Hydatellaceae

Flowering plants (angiosperms), with about 300,000–400,000 living species, are the largest and most diverse assemblage of land plants on our planet. They include many familiar and economically important plant groups such as the cereal grasses, legumes, and most fruits and vegetables. One of the major goals of systematic botany is to reconstruct the evolutionary history of this diverse lineage. Traditionally, hypotheses of evolutionary relationships have been based largely on morphological traits (for example, flower structure, stem anatomy), but current approaches also consider genetic evidence from one or a combination of the three genomes found in plants (plastid, mitochondrial, and nuclear). This type of work has provided many important insights into flowering plant evolution, and there has been substantial progress in reconstructing the plant tree of life. This knowledge has necessitated the production of a new classification scheme because some families and higher taxa were found not to be natural, and this framework now provides a solid evolutionary basis by which all aspects of comparative flowering plant biology can be focused.

Several major evolutionary lineages are currently recognized among living angiosperms (**Fig. 1**). These include three small lineages that split from the rest of the flowering plants before the major angiosperm radiation; these include the New Caledonian shrub *Amborella trichopoda*, water lilies (Nymphaeales), and woody Austrobaileyales. The other major lines include magnoliids (magnolias, laurels, and their relatives), eudicots (daisies, maples, oaks, poplars, etc.), and monocots (bananas, grasses, orchids, sedges, etc.). The discovery of additional major lineages of flowering plants, particularly among the well-studied lines near the very base of the flowering plant evolutionary tree, has not been expected because most flowering plant families have been sampled in molecular studies. The recent unexpected major realignment of the misunderstood and poorly known family Hydatellaceae, therefore, has taken the botanical world by surprise.

Family description. Hydatellaceae are a small family of minute (mature individuals are only a few centimeters in height; **Fig. 2**), nondescript, aquatic flowering plants that grow and flower in or at the edge of seasonal pools and swamps in Australia, New Zealand, and India. The family includes two genera (*Hydatella* and *Trithuria*, although these generic circumscriptions require careful study) and approximately 10 species characterized by narrow, linear leaves and highly reduced reproductive structures. Reproductive units in Hydatellaceae are unisexual or bisexual, and they include a series of sterile bracts (modified leaves associated with plant reproductive structures) that subtend tight aggregations of stamens (the male reproductive organ) and/or carpels (the female sex organ), each with no associated perianth (petals, sepals, or tepals). Current interpretations suggest that each reproductive unit in Hydatellaceae is a highly reduced inflorescence (a flower cluster segregated from any other flowers on the same plant, together with the stems and bracts associated with it) of simple, unisexual flowers, but it has also been hypothesized that the reproductive units might represent some sort of "prefloral" state that preceded the evolution of "standard" bisexual flowers, or that they might have arisen by reduction of a more classic flower structure, perhaps in response to life in an aquatic habitat.

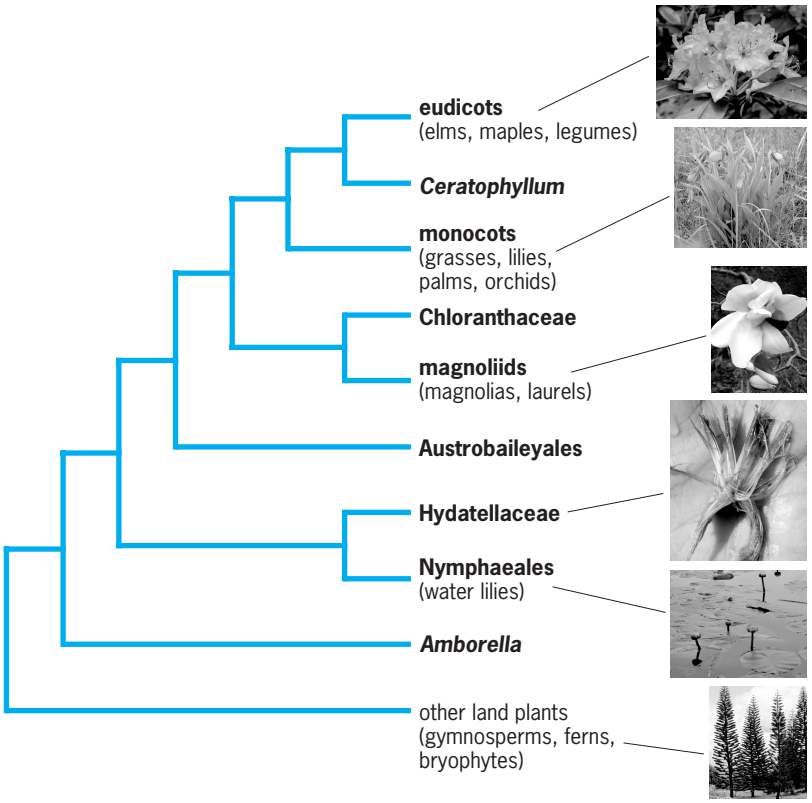

Fig. 1. Evolutionary tree showing the major flowering plant lineages and their relationships. Hydatellaceae and water lilies (Nymphaeales) are each other's closest relatives, and together they form a lineage that diverges near the base of the flowering plant evolutionary tree. (*Photographs by J. M. Saarela*)

Traditional classification. In early plant classifications, *Hydatella* and *Trithuria* were thought to be

Fig. 2. *Hydatella inconspicua* (Hydatellaceae) from Lake Kai Iwi, New Zealand. (*Photograph by Justin Goh, School of Biological Sciences, University of Auckland, New Zealand*)

Fig. 3. A species of water lily (*Nuphar* sp.) that is part of the lineage (Nymphaeales) most closely related to Hydatellaceae. (*Photograph by J. M. Saarela*)

monocots, a large lineage of plants often characterized as having parallel-veined leaves, floral parts in threes (that is, three petals, three sepals), and a single cotyledon (seed leaf). For over a century, these genera were included in the superficially similar monocot family Centrolepidaceae, which is closely related to grasses (Poaceae), sedges (Cyperaceae), and Australian rushes (Restionaceae). Like Hydatellaceae, the approximately 35 species of Centrolepidaceae are also small with linear leaves and highly reduced flowers and inflorescences, and they often co-occur with *Hydatella* and *Trithuria*. The two groups can be difficult to distinguish at normal magnification. In the 1970s, the German botanist U. Hamann published a careful morphological and anatomical study of Centrolepidaceae, and noted several major structural differences between *Hydatella* and *Trithuria* and the rest of the family and even other monocots, including differences in pollen, stomata (microscopic pores in leaves and stems that facilitate gas exchange), seeds, and ovules. Hamann concluded that if *Hydatella* and *Trithuria* are recognized as members of Centrolepidaceae, then that family would not be a natural unit. Consequently, he proposed a new plant family, Hydatellaceae, to accommodate *Hydatella* and *Trithuria*, and expressed hopes that this would emphasize their obscure characteristics and facilitate a search for their true evolutionary affinities. Nonetheless, in subsequent flowering plant classifications, Hydatellaceae continued to be treated as monocots—largely on the basis of their narrow, pointed leaves which resemble those of many grasses, sedges, and rushes—with multiple researchers noting major difficulties in identifying their nearest monocot relatives and calling for insight into their evolutionary affinities from molecular evidence.

DNA evidence. By examination of deoxyribonucleic acid (DNA) sequence data from multiple plastid and nuclear gene regions representing both Hydatellaceae genera, it was demonstrated that Hydatellaceae are not closely related to grasses or even other monocots. Unexpectedly, it was found that Hydatellaceae are in fact the closest living relatives of the aquatic water lily lineage (Nymphaeales) and are therefore part of a lineage that diverged near the base of the angiosperm phylogenetic tree (Fig. 1). The New Caledonian shrub species *Amborella trichopoda* is the only other lineage thought to have diverged from other flowering plants below this point, although the exact divergence order of *Amborella* and the Hydatellaceae-Nymphaeales lineage is not yet firmly established.

Morphological evidence. The surprising new home for Hydatellaceae illuminated by DNA evidence has prompted a careful reevaluation of its morphological characteristics, which previously (and incorrectly) had been used to place the family among monocots. Indeed, the inconspicuous, linear-leaved, and tiny-flowered Hydatellaceae are strikingly different in overall appearance compared to the often large-leaved and attractively flowered water lilies (**Fig. 3**), and it is likely because of this seeming disparity that the two groups had not previously been considered to be closely related. Upon close inspection, however, both lineages share several microstructural features, including several aspects of seed structure, stomata arrangement, pollen shape, and seed germination pattern, all of which provide additional evidence supporting a close relationship between these two lines. Surprisingly, these shared characters include many of those originally used to segregate Hydatellaceae from Centrolepidaceae. Such morphological evidence must be interpreted carefully and with caution as some of the shared characters also occur in other plant groups, including monocots, although they do not occur in consistent association. In cases like this, independent evidence from DNA can provide a new, informative, and relatively unbiased framework for interpreting morphology. This is a good example of the difficulties inherent in using morphological traits alone to uncover evolutionary relationships—it can be difficult to determine whether similar traits were inherited from a common ancestor, evolved independently in unrelated lineages, or were inherited initially but later lost (reversed in subsequent lineages).

Broader evolutionary implications. From a broader point of view, the new position for Hydatellaceae has important implications for understanding the early morphological, molecular, and ecological evolution of flowering plants as a whole. For example, the new placement for Hydatellaceae, with its simple, unisexual flowers, might provide insight into the origins of the "typical" bisexual flowers found in water lilies and many other angiosperms. Moreover, the addition of this branch near the base of the angiosperm phylogenetic tree might aid in clarifying the branching order of *Amborella* and

the Hydatellaceae-Nymphaeales line and determining what the closest living relatives of the flowering plants are. Discovery of Hydatellaceae material in the fossil record could potentially provide new insight into the timing of the origins of the angiosperms.

For background information *see* DEOXYRIBONUCLEIC ACID (DNA); FLOWER; NYMPHAEALES; PLANT EVOLUTION; PLANT KINGDOM; PLANT MORPHOGENESIS; PLANT PHYLOGENY; PLANT TAXONOMY in the McGraw-Hill Encyclopedia of Science & Technology.

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