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A MONOGRAPH OF THE FERN GENUS GONIOPHLEBIUM (POLYPODIACEAE)

GISELA RÖDL-LINDER*

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* Correspondence address: G. Rödl-Linder, 54 Plaza v. Humboldt, La Florida, La Pas, Bolivia.

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TAXONOMIC PART

1. SUMMARY AND INTRODUCTION

The present monographic study deals with the phylogenetic systematics of the goniophlebioid Polypodiaceae, with special reference to the Asian representatives. It includes the recognition and description of species of *Goniophlebium*, a full synonymy, and a reconstruction of their phylogeny.

This study concentrates on the analysis of 34 species earlier referred to *Polypodium* Linnaeus (sensu lato) with a (partly) goniophlebioid venation pattern and also includes a selection of free veined *Polypodium* species.

Status and nomenclature of the goniophlebioids are most ambiguous and show much variation. Several earlier attempts by other authors towards a natural classification have remained unsuccessful as is elucidated in a paragraph on the taxonomic history of the group.

In order to unravel the phylogenetic relationships within this group an analysis of characters, i.e. series of inferred homologous character states, was undertaken. They concern the morphology of the mature sporophyte, with respect to the rhizome, the rhizome scales, the gross morphology, the venation pattern, the indument, the sori, the paraphyses, the sporangia and the spores. Microscopical and submicroscopical features were included. Several of these characters were studied in detail for this group for the first time.

A selection of 90 character states was used in the datamatrix, which served as a prerequisite for cladistic analyses. Following the idea of evolution as descent with modification, relationships between (groups of) species are recognized by tracing their possession of shared derived character states (synapomorphies). The cladistic method primarily selected for the present study is CAFCA. It implies the deduction of transformation series from a chosen cladogram by application of outgroup comparison. In addition two other cladistic programs were applied, viz. PAUP and HENNIG86.

Observations regarding the development of gametophytes are reported. During her three years stay in the Philippines, the present author was able to study complete life cycles of the greater part of the Philippine species concerned. Special emphasis is given to growth from germination until maturity as well as to the location of indument, antheridia and archegonia. Results are presented and compared with informations given in the literature.

As to juvenile sporophytes, special attention is paid to the venation and to the indument. The presence, the period of development, the shape, the location and the persistency of acicular and glandular hairs as well as of laminar scales are the main observations reported on. Indument of juvenile and adult sporophytes is compared and differences are stated. A comparison between laminar and rhizome scales shows a number of morphological similarities.

Known data from literature about chromosome numbers are presented in a summarized form.

Geographical and ecological particularities were investigated. Areas of endemism are listed with their respective species. Collecting localities are indicated in detailed maps. All species are set in relation with defined climatic and rainfall patterns resulting in considerable support for groupings suggested by cladistic analyses. Altitudinal ranges are presented in separate diagrams for each species. Results of transplant experiments which were undertaken in the Philippines point out that morphological characters may show a great plasticity. These experiments also added important details to the author's species delineation.

The phylogenetic relationships between the species are correlated with the distribution areas. The biogeographical analysis suggests a close relationship between New Guinea, Celebes and the Philippine Islands. The Malay Peninsula and Sumatra appear closely related to each other as well as both these areas to Mainland Asia.

As a result of the morphological, cladistic, biological and geographical interpretation the Asian genus *Goniophlebium,* comprising 23 species, is recognized. Phylogenetic relationships within the inferred monophyletic genus are discussed. Cladistic analyses resulted in the recognition of a monophyletic group of nine species. This group (*G. percussum*-group) includes the type of the genus *Schellolepis* J. Smith, *S. percussa* (Cavanilles) Pichi Sermolli. Eight other species are accommodated in the *G. subauriculatum*-group, which includes the type of the genus *Goniophlebium, G. subauriculatum* (Blume) Presl. The remaining taxa build pairs of species of which the relationship to the *G. percussum*-group and *G. subauriculatum*-group could not be further resolved. Therefore, the present author has refrained from assigning a formal taxonomic rank to the *G. percussum*-group and the *G. subauriculatum*-group, although they are here proposed for the first time. It is expected that an even better phylogenetic resolution including the six remaining species will be obtained from further studies with modern experimental approaches. It is noteworthy that species which have always been regarded as closely related, e.g. *G. percussum* and *G. subauriculatum,* are now assigned to different groups. Uppermost frond segments and spores provide important characters for the delimitation of the well defined *G. percussum*-group. According to the new generic description all pinnatifid species, excluded by Copeland (1947) and Holttum (1968), are now accommodated in the genus *Goniophlebium.* Therefore, four species are newly combined.

The other eleven species studied are retained in *Polypodium.*

A scenario for *Goniophlebium* is given. The incorporation of the biogeographical history (evolution of morphological characters in space and time) leads to the postulation of a scenario on the two major monophyletic groups within the genus *Goniophlebium.* Copeland's (1915) perception of *Polypodium,* which was taken up by De la Sota (1973) and Ching (1978), is largely confirmed and the goniophlebioids from the Neotropics, North America and Eurasia are regarded to have evolved separately from those in the Asian (sub)tropics.

In the taxonomic part an emended description of the genus is given. The typification of the genus appeared most complex and had to receive much attention. The argumentation for the lectotypification of *Goniophlebium* is published separately. The species are described in detail and identification keys to all taxa are provided. The taxonomic part further contains also the full synonymy for specific and infraspecific taxa, information on the distribution and the habitat and last but not least notes on field and other relevant observations. Indices to taxonomic names as well as of the specimens studied are included.

GENERAL PART

2. MATERIAL AND METHODS

2.1. MATERIAL

Dried specimens from Asia of approximately 1500 collection numbers, partly with many duplicates, were studied from the following herbaria (the abbreviations follow the Index Herbariorum):

B	Botanisches Museum, Berlin-Dahlem.
BM	The Natural History Museum, London.
BO	Herbarium Bogoriense, Bogor.
BONN	Herbarium der Universität Bonn.
CAHP	College of Agriculture, University of the Philippines, Los Baños.
HBG	Herbarium Hamburgense.
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.
NY	The New York Botanical Garden, N.Y.
P	Muséum National d'Histoire Naturelle, Laboratoire de Phanérogamie, Paris.
PE	Institute of Botany, Academia Sinica, Peking.
PNH	Philippine National Herbarium, National Museum, Manila.
SING	Herbarium of the Botanic Gardens, Singapore.
TI	Botanical Institute, Tokyo.
U	Botanical Museum and Herbarium, Utrecht.

The greater part of taxa from Asia was studied alive. The author was able to do extensive fieldwork in the Philippines, and to a smaller extent in Southwest China (Yunnan and Sichuan). Her collections were cultivated in her private garden in Manila and are still in the Botanical Garden in Utrecht.

Thanks to the large collections from Costa Rica made by Prof. Hennipman and members of his team in 1986 there is as well abundant living material from America available, which was used for comparative studies.

2.2. METHODS

Rhizome and stipe/costa

For anatomical studies, pieces of rhizome and stipe/costa of dried material were softened by boiling them in a solution of glycerine in water. Fresh material had not to be treated in advance of sectioning it with a sharp razor blade by hand or by microtome. The sections were embedded in glycerine jelly to obtain semi-permanent microscope slides. Staining was not considered necessary to recognize vascular bundles and sclerenchyma strands and sheaths.

At least three different collections were studied from each species, if available.

Scales

Scales on rhizome and lamina were brushed with a strong solution of a detergent in water before pulling them off, in order not to break them in parts. After rinsing them in water they were mounted on slides with glycerine jelly.

At least 30 scales of five different collections were studied.

Venation pattern

To study the venation pattern in detail, lateral segments of fronds were cleared following Hennipman (1977), boiled in a solution of 5–10% KOH in water and bleached in pure household bleach. Projection photographs were taken with a standard magnification of two times.

Observations were first made on untreated material. One fertile and one sterile pinna, representative for each species, were photographed and used for detailed studies. In case of dried material the pinnae were remounted to the herbarium sheets.

Laminar indument and stomata

Pieces of epidermis were pulled off using a fine pair of tweezers and were embedded in glycerine jelly. For respective studies on living circinnate fronds, scales were removed first as described above. Then the young, still soft frond tissue was squashed under a cover glass in glycerine jelly.

At least ten measurements of stomata and of each type of indument per specimen were taken.

Receptacular paraphyses and sporangia

Sori were brushed with a strong solution of detergent in water, scraped of the frond with a pair of tweezers and mounted in glycerine jelly.

Five or more different collections were studied and at least ten sporangia and ten of each type of paraphyses per specimen were measured.

Spores

Spores were soaked with alcohol 96% and transferred to glycerine jelly for study with a light microscope (LM).

A representative selection of each species was studied and measured.

For studies with a scanning electron microscope (Cambridge SEM) spores were fixed on a standard specimen stub with doublesided tape and coated with gold before examination.

SEM studies are based on one or two collections, which were carefully selected after LM analysis.

Life cycles

To study the different stages of the life cycle of the Philippine species, spores were sown on agar medium and on sterilized tree fern fibre blocks. Spores were sown within 14 days of collection. Cultures were maintained under natural tropical light and temperature conditions under a plastic roof. They were fertilized every two weeks with a weak solution of inorganic fertilizer. In various stages of development gametophytes and juvenile sporophytes were fixed in FAPA (formaline 40%: 5; glacial acetic acid: 2.5; propionic acid: 2.5; alcohol 50%: 90). Further studies were carried out following the techniques explained above.

Complete life cycles in adequate numbers could only be obtained of some species from the Philippines because a few highland species did not develop well under lowland conditions. Cultivation on agar medium turned out less successful under natural conditions.

3. TAXONOMIC HISTORY OF GONIOPHLEBIUM

The genus *Goniophlebium* was created by Presl (1836) to accommodate the species earlier referred to as *Polypodium* sect. *Goniophlebium* by Blume (1830). Presl included apart from the paleotropical species also neotropical species with goniophlebioid venation. At the same place Presl recognized the genus *Marginaria* Bory (1825) which species he considered to have a slightly different goniophlebioid venation. Hooker and Bauer (1840) followed Presl. The genus *Marginaria* was illustrated by these authors with *M. verrucosa* (op. cit.: pl. 14 = *Goniophlebium percussum*), the genus *Goniophlebium* by *G. neriifolium* (pl. 70 = *Polypodium neriifolium*). In their discussion of *Marginaria piloselloides* (pl. 51 = *Polypodium piloselloides*) they communicated J. Smith's ideas about the generic circumscription and subdivision of *Goniophlebium* with which Hooker and Bauer did not agree. J. Smith's ideas were formalized soon after (J. Smith, 1841), and are of great interest. J. Smith recognized a genus *Goniophlebium* which he subdivided into four groups (referred to as sections by him; J. Smith, 1857), two of which with a goniophlebioid venation, i.e. the Asian *'Schellolepis'* with articulated pinnae and squamiferous sori and the American *'Goniophlebiae verae'* with continuous pinnae and naked sori. The genus *Marginaria* was in part referred to *Polypodium,* in part to *Goniophlebium.* In a later publication (J. Smith, 1866) he raised these four groups to generic rank. In his Historia Filicum (J. Smith, 1875) *Schellolepis* and *Goniophlebium* were together with *Phlebodium* combined into tribe Polypodieae sect. Goniophlebiae, whereas the other two groups were classified as genera into sect. Pleopelteae together with several other genera.

Contrary to J. Smith, Fée (1852) included in *Goniophlebium* also Asian goniophlebioid species. Moore (1857) construed a heterogeneous genus *Goniophlebium* including species presently referred to *Selliguea, Polypodium,* and *Goniophlebium.* Hooker (1864) merged *Marginaria* and *Goniophlebium* and treated them as *Polypodium* § [subgenus?] *Goniophlebium.* Christ (1897) adhered to a large genus *Polypodium* recognizing *Goniophlebium* and *Schellolepis* (*'Schellopsis'*) as pantropical subgroups, *Goniophlebium* with simple or pinnatifid fronds and *Schellolepis* with pinnate fronds. A large genus *Polypodium* was also recognized by Diels (1904).

A most important perception regarding the subdivision of the large and diverse genus *Polypodium* was achieved by Copeland (1915: 155): "... if *Goniophlebium* is made a genus in any natural sense, not any of the American ferns can be included," and "... *Goniophlebium* in America do not themselves represent a single line of descent." The typification of the genus *Goniophlebium,* as discussed by Copeland (1929), is incorrect. The American species with a goniophlebioid venation and the free veined species from the northern temperate zones, as well as the goniophlebioid species with pinnae continuous with the rhachis (e.g. *G. lachnopum, G. microrhizoma,* etc.) Copeland retained in *Polypodium.*

Christensen (1931) had no doubt that *Polypodium manmeiense* Christ is a free veined *Goniophlebium* (op. cit.: 315): "... in general aspect very like some forms of *P. vulgare,* on the other hand it comes very near *P. microrhizoma* Clarke" (a species with mostly goniophlebioid, rarely free venation and like *Polypodium manmeiense* with hairy soral paraphyses). "These and certain Asiatic species of *Goniophlebium* afford a strong basis ... that our common *P. vulgare*" (typus generis of *Polypodium*) "is a free-veined *Goniophlebium* ..." Christensen in Verdoorn's 'Manual of Pteridology' (1938) included *Goniophlebium* in the genus *Polypodium* which he considered a natural genus of c. 50 species in tropical and subtropical America and Asia–Polynesia, represented in the northern temperate region by a few, free veined species (*Polypodium vulgare* and related forms). Together with ten more genera he united *Polypodium* in Polypodioideae tribe Polypodieae and saw (op. cit.: 548) "... through some Asiatic species with somewhat more complicated venation the genus running into *Phymatodes,*" which he accommodated in the tribe Pleopeltideae. Especially with regard to these species from Eastern Asia Ching (1933, 1940) decided to merge *Goniophlebium* into *Polypodium* thereby rejecting the use of differences in venation as a distinguishing character between these two genera.

Holttum (1947), who recognized five groups within the Polypodiaceae, included *Goniophlebium* in *Polypodium* which he placed in the *Phymatodes* group. He accepted Christensen's (1931) idea that some Asian species bridged the gap between *Polypodium* (sensu Holttum) and *Phymatodes.* In a letter (pers. comm., 1985) he stated his belief that the free veined species from the Himalayan region belonged as well to the Asian genus *Goniophlebium.* Pichi Sermolli (1973), following Furtado (1949), designated *Goniophlebium articulatum* (Desvaux) Pichi Sermolli, an American species, as lectotype of the genus *Goniophlebium.* Hence, he referred *Goniophlebium* (sensu Copeland) to *Schellolepis* J. Smith. Pichi Sermolli (1977) recognized 14 groups within the Polypodiaceae, one of them including the genera *Polypodium, Marginaria, Schellolepis, Goniophlebium, Synammia, Thylacopteris, Hyalotricha,* and *Campyloneurum.*

In a revision of the Indian species Bir, Trikha & Vasudeva (1974) treated *Polypodium* apart from *Goniophlebium* only because of the basic idea of convenience in the field, thus separating the genera artificially by only one character, i.e. pinnae, at least the lower ones, articulate to the rhachis for *Goniophlebium* and pinnae not articulate for *Polypodium.*

In 1978 Ching split up *Polypodium* by creating three new genera: *Polypodiodes* [type: *P. amoenum* (Mettenius) Ching], which is accepted by Saiki (1987), *Polypodiastrum* [type: *P. argutum* (Hooker) Ching] and *Metapolypodium* [type: *M. manmeiense* (Christ) Ching]. According to Ching (1978) the latter was closest related to *Polypodium* Linnaeus (sensu stricto) and to *Thylacopteris* Kunze. Ching failed to provide distinguishing characters between his genera and *Polypodium* proper.

Contrary to Pichi Sermolli (1973, 1977), Tryon & Tryon (1982) considered *Goniophlebium* an Old World genus with articulate pinnae and not closely related to American elements.

As can be seen from the taxonomic history status and nomenclature of *Goniophlebium* are most ambiguous and show much variation.

4. MORPHOLOGY AND ANATOMY OF MATURE SPOROPHYTES

4.1. INTRODUCTION

After the recognition of terminal taxa analyses of the morphological and anatomical characters were executed. Character states (= different conditions of a character observed) were defined before the species were described. 117 characters were recognized; 341 character states were attributed to them. For practical reasons a selection of these character states has been used for the cladistic analyses (see chapter 9.2), following certain principles.

- Qualitative characters are more valuable than quantitative characters;
- constant characters within one species dominate over variable characters;
- character states present or absent in only one species (= autapomorphies) are meaningless;
- character types of venation and spores are recognized.

The character states are listed in table 1. Fourty characters are defined by 90 character states (numbered). The numbers given to character states in this table refer to the datamatrix used for cladistic analysis. Unnumbered character states refer to quantitative, variable or autapomorphous character states, which were left aside for the cladistic analyses.

Table 1.

characters	*character states*
rhizome	
transverse section	1) terete 2) dorsiventrally flattened
diameter size (mm)	< 2 2-4 4-6 6-8 8-10 > 10
colour	3) chalky/glaucous 4) brown (green in vivo)
distance of phyllopodia (cm)	< 1 1-3 1-5 > 5
arrangement of meristeles	5) regular circle 6) irregular circle
vascular strands	< 10 10-20 > 20
dark bundle sheaths	7) absent 8) present
sclerenchyma strands	9) absent 10) < 15 11) > 15 { 15-30 30-100 > 100
rhizome scales	
insertion	12) even and/or protruded 13) invaginated
colour	badious brunneous spadiceous ferrugineous orange

(Table 1 continued)

characters	*character states*
exposition	14) spreading 15) appressed
density	16) high or medium 17) low
persistency	high low
dimorphism	18) present 19) absent
general shape	20) deltoid 21) ovoid or irregular
apex shape	filiform acuminate round
basal flaps shape	22) round 23) pointed
basal flaps size	big short long medium/variating
attachment	24) perfoliate and/or 25) peltate [basifix
length (mm)	0.3–1.0 1.1–3.0 3.1–5.0 5.1–8.0
width (mm)	0.3–1.3 1.4–3.2 3.5–5.1
index	1–2 2–3 3–4 4–6
clathration of cell walls (CCW) centrally	very thick thick 26) present (dark) medium thin 27) absent (light)
marginally	very thick thick 28) present (dark) medium thin 29) absent (light)
CCW basally	very thick thick 30) present (dark) medium thin 31) absent (light)
colour of cell lumen	32) hyaline/colourless 33) yellowish to brown
clathrate marginal protrusions (CMP)	34) absent 35) present
CMP length apically	medium short long
CMP length basally	medium short long absent
glandular marginal hairs (GMH)	1 cell 36) present -2 cells -4 cells 37) absent
GMH frequency	high medium low
GMH position	terminal apical central basal absent
surface hairs	rhizoid 38) present glandular 39) absent
venation	
areolae first order A1	present absent
A1 shape	pentagonal hexagonal heptagonal
A1 index	0.75–1.00 1.00–2.00 2.00–3.25
A2	present absent

(Table 1 continued)

characters		*character states*
A3		present
		absent
A4		present
		absent
A5		present
		absent
marginal free veins (MFV) simple		absent
		only hydathode
		short
		long
MFV forked		present
		absent
empty irregular areolae		present
		absent
frequency of building empty irregular areolae		high
		low
		medium
hydathodes at marginal free veins		present
		absent
angle between primary and secondary vein		< 60°
		> 60°
type	40)	*percussum*
	41)	*subauriculatum*
	42)	*terrestre*
	43)	*vulgare*
sori, paraphyses, sporangia		
distribution pattern	44)	1(–2)-serial
	45)	–3–4-serial
relation to surface	46)	superficial
	47)	slightly sunken
	48)	deeply sunken
relation to costa/margin		medial
		costal
		marginal
shape		round
		oval
diameter (mm)		< 1
		1.0–2.0
		2.0–3.0
		3.0–4.0
receptacular hairy paraphyses (RHP)	49)	present
	50)	absent
RHP length (cells)		–5
		–13

characters		*character states*
RHP branching	51)	1–2 × glandular
	52)	–4–8 × glandular [and/or acicular
	53)	absent
receptacular scaly paraphyses (RSP)	54)	present
	55)	absent
RSP attachment	56)	perfoliate or peltate
	57)	palaceous
RSP shape	58)	linear
		rhomboid
		deltoid scalariform
	59)	round scalariform
RSP length (µm)		< 100
		100–200
		200–400
		> 400
RSP width (µm)		< 100
		100–200
		200–300
		> 300
RSP index		< 1.2
		1.2–1.5
		> 1.5
paraphyses persistence		high
		low
episporangial paraphyses (ESP)	60)	present (on capsule
	61)	absent [or on stalk)
ESP type		hairy
		scaly
total annulus cells		15–20
		21–25
additional cells between indurated annulus and stalk	64)	present (1 or 2)
	65)	absent
sporangial capsule length (µm)		< 230
		230–280
		280–330
		> 330
sporangial capsule width (µm)		< 200
		200–250
		250–300
		> 300

(Table 1 continued)

characters		*character states*
sporangial capsule index		0.9–1.0
		1.1–1.2
		1.3–1.6
gross morphology		
stipe diameter basal (mm)		< 2.5
		2.5–4.0
		4.0–6.5
		> 6.5
index length of stipe: length of blade		0.1–0.5
		0.5–0.8
		0.8–1.2
texture		thinly herbaceous
		firmly herbaceous
length max. of blade (cm)		-40
		-70
		-100
		> 100
index length of blade: width of blade		< 3.0
		3.0–4.0
		> 4.0
blade widest	66)	medially, subbasally or same width all along
	67)	basally
division apically		adnate
		pinnatifid
		pinnate
division medially		adnate
		pinnatifid
		pinnate
division basally		adnate
		pinnatifid
		pinnate
division	68)	at least partly adnate or pinnatifid
	69)	pinnate throughout
lateral segment shape apically		acute
		acuminate
		pungent
		obtuse
lateral segment shape basally	70)	cuneate or angustate
	71)	truncate
	72)	cordate or auriculate

characters		*character states*
lateral segment margin		entire
		serrate
		crenate
lateral segment attachment		sessile
		short-petiolate
		long-petiolate
lateral segment length (mm)		< 50
		50–100
		> 100
lateral segment index		< 5.0
		5.0–10.0
		> 10.0
terminal segment shape	73)	petiolate-conform
	74)	adnate-conform or coadunate
lateral segment length: terminal segment length		longer
		equal
		shorter
relation of basal segment: subbasal segment		equal
		shorter
deflexion	75)	present
	76)	absent
distance of basal segments (mm)		< 10
		10–25
		25–50
		> 50
indument		
number of terminal glands of laminar glandular hairs (LGH)		1
		2
		3
LGH length (cells)		2
		-3
		-4 (5)
		-11
LGH branching	77)	present (glandular and/or acicular)
	78)	absent
laminar acicular hairs (LAH)	79)	present (-4-8 cells long)
	80)	absent
LAH positioned at		margin
		rhachis and/or costa
		surface

(Table 1 continued)

characters	*character states*
LAH density	variable/medium high low
laminar bristles	present absent
laminar scales persistency	81) low, variable or [medium 82) high
petiolar acicular hairs	present absent
spores	
colour	hyaline to yellow yellow brownish orange
length (µm)	< 40 40–50 50–60 > 60
index (longitudinal view)	< 1.4 1.4–1.8 > 1.8
perispore appearance in LM	attached detached unconspicuous
perispore surface	smooth wrinkled reticulate equatorially crestate locally protruding [crestate
detailed outer surface ornamentation of perispore	smooth glebulate undulate granulate aculeate
equatorial excrescences of perispore	absent short long very long
equatorial excrescences twisting	present absent
globules on perispore	many few none
perispore	83) crests low, polarized equatorial excrescences absent (*subauriculatum*-type) 84) crests high, polarized, equatorial excrescences present (*percussum*-type) 85) crests locally protruding, polarized (*hendersonii*-type) 86) crests locally protruding, unpolarized (*dissimile*-type) 87) inconspicuous (*amoenum*-type)
outer ornamentation of the exospore	88) smooth 89) colliculate 90) (sub)verrucate
size of verrucae	equal decreasing

Characters used here are based on studies of mature sporophytes. They concern rhizomes, rhizome scales, fronds including gross morphology, venation pattern, laminar indument, sori with sporangia and paraphyses and spores, according to the traditional descriptive sequence. Terminal taxa with their respective numbers and abbreviations are listed below (table 2). Their numerical sequence follows the alphabetical order within their systematic groupings. In order to facilitate reading two- (for varieties three-)letter abbreviations are used when references are made to the terminal taxa in the course of the following chapters. See also fold-out page 423.

Table 2.

Terminal taxa

Goniophlebium percussum-group
BE = 1. *G. benguetense*
DE = 2. *G. demersum*
KO = 3. *G. korthalsii*
MB = 4. *G. mehibitense*
PC = 5. *G. percussum*
PS = 6. *G. persicifolium*
RA = 7. *G. rajaense*
SE = 8. *G. serratifolium*
TE = 9. *G. terrestre*

Goniophlebium subauriculatum-group
AM = 10. *G. amoenum*
AMl = 10a. *G. amoenum* var. *latedeltoideum*
AMc = 10b. *G. amoenum* var. *chinense*
AMa = 10c. *G. amoenum* var. *arisanense*
DL = 11. *G. dielseanum*
LA = 12. *G. lachnopum*
MA = 13. *G. manmeiense*
MI = 14. *G. microrhizoma*
PR = 15. *G. prainii*
PD = 16. *G. pseudoconnatum*
SU = 17. *G. subauriculatum*

Goniophlebium argutum-group
AR = 18. *G. argutum*
MZ = 19. *G. mengtzeense*

Terminal taxa

Goniophlebium formosanum-group
FO = 20. *G. formosanum*
NI = 21. *G. niponicum*
NIn = 21a. *G. niponicum* var. *niponicum*
NIw = 21b. *G. niponicum* var. *wattii*

Goniophlebium hendersonii-group
HE = 22. *G. hendersonii*
SA = 23. *G. subamoenum*

(Eur)Asian taxa retained in *Polypodium*
FA = 24. *P. fauriei*
SO = 25. *P. someyae*
VU = 26. *P. vulgare*

American taxa (p.p.) retained in *Polypodium*
BR = 27. *P. brasiliense*
CA = 28. *P. californicum*
DI = 29. *P. dissimile*
FR = 30. *P. fraxinifolium*
LO = 31. *P. loriceum*
SS = 32. *P. sessifolium*
(TR = 33. *P. triseriale* = *P. brasiliense*)

Next follows the description of the character states. Transformation series were established a posteriori. They are given in chapter 9.5. Character states which were omitted secondarily for the polished version of the datamatrix are not numbered here, to avoid confusion.

4.2. RHIZOME

The morphology and anatomy of the rhizome were studied in detail here for the first time.

Some features are best observed in the field. As the particulars are not complete for all species, they are not included in the analyses. The long creeping rhizome is spirally or vertically climbing or occasionally horizontally creeping. A remarkably high branching frequency was found in MZ, while conspicuously rare branching occurs in TE.

The growth habit, as stated in the taxonomic part, was observed for the seven Philippine species and a few Chinese species in the wild. For all other species information was taken from herbarium labels and literature and is not necessarily considered complete, especially for rarely collected species. For this reason the growth habit can only provide a limited parameter for cladistic analyses. A general trend from epiphytic towards epilithic growth was found in the *G. subauriculatum*-, *G. argutum*-, *G. hendersonii*-, and *G. niponicum*-group. In the *G. percussum*-group, however, a trend from epiphytic towards terrestrial growth was observed.

Other features are conclusive or nearly so in all species concerned. Phyllopodia are always present dorsally in two alternating rows. Their height varies within the species, but exceeds 5 mm only occasionally in PS. The anatomy of the rhizome exposes parenchymatous ground tissue, in which the vascular strands and in *Goniophlebium* also the sclerenchyma strands are embedded. The stele is a dictyostele, which shows a ring of bicollateral meristeles in cross section.

4.2.1. Morphology

Shape of cross section (character state nos. 1 & 2) — The rhizome of most species studied is perfectly terete. Three species (KO, RA and TE) have an always dorsiventrally flattened rhizome with a length/width index of 1.2–1.5, while in NIw terete as well as slightly flattened rhizomes with a length/width index of 1.0–1.3 were observed. In dried material these two conditions can be recognized best using thin cross sections which are soaked in a solution of detergent in water to reach their full extension. In KO, RA and TE character state no. 1 represents an apomorphous condition, while this is not clear for NIw. Since here the character state nos. 1 and 2 appear optionally, ecological reasons might be involved.

Diameter — The diameter of the rhizome varies between 1.2 and 14 mm. Diameter smaller or equal 2 mm apply only to SA and MI. In the case of TE, with flattened rhizome, measurements reach only 1.8–3.0 × 1.5–2.6 mm. The diameter exceeds 10 mm in BR and DI (American).

Colour (character state nos. 3 & 4) — The colour of the rhizome is brown when dried, yellowish to light green in vivo in all species except six from Asia. The rhizome of PD and SU is always white from a chalky wax layer, while AR, MZ, FO and NI have a wax layer which is quite thin and therefore appears bluish in vivo and whitish when dry.

Distance of phyllopodia — The phyllopodia are situated 0.2–5(–17) cm apart. In the species retained in *Polypodium*, there is a general tendency towards closer setting than in *Goniophlebium*, but no clear line can be drawn due to many overlaps in the character states. In RA and TE the largest distances were measured with 2–7 cm for RA and 4–5(–17) cm for TE.

Roots — Roots are situated ventrally, generally in two rows, in DI in up to five irregular rows. They are branched in all but FO, dark brown and covered with unicellular, ferrugineous hairs. In vivo they dry up and stop growing if the rhizome is not attached to any substrate. The roots of FO, however, are surrounded by a green parenchymatous tissue and therefore remain alive. Root characters are not scored in the datamatrix, since the only outstanding difference is an autapomorphy.

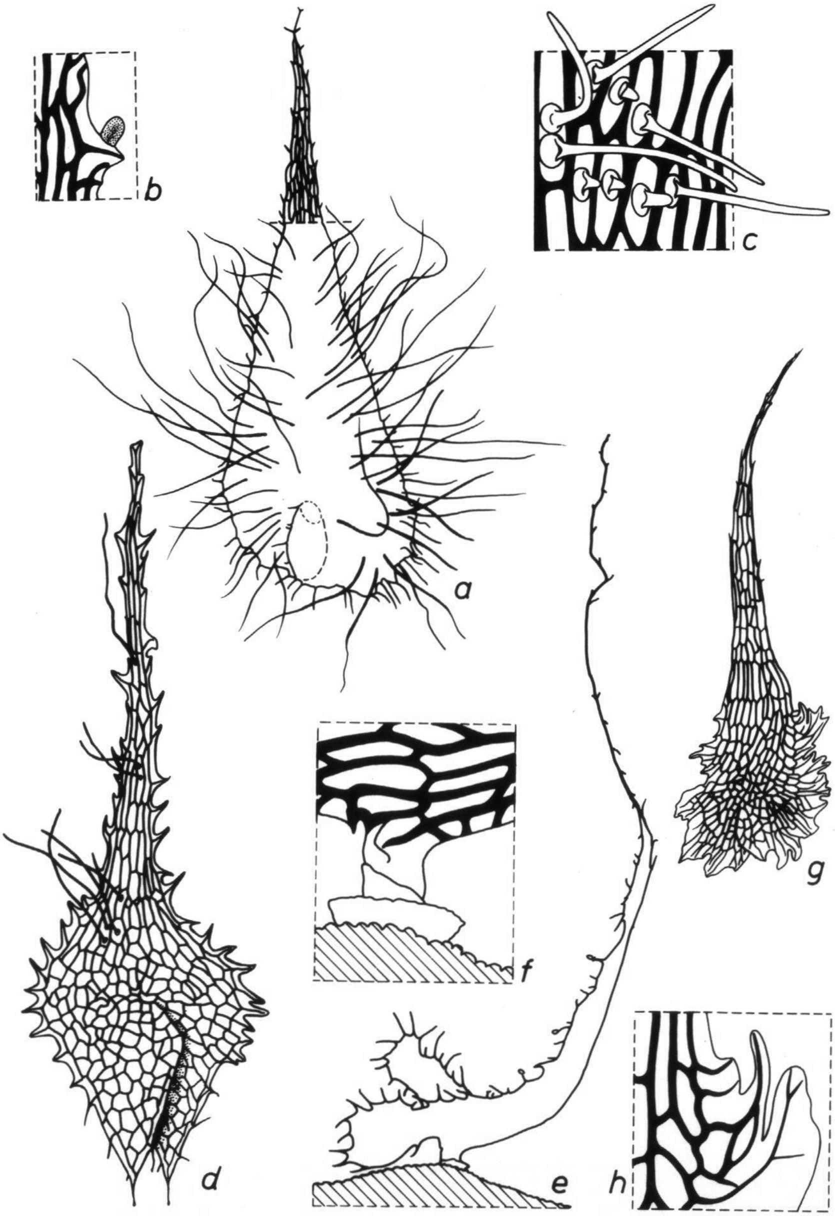


Fig. 1. Rhizome scales. — a–c. *Goniophlebium persicifolium:* a. outline with rounded basal flaps, × 25; b. detail of margin with protrusion and glandular cell, × 135; c. detail of surface with rhizoid hairs, × 135. — d. *G. percussum:* pointed basal flaps, × 25. — e–f. *G. lachnopum:* outline with filiform apex, × 25; f. detail of stalk insertion, × 135. — g–h. *G. terrestre:* g. rhizome scale not clathrate at margin of basal flaps, × 25; h. detail of margin of basal flaps, × 135.

4.2.2. Anatomy

Stele (character state nos. 5 & 6) — The stele in *Goniophlebium* appears as a regular circle in the transverse section while in FA, BR, FR and CA, species retained in *Polypodium,* vascular strands are arranged in a deformed circle.

Number of vascular strands — The number of vascular strands ranges from 5 to 22. There is a general tendency of thinner rhizomes to contain fewer vascular strands.

Dark bundle sheaths (character states 7 & 8) — To detect this character rhizomes have to be cross sectioned not too close to the growing tip, since at this point sclerification may not have started yet. In AM (AMc) and AR both conditions can be present. In one case the rhizome of AR shows a hollow, central cylinder, surrounded by a sclerenchyma sheath, which is scored as an abnormality.

Number of sclerenchyma strands (character state nos. 9, 10 & 11) — Dark sclerenchyma strands pass longitudinally through the rhizomes of all *Goniophlebium* species, varying in number from 1 to more than 100. Rhizomes of AM, AR, BE, MB, SE and SU contain more than 100, of KO, TE and NIw less than 15 strands. In species retained in *Polypodium* sclerenchyma strands are absent.

4.3. Rhizome scales (fig. 1)

The scales studied are those on well developed apical parts of the rhizome. Taken from the growing tip they have not reached their final extent of clathration yet, taken from the phyllopodium they are frequently longer and can differ as far as the indument is concerned. Rhizome scales of *Goniophlebium* are one cell layer thick throughout. They easily break off their stalks when taken for studies. In some species of *Polypodium* stalks remain attached to the scales which are several cell layers thick at the stalk attachment point. Length and thickness of stalks vary within the species studied.

The terms used to explain locations are illustrated in figure 2.

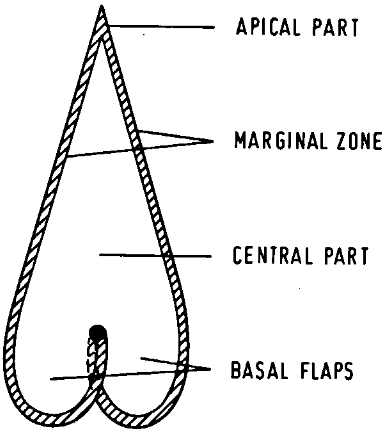


Fig 2. Schematic illustration of terms used to describe rhizome scales.

Insertion (character state nos. 12 & 13) — Scales may be inserted on a protrusion or evenly or in an invagination of the rhizome cortex. The first two conditions occur frequently within one specimen and have been combined.

Colour — Five different shades of brown were recognized for rhizome scales. This character, however, is not very stable. Light exposure, humidity, substrate consistency and age can change or influence the colour. In addition, the shades of colours are closely related to the grade of clathration of cell walls. Scales with heavily lignified cell walls appear darker than scales with thin cell walls. The cells themselves are either colourless and hyaline or yellowish to yellow. However, in scales with clathrate cell walls the colour of the lumen is indistinct. For these reasons this character has not been used for the final datamatrix.

Exposition (character state nos. 14 & 15) — All rhizome scales are at least basally appressed to the rhizome. Character state no. 14 concerns only the spreading of medial to apical parts of scales.

Density (character state nos. 16 & 17) — The density of the scales is high, if they cover the rhizome the way its surface cannot be seen. If the density is noted as medium, the surface of the rhizome is obviously visible between the scales. Low density means that scales are scattered somehow remote from each other. High and medium density were combined (character state no. 16) as distinction has been found rather difficult.

Persistence — If rhizome scales are optionally caducous, their persistence is described as low. This condition was stated in about half of all *Goniophlebium* species. The fact that parts of scales break off easily, as in AR and MZ, cannot be subsumed under the aspect of persistency. For all *Polypodium* species studied the persistency was scored as high. This character was not retained in the datamatrix, because clear judgement can only be secured from studies with fresh material (rhizome scales may be lacking in herbarium sheets for other reasons).

Dimorphism (character state nos. 18 & 19) — Dimorphism here refers to the occurrence of both round and deltoid rhizome scales. The latter are superimposed on several layers of the first. This situation was observed in AR and MZ. Details of the round form are explained in the respective descriptions of the species. Information considered in the datamatrix concerns only the deltoid form.

The same kind of dimorphism was reported from four species of *Drynaria* (Roos, 1985).

General shape (character state nos. 20 & 21) — All *Goniophlebium* species have more or less narrowly deltoid rhizome scales. In FR and LO they are ovoid. FA with rather large, extremely thin and closely appressed rhizome scales, though easily breakable, posed some difficulties. The condition ovoid in this case is an assumption.

Apex — The apex of ovoid rhizome scales is rounded. Deltoid rhizome scales with a pointed apex are described as acuminate, in case of a thin extension of the apex as filiform. Because of the close relation of this character to the general shape it has been neglected for the revised datamatrix.

Shape of basal flaps (character state nos. 22 & 23) — Correlated with the pseudopeltate attachment of the rhizome scales in all *Goniophlebium* species the basal part is divided into two flaps. They are mostly rounded but in seven species pointed (BE, DL, LA, SE, SU, MI, SO).

Size of basal flaps — Large, overlapping flaps and short auricles were noted. Long flaps correlate in most cases with character state no. 23. Since in six species all kind of variations occur, these conditions have been omitted in the final datamatrix.

Attachment (character state nos. 24 & 25) — Only FA, FR, LO, CA and VU (species retained in *Polypodium*) have peltately attached rhizome scales. In CA peltate and pseudopeltate attachment was observed. Pseudopeltate and basifix attachment have been combined in character state no. 24, since the basifix condition (HE, PR, SA) never occurs separate from the pseudopeltate condition.

Length, width, index — The length of the rhizome scales varies between 0.3 and 8.0 mm. In the majority of species they are less than 5 mm long. In LA and SU (*Goniophlebium*) as well as in FR, LO and VU (*Polypodium*) they can measure up to 8 mm.

Measurements of width of rhizome scales range from 0.3 to 5.1 mm. However, rhizome scales exclusively wider than 1.3 mm but not exceeding 3.2 mm were observed in FR, BR, LO, VU (all *Polypodium*) only.

The length/width index of rhizome scales in most species varies between 2 and 4, only for LO the index is less than 2. Three species belonging to *Goniophlebium* (LA, PR, SU) and four species of *Polypodium* studied (DI, BR, CA, VU) can reach index values of 4 to 6. Nevertheless, taking into account that 80% of all species show two or three overlapping conditions, this character has been neglected for the analyses.

Clathration of cell walls (character state numbers 26, 27, 28, 29, 30 & 31) — Lignification of primordial walls of rhizome scales is most common in *Goniophlebium*. Three of the *Polypodium* species (FA, CA, VU) were scored without any clathration.

A comparison of relative thickness of lignified cell walls has been rejected for the final datamatrix since it is difficult to judge. In *Goniophlebium* species the cell walls of rhizome scales are equally thick throughout or decrease in thickness towards their base. Rhizome scales of DE, DL and TE are never clathrate at the margin of the basal flaps. In FO all cell walls are thickly lignified throughout. As stated earlier, all rhizome scales of *Goniophlebium* are perfoliate.

In contrast, the cell walls of the peltate rhizome scales, found in *Polypodium* p.p., are thickest centrally as in FR or marginally as in LO. Thus, neglecting degree and graduation of thickness, only present or absent statements of clathration were counted for the analyses.

Colour of cell lumen (character state nos. 32 & 33) — Any shade of yellow to brownish is united in character state no. 33 and opposes a colourless, hyaline cell lumen. Except for SO rhizome scales of all species retained in *Polypodium* have a yellowish to brownish cell lumen.

Clathrate marginal protrusions (character state nos. 34 & 35) — The earlier idea of differentiating between a relative length of clathrate marginal protrusions at apex and base of the scales has finally been rejected in the datamatrix due to the degree of variability found within the species, associated with the structural complexity. In addition, there is some correlation with character state nos. 30 and 31. In case a clathration of cell wall is absent basally, clathrate marginal protrusions are necessarily absent as well. Thus, only the absent and present conditions for this character have been retained. FO is the only species of *Goniophlebium* without clathrate marginal protrusions at the rhizome scales, while this condition is common in *Polypodium.*

Glandular marginal hairs (character state nos. 36 & 37) — Character states concerning position and frequency of glandular marginal hairs were omitted since ecological factors as well as ageing processes appear influential (see chapter 6.2).

Glands, respectively glandular hairs were observed terminally at the apex of scales, terminally at the two basal flaps or all around the margin. If only present at terminal ends of the rhizome scale their frequency is considered low.

In the majority of species the marginal hairs of rhizome scales consist of simple glands only. In four *Goniophlebium* species (PS, PD, TE, MI) and in two *Polypodium* species (DI, LO) 2-celled glandular hairs have been found apart from simple glands. At rhizome scales of BR even 1–4-celled glandular hairs are present. In FA, FR, CA, VU glandular hairs at margins of rhizome scales are absent. '1' in condition no. 36 states the presence of glandular hairs irrespective its length; '1' in condition no. 37 codes the absence of any glandular hairs.

Surface hairs (character state nos. 38 & 39) — The presence of glandular surface hairs are common in scales covering young circinnate fronds. It is assumed that they dry up in older stages of the scale. This is the reason why a separate character state for glandular surface hairs has not been retained. Rhizoid hairs are mostly inserted adaxially on cells of the upper surface of the rhizome scales. In SU they were found abaxially as well.

4.4. FRONDS

The fronds are monomorphic, petiolate and articulate to the phyllopodia on the rhizome.

The number of vascular strands at the base of the stipe is somehow related to its diameter and varies between 4 and 20. There are always two big anterior strands and several small posterior strands, but in VU and SO only 2 vascular strands were observed. To describe their transition from the base of the stipe towards the apex of the rhachis four types were recognized (fig. 3).

The two main strands unite below the base of the lamina and build one. During its run through the rhachis small vascular strands split off to supply the lateral segments. The smaller strands, if present, run together with each other, while passing the rhachis, ending up in one small strand. Only at the apex of the rhachis the anterior and the posterior strand unite.

In the *G. percussum*-group the two anterior strands run through the rhachis separately and unite only towards the apex of the rhachis.

In SU and FR the two anterior strands run together below the lamina, separate again and reunite towards the apex of the rhachis.

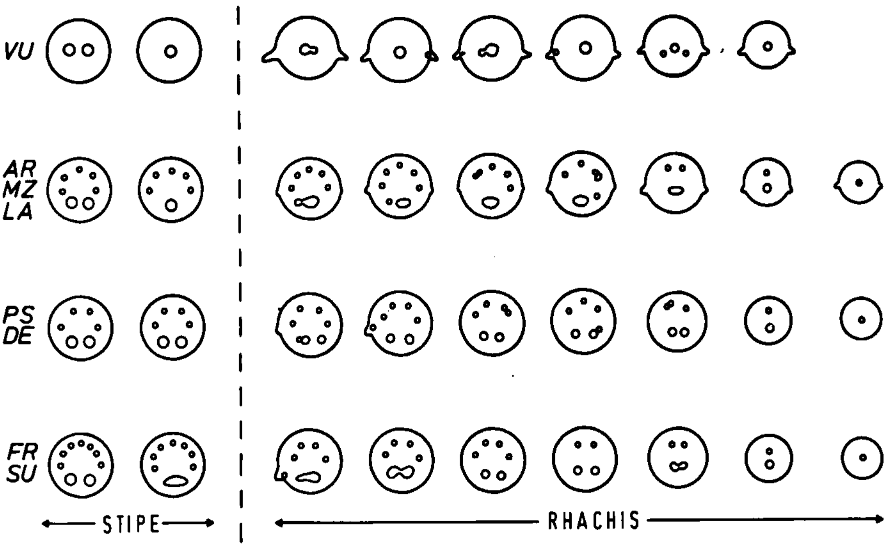


Fig. 3. Series of cross sections through stipe and rhachis of eight species (schematic).

This character is not used for the cladistic analyses, because the number of sequential sections of stipe and rhachis produced has not been sufficient. Ching (1933) stressed the fusion of vascular strands as an important character state defining the genus *Polypodium* in comparison with *Lepisorus*, *Microsorum*, and *Phymatodes*, where vascular strands do not unite while running through the rhachis.

In mature fronds the stomata are restricted to the lower surface and are situated in between the epidermis cells. Extensive studies of stomata within the family of Polypodiaceae were carried out by Sen & Hennipman (1981). Using their terminology, in all the groups recognized in the present paper the polocytic, copolocytic and anomocytic types are represented.

4.4.1. Gross morphology

Stipe diameter basally — Measurements of stipe in cross section near base reach from 1.0 to 9.5 mm across. Only some species show a basal diameter greater than 4 mm (DE, MB, PC, PS, PD, SE, DI, BR). Like most of the quantitative characters this character was not taken into account for the polished datamatrix. Small as well as large diameter sizes are represented throughout all groups.

Index length of stipe/length of blade — Indices of length of stipe to length of blade vary between 0.1 and 1.2.

Texture of the lamina — The character states recognized at first instance have later been omitted due to their similar nature apart from a certain variability within the taxa. As described before (Rödl-Linder, 1987), plants of one species can develop thinly or firmly herbaceous blades, depending on the habitat.

Maximal length of blade and length/width index — The maximal length of blade was noted between 15 and 215 cm. Longer blades tend to pend while shorter blades stand upright. Species which sometimes develop drooping fronds (PC, PS, SE, SU) were as well observed with short upright fronds. In these cases the length/width index cannot constitute a substantial factor. KO has with 1.0 to 1.1 the lowest index value. Outstandingly narrow fronds, with an index always greater than 4, were encountered in HE and MA.

Position of the blade's largest width (character state nos. 66 & 67) — This is an important character for describing the shape of the blade. Conditions as largest width medially, subbasally or same width all along the blade were found varying within species and constitute character state no. 66. Within the *G. percussum*-group a triangular shape of the blade, i.e. blade widest basally, is prevailing.

Division of the blade (character state nos. 68 & 69) — In describing the division of the blade one has to pay attention to the apical, medial and basal part of the blade. The whole blade can be pinnate, which means here that all lateral segments are articulate to the rhachis (plate 2b). This is the case in the *G. percussum*-group. The following three conditions were combined to define character state no. 68. Lateral segments are pinnate medially to basally at the blade only, but adnate to the rhachis towards the apex of the blade. Or all lateral segments are adnate to the rhachis, or the blade is pinnatifid throughout, i.e. deeply incised almost to the rhachis.

Earlier authors (J. Smith, 1866; E.B. Copeland, 1929) emphasized the pinnate, articulate condition of this character to separate the Asian from the American goniophlebioids. They have failed, as already stated by Ching (1933), as they did not take into consideration the presence of species with partly articulate and partly adnate lateral segments (AR, MZ, PR, PD, SU).

Shape of the lateral segment at its apex — Terms as obtuse, acute, pungent and acuminate were used to describe the apex of the lateral segments. This character was neglected for the analyses, as it showed much variation.

Shape of the lateral segment at its base (character state nos. 70, 71 & 72) — Logically the conditions of this character do not apply to pinnatifid species. Character state no. 71 overlaps in some species with no. 70, in other species with no. 72. In only one species (DE) all three conditions were observed.

Margin of lateral segments — The margin can be entire, crenate, serrate or any combination of the three. Some species are always obviously serrate, respectively serrulate (AR, HE, BE, DE, KO, MB, SE, SA). This character was not used for the cladistic analyses.

Attachment of lateral segments — The three conditions recognized are not applicable for pinnatifid blades. Lateral segments are either sessile, short or long-petiolate. These conditions are closely related to character state nos. 70 to 72 and have, therefore, been omitted in the final datamatrix.

Length and width of lateral segments, length/width index — Measurements were taken from the longest lateral segment available on a frond. Length/width indices range between 3 and 12 (and 22). These character states were neglected in the final datamatrix as these characters show much overlapping.

Shape of terminal segment (character state nos. 73 & 74) — The terminal segment can be conform to the lateral segments and petiolate continuous with the rhachis (figs. 50a, d & 51a). This condition, character state no. 73, appears correlated with character state no. 69; both character states represent a support in the cladistic analyses for the *G. percussum*-group. However, since they are also morphologically related, this coincidence does not strengthen the support. The matter is similar for character state no. 74, i.e. adnate-conform terminal segment or coadunate, gradually much reduced terminal segment (figs. 51e-f & 52a–d), which is correlated with character state no. 68.

Length of longest lateral segment in proportion to length of terminal segment — For the descriptions of species which have a terminal segment conform to the lateral segments a relation was established between the length of the longest lateral and the terminal segment. Because of many mutual overlaps the character states (longer, equal, shorter) were omitted in the final datamatrix.

Deflexion of lateral segments at the base of the blade (character state nos. 75 & 76) — In six species both conditions were found (HE, PD, SU, SO, MI, FA). For all other species these character states are distinctive.

Distance between basal and subbasal segments — Measurements were taken between the midribs of basal and subbasal segments. The extremes are represented by NI and MA (5 to 9 mm) and PC and PS (20 to 60 mm). However, the occurrence of high variation within these limits led to the discard of this character.

4.4.2. Venation pattern

Venation patterns of adult fronds were studied by various authors including J. Smith (1866), Beddome (1866, 1876) and Copeland (1947). That of juvenile leaves was described by Mitsuta (1984), at least for some of the species concerned.

The goniophlebioid Polypodiaceae are named after their characteristic venation pattern. *Goniophlebium* is derived from the greek 'goni', meaning angle, and 'phleps', meaning vein. The name refers to the veins which are forking and anastomosing to build a series of angular areolae, each with one included excurrent free vein.

Veins are either slightly immersed or prominent. Prominence is caused by a sclerification of the vascular bundles. This character, however, shows much variation even within one species.

In most of the species the venation is easily to be recognized. The venation is sometimes indistinct in NI and occasionally so in SU, because of the well developed acicular laminar indument.

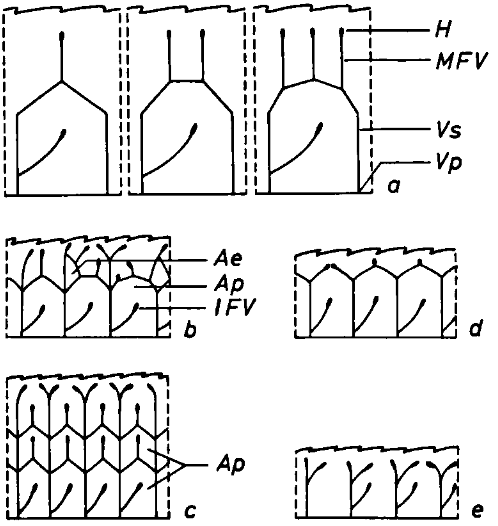


Fig. 4. Schematic illustration of terms used to describe goniophlebioid venation patterns. — a: primary areolae, H = hydathode, MFV = marginal free vein, Vp = primary vein, Vs = secondary vein. — b: *subauriculatum*-type, Ae = empty areola, Ap = primary areola, IFV = included free vein. — c: *percussum*-type, Ap = primary areola. — d: *terrestre*-type. — e: *vulgare*-type.

Within the family of Polypodiaceae the goniophlebioid venation pattern is generally regarded as structurally simple and phylogenetically derived (Copeland, 1929; Holttum, 1947; De la Sota, 1973). Species like HE and MI which are optionally goniophlebioid or free-veined demonstrate a high plasticity in the expression of this character. In addition, in all species the lateral segments show free venation at their apex. Consequently, goniophlebioid and free venation are here considered simple venation types which should not be used as the sole character to discriminate between genera. For this and other reasons MA, with always a free venation, is included in the genus *Goniophlebium*.

The ontogenetic development of the venation pattern shows an increasing complexity. Certain irregularities observed in juvenile fronds are discussed in chapter 6. In some American species (BR, FR) an irregular venation was observed in adult fronds. Included excurrent free veins of costal areolae can be either absent, present as one forked vein, or present as two veins touching each other and forming one common hydathode.

The terminology used here is explained in figure 4.

The venation was described from central parts of sterile lateral segments, since fertile ones are sometimes slightly reduced in width.

Costal primary areolae — Costal primary areolae are present in the majority of the taxa concerned. They are absent in three species (MA, FA, VU) and optionally present in six species (HE, LA, SO, MI, LO, CA).

Shape of costal primary areolae — The shape of a costal primary areola is determined by two criteria. It can be penta-, hexa- or heptagonal depending on the number of excurrent marginal free veins (fig. 4a). For taxa with multiserial primary areolae it is always pentagonal (fig. 4c). The shape can also be more or less round or elongated. This is indicated through a length/width index, which varies between 0.75 and 3.25. An index value exclusively smaller than 1 has been scored for HE only. The most common values found are between 1 and 2. For MB, PC, PS and CA these indices are always greater than 2.

Series of primary areolae — The number of series of primary areolae is necessarily correlated with the width of the lateral segments. Species with multiserial primary areolae occur within the *G. percussum*-group and in a few American goniophlebioids. In BE and SE (*G. percussum*-group) as well as in PR and SU (*G. subauriculatum*-group) representatives from Southeast Asia, a second row of primary areolae is occasionally present.

Marginal free veins and empty areolae — Marginal free veins, excurrent from areolae are found simple or forked and end, except in BR, in a hydathode. The length of these free veins can be more or less constant or variable within species. They can even be absent, thus only a hydathode is found at the touching point of two veins which form an areola. If marginal free veins anastomose with each other, they either form irregular empty areolae without an included vein (fig. 4b) or a regular series of primary areolae with an included free vein (fig. 4c). In some species the frequency of forming empty areolae was found higher than in others.

Angle between primary and secondary veins — In the *vulgare*-type of venation, which is described below, the angle between primary and secondary veins is always less than 60°. This also holds for two species of the *G. percussum*-group (BE, PS) and three American species (DI, BR, FR).

Venation types (character state nos. 40, 41, 42 & 43) — Given all the information on venation patterns, four venation types are recognized.

1. *percussum*-type: veins anastomose into series of regular primary areolae from costa towards margin (fig. 4c);
2. *subauriculatum*-type: veins anastomose into one (rarely two) series of regular primary areolae. Simple or forked marginal free veins form irregularly empty areolae (fig. 4b);
3. *terrestre*-type: veins anastomose into one series of enlarged regular primary areolae. Marginal free veins are minute or absent (fig. 4d);
4. *vulgare*-type: veins are free, once or twice forked or with occasional anastomoses (fig. 4e).

4.4.3. Indument

Laminar indument of Polypodiaceae was extensively studied by Baayen & Hennipman (1987). The terminology used in their publication is adopted here. Corresponding sterile soral structures (receptacular paraphyses) will be treated separately.

Laminar glandular hairs are present in all goniophlebioid Polypodiaceae. They are about 0.1 mm long and their position can vary intraspecificly. Their density is generally higher at the lower surface and less at the upper surface and along the margin of the lamina. In SS glandular hairs were observed very rarely only.

Length of glandular hairs (in cells) — Laminar glandular hairs consist at least of two cells, a basal non-glandular cell and a glandular cell. In half of all taxa concerned glandular hairs, 2–3(–4–5) cells long, were found. FA develops hairs which can get up to 11 cells long.

Number of terminal glands on glandular hairs — One or two terminal glands were found in BE, DE, PC, SE, TE, SU, FO and CA. In only one species (PS) 1–3 terminal glands on one basal cell were encountered.

Branched glandular hairs (character state nos. 77 & 78) — Laterally branching glands at glandular hairs occur in PC, PS, PD, SE and SU. Only in PC also an acicular branch were found.

Acicular hairs (character state nos. 79 & 80) — Acicular hairs develop already in an early stage of the juvenile frond, but still later than glandular hairs (see chapter 6.2).

Densely set acicular hairs cause a hirsute appearance of the lamina. They may be caducous or persistent to a certain extent in adult fronds even on the same rhizome (Rödl-Linder, 1987). Consequently, character state no. 79 refers to an optional presence, while character state no. 80 states a permanent absence of acicular laminar hairs. In this aspect the author fails to confirm the idea of Baayen & Hennipman (1987) who assumed a presence of acicular hairs in all species of *Goniophlebium* (*'Schellolepis'* sensu Pichi Sermolli).

In certain species acicular hairs can get longer than in others. With 2–8 cells the longest acicular hairs were found in BE.

In some species they occur only along costa and rhachis, in others they are distributed all over upper and lower surface and along the margin of lateral segments. For NI, FO and DI a permanent high density of acicular hairs all over the lamina was recorded.

When acicular hairs occur on the lamina they are not necessarily met at the stipe as well. If petiolar acicular hairs are present, they reach the same length as the laminar ones.

Bristles — More or less lignified bristles were observed in one species (MB) only. They are single or arranged in small tufts on the upper surface of the lamina mainly around the soral pustules.

Scale persistence (character state nos. 81 & 82) — Laminar and petiolar scales correspond structurally with the rhizome scales (see chapter 6.2.3). The presence of scales at stipe and lamina was observed in all species.

Their persistence in adult fronds pertains mainly to rhachis and costa at the lower surface of the lamina and to the basal part of the stipe. The persistence is characteristically high in in DE, LA, PD, SU, and AM. This condition is described by character state no. 82.

4.4.4. Sori, paraphyses and sporangia

Sori

Distribution patterns of sori (character state nos. 44 & 45) — Sori are arranged in regular series and are located terminally on included free veins. In one Asian (KO) and several American species there can be up to 3 (4) rows of sori on either side of the costa.

Relation of sori to surface of the lamina (character state nos. 46, 47 & 48) — Most species of the *G. percussum*-group have more or less sunken sori (except KO, SE, TE). In all other but two species (PD, SU) of *Goniophlebium* sori are situated superficially. In only one American species (BR) sunken sori were recorded.

Position of sori in relation to costa and margin — This character is only applicable for taxa with a uniserial distribution pattern of the sori. Sori can either be situated closer to the costa, medially between costa and margin or closer to the margin.

Shape and size of sori — Sori are usually perfectly round except in DL and MI. In these two Himalayan species they tend to be slightly oval.

The diameter of the sorus displays another quantitive, variable character. Smallest sori were noted for MB and DI with 0.4–0.8 mm, largest sori for RA and CA (VU) with 2.1–3.0(–4.0) mm in diameter.

Paraphyses (fig. 5)

As mentioned earlier paraphyses of Polypodiaceae were treated by Baayen & Hennipman (1987): "Paraphyses are regarded as receptacular or sporangium-born hairs being part of the remaining frond indument, and therefore not as sporangia." Nearly all paraphyses which were observed in the course of this study are described in full detail and beautifully illustrated in the publication above mentioned.

It was first assumed that a terminal gland occurs in all types of paraphyses. However, such a gland is absent in the deltoid and rhomboid scaly paraphyses of BE. Tips of scales or terminal glands may break off easily. In such cases glands appear to be lacking in other species as well.

Receptacular hairy paraphyses (character state nos. 49 & 50) — Receptacular hairy paraphyses were found in all Asian species studied. In MA and MI only a length of up to 3 or 4 cells was encountered, while in other species they might get longer, reaching up to 13 cells in FO.

Branched receptacular hairy paraphyses (character state nos. 51, 52 & 53) — Frequently hairy paraphyses are simple, in some species optionally once (rarely twice) branched (BE, PR, DL, SO, AM). A special situation was found in FO and NI which is defined by character state no. 52. Hairy paraphyses of the first have up to 5 glandular and up to 2 acicular branches. Hairy paraphyses of NIn present up to 4 and of NIw up to 8 glandular branches.

Receptacular scaly paraphyses (character state nos. 54 & 55) — Scaly paraphyses are present in sori of all species belonging to *Goniophlebium* except in FO, NI, MI and MA as well as in all species retained in *Polypodium,* except SO. Scaly paraphyses of AM deserve a special notice. Because of a very slight clathration they appear less clearly dentate than those of all other species.

Scaly soral structures, not reported before, were observed as an autapomorphy of BE. These paraphyses consist of an uniseriate stalk and a few thick terminal cells which are heavily clathrate, thus appearing brown. Similar structures were found in *Solanopteris bifrons* by Baayen & Hennipman, however without any clathration.

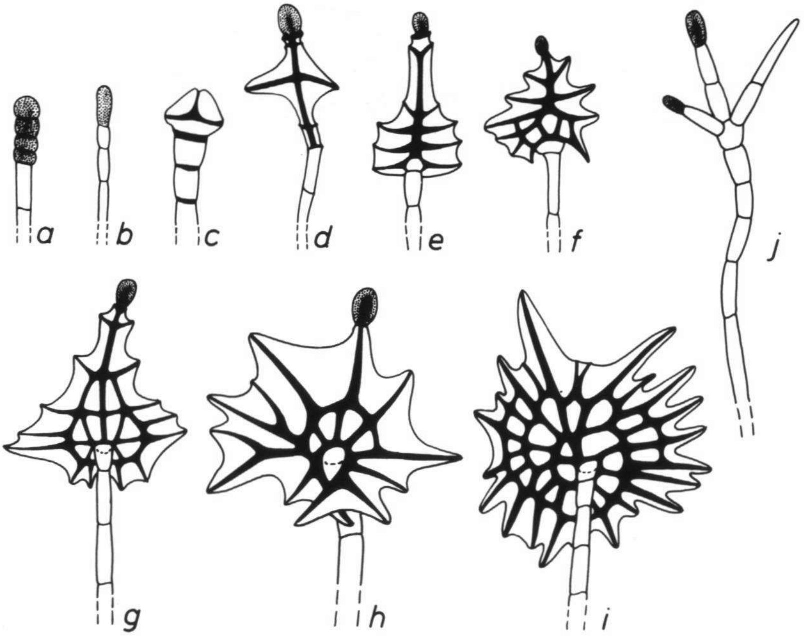


Fig. 5. Different kinds of soral paraphyses, arranged according to increasing complexity, × 135. — a & c. *Goniophlebium benguetense*. a: hairy paraphysis with 4 thickened terminal cells; c: rhomboid scaly paraphysis without terminal gland. — b & d. *G. dielseanum*. b: unbranched hairy paraphysis; d: scaly paraphysis, 2 cells wide with terminal gland, attachment palaceous. — e & j. *G. terrestre*. e: see d; j: deltoid scaly paraphysis, more than 2 cells wide, attachment peltate. — f. *G. persicifolium:* same as j, but attachment palaceous. — h. *G. mengtzeense:* rounded scaly paraphysis, attachment perfoliate. — i. *G. lachnopum:* stellate scaly paraphysis without terminal gland, attachment peltate. — j. *G. formosanum:* branched receptacular hairy paraphysis.

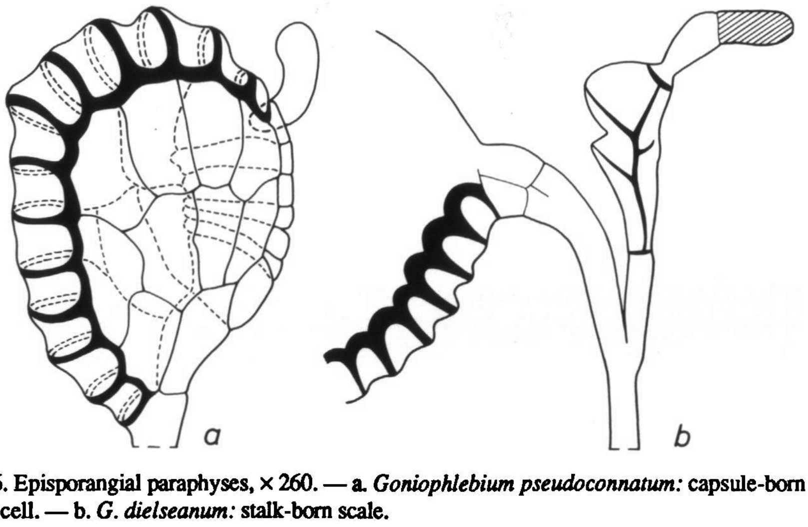


Fig. 6. Episporangial paraphyses, × 260. — a. *Goniophlebium pseudoconnatum:* capsule-born glandular cell. — b. *G. dielseanum:* stalk-born scale.

Attachment of receptacular scaly paraphyses (character state nos. 56 & 57) — Character state no. 56 defines a peltate or perfoliate attachment of the scaly paraphyses to a uniseriate stalk. In the complementary condition scaly paraphyses are palaceously attached. In LA, SU, AM, SA and TE both conditions occur.

Shape of receptacular scaly paraphyses (character state nos. 58 & 59) — Hairs and scales with clathrately thickened cell walls are considered 'scaly' in the present paper. Therefore 'intermediates between scales and uniseriate hairs' as indicated in Baayen & Hennipman (1987) are regarded as linear scales here (character state no. 58).

Basally attached, clathrate paraphyses, whether diamond-shaped or triangular, 2 or more cells wide, are considered structurally related (Baayen & Hennipman, 1987, ad plate 10). Less common are scaly paraphyses with stellate or deltoid blades which are peltately attached.

More or less deltoid scales were recorded for all Asian species apart from PD and SO. Rounded scales are defined by character state no. 59.

Size of receptacular scaly paraphyses (excluding linear scales) — Smallest scaly paraphyses were measured for PS which measure between 90–110 um × 60–80 μm, largest size occurs in SA, 450–700 × 210–400 μm. Length/width indices in all scales were calculated between 0.9 and 2.1. With respect to the different types of scaly paraphyses, the present types represent extremely variable quantitative characters.

Persistence of receptacular scaly paraphyses — Copeland (1947) assumed ephemeral paraphyses in a way that in certain stages of maturity none of them could be found in a sorus any more. This is not confirmed here. Hairy as well as scaly paraphyses can fall off to a certain extent but some of them are permanent.

Episporangial paraphyses (character state nos. 60 & 61; fig. 6) — Episporangial paraphyses (character state no. 60) may be branching from the stalk as in LA, DL, AM, MI, and MA, or may be inserted at one of the epistomium cells of the capsule. The latter condition occurs only occasionally in PD. Condition no. 61 states the absence of any episporangial paraphyses.

Type of episporangial paraphyses (character state nos. 62 & 63) — If present, episporangial paraphyses are either hairy or scaly. Glandular hairs with one or two basal cells were found branching from sporangial stalks in LA, MI and MA. Scaly ones are stalk-born in AM and DL.

A single gland only was observed on capsules of PD. Single glands positioned at one of the epistomium cells were not reported from any other species of the family.

Sporangia

Sporangial capsules are situated terminally on stalks which are triserial at their apex. The vertical annulus consists of 12–14 indurated, 3–4 epistomium, 2 stomium and 3–4 hypostomium cells.

Contrastomium cells (character state nos. 64 & 65) — The cells between indurated annulus and stalk which are on the opposite side of the stomium are called contrastomium cells in this study. In FA and SO one or two contrastomium cells were observed, i.e. hyaline cells between indurated annulus and stalk opposite of the stomium. This condition was illustrated before for species of other genera [e.g. *Platycerium bifurcatum* (Cavanilles) Christensen] by Haider (1954).

Size of sporangial capsules — Length, width and respective ratio of capsules were found to be varying to a great extent. Relatively small capsules were noted for PD, SU, DL, FO, MI, MA and LO. A length/width ratio always less or equal 1.0 was calculated for capsules of FO and SS. The values for all other species take place somewhere between 0.9 and 1.6.

4.5. SPORES

The monolete spores are concavo- to plano-convex like those of all Polypodiaceae. Spores of DL, AM, MI and FR remain hyaline, while mature spores of all other taxa are yellowish to brownish. The descriptive terms used correspond with those applied by van Uffelen & Hennipman (1985). Others were illustrated by Stearn (1983).

Size of spores — Measurements are taken at the outline of the exospore with light-microscopical magnification. The largest width in polar view shows more or less equal dimensions with the largest width in lateral view. Outstandingly short spores, with a length exclusively smaller than 45 µm, were encountered in PC, PS, SU and DL. Relatively long spores, optionally longer than 60 µm, were found in a number of species from all groups (KO, RA, HE, LA, NI, FA, SS, CA, VU). However, there are many overlapping sizes in between. Length/width indices reach from 1.3 to 1.9, hence the outline is ellipsoidal.

Attachment and folding of perispore (character states nos. 83, 84, 85, 86 & 87) — The appearance of the perispore in the light microscope can be either inconspicuous or distinct. In the latter case two types are recognised, one with most parts attached to the exospore, the other appearing quite detached from the exospore.

Character state nos. 83 to 87 refer to folding-types of the perispore as seen with the LM and SEM (plates 3 & 4).

— *subauriculatum*-type: crestae low and polarized, equatorial excrescences absent;
— *percussum*-type: crestae high and polarized, equatorial excrescences present;
— *hendersonii*-type: crestae locally protruding and polarized, equatorial excrescences absent or present;
— *sessifolium*-type: crestae locally protruding and unpolarized; equatorial excrescences absent;
— *amoenum*-type: crestae and equatorial excrescences absent (perispore not differentiated).

The *percussum*-type is characteristic for the perispore in the *G. percussum*-group. MB with the *hendersonii*-type represents an exception. SU, PD, MZ, LA and PR show the *subauriculatum*-type of perispore.

Outer surface ornamentation of the exospore (character state nos. 88, 89 & 90) — Differences between a smooth and colliculate or verrucate ornamentation can be distinguished in light-microscopical preparations, while a pustulate surface can only be recognized with the SEM. All species of the *G. percussum*-group and only a single American species (DI) have a rather smooth exospore. All other taxa show some kind of exospore ornamentation. A rather colliculate exospore is found in all species of the remaining groups and in some species of *Polypodium*. A verrucate exospore, showing a decrease in the size of the verrucae towards the distal pole, is found in spores of FA, BR, FR, CA and VU.

Equatorial excrescences of perispore at the lateral poles — The presence respectively absence of equatorial excrescences is included in the typification of the perispore. With the exception of AR they were observed only in species of the *G. percussum*-group. They are mostly short, about 1/9 in proportion to the length of the spore. In TE the excrescences reach c. 1/4 of the length of the spore, i.e. long. In KO they can even get longer than the spore itself, i.e. very long. The short excrescences may occasionally be twisted in PC.

Detailed outer surface ornamentation of the perispore — The smooth condition is common within the Polypodiaceae and, therefore, considered plesiomorphous. Derived conditions are represented by minute elevations which are described as glebulate, undulate and granulate in the taxonomic part.

Superimposed wrinkles were observed in the perispore of a number of species studied. SE is the only species of the *G. percussum*-group with a wrinkled perispore.

Globules, i.e. spherical deposits attached to the surface of the perispore, are found in some species of all groups. They are irregularly scattered and vary considerably in number and size.

5. GAMETOPHYTES

5.1. INTRODUCTION

Since Bower (1923), who interpreted the gametophyte as little important for fern classification, the opinion about the value of the gametophyte for comparative studies has changed considerably. The sequence of cell divisions at spore germination, the developmental stages, the morphology of the adult thallus as well as type and location of hairs and sex organs are assumed significant for an understanding of the evolution and phylogeny of the major taxonomic groups of ferns.

Nayar & Kaur (1971) associated the spore germination within the subfamily Polypodioideae with the *Gleichenia*- or sometimes *Vittaria*-type. They classified the patterns of spore germination on the basis of the planes of cell divisions (in relation to the polarity of the spore) and directions of growth of the primary rhizoid and the prothallus. They stated that in the *Gleichenia*-type cell divisions take place by formation of walls parallel to the polar axis of the spore. Nayar & Kaur (1971: 302): "In the *Vittaria*-type of germination a rhizoid initial is cut off at the proximal pole of the spore parallel to the equatorial axis. The prothallial initial then divides by a wall perpendicular to the first wall into two equal daughter cells, one of which remains quiescent and the other, by a series of divisions by walls parallel to the second wall, grows into a germ filament."

5.2. OBSERVATIONS AND DISCUSSION; CONCLUSION

The gametophytes of BE, PC and PS (*G. percussum*-group), PD and SU (*G. subauriculatum*-group) and MZ (*G. argutum*-group) were cultivated from spores sown within two weeks after collecting. The following observations are reported in chronological sequence:

- Germination of spores occurs within one to two weeks after sowing. First one rhizoid grows out of the spore.
- The plane of first cell division cannot be recognized, because of the permanent crestate perispore.
- The protonema stage reaches 3–4(–6) cells.
- Subsequent transverse divisions in the apical region result in the formation of a spatulate cell plate.
- During progressive development of the cell plate papillae are formed on surface and margin, which occasionally extend to soft hyaline rhizoids. Location and number of rhizoids show variation within and between the species.
- When the size of the gametophyte reaches c. 300 to 700 μm in diameter, the obconical apical meristematic cell initiates the formation of a sinus. From then on the gametophyte is cordate.
- The cordate thallus develops a 'midrib' on its lower surface, consisting of a longitudinal row several cells thick.
- Only in PS the wings of the cordate prothallus frequently overlap before reaching maturity.
- One-celled, club-shaped glandular hairs, 30–55 μm long, appear first marginally, then also on the upper surface. In PD and MZ hairs on lower surface are only found after the formation of antheridia. Secretion by hairs is observed after maturity of the sex organs only.
- Maturity is reached at the earliest eight to ten weeks after spore germination.
- In the mature gametophyte the 'midrib' is c. 6–12 cells wide and 4–5 cells thick.
- Rhizoids are found abundant on the upper surface, less so on the lower surface. They turn brown and become stiffer upon age.
- Antheridia develop earlier than archegonia on the same thallus. Antheridia are located on or near the 'midrib' towards the anterior end of the thallus. Archegonia are located on or near the 'midrib' towards the posterior end of the thallus. The number of archegonia is about three to five times higher than the number of antheridia.

- The subglobose antheridia consist of a slender disc-shaped base cell, a wider ring cell and a smaller cap cell. They include the central spermatogenous cell. Diameters of ring cells are measured between 40 and 60 µm.
- Archegonia are found with 3–4 projecting neck cells. They are straight and semiglobose with a basal diameter between 30 and 45 µm.
- Within two weeks after fertilization young sporophytes with two to three fronds are produced.
- Proliferation of gametophytes occur if no fertilization has taken place or if unfavourable conditions have prevailed.

Unlike the spore germination, Nayar & Kaur (1969, 1971) referred the prothallial development within the Polypodioideae to the *Drynaria*-type. This assumption was confirmed in gametophytes of the Philippine *Goniophlebium* species.

Gametophytes of only a few goniophlebioids were studied before. The gametophyte of AM was described by Nayar (1962) as generally a little longer than broad. This is confirmed here for certain other species belonging to the *G. subauriculatum*-group and to the *G. argutum*-group (PD, SU, MZ). It could not be confirmed for species of the *G. percussum*-group (BE, PC, PS). Highly branched hairs, as reported by Nayar (1962), were not observed. The antheridia were characterized by Nayar having a columnar basal cell and a large cap cell, i.e. its diameter being almost equal to the diameter of the entire antheridium. They were found bent away from the anterior end (sinus) of the thallus and often laying parallel to its surface. Even short-stalked antheridia were reported. For the Philippine species all this is not the case, as it is described above.

The description of the gametophyte of the neotropical species DI (*'Polypodium chnoodes'*) by Atkinson & Stokey (1970) differs from the authors' observations on the Philippine species especially as to the following statements: In DI archegonia develop earlier than antheridia and cover much of the 'midrib', while antheridia are found at the posterior portion of the 'midrib' or the wings. The neck of the mature archegonium is bent away from the anterior end. The antheridia are elongated (as in *Polypodium vulgare*) and are optionally stalked. The differences with the Philippine species are stated above. According to Atkinson & Stokey (1970) secretory glandular hairs appear only by the time the thallus is seven months old. They were not observed by the present author nor were branched hairs, which might, however, develop only at a later stage.

De la Sota (1973: 234) assumed that "recent studies on prothalli have given perhaps the most productive and successful evidence on the relationships within the Polypodiales, although their knowledge is still sporadic." Comparing the present results with evolutionary trends stated by him a number of characters are to be considered 'primitive', i.e. large prothalli with a thick 'midrib', short filamentous stage, slow growth (several months between spore germination and egg fertilization). As to the sex organs the results found for the Philippine species rather correspond with De la Sota's description of 'advanced' characters, i.e. small antheridia with a wall composed of three cells, round opercular cell, archegonia with a short neck.

Knowledge on gametophytes is still too scanty for comparative analysis.

6. JUVENILE SPOROPHYTES

6.1. INTRODUCTION

Juvenile plants (or parts of it) are plants that have not yet reached the mature fertile stage. Juvenile fronds are most prominent in ferns because of the heteroblastic series of successive sterile fronds formed by the sporophyte prior to the formation of fertile fronds. The development of shape and venation of heteroblastic frond series was observed especially in SU (fig. 7) and 6 other species occurring in the Philippines (BE, MZ, PC, PS, PD, TE).

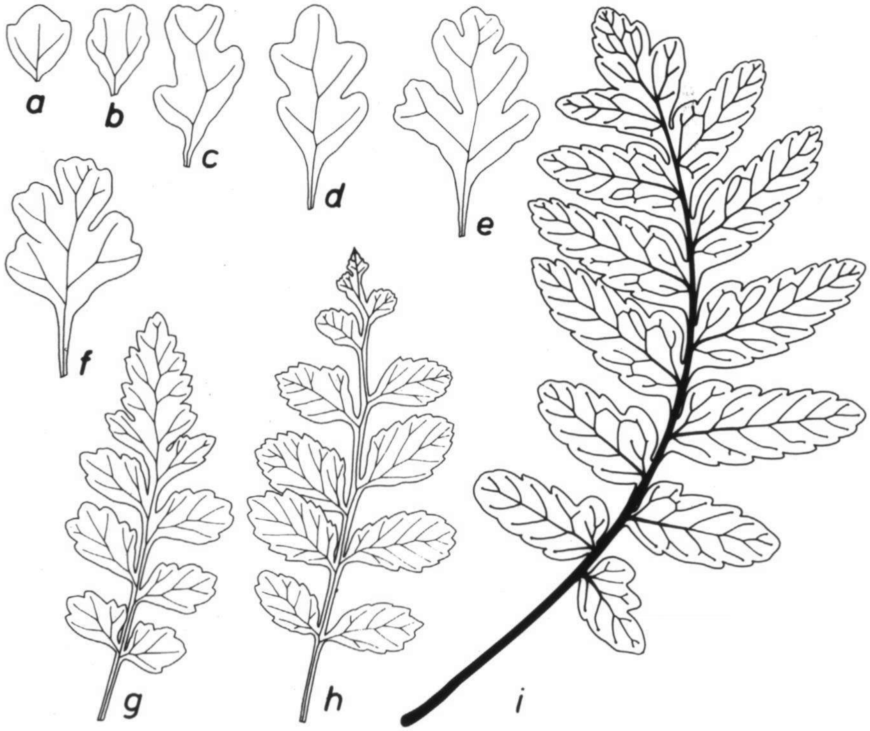


Fig. 7. *Goniophlebium subauriculatum:* series of selected young sporophytic fronds, arranged according to increasing complexity of venation pattern.

In principle they all start with a wedge-shaped to roundish-oval frond narrowed towards the base and the margin variously lobed. The pictured fronds are arranged according to increasing complexity of the venation, which coincides with an increase in size and in the grade of division. A clear differentiation into stipe and lamina is recognized in the earliest fronds. The veins are simply forked and start anastomosing at a stage where fronds are incised to the rhachis and lateral segments are numerous. At the beginning of this process either included free veins as well as areolae are built more or less simultaneously as in SU, or empty areolae appear first as in TE.

A similar observation was made by Mitsuta (1984) concerning juvenile fronds of AR. He described that veins anastomose without included veins at first, and succeedingly with simple excurrent included veins in the costal areolae. Mitsuta's notice of occasional irregularities in venation pattern like plural and/or forked included veins or subdivided primary areolae by continuous included veins specially in adult sterile fronds of PC is confirmed here. These irregularities are also remarkably frequent in BR and FR and in juvenile fronds of all species.

Juvenile fronds should not be mistaken for young fronds which include immature stages. In the following special attention is paid to the laminar and petiolar indument, which is identical in circinnate stages. It became obvious that fronds in a late circinnate stage show the highest variation of indument. Therefore hairs and scales present at this stage served as a basis for the following comparison between indument of juvenile and mature sporophytes. This study was carried out with a selection of eight *Goniophlebium* and four *Polypodium* species, i.e. BE, MZ, PC, PS, PD, SU, TE, FO, DI, BR, LO, VU.

6.2. INDUMENT

6.2.1. Acicular hairs

Acicular hairs develop later than glandular hairs and scales. Generally they are 1–3 cells longer on the mature than on the juvenile sporophyte, except in PC where they were found longer in the juvenile leaves. In PS and occasionally in SU they fall off upon ageing. Acicular hairs never occur in MZ, TE and BR. In BE, PC, SU, FO and DI acicular hairs are placed all over the upper and lower surface in various density. In PS (juvenile!) and LO they are found only along veins. Juvenile fronds of PD show acicular hairs along margins and veins, while in mature fronds they are positioned all over except marginally, as they are in all stages of VU. This comparison is shown in table 3. Petiolar acicular hairs occur only in FO and DI and occasionally in SU on mature sporophytes.

6.2.2. Glandular hairs

Uni- and biseriate, multicellular glandular hairs were only observed during juvenile stages of MZ, FO, DI, BR, LO and VU. The case is similar for all kinds of intermediates between these hairs and linear scales, which are also ephemeral towards the end of the uncoiling procedure. Table 4 presents the development of short glandular hairs. Paying attention to the number of terminal and of laterally branching glands a certain decrease is notable. Presumably, glands tend to dry out when the protective function of the crosier is missing. Only in DI abundant secretory hairs, 3–4 cells long, were observed during juvenile stages. They resemble the densely set acicular hairs, but have a club-shaped terminal cell.

Table 3.

	acicular hairs			
	juvenile lamina		mature lamina	
species	length (cells)	position	length (cells)	position
MZ	absent	–	absent	–
TE	absent	–	absent	–
BR	absent	–	absent	–
PS	2–8	along veins	absent	–
LO	2–4	along veins	2–5	along veins
VU	2–4	on surface	2–5	on surface
PD	2–4	along veins along margin	2–8	on surface
BE	2–5	on surface along margin	2–8	on surface along margin
PC	2–8	on surface along margin	2–5	on surface along margin
SU	2–6	on surface along margin	(2–8)	on surface along margin
FO	2–3	on surface along margin	2–4	on surface along margin
DI	2–6	on surface along margin	2–8	on surface along margin

6.2.3. Scales

Below follows a description of scales found on circinnate juvenile fronds.

— BE: scales deltoid, index 5.4–9.0, pseudopeltate, apex filiform, cell walls thinly clathrate throughout, marginal protrusions clathrate, short all along margin, terminal gland 1, basal glands 2.

— MZ: scales deltoid, index 7.6–9.1, pseudopeltate, apex filiform, cell walls thickly clathrate throughout, marginal protrusions clathrate, long all along margin, terminal gland 1, basal glands absent.

— PC: scales deltoid, index 1.8–3.5, basifix or pseudopeltate, apex acuminate, cell wall thinly clathrate throughout, marginal protrusions clathrate, getting longer towards base, terminal glands 1–2, basal glands 2–4.

— PS: scales deltoid, index 1.7–4.5, pseudopeltate, apex acute to acuminate, cell walls clathrate throughout, marginal protrusions clathrate, variable in length, terminal glands 1–3, basal glands absent.

Table 4.

species	glandular hairs			
	juvenile lamina		mature lamina	
	number of terminal glands	number of lateral branches	number of terminal glands	number of lateral branches
BE	1–2	1–3	1–2	absent
MZ	1–2	1–3	1	absent
PC	2	1–2	1–2	1–2
PS	2	1	1(–3)	1
PD	2	1	1	1
SU	2	1	1–2	1
TE	2	absent	1–2	absent
FO	1–3	1–2	1–2	absent
DI	1–2	absent	1	absent
BR	1–2	absent	1	absent
LO	1	0(–1)	1	absent
VU	1	absent	1	absent

— PD: scales deltoid, index 4.4–5.0, basifix or pseudopeltate, apex acute to filiform, cell walls thinly clathrate throughout, marginal protrusions clathrate, variable in length, terminal glands 1–2, basal glands 2.

— SU: scales deltoid, index 2.8–9.8, basifix or pseudopeltate, apex acute to filiform, cell walls clathrate throughout, marginal protrusions clathrate, variable in length, terminal glands 1–2, basal glands 0–4.

— TE: scales deltoid, index 2.1–5.0, pseudopeltate, apex acute to filiform, cell walls clathrate throughout, marginal protrusions clathrate, long all along margin, terminal gland 1, basal gland 0–2.

— FO: scales deltoid, index 2.8–3.0, pseudopeltate or palaceous, apex acute, cell wall thickly clathrate, mainly centrally, marginal protrusions absent, terminal glands 2–3, basal glands 0–6.

— DI: scales deltoid, index 2.5–5.8, pseudopeltate or palaceous, apex filiform, cell walls thinly clathrate, mainly centrally, marginal protrusions hyaline, short, mainly basally, terminal gland 1, basal glands 2.

— BR: scales lanceolate to deltoid, index 3.0–5.1, palaceous, apex acuminate to filiform, cell walls very thinly clathrate, marginal protrusions hyaline, short, mainly apically or absent, terminal gland 1, basal glands 0–4.

— LO: scales deltoid to ovoid, index 1.3–1.9, basifix or pseudopeltate, apex acute to filiform or obtuse, cell walls thickly clathrate, mainly centrally, marginal protrusions hyaline, variable in length, terminal gland 1, basal glands 0–2.

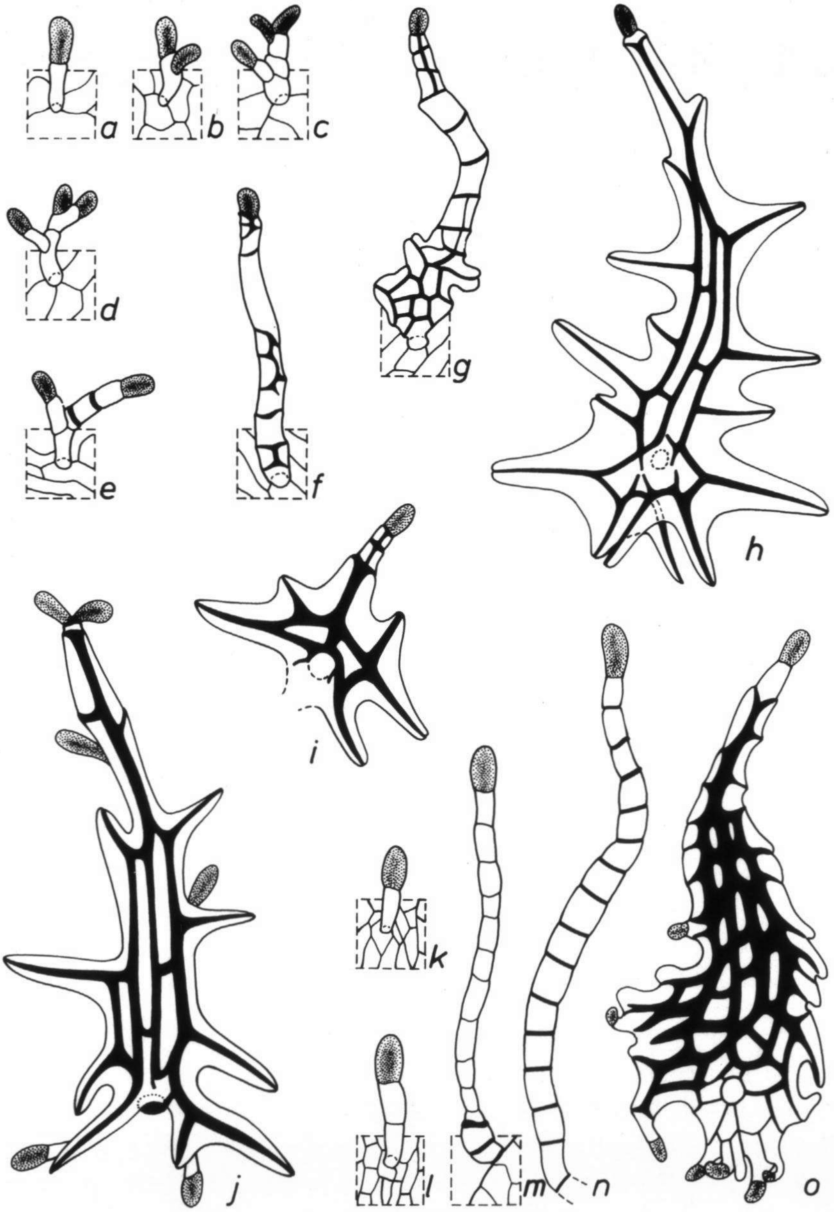


Fig. 8. Glandular indument on juvenile laminas of *Goniophlebium*, × 135. a–g. *Goniophlebium mengtzeense*; h. *G. benguetense*; i. *G. terrestre*; j. *G. subauriculatum*. — Glandular indument on juvenile laminas of some American goniophlebioids, × 135. k–m. *Polypodium triseriale*; n, o. *P. loriceum*.

— VU: scales lanceolate to deltoid, index 4.6–6.6, palaceous, apex filiform, clathration of cell walls absent, marginal protrusions hyaline, short or absent, terminal gland 1, basal glands absent.

Scales are ephemeral to a great extent. In a few species (AM, LA, PD) they are persistent, mainly along rhachis and costa. The scaly stipes of adult sporophytes of PD deserve special notice. As on glandular hairs also on the scales of mature fronds less terminal glands are found.

Different glandular hairs and scales found on juvenile laminas of Asian respectively American goniophlebioids are illustrated in figure 8.

Comparison between laminar and rhizome scales of juvenile sporophytes

Laminar scales are always appressed to the frond surface, while rhizome scales of certain species are spreading at their middle to apical part (see chapters 15 and 17).

The typical shape of rhizome scales, as described in the taxonomic part, can also be recognized among the laminar scales. However, laminar scales appear generally more variable in shape. Indices of laminar scales are higher in BE, MZ, BR and VU. In all other species studied these indices correspond but show a wider range.

Rhizome scales of all Asian species are pseudopeltate, rarely also basifix, those of LO and VU are peltate. Laminar scales present intraspecificly a variation of different kinds of attachment.

The clathration of cell walls in laminar and rhizome scales is strikingly similar with two exceptions. Rhizome scales of DI are centrally thickly, laminar scales of the same species thinly clathrate. However, the thickness of laminar and rhizome scales is decreasing towards the margin of the scale. Cell walls of rhizome scales of LO were found marginally thickly clathrate and centrally hyaline, while laminar scales show the opposite. In Asian species, where clathrate marginal protrusions occur on rhizome scales (except on rhizome scales of FO), they occur also on laminar scales. Minor modifications were observed, e.g. basal protrusions at rhizome scales of TE are not clathrate, but at laminar scales they are. American species, where clathrate cell walls are marginally not protruding, show the same feature at laminar scales. In addition, the hyaline cell lumen is occasionally slightly projecting.

Rhizoid surface indument was only found on rhizome scales.

7. KARYOLOGY

The existing knowledge of chromosome numbers in *Goniophlebium* is quite limited. Respective records have been found in Chiarugi (1960) and Fabbri (1963, 1965), where further references are given. They concern seven species only. In all these cases meiotic counts are listed. The known data are summarized in table 5. More research has been done on the polyploid *Polypodium vulgare*-complex. For reasons of comparison, data found in the literature about Asian species retained in *Polypodium* are also listed here.

Table 5.

species	meiotic (n)	mitotic (2n)	ploidy	references
PC	c. 37	–	diploidy	Manton, 1954b
PS	c. 37	–	diploidy	Manton, 1954b
AM	37	–	diploidy	Malhotra & Mehra, 1961
	c. 37	–	diploidy	Pal, 1961
	36	72	diploidy euploidy ?	Patnaik & Panigrahi, 1963
LA	37	–	diploidy	Malhotra & Mehra, 1961
	36	–	diploidy euploidy ?	Patnaik & Panigrahi, 1963
MI	37	–	diploidy	Malhotra & Mehra, 1961
	36	–	diploidy euploidy ?	Patnaik & Panigrahi, 1963
SU	c. 37	–	diploidy	Manton, 1954b
	37	–	diploidy	Holttum & Roy, 1965
AR	37	–	diploidy	Malhotra & Mehra, 1961
	36	–	diploidy	Patnaik & Panigrahi, 1963
FA	37	–	di	Evans, 1963
	37	–	di	Mitui, 1965
VU	74	–	tetra	Manton, 1947, 1950, 1951
	74	–	tetra	Sorsa, 1954, 1958, 1962

The given haploid chromosome numbers are mostly 37 and rarely 36; 36 chromosomes were found in four species (AR, AM, LA, MI) by Patnaik & Panigrahi who suggested a possible euploidy for the latter three. Taking into account the indications for hybrids and polyploids, as given by Hennipman (1977), only AM might possibly show euploidy. This species shows much variation in morphology as well as in habitat preferences. A similar case is suggested for SU. For this species the author was able to demonstrate that the extreme morphological variability is caused by external factors like light exposure, temperature, altitude and humidity (see chapter 8.3.).

The karyology of KO and TE, two local species of the *G. percussum*-group, should be examined because of deviating spores. The very limited fertile herbarium material of KO shows in part aborted spores. TE has all its spores normally shaped, but the number of spores per sporangium varies between 30 and 50. The sporangia of all other Philippine species contain 64 spores.

The present author has not been able to study the karyology of the *Goniophlebium* species herself. Chromosomal information, associated with the study of isozymic data is expected to be a powerful tool for testing systematic hypotheses.

8. GEOGRAPHY AND HABITAT

8.1. DISTRIBUTION

Goniophlebium, as delineated here, is an exclusively Asian genus which ranges from the Northwestern Himalayan region (Pakistan) to the South Pacific (Samoan Islands) and from Luo Shan in Shantung (China) to the Great Dividing Range (Queensland). The present distribution of the whole genus is shown in figure 9. The

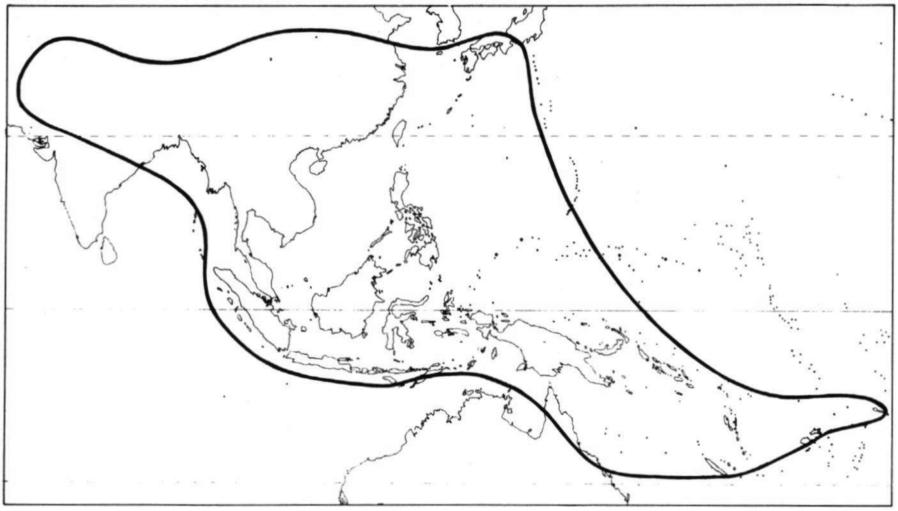


Fig. 9. Present distribution of the genus *Goniophlebium* (Blume) Presl.

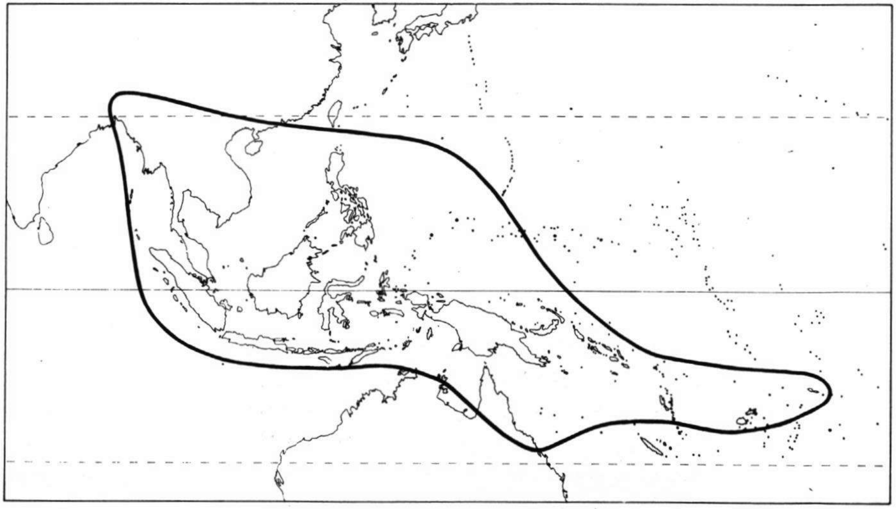


Fig. 10. Distribution area of the *Goniophlebium percussum*-group.

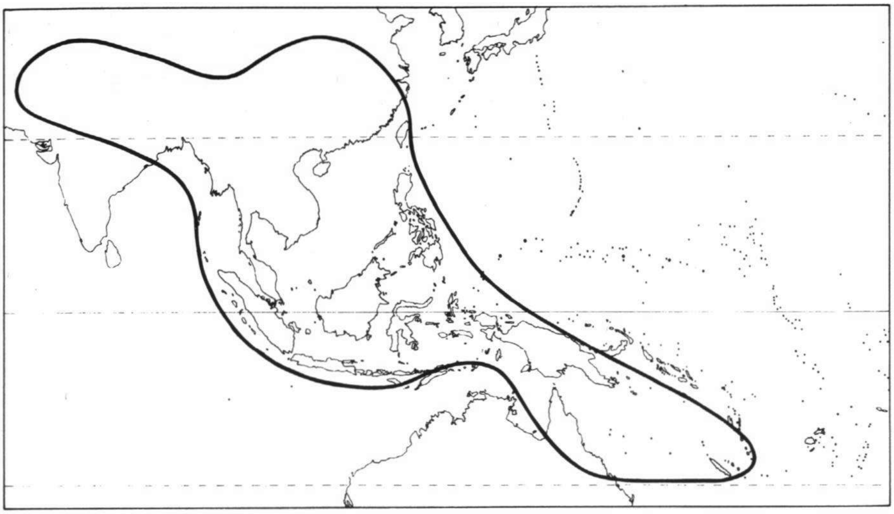


Fig. 11. Distribution area of the *Goniophlebium subauriculatum*-group.

distribution of selected groups is given. Figures 10 and 11 display the distribution areas of taxa belonging to the two largest groups of *Goniophlebium,* i.e. *G. percussum*-group and *G. subauriculatum*-group.

The *G. percussum*-group is mainly restricted to tropical Southeast Asia and does only slightly exceed the tropic of Cancer. Most of the other species are confined to Central and East Asia. However, the distribution of three of them (PR, PD, SU) overlaps the greater part of the area of the *G. percussum*-group.

The distribution of the individual species from Asia is illustrated in figures 12 to 24 on pages 319–324.

The sequence follows the list of terminal taxa as much as possible (see chapter 4.1 and fold-out page 423).

8.2. HABITAT

Kreeb (1983) stresses the influence of a complex ecological interaction on vegetation: "Die Vegetation ist nur ein Teil des gesamten Oekosystems. ... Sie wird nur verständlich, wenn alle Zusammenhänge ... berücksichtigt werden. Eine Vegetationsanalyse bedarf daher ... insbesondere der Klärung des oekologischen Wirkungsgefüges." Therefore, different aspects of environmental patterns are here discussed in association with the individual taxa. Respective patterns are adopted from Faniran & Jeje (1983), where further references are given. Faniran considered the climate classes defined by Koeppen as fairly accurate compared with others. Table 6 (on page 325) shows the species in a relation to climate classes.

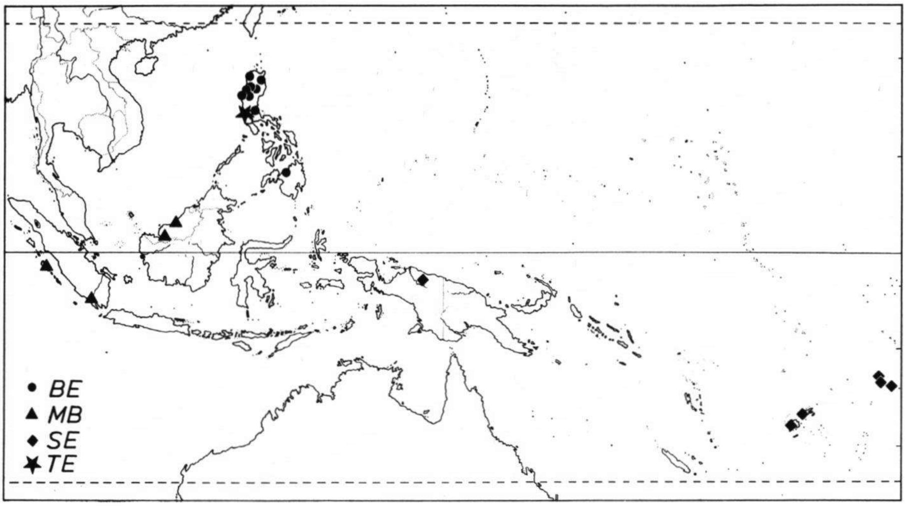


Fig. 12. Collecting sites of *Goniophlebium benguetense* (Copeland) Copeland, *G. mehibitense* (Christensen) Parris, *G. terrestre* Copeland, and *G. serratifolium* Brackenridge.

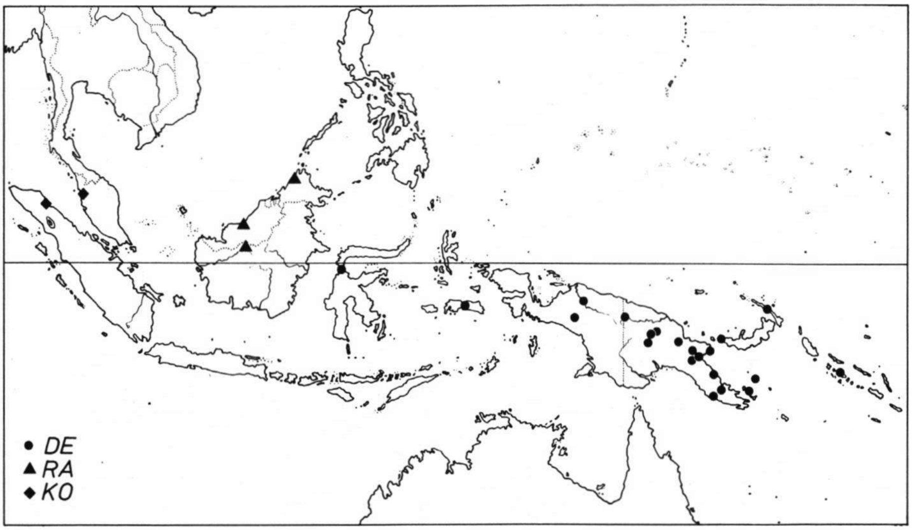


Fig. 13. Collecting sites of *Goniophlebium demersum* (Brause) Rödl-Linder, *G. korthalsii* (Mettenius) Beddome, and *G. rajaense* (Christensen) Parris.

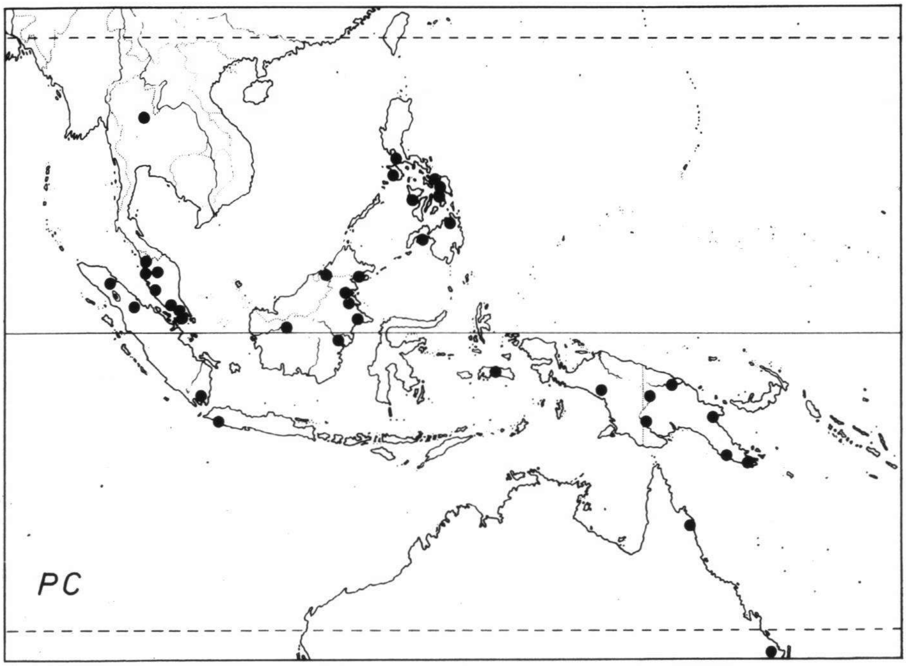


Fig. 14. Collecting sites of *Goniophlebium percussum* (Cavanilles) Wagner et Grether.

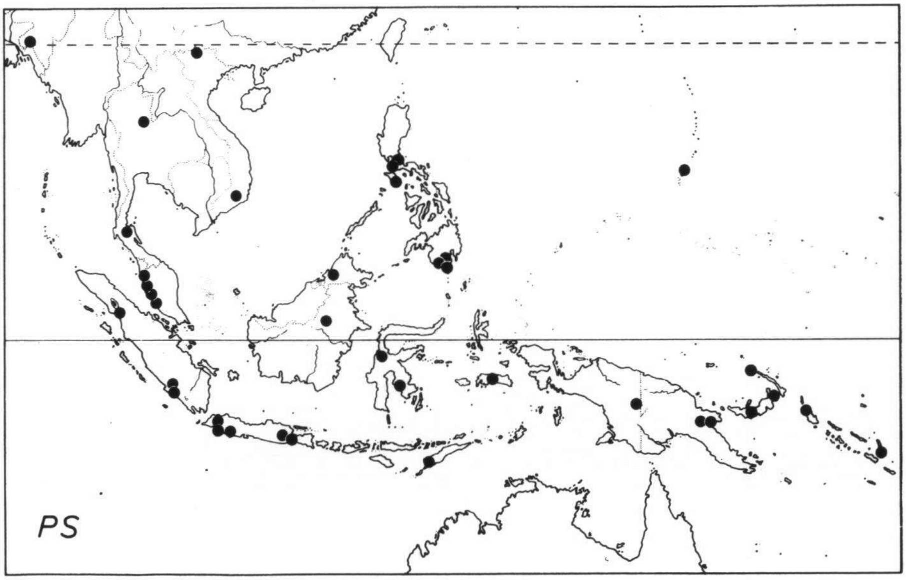


Fig. 15. Collecting sites of *Goniophlebium persicifolium* (Desvaux) Beddome.

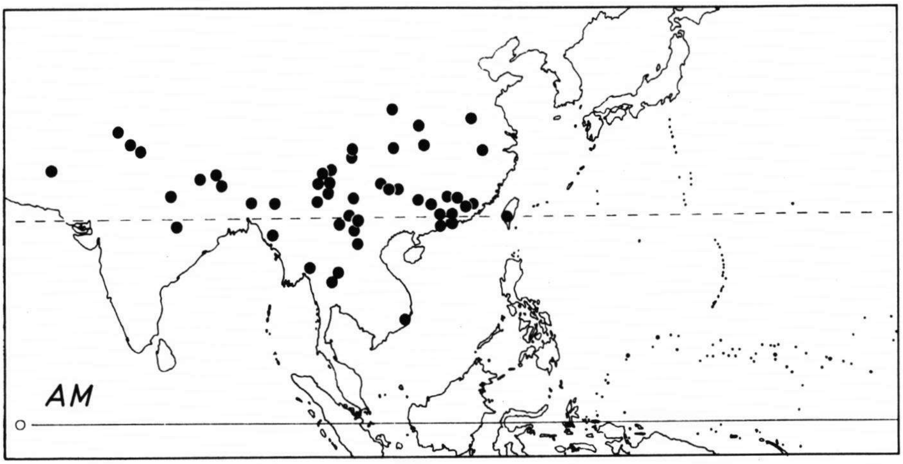


Fig. 16. Collecting sites of *Goniophlebium amoenum* (Mettenius) Beddome.

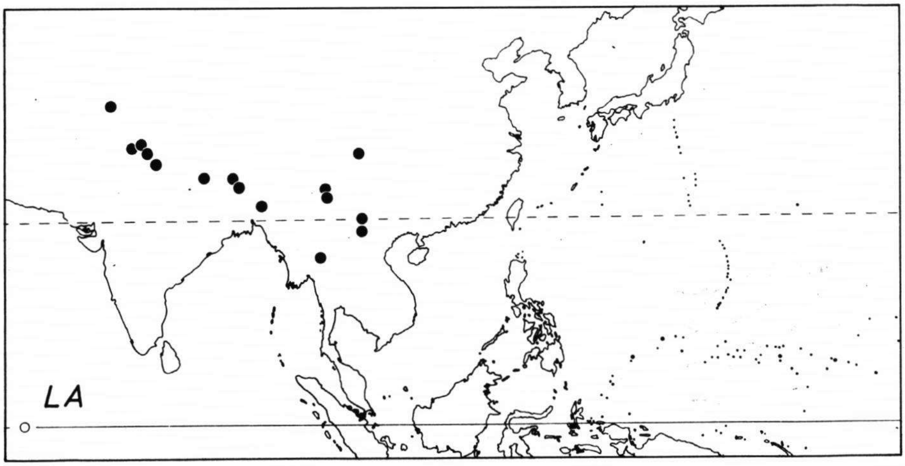


Fig. 17. Collecting sites of *Goniophlebium lachnopum* (Hooker) Beddome.

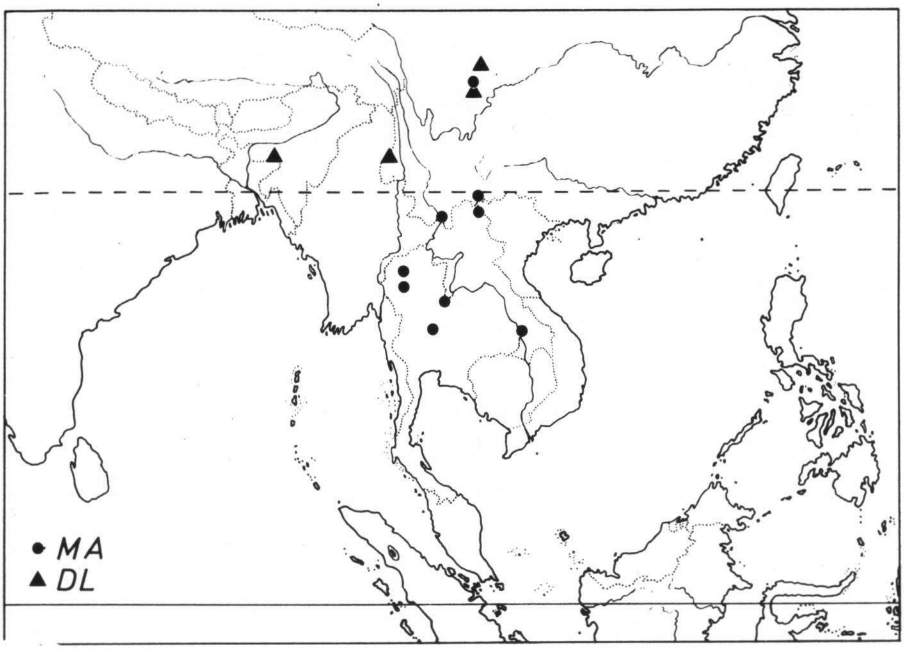


Fig. 18. Collecting sites of *Goniophlebium dielseanum* (Christensen) Rödl-Linder and *G. manmeiense* (Christ) Rödl-Linder.

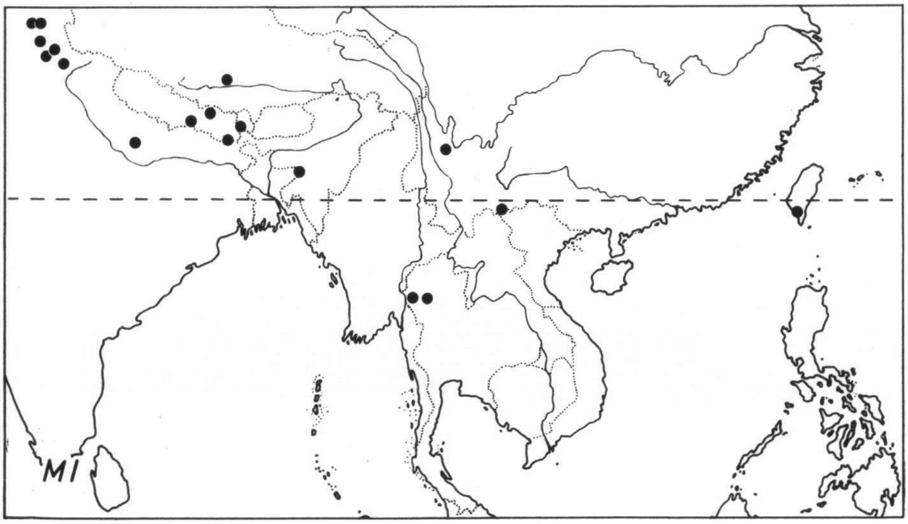


Fig. 19. Collecting sites of *Goniophlebium microrhizoma* (Baker) Beddome.

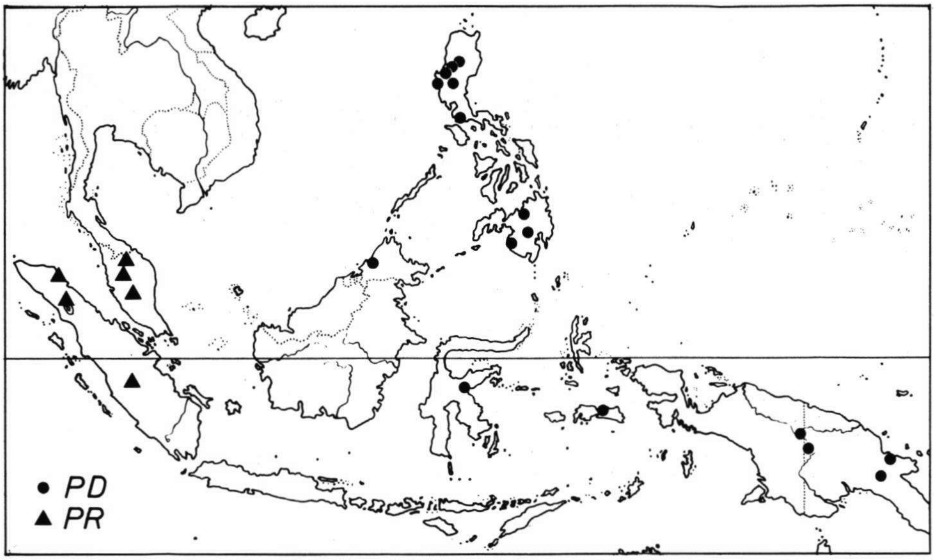


Fig. 20. Collecting sites of *Goniophlebium prainii* Beddome and *G. pseudoconnatum* (Copeland) Copeland.

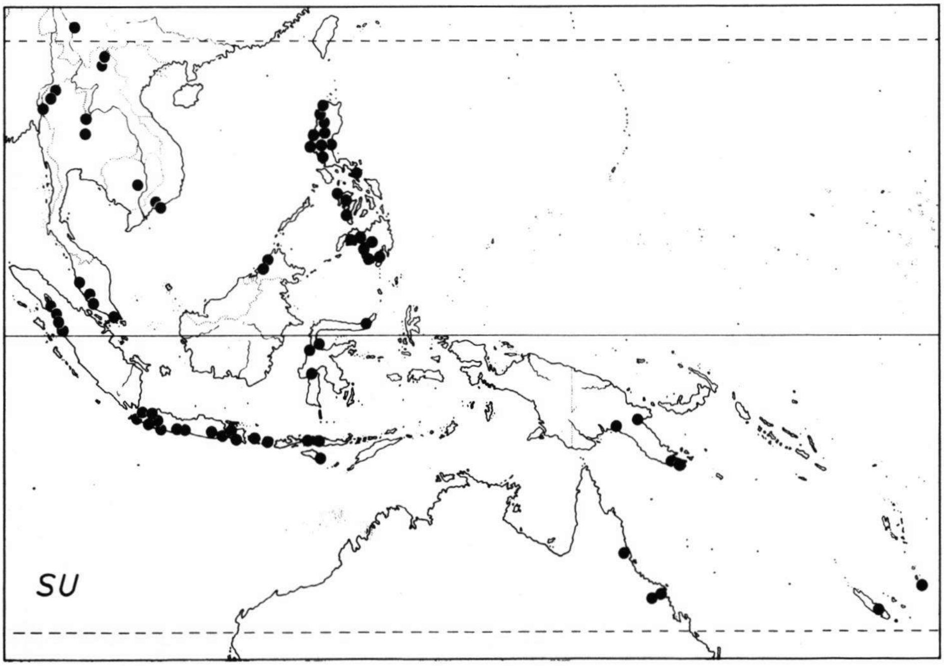


Fig. 21. Collecting sites of *Goniophlebium subauriculatum* (Blume) Presl.

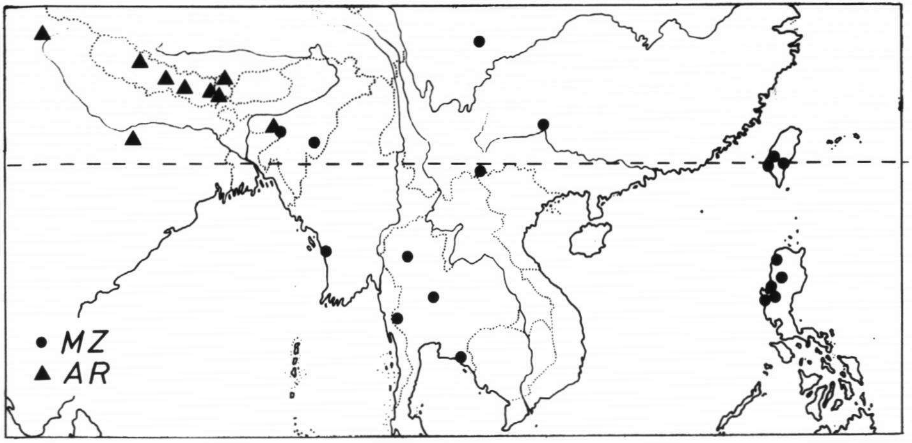


Fig. 22. Collecting sites of *Goniophlebium argutum* (Hooker) J. Smith and *G. mengtzeense* (Christ) Rödl-Linder.

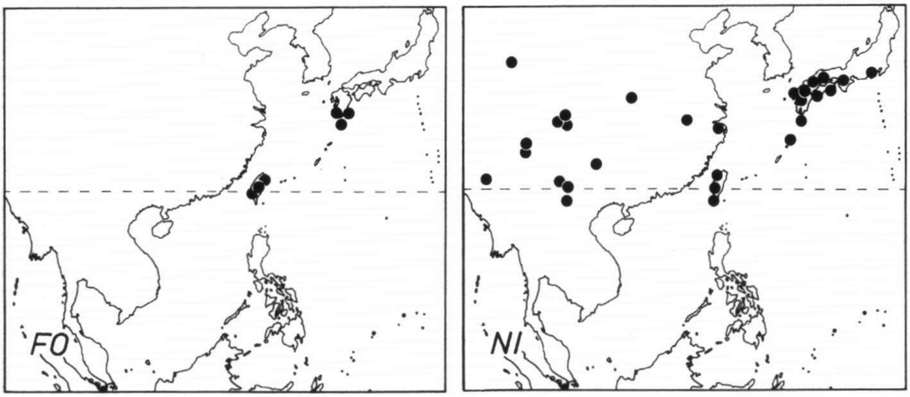


Fig. 23. Collecting sites of *Goniophlebium formosanum* (Baker) Rödl-Linder (left) and *G. niponicum* (Mettenius) Beddome (right).

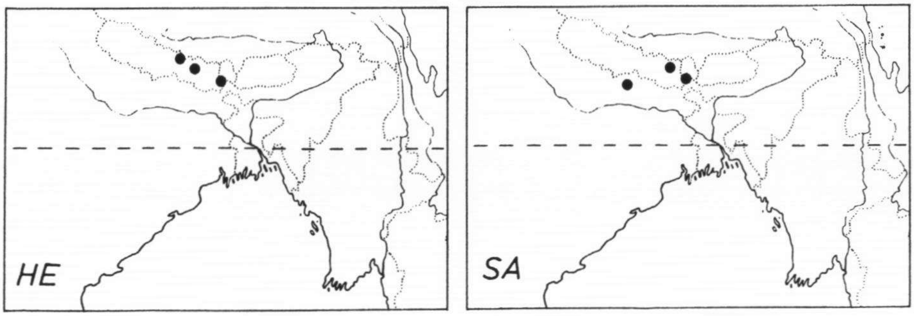


Fig. 24. Collecting sites of *Goniophlebium hendersonii* Beddome (left) and *G. subamoenum* (Clarke) Beddome (right).

Table 6. Climatic patterns applied on individual taxa.

	climate classes, after Koeppen			
species	tropical rainforest	marine west coast	humid subtropical	tropical savannah
BE	+	–	–	–
DE	+	+	–	–
KO	+	–	–	–
MB	+	–	–	–
PC	+	+	–	–
PS	+	+	(+)	–
RA	+	–	–	–
SE	+	–	–	–
TE	+	–	–	–
AM	+	–	+	+
DL	–	–	+	–
LA	(+)	–	+	–
MA	–	–	+	+
MI	(+)	–	+	–
PR	+	–	–	–
PD	+	–	–	–
SU	+	+	(+)	+
AR	–	–	+	+
MZ	+	–	+	+
FO	+	–	+	–
NI	–	–	+	+
HE	+	–	+	–
SA	–	–	+	–

As it becomes obvious from this table the *G. percussum*-group is mainly represented in tropical rainforest climate, while the majority of the other groups occurs in humid subtropical climate. Tropical savannah climate is touched by certain taxa of all but the *G. percussum*-group.

As defining criterion of the humid tropics the balance between precipitation and evapotranspiration is generally accepted. This balance is mainly influenced by temperature and moisture. The amount of rainfall is determined by several factors like form of surface, wind direction relative to coastal orientation and distance from the ocean. Faniran & Jeje (1983) gave an illustration of mean annual precipitation, which is used here as a basis for association.

The results correspond more or less with those of the climate patterns. Species of the *G. percussum*-group are confined to areas with a minimum of 1000 or 2000 mm of rainfall per year. In the other groups the majority of species occurs in regions with

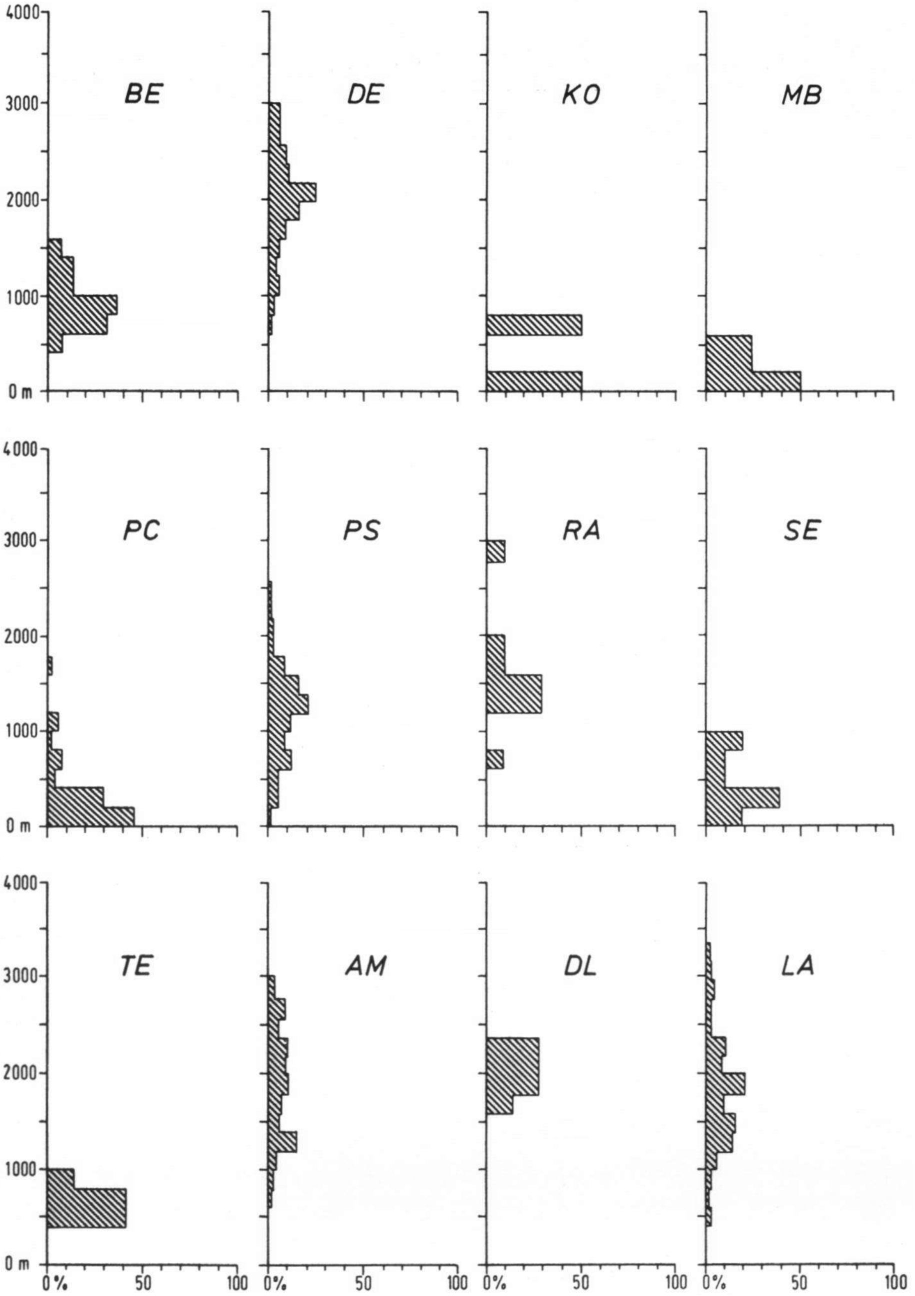


Fig. 25. Histogram of altitudinal ranges of the individual taxa. Horizontally: percentage of records (%); vertically: altitudinal zone (m).

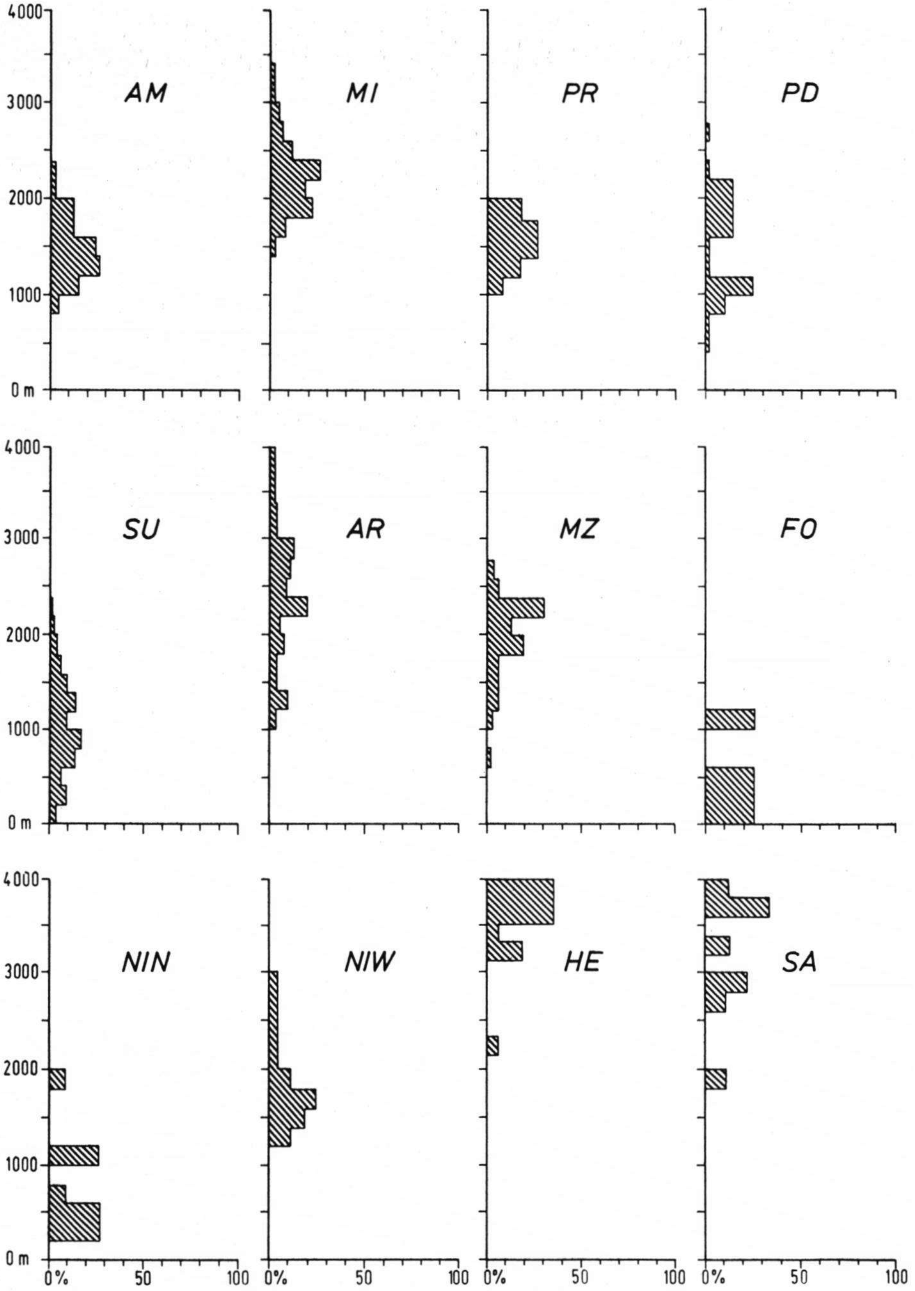


Fig. 26. Histogram of altitudinal ranges of the individual taxa. Horizontally: percentage of records (%); vertically: altitudinal zone (m).

a minimum of 1000 mm. However, a notable number of species can as well survive with less rainfall (between 500 and 1000 mm). Only PR requires more than 2000 mm rainfall per year.

The vegetation patterns of the humid tropics are characterized by forests and savannahs. The latter do not apply for *Goniophlebium*. Richards (1952) classified the plant communities 'forest' into three groups:

— tall evergreen forest or primary forest: characterized by tall buttressed emergents, interwined by lianas with abundance of epiphytes and sparse undergrowth;

— secondary forest: characterized by a thick tangle of light-loving plants, usually denser than the lower stories of the primary forest. It results from anthropogenic interference;

— dry forest: characterized by deciduousness and the presence of a shrub layer, contains (in Southeast Asia) mostly *Tectona grandis* and *Dendrocalamus gigantea.*

Most species of the *G. persussum*-group occur in the first two forest types, except DE and PS, which are also reported from the third type. On the contrary, in the *G. subauriculatum*-group only PR and PD are restricted to primary and secondary forests. All other taxa can be found in all three forest types. Giving a short view to the geological patterns it can be said that all species of *Goniophlebium* occur in areas with different kinds of sedimentary rocks or rarely with vulcanics.

The arrangement of vegetation is not only determined by longitudinal and latitudinal coordinates, but is, considering the sequence of altitudinal lines, three-dimensional. Therefore, histograms of altitudinal ranges of the individual species are given in figures 25 & 26.

The geographically widespread species from either group inhabit also large altitudinal zones (table 7).

Table 7.

PC	0 – 1650 m
PS	150 – 2200 m
AM	400 – 4200 m
SU	10 – 2400 m
NI	1300 – 3000 m

Generally, it can be noticed that sizes of distribution areas and altitudinal zones appear correlated. TE, the most limited endemic species, grows only in a range from 500–850 m. In addition, it can be pointed out that members of the *G. percussum*-group occupy in general lower altitudes than members of the other groups.

8.3. TRANSPLANT EXPERIMENTS

During the fieldwork in the Philippines the author collected representative collections of living material of all Philippine species for cultivation in her private garden in Manila (14° 21' N, 121° 00' E, alt. 30 m).

From each species at least seven living specimens were carefully sampled and all replanted within two to five days in similar soil to the one from the collecting site. Plants were watered once to twice daily. Table 8 shows the number of collection sites and respective altitudes for species used for transplant experiments.

Table 8.

species	number of sites	altitude (m)
BE	8	500 - 1500
PC	4	300 - 1000
PS	5	300 - 1500
TE	1	500 - 850
PD	5	1000 - 2400
SU	12	300 - 2400
MZ	7	1200 - 2400

For plants of PC, PS, and TE remarkable changes were not observed.

SU and BE were found to be able to survive well under different conditions. However, they adapted their phenotype under different environmental conditions. Not only altitude together with humidity and temperature, but also light exposure was found to be a morphologically determining factor. The 'mountain form' is generally small and has a firm texture. If transferred to the lowlands, it develops drooping fronds, with a thin texture. Light exposure intensifies characters which are typical for the 'mountain form'. These observations, although admittedly few in number, nevertheless do suggest a great plasticity of morphological characters.

Plants of MZ and PD reacted quite differently. The plants died despite of continuous attention given to them. The experiments with these species were repeated several times with the same result. The observations on these species rather suggest that MZ and PD are true highland plants without having the capacities to survive under tropical lowland conditions.

Additional information was obtained from the species cultivated at Utrecht. Plants of SU and BE were transferred from a greenhouse with tropical conditions to a greenhouse with temperate conditions. It was observed that in this case a plant showing a 'lowland form' could change to 'mountain form'. The reversibility of phenetic characters is understood as adaptation without genetic modification.

Referring to the classic transplant experiments of Clausen, Keck & Hiesey (1940, 1948), which already demonstrated genetic variation in response to climate, PD could have speciated from SU. An alteration of the genotype could have been caused by environmental influences. The time scale for such speciations is definitely very variable. Davies & Snaydon (1976), for example, record a period of only six years for the genetic divergence of populations of *Anthoxanthum odoratum* in response to a change in soil chemistry and competitive interactions.

9. PHYLOGENY

9.1. METHODOLOGY; PROCEDURE

The method primarily used here for phylogenetic reconstruction is developed by Zandee (CAFCA) and employs group compatibility analysis (Zandee & Geesink, 1987). Group compatibility combines the approach of parsimony and compatibility and incorporates as a method four steps:

1. recognition of cladogenetic units (clada);
2. establishment of relationship among cladogenetic units (group compatibility);
3. recognition of maximal complete sets of mutual compatible cladogenetic units (cliques);
4. evaluation of cladograms (cliques) with respect to the distribution of character states among taxa (parsimony).

The procedure is elaborated in full detail in Roos (1985) and will not be repeated here extensively. However, some explanations seem to be necessary. Following the character analysis in the present study a binary coded datamatrix was established indicating a present ('1') respectively absent ('0') condition of character states. First, the datamatrix was transcribed by the program into partially monothetic sets. A character state shared by a number of taxa defines this set of taxa (cladon). Pairs of sets of taxa that exclude or include each other are called compatible. Overlapping character state distributions within sets of taxa require additional interpretation and are not considered compatible by definition, and thus require special explanation. Between all mutually compatible groups of sets of taxa (cliques) the largest cliques were selected by the program. For a number T of terminal taxa, a fully resolved, i.e. dichotomous cladogram has T-1 internal nodes and T terminal nodes. In case the clique size is less than 2T-1 the cladogram is not fully resolved.

As the selection criterion for best cladograms the lowest value of contradiction minus support was chosen, i.e. the difference between the total number of homoplasious events (number of times the character state is required to originate independently) and the total number of character states that require only a single origin (i.e. character states that define a single node). In the present case several cladograms have similar quality (low selection value, supported by a large number of character states). The greater number of the cladograms show a continued reappearance of certain groupings. Supporting character states were examined for biological quality and tested for apo- respectively plesiomorphy by outgroup comparison. Additional biological inferences were helpful to take final decisions. Where a clear decision seemed not justified, cladograms of equal quality were taken into account.

It has to be emphasized that the search was not only for one cladogram showing the lowest value of contradiction minus support, but for one or more of the best cladograms (showing relatively low values) that are considered biologically significant.

The present method is automatically leading to rooted cladograms. According to the outgroup rule, the ingroup is monophyletic when it holds character states absent in the sistergroup and outgroup.

Such character states are apomorphous. This is the case for all clada within cladograms characterized by partially monothetic sets, with exception of the basal node. For this basal node an outgroup is not provided in the datamatrix. The supporting character states of basal clada were compared with character states found in other closely related Polypodiaceae (global outgroup comparison). At each level local outgroup comparison was applied, e.g. for the basal node of *Goniophlebium* the supporting character states were tested against the character states of the other goniophlebioids retained in *Polypodium*. For the basal node in the *G. percussum*-group the character states are tested against their presence in the species of the other groups and vice versa (local outgroup comparison).

The number of character states available relative to the number of taxa was obviously insufficient for a complete dichotomous resolution. Therefore, for several main branches a separate analysis has been run making use of all characters (secondary analysis).

Finally transformation series for character states in the cladogram chosen were set up using local outgroup comparison.

9.2. DATAMATRICES

The initial taxonomic work followed by character analysis resulted in a datamatrix of 341 character states for 117 characters using 34 terminal taxa. Two of them (NIw, TR) were finally not accepted as evolutionary species. In the first approach no character or character state was weighted a priori. Since the capacity of available computers proved to be insufficient for such a large datamatrix, CAFCA analyses had to be run independently for seven separate units, each containing characters of certain parts of the sporophyte, i.e. rhizome, rhizome scales, venation, gross morphology, frond indument, sori and spores. The number of different cladograms per unit was rather low (rhizome: 14; rhizome scales: 4; venation: 13; gross morphology: 1; frond indument: 6; sori: 9; spores: 1). However, the groupings obtained showed no clear similarities among each other. This was due to a considerable number of paraphyletic species involved. In addition, important distinguishing characters concern a few parts of the sporophyte only. Separate analyses based on certain parts of the plant can therefore not result in similar cladograms.

In order to make the datamatrix suitable for the computer capacity available, it had to be polished. The criteria applied for the polishing process, i.e. the judgement on the strength of character states were: variation within species, differentiation among species and morphological regularity, and structural complexity.

Finally used was a datamatrix comprising 90 character states for 40 characters with respect to 32 terminal taxa (table 9).

Table 9. Binary datamatrix, used for cladistic analyses.

Horizontally: terminal clada (according to table 2); vertically: character states 01–90, in complementary sets.

	AM	AR	BE	DE	DL	HE	KO	LA	MB	MZ	PC	PS	PR	PD	RA	SE	SA	SU	TE	FA	FO	MA	MI	NI	SO	VU	BR	CA	DI	FR	LO	SS
01:	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1
02:	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
03:	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0
04:	1	0	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	0	1	1	0	1	1	0	1	1	1	1	1	1	1	1
05:	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	1	0	1	1
06:	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0
07:	1	1	0	1	0	0	1	0	1	0	1	1	1	1	1	1	1	1	1	0	1	0	0	1	0	0	0	0	0	1	1	1
08:	1	1	1	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	1	1	1	1	0	0	0
09:	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	1	1	1	1
10:	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
11:	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0
12:	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	0	1	1	1	1	0	0	0	0
13:	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	1	1	1	1
14:	0	1	1	1	1	1	0	1	1	1	0	0	1	1	0	1	1	1	1	0	0	0	0	1	1	0	0	0	1	0	0	0
15:	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	1	1	1	1	0	0	1	1	1	0	1	1	1
16:	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	1
17:	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0
18:	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19:	1	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
20:	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	0	1
21:	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0
22:	1	1	0	1	0	1	1	0	1	1	1	1	1	1	1	0	1	0	1	1	1	1	0	1	0	1	1	1	1	1	1	1
23:	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0
24:	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	1	0	0	1
25:	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0
26:	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	0	0	1	0	1	1	0	1
27:	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	1	0	0	1	0
28:	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	0	1	0	1	1
29:	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	1	0	0
30:	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	0	0	0	1	0	1	1
31:	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	1	0	0
32:	0	1	0	1	0	1	0	1	0	1	0	0	0	1	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0
33:	1	0	1	0	1	0	1	0	1	0	1	1	1	0	1	1	0	1	0	1	1	1	0	1	0	1	1	1	1	1	1	1

(Table 9 continued)

	AM	AR	BE	DE	DL	HE	KO	LA	MB	MZ	PC	PS	PR	PD	RA	SE	SA	SU	TE	FA	FO	MA	MI	NI	SO	VU	BR	CA	DI	FR	LO	SS
34:	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	0	0
35:	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1	0	1	1	1
36:	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	0	1	0	1	1
37:	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	0	0
38:	1	0	0	1	1	0	0	1	1	0	1	1	0	1	1	0	1	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0
39:	0	1	1	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	1	0	1	0	0	1	0	1	1	1	1	1	1	1
40:	0	0	0	0	0	0	1	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1
41:	1	1	1	0	1	1	0	1	0	1	0	0	1	1	0	1	1	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0
42:	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
43:	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	1	0	0	0	0
44:	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	1	1
45:	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0
46:	1	1	0	0	1	1	1	1	0	1	0	0	1	0	0	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1
47:	0	0	1	1	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
48:	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
49:	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
50:	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
51:	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
52:	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
53:	0	1	0	1	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0
54:	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0
55:	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	1	1	1	1	1	1
56:	1	1	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0
57:	1	0	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
58:	1	0	1	1	1	1	1	0	0	0	1	1	1	0	1	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0
59:	1	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
60:	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
61:	0	1	1	1	0	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1
62:	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
63:	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
64:	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0
65:	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	1
66:	1	1	1	1	0	1	0	1	0	1	0	0	1	1	0	0	1	1	0	1	1	1	1	1	1	1	0	1	1	1	1	0
67:	0	0	0	0	1	0	1	0	1	0	1	1	0	0	1	1	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1
68:	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1
69:	0	0	1	1	0	0	1	0	1	0	1	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0

(Table 9 continued)

	A	A	B	D	D	H	K	L	M	M	P	P	P	P	R	S	S	S	T	F	F	M	M	N	S	V	B	C	D	F	L	S
	M	R	E	E	L	E	O	A	B	Z	C	S	R	D	A	E	A	U	E	A	O	A	I	I	O	U	R	A	I	R	O	S
70:	0	1	0	1	0	0	1	0	0	0	1	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1
71:	0	0	1	1	0	0	0	0	1	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
72:	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
73:	0	0	1	1	0	0	1	0	1	0	1	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
74:	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1
75:	1	0	1	1	0	1	0	1	0	0	0	0	1	1	0	0	1	1	1	1	1	0	1	1	1	1	0	0	0	0	1	1
76:	0	1	0	0	1	1	1	0	1	1	1	1	0	1	1	1	0	1	0	1	0	1	1	0	1	0	1	1	1	1	0	0
77:	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
88:	1	1	1	1	1	1	1	1	1	1	0	0	1	0	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
79:	1	0	1	1	0	0	0	1	0	0	1	0	1	1	0	1	1	1	0	1	1	0	0	1	0	1	0	1	1	0	1	0
80:	0	1	0	0	1	1	1	0	1	1	0	1	0	0	1	0	0	0	1	0	0	1	1	0	1	0	1	0	0	1	0	1
81:	0	1	1	0	1	1	1	0	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
82:	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
83:	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
84:	0	1	1	1	0	0	1	0	0	0	1	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
85:	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
86:	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
87:	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	1	0
88:	0	0	1	1	0	0	1	0	1	0	1	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
89:	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	0	1	1	0	0	1	1	1	1	1	0	0	0	0	0	1	1
90:	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	1	0	0

9.3. CLADISTIC ANALYSIS OF THE GONIOPHLEBIOID POLYPODIACEAE

From the datamatrix 121 partially monothetic sets can be read off. Most of these sets are defined by one single character state. The species of only few sets share two character states. The maximum cliques comprise 16 internal nodes and 0 terminal nodes which are partially monothetically defined. As the maximum clique size found (16) is much less than twice the number of taxa minus one (2T-1; in this case 65) the resulting cladograms show a considerable number of polychotomies.

All together 20 cliques were found and cladograms were selected by the CAFCA program according to their difference between the total of homoplasious events (contradiction) and the total of single origins (support). In addition, they were evaluated by judging their supporting character states and implied homoplasies. The selected cladograms as interpreted below determine the frame on the higher hierarchical level. The results serve as the basis for further cladistic analysis on the lower level.

Comparing the cladograms based on these 20 cliques, the amount of support ranges from 22 to 24, the number of contradiction from 63 and 69. Hence the value of the selection criterion (contradiction minus support) varies between 39 and 47.

As to the groupings found, there is a certain pattern to be observed. In all cladograms the following groups are built up:

group number	species
1	DE, TE, MB, PC, BE, KO, PS, RA, SE
2	LA, PD, MA, MI, AM, DL
3	FO, NI

Group 1 has to be regarded as undisputable, the affirmation will be discussed later on. Twelve of the 20 cladograms share in addition the groups 4 and 5:

group number	species
4	AR, MZ
5	DI, SS, VU, BR, CA, FR, LO, , FA, SO

Group 5 is strongly supported by character state no. 9, i.e. sclerenchyma strands in rhizome absent. Group 2 is based on character state no. 60, i.e. episporangial paraphyses present. Being rather doubtful about the homology of all types of episporangial paraphyses, whether branching from stalk or growing on capsule, the recognition of this cladon will be discussed later. Character state no. 18 (dimorphism of rhizome scales present) defining group 4 is no doubt apomorphous, as well as state no. 52 (receptacular hairy paraphyses 4–8 times branching) supporting group 3; both are regarded significant character states.

When concentrating on the higher hierarchical level there are four different types of cladograms. Three of them show identical groupings, differing in the outgroup position only. The other one places a part of the less steady grouping (group 5) in the outgroup position and integrates certain members of it (species SO, DI, LO, SS) in the ingroup and sistergroup. For each type the most parsimonious cladogram will be separately discussed.

Type 1: A cladogram with selection value 39 has group 1 in the outgroup position (fig. 27). The two supporting character states nos. 69 and 73 are morphologically correlated, i.e. all lateral segments articulate with the rhachis; terminal segment petiolate and conform with lateral segments. The other branch is supported by the complementary character state nos. 68 and 74. By the cladogram evaluation as well as the outgroup comparison with other Polypodiaceae they proved to be plesiomorphous. Therefore, the branch comprising the groups 2, 3, 4, 5 and species HE, PR, SA, SU is rejected, creating a basal polychotomy of five groups and four single taxa (fig. 28).

Type 2: A cladogram with selection value 39 has group 4 in the outgroup position (fig. 29). The single supporting character state no. 18, i.e. dimorphism of rhizome scales present, is a special feature and definitely apomorphous. The other branch is supported by the complementary character state no. 19. Therefore, this branching is also rejected; it results in the same cladogram as the first (fig. 28).

Type 3: A cladogram with selection value 42 has group 2 in the outgroup position (fig. 30). Character state no. 61, i.e. absence of episporangial paraphyses on stalk, is plesiomorphous and breaks the branching down to the same level as before (fig. 28).

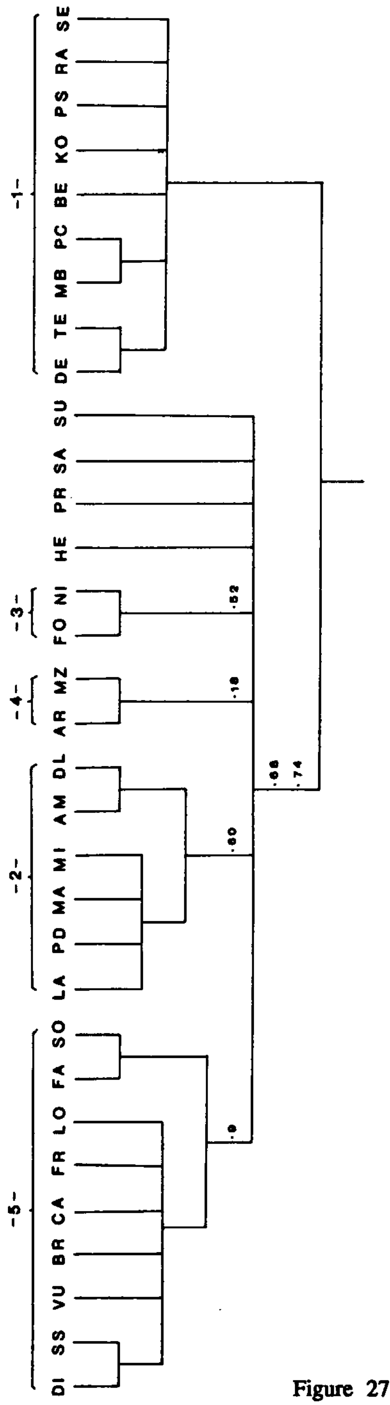

-1-
SE
RA
PS
KO
BE
PC
MB
TE
DE
SU
SA
PR
HE
-3-
NI
FO
-4-
MZ
AR
-2-
DL
AM
MI
MA
PD
LA
-5-
SO
FA
LO
FR
CA
BR
VU
SS
DI
.52
.18
.66
.74
.60
.9

Figure 27.

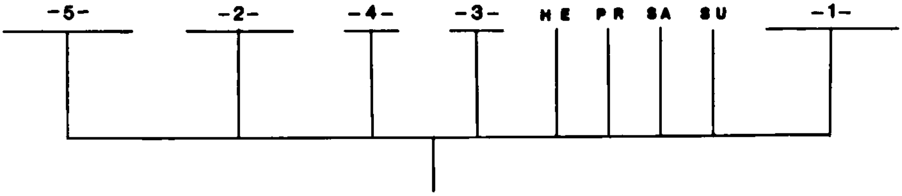


Figure 28.

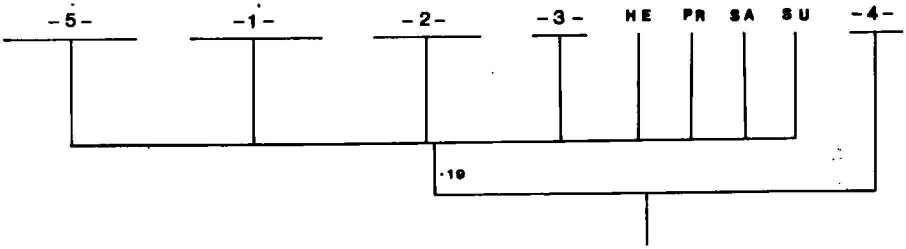


Figure 29.

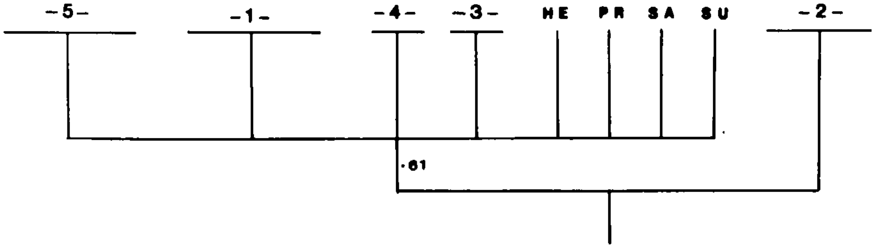


Figure 30.

Type 4: In the last type of cladogram with selection value 40 (fig. 31) a part of group five appears as outgroup. The branch comprising ingroup and sistergroup is defined by character state no. 28, i.e. marginal clathration of cell walls present, which is plesiomorphous as can be demonstrated by outgroup comparison with other Polypodiaceae. After rejecting this branch the cladogram shows a basal trichotomy. The remaining three groups are exclusively splitted according to their respective surface of exospore. This support is rather weak, since an artificial classification based on only one type of character would result. Hence it is not selected.

DI and SS, two closely related American species, deserve special notice. They show similarities with some of the Asian goniophlebioids in two aspects, i.e. the crestate perispore and the possible presence of clathrate marginal protrusions at the

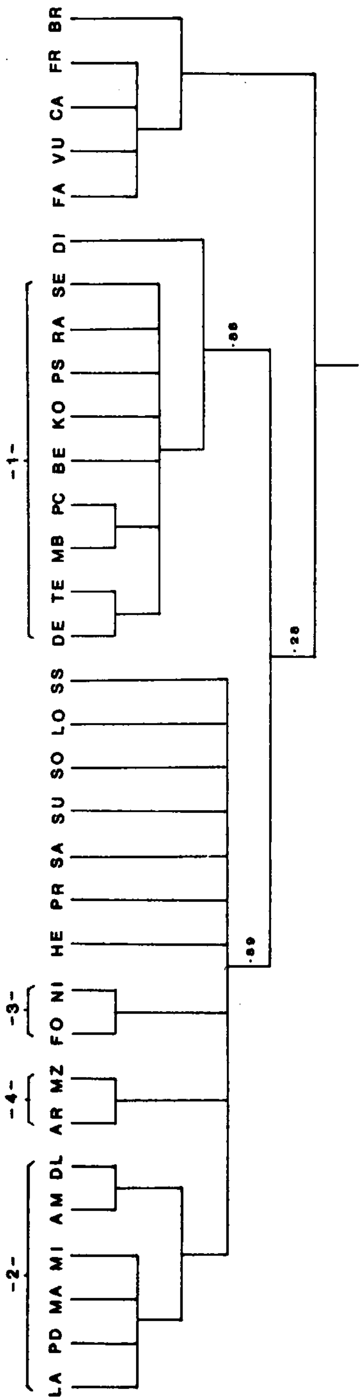


Figure 31.

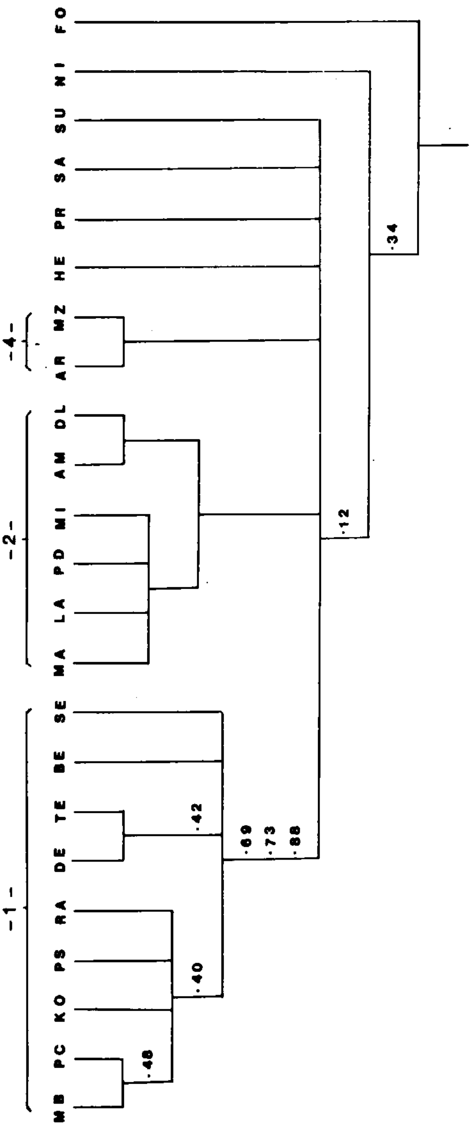


Figure 32.

rhizome scales. However, the absence of sclerenchyma strands in the rhizome and of any sterile structures in the sori seem to justify their position within group no. 5. Hence, the similarities have to be assumed as being the result of parallel development.

So far only one cladogram (fig. 28) remains. This cladogram shows a basal polychotomy and since no outgroup has been detected, the analysis could be considered as arrived at a dead end. However, there are reasons enough to set apart group 5 at this point. Assuming reversals for the development of receptacular sterile structures in FA and SO, the combination of character states nos. 9, 50 and 55 are considered a strong support for accepting group 5 as an outgroup, especially with respect to the representation of characters concerning the vegetative as well as the reproductive part of the plant. In addition the striking geographical distinction has to be taken into account. Members of this group occur mainly in tropical and to a smaller extent in subtropical America with an extention of species FA and SO to Japan. Paying attention to the hypotheses of origin and migration of the Polypodiaceae as stated by De la Sota (1973) there is another reason to favour this splitting. This topic shall be discussed later on. The taxa combined in group 5 are considered paraphyletic and represent only a small selection of the American species concerned. There is a chance of finding more support, when comparing *Goniophlebium* with possible monophyletic groups or eventually new genera (R. Hensen, Utrecht, in preparation). This choice of outgroup is also in accordance with the latest results of studies on the *Polypodium vulgare*-complex which were executed applying advanced methods. The electrophoretic mobility of genetic markers, e.g. isozymes or allozymes, was used to resolve difficulties in this respect (C.H. Haufler, Kansas). Accordingly it is suggested to retain the species of group 5 in the genus *Polypodium*.

Group 1, as defined in the basal cladogram (fig. 28) comprises a monophyletic group. As stated before, this group is represented in all selected cladograms (and in the analysis of the unpolished datamatrix run on gross morphological characters as well).

However, the problem is posed by the remaining 7 branches. When group 5 is excluded, new partially monothetic sets of terminal taxa can become possible which are not present in the overall analysis. For that reason a cladistic analysis without the *Polypodium* species has been run.

9.3.1. Cladistic analysis of Goniophlebium

The best cladogram (fig. 32) coincides in principle with the basal cladogram (fig. 28), but separates the two members of group 3 (NI, FO) in different levels. Group 1 reaches a higher degree of resolution.

Character state no. 34 is considered apomorphous if compared to the species retained in *Polypodium*. For SO, a critical species from Japan, a reversal for this character state has been assumed. Character state no. 12 is a strong support for the branch containing group 1, 2, 4 and HE, PR, SA and SU (fig. 33). The critical position of SO shall be discussed later on.

Another cladogram (fig. 34) gives an interesting option, even though it is less plausible by its selection value. In this case group 1 and the rest of the species repre-

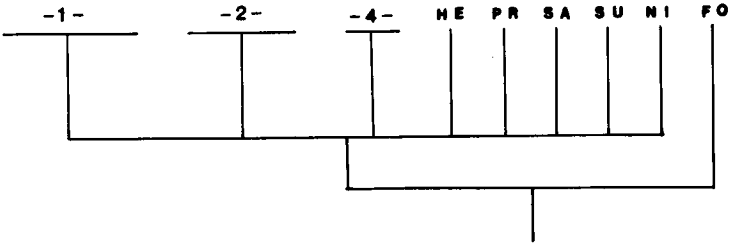


Figure 33.

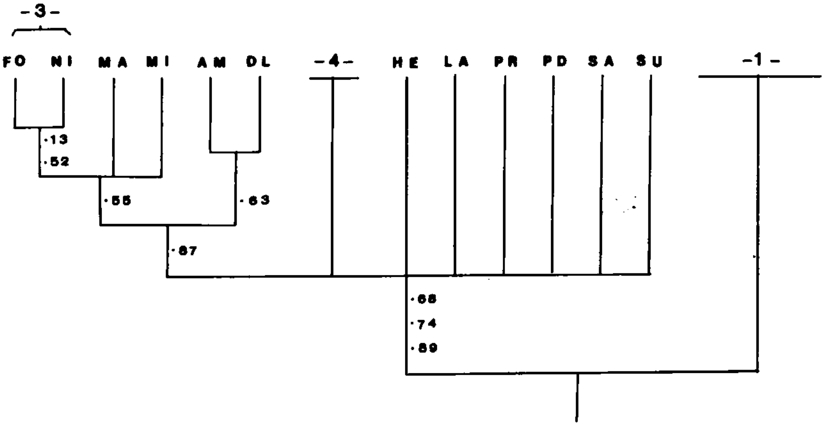


Figure 34.

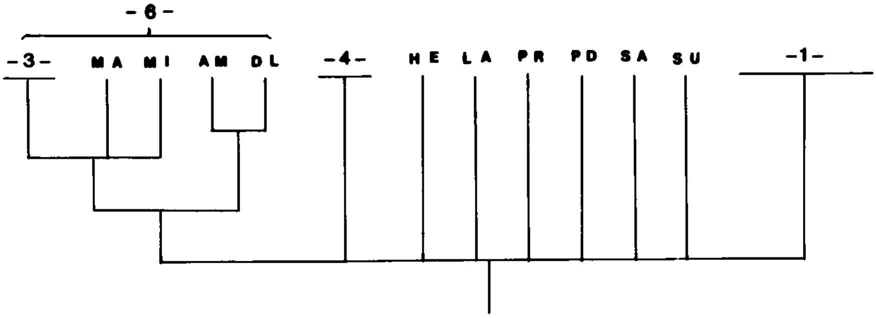


Figure 35.

sent sister groups. The two basal branches are supported by three complementary character states each. Conditions 68 and 74 are morphologically correlated, as discussed earlier, and are both plesiomorphous when compared with the outgroup. Character state no. 89, i.e. exospore with globular excrescences, is also a plesiomorphous condition. For this reason this branch has to be broken down (fig. 35).

The former group 2 is split and newly combined with NI and FO instead of LA and PD. AM and DL build a very robust subtree, being paired in 100% of the cladograms and based on character state no. 63, i.e. scaly episporangial paraphyses branching from the stalk. This structural novelty has not been observed before. The cladon including FO, NI, MA and MI is well defined by character state no. 55.

The branch comprising group 3, MA, MI, AM and DL, is supported by a common spore type (*amoenum*-type, plate 4b) and here called group no. 6. Character state no. 87 concerns only the inconspicuous perispore but for all taxa of this branch this condition is combined with an exospore with globular excrescences. This unique combination of character states (strictly monothetic set) acts apomorphously when compared with the outgroup, again assuming a parallelism for the critical species SO. However, the value of exospore and perispore characters is considered rather low within the family of Polypodiaceae due to their liability to parallel developments (Hennipman, 1990, in press).

Especially when character states have been sorted out beforehand, the value of contradiction minus support cannot stand as sole selection criterion. For this reason both resulting cladograms have been accepted attending to their biological inferences and implied homoplasies. No decision was taken at this stage in favouring one of the two. Therefore, separate analyses for the undisputed group 1 and for the group comprising the remaining taxa have been executed.

9.3.2. Cladistic analysis of the Goniophlebium percussum-group

This group was never suggested before and is considered here a monophyletic group. Apparently the relationships within this group are difficult to trace, in view of the large number of cliques found (84).

Apart from the set of nine terminal taxa, the analysis of the *G. percussum*-group resulted in 39 partially monothetic sets. Compared to the overall analysis respectively more sets are now defined by two or three character states. For these 39 sets, a total of 84 cliques comprising 11 nodes (6 internal and 5 terminal nodes) were discovered. This is less than 2T-1. That means that the resulting cladograms are still not completely resolved.

The number of supporting character states varies from 31 to 39, the number of homoplasies from 12 to 16. The overall values of contradiction minus support reach from –15 to –27.

Out of the most parsimonious cladograms (criterion values: –27, –26, and 6 with 25) the two best were chosen. They display different groupings except for the species pair MB and PC, which is steady also in almost all cladograms of other analyses. The amount of support is for both cliques 39, the number of implied homoplasies 12 and 13. The first cladogram (fig. 36) separates BE at its base. Both supporting character states of the branch comprising the other eight taxa, nos. 7 and 53, prove to be plesiomorphous, when compared to the outgroup. Accordingly, this cladon has to be rejected.

The next level cladon is defined by a single character state, no. 22, referring to the presence of round basal flaps on the rhizome scales. Also this branch cannot stand

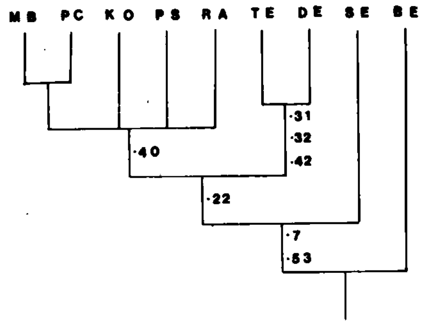


Figure 36.

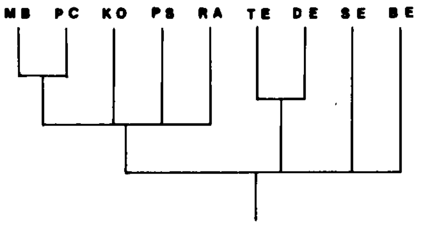


Figure 37.

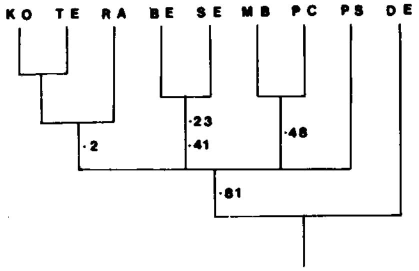


Figure 38.

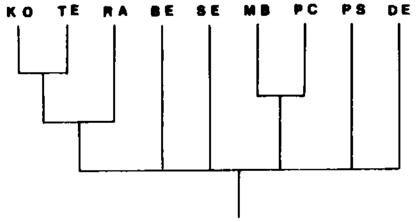


Figure 39.

when tested by outgroup comparison. MB, PC, KO, PS and RA are combined in one cladon due to their common venation type (*percussum*-type). This condition is apomorphous within all true *Goniophlebium* species. The cladon pairing TE and DE is partially monothetically defined by three character states. Condition 31 is scored as well for one species of the *G. subauriculatum*-group (DL). Nevertheless, this represents a strong support considering the lacerate appearance of the basal flaps of rhizome scales in TE and DE compared with those of DL. This is due to the combination of condition 31 and the length of cells in the basal flaps. Character state no. 32, i.e. hyaline/colourless cell lumen in rhizome scales, is considered ambiguous and plesiomorphous. Character state no. 42, i.e. the type of venation with a row of enlarged areoles and almost no marginal free veins, is significant and apomorphous. Following this interpretation the resulting cladogram pictures four basal polychotomies (fig. 37).

The second cladogram under discussion (fig. 38) separates DE at its base. The cladon with the other eight taxa is supported by character state no. 81, a weak character state which is found plesiomorphous when compared with the outgroup. The combination of the three terminal clada KO, TE and RA is based on the presence of a slender, dorsiventrally flattened rhizome, which is regarded apomorphous. The cladon uniting BE and SE is supported by the two plesiomorphous character state

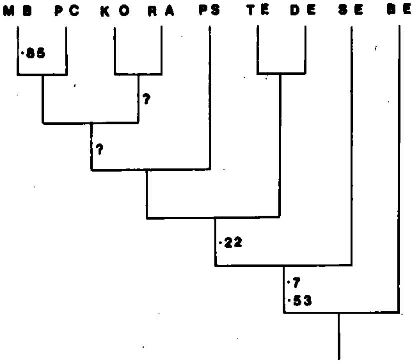


Figure 40.

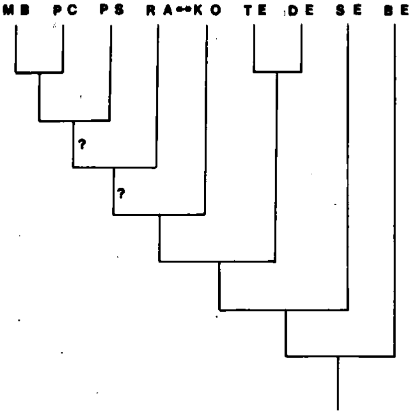


Figure 41.

nos. 23 and 41 and is therefore rejected. The cladon comprising MB and PC is well defined by character state no 48. Consequently, the resulting cladogram (fig. 39) displays six basal branches.

The first of the two resulting cladograms is best supported, however not fully resolved. It is exactly congruent with group 1 in chapter 9.3.1 and was chosen for a secondary analysis.

In the secondary analysis three cladograms of equal quality were found. They are fully resolved but some of the clada cannot be partially monothetically defined. Two cladograms are pictured in figures 40 & 41. The third one shows KO and RA in exchanged positions. In all three cladograms two internal and four terminal nodes remain undefined. Obviously in the polished data matrix there were not enough character states available. However, it was possible to find adequate support with strictly monothetical sets, i.e. unique combinations of character states.

This procedure was managable by computer for the five most critical species only (MB, PC, PS, RA, KO). Since the differences in value of the selection criterion are to be neglected (–34 to –36), there is no reason to favour one of the three options. The cladogram depicted in figure 41 is used here to continue with the analyses. The cladon comprising MB, PC and PS is based on a unique combination of 32 character states. The cladon comprising MB, PC, PS and RA is defined by a strictly monothetic set of 31 character states. The cladon comprising MB, PC, PS, RA and KO is supported by the combination of 28 character states. Also all terminal taxa can be defined this way.

9.3.3. Cladistic analysis of Goniophlebium, excluding the G. percussum-group

The analysis of the Asian *Goniophlebium* species excluding the *G. percussum*-group results in the recognition of 61 partially monothetic sets excluding the set of all 14 terminal taxa. These partially monothetic sets were ordered into five maximum cliques with a clique size of 15 (10 internal and 5 terminal nodes). The resulting

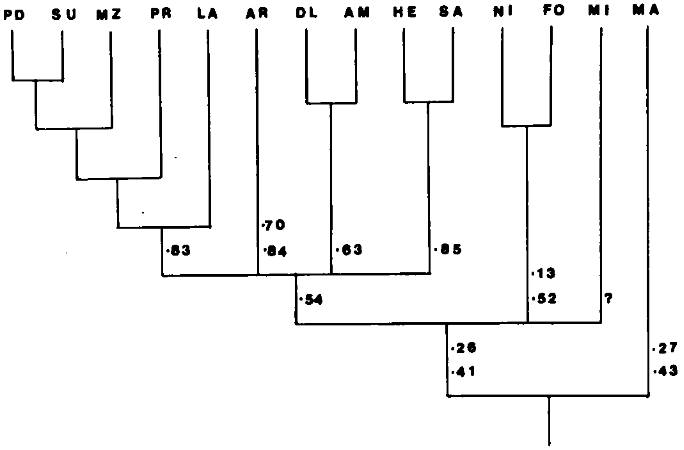


Figure 42.

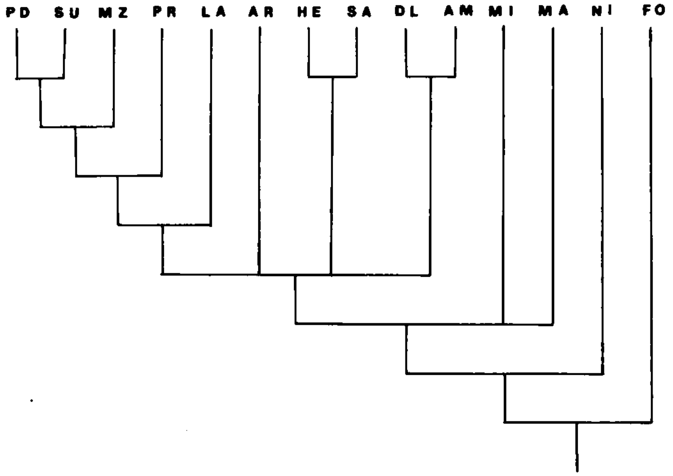


Figure 43.

cladograms are not fully resolved. The selection value between −5 and −10 was calculated on the basis of contradiction (27 to 29) minus support (34 to 37). After evaluation of the best cladogram (fig. 42) with a selection value of −10 and the second best (fig. 43) with a selection value of −8 the resulting cladograms were found more or less equal. The difference concerns a well supported combination of NI and FO in the more parsimonious case. The cladon uniting all taxa concerned

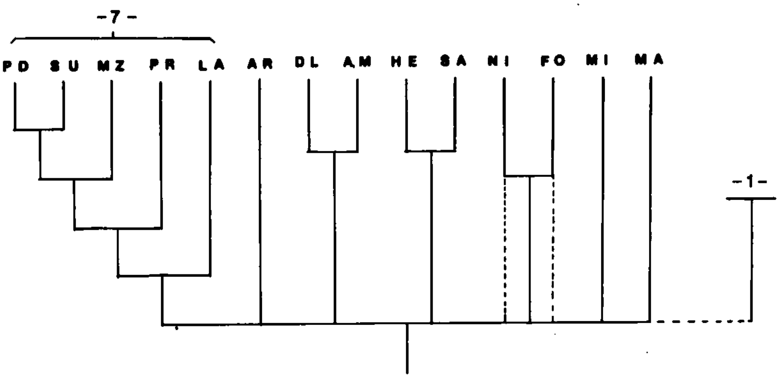


Figure 44.

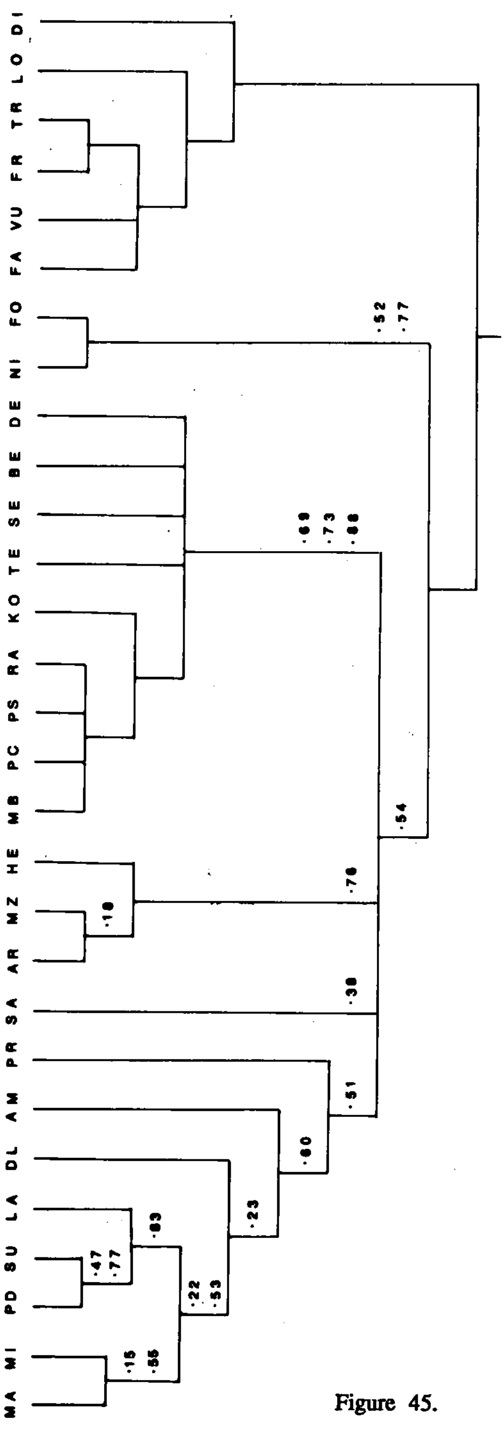
except MA is based on character state nos. 26 and 41. Character state no. 26 has to be interpreted as plesiomorphous when compared with the *G. percussum*-group. Character state no. 41 refers to the type of venation (*subauriculatum*-type), which is met also in two taxa of the outgroup (BE, SE). This fact suggests the rejection of the basal branch. The next level branch, defined by the plesiomorphous character state no. 54, has as well been broken down. The resulting diagram is shown in figure 44.

The remaining branches are apomorphously supported. The new group comprising PD, SU, MZ, PR and LA is here called group 7. It deserves notice that the earlier frequently found grouping of LA, PD, MA, MI, AM and DL (group 2 in chapter 9.3) does not reappear here. This fact could justify the assumption of the different types of episporangial paraphyses not being homologous structures. Surprisingly the earlier constant pairing of MZ and AR (group 4) is not represented in any of the five maximum cliques, although closest relationship is well supported.

Unlike the cladogram of the *G. percussum*-group, the resulting cladogram of the present group is not fully resolved, even when based on strictly monothetic sets. This fact can indicate either a paraphyly of the present group, or point to an insufficiency of the character states. The resolution achieved is equal to the resolution in the overall analysis. Consequently, there are now three larger groupings suggested besides of the *G. percussum*-group, i.e. group no. 2 (MA, MI, PD, LA, AM, DL) in figure 33, group no. 6 (NI, FO, MA, MI, AM, DL) in figure 35, and group no. 7 (PD, SU, MZ, PR, LA) in figure 44. There are, however, no biological reasons to favour any of them.

9.4. CHOICE OF THE CLADOGRAM OF THE GENUS GONIOPHLEBIUM

Integrating the results obtained through separate analyses of the groups, there are the three cladogram options. To facilitate a decision, two additional cladistic methods, i.e. HENNIG86 (Farris, 1988), and PAUP (Swofford, 1985) were applied.


DI
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TE
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·52
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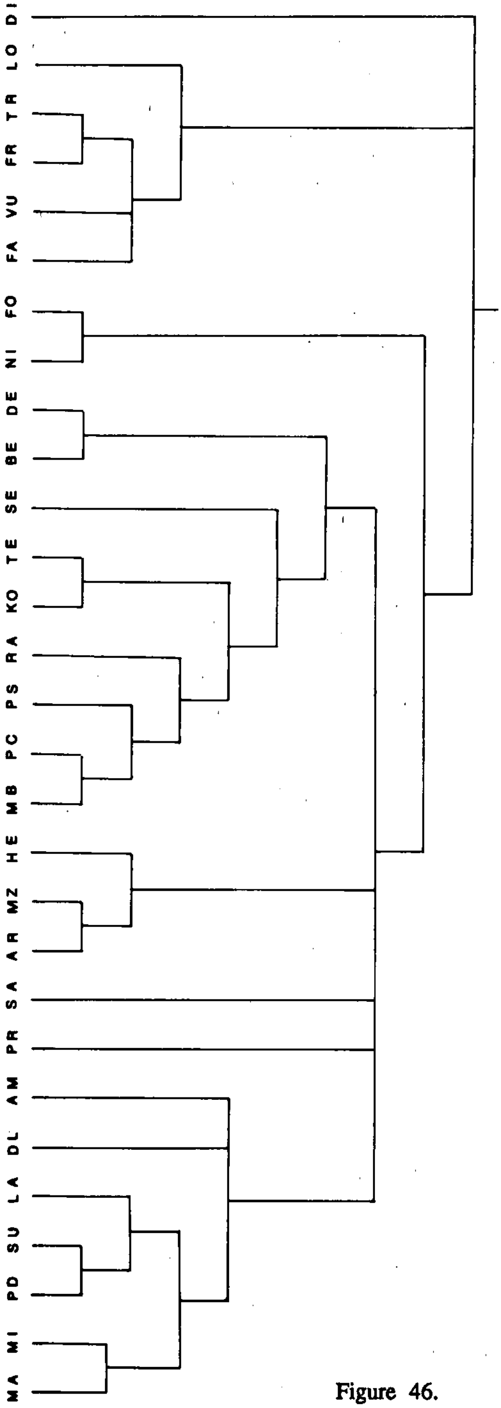
Figure 45.


DI
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AR
SA
PR
AM
DL
LA
SU
PD
MI
MA

Figure 46.

These two computer programs use the same method. They follow the Wagner criterion, i.e. the principle of maximum parsimony, and need the a priori designation of an outgroup. This means that the starting characters of the transformation series are already defined, since the character states of the outgroup are plesiomorphous by definition. An initial tree is calculated, in which taxa are arranged according to their phenetic similarity. Branch swapping helps to find equally or more parsimonious trees. Certain algorithms are used to ameliorate the efficiency and effectiveness of the programs. These two methods result in consensus trees, which are presented in figures 45 & 46. In all cases the *G. percussum*-group is monophyletic and well defined, whereas the group of remaining species appears paraphyletic and variously grouped. The *G. percussum*-group is situated at a lower level than NI and FO. According to the resulting cladograms found with HENNIG86 and PAUP, NI and FO take an uncertain generic position. As to the CAFCA analyses, these two species or at least NI are included in the genus *Goniophlebium.*

The supporting character states in the PAUP consensus tree are marked. Many of the internal clada were discussed earlier. The branch comprising AR, MZ and HE is only weakly supported. Character state no. 76, i.e. deflexion of the lowermost pinnae absent, is not accepted as sole support due to its variability in other species. Character state no. 38 at the base of SA, i.e. surface indument on rhizome scales present, implies homoplasies in many cases and is therefore not considered a strong support either.

In CAFCA, HE and SA represent sister taxa due to the *hendersonii*-type of perispore. They have similar distribution and habitat and are morphologically difficult to distinguish (see taxonomic part). They have not been grouped with other species in CAFCA. The *hendersonii*-type of perispore is conspicuously crestate as in SU, PD, MZ, AR, PR and LA, even though the crestae are locally protruding (plate 4a). This could serve as a reason to incorporate HE and SA in group 6.

The cladon including MA, MI, PD, SU, LA, DL, AM and PR is well supported by character state no. 51, i.e. receptacular hairy paraphyses 1 or 2 times branching. The next lower level is based on character state no. 60, i.e. episporangial paraphyses present. MA, MI, PD, SU and DL are combined due to character state no. 23, i.e. basal flaps of the rhizome scales pointed. PD, SU and LA share the important character state nos. 56, 59 and 83.

Most similarities with the HENNIG86 and PAUP consensus trees can be detected in the CAFCA cladograms in figure 28, respectively in figure 33. However, the CAFCA tree does not pair PD and SU as sister species, which is, however, strongly supported by biological and geographical data (see taxonomic part) and therefore accepted.

In the CAFCA cladogram in figure 44 the position of AR is not satisfying. Due to the cuneate basal shape of lateral segments and the *percussum*-type of perispore, AR has been placed on its own. These two character states are common in the *G. percussum*-group and parallel developments have to be assumed. In all but the cladistic analyses, discussed in chapter 9.3.3, MZ and AR represent sister taxa. The same situation results from HENNIG86 and PAUP. The two species share obvious synapomorphies, i.e. the unique appearance of superposed dimorphous rhizome scales and the adnate-conform terminal frond segment. Therefore, it has been decided to accept MZ and AR as sister taxa. MZ and AR share character state no. 3, i.e. rhizome chalky or glaucous, with PD and SU. In addition, these four species share character state nos. 56 and 59, i.e. receptacular scaly paraphyses peltate and round, with LA.

No objections were brought foreward against the cladogram in figure 35. Group 6 and group 7 are exclusively supported by exospore and perispore characters. In addition these two groups were not found combined in any of the cladograms, even though the author would have intuitively favoured these groupings.

For the time being the author likes to suggest a phylogenetic tree based on the best groupings in PAUP, HENNIG86 and CAFCA (figs. 45, 46 & 47).

Although NI and FO represent themselves in an uncertain generic position as to PAUP and HENNIG86, following CAFCA results these two species were included in the genus *Goniophlebium*. Thus, *Goniophlebium* has to be accepted as a genus with actually five groups, the *G. percussum*-group, the *G. subauriculatum*-group, the *G. argutum*-group, the *G. hendersonii*-group and the *G. niponicum*-group.

CAFCA was chosen as a quite objective respectively strict approach to trace phylogenetic relationships within a group of related species. In contrast to HENNIG86 and PAUP, it is a restricted parsimony method which requires an extra assumption in the case of a lost character state, and applies compatibility. Different tree selection criteria can be chosen. Consequently, the minimum length tree is not necessarily accepted as the best tree. Outgroup taxa can be included in the analysis and results are not influenced by arbitrary or erroneous polarity decisions made a priori. Since CAFCA proposes a set of possible alternative cladograms, the researcher is obliged to reconsider his biological inferences used for character state distinction. Choices are made by considering auxiliary motives as biogeographical patterns and ecological or evolutionary processes. In the ultimate phase of defining the phylogenetic tree subjective criteria might even dominate, but at this point the choices are already clearly limited.

9.5. TRANSFORMATION SERIES

Transformation series are based on the phylogeny which is pictured in figure 47 and were established a posteriori. As commented upon in chapter 10.2, the modification of character states in the course of evolution can only be traced in monophyletic groups. Character states implying several homoplasious events are neglected. It is remarkable that for all micromorphological characters the amount of parallelisms and reversals appears very high. Consequently, only a few important transformation series are given for the two major groups. The sequence of character states follows the one of chapter 4.1.

Rhizome terete → dorsiventrally flattened; this transformation occurs only in the *G. percussum*-group. For all species of the *G. subauriculatum*-group the rhizome is terete.

Rhizome colour brown → chalky; this transformation occurs only in the *G. subauriculatum*-group. All species of the *G. percussum*-group have a brown rhizome.

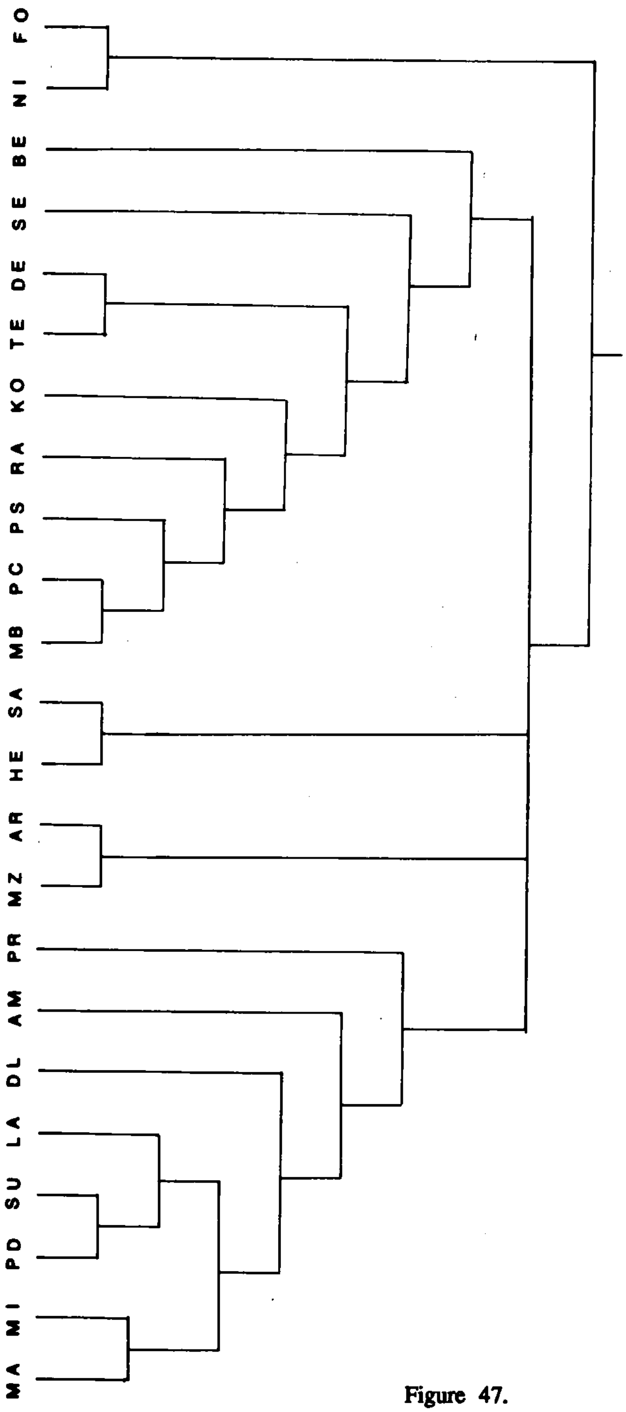

Figure 47.

Venation *subauriculatum*-type → *terrestre*-type → *percussum*-type; this transformation occurs in the *G. percussum*-group.

Venation *subauriculatum*-type → *vulgare*-type; this transformation occurs in the *G. subauriculatum*-group.

Receptacular scaly paraphyses present → absent; this transformation occurs in the *G. subauriculatum*-group only. In all species of the *G. percussum*-group receptacular scaly paraphyses are present.

Blade widest medially to subbasally → basally; this transformation occurs in the *G. percussum*- and in the *G. subauriculatum*-group. In the latter case it is followed by a reversal.

Articulate lateral segments basally truncate (cordate) → cuneate; this transformation applies only for the *G. percussum*-group.

10. THE MONOPHYLY AND SYSTEMATIC POSITION OF GONIOPHLEBIUM

10.1. DELIMITATION OF THE GENUS

A modern systematic approach to describe taxonomic units is the search for concepts which are based on genetic discontinuities in the course of evolution. As is concluded from the symposium on the 'Species concept in Pteridophytes' (Haufler, 1989), ongoing studies are continuously modifying the theoretical and practical perception of species. Therefore, dynamic definitions are needed as working hypotheses.

A genus is here understood as a passive historical entity resulting from continuing evolution. The ancestral species and all its descendents, when recognized as a monophyletic group of species, can be combined in a genus.

In order to elucidate the delimitation of the goniophlebioids as to genera, a larger array of species was at first included in the study of the goniophlebioids, including all representatives from the Himalayas and Eastern Asia as well as a selection of species occurring in the New World tropics.

If a classification is really natural and a genus is regarded as an evolutionary entity of species the author agrees with the hypothesis of Copeland (1915: 155): "The so-called *Goniophlebium* of the American tropics can in no way bear the name of the real *Goniophlebium* of the Old World ..." and "... the species assigned to *Goniophlebium* in America do not themselves represent a single line of descent." In contrast, Ching (1933) considered the New World species belonging to a phyletically natural distinct line of descent, which was treated under *Lepicystis* J. Smith by Diels. The results of the present study rather support Copeland's intuitive views. Regarding Ching (1933) it can be mentioned that this author confined himself to the species with peltate, orbicular rhizome scales. The generic delimitation of *Goniophlebium* needs discussion in view of the existence of a number of species not dealt with in detail by Copeland and Ching.

The rhizome scales of the neotropical species DI and SS resemble those of true *Goniophlebium*. They are in all cases pseudopeltate and deltoid. The rhizome scales of FO hold a somewhat distinct position for their lack of marginal clathrate protrusions. These are characteristic for all other species accepted in *Goniophlebium*, while they are absent in all American goniophlebioids. Clathration of cell walls occurs in Asian and American species, but not in FA, CA and VU (*Polypodium vulgare*-complex p.p.).

A real critical position is held by SO, an endemic species of Japan. It is retained in *Polypodium* here, due to the absence of sclerenchyma strands in the rhizome. This condition, which is not apomorphous when applying global outgroup comparison, is shared by all American goniophlebioids and the Asian species SO, FA and VU. The venation of SO is attributed to the *vulgare*-type. Contrastomium cells were found, an apomorphous condition shared with FA which is also endemic to Japan. Nevertheless, a number of other character states connect SO with *Goniophlebium*, e.g. the presence of receptacular hairy and scaly paraphyses which are absent in all American goniophlebioids. Only some members of the *Polypodium vulgare*-complex have hairy paraphyses. The characteristics of the rhizome scales of SO correspond fully with those described for *Goniophlebium*. The same is the case for the *amoenum*-type of exospore and perispore, which would place SO somewhere between AM and MI, if it was integrated in *Goniophlebium*. So far, it can only be assumed that a number of homoplasious events have taken place, which brought this taxon in an ambiguous systematic position.

As elaborated in the taxonomic history, the group under study has been subdivided by earlier authors in different ways. Ching (1933) criticized Copeland's (1929) generic separation of *Goniophlebium* from *Polypodium*, which was based on the articulate nature of the lateral pinnae. Ching considered such a distinction as entirely broken down in the presence of partly pinnate species. He suggested the two sections *Eupolypodium* and *Goniophlebium* within *Polypodium*, based on free respectively goniophlebioid venation. Herewith he followed Christensen (1931), who pointed out the intermediate type of venation in some species. Copeland (1947) stuck to his earlier delimitation in lack of any better solution. However, he admitted an intimate relationship of *Goniophlebium* to the group of Asian species with pinnatifid fronds. Ching (1978) tried to solve the problem in giving generic rank to three groups, which are *Polypodiodes* with pinnatifid fronds and goniophlebioid venation, *Polypodiastrum* with partly pinnate/pinnatifid fronds and goniophlebioid venation and *Metapolypodium* with pinnatifid fronds and free venation. Thus he simply set artificial lines to master the problem of the intermediate character states. He did not succeed in recognizing effective distinctive lines. Just to give two examples: He included NIw, which has a glabrous rhizome, even with specific rank into *Polypodiodes* and considered a densely scaly rhizome as one of the descriptive characters of the genus. He included also HE (*'Polypodium atkinsonii'* Christensen) and MI, known to have sometimes a free venation, in this genus. However, he described the venation as one row of costal areolae with included free vein. Therefore, this generic delimitation is not very useful. Trying to accommodate further species according to the distinguishing characters given, one will fail. In addition, Ching has rather neglected the truly pinnate species from Southeast Asia.

In conclusion, the genus *Goniophlebium* as presently combined is a monophyletic group of simple-veined species with longitudinal sclerenchyma strands in the rhizome and deltoid, pseudopeltate and clathrate rhizome scales. *Goniophlebium* is confined to the Old World (sub)tropics.

10.2. DELIMITATION OF THE GROUPS

A phylogenetic tree represents the historical sequence of speciation events and the biological and geographical developments. With the help of phylogenetic analyses monophyletic groups can be hypothesized. Monophyletic groups include the ancestral species and all of its descendents within an evolutionary lineage and allow therefore a phylogenetic reconstruction. The modification of character states in the course of evolution can be traced. Paraphyletic groups are not regarded as continuous building blocks in phylogenetic reconstruction.

The cladistic analyses for the species under study result in the recognition of the *G. percussum*-group (see fig. 41), a distinct monophyletic group of nine taxa. Its members share three apomorphies dealing with gross morphological and sporal structures. Apart from the criterion of monophyly, classification should preferably include groups of practical use. The distinctive character states describing the *G. percussum*-group are repeated here: All lateral segments are articulate to the rhachis, the terminal segment is petiolate – conform with the lateral segments, and the smooth exospore is surrounded by a crestate perispore with equatorial excrescences. An identical frond division occurs in *Drynaria rigidula* and in *Aglaomorpha speciosa* which, however, do not share other character states with this group. It is suggested that the *G. percussum*-group includes two smaller monophyletic groups. The first one consists of MB, PC, KO, PS and RA, and is based on a shared venation type. The other one pairs TE with DE because of two shared apomorphous character states concerning venation and rhizome scales.

Based on biologically best supported groupings found by different cladistic programs (see fig. 47), eight of the 14 remaining taxa are accepted as a monophyletic group, i.e. the *G. subauriculatum*-group. The other six taxa represent three sister pairs, i.e. AR and MZ, HE and SA, and NI and FO. For the time being the latter pair is included in the genus *Goniophlebium,* although its generic position is uncertain.

The latter four groups can only be distinguished micromorphologically. Character states that describe the groups are found in rhizome scales (*G. argutum*-group), spore type (*G. hendersonii*-group) and paraphyses (*G. subauriculatum*-group, *G. niponicum*-group).

10.3. SYSTEMATIC POSITION OF GONIOPHLEBIUM

Goniophlebium was most commonly regarded as a part of *Polypodium,* which is running into *Phymatodes.* As to Copeland (1915: 155) "... no natural line can be drawn between *Goniophlebium* and *Phymatodes* ...' Christensen (1938) indicated some Asian species of *Polypodium* with a somewhat more complicated venation, while Holttum (1947) mentioned some Asian species of *Phymatodes* with rather simple venation, as bridging the gap between *Polypodium* (incl. *Goniophlebium*) and *Phymatodes. Polypodium veitchii* was pointed out by Ching (1933) as a link between the two genera. Copeland (1929) suggested a relationship between *Goniophlebium* and *Microsorum* sensu Copeland, i.e. including *Phymatodes.* Holttum (1949) placed *Polypodium* (including *Goniophlebium*) in the *Phymatodes* group together with *Selliguea, Pycnoloma, Grammatopteridium,* and *Lecanopteris.*

In considering *Goniophlebium* a separate genus, Copeland was followed by Bir et al. (1974). Holttum (1968), revising his earlier opinion, also accepted the generic position of the genus, as did Pichi Sermolli (1973), but under the name of *Schellolepis.*

As emphasized by Christensen (1928), the closest relatives of *Polypodium vulgare* are species found in both hemispheres along its southern boundary, with veins more or less reticulate. Between such species with occasional or irregular anastomoses of veins and those with a regular row of areolae Christensen did not see any chance at all to refer them to different genera. However, it has been demonstrated here that *Polypodium vulgare* shares more similarities with the goniophlebioids from the New World than with those from the Old World tropics. In the present sense *Polypodium vulgare* does not represent a free-veined *Goniophlebium,* as was proposed by Christensen (1931). It is demonstrated here that a simplification of veins must have developed independently in America and Asia. This has further contributed to the existing confusion.

The relationships of *Goniophlebium* to other genera of the family are still unclear and those reported in the literature need further testing. Hennipman (1989) provisionally included *Goniophlebium* in *Polypodium* sensu lato, tribe Polypodieae.

10.4. DELIMITATION OF THE SPECIES

The species problem is still unsolved. Presently, theoretical biologists as well as systematists tend to consider the evolutionary species concept as the most comprehensive. This evolutionary interpretation includes the recognition of morphological characteristics (morphological concept), the knowledge about breeding and isolation data, about ecological and geographical ranges (biological concept) and the reconstruction of genealogical relationships as a historical parameter.

The evolutionary species concept does not only recognize divergent (primary) species, but also hybrid (secondary) species, due to their spatio-temporal identity. This fact is continuously gaining importance as biologists become aware that hybrid species are very common, especially among ferns. In addition, relationships might appear more and more confusing considering the hypothesis that primary species could have evolved from paleopolyploids through consistent diploidization, i.e. gene silencing (Barrington et al., 1989). In this case primary species would represent diploidized secondary species.

The author's information about such biological features, e.g. intraspecific variability and morphological variability in relation to habitat conditions is mainly based on field experiences in the Philippines.

All intraspecific taxa refer to non- or geographically defined varieties with 'insignificant' morphological differences.

According to the transplant experiments as explained in chapter 8.3, the presence of not only a different phenotype, but also a different genotype was carefully considered. Therefore, e.g. the xerophytic varieties of AM, LA and MI, as recognized by Mehra (1939) and Mehra & Bir (1964), are not accepted as taxa by the present author, assuming a similar process as in the 'mountain form' of SU, which appears to be reversible when environmental conditions are altered.

NIw, which was accepted as species by Tagawa (1949), Ching (1978) and Satija & Bir (1985), served as terminal cladon during cladistic analyses using morphological data sets. However, it was rejected as an evolutionary species finally, and is considered a variety of NI. This is in accordance with earlier authors. The main phenetic difference, the 'naked rhizome', is disproved by the presence of rhizome scales, which are set in rare small tufts. Unfortunately, NI and NIw were not studied in the field and their attitude in different habitats could not be observed. TR was recognized as conspecific with BR.

Similar reflections were applied for all taxa and 23 species were finally accepted. In order to test and improve the quality of the present species delimitation more experimental genetic, biochemical and molecular studies will be necessary.

11. BIOGEOGRAPHICAL ASPECTS

An evaluation of the species distribution revealed the following areas of endemism (table 10).

Table 10. Areas of endemism.

Sichuan, Yunnan, Assam	1
Tibet, Nepal, Sikkim, Assam	2
Taiwan	4
Philippines	6
Malay Peninsula	7
Borneo	8
Sumatra	9

The numbering follows a geographical direction from North to South and from West to East.

To these the following miscellaneous areas are added (table 11).

Table 11. Miscellaneous areas.

Japan	3
Indo-China, Thailand	5
Celebes, Java, Lesser Sunda Islands	10
New Guinea and adjacent islands	11
South Pacific	12
Australia	13

The numbering follows a geographical direction from North to South and from West to East.

Thirteen taxa, about half of the genus, are confined to restricted areas. Endemism in this sense is either referring to a certain region or to a very limited locality as in the case of TE, which is restricted to Mt. Makiling in the Philippines only. Celebes, a highly endemic area for *Lecanopteris* (Hennipman, pers. comm.), is inhabited by four rather widely distributed species of the present genus.

The only species inhabiting extremely disjunct areas is SE. This species was until now considered endemic to the Fiji and Samoa Islands. However, one specimen from West New Guinea is regarded conspecific (*Brass 14045*, MICH, type of *G. subcordatum* Copeland).

Five taxa (PC, PS, AM, NI, SU) are widespread. PC, PS and SU are represented north and south of the equator ranging from Indo-China to Queensland. AM and NI show a latitudinal expansion over mainland Asia and Taiwan, NI even reaching Japan.

Five taxa spread over smaller continuous areas. LA, MI and MZ were mainly found in the Himalayas; MI extends to Taiwan and MZ to Luzon. The distribution of DE includes Celebes, New Guinea and the Solomon Islands. The area occupied by PD reaches from the Philippines to New Guinea, touching the Northeastern part of Borneo and Celebes.

Table 12 relates species with areas. The numbers used correspond with those introduced in tables 10 and 11.

Assuming that the reconstructed phylogeny is correct, the species-related areas can be matched with the phylogenetic history of the two major groups (fig. 47) of *Goniophlebium*. Relevant branches of the area-cladogram of the *G. percussum*-group are shown in figure 48a–c as well as of the *G. subauriculatum*-group in figure 49a & b. Area-cladograms suggest a possible hypothesis on historical relationships among areas. According to Nelson & Platnik (1981) it can be assumed that the widespread species either expanded their range through dispersal or they failed to speciate in response to vicariance events. Further speciation of widespread species in endemic areas might still occur in the future.

Table 12.

	B	D	K	M	P	P	R	S	T	A	D	L	M	M	P	P	S	A	M	F	N	H	S
	E	E	O	B	C	S	A	E	E	M	L	A	A	I	R	D	U	R	Z	O	I	E	A
1						+				+	+	+	+	+			+		+		+		
2										+		+		+				+	+		+	+	+
3																			+	+			
4										+									+	+	+		
5					+	+				+		+	+	+			+		+		+		
6	+				+	+			+							+	+		+				
7			+		+	+									+		+						
8				+	+	+	+									+	+						
9			+	+	+	+									+		+						
10		+			+	+										+	+						
11		+			+	+		+								+	+						
12								+															
13					+												+						
	B	D	K	M	P	P	R	S	T	A	D	L	M	M	P	P	S	A	M	F	N	H	S
	E	E	O	B	C	S	A	E	E	M	L	A	A	I	R	D	U	R	Z	O	I	E	A

According to the area-cladogram of the *G. percussum*-group, Celebes, Java, the Lesser Sunda Islands, New Guinea and the Philippines are biogeographically closely related. The same relationship is suggested by the area-cladogram of the *G. subauriculatum*-group but also including Borneo. A closer relationship between Sumatrà and the Malay Peninsula (fig. 48b) is followed to the one between Sumatra and Borneo (fig. 48c). Two equally parsimonious cladograms of the *G. percussum*-group provide both options. However, the close relationship between Sumatra and the Malay Peninsula is also suggested by the area-cladogram of the *G. subauriculatum*-group. As also illustrated in figure 49a, Sumatra, the Malay Peninsula and mainland Asia are biogeographically closer related to each other than to any other area.

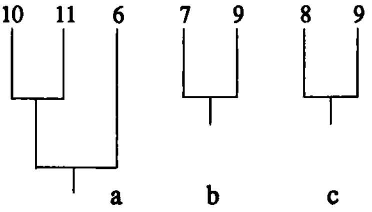

Fig. 48. Relevant branches of the area-cladogram of the *Goniophlebium percussum*-group.

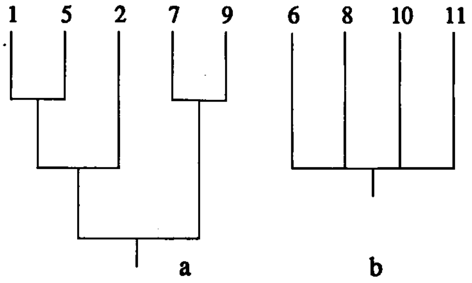

Fig. 49. Relevant branches of the area-cladogram of the *Goniophlebium subauriculatum*-group.

12. A SCENARIO FOR GONIOPHLEBIUM

12.1. VIEW OF PREVIOUS AUTHORS

Few pteridologists speculated on the phylogeny of the goniophlebioid ferns in relation to their geographical distribution. Two contradictory ideas have been stated by Christensen (1928) and Copeland (1909, 1929) respectively. The first assumes *Polypodium* to be derived from a goniophlebioid, tropical stock, while the latter considers it easy to picture *Goniophlebium* (in the present sense) as a derivative of *Polypodium.* Bir & Trikha (1979) followed Copeland suggesting that *Goniophlebium* evolved from *Phymatodes* through *Polypodium.*

De la Sota (1973: 239) understands *Polypodium* like a mosaic of groups of species complexes (*Polypodium vulgare-*, *P. polypodioides-*, *P. squamatum-*, ... and *P. loriceum-*), each of them having a 'homogeneous composition' but mutually not closely related. "This genus (*Polypodium*) is almost exclusive to the Neotropics with a few elements in Africa and Eastern Asia ..." *Goniophlebium* and *Thylacopteris* are cited as the only two simple veined genera of the Polypodiaceae of the Paleotropics.

Ching (1978: 31) offers a similar intuitive perception of *Polypodium*: "... there are no Neotropical polypodioid genera and their representatives in South Eastern Asia or vice versa ... *Polypodium* (sensu stricto) ... is strictly a temperate, northern Eurasian, North Eastern Asian and North American genus ... In tropical and subtropical Asia, the genus *Polypodium* is replaced by its allies ..." The term 'replaced' does in fact not explain any relationship, but Ching expresses clearly that the two major polypodioid (goniophlebioid) groups were not mutually related and have developed independently in their respective areas.

Ching's concept is supported by De la Sota's hypothesis of a migratory circle from Southeast Asia along the Antarctic coasts to the Neotropics, where species have evolved independently from those in the Paleotropics. Later this circle could have been completed with the bridge of North America – Eurasia.

12.2. INTRODUCTION

An explanation for the absence of any representative of this group in Africa might be that it only arose after separation of Gondwana in Africa and Papaustralia, which was caused by sea floor spreading according to generally accepted hypotheses about 120–140 million years ago (Powell et al., 1981). Together with the fact that fossil evidences of goniophlebioid Polypodiaceae have not been reported so far, one may conclude to deal with a relatively recent genus. Ching (1933) interpreted the internal instability of the group as an indication for a still very active evolution within a relatively recent genus *Polypodium* (including *Goniophlebium*).

Since a fully resolved cladogram for the genus could not be obtained, five groups of species are recognized in *Goniophlebium.* A scenario of the biogeographical history concerning the two largests groups may be a plausible support for the phylogeny of the genus as a whole.

Speciation events are considered determined by the chronology of environmental events. If speciation occurs after a vicariance event, a simultaneous speciation in several sympatric species or taxonomic groups can be expected. Similar speciation patterns in different groups are likely to be found.

If, however, speciation occurs after dispersal, parent species and daughter species can easily be allopatric. Speciation patterns are then probably different from that in other taxonomic groups (hypothesis of dispersal and vicariance model, Hovenkamp, 1986, following Nelson & Platnick, 1981).

Goniophlebium is obviously not represented in Africa. Understanding *Goniophlebium* as a relatively recent, monophyletic genus it could, therefore, be imagined that the common ancestor of its groups arose in Papaustralia, after the separation of East Gondwana and Africa.

Two centres of diversification can be recognized. One, in the Himalayan area, is characterized by quite variable climatic and ecological conditions. The second, in Southeast Asia, shows an insular type of diversification, however, under relatively uniform external factors.

12.3. A SCENARIO FOR THE GONIOPHLEBIUM PERCUSSUM-GROUP

SE and DE might have evolved from BE through sympatric speciation in Papaustralia. Since the distribution of SE nowadays reaches from New Guinea to the Fiji and Samoa Islands, it is assumed that SE was existent before any further splitting of these regions off Papaustralia. The population which was later moved to the South Pacific failed to speciate. The population of DE which rafted along with the land masses of today's Philippine Islands could have speciated allopatrically to TE. BE must have been defined to the same land masses or become later extinct in New Guinea. The divergence of TE and DE could as well be assumed after the separation of the Philippines from New Guinea. The unique venation-type (*terrestre*-type) shared by TE and DE, which arose from the *subauriculatum*-type, could serve as an argument for a later allopatric speciation of DE through dispersal to New Guinea.

With the next step the *percussum*-type of venation developed.

For the group of KO, RA, PS, PC and MB a more or less simultaneous insular type of diversification might have been performed. One could imagine an ancestral species spread over the Sunda Shelf during relatively recent glacial times of the Pleistocene. A following sealevel rise might have caused an independent development of island populations. This would explain the close morphological relationship between these taxa, which gives the impression that only limited anagenetic change occurred. PC and PS, widespread, might have expanded their range through dispersal.

12.4. A SCENARIO FOR THE GONIOPHLEBIUM SUBAURICULATUM-GROUP

The greater part of species belonging to the *G. subauriculatum*-group is restricted to mainland Asia. In this case less options for the scenario are provided.

PR is confined to Sumatra and the Malay Peninsula. In case Sumatra and the Malay Peninsula were connected with mainland Asia, as suggested by the biogeographical analysis, AM might have speciated sympatrically from PR. AM and DL also show a sympatric speciation, DL being areawise more restricted. Dispersal of AM to Taiwan is suggested. LA could as well have sympatrically speciated from its ancestor. The branch comprising PD, SU and LA developed stellate, peltate scaly paraphyses, while scaly paraphyses ceased in the sister pair MI and MA. SU might then have dispersed and largely expanded towards Southeast Asia. This coincided with quite obvious morphological diversification, e.g. rhizome chalky, lateral segments for the greater part articulate. PD, its mountainous sister species occurs within the distribution area of SU. Sympatric speciation is suggested. The same process could be assumed for MI and MA. In this case MI is representing the sister species with the larger distribution area.

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Plate 1. ***Goniophlebium mengtzeense*** **(Christ) Rödl-Linder. a. Population on rocky slope, in shade, Luzon, Mt. Sto. Tomas, alt. 2000 m; b. individual plants on rotten trunk, Luzon, Mt. Data, alt. 2320 m. —** ***G. pseudoconnatum*** **(Copeland) Copeland. c. Terrestrial population along trail to Mt. Sto. Tomas, in slight shade, alt. 1800 m; d. population, epilithic on mossy rocks, Luzon, between Banaue and Bontoc, alt. 1700 m (exsiccata: a.** ***Rödl-Linder 100*****; b.** ***161*****, c.** ***93*****, all L).**

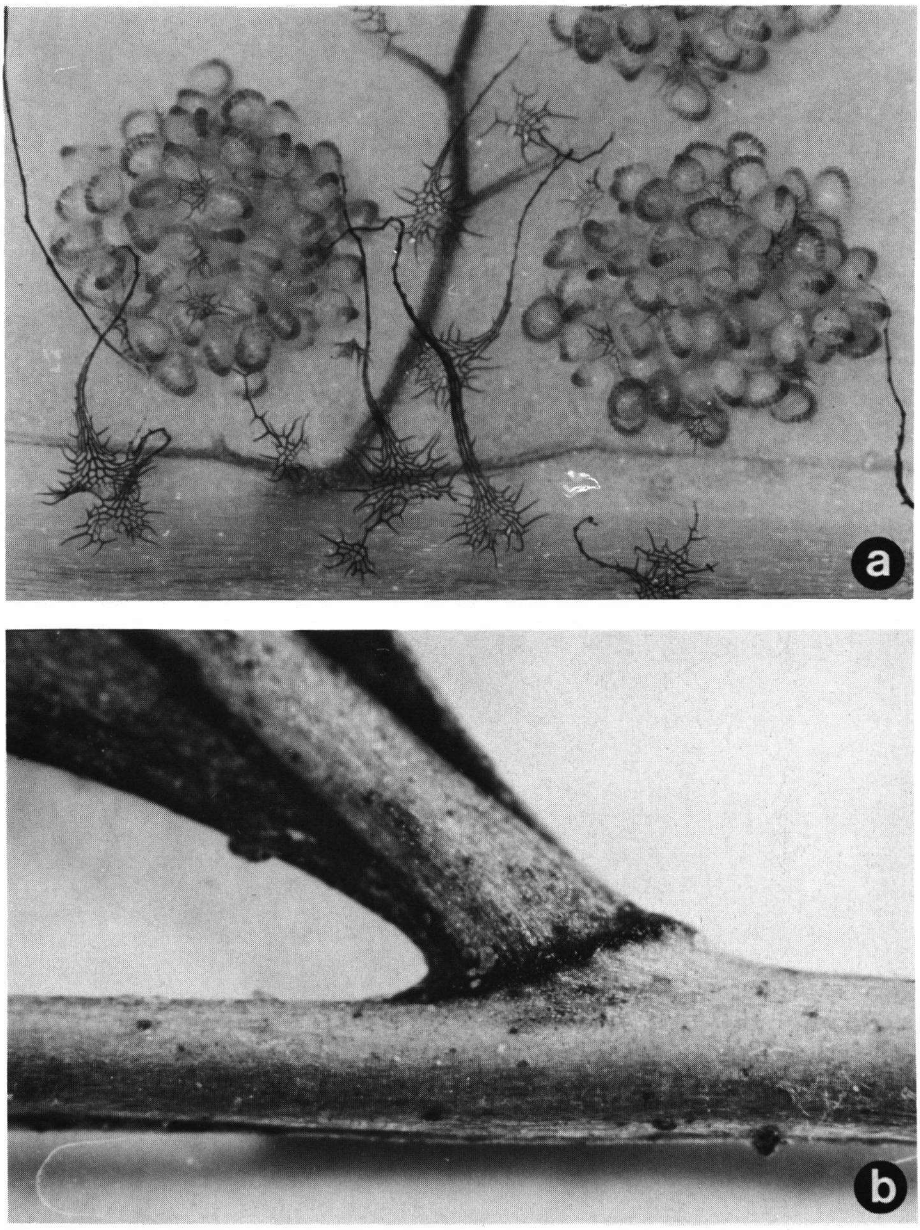

Plate 2. a. *Goniophlebium lachnopum* (Hooker) Beddome, lower surface of fertile frond showing sorus and laminar scales with filiform apex, × 100. — b. *G. persicifolium* (Desvaux) Beddome, articulation of pinna, × 30.

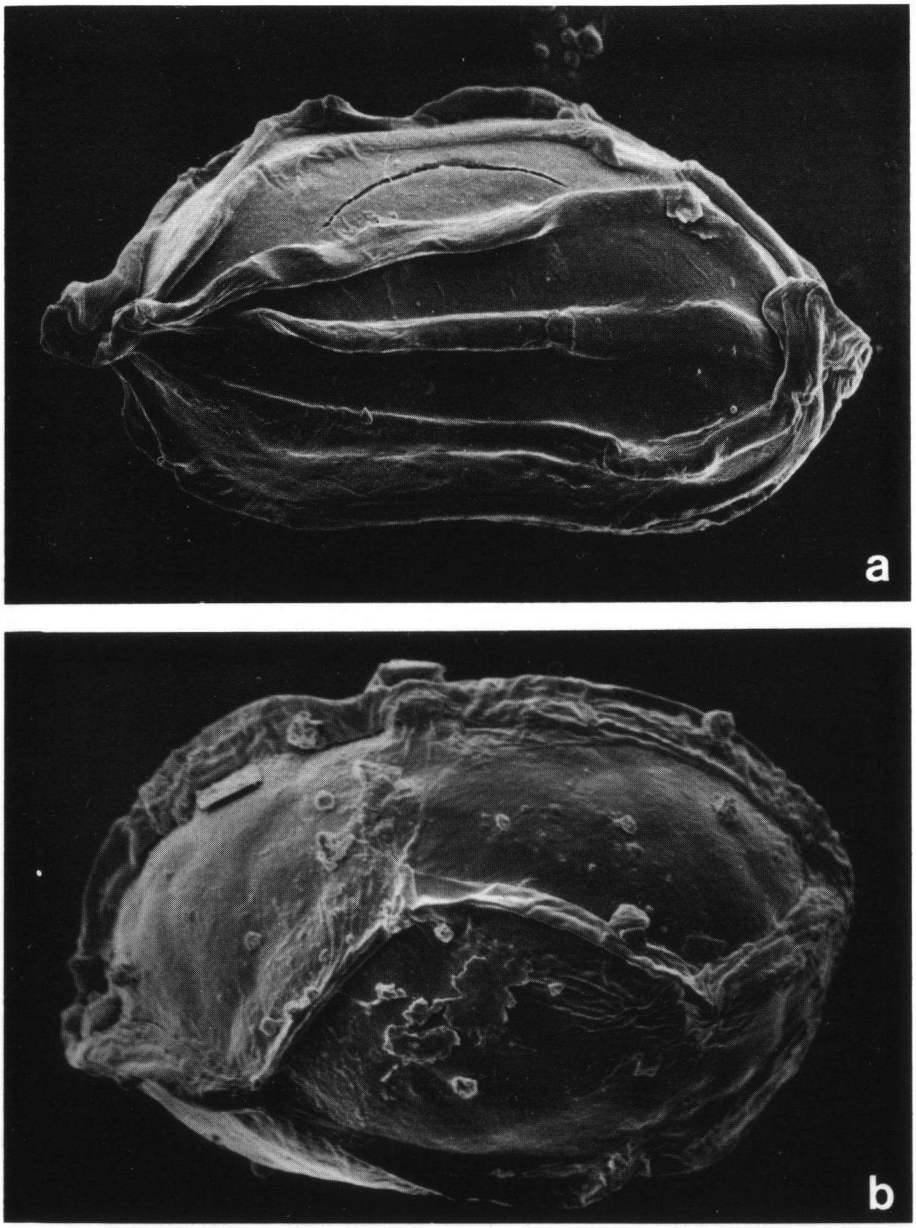

Plate 3. Spores: a. *percussum*-type, *Goniophlebium percussum* (Cavanilles) Wagner et Grether; 10 µm = 20 mm. — b. *subauriculatum*-type, *G. subauriculatum* (Blume) Presl; 10 µm = 23 mm (a. *Rödl-Linder 146*, L; b. 86GR00010 greenhouse Utrecht).

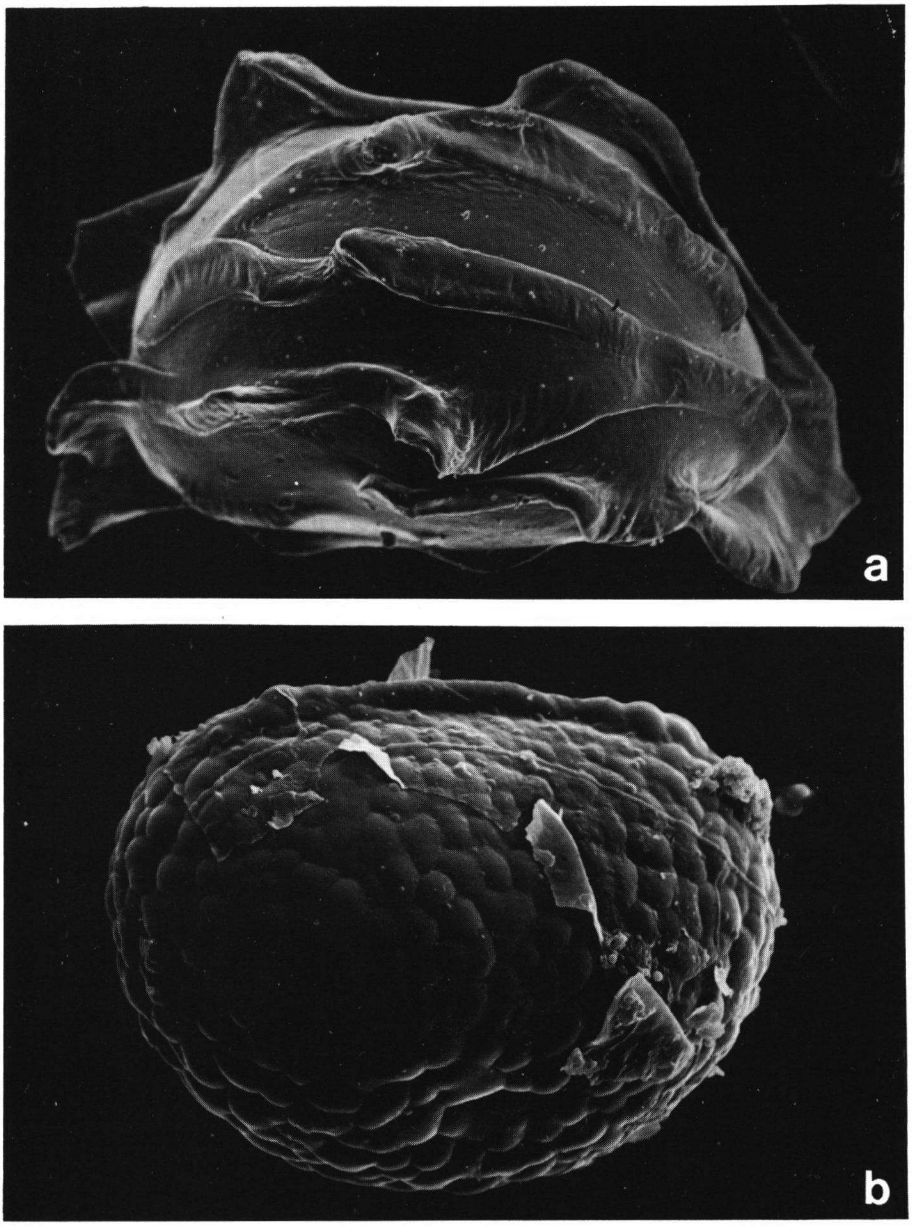

Plate 4. Spores: a. *hendersonii*-type, *Goniophlebium mehibitense* (Christensen) Parris; 10 µm = 16 mm. — b. *amoenum*-type, *Polypodium someyae* Yatabe; 10 µm = 17 mm (a. *Jermy 14002*, U; b. *Saida s.n.*, B).

TAXONOMIC PART

14. PRESENTATION OF DATA

In the taxonomic part the species of the genus *Goniophlebium* are ordered in five groups, which have been given formal recognition. Within the groups the species are alphabetically arranged. Asian representatives of species retained in *Polypodium* are treated separately.

A full synonymy is given for each taxon. Basionyms with respective homotypic synonyms are listed chronologically, as are the heterotypic synonyms. Selected literature is included. All pages concerned are cited, not only the first page as is usually done. Author's names are cited in full. Nearly all the type collections have been studied, except those marked with 'not traced'. Herbaria where the type specimens have been searched in vein are mentioned. Herbaria are abbreviated according to the Index Herbariorum. Lectotypes have generally been indicated only for taxa accepted in this paper. Nomina nuda and nomina illegitima are listed.

The description of the species refers to character states recognized in adult sporophytes. As stated in chapter 2.1, exsiccated as well as living material (wild and cultivated) have contributed to the results. The numbers of herbarium collections per species seen is listed in table 13. Rare collections are listed in detail after the description of the respective species. Living material has been studied of species nos. 1, 5, 6, 9, 10, 13, 15, 18, 21, 23, 26, 27, 29, 30, 31 and 33, which are cultivated in the botanic gardens in Utrecht. The descriptions are based on 341 conditions recognized (see chapter 4.1) Their arrangement coincides with the sequence of character states in chapters 4.2 to 4.5. These chapters further present explanations of the terminology and all character states.

The distributions are noted according to the order of geographical regions accepted at Kew. The abundance ratio of each species throughout its geographical range can be interpreted approximately from the distribution maps (figs. 12–24). Only herbarium collections with precise indications of localities have contributed to the maps; in the same way only precise indications of altitudes were used for the histograms (figs. 25 & 26). The material of Nessel's herbarium (BONN) has not been fully taken into consideration due to certain inconsistencies in the indication of localities. The percentage of specimens used for these illustrations is displayed in table 13.

The habitat of a number of species has been observed in the field. Additional information has been taken from herbarium labels.

Notes are added for special remarks and additional data, when necessary. The chromosome numbers have been taken from the literature indicated in chapter 7. The author's personal collection is kept in L.

Drawings of specimens in outline have been made from dried material on translucent paper in natural size. Only afterwards they have been scaled down.

The keys have been established using character states described in chapter 4 or in the notes. Keys to infraspecific taxa are given under the species.

Dubious and excluded species are listed separately.

Table 13.

number	species	specimens seen	number of different localities used for maps	% of total	number of data used for altitudinal ranges	% of total
01	BE	32	9	28.1	17	53.1
02	DE	71	21	29.5	68	95.8
03	KO	9	2	22.2	2	22.2
04	MB	6	4	66.7	4	66.7
05	PC	101	35	34.6	44	44.0
06	PS	135	43	31.8	77	57.0
07	RA	10	3	30.0	10	100.0
08	SE	23	5	21.7	8	36.4
09	TE	7	1	14.3	7	100.0
10	AM all var.	192	50	26.0	107	55.7
11	AR	62	10	16.1	36	58.1
12	DL	7	4	57.1	4	57.1
13	FO	14	6	42.9	2	14.3
14	HE	23	3	13.0	17	73.9
15	LA	76	15	19.7	44	57.9
16	MA	24	9	37.5	16	66.7
17	MZ	76	17	22.4	55	72.4
18	MI	61	19	31.1	43	70.5
19a	NIn	51	24	47.1	11	21.6
19b	NIw	10	5	50.0	9	90.0
20	PR	15	6	40.0	8	53.3
21	PD	37	18	48.6	24	64.9
22	SA	9	3	33.3	9	100.0
23	SU	260	90	34.6	137	52.7
24	FA	24	14	58.3	0	0.0
25	SO	8	2	25.0	0	0.0

15. GONIOPHLEBIUM

Goniophlebium (Blume) Presl, Tent. Pterid. (1836) 185; Beddome, Ferns Brit. Ind. (1865) 5, 6; (1866) 163, 206; Handb. (1883) 316; Fée, Gen. (1852) 254, 255; Moore, Ind. Fil. 1 (1857) 73; Copeland, Univ. Calif. Publ. Bot. 16 (1929) 109; Gen. Fil. (1947) 181; Farwell, Amer. Midl. Naturalist 12 (1931) 295, 296; Zijlstra et al., Taxon 36 (1987) 759. — ***Polypodium*** sect. ***Goniophlebium*** Blume, Flora Javae Filices (1830) 132; Diels in Engler & Prantl, Nat. Pflanzenfam. 1 (1900) 311. — ***Polypodium*** subg. ***Goniophlebium*** Christensen, Contr. U.S. Nation. Herb. 26 (1931) 315, 316. — Lectotypus generis [Rödl-Linder, Tryon & Zijlstra, Taxon 39 (1990) in press]: ***Goniophlebium subauriculatum*** (Blume) Presl (basion. ***Polypodium subauriculatum*** Blume).

Schellolepis J. Smith, Ferns Brit. & For. (1866) 82, 83, Hist. Fil. (1875) 92, 93; Pichi Sermolli, Webbia 28 (1973) 468. — *Goniophlebium* sect. *Schellolepis* J. Smith, Journ. of Bot. 4 (1841) 56, 57, Cat. Ferns (1857) 3. — Lectotypus generis (J. Smith, 1875): *Schellolepis percussa* (Cavanilles) Pichi Sermolli, syn. *Polypodium verrucosum* (Mettenius) Wallich ex Hooker, syn. *Goniophlebium percussum* (Cavanilles) Wagner et Grether.

Polypodiodes Ching, Acta Phytotax. Sin. 16 (1978) 26, 27. — Typus generis: *Polypodiodes amoena* (Mettenius) Ching, syn. *Goniophlebium amoenum* (Mettenius) Beddome.

Polypodiastrum Ching, Acta Phytotax. Sin. 16 (1978) 27, 28. — Typus generis: *Polypodiastrum argutum* (Hooker) Ching, syn. *Goniophlebium argutum* (Hooker) J. Smith.

Metapolypodium Ching, Acta Phytotax. Sin. 16 (1978) 28, 29. — Typus generis: *Metapolypodium manmeiense* (Christ) Ching, syn. *Goniophlebium manmeiense* (Christ) Rödl-Linder.

Ferns, moderate to large-sized, usually epiphytic or epilithic, spirally or vertically climbing, occasionally terrestrial, linearly creeping, fronds upright or pendent. *Rhizome* long creeping, usually terete, rarely dorsiventrally flattened, branched, 1.2–11 mm in diam., brown (in vivo green), glaucous or chalky, clothed with scales, phyllopodia more or less prominent, situated dorsally in 2 alternating rows, 0.5–5(–17) cm apart, roots situated ventrally in 2 rows or irregularly; anatomy: ground tissue parenchymatous, number of vascular strands 6–22, related to diameter of rhizome, arranged in a regular circle, dark bundle sheaths present or absent, black sclerenchyma strands longitudinal, present in specific numbers 3–>100, scattered in the ground tissue. *Rhizome scales* inserted evenly, on protrusions or in invaginations, different shades of brown, appressed or obliquely spreading, more or less densely set, usually perfoliate, rarely basifix, mostly monomorphic, narrowly deltoid, up to 5(–8) mm long, apex acuminate to filiform, basal flaps round or pointed, rarely dimorphic, as above and round, up to 0.1 mm in diam., usually cell walls dark clathrate throughout, rarely hyaline basally or centrally, cells hyaline to yellow, clathrate marginal protrusions present except in one species, marginal glands more or less frequent, rhizoid surface indument present or absent, glandular surface indument rare, situated abaxially. *Fronds* monomorphic, articulate to rhizome, petiolate; stipe terete, in cross section near base 0.1–1.0 cm across, vascular strands 4–20, unifying towards the apex of the rhachis, dark bundle sheaths present, index length of stipe/length of blade 0.2–0.9; blade herbaceous, index length/width (1.0–)1.5–5.3, widest medially to basally, pinnate to pinnatifid; lateral segments in an angle of 180° towards each other (in vivo), number relative to length of blade, lanceolate to linear, apically obtuse to pungent, margin entire, crenate or serrate; terminal segments petiolate- or adnate-conform with lateral segments or coadunate, basal segments 0.6–6.0 cm apart from subbasal segments, sometimes shorter, somtimes deflexed. *Venation:* 1–4 series of areolae at each side of costa, each areola including a free vein, marginal free veins with terminal hydathodes, sometimes forked, sometimes irregularly anastomosing. *Laminar indument:* glandular hairs present, about 0.1 mm long, 2–5 cells long, acicular hairs unbranched, present or absent, scales sparsely set, generally similar to rhizome scales (see note 1), more or less persistent. *Sori* exindusiate, usually uniserial at each side of costa, in only one species uni- to triserial, situated terminal at included free veins, superficial or sunken, mostly round, rarely slightly oval, 0.4–3.0 mm in diam.; receptacular hairy paraphyses present, receptacular scaly paraphyses in all but four species present, attached to uniseriate stalks, clathrate, peltate or palaceous, linear, stellate or deltoid scalariform; sporangial capsule index length/ width 1.0–1.5, annulus vertical, incomplete, indurated cells 11–15, stomium cells 2, cells in total 16–24. *Spores* per sporangium c. 64, bilateral, oblong (polar view), plano- to concavo-convex (lateral view), hyaline, yellow or brownish, exospore smooth or colliculate, perispore inconspicuous or crestately folded, detailed outer surface ornamentation of perispore quite smooth, globules present or absent, excrescences of perispore at lateral poles present or absent.

Chromosomes. n = 36, 37; 2n = 72. For details see chapter 7.

Gametophyte. Cordate. For details see chapter 5.

Distribution. Nepal; Sikkim; India (Kashmir, Punjab, Himachal Pradesh, Uttar Pradesh, Assam); Burma; Indo-China; Thailand; Japan; West, South-Central & Southeast China; Hongkong; Taiwan; Malesia; Australia (Queensland); Pacific: Melanesia, New Caledonia, Fiji, Samoa, Micronesia. Fig. 9.

Habitat. Primary and secondary forest, (sub)tropical, climbing or creeping; epiphytic, epilithic or terrestrial; shaded or exposed; alt. (0–)250–2400(–4000) m.

Notes. 1. For the detailed description of differences between laminar scales and rhizome scales see chapter 6.2.3.

2. The typification of *Goniophlebium* has received much attention. Copeland (1929, 1947), Farwell (1931) and Zijlstra et al. (1987) have been overlooking the fact that *Polypodium cuspidatum* Blume is an invalid name. *Goniophlebium subauriculatum* Blume has been designated as lectotype (Rödl-Linder et al., 1990, in press).

3. Synonyms have been listed only when their type species are part of this genus. Other genera to which species of the present genus have been referred include *Cyathea* and *Marginaria*.

4. Etymology. The name *Goniophlebium* derives from the greek words 'goni', meaning angle and 'phlebs', meaning vein. The name refers to the characteristic venation pattern as described in chapter 4.4.2.

16. KEY TO THE SPECIES OF GONIOPHLEBIUM

1a. Lateral segments are articulate; terminal segment petiolate-conform. Exospore smooth .... *percussum*-group – 2

b. Lateral segments are at least at apex of frond adnate to rhachis; terminal segment adnate-conform or coadunate. Exospore with globular excrescences other groups – 10

2a. Venation *subauriculatum*-type (fig. 4b). Basal flaps of rhizome scales pointed 3

b. Venation *percussum*- or *terrestre*-type (fig. 4c & d). Basal flaps of rhizome scales round 4

3a. Terminal segment as long as or longer than longest lateral segment. Dark bundle sheaths in rhizome absent. Rhomboid receptacular paraphyses (fig. 5c) present. The Philippines .... **1. G. benguetense**

b. Terminal segment shorter than longest lateral segment. Dark bundle sheaths in rhizome present. Rhomboid receptacular paraphyses absent. New Guinea, Fiji and Samoa Islands .... **8. G. serratifolium**

4a. Veins forming one row of enlarged areolae. Cell lumen of rhizome scales colourless; clathration of cell walls basally at rhizome scales absent 5
b. Veins forming multiserial areolae. Cell lumen of rhizome scales yellowish to brownish; clathration of cell walls also basally of rhizome scales present . . 6

5a. Stipe in cross section near base < 2 mm; length of blade < 20 cm; blade widest basally . . . . **9. G. terrestre**
b. Stipe in cross section near base > 3 mm; length of blade > 30 cm; blade widest medially to subbasally . . . . **2. G. demersum**

6a. Rhizome dorsiventrally flattened; number of sclerenchyma strands in rhizome < 20; length/width index of sporangial capsules < 1.2 7
b. Rhizome terete; number of sclerenchyma strands in the rhizome > 40; length/width index of sporangial capsules > 1.2 8

7a. Length/width index of lamina < 1.2. Sori up to triserial. Perispore with very long equatorial excrescences . . . . **3. G. korthalsii**
b. Length/width index of lamina > 1.5. Sori uniserial. Perispore with short equatorial excrescences . . . . **7. G. rajaense**

8a. Base of lateral segments truncate. Laminar bristles present. Linear receptacular scaly paraphyses absent . . . . **4. G. mehibitense**
b. Base of lateral segments angustate. Laminar bristles absent. Linear receptacular scaly paraphyses present 9

9a. Sori in diameter < 1.0 mm, deeply sunken, surrounded by a ring of dark paraphyses. Laminar acicular hairs present . . . . **5. G. percussum**
b. Sori in diameter > 1.5 mm, slightly sunken, ring of dark paraphyses absent. Laminar acicular hairs absent . . . . **6. G. persicifolium**

10a. Receptacular scaly paraphyses absent 11
b. Receptacular scaly paraphyses present 14

11a. Rhizome in diameter > 4 mm. Insertion of rhizome scales in invaginations. Angle between primary and secondary vein > 60° 12
b. Rhizome in diameter < 3.5 mm. Insertion of rhizome scales at even rhizome. Angle between primary and secondary vein < 60° 13

12a. Parenchymatous sheath around roots present. Clathrate marginal protrusions at rhizome scales absent. Receptacular hairy paraphyses with glandular and acicular branches . . . . **20. G. formosanum**
b. Parenchymatous sheath around roots absent. Clathrate marginal protrusions at rhizome scales present. Receptacular hairy paraphyses with glandular branches only . . . . **21. G. niponicum**

13a. Width of blade 3–5 cm. Clathration of cell walls centrally at rhizome scales absent. Globules at perispore absent . . . . **13. G. manmeiense**
b. Width of blade 6–12 cm. All cell walls of rhizome scales clathrate. Globules at perispore present . . . . **14. G. microrhizoma**

14a. Perispore inconspicuous. Scaly episporangial paraphyses occasionally branching from stalk 15
b. Perispore crestately folded. Scaly episporangial paraphyses absent 16

15a. Rhizome scales spreading. Fronds divided down to the rhachis. Laminar scales ephemeral. Sori occasionally slightly oval . . . . **11. G. dielseanum**
b. Rhizome scales appressed. Fronds divided to somewhat apart of the rhachis. Laminar scales along rhachis of lower surface persistent. Sori round **10. G. amoenum**

16a. Number of sclerenchyma strands in rhizome < 30. Perispore *hendersonii*-type (plate 4a) 17
b. Number of sclerenchyma strands in rhizome > 30; perispore *subauriculatum*- or *percussum*-type (plate 3a & b) 18

17a. Length/width index of lamina > 3.5; index length stipe/lamina < 4.5. Spores brown . . . . **22. G. hendersonii**
b. Length/width index of lamina < 3.5; index length stipe/lamina > 4.5. Spores yellow . . . . **23. G. subamoenum**

18a. Margin of lateral segments minutely serrate. Marginal free veins simple; irregular empty areolae absent. Short equatorial excrescences at perispore present **18. G. argutum**
b. Margin of lateral segments entire and/or crenate and/or roughly serrate. Marginal free veins forked to build irregular empty areolae. Equatorial excrescences at perispore absent 19

19a. Rhizome brown (in vivo green). Articulate lateral segments absent 20
b. Rhizome glaucous or chalky. Articulate lateral segments at least at lower half of fronds present 21

20a. Length of lateral segments 25–45 mm. Marginal glands along rhizome scales many. Peltate stellate receptacular paraphyses present. Himalayas **12. G. lachnopum**
b. Length of lateral segments 100–150 mm. Marginal glands along rhizome scales rare. Peltate stellate receptacular paraphyses absent. Malay Peninsula and Sumatra . . . . **15. G. prainii**

21a. Sori superficial. Dimorphous rhizome scales above each other. Branched glandular laminar hairs absent . . . . **19. G. mengtzeense**
b. Sori slightly sunken. Dimorphous rhizome scales absent. Branched glandular laminar hairs present 22

22a. Rhizome scales ferrugineous. Length/width index of rhizome scales 4.2–6.0. Palaceous deltoid receptacular paraphyses present **17. G. subauriculatum**
b. Rhizome scales brunneous. Length/width index of rhizome scales 3.8–4.1. Palaceous deltoid receptacular paraphyses absent **16. G. pseudoconnatum**

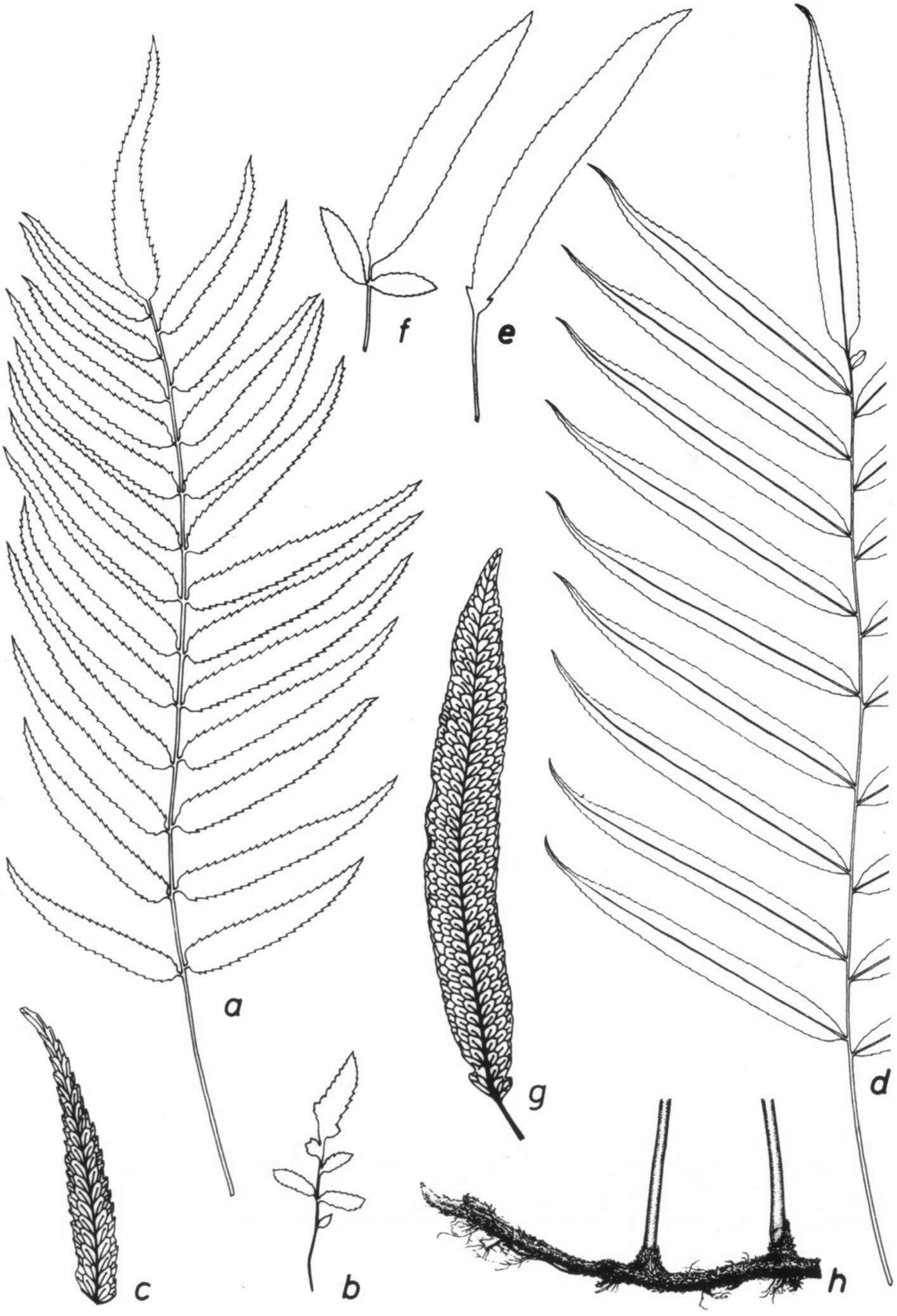

Fig. 50. *Goniophlebium benguetense* (Copeland) Copeland. a. Adult frond, × 0.5; b. juvenile frond, × 0.5; c. venation pattern, × 0.75. — *G. persicifolium* (Desvaux) Beddome. d. Adult frond, × 0.12; e, f. juvenile fronds, × 0.5; g. venation pattern, × 0.75; h. rhizome, × 0.5

17. DESCRIPTIONS

17.1. GONIOPHLEBIUM PERCUSSUM-GROUP

1. Goniophlebium benguetense (Copeland) Copeland — Fig. 50a–c.

Goniophlebium benguetense (Copeland) Copeland, Fern Fl. Philip. 3 (1960) 461; Rödl-Linder, Philip. Journ. Sc. 116 (1987) 153, 154. — *Polypodium benguetense* Copeland, Philip. Journ. Sc. 1, Suppl. 2 (1906) 256, 257. — *Schellolepis benguetensis* Pichi Sermolli, Webbia 28 (1973) 470. — Type: *E.B. Copeland 1829* (*'1892'*), Benguet, Ambuklao, 750 m alt., 'ad terram', 25-10-1905 (MICH; iso P, B).

Polypodium mengtzeense auct. non Christ: Copeland, Philip. Journ. Sc. 1, Suppl. 2 (1906) 161, pl. 21.

Mostly terrestrial and linearly creeping, sometimes epiphytic and vertically or spirally climbing. *Rhizome* terete, 2–3 mm in diam., brown, phyllopodia 0.5–1.0 cm apart, vascular strands 7–10, dark bundle sheaths absent, sclerenchyma strands > 100. *Rhizome scales* evenly inserted, badious, spreading, densely set, persistent, perfoliate, monomorphic, deltoid, index 2.5–2.9, 1.5–2.0 by 0.4–0.7 mm, apex filiform, basal flaps pointed, cell walls clathrate throughout, cells yellowish, clathrate marginal protrusions longer at base, marginal glands situated all along, frequent, surface indument absent. *Fronds:* blade herbaceous, index 1.5–1.7, 12–28 by 8–16 cm, widest medially to subbasally, pinnatifid, lateral segments index 6.7–9.0, 70–90 by 7–10 mm, apex pungent, base truncate, sessile to shortly petiolate, margin serrate, terminal segment conform to lateral segments, equally long or slightly shorter than longest lateral segment, basal segments 12–25 mm separate from subbasal segments, sometimes shorter, deflexed; stipe in cross section near base 1.5–2.5 mm across, index length of stipe/length of blade 0.6–0.9. *Venation:* primary areolae uniserial, index 1.75–2.00, marginal free veins 1/3 length of areolae, 1–3 per areola, unforked, empty anastomoses sometimes present, angle between secondary and primary veins 40–50°. *Indument:* laminar glandular hairs unbranched, 2 cells long, including 1–2 terminal glands, laminar acicular hairs 2–8 cells long, situated all over lamina, density low, laminar scales fugaceous, petiolar acicular hairs absent. *Sori* uniserial, slightly sunken, medial between costa and margin, round, 0.8–1.1 mm in diam.; receptacular hairy paraphyses –10 cells long, 1 glandular branch sometimes present, receptacular scaly paraphyses clathrate, palaceous, linear, rhomboid, deltoid, 2 or more cells wide, index 1.2, 120–170 by 100–140 µm, persistent; episporangial paraphyses absent, sporangial capsule index 1.2–1.3, 220–260 by 170–220 µm, annulus with 19–21 cells, including 11–13(–14) indurated cells. *Spores* yellow, index L/P 1.5–1.7, 25–30 by 45–50 by 30–35 µm; exospore smooth; perispore widely detached, crestae situated parallel to the equatorial axis, building short excrescences at lateral poles, detailed outer surface ornamentation smooth, globules absent or few.

Distribution. Philippines: Luzon. Fig. 12.

Habitat. Secondary forest; mostly terrestrial on mossy ground, sometimes epiphytic on pine-trees; generally shaded, rarely exposed; alt. 500–1500 m.

Notes. 1. Plants growing in sunny and dry places are smaller in size. The colour of the fronds is lighter green, the texture more firm, the pinnae contracted, the sori deeper sunken and the margin less serrate, e.g. *Rödl-Linder 153*. In the shade the margin can even be serrulate and the longest fronds can be pendent.

2. Copeland himself misidentified some specimens of *G. benguetense* as *G. integrum,* although *G. integrum* is a later synonym for *G. subauriculatum,* which is very distinct from *G. benguetense* (see also Rödl-Linder, 1987).

3. *Rödl-Linder 85* is somewhat abnormal; the lateral segments are basally auricled and the uppermost pair of pinnae are adnate.

2. Goniophlebium demersum (Brause) Rödl-Linder, *comb. nov.*

Polypodium demersum Brause, Bot. Jahrb. (1912) 44, 45. — Type: *L. Schultze (33) 9,* Papua New Guinea: 'Kaiser-Wilhelmsland, Lager Hochmoos', 1600 m alt. (B; BM, fragm. of holo).

Goniophlebium subimpressum Copeland, Univ. Calif. Publ. Bot. 18 (1942) 226. — Type: *Clemens 41222* (MICH).

Epiphytic and vertically climbing, epilithic, terrestrial. *Rhizome* terete, 3–5 mm in diam., brown, phyllopodia 1.0–4.5 cm apart, vascular strands 7–10, dark bundle sheaths present, sclerenchyma strands 60–90. *Rhizome scales* evenly inserted or on protrusions, spadiceous, spreading, densely set, persistent, perfoliate, monomorphic, deltoid, index 1.5–2.0, 2.0–5.0 by 1.3–2.6 mm, the apex acuminate, basal flaps round, clathration of cell walls thin, basally absent, cells hyaline, clathrate marginal protrusions absent at the base, marginal glands situated terminally and basally, rare, surface indument absent. *Fronds:* blade herbaceous, index 2.0–2.8, 40–70(–100) by 20–25 cm, widest medially to subbasally, pinnate, lateral segments 110–190 by 5–15 mm, index 7.3–22.0, apex pungent, base cuneate to truncate, rarely cordate, sessile, margin serrate, terminal segment conform to lateral segments, half as long as longest lateral segment, basal segments 20–30 mm separate from subbasal segments, shorter, deflexed; stipe in cross section near base 3.0–5.0 mm across, index length of stipe/length of blade 0.4–0.6. *Venation:* primary areolae uniserial, index 1.5–1.6, marginal free veins very short or only hydathodes, 1 per areola, unforked, empty anastomoses absent, angle between secondary and primary veins 60–70°. *Indument:* laminar glandular hairs unbranched, 2–3 cells long, including 1–2 terminal glands, the laminar acicular hairs 2–4 cells long, situated along rhachis and costa, density variable, laminar scales persistent, petiolar acicular hairs absent. *Sori* uniserial, slightly sunken, marginal, round, 1.2–2.2 mm in diameter; receptacular hairy paraphyses –10 cells long, unbranched, receptacular scaly paraphyses clathrate, palaceous, linear, deltoid, 2 or more cells wide, index 1.0–1.4, 100–200 by 100–140 µm, ephemeral; episporangial paraphyses absent, sporangial capsule index 1.4–1.5, 355–365 by 235–265 µm, annulus with 18–21 cells, including (12–)13–14 indurated cells. *Spores* yellow, index L/P 1.4–1.6, 30–40 by 50–55 by 35–40 µm; exospore smooth; perispore widely detached, crestae situated parallel to the equatorial axis, building short excrescences at lateral poles, detailed outer surface ornamentation smooth, globules absent.

Distribution. Malesia: Celebes (see note 2), Moluccas (Seram), New Guinea; Solomon Islands. Fig. 13.

Habitat. Rainforest; epiphytic on mossy or rotten tree trunks and branches; epilithic and terrestrial on mossy, wet ridges; reported from *Nothofagus grandis* Steenis and *Nothofagus pullei* Steenis; alt. 800–3000 m.

Notes. 1. Copeland (herb. Copel. MICH) frequently misidentified specimens of *G. demersum* as *G. tomentellum* which is *G. subauriculatum.*

2. The only record from Celebes is *Meijer 9565* (L).

3. *Brass 22803* and *24594* (L) are slightly abnormal having the terminal and uppermost pinnae adnate.

3. Goniophlebium korthalsii (Mettenius) Beddome

Goniophlebium korthalsii (Mettenius) Beddome, Handb., Suppl. (1892) 91. — *Polypodium korthalsii* Mettenius, Ann. Mus. Bot. Lugd. Bat. 2 (1866) 223; Baker in Hooker & Baker, Syn. Fil., ed. 1 (1867) 345; Holttum, Rev. Fl. Malaya 2 (1954) 204, 205. — *Schellolepis korthalsii* Pichi Sermolli, Webbia 28 (1973) 470. — Type: *Korthals s.n.*, Sumatra 'occidentalis' (L, herb. no. 908.303-91; iso BO, L).

Epiphytic. *Rhizome* dorsiventrally flattened, 3–4 by 2–3 mm in diam., brown, phyllopodia 1.5–4.5 cm apart, vascular strands 9–12, dark bundle sheaths present, sclerenchyma strands 4–8. *Rhizome scales* evenly inserted, brunneous, appressed, quite densely set, ephemeral, perfoliate, monomorphic, deltoid, index 1.8–6.1, 1.7–4.9 by 0.6–0.8 mm, apex filiform, basal flaps short and round, clathration of cell walls getting thinner towards base, cells yellowish, clathrate marginal protrusions longer at base, marginal glands situated terminally and basally, rare, surface indument absent. *Fronds:* blade herbaceous, index 1.0–1.1, 26–38 by 26–35 cm, widest at base, pinnate, lateral segments index 5.0–5.2, 125–175 by 24–35 mm, apex acuminate, base cuneate to angustate, sessile to shortly petiolate, margin crenate to serrate, terminal segment conform to lateral segments, equally long as longest lateral segment, basal segments 25–30 mm separate from subbasal segments, equally long, patens; stipe in cross section near base 3–4 mm across, index length of stipe/ length of blade 0.2–0.3. *Venation:* primary areolae 2–3-serial, index 1.8–2.0, marginal free veins max. 1/3 length of costal areolae, 1 per areola, simple or forking, empty anastomoses frequent, angle between secondary and primary veins 60–70°. *Indument:* laminar glandular hairs unbranched, 2 cells long, including 1 terminal gland, laminar acicular hairs absent, laminar scales sometimes persistent, petiolar acicular hairs absent. *Sori* 1–3-serial, superficial, round, 1.5–2.0 mm in diam.; receptacular hairy paraphyses –6 cells long, unbranched, receptacular scaly paraphyses clathrate, palaceous, linear, deltoid, 2 or more cells wide, index 0.9–1.6, 76–140 by 76–153 µm, persistent; episporangial paraphyses absent, sporangial capsule index 1.1–1.2, 320–335 by 265–295 µm, annulus with 20–22 cells, including 12–13 indurated cells. *Spores* yellowish, index L/P 1.3–1.4, 35–45 by 50–60 µm; exospore smooth; perispore for the greater part attached, crestae situated parallel to the equatorial axis, building very long excrescences at lateral poles, detailed outer surface ornamentation smooth, few globules present.

Distribution. Peninsular Malaysia (Perak), North Sumatra. Fig. 13.

Habitat. Wet and swampy areas; epiphytic, clinging in thick clusters to the stems of trees; abundant drooping from trees; alt. 0–30(–800) m.

Notes. 1. Unique in Asia because the distribution pattern of the sori can be one- to three-serial. The perispore has remarkably long equatorial excrescences at the lateral poles.

2. Mature spore material is rare. Measurements have therefore been taken from very few spores only.

3. Collections are rare. Perak: *Allen 2647* (SING). Sumatra: *Brooks 85* (L, MICH), *180* (MICH); *King 2943* (M, SING); *Korthals s.n. '46'* (BO, L).

4. Goniophlebium mehibitense (Christensen) Parris

Goniophlebium mehibitense (Christensen) Parris, Brit. Fern Gaz. 12 (1980) 118. — *Polypodium mehibitense* Christensen, Mitt. Inst. allgem. Bot. Hamb. 7 (1928) 159. — Type: *H. Winkler 706*, West Borneo, Bukit Mehibit, 500 m alt., 'epiphytic', 09-12-1924 (HBG).

Polypodium papilliferum Holttum, Journ. Mal. Br. R. As. Soc. 6 (1928) 22. — Type: *C. Boden Kloss 14800*, Sumatra, Sipora (SING).

Epiphytic. *Rhizome* terete, 5–6 mm in diam., brown, phyllopodia 2–4 cm apart, vascular strands 11–13, dark bundle sheaths present, sclerenchyma strands > 100. *Rhizome scales* evenly inserted, brunneous, spreading, densely set, ephemeral, perfoliate, monomorphic, deltoid, index 2.8–4.9, 1.4–4.4 by 0.5–0.9 mm, apex acuminate, basal flaps round, cell walls clathrate throughout, cells yellowish, clathrate marginal protrusions longer at base, marginal gland situated only terminal, surface indument rhizoid. *Fronds:* blade herbaceous, index 2.2–3.1, 45–69 by 20–22 cm, widest at base, pinnate, lateral segments index 7.2–7.3, 110–130 by 14–18 mm, apex pungent, base truncate, sessile, margin serrate, terminal segment conform to lateral segments, half or third as long as longest lateral segment, basal segments 30–40 mm separate from subbasal segments, equally long, patens; stipe cross section near base 3.5–4.5 mm across, index length of stipe/length of blade 0.3–0.4. *Venation:* primary areolae biserial, index of costal areolae 3.15–3.25, marginal free veins max. 1/3 length of costal areolae, 1 per areola, unforked, empty anastomoses absent, angle between secondary and primary veins 60–70°. *Indument:* laminar glandular hairs unbranched, 2 cells long, including 1 terminal gland, laminar acicular hairs absent, laminar scales sometimes persistent, petiolar acicular hairs absent. *Sori* uniserial, deeply sunken, costal, round, 0.4–0.5 mm in diam.; receptacular hairy paraphyses –10 cells long, unbranched, receptacular scaly paraphyses clathrate, paleaceous, 2 cells wide, index 1.6, 100 by 65 µm, ephemeral; episporangial paraphyses absent, sporangial capsule index 1.6, 320–385 by 200–240 µm, annulus with 20–23 cells, including 13–15 indurated cell. *Spores* brownish, index L/P 1.4–1.6, 30–35(–40) by 45–60 by 25–35 µm; exospore smooth; perispore widely detached, crestae situated parallel to the equatorial axis, locally protruding, building short excrescences at lateral poles, detailed outer surface ornamentation smooth, few globules present.

Distribution. Sumatra, Borneo. Fig. 12.

Habitat. Several types of forest (e.g. dipterocarp, alluvial, mixed lowland limestone forest); epiphytic on small trees, c. 1.5 m from ground; alt. 100–300 m.

Notes. 1. Unique because of the presence of laminar bristles and the strikingly papilliform sori.

2. Collections are rare. Sumatra: *Boden Kloss 14800* (SING); *Burchardt 11125* (NY). Borneo: *Jermy 13988, 14002* (U); *Richards 1562* (SING); *Winkler 706* (BM).

5. Goniophlebium percussum (Cavanilles) Wagner et Grether

Goniophlebium percussum (Cavanilles) Wagner et Grether, Occ. Pap. Bishop Mus. 19 (1948) 88; Copeland, Fern Fl. Philip. 3 (1960) 460; Rödl-Linder, Philip. Journ. Sc. 116 (1987) 155. — *Cyathea percussa* Cavanilles, Descr. (1801) 548. — *Schellolepis percussa* Pichi Sermolli, Webbia 28 (1973) 470. — *Polypodium cyathoides* Swartz, Syn. Fil. (1806) 37, nom. nov., non *Polypodium percussum* Cavanilles (1801); Christensen, Dansk Bot. Ark. 9 (1937) 29. — *Goniophlebium cyathoides* Hosokawa, Trans. Nat. Hist. Soc. Formosa 32 (1942) 286. — *Polypodium cyathoides* Swartz f. *typicum* Christensen, Ark. for Bot. 9 (1910) 39, nom. illeg. [ICBN art. 34.1]. — Type: *Luis Née*, Marianas (not traced in MA; 1 pinna in S-PA, see note 3).

Marginaria verrucosa [*Polypodium verrucosum* Wallich, Cat. (1828) no. 296, nom. nud.] Hooker & Bauer, Gen. Fil. (1838) ad pl. 14. — *Goniophlebium verrucosum* J. Smith, Cat. (1857) 4; Beddome, Handb. (1883) 324. — *Schellolepis verrucosa* J. Smith, Ferns Brit. & For. (1866) 83; Hist. Fil. (1875) 93. — *Polypodium verrucosum* Mettenius, Farngatt. Polypod. (1857) 81; Hooker, Gard. Ferns (1864) pl. 41; Spec. Fil. 5 (1863) 31; Baker in Hooker & Baker, Syn. Fil., ed. 2 (1883) 344; Diels in Engler & Prantl, Nat. Pflanzenfam. 1 (1899) 312, fig. 163: C–E; Copeland, Philip. Journ. Sc. 2 (1907) 139; Holttum, Rev. Fl. Malaya 2 (1954) 206, fig. 106. — *Polypodium cyathoides* Swartz var. *verrucosum* Christensen, Ark. for Bot. 9 (1910) 39, nom. illeg. [ICBN art. 34.1]. — Type: *Wallich 296*, Penang & Singapore, 1822 (K, herb. Hookerianum).

Polypodium cuspidatum auct. non Don: Mettenius, Farngatt. Polypod. (1857) 81, c. syn.

Polypodium koningsbergeri auct. non van Alderwerelt van Rosenburgh: Christensen, Dansk Bot. Ark. 9 (1937) 29.

Goniophlebium rotense auct. non Hosokawa: Hosokawa, Trans. Nat. Hist. Soc. Form. 32 (1942) 286.

Epiphytic and vertically or spirally climbing, terrestrial and linearly creeping. *Rhizome* terete, 5–10(–11) mm in diam., brown, phyllopodia 1.5–2.5 cm apart, vascular strands 14–19, dark bundle sheaths present, sclerenchyma strands 70–100. *Rhizome scales* evenly inserted, ferrugineous, appressed, densely set, ephemeral, perfoliate, monomorphic, deltoid, index 2.8–3.6, 2.5–4.0 by 0.7–1.3 mm, apex acuminate, basal flaps round, cell walls clathrate throughout, cells yellow, clathrate marginal protrusions slightly shorter at base, marginal glands situated terminally and basally, rare, surface indument rhizoid. *Fronds:* blade firm herbaceous, index 2.1–4.4, 38–99(–200) by 18–38(–45) cm, widest at base, pinnate, lateral segments index 6.2–6.8, 125–205 by 20–30 mm, apex acuminate, base shortly angustate, shortly petiolate, margin entire to crenate, terminal segment conform to lateral segments, slightly longer than longest lateral segment, basal segments 20–60 mm separate from subbasal segments, equally long, patens; stipe in cross section near base 3.5–5.0 mm across, index length of stipe/length of blade 0.2–0.6. *Venation:* primary areolae 3–4-serial, index of costal areolae 2.0–2.4, marginal free veins max. 1/3 length of costal areolae, 1 per areola, simple and forking, empty anastomoses frequent, angle between secondary and primary veins 70–75°. *Indument:* laminar glandular hairs sometimes with an acicular or a glandular branch (see note 4), 2 cells long, including 1–2 terminal glands, laminar acicular hairs 2–5 cells long, situated all over lamina, density low, laminar scales fugaceous, petiolar acicular hairs absent. *Sori* uniserial, deeply sunken, costal, round, 0.8–1.0 mm in diam.; receptacular hairy paraphyses –8 cells long, unbranched, receptacular scaly paraphyses clathrate, palaceous, linear, deltoid, 3 or more cells wide, index 1.2–1.3, 230–250 by 180–200 µm, persistent; episporangial paraphyses absent, sporangial capsule index 1.2–1.5, 210–300 by 170–205 µm, annulus with 20–22 cells, including 12–13(–14) indurated cells. *Spores* yellow, index L/P 1.7–1.8, 20–25 by 40–45 by 20–25 (–35) µm; exospore smooth; perispore widely detached, crestae situated parallel to the equatorial axis, building short excrescences at lateral poles (see note 2), detailed outer surface ornamentation smooth, globules absent.

Chromosomes. n = 37.

Distribution. Thailand; Malesia: Peninsular Malaysia, Singapore, Sumatra, Java, Borneo; Philippines, New Guinea; Australia: Queensland. Fig. 14.

Habitat. Several types of primary and secondary forest (dipterocarp, pine, peat swamp); epiphytic on mossy, often rotten tree trunks; terrestrial in wet, loose soil; reported from crown of *Dactylocladus stenostachys* Oliv. and amongst persistent leaf bases of savannah fan palms; alt. 0–1100(–1650) m.

Notes. 1. The width of the lateral segments is quite variable.

2. The equatorial excrescences at the lateral poles are twisted.

3. Christensen (1910) studied one pinna of the type specimen in Swartz' herbarium (S-PA) which could not be traced.

4. Laminar glandular hairs have sometimes an acicular branch which has not been observed in any other species.

5. Juvenile fronds of the present species have very long terminal segments as have those of *G. persicifolium* (see fig.50e, f), e.g. *Rödl-Linder 207* and *119b.*

6. The fertile pinnae are sometimes contracted and drooping. The rhachis is extremely flexible which makes fresh material easily distinguishable from *G. persicifolium,* even when sterile. This species is otherwise very similar to *G. persicifolium.* A list of diagnostic characters of adult plants is given below.

	percussum	*persicifolium*
rhizome		
sclerenchyma strands	70–100	40–50
rhizome scales		
marginal glands	absent	present
laminar indument		
acicular hairs	present	absent
sori		
relation to surface	deeply impressed	slightly impressed
diameter (mm)	< 1.5	> 1.5
dark scaly paraphyses	ring-like arranged	absent

6. Goniophlebium persicifolium (Desvaux) Beddome — Fig. 50d–h.

Goniophlebium persicifolium (Desvaux) Beddome, Ferns Brit. Ind., Suppl. (1876) 21, (*'persicaefolium'*); Copeland, Fern Fl. Philip. 3 (1960) 459, 460; Rödl-Linder, Philip. Journ. Sc. 116 (1987) 157, 158. — *Polypodium persicifolium* Desvaux (*'persicaefolium'*), Mag. Ges. Naturf. Freunde Berlin 5 (1811) 316; Baker in Hooker & Baker, Syn. Fil., ed. 1 (1867) 344; Holttum, Rev. Fl. Malaya 2 (1954) 206, 207. — *Schellolepis persicifolia* Pichi Sermolli, Webbia 28 (1973) 470. — Type: *Anon. s.n.*, Java (P-Juss, fragm. of holo).

Polypodium grandidens Kunze [Ind. Fil. Hort. Bot. Lips. (1843) nom. nud.] ex Mettenius, Bot. Zeit. 4 (1846) 423; Linnaea 23 (1850) 278, 318, 319; Mettenius, Ind. Fil. Hort. Bot. Lips. (1856) 33, pl. 23; Hooker, Spec. Fil. 5 (1863) 31. — *Goniophlebium grandidens* Fée, Gen. (1852) 255. — Type: a cultivated specimen (LZ, destroyed).

Polypodium colpothrix Kunze in Mettenius, Linnaea 23 (1850) 276, nomen, 316; Mettenius, Ind. Fil. Hort. Bot. Lips. (1856) 33. — Type: a cultivated specimen ex Hort. Bot. Amsterdam, 1848 (LZ, destroyed).

Polypodium phlebodioides Copeland, Polypod. Philip. (1905) 123; Philip. Journ. Sc. 1, Suppl. 2 (1906) 162. — Type: *E.B. Copeland 1762a*, Mindanao, Mt. Apo, 1300 m alt., 'epiphyte on tree trunk', 27-10-1904 (MICH).

Polypodium integrius Copeland (*'integriore'*), Philip. Journ. Sc. 2 (1907) 139. — Type: *E.D. Merrill 6005*, Mindoro, Mt. Halcon, 2200 m alt., -11-1906 (PNH, destroyed in 1945; iso MICH).

Polypodium koningsbergeri van Alderwerelt van Rosenburgh, Bull. Dépt. Agric. Ind. néerl. 18 (1908) 21, 22, non Rosenstock (1912); Christensen, Ark. for Bot. 9 (1910) 38; Dansk Bot. Ark. 9 (1937) 29, q.n.s. — Type: *van Alderwerelt van Rosenburgh s.n.*, Java, Preanger Regencies (not traced in BO, see note 3).

Polypodium persicifolium Desvaux var. *mettenii* Rosenstock, Feddes Repert. 13 (1914) 220. — Type: *Winkler 77a*, Sumatra, in 'terra Batacorum', 1911 (not traced in HBG and P).

Goniophlebium ponapense Copeland, Occ. Pap. Bishop Mus. 15 (1939) 90, fig. 9; Hosokawa, Trans. Nat. Hist. Soc. Formosa 31 (1941) 476. — Type: *M. Takamatsu 1045*, Micronesia, Caroline Is., Ponape, Tolotom, 11-02-1936 (not traced in MICH); paratype: *M. Takamatsu 971* (MICH).

Goniophlebium rotense Hosokawa, Trans. Nat. Hist. Soc. Formosa 31 (1941) 476; ibid. 32 (1942) 286, q.n.s. — Type: *T. Hosokawa 7622*, Micronesia, Marianas, Rota I., 13-07-1934 (TAI).

Polypodium cuspidatum auct. non Don (1825) c. syn. hom.: Presl (1825): Blume, Enum. (1828) 132, 133; Flora Javae Filicum (1830) 132; (1847) pl. 82; Mettenius, Farngatt. Polypod. (1857) 81; Hooker, Spec. Fil. 5 (1863) 32. — *Goniophlebium cuspidatum* auct. non (Don) Presl, Tent. Pterid. (1836) 186; Beddome, Ferns Brit. Ind. (1865) pl. 79. — *Schellolepis cuspidata* auct. non (Don) J. Smith, Ferns Brit. & For. (1866) 82.

Epiphytic and vertically or spirally climbing, terrestrial and linearly creeping. *Rhizome* terete, 5–10 mm in diam., brown, phyllopodia 2–3 cm apart, vascular strands 10–17, dark bundle sheaths present, sclerenchyma strands 40–50. *Rhizome scales* evenly inserted, ferrugineous, appressed, densely set, ephemeral, perfoliate, monomorphic, deltoid, index 2.2–3.3, 1.8–5.0 by 0.8–1.5 mm, apex acuminate, basal flaps round, cell walls clathrate throughout, cells yellowish, clathrate marginal protrusions slightly longer at base, marginal glandular indument 1–2 cells long, situated all along, frequent, surface indument rhizoid. *Fronds:* blade firm herbaceous, index 1.5–3.9, 35–60(–150) by (14–)20–38 cm, widest at base, pinnate, lateral segments index 8.8–10.0, 200–220 by 20–25 mm, apex acuminate, base angustate, long petiolate, margin entire to crenate, in a Malayan variation serrate, terminal segment conform to lateral segments, equally long or slightly longer than longest lateral segment, basal segments 30–60 mm separate from subbasal segments, equally long, patens; stipe in cross section near base 3.0–4.5 mm across, index length of stipe/ length of blade 0.5–0.7. *Venation:* primary areolae 2–4-serial, index of costal areolae 2.00–2.75, free veins max. 1/3 length of areolae, 1 per areola, simple and forking, empty anastomoses frequent, angle between secondary and primary veins 50–60°. *Indument:* laminar glandular hairs sometimes with a glandular branch, 2 cells long, including 1–3 terminal glands, laminar acicular hairs absent, laminar scales fugaceous, petiolar acicular hairs absent. *Sori* uniserial, slightly sunken, costal, round, 1.8–2.2 mm in diam.; receptacular hairy paraphyses –6 cells long, unbranched, receptacular scaly paraphyses clathrate, palaceous, linear, deltoid, 2 or more cells wide, index 1.4–1.5, 90–110 by 60–80 µm, ephemeral; episporangial paraphyses absent, sporangial capsule index 1.4–1.5, 235–275 by 155–195 µm, annulus with 20–21 cells, including 12–13 indurated cells. *Spores* yellow, index L/P 1.6–1.8, 20–25 by (35–)40–45 by 25–30 µm; exospore smooth; perispore for the greater part attached, crestae situated parallel to the equatorial axis, building short excrescences at lateral poles, detailed outer surface ornamentation smooth, globules absent.

Chromosomes. n = 37.

Distribution. India: Assam; China (Kwangsi); Thailand; Vietnam; Malesia: Peninsular Malaysia, Sumatra, Java, Borneo, Celebes, Moluccas (Seram), Philippines (Luzon, Mindanao), New Guinea; Solomon Islands; Marianas, Caroline Islands. Fig. 15.

Habitat. Different types of primary and secondary forest (e.g. *Castanopsis, Altingia, Podocarpus*); mostly high or low epiphytic on rotten or living tree trunks, shaded or partially exposed, rarely terrestrial in wet loose soil; alt. 150–1900 m.

Notes. 1. The fern described as *Polypodium grandidens* originates from the Malay Peninsula. The differences regard the margin of the lateral segments which is strongly serrate and the rhizome scales which are dark brown with two-celled marginal glands.

2. The material studied shows much variation in the length of blade – short upright or long pendent – which is not of specific importance.

3. In his letter of 25-06-1988, Dr. Soedarsono Riswan, Head of Herbarium Bogoriense, informed me about the absence of the type specimen of *Polypodium koningsbergeri* in BO.

7. Goniophlebium rajaense (Christensen) Parris

Goniophlebium rajaense (Christensen) Parris, Brit. Fern Gaz. 12 (1980) 118. — *Polypodium rajaense* Christensen, Mitt. Inst. allgem. Bot. Hamb. 7 (1928) 159. — *Polypodium integrius* Copeland var. *rajaense* Christensen, Ind. Fil., Suppl. 3 (1934) 151, 157. — Type: *H. Winkler 980b*, West Borneo, Bukit Raja, 1400 m alt., 'epiphytic', 20-12-1924 (HBG).

Epiphytic. *Rhizome* dorsiventrally flattened, 3–4 by 2–3 mm in diam., brown, phyllopodia 2–7 cm apart, vascular strands 10–12, dark bundle sheaths present, sclerenchyma strands 15–20. *Rhizome scales* evenly inserted, ferrugineous, appressed, quite densely set, persistent, perfoliate, monomorphic, deltoid, index 2.6–2.9, 1.7–3.4 by 0.6–1.2 mm, apex filiform, basal flaps round, cell walls clathrate throughout, getting thinner at base, cells yellowish, clathrate marginal protrusions longer at base, marginal glands situated terminally and basally, rare, surface indument rhizoid. *Fronds:* blade herbaceous, index 1.7–1.9, 50–60 by 26–30 cm, widest at base, pinnate, lateral segments index 7–10, 150–190 by 15–27 mm, apex acuminate, base angustate, shortly petiolate, margin entire to crenate, terminal segment conform to lateral segments, equally long or slightly shorter than longest lateral segment, basal segments 20–30 mm separate from subbasal segments, equally long, patens; stipe in cross section 3–4 mm across, index length of stipe/length of blade 0.5. *Venation:* primary areolae triserial, index of costal areolae 1.2–1.4, marginal free veins max. 1/3 length of costal areolae, 1 per areola, simple or forking, empty anastomoses quite frequent, angle between secondary and primary veins 65–75°. *Indument:* laminar glandular hairs unbranched, 2 cells long, including 1 terminal gland, laminar acicular hairs absent, laminar scales fugaceous, petiolar acicular hairs absent. *Sori* uniserial, slightly sunken, costal, round, 2–3 mm in diam.; receptacular hairy paraphyses –8 cells long, unbranched, receptacular scaly paraphyses clathrate, palaceous, linear, deltoid, 3 or more cells wide, index 1.1–2.0, 90–410 by 80–205 µm, persistent; episporangial paraphyses absent, sporangial capsule index 1.2, 255–275 by 205–225 µm, annulus with 17–20 cells, including 12–14 indurated cells. *Spores* yellowish, index L/P 1.4–1.6, 35–45 by 55–65 by 40–45 µm; exospore smooth; perispore for the greater part attached, crestae situated parallel to equatorial axis, building short excrescences at lateral poles, detailed outer surface ornamentation smooth or glebulate, many globules present.

Distribution. Borneo (Mt. Kinabalu, Mt. Penrissen). Fig. 13.

Habitat. Different types of primary forest (oak, chestnut); epiphytic, c. 4.50 m from ground on fallen tree trunk; on sedimentaries, friable soil; alt. 650–2000 (–2900) m.

Notes. 1. *Chai S 34010* (K, L): 'Sori dark brown.'

2. Collections are rare. *L.B. & E.C. Abbe 9979* (NY); *Chai S 34010* (K, L); *Clemens 29484* (BO, L, NY), *30612* (BM, NY), *32447* (M, MICH, NY), *33081* (BO); *Holttum 25393* (BO); *Mjöberg 50* (BM); *Winkler 980* (BM), *980b* (HBG).

8. Goniophlebium serratifolium Brackenridge

Goniophlebium serratifolium Brackenridge, U.S. Expl. Exped. 16 (1854) 35. — *Polypodium subauriculatum* Blume var. *serratifolium* Hooker, Spec. Fil. 5 (1864) 33, p.p. — *Polypodium serratifolium* Diels ['(Brackenridge) Hooker'], in Engler & Prantl, Nat. Pflanzenfam. 1 (1899) 312. — Type: *Brackenridge s.n.*, Fiji Is. (US, herb. no. 62502).

Goniophlebium subcordatum Copeland, Univ. Calif. Publ. Bot. 18 (1942) 226. — Type: *Brass 14045*, New Guinea, 'West Irian', Idenburg River, -04-1939 (MICH).

Polypodium subauriculatum auct. non Blume: Baker in Hooker & Baker, Syn. Fil., ed. 1 (1867) 344; Hayata, Bot. Mag. Tokyo 23 (1909) 79, 80.

Epiphytic, terrestrial. *Rhizome* terete, 4–6 mm in diam., brown, phyllopodia 1–2 cm apart, vascular strands 6–13, dark bundle sheaths present, sclerenchyma strands > 100. *Rhizome scales* evenly inserted, badious, spreading, densely set, persistent, perfoliate, monomorphic, deltoid, index 3.2–3.9, 2.6–3.9 by 0.8–1.0 mm, apex acuminate, basal flaps pointed, cell walls thinly clathrate throughout, cells yellowish, clathrate marginal protrusions present, marginal glands situated at base, frequent, surface indument absent. *Fronds:* blade herbaceous, index 2.2–3.0, 50–150 by 23–50 cm, widest at base, pinnate, lateral segments index 12.7–18.5, 140–240 by 11–13 mm, apex acuminate, base cuneate, rarely truncate, sessile, margin serrate, terminal segment conform to lateral segments, half as long as longest lateral segment, basal segments 30–40 mm separate from subbasal segments, equally long, patens; stipe in cross section near base 4.0–9.5 mm across, index length of stipe/length of blade 0.7–0.9. *Venation:* primary areolae 1–2-serial, index of costal areolae 1.5–1.9, marginal free veins max. 1/2 length of costal areolae, 1–3 per areola, simple and rarely forking, empty anastomoses frequent, angle between secondary and primary veins 60–70°. *Indument:* laminar glandular hairs sometimes with a glandular branch, 2–3 cells long, including 1–2 terminal glands, laminar acicular hairs 2–4 cells long, situated marginally, density low, laminar scales quite persistent, petiolar acicular hairs absent. *Sori* uniserial, superficial, costal, round, 1.5–3.0 mm in diam.; receptacular hairy paraphyses –5 cells long, unbranched, receptacular scaly paraphyses clathrate, palaceous, linear, deltoid, 2 cells wide, index 1.0–1.5, 100–200 by 100–130 µm, persistent; episporangial paraphyses absent, sporangial capsule index 1.1, 240–305 by 215–285 µm, annulus with 19–20 cells, including 11–12 indurated cells. *Spores* yellowish, index L/P 1.7–1.8, 25–30 by 45–50 by 25–30 µm; exospore smooth; perispore for the greater part attached, crestae situated parallel to equatorial axis, wrinkled, building short excrescences at lateral poles, detailed outer surface ornamentation smooth, globules absent.

Distribution. West New Guinea; Fiji and Samoa Islands. Fig. 12.

Habitat. Epiphytic in dense forest; terrestrial in ridge forest; alt. 50–1000 m.

Notes. 1. This species has been considered endemic in the Fiji and Samoan Islands. The type specimen of Copeland's *G. subcordatum* is the only record from New Guinea.

2. A clear-cut species which has formerly been confused with *Polypodium subauriculatum* Blume by Hooker (1864) and Hayata (1909). Conspicuous differences concern the rhizome which is not chalky, the terminal frond segment which is conform to the lateral segments, the base of the lateral segments which is cuneate (truncate), the spores with short lateral excrescences, and the receptacular scaly paraphyses which are palaceous.

9. Goniophlebium terrestre Copeland — Fig. 50a–d.

Goniophlebium terrestre Copeland, Philip. Journ. Sc. 56 (1935) 106, 107, pl. 13, 14; Fern Fl. Philip. 3 (1960) 460; Rödl-Linder, Philip. Journ. Sc. 116 (1987) 161. — *Schellolepis terrestris* Price, Kalikasan, Philip. Journ. Biol. 3 (1974) 178. — Type: *E.B. Copeland 272*, Mt. Makiling, 500 m alt., -12-1932 (PNH, destroyed in 1945; iso MICH).

Epiphytic and vertically climbing, epilithic or terrestrial and linearly creeping. *Rhizome* dorsiventrally flattened, 1.8–3.0 mm by 1.5–2.6 mm in diam., brown, phyllopodia 4–5(–17) cm apart, vascular strands 6–9, dark bundle sheaths present, sclerenchyma strands 3–11. *Rhizome scales* evenly inserted, spadiceous, spreading, densely set, persistent, perfoliate, monomorphic, deltoid, index 3.5–4.3, 3.0–4.7 by 0.8–1.1 mm, apex filiform, basal flaps round, cell walls clathrate, except at base, cells hyaline, marginal protrusions not clathrate at base, marginal glandular indument 1–2 cells long, situated all along, rare, surface indument absent. *Fronds:* blade thinly herbaceous, index 1.3–1.7, 7–19 by 4–14 cm, widest at base, pinnate, lateral segments index 6.0–7.5, 45–90 by 6–15 mm, apex acuminate, base cuneate or shortly angustate, sessile or shortly petiolate, margin entire to serrate, terminal segment conform to lateral segments, equally long or slightly longer than longest lateral segment, basal segments 13–25 mm separate from subbasal segments, equally long, patens; 1.1–1.8 mm in basal diam., index length of stipe/length of blade 0.5–0.8. *Venation:* primary areolae uniserial, index 1.2–1.6, marginal free veins max. 1/5 length of areolae or only hydathodes, 1 per areola, not forking, empty anastomoses absent, angle between secondary and primary veins 60–70°. *Indument:* laminar glandular hairs unbranched, 2 cells long, including 1–2 terminal glands, laminar acicular hairs absent, laminar scales fugaceous, petiolar acicular hairs absent. *Sori* uniserial, superficial, medial to marginal, round, 1.6–2.0 mm in diam.; receptacular hairy paraphyses –6 cells long, unbranched, receptacular scaly paraphyses clathrate, peltate or palaceous, linear, deltoid, 2 or more cells wide, index 1.5, 210–320 by 140–210 µm, persistent; episporangial paraphyses absent, sporangial capsule index 1.4, 285–340 by 205–245 µm, annulus with 21–22 cells, including 13–14 indurated cells.*Spores* yellow, index L/P 1.5–1.7, 30–40 by 45–60 by 35–45 µm; exospore smooth; perispore for the greater part attached, crestae parallel to equatorial axis, building long (c. 1/4 length of spore) excrescences at lateral poles, detailed outer surface ornamentation undulate, many globules present.

Distribution. Philippines: Luzon (Mt. Makiling). Fig. 12.

Habitat. Primary forest (mossy); low epiphyte on tree trunks; epilithic on mossy or bare rocks, rarely terrestrial in loose humus; alt. 500–850 m.

Notes. 1. Only 30–50 spores per sporangium have been counted.

2. The present species is small-sized with a thin rhizome. Plants growing in deep shade have a dark green colour compared to those growing exposed to light.

3. In young fronds rhachis as well as stipe are slightly winged which has not been observed in any of the other species belonging to the *G. percussum*-group.

4. This species was, even under variable climatic conditions, successfully grown in Utrecht, while in the author's garden in Manila it never developed fertile fronds.

5. The restricted altitudinal range of this species is noteworthy.

6. Collections are rare. *Copeland PPE272* (MICH); *Orlido 74* (CAHP); *Price 286, 498* (CAHP); *Rödl-Linder 51, 134, 136* (L).

17.2. GONIOPHLEBIUM SUBAURICULATUM-GROUP

10. Goniophlebium amoenum (Mettenius) Beddome — Fig. 51e–h.

Goniophlebium amoenum (Mettenius) [J. Smith, Journ. Bot. 4 (1842) 57, nom. nud.] Beddome, Ferns Brit. Ind. 1 (1866) 5, pl. 5. — *Polypodium amoenum* [Wallich, Cat. (1828) no. 290, nom. nud.] Mettenius, Farngatt. Polypod. (1857) 80; Hooker, Spec. Fil. 5 (1863) 24; Clarke,

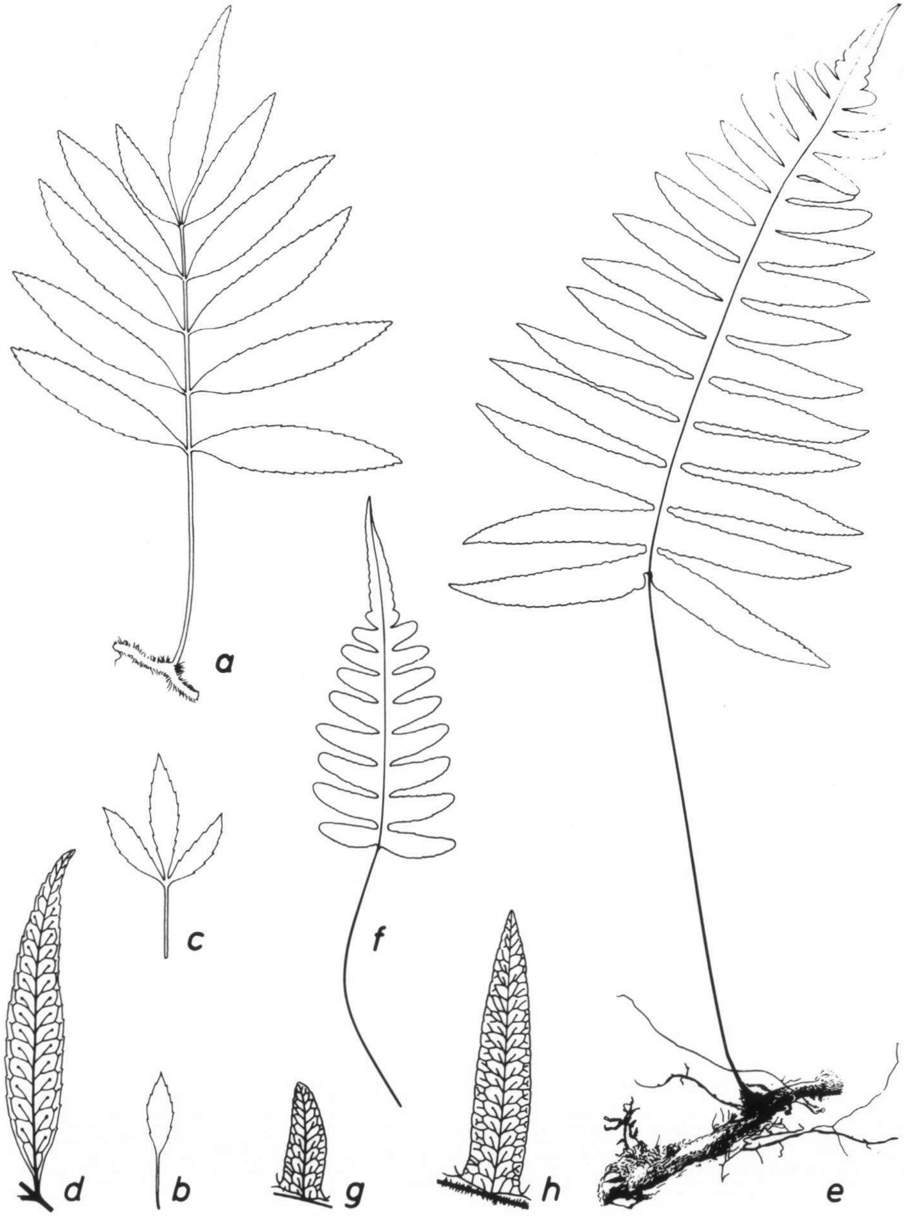

Fig. 51. *Goniophlebium terrestre* Copeland. a. Adult plant, × 0.5; b, c. juvenile fronds, × 0.5; d. venation pattern. — *G. amoenum* (Mettenius) Beddome. e. Adult plant, × 0.5; f. juvenile frond, × 0.5; g, h. venation pattern, × 0.75.

Trans. Linn. Soc. London, ser. 2, 1 (1880) 550; Diels in Engler & Prantl, Nat. Pflanzenfam. 1 (1899) 311, 312; Christ, Bull. Acad. Géogr. Bot. 1 (1902) 203; Christensen, Acta Horti Gotoburg. 1 (1924) 99, Contr. U.S. Nation. Herb. 26 (1931) 316; Wu, Sunyatsenia 3 (1932) 264, pl. 123; Ching, Contr. Inst. Bot. Acad. Peiping 2 (1933) 43; Icon. Fil. Sin. 2 (1934) ad pl. 99; Tagawa, Acta Phytotax. Geobot. 8 (1939) 234; Mem. Coll. Sc. Univ. Kyoto ser. B, 21 (1954) 73, 74. — *Marginaria amoena* Presl, Tent. Pterid. (1836) 188. — *Schellolepis amoena* J. Smith, Hist. Fil. (1875) 93. — *Polypodiodes amoena* Ching, Acta Phytotax. Sin. 16 (1978) 27. — Type: *Wallich 290*, Nepal (K, herb. Hookerianum).

Polypodium amoenum Mettenius var. ? *tonglense* Clarke, Trans. Linn. Soc. London ser. 2, 1 (1880) 550; Bir, Trikha & Vasudeva, New Bot. 1 (1974) 150. — Type: *C.B. Clarke s.n.*, Tonglo, Sikkim, 3300 '330' m alt. (K).

Polypodium yunnanense Franchet, Bull. Soc. Bot. France 32 (1885) 29; Christ, Bull. Soc. Bot. France 52, Mém. 1 (1905) 13. — *Goniophlebium yunnanense* Beddome, Handb., Suppl. (1892) 88, 89; Ching, Contr. Inst. Bot. Acad. Peiping 2 (1933) 46. — Type: *Delavay 68*, Yunnan, Mao-Kon-Tchang, 'supra Ta-Pin-Tze', 27-08-1883 (not traced in P).

Polypodium amoenum Mettenius f. *pilosum* Clarke, Journ. Linn. Soc. London Bot. 24 (1888) 417; Beddome, Handb., Suppl. (1892) 89, 'var.'. — Syntypes: *C.B. Clarke 44274*, Shillong, 26-06-1886 (K); *id. 44822*, Khasia, 02-09-1886 (K, see note 4).

Polypodium amoenum Mettenius var. *chinense* Ching, Contr. Inst. Bot. Acad. Peiping 2 (1933) 45. — *Polypodium subamoenum* Clarke var. *chinense* Christ, Nuov. Giorn. Bot. Ital. 4 (1897) 99. — Syntypes: *J. Giraldi s.n.*, Tun-u-sse 'in Shen-si meridionali', 16–18-06-1894 (P); *idem s.n.*, Hua-tzo-pin, 20-06-1894 (P); *idem s.n.*, Thae-peisan, -10-1894, 1895 (P).

Polypodium valdealatum Christ, Bull. Herb. Boissier 7 (1899) 4, 5. — Type: *A. Henry 11513*, Mengtze, 'North mountain forests', 2700 m alt. (iso NY).

Polypodium amoenum var. *latedeltoideum* Christ, Bull. Acad. Géogr. Bot. (1907) 142. — Type: *Esquirol s.n.*, Kouy-Yang (not traced in P).

Polypodium duclouxii Christ, Notul. Syst. [Paris] 1 (1909) 34; Ching, Icon. Fil. Sin. 2 (1934) ad pl. 99. — *Polypodium amoenum* Mettenius var. *duclouxii* Ching, Contr. Inst. Bot. Acad. Peiping 2 (1933) 46, 47. — Lectotype (Ching, 1933): *Ngoueou & Ducloux 130*, Hay-y, 'près de Son-lan' (P, herb. Christ).

Polypodium amoenum Mettenius var. *pilosum* Rosenstock, Feddes Repert. 13 (1914) 134; Ching, Contr. Inst. Bot. Acad. Peiping 2 (1933) 45, 46, 'forma *pilosa* Rosenstock'. — Type: *Cavalerie 2789*, Kuy-tcheou, Pin-fa (P, see note 4).

Polypodium arisanense Hayata, Icon. Pl. Form. 4 (1914) 243, fig. 170, non Rosenstock (1915); DeVol & Kuo, Fl. Taiwan 1 (1975) 202. — *Marginaria arisanense* Nakai ex Itô, Journ. Jap. Bot. 11 (1935) 94. — Type: *B. Hayata & S. Sasaki s.n.*, Mt. Arisan, 2300–2700 m alt., -01-1912 (TI).

Polypodium bonatianum Brause, Hedwigia 54 (1914) 207, 208, pl. 3: fig. 1. — Type: *Maire 6527*, Yunnan, Tong-tchouan, 2800 m alt., -09-1910 (P; B, fragm. of holo).

Polypodium amoenum Mettenius var. *xerophyticum* Mehra & Bir, Res. Bull. Punjab Univ. Sci. 15 (1964) 166; Bir, Trikha & Vasudeva, New Bot. 1 (1974) 150, fig. 30–33. — Type: *S.S. Bir 1050*, Sikkim, near Simdong, 3300 m alt., 26-07-1958 (not traced in the Panjab University herbarium).

Polypodium subamoenum auct. non Clarke: Christ, Bot. Gaz. 51 (1911) 346.

Epiphytic and vertically climbing; epilithic, terrestrial and horizontally creeping. *Rhizome* terete, 4–6 mm in diam., brown, phyllopodia 1–5 cm apart, vascular strands 8–17, dark bundle sheaths present or absent, sclerenchyma strands 50–100. *Rhizome scales* evenly inserted or on protrusions, badious, appressed, densely set, persistent, perfoliate, monomorphic, deltoid, index 2.0–2.4, 1.5–4.4 by 0.7–1.9 mm, apex acuminate, basal flaps round, clathration of cell walls getting thinner towards base, cells yellowish, clathrate marginal protrusions absent at base, marginal glands situated apically, terminally and basally, rare, surface indument rhizoid, rarely abaxially glandular. *Fronds:* blade herbaceous, index 1.6–3.2, 14–51 by 8–27 cm, widest subbasally, pinnatifid, lateral segments index 7.1–7.5, 50–150 by 7–20 mm, apex acute, rarely obtuse, margin crenate to serrate, terminal segment coadunate, basal segments 8–20 mm separate from subbasal segments, sometimes shorter, deflexed; stipe in cross section near base 2–4 mm across, index length of stipe/ length of blade 0.5– 0.8. *Venation:* primary areolae uniserial, index 1.8–2.3, marginal free veins max. 1/2 length of areolae, 2–3 per areola, simple and forking, empty anastomoses rare, angle between secondary and primary veins 60–70°. *Indument:* laminar glandular hairs unbranched, 2 cells long, including 1 terminal gland, laminar acicular hairs 2–3 cells long, situated all over lamina, density variable, laminar scales persistent, petiolar acicular hairs absent. *Sori* uniserial, superficial, medial between costa and margin, round, 1–2 mm in diameter; receptacular hairy paraphyses –7 cells long, 1 glandular branch sometimes present, receptacular scaly paraphyses hyaline or very light clathrate, peltate or palaceous, linear, stellate and deltoid 2 or more cells wide, index 1.0, 100–241 by 100–240 µm, persistent; episporangial scaly paraphyses rarely branching from stalk, sporangial capsule index 1.1–1.2, 200–300 by 170–270 µm, the annulus with 16–20 cells, including 11–13 indurated cells. *Spores* hyaline, index L/P 1.6–1.9, 25–30 by 45–50 by 25–30 µm; exospore subverrucate; perispore inconspicuous, wrinkled, excrescences at lateral poles absent, the detailed outer surface ornamentation undulate, globules absent.

Chromosomes. n = 36, 37; 2n = 72.

Distribution. Tibet; Nepal; Sikkim; India: , Punjab, Himachal Pradesh, Assam; Burma; China: Hupeh, Sichuan, Kweichow, Yunnan, Anhwei, Kiangsi, Kwantung, Kwangsi; Thailand; Laos; Vietnam; Taiwan. Fig. 16.

Habitat. Different types of primary and secondary forest (moist, evergreen), bushwood; epiphytic, low on mossy trees; epilithic on mossy cliffs or muddy walls; terrestrial in humus-rich walls; shaded or exposed; reported on oak-trees; alt. 400–4200 m.

Notes. 1. The present species is the type of *Polypodiodes* Ching.

2. A clear-cut species which is highly variable in characters like frond size, density of acicular hairs, texture of blade and width of lateral segments respectively lobes in between. The shape of the apex of the lateral segments can vary between acute and obtuse even within one frond, e.g. *Wilson 2648* (B, P), which was misidentified as *subamoenum* by Christ (1911). The sclerification of the veins is variable, e.g. in *Cavalerie 2787* (NY) and *Rödl-Linder 209* (L) (juvenile as well as adult) all veins are sclerified.

3. Ching considers his *Polypodium pseudo-amoenum* (ined.) belonging here. However, because of differences in venation and rhizome scales the type, *H.T. Tsai 60864* (PE) does not belong to *Goniophlebium* (see E 4).

4. *Polypodium amoenum* Mettenius f. *pilosum* Clarke and var. *pilosum* Rosenstock have different types.

KEY TO THE VARIETIES

1a. Laminar acicular hairs rare; dark bundle sheaths in rhizome present 2
b. Laminar acicular hairs frequent; dark bundle sheaths in rhizome absent
b. var. chinense
2a. Index of blade < 2; index of widest lateral segment < 7.5 (widespread)
a. var. latedeltoideum
b. Index of blade > 2; index of widest lateral segment > 7.0 (Taiwan)
c. var. arisanense

a. var. **latedeltoideum** Christ

Goniophlebium amoenum (Mettenius) Beddome. — *Polypodium valdealatum* Christ.

Rhizome: dark bundle sheaths present. *Fronds:* blade index l/w < 2, widest lateral segment index l/w < 7.5. *Indument:* laminar acicular hairs rare.

Distribution. See the species.

Habitat. See the species.

b. var. **chinense** Ching

Polypodium amoenum var. ? *tonglense* Clarke. — *Polypodium yunnanense* Franchet. — *Polypodium amoenum* f. *pilosum* Clarke. — *Polypodium amoenum* var. *pilosum* Rosenstock. — *Polypodium bonatianum* Brause. — *Polypodium amoenum* var. *xerophyticum* Mehra & Bir.

Rhizome: dark bundle sheaths absent. *Fronds:* blade index 1.6–3.0, widest lateral segment index < 7.0. *Indument:* laminar acicular hairs frequent.

Distribution. See the species.

Habitat. See the species.

Note. In juvenile as well as in adult plants from the same collecting place dark bundle sheaths are absent, e.g. *Rödl-Linder 210, 219.*

c. var. **arisanense** Rödl-Linder, *stat. nov.*

Basionym: *Polypodium arisanense* Hayata.

Rhizome: dark bundle sheaths present. *Fronds:* blade index > 2, widest lateral segment index > 7.0. *Indument:* laminar acicular hairs rare.

Distribution. Taiwan (Mt. Arisan).

Habitat. See the species.

Note. Collections are rare. *Faurie 582, 589* (L); *Linsley 107* (NY); *Sasaki s.n.* (MICH, herb. no. 380083); *Tagawa 791* (K, MICH).

11. **Goniophlebium dielseanum** (Christensen) Rödl-Linder, *comb. nov.*

Goniophlebium dielseanum (Christensen) Rödl-Linder. — *Polypodium leuconeuron* Diels, Bot. Jahrb. 29 (1900) 203, nom. illeg., non Christ (1900). — *Polypodium dielseanum* Christensen, Ind. Fil. (1906) 522, nom. nov.; Acta Horti Gotoburg. 1 (1924) 99; Ching, Contr. Inst. Bot.

Acad. Peiping 2 (1933) 32, 50. — *Polypodiastrum dielseanum* Ching, Acta Phytotax. Sin. 16 (1978) 28. — Type: *B. von Resthorn 398*, 'f. Aug.!', Nanchuan: Tanchiawan, 'Felshöhlen' (K).

Polypodium wilsonii Christ, Bull. Acad. Geogr. Bot. (1906) 104. — Type: *E.H. Wilson 5336*, Western China, -07-1903 (P).

Polypodium meyii Christ, Notul. Syst. [Paris] 1 (1909) 33, 34. — Syntypes: *Mey & Ducloux 137*, 12-06-1907, Yunnan: Sonchan, Tchen-hiong, pref. Tchaotong (P); *idem 5089*, ibid. (P).

Epilithic. *Rhizome* terete, 3–4 mm in diam., brown, phyllopodia 1–2 cm apart, vascular strands 10–15, dark bundle sheaths absent, sclerenchyma strands 60–80. *Rhizome scales* evenly inserted, ferrugineous, spreading, densely set, persistent, perfoliate, monomorphic, deltoid, index 2.8–3.1, 2.6–3.4 by 0.9–1.1 mm, apex acuminate, basal flaps pointed, clathration of cell walls getting thinner from apex towards base, absent at base, cells yellow, clathrate marginal protrusions absent at base, marginal glands situated terminally, apically and basally, frequent, surface indument rhizoid. *Fronds:* blade herbaceous, index 1.3–1.5, 25–36 by 19–25 cm, widest at base, deeply pinnatifid, lateral segments index 10.5–11.4, 95–125 by 9–11 mm, apex acute, base adnate, lowest lateral segment abaxially free, margin serrate, terminal segment conform to lateral segments, half as long as longest lateral segment, basal segments 20 mm separate from subbasal segments, equally long, patens; stipe in cross section 2–3 mm across, index length of stipe/length of blade 0.7–0.9. *Venation:* primary areolae uniserial, index 1.6–2.0, marginal free veins c. 1/2 length of areolae, 2–3 per areola, mostly simple, rarely forking, empty anastomoses rare, angle between secondary and primary veins 65–80°. *Indument:* laminar glandular hairs unbranched, 2 cells long, including 1 terminal gland, laminar acicular hairs absent, laminar scales fugaceous, petiolar acicular hairs absent. *Sori* uniserial, superficial, medial between costa and margin, slightly oval, 1.2 mm in diam.; receptacular hairy paraphyses –6 cells long, 1 glandular branch sometimes present, receptacular scaly paraphyses clathrate, palaceous, linear, deltoid, 2 cells wide, index 1.0–1.4, 90–177 by 90–128 μm, persistent; episporangial scaly paraphyses rarely branching from stalk, sporangial capsule index 1.1–1.2, 205–235 by 175–205 μm, annulus with 17–20 cells, including 12–14 indurated cells. *Spores* hyaline, index L/P 1.5–1.8, 25–30 by 40–45 by 25–30 μm; exospore colliculate; perispore inconspicuous, wrinkled, excrescences at lateral poles absent, detailed outer surface ornamentation undulate, globules absent.

Distribution. China: Sichuan, Yunnan; India: Assam. Fig. 18.

Habitat. In thickets, at roadside; epilithic; shaded or exposed; alt. 1700–2200 m.

Notes. 1. Collections are rare. China: *W.P. Fang 2736, 3055* (P), *2745* (K), *8066* (NY); *Maire s.n.* (P); *Mey & Ducloux 137* (P); *Resthorn 398* (K); *Wilson 5336* (P). Assam: *Hooker s.n.* (K).

2. This distinct species has been considered close to *Goniophlebium subauriculatum* by Christensen (1924) and Ching (1933) (*'Polypodium subauriculatum'*). The striking differences to *subauriculatum* concern the rhizome which is not chalky but green, the sori which are not round but slightly oval, all lateral segments which are not articulate but adnate to the rhachis and the receptacular scaly paraphyses which are not peltate but always palaceous.

12. Goniophlebium lachnopum (Hooker) Beddome

Goniophlebium lachnopum (Wallich ex Hooker) Beddome, Ferns Brit. Ind. 2 (1868) 163, pl. 163; Handb. (1883) 319. — *Polypodium lachnopum* [Wallich, Cat. (1828) no. 310, nom. nud.] Hooker, Ic. Pl. (1854) pl. 952; Cent. Ferns (1854) pl. 52; Spec. Fil. 5 (1863) 25; Mett., Farngatt. Polypod. (1857) 75; Clarke, Trans. Linn. Soc. London, ser. 2, 1 (1880) 551; Ching, Contr. Inst. Bot. Acad. Peiping 2 (1933) 48, 49; Icon. Fil. Sin. 2 (1934) pl. 95. — *Schellolepis lachnopa* J. Smith, Hist. Fil. (1875) 93. — *Polypodiodes lachnopa* Ching, Acta Phytotax. Sin. 16 (1978) 27. — Lectotype: *Wallich (Nepal) 310,* 1820 (see notes 1 & 2) (K, herb. Hookerianum).

Polypodium garrettii Wright in Ching, Contr. Inst. Bot. Acad. Peiping 2 (1933) 49, 50. — Type: *H.B.G. Garrett 382,* Da-pa-mown, 23-06-1927 (K; iso K).

Polypodium lachnopum Hooker var. *xerophyticum* Mehra, Panjab Univ. Bot. Publ. 7 (1939) 22, nom. illeg.

Epiphytic, epilithic. *Rhizome* terete, (2–)3–4 mm in diam., brown, phyllopodia 0.5–2.0 cm apart, vascular strands 8–16, dark bundle sheaths absent, sclerenchyma strands 39–100. *Rhizome scales* evenly inserted or on protrusions, badious, spreading, densely set, persistent, perfoliate, monomorphic, deltoid, index 3.6–4.2, 1.8–8.0 by 0.5–1.9 mm, apex filiform, basal flaps variable, frequently pointed, cell walls clathrate throughout, getting thinner at base, cells hyaline, clathrate marginal protrusions same length all along, marginal glands situated all along, frequent, surface indument rhizoid or absent. *Fronds:* blade thinly herbaceous, index 3.6–5.3, 18–48 by 5–9 cm, widest subbasally, pinnatifid, lateral segments index 5.0–5.6, 25–45 by 5–8 mm, apex acute, margin entire to crenate, terminal segment coadunate, basal segments 6–10 mm separate from subbasal segments, shorter, deflexed; stipe 1.5–3.0 mm in basal diam., index length of stipe/length of blade 0.1–0.5. *Venation:* primary areolae rarely not closing, index 1.05–1.30, marginal free veins max. 1/3 length of areolae, 1–2 per areola, unforked, empty anastomoses rare, angle between secondary and primary veins 65–75°. *Indument:* laminar glandular hairs unbranched, 2–4 cells long, including 1 terminal gland, laminar acicular hairs 2–4 cells long, situated all over lamina, density low, laminar scales persistent, petiolar acicular hairs sometimes present. *Sori* uniserial, superficial, medial to costal, round, 0.5–1.0 mm in diam.; receptacular hairy paraphyses –8 cells long, unbranched, receptacular scaly paraphyses clathrate, peltate, stellate and palaceous, deltoid, 3 or more cells wide, index 1.3–2.9, 205–765 by 70–580 µm, ephemeral; episporangial hairy paraphyses 0–2, branching from stalk, sporangial capsule index 1.0–1.2, 220–305 by 225–255 µm, annulus with 16–20 cells, including 11–14 indurated cells. *Spores* brownish, index L/P 1.5–1.7, 30–40 by 50–65 by 30–40 µm; exospore colliculate; perispore for the greater part attached, wrinkled, crestae parallel to the equatorial axis, detailed outer surface ornamentation undulate, globules absent.

Chromosomes. n = 36, 37.

Distribution. Nepal; Sikkim; India: Punjab, Himachal Pradesh, Assam; China: Yunnan; North Thailand. Fig. 17.

Habitat. Primary and secondary forest; epiphytic, epilithic or growing away from any substrate up to 30 cm free in the air; alt. (500–)1150–3200 m.

Notes. 1. Wallich's type specimen of 1820 corresponds exactly with Wright's type of *Polypodium garrettii*.

2. As already recognized by Clarke (1880), different species are mixed on the same sheets of Wallich's material of 1821 and 1829, i.e. *G. lachnopum* and *G. microrhizoma*.

3. Specimens of *G. lachnopum*, *G. hendersonii*, and *G. microrhizoma* are frequently confused. Important distinguishing characters concern the rhizome, the rhizome scales, the margin of lateral segments and the spores. *Goniophlebium lachnopum* ('lachno' means in Greek woolly) is easily recognized by the long, spreading rhizome scales. The perispore is crestate parallel to the equatorial axis. The margin of the lateral segments of *G. hendersonii* is obviously serrate and its spores are surrounded by a perispore with locally protruding crests. The rhizome of *G. microrhizoma* is comparatively thin, which becomes even more obvious due to the short, appressed rhizome scales. The perispore is inconspicuously attached to the exospore.

4. The density of the laminar indument is quite variable. The filiform apex of laminar scales exceeds sometimes 5 mm.

5. The rhizome branches frequently.

13. Goniophlebium manmeiense (Christ) Rödl-Linder, *comb. nov.*

Polypodium manmeiense Christ, Bull. Herb. Boissier 6 (1898) 870, 871 (see note 1); Christensen, Acta Horti Gotoburg. 1 (1924) 98, 99; Contr. U.S. Nation. Herb. 26 (1931) 315; Ching, Contr. Inst. Bot. Acad. Peiping 2 (1933) 41; Icon. Fil. Sin. 2 (1934) ad pl. 94. — *Metapolypodium manmeiense* Ching, Acta Phytotax. Sin. 16 (1978) 29. — Type: *A. Henry 10081*, Yunnan, 'South of Red River from Manmei', 2000 m alt. (P; iso B, NY).

Polypodium scalare Christ, Bull. Soc. France 52, Mém. 1 (1905) 14, nom. illeg. [ICBN art. 63.1]. — Type: *A. Henry 13036*, Yunnan, North West mountains, Sze-mao, 'cliffs', 2000 m alt. (P; iso NY, P, see note 2).

Polypodium pseudodimidiatum Christ, Bull. Soc. France 52, Mém. 1 (1905) 14, nom. illeg. [ICBN art. 63.1]. — Type: *A. Henry 13036*, Yunnan, North West mountains, Sze-mao, 'cliffs', 2000 m alt. (P; iso NY, P, see note 2).

Polypodium simulans Baker, Kew Bull. (1906) 13. — Type: *Hancock 152*, Yunnan, Mengtze, 'on limestone rocks', 2000–2300 m alt. (K).

Metapolypodium kingpingense Ching et Chu, Acta Phytotax. Sin. 16 (1978) 29. — Type: *W.M. Chu et al. 6519*, Yunnan, King-Ping, in rupibus, 700 m (not traced in PE).

Epiphytic, epilithic, terrestrial. *Rhizome* terete, 2.5–3.5 mm in diam., brown, phyllopodia 0.5–4.5 cm apart, vascular strands 7–9, dark bundle sheaths absent, sclerenchyma strands 40–80. *Rhizome scales* evenly inserted, brunneous, appressed, densely set, persistent, perfoliate, monomorphic, deltoid, index 2.1–3.0, 1.3–3.5 by 0.6–1.2 mm, apex acuminate, basal flaps round, clathration of cell walls absent at centre, present marginally and basally, cells yellowish, clathrate marginal protrusions slightly longer at base, marginal glands situated all along, frequency variable, surface indument rhizoid. *Fronds:* blade thinly herbaceous, index 4.8–6.8, 15–34 by 3–5 cm, widest medially or same width all along blade, deeply pinnatifid, sometimes adnate, lateral segments index 4.5–5.6, 18–28 by 4–5 mm, apex obtuse or acute, margin entire to crenate, terminal segment obviously narrow and crenate, equally long as longest lateral segment, basal segments 5–9 mm separate from subbasal segments, rarely shorter, patens; stipe in cross section near base 1.5–2.0 mm across, index length of stipe/length of blade 0.3–0.4. *Venation:* primary areolae absent, free veins once forking, empty anastomoses absent, angle between secondary and primary veins 45–55°. *Indument:* laminar glandular hairs unbranched, 2 cells long, including 1 terminal gland, laminar acicular hairs absent, laminar scales fugaceous, petiolar acicular hairs absent. *Sori* uniserial, superficial, medial to marginal, round, 1.2–1.8 mm in diam.; receptacular hairy paraphyses –3 cells long, unbranched, receptacular scaly paraphyses absent; episporangial hairy paraphyses sometimes branching from stalk, sporangial capsule index 1.1, 190–210 by 170–195 µm, annulus with 17–20 cells, including 12(–13) indurated cells. *Spores* yellowish, index L/P 1.6–1.8, 25–30 by 40–45 by 25 µm; exospore pusticulate; perispore inconspicuous, smooth, excrescences at lateral poles absent, detailed outer surface ornamentation granulate, globules absent.

Distribution. India: Assam; China: Sichuan, Yunnan; North Thailand; Laos; Cambodia. Fig. 18.

Habitat. Dense evergreen forest; epiphytic on mossy tree trunks, epilithic on mossy limestone rocks, terrestrial; generally shaded; alt. (900–)1200–2350 m.

Notes. 1. The present species is the type of *Metapolypodium* Ching.

2. Christ (1905) newly described *Polypodium scalare* and *P. pseucodimidiatum* on the same page and based the two species on the same type.

3. The terminal frond segment is typically caudate: See also Ching (1934) pl. 94.

4. Diagnostic characters to distinguish *G. microrhizoma* and *G. manmeiense* are given in the list below:

	microrhizoma	*manmeiense*
rhizome		
diameter (mm)	1.3–1.8(–3)	2.5–3.5
venation	mostly 1 row of areolae, sometimes partly free	free
sori		
position	medial to costal	medial to marginal
shape	slightly oval	round
blade		
width (cm)	6–12	3–5
widest	(sub)basal	equally wide throughout
spores		
exospore	colliculate	pustulate
perispore globules	few	absent

14. Goniophlebium microrhizoma (Baker) Beddome

Goniophlebium microrhizoma (Baker) Beddome, Ferns Brit. Ind., Suppl. (1876) 21, pl. 384. — *Polypodium microrhizoma* Clarke ex Baker in Hooker & Baker, Syn. Fil., ed. 2 (1883) 511; Clarke, Trans. Linn. Soc. London, ser. 2, 1 (1880) 551; Christensen, Contr. U.S. Nation. Herb. 26 (1931) 315; Ching, Contr. Inst. Bot. Acad. Peiping 2 (1933) 47; Icon. Fil. Sin. 2 (1934) ad pl. 96; Tagawa, Acta Phytotax. Geobot. 4 (1935) 145; Bir, Trikha & Vasudeva, New Bot. 1 (1974) 147. —*Polypodiodes microrhizoma* Ching, Acta Phytotax. Sin. 16 (1978) 27. — Lectotype: *H.J. Elwes s.n.*, Sikkim, Lachong, 3300 m alt., -12-1872 (K, the one frond on the sheet, which is *G. microrhizoma*, not the other three fronds, which are *G. hendersonii* Bedd.).

Polypodium taliense Christ, Bull. Soc. Bot. France 52, Mém. 1 (1905) 13, 14. — Type: *Delavay 27*, China, Tapin-tze, près de Tali, 29-08-1883 (P).

Polypodium deorsipinnatum Copeland, Philip. Journ. Sc. 38 (1929) 152. — Type: *U. Faurie 581*, Taiwan, Mt. Arisan, 'in rupibus', 2500 m alt., -06-1914 (P; iso B, L, NY, see note 2).

Polypodium fieldingianum Kunze ex Mettenius, Farngatt. Polypod. (1857) 75. — *Goniophlebium fieldingianum* Moore, Ind. Fil. (1862) 389; Beddome, Handb., Suppl. (1892) 90, q. specim. s.; Ching, Contr. Inst. Bot. Acad. Peiping 2 (1933) 52, q. specim. s. — Type: *Fielding, Hofmeister*, Himalaya (LZ, destroyed).

Polypodium microrhizoma Baker var. *xerophyticum* Mehra, Panjab Univ. Bot. Publ. 7 (1939) 22, nom. illeg.

Polypodium subapertum Rosenstock, nom. nud. (see note 2).

Epiphytic, epilithic. *Rhizome* terete, 1.3–1.8(–3.0) mm in diam., brown, phyllopodia 0.5–3.0 cm apart, vascular strands 11–12, dark bundle sheaths absent, sclerenchyma strands 20–70. *Rhizome scales* evenly inserted, brunneous, appressed, densely set, persistent, perfoliate, monomorphic, deltoid, index 2.8–3.3, 1.4–3.3 by 0.5–1.0 mm, apex acuminate, basal flaps pointed, clathration of cell walls getting thinner towards base, cells hyaline, clathrate marginal protrusions all along, marginal glandular indument 1–2 cells long, situated all along, frequency variable, surface indument rhizoid. *Fronds:* blade thinly herbaceous, index 2.6–3.3, 16–40 by 6–12 cm, widest basally to subbasally, pinnatifid, lateral segments index 5.0–5.6, 30–45 by 6–8 mm, apex acute, margin crenate to serrate, terminal segment coadunate, basal segments 10–15 mm separate from subbasal segments, shorter, sometimes deflexed; stipe in cross section near base 1.0–1.5 mm across, index length of stipe/ length of blade 0.3–0.6. *Venation:* primary areolae uniserial, rarely not closing, index 1.3–1.5, marginal free veins max. 1/3 length of areolae, 1–2 per areola, simple or forking, empty anastomoses absent, angle between secondary and primary veins 50–60°. *Indument:* laminar glandular hairs unbranched, 2 cells long, including 1 terminal gland, laminar acicular hairs absent, laminar scales fugaceous, petiolar acicular hairs absent. *Sori* uniserial, superficial, medial to costal, round to oval, 1.5 mm in diam.; receptacular hairy paraphyses –4 cells long, unbranched, receptacular scaly paraphyses absent; episporangial hairy paraphyses sometimes branching from stalk, sporangial capsule index 1.1–1.2, 180–250 by 160–200 µm, annulus with 17–20 cells, including (11–)12(–13) indurated cells. *Spores* hyaline, index L/P 1.7–1.9, 25–30 by 45–50 by 20–25 µm; exospore colliculate; perispore inconspicuous, smooth, excrescences at lateral poles absent, detailed outer surface ornamentation smooth to undulate, few globules present.

Chromosomes. n = 36, 37.

Distribution. Nepal; India: Punjab, Himachal Pradesh, Assam; China: Yunnan; North Thailand. Fig. 19.

Habitat. Dense evergreen forest; epiphytic on mossy tree trunks, epilithic on mossy rocks; shaded; sometimes locally abundant, sometimes locally rare; alt. 1500–3300 m

Notes. 1. Ex descriptione *Polypodium fieldingianum* Kunze ex Mettenius belongs here because of oval sori and free venation.

2. The isotype of *Polypodium deorsipinnatum* Copeland (NY) is annotated as type of *P. subapertum* Rosenstock, an unpublished name.

15. Goniophlebium prainii Beddome

Goniophlebium prainii Beddome, Journ. of Bot. 31 (1893) 226. — *Polypodium prainii* Christensen, Ind. Fil. (1906) 556; Holttum, Rev. Fl. Malaya 2 (1955) 204; Satija & Bir, Polypod. Ferns India (1985) 15. — *Polypodiastrum prainii* Ching, Acta Phytotax. Sin. 16 (1978) 28, Acta Bot. Yun. 1 (1979) 31, comb. illeg. (see note 3). — Type: *Scortechini s.n.*, Perak (P).

Epiphytic. *Rhizome* terete, 3.5–4.5 mm in diam., brown, phyllopodia 1.5–2.0 cm apart, vascular strands 11–14, dark bundle sheaths present, sclerenchyma strands 50–60. *Rhizome scales* evenly inserted or on protrusions, brunneous, spreading, densely set, ephemeral, perfoliate or basifix, monomorphic, deltoid, index 3.5–5.2, 2.1–7.3 by 0.4–2.1 mm, apex filiform, basal flaps round, cell walls clathrate throughout, cells yellowish, clathrate marginal protrusions basally absent, marginal glands situated centrally, rare, surface indument absent. *Fronds:* blade herbaceous, index 1.1–1.6, 20–45 by 18–28 cm, widest subbasally, pinnatifid, lateral segments index 7.7–10.0, 100–150 by 13–15 mm, apex acuminate, base in lower quarter of frond abaxially cordate, margin entire to crenate, terminal segment coadunate, basal segments 15–45 mm separate from subbasal segments, equally long, deflexed; stipe in cross section near base 3–4 mm across, index length of stipe/length of blade 0.6–0.8. *Venation:* primary areolae 1–2-serial, index of costal areolae 1.1–1.3, marginal free veins max. 1/2 length of costal areolae, 1–3 per areola, simple and forking, empty anastomoses frequent, angle between secondary and primary veins 60–70°. *Indument:* laminar glandular hairs unbranched, 2–4 cells long, including 1 terminal gland, laminar acicular hairs 2–5 cells long, situated along costa and rhachis, density medium, laminar scales sometimes persistent, petiolar acicular hairs 4–5 cells long. *Sori* uniserial, rarely biserial, superficial, costal, round, 1.5–2.0 mm in diam.; receptacular hairy paraphyses –8 cells long, 1 glandular branch sometimes present, receptacular scaly paraphyses clathrate, palaceous, linear, deltoid, 2 cells wide, index 1.6–2.0, 140–280 by 90–140 µm, ephemeral; episporangial paraphyses absent, sporangial capsule index 1.2–1.3, 250–280 by 200–220 µm, annulus with 17–22 cells, including 12–13 indurated cells. *Spores* yellowish, index L/P 1.5–1.6, 25–31 by 40–45 by 25–30 µm; exospore pustulate; perispore for the greater part attached, reticulately wrinkled, excrescences at lateral poles absent, detailed outer surface ornamentation smooth, globules absent.

Distribution. Peninsular Malaysia (Perak, Pahang, Selangor); North Sumatra. Fig. 20.

Habitat. Primary and secondary forest; epiphytic on mossy, rotten tree trunks, near ground level; shaded or exposed; alt. 1100–1900 m.

Notes. 1. *Surbeck 1005* (L): 'An den totlaufenden Nerven auf der Oberseite weisse oder durchscheinende Pünktchen', which are hydathodes.

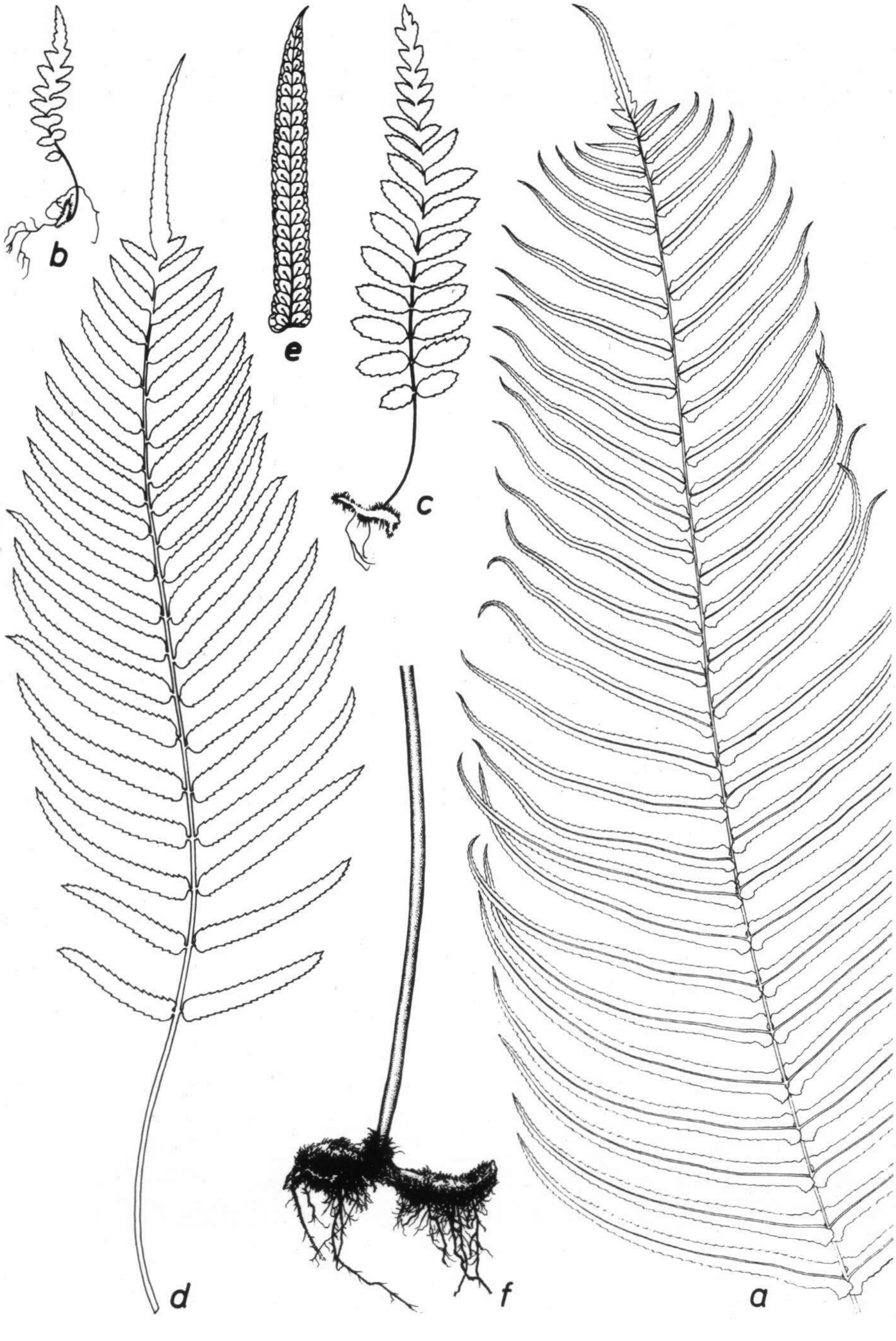

Fig. 52. *Goniophlebium pseudoconnatum* (Copeland) Copeland. a. Adult frond, × 0.12; b–d. juvenile fronds, × 0.5; e. venation pattern, × 0.75; f. rhizome, × 0.5.

2. According to Beddome's (1893) original description the sori are situated in one or two series. However, specimens with two series of sori have not been encountered by the present author.

3. Ching (1979) erroneously made the combination *Polypodiastrum prainii* (Beddome) Ching which was already earlier published by the same author (Ching, 1978).

16. Goniophlebium pseudoconnatum (Copeland) Copeland — Fig. 52.

Goniophlebium pseudoconnatum (Copeland) Copeland, Fern Fl. Philip. 3 (1960) 462; Rödl-Linder, Philip. Journ. Sc. 116 (1987) 158, 159. — *Polypodium pseudoconnatum* Copeland, Philip. Journ. Sc. 1, Suppl. 2 (1906) 161, pl. 22; Wu, Sunyatsenia 3 (1932) 268, pl. 125. — Lectotype (Rödl-Linder, 1987): *E.B. Copeland 1904a*, Luzon, Lepanto, Bagnen, 1900 m alt., 04-11-1905 (MICH).

Epiphytic and linearly or spirally climbing; epilithic or terrestrial, horizontally creeping. *Rhizome* terete, 5.0–7.5(–10) mm in diam., chalky, phyllopodia 3–5 cm apart, vascular strands 13–15, dark bundle sheaths present, sclerenchyma strands 30–50. *Rhizome scales* inserted on protrusions, brunneous, spreading, densely set, ephemeral, perfoliate, monomorphic, deltoid, index 3.8–4.1, 4.0–5.0 by 1.0–1.3 mm, apex filiform, basal flaps round, cell walls clathrate throughout, cells hyaline, clathrate marginal protrusions same length all along, marginal glandular indument 1–2 cells long, situated all along, frequent, surface indument glandular, abaxially, very rare. *Fronds:* blade herbaceous, index 0.4–0.6, 26–150 by 8–31 cm, widest subbasally or equally wide throughout, pinnate, lateral segments index 11.7–12.5, 100–140 by 8–12 mm, apex pungent, base cordate, auricled or truncate, sessile, at uppermost part of frond adnate, margin crenate, terminal segment coadunate, basal segments 15–35 mm separate from subbasal segments, sometimes shorter, sometimes deflexed; stipe in cross section near base 2.5–5.0 mm across, index length of stipe/length of blade 0.4– 0.6. *Venation:* primary areolae uniserial, index 1.2–1.4, marginal free veins max. 1/3 length of areolae, 1–3 per areola, simple and forking, empty anastomoses sometimes present, angle between secondary and primary veins 65–80°. *Indument:* laminar glandular hairs sometimes with glandular branch, 2 cells long, including 1 terminal gland, laminar acicular hairs 2–8 cells long, situated all over lamina, density variable, laminar scales persistent, petiolar acicular hairs absent. *Sori* uniserial, slightly sunken, medial between costa and margin, round, 1.5–2.0 mm in diam.; receptacular hairy paraphyses –6 cells long, unbranched, receptacular scaly paraphyses clathrate, peltate, stellate, index 1.1–1.2, 200–240 by 180–200 µm, persistent; episporangial paraphyses 2–3 cells long, including 1 terminal gland, attached onto first or second epistomium cell, rare (± on 15% of the capsules), sporangial capsule index 1.4, 215–235 by 155–165 µm, annulus with 18–20 cells, including 11–12 indurated cells. *Spores* yellow, index L/P 1.6–1.8, 25 by 40–45 by 20–30 µm; exospore colliculate; perispore for the greater part attached, crestae parallel to the equatorial axis, wrinkled, excrescences at lateral poles absent, detailed outer surface ornamentation smooth, few globules present.

Distribution. Borneo, Philippines (Luzon, Mindanao), Celebes, Moluccas (Seram), New Guinea. Fig. 20.

Habitat. Different types of primary and secondary forest (mossy, montane, evergreen); epiphytic on mossy tree trunks, epilithic on lime rocks, terrestrial on rocky, loose ground; mostly shaded; reported from *Pandanus* spec.; alt. (500–)900–2700 m.

Notes. 1. *Cuming 203* (L, P, K), identified as *Polypodium pallens* Blume by Mettenius (1857), as *P. tomentellum* Christensen by Copeland (1960), as *P. subauriculatum* Blume var. *serratifolium* Hooker by Hooker (1864) is *Goniophlebium pseudoconnatum*.

2. The present species is reported from China by Wu (1932: pl. 125), which is drawn from *Sin 8973*, Ku-Chen, 'on rocks', 09-05-1929. The present author was unable to trace Chinese material of the present species in PE. Therefore the distribution in China needs verification.

3. The outline of the fronds of *Goniophlebium pseudoconnatum* and *G. subauriculatum* is similar. The medial and lower pinnae of the present species are mostly 'more strictly opposite and more cordate, thus appearing connate' (Copeland, 1960: 462). Diagnostic characters to distinguish *G. pseudoconnatum* and *G. subauriculatum* are listed below.

	pseudoconnatum	*subauriculatum*
rhizome		
sclerenchyma strands	30–50	> 100
rhizome scales		
colour	brunneous	ferrugineous
marginal glandular hairs	2 cells long	1 cell long
fronds		
colour (in vivo)	dark green	light green
stipe and rhachis	firm, upright or pendent	very flexible drooping
sori		
diameter (mm)	1.5–2.0	1.0–1.5
episporangial paraphyses	present (on c. 15% of the capsules)	absent

4. *Gonophlebium pseudoconnatum* and *G. subauriculatum* have been collected side by side in the mossy forest of Mt. Sto. Tomas, Luzon, at 2000 m altitude. The first hardly developed under lowland conditions, whereas the latter grew very well in the author's garden.

5. *Kato et al. C-7710* (L) is slightly abnormal. The terminal segment is conform to the lateral segments, which is usually the case in species of the *G. percussum*-group.

17. **Goniophlebium subauriculatum** (Blume) Presl

Goniophlebium subauriculatum (Blume) Presl, Tent. Pterid. (1836) 186; J. Smith, Cat. Ferns (1857) 3; Beddome, Handb. (1883) 322, 323, fig. 173; Copeland, Fern Fl. Philip. 3 (1960) 461; Satija & Bir, Polypod. Ferns India (1985) 17; Rödl-Linder, Philip. Journ. Sc. 116 (1987) 159. — ***Polypodium subauriculatum*** Blume, Enum. (1828) 133; Flora Javae Filicum (1830) 132; ibid. (1847) pl. 83; Mettenius, Ind. Fil. Hort. Bot. Lips. (1856) 33; Farngatt. Polypod. (1857) 81; Hooker, Spec. Fil. 5 (1863) 32, 33; Baker in Hooker & Baker, Syn. Fil., ed. 1 (1867) 344,

q. n. s.; Clarke, Journ. Linn. Soc. London Bot. 24 (1888) 417; Copeland, Philip. Journ. Sc. 2 (1907) 139; Hayata, Bot. Mag. Tokyo 23 (1909) 79, 80, q. n. s.; Ching, Contr. Inst. Bot. Acad. Peiping 2 (1933) 51; Tagawa, Mem. Coll. Sc. Univ. Kyoto, ser. B, 21 (1954) 75; Holttum, Rev. Fl. Malaya 2 (1955) 207, fig. 108. — *Schellolepis subauriculata* J. Smith, Ferns Brit. & For. (1866) 82; Hist. Fil. (1875) 93; Price, Thesis: Univ. Philip. Los Baños (1975) 203, 204. — *Marginaria subauriculata* Nakai ex Itô, Journ. Jap. Bot. 11 (1935) 95, q. n. s. — Type: *Blume 130*, 'crescit in truncis vetustis arborum Javae' (L, herb. no. 980.286-630; iso L).

Polypodium pallens Blume, Flora Javae Filicum (1847) 177, 178, pl. 84; Mettenius, Farngatt. Polypod. (1857) 81. — *Goniophlebium pallens* Presl, Tent. Pterid. (1836) 186; J. Smith, Journ. of Bot. 3 (1841) 396. — *Schellolepis pallens* J. Smith, Hist. Fil. (1875) 93. — Type: *Kuhl & van Hasselt 206*, Java (L).

Goniophlebium reinwardtii de Vriese, Ned. Kruidk. Arch. 1 (1847) 257; Fée, Gen. (1852) 255, *'reinwardtianum'*. — *Polypodium reinwardtii* Kunze, Linnaea 23 (1850) 283, nom. illeg., non Presl (1836); Mettenius, Ind. Fil. Hort. Bot. Lips. (1856) 33, nom. illeg.; Baker in Hooker & Baker, Syn. Fil., ed. 2 (1883) 344, nom. illeg. — Type: *van Gesker s.n.*, 'in silvis montis Gede', Java (L).

Goniophlebium pleopeltis Fée, Gen. (1852) 256; J. Smith, Ferns Brit. & For. (1866) 82. — Type: *Lobb 263*, Java (K).

Goniophlebium molle Beddome, Ferns Brit. Ind. 2 (1868) 206, pl. 206; Handb. (1883) 322, pl. 172; Satija & Bir, Polypod. Ferns India (1985) 15, 16. — *Polypodium puberulum* Baker in Hooker & Baker, Syn. Fil., ed. 1 (1867) 344, nom. nov., nom. illeg., non Schlechtendal et Chamisso (1830) [nec *Polypodium molle* Schreber (1771), nec Jacquin (1789)]. — *Polypodium beddomei* Baker in Hooker & Baker, Syn. Fil., ed. 2 (1883) 344, nom. nov.; Christensen, Ind. Fil. (1906) 513; Ching, Contr. Inst. Bot. Acad. Peiping 2 (1933) 50, 51. — *Polypodiastrum molle* Ching, Acta Phytotax. Sin. 16 (1978) 28. — Type: *C.S. Parish s.n.*, Burma (K).

Polypodium molliculum Copeland, Fragm. Fl. Philip. 3 (1905) 190, nom. illeg., non Link (1841); Philip. Journ. Sc. 1, Suppl. 2 (1906) 162. — *Polypodium tomentellum* Christensen, Ind. Fil. (1906) 570, nom. nov. — *Goniophlebium tomentellum* Copeland, Fern Fl. Philip. 3 (1960) 461, 462. — *Schellolepis tomentella* Pichi Sermolli, Webbia 28 (1973) 470; Price, Thesis: Univ. Philip. Los Baños (1975) 204. — Type: *Elmer 6506*, Baguio, 'epiphyte on pine trees' (PNH, destroyed in 1945)

Goniophlebium integrum Copeland, Philip. Journ. Sc. 81 (1952) 42; Fern Fl. Philip. 3 (1960) 461. — Type: *Merrill 7814*, Benguet Prov., -05-1911 (MICH).

Polypodium metamorphum Kunze, nom. nud. (see note 5).

Epiphytic and vertically or spirally climbing, epilithic or terrestrial and linearly creeping. *Rhizome* terete, 5.0–6.5(–10.0) mm in diam., chalky, phyllopodia 0.5–3.0 cm apart, vascular strands 10–13, dark bundle sheaths present, sclerenchyma strands > 100. *Rhizome scales* inserted on protrusions, ferrugineous, spreading, densely set, ephemeral, perfoliate, monomorphic, deltoid, index 4.2–6,0, 3.0–6.0 by 0.6–1.0 mm, apex filiform, basal flaps pointed, cell walls thinly clathrate throughout, cells yellow, clathrate marginal protrusions longer at base, marginal glands situated all along, frequent, surface indument rhizoid. *Fronds:* blade herbaceous, index 2.1–5.0, 20–95(–250) by 7–45(–50) cm, widest medially to basally or equally wide throughout, pinnate, lateral segments index 6.7–8.9, 80–120 by 9–18 mm, apex pungent, base cordate or auricled, rarely truncate, sessile or shortly petiolate, at uppermost part of frond adnate, margin crenate to serrate, terminal segment coadunate, basal segments 15–35 mm separate from subbasal segments, sometimes shorter, sometimes deflexed; stipe in cross section near base 1.8–3.3 mm across, index length of stipe/length of blade 0.2–0.7. *Venation:* primary areolae 1–2-serial, index of costal areolae 1.3–1.7, marginal free veins max. 1/3 length of areolae, 1–3 per areola, simple and forking, empty anastomoses frequent, angle between secondary and primary veins 60–70°. *Indument:* laminar glandular hairs sometimes with glandular branch, 2 cells long, including 1–2 terminal glands, laminar acicular hairs 2–8 cells long, situated all over lamina, density variable, laminar scales persistent, petiolar acicular hairs sometimes present. *Sori* uniserial, slightly sunken, medial to costal, round, 1.0–1.5 mm in diam.; receptacular hairy paraphyses –6 cells long, unbranched, receptacular scaly paraphyses clathrate, peltate, stellate and palaceous, deltoid, 3 or more cells wide, index 1.2, 240–260 by 200–220 μm, persistent; episporangial paraphyses absent, sporangial capsule index 1.2, 190–225 by 165–190 μm, annulus with 20–22 cells, including 12–13 indurated cells. *Spores* yellowish, index L/P 1.5–1.8, 20–25 by 35–40 by 25 μm; exospore colliculate; perispore for the greater part attached, crestae parallel to the equatorial axis, wrinkled, excrescences at lateral poles absent, detailed outer surface ornamentation undulate, globules absent.

Chromosomes. n = 37.

Distribution. China: Yunnan (see note 4); Thailand; Laos; Cambodia; Vietnam (see note 3); Malesia: Peninsular Malaysia (Perak, Pahang, Selangor), Singapore, Sumatra, Java, Borneo, Philippines (Luzon, Mindanao, Bonito, Panay, Negros), Celebes, Lesser Sunda Islands (Bali, Sumba, Sumbawa, Flores), New Guinea; Australia: Queensland; New Caledonia. Fig. 21.

Habitat. Different types of primary and secondary forest (montane, mossy rain, pine, *Castanopsis, Altingia, Podocarpus*); epiphytic, high or low on rotten and living tree trunks, reported on tea bush, epilithic on limestone or in wet clefts between rocks; shaded or exposed; alt. 250–2400 m.

Notes. 1. Copeland's (1960) main distinctive character for *Goniophlebium tomentellum* being persistently hirsute could not be confirmed. Juvenile plants of *G. subauriculatum* are hairy and the hairiness may persist to some extent in older plants. The present author has seen every gradation in hairiness, even on adult fronds growing at the same rhizome, e.g. *Rödl-Linder 204* sheet 1 & 2.

2. Above 1500 m *G. subauriculatum* can appear as a kind of 'mountain form', which is exactly *Polypodium pallens* Blume. It develops short upright fronds and the pinnae are narrow with a firm texture, a truncate base and a less serrate margin. Growing these specimens under lowland conditions, the newly developed fronds look like any *G. subauriculatum* specimen collected from the lowlands, i.e. long, drooping fronds with very flexible rhachis, pinnae thin herbaceous with the margin serrate and the base auricled, e.g. *Rödl-Linder 154, 154B* and *165, 165B*.

3. The present species has been reported from the Himalayas and Burma by Satija & Bir (1985).

4. Only one record from China has been seen, i.e. *Henry 13145* (B, NY).

5. Mettenius (1856) discusses *Polypodium metamorphum* Kunze, based on a juvenile specimen in the 'Botanischer Garten', Leipzig, taken from a plant which developed later in a *G. ('Polypodium') subauriculatum* proper.

6. The present species is the lectotype of *Goniophlebium*.

17.3. GONIOPHLEBIUM ARGUTUM-, HENDERSONII- AND NIPONICUM-GROUP

18. Goniophlebium argutum (Hooker) J. Smith

Goniophlebium argutum (Wallich ex Hooker) J. Smith, Journ. of Bot. 4 (1841) 57; Beddome, Ferns Brit. Ind. 1 (1866) 6, pl. 6; Tagawa, Mem. Coll. Sc. Univ. Kyoto, ser. B, 21 (1954) 74, 75, p.p.; Copeland, Fern Fl. Philip. 3 (1960) 462, p.p. — *Polypodium argutum* [Wallich, Cat. (1828) no. 308, nom. nud.] Hooker, Spec. Fil. 5 (1864) 32; Baker in Hooker & Baker, Syn. Fil., ed. 2 (1883) 511; Clarke, Trans. Linn. Soc. London, ser. 2, 1 (1880) 551, p.p; Christensen, Contr. U.S. Nation. Herb. 26 (1931) 316, p.p.; Wu, Sunyatsenia 3 (1932) 266, pl. 124, p.p.; Ching, Contr. Inst. Bot. Acad. Peiping 2 (1933) 51, 52, p.p.; Tagawa, Acta Phytotax. Geobot. 7 (1938) 188, 189, p.p. — *Schellolepis arguta* J. Smith, Hist. Fil. (1875) 93. — Type: *Wallich 308*, Nepal, Kamaon (K, herb. Hookerianum; iso K).

Epiphytic. *Rhizome* terete, 4.5–6.5(–8.0) mm in diam., glaucous, phyllopodia 1.5–2.0 cm apart, vascular strands 13–22, dark bundle sheaths absent (see note 1), sclerenchyma strands > 100. *Rhizome scales* evenly inserted, spadiceous, quite densely set, perfoliate, dimorphic: I) spreading, ephemeral, deltoid, index 2.2–2.6, 1.2–2.0 by 0.5–0.8 mm, apex acuminate, basal flaps round; II) at base of I), appressed, persistent, round, 0.06–0.1 mm in diam.; I & II) cell walls clathrate throughout, cells hyaline, clathrate marginal protrusions short all around, marginal glands situated terminally and basally, rare, surface indument absent. *Fronds:* blade herbaceous, index 1.5–2.4, 30–60(–70) by 20–25 cm, widest medial or same width all along blade, pinnate, lateral segments 100–170 by 13–20 mm, index 7.7–8.5, apex pungent, base obliquely cuneate, sessile, at apical third of blade adnate and decurrent, margin serrate, terminal segment conform to lateral segments, 1/3 longer or equally long as longest lateral segment, basal segments 25–45 mm separate from subbasal segments, equally long, patens; stipe in cross section near base 2.5–3.5 mm across, index length of stipe/length of blade 0.2–0.3. *Venation:* primary areolae uniserial, index 1.5–1,7, marginal free veins half as long as areolae, 1–3 per areola, simple or forking, empty anastomoses sometimes present, angle between secondary and primary veins 60–70°. *Indument:* laminar glandular hairs unbranched, 2 cells long including 1 terminal gland, laminar acicular hairs absent, laminar scales fugaceous, petiolar acicular hairs absent. *Sori* uniserial, superficial, medial between costa and margin, round, 1.5–2.5 mm in diam.; receptacular hairy paraphyses –7 cells long, unbranched, receptacular scaly paraphyses clathrate, peltate, deltoid, 3 or more cells wide, index 1.3, 200–400 by 150–300 µm, persistent; episporangial paraphyses absent, sporangial capsule index 1.2–1.4, 270–300 by 200–250 µm, annulus with 22–24 cells, including (12–)13–15 indurated cells. *Spores* brownish, index L/P 1.3–1.4, 40–45 by 55–60 by 30–35 µm; exospore colliculate; perispore widely detached, wrinkled, crestae parallel to the equatorial axis with short excrescences at lateral poles, detailed outer surface ornamentation smooth, glebulate, few globules present.

Chromosomes. n = 36, 37.

Distribution. Nepal; Sikkim; India: Punjab, Himachal Pradesh, Assam; North Burma. Fig. 22.

Habitat. *Rhododendron* forest, moist, dark; epiphytic, e.g. on *Rhododendron arboreum* Smith; alt. 1100–3000(–3850) m.

Notes. 1. Dark bundle sheaths have been observed in only one specimen, i.e. *Kari 71* (P).

2. The equatorial excrescences at the lateral poles of the spores are noteworthy. Equatorial excrescences are otherwise only present in the *G. percussum*-group.

3. *Goniophlebium argutum* and *G. mengtzeense* have twice been found mounted together on a single sheet, *Griffith s.n.*, Darjeeling (B) and *Anon. s.n.*, Himalayas (L, herb. no. 908 296-446).

4. *Mann s.n.*, Khasi Hills, -07-1888 (SING) is intermediate between *G. argutum* and *G. mengtzeense* concerning the base of the lateral segments.

5. Former authors generally merged specimens of *G. mengtzeense* with specimens of *G. argutum*. However, they represent distinct species which can be recognized by the following characters:

	argutum	*mengtzeense*
venation		
marginal free veins simple	long	short
marginal free veins forking	present	present
empty anastomoses	present	absent
lateral segments		
basal shape	obliquely cuneate	cordate, auricled, (truncate)
spores		
colour	brownish	yellowish
index L/P	1.3–1.4	1.7–1.8
perispore		
equatorial excrescences	short	absent
globules	present	absent

19. Goniophlebium mengtzeense (Christ) Rödl-Linder

Goniophlebium mengtzeense (Christ) Rödl-Linder, Philip. Journ. Sc. 116 (1987) 154. — *Polypodium mengtzeense* Christ, Bull. Herb. Boissier 6 (1898) 869; Copeland, Philip. Journ. Sc. 1, Suppl. (1906) 161, pl. 21, q. n. s.; ibid., Suppl. 2: 256; Hu et Ching, Icon. Fil. Sinic. 1 (1930) pl. 42. — *Polypodium argutum* Wallich ex Hooker var. *mengtzeense* Christ, Bull. Acad. Géogr. Bot. (1909) 177. — *Polypodiastrum mengtzeense* Ching, Acta Phytotax. Sin. 16 (1978) 28. — Lectotypes (Rödl-Linder, 1987): *A. Henry 10964B*, Yunnan: Mengtze mountains, 2000 m alt. (P; iso K); *A. Henry 9054* (para B, K, NY, see note 6).

Polypodium argutum Wallich ex Hooker forma *khasianum* Clarke, Journ. Linn. Soc. London Bot. 24 (1888) 417, 418. — Syntypes: *C.B. Clarke s.n.*, 'exempla Khasiana omnia nisi exemplum Simons 282' (K).

Polypodium aspersum Baker, Kew Bull. (1898) 231, nom. illeg. [ICBN art. 63.1]. — Type: *A. Henry 9054*, Yunnan: Mengtze mountains to SE, 2000 m alt. (K; iso B, NY, see note 6).

Polypodium taiwanianum Hayata, Bot. Mag. Tokyo 23 (1909) 80; Tagawa, Acta Phytotax. Geobot. 7 (1938) 188, Mem. Coll. Sc. Univ. Kyoto, ser. B, 21 (1954) 74, 75. — *Marginaria taiwaniana* Nakai ex Itô, Journ. Jap. Bot. 11 (1935) 95. — *Polypodiastrum taiwanianum* Ching, Acta Phytotax. Sin. 16 (1978) 28. — Type: *Kawakami & Mori 2361*, Taironkosha, -11-1906 (TI).

Polypodium subauriculatum auct. non Blume: Baker in Hooker & Baker, Syn. Fil., ed. 1 (1867) 344.

Polypodium argutum auct. non Hooker: Wu, Sunyatsenia 3 (1932) 266, pl. 124, p.p.; Tagawa, Acta Phytotax. Geobot. 7 (1938) 188, 189, p.p.

Goniophlebium argutum auct. non J. Smith: Tagawa, Mem. Coll. Sc. Univ. Kyoto, ser. B, 21 (1954) 74, 75, p.p.; Copeland, Fern Fl. Philip. 3 (1960) 462, p.p.

Epiphytic and horizontally or vertically climbing, epilithic or terrestrial and linearly creeping. *Rhizome* terete, 3.5–5.0 mm in diam., glaucous, phyllopodia 1.5–2.0 cm apart, vascular strands 8–15, dark bundle sheaths absent, sclerenchyma strands 40–90. *Rhizome scales* evenly inserted, spadiceous, spreading, quite densely set, perfoliate, dimorphic; I) spreading, ephemeral, deltoid, index 3.4–3.6, 1.7–3.9 by 0.5–1.1 mm, apex filiform, basal flaps round; II) at base of I), appressed, persistent, round, 0.06–0.1 mm in diam.; I & II) clathration of cell walls getting slightly thinner at base, cells hyaline, clathrate marginal protrusions slightly longer at base, marginal glands situated all around, quite frequent, surface indument absent. *Fronds:* blade herbaceous, index 2.5–4.0, 20–60(–70) by 8–15(–20) cm, widest medially or equally wide throughout, pinnate, lateral segments index 8.0–8.5, 80–110 by 10–13 mm, apex pungent, base cordate or auricled, rarely truncate, sessile, at least at apical third of blade adnate and decurrent, margin entire to crenate, terminal segment conform to lateral segments, same length or slightly longer than longest lateral segment, basal segments 15–45 mm separate from subbasal segments, equally long, patens; stipe in cross section near base 2.0–3.5 mm across, index length of of stipe/length of blade 0.2–0.7. *Venation:* primary areolae uniserial, index 1.50–1.75, marginal free veins max. 1/3 length of areolae, 1–3 per areola, unforked, empty anastomoses rare, angle between secondary and primary veins 60–70°. *Indument:* laminar glandular hairs unbranched, 2–5 cells long, including 1 terminal gland, laminar acicular hairs absent, laminar scales sometimes persistent, petiolar acicular hairs absent. *Sori* uniserial, superficial, medial between costa and margin, round, 0.8–1.5 mm in diam.; receptacular hairy paraphyses –6 cells long, unbranched, receptacular scaly paraphyses clathrate, peltate, stellate and deltoid, 3 or more cells wide, index 1.1, 150–250 by 140–250 μm, persistent; episporangial paraphyses absent, sporangial capsule index 1.1, 220–260 by 200–240 μm, annulus with 19–23 cells, including 12–13 indurated cells. *Spores* yellow, index L/P 1.7–1.8, 30–35 by 55–60 by 35 μm; exospore colliculate; perispore for the greater part attached, crestae parallel to the equatorial axis, excrescences at lateral poles absent, detailed outer surface ornamentation smooth, globules absent.

Distribution. Japan (see note 7); Nepal; India: Assam; China: Yunnan, Kwangsi; Taiwan; Thailand; Laos; Vietnam; Philippines (Luzon). Fig. 22.

Habitat. Primary and secondary forest; mostly epiphytic on mossy tree trunks, rarely epilithic on humid cliffs or terrestrial under shrubs; alt. 1200–2700 m.

Notes. 1. The rhizome branches frequently and is hence intermingling when growing in clusters.

2. *Goniophlebium mengtzeense* seems to be seasonal. During a field trip in Luzon in November (end of rainy season) only yellow-brownish fronds have been found,

which were all adult and fertile but overmature with dark yellow sori. In June (beginning of rainy season) all specimens found were fresh and light green. Many juvenile, also sterile fronds were present and fertile fronds were not mature yet with pale yellow sori. This plant hardly grows under lowland conditions.

3. Some collections appear to be slightly different, the margin of pinnae being more serrate and the pinnae being situated alternately, e.g. *Jacobs 7453*, Mt. Tabayoc (L, PNH, CAHP) and *Rödl-Linder 108*, Mt. Pulog (L).

4. Specimens from Taiwan have sometimes prolonged auricles at the lateral segments, e.g. *Chen 2472* (L).

5. Specimens from Taiwan and North Thailand have generally bigger fronds and thicker rhizomes with the scales more densely set.

6. The specimens seen of *Henry 9054* (B, K, NY), type of *Polypodium aspersum* Baker and paratype of *Polypodium mengtzeense* Christ (1898) are somewhat abnormal, concerning the scattered sori.

7. Only one record from Japan has been seen, i.e. *Nakazawa 16012*, Tyoazyn (TI).

20. Goniophlebium formosanum (Baker) Rödl-Linder, *comb. nov.*

Polypodium formosanum Baker, Journ. of Bot. 23 (1885) 105; Ogata, Icon. Fil. Jap. 3 (1930) pl. 135; Yamamoto, Journ. Soc. Trop. Agric. Taiwan 10 (1931) 286, 287; Ching, Contr. Inst. Bot. Acad. Peiping 2 (1933) 43; Tagawa, Mem. Coll. Sc. Univ. Kyoto, ser. B, 21 (1954) 72, 73; DeVol & Kuo, Fl. Taiwan (1975) 202, 203. — *Marginaria formosana* Nakai ex Itô, Journ. Jap. Bot. 11 (1935) 94; Itô, Bot. Mag. Tokyo 53 (1939) 27. — *Polypodiodes formosana* Ching, Acta Phytotax. Sin. 16 (1978) 27. — Type: *W. Hancock 50*, Taiwan, Tamsui (K).

Polypodium liukiuense Christ, Bull. Herb. Boissier 1 (1901) 1014; Yamamoto, Journ. Soc. Trop. Agric. Taiwan 10 (1931) 287; Tagawa, Mem. Coll. Sc. Univ. Kyoto, ser. B, 21 (1954) 72, 73. — Type: *U. Faurie 4570*, Yakusima I., Kyuoyu, -07-1900 (P).

Epiphytic, epilithic. *Rhizome* terete, 5–6 mm in diam., glaucous, phyllopodia 0.8–2.0 cm apart, vascular strands 11–13, dark bundle sheaths present, sclerenchyma strands 50–60. *Rhizome scales* inserted in invaginations, brunneous, appressed, disperse, ephemeral, perfoliate, monomorphic, deltoid, index 1.8–2.2, 1.1–1.3 by 0.5–0.7 mm, apex acuminate, basal flaps round, cell walls very thickly clathrate throughout, cells yellow, clathrate marginal protrusions absent, marginal glands situated all along, frequent, surface indument absent. *Fronds:* blade herbaceous, index 2.6–3.1, 26–50 by 10–16 cm, widest subbasally, pinnatifid, lateral segments index 6.3–7.1, 50–70 by 7–11 mm, apex acute, margin entire, terminal segment coadunate, basal segments 15–18 mm separate from subbasal segments, shorter, deflexed; stipe in cross section near base 2–3 mm across, index length of stipe/length of blade 0.4–0.8. *Venation:* primary areolae uniserial, index 0.9–1.2, marginal free veins max. 1/2 length of areolae, 1–3 per areola, simple or forking, empty anastomoses frequent, angle between secondary and primary veins 60–70°. *Indument:* laminar glandular hairs unbranched, 2–3 cells long, including 1–2 terminal glands, laminar acicular hairs 2–4 cells long, situated all over lamina, density high, laminar scales fugaceous, petiolar acicular hairs 2–4 cells long. *Sori* uniserial, superficial, medial to costal, round, 1.5–2.0 mm in diam.; receptacular hairy paraphyses –13 cells long, –5 glandular and –2 acicular branches present, receptacular scaly paraphyses absent; episporangial paraphyses absent, sporangial capsule index 0.9–1.0, 200–210 by 200–220 μm, annulus with 17–20 cells, including 11–14 indurated cells. *Spores* yellow, index L/P 1.4–1.9, 25–35 by 45–55 by 25–35 μm; exospore subverrucate; perispore inconspicuous, smooth, excrescences at lateral poles absent, detailed outer surface ornamentation smooth, few globules present.

Distribution. Japan: Kyushu, Ryukyu; Taiwan. Fig. 23.

Habitat. Subtropical primary forest; forest border; epiphytic on tree trunk; epilithic; alt. 200–1200 m.

Notes. 1. Rhizome scales as well as laminar scales have no clathrate marginal protrusions (illustrated by Ogata, 1930), which is common among the Neotropical species.

2. The root structure is remarkable. The roots are unbranched and surrounded by a parenchymatous sheath.

21. **Goniophlebium niponicum** (Mettenius) Beddome

Goniophlebium niponicum Beddome, Handb., Suppl. (1892) 90. — *Polypodium niponicum* Mettenius, Annls. Mus. Bot. Lugd. Batav. 2 (1866) 222; Diels, Nat. Pflanzenfam. 1 (1899) 312; Christensen, Acta Horti Gotoburg. 1 (1924) 99; Ching, Contr. Inst. Bot. Acad. Peiping 2 (1933) 42; Tagawa, Mem. Coll. Sc. Univ. Kyoto, ser. B, 21 (1954) 71, 72; Satija & Bir, Polypod. Ferns India (1985) 11, 12. — *Marginaria niponica* Nakai ex Itô, Journ. Jap. Bot. 11 (1935) 95. — *Polypodiodes niponica* Ching, Acta Phytotax. Sin. 16 (1978) 27. — Type: *Bürger s.n.*, Japan (L, herb. no. 908.308-288, herb. Von Siebold, one sterile frond).

Polypodium niponicum Mettenius var. *wattii* Beddome,. Journ. of Bot. (1888) 235; Christ, Bull. Herb. Boissier 6 (1898) 870, q. specim. s. '*Polypodium nipponicum*'; Ching, Contr. Inst. Bot. Acad. Peiping 2 (1933) 42; Christensen & Tardieu, Notul. Syst. [Paris] 8 (1939) 183. — *Goniophlebium niponicum* Beddome var. *wattii* Beddome, Handb., Suppl. (1892) 90. — *Polypodium wattii* Tagawa, Journ. Jap. Bot. 22 (1949) 163; Satija & Bir, Polypod. Ferns India (1985) 15. — *Polypodiodes wattii* Ching, Acta Phytotax. Sin. 16 (1978) 27. — Type: *Watt 5852*, Manipur, Koupra, 1300–2000 m alt. (iso B, P).

Polypodium bodinierii Christ, Bull. Acad. Géogr. Bot. 1 (9) (1902) 203. — Syntypes: *Bodinier & Laborde 2031*, China, prov. Kouy-Tcheou, Tsin-gay, 'rochers de la montagne de Kaoschay', -12-1897 (P) & 15-03-1898 (P).

Polypodium niponicum Mettenius var. *laevipes* Franchet ex Christ, Bull. Soc. France 52, Mém. 1 (1905) 13; Christensen, Acta Horti Gotoburg. 1 (1924) 99. — Syntypes: *Henry 10179*, Yunnan, Mong-Tze (B, NY, P); *Soulié 1628*, China, Haute-Mékong (P).

Polypodium silvestrii Christ, Notul. Syst. [Paris] 1 (1909) 58. — Type: *G. Silvestre 62*, China, Hou-pe, Ma-kia-keon, 700 m alt., -04-1907 (P).

Polypodium longkyense Rosenstock, Feddes Repert. 13 (1914) 134; Ching, Contr. Inst. Bot. Acad. Peiping 2 (1933) 41. — Type: *Maire s.n.*, China, Yunnan, Long-ky, 300 m alt., 1912 (not traced in B, P, NY).

Polypodium transpianense Yamamoto, Journ. Soc. Trop. Agric. Taiwan 3 (1931) 236; Tagawa, Acta Phytotax. Geobot. 10 (1941) 286, 287; Mem. Coll. Sc. Univ. Kyoto, ser. B, 21 (1954) 72; DeVol & Kuo, Fl. Taiwan (1975) 203. — *Marginaria transpianensis* Itô, Journ. Jap. Bot. 11 (1935) 95. — *Polypodiodes transpianensis* Saiki, Journ. Phytogeogr. Tax. 35 (1987) 80. — Type: *Y. Yamamoto s.n.*, Taiwan, prov. Taihoku, Mt. Pianon, Rato-gun, 04-09-1925 (not traced in TAI, TI).

Polypodium raishaense Rosenstock, Hedwigia 56 (1915) 346; Tagawa, Acta Phytotax. Geobot. 5 (1936) 108; Mem. Coll. Sc. Univ. Kyoto, ser. B, 21 (1954) 73; DeVol & Kuo, Fl. Taiwan (1975) 202, 203; Saiki, Journ. Phytogeogr. Tax. 35 (1987) 80. — *Marginaria raishaensis* Nakai ex Itô, Journ. Jap. Bot. 11 (1935) 95; Itô, Bot. Mag. Tokyo 53 (1939) 27. — Type: *Faurie 219*, Taiwan, Raisha, 'ad arborum truncos', 1200 m alt., -03-1914 (iso B, NY, TI).

Marginaria pseudoformosana Tagawa, Acta Phytotax. Geobot. 3 (1934) 94; ibid. 5 (1936) 108. — Type: *J. Ohwi 364*, Taiwan, prov. Taitô 'inter Taizywin et Syussuiha', -04-1933 (not traced in KYO).

Polypodium amamianum Tagawa, Journ. Jap. Bot. 23 (1949) 78; Itô, Bot. Mag. Tokyo 53 (1939) 27; Tagawa, Mem. Coll. Sc. Univ. Kyoto, ser. B, 21 (1954) 72. — *Polypodiodes amamiana* Saiki, Journ. Phytogeogr. Tax. 35 (1987) 80. — Type: *G. Koidzumi s.n.*, Japan, Ryukyu I., Amami-Osima, Mt. Yuwan, 05-05-1923 (KYO; iso L).

Epiphytic, epilithic. *Rhizome* terete or dorsiventrally flattened, 4.0–6.0 mm in diam., glaucous (see note 1), phyllopodia 0.5–3.0 cm apart, vascular strands 8–16, dark bundle sheaths present, sclerenchyma strands 1–10 or 50–60. *Rhizome scales* inserted in an invagination, badious, spreading or appressed, quite densely set or very rare, ephemeral, perfoliate, monomorphic, deltoid, index 4.0–5.0, 1.6–4.0 by 0.4–0.8 mm, apex acuminate, basal flaps round, clathration of cell walls throughout, slightly thicker centrally, cells yellowish, clathrate marginal protrusions all along, marginal glands situated terminally and basally, rare, surface indument absent. *Fronds:* blade herbaceous, index 2.7–4.0, 11–38 by 4–10 cm, widest medially to subbasally, pinnatifid, lateral segments index 3.1–8.3, 22–50 by 3–13 mm, apex obtuse to acute, margin entire, rarely crenate, terminal segment coadunate, basal segments 5–14 mm separate from subbasal segments, shorter, deflexed; stipe in cross section near base 1.0–2.8 mm across, index length of stipe/length of blade 0.3–0.6. *Venation:* primary areolae uniserial, index 1.6–2.0, marginal free veins c. 3/4 length of areolae, 1–2 per areola, simple or forking, empty anastomoses rare, angle between secondary and primary veins 60–70°. *Indument:* laminar glandular hairs unbranched, 2–3 cells long, including 1 terminal gland, laminar acicular hairs 2–5 cells long, situated all over lamina, density variable, laminar scales sometimes persistent, petiolar acicular hairs 2–5 cells long. *Sori* uniserial, superficial, medial to costal, round, 1–2 mm in diam.; receptacular hairy paraphyses –10 cells long, –8 glandular branches present, persistency variable, receptacular scaly paraphyses absent; episporangial paraphyses absent, sporangial capsule index 1.1–1.3, 200–330 by 170–260 µm, annulus with 15–22 cells, including (11–)13(–15) indurated cells. *Spores* yellowish, index L/P 1.4–1.5, 25–40(–45) by 50–65 by 30–45 µm; exospore subverrucate; perispore inconspicuous, smooth, excrescences at lateral poles absent, detailed outer surface ornamentation smooth, few globules present.

KEY TO INFRASPECIFIC TAXA

1a. Rhizome scales present, quite densely set; sclerenchyma strands in rhizome 50–60; receptacular hairy paraphyses with –8 glandular branches
a. var. niponicum

b. Rhizome scales very rarely present, set in small tufts; sclerenchyma strands in rhizome 1–9; receptacular hairy paraphyses with –4 glandular branches
b. var. wattii

a. var. niponicum

Polypodium niponicum Mettenius. — ***Polypodium bodinierii*** Christ. — ***Polypodium silvestrii*** Christ. — ***Polypodium longkyense*** Rosenstock. — ***Polypodium transpianense*** Yamamoto. — ***Polypodium raishaense*** Rosenstock. — ***Marginaria pseudoformosana*** Tagawa. — ***Polypodium amamianum*** Tagawa.

Rhizome: terete, sclerenchyma strands 50–60. *Rhizome scales* quite densely set, spreading. *Fronds:* blade firmly herbaceous, widest subbasally, lateral segments index 5.0–8.3, basal segments 5–9 mm separate from subbasal segments. *Sori:* receptacular hairy paraphyses with –8 glandular branches, persistent. *Spores:* index L/P 1.4–1.5.

Distribution. Japan: Honshu, Shikoku, Kyushu, Ryukyu; Tibet; India: Assam; China: Hupeh, Sichuan, Kweichow, Yunnan, Anhwei, Chekiang, Hunan, Kwangtung; Taiwan; Vietnam. Fig. 23.

Habitat. Dense, mixed, subtropical primary forest; moist, loamy, shady, steep slopes; dry sandy thicket; epiphytic on tree trunks; epilithic on stone walls; sometimes rare, sometimes common; shaded or exposed; alt. 300–1200 m.

Notes. 1. One specimen with a conspicuously thin rhizome (3.6 mm) does not appear glaucous and has many marginal glandular hairs on the laminar scales, i.e. *Maire s.n.*, Nov. 1912, Long-ky (P).

2. The density of acicular laminar hairs is mostly high, hence the venation is not visible. Only rarely the density is low and the venation is clearly visible, e.g. *Faurie 219* (NY, type of *Polypodium raishaense* Rosenstock).

b. var. wattii Beddome

Goniophlebium niponicum Beddome var. ***wattii*** Beddome. — ***Polypodium niponicum*** Mettenius var. ***laevipes*** Franchet ex Christ.

Rhizome: terete or dorsiventrally flattened, sclerenchyma strands 1–9. *Rhizome scales* very rare, set in small tufts, appressed. *Fronds:* blade thinly herbaceous, widest medially to subbasally, lateral segments index 3.1–3.8, basal segments 8–14 mm separate from subbasal segments. *Sori:* receptacular hairy paraphyses with –4 glandular branches, fugaceous. *Spores:* index L/P 1.6–1.8.

Distribution. Tibet; India: Assam; China: Yunnan; Vietnam.

Habitat. Humid forest; alt: 1300–3000 m.

Notes. 1. Collections are rare. China: *Henry 10179* (B,NY,P); *Ludlow 12134* (PNH); *Soulié 1628sn* (P); *Teng 8019* (PE); *Tsai 51769* (SING); *Wang C.W. 65137* (PE); *T.T. Yue 19167, 23032* (PE). Assam: *Meebold A 4794* (B); *Watt 5852* (B, P). Vietnam: *Poilane 25596* (P).

2. Evidently, the altitude is a decisive factor for the varieties. Var. *niponicum* appears between 300 and 1200 m, while the altitudinal range of var. *wattii* reaches from 1300 to 3000 m.

22. Goniophlebium hendersonii Beddome

Goniophlebium hendersonii Beddome, Ferns Brit. Ind., Suppl. (1876) 21, pl. 383; Handb. (1883) 320, 322, nom. leg. [ICBN art. 72]. — *Polypodium hendersonii* Atkinson ex Baker in Hooker & Baker, Syn. Fil. (1874) 511, nom. illeg., non Lowe (1858); Clarke, Trans. Linn. Soc. London, ser. 2, 1 (1880) 550, 551; Ching, Contr. Inst. Bot. Acad. Peiping 2 (1933) 48. — *Polypodium atkinsonii* Christensen, Ind. Fil. (1906) 511, nom. nov.; DeVol, Taiwania 10 (1964) 151, pl. 10; Bir et al., New Bot. 1 (1974) 147, 148; DeVol & Kuo, Fl. Taiwan 1 (1975) 202, 203, pl. 70.— *Polypodiodes atkinsonii* Ching, Acta Phytotax. Sin. 16 (1978) 27, nom. illeg. [ICBN art. 72]. — Lectotype (Ching, 1933): *Atkinson s.n.*, Sikkim, 3300–3700 m alt. (K).

Epiphytic, epilithic. *Rhizome* terete, c. 3 mm in diam., brown, phyllopodia 1–2 cm apart, vascular strands 7–10, dark bundle sheaths absent, sclerenchyma strands 15–25. *Rhizome scales* inserted on protrusions, brunneous, spreading, densely set, ephemeral, perfoliate, sometimes basifix, monomorphic, deltoid, index 2.6–3.2, 1.6–3.5 by 0.5–1.3 mm, apex filiform, basal flaps round, cell walls clathrate throughout, cells hyaline, clathrate marginal protrusions slightly longer at base, marginal glands situated all along, frequent, surface indument absent. *Fronds:* blade thinly herbaceous, index 4.6–5.0,15–23 by 3–5 cm, widest medially to subbasally, deeply pinnatifid or adnate, lateral segments index 2.5–3.1, 15–25 by 6–8 mm, apex acute or obtuse, margin obviously serrate, apical segment coadunate, basal segments 7–10 mm separate from subbasal segments, shorter, sometimes deflexed; stipe in cross section near base 2.5–3.5 mm across, index length of stipe/length of blade 0.2–0.3. *Venation:* primary areolae uniserial (see note 2), index 0.75–0.80, marginal free veins 1/3 length of areolae, 1–3 per areola, unforked, empty anastomoses absent, angle between secondary and primary veins 65–75°. *Indument:* laminar glandu-lar hairs unbranched, 2–3 cells long including 1 terminal gland, laminar acicular hairs absent, laminar scales sometimes persistent, petiolar acicular hairs absent. *Sori* uniserial, superficial, medial to costal, round, 1.0–2.0 mm in diam.; receptacular hairy paraphyses –10 cells long, unbranched, receptacular scaly paraphyses clathrate, palaceous, linear, deltoid, 3 or more cells wide, index 1.6–2.7, 270–410 by 100–255 μm, ephemeral; episporangial paraphyses absent, sporangial capsule index 1.1, 310–340 by 270–310 μm, annulus with 19–20 cells, including 11–15 indurated cells. *Spores* brownish, index L/P 1.3–1.4, 40–45 by 55–60 by 40–45 μm; exospore smooth; perispore widely detached, reticulate and wrinkled, crestae locally protruding, excrescences at lateral poles absent, detailed outer surface ornamentation smooth, few globules present.

Distribution. Tibet; Nepal; Sikkim; India: Assam; Taiwan. Fig. 24.

Habitat. Cloud forest; epiphytic on pine trees, junipers, *Quercus* spec. and *Rhododendron arboreum* Smith, epilithic on damp, rocky cliffs; altitude 2300–4000 m.

Notes. 1. The margin of the lateral segments is conspicuously serrate.

2. DeVol (1964) reports specimens from Taiwan with veins partly free forking, partly anastomosing.

23. Goniophlebium subamoenum (Clarke) Beddome

Goniophlebium subamoenum (Clarke) Beddome, Handb. (1883) 317. — ***Polypodium subamoenum*** Clarke, Trans. Linn. Soc. London, ser. 2, 1 (1880) 550, pl. 82: fig. 2; Christ, Bot. Gaz. 51 (1911) 346, q. n. s.; Christensen, Acta Horti Gotoburg. 1 (1924) 99; Ching, Contr. Inst. Bot. Acad. Peiping 2 (1933) 47, 48; Bir, Trikha & Vasudeva, New Bot. 1 (1974) 148. — ***Polypodiodes subamoena*** Ching, Acta Phytotax. Sin. 16 (1978) 27. — Lectotype (Ching, 1933): *C.B. Clarke 13494A*, Tumbok 1000, Sikkim, 09-10-1870 (K; iso K).

Rhizome terete, 1.2–2.0 in diam., brown, phyllopodia 1–3 cm apart, vascular strands 6–8, dark bundle sheaths present, sclerenchyma strands 20–30. *Rhizome scales* evenly inserted, brunneous, spreading, densely set, persistent, perfoliate, monomorphic, deltoid, index 2.5–3.4, 2.3–4.4 by 0.9–1.3 mm, apex acuminate, basal flaps round, clathration of cell walls thin, sometimes absent at base, cells hyaline, clathrate marginal protrusions short all along, marginal glands situated basally, centrally and terminally, quite frequent, surface indument rhizoid. *Fronds:* blade herbaceous, index 2.0–2.8, 12–28 by 6–13 cm, widest basally to subbasally, pinnatifid, lateral segments index 4.5–5.5, 25–35 by 5–7 mm, apex obtuse, sometimes acute, margin obviously serrate, terminal segment coadunate, basal segments 6–10 mm separate from subbasal segments, shorter, deflexed; stipe in cross section near base 0.9–1.1 mm across, index length of stipe/length of blade 0.5– 0.9. *Venation:* primary areolae uniserial, index 0.9–1.5, marginal free veins max. 1/2 length of areolae, 1–3 per areola, simple or forking, empty anastomoses rare, angle between secondary and primary veins 60–70°. *Indument:* laminar glandular hairs unbranched, 2–3 cells long, including 1 terminal gland, laminar acicular hairs absent, laminar scales quite persistent, petiolar acicular hairs absent. *Sori* uniserial, superficial, medial between costa and margin, round, 1.5–2.0 mm in diam.; receptacular hairy paraphyses –6 cells long, unbranched, receptacular scaly paraphyses clathrate, peltate or palaceous, linear, deltoid, 2 or more cells wide, index 1.7–2.1, 450–700 by 210–400 µm, persistent; episporangial paraphyses absent, sporangial capsule index 1.1–1.2, 300–390 by 280–330 µm, annulus with 17–20 cells, including 12–14 indurated cells. *Spores* yellowish, index L/P 1.5–1.6, 30–40 by (45–)50–60 by 35–40 µm; exospore colliculate; perispore widely detached, crestae parallel to the equatorial axis, locally protruding, excrescences at lateral poles absent, detailed outer surface ornamentation smooth, few globules present.

Distribution. Nepal; Sikkim. Fig. 24.

Habitat. Dense primary forest; epiphytic on mossy tree trunks; epilithic on mossy rocks; deeply or slightly shaded; alt. (1900–)2800–4000 m.

Notes. 1. Collections are rare. *Clarke 13381A, 25590, 25596B, 25635C* (K); *Gamble 8377* (P); *Kanai et al. 725179, 725301, 725303B* (TI); *Khwaunju 1242* (K).

2. Some differences between *Goniophlebium subamoenum* and *G. amoenum*, which are stressed by Ching (1933), are here not considered characteristic, i.e. reduced size, subvillose leaves, thinner texture, bright brown colour when dried. The presence of entire rhizome scales as stated by Ching (1933) is not confirmed.

3. A list of diagnostic characters is given below:

	amoenum	*subamoenum*
rhizome		
diameter (mm)	4.0–6.0	1.2–2.0
sclerenchyma strands	50–100	20–30
sori		
receptacular scaly paraphyses clathration	light	dark
fronds		
lateral segments margin	crenate to serrate	obviously serrate

4. *Goniophlebium hendersonii,* a species with slightly wider distribution but same habitat is hard to distinguish from *G. subamoenum.* A list of diagnostic characters is given below:

	hendersonii	*subamoenum*
rhizome		
diameter (mm)	2.9–3.2	1.2–2.0
dark bundle sheaths	absent	present
fronds		
index length stipe/length blade	< 4.5	> 4.5
index blade	> 3.5	< 3.5
index lateral segment	< 3.5	> 3.5
laminar indument		
acicular hairs	absent	present
spores		
colour	brownish	yellowish

17.4. SPECIES DUBIAE ATQUE SPECIES EXCLUSAE

Species dubiae

D1. Polypodium knightii Baker, Gard. Chron. (1903) 245. — Type: A cultivated specimen ex Hort. Sander, originating from Australia.

Note. Only one sterile herbarium specimen has been seen. One sterile living specimen has been seen in the Botanischer Garten, Berlin. The venation is irregularly goniophlebioid, some costal areolae are empty, i.e. they have no included free veins, but are subdivided by a tertiary vein.

D2. Polypodium lampongense Zollinger, Syst. Verz. (1854) 37, nom. nud., 48; Baker in Hooker & Baker, Syn. Fil., ed. 1 (1867) 344. — Type: *H. Zollinger 756,* 16-09-1845, Sumatra, Lampong, prope Telok Betung (not traced in B, P).

Note. Ex descriptione: 'Prope *Polypodium subauriculatum* Bl. ponendum ... pinnis cordatis deorsum subauriculatis ... soris obsolete 3-serialibus.' The only Asian *Goniophlebium* with three-serial sori is *G. korthalsii* which is also reported from Sumatra, but with pinnae basally cuneate to angustate.

Species Goniophlebio exclusae

E1. Polypodium (Goniophlebium) bourrettii Christensen & Tardieu-Blot, Notul. Syst. [Paris] 8 (1939) 183. — Syntypes: *Bourret s.n.*, -03-1921, Vietnam, Tonkin, Pia Bioc (P); *Colani 4870,* Vietnam, Tonkin, near Chobo, alt. 500 m (P).

Note. This species differs from *Goniophlebium* in the *vulgare*-type of venation and the absence of paraphyses. Concerning venation, rhizome scales and spores it is similar to *Polypodium someyae,* from which it differs in the paraphyses. Besides the types no other specimen has been seen.

E2. Polypodium erythrocarpum Kuhn ex Mettenius, Linnaea 36 (1869) 135; Baker in Hooker & Baker, Syn. Fil., ed. 2 (1883) 511; Diels, Bot. Jahrb. 29 (1900) 203; in Engler & Prantl, Nat. Pflanzenfam. 1 (1899) 312; Christensen, Ind. Fil. (1906) 525. — *Goniophlebium erythrocarpum* Beddome, Fern Brit. Ind., Suppl. (1876) 21, pl. 382; Handb. (1883) 319, pl. 171, 320. — *Phymatopsis erythrocarpa* Ching, Acta Phytotax. Sin. 9 (1964) 191. — *Crypsinus erythrocarpus* Tagawa in Hara, Fl. E. Himal. (1966) 491. — *Phymatopteris erythrocarpa* Pichi Sermolli, Webbia 28 (1973) 462. — Type: *Hooker s.n.,* India orientalis, Sikkim, 2700–3700 m alt. = **Selliguea.**

Note. Baker (1883), Diels (1899, 1900) and Christensen (1906) consider this species as goniophlebioid. Beddome (1883) mentions that Clarke transferred the species to *Pleopeltis* because of its distinct venation. Not only the venation but also the coriaceous texture exclude this species from *Goniophlebium.*

E3. Polypodium moupinense Franchet, Nouv. Arch. Mus. [Paris] 2 (1883) 159. — *Goniophlebium moupinense* Beddome, Handb., Suppl. (1892) 91. — Type: *A. David s.n.*, -03-1869, China, Moupine (not traced in P). = **Selliguea** (?).

Note. Ex descriptione this species differs from *Goniophlebium* in the ovate rhizome scales and the simple, coriaceous, glaucous and dimorphic fronds.

E4. Polypodium pseudo-amoenum Ching, Contr. Inst. Bot. Acad. Peiping 2 (1933) 45, nom. nud., 'in herb.' — *Polypodiodes pseudo-amoena* Ching, Acta Phytotax. Sin. 16 (1978) 27, comb. illeg. — Type: *H.T. Tsai 60864* (PE).

Note. Ching cited and newly combined this name and annotated a type in PE. A description has never been published. (See also note 3 of species 10, *Goniophlebium amoenum*).

E5. Polypodium veitchii Baker, Gard. Chron. 14 (1880) 494; Christensen, Ind. Fil. (1906) 573; Ching, Contr. Inst. Bot. Acad. Peiping 2 (1933) 33. — *Phymatopsis veitchii* Itô, Journ. Jap. Bot. 11 (1935) 100. — *Crypsinus veitchii* Copeland, Gen. Fil. (1947) 206. — Type: *Maries 2294,* Japan (K).= **Selliguea.**

Note. This species is considered goniophlebioid by Baker (1880) and Christensen (1906). Ching (1933) puts it in *Phymatodes* due to its venation. Besides of the distinct venation the rhizome scales are not clathrate which excludes the present species from *Goniophlebium*.

E6. The Neotropical species referred to *Goniophlebium* are excluded.

17.5. POLYPODIUM SPECIES STUDIED IN COMPARISON WITH GONIOPHLEBIUM SPECIES

The generic identity of *Goniophlebium* being at stake, the author studied quite a number of species of *Polypodium* (sensu lato) throughout its geographical range. Neotropical species with a *Lepicystis*-type of scales were excluded, since they are not as the closest relatives of *Goniophlebium*. The results include the recognition of a genus *Goniophlebium* occurring exclusively in Asia. All other species are provisionally retained in *Polypodium*. The genus *Polypodium* is typified by *Polypodium vulgare* Linnaeus. This species is here referred to a group of species of which the Asian representatives with a (partly) free venation are described below to facilitate a comparison between these and the *Goniophlebium* species. The genus *Thylacopteris* might well be related to this Asian group of *Polypodium*. The complex of *Polypodium vulgare* and its relatives is presently studied by C. Haufler, Kansas. The Neotropical goniophlebioid species are presently studied by other researchers in the Polypodiaceae project (e.g. R. Hensen, Utrecht).

Since the Neotropical species studied are definitely heterophyletic, it is of interest to list not only character states distinguishing all of them from *Goniophlebium*, but also character states which are different in some of the species only.

Rhizome: vascular strands arranged in an irregular circle (FA, SO, BR, CA, FR), sclerenchyma strands absent (all species). *Rhizome scales:* peltate (FA, CA, FR, LO, BR), ovoid (FR, LO), clathrate marginal protrusions absent (FA, VU, BR, CA, FR, LO, SS). *Fronds:* lateral segments include an angle of c. 100° towards each other, in vivo (SS, BR, FR). — *Venation: vulgare*-type (FA, SO, VU, CA). *Sori:* receptacular hairy paraphyses absent (all species except SO), receptacular scaly paraphyses absent (all species except SO), contrastomium cells at sporangial capsule present (FA, SO). *Spores: vulgare*-type (FA, VU, BR, CA, FR, LO).

24. Polypodium fauriei Christ

Polypodium fauriei Christ, Bull. Herb. Boissier 4 (1896) 672; Ching, Contr. Inst. Bot. Acad. Peiping 2 (1933) 40; Tagawa, Mem. Coll. Sc. Univ. Kyoto, ser. B, 21 (1954) 71. — Lectotype: *Faurie 6009*, 'ruines de chateau de Morioka', 17-08-1890 (P).

Polypodium vulgare Linneus var. *japonicum* Franchet & Savatier, Enum. Pl. Jap. 2 (1876) 244. — *Polypodium japonicum* Maxon, Fern. Bull. 10 (1902) 42, 43, nom. illeg., non Houttuyn (1783); Makino, Bot. Mag. Tokyo 19 (1905) 139, 140; Ogata, Icon. Fil. Jap. 2 (1929) pl. 85. — Type: *Ono 1544*, Japan, Sendai prov. (not traced in P).

Epiphytic. *Rhizome* terete, 3–4 mm in diam., yellowish, phyllopodia 0.5–1.0 cm apart, vascular strands 10–15, dark bundle sheaths absent, sclerenchyma strands absent. *Rhizome scales* inserted in invaginations, orange, appressed, densely set, persistent, peltate, shape indistinguishable, index 1.4–2.0, 1.9–2.7 by 1.3–1.4 mm, apex round, basal flaps round, clathration of cell walls absent, cells yellow, clathrate marginal protrusions absent, marginal glands absent, surface indument rhizoid. *Fronds:* blade firm herbaceous, index 3.0–4.6, 9–32 by 3–7 cm, widest medially, pinnatifid, lateral segments index 7.0–8.3, 25–35 by 3–5 mm, apex acute, margin entire to crenate, terminal segment coadunate, basal segments 9–11 mm separate from subbasal segments, shorter, sometimes deflexed; stipe in cross section near base 1.0–1.5 mm across, index length of stipe/length of blade 0.1–0.3. *Venation:* primary areolae absent, free veins twice forked, empty anastomoses absent, angle between secondary and primary veins 40–50°. *Indument:* laminar glandular hairs unbranched, 2(–11) cells long, including 1 terminal gland, laminar acicular hairs 2–5 cells long, situated all over lamina, density variable, laminar scales fugaceous, petiolar acicular hairs sometimes present. *Sori* uniserial, superficial, medial between costa and margin, round, 1.5 mm in diam.; receptacular hairy paraphyses –8 cells long, unbranched, receptacular scaly paraphyses absent; episporangial paraphyses absent, sporangial capsule index 1.1, 285–335 by 255–315 µm, annulus with 21–25 cells, including 12–15 indurated cells. *Spores* yellowish, index L/P 1.6–1.8, 30–40 by 55–70 by 35–40 µm; exospore verrucate; perispore inconspicuous, wrinkled, excrescences at lateral poles absent, detailed outer surface ornamentation undulate, globules absent.

Chromosomes. n = 37.

Distribution. Japan: Hokkaido, Honshu, Kyushu; Korea: Quelpart I.

Habitat. Mountain forest; epiphytic on mossy tree trunks; altitude low and middle.

Notes. 1. Ex descriptione Christ (1896) 673: "... à rachis fortement enroulé latéralement, jusqu'à former une spirale ..."

2. The present species has (one to) two sporangial contrastomium cells. This has been illustrated before by Ogata (1929).

3. More details on the distribution are given in Kurata & Nakaike (1981).

25. Polypodium someyae Yatabe

Polypodium someyae Yatabe, Bot. Mag. Tokyo 5 (1891) 245, pl. 27; Ching, Contr. Inst. Bot. Acad. Peiping 2 (1933) 46, 47, q.n.s.; Tagawa, Mem. Coll. Sc. Univ. Kyoto, ser. B, 21 (1954) 74. — *Polypodium someyae* Yatabe var. *someyae* Tagawa, Mem. Coll. Sc. Univ. Kyoto, ser. B, 21 (1954) 74. — *Marginaria someyae* Nakai ex Itô, Journ Jap. Bot. 11 (1935) 95. — *Polypodiastrum someyae* Ching, Acta Phytotax. Sin. 16 (1978) 28. — Type: *T. Someya s.n.*, Mt. Myogi, prov. Kozuke, -09-1887 (TI).

Polypodium someyae Yatabe var. *awaense* Tagawa, Mem. Coll. Sc. Univ. Kyoto, ser. B, 21 (1954) 74. — Type: *G. Nakai 4088*, Higasisemitani, Kamikito-gun, 'on mossy rocks in mountain forest', 500 m alt., 28-09-1949 (KYO).

Epilithic. *Rhizome* terete, 2.5–4 mm in diam., brown, phyllopodia 1–3 cm apart, vascular strands 7–8, dark bundle sheaths absent, sclerenchyma strands absent. *Rhizome scales* inserted on protrusions, spadiceous, spreading, densely set, persistent, perfoliate, monomorphic, deltoid, index 2.5–2.8, 1.9–3.0 by 0.8–1.0 mm, apex acuminate, basal flaps pointed, cell walls thinly clathrate except at centre, cells hyaline, clathrate marginal protrusions short all around, marginal glands situated terminally and basally, rare, surface indument rhizoid. *Fronds:* blade thinly herbaceous, index 1.4–1.8, 14–22 by 10–12 cm, widest subbasal, pinnatifid, lateral segments index 4.6–5.5, 55–70 by 10–15 mm, apex acute, margin crenate, terminal segment conform to lateral segments, 1/3 shorter than longest lateral segment, basal segments 10–13 mm separate from subbasal segments, shorter, sometimes deflexed; stipe in cross section near base 1.0–1.5 mm across, index length of stipe/length of blade 0.6. *Venation:* primary areolae uniserial, sometimes not closing, index 1.7–2.3, marginal free veins max. 1/3 length of areolae, 1–3 per areola, simple or forking, empty anastomoses rare, angle between secondary and primary veins 40–50°. *Indument:* laminar glandular hairs unbranched, 2–3 cells long, including 1 terminal gland, laminar acicular hairs absent, laminar scales sometimes persistent, petiolar acicular hairs absent. *Sori* uniserial, superficial, medial to marginal, round, 1–2 mm in diam.; receptacular hairy paraphyses –4 cells long, 1–2 glandular branches sometimes present, receptacular scaly paraphyses clathrate, peltate or palaceous, linear, stellate, index 1.0–1.1, 100–215 by 90–215 μm, persistent; episporangial paraphyses absent, sporangial capsule index 0.9–1.2, 255–355 by 275–305 μm, annulus with 16–22 cells, including (9–)12–13(–14) indurated cells. *Spores* yellow, index L/P 1.3–1.4, 40 by 50–55 by 35–40 μm; exospore colliculate; perispore inconspicuous, smooth, excrescences at lateral poles absent, detailed outer surface ornamentation smooth, few globules present.

Distribution. Japan: Honshu: Mt. Myogi, Shikoku: Kito-mura.

Habitat. Mountain forest; epilithic on mossy rocks; alt. 500 m.

Notes. 1. Collections are rare: *Anonymus s.n.* (K); *Iba 77* (TI); *Nakai 4088* (KYO), type of *Polypodium someyae* var. *awaense*; *Ogata s.n.* (TI); *Saida s.n.* (B); *Sakwai s.n.* (B); *Someya s.n.* (TI); *Tanaka s.n.* (PE).

2. *Sakurai s.n.*, 16-07-1906 (B): 'Mt. Myogi, nur hier endemisch, doch nicht mehr vorhanden.'

3. Vernacular name: Myogi-shida (Japanese).

4. A distinct species with characteristic venation and one contrastomium cell in the sporangium (see also *Polypodium fauriei*).

5. The present species is critical, since sclerenchyma strands in the rhizome are absent, like in all American goniophlebioids and receptacular scaly paraphyses are present, like in all Asian goniophlebioids.

6. More details on the distribution are given in Kurata & Nakaike (1981).

18. INDEX OF SPECIMENS

Table 14. Living specimens studied from the Utrecht greenhouse.

no.	species	greenhouse numbers
12	*Goniophlebium lachnopum*	86GR00185 82GR00114 Kew 337.7702 899
20	*Goniophlebium formosanum*	85GR00163 85GR00092
26	*Polypodium vulgare*	85GR00238
27	*Polypodium brasiliense* (*P. triseriale*)	81GR00101 86GR01277 82GR00272 86GR00097 86GR00067
29	*Polypodium dissimile*	86GR00785 82GR00276 82GR00182 86GR00904
30	*Polypodium fraxinifolium*	86GR00924
31	*Polypodium loriceum*	86GR00793 83GR00569 82GR00269 82GR00115 84GR00315

Collections are referred to accepted names as specified on fold-out page 423. Only collections with name and number are included. For mixed collections all identifications are listed. Institutional series are neglected. Type specimens are included; those of synonyms are listed with the number of the accepted species. In case of groups of collectors only the name of the first is listed.

Abbe 9979: 7 — Abdullah 120: 6 — Addison 37195: 6 — Adelbert 30: 6 — Ahmed 1: 5 — Alcasid 45: 19 — Allen, see Molesworth Allen — Alston 12463: 17; 12882: 17; 14917: 15; 15684: 17; 15749: 16; 16356: 16 — Anderson 10006: 5 — Anonuevo 21: 17.

Backer 129: 17; 10224: 5; 14199: 6; 25886: 17 — Bakhuizen van den Brink 2334: 17; 2522: 5; 6201: 17 — Balansa 1822: 10 — Bamler, L. 186: 6 — Bamler, M.G. 247: 2 — Barker LAE 66831: 2; LAE 67489: 2 — Barnes 974: 17 — Bartlett 8659: 6 — Bartholomew 356: 10 — Bartsch 262: 17; 484: 17; 501: 17 — Beguin 57: 17 — Berol 54: 17 — Betche 43: 8 — van Beusekom 865: 6; 1290: 19; 1333: 12; 2215: 19 — Bir 1050: 10 — Bista 674439: 12 — Bloembergen 3388: 17 — Blume 126: 17; 129: 17; 130: 17; 135: 6 — Boden Kloss 14800: 4 — Bodinier & Laborde 2031: 21a; 2041i: 10; 2041ii: 10; 2323i: 10; 2323ii: 10 — du Bois-Reymond 42: 21a — Bor 16262: 18 — Bor's Coll. 82: 12; 1015: 10 — van Borssum Waal-

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20. INDEX TO TAXONOMIC NAMES

Accepted names are in roman type; new combinations are in **bold type**; synonyms in *italics*. The numbers refer to the respective number of the accepted species. *Goniophlebium:* p. 371; Species dubiae (D): p.412; Species exclusae (E): p. 413.

Abbreviations and numbers of species

Goniophlebium percussum-group

BE = 1. *G. benguetense*
DE = 2. *G. demersum*
KO = 3. *G. korthalsii*
MB = 4. *G. mehibitense*
PC = 5. *G. percussum*
PS = 6. *G. persicifolium*
RA = 7. *G. rajaense*
SE = 8. *G. serratifolium*
TE = 9. *G. terrestre*

Goniophlebium subauriculatum-group

AM = 10. *G. amoenum*
AMl = 10a. *G. amoenum* var. *latedeltoideum*
AMc = 10b. *G. amoenum* var. *chinense*
AMa = 10c. *G. amoenum* var. *arisanense*
DL = 11. *G. dielseanum*
LA = 12. *G. lachnopum*
MA = 13. *G. manmeiense*
MI = 14. *G. microrhizoma*
PR = 15. *G. prainii*
PD = 16. *G. pseudoconnatum*
SU = 17. *G. subauriculatum*

Goniophlebium argutum-group

AR = 18. *G. argutum*
MZ = 19. *G. mengtzeense*

Goniophlebium formosanum-group

FO = 20. *G. formosanum*
NI = 21. *G. niponicum*
NIn = 21a. *G. niponicum* var. *niponicum*
NIw = 21b. *G. niponicum* var. *wattii*

Goniophlebium hendersonii-group

HE = 22. *G. hendersonii*
SA = 23. *G. subamoenum*

(Eur)Asian taxa retained in *Polypodium*

FA = 24. *P. fauriei*
SO = 25. *P. someyae*
VU = 26. *P. vulgare*

American taxa (p.p.) retained in *Polypodium*

BR = 27. *P. brasiliense*
CA = 28. *P. californicum*
DI = 29. *P. dissimile*
FR = 30. *P. fraxinifolium*
LO = 31. *P. loriceum*
SS = 32. *P. sessifolium*
(TR = 33. *P. triseriale* = *P. brasiliense*)