cm long, near the base 2–3 mm thick, with 5–7 vascular bundles; lamina index 1–4, widest below or about the middle, 30–92 by 15–30 cm, without the terminal segment 9–32, the terminal segment 20–60 cm long, herbaceous, dark green, with a spherical subterminal bulbil (situated rather close to the apex); rhachis not winged; pinnae ± alternate, 9–17, 20–45 mm apart; central pinnae index 4–7, widest about the middle, 11.5–22 by 1.8–3.8 cm, base symmetrical, cuneate, margin ± entire, without teeth or spines, apex acute to caudate; the two lowermost pinnae 0–3 mm stalked, conform to the central pinnae; *terminal segment* ± conform to the central pinnae or flagelloid, subarticulate to the rhachis; *venation pattern*: veins ± irregularly reticulate, areoles decreasing in size towards the margin, otherwise varying in size and shape, especially the larger areoles with mostly one simple, excurrent, included free vein, see also fig. 87: c, d. *Fertile leaves* (but 3 complete ones available) 51, 63, and 84 cm long; petiole 27–51 cm long; laminas: 20, 24, and 33 cm long resp., c. 7 cm wide, the terminal segment 5.5, 6, and 7.5 cm long resp.; pinnae 9–15, 30–60 mm apart; central pinnae index 5–7, widest about the middle, 4–4.5 by c. 0.8 cm; the two lowermost pinnae 1–3 mm stalked. *Sporangia* inserted all over the lower surface. Spores: normal spores not available.

MADAGASCAR. Northwestern. Sambirano, Manongarivo Massif: *Perrier de la Bâthie 7490 p.p.* (type); Be Kilus Mts.: *Last s.n.* (BM, K); Bealanana Dist.: *Dufournet s.n.* (P).

*Habitat*. 'Bois rocailleux au-dessous de 500 m d'alt.' (type).

*Spores*. *Last s.n.* (K): all abnormal, shrivelled; perispore very strongly cristate (or folded?). *Perrier de la Bâthie 7490* (P): all three fertile leaves with immature sporangia only.

*Notes*. 1. A distinct fern because of its scales, leaf architecture, and venation pattern. The one fertile leaf available with ± mature sporangia shows abnormal spores only. The venation pattern may well be intermediate between that of *B. humblotii* (with which it shares the large and firm scales, the shape of the terminal segment, and the subterminal bulbil) and *B. auriculata* (with which it shares the shape of the pinnae and particulars of the venation pattern).

Bonaparte and Copeland related *B. longiflagellata* to *B. heteroclita* because of the flagelloid leaves. Christensen and Tardieu-Blot related it to, or included it in *B. acrostioides* because of supposed similarities in the venation pattern which is, however, much different when studied in detail.

The identity of *B. longiflagellata* is not sufficiently clear to me; it possibly represents a hybrid between *B. humblotii* (with which it was found to grow together in two of the three localities from which it is known) and *B. auriculata* (obviously locally common in Madagascar).

2. The type material shows two types of sterile leaves: one (with which the fertile leaves occur in association) with the terminal segment conform to the pinnae, the other with the terminal segment long-flagelloid.

3. Copeland's remarks on *Campium humblotii* were based on material of *B. longiflagellata*. He studied the collection of J. F. Last ('J. B. Last'), from N.W. ('N.E.') Madagascar collected in 1890 ('1900'), and overlooked Bonaparte's publication of *Leptochilus longiflagellatus*.

#### D. 6. *Bolbitis sagenioides* (Kuhn) Ching

*B. sagenioides* (Kuhn) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 50.—*Chrysodium sagenioides* Kuhn, Linnaea 36 (1869) 63; Verh. Zool. Bot. Ges. Wien 19 (1869) 570; Copel., Philip. J. Sc. 37 (1928) 393.—*Leptochilus sagenioides* C. Chr., Ind. Fil. (1906) 307.—Type: *Milne 337*, Melanesia, New Hebrides, Aneityum (iso in K).

*Campium samoense* Copel., Philip. J. Sc. 37 (1928) 372, fig. 26, pl. 19.—*B. samoensis* C. Chr., Ind. Fil., Suppl. 3 (1934) 50.—Type: *Powell s.n.*, Melanesia, Samoa Is. (GH, 'Kew Distr. no. 1173'; iso in BM). *Acrostichum repandum* auct. non Bl.: auct. p.p.

*B. lonchophora* auct. non (Kunze) C. Chr.: C. Chr., Bull. Bish. Mus. 117 (1943) 104, p.p.

Rhizome unknown. *Sterile leaves* pinnate (only one complete leaf available), 60 cm long; petiole 25 cm long; lamina index 1–3, widest somewhat below the middle, 35–40 cm long, without the terminal segment 15–21 cm, the terminal segment 15–25 cm long; pinnae 10–17, otherwise intermediate between those of *B. quoyana* and *B. rivularis*; terminal segment triangular. *Fertile leaf* 85 cm long (only one complete leaf available); petiole 50 cm long; lamina index 1–4, 33–42 cm long, without the terminal segment 25–35, the terminal segment 7–10 cm long; pinnae 12–23. *Sporangia* inserted all over the lower surface. Spores with a smooth cristate perispore.

SOLOMON Is. Guadalcanal: *Braithwaite RSS 4090* (K, L, ster.).

NEW HEBRIDES. Aneityum: *Herus 107* (B, BM, G, P); *Kajewski 893* (BISH, BO, GH, US); *Milne 337* (type of *Chrysodium sagenioides*); *Morrison s.n.* (K).

SAMOA Is. *Powell s.n.* (type of *Campium samoense*); *Reinecke 5a* (P).

**Habitat.** 'On steep rocky slope by river' (*Braithwaite RSS 4090*); 'mountain woods' (*Herus 107*).

**Spores.** *Kajewski 893* (BO, GH, US), *Powell s.n.* (holotype of *Campium samoense*): the greater part normal. *Herus 107* (B): the greater part normal, several sporangia filled with abnormal spores only. *Herus 107* (BM), *Powell s.n.* (isotype of *Campium samoense*, BM), *Kajewski 893* (BISH): all or the greater part abnormal, or in part also with aborted S.M.C.'s.

**Note.** The mostly incomplete specimens are intermediate between those of *B. quoyana* and *B. rivularis* and likely to have sprung from hybridization. Copeland (1928) thought *Campium samoense* 'more particularly related to *Campium lonchophorum*' (= *B. lonchophora*). He later (Bull. Bish. Mus. 93, 1932, 15) thought the type specimen an aberrant individual 'better regarded a form of *Campium lonchophorum*', with which Christensen (1943) agreed.

#### D. 7. *Bolbitis tonkinensis* (C. Chr.) Iwatsuki

*B. tonkinensis* (C. Chr.) Iwatsuki, Acta Phytotax. Geobot. 18 (1959) 49; Tagawa & Iwatsuki, Acta Phytotax. Geobot. 25 (1971) 18.—*Egenolfia tonkinensis* C. Chr. in Ching., Bull. Fan Mem. Inst. Biol. 2

1931) 306; Tardieu-Blot & C. Chr., Not. Syst. 7 (1938) 99; in Lecomte, Fl. Gén. I.-C. 7 (1941) 424, p.p.—Type: *Herb. École Sup. Agric. & Sylvic. Hanoi 3396* (Colani leg.), Vietnam, Tonkin, Lang-Son (BM; iso in BM, P, UC, US).

Spores with a smooth cristate perispore. Amply described by Christensen.

VIETNAM. Tonkin. Long-Son: *Herb. École Sup. Agric. & Sylvic. Hanoi 3396* (type). Gia-hoa: *Herb. École Sup. Agric. & Sylvic. Hanoi 3412* (BM, C, UC, all ster.).

THAILAND. Northern. Chiengrai: *Winit 1022* (= *E. Smith 1674*) (K).

Habitat. Moist forest. Altitudinal records: 100 m (type), 550–590 m (*Winit 1022*).

Spores. Isotype (US): the greater part normal. Holotype: the greater part abnormal, mostly shrivelled. *Winit 1022* (K): all abnormal.

Note. I agree with Christensen that the present species, based on two rather different collections one of which sterile, is closely related to *B. sinensis*. Christensen gave several differential characters of which the following more or less hold. Petiole and rhachis—the costa far less so—covered with  $\pm$  permanent scales; the dark colour of the dried leaves which is unlike that of *B. sinensis* agreeing with that sometimes found in *B. appendiculata* ssp. *appendiculata*; the shape of the lobes of the sterile pinnae, which is  $\pm$  subfalcate with an acute apex (usually straight and rounded in *B. sinensis*). The latter feature varies considerably when different parts of the type material are compared. The perispore is cristate whereas it is cristate-undulate in *B. sinensis*. A cristate but reticulate perispore is found in *B. appendiculata*. Here possibly also belong the specimens enumerated under *B. sinensis*, note 2c.

#### D. 8. *Acrostichum flabellifolium* Link

*A. flabellifolium* Link, Fil. Spec. Hort. Berol. (1841) 165; C. Chr., Ind. Fil. (1906) 8.—Type: a specimen cultivated at Berlin (*n.v.*).

Note. The fern was described from sterile material; the description may cover *B. heteroclita*. The name '*Acrostichum flabelliforme* Link' (sphalm.) was found written on several sheets of mostly cultivated material of *B. heteroclita*.

#### D. 9. *Asplenium* ? *setosum* Presl

*A. ? setosum* Presl, Rel. Haenk. 1 (1825) 42; C. Chr., Ind. Fil. (1906) 132; Holttum, Nov. Bot. Univ. Carol. Prag. (1968) 11.—Type: *Haenke s.n.*, Philippines, Luzon (*n.v.*).

Christensen (1906) thought it a *Diplazium*. Copeland (Fern Fl. Philip., 1960, 418) regarded it as a synonym of *Asplenium serrulatum* Presl and suggested that the latter species might be an *Egenolfia*. Holttum identified the type of *A. serrulatum* as *Diplazium esculentum* (Retz.) Swartz. He further considered *Asplenium setosum* to be an *Egenolfia*. From the description given by Presl I judge *A. setosum* to represent *Bolbitis rhizophylla* (Kaulf.) Hennisman.

#### D. 10. *Campium punctulatum* Presl

*C. punctulatum* Presl, Tent. Pterid. (1836) 239, pl. 10: fig. 22.—Type: unknown.

*Heteroneuron preslianum* auct. non Fée, Hist. Acrost. (1845) 92, pl. 39: i ('*Heteroneuron*'); auct. p.p.

In the original description Presl referred to *Acrostichum punctulatum* auct. non Swartz: Presl, Rel. Haenk. 1 (1825) 16 ('*Acrostichum punctulatum* Presl nec Lin.'). The name *Campium punctulatum* the epithet of which is regarded as new in the genus *Campium*, was validly published as it so happened that Presl gave data about its anatomy and venation pattern in the generic description. However, these data do not permit to ascertain its identity.

The drawing of the venation pattern does not apply to material of a species known from the Philippines, and therefore could not have been taken from Haenke's specimens upon which Presl based *Acrostichum punctulatum* auct. non Swartz. The drawing said to represent the venation pattern of part of a fertile leaf comes nearest to that of a sterile leaf of *B. presliana* (with which it agrees most), *B. subcrenata*, *B. × lancea*, or *B. × prolifera*. The anatomical data given are too general as to give further clues to its identity.

Prof. Holttum kindly searched for the type when studying Presl's herbarium (Holttum, Nov. Bot. Univ. Carol., Praq., 1968, 8). He traced a sheet with three sterile leaves the largest of which is similar to one of the leaves illustrated by Fée (1845) as *Heteroneuron preslianum*. The sheet is annotated as '*Campium punctulatum* Presl' and 'In Luzon ad portum Sorzogon legit Haenke'. As *B. presliana* is endemic to southern India, the locality as well as the collector are erroneous. I have correlated the details of the venation pattern as given in Presl's drawing with that of the sterile leaves mentioned above as well as with sterile and fertile leaves of the type of *Heteroneuron preslianum*, assuming that Hügel's collection was available to Presl as early as 1836. Presl's rather schematical drawing does not match the venation patterns of any part of any of the leaves in sufficient detail.

#### D. 11. [*Panna Mara-maravara*, Rheede, Hort. Malab. 12 (1703) 39, pl. 19.]

In the original description of *Acrostichum flagelliferum* (= *B. subcrenata*), Hooker & Greville referred to Rheede. The identity of Rheede's plant cannot be ascertained as an herbarium of Rheede is unknown (Stafleu, Taxonomic Literature, 1967, 390), and the illustration rather poor. The plant represents either *B. subcrenata* var. *prolifera*, to which it was also referred by Beddome (Handb. Ferns Br. India, 1883, 437) (as *Gymnopteris subcrenata*), or *B. heteroclita* which is not indigenous to southern India but cultivated. The name is given here because of the medicinal use attributed to this fern by Rheede: 'Cum saccharo in syrumpum redacta, tussim, morbum endemium; omnia pulmonum vitia, dispnaeam, morbum lunaticum, phthisin curat'.

#### D. 12. *Leptochilus stolonifer* Christ

*L. stolonifer* Christ, Bull. Herb. Boiss. II, 6 (1906) 1004; v.A.v.R., Handb. Malayan Ferns (1908) 739.—

Type: *Loher s.n.*, Philippines, Angilog. iii-1906 (*n.v.*). = *Bolbitis* spec.

In the original description Christ referred this fern to *Leptochilus cuspidatus* (Presl) C. Chr. (= *B. repanda*). This fern may be synonymous to *B. heteroclita*, but the venation pattern as given by Christ is deviating.

### Sectio dubiosa

#### D. 13. Sect. *Lysidictyon* Iwatsuki

Sect. *Lysidictyon* Iwatsuki, Acta Phytotax. Geobot. 18 (1959) 47.—Type: *Bolbitis laxireticulata* Iwatsuki. (= *spec. dub.*).

Iwatsuki included three species in Sect. *Lysidictyon*, but mentioned the type species only. The only two other taxa mentioned in the discussion are *B. × singaporensis* (*p. spec.*) and *B. sinensis* (ser. *Egenolfianae*).

### Nomen dubium

#### D. 14. [*Bolbitis labrusca* (C. Chr.) Ching]

[*B. labrusca* (Christ ex C. Chr.) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 48, *nom. nud.*—*Leptochilus labrusca* C. Chr., Ind. Fil. (1906) 386, *nom. nud.*].

Christensen (1906) referred to *Acrostichum labrusca* Christ, Ann. Mus. Congo Bot. V, 1 (1903) 10 (which is not listed in the Index), where it is not found as already stated by Copeland (Philip. J. Sc. 37, 1928, 402). As becomes clear from the preface of Christensen's Index, Christ assisted Christensen in various ways during the preparation of the MS of the Index. Christensen obviously included the name on the authority of Christ who expunged the species later.

### EXCLUDED

E. 1. *Bolbitis guianensis* (Aublet) Kramer, Acta Bot. Neerl. 3 (1954) 486, *comb. invalid.* (Art. 33); Vareschi in Lasser, Fl. Venezuela 1 (1969) 376.—*Polypodium guianense* Aublet, Hist. Pl. Guian. (1775) 962.—*Acrostichum guianense* Baker, Fl. Brasil. 1 (1870) 591.—*Gymnopteris guianensis* Christ, Bull. Herb. Boiss. II, 1 (1901) 70.—*Leptochilus guianensis* C. Chr., Bot. Tidsskr. 26 (1904) 288, fig. 1.—Type: *n.v.* = *Lomagramma guianensis* (Aublet) Ching, Amer. Fern J. 22 (1932) 17.

For heterotypic synonyms see C. Chr. (op. cit.) and Morton (Contr. U.S. Nat. Herb. 38, 1967, 65).

Note. With the otherwise Asian representatives of the genus *Lomagramma* the present species agrees as to the scandent rhizome, the articulated pinnae, the venation pattern, and the presence of paraphyses between the sporangia. It differs from the other species in the pinnatifid (not entire) terminal segment which is continuous (not artic-

ulate) with the rhachis, and in the well-developed cristate perispore (scarcely visible or absent in the other species). According to Ching (op. cit.) it was Christensen's opinion to segregate the present fern as a distinct genus. Holttum (Gard. Bull. S. S. 9, 1937, 196) excluded this fern from *Lomagramma* and suggested this to be a rather unusually aberrant species of *Bolbitis* only. More recently Holttum (*in litt.*) agreed with Christensen. As the leaf shape can be regarded a retention of a juvenile condition as found in the bathyphylls of Asian species, the assignment of the present species to *Lomagramma* seems the best solution.

**E. 2.** *Bolbitis laciniata* (Hooker) Abeywickr., Ceylon J. Sc. sect. A, Bot. 13 (1956) 22, *nom. invalid.* (Art. 33).—*Acrostichum variable* Hooker var. *laciniatum* Hooker, Spec. Fil. 5 (1864) 277.—*Campium laciniatum* Copel., Philip. J. Sc. 37 (1928) 354, pl. 7.—*Leptochilus laciniatus* Ching, Bull. Fan. Mem. Inst. Biol. 4 (1933) 344. = *Leptochilus decurrens* Bl., see Sledge, Ann. Mag. Nat. Hist. ser. 12, 9 (1956) 865–877.

**E. 3.** *Bolbitis macrophylla* (Kunze) Maxon & Morton, Bull. Torr. Bot. Cl. 65 (1938) 375.—*Meniscium macrophyllum* Kunze, Flora 22 (1839) Beibl. 44.—*Phegopteris macrophylla* Mettenius, Fil. Lechl. 2 (1859), 24, *quoad nomen solum?*—*Nephrodium macrophyllum* Keyserling, Polyp. & Cyath. Herb. Bung. (1873) 48, *comb. illeg.*, *non* Baker in Hooker & Baker, Syn. Fil. (1868) 300.—*Dryopteris macrophylla* C. Chr., Ind. Fil., Suppl. 1 (1913) 35.—Type: *n.v.* = *Thelypteris macrophylla* (Kunze) Morton, Amer. Fern J. 61 (1971) 17.

**Note.** The main argument for Maxon & Morton to exclude this dimorphic fern from *Dryopteris* (*s.l.*, including the thelypteroid ferns) was that the sporangia are not borne on a definite receptacle (as in all other species of this genus) but are regularly distributed over the whole surface. The thelypteroid identity of this fern became irrefutable after the study of the anatomy, the indument, and the spores. After my information (*in litt.*) to Mr. Morton, the fern got its proper place.

**E. 4.** *Bolbitis mollis* (Copel.) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 49.—*Campium molle* Copel., Philip. J. Sc. 37 (1928) 390, fig. 41, pl. 29.—Type: *G. Gardner s.n.*, Brazil ('Ceylon') (K). = *Cyclodium meniscioides* (Willd.) Presl.

**Notes.** 1. Hooker (Spec. Fil. 5, 1864, 262) referred the collection of Gardner to *Acrostichum virens* (= *Bolbitis virens* (Hooker & Grev.) Schott). Hooker supplied a short description of the specimen and thought it 'probably a distinct species'. Copeland newly described this common American fern in a genus which at that time he confined to the Old World.

2. The specimen has been mislabelled; G. Gardner collected in both Brazil and Ceylon (Britten & Boulger, A biogeographical index etc., 2nd ed., 1931, 119).

- E. 5. *Bolbitis neglecta* (F. M. Bailey) Morton, Contr. U.S. Nat. Herb. 38 (1973) 215.—for complete synonymy see Hennipman, Blumea 13 (1966) 397. = *Pteridoblechnum neglectum* (F. M. Bailey) Hennipman, l.c.
- E. 6. *Bolbitis ovata* (Copel.) Ching in C. Chr., Ind., Fil., Suppl. 3 (1934) 49.—*Leptochilus ovatus* Copel., Philip. J. Sc. 9 (1914) Bot. 229.—*Campium ovatum* Copel., Philip. J. Sc. 28 (1937) 354, fig. 9, pl. 6.—*Paraleptochilus ovatus* Copel., Gen. Fil. (1947) 198.—Type: C. J. Brooks 155.S., Sumatra, Bencoolen, Lebong Tandai, ii-1913 (iso in BM). = *Colysis cf. pedunculata* (Hooker & Grev.) Ching.
- E. 7. *Bolbitis rawsonii* (Baker) Ching in C. Chr., Ind. Fil., Suppl. 3 (1934) 49.—*Acrostichum rawsonii* Baker, Ann. Bot. 5 (1891) 496.—*Campium rawsonii* Copel., Philip. J. Sc. 37 (1928) 400.—Type: Sir Rawson W. Rawson s.n., Mauritius, Grand River (K?, n.v.). = *Species incertae sedis*.

Note. Apart from the description nothing is known of this fern. Copeland copied Baker's original description verbatim without comment. Alston (J. Bot. 77, 1939, 283–286) did not mention it. The type specimen which should be at Kew was not traced neither by me nor by Dr. F. M. Jarrett (*in litt.*). I exclude it from *Bolbitis* as according to the description the rootstock is erect.

#### Excluded fossil:

- E. 8. *Bolbitis coloradica* R. W. Brown, U.S. Geol. Surv. Prof. Paper 221—D (1950) 49, pl. 12: fig. 6, 7.—Type: not indicated. = *Astralopteris coloradica* (R. W. Brown) Reveal, Tidwell & Rushford, Brigham Young Univ. Geol. Stud. 14 (1967) 239, pl. 1–6.

Note. Brown placed this Cretaceous fern in *Bolbitis* because of certain resemblances of this fern to *B. macrophylla* (Kunze) Maxon & Morton (= *Thelypteris macrophylla* (Kunze) Morton). Reveal *et al.* regarded it related to *Drynaria* (*Polypodiaceae*) because of properties of the venation pattern. This relationship seems doubtful in view of the derived character of *Drynaria* and the aspecific occurrence of the drynarioid venation within modern leptosporangiate ferns.

## 5. INDEX OF COLLECTIONS

The collections are referred to the number of the taxon in the Taxonomic Part. For mixed collections all indentifications are listed. Cultivated material and unnumbered collections are not included.

Specimens with institutional serial numbers are cited under these series. The collectors, who collected in such a series, are mentioned in the list with a cross-reference to the pertaining series.

Type specimens are marked with (T); they are not necessarily the type of the accepted species, but may belong to one of its synonyms.



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