Floral formulae updated for routine inclusion in formal taxonomic descriptions

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Abstract Building on two centuries of history, we advocate an expanded and maximally informative format for floral formulae to describe angiosperm flowers in formal taxonomic descriptions. Using standard typeface and Unicode character codes, the format can summarise a wide range of features, including: acropetal sequence of organ initiation, number and symmetry of each whorl of floral organs (bracts, sepals, petals [or tepals], androecium, gynoecium, ovules), position of the organs relative to each other, partial and/or complete fusion of organs, resupination, organ loss and suppression, and deviations from standard bisexuality. We use several complex flowers to demonstrate our view that all known flower morphs can be accurately represented by the updated format, and show how use of floral formulae can outline some unanswered questions regarding the floral organisation of the model organism *Arabidopsis*. Possible uses of floral formulae extend beyond static description of mature morphology into the comparative realm. When combined with phylogenies, they help to elucidate generalised groundplans, plesiomorphic architecture, and the location and polarity of particular character-state transitions. They can usefully be applied within as well as between species, to compare wildtype versus mutant morphs and different ontogenetic stages. Perhaps their greatest strengths are that they (1) require only a universally available typescript, and (2) bring a comprehensive uniformity to the description of flowers, acting as a checklist of features to be examined. We recommend that floral formulae become a routine component of diagnoses in protologues and other formal taxonomic (re)descriptions, functioning as a logical phenotypic counterpart to the DNA barcode.

Keywords *Antirrhinum*; *Arabidopsis*; Caesalpinioideae; floral diagram; floral formula; floral morphology; flower; Lecythidaceae; Orchidaceae; protologue; taxonomic description

INTRODUCTION

Two contrasting but complementary methods were developed during the nineteenth century to represent the fundamental architectures of angiosperm flowers. The pictorial approach was termed the floral diagram, whereas the textual approach was termed the floral formula (examples are given in Fig. 1). Both approaches were developed during the nineteenth century when they achieved a reasonable level of usage in mainstream literature (cf. Grisebach, 1854; Sachs, 1873; Eichler, 1875, 1878; Goebel, 1887). However, use of floral diagrams declined during the twentieth century, and floral formulae travelled even further into obscurity, despite the fact that they convey a great deal of information in a highly compact form using only standard typeface.

Here, we update the floral formula for a wide range of twenty-first century uses, and argue that the floral formula should be routinely included in formal (re)descriptions of angiosperm taxa. We broadly follow traditional iconography, but also propose some modifications based on symbols that have become widely available. A logical conclusion of the current drive to establish DNA barcodes to provide species identifications and accelerate species discovery (e.g., papers in Savolainen & al. 2005) should be inclusion of such barcodes in the protologue describing new species. However, even the most avid supporters of barcoding agree that this approach will not work efficiently for all plants. Floral diagrams, while extremely useful, cannot be inserted into standard text. We suggest that floral formulae represent a simple and user-friendly morphological counterpart to the DNA barcode.

Our pragmatic goals in preparing this advocacy were (1) to stimulate discussion in order to achieve a consensus format among the botanical community for the floral formula, and (2) to encourage the architects of the *International code of botanical nomenclature* to specify minimum levels of character-based information (including floral formulae) required in any formal taxonomic description.

HISTORICAL DEVELOPMENT OF FLORAL FORMULAE

Although the first attempt to describe floral structure via floral formulae was made by Cassel (1820), the first formulae that resemble those used today were developed by Martius (1828). Grisebach (1854) made especially extensive use of floral formulae. For many plant families and genera he annotated a much-reduced formula in which he gave the number for each floral whorl from the periphery to the centre of the flower (e.g., he annotated for Ranunculaceae “5, 5, ∞, ∞”, indicating 5 sepals, 5 petals, many stamens and many carpels). Sachs (1873) also made extensive use of both floral diagrams and floral formulae in his influential *Lehrbuch der Botanik* (for a translation of Sachs’ book see Goebel, 1887). He highlighted advantages of the formula over the diagram, noting that the former can be printed in “gewöhnlichen Typen” (i.e., ordinary typescript: Sachs, 1873: 519) and – perhaps more importantly – is capable of broader generalisation, because the figures can be replaced by letters as numerical coefficients.

Sachs (1873: 520) also developed a convention for generalised formulae. For example, the formula for Monocotyledonae, Kn Cn An+n Gn(+n), indicates that their flowers are typically composed of five alternating whorls, each with the same number of organs, and that two whorls are expressed as perianth whorls, two as staminal whorls and one usually as a carpellary whorl; the parenthetic (+n) at the end of the formula indicates that there is occasionally a second carpel whorl present (note that the parentheses here are not used to annotate fusion, but rather to indicate an alternative condition). Most petaloid monocots would have a value of 3 for “n”.

Eichler’s (1875, 1878) *Blüthendiagramme* set an admirable standard in comparative floral morphology by making extensive use of floral diagrams. In contrast, he was surprisingly cautious in employing floral formulae, using them only to summarise the “Typus” of families with relatively simple flowers. His approach emphasises the fact that floral formulae have never been universally accepted by the botanical community.

Sattler (1973) described the ontogeny of 50 plant species, annotating these taxa with floral diagrams and floral formulae. Interestingly – and typical of his philosophical viewpoint – Sattler (1973: xvii) noted that “the floral formula is interpretative, based on the conception that the flower is a modified monaxial shoot without axillary buds. Since this idea of the flower is the predominant one today and usually the only one dealt with in textbooks, the inclusion of the floral formula may facilitate understanding of the organogenetic description for those who have received classical botanical training. Those who do not wish to be biased by the interpretative nature of the floral formula … should disregard the floral formula.”

Most of the recent uses of floral formulae have provided relatively brief summaries that served merely to convey the typical number of organs present in each of the three or four categories of whorl. Ellstrand (1983: 119) mentioned only that the “5-5-5-3” floral formula (5 sepals, 5 petals, 5 stamens, 3 carpels) of *Ipomopsis aggregata* is both remarkably constant throughout its genus and also almost invariant in its family, Polemoniaceae. Tian & al. (2007: 262) summarised the flowers of the tepallate *Circaeaster agrestis* (Circaeasteraceae) by presenting “the number of the floral organs by using floral formulas $P_nA_nG_n$”, where the subscripts represent organ number. Judd & al. (2007) made extensive use of floral formulae in their popular textbook on plant systematics, though their formulae are highly simplified (without use of capitals for different organs) and are less accessible via normal typescript. Méndez & Gómez (2006: 225) generalised that “floral structure in angiosperms is usually represented by means of a floral formula, which summarises the number and arrangement of floral organs (sepals, petals, stamens and carpels).” In contrast, we are proposing the consistent use of more comprehensive floral formulae with a far wider range of applications.

A STANDARDISED FLORAL FORMULA FOR THE TWENTY-FIRST CENTURY

Building on the principles established by Sachs (1873), and after considerable discussion, we have developed an agreed set of guidelines and a resulting standardised format for presenting floral formulae. We believe that this protocol will serve the needs of the many diverse uses to which floral formulae could (and should) be applied. We now briefly consider the successive elements of the suggested common formula (Table 1):

Floral symmetry. — Following the terminology of floral symmetry laid down by Endress (1999, 2001), the following symbols are available to denote the main categories of floral symmetry: “*” for polysymmetry (=radial symmetry; with >2 symmetry planes), “↓” for median monosymmetry (=zygomorphy = dorsiventral symmetry; with a single symmetry plane in median direction), “→” for transversal monosymmetry (single symmetry plane in transverse direction), Ø” for oblique monosymmetry (single symmetry plane oblique), “┼” for disymmetry (with two symmetry planes; note that we prefer the symbol “┼” over the frequently used “+” because the latter is used here to separate different whorls of similar organs), and “∂” for true asymmetry (lacking symmetry planes; here we propose the symbol for a partial differential, because it is readily available on PCs and therefore more accessible than other previously suggested symbols).

Rudall & Bateman (2002: 435) argued that floral formulae can convey a more precise explanation of floral symmetry by reporting the symmetry of each successive organ whorl in the flower, rather than the entire flower, using a superscript that represents the number of observed symmetry planes. Accepting their objective but modifying their suggested method, we here propose to add the above-mentioned symbols for each organ category directly after the whorl that it qualifies. This follows the logic of the analytical method, in which the organ whorl is first identified, then quantified and finally qualified. For example, the cypripedioid orchid shown in Fig. 1A has a monosymmetric sepal whorl, a monosymmetric petal whorl vertically bisecting the labellum, a monosymmetric androecium vertically bisecting the column, and a polysymmetric inferior ovary. The “overall symmetry” of the mature (anthetic) flower, as it appears to floral visitors, can if required be annotated using the appropriate signature at the very beginning of the floral formula.

Organ abbreviation and sequence. — We have adopted as the basis of our format the four fundamental categories of whorl that characterise eudicots. These four categories formed the basis of the typically quadripartite ‘KCAG’ (or, in appropriate cases, the tripartite ‘PAG’) floral formulae advocated by Sachs (1873). They are listed centripetally (acropetally) from the periphery to the centre (base to apex) of the flower along the floral axis: K calyx (sepal number), C corolla (petal number), A androecium (stamen number), G gynoecium (carpel number). We indicate stamen fascicles using superscripts. For example, the three fascicles, each consisting of many stamens, of *Hypericum perforatum* are given as $A3^{\infty}$ (for discussion of the morphology and homologies of stamen fascicles see

Table 1. Symbols used in updated floral formulae (symbol description plus Unicode character code in parentheses; see text for a detailed discussion of each symbol).

Symmetry:	
↓	median monosymmetry (downwards arrow; Unicode: 2193)
→	transverse monosymmetry (sidewards arrow; Unicode: 2192)
Ø	oblique monosymmetry (Latin capital letter O with stroke; Unicode: 00D8)
┼	disymmetry (box drawings light vertical and horizontal; Unicode 253C)
*	polysymmetry (asterisk)
∂	asymmetry (partial differential; Unicode 2202)
Organs:	
B	bracteate (flower in the axil of subtending bract)
Bt	bracteolate (flower preceded by bracteole/s)
K	calyx (number of sepals) (superscript = sepaloid organ)
C	corolla (number of petals) (superscript = petaloid organ)
P	perigon (number of tepals)
A	androecium (number of stamen)
AX^{∞}	stamen fascicles (X = number of fascicles, highlighted with superscript infinity symbol)
AX↔X	obdiplostemonous androecium (X = number of stamens per whorl, connected by "left right arrow"; Unicode 2194)
AX↔	obhaplostemonous androecium (X = number of stamens followed by "left right arrow"; Unicode 2194)
G	gynoecium (number of carpels)
$\underline{G}$	superior ovary
-G-	half-inferior ovary
Ĝ	inferior ovary (capital G with circumflex; Unicode 011C)
V	number of o**V**ules per ovary
Va	**a**pical placentation
Vb	**b**asal placentation
Vc	free **c**entral placentation
Vm	**m**arginal placentation
Vp	**p**arietal placentation
Vx	a**x**ile placentation
®	resupination (registered sign; Unicode 00AE)
Others	
∞	"many" organs (i.e., >12) (infinity; Unicode 221E)
–	defined range of organ number (en-dash; Unicode 2013)
+ (plus)	connects different whorls of the same organ category
: (colon)	separates morphologically contrasting organs within one organ whorl
(x), [x], {x}	fusion of different organs (different kinds of bracket allow for a nested series of up to three levels of fused organs)
^{r}	organ reduction (superscript r)
^{0}	organ loss (superscript zero)
♀	female (pistillate) flower (female sign; Unicode 2640)
♂	male (staminate) flower (male sign; Unicode 2642)

Prenner & al., 2008). In groups that possess closely-spaced whorls of morphologically similar sepals and petals (such as many monocots), both K and C are replaced with P for tepals (the 'P' represents a perigon – one or more undifferentiated whorls subtending the inner floral organs).

We here argue for the addition of ovules as a fifth category of organ (see also Sattler, 1973). To avoid confusion of the letter O with a zero, we suggest that o**V**ules should be symbolised by V, yielding a pentapartite 'KCAGV' format. In addition to the number of ovules per ovary, we highlight the type of placentation (Va = **a**pical, Vx = a**x**ile, Vb = **b**asal, Vc = free **c**entral, Vp = **p**arietal, Vm = **m**arginal placentation).

If required, the presence or absence of flower-subtending bracts (B) and/or flower-preceding bracteoles (Bt) can be annotated at the beginning of the floral formula, immediately prior to K or P (for discussions of these organs and their value in floral ontogeny and inflorescence terminology see Prenner, 2004a; Prenner & al., 2009). Similarly, it is possible to highlight the existence of an epicalyx or calyculus at the beginning of the floral formula; for example 'B3' in *Tofieldia*. Each of these lettered abbreviations is followed by the number of organs present in that whorl, or in the case of ovules, the number per gynoecium. An observed range of organs is indicated with an en-dash (e.g., A3–6). If there are "many" organs the infinity symbol "∞" is traditionally used. We suggest that an appropriate threshold for introducing this symbol would be more than twelve organs within the whorl in question (greater numbers can be given if appropriate).

Annotation within a category of organ. — If more than one whorl is differentiable within a particular organ category, then the different whorls of a single organ category are connected with the plus symbol "+", scoring the outer whorl first. For example, the early-divergent orchid *Neuwiedia* has an outer androecial whorl of three stamens, two suppressed, and an inner whorl of three stamens, one suppressed, giving "$A2^0:1+1^0:2$" (cf. Kocyan & Endress, 2001).

Where further differentiation is evident within one whorl, these morphs can be distinguished using the colon symbol. Within each whorl, the annotated organ sequence begins with the adaxial (typically upper) side of the flower, followed by the organs on the abaxial (typically lower) side of the flower. For example, in a typical flower of the mint family (Lamiaceae) and in the classic model organism *Antirrhinum*, two petals form the upper lip and three petals form the lower lip. Such cases are annotated as $C_{(}2^{\text{upper lip}}:3^{\text{lower lip}}{}_{)}\downarrow$. Note that all five petals are basally fused; this feature is symbolised by the subscript brackets (see discussion below for details). If the adaxial organs are oriented lowermost as a result of 180° rotation of the pedicel and/or ovary (i.e., resupination, as seen in the majority of orchids), adaxial numbers should still be given before abaxial (i.e., following the "original" orientation), but the KCAGV floral formula should be prefixed with the "registered" sign "®" (Fig. 1A, B).

We view an obdiplostemonous androecium as one in which the outer stamen whorl is located opposite the petals and hence the law of alternating whorls is broken (contrary to the definition of Bachelier & Endress, 2009: 502). Obdiplostemony can be annotated with "↔" between the whorls, as in our example of *Geranium* (Fig. 1C, D) where the androecium is annotated as "A5↔5". If there is only one whorl of stamens and the law of alternating whorls is broken (i.e., the androecium is obhaplostemonous), as in Primulaceae, the location of the stamens opposite the petals can be indicated as "A5↔" (i.e., omitting the position of the second whorl of stamens).

Organ reduction is annotated as superscript "r", organ loss as superscript "0". If further differentiation of floral organs within a single whorl is required, it is possible to resort to superscript terms. For example, in the legumes, the exceptionally complex five-petalled corolla of the typical papilionoid flag blossom is designated as $C1^{\text{flag}}:2^{\text{wing}}:(2)^{\text{keel}}\downarrow$ (note that the two keel petals are the only petals that are fused, here indicated by parentheses; see following paragraph).

Organ fusion. — Fusion of different organs is indicated using various kinds of bracket. If several organs from different whorls are fused, this can be depicted using a specified sequence of three different types of brackets: "(x)" followed by "[x]" followed by "{x}". If the fusion is restricted to the basal or apical region of the specified organs, brackets are given in subscript or superscript, respectively. For example, in the typical disc flower of Asteraceae, the shared corolla–filament tube and apically fused anthers are annotated as follows: ${}_{[}C(5)\ A^{(}5^{)}{}_{]}$ (see more detailed discussion below under "Within-species applications: mutants and models").

Ovary position. — Ovaries can be either superior (with the outer floral organs inserted at the base of the ovary), inferior (with the outer floral organs inserted on top of the ovary, which appears as if the ovary is congenitally "sunken" into the flower base) or semi-inferior (with the outer floral organs inserted at or near the middle of the ovary; see Endress, 1994; Soltis & Hufford, 2002; Soltis & al., 2003). We here propose to annotate superior ovaries by underlining the "G" for gynoecium ("$\underline{G}$"), inferior ovaries by inserting the letter G with circumflex ("$\hat{G}$") and semi-inferior ovaries with hyphens placed immediately before and immediately after the letter G ("-G-").

Dioecy and related reproductive architectures. — As already noted, the development of floral formulae has been strongly influenced by the classic hermaphrodite eudicot flower that gave us the equally classic 'ABC' model of floral developmental control (e.g., Theissen & al., 2002). However, there exist more complex spatial arrangements where male and female reproductive functions are separated in different flowers (monoecy) or even on different individuals (dioecy), or where male or female function is suppressed in some but not all flowers (gynodioecy and androdioecy respectively) (Barrett, 2002).

For separate male (staminate) and female (pistillate) flowers, we recommend two separate floral formulae prefixed by ♀ or ♂, and linked by the word "plus".

■ EXAMPLES OF FLORAL FORMULAE FOR COMPLEX FLOWER ARCHITECTURES

It is tempting to use flowers with simple ratios of readily distinguished organ whorls to illustrate our format, such as Marsh Crane's-bill, *Geranium palustre* (Fig. 1C, D), with five sepals, five petals, ten stamens in two whorls (arranged obdiplostemonously) and a superior ovary of five fused carpels and ten ovules arranged in axile placentation:

K5* C5* A5↔5* $\underline{G}$(5)* Vx10

However, we are anxious to demonstrate that the format can readily accommodate more complex floral morphologies exhibiting less well-differentiated and/or partially fused

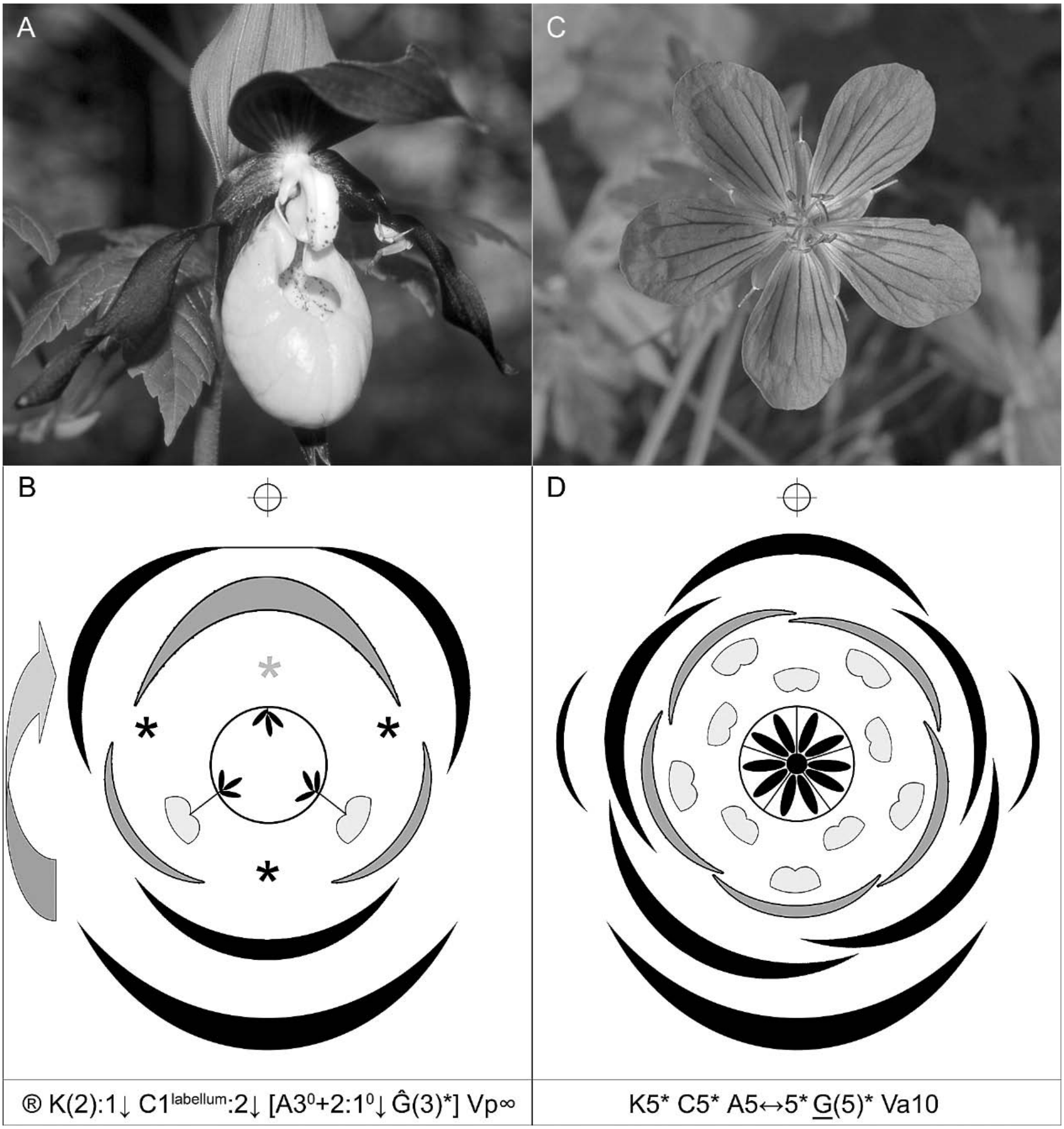

Fig. 1. Flower (A) and floral diagram and floral formula (B) of *Cypripedium calceolus*, a cypripedioid orchid (A by G. Prenner, B modified from Rudall & Bateman, 2002). Flower (C) and floral diagram and floral formula (D) of *Geranium palustre* (Geraniaceae) (C with permission from www.floracyberia.net; D modified from Eichler, 1878).

whorls (Fig. 1A, B). We have chosen our examples from the Asteraceae, Orchidaceae and Papilionoideae, the last of which is not readily convertible to a floral formula, according to Weberling (1989: 19).

The main challenge posed by typical Asteraceae is the basal and/or proximal fusion of floral organs. Use of superscript and/or subscript brackets allows representation of (1) fusion of the five petals to form a corolla tube, shown as “C(5)”; (2) formation of a corolla–filament tube by fusion of stamen filaments with basal parts of the corolla tube, subscript “$_{[}X_{]}$”; and (3) fusion of the anthers that form a tube, superscript “$^{(}X^{)}$”, through which the style will later emerge in order to secondarily present the pollen. Sepals are transformed into specialised hairs or scales (superscript “pappus”) and the inferior ovary consists of a pseudomonomerous gynoecium of two fused carpels with a single ovule in basal placentation. The floral formula for a typical radially symmetrical Asteraceae disc flower is therefore:

$$K^{pappus*}\ {}_{[}C(5)^{*}\ A^{(5)*}{}_{]}\ \hat{G}(1{:}1^{r})^{*}\ Vb1$$

In orchid flowers, the various elements of the androecium and gynoecium are fused into a single structure termed the gynostemium (column), and three to five of their presumed ancestral number of six stamens are suppressed (e.g., Rudall & Bateman, 2002, 2004). Orchids also show considerable diversification within particular organ whorls, notably the differentiation of a labellum from among the three petals. We here take as our example the resupinate flower (annotated with the prefixed registration sign) of Lady's Slipper, *Cypripedium calceolus* (Fig. 1A, B):

® K(2):1↓ C1^{labellum}:2↓ [A3^{0}+1^{0}:2↓ $\hat{G}$(3)*] Vp∞

Lastly, the floral formula for a typical papilionoid 'flag blossom' can be translated into a floral formula:

K(5)↓ C1^{flag}:2^{wing}:(2)^{keel}↓ A(5+4):1↓ $\underline{G}$1↓ Vm1–∞

The different types of petals (adaxial flag, lateral wing petals and abaxial keel petals) are annotated in superscript. The chosen formula denotes a species in which five stamen filaments of the outer whorl and four stamen filaments of the inner whorl are fused to an adaxially open sheath, whereas the tenth stamen, located in the adaxial position, remains free (as in the French bean, *Phaseolus vulgaris*). In brooms (*Genista* and its relatives), all ten stamen filaments form a closed filament tube, annotated as A(5+5), whereas in other species of the same subfamily, such as the pagoda tree (*Styphnolobium japonicum*), all ten stamens remain free, annotated as A5+5 (for details see Prenner, 2004b). The gynoecium consists of a single superior ovary that contains one to many ovules in marginal placentation.

In summary, we are confident that any flower can be converted into a floral formula with little if any loss of architectural information.

■ THE DIVERSE USES OF FLORAL FORMULAE

Comparative biology. — Thus far, we have discussed floral formulae as a means of summarising isolated, static floral morphologies. In fact, they have an additional role in comparative biology. Although comparison is most commonly confined to mature (anthetic) morphs representing different species, the method is equally applicable to comparisons within species, either of contrasting mutant floral morphs (e.g., Bateman & Rudall, 2006; Nutt & al., 2006) or of contrasting ontogenetic stages (e.g., Tsou & Mori, 2007).

Inferring groundplans. — Eichler's (1875) conservatism in deploying floral formulae usefully highlights two different uses of floral formulae, distinguishing empirical formulae that accurately reflect the actual appearance of one particular depicted taxon from theoretical floral formulae that aim to convey the fundamental essence of a range of evolutionarily related floral morphologies. 'Essential' formulae are sometimes termed a floral groundplan. Motivations for inferring groundplans differ. Some authors are seeking the 'ancestral' (in modern parlance, plesiomorphic) condition for the clade under scrutiny. Others are seeking a more dynamic comparison, either between putative plesiomorphic and apomorphic mature groundplans (perhaps exploring gains or losses of organs) or, less commonly, between juvenile and mature floral architectures in an ontogenetic series within a single species.

Groundplans are best inferred by vertically tabulating floral formulae (Tables 2, 3), which is the most effective available method of highlighting the architectural differences that distinguish between different floral morphs. For example, in Table 2 we have summarised floral formulae distributed throughout the text of the recent study of floral diversity in the legume subfamily Caesalpinioideae by Prenner & Klitgaard (2008), who demonstrated that even the most complex floral morphologies found in this group, such as that of the early-divergent *Duparquetia orchidacea*, can easily be encapsulated in the form of a floral formula (Table 2). Displaying all relevant formulae together in a tabular format enables the reader to easily track trends in flower evolution within this florally diverse subfamily. There is a widely accepted legume floral groundplan of K5 C5 A5+5 $\underline{G}$1 Vm1–∞, but the caesalpinioids show great diversity within this groundplan, using as their main evolutionary theme the fusion and/or suppression of organs (Table 2).

In Table 3 we have summarised floral formulae distributed throughout the text of the recent study of floral organogeny and

Table 2. Floral formulae of selected Caesalpinioideae compared with the floral groundplan of Leguminosae (derived from Tucker, 1998, 2000, 2002; Prenner & Klitgaard, 2008).

Caesalpinioideae						
Duparquetia orchidacea	B Bt	K4^{C}:1^{0}↓	C3:2^{r}↓	A$^{(4)}$:1^{0}+5^{0}↓	$\underline{G}$1↓	Vm2–5
Cercis canadensis	B Bt	K(5)↓	C5↓	A5+5↓	$\underline{G}$1↓	Vm∞
Petalostyles labicheoides	B Bt	K3:(2)^{C}↓	C5↓	A3:2^{r}+5^{0}↓	$\underline{G}$1^{C}↓	Vm∞
Labichea lanceolata	B Bt	K3:(2) ↓	C4:1^{0}↓	A2:3^{0}+5^{0}↓	$\underline{G}$1↓	Vm2–3
Dialium guineense	B Bt	K5↓	C1:4^{0}↓	A2:3^{0}+5^{0}↓	$\underline{G}$1↓	Vm2
Tamarindus indica	B Bt^{C}	K3:(2)^{C}↓	C3:2^{r}↓	A(3):2^{r}↓+4^{r}:1^{0}	$\underline{G}$1↓	Vm8–10
Brownea latifolia	B Bt^{C}	K3:(2)^{C}↓	C5*	A(5+4):1^{0}↓	$\underline{G}$1↓	Vm∞
Amherstia nobilis	B Bt^{C}	K3:(2)^{C}↓	C3:2^{r}↓	A(5+4):1^{0}↓	$\underline{G}$1↓	Vm1–6
Leguminosae groundplan	**B Bt**	**K5↓**	**C5↓**	**A5+5↓**	**$\underline{G}$1↓**	**Vm1–∞**

diversity in Lecythidaceae by Tsou & Mori (2007). Although each whorl, most notably the gynoecium, exhibits variation between the scored taxa, the most common formula is K6 C6 A∞ Ĝ(2–8) Vx1–∞. It is tempting to view this as a fundamental groundplan that provided the basis for evolutionary excursions into monosymmetry associated with smaller numbers and fusion of the sepals, and with deviations from the more common number of six petals (Table 3). This is of course only a first approximation which can act as a testable hypothesis in a phylogenetic background.

The opportunity exists in vertical tabulation to place first a full reference formula and then in subsequent formulae use a full stop to indicate identical codings to the reference formula, annotating only deviations from the reference formula (thus mimicking the tabulation of nucleotide and amino acid data in comparative molecular studies).

Phylogenetic applications: inferring plesiomorphic architectures and character evolution. — A modern researcher studying groundplans is most likely to be seeking a plesiomorphic 'ur-architecture' for a particular clade of species. This is best inferred by considering floral morphological characters within a phylogenetic framework based on morphological and/or molecular data. In theory, a floral formula could itself be viewed as constituting as a single phylogenetic character, paralleling similar discussions regarding whether sequences obtained from a single genic region constitute a single 'hypermultistate' character (e.g., Doyle, 1992). However, we would argue that, like a DNA sequence, a floral formula encompasses too much information to act as a single, highly multistate, character in a morphological cladistic matrix.

The greatest strength of floral formulae lies in providing an ideal checklist for characters that can be inserted into normal text, and should be coded in any phylogenetic study of angiosperm flowers. In addition, mapping floral formulae across the terminal branches of a phylogeny, whether morphological or molecular, readily identifies positions on the tree at which specific transitions in floral morphology take place, noting any potentially correlated shifts occurring on the same branch of the tree. It also determines the polarity of the transitions. For example, Rudall & Bateman (2002: figs. 13, 14) mapped shifts in partial and complete suppression of between three and five of the six plesiomorphic stamens among subfamilies of Orchidaceae, thereby clarifying how this suite of characters had evolved within the family.

Within-species applications: ontogenetic series. — The most extensive use of floral formulae in recent literature was by Tsou & Mori (2007) in their study of floral organogeny and diversity in Lecythidaceae. Inspired by Sattler (1973), the authors included symbols for postgenital fusion "<x>" and congenital fusion "(x)". Furthermore, they created an "ontogenetic floral diagram" to convey information on organ sequence and changes of floral symmetry during the course of floral ontogeny (see also Sattler, 1973). Such changes of symmetry patterns during development were already highlighted by Endress (1999), who listed and discussed a broad range of examples of shifts in symmetry during ontogeny. We believe that such changes during ontogeny remain under-studied, and that the translation into ontogenetic formulae could yield a better understanding of floral symmetry in general. Another potentially fruitful excercise would be to annotate different states of paedomorphosis during ontogeny into the format of an ontogenetic floral formula.

Within-species applications: mutants and models. — Although floral formulae have traditionally been used at the species level and above, they are equally applicable to any situation where comparison reveals a substantial qualitative

Table 3. Floral formulae in subfamilies Planchonioideae and Lecythidoideae (Lecythidaceae) (modified from Tsou & Mori, 2007; ovule numbers after Prance & Mori, 1977, 1979).

Planchonioideae						
Barringtonia racemosa	B Bt	K(4)*	C4*	A(∞)*	Ĝ(2–4)*	Vx2–3
Lecythioideae						
Grias peruviana	B Bt	K(4)*	C4*	A(∞)*	Ĝ(4–5)*	Vx2–4
Gustavia macarenensis	B Bt	K(4)*	C8⁎	A∞⁎	Ĝ(4–8)*	Vx7–93
Couroupita guianensis	B Bt	K6↓	C6*	A∞↓	Ĝ(6–7)	Vx30–115
Cariniana domestica	B Bt	K6↓	C6*	A∞↓	Ĝ(3)	Vx13–25
Cariniana micrantha	B Bt	K6↓	C6*	A∞↓	Ĝ(3)	Vx13–25
Cariniana decandra	B Bt	K(5)*	C5*	A(8–10)*	Ĝ(3)	Vx∞
Allantoma lineata	B Bt	K(5)*	C5*	A(30)*	Ĝ(4)*	Vx∞
Couratari sandwithii	B Bt	K6↓	C6↓	A∞↓	Ĝ(3)*	Vx?
Bertholletia excelsa	B Bt	K6↓	C6↓	A∞↓	Ĝ(4)↓	Vx5
Corythophora amapaensis	B Bt	K6↓	C6↓	A∞↓	Ĝ(3–4)↓	Vx5–8
Eschweilera rankiniae	B Bt	K6↓	C6↓	A∞↓	Ĝ(2)↓	Vx∞
Lecythis pisonis	B Bt	K6↓	C6↓	A∞↓	Ĝ(4)↓	Vx10–25
Generalised groundplan	**B Bt**	**K6**	**C6**	**A∞**	**Ĝ(2–8)**	**Vx1–∞**

shift in floral morphology. For example, Bateman & Rudall (2006) explored naturally occurring floral mutants of orchids, comparing mutant with wildtype morphs in the hope of better understanding the basis of floral evolution in the family. Comparing two varieties of the Green-flowered Helleborine, *Epipactis phyllanthes*, yields the following contrast:

Epipactis phyllanthes var. *vectensis*:
® ↓ K3* C1$^{\text{labellum}}$:2↓ [A2^0:1+3^0↓ Ĝ(3)*] Vp∞

Epipactis phyllanthes var. *phyllanthes*:
® * K3* C3* [A2^0:1+3^0↓ Ĝ(3)*] Vp∞

This comparison highlights a transition within the corolla between monosymmetric and polysymmetric floral morphs. Similarly, we can compare the orchid *Cephalanthera damasonium* with a contrasting morph that was originally described as a novel genus by Chen (1965) but was reinterpreted as a homeotic mutant of *Cephalanthera* by Bateman & Rudall (2006):

Cephalanthera damasonium:
® ↓ K3* C1$^{\text{labellum}}$:2↓ [A2^0:1+3^0↓ Ĝ(3)*] Vp∞

‘*Tangtsinia*’ *nanchuanica*:
* K3* C3* [A3+3^0* Ĝ(3)*] Vp∞

Here, another transition to monosymmetry in the corolla is mirrored by a similar transition in the outer (expressed) stamen whorl, suggesting a degree of developmental correlation and encouraging the particular model of floral developmental control in orchids advanced by Bateman & Rudall (2006), and tested by Mondragón-Palomino & Theissen (2009).

Astonishingly, even the best-known angiosperm model organisms, *Arabidopsis* and *Antirrhinum*, possess controversial floral architecture (e.g., Endress, 1992). Even in *Arabidopsis* – the cornerstone of the ‘ABC’ model of floral developmental control and the most intensively researched angiosperm species on the planet – there remain three significantly different interpretations of floral organisation, all of which show peculiarities that are important for discussion of floral structure (cf. Meyerowitz & al., 1991; Endress, 1992; Meyerowitz, 1994; Luo & al., 1996; see also Ronse De Craene, 2002). The flowers can be viewed as either (1) four-whorled with different organ numbers, (2) six-whorled with two organs each and the organs in the median plane are in pairs (except for the sepals), or (3) five-whorled with four organs each; two outer stamens lost and two carpels reduced:

4-whorled: K4┼ C4* A6┼ $\underline{\text{G}}$(2)┼ Vp∞
6-whorled: K2+2┼ C4* A2+4┼ $\underline{\text{G}}$(2)┼ Vp∞
5-whorled: K4┼ C4* A2:2^0+4┼ $\underline{\text{G}}$(2:2$^{\text{sterile}}$)┼ Vp∞

Selecting among these three alternative interpretations has downstream implications for the popular causal models conceived as general explanations of flower development in angiosperms (Meyerowitz & al., 1991; Meyerowitz, 1994).

CONCLUSIONS: THE FUTURE OF FLORAL FORMULAE

The floral formula is a powerful didactic tool. — A floral formula constitutes a compact, consistent, unified, semiquantitative description that requires only universally available typescript and Unicode character code. As such, it is a powerful tool to encourage consistency of floral description, effectively offering a checklist of available floral components and generating what might be termed an ‘identikit’ flower (especially in combination with floral diagrams). Preparing floral formulae encourages both more rigorous analysis of floral form and use of an explicit comparative approach (e.g., Stützel, 2002; Leins & Erbar, 2008). Once the few basic principles governing the format of a floral formula have been learned, formulae also become a valuable teaching tool, encouraging students to examine more closely the flowers put before them (e.g., Burrows, 2009).

Floral formulae are more concise than floral diagrams. — Some observers may argue that floral diagrams convey considerably more information regarding floral architecture than do floral formulae (Fig. 1). We consider both floral formulae and floral diagrams to be under-used tools in systematic studies of angiosperms, viewing them not as alternatives but as mutually supportive and complementary methods of summarising floral architectures. Our revised format for floral formulae upgrades the information content and flexibility of floral formulae. Only the relative sizes and orientations of organs within and between whorls cannot readily be depicted in a floral formula and, to compensate for this one deficit, features reflecting the axial extension of the flower – ovary position and the partial or complete fusion of organs – are more readily summarised as formulae than as diagrams. The greatest strength of floral formulae is their compactness and their exclusive use of typeface; unlike floral diagrams, they are readily employed within bodies of text.

Floral formulae should become a recommended element of formal taxonomic descriptions. — As defined in the glossary to the *ICBN* (*Vienna Code*; McNeill & al., 2006, footnote to recommendation 8A.4), the protologue is “everything associated with a name at its valid publication, i.e., description or diagnosis, illustrations, references, synonymy, geographical data, citation of specimens, discussion and comments.” Bateman (2009, in press) recently highlighted the incongruity evident in the *ICBN* between the plethora of articles and recommendations that regulate nomenclature and the designation of types on the one hand and the character content of the associated diagnosis/description on the other. There are no minimum requirements for the content of a botanical diagnosis (other than that it should be written in Latin: McNeill & al., 2006, article 36.1, 36A), an astonishing freedom that is in practice a recipe for anarchy in both diagnosis and subsequent identifications using that diagnosis. Bateman recommended that the content of diagnoses should be considered more seriously by the *ICBN*, taking into consideration recent initiatives in DNA barcoding (e.g., Tautz & al., 2003; Savolainen & al., 2005) that could lead to diagnoses wholly lacking in morphological information, written in the language of nucleotides rather than Latin.

We believe that a requirement (or, failing that, a recommendation) for routine inclusion of floral formulae in angiosperm diagnoses would bring some much-needed consistency to diagnoses, as well as acting as a *de facto* checklist for features of the flower that merit more detailed description.

Future developments. — We will continue to explore and, where possible, further expand the utility of floral formulae. Two areas where further progress could be made are to explore in greater detail the application of floral formulae to ontogenetic series, seeking to encapsulate heterochronic as well as heterotopic shifts in morphology (e.g., Gould, 1977; Alberch & al., 1979; Bateman, 1994), and to adapt the formulae for application to the (mostly dioecious) gymnosperms, both living and fossil. It is also our intention to encourage other authors to critique our present suggestions in print, with the ultimate goal of achieving a consensus notation for floral formulae.

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