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Authors

Nyman, Leslie Paul
Soediono, Noes
Arditti, Joseph

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OPENING AND RESUPINATION IN BUDS AND FLOWERS OF DENDROBIUM (ORCHIDACEAE) HYBRIDS¹

LESLIE PAUL NYMAN,* NOES SOEDIONO,† AND JOSEPH ARDITTI*

*Department of Developmental and Cell Biology, University of California, Irvine, California 92717; and †Flora Sari Orchids, Jalan Andara, Krukut, Pondok Labu, Jakarta Selatan, Indonesia

Observations of flower buds of *Dendrobium* Tomie 'Tokyo,' *D.* Indonesia, and seedlings of a *Dendrobium* hybrid flowering for the first time showed that all flower buds were borne with the labellum uppermost. Just before or during opening, the buds turned, positioning the lip below all other floral segments in a process known as resupination. The degree of turning depended on the orientation of the inflorescence relative to the ground and position of the pedicel. Individual flowers, at successive nodes along the inflorescence, alternated in turning clockwise and counterclockwise. Our results indicate that (1) only buds, flowers in the process of opening, and newly opened blossoms can undergo resupination; (2) mature flowers cannot reorient themselves if the angle of the inflorescence is changed; and (3) bending and twisting of the pedicel contribute to the final position of the flower.

Introduction

Resupination was defined by LEE (quoted without a reference or initials by AMES [1946]) as ". . . when the upper Lip of the Corolla looks toward the Ground, and the under Lip toward Heaven." JOHN LINDLEY (1853; cited in AMES [1938]) also described orchid flowers as being resupinate. This phenomenon has been attributed to torsion, twisting, or turning of the ovary, pedicel, or both (PFITZER 1882; ZIMMERMANN 1933; ZIEGENSPECK 1936). The result of resupination (usually a 180° turn) is generally to orient the flower so that the labellum is lowermost, regardless of the angle of the inflorescence (AMES 1938; WITHNER et al. 1974; SCHLECHTER 1977; GOH et al. 1982). Degrees of torsion may vary, and in *Hammarbya* (*Malaxis*) *paludosa* ". . . the ovarium [is] twisted twice as much . . . as usual" (DARWIN 1904), or 360°, and positions the labellum uppermost (AMES 1938). *Angraecum eburneum* also turns 360° (VAN DER PIJL and DODSON 1966).

Torsion may be clockwise or counterclockwise in *Spiranthes gracilis* and causes the entire inflorescence to appear spiral (AMES 1938). In *Trichopilia suavis* the flowers are oriented with the lip lowermost by a slight torsion of the pedicel rather than the ovary (AMES 1947). Some orchids are not resupinate, e.g., *Satyrium* (VAN DER PIJL and DODSON 1966). Others that are resupinate are borne with the labellum uppermost because their inflorescences are nodding and hanging (VAN DER PIJL and DODSON 1966). However, there are also species with

similar inflorescences in which the flowers turn and the labellum is lowermost (ZIMMERMANN 1933). Pistillate flowers of *Catasetum* are nonresupinate, whereas male blossoms may turn (SCHOMBURGK 1837; AMES 1945; DRESSLER 1981). The final position of the labellum depends on the species, degree of torsion, and position of the inflorescence (ZIMMERMANN 1933).

Resupination functions to place the labellum in a position that facilitates pollination (AMES 1948). This was apparently understood almost 200 yr ago (SPRENGEL 1793) but was explained more fully much later (DARWIN 1904; AMES 1938; VAN DER PIJL and DODSON 1966; DRESSLER 1981). Resupination has been used as a diagnostic character by systematists. However, there are very few studies of the process itself and the factors that control it (PFITZER 1882; ZIMMERMANN 1933; ZIEGENSPECK 1936; AMES 1938; GOH et al. 1982). This investigation was undertaken to establish the relationships among resupination and bud size, stage of development, and position of the inflorescence.

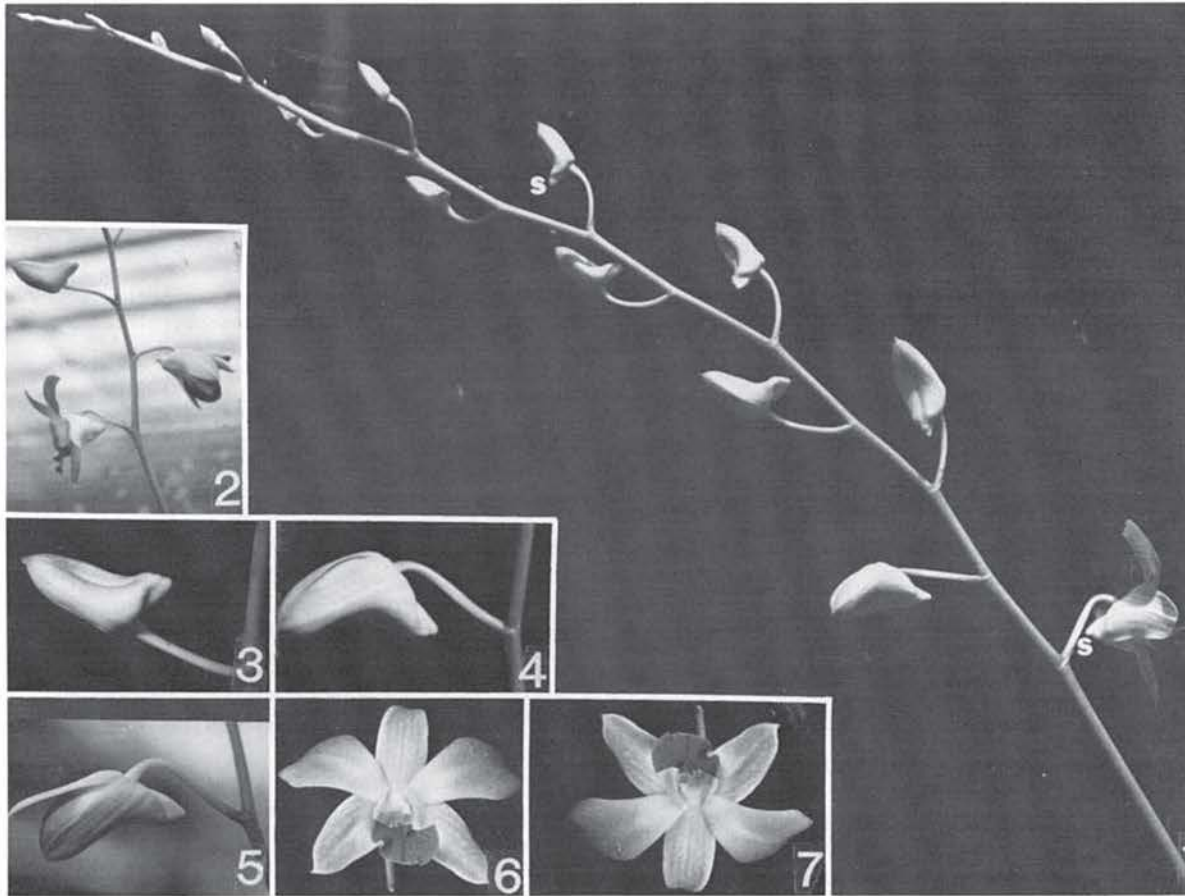
Material and methods

Racemes (figs. 1, 2), buds (figs. 3-5), and flowers (figs. 6, 7) of *Dendrobium* Indonesia and *D.* Tomie 'Tokyo' and seedlings of a *Dendrobium* hybrid flowering for the first time were observed at the Flora Sari Orchid Nursery in Jakarta, Indonesia. Diameters of buds were measured with calipers, and angles of inflorescences (relative to the ground), and buds and flowers (relative to the inflorescence) were determined with a protractor. At least 10 racemes and 60-80 buds were measured. To determine whether fully opened flowers were capable of torsion, the positions of inflorescences bearing such blossoms were altered. Theoretical degrees of torsion necessary to position the labellum lowermost were obtained by turning a cardboard flower model mounted on a metal rod tilted at 0°-90° to simulate various inflorescence angles.

¹ This paper is dedicated to the memory of Mrs. EMMA D. MENNINGER, a long-time generous supporter of orchid research.

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Address for correspondence and reprints: JOSEPH ARDITTI, Department of Developmental and Cell Biology, University of California, Irvine, California 92717.



FIGS. 1–7.—Racemes, buds, and flowers of *Dendrobium Tomie* 'Tokyo.' Fig. 1, A raceme in which the basal flower is fully open and completely resupinate; the bud above it has completed resupination and is starting to open; buds 3–9 from the base are in various stages of resupination; the pedicels of the remaining buds are bent and/or twisted, but resupination has not started. *s*, spur. Fig. 2, Unopened bud (top), a bud in the process of opening and resupination (middle), and a fully open, completely resupinate flower (bottom). Fig. 3, Nonresupinate bud. Fig. 4, Resupinate bud. Fig. 5, Resupinate bud that is starting to open. Fig. 6, Completely resupinate, fully open flower. Fig. 7, Rare, nonresupinate, fully open flower.

Observations

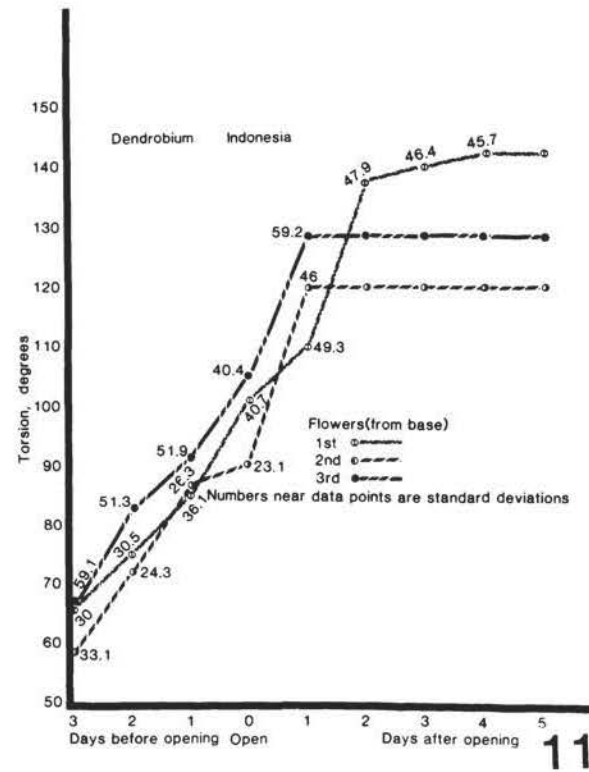
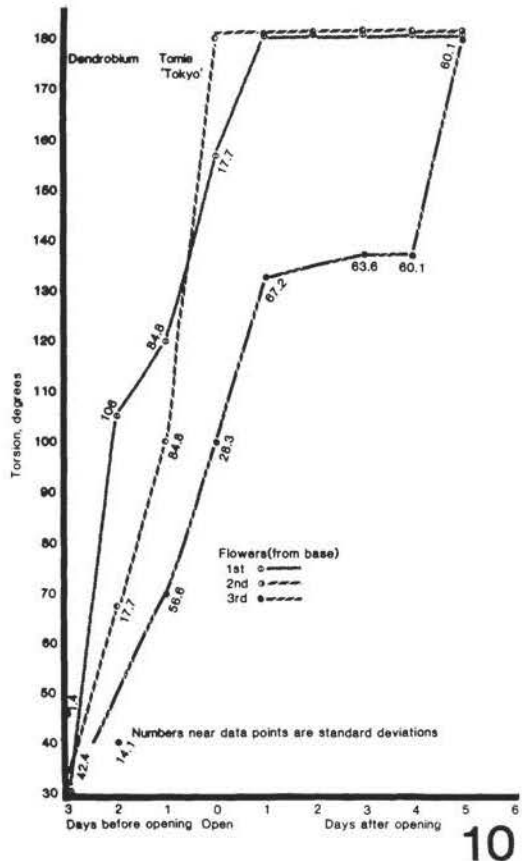
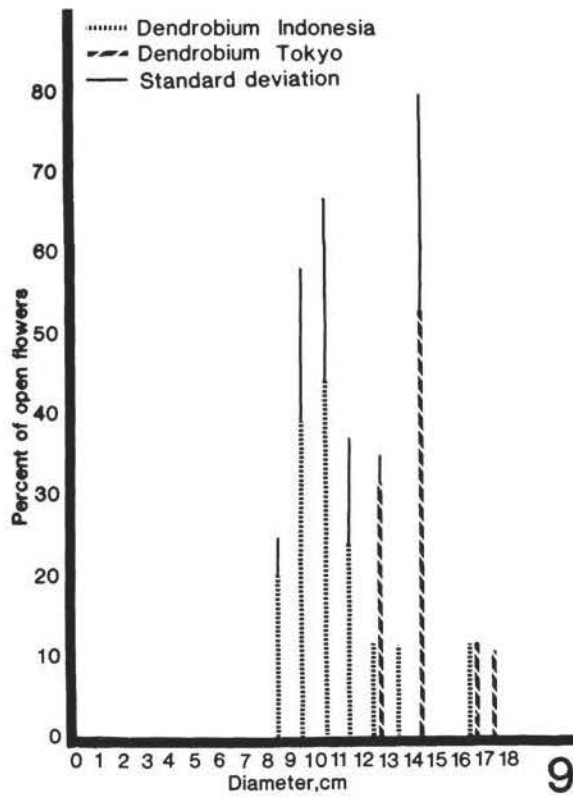
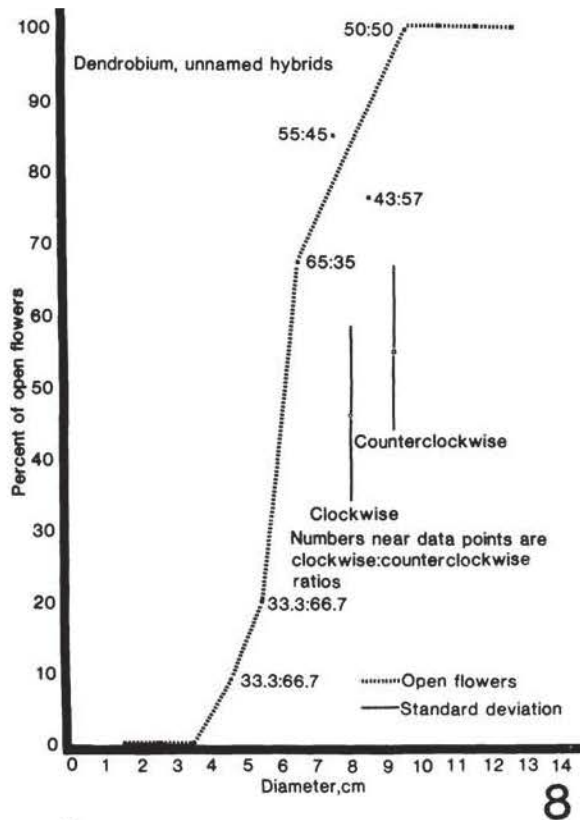
Very young buds of *Dendrobium Indonesia* and *D. Tomie* 'Tokyo' (fig. 1) were green, hard, and had spurs pointing upward (fig. 2, uppermost bud; fig. 3). Buds started to turn while relatively young (fig. 1, ninth bud from base) shortly before and during opening (fig. 2, third bud from base) and for a short period after the flower had opened. Perianth segments started to separate before or after (figs. 4, 5) torsion had been completed and the labellum had been positioned lowermost (fig. 6). Very few flowers were nonresupinate even after they had opened (fig. 7).

Some buds of the unnamed *Dendrobium* hybrid started to open on reaching a diameter of 3.5 mm. In general, opening started when the bud diameter was 4.0–4.9 mm, but all buds opened when their diameters were 9 mm (fig. 8). Buds of *D. Indonesia* started to open when their diameters were at least 8.0–8.9 mm. More than 40% of the buds

opened on reaching a diameter of 10.0–10.9 mm (fig. 9). Buds of *D. Tomie* 'Tokyo' started to open when their diameters were 12.0–12.9 mm. More than 50% opened by the time they reached a diameter of 14.0–14.9 mm (fig. 9).

Buds on any one inflorescence of the unnamed *Dendrobium* seedlings were generally resupinate alternately clockwise and counterclockwise (table 1). Clockwise:counterclockwise ratios of open flowers varied from 33.3%:66.7% through 50%:50% to 65%:35%; for all flowers the ratio was 46.4%:55.3% (fig. 8; table 2). The last ratio totals slightly more than 100% since the figures for each direction were averaged separately (fig. 8; table 2).

The model indicated that when inflorescences are at a 90° angle to the ground, buds must turn 180° to position the labellum lowermost and proportionately less when the flower stalks are tilted at a lesser angle (fig. 12). Resupination of ca. 90% of all buds was within 1 or 2 SDs of the values predicted by



FIGS. 8-11.—Opening and resupination of *Dendrobium* buds and flowers. Fig. 8, Bud size and opening and direction of resupination of buds of unnamed *Dendrobium* seedlings. Ratios (closed squares, dotted line) given at the data points were obtained from several racemes. The total ratios, $46.4 \pm 12.4:55.3 \pm 11.8$, (open squares, solid SD lines) were obtained by averaging each direction of torsion separately; therefore, the total is slightly higher than 100. Fig. 9, Bud diameters and opening in *D. Indonesia* and *D. Tomie 'Tokyo'*. Fig. 10, Resupination before and after opening of flowers of *D. Tomie 'Tokyo'*. Fig. 11, Resupination before and after opening of flowers of *D. Indonesia*. The horizontal portions of the curves in figs. 8, 10 (first and second day), and 11 (first, second, and third day) indicate that the position of the flowers did not change; i.e., resupination was completed. Resupination of such flowers was the same; consequently, there are no standard deviations and no numbers near the data points.

TABLE 1
RESUPINATION AND ITS DIRECTION IN FLOWERS OF AN
UNNAMED DENDROBIUM HYBRID

ANGLE OF INFLORESCENCE RELATIVE TO GROUND (°)	DEGREES OF TORSION ^a			Theoretical
	Clockwise	Counterclockwise	Average of all flowers ^b	
0	100.0 ± 103.9 ^c	108.0 ± 74.2 ^c	104.0 ± 79.8 ^c	90
10	300 ^d	100
40	225.0 ± 35.4	135.0 ± 33.2 ^c	165.0 ± 55.4 ^c	130
45	126.7 ± 35 ^c		100.0 ± 47.3 ^c	135
50	142.5 ± 187 ^c	63.0 ± 48.7 ^c	97.0 ± 92.5 ^c	140
60	180 ^d	150
70	113.0 ± 7.4	172.0 ± 2.9	138.0 ± 61 ^c	160
75	170 ^d	165
80	87.0 ± 32.2	118.0 ± 177 ^c	99.0 ± 29.7	170
90	111.0 ± 54.5 ^c	139.0 ± 34 ^c	125.0 ± 44.6 ^c	180

^a Value ± SD.

^b This average was calculated using the following formula:

(total clockwise + total counterclockwise/total number of flowers).

^c Theoretically expected degrees of torsion are within 1 SD.

^d Only one value available.

^e Theoretically expected degrees of torsion are within 2 SDs.

the model (tables 1, 3). When the positions of inflorescences of the unnamed *Dendrobium* seedlings bearing fully open flowers were altered, the blossoms did not change orientation.

Among the racemes of *D. Indonesia*, 33.3% had a perfect sequence of alternating clockwise and counterclockwise directions of turning. The remaining 66.7% had one sequence of two successive clockwise or counterclockwise torsions, but the direction of resupination for other buds alter-

nated (table 2). In *D. Tomie* 'Tokyo,' 50% of the inflorescences had a perfect sequence of alternate clockwise and counterclockwise resupination. The other half had two sequences in which two successive buds were resupinate in the same direction (table 2). Half of all open flowers of *D. Indonesia*

TABLE 2
DIRECTION OF RESUPINATION IN DENDROBIUM INDONESIA
AND *D. TOMIE* 'TOKYO'

	D.	D.
	Indonesia	Tomie 'Tokyo'
Sequence, % of racemes:		
All clockwise and counterclockwise	33.3	50.0
One repetition ^a	66.7	...
Two repetitions ^a		50.0
Clockwise torsion:		
% of total no. of open flowers	51.1	40.0
No. of open flowers per raceme ^b	2.6 ± 1	3.0 ± 1.4
Counterclockwise torsion:		
% of total no. of open flowers	48.9	60.0
No. of open flowers per raceme ^b	2.6 ± 1.1	4.5 ± 0.7

^a Clockwise followed by clockwise, or counterclockwise followed by counterclockwise.

^b Value ± SD.

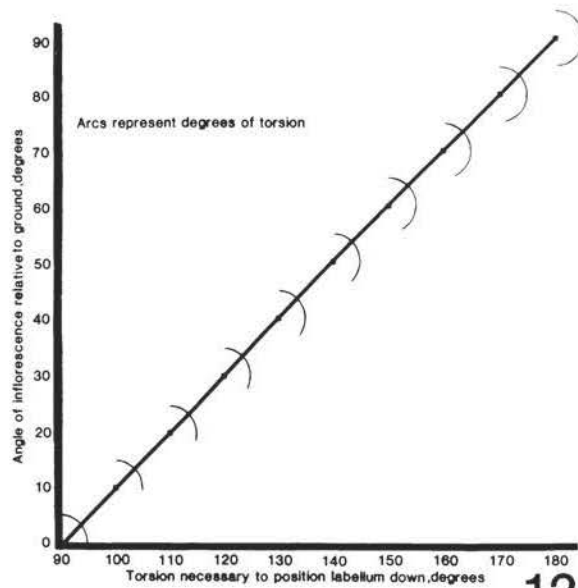


FIG. 12.—Torsion necessary to position the labellum (lip) in lowermost position as a function of the angle of the inflorescence relative to the ground. The arcs indicate degrees of torsion. Data were obtained from a model consisting of a cardboard flower mounted so that it could be turned on a metal bar, which was tilted to simulate angles of inflorescence relative to the ground.

TABLE 3
RESUPINATION OF FLOWERS OF DENDROBIUM INDONESIA
AND *D. TOMIE 'TOKYO'*

ANGLE OF INFLORESCENCE RELATIVE TO GROUND (°)	DEGREES OF TORSION ^a		Theoretical
	<i>D. Indonesia</i> Average	<i>D. Tomie 'Tokyo'</i> Average	
0	...	30.0 ± 14.1	90
5	95
10	100
15	111.7 ± 44.8 ^b	...	105
20	77.5 ± 15	90	110
25	55.0 ± 7.1	...	115
30	62.8 ± 22	92.5 ± 40.3 ^b	120
35	125
40	75.0 ± 37.5 ^c	...	130
45	135
50	83.3 ± 11.5	80 ^d	140
55	105 ^d	...	145
60	81.4 ± 36.1 ^c	112.5 ± 66.5 ^b	150
65	144.0 ± 41.6 ^b	...	155
70	90.7 ± 15.9	150 ^d	160
75	165
80	107.1 ± 35 ^c	180 ^d	170
85	175
90	136.7 ± 45.1 ^b	180 ^{b,d}	180

^a Value ± SD.

^b Within 1 SD of theoretically predicted degrees of torsion.

^c Within 2 SDs of theoretically predicted degrees of torsion.

^d Only one value available.

turned clockwise, and the rest were resupinate in a counterclockwise direction. In *D. Tomie 'Tokyo,'* the percentage of flowers that turned in a counterclockwise direction was slightly higher than in *D. Indonesia* (table 2).

In *D. Tomie 'Tokyo,'* the resupination of basal flowers on the day they opened was 157.5°, or 87.5% of the final torsion, which was 180° (fig. 10). The second flower from the base was completely resupinate (180°) at the time of opening. Resupination of the third flower at the time of opening was 100° or 55.6% of the completed torsion (fig. 10). The basal flower continued to turn for 1 day after opening, whereas the second was fully resupinate and the third completed its torsion in 4 days.

At the time of opening, resupination of the basal flowers on racemes of *D. Indonesia* was 101°, or 77% of the final theoretical value, and never reached 180° (fig. 11). Corresponding values for the second and third flowers from the base were 90.6° (75%) and 105° (81%), respectively (fig. 11). Resupination of the basal flower continued 4 days after opening. The second and third flowers continued to turn for 1 day after they opened (fig. 11).

Discussion

For these experiments it would have been preferable to use plants which are genetically identical.

A clone of a species would have been most desirable, but such clones are not available. Another problem with research that utilizes orchid blossoms is that many flowers and/or inflorescences are destroyed, and commercial growers (the only establishments that have enough plants and flowers) are generally unwilling to sustain the losses. Therefore, we were limited in our work to the available plants and flowers.

The parents of the unnamed hybrid were not divulged to us for commercial reasons. *Dendrobium Indonesia* (syn. *D. Arcuatum*) is a primary hybrid (*D. phalaenopsis* × *D. violaceo-flavens*). Like the overwhelming majority of all orchids, its parent species produce resupinate flowers. The plants we used were not a named clone of this hybrid. With *D. Tomie 'Tokyo'* (*D. Theodore Takiguchi* × *D. Jaquelyn Thomas*), we used a selected (and therefore named) clone of a more complex hybrid. The immediate parents as well as the species in its background (*D. phalaenopsis*, *D. stratiotis*, *D. gouldii*, *D. tokai*) produce resupinate flowers.

Each hybrid studied has a characteristic bud and flower size; therefore, it is not surprising that differences in bud size at the time of opening were observed. There is a positive correlation between bud diameter at the time of opening and mature flower size.

It is unlikely that the direction of torsion of an

individual flower would be of any ecological or evolutionary advantage. However, it is clear that the direction of turning is not random since we did not observe inflorescences in which all or even more than two adjacent blossoms turned in one direction. Torsion of basal buds may be in one direction, causing the second bud to turn in the other. The second blossom may then affect the turning of the one immediately above it. Also, the direction and sequence of turning may be established during the development of each bud. The observation that, when buds are missing, the sequence continues normally supports the second hypothesis. Existence of imperfect sequences would argue against both hypotheses presented here unless such imperfections are the result of damage, unexpected physiological changes, errors in data recording, or the hybrid nature of the plants. Leaves of *Aloe polyphylla* (Liliaceae) exhibit a clockwise and counterclockwise twist (JEPPE 1974; REYNOLDS 1974), but not enough information is available about this phenomenon to allow comparisons.

It may seem disturbing that not all buds turn to the extent predicted by the model or that resupination does not appear to be as constant and regular as claimed. However, resupination functions to place the labellum lowermost, and the amount of torsion per se is not the only factor that determines the final position of the flower because bending and twisting of the pedicel also have an important effect (PFITZER 1882; ZIMMERMANN 1933; ZIEGENSPECK 1936; AMES 1947, 1948). Torsion may play a major role, but it only completes the positioning of each blossom, and its extent is determined by the initial position of the bud and the raceme. For example, if the angle of the pedicel contributes 20° of the positioning of a flower on a 90° raceme, the required torsion would only be 160° and not 180° as predicted by the model. The contribution by the pedicel is technically difficult to measure, and it may change daily or more often in the same bud. Even with the unpredictability of the variations introduced by the pedicel, the observed torsion was within 1 or 2 SDs of the predicted values, indicating that resupination is a regular, constant, and reproducible process.

Some buds complete resupination before they open; others do not, and the open flowers continue to turn for up to 4 days. This and the fact that, after the process has been completed, the flowers no longer turn, even if their positions are changed, suggest that physiological and/or structural changes take place following completion of the process in *Dendrobium* flowers. These changes probably prevent further perception of the stimulus or stimuli that control resupination and/or render the flower incapable of turning.

In *Epipogon aphyllum*, *Dactylorhiza*, *Gymnadenia odoratissima*, *Platanthera bifolia*, and other orchids, pollination reverses the torsion (ZIEGENSPECK 1936), and the flowers are no longer resupinate. This suggests the involvement of auxin (because orchid pollen is a rich source of this hormone) and/or ethylene (since pollination induces production of the gas by orchid flowers) or other substances produced by pollen or pollinated orchid flowers (ARDITTI 1979; GOH et al. 1982). Participation of auxin is also indicated by (1) transport of ¹⁴C-IAA into ovaries from stigmas and (2) movement of auxin into receiver blocks from ovaries (STRAUSS and ARDITTI 1982). Auxin can, therefore, reach and affect ovaries and pedicels, i.e., the segments in which torsion and movement take place.

Buds of *Anacamptys pyramidalis* failed to turn when placed on a clinostat; only a few flowers of *Ophrys* were resupinate under similar conditions; and on racemes of *Goodyera repens* the oldest buds exhibited torsion, but the young ones did not (ZIEGENSPECK 1936). These findings have been interpreted to suggest that resupination occurs in response to gravity and is a special form of gravitropism (ZIEGENSPECK 1936; AMES 1946, 1948; SCHLECHTER 1977). They also indicated that the process cannot be stopped or reversed once it has been initiated (ZIEGENSPECK [1936] did not state the duration of the experiment). In *Cytisus laburnum* (Fabaceae), the axis of the inflorescence is erect while the flowers are in bud and the standards are uppermost. Later the inflorescence becomes pendent, and the position of each bud is changed placing the keel uppermost. When the flowers open, each ". . . twists round through nearly 180°, so that the standard is again brought uppermost" (VON MARILAUN 1896). If the young racemes are prevented from becoming pendent, the flower stalks fail to turn or do so to a very limited extent. This indicates that this process, which is very similar to orchid resupination, may be gravitropic. If so, this is an additional reason to believe that auxin and/or ethylene may be involved in both orchids and *C. laburnum*.

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