Phylogenetic Systematics of the Polypodiaceae (Filicales)*

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With 3 figures and 5 tables

Contents

A. General introduction

In his introductory statements to 'The Symposium on the Phylogeny and Classification of the Filicopsida' which was held in London, 1972, HOLTTUM, when dealing with 'dubious groups of relationships which would particularly repay investigation', mentioned the Polypodiaceae first (HOLTTUM, 1973: 6).

Talking about Polypodiaceae the present authors deal with the Polypodiaceae sensu stricto only, thus excluding the Cheiropleuriaceae, Dipteridaceae, Grammitidaceae, and also the Loxogrammaceae, taxa which were formerly (or are still) included in the Polypodiaceae sensu lato. As delineated in this way, this almost exclusively pantropical family consists of about 600 species and an indefinite number of genera.

The systematic problems in the family are the following:

1. The systematic position of the family in relation to other ferns;

2. The monophyly of the family;

3. The subdivision of the family into lower categories and especially genera;

4. The monographic treatment of the genera recognized, including the delimitation of species and their geographical distribution.

Under the covering law of evolution all these problems pertain to phylogenetic systematics. It is our aim to add to the knowledge about the phylogenetic relationships between the taxa comprising the family by the application of a cladistic analysis as given by WILEY (1981). This book starts from the basic principles of phylogenetic systematics as published by HENNIG (e.g. HENNIG, 1966) and at the same time assimilates additional knowledge about this discipline as published up to 1980.

I. Position of the family in relation to other ferns

DE LA SOTA (1973) discussed the relationship of the Polypodiaceae to the other ferns following PICHI SERMOLLI (1958, 1977). The latter's classification - 'the most natural classification' according to DE LA SOTA - starts from the idea that the Polypodiaceae (sensu PICHI SERMOLLI, i.e. including the loxogrammoid ferns), the Grammitidaceae, and the Cheiropleuriaceae form a monophyletic group. Within these three families DE LA SOTA reported the greatest number of similarities to exist between the Polypodiaceae and the Grammitidaceae. It is therefore surprising that DE LA SOTA refuted the alliance between Polypodiaceae and Grammitidaceae because of differences in geographical distribution apart from ecological differences.

HOLTTUM (1973) suggested a possible relationship between the Polypodiaceae (sensu HOLTTUM, i.e. including the loxogrammoid ferns) and the Davalliaceae because of similarities in rhizome and life

form, spores, scales, vascular anatomy, etc.,a relationship which
was not supported by JARRETT (1980) who regarded the similarities
between the two families as resulting from parallel evolution dic-
tated by epiphytism.

NAYAR (1970) held a still more different opinion about the alliance
of the Polypodiaceae (sensu NAYAR, i.e. excluding the loxogrammoid
ferns). He thought the Grammitidaceae to be related to the Cyathe-
ales whereas Polypodiaceae comprises 'the main line of evolution
from the primitive gleicheniaceous stock'. The Grammitidaceae to-
gether with the Aspleniaceae and the Thelypteridaceae should repre-
sent 'the aspleniaceous line' within the Cyatheales, whereby the
Grammitidaceae should 'represent a highly specialised line which
separated from the main stock rather early in the evolutionary his-
tory'. As far as the Polypodiaceae are concerned he stated: 'The
Loxogrammaceae appear to have separated from the main line (of po-
lypodiaceous ferns) earlier than the Dipteridaceae'. From this idea
it can be concluded that NAYAR regarded the Dipteridaceae as the
sister group of the Polypodiaceae which is, however, not reflected
in his linear classification of the families; he situated the Loxo-
grammaceae next to the Polypodiaceae.

JARRETT (1980) published a paper in order to state and discuss the
only 'radial change' she proposed after a long lasting general stu-
dy on the classification of all homosporous leptosporangiate ferns,
namely that the Polypodiaceae (sensu JARRETT, i.e. including the
loxogrammoid ferns) and the Grammitidaceae are related to the ad-
vanced indusiate ferns rather than to the gleichenioid group of
families as was proposed by BOWER (1928) and accepted by many au-
thors since. She implicitely accepted the monophyly of the Polypo-
diaceae (including the loxogrammoid ferns) as well as that of the
Grammitidaceae. Using the new evidence that has become available
from detailed studies on the stomata by VAN COTTHEM (1970, 1973)
she stated: 'The very different selection of types present in the
gleichenioid group and the Polypodiaceae provides significant evi-
dence against any phyletic link between the two groups'. It will
be set forth below that statements like this are contrary to phylo-
genetic reasoning, as inferred (aut)apomorphous characters do not
in themselves refute the possibility of a sister group relation-
ship.

JARRETT supplied very interesting new data about the configuration
of the cells of the capsule of the sporangium, which appears to be
of the same type in the Polypodiaceae and in the indusiate lepto-
sporangiate ferns. Whether this character state really can be used
to define the monophyly of the Polypodiaceae and these taxa, needs
further study; a similar type of configuration seems to occur in
Polytaenium (Vittariaceae). Another argument mentioned by JARRETT
to support her hypothesis regards similarities in indument of the
gametophyte. However, a similar indument, obviously also occurs in
the gymnogrammoid ferns. From the very interesting data given by
JARRETT it seems likely indeed that the relationship of the poly-
pods is not with the gleichenioid ferns but rather with 'advanced'
(and not neccessarily "advanced indusiate") families.

When trying to understand the argumentation used by the authors
mentioned above, it was especially the incompleteness of the data-
matrices used i.e. the distribution of the character states in the
taxonomic groups under discussion, that made a critical verifica-
tion problematical.

The above illustrates our general lack of knowledge to reach un-
animous conclusions when studying the systematics of the Polypo-
diaceae.

II. Monophyly of the family

When starting work on Polypodiaceae it became necessary to circum-
scribe the family in an undisputed way. Therefore, we delineated
the family to its narrowest sense thus also excluding the loxogram-
moid ferns. The family as thus construed is regarded to represent
a so-called 'A' group (in the sense of Aristotle). Its monophyly
has never been questioned although it must be admitted that there
are as yet no undisputed unique character states known to the au-
thors which support this monophyly.

III. Subdivision of the family into lower categories
and especially genera

Within the Polypodiaceae as delineated above, COPELAND (1947) re-
cognized 52 genera. On the other hand PICHI SERMOLLI (1977) recog-
nized as much as 63 genera. Still other generic concepts are com-
mon amongst present day pteridologists.

As a consequence the same species may be accommodated (and certain-
ly was so) in the genus *Polypodium* by one author, in *Microsorium*,
Phymatodes, etc. by other authors. This has resulted in an intri-
cate nomenclature which is unsurpassed in ferns, and may be so
even in plants.

As far as the arrangement of the genera is concerned opinions dif-
fer in a similar way. For instance, according to NAYAR (1970) the
Polypodiaceae 'is conceived as consisting of four nearly parallel
lines of evolution, all nearly equal in status, viz., Platycerioi-
deae, Microsorioideae, Pleopeltidoideae, and Polypodioideae'; 'sub-
family Crypsinoideae is conceived as derived directly from the Mi-
crosorioideae'. CRABBE & al. (1975) recognized the Grammitidaceae
(sensu CRABBE & al., i.e. including the loxogrammoid ferns), apart
from the Polypodiaceae. In the latter family they (provisionally)
recognized 57 genera which are accommodated in the subfamilies Dry-
narioideae, Platycerioideae, Microsorioideae, Pleopeltoideae, and
the Polypodioideae. PICHI SERMOLLI (1977) accommodated his genera
into 14 distinct groups which relationships he displayed in a phy-
letic tree of the family which he 'ventured to construct' (1977:
370, fig. 6). Other authors held a number of different views.

IV. Monographic treatment of the genera recognized, including the delimitation of species and their geographical distribution

It has been stressed several times by HOLTTUM (1973) and other authors that monographic work on critical groups should have first priority. However, when perusing the fern literature since 1950, monographs or critical revisions of fern generea are relatively scarce. This holds especially for genera of Polypodiaceae. Monographic work on inferred monophyletic genera, however, is a major subdiscipline in systematic research. Firstly, it provides the taxonomic information, i.e. the delimitation of the species, their nomenclature, diagnostic characters, etc. as well as their geographical distribution and habitat preferences. Secondly, a monograph should present a synthesis of evolutionary knowledge about the group, including the evolution in time (speciation events, anagenetic developments) and in space (the genesis of their geographical distribution also in relation to the evolution of land masses).

The recent publication of the monograph on *Platycerium* (HENNIPMAN & ROOS, 1982) is a first attempt towards this kind of monographic work. Other groups presently under investigation are the genus *Pyrrosia* by Mr. P. HOVENKAMP, Rijksherbarium, Leiden, and the drynarioid Polypodiaceae by the junior author.

V. Conclusions

The information given above illustrates the diversity of opinion regarding systematic research in Polypodiaceae. The existing differences as regards the systematics of this family originate primarily from lack of unanimity concerning the methodology of systematic research. In most publications it is difficult to find or infer the basic principles upon which classifications have been made. It is our opinion that the diversity of species in the Polypodiaceae first becomes intelligible when it is recognized that the differences have evolved in the course of phylogenesis. In other words it is our aim to add to the knowledge about the phylogenetic relationships of the taxa comprising the family. But when aiming at this, three fundamental questions should be posed (HENNIG, 1965), i.e. what is phylogenetic relationship; how is it established; and how is knowledge of it expressed in a way that misunderstandings are excluded. The following chapter enumerates in a condensend way the theory of phylogenetics as it has been set forth by WILEY (1981) and other authors, and as the present authors look upon it today.

B. Methodology

I. Introduction

Systematics is that part of comparative biology which studies the patterns that
can be recognized within the past and present diversity of organisms. In being
realists we look upon the world around us as a discontinuum comprising a varie-
ty of 'units'. The largest (basal) unit distinguished in comparative biology is
the species, whatever the species concept may be. Species can be abstracted in-
to unique sets of features which they possess (character states). Based on pat-
terns of similarities and differences it is possible to classify the species re-
cognized into a hierarchical system. Such a classification is basically an in-
formation storage system about characteristics of the organisms.

BROOKS (1981) pointed out that according to information theory, the best repre-
sentation of the information of objects to be stored is a hierarchical, dicho-
tomous system. The criterion of entropy is the test for such a system. This im-
plies the use of the lowest number of symbols (S-redundancy) and the highest
repetition of the symbols used (R-redundancy), to represent the full dataset.

Systematists nowadays follow the suggestion done by DARWIN that the underlying
order of the patterns within the diversity of life – the discontinuities as
seen at a certain time level – can be interpreted as the result of the evolutio-
nary processes that may lead to speciation events; the nature of these proces-
ses being irrelevant for the present paper. Evolution in its broadest sense is
defined as descent with modification. As a consequence, all organisms (and taxa)
share genealogical (evolutionary, phylogenetic) relationships. Because of these
genealogical relations in time, the diversity of life shows a hierarchical dyna-
mic continuum.

When the vital work of the delimitation of the species has been accomplished, it
is the task of the systematists to reconstruct the phylogenetic relationships
between the species recognized and to produce a classification reflecting these
relations (WILEY, 1981). In other words, the classifying criterion is the shared
possession of common ancestors, with the resulting classification representing
the historical sequence of speciation events. Speciation in this model is ge-
nerally, but not necessarily, regarded to be dichotomous. They can only be re-
cognized when accompanied by observable and inheritable changes in at least one
character in at least one of the two descendants. The resulting character state
(evolutionary novelty) is the documentation of that specific speciation event;
it is a unique feature that is present (either in its original or in an even
more derived state) also in all of the descendants of the ancestral species in
which the novelty arose. In order to fulfil the purpose of reconstruction of the
phylogenetic relationships between species, it is the task of the systematists
to analyse the features of the species and to hypothesize branching diagrams
representing the sequence of speciation events as documented by the respective
evolutionary novelties that arose as a result of speciation events. Such a no-
velty, i.e. the newly formed character state at a certain level of the hierarchy
(or level of universality), is called the apomorphic condition; the original
character ist called the plesiomorphic condition (which is an apomorphic charac-
ter state at a higher level of the hierarchy). Apomorphic character states have
a higher information content compared to plesiomorphic character states as they
are inherited to all lower level phylogenies, being at the same time unique at
that certain level (the latter is not true by definition for the plesiomorphic
character states).

In case of conflicting distribution of character states the test for such a sys-
tem is the common sense principle of parsimony. According to BROOKS (1981), the

organizing principles of the classifications of objects based on the criterion of entropy and of the classifications of species based on the criterion of parsimony, are identical.

In conclusion, a system reflecting the historical sequence of speciation events following linguistic criteria is the best way of classifying the diversity of living organisms; the methodology of phylogenetic systematics as proposed by HENNIG (and as emended by several later authors, see WILEY, op. cit.) is the most appropriate one to serve this purpose.

II. 3-taxon statements

Hypotheses about phylogenetic relationships are basically 3-taxon statements saying that species A and B are more closely related to each other than either of them is related to species C. In other words, species A and B - called sister groups by definition - are hypothesized to share a more recent common ancestor than one of them shares with species C. By definition, the combination of taxa A, B, and their conjectured common ancestor is called a monophyletic taxon. The test of this hypothesis, i.e. (A + B) is monophyletic, cannot be performed without introducing apart from taxon C, a fourth taxon D, and proceeds by application of the out-group rule (DE JONG, 1980; WATROUS & WHEELER, 1981, but excluding the implication of the use of the word 'related' as given in their definition) which will be examplified below.

In this way a system of sequential levels of universality, i.e. a cladogram, can be built. Each sequential triad of levels can be taken as the framework of of a 3-taxon statement (Fig. 1). By definition, character states characterizing a monophyletic taxon, e.g. taxon (A + B) are the apomorphic conditions. The alternative character states in the taxa C and D are the plesiomorphic condition.

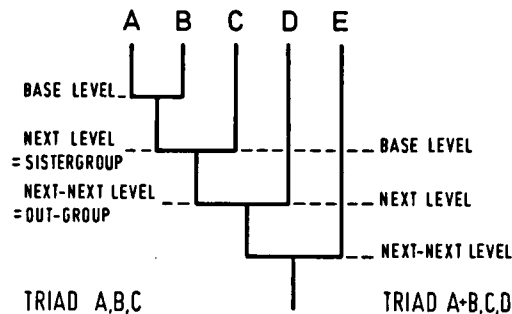Fig. 1: Triads of levels. (After ZANDEE, 1984; see also ELDREDGE & CRACRAFT, 1980, Fig. 2.17).

The conjecture of the monophyletic nature of taxa and its possible refutation also compels the consideration of possible alternative hypotheses (Fig. 2). These alternatives result from changing the mutual relative positions of the individual taxa in the 3-taxon statement (= 3-taxon statement permutations: ZANDEE, 1984).

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WILEY (1981) has argued that the criteria for testing synapomorphy are the same as those traditionally used for testing homology (i.e. the criteria of development, topology, morphology, etc.), as both homology and synapomorphy (as well as symplesiomorphy, i.e. the shared possession of a plesiomorphic condition in a number of species) refer to hypotheses about common ancestry. In other words a homology at one level is a synapomorphy at some higher level of universality.

When using WILEY's definition (1981: 121-122), characters of two or more taxa are homologues if these characters are found in the common ancestor of these taxa, or two characters (or a linear sequence of characters) are homologues if one is directly (or sequentially) derived from the other(s). Of a homologous pair of characters, the apomorphic character is the one that evolved directly from its pre-existing homologue, whereas the plesiomorphic character arose earlier in time and gave rise to the later, apomorphic character. For example, when we say that the presence of vascular tissue in ferns and monocots is a homologous feature, we are actually arguing that both taxa belong to a monophyletic group Tracheophyta (BREMER & WANNTORP, 1981) which has the presence of vascular tissue as a synapomorphy. A monophyletic group is a group comprising all descendants of one shared common ancestor and the ancestor himself. Conversely, an argument proposing the use of the presence of vascular tissue as a synapomorphy testing the monophyletic nature of the Tracheophyta is also an argument proposing all vascular tissue to be homologous.

Phylogenetic relations can only be given in a relative sense. The 2-taxon statement, given no other taxa, are always solved as there is only one possible cladogram (branching scheme of nested sets of taxa sharing apomorphies). Therefore, it has no sense to state that for instance *Platycerium coronarium* and *P. ridleyi* are relatives. It is only relevant to state that *P. coronarium* (A) and *P. ridleyi* (B) are more related to each other than one of them is related to *P. bifurcatum* (C), because in case of three taxa there are two other hypotheses about relationships possible, i.e. (A+C)-B, (B+C)-A. The 3-taxon statements are basic to phylogeny reconstruction as the whole phylogeny of life is a conjunction (of nearly infinite numbers) of 3-taxon statements taken the form as given above.

When dealing with three taxa, there are three different dichotomous cladograms possible as a result of 3-taxon statement permutations (Fig. 2; the trichotomous alternative is regarded an unsolved dichotomy). The selection of the possible cladograms can start from the analysis of character state distributions as they corroborate or refute the hypothesized monophyletic taxa, proceeded by selecting the best of the corroborated cladograms. It proceeds by the application of the principle of parsimony, i.e. by testing the hypothesized monophyletic status of the base level taxa involved (Fig. 1), which compels the availability of an outgroup, say taxon D.

Tab. 1: Distribution of 11 characters showing two different character states amongst taxon (A + B + C) and taxon D.

Characters		1	2	3	4	5	6	7	8	9	10	11
Taxa	A	0	0	0	1	0	1	1	0	0	1	1
	B	1	1	0	0	1	1	1	1	0	0	0
	C	1	1	1	0	0	1	1	0	1	0	1
	D	0	0	0	1	0	1	0	0	0	1	0

When reconstructing the phylogeny of A, B, and C in the present example we can start by treating these species as a so-called closed system, i.e. without re-

ferring to taxon D or to other taxa outside this particular 3-taxon problem, or without referring to other then a posteriori criteria, such as ontogeny and stratigraphy. As pointed out above, character states shared by two of the three taxa support their hypothesized monophyly, i.e. every similarity is a potential synapomorphy. In our example, there is (as usual) conflicting evidence (Fig. 2).

It is stressed that polarity is not designated a priori to the various character states found, as such designations are ad hoc decisions. As a consequence, the cladogram chosen is corroborated by the greatest number of shared character states, which are consequently synapomorphies (by definition). In Fig. 2, hypothesis I is supported by 2, hypothesis II by 3, and hypothesis III by 4 shared characters. Hypothesis III is chosen as it is the most corroborated one.
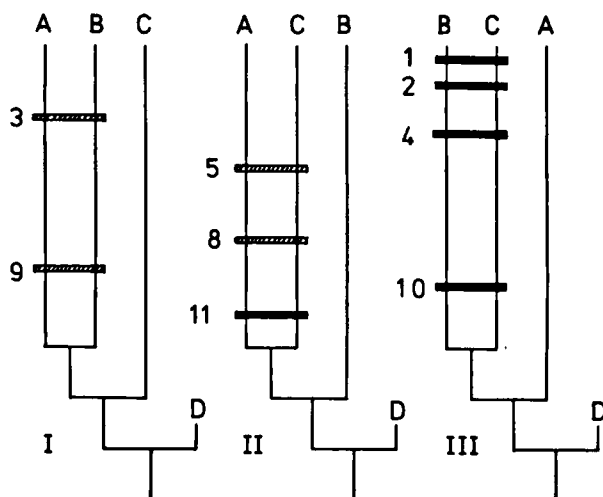

Fig. 2: The three possible hypotheses about the phylogenetic relationships between taxa A, B, and C; solid bars comprise the apomorphies after application of the out-group rule.

When the taxa A, B, C, and D are regarded a closed system and given the monophyly of each of the taxa A, B, C, and D separately, and of taxon (A + B + C), polarity of the character states found may be traced by the use of the out-group rule implying a test on the monophyly of taxa at the next higher level of universality, i.e. (A + B), (A + C), or (B + C). This rule is best defined by DE JONG (1980: 12) in the following way: 'If a character occurs in more than one state in a monophyletic group, the state that occurs also outside the group is likely to be the plesiomorphic state'. In the present example, the character state found in the group under study (taxon A + B + C) and also in the out-group (taxon D) is regarded to represent the plesiomorphic condition. Consequently, in case of characters showing two different states in the group under study, the alternative state represents the apomorphic condition.

Thus both character states supporting hypothesis I (character nos. 3 and 9) represent the plesiomorphic condition. As a consequence of this, hypothesis I must be refuted. Of the three characters which support hypothesis II only one (character no. 11) appears to represent the apomorphic condition, thereby corroborating the monophyletic nature of taxon (A + C). Hypothesis III is supported by 4 synapomorphies, which corroborate the monophyly of (B + C). Two out of the three possible hypothesis are corroborated. Hypothesis III is the most corroborated and the least rejected hypothesis. It is selected using the criterion of parsimony, minimizing the number of ad hoc hypothesis (homoplasies).

It should be remarked that the condition of character no. 11 found in the taxa A and C is according to this reasoning a 'true' apomorphy, though not a synapomorphy of these two species. For this character the ad hoc hypothesis is proposed saying that a similar apomorphic condition has been developed independently in the two taxa involved.

The present example is a simplification. Generally speaking, the introduction of a fourth taxon leads to the reconstruction of a new set of 15 (!) possible cladograms; see for instance PATTERSON (1980).

Using the methods as given above, characters are not a priori weighted. However, a systematist intuitively may regard character no. 11 to be of much more phylogenetic importance if compared with the other characters studied. As a consequence he will propose hypothesis II, regarding the 4 character states supporting hypothesis III as the result of parallel evolution. This intuitive approach increases the number of ad hoc hypotheses with 300 % (apart from the character weighting, which is in itself an ad hoc hypothesis).

In conclusion, the methodology outlined above starts with posing hypotheses about possible phylogenetic relationships between the species (taxa), followed by comparing the character states the species exhibit. The ultimate test whether the character state exhibited by a certain species represents the plesiomorphic or apomorphic condition of that particular character is the phylogenetic position within the hypothesized cladograms using the out-group rule.

The character transformations as dictated by the selected cladogram should be tested against 'the time factor', i.e. ontogeny and stratigraphy (HILL & CRANE, 1982), as well as against the lowest number of extra character changes thereby aiming at reduction of homoplasy (= parsimony sensu FELSENSTEIN, 1982). Finally, this results in the acceptance of the most parsimonious cladogram without a priori designation of polarity.

III. Practice

The theoretical implications as set forth above may lead to some difficulties when applied to the practice of systematic work. Basic to classifications of organisms is the delimitation of monophyletic groups. However, in selecting a group for studying its phylogenetic relationships, the group chosen does not necessarily has to be monophyletic. As relationships can only be given in a relative sense, also paraphyletic groups (for instance as defined by CHARIG, 1982) can be treated as if they were monophyletic. The results of a study of the members of a paraphyletic group or a group of which the monophyly is doubted, comprises a hypothesis about the phylogenetic relationships between the species studied (e.g. the modern species only, the neotropical species only, etc.) which should – by definition – not be contradictory to the hypothesis to be proposed in case all members of the monophyletic group, including all members of the paraphyletic group, were studied.

The application of phylogenetic systematics also implies the testing of every possible combination of three taxa (3-taxon statements) at each level of universality starting at the first base level, i.e. the (relatively most recent) species level (Fig. 1). Once a choice has been made for a particular 3-taxon statement at a certain level of universality, this is followed by reconsidering the parsimony of all lower level phylogenies. Such a procedure leads to an almost infinite number of statements. For example, the study of the phylogenetics of the genus *Platycerium* resulted in the recognition of 15 species using 34 diffe-

rent characters. In table 2 and 3 part of these characters and the distribution of their respective states amongst the species is reproduced from the original tabel in HENNIPMAN & ROOS (1982). For computer usage this character table can be modified for each of the character states into present/absent (1/0) statements resulting in a 15 x 93 data matrix (illustrated in table 4 and 5). Even such a supposedly manageable data matrix is hardly to compute taking into con-

Tab. 2: Characters of the plant and their presumed character states

Characters investigated	Plesiomorphic state	Apomorphic state(s)
I. Characters of the scales		
1. size and margin	size: 1.5–14 x 0.4–1.5 mm; margin: not flabelloid	a: 12–28 x 1.5–4.5 mm; not flabelloid b: 8–35 x 4–10 mm; flabelloid
2. shape of apex	acute to filiform	a: rounded
3. 'midrib'	present, entire, linear to narrow–triangular, in cross–section rounded	a: present, divided and/ or broad–triangular, in cross–section flattened or dumpbell-shaped b: absent
4. place of insertion of hairs	marginally and abaxially	a: in a marginal zone b: solely marginally
5. marginal indument	present	a: absent
6. implantation of indument	hairs sparsely to densely set	a: very densely set
7. shape of marginal trichomes	trichomes 1–6–celled; branched and unbranched; glandular and non–glandular; without protuberances	a: 1–8–celled; branched and unbranched; glandular and nonglandular; with protuberances a': mostly 1–5–celled a'': mostly 1–8–celled b: 1–2–celled, glandular and non–glandular; without protuberances c: 1–6–celled, unbranched; glandular; without protuberances

sideration all possibilities to be surveyed. One way of doing so is to eliminate all polythetic combinations of species and to use monothetic groups only (SHARROCK & FELSENSTEIN, 1975). The number of monothetic groups to be distinguished depends on the internal character conflicts as demonstrated by the particular data matrix. In case of the 3-taxon statement of the taxa A, B, and C, all three individual taxa should be monothetic. Also, A, B, C, together must form a monothetic group as well as the combination of two taxa of which the monophyly is tested. In other words, only monothetic groups are listed (in case of *Platycerium* about 350 groups) in order to search for the monophyletic group using 3-monothetic-taxon statements.

Tab. 3: Distribution of character states in *Platycerium*

Species	coronarium	ridleyi	bifurcatum	alcicorne	ellisii	madagascariense	andinum	quadridich.	elephantotis	wallichii	grande	holttumii	superbum	wandae	stemaria	Parallel development
Species no. if alphabetically arranged	4	11	3	1	6	9	2	10	5	14	7	8	13	15	12	
Character no. according to tab.1																
I. Scales																
1	x	x	o	o	o	o	o	o	o	o	●	●	●	●	o	
2	●	●	o	o	o	o	o	o	o	o	o	o	o	o	o	
3	●	●	o	o	o	x	x	o	o	o	x	x	x	o	o	P:x
4	x	x	x	o	o	o	o	o	o	-	●	●	●	●	o	
5	o	o	o	o	o	o	o	o	o	●	o	o	o	o	o	
6	o	o	o	o	o	o	o	o	o	-	●	●	●	●	o	
7	+	+	+	x	x	o	o	o	o	-	●'	●'	●	●	o	

Tab. 4: Characters of the scales (polarity not indicated, table 2, rearranged)

1.a. 1.5--4 x 0.4--1.5 mm; margin: not flabelloid
 b. 8--35 x 0.4--10 mm; margin flabelloid
 c. 12--28 x 1.5--4.5 mm; margin: not flabelloid

2.d. apex acute to filiform
 e. apex rounded

3.f. midrib present, entire, linear to narrow-triangular, in cross-section rounded
 g. midrib present, divided and/or broad-triangular, in cross-section flattened or dumbbell-shaped
 h. midrib absent

4.i. hairs absent

5.j. hairs marginally and abaxially inserted, sparsely to densely set

6.k. hairs in a marginal zone, very densely set
 l. hairs solely marginally inserted, sparsely to densely set

7.m. trichomes absent
 n. trichomes 1--6-celled, branched and unbranched, glandular and non-glandular, without protuberances
 o. trichomes 1--2-celled, glandular and non-glandular, without protuberances
 p. trichomes 1--6-celled, unbranched, glandular, without protuberances
 q. trichomes mostly 1--5-celled, branched and unbranched, glandular and non-glandular, with protuberances
 r. trichomes mostly 1--8-celled, branched and unbranched, glandular and non-glandular, with protuberances

Tab. 5: Datamatrix of characters of the scales based on table 4. — Character
state present (1), absent (0).

species nos.	4	11	3	1	6	9	2	10	5	14	7	8	13	15	12	
character nos.																
1.a.	0	0	1	1	1	1	1	1	1	1	0	0	0	0	1	
b.	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
c.	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	
2.d.	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	
e.	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2
3.f.	0	0	1	1	1	0	0	1	1	1	0	0	0	1	1	
g.	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3
h.	0	0	0	0	0	1	1	0	0	0	1	1	1	0	0	
4.i.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
5.j.	0	0	0	1	1	1	1	1	1	0	0	0	0	0	1	
6.k.	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	4,5,6
l.	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	
7.m.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
n.	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	
o.	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	7
p.	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	
q.	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	
r.	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	

However, even in case monothetic groups are taken into consideration only, the
number of possible cladograms could still be enormous. It is expected that the
most appropriate (parsimonious) hypothesis cannot be selected using advanced
computers, if at all possible. As yet, the correct application of the parsimony
criterion is still a major problem; it is presently under investigation by Dr.
M. ZANDEE, Leiden.

The necessity of an out-group. Most systematists concentrate on the systematics
of 'their' group; they treat their in-group as a closed system. However, as said
before, the resulting cladogram and the synapomorphies may change significantly
when the in-group is incorporated in higher level phylogenies. The parsimony
established in the in-group, therefore, could be ad hoc. As stated by WILEY
(1981: 112), this problem of ad hoc parsimony statements can be avoided when the
most highly corroborated next higher level phylogeny is accepted to be true
(which is in itself open to testing of course). The possible sister group of the
in-group is selected by perusing the literature and by a priori knowledge.

However, there is often ambiguity concerning the next higher level phylogeny.
In such cases a number of possible sister groups should be included amongst the
taxa of which a character analysis is made. Accordingly, the most parsimonious
hypothesis is calculated for each of the possible sister groups. Consequently,
the ad hoc choice is made in favour of that sister group which gives the most
unambiguous (resolved) hypothesis about the phylogenetic relations within the
in-group. This *objective* approach is different from character phylogeny.

Character phylogeny is the *heuristic* approach towards phylogenetics. Because of
the difficulties illustrated above, one may approach phylogenetics using charac-
ter phylogeny. In this case one does not start with hypotheses about phylogene-
tic relationships but with (ad hoc) hypotheses about the transformation in time
of the investigated characters and their respective states. A priori determina-
tion of the polarity of the characters is based on such 'criteria' as simple-

complex statements, ontogeny, stratigraphy, and 'out-group comparison'. 'Out-group comparison' is used here to determine those character states that can function to define monophyletic groups irrespective of the levels of universality within the in-group; as such it is not part of the selection of the corroborating characters that are valid tests of the hypotheses at the next lower level of universality.

This procedure helps in tracing groups of species that share unique character states. In other words, groups that are undisputed, representing 'true'A-groups (sensu Aristotle; see ELDREDGE & CRACRAFT, 1980). For example, stellate hairs are a unique feature within the Filicales, found in the polypodiaceous genera *Platycerium* and *Pyrrosia* only. Stellate hairs, therefore, may be regarded by intuition to represent a synapomorphy of these two genera.

One may object against the application of character phylogeny being a heuristic approach. Heuristics comprises a number of rules and agreements which (usually) indicate a quicker and better way towards results within the context of the theory. Besides, the results are open to testing!

The application of heuristics does not influence the axioms of biological systematics. For instance, the axiom that organic diversity has resulted from speciation events accompagnied by character modification(s) which resulted in genealogical relations between the species; these relations can be ascertained studying the characters which the species exhibit. Further, if there are contradictions, these should be explained by ad hoc hypotheses (e.g. parallelism, paedomorphosis) first, without questioning the axioms themselves. The axioms represent the paradigms (KUHN, 1962) or the 'hard core' of the research program (LAKATOS, 1970).

It should be admitted that character phylogeny has the disadvantage of ignoring possible alternative 3-taxon statements. On the other hand character phylogeny makes maximum use of biological information in an explicit and testible way, though in a (much) earlier stage than is permitted by the objective approach which strictly applies 3-taxon statements parsimony only.

When applying character phylogeny one often comes across conflicting evidence. In such cases one is forced to re-check the observations as well as reconsider the possible evolutionary significance of particular character states. This process of reciprocal illumination diminishes conflicts in the distribution of character states. It should be noted that reciprocal illumination is also implicit when applying the objective approach though after the construction of (conflicting) cladograms.

When as a result of applying character phylogeny a resolved cladogram is proposed, this cladogram should be tested using the 3-taxon statement permutations. For practical reasons set forth above, this can be performed only after condensing the cladogram into a smaller cladogram comprising the most corroborated monophyletic subgroups of the original cladogram as terminal taxa only. Consequently, the most parsimonious hypothesis regarding the relations between these groups can be computed (ignoring the polarities already designated). The same procedure can be applied for testing subgroups, as well as for solving the ambiguous relations between or within subgroups.

IV. Acknowledgements

C. Character phylogeny in Polypodiaceae

I. Introduction

The search for monophyletic groups within the family Polypodiaceae
has been attempted by means of character phylogeny of a selection
of the features of the sporophyte. Character analyses made so far,
or which are in progress, include the stomata (SEN & HENNIPMAN,
1981), scales, frond shape and venation patterns, paraphyses, and
spores (HENNIPMAN & SEN, in prep.). These studies are based on ma-
terial of the type species of the genera recognized by COPELAND
(1947) and other workers, as well as on a reasonable additional
selection of material of the other taxa that contribute to the va-
rious expressions of that particular character. A character analy-
sis is started by making a description of all the various morpho-
logical expressions of that character, followed by a classifica-
tion of these expressions in distinct morphological types. These
types are accordingly interpreted in terms of primitive and derived
character states. Using ontogenetic or other criteria the groups
of ferns that share a derived character state are regarded as pos-
sible monophyletic groups within the Polypodiaceae.

Character analysis makes maximum use of biological inference to
determine polarity of character states, i.e. to establish trans-
formation series. The hypothesized transformation series then are
used to construct the most parsimonious cladogram.

II. The spores

A study on the spores was made by the senior author together with
Dr. T. SEN, Kalyani, India (HENNIPMAN & SEN, in prep.). Traditio-
nally the spores of the Polypodiaceae are regarded to be uni-
formly bean-shaped, and lacking a perispore. From recent work
of especially LLOYD (1981), LUGARDON (1974, 1976), WAGNER (1974)
and others it was suggested that the spores in the Polypodiaceae
might be much diversified.

The study of the spores of about 150 species with light micro-
scopy and scanning electron microscopy, showed that the outer sur-
face ornamentation is variously structured. Representatives of the
different morphological types which could be recognized were ad-
ditionally studied with the transmission electron microscope.

Although we expected to find variation in the ultrastructure of the perispores, we unexpectedly came across surprising differences in the exospore as well. Using characteristics of the exospore, three distinct morphological types are presently recognized. Differences in the shape of the perispore may allow a further subdivision of especially one of these groups.

The three main types of spores are recognized using the criteria of canalization, banding and thickness of the exospore.

1. The *Polypodium vulgare* type

Exospore with canals near the aperture only; 1.5-2.0 µm thick; tangential bandings absent; microcanals absent.

2. The *Lepisorus* type

Exospore throughout with many small canals; 2-4 µm thick; tangential bandings of the spore present; microcanals absent.

3. The *Microsorium* type

Exospore with canals near aperture only; ca. 1 µm thick; tangential bandings absent; with microcanals.

According to a cladistic analysis, taxa should only be put together on the shared possession of derived character states. For the present study it suffices to inform the reader that the ultrastructure of the exospore as found in the *Lepisorus* type is unique in the Polypodiaceae and in all other Pteridophytes, therefore representing an obvious apomorphy. This means that the genera with this particular kind of exospore may constitute a monophyletic group. This group includes apart from the greater part of the traditional lepsiorioid ferns also *Dictymia* and *Phymatodes*, genera which are referred by other authors to different alliances. On the other hand such a group excludes the genus *Neocheiropteris* which is referred to the lepisorioid ferns by other authors. The study also resulted in the finding that the genus *Pleopeltis* consists of two distinct elements, already recognized as different genera by DE LA SOTA (1973), i.e. *Pleopeltis* s.s. (with spores of the *Microsorium* type) and *Lepisorus*. The recognition of the genus *Lepisorus* apart from a genus *Pleopeltis* s.s. is in contradiction with traditional views as expressed by for instance COPELAND (1947) and PICHI SERMOLLI (1977).

The finding of an unique ultrastructure in the spores of part of the Polypodiaceae is in itself a base for recognizing a characteristic monophyletic group of genera, including *Lepisorus, Drymotaenium, Lemmaphyllum, Phymatodes,* as well as several other genera.

III. Indument of fronds

From a detailed study of the indument of the sporophyte it could be confirmed that characteristic stellate hairs of a morphology

which is uniquely found in all pteridophytes, only occur in the genera *Pyrrosia* (including *Drymoglossum* and *Saxiglossum*) and *Platycerium*. This in itself is sufficient to regard these two genera to constitute a monophyletic group within the Polypodiaceae as was already suggested by HOLTTUM (1946). But generally speaking, the affinity of *Platycerium* to *Pyrrosia* was not regarded to be intimate. *Platycerium* was regarded an 'isolated' genus, which made CHING (1940) to propose even a separate family Platyceriaceae. The characteristic synapomorphy of the genus *Platycerium*, i.e. the unique frond dimorphism, was negatively interpreted by PICHI SER-MOLLI (1977) who thought a relationship between these two genera to be remote.

Within the group consisting of *Pyrrosia* and *Platycerium*, the genus *Platycerium* is monophyletic because of e.g. its unique frond dimorphism. The monophyly of *Pyrrosia* is, however far less obvious. The research undertaken by P. HOVENKAMP, Leiden, may contribute to trace the apomorphies necessary to define *Pyrrosia*.

IV. Conclusions

These two examples illustrate that the character analyses of detailed (microscopical and submicroscopical) structures may lead to the finding of character states (types) which can (provisionally) be regarded as uniquely developed structures. Such so-called apomorphic character states are used to define the larger subgroups within the Polypodiaceae, including genera. These well-defined monophyletic groups are then the subject of systematic research at a lower level of universality. As an example the phylogenetic relationships within the genus *Platycerium* will be discussed below.

D. Phylogenetic relationships in *Platycerium*

I. Introduction

The study of the phylogenetic systematics of the pantropical genus *Platycerium* (HENNIPMAN & ROOS, 1982) was started to find out the possibility to establish unambiguous phylogenetic relationships within this well-known group of ferns.

II. Subsequent steps of systematic research

1. Taxonomy: the recognition and circumscription of the species. The taxonomic study resulted in the recognition of 15 species, of which 6 occur in Africa including Madagascar, 8 in Asia and Australia, and 1 in tropical South America.

2. Selection of characters that show differences between the species; compilation of a complete synoptic table of species and their character states. Table 1 and 2, representing part of more elaborate data matrices given by HENNIPMAN & ROOS (1982), are given as examples.

3. The determination of polarities in the 34 characters studied. We hypothesized polarity for the characters using *Pyrrosia* as an 'out-group', irrespective of the level of universality of the character state itself. As pointed out above *Pyrrosia* can only be correctly used as the out-group for the first lower level phylogeny within *Platycerium* determining polarities at that particular level of universality only. Apart from 'out-group comparison' polarity was postulated using ontogenetic data.

4. The construction of the first version of the cladogram. Although there was much conflict as to the distribution of apomorphic character states in *Platycerium* which means that a large number of variously composed subgroups could be hypothesized reflecting the inferred apomorphic conditions of the characters investigated, we were able to select in this particular case two groups which were corroborated by 9 and 15 hypothesized apomorphies respectively. These two groups were regarded as undisputed monophyletic groups. Postulated apomorphies of other characters that were incongruent (i.e. characters of which the hypothesized apomorphies in fact did reject one of these groups) were regarded to be homoplasies. As a consequence, re-checking the polarity of these characters was executed in order to confirm the homoplasy. By doing so character weighing was avoided.

5. The construction of a second version of the cladogram is possible after elimination of (part of) the conflicting evidence as homoplasies. As a consequence, there appeared to exist several other corroborated subgroups. Re-checking of the polarities of the few remaining characters eventually led to an almost complete solution of the cladogram (Fig. 2). If necessary, it can be followed by another re-check, or by ad hoc choices by intuition. Nevertheless, it is likely that in many cases two or more possible cladograms appear to be even parsimonious.

6. The enumeration of all the characters that show homoplasies. Reciprocal illumination ('wechselseitige Erhellung') with biological data.

7. The comparison of the cladograms with the geographical distribution of the taxa recognized. In case the intrinsic characters studied did not result in one unambiguous cladogram, the geographical distribution of the taxa recognized, which is an extrinsic feature, can be used additionally. Also in this case, the criterion of parsimony must be applied, resulting in the selection of that (those) cladogram(s) which can be explained by the least number of dispersal or vicariance events (after the most parsimonious explanation of the development of the present distribution pattern has been established for each of the cladograms).

8. Description of a possible scenario of the inferred evolutionary history of the group, starting from the cladogram and using all information available about the group (stratigraphy, fossil record, geography, ontogeny, ecology, etc.).

III. Cladogram of *Platycerium* revisited

The cladogram of *Platycerium* as given in Fig. 2 is a slightly modified version of the one given earlier (HENNIPMAN & ROOS, 1982) thanks to Dr. BREMER (Stockholm), who indicated that is was possible to decrease the number of ad hoc statements in four characters showing parallelisms. Three of these characters corroborated the cladogram. For instance, in Table 2 and 3 character no. 3 shows parallel development for condition 'x'. Instead of argueing that this condition newly arose five different times, it is more parsimonious to postulate that within the *P. grande* group (species nos. 7, 8, 13, and 15; one of the two highly corroborated groups) condition 'x' arose only once. This defines the monophyly of the species 7, 8, and 13; consequently, the trichotomy in the original cladogram can be solved. Thus, the number of ad hoc hypotheses postulated to explain the distribution of this apomorphy within the species of this genus is decreased to three. This demonstrates that characters showing parallel development in a selected group of taxa, can still be used to define phylogenetic relationships within subgroups based on synapomorphies of other characters.

It seemed of interest to compare the character phylogeny approach to the strict application of the 3-taxon statement parsimony. For the application of the latter approach it is necessary to adjust the original character matrix in such a way that it can be handled by computer methods without character (state) weighing, and without a priori indications of apomorphies. Therefore, the original character table was modified into '0' and '1' statements (absent vs present statements). Such a table is illustrated in Table 4 and 5 which comprise the same part of the original character tables as illustrated in Tab. 2 and 3, respectively. Up till now the preliminary results do not suggest significant changes in the cladogram as presented here (Fig. 3); the matter is still under investigation by Dr. M. ZANDEE, Leiden.

E. General conclusions

A few years ago the Polypodiaceae were selected by the senior author as a research subject in view of its most ambiguous taxonomy and systematics. It was aimed to construct a classification reflecting the phylogenetic relationships within this family. Therefore, it became necessary to define the principles upon which such a classification should be based.

The present paper surveys the implications as well as the practical applications of the methodology of cladistic analysis as illustrated by WILEY (1981) and others, and as assimilated by the present authors. Besides, it demonstrates its (potential) value for the solution of systematic problems in Polypodiaceae and other groups of ferns.
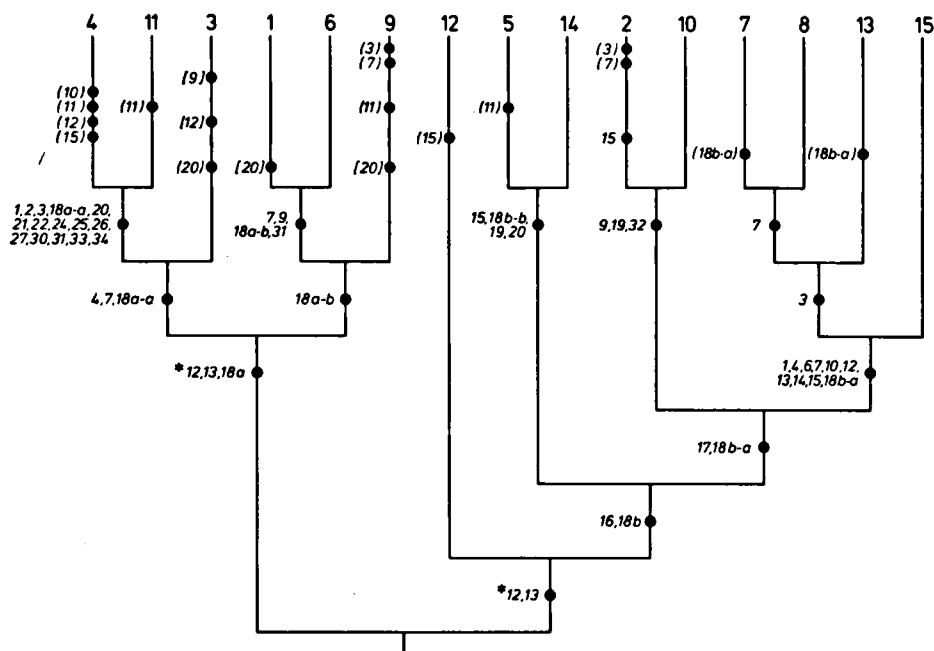
Fig. 3: The cladogram of *Platycerium* (HENNIPMAN & ROOS, 1982; slightly modified)
— The most resolved cladogram is given only. In case character nos. 12, 13, are
apomorphic in species nos. 4, 11, 3, 1, 6, and 9, the resulting cladogram in-
cludes a trichotomy comprising: (a) the monophyletic group of species nos. 4,
11, 3, 1, 6, and 9; (b) species no. 12; (c) the monophyletic group of species
nos. 5, 14, 2, 10, 7, 8, 13, and 15.

This being true, we finally may reach a more uniform approach to-
wards systematic research leading to less controversies among pte-
ridologists. As far as Pteridophytes are concerned, it is our pre-
sent interest to construct a classification of the major groups of
Pteridophytes applying a cladistic analysis and using all compari-
tive data presently known.

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