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The importance of anatomy and whole plant reconstructions in palaeobotany

D. L Dilcher

Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611-2035, USA

The nature of ancient plants can best be understood when whole extinct plants are reconstructed. Fossil plant reconstructions require a detailed knowledge of the anatomy and morphology of the fossils. Careful character analysis is important in the biosystematics of major plant groups. Birbal Sahni demonstrated this when he established a new group of plants based upon *Pentoxylon sahnii.*

Where are the dinosaurs, the pterodactyls, the coelacanths, the titanotheres, the giant sloths and the woolly mammoths of the plant world? If evolution is parallel in plants and animals, then the fossil record should also include extinct major groups as well as long-lived ancient lineages of plants. Fossil plants are too often thought of as ancient examples of living taxa, despite the fact that to do so denies evolution. People often tend to think of fossil plants in terms of living plants with which they are familiar. Perhaps compression fossils of isolated plant organs lack features that allow us to recognize them easily as extinct forms. I suggest in this paper that there is a need for palaeobotanists to reconstruct whole fossil plants, to study details of plant anatomy and morphology, and to search for characters that will allow us to draw clear distinctions between extinct and living plants. Just as the horse had a complex fossil history, and just as the dinosaurs represent an extinct major group of animals, there are similar patterns of complex fossil histories and extinctions of major groups in vascular land plants. And just as animals, such as the coelacanth or the horseshoe crab, exhibit stasis of form through long intervals of time, there are vascular plants that also exhibit similar stasis through geologic time.

Vascular land plants usually fall apart into leaves, stems and reproductive organs before they are deposited and fossilized. The effects of mosaic evolution may render the affinities of such dispersed fossil plant organs difficult to establish. A leaf may resemble one group of plants, the wood another and the reproductive organs a third group when in fact they all came from the same plant. These dispersed organs and their affinities are best understood by a detailed study of the anatomical details of the fossil. A thorough analysis of the anatomy of all fossil plants is not always possible. When plant anatomy is either not preserved or not analysed, information is limited, and it is easy to make mistakes concerning the affinities of individual organs as well as the major taxa to which such isolated plant parts are related.

Sahni[1], Krausel[2] and Harris[3] each demonstrated through their research the importance of plant anatomy in bringing together the scattered organs of extinct plants. They chose to study fossil plants that were structurally preserved, they developed special techniques to make anatomical preparations of fossil plant remains, and they endeavoured to extract the maximum anatomical detail possible from their fossil material. This was done because they realized that the external forms of the various organs of vascular plants (leaves, stems, reproductive organs) often lack critical distinguishing characters. Anatomical similarities of plant tissues from different organs provide important clues for placing the organs of fossil plants together in whole plant reconstuctions[4]. Often plant parts undergo little transport by wind and water prior to deposition and final burial. Thus various organs of a plant may continue to be closely associated after burial or in a few cases still attached to one another. Once the parts of a fossil plant are identified it can be studied as a single organism and compared to both the vast diversity of plants known only as fossils as well as those living today. It is only with such tedious and careful study that we can reconstruct the evolutionary history of plants. This was the style of research that Sahni undertook, promoted and taught.

One of the finest examples of bringing the parts of a plant together is the study of the Pentoxyleae which Sahni[1] presented as a new group of Jurassic age plants from the Rajmahal Hills of India (Figure 1). Sahni was able to assemble remains of the leaves, the stems and the female cones, each known by various form generic names. When the parts are assembled *Pentoxylon sahnii* Sriv. includes a set of characters unknown in any living or fossil group of gymnosperms, but combines characters of various major gymnosperm groups. *Pentoxylon sahnii* has in the past been proposed as ancestral to the angiosperms, but now is thought to share a common clade in angiosperm evolution[5].

Combining separated organs of plant fossils to produce whole plant reconstructions provides new insights into the nature of fossil plants and a better understanding of their evolution. Sometimes the combination of characters reveals a unique and extinct fossil plant with characteristics unknown in any plants living today. We see this in the Mesozoic plant *Pentoxylon*. The anatomy of the leaves, the nature of the female cones, the nature of the woody axis and the more recently described male cones[6] have influenced anatomists/morphologists to be cautious about indicating the relationships of *Pentoxylon*[7].

According to Stewart's[7] account of his investigation of the *Pentoxylon* type material, its affinities to other major groups of plants presents a dilemma. The wood is coniferous but arranged in segments, the leaves and the male pollen organs share cycad and cycadeoid characters, and the female cones are unique among the gymnosperms. Stewart identifies the Pentoxylales as a distinct group among other extinct Mesozoic orders of plants whose relationships are unclear; the Glossopteridales, Czekanowskiales, Caytoniales and Cycadeoidales. These Mesozoic plant groups have been looked at and considered at various times as logical candidates in our search for the origin of the angiosperms[8]. However there is no clear morphological or anatomical evidence which would exclude or selectively include any one of these groups as direct ancestors of the angiosperms.

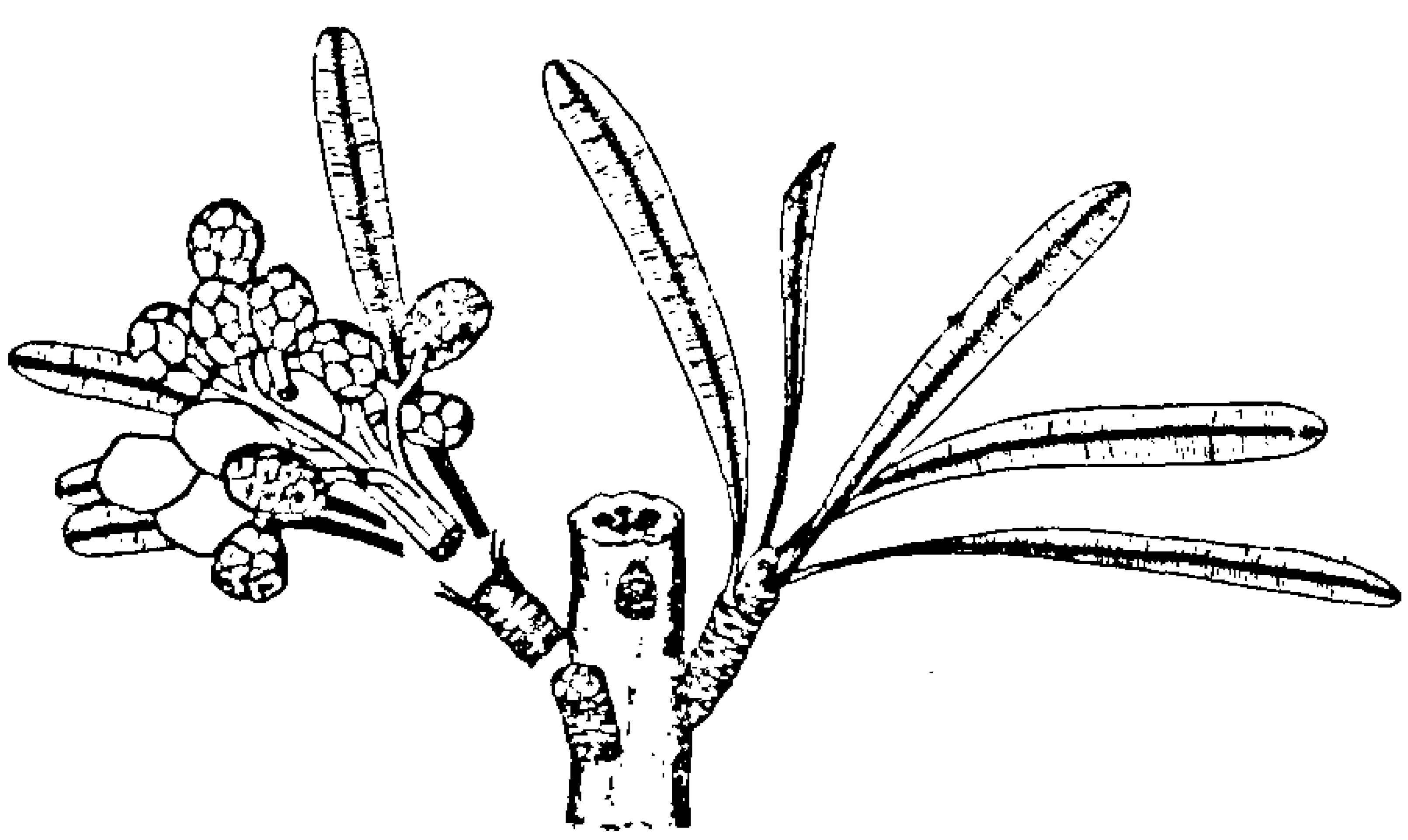

Figure 1. Reconstruction of *Pentoxylon sahnii*, showing stem, leaves and female cones (Sahni 1948).

Pentoxylon may hold many answers yet to be revealed concerning its relationship to extant taxa and other extinct taxa. These answers may be found by following the example of Sahni. We must study fossils as we study living plants, using anatomy and morphology, reassembling the isolated organs of the fossil plants and asking basic questions about the relationships of these unique extinct plants. This will give us a new understanding of plant evolution and will demonstrate how common extinction has been in the plant world.

There have been extinct major groups of plants such as the Palaeozoic Pteridospermales (seed ferns) and the Mesozoic Glossopteridales, Czekanowskiales, Cycadeoidales, Caytoniales and Pentoxylales. These Mesozoic plants lived at the time of the dinosaurs and played a critical role as vital elements in the ecosystems of that era. Certainly we need to recognize these extinct plants as we do their contemporaries, the dinosaurs and the pterodactyls. I would suggest that the evolution of the Palaeozoic seed ferns might be an important land plant radiation equivalent to that seen in the dinosaurs for vertebrate animals. It was a great discovery for Oliver and Scott[9] to realize that a particular type of seed was borne on fern-like leaves and thus establish a new major group of plants, the pteridosperms or seed ferns. Some of these seed ferns (such as *Medullosa*) were large trees with huge leaves, large seeds, complex pollen organs and complicated internal anatomy[7]. The evolution of the conifers, in particular the evolution of the female cone, has sometimes been likened to the progressive changes often illustrated for the evolution of the horse.

The extreme diversification of insects seems to co-occur with the early evolution and radiation of angiosperms. This is probably the result of the coevolution of both major groups of organisms. Many other animal groups have also influenced angiosperm evolution. Angiosperms show a secondary radiation in the early Tertiary, a time of radiation for both mammals and birds. Thus plant and animal evolution appear to be closely tied together[10]. Some mechanisms of evolution may be common to animals and plants for we see stasis in some aquatic animals and some very early aquatic angiosperms. Aquatic angiosperms, such as water lilies, are known from 100-million-year-old sediments and appear to be little changed from those known today. However, until the fossil plants are carefully reconstructed the full extent of their modern relationships cannot be validated.

Another group of flowering plants, the grasses, is

Figure 2. Reconstruction of *Archaenthus* in flower, showing stem, leaves, bud scale, sepals, petals, carpels, with upper left insert showing fruits (Dilcher and Crane 1984).

unknown before the Eocene[11]. Once established, they apparently underwent a rapid radiation and greatly influenced animal evolution[12].

Archaeanthus (Figure 2) is an extinct plant that has been reconstructed from isolated leaves, bud scales, sepals, petals, carpels, fruits and receptacles[13]. All of these organs can be assembled into a flowering axis and a fruiting axis. Each individual organ has similarities to the Magnoliales. This suggests that as early as 100 Ma each of these separate organs had already acquired characters known today in this order of angiosperms.

Reassembling the parts of a fossil plant is an essential process for the palaeobotanist interested in the evolution of plants. This can best be done by using anatomical and morphological data in order to reconstruct the whole plant. This method of research is not new in palaeobotany as we see from the research of Sahni, his teachers and contemporaries. However, until recently it has not been generally applied to the study of angiosperms. Now that characters and character changes are being examined more closely than ever before, by the help of cladistic analysis, the total number of characters available from reconstructed fossil plants is providing important new data that are essential to understanding the evolution of flowering plants.

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