The Phylogenetic Significance of Sciadonic (all-*cis* 5,11,14-20:3) Acid in Gymnosperms and Its Quantitative Significance in Land Plants

Sir:

Recent systematic investigations of the fatty acid compositions of seeds from Coniferophytes [this term is used here in the sense suggested by C.N. Page (1) to include *Ginkgo biloba*, the taxads, and the traditional conifers] that encompassed approximately 170 species (almost one-fourth of extant species) have shown that Δ5-unsaturated polymethylene-interrupted fatty acids (Δ5-UPIFA) are the rule in this plant subdivision. These fatty acids have been characterized in all families studied (2–11; Table 1), except in Phyllocladaceae, which do not seem to have been investigated as regards their seed lipid constituents. Among Δ5-UPIFA, sciadonic (all-*cis* 5,11,14-20:3) acid consistently occurs in all seeds analyzed (Table 1). This acid also has been repeatedly detected in the leaf lipids of all Coniferophyte families studied (12). It also is present in wood extracts, although in this case, the number of Coniferophyte species has been as yet limited to a few Pinaceae species (13,14). On the other hand, the presence of other Δ5-UPIFA, such as taxoleic (5,9-18:2), ephedrenic (5,11-18:2), pinolenic (5,9,12-18:3) or juniperonic (5,11,14,17-20:4) acids, is species- and apparently tissue-dependent (2–4,8,12–14). The presence of sciadonic acid in the seed (and probably the leaf and wood) lipids of all Coniferophyte families is thus a common biochemical feature that unites them all, supporting their monophyly. However, this observation in no way excludes the possibility of finding aberrant genera or species in new studies.

TABLE 1
Distribution of Sciadonic Acid in Gymnosperm Seed Lipids According to Their Subdivisions, Classes, and Families[a]

Subdivision	Class	Family	5,11,14-20:3[b]
Coniferophytes	Pinatae	Taxaceae	+
		Cephalotaxaceae	+
		Podocarpaceae	+
		Phyllocladaceae	?
		Araucariaceae	+
		Sciadopityaceae	+
		Cupressaceae	+
		Taxodiaceae	+
		Pinaceae	+
	Ginkgoatae	Ginkgoaceae	+
Cycadophytes	Gnetatae	Ephedraceae	+
		Welwitschiaceae	–
		Gnetaceae	–
	Cycadatae	Cycadaceae	+
		Zamiaceae	–
		Boweniaceae	?
		Stangeriaceae	?

[a]For the sake of clarity, orders are not presented. Sciadonic acid (all-*cis* 5,11,14-20:3) is always accompanied by some other Δ5-UPIFA.
[b]A plus sign denotes the presence of sciadonic acid, a minus sign denotes absence, and a question mark indicates that no species of the family have been analyzed. When sciadonic acid, and more generally, Δ5-UPIFA, are absent, cyclopropene (malvalic and sterculic) acids have been characterized.

Too few species among Cycadophytes have been analyzed to draw any conclusion for that subdivision. However, it is obvious that the Gnetatae class is heterogeneous, with *Ephedra* spp. (Ephedraceae) seeds containing fairly large amounts of Δ5-UPIFA including sciadonic acid (10) and *Welwitschia mirabilis* (Welwitschiaceae) (15) and *Gnetum* spp. (Gnetaceae) (16,17) seeds containing no such acids. In lieu of Δ5-UPIFA, the two latter families contain cyclopropene and sometimes cyclopropane fatty acids. However, the taxonomic rank of Gnetatae is still a matter of debate, as indicated by their alternative names indicating various taxonomic ranks, "chlamydosperms," "antophytes," and "gnetophytopsides." Cycadatae are even less well known than Gnetatae, as only two species have been described, *Cycas revoluta* (Cycadaceae) (2) and *Macrozamia communis* (Zamiaceae) (18). The seeds from the former species contain Δ5-UPIFA, whereas those from the latter are devoid of such acids, but contain cyclopropene acids. These partial observations, however, emphasize the lack of commonality in seed fatty acid compositions among Cycadophyte families, which otherwise occur in Coniferophyte families, united by the presence of sciadonic acid. However, the fact that some Cycadophyte families contain Δ5-UPIFA, including sciadonic acid, would be in favor of a strong link of these families with Coniferophytes.

We also wish to comment on the quantitative significance of sciadonic acid in lipids from land plants. Conifers are the most prominent components of the extant flora, and in the Northern Hemisphere, it is considered that one tree out of two is a conifer, and hence a gymnosperm. These plants, among some of the tallest (up to 100 m) and largest (diameter of up

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to 16 m) living organisms, thus represent a considerable biomass of land plants, far larger than mosses (bryophytes) and ferns (pteridophytes), which also are able to synthesize C_{20} Δ5-acids, but of the methylene-interrupted type (i.e., arachidonic and eicosapentaenoic acids) (19). In contrast, with the exception of a handful of species (20), angiosperms have apparently lost the capability to introduce supplementary Δ5-desaturation in unsaturated fatty acids, in particular in C_{20} acids, and contribute minimally to C_{20} Δ5-acids in the land plant biomass.

This leads to the apparent paradox that sciadonic acid, possibly along with juniperonic acid [another important C_{20} Δ5-UPIFA in conifer leaves (12)], whose 5,11-dienoic arrangement was formerly considered unusual (21), would be the most abundant and common C_{20} Δ5-unsaturated fatty acids in land plant biomass, at least in the Northern Hemisphere. The most intriguing aspect of this observation is that the abundance of such acids (but possibly not their prevalence) has likely lasted for over 250 million years, since the appearance of the earliest gymnosperms or progymnosperms during the Carboniferous period (22,23). The occurrence of C_{20} Δ5-UPIFA in higher plants may even have started earlier, as they have been characterized in the distantly-related extant *Equisetum* spp. [e.g., horsetail (19), a fern ally]. Considering the fact that C_{20} Δ5-UPIFA are present in most of the main gymnosperm families, it must be concluded that C_{20} Δ5-UPIFA have accompanied the emergence, radiation, and expansion of gymnosperms.

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