2006

The Good, The Bad, The Ugly: Using Naturally Occurring Terata to Distinguish the Possible from the Impossible in Orchid Floral Evolution

Richard M. Bateman
Natural History Museum, London

Paula J. Rudall
Royal Botanic Gardens, Kew

THE GOOD, THE BAD, AND THE UGLY: USING NATURALLY OCCURRING TERATA TO DISTINGUISH THE POSSIBLE FROM THE IMPOSSIBLE IN ORCHID FLORAL EVOLUTION

RICHARD M. BATEMAN[1,3] AND PAULA J. RUDALL[2]

[1]*Natural History Museum, Cromwell Road, London SW7 5BD, UK;* [2]*Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, UK*
[3]*Corresponding author (r.bateman@nhm.ac.uk)*

ABSTRACT

We interpret extensive field observations of terata in the context of recent insights into monocot phylogeny and evolutionary–developmental genetics to explore the evolution of the orchid flower. Our arguably typological classification of floral terata focuses on natural occurrences of three contrasting modes of peloria (restoration of actinomorphy in a formerly zygomorphic perianth) and three contrasting modes of pseudopeloria (lessening of the degree of zygomorphy shown by the evolutionarily preceding perianth). Dynamic evolutionary transitions in floral morphology are assigned to recently revised concepts of heterotopy (including homeosis: evolutionary transitions in position of expression) and heterochrony (evolutionary transitions in timing of expression), seeking patterns that delimit developmental constraints and allow inferences regarding underlying genetic controls. Lateral heterotopy, occurring within the whorl of three petals (including the labellum) or within the adjacent whorl of three sepals, is more frequent than acropetal heterotopy, and full basipetal heterotopy does not occur. Pseudopeloria is more likely than peloria to generate a radically altered yet functional perianth but is also more likely to cause acropetal modification of the fused filaments and style that constitute the characteristic gynostemium of orchids. We infer that at least one gene or gene complex controls style–stamen fusion, which requires the preadaptation of strongly developed epigyny, and another determines both stamen suppression and labellum formation adaxially. Our earlier hypothesis implicating genes of the TCP family has recently been challenged by empirical evidence of complex interactions between several MADS-box genes. Many transitions are highly iterative, and some are reversible (atavistic). Once heritability has been demonstrated, the most effective criteria for determining the most appropriate taxonomic status of a novel morph are the profundity of the phenotypic shift that it represents, the number and uniformity of the resulting populations, and whether the novel morph subsequently diversified to generate further morphs that retain the innovative features. Although morphological transitions attributable to heterochrony may be a more common driver of speciation than those attributable to heterotopy, we demonstrate that arguably all of the modes of instantaneous floral transition described in this paper have the ability to generate prospecies.

Key words: B-class genes, evolutionary–developmental genetics, floral evolution, heterochrony, heterotopy, MADS-box gene family, orchids, peloria, pseudopeloria, saltation, TCP gene family, terata.

I shall try to prove that sudden [and profound] mutation is the normal way in which nature produces new species and new varieties. These mutations are more readily accessible to observation and experiment than the slow and gradual changes surmised by Wallace and his followers, which are entirely beyond our present and future experience. The theory of mutations is a starting point for direct investigation, while the general belief in slow changes has [long] held back science from such investigation.

—Hugo DeVries, 1906 (ed. 2: 30), *Species and varieties: their origin by mutation*

Who could blame us if we would refer to orchids as monstrous lilies?
—J. W. Goethe, 1887, *Goethes Werke* (translated in Weber 2003: 8).

INTRODUCTION

General Introduction

Although teratology intrigued Greek natural philosophers and temporarily discomfited Linnaeus' (1744) belief in the immutability of species, the discipline peaked in the late nineteenth and early twentieth centuries, when "spontaneous" mutants observed in nature were widely regarded as indicators of possible evolutionary pathways (e.g., DeVries 1906; Worsdell 1916; Reychler 1928; Goldschmidt 1940). Although these views were determinedly suppressed later in the twentieth century by some of the more aggressive proponents of the New Synthesis, they have recently experienced a modest revival accompanying the emergence of the cross-disciplinary field of evolutionary–developmental genetics (= evo–devo: Cronk et al. 2002; Vergara-Silva 2003). Evo–devo focuses largely on the broader significance of artificially induced mutants in a few model organisms; the most notable examples are thale-cress, maize, and snapdragon, which is particularly relevant to this study because of its strongly bilaterally symmetrical flowers (e.g., Coen 1999).

In contrast, there have been few detailed comparative studies of naturally occurring mutants, even though such occurrences may reciprocally illuminate the nature of the genes and gene products that regulate floral development (Wardlaw 1965; Meyerowitz et al. 1989; Rudall and Bateman 2003). For example, species possessing zygomorphic (bilaterally symmetrical) flowers that spontaneously display reversion

Table 1. Glossary of terms relating to floral terata.

Products of Mutation

prospecies: a putatively recently evolved lineage possessing the essential intrinsic properties of a taxonomic species but yet to achieve levels of abundance and especially of longevity acceptable to most practicing taxonomists

teratos (plural terata): an individual showing a profound phenotypic change from its parent(s), irrespective of whether the underlying cause is heritable or ecophenotypic

hopeful monster: an individual showing a profound phenotypic change from its parent(s) that demonstrably reflects a heritable modification [a subset of teratos]

atavism (= reversion): an individual showing features lacked by its parents but possessed by more distant progenitors

peloria: a complete transition in symmetry of the perianth between parent and offspring [most commonly zygomorphy to actinomorphy; cf. pseudopeloria]

pseudopeloria (= semi-peloria): an incomplete transition in symmetry of the perianth between parent and offspring, such that another category of symmetry is approached but is not achieved

Phenotypic Transitions

heterochrony: temporal change in the expression of a feature between putative ancestor and putative descendant [cf. heterotopy]

paedomorphy: heterochronic shift where the feature is less well-expressed in the putative descendant than in the putative ancestor [cf. peramorphy]

peramorphy: heterochronic shift where the feature is better expressed in the putative descendant than in the putative ancestor

heterotopy: spatial (positional) change in the expression of a feature between putative ancestor and putative descendant (by duplication and/or translocation)

neoheterotopy: heterotopy where a feature is duplicated and does not replace a contrasting preexisting feature [cf. homeoheterotopy]

homeoheterotopy: heterotopy where a feature is duplicated or translocated and at least partially replaces a contrasting, preexisting feature

homeosis s.s.: homeoheterotopy where a feature is duplicated or translocated and wholly replaces a contrasting, preexisting feature [a subset of homeoheterotopy]

lateral homeosis: homeotic translocation occurring within the same floral whorl [cf. vertical homeosis]

vertical homeosis: homeotic translocation occurring between floral whorls

acropetal homeosis: vertical homeotic translocation occurring toward the axial apical meristem [cf. basipetal homeosis]

basipetal homeosis: vertical homeotic translocation occurring away from the axial apical meristem

to, or partial change toward, actinomorphy may provide insights into floral evolution. If they are heritable they may function as "hopeful monsters" (Goldschmidt 1940) or "prospecies" (Bateman and DiMichele 2002), theoretically capable of establishing new lineages.

The following discussions of the relevance of naturally occurring mutants to understanding orchid floral evolution require the use of a complex set of terms, some in common usage but others less so; in order to improve the intelligibility of this text we have included both a glossary (Table 1) and a terminological postscript.

The Normal Orchid Flower

The various distinctive features of orchid flowers are summarized in Fig. 1. The typical orchid flower resembles many other petaloid monocots in consisting of five fundamentally three-fold whorls. These whorls, listed acropetally in order of developmental initiation (Fig. 2), are: outer tepals (= "sepals": T1–3), inner tepals (= petals: t1–3), outer stamens (A1–3), inner stamens (a1–3), carpels/ovary. Orchids are unusual among "petaloid" monocots in that the tepals of the inner perianth whorl are in most cases readily differentiated from those of the outer whorl. Hence, they are often termed sepals and petals, respectively, despite the apparent lack of homology between the "sepals" of monocots and eudicots sensu Angiosperm Phylogeny Group (2003). Each fundamentally tripartite whorl of the orchid flower is in effect rotated by 180° relative to the adjacent whorls when viewed perpendicular to the axis. Moreover, the whorls are very closely spaced along the axis, permitting an unusually strong degree of synorganization and resulting in an unusually vertically compact flower. The characteristically fertile (i.e., potentially meiotic) three or more acropetal whorls are prone to partial or complete suppression of individual organs, and to partial or complete fusion of organs, both within and between whorls.

All orchids possess a bilaterally symmetrical gynostemium (= column), an unusual feature reflecting fusion of multiple organs. Specifically, the gynostemium comprises stamen filaments adnate to a syncarpous style on an ovary that contains vast numbers of minute mycoheterotrophic seeds. Overall, the flower is strongly epigynous ("hyper-epigynous"). All orchids also show partial or complete suppression of between three and five of the original six stamens observed in several putative sister groups to orchids, notably Hypoxidaceae. In all but the most primitive orchids the single remaining stamen generates 1–8 club-shaped masses of pollen, termed pollinia, that become attached to pollinating animals.

In most orchids at least the inner perianth whorl resembles the stamen whorls in being strongly zygomorphic. Bilateral symmetry is typically dictated most strongly by an especially well-differentiated labellum (t3). In many derived species the labellum is strongly ornamented and/or bears a potentially nectiferous spur as an aid to pollination. By functioning as a landing stage for pollinators in most orchid species the labellum is, along with the gynostemium, the biological focus of the flower. It is also the key reference point to allow observers to orient themselves around, and thus precisely describe, an orchid flower.

gynostemium =
congenitally fused
filaments and style

1(-3) abaxial stamens
expressed;
remainder suppressed

pollinium =
pollen grains
aggregated into
single mass

inferior ovary

vast number of minute
mycoheterotrophic ovules/seeds

pollinarium =
pollinium plus stalk
and viscid disc

resupination = 180° torsion
of pedical and ovary, typically
placing abaxial structures uppermost

bilateral symmetry
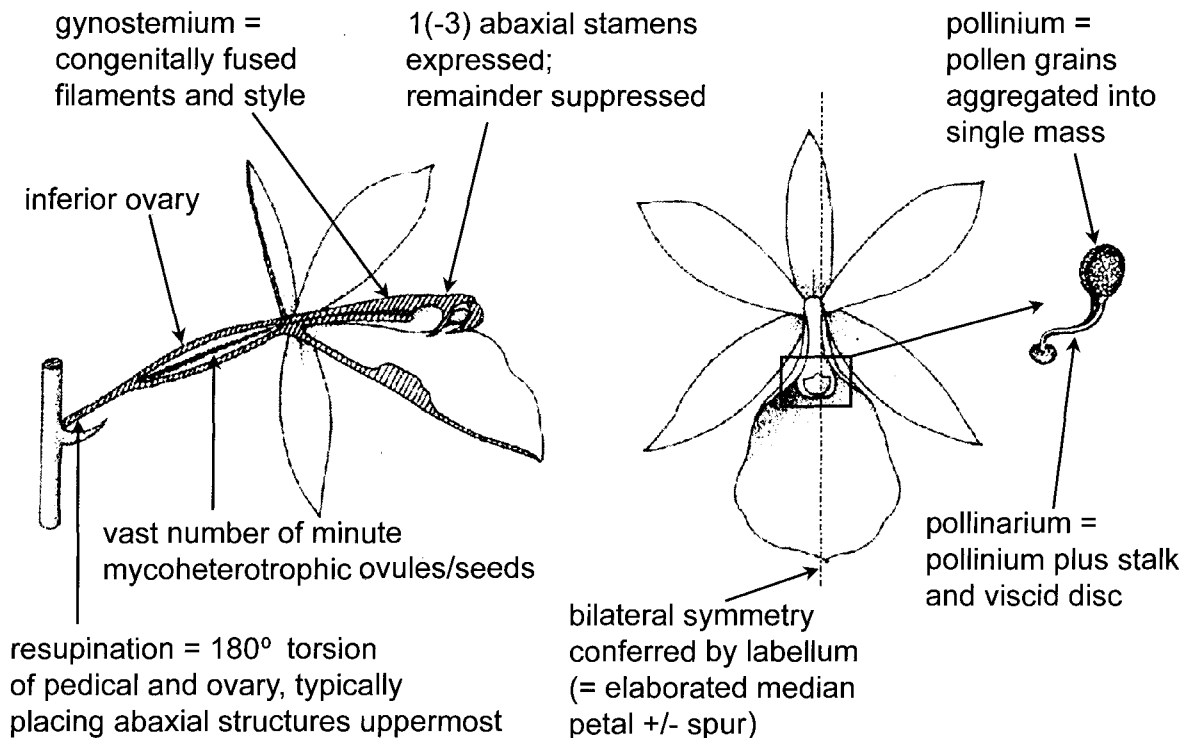conferred by labellum
(= elaborated median
petal +/- spur)

Fig. 1.—Characteristic morphological features of orchid flowers.

However, the final distinctive feature commonly exhibited by orchid flowers considerably complicates our spatial perception of the relative locations of individual organs. In most orchids the labellum is oriented lowermost (relative to the soil surface) of the six-perianth segments, as befits its role as a landing stage, but in developmental terms this is actually the adaxial (uppermost) rather than the abaxial (lowermost) portion of the flower. In orchids with erect inflorescences the labellum owes its downward orientation to 180° torsion of the ovary and/or pedicel, termed resupination (resupination is unnecessary in orchids that produce pendant inflorescences, where the labellum is already carried lowermost). Further complicating matters, a few orchid species (mainly, but not exclusively, those that are autogamous, or have ambulatory rather than aerial pollinators) routinely orient the labellum uppermost, some by abandoning resupination but others by exaggerating it to a full 360° rotation.

The Abnormal Orchid Flower

In recent reviews we have explored the terminology and evolutionary consequences of naturally occurring floral terata of orchids in considerable detail (Rudall and Bateman 2002), using the recently developed phylogenetic framework for orchids and related monocotyledons (cf. Chase 1999; Freudenstein and Rasmussen 1999; Bateman 2001; Freudenstein et al. 2004; Rudall and Bateman 2004), together with new insights into evolutionary–developmental genetics (Cronk et al. 2002; Johansen and Frederiksen 2002; Vergara-Silva 2003) and extensive field observations of terata (Rudall and Bateman 2002, 2003), in particular to examine the evolution of adnation and zygomorphy in these unusually strongly synorganized flowers. We subsequently compared

orchid floral terata with those observed in other characteristically zygomorphic plant groups, notably Lamiales sensu Angiosperm Phylogeny Group (2003), paying greater attention to the influence of the architecture of the inflorescence on the morphology of the aberrant flowers (Rudall and Bateman 2003). We then reviewed the patterns of stigma–style fusion (adnation) and stamen suppression evident in orchids in the broader context of the monocots as a whole (Rudall and Bateman 2004). Each of these discussions considered only morphological transitions, deliberately ignoring a further category of mutant orchids that involve transitions in the content or distribution across the flower of anthocyanin pigments.

In this paper we further extend our comparative morphological investigations of orchid flowers, drawing on a considerably enlarged data set with particular emphasis on temperate species, in order to:

(1) Briefly review the origin and phylogenetic distribution of features of the gynostemium and labellum, which reflect:
   – fusion and suppression in the androgynoecium
   – differential elaboration of specific perianth members.
(2) Briefly review variation in naturally occurring floral mutants, focusing on:
   – modifications to the perianth and, to a lesser degree,
   – expression/suppression of each of the six "ancestral" stamens.
(3) Categorize the mutant phenotypes using sets of more precise terms for:
   – static description of each morph, and especially,
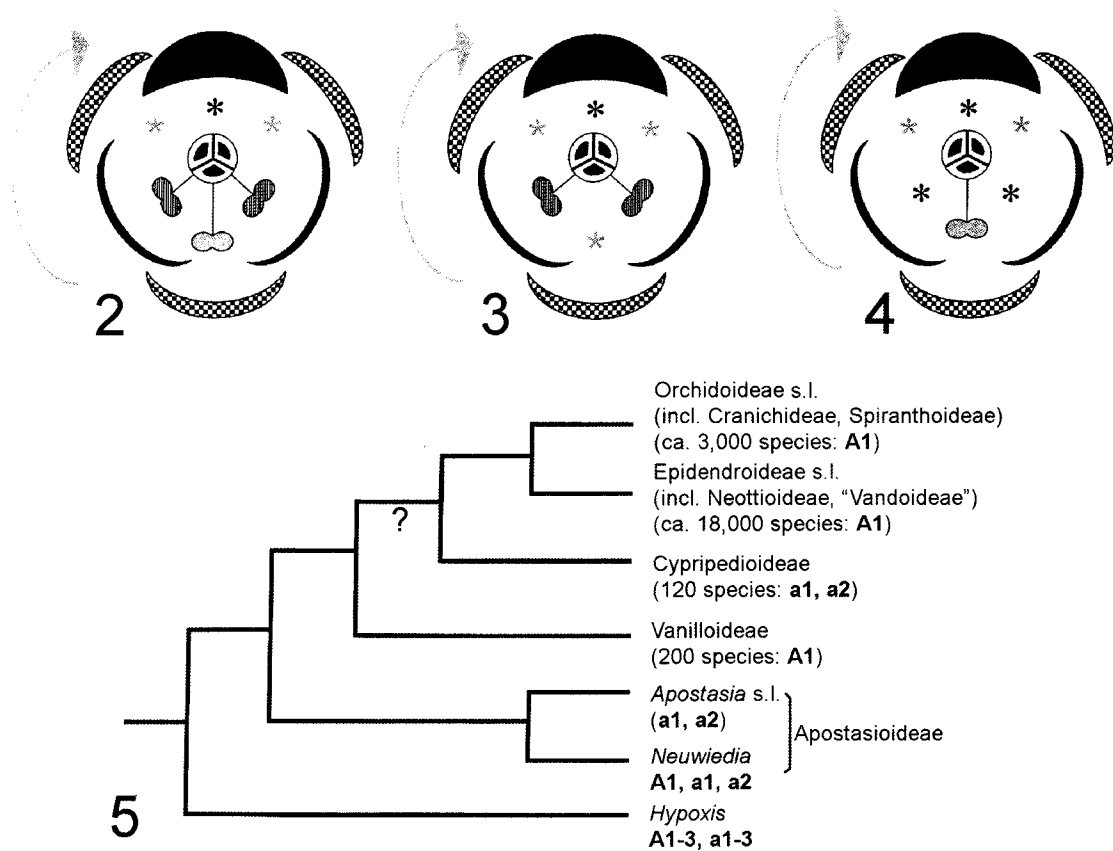   – dynamic transitions between pairs of closely related morphs.

Fig. 2–5.—The three main patterns of stamen suppression observed in Orchidaceae: the apostasioid *Neuwiedia* (2), cypripedioid (3), orchidoid-epidendroid (4). (5) Molecular phylogenetic relationships of the five subfamilies of Orchidaceae, summarizing stamen suppression patterns and species-level diversity. T = outer tepals ("sepals": checkerboard pattern), where T1 = median and T2+3 = lateral; t = inner tepals (petals: black), where t1+2 = lateral and t3 = median (labellum: larger); A = potential locations of outer stamens (pale); a = potential location of inner stamens (dark)—fertile stamens are shown as dumbbells, infertile/absent stamens as asterisks—central triradiate structure is the ovary. (Fig. 2–4 modified after Rudall and Bateman 2004, Fig. 4; Fig. 5 modified after Rudall and Bateman 2004, Fig. 13; see also Freudenstein et al. 2004.)

(4) Interpret semi-quantitatively the relative frequencies of mutant phenotypes in terms of:
- developmental processes and constraints and, to a lesser degree,
- evolutionary (and conservation) significance
- taxonomic treatment.

DESCRIBING SHIFTS IN FLORAL MORPHOLOGY

Stamen Suppression

Outgroup comparison suggests that orchid flowers are best viewed as having six potential locations for the expression of stamens, organized in an outer whorl of three locations (A1–3) that alternate with the three locations of a closely juxtaposed inner whorl (a1–3). In practice, three main arrangements of expressed stamens occur in Orchidaceae (Fig. 2–4). In each of the three arrangements, all three of the adaxial stamens are suppressed, though in some cases the inner adaxial stamen (a3) is represented by an infertile staminode. In the species-poor basally divergent subfamily, Apostasioideae, either all three of the abaxial stamens are expressed (a1 + a2 + A1: *Neuwiedia* Blume) or just the two inner abaxial stamens, leaving the third as an infertile staminode (*Apostasia* Blume). This a1 + a2 configuration also

characterizes Cypripedioideae. In contrast, the three remaining subfamilies, including the species-rich Orchidoideae and Epidendroideae, are all monandrous; they express only one fertile stamen, at the outer abaxial (A1) location (Rudall and Bateman 2002, 2004). Recent molecular phylogenies, though equivocal, suggest that the monandrous orchids may not be monophyletic (Fig. 5); suppression of all stamens but A1 has apparently occurred independently in the species-rich subfamilies Orchidoideae plus Epidendroideae versus the far less diverse Vanilloideae (e.g., Burns-Balogh and Bernhardt 1985; Freudenstein and Rasmussen 1999; Walker-Larsen and Harder 2000; Freudenstein et al. 2004).

Perianth Transitions: Categorization

In contrast to the stamens, all six of the perianth members are expressed in almost all orchids. They too are best viewed as two closely spaced whorls each consisting of three elements, the petals (t1–3) being inserted immediately acropetal to the sepals (T1–3) and alternating with them when viewed "vertically" (i.e., parallel to the ovary, which approximates the rotational axis of symmetry of the flower).

Rudall and Bateman (2002) elaborated a basic descriptive terminology for transitions from presumed wild type to ter-
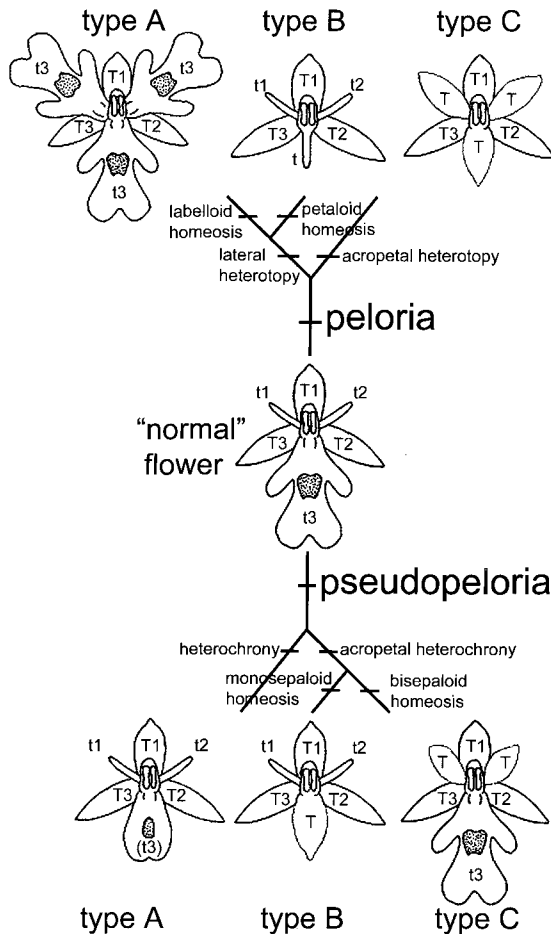
Fig. 6.—Diagrams of orchid perianth whorls (sepal and petal) illustrating the "normal," wild-type phenotype (center), three categories (types A–C) each of peloria and pseudopeloria, and the type of morphogenetic transition that each category represents. (Modified after Rudall and Bateman 2002, Fig. 3.)

atological orchid floral morphs that was first suggested by Bateman (1985) (cf. Fig. 6; Table 2). The main distinction recognized is between transitions that result in complete replacement of bilateral by radial symmetry in the perianth (true peloria) and those that reduce the degree of bilateral symmetry evident in the perianth but do not wholly eliminate it (a morphological shift that we term pseudopeloria).

Within the spectrum of peloria, three somewhat arbitrary categories are recognized. In type A peloria, the two lateral petals (t1, t2) are in effect replaced by additional median petals (labella, normally expressed only at t3). Type B peloria is the converse phenomenon, wherein the labellum is replaced by a third lateral petal. In type C peloria, three additional sepals replace all three petals—a third permutation of floral organs that generates a radially symmetrical perianth.

Three broad categories of pseudopeloria are also recognized. In type B pseudopeloria the labellum is replaced with a sepal, but the two lateral petals are unchanged. Type C pseudopeloria is the converse; the labellum is unaltered, but the two lateral petals are replaced by additional sepals. In type A pseudopeloria only the labellum is altered; its degree of differentiation from the remaining perianth segments is

reduced but not eliminated. Thus, unlike the other modes of peloria and pseudopeloria, it cannot be explained simply by translocating preexisting types of tepals (cf. Fig. 7–45).

Perianth Transitions: Description

As noted by Rudall and Bateman (2002), a more explanatory terminology can be generated by adapting the descriptors of evolutionary transitions between putatively ancestral and descendant morphologies put forward by Gould (1977), then quantified by Alberch et al. (1979), and later updated for the evolutionary–developmental genetics era by Baum and Donoghue (2002). When attempting to classify the many kinds of evolutionary–developmental change, the main dichotomy distinguishes between heterochrony, wherein the morphological shift is temporal only, and heterotopy, wherein the feature or features in question also shift positionally (Table 1; Fig. 6).

All three of the categories of peloria described above, together with two of the three categories of pseudopeloria, were ascribed by Rudall and Bateman (2002) to heterotopy. They recognized that, in the terminology of Baum and Donoghue (2002), all five categories constitute true homoeoheterotopy, wherein a feature is duplicated or translocated and at least partially replaces a morphologically contrasting, preexisting feature. In some examples the replacement is only partial (cf. Fig. 31–32, 39–40), but in the majority of examples the preexisting structure is wholly replaced by another comparable structure, thereby constituting a genuinely homeotic transformation. To cite two apparently straightforward kinds of transition, duplicated labella replace the two lateral petals in type A peloria (Fig. 9–16), and duplicated sepals replace the two lateral petals in type C pseudopeloria (Fig. 33–35).

However, these two types of transition also illustrate the reason why we further elaborated the terminology of Baum and Donoghue (2002). Although both kinds constitute bona fide homeosis, in the first kind the duplication plus translocation event occurs within the same whorl of the perianth, between the labellum (i.e., the median petal) and the lateral petals; this type of event is thus termed a lateral translocation. In contrast, the second kind of event involves translocation between the two perianth whorls; in this case, duplicated sepals are shifted "forwards" (inwards) from the sepal whorl to the petal whorl. We refer to this shift toward the axial apical meristem as acropetal homeosis. The (much rarer) converse shift, from petal whorl to sepal whorl, away from the axial apical meristem, is here termed basipetal homeosis (Fig. 31–32).

The sixth category of perianth transition, type A pseudopeloria, is arguably better explained in terms of heterochrony than heterotopy. These cases lack evidence of organ duplication or translocation, but rather involve the modification of the morphology of a preexisting structure. In peramorphic heterochrony that structure becomes larger and/or more elaborate, whereas in paedomorphic heterochrony it becomes smaller and/or less elaborate. The phenomenon of particular interest in this paper, type A pseudopeloria, involves paedomorphic simplification of the labellum (Fig. 25–30, 38). Evidence that this is heterochronic modification, rather than translocation, of a preexisting structure is provided by reten-

Table 2. Interpretation of putative ancestral and descendant morphs illustrated in Fig. 7–45 (NI = typical morph not illustrated).

Putative ancestor (Fig. #)	Putative descendant (Fig. #)	Category of perianth transition	Transition type	Morph occurs throughout inflorescence	Frequency of populations	Uniform populations	Taxonomic treatment of teratos
Peloria/Pseudopeloria in Perianth							
Ophrys insectifera L. (9)	same (10)	peloria A	lateral heterotopy	yes	rare	never	unnamed
Anacamptis (Orchis) papilionacea (L.) R. M. Bateman, Pridgeon & M. W. Chase (11)	same (12)	peloria A	lateral heterotopy	yes	rare	never	unnamed
Paphiopedilum cf. *insigne* Pfitzer (13)	same (14)	peloria A	lateral heterotopy	yes[c]	rare	never	unnamed
Phalaenopsis Blume hybrid (15)	same (16)	peloria A	lateral heterotopy	usually	[artificial]	[artificial]	unnamed
Phragmipedium (wallisii) (Rchb. f.) Garay (17)	*P. lindenii* (Lindl.) Dressler & N. H. Williams (18)	peloria B	lateral heterotopy	yes[c]	occasional	usually	species
Ophrys fuciflora (F. W. Schmidt) Moench s.l. (19)	same (20)	peloria B	lateral heterotopy	?yes	rare	never	unnamed
Ophrys araneola Rchb. (21)	same (22)	peloria B	lateral heterotopy	yes	rare	never	unnamed
Calochilus (robertsonii) Benth. (23)	*Thelymitra (cucculata)* (24)	?peloria C	acropetal heterotopy	yes	common	always	genus
Cephalanthera damasonium (Mill.) Druce (7)	"*Tangtsinia*" *nanchuanica* S. C. Chen (8)	?peloria C	acropetal heterotopy	?yes	rare	?never	genus
Epipactis phyllanthes var. *vectensis* D. P. Young (25)	var. *phyllanthes* (26)	pseudopeloria A	?paedomorphic heterochrony	yes	frequent	usually	variety
Plantanthera chlorantha Custer ex Rchb. (27)	var. ?*monstruosa* Mutel. (28)	pseudopeloria A	?paedomorphic heterochrony	yes	occasional	?never	variety[a]
Gymnadenia densiflora A. Dietr. (29)	"*Nigritella*" *austriaca* (Teppner & E. Klein) P. Delforge (30)	pseudopeloria A	?paedomorphic heterochrony	yes	common	always	genus[b]
Ophrys mammosa Desf. (31)	same (32)	pseudopeloria s.l.	basipetal partial heterotopy	?yes	rare	never	unnamed
Ophrys apifera Huds. (33)	subsp. *jurana* Ruppt. (34, 35)	pseudopeloria C	acropetal heterotopy	yes	occasional	sometimes	variety
Platanthera bifolia (L.) Rich. (36)	same (37)	?peloria C	acropetal heterotopy	yes	rare	never	unnamed
Platanthera bifolia (36)	same (38)	pseudopeloria A	?paedomorphic heterochrony	yes	occasional	?never	unnamed
Ophrys ferrum-equinum Desf. (39)	same (40)	pseudopeloria s.l.	acropetal partial heterotopy	unknown	rare	never	unnamed
Other Types of Transition							
Dactylorhiza fuchsii (Druce) Soó (NI)	same (41)	[additional pollinia expressed on labellum]		unknown	rare	never	unnamed
Ophrys fuciflora (19)	same (42)	[additional columns expressed on lateral petals]		unknown	rare	never	unnamed
Neottia (Listera) ovata (L.) Bluff & Fingerh. (NI)	same (43)	[pedicels and ovaries of adjacent flowers fused]		no	rare	never	unnamed
Epipactis purpurata Sm. (NI)	same (44)	[additional labellum expressed adjacent to original]		sometimes	occasional	never	unnamed
Ophrys insectifera (9)	same (45)	[four additional labella expressed in spiral]		unknown	rare	never	unnamed

[a] Originally mistakenly described as a bigeneric hybrid with *Pseudorchis* Ség. by McKean (1982).
[b] Implicitly treated as a subgenus in recent molecular phylogenetic studies.
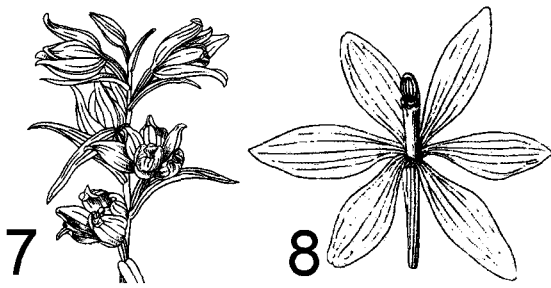[c] Difficult to assess as flowers are usually borne singly or in pairs.

Fig. 7–8.—Line drawings of *Cephalanthera damasonium* (left) and its presumed derivative via type C peloria, *Tangtsinia nanchuanica* (right); for interpretation of this pair of line drawings see Table 2. (Fig. 7 after Ross-Craig 1971, Plate 45; Fig. 8 after Chen 1982, Fig. 1.)

tion of vestigial features on the reduced labellum, such as distinctive markings and/or a rudimentary spur (Rudall and Bateman 2002). By definition, this form of heterochrony is confined to a single perianth whorl, namely the petals.

Admittedly, categorization of terata becomes difficult in cases where the labellum is simplified to a degree where it comes to resemble the sepals, and so could be viewed as representing either the paedomorphic labellum of type A pseudopeloria or the translocated sepal that causes type B pseudopeloria (Fig. 23–24, 36–37). Also problematic are cases where either the putatively ancestral or descendant floral morph possesses lateral petals that closely resemble the sepals, thereby compromising the supposed distinction between type C peloria and type B pseudopeloria (Fig. 7–8).

Non-Perianth Transitions

It is worth noting briefly that the terminology of heterotopy and heterochrony can usefully be expanded to include morphological floral transitions within or between the two apical-most whorls, the stamen and carpels, and between either of these meiotically competent whorls and either of the sterile perianth whorls. For example, we here illustrate orchids wherein additional pollinaria have been expressed on the labellum (Fig. 41) or on the lateral petals (Fig. 42), both examples constituting cases of basipetal partial heterotopy. Returning to heterochrony, the partial suppression of the outer adaxial stamen to generate a sterile staminode (a1: Fig. 4), which characterizes the majority of the species-rich monandrous orchids, can be viewed as an example of paedomorphosis; current evidence suggests that development of the stamen is arrested prematurely.

MATERIALS AND METHODS

Our semi-quantitative survey of orchid terata summarized here represents 25 years of our own field observations, together with examples generously donated to us by many professional and especially amateur orchidologists (notably Prof. Hans Reinhard, the late Derek Turner-Ettlinger, and, in aggregate, several members of the UK Hardy Orchid Society). This composite photographic record has been supplemented with literature surveys. This nonexperimental, field-based approach inevitably causes a bias toward species occurring in natural habitats of the temperate zones. However, we find this bias advantageous, as the relative success of the

novel morphs can more readily be monitored in natural conditions, providing a far more realistic appraisal of their evolutionary potential than is possible in the more popular but simpler, laboratory-based experimental systems that traditionally rely upon a few distantly related "model" species (cf. Rudall and Bateman 2002, 2003). One disadvantage is that the conservation concerns that inevitably surround studies of naturally occurring orchid populations in developed countries preclude collection of representative specimens for accession into the living collection and/or the herbarium, though seed is sometimes collected.

EVOLUTIONARY INTERPRETATION: PATTERNS

Our survey revealed that the most common categories of natural terata affecting the perianths of orchids are type A pseudopeloria (paedomorphic heterochrony within the petal whorl), which demonstrably affects ca. 20% of the British native orchid species recognized by Bateman (2004, in press), and type A peloria (replacement of lateral petals by additional labella, causing complete lateral heterotopy), which affects ca. 25% of British native orchid species. Next most frequent is the alternative form of lateral heterotopy, type B peloria (replacement of labellum by an additional lateral petal, also causing complete lateral heterotopy). Acropetal heterotopy (when at least one petal is replaced with a sepal) is far less common, and basipetal heterotopy (when at least one sepal is replaced with a petal) is very rare and never complete (i.e., does not achieve true homeosis: Fig. 32). Thus, modifications within whorls are far more common than those occurring between whorls toward the apical meristem, which in turn are far more common than those occurring between whorls away from the apical meristem.

Moreover, the six categories of modifications to the perianth vary considerably in their frequency of association with modifications to the gynostemium, which represents the fused product of the substantially reduced paired whorls of stamens and the many-ovulate carpels. Type A peloria is the category least likely to be accompanied by disruption to the morphology of the gynostemium, epitomizing a more general observation that development of the gynostemium is less readily disrupted by translocations of organs that are confined to a single perianth whorl than by translocations occurring between the two whorls. In some cases, the degree of morphological disruption to the perianth whorls is positively correlated with the degree of disruption to more detailed features; a good example is *Ophrys apifera* subsp. *jurana*, wherein the degree of acropetal development of sepals at locations previously occupied by lateral petals is correlated with progressive breakdown of the speculum markings on the labellum (cf. Fig. 33–35).

Together, these observations suggest the existence of at least two clines of gene expression. The more obvious and historically conserved gradient is basipetal–acropetal, determining the five fundamentally three-fold whorls (outer tepals, inner tepals, outer stamens, inner stamens, carpels) that together constitute the orchid flower. The more phylogenetically restricted adaxial–abaxial (broadly equivalent to "dorsal–ventral") gradient dictates the degree of bilateral symmetry shown by each of these five whorls. At maturity, a
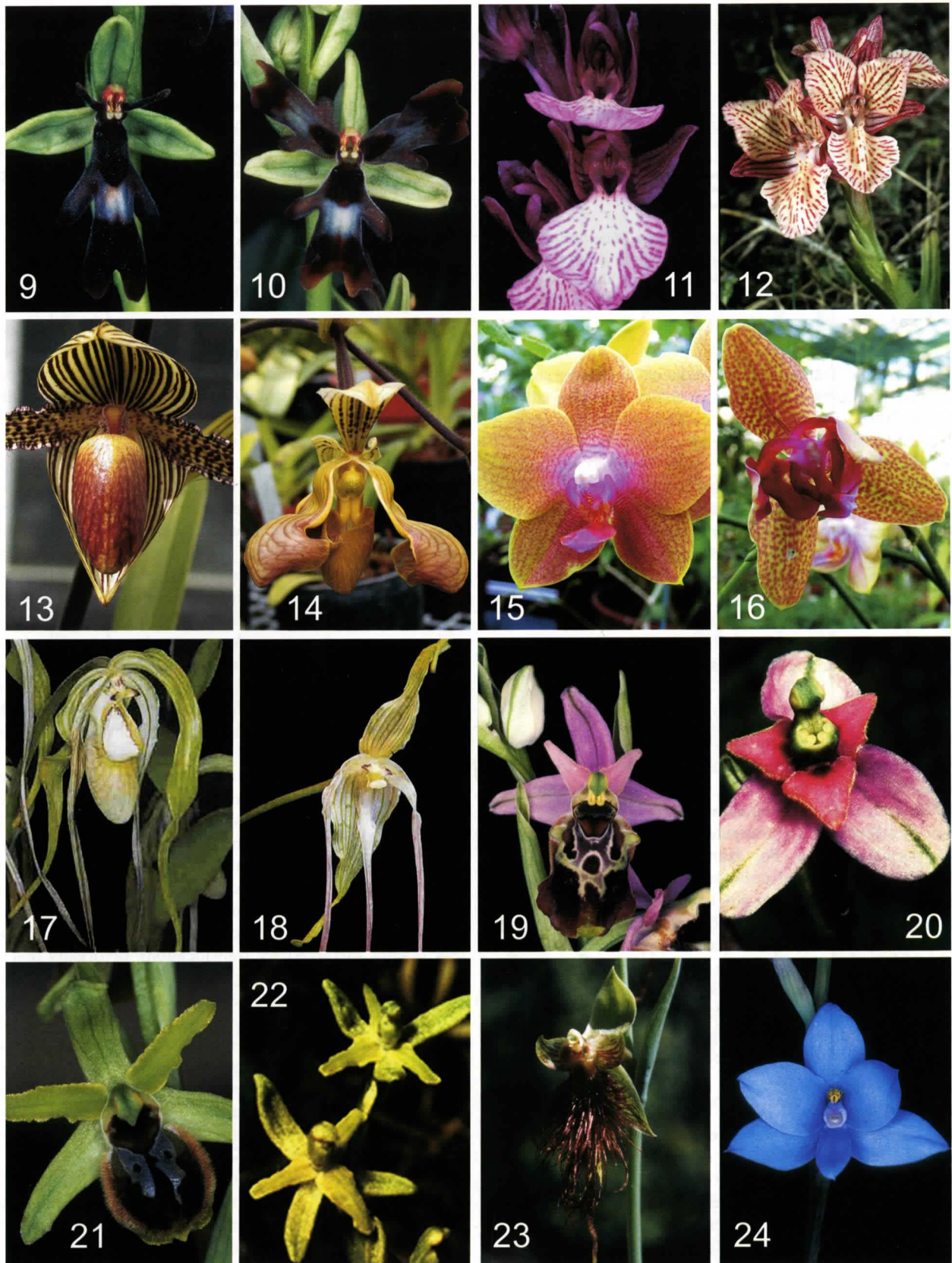
Fig. 9–24.—Photographed examples of peloric transitions between putative ancestral (left) and descendant (right) floral morphs; for interpretations of each pair of photographs see Table 2. (Magnifications vary. Photographs: R. Bateman Fig. 9–11, 19, 23, 24; P. Rudall Fig. 13–16; H. Reinhard Fig. 20, 22; P. Cribb Fig. 17, 18; P. Peisl Fig. 12; D. Turner-Ettlinger Fig. 21. See also Rudall and Bateman 2002, Fig. 10; 2003, Fig. 1.)
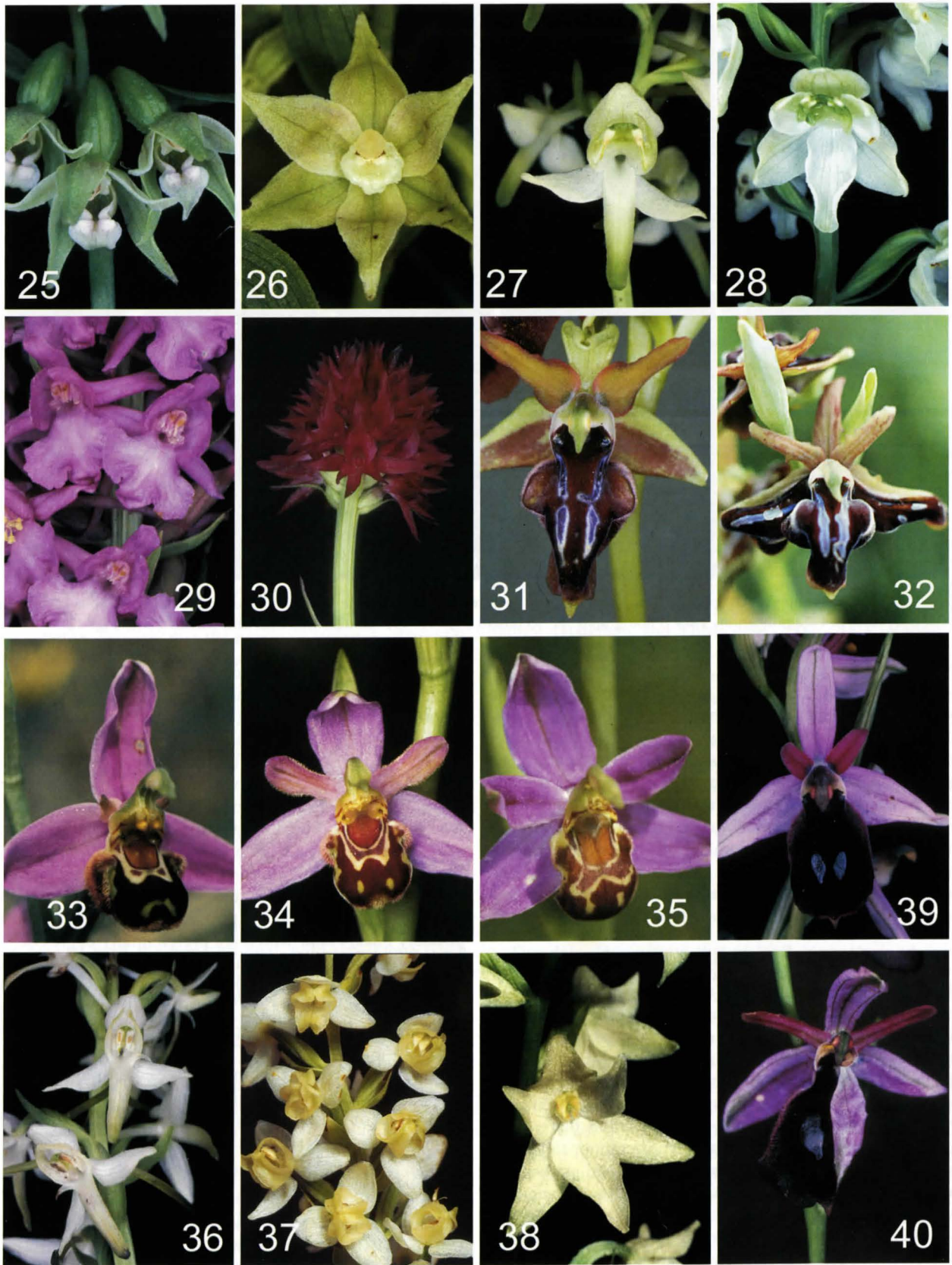
Fig. 25–40.—Photographed examples of pseudopeloric transitions between putative ancestral (left) and descendant (right) floral morphs; for interpretations of each pair or triplet of photographs see Table 2. (Magnifications vary. Photographs: D. Turner-Ettlinger Fig. 25, 26, 31, 33–35, 40; R. Bateman Fig. 27, 29, 30, 36, 39; H. Reinhard Fig. 37, 38; R. Bush Fig. 28; A. Hughes Fig. 32. See also Rudall and Bateman 2002, Fig. 10–12.)

Fig. 41–45.—Photographic examples of transitions not readily categorized as peloric or pseudopeloric; for interpretations of each photograph see Table 2. (Magnifications vary. Photographs: H. Reinhard Fig. 41–45; see also Bateman and Rudall 2002, Fig. 12.)

typical orchidoid or epidendroid flower (Fig. 1, 4) has a gynostemium wherein the ovary is slightly down-curved in the adaxial–abaxial plane, the two abaxial inner stamens are partially expressed as staminodes and the single abaxial outer stamen is fully expressed as two or more pollinaria. The single abaxial petal is more strongly developed than the two lateral petals, but all three sepals are approximately equally developed. Thus, the stamen whorls and the petal whorl in particular exhibit strong bilateral symmetry, which contributes substantially to the level of attraction to pollinators and thereby to the reproductive success of allogamous orchid flowers (e.g., Rudall and Bateman 2002).

EVOLUTIONARY INTERPRETATION: PROCESSES

The above observations lead us to infer that at least two key genes (or small suites of functionally linked genes) control the filament–style fusion, dominantly adaxial stamen suppression, and adaxial labellum formation (perhaps best viewed as over-expression) that together characterize orchids. The first suite controls synorganization, specifically the hyper-epigyny and filament–style adnation that permit the formation of the characteristic gynostemium; this operates predominantly along the acropetal–basipetal gradient. In contrast, the second suite controls adaxial stamen suppression and labellum formation, thereby generating zygomorphy in the gynostemium and perianth, respectively; this operates predominantly along the adaxial–abaxial gradient.

TCP Gene Family

We have previously argued (Bateman and Rudall 2003) that the obvious "null hypothesis" explanation for peloria

in orchids is over-expression or under-expression/suppression of gene families that have been implicated in cases of peloria in other families. This interpretation more heavily implicates TCP genes than the more widely discussed "ABC" MADS-box genes (cf. Bowman 1997; Cubas et al. 1999; Cubas 2002; Theissen et al. 2002). Control of the relevant aspects of floral morphology could at least partly reflect a balanced relationship between genes with "ventralized" expression, such as orthologues of *cycloidea, dichotoma,* and *teosinte branched1,* which are preferentially expressed adaxially, versus the less thoroughly researched genes with "dorsalized" expression, such as *divaricata* and possibly *backpetala,* which are preferentially expressed ventrally (reviewed by Almeida et al. 1997; Bateman and DiMichele 2002; Cubas 2002; Rudall and Bateman 2002, 2003; Vergara-Silva 2003). We further speculated that pseudopeloria (at least, type A pseudopeloria) may reflect modified expression of genes of more subtle effect, possibly expressed downstream from the coarser control exerted by the "classic" TCP genes. We also argued that at least some orchid terata may reflect changes in regulation rather than complete loss of gene function (Rudall and Bateman 2002).

MADS-Box Gene Family

However, more recent evidence has emerged to suggest that the MADS-box gene family, whose characterization in model organisms led to the benchmark ABC model of control of floral organ identity among whorls, may also be critical to floral development in petaloid monocots such as orchids. Elsewhere in this volume, Johansen et al. 2006 (see also Johansen and Frederiksen 2002; Johansen et al. 2002)

have used the vandoid (epidendroid) orchid *Cleisostoma* Blume to demonstrate that several MADS-box genes of the ABC categories, together with the "E" gene *sepallata,* are active in the flower during its later ontogenetic stages, when the detailed morphology of the gynostemium and labellum are established. Particularly notable is an apparent proliferation, and hypothesized subsequent subtle differentiation of expression, of B-class genes (i.e., the *pistillata*-AP3 group) in petaloid monocots (cf. Johansen et al. 2002, 2006; Kanno et al. 2003; Lamb and Irish 2003; Kim et al. 2004). In the classic dicot models, B-class expression is required for the production of petals and stamens (Coen 1999), and it has been assumed that in petaloid monocots expression has extended into the basal whorl of sepal-like petals (reviewed by Theissen et al. 2002); this has since been demonstrated in tulips (Kanno et al. 2003).

Within orchids, recognition of single B-class genes in the orchidoid *Orchis* L. (reported in Kim et al. 2004: *GLO* subfamily) and in the epidendroid *Oncidium* Sw. (Hsu and Yang 2002: *DEF* subfamily) was followed by a remarkable study of another epidendroid, *Phalaenopsis equestris* (Schauer) Rchb. f., by Tsai et al. (2004). This study used expressed sequence tagging to reveal the presence of no fewer than four B-class genes (*PeMADS2–5*). A gene tree based on protein sequences showed that all four paralogues were located in a distinct monocot clade within the *DEFICIENS/APETALA3* (rather than *GLOBOSA/PISTILLATA*) gene subfamily, yet only two of the four paralogues emerged as sisters. Extrapolation suggests that the common ancestor of orchids and grasses possessed at least two *DEF*-like genes, one presumably giving rise to *PeMADS3* and *4,* the other to the more divergent *PeMADS2* and *5.* First principles suggest that this diversity allows considerable latitude for these paralogues to interact with varying degrees of subtlety to differentiate the constituent organs of the orchid flower, especially with the likelihood of interactions extended to members of the *GLO* subfamily (e.g., *OrcPI*) and as-yet unidentified members of the *SEP* family (E-class genes).

The most intriguing aspect of the study of Tsai et al. (2004) was comparing sequences of the four paralogues taken from a wild-type plant and what we would term a type A peloric individual (cf. Fig. 16); remarkably, both plants were derived from the same original, wild-type clone (such divergence was termed somaclonal variation by Kaeppler et al. 2000). Although both *PeMADS2* and *5* were expressed in the sepals (T1–3), *PeMADS2* alone was sufficient for their normal development. *PeMADS2, 3,* and *5* were expressed in wild-type petals, but *PeMADS5* was not expressed in the two additional labella that replaced the wild-type lateral petals in the peloric mutant, suggesting that *PeMADS5* is critical for the development of non-labellar petals (t1 + t2). Relatively strong expression of *PeMADS3* and *4* was reported in wild-type labella, and that of *PeMADS4* extended to the two additional labella in the peloric mutant, indicating that it is critical for development of the labellum (t3). Moreover, expression patterns in the morphologically reduced gynostemium of the peloric mutant suggest influences from *PeMADS4* and *5,* which apparently initiates stamens.

As noted by Tsai et al. (2004: 841), "both disruption in promoter region and insertions in the fifth intron have occurred in both alleles of *PeMADS5* in [the] peloric mutant,"

indicating "chromosomal-level mutation." This evidence of a simple chromosomal rearrangement in one of a pair of otherwise genetically identical organisms that has profoundly and instantaneously altered the morphology of every floral whorl would surely have appealed to Richard Goldschmidt, arch-saltationist of the early twentieth century (e.g., Goldschmidt 1940).

Beyond Evo–Devo: Ecological Establishment of Phenotypic Novelties

Such controlled, laboratory-based and, above all, *comparative* studies are essential to identify the detailed DNA-based transitions that undoubtedly cause the phenotypic shifts documented in this paper. Nonetheless, even such hard-won breakthroughs in understanding the cause and phenotypic consequences of a particular mutation tell us little about the likely performance of the resulting mutant in the natural environment. Projects monitoring terata in nature not only provide useful first approximations of the relative probability of occurrence of various phenotypes (thereby acting as valuable guides for formulating laboratory studies in "evo–devo"), but they also demonstrate the short-term potential for establishment of such mutant lineages within a genuine ecosystem (see the introductory quote by DeVries 1906). It is the combination of generation of genetic novelty and subsequent filtration of those novelties by their happenstance environment that dictates evolutionary success or, far more frequently, failure (Bateman and DiMichele 2002, 2003; Rudall and Bateman 2003).

While we have no doubt that the vast majority of such mutants rapidly prove selectively disadvantageous, a small proportion will be at worst selectively neutral. Genetic drift would be unusually effective at driving to fixation such mutations, given the relatively low reproductive success and typically small effective population sizes of orchids (Tremblay et al. 2005).

SYSTEMATICS AND SPECIATION

Is Mutation-Based Teratology Iterative and Evolutionarily Reversible?

Our data demonstrate that at least some kinds of peloric and pseudopeloric transitions in at least some species are highly iterative, often occurring spontaneously and sporadically in several widely distributed populations of a single species; examples illustrated here include repeated cases of type A peloria in several species of *Ophrys* L. and *Dactylorhiza* Necker ex Nevski (e.g., Fig. 9, 10), type A pseudopeloria in both of the European species of *Platanthera* Rich. (Fig. 27, 28, 36, 38), and type C pseudopeloria in *Ophrys apifera* (Fig. 33–35). We therefore speculate that the underlying mutations must also be commonplace, the expression of the same gene (or, in the case of the loss of features, any element within the cascade of genes that together dictate the development of that feature) being affected in different populations. Moreover, as first principles suggest that most mutants fail to successfully establish themselves even in the short-term (Bateman and DiMichele 2002), the frequency of such mutations must be considerable in order to generate so many field observations of mature, reproductively competent

individuals. As well as providing interesting evolutionary case studies, the iterative nature of these mutations constitutes a potential model system to allow students of phylogeny reconstruction to compare well-established phenotypic and less well-established genotypic concepts of homoplasy (cf. Sanderson and Hufford 1996).

In addition to being demonstrably iterative, most transitions between contrasting floral organizations show some evidence of reversibility, unlike some other major biological transitions that have been phylogenetically mapped in orchids (e.g., autotrophy to mycoheterotrophy and allogamy to autogamy in tribe Neottieae: Bateman et al., in press). For example, all likely candidates as sister group of the orchids have six fully expressed stamens, but these are reduced to two or three fertile stamens in basal orchid subfamilies and to a single fertile stamen in more derived subfamilies (Fig. 5), co-occurring with varying numbers of staminodes (e.g., Kurzweil 1998). However, this trend is reversed in several of the terata illustrated here, which represent reinstatement of the developmental apparatus necessary to produce additional fertile stamens (e.g., Fig. 8, 20, 28; interestingly, however, none of these atavistic mutants appears to have established itself as a bona fide novel species). It seems likely that the complete loss of function in the photosynthetic apparatus that heralds a switch to a facultatively mycoheterotrophic lifestyle, and most likely results from a single point mutation, allows the remainder of that apparatus to enter "mutational free-fall," no longer constrained by its previously obligate function. Following this loss of developmental homeostasis, the lineage then has a preordained, irreversible future as an obligate mycoheterotroph, with crucial coevolutionary implications for both pollinators and mycorrhizae. This radical physiological shift often precedes substantial changes in vegetative morphology, but in many cases floral morphology (and its primarily reproductive function) pass through the transition to mycoheterotrophy virtually unaltered.

In contrast, an orchid that loses the ability to produce at least one fertile stamen per flower by definition loses the ability to reproduce altogether (or, to be more precise, to act as the male parent in any pollination event). Thus, suppression of stamens on orchids affects some but not all of the stamens in an orchid flower. Indeed, this appears to be a relatively subtle phenomenon, perhaps simply reflecting a hormonal cline that in turn reflects differential degrees of expression of a key gene across the dorsiventral axis of the flower. Such a control mechanism would lend itself readily to reversal to a more "primitive" ancestral condition (i.e., atavism: Table 1). In contrast, the presence of two closely spaced whorls of three perianth segments is undoubtedly plesiomorphic in Orchidaceae, and this tripartite arrangement is very rarely disrupted in orchid terata (e.g., Fig. 44, 45). Developmental constraints on the perianth appear strong, merely allowing shifts in the degree of morphological heterogeneity within and, less frequently, between whorls. Within this constraint, iterative mutation and atavism are once again commonplace.

Does Teratology Per Se Constitute Speciation?

Previous taxonomic treatments of peloric and pseudopeloric morphs have been highly inconsistent (Table 2). Some

have been the subjects of spectacular cases of mistaken identity, epitomized by the description of a supposed new intergeneric hybrid between *Platanthera* and *Pseudorchis* that was in fact based on the type A pseudopeloric *Platanthera chlorantha* here illustrated in Fig. 28 (cf. McKean 1982; Bateman 1985).

In our opinion, no non-heritable teratos merits taxonomic recognition, since by definition it is not a hopeful monster and thus is incapable of establishing a new evolutionary lineage. This principle ostensibly excludes terata where only a proportion of the flowers in the inflorescence are modified from wild type, thereby contravening the requirement of Rudall and Bateman (2003) that orchids typically show homogeneous peloria (all flowers on an indeterminate inflorescence are similarly modified). Of several examples available to us we have selected just two to illustrate here. The first is an isolated flower of *Neottia* (formerly *Listera*) *ovata* that possesses a single ovary but two lips, and is apparently the fusion product of two adjacent flowers (Fig. 43). This fusion may represent a somatic mutation in the floral primordium, or merely a non-heritable environmental perturbation such as damage inflicted on the floral primordium by an herbivorous insect. The second example is a specimen of *Epipactis purpurata* bearing two labella (Fig. 44). A population of the closely related but autogamous species *E. leptochila* Godfery (e.g., Bateman et al. in press) contained several individual plants wherein only the lowest flower on the inflorescence possessed two labella, the left labellum always developing behind the right, to generate a flower with seven perianth segments. A methylation effect of unusually subtle expression seems the most likely explanation for this remarkable example of an apparently heritable somatic instability.

It seems reasonable to assume that an inflorescence consisting entirely of uniformly modified flowers reflects a heritable cause—either chromosomal rearrangement (Wallbrunn 1987), point mutation, or methylation—but even this assumption is unreliable. Reychler (1928) demonstrated that a clonal line of *Cattleya* Lindl. plants reliably producing uniformly peloric flowers eventually reverted to wild type. We recently witnessed an even more striking example of several individuals of a *Phalaenopsis* hybrid that showed uniform type A peloria in all their inflorescences in 2003, but emerged uniformly wild type the following year after having been transferred to a contrasting environment of growth (cf. Fig. 15, 16). Both these examples may represent epigenetic methylation mutations that are clearly unstable, but nonetheless could permit at least limited heritability, as documented in the lamialean eudicots *Linaria vulgaris* Hill (Linné 1744; Cubas et al. 1999; Cubas 2002) and *L. purpurea* (L.) Mill (Rudall and Bateman 2003; C. Kidner and P. Rudall pers. obs. 2004).

Once heritability has been demonstrated (or is strongly suspected), the most effective criteria for determining the most appropriate taxonomic status of a novel morph are the profundity of the phenotypic shift that it represents, the number and "purity" (uniformity) of the resulting populations, and whether there is evidence that the novel morph subsequently diversified to generate further morphs that retain the novel features.

These principles are reasonably well reflected in the tax-

onomic treatment of the mutants listed in Table 2. The majority are rare morphs that fail to generate morphologically uniform populations and hence do not receive formal taxonomic treatment. Morphs that recur more frequently and/or occasionally form uniform populations are most commonly treated as varieties. Where they are largely stabilized they typically receive species recognition (e.g., *Phragmipedium lindenii*, Fig. 18), and where that stabilized lineage subsequently undergoes further speciation events (e.g., *Thelymitra* J. R. Forst. & G. Forst., Fig. 24; *Nigritella* Rich., Fig. 30), generic recognition is perhaps appropriate. The most obvious exceptions are the novel "genera" of neottioid orchids recognized by Chen (e.g., 1982), such as "*Tangtsinia*" (Fig. 8), which represent isolated occurrences of very small numbers of presumed mutants that at best merit recognition as forma.

Which Kinds of Terata Are Most Likely to Establish Species?

By pooling data on naturally occurring orchid terata from all sources, the contrasting modes of floral transition can be arranged hierarchically according to their relative evolutionary potential.

Although occurring most commonly, type A peloria appears least likely to result in bona fide speciation. It characteristically occurs sporadically in populations of many (indeed, we suspect in all widespread) orchid species, but rather than successfully forming uniform populations, type A peloric individuals tend to be ephemeral, presumably because in allogamous lineages at least they are strongly selected against by pollinator specificity. They show high turnover, appearing and disappearing with approximately equal regularity. The converse polarity of lateral heterotopy, type B peloria, is also fairly frequent (though less so than type A peloria), but it too tends to be ephemeral and rarely causes speciation (a notable exception being the origination of *Phragmipedium lindenii*, cf. Fig. 17, 18). Type C peloria, involving the acropetal transposition of sepals into the petal whorl, is uncommon and difficult to distinguish from type A pseudopeloria. If correctly assigned to type C peloria, the origin of the genus *Thelymitra* (Fig. 24) from within a strongly zygomorphic clade that includes *Calochilus* R. Br. (Fig. 23), and its subsequent diversification into an estimated 50 species, represents a clear example of an evolutionarily successful radical transition in floral morphology. In contrast, the single known occurrence of the supposed monotypic genus "*Tangtsinia*" probably represents a unique teratological experiment that is likely to prove transient (Fig. 7, 8).

Like type C peloria, types B and C pseudopeloria involve acropetal heterotopy and hence occur uncommonly. They too rarely establish the pure, relatively long-lived populations necessary for recognition as bona fide species. In contrast, type A pseudopeloria, interpreted here as reflecting paedomorphic heterochrony, not only generates occasional novel species but also rare novel genera capable of further speciation, albeit often via radical reproductive shifts such as autogamy and allopolyploidy. One particularly good example is the genus *Gymnadenia* R. Br., which has spawned at least three widespread lineages via paedomorphic shifts: two are single well-established species, *G. odoratissima* (L.)

Rich. and *G. frivaldii* Hampe ex Griseb. (Bateman et al., in press), while the third, "*Nigritella*," has expanded into a supposed genus of ca. 15 species (Bateman and DiMichele 2002; Fig. 29, 30).

Most orchid floral mutants not readily categorized as peloric or pseudopeloric can be judged from first principles to have very poor probabilities of successful establishment, though they can be useful for inferring developmental control mechanisms and/or homology assessment. For example, the partially sepaloid labellum illustrated in *Ophrys ferrumequinum* (Fig. 40) is likely to prove seriously dysfunctional but is a remarkably extreme example of fluctuating asymmetry (epigenetically mediated differential development of the same cell types across a particular structure: e.g., Rudall et al. 2002). It is also relevant to the long-running debate regarding the possible compound origin of the labellum through supposed fusion of the adaxial petal and two adjacent staminodes (reviewed by Rudall and Bateman 2002). Similarly, assuming that it reflects a heritable cause, the *Ophrys insectifera* flower that produced a spiral of five labella of progressively decreasing size (Fig. 45) is very unlikely to be successfully pollinated, given its reliance on pseudocopulation via solitary wasps. Nonetheless, it could constitute a useful model system for studying presumed loss of determinacy in a flower, an area of increasing interest to some evolutionary–developmental specialists (e.g., Rudall in prep.).

CONCLUSIONS

The overall conclusion is that morphological transitions attributable to heterochrony (pseudopeloria) may be a more common driver of speciation than those attributable to heterotopy (peloria). Nonetheless, we hope that we have demonstrated to the reader's satisfaction that at least some, and possibly all, of the modes of instantaneous (and iterative) floral transition described in this paper have the ability to generate at least some prospecies: derived, morphologically fairly uniform populations that have been documented as achieving at least modest longevity (Bateman and DiMichele 2002).

As evidenced in some excellent tomes (e.g., DeVries 1906; Worsdell 1916; Goldschmidt 1940), the evolutionary significance of such terata was given particular credence in the first half of the twentieth century, after Mendel's insights into patterns of allelic inheritance had been popularized, but before neoDarwinian orthodoxy had succeeded in switching the evolutionary emphasis from the genesis of heritable novelty to the supposed preeminence of models requiring directional or disruptive selection to favor some trivially distinct novelties at the expense of others across large panmictic populations. With a very few exceptions, plant teratology became a quaint retrospective discipline primarily of interest to historians of science (cf. Nelson 1967; Theissen 2000).

We hope that this paper will help to redress this balance, as we advocate combining elements of both paradigms and exploring them in vivo, in a phylogenetic context, and using a comparative approach. Given that each mutant prospecies of the kind illustrated here is the potential basis of a taxonomic species, longer term monitoring of naturally occurring mutants in the field is desirable to directly assess their rel-

ative evolutionary success (Bateman and DiMichele 2003; Rudall and Bateman 2003). Accumulating data are increasingly indicating that a remarkable plurality of speciation mechanisms is responsible for generating the extraordinary morphological and species-level diversity currently exhibited by Orchidaceae.

TERMINOLOGICAL POSTSCRIPT

Despite the undeniably challenging terminology employed in this paper (cf. Table 1), we are willing to risk accusations of hypocrisy by stating that evolutionary botany has been made unnecessarily complex by the reinvention or redefinition of several preexisting sets of morphological terms in other subdisciplines, most notably in the evolutionary–developmental genetics community. The resulting ambiguities would benefit from standardization.

We have already discussed the distinction between heterochrony and heterotopy, and the contradictory concepts represented by named categories within heterotopy, notably homeosis. In this context, the clarity brought to the topic by the definitions advocated by Baum and Donoghue (2002) merits wider dissemination and adoption.

Another obvious and troublesome example is the simple description of floral symmetry. For example, a zygomorphic flower by definition exhibits bilateral symmetry (defined by a single mirror plane) when viewed perpendicular to the subtending axis. However, when viewed lateral to the subtending axis such a flower apparently lacks any plane of bilateral symmetry, and from that perspective it can justifiably be described as asymmetric. In other words, symmetry is less in the eye of the beholder than in the perspective of the beholder. It would be preferable to define floral symmetry on the basis of a "full frontal" view perpendicular to the subtending axis, as encapsulated in floral diagrams (e.g., Fig. 2–4), and to reserve the term "asymmetric" for the relatively small number of flowers that lack any mirror planes when viewed from that perspective (see also Neal et al. 1998; Endress 2001; Rudall and Bateman 2002). Another partial solution would be to reinvigorate the nineteenth century predilection for floral formulae, in order to explore the architecture and symmetry of each individual whorl in the flower. Symmetry could easily be conveyed by adding to the formula the number of mirror planes evident in each floral whorl. Using this protocol, the information contained in the floral diagram of *Cypripedium* L. presented in Fig. 3 could equally well be conveyed as the floral formula K3³C3¹A0[a2¹G'($\bar{3}$)³]—or, if the distinction between K and C is considered inapplicable to petaloid monocots, as the modified formula T3³t3¹A0[a2¹G'($\bar{3}$)³].

Similarly popular in evo–devo circles are the terms dorsalized and ventralized, used most frequently to describe mutants of the best-known zygomorphic model flower, snapdragon (*Antirrhinum* L.). The wild type of this flower contains five petals of three distinct kinds: one is deemed to be ventral, two lateral, and two dorsal (e.g., Coen 1999). The *cycloidea* mutant operates by replacing the lateral and dorsal petals with duplicate ventral petals and is said to be ventralized. In contrast, the *backpetala* mutant replaces the lateral and ventral petals with duplicate dorsal petals and described as dorsalized. But the underlying concept of a dor-

siventral mirror plane denoting bilateral symmetry should not be concurrently regarded as an "altitudinal" concept reliably distinguishing physically upper from lower; this is precluded by the 180° rotation of the pedicel and/or ovary evident in most orchids that possess erect inflorescences. Thus, whereas the ventral portion of the flower is, as the term implies, closest to the ground in the non-resupinate snapdragon, it is *furthest* from the ground in a typical resupinate orchid. In an attempt to evade this potential confusion, we have consistently (e.g., Rudall and Bateman 2002, 2003, 2004; Bateman and Rudall 2003) used the terms adaxial for the portion of the axis generating the labellum and abaxial for the portion of the axis bearing the expressed stamen(s); these two terms are defined by both the position relative to the axial apical meristem and the sequence of initiation during ontogeny, which generally are evident before the late-stage onset of resupination.

However, the terms abaxial and adaxial do still serve to illustrate a further potential source of confusion for observers attempting to orient themselves around a phenotypically derived flower such as an orchid. When viewed from an evolutionarily plesiomorphic perspective, even an orchid flower is readily interpreted as consisting of a series of whorls of leaves that are increasingly modified relative to their plesiomorphic condition as the observer passes acropetally along the subtending axis from leaf to bract to sepal, and thence ultimately to carpel. This "bottom up" perspective emphasizes a lateral view of the flower, perpendicular to its axis. However, highly differentiated flowers that consist of closely spaced and phenotypically complex whorls are more instinctively viewed vertically, parallel to the axis and with the apical meristem at the epicenter. From this "top down" perspective, it is simpler to discuss the flower in terms of transitions from "inner" to "outer" whorls, moving away from the epicenter of the aggregate disk presented by the whorled (or helical) array of floral organs (and thus only coincidentally moving basipetally, down the axis).

Lastly, it has become commonplace to use the terms first, second, third, and fourth whorls to represent the sepals, petals, stamens, and carpels, respectively. Whereas this schema may adequately describes a typical eudicot, we hope that we have illustrated that it does not readily distinguish between phenotypically contrasting whorls of tepals or stamens in orchids, nor does it readily permit inclusive coding of other leaf-derived structures such as bracts that occur below the "first whorl" on the axis. In practice, like most other observers, we have found it impossible to avoid employing in our discussions both the "lateral" and "vertical" terminologies, but we hope that we have made more explicit the contrasting perspectives that they tend to represent.

LITERATURE CITED

ALBERCH, P., S. J. GOULD, G. F. OSTER, AND D. B. WAKE. 1979. Size and shape in ontogeny and phylogeny. *Paleobiology* **5**: 296–317.

ALMEIDA, J., M. ROCHETA, AND L. GALEGO. 1997. Genetic control of flower shape in *Antirrhinum majus*. *Development* **124**: 1387–1392.

ANGIOSPERM PHYLOGENY GROUP. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Bot. J. Linn. Soc.* **141**: 399–436.

BATEMAN, R. M. 1985. Peloria and pseudopeloria in British orchids. *Watsonia* **15**: 357–359.

———. 2001. Evolution and classification of European orchids: insights from molecular and morphological characters. *J. Eur. Orch.* **33**: 33–119.

———. 2004. Burnt tips and bumbling bees: how many orchid species currently occur in the British Isles? *Journal of the Hardy Orchid Society* **1**: 10–18.

———. In press. How many orchid species are currently native to the British Isles? *In* J. Bailey [ed.], Contributions to taxonomic research on the British and European flora. Botanical Society of the British Isles, London, UK.

———, AND W. A. DIMICHELE. 2002. Generating and filtering major phenotypic novelties: neoGoldschmidtian saltation revisited, pp. 109–159. *In* Q. C. B. Cronk, R. M. Bateman, and J. A. Hawkins [eds.], Developmental genetics and plant evolution. Taylor and Francis, London, UK.

———, AND ———. 2003. Genesis of phenotypic and genotypic diversity in land plants: the present as the key to the past. *Syst. Biodivers.* **1**: 13–28.

———, P. M. HOLLINGSWORTH, J. SQUIRRELL, AND M. L. HOLLINGSWORTH. In press. Phylogenetics: Neottieae. *In* A. M. Pridgeon, P. L. Cribb, M. W. Chase, and F. N. Rasmussen [eds.], Genera Orchidacearum, 4. Epidendroideae 1. Oxford University Press, Oxford, UK.

———, AND P. J. RUDALL. 2003. The good, the bad and the ugly: using natural terata to distinguish the possible from the impossible in orchid floral evolution. Third international monocot conference on the comparative biology of the monocotyledons. Rancho Santa Ana Botanic Garden, Claremont, California, USA, 31 Mar–4 Apr 2003. Abstract.

———, ———, AND K. E. JAMES. In press. Phylogenetic context, generic affinities and evolutionary origin of the enigmatic Balkan orchid *Gymnadenia frivaldii* Hampe ex Griseb. *Taxon.*

BAUM, D., AND M. J. DONOGHUE. 2002. Transference of function, heterotopy and the evolution of plant development, pp. 52–69. *In* Q. C. B. Cronk, R. M. Bateman, and J. A. Hawkins [eds.], Developmental genetics and plant evolution. Taylor and Francis, London, UK.

BOWMAN, J. L. 1997. Evolutionary conservation of angiosperm flower development at the molecular and genetic levels. *J. Biosci.* **22**: 515–527.

BURNS-BALOGH, P., AND P. BERNHARDT. 1985. Evolutionary trends in the androecium of the Orchidaceae. *Pl. Syst. Evol.* **149**: 119–134.

CHASE, M. W. 1999. Molecular systematics, parsimony, and orchid classification, pp. 81–88. *In* A. M. Pridgeon, P. J. Cribb, M. W. Chase, and F. N. Rasmussen [eds.], Genera Orchidacearum, Vol. 1. General introduction, Apostasioideae, Cypripedioideae. Oxford University Press, Oxford, UK.

———. 2001. The origin and biogeography of Orchidaceae, pp. 1–5. *In* A. M. Pridgeon, P. L. Cribb, M. W. Chase, and F. N. Rasmussen [eds.], Genera Orchidacearum, Vol. 2. Orchidoideae, part 1. Oxford University Press, Oxford, UK.

CHEN, S.-C. 1982. The origin and early differentiation of the Orchidaceae. *Acta Phytotax. Sin.* **20**: 1–20.

COEN, E. S. 1999. The art of the genes: how organisms make themselves. Oxford University Press, Oxford, UK. 396 p.

CRONK, Q. C. B., R. M. BATEMAN, AND J. HAWKINS (editors). 2002.

Developmental genetics and plant evolution. Taylor and Francis, London, UK. 543 p.

CUBAS, P. 2002. Role of TCP genes in the evolution of morphological characters in angiosperms, pp. 247–266. *In* Q. C. B. Cronk, R. M. Bateman, and J. A. Hawkins [eds.], Developmental genetics and plant evolution. Taylor and Francis, London, UK.

———, C. VINCENT, AND E. COEN. 1999. An epigenetic mutation responsible for natural variation in floral symmetry. *Nature* **401**: 157–161.

DEVRIES, H. 1906. Species and varieties: their origin by mutation, Ed. 2. Open Court, Chicago, Illinois, USA. 847 p.

ENDRESS, P. K. 2001. Evolution of floral symmetry. *Curr. Opinion Pl. Biol.* **4**: 86–91.

FREUDENSTEIN, J. V., AND F. RASMUSSEN. 1999. What does morphology tell us about orchid relationships? A cladistic analysis. *Amer. J. Bot.* **86**: 225–248.

———, C. VAN DEN BERG, D. H. GOLDMAN, P. J. KORES, AND M. W. CHASE. 2004. An expanded plastid DNA phylogeny of Orchidaceae and analysis of jacknife branch support strategy. *Amer. J. Bot.* **91**: 149–157.

GOLDSCHMIDT, R. 1940. The material basis of evolution. Yale University Press, New Haven, Connecticut, USA. 436 p.

GOULD, S. J. 1977. Ontogeny and phylogeny. Belknap, Cambridge, Massachusetts, USA. 520 p.

HSU, H.-F., AND C.-H. YANG. 2002. An orchid (*Oncidium* Gower Ramsey) *AP3*-like gene regulates floral formation and initiation. *Pl. Cell Physiol.* **43**: 1198–1209.

JOHANSEN, B., AND S. FREDERIKSEN. 2002. Orchid flowers: evolution and molecular development, pp. 206–219. *In* Q. C. B. Cronk, R. M. Bateman, and J. A. Hawkins [eds.], Developmental genetics and plant evolution. Taylor and Francis, London, UK.

———, ———, AND M. SKIPPER. 2006. Molecular basis of development in petaloid monocot flowers, pp. 151–158. *In* J. T. Columbus, E. A. Friar, J. M. Porter, L. M. Prince, and M. G. Simpson [eds.], Monocots: comparative biology and evolution (excluding Poales). Rancho Santa Ana Botanic Garden, Claremont, California, USA.

———, L. B. PEDERSEN, M. SKIPPER, AND S. FREDERIKSEN. 2002. MADS-box gene evolution: structure and transcription patterns. *Molec. Phylogen. Evol.* **23**: 458–480.

KAEPPLER, S. M., H. F. KAEPPLER, AND Y. RHEE. 2000. Epigenetic aspects of somaclonal variation in plants. *Pl. Molec. Biol.* **43**: 179–188.

KANNO, A., H. SAECKI, T. KAMEYA, H. SAEDLER, AND G. THEISSEN. 2003. Heterotopic expression of class B floral homeotic genes supports a modified ABC model for tulip (*Tulipa gesneriana*). *Pl. Molec. Biol.* **52**: 831–841.

KIM, S., M.-J. YOO, V. A. ALBERT, J. S. FARRIS, P. S. SOLTIS, AND D. E. SOLTIS. 2004. Phylogeny and diversification of B-function MADS-box genes in angiosperms: evolutionary and functional implications of a 260-million-year-old duplication. *Amer. J. Bot.* **91**: 2102–2118.

KURZWEIL, H. 1998. Floral ontogeny of orchids: a review. *Beitr. Biol. Pflanzen* **71**: 45–100.

LAMB, R. S., AND V. F. IRISH. 2003. Functional divergence within the *APETALA3/PISTILLATA* floral homeotic gene lineages. *Proc. Natl. Acad. Sci. U.S.A.* **100**: 6558–6563.

LINNÉ, C. VON. 1744. Dissertatio Botanica de Peloria. Amoenitates Academicae, Uppsala, Sweden. 1230 p.

MCKEAN, D. R. 1982. × *Pseudanthera breadalbanensis* McKean: a new integeneric hybrid from Scotland. *Watsonia* **14**: 129–131.

MEYEROWITZ, E. M., D. R. SMYTH, AND J. L. BOWMAN. 1989. Abnormal flowers and pattern formation in floral development. *Development* **106**: 209–217.

NEAL, P. R., A. DAFNI, AND M. GUIRFA. 1998. Floral symmetry and its role in plant–pollinator systems: terminology, distribution, and hypotheses. *Annual Rev. Ecol. Syst.* **29**: 345–373.

NELSON, E. 1967. Das Orchideenlabellum, ein Homologon des einfachen medianen Petalums der Apostasiaceen oder ein zusammengesetztes Organ? *Bot. Jahrb. Syst.* **87**: 22–35.

REYCHLER, L. 1928. Mutation with orchids. Goamaere, Brussels, Belgium. 163 p.

ROSS-CRAIG, S. 1971. Drawings of British plants, part 28. Hydrocharitaceae, Orchidaceae. G. Bell & Sons, Ltd., London, UK.

RUDALL, P. J., AND R. M. BATEMAN. 2002. Roles of synorganisation, zygomorphy and heterotopy in floral evolution: the gynostemium and labellum of orchids and other lilioid monocots. *Biol. Rev. (Cambridge)* **77**: 403–441.

————, AND ————. 2003. Evolutionary change in flowers and inflorescences: evidence from naturally occurring terata. *Trends Pl. Sci.* **8**: 76–82.

————, AND ————. 2004. Evolution of zygomorphy in monocot flowers: iterative patterns and developmental constraints. *New Phytol.* **162**: 25–44.

————, ————, M. F. FAY, AND A. EASTMAN. 2002. Floral anatomy and systematics of Alliaceae with particular reference to *Gilliesia*, a presumed insect mimic with strongly zygomorphic flowers. *Amer. J. Bot.* **89**: 1867–1883.

SANDERSON, M. J., AND L. HUFFORD (editors). 1996. Homoplasy: the recurrence of similarity in evolution. Academic Press, London, UK. 339 p.

THEISSEN, G. 2000. Evolutionary developmental genetics of floral symmetry: the revealing power of Linnaeus' monstrous flower. *Bioessays* **22**: 209–213.

————, A. BECKER, K. U. WINTER, T. MÜNSTER, G. KIRCHNER, AND

H. SAEDLER. 2002. How the land plants learned their floral ABCs: the role of MADS-box genes in the evolutionary origin of flowers, pp. 173–205. *In* Q. C. B. Cronk, R. M. Bateman, and J. A. Hawkins [eds.], Developmental genetics and plant evolution. Taylor and Francis, London, UK.

TREMBLAY, R., J. D. ACKERMAN, J. K. ZIMMERMAN, AND R. N. CALVO. 2005. Variation in sexual reproduction in orchids and its evolutionary consequences: a spasmodic journey to diversification. *Biol. J. Linn. Soc.* **84**: 1–54.

TSAI, W.-C., C.-S. KUOH, M.-H. CHUANG, W.-H. CHEN, AND H.-H. CHEN. 2004. Four *DEF*-like MADS-box genes displayed distinct floral morphogenetic roles in *Phalaenopsis* orchid. *Pl. Cell Physiol.* **45**: 831–844.

VERGARA-SILVA, F. 2003. Plants and the conceptual articulation of evolutionary developmental biology. *Biology and Philosophy* **18**: 249–284.

WALKER-LARSEN, J., AND L. D. HARDER. 2000. The evolution of staminodes in angiosperms: patterns of stamen reduction, loss, and functional re-invention. *Amer. J. Bot.* **87**: 1367–1384.

WALLBRUNN, H. 1987. Peloria in orchids. *Orchid Rev.* **95**: 360–367.

WARDLAW, C. W. 1965. Organisation and evolution in plants. Longman, London, UK. 499 p.

WEBER, A. 2003. Morphology and its renaissance in plant systematics, pp. 3–32. *In* T. Stuessy, V. Mayer, and E. Hörandl [eds.], Deep morphology: toward a renaissance of morphology in plant systematics. Gantner, Ruggell, Liechtenstein.

WORSDELL, W. C. 1916. Principles of plant teratology, Vol. 2. The Ray Society, London, UK. 296 p.