

THE PHYLLOCLADE OF *PHYLLOCLADUS* AND ITS POSSIBLE BEARING ON THE FOLIATE ORGANS OF CONIFEROPHYTES

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(Received August 11, 1978; Accepted September 16, 1978)

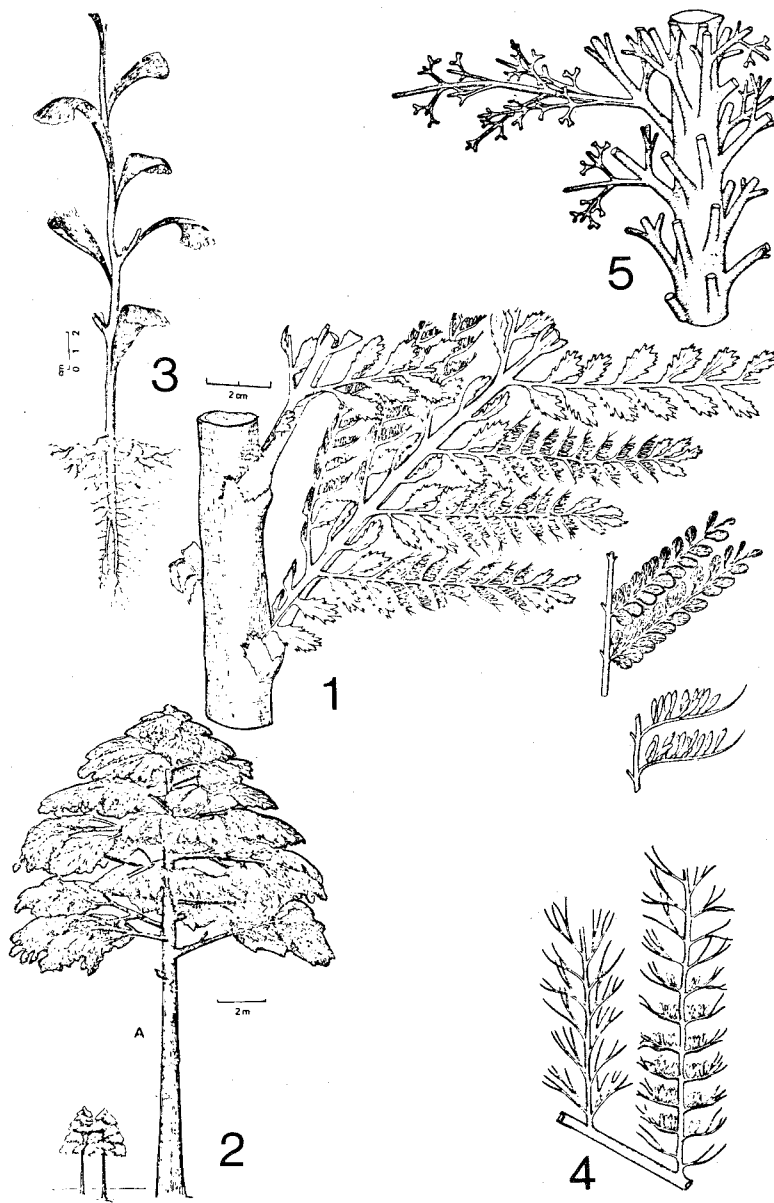
Abstract

The possible neotenic origin of the foliate organs of Coniferophytes is discussed. It is suggested that the simple foliate leaves of Coniferophytes have probably evolved convergently.

Introduction

Archaeopteris Dawson 1871 and *Callixylon* Zalessky 1911 are two widespread and well-known Devonian organ genera. Prior to 1960, these two organ genera were generally regarded as totally unrelated. *Archaeopteris*, according to some authors, represented either one of the earliest ferns or the ancestor of true ferns. *Callixylon* was treated as an early member of the gymnosperms and often classified under the Cordaitales because of its primary and secondary xylem structures, although no seeds have ever been found attached to its axis. Their systematic positions were changed abruptly by Beck's (1960) report of finding a frond of *Archaeopteris* attached to a stem which possessed distinct anatomical characteristics of *Callixylon* (Figs. 1 and 2). The organic connection of these two genera was thus securely established, with the older name *Archaeopteris* being retained. Its arborescent habit, megasporophyllous leaves, secondary growth, circular bordered pits, ray tracheids, collateral vascular bundles and heterosporous reproduction suggest that this plant possibly represents a link between the primitive Early and Middle Devonian psilophytes and the primitive Carboniferous gymnosperms. As a result, a new class, Progymnospermopsida, commonly known as progymnosperms, was created to accommodate *Archaeopteris* and allied genera which originally included *Aneurophyton*, *Eospermatopteris*, *Tetraxylopteris* (Fig. 5), *Protopitys* and *Pitys*. Extensive accounts of this new taxon have been prepared by Banks (1968), Bonamo (1975), Beck (1976) and others.

Beck (1966) postulated that the cycadophytic and coniferophytic gymnosperms might have evolved from two different branches of progymnosperms: the former evolving



Figs. 1–5. Reconstructions of some Devonian fossil plants.

Fig. 1. Portion of a branch of *Archaeopteris* with a fully expanded frond.

Fig. 2. Habit of *Archaeopteris*.

Fig. 3. *Eddya*, a probable sporeling of *Archaeopteris*.

Fig. 4. Two pinnae of *Archaeopteris fissilis* showing the dissected pinnules.

Fig. 5. Portion of the stem of *Tetraxylopteris* with dichotomously ramifying branches or leaves.

(Figures 1–5 after Bierhorst, 1971, originally from Beck 1960, 1967, etc.).

from the clamopityeans, and the latter, from '*Archaeopteris* or some similar genus'. This view has been generally adopted by Banks (1970), Bierhorst (1971) and others. In this paper, only the second point, that is, the probable phylogenetic relationships between progymnosperms and coniferophytes, with special reference to their foliate organs, is discussed.

Varying from one author to another, the coniferophytes are currently treated either as a division, or as a subclass. This taxon generally consists of the following orders: Ginkgoales, Cordaitales and Coniferales (containing Taxales), and sometimes also including Gnetales (e.g. Chamberlain 1935).

These two groups, Archaeopteridales (the most advanced member of the progymnosperms) and Coniferophytes, as Beck (1962) pointed out, are similar in their arborescent habit, secondary growth, circular bordered pits, ray tracheids, collateral vascular bundles and heterosporous reproduction. They also appear in the fossil record in a logical sequence. Their relationships are so intimate that Beck (1971, p. 783) went so far as to say: "The accumulated evidence suggests persuasively that *Archaeopteris* should be either considered, with related progymnosperms, as a separate major taxon, or be included in the Coniferophyta." Yet an obvious question one would raise is that how could a plant like *Archaeopteris* with huge bi-pinnate foliate organs be the ancestor to the coniferophytes which are exclusively simple leaved.

Attempts have been made to answer this question. Meeuse (1963), in a series of sketches (Fig. 6), suggested that the leaves of cordaites and conifers are homologous to the pinnules of *Archaeopteris*, while the simple leaf of *Ginkgo*, is a fusion of several pinnules. A more or less similar view was expressed by Beck (1970) who compares a long shoot of *Metasequoia* (a conifer) with several short shoots with the bi-pinnate frond of *Archaeopteris* (Fig. 7).

Our present knowledge on the foliate organ of *Archaeopteris* has been greatly improved as a result of anatomical studies of fossil materials by Carluccio et al. (1966) and by Beck (1970, 1971). Carluccio et al. (1966) found the so-called rachis and the axes of the so-called pinnae possess the radially symmetrical vascular system of a stem. They concluded that the foliar organ of *Archaeopteris* is not a bi-pinnate frond, but rather a planated lateral branch system. Beck accepted this view and further noted that the entire lateral branch system is subtended by a leaf which he had earlier (Beck 1962) designated as a stipule. Later, he (Beck 1971, p. 394) concluded that "The simple leaf is thought to have evolved in the progymnosperms by planation of an original three-dimensional ultimate branch system."

This intricate configuration of the lateral branch systems of *Archaeopteris* with branches in the axils of leaves of three different orders* reminded the present writer

* In the improved reconstructions of the complete lateral branch systems (or 'frond') of *Archaeopteris* as prepared by Beck (1971, his f. 55) and its fertile lateral branches (or fertile 'pinnae') as prepared by Philips et al. (1972, especially text Figs. 3 & 4), the ultimate branches (or sterile and fertile 'pinnules') appear to have subtended by a foliate structure (of the tertiary degree).

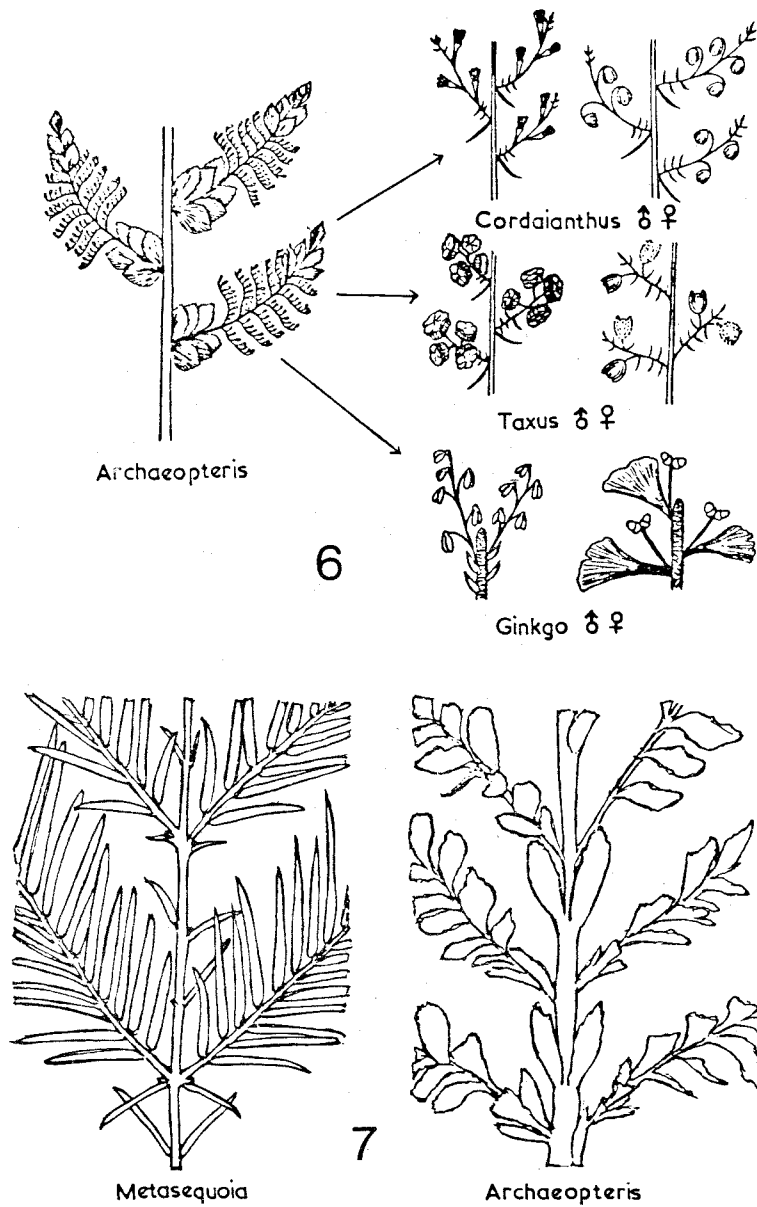


Fig. 6. Sketches showing the evolution of ovulate and pollenate branches of *Cordaianthus* (or *Cordaitanthus*), *Taxus* and *Ginkgo* from a part of the fertile frond of *Archaeopteris*. (After Meeuse, 1963).

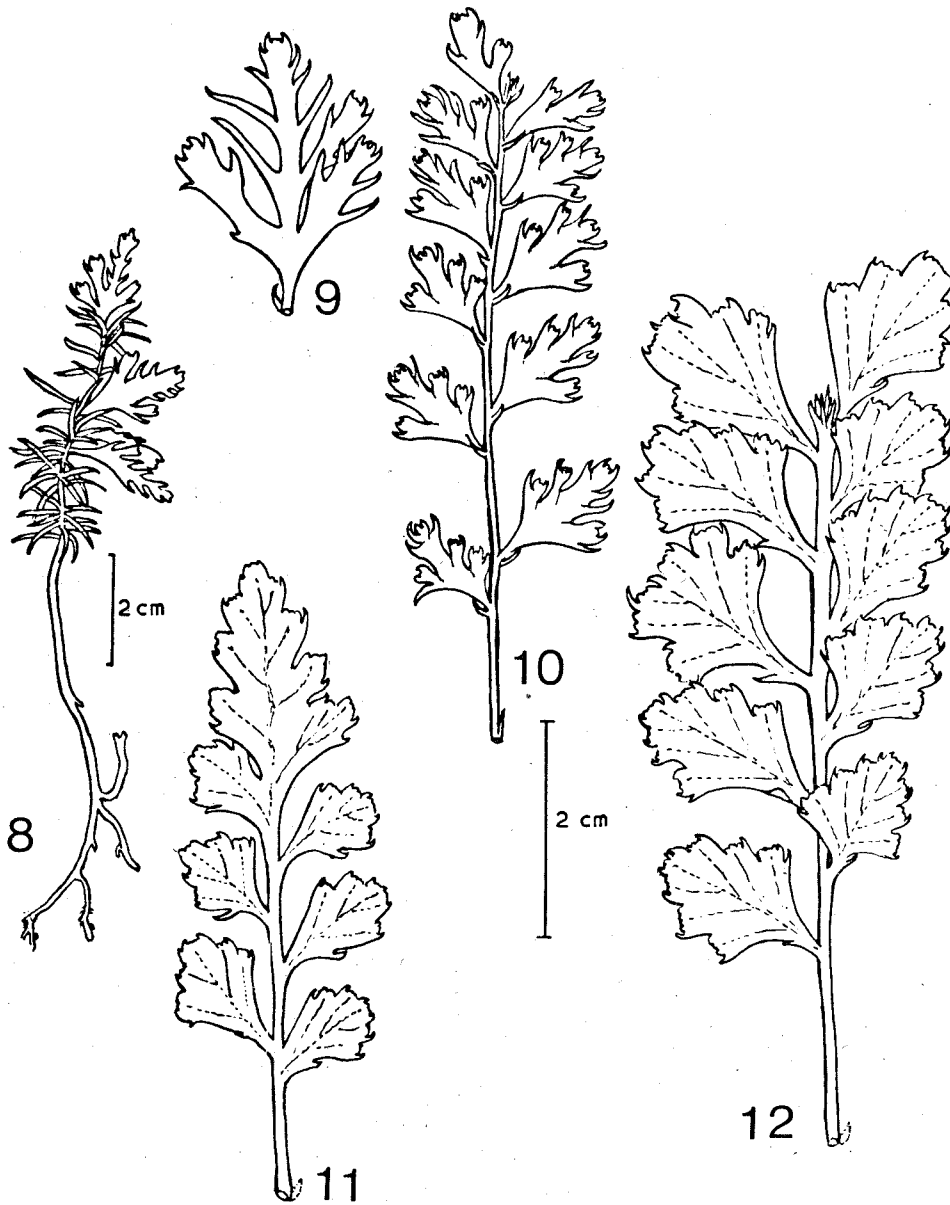
Fig. 7. Comparison between part of a long shoot of *Metasequoia* bearing short shoots with the lateral branch system or frond (in part) of *Archaeopteris*. (After photographs by Beck, 1970).

of his previous study (Keng 1963) on the phylloclades of *Phyllocladus*, a curious coniferous genus with four or five species found only in the Australasian and Malesian regions. Comparison of the lateral branch system of *Archaeopteris* with the pinnate phylloclade of *Phyllocladus* has been made (Keng 1974, 1977), some of the salient points can be further elaborated as follows.

The seedlings of *Phyllocladus*, especially the New Zealand species, *Ph. trichomanoides* D. Don, (Fig. 8) show the following features. From germination, there arises a pair of double-veined cotyledons. The plumule develops into a young shoot which bears a number of spirally arranged one-nerved juvenile leaves less than 1 cm long. In the axils of some of these juvenile leaves, the so-called phylloclades are developed. The earlier formed phylloclades (Fig. 9) are deltoid or rhomboid in outline, with the upper margins cut (*incisus*) or slashed (*laciniatus*); all the incisions are subtended by a single-veined leaf. The later-formed phylloclades on the seedlings (Fig. 10) are pinnate or partly bi-pinnate. They consist of 7–12 segments, sometimes possess a terminal bud. In the mature plant, the phylloclades (Figs. 11 and 12) are always pinnate and can reach a length of 10–12 cm. They consist of 7–10 (–12) segments. Sometimes they possess a large terminal bud, sometimes not. In the latter case, there is a large terminal segment instead which is often deeply lobed and always connected with one of the lateral segments or with both of them. It is particularly noteworthy that the terminal bud on the pinnate phylloclade, upon activation, can produce a whorl of 4–5 (–10) new pinnate phylloclades, and the main axis of the old pinnate phylloclade can thus transform into a true stem. Each segment is rhomboid to deltoid in outline, and is subtended by a leaf. The upper margins of the segments are undulately or shallowly lobed, and each lobation is invariably subtended by a subulate leaf, a large portion of which is embedded in the segment, only the apical portion emerging as a recurved needle.

Based on a collection of 24 Late Devonian specimens from New York, Beck (1967) was able to reconstruct a tiny plant with the aerial part about 20 cm tall which he named as *Eddyia sullivanensis* (Fig. 3). The leaves of this plant are flabelliform and are helically arranged. On the strength of the special feature of the bordered pits in groups on the radial walls of the secondary tracheids, Beck suggested that *Eddyia* could well be the sporeling (young sporophyte) of *Archaeopteris*. In some of the leaves axillary branch-like structures appeared to have existed, but unfortunately are not preserved. In spite of the absence or presence of the cotyledons and the difference in the morphology of the juvenile leaves (needle shaped, single-veined vs. flabelliform, multiple nerved), yet there exists a trifle of resemblance between the plausible sporeling of *Archaeopteris* and the seedling of *Phyllocladus*. It is particularly interesting to note that in both the sporeling and the seedling there is a tendency towards gradual increment of complexity in their foliate organs, i.e., lateral branches vs. phylloclades, until reaching the tertiary degrees in the leaf axils.

It is therefore suggested that the foliate organ of the putative ancestor of *Phyllocladus*, (and possibly of most of the coniferophytes) was probably bi-pinnate



Figs. 8–12. *Phyllocladus trichomanoides* D. Don.

Fig. 8. Seedling, the two cotyledons fallen off.

Fig. 9. An early formed phylloclade on the seedling, simple, but deeply lobed.

Fig. 10. A later formed phylloclade on the seedling, pinnate and partly almost bi-pinnate.

Fig. 11. A phylloclade from the mature plant, pinnate and without a terminal bud.

Fig. 12. A phylloclade from the mature plant, pinnate, but with a terminal bud.
(Figures 8 to 12, drawn from fresh material by Mrs. R.S. Keng).

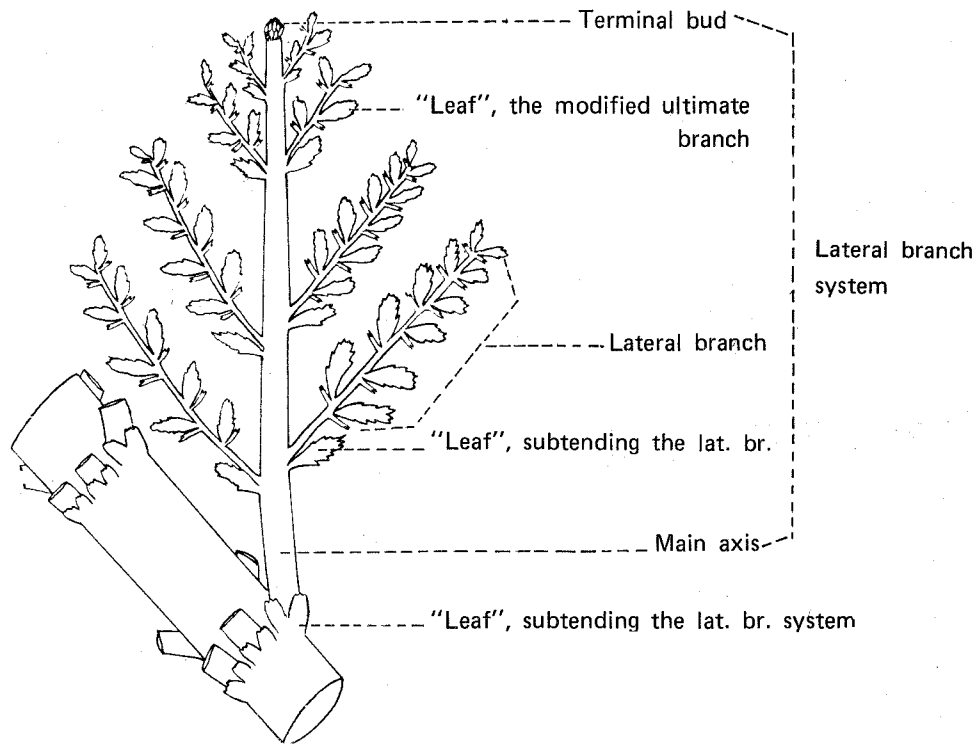


Fig. 13. The foliate organ of the putative ancestor of *Phyllocladus* (cf. Figs 1 and 10).

(Fig. 13). Morphologically it represented a lateral branch system (or 'frond'). It probably consisted of a main axis, a large terminal bud, and several pairs of lateral branches (or 'pinnae') with two rows of ultimate branches (or 'pinnules') along the branch-axes. It is also suggested that the branches of various degrees (namely the whole lateral branch system, the lateral branches and the ultimate branches) were subtended by a foliate structure. And these ultimate branches, like the subtending foliate structures of various degree, were probably originally three-dimensional, then planate and 'webbed', and finally turned into foliate structures which were eventually reduced into single-veined. In this connection, it is probably useful to bear in mind that in the primitive members of the Progymnosperms such as *Aneurophyton*, *Tetraxylopteris* (Fig. 5) etc., the whole plant was armed with protostelic, dichotomous branches which can hardly be rigidly defined either as a stem or a leaf yet probably served the functions of both.

The genus *Phyllocladus*, because of its unique foliate structures, and because of some of its morphological characters being intermediate between the Taxaceae and Podocarpaceae, has been elevated into a family rank (Core 1955, Keng 1973). The living conifers considered to be closely related to this genus are: *Podocarpus*, *Dacrydium* and other members of the Podocarpaceae, *Taxus*, *Amentotaxus* and other members

of the Taxaceae, and *Cephalotaxus* of the Cephalotaxaceae. All these genera, and furthermore, all the other living members of the coniferophytes, possess simple foliage leaves. It is particularly noted that the leaves of adult plants of *Cephalotaxus*, *Taxus*, *Amentotaxus*, *Dacrydium*, and most species of *Podocarpus* (with the exception of Sect. *Nageia*, a section which has recently been raised by de Laubenfels (1969) into a separate genus, *Decussocarpus*) are single-veined, morphologically and anatomically indistinguishable from the juvenile leaves found on their seedlings. One plausible explanation (Keng 1974) is that in a great majority of the coniferophytes their foliage leaves are a retention in the juvenile state, biologically known as neoteny, a subject recently reviewed and re-emphasized by Takhtajan (1972). The double-veined leaves of *Sciadopitys* (Taxodiaceae), as generally recognized, are a fusion of two single-veined leaves (Chamberlain 1935, p. 259). The true nature of the multi-nerved foliage leaves of *Podocarpus* Sect. *Nageia* (Podocarpaceae) *Agathis* (Araucariaceae) (both of the Coniferales) and *Cordaites* (of the Cordaitales), is not clear, but presumably they are formed through the fusion of many single veined leaves. The fanshaped dichotomously branched, multi-veined leaves of *Ginkgo* (of the Ginkgoales) as indicated in fossil records (Andrews 1947), appear to have evolved from the primal dichotomous branch systems by webbing.

Florin (1951), in his study of vegetative structures of the Late Carboniferous and Early Permian conifers, pointed out that there are two basic types of foliate organs among the most primitive conifers, which, for convenience, are generally classified under the family Lebachiaceae. In *Lebachia* and *Ernestiodendron*, their foliate organs are simple, subulate, single-veined leaves, which are rather similar to those of *Araucaria excelsa* R. Br., a living conifer of the Araucariaceae. Whereas in *Buriadia* and *Carpentieria*, their foliate organs are also simple, but dichotomously forked at the tip. In the former genus, they are thrice, twice to once forked, and in the latter, they are always once forked. These seem to be more likely a remnant of the telomic structure than the fusion of the single-veined leaves.

Thus it can be concluded that although the foliate organs of coniferophytes are uniformly simple leaved, their origin and nature might be different from one member to the other.

Literature Cited

- Andrews, H.N. Jr. 1947. Ancient plants and the world they lived in. Comstock, Ithaca. N.Y.
Banks, H.P. 1968. The early history of land plants. pp. 73-107. In E.T. Drake (ed.), Evolution and Environment Yale Univ. Press, New Haven.
Banks, H.P. 1970. Evolution and plants of the past. Wadsworth, Belmont.
Beck, C.B. 1960. Connection between *Archaeopteris* and *Callixylon*. Science **131**: 1524-1525.
Beck, C.B. 1962. Reconstruction of *Archaeopteris* and further consideration of its phylogenetic position. Amer. J. Bot. **49**: 373-382.
Beck, C.B. 1966. On the origin of gymnosperms. Taxon **15**: 337-339.
Beck, C.B. 1967. *Eddyia sullivanensis* Gen et sp. Nov., a plant of gymnospermic morphology from the Upper Devonian of New York. Palaeontographica **121B**: 1-22.
Beck, C.B. 1970. The appearance of gymnospermous structure. Biol. Rev. **43**: 379-400.

- Beck, C.B. 1971. On the anatomy and morphology of lateral branch system of *Archaeopteris*. *Am. J. Bot.* **58**: 758–784.
- Beck, C.B. 1976. Current status of the Progymnospermopsida. *Rev. Palaeobot. Palyn* **21**: 5–23.
- Bierhorst, D.W. 1971. *Morphology of vascular plants*. MacMillan, New York.
- Bonamo, P.M. 1975. The Progymnospermopsida: Building a concept. *Taxon* **24**: 569–579.
- Carluccio, L.W., F.M. Hueber, and H.P. Banks, 1966. *Archaeopteris macilentata*, anatomy and morphology of its frond. *Am. J. Bot.* **53**: 719–730.
- Chamberlain, C.J. 1935. *Gymnosperms, structure and evolution*. Chicago Univ. Press.
- Core, E.L. 1955. *Plant Taxonomy*. Prentice-Hall, Englewood.
- Florin, R. 1951. Evolution in cordaites and conifers. *Acta Hort. Berg.* **15**(11): 285–388.
- Keng, H. 1963. Aspects of morphology of *Phyllocladus hypophyllus*. *Ann. Bot.* **27**: 69–78.
- Keng, H. 1973. On the family Phyllocladaceae. *Taiwania* **18**: 142–145.
- Keng, H. 1974. The phylloclade of *Phyllocladus* and its possible bearing on the branch systems of progymnosperms. *Ann. Bot.* **38**: 757–764.
- Keng, H. 1977. *Phyllocladus* and its bearing on the systematics of conifers. pp. 235–251. In K. Kubitzki (ed.) *Flowering Plants – Evolution and Classification of higher categories* (Plat Syst. Evol. Suppl. 1), Springer-Verlag, Wien & New York.
- Laubenfels, D.J. De (1969). A revision of the Malesian and Pacific Rain Forest Conifers. I. Podocarpaceae, in part. *J. Arnold Arb.* **50**: 274–369.
- Meeuse, A.D.J. 1963. From ovule to ovary: a contribution to the phylogeny of the megasporangium. *Acta Biotheoret.* **16**: 127–182.
- Philips, T.L., Andrews, H.N. and Gensel, P.G. 1972. Two heterosporous species of *Archaeopteris* from the Upper Devonian of West Virginia. *Palaeontographica* **139B**: 47–71.
- Takhtajan, A. 1972. Pattern of ontogenetic alternations in the evolution of higher plants. *Phytomorphology* **22**: 164–171 (publ. 1974).

耿煊爲葉竹柏之葉狀莖及其與松柏類葉片之關係

耿 煊

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現代松柏類之葉形可能係停留在爲想祖先幼苗時期之狀態，未經繼續演發者。又該類植物中各種單葉可能係由不同來源輻合演化而成者。