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Circumscribing genera in the European orchid flora: a subjective critique of recent contributions

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Zusammenfassung/Summary:

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Die Abgrenzung von Gattungen oder anderen höheren Taxa erfolgt nach modernen Ansätzen weitestgehend auf der Rekonstruktion der Stammesgeschichte (Stammbaum-Theorie), mit Hilfe von großen Daten-Matrizen. Wenngleich aufgrund des Fortschritts in der DNS-Sequenzierungstechnik immer mehr Merkmale in der DNS identifiziert werden, ist es mindestens genauso wichtig, die Anzahl der analysierten Pflanzen zu erhöhen, um genaue Zuordnungen zu erschließen. Die größere Vielfalt mathematischer Methoden zur Erstellung von Stammbäumen führt nicht gleichzeitig zu verbesserten Methoden zur Beurteilung der Stabilität der Zweige innerhalb der Stammbäume. Ein weiterer kontraproduktiver Trend ist die wachsende Tendenz, diverse Datengruppen mit einzelnen Matrizen zu verquicken, die besser einzeln analysiert würden, um festzustellen, ob sie ähnliche Schlussfolgerungen bezüglich der Verwandtschaftsverhältnisse liefern. Ein Stammbaum zur Abgrenzung höherer Taxa muss nicht so robust sein, wie ein Stammbaum, aus dem man Details des Evolutionsmusters ableiten möchte, da höhere Klassifizierungen nur eine kleine Anzahl von besonders starken, zuverlässigen Zweigen erfordern. Die hier befürworteten priorisierten Regeln, um einen Stammbaum in Gattungen zu teilen, heben zunächst

die Monophylie und dann die Robustheit jener Zweige hervor, die ausgewählt wurden, um die Gattungen abzugrenzen. Ziel ist es, stabile Gattungsbeschreibungen zu generieren, die auch nach dem Erfassen von weiteren biosystematischen Daten nicht widerlegt werden. Diese Grundsätze werden veranschaulicht durch eine kritische Einschätzung einiger rezenter Studien, die versuchten, Gesichtspunkte zu Gattungsbeschreibungen, die von Bateman und Kollegen in Bezug auf die frühere Gattung *Orchis* s.l. aufgestellt wurden, zu verbessern. Es ist besonders wichtig, sowohl Stabilität als auch Widerspruchsfreiheit supra-spezifischer Taxonomie zu erreichen, indem man alle Gruppen europäischer Orchideen simultan betrachtet. Sporadisches Herausgeben zahlreicher kleinerer taxonomischer Überarbeitungen erzeugt ein taxonomisches und nomenklatorisches Chaos und sorgt dafür, dass die Meinungen einzelner Taxonomen gegenüber den wissenschaftlichen Prinzipien priorisiert werden.

Modern approaches to circumscribing genera and other higher taxa rely heavily on the reconstruction of phylogenies (evolutionary trees) from matrices of quantitative data. Although the number of characters included in DNA matrices is expanding rapidly as sequencing technology advances, increasing the number of plants analysed is at least as important for obtaining accurate relationships. Greater diversity of mathematical methods of building trees has not been matched by improved methods of assessing the relative strengths of branches within trees. Another counter-productive trend is an increased tendency to combine into single matrices diverse datasets that would better be analysed separately in order to determine whether they yield similar inferences of relationship. Less robustness is required in an evolutionary tree when it is used for delimiting higher taxa than when it is used to infer the details of evolutionary patterns, as higher classifications require only a small number of especially strong, reliable branches. The set of prioritised rules advocated here for dividing a tree into genera emphasises first monophyly and then the robustness of those branches that are selected to delimit the genera, with the aim of generating stable circumscriptions of genera that are very unlikely to be overturned when subsequent biosystematic data are gathered. These principles are illustrated by critically assessing several recent studies that sought to improve upon aspects of the generic circumscriptions enacted by Bateman and colleagues, focusing on the former genus *Orchis s.l.* It is especially important to achieve both stability and consistency of supraspecific taxonomy by simultaneously considering all groups of European orchids. Sporadically issuing numerous smaller taxonomic revisions creates taxonomic and nomenclatural chaos, and ensures that the opinions of individual taxonomists are prioritised above scientific principles.

Progress in phylogeny reconstruction: a personal view

The first DNA-based phylogenies (evolutionary trees) of European orchids, published 15 years ago, immediately ignited debates regarding the circumscription of genera that continue today, apparently unabated. In an attempt to better inform those debates, 11 years ago I prepared for orchid enthusiasts a detailed account of how and why phylogenies are reconstructed using explicit cladistic methods (Bateman 2001). As much of what I wrote at that time remains applicable, I will review fundamental issues only briefly here, noting in particular any relevant innovations or changes of emphasis that have developed through the last decade. The opinions that I express in this article are based on my own experience; many of my phylogeneticist colleagues would disagree with at least some of my views.

The first half of this article reviews the present state of phylogeny reconstruction as a scientific discipline, thus providing the necessary context for the second half of the article which critiques recent contributions to debates regarding the circumscription of genera of European orchids; this second section focuses on treatments of Subtribe Orchidinae that have been published during the three years that have passed since I last commented on these issues (Bateman 2009).

Nature of phylogenetic data

Phylogeny reconstruction is always based on an asymmetric matrix of individual plants scored for a reasonable number of characters that vary among the individuals. Thus, each cell within the matrix is scored for a particular character state. The characters scored can be morphological (e.g. external morphology, anatomy, development) or molecular (e.g. DNA/RNA bases, amino acids, proteins, base methylation). Sadly, use of morphological characters to actually build trees (as opposed to being ‘mapped’ across trees that have already been generated from molecular data) is declining in popularity, partly because it inevitably yields a limited number of characters and partly because it is more time-consuming to generate original data for morphology. Many authors now attempt to gather morphological and/or ecological data from previous literature. Although grazing the literature saves time and effort, it fails to add to, and even to adequately test, our collective knowledge, and (as we will see below) often perpetuates past errors.

Focusing on genetic characters, base sequences can be derived from three distinct genomes within a typical plant cell: genes from the nucleus are organised in chromosomes and inherited equally from both the ovule parent ('mother') and pollen parent ('father'), whereas genes from the organelles – plastids and mitochondria – are organised as single loops and are generally inherited only from the ovule parent. Each of these three genomes is not only inherited differently but also subject to contrasting processes of molecular evolution. Mitochondria have become the organelle of choice for studying higher animals but their mode of molecular evolution is sufficiently problematic that they are less commonly used to study higher plants, where plastids (a category of organelle absent from higher animals) have long been preferred.

Phylogenetic use of nuclear genes is complicated by the fact that, in classic genetic theory, at least one copy of each gene is inherited from the mother (seed parent) and another from the father (pollen parent); if those copies differ in base sequences this polymorphism will complicate any phylogenetic analysis. The looped DNA of plastids generally yields only one copy of each gene, making them simpler to analyse. However, under certain circumstances, a partial or even complete plastid genome can be transferred from one plant to another 'laterally', rather than being inherited 'vertically' from its mother. In cases where relatively recent hybridisation is suspected, both nuclear and plastid genes should be sequenced. The nuclear genes are likely to reveal conflicts between the maternal and paternal copies of genes, thus providing strong evidence that hybridisation has occurred. The associated plastid data will then allow us to determine which of the two parental species was the mother.

Constructing trees

Several categories of mathematical algorithm are now readily, and often freely, available for converting the accumulated data into a dichotomous tree (or, in the case of some methods, a set of optimal trees). Thus, anyone possessing basic IT competences can in theory produce their own phylogenies. The tree-building algorithms can differ greatly, both philosophically and practically. Parsimony has the advantage of being simple in theory and practice – a very small matrix can even be converted into trees without the aid of a computer. Unlike other methods, character states are preserved intact rather than being converted into probability statements, making the resulting trees more readily interpreted in terms of character evolution. However, parsimony trees are supposedly more vulnerable than some other trees to specific forms of statistical anomaly (such as long-branch attraction) that yield incorrect relationships. Also, a large matrix will usually generate many most-parsimonious trees, forcing the analyst to either choose between them or amalgamate them all into a less well-resolved consensus tree. The algorithm most commonly used in the 1980s and 1990s as an alternative to parsimony was neighbour joining, which is mathematically simple and generates only a single tree, but it too remains vulnerable to various kinds of statistical anomaly.

Consequently, likelihood methods of tree building were introduced, where the analyst must select from among a range of potential mathematical models of character evolution that vary in complexity; this raises the temptation for the analyst to choose the algorithm that results in the tree (and thus the mathematical model) that best fits their initial expectations of relationships. During the last decade, analysts of molecular data have increasingly resorted to mathematically complex Bayesian methods of tree building, which operate through a highly iterative process that cycles repeatedly between a hypothesis of relationships and the best fit of the data until a single mathematically preferred pattern of relationships eventually emerges. This method is supposedly more resistant to statistical anomalies than parsimony but shares with likelihood methods the handicap of being difficult to comprehend (i.e. it is a ‘black box’ method); it is virtually impossible to reconstruct the route by which the original characters have contributed to the resulting tree. It is my impression that many of today’s phylogeneticists are becoming increasingly skilled at the Information Technology aspects of phylogeny reconstruction but have lost sight of the central role played by character states in both constructing and interpreting evolutionary trees. It is essential that the key concepts underlying phylogeny reconstruction are preserved and adequately understood.

Comparing trees

We shall now consider the suite of statistics that have been developed in an attempt to determine the strengths of individual branches and thus the reliability of the relationships that they specify. Trees constructed using parsimony or likelihood methods almost always carry values from a bootstrap analysis, performed by repeatedly discarding some data from the matrix before comparing fresh sets of trees. In contrast, trees constructed using Bayesian methods are more likely to carry values for posterior probability, wherein the data effectively test the chosen prior parameters (the converse of likelihood estimates). Both bootstrap and posterior probabilities are expressed as percentages, and in theory, branches generating higher percentages are more reliable.

Initially, this statistical rationale had some logic – that is, when it was applied to morphological matrices, which inevitably contain a limited number of characters (rarely more than 50). However, these methods are less valuable when applied to increasingly character-rich molecular matrices, because the maximum value of 100% is rapidly reached (for example, a branch supported by just two unique character-state transitions typically gains a bootstrap value of about 67% and receives an even higher posterior probability). After reaching 100%, these measures are no longer able to discriminate between branches of contrasting strengths. Thus, given a typical DNA matrix rich in characters, most if not all branches will appear equally strong statistically when of course they are not; rather, we will have long since passed the threshold value at which these particular statistical methods are adequately informative.

A far less popular, but considerably more informative, measure of relative branch strength is provided by the decay index (= Bremer support). This is an arithmetic measure that increases in value with increasing branch strength; consequently, it is far more useful as it has no theoretical maximum value. Unfortunately, the decay index is difficult to calculate for matrices containing many species, and also it can be applied only to parsimony trees. It surprises me that more effort has not been made to develop comparable ‘open-ended’ statistics for Bayesian and likelihood tree-building algorithms.

Perhaps the worst aspect of these branch-support statistics is that they are commonly treated by analysts as demonstrating that an inferred relationship is *true* – for example, it is frequently said that a relationship supported by a bootstrap value greater than 80% and/or a posterior probability greater than 90% is reliable. Of course, this argument soon collapses when two trees generated from the same DNA samples but from different genes yield strongly contradictory relationships among species – relationships that are supported in both trees by bootstrap values and/or posterior probabilities of 100%! Rather than routinely hiding behind statistics, it then becomes necessary to further explore, and hopefully eventually explain, the incongruence between the contrasting trees generated from the two competing matrices – most likely by invoking one or more processes of genetic evolution.

Sampling taxa and characters

In my opinion, the most important of all the many factors that influence the rigour of a phylogenetic analysis is achieving an optimal balance between sampling individual plants and sampling characters. The amount of effort required to complete any molecular phylogenetic study is determined by how many species are selected for study, how many individual plants of each species (until recently, often just one) are sampled, how many genes per plant are sequenced, and how many variable bases (i.e. characters) are found in each gene. Particular attention has been paid to whether it is more important to maximise the number of species or the number characters – evidence to date suggesting that species sampling is paramount (e.g. Zwickl & Hillis 2002). A further consideration is that once an analyst has selected a set of ingroup species (those species that are of primary interest), how many additional 'outgroup' species should be analysed in order to root the tree (i.e. to identify the sequence in which branches diverge) and to test the monophyly of the ingroup. Only one outgroup species is needed to root the trees, but a larger number of outgroups is needed to test the monophyly of the ingroup.

Contrasting uses of phylogenies

I would argue that a crucial distinction exists between using a phylogenetic tree as the basis for a genus-level classification and using that same tree to infer the sequence of character-state transitions (i.e. biological innovations) that took place during the evolution of the group of species being studied. My preferred approach to converting a phylogenetic tree into a classification (discussed in greater detail below) highlights only a minority of all the branches present in the tree – generally those that receive the strongest statistical support (usually those branches that are relatively long). In contrast, when inferring the details of evolution in the group, or attempting to reconstruct the likely properties of a hypothesised shared ancestor occupying one of the internal nodes of the tree, it is usually necessary to assume that *all* of the branches in the tree, and the relationships that they suggest, are correct. In other words, it is considerably easier to derive a robust classification from a tree than to infer a robust evolutionary scenario from that same tree. Why, then, do classifications derived from phylogenetic trees remain controversial?

Circumscribing genera of European orchids using monophyly: the ongoing debate

There has been much discussion of the circumscription of European orchid genera in the 15 years that have elapsed since they were first subjected to the constraint of monophyly during the molecular phylogenetics revolution (Bateman et al. 1997, 2003, 2005; Pridgeon et al. 1997). Although the resulting monophyletic genera have become increasingly widely adopted (reviewed by Bateman 2009), they remain far from ubiquitous. However, most of the authors who are not yet convinced by the value of monophyly have simply chosen to ignore one or more of the re-circumscribed genera, rather than directly challenging the underlying principles of classification based on monophyly. The most notable exception was provided by Tyteca & Klein (2008), who offered several justifications why perceived morphological similarity and direct observations of apparent reproductive isolation should be prioritised above “almighty monophyly” when delimiting genera within European orchids. Their paper prompted a detailed critique by myself (Bateman 2009) that sought to clarify the principles underpinning monophyletic classification before systematically appraising each controversial genus-level group of European orchid species – a critique that soon drew a further, more conciliatory response (Tyteca & Klein 2009). I do not wish to reiterate here the many arguments put forward in this notable exchange – interested readers can readily consult the original papers. However, in order to further challenge continued critiques of these monophyletically delimited genera, it is necessary to repeat here the self-imposed rules that we used to produce our generic circumscriptions from an evolutionary tree. In my opinion, the following five rules are sufficient to generate an explicit, logical, robust and biologically justifiable classification from a tree generated from any substantial data-matrix, whether morphological or molecular. The desired properties, and resulting explicit rules of classification, are listed below in order of decreasing importance (cf. Bateman 2009, pp. 253–4):

Property 1: The classification should consist only of natural (evolutiona-rily inclusive, self-circumscribing) groups;

> **Rule 1:** Recognise only monophyletic groups (clades) evident in the tree.

Property 2: The classification shows considerable stability when further data of the same or other kinds are gathered;

> **Rule 2:** Preferentially divide the tree at branches that are relatively robust (and usually comparatively long); although evidence of robustness *within* a tree is provided by measures of statistical support, their limitations should be clearly understood (see discussion above).

Property 3: The classification generates taxa at the same rank that show similar levels of divergence in the characters that were used to construct the tree;

> **Rule 3:** Preferentially divide the tree at branches that receive similar levels of statistical support (such branches are typically of approximately equal length).

Property 4: The classification provides grouping information at every available rank;

> **Rule 4:** Minimise the proportion of branches in the tree that simultaneously represent more than one taxonomic rank (most notably, any terminal branch that represents not only a species but also a supposedly monotypic genus, such as *Chamorchis alpina* or *Steveniella satyrioides*).

Property 5: The classification minimises alterations necessary to existing Linnean names;

> **Rule 5:** Preferentially divide the tree in a way that minimises the need to (a) create new names and (b) create new combinations of existing names.

Although these rules focus on comparisons made *within* a single phylogenetic tree, I should note here that the strongest tests of the reliability of particular branches (and thus of potential genus-level circumscriptions) are provided by comparisons *between* trees that are based on the same range of species (ideally, the same individual plants) but on contrasting genes or genomes.

Having briefly reviewed conceptual and practical aspects of reconstructing phylogenetic trees, and summarised how best to convert an evolutionary tree into a genus-level classification, I will now illustrate these principles by critiquing two significant recent debates in generic circumscription of European orchids: (1) whether the genus *Orchis s.s.* (i.e. *sensu* PRIDGEON et al. 1997; BATEMAN et al. 2003) should be divided into two genera (e.g. TYTECA & KLEIN 2009; TYTECA et al. 2012), and (2) whether a recent molecular phylogeny that added mitochondrial and plastid sequence data to a subset of BATEMAN et al.'s nuclear ITS data (e.g. INDA et al. 2012) represents a significant advance over the ITS-only tree of BATEMAN et al. (2003) (compare Figs 1 and 2).

Should *Orchis sensu stricto* be divided into *Orchis sensu strictissimo* and '*Androrchis*'?

Background — The detailed exchange of views between TYTECA & KLEIN (2008) and BATEMAN (2009) led TYTECA & KLEIN (2009) to rapidly withdraw their suggestions for establishing novel non-monophyletic genera within *Anacamptis s.l.* and *Neotinea s.l.* – recommendations that were designed to achieve the questionable aim of restoring *Anacamptis pyramidalis* and *Neotinea maculata* as monospecific genera. However, TYTECA & KLEIN (2009) remained committed to dividing *Orchis s.s.* (i.e. *sensu* BATEMAN et al. 2003) into two groups – *Orchis sensu strictissimo*, possessing anthropomorphic flowers (epitomised by *Orchis militaris*), and the novel genus *Androrchis*, lacking anthropomorphic flowers (epitomised by *Orchis/Androrchis mascula*). TYTECA & KLEIN (2009) argued that this generic re-circumscription would not contravene DNA-based monophyly and (perhaps more convincingly) that the bipartite distinction is strongly supported by a degree of morphological, molecular and perhaps chromosomal divergence between the two groups, as well as good evidence of near-complete reproductive isolation (cf. KRETZSCHMAR et al. 2007; SCOPECE et al. 2010).

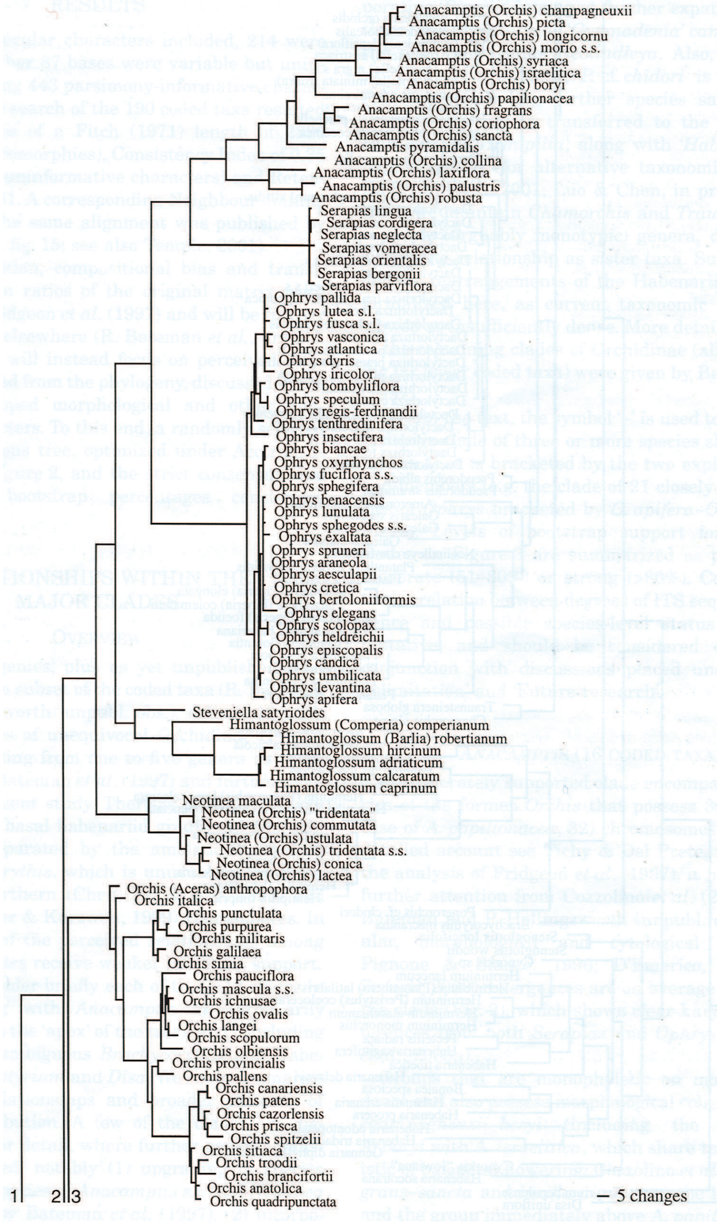


Fig. 1a: The Orchideae phylogeny of Bateman et al. (2003), based on nuclear ITS data.

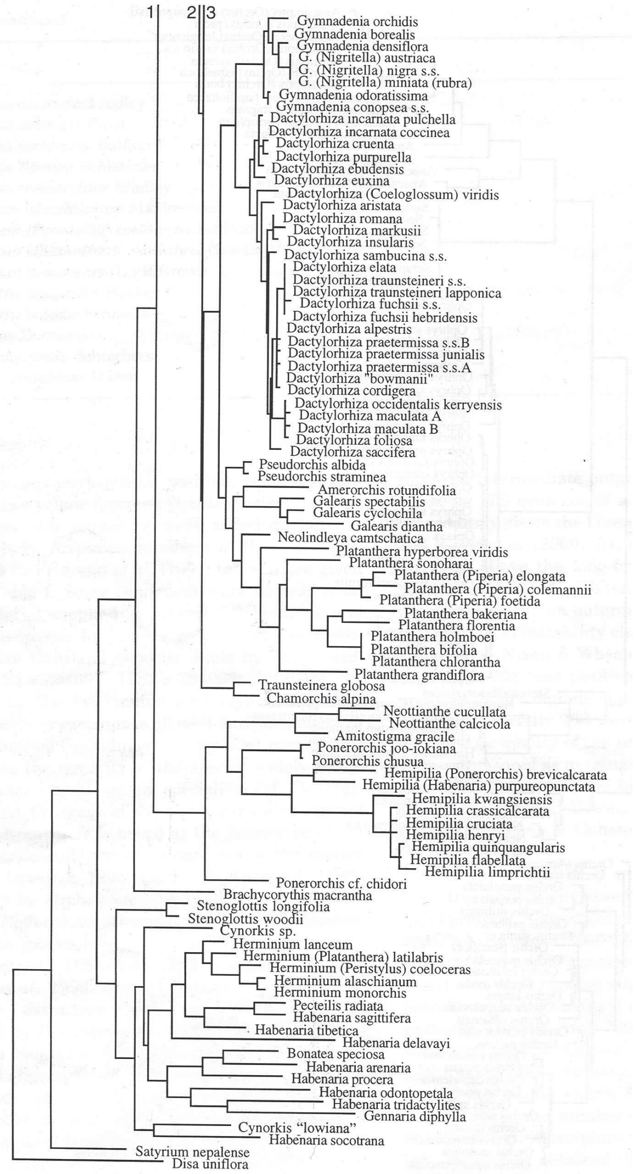


Fig. 1b: The Orchideae phylogeny of Bateman et al. (2003), based on nuclear ITS data (continued).

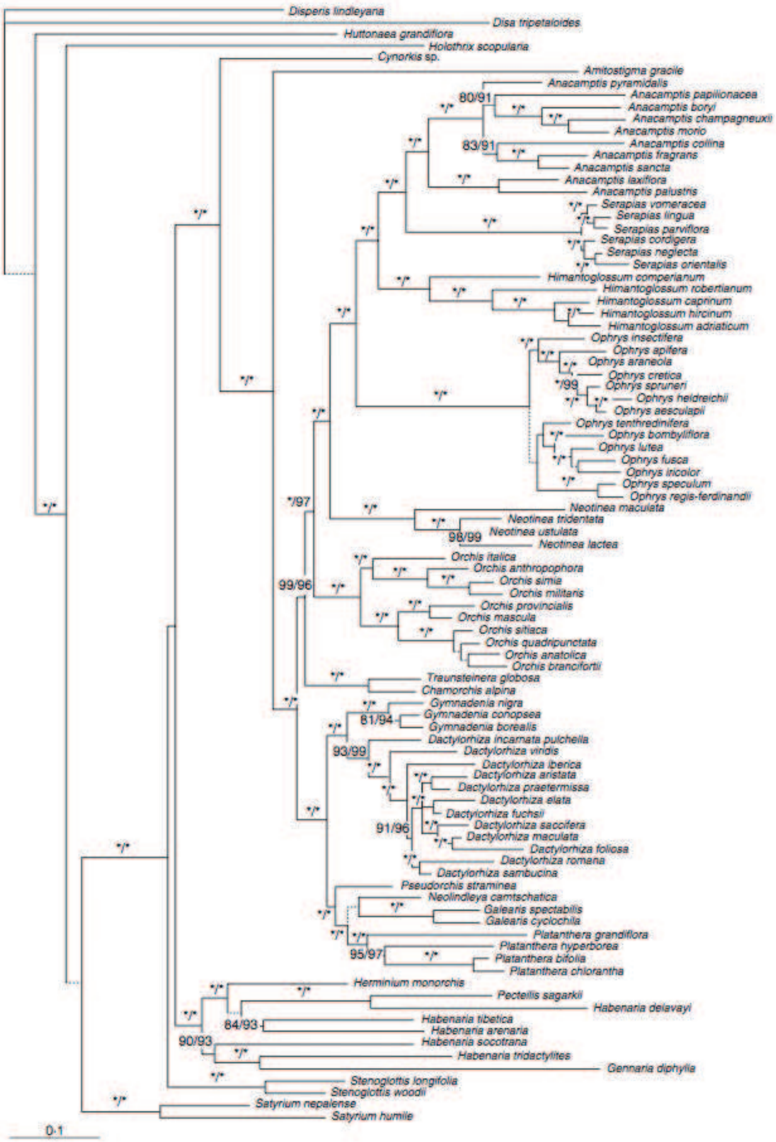


Fig. 2: The Orchideae phylogeny of Inda et al. (2012), based on data from nuclear ITS plus plastid *rpl16* plus mitochondrial *cox1*. Numbers before the slash are bootstrap values, those after the slash are posterior probabilities. Asterisks indicate values of 100%, whereas dashed lines indicate bootstrap values of less than 90%.

Tyteca & Klein (2009) soon received explicit support from a quantitative study of seeds of *Orchis s.l.* conducted by Gamarra et al. (2010, 2012), who reported reliable morphological differences between seeds of anthropomorphic and non-anthropomorphic species of *Orchis s.s.*, and suggested that this distinction further justified recognition of *'Androrchis'*. However, the arguments of Gamarra et al. (2012) do not withstand close scrutiny, as they: (1) were inconsistent, demonstrating a degree of diversity of seed morphology within *Anacamptis s.l.* that is at least as great as that observed within *Orchis s.s.* but nonetheless advocating retention of *Anacamptis s.l.* as single genus; (2) scored the seeds of anthropomorphic *Orchis s.s.* as being identical to the seeds of *Anacamptis papilionacea* and *A. collina* (their table 2), thereby showing that strong convergence in seed morphology can occur between groups that are only distantly related; and (3) formally proposed three sections of '*Androrchis'* (corresponding with Groups 5, 6 and 7 in Fig. 3) after having

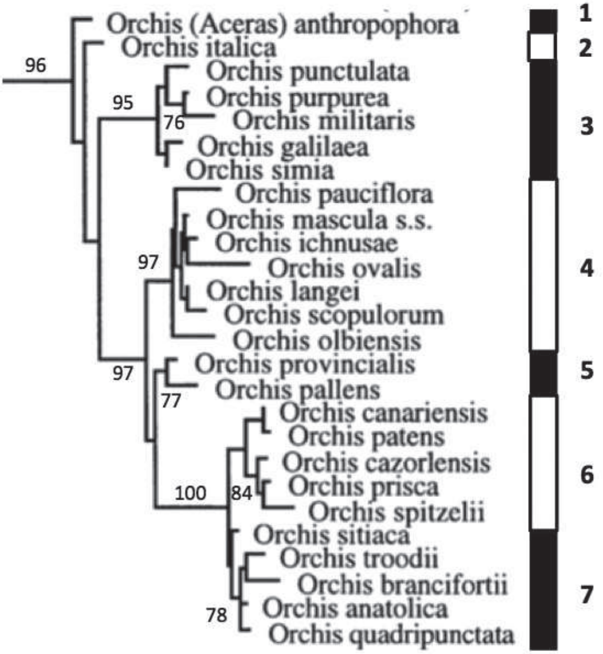
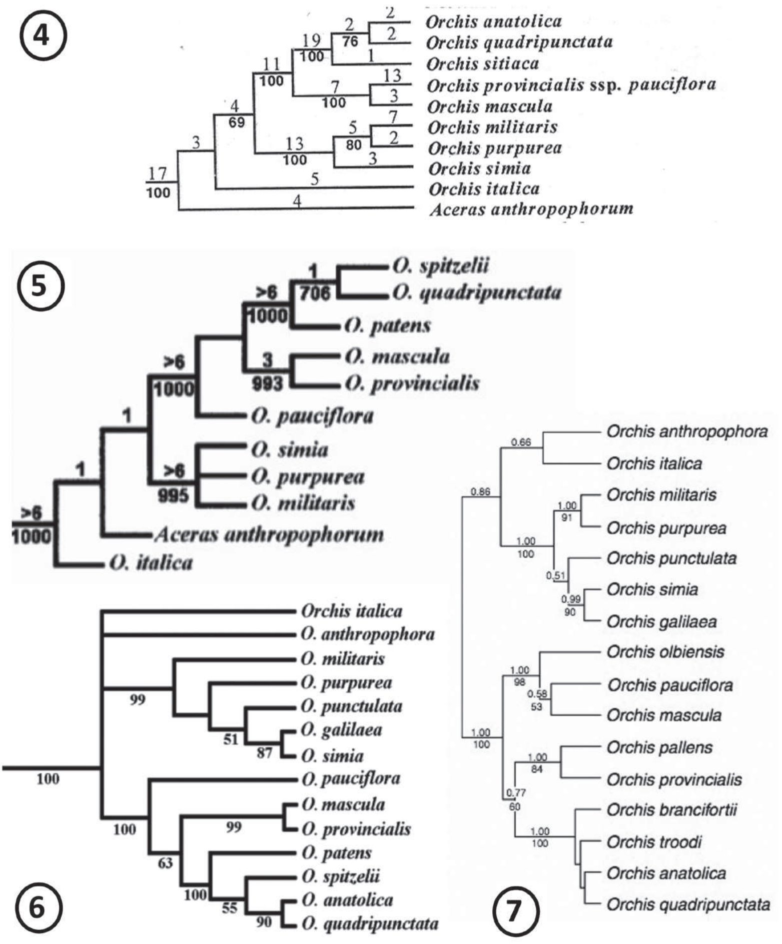


Fig. 3: The *Orchis s.s.* portion of the Orchideae phylogeny of Bateman et al. (2003), based on nuclear ITS data. Figures on branches are bootstrap percentages, and seven apparently monophyletic groups within the genus are numbered (see text).

demonstrated that seed morphology was uniform across the three groups. Taken together, these observations do not encourage prioritisation of seed morphology over other categories of taxonomic data when circumscribing genera of Orchidinae. Although seed data are a valuable contribution to basic taxonomic knowledge, when considered in isolation they offer far too few characters to permit meaningful taxonomic conclusions.

More recently, Tyteca et al. (2012) incorporated the seed-based morphological observations of Gamarra et al. into yet another advocacy of distinguishing at genus level between the anthropomorphic *Orchis sensu strictissimo* and *'Androrchis'*, offering several lines of evidence. Firstly, the *Orchis* ITS data of Bateman et al. (2003) were reanalysed using only a single outgroup and employing Bayesian tree-building methods, predictably yielding a topology (Fig. 8) that is congruent with the less well-sampled tree of Jacquemyn et al. (2011) (Fig. 7); these trees indicate that *'Androrchis'* is monophyletic but command limited statistical support (posterior probability = 0.86).

Moving on to consider extrinsic 'ethological' properties, Tyteca et al. argued that significant differences exist between anthropomorphic *Orchis* and *'Androrchis'* in pollinator spectra (data from Claessens & Kleynen 2011) and typical numbers of mycorrhizal partners (data from Jacquemyn et al. 2011). I have explained elsewhere, strongly and in considerable detail, why when circumscribing taxa we should prefer intrinsic properties such as morphology and DNA over extrinsic properties such as pollinators and mycorrhizal partners (Bateman et al. 2011). But in the case of *Orchis s.l.*, even the "supporting" extrinsic data themselves are unconvincing. Anthropomorphic *Orchis* species average 2.1 mycorrhizal partners relative to 1.4 in *'Androrchis'*, and the most striking feature of the two (admittedly crude) pollinator spectra is their overall similarity rather than dissimilarity. Both anthropomorphic *Orchis* and *'Androrchis'* are dominated by hymenopteran pollinators with subordinate dipterans and lepidopterans – the two groups differ meaningfully only in the greater average frequency of coleopteran pollinators in anthropomorphic *Orchis*, which is largely attributable to a single atypical species, *O. anthropophora*.



Figs 4–7: (4) The *Orchis s.s.* portion of the Orchideae phylogeny of Pridgeon et al. (1997), based on nuclear ITS data. Numbers above branches are branch lengths, those below branches are bootstrap values.
(5) The *Orchis s.s.* portion of the Orchideae phylogeny of Aceto et al. (1999), based on nuclear ITS data. Numbers above branches are values for the decay index, those below branches are bootstrap values.
(6) The *Orchis s.s.* portion of the Orchideae phylogeny of Cozzolino et al. (2001), based on nuclear ITS data and presented as a strict consensus tree. Numbers below branches are bootstrap values.
(7) A phylogeny of *Orchis s.s.* generated by Jacquemyn et al. (2011), based on nuclear ITS data provided by the present author. Numbers above branches are bootstrap values, those below branches are posterior probabilities.

Most intriguing of all was the decision of TYTECA et al. (2012) to conduct a morphometric comparison of five species of anthropomorphic *Orchis*, six species of *'Androrchis'* and, most remarkably, four putative species of the *Anacamptis* (formerly *Orchis*) *morio* group. The 22 characters measured were all metric or meristic (e.g. pigmentation characters were completely ignored) but nonetheless the data were rigorously analysed and yielded a credible outcome, specifically that *A. morio s.l.* is morphologically more similar to species of *'Androrchis'* than is either group to species of anthropomorphic *Orchis*. This result is hardly surprising, as the *A. morio* group is widely recognised as having undergone evolutionary convergence in floral morphology with the *Orchis mascula* group (i.e. with *'Androrchis'* p.p.: PRIDGEON et al. 1997, *et seq*.). I am confident that *Anacamptis* would show at least as much morphological diversity as anthropomorphic *Orchis* and *'Androrchis'* combined if members of the *laxiflora*, *coriophora*, *collina*, *papilionacea* and *pyramidalis* groups had been included in the morphometric analysis. Indeed, if the taxon sampling was extended further to include the *Gymnadenia conopsea* group, we would likely find that they most closely resembled *Anacamptis pyramidalis*, even though the two genera are only distantly related.

But even the above discussion misses the salient point. If TYTECA et al. and others prefer to prioritise overall morphological similarity (i.e. phenetic principles) over monophyly (i.e. cladistic principles) as the primary criterion for genus-level classification, then we should return to pre-1997 classifications of European orchids. Indeed, if phenetics is paramount, the evident strong morphological similarity of *'Androrchis'* to the *A. morio* group will require us to unite these two species groups within a single evolutionarily meaningless genus.

TYTECA et al. (2012, p. 30) concluded that "important criteria for the recognition of genera, as stressed by Stuessy [2009], are the phenetic gap between genera, which should be larger than between species of the same genus, the holophyletic [= monophyletic] nature of genera, and other elements of information that will help to improve the comparisons among taxa for purposes of generic circumscription". But monophyly has been prioritised by modern systematists precisely to *overcome* the chronic problems presented by phenetic approaches, which routinely misplace taxa that are highly morphologically deviant in artificial genera. Thus, it is neither practical nor desirable to award equal priority to both monophyly and phenetic distance, because these two methods often yield contrasting relationships and they are underpinned by radically different philosophies. It is certainly unacceptable to 'cherry-pick' which of these approaches is to be prioritised depending on the particular case-study that is under consideration (Bateman 2009). In my opinion, the most appropriate taxonomic use of morphometrically based phenetic approaches is the delimitation not of genera but rather of species and infraspecific taxa (Bateman 2001, 2012).

Present reappraisal—Here, I have chosen to explore the potential value of *'Androrchis'* by collating ten of the DNA-based trees that have been published since 1997 and that included at least eight species of *Orchis s.s.*, both anthropomorphic and non-anthropomorphic. The trees are illustrated in Figures 3–12, and some of the relevant properties of those trees are compared in Table 1.

The most significant figure to emerge from Table 1 is that all 26 widely recognised species of European *Orchis s.s.* were analysed by Bateman et al. (2003) and re-analysed by Tyteca et al. (2012), whereas the remaining nine studies average only 11 species. Moreover, some of the more recent studies lacked representatives of either one or two of the seven species groups recognised by Bateman et al. (Fig. 3), though to compensate, they added plastid and/or mitochondrial data to the basic nuclear ITS data sets used in eight of these ten studies. It is also worth noting that two separate ITS matrices were gathered in parallel, by Bateman and colleagues and by Cozzolino and colleagues (Aceto et al. 1999; Cozzolino et al. 2001), providing a useful independent test of data accuracy. A further development evident in Table 1 is the switch in 2011 from parsimony tree-building to Bayesian tree-building, and the consequent emphasis on questionable posterior probability values when assessing the relative strengths of branches.

Given that so many variable factors influence phylogeny reconstruction, it is not surprising that so many differences are evident among the resulting preferred trees (Figs 3–12). The most obviously problematic taxa are the readily recognised anthropomorphic species *Orchis* (*Aceras*) *anthropophora* and *O. italica*. In the parsimony trees presented in Figures 3–6 these species

Table 1: Summary of DNA-based phylogenetic trees that included significant numbers of species of *Orchis s.s.*

Study	**No. of species sampled (anthrop. + non-anthrop.)**	**Phylogenetic groups not sampled**	**Genic regions sequenced**	**Tree-building method**	**Branch support estimates**
Bateman et al. 2003	7+19	None	Nuclear ITS	Parsimony	Bootstrap
Pridgeon et al. 1997; Bateman et al. 1997	5+5	Patens	Nuclear ITS	Parsimony	Bootstrap
Aceto et al. 1999	5+6	None	Nuclear ITS	Parsimony	Bootstrap
Cozzolino et al. 2001	7+7	None	Nuclear ITS	Parsimony	Bootstrap
Jacquemyn et al. 2011[1]	7+9	Patens	Nuclear ITS[5]	Bayesian	Posterior probability
Tyteca et al. 2012[1]	7+19	None	Nuclear ITS[5]	Bayesian	Posterior probability
Inda et al. 2010 (1)[2]	5+6	Patens, Provincialis	Mitochondrial *cox1*	Parsimony	Bootstrap
Inda et al. 2010 (2)	5+6	Patens, Provincialis	ITS + mitochondrial *cox1*	Parsimony	Bootstrap
Inda et al. 2012 (1)	5+6	Patens, Provincialis[4]	Plastid *rpl16*	Bayesian	Bootstrap + Posterior probability
Inda et al. 2012 (2)	4+6	Patens, Provincialis[4]	ITS + *rpl16* + *cox1*	Bayesian	Bootstrap + Posterior probability
Bateman et al. 2008[3]	5+3	Patens, Provincialis	ITS + plastid microsats (4 regions)	Parsimony	Bootstrap

[1] Only a single species, *Traunsteinera globosa*, was used as outgroup

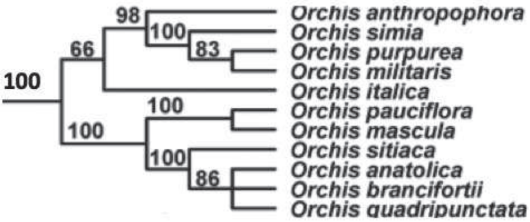
[2] Tree was not illustrated, as the topology was almost wholly unresolved

[3] Each species was represented by many samples

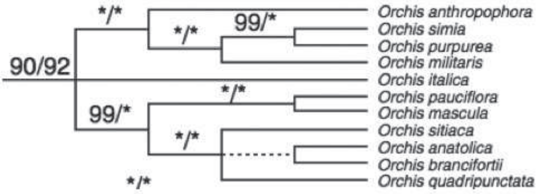
[4] The plant labelled *Orchis provincialis* (Chase-710) was actually *O. pauciflora* (cf. Pridgeon et al. 1997: 93)

[5] Data derived from Bateman et al. (2003)

⑧

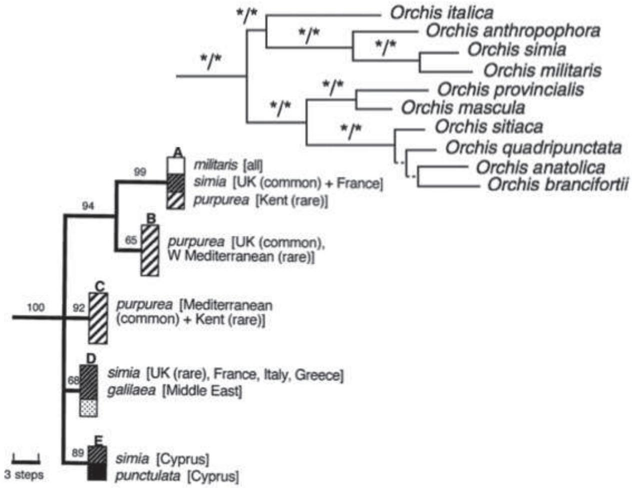


⑨



⑩

⑪



Figs. 8-11: A phylogeny of *Orchis s.s.* generated by Tyteca et al. (2012), based on nuclear ITS data provided by the present author. Numbers above branches are posterior probabilities.
Fig. 9: The *Orchis s.s.* portion of the Orchideae phylogeny of Inda et al. (2010), based on nuclear ITS plus mitochondrial *cox1* data. Numbers above branches are bootstrap values.
(10) The *Orchis s.s.* portion of the first Orchideae phylogeny of Inda et al. (2012), based on plastid *rpl16* intron data. Asterisks indicate values of 100%, whereas dashed lines indicate bootstrap values of less than 90%.
(11) The *Orchis s.s.* portion of the second Orchideae phylogeny of Inda et al. (2012), based on nuclear ITS plus plastid *rpl16* intron plus mitochondrial *cox1* data. Asterisks indicate values of 100%, whereas dashed lines indicate bootstrap values of less than 90%.

are shown as the two earliest-diverging species, making the anthropomorphic species paraphyletic relative to a monophyletic non-anthropomorphic group. Admittedly, these studies differ in whether *O. anthropophora* (Figs 3, 4) or *O. italica* (Fig. 5) is the first species to diverge, or whether their relationship is better treated as uncertain (Fig. 6). In the Bayesian trees (Figs 7, 8, 11) and the parsimony tree combining ITS and mitochondrial data (Fig. 9), the two species are earliest to diverge within a monophyletic anthropomorphic group, *O. italica* being sister to all other anthropomorphic species. The Bayesian plastid tree offers a compromise topology, the placement of *O. italica* being viewed as uncertain. Among the published trees, only those of Jacquemyn et al. (2011) and Tyteca et al. (2012) show *O. anthropophora* and *O. italica* as sister species (Figs 7, 8; admittedly, a similar result was recently obtained by Sramkó, Bateman et al. unpublished). All of the trees show the non-anthropomorphic species as a monophyletic group with 97–100% confidence estimates. But then confidence estimates in the trees are equally high for a *militaris* group (Group 3 in Fig. 3), a *mascula* group (Group 4) and a *patens* plus *quadripunctata* group (Groups 6+7), though the latter group is not evident where both groups were sampled but only poorly (Figs 5, 6). *Orchis provincialis* associates with the *mascula* group in poorly sampled trees but forms a separate, moderately well-supported group with *O. pallens* (Group 5) in better sampled trees (Figs 3, 7, 8).

If we consider a group of more closely related *Orchis* species (Fig. 3), the better-sampled trees (Figs 3, 7–11) suggest that the two non-anthropomorphic species within Group 7 that are characterised by strongly reduced, deeply three-lobed labella – *O. quadripunctata* and *O. brancifortii* – are not sister species (i.e. not collectively a natural group, despite their morphological similarity evident in Fig. 13). Rather, *O. quadripunctata* is seen as being more closely related to the co-occurring *O. anatolica* in some studies (Figs 3, 7, 8) but *O. brancifortii* is seen as being more closely related to *O. anatolica* in others (Figs 10, 11), even though it never co-occurs with *O. brancifortii*, which is confined to Italy. Moreover, none of these apparent relationships attracts strong statistical support, so they are undoubtedly unreliable.

Switching to the anthropomorphic species, the members of the *O. militaris* group (Group 3) differ considerably between trees, which agree only on a medium-strength relationship between *O. simia* and the morphologically similar *O. galilaea*. For this group, we now have the advantage of having accumulated and analysed many samples of several of these species, taken from a wide geographical spread and analysed for both nuclear ITS and plastid microsatellites (Bateman et al. 2008). The results of both datasets (cf. Fig. 12) suggest that relationships among these species that are implied by the remaining trees (Figs 3–11) are, at best, unreliable. Both *O. purpurea* and *O. simia* yielded three distinct ITS alleles and several plastid haplotypes, indicating that extensive gene exchange has occurred. Thus, adopting a traditional typological approach to phylogeny reconstruction, by using just one sample of each species to infer their evolutionary relationships (as in Figs 3–11), would at best yield a seriously simplistic picture.

I anticipate that, having reached this point in this essay, readers will by now be wondering whether DNA-based phylogeny reconstruction is so unreliable as to be meaningless; perhaps we would, after all, be better advised to continue with traditional approaches to plant classification, even though they are *ad hoc* and questionably scientific? However, it is important to remember that seven of the ten trees illustrated in Figures 3–12 are, in fact, small parts of larger trees based on species sampling that spanned much of Tribe Orchideae. If we consider the branch at the base of *Orchis s.s.*, we see that it is relatively long and robust in every one of these trees; only in the plastid tree of Inda et al. (2012: Fig. 9) does this branch attract less than a 100% bootstrap and/or posterior probability value. And this strong branch is found in every one of the relevant trees (the tree of Jacquemyn et al. [2011] and Tyteca et al. [2012] lacks a valid basal branch, as it included only one outgroup and so, by definition, could not test the monophyly of the ingroup – any test requires multiple outgroups).

It is the discovery of this strong underpinning branch in many different trees, based on several different kinds of DNA data – in other words, *congruence* among several studies – that convinces me that this particular branch provides the optimal position for the circumscription of an unquestionably monophyletic genus – in this case, *Orchis s.s.* of Bateman et al. (1997, 2003). In contrast, to circumscribe all of the non-anthropomorphic species as the genus *'Androrchis'* automatically creates an anthropomorphic genus that is

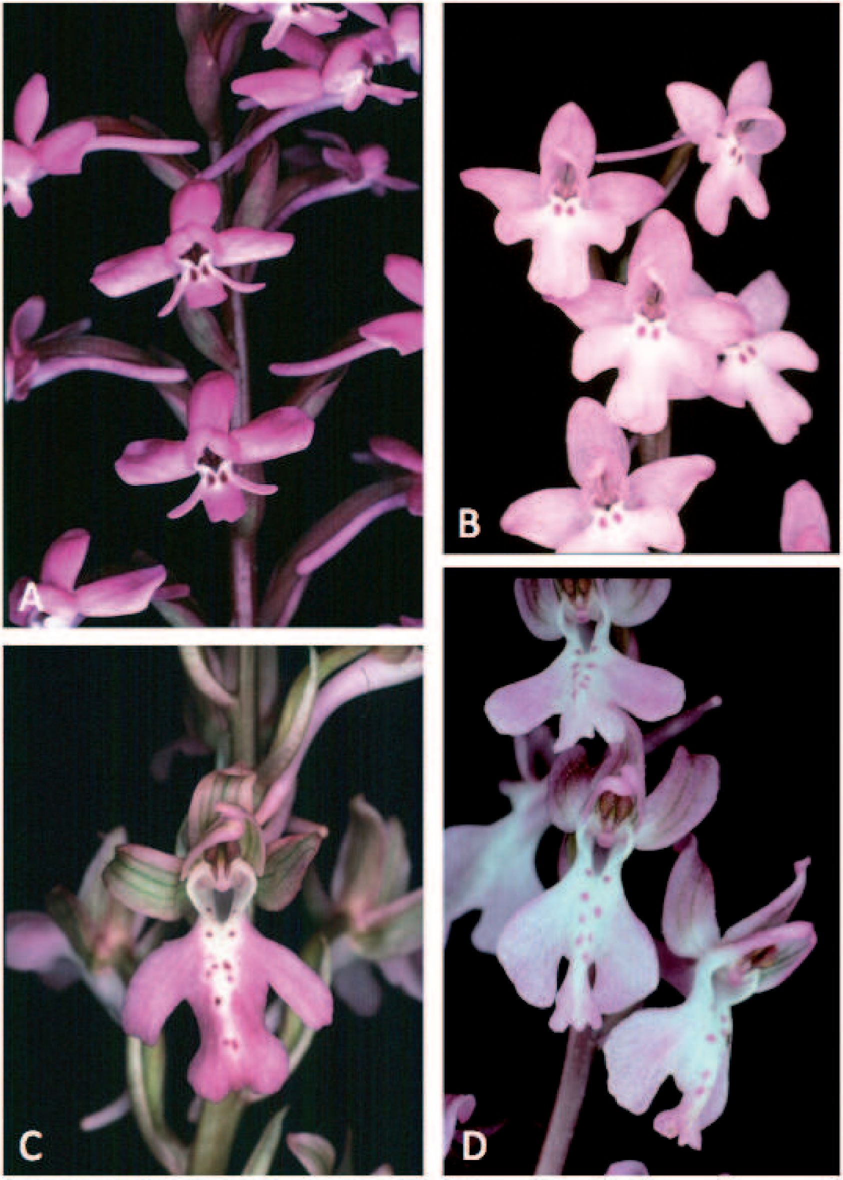


Fig. 12: Flowers of four closely related species of Group 7 of *Orchis s.s.*, reproduced at the same scale (horizontal dimension = 21 mm). (A) *Orchis brancifortii*, Sicily; (B) *Orchis quadripunctata*, Crete; (C) *Orchis sitiaca*, Crete; (D) *Orchis anatolica*, Chios. Images: R. BATEMAN.

questionably monophyletic (potentially fails Rule 1), and certainly is not molecularly robust (definitely fails Rule 2), despite the contrasting labellum shapes, seed morphology and substantial reproductive barrier. Recognition of *'Androrchis'* also requires division of the ITS tree (Fig. 1) using shorter branches than those separating other genera of Orchidinae (fails Rule 3). The rules for dividing a tree into genera, given above, are explicitly designed to maximise the likelihood of future stability within the context of a natural (i.e. monophyletic) classification; they are likely to survive the acquisition of further taxonomic datasets, however extensive. *'Androrchis'* does not meet these stringent criteria.

Tyteca et al. (2012, p. 30) concluded that "the main advantage of recognising *Orchis* and *Androrchis* as separate genera would be the homogeneous and consistent treatment of groups of species among Orchidinae". Ironically, it is because I subscribe to the same primary goal of achieving a consistent genus-level classification of European orchids that I continue to oppose the segregation of *'Androrchis'* from *Orchis s.s.*

The importance of considering the bigger picture

Exploring particular taxonomic issues in isolation is a high-risk strategy. The broader the taxonomic spectrum, and better the species sampling, that is encompassed by a particular phylogeny, the more reliable is the tree (e.g. Zwickl & Hillis 2002). The price paid by Inda et al. (2012) for adding data from plastid and mitochondrial genes to the original nuclear ITS matrix was reducing the number of species included to 92 (seven of which were outgroups), compared with 190 samples considered by Bateman et al. (2003). It is questionable whether adding two information-poor genic regions compensates for the reduced species sampling, particularly as the mitochondrial data alone had already proved incapable of discriminating among *any* genera of Orchidinae (Inda et al. 2010, fig. 1) (Fig. 10). And of course, the more reliable is the tree, the greater is the consistency that can be achieved when using it to circumscribe genera.

The rationale of applying explicit rules to ensure taxonomic consistency appears to have escaped Inda et al. (2012) when interpreting their own molecular phylogenetic trees. Discussing their combined ITS+*rpl16*+*cox1* tree, they accurately stated that "the detailed phylogenetic tree strongly supported the recently [sic] recircumscribed genetic concepts of BATEMAN and collaborators" (p. 71), and later "in general, our results support the changes in classification and nomenclature proposed by BATEMAN et al. (1997, 2003) … all genera [*sensu* BATEMAN et al.] belonging to the "core" Orchidinae (excluding the former Habenariinae) are monophyletic and strongly supported in the combined analysis". Nonetheless, INDA et al. (2012) could not resist making several *ad hoc* taxonomic suggestions, even failing to note the most radical innovation of their tree – the divergence of *Ophrys* before, rather than after, that of *Himantoglossum s.l.* (compare Figs 1 and 2) – in their haste to suggest (though fortunately not actually to enact) taxonomic changes: "Our combined analysis shows that the expanded *Anacamptis* concept is strongly supported and should be employed in taxonomic schemes for the subtribe, although our results do not end the debate over recognizing the *A. laxiflora* subgroup as a distinct genus" (p. 83). And later (p. 85), "*Gymnadenia* and the former *Nigritella* comprise a highly supported clade in both the plastid and combined analyses. These two taxa share several morphological traits that might support their merger, such as palmate-digitate tubers (also shared with *Dactylorhiza* and *Platanthera* [*sic*; its tubers are in fact fusiform]), two lateral, lobe-like stigmas and two pollinia, each with a caudicle. Nevertheless, morphology is, in this case, rather ambiguous, as other traits such as resupination support differentiation between these taxa. Further research is needed to clarify the relationships between these two orchid groups, but with just three accessions [of *Gymnadenia s.l.*] sampled, we cannot comment further."

These casual comments were made by INDA et al. (2012) without any accompanying discussion regarding which principles, beyond molecularly-determined monophyly, they might bring to bear in order to further improve the classification of Subtribe Orchidinae. Without subsidiary rules of the kind outlined above, monophyly does indeed become "almighty", thereby giving some credibility to the accusation levelled by TYTECA & KLEIN (2008) at the often unquestioning and superficial use of monophyly in many modern classifications. And having dismissed the idea that *Anacamptis pyramidalis* might justify continued recognition as a monotypic genus, despite its morphological distinctiveness, why did INDA et al. (2012) then invoke morphological characters when discussing whether *'Nigritella'* merits genus-level separation from *Gymnadenia*? With all the data now available demonstrating that

'Nigritella' arguably fails Rule 1 and certainly fails Rule 2 and Rule 3, why is "further research needed to clarify the relationships"? Will the relationships ever be "clarified" to an acceptable degree? Could we not just avoid all this ambiguity and argument by accepting that *'Nigritella'* and *Gymnadenia* are very molecularly similar, share many morphological characters, regularly hybridise where they co-occur, and together form an unquestionably monophyletic group? Doesn't it make far greater sense to accept this considerable body of evidence as being sufficient to justify having combined these former genera into a single genus, *Gymnadenia s.l.*? Ambiguous evidence means that the two former genera *might* each be monophyletic, but we have much greater confidence that the combined genus *is* monophyletic; surely it is better to divide the tree where we have identified perhaps 99% probability of monophyly rather than perhaps 50% probability?

The suggestion of Inda et al. (2012), made without explanation, that the (convincingly monophyletic) *Anacamptis laxiflora* group might merit genus-level separation from *Anacamptis* is an equally clear illustration of a reluctance to apply general principles and seek consistency by considering the bigger picture. *Anacamptis sensu* Bateman et al. undeniably encompasses considerable diversity, both molecularly and morphologically; this observation has led several authors to suggest that *Anacamptis s.l.* should be divided into two or more smaller genera (historically reviewed by Bateman et al. 1997). The most recent attempt was made by Delforge (2009), who chose to recognise five genera within *Anacamptis s.l.* The *Anacamptis laxiflora* group is molecularly distinct, morphologically distinct and undoubtedly monophyletic, thus passing Rules 1 and 2, so why not recognise it as a separate genus? Well, these statements apply with equal probability to the *A. coriophora* group and the *A. pyramidalis* group, so consistency would require us to similarly recognise these two groups as distinct genera, apparently supporting Delforge's arguments.

But having divided *Anacamptis s.l.* thus far, which genus name would we then apply to the residue of *Anacamptis*, containing species such as *A. morio*, *A. papilionacea* and *A. collina*, none of which are sisters? In other words, breaking up *Anacamptis s.l.* would contravene Rule 3. Also, if we scan across the entire Orchidinae tree (Fig. 1), we immediately see that several other monophyletic groups show degrees of molecular divergence equal to those of the subgroups within *Anacamptis s.l.* Consistency would require us to once again separate *Comperia* and *Barlia* from *Himantoglossum s.l.* (genera that, ironically, were first amalgamated by Delforge 1999) and to fragment *Platanthera* into several component genera (e.g. the Icelandic *P. hyperborea* would presumably revert to being *Limnorchis hyperborea*). We might even once again be tempted to partition *Orchis s.s.* into two or more groups, following Tyteca et al. (2012). Each of the resulting 'microgenera' of Orchidinae would contain few species, and collectively those species would show very limited molecular and morphological diversity. Although they would be monophyletic, and thus would be preferable to the polyphyletic 'macrogenus' that was *Orchis s.l.* prior to 1997, would such 'microgenera' really be as useful for classification as the medium-sized 'mesogenera' circumscribed by Bateman et al. (1997, 2003)? When answering this question, do bear in mind that genus is the only widely used rank below family and that the orchid family contains an estimated 25,000 species. Using these 'splitters' criteria for circumscribing (micro)genera, a family-wide classification of Orchidaceae would consist of at least 5,000 genera!

Another informative example of inappropriate use of phylogenetic information was provided recently by Jin et al. (2012). In order to assess the taxonomic status of the morphologically ambiguous Himalayan orchid *Habenaria griffithii*, these authors accumulated, largely from GenBank, 117 combined sequences from the plastid regions *rbcL* and *matK* sampled across Subfamily Orchidoideae, and within that taxonomic spectrum, 72 nuclear ITS sequences sampled from across Tribe Orchideae. The resulting consensus trees from the plastid and nuclear data matrices both placed *Habenaria griffithii* as sister to the distinct European habenariid *Gennaria diphylla*, a relationship that achieved 100% bootstrap and posterior probabilities in both the nuclear and plastid trees. Both trees also show long terminal branches subtending the two species – in other words, indicating that considerable molecular divergence has occurred since the two lineages separated. The authors therefore concluded that *'Habenaria' griffithii* should be segregated as a new monotypic genus, *Nujiangia griffithii*.

In making this decision, Jin et al. ignored several relevant facts. Firstly, the near-random selection of Orchideae species selected for inclusion in the analysis was guaranteed to generate false relationships, an outcome that is immediately evident when the trees of Jin et al. (2012) are compared with the better-sampled trees of Bateman et al. (2003) and Inda et al. (2010, 2012). Moreover, those previous studies revealed *Gennaria* to be a problematic 'wildcard' taxon; specifically, its long underpinning branch is prone to long-branch attraction, preferentially attracting as apparent sister-group other taxa that are similarly subtended by relatively long branches. Thus, any taxon appearing to be sister to *Gennaria* should be treated with suspicion, particularly when it is confined geographically to a different continent. When actually transferring *griffithii* from *Habenaria* to the supposed new genus *Nujiangia*, Jin et al. (2012) ignored any other generic transfers suggested by their tree. Even the few *Habenaria* species included by the authors form a single paraphyletic group in their ITS tree and two potentially monophyletic groups in their plastid tree (three groups if *H. griffithii* is included).

It is clear from their trees, as it has been clear from all previous phylogenetic trees, that the species-rich genus *Habenaria* is in desperate need of phylogenetically supported taxonomic revision, almost certainly requiring subdivision into several genera. But what is needed is a thorough, global monographic revision of the habenariids. As Jin et al. (2012, p. 68) themselves stated, "it is clear that many more species and genera and molecular markers are urgently needed to resolve the taxonomic problem of Orchideae" (strictly, of Habenariinae). How, then, does it help our understanding of relationships in this group to simply focus on one species and to create (even "tentatively") a new monotypic genus to accommodate that species, using as a justification a relationship with *Gennaria* that is almost certainly spurious. And in the unlikely event that the sister-group relationship inferred between *Habenaria griffithii* and *Gennaria diphylla* does ultimately prove to be correct, why not assign *H. griffithii* to *Gennaria*, rather than establishing two genera, both monotypic, as presumed sister genera? In this case (and in many others), DNA-based phylogenies have been produced but the results do not adequately justify the piecemeal taxonomic decisions then taken by the authors.

Taxonomy should be pursued as a genuinely scientific enterprise

In my opinion, taxonomic decisions involving the circumscription of genera have been taken far too casually by most orchid enthusiasts. Linnean binomial names are all too easy to create but extremely difficult to subsequently discredit. It is therefore essential that we can be confident that a formal Linnean name describes a meaningful biological and evolutionary entity – one that is assigned to the most appropriate taxonomic rank. When generating taxonomically useful datasets, such as the excellent seed descriptions of Gamarra et al. (2010, 2012), it is not necessary for authors of such papers to immediately make taxonomic changes on the basis of those highly restricted data. And when generating phylogenies primarily to answer evolutionary questions – for example, the study of Inda et al. (2012) focused more on inferring the timing and nature of divergences in pollination systems than on taxonomy – why succumb to the temptation to also make brief and inadequately justified taxonomic inferences? Many of the best-known students of European orchids have adopted a piecemeal approach to re-circumscribing genera, reclassifying species in relatively small groups over considerable periods of time, using a traditional approach based on 'intuitive morphology'. Such an approach is unlikely to lead to either accuracy or consistency. Even Tyteca & Klein (2008), in their admirably broad and detailed suggestion of an alternative classification of Orchidinae, omitted from their account those phylogenetically intermediate genera whose circumscription had not caused recent controversy, such as *Ophrys* and *Himantoglossum s.l.*

When circumscribing genera it is essential that we (a) simultaneously classify a wide range of species, (b) state and use explicit rules, and (c) apply those rules to extensive bodies of quantitative data, ideally spanning both the molecular and the morphological realms. This is not a task that can be satisfactorily addressed using *ad hoc* approaches.

I realise that the present article, in which I have emphasised key points by deliberately critiquing the work of selected colleagues, is liable to be viewed as a desperate attempt to defend the phylogeny, and resulting generic circumscriptions, enacted by Bateman et al. (1997, 2003). But my actual primary goal has been to explain more effectively the rationale that underlies those generic circumscriptions, and to argue that this rationale has not yet been damaged by the various criticisms that it has received during the subsequent 15 years (reviewed by BATEMAN 2009). I am not arguing that the phylogeny of BATEMAN et al. (2003) cannot be strengthened. However, I do not believe that their *circumscription of genera* can be improved upon.

Most notably, we are now on the brink of a flood of DNA sequence data that will be generated as next-generation sequencing becomes affordable to systematists (e.g. COTTON et al. 2013). These new sequencing technologies allow rapid generation of vast quantities of data; for example, it is becoming commonplace to sequence all of the *ca* 100 genes found in the DNA of a plastid, generating data for perhaps 160,000 bases from each plant analysed. Matrices of similar or much greater size will be obtained from the mitochondrial and nuclear genomes respectively. If a substantial percentage of these bases prove to be variable and hence can be used as characters in tree-building matrices, the resulting trees will have enormously long branches that will consequently earn exceptionally strong statistical support. So will this deluge of data finally provide us with the fabled 'one true tree'?

I think not. My fear is that the flood of sequence data will be immediately consolidated into vast global analyses – a 'black box' approach that is unlikely to lead to interpretations of the results that extend beyond crude assessments of statistical probability. If a more thoughtful and scientific approach *is* taken, we will see that trees generated from different genes and different genomes will continue to disagree with each other (albeit with greater statistical probability!) in details of relationships between some species and perhaps even between some generic circumscriptions, and such conflicts will continue to perplex those of us who wish to reconstruct the details of exactly how these groups of orchids evolved. However, I am confident that generating these exceptionally data-rich trees will *not* undermine the present genus-level circumscriptions, provided that the above rules continue to be applied. Stability and predictivity constitute the greatest advantages of circumscribing genera using only the most robust phylogenetic branches.

I will close this essay by predicting that the only remaining taxonomic changes in European orchids at genus level are likely to affect two traditionally circumscribed genera that are dominantly tropical and subtropical and are unusually species-rich, though each is represented by only one species in the European orchid flora. Current evidence suggests that *Malaxis monophyllos* is not closely related to the type species of *Malaxis*, and *Habenaria tridactylites* is not closely related to the type species of *Habenaria* (both generitypes are endemic to eastern USA). But until phylogenetically broad molecular trees have been published that span the full taxonomic range of these dominantly tropical and subtropical groups, it would be not just premature but even scientifically reckless to attempt to rename the genera containing these species on the basis of traditional taxonomic whims – or even on the basis of rigorous phylogenetic analyses, if those analyses do not include an adequate spectrum of relevant species that occur outside Europe.

Perhaps, by some miracle, we could now agree that the genus-level circumscription of European orchids, as summarised in the global *Genera Orchidacearum* project (Pridgeon et al. 1999, *et seq*.), is already optimal? We would then be free to concentrate our research efforts on addressing a far more challenging and open-ended topic – the optimal circumscription of *species* (Bateman 2012).

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