

BOTANY

New home for tiny aquatics

Else Marie Friis and Peter Crane

A shake-up of current thinking about the evolution of the angiosperms — the flowering plants — is a consequence of the relocation of a hitherto obscure branch on the angiosperm evolutionary tree.

Many new constellations in the angiosperm evolutionary tree have come to light as relationships within the flowering plants have been explored using molecular analyses^{1,2}. Some of these changes were not unexpected. But others have resulted in fundamental reinterpretations of angiosperm evolution^{3,4}.

On page 312 of this issue, Saarela *et al.*⁵ report one of the most striking realignments required so far. They find that the diminutive, moss-like, aquatic plants *Hydatella* and *Trithuria*, which are members of the family Hydatellaceae and were thought to be monocots close to grasses, are actually the closest living relatives of water-lilies and their allies (Fig. 1). This new-found position for the Hydatellaceae, near the point at which water-lilies (order Nymphaeales) diverged from other flowering plants, could scarcely be more attention-grabbing. On the evidence of Saarela and colleagues' analyses⁵, and given other generally accepted relationships at the base of the angiosperm evolutionary tree^{2,3}, only a single angiosperm species, *Amborella trichopoda*, diverged from other flowering plants below this point.

But is this new discovery simply a minor matter of phylogenetic tidying up? After all, the Hydatellaceae are a small family; their position has long been uncertain⁶; and the unexpected is bound to crop up when relationships in a group the size of flowering plants (some 350,000–400,000 extant species) are looked at more carefully.

At one level, as Saarela *et al.*⁵ point out, repositioning of the Hydatellaceae conforms to, rather than overthrows, current ideas of relationships among the extant representatives of early angiosperm lineages. These ideas have come to look increasingly secure, as more genes and more plants have been incorporated into molecular phylogenetic analyses. The Hydatellaceae associate with the Nymphaeales based on the new molecular data, and the relationship seems to be well corroborated. Many of the morphological characteristics of the Hydatellaceae, at least in so far as they are known, also make more sense in the context of the Nymphaeales than in the context of grasses and their relatives. And it is convenient that the

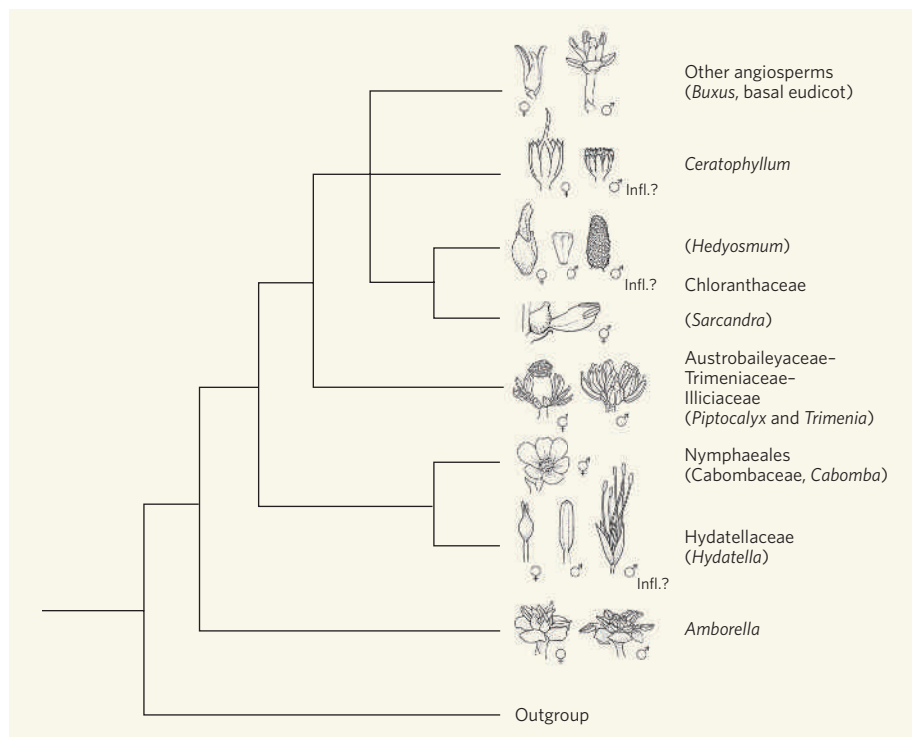


Figure 1 | A new branch near the root of the angiosperm evolutionary tree. *Amborella* remains the sister group to all other flowering plants, but the Hydatellaceae join the Nymphaeales (water-lilies) as the next diverging subsidiary branch of the tree. This new alignment⁵ raises questions about the origin of classic bisexual flowers in the Nymphaeales and other angiosperms. The unisexual flowers of Hydatellaceae — with male and female flowers consisting of a single organ only (stamen and carpel, respectively), aggregated in dense unisexual or bisexual inflorescences — contrast with the solitary, bisexual flowers of the Cabombaceae, represented here by *Cabomba*, which were previously regarded as the basic condition in the Nymphaeales. More generally, simple and often unisexual flowers occur among several early-diverging angiosperm lineages, for example in the Trimeniaceae (*Piptocalyx*, *Trimenia*) and Chloranthaceae (*Sarcandra*, *Hedyosmum*), as well as early-diverging eudicots (*Buxus*). But whether this simplicity reflects the basic phylogenetic condition or ecological adaptation is an open question. Flowers of *Amborella* are also small, and functionally unisexual, but female flowers have staminodes, indicating a basic bisexual organization. In this situation, interpretations of character evolution depend on the position of the root of the phylogenetic tree, and may also be sensitive to the addition of new taxonomic groups. Infl, inflorescence (flower cluster). (Drawings by P. von Knorring.)

Hydatellaceae, as a family of aquatic plants, link to the Nymphaeales rather than to the other, mainly woody, plants that make up the root of the angiosperm evolutionary tree. In this position they do not further complicate ideas about the evolution of life in an aquatic habitat.

For other traits, however, repositioning the Hydatellaceae raises questions that add to an already long list of unresolved issues in early

angiosperm evolution, particularly with regard to features that are perhaps too easily interpreted as 'reduced', 'lost' or 'absent'. At some point it may become more straightforward to infer that some early angiosperms never had certain features, rather than had them and then lost them.

For example, does the seemingly simple floral morphology of the Hydatellaceae reflect



Figure 2 | *Trithuria* — not previously on the radar screen of most specialists.

'reduction', or might it represent an early 'pre-floral' stage of angiosperm evolution in which the classic bisexual flower, with its whorls of three or more different organs, was not yet fully formed? Flowers of the Hydatellaceae — along with those of other early-diverging angiosperm lineages (for example, fossil and living *Hedyosmum*⁷ and other members of the Chloranthaceae) — could hardly be more simple (Fig. 1). It is possible, in the case of the Hydatellaceae, as well as *Ceratophyllum* and perhaps the fossil *Archaeofructus*^{8,9}, that the simple flowers reflect loss of floral parts associated with life in a submerged habitat, as has happened in other aquatic angiosperm lineages. But here, near the base of the angiosperm phylogenetic tree, it is difficult to be sure whether floral simplicity signals ecological adaptation or the basic phylogenetic condition. If it is the latter, it would have profound implications for ideas on the early evolution of the classic angiosperm flower.

It will take some time to digest all the implications of suddenly introducing a new plant family into discussions of early angiosperm evolution. *Hydatella* and *Trithuria* (Fig. 2) have not been on the radar screen of most specialists working on the subject, and there are many pieces of this puzzle still to work out. Certainly, repositioning the Hydatellaceae as the closest living relatives to the Nymphaeales will dramatically influence ideas about the early evolution of water-lilies and their allies, and it will modify important details of character evolution at the base of the angiosperm tree. Whether it will also affect the rooting of the angiosperm tree as a whole, perhaps in ways that would displace *Amborella* to a less prominent position, remains to be seen. Identification of angiosperm precursors in the fossil record would probably have an even greater impact.

It is also relevant that several species of Hydatellaceae have been described only in the past 25 years. It seems likely that more will come to light, and there may also be revelations among the several hundred plant species that are described as new to science every year. Examples such as the Hydatellaceae, and the

Australian conifer genus *Wollemia*¹⁰ discovered a little over a decade ago as a 'living fossil', illustrate the inadequacy of our knowledge of plant diversity at a time when so much is being destroyed or is under serious threat.

Hydatella and *Trithuria* will inevitably be the subject of detailed investigation in the coming years. But whatever the outcomes of these studies, the radical realignment discovered by Saarela *et al.*⁵ should remind us not to become too comfortable with the current picture of early angiosperm relationships, and especially with the details of character evolution that they imply. There will be more surprises as new plants are added to the mix. They will come not just from our gradually improving knowledge of living plants, but more especially from our exploration of the riches of the plant fossil record — both for early angiosperms and for their elusive relatives among other seed plants. ■

Else Marie Friis is in the Department of

Palaeobotany, The Swedish Museum of Natural History, Box 50007, 104 05 Stockholm, Sweden. Peter Crane is in the Department of the Geophysical Sciences, The University of Chicago, Chicago, Illinois 60637, USA. e-mails: elsemarie.friis@nrm.se pccrane@geosci.uchicago.edu

1. Chase, M. W. *et al.* *Ann. Missouri Bot. Gard.* **80**, 528–580 (1993).
2. Soltis, D. E., Soltis, P. S., Endress, P. K. & Chase, M. W. *Phylogeny and Evolution of Angiosperms* (Sinauer, Sunderland, MA, 2005).
3. Qiu, Y.-L. *et al.* *Nature* **402**, 404–407 (1999).
4. Endress, P. K. & Igersheim, A. *Int. J. Plant Sci.* **161**, S211–S223 (2000).
5. Saarela, J. M. *et al.* *Nature* **446**, 312–315 (2007).
6. Dahlgren, R. M. T., Clifford, H. T. & Yeo, P. F. *The Families of the Monocotyledons: Structure, Evolution, and Taxonomy* (Springer, Berlin, 1985).
7. Friis, E. M., Pedersen, K. R. & Crane, P. R. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **232**, 251–293 (2006).
8. Sun, G. *et al.* *Science* **296**, 899–904 (2002).
9. Friis, E. M., Doyle, J. A., Endress, P. K. & Leng, Q. *Trends Plant Sci.* **8**, 369–373 (2003).
10. Jones, W. G. *et al.* *Telopea* **6**, 173–176 (1995).

PHYSICAL CHEMISTRY

The peripatetic proton

James T. Hynes

The way in which protons are transferred between acids and bases has been known in general terms for decades. But the details of the process are complex, and only now is the full proton itinerary becoming clear.

Proton transfer is a headline player in many arenas of chemistry and biology. To name just a few, the process lies at the heart of the chemistry of acids and bases in solution, the workings of enzymes, and transport mechanisms in biological membranes and photosystems^{1,2}. A broad-brush picture of how protons are transferred between acids and bases in aqueous solution was painted in the 1950s and 1960s, in classic work by Eigen³ and Weller⁴. Writing in *Angewandte Chemie International Edition*, Mohammed *et al.*⁵ enlarge that picture and add more detail. They build on earlier, related experiments of their own and those of others to show how modern, ultra-rapid techniques can illuminate the myriad, sometimes indirect, molecular pathways between acid and base that a proton can follow.

An acid is a substance that likes to donate protons; a base is a substance that is inclined to accept them. Mohammed *et al.* used laser excitation to 'trigger' the departure of a proton from the light-sensitive acidic molecule pyranine. This acid can be written ROH, where R is an organic group and OH a hydroxyl group. As a proton is simply a hydrogen atom stripped of its electron, its progress can be tracked by identifying, through spectroscopy, where the 'H' appears in the chemical products of the subsequent reactions.

Using ultra-fast infrared vibrational

spectroscopy as a structural probe, the authors could in their experiments reconstruct the dynamics of the proton's entire voyage — from its departure from ROH, leaving behind the base RO[−], to its ultimate destination, a negatively charged base molecule, denoted B[−]. This base molecule is actually a trichloroacetate anion, [−]OOCCL₃, to which the proton attaches itself to produce a carboxylic acid, or BH in our notation. Different concentrations of the base, from 1 to 3 mol l^{−1}, helped the authors to unravel the exact proton-transfer dynamics.

The authors' first significant finding⁵ is that infrared bands characteristic of absorption by RO[−] are observed on a timescale of less than 150 femtoseconds (1 femtosecond is 10^{−15} s) after the initial laser excitation. These are not, however, immediately accompanied by the appearance of any absorption band corresponding to BH. Indeed, at a B[−] concentration of 2 mol l^{−1}, protonation to form BH is incomplete even after 700 picoseconds — more than 1,000 times longer than it takes for ROH to be deprotonated.

So where is the proton in the meantime? Making intermediate stops at water molecules, say Mohammed and colleagues. They observe a signal indicating the presence of hydronium ions, H₃O⁺, on the same short timescale as the RO[−] absorption band. They argue that this