

A Revision of *Alloschemone* Schott (Araceae: *Monstereae*)

J. Bogner

Botanischer Garten München
Menzinger Straße 63
D-80638, München, Germany

P. C. Boyce

Herbarium, Royal Botanic Gardens, Kew
Richmond, Surrey, TW9 3AB, U.K.

C. M. Sakuragui

Departamento de Biologia
Universidade de Maringá
Av. Colombo, 5790
CEP 87020-000 Maringá PR, Brazil

ABSTRACT

The genus *Alloschemone* Schott is revised. One new species, *A. inopinata* Bogner & P. C. Boyce, is recognized, and an expanded description of *A. occidentalis* (Poepp.) Engl. & K. Krause is presented. The distinguishing characters of the genus are discussed, especially with regard to the genus *Scindapsus* Schott, from which *Alloschemone* has been considered inseparable. Both genera have unilocular ovaries with basal placentation with one ovule; *Alloschemone* differs from *Scindapsus* by a pinnatifid leaf lamina (entire in *Scindapsus*), shoot architecture, anatomical differences, and Neotropical distribution (*Scindapsus* Paleotropical). Our new species has fused filaments, a unique character in *Monstereae*, and further differs from *A. occidentalis* by the narrower leaf pinnate separated by an oblong sinus. Seeds, often diagnostically very useful in *Monstereae*, are still unknown in *Alloschemone* and are highly desirable.

INTRODUCTION

Generic delimitation within Araceae tribe *Monstereae* has long been subject to differing interpretations. Mayo *et al.* (1997) recognize eight genera for the tribe: *Alloschemone* Schott, *Amydrium* Schott, *Epi-*

premmum Schott, *Monstera* Adans., *Rhopidophora* Hassk., *Rhodospatha* Poepp., *Scindapsus* Schott and *Stenospermation* Schott. The genera are mostly separated on gynoecial characters, notably locule number, ovule (and thus seed) number, placenta position, seed shape and endosperm presence or absence. Due to their great plasticity, vegetative characters alone are of little use for generic determination. In the past some botanists have sought to reduce several genera into one (e.g. Bakhuizen van den Brink 1958; Hotta 1970). However, recent work on vegetative anatomy (e.g. French & Tomlinson, 1981) and floral anatomy (e.g. Carvell, 1989) has shown that these 'weak' genera are probably soundly based.

Previously *Alloschemone* has been treated as part of *Scindapsus* (e.g. Madison, 1976) due to shared gynoecial characters. However, Madison (1979), French & Tomlinson (1981) and Carvell (1989) have demonstrated convincingly that *Alloschemone* is not only distinct from *Scindapsus* but also probably not closely related.

HISTORY

Schott (1858) established *Alloschemone* (as *Alloschemone poeppigiana* Schott, *nom. illeg.*) for *Scindapsus occidentalis* Poepp. (Poeppig 1845) based on a collec-

tion made by Eduard Poeppig in 1831 at Ega (modern Tefé) in Brazilian Amazonas. Poeppig produced a good description of his new species, which is fortunate since the single spadix collected was lost. In separating *Alloschemone* from *Scindapsus*, Schott (1858, 1860) cited the disjunct distribution of Poeppig's species (*Scindapsus* is wholly Paleotropical) and the divided leaf lamina (*Scindapsus* leaf laminae are always entire).

Koch (1856) and Bentham & Hooker (1883) included *Alloschemone* in the Neotropical genus *Monstera* but this was never universally followed. Engler and others (Engler, 1879, 1889; Engler & Krause, 1908) recognized *Alloschemone* but with the caveat 'genus dubium, imperfecte cognitum'. Madison (1976) argued that the leaf shape and disjunct distribution of *Alloschemone* were secondary to the gynoeceal characters. *Alloschemone* and *Scindapsus* have a unilocular ovary with a single ovule on a basal placenta and Madison concluded that the genera should be united. Later, based on observations along the Rio Negro in Brazilian Amazonas, Madison reported that the growth habit of *Alloschemone* was so different to that of *Scindapsus* that he subsequently considered *Alloschemone* to be a distinct genus (Madison, 1979).

French and Tomlinson (1981) surveyed vascular patterns in the stems of *Monsteroideae*. They found that in *Alloschemone* the course of the vascular bundles in the stem central core differed from that of all other vining *Monstereae* while *Scindapsus* showed similarities to *Monstera*, *Rhabdophora*, *Epipremnum* and *Amydrium*.

Carvell (1989) showed the floral vasculature of *Alloschemone* to be substantially different to that of *Scindapsus* but similar to that of *Monstera deliciosa* Liebm. *Alloschemone* also shares some features in its vasculature typical of *Rhodospatha* and *Stenospermation*. Much of Carvell's work involved studying vestigial tepals at the base on the flowers. *Monstereae* has naked flowers (i.e. lacking a perigon), although Carvell found that many species studied have traces of vestigial tepals, in-

cluding *Alloschemone*. Unfortunately the distribution of species with vestigial tepals is, in this instance, of little taxonomic significance.

Alloschemone has been seldom collected. Following Poeppig's original gathering it was recollected by B. A. Krukoff in 1934 and then by M. Madison in 1978. The same year it was also found by staff from the Instituto Nacional de Pesquisas de Amazônia (INPA) while working on the Projeto Flora Epífita; in 1982 T. Plowman made what was then the best collection. In 1977 sterile specimens were collected by Kirkbride *et al.* in Rondonia state, Brazil and in 1987 Solomon made the only known collection from Bolivia. Recently a fine collection has been made by C.M. Sakuragui at Tefé. This collection, which includes for the first time pre-adult shoots and inflorescences in spirit, forms the basis for the expanded description presented below. All collections seen by us originate from Brazilian Amazonia and Bolivia (Dept. Pando).

Alloschemone has been introduced into cultivation only once, from the 1978 Madison collection (*Madison 6310*, see Croat, 1986). However, there has been some confusion as to the origin of the plant in cultivation under this number and it seems that it may have become mixed. A specimen of this Madison collection grown by one of us (J.B.) flowered after several years in cultivation and proved to be *Monstera spruceana* (Schott) Engl.

RELATIONSHIPS

The maintenance of *Alloschemone* as a genus is well supported, but its generic relationships are less clear. Gynoeceal characters are important for the delimitation of genera in *Monstereae*. *Alloschemone* and *Scindapsus*, the only genera with a single basal ovule in a unilocular ovary, would appear to be closely allied. However, other characters do not support this assumption. *Alloschemone* and *Scindapsus* differ in features of vegetative and floral anatomy, shoot architecture, leaf shape and geographical distribution. Gynoeceal char-

acters aside, *Alloschemone* is most similar to the Neotropical genera of *Monstereae*. *Alloschemone* has a chromosome number of $2n = 84$ and would be hexaploid if a basic number of $x = 14$ is considered. Two Neotropical genera, *Stenospermation* and *Rhodospatha*, have $2n = 28$, *Rhodospatha* also $2n = 56$, while *Monstera* and the other genera of the *Monstereae* have a certain number of $2n = 60$; some other numbers have been published but must be confirmed. The chromosome number of $2n = 84$ for *Alloschemone* suggests a closer relationship to *Rhodospatha* and *Stenospermation*. All counts cited are from work by Dr Gitte Petersen (Petersen 1989).

VEGETATIVE ANATOMY

French & Tomlinson (1981) investigated the vascular patterns in stems of subfamily *Monsteroideae*. Their findings mostly support the infrageneric classification proposed by Engler & Krause (1908) and also Mayo *et al.* (1997). French & Tomlinson defined three groups; 'Group 1' and '2' together equating to *Monstereae*, 'Group 3' to tribe *Spathiphyllaeae*. *Alloschemone* has vascular patterns not fitting one of these groups.

'Group I' has simple vascular bundles with the axial bundles formed by the aggregation of small traces branching from existing bundles. Bud traces are prominent, enter the central cylinder at the node, are superficially attached and frequently asymmetrically organized, five genera: *Amydrium*, *Epipremnum*, *Monstera*, *Rhaphidophora*, and *Scindapsus*.

'Group II' is essentially very similar, differing most notably in the presence of some compound vascular bundles, two genera: *Rhodospatha*, *Stenospermation*.

'Group III' has amphivasal vascular bundles forming a highly condensed, irregularly branching system. Bud traces are inconspicuous and do not form nodal arcs, two genera: *Holochlamys*, *Spathiphyllum*.

Alloschemone lacks basally aggregated axial vascular bundles and has a 'Rhaphis-like' (see Zimmerman & Tomlinson, 1972) upward branching of the leaf trace. This

arrangement of characters is unknown elsewhere in *Monsteroideae*.

After R. Keating's unpublished anatomical data the following leaf data can be summarized here (with permission).

Leaf lamina: surface with a smooth, thin cuticle, epidermis cells undulate adaxially, but polygonal abaxially, with straight anticlinal walls at the cell base. Stomata abaxial, level with the surface and brachyparacytic to brachyparahexacytic; subsidiary cells narrow and rounded. Palisade cells of the mesophyll short, with 6–8 spongy layers, air cavities accounting for up to 60% of this layer. There are small cavities at the palisade/spongy boundary and larger cavities regularly spaced within the spongy layer. Collenchyma weakly developed abaxially at the mid-rib, with thin wall layering on epidermal and subepidermal walls. Mid-rib with one to two vascular bundles. The xylem has small protoxylem cells and two to five medium-sized metaxylem cells. The phloem is a small irregular strand. Sclerenchyma fibers ensheathing larger vascular bundles. Trichosclereids are present in small clusters in air cavities just beneath the palisade layer, larger trichosclereids (up to 40–50 μm) in bigger air cavities deeper in the spongy layer. Tannin cells with dark contents are scattered and very common in the mesophyll. Raphide cells are large, thin-walled and elongate, filled with multiple crystals. Druses are very common in small cells in the palisade layer.

Petiole: chloroplasts sparse in the outer ground tissue. Ground tissue is divided into cortex and central cylinder, the cortex with eight to ten paranchyma layers and central cylinder delimited by bands of fibers. Air cavities are numerous throughout ground tissue. The vascular bundles are scattered and numerous in the central cylinder. Sclerenchyma fibers ensheathing the vascular bundles. Trichosclereids are numerous in all ground tissue. There are also unusual crystals of small or large aggregations of fine or coarse prismatics throughout the ground tissue and these do not resemble typical druses.

POLLEN MORPHOLOGY

Grayum (1992) studied the pollen grains of *Alloschemone occidentalis* from the Krukoff 7162 collection (NY). The pollen grain of this collection is not fully zonate (=sulcate), ellipsoid and with a shallowly foveolate exine. Grayum was not satisfied with the examined material and said "... additional fertile collections of this little-known species are needed" (Grayum 1992:15).

We studied pollen material of *Plowman et al.* 12207 for which there are several duplicates all with abundant pollen. However, it turned out much more problematic than Grayum's study when examined with SEM. The Plowman collection also shows ellipsoid pollen but with a very inconspicuous sulcus best described as "hardly bordered diffuse germination field." The exine is more-or-less rough (compare Figs. 3–5 with Grayum 1992:55, Figs. 107–108).

We must agree with Grayum and say that more and better material is needed to give a clear interpretation of the pollen grains.

FLORAL ANATOMY

Carvell (1989) reported that floral vascular anatomy supports the integrity of *Monstereae* (*sensu* Engler & Krause, 1908; Mayo *et al.*, 1997). Genera are generally supported by differences in floral vasculature. Carvell met with problems interpreting the variability of vascular traces in *Rhaphidophora* and *Epipremnum*. This, particularly for *Epipremnum*, cast some doubt on generic integrity. However, the percentage of variability appeared to partly be an artifact of limited sampling and, despite these problems, sufficient data were found to show that a close relationship between *Epipremnum*, *Amydrium* and *Scindapsus* was unlikely and that furthermore these genera have little to do with *Alloschemone*.

Carvell (1989) found that *Alloschemone* has two rings of gynoecial traces, the inner trace terminating along the stylar canal, the outer trace arching to a position adjacent to the stylar canal. This is similar to

the condition in *Monstera deliciosa* although *M. deliciosa* lacks the arching pattern of the outer vascular ring traces. Arching vascular traces are diagnostic for *Rhodospatha* and *Stenospermation* but both have only a single ring of traces. *Scindapsus* has a single ring of vascular traces terminating adjacent to the stylar canal but these do not arch. Carvell concluded that the flowers of *Alloschemone* were anatomically distinct from *Scindapsus* but showed some similarities to *Rhodospatha*, *Stenospermation* and *Monstera*.

SHOOT ARCHITECTURE

Alloschemone displays a mature (fertile) shoot architecture that is very unusual in *Monstereae* (Madison, 1979; Sakuragui, pers comm.). Mature fertile stems of *Alloschemone* bear foliage leaves interposed by up to six nodes each bearing a cataphyll. This type of shoot architecture is very rare in *Monstereae* and occurs otherwise only in shoots of, e.g. *Rhaphidophora decursiva* (Roxb.) Schott, *Amydrium humile* Schott and *A. medium* (Zoll. & Moritzi) Nicolson. The seedling *Alloschemone* are still unknown.

There are three climbing Neotropical *Monstereae* genera: *Alloschemone*, *Monstera* and *Rhodospatha*. *Monstera* has the most diverse shoot architecture. Madison (1977) describes seven types of 'heteromorphic shoots' for *Monstera*, defined primarily by leaf development sequences. Madison's *Monstera* models include seedling data and the occurrence of skototropic shoots (see Strong & Ray, 1975), data currently not available for *Alloschemone*. However, comparison of mature and fertile shoot data available for *Alloschemone* suggests that none of Madison's *Monstera* models match *Alloschemone*.

Little data are available for shoot architecture in *Rhodospatha*. Observations of herbarium specimens suggest that *Rhodospatha* species have fairly 'conventional' shoots with regularly produced foliage leaves. A specimen of *R. oblongata* Poepp. (*Harley et al.* 18193 (K)) has a foraging flagellum, suggesting a growth pattern

similar to Madison's Fig. 27 (Madison 1977: 23 Fig. 27, *M. siltepecana* Matuda) or Fig. 29 (Madison 1977:23 Fig. 29, *M. acuminata* C. Koch). There is no evidence of foraging shoot production in *Alloschemone*. Little data exist for seedlings of *Rhodospatha*. The few juvenile specimens in Kew herbarium suggest that *Rhodospatha* produce conventional foliage leaves soon after germination but it is not clear whether plants pass through a 'stolon-like' (see Madison 1977:17–20) seedling stage.

The fourth Neotropical monsteroide genus, *Stenospermaton*, is a genus of epiphytes or terrestrial herbs. However, several species produce elongated root-climbing shoots but are not as vine-like as other genera. The shoot architecture of *Stenospermaton* will not be discussed further here.

In the Paleotropics one genus of *Monstereae* (*Epipremnum*) is an obligate climber and four genera have almost all species climbing, namely *Amydrium* (5 spp., one non-climbing), *Rhaphidophora* (ca. 100 spp., two none-climbing), *Scindapsus* (ca. 35 spp., five none-climbing). Of these genera *Scindapsus* has the most diverse shoot architecture of any Paleotropical monsteroide genus, with four distinct patterns. One species, *Scindapsus certhios* P. C. Boyce, has long root-climbing sterile shoots bearing cataphylls and scattered, somewhat depauperate, foliage leaves. These shoots later produce scattered fertile shoots with distichously arranged fully developed foliage leaves functioning as a litter basket. The sterile climbing stage of *S. certhios* is superficially similar to that of *Alloschemone* but the similarity between the genera does not extend to the fertile shoots. This type of shoot function differentiation occurs elsewhere in *Monstereae* (e.g. *Rhaphidophora schlechteri* K. Krause) and in tribe *Philodendreae* (e.g. *Philodendron linnaei* Kunth) and is probably not of taxonomic significance.

LEAF SHAPE

Leaf shape is of less use for determining generic affiliations. With the possible ex-

ception of tribe *Anthurieae* (sole genus *Anthurium* Schott) *Monstereae* displays the greatest range of leaf shape in the Araceae. Even individual genera have a bewildering range of leaf types (see, e.g. Madison, 1977). However, it is interesting to compare the distribution of divided leaves among genera. Two genera of Neotropical *Monstereae* have divided leaves, namely *Alloschemone* and *Monstera*. Sterile specimens of some *Monstera* species (especially *M. spruceana*) are superficially similar to *Alloschemone*, although *M. spruceana* is easily distinguished by having more than one primary lateral vein per pinna. Much has been written about the significance of split and perforated leaves in vining Araceae (e.g. King, 1962; Taylor & Sexton, 1972) but there is no conclusive evidence as to the precise function of these features.

In the Paleotropics, two species of *Epipremnum*, four species of *Amydrium* and nine species of *Rhaphidophora* have divided leaves. Other features, especially gynoecial characters, separate *Rhaphidophora* and *Amydrium* from *Alloschemone* and a close relationship between these genera seems unlikely. *Epipremnum* is overall more similar to *Alloschemone*. However, the species with divided leaves, *E. pinnatum* (L.) Engl. and *E. aureum* (Linden & André) Bunting are anomalous in the genus by characters including stem sculpturing and inflorescence presentation and require further study.

As noted above, *Scindapsus* is indistinguishable from *Alloschemone* on gynoecial characters but leaf shape and shoot architecture are distinct.

DISTRIBUTION

Alloschemone is known only from Brazil and Bolivia. Sterile collections from Venezuela tentatively assigned to *Alloschemone* have all proved to belong to *Monstera*. All genera of *Monstereae* recorded for the Neotropics (i.e. *Alloschemone*, *Monstera*, *Rhodospatha* and *Stenospermaton*) are not found outside of Mexico, Central and

South America and the Caribbean except as introductions.

Scindapsus, as defined here, is strictly Paleotropical, occurring from India to the western Pacific (Samoa). Except for *Rhapidophora* (ca. seven, mostly undescribed, species in West Africa) all Paleotropical *Monstereae* genera are restricted to the area from the Ryukyu Islands and Okasawara Guntu (Bonin Islands) to northern Australia and from India to Rarotonga (Cook Islands).

TO WHAT IS *ALLOSCHEMONE* RELATED?

The available evidence suggests that *Alloschemone* is not closely related to *Scindapsus*. The similarities of the gynoeceum are probably derived independently by the loss of a gynoeceal septum. If the gynoeceum prior to septal loss had a few large seeds on an axial or deeply intrusive placenta (i.e. as in *Epipremnum* or *Amygdrium*) then the loss of the septum would most likely result in a basal placenta with fewer ovules and thus a single basal ovule could have arisen independently in both genera. The anatomical characters reviewed above suggest a link to Neotropical rather than Paleotropical genera. *Alloschemone* has unique stem anatomy but shares gynoeceal anatomical characters with all three genera of Neotropical *Monstereae*, basal placentation with *Stenospermation*, vining habit but not shoot architecture with *Monstera* and *Rhodospatha*, and divided leaves only with *Monstera*.

Much work on the phylogeny of the Araceae and related alismatid monocot families, is currently being undertaken using molecular techniques. Preliminary work on the phylogeny of the *Monstereae* supported a phylogenetic link between *Alloschemone*, *Stenospermation* and *Rhodospatha* (Tam, pers. comm.).

Alloschemone Schott, Gen. Aroid. App. (1858) & Prodr. Syst. Aroid. 358 (1860); Engl. in Martius, Fl. Bras. 3(2): 115 (1878) & in A. & C., DC., Monog. Phanerog. 2:267 (1879); Engl. &

Prantl, Die natürl. Pflanzenfam. II, 3 120 (1889); Engl. & K. Krause in Engl., Das Pflanzenr. 37 (IV.23B):117–118 (1908); Madison, Selbyana 1(4):325–327 (1976) & Aroidiana 2 (3):73 (1979); French & Tomlinson, Amer. J. Bot. 68(8): 1123–1124, 1128 (1981); Carvell, Fl. Anat. Pothoideae Monsteroideae 317–325, 525–528; (1989); Mayo et al., Genera of Araceae 125–126, Pl. 18.

Trichosclereids abundant. Robust to large evergreen root climber. Stem terete, epidermis smooth at first, becoming distinctly corky and longitudinally furrowed with age. Juvenile and pre-adult plants with long flagelliform shoots and sometimes forming sparse terrestrial colonies. Roots densely arising along entire length of climbing stem, terete, gray, tomentose, adhering firmly on the trunk. Juvenile leaves spreading, slightly scattered, 1–3 cataphyllary nodes between each foliage leaf, lamina entire, ovate to ovate-elliptic, apex acute, base slightly cordate to almost truncate, margin entire to shallowly divided (in more intermediate stage); petiole long, geniculate apically, sheath short. Adult leaves spreading, laxly recurved, scattered, up to six cataphyllary nodes between each foliage leaf; cataphylls long, often reaching almost the length of the petiole, at first membranous, light green, soon drying chartaceous and turning dark brown; petiole geniculate apically, thickened at base, sheath short, with margin incurved and smooth on older leaves; leaf lamina coriaceous, ovate-subcordate in outline, pinnatifid, mid-green, paler beneath, pinnae 4–6 on each side of the midrib, subalternate, separated from each other by a rounded or oblong sinus and often with curtailed pinna development at the base, falcate, acute, each pinna with only one primary lateral vein, secondary lateral veins more-or-less parallel pinnate, higher order venation reticulate. Inflorescence solitary, erect, (strongly sweet-fragrant on opening in *A. occidentalis*); peduncle shorter than petiole; spathe ovate-cymbiform, coriaceous, deciduous at anthesis,

convolute to half way, shallowly concave and gaping above at female receptivity, apex more-or-less obtuse, exterior creamy white, glossy, interior flushed pink; spadix shorter than spathe, sessile to short-stipitate, cylindrical, apex obtuse, pale yellow to dull pink or orange, stipe terete. Flowers bisexual, naked; stylar areas yellow. Stamens four, filaments flattened, free or partially to completely connate, shorter than gynoecium, thecae oblong, dehiscing by oblique apical short slit; pollen not fully zonate, ellipsoid, medium-sized (mean 46 μm), exine shallowly foveolate. Gynoecium with prismatic ovary, 1-locular, with abundant locular mucilage, ovule one, amphitropous, funicle bearing trichomes, placenta basal; stylar region densely packed with trichosclereids, stigma sessile, elliptic; often some gynoecia at base of spadix larger and apparently sterile and nectariferous. Fruit and seed unknown. Chromosome number $2n = 84$.

Type species—*Alloschemone poeppigiana* Schott, *nom. illeg.* (= *A. occidentalis* (Poepp.) Engl. & K. Krause).

Two species restricted to Brazil (Amazonas, Rondonia) and Bolivia (Dept. Pando).

Etymology: Greek *allos* (=other), *schemma*, *schêmâtos* (=form) and *ône* (=being); in allusion to the plant's habit, which looks different to other aroids.

Key to the species of *Alloschemone*

1. Pinnae of the leaf lamina broader (5–10 cm wide), sinus between the pinnae round; filaments of the stamens free **1. *A. occidentalis***
1. Pinnae of the leaf lamina narrower (2–3 cm wide), sinus between the pinnae oblong; filaments of the stamens connate **2. *A. inopinata***

1. *Alloschemone occidentalis* (Poepp.) Engl. & K. Krause in Engl., *Das Pflanzenr.* 37 (IV.23B):117 (1908)—*Alloschemone poeppigiana* Schott, *Gen. Aroid. App.* (1858), *nom. illeg. pro. A. occidentalis* (Poepp.) Engl. & K. Krause—*Scindapsus occidentalis* Poepp., *Nov.*

Gen. Spec. Pl. 3:88 (1845)—*Monstera occidentalis* (Poepp.) C. Koch ex Ender, *Ind. Aroid.* 4, 54 (1864); Koch in *Bonplandia* 4:4–10 (1856); Bentham & Hook.f, *Gen. Pl.* 3:992 (1883). Type: Brazil, Município de Tefé, Tefé ('Ega'), 1831, *Poeppig s.n.* ('Addenda 107') (holotype P; isotype LE). Figs. 1, 2(B–M), 3–5 & back cover C–D, F–J.

Robust to very large evergreen root climber, at least 5 m high when flowering. *Stem* in adult plants adherent, unbranched (unless apical meristem damaged and then reiterating from a node close to the damaged apex), terete, (1–)1.5–2.5 cm diam., internodes ca. 1 cm long, epidermis smooth at first, mid-green to pale gray or brown, becoming conspicuously longitudinally corky-winged with age. Juvenile and pre-adult plants with long, robust flagelliform shoots and sometimes forming sparse terrestrial colonies. *Roots* densely produced from entire climbing stem length, adhering firmly to tree trunk, cylindrical, 2–6 cm \times 2–3 mm diam., more-or-less grayish, appearing tomentose, because densely covered with 1–2 mm long root hairs. *Juvenile leaves* spreading, slightly scattered (one to three cataphyllary nodes between each foliage leaf), lamina lanceolate, ovate or ovate-elliptic, up to 17 \times 7 cm, apex acute, base cuneate to slightly cordate to almost truncate, margins entire to shallowly divided in pre-adult leaves, petiole up to 9 \times 0.3 cm, geniculum ca. 1 cm long; *adult leaves* laxly recurved, scattered (up to six cataphyllary nodes between each foliage leaf); *leaf lamina* thinly coriaceous, ovate-subcordate in outline, pinnatifid, 45–95 \times 48–66 cm, shining mid-green, paler beneath, pinnae subalternate, oblong-elliptic, 18–32 \times 5–10 cm, falcate, apex acute, lacinae extending 1–4 cm from midrib, separated by a narrow to broad, rounded sinus, and often with curtailed pinna development at the base, primary lateral veins 1 per pinna, secondary lateral veins parallel-pinnate, 15–17 on each side of pinna, higher order venation reticulate; *petiole* geniculate apically, thickened at base, (26–)30–70 \times

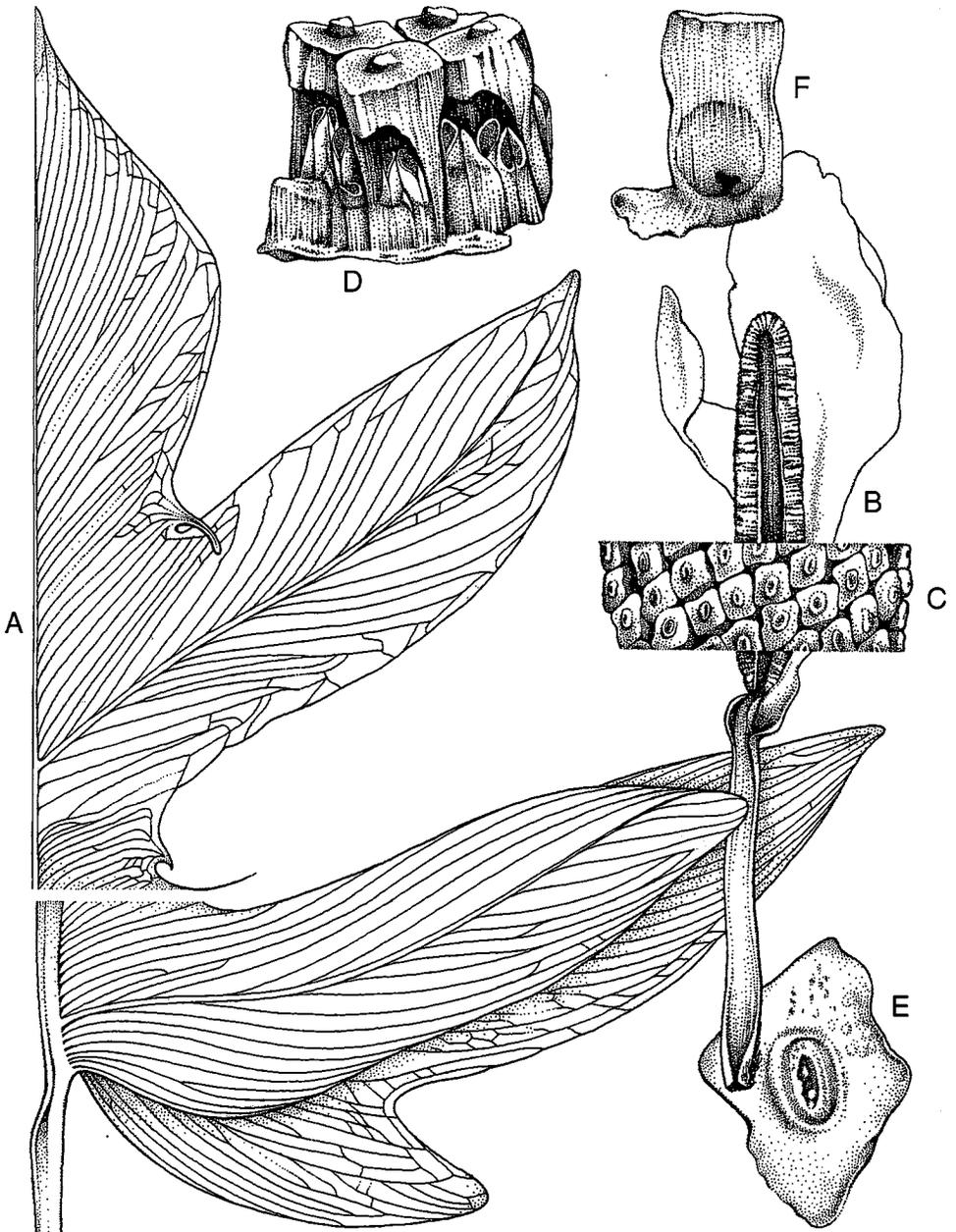


Fig. 1. *Alloschemone occidentalis*. **A** leaf tip and base, mid-portion omitted, basal part with left hand lobe folded over to show abaxial surface $\times \frac{1}{2}$; **B** inflorescence, spadix longitudinally sectioned and spathe damaged in nature $\times \frac{1}{2}$; **C** detail of post-anthesis spadix $\times 2$; **D** four flowers, three quarter view $\times 5$; **E** styler region, plan view $\times 10$; **F** gynoecium, longitudinal section with associated spadix axis tissue $\times 5$. A–B *Plowman et al.* 12207, C–F *Krukoff* 7162. Drawn by Emmanuel Papadopoulos.

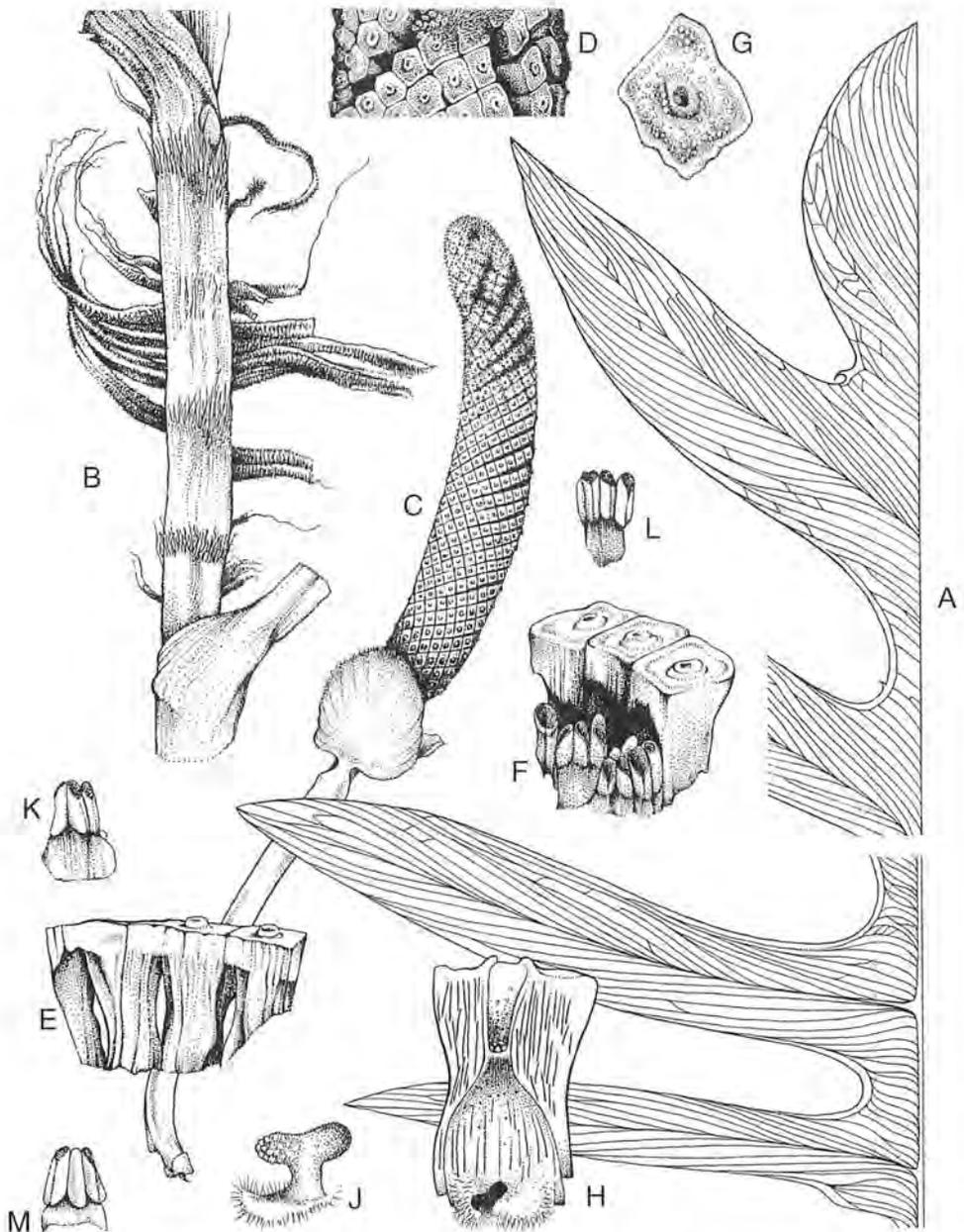


Fig. 2. **A.** *Alloschemone inopinata*. **A** leaf tip and base, mid-portion omitted $\frac{1}{2}$. **B–M** *Alloschemone occidentalis*. **B** young stem showing clasping roots, cataphyllary node scars and two foliar leaf petiole bases $\times \frac{2}{3}$; **C** inflorescence, with portion of spathe base $\times \frac{2}{3}$; **D** detail of pre-anthesis spadix $\times 1\frac{1}{2}$; **E** three flowers, side view $\times 4$; **F** three flowers, three quarter view $\times 4$; **G** stylar region, plan view $\times 6$; **H** gynoecium, longitudinal section showing abundant trichomes $\times 6$; **J** ovule $\times 10$; **K–M** anthers in adaxial, three quarter and abaxial view $\times 4$. **A** from *Projeto Flora Epifita 310*, **B–M** from *Plowman et al. 12207*. Drawn by Emmanuel Papadopoulos.

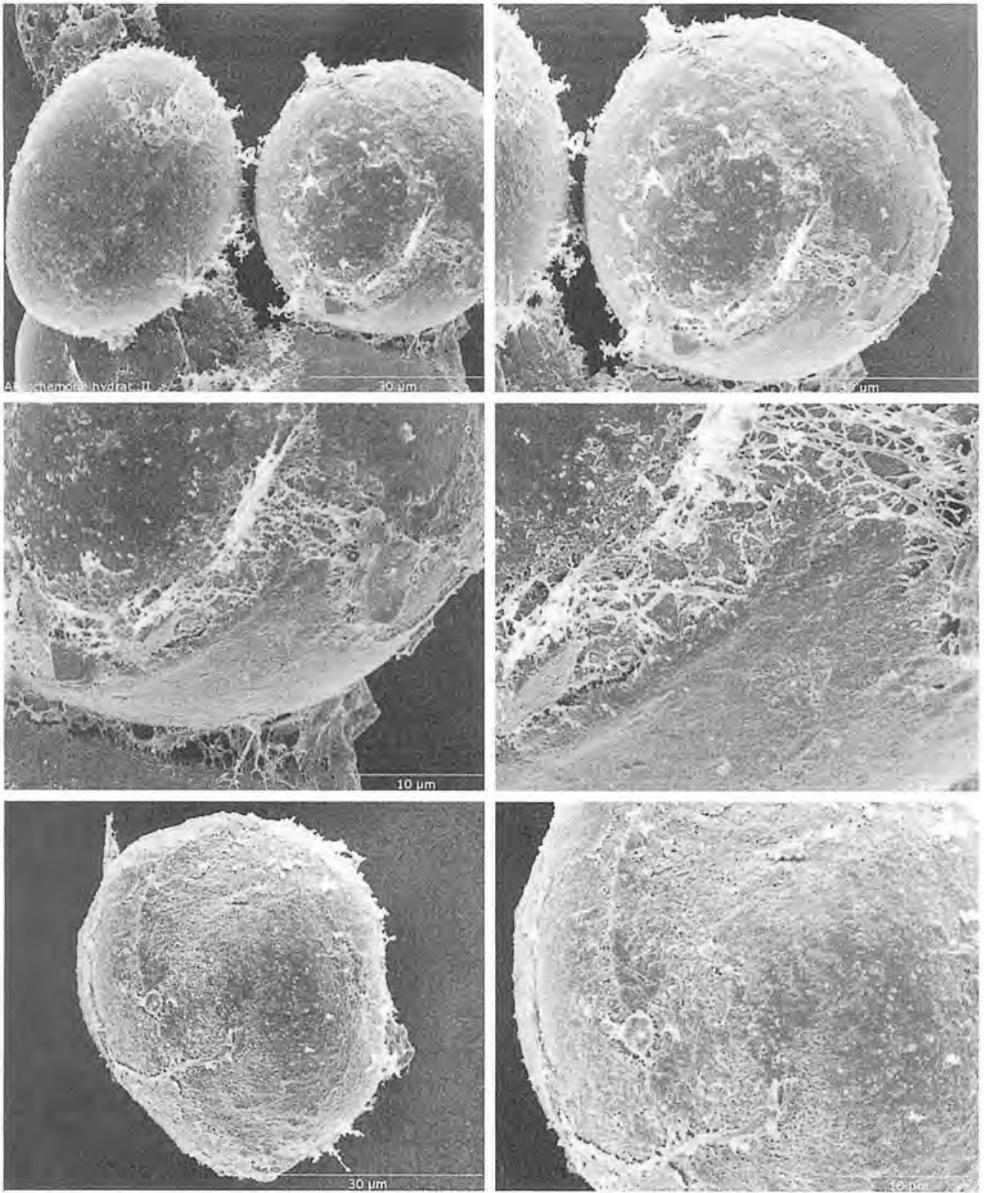


Fig. 3. *Alloschemone occidentalis*. Pollen SEM from *Plowman 12207*. SEM micrographs by M. Hesse.

(0.7–)1–1.5 cm, petiolar sheath short, 2–10 cm long, margins on older specimens incurved, smooth; geniculum 2–2.5 cm long. *Inflorescence* solitary, erect; peduncle erect, terete, 9–15 × ca. 2 cm diam., reddish; *spathe* deciduous, coriaceous, ovate-cymbiform, 17–20 × 7–9 cm, convolute to half way up, shallowly concave and gap-

ing above on opening, apex obtuse, exterior creamy white, glossy, interior flushed pink, strongly sweet-fragrant; *spadix* sessile to short-stipitate, cylindric, 10–12 × 2.5–3.5 cm, apex obtuse, stylar tissue pale yellow to dull pink or orange, also very sweet-fragrant; stipe terete, (0–)1.2 × ca. 3 cm. *Flowers*: bisexual, naked; *sta-*

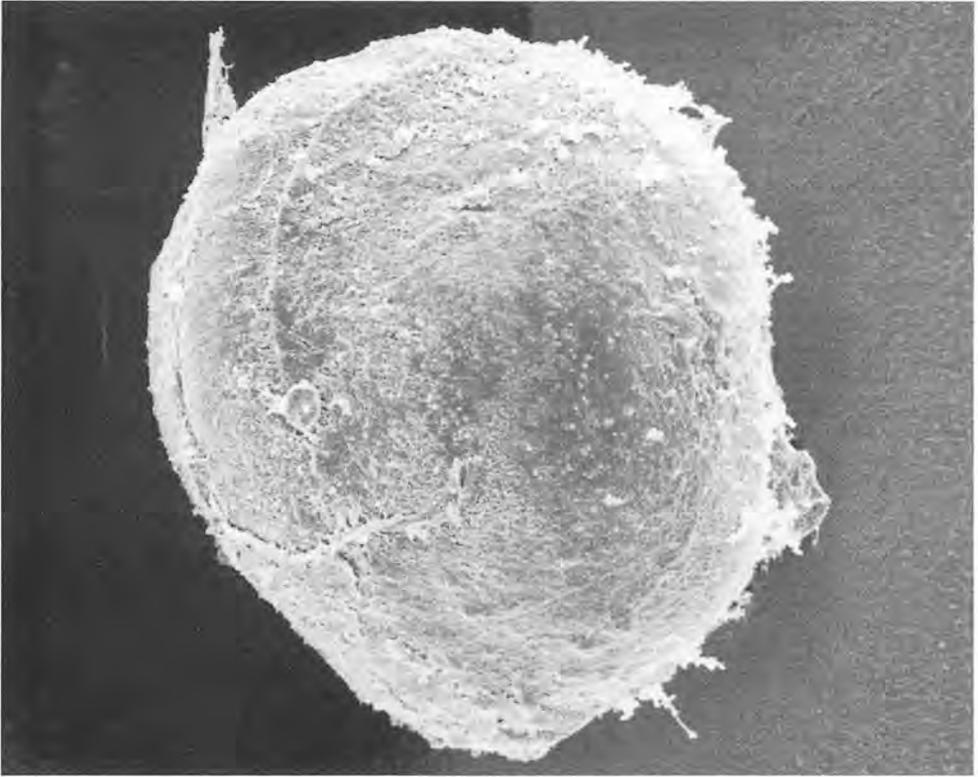


Fig. 4. *Alloschemone occidentalis*. Pollen SEM from *Plowman 12207*. The pollen is not acetolyzed; there is a little pollenkitt visible. SEM micrograph by M. Hesse.

mens 4, filaments flattened, free (4–)5–8 × 1–2 mm, thecae oblong, ca. 2mm long, dehiscent apically by an oblique, short slit. *Pollen* not fully zonate, ellipsoid, 44–46 × 27–28 μm, exine shallowly foveolate. *Gynoecium* prismatic, 8–9 × (2.5–)3.5–4 mm at top, below 2.5–3 mm wide (gynoecia at base of spadix larger, 8–9 × 4–6 mm, apparently sterile and nectariferous), stylar region densely packed with trichoscleroids, stigma prominent, elliptic in plan view 1.3–1.5 mm × ca. 1 mm, stigmas orientated longitudinally along the spadix axis; ovary 1-locular, with abundant locular mucilage; *ovule* 1, amphitropous, 1–1.2 mm tall, ca. 1.4 mm wide, funicle bearing trichomes, placenta basal. *Fruit* unknown. *Seed* unknown. *Chromosome number* 2n = 84.

Flowering—October to November; spathe and spadix strongly sweet-fragrant.

Distribution—Brazil (Amazonas, Rondonia), Bolivia (Dept. Pando).

Specimens seen—BRAZIL. Amazonas: No further data, *Hutchinson 8687, 8699* (UEC); Município de Humayta (Humaíta), Rio Madeira basin, plateau between Rio Livramento and Rio Ipixuna, 7–8 Nov. 1934, *Krukoff 7162* (GH, NY); Município de Maraã, Rio Japurá, near Maraã, Lago Maraã, 1°51'S, 65°36'W, 4–5 Dec. 1982, *Plowman et al. 12207* (INPA, K, MO, NY); Município de Tefé, Tefé ('Ega'), 1831, *Poeppig s.n.* ('Addenda 107') (holotype P, isotype LE); Município de Tefé, Tefé, road to airport, ca. 5 km from Tefé, 17 Oct. 1995, *Sakuragui 1050* (K, M; SPF). Rondonia: at km 11 on the road to Saldanha, close to Guajara-Mirim, 12 Jan. 1977 *Kirkbride jr., Lleras & Leite-Lleras 2712* (US).

BOLIVIA. Dept. Pando, Prov. Gral. Fred-

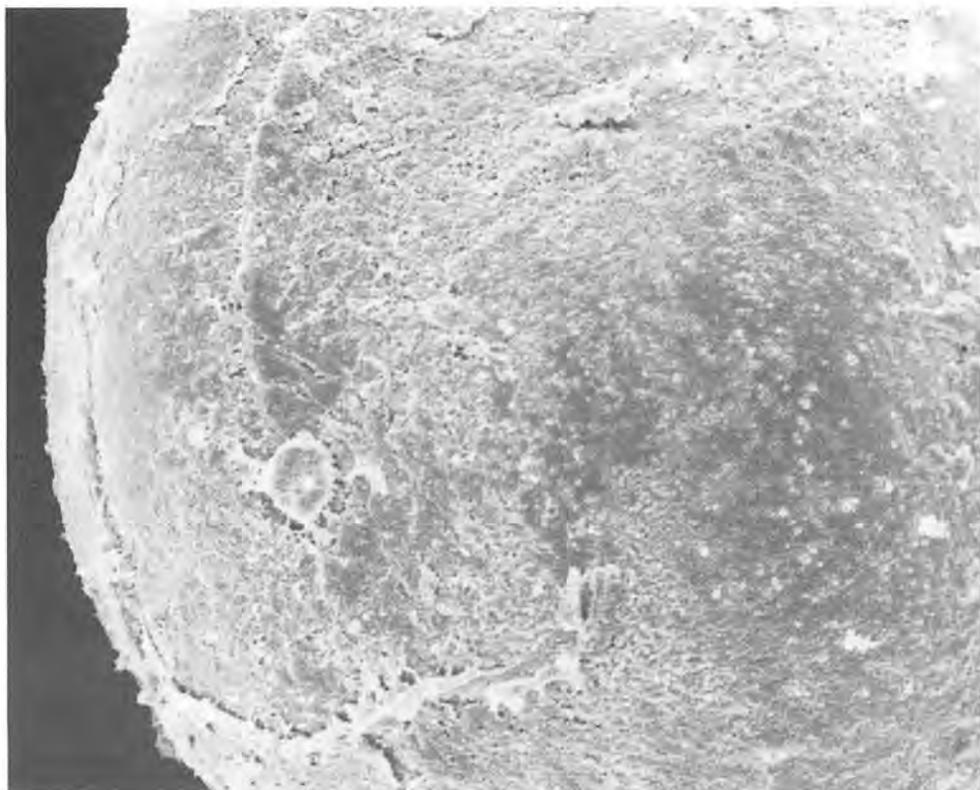


Fig. 5. *Alloschemone occidentalis*. Pollen SEM from *Plowman 12207* showing \pm rough, but not foveolate, exine. SEM micrograph by M. Hesse.

erico Roman, Rio Negro, 10°34'S, 66°06'W, 17 June 1987, *Solomon 17114* (MO).

Ecology—Caatinga, primary or degraded seasonal evergreen forest on terra firme of grayish clay or sandy clay with deep litter. 10–120 m.

2. ***Alloschemone inopinata*** Bogner & P.C. Boyce **sp. nov.**, differt ab *A. occidentalis* pinnis angustioribus (2–3 cm latis), sinus inter pinnis oblongo, filamentis staminorum connatis. Typus: Brazil, Amazonas, Rio Negro, mouth of the Rio Marié, 16 Oct. 1978, *Madison et al. 6310* (K, holotypus; INPA, MO, SEL, isotypi). Figs. 2(A) & back cover A–B, E.

Robust evergreen root-climber, several meters tall; *Stem* terete, outside corky in adult stage, 0.8–1.5 cm diam. Internodes

3–4 cm long, 3 nodes bearing cataphylls followed by foliage leaf (note by Madison); clasping roots covered densely with root hairs. *Juvenile leaves* unknown; *adult leaf* lamina pinnatifid; *petiole* 17–25 \times ca. 0.5 cm, geniculum 1–2 cm long, sheath short (ca. 1 cm long); *lamina* pinnatifid, 45–50 \times 35–40 cm, mostly 4 pinnae on each side, midrib quite strong, ca. 3 mm diam., 1 primary lateral vein running from the midrib into each pinna, pinnae 13–23 \times 2–3(–4) cm, acute to somewhat cuspidate, apex of upper pinnae turning upwards, ca. 15 secondary lateral veins on each side of the primary vein, these thinner, parallel-pinnate; higher order venation reticulate; sinus between the pinnae oblong, lacinae extending 1–1.5 cm from midrib. *Inflorescence* solitary; peduncle ca. 10 \times 0.7 cm; spathe deciduous; spadix cylindrical, ca. 11 \times 1.8 cm, apex obtuse.

Flowers bisexual; gynoecium ca. 5×4 mm, truncate, more-or-less rhombic in plan view; stigma broadly elliptic; *stamens* shorter than gynoecium, filaments connate, thecae oblong, dehiscent by a broad apical slit. *Fruit* and *seeds* unknown. Chromosome number unknown.

Flowering—October to December.

Distribution—Brazil (Amazonas).

Specimens seen—BRAZIL. Amazonas: Humaita, *Cid 8781* (INPA); Rio Negro, mouth of the Rio Marié, 16 Oct. 1978, *Madison et al.* 6310 (K, holotype; INPA, MO, SEL, isotypes); Rio Negro, mouth of the Rio Marié, 16 Oct. 1978, *Projeto Flora Epífita 310* (INPA); Humaita, *Teixeira et al.* 96 (INPA);

Ecology—Caatinga on terra firme. ca. 10 m.

REMARKS

The completely connate filaments of *Alloschemone inopinata* are unique not only in this genus but also in the whole of *Monstereae*. The *Krukoff 7162* collection clearly shows free filaments which are never connate partly at all. The *Madison 6310* collection has stamens where all filaments of a flower are connate, forming a ring. The *Plowman et al. 12207* collection shows both free filaments and also stamens where two are connate and thus this character is variable. The leaf pinnae of the *Plowman et al. 12207* collection are broader, and the sinus of the pinnae is more-or-less round, as it is in typical *A. occidentalis*. From the available material it is difficult to decide if *Alloschemone* comprises one very variable species or whether there are two, more narrowly defined species. For the present we believe that there are two species. We hope that this paper will stimulate people into trying to collect more, fertile, ideally fruiting, collections of this enigmatic genus.

The genus *Alloschemone* has a wide distribution (in Amazonian Brazil and one record is known from Bolivia) but it seems to be never common and occurs locally

only. This can be concluded from the few collections made within 170 years.

The seed structure is very important in the *Monstereae*, but fruits and seeds are still unknown for *Alloschemone*. Therefore, it would be very useful to get mature fruits. The living plants in cultivation grow only slowly, and it will take many years for them to reach a size for flowering and perhaps fruiting. Nevertheless it can be predicted from the structure of the ovule that the seed cannot be straight, it must be somewhat curved. Further, it would be very useful to know the structure of the testa, if endosperm is present or absent, and how the embryo is formed.

Mike Madison sent a color postcard picturing an Amerindian and a leaf in the upper left corner which is clearly an adult leaf of *Alloschemone occidentalis*. It is not known exactly where this photograph was taken.

Croat (1986 '1985':80–82, Figs. 1–3) pictured juvenile leaves as *Alloschemone occidentalis*, but these were later shown to belong to *Monstera spruceana*, when the plant flowered.

Plate 18 in Mayo *et al.* (1997), shows A–B, E, *Alloschemone inopinata*, and C–D, & F–J, *A. occidentalis*.

ACKNOWLEDGMENTS

The Keepers and Curators of the following herbaria are thanked for assistance during visits, and for the loan of material: GH, INPA, K, LE, MO, NY, P, SEL, SPF, UEG, US. Thanks are due to Emmanuel Papadopoulos and Eleanor Catherine for executing the illustrations, Gitte Petersen, Copenhagen for counting the chromosomes, Prof. M. Hesse, Wien, for the SEM micrographs of the pollen grains, Dr H. Roeßler, München, for providing the Latin diagnosis and to Prof. R. Keating, Edwardsville, Illinois, for additional anatomical data.

LITERATURE CITED

Bakhuizen van den Brink, R. C. 1958. Are *Epipremnum* Schott, *Rhaphidophora*

- Hassk., and *Monstera* Adans. congeneric? *Blumea* suppl. 4:91–92.
- Bentham, G. & J. D. Hooker, 1883. Araceae ('Aroideae'). *Genera Plantarum*, vol. 3:955–1000. Lovell Reeve & Co., London.
- Carvell, W. N. 1989. Floral anatomy of the *Potboideae* and *Monsteroideae* (Araceae) Unpublished Ph.D. Dissertation, Miami University, Oxford, Ohio.
- Croat, T. B. 1986 ('1985'). A new collection of the rare *Alloschemone occidentalis* (Poepp.) Engl. & Krause. *Aroideana* 8(3):80–82.
- Engler, A. 1879. Araceae. In A. & C. de Candolle, *Monographiae Phanerogamarum*, vol. 2:1–681. Masson, Paris.
- . 1889. Araceae. In A. Engler & K. Prantl (eds.), *Die natürlichen Pflanzenfamilien* 2(3):102–153. W. Engelmann, Leipzig.
- Engler, A. & K. Krause. 1908. Araceae—*Monsteroideae*. In A. Engler (ed.), *Das Pflanzenreich* 37(IV.23B):4–139. W. Engelmann, Leipzig.
- French, J. C. & P. B. Tomlinson. 1981. Vascular patterns in stems of Araceae: subfamily *Monsteroideae*. *Amer. J. Bot.* 68(8):1115–1129.
- Grayum, M. H. 1992. Comparative External Pollen Ultrastructure of the Araceae and Putatively Related Taxa. *Monographs Syst. Bot. Missouri Bot. Gard.* 43:1–167.
- Hotta, M. 1970. A system of the family Araceae in Japan and adjacent areas. *Mem. Fac. Sci. Kyoto Imp. Univ., Ser. Biol.* 4:72–96.
- King, H. W. 1962. The physiology of *Monstera deliciosa*. *J. Queckett Mic. Club*, Ser. 2, 32:125–136.
- Koch, C. 1856. *Monstera* und *Scindapsus*. *Bonplandia* 4:4–10.
- Madison, M. T. 1976. *Alloschemone* and *Scindapsus* (Araceae). *Selbyana* 1: 325–327.
- . 1977. A revision of *Monstera* (Araceae). *Contrib. Gray. Herb.* 207:3–100.
- . 1979. Notes on some aroids along the Rio Negro in Brazil. *Aroideana* 2(3):67–77.
- Mayo, S. J., J. Bogner & P. C. Boyce. 1997. *The Genera of Araceae*. xii + 370 pp. Royal Botanic Gardens, Kew.
- Petersen, G. 1989. Cytology and systematics of Araceae. *Nord. J. Bot.* 9:119–166.
- Poeppig, E. 1845. *Nova Genera ad Species Plantarum*, vol. 3. Leipzig.
- Schott, H. W. 1858. *Genera Aroidearum Appendix*. Ueberreuter, Vienna.
- . 1860. *Prodromus Systematis Aroidearum*, p. 358. Typis congregationis mechitharisticae, Vienna.
- Strong, D. R. & T. S. Ray. 1975. Host tree location behavior of a tropical vine (*Monstera gigantea*) by skototropism. *Science* 190:804–806.
- Taylor, S. E. & O. J. Sexton. 1972. Some implications of leaf tearing in Musaceae. *Ecology* 53:143–149.
- Zimmerman, M. H. & P. Tomlinson. 1972. The vascular system of monocotyledonous stems. *Bot. Gaz.* 133:141–155.