FOSSIL POLYPODIACEAE AND THEIR SPORES

GERDA A. VAN UFFELEN

Rijksherbarium / Hortus Botanicus, Leiden, The Netherlands

SUMMARY

In this publication emphasis is laid on the modern definition of the family *Polypodiaceae* (Filicales), which is based on an extensive study of Recent material and which is much restricted with respect to older circumscriptions of the family as usually applied by palaeobotanists. Fossils of ferns belonging to the family in the strict sense are extremely rare and those examined do not bear any spores suitable for study. Of the fossils attributed to the family in its traditional, large sense, only a small minority belongs to the family in its strict sense.

A survey of the few polypodiaceous fossils known to the author is given together with a list of non-polypodiaceous fossils that usually (sometimes tentatively) have been referred to the family *Polypodiaceae*.

INTRODUCTION

In palaeobotanical literature, as in the older actuobotanical literature (Diels, 1902; Christensen, 1938), the family *Polypodiaceae* is usually defined in a wide sense. In many publications (Arnold, 1964; Taylor, 1981; Meyen, 1987) it comprises a large part of the leptosporangiate ferns. This extremely wide concept of the family has no place in a natural classification, as it is probably not monophyletic: some groups in the family s.l. may be more closely related to groups outside that family than to the other groups within it (see, e.g., Holttum, 1949; Lovis, 1977).

In the polypodiaceous part of leptosporangiate ferns ever more supposedly monophyletic families have been recognized during the past fifty years (e.g., Crabbe et al., 1975; Kramer & Green, 1990). One of these is the family *Polypodiaceae* in its restricted sense.

One reason for the sometimes spectacular changes in taxonomic views is that for a long time it has been difficult to assess which characters in ferns best reflect natural relationships. In the course of this century the importance of soral characters has been reduced dramatically to the advantage of e.g. characters of the frond indument.

From the point of view of the palaeobotanist the way Recent fern classification keeps changing is very annoying. If actuopteridologists with their abundant data cannot come to a stable classification, why then should palaeobotanists bother to keep up with modern fern classification? Apart from this, the detailed classifications based on Recent material often are not directly applicable in palaeobotanic research: palaeobotanists usually have a broad concept of taxonomic groups, possibly due to

the large number of extinct taxa and to the usually small number of fossils available
to circumscribe a taxon. In the case of the *Polypodiaceae* the relatively small number
of fossilized leptosporangiate ferns available must play a role.

However, both palaeo- and actuopteridologists have important contributions to
make to the elucidation of relationships in ferns, and so to a stable, natural classifi-
cation.

To the Recent pteridologist, a detailed picture of relationships on which a classifi-
cation can be based is necessary in order to revise genera or groups of genera. There-
fore, the strict definition of *Polypodiaceae* is an important step towards a new, stable
classification.

In this publication a definition of *Polypodiaceae* in the strict sense will be given,
emphasizing those characters that appeared to be useful in assessing the taxonomic
position of Recent ferns. A more strict definition of this family and of the families
formerly thought to belong to the Polypodiaceae, will not render the palaeobotanist's
work more cumbersome – indeed, it may offer her or him some new characters for
study and an indication of the taxonomic importance of the characters used, based on
an extensive study of Recent material.

The approach adopted here, that is, to look for Fossil representatives of a small,
well-circumscribed group of Recent organisms, is unusual in palaeobotany. It has
not led to the results hoped for at the outset. However, it has shown up some pecu-
liar consequences (from the point of view of the actuobotanist) of the usual palaeo-
botanical approach, viz., study either all fossils from a certain age and place (includ-
ing representatives of taxonomically 'difficult' groups), or all Fossil representatives
of a (form-)taxon of which sufficient material is available.

THE FAMILY POLYPODIACEAE S.S.

Introduction

Ferns are usually treated as one division of the plant kingdom: the Filicophyta
(e. g., Andrews & Boureau, 1971) or Pteridophyta (e. g., Meyen, 1987). However,
opinions on rank and names within this division may vary considerably between
authors. The true ferns, that is excluding the so-called fern-allies (Psilotopsida, Lyco-
podiopsida, Equisetopsida), are usually all placed in the class Polypodiopsida (syn-
onyms: Pteropsida, Filicopsida) and contain the following groups with Recent
representatives: Ophioglossales, Marattiales, Osmundales, Filicales, Marsileales, and
Salviniales.

In the palaeobotanical literature the order Filicales includes usually 6–9 families
with Recent representatives (Andrews & Boureau, 1970; Taylor, 1981; Meyen, 1987).
*Schizaeaceae, Gleicheniaceae, Cyatheaceae, Dicksoniaceae, Matoniaceae, Davallia-
ceae, Hymenophyllaceae, Dipteridaceae*, and *Polypodiaceae* are the families generally
distinguished. The name *Polypodiaceae* is usually applied in its old-fashioned, broad
sense.

In the first half of this century, most actuopteridologists referred to the classi-
fication published by Diels (1902). So did Bower (1923), a pteridologist whose
morphological analysis of a great many ferns has formed a basis for many of the

earlier attempts at fern classification. In applying Diels' broad concept of the family *Polypodiaceae* (containing 114 genera and 4527 species), he described its main characters as follows: annulus vertical; sori marginal or superficial, and mixed (that is, the sporangia do not mature in a set order). His view corresponds with that of most palaeobotanists, who use the vertical annulus as the main character to recognize a 'polypodiaceous' fern.

In the course of this century, the polyphyletic origin of the *Polypodiaceae* s.l. has been indicated by many pteridologists (e.g., Copeland, 1947; Holttum, 1949; Lovis, 1977). This has resulted in a significant reduction in size of this family because several large, supposedly monophyletic families have been recognized in it, viz., *Adiantaceae, Dennstaedtiaceae, Thelypteridaceae, Aspleniaceae, Davalliaceae,* and *Blechnaceae.* The following groups are now also excluded from the *Polypodiaceae* s.s.: *Cheiropleuriaceae, Dipteridaceae, Grammitidaceae* (Hennipman et al., 1990; Jarrett, 1980), and, by some authors (Pichi Sermolli, 1974; Hennipman & Roos, 1983), *Loxogrammaceae.*

Lovis (1977), who has published on both Recent and Fossil ferns, uses the term 'polypodiaceous', in quotes, for all 'truly leptosporangiate ferns', that is, all ferns Bower (1928) called 'in an older terminology the Polypodiaceae.' They are characterized by 'the small leptosporangiate sporangium, containing only 64 spores, and the vertical annulus.' He described three main radiations within this group, between which the relations are unclear: the dennstaedtiaceous radiation of ferns with indusiate superficial sori (*Dennstaedtiaceae, Davalliaceae, Blechnaceae, Aspleniaceae, Dryopteridaceae, Thelypteridaceae, Lomariopsidaceae*), the adiantaceous radiation, with marginal or submarginal sori (*Adiantaceae* and *Parkeriaceae*) and the polypodiaceous radiation, characterized by naked superficial sori (*Polypodiaceae, Dipteridaceae, Cheiropleuriaceae, Grammitidaceae*). He applied the name *Polypodiaceae* in a restricted sense.

Recent research

For about ten years, the study of the family *Polypodiaceae* s.s. has been stimulated and coordinated from Utrecht, the Netherlands, by Hennipman (1984, 1985). Several studies have contributed to the knowledge about this family by way of monographs (*Platycerium:* Hennipman & Roos, 1982; *Drynarioideae:* Roos, 1986; *Pyrrosia:* Hovenkamp, 1986; *Lecanopteris* p.p.: Hennipman & Verduyn, 1987; *Goniophlebium:* Rödl-Linder, 1990; *Polypodium loriceum*-complex: Hensen, 1990; *Microsorum:* Bosman, 1991) and analyses of certain characters (stomata: Sen & Hennipman, 1981; venation patterns: Hetterscheid & Hennipman, 1984; paraphyses: Baayen & Hennipman, 1987a, b; spores: Van Uffelen & Hennipman, 1985; Hennipman, 1990; sporogenesis: Van Uffelen, 1990).

Circumscription of the Polypodiaceae s.s.

The most recent and detailed circumscription of the *Polypodiaceae* s.s. is given by Hennipman et al. (1990). They include 29 genera, two of which may also be placed in the separate family *Loxogrammaceae* (Pichi Sermolli, 1974; Hennipman &

Roos, 1983), and about 660 species in the family, which is a substantial reduction in size compared to Bower's treatment – even more so if one considers the large number of new fern species described since Bower's time.

The *Polypodiaceae* s.s. (*Loxogrammaceae* excluded) are relatively small, often epiphytic ferns with a creeping dorsiventral rhizome bearing scales (no hairs) and with a dictyostele.

The fronds are articulate to phyllopodia and deciduous, rarely persistent; they are usually simple, pinnatifid, or simply pinnate, rarely bipinnatifid, never regularly bipinnate or more divided; pedately, hastately, or dichotomously divided fronds are found in some genera. Frond dimorphy occurs in some genera: fronds may be differentiated into normal fronds and nest fronds for trapping litter; fertile fronds may differ dramatically from sterile ones, but many species have fronds of only one type. Venation is characteristically anastomosing, the areolae usually bearing one or more free veinlets, but in some genera open venation occurs (for venation see Hetterscheid & Hennipman, 1984; Mitsuta, 1981: figs. 1–270, 1982: figs. 1–113, 1983: figs. 1–355, 1984a: figs. 356–608, 1984b: figs. 750–904).

Sporangia are grouped in exindusiate sori on the lower surface of the lamina. Sori are usually round, but may be aggregated into linear coenosori (but never elongated along the veins as in *Asplenium*) or even cover the greater part of the lower lamina surface in case of fertile pinnae with a strongly narrowed lamina.

Sporangia usually have a 3-seriated stalk and a capsule with a vertical and interrupted annulus; they contain 64 spores, rarely 8 or 16.

Spores are monolete, the wall consisting of a smooth to verrucate or rugulate exospore of the blechnoid type, covered by a perispore that varies from very thin and closely adhering to the exospore, to very thick and complex.

NON-POLYPODIACEOUS FOSSILS

Under this heading those macrofossils are mentioned that in the standard works by Andrews & Boureau (1970), Taylor (1981), and by some others, have been placed in the family *Polypodiaceae* s.l. They do not belong to the family *Polypodiaceae* s.s. For Recent ferns, Kramer & Green (1990, including Hennipman et al. on *Polypodiaceae*), is used as the work of reference. For each genus, another family assignment is indicated wherever possible.

1. Acrostichum L. (*Pteridaceae–Pteridoideae*)

The Recent genus *Acrostichum* is related to the genus *Pteris*. Fossil finds include *Acrostichum anglicum* Collinson, based on dispersed sporangial masses and individual sporangia with trilete spores from the British Tertiary. Various plant parts (see Andrews & Boureau, 1970; Taylor, 1981), such as rhizomes bearing petioles and sterile and fertile pinnae with sporangia containing trilete, smooth spores, have been described as *Acrostichum ?aureum* L. by Wilde (Middle Eocene, Messel) or as *Acrostichum preaureum* by Arnold and Daugherty (Eocene, Clarno chert beds). They are supposed to be conspecific with the Recent species *Acrostichum aureum* by Barthel (1976) and Wilde (1989).

2. Adiantites Göppert (incertae sedis)

According to Lovis (1977) 'records of *Adiantites* need to be evaluated with particular circumspection, since this is a form-genus to which are attributed Carboniferous and Permian fossils which are not even ferns at all, but pteridosperms.' Fossils placed in this genus are, e.g., *Adiantites latifolius* Andreánszky (Miocene of Kerecsend, Hungary; a leaf like the Recent *Adiantum reniforme* L.), *Adiantites lindsayoides* Seward from the Jurassic, and *Adiantites oblongifolius* Göppert from the Lower Carboniferous (see Andrews & Boureau, 1970). In the descriptions the frond parts are said to be like those of *Adiantum* (*Pteridaceae–Adiantoideae*) or *Lindsaya* (= *Lindsaea, Dennstaedtiaceae–Lindsaeoideae*).

3. Adiantum L. (*Pteridaceae–Adiantoideae*)

Fossils described in the genus *Adiantum* are *A. anastomosum* Brown (Eocene), of which the generic name is doubtful as the species is based on poor material (Andrews & Boureau, 1970), and *Adiantum francisi* Ball (Eocene), of which Andrews & Boureau (1970) state that it is based on only one pinna.

4. Allantodiopsis erosa Knowlton et Maxon (incertae sedis)

This fossil from the Paleocene of Colorado (see Andrews & Boureau, 1970) is definitely non-polypodiaceous because of its sori, which are elongated along the veins.

5. Aspidistes Harris
Aspidistes thomasi (*Thelypteridaceae* ?)
Aspidistes beckeri and *A. sewardi* (*Matoniaceae* ?)

Three fossil species have been described in the genus *Aspidistes*. The type species is *A. thomasi* (Harris, 1961) from the Yorkshire Jurassic. Harris mentions no definite, obvious relationship but 'Aspideae?', a name not concurrent with nomenclatural practice (Greuter et al., 1988). Andrews & Boureau (1970) assign it to the family *Polypodiaceae* s.l. and state that 'il serait le plus ancien fossile de *Polypodiaceae* connu.' As to its affinities, Lovis (1975) states that 'though no living thelypteroid possesses all the characteristics of *Aspidistes thomasi*, there is no character of this fossil which cannot be matched somewhere amongst modern Thelypteridaceae.'

Of *Aspidistes beckeri* (Lorch, 1967) from the Jurassic, the venation and arrangement of the sori have been preserved, but not the sporangia and spores. Lovis (1977) writes 'It is unfortunate that this fossil should have been placed in the same genus as *A. thomasi*, since these two species are almost certainly unrelated. The true affinity of *A. beckeri* is problematical, but it is surely not thelypteridaceous, and it need not necessarily be a 'polypodiaceous' fern. On the contrary, the curious venation suggests to me the possibility that it may be a member of the *Matoniaceae* ...' *Aspidistes sewardi* from Lower Cretaceous rocks in England (Watson, 1969) is a pinna fragment, resembling *A. beckeri*, but 'just as distinct from *A. thomasi*' (Lovis, 1977). He states that both fossils are probably matoniaceous ferns.

6. Asplenium L. (*Aspleniaceae*)

Many different, probably not very closely related fossils, dating from the Lower Cretaceous onward, have been placed in the genus *Asplenium* (Lovis, 1977). For instance, *Asplenium alaskanum* Hollick (Tertiary, see Andrews & Boureau, 1970) is not an *Asplenium,* but is more likely to be a *Diplazium (Dryopteridaceae–Athyrioideae)* (Hovenkamp, pers. comm.).

7. Astralopteris Tidwell, Rushforth & Reveal (incertae sedis)

The Cretaceous fossil fern *Astralopteris coloradica* was first described by Brown in the Recent genus *Bolbitis (Lomariopsidaceae)* (see Hennipman, 1977). The species was based on sterile material only, and as soon as they had studied fertile material of the species, Tidwell, Rushforth & Reveal (1967) placed it in the newly-erected genus *Astralopteris.* They mention that Lellinger, an actuopteridologist, found it to resemble most closely species of the Recent genus *Drynaria,* a member of the *Polypodiaceae* s.s. Lovis (1977) states that it resembles in particular *Drynaria rigidula* (Schwartz) Bedd. in pinna shape and soral distribution. Hovenkamp (pers. comm.), an actuopteridologist, states that this fossil does not belong to the *Polypodiaceae,* as the innervation of the sori looks atypical for any *Polypodiaceae* (see Roos, 1986: pl.30–34, 37, 38, 40).

8. Dennstaedtia Bernhardi (*Dennstaedtiaceae–Dennstaedtioideae*)

Of the Recent genus *Dennstaedtia,* two species are mentioned by Andrews & Boureau (1970): *D. americana* Knowlton (Paleocene) and *D. tschuktschorum* Kryshtofovich (Cretaceous).

9. Dennstaedtiopsis Arnold et Daugherty (incertae sedis)

Dennstaedtiopsis aerenchymata Arnold & Daugherty (Eocene) is described as polypodiaceous by Taylor (1981): 'horizontally oriented rhizomes that bear alternately arranged, distinctly spaced pinnae ... the distal portions of the frond are not known ...'; Andrews & Boureau (1970) conclude that it is an aquatic fern, the fossil consisting of mineralized rhizomes and petiole bases; they place it in the subfamily *Dennstaedtioideae (Dennstaedtiaceae).* It is definitely non-polypodiaceous, as *Polypodiaceae* s.s. have a highly dissected stele (dictyostele).

10. Dryopteris Adans. (*Dryopteridaceae–Dryopteridoideae*)

Dryopteris meeteetseana Brown (Paleocene); cited by Andrews & Boureau (1970) as being the best conserved polypodiaceous fossil, although the spores have not been preserved.

11. Leptochilites Andreánszky (incertae sedis)

Leptochilites sarmaticus has been described by Andreánszky (1959, Miocene). He states that it is a sterile fern pinna, which has not been completely conserved. There-

fore he concludes 'eine Einreihung in eine echte Gattung nicht richtig und zogen wir vor, eine künstliche Gattung aufzustellen.' Although the depicted pinna may be polypodiaceous, data on the soral disposition are needed to verify this.

12. Onoclea L. *(Dryopteridaceae–Athyrioideae)*

Onoclea hesperia Brown (Paleocene) is cited by Taylor (1981) as being polypodiaceous. Andrews & Boureau (1970) find it to be rather like the Recent species *O. sensibilis* and conclude that it should be included in that species. Material placed by Andreánszky (1959, Miocene) in *Onoclea sensibilis* consists of just one badly conserved pinna. The material of *O. inquirenda* Hollick (Cretaceous) is cited by Andrews and Boureau as being of poor quality. *Onoclea sensibilis* L. var. *fossilis* Newberry (Oligocene?) is also based on poor material.

13. Polypodites Göppert (incertae sedis)

The Fossil genus *Polypodites* has been based by Göppert (1836) on a non-polypodiaceous fossil he named *Polypodites mantelli*. It is not clear why he removed the species *Lonchopteris mantelli* to this new genus. Göppert placed 7 species in his new genus, some of them dating from the Carboniferous. As he also placed several bipinnatifid species in the genus (e.g., *Polypodites elegans*), not all the species assigned to the genus fall within the *Polypodiaceae* s.s. Much of the material (e.g., that of *P. lindleyi*) is very fragmentary.

Subsequently, many species have been placed in the genus (see Jongmans & Dijkstra, 1963; Dijkstra & Van Amerom, 1985; Andrews & Boureau, 1970). Later additions include *Polypodites polysorus* Prynada and *P. verestchaginii* Krassilov, both depicted in Krassilov (1967). *Polypodites polysorus* probably belongs in the family *Cyatheaceae* because of the branching pattern, the 'knobbly' sori, and the trilete spores (Hovenkamp, pers. comm.), while *Polypodites verestchaginii,* which is sterile, may belong to the families *Pteridaceae* or *Thelypteridaceae.*

14. Polypodium L. *(Polypodiaceae–Polypodioideae)*

Lovis (1977) described *Polypodium oregonense* Fontaine as 'utterly unlike ... any known genus of *Polypodiaceae* (s.s.) and ... more consistent with *Cyatheaceae,* though without proper study this suggestion has scarcely more merit than Fontaine's determination.'

Other species described in the genus *Polypodium* (see Fossilium Catalogus = Jongmans & Dijkstra, 1963; Dijkstra & Van Amerom, 1985) will be treated in a subsequent publication on Fossil species of *Polypodium.*

15. Pteridium Scopoli *(Dennstaedtiaceae–Dennstaedtioideae)*

Pteridium calabazensis (Dorf) Graham (Miocene, Pliocene) is regarded as the fossil equivalent of the Present species *Pteridium aquilinum* (L.) Kuhn, which is also found as an abundant Pleistocene fossil (Andrews & Boureau, 1970). It is not regarded as a polypodiaceous fern.

16. Pteris L. (*Pteridaceae–Pteridoideae*)

Pteris palaeoaurita Kovács (Miocene) is based on sterile material, so that its place in the genus is uncertain and provisional (Andreánszky, 1959).

17. Salpichlaena Hooker (*Blechnaceae–Blechnoideae*)

The Fossil species *Salpichlaena anceps* (Lesquereux) Knowlton (Paleocene) is rather like the Recent species *Salpichlaena volubilis* according to Andrews & Boureau (1970).

18. Woodwardia J.E. Smith (*Blechnaceae–Blechnoideae*)

The Recent genus *Woodwardia*, like the Recent genus *Onoclea*, used to be placed in the *Polypodiaceae*. Andrews & Boureau (1970) note a close resemblance between sterile fronds of the two genera, which are now placed in two different families (*Blechnaceae* and *Dryopteridaceae*, respectively). Andrews and Boureau mention the Fossil species *Woodwardia arctica* (Heer) Brown (Paleocene), which includes *W. maxoni* Knowlton, based on fertile frond parts, and *W. columbiana* Knowlton (Pleistocene?).

POLYPODIACEOUS FOSSILS

1. Aglaomorpha heraclea (Kunze) Copel.

In the beginning of this century, Tobler found a 5 cm long fertile part of a fossil fern frond in Palembang Province, Sumatra, dated as Tertiary, possibly Upper Miocene in age. Kräusel (1932) showed it to Christ, and they identified it as a basal pinna of a fertile frond of *Polypodium quercifolium* L. [= *Drynaria quercifolia* (L.) J. Smith], basing their identification on the place of the sori, the venation pattern, and the thickness of the veins. Roos, in his monograph of the drynarioid ferns (1986), assigned it to *Aglaomorpha heraclea* (Kunze) Copel. The Natural History Museum in Basel kindly lent me the specimen. Although Kräusel states that some spores were present at the time he studied the fossil ('Vereinzelt sind auch Sporen vorhanden, einzeln oder in Paketen bis zu vieren vereinigt ...'), I did not find any spores suitable for further study.

2. Polypodium L. species

In 1937, MacGinitie described a fossil found in Redding Creek, California under the name of *Polypodium fertile*: 'This fossil in all its characters is nearly identical with the living *Polypodium vulgare* var. *occidentale* Hook.' It certainly looks like a *Polypodium*, but, despite the epithet, no sporangia or spores have as yet been found preserved on the specimens. Further study has shown the Weaverville flora to be Miocene rather than Eocene in age (Doyle, pers. comm.).

A fossil found in the Fortuna Mine near Bergheim in Germany during an excursion in which palaeobotanists from Utrecht took part, has been brought to my attention by Van den Burgh. It comes from the Rottonschichten Formation, and dates

from the Brunssumien (Pliocene). It can be assigned to the *Polypodiaceae* s. s. and is probably a species of *Polypodium*. It will be further described and published by Van Uffelen and Van der Burgh. Some spores were found and studied with the scanning electron microscope. They are clearly monolete, but too young to conclude anything about the surface pattern of the mature spore. The fossil is deposited in Utrecht under the number 11409.

In the same publication, several Fossil species of *Polypodium* as listed in the Fossilium Catalogus (Jongmans & Dijkstra, 1963; Dijkstra & Van Amerom, 1985) will be treated.

3. Protodrynaria takhtajanii Vikulin et Bobrov

This new, for the present monotypic genus (Vikulin & Bobrov, 1987) has been based on a fossil found in 1982–83 by Vikulin in the Paleogene (Upper Eocene–Lower Oligocene) of Tim, c. 450 km south of Moscow. It consists of a fern frond fragment. The description of the genus reads: 'Rachis very strong, fronds pinnate, with deep sinuses. Sori round, placed between the veins in a double row on both sides of the pinna's main vein. Nervature drynarioid, second order veins very prominent.' The presence of any spores or sporangia is not mentioned. The new fossil species is compared with the recent species *Drynaria mollis, D. sinica, D. propinqua, D. quercifolia,* and *Crypsinus laciniatus*. For comparison, only the macromorphology of the frond and the shape and placement of the sori has been used. Unfortunately, the authors did not yet have Roos (1986) at their disposal, which is the most recent monograph of the drynarioid ferns. Without further details on venation and spores, this fossil could also be placed in the genus *Selliguea* (including *Crypsinus*), on which Hovenkamp is preparing a monograph.

<center>SPORAE DISPERSAE</center>

Introduction

The need to name dispersed spores may pose severe problems to the palaeobotanist. A strict morphographic approach seems to be indicated, although speculation on the plant that produced the spores is necessary in order to establish their place in the natural system of the plant kingdom as soon and as accurately as possible. Once a resemblance between a spora dispersa and a Recent (or Fossil) taxon has been published, it is difficult to reappraise such a claim. However, as a result of the more general use of SEM (scanning electron microscopy), especially in combination with TEM (transmission electron microscopy) observations, many 'resemblances' indicated may turn out to be so slight as to be of no taxonomic consequence. The recent publication of standard works on the spores of Recent ferns and their allies have greatly facilitated comparison. Recent polypodiaceous fern spores have been treated lately in the following publications, which also include SEM pictures: Lloyd (1981, *Polypodium*), Tryon & Tryon (1982, ferns and fern-allies), Van Uffelen & Hennipman (1985, *Pyrrosia*), Hennipman (1990, *Polypodiaceae*), Tryon & Lugardon (1991, ferns and fern-allies, also with TEM).

Exospore and perispore

The exospore ('exine') is defined as 'the main wall of the sporoderm consisting of sporopollenin, including the aperture; homologous to exine' by Tryon & Lugardon (1991). Lugardon (1971), in his study on the ultrastructure of exospore formation in the homosporous ferns (i.e., the orders Ophioglossales, Marattiales, Osmundales, and Filicales), states that all ferns belonging to the order Filicales, except for the Gleicheniaceae, have a similar type of exospore, the blechnoid type, which is formed in basically the same way in all spores of this type. Therefore, the ultrastructure of the exospore, and its formation as studied with TEM is of no use in identifying polypodiaceous spores as such, as many other families have the same type of exospore ultrastructure. However, variations in exospore morphology do occur, and the ultrastructure of the mature exospore may be diagnostic on a generic or suprageneric level (see e.g. Hennipman, 1990, and Tryon & Lugardon, 1991). Moreover, exospore surface patterns show much variation, not only in mature spores, but also during sporogenesis. The variation in mature spores has been obvious from the first LM studies onward, but SEM has enabled palynologists to make a closer study of the surface patterns of both exospore ('exine') and perispore ('perine') in mature spores (Tryon & Tryon, 1982; Tryon & Lugardon, 1991).

Recently it has become feasible to study the succession of patterns during exospore deposition with SEM (Van Uffelen, 1990). Such a study of surface patterns during sporogenesis in several Recent species of *Polypodiaceae* has shown that, apart from differences in spore shape and size, different patterns succeed each other, while this ontogenetic series of patterns is characteristic on a (sub)generic or suprageneric level (Van Uffelen, 1987, 1990). Potonié (1962) already indicated that immature spores as often found in closed sporangia ('in situ') may look very different from sporae dispersae of the same species, which usually have been shed spontaneously from ripe sporangia. This may be caused either by the absence of one or more of the last-deposited exospore layers, or by the absence of the perispore on the spores 'in situ'. It may also be the result of the loss of the perispore layer during fossilization of sporae dispersae.

The presence of a true perispore in Recent ferns, defined by Tryon & Lugardon (1991) as 'the outer wall of the sporoderm consisting of material distinct from the exospore sporopollenin, and formed later than the exospore', has been a matter of debate over the years. However, TEM studies (Lugardon, 1978) have shown that all fern spores and most spores of the fern-allies do have a perispore, albeit sometimes a very thin and inconspicuous one, and therefore visible only on TEM sections. In the light of these fairly recent findings, the possibility of a perispore still being present in Fossil spores should be reconsidered.

Variability

On the one hand, spore surface patterns in one Recent species of ferns may exhibit a rather large variation, especially in the size and spacing of perispore elements (e.g., in *Drynaria sparsisora,* Van Uffelen, 1990, or in several species of *Pyrrosia,* Van Uffelen & Hennipman, 1985). In the study of Fossil sporae dispersae it is difficult to

assess whether the differences found between two samples (differing in time and/or in space) correspond to differences between taxa, or fall within the infraspecific variation. Therefore, well-circumscribed morphological differences should result in the description of different form-species, because different form-species are easily lumped once the conspecifity of such form-species with a variable Recent or Fossil taxon is established. However, the assignment of different names to form-species that are morphologically more or less identical, merely because they are found in different places and/or ages, does not serve any practical purpose and impedes an evaluation of the occurrence of the same type of spore in different places and/or in different ages of geological time.

The striking variability in spore characters within one Recent group of ferns, e.g., within the family *Polypodiaceae* (Hennipman, 1990) or the families *Aspleniaceae, Thelypteridaceae,* and *Dryopteridaceae* (Tryon & Lugardon, 1991), does not always reflect relationships as established by other characters: similar ranges of variability are found within different monophyletic groups. These instances of parallel evolution are annoying to a palaeobotanist who has to rely heavily on spore characters. It may be caused by a long-retained genetic predisposition to develop many different characters, of which some are developed in preference to others in the course of evolution (see Van Uffelen, 1991). Van Steenis (1986) noted the fact that evolutionary changes in pollen and spore morphology may result from the influence of aspects of the environment different from those causing changes in the morphology of the rest of the plant. However, after a survey of literature, Wagner (1974) concluded that in general 'there is a good overall correlation of spore type with the family–subfamily levels of classification.' In the polypodiaceous genus *Pyrrosia,* Van Uffelen & Hennipman (1985) found the perispore types encountered in the genus to concur reasonably well with the infrageneric groups Hovenkamp (1986) proposed in his monograph of the genus.

On the other hand, the fact that form-species or form-genera of spores may contain spores of quite different origin reflects the Recent situation, where in many not very closely related taxa similar spores may be found. In the *Thelypteridaceae, Aspleniaceae,* and *Dryopteridaceae* the same type of perispore may be present in genera of these different families. In the *Polypodiaceae* s.s., in *Pyrrosia angustata* and several species of *Goniophlebium,* a similarly folded perispore is found. Spores of *Davallia (Davalliaceae)* may be similar to those of species of *Polypodium.* The spore surface of species of the *Pyrrosia subfurfuracea*-type (*Polypodiaceae*), with a smooth exospore covered by a thin perispore that contains globules of exospore material, looks strikingly similar to that of *Lygodium microphyllum (Schizaeaceae),* where the exospore surface is verrucate, and covered by a thin perispore. The latter example also indicates an important limitation of SEM-studies of the spore surface only – the structure of the wall remains unknown, unless broken spores are included in the study (see Van Uffelen & Hennipman, 1985). Therefore LM or even TEM studies are advisable in order to determine which part of the surface pattern is contributed by the exospore, and which by the perispore. Both exospore and perispore characters may be important in determining relationship.

An example of the difficulties in interpreting wall structure when using LM data only, is found in Krutzsch (1967): *Verrucatosporites alienus* is said to be similar to

the spores of *Pyrrosia lanceolata,* which have an almost smooth exospore covered by a thick, pronouncedly verrucate perispore, and to those of *Microsorum diversifolium* (= *Phymatosorus diversifolius,* see Bosman, 1991), where the verrucate exospore is covered by a thin perispore. Other form-species in this form-genus, e.g. *Verrucatosporites favus,* are said to resemble spores of species of *Polypodium,* which also have a verrucate exospore covered by a thin perispore.

Polypodiaceous and non-polypodiaceous sporae dispersae

Monolete sporae dispersae have been found since the Lower Devonian (Traverse, 1988) and were produced by such diverse plant groups as sphenopsids, lycopsids, and Marattiales.

A general inventory of the form-genera that are often referred to the *Polypodiaceae,* be it s.s. or s.l., is difficult to give: members of almost all monolete form-genera have at some time or other been indicated as having affinities with this family. I exclude the possibly trilete spores of *Loxogrammaceae* (genera *Anarthropteris* and *Loxogramme*) from this review. The spores of the families *Loxogrammaceae* and *Grammitidaceae* are supposed to be more similar to each other than to those of the family *Polypodiaceae* s.s. (Tryon & Lugardon, 1991), although others regard the *Loxogrammaceae* as more closely related to the *Polypodiaceae* than to the *Grammitidaceae* (e.g., Hennipman et al., 1990).

It has been current practice (Andrews & Boureau, 1970) to regard sporae dispersae of the form-genera *Laevigatosporites* Ibrahim, *Verrucatosporites* Thomson et Pflug, and *Polypodiidites* Ross as belonging to the family *Polypodiaceae* s.l.

Laevigatosporites spores (syn. *Monolites,* see Krutzsch, 1967) have been produced over a long period (Paleozoic to Present, see Traverse, 1988) by organisms belonging to very different groups, such as sphenopsids, lycopsids, *Pecopteris, Scoleopteris,* and *Zeilleria*; they may belong to any group with a smooth exospore covered by a more or less pronounced perispore, which is usually lost during fossilization. For instance, Salard (1975, Tertiary) found a specimen of the form-genus *'Monolites'* and mentioned it to resemble the spores of *Equisetum debile.* Therefore, no conclusions may be drawn as to the presence of *Polypodiaceae* s.s. or s.l. in any age or place where *Laevigatosporites* spores have been found. Ultrastructural study may yield some data on possible relationships, but as exospore formation and ultrastructure in *Polypodiaceae* s.s. much resemble the process in many other families (Lugardon, 1971), ascribing spores of this form-genus to the *Polypodiaceae* s.s. may always be doubtful.

Many spores placed in the form-genus *Verrucatosporites* Pflug may be polypodiaceous, as many Recent species of the family have a verrucate exospore (e.g., species of *Drynaria, Microsorum, Polypodium,* and *Pyrrosia*). Therefore, careful comparison of SEM pictures of exospore surfaces of *Verrucatosporites* spores with those of Recent ones may yield information on the provenance of some of these sporae dispersae. Unfortunately, exospore surfaces of spores from different genera may be rather alike, e.g., the polygonal bases of closely packed verrucae being the result of basal similarities in the process of exospore formation (see Van Uffelen, 1991). For instance, Salard (1975), in a publication on Tertiary sporae dispersae from Cameroun,

mentions *Verrucatosporites* aff. *alienus* to be possibly related to either *Microsorum diversifolium* or *Polypodium vulgare*. She suggests that *Verrucatosporites favus* subsp. *pseudosecundus* may be related to *Psilotum triquetrum,* a Recent species from a family of doubtful affinities, which may be placed in the Filicales because of the similarities of the spores and their formation (Tryon & Lugardon, 1991), but is also often placed in a different order, the Psilotales. She also compares *Verrucatosporites tenellis* Krutzsch to the spores of the Recent *Pyrrosia schimperiana,* although the latter one has slightly bigger verrucae. It is difficult to assess how many differences in size of the spores itself and of the sculptural elements of the spore wall may be accounted for by infraspecific variation.

Other spores attributed to *Verrucatosporites* by Salard (1975), such as *V. usmensis* Krutzsch, have been compared to the Recent fern species *Stenochlaena palustris* (*Blechnaceae*). Another verrucate spore, *Gemmatosporis gemmatoides* Krutzsch she states to be like *'Pyrrosia ebertiartii'* (= *Pyrrosia lingua* or *P. serpens*), where the verrucate spore surface is formed by a thick perispore. This is an example of comparing pictures without consulting a Recent botanist about ecology and spore production of the plants mentioned. For instance, *Pyrrosia lingua* var. *heteractis* usually produces very few spores, so that the chance of finding any in a sediment is extremely small.

The form-genus *Polypodiidites* contains monolete spores that may be produced by *Polypodiaceae* s.s. In his publication on Neogene palynomorphs from Papua New Guinea, Playford (1982) supposes the verrucate *Polypodiidites* spec. to belong to a Recent species of the *Polypodiaceae,* such as *Microsorum diversifolium* (Willd.) Copel. or *Polypodium vulgare* L.; Tryon & Lugardon (1991) take it to be similar to spores of extant *Aglaomorpha meyeniana* (from Taiwan or the Philippines), *A. coronans, Drynaria delavayi* (both from the mainland of Southeast Asia), or to species of *Microgramma* or *Polypodium* 'not currently reported from New Guinea' – however, none of the species mentioned here occur in New Guinea, and *A. meyeniana* is probably ruled out by the perispore being verrucate, and not the exospore (Roos, 1986).

Tryon & Lugardon (1991) also attribute *Polypodiidites* spores found by Playford (1982) in the Neogene of Papua New Guinea to the Recent genus *Selliguea*; however, as they do not specify which of the two species of *Polypodiidites, P. usmensis* (Van der Hammen) Hekel with discrete, dispersed verrucae, or *Polypodiidites* spec. with close-spaced, smooth, rounded verrucae, it is difficult to assess this statement. The spores of *Polypodiidites* spec. are more similar to those of extant *Selliguea* than those of *P. usmensis,* but in my opinion they may belong to any other polypodiaceous genus. Playford mentions possible affinities of *Polypodiidites usmensis* with *Microsorum diversifolium* (Willd.) Copel. or *Polypodium vulgare* L., but also with 'the climbing swamp fern *Stenochlaena palustris* (Burm. f.) Beddome of the family *Blechnaceae.'* Hovenkamp (pers. comm.) agrees with this suggestion, as this fern species produces spores in abundance, in an environment where fossilization must be relatively easy.

Despite their misleading name, spores of the form-genus *Polypodiaceoisporites* Potonié are trilete and are usually linked with spores of Recent species of *Pteris* (*Pteridaceae*).

Spores of *Stenochlaenidites papuanus* (Cookson) Khan from the Upper Miocene of Papua New Guinea are described by Playford (1982) as having an exine with 'verrucae that are mostly arranged uniserially to form crenate or knobbly ridges', and sees the form-genus as identical with spores produced by *Stenochlaena laurifolia* Presl. The SEM pictures plus description ('exospore forms the contours; perispore laminate, thin') by Tryon & Lugardon (1991) indeed show a remarkable likeness. However, Tryon & Lugardon (1991) state that 'the size and surface of the fossil material clearly correspond to spores of *Goniophlebium* species, several of which presently occur in New Guinea', but they forget that the folds in Recent *Goniophlebium* spores are formed by the perispore. In this case, either Playford has interpreted a fossilized perispore as part of the exine, or Tryon and Lugardon are mistaken.

PALAEOBOTANY AND NOMENCLATURE

Among palaeobotanists, much discussion has been held over nomenclatural issues (e.g., Cleal, 1986; Collinson, 1986; Hughes, 1986). However, they do not touch upon a problem faced by actuobotanists making an inventory of Fossil representatives or relatives of a Recent taxon. The problem in question is caused by the essential rigidity of the type method as imposed by the International Code of Botanical Nomenclature (Greuter et al., 1988):

1) A specific epithet, once given, always stays with the material cited in the original publication.
2) A new generic name always stays with the species on which it has originally been based.

In the case of names for Fossil plants or plant parts, this means that great care has to be taken not to coin any name indicating a relationship with another taxon – such a name stays with the material forever, even if the supposed relationship turns out to be debatable or incorrect. A case in point is the genus *Polypodites*, most species of which do not belong to the family *Polypodiaceae* s.s. at all. The species placed in this genus after its publication by Göppert (1836) may belong in such different families as *Cyatheaceae, Dipteridaceae,* or *Thelypteridaceae* (Hovenkamp, pers. comm.). Even the type species of the genus, *Polypodites mantelli,* is only distantly related to the *Polypodiaceae*. Another example is *Leptochilites,* a sterile frond part, where the name is based on a superficial likeness with fronds of the fern *Leptochilus* (Andreánszky, 1959).

These considerations are also relevant to the application of Recent generic names to Fossil material, which is current practice from the Cretaceous onward (Collinson, 1986). Considering that assignment of a Fossil species to an existing genus always leaves the possibility of transferring it to another genus, it is much less confusing to assign a new Fossil species of slightly uncertain affinity to an existing Recent (or Fossil) genus than to erect a new Fossil genus with a suggestive, undeletable name! Collinson (1986) also points out that 'casual' assignment of fossils to modern taxa is 'a matter for peer review and subsequent confirmation or revision', and I regard this as less of a problem than having to use a permanent name that wrongly suggests a relationship.

Bolbitis coloradica (Brown, 1950) may serve as an example. The name is based on part of a sterile frond. The finding of corresponding fertile pinnae necessitated its removal from the genus *Bolbitis* and the erection of a new genus, *Astralopteris* (Tidwell et al., 1967), the name referring to the fact that it is indubitably a fern, and to the arrangement of the sori.

However, in this matter the palaeobotanist has to choose between the Scylla of instating undeletable, possibly 'wrong' names and the Charybdis of ending up with genera including such diverse species that they cannot possibly represent monophyletic groups, which may seriously impede biostratigraphical and palaeoecological studies (Cleal, 1986). Form taxa pose a slightly different problem. They are erected for the purpose of grouping organs that are similar in morphology, irrespective of their possible taxonomic origin, the form species to be incorporated in a 'complete' taxon as soon as more information becomes available (e.g., more fossil material, or ultrastructural data). As the taxonomic affinities of plant parts often are ambiguous (e.g., Van Steenis, 1986), no indication of relationship should be made in the generic name – it is much more convenient to apply features of the plant part in coining a name, as in *Laevigatosporites* and *Verrucatosporites*. The name *Polypodiaceoisporites* may illustrate the confusion caused by coining a name referring to an existing taxon: the spores are trilete and show no affinity to the family *Polypodiaceae* s.s. The latter has monolete spores, with very few exceptions in some species of *Loxogramme,* of which the spores are easily distinguished by their wall structure.

THE ORIGIN OF THE POLYPODIACEAE

The extreme paucity of polypodiaceous fossils may be caused by the fact that, like Recent *Polypodiaceae,* most of the now extinct *Polypodiaceae* were epiphytes with fronds that, when reaching the end of their life span, deteriorated on the plant and then fell from the plant, one by one. Collinson (1978) states: 'Any organ which is shed from the plant represents a more likely potential fossil than a structure decaying on the plant.' Only a catastrophe would yield an entire plant with several non-decayed fronds ready for fossilization (in the case of epiphytic ferns, e.g., the host tree falling over, followed by inundation or a volcanic eruption). Thomas & Spicer (1987) have described the small chance of any such potential fossil becoming a real fossil, available for study by a palaeobotanist.

Although Lovis (1975) stresses the importance of fossil evidence in estimating the age of a group, the absence of fossils of a taxonomic group should not be seen as final evidence of the absence of such a group in the period under discussion, considering the small chance of any living plant ever to become a fossil.

Detailed recent analyses by actuobotanists of the systematics of some genera in the *Polypodiaceae* s.s. have yielded the latest supposed relationships, thereby inferring evolutionary history, i.e., the order in which the different parts of the group under study have been split off. This, together with the data on the biogeography of the species plus knowledge of the geological history of the areas concerned, has led to some conclusions about the age of the family. As Hovenkamp (1986) states: 'Recent advances in geophysics ... have confirmed that the splitting of land masses is a plausible mechanism to be held responsible for large-scale speciation.'

If one assumes that the breakup of Gondwanaland corresponds to dichotomies low down in the reconstructed phylogenetic trees of groups with a pan- or palaeotropical distribution (see Hovenkamp, 1986: fig.15), then the origin of such groups (in this case, of genera in the *Polypodiaceae* s.s.) lies before this event, which took place in the Lower Cretaceous (120–140 m.y. B.P.). There is, however, some danger of 'channelling' of argument in this assumption; especially in groups with a pan- or palaeotropical distribution, once it is assumed that large-scale speciation is probably mainly due to vicariance (and not to migration), then only the Gondwanaland breakup is indicated as the main cause of vicariance. Furthermore, a proper analysis of relationships is handicapped by the sometimes extreme difficulty in circumscribing monophyletic groups for study in this family (Hensen, 1990; Bosman, 1991).

In his monograph on the drynarioid *Polypodiaceae,* Roos (1986) mentions a fossil described by Kräusel (1932), which probably dates from the Miocene (c. 10 m.y. B.P.), as conspecific with the Recent species *Aglaomorpha heraclea* (Kunze) Copel. In his chosen cladogram (Roos, 1986), five bifurcation events have led to the origin of this species, so the age of this group of *Polypodiaceae* must date even further back. Another approach, biogeographic analysis, leads to the supposition that the moment of separation of Africa, India and Ceylon, and the rest of the Palaeotropics falls within the history of the drynarioid *Polypodiaceae.*

Hovenkamp (1986) assumes that the basal dichotomy in his cladogram of *Pyrrosia* refers to the breakup of Gondwanaland into Africa and a part consisting of India, Australia, and Antarctica. Therefore, the genus must already have been in existence before 120–140 m.y. B.P. Like many other authors, he also stresses the close relationship between the genera *Pyrrosia* and *Platycerium,* which are usually placed together in a subfamily of the *Polypodiaceae,* the *Platycerioideae.* About relationships within the genus *Platycerium* some debate has been going on, but taking the centre of origin to be Africa, Hennipman & Roos (1982) conclude that the platycerioids must already have been in existence before the breakup of Gondwanaland.

How many genera in the family are of later origin is still a matter of debate. Rödl-Linder, in her monograph on the genus *Goniophlebium* (1990), states that 'it only arose after separation of Gondwana in Africa and Papaustralia', and considers the genus a 'relatively recent' one. She bases this conclusion on the absence of representatives of the genus in Africa, but also considers the total lack of fossils significant in this respect, which I think is no strong argument in this group of ferns, as fossil representatives of other genera of *Polypodiaceae* are also extremely rare.

Hereby the paradox is established that the time of origin of the *Polypodiaceae,* which was estimated to be Jurassic by uncritical assignment of many and various fossils to the family sensu latissimo (Emberger, 1968), is now again postulated to be Jurassic by a more devious method, although this is no longer supported by actual fossil evidence – the first truly polypodiaceous fossil (*Protodrynaria takhtajanii*), dating from the Upper Eocene–Lower Oligocene. Lovis (1977) states that 'it would seem that the Malaysian region has been peculiarly favourable as a refuge for the survival of the more immediate descendants of some elements of the Jurassic fern flora.' The Malaysian flora, being so rich in *Polypodiaceae* s.s., may be regarded as a confirmation of this statement.

ACKNOWLEDGEMENTS

REFERENCES

ANDREÁNSZKY, G. 1959. Die Flora der Sarmatischen Stufe in Ungarn. Akadémiai Kiado, Budapest.

ANDREWS, H.N., & E. BOUREAU. 1970. VI. Classe des Leptosporangiopsida. In: E. Boureau (ed.), Traité de Paléobotanique. T. IV fasc. I. Filicophyta: 257–406. Masson et Cie, Paris.

ARNOLD, C.A. 1964. Mesozoic and Tertiary fern evolution and distribution. Mem. Torrey Bot. Club 21 (5): 58–66.

BAAYEN, R.P., & E. HENNIPMAN. 1987a. The paraphyses of the Polypodiaceae (Filicales). I. General part. Beitr. Biol. der Pflanzen 62: 251–316.

BAAYEN, R.P., & E. HENNIPMAN. 1987b. The paraphyses of the Polypodiaceae (Filicales). II. Taxonomic part. Beitr. Biol. der Pflanzen 62: 317–347.

BARTHEL, M. 1976. Farne und Cycadeen. In: Anh. des Zentralen Geologischen Instituts. Paläontologische Abhandlungen H26: Eocene Floren des Geiseltales: 439–490 + Taf. 72–88.

BOSMAN, M.T.M. 1991. A monograph of the fern genus Microsorum (Polypodiaceae). Leiden Bot. Series 14: 1–161.

BOWER, F.O. 1923. The ferns (Filicales). Vol. I. Analytical examination of the criteria of comparison. Cambridge University Press, 359 pp.

BOWER, F.O. 1928. The ferns (Filicales). Vol. III. The leptosporangiate ferns. Cambridge University Press, 306 pp.

BROWN, R.W. 1950. Cretaceous plants from Southwestern Colorado. Geol. Survey Prof. Paper 221-D: 45–66.

CHRISTENSEN, C. 1938. XX. Filicinae. In: F. Verdoorn (ed.), Manual of Pteridology: 522–550. Nijhoff, The Hague.

CLEAL, C.J. 1986. Identifying plant fragments. In: R.A. Spicer & B.A. Thomas (eds.), Systematic and taxonomic approaches in palaeobotany. Syst. Ass. Special Volume 31: 53–65. Clarendon Press, Oxford.

COLLINSON, M.E. 1978. Dispersed fern sporangia from the British Tertiary. Ann. Bot. 42: 233–250.

COLLINSON, M.E. 1986. Use of modern generic names for plant fossils. In: R.A. Spicer & B.A. Thomas (eds.), Systematic and taxonomic approaches in palaeobotany. Syst. Ass. Special Volume 31: 91–104. Clarendon Press, Oxford.

COPELAND, E.B. 1947. Genera Filicum. The genera of ferns. Chronica Botanica Co., Waltham, Massachusetts, 247 pp. + 10 pl.

CRABBE, J.A., A.C. JERMY & J.T. MICKEL. 1975. A new generic sequence for the pteridophyte herbarium. Fern Gaz. 11: 141–162.

DIELS, L. 1902. Polypodiaceae. In: A. Engler & K. Prantl (eds.), Die natürlichen Pflanzenfamilien I, 4: 139–339. Wilhelm Engelmann Verlag, Leipzig.

DIJKSTRA, S.J., & H.W.J. VAN AMEROM. 1985. Filicales, Pteridospermae, Cycadales, incertae sedis. 2. Supplement. In: S.J. Dijkstra (ed.), Fossilium Catalogus. II: Plantae, Pars 91, Kugler Publications, Amsterdam.

EMBERGER, L. 1968. Les plantes fossiles. Masson et Cie, Paris, 758 pp.

GÖPPERT, H.R. 1836. Die Fossilen Farrnkräuter. Systema Filicum Fossilium. Nova Acta Acad. Caes. Leopoldino-Carol. Nat. Curios. 17 (Suppl.): 1–486 + 44 pl.

GREUTER, W., H.M. BURDET, W.G. CHALONER, V. DEMOULIN, R. GROLLE, D.L. HAWKSWORTH, D.H. NICHOLSON, P.C. SILVA, F.A. STAFLEU, E.G. VOSS & J. MCNEILL (eds.). 1988. International code of botanical nomenclature, adopted by the Fourteenth International Botanical Congress, Berlin, July–August 1987. Regnum Veg. 118.

HARRIS, T.M. 1961. The Yorkshire Jurassic Flora. I. Thallophyta–Pteridophyta. Brit. Mus. (Nat. Hist.), London.

HENNIPMAN, E. 1977. A monograph of the fern genus Bolbitis (Lomariopsidaceae). Leiden Bot. Series 2: 1–331.

HENNIPMAN, E. 1984. A new approach to the systematics of the Polypodiaceae (Filicales). Taxon 33: 140–141.

HENNIPMAN, E. 1985. Progress report of the Polypodiaceae project. Taxon 34: 354–355.

HENNIPMAN, E. 1990. The significance of the SEM for character analysis of spores of Polypodiaceae (Filicales). In: D. Claugher (ed.), Scanning Electron Microscopy in taxonomy and functional morphology. Syst. Ass. Special Volume 41: 23–44. Clarendon Press, Oxford.

HENNIPMAN, E., K.U. KRAMER & P. VELDHOEN. 1990. Polypodiaceae. In: K.U. Kramer & P.S. Green (eds.), I. Pteridophytes and gymnosperms: 203–230. In: K.Kubitzki (ed.), The families and genera of vascular plants. Springer Verlag, Berlin etc., 404 pp.

HENNIPMAN, E., & M.C. ROOS. 1982. A monograph of the fern genus Platycerium (Polypodiaceae). Verh. Kon. Ned. Akad. Wetensch. Natuurk. Ser. 2, Vol. 80, Amsterdam, 126 pp.

HENNIPMAN, E., & M.C. ROOS. 1983. Phylogenetic systematics of the Polypodiaceae (Filicales). Verh. naturw. Ver. Hamb. (NF) 26: 321–342.

HENNIPMAN, E., & G.P. VERDUYN. 1987. A taxonomic revision of the genus Lecanopteris (Polypodiaceae) in Sulawesi, Indonesia. Blumea 32: 313–19.

HENSEN, R.V. 1990. Revision of the Polypodium loriceum-complex (Filicales, Polypodiaceae). Nova Hedwigia 50 (3–4): 279–336.

HETTERSCHEID, W.L.A., & E. HENNIPMAN. 1984. Venation patterns, soral characteristics, and shape of the fronds of the microsorioid Polypodiaceae. Bot. Jahrb. Syst. 105 (1): 11–47.

HOLTTUM, R.E. 1949. The classification of ferns. Biol. Rev. 24: 267–296.

HOVENKAMP, P.H. 1986. A monograph of the fern genus Pyrrosia (Polypodiaceae). Leiden Bot. Series 9: 1–280.

HUGHES, N.F. 1986. The problems of data-handling for early angiosperm-like pollen. In: R.A. Spicer & B.A. Thomas (eds.), Systematic and taxonomic approaches in palaeobotany. Syst. Ass. Special Volume 31: 233–51. Clarendon Press, Oxford.

JARRETT, F.M. 1980. Studies in the classification of the leptosporangiate ferns: I. The affinities of the Polypodiaceae sensu stricto and the Grammitidaceae. Kew Bull. 34 (4): 825–833.

JONGMANS, W.J., & S.J. DIJKSTRA. 1963. Filicales, Pteridospermae, Cycadales. In: S.J. Dijkstra (ed.), Fossilium Catalogus. II: Plantae, Pars 54, Uitgeverij Junk, 's-Gravenhage.

KRAMER, K.U., & P.S. GREEN (eds.). 1990. I. Pteridophytes and gymnosperms. In: K. Kubitzki (ed.), The families and genera of vascular plants. Springer Verlag, Berlin etc., 404 pp.

KRASSILOV, V.A. 1967. Early Cretaceous flora of southern Primorye (far east) and its significance for the stratigraphy. Nauka, Moscow. (In Russian.)

KRÄUSEL, R. 1932. Fossile Pflanzen aus dem Tertiär von Süd-Sumatra. Verh. Geol. Mijnbouwk. Genootschap Ned. en Kol. Geol. Serie 9: 5–7.

KRUTZSCH, W. 1967. Atlas der mittel- und jungtertiären dispersen Sporen- und Pollen- sowie der Mikroplanktonformen des nördlichen Mitteleuropas. Lieferung IV und V: Weitere azonotrilete (apiculate, murornate), zonotrilete, monolete und alete Sporenformen. VEB Gustav Fischer Verlag Jena, 232 pp.

LLOYD, R.M. 1981. The perispore in Polypodium and related genera (Polypodiaceae). Can. J. Bot. 59: 175–189.

LORCH, J. 1967. A Jurassic flora of Maktesh Ramon, Israel. Israel J. Bot. 16: 131–55 + pl. 163–180.

LOVIS, J.D. 1975. Aspidistes thomasii – a Jurassic member of the Thelypteridaceae. Fern Gaz. 11 (2–3): 137–140.

LOVIS, J.D. 1977. Evolutionary patterns and processes in ferns. In: R.D. Preston & H.W. Woolhouse (eds.), Advances in Bot. Research 4: 229–415.

LUGARDON, B. 1971. Contribution à la connaissance de la morphogenèse et de la structure des parois sporales chez les Filicinées isosporées. Thesis, Univ. P. Sabatier, Toulouse, 257 pp. + 51 pl.

LUGARDON, B. 1978. Isospore and microspore walls of living pteridophytes: identification possibilities with different observation instruments. Proc. 4th Int. Palyn. Conf., Vol. I: 152–163 + 2 pl.

MACGINITIE, H.D. 1937. Eocene flora of Western America. III. The flora of the Weaverville Beds of Trinity Country, California; with descriptions of the plant-bearing beds. Carnegie Institution of Washington, Publ. no. 465: 83–151 + 15 pl.

MEYEN, S.V. 1987. Fundamentals of Palaeobotany. Chapman and Hall, London, 432 pp.

MITSUTA, S. 1981. Venation of Lepisorus and Pleopeltis (Polypodiaceae). Acta Phytotax. Geobot. 32): 147–164.

MITSUTA, S. 1982. Venation and trichomes of the Drynarioid ferns (Polypodiaceae). Acta Phytotax. Geobot. 33: 264–275.

MITSUTA, S. 1983. Studies in the venation and systematics of Polypodiaceae. I. Venation (1). Mem. Fac. Sc. Kyoto Univ. ser. Biol. VIII (2): 123–150.

MITSUTA, S. 1984a. Studies in the venation and systematics of Polypodiaceae. II. Venation of Polypodiaceae (2) and of some other ferns. Mem. Fac. Sc. Kyoto Univ. ser. Biol. IX (1): 57–85.

MITSUTA, S. 1984b. Studies in the venation and systematics of Polypodiaceae. III. Comments on generic classification of Polypodiaceae and notes on venation and systematics of Polypodiaceae. Mem. Fac. Sc. Kyoto Univ. ser. Biol. IX (2): 133–155.

PICHI SERMOLLI, R.E.G. 1974. Fragmenta Pteridologiae. V. Webbia 29: 1–16.

PLAYFORD, G. 1982. Neogene palynomorphs from the Huon Peninsula, Papua New Guinea. Palynology 6: 29–54.

POTONIÉ, R. 1962. Synopsis der Sporae in situ. Die Sporen der fossilen Fruktifikationen (Thallophyta bis Gymnospermophyta) im natürlichen System und im Vergleich mit den Sporae dispersae. Beihefte zum Geologischen Jahrbuch 52: 204 pp. + 19 Taf.

RÖDL-LINDER, G. 1990. A monograph of the fern genus Goniophlebium (Polypodiaceae). Blumea 34: 277–423.

ROOS, M.C. 1986. Phylogenetic systematics of the Drynarioidae (Polypodiaceae). Verh. Kon. Ned. Akad. Wetensch. Natuurk. Ser. 2, Vol. 85, Amsterdam.

SALARD, M. 1975. A propos de la microflore cryptogamique tertiaire du bassin sédimentaire côtier du Cameroun. Revue de Micropaléontologie 18 (2): 97–116.

SEN, U., & E. HENNIPMAN. 1981. Structure and ontogeny of stomata in Polypodiaceae. Blumea 27: 175–201.

STEENIS, C.G.G.J. VAN. 1986. The fossil pollen record and the age and distribution of angiosperm plant families – some paradoxes explained. Trans. Bot. Soc. Edinburgh, 150th Anniv. Suppl.: 33–49.

TAYLOR, T.N. 1981. Paleobotany – an introduction to fossil plant biology. MacGraw-Hill Book Company, 589 pp.

THOMAS, B.A., & R.A. SPICER. 1987. The evolution and palaeobiology of land plants. Croom Helm, London/Sydney, 309 pp.

TIDWELL, W.D., S.R. RUSHFORTH & J.L. REVEAL. 1967. Astralopteris, a new Cretaceous fern genus from Utah and Colorado. Brigham Young University Geology Studies 14: 237–240 + 6 pl.

TRAVERSE, A. 1988. Paleopalynology. Unwin Hyman, Boston, 600 pp.

TRYON, A.F., & B. LUGARDON. 1991. Spores of the Pteridophyta. Surface, wall structure, and diversity based on electron microscope studies. Springer Verlag, New York etc., 648 pp.

TRYON, R.M., & A.F. TRYON. 1982. Ferns and allied plants. With special reference to Tropical America. Springer Verlag, New York, 857 pp.

UFFELEN, G.A. VAN. 1987. Sporogenesis in Polypodiaceae (Filicales) (abstract). In: W. Greuter, B. Zimmer & H.-D. Behnke (eds.), Abstracts of the General Lectures, Symposium Papers and Posters presented at the XIV International Botanical Congress, Berlin, 1987: 269.

UFFELEN, G.A. VAN. 1990. Sporogenesis in Polypodiaceae (Filicales). I. Drynaria sparsisora (Desv.) Moore. Blumea 35: 177–215.

UFFELEN, G.A. VAN. 1991. The control of spore wall formation. In: S. Blackmore & S.H. Barnes (eds.), Pollen and Spores, Patterns of Diversification. Syst. Ass. Special Volume 44: 89–102. Clarendon Press, Oxford.

UFFELEN, G.A. VAN, & E. HENNIPMAN. 1985. The spores of Pyrrosia Mirbel (Polypodiaceae), a SEM study. Pollen et Spores 27 (2): 155–197.

VIKULIN, S.V., & A.E. BOBROV. 1987. A new fossil genus Protodrynaria (Polypodiaceae) from the paleogene flora of Tim (the south of the middle Russian upland). Botanitscheski shurnal 72 (1): 95–98 + 2 pl. (In Russian.)

WAGNER, Jr, W.H. 1974. Structure of spores in relation to fern phylogeny. Ann. Missouri Bot. Gard. 61: 332–353.

WATSON, J. 1969. A revision of the English Wealden flora. I. Charales–Ginkgoales. Bull. Br. Mus. Nat. Hist. (Geol.) 17 (5): 209–254, 6 pl.

WILDE, V. 1989. Untersuchungen zur Systematik der Blattreste aus dem Mitteleozän der Grube Messel bei Darmstadt (Hessen, BRD). Cour. Forsch.-Inst. Senckenberg 115: 1–213.