Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen,
Afd. Natuurkunde, Tweede Reeks, Deel 80

A monograph of the fern genus *Platycerium* (Polypodiaceae)

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North-Holland Publishing Company, Amsterdam, Oxford, New York, 1982

This monograph is dedicated to our friend Pieter (G.J.) de Joncheere in view of his friendship and scientific support during the time we all worked together at the Rijksherbarium, Leiden.

G.J. DE JONCHEERE.

Phot. C.G.G.J. van Steenis, 1955

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Accepted for publication: June 1982

Published: December 1982

ISBN 0-4448 5569-6

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GENERAL PART

1. Introduction and summary

The present monograph deals with the systematics of the genus *Platycerium* (staghorn ferns; Polypodiaceae). It is part of the studies on Polypodiaceae started by the senior author (E.H.) several years ago when working at the Rijksherbarium, Leiden. The junior author (M.C.R.) participated in this study to fulfil part of the requirement for the MSc degree in Biology, University of Leiden.

The genus *Platycerium* has received much attention of systematists in this century. Straszewski (1915) studied the morphology of the sporophyte in detail also postulating relationships. Joe composed a world monograph of the genus (Joe, 1964), a detailed morphological study on the rhizome scales (Joe Hoshizaki, 1970), and a study on the general morphology and phylogeny of the genus (Joe Hoshizaki, 1972). The phylogenetic considerations given by these authors were, however, strongly doubted by the senior author and Mr G.J. de Joncheere who took interest in the genus already long ago. Therefore, it was decided to provide a detailed account on selected morphological features, and to trace phylogenetic relationships following a cladistic analysis. The present study thus includes discussions on the interpretation of morphological properties in the sense of primitive (plesiomorphic) and derived (apomorphic) character states.

As far as the taxonomy of the genus is concerned Joe (1964) recognized 17 species. In the following years two species were reduced to one (De Joncheere, 1968), and two new species were described (De Joncheere and Hennipman, 1970). Important nomenclatural contributions were published by De Joncheere (1967, 1974). These new results were assimilated by Joe Hoshizaki (1970, 1972) who recognized 18 species. In the present study the four species Joe Hoshizaki attributed to the *Platycerium bifurcatum* alliance are reduced to infraspecific taxa of *P. bifurcatum*; accordingly, 15 species are enumerated in this monograph.

The geographical distribution of the taxa has never been studied into sufficient detail before. Our geographical data are based on the herbarium material as far as present in the important herbaria of the world as well as on extensive field work. This makes it possible for the first time to present a detailed geographical distribution of the species occurring in the wild.

Generally speaking the number of collections studied appeared to be rather limited, the herbarium specimens being often incomplete or fragmentary, and mostly badly labelled. Additional to the herbarium material, living material of a number of species was studied by the senior author in the wild in various parts of Asia and in Australia, whereas the rare *Platycerium ridleyi* was studied by the junior author in Sumatra

(Franken en Roos, 1982). Living sporophytes of all species were studied from material grown in botanic gardens. Living material revealed to be of primary importance for the study of the position and overall shape of the fronds as well as for the study of microscopical features. Spores of the living species studied were cultivated in a phytotron at the Leiden Botanic Garden. Knowledge of the juvenile fronds of some species appeared to be essential in relation to establishing transformation series pertaining to frond shape and indument of the rhizome scales.

Further, a large number of photographs of wild and cultivated plants were studied. Amongst these are photographs of two formerly incompletely known endemic species from Madagascar, made by Mr. J. Bogner, Munich. The General Part of this paper incorporates, apart from other subjects, the results of our morphological studies, and the phylogenetic relations in the genus including a cladogram. In the Taxonomic Part the descriptions of the features studied for making the transformation series are given under each of the taxa. This part further includes keys, full synonymy, and geographical distribution of all taxa.

2. Acknowledgements

It is our pleasure to express our gratitude to Mr G.J. de Joncheere who introduced the senior author into this fascinating genus and who put at our disposal all his knowledge and material accumulated by him during many years.

The help of the Directors of the herbaria and the botanic gardens which sent material is greatly appreciated. A number of institutes were visited by (one of) us.

We like to mention the cooperation of the late Dr D.E. Meyer, Berlin; Miss F. Billiet, Brussels; Dr F.M. Jarrett, Dr B.S. Parris, Mr P.J. Edwards, and Mr J. Woodhams, Kew; Mr B. Johns, Lae; Prof. Dr C. Kalkman, Leiden; Mr A.C. Jermy, London; Mr. J. Bogner and Dr A. Kress, Munich; Dr F. Badré, Paris; and Prof. Dr K.U. Kramer, Zürich.

Mr J. Bogner, Munich, provided us with living plants he earlier collected in Madagascar, as well as with numerous photographs of species from Madagascar taken from the wild. The authorities of the Botanic Garden of the University, Leiden, and especially its present director, Dr G.J.M.C. van Vliet, and Mr A. Mulder spent much time and energy in cultivating all stag horn fern species succesfully.

Several colleagues sent spores or juvenile sporophytes for cultivation; others sent photographs of specimens taken from the wild.

Fieldwork in Asia and Australia was possible due to invaluable cooperation of especially Mr B. Gray and Mr D.L. Jones (C.S.I.R.O., Australia); Mr Chamlong Phenghklai (Forest Herbarium, Bangkok, Thailand); Prof. Dr E. Soepadmo (University of Malaya, Kuala Lumpur); Mr Soetrisno Soewoko (P.P.A. Jambi, Sumatra); Director and staff members of BIOTROP, especially Dr Y. Laumonier (Bogor, Java). Invaluable technical help was received from Mr B. Kieft, Leiden (photographs), Mr H. Rypkema, Utrecht (drawings), and Mrs F. Kok, Miss E. Leenart, and Miss W. Sloot (typists at Utrecht).

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

3. Material and Methods

3.1 MATERIAL

Dried specimens were studied from the following herbaria. (The abbreviations follow the Index Herbariorum).

A	The Arnold Arboretum of Harvard University, Cambridge, Mass.
B	Botanisches Museum, Berlin-Dahlem
BM	British Museum (Natural History), London
BO	Herbarium Bogoriense, Bogor
BR	Jardin Botanique de l'Etat, Bruxelles
BRI	Botanic Museum and Herbarium, Botanic Gardens, Brisbane
C	Botanical Museum and Herbarium, Copenhagen
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.
NSW	National Herbarium of New South Wales, Sydney
P	Muséum National d'Histoire Naturelle, Laboratoire de Phanérogamie, Paris
S	Botanical Department, Naturhistoriska Riksmuset, Stockholm
SING	Herbarium of the Botanical Gardens, Singapore
U	Botanical Museum and Herbarium, Utrecht
UC	Herbarium of the University of California, Berkeley, Cal.
US	United States National Museum, Department of Botany, Washington, D.C.
W	Naturhistorisches Museum, Wien
Z	Botanischer Garten und Institut für Systematische Botanik der Universität Zürich

In addition, living specimens were studied from a number of botanic gardens of which the following were in particular important for our studies:

Botanischer Garten und Botanisches Museum Berlin-Dahlem, Berlin
Kebun Raya Indonesia, Bogor (Botanical Gardens of Indonesia)
Royal Botanic Gardens, Kew
Botanic Garden of the University, Leiden
Botanischer Garten, Munich
Botanic Gardens, Singapore
Botanischer Garten der Universität, Zürich

3.2 METHODS

Preparations of scales and spores were made in accordance with Hennipman (1977). Of spores embedded in glycerine jelly the E_1, E_2, and P values are given. Of each species 20 mature spores of three different sheets were measured. Stellate hairs, sporangia and paraphyses were softened in Kodak Foto-Flo 200 (Kramer, 1957), scraped from the dried fronds, and embedded in glycerine jelly.

The measurements of the number, length, and width of the rays of mature stellate hairs as occurring on upper and lower side of the foliage fronds, and paraphyses, the measurements of the sporangia (i.e. length, width, and number of each type of annular cells) are averages of 75 counts, each data set taken from three different specimens of each taxon. Spores, stellate hairs, paraphyses, and sections of the mesophyll of three different specimens of all taxa were also studied with the S.E.M. following standard procedures.

Gametophytes and juvenile sporophytes were grown in a climate room (phytotron) in which tropical lowland conditions were simulated following otherwise standard procedures. Vouchers of cultivated specimens are deposited in the Rijksherbarium, Leiden (L), and in the herbarium of the State University of Utrecht (U).

3.3 METHODOLOGY

According to the theory of phylogenetic systematics as proposed by Hennig (1966, 1975), species can only be grouped together if they share the same derived character states (synapomorphies).

The groups of species delineated, necessarily must be monophyletic, i.e. all species of such a group share a common ancestor, and all descendants and the ancestral species have to be included in that group. This implies that in order to establish monophyletic groups one has to generate a sufficient number of apomorphies connecting different numbers of taxa of the same rank. Usually, a large number of characters must be examined for all species, and the various expressions of a certain feature as found within the genus have to be interpreted in the sense of plesiomorphic (primitive) and apomorphic (derived) character states. Transformation series for each character should be established. A morphological feature is here defined as one of the various morphological structures present that has been given a name or can be shortly described; a morphological character is a feature selected for a particular study.

The cladistic analysis of the present investigation of *Platycerium* includes:

1. Inventarisation of (a great number of) features in order to obtain the number of transformation series necessary for grouping the species in monophyletic groups using the criterion of shared apomorphic character states. It appeared that the herbarium material was not sufficient to meet the requirements for this procedure. Therefore many efforts were undertaken to study living plants in the field and in botanic gardens. This living material allowed us to study, amongst other things, the juvenile fronds, the position, shape, and colour of the base fronds, the position, shape, and number of the foliage fronds, including the number of the soral patches per frond.

2. The denotation of the various character states encountered in terms of plesiomorphic and apomorphic, and the actual establishment of the transformation series for each character by out-group comparison and (where necessary) by ontogenetic or other criteria (De Jong, 1980; Watrous & Wheeler, 1981).

Table 1 provides the various character states for each character, whereas Table 2 gives the character states of all the characters used in this study for all the taxa recognized. See Chapter 5 for explanations.

4. Taxonomic history of the genus

The genus *Platycerium* was created by Desvaux (1827) who enumerated four species, *P. alcicorne, P. angustatum* (= *P. bifurcatum), P. coronarium* and *P. stemaria.* However, the genus dates back to Plukenet (1705, reprinted in 1769) the first botanist who described a *Platycerium* species, using the phrase name ,,Neuroplatyceros aethiopicus, nervosus folii cornu cervinum referentibus'' (= *P. alcicorne*).

Müller (1785) validly described a second species, *Osmunda coronaria* (= *P. coronarium*). Three more species were described in the large genus *Acrostichum*, i.e. *Acrostichum bifurcatum* (Cavanilles, 1799), *A. stemaria* (Palisot de Beauvois, 1803) and *A. alcicorne* (Swartz, 1801).

Gaudichaud (1826) added the tentative name *Alcicornium* (nomen nudum) between brackets to the name *Acrostichum alcicorne* without further comment. As this name is the oldest generic name available, Underwood later (1899, 1905) (incorrectly) accommodated all the species into this genus. Pichi Sermolli (1953) doubted the validity of the name *Alcicornum* and subsequently proposed to treat the name *Platycerium* as a nomen conservandum. In 1954 the Subcommittee for Generic Names of Pteridophyta was of opinion that the name *Platycerium* does not need conservation being the first validly and legitimately published name available. The name *Alcicornium* is illegitimate for reasons elaborately set forth by De Joncheere (1967).

J. Smith (1842) enumerated four species, first mentioning *P. grande*, – an invalidly published name taken from an unpublished MS of A. Cunningham – apart from *P. alcicorne* (with the synonym *P. angustatum*), *P. biforme* (= *P. coronarium*) and *P. stemaria.* In 1875, J. Smith enumerated five species adding *P. wallichii.* This author also typified the genus by *Acrostichum alcicorne* Swartz. Fée (1845) in his 'Histoire des Acrostichées' validated Plukenet's name *Neuroplatyceros*, this being a later homonym of *Platycerium*, recognizing also four species including *Neuroplatyceros grandis* (= *P. grande*). He arranged them into two subgenera, i.e. *Platyceria* and *Scutigera (Neuroplatyceros biformis* = *P. coronarium).*

During the second half of the nineteenth century several species were newly described. Diels (1902) listed 10 species. He placed the genus in the Polypodiaceae, subfam. Acrosticheae – a very unnatural assemblage –, tribe Platyceriinae, in which he also included the genus *Cheiropleuria* (= Cheiropleuriaceae). Underwood (1905) largely followed Diels, but accommodated *Platycerium* and *Cheiropleuria* in the Polypodiaceae, tribe Alcicorniae. This author enumerated 13 species in *Alcicornium* (= *Platycerium*).

Straszewski (1915), a pupil of Goebel, made an extensive morphological study of the genus also using cultivated material. He recognized 17 species including five species here referred to *P. bifurcatum*. Bower (1928) related the genus to a heterogeneity of Polypodiaceae including *Cheiropleuria* and *Dipteris*. Ching (1940) created a new family Platyceriaceae to accommodate *Platycerium* only, and typified the genus by *P. alcicorne* (Willem.) Desvaux. Pichi Sermolli (1953) incorrectly proposed *P. stemaria* as the type species of the genus. The nomenclature of the genus and its type species was lucidly set forth by De Joncheere (1967, 1974). Joe (1964) recognized 17 species, including both *P. wandae* and *P. wilhelminae-reginae* which are synonymous (De Joncheere, 1968), as well as four species in the *P. bifurcatum* alliance.

An important paper (Joe Hoshizaki, 1970) dealt with the morphology of rhizome scales. Joe Hoshizaki (1972) eventually recognized 18 species including the two new species of giant staghorn ferns described by De Joncheere and Hennipman (1970). Details on true *P. grande* were given by Hennipman *et al.* (1977). Nayar (1970) placed the genus together with *Pyrrosia* in Polypodiaceae subfam. Platycerioideae which was accepted by De la Sota (1973). Pichi Sermolli (1977) treated the genus separately as one of the 14 groups he recognized within the Polypodiaceae.

5. Morphology and anatomy; character states

5.1 INTRODUCTION

Representatives of *Platycerium* have been studied in detail by Straszewski (1915), Bower (1928), Joe (1964) and Joe Hoshizaki (1970, 1972). Straszewski analysed living plants grown at Munich, especially those of *P. stemaria* and *P. grande* auct. (= *P. suberbum*). His publication regards the ontogeny of the foliage fronds, the anatomy of the petiole and the mesophyll of the fronds. Joe studied all the species and dealt in particular with the scales, the shape of the fronds, petiole anatomy, soral structure, indument, and juvenile fronds of some species.

The present study also covers all the species. We have concentrated on the morphology of the rhizome scales including the marginal and abaxial scale indument, the shape of the fronds, soral structures including detailed LM and SEM studies of stellate hairs, sporangia, spores, and paraphyses. The characters selected for this study and their character states are given in table 1 and 2. The numbers given in these tables correspond to the numbers of the properties as given in the following description of the respective morphological characters. The designations plesiomorphic and apomorphic are proposed as a result of outgroup comparison, and – in some cases – as a result of knowledge of the ontogeny of the character states as seen in mature parts (*i.e.* parts as occurring in specimens showing meiospores).

5.2 RHIZOME

The rhizome is stout, cilindrical or dorsiventrally flattened, short, in most of the species capable to vegetative reproduction, densely set with often conspicuous scales. Joe Hoshizaki (1972) recognized two different types of steles, *i.e.* the dictyostele proper and the polycyclic-dictyostele. Both types of steles are present in *P. bifurcatum*. From her drawings it appears that relevant anatomical structures, *e.g.* the width of the vascular strands, show variation within one taxon. For this reason and for practical reasons, a detailed study on the rhizome anatomy was omitted.

5.3 SCALES

5.3.1 *Introduction*

In the literature but little attention has been paid to the study of the scales of *Platycerium* except Joe Hoshizaki (1970). This author was the first to describe the morphology of the scales of all the species in detail as seen from cultivated material. She convincingly demonstrated the great variation in the general and microscopical structures of the scales. As her interpretation of the data on scales played an important role in her phylogenetic classifications, scales were included amongst the properties of the sporophytes selected for our studies. Mature scales of herbarium specimens of wild material as well as scales taken from living and cultivated plants preserved on F.A.P.A. of all the species were studied.

In *Platycerium* scales occur on the rhizome and the phyllopodia of the foliage fronds only. They are most conspicuous on the apex of the rhizome. Within one species they may vary somewhat in the morphology and anatomy depending on age. Mature scales are here defined as the scales with an indument showing mature glandular cells. Old scales usually show loss or senescence of the indument and marginal zone, as well as increased lignification of the cell-walls, particularly of those cells that form the so-called 'midrib' (better called pseudo-midrib), if present. A midrib comprises a central row of blackish sclerenchyma cells, which in a few species is divided into two ridges in the lower half.

The indument of the scales comprises 1-celled glandular or non-glandular trichomes, and uniseriate branched or unbranched hairs. The hairs of the scales are generally set densiest and are (slightly) better developed morphologically in the upper half; these hairs were studied. In all the species linear, small-sized, membranous, and otherwise undifferentiated scales ('fibrils', Joe Hoshizaki, 1970) occur scattered between the mature ones. The aberrant scales are here regarded as normal scales which are arrested in their development at an early age.

5.3.2 *Properties of the scales*

Character no. 1. Size and marginal zone

A number of species (*P. coronarium*, the species of the *P. grande*-group, and *P. ridleyi*) have relatively large-sized scales not found in *Pyrrosia* (or elsewhere in the Polypodiaceae). Two different types of large-sized scales are recognized, one with the margin not differentiated like in the small-sized scales (Table 1:1a), and one with a so-called flabelloid margin (Table 1:1b). The latter type of scale is a remarkable apomorphic structure. Joe Hoshizaki (1970) suggested that the flabelloid margin arose through lateral fusion of free marginal cells followed by fusion of hairs: "If the free hairs in a non-flabelloid margin unite, a very broad, flabelloid margin as found in *P. coronarium* and *P. ridleyi* is formed. The cells of these broad flabelloid margins are orientated like many of the 'free' marginal hairs in *P. grande* [= *P. suberbum*]". This seems indeed a probable mechanism. It is, however, unlikely for two reasons that glandular hairs as found in the *P. grande*-group are involved. First, the multicellular marginal hairs of the scales of *e.g. P. suberbum* are usually not terminated by a glandular cell. Second, the hairs of the scales of *P. superbum* are inserted in a marginal zone, whereas the insertion of the flabellum and its glandular trichomes is strictly marginal. Hairs inserted in this way as well as strictly glandular hairs are a characteristic of *P. bifurcatum*. Moreover, this species has hairs that gradually increase in length towards the apex. A situation parallelled by the flabelloid margin, which also widens towards the apex.

Character no. 2. Shape of the apex

The acute to filiform apex terminated by a glandular 'hair', also present in the outgroup *Pyrrosia*, is selected as the plesiomorphic state. Scales with rounded apices still show the, often less conspicuous, apical hair. It is noteworthy that in *P. wallichii*, the scales of which lack a marginal indument, this apical hair is always present.

Character no. 3. 'Midrib'

A number of species have scales with a medially situated, longitudinal midrib. Such a midrib is otherwise absent from the scales of the Polypodiaceae. Its presence in *Platycerium* is intuitively regarded an apomorphy of the genus and consequently a plesiomorphy within the genus in view of the occurrence of more complex large-sized scales without a midrib (*P. grande, P. holttumii,* and *P. suberbum*), or with an even more complex structured midrib (*P. coronarium* and *P. ridleyi*). Functional outgroup comparison within the genus suggests the latter two types of scales to represent two different apomorphies (Table 1: 3a, 3b). The scale with a midrib as supposed to be present in the ancestral species is retained in *P. alcicorne, P. ellisii* (= *P. alcicorne*-group); *P. bifurcatum* (= *P. bifurcatum*-group p.p.); *P. elephantotis, P. wallichii* (= *P. elephantotis*-group); *P. quadridichotomum* (= *P. andinum*-group p.p.); *P. stemaria* (= *P. stemaria*-group); *P. wandae* (= *P. grande*-group p.p.).

Character no. 4. Place and insertion of the hairs

Hairs are variously inserted on the scales. In most of the species the hairs are inserted marginally and – though not always easily perceivable – abaxially as in the scales of *Pyrrosia* (Nayar, 1961). This condition is therefore regarded as plesiomorphic. The conditions showing the hairs inserted exclusively marginally (Table 1: 4b), or inserted in a narrow marginal zone (Table 1: 4a), are regarded apomorphic states.

Character no. 5. Marginal indument

The absence of an indument in *P. wallichii* is regarded a reduction, in view of the homologous occurrence of indument in *Pyrrosia*, consequently representing an apomorphic state. On the margin of the scales of this species small projections occur ('papillae', Joe Hoshizaki, 1970).

Character no. 6. Implantation of the indument

In view of the densitites of the marginal hairs on the scales as seen in *Pyrrosia* (and in the other Polypodiaceae), we regard the situation in which these hairs are proportionally very densely set (in the *P. grande*-group), as an apomorphic state.

Character no. 7. Shape of the trichomes

The several types of indument as present in *Platycerium* are different from those found in the sister genus *Pyrrosia*. Using ontogenetic data (see Chapter 5.3.3.), the presence of 1–6-celled, branched and unbranched, glandular and non-glandular hairs without protuberances (small projections of the cells of the hairs) is regarded to represent the plesiomorphic state. Three apomorphic states are recognized, which could not be classified into a single transformation series. They are regarded specializations in three different phylogenetic lines (see Table 1:7a–c).

5.3.3 *Notes on the indument of the scales in relation to the ontogeny of the indument of the fronds*

The hairs on the scales of some species may have terminally two (or several, Joe Hoshizaki, 1970) acicular apical cells, a condition approaching the stellate hairs as found on the juvenile fronds. Joe Hoshizaki (1970) and Stokey & Atkinson (1954) therefore discussed the relationship between the stellate hairs of the fronds and the hairs on the scales. Already Straszewski (1915) studied the indument on the first sporophytic fronds of *P. stemaria.* He was of opinion that the stellate hairs developed from 1-celled glandular trichomes ('Die Primärblätter sind .... mit Sternhaaren besetzt, welche sich aus zuerst einzelligen Drüsenhaaren entwickeln'). Joe Hoshizaki agreed with Straszewski, stating that the development of the stellate hairs starts as 'a glandular cell which divides apically into successive glandular cells that elongate and flatten into rays'. However, this could not be confirmed by the present authors. We find that the first formed fronds of *Platycerium* (and *Pyrrosia* species) show a fascinating diversity of increasingly complex hairs.

When studying the hairs of successive juvenile fronds, all kinds of intermediates can be found between a 1-celled glandular trichome and the mature, non-glandular, stellate hair. According to our observations, the first trichomes formed on the juvenile fronds are glandular cells. More complex stages of the trichome include a 2-celled glandular hair, a 3-celled hair consisting of a basal cell bearing either two glandular cells, or a glandular and a non-glandular (acicular) cell, or two non-glandular cells. The juvenile stellate hairs of the juvenile fronds include trichomes and hairs, which are ± similar to the hairs found on the scales of part of the species. These different morphologies point to the suggestion that the glandular and non-glandular apical cells found on the trichomes are homologous structures which formation seems primarily determined by the developmental phase of the juvenile frond. In our evaluation of the features of the scale we have regarded the types of indument, consisting of 1–6-celled, branched and unbranched, glandular and non-glandular hairs, similar to the variety of hairs found on the juvenile sporophytic frond, to represent the plesiomorphic condition. This condition is found on the scales of *e.g. P. andinum, P. elephantotis* and *P. stemaria.* Three different apomorphic character states are here regarded scales that have branched hairs the cells of which bear protuberances, scales that have unbranched hairs, and scales with either 1-celled trichomes or without any indument.

From the study of the juvenile stellate hairs it becomes likely, that the different types of hairs as found on the scales, can be understood best in terms of arrested (neotenic) development followed by successive morphological radiation. This result is quite different from that of Joe Hoshizaki (1970) who did not provide an unambiguous transformation series as regards the scale-indument. She explains the various types of hairs on the scale, starting from the three 'lines of evolution' which are intuitively based: 'Only after I had arrived at the probable evolution of the species did I examine the rhizome scales in detail to determine how their features correlated with the patterns I had determined.' (p. 144).

5.4 THE FRONDS

5.4.1 *Introduction*

Frond dimorphism of the genus is eye-catching and a striking apomorphy. Although this feature has developed parallelly in other ferns, its extent in *Platycerium* is not only unique for the Polypodiaceae, but for the leptosporangiate ferns as a whole. It seems to have been developed to meet the various biological functions of plants living in a particularly extreme habitat (see Chapter 7). According to Joe Hoshizaki (1972) and others, this dimorphism is a response to the epiphytic habitat, ensuring better absorption of water and nutrients by humus collection as well as a better protection of the roots (see also Chapter 7). Presumably associated with this is the loss of the photosynthetic functions of the base fronds of some species.

Joe Hoshizaki (1972) was the first to give a general survey of the morphology of the fronds of all species. She discussed base and foliage fronds in relation to each other and in relation to the 'lines of evolution' she recognized. As regards the terminology of the fronds we follow Joe Hoshizaki, who in her latest publication (1972) used the terms 'base fronds' and 'foliage fronds' (which are structurally very different). During our studies we have come across large variations in the morphology of the heteroblastic fronds as occurring in different species.

5.4.2 *Properties of the base fronds*

Base fronds are fronds that are non-articulate to the rhizome, usually sessile, rarely shortly stalked, at least with the basal part appressed to the substratum, sterile and persistent, veins prominent or immersed. The base fronds of one specimen together constitute either a ± spherical 'nest' or a more or less conspicuous 'basket'.

The lower part of the base frond is rather uniform in shape, the margin varying from entire to sinuate. A very conspicuous feature of the greater part of the species regards the fringe, a membranaceous, foliaceous, curled 'frill' or 'collar' situated near to or around the place of insertion. The shape of the upper part of the base frond is much diversified, varying from ± round to wedge-shaped, either (intricately) lobed or entire.

Character no. 8. Way of attachment; prominence of veins

These two features are treated together as both are related to the vascularisation of the frond. Two different apomorphic states are recognized by functional out-group comparison within the genus, each occurring in one species only, i.e. fronds inconspicuously stalked, veins forming a waffle-pattern (Table 1:8a), and fronds more or less conspicuously stalked, veins not forming a waffle-pattern (Table 1:8b).

Character no. 9. Colour of mature fronds

The condition in which the base fronds retain their assimilating function until new fronds are formed represents the plesiomorphic state. Consequently, base fronds which become brown soon after maturation, obviously functioning primarily to support the root function of the plant, display an apomorphic state (Table 1:9a). Brownescence of the base fronds does not seem to be an adaptation to a dry season: in monsoon Thailand *P. holttumii* (green base fronds) locally grows intermingled with *P. wallichii* (brown base fronds). The base fronds of these species are elaborately lobed which makes the statement of Joe Hoshizaki (1972) unjustified, that only base fronds with reduced foliar extensions turn brown rather early.

The characteristic dark green colour of only the mature base fronds of *P. madagascariense* obviously represents another apomorphic state.

A different interpretation of the colour of the base fronds seems possible. It starts from the idea that the fronds of the ancestral species primarily supported the root function irrespective of a possible continuation of the (additional) function of the base fronds as an assimilating organ. In case the ancestral species had brownescent base fronds, green base fronds necessarily developed secondarily and independently in different phylogenetic lines, which is less parsimonious.

Character no. 10. Position of the old fronds

Recurving old base fronds are found in the species with large-sized lobed base fronds. The old base fronds turn brown and bend inwards after the formation of new ones; they eventually decay together with the litter caught during their life. The (mechanical?) process of recurving is not well understood. In view of out-group comparison it is an apomorphy.

Character no. 11. Water storage tissue. Plate 9b

According to functional out-group comparison in *Platycerium* the original condition of the mature mesophyll is represented by well-developed, cork-like parenchyma tissue rich in intercellular spaces. Two different states have developed, i.e. loss of water storage tissue (Table 1:11a; *P. madagascariense* and *P. ridleyi*), and elongation of the cells in the basal region of the base fronds due to increase of intercellular spaces (Table 1:11b; *P. coronarium* and *P. elephantotis*).

5.4.2.1 Upper part of the base frond

Character nos. 12, 13. Position, shape, and incisions. – Fig. 1

The possibly related genera in the platycerioids lack the differentiation of the fronds into base fronds and foliage fronds, so well-developed in *Platycerium*. The ancestral condition of the base frond in the present genus presumably comprised undifferentiated, (tufted!) erect fronds, a situation which is found in part of the mature members of *Pyrrosia* and other Polypodiaceae. In *Platycerium* such a condition is commonly found in juvenile plants, which often have lanceolate fronds, the base of which (narrowly) wedge-shaped or acute, the venation monopodial (!) (Stokey & Atkinson, 1954). Such fronds, but with an anastomosed venation, may be formed by (much) older plants as well (e.g. *P. elephantotis* and *P. stemaria*). Within the genus we distinguish the following types of base fronds:

- fronds with a well-developed, markedly erect, wedge-shaped upper part which is either entire (*P. elephantotis, P. quadridichotomum*, and *P. stemaria*), or provided with two main, erect lobes (*P. andinum*) (Fig. 1: Alternative 1:p, Alternative 2:b).
- fronds appressed, kidney-shaped, margin entire or slightly lobed (*P. alcicorne, P. bifurcatum* p.p., *P. ellisii, P. madagascariense*, and *P. ridleyi*) (Fig. 1: Alternative 1:a; Alternative 2:p).
- fronds with a well-developed, markedly erect, elliptical upper part with many dissimilar lobes (*P. bifurcatum* p.p. and *P. coronarium*) (Fig. 1: Alternative 1:a'; Alternative 2:a).
- fronds like the first type given above, but with many ascending lobes of varying shape (*P. wallichii*) (Fig. 1: Alternative 1:b; Alternative 2: b-a).
- fronds with a well-developed, spreading, wedge-shaped upper part with many similar lobes (*P. grande, P. holttumii, P. superbum*, and *P. wandae*) (Fig. 1: Alternative 1:c; Alternative 2: b-b).

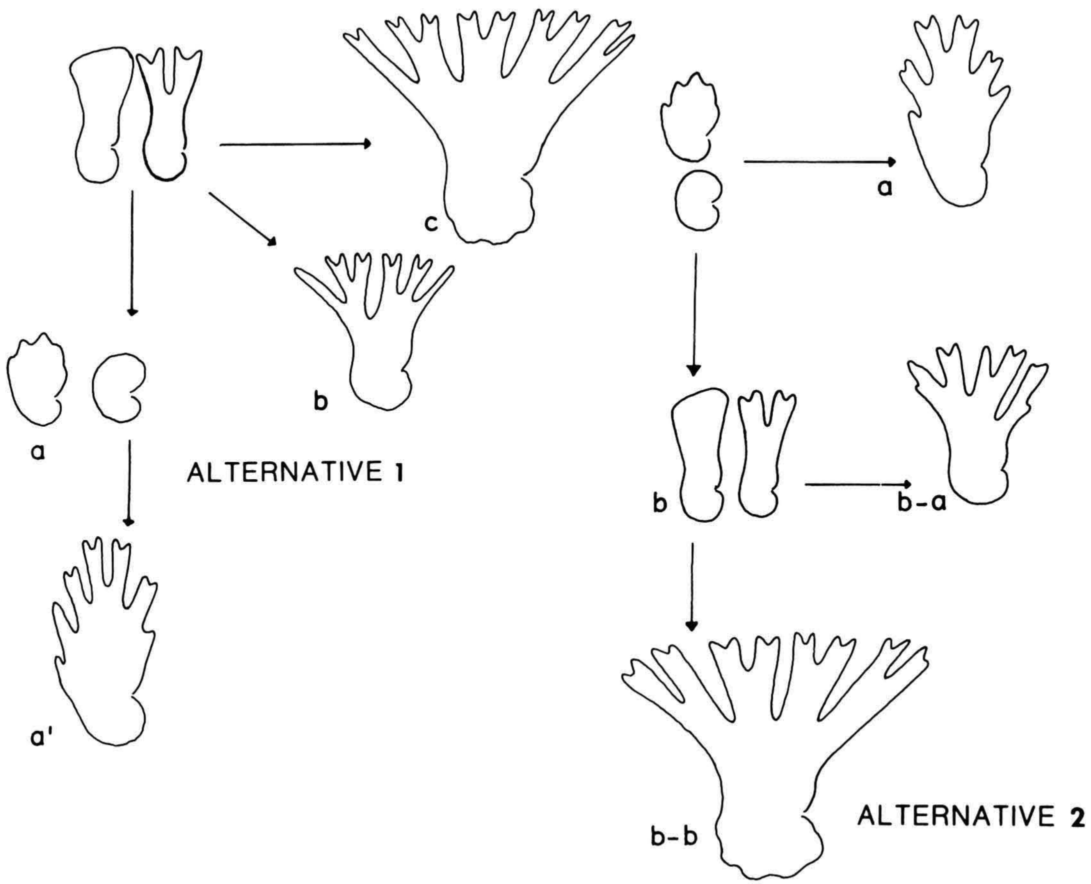

Fig. 1. Two alternative transformation series for the character states of character nos. 12, 13: position, shape, and incisions of the base frond.

– a. Alternative 1, the plesiomorphic condition being a base frond with an erect upper part. – b. Alternative 2, the plesiomorphic condition being an appressed kidney-shaped base frond. The symbols refer to the character states mentioned in the text and in Table 1.

When trying to understand these different types as plesiomorphic or apomorphic character states, the following observations are of interest. Detailed examination of the base fronds of *P. coronarium* and those of the *P. grande*-group revealed them to be essentially different; those of *P. coronarium* being similar to those of *P. bifurcatum* ssp. *willinckii*; those of the *P. grande*-group rather resembling those of *P. andinum*. Joe Hoshizaki (1972) did not differentiate between the base fronds of *P. coronarium* and those as found in the *P. grande*-group, which she regarded similar.

The juvenile base fronds of the *P. grande*-group show that entire, ± appressed, and ± erect, kidney-shaped base fronds precede the multi-lobed giant fronds formed later during their development. Joe Hoshizaki (1972, Pl. 2:21, 23) already nicely demonstrated the blastogeny of the base fronds of *P. suberbum* (and of *P. alcicorne*), which could be confirmed.

Further, the fronds of the species of the *P. grande*-group are unique having the uppermost parts of the fronds horizontally spreading, forming both a majestic basket and a 'roof' under which the foliage fronds develop. This is a significant difference with the base fronds of *P. wallichii* which are at first sight rather similar as to the overall shape. The overall similarity in the morphology of the base fronds of the *P. alcicorne*-group and the *P. bifurcatum*-group (type b, c) does not indicate sister group relationship (see below, Alternative 2).

Using the morphological data given above, it is possible to provide two different transformation series, the first of which seems the most likely one. This transformation series (Fig. 1a) starts from the idea that base fronds with an erect upper part represent the plesiomorphic condition as during ontogeny (Joe Hoshizaki, 1972, pl. 2:21, 23) the formation of laterally inserted, ± kidney-shaped base fronds is preceded by (more) basally inserted, ± erect fronds. From this condition three different apomorphic character states resulted. This hypothesis does imply monophyly of the species with base frond types b and c.

The second transformation series (Fig. 1b) shows the kidney-shaped base frond to be plesiomorphic. The sole argument for this is that during maturation of base fronds produced by mature plants, the young (not juvenile!) base fronds are at first kidney--shaped, the foliar extensions of which developing later.

It is of interest to note that the kidney-shaped base fronds are always found growing appressed to the substratum, a growth habit surely representing a derived condition. In case the kidney-shaped fronds are structurally associated with an appressed habit (what seems plausible), the kidney-shaped fronds, consequently, also represent an apomorphic state.

Joe Hoshizaki explained the morphological variation in terms of an archetype. She regarded the most foliaceous, so-called generalized frond, the ancestral state, a frond she regarded close to the frond present in e.g. *P. wandae, P. andinum*, and *P. stemaria*. On the other hand, entire fronds like present in e.g. *P. elephantotis, P. stemaria*, amd *P. alcicorne*, were regarded as characteristics of 'advanced' species. According to her reasoning the frond shape as found in *P. bifurcatum* ssp. *willinckii* should represent the ancestral state from which the appressed type of base frond as found in the other subspecies can be derived.

Following the above statement that the frond-shape as occurring in *P. elephantotis* and *P. stemaria* is the plesiomorphic condition, it can be accordingly suggested that the basket as occurring in these species, also represents a plesiomorphic condition if compared with the ± spherical nest as occurring in the species of the *P. alcicorne*--group and in *P. ridleyi*, and the elaborate basket as found in the species of the *P. grande*-group, *P. coronarium*, and *P. wallichii*. Obviously, the ancestral species with a basket as found in *P. elephantotis* and *P. stemaria* gave rise to species with two different strategies as far as the collecting of external material is concerned.

1. The increase of the significance of the basket for the collecting of external material leading to the gigantic basket (the species of the *P. grande*-group, *P. coronarium*, and *P. wallichii*). 2. The loss of the capacity of the basket to collect external material, the mineral and organic food being supplied solely by insects and other animals inhabiting a ± spherical nest (*P. alcicorne, P. ellisii, P. madagascariense,* and *P. ridleyi*).

5.4.2.2 Lower part of the base frond

Character no. 14. Margin

Resulting from functional out-group comparison, an entire margin is regarded the plesiomorphic condition. Two different apomorphic states are recognized, i.e. the sinuate margin as found in the species of the *P. grande*-group and a denticulate margin (*P. madagascariense*).

Character no. 15. Fringe ('collar', 'frill'). Plate 7

A number of species have developed a more or less distinct fringe. Three different apomorphic types are recognized in view of differences in position (situated around the stipes or above the stipes only), and margin (sinuate or denticulate). The fringes as found in the *P. grande*-group and in *P. madagascariense* are very characteristic. The fringes as occurring in *P. andinum, P. coronarium, P. elephantotis, P. stemaria,* and *P. wallichii* are only conspicuous in large-sized specimens. See also Chapter 6.2: Parallel developments.

5.4.3 Properties of the foliage fronds and the soral patches. – Fig. 2–4

Foliage fronds are fronds that are articulated to the rhizome, stalked, erect or pendulous, usually fertile, and deciduous. The sporangia are always arranged in an

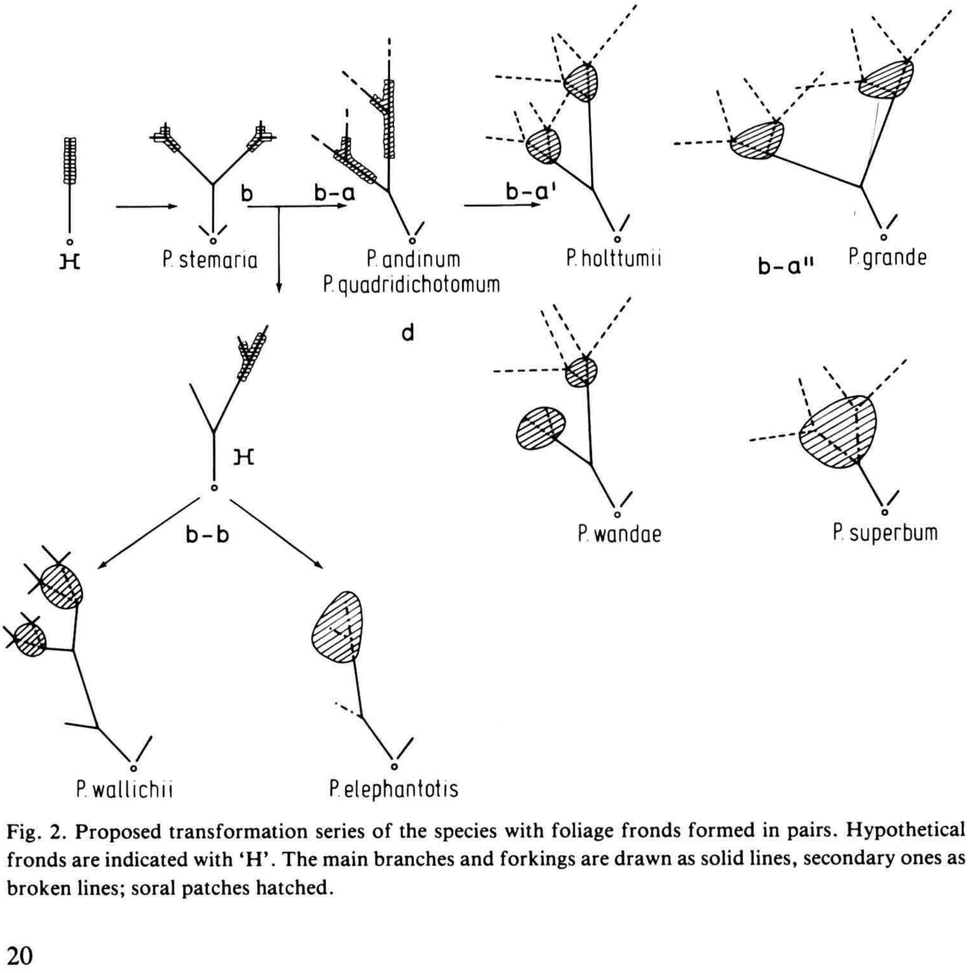

Fig. 2. Proposed transformation series of the species with foliage fronds formed in pairs. Hypothetical fronds are indicated with 'H'. The main branches and forkings are drawn as solid lines, secondary ones as broken lines; soral patches hatched.

acrostichoid pattern, i.e. they are inserted in indefinite numbers and order close together covering more or less large areas of the lower surface of the lamina. The shape and location of this so-called 'soral patch' shows variation.

As to shape the foliage fronds show great diversity. The general symmetry of the frond may be either symmetrical or asymmetrical. Some species have entire fronds with the soral patch situated terminally (somewhat away from the margin). Other species display a lamina which consists of dichotomously branched laminar straps. Still other species have a complex lamina consisting of a basal wedge-shaped part bearing the soral patch(es) apart from a terminal part comprising dichotomously branched lateral segments ('appendages'). A most remarkable lamina is the one composed of elaborately dichotomously branched laminar straps apart from a stalked shell-shaped or spoon-shaped soral patch ± laterally situated in the basal part.

The shape, including the lobing pattern of the mature fronds in *Platycerium* is determined by the formation of a number of ± equally well-developed meristems instead of one main apical meristem as is the rule in ferns. As a consequence the mature fronds of *Platycerium* lack a midrib or rhachis showing several 'primary' veins instead. It is of interest to note that the first formed juvenile fronds of *Platycerium* are ± symmetrical, entire, still showing a distinct rhachis. From the above it is concluded that the absence of one main (apical) meristem in mature plants of *Platycerium* should be regarded as an apomorphy of the genus.

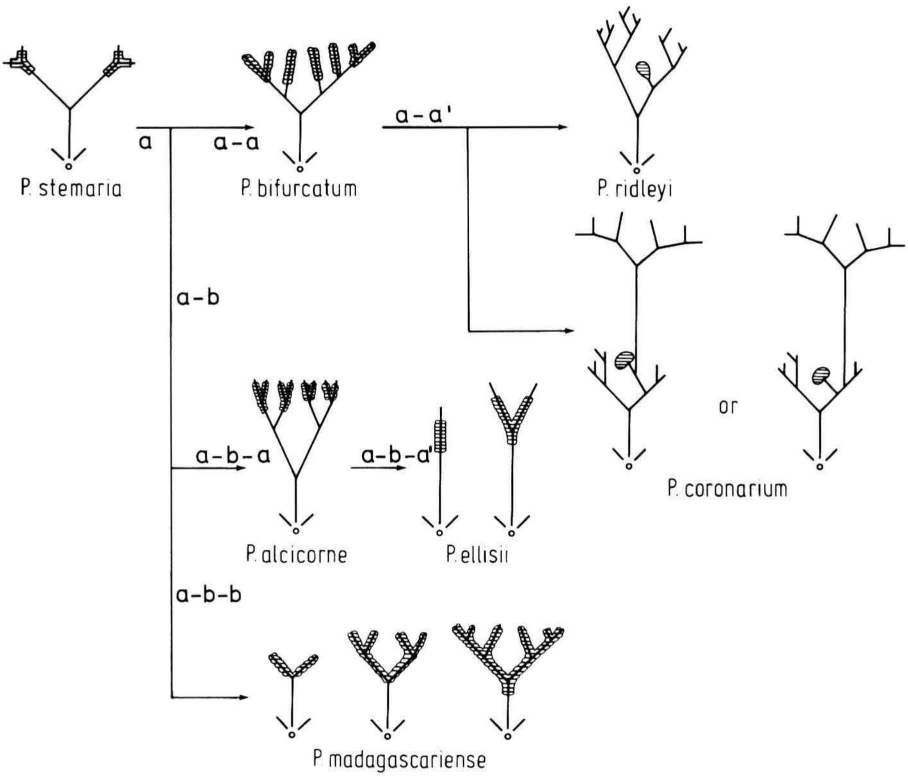

Fig. 3. Proposed transformation series of the species with foliage fronds formed in an undetermined number. The main branches and forkings are drawn as solid lines, secondary ones as broken lines; soral patches hatched.

Foliage fronds are produced either in pairs or in an indefinite order. When produced in pairs, the two fronds may be arranged side by side in one plane, each of them constituting the usually asymmetrical half of a symmetrical pattern ('bilateral symmetrical pattern').

Character no. 16. The number of fronds maturing at the same time

In part of the species the number of fronds formed at regular intervals (e.g. the start of the dry season: *P. wallichii,* Plate 1, 8b) is two, whereas in other species – like in *Pyrrosia* and in other Polypodiaceae – the number of fronds formed is undetermined (e.g. *P. bifurcatum,* Plate 3). The latter condition is a plesiomorphy.

It is noteworthy that in species with fronds formed in pairs the two fronds are arranged in a bilateral symmetrical pattern. This arrangement is regarded an apomorphic state. The species with an undetermined number of fronds formed at a time, also have their foliage fronds arranged in two rows, but there is no bilateral symmetrical pattern formed by neighbouring fronds.

Character no. 17. Development of the fertile and sterile segments

The shape of the mature fronds is arrived at in two ways. In the *P. andinum*-group and the *P. grande*-group the ultimate segments are formed after completion of the initiation of the soral patches (Plate 8a). In the *P. andinum*-group the secondary elongation follows the existing frond architecture, whereas in the species of the *P. grande*-group so-called secondary branches ('lateral appendages') are formed on the foliage frond. In the other species (and in the sister genus *Pyrrosia*) the initiation of the ultimate branches occurs simultaneously with the initiation of the soral patches.

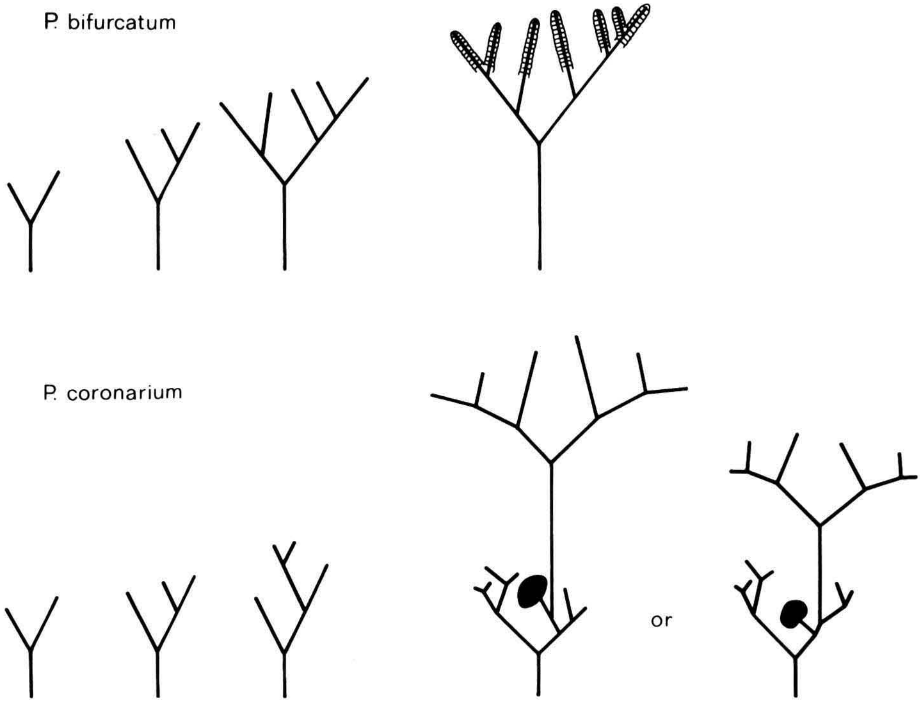

Fig. 4. Frond shape of the successive foliage fronds formed during ontogeny of the sporophytes of *Platycerium bifurcatum* and *P. coronarium.*

Character no. 18. Shape. – Fig. 2, 3

The simplest type of frond, the entire frond, is found in *P. elephantotis* (Plate 6; Fig. 22a). This frond does not represent the plesiomorphic condition, being unique for its broadened oblique upper part.

Entire, lanceolate, acute or once-forked fronds are a characteristic of *P. ellisii* (Fig. 13a). The entire fronds remind those of certain *Pyrrosia* species in general outline. Similar fronds also occur as juvenile fronds in *P. alcicorne, P. bifurcatum,* and *P. stemaria*. One may postulate that the shapes of the mature fronds of the latter three species are further elaborations of the fronds as found in *P. ellisii*. However, this does not seem to be correct for two reasons. First, *P. ellisii* occurs in a rather extreme habitat in Madagascar where a reduction (arrestment) of the fronds could be anticipated as a probable adaptation. Second, *P. ellisii* is synapomorphic with *P. alcicorne* (and not with *P. bifurcatum* and *P. stemaria*) for the character nos. 7 and 31. As a result of outgroup comparison we like to propose an alternative view which implies that the frond of *P. ellisii* is a derivation of a frond as found in *P. alcicorne*, hence representing an apomorphic state.

The type of foliage frond that follows next as to morphological complexity is the frond as found in *P. stemaria* (Fig. 27a). This type of frond may have arisen through hypothetical frond shapes which are characteristic for mature *P. ellisii* (Fig. 3).

The foliage fronds of *P. ellisii* and *P. stemaria* show variation as to their symmetry: both symmetrical and asymmetrical fronds are being formed. Strictly symmetrical fronds are formed in the sister genus *Pyrrosia*, and therefore it may seem obvious to regard the symmetrical frond as found in some *Platycerium* species to represent the plesiomorphic condition. However, as pointed out above, the morphology of the fronds in *Platycerium* is determined by the presence of several ± equally well-developed apical meristems. Consequently, a frond-shape showing some instability as to its symmetry reflecting the undetermined distribution of apical meristems which might have been present when the original apical meristem was replaced, may represent the plesiomorphic condition in the genus. Both consistently ± symmetrical fronds as well as asymmetrical fronds then are apomorphic states.

If we start from a foliage frond as present in *P. stemaria* two main lines of frond differentiation can be distinguished.

The first line shows fronds with a pattern of lobing which is rather similar to the 'Rhacopteris type of overtopping' as defined by Zimmermann (1959) for branching patterns. The simplest shape of this line is represented by the fronds of *P. andinum* (Fig. 15a) and *P. quadridichotomum* (Fig. 15b; both with secondary growth of segments; see character no. 17). A frond with a shape like this may have developed into two different sublines, *i.e.* the fronds as found in the *P. grande*-group, and the fronds as present in *P. wallichii* and *P. elephantotis* (Fig. 2).

The species of the *P. grande*-group show much variation as to frond-shape. Two species of this group, *P. grande* (Fig. 24a) and *P. superbum* (Fig. 29a), have symmetrical fronds which seems a secondary development. The fronds of *P. superbum* showing one soral patch only, may have originated from fronds with two soral patches each on one of the main lobes, either by reduction of one lobe or by fusion of the two lobes. The fact that juvenile fronds of *P. superbum* are symmetrical as well as the observation by Joe Hoshizaki (1972) and ourselves, that occasionally undeeply lobed symmetrical foliage fronds are formed in specimens of this species kept in cultivation, suggests a process of fusion rather than a process of reduction alone.

The species representing the second subline, *P. elephantotis* (Fig. 22a) and *P. wallichii* (Fig. 22e) (= the *P. elephantotis*-group), have one of the two main branches either absent (*P. elephantotis*) or reduced into an entire to twice-forked, relatively small, sterile segment (*P. wallichii*). This interpretation of the frond shape of *P. wallichii* is supported by the morphology of its juvenile and young fronds which show (the initiation of) these two main branches to be present at a time before the differentiation of the one main lobe into two fertile branches has taken place. The formation of the two fertile segments is a later differentiation following the branching of the frond into main segments, the further development of one of these being retarded later.

In *P. wallichii* the marginal forkings of the fronds are formed simultaneously with the soral patches. In *P. elephantotis* such elaborations are absent. It is difficult to ascertain if the marginal forkings of the fronds of *P. wallichii* represent a plesiomorphic or an apomorphic state. It seems possible that the foliage frond of the ancestral species of *P. wallichii* and *P. elephantotis* were less elaborately lobed than those of *P. wallichii*. The asymmetrical foliage frond of *P. elephantotis* is an apomorphic development, resulting from either a complete reduction of one main branch and subsequent fusion of the remaining segments, or by fusion alone.

The tendency of fusion of segments seems a characteristic of the species of this line. In agreement with this is the observation that the first formed, rather small-sized, foliage frond of *P. grande* in cultivation at Leiden, was far more deeply divided into two main (fertile) lobes than were the much larger foliage fronds formed later.

The second line of frond differentiation also starts with a frond type as found in *P. stemaria*. Fronds of this line are always formed in undetermined numbers. Using the criterion of symmetry, two main groups of species can be distinguished.

More or less symmetrical fronds are found in *P. alcicorne* (Fig. 13e), *P. ellisii* (Fig. 13a), and *P. madagascariense* (Fig. 27e), the condition being least stable in *P. ellisii*. The pattern of lobing of the fronds of *P. madagascariense* resembles that of *P. alcicorne* except for the largest-sized fronds. The lobing pattern of these recalls that found in *P. bifurcatum* var. *hillii*, obviously a parallel development. The symmetry of the fronds of *P. alcicorne* is rather consistent, and represents an apomorphic state. It is far less consistent in its juvenile fronds which recalls the situation as found in *P. ellisii*.

The fronds of *P. bifurcatum* (Plate 3; Fig. 17a, e; Fig. 18a, e), *P. coronarium* (Fig. 20e), and *P. ridleyi* (Fig. 20a) are basically asymmetrical. The juvenile fronds of *P. coronarium* and those of *P. bifurcatum* (Fig. 4) are similar, which makes them part of the same transformation series. The basally situated main lobes of the foliage fronds of *P. coronarium*, and the foliage fronds of *P. ridleyi* show a pattern of lobing which is rather similar to the 'Sphenopteris type of overtopping' (Zimmermann, 1959), the distal main lobe of *P. coronarium* has a pattern of lobing analogous to the 'Adiantum type of overtopping' (Zimmermann, 1959). The shell-shaped soral patch as found in *P. coronarium* and *P. ridleyi* is a striking apomorphic structure, probably homologous with one ultimate fertile lobe of a *P. bifurcatum*-like frond. In this connection, it is noteworthy that the ± 10 cm long, young, foliage fronds of *P. elephantotis* are spoon-shaped. Obviously this is a result of a process whereby the increase in size of the apical region is less than the increase in size of the other parts. The processes underlying this may be also present during the formation of the fertile lobes in *P. coronarium* and *P. ridleyi.* If compared with the fronds of *P. stemaria*, the fronds of all the species of this second line, except those of *P. ellisii* (which represents a reduction, see above) show an increase in the number of ultimate lobes (an apomorphic state of this group) rather than an increase in fusion of segments (which is the case, as already mentioned, in the species of the first line).

In conclusion, the above observations make it possible to arrange the fronds of all the species except those of *P. stemaria* in the following types (the symbols refer to those mentioned in Fig. 2, 3, and Table 1):

a.	Fronds with a fixed (a)symmetry, and with many primary forkings.
a-a.	Fronds asymmetrical, ± 3-times forked, growth of sterile segments after formation of soral patches absent.
a-a′.	Ibid.; fronds more than 3-times forked.
a-b.	Fronds symmetrical, 0–3-times forked, growth of sterile segments after formation of soral patches absent.
a-b-a.	Ibid.; 2–3-times forked, ultimate lobes ± equally-long.
a-b-a′.	Ibid.; fronds ± symmetrical, 0–1-times forked.
a-b-b.	Fronds symmetrical, 1–3-times forked, ultimate lobes often unequally-long, growth of sterile segments after formation of soral patches absent.
b.	Fronds with a fixed asymmetry, with two main branches, with or without growth of sterile segments after formation of soral patches.
b-a.	Fronds asymmetrical, 2–4-times forked, elongation of sterile segments after formation of soral patches present.
b-a′.	Ibid.; with two main branches; which become elaborately branched after the formation of soral patches.
b-a″.	As b-a′, but fronds secondarily symmetrical, either undivided or with two main branches.
b-b.	Fronds asymmetrical, one main branch reduced, growth of sterile segments after formation of soral patches absent.

Character no. 19. Position of the fertile frond and soral patch

In epiphytic Polypodiaceae (e.g. *Pyrrosia, Drynaria*), the (fertile) fronds are spreading or erect with the sori exposed horizontally or situated away from the plant. This condition is regarded the plesiomorphic state within *Platycerium*. The conditions in which the foliage fronds are pendulous with the soral patch exposed horizontally, or pendulous with the soral patch facing the plant, represent two different apomorphies.

Character no. 20. Shape of the segments that bear the soral patch; the location of the soral patch

Starting from a hypothetical frond type (as found in *Pyrrosia*), which is an entire frond showing a soral patch not quite reaching the apex, the fronds of *Platycerium* can be thought to have been originated by breaking up of the apical meristem. Therefore, the wedge-shaped soral patch situated terminally on the terminal and lateral segments and/or around the ultimate sinusses is regarded the plesiomorphic condition. An advanced condition then is a frond with linear and elongated segments bearing the soral patches. These fronds have the soral patches either on terminal or lateral segments, or medially on (pen-)ultimate segments. Another apomorphic state is a frond with spoon- or kidney-shaped segments which are laterally inserted.

5.5 THE SPORANGIA AND SPORES

Characters nos. 21–26: sporangia (Fig. 9); *27:* spores (Plate 9d, e)

According to Wilson (1959) the sporangia of the *Platycerium* species do not differ in any fundamental aspect from those of the other species of the Polypodiaceae.

As far as the sporangia are concerned, a detailed investigation was made of the number of cells of the hypostomium, the epistomium, the indurated annulus cells, and the total number of annulus cells. Except for the number of indurated annulus cells (and consequently also the total number of annulus cells), all species are homogeneous showing a condition as typical for Polypodiaceae, except for *P. coronarium* and *P. ridleyi* which are markedly different. For each character of the sporangia and spores, all the species have the same condition, also found in *Pyrrosia* except for *P. coronarium* and *P. ridleyi* (which share characters states nos. 21, 22, 24–27) or *P. ridleyi* (character no. 23). As a consequence of out-group comparison the morphologically unique states as found in the latter two species are regarded apomorphies.

5.6 STELLATE HAIRS AND PARAPHYSES

Character nos. 28, 29: stellate hairs (Plate 10); *30–34*: paraphyses (Plate 11). The platycerioid Polypodiaceae (*Platycerium, Pyrrosia* s.l., incl. *Drymoglossum* and *Saxiglossum*) are characterized by the presence of stellate hairs on their fronds. Stellate hairs in *Platycerium* were studied from either side of the base and foliage fronds. S.E.M. studies showed that the stellate hairs on the base fronds, and the foliage fronds are not markedly different.

Fig. 5 shows the variation in the number of rays per stellate hair and paraphyse of each taxon in the genus. The calculated numbers do not provide characteristics for individual taxa. When comparing the mean values of the number of rays of the stellate hairs on the lower, and the upper side, and of the paraphyses (Fig. 6), this value is the lowest for the stellate hairs occurring on the upper side, being similar for those occurring on the lower side and the paraphyses.

Fig. 7 shows the mean average length of the rays of the stellate hairs (character no. 28) on both lower and upper side of the foliage fronds, and of the paraphyses (character no. 32) arranged according to subsequent values of the mean average length of the stellate hairs of the upper side, as well as arranged for the taxonomic groups recognized. The variation is continuous if the figures for all the taxa are considered together. It is noteworthy that in *P. elephantotis* and *P. wallichii* the paraphyses have rays which are longer than those of the stellate hairs (shorter in all other species) representing an apomorphic condition. Besides, the absolute length of the rays of the paraphyses of these species represents an extreme. Fig. 7 further shows that in the *P. alcicorne*-group and *P. madagascariense* the data are significantly different from those encountered in the other species. The variation in the length of the rays of the stellate hairs, and of the paraphyses is the largest in *P. bifurcatum* being even greater in the *P. bifurcatum*-group (incl. *P. coronarium* and *P. ridleyi*). The situation in *P.*

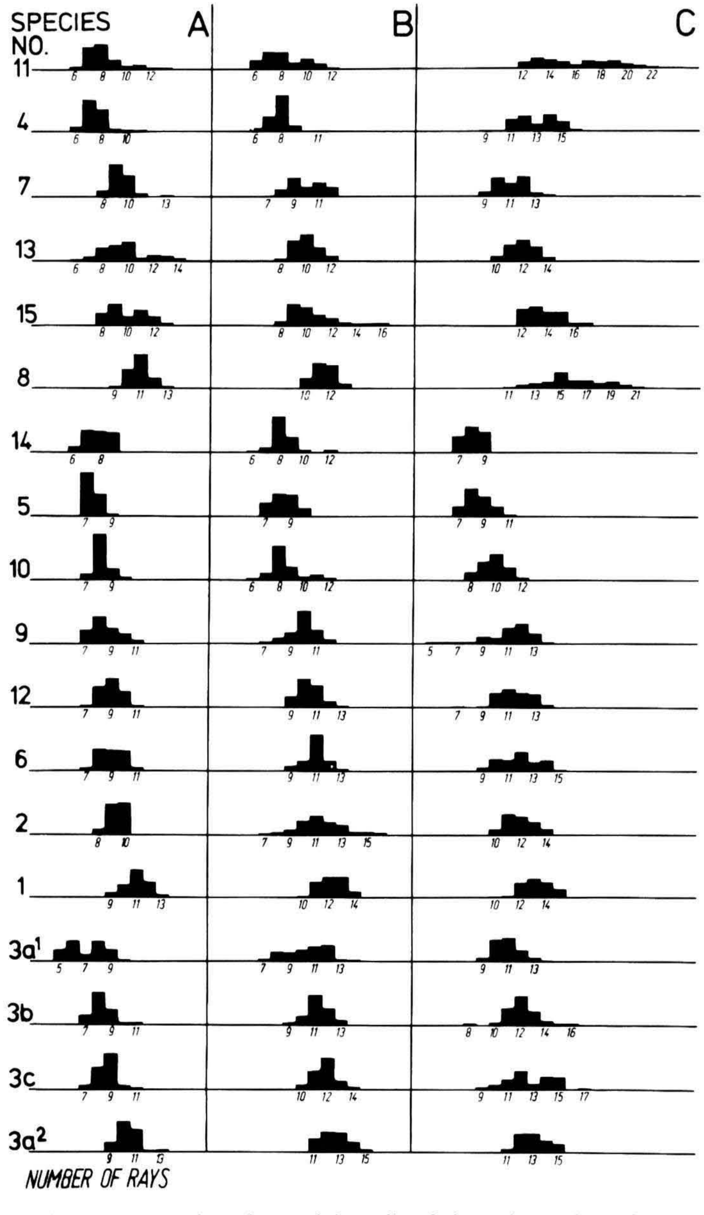

Fig. 5. Diagrams showing the number of rays of the stellate hairs and paraphyses for all taxa. The values given for each number are percentages of the total number of countings. The data of *P. coronarium* and *P. ridleyi* (species nos. 11 and 4), and the species of the *P. grande*-group (species nos. 7, 13, 15, 8) are listed first, those of the infraspecific taxa of *P. bifurcatum* (species no. 3) last. The sequence of the other species follows the minimum number of rays found in the stellate hairs occuring on the upper side of the frond. – A. Stellate hairs of the upper side of the foliage frond. – B. Id., beneath. – C. Paraphyses.

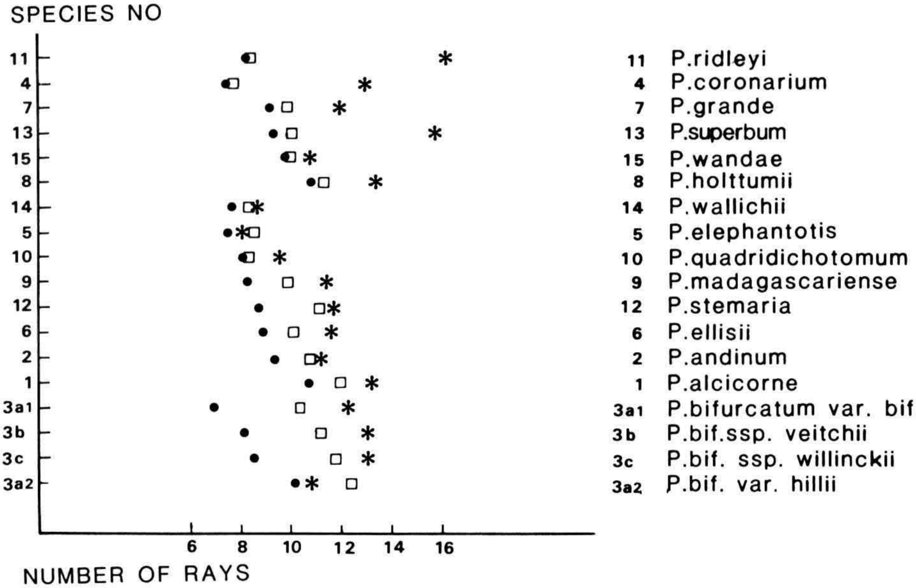

Fig. 6. The mean values of the number of rays of stellate hairs and paraphyses. Black dots: the mean value of the number of rays of the stellate hairs on the upper side of the foliage frond; squares: id., lower side; asterisks: id., paraphyses.

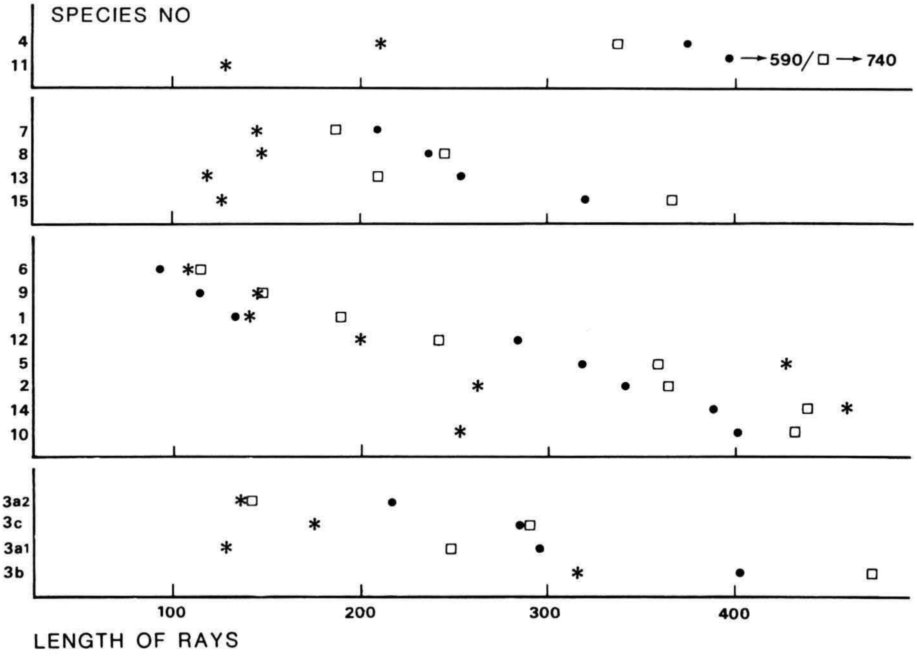

Fig. 7. The mean length of the rays of stellate hairs and paraphyses of the foliage frond of all taxa. The species are listed as in Fig. 5; for legend see Fig. 6.

ridleyi represents an other extreme. The variation is comparatively small in the species comprising the *P. alcicorne*-group (*P. alcicorne* and *P. ellisii*), and *P. madagascariense*. The rays of the stellate hairs of *P. ellisii* further shows a distinctive flat marginal zone apart from an acute apex (character no. 29). The rays of the paraphyses of *P. alcicorne* and *P. ellisii* are characteristic, being short ± flat (character no. 31). As far as the *P. grande*-group (*P. grande, P. holttumii, P. superbum*, and *P. wandae*) is concerned, the rays of the stellate hairs of *P. wandae* are far longer than those found in the other species. *P. stemaria* shows intermediacy for these features of the stellate hairs.

Fig. 8 shows the mean average width of the rays of the stellate hairs of the lower and the upper side of the foliage fronds, and of the paraphyses. *P. superbum* is different from the other species showing stellate hairs with relatively narrow rays (see character no. 31). Relatively wide rays of the paraphyses are a characteristic of *P. coronarium* and *P. ridleyi* (character no. 33).

Within the respective groups the species are arranged following the sequence of the values of the width of the stellate hairs above (which is similar to an arrangement based on the data of the stellate hairs beneath, except for *P. madagascariense* and *P. ridleyi*) Generally speaking the width of the stellate hairs above and beneath are similar, whereas the width of the paraphyses may be much wider.

In the *P. bifurcatum*-group, the width of the paraphyses is conspicuously wider than

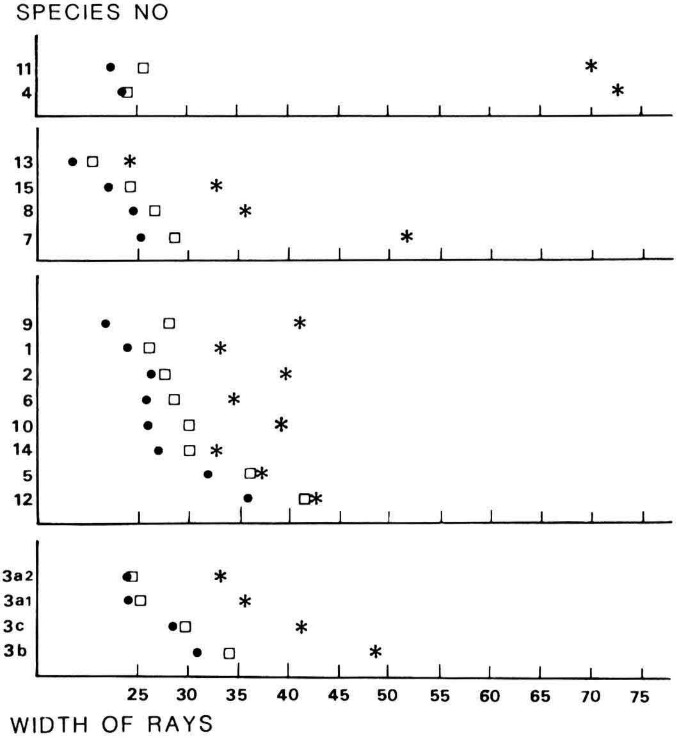

Fig. 8. The mean width of the rays of stellate hairs of the foliage frond and paraphyses of all taxa. The species are listed as in Fig. 5; for legend see Fig. 6.

the width of the respective stellate hairs, the situation realized in *P. coronarium* and *P. ridleyi* forming an extreme.

The situation in the *P. grande*-group is rather diverse. The extremes are represented by *P. superbum* (with rather uniform data and relatively narrow rays) and *P. grande* (with the data on stellate hairs rather different from those of the paraphyses which are wider). In the remaining species the data regarding *P. elephantotis* and *P. stemaria* are somewhat different if compared with those of the other species. First, the rays of the stellate hairs on both the upper and the lower side are wider; second, the width of the rays of the stellate hairs of the lower surface and that of the paraphyses is about equal.

The index of the stellate hairs in *P. ridleyi* represents an extreme. The indices of the paraphyses of *P. elephantotis* and *P. wallichii* are significantly different from those of the other species.

The paraphyses of *P. coronarium* and *P. ridleyi* (Plate 12) are very characteristic being long-stalked (character no. 34) and having the rays in a tuft, *i.e.* inserted terminally as well as subterminally on the stalk. In the other species the rays are inserted ± terminally only. The rays of the paraphyses of *P. ridleyi* are further unique being short-clavate.

TABEL I. CHARACTERS OF THE PLANT AND THEIR PRESUMED CHARACTER STATES

	Characters investigated	Plesiomorphic state		Apomorphic state(s)
I.	Characters of the scales			
1.	size and margin	size: 1.5–14 x 0.4–1.5 mm margin: not flabelloid	a:	12–28 x 1.5–4.5 mm; not flabelloid
			b:	8–35 x 0.4–10 mm; flabelloid
2.	shape of apex	acute to filiform	a:	rounded
3.	'midrib'	present, entire, linear to narrow-triangular, in cross-section rounded	a:	present, divided and/or broad-triangular, in cross-section flattened or dumpbell-shaped
			b:	absent
4.	place of insertion of hairs	marginally and abaxially	a:	in a marginal zone
			b:	solely marginally
5.	marginal indument	present	a:	absent
6.	implantation of indument	hairs sparsely to densely set	a:	very densely set
7.	shape of the marginal trichomes	trichomes 1–6-celled; branched and unbranched; glandular and non-glandular; without protuberances	a:	1–8-celled; branched and unbranched; glandular and non-glandular; with protuberances
			a':	mostly 1–5-celled
			a'':	mostly 1–8-celled
			b:	1–2-celled, glandular and non-glandular; without protuberances
			c:	1–6-celled, unbranched; glandular; without protuberances
II.	Characters of the base fronds			
	General; architecture			
8.	way of attachment; prominence of veins	sessile; veins ± immersed	a:	inconspicuously stalked; veins forming a waffle pattern
			b:	conspicuously stalked; veins prominent, no waffle pattern
9.	colour of mature fronds	green	a:	brown
			b:	dark green

	Characters investigated	Plesiomorphic state		Apomorphic state(s)
10.	position of old fronds	erect or appressed	a:	recurved
11.	water storage tissue; shape of cells near the base	present; cells spherical	a:	absent
			b:	present; cells cylindrical
	Upper part of base fronds			
	Alt. 1.			
12,13	position, shape and incisions	well-developed, markedly erect, wedge-shaped, margin entire or with two main lobes	a:	appressed, kidney-shaped, margin entire or slightly lobed
			a′:	well-developed, markedly erect, elliptical with many dissimilar lobes
			b:	well-developed, markedly erect, wedge-shaped, with many ascending lobes of varying shape
			c:	well-developed, spreading, wedge-shaped with many similar lobes
	Alt. 2.			
12,13	position, shape and incisions	appressed, kidney-shaped, margin entire or slightly lobed	a:	well-developed, markedly erect, elliptical with many dissimilar lobes
			b:	well-developed, markedly erect, wedge-shaped, margin entire or with two main lobes
			b-a:	well-developed, markedly erect, wedge-shaped, with many ascending lobes of varying shape
			b-b:	well-developed, spreading, wedge-shaped with many similar lobes
14.	margin	entire	a:	± sinuate
			b:	denticulate
15.	fringe (collar, frill)	absent or inconspicuous	a:	conspicuous, encircling the stipes, margin entire or sinuate
			b:	conspicuous, encircling the stipes, margin denticulate
			c:	± conspicuous, situated above the stipes only, margin ± entire

	Characters investigated	Plesiomorphic state	Apomorphic state(s)	
III.	Foliage fronds and soral patches (= s.p.)			
	General; architecture			
16.	number of fronds maturing at the same time	number is undetermined	a:	2
17.	development of fertile and sterile segments	development simultaneous	a:	fertile and sterile segments develop in succession
18.	shape: symmetry; no. of forkings, resp. development of main branches; growth of sterile segments after formation of s.p.	not fixed; 1–2; absent	a:	with a fixed (a)symmetry, many primary forkings
			a-a:	asymmetrical; 3; absent
			a-a':	asymmetrical; more than 3; absent
			a-b:	symmetrical; 0-3; absent
			a-b-a:	symmetrical; 2-3; ultimate lobes ± equally-long
			a-b-a':	± symmetrical; 0-1
			a-b-b:	symmetrical; 1-3; ultimate lobes often unequally-long
			b:	with a fixed asymmetry, with secondary forkings or such forkings absent
			b-a:	asymmetrical; 2-4, elongation of segments present
			b-a':	asymmetrical with 2 main branches; present, many lobes
			b-a'':	symmetrical; undivided or with 2 main branches
			b-b:	asymmetrical; one main branch reduced; absent
19.	position of frond and s.p.	fronds, or main branches of fronds erect or spreading; s.p. situated away from the plant or s.p. horizontally exposed	a:	fronds pendulous from the base; s.p. horizontally exposed
			b:	id.; s.p. eventually facing the plant
20.	shape of the segments that bear the s.p.; location of s.p.	wedge-shaped; terminally on terminal and lateral segments	a:	segments linear or elongate; on terminal and lateral segments
			b:	id.; medially on (pen-)ultimate segments
			c:	segments spoon- or kidney-shaped; on lateral segments

	Characters investigated	Plesiomorphic state		Apomorphic state(s)
	Sporangium			
21.	width	mean average width 210–320 μm	a:	mean average width 140–150 μm
22.	number of indurated cells	12–24	a:	9–11
23.	position of the stomium	lateral	a:	apical
24.	shape and length of the stalk	(2–)3-seriate; 0.1–0.5 mm long	a:	1-seriate; 1.5–2.0 mm long
25.	dehiscence of paraphyses	absent	a:	present
26.	number of spores per sporangium	64	a:	8
27.	perispore	indistinct	a:	distinct, flaky
	Indument			
28.	stellate hairs: length of rays	75–475 μm	a:	longer than 575 μm
29.	id.: differentiation and shape	undifferentiated, apex filiform	a:	with a narrow flat marginal zone, apex round or acute
30.	paraphyses: insertion of rays	terminal	a:	subterminal and terminal
31.	id. shape of rays	undifferentiated, involute to canaliculate	a: b: c:	flat or convex spine-like short-clavate
32.	id.: mean average length of rays	100–325 μm	a:	longer than 425 μm
33.	id.: width of rays	20–60 μm	a:	wider than 60 μm
34.	id.: stalk	short	a:	long

Explanation of symbols used for apomorphic states:

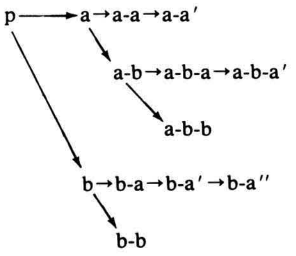

TABLE II. DISTRIBUTION OF CHARACTER STATES IN PLATYCERIUM

Species	P. coronarium	P. ridleyi	P. bifurcatum	P. alcicorne	P. ellisii	P. madagascariense	P. andinum	P. quadridich.	P. elephantotis	P. wallichii	P. grande	P. holttumii	P. superbum	P. wandae	P. stemaria	Parallel development
Species no. if alphabetically arranged	4	11	3	1	6	9	2	10	5	14	7	8	13	15	12	
Character no. according to table I																
I Scales																
1	x	x	○	○	○	○	○	○	○	○	●	●	●	●	○	
2	●	●	○	○	○	○	○	○	○	○	○	○	○	○	○	
3	●	●	○	○	○	x	x	○	○	○	x	x	x	○	○	P:x
4	x	x	x	○	○	○	○	○	○	–	●	●	●	●	○	
5	○	○	○	○	○	○	○	○	○	●	○	○	○	○	○	
6	○	○	○	○	○	○	○	○	○	–	●	●	●	●	○	
7	+	+	+	x	x	○	○	○	○	–	●′	●′	●	●	○	
II Base fronds																
Gen. archit.																
8	○	x	○	○	○	●	○	○	○	○	○	○	○	○	○	
9	○	○	●○	●	●	x	●	●	○	●	○	○	○	○	○●	P:●
10	●	○	○	○	○	○	○	○	○	○	●	●	●	●	○	P
11	x	●	○	○	○	●	○	○	x	○	○	○	○	○	○	P
Upper part																
12, 13 alt. 1.	●′	●	●●′	●	●	●	○	○	○	x	+	+	+	+	○	
12, 13 alt. 2. a.	●	○	○●	○	○	○	–	–	–	–	–	–	–	–	–	
12, 13 alt. 2. b.	–	○	–	○	○	○	●	●	●	●	●	●	●	●	●	
12, 13 alt. 2. b-a	–	–	–	–	–	–	○	○	○	●	–	–	–	–	○	
12, 13 alt. 2. b-b							○	○	○	–	●	●	●	●	○	
Lower part																
14	○	○	○	○	○	x	○	○	○	○	●	●	●	●	○	
15	+	○	○	○	○	x	+	○	+	+	●	●	●	●	+	P: +
III Foliage fronds																
Gen.; archit.																
16	○	○	○	○	○	○	●	●	●	●	●	●	●	●	○	
17	○	○	○	○	○	○	●	●	○	○	●	●	●	●	○	
18 a	●	●	●	●	●	●	–	–	–	–	–	–	–	–	○	
18 a-a	●′	●′	●	–	–	–									○	
18 a-b	–	–	–	●	●′	x									○	
18 b	–	–	–	–	–	–	●	●	●	●	●	●	●	●	○	
18 b-a							●	●	–	–	●″	●′	●″	●′	○	P:●″
18 b-b							–	–	●	●	–	–	–	–	○	
19	○	○	○	○	○	○	x	x	●	●	○	○	○	○	○	
20	+	+	●	●○	○	●○	x	x	○	○	○	○	○	○	○	P:●

TABLE II. DISTRIBUTION OF CHARACTER STATES IN PLATYCERIUM

Species	P. coronarium	P. ridleyi	P. bifurcatum	P. alcicorne	P. ellisii	P. madagascariense	P. andinum	P. quadridich.	P. elephantotis	P. wallichii	P. grande	P. holttumii	P. superbum	P. wandae	P. stemaria	Parallel development
Sporangium																
21	•	•	o	o	o	o	o	o	o	o	o	o	o	o	o	
22	•	•	o	o	o	o	o	o	o	o	o	o	o	o	o	
23	o	•	o	o	o	o	o	o	o	o	o	o	o	o	o	
24	•	•	o	o	o	o	o	o	o	o	o	o	o	o	o	
25	•	•	o	o	o	o	o	o	o	o	o	o	o	o	o	
26	•	•	o	o	o	o	o	o	o	o	o	o	o	o	o	
27	•	•	o	o	o	o	o	o	o	o	o	o	o	o	o	
Indument																
28	o	•	o	o	o	o	o	o	o	o	o	o	o	o	o	
29	o	o	o	o	•	o	o	o	o	o	o	o	o	o	o	
30	•	•	o	o	o	o	o	o	o	o	o	o	o	o	o	
31	+	+	o	•	•	o	o	o	o	o	o	o	x	o	o	
32	o	o	o	o	o	o	o	o	•	•	o	o	o	o	o	
33	•	•	o	o	o	o	o	o	o	o	o	o	o	o	o	
34	•	•	o	o	o	o	o	o	o	o	o	o	o	o	o	

code used for indicating polarity in transformation series:

p = o = plesiomorphic
a = • = apomorphic in case p → a : o → •
a′ = •′
a″ = •″ } apomorphic in case p → a → a′ → a″ : o → • → •′ → •″
b = +
c = x } apomorphic in case

$$\left.\begin{tikzcd} & a \\ p \arrow[ur] \arrow[r] \arrow[dr] & b \\ & c \end{tikzcd}\right\} : \begin{tikzcd} & o \\ o \arrow[ur] \arrow[r] \arrow[dr] & + \\ & x \end{tikzcd}$$

6. Phylogenetic relationships

6.1 THE CLADOGRAM

6.1.1 *Introduction*

The polarity of the morphoclines recognized in the characters used for establishing the hypothesized cladogram has been determined by comparing various outgroups (De Jong, 1980; Watrous and Wheeler, 1981). The unambiguous taxonomic outgroup selected for *Platycerium* is the genus *Pyrrosia* because of the synapomorphy of specialized stellate hairs. This determines polarity in character nos. 1, 2, 3, 16–19, 21–26, 29–31, 33 and 34. The groups based on synapomorphy of these characters were in turn used as the functional outgroups for establishing polarity in character nos. 4–7, 10–14, 20, 27, 32. (Because of the autopomorphy of species no. 14 for character no. 5, the polarity of character nos. 4, 6, and 7 could be determined).

However, using outgroup comparison only, the polarity of character nos. 7, 12, 13, 15, and 18 could not be given with certainty. In these cases the polarity is proposed using ontogenetic data. Nevertheless, alternative transformation series had to be included for character nos. 12, 13.

The plesiomorphic and apomorhic states recognized for 34 characters are enumerated in Table II. This table shows that the apomorphic states of the various characters when treated individually, suggest different monophyletic groups. To minimize the influence of parallel developments so common in ferns, only the groups of species that share at least the same apomorphic state of three different characters are regarded possible monophyletic groups. The groups are enumerated in a sequence that reflects the total number of shared apomorphic character states.

6.1.2 *Groups within the genus*

Group A. Species nos. 4 and 11

Platycerium coronarium and *P. ridleyi* share 15 apomorphic states (scales: character nos. 1–3; base frond: none; foliage frond: character nos. 18, 20–22, 24–27, 30, 31, 33, 34, of which 10 refer to the reproductive organs including the paraphyses).

Group B. Species nos. 7, 8, 13, and 15

Platycerium grande, P. holttumii, P. superbum, and *P. wandae* share 9 apomorphic states (scales: character nos. 1, 4, 6, 7; base fronds: character nos. 12–15; foliage fronds: character no. 18).

Group C. Species nos. 1 and 6

Platycerium alcicorne and *P. ellisii* share 3 different apomorphic states of which 2 refer to microscopical characters of the indument of the scales (character no. 7) and paraphyses (character no. 31), and one to the foliage fronds (character. no. 18).

Group D. Species nos. 2 and 10

Platycerium andinum and *P. quadridichotomum* share 3 different apomorphic states of the foliage fronds (character nos. 18–20).

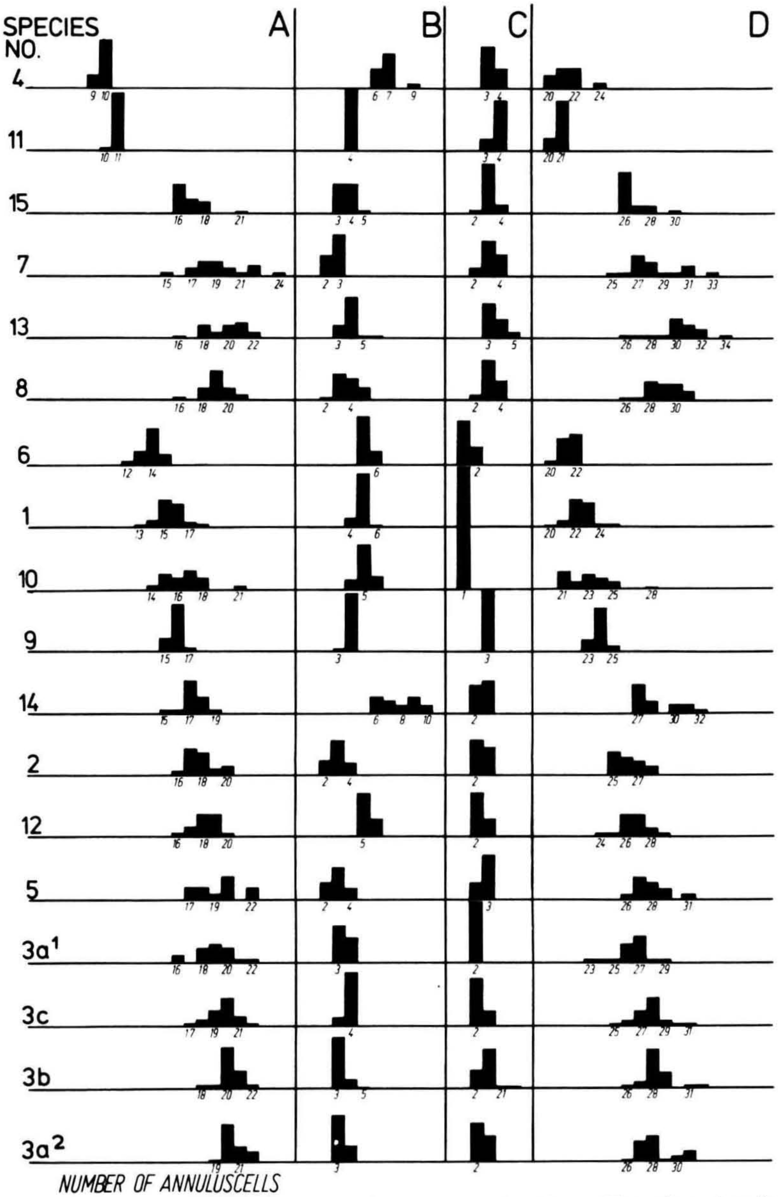

Fig. 9. Diagrams showing the number of annulus cells for all taxa. The values given for each number are the percentages of the total number of countings of each category. The species are listed as in Fig. 5. – A. No. of indurated cells. – B. No. of hypostomium cells. – C. No. of epistomium cells. – D. Total no. of annulus cells.

Group E. Species nos. 3, 4, and 11

Platycerium bifurcatum, P. coronarium, and *P. ridleyi* share 3 different apomorphic states (character nos. 4, 7, 18), of which the first two refer to the scales and the third to the foliage fronds. Species no. 3 shares also one apomorphic state with species nos. 1 and 9 (character no. 20). A relationship between species nos. 1, 3, and 9 is less parsimonious as they have only one synapomorphy in common, whereas species no. 1 shares 3 apomorphies with species no. 6 (see above: C). Character no. 20 will therefore be discussed as a possible parallel development (see Chapter 6.2).

Group F. Species nos. 5 and 14

Platycerium elephantotis and *P. wallichii* share 3 different apomorphic states (character nos. 18, 19, 32) of which 2 refer to the foliage frond, and one to the paraphyses.

6.1.3 *The construction of a cladogram*

When comparing the apomorphic character states that establish the groups A–F mentioned above, it becomes clear that they are not contradictory as to nesting sets of species. On the other hand the groups established do not make it possible to present a complete cladogram: it are especially the relations between the groups mentioned above, and the relations between the species of group B, that need further clarification.

For this purpose we have available the character states that have not been used before in establishing the groups A–F. However, these characters do not show congruences in nesting sets of species. Therefore, these character states are weighed against the character states that show congruence for group A (based on 15 synapomorphies) and B (based on 9 synapomorphies), groups that we regard undisputedly monophyletic. Consequently, we propose to regard all other apomorphic character states shared by other species and only part of the species of either two groups (character nos. 3, 9, 10, 11, 15) as necessarily the result of parallel development or misinterpretation of character states. These characters are disregarded for the establishment of other groups; they will be discussed separately in Chapter 6.2. Nevertheless, they may be of use for suggesting possible relationships between the taxa of which the sister group relations could not be established otherwise.

According to the reasoning given above a cladogram is proposed (fig. 10) based on the following monophyletic groups.

Group 1. The *P. coronarium*-group (species nos. 4 and 11; group A): *P. coronarium* and *P. ridleyi.*

Group 2. The *P. grande*-group (species nos. 7, 8, 13 and 15; group B): *P. grande, P. holttumii, P. superbum,* and *P. wandae.*

Within this group *Platycerium grande* and *P. holttumii* are sister species according to character no. 7 (marginal indument of the scales). This information is contradictory to that of character no. 18b which in turn is contradictory to character no. 3. However, the information of the latter character is disregarded, the character being liable to parallel evolution. The relationship of the group formed by *P. grande* and *P. holttumii* to *P. superbum* and *P. wandae* is ambiguous. Character no. 3 (absence of a midrib) nests *P. grande, P. holttumii*, and *P. superbum*. But as pointed out above scales did show much parallel evolution.

Group 3. The group formed by *P. alcicorne* and *P. ellisii* (species nos. 1 and 6; group C).

Group 4. The *P. andinum*-group (species nos. 2 and 10; group D): *P. andinum* and *P. quadridichotomum*.

Group 5. The *P. bifurcatum*-group (species nos. 3, 4, and 11; group E): *P. bifurcatum, P. coronarium*, and *P. ridleyi*.

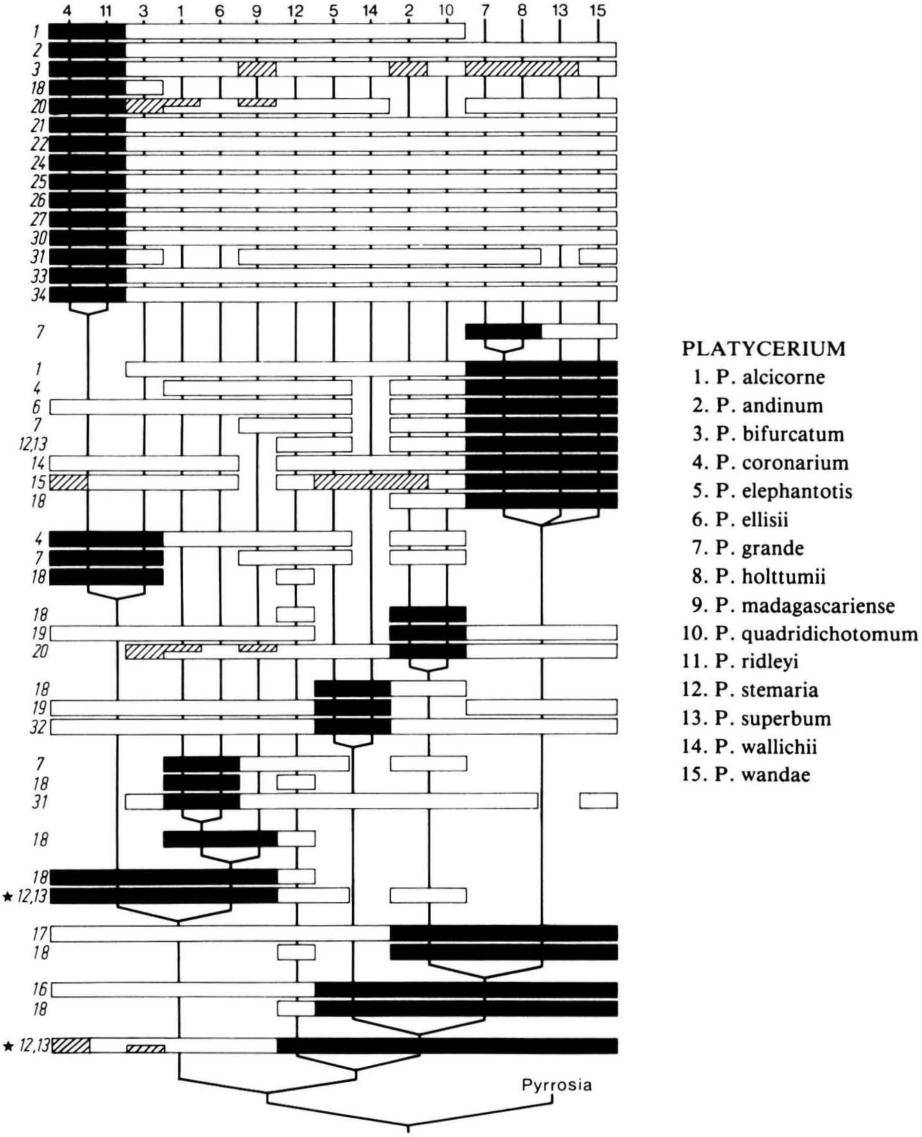

Fig. 10. Cladogram based on characters summarized in Table 1 and 2; apomorphic character states are in solid black bars; (relatively) plesiomorphic character states are in open bars; apomorphic character states due to inferred parallelism are in hatched bars; asterisks: an alternative hypothesis of the polarity of this character is included.

Group 6. The *P. elephantotis*-group (species nos. 5 and 14; group F): *P. elephantotis* and *P. wallichii.*

Group 7 = Group 5 + Group 3, and *P. madagascariense*

The species of the *P. alcicorne*-group and the *P. bifurcatum*-group share apomorphic states of the foliage fronds (character no. 18). This monophyly is supported by the shape of the base fronds (character nos. 12, 13; Alternative 2; Alternative 1 is non-informative as the species of these groups show the plesiomorphic condition for these characters).

Group 8 = Group 2 + Group 4

The sister-group of the *P. grande*-group is not obvious. When chosing alternative 1 of character nos. 12, 13 (Fig. 1), its sister-group is either the *P. andinum-*, or *P. elephantotis*-group, or *P. stemaria,* or a combination of these; Alternative 2 is non--informative because of plesiomorphy. However, the *P. andinum-, P. elephantotis-,* and the *P. grande*-group share the apomorphy of character no. 16 (foliage fronds formed in pairs). Secondary elongation of the segments of the foliage fronds relates the *P. grande*-group to the *P. andinum*-group.

Group 9 = Group 8 + Group 6

This follows from the synapomorphy of the formation of foliage fronds in pairs.

Group 10. *P. stemaria*

The position of *P. stemaria* in the cladogram is determined by character nos. 12, 13, alternative 1 (Fig. 1). Otherwise the species shows all its characters in the plesiomorphic state.

6.2 PARALLEL DEVELOPMENTS

A number of character states revealed to be incongruent with those that determine the monophyly of the groups 1-10 as listed above.

Character no. 3

A 'midrib' of the scales is absent in species nos. 2, 7, 8, 9, and 13, which belong to three different monophyletic groups from three different continents, also showing various habitat preferences.

The absence of a midrib on the scales seems an obvious parallel development. It is remarked that the presence of a midrib is not always consistent, which may indicate that the loss of a midrib may be rather of a general nature.

Character no. 9

Withering of base fronds occurs in five different monophyletic groups from three different continents, which show various habitat preferences. It is obviously a parallel development. The species of the *P. andinum*-group have brown base fronds, those of the species of its possible sister group, the *P. grande*-group, have green base fronds. In the *P. alcicorne*-group this character is variously expressed: the base fronds of *P. alcicorne* and *P. ellisii* are brown whereas those of their sister group, *P. madagascariense*, are of a characteristic dark green colour.

Withering of base fronds, therefore, seems not an obvious adaptation to a seasonally dry habitat. In monsoon Thailand, *P. holttumii* (green base frond) and *P. wallichii* (brown base frond) are sometimes found growing intermingled (comm. Dr C.F. van Beusekom and Drs R. Geesink).

Character no. 10

Recurving old base fronds occur in members of two monophyletic groups, the species of the *P. grande*-group, and in *P. coronarium*. The recurving of base fronds is likely to represent a parallel development in part of the species from tropical Asia. This character may be correlated with the (large) size and the pronounced lobings of the base frond.

Character no. 11

Loss of water storage tissue obviously arose independently in *P. madagascariense* and *P. ridleyi*, which are not closely related. The same holds for *P. coronarium* and *P. elephantotis* which have elongated mesophyll cells near the base of the fronds. The significance of the differentiation of this feature is not obvious. Either of the two different apomorphic states recognized occur in two unrelated African species inhabiting areas which are dry during a significant part of the year.

Characters nos. 12 and 13

Appressed base fronds occur in two monophyletic groups. They comprise two species of the *P. bifurcatum*-group (*P. bifurcatum* p.p. and *P. ridleyi*), and the species of the *P. alcicorne*-group (*P. alcicorne, P. ellisii,* and *P. madagascariense*).

The upper part of the base fronds in the remaining taxa of group 5 (*P. coronarium* and *P. bifurcatum* p.p.) are variously lobed. The occurence of appressed base fronds in small plants of *P. bifurcatum* and *P. coronarium* suggests that the lobed condition of the mature base fronds represents an apomorphic state. Still, the lobing of the base fronds of these two species does not represent a shared apomorphic state, as *P. coronarium* is the undoubted sister species of *P. ridleyi* and not of *P. bifurcatum*. Lobing of base fronds in this group therefore seems explained best as a parallel development. This being true, the ancestral condition of the base frond in the species of the *P. bifurcatum*-group and the *P. alcicorne*-group is the appressed base frond. It is suggested that the ancestral condition was retained in *P. alcicorne, P. ellisii,* and *P. bifurcatum* p.p., and variously further developed in *P. madagascariense* and the species of the *P. bifurcatum*-group (*P. bifurcatum* p.p. and *P. coronarium*: base fronds lobed; *P. ridleyi*: base fronds ± appressed, stalked, with a prominent venation). The capacity to further diversification of the base frond constitutes in itself an apomorphic state.

The development of wedge-shaped base fronds with about equally-long lobes has obviously occured twice in the evolution of the genus in Asia. It occurs in all the species of the *P. grande*-group and – in a slightly different way – in *P. wallichii* (which sister species – the African *P. elephantotis* – has entire base fronds). Lobing of fronds took place independently also in other phylogenetic lines incl. *P. bifurcatum, P. coronarium*, and *P. andinum.*

Character no. 15

The types of fringes 15a and 15b are conspicuous and characteristic. This is far less so with fringe type 15c which is usually only conspicuous in large-sized specimens. Leaving out *P. coronarium* in which this type of fringe is a parallel development in view of its relationship with *P. ridleyi* (and *P. bifurcatum*), the remaining species comprise the species of groups 4, 6, and 11, with the exception of *P. quadridichotomum* (in which this character may be lost secondarily). Although somewhat speculative, the data may suggest that ± conspicuous fringes, occurring above the stipe only, represent the original condition in the species of these groups. From this condition the spectacular fringes as occurring in the species of the *P. grande*-group obviously arose.

Character nos. 18a, 18b-a

More or less distinct bilateral symmetrical fronds are present in *P. bifurcatum* var. *hillii* and in the larger-sized multi-lobed fronds of *P. madagascariense*. They represent parallel developments (*e.g.* the sister group of var. *hillii* is undoubtedly var. *bifurcatum*).

Symmetrical fronds also occur in two species of the *P. grande*-group. From characters of the scales it is suggested that *P. grande* and *P. holttumii* (both with two soral patches) are sister species. Whether this is also the case with *P. superbum* and *P. wandae* needs further support.

Character no. 20a

Linear segments may represent the original apomorphic condition in the *P. alcicorne*- and *P. bifurcatum*-group.

The fronds of *P. ellisii* are aberrant because they retain a morphologically different juvenile condition which, though more advanced, is nevertheless morphologically simpler.

As *P. coronarium* and *P. ridleyi* belong to the *P. bifurcatum*-group, their fronds should be understood as derivations of fronds with linear segments. This is not too difficult in view of the morphology of other structures formed by these species, including base fronds.

6.3 DISCUSSION

The phylogenetic relations proposed by us are based on a character analysis of selected features which are accordingly interpreted following a cladistic analysis. The phylogenetic relations given by Joe Hoshizaki are based on Wagner's Groundplan Divergence Method (see Wagner, 1981). In both methods, relations are based on derived character states only.

The many differences between the diagram as presented by Joe and the cladogram presented here are mainly due to different interpretations of the morphological expressions. Examples are the interpretation of the scales with the flabelloid margin as found in *P. coronarium* and *P. ridleyi*, the brownescence of the base fronds, and the shape of the fronds. Also, Joe Hoshizaki obviously adhered much to the view of Straszewski that the groups sharing the same geographical distribution are monophyletic, an idea that is false (*e.g.* De Jong, 1980).

According to Joe Hoshizaki, the original condition as regards the flabelloid margin of the scales of *P. coronarium* and *P. ridleyi* should be a margin with hairs like those found in the *P. grande*-group. However, the flabelloid margin as found in *P. coronarium* and *P. ridleyi* is one cell thick consisting of rows of cells, arranged perpendicularly to the margin, often terminated by 1–2-celled, glandular trichomes. The hairs of the scales as found in the *P. grande*-group on the other hand are branched, inserted in a marginal zone, and usually non-glandular. If present, the glandular cell is situated in the basal part of the hair, not terminally. According to us it is more plausible that the ancestral condition is represented by a type of indument as found on the scales of *P. bifurcatum*. Exclusively this species has glandular, marginal inserted hairs; and hairs increasing in length towards the apex, a situation parallelled by the increase in width of the flabelloid margin of the scales of *P. coronarium* and *P. ridleyi*. In our view it is therefore unlikely that the flabelloid margin arose by fusion of hairs like those present in the *P. grande*-group; Joe Hoshizaki reported a narrow flabelloid margin in the scales of the species of the *P. grande*-group which could not be confirmed.

Joe Hoshizaki (1970: 155) mentioned the similarity between some types of scale indument and the stellate hairs of the fronds, to which we agree. She tried to establish a transformation series for the types of scale indument by reduction from the stellate hair-like type. Therefore, she explained the diversities of the scale indument by suggesting increasing complexity starting from scales without hairs, showing simple 'papillae' only (as found in *P. wallichii*) as well as by reduction of complex types. In our interpretation, the condition in which all stages from simple 1-celled trichomes to stellate hairs are present, is plesiomorphic. This condition comprises ontogenetic stages of stellate hairs, as can be found on juvenile fronds. Starting from this, three phylogenetic lines are proposed, one characterized by the tendency to form increasingly complex, usually non-glandular, many-celled hairs with protuberances, the other characterized by 1-celled trichomes (through neotenic development) or many-celled usually glandular hairs increasing in length and liable to lateral fusion.

As regards the loss of the assimilating function of the base frond, we agree with Joe Hoshizaki that the withering of mature base fronds is a derived character. However, this study (out-group comparison) shows that this condition resulted from parallel development.

As regards the shape of the base frond we propose two alternative transformation series which share essential elements with those given by Joe Hoshizaki. Differences between the latter and the present authors include the interpretation of the base fronds of *P. andinum*, as well as those of *P. grande* and relatives, and *P. coronarium*. The synapomorphy of the base fronds of *P. coronarium* and *P. bifurcatum* (*p.p.*) is a surprising result of our investigations.

The transformation series proposed for the shape and position of the foliage fronds and of the soral patches differ significantly from those given by Joe Hoshizaki. We like to mention in particular the interpretation of the foliage fronds of *P. coronarium* and *P. ridleyi* which in our view are not synapomorphic with those found in the species of the *P. grande*-group in spite of certain similarities. See Fig. 3.

The very striking feature of the formation of asymmetrical foliage fronds in pairs in a bilateral symmetrical pattern, instead of the formation in an undetermined number in an undetermined pattern, as found in other species with asymmetrical fronds, is noteworthy. Among other things, this had led us to assume a close relationship between *P. elephantotis* and *P. wallichii*. Further, we postulate a hypothesis about the original condition of the foliage fronds in the genus implying a different plesiomorphic state within the genus, than the original condition as seen by Joe Hoshizaki. This author inferred, from the foliage fronds present in the genus, a 'generalized' frond (in typological sense), which she regarded as the ancestral type. We propose a hypothetical plesiomorphic state and the relatively plesiomorphic conditions within the genus by outgroup comparison and where necessary by using ontogenetic data.

It is rather unfortunate that Joe Hoshizaki (1972), in her discussions, uses the idea of 'primitive species'. The fact that for each character one can establish the plesiomorphic condition and that modern species may have a number of their characters in the plesiomorphic state, does not imply the existence of recent modern primitive species.

From the above it is clear that the cladogram given in the present paper is different from the 'ground-plan diagram' of Joe Hoshizaki; the most conspicuous differences are: the position of *P. coronarium* and *P. ridleyi* as the sister group of *P. bifurcatum*, the only remote relationship of this group to the *P. grande*-group, and the sister group relation between *P. elephantotis* and *P. wallichii*. Joe Hoshizaki placed *P. elephantotis* as a derivative of *P. stemaria*, and she regarded *P. wallichii* as closely related to the *P. grande*-group. Sister group relations exist between the *P. alcicorne*-group and the *P. bifurcatum*-group. Joe relates the *P. alcicorne*-group to *P. quadridichotomum* which is not a close relative.

The morphological differences between the closely related *P. coronarium* and *P. ridleyi* seems the product of rather recent speciation, and indicates a genetic plasticity. This plasticity is also found in *P. bifurcatum*, their sister group, and the only species in the genus in which we were able to recognize distinct subspecies.

7. Habitat

7.1 GENERAL

The greater part of the species of *Platycerium* generally or exclusively (*P. coronarium, P. ridleyi,* and the species of the *P. grande*-group) occur as epiphytes, occasionally growing on rocks or cliff-faces. Only a few taxa are generally (*P. quadridichotomum*) or exclusively (*P. bifurcatum* ssp. *veitchii*) epilithic. *P. quadridichotomum* is found on limestone, whereas *P. bifurcatum* ssp. *veitchii* is confined to sandstone or basalt.

The species of this pantropical (in Australia subtropical also) genus show variation as to their climatological preferences, inhabiting (sub-)tropical everwet areas, as well as (sub-)tropical monsoon areas, with a more or less severe dry period.

As to the altitude, it appears that all species occur in the lowlands (up to 750 m). Only some species are found at higher elevations as well, extremes being *P. bifurcatum* ssp. *willinckii* (up to 2000 m or more, perhaps specimens escaped from cultivation?) and *P. elephantotis* (up to 1850 m). Other species are found exclusively at low elevations only, e.g. *P. ridleyi* (below 200 m), *P. quadridichotomum* (below 250 m), *P. andinum,* and *P. ellisii* (below 400 m). The altitudinal range of *P. grande* is unknown.

The species inhabit a great variety of forests (primary, secondary; dense, open; hygrophyl, mesophyl; evergreen, deciduous), sometimes also occurring in more open landscapes, like savannas (*P. elephantotis,* which points to a distribution in less wet areas if compared with *P. stemaria*) or shrubberies (*P. bifurcatum*). Also cultivated environments are inhabited by some species, like plantations (*P. alcicorne, P. coronarium, P. elephantotis, P. stemaria,* and *P. wandae*), or open disturbed places (*P. coronarium*). Boyer (1964) reported that *P. stemaria* is generally found in hygrophyllous or humid mesophyllous forests, whereas *P. elephantotis* is generally confined to (humid) mesophyllous forests; in some places with humid mesophyllous forest the species occur together. In general, most of the species do not have a strict and distinct habitat preference.

Most of the species are recorded to be heliophyllous (*e.g. P. elephantotis, P. ridleyi*), others inhabit shady places as well as places exposed to the sun (e.g. *P. coronarium, P. stemaria*), or shady places only (*P. wandae*). In regions, where *P. coronarium* and *P. ridleyi* occur together (according to field observations of the junior author in Berbak Nature Reserve, E. Sumatra), the latter species grows on the high branches of emergents, whereas the former species grows on lower branches in the shade. Motley (Labuan 1., Sabah) made similar observations (Ridley, 1908). However, *P. coronarium* is also reported to grow exposed to the sun (in areas where

P. ridleyi does not occur?) (Holttum, 1954). The habitat preferences of *P. ridleyi* are discussed in detail elsewhere (Franken & Roos, 1982).

The ancestral species of *Platycerium* and *Pyrrosia* acquired stellate hairs very probably as an adaptation against dry periods, which is interesting in view of the rich morphological diversification of the species presently inhabiting the everwet tropics.

7.2 A COMPARISON OF THE HABITAT PREFERENCES OF THE SPECIES INHABITING THE SAME GEOGRAPHICAL AREA

The species of Madagascar

The genus is represented by four species in Madagascar, of which three are endemic.

The phytogeography of the ferns of this island was described in detail by Perrier de la Bâthie (in C. Christensen, 1932). This author distinguished several phytogeographical districts, which are largely correlated with climate. Perrier de la Bâthie listed the characteristic fern species for each of the districts.

The distribution area of *P. quadridichotomum* (*P. stemaria p.p.,* sensu Christensen) is within the 'Western District' (Fig. 14). Scattered in this area are humid places (*e.g.* vallies) with a different floristic composition. But in general, this district endures a pronounced dry season (± 6 months). During this period the foliage fronds of *P. quadridichotomum* shrivel up, showing a characteristic bony appearance (Plate 4b).

P. ellisii on the other hand, occurs in the eastern part only, the most humid area of the island. It should be a characteristic species of the 'Eastern District' of Perrier de la Bâthie, to which it is largely confined (apart from one locality near Tananarive; Fig. 14).

Perrier de la Bâthie reported *P. madagascariense* to occur in the 'Central District' only. This district shows much altitudinal variation; it has a humid climate. The distribution map (Fig. 14), however, shows *P. madagascariense* to occur also somewhat beyond the border between the Eastern and the Central Districts, though generally at higher elevations (300–700 m) than does *P. ellisii* (below 400 m), which is confined to the Eastern District.

P. alcicorne (*P. stemaria p.p.* sensu Christensen) is in Madagascar confined to the south-eastern part. Examination of the distribution area with the phytogeographical districts, shows this species to occur in both the Eastern and the Central Districts, as described by Perrier de la Bâthie.

The species of mainland Africa

There are three species of *Platycerium* occuring in mainland Africa, two of which are endemic. When comparing the distribution maps of the species of the African continent with the climatological map of Landsberg *et al.* (1966), the following observations are of interest. In mainland Africa, *P. alcicorne* is confined to the wettiest parts occurring locally along the east coast, showing a relict-like distribution pattern. This pattern supports the common suggestion (Aubréville, 1949), that the climate of Africa in the past was more humid than it is nowadays. According to Boyer (1964), in her ecological study of *P. elephantotis* and *P. stemaria*, the latter species prefers a more humid habitat than does the former. Examination of the distribution maps of these species (Fig. 23, 28) with the climatological map confirms this idea, showing *P.*

stemaria to be common in the wet western parts of the continent, *P. elephantotis* being more frequent in the (less wet) eastern part (also occurring in areas with a dry season). This species is absent from the (very humid) Congo basin. The study of Boyer is reported in detail elsewhere (Chapter 7.4).

The species of Asia and Australia

The genus is most diversified in Asia and Australia, from which eight species are recognized. As far as the Asian and Australian species are concerned, *P. holttumii* and *P. wallichii* inhabit the monsoon areas of southeastern continental Asia. *P. coronarium* and its sister species *P. ridleyi*, are restricted to the everwet parts of western Malesia, whereas *P. wandae* is found in humid forest types in New Guinea. *P. superbum* occurs in the wet parts of the East-Australian coastal zone, extending beyond the tropics into the everwet warm-temporate subtropics. *P. bifurcatum* is a widespread and much diversified species occurring in southern and eastern Malesia and in eastern Australia. This species too, extends beyond the tropics into the warm-temporate subtropical areas of eastern Australia. Generally it is found growing in areas with a more or less pronounced dry season. The habitat preferences of the infraspecific taxa recognized in *P. bifurcatum* are discussed in the Taxonomic Part.

The species of South America

The sole, endemic species of South America, *P. andinum*, is restricted to a few localities in everwet vegetations at the foot of the Andes.

7.3 THE 'NEST' OF THE FERNS AS A HABITAT

Platycerium species are primary epiphytes of which the base fronds are ± persistent, creating an environment ('bulb', 'basket', 'nest') suitable for other organisms.

Irrespective of the shape of the basket or nest, they are generally inhabited by numerous animals, mainly arthropods, suggesting that in tropical (monsoon) forests, the larger epiphytes may be of importance as providers of nest facilities for the many animals living in the forest canopy.

The greater part of the *Platycerium* species have colonies of ants in their bulb or nest, formed by the base fronds. Especially those species with a huge erect or spreading nest or basket are favoured by ants. Also small(er) species, like *P. madagascariense* and *P. ridleyi* – with kidney-shaped base fronds, forming a bulb – are suited for ants. These species have very pronounced and thickened veins in the base fronds, keeping them in a ± spherial shape. Ants inhabit the open spaces between the successive permanent base fronds.

Symbiotic tendencies are recorded in several species. It is noteworthy that *P. ridleyi* and a *Lecanopteris* species (*e.g. L. crustacea* Copel.) always (?) are the sole epiphytes on their hosttree (often) growing intermingled (Franken & Roos, 1982).

An interesting example of symbiosis is that between *P. madagascariense* and *Cymbidiella rhodochila* Rolfe (Orchidaceae). The symbiosis seems obligatory for the orchid, the roots of which fill the spaces between the base fronds of the fern (Plate 5), but not for the fern (pers. comm. Mr J. Bogner).

Orchids or other flowering plants are reported to grow in baskets of *Platycerium* *holttumii*. The same holds for other conspicuous epiphytic ferns like drynarioids, some species of *Asplenium*, etc.

7.4 THE ECOPHYSIOLOGY OF *Platycerium elephantotis* AND *P. stemaria* (BOYER, 1964)

Boyer, in a very interesting publication (in French), studied the ecophysiology of two African staghorn ferns, i.e. *Platycerium elephantotis* and *P. stemaria*, both in their natural habitat and in cultivation. The field observations were made in Ivory Coast, in areas where the species occur separately as well as in areas where they occur intermingled.

Boyer followed the plant growth during the year. In Ivory Coast the climatological conditions generally include a short and a long dry season apart from two wet seasons. In the wet season following the main dry period, four new base fronds are formed, of which the two outer ones retain their green colour until the subsequent main dry season. Then they soon die and become brown. New foliage fronds are formed soon after the formation of the base fronds; they eventually die in the main dry season, but not until the sporangia have matured and the spores are shed in this dry period.

Gametophytes and juvenile sporophytes are formed within 3 to 4 months during the wet season, following the main dry season. The juvenile plants wilt in the subsequent short dry period, but are able to restore turgor when the rain starts again. Boyer suggested that the growing behaviour of the plant is determined by external factors only. This suggestion is in our view supported by the fact that these plants show continous growth in cultivation under everwet conditions. In this context it seems of interest to note that the elaborate frond morphology of the *Platycerium* species that inhabit the everwet tropics or areas without severe dry periods, is regarded by the present authors a secondary development. This secondary development may well have become realized only, when water became a less limiting growth factor, *viz*. the complex morphology of *P. coronarium*, in relation to that of *P. bifurcatum*, or the size of *P. andinum* if compared with that of *P. quadridichotomum*.

Boyer studied in particular the mineral nutrition and the water ecophysiology of both the gametophyte and the sporophyte. She analyzed the detritus within the basket and found it to consist mainly of remnants of base fronds, much less so of material from outside. Further, the decomposition of the material in the basket was very slow, in spite of good aeration, good water supply, and a well-developed microflora.

As a result, there is a very regular mineral supply of the plant, mainly from its own, decaying material (a ± closed system). The most important minerals are variously accumulated. Calcium was mainly found in the dead parts of the basket, whereas potassium was almost exclusively located in the living parts of the plant. According to Boyer, potassium seems to be a limiting factor for growth in *Platycerium*. She further noticed that germination of spores is inhabited by calcium, which seems the present authors a possible explanation for the fact that generally, juvenile *Platycerium* plants are absent from the basket.

Transpiration is proportionally greater in small plants if compared with larger ones, and a ± spherical nest is found in (part of the) small-sized taxa as a likely adaptation to drought, supposing that the food supply is not a limiting factor for plant growth. This trend is visible within the *P. bifurcatum* complex. The ssp. *bifurcatum* var. *hillii* is rather small-sized, with a ± spherical nest of base fronds. A ± prominent basket is present in the medium-sized ssp. *bifurcatum* var. *bifurcatum*. The largest representatives, ssp. *willinckii* (and ssp. *veitchii*) show a well-developed basket. Within the genus species with a ± spherical nest are comparatively small-sized; they are generally restricted to regions with a conspicuously dry period.

8. The systematic position of the genus

There has been some confusion about the relationships of *Platycerium* with the other genera of the polypodiaceous ferns. Earlier authors regarded *Platycerium* related to *Cheiropleuria, Christiopteris,* and *Dipteris, e.g.* Bower (1928) and Christensen (1938). Diels (1902) described a tribe Platyceriinae within a subfamily Acrosticheae within the Polypodiaceae, including *Platycerium* and *Cheiropleuria.* Copeland (1947) thought the affinity of *Platycerium* to *Cheiropleuria, Christiopteris,* and *Dipteris* to be not intimate, suggesting a more evident resemblance of *Platycerium* to *Pyrrosia*. However, the present genus was always seen as an isolated one, which made Ching (1940) to propose a separate family Platyceriaceae (*nom. illeg.*, see Jarrett, 1980). In spite of its characteristic features, *e.g.* the frond dimorphy, Platycerium does not show important distinctive characters to support the recognition of a separate family (Pichi Sermolli, 1977). Nowadays, especially because of the presence of stellate hairs in both genera, *Platycerium* is generally regarded to be related to *Pyrrosia*. Holttum (1946, 1949) was the first to suggest this idea, which is adopted by subsequent authors. Pichi Sermolli (1977) thought this relationship to be remote, as the only evidence which indicate it should be the presence of stellate hairs. Nayar (1970) set forth that also other characters point to a close relationship between *Pyrrosia* and *Platycerium*; he described a new subfamily Platycerioideae within the Polypodiaceae, including *Drymoglossum, Platycerium,* and *Pyrrosia*. Joe Hoshizaki (1972) and Crabbe *et al.* (1975) followed the idea of Nayar. However, Joe Hoshizaki noted that the genera have diverged widely from each other and their ancestor. In the present study *Platycerium* and *Pyrrosia s.l.* (including *Drymoglossum* and *Saxiglossum*) are regarded sister genera, comprising a monophyletic group within the Polypodiaceae, characterized by the apomorphic character states of stellate hairs.

9. Notes on specific delimitation

The recognition of different species is only possible when at least one character state can be perceived which developed as a consequence of genetic incompatibility between the newly formed species. Our studies to trace the phenetically distinct elements within the genus are based on the study of morphology and anatomy of mature sporophytes only. It appeared possible to accomodate the far greater part of the material into a number of morphologically distinct elements which kept their morphological characteristics when taken into cultivation; no intermediate forms being found. These elements have been given specific status.

The remaining material, *P. bifurcatum* of the present study, displayed a morphological heterogeneity, which could be correlated with geographical and ecological differences, although intermediate forms were traced. The morphological characteristics of these elements as present in typical herbarium specimens could not be verified from the specimens studied from cultivated material which showed great plasticity (in part also due to hybridization between the geographically distinct taxa recognized). Therefore, these taxa are given infraspecific rank.

10. The geographical distribution

The phytogeography of a monophyletic group is the result of a process affected by the following factors.

1. The age and place of origin of the group. Unknown in *Platycerium*.
2. The number of branchings in the cladogram (number of speciation processes). In Platycerium this is known for the recent species only; there is no knowledge about branches that have become extinct during the evolution of the genus. The rate of evolution of the various branches is unknown.
3. The distribution of the landmasses in time.
4. The paleoclimatology.
5. The dispersal quality of the *Platycerium* species, of which almost nothing is known, except that the greater part of the species occur in restricted distribution areas.
6. The suitability of the various biotas to accomodate *Platycerium* species.

The genus *Platycerium* is widely distributed and most diversified in Africa. This is noteworthy as, generally speaking, Africa is proportionally poor in tropical ferns if compared with Asia and America. This adds to the suggestion that the ancestor of these hairy ferns was resistent to drought (for at least part of the year). From the remarks made above any approach towards the phytogeography of *Platycerium* species seems rather speculative. Still we feel the need to further interest the reader in this subject.

Assuming that:

a. the cladogram includes *all* branches of the genus (no extinction of species others than the ancestral species of those given in cladogram),

b. the rates of evolution of the various branches do not show marked differences,

c. dispersal and vicariance are potentially equally important for establishing the distribution pattern, we have estimated the most parsimonious development of the present distribution pattern (Cracaft, 1975).

The age of origin of the genus *Platycerium* being unknown, we started with the idea that the genus arose on one of the present continents. Therefore, we have calculated the number of dispersal events necessary to explain the present day distribution, starting from Africa (Fig. 11a), S. America, S.E. Asia, Australia, and Malesia respectively. It appears that the most parsimonious explanation is to take Africa as the centre of origin. This implies that the ancestral African species of the *P. andinum*-group was dispersed from Madagascar to S. America, and that Australia was reached by two dif-

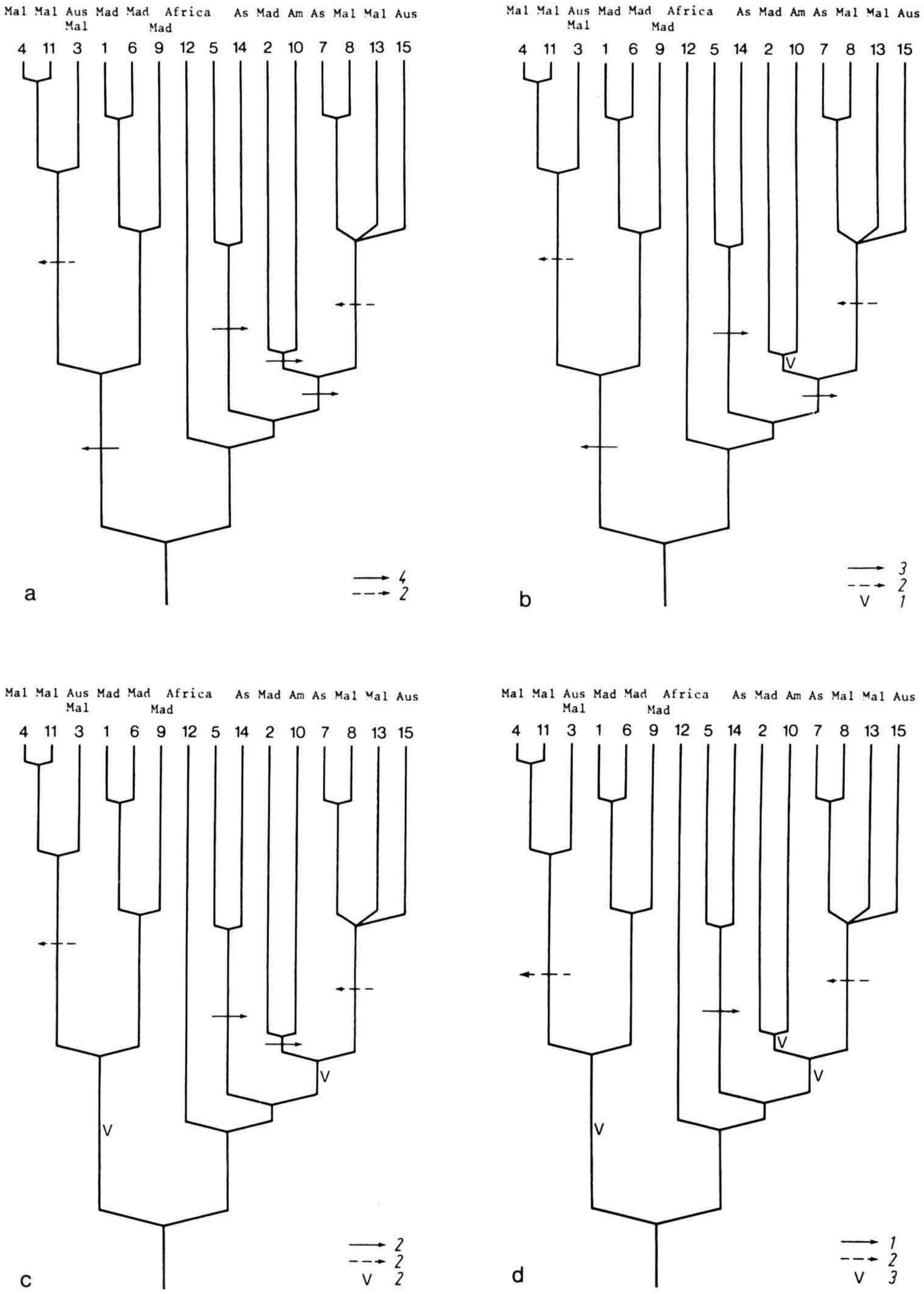

Fig. 11. Phylogenetic trees showing the number of events of long and short distance dispersal necessary for explaining the present distribution. Solid arrows represent events of long distance dispersal, dotted arrows events of short distance dispersal, V events of vicariance.

– a. Starting from Africa as the centre of origin. – b. Starting from a land mass consisting of Africa + S. America. – c. id. Africa + Australia. – d. Starting from Gondwanaland. – Am = America; As = continental Asia; Aus = Australia; Mad = Madagascar; Mal = Malesia.

ferent taxa (at different times?) either directly or through S.E. Asia. This reasoning assumes the general validity of long distance dispersal.

If we start from the idea that the genus originated earlier, i.e. at the time that one or more of the continents were mutually connected (theory of the Plate Tectonics), the land mass formed by the combination of Africa and Australia (Fig. 11c) appears to be a parsimonious one, though geologically (Dietz & Holden, 1970) less likely. In this model it is implicite that vicariance effected the geographical distribution of two of the four different evolutionary lines that had developed on the combined continents earlier. An equally parsimonious combination is that of Africa and S. America (Fig. 11b), which is in accordance with existing geological data (Dietz & Holden, *l.c.*). The latter model consequently explains the present distribution of *P. andinum* and *P. quadridichotomum* by supposing that the original distribution area of their ancestral species included very large parts of Africa and S. America, the present distribution of the two species being relict-like. When suggesting an origin of the genus in Gondwanaland (Fig. 11d), the presence of sister groups in Africa (western Gondwanaland) and Australia (eastern Gondwanaland), and that of sister groups between America and Africa can be both explained by vicariance. The development of the present distribution of the sister species *P. elephantotis* and *P. wallichii* can be variously explained: 1. via Australia and Malesia, which seems less likely, as no members of this group occur there. 2. via drift of the Indian continent. This seems unlikely as the genus is absent from S. India or Ceylon. 3. via Arabia. 4. via direct long distance dispersal.

The modern distribution pattern of the species can also be understood in terms of vicariance alone, when presuming the origin of the genus at a time when the Tethys sea did not exist or did not function as an actual barrier. The alternatives given should be viewed in relation to our present knowledge of the fossil platycerioid ferns, which is, however, nil. According to Harris (see Lovis, 1977) during the Jurassic (± 190–135 m.y. ago, the era during which the Tethys sea developed) the fern flora of Laurasia included elements which are considered as representatives of recent families, e.g. Thelypteridaceae (Yorkshire Jurassic: *Aspidistres*). This finding means that the ancestors of the main groups of leptosporangiate ferns may have arosen even earlier. Also, it is not improbable that the ancestors of the different groups within the polypodiaceous ferns already existed during the time of the breaking up of the continents (± 180–100 m.y. ago). Therefore, an early origin of one of the most conspicuous and presently most diversified groups of the Polypodiaceae, the platycerioid ferns, seems possible indeed, which implies a centre of origin of *Platycerium* in Gondwanaland.

CONCLUSIONS

The facts mentioned above point to Africa as the centre of origin of the genus. In case of an origin of the genus during a time that land masses were still combined it is plausible that the genus originated on a land mass consisting of at least Africa and Australia, and including a possible origin on Gondwanaland.

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Plate 1. *Platycerium wallichii*, a mature specimen growing as a high-epiphyte in hill evergreen forest along streams in northern Thailand (Sop Aep village, Payap; *Hennipman 3472*), shown by girls of the local Karen tribe in typical dress. – Phot. E. Hennipman.

Plate 2. *Platycerium holttumii* growing as high-epiphytes on *Shorea torrellii* (Dipterocarpaceae) in dry evergreen forest in northeastern Thailand (Ban Na Luang village, Udawn; *Hennipman 3968*, paratype). – Phot.: E. Hennipman.

Plate 3. *Platycerium bifurcatum* ssp. *willinckii* grown as an ornamental fern in a garden in Bogor (Java). – Phot.: M.C. Roos.

Plate 4. *Platycerium quadridichotomum*, an endemic from Madagascar, growing in the 'Massif de l'Ankarana'. a. habit in the rainy season; b. habit in the dry season. – Phot. a, b: J. Bogner.

Plate 5. *Platycerium madagascariense*, an endemic from Madagascar, growing in the Zahamena area. a. a clone living in association with *Cymbidiella rhodochila* (Orchidaceae); the ultimate segments of the foliage fronds are commonly gnawed by animals; b. cross-section through the 'bulb' formed by the subsequent base fronds, showing the white roots of *Cymbidiella rhodochila* inhabiting the spaces between the fronds. – Phot. a. b: J. Bogner.

Plate 6. *Platycerium elephantotis* growing as a high-epiphyte on *Ceiba pentandra* (Bombacaceae) in Zaire (near Rutshuru in the plain south of Lake Edwards; *Pichi Sermolli 4518*). – Phot. R.E.G. Pichi Sermolli.

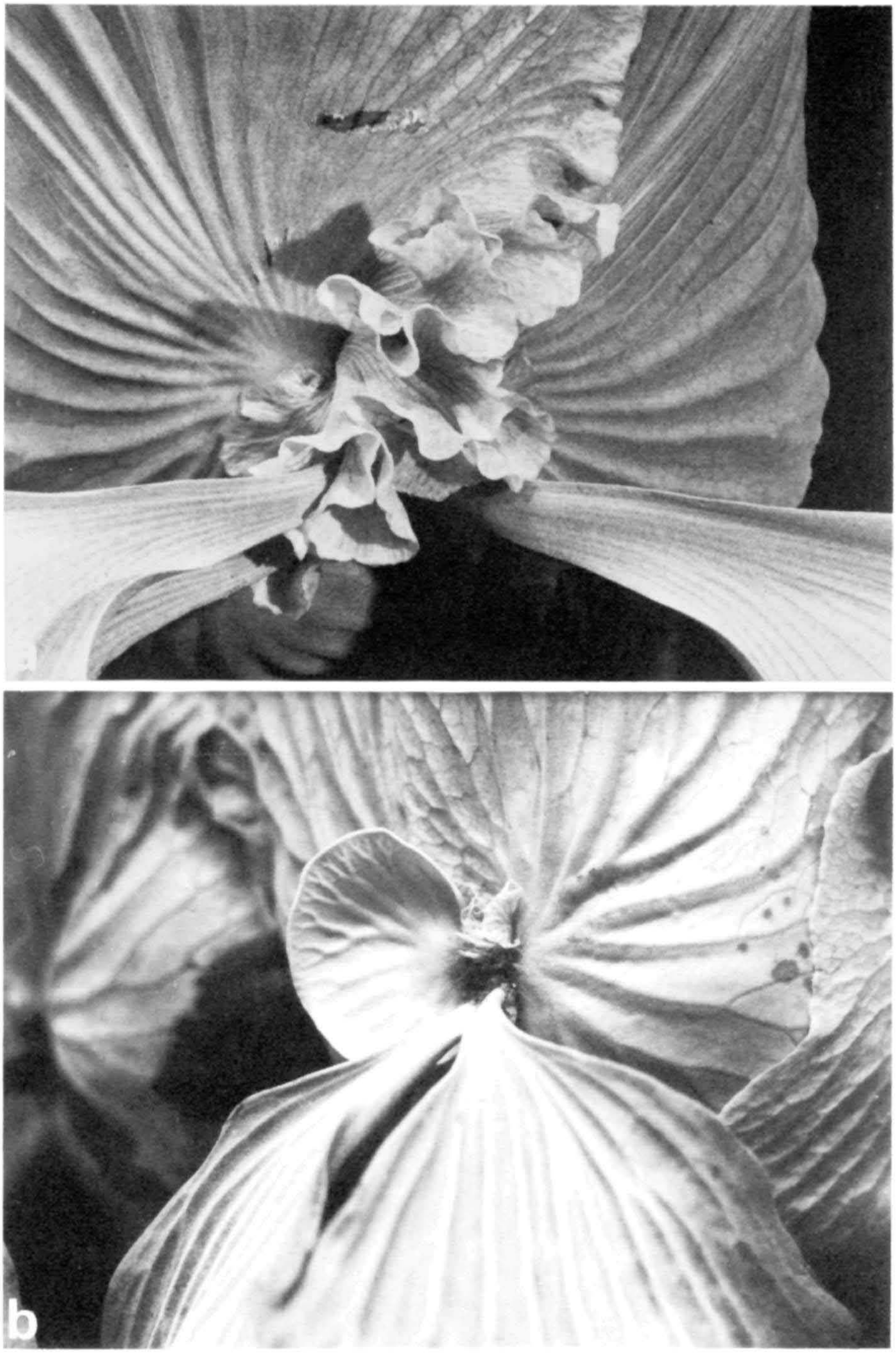

Plate 7. a. *Platycerium grande*, fringe of the base frond encircling the stipe of the foliage fronds; note the densely set (stellate) hairs on the base fronds. – b. *P. elephantotis*, detail of a mature specimen growing in the Botanic Garden, Munich, showing the rhizome apex densely covered with rhizome scales and the fringe of the base fronds being situated above the stipes of the foliage fronds only. – Phot. a.: B. Kieft; phot. b.: E. Hennipman.

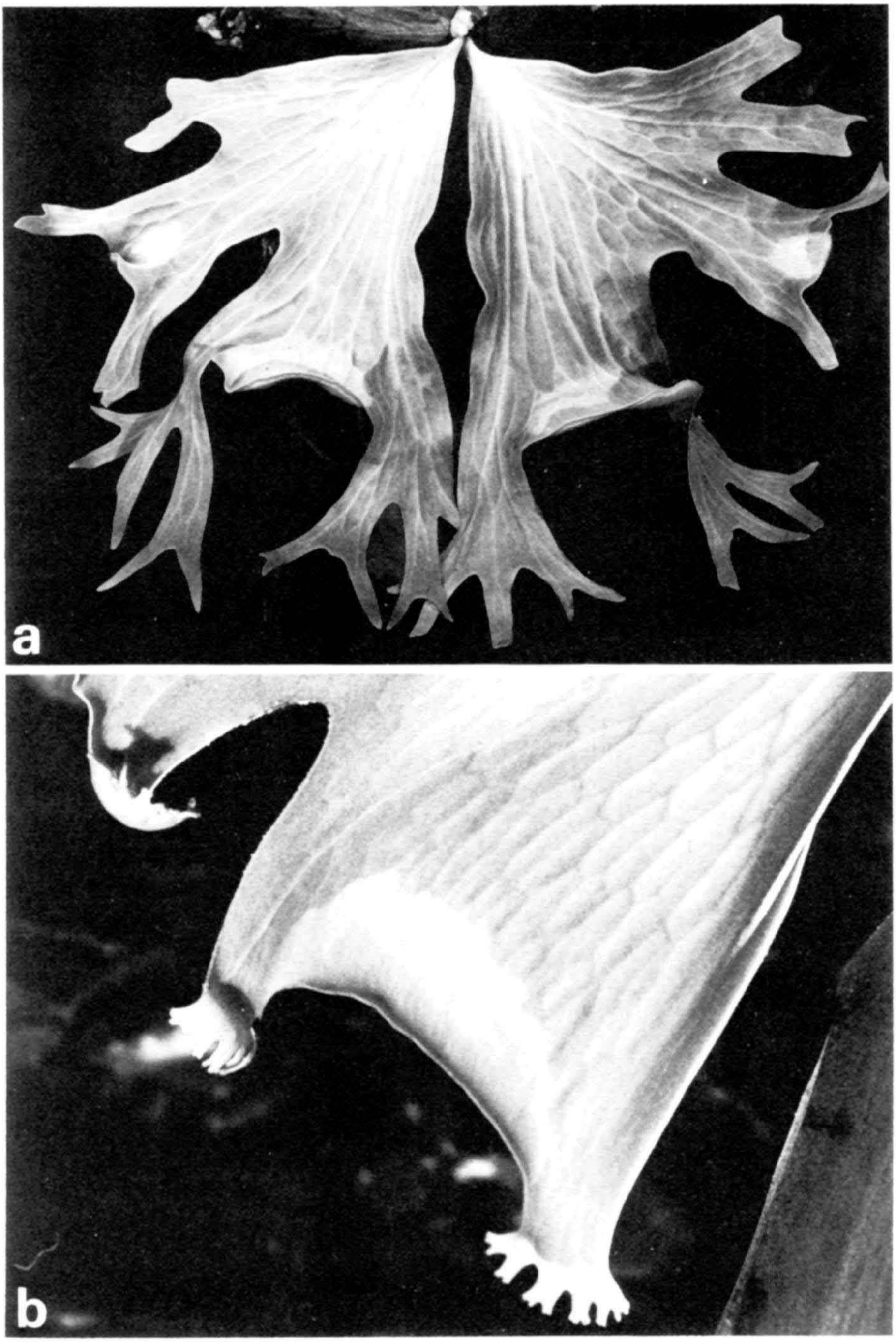

Plate 8. a. *Platycerium wallichii*, a mature specimen cultivated in the Botanic Garden, Leiden, showing the foliage fronds formed in pairs; the fronds being pendulous except for the soral patches which are horizontally exposed. – b. *P. grande*, detail of a young foliage frond of a specimen cultivated in the Botanic Garden, Leiden, showing the initiation of the soral patches prior to the elongation of the lateral appendages. – Phot. a, b: B. Kieft.

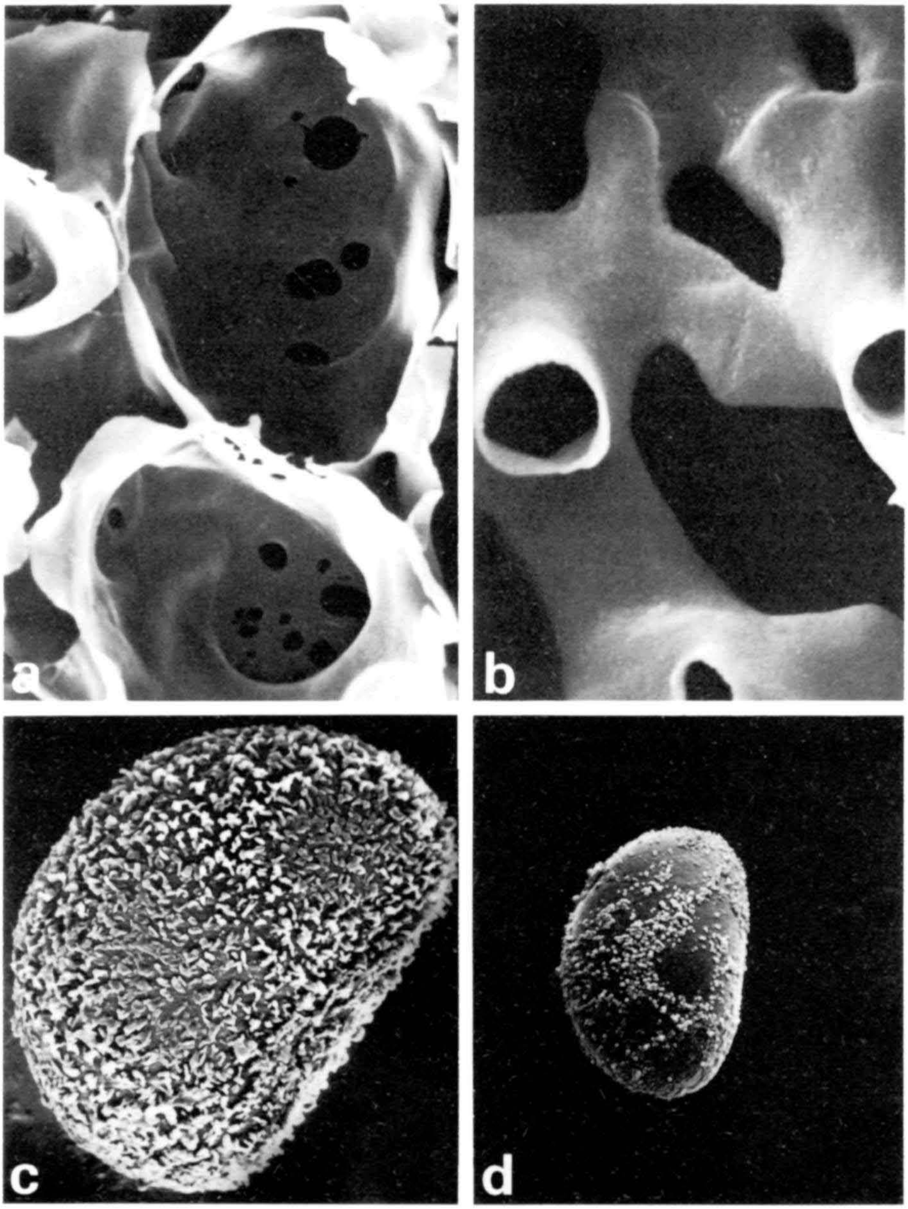

Plate 9. a, b. Waterstorage tissue, x 650. a. *Platycerium quadridichotomum*; b. *P. elephantotis* (a. *Peter 8274*, BR; b. *Cours 5462*, P). – c, d. Spores, x 700. c. *Platycerium ridleyi*; d. *P. bifurcatum* ssp. *veitchii* (c. *Meijer 2274*, L; d. *Henderson et al. s.n.*, L).

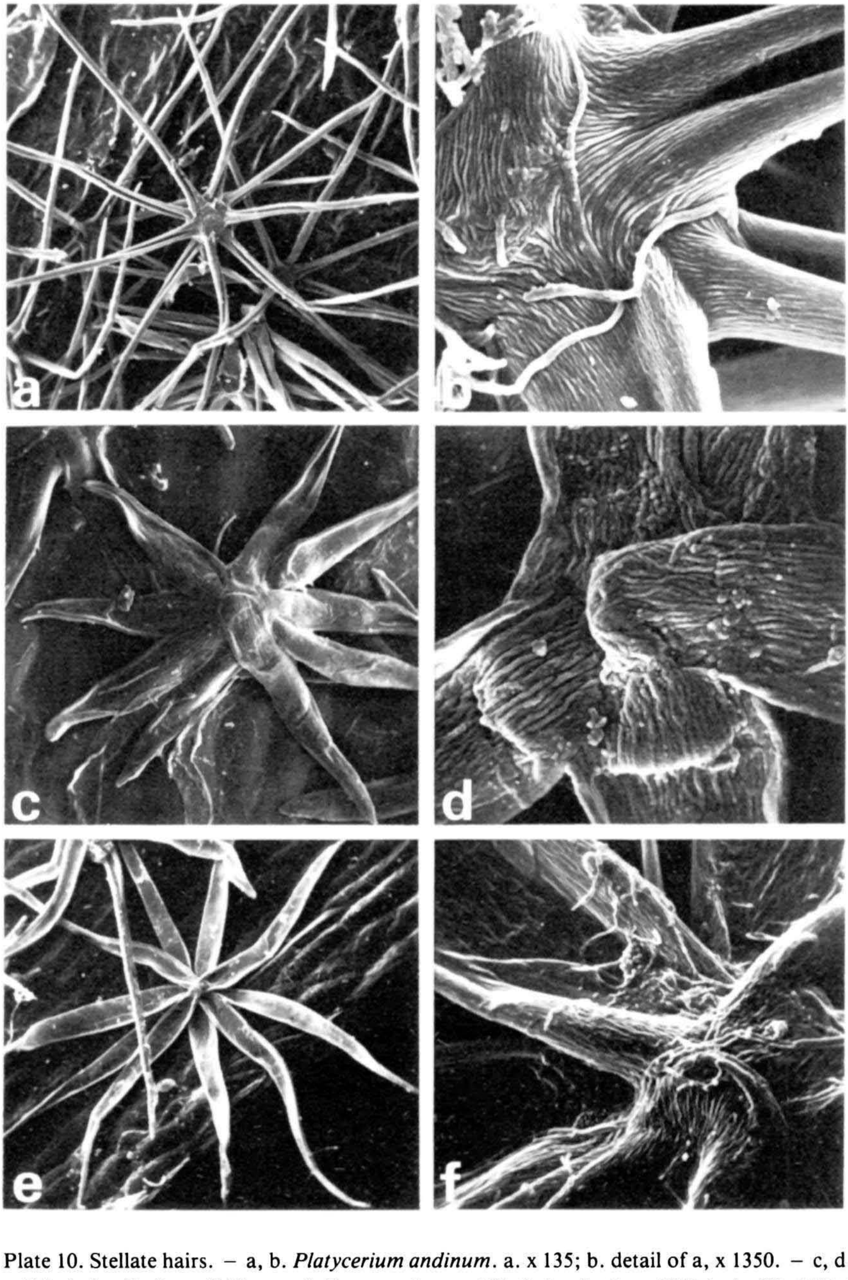

Plate 10. Stellate hairs. – a, b. *Platycerium andinum*. a. x 135; b. detail of a, x 1350. – c, d. *P. ellisii*. c. x 135; d. detail of c, x 1350. – e, f. *P. stemaria*. e. x 135; f. detail of e, x 1350 (a, b. *Ule 6520*, L; c, d. *Lam & Meeuse 6038*, L; e, f. *De Joncheere BCO 68*, L).

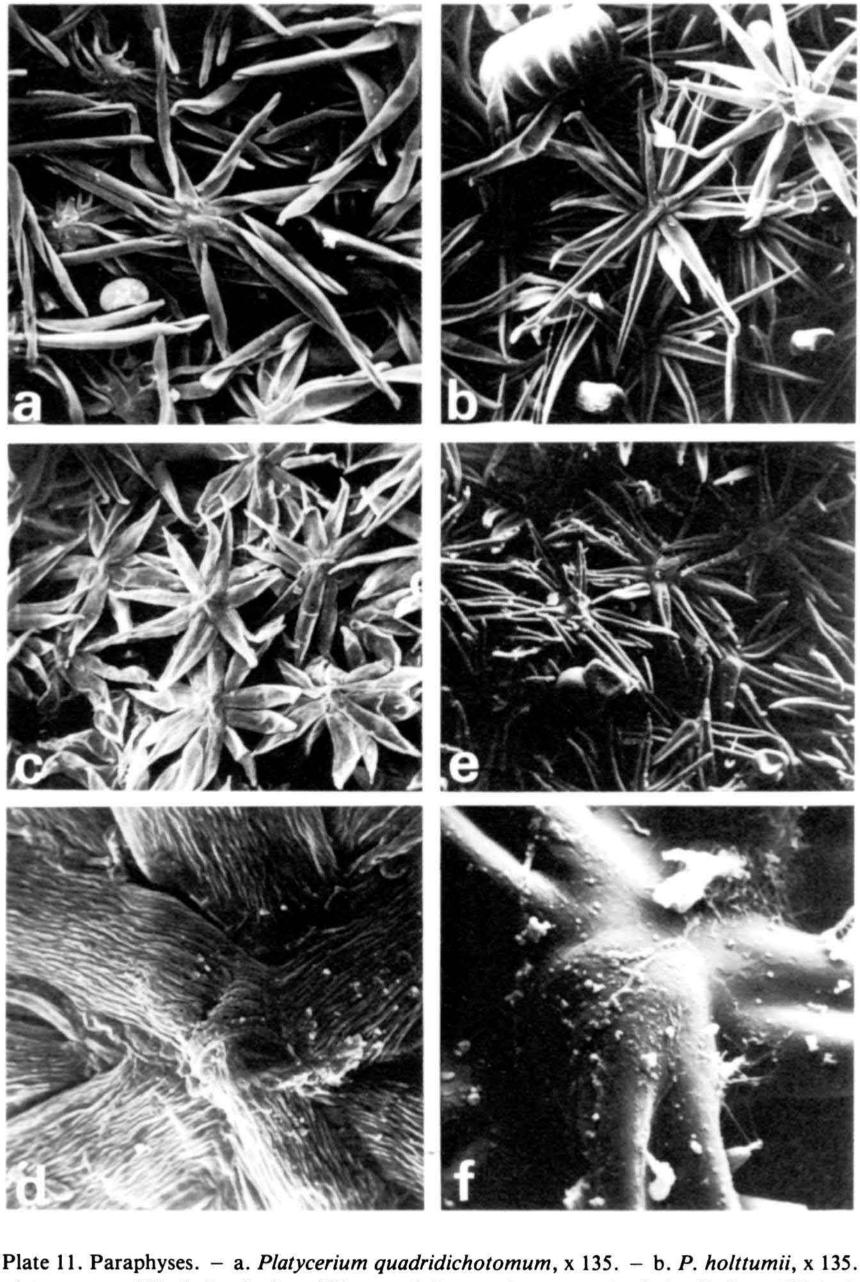

Plate 11. Paraphyses. – a. *Platycerium quadridichotomum*, x 135. – b. *P. holttumii*, x 135. – c, d. *P. alcicorne*. c. x 135; d. detail of c. x 700. – e, f. *P. superbum*. e. x 135; f. detail of e, x 700 (a. *Leandri 524*, P; b. *Collins 143*, K; c, d. *Schlieben 11155*, M; e, f. *Fraser s.n.*, BM).

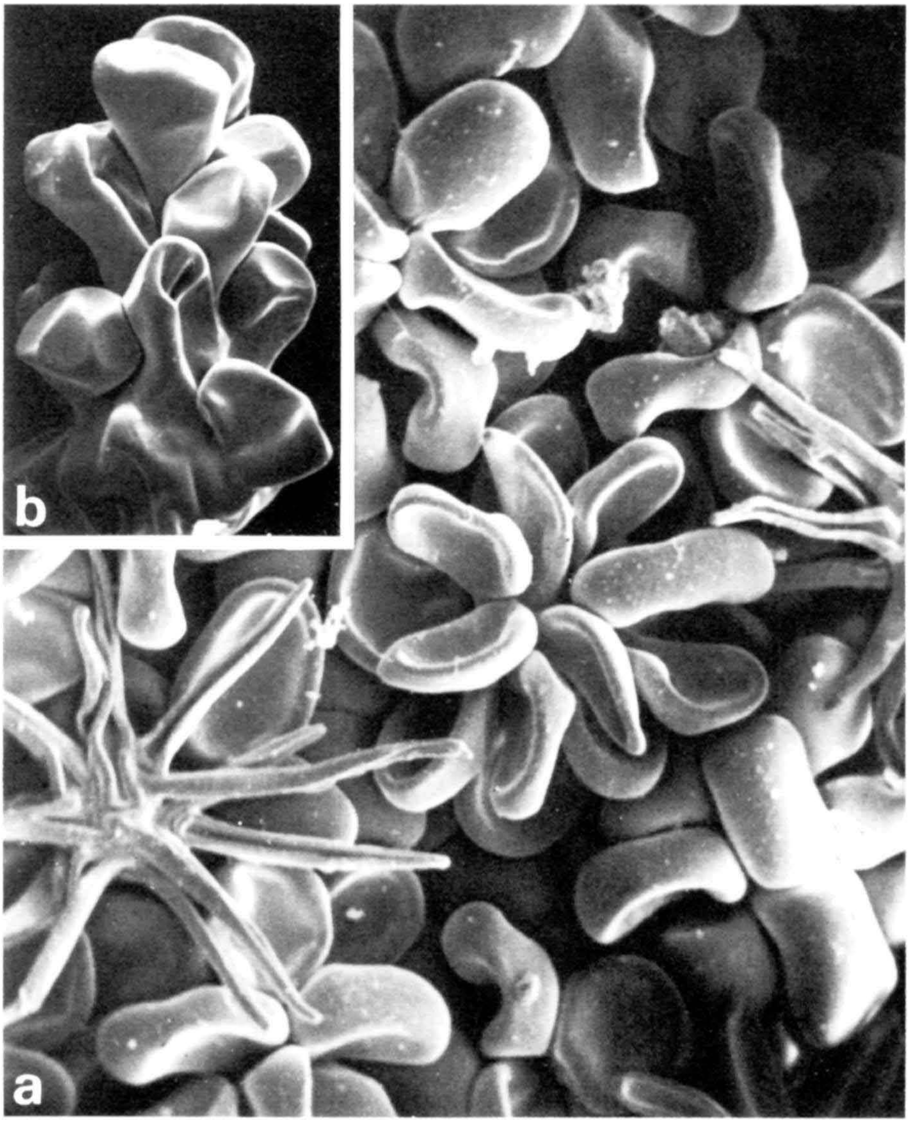

Plate 12. Paraphyses of *Platycerium ridleyi*, x 350. a. Surface view of the soral patch showing paraphyses and stellate hairs; b. lateral view of apical part of a paraphyse (*Gibot 36975*, K).

TAXONOMIC PART

1. Presentation of data. — Fig. 12

In the Taxonomic Part, the taxa are presented in an alphabetical sequence. We have refrained from giving formal status to the various infrageneric groups recognized in the General Part for fundamental reasons (see for instance Eldredge and Cracraft, 1980). For each of the taxa the synonymy is listed in full. Basionyms and the homotypic synonyms are listed together in chronological order, as are the heterotypic synonyms. A relevant selection of the literature is included. The abbreviations for the names of the authors are according to the Kew Index of Author Abbreviations; for names not included in this index, the authors choose convenient abbreviations. Nearly all type collections have been studied; those not seen by the authors are designated 'not traced' or 'n.v.' (not seen). The abbreviations used for the herbaria are according to the Index Herbariorum. The material studied included herbarium specimens as well as living material, both adult and juvenile (if present).

As the greater part of the species is large-sized, the herbarium specimens often comprise incomplete material only. Also, of a large number of species only a few herbarium collections are present in the herbaria. Additional living complete material of all taxa (wild and cultivated) contributed essentially to our work. A large collection of photographs, taken from wild and cultivated specimens, formed another important source of information.

The adult condition is described for each character. When necessary juvenile and aberrant conditions are separately discussed in notes. The condition of a character which occurs only rarely, is given between brackets.

The *'midrib'* of the scales comprises a central row of sclerenchyma cells, sometimes divided into 2 ridges. As to the indument of the scales, small projections of the cells of the hairs are called *protuberances*. *Glandular cells* are ± pear-shaped with a yellow or brown content. *Acicular cells* are usually long and slender, sometimes short-conical, never being glandular.

The term *trichomes* is used for all indumental enations on the scale, whereas 2- or more-celled uniseriate trichomes are called *hairs*.

The *flabelloid margin* as found on the scales of *P. coronarium*, and *P. ridleyi* comprises a very thin membranous marginal zone, which is one cell-layer thick, and of which the cells are arranged in rows, perpendicular to the margin. The *shape* of the scales is indicated by the index (length/width ratio) and the place where the scale is widest.

Withering of the base frond occurs when just after its maturation, the frond turns brown, loosing its photosynthetic function.

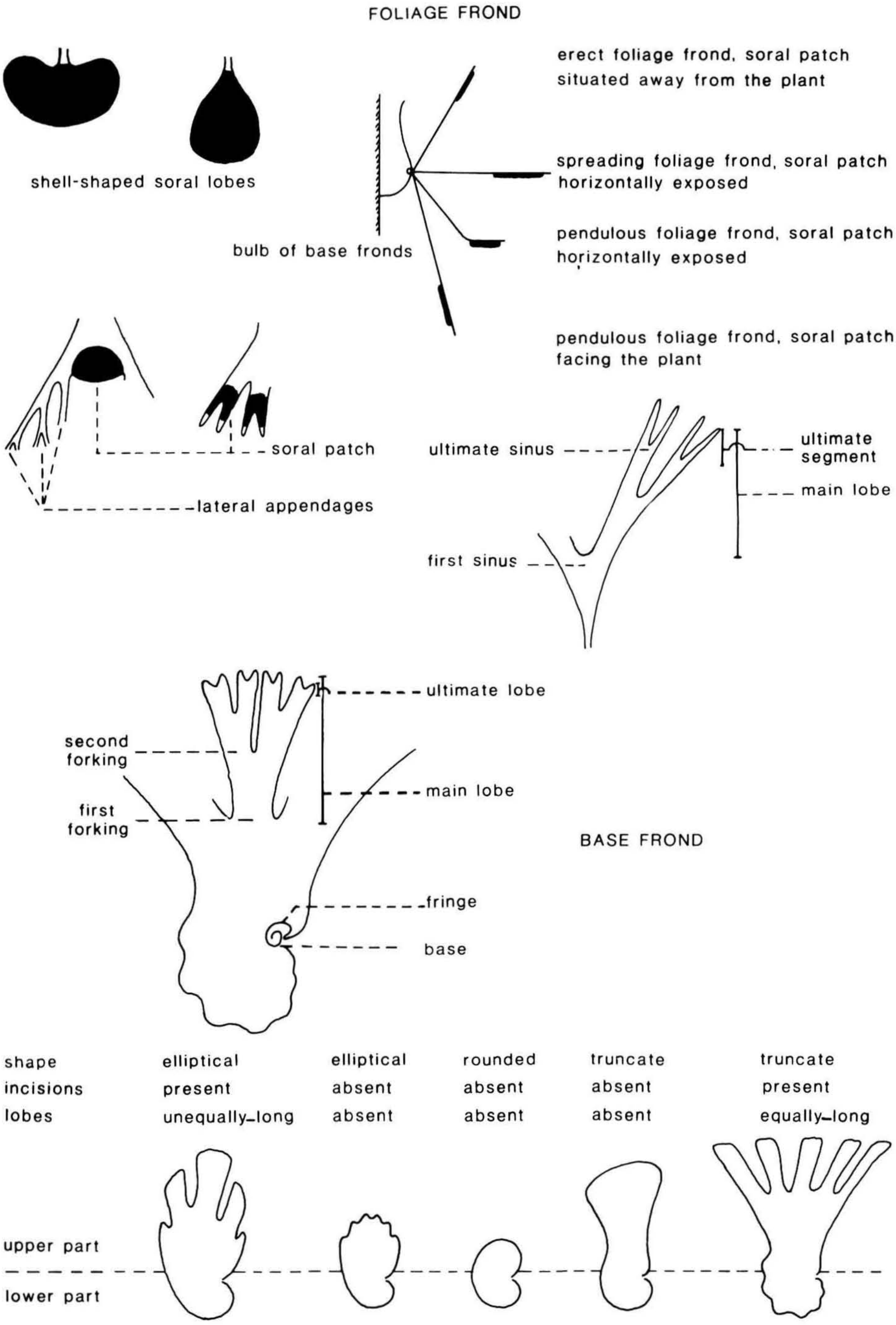

Fig. 12. Illustration of descriptive terms.

The *fringe* is a foliaceous curled 'frill' or 'collar', situated near to or around the base of the base frond.

The *water storage tissue* comprises the tissue in the thickened basal part of the base frond, consisting of cells with ± large intercellular spaces. *Veins* are called *prominent* in case they project markedly from the surface, being distinct all over the base frond; *immersed* veins are those veins that are immersed at least in the (thickened) basal part of the frond, sometimes becoming ± pronounced in the foliaceous upper part.

When foliage fronds are formed in pairs they may be arranged into a *bilateral symmetrical pattern* with a vertical plane of symmetry through the rhizome apex. The *length* of the foliage fronds is given only, the width is often very difficult to establish in species with elaborately forked fronds. When the *texture* of the foliage fronds is firm and thick, it is described as leathery, when it is rather thick (in most of the species) it is described as pergamentaceous.

The *soral patch* is defined as the area on the foliage fronds, where the sporangia and paraphyses are inserted, whereas the *soral lobe* is a shell-shaped soral patch.

The *measurements* of the sporangia are taken from sporangia in lateral view, the sizes of the rays of the stellate hairs are taken from such hairs in apical view, the sizes of the spores given are those as seen from spores in lateral view and in polar view.

The *distribution* given follows political boundaries. The frequency of distribution of each taxon throughout its geographical area can be inferred from the density of dots on the distribution maps. The maps are compiled from herbarium collections with precise localities. The *habitat* is described using the – often very scanty – information on the herbarium labels; a number of species has been studied in the field. *Notes* have been added to all species, including various kinds of additional information (mainly morphological and taxonomical).

Illustrations of frond shapes and scales are generalized; they are based on herbarium and living material. In these drawings glandular cells are hatched whereas soral patches are given in solid black. The illustrations of the transformation series are all schematical.

The *key* to the species is based on the characters given in Table 1 and 2. As much as possible only macroscopical characters have been used.

2. PLATYCERIUM

Platycerium Desv., Mém. Soc. Linn. Paris 6 (1827) 213; Blume, Fl. Javae (1828) 43; C. Presl. Tent. Pterid. (1836) 239; Hooker, Gen. Fil. (1842) t. 80B; J. Smith, Hook. J. Bot. 4 (1842) 153; C. Presl, Epim. bot. (1851) 152; Mettenius, Filices Horti Bot. Lips. (1856) 26; T. Moore, Index Fil. (1857) 22; Hooker, Spec. Fil. (1864) 282; Bedd., Ferns Brit. Ind. (1866) 108; J. Rotschild *et al.*, Fougères 1 (1867) 185; Baker in Hooker & Baker, Syn. Fil. (1868) 425; E.J. Lowe, Ferns 7 (1868) 153; Mettenius, Annls Mus. Bot. L.B. 4 (1868–'69) 170; J. Smith, Hist. Fil. (1875) 122; Bedd. Handb. Ferns Br. Ind. ed. 2 (1892) 444; J. Smith, Ferns Br. & For. (1896) 120; Christ, Farnkr. Erde (1897) 124; Carruth., J. Bot., Lond. 38 (1900) 123–125; F.M. Bailey, Queensl. Fl. 6 (1902) 1994; Diels in E. & P., Nat. Pfl. Fam. 1,4 (1902) 336; Copel., Dep. int. Bur. Govern. 28 (1905) 138; v.A.v.R., Mal. Ferns (1908) 707; Engl., Pflanzenw. Afr. 2 (1908) 58; Poisson, Revue hort. 10 (1910) 458, 530; Wigman jr., Teysmannia 21 (1910) 150; Strraszewski, Flora, Jena 108 (1915) 271; Ridley, J. Malay. Brch R. Asiat. Soc. 4,1 (1926) 109; Copel., Univ. Calif. Publs Bot. 16 (1929) 103; C. Chr., Dansk Bot. Ark. 7 (Pterid. Mad.) (1932) 171; Backer & Posthumus, Varenfl. Java (1939) 246; Ching, Sunyatsenia 5,4 (1940) 256; Tardieu & C. Chr. in Lecomte, Fl. Gén. Indo-Chine 7,2 (1941) 445; Copel., Gen. Fil. (1947) 179; Pichi Sermolli, Webbia 9,2 (1953) 434; Tardieu, Mém. Inst. fr. Afr. noire 28 (1953) 208; Holttum, Fl. Mal. 2 (Ferns) (1954) 137; Subcommittee for Pteridophyta, Taxon 3 (1954) 70; Copel., Fern Fl. Philipp. 3 (1960) 457; Tardieu, Polyp. 2 in Humbert, Fl. Mad. (1960) 94; Tindale, Contr. N.S.W. Herbarium, Flora Ser. 208–211 (1961) 25; Joe, Baileya 12,3 (1964) 69; Morton, Baileya 12 (1964) 36; Tardieu in Aubrév., Fl. Cameroun 3 (1964) 332; Fl. Gabon 8 (1964) 196; De Jonch., Blumea 15,2 (1967) 445; Joe Hoshizaki, Am. Fern J. 60 (1970) 144; N.C.W. Beadle, Fl. Sydney Reg. (1972) 72; Joe Hoshizaki, Biotropica 4 (1972) De Jonch., Blumea 22 (1974) 55; D.L. Jones & Clemesha, Austr. ferns (1976) 223, id. 2nd ed. (1980) 180. – *Acrostichum* L. subg. *Neuroplatyceros* [(Plukenet)] Endl., Gen. Pl. 1 (1836) 59. – [*Neuroplatyceros* Plukenet, Amlth. Bot. (1705) 151]. *Neuroplatyceros* Fée, Mém. Fougeres 2, Acrost. (1845) 25; Mém. Fougères 5, Gen. Fil. (1850–'52) 62. – *Neuroplatyceros* Fée subg. *Platyceria* Fée, Mém. Fougères 2, Acrost. (1845) 104; Mém. Fougères 5, Gen. Fil. (1850–'52) 62. – *Platycerium* Desv. subg. *Platyceria* (Fée) T. Moore, Ind. Fil. (1857) 22. – *Acrostichum* L. subg. *Platycerium* (Desv.) Kunze, Bot. Ztg. 6,6 (1848) 102. *Platycerium* Desv. sect. *Euplatycerium* Diels in E. & P., Nat. Pfl. Fam. 1,4 (1902) 339; v.A.v.R., Mal. Ferns (1908) 707; Mal. Ferns Suppl. (1917) 421; – Lectotype (J. Smith, 1875): *Acrostichum alcicorne* Swartz (= *P. alcicorne* Desv.).

Alcicornium Gaudich., Freychin. Voy. Bot. (1826) 48, *nom. illeg.*; Underwood, Mem. Torrey bot. Club 6 (1899) 275; Bull. Torrey bot. Club 30 (1903) 672; 32 (1905) 588. – Type: *Alcicornium vulgare* Gaudich., *nom. illeg.* (= *P. bifurcatum* (Cav.) C. Chr.).

Neuroplatyceros (Pluk. *ex* Endl.) Fée subg. *Scutigera* Fée, Mém. Fougères 2, Acrost. (1845) 104; Mém. Fougères 5, Gen. Fil. (1850–'52) 62. – *Platycerium* Desv. subg. *Scutigera* (Fée) T. Moore, Ind. Fil. (1857) 22; Diels in E. & P., Nat. Pfl. Fam. 1,4 (1902) 339; v.A.v.R., Mal. Ferns (1908) 707; Mal. Ferns suppl. (1917) 421. – Type: *Neuroplatyceros biformis* (Blume) Fée (= *P. coronarium* (König *ex* Müller) Desv.).

Herbs, generally epiphytic, sometimes epilithic, growing solitary, or in clusters. – *Rhizome* stout, cilindrical or dorsiventrally flattened, usually forming lateral shoots from which new plants emerge, densely set with overlapping scales, dictyostelic. – *Scales* usually basally-attached, rarely (*P. bifurcatum p.p.*) peltate, index 3–20 (–30) widest about or below the middle, 2–28 by 0.4–8.5 (–10) mm, base usually truncate, sometimes rounded, margin entire, straight to slightly convex, sometimes flabelloid, apex usually acute to filiform, sometimes rounded, papery or thin-coriaceous, opaque, brownish, midrib often present, variously shaped, brownish to blackish; indument: hairs variously shaped; apical hair always present, glandular; other hairs usually present, rarely (*P. wallichii*) absent, situated marginally, usually also abaxially, sometimes in a narrow marginal zone (*P. grande*-group), sparsely to very densely set and best developed in especially the upper half of the scale, unbranched or branched, sometimes with protuberances (the *P. grande*-group), 2–8-celled, 25–1000 μm long, thin-walled; apical cell either cylindrical, glandular, light-brown, or apical cell cone- to needle-shaped, non-glandular, hyaline, always of the same size in branched and unbranched hairs of one species, other cells cylindrical, hyaline; 1-celled trichomes usually present, glandular or non-glandular. – *Base fronds* non-articulate to the rhizome, usually sessile, rarely shortly stalked, in most of the species forming a so-called nest or basket, sterile, persistent, greyish green to dark green, or brown, variously densely covered with stellate hairs, especially above, old fronds appressed, erect or recurved, upper part erect, spreading or appressed to the substratum, variously shaped, and -incised, lower part appressed to the substratum with the margin entire, sinuate or dentate, with or without a fringe ('frill', 'collar'); venation and texture various, water storage tissue, if present, variously structured near the base. – *Foliage fronds* articulate to the rhizome, formed in pairs (in a symmetrical pattern) or in an undetermined number, fertile and sterile parts of fertile fronds developing simultaneously or in succession, variously shaped, entire to many times forked, erect to pendulous, usually fertile, (shortly) stalked, the base (narrowly) wedge-shaped, with 1–many variously shaped, initiated, positioned and exposed soral patches, decideous, green, variously densely covered with stellate hairs, especially beneath; venation various, texture usually thick-pergamentaceous, sometimes leathery. – *Sporangia* biconvex, ellipsoid or ± spherical, (200–)250–400(–450 by (130–)200–300(–350) μm, index 1.1–1.5(–2.3), annulus cells: 20–30(–34), indurated cells: (9)10–22(–24), epistomium cells: (2)3–7(–9), stomium cells: 2, hypostomium cells: 1–4(5), stomium mostly laterally, rarely apically situated (*P. ridleyi*), stalk usually (2)3-seriate, 0.1–0.5 mm long, or sometimes 1(–3)-seriate, 1.5–2.0 mm long, spores: usually 64, sometimes 8, bean-shaped, 60–105 by 30–75 by 30–75 μm, perispore usually indistinct, sometimes distinct, flaky; dehiscence of paraphyses and sporangia usually absent, sometimes present. – *Indument*: stellate hairs with (5–)7–12(–16) rays which are terminally inserted, usually undifferentiated with apex filiform, sometimes with a narrow flat marginal zone with apex round or acute, 75–475(–900) by 15–45 μm; paraphyses with (5–)7–15(–24) rays, usually terminally, sometimes also subterminally inserted, usually undifferentiated, involute to canaliculate, sometimes either flat or convex, or spine-like, or short-clavate, 80–450(–600) by (20–)25–50(–90) μm; usually short-stalked (less than 1 mm long), sometimes long-stalked (up to more than 2.5 mm long).

Chromosomes. N = 37, 2N = 74 (Löve, Löve & Pichi Sermolli, 1977; Lovis, 1977).

Distribution. Pantropic, in E. Australia also subtropical. Widely distributed in the Palaeotropics; in the Neotropics with only one local species.

Habitat. Generally epiphytic, sometimes epilithic; generally in forests, sometimes in cultivated areas or open landscapes; in everwet or monsoon areas; altitudinal range 0–750(–2000) m.

Notes. 1. The colour of the scales turns darker upon drying.

2. The marginal cells of many species often show lateral thickenings ('papillae', Joe, 1970) which are rather conspicuous in scales without (a well-developed) indument, and especially in *P. wallichii*.

3. Withering of the base fronds starts from the point of attachment of the base frond, whereas the decay of the base fronds starts from the foliaceous marginal upper parts.

3. Key to the species

1. Foliage fronds with 1 soral patch situated on a separate, stalked, shell-shaped, lobe; scales: margin flabelloid, apex rounded, midrib split at the base, and/or ▵-shaped 2

1. Foliage fronds with 1 to many soral patches situated on sessile segments or in sinusses; scales: margin narrow (not flabelloid), apex acute to filiform, midrib (if present) entire 3

2. Foliage fronds long-pendulous, fertile lobe kidney-shaped; upper part of base fronds deeply lobed, veins immersed .... **4. P. coronarium**

2. Foliage fronds erect, fertile lobe obovate or elliptical; upper part of base frond entire or slightly sinuate; veins very prominent .... **11. P. ridleyi**

3. Soral patches 1–2, wedge-shaped or semicircular with lateral appendages; upper part of base fronds deeply lobed; lobes many, equally-long 4

3. Soral patches 1–many, linear, deeply lobed, or wedge-shaped; without lateral appendages, upper part of base fronds entire or lobed; lobes either 2, equally-long, or many and unequally-long 8

4. Foliage fronds with 3 main lobes, 2 of which with one soral patch; scales 0.2–0.7 mm wide; mature base fronds brown .... **14. P. wallichii**

4. Foliage fronds, entire with 1 soral patch, or divided into 2 main lobes each of which with one soral patch; scales 1.0–5.0 mm wide; mature base fronds green 5

5. Foliage fronds with 1 soral patch .... **13. P. superbum**

5. Foliage fronds with 2 soral patches 6

6. Foliage fronds symmetrical, consisting of 2 equal halves .... **7. P. grande**

6. Foliage fronds assymetrical 7

7. Soral patches with lateral appendages; scales without a 'midrib'. Mainland Asia .... **8. P. holttumii**

7. The proximal soral patch without lateral appendages; scales usually with a 'midrib'. New Guinea .... **15. P. wandae**

8. Foliage fronds entire with a broadly rounded apex; mature base fronds erect, grass-green .... **5. P. elephantotis**

8. Foliage fronds usually at least once divided, sometimes entire with an acute apex; mature base fronds either erect, brown, or appressed, dark green 9

9. Mature base fronds dark green, the lower margin denticulate, with a conspicuous fringe encircling the stipes, veins raised forming a waffle pattern. Madagascar .... **9. P. madagascariense**

9. Mature base fronds brown, the lower margin entire, without or with a fringe situated above the stipe only; veins immersed.......................... 10

10. Foliage fronds entire with the soral patch situated terminally, or 1(–2)–times forked with the soral patches wedge-shaped and situated around the sinusses 11

10. Foliage fronds 2–many times divided, the soral patches linear or with linear or elongated lobes.. 12

11. Upper part of base fronds erect, foliage fronds spreading, 1(–2)–times divided. Mainland Africa....................................... **12. P. stemaria**

11. Upper part of base fronds appressed, foliage fronds erect, entire or once lobed. Madagascar.. **6. P. ellisii**

12. Ultimate parts of the fertile segments sterile; 2 foliage fronds formed at the same time.. 13

12. Ultimate parts of the fertile segments fertile; the number of foliage fronds formed at a time undetermined.. 14

13. Upper part of the base fronds with 2 main lobes; scales without a 'midrib'; fertile foliage fronds 100–(more than?) 200 cm long. S. America..... **2. P. andinum**

13. Upper part of the base fronds entire; scales with a 'midrib'; fertile foliage fronds 15–50 cm long. Madagascar.................... **10. P. quadridichotomum**

14. Foliage fronds ± asymmetrical, usually spreading or pendulous, sometimes erect, main vein reaching to up to 1/3 of the undivided basal part of the frond; scales: marginal hairs glandular, 2–7-celled. Australia, E. Malesia........... .... **3. P. bifurcatum**

14. Foliage fronds symmetrical, erect, main vein reaching to up to more than halfway of the undivided basal part of the frond; scales: marginal and abaxial trichomes glandular or non-glandular. 1–2-celled. Africa, Madagascar................ .... **1. P. alcicorne**

4. Descriptions

1. **Platycerium alcicorne** Desvaux. – **Fig. 13e–13f, 14, 28.**

P. alcicorne Desv., Mém. Soc. Linn. Paris 6 (1827) 213; Blume, Fl. Javae (1828) 46, *p.p.*; C. Presl. Epim. bot (1851) 153, *p.p.*; Hooker, Spec. Fil. (1864) 282, *p.p.*; J. Rothschild et al., Fougères 1 (1867) 186, Fig. 34, *s.n.*, *p.p.*; Baker in Hooker & Baker, Syn. Fil. (1868) 425, *p.p.*; E.J. Lowe, Ferns 7 (1868) 153, Fig. 63, *s.n.*, *p.p.*; Mettenius, Annls Mus. Bot. L.B. 4 (1868–69) 170, *p.p.*; Benth., Fl. Austr. 7 (1878) 781 *p.p.*; F. Muell., Sec. syst. cens. Austr. pl. 1 (1889) 234, *p.p.*; Racib., Pterid. Fl. Buitenz. (1898) 57, *p.p.*; Carruth., J. Bot., Lond. 38 (1900) 125, *p.p.*; F.M. Bailey, Queensl. Fl. 6 (1902) 1995, *p.p.*; De Jonch., Blumea 15,2 (1967) 445, Pl. 1, Fig. 1:2; Schelpe, Contr. Bolus Herb. 1 (1969) 89; De Jonch., Blumea 22 (1974) 55; Schelpe & Diniz in Mendes, Fl. Moçamb. Pterid. (1979) 148. – *Acrostichum alcicorne* Swartz, Schrader, J. Bot. 1800, 2 (1801) 11, *nom. illeg.*; Syn. Fil. (1806) 12, 196, *p.p.*; Schkuhr, Krypt. Gew. (1809) 1, Pl. 2; R. Brown, Prodr. Fl. Nov. Holl. (1810) 145, *p.p.*; Sprengel, Syst. Veg. (1827) 35, *p.p.*; Blume, Enum. Pl. Javae (1828) 103, *p.p.*; Turpin, Dict. Sc. Nat. (1826–'29) Pl. 82; Link, Hort. Reg. Bot. Ber. (1833) 47, *p.p.*; Kunze, Bot. Ztg. 6 (1848) 102, *p.p.* – *Elaphoglossum alcicorne* Keys., Pol. Cyath. Hb. Bung. (1873) 37. – Type: *Herb. Sloane vol. 102, fol. 194*, Comores, Johanna I. (*Adair leg.*?, see Schelpe, 1969) (BM).

Acrostichum alcicorne Willem., Usteri. Ann. Bot. 18 (1796) 61; Willd., Spec. Pl. 5 (1810) 111 *p.p.*; – *Neuroplatyceros alcicornis* (Willem.) Fée, Mém. Fougères 2 (Acrost.) (1845) 102, *p.p.*; – *P. alcicorne* (Willem.) Desv.; Copel., Gen. Fil. (1947) 179, *p.p.*, *nom. illeg.* – *P. alcicorne* (Willem.) Tardieu, Not. Syst. (Paris) 15 (1959) 417, Pl. 1: Fig. 1, 2, *nom. illeg.*; in Humbert, Fl. Madag. (1960) 96, Fig. 22: 1, 2; - Type: *Stadtmann,* Madagascar (not traced; see De Joncheere, 1967).

P. vassei Poisson, Revue hort. 10 (1910) 530; Anonymous, Bull. misc. Inf. R. bot. Gdns Kew (app. 3) (1911) 107; C. Chr., Ind. Fil., Suppl. 1 (1913) 55; Straszewski, Flora, Jena 108 (1915) 307, Fig. 23; Morton, Baileya 12 (1964) 36; Joe, Baileya 12 (1964) 101, Fig. 46; Joe Hoshizaki, Am. Fern J. 60 (1970) Pl. 19: fig. 19; Biotropica 4 (1972) 95, Pl. 1: Fig. 1, Pl. 2: Fig. 6, 20, 21, Pl. 3: Fig. 6, Pl. 5: Fig. 2, 10, Pl. 7: Fig. 6, Pl. 8: Fig. 6; – Type: a cultivated specimen; origin: Moçambique, *Vasse leg.* (n.v.).

P. bifurcatum auct. non (Cav.) C. Chr. *quoad specim. Afr. solem*: Engl., Pflanzenw. Afr. 2 (1908) 59; Domin. Bibltca Bot. 85, 1 (1915) 196; C. Chr. in Bonap., Notes Pterid. 16 (1925) 135; Backer & Posthumus, Varenfl. Java (1939) 247.

P. stemaria auct. non (Beauv.) Desvaux: Turpin, Dict. Sc. Nat. (1816–1829) 245; C. Chr., Ind. Fil. (1906) 496; Dansk bot. Ark. 7 (1932) 171.

Alcicornium stemaria auct. non (Beauv.) Underwood: Underwood, Bull. Torrey bot. Club 32 (1905) 595, *p.p.*

P. confusum Blume *ex* Mettenius, Annls Mus. Bot. L.B. 4 (1868–'69) 170, *nomen.*

Epiphytic, growing in clusters. – *Scales* basally attached, index 4.5–10 (–13), widest at or somewhat above the base, 3.5–12.0 by 0.5–1.5 mm, base usually truncate, sometimes rounded, margin usually ± straight to slightly convex throughout, sometimes slightly concave near the filiform apex, not flabelloid, thin-coriaceous, light- to red-brown, midrib undivided, linear or narrow-triangular, in cross-section round to elliptic; indument: hairs sparsely set, situated marginally and abaxially, unbranched 2(–3)-celled, 30–175 μm long, without protuberances; apical cell usually

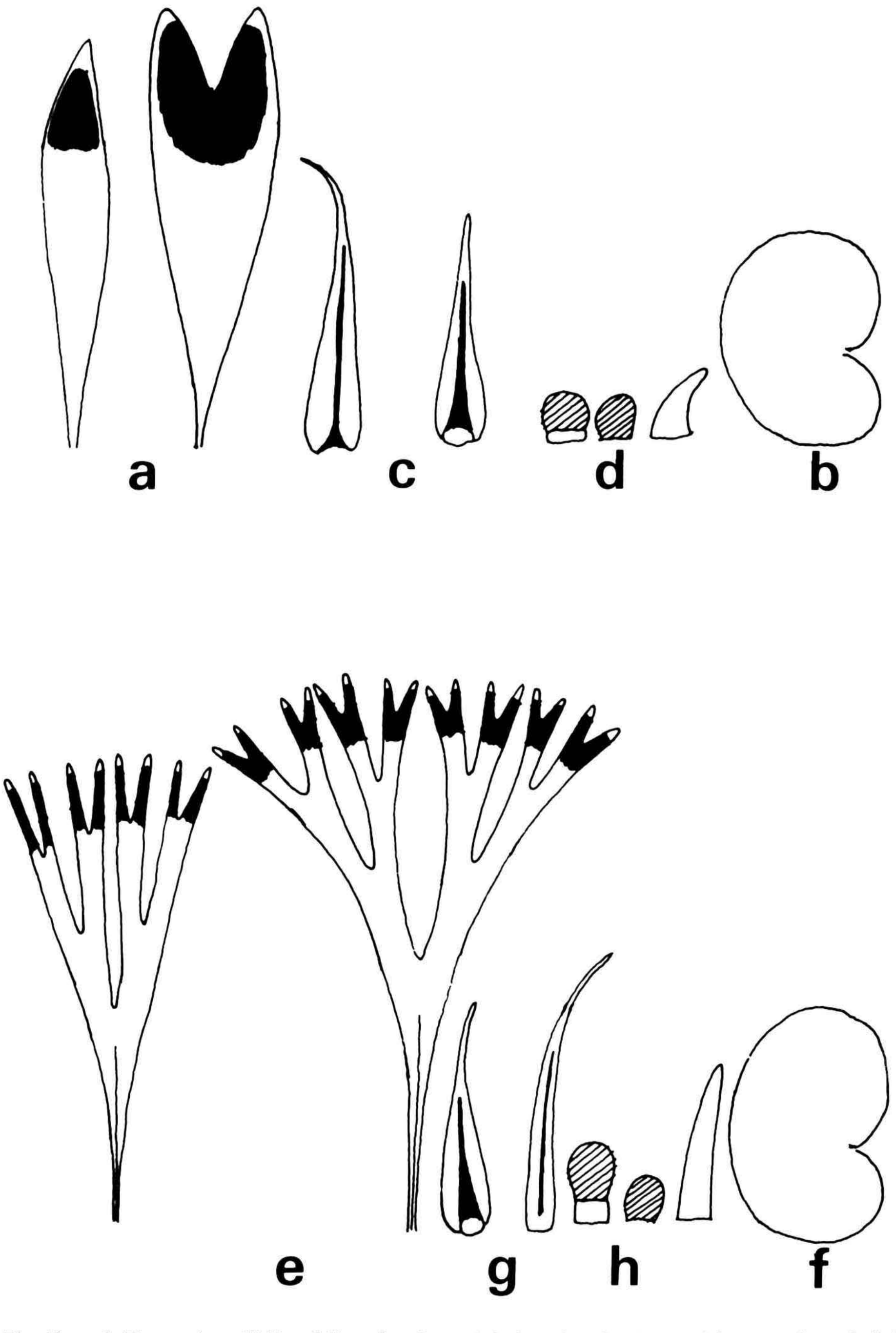

Fig. 13. a–d. *Platycerium ellisii*. a. foliage fronds x 1/8; b. base frond, x 1/8; c. rhizome scales, x 8; d. indument of scales, x c.200.

– e–f. *P. alcicorne*. e. foliage fronds, x 1/8; f. base frond, x 1/8; g. rhizome scale, x 6; h. indument of scales, x c.200.

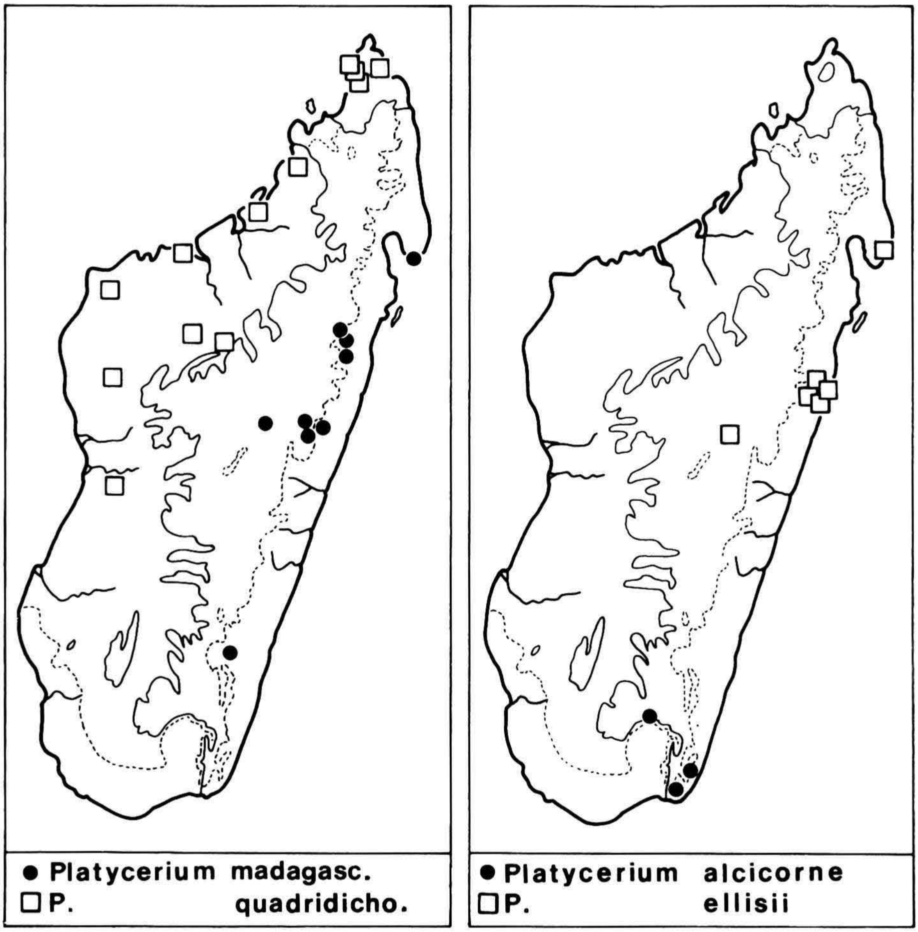

Fig. 14. Distribution of the *Platycerium* species of Madagascar: *P. madagascariense, P. quadridichotomum, P. alcicorne*, and *P. ellisii*.

glandular, 20–45 μm long, situated on 2(–3)-celled hairs, 30–115 μm long, sometimes non-glandular, 75–175 μm long, situated on 2-celled hairs, 75–175 μm long; 1-celled trichomes glandular or not. – *Base fronds* sessile, withering, old fronds appressed, 20–35 by 15–25 cm; upper part appressed, rounded, margin entire, lower part with the margin entire, without fringe; veins immersed, water storage tissue present, cells spherical. – *Foliage fronds* (sterile and) fertile, maturing in an undetermined number, fertile and sterile parts of fertile frond developing simultaneously, erect, symmetrical, wedge-shaped, 25–85 cm long, pergamentaceous, 2–3 times dichotomously forked, lobes equally-long, soral patches generally 4 or 8 per frond, situated away from the plant on the ultimate segments and often also around the ultimate sinusses, angustate–linear, 2–20 by 1–6 cm. – *Sporangia* 250–300 by 210–240 μm, index 1.2–1.3, annulus cells (20)21–23(–25), indurated cells: (13–)15, 16(–18), epistomium cells: (3)4(5), hypostomium cells: 1, stomium situated laterally, stalk (2)3-seriate, 0.1–0.3 mm long, spores: 64, 65–70 by ± 40 by 40–45 μm, perispore indistinct; dehiscence of paraphyses and sporangia absent. – *Indument*: stellate hairs with

(9)10–12(13) rays which are undifferentiated 100–250 by 22–30 μm, apex filiform; paraphyses shortly stalked, with (10–)12–15(16) rays, terminally inserted, flat or convex, 100–180 by 25–40 μm.

Chromosomes. N = 37 (Löve, Löve & Pichi Sermolli, 1977).

Distribution. Kenya, Tanzania, Rhodesia, Moçambique, Comores (Grande Comore, Anjouan, Mayotte), Madagascar, Mascarenes (Reunion, Mauritius).

Habitat. Epiphytic, locally frequent in different types of (humid) forests, several times reported from *Brachystegia spiciformis* Benth. (Ceasalpinioidae, Leguminosae), also in plantations, 5–20 m above the ground. Altitude: 0–600 m.

Notes. 1. A clear-cut species which shows much resemblance to *P. bifurcatum* with which it has been confused especially by the early authors. The most marked gross-morphological differences include the difference in veining of the foliage frond (*P. alcicorne*: main vein reaching to more than halfway of the undivided basal part of the frond; *P. bifurcatum*: main vein reaching to up to one third of the undivided basal part of the frond), the architecture of the foliage fronds, and the colour and architecture of the base fronds.

2. The base fronds of the present species are basically similar to those found in *P. ellisii* and in *P. bifurcatum* var. *hillii*.

3. The shape of the juvenile foliage fronds resembles that of the mature fronds of *P. stemaria*. The position and shape of the soral patches of the present species is comparable to that of *P. stemaria*.

2. **Platycerium andinum** Baker. – **Fig. 15a–15d, 16.**

P. andinum Baker, Ann. Bot. 5 (1891) 496; Christ, Farnkr. Erde (1897) 125, Fig. 353; Diels in E. & P., Nat. Pfl. Fam. 1, 4 (1902) 339; C. Chr., Ind. Fil. (1906) 496; Christ, Geogr. Farne (1910) fig. 58; Straszewski, Flora, Jena 108 (1915) 307, Fig. 29; Joe, Baileya 12 (1964) 78, Fig. 34; Joe Hoshizaki, Am. Fern J. 60 (1970) Pl. 19: Fig. 14; Biotropica 4 (1972) 95, Pl. 2: Fig. 1, Pl. 3: Fig. 1, Pl. 5: Fig. 5, Pl. 7: Fig. 1, Pl. 8: Fig. 1. – *Alcicornium andinum* Underwood, Bull. Torrey bot. Club 32 (1905) 593. – Lectotype: *Spruce 4739*, Peru, Dept. Loreto, Tarapoto, 1855–1856 (K, holo, 2 sh.; P); Paratype: *Pearce 786*, Bolivia, Paquicha (K, 3 sh.; W).

P. alcicorne auct. non Desvaux, *quoad specim. Americ. solum*: Hooker, Fil. Ex. (1859) Pl. 97; Spec. Fil. 5 (1864) 282; Baker in Hooker & Baker, Syn. Fil. (1868) 425; E.J. Lowe, Ferns 7 (1868) 153.

Epiphytic, growing in clusters. – *Scales* basally attached, index 8–22, widest at or somewhat above the base, 5.0–17.0 by 0.4–1.4 mm, base truncate, margin slightly convex in the basal and middle part, slightly concave to ± straight in the apical part, not flabelloid, apex acuminate to filiform, papery, light- to red-brown, the basal and central part darker, midrib absent; indument: hairs sparsely set, situated marginally and in the apical part also abaxially, branched or unbranched 2–4(–6)-celled, 50–400 μm long, unbranched hairs 2–3-celled, longest branches of branched hairs 2–3-celled, without protuberances; apical cell either glandular, 40–85 μm long, situated terminally on at least one branch of the branched hairs, or apical cell non-glandular, 65–250 μm long, situated on branched hairs; 1-celled trichomes non-glandular. – *Base fronds* sessile, withering, old fronds erect, 40–60 (–100) by 15–30 (or more?) cm; upper part erect, wedge-shaped, 1, 2(3) times dichotomously forked, segments of the same order equally-long, lower part with margin entire, fringe ± conspicuous, situated above the stipe only, margin entire; veins immersed, water storage tissue present, cells spherical.

– *Foliage fronds* (sterile and) fertile, maturing in pairs in a bilateral symmetrical pattern, fertile and sterile parts of fertile frond developing in succession, pendulous, asymmetrical, linear-wedge-shaped, 100 to more than 200 cm long, 3–5 times ± dichotomously forked, pergamentaceous, soral patches generally 2 or 4, facing the plant, reaching from near the first sinus to up to above the ultimate sinus or spread medially within this area, linear, 15–50 by 3–8 cm. – *Sporangia* 275–310 by 220–250 μm, index 1.2–1.3, annulus cells: 25–28, indurated cells: (16)17–20, epistomium cells: 3–5, hypostomium cells: 2, 3, stomium situated laterally, stalk (2)3-seriate, 0.1–0.3 mm long, spores: 64, 65–75 by 40–50 by 40–50 μm, perispore indistinct; dehiscence of paraphyses and sporangia absent. – *Indument*: stellate hairs with (8)9–11(–13)

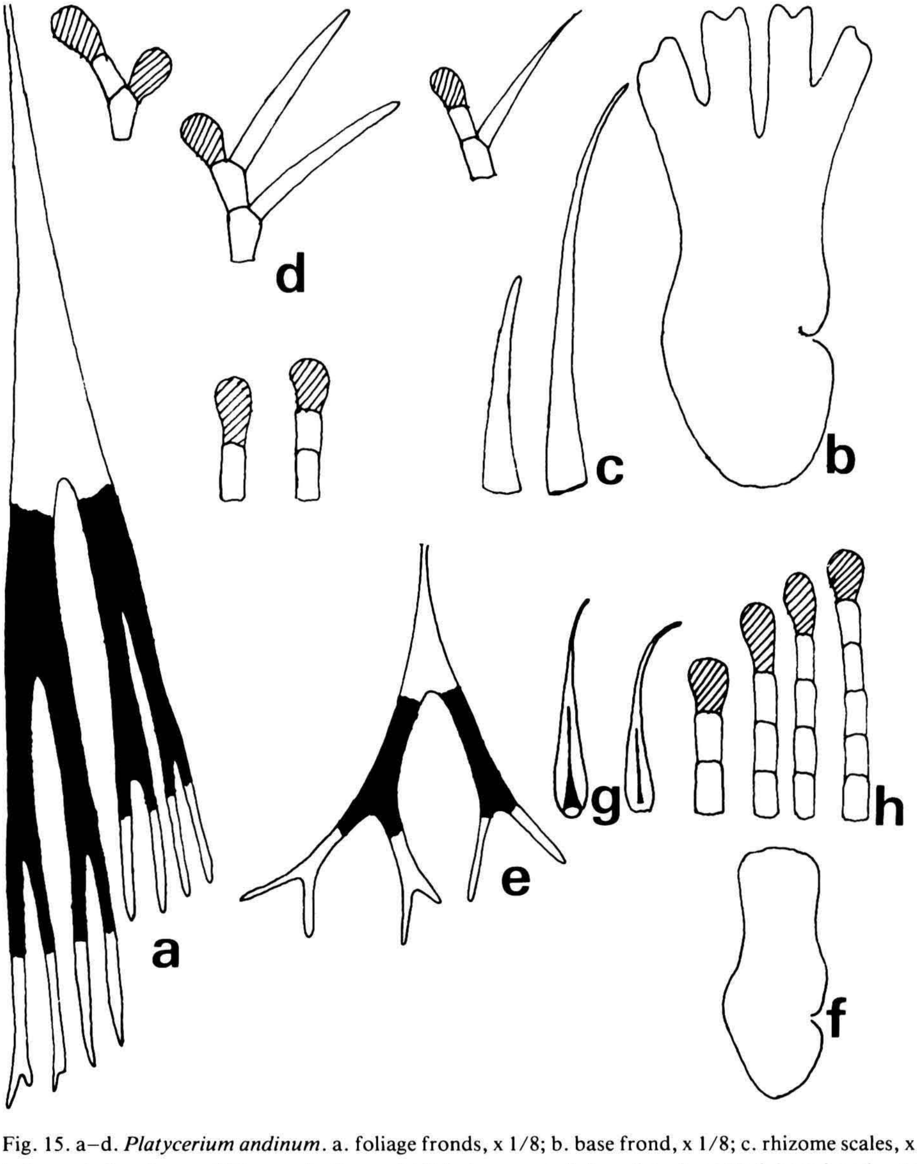

Fig. 15. a–d. *Platycerium andinum*. a. foliage fronds, x 1/8; b. base frond, x 1/8; c. rhizome scales, x 6; d. indument of scales, x c.200. – e–h. *P. quadridichotomum*. e. foliage frond, x 1/8; f. base frond, x 1/8; g. rhizome scales, x 6; h. indument of scales, x c.200.

rays, which are undifferentiated, 250–450 by 25–30 μm, apex filiform; paraphyses shortly stalked, with (5–)9–13(14) rays, terminally inserted, undifferentiated, involute to canaliculate, 190–350 by 30–50 μm.

Distribution. Peru, Bolivia.

Habitat. But little information available on the labels of the 8 collections studied. Epiphytic in forest. Altitude: 350–400 m.

Notes. 1. A distinct species easily recognized by its characteristic base fronds showing only two equally-long, erect, main lobes, and soral patches situated medially (as in *P. quadridichotomum*).

2. Clusters of plants of *P. andinum* may become so voluminous and heavy that they cause the break-down of the big branches on which they are epiphytic (*Spruce 4739*, P).

3. The first sinus may show a small but conspicuous lobe-like projection.

4. *Pierce s.n., s.d.* (W) has a – rather illegible – label with the locality 'Ecuador'.

3. Platycerium bifurcatum (Cav.) C. Chr. – Fig. 17–19; Plate 3.

P. bifurcatum (Cav.) C. Chr., Ind. Fil. (1906) 496; Wigman jr., Teysmannia 21 (1910) 164c. Fig.; Domin, Biblthca Bot. 85,1 (1915) 196, p.p.; Straszewski, Flora, Jena 108 (1915) 306, Fig. 1, 2, 36, 37, 41; Backer & Posthumus, Varenfl. Java (1939) 217, p.p.; Tindale, Contr. N.S.W. natn. Herb. Flora Ser. 208–211 (1961) 26; Joe, Baileya 12 (1964) 83, Fig. 36: a, Fig. 55: 9, 10, 12–14, 19; Jonch., Blumea 15,2 (1967) 450, Fig. 3; Joe Hoshizaki, Am. Fern J. 60 (1970) Pl. 19: Fig. 23; N.C.W. Beadle, Fl. Sydney Reg. (1972) 72; Joe

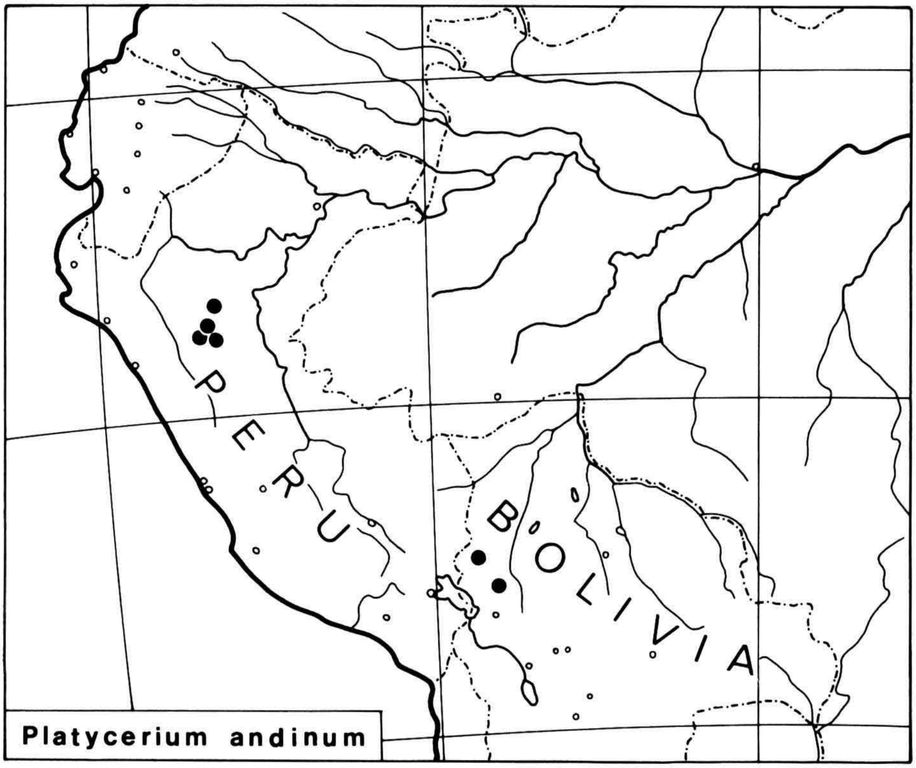

Fig. 16. Distribution of *Platycerium andinum*.

Hoshizaki, Biotropica 4 (1972) 94, Pl. 1: Fig. 2, Pl. 2: Fig. 10, Pl. 3: Fig. 10, Pl. 6: Fig. 14, Pl. 7: Fig. 10, Pl. 8: Fig. 10; Jones & Clemesha, Austr. ferns (1976) 234, Fig. 214; id. 2e ed. (1980) 181, Fig. 243. – *Acrostichum bifurcatum* Cav., Ann. Hist. Nat. Madrid (1799) 105; Descr. Pl. (1802) 241. – *Alcicornium bifurcatum* (Cav.) Underwood, Bull. Torrey bot. Club 32 (1905) 594. – *P. bifurcatum* (Cav.) C. Chr. var. *normale* Domin, Biblthca Bot. 85,1 (1915) 196, *comb. illeg.* – *P. bifurcatum* (Cav.) C. Chr. var. *bifurcatum*, Joe, Baileya 12 (1964) 84, Fig. 36: b–h, 55: 14. – Type: Née, Australia, N.S. Wales, Port Jackson (MA, *n.v.*).

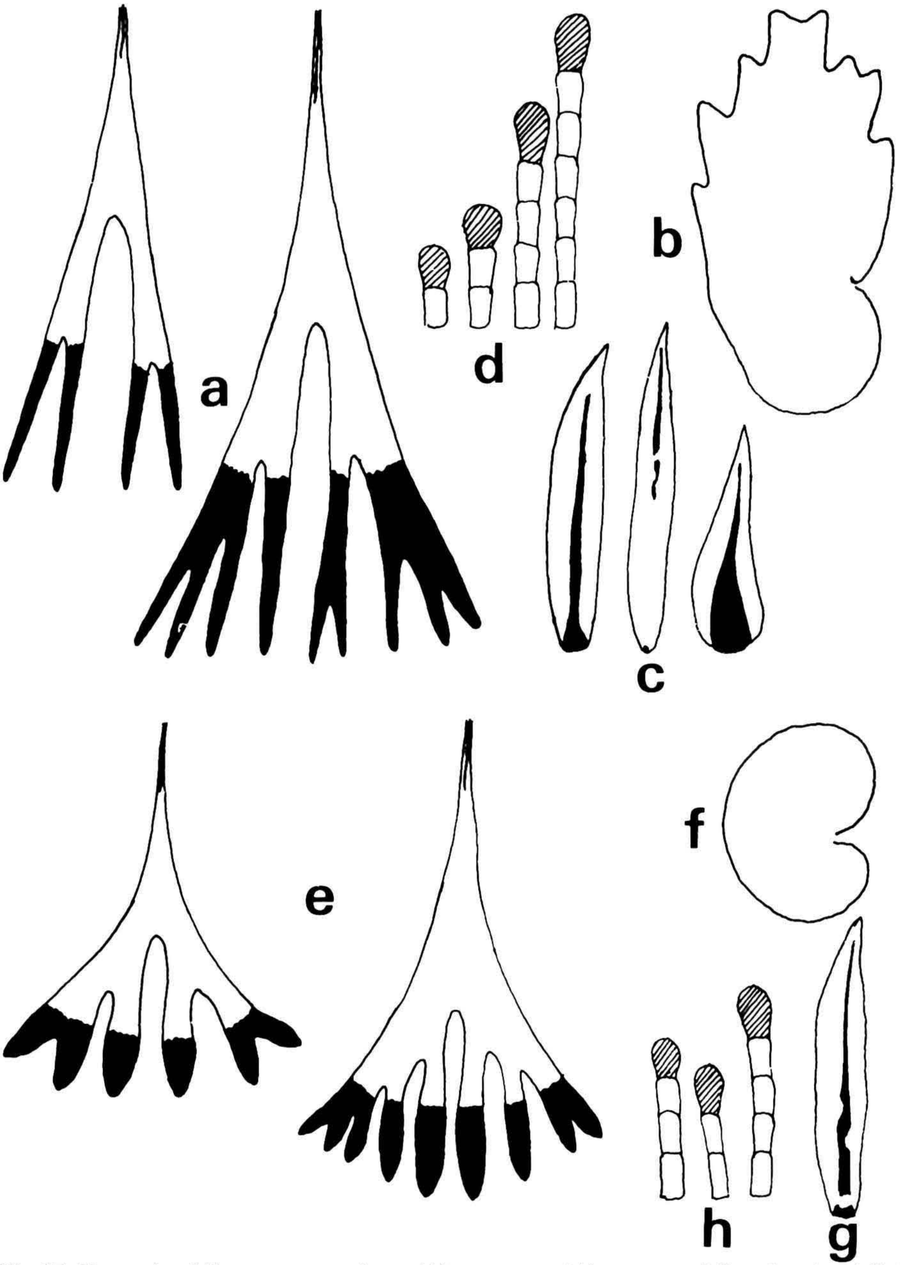

Fig. 17. *Platycerium bifurcatum*. – a–d. ssp. *bifurcatum* var. *bifurcatum*. a. foliage fronds, x 1/8; b. base frond, x 1/8; c. rhizome scales, x 6; d. indument of scales, x c.200. – e–h. ssp. *bifurcatum* var. *hillii*. e. foliage fronds, x 1/8; f. base frond, x 6; g. rhizome scale, x 6; h. indument of scales, x c.200.

Alcicornium vulgare Gaudich, Freycin. Voy. Bot. (1826) 307, *nom. illeg.* – Type: not traced.

Platycerium angustatum Desvaux, Mém. Soc. Linn. Paris (1872) 213. – Type: *Anonymus s.n.*, Australia (P., herb. Desvaux).

Platycerium willinckii T. Moore, Gdnrs' Chron, 3 (1875) 302, Fig. 56 (excellent); v.A.v.R., Mal. Ferns (1908) 710; Poisson, Revue hort. 10 (1910) 460; Wigman jr., Teysmannia 21 (1910) 164 c. Fig.; Straszewski, Flora, Jena 108 (1915) 306; v.A.v.R., Mal. Ferns, Suppl. (1917) 422; Joe, Baileya 12 (1974) 110, Fig. 50–54, 55: 1–7; Joe Hoshizaki, Am. Fern J. 60 (1970) Pl. 19: Fig. 12, 21; Biotropica 4 (1972) 94, Pl. 1: Fig. 3, 6,

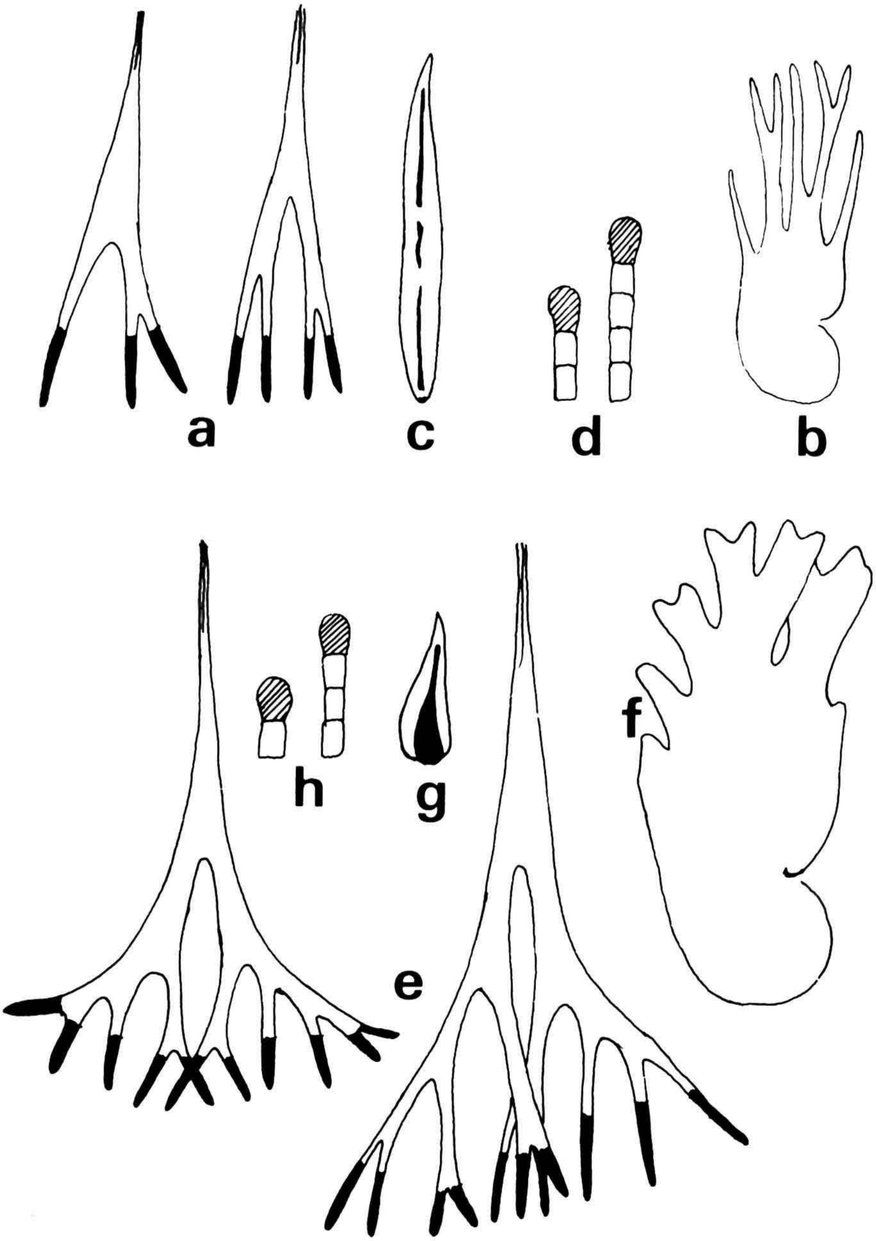

Fig. 18. *Platycerium bifurcatum*, a–d. ssp. *veitchii*. a. foliage fronds, x 1/8; b. base frond, x 1/8; c. rhizome scale, x 6; d. indument of scales, x c.200. – e–h. ssp. *willinckii*. e. foliage fronds, x 1/8; f. base frond, x 1/8; g. rhizome scale, x 6; h. indument of scales, x c.200.

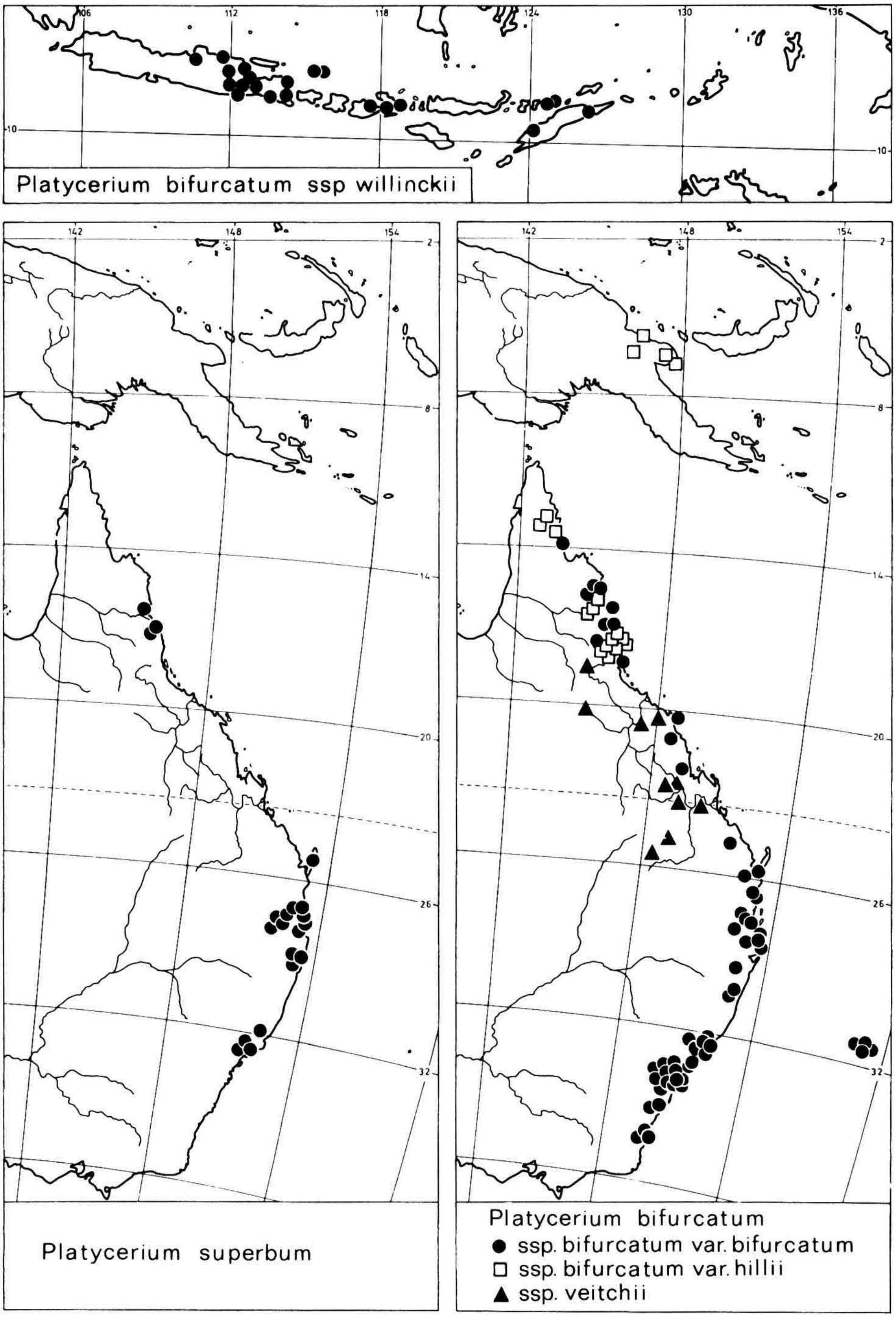

Fig. 19. Distribution of *Platycerium bifurcatum* and *P. superbum*.

Pl. 2: Fig. 8, Pl. 3: Fig. 8, Pl. 6: Fig. 8, Pl. 7: Fig. 8, Pl. 8: Fig. 8. Joe Hoshizaki, Fern Gr. Man. (1979) 210, c. Fig. – *Alcicornium willinckii* (T. Moore) Underwood, Bull. Torrey bot. Club 32 (1905) 596. – Type: a specimen cultivated by Messrs. Veitch & Sons, Chelsea, 1873; origin: Java, *Willinck leg.* (K, not traced).

Platycerium hillii T. Moore, Gdnrs' Chron. 10 (1878) 51, 429, Fig. 6, 74, 75; Straszewski, Flora, Jena 108 (1915) 306; Joe, Baileya 12 (1964) 92, Fig. 41, 55: 15–18; Joe Hoshizaki, Am. Fern J; 60 (1970) Pl. 18: Fig. 4, Pl. 19: Fig. 13, 24; Biotropica 4 (1972) 94, Pl. 2: Fig. 11, Pl. 3: Fig. 11, Pl. 6: Fig. 15, Pl. 7: Fig. 11, Pl. 8: Fig. 11; Jones & Clemasha, Austr. ferns (1976) 234, Fig. 215, id. 2e ed. (1980) 181, Fig. 244. – *P. alcicorne* Desvaux var. *hillii* F.M. Bailey, Syn. Queensl. Fl. (1883) 724; Queensl. Fl. 6 (1902) 1995; Poisson, Revue hort. 10 (1910) 458. – *Alcicornium hillii* (T. Moore) Underwood, Bull. Torrey bot. Club 32 (1905) 595. – *P. bifurcatum* (Cav.) C. Chr. var. *hillii* (T. Moore) Domin, Biblthca Bot. 85, 1 (1915) 197, Fig. 46. – Type: a specimen cultivated by Messrs. Veitch & Sons, Chelsea; origin: Australia, Queensland, *W. Hill leg.* (K).

Alcicornium veitchii Underwood, Bull. Torrey bot. Club 32 (1905) 596. – *Platycerium veitchii* (Anonymous, Gdnrs' Chron. 3, 19 (1896) 652) C. Chr., Ind. Fil. (1906) 497; Poisson, Revue hort. 10 (1910) 459; Straszewski, Flora, Jena 108 (1915) 306, Fig. 33; Joe Baileya 12 (1964) 104, Fig. 47, 55: 20; Joe Hoshizaki, Am. Fern J. 60 (1970) Pl. 18: Fig. 3, Pl. 19: Fig. 22; Biotropica 4 (1972) 94, Pl. 2: Fig. 9, Pl. 3: Fig. 9, Pl. 6: Fig. 13, Pl. 7: Fig. 9, Pl. 8: Fig. 9; Jones & Clemesha, Austr. ferns (1976) 237, Fig. 217; id. 2e ed. (1980) 183, Fig. 246. – Type: a specimen cultivated by Messrs. Veitch & Sons, Chelsea (K, not traced).

Platycerium sumbawense Christ, Warb. Monsun. 1 (1900) 64; Diels in E. & P., Nat. Pfl. Fam. 1,4 (1902) 339; v.A.v.R., Mal. Ferns (1908) 709; Christ, Annls Jard. bot. Buitenz. Suppl. 3 (1910) 8, Pl. 1; Poisson, Revue hort. 10 (1910) 459; Wigman jr., Teysmannia 21 (1910) 164; v.A.v.R., Mal. Ferns, Suppl. (1917) 422. – *Alcicornium sumbawense* (Christ) Underwood, Bull. Torrey bot. Club 32 (1905) 596. – Type: *Warburg 17266*, Lesser Sunda Is. Sumbawa, Donggo Mts (B).

P. bifurcatum (Cav.) C. Chr. var. *subrhomboideum* Domin, Biblthca Bot. 85,1 (1915) 198, Fig. 47; Joe, Baileya 12 (1964) 85, fig. 37: a. – Type: *Domin s.n., 1910*, Australia, N.E. Queensland, Yarraba (n.v.).

P. bifurcatum (Cav.) C. Chr. var. *lancifera* Domin, Biblthca Bot. 85,1 (1915) 198, Fig. 48; Joe, Baileya 12 (1964) 85, fig. 37: b, 55: 11. – Paratypes: *Domin s.n., 1910,* Australia, N.E. Queensland, Yarraba (n.v.) and *Domin s.n., 1910,* Australia, Tambourine Mts (n.v.).

Acrostichum alcicorne p.p., auct., non Swartz (1801): Swartz, Syn. Fil. (1806) 12, 196; R. Brown, Prodr. Fl. Nov. Holl. (1810) 145; Willd., Spec. Pl. 5 (1810) 111; Sprengel, Syst. Veg. (1827) 35; Blume, Enum. Pl. Javae (1828) 10; Link, Hort. Reg. Bot. Ber. (1833) 47. – *Platycerium alcicorne p.p. auct., non* Desvaux: Blume, Fl. Javae (1828) 46; C. Presl, Epim. bot. (1851) 153; Kunze, Linnaea 23 (1850) 474; Mettenius, Filices Horti Bot. Lips. (1856) 26, Pl. 4: 1–3; Hooker Spec. Fil. 5 (1864) 282; J. Rothschild *et al.*, Fougères 1 (1867) 186, Fig. 34, *s.n.*; Baker in Hooker & Baker, Syn. Fil. (1868) 425; E.J. Lowe, Ferns 7 (1868) 157, Fig. 63; Mettenius, Annls Mus. Bot. L.B. 4 (1868–'69) 170; Luerssen, J. Mus. Godeffroy 3 (1873) 8; F.M. Bailey, Handb. Ferns Queensl. (1874) 13; Benth., Fl. Austral. (1878) 780; F.M. Bailey, Fernw. Austral. (1881) 74; Syn. Queensl. Fl. (1883) 723; Christ, Farnkr. Erde (1897) 124; Racib., Pterid. Fl. Buitenz. (1898) 57; F.M. Bailey, Queensl. Fl. 6 (1902) 1995; Diels in E. & P., Nat. Pfl. Fam. 1,4 (1902) 339, Fig. 176, 177; A. Poisson, Revue hort. 10 (1910) 458. – *Neuroplatyceros alcicornis* (Willem.) Fée, Mém, Fougères 2 (Acrost.) (1845) 120 *p.p.*

Epiphytic and epilithic, growing in clusters. – *Scales* basally-attached to peltate, index 3–8(–25), widest usually near the base, sometimes widest about or above the middle, 1.5–11.0 by 0.3–1.3 mm, base truncate to cordate, margin straight to slightly convex, not flabelloid, apex acute to acuminate, papery to thin-coriaceous, red-brown, midrib undivided, linear to (narrow-)triangular, in large scales often interrupted with the basal parts usually lacking, in cross-section ± rounded; indument: hairs sparsely set, situated marginally, unbranched, 1–6-celled, 50–1000 μm long, without protuberances; apical cell glandular, rarely non-glandular in ssp. *veitchii*, 25–60 μm long; 1-celled-trichomes usually glandular, rarely non-glandular in spp. *veitchii.* – *Base fronds* sessile, withering, old fronds erect or appressed, 18–60 by 8–45 cm; upper part erect or appressed, rounded to elliptical, either entire, or sinuate, or up to 4 times dichotomously forked, lobes unequally-long, lower part of frond with the margin entire, without conspicuous fringe; veins immersed, water storage tissue present, cells spherical. – *Foliage fronds* (sterile and) fertile, maturing in an undetermined number, fertile and sterile parts developing simultaneously, either erect, or spreading, or pendulous, usually asymmetrical, sometimes ± symmetrical, wedge-shaped (to spathulate), 25–100 cm long, pergamentaceous, 2–5 times dichotomously lobed, soral patches 1–10, situated either away from the plant or horizontally exposed, or facing the plant, inserted in the apical part, angustate to linear, or with several acute lobes when reaching beyond the (pen-)ultimate sinusses, 1–22 by 0.5–7.5 cm. – *Sporangia* 235–375 by 200–280 μm, index 1.1–1.5, annulus cells: (23–)26–29(–32), indurated cells: (16–)18–22, epistomium cells: 3, 4(5), hypostomium cells: 2, 3(–5), stomium situated laterally, stalk (2)3-seriate, 0.1–0.3 mm long, spores: 64, 60–80 by 30–55 by 30–55 μm, perispore indistinct, dehiscence of paraphyses and sporangia absent. – *Indument*: stellate hairs with 5–12(–15) rays, which are undifferentiated, 100–565 by 20–40 μm, apex filiform; paraphyses shortly stalked, with (8–)10–15(–17) rays, terminally inserted, undifferentiated, involute to canaliculate, 90–430 by 25–55 μm.

Chromosomes. N = 37 (ssp. *bifurcatum*; Löve, Löve & Pichi-Sermolli, 1977).

Distribution. Java, Lesser Sunda Isl. (Kangean Arch., Lombok, Sumbawa, Flores, Alor, Timor), New Guinea, E. Australia (subtropic!).

Habitat. In several kinds of forests or in more open primary and secondary vegetations. Altitude: 0–2000 m. Locally the most common and dominant epiphyte.

Notes. 1. A polymorphic species which is habitually close to *P. alcicorne*. For differences see *P. alcicorne*, notes 1 and 2. The infraspecific taxa here recognized have been given specific status by several other authors (*e.g.* Joe Hoshizaki, 1972, Jones & Clemesha, 1976, 1980). Although these taxa are geographically and/or ecologically distinct, it is inferred from our studies of the material kept in cultivation that genetic isolation between these taxa has not been realized: all taxa easily hybridize with each other producing fertile offspring showing a wealth of morphologically different forms.

2. The shape of the base frond of especially ssp. *willinckii* (the most western subspecies, which distribution area borders on that of *P. coronarium*) is similar to that found in *P. coronarium*.

3. The present species is commonly cultivated by private and commercial plant growers. The cultivated forms include dwarfs (*P. 'pygmaeum'*), very hairy forms (*P. 'lemonei'*; a cross between ssp. *willinckii* and ssp. *veitchii*: Franks, Wendy B.P., 1969: Platycerium – Fern Facts. Private Printing, Los Angelos, Cal.), as well as various forms based on characteristics of the foliage fronds. For details see Joe, *op. cit.*, 1964, and Franks.

KEY TO THE INFRASPECIFIC TAXA

1. Scales up to 5 mm long; base fronds up to 70 cm long, upper part elliptical, forked, lobes (broadly) angustate; foliage fronds pendulous, ultimate segments angustate to linear triangular. . . . . **3c. ssp. willinckii**

1. Scales usually more than 5 mm long; base fronds up to 50 cm long, upper part rounded to elliptical, either entire, or sinuate, or forked with the lobes linear;

foliage fronds spreading to erect, ultimate segments angustate to linear triangular, or elliptical to obovate 2

2. Base fronds 8–15 cm broad, upper part elliptical with linear lobes; foliage fronds 2-times forked, very densely set with hairs, epilithic .... **3b. ssp. veitchii**

2. Base fronds (12–)15–45 cm broad, upper part rounded to elliptical, entire to distinctly sinuate; foliage fronds 2–5 times forked, sparsely to densely set with hairs, usually epiphytic, rarely epilithic 3

3. Base fronds with the margin of the upper part entire; foliage fronds all erect, ± symmetrical, sparsely set with hairs, ultimate segments angustate, elliptical to obovate .... **3a2. ssp. bifurcatum var. hillii**

3. Base fronds with the margin of the upper part ± sinuate; foliage fronds mostly spreading, asymmetrical, densely set with hairs, ultimate segments linear to narrowly triangular .... **3a1. ssp. bifurcatum var. bifurcatum**

3.a. **ssp. bifurcatum. – Fig. 17, 19.**

P. bifurcatum. – *P. angustatum*. – *P. hillii*. – *P. bifurcatum* var. *subrhomboideum*. – *P. bifurcatum* var. *lancifera*.

Epiphytic, rarely epilithic. – *Scales*: index 3–17(–25), widest below or above the middle, 1.5–11 by 0.3–1.3 mm, papery; indument (1)2–6-celled hairs, 50–1000 μm long, apical cell glandular, 25–55 μm long. – *Base fronds* 20–50 by 12–45 cm, upper part rounded (to elliptical), margin entire to sinuate. – *Foliage fronds* erect or variously spreading, asymmetrical or ± symmetrical, wedge-shaped to spathulate, 25–90 cm long, 2–5 times forked, ultimate segments ± linear or narrowly triangular, or angustate, elliptical to obovate, short- to long-sized, sparsely to densely set with hairs. – *Sporangia* 235–320 by 200–230 μm, index 1.1–1.4, annulus cells: (23–)26–31, indurated cells: (16–)18–22, epistomium cells: 3, 4, hypostomium cells 2, 3; spores 60–65 by 30–40 by 30–40 μm – *Indument*: stellate hairs with (5)6–13(–15) rays, 100–370 by 20–30 μm; paraphyses with (8–)10–13(–16) rays, 90–170 by 25–45 μm.

Distribution. New Guinea, E. Australia.

Habitat. in primary and secondary forests, or in more open vegetations (savannah-forest, or brusheries). Altitude: 0–1200 m.

Note. Joe Hoshizaki (1972) reported upon a typical specimen of *P. bifurcatum* from Cairns, Australia which took on the appearance of '*hillii*' when kept in cultivation, a result which reinforced her suspicion that '*P. hillii* is only a form of the plastic species *P. bifurcatum*'. The *P. bifurcatum* ssp. *bifurcatum* specimens found at Cairns (lowland) by the senior author usually belong to var. *hillii*.

3.a.1. **var. bifurcatum. – Fig. 17a–17d.**

For synonyms see ssp. *bifurcatum, P. hillii* excepted.

Scale-indument with hairs 50–1000 μm long. – *Base fronds* 20–50 by 15–45 cm, upper part rounded to ± elliptical, margin more or less distinctly sinuate. – *Foliage fronds* variously spreading, asymmetrical, wedge-shaped, 35–90 cm long, ultimate segments ± linear or narrowly triangular, densely set with hairs. – *Sporangia* 235–275 by 200–220 μm, index 1.1–1.3. indurated cells: (16–)18–20(–22), hypostomium cells: 2, annulus cells: (23–)26, 27(–29). – *Indument*: stellate hairs with 5–12(–14) rays, 185–370 by 20–30 μm; paraphyses with (8–)11–14(–16) rays, 90–165 by 30–45 μm.

Distribution. E. Australia, especially the interior tablelands.

Habitat. See the subspecies.

3.a.2. var. hillii. (T. Moore) Domin. – Fig. 17e–17h.

P. hillii.

Scale-indument with hairs 100–300 μm long. – *Base fronds* 20–40 by 12–24 cm; upper part rounded, margin entire. – *Foliage fronds* erect, usually symmetrical, sometimes asymmetrical (wedge-shaped to) spathulate, 25–70 cm long, ultimate segments angustate, elliptical to obovate, sparsely set with hairs. – *Sporangia* 255–320 by 205–230 μm, index 1.2–1.4, annulus cells: (26)27–31; indurated cells: (17–)19–21(22), hypostomium cells: 2–3. – *Indument:* stellate hairs with 9–14(15) rays, 100–270 by 20–25 μm; paraphyses with (9)10–12(–14) rays, 100–170 by 25–45 μm.

Distribution. New Guinea, E. Australia, especially in coastal areas.

Habitat. See the subspecies.

Note. This variety is known from New Guinea by only a few collections from adjacent sites. Joe Hoshizaki (1977) reported Mr Todd's (N.S.W., Australia) suggestion saying that this taxon could have been introduced.

3.b. ssp. veitchii. (Underwood) Hennipman & Roos, stat.nov. – Fig. 18a–18d, 19.

Alcicornium veitchii.

Epilithic. – *Scales*: index 3.5–18, widest near the base, 1.5–7.5 by 0.3–1.2 mm, papery; indument 1–6-celled hairs, 85–400 μm long, apical cell glandular, 30–60 μm long. – *Base fronds* 20–45 by 8–15 cm, upper part elliptical, consisting of unequally long-sized, up to 2 times forked linear lobes. – *Foliage fronds* erect (to spreading), asymmetrical (narrowly) wedge-shaped, 25–70 cm (or more) long, 2–3 times forked, ultimate segments linear to narrowly triangular, short- to medium-sized, very densely set with hairs. – *Sporangia* 320–375 by 245–280 μm, index 1.2–1.5, annulus cells: (26–)28–29(–32), indurate cells: (18–)20–21(22), epistomium cells: 3(–5), hypostomium cells: 2, 3(–5), spores 70–80 by 45–55 by 45–55 μm. – *Indument*: stellate hairs with 7–13 rays, 380–565 by 25–40 μm; paraphyses with (9)10–15(–17) rays, 205–430 by 40–55 μm.

Distribution. E. Australia.

Habitat. Exposed on basalt and sandstone in open shrub vegetations, in areas with a pronounced dry season. Altitude: 600–650 m.

Note. 1. Typical base fronds showing very narrow linear lobes are not always produced in cultivated specimens.

2. According to Mr. Bruce Gray and Mr. David Jones (pers. comm.) this taxon is locally quite abundant, but the patches are really small. The plants form huge clumps with uniform foliage fronds up to 1 m long; they grow exposed on rocks (or tree roots) in rocky areas (lava, granite) with scrubby stuff.

3.c. ssp. willinckii. (T. Moore) Hennipman & Roos, stat.nov. – **Fig. 18e–18h; Plate 3.**

P. willinckii. – *P. sumbawense.*

Epiphytic. – *Scales*: index 4–8(–10), widest near the base, 1.5–4.5 by 0.3–0.8 mm, thin-coriaceous; indument (2)3–5-celled hairs, 120–200 μm long, apical cell glandular, 25–50 μm long. – *Base fronds* up to 70 by up to 50 cm, upper part elliptical, consisting of up to 4 times forked, unequally long-sized, angustate lobes. – *Foliage fronds* ± pendulous, asymmetrical, wedge-shaped (to spathulate), 25–90 cm long, up to 5 times forked, ultimate segments ± angustate triangular, short to medium-sized, densely set with hairs. – *Sporangia* 300–340 by 235–270 μm, index 1.2–1.4, annulus cells: (25)26–29(–31), indurated cells: 17–22, epistomium cells: (3)4, hypostomium cells: 2–3; spores 65–80 by 35–45 by 35–50 μm. – *Indument*: stellate hairs with (7)8–12(13) rays, 240–330 by 25–35 μm; paraphyses with (11)12–15 rays, 125–225 by 35–50 μm.

Distribution. Java, Lesser Sunda Is.

Habitat. Primary and secondary monsoon forest. Altitude: 0–2000 m.

Notes. 1. Complete base fronds of large-sized specimens were not available in the herbarium material.

2. Vernacular name: Tama halota, Sang sebák, and Batá taná ti (Alor).

4. Platycerium coronarium (König *ex* Müller) Desvaux. – **Fig. 20e–20h, 21.**

P. coronarium (König *ex* Müller) Desvaux, Mém. Soc. Linn. Paris 6 (1827) 213; C. Chr. Ind. Fil (1906) 664; v.A.v.R., Mal. Ferns (1908) 711; Wigman jr., Teysmannia 21 (1910) 163; Straszewski, Flora, Jena 108 (1915) 305, Fig. 21: a, 26–28; Copel., Sarawak Mus. J. 2, 3, 7 (1917) 389; Backer & Posthumus, Varenfl. Java (1939) 248, Fig. 62; Tardieu & C. Chr. in Lecompte, Fl. Gén. Indo-Chine 7 (1941) 445, Fig. 52: 1 (in the Fig. it is called P. grande); Holttum, Fl. Malaya 2 (Ferns) (1954) 138, Fig. 57; Copel., Fern Fl. Philipp. 3 (1960) 458; Joe, Baileya 12 (1964) 86, Fig. 38: a, b; Jonch., Blumea 15, 2 (1967) 446; Joe Hoshizaki, Am. Fern J. 60 (1970) Pl. 18: Fig. 2, Pl. 19: Fig. 29; Biotropica 4 (1972) 95, Pl. 2: Fig. 17, Pl. 4: Fig. 21, 22, Pl. 6: Fig. 21, Pl. 7: Fig. 17, Pl. 8: Fig. 17; Yong, Nature Malaysiana 2, 4 (1977) 35 c. Figs. – *Osmunda coronaría* König *ex* Müller, Naturf. 21 (1785) 197, Pl. 3. – *Alcicornium coronarium* (König *ex* Müller) Underwood, Bull. Torrey bot. Club 32 (1905) 594. – Lectotype (choosen by De Joncheere 1967): Plate in Müller, 1785 (This Plate shows a typical fertile frond, but the base frond shown is a typical one of *P. ridleyi*, and must therefore be excluded from the type).

Acrostichum biforme Swartz, Schrader J. Bot. 1800, 2 (1801) 11, *nom. illeg.*; Syn. Fil. (1806) 12; Willd., Spec. Pl. 5 (1810) 111; Sprengel, Syst. Veg. (1827) 35; Kunze, Bot. Ztg. 6,6 (1848) 102. – *P. biforme* (Swartz) Blume, Fl. Javae (1828) 43, Pl. 18: fig. 1–4, *nom. illeg.*; J. Smith, Hook. J. Bot. 3 (1841) 402; C. Presl. Epim. bot. (1851) 154; Hooker, Gdnrs' Chron. (1858) 764; Spec. Fil. 5 (1864) 285; Bedd., Ferns Brit. Ind. (1866) 109, Pl. 109; Baker in Hooker & Baker, Syn. Fil. (1868) 425; Mettenius, Annls Mus. Bot. L.B. 4 (1868–'69) 170; Cesati, Atti R. Accad. Sci. F. & M. Napoli 7 (1876) 124; Bedd., Handb. Ferns Br. Ind. ed. 2 (1892) 445, Fig. 273; Christ, Farnkr. Erde (1897) 127, Fig. 359; Racib., Pterid. Fl. Buitenz. (1898) 57; Diels in E. & P., Nat. Pfl. Fam. 1, 4 (1902) 339, Fig. 177: B, C; Copel., Dep. int. Bur. governm. 28 (1905) 138; Ridley, J. Straits Brch R. Asiat. Soc. 50 (1908) 56; Poisson, Revue hort. 10 (1910) 458; Ridley, J. Malay. Brch R. Asiat. Soc. 4, 1 (1926) 110. – Lectotype (choosen by De Joncheere 1967): Plate 3 in Muller, 1785.

Epiphytic, growing in clusters. – *Scales* basally-attached, index (2)3–5, widest about the middle, 15–35 by 4–10 mm, base truncate, margin slightly convex, with a flabelloid zone ± 1.5–3.5 mm wide, apex rounded, papery to thin-coriaceous, red brown, midrib divided, broad triangular, medially consisting of two conspicuous lateral ridges, in cross-section dumpbell-shaped; indument: hairs densely set, situated marginally, unbranched, 2(3)-celled, 35–75 μm long, without protuberances; apical

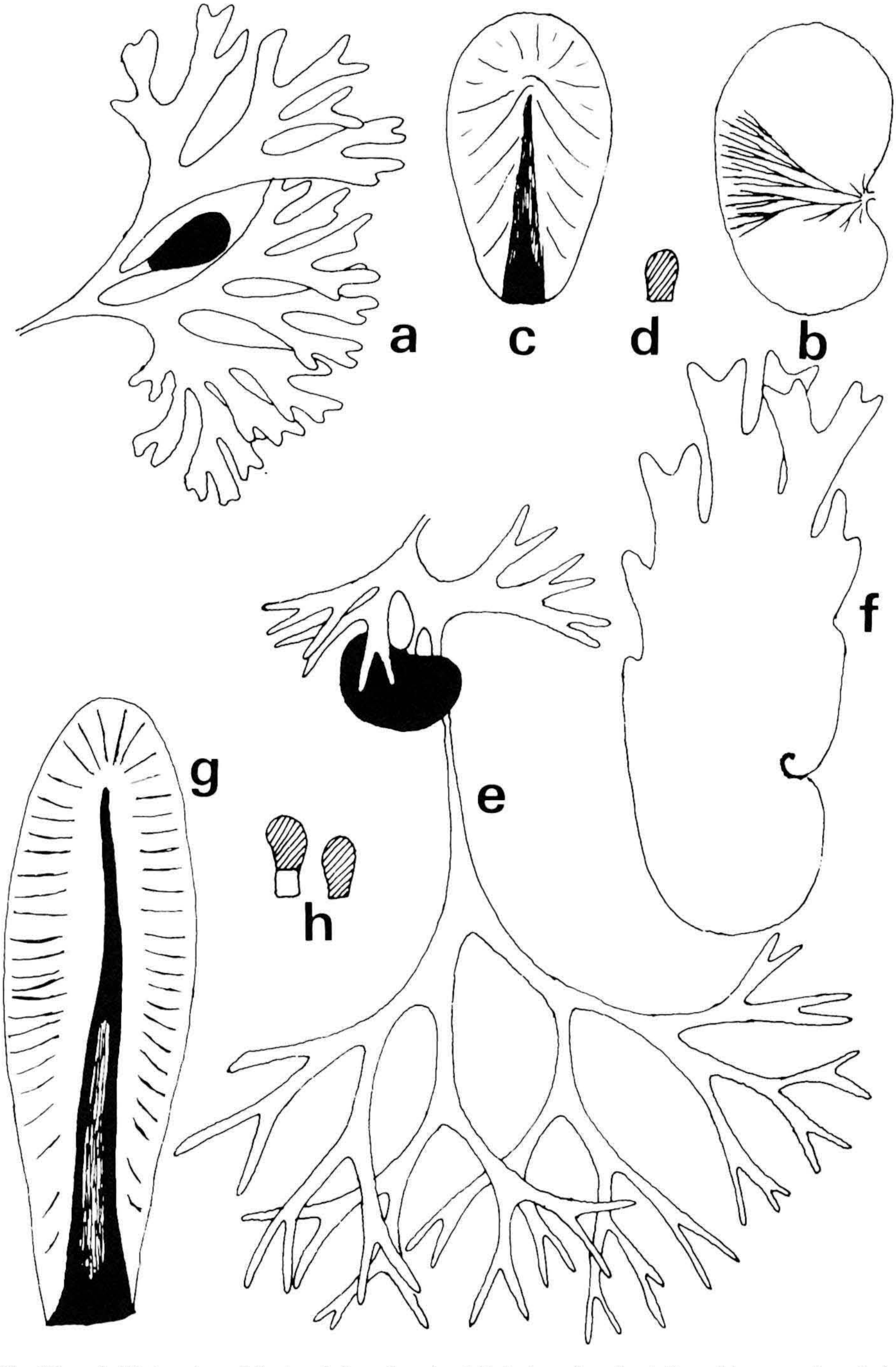

Fig. 20. a–d. *Platycerium ridleyi*. a. foliage frond, x 1/8; b. base frond, x 1/8; c. rhizome scale, x 6; d. indument of scales, x c.200. – e–h. *P. coronarium*. e. foliage frond, x 1/8; f. base frond, x 1/8; g. rhizome scale, x 6; h. indument of scales, x c.200.

cell always glandular, 35–50 μm long, 1-celled trichomes commonly present, glandular. – *Base fronds* sessile, green, old fronds recurving, 50–110 by 25–55 cm; upper part erect, elliptical, 2–5 times dichotomously lobed, lobes unequally-long, lower part with entire margin, fringe conspicuous, situated above the stipe only, margin entire; veins immersed, water storage tissue present, cells cylindrical. – *Foliage fronds* (sterile and) fertile, maturing in an undetermined number, fertile and sterile parts of fertile fronds developing simultaneously, basal part of frond spreading, otherwise pendulous, fronds asymmetrical, angustate, elliptical or obovate, 50–125 (or more) cm long, 3–7 times forked with 4 main lobes, pergamentaceous, central lobe sterile, long-pendulous (3)4–6 times forked, basal lobes two, sterile, ± spreading, 2–4 times forked, central lobe, fertile, horizontally exposed, either shell-shaped, or kidney-shaped, or semi-circular, 7–36 by 5–20 cm, stalk 2–7 cm long. – *Sporangia* 200–235 by 140–160 μm, index 1.3–1.6, annulus cells: 20–22(–24), indurated cells: 9, 10, epistomium cells: 6, 7(–9), hypostomium cells: 3, 4, stomium situated laterally, stalk 1(–3)-seriate, 1.5–2.0 mm long, spores: 8, 80–95 by 55–65 by 55–65 μm; perispore distinct, flaky; dehiscence of paraphyses and sporangia present. – *Indument*: stellate hairs with 7, 8 rays, which are undifferentiated, 280–450 by 20–25 μm, apex filiform; paraphyses long-stalked, with 12–20 rays, terminally and subterminally inserted, short-clavate, 155–265 by 60–85 μm.

Distribution. Birma, Thailand, Vietnam, Sumatra, Malay Peninsula,

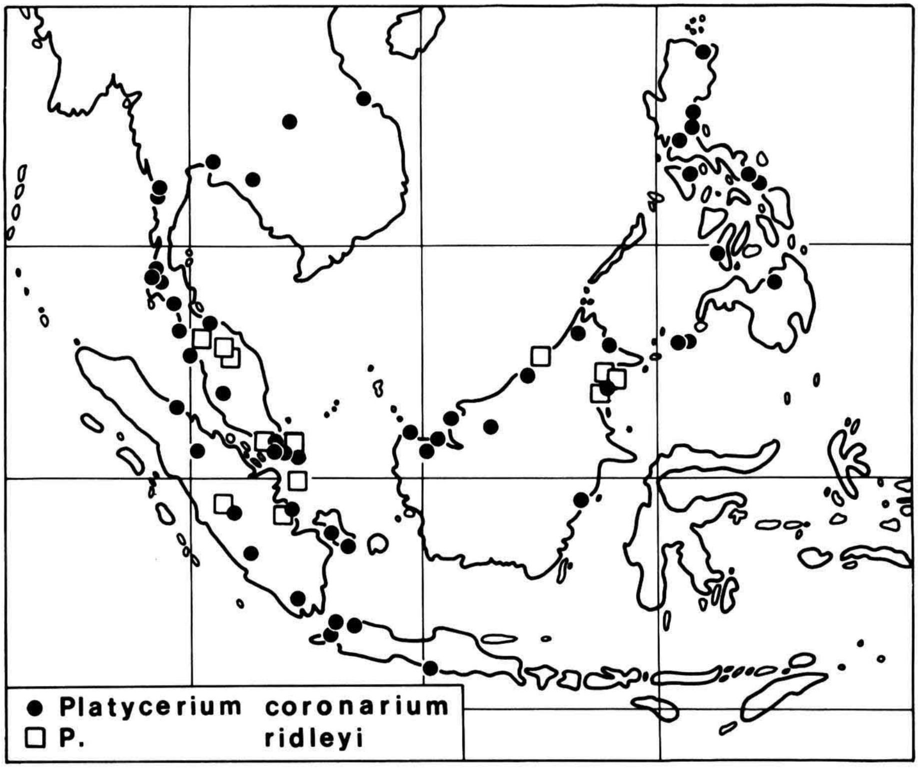

Fig. 21. Distribution of *Platycerium coronarium* and *P. ridleyi*.

Singapore, Riau Arch., Bangka, Java, Anambas Arch., Borneo (N. and E.), Philippines (Mindoro, Luzon, Samar, Negros, Mindanao).

Habitat. In everwet primary and secondary forests, also in plantations and otherwise disturbed place, growing on shaded low branches as well as on high branches exposed to the sun. Altitude: 0–500(–1000) m.

Notes. 1. The present species is one of the most beautiful epiphytes of the everwet malesian lowlands. It is locally very common, also as an ornamental plant. The species is close to *P. ridleyi*, with which it differs strikingly in architecture of the base fronds (± similar to those of *P. bifurcatum* ssp. *willinckii*), and position of the foliage fronds (pendulous in *P. coronarium*, erect in *P. ridleyi*).

2. Dehiscence of all paraphyses and sporangia at the same time is a characteristic of the present species and *P. ridleyi*.

3. So-called 'fibrils' were occasionally found amongst the larger-sized rhizome scales; according to Joe Hoshizaki (1970) they should be lacking in *P. coronarium*.

4. Vernacular names: Semung bidadari (Perak, Malay, Peninsula), Limbo (Kalantau, Malay Peninsula), Kojang (Bangka).

5. Uses. *SF 13618 (Burkill & Haniff*, SING) has the annotation 'ashes are rubbed over the body for spleen disease'.

5. **Platycerium elephantotis** Schweinf. – **Fig. 22a–22d, 23; Plate 6, 7b.**

P. elephantotis Schweinf., Bot. Ztg (1871) 361 *c. fig.*; Kuhn, Decken's Reisen O.-Afr. 3, 3 (1879) 54; Christ, Farnkr. Erde (1897) 127; Schelpe, Contr. Bolus Herb. 1 (1969) 88; De Jonch., Blumea 22 (1974) 55; Schelpe, Consp. Fl. Angol. (1977) 113; Schelpe & Diniz in Mendes, Fl. Moçamb., Pterid (1979) 147. – Type: *Schweinfuhrt 3120*, Central Africa, Sudan (Niamniam), Mando's village (K, iso; B, drawing).

Platycerium angolense Wellwitsch *ex* Baker in Hooker & Baker, Syn. Fil. (1868) 425, *nomen illeg.*; Christ. Farnkr. Erde (1897) 127; Welwitsch, Gdnrs' Chron. 23 (1898) 155, Fig. 62; Carruth., J. Bot., Lond. 38 (1900) 125; Diels in E. & P., Nat. Pfl. Fam. 1, 4 (1902) 339; De Wild., Miss. E. Laurent 1 (1905) 13, Fig. 3, 4; C. Chr., Ind. Fil. (1906) 496; Eng., Pflanzenw. Afrik. 2 (1908) 58, Pl. 3; Poisson, Revue hort. 10 (1910) 458; Straszewski, Flora, Jena 108 (1915) 306, Fig. 39; Tardieu, Mém. Inst. fr. Afr. noire 28 (1958) 208, Pl. 41: Fig. 2; Alston in Hutchinson & Dalziel, Fl. W. Trop. Afric., Suppl. Ferns (1959) 46; Tardieu in Aubrév., Fl. Cameroun 3 (1964) 334; Fl. Gabon 8 (1964) 196, Pl. 31: Fig. 2; Joe, Baileya 12 (1964) 80, Fig. 35: a–c; Morton, Am. Fern J. 60 (1970) 11; Joe Hoshizaki, Am. Fern J. 60 (1970) Pl. 19: Fig. 15; Biotropica 4 (1972) 95, Pl. 2: Fig. 4, Pl. 3: Fig. 4, Pl. 5: Fig. 8, Pl. 7: Fig. 4, Pl. 8: Fig. 4. – *Alcicornium angolense* (Welwitsch ex Baker) Underwood, Bull. Torrey bot. Club 32 (1905) 593. – Type: *Welwitsch 160*, Angola, Golungo Alto Distr. (K, holo; BM).

Platycerium velutinum C. Chr., Dansk Bot. Ark. 9,3 (1937) 69; Ind. Fil., Suppl. 4 (1965) 223. – Type: Humbert 8695, Zaïre, Kivu, S. of Lake Edward, alt. c. 1300 m (P, holo; BR).

P. aethiopicum p.p. auct., non Hooker: Baker in Hooker & Baker, Syn. Fil. (1868) 425.

Generally epiphytic, occasionally epilithic, growing in clusters. – *Scales* basally-attached, index 8–16, widest usually near the base, sometimes wides about the middle, 5–13 by 0.5–1.5 mm, base truncate, margin ± straight, not flabelloid, apex acuminate to filiform, (reddish-)brown, midrib undivided, linear or narrow-triangular, in cross-section ± rounded; indument: hairs sparsely set, situated marginally and abaxially, usually branched, sometimes unbranched, 1–5-celled, 35–250 μm long, without protuberances, unbranched hairs 1–4 celled, longest branches of branched hairs 2–3 celled; apical cell either glandular, 30–50 μm long, situated terminally on part of the 2-celled hairs and on all 3–4-celled unbranched hairs, as well as on usually one branch of branched hairs, or apical cell non-glandular, 50–250 μm long, situated terminally on part of the 2-celled hairs and always on at least one branch of branched hairs; 1-celled trichomes glandular or not. – *Base fronds* sessile, green, old fronds erect, 30–75 by 10–30 cm; upper part erect, wedge-shaped, apex truncate, margin ± entire, lower part with entire margin, fringe conspicuous, situated above the stipe only, margin entire; veins immersed, water storage tissue present, cells cylindrical. – *Foliage fronds* (sterile and) fertile, maturing in pairs in a bilateral sym-

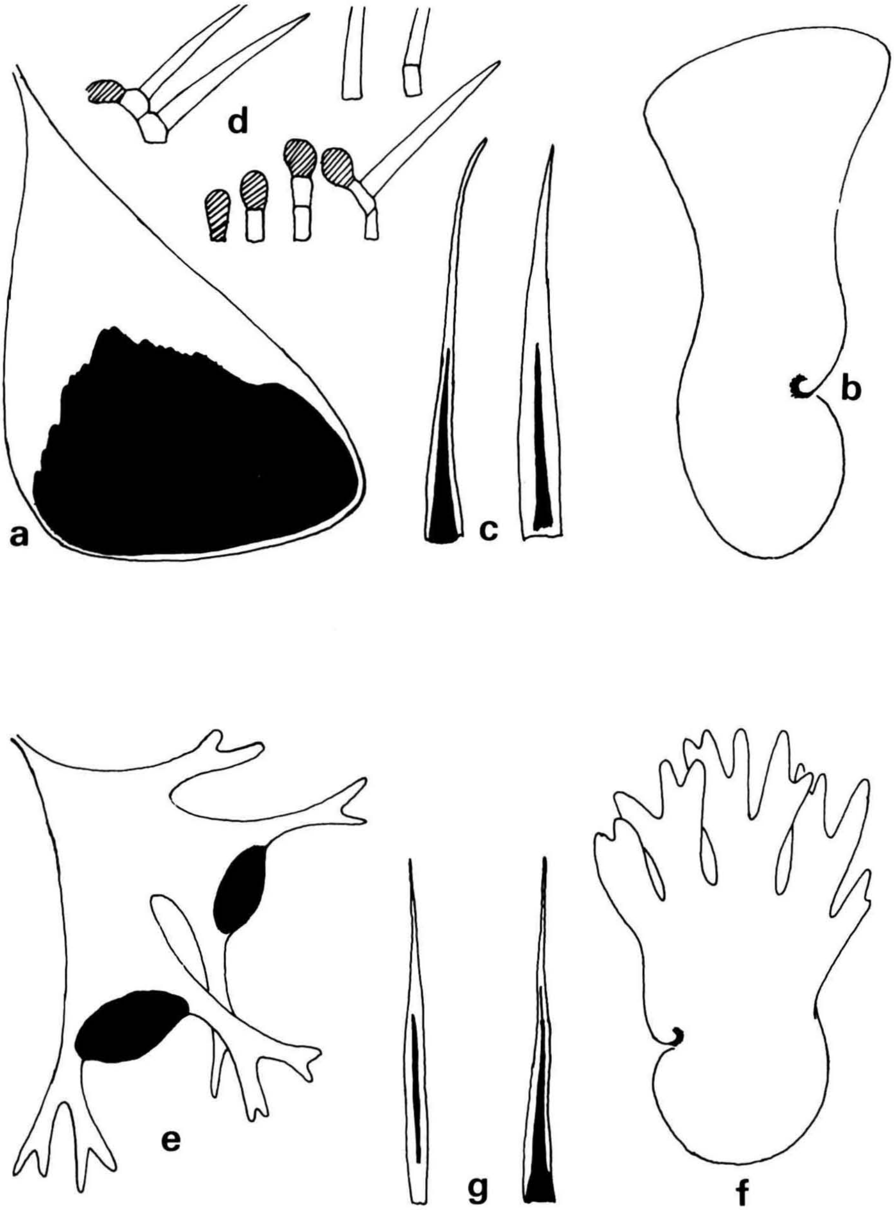

Fig. 22. a–d. *Platycerium elephantotis*. a. foliage frond, x 1/8; b. base frond, x 1/8; c. rhizome scales, x 6; d. indument of scales, x c.200. – e–g. *P. wallichii*. e. foliage frond, x 1/8; f. base frond, x 1/8; g, rhizome scales, x c.200.

metrical pattern, fertile and sterile parts of fertile fronds developing simultaneously, pendulous, asymmetrical, obovate, entire, 40–75 cm (by 20–55 cm), leathery, soral patch one, horizontally exposed, situated in the apical part, semi-rounded to transverse-obovate, 20–40 by 10–40 cm. – *Sporangia* 275–310 by 230–265 µm, index 1.1–1.2, annulus cells: (26)27–29(–31), indurated cells: 17–20(–22), epistomium cells: 3–5, hypostomium cells: 2, 3, stomium situated laterally, stalk (2)3-seriate, 0.1–0.3 mm long, spores: 64, 75–85 by 50–60 by 50–60 µm, perispore indistinct; dehiscence of paraphyses and sporangia absent. – *Indument*: stellate hairs with (6)7–9(–12) rays, which are undifferentiated, 250–475 by 30–40 µm, apex filiform; paraphyses shortly stalked, with 7–9 rays, terminally inserted, undifferentiated, involute to canaliculate, 280–575 by 30–45 µm.

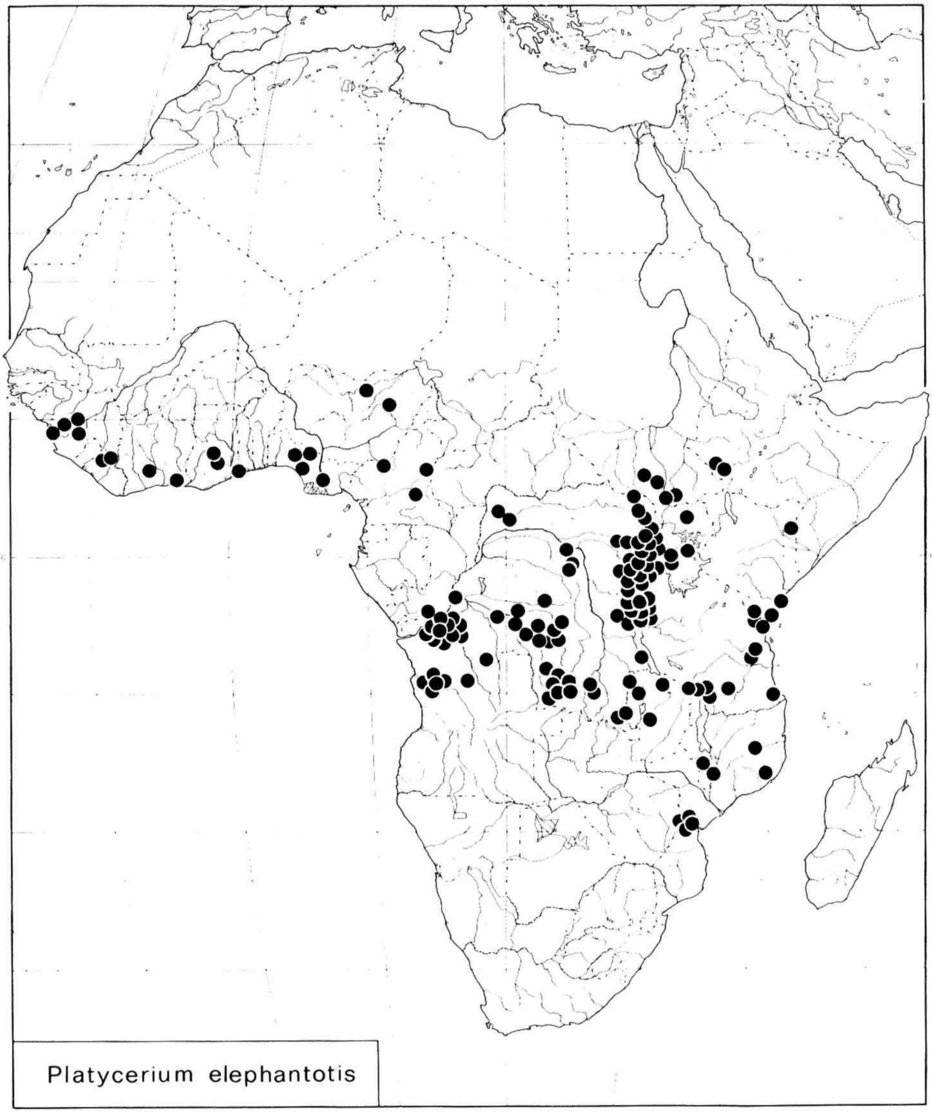

Fig. 23. Distribution of *Platycerium elephantotis*.

Chromosomes. N = 37 (Löve, Löve & Pichi-Sermolli, 1977).

Distribution. Senegal, Guinea, Sierra Leone, Liberia, Ivory Coast, Ghana, Togo, Dahomey, Nigeria, Cameroun, Sudan, Ethiopia, Congo (Braz.), Zaire, Angola, Burundi, Uganda, Kenya, Angola, Tanzania, Malawi, Zambia, Moçambique.

Habitat. Generally epiphytic (2–50 m high on trees), occasionally epilithic, in several types of primary and secondary forests, and in savannahs, also in plantations. Altitude: 200–1500(–1800) m.

Notes. 1. This species is widely distributed in Africa, reaching from the west to the east coast. It is absent from the islands west and east of the tropical mainland and also from large parts of the humid Congo basin. Generally, it occurs in drier habitats than does *P. stemaria*.

2. According to the field data recorded on the labels, the present species is locally abundant; it is commonly found in galery forests where it grows on a variety of trees. A marked number of collections was taken from *Elaeis guinensis* Jacq. (Palmae).

3. The leathery texture of the foliage fronds and the (ex-)position of the soral patch is similar to that found in *P. wallichii*.

4. Vernacular name: Yaka-yaka (Zaire, Kisantu), Liombombo (Zaire, dial. Turumbu), Pepelegbuku and Peperebuku (Zaire).

5. Usage: The juice squeezed out of green fronds is given to children against Malaria tropica (malaria spasms) (*Haerdy 475*, Tanzania; BR, G).

6. Platycerium ellisii Baker. – Fig. 13a–13d, 14.

P. ellisii Baker, Journ. Linn. Soc. 15 (1876) 421; Hooker, Icones plant. 7 (1887) Pl. 1695; Baker, Ann. Bot. 5 (1891) 496; Christ. Farnkr. Erde (1897) 127; Diels in E. & P., Nat. Pfl. Fam. 1,4 (1902) 339; C. Chr., Ind. Fil. (1906) 496; Poisson, Revue hort. 10 (1910) 458; Straszewski, Flora, Jena 108 (1915) 306; C. Chr., Dansk Bot. Ark. 7 (1932) 172; Tardieu, Not. Syst. (Paris) 15 (1959) 420, Pl. 2: Fig. 4; in Humbert, Fl. Madag. (1960) 95, Pl. 21: Fig. 4; Joe, Baileya 12 (1964) 88, Fig. 39: a, b; Joe Hoshizaki, Am. Fern J. 60 (1970) Pl. 19: 20; Biotropica 4 (1972) 95, Pl. 1: Fig. 7, Pl. 2: Fig. 7, Pl. 3: Fig. 7, Pl. 5: Fig. 11, Pl. 7: Fig. 7, Pl. 8: Fig. 7. – *Alcicornium ellisii* (Baker) Underwood, Bull. Torrey bot. Club 32 (1905) 594. – Type: *Ellis s.n., 1870*, Madagascar (K).

Platycerium diversifolium Bonap., Notes Pterid. 4 (1917) 84. – *P. ellisii* Baker var. *diversifolium* C. Chr., Dansk Bot. Ark. 7 (1932) 172; Joe, Baileya 12 (1964) 89. – Type: *Perrier de la Bâthie 7932*, Madagascar, Côte d'Est, Masoala, Marambo (P).

Epiphytic, growing in clusters. – *Scales* basally-attached, index 3.5–8.5, widest near the base, 4.0–8.0 by 0.7–1.4 mm, base truncate to rounded, margin slightly convex, not flabelloid, apex acuminate, thin-coriaceous, red-brown, midrib undivided, linear or narrow-triangular, in cross-section ± rounded; indument: hairs sparsely set, situated marginally and abaxially, unbranched, 2-celled, 25–50 μm long, without protuberances; apical cell glandular, 15–35 μm long; 1-celled trichomes glandular, 15–35 μm long, or non-glandular, 40–125 μm long. – *Base fronds* sessile, withering, old fronds appressed, 20–30 by 15–20 cm; upper part appressed, rounded, margin entire, lower part with margin entire, without fringe; veins immersed, water storage tissue present, cells spherical. – *Foliage fronds* (sterile and) fertile, maturing in an undetermined number, fertile and sterile parts of fertile fronds developing simultaneously, erect, often symmetrical, sometimes asymmetrical, wedge-shaped to obovate, 30–60 cm long, entire or one time lobed, pergamentaceous, 1 (rarely 2) soral patch(es), situated away from the plant, in the apical part, oblong or with two angustate, acute lobes mostly reaching around the sinus, 4–20 by 2–20 cm. – *Sporangia* 290–330 by 210–240 µm, index 1.2–1.5, annulus cells: (20)21, 22, indurated cells: (12)13–15, epistomium cells: 3(4), hypostomium cells: 1, 2, stomium situated laterally, stalk (2)3-seriate, 0.1–0.3 mm long, spores: 64, 65–70 by 40–45 by 40–45 µm, perispore indistinct; dehiscensce of paraphyses and sporangia absent. – *Indument*: stellate hairs with (7)8–11(–13) rays, 75–150 by 25–35 µm, which have a narrow, flat marginal zone, apex round or acute; paraphyses shortly stalked, with 10–14 rays, terminally inserted, flat or convex, 80–140 by 30–40 µm.

Distribution. Madagascar.

Habitat. Humid forests. Altitude: 0–400 m.

Notes. 1. The present species has characteristic, morphologically simple foliage fronds resembling those found in juvenile specimens of *P. alcicorne* and *P. stemaria.* Unforked foliage fronds of the present species are usually asymmetrical, whereas in general the once-forked ones are symmetrical showing a soral patch similarly positioned as that found in *P. stemaria.*

2. *P. ellisii* is confined to the phytogeographic region indicated as 'Domaine de l'Est' by Perrier de la Bâthie (in C. Christensen, op. cit., 1932). It is allopatric with its sister species *P. alcicorne*, and in part sympatric with *P. madagascariense.*

3. Vernacular name: Ranala (language: Mag.).

7. **Platycerium grande** (Fée) Kunze. – **Fig. 24, 25; Plate 7a, 8a.**

P. grande J. Smith, Hook. J. Bot. 3 (1841) 402, *nom. nud.*; Hook. J. Bot. 4 (1842) 153, *nom. nud*; Kunze, Linnaea 23 (1850) 474, *p.p.*; C. Presl., Epim bot. (1851) 154; Mettenius, Filices Horti Bot. Lips (1856) 26 *p.p.*; Hooker, Gdnrs' Chron. (1858) 764; Spec. Fil. 5 (1864) 284; F. Muell., Fragm. Phytog. Austr. 5 (1866) 139; Baker in Hooker & Baker, Syn. Fil. (1868) 425; E.J. Lowe, Ferns 7 (1868) 159, Fig. 64, s.n.; Mettenius, Annls Mus. Bot. L.B. 4 (1868-'69) 170; Luerssen, J Mus. Godeffroy 3 (1873) 8; Benth.; Fl. Austral. 7 (1878) 781; F.M. Bailey, Fernw. Austral. (1881) 74; Syn. Queensl. Fl. (1883) 724; Bedd., Handb. Ferns Br. Ind. ed. 2 (1892) 445; J. Smith, Ferns Br. & For. (1896) 121; Christ, Farnkr. Erde (1897) 127; Annls Jard. bot. Buitenz. 15 (1898) 182; Racib., Pterid. Fl. Buitenz. (1898) 57; F.M. Bailey, Queensl. Fl. 6 (1892) 1995; Diels in E. & P., Nat. Pfl. Fam. 1,4 (1902) 339; Copel., Dep. int. Bur. Govern. 28 (1905) 138; C. Chr., Ind. Fil. (1906) 496; v.A.v.R., Mal. Ferns (1908) 708; Copel., Leafl. Philipp. Bot. 3 (1910) 850; Poisson, Revue hort. 10 (1910) 459; Domin. Biblthca bot. 85, 1 (1915) 198; Straszewski Flora, Jena 108 (1915) 305, Fig. 8–11, 16, 31, 38, 40; Ridley J. Malay. Brch R. Asiat. Soc. 4,1 (1926) 109; Tardieu & C. Chr. in Lecomte, Fl. Gén. Indo-Chine 7,2 (1941) 446; Copel, Fern Fl. Philipp. 3 (1960) 458; Tindale, Contr. N.S.W. natn. Herb. Flora Ser. 208–211 (1961) 28; Joe, Baileya 12 (1964) 91; De Jonch. & Hennipm., Brit. Fern Gaz. 10,3 (1970) 113, Pl. 9; Joe Hoshizaki, Am. Fern J. 60 (1970) Pl. 18: Fig. 5, 8, Pl. 19: Fig. 28; Biotropica 4 (1972) 95, Pl. 2: Fig. 15, pl. 4: Fig. 14, Pl. 6: Fig. 19, Pl. 7: Fig. 15, Pl. 8: Fig. 15; Hennipm. et. al., Fern Gaz. 12,1 (1979) 47, Fig. 1, 2; – *Neuroplatyceros grandis* Fée, Mém. Fougères 2 (Acrost.) (1845) 103, *p.p.* – *Alcicornium grande* Underwood, Bull. Torrey bot. Club 32 (1905) 594, *p.p.* – *P. grande* (Fée) Kunze var. *normale* Domin. Biblthca bot. 85, 1 (1915) 200, *p.p., nom. illeg.* – - Type: *Cuming 157*, Philippines, Luzon (BM).

Epiphytic, growing solitary. – *Scales* basally-attached, index 3.5–8.0, widest near the base, 12.5–22.0 by 2.0–4.5 mm, base truncate, margin ± straight to slightly convex, not flabelloid, apex acute, papery, brownish with the basal and central part darker, midrib absent; indument: hairs very densely set, situated in a narrow marginal zone, branched or unbranched, 1–7-celled, 60–900 µm long, the greater part with protuberances; apical cell usually non-glandular, 60–300 µm long, situated on (1–)3–7-celled hairs, 100–900 µm long, sometimes apical cell glandular, 35–75 µm

Fig. 24. *Platycerium grande*. a. foliage frond, x 1/8; b. base frond, x 1/8; c. rhizome scales, x 6; d. indument of scales, x c.200.

long, situated on 2–3(4)-celled hairs, 60–125 μm long; 1-celled trichomes rarely present, non-glandular. – *Base fronds* sessile, green, old fronds recurring, 80–110 by 90–180 cm; upper part spreading, wedge shaped, apex truncate, 3–5 times dichotomously lobed, lobes equally-long, lower part with sinuate margin, fringe conspicuous, encircling the stipes, margin entire or sinuate; veins immersed, water-storage tissue present, cells spherical. – *Foliage fronds* fertile (rarely sterile), maturing in pairs, fertile and sterile parts of fertile fronds developing in succession, spreading, lateral appendages pendulous, fronds symmetrical, wedge-shaped, 50–120 cm long, pergamentaceous, with 2 wedge-shaped main lobes, each bearing one ± semi-circular, horizontally exposed soral patch, situated in the sinus, 7–35 by 2–22 cm, flanked on both sides by 3–7 times forked lateral appendages. – *Sporangia* 315–365 by 240–285 μm, index 1.2–1.4, annulus cells: (25–)27–31(–33), indurated cells: (15–)17–22(–24), epistomium cells: 3, 4, hypostomium cells: (2)3, 4, stomium situated laterally, stalk (2)3-seriate, 0.1–0.5 mm long, spores: 64, 65–80 by 45–50 by 45–50 μm, perispore indistinct; dehiscence of paraphyses and sporangia absent. – *Indument*: stellate hairs with (8–)9–10(–13) rays, which are undifferentiated, 155–240 by 20–30 μm, apex filiform; paraphyses shortly stalked, with 10–14(–16) rays, terminally inserted, undifferentiated, involute to canaliculate, 120–175 by 45–60 μm.

Distribution. Philippines (Luzon (?), Ticao, Cebu, Mindanao).

Habitat. No information available.

Notes. 1. The present species belongs to the impressive giant staghorn ferns, together with *P. holttumii, P. superbum,* and *P. wandae.* All have wedge-shaped foliage fronds, either divided into two wedge-shaped main lobes or undivided, with one or two large, semi-circular, soral patch(es) situated in the ultimate sinus and flanked by secondarily elongated lateral appendages. The base fronds, of which the upper part is spreading, form a huge basket, in which even shrubs may grow. The main differences between the four giants-taghorn species concern the shape and symmetry of the foliage fronds, as well as microscopic properties of the scale (*i.e.* indument, midrib).

2. The shape of the young foliage fronds, and the position of the soral patch just before the elongation of the lateral appendages, is essentially similar to that found in mature foliage fronds of *P. stemaria.*

8. Platycerium holttumii De Jonch. & Hennipm. – Fig. 25, 26; Plate 2.

P. holttumii De Jonch. & Hennipm., Brit. Fern Gaz. 10,3 (1970) 116, Pl. 12: Fig. 1–3; Joe Hoshizaki, Am. Fern J. 60 (1970) Pl. 19: Fig. 26; Biotropica 4 (1972) 95, Pl. 1: Fig. 9, Pl. 2: Fig. 13, Pl. 4: Fig. 15, Pl. 6: Fig. 18, Pl. 7: Fig. 13, Pl. 8: Fig. 13. – Type: *Hennipman 3968*, Thailand, Eastern, Nakohn Ratchasima, Prachinburi, Khao (Mt) Jai Nat. Park, c. 500 m alt. (L, holo; BKF, KYO).

P. grande auct. non (Fée) Kunze, *quod specim. Asii continent.*

Epiphytic, growing solitary. – *Scales* basally-attached, index 5–9, widest at the base, 17–28 by 2.5–4.5 mm, base truncate, margin straight to slightly convex, not flabelloid, apex acute to acuminate, papery, brownish, midrib absent; indument: hairs very densely set, situated in a narrow marginal zone, branched or unbranched, (1–)5–8-celled, 15–1000 μm long, the greater part with protuberances; apical cell usually non-glandular, 35–350 μm long, situated on (2–)5–8-celled hairs up to 1000 μm long, sometimes apical cell glandular, 20–50 μm long, situated on 2, 3-celled, unbranched hairs and on branches of 3–4-celled branched hairs; 1-celled trichomes rarely present, glandular or non-glandular. – *Base fronds* sessile, green, old fronds recurving, 90–115 by 90–135 cm; upper part spreading, wedge-shaped, the apex truncate, 3–6 times dichotomously lobed, lobes equally-long, lower part with sinuate margin, fringe conspicuous, encircling the stipes, entire or sinuate; veins immersed, water storage tissue present, cells spherical. – *Foliage fronds* fertile (rarely sterile), maturing in pairs in a bilateral symmetrical pattern, fertile and sterile parts of fertile fronds developing in succession, spreading, lateral appendages pendulous, fronds asymmetrical, wedge-shaped, 95–125 cm long, pergamentaceous, with 2 wedge-shaped main lobes, each bearing one ± semi-circular, horizontally exposed soral patch, situated in the sinus, 10–45 by 8–35 cm, flanked on both sides by 3–5 (central lobe) or 2–3 (lateral lobe) times forked lateral appendages. – *Sporangia* 325–375 by 235–290 μm, index 1.2–1.5, annulus cells: (26–)28–31, indurated cells: (16–)18–21, epistomium cells: (3)4–6, hypostomium cells: (2)3, 4, stomium situated laterally, stalk (2)3-seriate, 0.1–0.5 mm long, spores: 64, 65–85 by 40–55 by 40–50 μm, perispore indistinct; dehiscence of paraphyses and sporangia absent. – *Indument*: stellate hairs with (9)10–12(13) rays, which are undifferentiated, 195–300 by 20–30 μm, apex filiform; paraphyses shortly stalked, with 12–15(–17) rays, terminally inserted, spine-like, 115–185 by 30–45 μm.

Distribution. Thailand, Cambodia, Laos, Vietnam, Malay Peninsula.

Habitat. Epiphytic in evergreen or deciduous forests in monsoon areas. Altitude. 0–700 m.

Notes. 1. This species is partly sympatric with *P. wallichii*; the two species may grow intermingled.

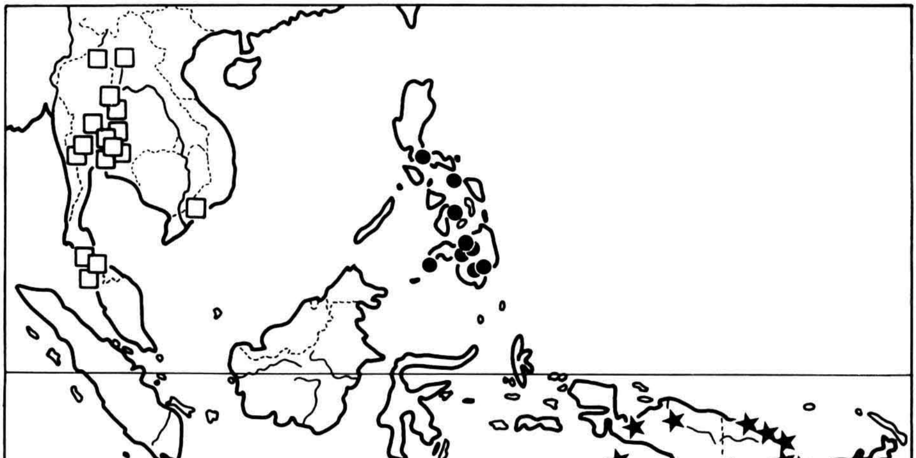

Fig. 25. Distribution of *Platycerium grande, P. holttumii*, and *P. wandae*.

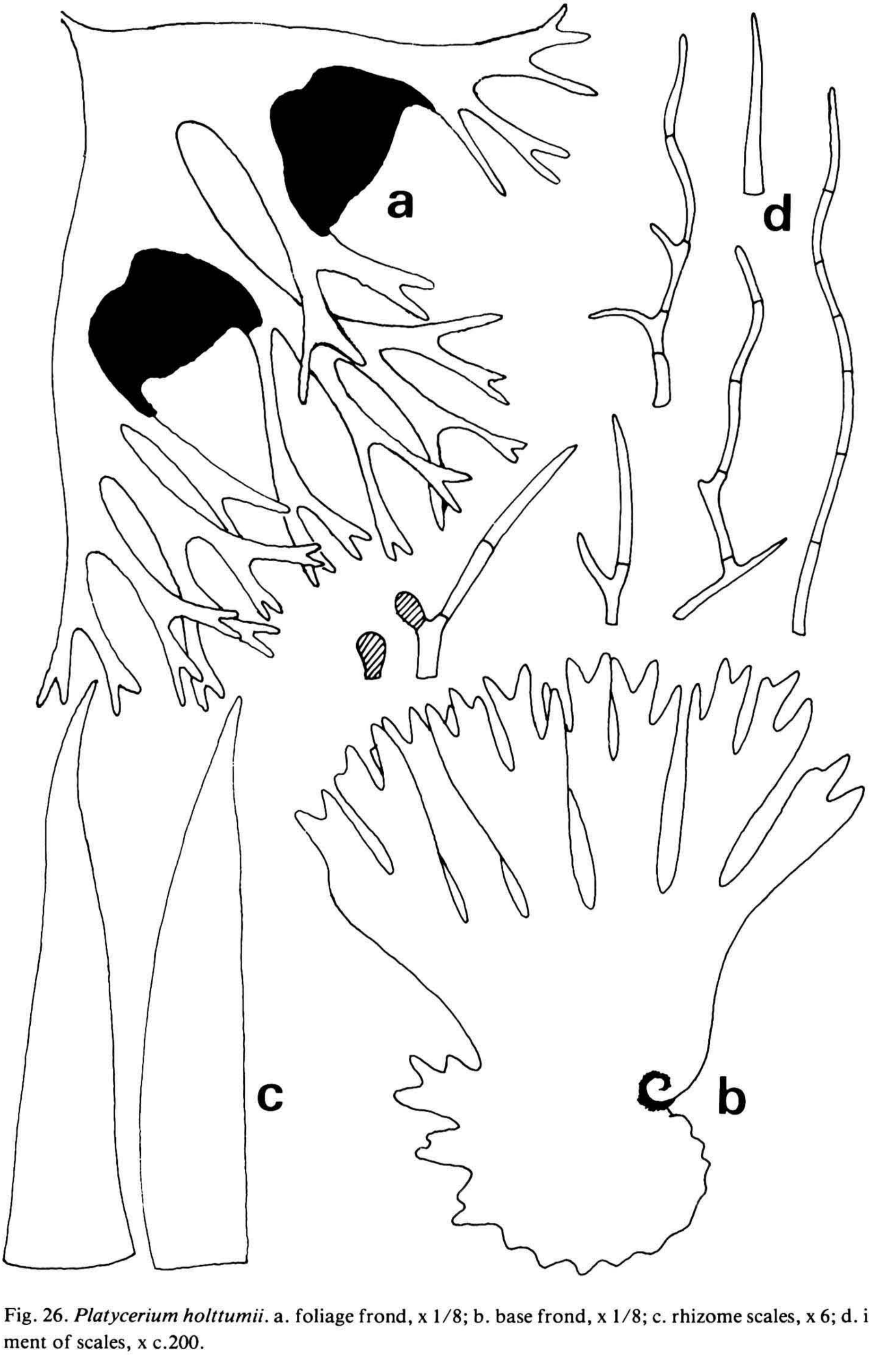

Fig. 26. *Platycerium holttumii*. a. foliage frond, x 1/8; b. base frond, x 1/8; c. rhizome scales, x 6; d. indument of scales, x c.200.

2. The precise locality in Cambodia is not traced. The distribution of *P. holttumii* in Indo-China is incompletely known.

3. Uses. According to the field data recorded on the herbarium specimens, the fronds are used in making tea.

4. See notes to *P. grande* and to *P. wallichii.*

9. Platycerium madagascariense Baker. – Fig. 14, 27e–27h; Plate 5.

P. madagascariense Baker, Journ. Linn. Soc. 15 (1876) 421; id. 16 (1877) 205; Ann. Bot. 5 (1891) 496; Diels in E. & P., Nat. Pfl. Fam. 1,4 (1902) 339; C. Chr., Ind. Fil. (1906) 496; Poisson, Revue hort. 10 (1910) 458; Straszewski. Flora, Jena 108 (1915) 306, Fig. 35; C. Chr., Dansk Bot. Ark. 7 (1932) 172; Tardieu, Not. Syst. (Paris) 15 (1959) 420, Pl. 2: Fig. 1–3; in Humbert, Fl. Madag. (1960) 96, Pl. 21: 1–3; Joe, Baileya 12 (1964) 94, Fig. 42: Joe Hoshizaki, Am. Fern J. 60 (1970) Pl. 19: Fig. 18; Biotropica 4 (1972) 95, Pl. 2: Fig. 5, Pl. 3: Fig. 5, Pl. 5: Fig. 9, Pl. 7: Fig. 5, Pl. 8: Fig. 5. – *Alcicornium madagascariense* (Baker) Underwood, Bull. Torrey bot. Club 32 (1905) 595. – Type: *Pool s.n., 1876*, Madagascar (K, holo; M).

P. madagascariense Baker var. *humblotii* Poisson, Revue hort. (Paris) 10 (1910) 459. – Type: *Humblot 208*, Madagascar (P).

Epiphytic, growing in clusters. – *Scales* basally-attached, index 3.5–14, widest at the base, 3.5–10 by 0.4–1.2 mm, base truncate to rounded, margin slightly convex, not flabelloid, apex acuminate (to filiform), papery to thin-coriaceous, red-brown, the central part often somewhat darker, midrib absent; indument: trichomes sparsely set, situated marginally and abaxially, unbranched, 1–3(4)-celled, 30–120 μm long, without protuberances; apical cell glandular, 15–30(–50) μm long; 1-celled trichomes rarely present, glandular or non-glandular. – *Base fronds* inconspicuously stalked, green, darkening, old fronds appressed, 10–35 by 8–22 cm; upper part appressed, round, margin minutely dentate, lower part with minutely dentate margin, fringe conspicuous, encircling the stipes, margin minutely dentate; veins prominent, forming a waffle-pattern, water storage tissue absent. – *Foliage fronds* (sterile and) fertile, maturing in an undetermined number, fertile and sterile parts of fertile frond developing simultaneously, erect, symmetrical, wedge-shaped, 10–30 cm long, 1–3 times forked, pergamentaceous, soral patches 1 or 2, situated away from the plant on the (pen-)ultimate segments, usually reaching to below the first sinus, acute or with several acute lobes, 4–16 by 3–39 cm. – *Sporangia* 325–400 by 290–335 μm, index 1.0–1.3, annulus cells: (23)24(25), indurated cells: (14)15(16), epistomium cells: (2)3, hypostomium cells: 3, stomium situated laterally, stalk (2)3-seriate, 0.1–0.3 mm long, spores: 64, 65–75 by 45–55 by 45–55 μm, perispore indistinct; dehiscence of paraphyses and sporangia absent. – *Indument*: stellate hairs with (7)8–10(–12) rays, which are undifferentiated, 95–180 by 20–35 μm, apex filiform; paraphyses shortly stalked, with (7–)10–13(14) rays, terminally inserted, undifferentiated, involute to canaliculate, 130–170 by 30–50 μm.

Distribution. Madagascar.

Habitat: Epiphytic in forest. Altitude. 300–700 m.

Notes. 1. The base frond of the present species has a number of unique characters, *i.e.* the arrangement of old fronds into globular structures, the dark green colour, the fronds which are stalked, the prominent venation (like in *P. ridleyi*) showing a waffle-pattern (absent in *P. ridleyi*), and the lack of water storage tissue.

2. The present species is often reported to grow in association (symbiosis) with *Cym-*

bidiella rhodochila Rolfe (Orchidaceae). The roots of the orchid grow into the open spaces (also inhabited by ants) between the old base fronds.

3. A significant number of foliage fronds collected from the field have the upper margin irregularly eradicated by animals. Excellent undamaged specimen are being cultivated by Mr. J. Bogner in Munich.

4. Mature foliage fronds show much variation. The most elaborate fronds remind of those found in *P. bifurcatum* having the central lobes not forked. The soral patch is proportionally large, often completely covering the upper half of the frond.

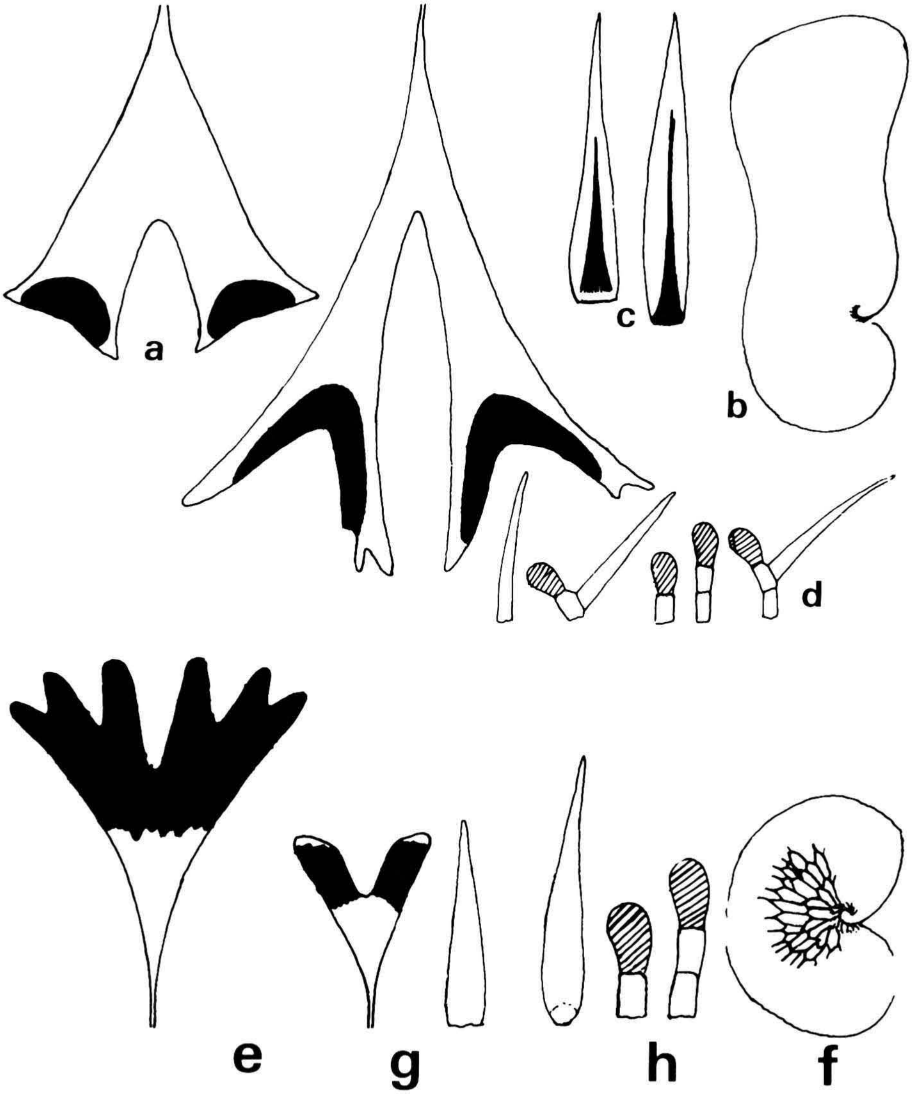

Fig. 27. a–d. *Platycerium stemaria*. a. foliage fronds, x 1/8; b. base frond, x 1/8; c. rhizome scales, x 6; d. indument of scales, x c.200. – e–h. *P. madagascariense*. e. foliage fronds, x 1/8; f. base frond, x 1/8; g. rhizome scales, x 6; h. indument of scales, x c.200.

5. According to Perrier de la Bâthie (in Christensen *op. cit.* 1932) this species should occur exclusively in the phytogeographical district indicated as 'Domaine Central'. However, the distribution map of the present species (fig. 14) shows that it also occurs in the 'Domaine d'Est'.

6. This species has relatively large-sized indurated annulus cells.

7. Leaves of *Dilobeia thouarsii* R & S (Proteac.) from Madagascar were identified by Fée as '*Drynaria vel Platycerium*' (Goudot, 1833, G), and by Christ as *Platycerium madagascariense* (Rusillon 74, G).

10. Platycerium quadridichotomum (Bonap.) Tardieu. – **Fig. 14, 15e–15h; Plate 4.**

P. quadridichotomum (Bonap.) Tardieu, Not. Syst. (Paris) 15 (1959) 420, Pl. 1: Fig. 3–5; in Humbert, Fl. Madag. (1960) 98, Pl. 22: Fig. 3–5; Joe, Baileya 12 (1964) 96, Fig. 43; C. Chr., Ind. Fil., Suppl. 4 (1965) 223; Joe Hoshizaki, Am. Fern J. 60 (1970) Pl. 19: Fig. 17; Biotropica 4 (1972) 95, Pl. 1: Fig. 5, Pl. 2: Fig. 2, Pl. 3: Fig. 2, Pl. 5: Fig. 6, Pl. 7: Fig. 2, Pl. 8: Fig. 2. – *P. bifurcatum* (Cav.) C. Chr. var. *quadridichotomum* Bonap., Notes Pterid. 4 (1917) 84. – Type: *Perrier de la Bâthie 7720*, W.-Madagascar, Haute Bemarivo (Boina) (P).

Usually epilithic, often epiphytic, growing in clusters. – *Scales* basally-attached, index 2.5–7(–10), widest at the base, 2–5 by 0.4–1.2 mm, base truncate to rounded, margin slightly convex to slightly concave, not flabelloid, apex acuminate, thin-coriaceous, light-brown, midrib undivided, linear to narrow-triangular, in cross-section ± rounded; indument: hairs sparsely set, situated marginally and abaxially, unbranched, 3–6-celled, (60–)80–220 μm long, without protuberances; apical cell glandular, 35–85 μm long; 1-celled trichomes rarely present, glandular or non-glandular, 60–150 μm long. – *Base fronds* sessile, withering, old fronds erect, 18–40 by 7–17 cm; upper part erect, wedge-shaped, apex truncate, margin entire or irregularly dentate, lower part with entire margin, without a fringe; veins immersed, water storage tissue present, cells spherical. – *Foliage fronds* (sterile and) fertile, maturing in pairs in a bilateral symmetrical pattern, fertile and sterile parts of fertile frond developing in succession, pendulous (spreading when young), asymmetrical, wedge-shaped, 15–40 cm long, 2–4 times dichotomously forked, texture pergamentaceous, soral patches usually 2, sometimes 4, facing the plant, reaching from near the first sinus to up to the ultimate sinus or spread medially within this area, angustate or with 2 lobes, 0.5–8.5 by 0.2–2.5 cm. – *Sporangia* 240–275 by 215–240 μm, index 1.1–1.2, annulus cells 21–25(–28), indurated cells: (14)15–18(–21), epistomium cells: (3)4(5), hypostomium cells: 1, stomium situated laterally, stalk (2)3-seriate, 0.1–0.3 μm long, spores: 64, 60–70 by 35–40 by 35–40 μm, perispore indistinct; dehiscence of paraphyses and sporangia absent. – *Indument*: stellate hairs with (6–)8, 9(–12) rays, which are undifferentiated 320–510 by 20–35 μm, apex filiform; paraphyses shortly stalked, with 8–11(12) rays, terminally inserted, undifferentiated, involute to canalicute, 180–325 by 30–50 μm.

Distribution. Madagascar.

Habitat: Usually epilithic; locally common in forests on limestone, in areas enduring a severe dry period of ± 6 months of the year. Altitude: 0–250 m.

Notes. 1. The present species is easily recognized by the medially situated soral patches, a condition similarly found in *P. andinum*. However, the two species differ in size, characters of the scales (*e.g.* midrib, indument), and the morphology of the upper part of the base fronds (entire or irregularly dentate in *P. quadridichotomum*, with two equally-long lobes in *P. andinum*). Photographs of wild specimens of *P. quadridichotomum* made by Mr. J. Bogner, indicate the secondary elongation of the sterile parts of the foliage fronds. Juvenile foliage fronds resemble those found in *e.g. P. stemaria*.

2. During the long dry season the plants have longitudinally recurved (involuted) foliage fronds exposing the densely hairy lower surface. Herbarium specimens collected in that period, therefore, show a characteristic 'bony' appearance. In spite of its occurrence in temporarily very dry areas, the morphology and density of the stellate hairs of this species are not strikingly deviating from those found in *Platycerium* species preferring wetter habitats.

3. The species is confined to the western and northern part of Madagascar, phytogeographically indicated as 'Domaine de l'Ouest' by Perrier de la Bâthie (in C. Christensen, *op. cit.* 1932). It is allopatric with the other species from Madagascar.

4. Vernacular name: Ramandrakotra (region of Ambobaka).

5. Uses. An infusion made of fronds and roots of the present species is used against intestinal troubles and hypertrophy of the milt or heart (*Anonymous 319, 24-11-1942 [Herb. Jard. bot. Tananarive 5447]*, P).

11. Platycerium ridleyi Christ. – Fig. 20a–20d, 21.

P. ridleyi Christ, Annls Jard. bot. Buitenz., Suppl. 3 (1909) 8, Pl. 2; C. Chr., Ind. Fil., Suppl. 1 (1913) 55; Straszewski, Flora, Jena 108 (1915) 305; v.A.v.R., Mal. Ferns, Suppl. (1917) 422; Ridley, J. Malay. Brch R. Asiat. Soc. 4,1 (1926) 110; Holttum, Fl. Malaya 2 (Ferns) (1954) 140; Joe, Baileya 12 (1964) 96, Fig. 44; Joe Hoshizaki, Am. Fern J. 60 (1970) Pl. 19: Fig. 30, Biotropica 4 (1972) 95, Pl. 1: Fig. 8, Pl. 2: Fig. 18, Pl. 4: Fig. 23, Pl. 6: Fig. 22, Pl. 7: Fig. 18, Pl. 8: Fig. 18; Anonymous, L.A.I.F.S. 6,9 (1979) 271, c. Figs.; Franken & Roos, Am. Fern J. 72,1 (1982) 12. – *P. biforme* (Swartz) Blume var. *erecta* Ridley, J. Straits Brch. R. Asiat. Soc. 50 (1908) 56. – Type: *Ridley SF 10830*, Singapore, Bukit Timah (SING, holo; P).

P. coronarium (König ex Müller) Desv. var. *cucullatum* v.A.v.R., Bull. Dépt. agric. Ind. néerl. 18 (1908) 25; Mal. Ferns (1908) 711; Wigman jr., Teysmannia 21 (1910) 163. – Type: *Teysmann, s.n.*, Lingga Arch. (SING).

Epiphytic, growing with several specimens in one hosttree, but not in clusters. – *Scales* basally-attached, index 1.5–2, widest about the middle, 8–15 by 4–9 mm, base truncate, margin convex, with a flabelloid zone up to 3.5 mm wide, apex rounded, thin papery, red- or yellow-brown, midrib broad triangular, in cross-section flattened; indument: trichomes densely set, situated marginally, unbranched, 1(–2)-celled, 35–110 μm long, without protuberances; apical cell glandular 35–50 μm long. – *Base fronds* conspicuously stalked, green, old fronds appressed, 20–50 by 20–40 cm; upper part appressed, ± rounded, margin entire, lower part with margin entire, without a fringe; veins prominent, not forming a waffle-pattern, water storage tissue absent. – *Foliage fronds* (sterile and) fertile, maturing in an undetermined number, fertile and sterile parts developing simultaneously, erect, asymmetrical, ± kidney-shaped, 25–50 cm (or more) long, 5–8 times dichotomously forked, pergamentaceous, forming 2 unequal parts, 1 sterile, 4–6 times forked and 1 fertile, 4–7 times forked, with a central soral lobe, shell-shaped, elliptical to obovate, horizontally exposed, 5–17 by 3–15 cm, stalk 2–10 cm long. – *Sporangia* 270–330 by 130–150 μm, index 1.9–2.4, annulus cells: (20)21, indurated cells: (10)11, epistomium cells: 4, hypostomium cells:

(3)4, stomium situated apically, stalk 1(–3)-seriate, 1.5–2.0 μm long, spores: 8, 90–105 by 65–75 by 65–75 μm, perispore distinct, flaky; dehiscence of paraphyses and sporangia present. – *Indument*: stellate hairs long-stalked, with (6)7–9(–11) rays, which are undifferentiated, 350–940 by 20–30 μm, apex filiform; paraphyses with 11-15 rays, terminally and subterminally inserted, short-clavate, 100–150 by 55–95 μm.

Distribution. (Thailand), Sumatra, Malay Peninsula, Singapore, Lingga Arch., Borneo (N.E.).

Habitat. Epiphytic in very humid forest types (*e.g.* swamps), growing on high branches (more than 25 m above the ground) exposed to the sun. Altitude: 0–200 m.

Notes. 1. The morphology of the scale is essentially similar to that of *P. coronarium* except for the texture (very thin and brittle in *P. ridleyi*) and the shape of the midrib which is undivided and less conspicuous in the present species (*Franken & Roos 340*; L, U). Non-glandular one-celled trichomes (not reported by Joe Hoshizaki, 1970) occur occasionally scattered between the glandular ones.

2. See notes 1, 2, to *P. coronarium* and note 1 to *P. madagascarience.*

3. The sterile parts of the foliage fronds of the present species are far more branched than the homologous basal part of the foliage fronds of *P. coronarium.*

4. The present species grows solitary and not in clusters (colonies) like does *P. coronarium*. Usually large numbers of plants (10 or more) are present on one hosttree. It grows (always?) in association with a *Lecanopteris* species (*e.g. L. crustacea* Copel., see Franken & Roos, 1982).

5. Vernacular name: Tiapakoe (Dadazan B. Tuhan).

12. **Platycerium stemaria** (Beauv.) Desv. – **Fig. 27a–27d, 28.**

P. stemaria (Beauv.) Desv., Mém. Soc. Linn. Paris (1827) 213; C. Presl, Epim. bot. (1851) 154; Kuhn, Fil. Afric. (1868) 58; E.J. Lowe, Ferns 7 (1868) 62, 155, *c. fig.*; J. Smith, Hist. Fil. (1875) 124, Pl. 5; Baker, J. Linn. Soc. 15 (1876) 421; Kuhn, Deckens' Reisen Ost-Afrik. 3,3 (1879) 53; J. Smith, Ferns Br. & For. (1896) 121 c. Fig.; Christ, Farnkr. Erde (1897) 126, Fig. 354; Diels in E. & P., Nat. Pfl. Fam. 1,4 (1902) 339; De Wild., Miss. E. Laurent 1 (1905) 11 & 2 (1905) Pl. 2; C. Chr., Ind. Fil. (1906) 496, *p.p.*; Straszewski, Flora, Jena 108 (1915) 307, Fig. 3–7, 12–15, 18–22, 32, 42; C. Chr., Dansk Bot. Ark. (1932) 172, *p.p.*, Tardieu, Mém. Inst. fr. Afr. noire 28 (1953) 210, Pl. 41: Fig. 1; Alston in Hutchinkon & Dalziel, Fl. W. Trop. Afr., Suppl., Ferns (1959) 46; Joe, Baileya 12 (1964) 99, Fig. 45; Tardieu in Aubrév., Fl. Cameroun 3 (1964) 335, Pl. 53: Fig. 1; Fl. Gabon 8 (1964) 198, Pl. 31: Fig. 1; De Jonch., Blumea 15, 2 (1967) 445, Fig. 1; Schelpe, Contr. Bolus Herb. 1 (1969) 89; Joe Hoshizaki, Am. Fern J. 60 (1970) Pl. 19: Fig. 9, 16; Biotropica 4 (1972) 95, Pl. 2: Fig. 3, Pl. 3: Fig. 3, Pl. 5: Fig. 3, 7, Pl. 7: Fig. 3, Pl. 8: Fig. 3; Schelpe, Consp. Fl. Angol (1977) 114. – *Acrostichum stemaria* Beauv., Fl. d'Oware Benin 1 (1803) 2, Pl. 2; Turpin, Dict. Sc. Nat. (1816–'29) 244. – *Neuroplatyceros aethiopicus* Fée, Mém. Fougères 2 (Acrost.) (1845) 103, Pl. 64. – *P. aethiopicum* (Fée) Hooker, Gard. Ferns (1862) Pl. 9; Spec. Fil. 5 (1864) 283; Baker in Hooker & Baker, Syn. Fil. (1868) 425; Baker, Ann. Bot. 5 (1891) 496, p.p.; Poisson, Revue hort. 10 (1910) 458. – *Alcicornium stemaria* (Beauv.) Underwood, Bull. Torrey bot. Club 32 (1905) 595. – *P. stemaria* (Beauv.) Desv. var. *stemaria*, Joe, Baileya 12 (1964) 99, fig. 45: a–c, e–g. – Type: *Palisot de Beauvois s.n.*, Nigeria (Oware) (P-JUS, cat. 1008).

P. stemaria (Beauv.) Desv. var. *laurentii* de Wild., Miss E. Laurent 1 (1905) 12, fig. 2 & 2 (1905) pl. 3; Joe, Baileya 12 (1964) 101, fig. 45: d. – Type: *Em. & M. Laurent s.n., 29-1-1904*, Zaïre, Eala (BR; K, phot.).

Acrostichum alcicorne auct. non Swartz (1801) *p.p.*: Swartz, Syn. Fil. (1806) 12, 196; Wild., Spec. Pl. 5 (1810) 111; Sprengel, Syst. Veg. (1827) 35.

P. alcicorne p.p. auct., non Desv.: J. Rothschild *et al.*, Fougères 1 (1867) 186.

Usually epiphytic, rarely epilithic, growing in clusters. – *Scales* basally-attached, index 7–15, widest somewhat above the base, 5–14 by 0.5–1.7 mm, base truncate, margin straight to slightly convex, not flabelloid, apex acuminate (to filiform), papery, light-brown, midrib undivided, linear or narrow-triangular, in cross-section rounded; indument: hairs sparsely set, situated marginally and abaxially, usually unbranched, sometimes branched, 2–4-celled, 40–200 μm long, without protuberances; apical cell of unbranched hairs usually glandular, 30–50 μm long, sometimes in 2-celled hairs, non-glandular, 60-170 μm long, apical cells of a branched hair always glandular and non-glandular; 1-celled trichomes occasionally present, non-glandular. – *Base fronds* sessile, withering, old fronds erect, 30–60 by 15–30 cm; upper part erect, wedge-shaped, apex truncate, margin entire (‘*stemaria*’) or irregular dentate

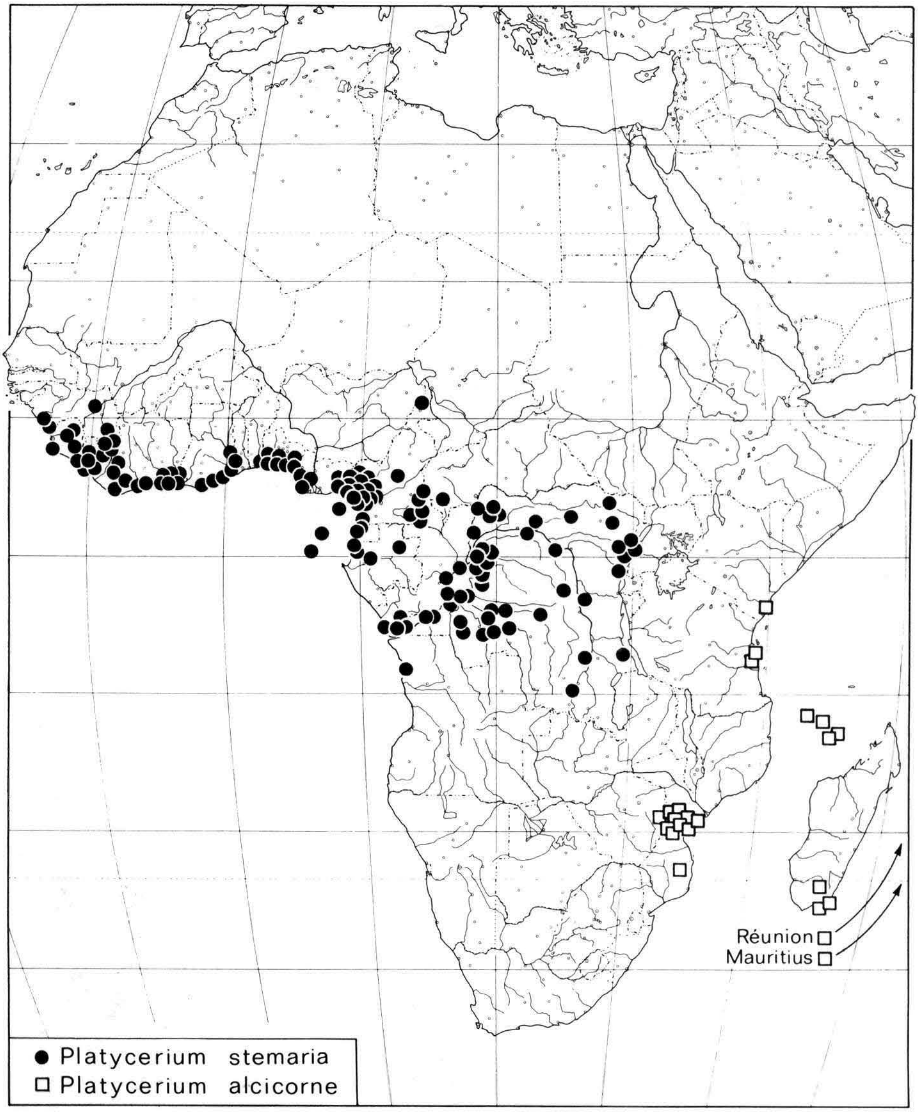

Fig. 28. Distribution of *Platycerium alcicorne* and *P. stemaria*.

(*'laurentii'*), lower part with entire margin, fringe conspicuous, situated above the stipe only; veins immersed, water storage tissue present, cells spherical. – *Foliage fronds* (sterile and) fertile, maturing (in pairs or) in an undetermined number, fertile and sterile parts of fertile frond develop simultaneously, spreading (*'laurentii'* ± pendulous), ± symmetrical, wedge-shaped, 30–90 cm long, 1, 2 times dichotomously forked, pergamentaceous, soral patches 2, situated around the ultimate sinusses (var. stemaria) or apically (*'laurentii'*), horizontally exposed, (in *'laurentii'* ± facing the plant), broad-triangular to U-shaped, apex entire (*'stemaria'*) or irregularly dentate (*'laurentii'*) 7–30 by 5–22 cm. – *Sporangia* 295–315 by 230–250 μm, index 1.2–1.3, annulus cells (24–)26–28(29), indurated cells: (16)17–19(20), epistomium cells: 4, 5, hypostomium cells: 2, 3, stomium situated laterally, stalk (2)3-seriate, 0.1–0.3 μm long, spores: 64, 70–80 by 45–50 by 45–50 μm, perispore indistinct, dehiscence of paraphyses and sporangia absent. – *Indument:* stellate hairs with (7)8–13(–16) rays, which are undifferentiated, 215–325 by 30–50 μm, apex filiform; paraphyses shortly stalked, with 9–15 rays, terminally inserted, undifferentiated, involute to canaliculate, 160–245 by 35–50 μm.

Distribution. Senegal, Guinea, Sierra Leone, Liberia, Ivory Coast, Ghana, Togo, Dahomey, Nigeria, Saô Tomé, Principe, Fernando Poo, Cameroun, Central African Empire, Spanish Guinea, Gabon, Congo (Brazz.), Cabinda, Zaire, Angola, Uganda.

Habitat. High-epiphyte (up to 45 m high) in rather humid types of forests, sometimes in plantations or village gardens, growing either exposed to the sun or in more shady situations; locally common. Altitude: 0–1000 m.

Notes. 1. The whole distribution area of the present species (Fig. 28) is largely within that of *P. elephantotis*. It is also present on the islands off the west coast of the continent where *P. elephantotis* is absent; it is absent from the eastern part of mainland Africa where *P. elephantotis* is present. *P. stemaria* requires a wetter habitat than does *P. elephantotis* (Boyer, 1964). The two species may grow intermingled, and may be difficult to distinguish unless mature.

2. De Wildeman (op.cit., 1905) described a var. *laurentii* which may need taxonomic recognition. The differences between this and typical *P. stemaria* concern size (var. *laurentii* being much more larger), and the apices of the fronds, ± entire in var. *stemaria*, irregularly dentate or laciniate in var. *laurentii*. These differences are not caused by polyploidy (*pers. comm.* Mr. P.H. Hovenkamp, who estimated the chromosome number of a specimen cultivated in the Botanic Garden, Leiden).

3. The soral patch is conspicuous because of the dark red-brown colour and the somewhat heminitidoid arrangement of the sori.

4. The present species is reported from quite a number of different host trees. It is commonly reported from plantations of *Elaeis guinensis* Jacq. (Oil palm) and *Cocos nucifera* L. (Coconut).

5. Vernacular name: M'balagimbe (Kugombe, Zaïre), Ententembe (Bokuma, Zaire).

6. Uses. The species is locally used in childbirth (*Scott-Eliott 4103*, K).

13. **Platycerium superbum** De Jonch. & Hennipm. – **Fig. 19, 29.**

P. superbum De Jonch. & Hennipm., Brit. Fern Gaz. 10, 3 (1970) 114, Fig. 4; Joe Hoshizaki, Biotropica 4 (1972) 95, Pl. 1: Fig. 4, Pl. 2: Fig. 16, 22, 23, Pl. 4: Fig. 17, Pl. 6: Fig. 20, Pl. 7: Fig. 15, Pl. 8: Fig. 16; Jones & Clemesha, Austr. ferns (1976) 236, Fig. 216; id. 2e ed. (1980) 182, Fig. 245. – Type: *Cunningham s.n.*, Australia, Queensl., Moreton Bay (K).

P. grande (Fée) Kunze var. *tambourinense* Domin, Biblthca bot. 85,1 (1915) 200; Joe, Baileya 12 (1964) 91. – Type: *Domin s.n., 1910*, Tambourine Mts, Australia (n.v.).

P. biforme auct., non Blume: Hooker, Gen. Fil. (1842) 7 Pl. 80B; Curtis's Bot. Mag. 2 (1846) 2; Ettingsh., Farnkr. Jetztw. (1865) 26, Pl. 19: Fig. 1–5.

P. grande auct., non (Fée) Kunze, *quoad specim. Austral. solem*: Ridley, J. Malay. Brch R. Asiat. Soc. 4,1 (1926) 109; Backer & Posthumus, Varenfl. Java (1939) 218; Tardieu & C. Chr. in Lecomte, Fl. Gén. Indo-Chine 7,2 (1941) 446; Copel., Fern Fl. Philipp. 3 (1960) 458; Tindale, Contr. N.S.W. natn. Herb. Flora Ser. 208–211 (1961) 28; Joe, Baileya 12 (1964) 91, Fig. 40.

Epiphytic, rarely epilithic, growing solitary. – *Scales* basally-attached, index 3–8(–14), widest usually somewhat below the middle, rarely widest at the base, 12–21 by 1.5–5 mm, base truncate, margin straight to convex, not flabelloid, apex acute, thin-coriaceous, brownish, sometimes with a much darker central part, midrib absent; indument: hairs very densely set, situated in a narrow marginal zone, branched or unbranched, 1–5(–8)-celled, 25–700 μm long, the greater part with protuberances; apical cell usually non-glandular, 50–300 μm long, situated on 2–5(–8)-celled hairs, 25–700 μm long, sometimes apical cell glandular, 30–60 μm long, situated on 2-celled, unbranched hairs and on branches of 3–5-celled, branched hairs; 1-celled trichomes occasionally present, non-glandular. – *Base fronds* sessile, green, old fronds recurving, 90–160 by 75–150 cm; upper part spreading, wedge-shaped, the apex truncate, 3–4 times dichotomously forked, lobes equally-long, lower part with sinuate margin, fringe conspicuous, encircling the stipes, margin entire or sinuate; veins immersed, water-storage tissue present, cells spherical. – *Foliage fronds* fertile (rarely sterile), maturing in pairs (sometimes single), fertile and sterile parts of fertile frond develop in succession, spreading, lateral appendages pendulous, fronds bilateral symmetrical, wedge-shaped, 75–160 cm long, pergamentaceous, soral patch 1, ± semi-circular, horizontally exposed, situated in the sinus, 10–42 by 9–68 cm, flanked on both sides by 3–5 times forked lateral appendages. – *Sporangia* 370–440 by 240–300 μm, index 1.4–1.6, annulus cells: (26–)30–32(–34), indurated cells: (16–)18–22, epistomium cells: 4, 5(–7), hypostomium cells: 3–5, stomium situated laterally, stalk (2)3-seriate, 0.1–0.5 mm long, spores: 64, 90–110 by 55–65 by 55–65 μm, perispore indistinct, dehiscence of paraphyses and sporangia absent. – *Indument:* stellate hairs with (6–)8–12(–16) rays, which are undifferentiated 115–345 by 15–20 μm, apex filiform; paraphyses shortly stalked, with 11–21 rays, terminally inserted, undifferentiated, involute to canaliculate, 85–150 by 20–30 μm.

Distribution. E. Australia (tropical and subtropical).

Habitat. Forests. Altitude: 0–900 m.

Notes. 1. This species differs from the other giant staghorn ferns by having symmetrical foliage fronds with only one soral patch. However, in cultivation juvenile plants may show variation as to the shape of the foliage fronds distinctly asymmetrical fronds occur as well as fronds with a medial incision. Also, in cultivated plants the foliage fronds often mature solitary. In case the foliage fronds with only one soral patch of the present species is the result of fusion of a frond type with two main lobes,

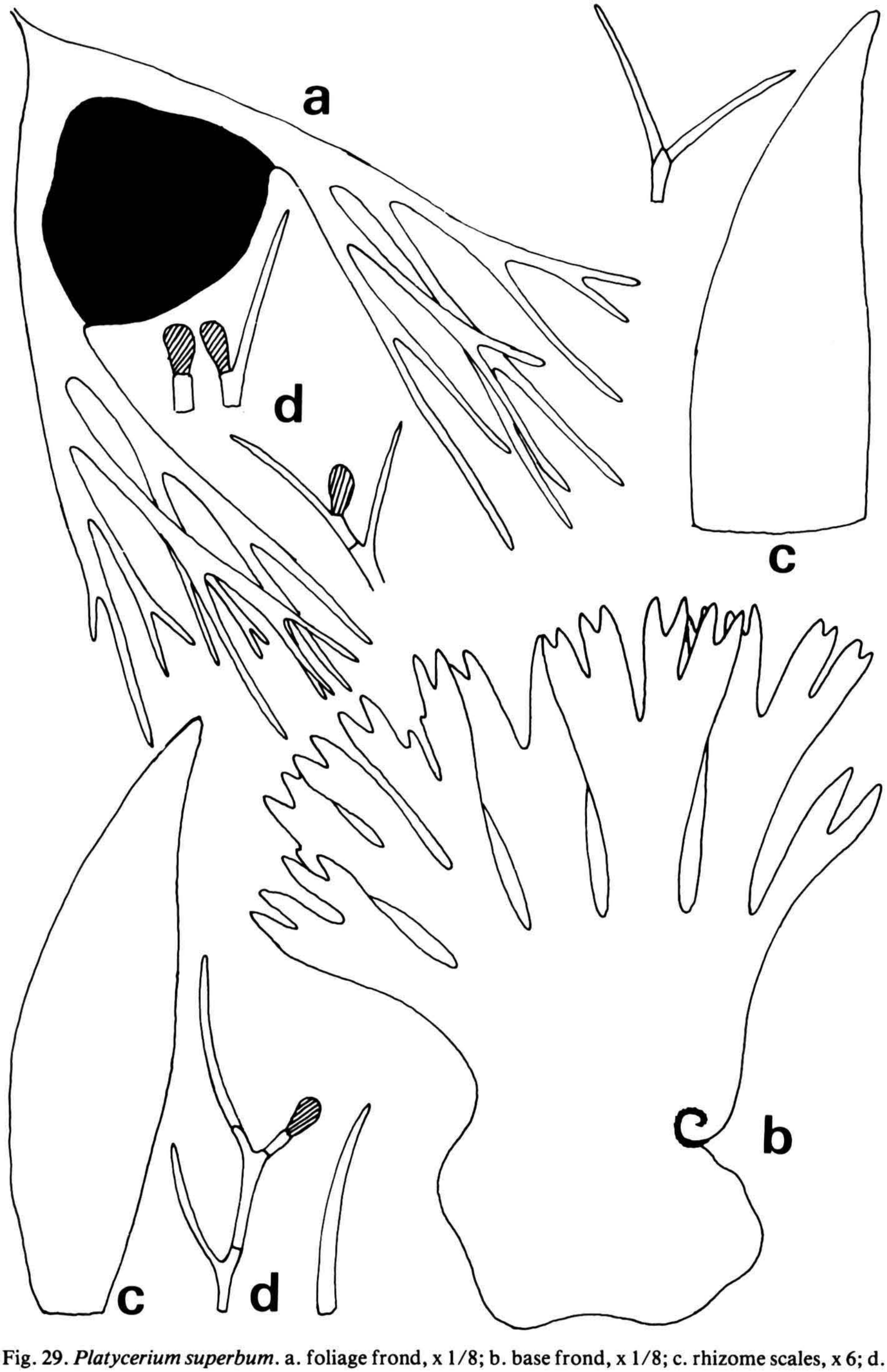

Fig. 29. *Platycerium superbum*. a. foliage frond, x 1/8; b. base frond, x 1/8; c. rhizome scales, x 6; d. indument of scales, x c.200.

it may have become variable as to its shape and to the formation in pairs. Or, better to say, it has not reached a stable condition.

2. See note to *P. grande.*

3. The segments of the lateral appendages of the present species are more narrow and more acute than those of *P. grande* and *P. wandae.*

4. According to Mr. Bruce Gray and Mr. David Jones the present species is commonly found in (somewhat dry) rain forests, especially near its margins along streambanks. It occurs generally epiphytic though sometimes on large boulders (where there is a break in the rain forest), or exposed on rocks in gorges. It grows at sealevel in its southern habitats being submontane in northern Australia. It is the dominant epiphyte in the rainforest near Atherton as was experienced during the first field trip of the International Association of Pteridologists, 1981.

14. **Platycerium wallichii** Hooker. – **Fig. 27e–27g, 30; Plate 1, 8b.**

P. wallichii Hooker, Gardnrs' Chron. (1858) 764; Fil Ex. (1859) Pl. 97; Spec. Fil. 5 (1864) 284; Bedd., Ferns Brit. Ind. (1866) Pl. 108; Baker in Hooker & Baker, Syn, Fil. (1868) 425; Bedd., Handb. Ferns Br. Ind., ed. 2 (1892) 334, Fig. 272; Christ. Farnkr. Erde (1897) 127; Diels in E. & P., Nat. Pfl. Fam. 1,4 (1902) 339; C. Chr., Ind. Fil. (1906) 497; v.A.v.R., Mal. Ferns (1908) 708; Wigman jr., Teysmannia 21 (1910) 164; Poisson, Revue hort. 10 (1910) 459; Straszewski, Flora, Jena 108 (1915) 305, Fig. 24, 30, 34; Holttum, Fl. Malaya 2 (Ferns) (1954) 141; Joe, Baileya 12 (1964) 105, Fig. 48: a–c; Joe Hoshizaki, Am. Fern J. 60 (1970) Pl. 19: Fig. 25; Biotropica 4 (1972) 95, Pl. 2: Fig. 12, Pl. 4: Fig. 20, Pl. 6: Fig. 16, Pl. 7: Fig. 12, Pl. 8: Fig. 12. – *Alcicornium wallichii* (Hooker) Underwood, Bull. Torrey bot. Club 32 (1905) 596. – Lectotype: *Wallich 19*, 'Irawaddy R. (1826) & Martaban str. (1827)' (K, herb. Hooker); Paratype: *Wallich 19* (BM).

Epiphytic, rarely epilithic, growing with several specimens in one hosttree, but not in clusters. – *Scales* basally-attached, index 11–23(–30), widest somewhat above the base (3–)5–12 by 0,2–0,7 mm, base truncate, margin straight to slightly convex, not flabelloid, apex filiform, papery, light-brown, midrib undivided, linear or narrow-triangular, in cross-section rounded; indument: hairs and 1-celled trichomes absent. – *Base fronds* sessile, withering, old fronds erect or recurving, 20–65 by 20–50 cm; upper part erect, wedge-shaped, apex ± truncate, 3–5-times irregularly forked, lobes ± equally-long, lower part with entire margin, fringe conspicuous, above the stipe only; veins immersed, water storage tissue present, cells spherical. – *Foliage fronds* (sterile and) fertile, maturing in pairs in a symmetrical pattern, fertile and sterile parts of fertile fronds develop simultaneously, pendulous, asymmetrical, wedge-shaped, 25–75 cm long, leathery, with 3 unequal main lobes, the medial one the largest, fertile, soral patch ± semi-circular, situated in the ultimate sinus, horizontally exposed, 5–20 by 3–15 cm, flanked on both sides by 2–3 times forked appendages, the central one medium-sized, fertile, soral patch ± semi-circular, situated in the ultimate sinus, horizontally exposed, 4–16 by 2–11 cm, flanked on both sides by unforked or 1 time forked appendages, lateral one the smallest, sterile, unforked to up to 2 times forked. – *Sporangia* 305–355 by 265–295 μm, index 1.1–1.3, annulus cells: 27–32, indurated cells: (15–)17, 18(19), epistomium cells: 5–9, hypostomium cells: 2, 3, stomium situated laterally, stalk (2)3-seriate, 0.1–0.3 mm long, spores: 64, 85–95 by 40–50 by 40–50 μm, perispore indistinct, dehiscence of paraphyses and sporangia absent. – *Indument*: stellate hairs with (6)7–9(10) rays, which are undifferentiated 335–530 by 25–35 μm, apex filiform; paraphyses shortly stalked, with 7–10(11) rays, terminally inserted, undifferentiated, involute to canaliculate, 325–595 by 25–40 μm.

Distribution. E. India, Birma, Thailand, China (reported by Prof. R.C. Ching and Prof. Z.H. Wang from Yunnan on the border of Upper Burma; Poster, I.B.C./Sydney, 1981).

Habitat. Locally common in evergreen and deciduous monsoon forests. Altitude: 0–750(–1500?)m.

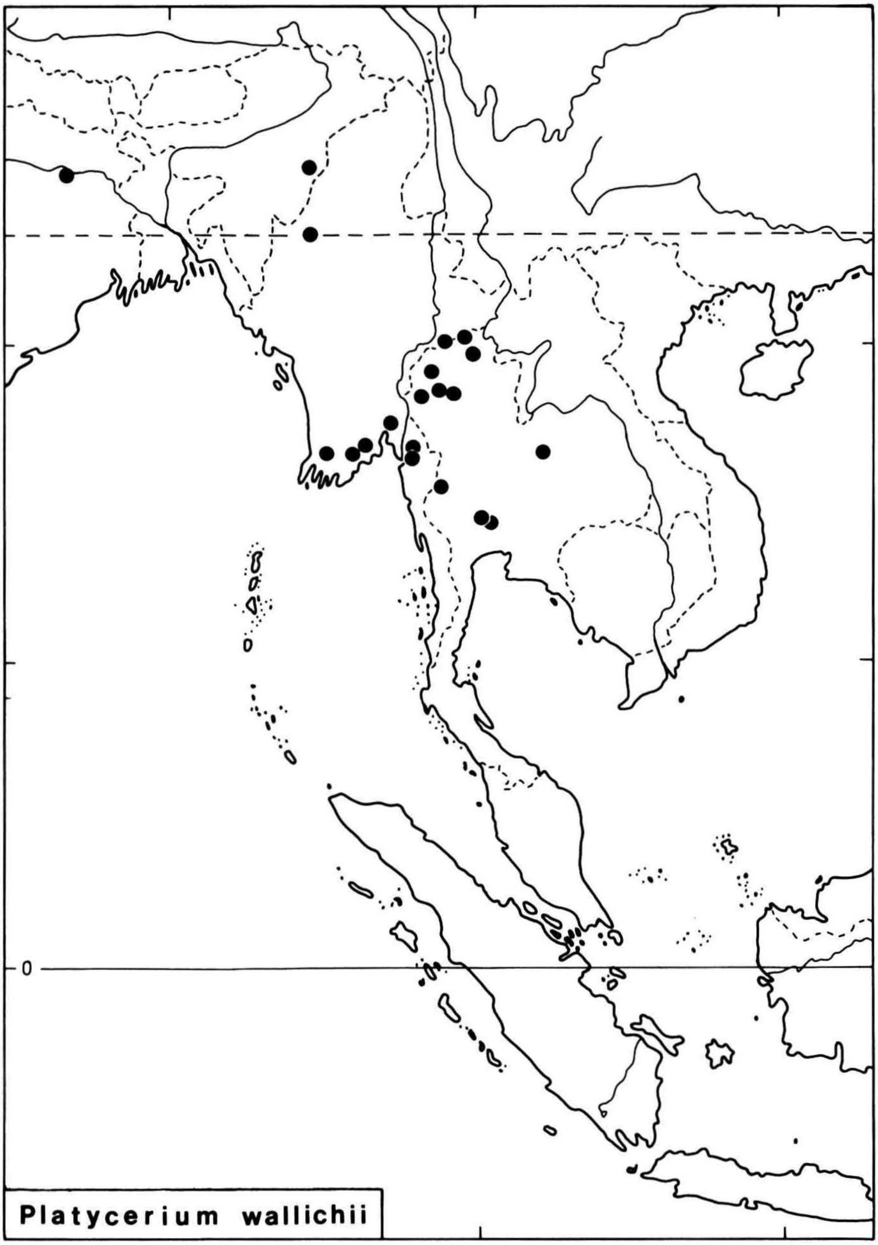

Fig. 30. Distribution of *Platycerium wallichii*.

Notes. 1. A clear cut species though sometimes confused with *P. holttumii* (also having strongly asymmetrical foliage fronds with two soral patches) with which it is in part sympatric. The two species are easily distinguished because of differences in scales (shape, indument, midrib), withering and shape of base fronds (absent in *P. holttumii*), and structure and development of the foliage fronds.

2. The architecture of the foliage frond is unique, showing a sterile lobe, and the largest soral patch being situated on the medial, and also otherwise most developed from lobe (Plate 8a). This situation is quite different from that found in *P. wandae* (in which the largest soral patch is situated on the lateral main lobe which shows the least developed sterile structures), or in *P. grande* (with two equally-sized soral patches and sterile structures).

3. See note to *P. elephantotis*.

4. Vernacular name: Zawgyi mo saik (Webula, Birma), Zaw-ji-moak-seik (Thandaung, Birma), Mêng bkân (Thailand, lang. Rarien).

15. **Platycerium wandae** Racib. – **Fig. 25, 31.**

P. wandae Racib., Bull. int. Acad. Sci. Lett. Cracovie (1902) 58; C. Chr., Ind. Fil. (1906) 497; v.A.v.R., Mal. Ferns (1908) 709; Wigman jr., Teysmannia 21 (1910) 164; Poisson, Revue hort. 10 (1910) 460; Straszewski, Flora, Jena 108 (1915) 306; Joe, Baileya 12 (1964) 107; De Jonch., Blumea 16,1 (1968) 109, Fig. 1, 2; Joe Hoshizaki, Am. Fern J. 60 (1970) Pl. 18: Fig. 7, Pl. 19: Fig. 27; Biotropica 4 (1972) 95, Pl. 2: Fig. 14, Pl. 4: Fig. 16, Pl. 6: Fig., 17, Pl. 7: Fig. 14, Pl. 8: Fig. 14. – Type: a specimen cultivated in the Botanic Gardens, Bogor; origin: *Meywes s.n., 1899,* N.W. New Guinea ('Von Doreh an der nordwestlichen Küste des holländischen Neu Guinea...') (*n.v.*).

P. wilhelminae-reginae v.A.v.R., Bull. Dépt. agric. Ind. néerl. 18 (1908) 24, Pl. 6, 7; Wigman jr., Teysmannia 21 (1910) 164 c. Fig.; Poisson, Revue hort. 10 (1910) 529; C. Chr., Ind. Fil., Suppl. 1 (1913) 55; v.A.v.R., Mal. Ferns, Suppl. (1917) 421; Joe, Baileya 12 (1964) 109, Fig. 49. – *Alcicornium wilhelminae-reginae* v.A.v.R., Bull. Dépt. agric. Ind. néerl. 18 (1908) 24, *nomen illeg.* – Type: *v.A.v.R. s.n., 1908,* a specimen cultivated the Botanic Gardens, Bogor, cult. no. II K (V, 2), (BO, holo; L).

Epiphytic, growing solitary. – *Scales* basally-attached, index 7–12, widest about the middle, 14–26 by 1.5–3 mm, base truncate, margin slightly convex, not flabelloid, apex acute to acuminate, thin-coriaceous, (light) red-brown, midrib undivided, linear or narrow-triangular, often interrupted, in cross-section rounded; indument: hairs very densely set, situated in a narrow marginal zone, branched or unbranched, 2, 3(–5)-celled, 25–400 μm long, with or without protuberances; apical cell usually non-glandular, (25–)100–350 μ long, occasionally glandular, 40–60 μm long; 1-celled trichomes commonly present, non-glandular. – *Base fronds* sessile, green, old fronds recurving, 100–125 by 100–135 cm; upper part spreading, wedge-shaped, apex truncate, 4–6 times dichotomously forked, lobes equally-long, lower part with sinuate margin, near point of attachment with aphlebia-like structures, fringe conspicuous, encircling the stipes, the margin with aphlebia-like structures; veins immersed, water storage tissue present, cells spherical. – *Foliage fronds* fertile (rarely sterile), maturing in pairs in a symmetrical pattern, fertile and sterile parts of fertile frond develop in succession, spreading, lateral appendages pendulous, asymmetrical, wedge-shaped, 50–135 cm long, pergamentaceous, with 2 unequal, wedge-shaped main lobes, each bearing one semi-circular to transverse-angustate elliptical, horizontally exposed soral patch, situated in the ultimate sinus, 7–33 by 20–60 cm, flanked on both

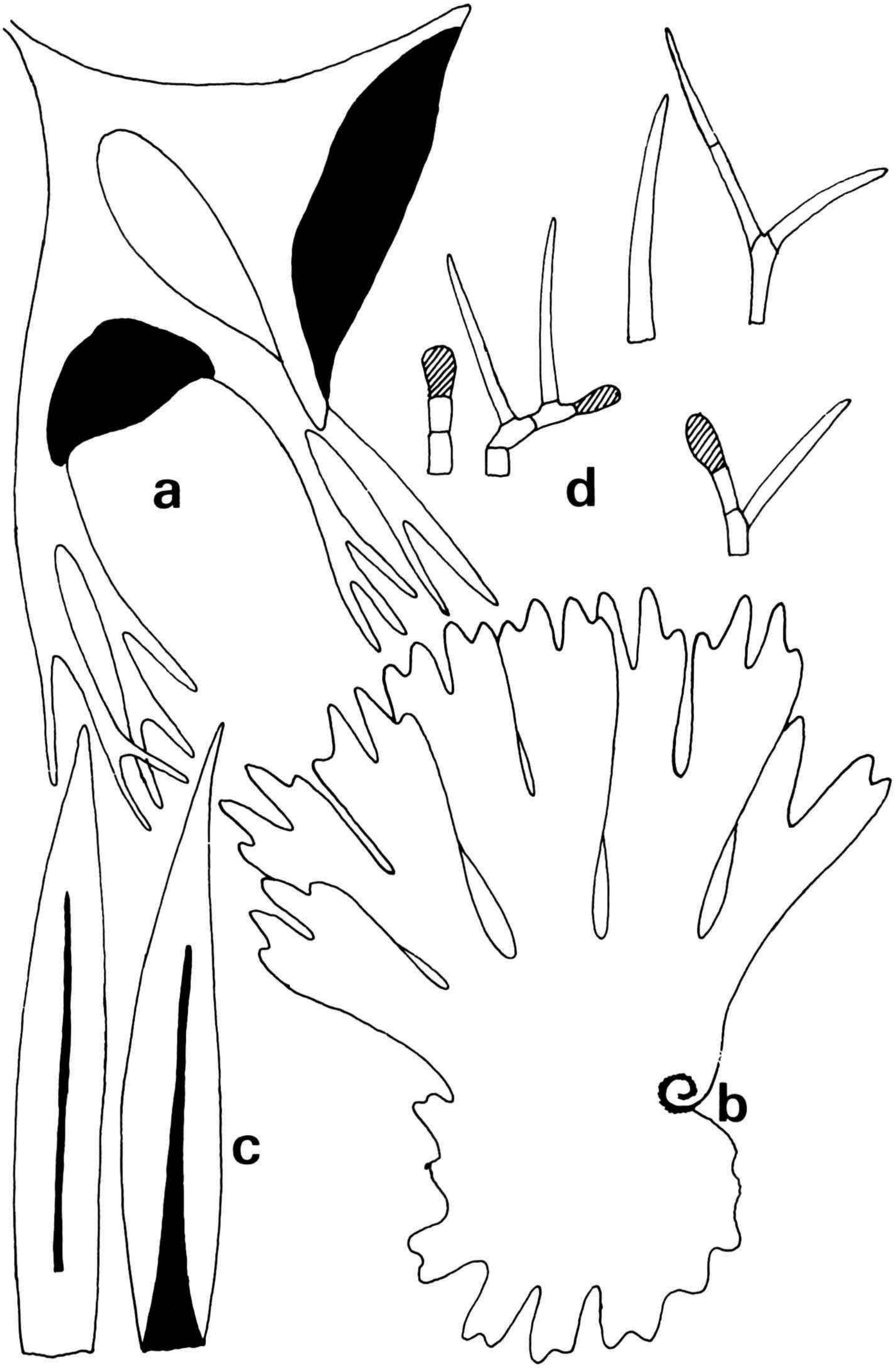

Fig. 31. *Platycerium wandae*. a. foliage frond, x 1/8; b. base frond, x 1/8; c. rhizome scales, x 6; d. indument of scales, x c.200.

sides by 3–4 times forked (medial lobe) or not forked (lateral lobe) lateral appendages. – *Sporangia* 300–350 by 210–250 μm, index 1.3–1.6, annulus cells: 26–28(–30), indurated cells: 16–18(–21), epistomium cells: 4, 5(6), hypostomium cells (2)3(4), stomium situated laterally, stalk (2)3-seriate, 0.1–0.5 mm long, spores: 64, 65–70 by 35–40 by 35–40 μm, perispore indistinct, dehiscence of paraphyses and sporangia absent. – *Indument*: stellate hairs with (7)8–12(13) rays, which are undifferentiated, 250–435 by 25–35 μm, apex filiform; paraphyses shortly stalked, with (9)10–12(–14) rays, terminally inserted, undifferentiated, involute to canaliculate, 80–170 by 25–40 μm.

Distribution. New Guinea.

Habitat. Epiphytic in the middle layer of rain forests, 10–25 m above the ground. Altitude: 0–1000 m.

Notes. 1. The present species is easily distinguished from the other three species of the *P. grande*-group showing foliage fronds with two main lobes, the lateral one of which without lateral appendages. The scales of this species are conspicuously different from those of its closests relatives because of the high shape-index, the presence of a midrib, and the proportionally few-celled hairs with or without protuberances. The scales show similarities with those found in *P. andinum, P. elephantotis*, and *P. stemaria*. See also note to *P. superbum*.

2. The present species grows in dry lower montane rainforest and lowland swamp forest as a high canopy species. It also occurs in the lowland zone on *Hevea brasiliensis* (Rubber), and *Cocos nucifera* (Coconut), and on planted *Pithecellobium samar* (Rain tree). Locally abundant (*pers. comm.* Mr. R.J. Johns and Dr. B.S. Parris).

3. *Platycerium wandae* has been spotted once in the Vogelkop Peninsula, West Guinea by Dr. W. Vink (Leiden).

4. Vernacular name: Áppáng (Papua).

5. The collecting of *Platycerium* species

The number of specimens accumulated in the herbaria is comparatively small. Besides, a proportionally large number of these comprise incomplete or scrappy material. This holds for the large-sized species in particular. This situation seems due to the fact that *Platycerium* grows mostly (high-)epiphytic, far beyond human reach, and also to the experience that they are not easy to preserve because of their spatial structure, including a so-called basket of base fronds. Further, plant collectors when preserving base fronds are not seldomly terribly bitten by numerous ants and other animals inhabiting the basket.

For those who start collecting *Platycerium* we like to provide the constituents of an ideal collection.

1. Preserve complete, mature (*i.e.* with mature sporangia and spores), foliage fronds. In case the fronds are large-sized one should make a description (or photograph) of the complete frond architecture before the specimen is cut into parts.
2. Preserve a complete base frond. The easiest way to do this is by bringing one hand holding a sharp knife between the outer and – first – inner base frond, loosening the outer base frond from the roots (which are usually abundantly represented between the base fronds), as well as from the rhizome. Flattening of the large-sized fronds may need extra weight. The fringe of the large-sized species is often better preserved when it is separated from the frond.
3. Preserve young, mature, foliage, and base fronds to show the maturation of parts.
4. Preserve the rhizome-apex, including young and mature rhizome-scales, preferably connected with a foliage frond.
5. Preserve complete juvenile specimens showing the (different) juvenile fronds as well as the organization of the base fronds.
6. Preserve a (sterile) voucher specimen of the host tree.
7. Annotations. Photographs or drawings should be made of the plant in their habitat, as well as of the complete base frond and foliage frond. The following items should be recorded:

a. Locality.
b. Habitat and frequency of the (juvenile and mature) plants, including their height above the ground, height of the host tree, forest type, etc.

c. Branching of the rhizome if present. This can be inferred when plants of various ages grow together in clumps (colonies).
d. Number of mature foliage fronds present on the plant.
e. Position of the respective parts of the mature and old base fronds.
f. Position of the sterile parts and the soral patch(es) of the foliage fronds.

6. Material recommended for further collecting

Herbarium material of all the species is in one way or another insufficiently represented in the herbaria. Therefore, all the species are enumerated below and the herbarium material required indicated. Of all the species juvenile fronds are wanted. It is appreciated if plant collectors deposit at least one or two duplicates of their collections in one of the greater herbaria of the world, or in the herbarium of the University of Utrecht to which the authors are presently connected.

It is remarked that several species, including *P. andinum* (South America), *P. grande* (Philippines) and *P. ridleyi* (Malaya, N. Borneo) have become locally very rare. Plant collectors are therefore requested not to collect the complete plant in case only one specimen is found. In such cases the collecting of only a foliage frond may suffice. When living spores of such plants are available it is appreciated to distribute these amongst botanical gardens including the botanical gardens of the Universities of Leiden and Utrecht.

1. *Platycerium alcicorne*: Collections from Madagascar.
2. *P. andinum*: Large-sized fronds; present distribution in South America insufficiently known; modern collections are scarce.
3. *P. bifurcatum*: Complete collections of ssp. *bifurcatum* from New Guinea, and of ssp. *willinckii*, and ssp. *veitchii*.
4. *P. coronarium*: Complete specimens in particular those from mainland Asia.
5. *P. elephantotis*: Complete collections with detailed ecological data; the present species is well-represented in the herbaria otherwise.
6. *P. ellisii*: Complete collections; distribution of this endemic of Madagascar is insufficiently known.
7. *P. grande*: Complete collections; distribution of this endemic from the Philippines is insufficiently known.
8. *P. holttumii*: Complete collections in particular those from Indo-China.
9. *P. madagascariense*: Complete collections.
10. *P. quadridichotomum*: Large-sized foliage fronds collected in the dry and in the rainy season.
11. *P. ridleyi* (locally already extinct): Complete foliage fronds and base fronds.
12. *P. stemaria*: Complete collections of 'var. *laurentii*' which taxonomic status and distribution is insufficiently known; living spores of collections from various parts of its distribution area.

13. *P. superbum*: Complete collections, though otherwise well-represented in herbaria.
14. *P. wallichii*: Complete collections of large-sized specimens.
15. *P. wandae*: Complete collections; distribution in New Guinea insufficiently known.

7. Index of collections

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