

The second Linnaean revolution: DNA sequencing and its impact on traditional taxonomy

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Carl Linnaeus (1707–1778), the father of modern taxonomy, would never have conceived of DNA, let alone the impact it would have on the classification system that was named in his honour.

The Linnaean classification system, also called the binomial system of nomenclature, is still in use today. It is a method of classifying living organisms by combining a genus name with a unique species name to identify an organism. For example, the scientific (binomial) name for humans is *Homo sapiens*.

Traditionally, taxonomy was an exercise in classification that used mainly morphological features (size, shape, colour, and many other visible characters) to not only group organisms into genera and species, but also into families, orders, phyla, as well as other intermediate ranks used mainly by taxonomists themselves, such as sections and subgenera, subfamilies, suborders, etc.

Sometimes these morphological features were supplemented by other information such as chromosome

number, but none of the data traditionally collected by taxonomists to help with classification gave much certainty over evolutionary relationships. DNA sequencing has changed all this.

The development of the DNA sequencing technique in the 1980s³ has made it possible to obtain what are termed phylogenetic trees, showing the evolution of organisms going back hundreds of millions of years. Increasing sophistication in DNA sequencing technology and the falling costs of sequencing now make it practical for any taxonomist to produce sequences for a group of organisms, and then to fit these into a larger data set obtainable from GenBank, the international repository for DNA sequences. A phylogenetic tree constructed from DNA sequences will show, with varying degrees of certainty and resolution, the evolutionary relationships of the species sampled.

The impact of this on the taxonomy of organisms in the last 20 years has been considerable. Traditional classifications are now being

examined for their agreement with phylogeny (the evolutionary history of an organism). While in many cases the traditional schemes are in good agreement with DNA-based phylogenies, in other cases they are not.

The problem of paraphyly

One of the challenges for taxonomy now is to translate a phylogeny into a classification. Particularly vexing is the issue of *paraphyly*. The practice of representing evolutionary relationships between species as a tree diagram is relatively new, and has highlighted a problem in traditional classifications. A *monophyletic group* (Fig. 1A) is a 'natural' group or lineage that contains all descendants of a single common ancestor. A *paraphyletic group* (Fig. 1B) is one that contains only some of the descendants, and so a paraphyletic genus contains some but not all species with a particular ancestor⁴. When this situation arises the excluded species are usually transferred to another genus. DNA sequencing shows that such paraphyletic groups are extremely common. At the moment there is a lack of consensus among taxonomists whether classifications should exclude paraphyletic groups.

Hebe and *Veronica*

The most notable example of DNA sequencing results revealing paraphyly in the classification that is relevant to New Zealand involves the world-wide plant genus *Veronica*. DNA sequencing carried out in Europe, Australia and New Zealand show that at present *Veronica* is a paraphyletic genus. The species that

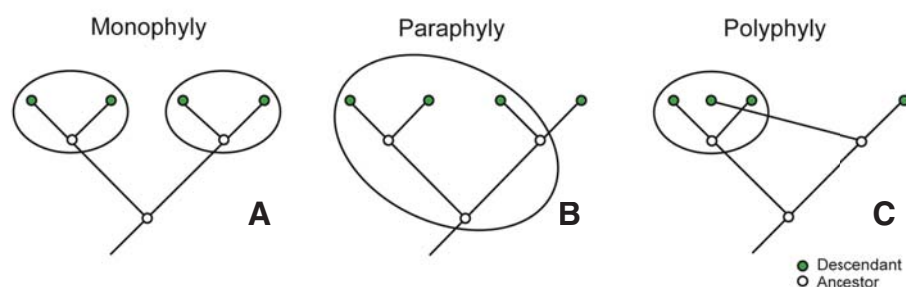


Fig. 1 Monophyly, paraphyly, and polyphyly in phylogenetic trees: **A**, monophyletic groups include *all* the descendants of a particular species. It's complete, and doesn't contain any species that are not descendants of that root ancestor species. A classification system made up only of monophyletic genera is considered to be a desirable aim in taxonomy; **B**, a paraphyletic group is one that is incomplete, i.e., it contains only some of the species that are descendants of the root ancestor species; **C**, a *polyphyletic group* contains some or all of the descendants, but not the common ancestor.

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³ See the previous article by Glenny et al. (pp. 8–9).

⁴ To further complicate matters, a third situation may occur where the group contains some or all of the descendants, but not the common ancestor – this is called polyphyly (Fig. 1C).

are not included in *Veronica* are the 90 or so species in the New Zealand genus *Hebe*.

Many New Zealanders regret the idea that a name in common use like *Hebe* might be dispensed with, but phylogenetic taxonomists like Professor Phil Garnock-Jones at Victoria University believe that classifications need to be aligned with what we now know about evolutionary relationships. Recently, Garnock-Jones and his colleagues published a full set of formal combinations under *Veronica* for the hebes (Garnock-Jones et al., 2007). These formal combinations (species, subspecies, varieties, etc.) mean that the names under *Veronica* are now available for use⁵.

Many taxonomists, in New Zealand as well as overseas, have argued strongly against making the many changes that would result from this realignment process, claiming it would seriously destabilise classification schemes now in place. They argue that stability in names is a valuable attribute of a classification that makes it useful, particularly to non-taxonomists. Such taxonomists are prepared to accept paraphyly in classifications.

In the example above, evolutionary taxonomists argue that it doesn't make sense to nest *Hebe* within *Veronica* and give them both the rank of genus. Two solutions are possible: to combine all species into a single large monophyletic genus, *Veronica*, or to divide *Veronica* into numerous monophyletic genera. Either way, changes to the classification are necessitated by alignment of a classification with phylogeny.

Mike Bayly and Allison Kellow, in their recent book *An illustrated guide to New Zealand Hebes* (Bayly and Kellow, 2006), discussed in detail the pros and cons of adopting *Veronica* as the genus for New Zealand hebes. They argued that it might be best to split *Veronica* into a number of smaller genera, retaining *Hebe* as one of them. They suggested that what are currently subgenera within *Veronica* (Fig. 2) could be regarded as genera alongside *Hebe*.

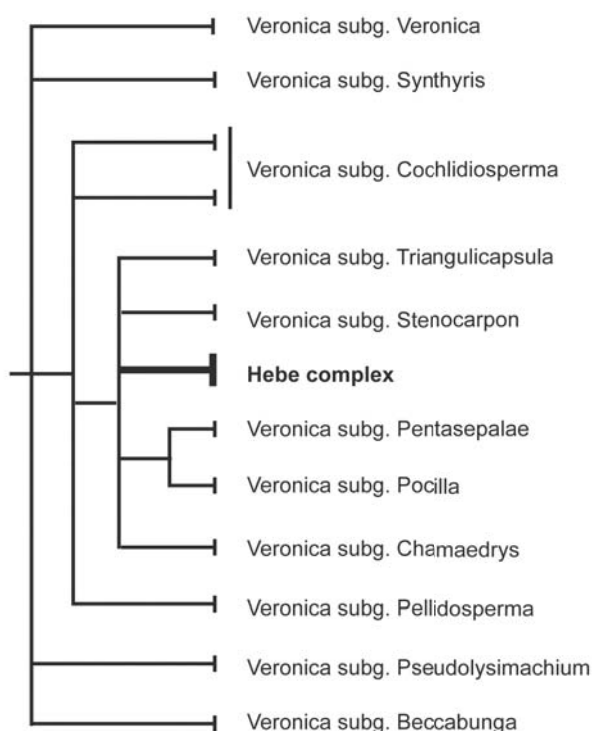


Fig. 2 Phylogenetic tree showing the relationship of the *Hebe* complex to *Veronica*. Reproduced with permission from Bayly and Kellow (2006, fig. 6).

Genus and family level changes to the New Zealand native flora

The Angiosperm Phylogeny Group (APG) is a group of flowering plant taxonomists who aim to incorporate phylogenetic hypotheses derived from DNA sequencing into an updated and practical classification system that follows the rules of the International Code of Botanical Nomenclature⁶. In 2003 they produced an overall classification of the flowering plants.

We have already outlined the genus level issues with *Hebe* and *Veronica*. Following the APG classification (and the underlying studies that support it), *Hebe*, *Veronica*, and related genera (see list that follows) are now placed in the Plantaginaceae family, rather than Scrophulariaceae. Many other plant groups have been similarly changed.

Cordyline is a well known genus, particularly because of the iconic and widely grown New Zealand cabbage tree, *C. australis*. Perhaps less well known is the long-standing uncertainty of which family to place this distinctive genus in. There are a multitude of earlier placements including the Agavaceae,

Asparagaceae, Asphodelaceae, Asteliaceae, Dracaenaceae, Liliaceae, and Lomandraceae. DNA evidence has concluded that the correct family for *Cordyline* is Laxmanniaceae. *Arthropodium*, the rengarenga lily, has also been included in this family.

While the Orchidaceae family remains a natural (monophyletic) group, there have been extensive changes to the Australasian orchids, particularly at the genus level as a result of both morphological and

DNA-sequencing work. For New Zealand, these new names are incorporated in the recently published book *Wild orchids of the lower North Island* (de Lange et al., 2007)⁷. However, the DNA sequencing work has not been fully published and many of the new names are not accepted by all taxonomists working in the family.

There have also been major changes in the Australasian epacrids. DNA phylogenies reject the southern heath family Epacridaceae because it was nested within the Ericaceae. As a consequence, the New Zealand genera *Archeria*, *Dracophyllum*, *Epacris*, *Leucopogon*, and *Pentachondra* are now placed in a larger Ericaceae. In addition, molecular and morphological work done in Australia on the epacrids has led to major rearrangements in the genera. New Zealand species that were placed in *Cyathodes* and *Leucopogon* have now been reassigned to new genera *Androstoma*, *Leptecophylla* and *Acrothamnus*. This work is incomplete, as *Cyathodes pumila*, *Leucopogon fraseri* and *L. nanum* have no place in the new generic scheme.

⁵ Ironically, the first New Zealand hebes to be described were under the name *Veronica*, and it took many years for the horticultural trade to accept the formal change to *Hebe*!

⁶ See <http://www.mobot.org/MOBOT/research/APweb/welcome.html>.

⁷ Reviewed in this issue (pp. 31–32).

Other changes affecting New Zealand native genera are:

Acanthaceae for *Avicennia* (rather than Avicenniaceae);

Amaranthaceae for *Atriplex*, *Chenopodium*, *Einadia*, *Sarcocornia*, and *Suaeda* (rather than Chenopodiaceae);

Araceae for *Lemna* and *Wolffia* (rather than Lemnaceae);

Argophyllaceae for *Corokia* (rather than Escalloniaceae or Corokiaceae);

Atherospermataceae for *Laurelia* (rather than Monimiaceae);

Calceolariaceae for *Jovellana* (rather than Scrophulariaceae);

Celastraceae for *Stackhousia* (rather than Stackhousiaceae);

Hemerocallidaceae for *Dianella* (rather than Phormiaceae), *Herpolirion* (rather than Anthericaceae), *Phormium* (rather than Agavaceae, Phormiaceae, etc.), and *Xeronema* (rather than Phormiaceae);

Hypericaceae for *Hypericum* (rather than Clusiaceae);

Ixerbaceae for *Ixerba* (rather than Grossulariaceae or Brexiaceae);

Lamiaceae for *Teuclidium* and *Vitex* (rather than Verbenaceae);

Malvaceae for *Entelea* (rather than Tiliaceae);

Phrymaceae for *Glossostigma*, *Mazus*, and *Mimulus* (rather than Scrophulariaceae);

Phyllanthaceae for *Oreoporphantha* and *Poranthra* (rather than Euphorbiaceae);

Plantaginaceae for *Callitriche* (rather than Callitrichaceae); *Chionohebe*, *Gratiola*, *Heliohebe*, *Leonohebe*, *Limosella*, *Ourisia*, *Parahebe*, *Veronica* [including hebes] (rather than Scrophulariaceae); and *Plantago*;

Portulacaceae for *Hectorella* (rather than Hectorellaceae);

Quintiniaceae for *Quintinia* (rather than Escalloniaceae [possibly]);

Rousseaceae for *Carpodetus* (rather than Escalloniaceae);

Santalaceae for *Korthalsella* (rather than Viscaceae);

Scrophulariaceae for *Myoporum* (instead of Myoporaceae);

Theophrastaceae for *Samolus* (rather than Primulaceae).

Of course these changes and many others will affect the placements of the non-native cultivated and naturalised flora as well, not only in New Zealand but throughout the world.

It is likely that most of these changes will gain acceptance. Above all, these changes are aimed at producing a more natural (phylogenetic) classification that reflects true relationships between plant groups.

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International Codes of Nomenclature

Zoological, Botanical, and Bacterial codes (Wikipedia, 2008a) have developed since the time of Linnaeus, and are amended by international gatherings of taxonomists. The Botanical Code of Nomenclature is amended by botanical congresses that meet every four years, and because the numbers of taxonomists attending these congresses are large and voting rights are held by all, it is virtually impossible to gain majority support for any radical amendments.

The PhyloCode

A number of evolutionary taxonomists have proposed a PhyloCode (Cantino and de Queiroz, 2007), a set of rules in which no rank is assigned to names above species level. At present the ranks of genus and family are compulsory, meaning that every species must be assigned to a genus and family. Under the PhyloCode, only species rank would be compulsory, and genus and family ranks would disappear. There would still be a hierarchy in the names, but there would be more flexibility over what groups were recognised.

In the case of *Veronica* and *Hebe*, the flexibility over naming would mean that both *Veronica* and *Hebe* could continue to be used, and a hierarchy would be provided that would show that *Hebe* is nested within *Veronica*.

The main obstacle to the PhyloCode becoming popular is the loss of the binomial naming system that has its origin with Linnaeus. *Hebe subalpina* is the binomial for a common New Zealand species, in which the first name is shared with all other hebes, but the second name qualifies it uniquely: there is only one species with that binomial. Under the PhyloCode, there would be no fixed rank of genus with the result that the familiar binomial system would be discontinued. No good alternative involving the substitution of uninomials has been put forward.

As Wikipedia (2008b) says, "The PhyloCode is controversial. The number of supporters for official adoption of the PhyloCode is still small, and it is uncertain, as of 2007, when the code will be implemented and how widely it will be followed."

A number of taxonomists have begun to publish names under the PhyloCode, and while these names don't have official standing under the existing codes of nomenclature, they present a challenge to orthodoxy: if enough taxonomists publish in this way and they are adopted by others, they will gain de facto standing.