

Generic delimitation and phylogenetic uncertainty: an example from a group that has undergone an explosive radiation

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Abstract. Phylogenetic trees can provide a stable basis for a higher-level classification of organisms that reflects evolutionary relationships. However, some lineages have a complex evolutionary history that involves explosive radiation or hybridisation. Such histories have become increasingly apparent with the use of DNA sequence data for phylogeny estimation and explain, in part, past difficulties in producing stable morphology-based classifications for some groups. We illustrate this situation by using the example of tribe Mirbelieae (Fabaceae), whose generic classification has been fraught for decades. In particular, we discuss a recent proposal to combine 19 of the 25 Mirbelieae genera into a single genus, *Pultenaea sens. lat.*, and how we might find stable and consistent ways to squeeze something as complex as life into little boxes for our own convenience.

Why name and classify organisms?

Giving names to things and placing them in classification frameworks are common human activities. There are many possible ways to name and classify organisms, with different classification systems reflecting different needs or priorities. In our society, medical scientists classify hepatitis viruses according to the disease symptoms they produce, conservationists classify species according to how likely they are to go extinct, foresters classify trees according to their usefulness as timber or firewood, and so on.

Similarly, a taxonomic classification serves several specific purposes:

1. Referring to a taxon; the name provides a link to all other information about a taxon,
2. Setting stable boundaries; the name and classification tell us where a taxonomic entity begins and ends, at least for a particular slice of evolutionary time, and
3. Summarising relationships; the name and classification tell us which organisms are related to a taxon and some measure of how closely they are related.

Historically, taxonomic classifications have met these aims by grouping together organisms with a morphological resemblance regardless of their phylogeny, because this made taxa easier to memorise (Stevens 1997, 2002). But since biology operates within an evolutionary framework, systematics should, where possible, reflect the evolutionary relationships between organisms regardless of superficial resemblance. Users of scientific names (specifically

binomials) usually assume that species in the same genus are more closely related to each other than to species in other genera. To satisfy that assumption of relatedness in an evolutionary sense, and to make classification predictive, monophyly is used as the primary criterion for delimiting taxa (de Queiroz and Donoghue 1988, 1990). Increasingly, DNA sequence-based phylogenies are used to estimate monophyly. Such phylogenies show the ‘true’ relationships between organisms that might previously have been obscured by parallel or convergent evolution or considerable morphological modification.

Since phylogenies are composed of a nested set of monophyletic groups, choosing which clade to designate a taxon is not necessarily a straightforward process. Organisms do not mark themselves as ‘genus 1’ and ‘genus 2’: these categories are human constructions imposed on the ever-evolving continuum of the tree of life, and there is no objective method of imposing them (Stevens 2002; Scotland and Sanderson 2004). In order to make decisions about how to delimit taxa using phylogenies, we need to consider the reasons why we make taxonomic classifications and the ways they are used. Two primary issues that impact on the end uses of names are nomenclatural stability and taxonomic equivalence.

Nomenclatural stability

Nomenclatural stability has become a major point of debate among systematists in recent years, given the amount of higher-level taxonomic revision that has taken place

since molecular data for phylogenetic reconstruction became widely accessible. In particular, genus names present a special case because of the binomial system for naming species. Since changes to genus names change the names of all species in the genera affected, there is a strong demand for stability in genus names. The best way to achieve the desired stability is to recognise only well-supported monophyletic groups as genera – groups that are likely to be robust to new data and new analyses. This might require shifting a generic boundary to correspond to a clade that is more robust than the clade(s) currently recognised as belonging to the genus. It means, for example, avoiding making genera within topological features that are not well resolved, such as large polytomies, if it leaves a paraphyletic residual of species that cannot be grouped into well-supported clades at the same level.

Natural classification and taxonomic equivalence

The historical demand that classifications should be easy to remember meant that reflecting ‘natural’ relationships in classification was not given priority, even for those who believed it was possible or desirable (e.g. Bentham, see Stevens 1997, 2002). Even now, taxonomic decisions are often based on subjective criteria (Brummitt 2002; Genner *et al.* 2004). For example taxonomists generally exhibit a preference for circumscribing genera that are not too big and not too small (Clayton 1972), thereby enforcing an unrealistic classification onto some groups and under-representing very large and very small genera (Scotland and Sanderson 2004). Memorability is no longer a major issue because (a) now there are too many taxa recognised to be able to memorise them all, (b) there are tools available (such as keys) to identify taxa, and (c) priority has shifted to reflecting phylogeny. We are now not constrained to artificially limit the number of species in a genus to a memorable size and can attempt to produce classifications that better reflect the evolutionary history of lineages.

What constitutes a ‘natural’ or ‘scientific’ classification? If a ‘natural’ classification should reflect evolutionary relationships, what does it require besides well-supported monophyly? Evolution proceeds by the splitting and diverging of lineages, resulting in an overall hierarchical pattern of relationships among lineages, although not all relationships among lineages will be hierarchical (see below). In the case of a speciation event resulting in two monophyletic daughter species (sister taxa), it is logical to consider both sister species as being of equal taxonomic rank (species). Extrapolating this through time, all sister groups should be considered of equal rank because all sister taxa (genera, families etc) were once sister species, irrespective of how many taxa each now comprises. Similarly, if speciation results in three daughter taxa, all three should be considered as equal in rank.

Phylogenetic trees comprise nested hypotheses of sister taxon relationships and it is from these that we attempt to

classify organisms. Our current binomial naming system does not require us to assign rank to every sister taxon relationship, but to make decisions about the rank of genus and species. Thus, having decided on the level of genus for one taxon, it follows that its sister lineage is also treated as a genus.

What is taxonomic equivalence and why strive for it? Taxonomic equivalence is important in applied biology. Biologists, as well as non-specialists, generally assume that named genera are evolutionarily equivalent units. For example, estimates of global biodiversity and hotspots for conservation typically use rank – number of species or genera or families – to compare regions or assess performance objectives (e.g. Williams *et al.* 1994; Desmet *et al.* 2002; Doerries and Van Dover 2003; Lei *et al.* 2003; Fukami *et al.* 2004). Non-equivalence of taxonomic rank among groups leads to overestimation of biodiversity for some groups relative to that of others. When government departments and community organisations prioritise funding of recovery plans for threatened or rare taxa, taxonomic non-equivalence can bias their decisions.

Taxonomic equivalence is also important in other empirical and theoretical studies, particularly synthetic reviews. For example, biogeographic studies typically use comparisons among higher taxa (e.g. Lee *et al.* 2001; Sanmartín and Ronquist 2004).

The problem of non-monophyly

The evolution of organisms does not always follow a simple bifurcating hierarchy (Hoelzer and Melnick 1994). There is mounting evidence that many recognised species (including those circumscribed using the biological species concept) are not monophyletic (Lee 1995; Crisp and Chandler 1996; Funk and Omland 2003)—about 23% of animal species (Funk and Omland 2003) and probably an even greater percentage of plant species (Crisp and Chandler 1996). Paraphyly might be indicated by gene trees whose topologies do not agree or by one species being nested within another (Crisp and Chandler 1996; Baum and Donoghue 1995; Maddison 1997; Funk and Omland 2003). Because higher taxa were once species they too, might be non-monophyletic.

Over time, extinction of some lineages can lead to the remaining lineages becoming monophyletic (Maddison 1997). Thus, the stage in the evolution of a lineage when a classification is imposed partly determines whether a lineage appears monophyletic and amenable to our enforced classification. A group that today appears non-monophyletic or has conflicting gene trees might, with lineage sorting and extinction over time, resolve into fewer well-supported monophyletic groups.

A cladogram derived naively from combined data (i.e. without assessing incongruence among partitions) may obscure non-monophyly by forcing the relationships among taxa into a tree-like branching pattern. Additionally, cladograms, which do not show branch lengths, might show

sister relationships and their support but they do not inform us about the amount of time or divergence between taxa. Consideration of all available data should allow more stable, evolutionarily-informative, taxonomic decisions.

Example: *Mirbelieae*

The Australian endemic tribe *Mirbelieae* (Fabaceae) provides a good illustration of these issues. *Mirbelieae* currently contains 25 genera and 675 species, accounting for about two thirds of the Australian papilionoid species. Tribe *Bossiaeeae* (six genera, 60 species) is nested within *Mirbelieae* (Crisp and Cook 2003a) and therefore is also included here. Recent embryological work has shown that five genera of *Mirbelieae* (*Daviesia*, *Sphaerolobium*, *Gompholobium*, *Viminaria* and *Erichsenia*), and all of *Bossiaeeae* (*Goodia*, *Bossiaea*, *Platylobium*, *Ptychosema*, *Aenictophyton* and *Muelleranthus*) share a set of characters known as ‘giant antipodals’ (GA) type embryology. The remaining 20 genera of *Mirbelieae* possess another embryology type known as the ‘no antipodals’ (NA) type (Crisp and Cook 2003a). Each of the seven clades *Daviesia*, *Sphaerolobium*, *Gompholobium*, *Viminaria* + *Erichsenia*, *Goodia*, *Bossiaea* + *Platylobium* and *Aenictophyton* + *Ptychosema* + *Muelleranthus* have strong support for monophyly from multiple molecular datasets [*trnL*, ITS (Crisp and Cook 2003a), *trnL-F*, *ndhF* (Cook and Crisp unpubl. data)], as does the NA genus *Isotropis* (10 species) [*trnL-F*, ITS, *ndhF* (Crisp and Cook 2003a; Orthia *et al.* 2005)]. The remaining 19 genera of *Mirbelieae* (470 species), referred to here as *Pultenaea sens. lat.* (previously known as the *Mirbelia* group, e.g. Crisp and Cook 2003a), form a strong clade with very high support and a long branch at the basal node (Fig. 1). This clade is consistently reproduced regardless of the genomic region (*trnL-F*, *ndhF*, *trnK*, *psbA-trnH*, ITS, ETS) or analysis method (MP, ML, distance, Bayesian) used to construct trees (Chandler *et al.* 2001; Crisp and Cook 2003a, 2003b; Orthia *et al.* 2005). The relationships between these nine clades (the seven GA clades, *Isotropis* and *Pultenaea sens. lat.*) are not well resolved; a combined *trnL*-ITS tree shows them forming a near polytomy, in which *Isotropis* is placed as sister to *Pultenaea sens. lat.* with weak support (Fig. 1) (Crisp and Cook 2003a). However, it is clear that *Pultenaea sens. lat.*, with 19 genera, is more or less equivalent in evolutionary age to the other lineages in *Mirbelieae* and *Bossiaeeae*, each with only one, two or three genera. Effectively, all the taxa that are the evolutionary equivalents of *Pultenaea sens. lat.* are genera. *Isotropis*, the most likely sister group of *Pultenaea sens. lat.*, is a genus. Therefore, Crisp and Cook (2003a) proposed that all of *Pultenaea sens. lat.* be treated as a single genus.

Most *Pultenaea sens. lat.* genera were first described in the 18th and 19th centuries and revised by Bentham (1864) in *Flora Australiensis*. Cladistic analyses of morphological,

cytological and/or DNA sequence data for the taxa over the past twenty years led to the description of two new genera, *Almaleea* (Crisp and Weston 1991) and *Stonesiella* (Crisp *et al.* 1999), the informal proposal of new genus *Otione* (Crisp and Weston 1995), and the sinking of *Brachysema*, *Nemcia* and *Jansonia* into *Gastrolobium* (Chandler *et al.* 2001). However, morphological and molecular characterisation of several lineages remains poor. Molecular trees show that some *Pultenaea sens. lat.* genera—*Mirbelia* (32 species), *Chorizema* (27), *Podolobium* (6) and *Pultenaea* (116) – are strongly paraphyletic (Crisp and Cook 2003a, 2003b; Orthia *et al.* 2005).

Revising generic delimitation in *Pultenaea sens. lat.*

Under a strict cladistic approach to classification, if current genera were to be maintained as far as possible, *Mirbelia*, *Chorizema*, *Podolobium* and *Pultenaea* would need to be split up further into new genera. However, splitting these genera poses major problems. First, neither these genera nor most of their infrageneric clades can be diagnosed by a simple morphological trait or set of traits. Even though *Pultenaea sens. lat.* taxa appear to show a wide range of morphological diversity, this consists of multiple combinations of a relatively small number of characters (Crisp and Cook 2003b; Orthia *et al.* 2005).

Second, there are supported topological conflicts between trees constructed using different genomic regions. One of the most striking examples of conflicting trees is in the placement of the *Podolobium ilicifolium* group—*trnL-F* and ITS each place it in different parts of the tree with high support (Fig. 2). Other conflicts include differing support levels and topologies for the ‘spiny *Mirbelia*’ group, supported conflicting placement of *Mirbelia rubiifolia* and different relationships between *Pultenaea* clades, albeit with low support levels (Crisp and Cook 2003b; Orthia *et al.* 2005). There are no objective criteria to follow in choosing which tree to use as the basis for a new generic classification.

The third problem with continuing the splitting approach is the small size of the genera that would result. The polytomy at the base of *Pultenaea sens. lat.* is comprised of nearly 40 clades, all of which must become genera under this approach, and many of which contain fewer than 10 species. Already there are three monotypic genera (*Callistachys*, *Euchilopsis*, *Stonesiella*) and seven genera with 2–10 species (*Oxylobium*, *Podolobium*, *Eutaxia*, *Latrobea*, *Almaleea*, *Otione*, *Urodon*) and the further split of *Mirbelia*, *Chorizema* and *Pultenaea* would add at least ten small genera. Taxonomic splitting tends to regress into yet more splitting in an attempt to maintain monophyletic genera. Increasingly, workers are likely to waste resources as they search for the right gene or the right character to extract the fine details of an ultimately unresolvable pattern. There is nothing wrong in principle with the circumscription of small or monotypic genera: the ditopic clade of *Viminaria* + *Erichsenia* is equivalent to the

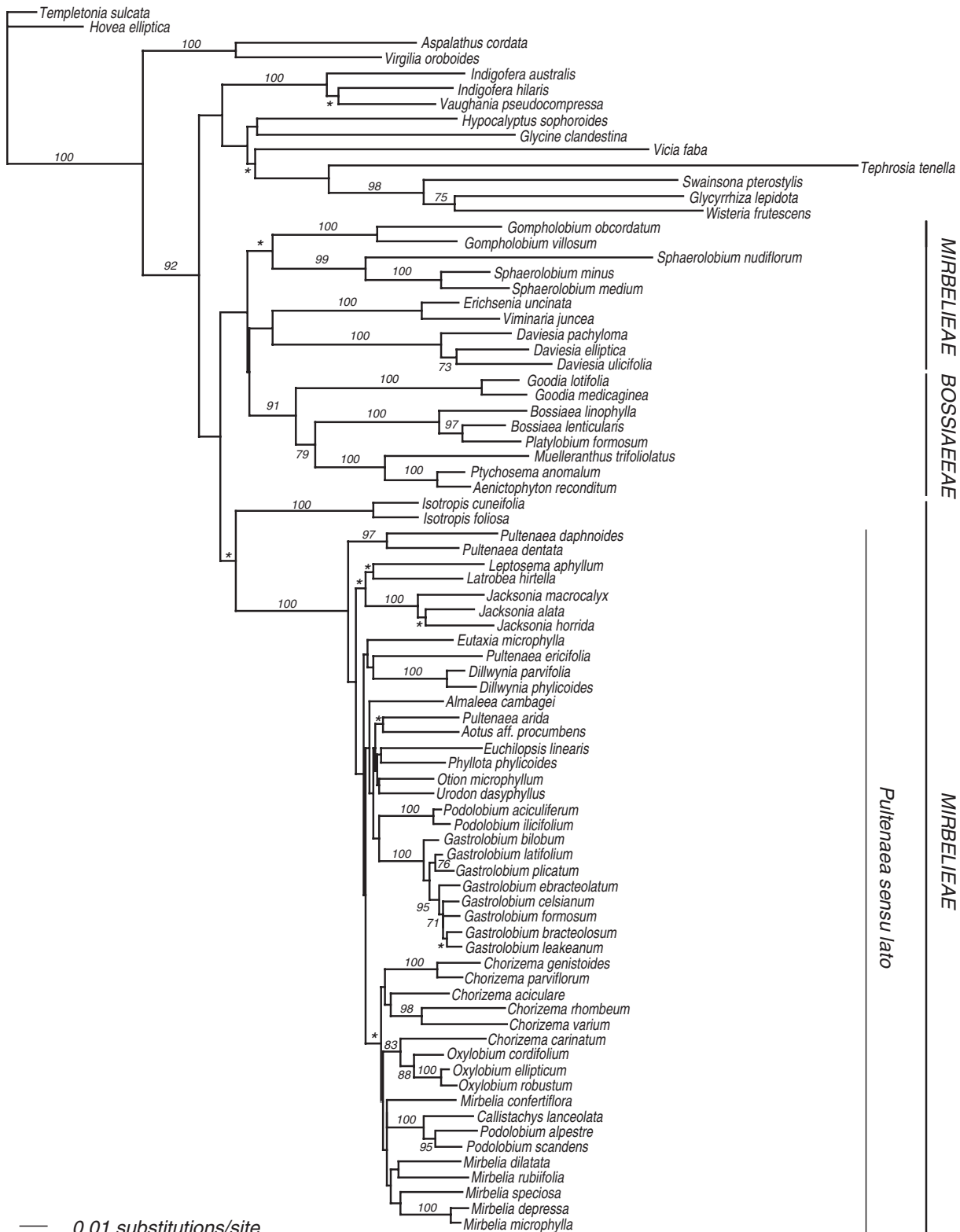


Fig. 1. Phylogram of the Fabaceae tribes Mirbelieae and Bossiaeeae, with *Pultenaea sens. lat.* showing an explosive radiation—short basal nodes subtended by a long stem. Modified from Crisp and Cook (2003a, fig. 2). Numbers on branches are bootstrap scores. *50 ≤ BS ≤ 69.

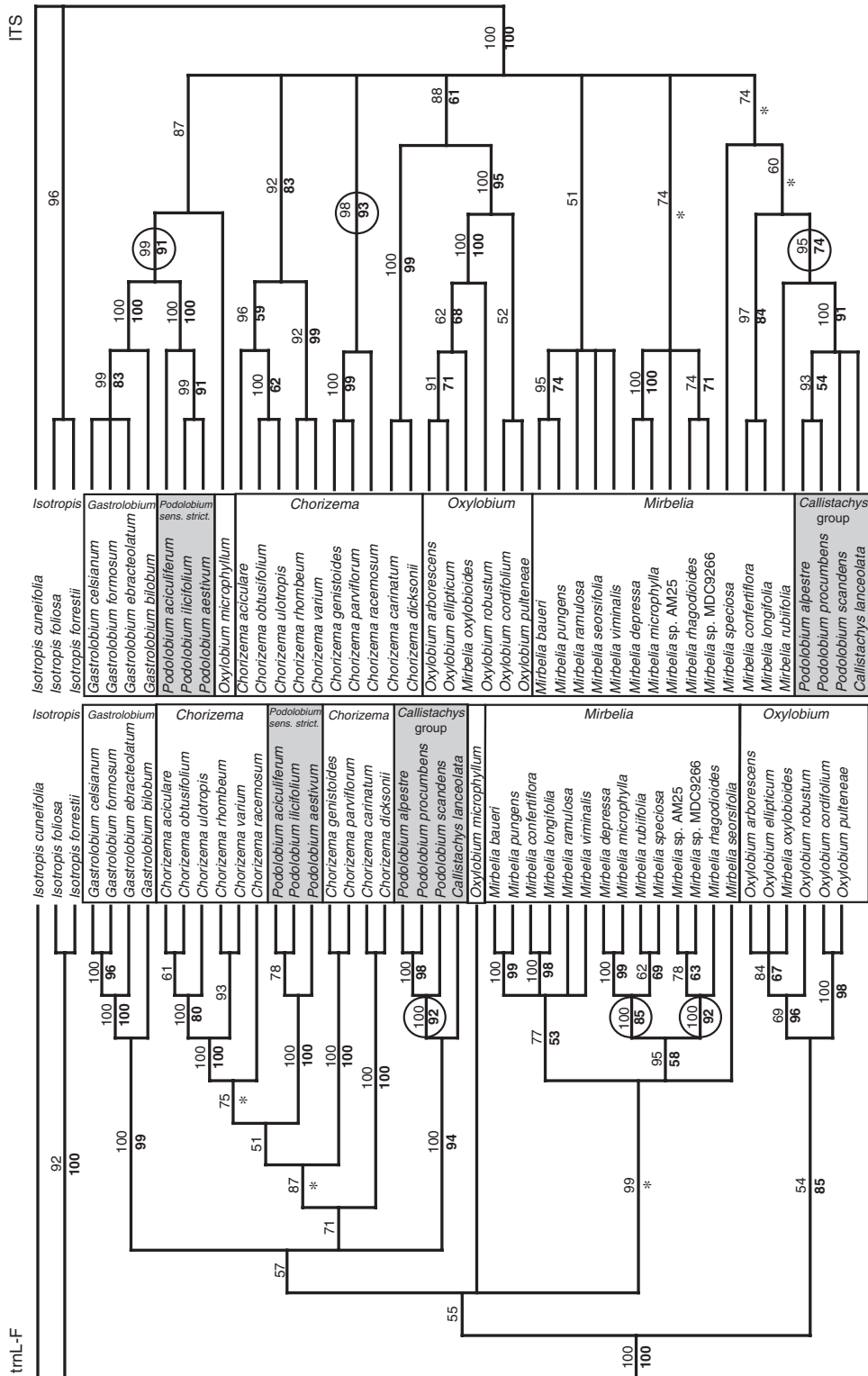


Fig. 2. Phylogeny of *Pultenaea sens. lat.* (in part) estimated from ITS sequences (right) and *trnL-F* (left), modified from Crisp and Cook (2003b). Terminals are grouped according to current generic placement. *Podolobium* (highlighted by grey boxes) comprises two groups, each showing different sister taxon relationships in each tree. Numbers above branches are Bayesian posterior probabilities; below are bootstrap scores from maximum parsimony (asterisks indicate branches from the MP strict consensus tree with bootstrap < 50). Circles indicate well-supported nodes that conflict between trees.

speciose *Daviesia* in evolutionary age, so is justifiable as a genus. But the age of the existing *Pultenaea sens. lat.* genera is young compared with those such as *Daviesia*. If *Pultenaea sens. lat.* were to be split into small stable genera, each would be accorded the same status as that of other genera in tribes Bossiaceae and Mirbelieae. That is, although many of the *Pultenaea sens. lat.* genera would differ from each other only as much as sections within *Daviesia*, they would each have the same status of the whole of *Daviesia*.

The fourth, related, problem is that inappropriate comparisons might be made. If there were a question of whether to fund a conservation program for *Euchilopsis* or *Erichsenia*, the current classification makes it seem a difficult choice because both genera are monotypic. However, considering the phylogeny and phylogenetic diversity (Faith 1994), it is clear that the loss of *Euchilopsis*, with *c.* 470 close relatives, will be much less than the loss of *Erichsenia*, with only one. Although *Euchilopsis* is divergent from other *Pultenaea sens. lat.* taxa, underlying genetic distance is not great compared with the differences among *Daviesia*, *Isotropis* and their sister lineages (including *Pultenaea sens. lat.*), and finer splitting of *Pultenaea sens. lat.* will only make this disparity worse.

The problems within this group might be due to the relative youth of the radiation within the crown group of *Pultenaea sens. lat.*, compared with the much older radiation that gave rise to the *Pultenaea sens. lat.* lineage and its sisters. Given enough evolutionary time, the conflicts present in the *Pultenaea sens. lat.* group and the problem of having numerous species-poor lineages might largely disappear. Lineage sorting and extinction over time might make originally non-monophyletic groups eventually appear monophyletic in trees. So, workers three million years in the future might find *Pultenaea sens. lat.* lineages quite amenable to neat generic delimitation, with the lineages we currently know as '*Daviesia*' and '*Isotropis*' best elevated to tribe or family level (or extinct, who knows?). At the moment though, it is inappropriate to split *Pultenaea sens. lat.* into multiple genera because in doing so we would introduce greater taxonomic inequivalence, maintain instability and enforce monophyly on reticulate groups within it.

Our proposal to lump *Pultenaea sens. lat.* into a single genus would avoid the instability that is inherent in the current classification. *Pultenaea sens. lat.* as a whole forms a very robust, consistently supported clade that is unequivocally monophyletic. Additionally, it is evolutionarily equivalent to other genera in Mirbelieae and Bossiaceae, unified in embryology and has a long stem that indicates clearly where a taxonomic boundary should be drawn. Such a genus would remain nomenclaturally stable. In the short term, formalising *Pultenaea sens. lat.* as a single genus would create nomenclatural disruption. Eighteen generic names would be reduced to subgenus level or disappear and *c.* 108 of 470 species would require a change of both generic and

specific epithets. Nevertheless, we believe that short-term disruption is acceptable because we are certain that it will lead to long term stability. In the case of *Pultenaea sens. lat.*, all available evidence from multiple genes and analyses, embryology and morphology supports the change.

Conclusions

The taxonomic problems within *Pultenaea sens. lat.* reflect the manner in which it evolved: by explosive radiation, the more or less simultaneous generation of multiple lineages. The explosive radiation might have occurred when populations of the ancestral species rapidly expanded into new territory. Perhaps this was followed by range contraction after environmental change, fragmenting populations to form many new species. Nuclear and chloroplast alleles might have sorted differentially and thus created conflict between trees. There might also have been some horizontal transfer of genetic material between lineages during this radiation, leading to further conflicts (see Crisp and Cook 2003*b*). This is probably not an unusual scenario; speciation is not always a neatly bifurcating process in which species are immediately reproductively isolated, and gene trees are likely to remain in conflict for a long period following speciation. Phylogenies of other taxa have topologies that suggest explosive radiation events (Hoelzer and Melnick 1994; Vijverberg *et al.* 1999; Mummehoff *et al.* 2001; Kadereit *et al.* 2003; Quinn *et al.* 2003) and hybridisation is thought to have played a role in the evolutionary history of other plant lineages (McKinnon *et al.* 2001; Gross *et al.* 2003; Arnold 2004). Taxa diverging in allopatry might have secondary contact in the later stages of speciation, causing lineage reticulation.

Conflict among datasets and non-equivalence of taxa probably occur in many groups, including groups far less speciose than Mirbelieae. Such problems might not be evident unless multiple DNA regions from different genomes are sequenced and analysed separately, rather than being lumped *a priori* for 'total evidence' analysis. Attempting to force all nodes in a taxon phylogeny to be dichotomous is problematic and misguided. Taxonomic equivalence can only be properly assessed using comparative studies and by taking account of branch lengths and support values. However, many phylogenetic studies do not show phylograms and/or ignore low support values on major branches. We conclude that studies that do not thoroughly explore the evolutionary history of the study group in these ways might be making erroneous or premature judgements about taxonomic boundaries that ultimately perpetuate instability.

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