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A revision of the saprophytic orchid genera *Wulfschlaegelia* and *Uleiorchis*

By

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With 9 figures

Abstract

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The present revision deals with four species in two saprophytic genera of Orchidaceae in the Neotropics: *Wulfschlaegelia* and *Uleiorchis*. This is in continuation of a series of revisions of Burmanniaceae, saprophytic Gentianaceae, and Triuridaceae for Flora-Neotropica (MAAS & Collaborators 1986).

Keywords: Orchidaceae, Neotropics, saprophytism, taxonomy, *Wulfschlaegelia*, *Uleiorchis*.

Introduction

SCHLECHTER (1926, 1927) revised the classification of the Orchidaceae, dividing the family into two subfamilies and recognizing three tribes in the monandrous orchids; his classification has been widely used. GARAY (1960, 1972) raised each of the three monandrous tribes of SCHLECHTER to subfamily status, thus increasing the total number of orchidaceous subfamilies to five. Both authors treated *Wulfschlaegelia* as a member of the tribe Cranichidinae. Recent workers find that the monandrous orchids with soft, mealy pollinia are a polyphyletic and paraphyletic grade, some are relatively closely related to the subfamily Orchidoideae; some, like the Vanillaee, are very distinctive and may merit subfamilial status, while others are closely related to the advanced Epidendroideae (DRESSLER & CHASE 1995).

The genus *Wulfschlaegelia* Reichenbach f. (1863) was based on *Cranichis aphylla* Swartz. That *Wulfschlaegelia* has been listed as a member of the

Cranichidinae by many subsequent authors must be ascribed to taxonomic inertia. The Cranichidinae are characterized by a dorsal anther on a tapering column and a small, terminal viscidium; the pollinia are generally clavate, with the pollinia narrowed to the point of attachment of the viscidium. In *Wulfschlaegelia* the anther is largely embedded in a very short column, and the viscidium is associated with the ventral side of the anther. The anther is very unusual, but may be a modification of the incumbent anther found in most epidendroid orchids. The pollinia are sectile, with narrow ellipsoid massulae. Sectile pollinia occur in a number of groups, including the Cranichideae-Goodyerinae, but not the Cranichidinae, which in the strict sense have rather firm, brittle pollinia. The Gastrodieae are characterized by incumbent anthers, sectile pollinia, and viscidia ventral to the anther. STERN et al. (1993) have studied the anatomy of the "Spiranthoid" groups, including the Cranichideae. Dr. STERN is just beginning his work with *Wulfschlaegelia* and the Gastrodieae, but he can already assure us (pers. comm.) that the anatomy of *Wulfschlaegelia* is quite unlike anything in the Cranichideae.

The seed structure of *Wulfschlaegelia* is referred to the *Gastrodia* type by ZIEGLER (1981), though he also sees some resemblances to the *Goodyera* seed type. SCHILL & PFEIFFER (1977) show that the pollen structure of *Wulfschlaegelia* is very unlike that of the Cranichideae; they did not examine (other) members of the Gastrodieae, but HESSE et al. (1989) illustrate the pollen surface of *Gastrodia sesamoides*, with structure very like that of *Wulfschlaegelia*. DRESSLER (1980) discusses the features of *Wulfschlaegelia* and, impressed by its unique features, assigns it to a new tribe, *Wulfschlaegeliaceae*. In 1983, however, he reduces this to a subtribe *Wulfschlaegeliinae* in the tribe Gastrodieae.

The genus *Uleiorchis* was created by HOEHNE (1944), based on a species originally placed in *Wulfschlaegelia* by COGNIAUX (1895). DRESSLER's 1981 classification lists *Uleiorchis* as a member of subtribe *Gastrodiinae* in the tribe Gastrodieae. The tribe Gastrodieae at that time also includes the subtribes *Nerviliinae* and *Rhizanthellinae*. In DRESSLER's 1993 survey, the Gastrodieae are regarded as part of a diverse and probably paraphyletic "primitive Epidendroid grade", and appear much modified. They now include the subtribes *Gastrodiinae*, *Epipogiinae*, and *Wulfschlaegeliinae*. SZLACHETKO (1995) narrows down the concept in excluding *Epipogiinae*, thus leaving only the other two subtribes.

Molecular systematics is making great strides in clarifying orchid relationships, but this work usually involves chloroplast genes, which may be hard to find in these obligate mycotrophic groups, even when live material is available.

SEM studies of trichomes and seeds

For SEM studies, dried material or material preserved in spirit was gold-palladium coated for three minutes using an EMSCOPE sputtercoater, and examined through a Dualstage ISI Scanning Electron Microscope at 10 kV (for the seeds) and a Cambridge

Stereoscan at 10 kV (for the trichomes). For the examinations of trichomes and seeds, one or two representative specimens were used. *Uleiorchis* being glabrous as far as known, trichomes were studied in *Wulschlaegelia* only. Seeds of *Uleiorchis liesneri* were not available and could not be investigated.

Trichomes

Wulschlaegelia aphylla (Figs. 1a, c, e, g, 2b, c)

Material investigated: *Hatschbach* 26342, *Hatschbach & Guimarães* 16053.

Trichomes grouped in dense clusters particularly near top of the stem (Fig. 1a), almost lacking near the base; 0.2–0.5 mm long, simple or branched, stalked, pluricellular (number of cells varying from 3–12; Figs. 1c, e, 2b, c), the cells swollen and gland-like, separated by constrictions (Fig. 1e), basal cell tapering towards base, walls smooth. Fig. 1g shows the remnants of the basal cell with a membranous-like tissue in the centre.

Wulschlaegelia calcarata (Figs. 1b, d, f, h, 2a)

Material investigated: *Born et al.* 41, *Maas et al.* 7901.

Trichomes distributed evenly, densely so near top of the stem (Fig. 1b), less densely towards the base, 0.1–0.6 mm long, simple (Fig. 1h), or with 2–3 (or more) branches over most of the length or only near the top (Figs. 1d, f, 2a), stalked, pluricellular, cells swollen or not but not appearing gland-like, not separated by constrictions (Figs. 1f, 2a), terminal cell elongate, apex rounded (Fig. 1f), basal cell tapering towards base and shorter than remaining cells. (Fig. 2a), walls smooth.

Seeds

Wulschlaegelia aphylla (Fig. 3a, b)

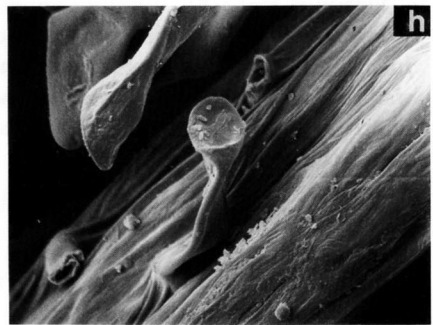
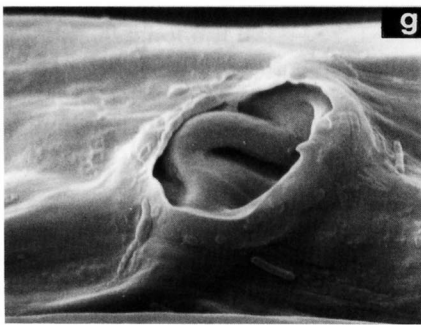
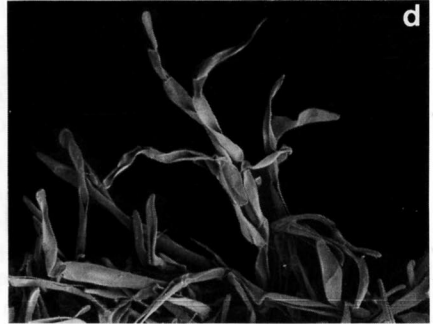
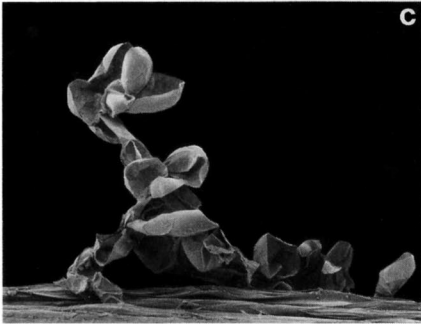
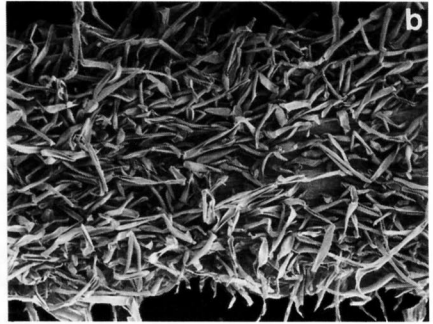
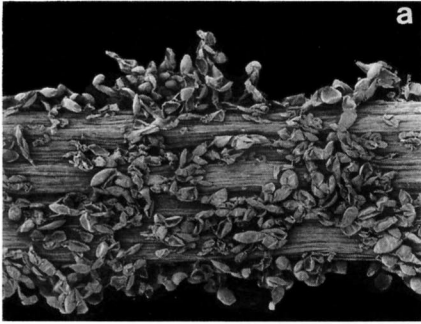
Material investigated: *Mamede et al.* 388, *Hatschbach & Guimarães* 16053.

Seeds filiform to fusiform, poles rounded, 750–1100 μm long, 90–125 μm wide, length/width ratio = 9. Epidermal cells oblong to rectangular, arranged in parallel longitudinal rows; anticlinal walls and cell junctions distinctly raised, smooth, straight; outer periclinal walls sunken, surface smooth with longitudinal oblique thickenings.

Wulschlaegelia calcarata (Fig. 3c, d)

Material investigated: *Maas et al.* 7091.

Seeds filiform to fusiform, poles acute to rounded, 1280–1840 μm long, 80–120 μm wide, length/width ratio = 16. Epidermal cells oblong, arranged in



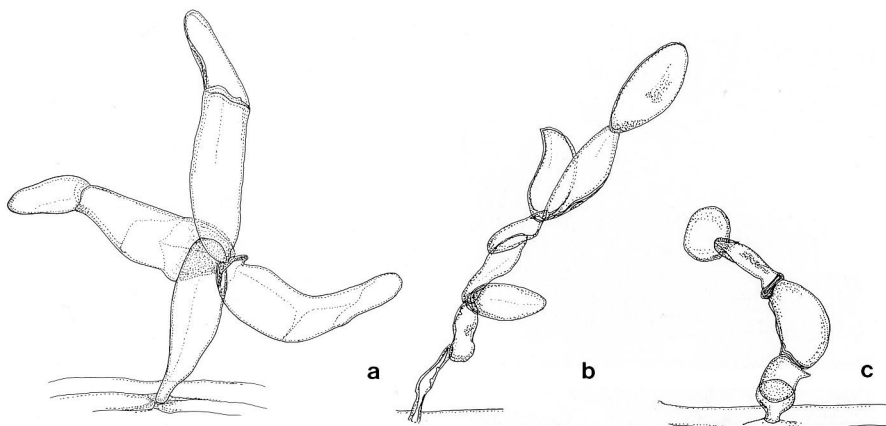


Fig. 2. Light-optical study of trichomes of *Wulfschlaegelia*. — a, *W. calcarata*, $\times 66$; b, c, *W. aphylla*, different branching patterns, $\times 66$, Drawings by M. G. BORN.

parallel longitudinal rows; anticlinal walls and cell junctions distinctly raised, smooth, straight; outer periclinal walls sunken, surface smooth with longitudinal and striate oblique thickenings.

Uleiorchis ulaei (Fig. 3e, f)

Material investigated: *Born et al. 70*.

Seeds filiform to fusiform, twisted, poles acute, 1625–2700 μm long, 70–120 μm wide, length/width ratio = 23. Epidermal cells oblong, arranged in parallel longitudinal rows; anticlinal walls and cell junctions distinctly raised, smooth, straight, outer periclinal walls sunken, surface smooth, with longitudinal, oblique thickenings.

Conclusions

The two species of *Wulfschlaegelia* are characterized by two different trichome types by which the species can be well distinguished from each other.

Fig. 1. SEM study of trichomes of *Wulfschlaegelia* — a, c, e, g, *W. aphylla*: a, trichomes near tip, $\times 22$; c, branching pattern of hair, $\times 70$; e, hair with base cell, $\times 146$; g, remnant of base cell, $\times 1714$. b, d, f, h, *W. calcarata*: b, trichomes near tip, $\times 23$; d, branching pattern of hair, $\times 50$; f, two 3-branched trichomes, $\times 140$; h, simple branched hair, $\times 305$.

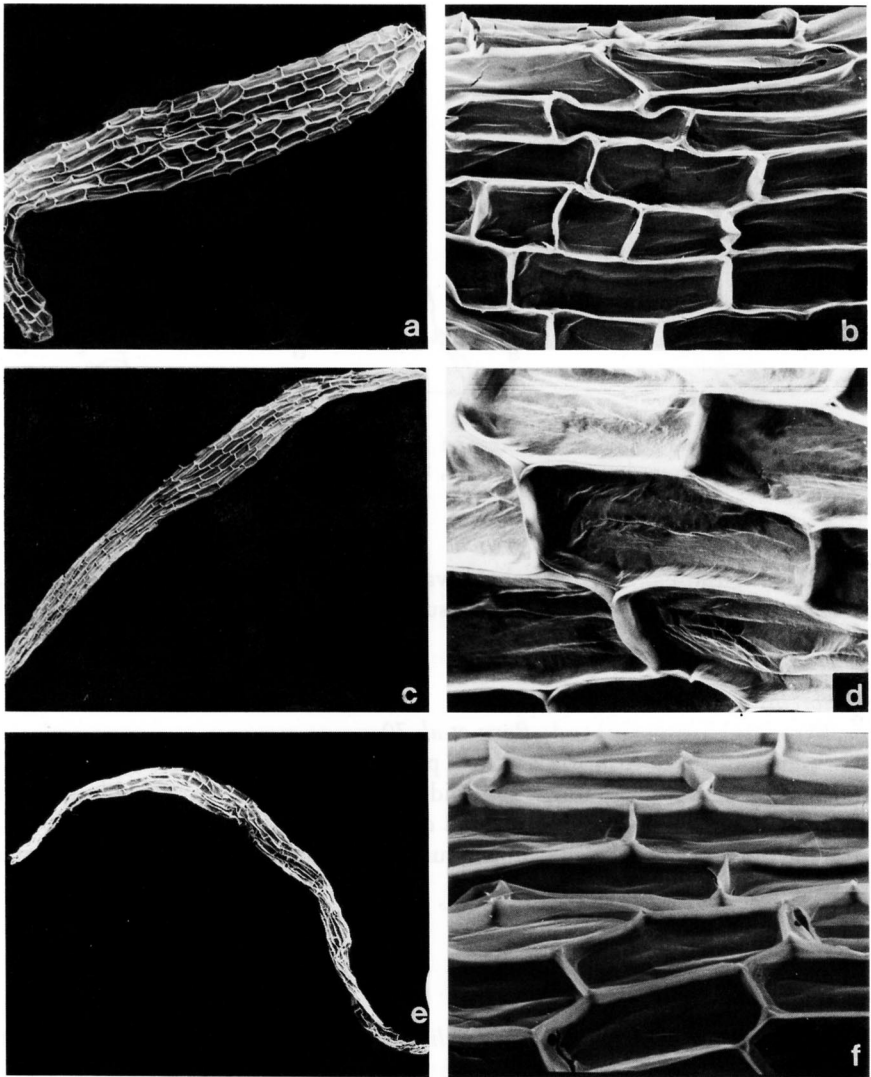


Fig. 3. Seeds of *Wulfschlaegelia* and *Uleiorchis*. — a, b, *W. aphylla*: a, seed, $\times 63$; b, detail of seed, $\times 25$. c, d, *W. calcarata*: c, seed, $\times 26$; d, detail of seed, $\times 442$. e, f, *U. ulaei*: e, seed, $\times 25$; f, detail of seed, $\times 326$.

W. aphylla has clustered hairs (Fig. 1a) consisting of swollen cells separated by constrictions (Figs. 1c, e, 2b, c). *W. calcarata* has hairs evenly distributed (Fig. 1b), consisting of more or less swollen cells not separated by constrictions (Figs. 1f, 2a).

The seeds of the three species studied are highly similar and do not allow to distinguish between the species, notwithstanding the shorter length of the seeds of *W. aphylla*.

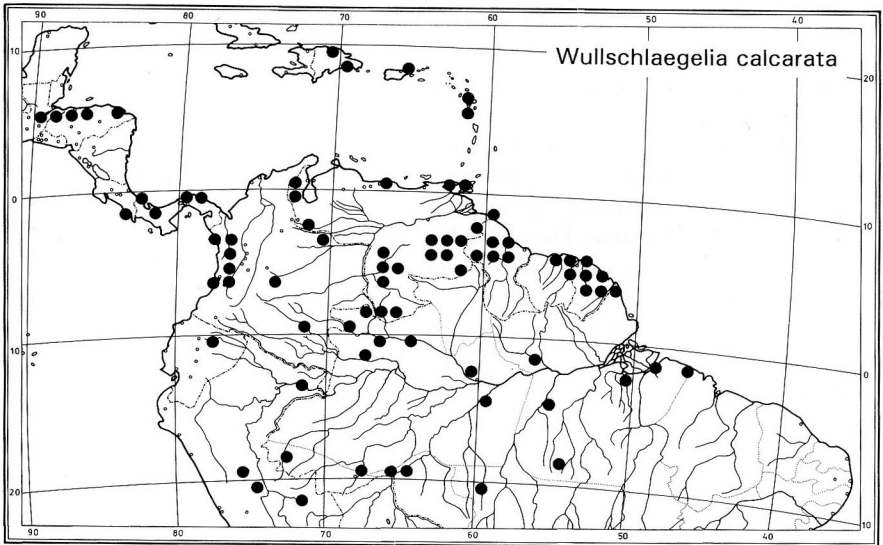
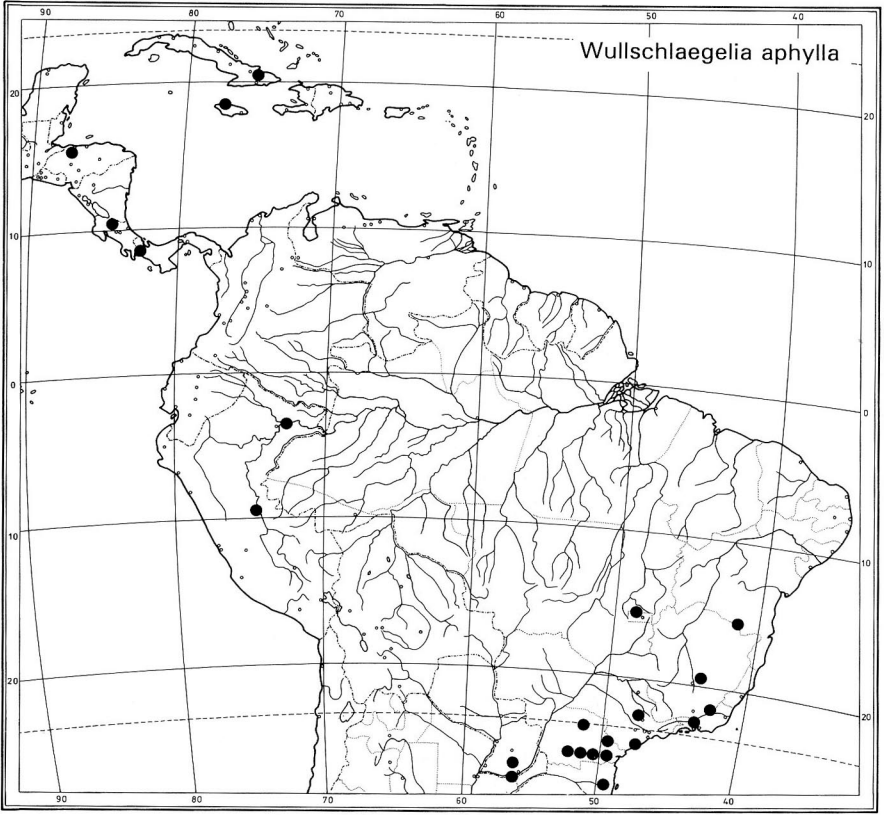
Distribution

There is an obvious contrast between the distribution pattern of *Wulfschlaegelia aphylla* on one hand, and that of *Wulfschlaegelia calcarata* and *Uleiorchis ulaei* on the other hand. It seems too early to say anything about *Uleiorchis liesneri* now, that species being known so far from a single collection in Amazonian Venezuela at a rather high elevation.

Wulfschlaegelia aphylla exhibits a peculiar bimodal distribution pattern (Fig. 4). The species occurs in Cuba, Jamaica, Honduras, Costa Rica, and Panama, in rain forest up to 600 m. The other part of the area includes Amazonian Peru, SE Brazil extending to Rio Grande do Sul in the South, and Paraguay. According to the notes on the herbarium material it appears that *W. aphylla* prefers a relatively dry vegetation type like woodlands in open field, wood islands on slopes of creek and river valleys, on sandstone slopes, and outcrops up to 1400 m, and savanna forest. Specimens were also collected in *Araucaria* forest with an annual temperature between 13–18 °C and an annual rainfall between 1000–2500 mm.

Wulfschlaegelia calcarata shows a more continuous distribution pattern: from the Dominican Republic (ca. 19° N lat.) to ca. 11° S lat. in Brazil. It is known from various forest types: premontane wet forest, primary and secondary rain forest in river valleys and on ridge tops above rocky savannas, in *Mora* forest (Guyana), in high savanna forest and often on stream edges and river slopes around falls in the non-flooded zone. It sometimes grows on moss-covered stumps or among roots and buttresses of trees (sometimes in association with *Uleiorchis ulaei*), according to notes accompanying several collections from Venezuela and the Guianas. Data from herbarium material show that *W. calcarata* occurs on mixed white sand and red clay, deep humous soil, grey clay-silt soil, or lateritic gravelly soil (Guianas).

It seems that *W. aphylla* occurs only at the periphery of the area of *W. calcarata* (Fig. 4). The latter, as said above, shows a more continuous distribution pattern. An explanation for this difference is not readily apparent. Maybe *W. aphylla* had been excluded by competition on wetter vegetation types or maybe they are associated with a different type of mycorrhizal fungi. If they are epiparasites, the distribution of host species could determine their location (BLACK 1980).



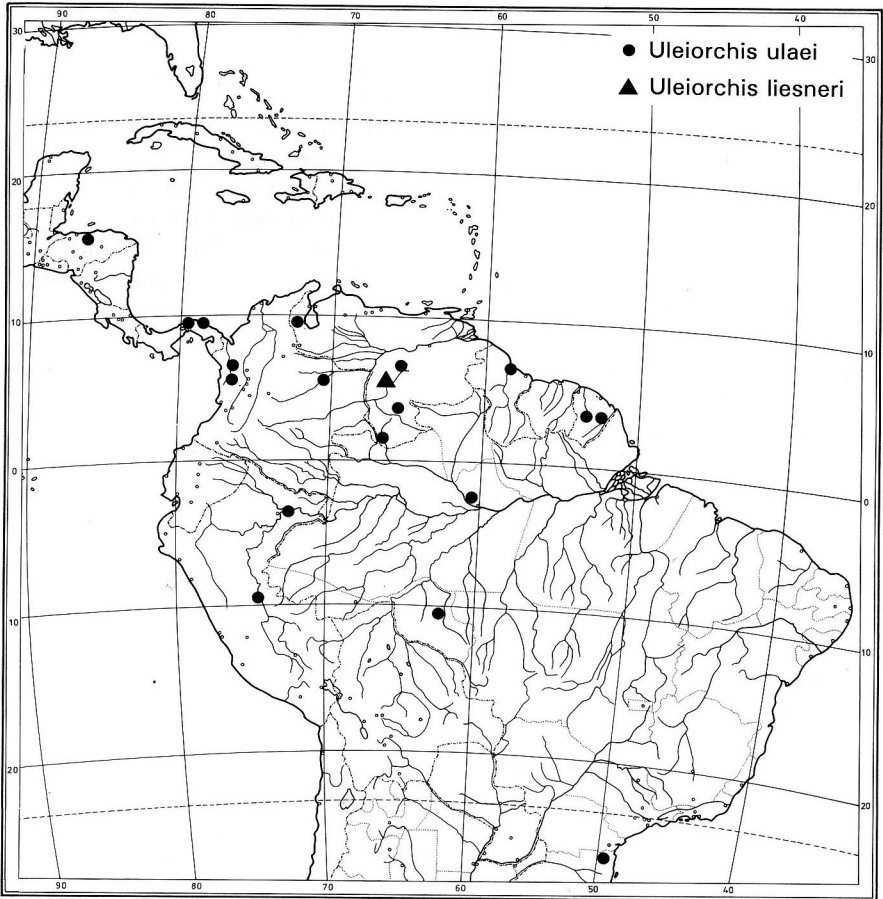


Fig. 5. Distribution map of *Uleiorchis ulaei* and *U. liesneri*.

Uleiorchis ulaei shows the same distribution pattern as *Wulfschlaegelia calcarata* (Fig. 5). Although *Uleiorchis ulaei* occurs in the same area, there are gaps in the distribution pattern most likely due to scarcity of collections. *Wulfschlaegelia calcarata* and *Uleiorchis ulaei* are known from lower elevations than *Wulfschlaegelia aphylla*: most of the specimens were collected between sea level and 600 m. There are only two collections known between 750–1400 m.

Fig. 4. Distribution maps of *Wulfschlaegelia aphylla* and *W. calcarata*, respectively.

Ecology

Species of *Wullschlaegelia* and *Uleiorchis* are terrestrial, saprophytic herbs with roots of the bird's nest or morning star type, i.e., more or less fleshy roots crowded and oriented like the rays of a star or forming bird's nest-like clumps. In *Uleiorchis* there is also a tuber-like rhizome part. *Wullschlaegelia* lacks such a tuber, but, instead, some of its roots appear swollen and resemble tubers. A general trait in saprophytes is the lack of root trichomes (JOHOW 1885). Such a root pattern often occurs in saprophytic plants thriving in a humous substrate (JOHOW op. cit.), like decaying leaves, leaf mould, or hummocks, although they sometimes grow on moss-covered stumps or dead decaying wood. They can be found in scattered, little groups or more regularly distributed.

The term saprophyte is used for any plant that does not produce its own food by photosynthesis, but uses external organic material (through decomposition of other plants) as a primary energy source instead. Saprophytes generally live in symbiosis with mycorrhizal fungi. There is an exchange of nutrients by transport of carbohydrate from the fungus to the orchid plant, and transport of amino acids from the orchid to the fungus. However, the mechanism and the equality of the transport is not clear. INGOLD (1961) suggested three possibilities. First, the fungus living in the soil outside and in close touch with the host, breaks down insoluble organic material and liberates soluble substances, such as sugars, which then are taken up by the host. Secondly, fungal hyphae in the soil translocate organic food into the living fungal cells in the host and this may then diffuse into the orchid cells. Thirdly, soluble organic food becomes available by breakdown of the hyphae in the zone between the infected and the non-infected cells of the host (FURMAN & TRAPPE 1971; INGOLD 1961). Generally, there are two types of mycorrhiza: ectomycorrhiza, where the fungus does not penetrate the cells, and endomycorrhiza where the fungus does penetrate the cells. In the present case of ectomycorrhiza, the fungus forms a mycelial layer around the outside of the roots.

For most green orchids the association with a special fungus is indispensable if their seeds are to germinate and become established. They are dependent on their mycorrhiza until they photosynthesize. In the saprophytic orchids this association is obligatory for their whole lifespan.

Some saprophytic plants are connected via their mycorrhiza to the roots of photosynthesizing plants. The former can indirectly parasitize the latter via connecting mycelium. This linked system is best regarded as the components of interacting plants (FURMAN & TRAPPE 1971, INGOLD 1961). It has been demonstrated that there is transport of nutrients from the green host via the fungus to the saprophyte (BLACK 1980). In this situation *Armillaria* (Agaricales) was involved as an endophyte rather than the more commonly associated *Rhizoctonia* (Aphyllphorales; both fungus orders belonging to Basidiomycetes) (HUDSON 1986). This form of epiparasitism might explain the scattered distri-

bution pattern of saprophytes because the distribution of host species may determine their location (BLACK 1980).

The roots of both genera were studied anatomically. The first author examined transverse sections of the root of *Uleiorchis ulaei* made by TH. W. KUYPER (Wijster, The Netherlands). In these she found in the outer cortex living hyphae, which seemed to belong to a species of *Rhizoctonia*. Also digested hyphae were observed, and a more or less puzzle-shaped structure which could not be identified.

Transverse sections of the roots of *Wullschlaegelia calcarata* had been studied earlier by R. SINGER in 1978 (Manaus, Brazil: pers. comm. by Mr. TED ST. JOHN). He then discovered two fungi: one with septate hyphae, and one with narrow mycelium with numerous but clampless septa and brown walls, which might belong to a member of Aphyllophorales. As the latter type did not show any sign of penetrating the cells, it could not be determined if it was parasitic or saprophytic. Transverse sections of roots of the same species made by the first author herself and KUYPER could confirm the preliminary observations by SINGER. Unfortunately, roots of *W. aphylla* could not be studied, because no material in spirit was available.

Pollination and dispersal

Very little, if anything, is known about the pollination of the two genera. They are generally thought to be self-pollinating. The flowers in *Wullschlaegelia* do not have any marked colours. In contrast, however, an excellent photograph of *Uleiorchis ulaei* taken recently in Saül (French Guiana) by CAROL GRACIE shows flowers with a fairly conspicuously yellow-and-brown coloured lip (CHRISTENSON 1997). No discernable aroma has ever been reported from the flowers of either genus. The pollinia in *Wullschlaegelia* do have a prominent viscidium; so if the flowers are self-pollinating, the viscidium may be non-functional (DRESSLER 1981, pp. 199–200). It could be of interest, though, that the first author, when she visited French Guiana in 1991, observed flies sitting on a fruiting plant of *Wullschlaegelia calcarata* (Fig. 6). Although these flies perhaps were merely accidental visitors, it might be worthwhile to investigate if there possibly exists a more close relationship between plant and insect as well. This equally applies to the flower colour in *Uleiorchis ulaei* noted above which still seems to suggest a potential attraction to insects, and merits further attention.

The seeds of *Wullschlaegelia* and *Uleiorchis* (not seen in *U. liesneri*), as in most orchids, are tiny, light-weight and are produced in large amounts which increases their chances of successful germination and survival. The minute size of the seeds makes them optimally suited to dispersal by air currents, but in the understory of tropical rain forests such currents may not be sufficiently effective. It has been hypothesized that most of the forest-dwelling saprophytic species are dispersed with the help of water from small streams or the runnels after



Fig. 6. *Wulfschlaegelia calcarata* in fruiting stage, visited by flies; French Guiana. Photograph by M. G. BORN.

heavy rains (BOUMAN 1992: pers. comm.). In French Guiana, *W. calcarata* was found on creek or river slopes and flowered at the end of the dry season! Possibly the seeds are splashed out of the fruit during heavy showers.

U. ulaei has very thick and fleshy roots. They may be an adaptation for vegetative propagation. ULE suggested this already in his letter dated 1 Dec. 1888 which was attached to the herbarium material in BR “.. la manière de croître est intéressante, car le rhizome parait se renouveler tous les ans formant un anneau des racine longues..”. In French Guiana this species was found on the same location for many years (MORI 1991: pers. comm.), which might well be an indication of vegetative reproduction. Another possibility, as suggested by

E. A. CHRISTENSON (pers. comm.), is that the fleshy roots form a storage system to support the flowering and fruiting.

Systematic treatment

Material and methods

This revision is based on study of material from the following herbaria: A, AAU, AMES, B, BM, BR, BRG, C, CAY, COL, CR, F, FLAS, G, GH, GOET, HBG, IAN, JBSD, K, L, LL, MEXU, MICH, MO, MY, NY, P, RB, S, SP, U, UC, US, USM, VEN, WU.

For describing shapes, the terminology recommended by the SYSTEMATICS ASSOCIATION COMMITTEE FOR DESCRIPTIVE TERMINOLOGY (1962) was followed.

Floral measurements of *Wulfschlaegelia aphylla* were made on herbarium material. Such measurements, due to shrivelling, generally will give lower values than correspond to the living plant. The measurements of *Wulfschlaegelia calcarata* and *Uleiorchis ulaei* could be taken from collections preserved in spirit. For *Uleiorchis liesneri* the values were copied from the protologue by CARNEVALI & RAMÍREZ (1993).

I. *Wulfschlaegelia* Reichenbach f., Bot. Zeitung (Berlin) 21: 131. 1863; Foldats, Fl. Venezuela 15(1): 101. 1969; Hoehne, Fl. Brasília 12(2): 91. t. 62. 1945; Garay, Fl. Ecuador 9: 230. 1978. — Type: *Wulfschlaegelia aphylla* (Swartz) Reichenbach f. (≡ *Cranichis aphylla* Swartz).

The genus *Wulfschlaegelia* is named after HEINRICH RUDOLPH WULFSCHLÄGEL, a nineteenth-century German missionary in Antigua and Suriname, bishop of the community Berthelsdorf, Herrnhut.

Terrestrial, saprophytic, hairy herbs. Rhizome ascending, roots of the bird's nest or morning star type, consisting of a fascicle of fusiform, glabrous tubers. Leaves scale-like, brown, appressed, semitransparent, sessile, concave. Stems dirty white, erect, simple, covered with brownish trichomes. *Inflorescence* a subdense terminal, bracteate raceme. *Flowers* white, erect, covered with brownish pluricellular trichomes, resupinate or not. Sepals and petals dirty white, appressed, 1-veined, connivent, dorsal sepal free, lateral sepals fused with the column foot forming a spur-like chin, petals free. Lip white, entire, sessile, concave. Column white, erect, broadly ovoid, extended at its base into a long foot which bears the lip, surrounded by columnar tissue which is attached to the dorsal side of the anther, the rostellum white, beak-like. Anther white, erect, sessile, dorsal, obtuse, thick and fleshy, thecae curved. Stigma entire, projecting beneath the rostellum, softly hairy at the apex. Pollinia 2, white, sectile, with a viscidium. Ovary fusiform, sparsely covered with pluricellular trichomes, becoming glabrous with age. *Fruit* dirty white, ovoid, with 6 thickened ribs persisting after dehiscence. Seeds white, filiform.

Distribution: A genus with two species. Throughout the Neotropics; in Central America from Guatemala to Panama; in the West Indies in Cuba, Jamaica, the Dominican Republic, Puerto Rico, and Guadeloupe; in South America from Colombia to the southeastern part of Brazil and eastern Paraguay.

Key to the species of *Wullschlaegelia*:

- 1a. Stems and flowers covered with clustered trichomes consisting of swollen, gland-like cells (Figs. 1a, c, e, g, 2b, c); flowers non-resupinate . *W. aphylla*
- 1b. Stems and flowers covered with regularly distributed trichomes, the cells not appearing gland-like (Figs. 1b, d, f, h, 2a); flowers resupinate . *W. calcarata*

1. ***Wullschlaegelia aphylla*** (Swartz) Reichenbach f., Bot. Zeitung (Berlin) 21: 131. 1863; Fawcett & Rendle, Fl. Jamaica 1: 30. pl. 3, 23–25. 1910; Hoehne, Fl. Brasília 12(2): 91. t. 62. 1945; Foldats, Fl. Venezuela 15(1): 101. 1969. ≡ *Cranichis aphylla* Swartz, Prodr. 120. 1788; Swartz, Fl. Ind. Occid. 3: 1421. t. 29. 1806 [1804?]. — Type: Jamaica, mountains of Clarendon, *Swartz s.n.* (holotype, BM). Fig. 7.

Herbs, 15–40 cm high. Roots 2–7 cm long, additionally with a few roots 1–1.5 mm in diam. Stems more or less densely covered with simple or 2–more-branched clustered trichomes, becoming nearly glabrous near the base; trichomes dark brown, 0.2–0.5 mm long, composed of 3–12 glandular-globose cells, basal cell tapering towards base, walls smooth. Leaves linear-triangular to narrowly ovate, (3–)3.5–4.5(–5) mm long, 1–1.5 mm wide, base obtuse to broadly cuneate, apex acute to acuminate. *Inflorescence* a 16–26-flowered raceme 6–10(–12) cm long. Bracts dark brown, saccate, semitransparent, scale-like, appressed, linear-triangular to narrowly ovate, (2–)2.5–3.5(–4) mm long, 0.8–1 mm wide, glabrous, base obtuse to broadly cuneate, apex acute to acuminate. Pedicels dirty white, (1–)1.4–2.2(–3) mm long, sparsely covered with pluricellular trichomes to glabrous. *Flowers* non-resupinate, with a spur-like mentum, sparsely covered with pluricellular trichomes. Sepals membranous, dorsal side sparsely covered with brown pluricellular trichomes. Dorsal sepals oblong-ovate, 1.6–2 mm long, 0.8–1 mm wide, apex acute to obtuse. Lateral sepals triangular, more or less concave, 1.8–2.5(–3) mm long, 1–1.2 mm wide, base asymmetric, oblique, extended into an oblong-ovoid short spur 0.5–0.6 mm long, apex acute to obtuse. Petals oblong-ovate, 1.5–1.8(–2) mm long, 0.6–0.8(–1) mm wide, glabrous, apex acute to obtuse. Lip uppermost, inserted at apex of column foot, almost completely enclosed by the lateral sepals, membranous, concave, 5-veined, oblong-ovate, 3–3.5 mm long, 1.3–1.5 mm wide, glabrous but upper part of dorsal side sparsely covered with trichomes, apex rounded to apiculate. Column 1–1.3 mm long, including foot, 0.4–0.6 mm wide at apex. Anther 0.6–1 mm long, 0.5–0.6 mm wide. *Fruit* 5–7 mm long. Seeds 0.7–1.1 mm long, 0.1 mm wide.

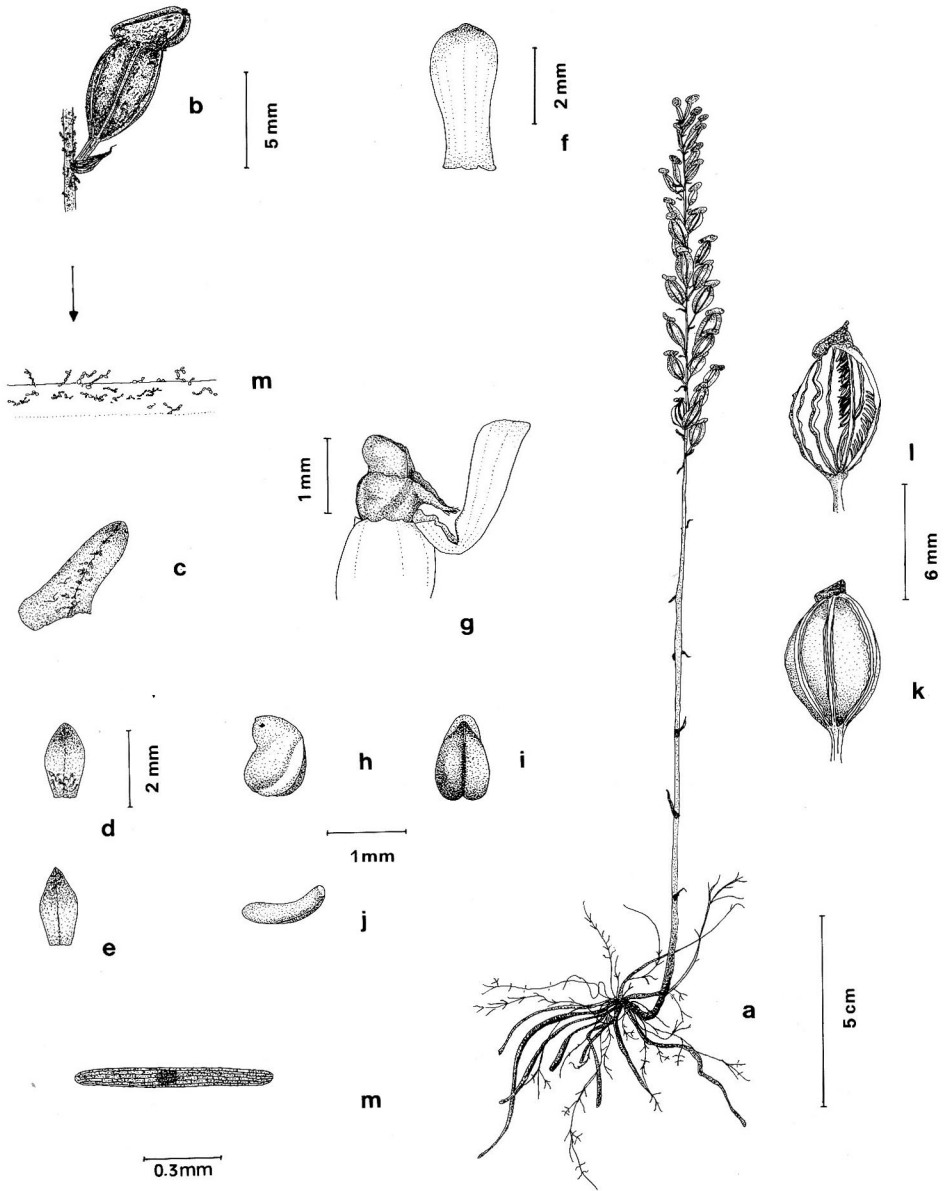


Fig. 7. *Wullschlaegelia aphylla*. (a, b, k, l, *Brade* 193; c–g, m, *Hatschbach* 26342; h–j, *Dusén* 9479). — a, Habit; b, flower; c, lateral sepal; d, dorsal sepal; e, petal; f, lip; g, column with column foot and attached lip, sepals and petals removed, lip slightly depressed; h, i, anther, lateral view and front view; j, pollinia; k, fruit; l, dehisced fruit; m, seed. Drawings by M. G. BORN.

Distribution: (Fig. 4): Central America from Honduras to Panama, the Greater Antilles (Cuba and Jamaica), Amazonian Peru (2 collections), SE Brazil, and Paraguay. In various forest types, viz. primary forest, interiors of woodlands in open field, woodlands with *Araucaria*, forest on slopes; at elevations from sea level to 1400 m. Flowering and fruiting from September through May, but most flowering specimens were collected in December, January and February.

Specimens examined: HONDURAS. Atlántida: Lancetilla Valley, near Tela, alt. 20–600 m, 6 Dec 1927–20 Mar 1928, *Standley 52777* (AMES).

COSTA RICA. Guanacaste: Parque Rincón de la Vieja, Hacienda Santa María, alt. 800–1000 m, 11 Oct 1987, *Herrera & Rivera 865* (MO, SEL).

PANAMA. Bocas del Toro: road to Chiriquí Grande, 10 miles from continental divide, alt. 350–500 m, 10 Mar 1986, *McPherson 8758* (MO).

CUBA. Monte Verde, Sep 1859–Jan 1860, *Wright 1691* (BM, G, GOET, GH, K, MO, S, W); Monte Verde, 21 Sep 1860, *Wright s.n.* (K, W).

JAMAICA. Bethabara, 1849, *Wulfschlaegel 1071* (M, W); Interior of St. Ann, Dec 1843, *Purdie s.n.* (K).

PERU. Huánuco: Finca “Panguana”, 1 hour walk from Llullapichis (on Río Pachitea), 25 Jan–Feb 1975, *Dressler 4940* (FLAS). Loreto: Maynas, Yanamono Tourist Camp, Río Amazonas, Indiana-Río Napo, alt. 130 m, 24 Jan 1983, *Gentry et al. 39695 A* (MO).

BRAZIL. Goiás: Pico dos Pirineus, road to Niquelandia, alt. 1400 m, 28 Jan 1968, *Irwin et al. 19384* (NY). Minas Gerais: Lagoa Santa, 12 Jan 1865, *Warming s.n.* (BR, C). Paraná: Ponta Grossa, 5 Mar 1910, *Dusén 9479* (S); Palmeira, *Freitas SP69697* (SP); Mun. Lapa, Rio Passa Dois, 15 Feb 1967, *Hatschbach 15991* (NY, US); Mun. Ponta Grossa, Parque Vila Velha, Vila Velha, 15 Feb 1967, *Hatschbach & Guimarães 16053* (AMES, B, F, GH, K, L, MO, NY, US); Mun. Lapa, Santo Amare, 16 Mar 1967, *Hatschbach 16162* (L, UC); Guarapuava, Candi, 19 Feb 1971, *Hatschbach 26342* (NY, UC); Fazenda Reserva, 85 km SW of Guarapuava, alt. 800–1050 m, 13 Mar 1967, *Lindeman & de Haas 4855* (A, K, NY, U). Rio de Janeiro: Corcovado Range, alt. 300–700 m, 29 Jan 1924, *Bailey & Bailey 703* (AMES); Tijuca, 24 Jan 1932, *Brade 193* (AMES); without location, 1830, *Gaudichaud-Beaupré 43* (G); Corcovado, between botanical garden of Lagoa and Corcovado, 18 Dec 1892, *Glaziov 16* (BR); Rio de Janeiro, in the vicinity of the Horto Florestal, 23 Dec 1926, *Kuhlmann 918* (RB). Rio Grande do Sul: São Leopoldo, 15 Jan 1936, *Orth SP50546* (= *Rambo 2701*) (SP); Pestana, near Ijuí, 10 Feb 1956, *Pivetta 1146* (B); Palmeira, Rio Uruguay, 12 Feb 1951, *Rambo 49971* (B, S); Fazenda do Arroio near Osorio, 25 Jan 1958, *Rambo 63629* (S). Santa Catarina: Rio do Sul, alt. 400 m, 27 Jan 1959, *Reitz & Klein 8386* (US). São Paulo: Raiz de Serra, *Edwall 4046* (BR); Floresta, Mun. Santa Barbara, 21 Jan 1921, *Hoehne SP5063* (SP); Iguape, Reserva Ecológica da Juréia, trail to Figueira Grande, alt. 140 m, 18 Dec 1990, *Mamede et al. 388* (SP, U).

PARAGUAY. Alto Paraná: Alto Paraná, Oct 1909, *Fiebrig s.n.* (AMES). Caaguazú: Paso Yobay, Dec 1933, *Jorge 26* (AMES). Guaira: Santa Barbara, near Villarica, Dec 1981, *Balansa 3010* (BM, K, L).

2. *Wulfschlaegelia calcarata* Benth, J. Linn. Soc., Bot. 18: 342. 1881; Hoehne, Fl. Brasílica 12(2): 91. t. 62. 1945. — Type: Brazil. Amazonas: near Ipanoré, Rio Uaupés (“fl. Vaupés, prope Panuré”), Jan 1853, *Spruce 2847* (holotype, K; isotypes, BR, W). Fig. 8.

Herbs, 20–35 cm high. Roots 2–7 cm long, additionally with a few roots 1–1.5 mm in diam. Stems densely covered with simple or 2–more-branched trichomes, sparsely towards the base; trichomes dark brown, 0.1–0.4(–0.6) mm long, simple or branched, the basal cell tapering towards base, branches consisting of one to several cells, terminal cell elongate with rounded apex, walls smooth. Leaves linear-triangular to narrowly ovate, 1.5–2.5(–3.5) mm long, 0.9–1(–1.4) mm wide, glabrous, base slightly oblique, apex acute to obtuse. *Inflorescence* a 5–14(–18)-flowered raceme 3–7(–9) cm long. Bracts dark brown, triangular-ovate, (2–)2.5 mm long, 0.8(–1) mm wide, glabrous, base obtuse to broadly cuneate, apex acute. Pedicels dirty white, (2–)2.5 mm long, sparsely covered with pluricellular trichomes to glabrous. *Flowers* resupinate, with a spur-like mentum, sparsely to densely covered with pluricellular trichomes. Sepals membranous, dorsal side covered with brown, pluricellular trichomes. Dorsal sepal narrowly ovate, (1.5–)2 mm long, 0.6–0.8 mm wide, apex acute to obtuse. Lateral sepals triangular-ovate, more or less concave, 3.5(–4) mm long, 1.1 mm wide, base asymmetric, oblique, extended into a oblong-ovoid long spur 0.8–1.1 mm long, apex acute to obtuse. Petals broadly ovate, 1.8 mm long, 1 mm wide, apex acute, glabrous, but adaxially sparsely covered with pluricellular trichomes. Lip⁴ lowermost, inserted at apex of column foot, almost completely enclosed by the lateral sepals, membranous, 5–9-veined, oblong-obovate, 4(–5) mm long, 1.6–2 mm wide, glabrous, but outer parts sparsely covered with pluricellular trichomes, apex rounded to apiculate. Column 1.2–1.3 mm long, including foot, 0.8 mm wide at apex. Anther apex bending backwards, 1.1 mm long, 0.6–0.8 mm wide. Ovary 4.5–5(–6) mm long, densely covered with pluricellular trichomes, ribs very sparsely covered with trichomes or glabrous. *Fruit* 5–11.5 mm long. Seeds 1.3–1.8 mm long, 0.1 mm wide.

Distribution (Fig. 4): Central America from Guatemala to Panama, the Greater Antilles (Dominican Republic and Puerto Rico), the Lesser Antilles (Guadeloupe, Dominica), and throughout tropical South America. In various forest types, viz. high rain forest, premontane wet forest, hillside forest, and ridgetops; at elevations from sea level to 600 m, only two collections known from between 750–1400 m. Flowering and fruiting in the Guianas from August till June, in Colombia from January till April, in Venezuela and Brazil throughout the year, but with peaks in March–May and in October–November, respectively.

Specimens examined: GUATEMALA. Alta Verapaz: 2 km S of Jolomylix, Telemán, Panzós, alt. 750 m, 20 Jul 1988, *Martínez S. et al. 22869* (MEXU). Izabal: Lago Izabal, alt. 0–600 m, 22 Apr 1966, *Jones et al. 3012* (F, LL, MICH, NY, U, US); Punta Palma, across bay from Puerto Barrios, alt. 0–1 m, 23 Feb 1940, *Steyermark 39861* (F).

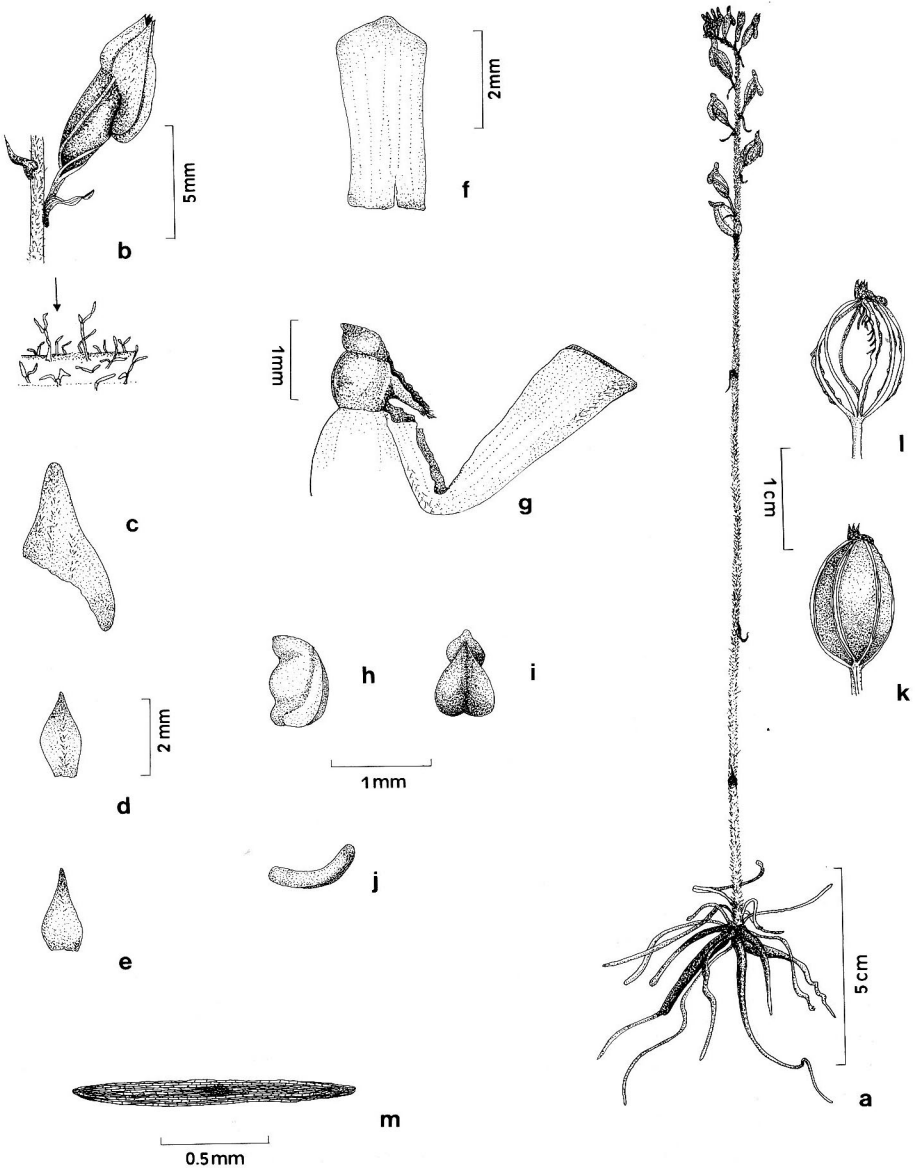


Fig. 8. *Wulfschlaegelia calcarata*. (a–j, *Born et al. 41*; k–m, *ter Steege s.n.*). — a, Habit; b, flower; c, lateral sepal; d, dorsal sepal; e, petal; f, lip; g, column with column foot and attached lip, sepals and petals removed, lip slightly depressed; h, i, anther, lateral view and front view; j, pollinia; k, fruit; l, dehisced fruit; m, seed. Drawings by M. G. BORN.

HONDURAS. Atlántida: Mpio. Esparta, 41.5 km E of Tela on Tela-Ceiba Hwy., then ca. 6 km N on old lumber road, alt. 100–200 m, 11 Apr 1994, *Brant & Zuñiga 2808* (MO); 10 km SW of La Ceiba, base of N slope of Pico Bonito, alt. 80–180 m, 10 May 1993, *Liesner 26169* (MO). Gracias a Dios: Camp Tiro, 2 miles NW of Bulebar on third northern branch of Quebrada Tiro, tributary of Río Platano, Apr 1980, *Saunders 1297* (MO).

COSTA RICA: Limón: Fila Carbon, W of Cahuita, alt. 150 m, 13 Feb 1991, *Maas et al. 7901* (CR, MO). Puntarenas: Reserva Forestal Golfo Dulce, Península de Osa, Alto Los Mogos, alt. 100 m, 5 Feb 1991, *Maas et al. 7843* (CR, MO).

PANAMA. Coclé: ridge NW of Río Blanco del Norte, between Caño Sucio and Río Blanco del Norte, alt. 350 m, 20 Feb 1982, *Knapp 3669* (MO). Colón: N from Río Escandaloso towards Cerro Bruja, alt. 450 m, 27 Apr 1978, *Hammel 2729* (MO); El Llano-Carti Road, 12 mls. above Pan-American Hwy., alt. 200–500 m, 26–27 Mar 1973, *Liesner 1150* (MO); between El Llano and Carti, 12–15 km N of El Llano, alt. 400 m, 3 Mar 1976, *Taylor 13211* (K). San Blas: Km 26.5, 9°19' N, 78°55' W, alt. 200 m, 8 Apr 1985, *de Nevers et al. 5247* (MO).

DOMINICAN REPUBLIC. Santo Domingo, Peninsula de Samaná, Santa Barbara de Samana at Río Tito, alt. 275 m, 12 Jun 1930, *Ekman H15273* (AMES, C, G, GH, K, NY, S, U); La Manaclita, La Vega, alt. 400–600 m, 25 Jun 1969, *Liogier 15834* (NY); Santo Domingo, between El Valle and Arenitas, Sabana de la Mar, 27 Apr 1974, *Liogier 21627* (JBSD).

PUERTO RICO. Mt. El Yunque, Apr 1924, *Dale s.n.* (NY); El Verde, Luquillo Mts., alt. 400–500 m, 18 Apr 1964, *Liogier 10854* (GH); Tabonuco forest, Luquillo National Forest, alt. 350–370 m, 1 Jul 1977, *Luteyn & Lebrón-Luteyn 5118* (NY); Luquillo Experimental Forest, Sonodora El Verde, alt. 280–300 m, 31 Mar 1985, *Maas 6454* (U).

GUADELOUPE. Pointe-Noire, Le Piton, alt. 550 m, 18 Sep 1974, *Jérémie 163* (P).

DOMINICA. SE slope of Morne Couronne near Point Lolo, alt. 300–450 m, 24 Apr 1964, *Ernst 1160* (GH, US); La Chaudière, Hampstead River, ca. 2 miles from mouth, alt. 100 m, 10 May 1940, *Hodge 3596* (NY, AMES); Carib trail between Riversdale and Deux Branches, 27 May–2 Jun 1950, *Howard 11766* (A); NW slopes of Morne Diablotins, near Syndicate, alt. 650 m, 15 Sep 1983, *Whitefoord 3644* (BM).

COLOMBIA. Amazonas-Vaupés: Río Apaporis, between Ríos Pacoa and Kananarí, alt. 250 m, 11 Jul 1951, *Schultes & Cabrera 13051* (AMES). Chocó: 1.5 km NE of Camp Curiche, ca. 4.5 km E of Curiche, 21 Mar 1967, *Duke & Idrobo 11324* (NY, U); near Quibdó, alt. 30–50 m, 23 Apr 1975, *Forero et al. 1122-A* (COL); mouth of Río Atrato, Beté, alt. 50–60 m, 4 Apr 1982, *Forero et al. 8868* (COL); mouth of Río Atrato, Beté, alt. 50–60 m, 6 Apr 1982, *Forero et al. 8956* (COL); Mecana, Ridge N of Río Mecana, alt. 300–400 m, 6 Mar 1983, *Juncosa & Gentry 715* (MO); Río Condoto, between Quebrada Guarapo and Mandinga, alt. 120–180 m, 22–28 Apr 1939, *Killip 35171* (AMES, US). El Valle: Río Calima, La Trojita, alt. 5–50 m, 19 Feb–10 Mar 1944, *Cuatrecasas 16559* (F);

Río Raposo, Mountain ridge NW of Rockefeller Camp, 26 Mar 1963, *Fernández-Pérez 6034* (COL); Córdoba, alt. 50–100 m, 17 Feb 1939, *Killip & García 33443* (US). Santander: vicinity of Barrancabermeja, Magdalena Valley, between Ríos Sogamoso and Colorado, alt. 100–500 m, 16–19 Jan 1935, *Haught 1520* (US). Vichada: Río Vichada, near San José de Ocuté, alt. 100 m, 3 May 1939, *Haught 2803* (US).

VENEZUELA. Amazonas: Río Negro, Cerro de la Neblina, Camp on Río Mawarinuma, alt. 140 m, 28 Nov 1983, *Anderson 13375* (VEN); Río Negro, near Loma de las Pinas, 1.5 km S of Neblina Base Camp, alt. 215 m, *Bell 410* (VEN); Río Negro, N part of Cerro Aracamuni, alt. 1415 m, 16–18 Oct 1987, *Delascio & Liesner 13527* (VEN); Dep. Atabapo, N flank of Cerro Duida, 2 km S of Culebra, alt. 700 m, Apr 1990, *Ang. Fernández 7760* (U); Cerro Neblina, Base camp, Río Mawarinuma, alt. 140 m, 2 May 1984, *Gentry & Stein 47088* (VEN); Dep. Atures, Valley of Río Coro-Coro, W of Serranía de Yutajé, alt. 1100 m, 10 Mar 1987, *Holst & Liesner 3404* (VEN); Río Negro, between km 4–20 of the road from San Carlos to Solano, alt. 120 m, 15 Sep 1980, *Huber & Medina 5644* (U, VEN); IVIC study site, 4 km NE of San Carlos de Río Negro, alt. 120 m, 4 Apr 1979, *Liesner 6140* (VEN); Conuco, 4 km NE of San Carlos de Río Negro, alt. 120 m, 1 May 1979, *Liesner 7112* (VEN); 0 to 5 km NE of San Carlos de Río Negro, 20 km S of Río Negro and Brazo Casiquiare, alt. 120 m, 5 May 1979, *Liesner 7229* (VEN); 8 km NE of San Carlos de Río Negro, 20 km S of Río Negro and Brazo Casiquiare, alt. 120 m, 8 May 1979, *Liesner 7291* (VEN); 4 km NE of San Carlos de Río Negro, 20 km S of Río Negro and Brazo Casiquiare, alt. 120 m, 17 May 1979, *Liesner 7510* (MO, VEN); 0 to 2 km NE of San Carlos de Río Negro, alt. 120 m, 20 Jan 1980, *Liesner 8469* (MO, VEN); Río Negro, 0 to 1 km W of Cerro de La Neblina, Base Camp on Río Mawarinuma, alt. 140 m, 13 Mar 1984, *Liesner 16563* (VEN); Río Negro, 0 to 1 km W of Cerro de La Neblina, Base Camp on Río Mawarinuma, alt. 140 m, 27 Nov 1984, *Liesner & Kral 17330* (MO, VEN); Dep. Atures, Río Coro-Coro, W of Serranía de Yutajé, 6 to 8 km N of Yutajé, alt. 320 m, 28 Feb 1987, *Liesner & Holst 21499* (VEN); base of Piedra de Cucuy, alt. 100–200 m, 28 Oct 1987, *Maas et al. 6873* (NY); Río Negro, Cerro de la Neblina Expedition Base Camp along Río Baria, alt. 140 m, 12 Apr 1984, *Plowman & Thomas 13560* (F); Cerro Yapacana, between base camp and savanna, alt. 125 m, 7 May 1970, *Steyermark & Bunting 103205* (AMES, VEN); Distr. Alto Orinoco, 200 km SE of La Esmeralda, between airstrip and Río Orinoco, alt. 120 m, 1 Apr 1995, *Zimmermann et al. 148* (U). Apure: Reserva Forestal San Camilo, Quebrada La Azulita, SW of San Camilo (El Nula), alt. 280 m, 30 Mar 1968, *Steyermark et al. 101608* (NY); Reserva Forestal San Camilo, Quebrada La Azulita, SW of San Camilo (El Nula), alt. 280 m, 30 Mar 1968, *Steyermark et al. 101645* (VEN). Bolívar: region of Ríos Icabaru and Hacha, alt. 450–850 m, 12 Jan 1956, *Bernardi s.n.* (NY); La Paragua, alt. 286 m, 20 Apr 1943, *Cardona 452* (US); Ocla, SE of El Dorado, 13 Mar 1970, *Ant. Fernández 1067* (MY); Aurukima, near Río Lapo, Río Paragua, between Guaiquinima and Río Torono, alt. 280 m, 13 Apr 1943, *Killip 37438* (US); 5 km

S of El Pauji, “El Abismo”, Río Samay, affluent of Icabarú, alt. 520 m, 24 Oct 1985, *Liesner & Holst 19030* (VEN); Gran Sabana, 10 km SW of Karaurin-tepuí at junction of Ríos Karaurin and Asadon, alt. 900–1000 m, 21 Apr 1988, *Liesner 23558* (VEN); Chimantá Massif, Torono-tepuí, between Río Tirica and forest slope, alt. 755–1395 m, 6 Mar 1955, *Steyermark & Wurdack 1288* (AMES, NY); Chimantá Massif, Abácapa-tepuí, Río Abácapa, alt. 420 m, 30–31 Mar 1953, *Steyermark 74776* (AMES, F, NY); Río Bonita, Sierra Maigualida and Sierra Cervatana, alt. 300–500 m, 26 Apr 1966, *Steyermark & Gibson 95746* (AMES, F, NY, VEN), 95776 (VEN); Lower Río Orinoco, 1896, *Rusby & Squires s.n.* (NY). Miranda: Cerros del Bachiller, above Quebrada Bachiller, S of Caño Rico and Bachiller, alt. 20–690 m, 21, 27–28 Mar 1978, *Steyermark & Davidse 116549* A (U). Sucre: Peninsula de Paria, Distr. Mariño, Río Arriba, affluent of Río Santa Isabel, NW of Irapa, alt. 800–1000 m, 11 Jul 1972, *Dumont et al. VE-7534* (VEN); Peninsula de Paria, Cerro Patao, N of Puerto de Hierro, NE of Güiria, alt. 875 m, 25–26 Jul 1962, *Steyermark & Agostini 91334* (AMES). Zulia: 55 km SW of Machiques, Aricuaísa, Río Aricuaísa, alt. 100–250 m, 24–25 Mar 1982, *Liesner & González 13144* (MO, VEN).

TRINIDAD. 4 mls. E of Arima, 15 Mar 1920, *Britton et al. 597* (NY, US); Caroni North Bank Road, 21 Mar 1920, *Britton & Mendelson 838* (NY); Aripo Savanna, 14 Apr 1921, *Britton & Britton 2942* (NY, US); Toco Road, Valencia, 16 Apr 1920, *Britton et al. s.n.* (NY); Santa Cruz, on the mountain ridge of Providence Estate, 23 Apr 1908, *Broadway 2248* (AMES, BM, G); Mt. Harris, Central Range, 27 Apr 1930, *Broadway 7550* (BM, K, MO); Arima, 7 Mar 1905, *Dannouse s.n.* (AMES); locality unknown, 1877–1880, *Fendler 756* (K, NY); Aripo, Apr 1896, *Hart s.n.* (AMES); Las Lapas Trace, Blanchisseuse Saddle, alt. 510 m, 1 Jun 1962, *Purseglove 6441* (K, NY); Las Lapas Trace, alt. 500 m, 4 Jul 1962, *van Steenis 20295* (L).

GUYANA. Cuyuni River, Oct 1904, *Bartlett 8149* (BRG); Cuyuni River, Oct 1904, *Bartlett 8298* (BRG); 20 km N of Mt. Roraima, Mar 1980, *Brandham s.n.* (K); Cuyuni River, Kamaria Road, alt. 30 m, 10 Feb 1931, *T.A.W. Davis 1023* (K); Waini River, NW Distr., 3–18 Apr 1923, *de la Cruz 3625* (NY, F, GH); Essequibo River, Groete Creek, 6 Apr 1944, *Forest Dept. Brit. Guiana 4705* (= *Fanshawe 1969*) (K); Tumatumari, Potaro River, 3–5 Jan 1920, *Hitchcock 17351* (AMES, NY, US); Edu Swamp, Aruka River, 15 Sep 1897, *Im Thurn 225* (K); Mazaruni River, 2 to 8 km W of Kamarang, alt. 450–550 m, 18 Aug 1977, *Maas et al. 2523* (U); near Kamarang, alt. 450 m, 8 Nov 1979, *Maas & Westra 3976* (U), 4136 (U); ibidem, 11 Nov 1979, *Maas & Westra 4248* (K, NY, U); Essequibo River, Groete Creek, Kamuni Creek, 20 Apr 1944, *Maguire & Fanshawe 22921* (AMES, K, NY); Tokomaku Creek, Amakura River, NW Distr., 22 Mar 1935, *Myers 4993* (K); Lower Barama River, NW Distr., 25 Mar 1935, *Myers 5006* (K); Cuyuni River, Kamaria Road, Feb 1931, *Record 1023* (RB); Essequibo River, Moraballi Creek, near Bartica, alt. sea level, 15 Oct 1929, *Sandwith 455* (K); Essequibo River, Moraballi Creek, near Bartica, alt. sea level, 22 Oct 1929, *Sandwith 501* (K); below Kaieteur Falls, gorge of Potaro River, 10 Sep 1937,

Sandwith 1479 (AMES, K); Mabura Hill area, *ter Steege s.n.* (U); no data (?), *Forest Dept. Brit. Guyana 3055* (K).

SURINAME. Near Zanderij, *Florschütz & Florschütz 748* (U); Nassau Mts., near km 2.5, 12 Oct 1953, *Geijskes 189* (U); Jodensavanne-Mapane kreek area near Kamp 8, 8 Dec 1954, *Lindeman 6710* (AMES, U).

FRENCH GUIANA. Road to St. Elie, near km 15, SW of Sinnamary, 29 Nov 1977, *Berg 777A* (U), *777B* (U); Basin of Approuague River, Station des Nouragues, alt. 80–100 m, 4 Aug 1991, *Born et al. 39* (U); ibidem, 23 Aug 1991, *Born et al. 41* (NY, U); ibidem, 14 Sep 1991, *Born et al. 67* (U); Mt. des Trois Pitons, NW of St. Georges de l'Oyapock, alt. 250–300 m, 22 Jan 1981, *Cremers 7008* (CAY, P); Piste de St. Elie, PK 14, 3 Oct 1982, *Feuillet 194* (CAY); Piste de St. Elie, Layon Sabatier, 13 Nov 1983, *Feuillet 1114* (CAY); Piste de St. Elie, CD-21, km 15.7, alt. 100 m, 15 Sep 1987, *Hahn 3763* (MO); Cayenne, 1839, *Leprieur "164"* (G); Approuague River, E of Sauts Mapaou, W of Picard, alt. 0–60 m, 5 Sep 1991, *Martens et al. 1* (U); Saül, near Eaux Claires on sentier Botanique, alt. 200–400 m, 15 Nov 1990, *Mori et al. 21679* (NY, U); Approuague River, Crique Calebasse, along banks of the Maïs Falls, 7 Sep 1967, *Oldeman 2794* (CAY), *2796* (CAY); base of Organabo River, alt. 10 m, 22 Mar 1988, *Philippe 182* (CAY); Roche Fendé near confluence with le Comté, right bank of river, 20 Jan 1977, *Veyret 1489* (CAY).

ECUADOR. Napo: Tena, 6 km along Río Pano, alt. 600 m, 12 Jun 1968, *Holm-Nielsen & Jeppesen 651* (AAU).

PERU. Huánuco: Tingo Maria, 18 Aug 1940, *Asplund 13170* (S). Loreto: Río Ampiyacu, surroundings Pucaurquillo, 13 Mar 1981, *E.W. Davis et al. 867* (F); km 26 of road Yurimaguas–Tarapoto, alt. 200 m, 22 Aug 1986, *Knapp 8140* (MO). Madre de Dios: Manu, Parque Nacional Manu, Pakitsea station, Tachigali, trail, 4 km N of camp, alt. 350 m, 11 Sep 1989, *Foster & Beltran 13172* (USM). Pasco: Oxapampa, Pichis Valley, Puerto Bermúdez, 2 km SW of town, alt. 300 m, 2 Sep 1982, *Foster 8560* (MO). San Martín: Prov. Mariscal Cáceres, Distr. Campanilla, left bank of Río Huallaga, alt. 390–400 m, 16 Jul 1970, *Schunke V. 4121* (F).

BRAZIL. Acre: Rio Juruá-Mirím, Jul 1901, *Ule 5741* (G). Amazonas: Rio Negro, Morcêgo, 18 May 1948, *Black 48-2766* (IAN); Reserva Forestal Ducke, N of Manaus, Igarapé Acará, alt. 60–70 m, 21 Sep 1974, *Ebrendorfer 74921/23* (WU); Reserva Forestal Ducke, N of Manaus, Igarapé Acará, 29 Sep 1977, *Maas et al. 3079* (MO, U); between Rio Marié and Morro Ximaio, 7 Jul 1979, *Poole 1905* (NY); basin of Rio Demení, vicinity of Tototobi, 2 Mar 1969, *Prance et al. 10389* (NY, US); basin of Rio Negro, Rio Cuieras, below mouth of Rio Brancinho, 25 Sep 1971, *Prance et al. 14831* (NY); basin of Rio Negro, Tapurucuara by road to airport, 17 Oct 1971, *Prance et al. 15371* (INPA, NY). Mato Grosso: Rio Aripuaña, road from Nucleo Pioneiro to Rio Juruena, 1973, *Prance et al. 19900* (K, NY, U). Pará: road between Rios Nhamundá and Trombetas, Igarapé Jamari, *Hoogmoed & Pires S-40* (U); near Belém, Reserva Mocambo (EMBRAPA), 17 Oct 1990, *Maas et al. 7779* (MG, U); km 81 of Hwy. Belém-Brasília,

14 Dec 1959, *Oliveira* 293 (IAN); km 15–18.5 of line SW of Ilha de Breu, 3 Oct 1962, *Prance et al.* 1521 (NY); Cachoeira de Curuá, N slope of Serra Cachimbo, alt. 300 m, 4 Nov 1977, *Prance et al.* 24835 (NY); BR 230 Transamazon Hwy., 27 km NE of Itaituba, 27 Nov 1977, *Prance et al.* 25803 (NY).

BOLIVIA. Pando: W bank of Río Madeira, 10 km above Abuña, 21 Nov 1968, *Prance et al.* 8746 (INPA, NY).

The two species of the genus *Wulfschlaegelia* have been confused for many years due to wrong determinations and incorrect illustrations. The illustration by DUNSTERVILLE & GARAY (1966), for example, shows a plant with resupinate flowers and the trichomes of *W. calcarata*, but it is misidentified as “*W. aphylla*”. FOURNET (1978) perpetuated the error in his flora of Guadeloupe and Martinique, as was also done by GARAY & SWEET in Flora of the Lesser Antilles (1974). The drawings in Flora Brasílica (HOEHNE 1945), and Flora Brasiliensis (COGNIAUX 1895) are very confusing because both *W. aphylla* and *W. calcarata* are depicted with non-resupinate flowers. The detailed drawings incorrectly show a flower of *W. calcarata* with a short spur-like chin, and that of *W. aphylla* with a long chin.

In fruiting stage the differences may appear less obvious, because in *W. calcarata* the pedicels under the developing capsules more or less tend to twist back, away from the resupinate position. However, in the top part of the inflorescence resupinate flowers can always be found.

To summarize, the differences between these two species are clear. *W. aphylla* has non-resupinate flowers, with the lip on the upper (adaxial) side of the flower. The trichomes look gland-like due to swollen cells with constrictions in between (Fig. 1a). *W. calcarata* has resupinate flowers, with the lip on the lower (abaxial) side of the flower. The trichomes do not look gland-like, the cells being without constrictions in between (Fig. 1b).

II. *Uleiorchis* Hoehne, Arch. Bot. São Paulo 1(6): 129. t. 144. 1944; Hoehne, Fl. Brasílica 12(2): 93. t. 62. 1945. — Type: *Uleiorchis ulaei* (Cogniaux) Handro (≡ *Wulfschlaegelia ulaei* Cogniaux).

Named after ERNST HEINRICH ULE, German botanist and well-known explorer of the Amazon region and the Brazilian highlands. With the type specimen in BR there was a letter written by ULE dated 1 Dec 1988 with the following text: “...Je profite l’occasion de vous envoyer un genre de une orchidée saprophytique possiblement nouveau. Cette orchidée j’ai trouvé le 10 de Novembre sur le sommet d’une montagne, mais fleurissante peu de temps, je ne pus la découvrir plus tard avec fleurs. La manière de croître est intéressante, car le rhizome paraît se renouveler tous les ans formant un anneau des racines longues...” (I take the opportunity to send you a possibly new genus of saprophytic orchids. I found this orchid on November 10th on the summit of

a mountain, but, since it flowers a short time, I could not find it in flower later. The way of growing is interesting, because the rhizome appears to renew itself every year by forming a ring of long roots.)

Terrestrial, saprophytic, glabrous herbs. Rhizome consisting of a series of one or more, thick, verrucose tubers. Roots thin, in a rosulate cluster at the base of the stem. Leaves scale-like, membranous, sessile. Stems erect, glabrous. *Inflorescence* a terminal, bracteate raceme or clustered racemes, or a solitary flower. *Flowers* glabrous. Sepals and petals united for most of their length except for a ventral slit down to the base. Lip simple, free, ecallose. Column with broad, V-shaped stigmatic surface. Anther erect, fleshy, terminal. Pollinia white, soft, granular. Ovary 6-ribbed. *Fruit* a 6-ribbed capsule. Seeds (as far as seen) white, filiform.

Distribution: A genus with two species known from Central America and tropical South America.

Key to the species of *Uleiorchis*, after CARNEVALI & RAMÍREZ (1993):

- 1a. Lip 5 times or more as long as wide, 15–16 mm long, longer than or subequalling the perianth cup. *U. liesneri*
 1b. Lip 2.5–3 times as long as wide, up to 13 mm long, shorter than the perianth cup. *U. ulaei*

1. *Uleiorchis ulaei* (Cogniaux) Handro, Arch. Bot. São Paulo, n.s. 3(4): 175. 1958; Foldats, Fl. Venezuela 15(1): 99. 1969; Veyret, Adansonia, ser. 2, 20(1): 141. t. 142. 1980. Fig. 9.

≡ *Wulfschlaegelia ulaei* Cogniaux in Martius, Fl. Bras. 3(4): 244. 1895. — Type: Brazil. Santa Catarina: Mts. of Garcia, Blumenau, 10 Nov 1888, *Ule 1000* (holotype, BR; isotypes, HBG, RB, US).

≡ *Uleiorchis cogniauxiana* Hoehne, Arch. Bot. São Paulo 1(6): 129. t. 144. 1944; Hoehne, Fl. Brasília 12(2): t. 92. 1945, illegitimate name as *Wulfschlaegelia ulaei* is cited in synonymy.

Herbs, 10–15(–20) cm high. Rhizome bearing tubers interconnected by short verrucose rhizome, 2–7(–9) cm long, glabrous. Roots 2–6(–11) cm long. Stems pale white. Leaves pale white to pale brown, broadly triangular-ovate, 5–6.2 mm long, 5 mm wide at the base, glabrous, base oblique, apex obtuse. *Inflorescence* a 1–6-flowered raceme 2–8 cm long. Bracts pale white to pale brown, erect, membranous, scale-like, covering pedicel and ovary, closely fitting at their base, narrowly triangular-ovate, 5-veined, 6.2–7 mm long, 2–2.5 mm wide at the base, glabrous, base oblique, apex acute. Pedicels pale white, erect to spreading, 1–2 mm long, glabrous. *Flowers* campanulate, white with a tinge of lilac or pale brownish white, lip yellow with brown or sepia patch at base, erect to spreading. Perianth cup membranous, 15–18 mm long, the free apical parts not spreading. Free parts of sepals triangular, margins involute, 3.5–4.5 mm long, glabrous, apex

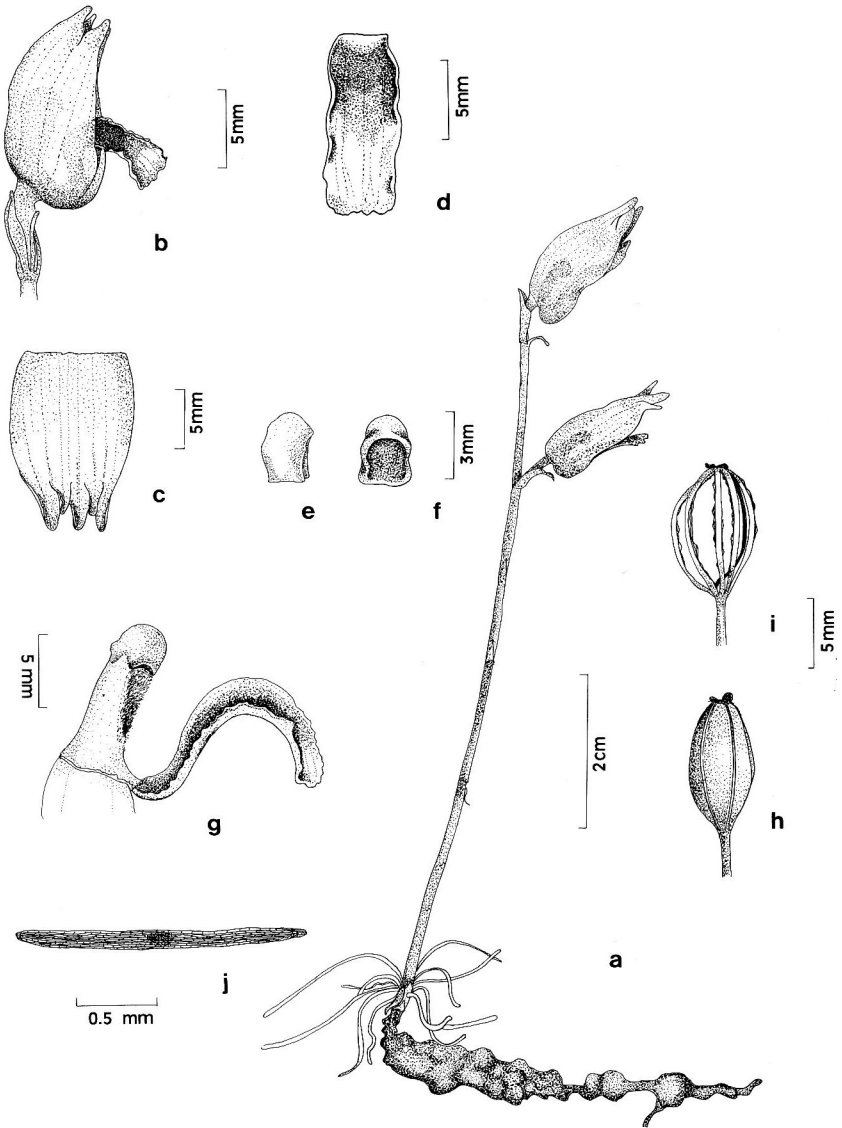


Fig. 9. *Uleiorchis ulaei*. (a, *Sastre 6212*; b–j, *Mori 21644*. — a, Habit; b, flower; c, connate sepals and petals; d, lip; e, f, anther, lateral view and front view; g, column, column foot with attached lip, sepals and petals removed, lip slightly depressed; h, fruit; i, dehiscent fruit; i, seed. Drawings by M. G. BORN.

acute-obtuse. Free parts of petals triangular, margins involute 2.5–3 mm long, apex acute-obtuse. Lip fleshy, especially in the basal part, inserted at the apex of the column foot, more or less concave, oblong-ovate, edges undulate, 10–16 mm long, 3–6 mm wide, apex covered with dark brown papillae. Column white, erect, oblong-ovate, 8–9 mm long, glabrous dorsally, covered with single trichomes ventrally. Anther white, erect, 3 mm long. Ovary dirty white to light brown, oblong-ovoid, 4 mm long, glabrous. *Fruit* stiffly erect relative to pedicel, dirty white, ovoid, ribs thickened, persisting after dehiscence, 12–25 mm long. Seeds white, 1.6–2.7 mm long, 0.1 mm wide.

Distribution (Fig. 5): Honduras, Panama, Colombia, Venezuela, Peru, the Guianas, and SE Brazil. In primary forest along streams and slopes near rivers, and in non-flooded forest, from sea level to 500 m. Flowering and fruiting from February through June and from September through December, most flowering specimens collected in April.

Specimens examined: HONDURAS. Atlántida: Campamento Quebrada Grande, 10 km W of La Ceiba, base of N slope of Pico Bonito, alt. 80 m, 13 May 1993, *Liesner 26255* (MO).

PANAMA. Canal Zone: Military Reserve Fort Sherman between Gatun and Pina, alt. 0–170 m, 2 Apr 1973, *Liesner 1367* (MO). San Blas: km 25 of El Llano-Cartí Road, alt. 200 m, 8 Apr 1985, *de Nevers et al. 5248* (MO).

COLOMBIA. Chocó: mouth of Río Atrato, Beté, alt. 50–60 m, 3 Apr 1982, *Forero et al. 8856* (COL, MO); *ibidem*, 4 Apr 1982, *Forero et al. 8869* (COL); *ibidem*, 6 Apr 1982, *Forero et al. 8957* (COL); Mecana, ridge N of Río Mecana, alt. 300–400 m, 6 Mar 1983, *Juncosa & Gentry 714* (MO); Río Atrato, Loma de Belen, Mun. Guayabal, 10 km below Quibdó, 24 Apr 1982, *Prance 28066* (NY).

VENEZUELA. Amazonas: Río Negro, 0 to 2 km E of Cerro La Neblina, Base Camp, Río Mawarinuma, alt. 140 m, 20 Feb 1984, *Liesner 16129* (VEN); Distr. Alto Orinoco, La Esmeralda, alt. 120 m, 7 Apr 1995, *Zimmerman 156* (U). Bolívar: Río Bonita, Sierra Maigualida and Sierra Cervatana, alt. 300–500 m, 26 Apr 1966, *Steyermark & Gibson 95775* (F, NY, US, VEN). Zulia: 55 km SW of Machiques, Aricuaisa, base of Río Aricuaisa, alt. 100–250 m, 24–25 Mar 1982, *Liesner & González 13177* (MO, VEN).

GUYANA. 7.5 mls. of Bartica–Potaro Road, 26 Nov 1947, *Forest Dept. Brit. Guyana 5585* (= *Fanshawe 2786*) (K).

FRENCH GUIANA. Saül, near Crique Eaux Claires, Chemin Botanique, alt. 200–300 m, 25 Nov 1991, *Born et al. 70* (U); *ibidem*, 13 Nov 1990, *Mori et al. 21644* (NY, U); Approuague River, Rivière Arataye, Saut Pararé, 20 Oct 1978, *Sastre 6212* (CAY).

PERU. Huánuco: Pachitea, Puerto Inca, 15 Sep 1982, *Foster 8823* (USM). Loreto: Maynas, Indiana, Yanamono, Río Amazonas, alt. 106 m, 28 Sep 1988, *Vásquez & Jaramillo 11079* (MO).

BRAZIL. Amazonas: Reserva Forestal Ducke W of Manaus, Igarapé Acará, 29 Sep 1977, *Maas et al. 3076* (INPA: lost in a fire). Rondônia: Jarú, Igarapé Paraíso, Ponto I, 2 Oct 1986, *Martuscelli 272* (SP).

2. *Uleiorchis liesneri* Carnevali & I. Ramírez, *Novon* 3(2): 105. f. 3. 1993. — Type: Venezuela. Amazonas: Dep. Atures, lower forested E slope of unnamed 1760 m peak, 8 km NW of Yutajé, 1050–1200 m, 13 Mar 1987, *Liesner & Holst 21893* (holotype, VEN: n.v.; isotype, MO).

Herbs, 15–33 cm high. Rhizome tubers narrowly fusiform, ca. 3 cm long, 3–10 mm thick. Stems 1–2 mm thick, simple or once-branched. Leaves 4–5 m long, 3 mm wide, ovate, apex acute to subacuminate. *Flowers* solitary at stem apex, 'pinkish-tan with yellow at apex of projection' [= column foot?]. Perianth cup corsally 14–16 mm long, 17–18 mm long ventrally from base of column foot. Free parts of sepals and petals 0.5–1.5 mm long, triangular-elliptic, acute to truncate, sepaline parts somewhat longer. Lip 15–16 mm long, 3–3.2 mm wide, narrowly oblong-elliptic, concave, almost rounded to broadly obtuse at the apex, hinged to the column foot by a claw 1 mm long, ventral face finely and densely black-verruculose on the sides. Column 8–10 mm long, with foot 4.5–5.5 mm long. *Fruit* obovoid, 10–12 mm long, on a pedicel up to 12 mm long. Seeds not seen.

Distribution (Fig. 5): Known only from the type collection. The description is largely drawn from the protologue.

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Numerical list of taxa

- I. 1. *Wulfschlaegelia aphylla* (Sw.) Rchb. f.
 2. *W. calcarata* Benth.
 II. 1. *Uleiorchis ulaei* (Cogn.) Handro
 2. *U. liesneri* Carnevali & I. Ramírez

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* Collections marked with an asterisk came in after completion of the text.