ADDITIONS TO THE COSTA RICAN MYOXANTHUS (ORTHIDACEAE: PLEUROTHALLIDINAE)
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ABSTRACT. *Pleurothallis cerea*, a species described based on a specimen collected by Lankester in Costa Rica, and commonly placed under the synonymy of *Myoxanthus octomeriae* or *M. congestus*, is here recognized as distinct. The species is easily distinguished by the shape and size of the leaf, as well as various floral details, especially of the lip. A new combination, tentatively suggested by Carl Luer but never published, is required and therefore validated. Additionally, the vegetatively striking *Myoxanthus affinis* is recorded from Costa Rica for the first time based on two recent collections. The species is variable within its broad distribution from Colombia to Bolivia and, although differences with the original material from Peru are evident, we cannot be sure at this time that ours represents a different species. Both species are described and illustrated based on living plants.

KEY WORDS: Carl Luer, *Myoxanthus affinis*, *M. octomeriae*, *Pleurothallis cerea*, taxonomy

Introduction. *Myoxanthus* (Orchidaceae: Pleurothallidinae) was proposed by Poeppig and Endlicher (1835) to accommodate a species collected by the first author in Peru, *Myoxanthus monophyllus* Poepp. & Endl. The genus was, however, soon treated as a synonym of *Pleurothallis* R. Br. by Lindley (1836), and its only species was transferred to the latter as *Pleurothallis poeppigii*. The second attempt to propose a new generic name for a species of *Myoxanthus* was made by Karsten (1847), when he proposed the genus *Duboisia*, later renamed *Duboisia-Reymondia* H. Karst. due to a preexisting name in the Solanaceae (Karsten 1848). Both were treated as synonyms of *Pleurothallis* by Reichenbach (1852). The proposal of *Chaetocephala* Barb. Rodr. (1882) was the third attempt at recognition for the species of *Myoxanthus* as segregates from *Pleurothallis*. But that genus was also placed under *Pleurothallis* shortly after, on this occasion by Cogniaux (1896).

The situation would remain virtually unchanged for almost a century, and it is not until 1982 that Luer reconsiders this group of species, and segregates them from *Pleurothallis*. He described one new species and transferred 33 others to his newly re-circumscribed *Myoxanthus*, with the previously mentioned *Chaetocephala*, *Duboisia* and *Duboisia-Reymondia* among its synonyms. The establishment of the genus was supported by the anatomical studies made by Pridgeon and Stern (1982). A few years after, Luer (1986) broadened the circumscription of *Myoxanthus* by transferring *Pleurothallis aspasicensis* Rchb.f. and *Pleurothallis pan* Luer, later selected as type species of *Myoxanthus* subgen. *Satyria* Luer, and *Myoxanthus* subgen. *Silenia* Luer respectively, and their allies to the genus. In his monograph of *Myoxanthus*, Luer (1992) included 47 species and divided them into three subgenera, *Myoxanthus* subgen. *Myoxanthus* (with sections *Antenella* Luer, *Myoxanthus*, and *Scandentia* Luer), *Myoxanthus* subgen. *Satyria*, and *Myoxanthus* subgen. *Silenia*. The morphological features of the seven members of subgenera *Silenia* and *Satyria* were very unlike the species of subgenus *Myoxanthus*, shedding doubt on their affinities within the genus. Reconsidering his initial interpretation, Luer (1995) transferred the two sections to *Pleurothallis* subgen. *Acianthera* (Scheidw.).
The DNA evidence published by Pridgeon, Solano and Chase (2001) showed that *Myoxanthus* is indeed not closely related to *Pleurothallis*, and that it is monophyletic with the exclusion of the species belonging to subgen. *Silenia* and subgen. *Satyria*. These two subgenera were finally segregated into a novel generic concept under the name *Echinosepala* Pridgeon & M.W Chase (Pridgeon & Chase 2002). Karremans (2016) suggests that *Echinosepala* and *Myoxanthus* are sister genera within the Restrepia affinity, which is the same we have found in our own unpublished analyses, albeit with weak support.

*Myoxanthus* as defined by Pridgeon (2005) and Karremans (2016) is an easily recognizable and monophyletic genus within the Pleurothallidinae with some 49 accepted species, distributed from southern Mexico, throughout Central America, to Bolivia and Brazil (Luer 1986, 1992). The highest diversity is found in Ecuador (with 25 species), Colombia (14 species), Peru (13 species) and Venezuela (11 species). The genus has one of the broadest altitudinal distributions within the Pleurothallidinae, ranging from 3 m (in Brazil) to 3200 m (in Colombia) (Pridgeon 2005), but being more frequent at elevations between 1000 and 2500 m (Luer 1992).

The plants of *Myoxanthus* are epiphytes, lithophytes, or occasionally terrestrial, herbs, with caespitose, repent, or scandent habits, characterized by having rhizomes and ramicauls with hispidulous, scurfy sheaths (Luer 1992) with unicellular trichomes arranged in lines perpendicular to the axis of the stem (Pridgeon & Stern 1982). The sepals are usually fleshy and often pubescent, the laterals usually connate; the petals are usually linear, fleshy or thickened toward the apex, sometimes with osmophores (Luer 1982). The lip is thick, variously shaped, and delicately hinged to a thick column-foot. The column is semiterete, variably winged or toothed, the anther is ventral, with a pair of ovoid pollinia, brought together by a pair a whale-tail like caudicles. The anther cap is cellular-glandular, often ciliate, fimbriate or papillose on the upper edge (Luer 1992).

Pupulin (2002) cited seven species of *Myoxanthus* in his catalogue of the orchids of Costa Rica, whereas Luer (2003) would include only five of them in the *Manual de Plantas*, and only mentioning *Myoxanthus exasperatus* (Lindl.) Luer and *Myoxanthus trachychlamys* (Schltr.) Luer, as cited by the first, but without expressly excluding them. With the later addition of *Myoxanthus sotoanum* Pupulin, Bogarin & Mel. Fernández, a new species similar to *M. scandens* (Ames) Luer, published by Pupulin, Bogarin and Fernández (2010), eight species of *Myoxanthus* are currently reported for the country. Two additional species are here recognized for the flora of the country, bringing the total to ten. One, *Myoxanthus affinis* (Lindl.) Luer, is newly reported based on two recent collections, while *Pleurothallis cerea* Ames, a species described from Costa Rica and commonly placed under the synonymy of *Myoxanthus octomeriae* (Schltr.) Luer or *M. congestus* (A. Rich. & Galeotti) Soto Arenas, is recognized as a distinct species and transferred to *Myoxanthus*.

**Taxonomic treatment**

*Myoxanthus affinis* (Lindl.) Luer, Selbyana 7: 35. 1982.


TYPE: Peru. Dept. of San Martín: Lithophytic, Province of Chachapoyas, 1835, *Mathews 1899* (holotype, K; photo of type!; Fig. 1).


TYPE: Peru. Dept. of San Martín: Lithophytic near Chachapoyas, 1840, *Mathews 3187* (holotype, G; photo of type!).


TYPE: Ecuador. Prov. of Morona Santiago: Andes east of Sigsig, 1887, *F. C. Lehmann 6511* (holotype, K; photo of type!; Fig. 2).

*Plant* large, epiphytic, densely caespitose. *Roots* flexuous, branching, 1–2 mm in diameter. *Ramicauls* stout, erect, up to 70 cm long, 3–5 mm in diameter, enclosed by overlapping, tubular sheaths. *Sheaths* light brown, papyraceous, 6–10 cm long, covered by trichomes except the uppermost, trichomes dark, disposed in rows perpendicular to the ramicaul axis. *Leaf*
FIGURE 1. Holotype of Pleurothallis affinis Lindl. (= Myoxanthus affinis) deposited at K. Reproduced with the kind permission of the Director and the Board of Trustees Royal Botanic Gardens, Kew.
Figure 2. Holotype of *Pleurothallis furfuracea* F.Lehm. & Kraenzl. (= *Myoxanthus affinis*), deposited at K. Reproduced with the kind permission of the Director and the Board of Trustees Royal Botanic Gardens, Kew.
erect, chartaceous, elliptic, acute to shortly acuminate, 15–27 × 5–10 cm, cuneate basally into a twisted petiole, 1.0–1.5 cm long. Inflorescences many, emerging from the apex of the rami culum, enclosed by a papyraceous sheath 6–8 mm long, appearing successively, several flowering simultaneously, racemose, developing a single flower, the remainder of the raceme vestigial, peduncles persistent and thus becoming subfas ciculate with time, 8.0–12.0 × 0.5 mm, with purple trichomes; floral bracts infundibular, 2–5 mm long, with purple trichomes, enclosing the pedicel and the base of the ovary; pedicel stout, 2–3 × 1 mm, with a few purple trichomes. Ovary cylindrical, glandular, 2 × 1 mm. Sepals greenish-yellow, with a few purple points abaxially; dorsal sepal narrowly ovate, acute, 7.0–9.0 × 2.5–3.0 mm, 5-veined, margins lightly glandular; lateral sepals connate at the base, narrowly ovate, acute, 7.0–9.0 × 1.5–2.0 mm, 4-veined; petals greenish-yellow, translucent basally, narrowly ovate-triang ular, acute with apex narrowly rounded, 7.0–9.0 × 1.5–2.0 mm, thickened above the middle, conspicuously glandular along the margins, 3-veined; lip white to yellowish, with purple margins, 3-veined, ovate-trilobulate, 2 × 1 mm, lateral lobes erect, margins serrulate to crenulate, apex obtuse, irregular, sometimes slightly emarginate with an apicule, the disc with a low pair of longitudinal, purple carinae, papilllose to verrucose in the center, the base subtruncate, hinged to the apex of the column foot; column greenish-white, winged, stout, semiterete, slightly arched, 2.0–2.5 × 1.0 mm, irregular and purple at the apex, with a pair of acute teeth, the foot concave, stout, 1 mm long. Anther cap white, with purple in the middle; 0.5 × 0.5 mm; pollinia two, yellow, ovoid, laterally flattened, 0.3 mm wide, with a pair of small, flat, white caudicles.

Note: This description is based only on the Costa Rican material of this species.

Material studied. Costa Rica. Cartago: Jiménez, Pejibaye, La Marta, laderas del Río Gato. Reserva Biológica La Marta, sendero Tepemecines, bosque muy húmedo premontano. 9°46’52”N, 83°41’15”W, 790 m, 27 de marzo 2016, A. P. Karremans, M. Contreras Fernández, C. Mora, I. Pérez & J. Velásquez 6990 (JBL-Spirit!; Fig. 3). Cartago: Turrialba, Tayutic, Jicotea, Finca La Pradera. Bosque muy húmedo premontano. 9°47’06.79” N, 83°32’49.48” W, 1073 m, epífitas en vegetación madura a orillas de una quebrada, 22 de septiembre 2016, G. Rojas-Alvarado, I. Chinchilla, M. Díaz & A. P. Karremans 69 (JBL-Spirit!; Fig. 4). No additional specimens from Costa Rica were found at JBL, UCR, INB-UCR, USJ or SEL.

Distribution and ecology. Widely distributed from Costa Rica to Peru and Bolivia, where it has been reported to grow at elevations between 350 and 2500 m. In Costa Rica, this large and characteristic species had not been collected until very recently in the premontane very wet forests of Turrialba and Jiménez in Cartago (Fig. 5), a well botanized area where the species has somehow passed overlooked. It flowered in cultivation from December to February.

This species was first collected in Chachapoyas, Peru, by Mathews in 1835, and was described later by Lindley as Pleurothallis affinis. Luer (1992) considered Myoxanthus affinis a variable species and included two other names as synonyms under it. The first, Pleurothallis rigidifolia, was described by Reichenbach in 1855 based on a plant also collected by Mathews in the same locality where he collected the type of P. affinis. The second, Pleurothallis furfuracea, was described by Lehmann and Kraenzlin in 1899, based on a plant collected in Ecuador.

Even though there are observable morphological differences between the types of P. affinis, P. rigidifolia and especially P. furfuracea, the original descriptions of the first two are too vague to allow for a detailed comparison. Across the wide range of this species it seems to be quite variable, and there is apparently little consistency in some of the diagnostic features that could be used to distinguish them. At Selby there are several sketches of diverse individuals of this species prepared by Luer, and illustrations by other authors have appeared in several local floras. The illustrations clearly show variation in the presence and absence of trichomes on the sepals, the shape and ornamentation of margins of the petals, the shape of the lip and the ornamentation of the apex of the column, and none seem to be consistent. Especially outstanding is the variation in the width of the leaf. The Costa Rican material (Fig. 3–4) consistently has very broad, chartaceous leaves, quite unlike those of type specimen from Peru (Fig. 1). Nevertheless, the type specimen of P. furfuracea from Ecuador (Fig. 2) shows a habit much like that of the Costa Rican specimens il-
Illustrated here, and we have no doubt that they represent the same species. It is possible that more than a single species are currently treated under the name *M. affinis*, but we concur with Luer that at this time it is impossible to set these entities apart.

In Costa Rica, *Myoxanthus affinis* is easily distinguished from all other *Myoxanthus* species by its outstanding vegetative features. It is the only species with ramiicauls that reach up to 70 cm tall, bearing large, chartaceous, elliptic leaves. The less developed stems of *M. affinis* are rivaled in size only by well developed plants of *Myoxanthus cereus* (Ames) Luer ex Rojas-Alv. & Karremans, which is also treated here. But the latter can be easily distinguished by its coriaceous leaves (vs. chartaceous leaves), sheaths of the ramiicaul with shedding trichomes (vs. sheaths of the ramiicaul with persistent trichomes), flowers with ovary 5–6 mm long (vs. ovary 2 mm long), peduncles 1–2 mm long (vs. peduncles 8–12 mm long) sepals oblong-ovate and obtuse (vs. sepals narrowly ovate and acute), and petals glabrous (vs. petals with glandular margins).

*Myoxanthus cereus* (Ames) Luer ex Rojas-Alv. & Karremans, **comb. nov.**

**Bas.** Pleurothallis *cerea* Ames, Schedul. Orchid. 4: 19, 1923.

**TYPE:** Costa Rica. Provincia de Cartago: Agua Ca-

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**Plant** medium, epiphytic, subcaespitose, rhizome stout, covered by hispidulous sheaths. **Roots** flexuous, branching, 1–3 mm in diameter. **Ramiicauls** stout, erect, up to 45 cm long, 3–5 mm in diameter, thicker basally, enclosed by overlapping, tubular sheaths. **Sheaths** light brown to whitish, papyracceous, 5–9 cm long, with dark trichomes disposed in rows perpendicular to the ramiicaul axis, deciduous leaving scars. **Leaf** coriaceous, elliptic, acute, 17.0–23.0 × 4.5–7.5 cm, cuc-neate basally into a 1 cm long petiole. **Inflorescences** many, emerging from the apex of the ramiicaul, appearing successively, several flowering simultaneously, racemose, developing a single flower, the remainder of the raceme vestigial, peduncles persistent and thus becoming subfasciculate with time, 1–2 mm long; **floral bracts** infundibular, with purple trichomes, 3–6 mm long, enclosing the pedicel; **pedicel** stout, 3–4 mm long. **Ovary** cylindrical, glandular, 5.0–6.0 × 1.0–1.5 mm. **Sepals** white to cream above the middle, 3-veined, glabrous, thickened above the middle, **dorsal sepal** oblong-ovobate, obtuse, 10.0–10.5 × 3.0–3.5 mm, 3-veined, **lateral sepals** free to connate only at the base, oblong-ovate, obtuse, 8.0–9.0 × 2.5–3.0 mm, **petals** white to cream, glabrous, narrowly oblong-ovate, obtuse, 9.0 × 2.0–2.5 mm, thickened above the middle, 3-veined; **lip** white, with purple margins, oblong, 2 × 1 mm, 3-veined, apex obtuse, apiculate, the disc with a minute pair of longitudinal lamellae in the middle, papillose-verrucose in the center, the base truncate, hinged on the apex of the column foot; **column** white, winged, stout, semiterete, 2 × 1 mm, apex with a pair of acute teeth, the foot concave, stout, 1 mm long, with light purple at the apex. **Anther cap** purple with white margins, granular, apex verruculose, 0.6 × 0.5 mm, **pollinia** two, yellow, ovoid, laterally flattened, 0.3 mm wide, with a pair of small, flat, white caudicles.

Figure 6. Holotype of Pleurothallis cerea Ames (≡ Myoxanthus cereus), deposited at K. Reproduced with the kind permission of the Director and the Board of Trustees Royal Botanic Gardens, Kew.
sobre el Río. 9°57’16” N, 83°46’12” W, 1800 m, 31 de enero 2005, A. P. Karremans 754 (JBL-Spirit!). Cartago: Cartago, San Nicolás, Cerros la Carpintera, Campo Iztáru. Bosque remanente. 9°53’18.1” N, 83°58’08.0” W, 1750 m, 26 de octubre 2014, A. Cascante 2444 (USJ!; Fig. 8). Costa Rica. Without further collection data, 14 de noviembre 1978, Mora de Retana s.n. (USJ!). Costa Rica. Without further collection data, A. Endrés s.n. (W-0019911!).

**Distribution and Ecology.** This species is currently only known from a few localities around Cartago in Costa Rica. It is found as an epiphyte in lower montane and premontane very wet forest, at elevations between 974 and 1800 m (Fig. 9). It flowered in cultivation from December to April.

The type specimen of *Pleurothallis cerea* Ames was collected by Charles Lankester in Cartago, Costa Rica, and described by Oakes Ames in 1923. Luer (1992) placed *P. cerea* under the synonymy of *Myoxanthus octomeriae*, a species based on a plant collected by Powell from Panama. Nevertheless, Luer did note differences between the two species, and in 1991 annotated a specimen collected by Endrés from Costa Rica as “*M. cereus* (Ames) Luer”, a combination which he never published. When Soto (2008) revised the taxonomy of the Mexican *Myoxanthus*, he reduced *M. octomeriae*, with all its synonyms, to the synonymy of the older *M. congestus*, a name based on material from Mexico. However, he also noted the odd features of *P. cerea*, especially in the size and shape of the leaf and in the lip structure.

Here we formally recognize the distinctness of *M. cereus* from *M. congestus* (= *M. octomeriae*), both of which are found in Costa Rica. *Myoxanthus cereus* is distinguished from *M. congestus* by the larger, elliptic leaves 17.0–23.0 × 4.5–7.5 cm (vs. smaller, narrowly elliptic 5.0–15.0 × 2.0–4.5 cm), sepals oblong, obtuse and glabrous (vs. ovate, acute with minute warts externally), lip apex obtuse, apiculate, with a pair of longitudinal lamellae in the middle (vs. lip apex acute, without an apicule, lacking lamellae), anther cap shortly verrucose at the apex (vs. anther cap conspicuously dorsally papillose). *Myoxanthus cereus* is apparently endemic to the Atlantic watershed of the mountains of the Central Valley in the province of Cartago, where it is found growing above 1000 m in elevation. It has not been found growing sympatrically with *M. congestus*,...
a species that is more commonly found at lower elevations on both Atlantic and Pacific watersheds of the Costa Rican mountain chains.

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