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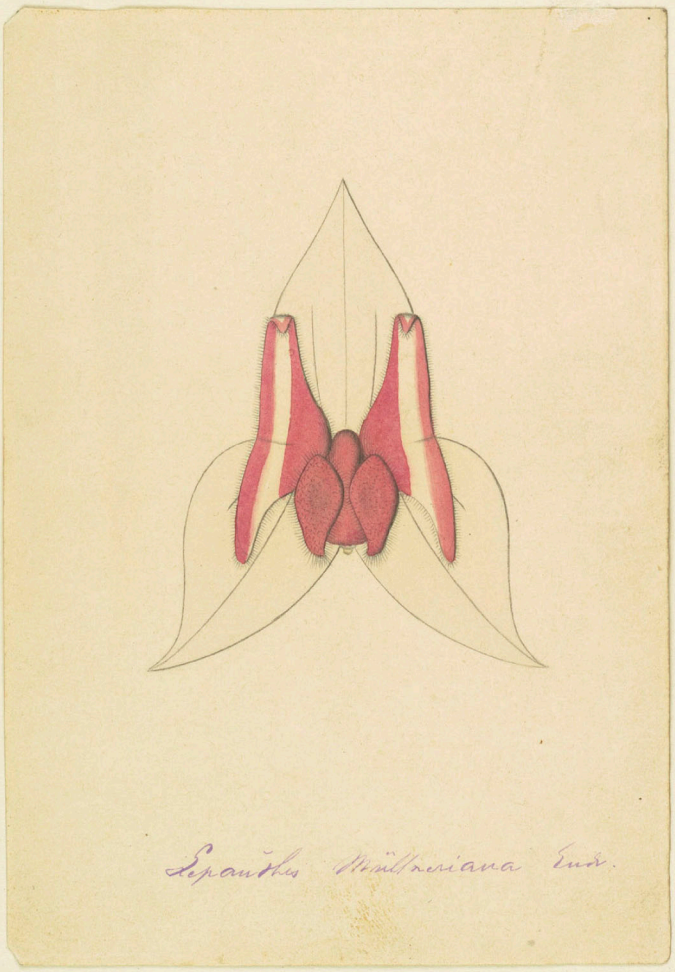

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INTERNATIONAL JOURNAL ON ORCHIDOLOGY

This issue of Lankesteriana
is dedicated to te memory of
Luis Diego Gómez Pignataro
(1944-2009)
a passionate humanist and biologist,
mentor of Costa Rican natural sciences,
a friend

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LORD OF THE FLIES: POLLINATION OF *DRACULA* ORCHIDS

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Abstract. The labellum of *Dracula* orchids looks and smells like mushrooms, and biologists have long hypothesized mushroom mimicry in which mushroom-associated (mycophilous) flies accidentally pollinate these flowers while laying their eggs. In the cloud forest of Ecuador, we observed flower morphology, pollinators and the mechanisms of pollination in two species, *Dracula lafleurii* Luer & Dalström and *D. felix* (Luer) Luer. The orchids are visited and pollinated by drosophilid mycophilous flies of the genus *Zygothrica*, which normally complete part of their life cycles on mushrooms. While these flies court and mate in the flowers, and in the process, pollinate them, they apparently do not lay their eggs in the flowers. The pollination mechanism of *Dracula* occurs when pollinators' thoraces are trapped by the incurved flaps of the rostellum which creates an angle between the scutellum and the abdomen for the removal and deposition of the pollinia, a novel feature previously not describe in orchids.

Resumen. La forma y el olor de los labelos de las orquídeas del género *Dracula* se asemejan a hongos, y por mucho tiempo se ha mantenido la hipótesis de que estas orquídeas mimetizan hongos y dípteros con ciclos de vida asociados con los hongos (micófilos) accidentalmente polinizarían estas flores mientras ovopositan. La morfología floral, los polinizadores y mecanismos de polinización fueron estudiados en *Dracula lafleurii* Luer & Dalström and *D. felix* (Luer) Luer en un bosque nublado de Ecuador. Estas orquídeas son efectivamente visitadas en su mayoría por moscas micófilas pero son polinizadas únicamente por moscas drosofilidas del género *Zygothrica* cuyos ciclos de vida están estrechamente asociados con hongos. Estas moscas realizan despliegues de cortejo y apareamiento en las superficies de las flores de *Dracula* estudiadas y en este proceso también las polinizan, aparentemente sin ovopositar. El mecanismo de polinización de *Dracula* ocurre cuando los tóraxes de los polinizadores son atrapados por los márgenes incurvados del rostelo, lo cual crea un ángulo entre el escutelo y el abdomen apropiado para la remoción y deposición de los polinios, una característica que hasta ahora no había sido reportada en las orquídeas.

Key words: cloud forest, fly pollination; mycophilous; odor; pollinator behavior; *Zygothrica*

Introduction. Orchids in the genus *Dracula* have long been suspected to be mushroom mimics. They have a cupped labellum that is usually lined with parallel or radiating ridges that resembles the cap and gills of an inverted mushroom, dark-spotted sepals on a light background, long sepaline tails, and sometimes a mushroom-like odor. These characteristics suggest that *Dracula* flowers attract saprophagous or mycophagous insects that accidentally act as pollinators (Van der Pijl & Dodson 1966, Vogel 1978, Endress 1996, Proctor *et. al*. 1996, Pridgeon *et al.* 2005). Moreover, Vogel (1978) hypothesized a pollination mechanism in which the pollinia adhere to the backs of small mycophagous flies while they attempt to lay eggs on the flowers.

Dracula is a genus of unusual orchids that occurs in the moist and shady montane cloud forests of tropical America. The name means little dragon and pays homage to the 'chimaera' of Reichenbach (Luer 1993), as well as to the extravagant display of the flowers' widespread sepals with long, pendant sepaline tails that resemble flying bats (Luer 1978, Luer 1993). Comprising ca. 148 mostly epiphytic

species, *Dracula* can be found mostly in pristine forests and less frequently in disturbed habitats from southern Mexico to Peru (Luer 1993). The genus *Dracula* belongs to the most diverse subtribe of Neotropical orchids, the Pleurothallidinae, which comprises 5 to 8% of the floristic diversity of the Neotropics (Jørgensen & León-Yánez, 1999), and are a mostly fly-pollinated group (Van der Pijl & Dodson 1966, Chase 1985, Dressler 1993, Duque 1993, Christensen 1994, Endress 1996, Borba & Semir 2001, Pridgeon *et al*. 2001, Van der Cingel 2001, Blanco & Barboza 2005, Pridgeon 2005, Albores-Ortiz & Sosa, 2006, Barbosa *et al*. 2009).

In this paper we describe the pollination biology of these remarkable putative mushroom mimics in their native habitats, with a particular focus on the diversity and visitation rates of floral visitors to the flowers of *Dracula lafleurii* Luer & Dalström with a few additional observations from *D. felix* (Luer) Luer.

Material and methods

Species and study sites.- Field studies were conducted during the rainy season (January to May) of 1999 and 2002 at Los Cedros Biological Reserve in northwestern Ecuador (00˚18.519'N, 78˚46.760W), in the buffer zone of the Cotacachi-Cayapas Ecological Reserve. The Los Cedros Reserve protects 6600 hectares of montane cloud forest from 1200 to 2200 m elevation. Due to the altitudinal gradient, a wide diversity of microhabitats can be found in this reserve where 14 *Dracula* species have been reported (Luer and Escobar 1994, www.tropicos.org). The local annual rainfall reaches 3225 mm with a pronounced dry period during the months of June and July (J. de Coux, pers. comm. 2002). Two *Dracula* species that occurred at different elevations and microhabitats within Los Cedros Biological Reserve were studied. Plants of *Dracula lafleurii* were abundant along the Los Cedros River, in the lower region of the reserve (from 1260 to 1300m). *Dracula felix* occurs at higher elevations, along the mountain ridges above the research facilities (1640-1800m).

Floral morphology.- The floral morphology and secretions of these flowers were examined. The flowers produced no measurable nectar, so to determine whether small amounts of sugar were nonetheless present, we rubbed Combur® test strips to 8 flowers from approximately 5 individual plants per species (it is not always possible to determine genetic individuals due to sympodial growth and close proximity) on the first day of anthesis.

Floral visitors.- All observations were performed between 0600 to 1700 hr, with 760 hr of observations being made. Detailed observations of insect activity were registered for 5 and 47 flowers of *Dracula lafleurii* and *D. felix*, respectively. Pollinia removal or deposition was observed with a 10x-magnifying lens and complemented with photographic documentation. Notes were taken on the behavior of the visiting flies used the terminology defined by Grimaldi (1987). After observations were completed, some visitors and pollinators were captured with an aspirator or small plastic bags and then preserved in 70% ethanol for identification. Herbarium specimens of the plants (*L. Endara 289-L. Endara 305*) were deposited in the herbarium of the Pontificia Universidad Católica del Ecuador (QCA). Fly specimens were identified by D. Grimaldi and deposited in the Division of Invertebrate Zoology of the American Museum of Natural History. Identifications of drosophilids required dissection of male genitalia and examination with compound microscopy.

Results

Flower morphology.- *Dracula felix* and *D. lafleurii* have different inflorescence orientation and floral presentation (Luer 1993). *Dracula felix* produces erect or ascending peduncles that bear a single cup-shaped flower (Fig. 1a). Unlike *D. felix,* but similar to the majority of the species in the genus, the flowers of *Dracula lafleurii* resemble an open umbrella and are borne from descending, spreading peduncles (Fig. 1b). When fully open, the flower faces downward and the sepaline tails (long tail-like extensions of the sepals, 8-9 cm long) expand outwards. The two species have different degrees of floral pubescence and color patterns (Fig 1a versus 1b). In both species, the petals are parallel to the column (gynoecium) and are small (3 mm long x 2 mm wide), oblong structures with the lamina containing central brown to purple spots, and a bivalvate, papillate apex, a diagnostic character of this genus (Luer 1993, see

FIGURE 1. A — *Dracula felix* showing mass flowering and cup-shaped flowers; B — *Dracula lafleurii* showing successive flowering and umbrella-like flowers; C — Glossy film on labellum of *D. lafleurii,* which is present only on the first day the flowers are open (anthesis); D — *Zygothrica* flies landing on sepaline tails of *D. lafleurii*; E — *Hirtodosophila* sp. (left) and *Zygothrica antedispar* (right) lapping the epichile of *D. laffleurii*; F — *Zygothrica paraldrichi* performing the "scissoring" wing display on a flower of D. *laffleurii*.

Fig. 2c). The column is a rigid structure of the same size or slightly longer than the petals (3 mm long x 1.5 mm wide excluding the column foot) and in both species it contains small raphide encrustations (intracellular crystals; Fig. 2a). The apex of the column is irregularly dentate and contains the anther

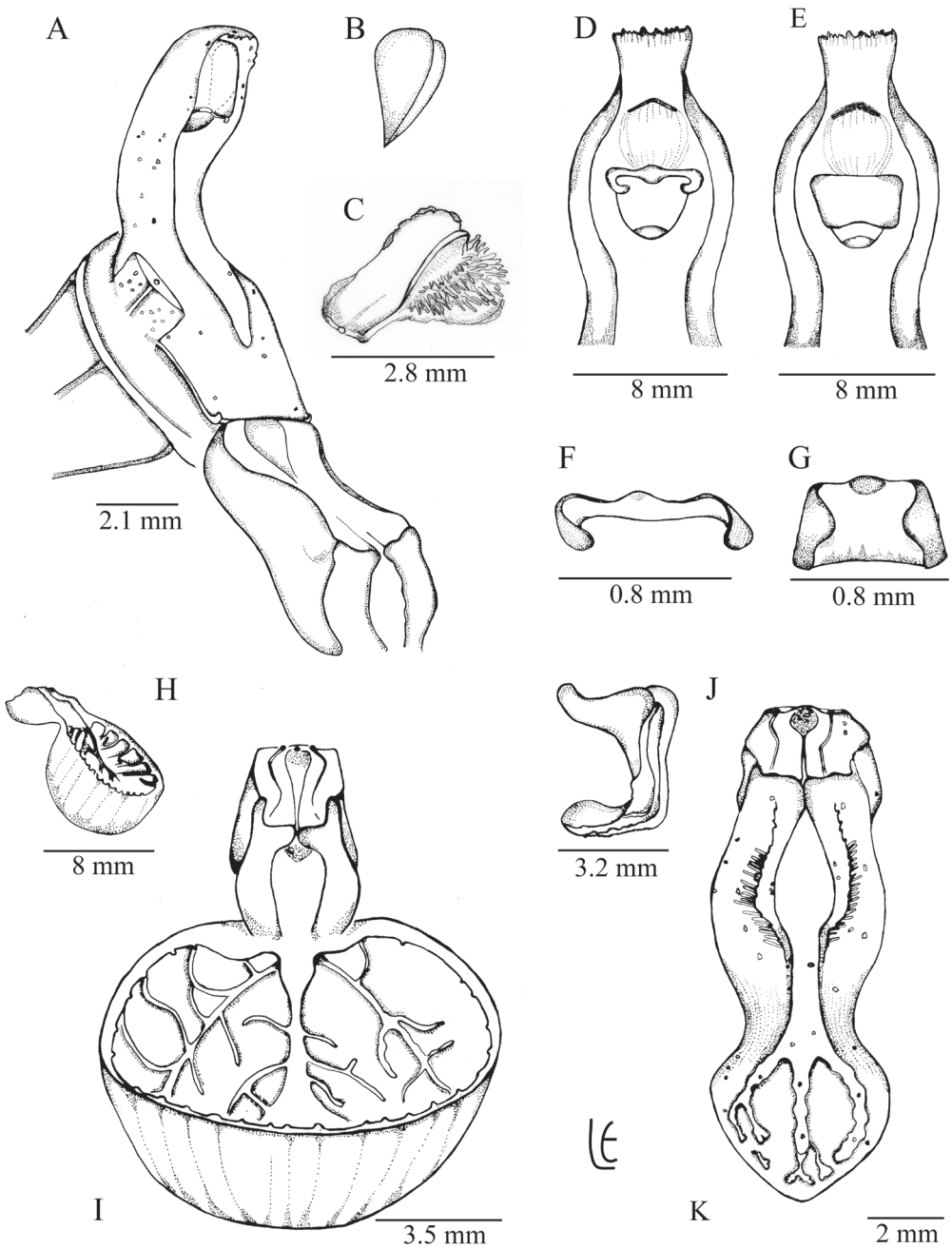

FIGURE 2. Reproductive organs of *Dracula lafleurii* (A-I) and *D. felix* (J-K); *Dracula laffleurii*: A — Column and hypochile with raphide crystals, petals and sepals have been removed; B — pollinia; C — bivalvate petal; D — ventral view of the column, rostellum in open position, pollinia removed; E — ventral view of the column, rostellum in closed position, pollinia removed; F — frontal view of the rostellum; G — ventral view of the rostellum; H — lateral view of the labellum; I — frontal view of the labellum; J — lateral view of the labellum of *Dracula felix* K — frontal view of the labellum of *D. felix* showing raphides. Illustrations by Lorena Endara.

bed with two waxy, subhemispherical pollinia (Fig. 2b), which are separated from the stigmatic cavity by a rostellar flap with incurved margins (Fig. 2d, e, f, g). The labellum is flexibly attached to the base of the column by membranous tissue of labellar origin, which provides elasticity and allows movement of the labellum (Fig. 2a). The labellum is divided in two sections: a basal, narrow portion (hypochile) and a distal, expanded, usually concave segment (epichile) with the appearance of the gills of an inverted mushroom. In both species, the hypochile is a complex structure that has a central cleft with sinuous lateral margins (Fig. 2h, i, j, k).

The epichiles of *Dracula lafleurii* and *D. felix* differ greatly. In *D. lafleurii* it is subglobose with a complex inner arrangement of lamellae that radiate from the hypochile and branch outwards (Fig. 2i). Its outer surface is smooth and is covered by a lustrous film on the first day of anthesis (Fig. 1c). The epichile of *D. felix* is pandurate, shallow and concave with a rather simple network of lamellae with small raphides (Fig. 2 k). The lustrous film that is present in *D. lafleurii* was not detected in *D. felix*. The column, petals, and labellum hypochile frame a small space, here designated as the columnar chamber. In *D. lafleurii*, the columnar chamber measures 2.5 x 1.5 x 3.4 mm, while *D. felix* measures 1.5 x 1.3 x 3 mm (height, width and depth respectively).

Flowering patterns and flower longevity.- The two orchid species have very different flowering patterns. Each *Dracula lafleurii* plant produces flowers in succession that are open for 11± 4.5 days (n=8). Each inflorescence produces three to six flowers per season (primarily December to late May). In contrast, each *D. felix* plant has a single, synchronous, massive flowering event with 50 or more flowers/plant/year (depending on size of plant), and the flowers are open for 10±3 days (n=40). The flowering period of *D. felix* varies between early January and late February, depending on the year, but within a year the mass flowering lasts only a couple of weeks. (In 1999 7-21 February; in 2002 1-15 January; in 2008 15-31 January, and in 2009 a few were flowering in the 4th week of December, but many more had buds). We did not find evidence for sugary floral rewards; Combur® strips laid on exudates had no reaction, indicating a lack of reducing sugars.

Floral visitors and their behavior.- Most visitors of *Dracula lafleurii* and *D. felix* were flies of the family Drosophilidae, and most of them were species of *Zygothrica* (Table 1). With the exception of specimens 10 (*Cladochaeta* sp.), 22 (*Drosophila* [*Sophophora*] sp.), and 27 and 29 (*Drosophila bromeliae* species group), all of the drosophilids in this study are largely mycophilous. No significant difference in fly sex ratios was documented, but differences were found in the composition of the guilds visiting the two species (Table 1). Visitors of *D. lafleurii* and *D. felix* behaved differently and are thus described separately below.

Dracula lafleurii.- The total number of fly visits/flower varied from four to 22 (n= 5 flowers), with the majority of visits (64%) occurring between 0900 and 1300 hr. The earliest visit was at 07:43 and the latest at 15:58. On the first day of anthesis no visits were recorded, which coincides with the period when the labellum had a lustrous appearance (Fig. 1c). Visitation started on the second day and was most intense during the third through fifth days of anthesis, with 85% of the recorded visits taking place on these three days (Fig. 4a). Visitation rates were 72 visits/5 flowers/55 hours = 0.26 visitors/flower/hour and the pollinia were removed from all five flowers. The flies landed either on the epichile, the inner surface of the sepals, or on the sepaline tails. Flies often perched on the sepaline tails, or they followed them toward the inner blade of the sepal and sometimes the epichile was reached (Fig. 1d). Landing was followed by resting, or by one of two activities: combing the wings with the hind legs, or repetitive lapping at the surface of the flower with their proboscis. The latter activity is the most commonly performed by visiting flies (Fig. 1e). We observed flower guarding and fidelity of flies to particular flowers. The flies spent a long time in the flowers, averaging 70.8 minutes per visit (range = <1-323 min). Visit duration depended on the day since the flower opened (ANOVA $F\ 2.19_{6,85}$, P=0.0510; Fig. 4b), with no visits occurring on the first and last (7th) days of observation.

Flies congregate on the inner surface of the sepaline blades or on the inner and outer portions of the labellum's epichile. During periods of high visitation (7 to 18 flies simultaneously) an interesting display of interactions occurred among visitors. Flies posed on the sepals or the epichile, or advancing towards

Table 1. Visitors to flowers of *Dracula felix* and *D. lafleurii*. Specimens that removed pollinia are marked with an asterisk (*), specimens that deposited pollinia are marked with a double asterisk (**), n/d indicates no data. Abbreviations: aff.=affinity, sp.=species, n. sp.=new species.

Dracula felix

Family	**Visitors**	♀	♂
Drosophilidae	*Cladochaeta* sp.	1	
	Zygothrica sp. 1 aff. *candens-ptilialis*		1
	Zygothrica sp. 4 aff. *spiculirostris*, n. sp.		2
	Zygothrica sp. 5 aff. *spiculirostris*, n. sp. *,**	1	1*,**
Sphaeroceridae	*Pterogramma* sp.	n/d	n/d
Staphylinidae	Subfm. Aleocharinae	n/d	n/d

Dracula lafleurii

Family	**Visitors**	♀	♂
Drosophilidae	*Drosophila* sp. (*bromeliae* group)	1	1
	Drosophila sp. (subgenus *Sophophora*)		1
	Hirtodrosophila sp. 1		1
	Hirtodrosophila sp. 2 near *levigata-glabrifrons*	1	1
	Zygothrica antedispar	3	3*
	Zygothrica paraldrichi	2	1
	Zygothrica sp.3 near *bilinefilia*	2	2
	Zygothrica sp. 7 *vittatifrons* group	3	
	Zygothrica sp. 8 *vittatifrons* group	1**	
	Zygothrica sp. 9 *vittatifrons* group	1*	
	Zygothrica sp. 10 *vittatifrons* group	1*	
Lauxaniidae	*Minettia* sp.	n/d	n/d

it, engaged in semaphoring (slow, repetitive, side-to-side movements made with the wings when they are extended 45˚ from each other and raised 45˚ above the abdomen), flicking (wings extended slowly and alternately more than 90˚ from their resting position over the abdomen), scissoring (wings simultaneously and rapidly extended about 90˚ to the longitudinal axis of the body) and vibrating wing movements (Figs. 1f, 3a). *Zygothrica antedispar* advanced towards the labellum performing a different wing movement than those aforementioned. These flies lift the left wing followed by both wings and combine this with repeated lapping at the surface of the flowers. Foreleg slashing and head butting were less frequently displayed. *Hirtodrosophila* and the *Drosophila bromeliae* group visitors especially displayed these aggressive behaviors, displacing other flies in the epichile or the ones entering the columnar chamber. Some individuals of *Zygothrica* remained on the upper proximal surface of the labellum during their visit.

Dracula felix.- The massive flower production of this species, the erratic behavior of the small flies, and their superficial similarity to each other made it impossible to record visit duration for individual insect species, so we report only the number of visits. Normally, flies landed on the internal blade of the dorsal sepal and moved rapidly into the flower, lapping and sucking the inner surface of the sepals and eventually reaching the labellum. Visitation rates were high: 70 visits/47 flowers/1.25 hrs = 1.19 per flower per hour. Like in *D. lafleurii*, we observed flower guarding and fidelity of flies to particular flowers (Fig. 3b), but this was less pronounced on *D. felix*. Unlike in *D. lafleurii*, we never observed mating in the flowers of *D. felix*.

In addition to flies, web-building spiders (Fig. 3c) and staphylinid beetles of the subfamily Aleocharinae were occasionally observed in *Dracula* flowers.

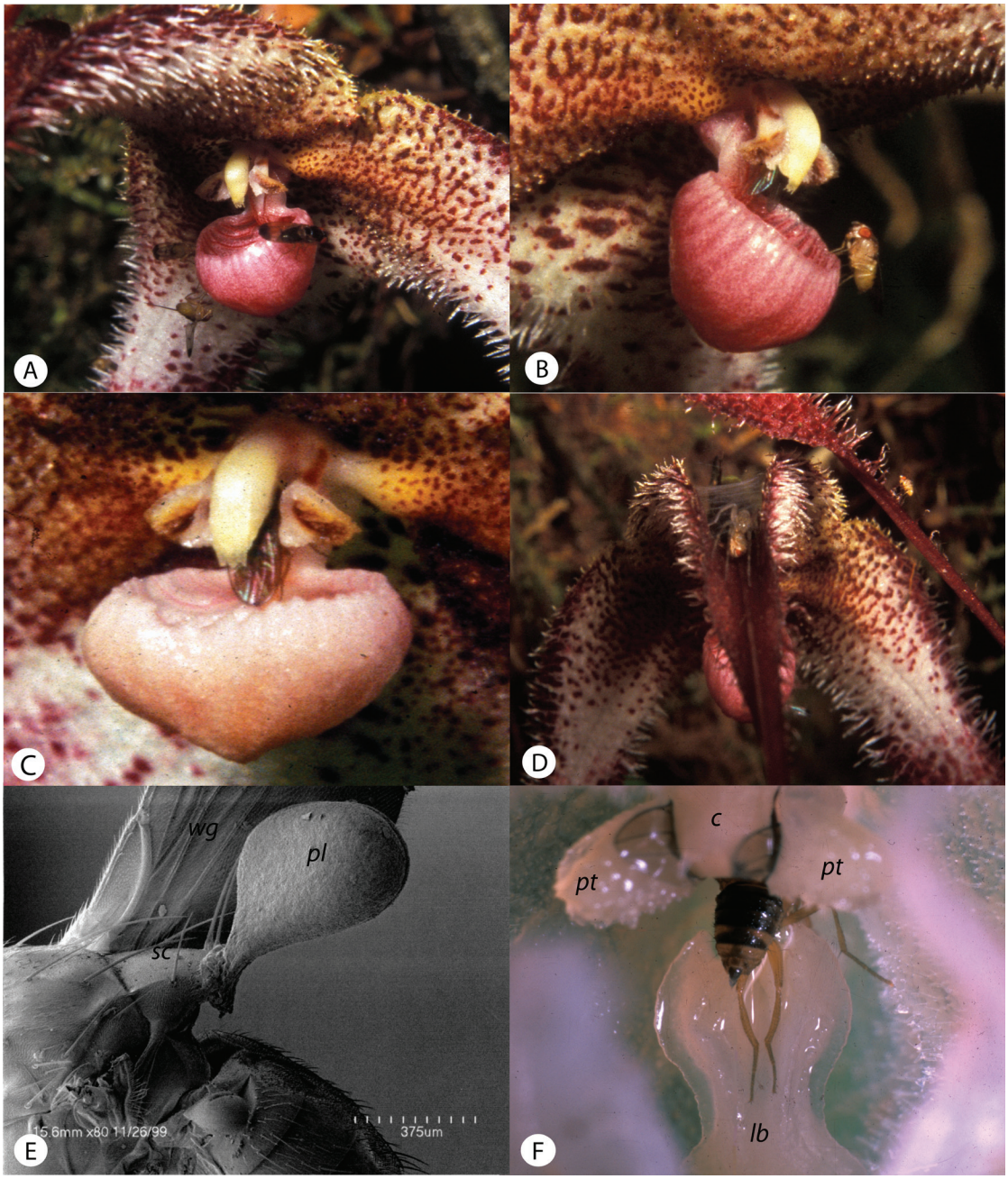

Figure 3. A — Lapping and semaphoring behavior displayed by visitors of *Dracula lafleurii* and territorial behavior on labellum; B — *Zygothrica* territorial behavior on *D. laffleurii* lip; C — A spider capturing flies on the dorsal sepal of *D. lafleurii*; D — *Zygothrica* sp. entering the columnar chamber of *D. lafleurii;* E — SEM of the pollinia of *D. lafleurii* attached to the scutellum of *Zygothrica antedispar*; *wg:* wing, *pl:* pollinia, *sc:* scutellum; F — *Zygothrica* sp. 5 (aff. *spiculirostris*) trapped in columnar chamber of *Dracula felix*; *c*: column, *pt*: petal, *lb*: labellum.

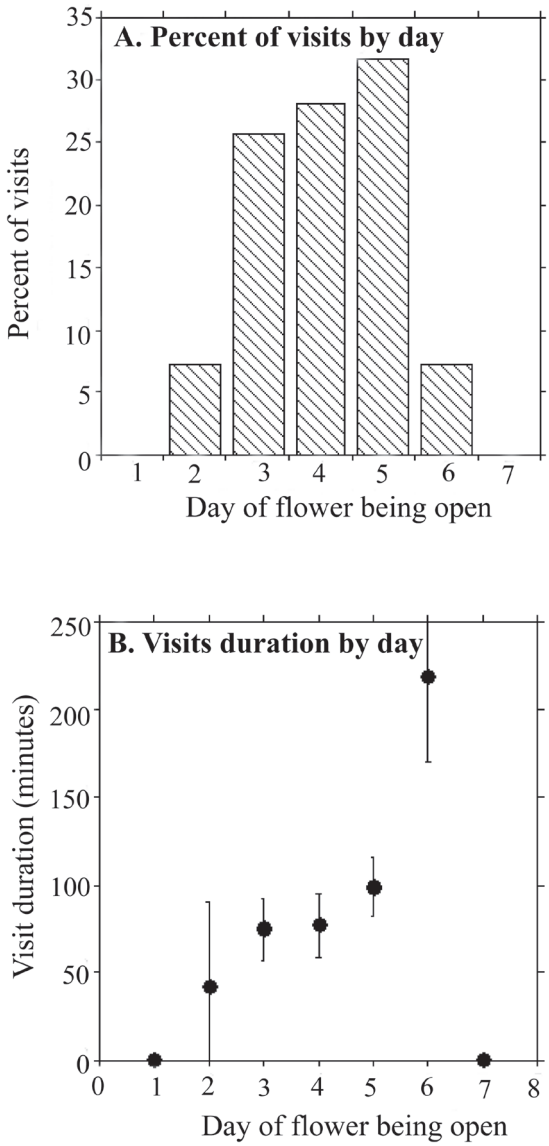

FIGURE 4. Summary of visitation by flying insects to *D. lafleurii* for each day the flowers were open (n=5 flowers, 72 visitors). A — percentage of total visits by day; B — duration of visits by day (mean ± s.e.).

Pollination mechanism

Dracula lafleurii.- Flies that lap at the inner surface of the labellum epichile are guided by lamellae that radiate from the hypochile. The wings lie over the abdomen and touch the apex of the column; the fly enters into the columnar chamber (Fig. 3d) and advances towards the base of the hypochile while constantly lapping the surface. The hind legs reach a slope on the margins of the distal portion of the hypochile and the fly makes repeated attempts to advance towards the base of the hypochile, but the mid and hind legs slide on this slope, slightly pushing the labellum away from the column. The thorax of the fly is then trapped by the incurved margins of the claw-like rostellar flap (Fig. 2f, g) and attempts of the fly to move further or escape are unsuccessful. The fly's movements are interrupted by short pauses in which the legs stop moving, the labellum returns to its normal position, and the fly is gently pressed against the column. The ventral part of the fly's body rests on the central cleft of the hypochile and the thorax and abdomen form an angle that leaves the scutellum free. After alternating periods of activity and pause, the scutellum becomes coated with a sticky fluid secreted by the rostellum, which then sticks to the caudicles of the pollinia (Fig. 3e). The rostellum remains partially attached to the fly as the fly backs out and pulls the pollinia out of the anther bed. Simultaneously, the rostellum is pulled forward and covers the stigmatic cavity (Fig. 2d, e). The loaded fly is released from the rostellum, the anther cap falls and the fly immediately leaves the columnar chamber. The duration of the process from initial trapping to pollinia removal varied from 47 to 65 minutes and was performed by three species of *Zygothrica*: *Z. antedispar* and *Zygothrica* spp. 9 and 10. Once liberated, flies loaded with pollinia fell into the epichile or flew to the sepals, sepaline tails or to other flowers, but no case did flies remain for extended periods in the same flower. Curiously, flies loaded with pollinia flew to other flowers and immediately tried to enter the columnar chamber of other *D. lafleurii* flowers. No deposition of pollinia in the stigmatic cavity was observed in this species. One fly (*Zygothrica* sp. 8) was found trapped in the columnar cavity probably after depositing pollinia.

Dracula felix.- The pollination process resembles that of *D. lafleurii*, with the main difference being that the flies visiting and pollinating these smaller flowers enter directly into the columnar chamber. *Zygothrica* spp. 1, 4, 5, and 8 removed pollinia, but the only pollinia deposition observed was conducted by *Zygothrica* cf. *antedispar*. *Zygothrica* spp. 4 and 5 are undescribed

species closely related to *Z. spiculirostris*, all of which have a distinctive, long, fine proboscis. When a fly loaded with pollinia enters the columnar chamber, the pollinia lodge into the sticky stigmatic cavity and the fly is trapped again. Flies will then spread their wings 45˚ apart and these become pressed against the column by the inner surface of the bivalvate petals. One observed fly was liberated after the pollinia deposition, but it was common to find dead flies trapped in flowers with developing capsules in this species (Fig. 3f).

Post-pollinia removal and post pollination effects

After the pollinia have been removed in *Dracula lafleurii* and *D. felix* the rostellum moves partially forward, covering the stigmatic cavity. The rostellum returns to its original position a few minutes after the pollinia have been removed. After the deposition of pollinia, the stigmatic cavity engulfs the pollen masses and the column starts to swell. After the 7th day of being open, or after pollinia removal, flowers of *D. lafleurii* become darker at the junction of the lateral and dorsal sepals. The mobility of the labellum and its relative position to the column loosen and the labellum separates from the column. After pollinia removal or the 5th day of the flowers being open, the fragrance stops being mushroom-like and becomes sweet instead.

Discussion

We have shown that the flowers are attractive to mycophilous flies, and that these insects pollinate them. Several species of *Zygothrica* and the closely related drosophilid genus *Hirtodrosophila* are attracted to these orchids (Courtney *et al*. 1990, Grimaldi 1990). Both genera are well known to congregate at fungi, particularly at white ones. A number of the flies we found were undescribed. This genus is large, and primarily Neotropical with approximately 120 described species and perhaps an additional 100 as yet undescribed species (Grimaldi 1987); it is only partially revised taxonomically.

We observed that some *Zygothrica* species aggressively defend their territory from other males on the sepals of a *Dracula* flower, while others defend their territory on top of the labellum, analogous to the pilei of mushrooms in the same way that some *Zygothrica* partition their territories on mushrooms (Burla 1990). In contrast, other non-*Zygothrica* visitors approached any small dark insect silhouetted against the white surface and displayed various wing movements regardless of conspecificity. The aggregation and courtship behavior triggered by small dark forms suggests that the small dots on most *Dracula* sepals may serve as a visual attractant for these mycophilous flies. Moreover, the pigmented wings of *Z. paraldrichi* (Fig. 1f, showing scissoring movement) and *Z. antedispar* bear remarkable resemblance to the petals of most *Dracula* species, leading us to hypothesize that the petals could trigger mating behavior in the flies and prompt them to approach the columnar chamber. While we observed courtship and mating in the flowers, no eggs were discovered in the flowers.

Fragrances are likely to be important for attracting the flies that visit *Dracula*. While *Dracula felix* has little human-observable fragrance, *D. lafleurii* smells mushroom-like and mushroom fragrance compounds have been isolated from other *Dracula* species (Kaiser 2006). Flies approached *D. lafleurii* flowers with a seemingly scent-oriented flight (directly, in a spiral or in a zigzag pattern), and some hovered near the labellum before landing on it. Other visitors hovered at 5 cm or less in front of the flower before landing on the sepals. To understand the links between fragrance, mimicry and pollinator behavior, future work with *Dracula* fragrances should document the extent of natural variation and selection acting on it.

The number and diversity of *Zygothrica* flies coming to *Dracula* flowers was remarkable, with at least five species of drosophilids from the present study being new to science. *Zygothrica* flies were the only ones that carried pollinia and are the best suited as pollinators of the insect visitors observed. For example, it is unlikely that *Cladochaeta* and *Hirtodrosophila* visitors, due to their smaller size, would be able to remove or deposit pollinia. However, it is interesting that two of these three fly genera are primarily mycophagous (Grimaldi & Nguyen 1999). The larvae of *Minnetia* and *Pterogramma* are saprophagous and those of *Cladochaeta* are mostly parasites of spittlebugs or they feed within flowers (Grimaldi & Nguyen 1999). In the case of *Minnetia,* large quantities of fungal spores and hyphae are usually present in their guts (Broadhead 1984).

While a number of species of *Zygothrica* visited each species of *Dracula*, the two orchids did not share visitors (Table 1). This is not too surprising given that these particular orchids mostly grow in different habitats (mountain ridges for *D. felix* and river valleys for *D. lafleurii),* and the flowers are very different in overall size and morphology (see figures). However, hybridization has been reported for other *Dracula* species growing in *ex situ* (Luer 1989) and several specimens with unclear species boundaries and putative natural hybrids have been collected in disturbed sites (Endara pers. obs.). Given our data showing that many species of *Zygothrica* flies can remove pollinia from *Dracula* orchids, and studies that have shown little specificity of mycophagous flies to particular mushrooms (Courtney *et al.* 1990), rampant hybridization would seem likely.

An important question remains: What is the nature of the film that forms on the labellum the first day the flowers are open? Do these flowers provide fluid nutrition through the production of putrefying or deliquescing fluid? Repetitive lapping by *Zygothrica* and other flies suggest that the flies are grazing on some sort of liquid film. The lack of sugar indicated by the tests could have resulted from several factors, including: (1) not testing on the proper day (we only tested on the first day the flowers were open, though that was also the only time we saw anything that could be interpreted as a liquid), (2) low concentrations of sugars, (3) tests that are not sensitive to the sugars present in this film or, (4) a film that is composed mostly of lipids, proteins, or amino acids that could serve as growth medium to yeast that is part of mycophilus flies (Labandeira, 2005). Alternatively, the lapping behavior is reminiscent of the same behavior exhibited by *Drosophila* males during courtship (Sturtevant 1915, Howard and Blomquist 1982; Ferveur 2007).

Synthesis and Conclusions.- Similar to mushrooms, *Dracula* flowers serve as shelters and rendezvous sites for flies during the prolonged rainy season, a potential explanation for the tendency of extended visits by these flies (Fig. 4b). Despite the violent disturbances caused to the flowers by droplets of water, the spreading sepals create a roof-like structure that protects the flower's reproductive organs and insect visitors. The incurved margins of the rostellar flap and the base of the petals, so crucial in pollination, also play an important role in preventing the expulsion of the pollinator from the flower during rainy periods. The incurved margins of the rostellar flap of *Dracula* flowers were not mentioned in the original species descriptions, which is not surprising since these structures are minute. To our knowledge, the only previous account of this structure an illustration of the column of *Dracula bella (formerly Masdevallia bella*, Woolward 1896), which shows a frontal view of the rostellum's incurved margins. The importance of this structure would not have been noticed until their role in the pollination mechanism was observed.

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CALLUS GROWTH AND PLANT REGENERATION IN *LAELIA SPECIOSA* (ORCHIDACEAE)

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Resumen. *Laelia speciosa* es una orquídea epífita amenazada, endémica de México. Se considera que la reproducción asexual *in vitro* puede ser una de las acciones para contrarrestar la extracción masiva de individuos de sus poblaciones naturales, al ofrecer plantas de calidad en el mercado. El crecimiento y diferenciación de callo derivado de explantes de hojas de *L. speciosa* fueron investigados en el medio de Murashige y Skoog (MS) con 30 g l^{-1} de sacarosa y cinco concentraciones (0.0, 0.25, 0.5, 1.0, y 2.5 g l^{-1}) de ácido naftalenacético (ANA) en combinación con benziladenina (BA, 0.0, 0.25, 0.5, 1.0, y 2.5 g l^{-1}). Explantes de hojas de plántulas cultivadas *in vitro* fueron efectivos para la formación de callo en el medio MS suplementado con 2.5 mg l^{-1} BA, mientras que explantes de hojas maduras no respondieron. El diámetro del callo en promedio por explante de hoja fue de 1.25 cm después de ocho semanas de cultivo. El mejor desarrollo de PLBs se reportó en el medio MS suplementado con 2.5 mg l^{-1} ANA and 1 mg l^{-1} BA. La formación de plántulas se logró exitosamente en MS suplementado con 0.5 mg l^{-1} de ANA y 0.1 mg l^{-1} de GA_3. Dichas plántulas fueron aclimatadas exitosamente en invernadero con una tasa de supervivencia de 70%.

Abstract. *Laelia speciosa* is an endangered epiphytic orchid, endemic to México. It is thought that the asexual reproduction *in vitro* could be one of the actions to counteract the massive extraction of individuals from their natural populations. The growth and differentiation of callus tissues derived from leaf explants of *L. speciosa* were investigated in Murashige and Skoog medium (MS) with 30 g l^{-1} sucrose and five concentrations (0.0, 0.25, 0.5, 1.0, and 2.5 g l^{-1}) of naphthaleneacetic acid (NAA) with benzyladenine (BA) (0.0, 0.25, 0.5, 1.0, and 2.5 g l^{-1}). Leaf explants from *in vitro* plantlets formed callus tissue on MS medium supplemented with 2.5 mg l^{-1} BA while mature leaves did not respond. Diameter of the callus tissues averaged 1.25 cm after eight weeks of culture. PLBs development was achieved on MS medium supplemented with 2.5 mg l^{-1} NAA and 1 mg l^{-1} BA. The formation of plantlets was successfully obtained in MS supplemented with 0.5 mg l^{-1} of NAA and 0.1 mg l^{-1} of gibberellic acid (GA_3). Obtained plantlets were successfully acclimatized in a greenhouse with a survival rate of 70%.

Key Words*: Laelia speciosa*, endangered orchid, callus, plant regeneration.

Abbreviations: BA: benzyladenine; GA3: Gibberellic acid; MS: Murashige and Skoog medium; NAA, α-naphthaleneacetic acid; PLBs: Protocorm-like bodies

Introduction. It is thought that asexual reproduction is a valuable tool in the massive propagation of many orchids (Rao 1977, Arditti & Ernst 1993). Several species, varieties and hybrids have been asexually micropropagated, such as *Acampe praemorsa, Cattleya* spp., *Cymbidium* spp., *Dendrobium* spp., *Epidendrum radicans*, *Renanthera imschootiana, Laelia* spp., *Phalaenopsis* spp., *Doritaenopsis* spp.,

among others. Efficient micropropagation methods to obtain many plants for commercial purposes or for their conservation have been reported (Seeni & Latha 1992, Nayak *et al.* 1997ab, Chen *et al.* 2002, Park *et al.* 2003, Roy & Banerjee 2003, Santos-Hernández *et al.* 2005, Lavrentyeva & Ivannikov 2007).

Laelia speciosa (HBK) Schlechter, is commonly known as "flor de mayo" (flower of May); "flor grande" (big flower); "flor de corpus" or "corpo" (flower of the Day of the Holy Corpse); "tlacuxóchitl", "deantza", "itzámahua" (Purépecha) (Halbinger & Soto 1997, Ávila-Díaz pers. obs.). It is an epiphytic orchid endemic to the central part of Mexico, including the oak forests of the Sierra Madre Occidental, of the Sierra Madre Oriental, the southern part of the Altiplanicie Mexicana (Mexican Plateau), and the Eje Neovolcánico Transversal (Trans-Mexican Volcanic Belt) (Halbinger & Soto 1997, Ávila-Díaz & Oyama 2007). It blooms from April to June, and produces an inflorescence with 1 to 2 large, pale or dark pink-lilac to purplish flowers. The plants of this species are grown in home gardens and they are also used in religious ceremonies as well as to extract mucilage from pseudobulbs to make a paste with the pith of corn, which is used for making religious figures (Miranda 1997, Hágsater *et al.* 2005). Thousands of plants of *L. speciosa* are usually harvested from their natural habitats, which has caused local extinctions. *Laelia speciosa* is listed as endangered species by official Mexican law (NOM-059-ECOL) (Salazar-Chávez 1996, Halbinger & Soto 1997, Ávila-Díaz & Oyama 2007).

Therefore, it is important to develop a system for *in vitro* asexual propagation of *L. speciosa* and to obtain high-quality plants that could be an alternative for commercialization and, in this way, to diminish the pressure that exists over their natural populations.

A successful protocol for *in vitro* propagation of *L. speciosa* by seed germination has been already developed with conservation purposes (Avila-Díaz *et al.* 2009). However, plantlet regeneration from vegetative explants has not been reported for this species. Therefore, this study aimed induction of calluses and regeneration of plantlets derived from them through PLBs proliferation.

This work is part of a multidisciplinary project in which diverse aspects of conservation biology of this species have been studied. It also contemplates the work done with local human communities. It is our hope that the results from this investigation can be applied to establish a sustainable management of this highly-appreciated orchid.

Material and methods

Callus induction. — Leaf segments of 6 month-old *in vitro Laelia speciosa* plantlets obtained by seed culture (Ávila-Díaz *et al.* 2009), were used as explants. Also, leaf explants from mature plants were tested, which were surface-disinfected with 15% Neutral Plus Hyclin (concentrated liquid detergent) (HYCEL of Mexico, Mexico D.F.) for 5 min, followed by 70% ethanol for 5 min, 3% hydrogen peroxide for 5 min, 1.2% sodium hypochlorite for 15–20 min, and then rinsed three times with sterile-distilled water in a laminar flow cabinet.

Leaf segments of 0.5 cm in length and 0.3 to 0.5 cm in width, with the under surface of the leaf placed in contact with the culture medium, were cultured on MS basal medium (Murashige & Skoog 1962) supplemented with NAA (0.25, 0.5, 1.0, and 2.5 g l^{-1}) in combination with BA (0.25, 0.5, 1.0, and 2.5 g l^{-1}) using MS without plant growth regulators (PGRs) as control treatment. Each treatment consisted of five 120 ml-glass jars, and each of them contained 25 ml of the medium. Five leaf explants were placed in each jar. They were closed with clear plastic caps of Sigma, Co. St. Louis, Missouri, USA.

Microscopic observations were carried out after 60 days of culture with a SMZ800 Nikon stereo microscope (México, D.F.). The size of the diameter of callus was registered.

Data were analyzed using one way ANOVA and HSD Tukey Post Hoc test. The SPSS 15.0 program for Windows (SPSS Inc. Chicago, IL, USA) was used for data analysis.

PLBs proliferation. — Eight week-old callus sections grown on the optimal medium for callus induction were segmented into approximately 0.5 cm diameter segments. Five callus segments were placed on 10 ml of culture medium poured into 45 mm diameter disposable Petri dishes with the same combinations of NAA/BA than in the previous experiment. Five replicates were established per treatment. After

Table 1. Callus growth (diameter, cm) in leaf explants of *Laelia speciosa* after 60 days of culture.

		NAA (mg l^{-1})				
		0	**0.25**	**0.5**	**1**	**2.5**
BA (mg l-1)	**0**	0 ± 0 ^{e}	0.1 ± 0.01 ^{e}	0 ± 0 ^{e}	0 ± 0 ^{e}	0 ± 0 ^{e}
	0.25	0.25 ± 0.02 ^{d}	0 ± 0 ^{e}	0 ± 0 ^{e}	0.49 ± 0.03 ^{c}	0 ± ^{e} 0
	0.5	0.51 ± 0.04 ^{c}	0.46 ± 0.03 ^{c}	0.55 ± 0.03 ^{c}	0 ± 0 ^{e}	0 ± 0 ^{e}
	1	0.48 ± 0.04 ^{c}	0.52 ± 0.03 c ^{c}	0 ± 0 ^{e}	0 ± 0 ^{e}	0 ± 0 ^{e}
	2.5	1.25 ± 0.06 ^{a*}	0.75 ± 0.02 ^{b}	0.50 ± 0.03 ^{c}	0 ± 0 ^{e}	0 ± 0 ^{e}

Means with different letters are significantly different at $p = 0.000$

eight weeks, the average number of PLBs per callus segment was estimated. Moreover, the mean length was recorded. In addition, the overall appearance of the cultures was registered. Analysis of data for PLBs proliferation was done by one way ANOVA and HSD Tukey Post Hoc test. The SPSS 15.0 program for Windows (SPSS Inc. Chicago, IL, USA) was used for all data analysis.

Plantlet development. — PLBs were further developed on MS medium supplemented with 0.1 mg l^{-1} GA_3 and 0.5 mg l^{-1} NAA. This nutrient medium was selected from previous experiments (Avila-Díaz *et al.* 2009).

General culture conditions. — All micropropagation and plantlet development media were based on the MS formulation with 3% sucrose and 0.7% BIOXON bacteriological agar (Becton, Dickinson of Mexico, Cuautitlan Izcalli, Mexico). Growth regulators were added in different concentrations and combinations before autoclaving. The pH of the media was adjusted to 5.7±0.1 before agar was added. Media were autoclaved for 20 minutes at 121°C. All cultures were kept in a growth chamber at 25±1°C under a 16-hour photoperiod of 36 µmol m^{-2} s^{-1} provided by fluorescent tubes (60W).

Acclimatization. – Plantlets of approximately 5 cm in length, obtained on the MS medium supplemented with 0.5 mg l^{-1} NAA and 0.1 mg l^{-1} of GA_3, were transplanted in wet tezontle (volcanic gravel) - oak bark (1:1) into plastic flats, and were covered with a clear plastic lid. Lids were gradually opened every 2 days until they were completely removed after 15 days as was recommended by Ávila-Díaz *et al.* (2009). Plantlets were watering each 8 days and survival was recorded after 30 days.

Results

Callus induction. — The leaf explants from mature plants did not show any growth when cultured *in vitro* and finally turned necrotic, while those obtained from plantlets growing *in vitro* formed callus. Significant differences among the media tested were observed at 60 days following culture ($F = 178.81$, $df = 24$, $p = 0.000$). Tissues of *L. speciosa* incubated on media with NAA alone (0.25 mg l^{-1}) and with NAA/BA (1.0/ 0.25 mg l^{-1}), developed callus (Table 1) although the treatment with 2.5 mg l^{-1} of BA without NAA carried the best growth of *L. speciosa* callus (1.25 cm-diameter and the best quality with light-green color) (Fig. 1A). This treatment was significantly higher than all other investigated. Low dosis (0.25 mg l^{-1}) of NAA with 2.5 mg l^{-1} of BA was the second best treatment for callus growth (Table 1).

PLBs proliferation. — Induction of *L. speciosa* PLBs showed significant differences among the media tested ($F = 64.11$, $df = 24$, $p = 0.000$). Treatments that generated significantly higher number of PLBs were MS medium with 2.5 mg l^{-1} NAA with 1.0 mg l^{-1} of BA, MS medium with 2.5 mg l^{-1} of BA, and 0.5 mg l^{-1} NAA with 0.5 mg l^{-1} BA 60 days following culture (Fig. 1B, Fig. 2). PLBs grown on 2.5 mg l^{-1} NAA /1.0 mg l^{-1} BA showed longer mean length (0.7 mm) than the 2.5 mg l^{-1} BA (0.4 mm) and 0.5 mg l^{-1} NAA with 0.5 mg v BA (0.5 mm) treatments, also on 2.5 mg l^{-1} NAA /1.0 mg l^{-1} BA medium the development of one or two roots of up to 2 cm long with velamen was obtained (Fig. 1C), whereas the other media did not induced any root.

Plantlet development. — PLBs developed successfully

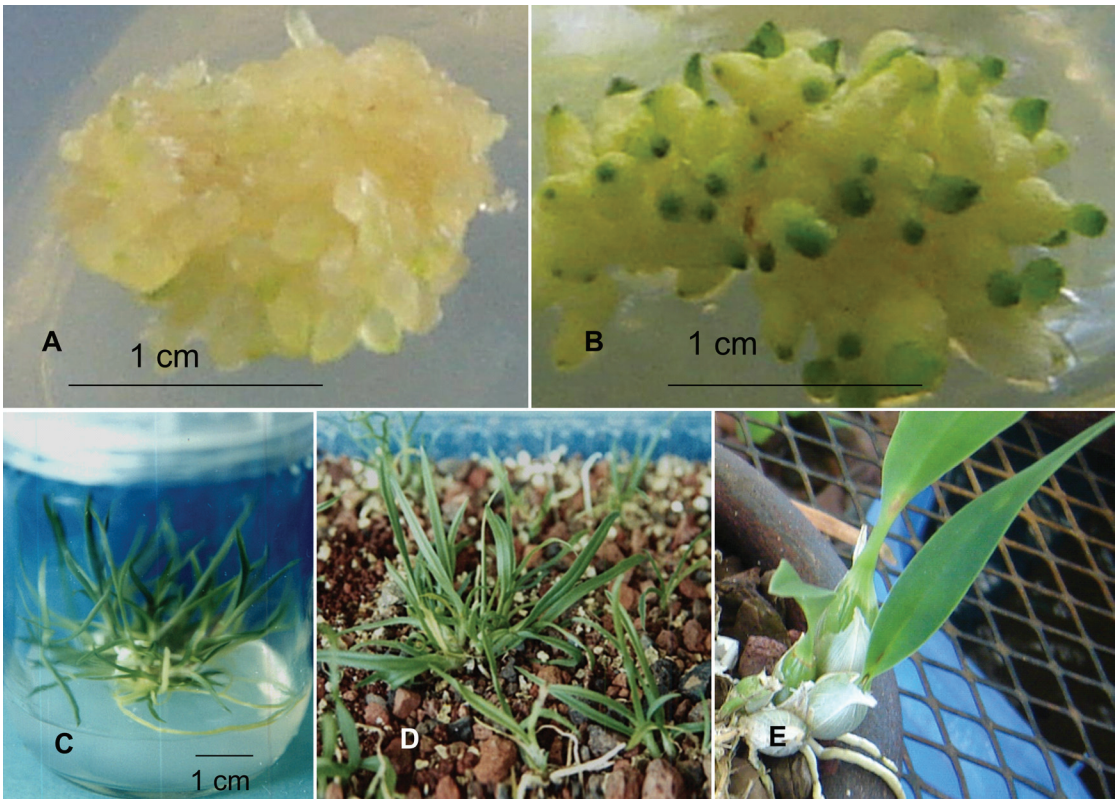

FIGURE 1. A — Callus formation in *Laelia speciosa* on MS media with 2.5 mg l^{-1} of BA. B — Proliferation of PLBs protocorm-like bodies on MS medium supplemented with 2.5 mg l^{-1} NAA and 1 mg l^{-1} BA. C — Plantlets with roots subcultured on MS supplemented with 0.5 mg l^{-1} of NAA and 0.1 mg l^{-1} of GA3. D — Plantlets acclimatized in greenhouse for 30 days. E — Three years old plantlets to be used for hand crafts.

to plantlet on the selected nutrient medium (Avila-Díaz *et al.* 2009). When they reached 3 cm in height they were transplanted to the greenhouse for their acclimatization.

Acclimatization. — Survival of plantlets of *L. speciosa* transferred in tezontle-oak bark substrate was 70% in the greenhouse (Fig. 1D, 1E).

Discussion

According to the results of this work, the use of *L. speciosa* leaf segments from *in vitro* grown plantlets as explants can be considered effective for the asexual propagation of this species. Other micropropagation studies in epiphytic orchids have shown that different sections of the plants can be used as explants, such as: flower stalk sections, buds, leaf primordium, tip and basal part of the leaves, shoot-tips, root tips (Arditti *et al.* 1972, Seeni & Latha 1992, Nayak *et al.* 1997a, 1997b, Chen *et al.* 2002, Park *et al.* 2003, Roy & Banerjee 2003, Santos-Hernández *et al.* 2005, Lavrentyeva & Ivannikov 2007). In general, it has been reported that the young tissues are more adequate than mature ones for the induction of PLBs or shoots (Seeni & Latha 1992, Murthy & Pyati, 2001). In many cases, such as in our experiments, explants from *in vitro* cultures have given successful results (Nayak *et al*. 1997a, Murthy & Pyati, 2001, Chen *et al.* 2002, Park *et al.* 2003, Salazar & Mata 2003, Condemarín-Montealegre *et al.* 2007, Lavrentyeva & Ivannikov 2007).

The induction of callus in *L. speciosa* on MS medium supplemented with NAA resembles the results of Avila-Díaz *et al.* (2009), using complete seedlings grown *in vitro* as explants; nevertheless, in this particular investigation, we obtained higher induction

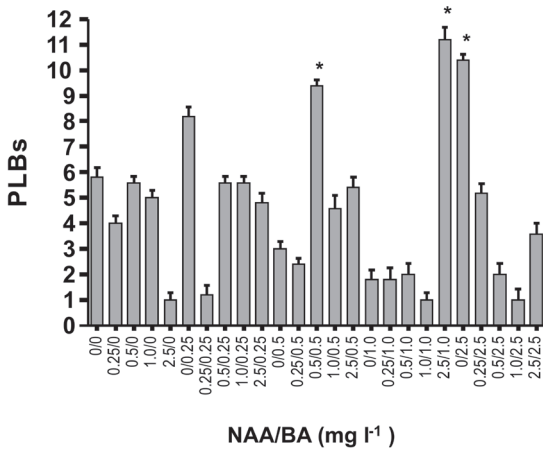

Figure 2. Mean number of PLBs after 60 days of subculture of leaf explants on media with NAA and BA. Treatments that generated significantly higher number of PLBs are marked with *.

rates when BA was added to the MS media using plantlet's leaves as explants. The induction of callus in *L. speciosa* with high concentrations of BA (2.5 mg l^{-1}), whether alone or in combination with NAA (0.25 mg l^{-1}), is similar to what has been reported for other orchid species; the callus induction is favored by the addition of cytokinins along or in combination with auxins as in the case of *Dendrobium fimbriatum*, in which optimum callusing was recorded in the presence of 1.0 mg l^{-1} BAP and 0.5 mg l^{-1} NAA (Roy & Banerjee 2003). In *Epidendrum radicans*, small transparent tissues enlarged and developed calluses when cultured with thidiazuron (TDZ) under light (Chen *et al.* 2002).

The cytokinin and auxin balance is also important in PLBs formation. A concentration of 2.5 mg l^{-1} NAA and 1 mg l^{-1} BA induced the highest formation of the largest PLBs in *L. speciosa*. In many orchids, PLB or shoot induction has been accomplished with cytokinins alone or in combination with auxins. The response to different concentrations is variable, depending on the species. For example, in *Epidendrum radicans* homogenized PLB tissues produced by blending were used as explant to test the effects of four cytokinins. The best response on number of PLBs per tube was found on a basal medium supplemented with 1 mg l^{-1} BA (Chen *et al.* 2002). However, in *Acampe praemorsa* shoot buds were induced on MS medium supplemented with 1 mg l^{-1} TDZ, while shoot elongation and leaf expansion were promoted with 0.5 mg l^{-1} BA and 2.0 mg l^{-1} NAA (Nayak *et al*. 1997a). On the other hand, in *Aerides maculosum*, *Mormodes tuxtlensis* and *Cuitlauzina pendula*, PLBs or shoots were inducted with BA alone (Murthy & Pyati 2001, Salazar & Mata 2003) and in *Lycaste skinneri* with NAA alone (Salazar & Mata 2003).

The plantlet survival rate during acclimatization (70%) is close to that reported by Ávila *et al*. (2009) for *L. speciosa* seedlings cultivated *in vitro* (77.5%). More investigation is recommended about acclimatization of this species to increase its survival.

The method of asexual propagation developed in this study for *L. speciosa is* efficient. 28 plants can be obtained from each single explant in 10 to 12 months and if the callus is subcultured, it is possible to obtain much more individuals. This is considered useful for an abundant production of orchids, which can be used for commercialization of ornamental plants or for the elaboration of arts and crafts.

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ORCHID ITINERARIES OF AUGUSTUS R. ENDRÉS IN CENTRAL AMERICA: A BIOGRAPHIC AND GEOGRAPHIC SKETCH

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Abstract. A.R. Endrés, as he was known until recent research revealed most of his relevant biographical data, was the most important orchid collector to visit Costa Rica. Besides collecting the type specimens for some one hundred new orchid species, he discovered, described and illustrated thousands of orchid plants, most of which remained still undescribed during his life time. One of the outstanding aspects of the collections made by Endrés in just a few years in the post-colonial Costa Rica of the Nineteenth century is his impressive knowledge of the country, in terms of geographical coverage, which in several cases extended beyond the limits of the already explored territories. The present paper presents for the first time the most important biographical facts about Endrés' life and his orchidologic work in Central America. The main exploratory routes made by Endrés are highlighted in the framework of the social geography of his time, and a complete catalogue of the localities where he made his orchid collections, referenced to modern geographical coordinates, is presented.

Resumen. A.R. Endrés, como fue conocido hasta que investigaciones recientes revelaron gran parte de sus datos biográficos relevantes, fue el más importante colector de orquídeas que jamás visitó Costa Rica. Además de recolectar los especímenes tipo de casi un centenar de nuevas especies de orquídeas, Endrés descubrió, describió e ilustró miles de plantas de orquídeas, muchas de ellas aún sin describir a la época de sus hallazgos. Uno de los rasgos sobresalientes de las colecciones llevadas a cabo por Endrés en la Costa Rica post-colonial del siglo diecinueve es su impresionante conocimiento del país, en términos de cobertura geográfica, que en muchos casos se extiende más allá de los límites de los territorios ya explorados en estos entonces. El presente trabajo presenta por vez primera los datos biográficos más importantes de Endrés y de su trabajo orquidológico en América Central. Se resaltan las rutas exploratorias más relevantes realizadas por Endrés, explicándolas en el marco de la geografía social de su época y se presenta un catálogo completo de las localidades en las que realizó sus colectas, referenciándolas con coordenadas geográficas modernas.

Key Words: Augustus R. Endrés, botanical history, orchidology, Costa Rica, geography

"There is a young man by the name of A. R. Endrés living in Costa Rica, who has devoted the past four or five years to investigating the Botany of the interior of that republic. He is still devoted to that purpose and has made many important discoveries of new plants.

I have no doubt that you might draw him into correspondence with you, altho' his correspondence is chiefly with European botanists, and particularly with Reichenbach, the distinguished orchidologist of Germany, to whom Mr. Endrés sends the major portion of his collections for description and publication" (John M. Dow, 1873).

Introduction. The disclosure of Costa Rican orchid diversity during the second half of the Nineteenth century is profoundly indebted to the exploratory and botanical work by Augustus R. Endrés. Heinrich Gustav Reichenbach (1870, 1871, 1872a, 1872b, 1872ca, 1872d, 1872e, 1873, 1874a, 1874b, 1875a, 1875b, 1875c, 1875d, 1876, 1877a, 1877b, 1881, 1883), George Nicholson (1886), Friedrich Richard

Rudolf Schlechter (1921), Friedrich Wilhelm Ludwig Kränzlin (1920, 1921, 1922, 1923, 1925), Carlyle August Luer (1992, 1995, 1996, 1999), and Franco Pupulin (2001), described almost one hundred orchid species on the basis of plants collected by Endrés during his journey in Costa Rica. The type specimens collected by Endrés belong today to several orchid genera, such as *Ada* Lindl., *Barbosella* Schltr., *Barkeria* Knowles & Westc., *Benzingia* Dodson, *Chondroscaphe* (Dressler) Senghas & Gerlach, *Cischweinfia* Dressler & N.H. Wiliams, *Cryptarrhena* R.Br., *Dichaea* Lindl., *Epidendrum* L., *Huntleya* Batem. ex Lindl., *Kefersteinia* Rchb.f., *Lepanthes* Sw., *Lockhartia* Hook., *Lycaste* Lindl., *Masdevallia* Ruiz & Pav., *Maxillaria* Ruiz & Pav., *Maxillariella* M.A. Blanco & Carnevali, *Miltoniopsis* Godefr. & Leb., *Nitidobulbon* I. Ojeda, Carnevali & G.A. Romero, *Oncidium* Sw., *Pleurothallis* R.Br., *Pleurothallopsis* Porto & Brade, *Polycycnis* Rchb.f., *Restrepia* Kunth, *Scaphosepalum* Pfitz., *Scaphyglottis* Poepp. & Endl., *Sievekingia* Rchb.f., *Sigmatostalix* Rchb.b., *Stanhopea* Frost. ex Hook., *Stelis* Sw., *Stenotyla* Dressler, *Telipogon* Kunth, *Trichocentrum* Poepp. & Endl., *Trisetella* Luer, and *Zootrophion* Luer.

The thousands of plants, sketches, analytical drawings, habitat notes and botanical descriptions prepared by Endrés from 1866 to 1874, when he mostly resided in Costa Rica and now at the Herbarium and the Archives of the Natural History Museum in Vienna (NHMW), form an extraordinary legacy, still today largely waiting for in-depth scrutiny and interpretation. Besides the relatively few taxa based on his Costa Rica gatherings, Endrés collected, illustrated and described literally hundreds of species that were still new to the science at the time of his findings. These materials are now fully accessible to the public through the web page of the NHMW (2010), where high-resolution digital images of Endrés' botanical legacy were made available thanks to a joint effort by the NHMW, the University of Costa Rica, and the Jany Renz Herbarium at the University of Basel.

Very little, however, was traditionally known about Endrés himself, with the exception of the preliminary attempts at biographical sketches offered by Luer (1995) and variously taken up again by Atwood and Mora-Retana (1992-1993), Ossenbach (2003, 2009), and Pupulin and Ossenbach (2005).

One of the outstanding aspects of the collections made by Endrés in just a few years in the post-colonial Costa Rica of the Nineteenth century is his impressive knowledge of the country, in terms of geographical coverage. Several of the localities indicated by Endrés in his notes, or affixed to the dry specimens and drawings he regularly sent to his main correspondent, Prof. Reichenbach at Hamburg, were at that time at the extreme bounds of the known territories of a still unexplored country. Some of them correspond today to prosperous villages and towns, but they are recorded by Endrés just as the farms and hamlets, mines, pastures, trails, or simple sites, as they were at the time he visited these localities for the first time. The present paper is a first attempt to produce a complete catalogue of the itineraries and the localities where Endrés made his orchid collections, explaining them in the framework of the social geography of Nineteenth Century Costa Rica, and giving them a modern geographical reference (Appendix 1).

The only exception, and one that can only be explained by sheer lack of time, is that there is not a single orchid specimen collected by Endrés in the mountain pass of La Palma, to the North and Northwest of San José, in the saddle between the Barva and Irazú volcanoes. Although easily accessible through the old trail to Carrillo, this area was not explored until the first decades of the Twentieth Century, when the Brade brothers, Wercklé, Tonduz, and many others discovered dozens of new species, mostly described by Rudolf Schlechter.

Augustus R. Endrés (1838—1874) . A few days after Christmas, in the last days of the year 1866, a young botanist of just 28 years of age landed at Greytown (=San Juan del Norte) on the Caribbean coast of Nicaragua (Endrés, 1867). Augustus R. Endrés, born in the small village of Herbitzheim in Alsace as the son of the local school teacher on November 27, 1838 (Herbitzheim, 2008) had preceded his family, who emigrated some years later to the United States, and arrived in New York sometime in the year of 1855 (Archives départementales du Bas-Rhin, 2010a, 2010b). Eleven years later, on December 13, 1866, Endrés was granted U.S. citizenship and received an American passport (United States National Archives and Records Administration, 2008, 2008b). On the same day, and with a freshly signed contract in his

FIGURE 1. Map of Costa Rica by Wagner & Scherzer. The most modern map of the country available at the time of Endrés' arrival. In Wagner & Scherzer, 1856.

pocket to collect orchids for James Bateman of England and Heinrich Gustav Reichenbach, Director of the Hamburg Botanical Garden, he applied for a passport, with which he embarked on the next available ship to Central America (Endrés, 1871). However, although being born as a citizen of the French Empire and having obtained the United States nationality, Endrés remained, through the rest of his short life, faithful to his German extraction, culture and language.

Over the next seven and a half years Endrés would become a legendary figure in the botanical exploration of Costa Rica and undoubtedly the most important orchidologist who ever visited the Central American countries (Fig. 1—2). In 1871 he rescinded his contract with Bateman and Reichenbach and went into an agreement with the house of Veitch, which lasted until 1873 (Endrés, 1871; Veitch, 1906).

On January 12, 1874, shortly before leaving Costa Rica, Endrés wrote in San José his last known letter to Captain John M. Dow. Having failed in achieving the celebrity and prosperity he always dreamed of, his words were full of bitterness: *"Reichenbach has lately repeated his proposal of buying my dried orch. collections and I fear our first interview will be a stormy one. I begin to consider these cabinet-celebrities as vampires nourishing their inflated fame at the cost of the lifeblood of those poor fools they condescendingly call "collectors", and I am thoroughly disgusted, at moments, with the pursuits I have so passionately followed for seven years"* (Endrés, 1874).

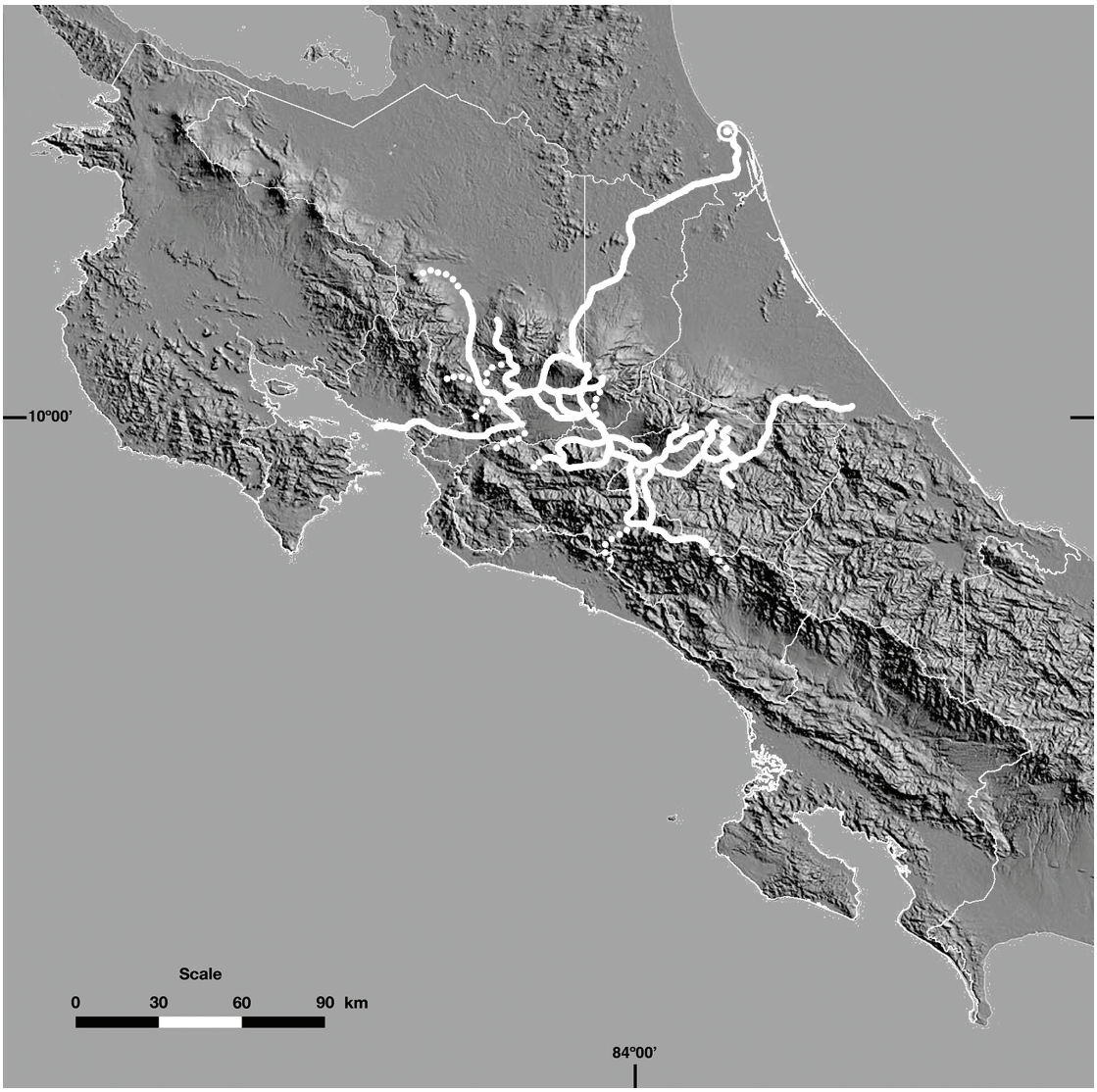

FIGURE 2. General map of the known itineraries by A.R. Endrés in Costa Rica.

In April of 1874 Endrés left Costa Rica on a journey from which he would never return. After traveling to Puntarenas and sailing from there to Panama, he embarked to Europe in April of 1874 (Endrés, 1874). During the early summer of 1874 he met with Reichenbach in Hamburg. Nothing is known about their conversation, except for a brief note by Reichenbach who in 1875 wrote that he had had *"a few delightful days, full of Orchid talk and chat, with Messrs. Roezl and Endres at Hamburg"* (Reichenbach, 1875b).

On July 15 of that year he embarked again for America, this time in the company of the famous Czech plant collector Benedikt Roezl, landing on August 2 in New York (United States National Archives and Records Administration, 2008c). After a short excursion with Roezl to Niagara Falls, he sailed to Barranquilla, on the Caribbean coast of Colombia. During the last week of October he continued on what would be his last collecting excursion, this time eastwards to the Sierra Nevada of Santa Marta. After falling ill with pleurisy in the small village of San

Figure 3. King Street in Greytown. *In* Vargas, 2008.

Antonio, at 3,000 feet altitude on the northeastern slope of the Sierra, he was brought by local Indians to the costal village of Dibulla, where, in the words of Franz Flux, officer of the German Consulate in Barranquilla, *"he started on his journey to the afterworld at the end of November* [of 1874]*"* (Flux, 1875).

The orchid itineraries of Augustus R. Endrés in Costa Rica

The 'far' Northeast and the road of Sarapiquí. — After arriving in Greytown, Endrés spent several months in the Atlantic region of Nicaragua and Costa Rica. According to undocumented reports, Endrés settled temporarily with English and German colonists along the San Carlos and Sarapiquí rivers (L.D. Gómez, pers. comm. 2008). There he worked at least part-time with a Mr. Koschny in beginning a plantation of native rubber and nutmeg (Gómez, L. D. in Luer, 1995).

The port of Greytown, and the rivers San Juan and Sarapiquí were part of the "road of Sarapiquí", at that time the only route connecting the highland valleys of Costa Rica and the Caribbean coast. Travelers embarked in Greytown (Fig.3) on primitive canoes and after navigating the treacherous sandbars on the mouth of the San Juan went up the river and continued into the Sarapiquí until they reached the village of El Muelle, the only available river landing on this stream. From there, on foot and on mules, travelers took the trail to the villages of La Virgen and San Miguel through virgin forests and climbed over the mountain pass of El Desengaño, descending from an altitude of almost 10,000 feet to Costa Rica's Central Valley and the country's capital, San José (Fig. 4). Only passable during the dry season, the road was equally important to travelers and for the import of goods into the country. Costa Rica's first piano and first printing press came into the country via Greytown and Sarapiquí.

The first notice of this route dates back to 1620, when Diego de Mercado, at the request of the Spanish authorities, who were interested in finding a way between the Atlantic and the Pacific because

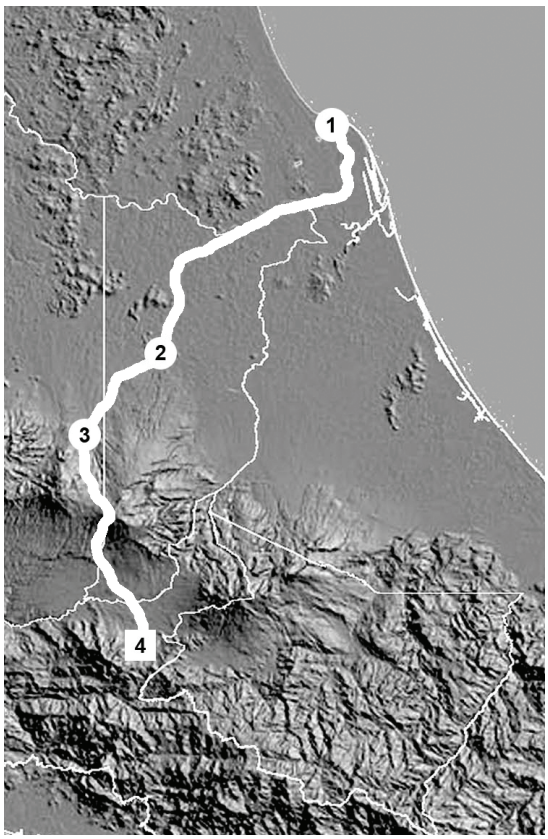

Figure 4. The 'far' Northeast and the road of Sarapiquí. 1 - San Juan (Greytown). 2 - Muelle. 3 - San Miguel. 4 - San José.

of the insalubrity of Panama, submitted a report to the government in Guatemala in which he stated that he had found the desired communication along two different routes. "The first one navigating upstream along the 'Desaguadero' [the Drainage, or the San Juan River] to the mouth of the Sarapiquí, then upstream for more than twenty leagues and from that point to the Royal Embarkment (the mouth of the Tempisque River on the Pacific coast). The road was of 'hard earth and not marshy'…" The other route consisted in what was later known as the Nicaragua Canal, sailing the San Juan River upstream to the Lake of Nicaragua and building from there a canal to the Pacific Coast (Secretaría de Gobierno, 1924).

Shortly after Costa Rica's independence from Spain in 1821, Richard Trevithick (1771–1833), a British inventor and mining engineer, whose most significant success had been the high pressure steam engine and the first full-scale working railway steam locomotive, arrived in Costa Rica hoping to develop mining machinery. He spent time looking for a practical route to transport ore and equipment, settling on using the San Juan River, the Sarapiquí River, and then a railway to cover the remaining distance. Trevithick had in mind a steam-driven and not a mule-driven railway. After almost loosing his life along the route, Trevithick abandoned the idea in 1827, returned to England and never came back to Costa Rica (Gutiérez Braun, 1981). The road of Sarapiquí lost importance against the route from Costa Rica's Pacific port of Puntarenas to Panama and Colón once the railroad across the Isthmus of Panama was inaugurated in 1855.

A more easterly route to the road of Sarapiquí was built in 1880, which communicated San José with the Sucio River and joined there the new railroad to Port Limón. It was named the 'road of Carrillo', in remembrance of President Braulio Carrillo (1800-1845) who had first envisioned the need for better communications with the Atlantic region. Finally, the railroad between San José and Port Limón was completed in 1890. However, the road of Sarapiquí, expanded in the early 1900's for the circulation of motor vehicles, remained the most important access to Costa Rica's Atlantic region until the late 1960's, when the present roads to Port Limón (the first over Turrialba and Siquirres and the second other over the Zurquí tunnel) were inaugurated.

Endrés first known orchid collection in Costa Rica, a specimen of *Dichaea trulla* Rchb. f., carries the date "1866" (W *Rchb-Orch* 18037/W 0019163, Fig. 5) and was undoubtedly collected in the Caribbean watersheds of the Sarapiquí and San Juan rivers, where this species is still fairly common. There is no mention of other plant collections by Endrés along the "road of Sarapiquí", but we know that he arrived in San José on May 25, 1867, after following this route. In a letter of that date to Capt. John M. Dow, Endrés writes about having 'lately' received a letter from a Mr. Buchanan [of New York] in Greytown, indicating that he had been living in that region from December 1866 until at least March or April of 1867. In said letter to Dow he states that he *"arrived here* [in San José] *this morning"* (Endrés, 1867).

It is interesting that Endrés' first impression of Costa Rica was that *"it* […] *would be a useless waste*

Figure 5. *Dichaea trulla* Rchb. f. (W *Rchb-Orch* 18037/W 0019163). Endrés first known collection of a orchid in Costa Rica.

of time and labor to collect anything here" as he wrote to Dow (Endrés, 1867). He was under the impression that the collectors who had visited the country before him had already taken *"all that could be found within the country"*. It is fortunate that he apparently changed his mind. In the years to come, Endrés traveled throughout Costa Rica, reaching every region that was accessible at that time. The exceptions where the North and Northwestern regions (the westernmost part of the province of Alajuela and the region of Guanacaste), where orchids were large in quantity but small in diversity (and thus of little interest to Endrés), and the Pacific and Atlantic coastal regions of Southeastern Costa Rica, practically inaccessible at that time and only partially surveyed during the last two decades of the 19 century by explorers like the American geologist William Gabb, Archbishop Bernard A. Thiel, and the Swiss naturalist Henri Pittier. One of the smallest Central American countries, Costa Rica had in 1868 just about 128,000 inhabitants (Paniagua, 1943: 44). Large portions of the country were still covered by virgin forests that were fertile ground for plant collectors. As an example, Endrés wrote on one of his herbarium specimens (*Ornithidium*, W *Rchb-Orch* 35997/0018715), that it could be found *"by thousands, north of Santa María."*

The 'near East': the road to Turrialba, the Turrialba volcano, Turrialba and surroundings (1867 and second half of 1872). — The region of Turrialba was the first to be explored in Costa Rica by Endrés (Fig. 6). As he wrote to Spencer F. Baird, "*In June 1867, I left a jar of Hummers* [=hummingbirds] *preserved in spirits, at the "Angostura…"* (Endrés, 1869). He referred to the small village of Angostura, just East of the city of Turrialba, and to his activities as collector of birds, which he alternated with his main objective, the orchids. There is a list of birds at the United States National Museum, all collected by Endrés in Costa Rica. Of these, we find 37 specimens

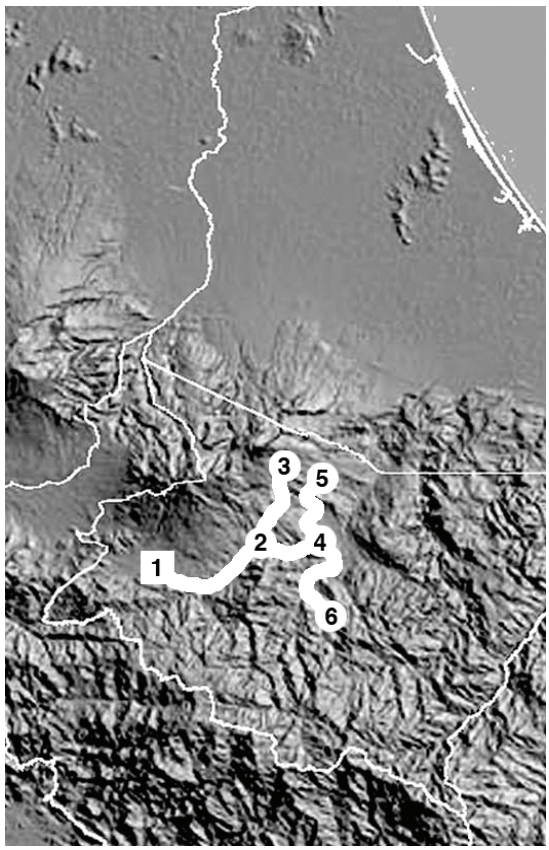

Figure 6. The 'near East': the road to Turrialba, the Turrialba volcano, Turrialba and surroundings. 1 - Cartago. 2 – Juan Viñas. 3 – Turrialba volcano. 4 - Turrialba. 5 – Santa Cruz. 6 - Pejibaye.

of hummingbirds (Family Trochilidae) and one specimen of jacamar (Family Galbulidae). Two of the hummingbird specimens were described by Lawrence as new species: *Eupherusa nigriventris* (Fig. 7) and *Glaucis aeneus*. Others proved to be new records for *the fauna of the State*, in the words of Baird (1869).

He would return to the area some years later. In a letter to Dow of September, 1872, he wrote that he had *"lately scaled the Volcan de Turialba"* (Endrés, 1872). It is probable that this excursion to the volcano was part of his failed excursion to Talamanca, which took place in May of 1872. Also possible is that Endrés stayed on that occasion (May-September 1872) for a longer period of time in the area of Turrialba, traveling and collecting in the neighborhood of that city.

On his way to the volcano, Endrés must have stopped at the house of Eusebio Ortiz, a place which he had visited before and that is mentioned frequently on his herbarium labels, described by Endrés as follows: *"Sitio* [site] *de Eusebio Ortiz. Southwestern slopes of Vulc. Turialba. Road from Cartago to Turialba. After crossing the river Birris, where the same gentleman possesses a saw-mill, one takes the cuesta* [steep incline on a road] *(Iglesias' new road) and before reaching the height, follows on the left until reaching the Potrero* [pasture] *where a house is found at a altitude of about 5,000 feet"* (Endrés, 1869b). On the road from Cartago to Turrialba, Endrés collected in Paraíso, Cervantes, Birrís, Quebrada Honda, Naranjo, Juan Viñas, Chiz and Colorado. To the North of Turrialba he names Guayabo. To the Southeast we have seen labels from Atirro, Bóveda, and Angostura, where he probably stayed at the house of the German teacher Karl Lammich (Lammich had arrived at Angostura as part of the group that attempted to establish a German colony under the direction of Baron Alexander von Bülow. The attempt ended in 1854 as a total failure and most Germans abandoned the area, but Lammich stayed behind and lived for years at Angostura). To the South and Southeast he was in Pejibaye, Azul and Tucurrique, connecting from there again through Guatuso and Tejar with the southern part of Cartago and the road to San José.

The 'far' East: the Atlantic Region (May 1872). — Endrés excursions to the Atlantic region had probably the city of Cartago as their point of origin (Fig. 8), and were related to the construction of the railroad from San José to Puerto or Port of Limón. In October of 1872 Endrés wrote to Dow about his intention of forming a collection of plants with the help of Wilhelm Nanne (then in charge of the construction of the railway) and said he hoped that *"he may give the necessary instructions to his staff of engineers for the purpose"*. Endrés was also offered to take part in the exploration of the region of Talamanca by W.M. Gabb (1839-1878, an American geologist who was hired in 1873 by Minor Keith, the builder of the railroad to Limón, to explore the region of Talamanca in search of the legendary gold mines of Río la Estrella and Tisingal, *"for the purpose of working out a report on the vegetation of the eastern coast"*. And speaking of Talamanca, he wrote that *"Last May* [1872] *already, I started in that direction but was dissuaded before I reached Limon"* (Endrés,

Figure 7. *Eupherusa nigriventris* Lawrence. A new species of hummingbird coollected by Endrés. Illustration by José Alberto Pérez Arrieta.

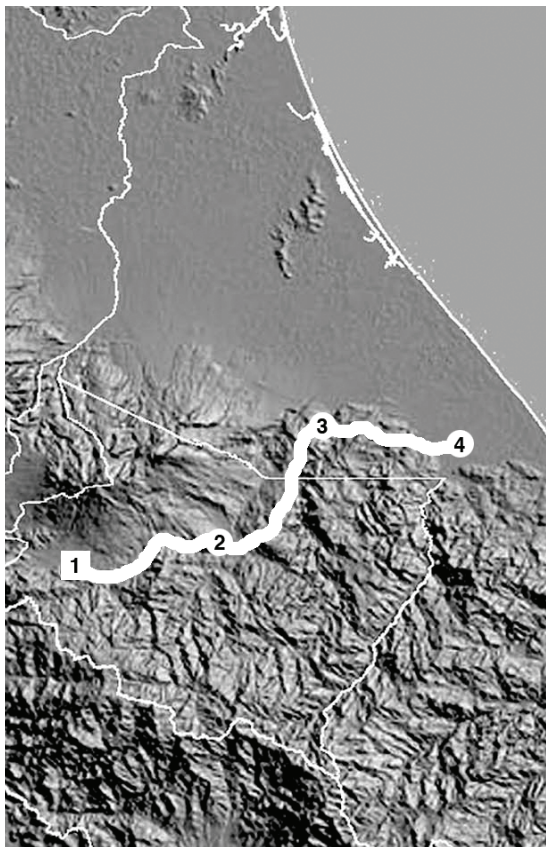

FIGURE 8. The 'far' East: the Atlantic Region. 1 - Cartago. 2 –Turrialba. 3 – Siquirres. 4 - Matina.

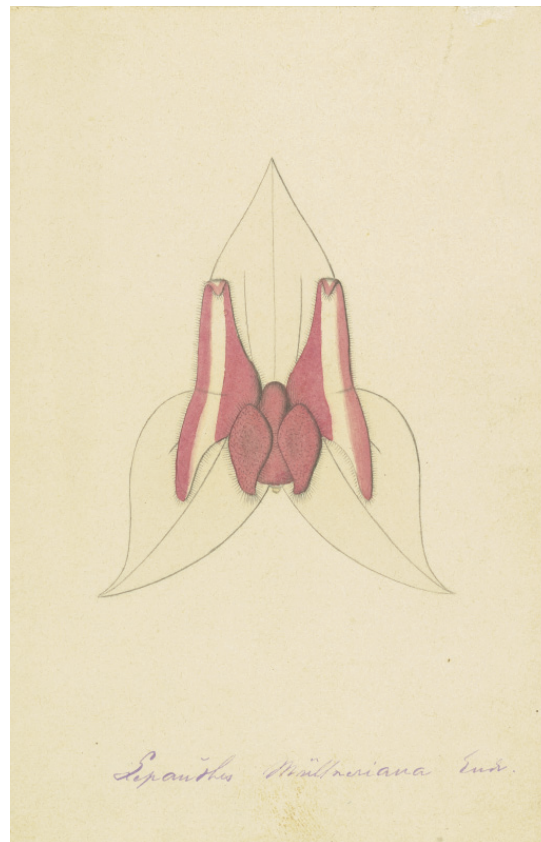

FIGURE 9. *Lepanthes muellneriana* [= *Lepanthes candida* Endrés ex Luer] (W *Rchb-Orch* 7618/0019675). Dedicated by Endrés to Georg Muellner, his host at Hacienda Caño Seco.

1872b). It was undoubtedly during this excursion that he met Georg Müllner at his Hacienda Caño Seco, and Müllner's hospitality which earned him the dedication of *Lepanthes muellneriana* (an unpublished name by Endrés for *Lepanthes candida* Endrés ex Luer; W *Rchb-Orch* 7618/W0019675, Fig. 9). Müllner and his partner, another German by the name Schäfer, had held important positions in the railway company (Bovallius, 1974) and it is therefore probable that it was Nanne, who was directing the construction of the railway, who referred Endrés to Caño Seco. Nanne was rewarded with the dedication by Endrés of *Lepanthes nanneana* (a manuscript, unpublished name for *Lepanthes bradei* Schltr.; W *Rchb-Orch* 7620/W0019685, Fig. 10).

It was in preparation of his excursion to Talamanca that Endrés read Valentini's manuscript about the discovery and conquest of the Atlantic region of Central America (Valentini, 1869) and Wagner and Scherzer's famous book about Costa Rica (Wagner and Scherzer 1856). A reference to these works is given by Endrés in his 'Notizbuch II' (Endrés, 1870). Endrés extracted from Wagner and Scherzer a vocabulary of words of the Bribrí language (spoken by the natives of Talamanca), with its translation into German. Several specimens of *Ionopsis*, one of them bearing the label *'Common in Atlantic coast betw. Pacuare & Matina in the Cacao haciendas del "Bejuco"'* (W *Rchb-Orch* 35959/W0019741) were collected during that excursion. Moreover, many of his collections on the route from Angostura to the Atlantic ocean are labeled "May", which is coincident with the indication in the above mentioned letter (Endrés, 1872b). Finally, in his letter to Endrés of October1872, Captain Dow wrote: *"I am also glad to hear you have got some first [orchids]*

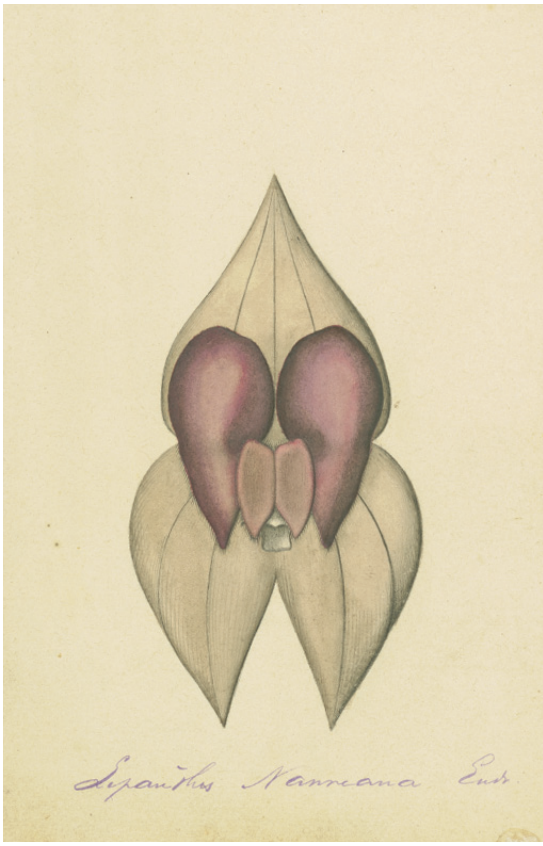

Figure 10. *Lepanthes nanneana* [= *Lepanthes bradei* Schltr.] (W *Rchb-Orch* 7620/0019685). Endrés' tribute to Wilhelm Nanne.

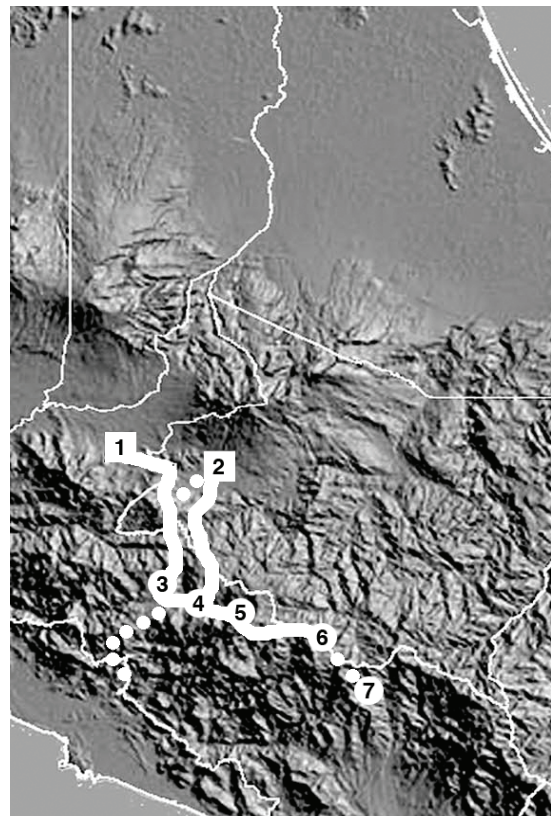

Figure 11. South and Southeast of Cartago, the ascend to the Páramo de Vueltas and Cerro Buena Vista, and the 'new' road to Térraba. 1 – San José. 2 - Cartago. 3 – San Pablo. 4 – Copey. 5 – Cerro Vueltas. 6 – Cerro de la Muerte. 7 – División.

from the rivers of the eastern slope of the Cordillera" (Dow, 1872b). Molina had described the road to Matina as "extremely laborious", having to pass through large rivers without bridges, and large swamps. One had to rent horses in Cartago and ride through Turrialba to the Matina river, and take boats from there to the mouth of the river on the Atlantic shore. The journey took almost a whole month (Molina 1851).

Although the locality of Fajardo (near Ujarrás, on the Reventazón River) lies on the original route which was proposed for the railroad, we do not know if Endrés' orchid collections in that area (Fajardo, Ujarrás, Orosi) were made during the excursion sponsored by W. Nanne or on a different occasion. Let us remember that the railroad was originally planned to run along the Eastern bank of the Reventazón, but the rocks of Fajardo proved to be an insurmountable obstacle. The route was afterwards changed to the Western bank of the river, running from Cartago to Cervantes, Juan Viñas and Turrialba.

South and Southeast of Cartago, the ascent to the Páramo de Vueltas (also called Páramo de Dota) and Cerro Buena Vista, and the 'new' road to Térraba. — There were two routes into the Talamanca mountain range (Fig. 11). The first went from San José through Desamparados and Tablazo to Corralillo and Frailes, and from there to Boca de Dota (named also Atarrazú, today the city of San Marcos de Tarrazú). In Tarrazú there is frequent mention by Endrés of the "savannas of Ramón Zúñiga". Ramón Zúñiga Barahona had been one of the founders of the village and probably another of the many people whose hospitality was enjoyed by Endrés during his

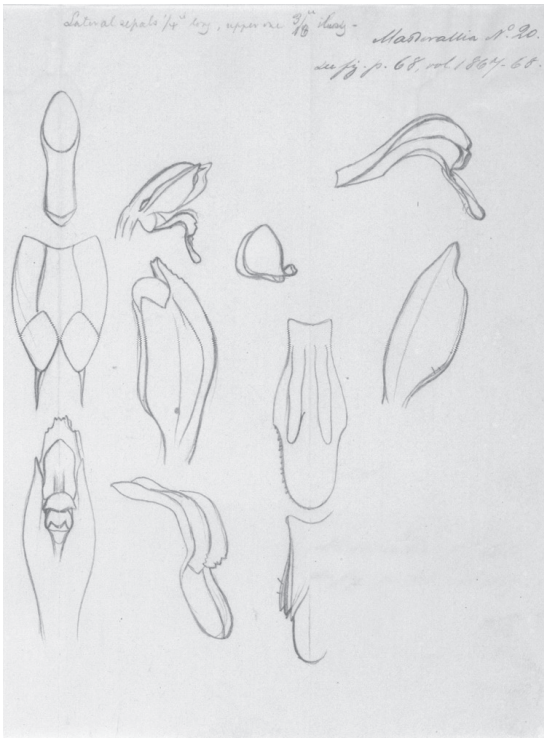

FIGURE 12. *Masdevallia* [= *Scaphosepalum mycrodacylum* Rolfe] (W *Rchb-Orch* 38548/W0020768). Collected by Endrés in Atarrazú.

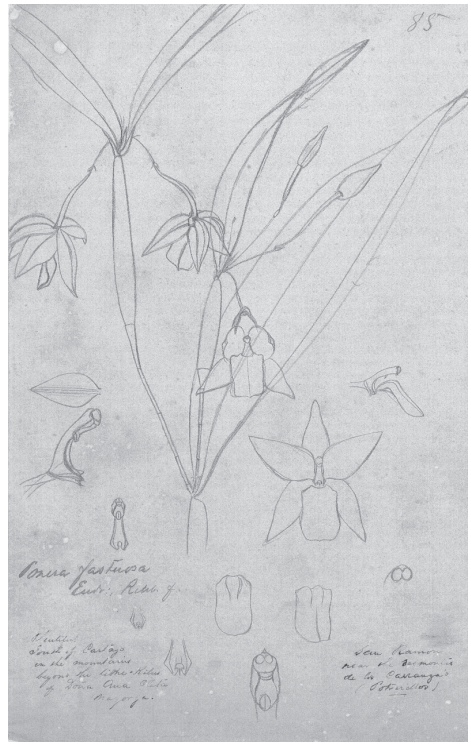

FIGURE 13. *Ponera fastuosa* [= *Scaphyglottis pulchella* (Schltr.) L.O.Williams] (W *Rchb-Orch* 33226/W0020722). Collected by Endrés on the road from Cartago to San Cristóbal and Copey.

travels. Santa María de Dota was founded somewhat later by settlers who came from Tarrazú and from there a road was built to the hamlet of Copey.

The second route started from Cartago, and went through El Tejar, were Endrés mentions the lime-kilns of Ana Cleta Mayorga [1809-1877, a rich widow, owner of an important coffee farm near Paraíso, and one of the first women in Costa Rica who took an active part in politics (Gutiérrez Braun, 1981)], passed near Pizirres (where he stayed at the house of Rafael Calderón) and went on to Estrella and Copey, following more or less the course of the present Pan-American Highway.

Both routes interconnected through the road from Cartago through Tobosi to Corralillo, and Endrés mentions a number of different localities in this area in his collections, such as Copalchí, Alumbre and the road to Palo Blanco.

From the indications on his herbarium sheets, it seems that Endrés traveled both of the routes to the region of Dota. From the first, Endrés recorded *Masdevallia* (= *Scaphosepalum microdactylum* Rolfe; W *Rchb-Orch* 38548/W0020768, Fig. 12) and *Trichocentrum saundersianum* (= *Trichocentrum pfavii* Rchb. f.; W *Rchb-Orch* 37148/W0020946), while from the route to Copey he gathered *Ponera fastuosa* (= *Scaphyglottis pulchella* (Schltr.) L.O. Wms.; W *Rchb-Orch* 33226/W0020272, Fig. 13) and *Platystele propinqua* (Ames) Garay (W *Rchb-Orch* 38623/W0020363).

From Copey, Pedro Calderón started, in 1866, to explore a trail across the mountains, trying to reach the Valley of El General and the region of Térraba. Calderón, a native of San Ramón, was accompanied by his son-in-law Juán López. While Pedro Calderón spent months at a time in the mountains, his son-in-law returned every three months to San Ramón, to visit his family, a journey of over two weeks each way. It may well be that Endrés learned about this area from Juan López, and that he decided to travel with him when

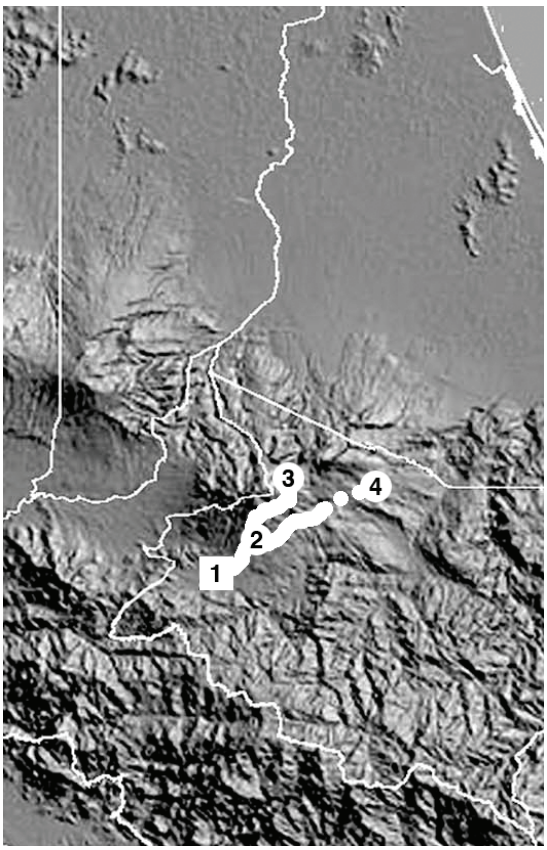

Figure 14. North of Cartago: the slopes of the Irazú volcano. 1 - Cartago. 2 – San Rafael. 3 – Irazú volcano. 4 – Santa Cruz.

Figure 15. Ascent to the Irazú volcano. In Vargas, 2008.

he returned to the mountains. Calderón and López received shelter and supplies from Patricio Granados, a landowner in Copey who is often named (as *"the savanna de los Granados"*) by Endrés on his labels. Endrés makes specific mention on one of his labels (W *Rchb-Orch* 38502/W0019335, Fig. 18) of Calderón's trail (the 'Picada de Pedro Calderón') and on several of his specimens from Dota mentions 'the [new] road to Térraba', not to be confused with the "old road to Térraba", which went from Tarrazú on a south-westerly course to the Pacific plains in the neighbourhood of Quepos. Endrés traveled on the first part of this "old" road and collected as far as Cerro Pito (see, among others, W *Rchb-Orch* 38627/W0021719).

North of Cartago: the slopes of the Irazú volcano. — Although no exact date is known for his excursion, Endrés collected on the slopes of the Irazú volcano (Fig. 14—15). In his description of the flora of the Turrialba volcano, he writes to Dow (Endrés, 1872): *"... yet the flora is much the same as that of the contiguous Volc. Irazú, interspersed with a few sp. from the crest of Dota."* Clearly, he had been on the Irazú and in Dota before ascending to the Turrialba. Endrés names several collecting localities in this area: Cot, Potrero Cerrado, Pascón (near Pacayas), 'Felipe Díaz' (a Spanish conqueror, who in 1569 had been granted a large part of Cot and its neighborhood) and Cerro Grande (W *Rchb-Orch* 38538/W0019322; W *Rchb-Orch* 36720/W0021668; and many others).

The Northwest: San Ramón and surroundings and the road to San Carlos (1867-1874). — The town of San Ramón was not only the favorite collecting area for Endrés, but for most of his time in Costa Rica also

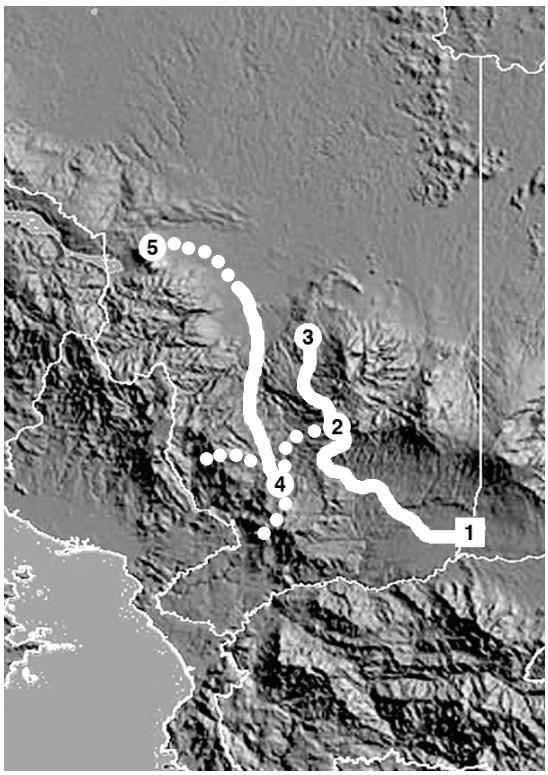

FIGURE 16. The Northwest: San Ramón and surroundings and the road to San Carlos. 1 - Alajuela. 2 – Zarcero. 3 – Ciudad Quesada. 4 – San Ramón. 5 – Arenal Volcano.

FIGURE 17. San Ramón, ca. 1880. Courtesy of Álvaro Castro H.

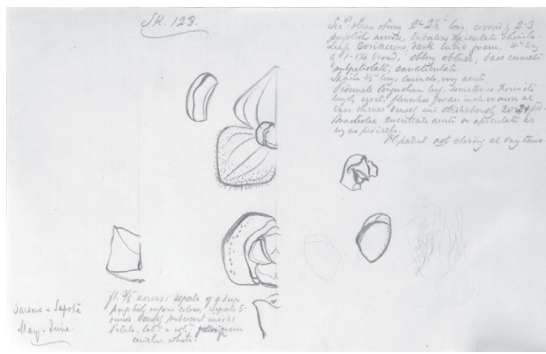

FIGURE 18. *Stelis argentata* Lindl. (W *Rchb-Orch* 142213/W1889-0142213). Collected in Zarcero, along the 'old' road to San Carlos.

his place of residence (Fig. 16). From his letters to Captain Dow and Prof. Baird we know that he lived in San Ramón at least from November 1867 until April 1874. In September of 1872 he even bought a piece of property in the center of the town (Archivos Nacionales, 2008; Fig. 17). At least four herbarium specimens with collecting localities close to San Ramón (Quebrada Verde, Cerros de los Palmares) are dated in 1867, a clear indication that this area was explored by Endrés from the very beginning of his stay in Costa Rica.

Endrés first came to San Ramón in the last half of 1867, after he was named superintendent for the construction of the road to San Carlos, which led from the district of Los Ángeles (to the North-Northwest of San Ramón) to the Cataratas River and from there to the *"navigable waters of the San Carlos River"* (Endrés, 1869). This is the route which Endrés calls "the road to San Carlos" or "the new road to San Carlos". However, in a few cases Endrés mentions "the old road to San Carlos". This road went from Alajuela to Grecia and passed through Zarcero, Zapote and the La Vieja River. It had been opened in 1850 by the expedition of Martínez and Toledo and was of military importance during the campaign of 1856 against the troops of William Walker (Hilje, 2008). After the war, it was abandoned. In Endrés' time it must have been no more than a trail (W *Rchb-Orch* 142213/W1889-0142213; Fig. 18).

Living in San Ramón, Endrés could travel in any direction and find undisturbed forests, ideal for his purposes. Journeys of no more than 1-3 days brought him to the North, to the hacienda of Ramón Rodríguez Solórzano (one of the founding fathers and the first mayor of San Ramón) at Silencio, the ford at the San Lorenzo River, to Quebrada Verde (near Balsa), and reaching as far as the headwaters of the San Carlos River. The trail to San Carlos, at the ford of the San Lorenzo River, was also known as 'picada de Nelson', or 'Nelson's path', and Endrés mentions the house of

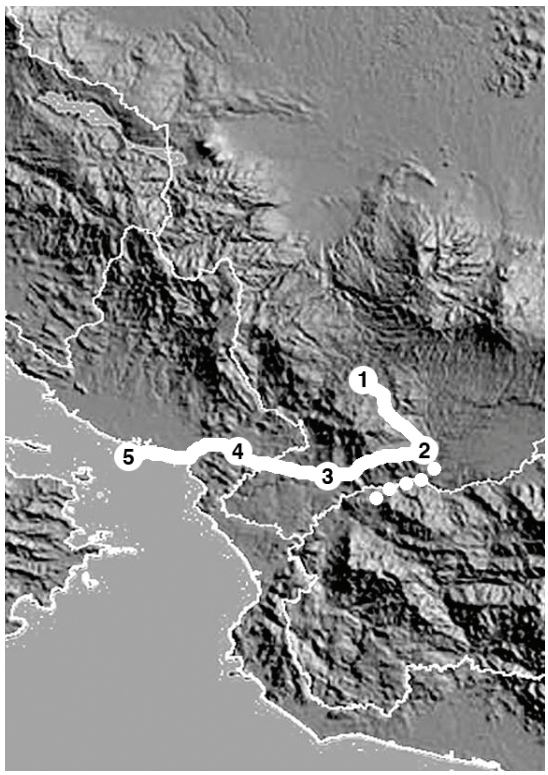

Figure 19. The West: the road from San Ramón to Puntarenas. 1 – San Ramón. 2 – Atenas. 3 – San Mateo. 4 – Esparza. 5 – Puntarenas.

Figure 20. *Brassavola nodosa* (L.) Lindl. (W *Rchb-Orch* 5522/W0019047). *"Along the Pacific shore, near Chacarita."*

P. Nelson in this area. His incursions to the Arenal Volcano (called at that time 'Cerro de los Guatusos') were surely coincidental with his travels during the construction of the road to San Carlos.

To the Northeast, passing through the hacienda of Julián Volio (the village of Volio of present days) he collected in Zarcero, Palmira, Laguna, Zapote and Tapezco. A note in his "Notizbuch II" (Endrés, 1870) reads *"Sarcero, June 10th, 1871"*. To the Southeast we have seen specimens from Palmares, Candelaria, San Roque and Grecia. To the Southwest he collected in Río Jesús and the lime-kilns of La Calera. To the South he described plants from Dujardin's Hacienda La Francia and to the Northwest from La Paz, Potrerillos, and the rivers Piedras and Barranca. Near Potrerillos he mentions the "lands of Teresa Rodríguez", meaning undoubtedly Teresa de Jesús Rodríguez Vega, the widow of Pioquinto Alvarado Arrieta (1816-1843), another of the founding fathers of San Ramón.

The West: the road from San Ramón to Puntarenas. — The 'National Road', connecting the capital city of San José and the port of Puntarenas, on the Pacific, was built between 1844 and 1846 and was the only road apt for oxcarts in Central America at that time. Although Endrés probably could have found a shorter route to Puntarenas, it seems clear, from his letters, that he traveled always first to Atenas (through Palmares and Candelaria), and then on the National Road to San Mateo, rivers Paires and Jesús María, Esparza, Barranca and Chacarita until reaching the harbour (Fig. 19). All of these places are well documented on orchid collections by Endrés, who still uses for this road the name "Camino Real" [Royal road] from Costa Rica's colonial times (i.e., W *Rchb-Orch* 38586/W0020193; W *Rchb-Orch* 5522/W0019047, Fig. 20). Other collecting localities of Endrés near this route are Río Grande, Balsa and Picagres.

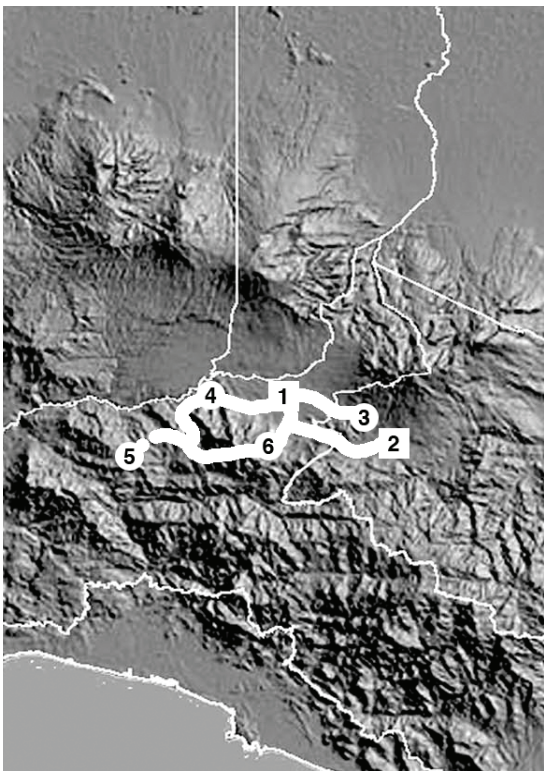

FIGURE 21. South, Southeast, and Southwest of San José. 1 – San José. 2 – Cartago. 3 – Tres Ríos. 4 – Santa Ana. 5 – Santiago. 6 – Aserrí.

His visits to Puntarenas had seemingly always the same purpose, which was to meet his friend and mentor Captain John Melmoth Dow, but this route was also important for Endrés because it was via Puntarenas that he received his mail and that he sent his plants and herbarium specimens.

SOUTH, SOUTHEAST, AND SOUTHWEST OF SAN JOSÉ. — There are no documents to tell us when Endrés collected in this area. According to L.D. Gómez (pers. comm. 2006), we assume that, in the first months of residence in Costa Rica, he lived for some time in San José, and this may have been the time to explore the surroundings of the city (Fig. 21). He could have taken the route to Aserrí and from there to Tabarcia and Pacaca exploring on the way the mountains of Tablazo and Cerro del Dragón (all named on his herbarium labels: W *Rchb-Orch* 36218/W0019352, Fig. 22). He also collected on the hills of Carpintera (to the East of San José) and Pico Blanco, to the Southwest. When

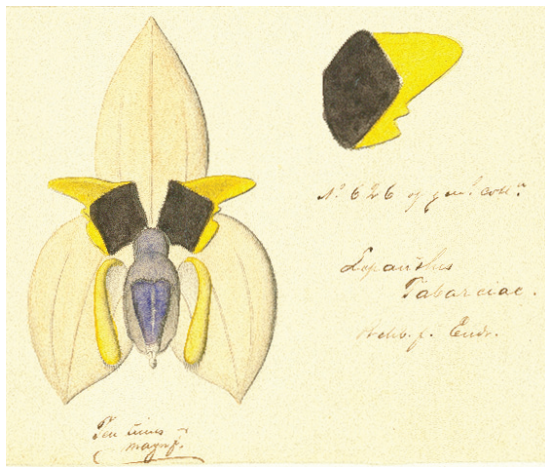

FIGURE 22. *Lepanthes inescata* Luer (W *Rchb-Orch* 36218/W0019352). Named by Endrés *Lepanthes tabarciae*, after the village of Tabarcia, southeast of San José.

travelling from San José to Cartago, Endrés seemingly always used the old colonial road, from San José to Desamparados and from there over Patarrá and Tobosi to Tejar and Cartago, thus traveling along the southern flank of the Carpintera mountains, rather than over the 'modern' road through Tres Ríos. This road was known as the "camino por lo alto" [road along the heights] or Cavallón's road [Juan de Cavallón y Arboleda (1524-1565) was a Spanish conqueror who in 1561 founded Garcimuñoz, the first Spanish city in Costa Rica's central valley, situated at the present location of Desamparados].

THE CENTRAL MOUNTAIN RANGE (POÁS AND BARVA VOLCANOES). — Again, we have no dates for Endrés' collections along the southern slope of the Central Mountain Range. However, he names frequently localities along the route to the Poás (also called by him 'Volcan de los Votos') and Barva volcanoes and seems to be quite familiar with that area (Fig. 23). San Isidro, Itiquís River, Desengaño, Poás and Barba are names which are often found on the herbarium specimens preserved in Vienna. Charles Lankester, who seems to have been familiar with Endrés' itineraries, wrote about Varablanca, a locality on the pass of Desengaño: *"Endrés worked it, but probably mainly for horticultural stuff!"* (Lankester, 1923). North of the village of Barva, Endrés seems to have been acquainted with Pío

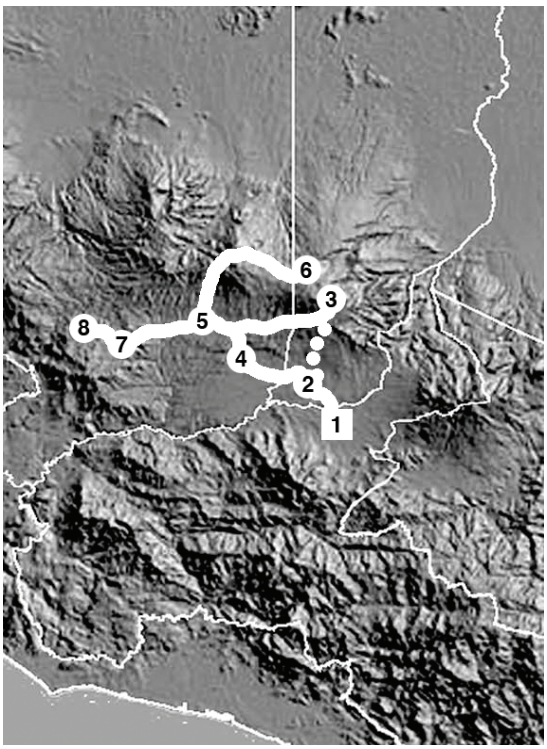

Figure 23. The Central Mountain Range (Poás and Barva volcanoes). 1 – San José. 2 – Heredia. 3 – Poás volcano. 4 – Alajuela. 5 – Sarchí. 6 – Varablanca. 7 – Palmares. 8 – San Ramón.

Figure 24. *Fregea batemanniana* [= *Sobralia amabilis* (Rchb.f.) L.O. Williams] (W Rchb-Orch 16179-W0019788). Collected by Endrés on the southern slopes of the Barva volcano.

Murillo, the owner of a large farm close to the crater of the Barva volcano.

It is clear that Endrés was well acquainted with this region. One of his notes on a herbarium sheet preserved at Vienna (W *Rchb-Orch* 36911/W0021520) reads: *"Plenty of the Poas Sobralia along the road from Alajuela (Camino de las Canoas) to Desengaño, some 2,000 yds. above Casorla's Hacienda growing on the respaldos* [embankments of the road] *(terrestrial). Further up towards where the "Tambor" river crosses the road, Odontoglossum cariniferum with ovate oblong,* [...] *bulbs, ovate acute leaves and a 2-3 ft. long erect stout 50-60 fl. panicled peduncle and rachis somewhat glaucous. On the same spot a pendulous 8 in. long Epidendrum with lanceolate acuminate fleshy green leaves flat* [...] *behind. Flowers in a slender fine branched irregular short panicle, pale* [...] *lilac, spurred, small, inconspicuous. Sept. Oct. Among the Poas Sobralia, Fregea Batemanniana with deep purplish carmine flower, the base of labellum white blotched with deep crimson. Above Santa Bárbara plenty of Epidendrum campylostalix, Odontoglossum pulchellum ? the Candelaria & Poás variety. Above San Isidro (Alajuela) Epidendrum campylostalix, Lycaste candida, Odontoglossum pulchellum and some plants of Odontoglossum cariniferum* (W *Rchb-Orch* 38546/W0019496; Fig. 24).

A man named José Mora seems to have been Endrés' guide to the Poás volcano. In his Notizbuch II (Endrés, 1870) Endrés mentions a 6-day journey to the volcano, for which Mora was paid $4,50 (Pesos, the Costa Rican currency of that time).

The journey of augustus R. Endrés to Panama. — Endrés traveled to Panama sometime between May 1871 and April 1872 (Fig. 25). In September 1872 Endrés wrote to Dow from Puntarenas *"for the first time since my visit to the isthmus have I come down to the port..."* (Endrés, 1872), remembering his

FIGURE 25. The journey of Augustus R. Endrés to Panama.

visit to Panama which had the purpose of delivering in good conditions to the transatlantic steamer a shipment of orchids to Veitch. As Dow wrote later to Endrés: *"I am sorry the Messrs. Veitch were not satisfied with the remittance you took so much pain to accompany to Aspinwall"* (Dow, 1872c). From his few collection dates, it can be assumed that he arrived in Panama sometime in June of 1871 and embarked for his return to Costa Rica on April 12, 1872. This means that he could have been as much as 10 months away from San Ramón. The main purpose of this trip was clearly not the collection of orchids, of which barely a dozen can be found in the archives of the NHMW (W *Rchb-Orch* 5547/ W0020710; Fig. 26).

Also, in *Hortus Veitchii* (Veitch, 1906), concerning *Epidendrum lindleyanum*, one reads: "The variety Centerae was introduced by us from Costa Rica, in 1873, through M. Endres; and dedicated to Mrs. Center, the wife of the then superintendent of the Panama Railway". Endrés was obviously familiar with Panama, the railway and its officials and the fact that Endrés had suggested

FIGURE 26. *Schomburgkia* [= *Caularthron bilamellatum* (Rchb. f.) R.E. Schult.] (W *Rchb-Orch* 5547/ W0020710). Collected by Endrés at San Pablo Station, Panama railroad.

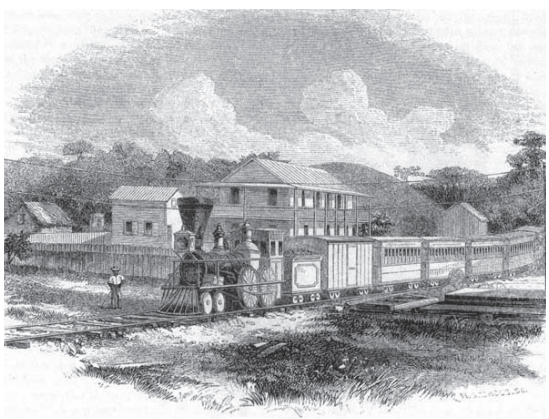

FIGURE 27. San Pablo Station, Panama Railroad. In Vargas, 2008.

the name *Restrepia centereana* for the specimen of *Restrepia trichoglossa* collected by him, we presume that the superintendant's wife had made quite an impression on him.

We also presume that Endrés was using the railway to reach the eastern seaboard of Central America to sail home to Europe as there was no deep-sea port on the Atlantic coast of Costa Rica. One therefore wonders if the superintendant was aware of the honour subsequently bestowed on his wife by a passing stranger – if indeed he was just a passing stranger (Manning, 2008). The localities indicated by Endrés on his specimens are all referred to the railway, namely three of its stations: San Pablo (Fig. 27), Obispo, and Matachín.

Endrés introduction to Alexander Center and his family must again have been the work of John M. Dow. Dow was a good friend of the family. In April 1872 he wrote to his wife: *"... knowing of my intimacy with the Center family..."* and further on, in the same letter: *"... so far as their society is concerned I would not ask for more agreeable company than they* [Mrs. Center and her daughters] *have proved themselves to be"* (Dow, 1872).

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Archives départementales du Bas-Rhin (in Strasbourg), 2010. Document 1TP/PRI374: letter from Philippe Endrés to the Prefect of the Department du Bas-Rhin, indicating that his son Auguste is living with his grandfather Auguste Reeb in New York at that time, July 18, 1857.

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Appendix 1. Endrés' collecting localities.

Locality name on Endrés label	Coordinates	Note
	Costa Rica	
Acosta (Mina)	Unknown locality	Probably a gold mine - near San Ramón.
Aguacaliente (Agua Caliente)	1440 m, 9°51'N 83°56'W	Town in the E Valle Central, SW of Cartago
Alajuela	951 m, 10°01'N 84°13'W	City in the W Valle Central; capital of Prov. Alajuela
Alumbre	1550 m. 9°48'N 84°02'W	Village on the slope of the Cordillera de Talamanca, SW of Cartago
Angostura	543 m, 9°53'N 83°40'W	Site to the SE of Turrialba
Arenal [Volcano]	1633 m, 10°28'N 84°42'W	Isolated peak near the southern end of the Cordillera de Guanacaste; most active volcano in Costa Rica. At Endrés' time it was not known that it was a volcano and was called 'Cerro de los Guatusos', which is the name used by Endrés on his specimens
Arenilla	1388 m, 9°52'N 83°48'W	Old name for Guadalupe. Suburb of Cartago, to the SW of the town
Atenas	696 m, 9°58'N 84°23'W	Town in the W Valle Central; railroad station
Atirro	597 m, 9°50'N 83°40'W	Village to the SSE of Turrialba.
Atlantic (sultry lowlands of the)	The region between Siquirres and the coast	We assume that Endrés collected along the proposed railroad to Limón. As a matter of fact, he intended to explore Talamanca (in May 1872) but in his letter to Capt. Dow of Oct. 18, 1872 he writes: *"I was dissuaded before I reached Limón"*
Azul, Quebrada	800 m, 9°47'N 83°44'W	Creek in the N Cordillera de Talamanca; a tributary of the Río Pejibaye. Also Finca Azul, at the confluency of the Quebrada with the Río Pejibaye
(La) Balsa de Atenas (de Río Grande; de Tárcoles) (spelled by Endrés 'Balza')	425 m, 9°57'N 84°23'W	Railroad station in W Valle Central, S of Atenas
Barranca (1)	27 m, 9°59'41"N 84°43'29"W	Village 7 miles to the E of Puntarenas
Barranca (2)	614 m, 10°05'N 84°32'W	Hamlet 4 miles West of San Ramón
Barva (or, Barba)	1177 m, 10°02'N 84°08'W	NW suburb of Heredia
Barva volcano (spelled by Endrés 'Barba')	2906 m, 10°08'N 84°06'W	In the Central Mountain Range, 15 miles to the N of San José
Birrís (spelled by Endrés 'Virrís')	1253 m, 9°53'N 83°47'W	Village along the Río Birrís, just NE of Cervantes
Boquerón	1793 m, 9°90'N 83°50'W	Village N of Cartago, about 1 mile E of Cot, on the slopes of Irazú volcano
Bóveda	726 m, 9°54'N 83°39'W	Village to the W of Turrialba, on the road to Siquirres, between Eslabón and Pavones
Buena Vista, Cerro and Páramo	3491 m, 9°35'N 83°45'W	Mountain and highland plain in the Cordillera of Talamanca
Buena Vista (de San Carlos)	850 m, 10°17'N 84°28'W	Town on the westernmost slope of the Cordillera Central, SW of Ciudad Quesada

Locality name on Endrés label	Coordinates	Note
Cacao, Río	800 m, 9°59'N 84°26'W	River draining the E slope of the Montes del Aguacate, flowing just N of Atenas; a tributary of the Río Grande de Tárcoles
(La) Calera (de San Ramón)	1100 m, 10°01'N 84°29'W	Site on the S slope of the Montes del Aguacate
Calvario on the cliffs		Road to Limón (?). A Calvary (stations of the Cross), somewhere along the Limón road, then under construction. Probably a collecting locality during his intended trip to Talamanca, in May 1872
Camino de Boruca		The road to the lowlands of Boruca, after crossing the Cerro Buena Vista
Candelaria	1010m, 10°02'N 84°25'W	Village about 2 miles S of Palmares, on the road to Atenas
Candelaria (Cerros de)	1000–2100 m, 9°43–50'N 84°00–07'W	A mountainous region, part of the N Cordillera de Talamanca, comprising the drainage basins of the Ríos Tarrazú, Alumbre, and Santa Elena
Candelaria, Río (Grande de)	1100 m, 9°47'N 84°06'W	Major river draining the S slope of the Cerros de Escazú, portions of the N Cordillera de Talamanca, etc., formed by the confluence of the Río Alumbre and the Río Tarrazú; an affluent (with the Río Pirrís) of the Río Parrita
Carmen, Llanos del	Plain to the SW of Alajuela	Site between Turrúcares and Alajuela (occupied today in great part by the industrial zone of El Coyol)
Carpintera, Cerro(s) de la (spelled by Endrés 'Carpintaria')	1870 m, 9°53'N 83°49'W	Serranía at the S margin of the Valle Central, connecting the Cordillera de Talamanca and the Cordillera Central
Carranza´s, Camino de los		San Ramón. Path near Potrerillos
Cartago	1426 m, 9°52'N 83°55'W	City in the E Valle Central; capital of Prov. Cartago
Cataratas de San Ramón		Village in the district of Los Ángeles de San Ramón, near the confluence of the rivers Balsa and Cataratas (not shown on modern maps)
Cervantes	1441 m, 83°49'W, 9°53'N	Village E of Cartago, on the road to Turrialba
Chacarita	4 m, 84° 45' W 10° 00' N	Hamlet 3 miles E of Puntarenas
Chiz (as "Chis") the Río Chiz	835 m, 9°52'N 83°43'W	Small hamlet to the SE of Juan Viñas, on the banks of
Chiz, Río (as " Chis	829 m, 9°52'N 83°43'W	A tributary of the Río Reventazón
Coliblanco	2350 m. 9°57'N 83°48'W	Town on the SE slope of Volcán Irazú
Colorado (Heights of)	1000 m, 83° 42' W 9° 55' N	Hamlet WNW of Turrialba
Copalchí (spelled 'Colpachí')	1854 m, 9°48'N 84°02'W	Village SW of Cartago, on the road to Frailes
Corralillo	1665 m. 9°48'N 84°01'W	Town 15 km SW of Cartago
Cot	1820 m, 9°54'N 83°452'W	Village to the NE of Cartago, on the road to Irazú volcano
Desengaño, Paso del (or Alto del)	1899 m, 10 10'N 84 10'W	Mountain pass between the Poás and Barva volcanoes. Historically important as the route to the lowlands of Sarapiquí

Locality name on Endrés label	Coordinates	Note
Dota, Boca de	1404 m. 9°40'N 84°01'W	Site located to the South of where the village of San Marcos de Tarrazú was later founded. Today known as Santa Marta de San Lorenzo de Tarrazú
Dragón, Cerro (better known as Cerro Caraigres)	2508 m, 9°43'N 84°08'W	Geologically complex and intriguing subsidiary peak in the N part of the Cordillera de Talamanca; also known as Cerro de Los Cuarteles
Escazu's, Camino de los		San Ramón. Path near Potrerillos
Esparza	168 m, 10 00' N 84 40' W	Town on the old road to Puntarenas
Fajardo	1000 m, 9° 51' N 83° 43' W	Site north of the Cachí dam on the Reventazón river. Narrow gorge also known as 'Puente [bridge] de Fajardo' or 'Rocas [rocks] of Fajardo'
Felipe Diaz (La Cañada de Felipe Días)	9° 58' N 83° 54' W	Today simply "La Cañada". Village to the SW of Irazú volcano, 1.5 miles NE ofLlano Grande. Named after a Spanish conqueror who received land grants on the slopes of Irazú volcano back in 1569
Frailes, Los	1596 m, 9° 45' N 84° 40' W	Village on the road from Desamparados to Tarrazú and Dota. Frailes, Spanish for *friars*, was a community of friars from the order of St. Francis, established in the area in the last quarter of the 18th century
Garita, La	675 m, 9 59' 30'' N 84 19' 00'' W	Village 2.5 miles N of Turrúcares, on the road from Alajuela to Atenas
Granados, Savanna de los	2200 m, 9°38'N 83°55'W	House and pastures of Patricio Granados, in Copey de Dota. Town in the Cordillera de Talamanca, E of Santa María de Dota
Grande, Cerro, Cartago	2539 m, 10 00' N 83 50' W	Mountain southwest of Turrialba volcano
Grande de Tárcoles, Río		Formed by the confluence of the rivers Grande de San Ramón and Virilla, near Atenas
Grecia	1015 m, 10°04'N 84°18'W	Town in the W Valle Central, between Sarchí (Norte) and San Pedro de Poás
Guatuso	1390 m, 9°49'N 83°57'W	Town at the S edge of the E Valle Central, SW of Cartago
Guayabo (1) (spelled by Endrés often 'Guayavo')	800 m, 9°58'N 83°38'W	Turrialba. Site NE of Turrialba; small hamlet at the the confluence of the Guayabo and Reventazón Rivers
Guayabo (2), Hacienda de (Finca) (spelled often'Guayavo')	900 m, 9°58'N 83°40'W	Site N of Turrialba; once owned by Mme. Amparo de Zeledón, noted patron of orchid collectors. The Guayabo, National monument is nearby at 1050 m, 9°58'N 83°41'W. Archeological site on the E slope of Volcán Turrialba.
"Hacienda de don Pío Murillo		Close to the crater of the Barva volcano. A farm from Spain in 1821. Murillo had been one of the first to explore the routes to the region of Sarapiquí in the years of 1832 and 1833
"Hacienda la Francia"	1070 m, 10°04°N 84°28°W	Coffee farm property of the Frenchman Victor Dujardin, in the district of San Rafael de San Ramón. The farm was located in what is today the center of the village and the street on the north side of the church is still called "La Francia"

Locality name on Endrés label	Coordinates	Note
Honda, Quebrada (1)	1014 m, 9°53'N 83°47'W	Creek draining the SE foothills of Volcán Irazú; a tributary of the Río Reventazón. N.B.: "Quebrada Honda" is one of the most common place names in Costa Rica. This is perhaps the most important one botanically, but there are others, and some cannot be localized with certainty
Honda, Quebrada (2)	900 m, 9°58'N 84°28'W	Creek with its source near Zapote, some 3.5 miles South of Santiago de San Ramón, flowing into the Río Machuca. Also a site with the same name about 1.3 miles North of Desmonte, probably an abandoned mine
Iglesias, Mina		Site (mine) along or near the Río Barranca, Puntarenas
Irazú volcano	3432 m, 9°49'N 83°50'W	In the Central Mountain Range, 20 miles Northeast of Cartago
Itiquís (Cabecera del río)	1295 m, 10°04'N 84°11'W	Headwaters of Itiquís River on the southwestern slope of Barva volcano
Jardín (El)	2230 m, 9°43'N 83°58'W	Town in the Cordillera de Talamanca SW of El Empalme, along the road to Santa María de Dota
Jesús María, Río	100–200 m, 9°58'N 84°37'W	River draining the Montes del Aguacate, flowing to the sea at Tivives
Jilguero (spelled 'Cilguero')	779 m, 10° 25'N 84°43'W	Hamlet on the SW slope of Cerro Chato, about 3 miles S of Arenal volcano
Jorco, Río	230–600+ m , 9°47–48'N 84°15–19'W	A tributary of the Río Grande de Candelaria
Juan Viñas, Río	9°56'N 83°47'W (headwaters)	Today known as Río Maravilla. Its headwaters are just SE of Santa Teresa, on the SE slope of Volcán Irazú, NE of Capellades. A tributary of the Chiz River, who is a tributary of the Reventazón
Laguna de Zarcero (or de Alfaro Ruiz)	1850 m, 10°13'N 84°20'W	Town on the W slope of the Cordillera Central, just NW of Zarcero along the road to Ciudad Quesada
Legua (Cuesta de la)		San Ramón de Alajuela, camino a San Carlos (?)
Legua de Desamparados	1649 m. 9°45'N 84°08'W	Today known as Legua de Aserrí. Village to the N. of Aserrí
Lluvioso, Cerro (?)		
Macacona (de Esparza)	243 m, 10°00'N 84°39'W	Town along the Carretera Interamericana, just NE of Esparza
(La) Matina	11 m, 10°05'N 83°18'W	Railroad station on the Llanura de Santa Clara, near the upper Río Matina
(La) Mina, Cerro	400 m. 10°03'N 84°40'W	Hill about 9 km SE of Miramar
Mina San Gerardo	500 m, 10°03'N 84°35'W	Abandoned gold mine in the mine district near the confluence of the rivers Jesús and Barranca
Monte Redondo	1140 m, 9°48'N 84°08'W	Town in the valley of the Río Grande de Candelaria
Naranjo (de Juan Viñas)	1242 m, 9°53'N 83°46'W	Town just W of Juan Viñas
Navarro	1100 m, 9°48'N 83°53'W	Town in the N Cordillera de Talamanca, in the valley of the Río Agua Caliente, near its confluence with the Río Navarro

Locality name on Endrés label	Coordinates	Note
Ochomogo	1500 m, 9°53'N 83°57'W	Mountain pass along the main road between San José and Cartago, dividing the central highland of Costa Rica into the Eastern and Western Valley
Ojo de Agua (1)	840 m, 9°58'N 84°13'W	Railroad station in the Valle Central, S of Alajuela
Ojo de Agua (2)	2980 m, 9°37'N 83°49'W	Site near Cerro de las Vueltas, Cartago
Orosi	1051 m, 9°48'N 83°52'W	Town in the N Cordillera de Talamanca, in the valley of the Río Grande de Orosi
Pacaca	799 m, 9°55'N 84°15'W	Former name for Colón (Ciudad; Villa), town in the W Valle Central
Pacuare, Río	70 m, 10°05'41"N 83°29'18"W (where Siquirres–Limón highway crosses river); 10°05'26"N 83°29'20"W (at Northern Railroad crossing)	River draining the N Cordillera de Talamanca, flowing to the sea between Parismina and Puerto Limón
Paires, Río (as 'Payres')		River to the W of Esparza. A tributary of Río Jesús María
Palmares, Cerros de los	1353 m, 10°05'N 84°25'W	19th century denomination for the hills to the East of San Ramón and Palmares, whith the Cerro del Espíritu Santo as one of its main elevations
Palmira, Cerro	2184 m, 10°12'N 84°21'W	Promontory in the W portion of the Cordillera Central, SE of Palmira de Alfaro Ruiz; an extinct volcano
Palo Blanco	1700 m, 9°49'N 83°58'W	Site on the slope above San Isidro de Cartago
Paquita, Río	80 m, 9°31'N 84°06'W	River draining the Cordillera de Talamanca, flowing to the sea (Boca Damas) just N of Puerto Quepos
Paraíso	1350 m, 9°50'N 83°51'W	Town W of Cartago, on the road to Turrialba
Parrita, Río		Major river draining the Cordillera de Talamanca, formed by the confluence of the Río Grande de Candelaria and the Río Pirrís
Parrita Grande, Río		Old name for the upper part of the Río Pirrís, in the region of S. Marcos de Tarrazú and Sta María de Dota
Pascón	1742 m, 9°55'N 83°48'W	Hamlet 1.3 miles SW of Pacayas, NE of Cartago
Patarrá	1170 m, 9°53'N 84°02'W	SE suburb of San José
(La) Paz de San Ramón	1110 m, 10°08'N 84°32'W	Village in the Cordillera de Tilarán, NW of San Ramón
Peje, Río	100 m, 10°24'N 84°30'W	River draining the northernwesternmost slopes of the Cordillera Central; a tributary of the Río San Carlos
Pejibaye (as "Pejivalle")	650 m, 9°48'N 83°43'W	Town in the N Cordillera de Talamanca, along the Río Pejibaye
Pejibaye, Río	750 m, 9°47'N 83°43'W	River draining the N part of the Cordillera de Talamanca; a tributary of the Río Reventazón
Pelón, Cerro	926 m, 9°43'N 84°24'W	Hill in the Puriscal region, S of Salitrales
Picagres	600 m, 9°54'N 84°21'W	Village about 5 miles NW of Puriscal, on the SE slope of the Río Grande de Tárcoles
Pico Blanco, Cerro	2428 m, 9°87'N 84°14'W	Second highest mountain of the Cerros de Escazú, SW of San José

Locality name on Endrés label	Coordinates	Note
Piedras (Río)		A tributary of the Río Barranca, NW from San Ramón
Picada de Pedro Calderón		Trail established in 1866 which led from Santa María de Dota over Copey and the Páramo de Vueltas to the Valley of El General. Pedro Calderón Ureña started -together with his son-in-law Juan López Alfaro- from the village of Copey de Dota, and used the house of Patricio Granados as his base camp (see other collections by Endrés referring to the "savanna de los Granados")
Pito, Cerro El	1460 m, 9°35'N 84°04'W	Promontory SW of San Marcos de Tarrazú; sometimes given as "Alto de La Pita"
Pizirres	2000 m, 9°48'N 84°01'W	Today known as "Calle Pizirres", site in the district of Patio de Agua (Tejar)
Poás, Volcán (Massif du)	2708 m, 10°11'N 84°14'W	Major, active volcano in the Cordillera Central; formerly known as "Volcán de Los Votos" (or "Botos")
Potrerillos, San Ramón	ca. 1000 m, 10°07'00" N 84°32'12" W	small village near Piedades Norte
Potrero Cerrado	2196 m, 9°55'N 83°52'W	Village on the road from Cartago to the Irazú volcano
Pozón (Cerros del)		San Ramón (?)
Quebrada Verde	1020 m, 10°12'N 84°30'W	Creek in the Cordillera de Tilarán, just NW of La Balsa; a tributary of the Río Balsa
Quemado, Cerro		Near Santa María de Dota (?)
Reventazón (Río; River)	80 m, 10°06'45"N 83°31'36"W (measured at benchmark 80, bridge just west of Siquirres)	Major river draining the S Cordillera Central, E Valle Central, and N Cordillera de Talamanca, formed by the confluence of the Río Agua Caliente and the Río Grande de Orosi; a tributary of the lower Río Parismina. The upper portions of the river (above ca. 330 m) are in Prov. Cartago. According to local usage (but not maps), "Río Reventazón" includes the Río Grande de Orosi
Río Grande de San Ramón		River with its headwaters near the village of Volio, N of San Ramón. It flows S, E and S until about 3 miles S of Atenas, where it meets the Río Virilla. From that point on to its mouth in the Pacific it receives the name of Río Grande de Tárcoles
Río Grande	485 m, 9°57'N 84°21'W	Village to the SE of Atenas
Río Jesús (de San Ramón)	870 m, 10°02'N 84°31'W	Town along the Carretera Interamericana, between San Ramón and Esparza; formerly called "San José de San Ramón"
Río Saíno (or Quebrada Saíno, spelled by Endrés 'Sajino')		Creek about 6 miles north of Zarcero, flows into the Tapezco River
Salvaje (Alto or Cerro del)	2000 m, 9°51'N 84°10'W	Peak in the Cerros de Escazú, about 6 km to the E of Palmichal de Acosta
San Carlos	150 m	Atlantic cantón of Prov. Alajuela; the name technically refers to the entire cantón, but is frequently used narrowly for Ciudad Quesada, or very broadly (in the sense of "Llanura de San Carlos" = San Carlos valley) to include portions of adjacent cantones

Locality name on Endrés label	Coordinates	Note
San Cristóbal (de Candelaria)	1710 m, 9°47'N 84°01'W	Town in the N Cordillera de Talamanca
San Francisco de San Ramón	911 m, 10°05'N 84°33'W	Town in the Cordillera de Tilarán, W of San Ramón
San Gerardo		Gold (?) mine in the district of Santiago, SW of San Ramón
San Isidro (de Alajuela)	1360 m, 10°05'N 84°12'W	Village 5.5 miles NNE of Alajuela
San José	1160 m, 9°56'N 84°05'W	City in the Valle Central; capital of Costa Rica and of Prov. San José
San Juan de San Ramón	1140 m, 10°07'N 84°28'W	N suburb of San Ramón
San Lorenzo, Río	330 m, 10°18'N 84°33'W	River draining the N slope of the Cordillera de Tilarán; an affluent (with the Río Balsa) of the Río Jabillos
San Mateo	254 m, 9°57'N 84° 31'W	Village 2.2 miles N of Orotina
San Miguel de Desamparados	1200 m , 9°52'N 84°04'W	S suburb of San José
San Pablo [de San Mateo; de Puriscal; de Turrubares]	373 m, 9°54'N 84°27'W	Town in the valley of the Río Grande de Tárcoles; properly belongs to the Cantón de Turrubares
San Pedro de Poás (de Alajuela)	1145 m, 10°05'N 84°15'W	Town NW of Alajuela, on the S slope of Volcán Poás; formerly known as San Pedro de La Calabaza
San Ramón	1050 m, 10°05'N 84°28'W	Major town in the W Valle Central
San Roque	1088 m. 10°17'N 84°17'W	Village to the N of Grecia
Santa Ana	900 m, 9°56'N 84°11'W	Town in the Valle Central, S of Alajuela and W of San José
Santa María (de Dota)	1548 m	Town along the Río Pirrís, in the N part of the Cordillera de Talamanca. We remember the name in *Lepanthes dotae* Endres ex Luer
(Fila de) Santa María (de Dota)		Chain of hills about 2 miles south of S.ta María de Dota
Santo Domingo de Vara Blanca	1500 m, 10°13'N 84°08'W	Site on the NW slope of Volcán Barva
Santiago (de Puriscal)	1102 m, 9°51'N 84°19'W	Main town in the Puriscal region, SW of Ciudad Colón; nowadays, the town is usually called simply "Puriscal"
Silencio de San Ramón (El)	1130 m, 10°10'N 84°28'W	Site in the Cordillera de Tilarán, N of San Ramón
Sitio (El)		A farm property of Don Eusebio Ortiz to the NE of Juan Viñas. A resting place for those who ascended the Turrialba volcano. In Seebach's description of his ascent, he writes: *"At 11 a.m. we arrived at a small plateau on which one can see a pasture with a house and some huts. This pasture is the 'Sitio de Eusebio Ortiz' and the last colony or hamlet in the proximity of the Turrialba."* (Liceo de Costa Rica, 1922: 19)
Tabarcia (spelled often 'Taburcia')	817 m, 9°51'N 84°14'W	Town at the SW base of the Cerros de Escazú. One of Endrés' discoveries (*Endrés 626*) was named by him *Lepanthes tabarciae*, known today as *Lepanthes inescata* Luer
Tablazo	1983 m, 9°50'N 84°03'W	Promontory on the S skyline of the Valle Central, between the Cerros de Escazú and the Cerros de La Carpintera, on the divide between the Río Virilla and the Río Grande de Candelaria

Locality name on Endrés label	**Coordinates**	**Note**
Tapesco (or Tapezco) de Zarcero	1860 m, 10°13'N 84°23'W	Town in the westernmost Cordillera Central, just NW of Zarcero along the road to Ciudad Quesada
Tapesco River	1600–1700 m	ca. 6 miles N of Zarcero
Tarrazú (Río)	1800 m, 9°46'N 83°59'W	River to the SE of Cartago, with headwaters near La Sierra
Tarrazú (San Marcos de)	1404 m. 9°40'N 84°01'W	Village on the Río Pirrís, formerly known as 'Atarrazú', which is the name used by Endrés
(El) Tejar	1380 m, 9°51'N 83°57'W	SW suburb of Cartago
Tobosi	1400 m, 9°50'N 83°59'W	Town along the Río Purires, at the extreme SE corner of the E Valle Central
Trinchera (Finca la)	90 m, 10°30'N 84°15'W	Farm and hamlet 4 miles N of Pital de San Carlos
Tucurrique	777 m, 9°52'N 83°44'W	Town along the Río Reventazón, SW of Turrialba
Turrialba (spelled 'Turialba')	650 m, 9°54'N 83°42'W	Major town at the SE base of Volcán Turrialba, in the valley of the Río Reventazón
Turrialba, Río	500–600 m, 9°54'N 83°39'W	River draining the S slope of Volcán Turrialba; a tributary of the Río Reventazón
Ujarrás (spelled 'Ujarráz')	1025 m, 9°50'N 83°46'W	Village in the valley of Orosi
Volio, Potrero, Quebrada, Hacienda	1200 m, 10°0'N 84°27'W	Formerly the farm of the prosperous family of don Julián Volio, today a small village to the N of San Ramón
Zapote (spelled 'Sapote')	1544 m, 10°13'N 84°22'W	Village on the road from Naranjo to San Carlos
Zarcero (spelled 'Sarsero')	1782 m, 10°11'N 84°20'W	Village on the road from Naranjo to San Carlos
	Panama	
Matachín Station		Station of the Panama Railroad, close to the confluence of the Chagres and Obispo Rivers
Obispo Station		Station of the Panama Railroad, just E of Matachin, on the Obispo River
San Pablo Station		Station of the Panama Railroad, about half a mile south of the bridge over the Chagres River

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Camaridium lankesteri (Ames) M.A.Blanco, ***comb. nov.*** 7(3): 520. 2007.

Camaridium longicolumna (J.T.Atwood) M.A.Blanco, ***comb. nov.*** 7(3): 520. 2007.

Camaridium lutheri (J.T.Atwood) M.A.Blanco, ***comb. nov.*** 7(3): 520. 2007.

Camaridium meleagris (Lindl.) M.A.Blanco, ***comb. nov.*** 7(3): 520. 2007.

Camaridium micranthum M.A.Blanco, ***nom. nov.*** 7(3): 520. 2007.

Camaridium microphyton (Schltr.) M.A.Blanco, ***comb. nov.*** 7(3): 520. 2007.

Camaridium mombachoense (A. H. Heller ex J.T.Atwood) M.A.Blanco, ***comb. nov.*** 7(3): 520. 2007.

Camaridium monteverdense (J.T.Atwood & G.Barboza) M.A.Blanco, ***comb. nov.*** 7(3): 521. 2007.

Camaridium neglectum (Schltr.) M.A.Blanco, ***comb. nov.*** 7(3): 521. 2007.

Camaridium obscurum (Linden & Rchb.f.) M.A.Blanco, ***comb. nov.*** 7(3): 521. 2007.

Camaridium oestlundianum (L.O.Williams) M.A.Blanco,

comb. nov. 7(3): 521. 2007.

Camaridium paleatum (Rchb.f.) M.A.Blanco, ***comb. nov.*** 7(3): 521. 2007.

Camaridium praestans (Rchb.f.) M.A.Blanco, ***comb. nov.*** 7(3): 521. 2007.

Camaridium pygmaeum M.A.Blanco, ***nom. nov.*** 7(3): 521. 2007.

Camaridium ramonense (Schltr.) M.A.Blanco, ***comb. nov.*** 7(3): 521. 2007.

Camaridium rhombeum (Lindl.) M.A.Blanco, ***comb. nov.*** 7(3): 521. 2007.

Camaridium scalariforme (J.T.Atwood) M.A.Blanco, ***comb. nov.*** 7(3): 521. 2007.

Camaridium sigmoideum (C. Schweinf.) M.A.Blanco, ***comb. nov.*** 7(3): 521. 2007.

Camaridium soconuscanum (Breedlove & D. Mally) M.A.Blanco, ***comb. nov.*** 7(3): 521. 2007.

Camaridium standleyi M.A.Blanco, ***nom. nov.*** 7(3): 521. 2007.

Camaridium stenophyllum (Schltr.) M.A.Blanco, ***comb. nov.*** 7(3): 521. 2007.

Camaridium strumatum (Endres & Rchb.f.) M.A.Blanco, ***comb. nov.*** 7(3): 521. 2007.

Camaridium suaveolens (Barringer) M.A.Blanco, ***comb. nov.*** 7(3): 521. 2007.

Camaridium synsepalum (J.T.Atwood) M.A.Blanco, ***comb. nov.*** 7(3): 521. 2007.

Camaridium tigrinum (C. Schweinf.) M.A.Blanco, ***comb. nov.*** 7(3): 521. 2007.

Camaridium tricarinatum (J.T.Atwood) M.A.Blanco, ***comb. nov.*** 7(3): 522. 2007.

Camaridium tuberculare (J.T.Atwood) M.A.Blanco, ***comb. nov.*** 7(3): 522. 2007.

Camaridium tutae (J.T.Atwood) M.A.Blanco, ***comb. nov.*** 7(3): 522. 2007.

Camaridium vaginale (Rchb.f.) M.A.Blanco, ***comb. nov.*** 7(3): 522. 2007.

Camaridium valerioi (Ames & C. Schweinf.) M.A.Blanco, ***comb. nov.*** 7(3): 522. 2007.

Camaridium vittariifolium (L.O.Williams) M.A.Blanco, ***comb. nov.*** 7(3): 522. 2007.

Chondroscaphe endresii (Schltr.) Dressler, ***comb. nov.*** 3: 28. 2002.

Christensonella cepula (Rchb.f.) S. Koehler, ***comb. nov.*** 7(3): 522. 2007.

Christensonella neowiedii (Rchb.f.) S. Koehler, ***comb. nov.*** 7(3): 522. 2007.

Christensonella pacholskii (Christenson) S. Koehler, ***comb. nov.*** 7(3): 522. 2007.

Christensonella squamata (Barb.Rodr.) Carnevali, ***comb. nov.*** 7(3): 523. 2007.

Comparettia sotoana Pupulin & G.Merino, ***sp. nov.*** 9(3): 400. 2010.

Coryanthes kaiseriana G. Gerlach, ***sp. nov.*** 8: 23. 2003.

Coryanthes maduroana G. Gerlach, ***sp. nov.*** 70

Crossoglossa sotoana Pupulin & Karremans, ***sp. nov.*** 9(3): 444. 2010.

Cryptocentrum Benth. subgenus *Anthosiphon* (Schltr.) Carnevali, ***comb. et stat. nov.*** 7(3): 543. 2007.23

Deiregyne densiflora (C.Schweinf.) Salazar & Soto Arenas, ***comb. nov.*** 9(3): 502. 2010.

Dendrophylax monteverdi (Rchb.f.) Ackerman & Nir, ***comb. nov.*** 53

Dichaea elliptica Dressler & Folsom, ***sp. nov.*** 3: 25. 2002.

Echinella vittata (Pupulin & M.A.Blanco) Pupulin, ***comb. nov.*** 4: 17. 2002.

Echinorhyncha antonii (Ortiz) Dressler, ***comb. nov.*** 5(2): 94. 2005.

Echinorhyncha Dressler, ***gen. nov.*** 5(2): 94. 2005.

Echinorhyncha ecuadorensis (Dodson) Dressler, ***comb. nov.*** 5(2): 94. 2005.

Echinorhyncha litensis (Dodson) Dressler, ***comb. nov.*** 5(2): 94. 2005.

Echinorhyncha vollesii (Gerlach, Neudecker & Seeger) Dressler, ***comb. nov.*** 5(2): 94. 2005.

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Encyclia cajalbanensis Mújica, Bocourt & Pupulin, ***sp. nov.*** 4(3): 211. 2004.

Encyclia monteverdensis M. A. Díaz & Ackerman, ***sp. nov.*** 50

Epidendrum cancanae (P.Ortiz) Hágsater, ***comb. nov.*** 5(1): 73. 2005.

Epidendrum fuscinum (Dressler) Hágsater, ***comb. nov.*** 5(1): 73. 2005.

Epidendrum jalcaënse Chocce, Dalström, Hágsater & Arnaiz, ***sp. nov.*** 9(3): 529. 2010.

Epidendrum macdougalli (Hágsater) Hágsater, ***comb. nov.*** 5(1): 74. 2005.

Epidendrum misasii Hágsater, ***nom. nov.*** 5(1): 74. 2005.

Epidendrum montis-narae Pupulin & L.Sánchez S., ***sp. nov.*** 1: 7. 2001.

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Epidendrum parviexasperatum (Hágsater) Hágsater, ***comb. nov.*** 5(1): 74. 2005.

Epidendrum sotoanum Karremans & Hágsater, ***sp. nov.*** 9(3): 405. 2010.

Epidendrum stolidium Hágsater, ***nom. nov.*** 5(1): 74. 2005.

Epidendrum × *monteverdense* (Pupulin & Hágsater) Hágsater, ***comb. nov.*** 5(1): 74. 2005.

Epidendrum zunigae Hágsater, Karremans & Bogarín, ***sp. nov.*** 8(2): 63. 2008.

Euryblema anatonum (Dressler) Dressler, ***comb. nov.*** 5(2): 94. 2005.

Euryblema andreae (Ortiz) Dressler, ***comb. nov.*** 5(2): 94. 2005.

Euryblema Dressler, ***gen. nov.*** 5(2): 94. 2005.

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Guarianthe aurantiaca (Bateman ex Lindl.) Dressler & W.E.Higgins, ***comb. nov.*** 7: 38. 2003.

Guarianthe bowringiana (Veitch) Dressler & W.E.Higgins, ***comb. nov.*** 7: 38. 2003.

Guarianthe Dressler & W.E. Higgins, ***gen. nov.*** 7: 37. 2003.

Guarianthe patinii (Cogn.) Dressler & W.E.Higgins, ***comb. nov.*** 7: 38. 2003.

Guarianthe skinneri (Bateman) Dressler & W.E.Higgins, ***comb. nov.*** 7: 38. 2003.

Inti bicallosa (Rchb.f.) M.A.Blanco, ***comb. nov.*** 7(3): 524. 2007.

Inti chartacifolia (Ames & C. Schweinf.) M.A.Blanco, ***comb. nov.*** 7(3): 524. 2007.

Inti M.A.Blanco, ***gen. nov.*** 7(3): 524. 2007.

Ixyophora aurantiaca (Senghas & Gerlach) Dressler, ***comb. nov.*** 5(2): 95. 2005.

Ixyophora carinata (Ortiz) Dressler, ***comb. nov.*** 5(2): 95. 2005.

Ixyophora Dressler, ***gen. nov.*** 5(2): 95. 2005.

Ixyophora viridisepala (Senghas) Dressler, ***comb. nov.*** 5(2): 95. 2005.

Lankesterella glandula Ackerman, ***sp. nov.*** 49

Lepanthes arenasiana Bogarín & M.Fernández, ***sp. nov.*** 9(3): 487. 2010.

Lepanthes gerardensis M.A.Blanco, ***sp. nov.*** 8: 19. 2003.

Lepanthes montis-narae Pupulin, Bogarín & C. Smith, ***sp. nov.*** 9(3): 425. 2010.

Lepanthes sotoana Pupulin, Bogarín & C. Smith, ***sp. nov.*** 9(3): 427. 2010.

Ligeophila gavilanensis Ormerod & G.A.Romero, ***sp. nov.*** 9(3): 513. 2010.

Lophiaris natalieae Balam & Carnevali, ***sp. nov.*** 9(3): 522. 2010.

Lycaste bruncana Bogarín, ***sp. nov.*** 7(3): 543. 2007.

Malaxis brevis Dressler, ***sp. nov.*** 4(1): 97. 2004.

Malaxis insperata Dressler, ***sp. nov.*** 4(1): 97. 2004.

Malaxis rostratula Dressler, ***sp. nov.*** 4(1): 97. 2004.

Malaxis triangularis Dressler, ***sp. nov.*** 4(1): 97. 2004.

Mapinguari auyantepuiensis (Foldats) Carnevali & R. Singer, ***comb. nov.*** 7(3): 525. 2007.

Mapinguari Carnevali & R. Singer, ***gen. nov.*** 7(3): 525. 2007.

Mapinguari desvauxianus (Rchb.f.) Carnevali & R. Singer, ***comb. nov.*** 7(3): 525. 2007.

Mapinguari foldatsianus (Carnevali & I.Ramírez) Carnevali & R. Singer, ***comb. nov.*** 7(3): 525. 2007.

Mapinguari longipetiolatus (Ames & C.Schweinf.) Carnevali & R. Singer, ***comb. nov.*** 7(3): 525. 2007.

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Masdevallia vilcabambensis L. Valenz. & Suclli, ***sp. nov.*** 8(1): 17. 2008.

Maxillariella acervata (Rchb.f.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 528. 2007.

Maxillariella alba (Hook.f.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 528. 2007.

Maxillariella anceps (Ames & C. Schweinf.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 528. 2007.

Maxillariella appendiculoides (C. Schweinf.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 528. 2007.

Maxillariella arbuscula (Lindl.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 528. 2007.

Maxillariella brevifolia (Lindl.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 528. 2007.

Maxillariella caespitifica (Rchb.f.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 528. 2007.

Maxillariella cassapensis (Rchb.f.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 528. 2007.

Maxillariella caucana (Schltr.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 528. 2007.

Maxillariella cobanensis (Schltr.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 528. 2007.

Maxillariella costaricensis (Schltr.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 528. 2007.

Maxillariella curtipes (Hook.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 528. 2007.

Maxillariella densifolia (Poepp. & Endl.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 528. 2007.

Maxillariella diuturna (Ames & C. Schweinf.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 528. 2007.

Maxillariella elatior (Rchb.f.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 528. 2007.

Maxillariella estradae (Dodson) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 528. 2007.

Maxillariella funicaulis (C. Schweinf.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 528. 2007.

Maxillariella graminifolia (Kunth) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 528. 2007.

Maxillariella guareimensis (Rchb.f) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 528. 2007.

Maxillariella houtteana (Rchb.f.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 528. 2007.

Maxillariella infausta (Rchb.f.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 529. 2007.

Maxillariella lawrenceana (Rolfe) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 529. 2007.

Maxillariella linearifolia (Ames & C. Schweinf.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 529. 2007.

Maxillariella longibracteata (Lindl.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 529. 2007.

Maxillariella luteorubra (F.Lehm. & Kraenzl.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 529. 2007.

Maxillariella M.A.Blanco & Carnevali, ***gen. nov.*** 7(3): 543. 2007.527

Maxillariella mexicana (J.T.Atwood) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 529. 2007.

Maxillariella microdendron (Schltr.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 529. 2007.

Maxillariella nitidula (Rchb.f.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 529. 2007.

Maxillariella oreocharis (Schltr.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 529. 2007.

Maxillariella pardalina (Garay) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 529. 2007.

Maxillariella pastensis (Rchb.f.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 529. 2007.

Maxillariella ponerantha (Rchb.f.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 529. 2007.

Maxillariella procurrens (Lindl.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 529. 2007.

Maxillariella prolifera (Sw.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 529. 2007.

Maxillariella purpurata (Lindl.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 529. 2007.

Maxillariella robusta (Barb. Rodr.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 529. 2007.

Maxillariella sanguinea (Rolfe) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 529. 2007.

Maxillariella spilotantha (Rchb.f.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 529. 2007.

Maxillariella stenophylla (Rchb.f.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 530. 2007.

Maxillariella stictantha (Schltr.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 530. 2007.

Maxillariella tenuifolia (Lindl.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 530. 2007.

Maxillariella tuerckheimii (Schltr.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 530. 2007.

Maxillariella variabilis (Bateman ex Lindl.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 530. 2007.

Maxillariella vinosa (Rolfe) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 530. 2007.

Maxillariella vulcanica (F.Lehm. & Kraenzl.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 530. 2007.

Maxillariella × *yucatanensis* (Carnevali & R. Jiménez) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 530. 2007.

Maxillariella xanthorhoda (Schltr.) M.A.Blanco & Carnevali, ***comb. nov.*** 7(3): 530. 2007.

Mormolyca acutifolia (Lindl.) M.A.Blanco, ***comb. nov.*** 7(3): 531. 2007.

Mormolyca aureoglobula (Christenson) M.A.Blanco, ***comb. nov.*** 7(3): 531. 2007.

Mormolyca chacoensis (Dodson) M.A.Blanco, ***comb. nov.*** 7(3): 531. 2007.

Mormolyca cleistogama (Brieger & Illg) M.A.Blanco, ***comb. nov.*** 7(3): 531. 2007.

Mormolyca dressleriana (Carnevali & J.T.Atwood) M.A.Blanco, ***comb. nov.*** 7(3): 531. 2007.

Mormolyca hedwigiae (Hamer & Dodson) M.A.Blanco, ***comb. nov.*** 7(3): 531. 2007.

Mormolyca lehmanii (Rolfe) M.A.Blanco, ***comb. nov.*** 7(3): 531. 2007.

Mormolyca moralesii (Carnevali & J.T.Atwood) M.A.Blanco, ***comb. nov.*** 7(3): 531. 2007.

Mormolyca pudica (Carnevali & Tapia-Muñoz) M.A.Blanco, ***comb. nov.*** 7(3): 531. 2007.

Mormolyca richii (Dodson) M.A.Blanco, ***comb. nov.*** 7(3): 531. 2007.

Mormolyca rufescens (Lindl.) M.A.Blanco, ***comb. nov.*** 7(3): 531. 2007.

Mormolyca sanantonioensis (Christenson) M.A.Blanco, ***comb. nov.*** 7(3): 531. 2007.

Mormolyca schlimii (Linden & Rchb.f.) M. A.Blanco, ***comb. nov.*** 7(3): 531. 2007.

Mormolyca sotoana (Carnevali & Gómez-Juárez) M.A.Blanco, ***comb. nov.*** 7(3): 531. 2007.

Mormolyca suarezorum (Dodson) M.A.Blanco, ***comb. nov.*** 7(3): 531. 2007.

Mormolyca tenuibulba (Christenson) M.A.Blanco, ***comb. nov.*** 7(3): 531. 2007.

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Ornithidium adendrobium (Rchb.f.) M.A.Blanco & Ojeda, ***comb. nov.*** 7(3): 532. 2007.

Ornithidium affine (Poepp. & Endl.) M.A.Blanco & Ojeda, ***comb. nov.*** 7(3): 532. 2007.

Ornithidium cachacoense (J.T.Atwood) M.A.Blanco & Ojeda, ***comb. nov.*** 7(3): 532. 2007.

Ornithidium canarense (J.T.Atwood) M.A.Blanco & Ojeda, ***comb. nov.*** 7(3): 532. 2007.

Ornithidium condorense (J.T.Atwood) M.A.Blanco & Ojeda, ***comb. nov.*** 7(3): 532. 2007.

Ornithidium donaldeedodii Ackerman & Whitten, ***sp. nov.*** 9(3): 509. 2010.

Ornithidium fasciculatum (C. Schweinf.) M.A.Blanco & I. Ojeda, ***comb. nov.*** 8(1): 15. 2008.

Ornithidium fimbriatilobum (Carnevali & G. A. Romero) M.A.Blanco & Ojeda, ***comb. nov.*** 7(3): 532. 2007.

Ornithidium gualaquizense (Dodson) M.A.Blanco & Ojeda, ***comb. nov.*** 7(3): 532. 2007.

Ornithidium haemathodes (Ruiz & Pav.) M.A.Blanco & Ojeda, ***comb. nov.*** 7(3): 532. 2007.

Ornithidium lasallei (Foldats) M.A.Blanco & Ojeda, ***comb. nov.*** 7(3): 532. 2007.

Ornithidium machinazense (D. E. Benn. & Christenson) M.A.Blanco, ***comb. nov.*** 7(3): 532. 2007.

Ornithidium maldonadoense (J.T.Atwood) M.A.Blanco & Ojeda, ***comb. nov.*** 7(3): 532. 2007.

Ornithidium minutiflorum (D. E. Benn. & Christenson) M.A.Blanco & Ojeda, ***comb. nov.*** 7(3): 533. 2007.

Ornithidium nicaraguense (Hamer & Garay) M.A.Blanco & Ojeda, ***comb. nov.*** 7(3): 533. 2007.

Ornithidium oxapampense (J.T.Atwood) M.A.Blanco & Ojeda, ***comb. nov.*** 7(3): 533. 2007.

Ornithidium patellum (J.T.Atwood) M.A.Blanco & Ojeda, ***comb. nov.*** 7(3): 533. 2007.

Ornithidium patulum (C. Schweinf.) M.A.Blanco & Ojeda, ***comb. nov.*** 7(3): 533. 2007.

Ornithidium pseudonubigenum (J.T.Atwood) M.A.Blanco & Ojeda, ***comb. nov.*** 7(3): 533. 2007.

Ornithidium pustulosum (J.T.Atwood) M.A.Blanco & Ojeda, ***comb. nov.*** 7(3): 533. 2007.

Ornithidium rauhii (D. E. Benn. & Christenson) M.A.Blanco & Ojeda, ***comb. nov.*** 7(3): 533. 2007.

Ornithidium repens (L.O.Williams) M.A.Blanco & Ojeda, ***comb. nov.*** 7(3): 533. 2007.

Ornithidium rigidum (Barb. Rodr.) M.A.Blanco & Ojeda, ***comb. nov.*** 7(3): 533. 2007.

Ornithidium scandens (D. E. Benn. & Christenson) M.A.Blanco & Ojeda, ***comb. nov.*** 7(3): 533. 2007.

Ornithidium scullianum (J.T.Atwood) M.A.Blanco & Ojeda, ***comb. nov.*** 7(3): 533. 2007.

Ornithidium sillarense (Dodson & Vásquez) M.A.Blanco & Ojeda, ***comb. nov.*** 7(3): 533. 2007.

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Pescatorea lalindei (Linden) Dressler, ***comb. nov.*** 5(2): 95. 2005.

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Porroglossum porphyreum G.Merino, A.Doucette & Pupulin, ***sp. nov.*** 9(3): 465. 2010.

Prosthechea micropus (Rchb.f.) W.E.Higgins, ***comb. nov.*** 4(3): 223. 2004.

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Rhetinantha aciantha (Rchb.f.) M.A.Blanco, ***comb. nov.*** 7(3): 534. 2007.

Rhetinantha acuminata (Lindl.) M.A.Blanco, ***comb. nov.*** 7(3): 534. 2007.

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