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# Relationships between floral characters, pollination mechanisms, life forms, and habitats in Araceae

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The floral traits of the inflorescences of angiosperms have coevolved to ensure and maximize pollination success. Other factors believed to influence floral architecture are external (for example, ecological) to the inflorescence. In order to understand the relationships between such factors and floral characters, 12 floral traits were measured in 54 species of Araceae. An analysis was performed to determine how these traits are linked to the following: (1) self-pollination capacity; (2) life form (evergreen versus seasonally dormant); (3) climatic conditions; and (4) type of pollinator (i.e. flies, bees, or beetles). A significant difference was found between the pollen to ovule ratio of the species able to self-pollinate and those unable to self-pollinate. Evergreen and tropical aroids produced a larger number of gametes than did seasonally dormant and temperate taxa. Finally, several floral traits, such as pollen volume and number, number of female flowers, and flower sexual type (unisexual or bisexual), showed clear differences between the three pollinator types. Variations in floral traits between the different life forms and climatic conditions are discussed with respect to pollination efficiency and properties of the growing season. The pollen to ovule ratio cannot be considered as an accurate indicator of breeding systems in aroids because of the particular pollination ecology of the family. © 2008 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2008, **156**, 29–42.

ADDITIONAL KEYWORDS: bee – beetle – climatic conditions – fly pollination – life cycle – pollen to ovule ratio – pollination syndrome.

## INTRODUCTION

Angiosperms have evolved a complex reproductive structure (i.e. the flower) which functionally ensures their reproduction. Floral architecture is directly linked to pollination, and therefore presents characters which have coevolved in order to ensure and maximize pollen transfer right up to the ovule (reviewed in Cruden, 2000) and, thus, the probability of reproduction (Cruden, 2000; Fenster *et al*., 2004). The relationship between floral characters and breeding system has been studied extensively (reviewed in Cruden, 2000), but other factors not physically linked to the inflorescence (i.e. external to the inflorescence) may also influence the floral architecture. Such external (for example, ecological) factors include, for example, pollinator types, life form, and habitats. However, contrary to the 'internal' relationships (i.e. within the inflorescence) between the floral characters, these external relationships have rarely been properly studied in angiosperms at the family level (Raven, 1979; Plitmann & Levin, 1990; Ramirez & Seres, 1994; Jürgens, Witt & Gottsberger, 2002; Chouteau, Barabé & Gibernau, 2006a).

After studying 80 different species, Cruden (1977) concluded that the pollen to ovule (P/O) ratio was related to the plant breeding system and pollination efficiency: 'The more efficient the transfer of pollen is, the lower the P/O should be' (Cruden, 1977). Some recent studies have more or less confirmed the

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*Corresponding author. E-mail: gibernau@cict.fr relationship between the P/O ratio, the breeding system, and pollination efficiency (Schoen, 1977; Lord, 1980; Wyatt, 1984; Campbell, Famous & Zuck, 1986; Philbrick & Anderson, 1987; Ritland & Ritland, 1989; Plitmann & Levin, 1990; Mione & Anderson, 1992; Lopez *et al*., 1999; Jürgens *et al*., 2002; Wang, Zhang & Chen, 2004; Wang *et al*., 2005), whereas others have not found any such relationship (Gallardo, Dominiguez & Munoz, 1994; Ramirez & Seres, 1994; Wyatt, Broyles & Lipow, 2000; Chouteau *et al*., 2006a; Chouteau, Barabé & Gibernau, 2006b). These studies also mentioned the existence of factors, such as habitat, pollen vectors, and pollination mechanisms, which could influence floral morphology and the P/O ratio, but such factors were never tested (Small, 1988; Cruden, 2000; Jürgens *et al*., 2002; Chouteau *et al*., 2006a). According to Cruden (2000), variations in floral traits reflect variations in pollinator efficiency in different habitats. Such variations in the P/O ratio and floral traits for a given pollinator have been documented (Plitmann & Levin, 1990; Ramirez & Seres, 1994). In addition, factors as diverse as arboreal or terrestrial habits and perennial or annual life cycles seem to be important for an understanding of the floral architecture and the ranges of the P/O ratio in relation to the breeding system (Raven, 1979; Plitmann & Levin, 1990; Ramirez & Seres, 1994; Jürgens *et al*., 2002; Chouteau *et al*., 2006a). In this study, such factors are investigated in the Araceae.

The Araceae comprises 107 genera and more than 3300 species (Mayo, Bogner & Boyce, 1997). Two main types of inflorescence can be found in this family: (1) those with only bisexual flowers, represented by the genus *Anthurium*; and (2) those with unisexual flowers, represented by the genus *Philodendron*.

For inflorescences of the *Anthurium* type, there is no spatial pattern as bisexual flowers are present all along the inflorescence. For inflorescences of the *Philodendron* type, the female flowers are located in the lower portion and the male flowers in the upper portion. An intermediate zone of sterile male flowers is present in certain genera (for example, *Caladium*, *Philodendron*), and, in others, a terminal appendix without flowers (for example, *Arum*) is present above the male flowers, which has diverse functions, such as odour and heat production (Vogel & Martens, 2000). Aroids are present on all continents between the latitudes 50°N and 35°S (Mayo *et al*., 1997). They can be epiphytic, hemi-epiphytic, terrestrial, geophytic, helophytic, or free-floating plants; they can be evergreen or seasonally dormant (Mayo *et al*., 1997). Pollination is mainly accomplished by insect vectors as diverse as beetles, bees, and flies (Gibernau, 2003).

To date, the relationships between breeding system and floral characters in aroids have been studied at the intragenus level only for *Anthurium* and *Philodendron* (Chouteau *et al*., 2006b). These studies did not show any relationship between the P/O ratio and breeding system, and it is believed that the P/O ratio is not an indicator of breeding system at this level for aroids (Chouteau *et al*., 2006b). The only study available at the family level (Chouteau *et al*., 2006a), conducted on a limited number of species (for example, nine French Guianese aroids), clearly showed a relationship between the P/O ratio and the breeding system opposite to the findings of Cruden (1977). In addition, in Araceae, it is thought that a link exists between the P/O ratio and the type of pollination mechanism, habitat, and growth mode. Terrestrial, helophytic, and geophytic species have higher P/O ratios than hemi-epiphytic species (Chouteau *et al*., 2006a).

In order to understand floral architecture in relation to certain ecological factors external to the inflorescence, the following questions were addressed: (1) are the P/O ratio and self-pollination linked in aroids at the family level?; (2) are floral traits influenced by life form?; (3) are floral traits influenced by climatic zone?; (4) do floral traits and the P/O ratio vary in relation to pollinator type (for example, pollination syndromes)?

## MATERIAL AND METHODS

This study was conducted on 54 species belonging to 32 genera of Araceae sampled from the living collections of the Montreal and Missouri Botanical Gardens and the Montreal Biodôme, as well as from the field in French Guiana (see Appendix). The species listed in Table 1 were sampled during their flowering period. Voucher specimens were deposited at the Marie-Victorin Herbarium (MT).

For species with unisexual flowers, inflorescences were collected during the first day of the flowering cycle, when the spathe is open but before the pollen is released. For each inflorescence, the total numbers of female, male, and bisexual flowers were counted; however, in some cases when the male flowers could not be isolated, the total number of male flowers was estimated. To estimate the number of male flowers, a 5 mm slice was cut in the middle of the male zone and the number of stamens over its entire surface was counted. The total number of stamens was obtained by multiplying the number of stamens on the slice by the total length of the male zone and dividing by five. The male zone was considered to be a cylinder and its height was measured with a digital calliper (±0.01 mm). The total number of male flowers was determined by dividing the total number of stamens on the inflorescence by the mean number of stamens per flower counted on 30 flowers from three separate

**Table 1.** Climatic region, life form, growth mode, pollinator, floral traits measured, and self-pollination capacity for 54 aroid species in 32 genera

|  | Climatic region | Life form | Growth mode | Pollinator | Stigma area per flower (mm$^2$) $N \geq 30$ | Pollen grain volume (ìm$^3$) $N \geq 30$ | Male flower number per inflorescence $N \geq 3$ | Female flower number per inflorescence $N \geq 3$ | Pollen grain number per male flower $N \geq 27$ | Pollen grain number per inflorescence $N \geq 3$ | Ovule number per flower $N \geq 30$ | Ovule number per inflorescence $N \geq 3$ | P/O ratio of inflorescence $N \geq 3$ | Self-pollination capacity |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Alocasia* sp. | Trop | E | T | Fly | 3.14 ± 0.43 | 22 449* | 153 ± 11 | 51 ± 2 | 11 399 ± 3482 | 1 739 446 ± 6 599 | 9.3 ± 0.9 | 459 ± 25 | 3 795 ± 196 |  |
| *Alocasia macrorhizos* (L.) G. Don | Trop | E | T | Fly | 1.68 ± 0.05 | 33 944 ± 1 973 | 162 ± 23 | 110 ± 15 | 47 310 ± 5591 | 7 679 920 ± 1 266 074 | 11.8 ± 0.7 | 1 303 ± 201 | 5 885 ± 98 | No |
| *Alocasia portei* Schott | Trop | E | T | Fly | 1.93 ± 0.49 | 45 293 ± 6 595 | 491 ± 33 | 111 ± 11 | 18 910 ± 4 240 | 9 257 149 ± 437 165 | 6.3 ± 0.6 | 707 ± 44 | 13 129 ± 1 129 | Yes |
| *Anaphyllopsis americana* (Engl.) A. Hay | Trop | S | H |  | 0.29 ± 0.01 | 14 847 ± 2 405 | 129 ± 30 | 129 ± 30 | 106 324 ± 34 724 | 17 074 965 ± 53 995 780 | 1.0 ± 0.0 | 129 ± 30 | 106 324 ± 34 724 | No |
| *Anchomanes difformis* (Blume) Engl. | Trop | S | G |  | 0.50 ± 0.11 | 26 521* |  | 141 ± 133 |  | 4 886 303 ± 5 494 704 | 1.0 ± 0.0 | 141 ± 133 | 29 232 ± 11 222 |  |
| *Anthurium harrisii* (Grah.) G. Don | Trop | E | E | Bee | 1.08 ± 0.17 | 3 172 ± 794 | 369 ± 55 | 369 ± 55 | 35 488 ± 6 683 | 13 106 904 ± 2 208 933 | 2.0 ± 0.0 | 738 ± 110 | 17 743 ± 2 284 | No |
| *Anthurium longistamineum* Engl. | Trop | E | E | Bee | 0.57 ± 0.07 | 2 579 ± 334 | 1742 ± 326 | 1742 ± 326 | 27 499 ± 10 143 | 47 904 129 ± 13 316 890 | 2.0 ± 0.0 | 3 484 ± 652 | 14 166 ± 5 279 | Yes |
| *Anthurium schlechtendalii* ssp. *schlechtendalii* Kunth | Trop | E | E | Bee | 0.33 ± 0.05 | 6 858 ± 1 233 | 2215 ± 54 | 2215 ± 54 | 36 882 ± 3269 | 81 725 717 ± 4 616 231 | 2.0 ± 0.0 | 4 430 ±E 108 | 18 441 ± 1 001 | Yes |
| *Anubias barteri* Schott | Trop | E | H | Beetle | 0.56 ± 0.02 | 7 238* | 105 ± 41 | 54 ± 9 | 55 782 ± 23 413 | 6 397 989 ± 5 057 274 | 37.8 ± 1.5 | 2 060 ± 347 | 3 360 ± 3 021 | No |
| *Anubias heterophylla* Engl. | Trop | E | H | Beetle | 0.07 ± 0.01 | 15 598* | 62 ± 36 | 54 ± 12 | 86 699 ± 23 685 | 5 725 785 ± 4 326 564 | 20.7 ± 0.8 | 1 129 ± 264 | 4 749 ± 2 718 | No |
| *Arisaema dracontium* (L.) Schott | Temp | S | G | Fly | 0.01 ± 0.01 | 5 575* | 27 ± 9 | 185 ± 37 | 47 832 ± 12 065 | 1 346 202 ± 674 186 | 3.5 ± 0.5 | 640 ± 126 | 2 172 ± 1 044 |  |
| *Arisaema triphyllum* (L.) Schott | Temp | S | G | Fly | 0.62 ± 0.01 | 8 768 ± 929 | 41 ± 7 | 68 ± 6 | 34 299 ± 6 207 | 1 385 094 ± 2 910 | 5.3 ± 0.4 | 365 ± 38 | 3793 | No |
| *Arum cylindraceum* Gasp. | Temp | S | G | Fly |  | 17 157* | 69 ± 15 | 51 ± 10 | 6 830 ± 1 161 | 510 620 ± 95 040 | 3.8 ± 0.4 | 199 ± 39 | 2512 ± 424 | No |
| *Arum italicum* Mill. | Temp | S | G | Fly |  | 17 157* | 144 ± 26 | 52 ± 12 | 7 496 ± 1 109 | 1 048 468 ± 260 598 | 5.8 ± 1.6 | 311 ± 138 | 4 221 ± 1 323 | No |
| *Arum maculatum* L. | Temp | S | G | Fly |  | 12 770* | 106 ± 31 | 31 ± 11 | 5 485 ± 1 198 | 550 345 ± 257 435 | 4.8 ± 1.4 | 161 ± 108 | 4 596 ± 1 910 | No |
| *Caladium bicolor* (Aiton) Vent. | Trop | S | G | Beetle | 0.83 ± 0.06 | 35 494 ± 7 882 | 152 ± 43 | 194 ± 16 | 7 649 ± 2 577 | 1 136 430 ± 118 013 | 8.0 ± 0.0 | 1 556 ± 130 | 729 ± 14 | No |
| *Cercestis stigmaticus* N.E. Br. | Trop | E | HE | Beetle | 1.85 ± 0.02 | 95 322 ± 3 824 | 221 ± 78 | 46 ± 10 | 11 087 ± 2 931 | 2 409 590 ± 632 299 | 1.0 ± 0.0 | 46 ± 10 | 51 610 ± 1 825 | No |
| *Colocasia esculenta* (L.) Schott | Trop | S | G | Fly | 0.76 ± 0.07 | 6 027 ± 799 | 490 ± 59 | 207 ± 51 | 18 199 ± 7 513 | 9 112 362 ± 4 291 846 | 41.6 ± 8.5 | 8 646 ± 2 264 | 1 023 ± 228 | No |
| *Colocasia fallax* Schott | Trop | S | G | Fly | 0.01 ± 0.01 | 27 198 ± 4 761 | 165 ± 7 | 123 ± 9 | 36 615 ± 3 974 | 6 067 225 ± 753 821 |  | 3 782 ± 441 | 1 626 ± 389 | No |
| *Culcasia saxatilis* A. Chev. | Trop | E | T | Beetle | 0.48 ± 0.04 | 17 157* | 114 ± 17 | 22 ± 4 | 13 932 ± 1 384 | 1 599 376 ± 300 207 | 1.0 ± 0.0 | 22 ± 4 | 72 735 ± 381 | No |
| *Dieffenbachia oerstedii* Schott | Trop | E | T | Beetle | 7.06 ± 0.67 | 508 047* | 210 ± 33 | 39 ± 6 | 8 421 ± 2 375 | 1 722 299 ± 357 475 | 1.0 ± 0.0 | 39 ± 6 | 45 577 ± 14 878 | Yes |
| *Dieffenbachia seguine* (Jacq.) Schott | Trop | E | T | Beetle |  | 258 154* | 286 ± 47 | 39 ± 6 | 9 788 ± 1 379 | 2 754 300 ± 205 628 | 2.2 ± 0.1 | 85 ± 18 | 33 276 ± 6 453 | Yes |
| *Dracontium polyphyllum* L. | Trop | S | G | Fly | 0.38 ± 0.03 | 11 312 ± 4 243 | 127 ± 8 | 127 ± 8 | 138 632 ± 60 282 | 21 111 163 ± 3 360 695 | 3.0 ± 0.0 | 381 ± 25 | 55 238 ± 5 130 | No |
| *Dracunculus vulgaris* Schott | Trop | S | G | Fly | 0.63 ± 0.12 | 47 712* |  | 211 ± 110 |  | 3 546 327 ± 2 092 984 | 3.9 ± 0.3 | 844 ± 441 | 4 116 ± 327 |  |
| *Gonatopus angustus* N.E. Br.† | Trop | S | G |  | 2.26 ± 0.09 | 229 847* | 49 | 40 | 4 499 ± 436 | 220 451 | 2.0 ± 0.0 | 80 | 2 756 | No |
| *Gonatopus boivinii* (Decne.) Engl. | Trop | S | G |  | 1.76 ± 0.13 | 229 847* | 195 ± 19 | 101 ± 2 | 3 192 ± 1 282 | 677 820 ± 20 858 | 2.0 ± 0.0 | 202 ± 5 | 3 345 ± 96 |  |
| *Homalomena rubescens* Kunth | Trop | E | T |  | 1.34 ± 0.06 | 3 156 ± 1 469 | 563 ± 5 | 135 ± 20 | 40 565 ± 9 410 | 22 855 411 ± 3 732 359 | 39.7 ± 3.2 | 10 907 ± 836 | 2 114 ± 504 | No |
| *Homalomena philippinensis* Engl.† | Trop | E | T |  | 0.12 ± 0.01 | 3 053* | 125 | 66 | 1 300 ± 225 | 162 557 | 55.0 ± 1.0 | 3630 | 44 |  |

**Table 1.** *Continued*

| | Climatic region | Life form | Growth mode | Pollinator | Stigma area per flower (mm$^2$) $N \geq 30$ | Pollen grain volume (ìm$^3$) $N \geq 30$ | Male flower number per inflorescence $N \geq 3$ | Female flower number per inflorescence $N \geq 3$ | Pollen grain number per male flower $N \geq 27$ | Pollen grain number per inflorescence $N \geq 3$ | Ovule number per flower $N \geq 30$ | Ovule number per inflorescence $N \geq 3$ | P/O ratio of inflorescence $N \geq 3$ | Self-pollination capacity |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Monstera adansonii* Schott | Trop | E | HE | Bee | 0.57 ± 0.05 | 51 870 ± 10 621 | 230 ± 44 | 230 ± 44 | 57 203 ± 8 289 | 12 985 938 ± 219 9319 | 4.0 ± 0.0 | 922 ± 179 | 14 300 ± 2072 | No |
| *Montrichardia arborescens* (L.) Schott | Trop | E | H | Beetle | 11.16 ± 0.22 | 720 667 ± 129 288 | 448 ± 118 | 73 ± 12 | 19 445 ± 5 316 | 8 727 761 ± 3 394 104 | 1.0 ± 0.0 | 73 ± 12 | 119 020 ± 42 929 | Yes |
| *Montrichardia linifera* (Arruda) Schott | Trop | E | H | Beetle | | 434 892* | 649 ± 36 | 122 ± 22 | 17 251 ± 8 292 | 11 397 606 ± 5 920 738 | 1.0 ± 0.0 | 122 ± 22 | 92 355 ± 45 682 | |
| *Peltandra virginica* (L.) Schott | Temp | S | H | Fly | 0.57 ± 0.02 | 11 494* | 185 ± 13 | 43 ± 21 | 19 666 ± 5 630 | 3 656 094 ± 491 645 | 3.2 ± 0.4 | 142 ± 74 | 28 744 ± 11 568 | No |
| *Philodendron erubescens* C. Koch & Augustin | Trop | E | HE | Beetle | 1.04 ± 0.12 | 63 218 ± 11 383 | 765 ± 40 | 775 ± 129 | 7 054 ± 3 471 | 5 331 093 ± 2 265 953 | 15.7 ± 0.9 | 12 234 ± 2806 | 469 ± 292 | No |
| *Philodendron pedatum* Kunth | Trop | E | HE | Beetle | 1.28 ± 0.09 | 83 061 ± 39 695 | 964 ± 356 | 1060 ± 76 | 17 359 ± 7 656 | 17 840 873 ± 1 162 0431 | 34.1 ± 2.0 | 36 148 ± 3163 | 484 ± 297 | No |
| *Philodendron squamiferum* Poepp. & Endl. | Trop | E | HE | Beetle | 1.06 ± 0.54 | 47 680 ± 26 117 | 1258 ± 345 | 641 ± 36 | 14 679 ± 4 450 | 17 768 841 ± 90 404 | 25.8 ± 3.4 | 16 478 ± 1231 | 1 081 ± 86 | No |
| *Pinellia tripartita* (Blume) Schott | Temp | S | G | Fly | 0.017 ± 0.01 | 12 770* | | 67 ± 8 | | 856 848 ± 5 159 | 1.0 ± 0.0 | 67 ± 8 | 6 443 ± 777 | . |
| *Pistia stratiotes* L. | Trop | E | FF | | 1.61 ± 0.17 | 10 305* | 1 ± 0 | 1 ± 0 | 2 033 ± 1 464 | 2 033 ± 1464 | 22.3 ± 1.5 | 22 ± 1 | 90 ± 66 | No |
| *Pseudodracontium fallax* Serebr. | Trop | S | G | | 0.50 ± 0.05 | 57 905* | 94 ± 5 | 95 ± 33 | 17 582 ± 3 049 | 1 671 158 ± 251 408 | 1.0 ± 0.0 | 94 ± 33 | 18 642 ± 3942 | |
| *Rhaphidophora schottii* Hook† | Trop | E | HE | Beetle | 0.19 ± 0.02 | 18 816* | 991 | 991 | 98 766 ± 7 750 | 97 877 106 | 1.0 ± 0.0 | 991 | 98 766 | |
| *Spathiphyllum friedrichsthalii* Schott | Trop | E | T | Bee | 0.77 ± 0.07 | 10 865 ± 929 | 171 ± 32 | 171 ± 32 | 25 932 ± 9 602 | 4 545 879 ± 1 851 630 | 9.0 ± 0.0 | 1539 ± 296 | 2 881 ± 833 | No |
| *Spathiphyllum patinii* (Mast.) N.E. Br. | Trop | E | T | Bee | 0.64 ± 0.06 | 18 470 ± 1 266 | 118 ± 12 | 118 ± 12 | 21 987 ± 10 934 | 2 598 082 ± 1 292 262 | 9.0 ± 0.0 | 1065 ± 109 | 2 467 ± 1 211 | No |
| *Spathiphyllum wallisii* Regel | Trop | E | T | Bee | 0.56 ± 0.11 | 12 198 ± 865 | 126 ± 31 | 126 ± 31 | 38 455 ± 7 213 | 4 917 462 ± 1 774 087 | 9.0 ± 0.0 | 1141 ± 279 | 4 235 ± 892 | No |
| *Stenospermation longipetiolatum* Engl. | Trop | E | E | | 0.77 ± 0.05 | 75 123 ± 11 638 | 179 ± 5 | 179 ± 4 | 2 599 ± 433 | 465 291 ± 63 295 | 5.4 ± 0.5 | 969 ± 26 | 481 ± 78 | No |
| *Stenospermation sessile* Engl.† | Trop | E | E | | 0.50 ± 0.03 | 38 792* | 206 | 206 | 9 399 ± 721 | 2 609 196 | 4.0 ± 0.0 | 824 | 3166 | No |
| *Synandrospadix vermitoxicus* (Griseb.) Engl.† | Trop | S | G | | 0.19 ± 0.04 | 61 600* | 275 | 28 | 16 466 ± 2 106 | 4 528 150 | 4.0 ± 0.0 | 112 | 40 429 | |
| *Syngonium angustatum* Schott | Trop | E | HE | Beetle | 0.53 ± 0.01 | 76 335 ± 5 819 | 158 ± 32 | 52 ± 4 | 12 799 ± 4 823 | 2 111 784 ± 1 287 717 | 2.0 ± 0.0 | 104 ± 8 | 19 866 ± 10 760 | No |
| *Syngonium auritum* (L.) Schott | Trop | E | HE | Beetle | 6.22 ± 0.77 | 27 012 ± 4 052 | 554 ± 222 | 91 ± 26 | 70 541 ± 14 704 | 39 737 310 ± 18 838 639 | 1.0 ± 0.0 | 91 ± 26 | 42 2107 ± 85 191 | No |
| *Syngonium ruizii* Schott | Trop | E | HE | Beetle | 0.78 ± 0.11 | 47 712* | 75 ± 19 | 353 ± 49 | 8 090 ± 3 175 | 594 886 ± 4729 | 4.0 ± 0.0 | 1413 ± 197 | 428 ± 70 | |
| *Syngonium schottianum* H. Wendl. ex Schott† | Trop | E | HE | Beetle | 10.06 ± 1.32 | 220 893* | 868 | 173 | 17 933 ± 3 564 | 15 853 152 | 2.0 ± 0.0 | 346 | 45 818 | No |
| *Typhonium trilobatum* (L.) Schott | Trop | S | G | Beetle | 0.12 ± 0.01 | 24 429* | | 174 ± 16 | | 837 676 ± 189 880 | 1.0 ± 0.0 | 174 ± 16 | 4 783 ± 624 | |
| *Typhonium violifolium* Gagnep. | Trop | S | G | Beetle | 0.19 ± 0.03 | 17 157* | | 16 ± 2 | | 234 064 ± 50 668 | 1.0 ± 0.0 | 16 ± 2 | 15 210 ± 5 293 | |
| *Xanthosoma conspurcatum* Schott† | Trop | S | G | Beetle | 0.78 ± 0.08 | 38 792* | 103 | 76 | 8 865 ± 737 | 913 095 | 16.6 ± 0.9 | 1261 | 723 | No |
| *Zamioculcas zamiifolia* (Lodd.) Engl. | Trop | S | G | | 2.59 ± 0.24 | 145 683 ± 43 782 | 94 ± 14 | 50 ± 6 | 5 415 ± 376 | 513 985 ± 109 275 | 2.0 ± 0.0 | 101 ± 12 | 5 060 ± 444 | No |
| *Zomicarpella amazonica* Bogner | Trop | E | G | | 0.07 ± 0.01 | 3 591* | | 8 ± 1 | | 273 891 ± 19 952 | 3.5 ± 0.5 | 28 ± 1 | 9 607 ± 466 | |

Climatic region: Temp, temperate; Trop, tropical. Life form: E, evergreen; S, seasonally dormant. Growth mode: E, epiphyte; FF, free-floating; G, geophyte; H, helophyte; HE, hemi-epiphyte; T, terrestrial.

*Obtained from Grayum's (1992) data on pollen diameter (see 'Material and methods').

†Smaller sampling: $N \leq 2$ inflorescences.

inflorescences. As merosity in unisexual flowers usually varies, the number of stamens per flower can also vary.

For species with bisexual flowers, inflorescences were collected on the first day of pollen release. In the case of *Monstera* and *Stenospermation*, which have a short flowering cycle of approximately 7 days (Chouteau *et al*., 2006a), the inflorescences were collected just after the spathe had opened. For all these species, the total number of flowers was determined by counting all the flowers individually.

For both types of inflorescence, the number of ovules per flower was estimated by counting the number of locules on ten flowers and the number of ovules per locule for ten locules for each inflorescence collected. The ovule number per inflorescence was obtained by multiplying the mean number of ovules per flower by the mean number of flowers per inflorescence bearing ovules.

To estimate the number of pollen grains per inflorescence, three groups of five stamens were collected on inflorescences with flowers that could not be isolated and three groups of one flower on inflorescences with flowers that could be isolated. Each group of stamens or each flower was dissolved in 300 μL of 95% sulphuric acid for 5 days at 24 °C. The solution was then homogenized, and 1 μL was collected and carefully placed on a microscope slide. The number of pollen grains was counted for three independent replicates of 1 μL.

When three groups of five stamens were used, the total number of pollen grains per flower was obtained by multiplying the mean of the triplicate count by 300, dividing the result by five, and multiplying that by the number of stamens per flower. When three groups of one flower were used, the number of pollen grains per flower was obtained by multiplying the mean of the triplicate by 300. A complete pollen count was performed in triplicate for each inflorescence ($3 \times 5$ stamens or $3 \times 1$ flower per inflorescence). Standard deviations were calculated using the total number of pollen counts (generally $N = 9$) of the same species. The number of pollen grains per inflorescence was obtained by multiplying the mean number of pollen grains per flower by the mean number of flowers bearing pollen. In the same way, the pollen grain volume per inflorescence was obtained by multiplying the mean number of pollen grains per inflorescence by the mean pollen volume of the species concerned (see below). The size of the pollen grains was estimated by measuring the diameter of the polar and equatorial axes of the grains from dehisced anthers. Measurements were made with an ocular micrometer at ×630. The volume of a single pollen grain was estimated using the formula $\pi PE^2/6$ (Harder, 1998), where $P$ is the polar axis diameter and $E$ is the equatorial axis diameter. Generally, ten pollen grains per inflorescence were measured from three independent inflorescences (generally $N = 30$). In addition, for a few species listed in Table 1, the pollen grain volume was estimated using Grayum's (1992) data on pollen diameter and applying the formula $(4/3)\pi(D/2)^3$, where $D$ is the diameter.

The P/O ratio was calculated for the inflorescence by dividing the mean number of pollen grains per inflorescence by the mean number of ovules per inflorescence. For the dioecious *Arisaema triphyllum*, the P/O ratio was calculated by dividing the mean number of pollen grains per inflorescence of plants with male flowers by the mean ovule number per inflorescence of plants with female flowers. For all species, standard deviations were calculated using all the inflorescences from the same species (generally $N = 3$).

For each inflorescence studied, the stigma area (estimated as a circle) of ten flowers was calculated using the diameter (0.01 mm resolution) of the stigmas measured at ×20 magnification under a dissecting microscope equipped with an ocular micrometer and the formula $\pi D^2/4$, where $D$ is the measured diameter. To obtain the total stigmatic area of the inflorescences, the mean stigma area was multiplied by the mean number of flowers bearing stigmas for each species. When inflorescences bore fewer than ten female flowers, all the stigmas were measured.

A minimum of three inflorescences per species (Table 1) were bagged at the bud stage. After anthesis, if at least one inflorescence had set fruit, the species was considered to be potentially self-pollinating; if all the inflorescences withered without producing seeds, the species was considered to be unable to self-pollinate. These qualitative observations indicate only the potential for self-pollination rather than quantitative measurement.

The life form, growth mode, and climatic region were obtained using Mayo *et al*. (1997) and from personal observations. Species are considered to be seasonally dormant (seasonal) when they have a dormant stage each year associated with the loss of the aerial vegetative system, whereas evergreen species lose dormancy and the aerial vegetative system is present all year around. For the growth mode, species were categorized as epiphytic (non-parasitic plants growing on another plant and without having roots in contact with the ground at any moment during their life), hemi-epiphytic (plants growing on a host plant and having feeder roots in contact with the ground), terrestrial (plants which grow on the ground and lack subterranean stems), geophytic (plants having subterranean stems, implying a tuber or rhizome), helophytic (marsh or swamp plants growing in flooded ground with the foliage above the water), or free-floating (aquatic plants floating above the water without any anchor roots). Finally, the species were divided into two climatic regions: temperate and tropical (including subtropical, tropical, and equatorial regions).

*t*-test analyses were used to determine differences between groups for the variable measured (self-pollination capacity, life form, climatic zone, and growth mode) for all the species studied (SPSS 11.0.0, 2001). Differences in floral traits between the different types of pollinator were tested using analysis of variance (ANOVA) (Systat 8.0, 1998). Prior to the analysis, the P/O ratios were logarithmically transformed and the numbers of ovules were square-root transformed. In order to study the relationships between certain measured floral traits and the type of pollinating insect, a stepwise backward discriminant analysis was performed (Systat 8.0, 1998). The analysis was conducted for three types of pollinating insect (grouping variable) – bee, beetle, and fly – according to the data available in the literature (for a review, see Gibernau, 2003). Twenty species were coded as beetle-pollinated, 13 as fly-pollinated, seven as bee-pollinated, and 14 as unknown (see Table 1). Species with unknown pollinator types were used as complementary data and, after analysis, were classified into one of the three defined groups. The 12 floral traits (variables) available for all species were selected in order to test any discrimination between the three pollinator groups: flower stigma area, stigma per inflorescence, mean volume of a pollen grain, pollen volume per inflorescence, pollen number per inflorescence, number of ovules per flower and per inflorescence, P/O ratio, number of female flowers, sexual type of the flower, growth mode, and life form.

## RESULTS

Table 1 summarizes the floral traits, climatic region, life form, growth mode, pollinator type, and capacity for self-pollination for 54 species of aroids. Of the species studied, 41 had unisexually flowered inflorescences and 13 had bisexually flowered inflorescences. Thirty-two species were evergreen and all these were tropical or subtropical taxa with different growth modes (eight terrestrial, four helophytic, 13 hemi-epiphytic, five epiphytic, one free-floating, and one geophytic). Of the 22 seasonally dormant species, all were geophytes; seven were from temperate regions with a wide range of temperature variation between summer and winter, and 15 were tropical.

### P/O RATIO AND SELF-POLLINATION CAPACITY

Of the 39 species bagged for the self-pollination test, only six species set fruit and were therefore considered to be able to self-pollinate (Table 1). A significant difference (*t*-test: $t_{37} = 2.182$, $P = 0.036$) was found between the P/O ratio of the group potentially able to self-pollinate (mean log ± SD, 9.89 ± 0.55) and that unable to do so (mean log ± SD, 8.12 ± 0.34), with the latter group having a lower P/O ratio.

### FLORAL TRAITS WITH RESPECT TO LIFE FORM

Evergreen taxa had a significantly higher volume of pollen grains per inflorescence (*t*-test: $t_{31.49} = 2.872$, $P = 0.007$) and ovule number per inflorescence ($t_{46.37} = 2.183$, $P = 0.034$) than seasonally dormant taxa (Fig. 1A, B). This was mainly a result of the higher male ($t_{34.60} = 3.381$, $P = 0.002$) and female ($t_{32.25} = 2.699$, $P = 0.011$) flower numbers per inflorescence in evergreen taxa. In addition, the stigmatic area of a single flower ($t_{33.67} = 2.266$, $P = 0.030$) and of the inflorescence ($t_{29.68} = 3.792$, $P = 0.001$) was larger in evergreen taxa compared with seasonally dormant ones (Fig. 1C). Finally, the P/O ratio was not significantly different between evergreen and seasonal taxa ($t_{51.89} = 0.243$, $P = 0.809$; Fig. 1D).

### FLORAL TRAITS WITH RESPECT TO CLIMATIC ZONE

Because the evergreen taxa all came from tropical regions, no analysis was performed on this group. Floral trait comparisons were only performed between temperate and tropical seasonally dormant geophytic taxa (Fig. 2). Tropical geophytes (15 species) produced higher pollen volumes per grain (*t*-test: $t_{14.19} = 2.721$, $P = 0.016$) and per inflorescence ($t_{15.09} = 4.338$, $P = 0.001$; Fig. 2A), whereas the number of ovules per inflorescence was no different ($t_{16.87} = 1.392$, $P = 0.182$; Fig. 2B). They also showed a larger stigmatic area per inflorescence ($t_{15.22} = -3.418$, $P = 0.004$; Fig. 2C) than their related temperate geophytic taxa (seven species). No significant difference was found for the numbers of male ($t_{15} = 1.396$, $P = 0.183$) or female ($t_{20} = 1.543$, $P = 0.138$) flowers between tropical and temperate geophytes. Finally, the P/O ratio was not significantly different between tropical and temperate geophytes ($t_{19.44} = -0.513$, $P = 0.614$; Fig. 2D).

No significant differences in any of the considered floral traits were found between the different growth modes in the aroid species studied, suggesting that there are no clear relationships between the measured floral traits and the different growth modes. It is noteworthy that the growth modes were not independent of climatic zones and life forms, as, in our sampling, epiphytes and hemi-epiphytes are evergreen and tropical taxa, and terrestrials and geophytes are mainly seasonally dormant and temperate

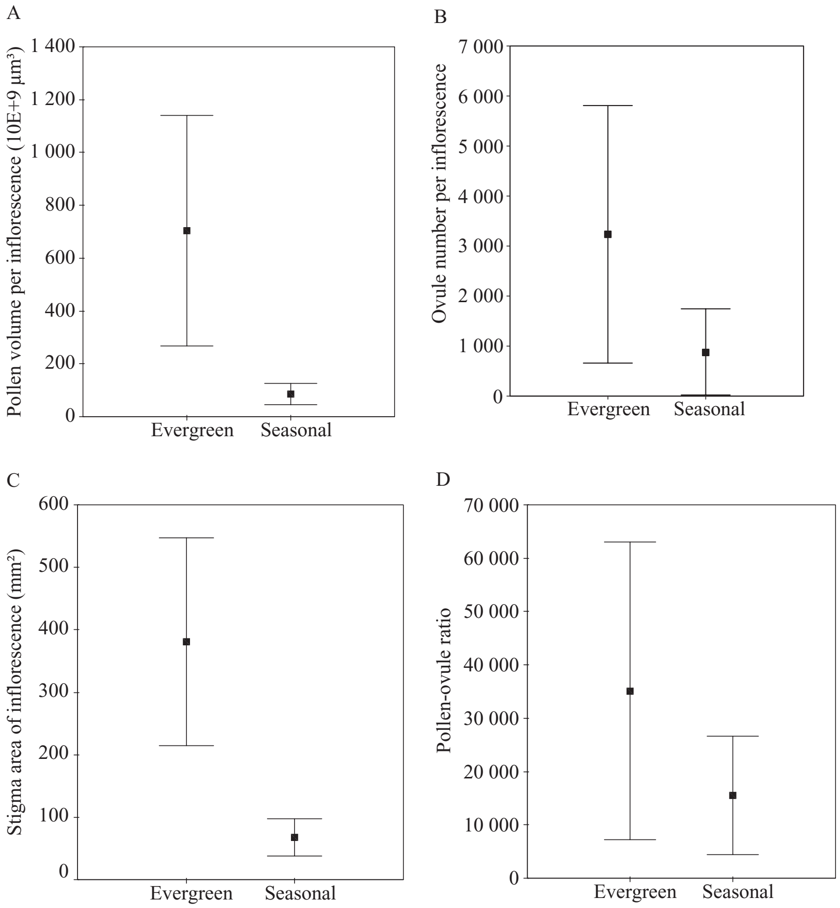

**Figure 1.** Differences in floral traits between evergreen and seasonally dormant taxa in the aroids studied. Means and 95% confidence intervals: A, pollen volume per inflorescence; B, ovule number per inflorescence; C, stigmatic area of inflorescence; D, pollen to ovule ratio.

taxa. More data are needed to study further the influence of this character on floral traits.

### Floral traits with respect to pollinator type

The stepwise backward discriminant analysis held back five variables, although certain other variables showed significant differences between pollinator types (Table 2): pollen volume per inflorescence, pollen number per inflorescence, number of female flowers, sexual type of the flower, and life form. The jackknifed classification matrix resulted in a total of 80% of the data being correctly classified (75% for beetle pollination, 77% for fly pollination, and 100% for bee pollination). The eigenvalues for the two axes were 14.60 and 0.52, respectively, with the corresponding canonical correlations of 0.97 and 0.59. Wilks' lambda test was significant (Wilks' lambda = 0.042, $P < 10^{-4}$). The standardized canonical discriminant functions for each variable are presented in Table 3. The three pollinator groups are very distinct with no overlap (see Fig. 3), but some species were misclassified (see below). The bee-pollinated group is characterized by species with bisexual flowers, an evergreen life form, and a large number of gynoecia (see Table 2). Beetle-pollinated species are characterized by a high pollen volume per inflorescence, a medium number of female flowers, and almost always bear unisexual flowers (see Table 2). Fly pollination is associated with species with low female flower numbers and a relatively small number of pollen grains per inflorescence (see Table 2).

Species classification is now considered according to pollinator type. Some species were misclassified: eight of 40. Four beetle-pollinated species were classified amongst fly-pollinated species, namely *Typhonium trilobatum*, *Typhonium violifolium*, *Caladium bicolor*, and *Xanthosoma conspurcatum* (see Fig. 3). Conversely, the three *Alocasia* fly-pollinated species were classified amongst beetle-pollinated species (see Fig. 3). The fly-pollinated *Dracontium polyphyllum*

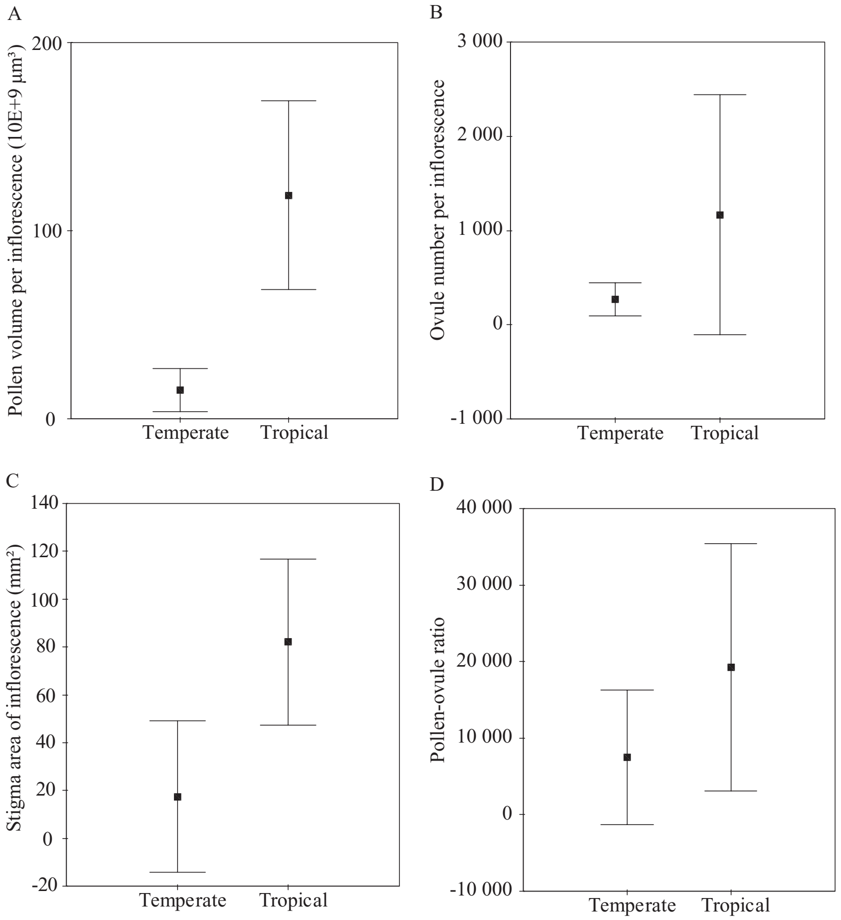

**Figure 2.** Differences in floral traits between the temperate and tropical seasonally dormant aroids studied. Means and 95% confidence intervals: A, pollen volume per inflorescence; B, ovule number per inflorescence; C, stigmatic area of inflorescence; D, pollen to ovule ratio.

was classified as bee-pollinated, close to *Anaphyllopsis americana*, an ‘unknown taxon’, but clearly stands in an intermediate position between fly- and bee-pollinated groups (see Fig. 3). The other species with unknown pollinators were tentatively classified as follows: the two *Stenospermation* species were considered to be bee-pollinated; the two *Homalomena* species, *Pistia stratiotes* and *Zomicarpella amazonica*, were classified as beetle-pollinated; and *Synandrospadix vermitoxicus*, *Pseudodracontium fallax*, the two *Gonatopus* species, and *Zamioculcas zamiifolia* were considered to be fly-pollinated (Fig. 3). The two *Gonatopus* species appear to be marginally separate (like *Zamioculcas zamiifolia*) from the other fly-pollinated species (Fig. 3). It should be noted that the classifications of the unknown species were not tested during the discriminant analysis, and thus must be considered as hypotheses to be validated in the field.

The P/O ratio was much higher in beetle-pollinated species (mean: 51 657) than in fly- (mean: 9807) and bee-pollinated (mean: 10 605) species, but these differences were not significant (Table 2). Pollen grain volume in relation to pollinator class displayed the same type of difference, with the pollen volume of beetle-pollinated species being significantly larger (mean: 123 595 $\mu m^3$) than that of related fly- (mean: 19 973 $\mu m^3$) and bee-pollinated (mean: 15 145 $\mu m^3$) species (Table 2). In the same way, the flower stigma surface was significantly larger in beetle-pollinated species (mean: 3.06 $mm^2$) than in fly- (mean: 0.85 $mm^2$) or bee-pollinated (mean: 0.65 $mm^2$) taxa (Table 2).

## DISCUSSION

### P/O RATIO AND BREEDING SYSTEM

Aroids seem to be a family whose inflorescences are adapted for out-breeding. Of all the species studied, only six showed an ability to self-pollinate. This result

**Table 2.** Group means (±standard error) used in the discriminant analysis for the different floral characters according to type of pollinator

| Floral character | Beetle pollination ($N = 20$) | Fly pollination ($N = 14$) | Bee pollination ($N = 7$) | Statistic values $F_{2,38}$ |
|---|---|---|---|---|
| Flower stigma area | 3.06 ± 0.87a | 0.85 ± 0.23b | 0.65 ± 0.09b | 3.44* |
| Stigma area per inflorescence | 431 ± 115a | 76.4 ± 20.3b | 453 ± 137a | 3.84* |
| Mean pollen grain volume | 123 595 ± 35 614a | 19 973 ± 3674b | 15 144 ± 6467b | 4.43* |
| Pollen volume per inflorescence | 10 ± 3.24 × $10^{11}$a | 1.04 ± 0.34 × $10^{11}$b | 2.22 ± 1.03 × $10^{11}$b | 3.59* |
| Pollen number per inflorescence | 1.2 ± 0.5 × $10^{7}$ | 0.48 ± 0.15 × $10^{7}$ | 2.39 ± 1.12 × $10^{7}$ | 2.13 |
| Ovule number per flower | 8.89 ± 2.67 | 9.59 ± 3.14 | 5.28 ± 1.34 | 0.38 |
| Ovule number per inflorescence | 3719 ± 1962 | 1286 ± 620 | 1903 ± 548 | 0.64 |
| Pollen to ovule ratio | 51 657 ± 21 224 | 9807 ± 3977 | 10 605 ± 2695 | 1.93 |
| Female flower number | 252 ± 74a | 103 ± 16a | 853 ± 321b | 7.99** |
| Flower sexual type† | 1.95 ± 0.05a | 1.93 ± 0.07a | 1 ± 0b | 52.1*** |
| Growth mode‡ | 2.8 ± 0.28a | 1.5 ± 0.23b | 4 ± 0.38c | 13.3*** |
| Life form§ | 1.2 ± 0.09a | 1.79 ± 0.11b | 1 ± 0a | 13.5*** |

The level of significance of the analysis of variance (ANOVA) results is coded as follows: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. Group means with different letters are significantly different (*post hoc* test $P < 0.05$).

†The flower sexual type was coded: 1, bisexual; 2, unisexual.

‡The growth mode was coded: 1, geophyte; 2, helophyte; 3, ground; 4, hemi-epiphyte; 5, epiphyte.

§The life form was coded: 1, evergreen; 2, seasonally dormant.

**Table 3.** Standardized canonical discriminant functions for each variable

| | Axis 1 | Axis 2 |
|---|---|---|
| Pollen volume per inflorescence | 0.059 | 0.405 |
| Pollen number per inflorescence | −1.643 | 0.217 |
| Number of female flowers | 0.831 | 0.077 |
| Sexual type of flower | −1.555 | 0.164 |
| Life form | −0.203 | −0.770 |

is confirmed by the fact that aroid inflorescences are dichogamous, with stigmas receptive before pollen release (Mayo *et al*., 1997). Self-pollination in some aroids could be a mechanism for eventually ensuring fertilization when pollinator frequencies are limited. In addition, genera, such as *Alocasia* (Yafuso, 1993; Miyake & Yafuso, 2003; M. Chouteau, pers. observ.), *Dieffenbachia* (Young, 1986; Beath, 1999), and *Montrichardia* (Gibernau *et al*., 2003), which are able to self-pollinate to some degree, present distinctive traits, such as thermogenesis, odour production, nectar production, and even movements of the spathe during the flowering cycle to attract entomophilous pollinators and ensure pollination. Because self-pollination is most probably a secondary mechanism in the aroid family, the assumption that the P/O ratio reflects the breeding or the compatibility system is not found to be true in this family. As suggested by Chouteau *et al*. (2006a), in Araceae, a higher P/O ratio is most probably the result of a less efficient pollination mechanism, and therefore, to ensure seed production, the plant could have evolved self-pollination mechanisms.

### Floral traits with respect to life form

Little is known about floral traits with respect to life form. Jürgens *et al*. (2002) found significant differences between perennial and annual Caryophylloideae in terms of various floral traits. Perennial flowers had larger numbers of pollen grains and ovules, and greater P/O ratios, than annual flowers. In the aroids studied, there were significant differences between seasonally dormant (perennial) and evergreen taxa. Evergreen taxa may invest more resources in the male reproductive function by producing a larger number of male flowers and larger pollen volumes per inflorescence than seasonally dormant taxa (which are all geophytic). Ovule numbers per inflorescence were also higher in evergreen taxa.

Two non-exclusive main hypotheses could explain these differences between evergreen and seasonally dormant taxa.

1. Evergreen taxa are able to photosynthesize all year around, and therefore can acquire more resources to be invested in male and female functions than can seasonally dormant taxa.
2. As seasonally dormant taxa produce very few inflorescences per year (generally one per growing season), they should have more efficient pollen

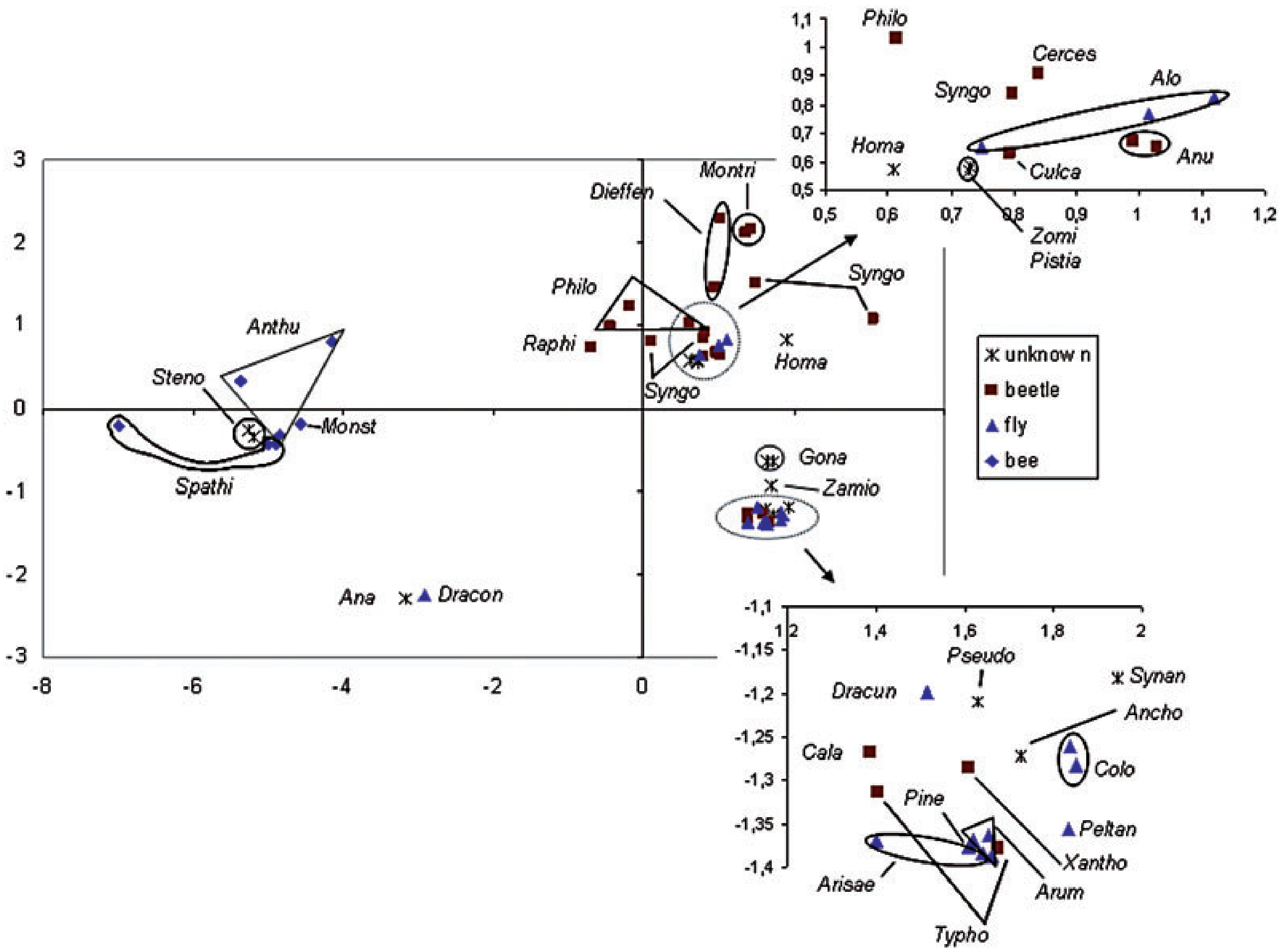

**Figure 3.** Graph of the discriminant analysis with two point clouds detailed (bottom and top). Species from the same genera are grouped together. Genera names are coded by the first three to six letters of their name (see Table 1).

transfer mechanisms in order to achieve pollination, leading to a decrease in the number and/or size of flowers and/or gametes. The stigmatic area per flower and per inflorescence is much smaller in seasonally dormant taxa than in evergreen taxa, which may support the hypothesis of higher pollination efficiency (Cruden, 2000).

### FLORAL TRAITS WITH RESPECT TO CLIMATIC ZONE

Of the seasonally dormant species studied, the temperate taxa, which are true perennials, had fewer pollen grains (mostly because of smaller pollen volumes) than their related tropical taxa. The mean pollen grain number per flower of the temperate (perennial) group is consistent with data published for the Caryophylloideae (Jürgens *et al.*, 2002). However, lower ovule numbers per flower and thus a higher P/O ratio were found for Araceae than for Caryophylloideae, even though both perennial Araceae and Caryophylloideae are xenogamous (Jürgens *et al.*, 2002). In the same way, differences between evergreen and seasonally dormant taxa, with lower gamete production and smaller stigma area per inflorescence for temperate (perennial) than tropical taxa, could result from a greater efficiency in pollen transfer (Cruden, 1977, 2000), because of the harsh climatic conditions and the shortness of the flowering season in temperate latitudes. Amongst the seasonally dormant taxa, all temperate species are known to be pollinated by flies, whereas tropical species are pollinated by beetles and bees.

### FLORAL TRAITS WITH RESPECT TO POLLINATOR TYPE

Eight of the 40 species were misclassified by the discriminant analysis, showing some mismatches between floral traits and pollinator types. In the case of *Xanthosoma conspurcatum*, a beetle-pollinated species classified amongst the fly-pollinated species, the pollen is shed in tetrads. This is very rare in the Araceae and only known from two genera: *Xantho-*

*soma* and *Chlorospatha* (Mayo *et al*., 1997). Consequently, if the tetrad is the functional pollen unit, the volume of *Xanthosoma* pollen (average of 38 798 μm$^3$) must be multiplied by four (155 168 μm$^3$), which is in accordance with the mean pollen volume (123 595 μm$^3$) of beetle-pollinated species. However, in most cases, there is good correspondence between floral traits and pollinator type. The selective pressure of the different types of pollinator has led to pollination syndromes (reviewed in Fenster *et al*., 2004): correlation of floral traits resulting in different types of floral architecture adapted to particular groups of pollinators. A few studies dealing with the subject have focused on the P/O ratio to explain the difference in pollination efficiency of the different types of pollinator. It was found that, in a tropical cloud forest community, the P/O ratio was higher in beetle- and fly-pollinated species than in bee-, bird- and bat-pollinated species (Ramirez & Seres, 1994). By contrast, no differences in P/O ratios were found amongst the species pollinated during the day (Lepidoptera, Hymenoptera, and Diptera) and night-pollinated (Lepidoptera) Caryophylloideae (Jürgens *et al*., 2002). Another floral trait that has been studied in relation to the pollinator is pollen grain size, which is believed to be optimal for collection and transportation by the pollinator without being lost (Wodehouse, 1935; Harder, 1998; Cruden, 2000). Our results show clearly that the P/O ratios of bee- and fly-pollinated species are similar, which is consistent with the literature (Cruden, 2000), suggesting that bees and flies have a similar pollination efficiency. The much higher P/O ratio of beetle-pollinated species, compared with other types of pollinator, lends credence to the hypothesis that beetles may be less effective pollinators. Pollen size was also much greater for beetle-pollinated species than the other classes of pollinator, which reinforces the hypothesis of pollen size being related to pollinator in order to maximize its transportation. The much higher P/O ratio and pollen grain volume of beetle-pollinated species suggest a much higher investment in pollen production by beetle-pollinated plants. Many beetles eat pollen, which is part of the plant's rewards for its pollinators (Bernhardt, 2000). Therefore, plants having pollen rewards would tend to show a higher pollen production to counterbalance the disadvantage of pollen loss by direct consumption in beetle pollinations. Although bees are known to harvest a pollen 'reward', the lower P/O ratio of this group could be explained by the bees being more efficient pollinators (Webb, 1984). In addition, the bee-pollinated aroids studied all provide other types of reward which could be favoured by the pollinator, such as stigmatic secretions and sweet scents that can be collected from *Anthurium* (Croat, 1980; Schwerdtfeger, Gerlach & Kaiser, 2002) and *Spathiphyllum* (Lewis *et al*., 1988; Gerlach & Schill, 1991; Yong, 1993), or resin known to be harvested for nest construction from *Monstera* (Ramirez & Gomez, 1978). Finally, the small pollen size of the bee-pollinated species renders harvesting by bees more difficult (Harder, 1998).

## CONCLUSION

Floral traits seem to be correlated with pollinator type (i.e. pollination syndromes; Fenster *et al*., 2004), life form, climatic conditions, and self-pollination capacity, whereas the growth mode has no apparent influence. The floral characters retained for the characterization of the pollinator type are pollen volume per inflorescence, pollen number per inflorescence, number of gyneocia, sexual type of the flower, and life form. The number of stamens of flowers could also be an important character, as suggested by the two male characters retained in the discriminant analysis: pollen number and volume. This aspect was not included in the analysis as it was not available for all the studied species. Further data are needed to verify this hypothesis. These results provide new insights into the understanding of specialized floral architecture in relation to pollinator type, and could help in identifying the pollination syndrome for a specific species. In addition, life form and climatic region are factors affecting investment in male and female functions in aroids. Temperate and seasonally dormant species show lower gamete production and smaller stigma areas, suggesting more efficient pollination mechanisms, in comparison with tropical and evergreen species. These differences could be attributed to the length and condition of the growing season, which would directly influence the energy pool of plants allocated to inflorescence production. The less energy plants have to invest in an inflorescence, the more efficient the pollination system. Finally, in aroids, the P/O ratio in relation to the breeding system behaves contrary to that found in other plant groups, suggesting that it may not be linked to the breeding system. It seems more likely that the P/O ratio is a measure of efficiency of pollen transfer.

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## APPENDIX

### Location collection and list of voucher specimens

| Species | Location (identification number) | Voucher number (herbarium) |
|---|---|---|
| *Alocasia* sp. | Missouri Botanical Garden (No 90145) | *Croat 90145* (UMO) |
| *Alocasia macrorrhizos* (L.) G. Don | Montreal Botanical Garden (No 1774-1956) | *Chouteau 15* (MT) |
| *Alocasia portei* Schott | Montreal Botanical Garden | *Chouteau 16* (MT) |
| *Anaphyllopsis americana* (Engl.) A. Hay | French Guiana | *Barabé 258* (MT) |
| *Anchomanes difformis* (Blume) Engl. | Missouri Botanical Garden (No Knecht.1) | *Knecht 1* (UMO) |
| *Anthurium harrisii* (Grah.) G. Don | Montreal Botanical Garden (No 635-1942) | *Barabé 253* (MT) |
| *Anthurium longistamineum* Engl. | Montreal Botanical Garden (No 1554-1958; No 3038-1959) | *Barabé 233* (MT) |
| *Anthurium schlechtendalii* ssp. *schlechtendalii* Kunth | Montreal Botanical Garden (No 2463-1954) | *Barabé 219* (MT) |
| *Anubias barteri* Schott | Montreal Botanical Garden (No 3548-1985) | *Chouteau 17* (MT) |
| *Anubias heterophylla* Engl. | Montreal Botanical Garden (No 1941-1999; No 1909-1999) | *Barabé 197* (MT) |
| *Arisaema dracontium* (L.) Schott | Missouri Botanical Garden (No 69905) | *Croat 69905* (UMO) |
| *Ariseama triphyllum* (L.) Schott | Montreal Botanical Garden (No 1984-2000) | *Barriault 25* (MT) |
| *Arum cylindraceum* Gasp. | Corsica | |
| *Arum italicum* Mill. | Corsica | *Barabé 182* (MT) |
| *Arum maculatum* L. | Corsica | |
| *Caladium bicolor* (Aiton) Vent. | Montreal Botanical Garden (No 2364-1992; No 1590-1995) | *Barabé 96* (MT) |
| *Cercestis stigmaticus* N.E. Br. | Montreal Biodôme (No 7078-1998) | *Barabé 239* (MT) |
| *Colocasia esculenta* (L.) Schott | Montreal Botanical Garden (No 1412-1998; No 1143-1999) | *Barabé 175* (MT) |
| *Colocasia fallax* Schott | Montreal Botanical Garden (No 1416-2002) | *Chouteau 18* (MT) |
| *Culcasia saxatilis* A. Chev. | Montreal Botanical Garden (No 4094-1984) | *Barabé 91* (MT) |
| *Dieffenbachia oerstedii* Schott | Montreal Botanical Garden (No 1834-1955) | *Chouteau 19* (MT) |
| *Dieffenbachia seguine* (Jacq.) Schott | French Guiana | *Chouteau & Lavallée 3* (MT) |
| *Dracontium polyphyllum* L. | Montreal Botanical Garden (No 484-1987; No 2464-1954) | *Barabé 50* (MT) |
| *Dracunculus vulgaris* Schott | Missouri Botanical Garden (No 942193) | *Croat 942193* (UMO) |
| *Gonatopus angustus* N.E. Br. | Montreal Botanical Garden (No 4106-1984) | *Barabé 101* (MT) |
| *Gonatopus boivinii* (Decne.) Engl. | Missouri Botanical Garden (No 69740) | *Croat 69740* (UMO) |
| *Homalomena rubescens* Kunth | Montreal Botanical Garden (No 1721-1955) | *Barabé 108* (MT) |
| *Homalomena philippinensis* Engl. | Missouri Botanical Garden (No 52988) | *Croat 52988* (UMO) |

APPENDIX *Continued*

| Species | Location (identification number) | Voucher number (herbarium) |
|---|---|---|
| *Monstera adansonii* Schott | French Guiana | *Chouteau & Lavallée 5* (MT) |
| *Montrichardia arborescens* (L.) Schott | French Guiana | *Barabé 263* (MT) |
| *Montrichardia linifera* (Arruda) Schott | French Guiana | *Chouteau & Lavallée 4* (MT) |
| *Peltandra virginica* (L.) Schott | Missouri Botanical Garden (No 96738) | *Croat 96738* (UMO) |
| *Philodendron erubescens* C. Koch & Augustin | Montreal Botanical Garden (No 2798-1950; No 1892-1957) | *Chouteau 12* (MT) |
| *Philodendron pedatum* Kunth | French Guiana | *Barabé 259* (MT) |
| *Philodendron squamiferum* Poepp. & Endl. | Montreal Botanical Garden (No 2365-1992; No 2201-1986) | *Barabé 136* (MT) |
| *Pinellia tripartita* (Blume) Schott | Missouri Botanical Garden (No 78128) | *Croat 78128* (UMO) |
| *Pistia stratiotes* L. | Montreal Botanical Garden (No 2627-1993) | *Chouteau 20* (MT) |
| *Pseudodracontium fallax* Serebr. | Missouri Botanical Garden (No 79452) | *Croat 79452* (UMO) |
| *Rhaphidophora schottii* Hook | Missouri Botanical Garden (No Kew 478-65-47801) | *Kew 478-65-47801* (UMO) |
| *Spathiphyllum friedrichsthalii* Schott | Montreal Botanical Garden (No 2577-1954) | *Chouteau 21* (MT) |
| *Spathiphyllum patinii* (Mast.) N.E. Br. | Montreal Botanical Garden (No 1779-1949; No 2229-1960) | *Barabé 189* (MT) |
| *Spathiphyllum wallisii* Regel | Montreal Botanical Garden (No 2471-1954; No 1231-1986) | *Barabé 105* (MT) |
| *Stenospermation longipetiolatum* Engl. | Montreal Biodôme (No 7267-1992; No. 7057-1998) | *Barabé 251* (MT) |
| *Stenospermation sessile* Engl. | Montreal Biodôme (No 7003-2000) | *Chouteau 22* (MT) |
| *Synandrospadix vermitoxicus* (Griseb.) Engl. | Missouri Botanical Garden (No 62836) | *Croat 62836* (UMO) |
| *Syngonium angustatum* Schott | Montreal Botanical Garden (No 1891-1942) | *Barabé 217* (MT) |
| *Syngonium auritum* (L.) Schott | Montreal Biodôme (No 7342-1992) | *Barabé 216* (MT) |
| *Syngonium ruizii* Schott | Missouri Botanical Garden (No 85-1656 Atwood) | *Atwood 85-1656* (UMO) |
| *Syngonium schottianum* H. Wendl. ex Schott | Montreal Biodôme (No 7013-1998) | *Barabé 212* (MT) |
| *Typhonium trilobatum* (L.) Schott | Missouri Botanical Garden (No 53260) | *Croat 53260* (UMO) |
| *Typhonium violifolium* Gagnep. | Missouri Botanical Garden (No HAR194) | *HAR 194* (UMO) |
| *Xanthosoma conspurcatum* Schott | Montreal Botanical Garden (No 1510-2003) | |
| *Zamioculcas zamiifolia* (Lodd.) Engl. | Montreal Botanical Garden (No 7324-1939) | *Barabé 84* (MT) |
| *Zomicarpella amazonica* Bogner | Missouri Botanical Garden (No 71763) | *Croat 71763* (UMO) |