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# Morphology and ecology of seedlings, fruits and seeds of Panamá: Vochysiaceae

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**SYNOPSIS** Seedlings, saplings, fruits and seeds of *Vochysia ferruginea* (Vochysiaceae) are described, and ecological data on these stages summarized, as part of the ongoing *Seedling Flora Project* centred on Barro Colorado Island, Panamá. Seedlings of two other species reported from Panamá are also described. The morphology of these stages is compared to that of other taxa in the family. The potential use of seed and seedling characters in phylogenetic studies within the family is discussed. Special attention is drawn to unusual two-parted cotyledonary stipules, ontogenetic changes in leaf hair morphology, and complex ptyxis and veneration of the embryonic cotyledons.

## INTRODUCTION

The aim of the *Seedling Flora Project*, initiated in 1985, is to produce an illustrated flora of seedlings, saplings, fruits and seeds for the neotropical forest centred on Barro Colorado Island, Panamá (see Garwood & Humphries, 1993; Garwood, 1994, 1995, in prep.). This is the account of *Vochysia ferruginea* Mart. (Vochysiaceae). It is the most abundant *Vochysia* in Panamá, common in the younger forests of Barro Colorado Island and Central Panamá; four other species are known, but only from a few collections (Robyns, 1967*a*, *b*; Croat, 1978; D'Arcy, 1987). Ranging from Central America through the Amazon basin, *V. ferruginea* is also the most widespread species in the genus, in contrast to most species which have relatively limited distributions (Stafleu, 1948). Because of its fast growth rate and valuable timber, *V. ferruginea* has been identified as a potentially important forestry species for use in plantations or managed secondary forests in the neotropics (Finegan, 1992; Condit et al., 1993; Butterfield & Fisher, 1994).

In this account, I describe the seedlings, saplings, fruits and seeds of *V. ferruginea*, and the seedlings of two other species known from Panamá, then compare these stages to those of other species in the family to identify characters of potential phylogenetic importance. Fruit and seed characters have been important in delimiting the

tribes and genera of Vochysiaceae; subgeneric classifications and keys to species, however, have been based almost solely on floral and vegetative characters (Warming, 1875; Stafleu, 1948–1954; Keay & Stafleu, 1953). There have been few comparative studies of the gross morphology or anatomy of fruits and seeds (Corner, 1976; Boesewinkel & Venturelli, 1987). Seedlings of few species have been described in detail (del Amo, 1979; Ricardi et al., 1987; Flores, 1993*a*, *b*).

## METHODS

Standard methods for germinating seeds, producing voucher specimens for each seed collection, growing and harvesting seedlings, collecting unvouchered seedlings (wildlings) from the forest, and manipulating the descriptive database were developed for the *Seedling Flora Project* (Garwood, 1994, 1995) and were used for this account. The detailed descriptions follow the standard format developed for the *Project*. Descriptive terms have been standardized for use across all families in the *Project*, but generally follow common use. See de Vogel (1980) for definitions of seedling-specific terms and Corner (1976) and Boesewinkel & Bouman (1984) for seed-specific terms. To facilitate identifying isolated seeds, the base of the

seed is arbitrarily defined as the part nearest the hilum, rather than using a reference point within the fruit. Leaf nodes of seedlings are numbered sequentially from the first leaf-bearing node above the cotyledons. The following less conventional terms are used: for length of pubescence or size of other surface features – minute (<0.1 mm), short (0.1–0.5 mm), long (0.5–1.0 mm), very long (> 1.0 mm); for relative thickness of the seed coat or pericarp layers compared to total width of the structure – very thick (> 25% width), thick (10–25%), thin (1–10%), and very thin (< 1%).

## VOCHYSIACEAE

**HABIT AND DISTRIBUTION.** Trees or shrubs, rarely subshrubs. Neotropical except for one very small African genus; 6–8 genera and c. 200 species, 3 genera and 8 species from Panamá, 1 genus and species known from Barro Colorado Island.

**TAXONOMIC REFERENCES.** Stafleu (1948), Keay & Stafleu (1953), Robyns (1967*a, b*), Cronquist (1981), D'Arcy (1987), Kawasaki (in press).

### *Vochysia* Aubl.

**HABIT AND DISTRIBUTION.** Trees, shrubs or rarely subshrubs. Neotropical; c. 100 species, 5 species in Panamá, 1 species known from Barro Colorado Island.

***Vochysia ferruginea* Mart.** in Mart. & Zucc., *Nov. Gen. sp. pl.* 1: 151, t. 92 (1824).

Fig. 1.

**HABIT AND DISTRIBUTION.** Trees, 6–35 m tall, of moist to wet lowland and premontane forests, usually in secondary forest. Nicaragua to Peru and Brazil.

**COLLECTIONS.** Panamá. Barro Colorado Island: *Garwood* 1630A (F, BM, PMA, adult vouchers), *Garwood* 1630B–F (seedlings), *Garwood* 2005 (seedlings), *Foster* s.n. (seedlings with fruit voucher); 50 seedlings to 37 cm tall examined.

### Fruits

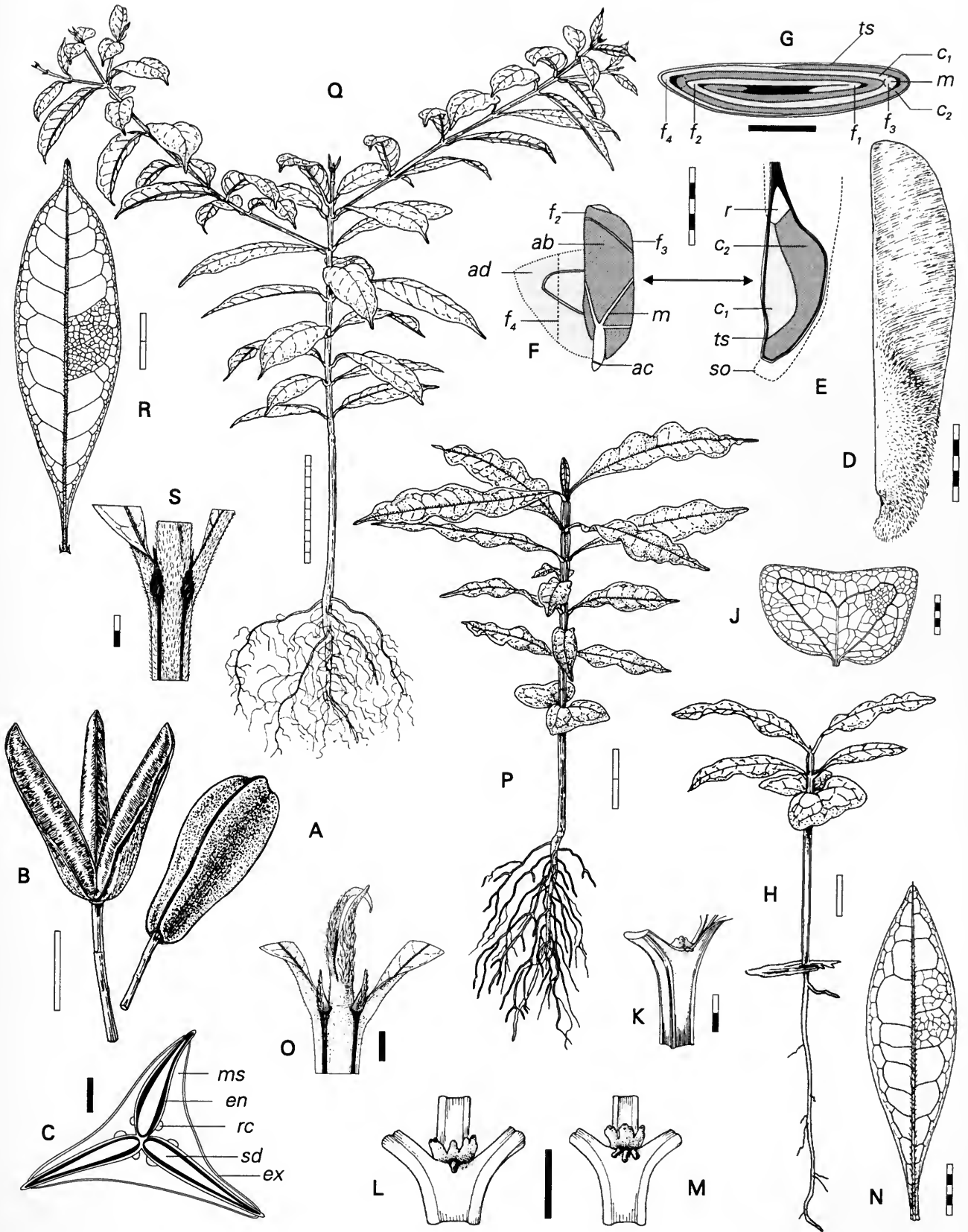
*Infructescences* terminal and upper-axillary thyrses, of 1- to 5-flowered helicoid cymose branches, usually with  $\leq 1$  fruit maturing per branch. Rachis densely short-pubescent, with hairs 2-branched,  $\pm$  sessile to short-stalked, appressed to ascending, straight to sinuous; lateral branches (including pedicels) 8–15 mm long, slightly to moderately pubescent. *Receptacles* undeveloped. *Stipes* absent. *Fruits* dry capsules, from superior ovaries. Capsules  $\pm$  woody, loculicidally dehiscent; completely septate; 17–26  $\times$  8–12  $\times$  8–12 mm; straight; oblong to obovate in outline, 3-lobed to 3-cleft in t.s., not compressed; margins entire; base rounded to abruptly truncate; apex rounded to slightly retuse, with stylar scar to 1 mm wide; surface dark brown to black-brown, dull, slightly to prominently warty, often irregularly clear- to white-scaly, glabrous. Seeds 1–3, 1 per

locule, intermediary, separated by mesocarp and endocarp, compressed laterally; long axis of seed radially parallel to long axis of fruit. *Placentae* axile. *Funicle* absent. *Valves* 3, dehiscent from apex, slightly spreading apart then each folding back, remaining firmly attached at base. *Fruit wall* thick, 0.4–1.5 mm wide, thickest centrally, 3-layered. *Exocarp* very thin,  $\approx$  0.05 mm wide,  $\pm$  hard-papery, dark brown to black-brown. *Mesocarp* thick, 0.2–1.3 mm wide, thickest centrally between locules, hard-spongy to  $\pm$  woody, with 2 large longitudinal resin-filled canals near axis between each pair of locules and several smaller chambers along locules (resin drying red-brown and glassy), light to medium brown. *Endocarp* thin,  $\approx$  0.1 mm wide, crustaceous, cream to light brown; inner surface smooth, minutely transversely fibrous, glabrous, glossy, medium brown-orange. When fruit unripe, exocarp grey-green.

### Seeds

Seeds 20–25  $\times$  5–6  $\times$  1–2 mm; hilar-anatropous; 1-winged; transversely half-obovate in outline, compressed and elliptic in t.s. in seminiferous area, planar in wing; margins constricted distally in seminiferous area on hilar side, constricted below wing on opposite side; base widely truncate; apex widely rounded; outer surface  $\pm$  smooth to slightly rough, minutely rough under hairs at higher magnification, densely long- to very long-pubescent, with hairs sinuous, appressed, light to medium brown-orange; glossy, medium brown to brown-orange, dark brown under hairs; not exfoliating. Wing lateral, fibrous,  $\approx$  15–17  $\times$  5–6 mm,  $\pm$  half-elliptic in outline, planar, asymmetrically rounded at apex, entire along margins, with curved ridge slightly raised,  $\pm$  flattened, extending from base to  $\frac{3}{4}$  length of wing and forming thickened straight margin; formed from very long, interwoven, testal hairs. Seminiferous area lateral,  $\approx$  10–11  $\times$  4–5 mm,  $\pm$  elliptic in outline, compressed, darker than wings, with short fringe of interwoven hairs on side opposite wing. *Aril* absent. *Sarcotesta* absent. *Hilum* basal, along straight side, exposed, flush, light brown, lighter than testa, linear, 7–10 mm long. *Micropyle* subbasal to marginal (visible internally at tip of radicle, possibly continuing through thickened ridge of wing and terminating along straight side past hilum), concealed externally. *Lens* absent. *Storage reserves* absent. *Embryo* large,  $\approx$  10–11 mm long, filling seminiferous area, straight,  $\pm$  oblong or ellipsoid, compressed; axis well-developed, with long 4-winged hypocotyl separated from very short radicle by annular ridge at collet, half-exposed; cotyledons well-developed, thin, with compressed obliquely supervolute ptyxis and convolute (*sensu* imbricate) vernation, with wider side of each cotyledon angled down and partially enclosing hypocotyl, with shape obscured by folding and base hidden within folded blade; plumule rudimentary. *Vascular bundle* half-lateral on hilar side, unbranched, thin, with tip exposed at end of hilum and fragments of the funicular bundle often exposed in hilum; passing through short raphe, terminating marginally at tip of seminiferous area. *Seed coat* very thin,  $\pm$  papery, undifferentiated at maturity. *Testa* very thin,  $\pm$  thicker under hilum and around micropyle,  $\pm$  papery, 1-layered, medium to dark brown, densely long-pubescent (see above); inner surface irregular and minutely rough, glabrous, glossy, dark brown. *Tegmen* absent.

**Fig. 1** *Vochysia ferruginea* Mart. Fruit: A, undehiscent fruit; B, dehiscent capsule; C, t.s. Seed: D, seed, lateral view; E, embryo in seminiferous region, with seed coat partially removed; F, embryonic cotyledon and radicle, with one side of cotyledon unfolded and second cotyledon removed to show primary veins, radicle, and angle of folding; G, t.s. through seminiferous region at level marked by arrow in E–F, view toward radicle and wing. Seedling: H, seedling; J, cotyledon; K, cotyledonary stipules, hypocotyl, and petiole ridges; L–M, cotyledonary stipules after epicotyl expands; N, first leaf; O, stipules at first node. Sapling: P, young sapling; Q, branched sapling; R, leaf at node 15; S, stipules at about node 20. Scale bars: black or black and white, 1 mm units; white only, 1 cm units. Symbols: ac, annulate collet; ab, abaxial surface of cotyledon; ad, adaxial surface of cotyledon; c<sub>1</sub>–c<sub>2</sub>, cotyledons 1 and 2; en, endocarp; ex, exocarp; m, midvein of cotyledon; ms, mesocarp; r, radicle; rc, resin canals; sd, seed; so, outline of seed (dotted line); ts, testa; f<sub>1</sub>–f<sub>4</sub>, folds of cotyledon.



*Seedlings and saplings*

Seedlings phanero-epigeal with photosynthetic cotyledons.

**DEVELOPMENT.** Radicle emerges from hilar side of seed near wing. Hypocotyl elongates into loop, then straightens, often carrying seed upward. Cotyledons emerge from seed and fully expand before first leaves are initiated. Shoot rest period is short during the cotyledon stage, about 1 month in sun and 3 months in shade. Seed reserves are exhausted by the end of this period, as albino seedlings die at the cotyledon stage without initiating any leaves. Growth is continuous, with a pair of leaves initiated about every month in sun and every 2–3 months in shade, although shade-produced leaves are smaller.

**ROOTS.** *Primary root* 30–50 × 0.6–0.8 mm, circular in t.s., slightly sinuous, cream to white, becoming medium orange-brown; narrow annular ridge encircles axis at collet, becoming indistinct with age; surface texture and colour between hypocotyl and root change conspicuously and abruptly at collet. *Secondary roots* to 0.2 mm wide, sinuous, very sparsely scattered along primary root. *Root hairs* appear abruptly and densely on primary root just below collet. *Sapling root system:* taproot thick, long-tapering; secondary roots ± thin and common along primary root; tertiary and higher order roots very fine and numerous.

**STEMS.** *Hypocotyl* 15–67 × 0.25–0.50 mm, ± square in t.s., becoming circular in t.s. and hollow with age; 4-ridged to 4-winged, each wing to 0.5 mm tall, continuing at apex into lower margin of cotyledon petiole and terminating at base abruptly above collet; glabrous; medium yellow-green to green, becoming dark brown or red-brown. *Epicotyl* 3–12 × 0.3–0.5 mm, ± square in t.s., becoming circular with age, 4-winged, each 0.3–1.0 mm tall and terminating apically in stipules, glabrous or sparsely short-pubescent, medium green to yellow-green. Hairs short, T-shaped (ratio of arm lengths ≈ 1:1), ± sessile, appressed, straight, and light brown to orange-brown. *Cataphylls* absent. *Internodes* 1–10, 2–15 mm long; later internodes to 34 mm; similar to epicotyl except later internodes becoming densely short- to long-pubescent, with hairs long, unequally 2-branched (arm length ratio to 8:1), short-stalked, ascending, and curved or sinuous or coiled. *Older stems* dark brown, with wings often red-brown, hollow, often sparsely pubescent with age; wood cream-coloured. *Lenticels* appearing on stems > 2 mm wide, sparse on stems 2–4 mm wide; mostly 0.5 mm long, ± round to elliptic, light brown, lighter on dark stems. *Buds:* Cotyledonary buds hidden in axils and inconspicuous above cotyledon scars, rarely protruding to ≈ 0.5 mm in older seedlings, moderately short-pubescent. Lateral buds usually slightly protruding out of axils, to 1 mm long at later nodes, moderately pubescent at early nodes to densely pubescent at later nodes, with accessory bud above sylleptic branches at later nodes. Terminal buds naked, partially covered by stipules, moderately short-pubescent at early nodes to densely long-pubescent at later nodes, with hairs light brown to orange-brown.

**COTYLEDONS.** Two, opposite, foliaceous, simple, petiolate, stipulate, emergent from seed, spreading apart, persistent at least until node 3 matures, falling sometime before node 9 matures (between 9 and 20 months). Blades 10–15 × 13–23 mm; straight, flat, depressed obovate, with right half (viewed from the lower abaxial side) usually slightly larger, 2-lobed to 2-cleft; apex of lobes obtuse to broadly obtuse; base emarginate or cordate, often asymmetrical with right lobe slightly larger, or half-rounded/half-cordate; margins entire. Blades glabrous; green above, lighter below. *Venation* palmate, 3-nerved; acro-brochidodromous, basal and perfect. Primary veins 3; moderate-sized; impressed to slightly raised above, moderately raised below; central primary vein forked, with straight stem  $\frac{1}{2}$ – $\frac{3}{4}$

distance to apex and branches slightly recurved; lateral primary veins basal, ≈  $\frac{3}{4}$  length of blade, straight to curved, diverging at narrowly acute angle, looped, joining branches of central vein to form large ± triangular to obovate intercostal area, the pair of intercostal areas usually spanning about 60–70% of the width of the cotyledons. Secondary veins moderate-sized basally along lateral primaries becoming fine apically; 16–24, 2–4 along midvein, 6–10 along lateral primaries, 6–10 along branches of midvein; mostly marginal, alternate along midvein;  $\frac{1}{6}$ – $\frac{3}{4}$  length of blade (mostly  $\frac{1}{6}$ – $\frac{1}{4}$  along branches of midvein), longest basally; mostly curved or arched along lateral primaries, hooked along branches of midvein, curved to zigzag along midvein, rarely scythe-shaped; diverging at narrowly acute angles (< 45°) basally on lateral primaries to perpendicular angles along branches of midvein; looped marginally, sometimes percurrent in intercostal area, mostly obtusely joined; slightly raised above, slightly raised below. Inter-secondary veins absent. Tertiary veins reticulate within intercostal area, looped in marginal area. *Petioles* 0.5–1.5 mm long, transversely oblong in t.s., straight to slightly curved, 2-ridged above, with ridges continuing into lateral primary veins, 4-winged along margin, with lower wings continuing into hypocotyl wings and upper wings terminating in fleshy knobs near centre of hypocotyl, glabrous. *Stipules* usually fused and interpetiolar, sometimes separate and paired; composed of two structures, both variable in shape and development. The lower part usually a ± conical projection between the petioles at the base of the upper marginal ridge of each petiole, sometimes with two or three separate projections or these absent, mostly 0.125–0.25 mm long, usually perpendicular to the stem, sometimes gland-like apically. The upper part usually a flattened interpetiolar scale-like outgrowth just above the petioles, initially folded over the terminal bud, becoming erect and visible as the epicotyl expands, 0.25–0.5 mm tall and 0.5–0.75 mm wide, ± transversely oblong to depressed ovate, usually 2- to 5-lobed or -cleft, but sometimes divided into two separate parts or unlobed, the apex of lobes gland-like when young; persistent, papery, green becoming light brown.

**LEAVES.** Opposite, decussate on trunk axis, distichous on branches; simple; short-petiolate, stipulate. Leaf blades 17–32 × 3–9 mm at first node; 20–67 × 5–20 mm at nodes 2–10; to 142 × 49 mm at later nodes; 65–125 × 25–37 mm on branches; straight; narrowly elliptic at nodes 1–3, narrowly elliptic or narrowly obovate at later nodes, elliptic or narrowly elliptic or narrowly obovate or linear-obovate on branches; apex narrowly obtuse or acuminate at nodes 1–10, acuminate to long-acuminate at later nodes and on branches, mucronate at most nodes; base mostly attenuate at early nodes, sometimes narrowly cuneate at later nodes, mostly acute on branches; margins entire, sometimes undulate. Blades green above, lighter below; flat between secondary veins above when fresh; papery; densely minutely pusticulate below (from internal crystals), but weakly so at nodes 1–2; densely minutely pusticulate above, with pustules usually white on larger leaves; slightly to moderately short- to long-pubescent on blade and veins below at early nodes becoming densely long- to very long-pubescent only on the midvein at later nodes; glabrous on blade above, slightly to moderately ± short-pubescent on midvein at early nodes to densely long-pubescent at later nodes; slightly to moderately short- to long-pubescent along margin, often also densely minute-pubescent when young at later nodes; pubescence light brown to orange-brown. Hairs on midvein above simple, ± erect, straight to slightly curved, mostly 0.5–0.75 mm long on first node, to 1–2 mm long on later nodes; those on blade and veins below T-shaped (ratio of arm lengths ≈ 1:1), ± sessile, appressed and straight at early nodes, mostly 0.25–0.75 mm long, becoming progressively more unequally 2-branched (ratio of arm lengths mostly

< 4:1 on blades but to 8:1 on midvein), short-stalked, ascending, curved or sinuous or coiled at later nodes; those on margins T-shaped or 2-branched (as above) and, at later nodes, also minute, simple, ± erect and sinuous. *Young leaves* conduplicate, spreading open before half-grown, densely pubescent, light green, rigid, erect to horizontal. *Venation* pinnate; brochidodromous. Midvein moderate-sized; straight; flush to slightly raised above, impressed at later nodes and when fresh, prominently raised below. Secondary veins ± fine; 14–17 on leaves at first node, 15–30 at nodes 2–10, to 30 at later nodes and on branches; alternate; mostly  $\frac{1}{6}$ – $\frac{1}{3}$  length of blade, longest centrally; mostly hooked or arched, sometimes also slightly zigzag; diverging at moderately acute angles (45°–65°); looped, sometimes diffusely looped basally on larger leaves, obtusely joined; slightly raised above, slightly raised below. Inter-secondary veins infrequent. Tertiary veins reticulate within intercostal area, looped in marginal area. *Petioles* 0.5–4.0 mm long, ≤ 2 mm long at nodes 1–10; ± circular in t.s., straight to slightly curved; shallowly channelled, with erect narrow margins above; sparsely to moderately pubescent. *Stipules* paired; 0.5–1.0 mm long at nodes 1–6, to 3 mm long at later nodes and on branches; simple, triangular to narrowly triangular; persistent, ± papery; densely pubescent, pale against dark older stems; the inner margin and base continuing to and perhaps above the petiole; the outer margin and base usually terminating abruptly, but sometimes forming a low interpetiolar ridge with the stipule of the opposite leaf as the stem thickens at early but not later nodes.

**ARCHITECTURE.** Trunk axis monopodial to at least 37 cm tall (based on one individual). Initial axis orthotropic. Branches plagiotropic but ± ascending, with leaves distichous through twisting of internodes; sylleptic; alternate and perpendicular at two consecutive nodes (semi-decussate); first produced 31–34 cm above the collet (at about nodes 17–18). First branch internode 60–75 mm long, much longer than superadjacent trunk internode (10–30 mm). First branch leaf half- to full-size of later branch leaves. Single or paired sylleptic secondary branches were produced on the primary branches 24–29 cm from the trunk. Leaves held horizontal. Several factors indicate that growth of the trunk axis above the branches stopped or slowed considerably while the branches were developing, so that overall growth of the trunk was rhythmic (see Fig. 1Q): the trunk axis was very short (about 4 cm long) compared to the length of the branches (28–38 cm long); it was non-woody and very thin compared to the woody internodes on the trunk below the branches and on the lower parts of the branches; and it had matured only one pair of leaves compared to 7–8 pairs on the branches. At the time of harvest, the trunk axis had re-initiated growth, although the primary and secondary branches were still elongating. Rhythmic growth, if substantiated, would suggest Massart's model.

### Ecology

**PHENOLOGY.** In Panamá, *Vochysia ferruginea* usually flowers from late March to early July, and sometimes to a lesser extent in September–October, and its fruits mature August–October (Croat, 1978). Ripe fruits were dehiscent and releasing mature seeds in October (Garwood 1630A). Elsewhere in Central America, it primarily flowers in April–June and October–December and fruits July–September and December–January (Croat, 1978; Flores, 1993b; Moreira & Arnáez, 1994).

**DISPERSAL.** When ripe, valves of the dark brown capsules open and fold back, exposing the glossy bright orange-brown endocarp and releasing the seeds. Seeds are wind-dispersed.

**VIABILITY.** Seeds remain viable for 2–3 months when stored at ambient temperature (24–26°C) and moisture levels if well-aerated

(Flores, 1993b). Flores (1993b) considers the seeds orthodox, although the initial moisture content of the seeds (23%) is rather high.

**GERMINATION.** Seeds germinate rapidly (13 days) at moderate percentages (39–50%) in both sun and shade in the growing house (this study). Other studies also report rapid germination (8–14 days) in the forest or growing house, but higher germination percentages (80–95%) (Flores, 1993b; Moreira & Arnáez, 1994).

**ESTABLISHMENT AND GROWTH.** The earliest stages of natural seedling establishment and growth have not been studied, although Flores (1993b) noted that germinating seeds and young seedlings suffered high predation from ants and other herbivores. Boucher et al. (1994) reported exceptional seedling densities and sapling growth after Hurricane Joan in Nicaragua in October 1989, which killed all adults in the population. Four months after the hurricane, there were 94 500 seedlings and saplings (0.1–1.5 m tall) per hectare, but few young trees (3.2–10 cm DBH). The extremely open canopy, created by the hurricane through defoliating and felling trees, favoured survivorship and growth of these juveniles, such that young trees were abundant four years later and were growing on average at about 1.4 cm DBH/year. Under the less open canopy of Barro Colorado Island, not recently if ever disturbed by hurricanes, similar-sized individuals (1–9.9 cm DBH) grew on average only 0.45 cm DBH/year, but larger individuals (> 10 cm DBH) grew more rapidly, 1.3–1.7 cm DBH/year (Condit et al., 1993).

The population dynamics and appropriate management strategies for this species may differ greatly in hurricane-prone areas such as Nicaragua compared to hurricane-free areas such as Panamá. Where hurricanes are common in the Caribbean, they occur mostly August–October during the period *Vochysia ferruginea* is maturing and dispersing its seeds. A hurricane occurring late in the season might blow the wind-dispersed seeds over large areas of disturbed forest, expanding the population. An earlier hurricane might kill adult trees before seeds could be matured and dispersed, preventing regeneration from seed and eliminating the local population, unless most regeneration comes from established shade-tolerant juveniles. It is not yet known whether seedling recruitment after disturbance is primarily from recently germinated seedlings from the current year's seed crop or older shade-tolerant juveniles surviving from previous years.

**Vochysia guatemalensis** Donn. Sm. in *Bot. Gaz.* **12**: 131, pl. 22 (1887).

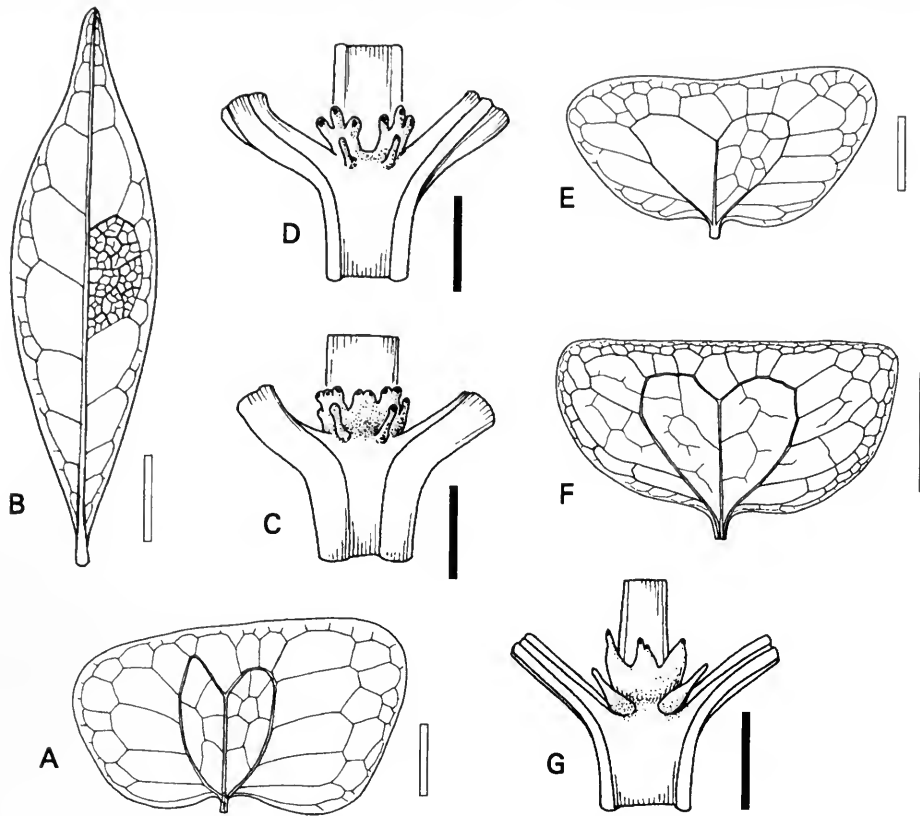
*Vochysia hondurensis* Sprague in *Bull. Misc. Inform., Kew* **1922**: 183 (1922).

Fig. 2A–D.

**HABIT AND DISTRIBUTION.** Trees, 30–55 m tall. Veracruz, México, to Panamá.

**COLLECTIONS.** **Belize.** Cayo District, Chiquibul: Palmar, Garwood 4031 (BM, seedlings with seed voucher); New Maria, *Monro* 867 to 871, *Monro, Howe & King* M4162X, M7231X, M7340X (seedlings) and M6002X (sapling); 28 seedlings to 17 cm tall examined, sapling height about 2 m.

**TAXONOMIC NOTE.** The seeds associated with Garwood 4031 unmistakably identify the seedlings to genus. If one accepts the synonymy of *Vochysia guatemalensis* and *V. hondurensis* (Standley & Steyermark, 1949; Gaos, 1978; Flores, 1993a), then only one species has been reported from Belize (Stafleu, 1948; Standley & Steyermark, 1949). That the mature leaves and stems are nearly glabrous supports the identification of these collections as *V. guatemalensis*.



**Fig. 2** *Vochysia guatemalensis* Donn. Sm. Seedling: A, cotyledon; B, first leaf; C–D, cotyledonary stipules. *Vochysia* sp. Seedling: E–F, cotyledons; G, cotyledonary stipules; E, Hampshire & Whitefoord 269; F–G, Garwood 135. Scale bars: black, 1 mm; white, 1 cm.

#### Seedlings and saplings

Seedlings phanero-epigeal with photosynthetic cotyledons.

**ROOTS.** *Primary root* 30–70 × 0.8–1.2 mm, circular in t.s., slightly sinuous, cream-coloured; narrow annular ridge encircles axis at collet, becoming indistinct with age. *Secondary roots* sinuous, scattered along primary root.

**STEMS.** *Hypocotyl* 50–85 × 1 mm, square to rectangular in t.s., becoming circular with age; 4-ridged or 4-winged, each wing < 0.25 mm tall, continuing at apex into lower margin of cotyledon petiole; glabrous; green. *Epicotyl* 5–22 × 1 mm, ± square in t.s. when young, becoming circular with age; 4-winged, each wing ≤ 0.25 mm tall and terminating apically in a stipule; glabrous; green. *Cataphylls* absent. *Internodes* 1–16, 3–5 mm long; 4-winged, each wing about 0.25 mm tall and terminating apically in a stipule; glabrous; green. Older stems light brown to grey-brown, hollow. *Buds*: Cotyledonary buds hidden in axils, sparsely pubescent. Lateral buds protruding out of axils, ≤ 0.5 mm long at nodes 1–15, sparsely short-pubescent at first node, becoming densely pubescent at later nodes. Terminal buds naked, sparsely pubescent at first node, becoming moderately pubescent at later nodes. Hairs on all buds clear to white, mostly ≤ 0.25 mm long.

**COTYLEDONS.** Two, opposite, foliaceous, simple, petiolate, stipulate, emergent from seed, spreading apart, persistent until at least leaves at nodes 2–3 mature. Blades 15–26 × 25–37 mm; straight, flat, ± depressed obovate, with right half (seen from lower or abaxial side) usually larger at both base and apex; apex truncate to emarginate, often obliquely so, rarely ± rounded; base cordate, rounded, to ±

truncate, often obliquely so; margins entire. *Venation* palmate, 3-nerved; acro-brochidodromous, basal and perfect. Primary veins 3, ± fine, slightly raised above, moderately raised below; central primary vein forked, with straight stem  $\frac{1}{2}$  to  $\frac{3}{4}$  distance to apex and branches slightly curved; lateral primary veins basal, about  $\frac{3}{4}$  length of blade, mostly curved, diverging at narrowly acute angle, looped, joining branches of central vein and forming ± small obovate or triangular intercostal area or rarely branching before joining the central vein and forming a ± indistinct intercostal area, the pair of intercostal areas, when distinct, usually spanning about 30–50% of the width of the cotyledon. Secondary veins moderate-sized basally along lateral primaries becoming fine apically; 12–16, 0–1 along midvein, 8–10 along lateral primaries, 4–5 along branches of midvein; mostly marginal; to  $\frac{2}{3}$  length of blade, longest basally; mostly arched or hooked; diverging at narrowly acute angles basally on lateral primaries to perpendicular angles along branches of midvein; looped marginally, acutely to obtusely joined; flush above, moderately raised below. *Petioles* 2–3 mm long, transversely oblong in t.s., 2-ridged above, with ridges continuing into lateral primary veins; 4-ridged along margins, the lower ridges continuing down into the ridges or wings on the hypocotyl and the upper ridges terminating at the stipules; glabrous. *Stipules* separate and paired or sometimes fused and interpetiolar, composed of two structures, both variable in shape and development. The lower part a pair of ± conical projections between the petioles near the base of the upper marginal ridge of each petiole, one or both sometimes absent, mostly 0.25–0.75 mm long, usually perpendicular to the stem, sometimes gland-like apically. The upper part usually a pair of flattened scale-like outgrowths between and just above the petioles, initially folded over



the terminal bud but becoming erect and visible as the epicotyl expands, each  $\pm$  ovate to rhombic, 0.5–0.75 mm tall and wide, the apex often 3-lobed and gland-like, the pair sometimes fused together, then 0.5–0.75  $\times$  0.75–1.5 mm tall and wide and the apex multilobed or irregular.

**LEAVES.** Opposite, decussate on seedling trunk axis, sometimes 3-whorled on sapling trunk axis; simple, short-petiolate; stipulate. Leaf blades 30–69  $\times$  11–19 mm at first node; 30–82  $\times$  13–17 mm at nodes 2–15, to 195  $\times$  52 mm on saplings; straight; narrowly obovate to narrowly elliptic at nodes 1–15 and on sapling; apex acuminate or long-acuminate, rarely acute at first node; bases cuneate to narrowly acute; margins entire. Blades green, papery at early nodes becoming subcoriaceous on larger saplings; sometimes moderately pustulate above and below on later leaves, the pustules pale above; the blade nearly glabrous when fully expanded, the midvein below often sparsely short-pubescent, but moderately to densely pubescent on the blade and midvein below and along margins when expanding leaves of seedlings are < 10 mm long. Hairs simple, basifixed, < 0.25 mm long, clear to white. *Venation* pinnate, brochidodromous. Midvein moderate-sized; straight; flush to slightly raised above, prominently raised below. Secondary veins thin, 14–22 at first node, to 22 at later nodes; alternate; mostly  $\frac{1}{4}$  to  $\frac{1}{3}$  length of blade, longest centrally; mostly hooked or arched, diverging at a moderately acute angle; looped, obtusely joined; slightly raised above and below. Intersecondary veins infrequent. Tertiary veins reticulate in intercostal area, looped in marginal area. *Petioles* 1 mm long at first node, to 2 mm long at nodes 2–15, to 7 mm on saplings; shallowly channelled, with erect narrow margins above. *Stipules* paired; 1.0–1.2 mm long at first node, to 1.7 mm long at nodes 2–15; simple, narrowly triangular; the inner margin and base continuing above the petiole and apparently terminating near the lateral bud; the outer margin and base usually terminating abruptly, but sometimes forming a low interpetiolar ridge with the stipule of the opposite leaf as the stem thickens at some early nodes; persistent; often sparsely short-pubescent toward the apex.

#### **Vochysia** sp.

Fig. 2E–G.

**COLLECTIONS.** Panamá. Colón Province: Santa Rita Ridge, *Garwood* 135 (seedlings with seed fragment); Chiriquí Province: Fortuna, *Hampshire & Whitefoord* 269 (BM, seedlings); 15 seedlings to 9 cm tall examined.

**TAXONOMIC NOTE.** Specific identification is not yet possible, as *Garwood* 135 had only a seed fragment attached and *Hampshire & Whitefoord* 269 lacked seeds altogether. In addition to *Vochysia ferruginea*, *V. allenii* Standl. & L.O. Williams, *V. jefensis* A. Robyns, and *V. speciosa* Warm. have been reported from eastern Panamá and *V. hondurensis* (= *V. guatemalensis*) from western Panamá (D'Arcy, 1987). As immature leaves of both collections have T-shaped hairs  $\geq$  0.25 mm long on the lower surfaces (see below), it is not *V. guatemalensis*, which has simple basifixed hairs < 0.25 mm long (see above). The T-shaped hairs on the first leaves ally it with *V. ferruginea*, but the cotyledons are about 1.5–2 times larger. Thus, the Chiriquí collection is a new species record for western Panamá. As the cotyledons from the Chiriquí collection are consistently larger than those from the Colón collection (Fig. 3), two species might be represented. Given their similarity and the paucity of material, they are described together below, with the few differences noted.

#### *Seedlings*

Seedlings phanero-epigeal with photosynthetic cotyledons.

**ROOTS.** *Primary root* 45–70 mm long, 1 mm wide, circular in t.s., slightly sinuous, medium brown.

**STEMS.** *Hypocotyl* 50–86  $\times$   $\approx$  1 mm long and wide,  $\pm$  square to rectangular in t.s., 4-ridged to 4-winged, each wing  $\leq$  0.25 mm tall and continuing at apex into lower margin of petiole; glabrous. *Epicotyl* (immature) 4-ridged or 4-winged, each wing  $\leq$  0.25 mm tall; glabrous. *Buds:* Cotyledonary buds hidden in axils (*Garwood* 135) or 0.75 mm tall and densely pubescent (*Hampshire & Whitefoord* 269).

**COTYLEDONS.** Two, opposite, foliaceous, simple, petiolate, stipulate, emergent from seed, spreading apart, persistent. Blades 14–21  $\times$  22–40 mm (14–17  $\times$  25–32 mm in *Garwood* 135, 19–21  $\times$  34–40 mm in *Hampshire & Whitefoord* 269); straight, flat, depressed obovate, with right side (viewed from lower or abaxial surface) usually larger than or sometimes equal to left side; apex truncate, emarginate, or cordate, sometimes obliquely so; base rounded, truncate or emarginate, sometimes unequal; margins entire. Blades green, glabrous. *Venation* palmate, 3-nerved; acro-brochidodromous, basal and perfect. Primary veins 3, moderate-sized; central primary vein forked, with straight stem  $\frac{2}{3}$  to  $\frac{3}{4}$  distance to apex and branches recurved; lateral primary veins basal, about  $\frac{3}{4}$  length of blade, mostly curved, diverging at narrowly acute angle, looped, joining branches of central vein to form  $\pm$  small obovate or triangular intercostal area, the pair of intercostal areas usually spanning about 40–50% of the width of the cotyledon. Secondary veins moderate-sized basally becoming fine apically; 10–16, 0–2 along midvein, 6–9 along lateral primaries, 3–5 along branches of midvein; mostly marginal;  $\frac{1}{3}$  to nearly full length of blade, longest basally; mostly arched to hooked, diverging at narrowly acute angles basally to perpendicularly apically; looped marginally, acutely to perpendicularly joined; flush above, moderately raised below. Tertiary veins reticulate within intercostal areas, looped in marginal areas. *Petioles* about 2 mm long, transversely oblong in t.s., 2-ridged above, with ridges continuing into the lateral primary veins; 4-ridged along margin, with lower ridges continuing into hypocotyl ridges and upper ridges terminating in the stipules; glabrous. *Stipules* usually fused and interpetiolar, sometimes separate and paired; composed of two structures, both variable in shape and development. The lower part a pair of  $\pm$  conical projections between the petioles near the base of the upper marginal ridge of each petiole, sometimes absent or bifid, mostly 0.25–0.5 mm long, usually perpendicular to the stem, sometimes gland-like apically. The upper part usually a flattened scale-like outgrowth between and just above the petioles, initially folded over the terminal bud but becoming erect and visible as the epicotyl expands,  $\pm$  transversely oblong to depressed ovate, 0.5–0.75  $\times$  0.75–1.0 mm tall, 3- to 5-lobed and gland-like at the apex, sometimes divided.

**LEAVES** (only immature leaves at first node present). Opposite, decussate on trunk axis; simple, short-petiolate. Blades moderately pubescent below and along margins when expanding blades are < 5 mm long, sparsely pubescent when half-expanded. Hairs 0.25–0.625 mm long, T-shaped, sessile, pale orange-brown. *Venation* pinnate, brochidodromous.

#### **Key to known seedlings of *Vochysia* in Panamá and Central America**

1. T-shaped hairs present on lower surface of young leaves at first and early nodes
2. Cotyledons 13–23 mm wide and 10–15 mm long ..... ***V. ferruginea***

2. Cotyledons 22–40 mm wide and 14–21 mm long ..... *V. sp.*
1. Simple basifixed hairs present on lower surface of young leaves at first and early nodes or hairs absent; cotyledons 25–37 mm wide and 15–26 mm long ..... *V. guatemalensis*

## DISCUSSION

Vochysiaceae is a moderate-size, primarily neotropical family divided into two tribes. Vochysieae includes *Vochysia* (100 species), *Callisthene* (12 species), *Salvertia* (1 species), and *Qualea* sensu lato (77 species, including *Ruizterania*); Erismeeae includes *Erisma* (16 species) and *Erismadelphus* (2 species), the only African taxa (Stafleu, 1948–1954; Keay & Stafleu, 1953; Marcano-Berti, 1969; Kawasaki, in press). The monotypic *Euphronia* (= *Lightia*), sometimes included in Vochysiaceae (Lleras, 1976; Cronquist, 1981) or segregated as the Euphroniaceae (Marcano-Berti, 1989, 1990), is not closely related to Vochysiaceae according to recent molecular studies (Litt et al., 1995) and will not be further discussed.

## Fruit

There are two basic types of fruit in Vochysiaceae (Warming, 1875; Stafleu, 1948–1954; Keay & Stafleu, 1953). The dehiscent trilocular capsules of Vochysieae, derived from superior ovaries, contain winged seeds. The indehiscent unilocular fruits of Erismeeae, derived from inferior to semi-inferior ovaries, have persistent enlarged winged calyx lobes. Within Vochysieae, fruits of *Callisthene* have a thick persistent central column and a fragile exfoliating exocarp not found in the other genera. Several of the 12 ovules per locule mature into seeds in *Qualea* (Stafleu, 1953); one or more of the few ovules per locule mature in *Callisthene*, (Stafleu, 1952). In *Vochysia* and *Salvertia*, however, only one of the two ovules in each locule usually develops into a mature seed (Warming, 1875; Stafleu 1948; Standley & Steyermark, 1949; Robyns, 1967a; Gaos, 1978; Moreira & Arnáez, 1994; this study), although two mature according to Flores (1993a, b).

Fruits of *Vochysia ferruginea* are typical of the genus (Stafleu, 1948), being 3-locular loculicidal capsules, oblong or obovate in outline and 3-angled. Variation in size, shape, and surface texture of fruits in *Vochysia* is not well-documented: fruits of many species are still unknown (Warming, 1875; Stafleu, 1948; but see van Roosmalen, 1985). The gross morphology of fruits has been little studied. Stafleu (1948) described the pericarp of the genus as consisting of a black or dark bluish exocarp 'strongly adhering to the shining golden-yellow endocarp', an observation repeated by later authors (Robyns, 1967a; van Roosmalen, 1985), but Flores (1993a, b) noted the presence of a well-developed mesocarp in both *V. ferruginea* and *V. guatemalensis*. In *V. ferruginea*, there is a brown to black exocarp, a light to medium brown spongy to woody mesocarp, thickest near the centre of the fruit, and a pale crustaceous endocarp of even thickness around each locule (Fig. 1C). The mesocarp is penetrated by longitudinal resin canals adjacent to the locules (Fig. 1C) and is also well-vascularized (Flores 1993a, b). In mature fruit, the endocarp is as well-developed around empty locules as around those filled with mature seeds, indicating that development of each locule is not dependent on the growth of fertilized ovules within it. The locules complete development before the seeds and determine the shape of the seed wing (Boesewinkel & Venturelli, 1987).

## Seed

Seeds are winged in the Vochysieae. The wings are large and unilateral in *Vochysia*, *Qualea*, and *Salvertia*, but small and circum-

ferential in *Callisthene*, and are formed from compacted testal hairs in *Vochysia* and *Salvertia*, but from extensions of the testa in *Qualea* and *Callisthene* (Warming, 1875; Stafleu, 1948–1953; Boesewinkel & Venturelli, 1987). The seeds of *V. ferruginea* are typical of the genus (Warming, 1875). The wing is on the anti-hilar side of the seed, and the micropyle extends along the seminiferous area and terminates near the hilum, as in *V. pygmaea* Bong. and *Salvertia* (Boesewinkel & Venturelli, 1987). In contrast, the wing of *Qualea* is on the hilar side of the seed, such that the micropyle extends along the anti-hilar margin of the wing and opens at the apex of the wing away from the hilum (Boesewinkel & Venturelli, 1987). The final shape of the wing in *Vochysia* is determined by the shape of the locule: the unicellular hairs grow upward from the testa to fill and take their shape from the empty locule (Boesewinkel & Venturelli, 1987). Hence, much of the variation in size and shape of seeds among species in *Vochysia* probably arises from differences in the size and shape of the mature locules.

There has been little work on seed anatomy of Vochysiaceae (Corner, 1976; Boesewinkel & Venturelli, 1987). Stafleu (1948, 1953) described the testa of *Vochysia* as brown, thin, and chartaceous, and the tegmen as very thin, paper white, and adhering to the testa, and the testa of *Qualea* as chartaceous. The mature seed coat of *V. pygmaea*, however, consists only of the outer layers of the testa, because the inner layers of the testa are crushed and the tegmen resorbed during development (Boesewinkel & Venturelli, 1987). The seed coat also appeared as one undifferentiated layer at maturity in *V. ferruginea* (this study), but Flores (1993a, b) described a dark exotesta distinct from the dead cell layers and air spaces of the mesotesta and endotesta and remnants of the tegmen in *V. ferruginea* and *V. guatemalensis*. In contrast, the mature seed coat of *Qualea densiflora* Warm. and *Callisthene* retains both the inner layers of the testa and tegmen (Boesewinkel & Venturelli, 1987). The seed coat of *Erisma* and *Erismadelphus* is thick and contains a large branched vascular bundle (Boesewinkel & Venturelli, 1987). The vascular bundle of *V. ferruginea*, hitherto undescribed in Vochysieae, is unbranched and terminates at the tip of the seminiferous area. The hilum of *V. ferruginea* (7–10 mm long) is longer than in *V. pygmaea* (3–4 mm long), and stretches over a greater proportion of the length of the winged seed (35–40% versus about 20%). Due to the long hilum, the seed type of *V. ferruginea* is described as hilar-anatropous.

Endosperm is absent in mature seeds of Vochysiaceae (Benthams & Hooker, 1867; Baillon, 1874; Warming, 1875; Petersen, 1896; Stafleu, 1948–1953; Standley & Steyermark, 1949; Robyns, 1967a; Gaos, 1978; Boesewinkel & Venturelli, 1987; Flores, 1993a, b). None was seen in *Vochysia ferruginea*. Occasional reports that endosperm is rarely well-developed (Cronquist, 1981; Niembro Rocas, 1989) do not appear well-founded. A thin, whitish aril, adhering to the testa, was reported in *V. guatemalensis* (Gaos, 1978) and in the family (Niembro Rocas, 1989); this appears to be a mistranslation of Stafleu's (1948) description of the tegmen (see above).

## Embryo

In all genera, the embryo of the mature seed is straight and the plumule and radicle poorly developed (Warming, 1875; Stafleu, 1948–1954). In *Vochysia ferruginea*, the embryonic axis is well-developed; the hypocotyl is relatively long compared to the poorly developed radicle, compressed, 4-winged, and annulate at the collet. The winged hypocotyl and annulate collet persist into the seedling stage, confirming the identification of the structures in the seed. In Vochysieae, the embryonic cotyledons are generally thin, foliaceous, and folded in various ways (see below), whereas, in Erismeeae,

they are thick, fleshy, and not or scarcely folded (Baillon, 1874; Warming, 1875; Boesewinkel & Venturelli, 1987; Kawasaki, in press). The cotyledons of *Erismadelphus* are plano-convex and slightly convolute at the margins (Boesewinkel & Venturelli, 1987), while those of *Erisma* are narrowly elongate and semi-cylindrical (Baillon, 1874), plano-convex (Boesewinkel & Venturelli, 1987), or flat (Stafleu, 1954).

The embryonic cotyledons have been described as unequal in *Vochysia* (Warming, 1875; Stafleu, 1948) and *Salvertia* (Stafleu, 1948), although no comparable information was given for *Qualea* or *Callisthene*. Unequal could mean either that each cotyledon is asymmetrical or that the two cotyledons are heterocotylar, differing in shape or size. Cotyledons are asymmetric in two species of *Vochysia* and one species of *Qualea* but symmetric in one species of *Vochysia* and *Salvertia* (Table 1), based on the illustrations of the unfolded embryo in Warming (1875). In *V. ferruginea*, each cotyledon is usually asymmetric, with the right side (viewed from the lower abaxial surface) larger, at least basally. The base of the smaller side tends to be rounded, and that of the larger side cordate, as in the expanded cotyledon of the seedling (Fig. 1J). The embryonic cotyledons of *V. ferruginea*, when unfolded, and the fully expanded cotyledons of the seedling (Fig. 1H, P), are isocotylar. The larger side of one cotyledon opposes the smaller side of the other on the embryo and seedling, hence, the two cotyledons are identical in shape, not mirror-images.

Most monographic and floristic works indicate that the embryonic cotyledons of Vochysiaceae are folded, but give insufficient detail to characterize the complex pattern of folding. It is usually unclear which component of folding is described: ptyxis, the folding of an individual organ such as a leaf in the bud or cotyledon in the seed, or vernation, the relationship of the immature organs to each other (Bell, 1991). Some terms, such as convolute, are used for both ptyxis and vernation but have different meanings (Bell, 1991). Definitions of terms vary considerably among authors.

In *Vochysia ferruginea*, each cotyledon is folded four times around the longitudinal axis of the embryo (Fig. 1E-G). The folds ( $f_1$ - $f_4$ ) are parallel to the radicle but not parallel to the midvein of the cotyledon (Fig. 1F). The margin of the larger side of the cotyledon (the right side as viewed from the lower abaxial surface) is on the exterior of the embryo, while the margin of the smaller side is in the interior. The folded smaller side is completely enclosed within the folded larger side. The inner margin is narrowly bent back with the adaxial surfaces appressed at the first fold ( $f_1$ ). Because of the oblique folding of the cotyledon, the base of the larger side of each asymmetric cotyledon is folded around the hypocotyl, nearly obscuring it (Fig. 1F). Except for the compressed nature of the embryo and distinct lines of folding, ptyxis is essentially supervolute (often called convolute) but oblique. It is not conduplicate, although the cotyledon appears to be folded around the midvein in cross-sections through the middle of the embryo (Fig. 1G). Vernation is essentially convolute *sensu* Bell (1991), although unusually compressed. Each cotyledon partially overlaps the other, with inner margins opposite near the centre of the embryo and outer margins opposite on the exterior (Fig. 1G). Confusingly, vernation is not convolute *sensu* Radford et al. (1974), because one rolled or supervolute cotyledon is not completely enclosed within a second rolled cotyledon.

Convolute vernation and supervolute ptyxis are also found in *Vochysia pygmaea*, *V. tucanorum* Mart., and *Salvertia convallari-dorea* A. St.-Hil., as seen in transverse sections of the embryo (Warming, 1875: figs 16-II, 17-II; Boesewinkel & Venturelli, 1987: fig. 10B). The embryos are less compressed and angular than in *V. ferruginea*, and the inner margins of the cotyledons overlap rather

than being folded back individually. Embryos of *V. guatemalensis*, *V. obscura* Warm., *V. tucanorum*, and *S. convallari-dorea* (Warming, 1875: figs 13, 16II, 17II; Flores, 1993a: fig. 9) are externally similar to that of *V. ferruginea*, and the position of the outer cotyledon margin is also consistent with convolute vernation. Ptyxis is probably oblique in most species because the hypocotyl is hidden, as in *V. ferruginea*, but may differ in *V. obscura*, given that the hypocotyl is well-exposed in spite of the deeply lobed cotyledon base. Although folding appears somewhat angular in section because the seed is compressed, cotyledons are not plicate in the sense of fan-like. Thus, there is one basic pattern of vernation and ptyxis for cotyledons of *Vochysia* and *Salvertia*, with minor variations, whether cotyledons are asymmetric or not.

Embryonic cotyledons of the genus *Vochysia* have previously been described as convolute or rolled (Bentham & Hooker, 1867; Petersen, 1896; Flores, 1993a, b), spirally convolute (Baillon, 1874), obliquely spirally convolute (Warming, 1875), spirally folded (Boesewinkel & Venturelli, 1987), and spirolobal (Stafleu, 1948). The cotyledons of the species discussed above are not spirolobal, a term now used for bent embryos with incumbent once-folded cotyledons (Duke, 1969; Radford et al., 1974). The remaining descriptions are not inconsistent with convolute vernation and/or obliquely supervolute (= convolute) ptyxis, but do not completely characterize ptyxis and vernation.

In *Qualea*, embryonic cotyledons have been described as convolute or rolled (Petersen, 1896; Boesewinkel & Venturelli, 1987) or convolute and plicate (Warming, 1875; Stafleu, 1953). The cotyledons of *Q. grandiflora* Mart. (Warming, 1875: fig. 8-II) are more complexly folded than in *Vochysia*, although the complete pattern cannot be resolved from the embryo and its cross-section. Supervolute ptyxis and convolute vernation, as in *Vochysia*, can be eliminated, however, and folding may be irregular but is not fan-like. The exposed margins of the cotyledon are very uneven, almost lobed. In contrast, the exposed cotyledon margins of *Q. multiflora* Mart. (Warming, 1875: fig. 7-II) are unlobed and parallel, similar to *Vochysia* except that they are close together on the exterior of the embryo. There appears to have been some folding around the longitudinal axis through the radicle, but the specific pattern is again unknown. In both species of *Qualea*, the folded cotyledons nearly obscure the embryonic axis. Thus, ptyxis and vernation appear very different in these two *Qualea* species compared to the homogeneous pattern observed in *Vochysia*.

Embryonic cotyledons in *Callisthene* have been described as plicate and/or convolute (Warming, 1875; Petersen, 1896; Stafleu, 1952; Boesewinkel & Venturelli, 1987). In *C. major* Mart. (Warming, 1875: fig. 3-II), the embryo is straight and compressed. Each cotyledon is irregularly folded, appearing more wrinkled (corrugate) than plicate on the surface; each margin is involute, folding back with the adaxial surfaces touching. The folded cotyledons are pushed together for most of their length and width, but the folds are only rarely synchronous between the two. The involute margin of the first cotyledon is exposed at the edge of the embryo and overlaps the involute but hidden margin of the second, whereas the exposed involute margin of the second cotyledon abuts, rather than overlaps, the hidden margin of the first. No standard terms describe this pattern of folding, but corrugate-involute ptyxis and semi-convolute or valvate-convolute vernation might be used. In contrast to other genera in Vochysiaceae, the embryonic axis is fully exposed and the embryo appears almost spatulate, except for the wrinkled slightly overlapping cotyledons.

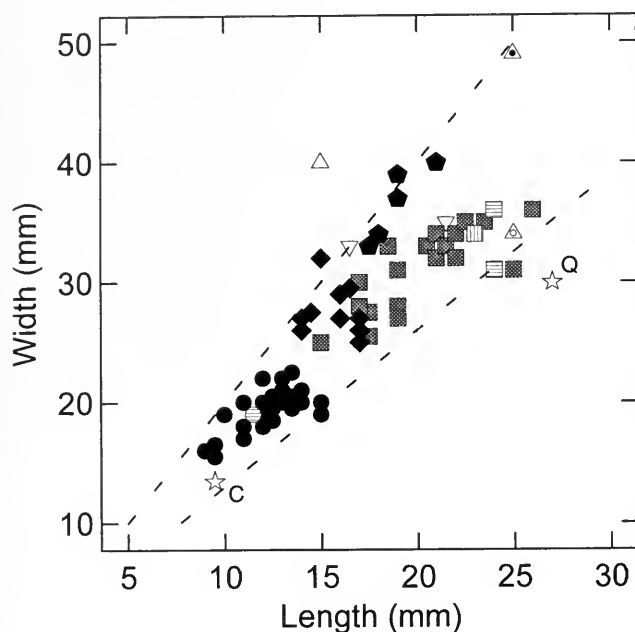
Embryos of *Vochysia*, *Qualea*, and *Callisthene* are rich in lipids and poor in starch, those of *Erisma* are poor in lipids and starch, and those of *Erismadelphus* are rich in lipids and starch (Boesewinkel &

Venturelli, 1987). The seeds of *V. hondurensis* are rich in protein, as well as lipids (Blanche et al., 1991).

## Seedling

There is little published information on seedlings and saplings of Vochysiaceae. Only *Vochysia duquei* Pilg., *V. guatemalensis*, and *V. ferruginea* (del Amo, 1979; Ricardi et al., 1987; Flores, 1993a, b; this study) have been described in detail. Limited data are available for ten additional species and some information can be inferred from the embryos of five species (Tables 1–2). In Erismeeae, cotyledons of *Erismadelphus* are cryptocotylar, hypogeal, and food-storing. Embryonic cotyledons of *Erisma* are also fleshy and food-storing, but it is not known whether these are cryptocotylar or phanerocotylar, or epigeal or hypogeal, after germination. No other information on seedlings is available for Erismeeae.

In Vochysieae, cotyledons are all phanerocotylar, epigeal, and foliaceous (Table 1). Where known, they persist after the first leaves are produced, and presumably continue to photosynthesize. In *Vochysia thyrsoidea* Pohl, they are the major photosynthetic organ



**Fig. 3** Relationship of cotyledon length and width in Vochysiaceae. *Vochysia* species: circles, *V. ferruginea* (Panamá: Garwood 1630; Garwood 2005; Foster s.n.; Costa Rica: Flores, 1993b); squares, *V. guatemalensis* (Belize: Garwood 4031; Monro 868–871, Monro et al. M4162X; del Amo, 1979; Costa Rica: Flores, 1993a); diamonds, *V. sp.* (Panamá: Hampshire & Whiteford 269); octagons, *V. sp.* (Panamá: Garwood 135); inverted triangles, *V. duquei* (Venezuela: Ricardi et al., 1987); open triangle, *V. surinamensis* (Guyana: Polak, 1992); triangle with black circle, *V. sp.* (French Guiana: Oldeman & Fundter, 1986); triangle with white circle, *V. thyrsoidea* (Brazil: Rizzini, 1965). Other genera (stars): C, *Callisthene major* (Brazil: Labouriau et al., 1964); Q, *Qualea grandiflora* (Brazil: Thomazini et al., 1973). Shading of symbols indicates country of origin: black, Panamá; cross-hatching, Belize; horizontal hatching, Costa Rica; vertical hatching, México; white, South America. Dashed lines represent width to length ratios of 2.0 (upper line) and 1.3 (lower line). Data are measurements of all seedlings in each collection, values cited in references, or my estimates from illustrations in references where values are not given. Overlapping points have been off-set by 0.5–1.0 mm to improve readability.

for many months (Rizzini, 1965). Cotyledons range from about 1 to 3 cm long and 1 to 5 cm wide (Fig. 3). They are smallest in *Callisthene major* and largest in an unidentified species of *Vochysia* (Fig. 3). Within *Vochysia*, those of *V. ferruginea* are the smallest (Fig. 3). Cotyledons are mostly 1.3 to 2.0 times wider than long in *Vochysia*, *Salvertia*, and *Callisthene*, but only 0.8 to 1.3 times wider than long in *Qualea*, and broadest above the middle in *Vochysia* and *Salvertia*. They are broadest around the middle in *Callisthene* and *Qualea* (Table 1; Fig. 3). They are asymmetric or symmetric in *Vochysia* (Fig. 1J and 2A, E–F), as in the embryos, but this may be variable within some species or collections (Table 1). The apex of *Q. grandiflora* was short-acuminate, that of *C. major* ± obcordate, and those of *Vochysia* truncate, rounded, retuse or rarely obcordate (Fig. 1J and 2A, E–F; Table 1). Venation can only be assessed in *Vochysia*, but the pattern is unusual. The midvein forks toward the apex, whether the apex is rounded or lobed, and two strong lateral primaries diverge from the base: in most species, the lateral primaries join with the recurved branches of the midvein to form triangular to obovate intercostal areas (Fig. 1J and 2A, E–F; Table 1). Smaller veins form one or more concentric series of loops around the central intercostal areas.

The cotyledonary stipules in the three species of *Vochysia* described in this study are unusual two-parted structures (Fig. 1K–M; Fig. 2C–D, G). The lower part usually consists of one to three narrow projections between the petioles, usually perpendicular to the hypocotyl, situated at the base of the upper (adaxial) surface of the petiole where the upper ridge or wing of the petiole terminates. The upper part consists of a flattened interpetiolar scale-like outgrowth just above the petioles, initially folded over the terminal bud but becoming erect and visible as the epicotyl expands, completely or partially divided or torn into two to five parts but rarely unlobed. The apex of the lower and/or upper parts often appears gland-like. Neither part appears to be fused over the petioles, and the axillary buds are often visible above the cotyledonary petiole. Although there was some intraspecific variation, the stipules of *V. ferruginea* usually had one lower projection and a lobed upper part and those of *V. guatemalensis* two lower projections and two separate upper parts. The reduced stipules of *V. guatemalensis* have also been described as 2–3 trichomes of a glandular nature (Flores, 1993a), but the thick 3-lobed pair of structures illustrated (fig. 7e) appear rather large and fleshy for trichomes and may be a different form of the variable structures described in this study. Two-parted cotyledonary stipules similar to those of *Vochysia* have not been seen in seedlings of more than 600 dicotyledonous species in 88 families surveyed from Panamá (Garwood, in prep.), although the fleshy cotyledonary stipules of *Lafaensia* (Lythraceae) are similar to the lower stipular parts of *Vochysia*.

Leaves are opposite at the early nodes in *Vochysia*, *Qualea*, and *Callisthene* (Table 2). In *Vochysia*, the pair of leaves at the first node is decussate with respect to the cotyledons and leaves at the second node (Table 2). In *Q. grandiflora*, the first pair of fully developed leaves is parallel to the cotyledons but decussate to the second pair of leaves (Table 2); a pair of 'prophylls' between the cotyledon and first pair of leaves (Thomazini et al., 1973) might be vestiges of the 'missing' pair of decussate leaves or homologous to the interpetiolar cotyledonary stipules of *Vochysia*. Leaves remain opposite into the adult stage in *V. ferruginea*, but become 3- then 4-whorled in *V. guatemalensis* sometime in the sapling stage. The initial axis of *C. major* appears to be plagiotropic, with opposite distichous leaves smaller than the cotyledons, but this will need confirmation because it is difficult to interpret details in the published photograph of the seedlings (Labouriau et al., 1964: fig. 26).

Stem characters are known only from *Vochysia*. The collet, the

**Table 1** Cotyledon characters in seedlings and embryos of Vochysiaceae.

Genus Species	Source	Emer- gence	Posi- tion	Devel- opment	Persistence		Width:Length Ratio	Shape	Base	Apex	Symmetry	Venation	Stipules
					node	months							
<i>Vochysia</i>													
<i>V. densiflora</i> Spruce	18*	–	–	F	–	–	1.7	2	5–7	8	A	–	–
<i>V. duquei</i> Pilg.	15	P	E	Fr	2	>1	1.6–1.9	2–3,6	4–6	3–5	S	1,2	+
<i>V. ferruginea</i> Mart.	6	P	E	F	3–8	>9	1.3–1.9	2	3–6	6–7	A	1–3	f+f,g
	10	–	E	–	–	–	–	–	–	–	–	–	–
	4b	P	E	F	2	–	1.6	2	6	5	S,A	1	f
<i>V. guatemalensis</i> Donn. Sm.	6	P	E	F	3	–	1.2–1.8	2	3–6	3–5	A	1–3	s+s,g
	10	–	E	–	–	–	–	–	–	–	–	–	–
	4a	P	E	F	1	–	1.2–1.3	2	6	4	A	1,4	s,g
	1,5	P	E	F	6	–	1.5	2	4–5	4	A	1,2	–
<i>V. obscura</i> Warm.	18*	–	–	F	–	–	1.4	2	7	4–5	S	–	–
<i>V. surinamensis</i> Stafleu	14	P	E	F?	6	–	2.7	1	–	3–4	–	–	–
<i>V. thyrsoides</i> Pohl	13	–	E	–	–	≈ 12	–	–	–	–	–	–	–
	16	P	E	Fr	1	>12	–	1	2	4	–	–	–
<i>V. tucanorum</i> Mart.	18*	–	–	F	–	–	1.6	2	6–7	3–4	A	–	–
<i>V. sp.</i> (Brazil)	2	P	E	F	–	–	–	1	–	–	–	–	–
<i>V. sp.</i> (Fr. Guiana)	11	P	E	F	–	–	2.1	2	4	5	S	2,5	–
<i>V. sp.</i> (Panamá)	6	P	E	F	1	–	1.4–2.1	2	3–5	4–6	S,A	1–3	s+f,g
<i>Salvertia</i>													
<i>S. convallaridorea</i> A. St.–Hil.	18*	–	–	F	–	–	1.6	2	2–3	4–5	S	–	–
<i>Qualea</i>													
<i>Q. grandiflora</i> Mart.	12	P	E	F	2	>6	–	–	–	–	–	–	–
	3	P	E	F	–	4	–	–	–	–	–	–	–
	17	P	E	F	2	>6	1.1	5	3–4	1	A?	–	P
<i>Q. multiflora</i> Mart.	18*	–	–	F	–	–	0.8–1.3	4	3	9	A	–	–
<i>Callisthene</i>													
<i>C. major</i> Mart.	8	P	E	F?	1–3?	–	1.2–1.5	3	–	5–6	–	–	–
	18*	–	–	F	–	–	1.2–1.6	–	–	–	–	–	–
<i>Erisma</i>													
<i>E. spp.</i>	7*	–	–	R	–	–	–	–	–	–	–	–	–
<i>Erismadelphus</i>													
<i>E. exsul</i> Mildbr.	9	C	H	R	–	–	–	–	–	–	–	–	–
<i>E. sp.</i>	9	C	H	R	–	–	–	–	–	–	–	–	–

Source: 1, del Amo 1979; 2, Duarte 1979; 3, Felipe & Dale 1990; 4a,b, Flores 1993a, b; 5, Gaos 1978; 6, Garwood, this study; 7, Kawasaki, in press; 8, Labouriau et al. 1964; 9, Miquel 1987; 10, Moreira & Arnáez 1994; 11, Oldeman & Fundter, 1986; 12, Paulilo et al. 1993; 13, Paviani & Haridasan 1988; 14, Polak 1992; 15, Ricardi et al. 1987; 16, Rizzini 1965; 17, Thomazini et al. 1973; 18, Warming 1875. \*, all characters based only on the embryonic cotyledon in the mature seed.

Emergence: P, phanerocotylar; C, cryptocotylar.

Position: E, epigeal; H, hypogeal.

Development: F, foliaceous; R, fleshy, presumably with stored reserves; r, somewhat fleshy or succulent, with reserves or stored water.

Persistence: measured as i) the last recorded leaf node to produce leaves while the cotyledons are still present (e.g. node=3, cotyledons still present when leaves produced at node 3) or ii) the length of time [months] that cotyledons persist after germination. These measures underestimate persistence when only the youngest seedling stages have been studied.

Width:Length Ratio: width divided by length.

Shape: 1, obtriangular to shallowly obtriangular, including 'triangular'; 2, depressed obovate; 3, transversely oblong; 4, very widely obovate; 5, transversely widely elliptic to transversely widely oblong; 6 transversely reniform, rectangular-reniform.

Base & apex: 1, short-acuminate; 2, acute; 3, rounded; 4, truncate; 5, retuse to emarginate; 6, cordate, obcordate, 2-lobed; 7, 2-cleft or -parted; 8, 3-lobed; 9, irregular. When blade is asymmetric, the base and/or apex may be unequal on the two sides (e.g. half-cordate, half-rounded) or oblique (e.g. obliquely truncate).

Symmetry of blade: A, asymmetrical; S, symmetrical.

Venation: 1, branches of forked central primary vein join lateral primaries forming a pair of obovate to triangular intercostal areas; 2, palmate or 3-nerved; 3, basal acro-brochidodromous; 4, basal actinodromous; 5, branches of central primary vein forked; lateral primaries each form a closed loop apically, terminating near but not joined directly to the tips of the central vein.

Stipules: s, usually separate; f, usually fused and interpetiolar; f+f, f+s, and s+s, two structures (fused or separate) present at cotyledonary node (first is lower structure, second is upper structure); g, gland-like; +, present; P, 'prophylls' present above cotyledons.

–, Information not available.

Characters in italics were inferred or estimated from illustrations in the citations, not from the text of the original author. Where authors identified the cotyledons as foliaceous, it was assumed that they were also phanero-epigeal.

junction of the radicle and hypocotyl, is annulate in at least three species (Table 2; Fig. 1F). The hypocotyl, epicotyl, and later internodes are usually square, with ridges or wings on each corner (Table 2). Ridges on the hypocotyl continue without interruption into the ridges on the lower margins of the cotyledonary petioles in *V. ferruginea* and *V. guatemalensis* (Figs 1K, 2G; Flores, 1993a, b). In contrast, the wings or ridges on the epicotyl and later internodes

terminate in small narrowly triangular to linear stipules at the top of each internode (Fig. 1O, S; Table 2), with the inner margin and base of the stipules apparently extending above the petiole but not attached to it. The winged stems do not originate directly from decurrent leaf bases, as sometimes suggested, because the attenuate base of the blade narrows into a medial pair of short thin ridges on the upper (adaxial) surface of the petiole, interrupting the lamina

**Table 2** Root, stem, and leaf characters in seedlings of Vochysiaceae.

Genus Species	Source	Collet	Hypocotyl	Epicotyl	Internodes	Phyllotaxis		Leaf stipules
						Nodes 1–2	Later nodes	
<i>Vochysia</i>								
<i>V. duquei</i>	15	a	s	s	–	o	–,v	+
<i>V. ferruginea</i>	6	a	s,w	s,w	s,w	o,d	o,d	+,s
	4b	c	s	–	–	o,d	o,d	–
<i>V. guatemalensis</i>	6	a	s,w	s,w	s,w	o,d	o,w	+,s
	4a	c	s,w	s,w	–	o,d	o,w	–
	1,5	c	c,w	s,w	s,w	o,d	o	+,i
<i>V. surinamensis</i>	14	–	–	–	s,w	o	o,v	–
<i>V. thyrsoidea</i>	13	c	t	–	–	–	–	–
<i>V. sp. (Panamá)</i>	6	–	s,w	w	–	o	–	–
<i>Qualea</i>								
<i>Q. grandiflora</i>	17	–	–	–	–	o,p	–	–
<i>Callisthene</i>								
<i>C. major</i>	8	–	–	–	–	o	a?	–

Sources and authorities for names: see Table 1.

Collet (junction of hypocotyl and primary root): a, annulate ridge present; c, constriction, abrupt change, or other feature present, but nature of structure not discernable from illustration.

Hypocotyl, Epicotyl, and Internode: cross-sectional shape of hypocotyl, epicotyl, and early internodes (about first ten), respectively: s, square to rectangular; c, circular; t, tuberos and circular, at least when older; w, 4 wings or ridges present.

Phyllotaxis:

Nodes 1–2: o, leaves at first node opposite; d, pair of leaves at first node decussate to both cotyledons and pair of leaves at second node; p, pair of leaves at first node parallel to cotyledons and decussate to pair of leaves at second node.

Later nodes: o, leaves opposite and decussate (at least to node 5, sometimes reported up to node 20); d, leaves opposite and decussate on larger seedlings, saplings, and adults; w, leaves whorled on larger seedlings or saplings (and adults), with three or four leaves per node, size of juveniles at time of transition from opposite to whorled leaves

unknown; v, juvenile leaves unknown, but adult leaves whorled; a, axis becoming plagiotropic with pairs of leaves distichous.

Leaf stipules: +, small, narrowly triangular to linear stipules present from the first node; i, stipules intrapetiolar; s, stipules separate.

–, Information not available.

Characters in italics were inferred or estimated from illustrations in the citations, not from the text of the original author.

between the blade and wings. It is unclear, however, whether the petiolar ridges are joined to the lateral extensions of the stipules.

Striking ontogenetic changes are seen in hair morphology in *Vochysia ferruginea* (this study). The epicotyl and first leaves are only sparsely pubescent below, but stems and leaves at higher nodes become progressively more densely pubescent. Hairs on early internodes and lower leaf surfaces are nearly sessile, appressed, and T-shaped, with straight arms of equal length; those on later leaves and stems are short-stalked, ascending to erect, 2-branched, with the longer arm curved to coiled and about eight times longer than the shorter arm. Hairs on the adult leaves are similar, except the branches are even more unequal in length (Garwood, pers. obs.). On seedlings to adults of *V. ferruginea*, hairs on the midrib above are always simple. In *Vochysia* sp. (Garwood 135 and Hampshire & Whitefoord 269), hairs on the epicotyl and eophylls were similar to those on *V. ferruginea*. In contrast, hairs on the young expanding leaves of *V. guatemalensis* were simple and basifixed, but these were usually sparse or absent on mature leaves (Flores, 1993a; this study). All parts of *V. duquei* are glabrous (Ricardi et al., 1987).

Seedlings from the Brazilian cerrado have a number of special morphological adaptations to the dry cerrado environment (Labouriau et al., 1964; Rizzini, 1965; Paviani & Haridasan, 1988). *Vochysia thyrsoidea* has ± fleshy succulent cotyledons, a thick watery hypocotyl which is mostly buried, minute eophylls which remain hidden between the cotyledons, greater growth of the taproot rather than shoot in the first few months, and a swollen subterranean organ which forms from the hypocotyl and upper part of the taproot in the first two years. *Qualea grandiflora* also forms a swollen under-ground organ.

## Phylogeny

There have been no phylogenetic analyses of relationships within Vochysiaceae. Since the completion of Stafleu's (1948–1954) monograph more than 40 years ago, the numbers of collections and species described have increased, but major systematic work has been limited to elevating one section of *Qualea* to *Ruizterania* (Marcano-Berti, 1969) and monographing *Erisma* (Kawasaki, in press). Fruit and seed characters have long been important in delimiting genera within the family, but the utility of seedling characters has been untested because seedlings have not been available for study. The potential of the new seedling and seed characters described above to contribute to phylogenetic and systematic studies is discussed here. If such traits look promising, data on more species should be collected.

Phanero-epigeal seedlings are reported only from Vochysieae, and crypto-hypogeal seedlings from Erismeae, following the current tribal division. In Vochysieae, shape characters of the foliaceous cotyledon fell into three groups corresponding to *Qualea*, *Callisthene*, and *Vochysia/Salvertia*, although some variation occurred in all groups. Symmetry of the cotyledons varied most in *Vochysia*, and veneration and ptyxis of the embryonic cotyledons in *Qualea*. Several traits generally uncommon in dicotyledon seedlings occur together in *Vochysia*, including unusual cotyledonary stipules and cotyledonary venation, annulate collet, and winged hypocotyls and early internodes, but these have not been assessed in many species or other genera. Supra-cotyledonary prophylls, also unusual in dicotyledon seedlings, were reported in one species of *Qualea*. The existence of considerable variation in cotyledon characters, and the presence of many unusual seedling characters in this small sample of

about 20 species (Tables 1–2), suggests further study of other taxa would be profitable.

Ontogenetic changes from the seedling to adult stages can also be important phylogenetic characters. In *Vochysia*, leaves of adults are either opposite or 3- or 4-verticillate, but the first seedling leaves of all species described are opposite (Table 2). In *V. guatemalensis*, leaves remain opposite at early seedling nodes, but gradually become 3- then 4-verticillate in larger saplings (Flores, 1993a). Although presence of opposite seedling leaves in all taxa would not be phylogenetically informative, the timing of the switch from opposite to verticillate leaves may provide a useful character. Adult leaves are also verticillate in *Salvertia* and some species of *Erismia*, but opposite in other taxa (Stafleu, 1948–1954).

Pronounced ontogenetic changes in hair morphology were observed in *Vochysia ferruginea*, but not in *V. guatemalensis*. Because studies of ontogenetic changes of trichomes on leaves of seedlings and adults have helped identify groups of species within the large and complex genera of *Solanum* and *Rhododendron* (Seithe 1979, 1980; Seithe & Anderson, 1982), further study would be warranted. Unfortunately, the morphology of hairs in *Vochysia* is poorly known. They have been described as simple or sometimes unicellular and 2-branched (Warming, 1875; Metcalfe & Chalk, 1950); hairs have arms of equal length and short stalks in at least one species (Shanmukha Rao & Vijayalakshmi Sarma, 1992). Stafleu (1952) indicated that simple and biramose hairs occurred in Vochysiaceae, but did not specifically describe those of *Vochysia* (Stafleu, 1948), although frequent references to ‘peculiar indumentum’ or ‘characteristic indumentum’ suggests that their morphology is unusual.

An examination of adult specimens of *Vochysia* at BM indicates that species with 2-branched or simple hairs are both common (Table 3). The distribution of simple and branched hairs is clearly not random with respect to the sections of *Vochysia* delimited by Stafleu (1948). Branched hairs are especially abundant in subsection Ferrugineae, which contains *V. ferruginea*. There was considerable variation among species in the morphology of the branched hairs of the adult stage, ranging from nearly sessile appressed T-shaped hairs with straight branches of equal length, to long-stalked erect 2-branched hairs with curled arms of equal or unequal length (Garwood, pers. obs.). In some species, the smaller arm was so reduced in length that the hair could easily be misinterpreted as simple, suggesting that at least some of the simple hairs in *Vochysia* might be derived from much-reduced branched hairs, as occurs in Malpighi-

aceae (Anderson, 1990). The range of hair morphology from the seedling to adult stages in *V. ferruginea* spans nearly the entire range of branched hairs seen in the genus. Therefore, examining the ontogeny of branched hairs might reveal similarities in the early stages that would be phylogenetically informative in comparison with other species of *Vochysia*, or other genera. Hairs are also simple or 2-branched in *Qualea* (Stafleu, 1953), but stellate in *Erismia* (Warming, 1875; Stafleu, 1954), and simple in *Callisthene* (Stafleu, 1952), *Salvertia* (Garwood, pers. obs.), and *Erismadelphus* (Garwood, pers. obs.).

Seed, fruit, and seedling characters also bear on the higher order relationships of the family. Vochysiaceae has usually been included in the Polygalales with Polygalaceae, Trigonaceae, Malpighiaceae, Xanthophyllaceae, Tremandaceae, and Krameriaceae (Dahlgren, 1980; Takhtajan, 1980; Cronquist, 1981). Boesewinkel & Venturelli (1987) used anatomy of the seed coat to reassess the position of the family in Polygalales. They concluded that only Polygalaceae and Xanthophyllaceae should be retained in the Polygalales, and that the relationship of Vochysiaceae and the remaining families needed further study. Reviewing numerous floral and vegetative characters in Malpighiaceae, Anderson (1990) decided that Malpighiaceae was most similar to Vochysiaceae and Trigonaceae and least similar to Polygalaceae and Krameriaceae. The presence of 2-branched unicellular hairs in Vochysiaceae, Trigonaceae, and Malpighiaceae, and their absence in Polygalaceae, also supports this grouping (Shanmukha Rao & Vijayalakshmi Sarma, 1992).

Recent molecular analyses of the angiosperms using the chloroplast gene *rbcL* also supported the break-up of the Polygalales, but not the grouping of Vochysiaceae with Malpighiaceae and Trigonaceae (Chase et al., 1993). Instead, Vochysiaceae, represented by *Qualea*, fell within the Myrtales. A more detailed study of Myrtales using the same gene confirmed the Myrtalean affinities of Vochysiaceae, represented by *Vochysia*, *Erismia*, and *Qualea* (Conti et al., 1996). Vochysiaceae was sister group to the Myrtaceae and these, with Heteropyxidaceae and Psiloxylaceae, formed the sister clade to that containing Melastomataceae, Memecylaceae, and other families. Work with chloroplast gene *matK* also supports placement of Vochysiaceae in Myrtales, but it falls between Myrtaceae (with Heteropyxidaceae and Psiloxylaceae) and Melastomataceae (with Memecylaceae) (P. Wilson, pers. comm.).

Previous systematic treatments based on morphology have never included Vochysiaceae in the Myrtales (Conti et al., 1996), regard-

**Table 3** Distribution of simple and branched hairs in *Vochysia*.

Section	Subsection	Number of species				
		Described by Stafleu (1948)	Examined for study	Type of hair		
Simple	Branched			Unknown		
Vochysiella	Decorticantes	10	6	6	0	0
	Calophylloideae	10	7	6	0	1
Ciliantha	Micranthae	11	9	8	0	1
	Lutescentes	23	13	6	4	3
	Discolores	3	2	0	2	0
	Chrysophyllae	1	1	1	0	0
	Megalanthae	5	3	3	0	0
	Ferrugineae	31	22	1	18	3
Pachyantha	–	3	0	–	–	–

Type of hair: simple, only simple unbranched hairs present on leaves, stems, and reproductive parts; branched, some or all of hairs present branched, including T-shaped hairs; unknown, specimens glabrous or hairs too small or dense to characterize. Leaves, stems, and inflorescences of one to several specimens of each species at BM monographed by Stafleu (1948) were examined under a 40x dissecting microscope.

ing this relationship as so remote that the presence of two of the most definitive Myrtales characters, vestured pits in the secondary xylem and bicollateral vascular bundles in the primary stem, was not considered significant (van Vliet & Baas, 1984). In retrospect, many vegetative characters of Vochysiaceae are equally at home in Myrtales (*sensu* Dahlgren & Thorne, 1984) as in Polygalales, including opposite or verticillate leaves with entire margins, brochidodromous venation, and stipules. The highly zygomorphic flowers with one fertile stamen are, however, unusual in the order (Conti et al., 1996). When a thorough morphological analysis of the relationship of Vochysiaceae within Myrtales is undertaken, several seedling and seed characters described for Vochysiaceae deserve further study.

Vochysiaceae share other vegetative characters with Myrtales, including the occasional presence of 2-branched unicellular or tufted hairs in Combretaceae, Lythraceae, and Myrtaceae (Metcalf & Chalk, 1950). Cotyledonary stipules, generally uncommon in dicotyledons, occur as rudimentary glandular structures in some Lythraceae, Onagraceae, and Myrtaceae, and as 2- to 3-lobed structures or glandular processes near the basal margins of the blade in other groups of Myrtaceae (Weberling, 1984). The latter type might be homologous to the unusual cotyledonary stipules of *Vochysia* (Flores, 1993a; this study), which are composed of an upper lobed part and lower possibly glandular part.

Wings are well-developed on adult stems in some Lythraceae and Penaeaceae, and often develop auricles at the apex, which are distinct from the rudimentary stipules found closer to the petioles (Weberling, 1984). In Lythraceae, auricled wings are already present at the seedling stage in *Lafoesia* (Garwood, in prep.). Wings are well-developed on seedlings of *Vochysia*, although usually reduced to ribs on adults (Stafleu, 1948; Garwood, pers. obs.). As the small stipules of *Vochysia* occur at the apex of the wings, they may be homologous to the auricles at the apex of the wings of these Myrtales, rather than the small, often dissected, stipules characteristic of Myrtales (Weberling, 1984). If so, *Vochysia* may lack true stipules. Herbarium specimens of *V. ferruginea* and *V. guatemalensis* seedlings were carefully examined for the presence of dissected or rudimentary stipules over the petioles, but none were seen (Garwood, pers. obs.). The occasional presence of a minute shrivelled structure, however, suggests that actively growing seedlings should be examined to verify whether minute caducous stipules are present but hidden by the small erect expanding leaves. In seedlings of Myrtaceae, auricles are lacking on the winged epicotyl and later internodes of *Psidium* and *Calycolpus* and on the winged hypocotyl of *Myrcia*, and wings are lacking in *Eugenia*, but all have rudimentary gland-like stipules (Garwood, in prep.).

Seeds of Vochysiaceae and Myrtales generally lack endosperm and arils and have straight or slightly curved embryos (Cronquist, 1981; Dahlgren & Thorne, 1984). A fibrous exotegmen and an endotestal crystal layer are found in *Qualea* and some Lythraceae, Combretaceae, and Onagraceae, but the exotegmen lacks fibres and is crushed in *Vochysia* and some Melastomataceae and Myrtaceae (Corner, 1976; Dahlgren & Thorne, 1984; Boesewinkel & Venturelli, 1987). The embryonic cotyledons are variously folded in Vochysiaceae and many Myrtales, with folding frequently described as 'spiral' in *Vochysia* as well as Combretaceae and Oliniaceae (Dahlgren & Thorne, 1984). As brief descriptions of vernation and ptyxis in Vochysiaceae are generally incomplete or incorrect (see above), further detailed studies should be carried out throughout the order.

## Ecology

Seed germination has been the most frequently studied aspect of the seed and seedling ecology of Vochysiaceae. Germination is usually rapid, occurring 1 week to 3 months after seed dispersal or sowing in species of *Vochysia*, *Salvertia*, and *Qualea* from both cerrado and rainforest (Rizzini, 1965; Thomazini et al., 1973; Macedo, 1977; Duarte, 1979; Sabatier, 1985; Paviani & Haridasan, 1988; de Godoy & Felipe, 1992a; Moreira & Arnáez, 1994; Flores 1993a, b; this study; M. Bustamante, pers. comm.; P.E. Oliveira, pers. comm.; P. Wilson, pers. comm.). Chemical or mechanical scarification of the seed coat, or its complete removal, may hasten germination in *Q. grandiflora* (Felippe, 1990; Felippe & Dale, 1990), but is not required (M. Bustamante, pers. comm.; P.E. Oliveira, pers. comm.; P. Wilson, pers. comm.). Germination is not inhibited by dark or shaded conditions in *Q. retusa* Spruce ex Warm., *Q. grandiflora*, or *V. ferruginea* (Macedo, 1977; Felippe, 1990; this study), although it can be somewhat depressed in direct sunlight (Flores, 1993b). Recently dispersed seeds of *V. maxima* Ducke buried under the leaf litter either lost viability or had germinated within 2 months (Viana, 1990). Thus, there is no indication of any type of seed dormancy in the family, and seeds should form transient, rather than persistent, seed banks under natural conditions.

Under artificial conditions, seeds of *Qualea cordata* Spreng., *Vochysia guatemalensis*, and *V. ferruginea* retained high viability for at least 2–3 months when stored at room temperature and humidity (de Godoy & Felipe, 1992a; Flores, 1993a, b), in spite of a relatively high initial moisture content in *Vochysia* (23–32%, fresh weight basis). Reducing the moisture content extended viability of the apparently orthodox seeds, although they were intolerant of chilling (Flores, 1993a). The potential to store seed should promote the ongoing silvicultural development of the family.

Seeds of all species are wind-dispersed, as indicated by the morphology of seeds of Vochysiaceae and indehiscent fruits of Erismaceae, except *Erisma calcaratum* (Link) Warm. from the Amazonian varzea, which is water-dispersed (Stafleu, 1954). In tropical forests, seeds of *Vochysia maxima* are dispersed near the parent, mostly  $\leq 30$  m from the trunk (Viana, 1990), seedlings of *V. maxima* and *V. ferruginea* persist in the shaded understorey (Viana, 1990; Garwood, pers. obs.), but growth is fast only in treefall gaps and larger openings (Viana, 1990; Boucher et al., 1994). In plantations, seedlings of *V. guatemalensis* and *V. ferruginea* can reach 2–3 m tall within three years (Flores 1993a, b). Thus, tall canopy *Vochysia* appear to be gap opportunists, regenerating from a persistent seedling bank following disturbances throughout the year. Regeneration of *Qualea* may follow a different pattern. Following a severe hurricane, most of the severely defoliated adults of *Q. paraensis* Ducke survived but there was no regeneration from seedlings or saplings; in contrast, all the equally abundant and severely defoliated adults of *V. ferruginea* died, but there was extensive regeneration from seedlings and saplings (Boucher et al., 1994). If this pattern is typical, species of *Vochysia* may be more amenable to sustainable management or plantation development than *Qualea*.

In the drier and more open cerrado, seedlings of *Qualea grandiflora*, *Q. cordata*, and *Vochysia thyrsoidea* appear to grow inherently slowly, with neither extra moisture nor nutrients promoting rapid growth (Rizzini, 1965; de Godoy & Felipe, 1992b; Paulilo et al., 1993; Felippe & Dale, 1990). Although the basis for the slow growth is not understood, many species develop special morphological adaptations to the cerrado environment, such as large subterranean storage organs and thick succulent cotyledons (Labouriau et al., 1964; Rizzini, 1965; Paviani & Haridasan, 1988).



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# A revision of the genus *Mandragora* (Solanaceae)

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**SYNOPSIS.** The Old World genus *Mandragora* L. (Solanaceae) is revised for the first time across its entire geographical range. The introduction reviews the extensive mythological and medicinal as well as the taxonomic history of the genus. On morphological and phenological grounds three geographically widely disjunct species can be distinguished: the Mediterranean *M. officinarum* L., the narrowly local Turkmenian endemic *M. turcomanica* Mizg. and the Sino-Himalayan *M. caulescens* C.B. Clarke. The generic monophyly of *Mandragora* L. as traditionally circumscribed is supported by cladistic analysis of morphological data. The ecological and historical phytogeography of the genus is discussed and alternative biogeographical scenarios are evaluated. Finally, a concise taxonomic treatment of the taxa is provided, based on the evidence of the preceding analyses.

## INTRODUCTION

The nightshade family (Solanaceae) is a cosmopolitan but predominantly tropical group and is especially well represented in the Neotropics. The family is of considerable economic importance. Food plants include potato (*Solanum tuberosum* L.), tomato (*Solanum lycopersicum* L. (= *Lycopersicon esculentum* Mill.)), pepper (*Capsicum annuum* L.) and aubergine (*Solanum melongena* L.). Another species of great commercial value is tobacco (*Nicotiana tabacum* L.). The family also contains ornamental plants such as garden petunias (species of *Petunia* Juss.) and the Chinese lantern (*Physalis alkekengi* L.). Many members of the family are poisonous, but several such as deadly nightshade (*Atropa belladonna* L.), henbane (*Hyoscyamus niger* L.) and thorn-apple (*Datura stramonium* L.) provide drugs traditionally used in medicine. The subjects of this study, the mandrakes (*Mandragora* L.), belong to this latter group of pharmaceutically interesting Solanaceae.

The long history of mythology and medicinal use of the mandrake combined with the variable morphology and phenology have led to considerable confusion in the classification of *Mandragora*. The nomenclatural situation is, considering the small size of the genus, amazingly chaotic. In particular the Mediterranean *Mandragora* is burdened with synonyms, and some authors (Mill, in litt.) have expressed doubts about the placement of the Himalayan mandrake in *Mandragora* at all. This study represents the first taxonomic revision of the genus over its entire range. We address the following main questions in this study. Firstly, which of the described *Mandragora* taxa are justifiable if the whole range of the morphological variation is considered? Secondly, is the genus as currently delimited (including the Himalayan mandrake, *M. caulescens*) monophyletic? Finally, does the phylogeny, combined with the distribution patterns of the taxa, support a particular historical biogeographical scenario and do the ecological requirements of the defined taxa impinge upon this?

## Mythological and medicinal history

The origin of the myth surrounding the mandrake root is hard to trace. It is clear, however, that the mandrake was a focus of superstition and belief in magic and demons for many centuries. The sometimes vaguely humanoid shape of the root and its potent, psychotropically active alkaloids are probably responsible for the long history of myths. However, the properties ascribed to the plant as a whole, and especially to its root, are highly ambiguous and the first references in Ancient Egypt and in the Bible remain controversial. Ornaments on the casket and throne from the tomb of Tutankhamun seem to depict mandrakes (Hepper, 1990; Roland, 1991). *Mandragora* is not known to be native in Egypt but may have been cultivated there. The Biblical 'Dudaim' is often said to be identical with *Mandragora* (Moldenke & Moldenke, 1952; Feinbrun-Dothan, 1978; Fleisher & Fleisher, 1994). Dudaim is mentioned in the Song of Solomon (7: 13) and in another passage from the Old Testament (Genesis 30: 14–18), according to which it was used in relation to fertility. The 'Moly' of Homer in his *Odyssey* is presumed to be the mandrake, as is the 'Baraa' of Flavius Josephus' *Jewish Wars*, where it is described as shining in the dark (*sic*) and is attributed exorcistic powers. Pliny in his *Natural History* and Dioscorides in *De Materia Medica* wrote that the mandrake was known as 'Circaeon' after Circe, the mythical sorceress who turned men into sexually supercharged swine (Marzell, 1975; Roland 1991; Fleisher & Fleisher, 1994). The Ancient Greeks and Romans considered the mandrake so potent and valuable as a narcotic and restorative plant that the collectors of its roots had to obey rigid ceremonial rules which were described by Theophrastus and Pliny (Randolph, 1905).

In Medieval Europe the plant was known as 'Alraune' in Germany and 'Main de gloire' in France. Carved to emphasize the anthropomorphic male or female character of the root, it was popular as an aphrodisiac, charm against sterility and love talisman alike. But the plant was soon connected with witchcraft; for example, Joan of Arc, who was tortured and burnt at the stake in 1431 as a heretic, was also accused of the witches' crime of possessing a mandrake (Thompson, 1934). It was believed that the plant grew under gallows and that the root owed its human shape to urine or sperm of unjustly hanged men. The gathering of the root was considered to be highly dangerous and dogs had to perform the supposedly lethal procedure of pulling out the plants, whereupon the roots would shriek so 'that living mortals hearing them run mad': Shakespeare, *Romeo and Juliet* Act IV (Randolph, 1905; Moldenke & Moldenke, 1952; Marzell, 1975; Roland, 1991; Talalaj et al., 1992; Fleisher & Fleisher, 1994). Perhaps the most interesting aspect of the mythology of the mandrake is convergent myths in the eastern area of the genus in the disjunct region of Central Asia, the Himalayas and China where *Mandragora* has a similarly long history of application and traditional use. For instance in Sikkim, the roots of *Mandragora caulescens*, called 'Lakshmana', were used in magical rites and in folk medicine (Mehra, 1979); and in Central Asia the mandrake, called 'Khaoma-soma', was considered a holy plant (Khlopina, 1979).

The mythology of the mandrake and its use in traditional medicine are hard to keep apart. In a wide range of applications it was used as an aphrodisiac, hypnotic, emetic and purgative, sedative and narcotic, for example as a pain-killer at childbirth as well as to relieve crucifixion agony (Duke, 1985; Talalaj et al., 1992); in fact, according to Heiser (1969), it has been questioned that Christ died on the Cross at all, suggesting that the vinegar supplied to him had contained the drug, inducing merely a deathlike trance. The secondary metabolites of major pharmaceutical importance are chiefly

tropane alkaloids and their esters. Staub (1962), Hegnauer (1973), Romeike (1978), Evans (1979) and Jackson & Berry (1979) list alkaloids of *Mandragora* and other Solanaceae. Tropane alkaloids occur mainly in the Solanaceae, but they are not entirely restricted to this family; other tropane alkaloids of importance include cocaine, found in the family Erythroxylaceae. However, esters with tropic or related acids of alkamines derived from tropane do seem to be restricted to the Solanaceae (Romeike, 1978).

The most important alkaloid components of *Mandragora* are: atropine, apoatropine, belladonnine, cuscohygrine, hyoscyamine, hyoscyamine-N-oxide, norhyoscyamine, scopolamine, 3 $\alpha$ -tigloyloxytropine, 3 $\alpha$ ,6 $\beta$ -ditigloyloxytropine, and 6 $\beta$ -hydroxyhyoscyamine. The root, stem, leaves, fruits and seeds of *Mandragora* all contain a different alkaloid profile. However, the root is considered to be the site of synthesis of the tropane alkaloids (Romeike, 1978) and is the most poisonous part of *Mandragora*, due to the high concentration therein. The total content of alkaloids in the root is around 0.4% (Kessler, 1951; Maugini, 1959; Duke, 1985), hyoscyamine being the most important constituent (Duke, 1985). In contrast, the berries are said to be sweet and edible in moderation (Viney, 1994). The synthetic pathways leading to the alkaloids in different taxa of the Solanaceae have been proposed to be homologous to each other (Tétényi, 1987) and to be a linear or spiralling phyletic sequence. Tropane alkaloids are effective as analgesics, anaesthetics, antispasmodics, and are used to increase the circulation, reduce secretions and dilate pupils. Scopolamine is a hypnotic (Duke, 1985) and achieved a notorious reputation as a 'truth-drug' in police and secret service investigations (Heiser, 1969). 'Quishen', a Chinese herbal medicine consisting of dried roots of *M. caulescens*, is used in Yunnan and Xizang as a ginseng substitute for all kinds of physical weaknesses (Xiao & He, 1983). In allopathic western medicine, however, the mandrake has largely lost its importance as valued source of alkaloids, although the plant itself is still surrounded by myth.

## Taxonomic history

### *The classification of Mandragora*

MEDITERRANEAN PLANTS. As mentioned above, considering the small size of the genus, there has been a fair amount of confusion in respect to the classification of *Mandragora*. The long taxonomic history, especially of the Mediterranean *Mandragora* species, led to a large number of often imprecisely defined species and subspecies or varieties. As a consequence, there is a plethora of names, and their somewhat indiscriminate use renders the meaning and reliability of identifications of specimens in herbaria, as well as in the literature, highly problematic. Here we present the taxonomic history of the Mediterranean part of the genus in periods, with examples of major taxonomic works and their treatment of the genus, in order to outline the main taxonomic trends through the centuries.

*Pre-Linnaean*: The Ancients distinguished two species that they called the female or black mandrake (*Mandragoras femina*), and the male or white mandrake (*Mandragoras mas*). These plants were described by both Dioscorides and Pliny (cf. Randolph, 1905 for translations), and this division was widely adopted, for instance by Parkinson (1629) and by Jean Bauhin et al. (1651) as late as the seventeenth century. The male mandrake corresponds to a spring flowering entity; the female mandrake represents an autumn flowering one. Caspar Bauhin (1623) and Tournefort (1719), on the other hand, each recognized three 'species'. Both authors listed *Mandragora fructu rotundo* and *M. flore subcaeruleo, purpurascete*.

Bauhin's third species was *M. fructu pyri* while Tournefort's was *M. flore subcaeruleo, foliis minoribus, fructu globoso*.

**Linnaeus:** In his *Hortus cliffortianus*, Linnaeus (1738) considered these variants as mere forms of a single species. In the first edition of *Species plantarum* (1753), he accordingly recognized only one species that he named *Mandragora officinarum*. Later, however, he changed his mind with respect to the distinctness of this taxon and placed it within his genus *Atropa*, calling it *Atropa mandragora* (Linnaeus, 1759, 1762).

**Post-Linnaean:** Linnaeus's idea of a single species did not last very long. The nineteenth and the first half of the twentieth centuries were characterized by an increasingly elaborate division of the genus (Table 1). Heldreich (1886) additionally described an infertile hybrid between two vernal entities: *Mandragora vernalis* Bertol. and *M. haussknechtii* Heldr., called *M. × hybrida* Haussk. & Heldr.

**Post-1950:** In recent decades, however, there has been a trend towards reversing this ever greater subdivision of the genus. In fact, since the 1950s there have been a number of proposals to re-adopt the two traditional, pre-Linnaean taxa only (Tercinet, 1950; Hawkes, 1972b; Jackson & Berry, 1979). This viewpoint was adopted in *Flora Europaea* (Hawkes, 1972a), using the names *Mandragora officinarum* L. for a vernal entity and *M. autumnalis* Bertol. for an autumnal one. However, *M. officinarum* L. might be considered an ambiguous name since it was formerly used for an autumnal entity as well (Greuter & Rechinger, 1967; see Table 1). Hawkes (1972b) rejected this reservation on the grounds of the priority, the wide use and the generic type status of the Linnaean epithet *officinarum*. Knapp in Jarvis et al. (1993) finally lectotypified *M. officinarum* L. with a specimen in the Bursar herbarium, to which no phenological data are attached.

**SINO-HIMALAYAN PLANTS.** In contrast to the Mediterranean plants, the classification of the disjunct Central and East Asian part of the genus was never as contentious and did not arouse much comment, in part reflecting its far younger taxonomic history. *Mandragora caulescens* was described by C.B. Clarke (1883) in Hooker's *The flora of British India* (Hooker fil. and Thomson labelled the specimens '*Scopolia humilis*' but this name was never published). *Anisodus caulescens* (C.B. Clarke) Diels and *A. mariae* Pascher, as well as *Mairella yunnanensis* H. Lév., were placed in synonymy with *Mandragora caulescens* in the *Flora of China* (Zhang et al., 1994). Grubov (1970) described a new species from Xizang, China which he named *Mandragora tibetica*, and Kuang Ko-zen & Lu An-ming (1978) described a new species found in Qinghai and Xizang which they named *Mandragora chinghaiensis*. In the *Flora of China* (Zhang et al., 1994) the latter two taxa were provisionally put into synonymy with *M. caulescens* until a more detailed revision could

establish their distinctiveness. *Mandragora shebbeari* C.E.C. Fischer, described from a single specimen from Xizang (Fischer, 1934), was transferred to the monotypic solanaceous genus *Przewalskia* by Grubov (1970). One attempt to subdivide *Mandragora caulescens* was made by Grierson & Long (1978) who split it into four subspecies (subsp. *caulescens*, subsp. *flavida* Grierson & Long, subsp. *purpurascens* Grierson & Long and subsp. *brevicalyx* Grierson & Long) differentiated on the basis of corolla colour and various morphometric characters, especially of flower parts.

**TURKMENIAN PLANTS.** Finally, *Mandragora turcomanica* Mizg. was described in 1942 from a small area (the Shevlan 'pocket', Mizgireva, 1955) near Kara Kala in the southwestern Kopet Dag in Turkmenistan. Only a few collections of this restricted endemic exist, and these are all to be found in herbaria of the former Soviet Union. Its status as a distinct taxon has never really been questioned, but only because so few specimens exist for comparison. Mizgireva (1955) worked for 12 years on the detailed anatomy and morphology of this species and her revision remains the best source for data on characters and their variation.

### *The position of Mandragora within the Solanaceae*

More than 200 years after the original outline by Jussieu (1789), the higher level classification of Solanaceae is far from being settled, and the placement of *Mandragora* in the various proposed classifications is just as controversial. In the following review, the most widely followed classifications of the Solanaceae are presented together with the positions of *Mandragora* and the other genera used in our cladistic analysis: *Anisodus* Link, *Atropa* L., *Lycium* L. and *Nicotiana* L.

In his artificial sexual system, Linnaeus (1753) placed *Mandragora* within his group Pentandria Monogyna, together with *Atropa*, *Lycium* and *Nicotiana*. Jussieu (1789) defined the 'order' Solaneae with *Mandragora* in group II (fructus baccatus) alongside *Atropa* and *Lycium*. *Nicotiana* on the other hand was placed in group I (fructus capsularis). In the nineteenth century, classifications became more elaborate and tribes and subtribes were established in order to approximate a more 'natural' classification. In Table 2, the three most widely adopted classifications of the Solanaceae in this period (Dunal, 1852; Bentham, 1876; Wettstein, 1895) are presented together with the more recent one of Baehni (1946).

The last few decades have seen the analysis of new types of data, such as DNA sequences (Olmstead & Sweere, 1994) and secondary plant metabolites (Tétényi, 1987), as well as application of cladistic methodology to morphological data (Hoare & Knapp, 1997). This has led to new hypotheses concerning relationships within the Solanaceae, as well as the placement of *Mandragora*. However, opinion still differs widely on whether *Mandragora* should be placed within the tribe Hyoscyameae (Hoare & Knapp, 1997; = *Atropeae sensu* Tétényi, 1987) or in an isolated, basal monogeneric tribe Mandragoreae (Olmstead & Sweere, 1994; Hunziker, 1995; Olmstead et al., in press).

## MATERIALS AND METHODS

### Material examined

This revision is based exclusively on herbarium specimens. The material examined includes the *Mandragora* specimens in the herbaria of The Natural History Museum of London (BM) and Kew (K) together with specimens borrowed from the following herbaria:

**Table 1** Post-Linnaean classifications of the increasingly subdivided Mediterranean taxa of *Mandragora*.

Classification type	Vernal species	Autumnal species
1 VERNAL, 1 AUTUMNAL TAXON Sprengel (1825)	<i>M. vernalis</i> Bertol.	<i>M. autumnalis</i> Bertol.
1 VERNAL, 2 AUTUMNAL TAXA Bertoloni (1835), Dunal (1852)	<i>M. vernalis</i> Bertol.	<i>M. officinarum</i> L. <i>M. microcarpa</i> Bertol.
2 VERNAL, 2 AUTUMNAL TAXA Heldreich (1886)	<i>M. vernalis</i> Bertol. <i>M. haussknechtii</i> Heldr.	<i>M. autumnalis</i> Spreng. <i>M. microcarpa</i> Bertol.
3 VERNAL, 2 AUTUMNAL TAXA Vierhapper (1915)	<i>M. mas</i> Garsault <i>M. hispanica</i> Vierh. <i>M. haussknechtii</i> Heldr.	<i>M. autumnalis</i> Bertol. <i>M. foemina</i> Garsault

**Table 2** Tribal classification of the Solanaceae and the position of *Mandragora* and the outgroup genera *Anisodus*, *Atropa*, *Lycium* and *Nicotiana*.

Author	Classification	Genera of this study
Dunal (1852)	Nolaneae	Nolanineae Grabowskieae Triguereae Solanaceae
	Solaneae	
		Solanineae Atropineae Lycineae
		Datureae Hyoscyameae Nicotianeae Retzieae Fabianeae Metternichieae Cestreae
		<i>Mandragora</i> <i>Atropa</i> <i>Lycium</i> <i>Anisodus (Scopolia)</i> <i>Nicotiana</i>
Bentham (1876)	Solaneae	Lyciinae
	Atropeae	
	Hyoscyameae Cestrineae Salpiglossidae	
		Hyoscyaminae Solaninae Mandragorinae
	Daturae Cestreae	Cestrinae Goetzeinae Nicotianinae
	Salpiglossidae	
		<i>Mandragora</i> <i>Atropa</i> <i>Lycium</i> <i>Anisodus (Scopolia)</i> <i>Nicotiana</i>
Wettstein (1895)	Nicandreae	Lyciinae
	Solaneae	
	Daturae Cestreae	Cestrinae Goetzeinae Nicotianinae
	Salpiglossidae	
		<i>Atropa</i> <i>Lycium</i> <i>Anisodus (Scopolia)</i> <i>Mandragora</i> <i>Nicotiana</i>
Baehni (1946)	Solaneae	Solaninae Sarachinae Margaranthinae Physalidinae Iochrominae Goetzeinae Discopodiinae Atropinae
	Atropeae	Markeinae Hyoscyaminae Parabouchetiinae
	Anthocercideae Nicotianeae	Nicotianinae Daturinae Nicandrinae
	Salpiglossidae	
		<i>Mandragora</i> <i>Atropa</i> <i>Lycium</i> <i>Anisodus (Scopolia)</i> <i>Nicotiana</i>

Berkeley (UC, JEPS), Edinburgh (E), Kunming (KUN), Palermo (PAL) and Reading (RNG). The collections of the Muséum National d'Histoire Naturelle in Paris (P) were examined on site during a research visit. Regrettably it was not possible to obtain any specimens, including the types, of *Mandragora turcomanica* and *M. tibetica* from St. Petersburg (LE) or *M. chinghaiensis* from Xining (HNWP).

Material with the same collection number or specimens collected at the same locality and at the same date were unified and treated as one sample. Unlocalized material or specimens with illegible, doubtful or very imprecise collection locality and collector data were excluded, cultivated material being the exception. Only collections with precise locality data are listed in the taxonomic account of the species. A complete listing of the specimens examined can be found in the Exsiccatae.

### Taxonomic concepts

The adopted taxonomic methodology in this study of herbarium material is necessarily largely pattern-oriented. If process-based terms like 'population' or 'hybrid' are used, these properties are only informally applied, i.e. inferred rather than rigidly defined, let alone experimentally circumscribed.

The adopted species concept is operational, i.e. the ability to distinguish between sets of specimens serves as the criterion for the delimitation of the terminal taxa (species). Cladistic analysis results in an estimate of these relationship between the species and the delimitation of higher level taxa, i.e. monophyletic groups and their hierarchical relationships. The requirement for a species description is thus at least one distinguishing qualitative, or discontinuous quantitative, diagnostic character state (monothetic species) or a unique set of character states (polythetic species) (cf. Nelson &

Platnick, 1981; Nixon & Wheeler, 1990). Morphological and phenological variation plus ecological and geographical information are the data that were collected from herbarium specimens and their labels respectively.

## Morphometrics

### Specimen sampling

The inherent weakness of the traditional herbarium record of a taxon for taxonomic studies is well known (Du Rietz, 1930; Anderson & Turrill, 1935; Anderson, 1941). For species that are well represented in herbaria, one can obtain a more or less accurate record of the general range of variation. Seldom or never, however, is it possible to calculate frequencies of the different variants and the resolution of the classification is limited by the lack of a random sample.

Plant variation also occurs on different hierarchical levels (cf. Bateman, 1989), which can become confused and overlap. In *Mandragora* the confounding of within-group and between-group variation is most pronounced in the Sino-Himalayan complex, due to the secondary growth of the plants during the late flowering and the fruiting period (ontogenetic variation, see Fig. 9, also Hoare & Knapp, 1997: fig. 5d). Combining all samples to a pooled matrix easily leads to a confusion of the two sources of variation which can seriously compromise interpretation of many applications of morphometric analyses (Gibson et al., 1984). Avoiding within-group variation, for example by calculating the mean or only considering the largest or smallest example of a particular character is not a solution, but merely reduces the total amount of variation encountered in a taxon, leading ultimately to a simplistic taxon delimitation. In the taxonomic process, characters and their variability necessarily have priority over all other considerations since taxa are attributed to characters—not the other way around (characters all attributed to individuals). It follows that the basal unit of investigation, the specimen, must be evaluated in respect to its variability. Therefore, maximal as well as minimal values of the flowering part measurements of each specimen were assessed, rather than solely mean or maximal values.

### Character sampling

A genus with a long taxonomic history is unlikely to yield any 'new' gross morphological characters which distinguish species. This is especially true when working with inadequate herbarium material (i.e. incomplete with much missing data and/or very old and often in poor condition). The emphasis in this study was thus much more on evaluating the traditional and obvious characters in respect to their ability consistently to delimit proposed taxa. The analysis was therefore carried out using the following data.

**GEOGRAPHY.** The entire distributional range of *Mandragora* was divided into 20 geographic areas. These are (1) Cultivated specimens, typically from botanic gardens north of the Alps, (2) North Africa, (3) Iberia, (4) northern Italy and Dalmatia, (5) peninsular Italy with Sardinia and Sicily, (6) mainland Greece, (7) Aegean islands, (8) Asia Minor, (9) Cyprus, (10) Levant, (11) Kopet Dag, (12) Nepal, (13) Sikkim, (14) Bhutan, (15) Arunachal Pradesh (Assam), (16) north Myanmar (Burma), (17) Yunnan, (18) Sichuan, (19) Qinghai and (20) Xizang.

**PHENOLOGY.** Flowering and fruiting dates were recorded, resulting in the cumulative reproductive period.

**MORPHOLOGY.** Corolla length, calyx length, fruit size, fruiting calyx length, leaf length, leaf length/width ratio. The corolla colour

of herbarium material is not reliably determinable and was thus only recorded if it was stated on the labels. The shape of the berry (globose or ovoid) was excluded as a character since it is not accessible through pressed herbarium material and is only rarely stated on the labels. Berry shape in the Solanaceae is quite variable and this variation is occasionally a developmental sequence (Bohs, 1994).

### Data analysis

Univariate and multivariate analyses were applied as a descriptive, explorative tool to study the joint relationships of the morphological, phenological and geographical variables of the specimens at hand. As mentioned above, since the examined specimens are not a random sample, the result of inferential data analysis with significance testing would be invalid. A cluster analysis or a cladistic analysis of the data at population level, on the other hand, was rejected on the grounds that these methods assume hierarchical relationships, an assumption that is not justified. Phenotypic characters may be distributed clinally or in a reticulate manner, but are unlikely to be strictly hierarchical (Crisp & Weston, 1993). If hierarchical structure exists, it would suggest that the populations have already undergone speciation and have to be treated as terminal taxa in the phylogenetic analysis. The explorative data analysis was performed on SYSTAT for the Macintosh Version 5.2 (Wilkinson, 1992).

**UNIVARIATE ANALYSES.** Phenological data are circular (Fisher, 1993). The reproductive period was thus analysed in a polar coordinate system. In order to dampen peak values, which might merely reflect a particularly high collecting effort, the collection proportion of each month was converted to its logarithm.

**MULTIVARIATE ANALYSES.** Ordination techniques reduce a data matrix of distances (similarities) among the samples to one or a few dimensions. These types of techniques seem to be most appropriate under a nonhierarchical model of infraspecific variation. Principal component analysis (PCA) is the method most commonly applied in multivariate systematics studies (James & McCulloch, 1990). It aims to show the eventual existence of distinguishable groups with discontinuous variation without *a priori* postulates of groups such as populations. Since data sets with missing data cannot be processed using PCA, only the most commonly represented characters of the herbarium specimens (see above and Table 3) were analysed. Fortunately, these are also the characters that are most commonly applied to differentiate between the traditionally recognized Mediterranean taxa. In contrast to many other analyses of specimen-based data, within-collection variation was accounted for by recording and analysing both minimal and maximal values of the flowering part lengths. Only fully developed and open flowers were considered and measured. The length/width ratio of the leaves was not included in the PCA analysis on the grounds that ratios are often not linearly related to the length measurements (Miles & Ricklefs, 1984). All the variables have been standardized (normalized) by the standard

**Table 3** Variables used in the principal component analysis of the Mediterranean complex.

Length measurements	Variable 1	Corolla length max.	mm
	Variable 2	Corolla length min.	mm
	Variable 3	Calyx length max.	mm
	Variable 4	Calyx length min.	mm
	Variable 5	Leaf length max.	cm
Phenology	Variable 6	Flowering time	month

deviation to obtain a variance of one and a mean of zero by performing the analysis on a correlation matrix.

Due to a lack of available specimens from Asia of the taxa *Mandragora caulescens* subsp. *brevicalyx*, *M. chinghaiensis*, *M. tibetica* and *M. turcomanica*, the discussion of variability among these taxa (and its implications on their delimitation) has to remain qualitative.

## Cladistics

Cladistic analysis is a parsimony-based search for hierarchical arrangements or patterns of terminal units (in most cases species). The premises are accordingly that there is a hierarchical structure of the taxa and therefore of the characters used to define them, and that the level of homoplasy in the chosen characters is low enough not to infer convergent groups. As a strictly numerical procedure, there is no need for additional models or assumptions relating to biological processes, such as reproduction or descent (Davis & Nixon, 1992). The resulting cladogram therefore represents a synapomorphy scheme, merely suggesting closeness of relationship due to recency of shared common ancestry. It might be congruent with the actual phylogenetic tree, featuring the ancestors and descendants; however, there are many possible phylogenetic trees compatible with one cladogram (Eldredge, 1979). The cladogram was rooted by means of outgroup comparison.

A phylogeny of the tribe Hyoscyameae based mainly on morphological characters was recently published by Hoare & Knapp (1997) suggesting that *Mandragora*, as traditionally defined, is monophyletic. To test the monophyly of *Mandragora* as a whole, we included in this analysis material of species representing two other genera of the Hyoscyameae, *Anisodus luridus* Link and *Atropa belladonna* (see Table 4). The three recognized terminal taxa of *Mandragora* represent the ingroup (*M. caulescens*, *M. officinarum*,

**Table 4** Taxa used in the cladistic analysis.

<i>Nicotiana glauca</i> Graham
<i>Lycium chinense</i> Mill.
<i>Anisodus luridus</i> Link
<i>Atropa belladonna</i> L.
<i>Mandragora officinarum</i> L.
<i>M. turcomanica</i> Mizg.
<i>M. caulescens</i> C.B. Clarke

**Table 5** Character set used in the cladistic analysis.

<b>Habit</b>
1. Woody plant (shrub or tree) 0; herb 1
<b>Root</b>
2. Tap-root: enlarged tap-root absent 0; present 1
<b>Stem</b>
3. Axis: condensed 0; first condensed, later elongated 1; elongated 2
<b>Leaves</b>
4. At anthesis: leaves clustered in a rosette 0; leaves alternate 1
<b>Inflorescence</b>
5. Type: numerous flowers in panicle 0; 1(–3) axillary flowers 1
<b>Corolla</b>
6. Shape: tubular-infundibuliform 0; campanulate-urceolate 1
<b>Fruit</b>
7. Type: berry 0; capsule 16
<b>Fruiting calyx</b>
8. Not enlarged in fruit 0; markedly enlarged in fruit 1
9. Without prominent ribs 0; with prominent ribs 1
<b>Seeds</b>
10. Embryo: not curved 0; curved circularly or in a spiral 1
11. Testal cells deep 0; shallow 1

**Table 6** Data matrix used in the HENNIG86 analysis

Taxon	Character			
	12345	67890	1	1
<i>Nicotiana glauca</i>	00200	01000	0	
<i>Lycium chinense</i>	00200	00001	0	
<i>Anisodus luridus</i>	11201	11111	0	
<i>Atropa belladonna</i>	10201	10001	1	
<i>Mandragora officinarum</i>	11011	10001	0	
<i>M. turcomanica</i>	11011	10101	?	
<i>M. caulescens</i>	11111	10111	1	

*M. turcomanica*). The outgroup, *Nicotiana glauca* Graham, was chosen based upon previous cladistic analyses of chloroplast DNA data sets (Olmstead & Palmer, 1992; Olmstead & Sweere, 1994; Olmstead et al., in press). *Lycium chinense* Mill. was included as an additional taxon (but not defined as an outgroup, see Tables 2 and 4).

Although acknowledging that there is no such thing as an *a priori* 'perfect cladistic character' (Thiele, 1993), the suggestion of Chappill (1989) and Stevens (1991) not to include purely morphometric, quantitative data in the cladistic analysis was followed. This limitation is feasible in view of the minimal size of the ingroup and the already established analysis of an extensive character set including quantitative character states (Hoare & Knapp, 1997). The characters used in the present work (Table 5) and their states are largely self-explanatory. The data matrix used in the analysis is presented in Table 6.

Cladistic analyses were undertaken with HENNIG86 (Farris, 1988) using the *ie* option (implicit enumeration) with all characters unordered, thus avoiding any character state change assumptions. The generated cladogram statistics include length (L), the number of character state changes on the tree, the ensemble consistency index (CI) which provides a measure of character fit on the cladogram (amount of homoplasy), and the ensemble retention index (RI) which expresses the fraction of similarities on the cladogram interpreted as synapomorphy (Farris, 1989). Both of these indices have an optimal value of 1.

## RESULTS AND DISCUSSION

### Species delimitation using morphometric analyses

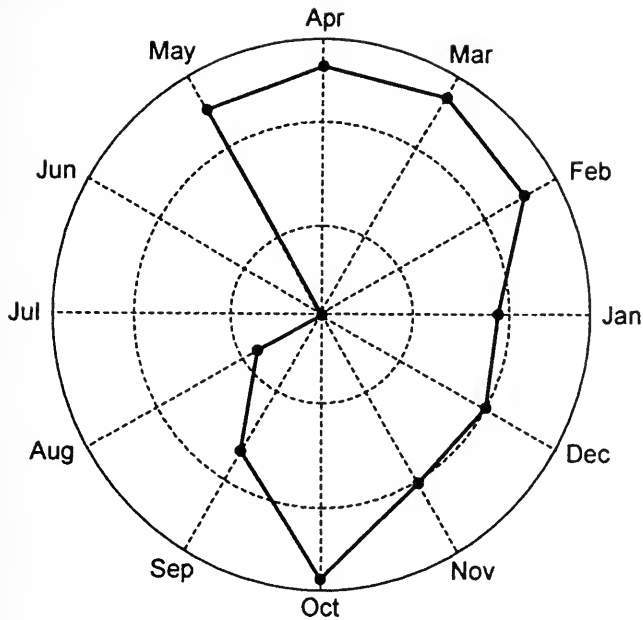
For the Mediterranean taxa a number of specific hypotheses were tested using the above described statistical analyses.

#### *Univariate analysis of reproductive period.—Are there two distinct vernal and autumnal taxa?*

By adopting the two species *Mandragora vernalis* and *M. autumnalis*, Sprengel (1825) argued against Linnaeus's unified *Mandragora officinarum* concept. Even in later, more elaborate classifications the division into these two major groups remained important (Table 1) since it was obvious that two groups with widely differing flowering periods would hardly be able to interbreed due to the seasonal isolation. So, is there evidence in the compiled Mediterranean data set that there are two phenologically distinct species? Figure 1 shows the distribution of the collecting dates (in flower or in fruit) as an indicator of the reproductive period.

It is evident that there is actually only one, very extensive period of reproductive activity from autumn to spring. In fact only during the hottest summer months does the cycle break. If conditions are





**Fig. 1** Relative distribution of the vegetative period of the Mediterranean complex (*Mandragora officinarum*) in the course of the year (logarithmized monthly fractions: for analysis see text).

favourable, the same individual can flower twice a year, in autumn and then again in spring, as can be seen from annotated herbarium material, especially from cultivated material in botanical gardens. The key factor is probably sufficient rainfall; for instance, sudden and widespread flowering after exceptionally heavy autumn rains was recorded from Tunisia (label data from Tomkinson 72). A more detailed discussion pertaining to the influence of the climate and the summer dormancy is given in the section on ecological biogeography below.

*Multivariate analysis of morphometric characters.* – Are there distinct clusters within the Mediterranean mandrakes that are recognizable from gross morphology?

The different eigenvector values of the PCA (Table 8) indicate the relative contribution of the variables. The first three axes (see Table 7) explain 92.2% of the variation if length measurements are considered only (Fig. 2a), and 87.1% of the variation if the analysis was run including the phenological variable of flowering time (Fig. 2b). In both cases it is obvious that no clear-cut clusters can be distinguished. Cryptic species may exist within the Mediterranean region but are likely to be revealed only if extensive, field-based studies over the entire range, as well as transplant experiments, are undertaken (Clausen et al., 1940). The information currently available does not justify recognition of more than a single species of Mediterranean mandrake.

Other characters traditionally applied in keys but not analysed quantitatively here include the following:

**Corolla colour:** Hawkes (1972b) considered the elaborate splitting of the vernal and autumnal groups as unjustified and recognized only the white-flowered vernal plants from northern Italy and Dalmatia as distinct from the remaining Mediterranean group. Restricted to only a small part of the total Mediterranean range, the white-flowered plant has often been considered as the most distinctive group (Heldreich, 1886; Vierhapper, 1915). The diagnostic value of this character which has been extensively used in past and current

**Table 7** Principal components (PC) of the Mediterranean complex. A: Length measurements only. B: Length measurements and flowering period combined.

Component	Eigenvalue	% of variance explained
A PC 1	3.248	64.97
PC 2	0.977	19.54
PC 3	0.383	7.66
B PC 1	3.328	55.47
PC 2	1.410	23.50
PC 3	0.490	8.17

**Table 8** Eigenvectors of the three most important axes (component loadings).

Variable	PC 1	PC 2	PC 3
A 1 Corolla length max.	0.885	0.023	0.131
2 Corolla length min.	0.875	0.011	0.435
3 Calyx length max.	0.898	0.114	-0.391
4 Calyx length min.	0.924	0.065	-0.147
5 Leaf length max.	-0.197	0.979	0.047
B 1 Corolla length max.	0.882	0.067	-0.160
2 Corolla length min.	0.851	0.189	0.042
3 Calyx length max.	0.897	0.123	0.066
4 Calyx length min.	0.905	0.156	0.175
5 Leaf length max.	-0.181	0.865	-0.453
6 Flowering time	-0.413	0.763	0.471

keys is minimal, however, if one considers that flowers are very variable in colour even within individuals (Jury et al. 12238 from Morocco, Jury & Jury 13111 from Spain).

**Fruiting calyx length:** The relative length of the accrescent fruiting calyx to the berry (longer: *M. autumnalis* or shorter: *M. officinarum*) has also been proposed as a diagnostic character (Hawkes, 1972b). Again, it seems that within-group variation is just as high, considering for instance a specimen housed in P of a cultivated plant which features two berries that are clearly shorter than the calyx, but three others which are longer.

**Leaf shape:** This is perhaps the most variable character of all. One can get at least an idea of the variability if the length to width ratios of mature leaves are compared. The variability within an individual ranges from 1.7:1–4:1 (in Reverchon s.n.) to 4.6:1–10.5:1 (in Welwitsch 159). The total variability within the whole set of examined specimens was found to be between 1.5:1–10.5:1.

Any distinction between *Mandragora officinarum* and *M. autumnalis* or any other splitting of the Mediterranean *Mandragora* on morphological or phenological grounds would be intentionally giving formal status to divergent ends of clines. Thus overlapping intermediates would be difficult if not impossible to assign to either of the taxa in any other way than arbitrarily. Extensive overlap and putative hybrids must be considered if aiming at expressing the whole range of variability. This confirms Meikle's (1985) doubts concerning the validity of the different proposed Mediterranean species. Although certain plants of particular populations are quite different in appearance from some plants of other populations, when the total pattern of variation over the entire range is considered, no diagnosable taxa within the Mediterranean complex of *Mandragora* are discernable. Further morphological support for the unification of the Mediterranean *Mandragora* comes from the anatomy of the tap roots which has been shown to be identical in vernal and autumnal taxa and in their chemical composition which is also similar (Jackson & Berry, 1979).

For *Mandragora turcomanica*, a statistically valid morphometric analysis is not feasible with the available literature data only. The

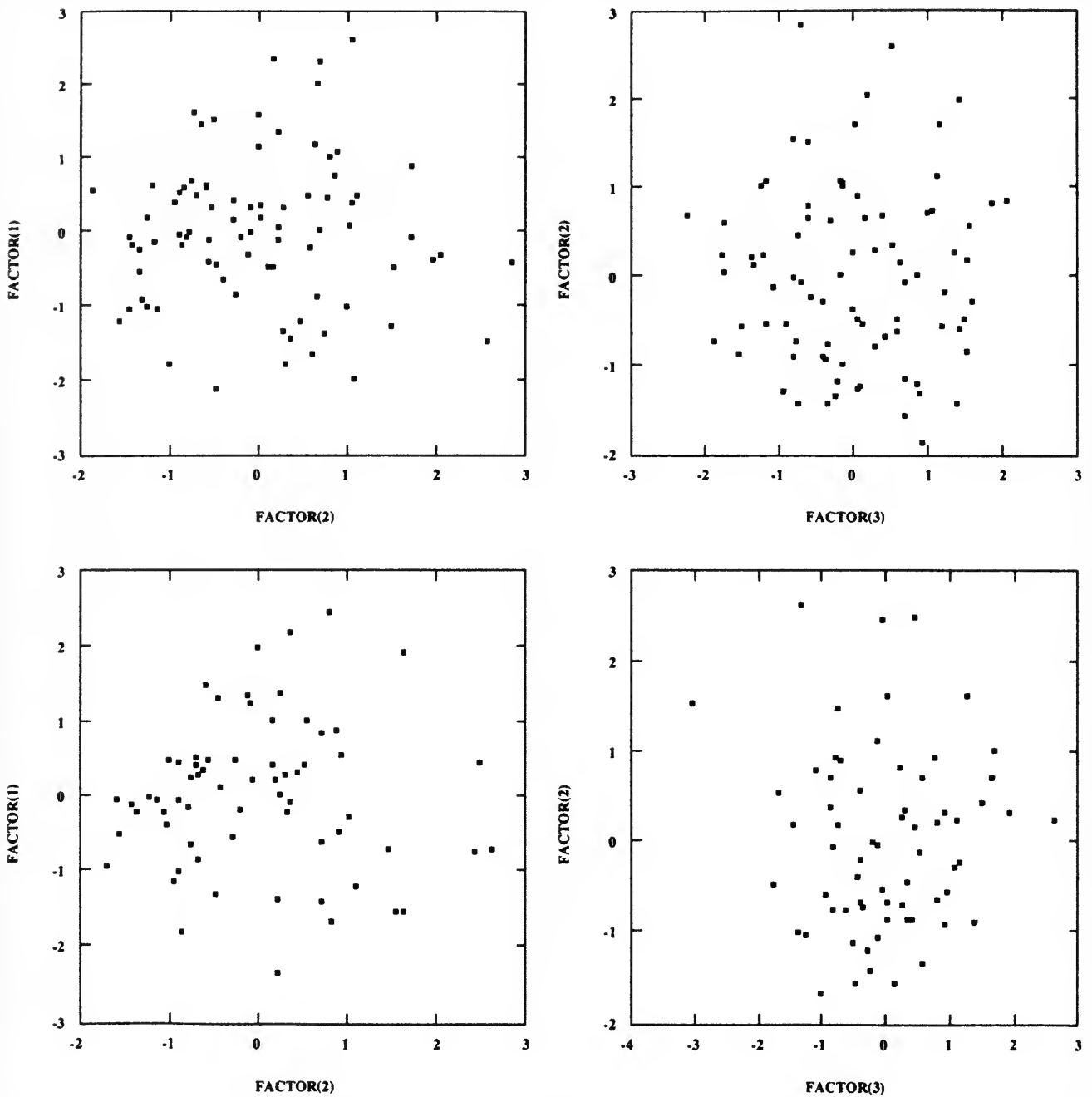


Fig. 2 Principal component analysis of the Mediterranean complex (*Mandragora officinarum*). Top pair: a. Bottom pair b. Left: PC 1,2. Right: PC 2,3.

range of the Turkmenian plants is so small that variability at population level is considered equivalent with the variability over the whole range. Mizgireva (1955) meticulously documented teratogenic forms of flowers and fruits of *M. turcomanica*, but did not cite field collected vouchers for these forms. She also documented huge variability in the shape and size of tap roots, and described the growth of the plant in detail, from seed germination to fruiting. *Mandragora turcomanica* is accepted as a distinct species on the grounds of the evidence given in Mizgireva (1942, 1955, 1978) and Lincevskij (1955). The whole plant is much larger than *M. officinarum*. The lower leaves ( $\pm 90 \times 60$  cm) are especially large resulting in a rosette with a diameter of 150–180 cm. *Mandragora turcomanica* blooms in both the autumn and the spring (Mizgireva,

1955, see taxonomic treatment), with different individuals in the population exhibiting one or the other flowering time. Geographically the species is isolated, occurring only in a narrowly restricted range, and within that range it is only found in localized regions (Mizgireva, 1955). It is also widely disjunct, being some 1500 km from the closest Mediterranean *Mandragora* population in the Near East and about 2500 km from the nearest Himalayan population in western Nepal.

In common with the Mediterranean mandrake, the Himalayan plants make up a complex with considerable variation in size, shape and colour of the flowers and leaves. The following questions are addressed:

*Is the recognition of the four infraspecific taxa sensu Grierson & Long within Mandragora caulescens sensible?*

After checking herbarium material from almost the entire range of *Mandragora caulescens* (north-western Sichuan and southern Qinghai excluded), Grierson & Long (1978) were well aware of the extreme variability of the morphological characters they used to describe their four subspecies. The characters used were corolla colour, calyx and corolla lengths and overall plant size. As with *Mandragora officinarum*, flower colour, according to observations of the fresh material given on herbarium labels, is variable within individuals as well as within local populations (e.g. Alden et al. 1185: 'flowers yellow to purplish-brown', Long et al. 266: 'corolla yellow, purple at base, inside and out', and Polunin 631: 'petals yellow with purple veins'). Colours probably merely reflect to what extent the yellow pigments are masked by purple ones. Grierson & Long (1978) were unable to find any diagnostic morphometric discontinuities. Their proposed classification is based on the rule that due to its type status, the holotype of *M. caulescens*, collected in Sikkim and representing an intermediate between the extremes of the 'typical' small, yellow-flowered plants and the large, purple-flowered ones, must retain the name *M. caulescens* (and must thus be given the subspecific epithet *caulescens*). They therefore split the complex not into two but into three subspecies representing the two extreme forms (subsp. *flavida* and subsp. *purpurascens*) and the intermediates (subsp. *caulescens*), and additionally described a fourth subspecies with a shorter calyx (subsp. *brevicalyx*) based on only two collections from Xizang. As a consequence, their classification is based on non-diagnostic, largely overlapping characters, rendering *M. caulescens* subsp. *caulescens* as a 'basket' taxon for any intermediates. Indeed, it might be hypothesized that there are at least two different species present within this complex with frequent

introgression of the sympatric populations. However, the many putative 'hybrids' linking them and resulting in an extensive overlap of their features make them unsuitable as terminal taxa for the cladistic analysis. Furthermore, a restrictive taxonomic concept as described earlier does not allow for the recognition of infraspecific taxa if their characters and their ranges are extensively overlapping.

*Are Mandragora tibetica and M. chinghaiensis distinct species or are they both conspecific with M. caulescens?*

As in the case of the Turkmenian mandrake, the unavailability of the types and a reasonable number of specimens renders the data somewhat meagre, so the original descriptions by Grubov (1970) for *Mandragora tibetica* and by Kuang & Lu (1978) for *M. chinghaiensis* must provide much of the necessary information. These descriptions, together with their accompanying keys, which distinguish the newly described species from *M. caulescens*, recognize the small, yellow-flowered plants as distinct from the larger, purple-flowered ones. Both new taxa are therefore covered by the range of variability given in Grierson & Long's (1978) subdivision of *M. caulescens* into four subspecies, which are defined only by overlapping differential characters and, as such, are not acceptable as distinct taxa. Indeed, a specimen in P. Polunin et al. 878, is annotated as *M. chinghaiensis* by Lu An-ming and is also an isotype of *M. caulescens* subsp. *flavida*. Some doubts must remain concerning *M. tibetica* and *M. caulescens* subsp. *brevicalyx* that together may represent a single distinct taxon with a very short calyx. An unusual specimen from western China (Wilson 4195 (K), no precise locality given) bears a single flower with a conspicuously narrow corolla. A note by Grierson and Long on the herbarium sheet suggests that they considered this specimen not conspecific or even congeneric with *M. caulescens*. Without further material, however, proposing a new taxon would be just as

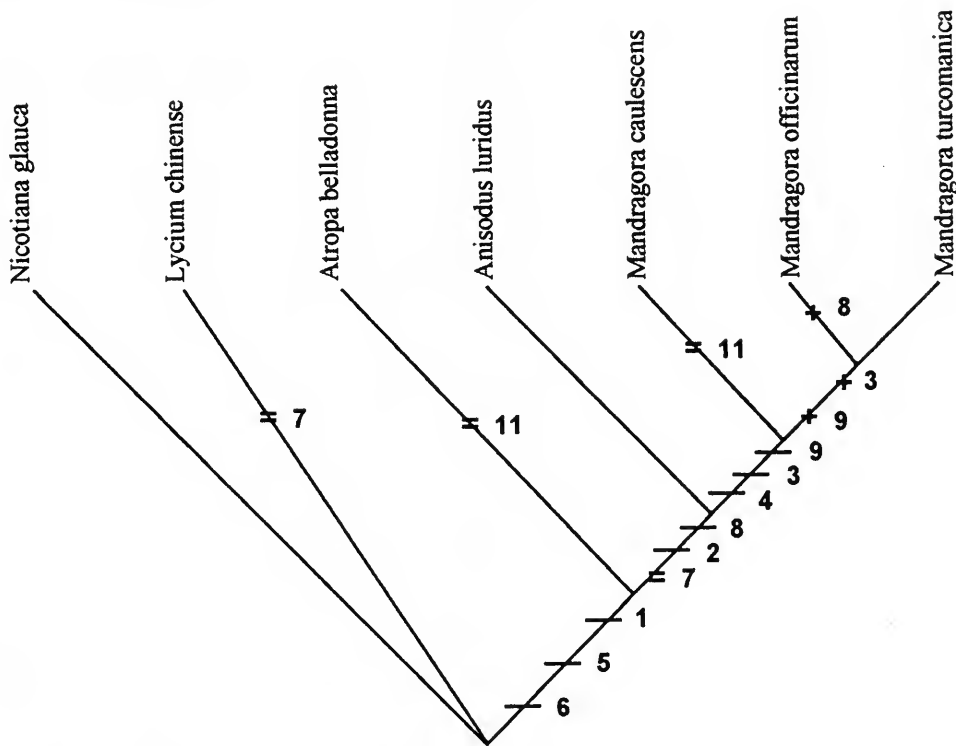


Fig. 3 The single most parsimonious cladogram from the HENNIG86 analysis. The characters are discussed in the text, and characters states are shown in Table 5. For characters marked on the branches of the cladogram: single lines indicate unambiguous synapomorphies, parallel lines parallelisms and crosses reversals (homoplasy).

speculative as disregarding the flower as a mere artefact of preparation. The synonymy presented in the taxonomic treatment here, especially in respect to the undercollected plants from central and northeastern Xizang, is therefore provisional and subject to confirmation once more material of both flowering and fruiting plants becomes available. Only then will it be possible to judge whether or not there exist distinct taxa not included within the range of variation of *M. caulescens*.

*Mandragora* is a genus with pronounced variability, both within and between individuals and therefore necessarily within the proposed polymorphic species. Furthermore, discordant variation in the applied gross morphological characters impedes a workable subdivision based on a whole set of differential characters, rather than just one (apparently non-existent) diagnostic character.

## Phylogeny

The cladistic analysis resulted in a single most parsimonious cladogram of length = 16, CI = 75 and RI = 73 (Fig. 3). The genus *Mandragora* defined in the traditional sense is monophyletic in our analysis: the species share synapomorphies in characters 3 (a condensed axis), 4 (leaves clustered in a rosette) and 9 (fruiting calyx with prominent ribs). If the inaperturate pollen known from *M. caulescens* and *M. officinarum* (see Hoare & Knapp, 1997 for details) is also found in *M. turcomanica*, this too would be a synapomorphy of the genus.

*Mandragora officinarum* and *M. turcomanica* are more closely related to each other than to *M. caulescens*. They share reversals in characters 3 (a condensed axis) and 9 (a fruiting calyx without prominent ribs), but no unambiguous synapomorphies. The peculiar life-cycle, i.e. the mode of development of the leaves and flowers, is evidence for a shared common ancestry of the Mediterranean-Turkmenian clade. Mizgireva (1955) also suggested this in her revision of the Turkmenian species. In order to determine more clearly the relationships among the three species of *Mandragora*, a different, probably field-based set of characters is necessary. Here, however, we are concerned more with the delimitation of terminal taxa, especially among the Mediterranean plants, and whether or not the genus as currently defined is monophyletic.

A comparison between alternative hypotheses concerning the position of *Mandragora* based on morphological, chemical and

molecular (chloroplast DNA) characters is given in Figure 4. The most pronounced discrepancy concerning the position of *Mandragora* is that the molecular data set (Fig. 4a) deviates from the morphological (Fig. 4c) and chemical ones (Fig. 4b) by attributing this genus a very independent position due to extremely divergent and autapomorphic cpDNA sequences. This is reflected in the proposal of a monogeneric tribe Mandragoreae (Olmstead et al., in press). Morphological and chemical evidence, on the other hand, suggests a placement within the tribe Hyoscyameae (Hoare & Knapp, 1997; = *Atropeae sensu* Tétényi, 1987). The present study is far too limited in its scope to allow any conclusions concerning higher level classification within the Solanaceae. However, it is clear that our limited data set supports the inclusion of *Mandragora* within the Hyoscyameae (synapomorphies in characters 1, 5 and 6) but, as mentioned above, a much larger and more field-based data set will be needed to address this problem. *Mandragora* is an anomalous genus in the family, both morphologically and in terms of molecules, but this should not prevent us from eventually identifying its true affinities and relatives given adequate data.

## Biogeography

The biogeography of an exclusively Laurasian genus within the Solanaceae is of interest because the family is largely Gondwanan in distribution. It is useful to approach biogeography from two different angles. Ecological biogeography considers a short temporal scale in evaluating ecological factors relevant for present-day distributions of taxa. Historical biogeography, on the other hand, is concerned with the change of distributions and the potential causes thereof on a long temporal scale. We attempt here to summarize some of the most important data with respect to the geographical distribution of *Mandragora*, both now and in the past, and pinpoint major gaps in knowledge.

### Ecological biogeography

The present approximate distribution of the genus is given in Figure 5. Apart from the herbarium material examined, the sources presented in Table 9 were used. Most comprehensive are the distribution data in Heldreich (1886) and Vierhapper (1915). *Mandragora* does not appear to penetrate into the Arabian Peninsula, being absent

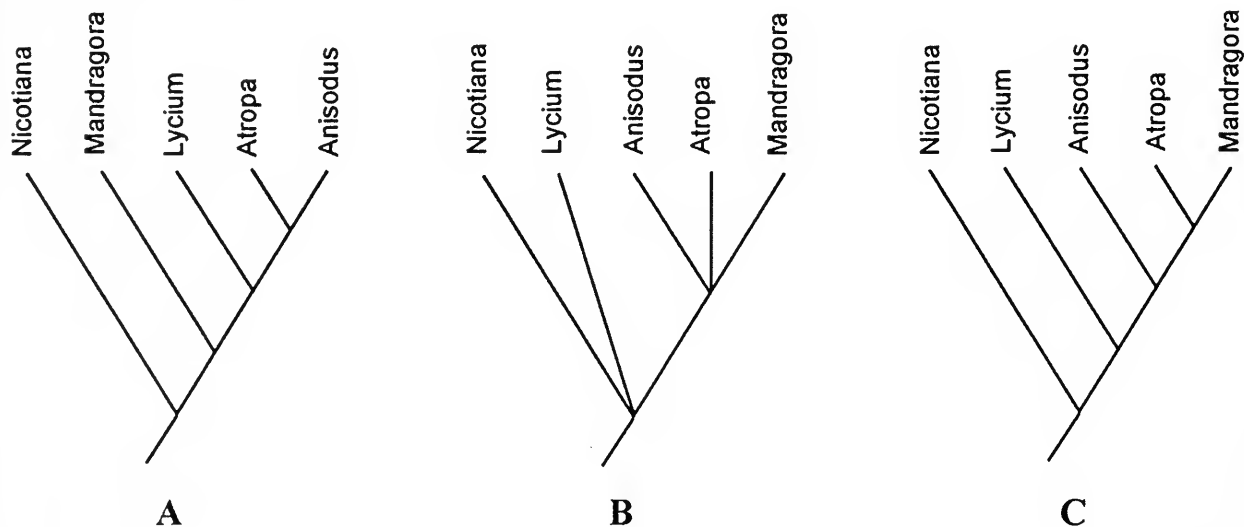


Fig. 4 Differing hypotheses of the relationships of *Mandragora* within the Solanaceae. a: Olmstead et al., in press, b: Tétényi, 1987, c: Hoare & Knapp, 1997.

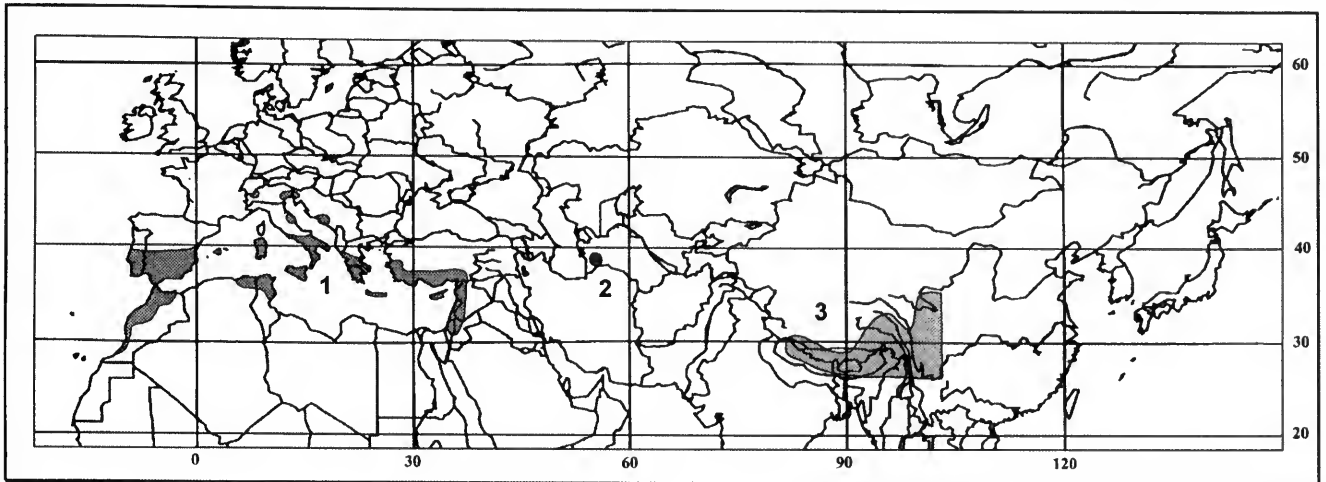


Fig. 5 Distribution of the genus *Mandragora*. 1) *M. officinarum*, 2) *M. turcomanica*, and 3) *M. caulescens*.

even in the most northern parts of Saudi Arabia (Migahid, 1989) as well as from Mesopotamia (Rechinger, 1964; Mouterde, 1979). The genus was naturalized in Malta in the nineteenth century but is now presumably extinct there (Borg, 1927; Maugini, 1959). *Mandragora* does not appear in works covering France and Corsica (Fournier, 1990), Albania (Demiri, 1983), Egypt (Täckholm, 1974; Boulos, 1995) or Libya (Siddiqi, 1978) and is presumed absent from these areas. Likewise, the genus is absent from the Macaronesian archipelagos of the Canaries, Madeira and the Azores (not recorded either by Hansen & Sunding, 1993; or Press & Short, 1994).

*Mandragora turcomanica* is found only in the Kopet Dag range of southern Turkmenistan. It has not yet been reported from the Iranian part of these mountains (Rechinger, 1972). In eastern Asia, *Mandragora* (*M. caulescens*) occurs in the central and eastern Himalaya

and southwestern China, but there are no records from the western extensions of these mountain ranges (Karakorum, Pamir, Hindu Kush and Tien Shan).

Apart from historical factors, dealt with below, the principal factor determining the geographical distribution of taxa on a large scale is typically climate. Although one might disagree on the relative importance of means and extreme values of various climatic variables, the prime importance of climate in general has long been accepted (Cain, 1944).

A convenient way of depicting and comparing different climates is by means of standardized diagrams. The purpose of the so-called ecological climate-diagrams is to portray the climate of a locality in a readily comparable way and visually to present the most important climatic factors affecting the growth of plants (Walter et al., 1975). By choosing a scale at which 10°C correspond to 20 mm precipitation, a relatively wet (dark) and relatively dry (light) season can be identified on the diagrams (Fig. 6). These climate diagrams make it evident that the range of *Mandragora* comprises not only quantitatively different climates but qualitatively different climate types. The amount and especially the main season of rainfall is particularly significant.

The Mediterranean climate is characterized by mild, rainy winters and hot, dry summers. Although the total amount of rainfall for other locations for *Mandragora officinarum* may differ somewhat from that presented here (Iraklio, on the northern coast of Crete, Fig. 6), the general aspect of a winter rainfall regime remains the same all over the Mediterranean basin, even extending towards Afghanistan and the Hindu Kush. The typical vegetation consists of adapted sclerophyllous vegetation, analogous to that found in the same climate type in California, Chile, the Cape region of South Africa and southwestern Australia.

The Kopet Dag is a Transcasian mountain range surrounded by the Irano-Turanian desert. The climate there represents a continental, dry version of the Mediterranean type with much lower rainfall (Fig. 6: Kizil-Arvat) and an extended summer arid period. During this dry summer, *Mandragora turcomanica* exhibits a long period of xerothermic dormancy (Kurbanov, 1994). Mizgireva (1955) suggested that *M. turcomanica* is much more cold-tolerant than its mediterranean congeners. The typical vegetation in the Kopet Dag consists of broadleaved deciduous forest in the moister microhabitats and open shrubland in drier areas.

The eastern part of the *Mandragora* range in the Sino-Himalayan

Table 9 Sources used for determining the overall distribution of the genus *Mandragora*.

Geographical area	Reference
Tunisia	Bouquet (1952), Pottier-Alapetite (1981)
Algeria	Quezel & Santa (1963)
Morocco	Jahandiez & Maire (1934)
Portugal	Amaral Franco (1984)
Spain (incl. Balearic Is.)	Lázaro é Ibiza (1907), Bonafè Barceló (1980), Valdés et al. (1987)
Italy (incl. Sicily, Sardinia)	Maugini (1959), Pignatti (1982), Cellinese et al. (1994)
Former Yugoslavia	Hayek & Markgraf (1931)
Greece (incl. Aegean Is.)	Halácsy (1902), Hayek & Markgraf (1931)
Turkey	Baytop (1978)
Cyprus	Meikle (1985), Viney (1994)
Syria	Post (1933), Feinbrun-Dothan (1978), Mouterde (1979)
Lebanon	Post (1933), Feinbrun-Dothan (1978), Mouterde (1979)
Israel	Post (1933), Feinbrun-Dothan (1978)
Jordan	Post (1933), Feinbrun-Dothan (1978)
Turkmenistan	Pojarkova (1955), Kurbanov (1994)
Nepal	Grierson & Long (1978)
India (Sikkim, Arunachal Pradesh)	Hara (1966), Grierson & Long (1978), Deb (1979)
Bhutan	Hara (1971), Grierson & Long (1978)
Myanmar	Grierson & Long (1978)
China	Grierson & Long (1978), Zhang et al. (1994), Zhang & Lu (1994)

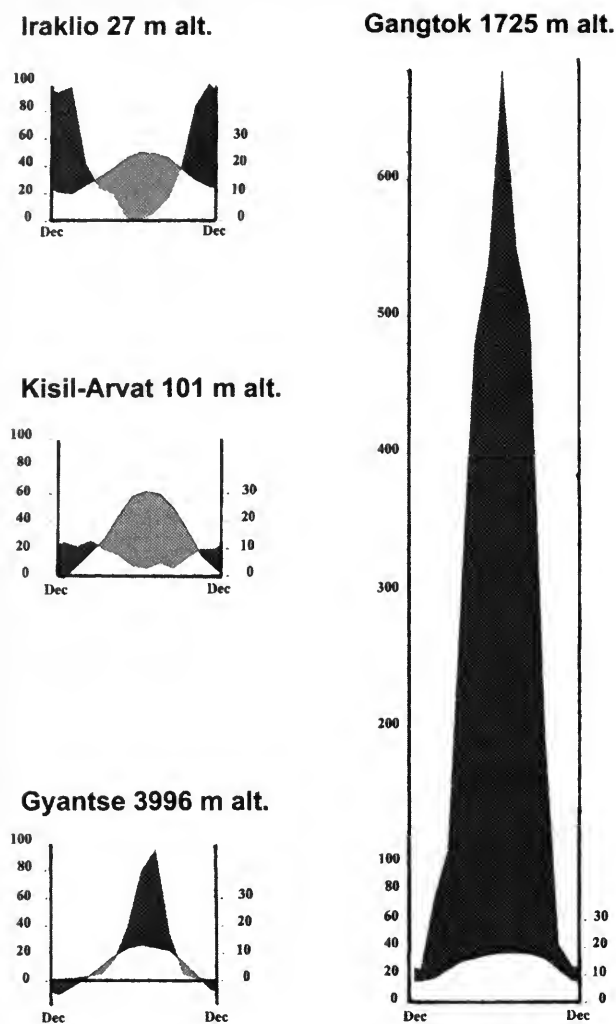


Fig. 6 Climate diagrams of four representative weather stations in three different climate regimes. Given are the rainfall and temperature curves, resulting in wet (dark shading) and dry (light shading) seasons. Based on Walter et al. 1975.

region is characterized by a completely different rainfall regime altogether. The influence of the monsoon renders not the winter but the summer the season of the highest rainfall. The amount of precipitation during the monsoon period, however, does vary enormously. The Himalayan chain functions as a rain screen resulting in high rainfall on the southern slope of the mountain range (Fig. 6: Gangtok) as well as in the southwestern Chinese mountains of Yunnan and Sichuan, and much lower rainfall in the inner regions of Xizang (Fig. 6: Gyantse). Even at high altitudes, winters are very mild in the high rainfall areas (see climate-diagram of Gangtok, about 1700 m above sea level) and snow is scarce. Generally speaking, the eastern Himalaya and southeastern Xizang, Sichuan and Yunnan enjoy a much more humid and milder climate than the western Himalaya and central Xizang. The locality data of the examined specimens suggest that the distributional boundary of the Himalayan mandrake towards the central Xizang highland lies within the 200–400 mm annual precipitation strip north of the main ranges. Due to the immense altitudinal gradient, the vegetation is strikingly zonal and ranges from subtropical forests to alpine scrub and meadows. The upper forest limit lies between about 3600 and 4200 m, the upper tree limit between 4200 and 4500 m. The belt in

between is characterized mainly by a succession of various *Rhododendron* species. This is the typical habitat of *Mandragora caulescens*. The permanent snow line lies at about 4800 m in the south and 5800 m in the north towards central Xizang (Walter, 1962).

Other factors affecting plant distribution, albeit on a smaller and less important scale, include soil type and competition. *Mandragora officinarum* especially grows in ruderal habitats, on clayey and nitrogen-rich soils. So far, it is not clear whether *M. caulescens* occurs on acidic (granitic) or base-rich (limestone) soils in the subalpine and alpine zone of the Himalaya. It cannot be ruled out that there might be two different, vicariant ecological groups as is often the case in the Alps, for example in *Rhododendron* (Walter, 1966). The type of climate and soil typically only indirectly determine the occurrence of a species in a certain locality, in that they affect the fitness of that species in relation to others (Walter, 1977). Both *Mandragora officinarum* and *M. turcomanica* seem more or less restricted to low-competition localities, representing typical *r*-species (good colonizers but poor competitors).

### Historical biogeography

The atemporal cladogram of a group together with historical evidence, namely paleoclimatic and paleogeographical data allow for the formulation of historical scenarios. A scenario is a model of the basic features (including space and time) of the evolutionary history of a group which can serve to stimulate directions of further investigation. However, the essentially speculative character of such a model renders it more like a tool than a serious scientific statement (Eldredge, 1979) and *ad hoc* assumptions are inevitable (Humphries & Parenti, 1986). In attempting to construct scenarios for the historical biogeography of any group, plate movement, eustasy (worldwide changes of sea level) and climate changes are considered the major factors to be considered (Hallam, 1981). In the case of the Solanaceae, virtually no fossil record is available (PaleoNet Listserv, <http://www.ucmp.berkeley.edu/Paleonet/>), thus historical hypotheses concerning *Mandragora* are inevitably founded on extant taxa only.

The Mediterranean region presents a very complex tectonic jigsaw puzzle, hard to resolve adequately (Hallam, 1981). It seems clear, however, that during most of the Tertiary, summer was the rainy season and only before the Pleistocene was there a shift towards the current pattern of rainfall in winter. The plants had to adapt and reduce activity during the dry summer months (Walter, 1977). The northern Mediterranean localities for *Mandragora* in northern Italy and on the Dalmatian coast are very patchy, resulting in a highly fragmented range there, and the precise status of these populations is uncertain. We have been unable to discover any modern collections from these regions (Cellinese et al., 1994) and some, or all, of the populations may no longer exist. Vierhapper (1915) maintained that these plants are Tertiary relics, the scattered remnants of a formerly larger, continuous range, that have been unable to adapt to the changing climate and still exhibit the vernal phenology type. Relict status based on Tertiary processes, however, is normally attributed to groups of far wider disjunct ranges than is the case here. Hawkes (1972a) based his definition of *M. officinarum* L. on these northern Italian and Dalmatian populations only, using corolla colour and phenology. On the evidence of our multivariate analyses, Hawkes's position is untenable, since the plants fall within the range of variation exhibited by the rest of the Mediterranean plants. It could be argued that the different corolla colour (white) of the northern Italian and Dalmatian plants, coupled with their discrete distribution is sufficient to recognize them at least at subspecific rank. We have already pointed out that the corolla colour is only an

apparent distinction, with similar colours occurring in populations outside northern Italy and Dalmatia. The somewhat isolated distribution alone is insufficient reason to recognize the Italian and Dalmatian plants as a separate taxon.

The close relationship between the Mediterranean and the Turkmenian mandrake as suggested by the cladistic analysis is reflected in a linked history of the regions particularly during the Tertiary. It can be proposed that in this period, after the Tethys Sea receded and the middle Asian mountains became exposed during their simultaneous uplift, a vicariance event of the Mediterranean and Turkmenian ancestors took place. Both extant species show a comparable adaptation to the aridization and change from a summer to a winter rainfall regime. In other words, *Mandragora turcomanica* can be seen as an example of a plant that has been evolving in isolation in Turkmenistan since the Tertiary from ancient Tethyan stock (Kurbanov, 1994). It is of some interest to note that there is a highly congruent pattern within *Atropa* where the disjunct distribution of the Turkmenian *Atropa komarovii* Blin. & Schal., consists of a very narrow range south of the river Sumbar only a few miles away from the *Mandragora turcomanica* population north of the river (Kurbanov, 1994).

The Sino-Himalayan area is of particular interest because of its position at the transition between the Palearctic and the Oriental floristic realms. The period of the collision of the Indian subcontinent with Asia is contentious but probably occurred in the Paleogene approximately 50 million years ago (Scotese et al., 1988) with the penetration of the Eurasian border continuing during the early Neogene (c. 20 millions years ago) (Dercourt et al., 1986). The connection between Tethys and the Mediterranean, on the other hand, probably did not close until the mid-Miocene (c. 15 million years ago) (Hallam, 1994). Climate changes during the Paleogene were severe. Temperatures increased up to the early Eocene (c. 55 million years ago) followed by a global cooling which marks the passage from a warm domain of the Mesozoic and early Palaeogene to the cool domain thereafter (Hallam, 1994). According to Rudman et al. (1989) much of the uplift in the Xizang plateau region occurred only in the last 5 to 10 million years (Plio-Pleistocene uplift). It must be assumed that the glaciation of the high altitude regions of the Sino-Himalayan area during the Pleistocene (Ice-Ages) was more or less complete, posing the question whether refugia further south and at lower altitudes might have served as speciation centres.

Schuster (1976) argued that the Indian plate served as a vehicle for the dissemination of Gondwanan taxa into Laurasia. But at the same time he expected that due to the migration through several climatic zones the Indian plate probably arrived with a rather depleted and altered flora and therefore only remnants of the original Gondwanan flora are recognizable in India today. If angiosperms were indeed on the Indian plate in early Cretaceous time, they could probably not be assigned to presently recognizable families. On the basis of a proposed late Triassic (c. 210 million years ago) start of the Indian plate migration, serious doubt is cast on the possibility that early Solanaceae could have been 'on board'. The main objection is that the plate drift simply occurred too early, before modern groups were in existence. However, other data (Smith et al., 1994) suggest that India did not break free from Gondwana until the late Jurassic to early Cretaceous (130–140 million years) or even near the Cretaceous-Tertiary boundary only 60–65 million years ago (Hallam, 1994). Lu & Zhang (1986) proposed southwestern China as a later, secondary speciation centre of the whole tribe Hyoscyameae on the grounds of its high species-richness.

A different biogeographical scenario proposes a migration from Gondwana to the Mediterranean basin. Migration routes that are

closed today were wide open in the Mesozoic. Indeed, massive and relatively unimpeded migrations from Gondwana to Laurasia might have been feasible until the late Cretaceous (Schuster, 1976). Contrary to the first scenario, the mandrake ancestors would therefore have spread eastwards from the Protomediterranean to the developing eastern Asian mountain ranges where the massive uplift possibly resulted in a vicariance event. The Mediterranean populations on the other hand would have had to adapt to the increasing aridization in the western part of the continent during the late Tertiary (Weinert, 1972) and thus slowly changed their mode of development from a summer flowering to a autumn-winter-spring flowering rhythm. Proskuryakova & Belyanina (1985) claim that the slow succession of the development phases, particularly of the germination, the long growth and flowering period and the large size of the plant speak for the great age of the Mediterranean group. They draw the conclusion that the Mediterranean section must be older, representing a Tertiary relic, than the apparently highly adapted Himalayan mandrake. The Himalayan mandrake, in fact, might have arisen from now-extinct ancestors as late as the Quaternary glaciations.

To conclude, the massive timespan covered in the Tertiary, the many fluctuations in climate and transgressions of the seas and the current very inaccurate timing of even the major events render definitive statements or falsifications concerning the above scenarios and the history of *Mandragora* hardly possible. In this context the distinction between a cladogram (what is more closely related?) and the actual phylogenetic tree (what is the ancestor?) must be stressed. The cladogram (Fig. 3) suggesting a more recent common ancestry of *Mandragora officinarum* and *M. turcomanica* is congruent with only one of the many possible trees equally resulting in this particular cladogram, which therefore represents a far less informative (more general) mode of expression. Thus, it does not allow for statements concerning the ancestor and does not imply that *Mandragora caulescens* is the older taxon. Nevertheless, it can be proposed that the major events affecting speciation and present distribution of *Mandragora* in the Mediterranean-Turkmenian area were probably the receding of the Tethys and the aridization of the climate in the Tertiary. In the Sino-Himalayan area, on the other hand, the collision of the Indian plate and the subsequent uplift of the Himalayan range, as well as the later glaciation periods during the Quaternary, are probably most important.

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## TAXONOMIC TREATMENT

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*Mandragora* L., *Sp. pl.* 1: 181 (1753). Type species: *M. officinarum* L.

Perennial herbs. Stout tap-root, often branched, sometimes vaguely anthropomorphic. Stem very short or with secondary growth during flowering and fruiting, sometimes branched. Leaves simple, normally entire, occasionally toothed. Inflorescence of typically solitary axillary, pedicellate flowers. Floral envelope actinomorphic. Calyx 5(6)-lobed, persistent, enlarged in fruit. Corolla 5(6)-lobed. Stamens 5(6), included, inserted in lower half of corolla-tube; filaments filiform, pubescent at base; anthers dorsifixed, dehiscent longitudinally. Ovary 2-locular; ovules numerous; style elongate; stigma capitate or somewhat bilobed. Fruit a fleshy, many seeded berry, globose or ovoid, borne beneath the leaves on nodding pedicel or lying on the ground. Seeds compressed; embryo curved.

FLORAL FORMULA.  $K(5) C(5) A5 \underline{G}(2)$

DIVERSITY AND DISTRIBUTION. Three disjunct species: Mediterranean region, central Asia, Sino-Himalayan region.

**PHENOLOGY AND HABITAT.** All three *Mandragora* species are geophytes with a conspicuous tap-root which is the perennating organ of these herbs, linking the annual vegetative periods. The Turkmenian mandrake with its prolonged dry season dormancy has been referred to as an ephemeroïd (Proskuryakova & Belyanina, 1985), its rhythm of development more closely related to the Mediterranean than to the Himalayan climatic cycle. Propagation is usually by seeds or vegetatively by underground buds on the tap-root. The species grow in open woodland, olive groves, grassland, fallow land, waysides, railway embankments, ruins, in rock crevices, grassy and stony mountain slopes and screes. The altitudinal range is 0–1200 and 3000–4900 m.

**ETHNOBOTANY.** Once important medicinal plants with a long tradition in mythology and superstition. All parts of the plant contain potent narcotic alkaloids.

**ETYMOLOGY.** Origin uncertain, possibly from the Greek  $\mu\alpha\nu\text{-}\delta\rho\alpha\gamma\omicron\rho\alpha\sigma$ , original meaning controversial; alternatively from the Sanskrit *mandros*, meaning sleep and *agora*, meaning object or substance (Thompson, 1934).

### Key to the species of *Mandragora*

- 1 Young leaves arranged in a cluster on top of a stem with scales, later along the secondarily elongated, sometimes branched stem; corolla yellow to dark purple; style not exceeding stamens. Sino-Himalayan. Alt. 3000–4900 m ..... 3. *M. caulescens*
  - Leaves permanently arranged in a rosette, the stem not elongating; corolla white to pale blue or violet; style exceeding stamens ..... 2
  - 2 Mature lower leaves in a large rosette of 150–180 cm; berries 40–60 mm in diameter. Turkmenian. Alt. 500–700 m ..... 2. *M. turcomanica*
  - Mature lower leaves in a rosette of less than 100 cm; berries less than 40 mm in diameter. Mediterranean. Alt. 0–1200 m ... 1. *M. officinarum*
1. *Mandragora officinarum* L., *Sp. pl.* 1: 181 (1753). Type: Herb. Burser IX: 26 (UPS-lectotype, designated by Knapp in Jarvis et al. (1993), microfiche-BM!).  
Figs 7, 8.
- ≡ *Atropa mandragora* L., *Syst. nat.* 10th ed.: 933 (1759), nom. illeg. (Art. 52.1).  
≡ *Mandragora foemina* Garsault, *Fig. pl. méd.* 3: 221, t. 363 p.p. (1764).  
≡ *Mandragora mas* Garsault, *Fig. pl. méd.* 3: 221, t. 363 p.p. (1764).  
≡ *Mandragora acaulis* Gaertn., *Fruct. sem. pl.* 2: 236, t. 131 (1791).  
≡ *Atropa humilis* Salisb., *Prodr. stirp. Chap. Allerton*: 132 (1796).  
≡ *Atropa acaulis* Stokes, *Bot. mat. med.* 1: 396 (1812).  
≡ *Mandragora autumnalis* Bertol., *Elench. plant. viv.*: 6 (1820).  
≡ *Mandragora vernalis* Bertol., *Virid. Bonon. veg.*: 6 (1824).  
≡ *Mandragora praecox* Sweet, *Brit. fl. gard.* 2: t. 198 (1827).  
≡ *Mandragora neglecta* G. Don ex Loudon, *Hort. brit.*: 71 (1830).  
≡ *Mandragora microcarpa* Bertol., *Comm. Mandrag.*: 12, t. 3 (1835).  
≡ *Mandragora haussknechtii* Heldr. in *Mitt. Geogr. Ges. Jena.* 4: 77, app. (1886).  
≡ *Mandragora* × *hybrida* Hausskn. & Heldr. in *Mitt. Geogr. Ges. Jena.* 4: 77 (1886).  
≡ *Mandragora hispanica* Vierh. in *Österr. Bot. Z.* 65: 132–133 (1915).

**ILLUSTRATIONS.** Wettstein (1895: fig. 12M-O); Feinbrun-Dothan

(1978: fig. 278); Pignatti (1982: figs on p. 518); Hoare & Knapp (1997: fig. 5c).

Plant virtually stemless. Root stout, often branched, very long. Leaves arranged in a rosette, leaf shape and size very variable, but usually elliptic to obovate, max. 45 cm long, length/width ratio 1.5–10, variously pubescent. Flowers borne in leaf axils. Pedicels very variable in length, max. 15 cm. Calyx 6–28 mm long, lobed  $1/2$ – $2/3$  of the way to the base, lobes 3–15 mm, acuminate, only slightly accrescent in fruit. Corolla 12–65 mm long, campanulate, greenish white to pale blue or violet, lobed  $1/2$  to nearly to the base, the lobes 6–60 mm. Stamens adnate to lower half of corolla; filaments 7–15 mm long; anthers 2.5–4.0 mm long, yellow to brown, sometimes pale blue. Style 8–20 mm long, exceeding stamens; stigma capitate. Fruit 5–40 mm in diameter, globose to ellipsoid, glossy yellow to orange when ripe, juicy, edible. Seeds 2.5–6.0 mm long, reniform, the surface reticulate, yellow to light brown.

**HABITAT.** Open woodland, olive groves, fallow land, waysides, railway embankments, ruins, crevices. Altitudinal range 0–1200 m.

**VERNACULAR NAME.** Mediterranean mandrake.

**PHENOLOGY.** Flowering September to April. Fruiting November to June.

**CONSERVATION STATUS.** Populations are scattered throughout the species range. Northern Italian populations are vulnerable (Cellinese et al., 1994) as they are apparently known only from old herbarium records and the present occurrence and abundance of these populations are unclear.

**DISTRIBUTION.** Circum-Mediterranean. (Tunisia, Algeria, Morocco, Portugal, Spain, Italy, former Yugoslavia, Greece, Cyprus, Turkey, Syria, Lebanon, Israel, Jordan).

**SELECTED SPECIMENS EXAMINED.** **TUNISIA.** Cap Bon, roadsides and orchards, 0–150 m, 6 October 1969, Tomkinson, M.J. 72, 72A (BM). Nabel, 60 m, 14 October 1907, Gandoger, M. 84 (K).

**MOROCCO.** Guercif, 144 km E. of Fes near 'La Kazbah', 38 km before the town of Guercif, 34°16'N, 3°45'W, 510 m, disturbed gravelly area by road, 3 November 1994, Jury, S.L. et al. 15434 (RNG); Gharb, c. 4 km NNE of Souk-El-Arbaa-du-Rharb on road to Ksar-El-Kebir, by bridge and salt works, 34°43'N, 6°00'W, 30 m, pasture between fields at side of salt pans, 7 November 1994, Jury, S.L. et al. 15701 (RNG); Zerhoun, c. 3 km NW of Moulay Idriss and 33 km from Meknes along road to Sidi Kacem and Tanger, 34°04'N, 5°33'W, 390 m, ruins of Roman city of Volubilis, 1 November 1994, Jury, S.L. et al. 15398 (RNG); Prerif Central, N. of Fes, on the road to Ouezzane, 34°22'N, 5°09'W, 210 m, roadside ruderal community, 24 October 1993, Jury, S.L. et al. 12634 (RNG); Haut Ouerrha, c. 50 km N. of Fes on the road between Fes-el-Bali and Ourtzarh, 34°33'N, 5°02'W, 120 m, in olive plantation on steep N-facing slope with *Zizyphus lotus*, 24 October 1993, Jury, S.L. et al. 12653 (RNG); Temara, 10 km S of Rabat, 0–30 m, sandy roadside, 14–20 October 1981, Lewalle, J. 10054 (BM, RNG); 5 km W. of Oued, Beht on Rabat-Meknes road, 33°52'N, 5°58'W, 400 m, 27 September 1991, Gardner, M.F. et al. 4885 (E, RNG); Loukkos, SW of Chefchaouen, on road to Ksar-el-Kebir, 35°1'N, 5°45'W, 120 m, in cultivated fields of wheat, 21 October 1993, Jury, S.L. et al. 12542 (RNG); Loukkos, c. 1 km E. of Larache on road to Asilah, c. 200 m from Oued Loukkos, 35°12'N, 6°08'W, 5 m, at side of road by salt pans, 28 October 1994, Jury, S.L. et al. 15237 (RNG); Tanga, just N. of airport, road to Cap Spartel, 35°45'N, 5°55'W, 35 m, fallow area at side of ploughed field with *Urginea maritima*, 16 October 1993, Jury, S.L. et al. 12217 (RNG); Tanga, E. on road to Sebta (Ceuta), Oued Dliane, 35°50'N, 5°39'W, 5 m, nitrophilous areas on fallow cultivated land on heavy clay alluvial plain, 17 October 1993, Jury, S.L. et al. 12238 (RNG); Allal-Tazi, close to the river Sedou, 1 November 1965, Taton, A. 1630 (BM).

**SPAIN.** Balears, Palma, between S. Sardina and S. Bernardo, 22 September 1913, Bianor & Sabasien 1877 (BM, E, P, RNG); Province Cadíz,





Fig. 7 *Mandragora officinarum*. a) Flowering, cultivated at RBG Kew, b) Fruiting, cultivated at RBG Kew.



**b**



**a**

Fig. 8 *Mandragora officinarum*. a) Flowering, *Heildreich* s.n. (E), b) Fruiting, *Reverchon* s.n. (E).

Chiclana, on clayey soil by the river, 10 January 1855, *Bourgeau, E.* 2304 (E, K, P); Torredonjimeno, 600 m, 10 December 1986, *Espinosa, A.* 870252 (K); alrededores de Córdoba, Cuesta del Espino, 2 December 1967, *Galiano, E.F. & Valdes, B.* 820 (E, RNG); Province Málaga, C 341 from Campillos to Ronda, 36°52'N, 5°00'W, 525 m, disturbed ground near new road cutting, 27 October 1990, *Gardner, M.F. & Knees, S.G.* 4769 (RNG); Province Cadiz, 23 km from Jerez de la Frontera, 36°32'N, 5°59'W, 130 m, ruderal area by road with abundant *Silybum marianum* below ruined castle of El Pedroso, 22 December 1993, *Jury, S.L. & Jury, L.C.* 13111 (BM, RNG); Province Jaén, Torredonjimeno, between Porcuna and Torredonjimeno, near Pilar de Moya, 500 m, roadside on chalky soil, 3 November 1979, *Ladero, M.* et al. 10605 (RNG); Málaga, near Churiana, 3 December 1957, *Partridge, F.* 2 (BM); Campamento, 9 November 1911, *Wolley-Dod, A.H.* 22 (BM).

**ITALY.** Sicily, Province Palermo, Madonie, near Polizzi, 950 m, rocky limestone slopes, 18 August 1964, *Davis, P.H.* 40134 (E); Sicily, Trapani, 200 m, steep slopes, 25 August 1964, *Davis, P.H.* 40182 (RNG); Sicily, Province Siracusa, Augusta, October–November 1911, *Vaccari, A.* 2326 (BM, K).

**FORMER YUGOSLAVIA.** Hercegovina, Dolnja Glavska, 6 May 1908, *Reiser, C.* s.n. (K); Sileski, near Ragusa, 500 m, 29 April 1909, *Maly, K.* s.n. (K).

**GREECE.** Near Corinth, 30 m, waste grounds and waysides, April 1931, *Atchley, S.C.* 819 (K); Crete, Frangokastello, 29 March 1973, *Barclay, C.* 3004 (K); Crete, Canea, 1 December 1943, *Bickerich, G.* 15324 (BM, K); Crete, Kolokithia, December 1977, *Bowen, H.J.M.* 694 (RNG); Crete, Agios Nikolaos, December 1983, *Bowen, H.J.M.* 3088 (RNG); Peloponnese, 5 km from Pilos on the road from Kalamata, 250 m, in cultivated fields near stream, 12 November 1973, *Brickell, C. & Mathew, B.* 8088 (K); Crete, Canea, frequent in hills and ditches throughout Crete up to 300 m, 1 January 1940, *Davis, P.H.* 1100 (E, K); Cyclades, Amorgos, 10 April 1940, *Davis, P.H.* 1438 (K); Dodecanese, Kos, Asfendion, 300–600 m, rocky slopes, 27 March 1965, *Davis, P.H.* 40478 (K); Crete, near Candia, Hagios-Deka, December 1913, *Duffour, C.* 1501 (P); Cyclades, Kea, 30 April 1961, *Gathorne-Hardy, E.* 14 (E); Dodecanese, Tilos, near chapel of Ayios Nicolaos c. 180 m above Livadia, 26 April 1962, *Gathorne-Hardy, E.* 139 (E); Crete, near Sitia, 150–200 m, on clayey soil, 30 October 1966, *Greuter, W.* 7821 (E); Near Corinth, Examillia, 8 February 1931, *Guiol, F.* 1731 (BM); Crete, Canea, on wasteland, 10 March 1883, *Reverchon, E.* 117 (BM, E, K, P, PAL); Dodecanese, Kos, by track near Asclepeion, 23 March 1985, *Townsend, C.C.* 85/11 (K); Dodecanese, Rhodes, 9 February 1914, *Vaccari, A.* 1141 (K); Crete, Nomos Lasithiou, Monastiraki, roadside, 5 April 1980, *Walree, A.M.* 22226 (BM).

**CYPRUS.** Kyrenia, fallow olive grove, 13 February 1949, *Casey, E.C.* 221 (K).

**TURKEY.** Province Mugla, Kemer-Kestep, 50 m, edge of fields, 29 March 1956, *Davis, P.H. & Polunin, O.* 25469 (BM, E, K); Side, 22 February 1966, *Baytop, A.* et al. 8504 (E).

**SYRIA.** Baniyas, 300 m, foot of hill, beneath tree, 11 March 1945, *Norris, F.H.* s.n. (BM).

**ISRAEL.** Jerusalem, fields, 800 m, 20 February 1908, *Meyers, F.* 4377 (E); Mount Carmel, upper Nahal Neshet, 2 km S. of Neshet, 32°45'N, 35°31'E, 280 m, terra rossa on hard limestone, 6 April 1989, *Danin, A. & Knees, S.G.* 1709 (RNG); Mount Gerizim, near Nablus, fields, 700 m, 22 December 1910, *Meyers, F.S. & Dinsmore, J.E.* 6377 (E); District Haifa, near Waldheim (Alloney Aba), open places in *Quercus ithaburensis* forest, 28 March 1942, *Davis, P.H.* 4166 (E, K).

The confusion surrounding specific epithets for the taxon we are here calling *Mandragora officinarum* is incredible. This morass has arisen for two basic reasons, firstly orthographic errors, and secondly, the confusion over the phenological status of type specimens. Orthographic errors made by early authors persist through floristic works, adding and compounding any ambiguities that may have arisen. A name often used in synonymy (or as a valid name) of *M. officinarum* is *Mandragora officinalis* Mill., said to be validly published in 1768 (see Jackson & Berry, 1979: 508, footnote). However, in the eighth edition of *The gardener's dictionary* (Miller, 1768), where Miller used Linnaean epithets for the first time, Miller actually used the epithet *officinarum* ('MANDRAGORA (*officinarum*)'), not *officinalis*. In the ninth edition (Miller & Martyn,

1807), the taxon was classified as *Atropa mandragora*, following *Systema naturae* (Linnaeus, 1759) and the second edition of *Species plantarum* (Linnaeus, 1762). *Mandragora officinalis* was cited in synonymy, with reference made to the illustrations produced to compliment the earlier editions (Miller, 1760). These illustrations bear no specific epithets, thus the 1807 reference to the epithet *officinalis* is almost certainly an orthographic error for the 1768 use of Linnaeus's epithet *officinarum*, which was not cited in synonymy in the ninth edition (Miller & Martyn, 1807). Thus the name *Mandragora officinalis* Mill. has persisted in the literature, but has no real nomenclatural standing.

Similarly, Bertoloni (1820) attributed the epithet *officinalis* (see below) to Willdenow, explicitly citing 'W. En.'. Willdenow (1809), in his *Enumeratio plantarum*, attributed the epithet *officinalis* to DeCandolle (in Lamarck & DeCandolle, 1805), where it is again attributed, in error, to Miller's *Gardener's dictionary*. Thus it is apparent that the numerous occurrences of the epithet *officinalis*, attributed to many authors, are traceable to a single orthographic error from Miller's 1767 edition of the *Gardener's dictionary*. Even if the epithet *officinalis* had nomenclatural standing, it would be invalid under Article 52.1 (see above), as it is homotypic with *Mandragora officinarum* L.: in DeCandolle (in Lamarck & DeCandolle, 1805) and Willdenow (1809), *Atropa mandragora* L. is cited in synonymy.

Assumptions as to the phenological status of type specimens has also led to confusion about the correct application of epithets (e.g. Jackson & Berry, 1979). Bertoloni (1820, 1824, 1835) contributed greatly to the confusion surrounding names for the Mediterranean mandrake. In a list of plants cultivated in the Botanic Gardens at Bologna (Bertoloni, 1820), he included two species of mandrakes: *Mandragora autumnalis*, which he coined as a new name, and *M. officinalis*, which he attributed to Willdenow. In a later work (Bertoloni, 1824) he designated two different taxa: *M. vernalis* and *M. officinarum*, explicitly citing Linnaeus as the source of the latter epithet. He put *M. officinalis* in synonymy with *M. vernalis* and put *M. autumnalis* in synonymy with *M. officinarum*. In *Commentarius de Mandragoris* (Bertoloni, 1835), he revised the genus and recognized three species: *M. vernalis*, *M. officinarum* and *M. microcarpa*. In synonymy he left out both of the previously used epithets, *autumnalis* and *officinalis*, which he may have considered to be superfluous.

The lectotype of *Mandragora officinarum*, selected from amongst the elements used by Linnaeus in his description, bears no phenological information at all. The specimen in Burser's herbarium is labelled 'Misnia, Lusatia', indicating it came from Germany. It is probable therefore that it is from a botanical garden, and since plants of *Mandragora* in northern European gardens usually bloom in spring, it has been assumed that this one did as well. This is not founded in fact, thus rendering much of the debate as to which name is the vernal or autumnal taxon irrelevant.

2. *Mandragora turcomanica* Mizg. in *Trudy Turkmen. Fil. Akad. Nauk SSSR. Ashkabad* 2: 165 (1942). Type: Turkmenistan, western Kopet Dag, Kara Kala region, southern foot of Mt Syunt, Schevlan valley, on scree slopes, 26 November 1938, *O.G. Mizgireva, M. Nastacalicz & G. Nastacalicz* s.n. (ASH-holotype; LE-isotype(?)).

ILLUSTRATIONS. Mizgireva (1942: figs 1, 2; 1955: figs 2–7, 9, 14, 15, 18, 19, 24); Belyanina (1982: figs 1, 2).

Plant virtually stemless. Leaves arranged in a rosette: lower leaves c. 90 × 60 cm, length/width ratio c. 1.3–1.5, broadly elliptical or ovate,

usually with large, irregular teeth in upper half, upper leaves smaller, oblong-ovate or broadly lanceolate, usually without large teeth, on both sides sparsely hairy, the hairs mostly arranged along veins. Flowers borne 1(–3) in leaf axils, occasionally the pedicels up to 2–6-flowered. Pedicels 2–3 cm long, 7–18 cm in fruit. Calyx 15–20 mm long, lobes 10–15 mm, acuminate, accrescent in fruit. Corolla 20–25 mm long, campanulate, violet or purple, with three narrow white stripes at base, the lobes c. 15 mm. Stamens c. 10 mm long, attached to lower half of corolla; filaments 6–7 mm, densely pubescent at the base and in the lower ½; anthers c. 4 mm long, pale blue. Style exceeding stamens; stigma capitate, slightly bilobed, green. Fruit 40–60 mm in diameter, glossy yellow to orange when ripe, pulpy, juicy, smelling of melons, edible. Seeds 4–5 × 6–7 mm, reniform, yellow to light brown.

**HABITAT.** Shrubland in ravines and on stony mountain slopes, especially among *Paliurus spina-christi* Mill. (Rhamnaceae). Altitudinal range 500–700 m.

**VERNACULAR NAME.** Turkmenian mandrake.

**PHENOLOGY.** Flowering October to March. Fruiting until June. Summer dormancy until autumn rains begin. Xerothermic ephemeroïd.

**CONSERVATION STATUS.** Only small populations in a restricted area within the Syunt-Khassardagh Reserve, and in the valleys of Chokhadgh, Shevlan, Altybai, Ekechinar, Sarymsakli and Dagdanli are known (Kurbanov, 1994). According to Mizgireva (1978) the population in the Syunt-Khassardagh reserve consists of fewer than a thousand plants.

**DISTRIBUTION.** Southwestern Kopet Dag. (Turkmenistan, ?Iran).

**SELECTED SPECIMENS EXAMINED.** No specimens were available for examination: the data here are drawn exclusively from the literature.

In the original article in which this species was described (Mizgireva, 1942) the type is cited as being in Ashkabad (ASH). Subsequently, in the *Flora of the USSR* (Lincevskij, 1955), the type was said to be in Leningrad (now St. Petersburg, LE) and this citation has been followed in other floristic works (Schönbeck-Temesy, 1972). Since we have been unable to obtain specimens from either herbarium, it is uncertain whether or not the holotype remains in ASH or has been transferred to LE, thus we have cited its location as in the original publication.

Mizgireva's (1955) detailed study of this species documented the flowering times (Mizgireva, 1955: fig. 16) of individual plants and clearly shows that some individuals flower in autumn (October and November) while others flower in spring (February and early March). This is the same situation as that in *Mandragora officinarum*, and is markedly different from that found in much of the rest of the flora of Kopet Dag (Mizgireva, 1978). Mizgireva (1955) stated that the differences between her species, *M. turcomanica*, and the Mediterranean mandrakes (separated by her into *M. officinarum* and *M. autumnalis*) were largely size of plant, colour of anthers and relative sizes of calyx and corolla. It is clear from her work that these characteristics are consistent throughout the range of wild and greenhouse grown material she examined, but since she cites no specimens, nor have we been able to examine any of the known specimens of *M. turcomanica*, an in-depth analysis of these characters relative to the range of variation found in *M. officinarum* awaits future study.

3. ***Mandragora caulescens*** C.B. Clarke, *Fl. Brit. Ind.* 4: 242 (1883). Type: India, Sikkim, Lachen, *Hooker* s.n. (K!)-lectotype, designated here by R. Mill.

Fig. 9.

= *Anisodus mariae* Pascher in *Feddes Repert. Spec. Nov.* 7: 227 (1909).

= *Mairella yunnanensis* H. Lév., *Cat. pl. Yun-Nan*: 199 (1916).

= *Anisodus caulescens* (C.B. Clarke) Diels in *Feddes Repert. Spec. Nov. Beih.* 12: 480 (1922).

= *Mandragora tibetica* Grubov in *Rast. Tsentral. Azii.* 5: 108–109 (1970).

= *Mandragora caulescens* subsp. *brevicalyx* Grierson & D.G. Long in *Notes Roy. Bot. Gard. Edinburgh* 36: 144 (1978).

= *Mandragora caulescens* subsp. *flavida* Grierson & D.G. Long in *Notes Roy. Bot. Gard. Edinburgh* 36: 143 (1978).

= *Mandragora caulescens* subsp. *purpurascens* Grierson & D.G. Long in *Notes Roy. Bot. Gard. Edinburgh* 36: 143 (1978).

= *Mandragora chinghaiensis* Kuang & A.M. Lu, *Fl. reip. pop. Sin.* 67: 159 (1978).

**ILLUSTRATIONS.** Grubov (1970: pl. IV, fig. 2; pl. V, fig. 2); Kuang & Lu (1978: fig. 36, 1–6). Hoare & Knapp (1997: fig. 5d).

Root stout, often branched. Stem present, max. 60 cm long. Leaves arranged in a cluster on top of the young stem above scale leaves, later along the secondary growth of the stem, max. 30 cm long, length/width ratio 1.9–5.5, oblanceolate or spathulate, glabrous to densely pubescent beneath, especially along the veins. Flowers borne in leaf axils, often nodding, pleasantly scented. Pedicels 5–10 cm long. Calyx 5–30 mm long, often nearly as long as corolla, lobed c. ¼ of the way to the base, accrescent in fruit. Corolla 5–30 mm long, campanulate to cup-shaped, yellow to purple, the venation usually darker, lobed about ¼ of the way to the base, the lobes 2–10 mm. Stamens adnate in lower half of corolla; filaments 3–10 mm; anthers 1–5 mm long, white to yellow. Style 3–6 mm long, not exceeding the stamens; stigma capitate, somewhat bilobed. Ovary 2.5–5 mm in diameter, globose. Fruit 10–25 mm in diameter, globose, pale greenish white or greenish yellow. Seeds 1.5–3.0 mm long, numerous, reniform, the surface pitted, yellow to light brown.

**HABITAT.** Grassy and stony slopes, open moorland, pastures and screes. Subalpine and alpine zone, especially among *Rhododendron* shrubs. Altitudinal range 3000–4900 m.

**VERNACULAR NAMES.** Himalayan mandrake. China: qie shen.

**PHENOLOGY.** Flowering April to September. Fruiting August to October.

**CONSERVATION STATUS.** Locally common. Not threatened.

**DISTRIBUTION.** Sino-Himalayan. (Nepal, India, Bhutan, Myanmar, China).

**SELECTED SPECIMENS EXAMINED.** **NEPAL.** Topke Gola, 27°39'N, 87°35'E, 3810 m, in short grassland, 3 July 1971, *Beer*, L.W. 8264 (BM); Tarakot, 28°53'N, 82°59'E, 3900 m, 25 May 1969, *Dobremez*, J.F. 175 (BM); Jangla Banyang, wet place, 3800 m, 5 June 1973, *Einarsson*, L. et al. 430 (BM); Ganesh Himalaya, Shior Khola, 4270 m, bouldery alpine meadow, *Gardner*, P.C. 479 (BM); Topke Gola-Tasagon, 3600–4350 m, 17 August 1977, *Ohashi*, H. et al. 775165 (BM); Langtang Valley, 28°14'N, 85°32'E, 4420 m, among rocks in turf, June 1949, *Polunin*, O. 631 (BM); 5 miles E. of Timure, oak wood, 4110 m, 3 July 1949, *Polunin*, O. 780 (BM); pass NW of Jumla, 6 miles Pansae Dara, 3050 m, growing in loose soil recently free of snow, 30 April 1952, *Polunin*, O. et al. 878 (BM); Dozam Schola, near Simikot, 3510 m, grass slopes, 2 June 1952, *Polunin*, O. et al. 4250 (BM); near Jumla, 3810 m, open grassy slopes, 14 July 1952, *Polunin*, O. et al.

13600



FAN MEMORIAL INSTITUTE  
OF BIOLOGY  
FLORA OF YUNNAN

Field No. 19843 Date AUG. 9, 1933  
Locality Upper Makiang Valley,  
(Chiang) Lungshihua  
Mt. slope open & stony  
place

Habit Herb Perennial  
Height 1 ft. 10 in.  
Leaf  
Flower  
Fruit  
Notes  
Common Name  
Family

Very young, immature, with  
calyx lobes open for period after  
Common

100 mm. 62  
Cultivar T. T. W.

*Mandragora caulescens* Clarke  
Det. A. J. C. Gribben & D. G. Long  
Bhutan Flora Project Oct. 1977



b



F. LUDLOW-G. SHERIFF  
Locality  
Alt. 1590  
Date 14. 5. 34.  
Description  
In deep shade woods, pink  
with green, red, orange, yellow  
flowers. ~~Stems~~ ~~leaves~~ ~~July 1934~~  
Stems, leaves yellow, 1937  
Bottle.

Dr. J. W. Greuter, Bern  
Mandragora caulescens Griseb.  
1856 v. 1, p. 93. (1)

*Mandragora caulescens* Clarke  
Det. A. J. C. Gribben & D. G. Long  
Bhutan Flora Project Oct. 1977

Approved  
R. R. Mill

a

Fig. 9 *Mandragora caulescens*. a) Early flowering, clustered, Ludlow & Sheriff 1590 (BM), b) Late flowering, stem elongating, Yü 19843 (E).

4668 (BM); Arun-Tamur watershed, Topke Gola, 3960 m, 11 May 1956, *Stainton, J.D.A.* 254 (BM); Balangra Pass, W. of Tibrikot, 29°06'N, 82°41'E, 3810 m, 28 May 1963, *Stainton, J.D.A.* 4263 (BM); Rolwaling, 27°55'N, 86°23'E, 3810 m, beneath small shrubs, 25 June 1964, *Stainton, J.D.A.* 4676 (BM); Khunde-Khumjung, 3820 m, 6 June 1952, *Zimmermann, A.* 688 (BM).

**INDIA. Sikkim:** Changu, 3960 m, in crevices of rocks, 28 June 1913, *Cooper, R.E.* 80 (E); Gnatong, 3960 m, peaty marsh, 31 August 1913, *Cooper, R.E.* 759 (E); Jongri, 4000–4200 m, 22 May 1960, *Hara, H.* et al. 443 (BM, K); Tungu, 3660–3960 m, 23 July 1849, *Hooker, J.D.* s.n. (K); Jongri, 4420 m, campsites towards Yakhut amongst *Juniperus* scrubs, 29 May 1990, *Kirkpatrick, G.* 53 (E); District Darjeeling, Phalut, 3350–3660 m, 30 May 1902, *Lace, J.H.* 2266 (E); West District, Bikbari, Choktsering Chhu valley; 27°30'53"N, 88°08'28"E, 3950 m, amongst scrub, 12 July 1992, *Long, D.G.* et al. 266 (E); Chulong, 4570 m, 12 September 1912, *Rhomoo, L.* 210 (E); Gamothang, 3960 m, 12 August 1913, *Rhomoo, L.* 1059 (E); Giagong, 3960 m, 6 September 1911, *Ribu & Rhomoo* 5492 (BM, E, K); Phalut, 3350–3660 m, 27 May 1911, *Smith, W.W.* 4593 (E); Jongri, 4000 m, in shelter of dwarf *Rhododendron* and *Juniperus*, 23 June 1983, *Starling, B.N.* et al. 92 (K); Tangshing campsite, 4000 m, open grazed areas among *Rhododendron* and around campsite, 24 June 1983, *Starling, B.N.* et al. 106 (K); summit of Sandakphu, 3660 m, small dense tufts amongst grass, 18 May 1881, *Watt, G.* 5373 (E, K). **Arunachal Pradesh (Assam):** Orka La, Bhutan frontier, 3960 m, on stony slopes, scattered, 7 June 1938, *Kingdon Ward, F.* 13840 (BM).

**BHUTAN.** Paco Chu, 4110 m, loose sandy crevice, 15 May 1966, *Bowes Lyon, S.* 3156 (BM); Phajudin Timpu, 3960 m, 5 August 1914, *Cooper, R.E.* 3232 (BM, E); Tare-La area, 3660 m, 19 May 1938, *Gould, B.J.* 109 (K); Laum Thang, 3900 m, in alpine herbage with moderate humidity, 18 May 1967, *Hara, H.* et al. 11973 (BM); Western Bhutan, 3510 m, among boulders above tree line, 17 June 1933, *Ludlow, F. & Sherriff, G.* 107 (BM); Byasu La, 4110 m, growing among stones on open hillside, 18 May 1937, *Ludlow, F. & Sherriff, G.* 3073 (BM); Cheli La, 3810 m in open moorland, 4 May 1949, *Ludlow, F.* et al. 16139 (BM); Pangotang, 3960 m, open hillside above fir zone, 27 May 1949, *Ludlow, F.* et al. 18986 (BM); Kantanang, Tsampa, 4110 m, among shrubs on steep hillside, 3 June 1949, *Ludlow, F.* et al. 19040 (BM); Shingbe, Me La, 3350 m, growing amongst other herbs and small shrubs, 16 May 1949, *Ludlow, F.* et al. 20645 (BM, E).

**MYANMAR (Burma).** Chenochi Pass, 3600 m, 3 July 1920, *Farrer, J.R.* 1694 (E).

**CHINA. Yunnan:** Diqing Prefecture, E. slope of Bai Ma Shan, 28°19'N, 99°05'E, 3895 m, among stones in *Abies* forest, 9 June 1993, *Alden, B.* et al. 1021 (E); Diqing Prefecture, Zhongdian County, above Napa Hai, N. of Zhongdian, 27°55'N, 99°34'E, 4000 m, forested ridge, snow-bed vegetation and dwarf *Rhododendron* scrub, 12 June 1993, *Alden, B.* et al. 1185 (E); western flank of the Lichiang range, 27°20'N, 3050–3350 m, open alpine pasture, June 1910, *Forrest, G.* 5999 (E, K); Lichiang range, 27°25'N, 3660–3960 m, July 1913, *Forrest, G.* 10474 (BM, E, K); western slopes of Likiang snow range, Yangtze watershed, 30 May–6 June 1922, *Rock, J.F.* 4211 (BM); Mo-ting shan, NE of Atuntze, eastern slopes of Yangtze-Mekong divide, 3660 m, along trail, June 1932, *Rock, J.F.* 22771 (E); slopes of Mt Gyi-na lo-ko, the second peak of the Yu-lung shan, 3660 m, in alpine meadows, April–May 1932, *Rock, J.F.* 25005 (BM, E); Chungtien, Chiren, 2200 m, grass slope, 17 May 1937, *Yü, T.T.* 11327 (KUN); Mekong-Salween divide, Chingpoh, 3800 m, alpine pasture lands, 14 June 1938, *Yü, T.T.* 19078 (E); Upper Kiukiang valley, Clulung Lungtsahmuru, 3700 m, mountain slope, open and grassy place, 9 August 1938, *Yü, T.T.* 19843 (E, KUN). **Sichuan:** Tien-chuan-hsien, 3500 m, 14 June 1936, *Chu, K.L.* 2791 (BM); mountains E. of Yungning, 27°48'N, 101° E, 3660 m, open stony pasture, June 1922, *Forrest, G.* 21407 (BM, E, K); mountains around Muli, 28°12'N, 101° E, 3660 m, July 1930, *Forrest, G.* 28416 (BM, E); Liuku-liangde, 27°48'N, 3700–4200 m, 18 May 1914, *Handel-Mazzetti, H.* von 2349 (K); Minya Konka snow range, S. of Tatsienlu, 4450 m, in meadows, July 1929, *Rock, J.F.* 17530 (E); Mu-li-ka-bu, 3600 m, mountain slope, grassy place, 18 May 1937, *Yü, T.T.* 5496 (KUN). **Qinghai:** Dari (Darlag) Xian, just N. of Manzhang, along the Manzhang He, between Dari and Banma, 33°17'51"N, 100°25'55"E, 4000 m, on moist rodent disturbed slope, 12 August 1993, *Ho, T.N.* et al. 1172 (E); Chindu Xian, Xiwu Xiang, E. of pass on road between Xiwu and the Szechwan border, 33°09'14"N, 97°32'35"E, 4250 m, damp slope with extensive pika warrens, 11 September 1996, *Ho, T.N.* et al. 3063 (BM). **Xizang:** Dotha, 3960 m, 20 June 1945,

*Bor & Kirat Ram* 20511 (K); Mt. Demula, Yiwei County, 4100 m, 23 August 1973, *Chinese Tibet Expedition 1973* 1214 (KUN); District Chengtang, Dingjie County, Ladang to Xingeng, 3800–4000 m, 9 June 1975, *Chinese Tibet Expedition 1975* 5679 (KUN); Londre Pass, Tsarong, Mekong-Salween divide, 28°14'N, 98°40'E, 3960 m, July 1921, *Forrest, G.* 19630 (UC/JEPS, P, K); Tha Chu valley, 3660 m, in clumps, alpine region, in stony pastures and on grassy slopes, 11 July 1950, *Kingdon Ward, F.* 19613 (BM); N. of Sanga Choling, 28°41'N, 93°02'E, 4110 m, on open grassy bank, 14 May 1936, *Ludlow, F. & Sherriff, G.* 1590 (BM); hills S. of Lhasa, 4420 m, ground left bare by melting snow, 6 June 1942, *Ludlow, F. & Sherriff, G.* 8676 (BM); hills S. of Lhasa, 4720 m, herb growing under boulders, 21 August 1942, *Ludlow, F. & Sherriff, G.* 9014 (BM); Pome, above Showa Dzong, 29°55'N, 95°25'E, 3350 m, open hillsides midst grass, 11 June 1947, *Ludlow, F.* et al. 13149 (BM, E); Sobhe La, near Tongyuk Dzong, Pome, 30°07'N, 94°54'E, 3510 m, 21 May 1947, *Ludlow, F.* et al. 13750 (BM, E); Province Kongbo, Nyima La, 29°38'N, 94°52'E, 3350 m, on dry ground under trees, 21 May 1947, *Ludlow, F.* et al. 15051 (BM, E); Lo La, Pachakshiri, 28°49'N, 93°59'E, 3810 m, in openings of *Rhododendron* forest, mostly above *Abies* zone, 15 May 1938, *Ludlow, F.* et al. 3776 (BM); Province Kongbo, south side of Lusha Chu, 29°20'N, 94°35'E, 3810 m, in *Lonicera* and *Berberis* scrub, 13 June 1938, *Ludlow, F.* et al. 4591 A (BM, E); valley above Tse, Tsangpo valley, 29°23'N, 94°22'E, 3350 m, in grassy banks under *Rhododendron*, *Ludlow, F.* et al. 4591 (BM).

The status and identity of the previously proposed subspecies of *Mandragora caulescens* (Grierson & Long, 1978) are discussed in the section on the species delimitation (p. 25). It is clear from our studies that *M. caulescens* is extremely variable and that a detailed field-based study over the entire species range is necessary.

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- Atherton, G.E. 793, *M. officinarum* (K); 812, *M. officinarum* (K); 998 *M. officinarum* (K)
- Baker, E.W. 149, *M. officinarum* (BM)
- Ball, J. s.n., *M. officinarum* (E)
- Barclay, C. 3004, *M. officinarum* (K)
- Bauer, K. & Spitzenberger, F. 53, *M. officinarum* (BM)
- Baytop, A., Tanker, N. & Sezik, E. 8504, *M. officinarum* (E)
- Beer, L.W. 8264, *M. caulescens* (BM)
- Bianor & Sabasien 1877, *M. officinarum* (BM, E, P, RNG)
- Bickerich, G. 15324, *M. officinarum* (BM, K)
- Biro, L. s.n., *M. officinarum* (K)
- Bor & Kirat Ram 20481, *M. caulescens* (K); 20511, *M. caulescens* (K)
- Bormüller, J. s.n., *M. officinarum* (K)
- Bourgeau, E. s.n., *M. officinarum* (K, P), 2304, *M. officinarum* (E, K, P)
- Bowen, H.J.M. 694, *M. officinarum* (RNG); 3088, *M. officinarum* (RNG)
- Bowes Lyon, S. 3156, *M. caulescens* (BM); 3239, *M. caulescens* (BM)
- Brickell, C. & Mathew, B. 8088, *M. officinarum* (K)
- Carr, J.W. s.n., *M. officinarum* (RNG)
- Casey, E.C. 221, *M. officinarum* (K)
- Chaboisseau, C. 575, *M. officinarum* (BM)
- Chatterjee, D. 75, *M. caulescens* (BM)
- Chinese Tibet Expedition 1973 1214, *M. caulescens* (KUN)
- Chinese Tibet Expedition 1975 5679, *M. caulescens* (KUN)
- Chu, K.L. 2791, *M. caulescens* (BM)
- Clarke, C.B. 34977, *M. caulescens* (K); 34983 A, *M. caulescens* (BM); 35704, *M. caulescens* (K)
- Clarke, E.D. s.n., *M. officinarum* (BM)
- Coincy, M.A. de s.n., *M. officinarum* (P)
- Cooper, R.E. 80, *M. caulescens* (E); 759, *M. caulescens* (E); 3232, *M. caulescens* (BM, E)
- Danin, A. & Knees, S.G. 1709, *M. officinarum* (RNG)
- Davis, P.H. 1100, *M. officinarum* (E, K); 1438, *M. officinarum* (K); 2108, *M. officinarum* (E, K); 4166, *M. officinarum* (E, K); 40134, *M. officinarum* (E); 40182, *M. officinarum* (RNG); 40478, *M. officinarum* (K)
- Davis, P.H. & Polunin, O. 25469, *M. officinarum* (BM, E, K)
- Delavay, J.M. s.n., *M. caulescens* (P); 263, *M. caulescens* (P); 1026, *M. caulescens* (P)
- Dhwoj, L. 513, *M. caulescens* (BM, E)
- Dinsmore, J.E. B 377, *M. officinarum* (E)
- Dobremez, J.F. 175, *M. caulescens* (BM)
- Duffour, C. 1501, *M. officinarum* (P)
- Economides, S. 1055, *M. officinarum* (K)
- Einarsson, L., Skärby, L. & Wetterhall, B. 430, *M. caulescens* (BM)
- Espinosa, A. 870252, *M. officinarum* (K)
- Ex Herb. Postian. apud Colleg. Syriens. Protest. 952, *M. officinarum* (BM)
- Farrer, J.R. 1694, *M. caulescens* (E)
- Fay, J.M. 815, *M. officinarum* (K); 864, *M. officinarum* (K)
- Forbes s.n., *M. officinarum* (UCJEPS)
- Forrest, G. 569, *M. caulescens* (E); 5999, *M. caulescens* (E, K); 10474, *M. caulescens* (BM, E, K); 19630, *M. caulescens* (UCJEPS, P, K); 21407, *M. caulescens* (BM, E, K); 26951, *M. caulescens* (P); 28416, *M. caulescens* (BM, E)
- Galiano, E.F. & Valdes, B. 820, *M. officinarum* (E, RNG)
- Gammie, G.A. s.n., *M. caulescens* (BM, E)
- Gandoger, M. s.n., *M. officinarum* (K); 84, *M. officinarum* (K); 8400, *M. officinarum* (K)
- Gardner, M.F., Jury, S.L. & Rejdali, M. 4885, *M. officinarum* (E, RNG)
- Gardner, M.F. & Knees, S.G. 4769, *M. officinarum* (RNG)
- Gardner, P.C. 479, *M. caulescens* (BM)
- Garnett, C.S. 33/5, *M. officinarum* (BM); 158/7, *M. officinarum* (BM)
- Gathorne-Hardy, E. 14, *M. officinarum* (E); 139, *M. officinarum* (E); 194, *M. officinarum* (E)
- Girgenti s.n., *M. officinarum* (BM)
- Gould, B.J. 109, *M. caulescens* (K)
- Greuter, W. 7821, *M. officinarum* (E)
- Guiol, F. 1731, *M. officinarum* (BM)
- Haig, E. s.n., *M. officinarum* (BM)
- Handel-Mazetti, H. von 2349, *M. caulescens* (K)

## EXSICCATAE

Arranged by collector, with collection numbers (s.n.: collections without collection number), species and herbaria.

- Al-Eisawi, D. & Al-Jallad, W. 2221, *M. officinarum* (BM)
- Alden, B., Alexander, J.C.M., Long, D.G., McBeath, R.J.D., Noltie, H.J. & Watson, M.F. 1021, *M. caulescens* (E); 1185, *M. caulescens* (E)
- Atchley, S.C. s.n., *M. officinarum* (BM); 315, *M. officinarum* (K); 819, *M. officinarum* (K)



- Hara, H., Kanai, H., Murata, G. Ohashi, H., Tanaka, O. & Yamazaki, T. 11973, *M. caulescens* (BM)
- Hara, H., Kanai, H., Murata, G., Togashi, M. & Tuyama, T. 443, *M. caulescens* (BM, K)
- Hardy, E. s.n., *M. officinarum* (BM)
- Hart, H.C. s.n., *M. officinarum* (BM)
- Hay, J.H. 1707, *M. officinarum* (K); H. 2484, *M. officinarum* (K)
- Helbaek, H. 74, *M. officinarum* (K)
- Heldreich, T. von s.n., *M. officinarum* (BM, E, K, P); 257 [1860], *M. officinarum* (BM); 257 [1857], *M. officinarum* (P); 257 [1859], *M. officinarum* (K); 2817 [1853], *M. officinarum* (P); 2817 [1860], *M. officinarum* (K, P)
- Higgins, E.K. s.n., *M. officinarum* (BM)
- Ho, T.N., Bartholomew, B. & Gilbert, M. 1172, *M. caulescens* (E)
- Ho, T.N., Bartholomew, B., Watson, M. & Gilbert, M. 3063, *M. caulescens* (BM)
- Hooker, J.D. s.n., *M. caulescens* (E, K-lectotype, P)
- Huguenin s.n., *M. officinarum* (BM)
- Jury, S.L., Achhal, A. & Mouks, H. & Upson, T.M. 12634, *M. officinarum* (RNG); 12653, *M. officinarum* (RNG)
- Jury, S.L., Aitlafkih, M., Hedderson, T. & Kahouadji, A. 15237, *M. officinarum* (RNG)
- Jury, S.L., Aitlafkih, M., Hedderson, T. & Rutherford, R. W. 15398, *M. officinarum* (RNG); 15434, *M. officinarum* (RNG); 15701, *M. officinarum* (RNG)
- Jury, S.L. & Jury, L.C. 13111, *M. officinarum* (BM, RNG)
- Jury, S.L., Rejdali, M., Taleb, A. & Upson, T.M. 12542, *M. officinarum* (RNG)
- Jury, S.L., Taleb, A. & Upson, T.M. 12217, *M. officinarum* (RNG); 12238, *M. officinarum* (RNG)
- Jussieu, A. de s.n., *M. officinarum* (P)
- King, G. s.n., *M. caulescens* (E); 4368, *M. caulescens* (P)
- Kingdon Ward, F. 13840, *M. caulescens* (BM); 19613, *M. caulescens* (BM)
- Kirkpatrick, G. 53, *M. caulescens* (E)
- Lacaita, C.C. s.n., *M. officinarum* (BM); s.n., *M. caulescens* (BM)
- Lace, J.H. 2266, *M. caulescens* (E)
- Ladero, M., Lopez Guadalupe, M., Molero, J. & Perez Raya, F. 10605, *M. officinarum* (RNG)
- Lange, J. s.n., *M. officinarum* (K, P)
- Laukkonen, P. 55, *M. officinarum* (K)
- Le Testu, G. s.n., *M. officinarum* (BM)
- Lewalle, J. 10054, *M. officinarum* (BM, RNG)
- Lojacono-Pojero, M. s.n., *M. officinarum* (BM)
- Long, D.G., McBeath, R.J.D., Noltie, H.J. & Watson, M.F. 266, *M. caulescens* (E)
- Lowne, B.T. s.n., *M. officinarum* (BM)
- Ludlow, F. & Sheriff, G. 107, *M. caulescens* (BM); 1590, *M. caulescens* (BM); 3073, *M. caulescens* (BM); 8676, *M. caulescens* (BM); 9014, *M. caulescens* (BM)
- Ludlow, F., Sherriff, G. & Elliot, H.H. 13149, *M. caulescens* (BM, E); 13750, *M. caulescens* (BM, E); 15051, *M. caulescens* (BM, E)
- Ludlow, F., Sherriff, G. & Hicks, J.H. 16139, *M. caulescens* (BM); 18986, *M. caulescens* (BM); 19040, *M. caulescens*, (BM); 20645, *M. caulescens* (BM, E)
- Ludlow, F., Sherriff, G. & Taylor, G. 3776, *M. caulescens* (BM); 4591 A, *M. caulescens* (BM, E); 4591, *M. caulescens* (BM)
- Maly, K. s.n., *M. officinarum* (K)
- Manberg, T. s.n., *M. caulescens* (K)
- Mavzomoustakis, G.A. 8, *M. officinarum* (BM)
- Mc Laren's collectors AC 67, *M. caulescens* (E, P)
- Meyers, F. 4377, *M. officinarum* (E)
- Meyers, F.S. & Dinsmore, J.E. 6377, *M. officinarum* (E); B 6377, *M. officinarum* (K)
- Mill, J.S. s.n., *M. officinarum* (K)
- Moreau, W.M. 62, *M. officinarum* (K)
- Norris, F.H. s.n., *M. officinarum* (BM)
- Ohashi, H., Kanai, H., Ohba, H. & Tateishi, Y. 775165, *M. caulescens* (BM)
- Olivier & Bruguère s.n., *M. officinarum* (P)
- Orphanides, T.G. 75, *M. officinarum* (BM, E, K, P)
- Paine, J.A. s.n., *M. officinarum* (K)
- Pantling, R. s.n., *M. caulescens* (K); 46387, *M. caulescens* (K)
- Partridge, F. 2, *M. officinarum* (BM)
- Pastor, J. & Valdes, B. s.n., *M. officinarum* (RNG)
- Perraudière, H. de la s.n., *M. officinarum* (P)
- Petter, F. s.n., *M. officinarum* (BM)
- Pichler s.n., *M. officinarum* (BM, E, K)
- Pignant s.n., *M. officinarum* (K)
- Piard, C.-J. 1757, *M. officinarum* (K)
- Polunin, O. 631, *M. caulescens* (BM); 780, *M. caulescens* (BM); 6616, *M. officinarum* (K)
- Polunin, O., Sykes, W.R. & Williams, L.H.J. 878, *M. caulescens* (BM, P); 4250, *M. caulescens* (BM); 4668, *M. caulescens* (BM); 4696, *M. caulescens* (BM)
- Pratt, A.E. 755, *M. caulescens* (BM, K, P)
- Probyn, F.M. 49, *M. officinarum* (K)
- Raulin, V. s.n., *M. officinarum* (P); 302, *M. officinarum* (P)
- Rechinger, K.H. 90, *M. officinarum* (BM); 3630, *M. officinarum* (BM, K)
- Reiser, C. s.n., *M. officinarum* (K)
- Reverchon, E. s.n., *M. officinarum* (BM, E, P, K); 117, *M. officinarum* (BM, E, K, P, PAL); 469 [1888], *M. officinarum* (BM, P); 469 [1890], *M. officinarum* (P)
- Rhomoo, L. 210, *M. caulescens* (E); 1059, *M. caulescens* (E)
- Ribu & Rhomoo 5492, *M. caulescens* (BM, E, K)
- Rock, J.F. 3597, *M. caulescens* (E); 3985, *M. caulescens* (P); 4211, *M. caulescens* (BM); 17530, *M. caulescens* (E); 22771, *M. caulescens* (E); 24750, *M. caulescens* (BM, E); 25005, *M. caulescens* (BM, E)
- Ross, H. s.n., *M. officinarum* (BM)
- Ross, H. 266, *M. officinarum* (E, K, P)
- Schneider, C. 3501, *M. caulescens* (E, K)
- Sintenis & Rigo 8, *M. officinarum* (K, PAL); 8a, *M. officinarum* (K)
- Smith, W.W. 4593, *M. caulescens* (E)
- Soulié, J.-A. 849, *M. caulescens* (P); 1252, *M. caulescens* (P); 2102, *M. caulescens* (P)
- Stainton, J.D.A. 254, *M. caulescens* (BM); 4263, *M. caulescens* (BM); 4676, *M. caulescens* (BM)
- Starling, B.N., Upward, E.M., Brickell, C.D. & Mathew, B. 92, *M. caulescens* (K); 106, *M. caulescens* (K)
- Syngrassides, A. 1464, *M. officinarum* (K)
- Taleb, A. 38, *M. officinarum* (RNG)
- Taton, A. 1630, *M. officinarum* (BM)
- Thomas, P. s.n., *M. officinarum* (K)
- Tilman, H.W. 23, *M. caulescens* (K)
- Todaro, A. s.n., *M. officinarum* (P)
- Todd, E. s.n., *M. officinarum* (BM)
- Tomkinson, M.J. 72, 72A, *M. officinarum* (BM)
- Townsend, C.C. 85/11, *M. officinarum* (K)
- Tozer, H.F. s.n., *M. officinarum* (K)
- Treffewy, A.W. 11, *M. officinarum* (K); 20, *M. officinarum* (K)
- Vaccari, A. 1141, *M. officinarum* (K); 2326, *M. officinarum* (BM, K)
- Virantonio s.n., *M. officinarum* (BM)
- Walree, A.M. 22226, *M. officinarum* (BM)
- Walsh, E. 113, *M. caulescens* (K)
- Watt, G. 5373, *M. caulescens* (E, K); 5436, *M. caulescens* (E, K)
- Welwitsch, F.M.J. s.n., *M. officinarum* (P); 159, *M. officinarum* (BM); 337, *M. officinarum* (P)
- White, M.F. s.n., *M. officinarum* (BM)
- Williams, L.H.J. 700, *M. caulescens* (BM)
- Wilson, E.H. 4192, *M. caulescens* (BM, K, P); 4194, *M. caulescens* (BM, K, P); 4195, *M. caulescens* (K)
- Wolley-Dod, A.H. 22, *M. officinarum* (BM)
- Yü, T.T. 5496, *M. caulescens* (KUN); 11327, *M. caulescens* (KUN); 19078, *M. caulescens* (E); 19843, *M. caulescens* (E, KUN)
- Zimmermann, A. 688, *M. caulescens* (BM)

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**TAXONOMIC INDEX**


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Accepted names are given in roman, synonyms in *italics*. An asterisk denotes a figure.

*Anisodus caulescens* (C.B. Clarke) Diels 34

*A. luridus* Link 22

*A. mariae* Pascher 34

*Atropa acaulis* Stokes 30

*A. belladonna* L. 30

*A. humilis* Salisb. 30

*A. mandragora* L. 30

*Lycium chinense* Mill. 22

*Mairella yunnanensis* H. Lévl. 34

*Mandragora acaulis* Gaertn. 30

*M. autumnalis* Bertol. 30

*M. caulescens* C.B. Clarke 34, 35\*

*M. caulescens* subsp. *brevicalyx* Grierson & D.G. Long 34

*M. caulescens* C.B. Clarke subsp. *caulescens* 34

*M. caulescens* subsp. *flavida* Grierson & D.G. Long 34

*M. caulescens* subsp. *purpurascens* Grierson & D.G. Long 34

*M. chinghaiensis* Kuang & A.M. Lu 34

*M. foemina* Garsault 30

*M. haussknechtii* Heldr. 30

*M. hispanica* F. Vierh. 30

*M. × hybrida* Hausskn. & Heldr. 30

*M. mas* Garsault 30

*M. microcarpa* Bertol. 30

*M. neglecta* G. Don ex Loudon 30

*M. officinarum* L. 30, 31\*, 32\*

*M. praecox* Sweet 30

*M. shebbeari* C.E.C. Fisch. 19

*M. tibetica* Grubov 34

*M. turcomanica* Mizg. 33

*M. vernalis* Bertol. 30

*Nicotiana glauca* Graham 22

*Przewalskia* Grubov 19

# The pteridophytes of São Tomé and Príncipe (Gulf of Guinea)

**ESTRELA FIGUEIREDO**

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**SYNOPSIS.** A catalogue of the pteridophytes of São Tomé and Príncipe is presented, with 156 taxa, 12 of which are endemic to the islands. Recent synonymy for the area is included. All collections examined are cited.

## INTRODUCTION

The most recent account of the pteridophytes of São Tomé and Príncipe (Gulf of Guinea) was produced by Alston in 1944. Since then several nomenclatural changes have taken place and new records have been added to the flora of the islands (e.g. Alston 1958, 1959).

The pteridophytes of the neighbouring island of Bioko (Fernando Po) have been recently revised by Benl (1978, 1980, 1982, 1988, 1991) who provided descriptions and keys to the taxa. The lack of an updated checklist for São Tomé and Príncipe and the difficulty in compiling the dispersed information on this group of plants have precluded its inclusion in recent floristic and biodiversity studies (Figueiredo, 1994).

The incorporation of several recent collections from São Tomé

and Príncipe at LISC, has revealed further new records and new areas of distribution for some taxa, and provided the basis for a revision of Alston's (1944) account.

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## DIVERSITY

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There are 153 indigenous taxa of pteridophytes in São Tomé and Príncipe occurring from sea level (e.g. *Acrostichum aureum* L., found in swamps and mangroves) to the highest peaks of the islands (e.g. *Grammitis* spp.), and belonging to 28 families and 60 genera. Three taxa were probably introduced, and became naturalized, *Pityrogramma calomelanos* (L.) Link (Alston, 1944), *Adiantum raddianum* C. Presl from the Neotropics (Alston, 1956a), and *Pteris vittata* L. (Alston 1958, 1959).

One hundred and thirty-seven taxa occur in São Tomé and 75 occur in Príncipe; 12 taxa are endemic to the islands. In Bioko, the pteridophyte richness is higher than in either São Tomé or Príncipe, with 208 taxa in 31 families (Benl, 1978). However, only four taxa (1.9%) are endemic to Bioko, while eight taxa are endemic to São Tomé (5.8%) and three are endemic to Príncipe (4%).

This difference in the percentage of endemics is less striking than the difference found for the angiosperms. In that group, Bioko has 3.6% endemic taxa, São Tomé has 13.4%, and Príncipe has 8.2% (Figueiredo, 1994).

*Asplenium* is the genus of pteridophytes with the largest number of taxa in São Tomé and Príncipe. Twenty-four taxa are represented, of which three are endemic.

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## CONSERVATION

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Twenty-five taxa collected in São Tomé and Príncipe in the nineteenth century have not been collected since, even though extensive collecting took place in the 1950s and also in the 1990s. Although some of these taxa, represented in the herbarium by a single collection, may be doubtful records, others were collected more than once by different collectors. The absence of these taxa amongst the collections made this century may indicate their rarity or extinction. For example, *Microlepia speluncae* (L.) T. Moore was collected in São Tomé by Don (s.l.), Quintas (Ilhéu das Rolas), and Welwitsch (Monte Café). Although Monte Café is a well collected area, visited by most botanists, this species has not been found during the last 100 years. Elsewhere in Africa, *M. speluncae* is rare and sporadic, occurring at low to medium altitudes.

Sixteen taxa are represented in herbaria by a single collection, either from São Tomé or from Príncipe (10 from São Tomé and 6 from Príncipe), which may indicate their rarity or even extinction. When Príncipe alone is considered, 27 of the total of 75 taxa have been collected only once. In this case, mistaken recordings or undercollecting are also a possibility. Several species are represented in herbaria by a single collection made by Barter, who visited Príncipe when stationed at Bioko, and therefore it is possible that there were some errors when the specimens were labelled. Príncipe remains poorly collected and recent collections of pteridophytes from that island were not available to confirm the presence of these taxa.

Seven taxa are apparently restricted to the Pico of São Tomé [*Asplenium friesiorum* C. Chr., *Ctenitis cirrhosa* (Schum.) Ching, *Grammitis molleri* (Baker) Schelpe, *G. tomensis* Schelpe, *Huperzia ophioglossoides* (Lam.) Rothm., *Lycopodium clavatum* L., and

*Xiphopteris oosora* (Baker) Alston] and five taxa are confined to the Pico of Príncipe [*Grammitis nigrocincta* Alston, *Hymenophyllum polyanthos* var. *mildbraedii* (Brause ex Brause & Hieron.) Schelpe, *Lomariopsis warneckeii* (Hieron.) Alston, *Selaginella squarrosa* Baker, and *Triplophyllum jenseniae* (C. Chr.) Holttum]. Most of these are high altitude pteridophytes which are also distributed on other African mountains. Two of these taxa, *Grammitis molleri* and *G. tomensis*, are very rare and endemic to the Pico of São Tomé. *Lycopodium clavatum* is cosmopolitan but, in the tropics, it is confined to mountains.

Of the twelve taxa endemic to São Tomé and Príncipe, two are apparently very rare, having been collected only once: *Selaginella monodii* Alston and *Sphaerostephanos elatus* subsp. *thomensis* Holttum.

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## COLLECTIONS

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### Historical collections

Exell (1944) gives a lively account of the early collectors in São Tomé and Príncipe. The majority of the earliest collections of pteridophytes from São Tomé and Príncipe were made by Don (in 1822), Curror (in 1839), Welwitsch (in 1853), Barter (in 1858), and Mann (in 1861). These collections are deposited at K (Curror, Barter, and Mann), BM (Don and Welwitsch), and LISU (Welwitsch).

In the late nineteenth century extensive collecting was made by the Portuguese collectors Moller, Quintas, and Newton. The original set of these collections is kept at COI, but duplicates were sent to several European herbaria. The duplicates were distributed as *Flora Africanae Exsiccata* (F.A.E.), a series in which different collections of the same taxon were grouped and distributed with the same number. For this reason, most F.A.E. labels refer to several localities and different collectors. After examining the original sets of the Moller, Quintas, and Newton collections, Exell (1944: 383–385) tried to link originals with duplicates. However, it seems that, for the pteridophytes, in most cases the original collections were scarcely labelled, lacking the information needed to link them to the duplicates distributed. Many F.A.E. duplicates sent from COI to K had a second label referring to a single collector. The numbering on these collector labels is unique to K specimens, as the original sets at COI are mostly unnumbered. Although the second label usually refers to a single collector and locality there is no certainty as to the correspondence between the specimen and the data. The information consisting of more than one locality, found on some F.A.E. and original set labels, is worthless and misleading because it is not possible to relate it to the specimens it is attached to. This information should be omitted when those collections are cited.

Together with the F.A.E. collections, the collections made by Chevalier in 1905 and Exell in 1932–33, the first sets of which are deposited, respectively, at P and BM, comprise the bulk of the material examined to produce Alston's account of the pteridophytes in Exell's Catalogue (1944).

### Recent collections

Only a few collections were made during the twenty years that followed Exell's expedition in 1932–33. The majority of recent collections were made during the years 1954–1973, and in the 1990s.

The first set of the collections made by Rozeira in São Tomé and Príncipe in 1954 is deposited at PO. However, several collections of pteridophytes cited in the literature (Alston, 1958) could not be located in that herbarium. A set of duplicates of Rozeira's collection is apparently deposited at BM (Exell & Rozeira, 1958) but could not be found in 1997. Some duplicates (with the name of the collector missing) exist at K. Based on Rozeira's collections, new records for the islands were published by Alston (1958) in the proceedings of the 'Conferência Internacional dos Africanistas Ocidentais', which took place in São Tomé in 1956.

During 1956 several botanists collected in São Tomé and Príncipe. As part of a Calypso expedition which took place in 1956–57, Rose made several collections in the two islands, including living material, which were deposited at P. In the same year, Monod and Thorold made important collections in São Tomé and Príncipe, which are deposited at BM. These collections were studied by Alston (1958, 1959) and resulted in several new records being added to the flora of the islands. Lains e Silva also collected in São Tomé in 1956. Although his collections have been cited in the literature, several numbers could not be found either at LISJC or LISU. In 1968–1973, Espírito Santo collected in both islands. The original sets of his collections are kept at LISJC and LISC, with some duplicates at BM and COI.

Recent collections of pteridophytes from São Tomé examined during this study were mainly made by Pinto Basto in 1990, Matos and Matos & Van Essche in 1994, and Lejoly in 1994–1995, and are deposited at LISC. Recent collections were also made by Paiva (COI), but these were not available for examination at the time of this study.

## CATALOGUE

The catalogue includes all the taxa of pteridophytes known to occur in São Tomé and Príncipe, arranged in alphabetical order, with synonyms and references to the literature for the area published since 1944. Synonyms already cited in Alston's (1944) work are omitted.

All the collections examined are cited in this catalogue. Collections cited in the literature are also included. Some of these specimens were not located (indicated in the text with 'not found'), and others were not available for study. Some of the collections cited but not seen by Alston (1944), probably at B, were not examined during this study; these are marked with a question mark. It is possible that a future study of the unseen material may reveal misidentifications by previous authors.

For each taxon, the collections are cited by alphabetical order of collectors, but collections from the same locality are grouped. Collections without locality are placed at the end of the specimens cited. These include *F.A.E.* and *Moller* collections with more than one locality on the labels. *F.A.E.* duplicates at K are cited under their *F.A.E.* number and reference is made to other labels and numbers if they exist.

Most of the localities provided by the collectors consist of the name of a plantation ('roça') or a river. For this reason, distribution maps based on these collections would be very inaccurate. Maps with 'roças' and other collecting localities mentioned in the text are provided, to allow for an estimate of the distribution of the taxa (Figs 1 and 2).

Data on habit, habitat, and ecology are lacking for the vast majority of the collections examined.

## Acrostichaceae

### Acrostichum L.

*Acrostichum aureum* L., *Sp. pl.* 2: 1069 (1753); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 85 (1944); Benl in *Acta Bot. Barcinon.* 38: 22 (1988).

**SÃO TOMÉ.** Porto Alegre, *Chevalier* 14194bis (P!), 14200 (P!), salt marshes, *Espírito Santo* 5131 (LISC!, LISJC!); Ilhéu das Rolas, *F.A.E. (Quintas)* 69 (BM!, LISU!), *Quintas* s.n. (COI!); Porto Alegre, Praia Jalé, Rio Malanza, swamp, *Matos* 7663 (LISC!); Perseverança, *Rose* 538 (P!).  
**PRÍNCIPE.** Santo António, salt marshes, *Espírito Santo* 5170 (LISC!, LISJC!), mangrove, *Monod* 12191 (BM!), mangrove, *Rose* 425 (P!); Rio Papagaio, swampy border, *Quintas* 1 (BM!, COI!); Praia General Fonseca, *Rozeira* 430 (PO!); s.l., *Welwitsch* 15 (BM!, LISU!).

DISTRIBUTION. Pantropical.

## Adiantaceae

### Adiantum L.

*Adiantum mettenii* Kuhn, *Filic. afr.*: 65 (1868) nomen; in *Jahrb. Königl. Bot. Gart. Berl.* 1: 338 (1881).

*Adiantum soboliferum* sensu auct. non Wall. ex Hook., *Sp. fil.* 2: 13, t. 74A (1858); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 82 (1944).

**SÃO TOMÉ.** Monte Forte, 50 m, *Quintas* s.n. (COI!, K!); s.l., *Don* s.n. (BM!).

DISTRIBUTION. Tropical Africa and Madagascar, extending to India and Philippines.

NOTE. This taxon has not been recorded in the islands since the nineteenth century.

*Adiantum philippense* L., *Sp. pl.* 2: 1094 (1753); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 82 (1944); Alston in Exell, *Suppl. Cat. Vasc. Pl. S. Tomé*: 7 (1956); Benl in *Acta Bot. Barcinon.* 32: 26 (1980).

**SÃO TOMÉ.** Casal Pires, waterfall, 200 m, *Espírito Santo* 110 (BM!, COI!, LISJC!); Boa Entrada, *Chevalier* 14518 (P); Rio do Ouro, 110 m, *Quintas* 1249 (BM!, COI!, LISJC!); Água Coimbra, 100 m, *Quintas* s.n. (COI!), *Moller & Quintas* s.n. (LISU!); Diogo Vaz, *Rozeira* 518 (PO!); Santa Catarina, between main house and Lembá, *Rozeira* 840 (PO!).

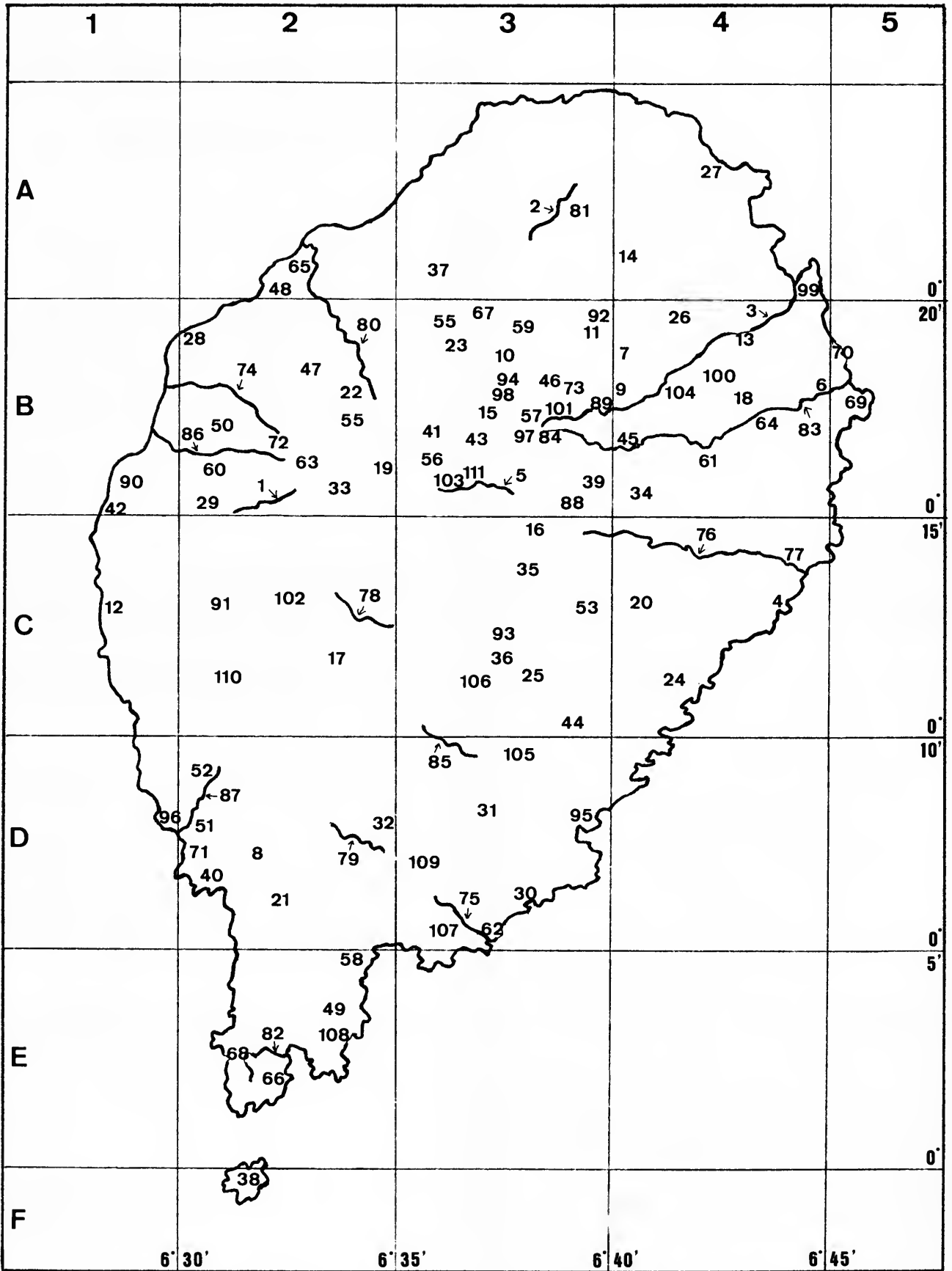
DISTRIBUTION. Palaeotropical.

*Adiantum raddianum* C. Presl, *Tent. pterid.*: 158 (1836); Alston in Exell, *Suppl. Cat. Vasc. Pl. S. Tomé*: 7 (1956); Alston in Exell & Rozeira in *Conf. Int. Afr. Oc.* 3: 79 (1958).

**SÃO TOMÉ.** Quinta da Graça, 600 m, *Espírito Santo* 124 (BM!, COI!, LISJC!); Pouso Alto, 490 m, *Espírito Santo* 4278 (LISC!, LISJC!); Monte Café, São Carlos, secondary forest, *Espírito Santo* 5048 (LISC!, LISJC!); São Nicolau, waterfall, on wet rocks, *Espírito Santo* 5178 (LISC!, LISJC!); Saudade, 900 m, *Exell* 399 (BM!, COI!); Ponta Figo, on the way to Morro Vilela, *Lains e Silva* 357 (LISU!); between Pico and Monte Castro, 1200–1800 m, mountain rainforest, *Lejoly* 95/13 (LISC!); Monte Café, 1010 m, *Monod* 11694 (BM!, COI!), *Oliveira & Noronha* s.n. (LISU!); NW of Pico, 1000–1200 m, *Monod* 12263 (BM!, COI!); Água Izé, common, *Pinto Basto* 199 (LISC!); Trás-os-Montes, Calvário, *Rozeira* 582 (PO!).

**PRÍNCIPE.** Esperança, near Ribeira Camarão, *Rozeira* 354 (PO!).

DISTRIBUTION. Cultivated American species, escaped and naturalized.



**Adiantum vogelii** Mett. ex Keyserl. in *Mém. Acad. Imp. Sci. Saint Pétersbourg ser. 7*, **22**(2): 8, 31 (1875); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 83 (1944); Tardieu-Blot in Aubrév., *Fl. Cameroun 3*: 147 (1964); Benl in *Acta Bot. Barcinon.* **32**: 26 (1980).

**PRÍNCIPE**. Santo António, *Monod* 12072 (BM!, COI!); Berimbau, *Newton* 18 (BM!, COI!, K!); *Newton* s.n. (K!); Cimáló, *Quintas* 36 (BM!, COI!); Esperança, between Montalegre and Máquina, *Rozeira* 378 (PO!); s.l., *Souza* s.n. (COI!).

**DISTRIBUTION**. W. tropical Africa to Angola, Zanzibar.

## Aspidiaceae (=Dryopteridaceae)

### Ctenitis (C. Chr.) C. Chr.

**Ctenitis cirrhosa** (Schum.) Ching in *Sunyatsenia* **5**: 250 (1940); Benl in *Acta Bot. Barcinon.* **40**: 41 (1991).

*Dryopteris crinobulbon* (Hook.) C. Chr., *Index filic.*, Suppl. 3: 84 (1934); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 61 (1944).

**SÃO TOMÉ**. Pico, 1850 m, *Mann* s.n. (B, K!-type of *Dryopteris crinobulbon*).

**DISTRIBUTION**. Tropical and SE Africa, Madagascar, Comoros and Mascarene Is.

**NOTE**. This taxon has not been recorded in the islands since the nineteenth century.

**Ctenitis lanuginosa** (Willd. ex Kaulf.) Copel., *Gen. fil.*: 124 (1947); Benl in *Acta Bot. Barcinon.* **40**: 41 (1991).

*Dryopteris lanuginosa* (Willd. ex Kaulf.) C. Chr., *Index filic.*: 273 (1905); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 62 (1944).

**SÃO TOMÉ**. S.l., *Mann* s.n. (K-not found).

**DISTRIBUTION**. Tropical and subtropical Africa, Madagascar, Comoros, Seychelles and Mascarene Is.

**NOTE**. This taxon has not been recorded in the islands since the nineteenth century.

### Didymochlaena Desv.

**Didymochlaena truncatula** (Sw.) J. Sm. in *J. Bot. (Hooker)* **4**: 196 (1841); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 66 (1944); Tardieu-Blot in Aubrév., *Fl. Cameroun 3*: 254 (1964); Benl in *Acta Bot. Barcinon.* **40**: 35 (1991).

**SÃO TOMÉ**. Rio Contador, 1270–1350 m, *F.A.E. (Moller)* 36 (BM!, LISU!); Trás-os-Montes, *Gama* s.n. (COI!); *Mollers* s.n. (COI!); Macambrará, 1270 m, *Moller* s.n. (COI!); Sela do Camelo, near Lembá, 200 m, *Rozeira* 3450 (PO!); Monte Café, 760–850 m, *Welwitsch* 67 (BM!, K!, LISU!).

**DISTRIBUTION**. Pantropical.

### Dryopteris Adans.

**Dryopteris pentheri** (Krasser) C. Chr., *Index filic.*: 284 (1905); Alston in Exell in *Bull. Inst. Franç. Afrique Noire ser. A*, **21**: 447 (1959); Benl in *Acta Bot. Barcinon.* **40**: 36 (1991).

*Dryopteris oligantha* sensu auct. non (Desv.) C. Chr., *Index filic.* Suppl. 3: 93 (1934); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 62 (1944).

**SÃO TOMÉ**. Pico, *Chevalier* 13651 (P), 14290 (P), *Moller* s.n. (COI-not found, P!); between Monte Café and Pico, *Chevalier* 14580 (P); Macambrará, *Exell* 131 (BM), 135 (BM); Trás-os-Montes, *Gama* s.n. (COI-not found), 800 m, *Quintas* 1286 (BM!, COI-not found), *Rozeira* 554 (K!, PO!); between Pico and Monte Castro, 6 km S. of Ponta Figo, mountain rainforest, 1200–1800 m, *Lejoly* 95/9 (LISC!); between Monte Quinas and Quinas Altas, *Monod* 12007 (BM!); Monte Café, 1010 m, *Monod* 11696 (BM!); Lagoa Amélia, 1300 m, *Quintas* 1291 (BM!, COI-not found), *Rose* 199 (P!); São Nicolau, near waterfall, *Rozeira* 182 (K!, PO!); Santa Catarina, Lembá, *Rozeira* 856 (K!); s.l., 1850 m, *Mann* (K!), *F.A.E. (Moller)* 39 (BM!, LISU!), *Moller* s.n. (COI-not found), *Quintas* 10 (K!).

**DISTRIBUTION**. Tropical and southern Africa.

<b>Fig. 1</b> São Tomé	23. Chamiço-3B	45. Milagrosa (Roça)-4B	68. Praia Jalé-2E	89. Rodia (Roça)-3B
1. Água Cardoso-2B	24. Colónia Açoreana (Roça)-4C	46. Monte Café (Roça)-3B	69. Praia Melão (Roça)-5B	90. Santa Catarina (Roça)-1B
2. Água Coimbra-3A	25. Cruzeiro (Roça)-3C	47. Monte Castro-2B	70. Praia Pantufo-5B	91. Santa Irene (Roça)-2C
3. Água Grande-3B-4B-4A	26. Diana (Roça)-4B	48. Monte Forte (Roça)-2A	71. Quijá-2D	92. Santa Margarida (Roça)-3B
4. Água Izé (Roça)-4C	27. Diogo Nunes-4A	49. Monte Mário (Roça)-2E	72. Quinas Altas -2B	93. Santelmo (Roça)-3C
5. Água Pinhão-3B	28. Diogo Vaz (Roça)-2B	50. Monte Quinas-2B	73. Quinta da Graça (Roça)-3B	94. São Carlos (Roça)-3B
6. Almas-4B	29. Dona Amélia (Roça)-2B	51. Monte Rosa (Roça)-2D	74. Ribeira Moça-1B-2B	95. São João dos Angolares-3D
7. António Soares-4B	30. Dona Augusta (Roça)-3D	52. Monte Verde-2D	75. Ribeira Peixe-3D	96. São Miguel (Roça)-1D
8. Bacelar-2D	31. Dona Eugénia (Roça)-3D	53. Morro Cantagalo-3C	76. Rio Abade-3C-4C	97. São Nicolau (Roça)-3B
9. Batepá-4B	32. Ermelinda (Roça)-2D	54. Morro Vigia -3B	77. Rio Abade (bridge) -4C	98. São Pedro-3B
10. Bemposta (Roça)-3B	33. Estação Sousa-2B	55. Morro Vilela-2B	78. Rio Campos-2C	99. São Tomé -4A
11. Benfica (Roça)-3B	34. Famosa-4B	56. Nova Ceilão (Roça)-3B	79. Rio Caué-2D	100. São Vicente-4B
12. Bindá (Roça)-1C	35. Formoso-3C	57. Nova Moca (Roça)-3B	80. Rio Contador-2A-2B	101. Saudade (Roça)-3B
13. Blu-blu-4B	36. Guaiquil (Roça)-3C	58. Novo Brasil (Roça)-2E	81. Rio do Ouro (Roça)-3A	102. Sela do Camelo-2C
14. Boa Entrada (Roça)-4A	37. Guarda (Roça)-3A	59. Novo Destino (Roça)-3B	82. Rio Malanza-2E	103. Trás-os-Montes (Roça)-3B
15. Bom Sucesso (Roça)-3B	38. Ilhéu das Rolas-2E-2F	60. Paga Fogo (Roça)-2B	83. Rio Manuel Jorge-3B-4B-5B	104. Trindade-4B
16. Bombaim (Roça)-3C	39. Jau (Roça)-3B	61. Pedroma (Roça)-4B	84. Rio Manuel Jorge (waterfall)-3B	105. Vale Carmo (Roça)-3D
17. Cabumbé-2C	40. Jov (Roça)-2D	62. Perseverança (Roça)-3D	85. Rio Miranda Guedes-3C-3D	106. Vieira Machado (Roça)-3C
18. Caixão Grande-4B	41. Lagoa Amélia-3B	63. Pico-2B	86. Rio Paga Fogo-1B-2B	107. Vila Aida (Roça)-3D
19. Calvário-2B	42. Lembá (Roça)-1B	64. Pinheira (Roça)-4B	87. Rio Xufexufe-2D	108. Vila Conceição (Roça)-2E
20. Cantagalo (Roça)-4C	43. Macambrará (Roça)-3B	65. Ponta Figo (Roça)-2A	88. Roça Nova (Roça)-3B	109. Vila José (Roça)-3D
21. Cão Pequeno-2D	44. Maria Fernandes-3C	66. Porto Alegre (Roça)-2E		110. Zagaia-2C
22. Cascata-2B		67. Pouso Alto (Roça)-3B		111. Zampalma (Roça)-3B.

The following collecting localities could not be located: Água Telha (Diogo Vaz), Água Telha (near Ribeira Moça), Casa do Pico (1935 m alt.), Casal Pires, Correia, Monte Figo, Magodinho, Morro Pempem (Trás-os-Montes), Quingombó, Santa Maria, Rio Santo António.

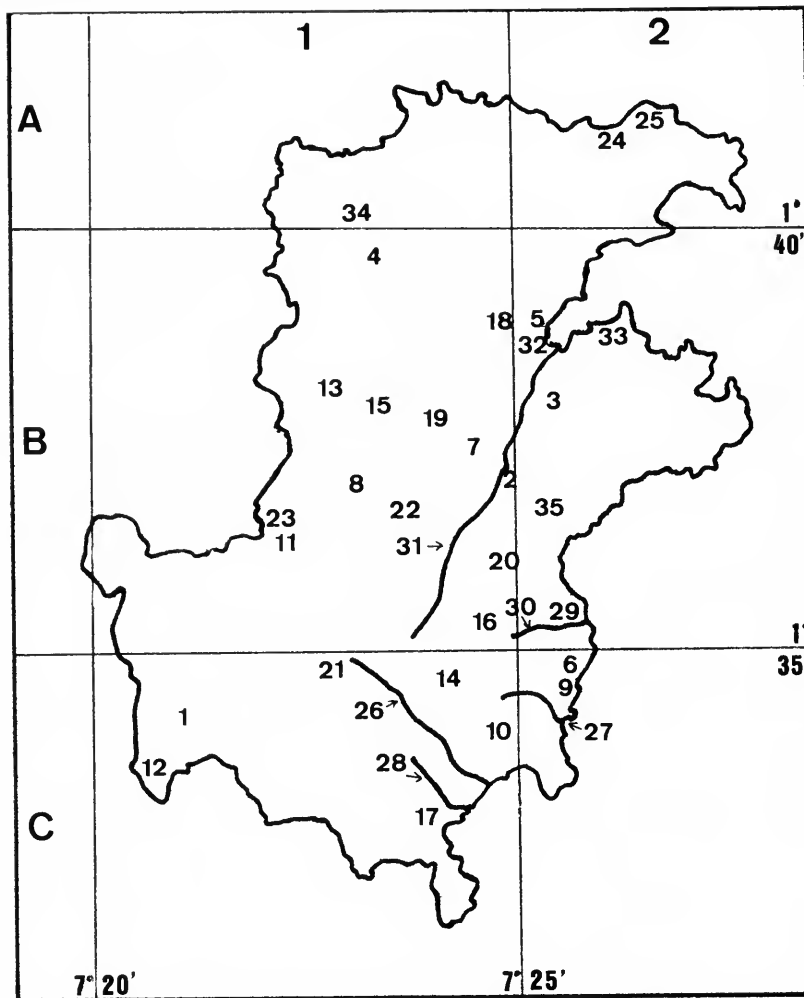


Fig. 2 Príncipe

- |                         |                                   |                              |                            |                            |
|-------------------------|-----------------------------------|------------------------------|----------------------------|----------------------------|
| 1. Barriga Branca-1C    | 8. Fundão-1B                      | 14. Meneorne-1C              | 21. Pico-1C                | 28. Ribeira Chimboto-1C    |
| 2. Bela Vista (Roça)-1B | 9. General Fonseca-2C             | 15. Montalegre (Roça)-1B     | 22. Pico Papagaio-1B       | 29. Ribeira Fria (Roça)-2B |
| 3. Berimbau-2B          | 10. Infante D. Henrique (Roça)-1C | 16. Morro do Leste-1B        | 23. Praia da Lapa-1B       | 30. Ribeira Jambere-1B-2B  |
| 4. Cajamanga-1B         | 11. Lapa (Roça)-1B                | 17. Neves Ferreira (Roça)-1C | 24. Praia das Burras-2A    | 31. Rio Papagaio-1B-2B     |
| 5. Cimãlô-2B            | 12. Mamas-1C                      | 18. Ôquê Gaspar (Roça)-1B    | 25. Precipício-2A          | 32. Santo António-2B       |
| 6. Dois Irmãos-2C       | 13. Máquina-1B                    | 19. Ôquê Nazaré-1B           | 26. Ribeira Bibi-1C        | 33. São João (Roça)-2B     |
| 7. Esperança (Roça)-1B  |                                   | 20. Ôquê Pipi-1B             | 27. Ribeira Cambungo-1C-2C | 34. Sundi (Roça)-1A        |
|                         |                                   |                              |                            | 35. Terreiro Velho-2B.     |

The following collecting localities could not be located: Porto Real, Ribeira Camarão and Rio Bambu-Porco.

### Lastreopsis Ching

**Lastreopsis** aff. **currori** (Mett. ex Kuhn) Tindale in *Victoria Naturalist* 73: 184 (1957); Tindale in *Contr. New South Wales Natl. Herb.* 3: 338 (1965).

*Aspidium nigritianum* Mett. ex Kuhn, *Filic. afr.*: 138 (1868).

*Dryopteris nigritiana* (Mett. ex Kuhn) Kuntze, *Revis. gen. pl.* 2: 813 (1891); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 62 (1944).

*Ctenitis nigritiana* (Mett. ex Kuhn) Alston in *Bol. Soc. Brot., ser. 2*, 30: 12 (1956).

**PRÍNCIPE**. Rio Bambu-Porco, 60 m, *Navel* 138 (LISU!), 141B (not found); Pico, *Rozeira* 2607 (PO!); s.l., *Barter* 1906 (K-type of *Aspidium nigritianum*, not found).

### Tectaria Cav.

**Tectaria** **angelicifolia** (Schum.) Copel. in *Philipp. J. Sci., ser. C, Bot.* 2: 410 (1907); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 66

(1944); Alston in Exell, *Suppl. Cat. Vasc. Pl. S. Tomé*: 7 (1956); Benl in *Acta Bot. Barcinon.* 40: 55 (1991).

**SÃO TOMÉ**. São Vicente, 200 m, *Espírito Santo* 42 (BM!, COI!, LISJC!); Bombaim, *Monod* 11886 (BM!); between São Tomé and Monte Café, *Welwitsch* 62 (BM!, LISU!); s.l., *F.A.E. (Moller & Quintas)* 43 p.p. (BM!, COI!, K also *Moller* 32!, LISU!), 550 m, *Welwitsch* s.n. (K!).

**PRÍNCIPE**. S.l., *Welwitsch* 12b (BM!, LISU!).

**DISTRIBUTION**. W. and Central tropical Africa

**Tectaria** **camerooniana** (Hook.) Alston in *J. Bot.* 77: 288 (1939); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 67 (1944); Tardieu-Blot in Aubrév., *Fl. Cameroun* 3: 291 (1964); Benl in *Acta Bot. Barcinon.* 40: 56 (1991).

**SÃO TOMÉ**. Macambrará to Zampalma, 900 m, ground fern, *Exell* 293 (BM!), 294 (BM!, COI!); between Bom Sucesso and Lagoa Amélia, primary forest, 1350–1420 m, *Matos & Van Essche* 7296 (LISC!); above Monte Café, 1010 m, *Monod* 11693 (BM!); between São Pedro and Lagoa Amélia, 1050



m, *Monod* 11711 (BM!); Calvário, 1200 m, *Monod* 11815 (BM!), 11817 (BM!); Lagoa Amélia, *Rose* 232 (P!); s.l., *F.A.E. (Moller)* 44 (BM!, COI!, LISJC!, LISU!, P!).

DISTRIBUTION. W. and Central tropical Africa.

**Tectaria fernandensis** (Baker) C. Chr., *Index filic.*, Suppl. 3: 179 (1934); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 67 (1944); Benl in *Acta Bot. Barcinon.* **40**: 57 (1991).

**SÃO TOMÉ.** Boa Entrada, *Chevalier* 14360 (P!), 14517 (P!); SW region, *Chevalier* 14591 (P!), 14617 (P!); São Miguel, 50 m, *Espírito Santo* 4742 (LISJC!); between Pico and Monte Castro, 6 km S. of Ponta Figo, mountain rainforest, 1200–1800 m, *Lejoly* 95/10 (LISJC!); São Miguel, Monte Verde, secondary forest, 10–150 m, *Lejoly* 95/84 (LISJC!); Pedroma, *Mocquerys* 125/126 (P!); São João dos Angolares, 80 m, *Newton* s.n. (COI!), 50 m, *Quintas* s.n. (COI!); Água Izé, common, *Pinto Basto* 211 (LISJC!); Perseverança, *Rose* 537 (P!); s.l., *Don* s.n. (BM!), *F.A.E. (Moller & Quintas)* 43 p.p. (LISJC!).

**PRÍNCIPE.** Between Ôquê Pipi and Morro do Leste, secondary forest, 350 m, ground fern, *Exell* 564 (BM!, COI!), 565 (BM!, COI!); Pico Papagaio, 600 m, ground fern, *Exell* 684 (BM!); s.l., *Barter* 1907 (K!), *Welwitsch* 12 (BM!, K!, LISU!).

DISTRIBUTION. W. and Central tropical Africa.

### **Triplophyllum** Holttum

**Triplophyllum buchholzii** (Kuhn) Holttum in *Kew Bull.* **41**: 251 (1986).

*Tectaria buchholzii* (Kuhn) Copel. in *Philipp. J. Sci.* **38**: 138 (1929) 'buckholzii'; Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 67 (1944).

*Ctenitis buchholzii* (Kuhn) Alston in *Bol. Soc. Brot.*, ser. 2, **30**: 11 (1956); Alston in Exell in *Bull. Inst. Franç. Afrique Noire ser. A*, **21**: 448 (1959).

**PRÍNCIPE.** Pico, 500–600 m, *Monod* 12119 (BM!), 800 m, *Rozeira* 886 (PO!), 911 (PO!), 2617 (PO!); Rio Bambu-Porco, 60 m, *Navel* 139B (LISU!); Infante D. Henrique, 250 m, *Rozeira* 2300 (PO!); Infante D. Henrique, old path to Ribeira Bibi, *Rozeira* 2391 (PO!); Mecomne, 200 m, *Rozeira* 2411 (PO!).

DISTRIBUTION. Ivory Coast to Zaïre.

**Triplophyllum fraternum** (Mett. ex Kuhn) Holttum in *Kew Bull.* **41**: 253 (1986).

*Aspidium fraternum* Mett. ex Kuhn, *Filic. afr.*: 132 (1868).

*Ctenitis fraterna* (Mett.) Tardieu in *Notul. Syst. (Paris)* **14**: 342 (1953).

var. **elongatum** (Hook.) Holttum in *Kew Bull.* **41**: 254 (1986).

*Nephrodium subquiquefidum* (P. Beauv.) Hook., *Sp. fil.* **4**: 130 (1862) var. *elongatum* Hook., *Sp. fil.* **4**: 130 (1862).

**PRÍNCIPE.** S.l., *Mann* 1861 (K!)-lectotype of *Nephrodium subquiquefidum* var. *elongatum*.

DISTRIBUTION. Endemic.

NOTES. The following collections are unlocalized but may have been collected in Príncipe, since there are no further collections from the continent: Niger Exped., *Barter* s.n. (K!), s.l., *Curror* s.n. (K!).

Based on the same type specimen, Pichi-Sermolli (1985) considered this fern to be a new species (*Ctenitis attenuata* Pic. Serm.) and later (Pichi Sermolli, 1991) transferred it to *Triplophyllum* with the name *T. attenuatum* (Pic. Serm.) Pic. Serm.

This taxon has not been recorded in the islands since the nineteenth century.

**Triplophyllum jenseniae** (C. Chr.) Holttum in *Kew Bull.* **41**: 253 (1986).

**PRÍNCIPE.** Pico, 850 m, *Rozeira* 1021 (PO!).

DISTRIBUTION. W. and Central tropical Africa.

**Triplophyllum principis** Holttum in *Kew Bull.* **41**: 246 (1986).

*Dryopteris variabilis* (Hook.) Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 64 (1944) var. *barteri* (Hook.) Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 64 (1944).

**PRÍNCIPE.** Ôquê Pipi, secondary forest, 300 m, ground fern, *Exell* 546 (BM!, COI!); between Ôquê Pipi and Morro do Leste, secondary forest, 350 m, ground fern, *Exell* 562 (BM!, COI!); above Infante D. Henrique, secondary forest, 300 m, ground fern, *Exell* 618 (BM!, COI!), 624 (BM!); Rio Bambu-Porco, 60 m, *Navel* 141a (LISU!); Ôquê Nazaré, 500 m, *Newton* s.n. (COI!); Infante D. Henrique, *Rose* 402 (P!), *Rozeira* 2370 (PO!); Neves Ferreira, *Rozeira* 2204A (PO!), 2205 (PO!); between Barriga Branca and Mamas, *Rozeira* 2552 (PO!); Mecomne, *Rozeira* 4299 (PO!); s.l., *Barter* 1927 (BM!, K!)-holotype, *Wilde* et al. 371 (WAG, cited by Holttum, l.c.).

DISTRIBUTION. Endemic.

**Triplophyllum protensum** (Afzel. ex Sw.) Holttum in *Kew Bull.* **41**: 247 (1986); Benl in *Acta Bot. Barcinon.* **40**: 45 (1991).

*Aspidium subquiquefidum* P. Beauv., *Fl. Oware* **1**: 34, t. 19 (1805).

*Dryopteris protensa* (Afzel. ex Sw.) C. Chr., *Index filic.*: 286 (1905); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 63 (1944).

**SÃO TOMÉ.** Bemposta, 600 m, *Moller* s.n. (BM!, COI!).

**PRÍNCIPE.** SW Esperança, 200 m, *Exell* 671a (BM!); São João, *Newton* s.n. (COI!); Infante D. Henrique, old path to Ribeira Bibi, *Rozeira* 2390A (PO!); Pico Papagaio, *Welwitsch* 16 (BM!, LISU!); s.l., *Souza* s.n. (COI!).

DISTRIBUTION. Widespread in W. and Central tropical Africa.

NOTE. Pichi Sermolli (1991) considered that the type of *Triplophyllum protensum* was a hybrid and described this taxon as a new species, *T. heudelotii* Pic. Serm. He considered *Triplophyllum subquiquefidum* (P. Beauv.) Pic. Serm. to be a distinct species. Of these two taxa only the latter was recorded for S. Tomé and Príncipe.

**Triplophyllum securidiforme** (Hook.) Holttum in *Kew Bull.* **41**: 242 (1986); Benl in *Acta Bot. Barcinon.* **40**: 43 (1991).

*Dryopteris securidiformis* (Hook.) C. Chr., *Index filic.*: 291 (1905).

*D. securidiformis* var. *nana* Bonap., *Not. pterid.* **14**: 211 (1923); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 64 (1944).

*Triplophyllum securidiforme* var. *nanum* (Bonap.) Holttum in *Kew Bull.* **41**: 243 (1986).

**SÃO TOMÉ.** Macambará, primary forest, 1050–1200 m, *Exell* 103 (BM!), 151 (BM!); Monte Café, 800 m, *Moller* s.n. (COI!); between Monte Quinas and Quinas Altas, *Monod* 12013 (BM!); São João dos Angolares, 200 m, *Quintas* s.n. (COI!); Ribeira Moça, *Rozeira* 2119 (PO!); between Ermelinda and Cabumbé, *Rozeira* 2819 (PO!), 2823 (PO!); Cantagalo, 400 m, *Rozeira* 3152 (PO!); Sela do Camelo, 200 m, *Rozeira* 3451 (PO!); Formoso, *Rozeira* 3537 (PO!); near Rio Miranda Guedes, *Rozeira* 3639 (PO!); Vieira Machado, 400 m, *Rozeira* 3666 (PO!); s.l., *F.A.E. (Moller & Quintas)* 40 (BM!, COI!, K also *Quintas* 44!, LISU!, P!).

**PRÍNCIPE.** Rio Bambu-Porco, 60 m, *Navel* 139A (LISU!), 141C (not found); Infante D. Henrique, *Rose* 409 (P!), 414 (P!); Neves Ferreira, *Rozeira* 2201 (PO!); Ribeira Camarão, *Rozeira* 2219 (PO!), 2220 (PO!), *Rozeira* 2268 (PO!); between Ribeira Jambere and Ribeira Fria, *Rozeira* 2237 (PO!); near Ribeira Cambungo, *Rozeira* 2239 (PO!); Infante D. Henrique, old path to Ribeira Bibi, *Rozeira* 2305 (PO!), 2326 (PO!); Infante D. Henrique, *Rozeira* 2374 (PO!); Mecomne, *Rozeira* 2408 (PO!); between Barriga Branca and Mamas, *Rozeira* 2562 (PO!); s.l., *Barter* 1929 (P!), *Mann* s.n. (K-not found).

DISTRIBUTION. W. and Central tropical Africa.

## Aspleniaceae

*Asplenium* L.

*Asplenium aethiopicum* (Burm.f.) Bech. in *Candollea* 6: 22 (1935); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 74 (1944); Benl in *Acta Bot. Barcinon.* 40: 24 (1991).

**SÃO TOMÉ.** Pico, primary forest, 1987 m, epiphyte, *Matos & Van Essche* 7381 (LISC!); Lagoa Amélia, 1430 m, epiphyte, *Matos* 7495 (LISC!); between Estação Sousa and Pico, primary forest, 1700 m, epiphyte, *Matos* 7554 (LISC!); Macambrará, 1270 m, *Moller* s.n. (COI!); Lagoa Amélia to São Pedro, 1200 m, *Quintas* 1392 (BM!, COI!); Monte Café, *Quintas* 1392 (LISJC!); s.l., *F.A.E. (Moller)* 31 (BM!, K!, LISU!), *Moller* s.n. (COI!).

DISTRIBUTION. Pantropical and subtropical.

*Asplenium africanum* Desv. in *Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk.* 5: 322 (1811); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 74 (1944); Benl in *Acta Bot. Barcinon.* 40: 6 (1991).

**SÃO TOMÉ.** Ilhéu das Roías, *Greeff* s.n. (B); near São Tomé, 8 m, *Moller* s.n. (COI!); Água Izé, frequent epiphyte, *Pinto Basto* 218 (LISC!); s.l., *Don* s.n. (BM!), *F.A.E. (Moller)* 21 (BM!, LISU!, P!).

**PRÍNCIPE.** Above Neves Ferreira, 200–350 m, epiphyte, *Exell* 650 (BM!, COI!); s.l., *Newton* (not found at COI).

DISTRIBUTION. W., Central, and E. Africa.

*Asplenium anisophyllum* Kunze in *Linnaea* 10: 511 (1836).

*Asplenium geppii* Carruth., *Cat. Afr. Pl.* 2: 269 (1901); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 78 (1944).

**SÃO TOMÉ.** Near São Pedro, 1280 m, *F.A.E. (Moller)* 26 (BM!, K also *Moller* 23!, LISU!); between Pico and Monte Castro, 6 km S. of Ponta Figo, mountain forest, 1200–1800 m, *Lejoly* 95/18 (LISC!); NW of Pico, 1350–1600 m, *Monod* 12226 (BM!); Lagoa Amélia, *Quintas* 1385 (BM!, COI!), *Rose* 206 (P!).

DISTRIBUTION. W. tropical Africa.

*Asplenium barteri* Hook., *Sec. cent. ferns*: t. 75 (1860); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 75 (1944); Tardieu-Blot in Aubrév., *Fl. Cameroun* 3: 192 (1964); Benl in *Acta Bot. Barcinon.* 40: 13 (1991).

**SÃO TOMÉ.** São Miguel, *Chevalier* 14491bis (P-not found); SW region, *Chevalier* 14618 (P!); Porto Alegre, *Chevalier* 14619bis (P!); Saudade and Pico, *F.A.E. (Moller)* 25 p.p. (BM!); São João dos Angolares, 80 m, *Newton* s.n. (BM!, COI!); Cruzeiro, 300 m, *Thorold* 2065 (BM!); s.l., *Matos* s.n. (LISC!).

**PRÍNCIPE.** Esperança, plantation, 100 m, on rocks, *Exell* 677 (BM!, COI!); W. of Pico, above Lapa, below 250 m, *Monod* 12100 (BM!); Pico, near Lapa, below 250 m, *Monod* 12103 (BM!); São João, 450 m, *Newton* 28 (BM!, COI!); Lapa (Oeste), *Quintas* 25 (BM!, COI!); s.l., *Barter* 1909 (K!), 1910 (K!).

DISTRIBUTION. Widespread in tropical Africa.

*Asplenium biafranum* Alston & F. Ballard in *Hooker's Icon. pl.* 34: t. 3367 (1938); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 75 (1944); Tardieu-Blot in Aubrév., *Fl. Cameroun* 3: 200 (1964); Benl in *Acta Bot. Barcinon.* 40: 23 (1991).

**SÃO TOMÉ.** Between Monte Café and Pico, *Chevalier* 14543 (P!); Macambrará, primary forest, 1050–1200 m, *Exell* 154 (BM!); Pico, primary forest, 1900–2020 m, *Lejoly* 94/581 (LISC!); between Lagoa Amélia and Chamiço, *Matos* 7528 (LISC!); Santa Maria, 1350 m, *Moller* s.n. (COI!);

Lagoa Amélia, 1400 m, *Monod* 11747 (BM!); Calvário, 1560 m, *Monod* 11834 (BM!); between Casa do Pico and Pico, 1950 m, *Monod* 11958 (BM!).

DISTRIBUTION. Benin, Bioko, Nigeria, Cameroun.

*Asplenium cuneatum* Lam., *Encycl.* 2: 309 (1786); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 75 (1944); Tardieu-Blot in Aubrév., *Fl. Cameroun* 3: 219 (1964).

**SÃO TOMÉ.** Trás-os-Montes, Morro Pempem, 1200 m, *Quintas* 1387 (BM!, COI!).

DISTRIBUTION. W. tropical Africa, tropical America, Polynesia.

NOTE. This taxon has not been recorded in the islands since the nineteenth century.

*Asplenium currorii* Hook., *Sp. fil.* 3: 82 (1860); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 75 (1944); Alston in Exell in *Bull. Inst. Franç. Afrique Noire ser. A*, 21: 445 (1959); Tardieu-Blot in Aubrév., *Fl. Cameroun* 3: 180 (1964).

**SÃO TOMÉ.** Macambrará, primary forest, 1050–1200 m, epiphyte, *Exell* 172 (BM!); between Pico and Monte Castro, 6 km S. of Ponta Figo, mountain forest, 1200–1800 m, *Lejoly* 95/29 (LISC!); between Bom Sucesso and Lagoa Amélia, primary forest, 1350–1420 m, *Matos & Van Essche* 7291 (LISC!); *Moller* s.n. (COI!); Lagoa Amélia, 1500 m, *Monod* 11722 (BM!); s.l., 550 m, *Welwitsch* 64 (BM!, LISU!).

**PRÍNCIPE.** Pico Papagaio, *Welwitsch* 24a (BM!); s.l., *Barter* 1900 (K-not found), *Mann* 1861 (K!), *Welwitsch* 24 (BM!, K-not found, LISU!).

DISTRIBUTION. W. tropical Africa.

*Asplenium dregeanum* Kunze in *Linnaea* 10: 517 (1836); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 76 (1944); Alston in Exell, *Suppl. Cat. Vasc. Pl. S. Tomé*: 7 (1956).

subsp. *brachypterum* (Kunze ex Houlston & T. Moore) Pic. Serm. in *Bull. Jard. Bot. Belg.* 55: 130 (1985); Benl in *Acta Bot. Barcinon.* 40: 28 (1991).

**SÃO TOMÉ.** Monte Café, 1200 m, epiphyte, *Espírito Santo* 164 (BM!, COI!, LISJC!); Macambrará, primary forest, 1050–1200 m, *Exell* 96 (BM!), 126 (BM!, COI!); Lagoa Amélia, 1200–1400 m, *Lains e Silva* 83 (LISU!), *Matos* 7493 (LISC!), 1400 m, *Monod* 11741 (BM!), 1400 m, *Quintas* 1349 (BM!, COI!), *Rose* 224 (P!), 240 (P!), *Rozeira* 154 (PO!), 1161 (PO!); Pico, primary forest, 1900–2020 m, epiphyte, *Lejoly* 94/580 (LISC!), 1950 m, *Moller* s.n. (COI!); between Bom Sucesso and Lagoa Amélia, primary forest, 1350–1400 m, epiphyte, *Matos & Van Essche* 7287 (LISC!); between São Pedro and Lagoa Amélia, 1050 m, *Monod* 11705 (BM!, COI!); Calvário, 1400 m, *Monod* 11852 (BM!); s.l., *F.A.E. (Moller)* 33 (BM!, COI!, K!, LISJC!, LISU!), *Mann* s.n. (K!), *Moller* s.n. (COI!).

DISTRIBUTION. Zaïre, Rwanda, Burundi.

*Asplenium emarginatum* P. Beauv., *Fl. Oware* 2: 6, t. 61 (1808); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 76 (1944); Alston in Exell, *Suppl. Cat. Vasc. Pl. S. Tomé*: 7 (1956); Tardieu-Blot in Aubrév., *Fl. Cameroun* 3: 192 (1964); Benl in *Acta Bot. Barcinon.* 40: 10 (1991).

**SÃO TOMÉ.** São Vicente, 200 m, common, *Espírito Santo* 35 (BM!, COI!, LISJC!, LISJC!); Monte Café, 800 m, *Moller* 349 (BM!, COI!); Santa Margarida, António Soares, *Rozeira* 1225 (PO!); s.l., *Don* s.n. (BM!), 800 m, *Quintas* 8 (K!).

**PRÍNCIPE?** (Beauvois, l.c.).

DISTRIBUTION. Widespread in tropical Africa.

*Asplenium erectum* Bory ex Willd., *Sp. pl.* 5: 328 (1810).

var. *usambarense* (Hieron.) Schelpe in *Bol. Soc. Brot., ser. 2*, 41:

207 (1967); Schelpe in Exell & Launert, *Fl. Zamb., Pteridophyta*: 176 (1970); Benl in *Acta Bot. Barcinon.* **40**: 16 (1991).

*Asplenium quintasii* Gand. in *Bull. Soc. Bot. France* **66**: 305 (1919); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 79 (1944); Tardieu-Blot in Aubrév., *Fl. Cameroun* **3**: 198 (1964).

**SÃO TOMÉ.** Monte Café, *Chevalier* 13673 (BM!, P!); Pico, 1850 m, *Exell* 345a (BM!), *Newton* s.n. (BM!, COI!), 1650 m, *Quintas* 1342 (BM!, COI!); type of *Asplenium quintasii*; between Pico and Monte Castro, 6 km S. of Ponta Figo, mountain forest, 1200–1800 m, *Lejoly* 95/19 (LISC!); between Pico and Ponta Figo, primary forest, 1600–1700 m, epiphyte, *Matos & Van Essche* 7389 (LISC!); Calvário, 1450 m, *Monod* 11826 (BM!).

DISTRIBUTION. Widespread in tropical Africa.

*Asplenium eurysorum* Hieron. in Engl. in *Bot. Jahrb. Syst.* **46**: 364 (1911); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 76 (1944).

**SÃO TOMÉ.** Pico, *Chevalier* 13659 (P!), primary forest, 1987 m, epiphyte, *Matos & Van Essche* 7382 (LISC!); Calvário, 920 m, *Espírito Santo* 5070 (LISC!, LISJC!); between Bacelar and Quijá, secondary forest, 160 m, *Espírito Santo* 5139 (LISC!, LISJC!); Macambrará, primary forest, 1050–1200 m, ground fern, *Exell* 132 (BM!), 1385 m, *Moller* s.n. (COI!); Ribeira Peixe, *Lains e Silva* 301 (LISU!); between Pico and Monte Castro, 6 km S. of Ponta Figo, mountain forest, 1200–1800 m, *Lejoly* 95/1 (LISC!); Santa Maria, 1260 m, *Moller* s.n. (COI!); between São Pedro and Lagoa Amélia, 1050 m, *Monod* 11714 (BM!); between Monte Quinas and Quinas Altas, *Monod* 12008 (BM!); s.l., *F.A.E. (Moller)* 28 (BM!, LISJC!, LISU!, P!).

**PRÍNCIPE.** Ôquê Nazaré, *Newton* 27 (BM!, COI!, P!); Pico Papagaio, *Welwitsch* 14 (BM!, K!, LISU!); s.l., *Barter* 1896b (K!).

DISTRIBUTION. Endemic.

*Asplenium exhaustum* (H. Christ) Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 76, f. 2 (1944); Alston in Exell in *Bull. Inst. Franç. Afrique Noire ser. A*, **21**: 445 (1959).

**SÃO TOMÉ.** Pico, *Chevalier* 14587 (P!-type); Cruzeiro, 300 m, *Thorold* 2072 (BM!); s.l., *Seabra* s.n. (BM!, COI!, LISU!).

DISTRIBUTION. Endemic.

*Asplenium formosum* Willd., *Sp. pl.* **5**: 329 (1810); Alston in Exell & Rozeira in *Conf. Int. Afr. Oc.* **3**: 79 (1958).

**SÃO TOMÉ.** Diogo Vaz, near Água Telha, *Rozeira* 518a (PO).

DISTRIBUTION. Pantropical.

*Asplenium friesiorum* C. Chr. in *Notizbl. Bot. Gart. Berlin-Dahlem* **9**: 181 (1924); Benl in *Acta Bot. Barcinon.* **40**: 22 (1991).

**SÃO TOMÉ.** Pico, 1950 m, *F.A.E. (Moller)* 27 (BM!, K!, LISU!, P!); between Casa do Pico and Pico, 1950 m, *Monod* 11957 (BM!).

DISTRIBUTION. Widespread in tropical Africa.

*Asplenium hypomelas* Kuhn, *Filic. afr.*: 104 (1868); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 78 (1944); Benl in *Acta Bot. Barcinon.* **40**: 31 (1991).

**SÃO TOMÉ.** Porto Alegre, *Chevalier* 13658 (P!); between Monte Café and Pico, *Chevalier* 14579 (P!); Lagoa Amélia, 1400 m, *Espírito Santo* 4069 (COI!, LISJC!), 1400 m, *Monod* 11735 (BM!, COI!), *Rose* 233 (P!), *Rozeira* 1129 (PO!); Calvário, secondary forest, 920 m, *Espírito Santo* 5074 (LISC!, LISJC!), 1200 m, *Monod* 11813 (BM!), *Rose* 150 (P!); Macambrará, primary forest, 1050–1200 m, ground fern, *Exell* 120 (BM!, COI!), 1200–1350 m, ground fern, 235a (BM!, COI!); Trás-os-Montes, *Gama* s.n. (COI!); between Pico and Monte Castro, 6 km S. of Ponta Figo, mountain forest, 1200–1800 m, *Lejoly* 95/16 (LISC!); between Bom Sucesso and Lagoa Amélia, primary forest, 1350–1420 m, *Matos & Van Essche* 7295 (LISC!); Rio Contador, 1400

m, *Moller* s.n. (COI!); W. of Pico, 1225 m, *Monod* 11996 (BM!); Pico, *Newton* s.n. (BM!, COI!); São Pedro, *Quintas* s.n. (COI!); s.l., *F.A.E. (Moller & Quintas)* 11 (BM!, COI!, K also *Moller* 10!, LISJC!, LISU!, P!), *Mann* s.n. (K!), *Quintas* s.n. (LISU!), *Souza* s.n. (COI!).

DISTRIBUTION. Widespread in tropical Africa, extending to S. and SE Africa.

*Asplenium inaequilaterale* Bory ex Willd., *Sp. pl.* **5**: 322 (1810); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 78 (1944); Benl in *Acta Bot. Barcinon.* **40**: 17 (1991).

**SÃO TOMÉ.** Ribeira Peixe, *Lains e Silva* 253 (LISU!), 254 (LISU!); Lagoa Amélia, 1430 m, *Matos* 7492 (LISC!); between Bom Sucesso and Macambrará, *Matos* 7605 (LISC!); Saudade, 750 m, *Moller* s.n. (COI!); Calvário, *Monod* 11856 (BM!); s.l., *F.A.E. (Moller)* 25 p.p. (BM!, LISJC!, LISU!), *Moller* 25 (BM!, COI!).

DISTRIBUTION. Widespread in tropical Africa, extending to S. and SE Africa and Madagascar.

*Asplenium lividum* Mett. ex Kuhn in *Linnaea* **36**: 100 (1869).

*Asplenium protensum* sensu auct. non Schrad. in *Gött. Gel. Anz.* **[1818]**: 916 (1818); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 79 (1944).

**SÃO TOMÉ.** Macambrará to Zampalma, 900 m, ground fern, *Exell* 296 (BM!, COI!); Água Pinhão, 850 m, *Quintas* 1283 (BM!, COI!).

DISTRIBUTION. E. and S. Africa, and S. America.

*Asplenium longicauda* Hook., *Sec. cent. ferns*: t. 69 (1860); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 78 (1944); Tardieu-Blot in Aubrév., *Fl. Cameroun* **3**: 186 (1964); Benl in *Acta Bot. Barcinon.* **40**: 9 (1991).

**PRÍNCIPE.** Between Ôquê Pipi and Morro do Leste, secondary forest, 350 m, ground fern, *Exell* 571 (BM!, COI!); Rio Bambu-Porco, 60 m, *Navel* 144 (LISU!, P!); s.l., *Barter* 1900 (K!-syntype).

DISTRIBUTION. W. tropical Africa, Madagascar.

*Asplenium megalura* Hieron. in Brause & Hieron. in Mildbr., *Wiss. Erg. Deut. Zentr.-Afr. Exped., Bot.* **2**: 17 (1910); Benl in *Acta Bot. Barcinon.* **40**: 23 (1991).

var. *molleri* (Hieron.) Tardieu in *Mém. Inst. Franç. Afrique Noire* **28**: 190 (1953).

*Asplenium molleri* Hieron. in Engl. in *Bot. Jahrb. Syst.* **46**: 371 (1911); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 79 (1944).

**SÃO TOMÉ.** Lagoa Amélia, 1400 m, epiphyte, *Espírito Santo* 4068 (COI!, LISJC!), crater rim, 1350 m, epiphyte, *Exell* 202 (BM!), 1430 m, rare epiphyte, *Matos* 7496 (LISC!); 1400 m, *Monod* 11779 (BM!); Macambrará, primary forest, 1200 m, epiphyte, *Exell* 228 (BM!); Bom Sucesso, 1075 m, *F.A.E. (Moller)* 29 (BM!, COI!, K!-type, LISU!); between Bom Sucesso and Lagoa Amélia, secondary forest, 1150–1300 m, *Matos & Van Essche* 7310 (LISC!); Calvário, 1400 m, *Monod* 11854 (BM!); W. of Pico, 870–1225 m, *Monod* 11905 (BM!); s.l., *Matos* s.n. (LISC!).

DISTRIBUTION. The species is widespread in tropical Africa. The variety is endemic to São Tomé.

*Asplenium nigritianum* Hook., *Sp. fil.* **3**: 223 (1860) et *Sec. cent. ferns*: t. 44 (1860); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 79 (1944); Alston in *Bol. Soc. Brot., ser. 2*, **30**: 10 (1956).

**SÃO TOMÉ.** S.l., *Mam* 1107 (K-not found).

**PRÍNCIPE.** Lapa (Leste), *Quintas* s.n. (BM!, COI!); s.l., *Barter* 1895 (BM!, K-not found), (probably Lapa), *Quintas* B (K!).

DISTRIBUTION. Tropical Africa.

NOTES. As shown by Alston (1956*b*), it was wrongly assumed that the type collection came from Bioko. In fact, *Asplenium nigritianum* does not seem to occur in Bioko.

Alston (1956*b*) referred to the type collection as *Barter* 225, explaining that Hooker mistook the date, 1859, for the number and then miscopied it as 1895 (in K specimen) or 1898 (in BM specimen). Since the specimen at K was not found, it was not possible to check its number. The collections of pteridophytes made by Barter which I examined range from no. 1886 to 1928, so it is likely that these figures refer to the number and not the date of collection. The type collection should be referred to as *Barter* 1895.

The species is poorly represented in herbaria. Neither the specimen *Barter* 1895 (K) nor *Mann* 1107 (K) could be located. In a handwritten document kept at BM, reference is made to a duplicate of the *Mann* collection kept at B.

This taxon has not been recorded in the islands since the nineteenth century.

***Asplenium paucijugum*** F. Ballard in *Hooker's Icon. pl.* **33**: t. 3287 (1935); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 79 (1944); Benl in *Acta Bot. Barcinon.* **40**: 8 (1991).

*Asplenium variabile* Hook., *Sp. fil.* **3**: 93, t. 185 (1860) var. *paucijugum* (F. Ballard) Alston in *Bol. Soc. Brot., ser. 2*, **30**: 7 (1956); Tardieu-Blot in *Aubrév., Fl. Cameroun* **3**: 184 (1964).

**SÃO TOMÉ.** Monte Café, 800 m, *F.A.E. (Moller)* 24 (BM!, COI!, LISJC!, LISU!); Lagoa Amélia, primary forest, 1400–1420 m, epiphyte, *Matos & Van Essche* 7410 (LISC!); NW of Pico, 1000–1350 m, *Monod* 12216 (BM!); s.l., 800 m, *Moller* 19 (K!), 550 m, *Welwitsch* 63 (BM!, LISU!).

**PRÍNCIPE.** Sundi, *Newton* 29 (BM!, COI!).

DISTRIBUTION. W., Central, and E. tropical Africa, Madagascar.

***Asplenium sandersonii*** Hook., *Sp. fil.* **3**: 147, t. 179 (1860); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 80 (1944); Benl in *Acta Bot. Barcinon.* **40**: 27 (1991).

**SÃO TOMÉ.** Macambará, primary forest, 1050–1200 m, epiphyte, *Exell* 144 (BM!, COI!); São Miguel, between Xufexufe and São Miguel, 400 m, epiphyte, *Matos* 7658 (LISC!); Pico, 1950 m, *Moller* s.n. (COI!); Bombaim, *Rose* 156 (P!); Dona Augusta, Dona Eugénia, epiphyte, *Rozeira* 1096 (PO!); Lagoa Amélia, 1400 m, epiphyte, *Sérgio* s.n. (LISU!); s.l., *F.A.E. (Moller)* 23 (BM!, K also *Moller* 21!, LISU!), *Mann* (not found), *Moller* s.n. (COI!).

DISTRIBUTION. Widespread in tropical and subtropical Africa.

***Asplenium unilaterale*** Lam., *Encycl.* **2**: 305 (1786); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 80 (1944); Benl in *Acta Bot. Barcinon.* **40**: 15 (1991).

**SÃO TOMÉ.** Pico, 1300–1900 m, *F.A.E. (Moller)* 30 (K-not found, LISU!); Pico, 1900 m, *Moller* s.n. (COI!); Rio Contador, 1300 m, *Moller* s.n. (COI!).

**PRÍNCIPE.** S.l., *Barter* 1917 (K!).

DISTRIBUTION. Palaeotropical.

NOTE. This taxon has not been recorded in the islands since the nineteenth century.

***Asplenium variabile*** Hook., *Sp. fil.* **3**: 93, t. 185 (1860); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 80 (1944); Benl in *Acta Bot. Barcinon.* **40**: 7 (1991).

**SÃO TOMÉ.** Ió Grande, São João dos Angolares, 50 m, *F.A.E. (Quintas)* 22 (K also *Quintas* 20!, LISU!); between Xufexufe and São Miguel, 400 m, epiphyte, *Matos* 7657 (LISC!); São João dos Angolares, 50 m, *Quintas* s.n. (COI!).

**PRÍNCIPE.** Between Ôquê Pipi and Morro do Leste, secondary forest, 350 m, on rocks, *Exell* 567 (BM!, COI!); W. of Pico, above Lapa, below 250 m, *Monod* 12099 (BM!); Rio Bambu-Porco, 60 m, *Navel* 140 (LISU!, P!); Pico, *Thorold* 2085 (BM!); s.l., *Mann* s.n. (K-not found).

DISTRIBUTION. W. tropical Africa.

NOTE. Alston (1944) cited the collection *Barter* 1910 (BM, K). At BM, only the specimen *Barter* s.n. (Niger Expedition) was found. *Barter* 1910 (K) is *Asplenium barteri*.

## Athyriaceae

### *Athyrium* Roth

***Athyrium newtonii*** (Baker) Diels in *Engl. & Prantl, Nat. Pflanzenfam.* **1**(4): 224 (1899); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 73 (1944).

**SÃO TOMÉ.** Pico, 1650 m, *Quintas* 1393 (BM!, COI!, LISJC!), 1650 m, *Quintas* s.n. (COI!); s.l., *Newton* 2 (K!-type), *Newton* s.n. (COI!), (probably Pico), 1650 m, *Quintas* 9 (K!).

DISTRIBUTION. Also in Uganda and Tanzania, above 1000 m.

NOTES. *Newton* 88 (K) cited by Alston (l.c.) is most probably a mistake for *Quintas* 9 (the number 88 after the collector's name is the date).

This taxon has not been recorded in the islands since the nineteenth century.

### *Diplazium* Sw.

***Diplazium arborescens*** (Bory) Sw., *Syn. fil.*: 92 (1806); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 73 (1944).

**SÃO TOMÉ.** Between Monte Café and Pico, *Chevalier* 14290 (P!); Pico, *Chevalier* s.n. (P!); Macambará, primary forest, 1050–1200 m, *Exell* 128 (BM!, COI!); Trás-os-Montes, *Gama* s.n. (COI!); between Lagoa Amélia and Chamiço, primary forest, 1400 m, *Matos* 7526 (LISC!); Monte Café, *Moller* s.n. (COI!); Lagoa Amélia, 1350–1380 m, *Monod* 11772 (BM!, COI!), *Rose* 234 (P!), *Rozeira* 1139 (K!, PO!); Cantagalo, 400 m, *Rozeira* 3157 (PO!); Formoso, *Rozeira* 3236 (PO!); Nova Ceilão, *Rozeira* 4905 (PO!); s.l., *F.A.E. (Moller)* 34 (BM!, COI!, K also *Moller* 28!, LISJC!, LISU!, P!), *Mann* 621 (P!), 1200 m, *Mann* s.n. (K!), *Moller* s.n. (COI!), *Rozeira* 2846 (PO!).

DISTRIBUTION. Also in Madagascar, Comoros, and Mascarene Is.

***Diplazium proliferum*** (Lam.) Thouars, *Esquisse fl. Tristan d'Acugna*: 35 (1804); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 73 (1944); Tardieu-Blot in *Aubrév., Fl. Cameroun* **3**: 237 (1964).

*Callipteris prolifera* (Lam.) Bory, *Voy. îles Afrique* **1**: 283 (1804); Benl in *Acta Bot. Barcinon.* **38**: 37 (1988).

**SÃO TOMÉ.** Between Bom Sucesso and Lagoa Amélia, *Almeida* s.n. (LISC!); Boa Entrada, *Chevalier* 14333 (P!), 14361 (P!) 14361bis (not found); Ribeira Peixe, S. of Cabumbé, secondary forest, 350 m, *Espírito Santo* 3916 (COI!, LISJC!); Morro Vigia, 800 m, *Espírito Santo* 4253 (LISC!, LISJC!); Monte Rosa, secondary forest, 50 m, *Espírito Santo* 4748 (LISC!, LISJC!); Trás-os-Montes, *Lains e Silva* 229 (LISU!); between Monte Castro and Ponta Figo, secondary forest, 500–1070 m, *Lejoly* 95/45 (LISC!); Dona Amélia, Santa Catarina, near Água Cardoso, *Matos* 7593 (LISC!); Pedroma, *Mocquerys* 89/90 (P!), 131/132 (P!); Nova Moca, near Monte Café, 90 m, *Moller* s.n. (COI!); Pinheira, *Moller* s.n. (COI!); Rodia, 540 m, *Moller* s.n. (COI!); Calvário, 1200 m, *Monod* 11816 (BM!); waterfall near São Nicolau, *Monod* 12037 (BM!, COI!), *Rozeira* 571 (PO!); Cruzeiro, *Rozeira* 765 (PO!); between Milagrosa and Rio Abade, near Formoso, *Rozeira* 3188 (PO!); on the way from Santa Irene to the river, *Rozeira* 3319

(PO!); Sela do Camelo, near Lembá, 300–700 m, *Rozeira* 3459 (PO!); Monte Café, 760 m, *Welwitsch* 60 (BM!, K!, LISU!); s.l., *Don* 49 (BM!), *F.A.E. (Moller)* 35 (BM!, COI!, LISJC!, LISU!, P!).

**PRÍNCIPE.** Between Ôquê Pipi and Morro de Leste, secondary forest, 350 m, ground fern, *Exell* 563 (BM!, COI!); Rio Bambu-Porco, 60 m, *Navel* 137 (LISU!, P!); Infante D. Henrique, *Rose* 413 (P!); Infante D. Henrique, near Ribeiro Chimboto, *Rozeira* 312 (PO!); Lapa, way to Pico, 300 m, *Rozeira* 915 (PO!); near Ribeira Camarão, *Rozeira* 2213 (PO!); Bela Vista, near main house, *Rozeira* 3916 (PO!).

DISTRIBUTION. Palaeotropical.

## Blechnaceae

### *Blechnum* L.

***Blechnum attenuatum*** (Sw.) Mett., *Fil. hort. bot. Lips.*: 64, t. 3, figs 1–6 (1856); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 80 (1944); Tardieu-Blot in Aubrév., *Fl. Cameroun* 3: 295 (1964); Benl in *Acta Bot. Barcinon.* 38: 63 (1988).

**SÃO TOMÉ.** Macambrará to Zampalma, primary forest, 800–1050 m, *Exell* 437 (BM!, COI!), 438 (BM!, COI!); between Casa do Pico and Pico, 1250 m, *Monod* 11960 (BM!).

DISTRIBUTION. Tropical and S. Africa, Madagascar.

## Cyatheaceae

### *Cyathea* Sm.

***Cyathea camerooniana*** Hook. in Hook. & Baker, *Syn. fil.*: 21 (1865); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 60 (1944).

var. ***currorii*** Holttum in *Kew Bull.* 36: 480 (1981).

*Alsophila camerooniana* var. *camerooniana* sensu auct. non (Hook.) R.M. Tryon in *Contr. Gray Herb.* 200: 30 (1970); Benl in *Acta Bot. Barcinon.* 31: 26 (1978).

**PRÍNCIPE.** Between Ôquê Pipi and Morro do Leste, secondary forest, 350 m, *Exell* 556 (BM!, COI!); Rio Bambu-Porco, 60 m, *Navel* 136 (COI!, K!, LISU!, P!, WAG); Infante D. Henrique, *Rose* 400 (P!); Infante D. Henrique, near Ribeiro Chimboto, *Rozeira* 325 (PO!); s.l., *Strickland* s.n. (BM!, COI-not found).

DISTRIBUTION. Apparently this variety occurs only in Príncipe, where the type (W. Africa, S. of Tropics, *Curror* s.n. (K!)) was probably collected.

***Cyathea manniana*** Hook. in Hook. & Baker, *Syn. fil.*: 21 (1865); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 60 (1944); Holttum in *Kew Bull.* 36: 472 (1981).

*Alsophila manniana* (Hook.) R.M. Tryon in *Contr. Gray Herb.* 200: 30 (1970); Benl in *Acta Bot. Barcinon.* 31: 27 (1978).

**SÃO TOMÉ.** Lagoa Amélia, 1400 m, *Espírito Santo* 5035 (LISC!, LISJC!), 1380 m, *Monod* 11763 (BM!), *Quintas* s.n. (COI!), *Rozeira* 1150 (PO!); Macambrará, primary forest, 1050–1200 m, *Exell* 244 (BM!); Pico, primary forest, 1900–2020 m, *Lejoly* 94/577 (LISC!), 1850 m, *Moller* s.n. (COI!); between Quinas Altas and Monte Quinas, *Monod* 12021 (BM!); between Casa do Pico and Pico, 1950 m, *Monod* 12242ter (BM!).

DISTRIBUTION. Widespread in tropical Africa.

***Cyathea welwitschii*** Hook. in Hook. & Baker, *Syn. fil.*: 21 (1865); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 60 (1944); Holttum in *Kew Bull.* 36: 475 (1981).

*Alsophila welwitschii* (Hook.) R.M. Tryon in *Contr. Gray Herb.* 200: 31 (1970).

**SÃO TOMÉ.** Macambrará, primary forest, 1050–1200 m, *Exell* 111 (BM!, COI!), 233 (BM!, COI!); Bom Sucesso, 1200 m, *F.A.E. (Moller)* 2 (K!, LISU!, P!), 1200 m, *Moller* s.n. (BM!, COI!); Pico, 1500–1850 m, *F.A.E. (Moller)* 3 (K!, LISU!), 1850 m, *Moller* s.n. (COI!); Trás-os-Montes, *Gama* s.n. (COI!), 900–1200 m, *Henriques* s.n. (P!); between Quinas Altas and Monte Quinas, *Monod* 12010 (BM!); Monte Café, 600 m, *Welwitsch* 66 (BM!, K!, LISU!); s.l., *Mann?* 41/1 (P!), *Mann* 1104 (K!-lectotype).

DISTRIBUTION. Endemic.

## Davalliaceae

### *Davallia* Sm.

***Davallia chaerophylloides*** (Poir.) Steud., *Nomencl. bot.* 2: 146 (1824); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 72 (1944); Alston in *Exell, Suppl. Cat. Vasc. Pl. S. Tomé*: 7 (1956); Benl in *Acta Bot. Barcinon.* 33: 27 (1982).

**SÃO TOMÉ.** São Vicente, 200 m, epiphyte, *Espírito Santo* 107 (BM!, COI!, LISJC!); Benfica, 350 m, epiphyte, *F.A.E. (Moller)* 9 (BM!, LISU!); Benfica, near Trindade, 350 m, *Moller* s.n. (COI!); Rio do Ouro, 350 m, *Moller* s.n. (COI!); near Diana, epiphyte, *Rozeira* 1210 (PO!); s.l., 460–600 m, *Welwitsch* 56 (BM!, K!, LISU!).

DISTRIBUTION. Widespread in tropical and S. Africa and Mascarene Is.

NOTE. Nootboom (1994) synonymized *Davallia chaerophylloides* with *D. denticulata* (Burm.f.) Mett. ex Kuhn var. *denticulata*.

### *Humata* Cav.

***Humata repens*** (L.f.) Diels in Engl. & Prantl, *Nat. Pflanzenfam.* 1(4): 209 (1899); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 71 (1944).

**SÃO TOMÉ.** São Miguel, *Newton* s.n. (P!).

DISTRIBUTION. Palaeotropical.

NOTES. Nootboom (1994) included *Humata* in *Davallia* [*D. repens* (L.f.) Kuhn].

This taxon has not been recorded in the islands since the nineteenth century.

## Dennstaedtiaceae (incl. Hypolepidaceae)

### *Blotiella* R.M. Tryon

***Blotiella currorii*** (Hook.) R.M. Tryon in *Contr. Gray Herb.* 191: 99 (1962); Benl in *Acta Bot. Barcinon.* 38: 29 (1988).

*Lonchitis currorii* (Hook.) Mett. ex Kuhn in Von der Decken's *Reisen Ost-Afr.* Bot. 3: 10 (1879); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 85 (1944); Alston in *Exell & Rozeira in Conf. Int. Afr. Oc.* 3: 79 (1958); Alston in *Exell in Bull. Inst. Franç. Afrique Noire ser. A.* 21: 441 (1959); Tardieu-Blot in Aubrév., *Fl. Cameroun* 3: 100 (1964).

**SÃO TOMÉ.** Nova Moca, 1100 m, *Quintas* 6 (K!, LISU!); Lagoa Amélia, 1400 m, *Quintas* 1262 p.p. (P!), 1400 m, *Quintas* 1455 (BM!, COI!, K!); s.l., *Quintas* 1287 p.p. (P!).

**PRÍNCIPE.** Infante D. Henrique, *Lains e Silva* 458 (LISU!), 459 (LISU!); Pico, 500–600 m, *Monod* 12109 (BM!), *Rozeira* 913 (PO).

DISTRIBUTION. W. tropical Africa, extending to Sudan and Zambia.

NOTE. *Newton* s.n. (P!), from Príncipe, cited but not seen by Alston (1944), consists of sterile young fronds.

**Blotiella glabra** (Bory) R.M. Tryon in *Contr. Gray Herb.* **191**: 99 (1962); Benl in *Acta Bot. Barcinon.* **38**: 31 (1988).

*Lonchitis glabra* Bory, *Voy. îles Afrique* **1**: 321 (1804); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 85 (1944).

*Lonchitis gracilis* Alston in Exell, *Suppl. Cat. Vasc. Pl. S. Tomé*: 7 (1956); Tardieu-Blot in Aubrév., *Fl. Cameroun* **3**: 102 (1964).

**SÃO TOMÉ**. Porto Alegre, *Chevalier* 14311 (P!); Pico, 1700–1900 m, *F.A.E. (Moller)* 13 (BM!, COI!, LISJC!, LISU!, P!), *Mann* s.n. (K!), 1750–1900 m, *Moller* s.n. (COI!); Lagoa Amélia, 1400 m, *Quintas* 1262 (BM!).

DISTRIBUTION. Tropical and S. Africa, Madagascar and Reunion.

**Blotiella mannii** (Baker) Pic. Serm. in *Webbia* **31**: 250 (1977); Benl in *Acta Bot. Barcinon.* **38**: 30 (1988).

*Lonchitis mannii* (Baker) Alston in *Bol. Soc. Brot., ser. 2*, **30**: 18 (1956); Alston in Exell & Rozeira in *Conf. Int. Afr. Oc.* **3**: 80 (1958).

**SÃO TOMÉ**. Macambrará, primary forest, 1050–1200 m, ground fern, *Exell* 239 (BM!, COI!), *Quintas* 1262A (BM!); Trás-os-Montes, *Quintas* 1287 (BM!, COI!); s.l., *Quintas* 1262 p.p. (COI!, P!).

**PRÍNCIPE**. Pico, *Rozeira* 903 (BM-not found, PO!), 800 m, *Rozeira* 912 (K!), 918 (K!, PO!), 600 m, *Rozeira* 1075 (K!).

DISTRIBUTION. W. tropical Africa.

**Histiopteris** (J.G. Agardh) J. Sm.

**Histiopteris incisica** (Thunb.) J. Sm., *Hist. fil.*: 295 (1875); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 86 (1944); Benl in *Acta Bot. Barcinon.* **38**: 25 (1988).

**SÃO TOMÉ**. Near São Pedro, *F.A.E. (Moller)* 19 (BM!, LISU!); Macambrará, 1280 m, *Moller* s.n. (COI!).

**PRÍNCIPE**. Ôquê Nazaré, *Newton* s.n. (COI!).

DISTRIBUTION. Pantropical.

NOTE. This taxon has not been recorded in the islands since the nineteenth century.

**Hypolepis** Bernh.

**Hypolepis sparsisora** (Schrad.) Kuhn, *Filic. afr.*: 120 (1868); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 82 (1944); Benl in *Acta Bot. Barcinon.* **38**: 27 (1988).

**SÃO TOMÉ**. Macambrará, primary forest, 1050–1200 m, *Exell* 112 (BM!, COI!), 1200 m, *Quintas* 4 (COI!-also with no. 1354, K!), 1200 m, *Quintas* 1354 (BM!, COI!, LISJC!); Trás-os-Montes, *Gama* s.n. (COI!).

DISTRIBUTION. Tropical and S. Africa, Madagascar, Comoros and Mascarene Is.

**Lonchitis** L.

**Lonchitis occidentalis** Baker in Hook. & Baker, *Syn. fil.*: 128 (1867); Benl in *Acta Bot. Barcinon.* **38**: 34 (1988).

*Anisosorus occidentalis* (Baker) C. Chr., *Cat. pl. mad., pter.*: 54 (1932); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 85 (1944).

**SÃO TOMÉ**. Macambrará, 1290 m, *Moller* s.n. (COI!); São João dos Angolares, 200 m alt, *Quintas* s.n. (COI!); s.l., *F.A.E. (Moller & Quintas)* 14 (BM!, K also *Moller* 11!, LISU!).

DISTRIBUTION. Widespread in tropical and SE Africa, Madagascar.

NOTE. This taxon has not been recorded in the islands since the nineteenth century.

**Microlepia** C. Presl

**Microlepia speluncae** (L.) T. Moore, *Index fil.*: 93 (1857); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 72 (1944); Benl in *Acta Bot. Barcinon.* **38**: 23 (1988).

**SÃO TOMÉ**. Ilhéu das Rolas, *Quintas* s.n. (BM!, COI!); Monte Café, 760 m, *Welwitsch* 56(2) (BM!, LISU!); s.l., *Don* s.n. (BM!), *F.A.E. (Moller & Quintas)* 10 (K-not found, LISU!), 760 m, *Welwitsch* 56 (K!, LISU!).

DISTRIBUTION. Palaeotropical, rare and sporadic.

NOTE. This taxon has not been recorded in the islands since the nineteenth century.

**Odontosoria** Fée

**Odontosoria chinensis** (L.) J. Sm. in Seem., *Bot. voy. Herald*: 430 (1857).

var. **divaricata** H. Christ in *J. Bot. (Morot), ser. 2*, **2**: 23 (1909).

*Stenoloma chinense* (L.) Bedd., *Handb. ferns Brit. Ind.*: 70 (1883) var. *divaricatum* (H. Christ) Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 73 (1944).

*Sphenomeris chusana* (L.) Copel. in *Bernice P. Bishop Mus. Bull.* **59**: 69 (1929) var. *divaricata* (H. Christ) Tardieu in Humbert, *Fl. Madag. et Comoros* **1**, fam. 5: 29 (1958).

*Sphenomeris chinensis* (L.) Maxon in *J. Wash. Acad. Sci.* **3**: 144 (1913) var. *divaricata* (H. Christ) Kramer in *Blumea* **15**: 572 (1968).

**SÃO TOMÉ**. Between Monte Café and Pico, *Chevalier* 14309 (P!-type of the var.); Calvário, 1500 m, ground fern, *Exell* 321 (BM!, COI!); Pico, 1500–1900 m, *F.A.E. (Moller)* 12 (BM!, COI!, LISJC!, LISU!), 1900 m, *Mollers*.n. (COI!), *Newton* s.n. (BM!, COI!); Trás-os-Montes, *Gama* s.n. (COI!); between Calvário and Estação Sousa, primary forest, 1500 m, *Matos & Van Essche* 7357 (LISC!).

DISTRIBUTION. Occurs also sporadically in tropical Asia and Oceania, and in Madagascar, Reunion, Mauritius and Seychelles.

NOTE. Kramer (1972) suggested that the collections *Moller*, *Gama*, *Exell*, *Newton* and *F.A.E. (Moller)*, cited above, might represent an undescribed species of *Sphenomeris* (= *Odontosoria*), noting that more material and field studies are required to resolve the problem.

**Pteridium** Gled. ex Scop.

**Pteridium aquilinum** (L.) Kuhn in Von der Decken's *Reisen Ost-Afr., Bot.* **3**: 11 (1879); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 86 (1944); Benl in *Acta Bot. Barcinon.* **38**: 35 (1988).

**SÃO TOMÉ**. Boa Entrada, *Chevalier* 13791 (P); between Macambrará and São Nicolau, secondary woodland, 1050 m, common, *Exell* 272 (BM!, COI!); Nova Moca, 800–900 m, *F.A.E. (Moller)* 17 (LISU!); between Morro Vigia and Guarda, *Rozeira* 688 (PO!); Pico, 1900 m, *Monod* 11920 (BM!); Monte Café, 760 m, *Welwitsch* 59 (BM!, LISU!); s.l., *Moller* s.n. (COI!), *Welwitsch* 57 (LISU!).

**PRÍNCIPE**. Cajamanga, *Rozeira* 633 (PO!); Pico Papagaio, *Welwitsch* 18 (BM!, LISU!).

DISTRIBUTION. Cosmopolitan.

**Elaphoglossaceae**

**Elaphoglossum** Schott ex J. Sm.

**Elaphoglossum acrostichoides** (Hook. & Grev.) Schelpe in *J. S.*

*African Bot.* **30**: 196 (1964); Schelpe in *Contr. Bolus Herb.* **1**: 29 (1969); Benl in *Acta Bot. Barcinon.* **40**: 71 (1991).

**SÃO TOMÉ.** Macambrará, *Exell* 153 (BM!); Calvário, *Monod* 11846 (BM!); Pico, *Rose* 311 (P!).

DISTRIBUTION. Widespread in tropical and subtropical Africa, Madagascar, Comoros and Reunion.

**Elaphoglossum aubertii** (Desv.) T. Moore, *Index fil.* **2**: 5 (1857); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 91 (1944); Schelpe in *Contr. Bolus Herb.* **1**: 32 (1969); Benl in *Acta Bot. Barcinon.* **40**: 75 (1991).

**SÃO TOMÉ.** Pico, 1900 m, *F.A.E. (Moller)* 63 (K also *Moller* 56!, LISU!), 1900 m, *Moller* s.n. (BM!, COI!); Calvário, 1550 m, *Monod* 11841 (BM!).

DISTRIBUTION. Widespread in tropical and subtropical Africa, Madagascar, Comoros and Mascarene Is.

**Elaphoglossum chevalieri** H. Christ in *J. Bot. (Morot)*, ser. 2, **2**: 23 (1909); Alston in Exell, *Suppl. Cat. Vasc. Pl. S. Tomé*: 8 (1956); Alston in Exell in *Bull. Inst. Franç. Afrique Noire ser. A*, **21**: 447 (1959); Schelpe in *Contr. Bolus Herb.* **1**: 33 (1969).

*Elaphoglossum clarenceanum* sensu auct. non (Baker) C. Chr., *Index filic.*: 304 (1905); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 92 (1944).

**SÃO TOMÉ.** Between Monte Café and Pico, *Chevalier* 14292bis (P!-type); Pico, 1950 m, *Moller* s.n. (COI!), *Rose* 298 (P!); Calvário, 1550 m, *Monod* 11837 (BM!); near Casa do Pico, 1930 m, *Monod* 11953 (BM!); E. of Pico, 1700 m, *Quintas* 1379 (BM!, COI!); s.l., *F.A.E. (Moller)* 64 (LISU!), *Henriques* 5/84 p.p. (K also labelled *F.A.E. (Moller)* 64!).

**PRÍNCIPE.** Pico, 700–800 m, *Monod* 12134 (BM!, COI!), above 300 m, *Thorold* 2087 (BM!).

DISTRIBUTION. W. tropical Africa, SE Africa.

**Elaphoglossum isabelense** Brause in Brause & Hieron. in *Bot. Jahrb. Syst.* **53**: 432 (1915); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 92 (1944); Tardieu-Blot in Aubrév., *Fl. Cameroun* **3**: 297 (1964); Benl in *Acta Bot. Barcinon.* **40**: 73 (1991).

**SÃO TOMÉ.** Between Monte Café and Pico, *Chevalier* 14540 (not found); Lagoa Amélia, *Exell* 221 (BM!), *Rose* 195 (P!); Macambrará, *Exell* 227 (BM!); Calvário, *Monod* 11823 (BM!); Rio Contador, 1450 m, *Quintas* 1356 (BM!, P!); s.l., *F.A.E. (Moller)* 62 (BM!, LISU!, P!), *Henriques* 5/84 p.p. (K!).

**PRÍNCIPE.** S.l., *Barter* 1903 (K!).

DISTRIBUTION. W. tropical Africa.

**Elaphoglossum salicifolium** (Willd. ex Kaulf.) Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 92 (1944); Tardieu-Blot in Aubrév., *Fl. Cameroun* **3**: 302 (1964); Benl in *Acta Bot. Barcinon.* **40**: 73 (1991).

*Elaphoglossum petiolatum* (Sw.) Urb., *Symb. antill.* **4**: 61 (1903) subsp. *salicifolium* (Willd. ex Kaulf.) Schelpe in *Contr. Bolus Herb.* **1**: 34 (1969).

**SÃO TOMÉ.** São João dos Angolares, *F.A.E. (Quintas)* 61 p.p. (BM!); Pico, *Rose* 315 (P!).

DISTRIBUTION. Tropical Africa, Madagascar, Comoros, Seychelles and Mascarene Is.

## Gleicheniaceae

### Dicranopteris Bernh.

**Dicranopteris linearis** (Burm.f.) Underw. in *Bull. Torrey Bot. Club* **34**: 250 (1907); Benl in *Acta Bot. Barcinon.* **31**: 23 (1978).

*Gleichenia linearis* (Burm.f.) C.B. Clarke in *Trans. Linn. Soc. London, Bot.* **1**: 428 (1880); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 93 (1944); Alston in Exell, *Suppl. Cat. Vasc. Pl. S. Tomé*: 8 (1956).

**SÃO TOMÉ.** Between Monte Café and Pico, *Chevalier* 14310 (P); Famosa, 400 m, *Espírito Santo* 71 (BM!, COI!, LISJC!); between Java and Bombaim, secondary forest, 520 m, *Espírito Santo* 5013 (LISC!, LISJC!); Macambrará to Zampalma, 1050 m, ground fern, *Exell* 298 (BM!, COI!); São Nicolau, 900 m, *Figueiredo & Arriegas* 52 (LISC!); Jou, *Lains e Silva* 331 (LISU!); between Monte Castro and Ponta Figo, secondary forest, 500–1070 m, *Lejoly* 95/35 (LISC!); Pico, summit, *Mann* (K!), 1800 m, *Moller* s.n. (COI!); between Calvário and Estação Sousa, primary forest, 1500 m, *Matos & Van Essche* 7358 (LISC!); Rio Contador, 1325 m, *Moller* s.n. (COI!); Calvário, 1100 m, *Monod* 11810 (BM!, COI!); Água Izé, common, *Pinto Basto* 198 (LISC!); Nova Moca, 750 m, *Quintas* 1465 (BM!, COI!, K!); between Vale Carmo and Guaiquil, *Rozeira* 18 (PO!); Trás-os-Montes, s.c. s.n. (COI!); s.l., *F.A.E. (Moller)* 1 (BM!, COI!, LISJC!, LISU!).

**PRÍNCIPE.** Infante D. Henrique, 200 m, common ground fern, *Exell* 654 (BM!, COI!); 240 m, *Lains e Silva* 467 (LISU!); Ôquê Nazaré, *Newton* s.n. (BM!, COI!); Pico Papagaio, 760 m, *Welwitsch* 19 (BM!, LISU!).

DISTRIBUTION. Pantropical.

## Grammitaceae

### Grammitis Sw.

**Grammitis ebenina** (Maxon) Tardieu in *Mém. Inst. Franç. Afrique Noire* **28**: 211, t. 42, figs 11–12 (1953); Schelpe in *Contr. Bolus Herb.* **1**: 3 (1969).

*Polypodium ebeninum* Maxon in *Bull. Torrey Bot. Club* **42**: 224 (1915); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 88 (1944).

**SÃO TOMÉ.** Cabumbé, 800 m, epiphyte, *Newton* s.n. (P!).

DISTRIBUTION. Also in St. Helena.

NOTE. This taxon has not been recorded in the islands since the nineteenth century.

**Grammitis mollerii** (Baker) Schelpe in *Bol. Soc. Brot.*, ser. 2, **40**: 162 (1966); Schelpe in *Contr. Bolus Herb.* **1**: 5 (1969).

*Polypodium mollerii* Baker in Henriq. in *Bol. Soc. Brot.* **4**: 154, t. 2, fig. B (1887); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 88 (1944).

**SÃO TOMÉ.** Pico, 1900 m, *F.A.E. (Moller)* 51 (BM!, COI!, LISJC!, LISU!, P!); s.l. (probably Pico), *Moller* 64 (K-holotype).

DISTRIBUTION. Endemic.

NOTE. This taxon has not been recorded in the islands since the nineteenth century.

**Grammitis nigrocincta** Alston in Exell in *Bull. Inst. Franç. Afrique Noire ser. A*, **21**: 444 (1959); Schelpe in *Contr. Bolus Herb.* **1**: 3 (1969).

*Grammitis* sp.; Alston in Exell & Rozeira in *Conf. Int. Afr. Oc.* **3**: 80 (1958).

**PRÍNCIPE.** Pico, 600 m, *Thorold* 2074 (BM!), *Monod* 12162 (BM!-holotype, COI!), *Rozeira* 921 (PO).

DISTRIBUTION. Also in Madagascar.

**Grammitis tomensis** Schelpe in *Contr. Bolus Herb.* **1**: 6 (1969).

**SÃO TOMÉ.** Pico, 2000 m, *Quintas* 11 (BM!-holotype, COI!); s.l. (probably Pico), *Newton* 11 p.p. (K).

DISTRIBUTION. Endemic.

NOTES. At BM there is another collection labelled *Quintas* 11 which consists of *Pteris tripartita*.

This taxon has not been recorded in the islands since the nineteenth century.

### **Xiphopteris** Kaulf.

**Xiphopteris cultrata** (Willd.) Schelpe in *Bol. Soc. Brot., ser. 2*, **41**: 217 (1967); Schelpe in *Contr. Bolus Herb.* **1**: 9 (1969); Benl in *Acta Bot. Barcinon.* **33**: 22 (1982).

*Polypodium cultratum* Willd., *Sp. pl.* **5**: 187 (1810) var. *elasticum* (Bory ex Willd.) Baker in Hook. & Baker, *Syn. fil.*: 327 (1867); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 87 (1944).

**SÃO TOMÉ.** Macambrará to Zampalma, primary forest, 800–1050 m, *Exell* 441 (BM!); between Bom Sucesso and Lagoa Amélia, epiphyte, *Matos* 7585 (LISC!); Lagoa Amélia, primary forest, 1400–1420 m, epiphyte, *Matos & Van Essche* 7412 (LISC!).

DISTRIBUTION. W. and Central Africa and tropical America.

**Xiphopteris oosora** (Baker) Alston in *Bol. Soc. Brot., ser. 2*, **30**: 26 (1956); Tardieu-Blot in Aubrév., *Fl. Cameroun* **3**: 325 (1964); Schelpe in *Contr. Bolus Herb.* **1**: 12 (1969); Benl in *Acta Bot. Barcinon.* **33**: 21 (1982).

*Polypodium oosorum* Baker in Henriq. in *Bol. Soc. Brot.* **4**: 154, t. 2, fig. A (1887); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 89 (1944).

**SÃO TOMÉ.** Pico, 1950 m, *Moller* s.n. (BM!, COI!); Pico, 1950 m, *F.A.E. (Moller)* 52 (BM!, K?, LISU!, P!); s.l. (probably Pico), *Moller* 1337 (K-holotype).

DISTRIBUTION. W. and E. tropical Africa, Madagascar.

NOTE. This taxon has not been recorded in the islands since the nineteenth century.

**Xiphopteris villosissima** (Hook.) Alston in *Bol. Soc. Brot., ser. 2*, **30**: 27 (1956); Schelpe in *Contr. Bolus Herb.* **1**: 8 (1969); Benl in *Acta Bot. Barcinon.* **33**: 23 (1982).

*Polypodium villosissimum* Hook., *Sp. fil.* **4**: 197 (1862); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 90 (1944).

**SÃO TOMÉ.** S.l., *Mann* s.n. (K), *Newton* (not found at COI).

DISTRIBUTION. W., E., and SE tropical Africa.

NOTE. This taxon has not been recorded in the islands since the nineteenth century.

## **Hemionitidaceae**

### **Coniogramme** Fée

**Coniogramme africana** Hieron. in *Hedwigia* **57**: 293 (1916); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 81 (1944); Tardieu-Blot in Aubrév., *Fl. Cameroun* **3**: 132 (1964); Benl in *Acta Bot. Barcinon.* **32**: 26 (1980).

**SÃO TOMÉ.** Macambrará to Zampalma, 900 m, ground fern, *Exell* 292

(BM!); Macambrará, primary forest, 1050–1200 m, ground fern, *Exell* 421 (BM!, COI!); Pico, 1800 m, *Moller* s.n. (COI!); W. of Pico, 1225 m, *Monod* 11994 (BM!); NW of Pico, 1225 m, *Monod* 11995 (BM!); Lagoa Amélia, *Rozeira* 1182 (PO!); s.l., *F.A.E. (Moller)* 58 (BM!, LISU!), *Mann* s.n. (K!), *Moller* s.n. (COI!).

DISTRIBUTION. Widespread in tropical Africa.

### **Pityrogramma** Link

**Pityrogramma calomelanos** (L.) Link, *Handbuch* **3**: 20 (1833) 'calomelas'; Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 81 (1944); Alston in Exell in *Bull. Inst. Franç. Afrique Noire ser. A*, **21**: 442 (1959).

var. **calomelanos**; Benl in *Acta Bot. Barcinon.* **32**: 30 (1980).

**SÃO TOMÉ.** Between Bom Sucesso and Macambrará, *Matos* 7611 (LISC!); Água Izé, *Pinto Basto* 215 (LISC!); near Bombaim, *Rozeira* 499 (PO!).

**PRÍNCIPE.** Santo António, *Monod* 12064 (BM!, COI!); s.l., *Barter* 1912 (K-not found).

DISTRIBUTION. A weed introduced from tropical America.

## **Hymenophyllaceae**

### **Hymenophyllum** Sm.

**Hymenophyllum capillare** Desv. in *Mém. Soc. Linn. Paris* **6**: 333 (1827); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 59 (1944); Tardieu-Blot in Aubrév., *Fl. Cameroun* **3**: 75 (1964); Benl in *Acta Bot. Barcinon.* **32**: 7 (1980).

**SÃO TOMÉ.** Pico, 1500–2000 m, *Moller* s.n. (BM!); W. of Pico, 1225–1430 m, *Monod* 11913 (BM!, COI!); Calvário, *Rose* 155 (P!); s.l., *F.A.E. (Moller & Quintas)* 5 p.p. (K also *Moller* 4!, P!).

DISTRIBUTION. Widespread in tropical Africa, Mascarene Is. and Tristan da Cunha.

**Hymenophyllum hirsutum** (L.) Sw. in *J. Bot. (Schrader)* **1800**(2): 99 (1801), emend. C.V. Morton in *Contr. U.S. Natl. Herb.* **29**: 155, 173 (1947); Tardieu-Blot in Aubrév., *Fl. Cameroun* **3**: 76 (1964); Benl in *Acta Bot. Barcinon.* **32**: 9 (1980).

*Hymenophyllum ciliatum* Sw. in *J. Bot. (Schrader)* **1800**(2): 100 (1801) var. *boryanum* (Willd.) Mett. ex Kuhn, *Filic. afr.*: 39 (1868); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 59 (1944).

**SÃO TOMÉ.** Between Monte Café and Pico, *Chevalier* 14292 p.p. (P!); Calvário, 1500 m, ground fern, *Exell* 327 (BM!, COI!), 1560 m, *Monod* 11835 (BM!, COI!); Lagoa Amélia, primary forest, 1400–1420 m, epiphyte, *Matos & Van Essche* 7414 (LISC!); Pico, 1500–2000 m, *Moller* s.n. (BM!, COI!); Bom Sucesso, 1150 m, *Moller & Quintas* s.n. (COI!); Bindá, *Newton* (P-specimen is missing from sheet); São Nicolau, 900 m, *Quintas* s.n. (LISU!); s.l., *F.A.E. (Moller & Quintas)* 5 p.p. (BM!, COI!, K!, LISJC!, LISU!, P!), *Quintas* s.n. (K!).

DISTRIBUTION. Pantropical and subtropical.

**Hymenophyllum polyanthos** Sw. in *J. Bot. (Schrader)* **1800**(2): 102 (1801).

var. **kuhnii** (C. Chr.) Schelpe in *Bol. Soc. Brot., ser. 2*, **40**: 156 (1966); Benl in *Acta Bot. Barcinon.* **32**: 6 (1980).

*Hymenophyllum kuhnii* C. Chr., *Index filic.*: 363 (1905); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 59 (1944); Alston in Exell & Rozeira in *Conf. Int. Afr. Oc.* **3**: 78 (1958); Alston in Exell in *Bull. Inst. Franç. Afrique Noire ser. A*, **21**: 441 (1959); Tardieu-Blot in Aubrév., *Fl. Cameroun* **3**: 72 (1964).



**SÃO TOMÉ.** Between Monte Café and Pico, *Chevalier* 14292 p.p. (P!), 14292ter (BM!, P!), 14551 (P!); SW region, *Chevalier* 14588 (P!); Calvário, 1500 m, ground fern, *Exell* 323 (BM!); between Lagoa Amélia and Chamiço, primary forest, 1250 m, epiphyte, *Matos* 7534 (LISC!); Pico, 1950 m, *Moller* s.n. (COI!), *Rose* 316 (P!), 319 (P!), *Rozeira* 967 (PO!); Trás-os-Montes, 800–1200 m, *Quintas* 1315 (BM!), COI-not found; s.l., *F.A.E. (Moller)* 4 p.p. (BM!, COI!), K also *Moller* 3!, LISJC!, LISU!, P!).

**PRÍNCIPE.** W. of Pico, 500–600 m, *Monod* 12113 (BM!); Pico, 500–600 m, *Monod* 12116 (BM!), 800–900 m, *Rozeira* 973 (BM-not found, PO), 600 m, epiphyte, *Thorold* 2073A (BM!).

**DISTRIBUTION.** Widespread in tropical Africa.

**Hymenophyllum polyanthos** Sw. in *J. Bot. (Schrader)* **1800**(2): 102 (1801).

var. **mildbraedii** (Brause ex Brause & Hieron.) Schelpe in *Garcia de Orta, ser. Bot.* **3**: 54 (1976).

*Hymenophyllum mildbraedii* (Brause ex Brause & Hieron.) Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 60 (1944); Alston in *Exell in Bull. Inst. Franç. Afrique Noire ser. A*, **21**: 441 (1959).

**PRÍNCIPE.** Pico, *Rozeira* 965 (K!), 600 m, epiphyte, *Thorold* 2073 p.p. (BM!), 900 m, *Thorold* 2084 p.p. (BM!).

**DISTRIBUTION.** Angola and Annobon.

**Hymenophyllum splendidum** Bosch in *Ned. Kruidk. Arch.* **5**(3): 192 (1863); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 60 (1944); Alston in *Exell in Bull. Inst. Franç. Afrique Noire ser. A*, **21**: 441 (1959); Tardieu-Blot in *Aubrév., Fl. Cameroun* **3**: 76 (1964); Benl in *Acta Bot. Barcinon.* **32**: 8 (1980).

**SÃO TOMÉ.** Macambrará, primary forest, 800–1050 m, *Exell* 439 (BM!, COI!); s.l., *F.A.E. (Moller & Quintas)* 5 p.p. (P!).

**PRÍNCIPE.** Pico, *Rozeira* 966 (K!), 600 m, epiphyte, *Thorold* 2073B (BM!), 900 m, epiphyte, *Thorold* 2084A (BM!).

**DISTRIBUTION.** Tropical Africa, extending to Tanzania.

### Trichomanes L.

**NOTE.** Recent work (Dubuisson, 1996) supports the division by earlier workers of the genus *Trichomanes* s.l. into several genera. Although the genus is treated here in its *sensu lato*, the names of the taxa in the segregate genera are also provided, when available.

**Trichomanes borbonicum** Bosch in *Ned. Kruidk. Arch.* **5**(2): 158 (as '185') (1861); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 57 (1944); Tardieu-Blot in *Aubrév., Fl. Cameroun* **3**: 88 (1964); Benl in *Acta Bot. Barcinon.* **32**: 22 (1980).

[**Vandenboschia borbonica** (Bosch) G. Kunkel in *Nova Hedwigia* **6**: 213 (1963)]

**SÃO TOMÉ.** Pico, 1500–2000 m, *Moller* s.n. (BM!, COI!); Trás-os-Montes, 1200 m, *Quintas* 1269A (BM!, COI!).

**DISTRIBUTION.** Widespread in tropical Africa, SE and S. Africa, Madagascar and Reunion.

**NOTE.** This taxon has not been recorded in the islands since the nineteenth century.

**Trichomanes crispiforme** Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 57 (1944); Alston in *Exell & Rozeira in Conf. Int. Afr. Oc.* **3**: 78 (1958); Tardieu-Blot in *Aubrév., Fl. Cameroun* **3**: 90 (1964).

**SÃO TOMÉ.** Cabumbé, *Newton* (P?).

**PRÍNCIPE.** Ôquê Pipi, secondary forest, 300 m, epiphyte, *Exell* 501 (BM!, COI!); W. of Pico, 500–600 m, *Monod* 12123 (BM!), 700–800 m, *Monod* 12143 (BM!); Pico, *Rozeira* 905 (BM-not found, PO); s.l., *Barter* 1918 (K-not found).

**DISTRIBUTION.** W. and Central tropical Africa.

**Trichomanes digitatum** Sw., *Syn. fil.*: 370 (1806); Alston in *Exell in Bull. Inst. Franç. Afrique Noire ser. A*, **21**: 441 (1959).

[**Microtrichomanes digitatum** (Sw.) Copel. in *Philipp. J. Sci.* **67**: 36 (1938)]

**SÃO TOMÉ.** Calvário, 1400 m, *Monod* 11855 (BM!, COI!).

**DISTRIBUTION.** Also in Madagascar, Mauritius, Reunion, Malaya and Borneo.

**Trichomanes erosum** Willd., *Sp. pl.* **5**: 501 (1810); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 58 (1944); Benl in *Acta Bot. Barcinon.* **32**: 16 (1980).

[**Microgonium erosum** (Willd.) C. Presl, *Gefässbündel Farrn.*: 27 (1847)]

*Trichomanes chamaedrys* Taton in *Bull. Soc. Roy. Bot. Belgique* **78**: 29, pl. 2, figs K-L (1946); Alston in *Exell & Rozeira in Conf. Int. Afr. Oc.* **3**: 78 (1958).

**SÃO TOMÉ.** Porto Alegre, *Chevalier* 14178 (P); Pico, 1900 m, *Moller* s.n. (COI!); São João dos Angolares, 80 m, *Newton* s.n. (BM!, COI!); Macambrará, 1200 m, epiphyte, *Quintas* 1269B (BM!, COI!); Bom Sucesso, *Quintas* s.n. (BM!, COI!); Ribeira Peixe, *Rozeira* 205 (BM-not found, PO); s.l., *F.A.E. (Moller & Quintas)* 6 (K!, LISU!), *Quintas* 3 (COI!).

**PRÍNCIPE.** S.l., *Barter* 1919 (K!).

**DISTRIBUTION.** Tropical Africa.

**Trichomanes mannii** Hook. ex Hook. & Baker, *Syn. fil.*: 75 (1867); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 58 (1944); Benl in *Acta Bot. Barcinon.* **32**: 17 (1980).

[**Gonocormus mannii** (Hook. ex Hook. & Baker) G. Kunkel in *Nova Hedwigia* **6**: 212 (1963)]

**SÃO TOMÉ.** Lagoa Amélia, *Exell* 203 (BM!, COI!); between São Pedro and Lagoa Amélia, 1050 m, *Monod* 11706 (BM!); Trás-os-Montes, 850 m, *Quintas* 1269 (BM!, COI!).

**DISTRIBUTION.** W., Central and E. Africa, Madagascar and Comoros.

**Trichomanes pyxidiferum** L., *Sp. pl.* **2**: 1098 (1753).

[**Vandenboschia pyxidifera** (L.) Copel. in *Philipp. J. Sci.* **67**: 53 (1938)]

var. **melanotrichum** (Schldtl.) Schelpe in *J. S. African Bot.* **30**: 181 (1964); Benl in *Acta Bot. Barcinon.* **32**: 24 (1980).

*Trichomanes melanotrichum* Schldtl., *Adumbr. pl.*: 56 (1832); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 58 (1944).

**SÃO TOMÉ.** São Nicolau, 900 m, *F.A.E. (Moller)* 7 (BM!, K!, LISU!), 950 m, *Moller* s.n. (COI!); Lagoa Amélia, *Rozeira* 1084 (K!); s.l. (probably São Nicolau), *F.A.E. (Moller)* 4 p.p. (P!).

**DISTRIBUTION.** Widespread in tropical and subtropical Africa.

**Trichomanes radicans** Sw. in *J. Bot. (Schrader)* **1800**(2): 97 (1801); Benl in *Acta Bot. Barcinon.* **32**: 14 (1980).

[**Vandenboschia radicans** (Sw.) Copel. in *Philipp. J. Sci.* **67**: 54 (1938)]

*Trichomanes giganteum* sensu auct. non Bory ex Willd., *Sp. pl.* **5**: 514 (1810); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 58 (1944).

**SÃO TOMÉ.** Macambrará, primary forest, 1050–1200 m, ground fern, *Exell*

185 (BM!, COI!), *Moller* s.n. (COI!); near São Tomé, 20 m, *Moller* s.n. (COI!); Pico, 1800 m, *Moller* s.n. (COI!), *Newton* s.n. (BM!, COI!); São Pedro, *Quintas* s.n. (COI!); s.l., *F.A.E. (Moller & Quintas)* 8 (BM-not found, COI!, LISU!, P!), *Mann* s.n. (K!).

DISTRIBUTION. W., Central and E. Africa, Madagascar, Comoros and Reunion.

*Trichomanes rigidum* Sw., *Prodr.*: 137 (1788).

[*Selenodesmium rigidum* (Sw.) Copel. in *Philipp. J. Sci.* **67**: 81 (1938)]

*Trichomanes cupressoides* Desv. in *Mém. Soc. Linn. Paris* **6**(2): 330 (1827); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 57 (1944); Alston in Exell & Rozeira in *Conf. Int. Afr. Oc.* **3**: 78 (1958).

SÃO TOMÉ. Maria Fernandes, secondary forest, 275 m, *Carvalho* 2 (LISC!); São Miguel, Monte Verde, secondary forest, 10–150 m, *Lejoly* 95/96 (LISC!).

PRÍNCIPE. Ôquê Nazaré, *Newton* s.n. (BM!, COI!); Pico, above Neves Ferreira, *Rozeira* 650 (BM-not found, PO), 683 (BM-not found, PO); Pico, *Rozeira* 907 (BM-not found, PO).

DISTRIBUTION. Widespread in tropical and subtropical Africa, tropical America.

## Lomariopsidaceae

### Bolbitis Schott

*Bolbitis acrostichoides* (Afzel. ex Sw.) Ching in C. Chr., *Index filic.* Suppl. 3: 47 (1934); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 68 (1944); Hennipman, *Monogr. fern genus Bolbitis*: 149 (1977); Benl in *Acta Bot. Barcinon.* **40**: 61 (1991).

SÃO TOMÉ. Near São Tomé, *F.A.E. (Moller)* 67 (K also *Moller* 41!, LISU!); Monte Café, 800 m, *Moller* s.n. (COI!); *Welwitsch* 63b (BM!, LISU!); São Pedro, 1100 m, *Quintas* s.n. (COI!).

DISTRIBUTION. Tropical Africa, Madagascar.

NOTES. *Moller* 63 (K), cited by Hennipman (1977), is probably a mistake for *F.A.E. (Moller)* 67.

This taxon has not been recorded in the islands since the nineteenth century.

*Bolbitis auriculata* (Lam.) Ching in C. Chr., *Index filic.* Suppl. 3: 47 (1934) et Alston in *J. Bot.* **72**, Suppl. 2: 3 (1934); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 68 (1944); Hennipman, *Monogr. fern genus Bolbitis*: 136 (1977); Benl in *Acta Bot. Barcinon.* **40**: 59 (1991).

SÃO TOMÉ. Boa Entrada, *Chevalier* 14335 (P!); Monte Café, *Moller* s.n. (COI!), 800 m, *F.A.E. (Moller)* 66 (BM!, LISU!, P!); Diogo Vaz, 150 m, *Quintas* s.n. (BM!, COI!, K!, LISJC!, P!); above Monte Café, *Welwitsch* 58 (BM!, LISU!).

PRÍNCIPE. Between Ôquê Pipi and Morro do Leste, secondary forest, 350 m, ground fern, *Exell* 572 (BM!); s.l., *Barter* 1899 (K-not found).

DISTRIBUTION. Tropical Africa, Madagascar, Mascarenes.

*Bolbitis fluviatilis* (Hook.) Ching in C. Chr., *Index filic.*, Suppl. 3: 48 (1934); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 69 (1944); Alston in Exell & Rozeira in *Conf. Int. Afr. Oc.* **3**: 78 (1958); Alston in Exell in *Bull. Inst. Franç. Afrique Noire ser. A*, **21**: 447 (1959); Tardieu-Blot in Aubrév., *Fl. Cameroun* **3**: 316 (1964); Hennipman, *Monogr. fern genus Bolbitis*: 142 (1977); Benl in *Acta Bot. Barcinon.* **40**: 60 (1991).

SÃO TOMÉ. São João dos Angolares, 200 m, *F.A.E. (Quintas)* 68 (BM!, COI!, LISU!); Rio Abade, 1300 m, *Quintas* s.n. (COI!).

PRÍNCIPE. Pico, 700–800 m, *Monod* 12137 (BM!); between Lapa and Pico, *Rozeira* 893 (PO); s.l., *Barter* 1897 (K), 1897bis (K!).

DISTRIBUTION. W. tropical Africa.

### Lomariopsis Fée

*Lomariopsis guineensis* (Underw.) Alston in *J. Bot.* **72**, Suppl. 2: 5 (1934); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 81 (1944); Tardieu-Blot in Aubrév., *Fl. Cameroun* **3**: 309 (1964); Benl in *Acta Bot. Barcinon.* **40**: 64 (1991).

SÃO TOMÉ. Ilhéu das Rolas, 120 m, *Quintas* 1164 (BM!, COI also labelled no. 35 from Monte Café!), *F.A.E. (Quintas)* 65 p.p. (BM!, COI!, K!-also *Quintas* 35); Monte Café, *Welwitsch* 68 (BM!, LISU!).

PRÍNCIPE. Esperança, 600 m, *Rozeira* 892 (K!).

DISTRIBUTION. W. tropical Africa to Angola.

*Lomariopsis hederacea* Alston in *J. Bot.* **72**, Suppl. 2: 5 (1934); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 81 (1944); Benl in *Acta Bot. Barcinon.* **40**: 70 (1991).

SÃO TOMÉ. Macambará, 1050–1200 m, epiphyte, *Exell* 189 (BM!), primary forest, 1050–1200 m, ground fern, *Exell* 315 (BM!, COI!); Rio Contador, 1300 m, *Moller* s.n. (COI!); s.l., *F.A.E. (Moller & Quintas)* 65 p.p. (BM!, COI!), *Moller* s.n. (COI!).

DISTRIBUTION. W. tropical Africa to Angola, Central Africa.

NOTE. *Barter* s.n. (K) from Príncipe was cited by Alston in the protologue of the species (paratype). *Barter* 1899 (K), also from Príncipe, was cited by Alston in 1944. The same collection (*Barter* 1899) was cited by Alston (1944) under *Bolbitis auriculata*. Neither of these collections was found under *Lomariopsis hederacea* at K. *Barter* 1899 (K) is *Bolbitis auriculata*. It is possible that both citations refer to *Barter* 1902 (K), a specimen of *L. warneckeii*.

*Lomariopsis warneckeii* (Hieron.) Alston in *J. Bot.* **72**, Suppl. 2: 6 (1934); Benl in *Acta Bot. Barcinon.* **40**: 70 (1991).

*Lomariopsis nigrescens* Holttum in *Kew Bull.* 1939: 627, figs 13 & 14 (1940); Alston in Exell in *Bull. Inst. Franç. Afrique Noire ser. A*, **21**: 447 (1959).

*Lomariopsis hederacea* sensu auct. non Alston in *J. Bot.* **72**, Suppl. 2: 5 (1934); Alston in Exell & Rozeira in *Conf. Int. Afr. Oc.* **3**: 79 (1958).

PRÍNCIPE. Pico, above Neves Ferreira, epiphyte, *Rozeira* 663 (BM-not found, PO!); Pico, epiphyte, *Thorold* 2086 (BM!); s.l., *Barter* 1902 p.p. (K!).

DISTRIBUTION. E. and SE Africa and Bioko.

NOTE. *Barter* 1902 (K) consists of two herbarium sheets. The one cited above is apparently a young plant (as noted by Holttum on the herbarium sheet), with pinnae smaller than in typical *Lomariopsis warneckeii*. The other sheet contains a larger specimen, referred to *L. hederacea* by Holttum, but with much larger and separated pinnae. Although the distinction between this species and the previous seems to be clear in material from the continent, some specimens from São Tomé and Príncipe show intermediate features.

## Loxogrammaceae

### Loxogramme (Blume) C. Presl

*Loxogramme lanceolata* (Sw.) C. Presl, *Tent. pterid.*: 215, t. 9, fig. 8 (1836); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 90 (1944); Benl in *Acta Bot. Barcinon.* **33**: 24 (1982).

**SÃO TOMÉ.** Macambrará, primary forest, 1200 m, epiphyte, *Exell* 230 (BM!); between Estação Sousa and Pico, 1700 m, *Matos* 7551 (LISC!); between Bom Sucesso and Lagoa Amélia, primary forest, 1350–1420 m, *Matos & Van Essche* 7290 (LISC!); Saudade, 780 m, *Moller* s.n. (COI!); NW of Pico, 1600–1800 m, *Monod* 12239 (BM!); Trás-os-Montes, *Quintas* s.n. (BM!, COI!); Novo Brasil, Monte Mário, *Rozeira* 4 (PO!); Cruzeiro, 300 m, *Thorold* 2069 (BM!).

**PRÍNCIPE.** S.l., *Barter* 1898 (K!).

**DISTRIBUTION.** Widespread in tropical and subtropical Africa.

## Lycopodiaceae

### Huperzia Bernh.

**Huperzia mildbraedii** (Herter) Pic. Serm. in *Webbia* **23**: 163 (1968); Benl in *Acta Bot. Barcinon.* **31**: 10 (1978).

*Lycopodium mildbraedii* Herter in *Hedwigia* **49**: 90 (1909); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 95 (1944).

**SÃO TOMÉ.** Lagoa Amélia, epiphyte, *Espírito Santo* 5032 (LISC!, LISJC!), primary forest, 1400–1420 m, epiphyte, *Matos & Van Essche* 7409 (LISC!), 1350 m, epiphyte, *Moller* s.n. (COI!), 1400 m, *Monod* 11734 (BM!); Calvário, 1500 m, *Exell* 317 (BM!, COI!), 1550 m, *Monod* 11832 (BM!); Macambrará, primary forest, 1050–1200 m, epiphyte, *Exell* 427 (BM!, COI!); Pico, 1700–1900 m, *F.A.E. (Moller)* 75 (BM!, K!, LISU!, P!), 1850 m, epiphyte, *Moller* s.n. (COI!), *Moller* s.n. p.p. (COI!), *Rose* 323 (P!); Bom Sucesso, 1250 m, epiphyte, *Moller* s.n. (COI!); Trás-os-Montes, 1100 m, *Quintas* 1321 p.p. (COI!); s.l., *F.A.E. (Moller)* 74 p.p. (BM!, COI!, LISU!), 1100–1400 m, *Moller* 76 (K!).

**PRÍNCIPE.** Pico Papagaio, 350 m, *Exell* 702 (BM!, COI!); W. of Pico, below 250 m, *Monod* 12097 (BM!); Pico, common up to 900 m, *Thorold* 2083 (BM!).

**DISTRIBUTION.** W. tropical Africa.

**Huperzia ophioglossoides** (Lam.) Rothm. in *Feddes Repert. Spec. Nov. Regni Veg.* **54**: 62 (1944).

**SÃO TOMÉ.** Pico, primary forest, 1900–2020 m, *Lejoly* 94/538 (LISC!), 1850 m, epiphyte, *Mollers* s.n. p.p. (COI!), *Rose* 328 (P!); s.l. (probably Pico), *F.A.E. (Moller)* 74 p.p. (LISU!).

**DISTRIBUTION.** Tropical, SE and S. Africa, Madagascar and Mascarene Is.

**Huperzia phlegmaria** (L.) Rothm. in *Feddes Repert. Spec. Nov. Regni Veg.* **54**: 62 (1944); Benl in *Acta Bot. Barcinon.* **31**: 9 (1978).

*Lycopodium phlegmaria* L., *Sp. pl.* **2**: 1101 (1753); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 96 (1944).

**SÃO TOMÉ.** Pico, *Chevalier* 13660 (P!); Lagoa Amélia, *Chevalier* 14307 (P!); Ribeira Peixe, Vila Irene, epiphyte, *Espírito Santo* 4601 (LISC!); São João dos Angolares, *F.A.E. (Quintas)* 76 (BM!, K!, LISU!, P!), *Quintas* s.n. (COI!); Perseverança, *Seabra* 183b (LISU!).

**PRÍNCIPE.** Between Terreiro Velho and Infante D. Henrique, plantation, 100 m, *Exell* 587 (BM!, COI!); Porto Real, *Rose* 483 (P!).

**DISTRIBUTION.** Palaeotropical.

**Huperzia verticillata** (L.f.) Trevis. in *Atti Soc. Ital. Sci. Nat.* **17**: 248 (1874); Benl in *Acta Bot. Barcinon.* **31**: 8 (1978).

*Lycopodium verticillatum* L.f., *Suppl. pl.*: 448 (1782); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 96 (1944); Tardieu-Blot in Aubrév., *Fl. Cameroun* **3**: 12 (1964).

**SÃO TOMÉ.** Bom Sucesso, 1200 m, *F.A.E. (Moller)* 73 (BM!, COI!, K!, LISU!, P!); Macambrará, 1100 m, *Moller* s.n. (COI!).

**DISTRIBUTION.** Tropical, SE and S. Africa, Comoros and Reunion, tropical America, and Polynesia.

**NOTE.** This taxon has not been recorded in the islands since the nineteenth century.

**Huperzia warneckei** (Herter ex Nessel) Pic. Serm. in *Webbia* **23**: 163 (1968).

*Lycopodium warneckei* (Herter ex Nessel) Alston in *Bol. Soc. Brot., ser. 2*, **30**: 20 (1956); Alston in Exell & Rozeira in *Conf. Int. Afr. Oc.* **3**: 81 (1958).

**SÃO TOMÉ.** Between São Miguel and Zagaia, primary forest, 170–400 m, *Matos & Van Essche* 7247 (LISC!); Trás-os-Montes, 1100 m, *Quintas* 1321 p.p. (COI!); Ribeira Peixe, between Vila José and Ermelinda, *Rozeira* 288 (PO!).

**DISTRIBUTION.** W. tropical Africa.

### Lycopodiella Holub

**Lycopodiella cernua** (L.) Pic. Serm. in *Webbia* **23**: 166 (1968); Benl in *Acta Bot. Barcinon.* **31**: 11 (1978).

*Lycopodium cernuum* L., *Sp. pl.* **2**: 1103 (1753); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 95 (1944); Sobrinho in *Portugaliae Acta Biol., Ser. B. Sist.* **3**: 393 (1952).

**SÃO TOMÉ.** Porto Alegre, *Chevalier* 14196 (P); São Nicolau, 1000 m, *Espírito Santo* 4448 (LISC!, LISJC!), 900 m, *Moller* s.n. (COI!); Macambrará, primary forest, 1200 m, *Exell* 94 (BM!); Santa Maria, 1300 m, *Exell* 196 (BM!, COI!), 1380 m, *Moller* s.n. (COI!); Lagoa Amélia, 1300 m, *Exell* 206 (BM!, COI!), crater swamp, 1300 m, *Exell* 209 (BM!), 1412 m, *Matos* 7504 (LISC!); Trás-os-Montes, *Gama* s.n. (COI!); road to Monte Mário, *Lains e Silva* 279 (LISU!); Pico, primary forest, 1900–200 m, *Lejoly* 94/546 (LISC!); Bom Sucesso, secondary forest, 1150 m, *Matos & Van Essche* 7459 (LISC!); Saudade, 950 m, *Moller* s.n. (COI!); above Monte Café, 1050 m, *Monod* 11679 (BM!); between Cascata and Morro Vilela, 700–1000 m, *Monod* 12202 (BM!); Santelmo, *Oliveira & Noronha* 6-B (LISU!); Monte Café, in forest and plantations, *Oliveira & Noronha* s.n. (LISU!); Trás-os-Montes, between Calvário and main house, *Rozeira* 527 (PO!); s.l., *Campos* 16 (COI!), *F.A.E. (Moller)* 77 (BM!, COI!, K!, LISU!).

**PRÍNCIPE.** Ôquê Pipi, secondary forest, 300 m, *Exell* 551 (BM!, COI!); Ôquê Gaspar, *Newton* s.n. (COI!); Ribeira Jambere, *Rozeira* 593 (PO!); Pico Papagaio, 900 m, *Welwitsch* 10 (BM!, LISU!).

**DISTRIBUTION.** Cosmopolitan.

### Lycopodium L.

**Lycopodium clavatum** L., *Sp. pl.* **2**: 1101 (1753); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 95 (1944); Tardieu-Blpt in Aubrév., *Fl. Cameroun* **3**: 16 (1964); Benl in *Acta Bot. Barcinon.* **31**: 10 (1978).

**SÃO TOMÉ.** Pico, 2000 m, *Chevalier* 13676 (P!), 2000 m, *F.A.E. (Moller)* 78 (BM!, COI!, K!, LISU!, P!), 1850 m, *Monod* 11919 (BM!, COI!), *Rose* 320 (P!).

**DISTRIBUTION.** Cosmopolitan.

## Marattiaceae

### Marattia Sw.

**Marattia fraxinea** Sm., *Pl. icon. ined.* **2**: t. 48 (1790); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 94 (1944); Benl in *Acta Bot. Barcinon.* **32**: 3 (1980); Pichi Sermolli in *Webbia* **23**: 332 (1969).

*Marattia robusta* Alston in Exell, *Suppl. Cat. Vasc. Pl. S. Tomé*: 8 (1956).

**SÃO TOMÉ.** Monte Café, primary forest, 1200 m, *Espírito Santo* 191 (BM!-holotype of *Marattia robusta*, COI!, LISJC!), 760 m, *Welwitsch* 70 (BM!, LISU!); Ribeira Peixe, S. of Cabumbé, secondary forest, *Espírito Santo* 3899 (COI!, LISJC!); Macambará, primary forest, 1050–1200 m, *Exell* 129 (BM!, COI!), 1250 m, *Moller* s.n. (COI!); Lagoa Amélia, 1200–1400 m, very common, *Lains e Silva* 88 (LISU!), 88a (LISU!), 1350–1380 m, *Monod* 11771 (BM!, COI!), *Rozeira* 1091 (PO!); São Miguel, Monte Verde, secondary forest, 10–150 m, *Lejoly* 95/88 (LISC!); between São Miguel and Zagaia, primary forest, 170–400 m, *Matos & Van Essche* 7239 (LISC!); Bom Sucesso, 1250 m, *Moller* s.n. (COI!); between São Pedro and Lagoa Amélia, 1050 m, *Monod* 11717 (BM!); São João dos Angolares, 150 m, *Quintas* s.n. (COI!); Porto Alegre, near Cão Pequeno, *Rozeira* 51 (PO!); between Lagoa Amélia and Calvário, *Rozeira* 1171 (PO!); Dona Augusta, *Rozeira* 1179 (PO); s.l., *F.A.E. (Moller & Quintas)* 71 (BM!, COI!, LISU!).

**PRÍNCIPE.** S.l., *Barter* 1916 (K!).

DISTRIBUTION. Palaeotropical.

NOTE. Pichi Sermolli (1969) considered that *Marattia robusta* was a strong form of *M. fraxinea* and that the plants from São Tomé might be recognized at infraspecific level. The collection from Príncipe is from a smaller plant (*M. fraxinea* s.s.).

## Nephrolepidaceae

### Arthropteris J. Sm.

**Arthropteris monocarpa** (Cordem.) C. Chr., *Cat. pl. mad., pter.*: 32 (1932); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 69 (1944); Alston in *Exell in Bull. Inst. Franç. Afrique Noire ser. A*, **21**: 445 (1959); Benl in *Acta Bot. Barcinon.* **33**: 35 (1982).

**SÃO TOMÉ.** Pico, *Campos* 77 (COI!), *Chevalier* s.n. (P!), primary forest, 1987 m, *Matos & Van Essche* 7385 (LISC!); Macambará, virgin forest, 1050–1200 m, *Exell* 121 (BM!), 1200–1350 m, 122a (BM!); Lagoa Amélia, crater swamp, 1300 m, ground fern, *Exell* 210 (BM!), 1430 m, epiphyte, *Matos* 7494 (LISC!); between Macambará and São Nicolau, secondary woodland, 1050 m, *Exell* 403 (BM!, COI!); Trás-os-Montes, *Gama* s.n. (COI!); between Pico and Monte Castro, 6 km S. of Ponta Figo, mountain rainforest, 1200–1800 m, *Lejoly* 95/23 (LISC!); Calvário and surroundings, primary forest, 1600–1620 m, epiphyte, *Matos & Van Essche* 7349 (LISC!); São João dos Angolares, 80 m, *Newton* s.n. (BM!, COI!); s.l., *Moller* s.n. (COI!), *F.A.E. (Moller)* 38 p.p. (BM!, LISJC!, LISU!, P!).

**PRÍNCIPE.** Porto Real, *Rose* 450 (P!); Pico, 950 m, *Thorold* 2082 (BM!).

DISTRIBUTION. Widespread in tropical Africa and Mascarene Is.

**Arthropteris orientalis** (J.F. Gmel.) Posth. in *Recueil Trav. Bot. Néerl.* **21**: 218 (1924); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 70 (1944); Tardieu-Blot in *Aubrév., Fl. Cameroun* **3**: 116 (1964); Benl in *Acta Bot. Barcinon.* **33**: 34 (1982).

**SÃO TOMÉ.** Between Monte Café and Pico, *Chevalier* 14562 (P!); Pico, *Moller* s.n. (COI-not found); Cruzeiro, 300 m, *Thorold* 2068 (BM!); s.l., *F.A.E. (Moller)* 38 p.p. (BM!, COI!, LISJC!, P!).

**PRÍNCIPE.** Rio Bambu-Porco, 60 m, epiphyte, *Navel* 143 (P!).

DISTRIBUTION. Widespread in tropical Africa and Mascarene Is.

**Arthropteris palisotii** (Desv.) Alston in *Bol. Soc. Brot., ser. 2*, **30**: 6 (1956); Benl in *Acta Bot. Barcinon.* **33**: 31 (1982).

*Arthropteris obliterata* sensu auct. non (R. Br.) J. Sm., *Ferns Brit. for.*: 163 (1866); C. Chr., *Index filic.*: 62 (1905); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 70 (1944).

**SÃO TOMÉ.** São João dos Angolares, 120 m, *F.A.E. (Quintas)* 47 (BM!, LISU!), 80 m, *Newton* s.n. (BM!, COI!), 120 m, *Quintas* s.n. (COI!); Água Pinhão, 650 m, *Quintas* 1454 (BM!, COI!); Monte Café, 760 m, *Welwitsch* 55 (BM!, K!, LISU!).

DISTRIBUTION. Tropical Africa, tropical Asia, Philippines.

### Nephrolepis Schott

**Nephrolepis biserrata** (Sw.) Schott, *Gen. fil.*: ad t. 3 (1834); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 70 (1944); Sobrinho in *Portugaliae Acta Biol., ser. B, Sist.* **3**: 392 (1952); Benl in *Acta Bot. Barcinon.* **33**: 36 (1982).

**SÃO TOMÉ.** Boa Entrada, *Chevalier* 13789 (P); between Monte Café and Pico, *Chevalier* 14291bis (P); São Miguel, 50 m, not frequent, *Espírito Santo* 4743 (LISC!, LISJC!); Água Izé, littoral, ground fern, *Exell* 482 (BM!, COI!), common epiphyte, *Pinto Basto* 214 (LISC!); Rio Contador, 1300 m, *Moller* s.n. (COI!); Bombaim, *Monod* 11887 (BM!); W. of Pico, *Monod* 11895 (BM!); between Quinas Altas and Monte Quinas, 520–750 m, *Monod* 12021 (BM!), 12022 (BM!); Santelmo, secondary forest, very abundant epiphyte, *Oliveira & Noronha* 23-A (LISU!); São Nicolau, Dependência Roça Nova, road to Trás-os-Montes, *Oliveira & Noronha* s.n. (LISU!); Ilhéu das Rolas, *Quintas* s.n. (COI!); Cruzeiro, 300 m, *Thorold* 2063 (BM!); s.l., *F.A.E. (Moller)* 46 (BM!, COI!, LISU!), *Moller* s.n. (COI!), *Ratray* s.n. (E), *Souza* s.n. (COI!).

**PRÍNCIPE.** Terreiro Velho, plantation, 200 m, ground fern, *Exell* 525 (BM!, COI!), 526 (BM!, COI!); s.l., *Ratray* s.n. (E), *Souza* s.n. (COI!), *Welwitsch* 23 (BM!, K!, LISU!), *Welwitsch* 23b (BM!, LISU!).

DISTRIBUTION. Pantropical.

**Nephrolepis pumicicola** F. Ballard in *Kew Bull.* [1955]: 467 (1955); Alston in *Exell in Bull. Inst. Franç. Afrique Noire ser. A*, **21**: 445 (1959); Tardieu-Blot in *Aubrév., Fl. Cameroun* **3**: 108 (1964); Benl in *Acta Bot. Barcinon.* **33**: 37 (1982).

**SÃO TOMÉ.** Lagoa Amélia, *Chevalier* 13650 (P!), 1412 m, *Matos* 7505 (LISC!), 1380 m, *Monod* 11759 (BM!); Pico, *Chevalier* 13659ter (P!); between Monte Café and Pico, *Chevalier* 14581 (P!); s.l., 1500 m, *Mann* 1106 (K!), *Mann* s.n. (P!).

DISTRIBUTION. Cameroun, Bioko.

**Nephrolepis undulata** (Afzel. ex Sw.) J. Sm. in *Bot. Mag.* **72**, *Comp.*: 37 [as '35'] (1846); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 71 (1944); Benl in *Acta Bot. Barcinon.* **33**: 39 (1982).

**SÃO TOMÉ.** São Nicolau, 870 m, *Espírito Santo* 5053 (LISC!, LISJC!); Macambará, coffee plantation, 1200 m, epiphyte, *Exell* 116 (BM!, COI!), primary forest, 1050–1200 m, epiphyte, *Exell* 190a (BM!); Lagoa Amélia, 1300 m, ground fern, *Exell* 212 (BM!); Trás-os-Montes, *Gama* s.n. (COI!); Santa Catarina, *Lains e Silva* 387 (LISU!); between Monte Castro and Ponta Figo, secondary forest, 500–1070 m, *Lejoly* 94/39 (LISC!); Pico, primary forest, 1900–2020 m, *Lejoly* 94/540 (LISC!); Nova Moca, 850 m, *Moller* s.n. (COI!); Saudade, *Moller* s.n. (COI!); Monte Café, 690 m, *Monod* 11669 (BM!), 600 m, *Thorold* 2061 (BM!); Bombaim, *Monod* 11885 (BM!); between Monte Quinas and Quinas Altas, *Monod* 12016 (BM!); NW of Pico, above Cascata, 1000 m, *Monod* 12267 (BM!); Água Izé, *Pinto Basto* 209 (LISC!); s.l., *Brentel* s.n. (COI!), *F.A.E. (Moller)* 45 (BM!, LISU!), *Mann* (not found).

**PRÍNCIPE.** Pico, summit, *Rozeira* 924 (PO!).

DISTRIBUTION. Widespread in tropical and S. Africa.

## Oleandraceae

### Oleandra Cav.

**Oleandra distenta** Kunze in *Bot. Zeitung (Berlin)* **9**: 347 (1851); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 69 (1944); Benl in *Acta Bot. Barcinon.* **33**: 28 (1982).

*Oleandra annetii* sensu auct. non Tardieu in *Notul. Syst. (Paris)* **14**: 332 (1953); Pichi Sermolli in *Webbia* **20**: 763 (1965) p.p. quoad

distr. São Tomé; Benl in *Acta Bot. Barcinon.* **33**: 30 (1982) p.p. quoad distr. São Tomé.

**SÃO TOMÉ.** Macambrará, primary forest, 1050–1200 m, epiphyte, *Exell* 237 (BM!); Nova Moca, 950 m, *Moller* s.n. (COI!); Bom Sucesso, 1250 m, *Moller* s.n. (COI!); Calvário, *Espírito Santo* 5058 p.p. (LISC!); São João dos Angolares, *Newton* s.n. (BM!, COI!); Trás-os-Montes, *Quintas* s.n. (COI!); Monte Café, *Welwitsch* 52 (BM!, LISU!); s.l., *F.A.E. (Moller & Quintas)* 48 (BM!, G, K also *Moller* 43!, LISU!).

**PRÍNCIPE.** S.l., *Barter* 1928 (K!).

**DISTRIBUTION.** Widespread in tropical and subtropical Africa and Mascarene Is.

**NOTE.** Some collections from São Tomé previously identified as *Oleandra annetii* Tardieu have squarrose rhizomes with abruptly subulate to gradually tapering scales and for this reason, they are here referred to *O. distenta* s.l.

## Ophioglossaceae

### Ophioglossum L.

**Ophioglossum costatum** R. Br., *Prodr.*: 163 (1810); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 94 (1944).

**SÃO TOMÉ.** Between Macambrará and São Nicolau, *Exell* 307 (BM-not found).

**DISTRIBUTION.** Widespread in tropical Africa, Asia, and Australasia.

**Ophioglossum reticulatum** L., *Sp. pl.* 2: 1063 (1753); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 94 (1944); Benl in *Acta Bot. Barcinon.* **33**: 3 (1982).

**SÃO TOMÉ.** Near São Pedro, 900–1200 m, *Chevalier* 14532 (P!); Magodinho, 50 m, *Espírito Santo* 4929 (LISC!, LISJC!); Macambrará, primary forest, 1050–1200 m, *Exell* 444 (BM!); Nova Moca, 800 m, *F.A.E. (Quintas)* 72 (BM!, COI!, K!, LISU!, P!), *Quintas* s.n. (COI!); Diogo Nunes, *Newton* s.n. (BM!, COI!, P!); Diogo Vaz, between Paga Fogo and Rio Paga Fogo, *Rozeira* 698 (PO!); s.l. (probably Nova Moca), *Quintas* 62 (K!), *Welwitsch* 30 (BM!, LISU!).

**DISTRIBUTION.** Pantropical and subtropical.

## Polypodiaceae

### Anapeltis J. Sm.

**Anapeltis lycopodioides** (L.) J. Sm., *Cult. ferns*: 6 (1857).

var. *owariensis* (Desv.) Benl in *Acta Bot. Barcinon.* **33**: 18 (1982).

*Polypodium lycopodioides* sensu auct. non L., *Sp. pl.* 2: 1082 (1753); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 88 (1944); Sobrinho in *Portugaliae Acta Biol., Ser. B, Sist.* **3**: 393 (1952).

*Microgramma owariensis* (Desv.) Alston in *Bol. Soc. Brot., ser. 2*, **30**: 20 (1956); Alston in *Exell & Rozeira in Conf. Int. Afr. Oc.* **3**: 80 (1958).

**SÃO TOMÉ.** Pico, *Chevalier* 13639 (P); Porto Alegre, *Chevalier* 14211 bis (P); Vila Conceição, 100 m, *Matos* 7718 (LISC!); Caixão Grande, 200 m, *Moller* s.n. (COI!); Trindade, 250 m, *Moller* s.n. (COI!); near São Tomé, *Moller* s.n. (COI!); Ribeira Peixe, epiphyte, *Oliveira & Noronha* 35-A (LISU!); Água Izé, epiphyte on plantation, *Pinto Basto* 206 (LISC!); Correia, 50 m, *Quintas* 1246 (BM!, COI!); Ilhéu das Rolas, *Quintas* s.n. (COI!); São Nicolau, 900 m, *Quintas* s.n. (LISU!); Ribeira Peixe, between Vila José and Ermelinda, epiphyte, *Rozeira* 236 (PO!); Diogo Vaz, *Rozeira* 869 (PO); s.l., *F.A.E. (Moller & Quintas)* 54 (COI!, BM!, LISJC!, LISU!), *Seabra* s.n. (COI!, LISU!).

**PRÍNCIPE.** Terreiro Velho, 200 m, epiphyte, *Exell* 534 (BM!, COI!); Porto Real, epiphyte, *Lains e Silva* 420 (LISU!); Sundi, epiphyte, *Monod* 12076 (BM!), *Thorold* 2080 (BM!); Berimbau, *Newton* 23 (BM!, COI!); Cimãlo, *Quintas* 43 (BM!, COI!); Infante D. Henrique, at the base of Dois Irmãos, epiphyte, *Rozeira* 435 (BM-not found, PO!); Esperança, 120 m, *Rozeira* 996 (PO), *Thorold* 2076 (BM!); Santo António, sea level, epiphyte, *Thorold* 2079 (BM!); s.l., *Ratray* s.n. (E, K!).

**DISTRIBUTION.** W. tropical Africa.

### Belvisia Mirb.

**Belvisia spicata** (L.f.) Mirb. ex Copel., *Gen. fil.*: 192 (1947); Alston in *Exell in Bull. Inst. Franç. Afrique Noire ser. A*, **21**: 444 (1959); Tardieu-Blot in Aubrév., *Fl. Cameroun* **3**: 342 (1964); Benl in *Acta Bot. Barcinon.* **33**: 12 (1982).

*Hymenolepis spicata* (L.f.) C. Presl, *Epimel. bot.*: 159 (1851); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 90 (1944); Sobrinho in *Garcia de Orta* **7**: 89 (1959).

**SÃO TOMÉ.** Calvário, secondary forest, 920 m, epiphyte, *Espírito Santo* 5075 (LISJC!); Ribeira Peixe, 140 m, epiphyte, *Lains e Silva* 248 (LISU!), 257 (LISJC-not found), 284 (LISJC-not found); Trás-os-Montes, 700 m, *Quintas* 1322 p.p. (BM!, COI!); Nova Moca, 1100 m, *Quintas* s.n. (LISU!); Ribeira Peixe, between Vila José and Ermelinda, *Rozeira* 272 (PO!); Cruzeiro, 300 m, *Thorold* 2067 (BM!), 300 m, 2071 (BM!); s.l., 900 m, *Quintas* 3 (K!).

**DISTRIBUTION.** Tropical Africa and Mascarene Is.

### Drynaria (Bory) J. Sm.

**Drynaria laurentii** (H. Christ ex De Wild. & T. Durand) Hieron. in Engl. & Drude, *Veg. Erde* **9**(2): 57, fig. 54 (1908); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 90 (1944); Benl in *Acta Bot. Barcinon.* **33**: 10 (1982).

**SÃO TOMÉ.** Monte Café, *Chevalier* 14291 (P!), 600 m, *Thorold* 2062 (BM!), 600–760 m, *Welwitsch* 69 (BM!, K!, LISU!); Blu-blu, 50 m, *Moller* s.n. (COI!); Água Izé, epiphyte, *Pinto Basto* 217 (LISC!); Diana, *Rozeira* 957 (PO!); Perseverança, *Seabra* 173 (LISU!); s.l., *Don* s.n. (BM!), *F.A.E. (Moller)* 57 (BM!, K also *Moller* 52!, LISU!).

**PRÍNCIPE.** S.l., *Welwitsch* 17 (BM!, K!, LISU!).

**DISTRIBUTION.** Tropical Africa.

**Drynaria volkensii** Hieron. in Engl. & Drude, *Veg. Erde* **9**(2): 57 (1908) nomen; in *Bot. Jahrb. Syst.* **46**: 393 (1911); Alston in *Exell & Rozeira in Conf. Int. Afr. Oc.* **3**: 80 (1958); Alston in *Exell in Bull. Inst. Franç. Afrique Noire ser. A*, **21**: 444 (1959); Benl in *Acta Bot. Barcinon.* **33**: 11 (1982).

**SÃO TOMÉ.** Nova Moca, 900 m, *Moller* s.n. (COI!); Cruzeiro, 300 m, *Thorold* 2066 (BM!); Água Izé, 180 m, *Thorold* 2092 (BM!).

**PRÍNCIPE.** Praia da Lapa, epiphyte, *Rozeira* 1902 (BM-not found, PO!); s.l., *Barter* 1921 (K!).

**DISTRIBUTION.** Widespread in tropical Africa.

### Microsorium Link

**Microsorium punctatum** (L.) Copel. in *Univ. Calif. Publ. Bot.* **16**: 111 (1929); Benl in *Acta Bot. Barcinon.* **33**: 14 (1982).

*Polypodium irioides* Poir., *Encycl.* **5**: 513 (1804); Alston in *Exell, Cat. Vasc. Pl. S. Tomé*: 88 (1944).

**SÃO TOMÉ.** Between Bom Sucesso and Lagoa Amélia, *Almeida* s.n. (LISC!); Boa Entrada, *Chevalier* 13788 (P!), 14375 (not found); São João dos Angolares, *F.A.E. (Quintas)* 55 (LISU!), *Quintas* s.n. (COI!); Água Izé, common epiphyte, *Pinto Basto* 203 (LISC!); s.l., *Mendonça* s.n. (P!), *Souza* s.n. (BM!, COI!).

**PRÍNCIPE.** Santo António, sea level, epiphyte, *Monod* 12189 (BM!); Sundi, 150 m, *Quintas* 62 (COI!); Esperança, 120 m, *Thorold* 2077 (BM!); Lapa, near sea level, *Thorold* 2089 (BM!), 2090 (BM!); s.l., *Ratray* s.n. (E), *Welwitsch* 25 (BM!, LISU!).

DISTRIBUTION. Palaeotropical.

### Phymatosorus Pic. Serm.

**Phymatosorus scolopendria** (Burm.f.) Pic. Serm. in *Webbia* **28**: 460 (1973); Benl in *Acta Bot. Barcinon.* **33**: 13 (1982).

*Polypodium phymatodes* L., *Mant. pl.* **2**: 306 (1771); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 89 (1944); Alston in Exell, *Suppl. Cat. Vasc. Pl. S. Tomé*: 8 (1956).

**SÃO TOMÉ.** Boa Entrada, *Chevalier* 13786 (P); Porto Alegre, *Chevalier* 14243 (K!); Famosa, 400 m, *Espírito Santo* 69 (BM!, COI!, LISJC!); Ilhéu das Rolas, plantation, 70 m, epiphyte, *Espírito Santo* 5110 (LISC!, LISJC!), *Quintas* s.n. (COI!); Água Izé, epiphyte, *Exell* 480 (BM!, COI!), epiphyte, *Pinto Basto* 201 (LISC!); bridge over R. Abade, *Figueiredo & Arriegas* 34 (LISC!); Rio Santo António, *Matos* 7646 (LISC!); Praia Pantufo, *Moller* s.n. (COI!); near Bâtepá, 500 m, *Moller* s.n. (COI!); Bombaim, epiphyte, *Monod* 11880 (BM!); NW of Pico, 1000 m, *Monod* 12268 (BM!, COI!); Quingombó, 100 m, *Newton* s.n. (COI!); Cruzeiro, 300 m, *Thorold* 2070 (BM!); Monte Café, 850 m, *Welwitsch* 51 (BM!, LISU!); s.l., *Don* s.n. (BM!), *F.A.E. (Moller & Quintas)* 56 (BM!, COI!, LISJC!, LISU!); *Mendonça* (COI!, K!), *Moller* s.n. (COI!), *Rozeira* 1 (PO!), *Seabra* s.n. (COI!).

**PRÍNCIPE.** Terreiro Velho, plantation, 200 m, ground fern, *Exell* 523 (BM!, COI!); Esperança, 120 m, *Thorold* 2075 (BM!), 2078 (BM!); Lapa, near sea level, *Thorold* 2091 (BM!); s.l., *Ratray* s.n. (E), *Welwitsch* 9 (BM!, K!, LISU!), 9bis (K!).

DISTRIBUTION. Palaeotropical.

### Platyserium Desv.

**Platyserium stemaria** (P. Beauv.) Desv. in *Mém. Soc. Linn. Paris* **6**: 213 (1827); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 91 (1944); Alston in Exell, *Suppl. Cat. Vasc. Pl. S. Tomé*: 8 (1956); Benl in *Acta Bot. Barcinon.* **33**: 9 (1982); Hennipman & Roos, *Monogr. fern genus Platyserium*: 108 (1982).

**SÃO TOMÉ.** São Vicente, 200 m, epiphyte, *Espírito Santo* 24 (BM!, COI!, LISJC!); near São Tomé, *Chevalier* 13726 (P!); Trindade, 250 m, *Moller* s.n. (COI!), *Quintas* s.n. (COI!); Rio do Ouro, 380 m, *Moller* s.n. (COI!); Diogo Vaz, epiphyte, *Rozeira* 829 (PO!); s.l., 250–350 m, *F.A.E. (Moller)* 70 (LISU!), *Mendonça* s.n. (K!, P!), 250 m, *Moller* 60 (K!).

**PRÍNCIPE.** Precipício, *Monod* 12178 (BM!); Praia das Burras, epiphyte, *Rozeira* 1029 (PO!); s.l., *Barter* 1886 (K!), *Welwitsch* 20 (K-not found, LISU!), 20b (BM-not found, LISU!).

DISTRIBUTION. W. and Central tropical Africa.

### Pleopeltis Humb. & Bonpl. ex Willd.

**Pleopeltis excavata** (Bory ex Willd.) Sledge in *Bull. Br. Mus. (Nat. Hist.) Bot.* **2**: 138 (1960); Benl in *Acta Bot. Barcinon.* **33**: 16 (1982).

*Polypodium preussii* Hieron. in Engl. in *Bot. Jahrb. Syst.* **46**: 386 (1911); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 89 (1944).

**SÃO TOMÉ:** Calvário, *Espírito Santo* 5058 p.p. (LISC!, LISJC!); Macambrará, primary forest, 1050–1200 m, epiphyte, *Exell* 113 (BM!); Lagoa Amélia, *Exell* 216 (BM-not found), 1412 m, *Matos* 7511 (LISC!), 1380 m, *Monod* 11758 (BM!), 1450 m, *Monod* 11768 (BM!, COI!); Macambrará to Zampalma, 900 m, epiphyte, *Exell* 295 (BM!); Pico, light woodland, 2000 m, epiphyte, *Exell* 341 (BM!), primary forest, 1900–2020 m, *Lejoly* 94/536 (LISC!), *Mann* (not found), primary forest, 1987 m, epiphyte, *Matos & Van Essche* 7386 (LISC!); Bom Sucesso, 1080 m, *F.A.E. (Moller & Quintas)* 53 (BM!, LISU!), *Moller* s.n. (COI!); near São Nicolau waterfall,

800 m, *Lains e Silva* 129 (LISU!); Casa do Pico, 1930 m, *Monod* 12250 (BM!); s.l., *Souza* s.n. (COI!).

DISTRIBUTION. Palaeotropical.

**Pleopeltis macrocarpa** (Bory ex Willd.) Kaulf. in *Berlin. Jahrb. Pharm. Verbundenen Wiss.* **21**: 41 (1820).

**SÃO TOMÉ.** Lagoa Amélia, primary forest, 1400–1420 m, epiphyte, *Matos & Van Essche* 7411 (LISC!).

DISTRIBUTION. Pantropical and subtropical

### Pyrrosia Mirb.

**Pyrrosia lanceolata** (L.) Farw. in *Amer. Midl. Naturalist* **12**: 245 (1931); Alston in Exell & Rozeira in *Conf. Int. Afr. Oc.* **3**: 80 (1958); Tardieu-Blot in Aubrév., *Fl. Cameroun* **3**: 340 (1964); Hovenkamp, *Monogr. fern genus Pyrrosia*: 191 (1986).

*Cyclophorus spissus* (Bory ex Willd.) Desv. in *Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk.* **5**: 301 (1811) var. *continentalis* Hieron. ex Engl. in Engl. & Drude, *Veg. Erde* **9**(2): 55, fig. 53 (1908); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 91 (1944).

**SÃO TOMÉ.** Cruzeiro, *Rozeira* 690 (BM-not found, PO).

**PRÍNCIPE.** Cimáló, *Quintas* 30 (BM!, COI!, P!, Z); Esperança, way to Montalegre, *Rozeira* 392 (PO!); Praia da Lapa, *Rozeira* 1944 (PO!); s.l., *Keulemans* s.n. (L), *Quintas* A (K!).

DISTRIBUTION. Palaeotropical.

### Psilotaceae

#### Psilotum Sw.

**Psilotum nudum** (L.) P. Beauv., *Prodr. aethéogom.*: 106, 112 (1805); Alston in Exell, *Suppl. Cat. Vasc. Pl. S. Tomé*: 9 (1956); Benl in *Acta Bot. Barcinon.* **31**: 21 (1978).

**SÃO TOMÉ.** Praia Melão, *Rozeira* 57 (PO!); s.l., *Don* s.n. (BM!).

DISTRIBUTION. Widespread in tropical and subtropical regions worldwide.

### Pteridaceae

#### Pteris L.

**Pteris atrovirens** Willd., *Sp. pl.* **5**: 385 (1810); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 83 (1944); Tardieu-Blot in Aubrév., *Fl. Cameroun* **3**: 166 (1964); Benl in *Acta Bot. Barcinon.* **38**: 16 (1988).

**SÃO TOMÉ.** Boa Entrada, *Chevalier* 13792 p.p. (P!); Pico, *Chevalier* 14617 (P!); Trás-os-Montes, *Gama* s.n. (COI!); between Quinas Altas and Monte Quinas, *Monod* 12009 (BM!, COI!); Água Izé, *Pinto Basto* 210 (LISC!); Pedroma, *Rozeira* 1370 (K!); s.l., *Don* s.n. (BM!), *F.A.E. (Moller)* 18 p.p. (BM!, COI!, LISU!, P!), *Moller* s.n. p.p. (COI!), *Moller* s.n. (COI!), *Ratray* s.n. (E, K!).

**PRÍNCIPE.** Esperança, *Navel* 146 (P!); Sundi, *Newton* 42 (COI!); Pico Papagaio, *Welwitsch* 22 (BM!, LISU!); s.l., *Jardim* (cited by Kuhn, 1868), *Ratray* s.n. (E).

DISTRIBUTION. W. tropical Africa.

**Pteris burtonii** Baker in *Ann. Bot. (London)* **5**: 218 (1891); Alston in Exell in *Bull. Inst. Franç. Afrique Noire ser. A*, **21**: 442 (1959); Benl in *Acta Bot. Barcinon.* **38**: 7 (1988).

**PRÍNCIPE.** S.l., *Fox* s.n. (BM!).

DISTRIBUTION. W. and E. tropical Africa.

NOTES. This taxon has not been recorded in the islands since the nineteenth century.

The collection *Walg* 71 (WAG), from São Tomé, was interpreted as a possible hybrid between *Pteris atrovirens* and *P. burtonii* by Benl (1988: 17).

***Pteris dentata*** Forssk., *Fl. aegypt.-arab.*: 186 (1775); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 84 (1944).

subsp. ***flabellata*** (Thunb.) Runemark in *Bot. Not.* **115**: 190 (1962); Benl in *Acta Bot. Barcinon.* **38**: 11 (1988).

*Pteris communata* sensu auct. non Kuhn in Von der Decken's *Reisen Ost-Afr., Bot.* **3**: 20 (1879); Alston in Exell in *Bull. Inst. Franç. Afrique Noire ser. A*, **21**: 442 (1959).

**SÃO TOMÉ**. Lagoa Amélia, 1400 m, *Monod* 11749 (BM!).

**PRÍNCIPE**. Esperança, 600 m, *Rozeira* 890 (K!).

DISTRIBUTION. Subtropical Africa, Madagascar, Mascarene Is., Ascension, St Helena.

***Pteris linearis*** Poir., *Encycl.* **5**: 723 (1804); Alston in Exell & Rozeira in *Conf. Int. Afr. Oc.* **3**: 79 (1958); Benl in *Acta Bot. Barcinon.* **38**: 18 (1988).

*Pteris biaurita* sensu auct. non L., *Sp. pl.* **2**: 1076 (1753); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 83 (1944).

**SÃO TOMÉ**. Boa Entrada, *Chevalier* 13792 p.p. (P); Ilhéu das Rolas, palm plantation, *Espírito Santo* 5145 (LISC!, LISJC!), *Rozeira* 74 (BM-not found, PO!); Bombaim, *Rozeira* 495 (PO); Santa Catarina, palm plantation, *Rozeira* 790 (K!); s.l., *Don* s.n. (BM!), *F.A.E. (Moller)* 16 (BM!, COI!, LISU!), 900 m, *Moller* 14 (K!), *Moller* s.n. (COI!), *Ratray* s.n. (E).

**PRÍNCIPE**. Ôquê Nazaré, *Carvalho* s.n. (COI!); Terreiro Velho, plantation, 200 m, ground fern, *Exell* 529 (BM!, COI!); s.l., *Welwitsch* 22b (LISU!).

DISTRIBUTION. Palaeotropical.

***Pteris paucipinnata*** Alston in Exell in *Bull. Inst. Franç. Afrique Noire ser. A*, **21**: 443 (1959); Benl in *Acta Bot. Barcinon.* **38**: 14 (1988).

*Pteris catoptera* sensu auct. non Kunze in *Linnaea* **18**: 119 (1844); Alston in Exell & Rozeira in *Conf. Int. Afr. Oc.* **3**: 79 (1958).

*Pteris quadriaurita* sensu auct. non Retz, *Observ. bot.* **6**: 38 (1791); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 84 (1944) p.p. quoad spec. São Tomé.

**SÃO TOMÉ**. Macambrará, primary forest, 1050–1200 m, ground fern, *Exell* 187 (BM!); between Pico and Monte Castro, 6 km S. of Ponta Figo, mountain rainforest, 1200–1800 m, *Lejoly* 95/11 (LISC!); Monte Café, 1010 m, *Monod* 11690 (BM!-holotype); Colónia Açoreana, *Rozeira* 267 (PO); Diogo Vaz, *Rozeira* 516 (PO); s.l., 350 m, *Welwitsch* 54 (BM!, LISU!).

**PRÍNCIPE**. Pico Papagaio, 600 m, ground fern, *Exell* 686 (BM!).

DISTRIBUTION. Bioko.

***Pteris pteridioides*** (Hook.) F. Ballard in *Kew Bull.* [1937]: 348 (1937); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 84 (1944); Tardieu-Blot in Aubrév., *Fl. Cameroun* **3**: 170 (1964); Benl in *Acta Bot. Barcinon.* **38**: 9 (1988).

**SÃO TOMÉ**. Trás-os-Montes, *Gama* s.n. (COI!); Macambrará, 1200 m, *Quintas* 5 (K!), 1200 m, *Quintas* 1352 (BM!, COI!, K!, P!).

DISTRIBUTION. Widespread in tropical and subtropical Africa.

NOTE. This taxon has not been recorded in the islands since the nineteenth century.

***Pteris similis*** Kuhn in Von der Decken's *Reisen Ost-Afr., Bot.* **3**: 21 (1879); Benl in *Acta Bot. Barcinon.* **38**: 18 (1988).

*Pteris atrovirens* sensu auct. non Willd., *Sp. pl.* **5**: 385 (1810); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 83 (1944) p.p.

**SÃO TOMÉ**. São Miguel, Monte Verde, secondary forest, 10–150 m, *Lejoly* 95/98 (LISC!); Água Izé, common, *Pinto Basto* 200 (LISC!); Monte Café, 760 m, *Welwitsch* 53 (BM!, LISU!); s.l., *Don* s.n. (BM!).

**PRÍNCIPE**. Between Ôquê Pipi and Morro do Leste, secondary forest, 350 m, ground fern, *Exell* 561 (BM!, COI!); Sundi, 150 m, *Quintas* 45 (BM!, COI!, K!, P!); Infante D. Henrique, *Rose* 407 (P!).

DISTRIBUTION. W. tropical Africa to E. Africa.

***Pteris togoënsis*** Hieron. in Brause & Hieron. in Engl. in *Bot. Jahrb. Syst.* **53**: 402 (1915); Benl in *Acta Bot. Barcinon.* **38**: 13 (1988).

**PRÍNCIPE**. S.l., *Barter* 1926 (K!).

DISTRIBUTION. W. tropical Africa to E. Africa.

NOTE. This taxon has not been recorded in the islands since the nineteenth century.

***Pteris tripartita*** Sw. in *J. Bot. (Schrader)* **1800**(2): 67 (1801); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 84 (1944); Benl in *Acta Bot. Barcinon.* **38**: 15 (1988).

**SÃO TOMÉ**. Boa Entrada, *Chevalier* 13720 (P!); Ilhéu das Rolas, *F.A.E. (Quintas)* 20 (BM!, LISU!), *Quintas* s.n. (COI!); s.l., *Don* s.n. (BM!); s.l., *Ratray* s.n. (E).

**PRÍNCIPE**. Sundi, littoral, *Quintas* 11 (BM!, COI!, K!, P!).

DISTRIBUTION. Pantropical.

***Pteris vittata*** L., *Sp. pl.* **2**: 1074 (1753); Alston in Exell & Rozeira in *Conf. Int. Afr. Oc.* **3**: 79 (1958); Alston in Exell in *Bull. Inst. Franç. Afrique Noire ser. A*, **21**: 443 (1959).

**SÃO TOMÉ**. Monte Café, 690 m, *Monod* 11671 (BM!), *Rozeira* s.n. (PO); Água Izé, *Pinto Basto* 216 (LISC!).

DISTRIBUTION. Pantropical. Alston (1958, 1959) suggested that this might be an escape from cultivation.

## Selaginellaceae

### Selaginella P. Beauv.

***Selaginella cathedrifolia*** Spring in *Mém. Acad. Roy. Sci. Belgique* **24**: 112 (1849); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 96 (1944); Tardieu-Blot in Aubrév., *Fl. Cameroun* **3**: 30 (1964); Benl in *Acta Bot. Barcinon.* **31**: 15 (1978).

**PRÍNCIPE**. Above Infante D. Henrique, secondary forest, 300 m, ground fern, *Exell* 629 (BM!); Pico Papagaio, 600 m, ground fern, *Exell* 687 (BM!, COI!); near Lapa, *Monod* 12094 (BM!); s.l., *Barter* 1931 (K!), *Curror* 3 (K!-type), *Mann* s.n. (K!).

DISTRIBUTION. W. and Central tropical Africa.

***Selaginella mannii*** Baker in *J. Bot.* **23**: 180 (1885); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 96 (1944).

**SÃO TOMÉ**. Between Monte Café and Pico, *Chevalier* 14552 (P!); Macambrará, primary forest, 1050–1200 m, *Exell* 95 (BM!, COI!), 106 (BM!), 168 (BM!), 1260 m, *Moller* s.n. (COI!); between Bom Sucesso and Calvário, primary forest, 1350–1400 m, *Matos & Van Essche* 7347 (LISC!); Bom Sucesso, 1250 m, *Moller* s.n. (COI!); Pico, 1900 m, *Moller* s.n. (COI!); Rio Contador, 1350 m, *Moller* s.n. (COI!); Lagoa Amélia, 1400 m, *Monod*

11784 (BM!); W. of Pico, 870–1225 m, *Monod* 11904 (BM!); Calvário, *Rose* 151 (P!); s.l., *F.A.E. (Moller)* 80 (BM!, COI!), K also *Moller* 75!, LISU!, P!), *Henriques* 4 (K!), 1500 m, *Mann* 1108 (K!-type).

**PRÍNCIPE.** Pico Papagaio, 600 m, ground fern, *Exell* 683 (BM!).

**DISTRIBUTION.** Endemic.

**Selaginella mollerii** Hieron. in Engl. & Prantl. *Nat. Pflanzenfam.* 1(4): 697 (1901); Alston in Exell, *Cat. Vasc. Pl. S. Tomé:* 97 (1944); Benl in *Acta Bot. Barcinon.* 31: 20 (1978).

**SÃO TOMÉ.** Pico, *Chevalier* 13668 (P!); Macambará, primary forest, 1050–1200 m, *Exell* 180 (BM!, COI!); Bom Sucesso, 1250 m, *Moller* s.n. (COI!); Rio Manuel Jorge, waterfall, 800 m, *Moller* s.n. (COI!); s.l., *F.A.E. (Moller)* 79 p.p. (BM type!, COI!, K!, LISU!).

**DISTRIBUTION.** Liberia, Nigeria, Bioko.

**Selaginella mollicepe** Spring in *Mém. Acad. Roy. Sci. Belgique* 24: 257 (1849); Alston in Exell, *Cat. Vasc. Pl. S. Tomé:* 97 (1944); Alston in Exell & Rozeira in *Conf. Int. Afr. Oc.* 3: 81 (1958); Benl in *Acta Bot. Barcinon.* 31: 20 (1978).

**SÃO TOMÉ.** Between Bacelar and Quijá, secondary forest, 160 m, *Espírito Santo* 5140 (LISC!, LISJC!); Ribeira Peixe, Cão Grande, primary forest, *Matos* 7636 (LISC!); between São Miguel and Zagaia, primary forest, 170–400 m, *Matos & Van Essche* 7238 (LISC!); Diogo Vaz, *Rozeira* 879 (PO).

**PRÍNCIPE.** Ôquê Pipi, secondary forest, 300 m, ground fern, *Exell* 500 (BM!, COI!); São João, 450 m, *Newton* s.n. (COI!), *Newton* 4 (K!); Pico Papagaio, 900 m, *Welwitsch* 11 (BM!, LISU!); s.l., *Curror* 2 p.p. (K!-type).

**DISTRIBUTION.** W. and Central tropical Africa.

**Selaginella monodii** Alston in Exell in *Bull. Inst. Franç. Afrique Noire ser. A*, 21: 440 (1959).

**SÃO TOMÉ.** Blu-blu, *Monod* 11806 (BM!-holotype, COI!).

**DISTRIBUTION.** Endemic.

**Selaginella myosurus** (Sw.) Alston in *J. Bot.* 70: 64 (1932).

**PRÍNCIPE.** S.l., *Curror* 2 p.p. (K!).

**DISTRIBUTION.** Tropical Africa.

**NOTE.** This taxon has not been recorded in the islands since the nineteenth century.

**Selaginella squarrosa** Baker in *J. Bot.* 23: 180 (1885); Alston in Exell in *Bull. Inst. Franç. Afrique Noire ser. A*, 21: 440 (1959).

**PRÍNCIPE.** Pico, 500–600 m, *Monod* 12111 (BM!).

**DISTRIBUTION.** Cameroun, Equatorial Guinea.

**Selaginella thomensis** Alston in Exell, *Cat. Vasc. Pl. S. Tomé:* 97, f. 3 (1944); Tardieu-Blot in Aubrév., *Fl. Cameroun* 3: 40 (1964).

**SÃO TOMÉ.** Between Santa Maria and Zampalma, 1200 m, *Exell* 261 (BM!, COI!); Macambará, primary forest, 1050–1200 m, *Exell* 423 (BM!-holotype, COI!); road Monte Café to São Nicolau, *Figueiredo & Arriegas* 121 (LISC!); Nova Moca, 890 m, *Moller* s.n. (COI!, K!); Pico, 1950 m, *Moller* s.n. (COI!); s.l., *F.A.E. (Moller)* 79 p.p. (BM!, K!, LISU!).

**DISTRIBUTION.** Sierra Leone, Nigeria, Cameroun.

## Sinopteridaceae

### Pellaea Link

**Pellaea doniana** Hook., *Sp. fil.* 2: 137, t. 125 fig. A (1858); Alston

in Exell, *Cat. Vasc. Pl. S. Tomé:* 82 (1944); Tardieu-Blot in Aubrév., *Fl. Cameroun* 3: 140 (1964); Benl in *Acta Bot. Barcinon.* 32: 29 (1980).

**SÃO TOMÉ.** Pico, *Don* s.n. (BM!-type); Ilhéu das Rolas, plantation, *Espírito Santo* 5106 (LISC!, LISJC!), *F.A.E. (Quintas)* 15 (K also *Quintas* 13!, LISU!), *Quintas* s.n. (COI!), *Rozeira* 92 (PO!).

**PRÍNCIPE.** Between Esperança and Fundão, primary forest, 300–350 m, *Exell* 739 (BM!).

**DISTRIBUTION.** Widespread in tropical Africa

## Thelypteridaceae

### Christella H. Lév.

**Christella dentata** (Forssk.) Brownsey & Jermy in *Brit. Fern Gaz.* 10: 338 (1973); Benl in *Acta Bot. Barcinon.* 38: 53 (1988).

*Dryopteris dentata* (Forssk.) C. Chr. in *Kongel. Danske Vidensk. Selsk. Naturvidensk. Math. Aft.* 8(6): 24 (1920); Alston in Exell, *Cat. Vasc. Pl. S. Tomé:* 61 (1944); Alston in Exell, *Suppl. Cat. Vasc. Pl. S. Tomé:* 7 (1956).

**SÃO TOMÉ.** Boa Entrada, *Chevalier* 13787 (P!), 14336 (P!); São Vicente, 200 m, *Espírito Santo* 41 p.p. (BM!, COI!, LISJC!); Novo Destino, 760 m, *Welwitsch* 61 (BM!, K!, LISU!); Monte Café, *Welwitsch* 65 (BM!, LISU!); s.l., *F.A.E. (Moller)* 42 p.p. (COI!, BM!), *Ratray* s.n. (BM!, E).

**PRÍNCIPE.** Ôquê Nazaré, *Newtons* s.n. (BM!, COI!); s.l., *Ratrays* s.n. (BM!, E).

**DISTRIBUTION.** Palaeotropical.

**Christella hispidula** (Decne.) Holttum in *Kew Bull.* 31: 312 (1976); Benl in *Acta Bot. Barcinon.* 38: 51 (1988).

*Dryopteris quadrangularis* (Fée) Alston in *J. Bot.* 75: 253 (1937); Alston in Exell, *Cat. Vasc. Pl. S. Tomé:* 63 (1944).

**SÃO TOMÉ.** Água Grande, 100 m, *Moller* s.n. (COI!); Saudade, 720 m, *Moller* s.n. (COI!); above Monte Café, 1010 m, *Monod* 11691 (BM!); between Monte Quinas and Quinas Altas, *Monod* 12006 (BM!).

**DISTRIBUTION.** Pantropical.

### Cyclosorus Link

**Cyclosorus striatus** (Schum.) Ching in *Bull. Fan Mem. Inst. Biol.* 10: 249 (1941); Benl in *Acta Bot. Barcinon.* 38: 55 (1988).

*Dryopteris striata* (Schum.) C. Chr., *Index filic.*: 294 (1905); Alston in Exell, *Cat. Vasc. Pl. S. Tomé:* 64 (1944).

**SÃO TOMÉ.** Lagoa Amélia, *Chevalier* 13653 (P).

**DISTRIBUTION.** Tropical Africa.

### Metathelypteris (H. Ito) Ching

**Metathelypteris fragilis** (Baker) Holttum in *J. S. African Bot.* 40: 127 (1974).

*Dryopteris fragilis* (Baker) C. Chr., *Index filic.*: 266 (1905); Alston in Exell, *Cat. Vasc. Pl. S. Tomé:* 62 (1944).

subsp. **guineensis** Benl in *Nova Hedwigia* 27: 150 (1976); Benl in *Acta Bot. Barcinon.* 38: 43 (1988).

**SÃO TOMÉ.** Macambará, primary forest, 1050–1200 m, *Exell* 133 (BM!); s.l., *Newton* 1 (K!).

**DISTRIBUTION.** Bioko.

**NOTE.** The collection cited by Holttum (l.c.) as *Newton* s.n. (K ex COI), 1885, is *Newton* 1 (K).



**Pneumatopteris** Nakai

**Pneumatopteris afra** (C. Chr.) Holttum in *Blumea* **21**: 306 (1973); Benl in *Acta Bot. Barcinon.* **38**: 57 (1988).

*Dryopteris oppositifolia* sensu auct. non (Hook.) C. Chr., *Index filic.*: 281 (1905); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 63 (1944) p.p. quoad pl. ex Príncipe.

*Cyclosorus afer* (H. Christ) Ching in *Bull. Fan Mem. Inst. Biol.* **10**: 242 (1941); Alston in Exell in *Bull. Inst. Franç. Afrique Noire ser. A*, **21**: 446 (1959).

**SÃO TOMÉ**. São Vicente, *Espírito Santo* 41 p.p. (LISC!); São Miguel, 50 m, *Espírito Santo* 4744 (LISC!); between Pico and Monte Castro, 6 km S. of Ponta Figo, mountain rainforest, 1200–1800 m, *Lejoly* 95/30 (LISC!); Pedroma, *Mocquerys* 39/40 (P!); between Quinas Altas and Monte Quinas, *Monod* 12023 (BM!); Água Izé, *Pinto Basto* 213 (LISC!); Lagoa Amélia, *Rose* 204 (P!), 231 (P!).

**PRÍNCIPE**. Terreiro Velho, plantation, 200 m, *Exell* 530a (BM!, COI!); between Ôquê Pipi and Morro do Leste, secondary forest, 350 m, ground fern, *Exell* 566 (BM!, COI!); Infante D. Henrique, *Rose* 398 (P!); s.l., *Barter* 1924 (K!), *Ratray* s.n. (E), 300 m, *Webwitsch* 21 (BM!, K!, LISU!), 21bis (K!).

DISTRIBUTION. Widespread in W. tropical Africa.

**Pneumatopteris oppositifolia** (Hook.) Holttum in *Blumea* **21**: 304 (1973); Holttum in *J. S. African Bot.* **40**: 157 (1974); Benl in *Acta Bot. Barcinon.* **38**: 62 (1988).

*Dryopteris oppositifolia* (Hook.) C. Chr., *Index filic.*: 281 (1905); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 63 (1944) p.p. quoad pl. ex São Tomé.

*Cyclosorus oppositifolius* (Hook.) Tardieu in *Notul. Syst. (Paris)* **14**: 346 (1953); Alston in Exell in *Bull. Inst. Franç. Afrique Noire ser. A*, **21**: 445 (1959).

**SÃO TOMÉ**. Between Lagoa Amélia and Calvário, primary forest, 150 m, ground fern, *Exell* 259 (BM!, COI!); Macambrará to Zampalma, 900 m, ground fern, *Exell* 297 (BM!); Trás-os-Montes, *Gama* s.n. (COI!); Ribeira Peixe, 140 m, frequent, *Lains e Silva* 268 (LISU!); Pico, 1500 m, *Mann* s.n. (K!-type); Lagoa Amélia, 1400 m, *Monod* 11748 (BM!); Calvário, 1200 m, *Monod* 11814 (BM!); between Quinas Altas and Monte Quinas, *Monod* 12018 (BM!); s.l., *F.A.E. (Moller)* 41 p.p. (BM!, COI!, LISU!, P!).

DISTRIBUTION. Bioko, Annobon.

**Pneumatopteris venulosa** (Kuntze) Holttum in *Blumea* **21**: 315 (1973); Benl in *Acta Bot. Barcinon.* **38**: 59 (1988).

*Dryopteris venulosa* Kuntze, *Revis. gen. pl.* **2**: 814 (1891); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 66 (1944).

*Cyclosorus elatus* (Mett. ex Kuhn) Alston in *Bol. Soc. Brot., ser. 2*, **30**: 13 (1956); Alston in Exell in *Bull. Inst. Franç. Afrique Noire ser. A*, **21**: 446 (1959).

**SÃO TOMÉ**. Boa Entrada, *Chevalier* 13680 (P!); Macambrará, primary forest, 1050–1200 m, ground fern, *Exell* 242 (BM!, COI!); Lagoa Amélia, 1400 m, *Monod* 11750 (BM!); s.l., *Don* s.n. (BM-not found), *F.A.E. (Moller)* 42 p.p. (K also *Moller* 39!, P!).

**PRÍNCIPE**. Esperança, *Navel* 145 (LISU!, P!).

DISTRIBUTION. Equatorial Guinea (continent, Bioko and Annobon).

**Pseudophegopteris** Ching

**Pseudophegopteris henriquesii** (Baker) Holttum in *Blumea* **17**: 15 (1969); Holttum in *J. S. African Bot.* **40**: 128 (1974).

*Polypodium henriquesii* Baker in *Henriq. in Bol. Soc. Brot.* **4**: 154, t.1 (1887).

*Dryopteris henriquesii* (Baker) C. Chr., *Index filic.*: 270 (1905); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 62 (1944).

*Thelypteris henriquesii* (Baker) Tardieu in *Notul. Syst. (Paris)* **14**: 344 (1953).

*Macrothelypteris henriquesii* (Baker) Pic. Serm. in *Webbia* **23**: 179 (1968).

**SÃO TOMÉ**. Trás-os-Montes, *Gama* s.n. (COI!); Nova Moca, *Moller* s.n. (COI!), 750 m, *Quintas* 1464 (COI!, LISJC!, P!); Macambrará, 1250 m, *Moller* s.n. (COI!); São Nicolau, waterfall, *Rozeira* 162 (PO!); Trás-os-Montes, Calvário, *Rozeira* 562 (PO!); s.l., *F.A.E. (Moller)* 49 (BM!, K!-also *Moller* 45, type, LISU!, P!), *Moller* 1 (BM!).

DISTRIBUTION. Endemic.

**Sphaerostephanos** J. Sm.

**Sphaerostephanos elatus** (Bojer) Holttum in *J. S. African Bot.* **40**: 167 (1974).

subsp. **thomensis** Holttum in *J. S. African Bot.* **40**: 167 (1974).

*Thelypteris mauritiana* (Fée) C.F. Reed in *Phytologia* **17**: 291 (1968) subsp. **thomensis** (Holttum) Viane in *Bull. Soc. Roy. Bot. Belg.* **118**: 54 (1985).

**SÃO TOMÉ**. S.l., *F.A.E. (Moller)* 41 p.p. (COI!, P!-type).

DISTRIBUTION. Endemic.

NOTE. This taxon has not been recorded in the islands since the nineteenth century.

**Vittariaceae****Anthrophyum** Kaulf.

**Anthrophyum immersum** (Bory ex Willd.) Mett. ex Hook. in Hook. & Baker, *Syn. fil.*: 393 (1868); Alston in Exell in *Bull. Inst. Franç. Afrique Noire ser. A*, **21**: 442 (1959).

**SÃO TOMÉ**. Monte Verde, secondary forest, 10–150 m, *Lejoly* 95/86 (LISC!); between Estação Sousa and Pico, primary forest, 1700 m, rare epiphyte, *Matos* 7553 (LISC!); Cruzeiro, 300 m, *Thorold* 2064 (BM!).

**PRÍNCIPE**. Pico, 950 m, *Thorold* 2081 (BM!).

DISTRIBUTION. Also in Liberia and Mascarene Is.

**Anthrophyum mannianum** Hook., *Sec. cent. ferns*: t. 73 (1860); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 87 (1944); Benl in *Acta Bot. Barcinon.* **33**: 6 (1982).

**SÃO TOMÉ**. Pico, light woodland, 2000 m, epiphyte, *Exell* 340 (BM!); near Rio Campos, primary forest, epiphyte, *Matos & Van Essche* 7441 (LISC!); between São Pedro and Lagoa Amélia, 1250 m, *Moller* s.n. (COI!); Macambrará, 1200 m, epiphyte, *Moller* s.n. (COI!); São João dos Angolares, 200 m, *Quintas* 54A (K!), *Quintas* s.n. (COI!); Lagoa Amélia, epiphyte, *Rozeira* 1097 (PO!); s.l., *F.A.E. (Moller & Quintas)* 60 (BM!, COI!, K!, LISJC!, LISU!), 1250 m, *Moller* 54 (K!).

DISTRIBUTION. Widespread in tropical Africa.

**Vittaria** Sm.

**Vittaria guineensis** Desv. in *Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk.* **5**: 325 (1811); Alston in Exell, *Cat. Vasc. Pl. S. Tomé*: 86 (1944); Tardieu-Blot in *Aubrèv., Fl. Cameroun* **3**: 124 (1964); Benl in *Acta Bot. Barcinon.* **33**: 7 (1982).

**SÃO TOMÉ**. SW region, *Chevalier* 14598 (P!); Calvário, 970 m, epiphyte,

*Espírito Santo* 5059 (LISC!, LISJC!); between Lagoa Amélia and Esperança, 1300 m, epiphyte, *Espírito Santo* 5156 (LISC!, LISJC!); between São Carlos and Bom Sucesso, secondary forest, *Espírito Santo* 5190 (LISJC!); São João dos Angolares, littoral, *F.A.E. (Newton)* 61 p.p. (BM!), 80 m, *F.A.E. (Quintas)* 61 p.p. (BM!, COI!, K!-mixed with *Barter* 1908, LISU!), *Newton* s.n. p.p. (COI!, P!); Ilhéu das Rolas, *Greeff* s.n. (B?); between Pico and Monte Figo, 6 km S. of Ponta Figo, mountain rainforest, 1200–1800 m, epiphyte, *Lejoly* 95/6 (LISC!); W. of Pico, 870–1225 m, *Monod* 11906 (BM!); Macambrará, 1200 m, *Quintas* s.n. (COI!); Ribeira Peixe, between Vila Aida and main house, epiphyte, *Rozeira* 291 (PO!).

**PRÍNCIPE.** Pico Papagaio, primary forest, 450 m, epiphyte, *Exell* 719 (BM!, COI!); Ôquê Gaspar, *Newton* 25 p.p. (BM!); s.l., *Barter* 1908 (K!-mixed with *F.A.E.* 61).

**DISTRIBUTION.** W. tropical Africa to Uganda.

**Vittaria owariensis** Fée. *Mém. foug.* 3: 21, t. 3, fig. 2 (1852); Alston in Exell, *Cat. Vasc. Pl. S. Tomé:* 87 (1944).

**SÃO TOMÉ.** São João dos Angolares, *F.A.E. (Newton)* 61 p.p. (BM!), *F.A.E. (Quintas)* 61 p.p. (BM!, P!), *Newton* s.n. p.p. (P!), *Quintas* s.n. (COI!); Vila Conceição, 100 m, epiphyte, *Matos* 7716 (LISC!); Rio Caué, epiphyte, *Rozeira* 30 (PO!); Rio Manuel Jorge, between Pinheira and Almas, epiphyte, *Rozeira* 83 (PO!); s.l., *Seabra* s.n. (COI!).

**PRÍNCIPE.** Ôquê Gaspar, *Newton* 25 p.p. (BM!, COI!); Porto Real, *Rose* 467 (P!); Infante D. Henrique, at the base of Dois Irmãos, epiphyte, *Rozeira* 480 (PO!); s.l., *Welwitsch* 13 (BM-not found, K!, LISU!).

**DISTRIBUTION.** W. tropical Africa.

## DOUBTFUL RECORDS

**Asplenium hemitomum** Hieron. in Engl. in *Bot. Jahrb. Syst.* 46: 365 (1911); Alston in Exell, *Cat. Vasc. Pl. S. Tomé:* 78 (1944); Benl in *Acta Bot. Barcinon.* 40: 20 (1991).

### PRÍNCIPE ?

**NOTE.** Alston (l.c.) recorded this species based on the collection *Barter* 1896a (K!) from Príncipe. *Barter* 1896 is a mixed collection, containing *A. hemitomum* and *A. eurysorum*. Since *Barter* also collected *A. hemitomum* in Bioko it is possible that a specimen of this species, from Bioko, was attached to the herbarium sheet with *A. eurysorum* from Príncipe.

**Ceratopteris cornuta** (P. Beauv.) Lepr. in *Ann. Sci. Nat. (Paris)* 19: 103, t. 4A (1830); Alston in Exell, *Cat. Vasc. Pl. S. Tomé:* 92 (1944).

**PRÍNCIPE ?** *Barter* (Kuhn, 1868).

**NOTE.** No specimens were seen at BM, K or P. However, at BM there is a specimen collected by *Barter* during the Niger Expedition, unlocalized, which could have been collected in Príncipe.

**Dryopteris manniana** (Hook.) C. Chr., *Index filic.:* 276 (1905); Benl in *Acta Bot. Barcinon.* 40: 38 (1991).

### SÃO TOMÉ ?

**NOTE.** No specimens were seen.

**Lastreopsis nigritiana** (Baker) Tindale in *Contr. New South Wales Natl. Herb.* 3: 245 (1963); Tardieu-Blot in Aubrév., *Fl. Cameroun* 3: 280 (1964); Benl in *Acta Bot. Barcinon.* 40: 51 (1991).

*Polypodium nigritianum* Baker in Hook. & Baker, *Syn. fil.:* 313 (1867).

### PRÍNCIPE ?

**NOTE.** No specimens were seen. Although there are references in the literature to the occurrence of this species in Príncipe, Tindale (1965) did not record it for São Tomé and Príncipe in his monograph of the genus.

**Lygodium microphyllum** (Cav.) R. Br., *Prodr.:* 162 (1810).

*Lygodium scandens* sensu auct. non (L.) Sw. in *J. Bot. (Schrader)* 1800(2): 106 (1801); Alston in Exell, *Cat. Vasc. Pl. S. Tomé:* 93 (1944).

**PRÍNCIPE ?** (*Barter*, 1860).

**NOTE.** No specimens were seen at BM or K. There are specimens of *Lygodium microphyllum* collected by *Barter* in 1859 during the Niger Expedition, some of which are unlocalized and could have been collected on the island. Being a lowland species, *L. microphyllum* might be extinct due to the extensive cultivation of these areas.

**Ophioglossum gramineum** Willd. in *Schrift. Akad. Erfurt:* 18, t. 1, f. 1 (1802); Tardieu-Blot in Aubrév., *Fl. Cameroun* 3: 46 (1964).

### SÃO TOMÉ ?

**NOTE.** No specimens seen.

**Trichomanes africanum** H. Christ in *J. Bot. (Morot), ser. 2,* 2: 21 (1909); Benl in *Acta Bot. Barcinon.* 32: 23 (1980).

[**Vandenboschia africana** (H. Christ) G. Kunkel in *Nova Hedwigia* 6: 213 (1963)]

### SÃO TOMÉ ?

**NOTE.** No specimens seen.

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