A morphometric study of ×Orchiaceras bergonii (Nanteuil) Camus and its parents (Aceras anthropophorum (L.) Aiton f. and Orchis simia Lamarck) in Kent*

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ABSTRACT

 \times Orchiaceras bergonii (Nanteuil) Camus (Aceras anthropophorum (L.) Aiton f. \times Orchis simia Lamarck), recently found in Kent and new to the British Isles, is described in detail. Morphometric comparison of the hybrid with its parent species has shown that it is intermediate in 17 of the 41 characters measured but resembles Aceras in six and O. simia in 18. It is similar to Continental plants of \times Orchiaceras bergonii; some characters appear to be expressed consistently in hybrids between Aceras and several species of Orchis. The status of the British \times Orchiaceras bergonii as a natural hybrid, and the value of Aceras R. Brown as a genus, are discussed. The need for accurate, quantitative diagnostic characters in Floras, and the considerable value of multivariate methods in the study of hybrids, are emphasized.

INTRODUCTION

Bigeneric hybrids between Aceras anthropophorum (L.) Aiton f. and species of Orchis L. section Orchis subsection Militares Parlatore are often recorded on the Continent (Nelson 1968; Peitz 1970; Davies et al. 1983), especially ×Orchiaceras bergonii (Nanteuil) Camus (1892) (A. anthropophorum × O. simia Lamarck); for synonyms see Peitz (1970). The frequent occurrence of this hybrid, particularly in France, shows that its parents share pollen vectors and that barriers to cross-fertilization are, at best, only partially effective. It also reflects their similar ecological preferences and geographical distributions in mainland Europe (Baumann & Künkele 1982). Aceras and O. simia both reach their northern limits in the British Isles, but curiously they have remained almost entirely allopatric. Aceras is locally frequent along the North Downs of Kent and Surrey, but rare elsewhere (Perring & Walters 1962); Druce (1886) reported only one Oxfordshire site for Aceras, and only one remains (Steel & Creed 1982). O. simia has always been confined to southern Oxfordshire, where it coexisted with O. militaris L. and was locally frequent until the mid-nineteenth century (Godfery 1933; Summerhayes 1951), but has since declined to a single viable population (Summerhayes 1951; Paul 1965). Consequently, in Britain, only one hybrid combination has been recorded involving O. simia (O. \times beyrichii A. Kerner = O. simia \times O. militaris) (Hunt 1975a), and none involving Aceras (Hunt 1975b).

In 1920, five plants of *O. simia* were found at Bishopsbourne, near Canterbury, Kent. In the same year, B. J. Brook collected two flowers of *O. simia* and one of *Aceras*, all apparently from this locality (**BM**). Unfortunately, *O. simia* only persisted at Bishopsbourne until 1923, and only one or two plants flowered each year (Summerhayes 1951), providing little opportunity for hybridization. However, in 1955, H. M. Wilks discovered another Kentish locality for *O. simia*

* Dedicated to the late Norman R. Campbell, orchid biometrician.

near Faversham (Wilks 1960), and this remains the only natural population of this species south of the Thames (Perring & Farrell 1977; Philp 1982); at present about 30-50 O. simia plants coexist with a similar number of Aceras. When we visited the locality on the 31st May 1985, we tentatively identified the first individual of ×Orchiaceras bergonii recorded in the British Isles.

MATERIALS AND METHODS

A biometric study was performed to appraise this initial identification and to assess the morphological variation shown by its presumed parent species. 41 characters were recorded for the putative hybrid and for every flowering plant of *O. simia* (10) and *Aceras* (8) present:

- A. Stem and inflorescence (7 characters).
- 1. Stem height, above ground level.
- 2. Stem diameter, above uppermost sheathing leaf.
- 3. Presence (1) or absence (0) of anthocyanins immediately below inflorescence.
- 4. Inflorescence length.
- 5. Number of flowers.
- 6. Bract length.
- 7. Ovary length.
- B. Leaves (7 characters).

Orchis and *Aceras* leaves are difficult to categorize. Basal leaves form a spreading rosette immediately above ground level. Sheathing leaves arise from the rosette but surround the stem (occasional leaves intermediate between these categories were arbitrarily classed as basal leaves). Cauline leaves arise from the stem above its base, and are usually much smaller than the lower leaves. Leaf shape (character 14) was assessed by determining the position of maximum width relative to length, on a scale 1-4 (1=0-10% of length; 2=11-25%; 3=26-50%; 4=>50%).

- 8. Number of basal leaves.
- 9. Number of sheathing leaves.
- 10. Number of cauline leaves.
- 11. Length of longest leaf.
- 12. Width of longest leaf (often=C13).
- 13. Width of widest leaf.
- 14. Shape of longest leaf (see above).
- C. Labellum (16 characters).

Fig. 1 summarizes nine measurements taken from each labellum, and explains the anthropomorphic terminology that we have adopted for simplicity to describe parts of the labellum. The colours of the 'torso' and 'limbs' of each labellum, and of the reverse surfaces of the outer perianth segments, were matched to the nearest colour block of the Royal Horticultural Society Colour Chart (Anonymous 1966) by I. Denholm. Patches of pigmented hairs characteristic of the 'torso' of *O. simia* are termed papillae.

- O. simu are termed papina
- 15. Maximum width.
- 16. Width of 'torso'.
- 17. Maximum length.
- 18. Length of 'torso'.
- 19. Presence (1) or absence (0) of 'tail'.
- 20. Length of 'tail' (if present).
- 21. Length of 'arm'.
- 22. Width of 'arm', measured halfway along length.
- 23. Length of 'leg'.
- 24. Width of 'leg', measured halfway along length.
- Colour of 'torso', on a scale 1-3 (1=pale straw yellow, R.H.S.11C; 2=greenish-grey, R.H.S.157C; 3=very pale lilac, R.H.S.76D).
- 26. Colour of 'limbs', on a scale 1-4 (1=yellowish-orange, R.H.S.15C; 2=purplish-red, R.H.S.64B; 3=reddish-purple, R.H.S.72B-C; 4=purple-violet, R.H.S.80B-C).
- 27. Number of papillae on 'torso'.
- 28. Distribution of papillae on 'torso', on a scale 1-3 (1=concentrated immediately below spur entrance, through to 3=distributed over most of 'torso').

398



FIGURE 1. Nomenclature of floral parts, and labellum dimensions measured. Numbers refer to characters listed in Materials and Methods.

- 29. Attitude of 'torso' relative to stem, on a scale 1-5 (1=parallel, through to 5=perpendicular).
- 30. Attitude of 'limbs' relative to 'torso', on a scale 1-4 (1=shallowly convex; 2=planar; 3=shallowly concave; 4=deeply concave).
- D. Spur (3 characters).
- 31. Length, from entrance to apex.
- 32. Diameter, halfway along length when viewed laterally.
- 33. Shape, on a scale 1-5 (1=strongly recurved, through to 5=strongly decurved).
- E. Inner perianth segments (2 characters).
- 34. Length.
- 35. Maximum width.
- F. Outer perianth segments (5 characters).
- 36. Length.
- 37. Maximum width.
- Colour of reverse surface, on a scale 1-2 (1=pale yellowish-green, R.H.S.154C-D; 2=pale/ very pale lilac, R.H.S.76C-D).
- 39. Presence (1) or absence (0) of peripheral and median linear markings on reverse surface.
- 40. Presence (1) or absence (0) of dispersed dots and/or dashes on reverse surface.
- G. Phenology (1 character).
- 41. Percentage of flowers in inflorescence fully open.

Some of the above characters were used to calculate the following ratios, which summarize the shapes of certain structures. The characters are numbered according to the above list and preceded by the letter 'C':

- a. Robustness of stem. C2/(C1+C2).
- b. Percentage of stem bearing flowers. $(100 \times C4)/C1$.
- c. Density of inflorescence (fls/cm). C5/C4.
- d. Length of bract relative to length of ovary. C6/(C6+C7).
- e. Shape of longest leaf. C12/(C11+C12).
- f. Roundness of labellum. C17/(C15+C17).
- g. Length of 'arms' relative to length of 'torso'. C21/(C18+C21).
- h. Length of 'legs' relative to length of 'torso'. C23/(C18+C23).
- i. Length of 'arms' relative to length of 'legs'. C21/(C21+C23).

Data were analysed by multivariate methods using the Rothamsted Genstat computer program (Alvey *et al.* 1977). Character 12 was discarded as it often duplicated character 13, and ratios (a) to (i) were omitted as they duplicate their component characters. The remaining 40 characters were used to compute a symmetrical matrix that quantified the similarities of pairs of data sets (i.e. plants) using the Gower Similarity Coefficient (Gower 1971) on unweighted data scaled to unit variance. This was used to construct a minimum spanning tree (Gower & Ross 1969) and subsequently to calculate principal coordinates (Gower 1966), compound vectors that incorporate positively or negatively correlated characters which are most variable and therefore of potential diagnostic value. Principal coordinates have previously been used to assess morphological relationships between orchid taxa (Bateman & Denholm 1983, 1985), but not those between orchid hybrids and their parental taxa.

VARIATION IN SINGLE CHARACTERS

Population means (and sample standard deviations) for O. simia, $\times Orchiaceras$ and Aceras are presented in Table 1.

CHARACTERS SEPARATING THE PARENTS

We define continuous metric characters and ratios as *taxonomically useful* if the parental standard deviations do not overlap (>67% discrimination) and *diagnostic* if twice the parental standard deviations do not overlap (>95% discrimination) (Fig. 2). Diagnostic scalar characters lack classes containing individuals of both species. Eleven characters and three ratios are taxonomically useless, and a further nine characters and two ratios are taxonomically useful but not diagnostic (i.e. give 67–95% discrimination; Table 1). They include the majority of the floral dimensions measured and all but one of the vegetative characters (e.g. stem height, leaf size and number), which are potentially strongly influenced by both ontogeny and environment; the four vegetative characters (one, stem diameter, diagnostic) classed as taxonomically useful here might be less useful at other sites which support more vigorous populations of *Aceras*. However, the remaining 20 diagnostic characters and four diagnostic ratios are probably generally applicable.

Compared with *Aceras*, *O. simia* has basal leaves that are broadest closer to their tips and much shorter bracts (about one quarter the length of the ovary rather than approximately equalling the ovary). Its tendency to have fewer, more closely-spaced flowers results in a shorter inflorescence forming a much smaller proportion of the total length of the stem. Its flowers open more or less simultaneously (the lower flowers may open slightly earlier (Wilks 1960) or slightly later (Ettlinger 1976) than the upper) to form a cylindrical inflorescence, whereas those of *Aceras* open gradually from the bottom upwards over a long period to form an acute conical inflorescence. The flowers of



FIGURE 2. Explanation of A) 'hybrid categories' (1–5) listed in Table 1, and B) character classes described in Characters Separating the Parents. \odot =value for ×*Orchiaceras*, •=mean for *Orchis simia*, \bigcirc =mean for *Aceras*; bars indicate standard deviations of parental taxa (¹=twice the standard deviation).

400

STUDY OF × ORCHIACERAS BERGONII

TABLE 1. COMPARISON OF CHARACTER VALUES FOR $\times ORCHIACERAS$ BERGONII WITH POPULATION MEANS (AND SAMPLE STANDARD DEVIATIONS IN PARENTHESES WHERE APPROPRIATE) OF PARENTAL POPULATIONS

Characters are numbered as in Materials and Methods. Italicized characters are taxonomically useful, bold characters are diagnostic (see Fig. 2). See Fig. 2 for explanation of 'hybrid category'.

Chara	leter	Units	O. sin	nia	imes Orchiaceras	Acera	S	Hybrid category
٨	1	mm	267	(68)	180	223	(46)	4
А.	2	mm	1 28	(0.0)	3 4	2 50	(40)	3
	2	111111	4.20	(0.77)	0	0	(0.32)	3
	3	mm	25.8	(8.0)	11	71 1	(25, 1)	1
	4 5	mm	17.6	(0.9)	6	22 1	(23.1) (11.5)	1
	5	122.122	1 9	(3.0)	7 9	52.1	(11.3)	5
	7	mm	7.0	(0.7)	6.8	6.2	(0.3)	3
В.	2	mm	1.9	(1.0)	0.0	1.0	(0.3)	1
	0		4.5	(0.3)	1	4.0	(0.6)	1
	9		1.0	(0.7)	1	1.1	(0.0)	1
	10		117	(0.5)	0	1.1	(0.4)	1
	11	mm	20	(24)	93	00	(29)	2
	12	mm	29	(3)	22	10	(3)	3
	13	mm	30	(0)	24	18	(3)	3
0	14		4.0	11.0	4	3.0	(0. 6)	2
C.	15	mm	12.2	(1.6)	11.0	4.1	(0.6)	2
	16	mm	1.84	(0.24)	1.7	1.23	(0.22)	2
	17	mm	12.7	(1.3)	13.0	9.9	(2.2)	2
	18	mm	7.8	(0.7)	7.8	7.1	(1.3)	2
	19		1.0		1	0.4		2
	20	mm	1.44	(0.57)	0.7	0.27 ^o	(0.21)	3
	21	mm	8.2	(0.8)	8.3	5.4	(1.4)	2
	22	mm	0.73	(0.07)	0.9	0.62	(0.08)	1
	23	mm	7.5	(1.3)	5.4	2.9	(1.1)	3
	24	mm	0.92	(0.15)	0.9	0.38	(0.09)	2
	25		3.0		2	1.0		3
	26		4.0		3	1.3		3
	27		28	(3)	6	0		3
	28		3.0		2	0		3
	29		2.4		2	1.0		2
	30		4.0		2	1.4		4
D.	31	mm	4.7	(0.8)	1.9	0		3
21	32	mm	1.69	(0.35)	1.6	0		2
	33		4.2	(0100)	4	Ő		2
F	34	mm	8.5	(1, 1)	6.6	4.9	(1, 2)	3
L .	35	mm	1 48	(0.24)	1.4	1.24	(0.37)	3
F	36	mm	11.3	(1.2)	8.0	6.4	(0.9)	3
1.	37	mm	47	(0, 9)	3.4	29	(0, 4)	3
	38	111111	2.0	(0.))	1	1.0	(0.4)	4
	30		0		1	1.0		4
	39		1.0		1	1.0		-
G	40	07.	100	(0)	100	52	(24)	2
U. Datia	41	70	0.016	(0, 002)	0.019	. 0.012	(24)	2
Ratio	a F	01-	0.010	(0.002)	6.1	32.1	(0.005)	2
	0	fle/cm	7.0	(1.0)	5.5	1 7C	(0.9)	2
	u a	IIS/CIII	0.10	(1.4)	0.52	4./	(1.7)	5
	u a ^a		0.19	(0.03)	0.55	0.10	(0.04)	4
	e		0.20	(0.02)	0.19	0.18	(0.05)	5
	I		0.51	(0.04)	0.54	0.71	(0.05)	2
	8		0.52	(0.03)	0.52	0.43	(0.03)	2
	n		0.49	(0.04)	0.41	0.29	(0.04)	3
	1		0.53	(0.03)	0.61	0.65	(0.00)	4

^a Values estimated for several plants lacking leaf tips. ^bMean of plants possessing 'tails'. ^cValue would have decreased as flowers higher in the inflorescence opened.

O. simia are generally larger (Fig. 3), especially in overall labellum width, 'leg' and outer perianth segment dimensions. 'Tails' are either absent in Aceras or much shorter than those of O. simia. The labella of Aceras are parallel to the stem and the 'limbs' are more-or-less parallel to the 'torso', whereas the labella of O. simia are inclined upward and the 'limbs' arc forward. The c.5 mm long, downward-curved spur of O. simia is represented only by a very shallow (<0.5 mm) 'nectar pit' in Aceras, and Aceras lacks the 25–30 papillae that adorn the 'torso' of O. simia. Pigmentation provides the most conspicuous differences between the species; O. simia has pale lilac outer perianth segments and 'torsos', deepening to purple-violet on the 'limbs', and anthocyanins are usually also present on the upper part of the stem, whereas Aceras has yellowish-green outer perianth segments, a straw yellow 'torso' with 'limbs' that often open purplish-red but fade to yellow-orange, and lacks stem anthocyanins. The outer perianth segments of O. simia bear dispersed purple-violet dots and dashes, in contrast to the peripheral and median linear, purplish-red markings of Aceras.

Interestingly, the ranges of labellum lengths obtained for both species in Kent are shorter than, and do not overlap with, ranges given in *Flora Europaea* by Soó (1980) for *O. simia*, and Moore (1980) for *Aceras*. Soó (1980) also described the bracts of *O. simia* as c.50% of the length of the ovary (they average 23% in Kent), its labellum as longer than wide (its length approximately equals its width in Kent), and its outer and inner perianth segments as c.10 mm long (the outer perianth segments average 11.3 mm but the inner only 8.5 mm in Kent).

COMPARISON OF THE HYBRID WITH ITS PARENTS

Characters of the putative hybrid have been assigned to one of five 'hybrid categories' in Table 1 according to their values relative to the standard deviations of the parental means. Fig. 2 explains these categories. The hybrid is morphologically more extreme than either parent (categories 1 and 5) in only six characters, and only two of these are taxonomically useful: it has a shorter inflorescence than O. simia and slightly longer bracts than Aceras. It resembles O. simia in 13 characters (category 2), including its orbicular leaves, the inclined position and more-or-less synchronous opening of its flowers, its wide labellum, 'torso' and 'legs', its long 'arms' and its small labellum roundness index, and resembles Aceras in five characters (category 4), including having its 'limbs' in the same plane as its 'torso' (Fig. 3), yellowish-green outer perianth segments, bracts that equal the ovaries in length, and in lacking stem anthocyanins. The hybrid is intermediate in 16 characters (category 3). Values for 14 of these do not fall within the standard deviations (continuous metric character) or classes (scalar characters) of either parent and therefore aid identification of the hybrid; they include several vegetative characters, 'leg', 'tail' and spur lengths, labellum colours, number and distribution of papillae, and outer and inner perianth segment dimensions. Its outer perianth segments also bear both the dispersed dots and dashes of O. simia and the peripheral and median lines of Aceras (Fig. 3).

The hybrid was a young plant flowering for the first time when measured (H. M. Wilks pers. comm. 1985) and consequently gave small values for most vegetative characters. When this is taken into account, the stem and leaves of the hybrid more closely resemble those of *O. simia*, although it has similar bracts to *Aceras*. Most of its labellum dimensions are also closer to *O. simia*, especially its overall width, but it has a shorter 'tail' and 'legs', and its 'limbs' occur in the same plane as its 'torso', resembling *Aceras*. Its labellum is intermediate in colour, and although it has the papillae and spur of *O. simia* the former are far fewer and the latter is much shorter. The outer and inner perianth segments of the hybrid are intermediate in size and bear markings characteristic of both parents.

This mixture of parental and intermediate characters is typical of hybrids between closely related species (Stace 1975).

MULTIVARIATE ANALYSES

Data for individual plants were subjected to multivariate analyses for two reasons: i) to test the a priori assignment of plants to one of the three categories (*Orchis*, \times *Orchiaceras*, *Aceras*) in Table 1, and ii) to investigate the potential for identifying and describing hybrids of superimposing

402









FIGURE 3. Comparison of the flowers of Orchis simia (A), \times Orchiaceras bergonii (B), and Aceras anthropophorum (C).



FIGURE 4. Minimum spanning tree superimposed onto a principal coordinates plot of PC1:PC2. Percentages are Gower Similarities (links within parental groups all exceed 92.5%). \bullet =Orchis simia, \bigcirc =Aceras anthropophorum, \bigcirc =×Orchiaceras bergonii.

a minimum spanning tree based on Gower Similarity Coefficients onto a principal coordinates analysis (Fig. 4).

The mean of the maximum similarities of individuals of *O. simia* and *Aceras* is only $51.6\pm6.4\%$, so it is not surprising that the parental species form two distinct groups separated by a wide morphological discontinuity on the very strong first coordinate (PC1). Within each parental group, separation on PC1 is slight and minimum spanning tree links between individuals are relatively strong, exceeding 92.5% maximum similarity. The hybrid occurs between the parental groups, slightly closer to the nearest *O. simia* than to the nearest *Aceras*. Its predictably weak minimum spanning tree links also suggest a greater overall similarity to *O. simia*.

Table 2 shows that PC1 is determined by all of the characters defined as taxonomically useful in Table 1, with diagnostic characters taking precedence. The much weaker PC2 represents seven vegetative characters (six taxonomically useless) that are influenced by the size of the plant; it is a 'vigour' coordinate. PC3 is governed by four of the six characters (five taxonomically useless) that yield values for the hybrid more extreme than both parents; it therefore separated the hybrid from all the other plants measured.

DISCUSSION AND CONCLUSIONS

The Kentish $\times Orchiaceras$ bergonii is very similar to plants of this parentage described by Continental orchidologists (Camus & Camus 1932; Nelson 1968; Peitz 1970). Indeed, similar combinations of characters are shown by hybrids of *Aceras* with other species of *Orchis* subsection *Militares* (Nelson 1968, plate 23; Peitz 1970, pp. 252–3; Sundermann 1980, p. 258). Vegetative characters are variable and often intermediate between the parents, but the hybrids usually resemble *Orchis* in inflorescence density and *Aceras* in bract size. Floral characters are more predictable; $\times Orchiaceras$ resembles *Orchis* in overall labellum shape (although 'leg' lengths are often intermediate), but is intermediate in 'tail' and spur lengths and perianth segment dimensions. It is also intermediate in pigmentation characters, and the papillae of *Orchis*, although present, are reduced in size and number. This consistency of expression in $\times Orchiaceras$ for many characters, irrespective of the parental species of *Orchis*, suggests that they are controlled by major genes whose dominance is relatively well-established.

STUDY OF × ORCHIACERAS BERGONII

TABLE 2. LIST OF CHARACTERS CONTRIBUTING APPRECIABLY TO THE FIRST THREE PRINCIPAL COORDINATES

See Materials and Methods for descriptions of numbered characters. Characters in normal typeface increase in value with increasing value of the vector, italicized characters decrease in value with increasing value of the vector.

Coordinate	Percentage of total variance accounted for	Characters contributing to the coordinates, listed in order of decreasing contribution
PC1	76.5	25, 28, 31, 40, 14, 27, 26, 15, 33, 32, 38, <i>39</i> , 30, 36, 23, 3, 24, 34, 29, 6, 20, 2, 16, 37, 41, 13, 21, <i>4</i> , 7
PC2	5.8	1, 18, 9, 5, 11, 17, 7
PC3	3.7	10, 8, 22, 6

The widespread occurrence of $\times Orchiaceras bergonii$ on the Continent shows that at least some insects, possibly bees (the pollen vectors of *O. simia* and *Aceras* have not, to our knowledge, been studied), visit both parents. However, field observations suggested that the Kent population of *O. simia* was not being naturally pollinated, so a successful programme of artificial pollination was introduced in 1958 (Wilks 1960) and is still performed annually (H. M. Wilks pers. comm. 1985). Thus, the Kentish $\times Orchiaceras$ could have arisen artificially, although it is more likely that natural pollination of *O. simia* does occur sporadically and that an insect paid a rare visit to an *O. simia* and an *Aceras*; two individuals, one of each taxon, have grown and flowered a few centimetres apart for several years (H. M. Wilks pers. comm. 1985).

Some authors (Bateman 1982; Davies *et al.* 1983) have argued that the frequent hybridization of *Aceras* with species of *Orchis* subsection *Militares* casts doubt on its usefulness as a monotypic genus. Although much shorter, the 'nectar pit' of *Aceras* is probably homologous with the spur of *Orchis*; its shallower depth and the shorter distance between the viscidia of *Aceras* merely indicate adaptation to smaller pollen vectors. With these exceptions, *Aceras* apparently lies within the range of variation encompassed by the eight European species of *Orchis* subsection *Militares*, and shares with them a chromosome number of 2n=42 (Sundermann 1980; Moore 1980; Soó 1980). Furthermore, introgression of *Aceras* and *Orchis* has been reported by several authors (Keller & Schlechter 1928; Peitz 1970), although the feasibility of identifying such hybrids has been questioned by Wollin (1972). Together, these facts suggest that *Aceras anthropophorum* would be more appropriately placed under *Orchis*.

Reliable identification of putative hybrids must rest entirely on morphological discrimination from the parents if they have identical chromosome numbers and other, less readily obtained, biosystematic data are not available. This requires careful and detailed measurement, not only of the hybrid but also of any potential parental taxa; our study would have been invalid if we had relied on descriptions of the parents in the literature as these can be misleading, e.g. in *Flora Europaea* (Moore 1980; Soó 1980).

Principal coordinates analysis is preferred to other multivariate methods of processing such data as it avoids the a priori identification of the parental taxa inherent in Wells hybrid distance diagrams (Adams 1982) and of hybrids in canonical variates analysis (Neff & Smith 1979). It is also preferable to projecting a hybrid onto a pre-ordinated canonical variates analysis (McNeill 1984), as the minimized intra-group distances mean that the suspected hybrid would be unlikely to occupy the same multivariate space as its putative parents even if it is merely a morphological extreme of one of the species. Superimposing a minimum spanning tree onto a principal coordinates plot of unweighted data scaled to unit variance has proved excellent for i) identifying the hybrid, ii) establishing its overall similarities to the parent taxa, iii) identifying characters most suitable for separating the parental taxa and distinguishing the hybrid, and iv) identifying characters most strongly influenced by vigour. Moreover, good separation of taxa has been achieved by principal coordinates analysis without maximizing the inter-taxon distances using the F-1 weighted similarities advocated by Whiffin (1977) and Adams (1982).

In this study, PC1 is much stronger than the other coordinates and separates the parental taxa, leaving a morphological discontinuity occupied only by the hybrid. PC2 reflects variation in vigour

in all the taxa measured, and PC3 identifies the few characters that separate the hybrid from both parents. This distribution of character types among the first three coordinates may be expected in instances of hybridization where i) the parental taxa are separated by a morphological discontinuity, ii) the hybrid plants are less numerous than either parent, and iii) most of the characters of the hybrid fall within or between the parental ranges (categories 2–4). As all three criteria are fulfilled by most examples of natural hybridization, principal coordinates analysis represents a powerful tool for investigating hybridization and deserves to be more widely used.

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STUDY OF × ORCHIACERAS BERGONII

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