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

Accepted: 21 September 2000

**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 sym-

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

Table 1 Continued

Plant species	M/N
Adiantaceae	
* <i>Adiantum bonatianum</i> Brause	1/0
<i>A. edgeworthii</i> Hook	4/0
<i>A. flabellulatum</i> L.	1/1
<i>A. malesianum</i> Ghatak	0/2
<i>A. philipense</i> L.	0/2
Hemionitidaceae	
<i>Coniogramme intermedia</i> Hieron	2/0
<i>C. rosthorni</i> Hieron	0/2
<i>C. simillima</i> Ching	2/0
<i>Gymnopteris bipinnata</i> Christ. var. <i>auriculata</i> (Franch.) Ching	0/2
<i>G. vestita</i> (Presl.) Underw.	1/1
Antrophyaceae	
<i>Antrophyum henryi</i> Christ	0/2
Vittariaceae	
<i>Vittaria flexuosa</i> Fee	0/1
Athyriaceae	
<i>Acystopteris tenuisecta</i> (Bl.) Tagawa	1/1
<i>Allantodia alata</i> (Christ) Ching	0/2
<i>A. dilatata</i> (Bl.) Ching	1/1
<i>A. doederleinii</i> (Luerss.) Ching	0/3
<i>A. laxifrons</i> (Rosent.) Ching	3/0
<i>A. megaphylla</i> (Bak.) Ching	0/2
<i>A. stenochlamys</i> (C. Chr.) Ching	0/2
<i>A. spectabilis</i> (Wall. ex Mett.) Ching	1/2
<i>Athyriopsis longipes</i> Ching	1/1
<i>A. persennii</i> (Kunze) Ching	1/1
<i>Athyrium anisopterum</i> Christ	0/3
<i>A. biserrulatum</i> Christ	2/0
<i>A. delicatulum</i> Ching et S. H. Wu	0/2
<i>A. dissitifolium</i> (Bak.) C. Chr.	1/1
<i>A. mackinnonii</i> (Hopi) C. Chr.	0/2
<i>A. mengtzeense</i> Hieron	2/0
<i>A. niponicum</i> (Mett.) Hance	0/2
<i>A. stigillosum</i> Moore	1/1
<i>Callipteris esculenta</i> (Retz.) J. Sm.	0/2
<i>Diplazium donianum</i> (Mett.) Tard.-Blot.	0/2
<i>D. splendens</i> Ching	1/1
<i>Dryoathyrium boryanum</i> (Willd.) Ching	0/3
<i>D. edentulum</i> (Kunze) Ching	1/1
<i>Lunathyrium dolosum</i> (Christ) Ching	0/2
<i>Monomelangium pullingeri</i> (Bak) Tagawa var. <i>daweishanicolum</i> W.M. Chu (ined.)	1/1
* <i>Pseudocystopteris atkinsonii</i> (Bedd.) Ching	0/1
Hypodematiaceae	
<i>Hypodematum crenatum</i> (Forsk) Kuhn	1/2
Thelypteridaceae	
<i>Ampelopteris prolifera</i> (Ketz.) Cop.	0/2
<i>Cyclogramma auriculata</i> (J.Sm.) Ching	1/1
<i>Cyclosorus acuminatus</i> (Houtt.) Nakai	0/2
<i>C. dentatus</i> (Forsk) Ching	0/2
<i>C. hokouensis</i> Ching	1/1
<i>C. mollicesculus</i> (Kuhn.) Ching	0/3
<i>C. parasiticus</i> (L.) Farwell	0/2
<i>C. subnigrescens</i> Ching et W. M. Chu (ined.)	0/3
<i>C. truncatus</i> (Pior.) Farwell	0/2
<i>Dictyocline griffithii</i> Moore	2/0
Thelypteridaceae	
<i>Glaphylopteridopsis erubescens</i> (Wall.) Ching	1/2
<i>Macrothelypteris toressiana</i> (Gaud.) Ching	1/1
* <i>Metathelypteris flaccida</i> Ching	0/1
<i>Parathelypteris beddomei</i> (Bak.) Ching	0/2
<i>P. hirsutipes</i> (Clarke) Ching	1/1
<i>Pronophrium gymnopteridifrons</i> (Hayata) Holtt.	0/2

Table 1 Continued

Plant species	M/N
<i>P. nudotum</i> (Roxb.) Holtt.	0/2
<i>P. simplex</i> (Hook.) Holtt.	0/3
<i>Pseudocyclosorus esquirolii</i> (Christ) Ching	1/2
<i>P. subochthodes</i> (Ching) Ching	0/2
<i>Pseudophegopteris pyrrhorachis</i> (Kze.) Ching	0/2
<i>P. yunkweiensis</i> (Ching) Ching	0/2
Aspleniaceae	
* <i>Asplenium cheilosorum</i> Kze. ex Mett.	1/0
<i>A. excisum</i> Presl.	0/3
<i>A. finlaysonianum</i> Hook.	0/2
<i>A. fuscipes</i> Bak.	0/2
<i>A. griffithianum</i> Hook.	0/2
<i>A. lushanense</i> C. Chr.	1/1
<i>A. normale</i> Don.	0/2
<i>A. pekinense</i> Hance	0/4
<i>A. praemosum</i> Sw.	0/3
<i>A. prolongatum</i> Hook.	0/3
* <i>A. tenuicaule</i> Hay.	0/1
<i>A. unilaterale</i> Lam.	0/2
<i>A. varians</i> Wall. ex Hook et Grev.	0/3
<i>A. wrightioides</i> Christ	0/2
<i>A. yunnanense</i> Franch	0/3
* <i>Neottopteris antrophyoides</i> (Christ.) Ching	0/1
* <i>N. simonsiana</i> (Hook.) J. Sm.	0/1
Blechnaceae	
<i>Blechnum orientale</i> L.	1/1
* <i>Brainea insignis</i> (Hook.) J. Sm.	0/1
<i>Woodwardia japonica</i> (L.f.) Sm.	2/0
* <i>W. unigemmata</i> (Makino) Nakai.	0/1
Peranemaceae	
<i>Acrophorus stipellatus</i> Moore	0/2
<i>Diacalpe christensenae</i> Ching	0/2
Dryopteridaceae	
<i>Acrorumohra diffracta</i> (Bak.) H. Ito	2/0
<i>Arachniodes globisora</i> (Hayata) Chin	2/0
<i>A. sporadosora</i> (Tagawa) Ching	0/2
<i>Cyrtomium caryotideum</i> (Wall. ex Hook et Grev.) Presl.	1/2
<i>f. caryotideum</i>	
<i>C. fortunei</i> J. Sm.	0/2
<i>Dryopteris basisora</i> Christ	0/2
<i>D. caroli-hopei</i> Fraser-Jenkins	0/2
<i>D. chrysocoma</i> (Christ) C. Chr.	0/3
<i>D. cochleata</i> (Don.) C. Chr.	0/2
<i>D. fructuosa</i> Christ	3/0
<i>D. lepidopoda</i> Hay.	0/3
* <i>D. marginata</i> (Wall. ex Clarke) Christ	1/0
<i>D. odontoloma</i> (Moore) C. Chr.	0/3
<i>D. sparsa</i> (Don.) Ktze.	2/0
<i>D. stenolepis</i> (Bak.) C. Chr.	0/2
<i>D. sublacera</i> Christ	1/1
<i>Polystichum alteruatum</i> Ching	0/2
* <i>P. chingae</i> Ching	0/1
<i>P. dielsii</i> Christ	0/2
<i>P. eximium</i> (Mett. ex Kuhn) C. Chr.	0/2
<i>P. jizhushanense</i> Ching	1/1
<i>P. pycnopterum</i> (Christ) Ching	0/2
<i>P. tsus-simense</i> (Hook.) J. Sm.	1/2
<i>Nothoperanema hendersonii</i> (Bedd.) Ching	0/2
Aspidiaceae	
* <i>Ctenitis membranifolia</i> Ching et C.H. Wang	0/1
<i>Ctenitopsis devexa</i> (Kze.) Ching et C. H. Wang	0/2
<i>C. glabra</i> Ching et C. H. Wang	0/3
<i>C. sagenioides</i> (Mett.) Ching	0/3
<i>C. setulaosa</i> (Bak.) C. Chr. et Tardieu	0/2
<i>C. subsageriacea</i> (Christ) Ching	0/2
<i>Pleocnemia winitei</i> Holtt.	0/5

**Table 1** Continued

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

**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)

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.

**Acknowledgements** This research was supported by the Key Laboratory for microbial Resources of Ministry of Education, P.R. China. The author thanks Professor Chu Weiming, Mr. Zhang Guangfei, He Zhaorong and Su Wenhua (The Institute of Geobotany and Ecology, Yunnan University) for help in sample collection, and thanks Professor Chu in particular for identifying the pteridophyte specimens. This research was supported financially by the Natural Science Foundation of Yunnan Province (98C003G; 1999C0008M).

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