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The arbuscular mycorrhizas of pteridophytes in Yunnan, southwest China: evolutionary interpretations

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Abstract The percentage of arbuscular mycorrhizal pteridophytes among 256 pteridophyte species distributed in Yunnan (southwest China) was found to be lower than that in angiosperms. In the pteridophytes, the occurrence of arbuscular mycorrhizas was low in sporophytes of fern-allies and leptosporangiates, whereas in the eusporangiates it was relatively high. From the standpoint of mycotrophism, the evolutionary trend in the Filicineae may be from constantly mycorrhizal to facultative mycorrhizal and finally to non-mycorrhizal plants.

Keywords Arbuscular mycorrhiza · Pteridophyte · Evolution

Introduction

Pteridophytes are of ancient origin and have special life cycles. They occupy a very important position in the origin and systematic evolution of vascular plants. Mycorrhizas between pteridophytes and fungi have been found in the fossil rhizomes of *Rhynia* and *Asteroxylon*, which were common in the Devonian to Carboniferous periods in the Paleozoic era, and these mycorrhizas were considered to be the earliest arbuscular mycorrhizas (Hass et al. 1994; Remy et al. 1994). Although having persisted through evolution for 3–4 hundred million years, the arbuscular mycorrhizal status of extant pteridophytes is still not clear.

A systematic investigation of the mycorrhizas of pteridophytes was carried out by Boullard (1957), who surveyed the mycorrhizas of more than 420 species of pteridophytes (mostly sporophytes and a few gametophytes). Boullard concluded that the "endophytic symbioses" existed in all pteridophytes except the aquatic ferns (*Marsileaceae, Salviniaceae* and *Isoetaceae*). It is much to be regretted that 75% of Boullard's material (roots and rhizomes) was taken from dried herbarium specimens and not from fresh plants, and that he did not study further the types of endophytic symbioses and the endophytic fungi. Cooper (1976) studied the vesicular-arbuscular mycorrhizas (VAM) of 101 species of pteridophytes in New Zealand and reached a similar conclusion to Boullard. Berch and Kendrick (1982), studying VAM of southern Ontario ferns and fern-allies, found no VAM in fern-allies sporophytes, but all eusporangiates in the Filicineae were arbuscular mycorrhizal. The occurrence of arbuscular mycorrhizas in the Filicineae was not as high as that reported by Boullard (1957) or Cooper (1976). The mycorrhizas of 89 species of ferns in Hawaii were surveyed by Gemma et al. (1992). They found 66 species to be mycorrhizal, but the highest proportion occurred in the leptosporangiates *Dicksoniaceae, Dryopteridaceae* and *Lindsaeaceae.* The occurrence of mycorrhiza in the eusporangiates was very low. It seems that pteridophytes distributed in different areas vary with respect to arbuscular mycorrhizas, and the mycorrhizal status of various species is still not clear.

Yunnan is located in tropical and subtropical areas of southwest China. About 1500 species of pteridophytes are to be found there. Here, we report on the occurrence of arbuscular mycorrhizas in these plants.

Materials and methods

The roots of pteridophytes were collected in different habitats from tropical and subtropical areas of Yunnan. Fresh roots from up-rooted plants were cut into 1- to 3-cm segments and fixed in FAA (formalin 5 ml, acetic acid 5 ml, 70% alcohol 90 ml) diluted to 50% before use. Where possible, at least two individuals of each species were collected in different habitats. The root samples were processed according to the method of Berch and Kendrick (1982) and their mycorrhizal status was determined under a compound microscope.

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Table 1 The arbuscular mycorrhizal status of sporophytes in different pteridophytes. For M/N, M and N indicate the number of arbuscular mycorrhizal and non-mycorrhizal individuals found, respectively

Plant species	M/N
Fern allies	
Huperziaceae	
Huperzia serrata f. longipetolata (Spring) Ching	0/3
Phlegmariurus henryi (Bak.) Ching	0/2
Lycopodiaceae	
Diphasiastrum complanatum (L.) Holub	0/3
Lycopodiastrum casuarinoides (Spring) Holub	0/2
Lycopodium japonicum Thunb.	1/2
Palhinhaea cernua (L.) Frane et Vasc.	0/5
Selaginellaceae	
Selaginella biformis A. Br.	1/1
S. chrysocaulos (Hook et Grev.) Spring	0/3
S. davidii Fr.	1/1
S. frondosa Warb.	1/3
S. helferi Warb.	0/2
S. involvens (Sw.) Spring	1/2
**S. monospora* Spring	0/1
S. picta A. Br.	1/1
S. pulvinata (Hook et Grev.) Maxim	1/1
S. remotifolia Spring	1/3
S. sanguinolenta (L.) Spring	1/1
S. delicatula (Desv.) Alston	1/4
Equisetaceae	
Equisetum debile Roxb	0/5
E. diffusum Don	0/3
Eusporangiates	
Ophioglossaceae	
Ophioglossum petiolatum Hook.	3/0
O. themale Kom.	2/0
O. reticulatum L.	7/0
Angiopteridaceae	
Angiopteris caudatiformis Hieron	5/0
A. hokouensis Ching	11/0
A. wangii Ching	14/0
A. yunnanensis Hieron	9/0
Archangiopteris bipinnata Ching	7/0
A. henryi Christ et Gies.	12/0
A. hokouensis Ching	8/0
A. subrotundata Ching	7/0
Christenseniaceae	
Christensenia assamica (Gifl.) Ching	7/0
Leptosporangiates	
Osmundaceae	
Osmunda japonica Thunb	2/0
Plagiogyriaceae	
Plagiogyria distinctissima Ching	1/1
Gleicheniaceae	
Dicranopteris gigantea Ching	0/3
D. pedata (Houtt.) Nakai	0/2
D. splendida (Hand.-Mazz.) Ching	0/2
Diplopterygium giganteum (Wall ex Hook.) Nakai	0/5
**D. glaucoides* (Ching) Ching	0/1
D. glaucum (Houtt.) Nakai	0/2
Sticherus laevigatus Presl.	0/2
Lygodiaceae	
Lygodium conforme C. Chr.	1/3
L. japonicum (Thunb) Sw.	0/2
Hymenophyllaceae	
Crepidomanes latealatum Cop.	0/3
Mecodium badium (Hook et Grev.) Cop.	0/2
M. blumeanum (Spring.) B. Nayar	0/3
**Trichomanes auriculatum* Bl.	0/1
Dicksoniaceae	
Cibotium barometze (L.) J. Sm.	0/2
Cyatheaceae	
Alsophila constularis Bak.	0/2
A. spinulosa (Hook.) Tryon	2/0
Gymnosphaera gigantea (Wall. ex Hook.) J. Sm.	0/2
G. podophylla (Hook.) Cop.	0/2
Sphaeropteris brunoniana (Hook.) Tryon	0/2
Monachosoraceae	
**Monachosorum henryi* Christ	1/0
Dennstaedtiaceae	
Dennstaedtia melanostipes Ching	2/0
D. scabra (Wall.) Moore	1/1
**Microlepia hookeriana* (Wall.) Presl	1/0
M. marginata (Houtt.) C. Chr.	2/0
M. marginata var. calvescens	2/0
M. pilosissima Ching	3/0
M. platyphylla (Don.) J. Sm.	0/2
M. rhomboidea (Wall.) Presl.	0/3
Lindsaeaceae	
Lindsaea ensifolia Sw.	0/2
L. javanensis Blome	0/2
L. orbiculata (L.) Mett.	3/0
L.odorata Roxb	0/2
Stenolomachusanum (L.) Ching	1/2
Hypolepidaceae	
Hypolepis punctata (Thunb.) Mett.	0/2
Pteridiaceae	
Pteridium revolutum (Bl.) Nakai	0/5
Pteridaceae	
Histiopteris incisa (Thunb.) J. Sm.	1/1
Pteris aspericaulis var. tricolor Moore	0/2
P. cretica var. laeta C. Chr. et Tard.-Blot	0/2
P. cretica var. nervosa(Thunb) Ching et S.H. Wu	0/2
P. dissitifolia Bak.	0/3
P. ensiformis Burm	0/2
P. esquirolii Christ	0/5
P. excelsa Gaud	0/4
P. linearis Poir.	0/2
P. semipinnata L.	0/3
P. setulosocostulata Hayata	1/1
P. vittata L.	0/3
**P. wangiana* Ching	0/1
Sinopteridaceae	
Aleuritopteris albomarginatata (Cll.) Ching	2/0
A. argentea (Gmel.) Tee	3/0
**A. duclouxii* (Christ) Ching	0/1
A. pseudofarinosa Ching et S.H Wu	0/2
Cheilosoria hancockii (Bak.) Ching et Shing	3/0
Leptolepidium subvillosum Shing et S.H. Wu	0/2
Onychium angustifrons Ching	0/2
O. contigium Hope	2/0
O. japonicum var.lucidum (Don) Christ	0/2
O. lucidum (Don) Spring	2/0
Pellaea mairei Brause	2/0
**Sinopteris grevilleoides* (Chr.) C. Chr. et Ching	0/1

Table 1 Continued

Plant species	M/N
Adiantaceae	
**Adiantum bonatianum* Brause	1/0
A. edgewothii Hook	4/0
A. flabellulatum L.	1/1
A. malesianum Ghatak	0/2
A. philipense L.	0/2
Hemionitidaceae	
Coniogramme intermedia Hieron	2/0
C. rosthorni Hieron	0/2
C. simillima Ching	2/0
Gymnopteris bipinnata Christ. var. auriculata (Franch.) Ching	0/2
G. vestita (Presl.) Underw.	1/1
Antrophyaceae	
Antrophyrum henryi Christ	0/2
Vittariaceae	
Vittaria flexuosa Fee	0/1
Athyriaceae	
Acystopteris tenuisecta (Bl.) Tagawa	1/1
Allantodia alata (Christ) Ching	0/2
A. dilatata (Bl.) Ching	1/1
A. doederleinii (Luerss.) Ching	0/3
A. laxifrons (Rosent.) Ching	3/0
A. megaphylla (Bak.) Ching	0/2
A. stenochlamys (C. Chr.) Ching	0/2
A. spectabilis (Wall.ex Mett.)Ching	1/2
Athyriopsis longipes Ching	1/1
A. ptersennii (Kunze) Ching	1/1
Athyrium anisopterum Christ	0/3
A. biserrulatum Christ	2/0
A. delicatulum Ching et S. H. Wu	0/2
A. dissitifolium (Bak.) C. Chr.	1/1
A. mackinnonii (Hopi) C. Chr.	0/2
A. mengtzeense Hieron	2/0
A. niponicum (Mett.) Hance	0/2
A. stigillosum Moore	1/1
Callipteris esculenta (Retz.) J. Sm.	0/2
Diplazium donianum (Mett.) Tard.-Blot.	0/2
D. splendens Ching	1/1
Dryoathyrium boryanum (Willd.) Ching	0/3
D. edentulum (Kunze) Ching	1/1
Lunathyrium dolosum (Christ) Ching	0/2
Monomelangium pullingeri (Bak) Tagawa *var. daweishan-nicolum* W.M. Chu (ined.)	1/1
**Pseudocystopteris atkinsonii* (Bedd.) Ching	0/1
Hypodematiaceae	
Hypodematium crenatum (Forsk) Kuhn	1/2
Thelypteridaceae	
Ampelopteris prolifera (Ketz.) Cop.	0/2
Cyclogramma auriculata (J.Sm.) Ching	1/1
Cyclosorus acuminatus (Houtt.) Nakai	0/2
C. dentatus (Forsk) Ching	0/2
C. hokouensis Ching	1/1
C. mollicesculus (Kuhn.) Ching	0/3
C. parasiticus (L.) Farwell	0/2
C. subnigrescens Ching et W. M. Chu (ined.)	0/3
C. truncatus (Pior.) Farwell	0/2
Dictyocline griffithii Moore	2/0
Thelypteridaceae	
Glaphylopteridopsis erubescens (Wall.) Ching	1/2
Macrothelypteris toressiana (Gaud.) Ching	1/1
**Metathelypteris flaccida* Ching	0/1
Parathelypteris beddomei (Bak.) Ching	0/2
P. hirsutipes (Clarke) Ching	1/1
Pronephrium gymnopteridifrons (Hayata) Holtt.	0/2
P. nudotum (Roxb.) Holtt.	0/2
P. simplex (Hook.) Holtt.	0/3
Pseudocyclosorus esquirolii (Christ) Ching	1/2
P. subochthodes (Ching) Ching	0/2
Pseudophegopteris pyrrhorachis (Kze.) Ching	0/2
P. yunkweiensis (Ching) Ching	0/2
Aspleniaceae	
**Asplenium cheilosorum* Kze. ex Mett.	1/0
A. excisum Presl.	0/3
A. finlaysonianum Hook.	0/2
A. fuscipes Bak.	0/2
A. griffithianum Hook.	0/2
A. lushanense C. Chr.	1/1
A. normale Don.	0/2
A. pekinense Hance	0/4
A. praemosum Sw.	0/3
A. prolongatum Hook.	0/3
**A. tenuicaule* Hay.	0/1
A. unilaterale Lam.	0/2
A. varians Wall. ex Hook et Grev.	0/3
A. wrightioides Christ	0/2
A. yunnanense Franch	0/3
**Neottopteris antrophyoides* (Christ.) Ching	0/1
**N. simonsiana* (Hook.) J. Sm.	0/1
Blechnaceae	
Blechnum orientale L.	1/1
**Brainea insignis* (Hook.) J. Sm.	0/1
Woodwardia japonica (L.f.) Sm.	2/0
*W. unigemmata (Makino) Nakai.	0/1
Peranemaceae	
Acrophorus stipellatus Moore	0/2
Diacalpe christensenae Ching	0/2
Dryopteridaceae	
Acrorumohra diffraeta (Bak.) H. Ito	2/0
Arachniodes globisora (Hayata) Chin	2/0
A. sporadosora (Tagawa) Ching	0/2
Cyrtomium caryotideum (Wall. ex Hook et Grev.) Presl. *f. caryotideum*	1/2
C. fortunei J. Sm.	0/2
Dryopteris basisora Christ	0/2
D. caroli-hopei Fraser-Jenkins	0/2
D. chrysocoma (Christ) C. Chr.	0/3
D. cochleata (Don.) C. Chr.	0/2
D. fructuosa Christ	3/0
D. lepidopoda Hay.	0/3
**D. marginata* (Wall. ex Clarke) Christ	1/0
D. odontoloma (Moore) C. Chr.	0/3
D. sparsa (Don.) Ktze.	2/0
D. stenolepis (Bak.) C. Chr.	0/2
D. sublacera Christ	1/1
Polystichum alteruatum Ching	0/2
**P. chingae* Ching	0/1
P. dielsii Christ	0/2
P. eximium (Mett. ex Kuhn) C. Chr.	0/2
P. jizhushanense Ching	1/1
P. pycnopterum (Christ) Ching	0/2
P. tsus-simense (Hook.) J. Sm.	1/2
Nothoperanema hendersonii (Bedd.) Ching	0/2
Aspidiaceae	
**Ctenitis membranifolia* Ching et C.H. Wang	0/1
Ctenitopsis devexa (Kze.) Ching et C. H. Wang	0/2
C. glabra Ching et C. H. Wang	0/3
C. sagenioides (Mett.) Ching	0/3
C. setulaosa (Bak.) C. Chr. et Tardieu	0/2
C. subsageriacea (Christ) Ching	0/2
Pleocnemia winitei Holtt.	0/5

Table 1 Continued

Plant species	M/N
Quercifilix zeylanica (Houtt.) Cop.	0/2
Tectaria coadunata C. Chr.	0/3
T. decurrens (Presl.) Cop.	0/4
T. dubia (Clarke et Bak.) Ching	0/2
T. hainanensis C. Chr.	0/2
T. hokouensis Ching	0/2
T. simonii (Bak.) Ching	0/2
T. variolosa (Wall) C. Chr.	0/2
T. yunnanensis (Bak.) Ching	0/2
Bolbitidaceae	
Egenolfia tokinensis C. Chr. in Ching	2/0
E. sinensis Maxon	2/0
Bolbitis heteroclita (Presl.) Ching	0/2
B. hokouensis Ching	0/2
Lomariopsidaceae	
**Lomariopsis spectabilis* Mett.	0/1
Nephrolepidaceae	
Arthropteris palisotii (Desv.) Alston	0/4
**Nephrolepis faleata* (Cav.) C. Chr.	0/1
Davalliaceae	
Araiostegia perdurans (Christ) Cop.	0/2
Dipteridaceae	
**Dipteris conjugata* (Kaulf.) Reinw.	0/1
Polypodiaceae	
Arthromeris mairei (Brause) Ching	0/2
Colysis diversifolia W. M. Chu	0/2
C. hokouensis Ching	0/2
C. pentaphylla (Baker.) Ching	0/2
Lepidogrammitis rostrama (Bedd.) Ching	0/3
Lepisorus contortus (Christ) Ching	0/3
L. macrosphaerus (Bak.) Ching	0/2
L. scolopendrium (Ham. ex Don) Mehra et Bir.	0/2
Microsorium carinatum W. M. Chu (ined.)	0/2
M. henryi (Christ) Kuo	0/2
**M. membranaceum* (Don) Ching	0/1
Polypodiaceae	
**M. punctatum* (L.) Cop.	0/1
**Neocheiropteris palmatopedata* (Bak.) Christ	0/1
Neolepisorus ovatus (Bedd.) Ching	0/2
N. sinensis Ching	0/2
Phymatopsis crenatopinnata (Clarke) Ching	0/3
P. nigrovenia (Christ) Ching	0/2
P. trisecta (Bak.) Ching	0/3
**Polypodiodes amoena* (Wall.) Ching	0/1
P. amoenum Wall. *var. pilosa* Clarke	0/2
Pyrrosia adnaseens (Sw.) Ching	0/2
P. gralla (Gies) Ching	0/2
P. lingua (Thunb.) Farwell	0/2
P. mollis (Kz.) Ching	0/2
P. subfurfuracea (Hook.) Ching	0/3
P. tonkinensis (Christ) Ching	0/2
**Tricholepidium maculosum* (Christ) Ching	0/1
Drynariaceae	
Drynaria propinqua (Wall.) J. Sm.	0/2
Loxogrammaceae	
Loxogramme ensiformis Ching	0/2

More than 50 root segments (0.5-1 cm) were examined for each root sample; if at least one segment contained arbuscules, then the plant was considered to be arbuscular mycorrhizal. Species found to be mycorrhizal in more than two places were considered to be constantly mycorrhizal. Species mycorrhizal in one ecological habitat but not in others were scored as facultative mycorrhizal. Species lacking arbuscules in root cortical cells were classified as non-mycorrhizal.

Results and discussion

Arbuscular mycorrhizal status of sporophytes in various taxa of pteridophytes

Of the 256 species surveyed, 20 species were fern-allies, 12 species were eusporangiates and 224 were leptosporangiates. These species and their mycorrhizal status are listed in Table 1. The arbuscular mycorrhizal status of the three groups is summarized in Table 2.

The occurrence of arbuscular mycorrhizas in the pteridophytes of Yunnan largely agrees with the report of Berch and Kendrick (1982) on the pteridophytes of Ontario, Canada. The thick, fleshy, infrequently branched and almost hair-free roots were usually arbuscular mycorrhizal, especially in the case of the eusporangiates (Table 1). In contrast, woody roots with dense clusters of root hairs and heavy pigmentation were rarely arbuscular mycorrhizal. More than two individuals were examined for the majority of the species. However, only one sample was examined in the case of 28 species (marked with * in Table 1) which were rare or difficult to collect from, e.g. crevices of cliffs or tall trees. This prevented any assessment of the variability in their mycorrhizal status.

The data in Table 2 reveal the much lower percentage (17%) of arbuscular mycorrhizal plants in the pteridophytes than in angiosperms (62%) (Trappe 1987). The results in Tables 1 and 2 also show the presence equally of facultative arbuscular mycorrhizal and non-mycorrhizal types but no constantly arbuscular mycorrhizal types among the sporophytes of fern-allies. In the Filicineae, all eusporangiates were heavily arbuscular mycorrhizal. In comparison, 71% of the leptosporangiates were non-mycorrhizal. From the point of view of arbuscular mycotrophism, there is probably no evolutionary trend between facultative mycorrhizal and non-

Table 2 The arbuscular mycorrhizal status of sporophytes in different taxa of pteridophytes. Percent of total species surveyed is given in parentheses (*CM* number of species constantly mycorrhizal, *FM* facultatively mycorrhizal, *NM* non-mycorrhizal, *SN* number of species surveyed)

Taxa	SN	CM	FM	NM
Fern allies	20	0 (0)	9 (45)	11 (55)
Eusporangiates	12	12 (100)	0 (0)	0 (0)
Leptosporangiates	224	32 (15)	31 (14)	161 (71)
Total	256	44 (17)	40 (16)	172 (67)

mycorrhizal types in the fern-allies. In contrast, there appears to be a trend in the Filicineae from constantly arbuscular mycorrhizal (eusporangiates) to non-mycorrhizal (leptosporangiates). This trend was especially obvious when the arbuscular mycorrhizal status of pteridophytes was considered in the context of different evolutionary stages.

Arbuscular mycorrhizal status of pteridophytes in different evolutionary stages

In the extant pteridophytes, the numbers of species, their frequency and the distribution of the Filicineae (eusporangiates and leptosporangiates) all exceed the fern-allies. Comparing the anatomy of Filicineae with the geological records (fossils) of pteridophytes, Bower (1959) found that ferns with simultaneous formation and maturation of sporangia in the sorus (Simplices) were predominant in the Palaeozoic Period. The dominant ferns of the Mesozoic Period, in addition to the Simplices, included many whose sporangia mature gradually from the center to the base of the sorus (Gradatae). Sporangia development in more recent ferns (Mixtae) is of the mixed type with formation and maturation in the sorus neither simultaneous nor gradual but mixed from the center to the base. Classifying the pteridophyte families listed by Ching (1978) into these three groups, *Helminthostachyaceae* to *Lygodiaceae* can be placed in the Simplices, *Hymenophyllaceae* to *Hypolepidaceae* in the Gradatae, and the families after *Pteridiaceae* in the Mixtae.

Using the Simplices, Gradatae and Mixtae to indicate three stages in the vertical evolution process of the Filicineae, the arbuscular mycorrhizal status of the pteridophytes surveyed in this research can be grouped as in Table 3. The occurrence of the arbuscular mycorrhizas in the three different evolutionary groups decreased progressively from Simplices to Mixtae. Constantly arbuscular mycorrhizal plants were 56% Simplices, 36% Gradatae and 12% Mixtae, whereas the proportion of non-mycorrhizal species increased gradually in these three groups (35%, 56% and 74%, respectively). The proportion of the interim facultative arbuscular mycorrhizal type varied little between the three classes. This apparent evolutionary process in the Filiniceae from mycorrhizal through facultative to non-mycorrhizal strongly supports the hypothesis of the mycotrophic origin of land plants (Pirozynski and Malloch 1975). This evolutionary progression has been of use in the further phylogenetic study of plants (Trappe 1987; Gemma et al. 1992). In addition, this evolutionary trend could explain the lower incidence of arbuscular mycorrhiza in pteridophytes than in angiosperms: pteridophytes originated earlier than angiosperms and have evolved further in the direction of non-mycorrhizal.

Table 3 The arbuscular mycorrhizal status of pteridophytes at different evolutionary stages. Percent of total species surveyed is given in parentheses (*CM* number of species constantly mycorrhizal, *FM* facultatively mycorrhizal, *NM* non-mycorrhizal, *SN* number of species surveyed)

Stage	SN	CM	FM	NM
Simplices	23	13 (56)	2 (9)	8 (35)
Gradatae	25	9 (36)	2 (8)	14 (56)
Mixtae	188	22 (12)	27 (14)	139 (74)
Total	236	43 (18)	32 (14)	161 (68)

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