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A MORPHOMETRIC ANALYSIS OF FLORAL CHARACTERS IN *MILTONIA SPECTABILIS* AND *MILTONIA SPECTABILIS* VAR. *MORELIANA* (MAXILLARIEAE: ONCIDIINAE)[1]

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ABSTRACT: Thirty-two floral morphological characters were measured in Brazilian populations of *Miltonia spectabilis* and *Miltonia spectabilis* var. *moreliana*. Canonical discriminant analysis and cluster analysis based on Mahalanobis' distances were employed to study morphological variation and delimitation of these two taxa. Differences in flowering times among populations and distribution were also considered. The two taxa were clearly distinct in all analyses. We therefore propose to recognize *M. spectabilis* var. *moreliana* as a distinct species, *M. moreliana*.

MILTONIA was described by Lindley (1837), with the Brazilian species *M. spectabilis* as the type. Although more than 20 Andean and Central American species have been either described or included in *Miltonia* (Hoehne, 1949), currently only nine species (Pabst and Dungs, 1977) are included in the genus, and most of these are strictly Brazilian: *M. anceps* Lindl., *M. candida* Lindl., *M. clowesii* Lindl., *M. cuneata* Lindl., *M. flavescens* Lindl., *M. kayasimae* Pabst, *M. regnelli* Rchb.f., *M. russeliana* Lindl. and *M. spectabilis*. Although *M. candida* and *M. cuneata* have been separated as the genus *Anneliesia* Brieger & Lückel (Brieger and Lückel, 1983; Senghas, 1997a; Senghas, 1997b), molecular data indicate the circumscription of Sweet (1978) to be a monophyletic group (Williams *et al.*, 2001).

Within *M. spectabilis,* there is a population that has been described as *M. spectabilis* var. *moreliana* Henfr., and these plants have a distinct darker color pattern when compared to the typical populations. Although in early literature some authors preferred to consider it a distinct species (Warner, 1867; Nicholson, 1886), in the last two centuries it has generally been treated as a variety, until the studies of Martins (1967), who studied 119 individuals of these two taxa. Most of these were included in this study; however, Martins (1967) organized the populations in a slightly different way in which he grouped them in four regions: region 1 (Bertioga—São Sebastião, SP), mean altitude 400m; region 2 (Serra dos Órgãos: Rodovia Rio de Janeiro—Petrópolis, RJ), mean altitude 800m; region 3 (Serra dos Órgãos: Petrópolis, RJ), mean altitude 600m; region 4 (Muqui, ES), mean altitude 250m. He also analyzed 14 plants of *M. spectabilis* var. *moreliana* from one region (adjoining portions of northern Espírito Santo and southern Bahia). He compared living material with descriptions and illustrations in the literature and considered geographic distribution and flowering times. Additionally, he measured four vegetative and eight floral measurements and calculated the average, standard deviation, and coefficient of variation, as well as applying *t*-tests for each variable. Although he found discontinuity between these two taxa, at that time computer facilities did not allow more complex multivariate analysis of the data. He also verified that flowering times of these two taxa were distinct and concluded they should be considered species.

Considering the size of Orchidaceae, there is a relatively small number of studies using morphometrics to assess population variability; mostly this has been focused on terrestrial temperate

[1] This paper was completed after the death of the third author and is therefore dedicated to his memory.

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TABLE 1. Populations of *M. spectabilis* var. *spectabilis* and *M. spectabilis* var. *moreliana* included in this study.

Taxon	Population	Code	Sample size	Latitude	Longitude	Elevation (m)
M. spectabilis var. *spectabilis*	Petrópolis, RJ	MSS1	81	22.51°S	43.18°W	810
	Toque-Toque Pequeno, SP	MSS2	25	23.76°S	45.41°W	1
	Cascata, RJ[1]	MSS3	6	—	—	—
	Muqui, ES	MSS4	3	20.95°S	41.35°W	250
	Angra dos Reis, RJ	MSS5	1	23.01°S	44.32°W	7
M. spectabilis var. *moreliana*	Pedro Canário, ES	MSM1	12	18.03°S	40.15°W	140
	Jussari, BA	MSM2	1	15.19°S	39.50°W	196
Total			129			

[1] This is a small village between Petrópolis, RJ, and Rio de Janeiro, RJ, which does not figure in most maps and for which we were unable to locate precise latitude, longitude, and elevation.

orchids (Bateman and Denholm, 1988; Bateman and Farrington, 1989; Dufrene, Gathoye, and Tyteca, 1991; Tyteca and Gathoye, 1993; Catling and Catling, 1994; Tyteca and Dufrene, 1994; Catling and Catling, 1997; Shaw, 1998; Catling and Brownell, 1999; Catling, Brownell, and Allen, 1999; Borba et al., 2002). We could find only five studies of this type that dealt with subtropical or tropical orchids (Morrison and Weston, 1985; Balfour and Linder, 1990; Ackerman and Galarza Perez, 1991; van den Berg and Martins, 1998; Borba et al., 2002).

Our aim in this research was to study the morphological variation of *M. spectabilis* and *M. spectabilis* var. *moreliana* in more depth with increased data and more powerful statistical analyses, taking also into account flowering data and geography.

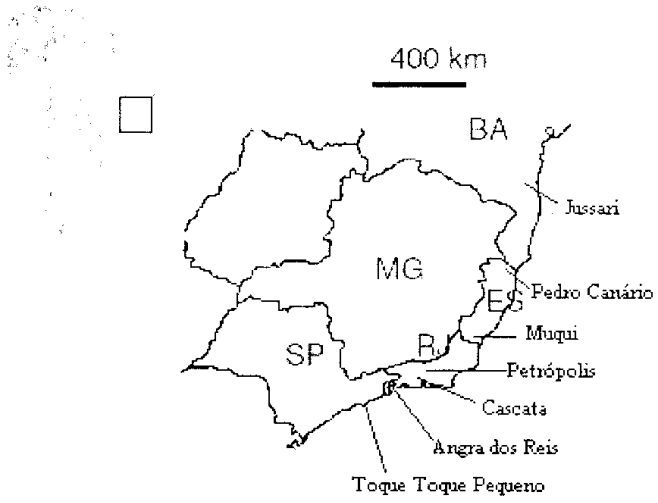

Fig. 1. Geographical location of populations of *M. spectabilis* var. *moreliana* (MSM1—Pedro Canário, ES; MSM2—Jussari, BA), *M. spectabilis* var. *spectabilis* (MSS1—Petrópolis, RJ; MSS2—Toque-Toque Pequeno, SP; MSS3—Cascata, RJ; MSS4—Muqui; MSM5—Angra dos Reis, RJ) included in this study. Legend: BA = Bahia, ES = Espírito Santo, MG = Minas Gerais, RJ = Rio de Janeiro, SP = São Paulo.

MATERIAL AND METHODS

A total of 129 individuals were sampled. These were randomly chosen within five populations throughout the range of *M. spectabilis* as well as two populations that could be assigned to variety *moreliana* based on flower color (Table 1; Fig. 1). All plants of these seven populations had been collected many years ago and kept under uniform growing conditions in the orchid collection of the Department of Genetics, ESALQ/USP, Piracicaba, São Paulo, Brazil. This was considered important as a way to control environmental variation and thus leave only genetic variation or that due to random variation among the studied plants. Several years ago, flowers of each individual were collected, dried, and attached to paper cards with the purpose of being used as vouchers and also to facilitate measurement. These cards are deposited at ESA.

For this study, 32 floral variables were measured (Table 2; Fig. 2) for only one flower per individual if there was more than one per voucher. Vegetative variables were not included. Plants belonging to the same geographical region, that is, neighboring localities with the same ecological and environmental conditions, were grouped as a single population. In this way, the typical form of *M. spectabilis* included five populations: MSS1—Petrópolis, Rio de Janeiro State, including Petrópolis county and neighboring districts of Bom Jardim, and Mantiqueira between the town of Petrópolis and the city of Rio de Janeiro;

TABLE 2. Floral measurements used as variables for the statistical analyses in this study.

Variable	Code
Largest length and width of the dorsal sepal	CSD[a], LSD[a]
Largest length and width of the lateral sepal	CSL[a], LSL[a]
Largest length and width of the petal	CPET[a], LEPT[a]
Peduncle length	CPED
Largest length and width of the lip	CLAB[a], LLAB[a]
Ovary length	COV
Length, width and thickness of the column	CCOL, LCOL, ECOL
Width of the lip taken at 20%, 40%, 60%, and 80% of its length	LAB20, LAB40, LAB60, LAB80
Width of the dorsal sepal taken at 20%, 40%, 60%, and 80% of its length	SD20, SD40, SD60, SD80
Width of the lateral sepal taken at 20%, 40%, 60%, and 80% of its length	SL20, SL40, SL60, SL80
Width of the petal taken at 20%, 40%, 60%, and 80% of its length	PET20, PET40, PET60, PET80
Length of the lip taken at 25%, 50%, 75% of its width	LAB25, LAB50, LAB75

[a] Also used by Martins (1967).

MSS2—Toque-Toque Pequeno, on the shore of São Paulo State; MSS3—Cascata, Rio de Janeiro State; MSS4—Muqui, Espírito Santo State; MSS5—Angra dos Reis, Rio de Janeiro State. *Miltonia spectabilis* var. *moreliana* was sampled in two localities: MSM1—Pedro Canário, Espírito Santo State, and MSM2—Jussari, Bahia State (Table 1; Fig. 1).

Initially, we performed univariate variance analyses and the *F*-test for each variable and calculated Pearson correlations for each pair of variables, considering the two taxa. Because the correlations were significant, we proceeded to multivariate analyses. Discriminant canonical analysis (DCA; Manly, 1994) was used as an exploratory analysis to verify the consistency of the two taxa as morphological groups and identify the main variables responsible for their distinction. These were similar to other studies in plant populations (Valero and Hossaert-McKey, 1991; Afzal-Rafii and Dodd, 1994) and orchids (Dufrêne, Gathoye, and Tyteca, 1991; van den Berg and Martins, 1998). Discriminant functions (Fisher, 1936; Manly, 1994) were obtained considering the two taxa as a way of testing whether the initial classification based on flower color was in agreement with morphological measurements.

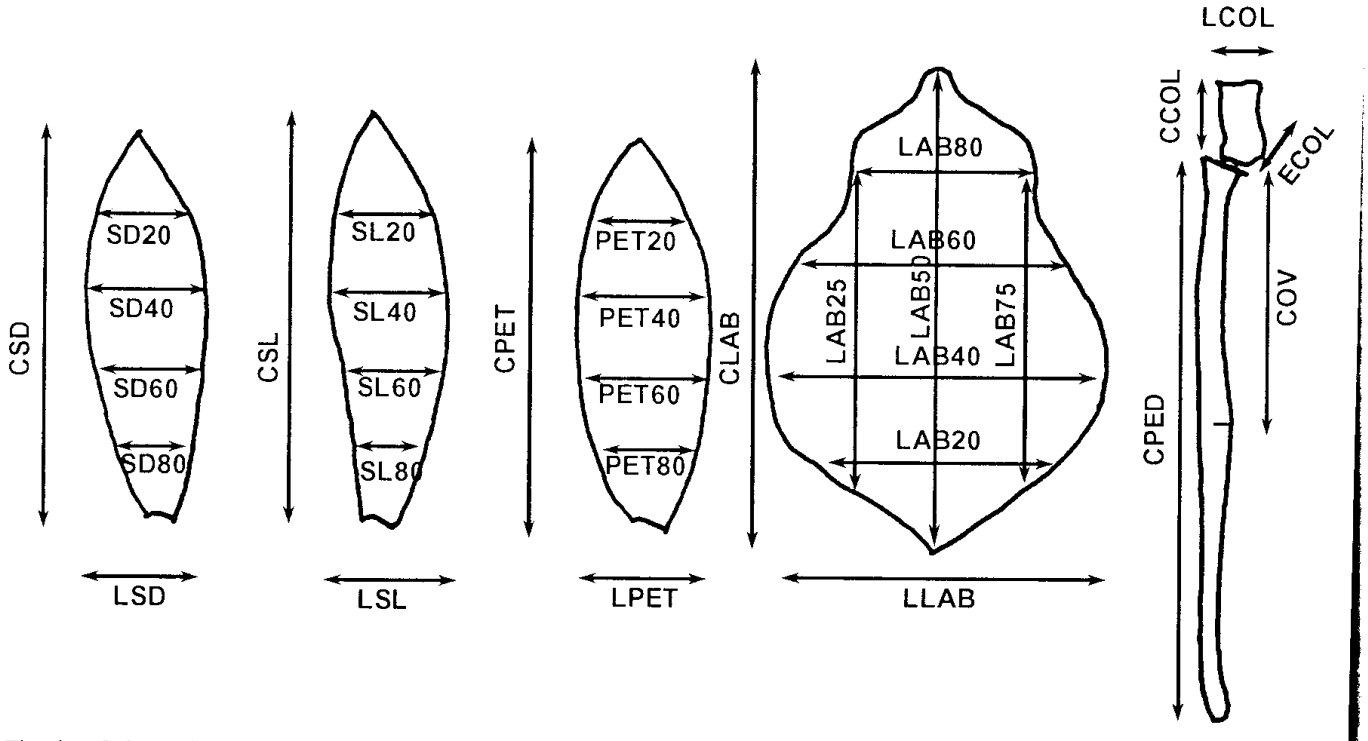

Fig. 2. Schematic representation of the 32 floral variables measured and analyzed in this study.

TABLE 3. A synopsis of analyses of variance (ANOVA), *F*-tests, coefficients of variation (CV%), and mean values for 32 variables in two groups: *M. spectabilis* var. *moreliana* (MSM), *M. spectabilis* var. *spectabilis* (MSS), and a general mean. SV = source of variation; DF = degrees of freedom; MS = mean square. Variable codes as in Table 2.

SV	DF	MS						
		CSC	LSD	CSL	LSL	CPET	LPET	CPED
Taxa	1	120.99[b]	50.09[c]	227.74[c]	88.45[c]	133.47[c]	121.87[c]	73.22[a]
Error	127	20.04	4.04	23.60	3.69	18.61	3.47	38.26
CV%		11.36	15.43	11.84	14.84	11.35	13.25	11.47
MSM mean		42.31	14.88	45.00	15.42	41.04	16.96	56.19
MSS mean		39.09	12.81	40.59	12.67	37.66	13.73	53.69
Gen. mean		39.41	13.02	41.03	12.95	38.00	14.06	53.94

SV	DF	MS						
		CLAB	LLAB	COV	CCOL	LCOL	ECOL	LAB20
Taxa	1	1263.62[c]	5556.06[c]	33.16[a]	0.10[a]	11.47[c]	30.26[c]	4655.55[c]
Error	127	27.22	26.70	21.92	1.19	1.07	1.59	15.77
CV%		11.32	14.57	15.66	11.54	14.22	16.86	13.76
MSM mean		55.46	55.08	28.39	9.50	6.38	6.04	46.81
MSS mean		45.07	33.28	30.07	9.47	7.38	7.65	26.85
Gen. mean		46.11	35.47	29.90	9.47	7.28	7.49	28.87

SV	DF	MS						
		LAB40	LAB60	LAB80	SD20	SD40	SD60	SD80
Taxa	1	5460.80[c]	5752.01[c]	74.48[c]	15.51[b]	3.86[a]	108.33[c]	48.96[c]
Error	127	28.23	29.38	9.45	3.23	3.74	2.58	1.53
CV%		15.20	19.14	16.15	19.33	15.66	14.34	14.60
MSM mean		54.39	48.27	21.30	8.26	12.88	13.93	10.31
MSS mean		32.78	26.09	18.77	9.41	12.30	10.89	8.27
Gen. mean		34.96	28.32	19.03	9.30	12.36	11.19	8.47

SV	DF	MS						
		SL20	SL40	SL60	SL80	PET20	PET40	PET60
Taxa	1	6.99[a]	25.18[c]	154.97[c]	25.70[c]	1.02[a]	98.76[c]	103.31[c]
Error	127	2.56	3.59	2.37	0.99	2.20	3.26	2.64
CV%		17.71	15.27	14.58	12.95	15.98	13.67	12.63
MSM mean		8.33	13.73	13.82	9.01	9.55	15.82	15.53
MSS mean		9.11	12.26	10.18	7.53	9.26	12.91	12.56
Gen. mean		9.03	12.41	10.55	7.67	9.29	13.20	12.86

SV	DF	MS			
		PET80	LAB25	LAB50	LAB75
Taxa	1	1.54[a]	255.97[c]	1144.22[c]	206.23[c]
Error	127	1.92	14.96	27.61	14.66
CV%		12.03	11.41	11.48	11.27
MSM mean		11.85	38.09	54.67	37.75
MSS mean		11.49	33.41	44.77	33.55
Gen. mean		11.53	33.88	45.77	33.98

[a] Non-significant in the *F*-test ($p > 0.05$).
[b] Significant in the *F*-test ($p \leq 0.05$).
[c] Significant in the *F*-test ($p \leq 0.01$).

Additionally, we performed DCA using as groups only the populations and not considering the taxa to which they belonged. This was important because we expected that if the taxa were really distinct the first pattern to appear should be that discriminating between them. In this analysis, we discarded populations MSS5 of *M. spectabilis* var. *spectabilis* and population MSM2 of

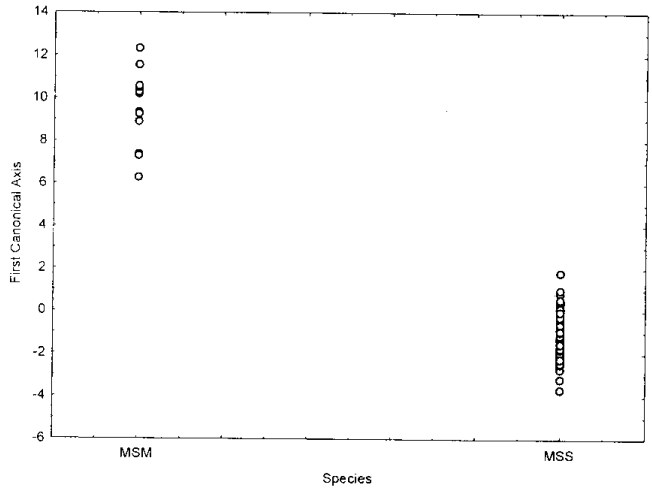

Fig. 3. Plot of the scores in the single canonical axis produced in the DCA using as groups only the two taxa. MSM = *M. spectabilis* var. moreliana, MSS = *M. spectabilis* var. *spectabilis*.

M. spectabilis var. *moreliana* because they were represented by only one individual, which would not allow the calculations for the canonical analysis. In this analysis, we extracted the quadratic Mahalanobis' distance to group the plants using UPGMA (Sokal and Michener, 1958; Manly, 1994).

We have also considered the distribution and flowering times (as a percentage of plants in flower per month) for each population. Martins (1967), comparing the plants and cultivation, field data, and reports in the literature, concluded that there was no difference between flowering times at Piracicaba and the natural habitats of the populations, and so we used the flowering times recorded on the cards, which therefore meant that our data were based on the plants under cultivation.

RESULTS

In the univariate analyses, we found significant differences between the two taxa for most of the variables (Table 3). If significant differences were found, the average values in *M. spectabilis* var. *moreliana* were higher, with exception of only LCOL, ECOL, and SD20 (Table 3). The overall correlation among pairs of variables was significant (not shown), and therefore we proceeded to multivariate analyses.

In the DCA considering the two taxa as groups, only one canonical axis is produced (the number of groups minus one), and this had an eigenvalue of 10.42. This axis completely separated one taxon from the other, showing the distinctness of the groups (Fig. 3). The main variables that contributed to this separation were the width of the floral organs, especially the lip, positively correlated to this axis (Table 4), and therefore with higher values in *M. spectabilis* var. *moreliana*. Width and thickness of the column (LCOL and CCOL) were negatively correlated to this axis and also contributed to the separation between the two taxa. The numerical classification of the individuals within these two taxa using the discriminant functions obtained from the data was 100% in accordance with the initial classification.

In the DCA among populations (Fig. 4), the first axis (responsible for 72.10% of the variation) completely separated the population of *M. spectabilis* var. *moreliana* from the other four belonging to the typical variety. The contribution of the original variables to this axis (Fig. 5) re-

TABLE 4. Canonical coefficients for 32 variables analyzed in this study, taking as groups *M. spectabilis* var. *spectabilis* and *M. spectabilis* var. *moreliana*. Variable codes as in Table 2.

Variable	Total canonical coefficient
CSD	0.22
LSD	0.31
CSL	0.28
LSL	0.42
CPET	0.24
LPET	0.49
CPED	0.13
CLAB	0.54
LLAB	0.83
COV	−0.11
CCOL	0.01
LCOL	−0.29
ECOL	−0.38
LAB20	0.88
LAB40	0.81
LAB60	0.82
LAB80	0.25
SD20	−0.20
SD40	0.09
SD60	0.52
SD80	0.47
SL20	−0.15
SL40	0.24
SL60	0.61
SL80	0.43
PET20	0.06
PET40	0.46
PET60	0.51
PET80	0.08
LAB25	0.36
LAB50	0.52
LAB75	0.33

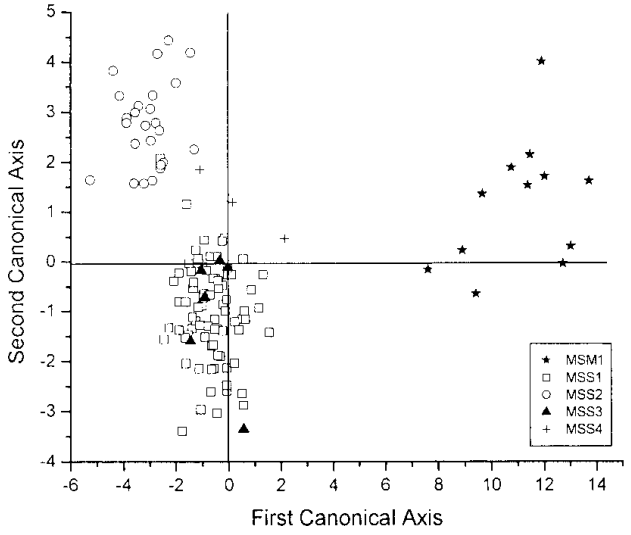

Fig. 4. Plot of the scores in the first two axes produced in the DCA using as groups the populations. *Miltonia spectabilis* var. *moreliana* (MSM1—Pedro Canário, ES), *M. spectabilis* var. *spectabilis* (MSS1—Petrópolis, RJ; MSS2—Toque-Toque Pequeno, SP; MSS3—Cascata, RJ; MSS4—Muqui, ES).

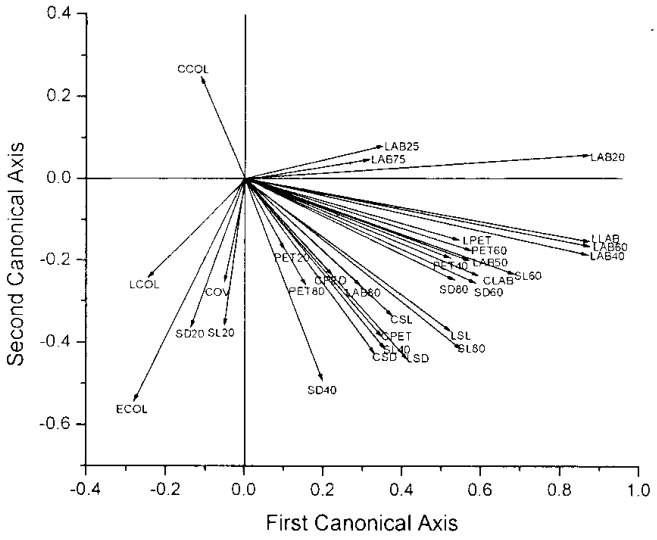

Fig. 5. Plot of the contribution of the original variables to the first two axes of the DCA using as groups the populations. Variable codes as in Table 2.

flected variation in the overall size of the flowers. They indicated that individuals belonging to the variety *moreliana* had larger lips and smaller columns. Additionally, they have the basally narrower sepals (as shown by SD20 and SL20) and shorter ovaries (COV). The second axis, explaining a much lower amount of variation (12.37%), showed intraspecific differentiation of the MSS2 population (Toque-Toque Pequeno) of *M. spectabilis* var. *spectabilis* in relation to the other three. Plants from this population were more similar to the variety *moreliana* in possessing longer, thinner columns as well as longer lips and narrower sepals.

The Mahalanobis' distances (Table 5) and the UPGMA tree (Fig. 6) also showed variety *moreliana* to be the most divergent from the typical populations of the species, similarly to previous univariate and multivariate analyses. Flowering time data (Fig. 7) showed a clear distinction between those of both varieties, with *M. spectabilis* var. *spectabilis* producing flowers mainly in October, whereas variety *moreliana* flowered mainly in June and July.

DISCUSSION

According to our morphological data of flower measurements, the two taxa studied here should be considered distinct based on the clearly distinct patterns observed in all analyses. This pattern of diversity was consistent with previous taxonomy based primarily on the color differences between *M. spectabilis* var. *spectabilis* and *M. spectabilis* var. *moreliana*. From a morphological point of view, the analyses showed that the flower measure means of variety *moreliana* do not overlap with the typical variety of the species (evident from the univariate analysis in which most means differed statistically between the two varieties), although single individuals may overlap.

Regarding the geographical distribution of these two taxa, Martins (1967) reported that the

TABLE 5. Mahalanobis' generalized distance (upper diagonal) between populations of *M. spectabilis* var. *moreliana* (MSM1—Pedro Canário, ES) and *M. spectabilis* var. *spectabilis* (MSS1—Petrópolis, RJ; MSS2—Toque-Toque Pequeno, SP; MSS3—Cascata, RJ; MSS4—Muqui, ES) and their *p*-values (lower diagonal).

	MSM1	MSS1	MSS2	MSS3	MSS4
MSM1	0	141.94	201.58	173.88	164.44
MSS1	0.0001	0	20.26	40.88	52.48
MSS2	0.0001	0.0001	0	55.20	66.63
MSS3	0.0001	0.0001	0.0001	0	103.71
MSS4	0.0001	0.0001	0.0001	0.0001	0

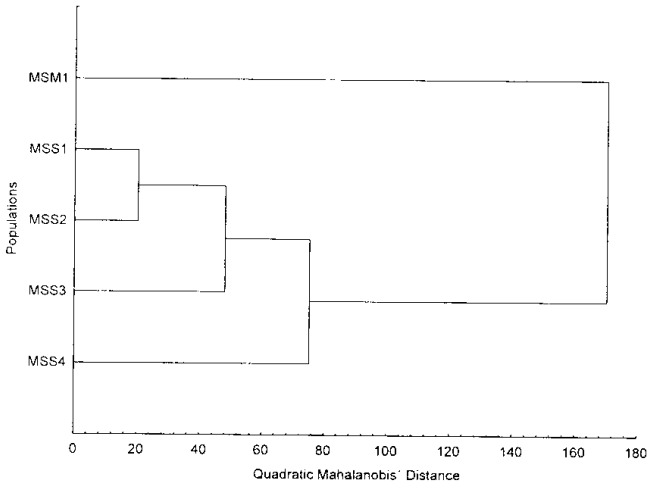

Fig. 6. Cluster analysis (UPGMA) of populations of *M. spectabilis* var. *moreliana* (MSM1—Pedro Canário, ES) and *M. spectabilis* var. *spectabilis* (MSS1—Petrópolis, RJ; MSS2—Toque-Toque Pequeno, SP; MSS3—Cascata, RJ; MSS4—Muqui, ES), based on the Mahalanobis' generalized distance calculated from the 32 variables included in this study.

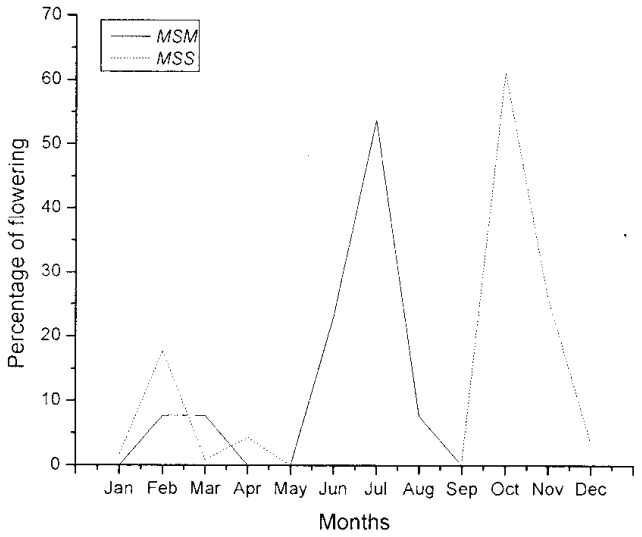

Fig. 7. Percentages of individuals in flower of *M. spectabilis* var. *spectabilis* (MSS) and *M. spectabilis* var. *moreliana* (MSM) in the collections at Piracicaba, São Paulo, Brazil.

variety *moreliana* occurs only in the northern part of Espírito Santo and the southern portion of Bahia, which are occupied by a rather distinct flora, called *formação perenifólia latifoliada higrófila Hileana* (Hilean latifoliate perennial-leafed hygrophylous forest; Lima, 1966). Additionally, this region corresponds to one of the proposed Pleistocene refugia of Haffer (1987). These would have been areas in which forest vegetation of the tropical lowlands remained during the last glaciation (Wisconsin-Würm) in the Quaternary. *Miltonia spectabilis* var. *moreliana* has been also reported as occuring the northern portion of the Orinoco Basin in Venezuelan State of Amazonas (Dunsterville, 1964; Dunsterville and Garay, 1965; Dunsterville and Garay, 1979). The typical variety of the species has a broader range in several localities in São Paulo, Rio de Janeiro, and Espírito Santo states, completely disjunct from the populations of the variety *moreliana*. This geographic isolation, which would drastically limit gene flow, contributes even more to morphological differentiation, as already stated by Martins (1967). Based on this evidence, it is clear that variety *moreliana* should be treated as a good species, as already suggested by Warner (1867) and emphasized by Martins (1967).

Key to the taxa

1. Flowers and lip smaller, petals 29–47 × 9–20 mm, lateral sepals 30.0–52.5 × 9.0–19.0 mm, dorsal sepal 30–50 × 9–19 mm, lip 34–61 × 21–45 mm, column 7.0–12.0 × 5.5–10.0 × 5.5–10.0 mm, peduncle 40–72 mm, ovary 20–44 mm, petals and sepals white or light pink . . . . . ***M. spectabilis***
2. Flowers and lip larger, petals 37–45 × 15–19 mm, lateral sepals 40–50 × 14–18 mm, dorsal sepal 38–49 × 13–18 mm, lip 46.0–60.0 × 42.0–61.5 mm, column 8.0–11.5 × 5–8.0 × 5–10.00 mm, peduncle 46–64 mm, ovary 17–34 mm, petals and sepals dark purple . . . . . ***M. moreliana***

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Miltonia spectabilis var. *aspersa* Rchb.f., *Gard. Chron.* n.s., 24: 70. 1885 ·

Miltonia spectabilis var. *bicolor* Nichols, *Dict. Gard.* 2: 369. 1886.

Miltonia spectabilis var. *lineata* Linden & Rodigas, *Lindenia* 2: 31 t. 62. 1886.

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Macrochilus fryanus Knowl. & Westc., *Flor. Cab.* 1: 93. T. 45. 1837.

Oncidium spectabile (Lindl.) Beer, *Prakt. Stud. Fam. Orch.* 293. 1863.

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Miltonia spectabilis var. *purpureo-violacea* Hook., *Bot. Mag.* 75 (ser. 3: vol. 5): t. 4425. 1849.

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