Taxonomic position of Phyllocladus and the classification of Conifers

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THE GENUS *Phyllocladus* Louis Claude Marie Richard occupies an equivocal position in the conifers. The opportunity to collect and study material of the hitherto little known species, *Phyllocladus hypophyllus* Hook. f., suggested a review of the perennial taxonomic problem surrounding this genus in the light of new information. The object of this paper is to re-assess the taxonomic position of *Phyllocladus* among the higher categories in the conifers.

The apparently conflicting morphological features of Phyllocladus lead to quite diverse taxonomic treatment of the genus, depending on the relative weight assigned to these features. For example, the leafy microsporophyll bearing two microsporangia at the base and the winged microspores resemble those of Podocarpus and allied genera; the erect ovules and the peculiar arillus structure appears to be similar to those of Taxus and allied genera. For this reason, there are two different ways of classifying this genus. The first is to consider Phyllocladus as representing a third taxon intermediate between Podocarpus and allies and Taxus and allies. The second is to regard Phyllocladus as a part of the taxon in which Podocarpus and its allies are included. There is also involved the question of the family concept of the Taxaceae. In a broad sense, Taxaceae contain both Podocarpus and its allies as well as Taxus and its allies; the former constitute the tribe Podocarpineae, and the latter, Taxineae. In a narrow sense, Taxaceae include Taxus and allied genera only, whereas Podocarpus and allied genera form a separate family, Podocarpaceae.

Thus far, four different ways of classifying the genus *Phyllocladus* have been proposed. These are as follows:—

A. Strasburger (1872); Kildahl (1908A)

Taxaceae (sensu lato)

- a. Podocarpineae (including Phyllocladus)
- b. Taxineae
- B. Pilger (1903)

Taxaceae (sensu lato)

- a. Podocarpineae
- b. Phyllocladineae (Phyllocladus)
- c. Taxineae

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- I. Podocarpaceae
 - a. Pherosphaeroideae (Pherosphaera)
 - b. Phyllocladoideae (Phyllocladus)
 - c. Podocarpoideae
- II. Taxaceae (sensu stricto)
- D. Core (1955)
 - I. Podocarpaceae
 - II. Phyllocladaceae (Phyllocladus)
 - III. Taxaceae (sensu stricto)

Superficially, the genus *Phyllocladus* is somewhat intermediate between *Podocarpus* and allied genera and *Taxus* and allied genera. However, the extensive morphological studies of Robertson (1906), Kildahl (1908), Young (1910) and Sinnott (1913), lead each of these authors independently to the same conclusion, namely, that *Phyllocladus* has far stronger affinities with *Podocarpus* and its allies than with *Taxus* and its allies. A summary of the important morphological characters of *Phyllocladus*, including the work of the previous authors, may be enumerated as follows. Resemblances to *Podocarpus* and allies and to *Taxus* and allies are marked with "P" and "T" respectively.

- 1. The microsporophyll bears two abaxial sporangia at the base (P).
- 2. The microspores have two air-filled wings (P).
- 3. The prothallial cells are present in the mature pollen grain (P).
- 4. The ovule is erect (T).
- 5. The arillus originates at the base of the ovule (T).
- 6. The megaspore membrane is strongly developed and spongy tissue is conspicuous (P).

Thus on morphological grounds, it appears reasonable to include *Phyllocladus* in that taxon which comprises *Podocarpus* and allies rather than with *Taxus* and allies. Nor does it seem reasonable to establish a distinct higher taxon for this genus alone.

A major controversy at the present time revolves around the grouping into higher taxa of the families of conifers. The seven commonly recognized families are: Taxaceae, Podocarpaceae, Araucariaceae, Cephalotaxaceae, Pinaceae, Taxodiaceae and Cupressaceae as originally proposed by Pilger (1926). Chamberlain (1934, p. 434), Janchen (1949) and others, on the one hand, suggest that the Taxaceae, Podocarpaceae and Cephalotaxaceae should be segregated from the manifestly cone-bearing families such as Araucariaceae, Pinaceae, Taxodiaceae and Cupressaceae. The former group is referred as Taxares or Taxales, and the latter, as Pinares (Chamberlain 1934) or Pinales (Janchen 1949). On

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the other hand, Florin (in Erdtman 1952), Pilger & Melchior (in Melchior & Wedermann 1954) and others emphasize that the ovule structure of Taxaceae is very different from that of the rest of the six families. The ovule in Taxaceae, according to Florin (1951, p. 376, f. 65), is always a direct continuation of "flower" axis, while in the other conifers (and Cordaitales), it is essentially terminal on more or less stalk-like lateral appendages of the "flower" axis. Therefore, according to Pilger & Melchior, the Taxaceae alone should be raised to the rank of an independent class, Taxopsida, co-ordinate with Coniferopsida. The latter comprises two orders, Cordaitales (fossil only) and Coniferales, with a number of families including Podocarpaceae.

Certainly some of the characteristics of the ovule of *Phyllocladus*, such as the presence of the arillus, its erect position, and the completely disappearance of the "sterile part of the flower" (Florin 1951, p. 364) are at least superficially similar to those of Taxaceae, although the true homologies are uncertain. Nevertheless, the development of one of the few laterally attached ovules—each representing a "female flower", according to the interpretation of Florin —in a female strobilus into a young seed which eventually assumes a pseudo-terminal position in *Phyllocladus hypophyllus* (Keng 1962 *f. 12 & f. 14*) is probably significant. It may possibly suggest a similar evolutionary trend from the unknown paleozoic gymnosperms to mesozoic *Taxus jurassica* and *Palaeotaxus rediviva* (cf. Florin 1951, p. 349, *f. 43a*) and to the Taxaceae of to-day. For this reason, Chamberlain's and Janchen's scheme of classification of conifers is perhaps a better approach to the phylogeny of this group than Florin's and Pilger & Melchior's.

In the light of the present writer's morphological observation on *Phyllocladus hypophyllus*, together with information drawn from the literature, it seems appropriate at the present time to:—

- 1. Retain *Phyllocladus* in the Phyllocladoideae, Podocarpaceae sensu Pilger (1926).
- 2. Assign the Podocarpaceae to the Taxares sensu Chamberlain (1934) or preferably Taxales sensu Janchen (1949).

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