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蕨类植物的 VA 菌根与蕨类植物系统演化关系的研究*

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摘要：通过对云南热带、亚热带生长的 256 种蕨类植物 VA 菌根的调查，发现蕨类植物 VA 菌根营养者所占的比例低于被子植物；在真蕨类植物中，植物具有由 VA 菌根营养经兼性 VA 菌根营养向自养方向进化的趋势。

关键词：蕨类植物，VA 菌根，系统进化
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Study on the Relationships between Vesicular Arbuscular Mycorrhiza and the Systematic Evolution of Pteridophyte

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Abstract: The mycorrhizal states of 256 species of pteridophytes which are naturally distributed in the tropical and subtropical areas of Yunnan (Southwest China) were surveyed. It was found that the percentage of vesicular arbuscular mycotrophic associated with pteridophytes are lower than the angiosperms. The evolutionary trend of filicineae may be from mycotrophism to facultative mycotrophism, and at last to autotrophism.

Key words: Pteridophyte; Vesicular arbuscular mycorrhiza; Systematic evolution

Pirozynski and Marlloch (1975) proposed a hypothesis of land plant mycotrophism origin. They suggested that only when an association formed between an ancient semi－aquatic alga and an aquatic fungus, could a plant colonize and evolve on land. This hypothesis was surpported by the facts that: 1) Mycorrhiza was a popular phenomenon in rhizomes fossils of the earliest land plants (Remy *et al*, 1994; Hass *et al*, 1994; Knoll, 1992); 2) The origin time of vascular plants was concordant with the vesicular arbuscular mycorrhizal fungi which was estimated based on nucleotide sequence divergence of 18S rDNA (Simon *et al*, 1992, 1993); 3) up to 80% of all terrestrial angiosperms were mycorrhized today, and the more ancient taxa, the higher mycorrhized (Trappe, 1987). Vesicular arbuscular mycorrhiza (VAM) or arbuscular mycorrhiza (AM) is the symbiotic association of Glomales fungi and plants. This symbiotic association takes an important role in plant mineral and water nutrition, it even could influence the biodiversity and the stability of the ecosystem (Hayman, 1982; van der Heijden et al, 1998). A lot of research has been reported on the VAM of trees, crops, fruit trees

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and horticultural plants. Research on the VAM of pteridophytes is very limited (Cooper, 1976; Berch *et al*, 1982; Gemma *et al*, 1992).

Pteridophyte has an ancient origin and special life cycle; It takes a very important position in the origin and systematic evolution of vascular plants. VAM formed by pteridophytes and vesicular arbuscular mycorrhizal fungi (VAMF, or arbuscular mycorrhizal fungi, AMF) has been found generally in the rhizomes fossils of *Rhynie* and *Asteroxylon* which were prosperous in the Devonian to Carboniferous Period in the Paleozoic Era, and this VAM was considered to be the earliest VAM (Remy *et al*, 1994; Hass *et al*, 1994). Processing the evolutionary course of 3 to 4 hundreds of millions years, the extant pteridophytes' mycorrhizal states, the role and the evolutionary trend of VAM in the systematic evolution of pteridophytes are still not clear. In this research work, the VAM states of 256 pteridophytes species in Yunnan were surveyed, and the VAMF which were associated with the pteridophytes were also isolated and identified (Zhao, 1998). The evolutionary trend of VAM in the systematic evolution of pteridophytes was formulated.

Materials and method

The roots of pteridophytes were collected in different habitats from tropical and subtropical areas of Yunnan. The fresh roots were cut into 1 ~ 3 cm and fixed in 1/2 FAA (formalin 5 mL, acetic acid 5 mL, 70% alcohol 90 mL, diluted two times when used). The samples were processed according to the method of Berch and Kendrick (1982), recorded the mycorrhizal states of the roots samples under the compound microscope. More than fifty of each 0.5 ~ 1 mm root sections were examined from each species, and if only one section was qualified with arbuscular, then the plant was considered as a mycorrhized species. In addition, if one species was mycorrhized in one ecological habitat, but not mycorrhized in another place, this species was registered as a facultative mycotrophic one; and if a species was found to be mycorrhized in more than two places, then this species was considered to be a mycotrophic plant, otherwise, the species was an autotrophic one.

Table 1 VA mycorrhizal states of sporophytes in different taxa of pteridophytes

Plant group	SN	MT	FM	AT
Fernallies	20	0 (0a)	9 (45)	11 (55)
Eusporangiates	12	11 (92)	1 (8)	0 (0)
Leptosporangiates	224	32 (15)	31 (14)	161 (71)
Total	256	43 (17)	41 (16)	172 (67)

Notes: SN = Species number surveyed; MT = Mycotrophic;
FM = Facultative mycotrophic;
AT = Autotrophic; a = percentage of each groups in the SN.

Results

VA mycorrhizal states of sporophytes in different taxa of pteridophytes

Of the 256 surveyed pteridophytes species, 20 species were fern allies, 12 species were eusporangiates and 224 were leptosporangiates. The VA mycotrophic, facultative VA mycotrophic and autotrophic species and their percentages in each of the three taxa were counted up in Table 1.

VA mycorrhizal states of pteridophytes in different evolutionary stages

In the extant pteridophytes, the species numbers, the amount and the distribution patterns of the filicineae (Eusporangiates and Leptosporangiates) are beyond compare with fern allies. Compared with the comparative anatomy of filicineae with the geological records (fossils) of pteridophytes, Bower (1959) found that the ferns with simultaneous formation and maturation of the sporangia in the sorus were those present mainly in the Palaeozoic Period, these ferns were called Simplices. The dominant ferns in the Mesozoic Period, in addition to the Simplices, included a large proportion of those with basipetal sequence of sporangia (the maturation of the sporangia in the sorus has a sequence, the sporangia mature from the center to the base of sorus gradually), this group was called as Gradatae; the development of sporangia in more recent ferns were mixed type, that is to say the formation and maturation of sporangia in the sorus were neither simultaneous nor gradual, but mixed from the center to the base of the sorus, these recent ferns were called as Mixtae. To settle the families listed in Ching's 'The Chinese fern families and genera: systematic arrangement and historical origin' (1978). The ferns from Helminthostachyaceae to Lygodiaceae could be placed in the Simplices, from Hymenophyllaceae to Hypolepidaceae could be placed in the Gradatae, and the families behind Pteridiaceae should be placed in the Mixtae. Taking the Simplices, Gradatae and Mixtae as three evolutionary stages in the vertical evolution process of the filicineae, the statistical data of the mycorrhizal states of the pteridophytes surveyed in this research were given in Table 2.

Table 2 The mycorrhizal states of ferns in different evolutionary stages

Groups	SN	MT	FM	AT
Simplices	23	12 (52a)	3 (13)	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)

Notes: SN = Species number surveyed; MT = Mycotrophic;
FM = Facultative mycotrophic;
AT = Autotrophic; a = percentage of each group in SN.

Discussion

The percentage of VA mycotrophic plants in the pteridophytes was relatively lower (just 17%, table 1) compared with angiosperms in which the VA mycotrophic plants was about 50% (Trappe, 1987). It was also found in table 1 that there were VA facultative mycotrophic and autotrophic types, but no VA mycotrophic type in the sporophytes of fern allies, and the percentages of the former two types in the fern allies were very close. In the filicineae, eusporangiates were heavily mycorrhized, 92% plants were VA mycotrophic, and there was no autotrophic type in the eusporangiates. However, 71% of the leptosporangiates were autotrophic. From the VA mycotrophism standpoint of view, there was probably no evolutionary trend between facultative and autotrophic types in the fern allies but, in the filicineae, there is a tendency for plants to have evolved from VA mycotrophism (eusporangiates) to autotrophism (leptosporangiates). This evolutionary trend was especially obvious when considering the VA mycotrophic states in the different evolutionary stages of pteridophytes.

In the three different evolved groups (see Table 2), the dependency of ferns on the VA mycotrophism was more and more less from Simplices to Mixtae, the mycotrophic plants were 52%, 36%

and 12% in the Simplices, Gradatse and Mixtae respectively, but the autotrophic percentage increased gradually in these three groups (it was 35%, 56% and 74% respectively). That is to say that mycotrophism decreased and autotrophism increased gradually in the Simplices, Gradatae and Mixtae. Facultative VA mycotrophism as an interim type varied little in the three groups. This evolutionary process of filiniceae from mycotrophism through facultative to autotrophism was certainly a strong argument for the hypothesis of the mycotrophism origin of land plants, and this evolutionary regularity also could be used in the phylogenetic study of plants (Trappe, 1987; Gemma *et al*, 1992). In addtion, this evolutionary trend could be easily used to explaine the fact that the mycotrophic percentage of pteridophytes was lower than that of angiosperms. Therefore, the origin of the pteridophytes was far earlier than that of angiosperms, that is to say the evolutionary history of pteridophytes was longer than that of the angiosperms, and the pteridophytes were evolved along the trend from mycotrophism to auotrophism. So the percentage of VA mycotrophic plants in pteridophytes certainly should be lower than that of angiosperms.

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