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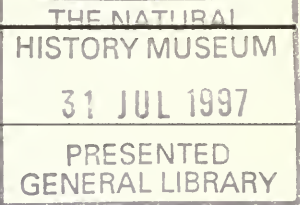
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Notes on the diatom species *Tetracyclus castellum* (Ehrenb.) Grunow with a description of *Tetracyclus pseudocastellum* nov. sp.

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SYNOPSIS. This paper reviews the evidence for retaining the taxon described by Ehrenberg as *Biblarium castellum* Ehrenb. (transferred to the genus *Tetracyclus* by Grunow). Consideration of numerous new names proposed since Ehrenberg establishes that *T. castellum* is a valid taxon which has been re-described several times during the period 1903-1983. While previously considered to be known only from a few fossil specimens, this paper establishes that it has been recorded as living (from Iceland). In addition, a better understanding of *T. castellum* has revealed a new fossil species from China, *T. pseudocastellum*.

INTRODUCTION

The diatom genus *Tetracyclus* Ehrenb. (Bacillariophyta) comprises at least 30 species, of which only five have been reported living, the remainder occurring exclusively as fossils (Williams, 1987, 1989, 1996). The taxonomy of the genus has more or less relied on the shape and dimensions of the valve as well as the frequency of particular valve characters, such as striae and ribs (Hustedt, 1914; Li, 1982a, b, 1984). While the majority of species are either elliptical or circular in valve outline, there are a few taxa that have more or less star-shaped valves. Two of these species, *T. emarginatus* (Ehrenb.) W. Sm. and *T. japonicus* (Petit) Temp. & H. Perag. have already been described in detail with both light and electron microscopy (Williams 1987, 1989). As a continuation of those studies, this paper describes a taxon Ehrenberg called *Biblarium castellum* Ehrenb. (= *T. castellum* (Ehrenb.) Grunow) and a new fossil species from Inner Mongolia, *T. pseudocastellum*. I also offer some notes on other taxa possibly confused with *T. castellum*. While this study is limited to light microscopy only, it will serve as a focus for the further study of specimens under the scanning electron microscope if and when appropriate material is discovered and becomes available.

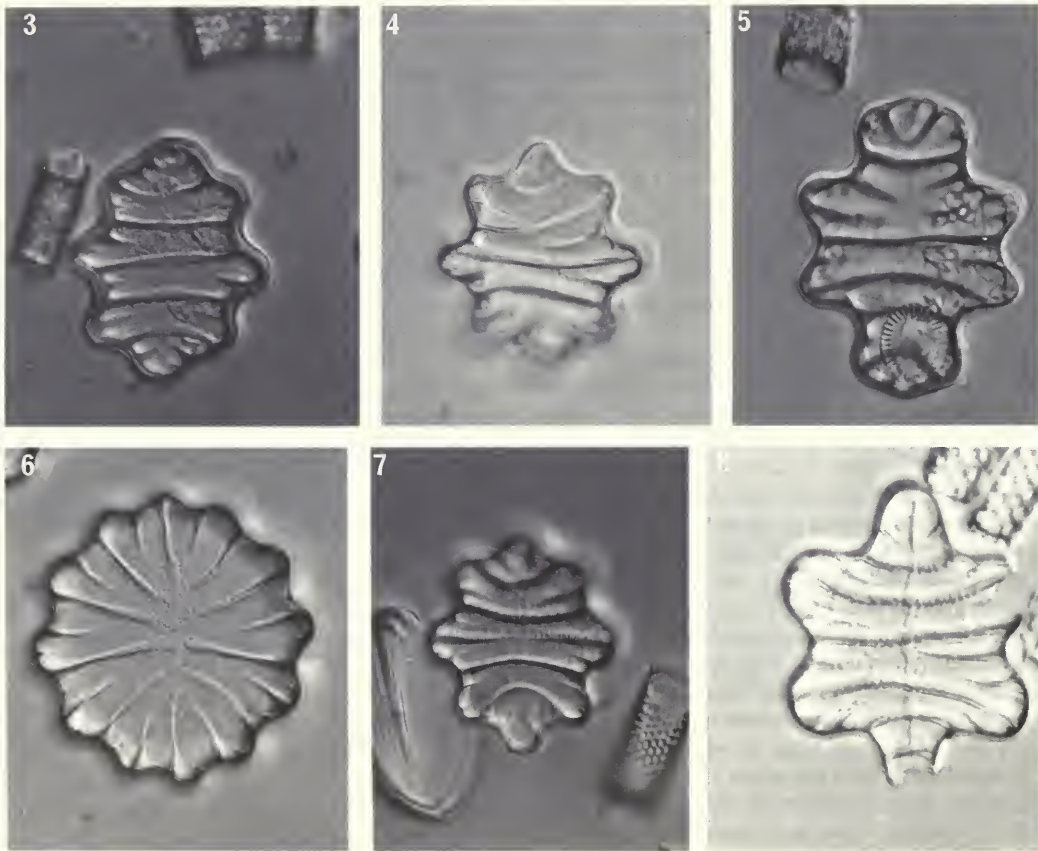
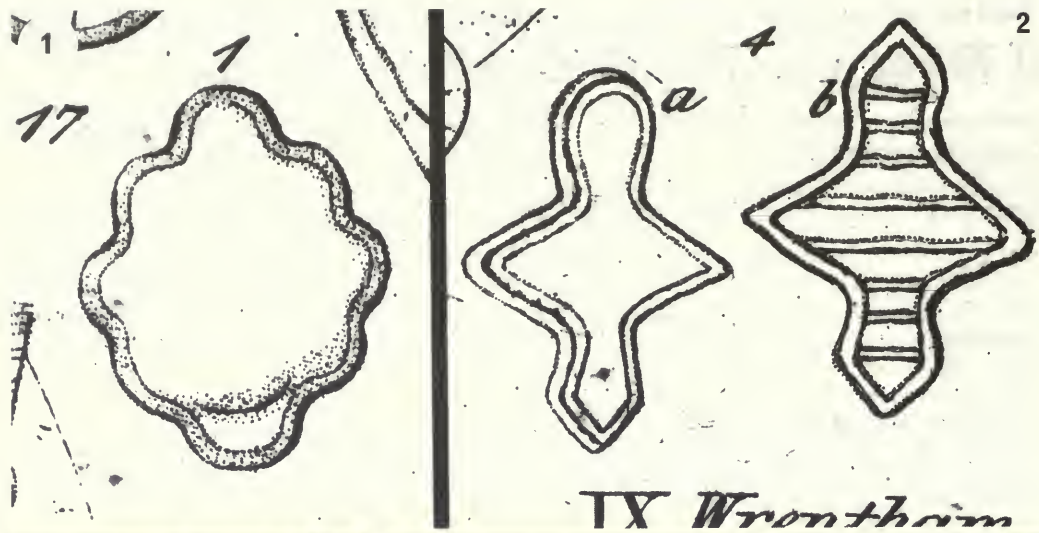
TERMINOLOGY

A number of papers dealing with the particulars of diatom valve terminology have been published in the last 15 years. For the siliceous parts of the diatom valve and girdle, Anonymous (1975),

and its updated version Ross et al. (1979), are the standard references followed in this study. Stosch (1975) presented the first detailed discussion on girdle band morphology and nomenclature. However, since his pioneering effort much has been discovered and some of the conclusions reached in his paper are subject to debate and undoubtedly will be modified in due course; some aspects of possible modifications have been discussed by Mann (1982), Williams (1985), and Round et al. (1990). Additional commentary relevant to *Tetracyclus* morphology can also be found in Williams (1985, 1987, 1989, 1996).

SYSTEMATIC DESCRIPTIONS

***Tetracyclus castellum* (Ehrenb.) Grunow** in *Verh. zool.-bot. Ges. Wien* **12**: 411 (1862). – *Tetracyclus japonicus* sensu Lupikina in *Nov. Sist. Nizsh. Rast.* [1965]: pl. 3, figs 1-3 (1965); Khursevich & Loginova, *Iskopaemaya Diatomovaya Flora Belorussii (Sistematicheskii Obzor)*: pl. 17, fig. 13 (1980); Khursevich in *Acta geol. hung.* **28**: pl. II, fig. 7 (1982). – *Tetracyclus stellare* sensu J.Y. Li in *Bull. Inst. Geol. chin. Acad. geol. sci.* **5**: pl. 1, fig. 18 (1982); J.Y. Li & Y.Z. Qi in *Proc. 8th Internat. Diat. Symp.*: pl. 2, figs 4, 5 (1986); Valeva & Temniskova-Topalova in *Fitologiya* **46**: pl. III, figs 11, 12 (1993). – *Tetracyclus stellare* var. *exinia* sensu VanLand. in *Micropaleontology* **31**: pl. 1, fig. 9 (1985). – *Tetracyclus* sp. Tscheremisina, *Diatomovaya Flora Neogenovykh Otlozhenii Pribaikal'ya (Tunkinskaya Kotolovina)*: pl. 6, fig. 2 (1973).
Figs 1, 3, 4, 7.



Figs 1, 3, 4, 7 *T. castellum*. Fig. 1: Reproduction of Ehrenberg (1854): pl. 33/2, fig. 1. Fig. 3: *Tetracyclus* '*costellatus*' from Temp. & Perag., *Diat. monde entier*, 2nd ed., slide no. 122, BM 68468, specimen 30 μ long. Fig. 4: *Tetracyclus elegans* var. *eximia* from Temp. & Perag., *Diat. monde entier*, 2nd ed., slide no. 122, BM 68468, specimen 25 μ long. Fig. 7: *T. 'costellatus'* var. *turris* from Temp. & Perag., *Diat. monde entier*, 2nd ed., slide no. 134, BM 68479, specimen 25 μ long.

Fig. 2 *Bibliarium elegans* reproduced from Ehrenberg (1854): pl. 33/2, fig. 4a, b.

Fig. 5 *T. emarginatus* var. *crassa* from Temp. & Perag., *Diat. monde entier*, 2nd ed., slide no. 122, BM 68468, specimen 40 μ long.

Fig. 6 *T. japonicus* from Temp. & Perag., *Diat. monde entier*, 1st ed., slide no. 79, BM 14331, specimen 55 μ long.

Fig. 8 *T. pseudocastellum*. Inner Mongolia, China, BM 81618, specimen 40 μ long.

Bibliarium castellum Ehrenb. in *Ber. Akad. Wiss. Berlin* [1843]: 47 (1843), *nom. nud.* – Ehrenb. in *Ber. Akad. Wiss. Berlin* [1845]: 73 (1845). – Ehrenb. in *Mikrogeol.*: pl. 33/2, fig. 1 (1854). Type: ‘Ad Bargusinam Sibiriae fossile’, Ehrenberg (1843: 47), specimens not located. Iconotype = pl. 33/2, fig. 1 in Ehrenberg (1854).

?*Tetracyclus islandica* Østrup in *Meddr dansk geol. Foren.* 6: 28, pl. 1, fig. 1 (1900). Type: Illagil, Iceland (K 384-holotype?).

Tetracyclus costellatus Héríb., *Diat. foss. Auvergne*: 16, pl. 8, fig. 12 (1902), *orth. var.*, corrected to *castellum* in Perag. *Cat. Diat.*: 920 (1903). Type: ‘Dépot de Celles, Cantal’ (BM 68468-isotype).

Tetracyclus costellatus var. *turris* Perag. & Héríb. in Héríb. *Diat. foss. Auvergne*: 39, pl. 8, fig. 13 (1902), *orth. var.*, corrected to *castellum* in Perag., *Cat. Diat.*: 920 (1903). Type: ‘Dépot d’Auxillac, Cantal’ (BM 68479-3-isotypes).

Tetracyclus elegans var. *eximia* Héríb. & Perag. in Héríb., *Diat. foss. Auvergne*: 16, pl. 8, fig. 15 (1902). Type: ‘Dépot de Celles, Cantal’ (BM 68468-isotype).

Tetracyclus stellare Héríb., *Diat. foss. Auvergne*: 31, pl. 11, fig. 23 (1903). Type: ‘Dépot de Joursac, Cantal’ (BM 68397–99-isotypes).

Tetracyclus stellare var. *eximia* (Héríb.) Hust. in *Abh. naturw. Ver. Bremen* 23: 98 (1914).

Tetracyclus lapponicus Tynni in *Bull. geol. Surv. Finl.* 320: 35, pl. 19, figs 10–15 (1982). Type: ‘Gyttya deposit of Sivakkapalo’ (GTL HH/80-holotype, not seen).

Tetracyclus chudjakovii Pushkar in *Paleobot. Fitostrat. Vostoka SSSR*: 114, pl. 22, figs 15–17 (1983) (AH CCCP 123/30-79-Û-holotype, not seen).

Valves with 8 equally spaced points somewhat resembling a ‘star’, 25–45 µ (n=10) in diameter, each tip curving at its margin (Li & Qi, 1986: pl. 2, fig. 4). Transapical ribs primary (25–45 in 10 µ), radiate; secondary and tertiary ribs present, extending into each point of the star and meeting at the sternum; striae in equidistant rows. Cingulum consisting of open septate bands. Septum small, not visible in a number of bands (= secondary copulae?) (Fig. 1, septum visible in Ehrenberg’s illustration; Li & Qi, 1986: pl. 2, fig. 5).

Material examined

Living

Iceland. ‘Illagil. Tinnárdalur, Skagafhordssýssel . . .’ (K 384, holotype? of *Tetracyclus islandica*).

Fossil

France. Cantal, Joursac, BM 68397-99 (Isotypes of *Tetracyclus stellare*, Temp. & Perag., *Diat. monde entier*, 2nd ed., nos 51–53); Cantal, Celles, BM 68468 (Isotype of *Tetracyclus costellatus*, *T. elegans* var. *eximia*, and *T. emarginatus* var. *crassa*, Temp. & Perag., *Diat. monde entier*, 2nd ed., no. 122); Cantal, Auxillac, BM 68479-3 (Isotype of *T. costellatus* var. *turris*, Temp. & Perag., *Diat. monde entier*, 2nd ed., nos 133–137).

U.S.A. Nevada, Esmeralda Co., SW of Loric Mountain and west of Tonopato Esmeralda formation, USGS 5078 (CAS 382005).

What is understood as *Tetracyclus castellum* is based upon type material from synonymous taxa, as Ehrenberg’s material is unavailable. In addition five valves were discovered in a fossil deposit from the U.S.A. (Tonopato Esmeralda formation, CAS 382005). As the species is known from so few specimens the synonymy requires further comment.

Bibliarium castellum – Ehrenberg (1843) described the species *Bibliarium castellum* from a fossil deposit in Siberia (‘Infusorien-

Lager von Bargusina im Gouvernement Irkutsk in Sibirien’, Ehrenberg, 1843: 46; ‘Ad Bargusinam Sibiriae fossile’, Ehrenberg, 1845: 73). Although Ehrenberg provided a reasonable (for his time) description (‘B. corpusculorum valvis (intermediis) ovatis obtusis, sinibus marginalibus utrinque quatuor. Laterales valvae nondum observatae’, Ehrenberg, 1845: 73), he offered only one illustration in the *Mikrogeologie* (Ehrenberg, 1854: pl. 33/2, fig. 1, reproduced here as Fig. 1). The specimen he chose to illustrate is clearly of a girdle band and provides no information on valve structure, of which Ehrenberg appeared to have no knowledge (‘Laterales valvae nondum observatae.’ Ehrenberg, 1845: 73). Ralfs (in Pritchard, 1861: 806) added nothing of significance to the species description, reproducing Ehrenberg’s figure (in Pritchard, 1861: pl. iv, fig. 44) and translating his 1845 text (‘Lateral view of central portion elliptic, with obtuse ends, and four marginal undulations . . . Lateral valves unknown’, Pritchard, 1861: 806). Although Grunow (1862: 411) transferred the species to the genus *Tetracyclus*, he also appears not to have investigated relevant material and again relied only on Ehrenberg’s description and figure. This approach continued with De Toni referring to Ehrenberg, Grunow, and Ralfs (all of whom used the same single specimen) for his own description of this species for which he was able to provide additional perspective: ‘Valvis late ovatis, obtusis, subrhomboideis, marginibus triundulatus...’ (De Toni, 1892: 748). In summary, *Tetracyclus castellum* has remained a valid name based on Ehrenberg’s one girdle band specimen for which type material has been unavailable for examination, one imagines, since Ehrenberg’s time. However, it is possible to suggest two things from this illustration of a girdle specimen: first, that the valves would be similar in shape, that is like an 8-pointed star; and second, that the girdle has a septum (Fig. 1).

Tetracyclus ‘costellatus’ – When Héribaud undertook his study of the fossil diatoms of Auvergne in France he made the new combination *Tetracyclus costellatus* based on *Bibliarium costellatum*, attributing the specific epithet to Ehrenberg (Fig. 3; Héribaud, 1902: 16, pl. 8, fig. 12). In the same volume, Tempère & Héribaud described the new variety *T. costellatus* var. *turris* (Fig. 7; Héribaud, 1902: 39, pl. 8, fig. 15), again with reference to the *Bibliarium costellatum* of Ehrenberg (Lauby [1910: 340], in a study of the same area, also used the name *T. costellatum*). Ehrenberg never used the name *costellatum* in connection with the genus *Bibliarium*. That Héribaud made an error with the name was identified by Peragallo (1903: 920) who corrected both names. Mills (1935: 1600) included *Tetracyclus costellatus* (and the variety *turris*) in his catalogue as a synonym of *T. castellum* (to compound confusion Mills misspelt *T. costellatus* as *T. constellatus*). VanLandingham acknowledged that Héribaud’s usage of the name *T. costellatus* was a misspelling of *castellum* (‘error? for *Bibliarium castellum* Ehrenberg 1843...’, VanLandingham, 1978: 3981) and included it as an orthographic variant of *T. castellum*.

Isotype material for *T. ‘costellatus’* and *T. ‘costellatus’* var. *turris* are available as part of Tempère & Peragallo’s *Diatomées du monde entier* exiccata set (2nd ed., slide no. 122, BM 68468; slide nos 133–137, BM 68479-83) and although rare, a few specimens have been examined (Figs 3, 7). In each case the valves are 8-pointed stars suggesting that they can be usefully compared with Ehrenberg’s *Bibliarium castellum*.

Tetracyclus elegans*, *T. elegans* var. *eximina*, *T. emarginatus* var. *crassa*, and *T. stellare – *Tetracyclus elegans* (Ehrenb.) Héríb. was based upon another Ehrenberg species, *Bibliarium elegans*, described from the same Siberian fossil deposit as *B. castellum* (Ehrenberg, 1854: 90, pl. 33/2, fig. 4a, b). Ehrenberg provided no description and only published illustrations of two specimens, one

valve and one girdle band (Ehrenberg, 1854, pl. 33/2, fig. 4a, b; reproduced here as Fig. 2). Ralfs transferred the species to *Tetracyclus*, providing a minimal description ('Inflations acute') and noting that 'Ehrenberg's figure of this species differs from *T. rhombus* merely in its more developed inflation' (Ralfs in Pritchard, 1861: 806–7). De Toni, however, differed from Ralfs and in his view likened *T. elegans* to *T. lacustris* Ralfs (= *T. glans* (Ehrenb.) Mills; see Williams, 1987). *T. rhombus* (Ehrenb.) Ralfs in Pritchard has been discussed in more detail in Williams (1996) and *T. glans* in Williams (1987). Briefly, Ehrenberg's original illustrations of *T. rhombus* included drawings of specimens from Siberia and a U.S.A. fossil deposit from Columbia River (Ehrenberg, 1854: pl. 33/12, figs 7, 8, pl. 33/2, figs 9, 9*, 10; see Williams, 1996, for notes on the Columbia River deposit). From the illustrations alone, it appears that specimens from Siberia (Ehrenberg, 1854: pl. 33/2, figs 9, 9*, 10) may indeed belong to *T. glans* (or some closely related species, e.g. *T. pagesi* Hér. or *T. stella* (Ehrenb.) Hér.; cf. Hustedt, 1914: 101, 105; Williams, in prep.) while the Columbia River specimens (Ehrenberg, 1854: pl. 33/12, figs 7, 8) are probably a small pre-auxospore stage of some elliptical-valved species (see Williams, 1990, 1996). Until Siberian material has been examined these conclusions must be considered unsubstantiated. However, it does explain Ralfs' and De Toni's conflicting views noted above.

Hér. & Peragallo unnecessarily transferred *Biblarium elegans* to *Tetracyclus* (Hér. & Peragallo, 1902: 16; Ralfs had already done so). However, part of their reason was to be able to describe further specimens they encountered in the 'Celles' deposit as *Tetracyclus elegans* var. *eximia* (Hér. & Peragallo, 1902: 16, pl. 8, fig. 15). Isotype material is available (Temp. & Peragallo, *Diat. monde entier* 2nd ed., slide no. 122, BM 68468) and, although only a few specimens were encountered, they are 8-pointed star-shaped valves like *T. castellum* (Fig. 4).

In a later volume of the same study, Hér. & Peragallo published another new species under the name of *Tetracyclus stellare* Hér. from the Joursac deposit of Cantal (Fig. 7; Hér. & Peragallo, 1903: 31, pl. 11, fig. 23). According to Hér. & Peragallo *T. stellare* is '... intermédiaire entre le *Tetracyclus castellum* et le *Tetracyclus elegans*, dont il nous paraît une forme dérivée' (Hér. & Peragallo 1903: 31). This is clearly referring to the shape of the valve outline. Hustedt concluded that *Tetracyclus elegans* var. *eximia* was perhaps better understood as a variety of *T. stellare* and that *T. elegans* was better understood as a variety of *T. lacustris* (= *T. glans*) and transferred both taxa accordingly (Hustedt, 1914, p. 97 for *elegans*, p. 98 for *stellare*; unfortunately, Hustedt refers to *stellare* as *stellaris* throughout his monograph). There is merit in Hustedt's decisions but once again, the absence of Ehrenberg's Siberian material makes judgment difficult. Nevertheless, inspection of specimens of *T. stellare* (as well as *T. elegans* var. *eximia*) indicates that there is as yet insufficient evidence to relate it most closely to either *T. elegans* or *T. glans* and is best considered as a synonym of *T. castellum*.

Finally, Hér. & Peragallo described a new variety of *Tetracyclus emarginatus*, *T. emarginatus* var. *crassa* Hér. & Peragallo (Hér. & Peragallo, 1902: 16, pl. 8, fig. 16; specimens from Temp. & Peragallo, *Diat. monde entier* 2nd ed., no. 122, BM 68468; Fig. 5). This taxon only superficially resembles *T. castellum* and should perhaps be considered in the context of *T. emarginatus* to which it appears more similar.

Tetracyclus islandica, *T. lapponicus*, and *T. chudjakovii* – Østrup described the new species *Tetracyclus islandica* from Illagil in Iceland (Østrup, 1900: 28, pl. 1, fig. 1). He made no attempt at a description but drew attention to the unusual shape which he felt

made its unique status obvious ('... som uden at kraeve naermere Beskrivelse, tydeligt fremgaar af Tab. nost. Fig. 1', Østrup, 1900: 28). There is only one relevant slide of type material present in C of which J.B. Hansen wrote: 'Østrup used to keep raw and cleaned material of everything but in a few cases where the material is scanty there are only slides available. You have got the only material I can find' (Hansen, pers. comm.). The specimens on this slide were rather rare and too poor to make useful micrographs. However, it was clear that the 'edges' of the valve were somewhat more rounded than in Østrup's published illustration, suggesting that it too should be considered a synonym of *T. castellum*. This is an interesting conclusion as it implies that *T. castellum* should properly be considered as a sixth (albeit rare) living species of *Tetracyclus*. Further material needs to be examined, especially using electron microscopy.

Tetracyclus lapponicus Tynni was described as a Neogene fossil from the 'Gyttya deposit in Finland' (Tynni, 1982: 35, pl. 19, figs 7, 10–15). Tynni suggested that it 'closely resembles the form *T. japonicus* described from the Neogene stratum of White Russia (Khursevich & Loginova 1980)'. Khursevich & Loginova's (1980) specimen is one of *T. castellum* (see below) and hence *T. lapponicus* should also be considered a synonym of *T. castellum*. Tynni remarks that '*T. ellipticus* var. *lancea* f. *subrostrata* Hust. – *T. lapponicus* with their intermediate forms constitute a transitional series... from which it becomes evident that *T. ellipticus* and *lapponicus* are closely related forms.' (Tynni, 1982: 35). Material has not been examined but evidence presented by Tynni (1982: pl. 19, figs 7, 10–15) does not seem to support his contention and he relies on an unconventional understanding of *T. ellipticus* var. *lancea* f. *subrostrata* (see Williams, 1996).

Finally, Pushkar described the new species *Tetracyclus chudjakovii* Pushkar (1983: 114, pl. 22, figs 15–17) also with an 8-pointed star-shaped valve and again probably a specimen of *T. castellum*.

SUMMARY. Specimens which appear to be *T. castellum* (not forgetting that this taxon was originally based on one illustration of a girdle band) have been described on a number of different occasions after Ehrenberg, from 1903 to 1983, including *T. 'castellatus'*, *T. elegans* var. *eximia*, *T. stellare*, *T. islandica*, *T. lapponicus*, and *T. chudjakovii*. No doubt much of this re-description is due to poor knowledge of genuine *T. castellum* specimens. To compound matters other errors have crept in, possibly due to peculiarities surrounding its nomenclature, especially an early confusion involving several different usages of the name *Tetracyclus japonicus*, clearly a different species from *T. castellum* as it has a valve like a 12-pointed star (Fig. 6, *T. japonicus* sensu stricto; see also Williams, 1989).

Other illustrations with different names include Lupikina (1965: pl. 3, figs 1–3) and Khursevich & Loginova (1980: pl. 17, fig. 13; see also Khursevich, 1982: pl. II, fig. 7; both illustrations are of the same specimen, the latter being turned upside down) who named specimens of this taxon *T. japonicus*; Li (1982b: pl. 1, fig. 18) and Valeva & Temniskova-Topalova (1993: pl. III: figs 11, 12) who named specimens *T. stellare*; VanLandingham (1985: pl. 1, fig. 9) who named specimens *T. stellare* var. *eximia*; and Tscheremisina (1973: pl. 6, fig. 2) who named specimens *Tetracyclus* sp. All these illustrations seem to be of the same taxon and should be considered representatives of *T. castellum*. More recently additional specimens have been encountered from Kamchatka (Ozornina, 1993 and pers. comm.).

One notable exception is the specimens illustrated by Li (1982a) and Li & Qi (1986) which they erroneously called *T. peragalli* Hér. (see Williams, 1990). Examination of relevant material from their Chinese deposit reveals specimens that more correctly belong to a new species, a description of which is given below.

Tetracyclus pseudocastellum D.M. Williams, sp. nov.
Fig. 8.

Tetracyclus peragalli sensu J.Y. Li & Y.Z. Qi in *Proc. 8th Internat. Diat. Symp.*: pl. 2, figs 3, 6 (1986).

Valves with 6 equally spaced points somewhat resembling a 'star', each point rounded at the margin, 20–45 μ ($n=7$) in diameter. Striae in equidistant rows; ribs predominantly primary, with few secondary ribs extending between the points of the star. Cingulum consisting of open septate bands (Li & Qi, 1986: pl. 2, figs 3, 6). Septum small, difficult to observe in a number of bands (those are possibly secondary copulae). Known only from type material.

TYPE. Late Miocene flora of Inner Mongolia, China. BM 81618, 'No: SZ₁₁-1 (9) IM, China', specimen marked number 5-holotype; IGC-Beijing SZ₁₁-1-01 IMS-isotype.

Material examined

China. *Miocene*, Den Hua Jiling Province and Shangdu County of Inner Mongolia, BM 81618, 'No: SZ₁₁-1 (9) IM, China'.

T. pseudocastellum is known only from the type locality and is easily distinguished by the number of points of the valve: 6 for *pseudocastellum* (Fig. 8), 8 for *castellum* (Figs 3, 4, 7), and 12 for *japonicus* (Fig. 6). Only the latter species is known from a detailed study of its morphology (Williams, 1989). Detailed comparison of valve and girdle structure of these species will allow them to be placed in relation to each other as well as other species of *Tetracyclus*. The (palaeo)biogeographical interpretation of the genus is largely around the Pacific rim, an understanding of the relationships of the species will allow a better understanding of the causes of this distribution (Williams 1996).

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A new species of *Calymperes* (Musci: Calymperaceae) from Peninsular Malaysia

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SYNOPSIS. *Calymperes woodii* L.T. Ellis, apparently endemic to areas of lowland rainforest in Negeri Sembilan, Peninsular Malaysia, is described and illustrated.

During March 1996 fieldwork was undertaken at Pasoh Forest Reserve, an area of lowland rainforest in eastern Negeri Sembilan, Peninsular Malaysia. Two collections from pristine forest within the reserve appear to represent a hitherto undescribed species of *Calymperes*. These specimens are identical with a collection made by G.H.S. Wood in 1954 from another area of lowland rainforest near the coast in western Negeri Sembilan – Sungei Manyala Forest Reserve. The new species is described here and named in honour of Wood who made the first collection.

Calymperes woodii L.T. Ellis, sp. nov.

C. subserrato M. Fleisch. affinis, sed foliis dimorphis, spathulatis, margine supra basin hyalinam polystrato. Type: Peninsular Malaysia, Negeri Sembilan, Sungei Manyala Forest Reserve, 10 miles SE of Port Dickson, FRI [Forest Research Institute] jungle plot 102, c. 18 m, 13 January 1954, G.H.S. Wood 1372 (BM–holotype; BM-K–isotype).

Plants reaching 0.5–1.0 cm high, in mats or as scattered shoots. Leaves curled when dry (often in one direction), erect to spreading (sometimes recurved) when moist, dimorphic (gemmiferous and nongemmiferous leaves). Nongemmiferous leaves mostly >3–4 mm long, lingulate to narrowly spatulate, with a calymperoid hyaline basal region; apices subtire to denticulate, broadly obtuse, usually apiculate. Costa ending immediately below leaf apex; in cross-section composed of dorsal and ventral bands of stereids separated by a single row of guide cells, dorsal and ventral surfaces formed by single layers of small chlorophyllose cells (Fig. 1q, r), superficial cells above hyaline leaf base subquadrate to shortly subrectangular in surface view, mostly 5–15(–22.5) × 7.5–12.5 μm (those forming the dorsal surface longer on average than those forming the ventral surface), sometimes smooth, usually with 1–2 blunt papillae, toward leaf apex many protruding subacutely to acutely. Chlorophyllose lamina occupying four-fifths or more of leaf length (above hyaline basal region), unistratose; cells 6–15 × 6–12.5 μm, isodiametric to slightly longer than broad, with 4–6 sides or rounded, thick-walled (Fig. 1i, j), each ventrally drawn out as a subacute to acute protrusion, dorsally pluripapillose (Fig. 1k, l). Hyaline lamina occupying leaf base, usually not sharply defined; composed of large, subquadrate to subrectangular, thin-walled, porose, hyaline cells; an intramarginal, unistratose band of linear, thick-walled cells, c. (1–)3–6 cells wide, extending from the leaf base toward the distal end of the hyaline lamina sometimes apparent (Fig. 1p), often obscure or absent. Leaf margin plane to inflexed, from a short distance above the hyaline base to the leaf apex formed by a subtire to denticulate, polystratose rib composed of isodiametric chlorophyllose cells (stereids sometimes present internally), most superficial cells protruding as small teeth (Fig. 1m–o); in hyaline base unistratose, subtire to irregu-

larly denticulate, formed by a band of short, broad irregularly polygonal, thin-walled hyaline cells (often with oblique cross-walls), 1–2(–4) cells wide (Fig. 1p). Gemmiferous leaves often erect and slightly exerted above nongemmiferous leaves, similar to nongemmiferous leaves but up to 5 mm long and sometimes more narrowly lingulate, possessing apices modified as gemma-bearing proboscises (Fig. 1f, g). Proboscis narrowly suboblong to linear, often curved slightly backwards at tip. Costa strong (usually thicker than in nongemmiferous leaves), extending into proboscis, ending below leaf apex. Lamina narrowing abruptly into proboscis and becoming tightly recurved, becoming plane above and forming a narrow margin around the tip of the costa, ending as a rounded to shortly pointed leaf apex. Gemmae arising in a radial mass from ventral surface of the costal apex, fusiform to clavate, multicellular, uniseriate, smooth (Fig. 1g). Axillary paraphyses produced in brush-like bunches, filamentous, usually exceeding 0.5 mm long, hyaline, multicellular, normally uniseriate (Fig. 1h). Rhizoids conspicuous around base of shoots, papillose, deep purplish red. Gametangia and sporophytes not seen.

DISTRIBUTION. *Calymperes woodii* appears to be endemic to Negeri Sembilan, Peninsular Malaysia.

HABITAT. *Calymperes woodii* has been collected in rainforest at c. 18 m and 100 m above sea-level. Shoots occur in loose mats, or are scattered over rotting logs or soft bark on the trunks of trees in shaded, damp situations.

ADDITIONAL SPECIMENS EXAMINED. Peninsular Malaysia, Negeri Sembilan, Pasoh Forest Reserve, 50 Hectare Plot: tree number 151601, c. 100 m, March 1996, *Ellis* 9601 (BM, FRIM); tree number 131666, 100 m, March 1996, *Ellis* 9602 (BM, FRIM).

DISCUSSION. The absence of sporophytes in the type and other specimens of *Calymperes woodii* makes the generic placement of this species a matter of strong probability, rather than absolute certainty. Features of the gametophyte in *C. woodii* bear a degree of superficial resemblance to those found in species of both *Calymperes* and *Syrrhopodon* (the two largest genera in the Calymperaceae). However, more features of *C. woodii* are *Calymperes*-like than *Syrrhopodon*-like. For example, the structure of the proboscis in the gemmiferous leaves is virtually identical to that of several species of *Calymperes* (Fig. 1f, g), particularly *C. graeffeanum* Müll. Hal. and *C. hispidum* Renaud & Cardot (both illustrated by Ellis, 1988). Another feature, more usually associated with *Calymperes* than *Syrrhopodon*, is the possession of an intramarginal rib in the hyaline basal region of the leaf. Although often obscure to the point of absence, such a rib can be demonstrated in some leaves of *C. woodii* (Fig. 1p). The presence of axillary paraphyses (lacking in *C. graeffeanum* and *C. hispidum*) is a feature of some closely interre-

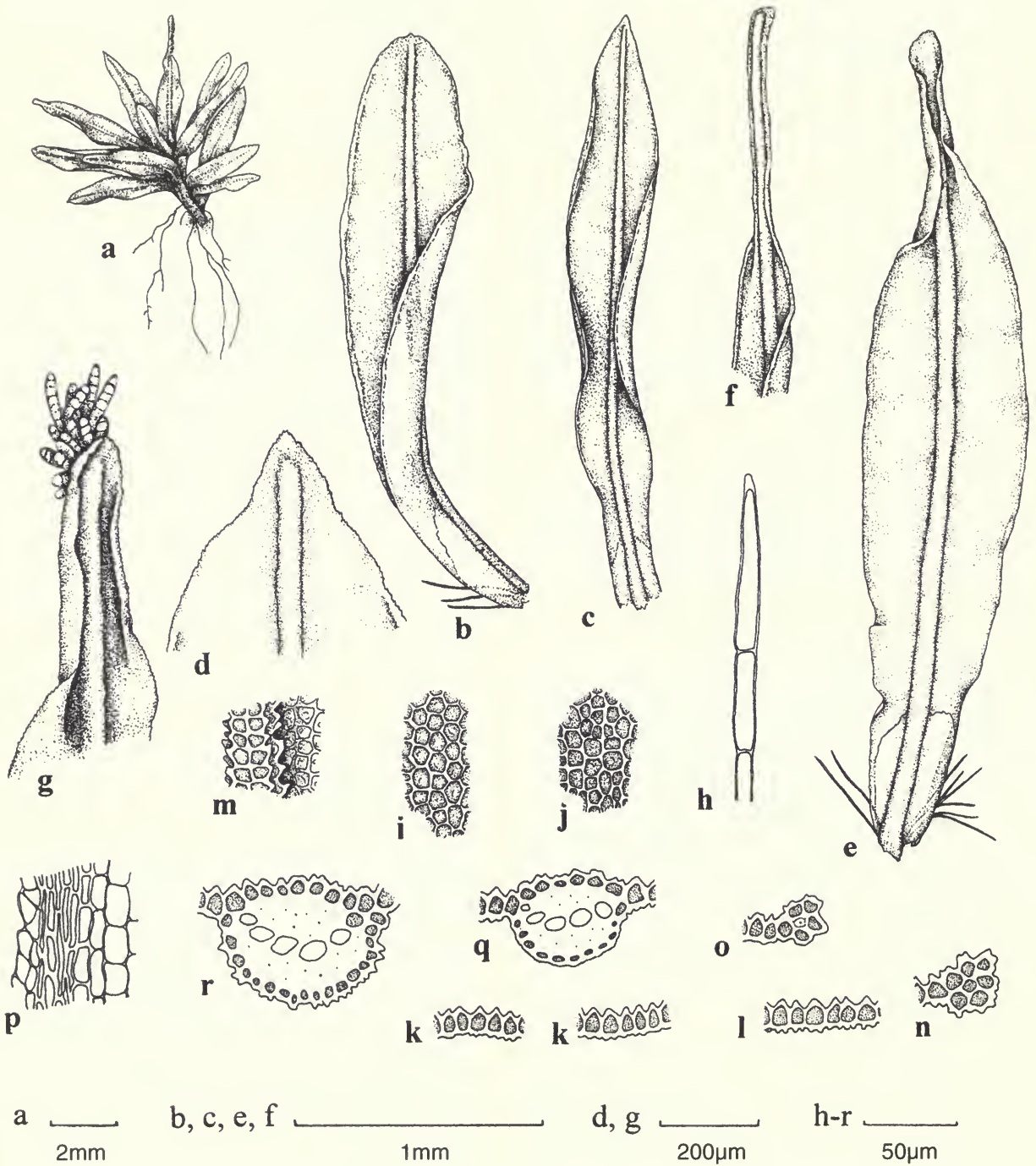


Fig. 1 *Calymperes woodii* L.T. Ellis a: habit (when moist); b–d: nongemiferous leaf (b, c: in ventral view, d: detail of apex); e–g: gemmiferous leaf (e: in dorsal view, details of apex in f: ventral view, and g: dorsal view); h: apex of axillary paraphysis; i–l: chlorophyllose lamina (i, j: ventral surface, k, l: in cross-section); m–o: margin above hyaline leaf base (m: ventral surface, n, o: in cross-section); p: margin in hyaline leaf base; q, r: costa at mid-leaf in cross-section. a, b, d, e, g–i, l–n, r Drawn from *Ellis* 9601 (BM). c, f, j, k, o–q Drawn from *Wood* 1372 (BM).

lated species of *Calymperes*, including *C. serratum* A. Braun ex Müll. Hal., *C. subserratum* M. Fleisch., and *C. subulatum* E.B. Bartram (all regarded as conspecific by Eddy (1990) and Menzel & Schultze-Motel (1990), but shown to be distinct by Reese & Streimann (1994)). *C. woodii* has axillary paraphyses (Fig. 1b, e, h) and shows some other similarities to *C. subserratum* and its relatives, such as the possession of leaves with a poorly defined hyaline base. However, the leaves of these other paraphyses-bearing species are monomorphic (i.e. gemmiferous leaves are unmodified) and narrowly strap-shaped. In contrast, the leaves of *C. woodii* are strongly dimorphic and mostly narrowly spatulate. The type specimen of *C. woodii* (Wood 1372) was originally erroneously identified as *C. subserratum*. In addition to the features mentioned above, the latter species has entirely unistratose leaf margins which are incurved to involute and largely subentire (toward the leaf apex a few teeth may occur); the cells of the chlorophyllose lamina are $<5-10(-12.5) \times <5-7.5 \mu\text{m}$ in surface view. The margins of the leaves in *C. woodii* are polystratose (Fig. 1n, o), plane to inflexed, and minutely denticu-

late with single-celled teeth; the cells of the chlorophyllose lamina are $6-15 \times 6-12.5 \mu\text{m}$ in surface view.

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A phylogenetic conspectus of the tribe Hyoscyameae (Solanaceae)

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SYNOPSIS. A cladistic analysis of the tribe Hyoscyameae (including *Atropa* and *Mandragora*) shows that *Atropa* and *Mandragora* are clearly part of the same monophyletic group as the traditional members of the tribe: *Hyoscyamus*, *Physochlaina*, *Anisodus*, *Atropanthe*, *Scopolia*, and *Przewalskia*. The group can further be divided into two main clades, one containing *Hyoscyamus* and *Physochlaina* and the other containing the rest of the genera. Characters used in the analysis are discussed and illustrated, and a conspectus of the genera with descriptions and lists of component species is provided. Introductory material includes a review of the nomenclatural history and the economic botany of the Hyoscyameae.

INTRODUCTION

The Solanaceae are an economically important, cosmopolitan family with over 2500 species. Members of the family are important to agriculture, with potatoes, tomatoes, peppers, and a host of minor fruit crops cultivated worldwide. Many species are also valuable to medicine, being used in both traditional and pharmaceutical treatments. The family is traditionally divided into two subfamilies. The Cestroideae, including petunias, the cestrums, and their relatives, usually have non-compressed, often prismatic seeds and tropane alkaloids. The Solanoideae, which contains the majority of the species in the family, including *Solanum* and its relatives, have compressed seeds and steroidal alkaloids. This traditional classifica-

tion has recently been challenged by cladistic analyses using chloroplast and nuclear DNA data sets, and the family can now be divided into approximately seven monophyletic groups (see Olmstead et al., in press).

The family is predominantly tropical in distribution, but the group variously defined as the tribe Hyoscyameae or subtribe Hyoscyaminae (see p. 13) is exclusively Eurasian and Middle Eastern, with no members in even the subtropics of the northern hemisphere (see Fig. 1). The six genera of the traditionally defined Hyoscyaminae (*Anisodus*, *Atropanthe*, *Hyoscyamus*, *Physochlaina*, *Przewalskia*, and *Scopolia*) and the genera of the Atropinae (*Atropa* and *Mandragora*) have often been considered related in the past (see p. 13) but are usually considered separately. As part of on-going studies into the generic phylogeny of the Solanaceae (Persson et al. 1994;

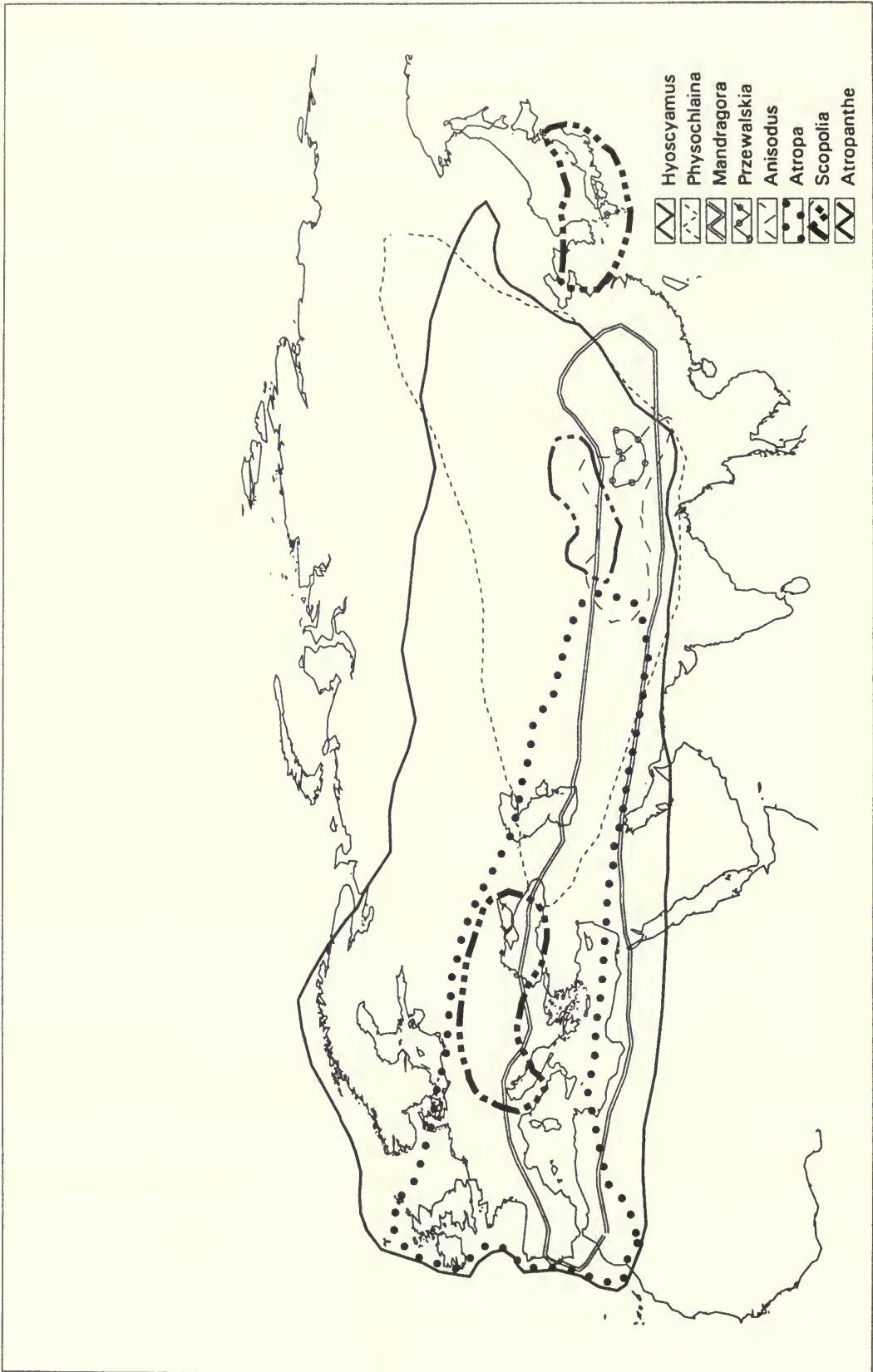


Fig. 1 Distribution of the genera of the Hyoscyameae.

Knapp et al., in press) we decided to examine the phylogenetic relationships of these eight genera using primarily morphological characters. We have attempted a preliminary generic delimitation, but several potential problems are highlighted in the analysis.

HISTORY OF CLASSIFICATION

The concept of the family Solanaceae was first used by A.L. de Jussieu in his *Genera plantarum* (1789) where he included 15 genera in the Solanaceae, all of which are still in current usage, including *Atropa*, *Hyoscyamus*, and *Mandragora*. He divided the family into three groups, the first with capsular fruits, the second having berries, and the third a group of miscellaneous taxa of less certain affinity with the rest of the family.

Following de Jussieu's work and continuing to the present, much effort has been put into the production of a classification system of the family which best reflects the relationships of the genera. G. Don (1838) was the first to recognize tribes within the family. He proposed seven tribes, largely on the basis of the corolla aestivation, characters of the stamens, fruit type, and embryo curvature. These features have been important in most subsequent classifications. Endlicher (1839) produced an alternative classification which was the first to recognize the tribe Hyoscyameae, composed of *Hyoscyamus*, *Anisodus*, and *Scopolia*. The characters by which he defined this group were a curved embryo, semi-circular cotyledons, and a bilocular capsule with circumscissile dehiscence. Endlicher placed *Atropa* and *Mandragora* in the heterogeneous tribe Solaneae, composed of genera with baccate fruits.

Miers (1849) proposed profound changes to the Solanaceae, with the erection of a new family Atropaceae. He considered this group to be intermediate between the Solanaceae and the Scrophulariaceae on the basis of corolla aestivation and symmetry of floral parts. Thus, the Atropaceae were characterized by having nearly isomeric flowers with imbricate or a peculiar aestivation. Within the Atropaceae Miers described 10 tribes, including Hyoscyameae (including the genera *Hyoscyamus*, *Scopolia*, *Physoclaina*, *Cacabus*, and *Thinogeton*) and Atropeae (including the genera *Atropa*, *Nicandra*, *Cliocarpus*, *Anisodus*, *Mandragora*, and *Lycium*). Miers stated that the Hyoscyameae formed a 'very natural tribe', but then contradicted himself by casting some doubt over the affinity of the last four genera with *Hyoscyamus*. Miers' hesitation over definition of the Hyoscyameae was clearly due to his uncertainty over the exact nature of corolla aestivation in all but *Hyoscyamus*. The Atropeae he distinguished by their supposedly baccate fruits, and the absence of an epigynous gland. Later (Miers, 1850), he reclassified *Anisodus* in the Hyoscyameae after seeing its circumscissile fruit and clearly imbricate corolla aestivation.

In 1852 Dunal published the account of Solanaceae for de Candolle's *Prodromus*. This treatment is the last published revision of all the known genera and species in the Solanaceae. It included 60 genera which were placed into two tribes, the Nolaneae and Solaneae. The latter group was subdivided into nine subtribes, including the Hyoscyaminae, defined using the same characters as Endlicher (1839) had used. Dunal recognized only *Hyoscyamus* and *Scopolia* in the Hyoscyaminae. Within *Scopolia* however, he included species now placed in *Physoclaina*, *Hyoscyamus*, *Anisodus*, and *Scopolia* s.s. which he defined as sections. His rationale for lumping these taxa under *Scopolia* was that they all differed from *Hyoscyamus* in the shape of their corolla and calyx. *Atropa* and *Mandragora* were placed in the large and heterogeneous subtribe Solanaeae. Within that subtribe the division Atropineae contained many of the genera of the family, including those as diverse as *Jaborosa* and

Discopodium. This group was diagnosed by its 5-parted calyx, campanulate corolla with valvate-plicate aestivation, and its baccate fruit.

In the second half of the nineteenth century two further treatments of Solanaceae appeared, those of Bentham (1876) and Wettstein (1895). These were produced at a time when many new species were being discovered as a result of botanical explorations to new regions of the world. Also at this time, Darwin had published his *Origin of species* (1859) and the theory of evolution by natural selection was beginning to have an impact on taxonomy. *Die natürlichen Pflanzenfamilien*, in which Wettstein's system was published, was the first major work to incorporate these ideas, although this had little direct impact on the classification of the Solanaceae. Both Bentham and Wettstein recognized a group centred on *Hyoscyamus*. Their classifications are summarized in Table 1.

Table 1 Classification of the Hyoscyameae according to Bentham (1876) and Wettstein (1895).

Bentham (1876)	Wettstein (1895)
Solaneae	Nicandreae
Atropeae: Including –	Solaneae:
<i>Lycium</i> L.	Lyciinae – incl. <i>Atropa</i> L.
<i>Atropa</i> L.	Hyoscyaminae – <i>Scopolia</i> Jacq.
<i>Mandragora</i> Juss.	<i>Physoclaina</i> Don.
Hyoscyameae: <i>Datura</i> L.	<i>Przewalskia</i> Maxim.
<i>Scopolia</i> Jacq.	<i>Hyoscyamus</i> L.
<i>Physoclaina</i> Don.	Solaninae
<i>Hyoscyamus</i> L.	Mandragorinae – incl.
Cestrineae	<i>Mandragora</i> Juss.
Salpiglossidae	Datureae
	Cestreae
	Salpiglossideae

Working extensively on the aestivation of the corolla and calyx, Baehni (1946) suggested pathways for the evolution of morphology in the family and proposed a new classification of the Solanaceae. He recognized five tribes, of which the Atropeae included the subtribe Hyoscyaminae. The genera which made up this subtribe were: *Hyoscyamus*, *Scopolia*, *Physoclaina*, *Tunaria*, *Vestia*, *Przewalskia*, *Petunia*, and *Nierembergia*. *Atropa* and *Mandragora* were placed in the subtribe Atropinae.

The most recent conspectus of the family (D'Arcy, 1979, revised and slightly modified in D'Arcy, 1991) is based on that of Wettstein with some modifications. In this system, 96 genera are included within the Solanaceae, representing about 2300 species. The hyoscyamoid group is recognized at the rank of tribe, and is composed of six genera: *Scopolia*, *Anisodus*, *Atropanthe*, *Przewalskia*, *Physoclaina*, and *Hyoscyamus*. This classification of the tribe Hyoscyameae follows that of Lu & Zhang (1986) who studied the Chinese members of the tribe. They listed the chief characters of the tribe as follows: embryo curved, ovary two-chambered with numerous ovules, connective between two anther cells inconspicuous, filaments inserted at the base or near the base of anthers, corolla lobes often imbricate in bud, calyx greatly enlarged after flowering and including the fruit, capsule with circumscissile dehiscence, and plants containing tropane alkaloid compounds. *Atropa* and *Mandragora* are both placed in the still large and heterogeneous tribe Solaneae, along with 33 other genera.

However, some work has cast doubt over this delimitation of the tribes. Tétényi (1987) examined the biosynthesis of alkaloids and steroids in the Solanaceae, and concluded that the family should be divided into four groups. He recognized the subfamilies Anthocercidoideae, Cestroideae, Solanoideae, and Atropoideae, based

largely on differences in the complexity of alkaloid biosynthetic pathways. Further evidence was taken from geographical and morphological data. On this basis, Tétényi placed the Hyoscyamineae, as defined by Lu & Zhang (1986), together with *Atropa* and *Mandragora* to form the subfamily Atropoideae. The subfamily was defined by its distinctive alkaloid-tropine ester synthesis relationship, where tropine esters are dominant forms (see Tétényi, 1987), imbricate corolla lobes, and Eurasian distribution.

Only Lu & Zhang (1986) have attempted to produce a phylogeny for the whole of the Hyoscyameae. This treatment has been used as the basis for the recent *Flora of China* account (Zhang et al., 1994). They did not include *Atropa* and *Mandragora* in their concept of the tribe because these genera possess baccate fruits. In their classification, *Scopolia* and *Anisodus* were considered the most primitive members of the group, with *Atropanthe* and *Przewalskia* being most closely related to them. These relationships were proposed on the basis of whether the genera showed relatively advanced or primitive characters. The primitive features were considered to be solitary flowers, an actinomorphic corolla, stamens inserted at the base of the corolla tube, and inaperturate pollen grains. However, there are a number of reasons to question their results. The first of these is doubt over the pollen descriptions given (see our results below). Secondly, they give no explanation as to how they reached their decisions regarding the evolution of characters, which could be interpreted differently. Finally, Lu & Zhang state themselves that their phylogenetic hypothesis should only be regarded as a basis for further study of the group.

Most recently, the Solanaceae have been the subject of molecular studies (Olmstead & Palmer, 1992; Olmstead & Sweere, 1994; Olmstead et al., in press). These chloroplast DNA based phylogenies do not include all the species or even all the genera of the family, but give ideas as to the potential monophyletic groupings of taxa. In cpDNA phylogenies based on the genes *rbcL* and *ndhF* (Olmstead & Sweere, 1994), *Atropa* is grouped with *Nolana* and *Lycium*. With restriction sites on the entire chloroplast genome, *Atropa* and *Hyoscyamus* together are sister to *Lycium* (Olmstead & Palmer, 1992). The most recent and as yet unpublished results of Olmstead et al. (in press) indicate that *Hyoscyamus*, *Physochlaina*, *Anisodus*, and *Atropa* (the only genera of the tribe used in the analysis) form a clear, well-defined monophyletic clade. These analyses do not contain enough taxa to draw clear conclusions as to the relationships of the genera, but they do clearly place the Hyoscyameae as defined here and by Tétényi (1987) together. However, *Mandragora* is extremely isolated in the cpDNA analysis and possesses many molecular autapomorphies (Olmstead et al., in press).

CHEMISTRY AND ECONOMIC BOTANY

Chemistry

The presence of abundant tropine alkaloids is characteristic of members of the Hyoscyameae. Tropine alkaloids are characterized by their five-member, nitrogen-containing rings and are found in several families in addition to the Solanaceae, most notably the Erythroxylaceae (Hegnauer, 1973; Romeike, 1978; Evans, 1979; Lounasmaa, 1988). The range and variety of tropine alkaloids in the Solanaceae arises from the esterification of various acids, such as acetic, propionic, and tiglic (see Evans, 1979) with hydroxytropines derived from amino acids such as ornithine, tryptophan, and phenylalanine. Hyoscyamine-type alkaloids, derived from phenylalanine, are also found in the Australian genera related to *Anthocercis*, the Chilean endemic *Latua* (Schultes & Hofmann, 1980), *Acnistus*, and *Salpichroa*, but are

in the highest concentrations in members of the Hyoscyameae (Romeike, 1978; Evans, 1979). The biosynthetic pathways leading to the hyoscyamine-type alkaloids are the most complex in the family, and are homologous in all the genera studied (Tétényi, 1987). The most abundant accumulated end-products in members of the Hyoscyameae are atropine, hyoscyamine, hyoscyne (=scopolamine), and tropine, but many other minor tropanes are also found. For complete lists of component alkaloids and a detailed discussion of tropine biosynthesis, see Evans (1979), Romeike (1978), and Tétényi (1987). Studies into the chemistry of these tropine alkaloids have not only provided data useful for classification, but also have provided insight into the effectiveness of these plants in traditional medicine (Qicheng, 1980; Xiao, 1981; Xiao & He, 1982).

Economic botany

The use of the Hyoscyameae in medicine has a long history. They have been recorded in the herbals of the ancient Greeks and in the ancient Chinese, Tibetan, and Indian pharmacopoeias (Deb, 1979; Bettolo, 1981, and see references below).

Hyoscyamus niger (henbane) has a long history of use over most of its range. The oldest of the Chinese herbals, *Shen Nung Pents'ao Jing* (thought to have been written some 2000–3000 years ago) describes the virtues of the seeds of henbane, lang-tang-tze, for curing toothache and for increasing vitality (Xiao & He, 1983). Later Chinese herbals document the use of lang-tang in a variety of illnesses and state that a tonic made from the plant allowed the patient to communicate directly with devils and spirits (Rätsch, 1992). Doctors of the Assyrian empire also used henbane for the cure of toothaches (Press et al., 1989). Dioscorides used henbane to induce sleep and relieve pain, and wrote of its properties in his *De materia medica* in A.D.77 (Stockwell, 1988). The herbals of the Middle Ages also contain numerous references to narcotic and dangerous properties of henbane (Arber, 1912). One of the best known of the English herbalists, John Gerard (1597), wrote scathingly of the fraudulent use of the smoke of henbane seeds to draw worms from the teeth. There is no doubt that the drug eased the pain of toothache, but the worms so miraculously removed by medical practitioners were nothing more than the tiny coiled embryos released from the seeds by the heat (Grieve, 1992). Culpeper, an astrological botanist (see Arber, 1912) writing in the first half of the seventeenth century, recommended an infusion of the leaves for the treatment of gout, swellings, and pains of the joints. He also believed the oil of the seed to be good for deafness and worms in the ears (Culpeper, 1826), thereby perpetuating the worm myth! Several species of *Hyoscyamus* are used in North Africa for both criminal and medicinal purposes (Boulos, 1983).

The *Coloured atlas of Tibetan medicine* (1704, see Xiao & He, 1983), a commentary on the much earlier complete manual of Tibetan medicine *Rygud bzhi* of 820, describes the use of the roots of *Przewalskia tangutica* to relieve pain and reduce swellings. The *Atlas* included illustrations of the plants used, and that of *P. tangutica* is botanically extremely accurate. The roots of *Physochlaina physaloides* are used in Mongolia as a tonic and a cure for asthma, those of *P. praealta* in Tibet as an analgesic (Xiao & He, 1983) and in India as a drug to dilate the pupils and to cure boils (Sharma & Singh, 1975). Roots of *Physochlaina infundibularis* were locally regarded as a sort of ginseng in the Chinese provinces of Shanxi and Henan. Several species of *Anisodus* have a long history of use in Tibetan medicine, as analgesics, anaesthetics, and antispasmodics, but dosages are very small and great care is needed as overdoses are known to cause delirium (Xiao & He, 1983).

In addition to their value as herbal remedies, some of these plants

gained reputations for their supposed magical properties, and became associated with numerous myths. Most notable are those surrounding the mandrake, *Mandragora officinarum* (Bouquet, 1936; Moldenke & Moldenke, 1952). The roots of this plant, which sometimes bear a resemblance to the human form, were believed to be the abode of evil spirits. The mandrake was said to scream when pulled from the ground, causing the death of the person uprooting it or anyone who heard the screams. To escape such a fate, people were said to use dogs to pull the plants up, and would drown the cries by blowing loudly on horns. Mandrakes were said to sprout from the sperm of hanged men, and so were to be found growing at the foot of gallows. Gerard (1597) ridiculed these myths as the hoaxes of charlatans, saying ‘...they are all and everie part of them false and most untrue for I myselfe and my servants also have digged up, planted and replanted very many.’ A mandrake is clearly identifiable on the thirteenth century Mappa Mundi in Hereford, a map showing the extent of the then-known world and many of its creatures. Numerous images of mandrakes adorn Egyptian tombs and tomb art and it may have been an important drug at that time. In the Old Testament mandrakes are mentioned in two places (in Genesis and in the Song of Solomon) in relation to the procreation of children, and the roots are carried in Eastern Europe as a charm against sterility (Mehra, 1979).

Mandragora was also associated with witchcraft, as were henbane and deadly nightshade, *Atropa belladonna*. The magical powers of these plants were believed to enable witches to fly (Stockwell, 1988). The celebrated sixteenth century Spanish physician A.F. de Laguna was probably the first to correlate the use of solanaceous drugs with witchcraft. The ointments used by supposed witches were composed of henbane, nightshade, and mandrake and caused hallucinations and delusions. He believed that witches were drug users and that the use of hallucinogenic drugs also increased suggestibility. Thus the confessions wrung from these people represented the delusional speech of deranged minds and were false (Schleiffer, 1979). Accounts of hallucinations experienced while using henbane and mandrake almost always involve flying sensations and some have suggested that the urge to move is a hallmark of the intoxication (Schleiffer, 1979).

The Hyoscyameae have continued to be employed in medicine right up to the present day. They make an important contribution to both modern and traditional medicine. In traditional medicine the use of these plants is found in Tibet, China, and in the Himalayan countries. They are used to treat swellings, bruises, asthma, to relieve pain, for the treatment of travel sickness, as antidotes to nerve gases, and as anaesthetics and sedatives. Extracts of species of *Physochlaina* and *Mandragora caulescens* are also used to make a tonic in Tibet, southern China, and Mongolia, which is administered to replenish weakness and to ‘warm the stomach’. Most of the Chinese species in the group are used in medicine in some way (Xiao & He, 1983; Zhang et al., 1994). *Hyoscyamus* is in the official British Pharmacopoeia (see Grieve, 1992) and has great importance in both the Ayurvedic and Unani medicinal systems of India (Dash & Kashyap, 1980; Thakur et al., 1989). The uses of this group of plants reflect the properties of their constituent alkaloids. The tropane alkaloids have been shown to be effective as analgesics, anaesthetics, antispasmodics, and to increase the circulation.

Today, five species are used commercially as a source of alkaloids in modern Western medicines. Hyoscyamine, or scopolomine, most important as a sedative, is extracted from *Scopolia carniolica*. Scopolomine is the infamous ‘truth serum’ – used unscrupulously to extract information from uncooperative persons. *Atropa belladonna* is the source of atropine, an antispasmodic used to treat asthma, colic, and eye diseases. *Hyoscyamus niger*, *H. albus*, and *H. muticus*

are grown for the extraction of hyoscyamine, atropine, and hyoscyamine.

This brief account highlights the importance of this group of plants for man. However, their beneficial effects are dependent on their wise use. All of these plants are potentially toxic and can cause death. Deadly nightshade, *Atropa belladonna*, is one of the most poisonous species of the group. This is clearly reflected in both the common and generic names of the plant: in Greek mythology Atropos was the Fate who held the shears to cut the thread of human life.

METHODS

Choice of taxa

Specimens studied were those at The Natural History Museum, London (BM) and the Royal Botanic Gardens, Kew (K). Living plants of some taxa were also examined. Individuals of *Anisodus luridus*, *Mandragora officinarum*, *Physochlaina orientalis*, *Atropa belladonna*, *Hyoscyamus albus*, *H. niger*, and *Scopolia carniolica* are all grown at Kew, and all but *Anisodus* and *Physochlaina* are grown at the Chelsea Physic Garden, London. *Scopolia carniolica* is also grown in the Harris Garden, Reading. Further details of the specimens studied are given in Appendix I and a complete database of all specimens studied is held at the University of Reading. Genera with more than one species were sampled, with species encompassing the range of variation used in the analysis. Taxa used in the analyses were: *Lycium chinense* Mill., *Datura innoxia* Mill., *Nicandra physalodes* Gaertn., *Anisodus luridus* Link, *Atropa belladonna* L., *Atropanthe sinensis* (Hemsl.) Pascher, *Hyoscyamus muticus* L., *Hyoscyamus niger* L., *Hyoscyamus senecionis* Willd., *Mandragora officinarum* L., *Mandragora caulescens* C.B. Clarke, *Physochlaina physaloides* (L.) G. Don, *Physochlaina praealta* (Dcne.) Miers, *Przewalskia tangutica* Maxim., and *Scopolia carniolica* Jacq.

Characters

The taxa were scored for variation in morphological and palynological characters. The morphological characters used were taken from the flowers, leaves, fruits, and seeds. A list of all the characters is given in Table 2, together with the coding used. Most of the characters are binary and self-explanatory. The data matrix used in the analyses is presented in Table 3.

The features of the spermoderm were determined by examining seeds prepared by enzyme etching (Lester & Durrands, 1984). Two seeds of each species were treated with a 1% solution of Driselase for 24 or 48 hours. The longer time was found to be necessary for the seeds of *Anisodus luridus*, *Atropa belladonna*, *Atropanthe sinensis*, *Mandragora officinarum*, *M. caulescens*, and *Przewalskia tangutica*. The seeds were rinsed with distilled water and allowed to dry before being examined with SEM. Seed measurements were made from 20 seeds when possible, and the average value recorded.

Table 2 Character set used in the cladistic analysis.

Inflorescence

0. Inflorescence type: raceme 0; solitary flowers 1; cyme 2
1. Flowers: pedicellate 0; sessile 1

Calyx

2. Calyx: tubular 0; campanulate–urceolate 1; cup-shaped 2
3. Calyx: actinomorphic 0; zygomorphic 1
4. Calyx: quite deeply lobed 0; very deeply lobed 1; shallowly lobed 2
5. Apices of calyx lobes: acuminate 0; rounded 1
6. Length of calyx: short (< 1 cm) 0; medium (1–3 cm) 1; long (> 3 cm) 2

Corolla

7. Corolla: flared 0; campanulate-urceolate 1; cup-shaped 2
8. Corolla: actinomorphic 0; zygomorphic 1
9. Corolla: uniform in colour 0; tube darker than the limb 1
10. Corolla lobes: quite deep 0; shallow 1; very deep 2
11. Apices of corolla lobes: rounded 0; acuminate 1
12. Length of corolla: short (< 2 cm) 0; medium (2 cm < x < 5 cm) 1; long (> 5 cm) 2
13. Width of corolla tube: narrow (< 1 cm) 0; broad (>1 cm) 1

Stamens

14. Filament insertion on the corolla tube: near middle 0; basal (< 1/3 of way up) 1; apical (> 1/2 way up) 2
15. Stamens: exerted from corolla tube 0; included 1
16. Stamens: regular 0; declinate 1

Stigma

17. Stigma: included in corolla tube 0; exerted 1

Fruiting calyx

18. Fruiting calyx: cup-shaped 0; ovoid 1; flared-urceolate 2; tubular 3
19. Fruiting calyx: little enlarged 0; inflated 1
20. Fruiting calyx: without prominent ribs 0; with prominent ribs 1
21. Fruiting calyx: membranous 0; subcoriaceous 1; coriaceous to woody 2

Fruit

22. Fruit: berry 0; capsule 1
23. Fruit: globose 0; cylindrical 1

Leaves

24. Leaves: ovate 0; cordate 1; lanceolate 2
25. Leaf margins: entire 0; variously incised 1
26. Leaves: arranged along the stem 0; a basal rosette 1

Seeds

27. Seeds: compressed 0; not compressed 1
28. Seeds: rectangular-subreniform 0; reniform 1; sublenticular 2
29. Seed size: medium (2.5–5 mm) 0; small (< 2.5 mm) 1; large (> 5 mm) 2
30. Seed colour: light brown or mustard yellow 0; dark brown 1
31. Spermoderm cells: deep 0; shallow 1
32. Walls of spermoderm cells: sinuate 0; straight 1

Trichomes

33. Glandular hairs: absent 0; with uniseriate glands only 1; with uni- and multi-seriate glands 2
34. Eglandular hairs: all simple 0; dendritic hairs present 1

Pollen

35. Number of apertures: three 0; none 1; more than three 2
36. Length of apertures: long, almost meeting at the poles 0; short 1
37. Tectum: present 0; absent 1
38. Supratracteal ornamentation: absent 0; isolated elements-scabrate 1; scabrate with gemmae 2; reticulate or striate 3

Chemistry

39. 3-tigloyloxytropine: absent 0; present 1
40. Belladonnine: absent 0; present 1
41. Tropine: absent 0; present 1

Table 3 Data matrix used in the cladistic analysis.

Character Number	0123456789	1111111111	2222222222	3333333333	44
<i>Lycium</i>	000000000	000000000	000000000	000000000	00
<i>Anisodus</i>	1021001100	0011110011	1210000110	1000121020	01
<i>Atropa</i>	0020101100	0011111100	0000000121	1101000031	11
<i>Atropanthe</i>	1020001100	0011111111	0110000100	0110000030	01
<i>H. muticus</i>	2111201011	0010000121	0211010001	0101100011	01
<i>H. niger</i>	2111001011	0010000121	0210010001	0102000011	01
<i>H. senecionis</i>	2010001010	2011000121	0211010001	0102000011	01
<i>M. caulescens</i>	1020111200	2011010000	0000201110	111001?111	10
<i>M. officinarum</i>	1020101000	2011110000	0000101112	000001?101	10
<i>P. physaloides</i>	0000000000	0000000111	0110100001	0002020011	01
<i>P. praealta</i>	0010000000	1110100121	0111100001	1002000031	01
<i>Przewalskia</i>	1000011000	0010210111	1210201100	1001000001	01
<i>Scopolia</i>	1021200000	1101110011	0110000110	01100?1011	01

Pollen for this study was taken from herbarium specimens at The Natural History Museum (see Appendix I), except in the case of *Scopolia carniolica*, in which pollen from live plants was studied. Pollen grains were prepared using the procedure of Erdtmann (1960). Acetolysed pollen grains were studied under the SEM and the light microscope. All chemical characters were taken from the literature, largely from Tétényi (1987) and Romeike (1978).

Tree construction

Cladistic analyses were undertaken with HENNIG86 (Farris, 1988) using the *ie** option (implicit enumeration) with all characters unordered. Tree statistics generated from HENNIG86 include the tree length (L), the ensemble consistency index (CI), and the retention index (RI). The ensemble consistency index (CI) is a measure of character fit on a scale of 0 to 1 and the ensemble retention index (RI) is the fraction of apparent synapomorphy in a character that is retained as synapomorphy on the tree (Farris, 1989). The genus *Lycium* was chosen as the outgroup for this analysis based on the cpDNA phylogenies produced for the Solanaceae in which *Lycium* is the sister group to the clade containing *Atropa* and *Hyoscyamus* (Olmstead & Palmer, 1992; Olmstead & Sweere, 1994; Olmstead et al., in press).

RESULTS AND DISCUSSION**Tree topology**

The HENNIG86 analysis produced a single most parsimonious tree of L=109, CI=52, and RI=58 (Fig. 2). The group can be broadly divided into two clades: the *Hyoscyamus* + *Physochlaina* clade and the rest of the genera (see Fig. 2). The *Hyoscyamus* + *Physochlaina* clade is defined by the following suite of synapomorphies: cordate leaves (character 24), very small seeds (character 29), glandular hairs with uniseriate and multiseriate glands (character 33), and pollen with isolated scabrate supratracteal elements (character 38). A close relationship between *Hyoscyamus* and *Physochlaina* has been pointed out by previous authors (Lu & Zhang, 1986). The genus *Physochlaina* is not, in our tree, a monophyletic group. This could be used as evidence for the suggestion that this genus should be reduced to synonymy within *Hyoscyamus*. The position of *P. praealta* does agree with the observations of Zhang & Lu (1984) who suggest this species may be intermediate between the two genera. The characters linking *P. praealta* to *Hyoscyamus* include the shape of the calyx and the fruit. However, if the pattern of branching is altered, such that the two species of *Physochlaina* do form a monophyletic group, then the tree is only one step longer. Clearly, this analysis does not provide convincing evidence either for the lumping of these genera or for keeping them separate.

The clade consisting of the rest of the genera in the tribe is defined by the following suite of synapomorphies: a racemose inflorescence (character 0), a medium length calyx (character 6, also present in *Hyoscyamus*) and corolla (character 12, occurring in many places on the tree), basal filament insertion (character 14), stamens included in the corolla tube (character 15), and non-compressed seeds (character 27). Within the clade, the only consistent groupings are *Scopolia* + *Anisodus* and *Atropa* + *Mandragora* (see p. 19). Relationships of the other genera are somewhat ambiguous, although *Przewalskia* is basal to the clade. Contrasting this with the proposed phylogeny of Lu & Zhang (1986) illustrates an important aspect of cladistics which distinguishes it from other purportedly phylogenetic approaches. Lu & Zhang (1986) hypothesize that *Przewalskia* is the

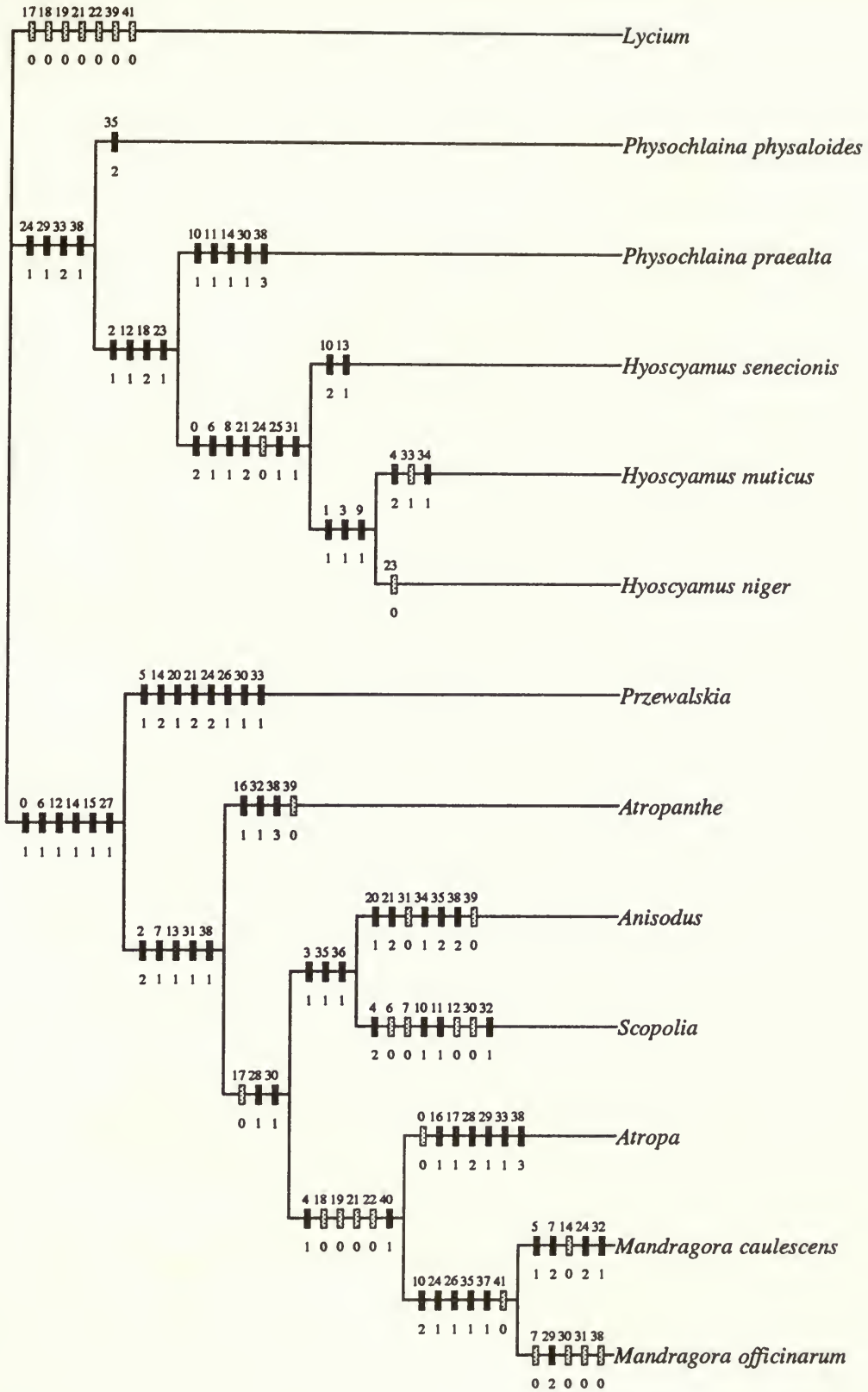


Fig. 2 The single most parsimonious cladogram from the HENNIG86 analysis. The characters are discussed in the text, and character states are shown in Table 2. For characters marked on the branches of the cladogram: unshaded marks indicate synapomorphies, stippled marks indicate reversals and parallelisms (homoplasy), and solid marks non-homoplastic synapomorphies.



a



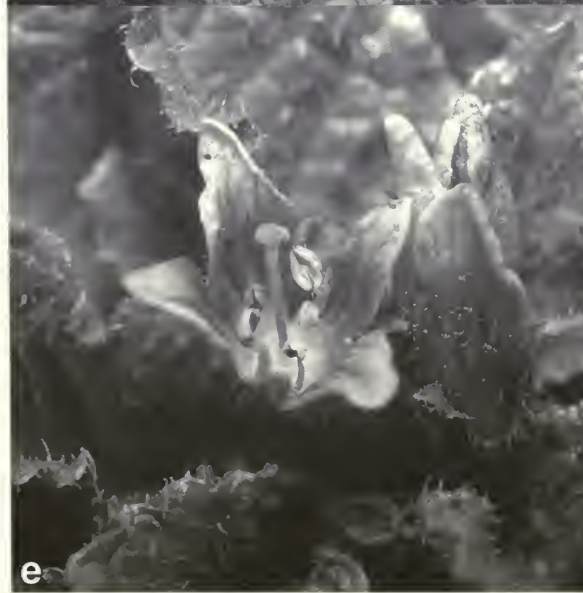
b



c



d



e



f



Fig. 4 a) Fruit of *Anisodus tanguticus* (photograph courtesy of M. Gilbert), b) Fruit of *Atropa belladonna*, Chelsea Physic Garden, c) Fruit of *Hyoscyamus niger*, Chelsea Physic Garden, d) Fruit of *Physochlaina orientalis*, RBG Kew.

most 'advanced' and thus, according to them, derived, taxon of the group. However, in our tree, this genus usually occurs at the base of the clade. This radical difference in placement is most likely due to the large number of autapomorphies (see Fig. 2) which distinguish *Przewalskia*. Automorphies are not informative about relationships.

Atropa and *Mandragora* cluster together and are nested well within the tribe as a whole. This is in agreement with Tétényi's (1987) system. Earlier classifications had not included *Atropa* or *Mandragora* within the tribe simply on the basis that they bear berries and not capsules. Characters which unite the two genera

include those of the fruiting calyx (shape, inflation, and texture), fruit type, and the presence of belladonnine. The close relationship of these two genera was implied in the classifications of some of the early botanists: Miers (1849), Dunal (1852), and Bentham (1876) all placed these two genera in the same tribe or subtribe. This link is also reflected in the naming of some of the species, for example, Linnaeus had described *Mandragora officinarum* in *Species plantarum* (1753), but in later editions he changed the name to *Atropa acaulis* (1762, 1764).

Fig. 3 a) Flowers of *Physochlaina orientalis*, RBG Kew, b) Flowers of *Hyoscyamus niger*, Chelsea Physic Garden, c) Flowers of *Scopolia carniolica*, Chelsea Physic Garden, d) Flowers of *Anisodus luridus*, RBG Kew, e) Flowers of *Mandragora autumnalis*, RBG Kew, f) Close-up of the flower of *Atropa belladonna* showing declinate stamens, Chelsea Physic Garden (photograph courtesy of J. Vogel).



Fig. 5 a) Fruiting plant of *Przewalskia tangutica* (photograph courtesy of M. Gilbert), b) Fruit of *Przewalskia tangutica* showing dehiscence (photograph courtesy of M. Gilbert), c) Fruit of *Mandragora officinarum*, RBG Kew, d) Fruiting plant of *Mandragora chinghaiensis* (photograph courtesy of M. Gilbert).

Character analysis

Rather than discussing in detail all of the characters and their distribution on the tree, we have chosen a few to discuss in detail. Some of these are characters that show little homoplasy on the tree, while others are those that surprisingly do not provide any phylogenetic evidence.

Morphological characters

3. CALYX SYMMETRY. An actinomorphic calyx is plesiomorphic in the tribe. This finding is contrary to studies completed for the family as a whole, with the most basal members possessing zygomorphic flowers (see Olmstead & Palmer, 1992; Olmstead et al., in press). Zygomorphy occurs twice on the tree, once in *Hyoscyamus* and as a

synapomorphy uniting *Scopolia* and *Anisodus*. In *Scopolia* and *Anisodus* the calyces are symmetrical except in their lobing. In *Scopolia*, one lobe is usually enlarged (Fig. 3c), and in *Anisodus* the lobing is very irregular (Fig. 3d, 4a). However, in the two species of *Hyoscyamus*, the asymmetry is manifested differently. In these species the calyx tube is curved, and the lobes show a gradation in size. The zygomorphic calyces of *Hyoscyamus* should probably not be equated with those of *Anisodus* and *Scopolia*. A more meaningful coding of this character may be to represent these as two independent states, or it could be divided into two characters; symmetry of the calyx lobes and of the calyx tube.

7. COROLLA SHAPE. A flared corolla is the plesiomorphic state for the tribe. Within the *Hyoscyamus/Physochlaina* clade, this character is conservative. In contrast to this, in the rest of the tribe, corolla

shape shows much homoplasy. It was difficult to divide shape into discrete states, although the cup-shaped flowers of *Mandragora caulescens* were quite distinct. Shape may in fact represent several independent characters, and so would be better coded as such. The problem then lies in determining just what these characters should be.

14. FILAMENT INSERTION. Lu & Zhang (1986), in their study of the Chinese members of this tribe, presumed that stamens inserted at the base of the corolla tube were a primitive feature. This analysis suggests that this should actually be regarded as a derived trait, occurring in two places on the tree. Basal stamen insertion is a synapomorphy of the *Przewalskia* clade (uniting all the genera save *Hyoscyamus* and *Physochlaina*) and occurs in *Physochlaina praealta*.

16. ARRANGEMENT OF THE STAMENS. Declinate stamens are found in both *Atropa* and *Atropanthe*. Consequently, this character is not indicative of shared ancestry and, in this analysis, is uninformative about generic relationships. It is possible that this feature is an adaptation for improving pollen deposition on insect pollinators. The flowers of these genera are held horizontally or are nodding, and the position of the anthers is such that they would brush the bodies of insects entering them (see Fig. 4f).

19. INFLATION OF THE FRUITING CALYX. An inflated fruiting calyx (Figs 4c, d, 5a) is a synapomorphy of the tribe in this analysis. The non-inflated calyx found in *Atropa* and *Mandragora* (Figs 4b, 5c, d) must therefore be considered to be derived within the tribe and is probably related to the method of seed dispersal in these plants. Both these genera produce fleshy or juicy berries. Those of *Atropa* are black and shiny when ripe, and are eaten by birds. The fruits of *Mandragora* are whitish, greenish, yellow, orange or purple, and are borne close to the ground, frequently hidden by leaves. These are eaten by small mammals or reptiles. In the other members of the tribe seed dispersal is effected by the seeds being shaken from the capsules. The fruits of *Przewalskia* become detached and behave as tumble weeds, releasing seeds as they are blown about by the wind (M. Gilbert, pers. comm.).

21. TEXTURE OF THE FRUITING CALYX. A subcoriaceous calyx is plesiomorphic in the tribe. *Atropa* and *Mandragora* are united by having membranous calyces. This seems to provide some support for the suggestion that the calyx has a protective function in other members of the tribe. Thickening of the calyx occurs in three places on the tree, in *Anisodus*, *Przewalskia*, and as a synapomorphy of *Hyoscyamus*.

26. LEAF ARRANGEMENT. A rosette arrangement of leaves occurs twice on the tree, in *Przewalskia* and *Mandragora*. The rosette habit has been thought to be an adaptation to habitat (Lu & Zhang, 1986), providing protection from wind and grazing animals, and ensuring maximum exposure to the sun. *Przewalskia* is found at high altitudes in arid grasslands and areas of frost heave (Fig. 5a), while *Mandragora* (see Fig. 5d) occurs in a wider range of habitats, which include stony slopes and screes in mountainous regions, grassland, and ruderal habitats.

27. SEED COMPRESSION. Compressed seeds are confined to the *Hyoscyamus* + *Physochlaina* clade, and so supports the division of the tribe into two groups. Non-compressed seeds are a synapomorphy of the other clade and are generally uncommon in the family (see Knapp, 1991). This character may be related to the development of the seeds, and possibly to seed dispersal.

29. SEED SIZE. Small seed size is a synapomorphy of the *Hyoscyamus* + *Physochlaina* clade, but is also found in *Atropa*. Small

seeds are often associated with capsular fruit in the Solanaceae (Souèges, 1907), but in the Hyoscyameae this ecological distinction appears not to hold true.

30. SEED COLOUR. In contrast to the genus *Solanum* and other tribes in the family (see Knapp, 1989; Knapp et al., in press; Knapp & Helgason, in press) seed colour provides little support for the tree topology, and has frequently changed in the Hyoscyameae. The explanation for this may lie in the function of the seed colour, or may reflect the ease with which these changes can occur.

32. SPERMODERM CELL WALLS. Whether the cell walls of the spermoderm are straight or sinuate is uninformative with respect to generic relationships, since straight walls are autapomorphic in both *Scopolia* and *Mandragora caulescens*. This is in contrast to the utility of cell wall shape as a character in studies of other groups of Solanaceae (Knapp & Helgason, in press).

34. PRESENCE OF DENDRITIC HAIRS. Dendritic hairs occur in both clades, in *Physochlaina* and *Anisodus*. This high level of homoplasy is also found in many other groups of Solanaceae (Knapp, 1991). Trichomes can have a multitude of functions, for example, protection against desiccation, ultra-violet radiation, and insect attack (Metcalfe & Chalk, 1983). Dendritic hairs, in comparison to simple hairs, may have advantages in any of these roles but no evidence exists for an adaptive role.

Pollen characters

35. NUMBER OF APERTURES. Triaperturate pollen grains are plesiomorphic in the tribe, as they are thought to be for the family Solanaceae and dicotyledons in general. This is contrary to the suggestion of Lu & Zhang (1986) that inaperturate pollen grains are ancestral in the Hyoscyameae. They (Zhang & Lu, 1984; Lu & Zhang, 1986) identified the pollen grains of *Anisodus tanguticus*, *A. luridus* (as *A. mairei*), *A. carniolicoides* (as *Scopolia carniolicoides*), and *A. acutangulus* as inaperturate, while our results clearly show (Fig. 7b) the grains of *A. luridus* to be porate. The potentially cryptic nature (see *Mandragora* p. 27, and Diez & Ferguson, 1984) of the apertures in the pollen grains of *Anisodus* needs further study. The two species which have pollen with more than three apertures, *Anisodus luridus* and *Physochlaina physaloides*, are unrelated. Increase in aperture number must therefore have occurred independently in these two taxa. Distribution of apertures in these two taxa differs radically. In *A. luridus* the six apertures are distributed randomly on the pollen grain, and the grains are pantoporate (Fig. 7b), whereas in *P. physaloides* the apertures are confined to the equator (Fig. 6a).

The principal functions of the pollen aperture are protection, harmomegathic responses (alterations in form accompanying changes in pollen grain hydration, see Blackmore & Barnes, 1986), ion exchange, and pollen tube germination. The significance of the number of apertures to each of these functions is unclear. Increase and irregularities in number of apertures does seem to be related to polyploidy, but cytological information is lacking for both these species (see Table 4).

36. LENGTH OF APERTURES. The presence of pores, rather than colpi, is a synapomorphy which unites *Anisodus* and *Scopolia* (see Fig. 7a, b). Reduction of aperture size may have occurred in response to an increasingly arid environment, reducing the risk of desiccation of the pollen grains. However, the ecology of these genera does not fit in with this, as they are typically plants of moist environments. This highlights the fact that we should be wary of making simplistic explanations about the adaptive significance of

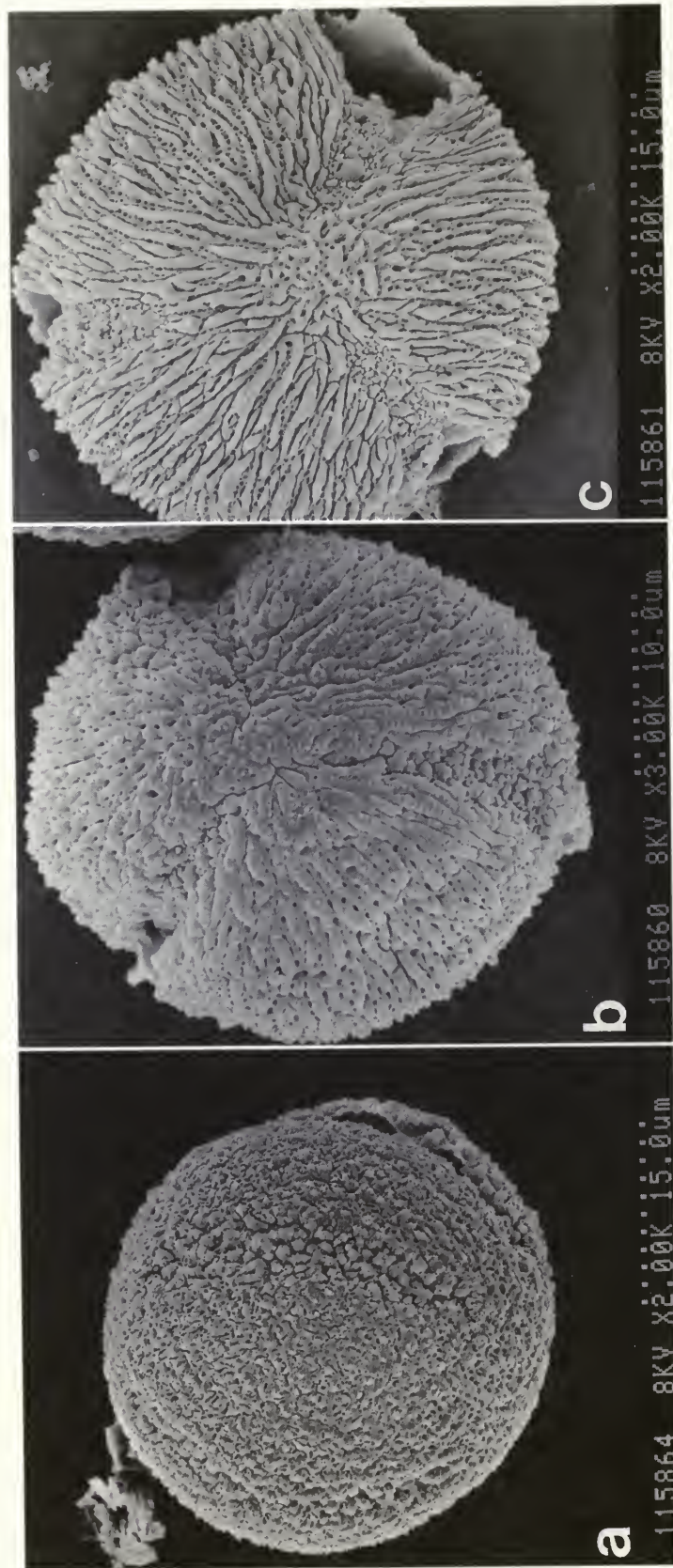


Fig. 6 Pollen morphology of the Hyoscyameae. Scale bars beneath photographs. a) *Physoclaina physaloides*, b) *Physoclaina praealta*, c) *Atropanthe sinensis*.

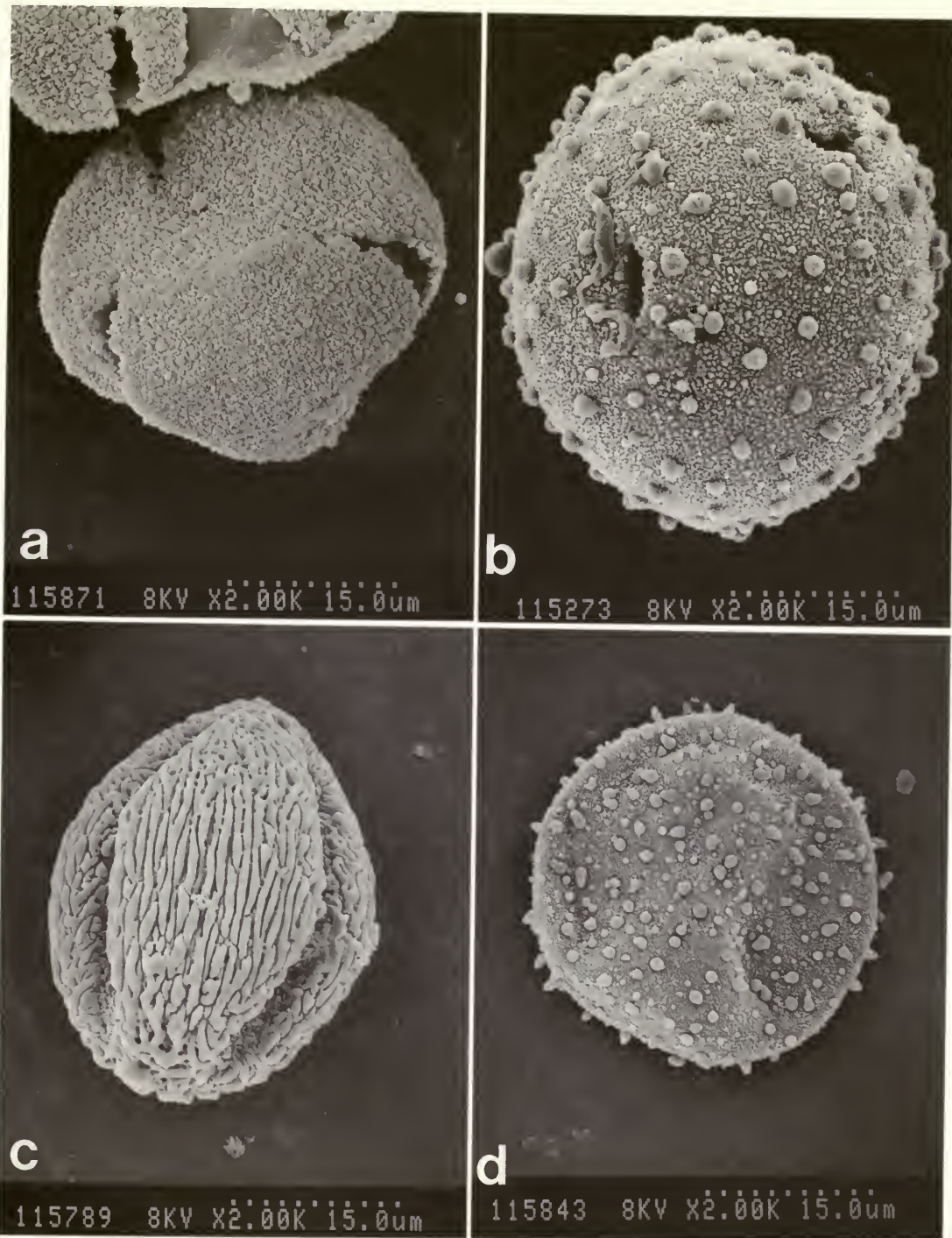


Fig. 7 Pollen morphology of the Hyoscyameae. Scale bars beneath photographs. a) *Scopolia carniolica*, b) *Anisodus luridus*, c) *Atropa belladonna*, d) *Mandragora caulescens*.

characters. Multiple functions of characters considerably complicate the issue. This is undoubtedly true for pollen apertures, where complexity of structure and a variety of alternative strategies make simplistic adaptive explanations unrealistic.

37. OCCURRENCE OF A TECTUM. The only taxa in which intectate pollen occurs, are the two species of *Mandragora*. This type of pollen is believed to be primitive for the angiosperms as a whole (Zavada, 1986). Lack of a tectum is perhaps related to the cryptaperturate condition in *Mandragora* (Diez & Ferguson, 1984).

The structure of the ectexine affects the physical properties of the wall, and this must influence the durability of the pollen and the exchange of materials across the wall.

38. SUPRATECTAL ORNAMENTATION. There is little concurrence between this character and the tree topology. This may be for two reasons. One possibility is that the ornamentation of the pollen grain may not be useful in revealing phylogenetic relationships in this group because of parallel evolution. This analysis does suggest that pollen with a reticulate pattern may have arisen independently in

Table 4 Chromosome numbers which have been recorded for the Hyoscyameae.

Species	Chromosome number	Reference
<i>Atropa belladonna</i>	2n = 72	Vasudevan, 1975
<i>Hyoscyamus muticus</i>	2n = 28	Al-Musawi, 1979
<i>Hyoscyamus niger</i>	2n = 34	Al-Musawi, 1979
<i>Hyoscyamus senecionis</i>	2n = 34	Al-Musawi, 1979
<i>Mandragora autumnalis</i>	2n = 96	Murin, 1978
	2n = 84	Hawkes, 1972
<i>Physochlaina praealta</i>	n = 41	Vasudevan, 1975
<i>Scopolia carniolica</i>	2n = 48	Vasudevan, 1975
		Hawkes, 1972

three lineages. The selection pressures which may have led to this are not known. The function of pollen sculpturing has been thought to be related to the pollen vector (Hemsley & Ferguson, 1985; Ferguson & Pearce, 1986), although in some groups of plants there is no apparent correlation between the vector and ornamentation type (Thanikaimoni, 1986). An alternative explanation is that the delimitation of the character states is not meaningful. This seems likely in view of the difficulty in deciding on character states due to uncertainty about pattern homology. For example, pollen grains which were scabrate and those with isolated granules were coded together, but perhaps these should have been coded separately. Pollen of *Anisodus* was unique in being scabrate with isolated gemmae (see Fig. 7b). This was coded separately from simply scabrate pollen. The importance of this distinction is unclear. Investigation into the development of sculptural patterns may shed some light on this area, and so help in the interpretation of changes in ornamentation type.

Chemical characters

39. PRESENCE OF 3-TIGLOYLOXYTROPANE. Presence of this compound is a synapomorphy for the tribe, but the distribution of the character on the tree is homoplasious. Either the ability to produce this compound has arisen up to four times in the tribe, or there have been reversals in *Anisodus* and *Atropanthe*.

40. PRESENCE OF BELLADONNINE. This character is a synapomorphy of *Atropa* + *Mandragora*.

41. PRESENCE OF TROPINE. The occurrence of tropine is a synapomorphy of the tribe in this analysis. However, there has been a reversal in this character in *Mandragora*.

Lu & Zhang (1986) identified a number of characters which they considered to be 'primitive' for the tribe. Among these were actinomorphic and solitary flowers, stamens inserted at the base of the corolla tube, and inaperturate pollen. They provided no explicit reasoning for their choices, and tried to place taxa on a gradient of 'advancement'. This analysis suggests that many of these features should be viewed as derived within the tribe. This draws attention to the futility of deciding *a priori* on criteria of 'advancement'. Decisions based on phylogenetic analyses rather than on intuition can be more easily justified.

The diversity of pollen types in the Hyoscyameae means that such characters cannot be used as synapomorphies of the group. Similarly, this source of data provides little information about generic relationships in the tribe. The differences in pollen morphology between some of the genera have been used in the past as evidence for their continued recognition (Zhang & Lu, 1984; Sandina & Tarasevich, 1982). Thus, the separation of *Scopolia*, *Atropanthe*, and *Anisodus* is supported by the palynological evidence. However, this is insufficient evidence on its own, because similar levels of varia-

tion are found within other genera such as *Physochlaina* (Zhang & Lu, 1984). There is no justification for emphasizing one source of data at the expense of others.

Chromosome numbers have not been used in this analysis, but may perhaps be of use in future work on this group. Initial work on the cytology of these plants suggests that this may be informative. The chromosome counts which have been completed are listed in Table 4. A chromosome number of $x=12$ is widely held to be primitive for the Solanaceae, with aneuploid reduction to $x=7$ in many lineages (Goodspeed, 1954; Olmstead & Palmer, 1992). Polyploidy is common and possibly has been an important factor in the evolution of the tribe. Whether ploidy levels in the Hyoscyameae are due to allopolyploidy or to simple chromosome doubling is not known.

Biogeography

The biogeography of the Hyoscyameae is of great interest because it is the only exclusively Eurasian group in the family, the rest of which is largely Gondwanan in distribution (see Symon, 1991). Two theories have been proposed for the origin of the Hyoscyameae. Lu & Zhang (1986) drew attention to the diversity of the tribe in south-western China. Eleven of the forty species of the Hyoscyameae are found here, five of which are endemic to this area (see Fig. 1). On this basis, they concluded that this area was probably 'the birthplace of hyoscyaminous plants'. However, there is a fundamental flaw in equating the centre of origin of a group with its centre of diversity: centre of origin arguments are often flawed (Humphries & Parenti, 1986) and these dispersal hypotheses always require external, often ad hoc, causes to explain patterns. Linking distribution with the history of the earth has proved a powerful method for understanding the processes that influence the patterns we observe (Nelson & Platnick, 1981; Humphries & Parenti, 1986). An alternative scenario to the centre of origin idea of Lu & Zhang (1986) was proposed by Symon (1991). He considered the distribution of this tribe to be consistent with the ancestral group being rafted north on the Indian plate. On meeting Eurasia, the group evolved in the developing Himalayas, and subsequently spread from there.

The geological history of the area occupied by members of the Hyoscyameae is remarkably complex. Although the group is largely Eurasian in distribution at present, the main areas occupied by the genera of the Hyoscyameae were once part of the Gondwana supercontinent. Much of South East Asia, including southern China, consists of terranes rifted from the margins of eastern Gondwana some time during the Jurassic (Hallam, 1994). The southern part of Tibet in the Himalayan mountains is thought to have been the southern margin of the Tethys Sea or still moving to collide with the Laurasian supercontinent in the early to mid Jurassic, while the northern part of the area is more consistent with a non-Gondwanan, Eurasian position. The Lhasa block collided with the other rifted terranes in the late Jurassic to early Cretaceous (Dewey, 1988). Apulia, including Turkey and present day Italy, was connected to Africa during the early Cretaceous, and rotated to collide with Eurasia about 80 million years ago (Hallam, 1994). The Indian plate is thought to have broken away from the Gondwanan land mass last of all, some time near the Cretaceous/Tertiary boundary between 65 and 60 million years ago (Hallam, 1994). The Eurasian-African collision closing the seaway to the Indo-Pacific occurred in the early Miocene, and brought the Middle East into contact with the major land masses of Eurasia. Climate change during the Neogene was probably important to the evolution and distributional patterns of land plants in these areas. The Himalayas have continued to uplift long after the initial collision event between India and Asia (Hallam, 1994) and this may have been a major factor in the general cooling of climate in the Neogene. The general pattern of the break-up of the

continents over geological time is thus consistent with the Hyoscyameae being a primarily Gondwanan group which has radiated extensively in Eurasia in more recent times.

The two main clades within the tribe have broadly overlapping distributions centred in the Himalayan and South China area. Distribution patterns within the *Hyoscyamus/Physochlaina* clade are somewhat confused due to widespread human utilization and distribution of these species. The genus *Physochlaina* is found in much of China, reaching north into Siberia and as far west as the Himalayas. Species of *Physochlaina* are predominantly plants of montane habitats. A possible scenario is that this genus arose with adaptation to high altitudes or to colder climates. This may have occurred during the development of the Himalayas, or alternatively this group might have evolved at low altitudes during later glaciations in the Quaternary. *Hyoscyamus* shows a much wider distribution and ecological amplitude. The majority of the species occur in the Middle East and the Mediterranean region, and it has been suggested that its occurrence in North Africa and northern Europe is a result of human dispersal (Symon, 1991). All species of *Hyoscyamus* occurring in India occur in Kashmir and the north of the country, perhaps lending support to the idea of a very early origin for the group. Adaptation to more arid and mediterranean climates seems to have occurred in many of the species. This may have arisen as the genus spread into more arid areas or during a period of increased aridity. Such conditions are thought to have developed in central Asia following the uplift of the Himalayas and the Tibetan plateau (Manabe & Broccoli, 1990). However, any hypotheses of biogeography and evolutionary history of *Hyoscyamus* will need to be tested using an in-depth phylogenetic analysis of the entire genus.

Within the other clade of the Hyoscyameae, similar ecological factors seem to have been important. The genera in this clade are largely isolated ecologically, growing in different elevational ranges and often in quite different microhabitats. *Przewalskia* is a narrow endemic from the Qinghai-Xizang Plateau of western China and Tibet, growing between 3200 and 5000 m. The evolution of *Przewalskia* may have occurred during the uplift of this region (Lu & Zhang, 1986). The timing of the Himalayan orogeny is uncertain. One theory is that the main orogenic events occurred in the Oligocene, at the same time as the Himalayas developed. Alternatively, uplift may have continued well into the Pliocene and palynological evidence supports this (Ruddiman et al., 1989). The prolonged uplift of the Himalayas (Ruddiman et al., 1989) and the concomitant expansion of grassland habitats at the expense of forests will have had a profound effect on the evolution of plants found in these areas.

The widely disjunct distribution of *Scopolia* (see Fig. 1) suggests that it was once more widespread. This explanation is favoured over one of long-distance dispersal because capsular fruits and small unornamented seeds, which are found in these plants, tend to be locally dispersed (Olmstead & Palmer, 1992). Lu & Zhang (1986) suggest that this genus was widespread during the Tertiary, but became much more restricted with the advance of ice-sheets over the continent during the Quaternary.

Atropa and *Mandragora* are both very widespread genera, occurring from southern Europe across to the Himalayas and the mountains of western China. Their animal-dispersed fruits and their widespread human use may have helped to expand their ranges considerably.

The analysis presented above is a first attempt at a complete phylogenetic classification of the Hyoscyameae. The resultant cladogram shows that two lineages can be identified within the group, one clade consisting of *Hyoscyamus* + *Physochlaina* and the other containing *Przewalskia* + the rest of the genera. Within the *Przewalskia* clade the relationships of the genera are somewhat

ambiguous, although *Anisodus* + *Scopolia* and *Atropa* + *Mandragora* always group together. The position of *Atropa* and *Mandragora*, clustering well within the tribe, provides evidence for including them in the Hyoscyameae and supports Tétényi's (1987) grouping. This is further corroborated by their distribution, since they form a phytogeographically coherent group with the Hyoscyameae (Symon, 1991).

GENERIC CONSPECTUS

This conspectus is intended as an overview of the taxonomy of the genera, but may require revision as more species are studied in detail. The synonymy has been taken in large part from recent floristic or monographic treatments, which are acknowledged and cited as part of each description. Much work remains to be done with the taxonomy and phylogeny of each of these genera and we hope that this conspectus will help future workers in these groups. Distributions for each of the species are given in general terms. More complete descriptions, especially for species occurring in China, can be found in the floristic works cited.

Artificial key to the genera of the Hyoscyameae

1. Fruit a fleshy or juicy berry, white, green, yellowish orange, purplish or black 2
Fruit a dry capsule, usually circumscissile 3
2. Berry white, green, purplish or yellowish orange at maturity, fleshy, usually held beneath the leaves; acaulescent (occasionally shortly caulescent) herbs with enlarged tap roots; flowers deeply lobed, actinomorphic 5. **Mandragora**
Berry black and juicy at maturity; plant an erect perennial to 1 m tall; flowers shallowly lobed, the stamens declinate 2. **Atropa**
3. Flowers solitary or in short inflorescences of 2–3 flowers 4
Flowers in elongate or branched inflorescences, the inflorescence usually with more than 5 flowers 7
4. Acaulescent herbs with long, fleshy taproots; leaves sessile; corolla narrowly tubular 7. **Przewalskia**
Erect, often branched perennials with well-developed above-ground stems; leaves variously petiolate; corolla not narrowly tubular 5
5. Corolla slightly zygomorphic, one petal larger than the rest; calyx lobes equal in size; anthers declinate at anthesis 3. **Atropanthe**
Corolla actinomorphic; calyx lobes usually unequal in size; anthers not declinate at anthesis 6
6. Corolla campanulate-urceolate, as wide as long, greenish; calyx lobes rounded at the tips 1. **Anisodus**
Corolla flaring, longer than wide, usually purplish without; calyx lobes strongly pointed, especially the elongate one 8. **Scopolia**
7. Inflorescences markedly one-sided, usually unbranched; corolla zygomorphic; calyx lobes spiny at the tips in fruit 4. **Hyoscyamus**
Inflorescences not markedly one-sided, usually branched; corolla actinomorphic; calyx lobes not spiny at the tips in fruit 6. **Physochlaina**

1. **Anisodus** Link, in Sprengel, *Syst. veg.* 1: 699 (1825). Type: *Anisodus luridus* Link. Figs 3d, 4a.

Robust subshrubs or perennial herbs, at least sometimes with a massive softly woody rootstock; glabrous or pubescent. Leaves alternate, petiolate, entire or dentate; sympodia difoliate. Inflorescences of solitary flowers borne in the leaf axils. Flowers

subactinomorphic; calyx campanulate-funnelform to funnelform, the lobes unequal in length and variable in shape, usually rounded at the tips; corolla campanulate, longer than or equal in length to the calyx; stamens inserted near the base of the corolla tube; pollen hexapantoporate with slightly elongated pori with rounded ends and scabrate-gemmate ornamentation (Fig. 7b); ovary bilocular, with a disc-like nectary. Fruit a globose or ovoid capsule, with circumscissile dehiscence; fruiting calyx much enlarged, sometimes enclosing the fruit and prominently ribbed, often laterally compressed. Seeds numerous, not markedly compressed. Grasslands and woodland edges, occasionally ruderal around towns and villages; 2800–4500 m.

LIST OF SPECIES (Zhang et al. 1994). *Anisodus acutangulus* C.Y. Wu & C. Chen, China; *Anisodus carniolicoides* (C.Y. Wu & C. Chen) D'Arcy & Zhang (*Scopolia carniolicoides* C.Y. Wu & C. Chen), S. China; *Anisodus luridus* Link (*Anisodus fischerianus* Pascher, *A. luridans* Link & Otto, *A. mairei* (H. Lev.) C.Y. Wu & C. Chen, *A. stemonifolius* G. Don, *A. stramonifolius* (Wall.) G. Don, *Nicandra anomala* Link & Otto, *Physalis stramonifolia* Wall., *P. stramonifera* Wall., *Scopolia anomala* (Link & Otto) Airy Shaw, *S. lurida* (Link) Dunal, *S. mairei* H. Lev., *S. stramonifolia* (Wall.) Shrestha, *Scopolina stramonifolia* (Wall.) Kuntze), *Whitleya stramonifolia* (Wall.) Sweet), India, Bhutan, Nepal, and China; *Anisodus tanguticus* (Maxim.) Pascher (*Scopolia tangutica* Maxim.), Nepal, China.

2. *Atropa* L., *Sp. pl.* 1: 181 (1753). Type: *Atropa belladonna* L. Figs 3f, 4b.

Perennial herbs; glabrous or slightly pubescent. Leaves alternate, petiolate, simple and entire. Inflorescences of solitary flowers borne in the leaf axils. Flowers actinomorphic; calyx campanulate; corolla tubular-campanulate, twice as long as the calyx, greenish purple or yellow; stamens inserted near the base of the corolla tube, declinate; pollen trizonocolporate with long, distinct colpi with sunken margins and striate-rugulate ornamentation (Fig. 7c); ovary bilocular, with an annular receptacular disc. Fruit a black, juicy berry; fruiting calyx somewhat enlarged but not enclosing the berry. Seeds numerous, sublenticular. Woodland and other shady habitats, rocky screes; 0–1800 m. (Hawkes, 1972; Schönbeck-Temesy, 1972).

LIST OF SPECIES (Harborne & Khan, 1993; Pojarkova, 1955; Schönbeck-Temesy, 1972; Baytop, 1979). *Atropa acuminata* Royle ex Lindl., Asia (India, Pakistan, Afghanistan, Mongolia, Iran); *Atropa baetica* Willk., Spain and Morocco; *Atropa belladonna* L. (*Atropa caucasica* Kreyer, *A. komarovii* Blin. & Schal., *A. lutescens* Blin. & Schal., *A. pallidiflora* Schönb.-Tem., *A. paschdewiczii* Kreyer), widespread in Central Europe and Asia to Iran.

3. *Atropanthe* Pascher in *Österr. Bot. Zeitschr.* 59: 329 (1909). Type: *Atropanthe sinensis* (Hemsl.) Pascher (basonym *Scopolia sinensis* Hemsl.).

Subshrubs or perennial herbs; glabrous. Leaves alternate, petiolate, simple and entire. Inflorescences of solitary flowers borne in the leaf axils. Flowers subactinomorphic; calyx tubular-campanulate; corolla slightly zygomorphic, with one petal lobe enlarged, tubular-campanulate, twice as long as the calyx; stamens inserted near the base of the corolla tube, declinate; pollen trizonocolporate with short, distinct colpi and striate-rugulate ornamentation (Fig. 6c); ovary bilocular with an annular disc. Fruit a globose capsule, with circumscissile dehiscence; fruiting calyx inflated, abruptly inserted on the pedicel. Seeds rectangular and somewhat compressed. Forest and ditches; 1400–3000 m. (Zhang et al. 1994).

LIST OF SPECIES (Zhang et al. 1994). *Atropanthe sinensis* (Hemsl.) Pascher (*Anisodus sinensis* Hemsl.), China.

4. *Hyoscyamus* L., *Sp. pl.* 1: 179 (1753). Type: *Hyoscyamus niger* L. Figs 3b, 4c.

Annual, biennial or perennial herbs; variously pubescent. Leaves alternate, sometimes forming a rosette, petiolate and simple, variously sinuate to dentate, rarely entire. Inflorescences of solitary flowers in the leaf axils, condensed to form usually secund, scorpioid cymes. Flowers zygomorphic, sessile or shortly pedicellate; calyx tubular-campanulate or urceolate, the lobes often spine-tipped; corolla campanulate or funnelform, the lobes unequal; stamens inserted near the base of the corolla tube; pollen trizonocolporate with long, distinct colpi and weakly striate ornamentation; ovary bilocular with an indistinct disc. Fruit a globose or ovoid capsule, with circumscissile dehiscence; fruiting calyx enlarged, enclosing the fruit, the lobes spine-tipped. Seeds reniform or discoid, strongly compressed. Fields, waysides, and hedges; 0–3600 m. (Zhang et al. 1994; Hawkes, 1972; Al-Musawi, 1979).

LIST OF SPECIES (Schönbeck-Temesy, 1972; Al-Musawi, 1979; Feinbrun-Dothan, 1978). *Hyoscyamus albus* L. (*Hyoscyamus arenarius* Dunal, *H. canariensis* Ker-Gawl., *H. clusii* G. Don, *H. major* Mill., *H. minor* Mill., *H. varians* Vis.), Mediterranean to Iraq and Egypt; *Hyoscyamus aureus* L., E. Mediterranean to NW Iraq, Sinai, and Egypt; *Hyoscyamus flaccidus* Wright, Arabia; *Hyoscyamus gallagheri* A.G. Mill. & J.A. Biagi, Oman; *Hyoscyamus grandiflorus* Franch., tropical Africa; *Hyoscyamus insanus* Stocks (*Hyoscyamus angulatus* Griff., *H. nutans* Schönb.-Tem., *H. orthocarpus* Schönb.-Tem., *H. rosularis* Schönb.-Tem., *H. tenuicaulis* Schönb.-Tem.), N. Africa and the Middle East; *Hyoscyamus leptocalyx* Stapf., W. Iran; *Hyoscyamus longipedunculatus* Townsend, Iraq; *Hyoscyamus malekianus* Parsa, Iran; *Hyoscyamus muticus* L. (*Hyoscyamus betaefolius* Lam., *H. boveanus* (Dunal) Ascher & Schweinf., *H. datora* Forsk., *H. falezlez* Coss., *Scopolia boveana* Dunal, *S. datora* (Forsk.) Dunal, *S. mutica* (L.) Dunal), N. Africa and the Middle East; *Hyoscyamus niger* L. (*Hyoscyamus agrestis* Kit., *H. auriculatus* Tenore, *H. bohemicus* F.W. Schmidt, *H. lethalis* Salisb., *H. pallidus* Waldst. & Kit., *H. persicus* Boiss. & Buhse, *H. pictus* Roth, *H. sypsiensis* C. Koch, *H. verviensis* Lej.), widespread in temperate Eurasia; *Hyoscyamus pusillus* L. (*Hyoscyamus micranthus* Ledeb., *H. pungens* Griseb.), Egypt to SW and C. Asia; *Hyoscyamus reticulatus* L. (*Hyoscyamus afghanicus* Pojark., *H. arachnoideus* Pojark., *H. camerarii* Fisch. & Mey., *H. coelosyriacus* Bornmuller, *H. issa-sadiqui* Parsa, *H. kopetdaghi* Pojark., *H. kotschyanus* Pojark., *H. kurdicus* Bornmuller, *H. leucanthera* Bornm. & Gauba, *H. multicaulis* Rech. f. & Edelb., *H. pinnatifidus* Schldl., *H. pojarkovae* Schönb.-Tem., *H. purpureus* Griseb., *H. squarrosus* Griff.), Egypt to SW Asia; *Hyoscyamus senecionis* Willd. (*Hyoscyamus pinnatisectis* Boiss.), Egypt through the Middle East; *Hyoscyamus tibesticus* Maire (*Hyoscyamus cylindrocalyx* Rech. f., *H. desertorum* (Asch.) Täckh.), N. Africa in Sahara to the Arabian peninsula; *Hyoscyamus turcomanicus* Pojark., Trans-Caspian area in Iran, Uzbekistan.

5. *Mandragora* L., *Sp. pl.* 1: 180 (1753). Type: *Mandragora officinarum* L. Figs 3e, 5c, d.

Perennial herbs from enlarged taproots; variously pubescent. Leaves alternate, forming a dense basal rosette, very short petiolate or sessile, simple, entire or dentate. Inflorescences of solitary flowers

in the leaf axils. Flowers actinomorphic; calyx flared or cup-shaped, deeply lobed, the lobes long-triangular; corolla flared or cup-shaped, deeply lobed; stamens inserted in proximal part of the corolla tube; pollen cryptaperturate with symmetrical pattern of endoaperture thinnings and gammate-baculate ornamentation (Fig. 7d); ovary bilocular, with an indistinct disc. Fruit a globose or ovoid, fleshy berry, yellow-orange, greenish or white flushed with purple, usually borne beneath the leaves; fruiting calyx slightly enlarged, not enclosing the berry. Seeds reniform, very large. Grasslands, woods, hedges and waysides, stony hillsides and screes; 0–4200 m. (Zhang et al., 1994; Hawkes, 1972).

LIST OF SPECIES (Pojarkova, 1955; Schönbeck-Temesy, 1972; Jackson & Berry, 1979; Zhang et al., 1994). *Mandragora autumnalis* Bertol. (*Mandragora femina* Gersault, *M. microcarpa* Bertol., *M. officinalis* Moris., *M. officinarum* Bertol., *M. officinarum* L. pro parte). Mediterranean; *Mandragora caulescens* C.B. Clarke (*Anisodus caulescens* (C.B. Clarke) Diels, *A. mariae* Pascher, *Mairella yunnanensis* H. Lev., *M. tibetica* Grubov.), Himalayas in India, Nepal, Bhutan, and China; *Mandragora chinghaiensis* Kuang & A.M. Lu, China, restricted to pika warrens (fide M. Gilbert); *Mandragora officinarum* L. (*Atropa acaulis* L., *Mandragora acaulis* Gaertn., *M. haussknechtii* Heldr., *M. hispanica* Vierhapper, *M. mas* Gersault, *M. neglecta* G. Don, *M. officinalis* Mill., *M. praecox* Sweet, *M. vernalis* Bertol.), widespread in Eurasia; *Mandragora turcomanica* Mizg., Turkmenistan near Caspian Sea, Russia.

6. **Physochlaina** G. Don, *Gen. Hist.* 4: 470 (1837). Type: *Physochlaina physaloides* (L.) G. Don (basionym *Hyoscyamus physaloides* L.). Figs 3a, 4d.

Perennial herbs; glabrous or variously pubescent. Leaves alternate, petiolate, simple, entire to sinuate. Inflorescences axillary or terminal, branched several times. Flowers actinomorphic; calyx tubular-campanulate to tubular-urceolate; corolla campanulate or funnellform, purplish; stamens inserted midway up the corolla tube; pollen either pentacolporate, occasionally tetracolporate, with long, indistinct colpi and scabrate ornamentation or trizonocolporate with long, distinct colpi and striate-rugulate ornamentation (Fig. 6a, b); ovary bilocular, with a fleshy, annular disc. Fruit a globose or oblong capsule, with circumscissile dehiscence; fruiting calyx subcoriaceous and inflated, longer than the capsule. Seeds reniform, compressed. Grasslands and forest edges; 800–4500 m. (Zhang et al., 1994; Pojarkova, 1955).

LIST OF SPECIES (Zhang et al., 1994; Kuang & Lu, 1981; Schönbeck-Temesy, 1972; Pojarkova, 1955). *Physochlaina capitata* A.M. Lu, China; *Physochlaina infundibularis* Kuang, China; *Physochlaina macrocalyx* Pascher, China; *Physochlaina macrophylla* Bonati, China; *Physochlaina orientalis* G. Don (*Hyoscyamus orientalis* (G. Don) Bieb., *Physochlaina dubia* Pascher, *Scopolia orientalis* (G. Don) Dunal), Caucasus to Iran; *Physochlaina physaloides* (L.) G. Don (*Atropa physaloides* Georgi, *Hyoscyamus physaloides* L., *Physochlaena dahurica* Miers, *Physochlaina physaloides* (L.) Miers, *P. pseudophysaloides* Pascher, *Scopolia physaloides* (L.) Dunal), China, Mongolia, Russia (Siberia); *Physochlaina praealta* (Dcne.) Miers (*Belenia praealta* Dcne., *Hyoscyamus praealtus* (Dcne.) Walp., *Physochlaina grandiflora* Hook., *P. urceolata* Kuang & A.M. Lu, *Scopolia praealta* (Dcne.) Dunal), China, Nepal, Pakistan, and India (Kashmir); *Physochlaina semenowii* Regel, central Asia.

7. **Przewalskia** Maxim. in *Bull. Acad. Petersb.* 27: 507 (1881).

Type: *Przewalskia tangutica* Maxim.
Figs 5a, b.

Perennial herbs, from an elongate fleshy taproot; pubescent, the trichomes glandular. Leaves alternate, forming a dense basal rosette, simple, entire. Inflorescences of clusters of flowers in the leaf axils. Flowers actinomorphic; calyx tubular-campanulate; corolla tubular-funnelform, greenish yellow or violet; stamens inserted in the distal part of the corolla tube; pollen trizonocolporate with long, distinct colpi and reticulate ornamentation; ovary bilocular, with an annular disc. Fruit a globose capsule, with circumscissile dehiscence; fruiting calyx much enlarged and the tube inflated with prominent reticulate veins, completely enclosing the much smaller fruit, the lobes constricted with incurved lobes. Seeds reniform. Open habitats on the Qinghai-Tibet plateau, sand dunes, road margins and areas of frost heave; 3200–5000 m. (Zhang et al., 1994).

LIST OF SPECIES (Zhang et al. 1994). *Przewalskia tangutica* Maxim. (*Mandragora shebbearei* C. Fischer, *Przewalskia robo-rowskii* Batalin, *P. shebbearei* (C. Fischer) Grubov), China.

8. **Scopolia** Jacq., *Obs. Bot.* 1: 32 (1764). Type: *Scopolia carniolica* Jacq.
Fig. 3c.

Perennial herbs; glabrous to minutely pubescent. Leaves alternate, petiolate, simple, entire. Inflorescences of solitary flowers in the leaf axils. Flowers subactinomorphic; calyx cup-shaped with irregular lobes, one usually much longer than the rest; corolla campanulate-funnelform, greenish yellow to reddish purple; stamens inserted near the base of the corolla tube; pollen trizonocolporate with long, indistinct colpi and scabrate ornamentation (Fig. 7a); ovary bilocular, with an annular disc. Fruit a globose capsule, with circumscissile dehiscence; fruiting calyx somewhat enlarged, enclosing the fruit. Seeds subreniform. Woodlands; 500–1500 m. (Lu & Zhang, 1986; Pojarkova, 1955).

LIST OF SPECIES (Sandina, 1980; Lu & Zhang, 1986). *Scopolia carniolica* Jacq. (*Hyoscyamus scopolia* L., *Scopolia atropoides* Bercht. & Presl, *S. caucasica* Kolesn., *S. hladnikiana* Fleishm., *S. parviflora* (Dunal) Nakai, *S. trichotoma* Moench, *S. tubiflora* Kreyer, *Scopolina atropoides* Schult.), Alps, Carpathian mountains, Caucasus; *Scopolia japonica* Maxim., Japan, Korea.

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APPENDIX I

Specimens examined for pollen analysis (all BM).

- Anisodus luridus* Link – Beer et al. 9410 (Nepal).
Atropa belladonna L. – Mohamed 146 (Morocco).
Atropanthe sinensis (Hemsl.) Pascher – Wilson 2594 (China, Hupeh).
Hyoscyamus muticus L. – Hildebrandt 71 (Egypt).
Hyoscyamus niger L. – Davis 52541 (Algeria).
Hyoscyamus senecionis L. – Thesiger 189 (Afghanistan).
Mandragora caulescens C.B. Clarke – Gardner 479 (Nepal); Polunin et al. 4696 (Nepal).
Physochlaina physaloides (L.) G. Don – Heward s.n., July 1847 (India).
Physochlaina praealta (Dcne.) Miers – Stacey & Winterbottom s.n. (China, Tibet).
Przewalskia tangutica Maxim. – Richardson 56 (China, Tibet).
Scopolia carniolica Jacq. – Harris Garden, University of Reading

A revision of *Solanum* section *Pterioidea*: Solanaceae

BRN 306450

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SYNOPSIS. *Solanum* section *Pterioidea* is a small group of ten species of Neotropical primary forest herbs and vines. The group is treated in this monograph as a unit for convenience, but cladistic analysis shows that it is almost certainly not monophyletic. The ten species are therefore placed in two monophyletic species groups: the *Solanum ternatum* species group, defined by its woody vining habit and large flowers, and the *Solanum mite* species group, defined by its conical rugose fruits and ovoid-reniform seeds with distinctive testal morphology. The history of nomenclature and composition of section *Pterioidea* s.l. are discussed. Illustrations and distribution maps are provided and photographs of several of the species show characters of the flowers, fruits, and seeds.

INTRODUCTION

Although it is one of the five or six largest genera of flowering plants, little monographic work has been done in *Solanum* L. (Solanaceae) (see D'Arcy, 1991). Taxonomic research effort has been concen-

trated on groups of economic importance, such as potatoes, tomatoes, morellas, and the spiny solanums. The genus is diverse, with some 1000 or more valid species (D'Arcy, 1991), but monographs do not exist for the majority of species groups in *Solanum*. As part of an ongoing research programme into the taxonomy and phylogeny of non-spiny solanums (see Knapp, 1986a; Knapp, 1989; Knapp,

1991a) we have investigated the small, primarily rainforest species of section *Pterioidea* with the aim of determining the monophyly of the group and the species boundaries within it. The section, whose members are characterized by a scorpioid cyme inflorescence which is axillary in position, is quite heterogeneous, and has apparently no close relatives (see p.33). It is clear from our analyses that the section as treated here is not strictly monophyletic and can be divided into two groups. We have called these groups the *Solanum mite* species group and the *Solanum ternatum* species group, following the convention of Whalen (1984). The true nature of the relationships between these two monophyletic lineages will only become clear with a large scale analysis of all non-spiny solanums. Several potential sister groups have been identified; these will be treated in future monographs, and larger scale relationships tested as more monophyletic groups are identified.

TAXONOMIC AND NOMENCLATURAL HISTORY

Solanum is most species rich in the New World tropics and subtropics, and thus many of the taxa have been described relatively recently. The last comprehensive treatment of the genus was by Dunal (1852) and while 900 species were treated in the *Prodromus*, at least 4000 specific epithets exist for *Solanum* at present. By convention and for convenience *Solanum* is usually divided into two main groups, the spiny solanums (subgenus *Leptostemonum*) and the non-spiny solanums (the rest: subgenera *Solanum*, *Brevantherum*, *Bassovia*, and *Potatoe* – D'Arcy, 1972, see Table 1). Taxonomy of non-spiny solanums has long been confused, and there is considerable disagreement as to monophyly within that portion of the genus. For a detailed history of the taxonomy of *Solanum* both before and after Dunal (1852) see Knapp (1989, 1991a) and Bohs (1994). Knapp (1989) also provides a list of recent monographs of sections of *Solanum*, to which can be added a monograph of *Solanum* section *Allophyllum* (Bohs, 1990) and the genus *Cyphomandra* (Bohs, 1994; now with all epithets transferred to *Solanum*, see Bohs, 1995).

Table 1 Characters used to define the major Neotropical subgenera of *Solanum* (after D'Arcy, 1972).

<i>Solanum</i> c. 1500–2000 species	
subgenus <i>Solanum</i>	Stout anthers, simple hairs, no spines
subgenus <i>Bassovia</i>	Stout anthers, simple hairs, pinnate leaves, axillary inflorescences, pointed fruits
subgenus <i>Brevantherum</i>	Stout anthers, entire leaves, dendritic or stellate hairs
subgenus <i>Potatoe</i>	Scandent species or herbs, pinnate leaves usually with interstitial leaflets, lateral inflorescences, articulated pedicels
subgenus <i>Leptostemonum</i>	Tapering anthers, stellate hairs, almost always with prickles

History of section *Pterioidea*

The first species of section *Pterioidea* to be described was *Solanum anceps* (as *Bassovia sylvatica*), described by Aublet (1775) from what is now French Guiana. Several more species were described by Ruiz & Pavón (1799) from collections made in Peru (*S. anceps*, *S. conicum*, *S. diffusum*, *S. incurvum*, *S. mite*, *S. ternatum*). Ruiz & Pavón noted the similarity between these taxa, and commented upon it in the *Flora peruviana et chilensis* (1799). In his *Histoire*

naturelle, médicale et économique de Solanum, Dunal (1813) attempted to treat taxonomically all known species of *Solanum* in a hierarchical fashion. He divided the genus into a series of nested groups, marked by different symbols (for a discussion of these and their significance to sectional nomenclature in *Solanum* see Knapp, 1983). The group composed of the species of section *Pterioidea* was explicitly given sectional rank ('la section désignée sous le nom *Pterioidea*') by Dunal, one of the few groups of taxa to be assigned rank in his 1813 monograph. In his section *Pterioidea* Dunal (1813) grouped together species sharing the following characters: '*Foliis impari-pinnatis; foliolis integerrimis acuminatis; pedunculis axillaribus aggregatis, petiolis brevioribus*. PTERIOIDEA.' The simple-leaved species (see Morphology for a discussion of the nature of leaf division in section *Pterioidea*) were not considered related to the pinnate-leaved species by Dunal (1813), and were placed in a heterogeneous group, with species now placed in either the genus *Lycianthes* or *Solanum* section *Geminata* (sensu lato, see Knapp, 1986a). In 1816, Dunal again grouped the pinnate-leaved species of section *Pterioidea* together, adding *S. seafortianum* (now recognized as a member of section *Jasminosolanum*) to the group. He did, however, recognize the similarities of the simple-leaved taxa, and put them in a group of their own, but without rank. In his *General system of gardening and botany*, one of the best compendia of flowering plants known at the time, George Don (1838) basically followed Dunal in separating the simple and pinnate species, but he put the pinnate taxa in his subsection *Potatoe* with the potatoes and their relatives, while the simple-leaved taxa were placed in subsection *Holophylla*, a large and very heterogeneous group of species. Walpers (1844) followed Don's system, but elevated Don's subsections to the rank of section. He retained the separation of the taxa based on leaf morphology and kept them in the groups where Don had placed them. In the *Prodromus* (1852) Dunal attempted a worldwide revision of all known species of *Solanum* – the last time this has been so done. In this work he radically re-organized his system of classification, creating an explicit hierarchical structure. Here, Dunal separated pinnate and simple-leaved species of section *Pterioidea*, putting the former in the group *Polybotryon* in subsection *Dulcamara* and the latter in the group *Bassovioides* in subsection *Micranthes* (see Table 2). He described no new species of either group, but included *S. pteleifolium* Sendtn. (as *S. pteleaeifolium*, see species treatment of *S. mite*) with the pinnate taxa and a group of little-known ambiguous simple-leaved species in the group *Bassovioides* (*S. cormanthum* Vell., *S. laurinum* Dunal, *S. lacteum* Vell., see Excluded Taxa for correct identification and placement of these taxa).

Table 2 Classification of the species of section *Pterioidea* in Dunal (1852).

Sectio I. *Pachystemonum*

Subsectio III. *Dulcamara*. – Cymis terminalibus, dein lateralibus alaribus axillaribusque; corollis 5-angulato-plicatis, 5-fidis, 5-partitisve, coeruleis vel albis; baccis globosis ovatisque.

** *Polybotryon*. – Foliis impari-pinnatisectis, segmentis, integerrimis, saepius acuminatis vel simplicibus indivisis; cymis subaxillaribus, pluribus, aggregatis vel solitariis, nonnunquam radicibus oppositis; corollis 5-fidis vel 5-partitis.

Subsectio IV. *Micranthes*. – Frutices suffruticesque; foliis integris, glabris, pilosis, tomentosis vel hispidis; calyce 5-fido, 1–2 lin. diam.; corollâ duplo triplove calyce longiore; baccâ globosâ ovatâque, cerasi vel olivae parvae magnitudine.

§ 3. *Bassovioides*. – Cymis subaxillaribus intrafoliaceis aut suboppositifoliis; foliis brevioribus 2, 3, 4 aggregatis vel subsolitariis.

The first taxonomist to recognize the close relationship between simple and pinnate-leaved taxa of what is now section *Pteroidea* was Georg Bitter (1912). In describing section *Polybotryon*, he clearly separated the taxa included in Dunal's 'Artengruppe *Polybotryon*' into those with axillary inflorescences and those with leaf-opposed or lateral inflorescences. Bitter explicitly grouped the pinnate and simple-leaved taxa together in his new section *Polybotryon*, stating that the axillary inflorescence was the grouping character. In the section he included *S. conicum*, *S. mite*, *S. trizygum*, *S. fraxinellum*, *S. quinquefoliolatum*, *S. chamaepolybotryon*, *S. diffusum*, *S. ternatum*, *S. pteleifolium*, *S. conjungens*, *S. hederiradiculum*, *S. angustialatum*, and *S. theobromophyllum*, most of which he described in the same paper. In 1921, Bitter united all of Dunal's (1852) various ambiguous grades (excluding the species he recognized as the segregate genus *Lycianthes*) possessing axillary inflorescences and elevated the group to subgeneric rank, as subgenus *Bassovia* (Aubl.) Bitter. He based its elevation in rank solely on the peculiar axillary inflorescence possessed by all species in the group.

Subsequent authors have for the most part followed Bitter in placing these species in a group of subgeneric rank diagnosed by possession of an axillary inflorescence (Seithe, 1962; Danert, 1967, 1970; Gilli, 1970; D'Arcy, 1972; D'Arcy, 1991). No attempts have been made to determine relationships with other groups of solanums. D'Arcy (1991) however, did include section *Pteroidea* as part of subgenus *Solanum* in his review of taxonomy of the Solanaceae. Child (1991) is the only author to place the section in subgenus *Potatoe* (G. Don) D'Arcy, but he did not explain clearly his reasons for doing so. From his introduction, it seems to be largely due to the herbaceous habit of many members of section *Pteroidea*, and perhaps due to their pinnate leaves. Recent cpDNA analyses of the Solanaceae (Olmstead & Palmer, 1991; Spooner et al., 1993) have not included members of section *Pteroidea*, thus it is still largely perceived as an isolated and morphologically very distinct group.

MORPHOLOGY AND NATURAL HISTORY

Species in section *Pteroidea* are all forest understory plants. Members of the group range from being herbs or semi-woody shrubs to 3 m to woody climbers up to 10 m in length. They occur in a wide range of elevations, but always in the deep shade of the forest understory (see Fig. 1a, b). Occasionally some species (e.g. *S. mite*) are found growing along roadsides or streams. *Solanum anceps* occurs at low elevations (at or near sea level) in the Amazon basin and *S. incurvum* to 3000 m in the Peruvian and Ecuadorian Andes. Most species are relatively rare in the habitats in which they occur, but some species (e.g. *S. chamaepolybotryon*) form what appear to be clonal groups.

Stems

Members of section *Pteroidea* are usually slender, single-stemmed shrubs (Fig. 2a) or herbs or are variously climbing. *Solanum mite* has occasionally been described on labels as a branching shrub, but this is not the common growth form for any species in the section. Most of the species will root along the stem; plants of *S. conicum* are apparently weak-stemmed, often falling over and rooting in that fashion. Other species in the group (e.g. *S. uleanum*) are trunk climbers, adhering to the substrate with small, adventitious roots (see Fig. 2b). The two species that we segregate as the *S. ternatum* species group (*S. ternatum*, *S. incurvum*) are quite woody climbers with lower stems up to 3 cm in diameter in some plants. Amongst the species of the *S. mite* species group, woodiness

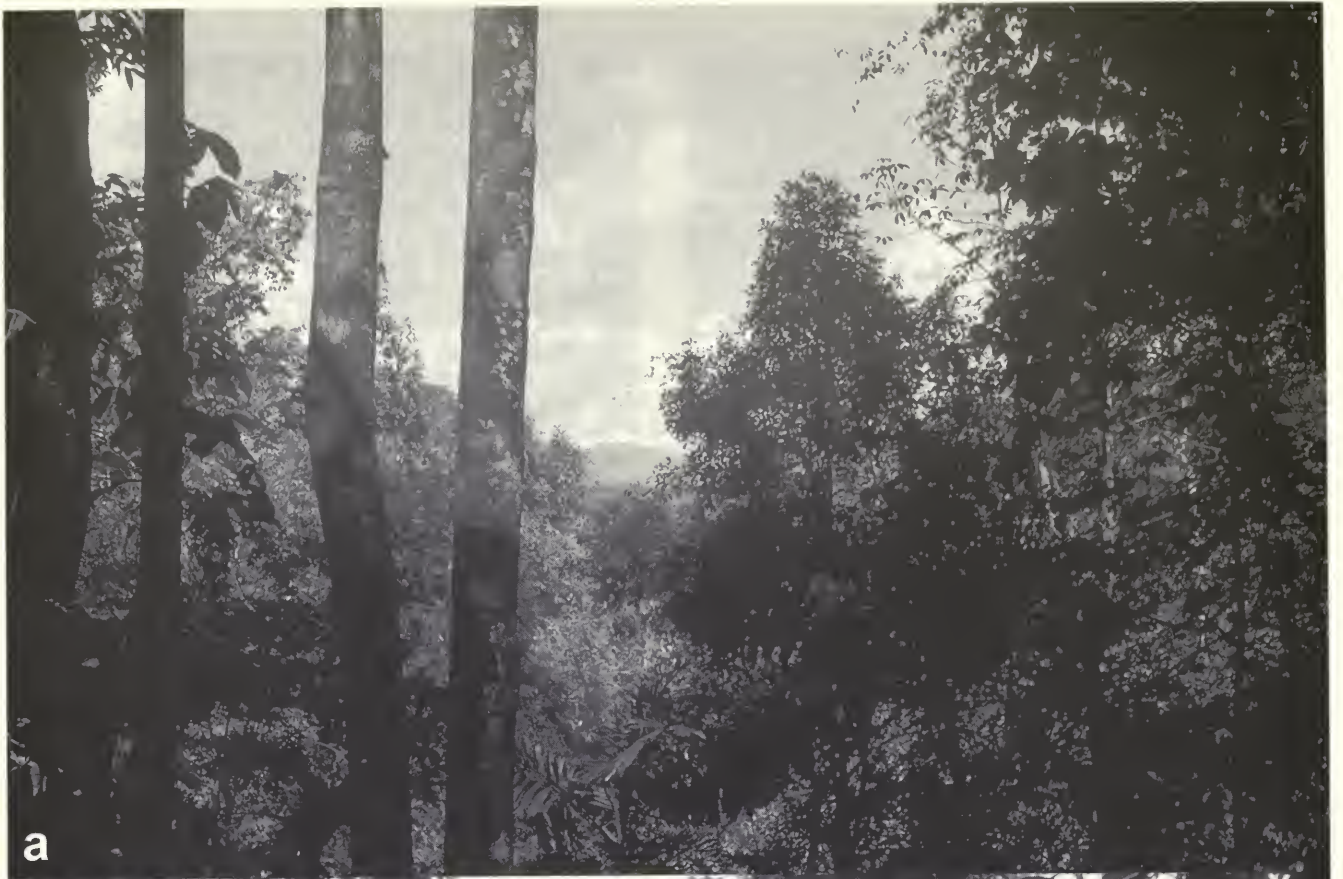
is only very weakly developed in *S. mite*. Plants range from quite small (a few centimetres in *S. conicum* and *S. chamaepolybotryon*) to more than a metre in height (e.g. *S. savanillense*, *S. mite*) to several metres long for some of the vining taxa.

In all *Solanum* species the young non-reproductive stem is monopodial with the leaves arranged in a 2/5 phyllotaxic spiral. When a stem begins its reproductive phase, sympodial growth begins (Danert, 1958; Bell & Dines, 1995). Each inflorescence is terminal and shoot continuation is initiated in the axil of the leaf subtending the inflorescence. A single lateral continuation of the shoot produces a monochasial growth pattern, a double one a dichasial pattern. In some species these two patterns occur in a single plant (Bell & Dines, 1995). Bell & Dines (1995) arrange species within the family along a continuum from monochasial to dichasial branching. The determining factor for pattern expression is dormancy of axillary buds in any given sympodial unit. Sympodial units in *Solanum* consist of leaves along each shoot terminating in an inflorescence. In the genus these units can vary from plurifoliate (members of section *Brevantherum*, section *Holophylla*, the *S. nitidum* species group, see Knapp, 1989) to unifoliate (section *Geminata*, see Knapp, 1986a). All members of section *Pteroidea* have what appear to be unifoliate sympodial units (see Fig. 3 for our working hypothesis of stem structure in the group). Danert (1967) was unsure whether the vegetative axis in section *Pteroidea* was monopodial or monochasial (as in the rest of *Solanum*), and urged further ontogenetic studies. Whether or not the unifoliate sympodia of section *Pteroidea* and those found elsewhere in the genus are homologous can really only be determined by such detailed ontogenetic studies.

Leaves

The leaves of members of section *Pteroidea* are generally petiolate (the petiole can be very short or absent in some species, most notably *Solanum angustialatum*), with pinnate, brochiodromous venation, and entire margins. Leaf shape has been used widely in section *Pteroidea* for determining relationships (see p. 32). The compound leaves have usually been described as imparipinnate, but are more strictly pinnatifid or deeply pinnately lobed, as thin wings of leaf tissue remain along the midrib or rachis. For the purposes of this treatment, these leaves will be referred to as pinnate, and the divisions will be described as leaflets. The petiole-like constriction at the base of the leaflets will be described as a petiolule. There are seven pinnate and three simple-leaved species in this section. The simple-leaved species, *S. incurvum*, *S. angustialatum*, and *S. anceps*, have entire margins; and in *S. anceps* leaf size, and to some extent leaf shape, is highly variable. Pinnate leaves are generally ternate to 9-jugate, with the terminal leaflet larger, and usually of a somewhat different shape than the paired leaflets. Leaflet numbers vary considerably within and between taxa, and exact numbers of leaflet pairs are generally not good distinguishing characteristics of species, although general trends to more or fewer leaflet pairs are good characters. Leaflet pairs are often not perfectly opposite and are occasionally markedly oblique at the base (e.g. *S. conicum*).

The leaves of members of section *Pteroidea* are often very dark green, a common trait in understory plants. Several species (e.g. *Solanum anceps*, *S. savanillense*, *S. uleanum*) develop deep purple leaf undersides in certain conditions. Populations are often highly polymorphic for this character, differing in plants growing side by side. Whether this is due to genetics or environment is unclear. Leaf texture is membranous, as is usually the case in forest understory plants, but the leaves of some species (e.g. *S. chamaepolybotryon*, *S. ternatum*) are quite rubbery in texture, often drying quite thick on



a



b

Fig. 1 a) Lowland forest habitat of *S. anceps*, *S. mite*, *S. conicum*, *S. uleanum*: Río Palcazu valley, Pasco, Peru, b) Cloud forest habitat of *S. trizygum*: Cerro Pando, Chiriquí, Panama.



Fig. 2 a) Herbaceous shrub habit of *S. conicum* (Knapp & Mallet 6456, Cusco, Peru), b) Climbing habit of *S. ulleanum* (Knapp & Mallet 6524, San Martin, Peru).



Fig. 3 Sympodial structure in *Solanum* section *Pterioidea* (modified from Danert, 1967).

herbarium sheets. *Solanum uleanum* has very thin and delicate leaves, particularly the juvenile plants.

Plants in the family Solanaceae are widely known for their toxic qualities derived from a diverse array of alkaloids, steroids, and phenolic glycosides (see Brown, 1987 for a review). Herbivorous insects found on the leaves of these plants are often restricted to the family, and many host-specific relationships have evolved. Among the most specialized herbivores on leaves of Solanaceae are the caterpillars of ithomiine butterflies (Nymphalidae: Ithomiinae). The adults of these butterflies are aposematic (Brown, 1987) and have evolved a wide array of colour patterns along the eastern slopes of the Andes. Host specificity of ithomiine larvae is common at species level in *Solanum* (Drummond & Brown, 1987). Very few host

Table 3 Ithomiine larval records from members of *Solanum* section *Pterioidea*.

Butterfly	Host plant	Country	Reference
<i>Oleria vicina</i> (Salvin)	<i>S. trizygum</i>	Costa Rica	Drummond & Brown, 1989
<i>Oleria makrena</i> (Hewitson)	<i>S. trizygum</i>	Venezuela	Drummond & Brown, 1989
<i>Oleria agarista</i> (Felder)	<i>Solanum</i> sp. section <i>Pterioidea</i>	Ecuador	Drummond & Brown, 1989
<i>Oleria janarilla</i> (Hewitson)	<i>S. anceps</i>	Peru	Drummond & Brown, 1989 (based on S.K. record)
<i>Oleria agarista agarista</i> (Felder)	<i>S. mite</i>	Ecuador	Beccaloni, 1995
<i>Oleria agarista agarista</i> (Felder)	<i>S. anceps</i>	Ecuador	Beccaloni, 1995
<i>Oleria</i> sp.	<i>S. anceps</i>	Ecuador	S.K. pers. obs.

records exist for members of section *Pterioidea*, perhaps due to their understory habitat, or to their small size. The only larvae reared (see Table 3) from members of section *Pterioidea* are species of *Oleria*, a diverse group along the eastern Andean slope. Larvae of *Oleria* feed on a wide variety of other solanums (and on the genus *Lycianthes*) so they are probably not specific to members of the section. Their oviposition behaviour is unusual in that most host-specific lepidoptera oviposit directly on the host plant itself. This behaviour may account for the paucity of records. The senior author has observed *Oleria* females (in Ecuador) testing plants of *S. anceps*, then ovipositing on a stick or another non-solanaceous plant some metres away. This may be a form of parasitoid avoidance behaviour, but detailed ecological field studies need to be carried out.

Inflorescences

The inflorescence of members of section *Pterioidea* is a scorpioid cyme with the flowers arranged in two rows along the axis. This inflorescence type is common to most species of *Solanum* and has been variously misinterpreted as a raceme by earlier authors (Dunal, 1852). The position of the inflorescence is probably morphologically terminal (see p. 33), but due to shoot and inflorescence rachis concaulescence and subsequent shortening of internodes (Danert, 1967) it is apparently axillary (Fig. 3). The growth of renewal shoots from axillary buds below the inflorescence causes axillary inflorescences in *Cyphomandra* (Bohs, 1994), but the situation in section *Pterioidea* needs detailed anatomical study to ascertain whether the axillary inflorescence is homologous in these two groups. In several species of section *Pterioidea* multiple cymes appear to emerge from each leaf axil. This has been attributed to insertion of a subsidiary shoot on the pleiochasial inflorescence some distance from other subsidiary inflorescences (Child, 1979), but no detailed anatomical work has been done to verify this. The nature of the inflorescence in section *Pterioidea* has been largely responsible for its problematic phylogenetic position and its separation as an isolated subgenus by previous authors (see above).

Inflorescence length is taken from the base to apex, including both the peduncle (length from base to first pedicel) and the rachis (the axis bearing pedicels). Generally in section *Pterioidea* the flowers occur only in the distal half to one third of the usually unbranched inflorescence. The pedicels are articulated at the base, never leaving pegs or prominent scars (see Anderson, 1977; Hawkes, 1990; Bohs, 1994). In any given inflorescence only a few, usually up to three, flowers will be open at a time, but the number of flowers per inflorescence can be determined by counting the number of pedicel scars or remnants. Pubescence of the inflorescence generally parallels that of the rest of the plant and hair types in the inflorescence do not differ from those found on leaves and stems.

Trichomes

Trichomes have traditionally provided many useful characters in *Solanum* taxonomy (Seithe, 1962; Roe, 1971; Seithe, 1979; Edmonds, 1982; Seithe & Anderson, 1982; Whalen, 1984; Knapp, 1991a). In section *Pterioidea*, however, the trichomes of all species are simple, uni- or multicellular, and uniseriate. Thus they have not been particularly useful taxonomic characters in the group. Both *S. anceps* and *S. mite* have variable degrees of pubescence, from densely pubescent to completely glabrous. When analysed as separate taxa during cladistic analysis, however, the pubescent and glabrous plants always are grouped as sister taxa, suggesting that pubescence is polymorphic, as in other groups of *Solanum* (Knapp, 1989). Whether degree of pubescence is developmental or genetic is not known in section *Pterioidea*, but in some groups of spiny solanums

(see Whalen et al., 1981; pers. obs. in Ecuador by Leo Roth of *S. marginatum*) lack of prickles is a single gene trait. The juvenile foliage and young leaves and shoots of most of the variably pubescent taxa are much more densely pubescent than mature leaves. *Solanum ternatum* has densely pubescent juvenile foliage (see Fig. 11, Knapp & Mallet 6626) but mature specimens are nearly always glabrate suggesting a developmental aspect to pubescence density. Plants described as *S. dendrophilum* (here treated as a synonym of *S. ternatum*) have dense pubescence more reminiscent of juvenile leaves than other mature individuals of *S. ternatum*.

Flowers

All species have actinomorphic, pentamerous flowers. The calyx is synsepalous and the corolla is sympetalous, although the floral tube is usually very short. The calyx lobes are usually much smaller than the corolla lobes and vary from broadly deltate to almost subulate in some collections of *Solanum anceps*. Pubescence of floral parts parallels that of the rest of the plant, but corolla lobes are generally glabrous except along the tips and margins. There are basically two types of corollas in section *Pterioidea*. In the *S. ternatum* species group the corolla is quite large (12–20 mm in diameter) and fleshy with the apices of the lobes usually planar at anthesis and somewhat cucullate (Fig. 4a). In the *S. mite* species group the corolla is much smaller, usually 5–10 mm (occasionally to 13 mm in *S. conicum*), with more membranous lobes that are usually strongly reflexed at anthesis (see Figs 4, 5). The corolla in both groups can be either white or pale pinkish purple, but many more collections record pigmented flowers in the *S. ternatum* species group than in the *S. mite* species group. All species have five yellow stamens of equal length inserted at the base of the corolla. The filament bases occasionally form a minute tube, but we are unconvinced of its value as a taxonomic character as emphasized by previous authors (Barboza & Hunziker, 1991). Considerable variation exists as to length or even presence of the tube, and its size is variable enough within species to not warrant its use as a taxonomic character. Anthers in members of the *S. mite* species group are shorter and stouter in relation to the corolla lobes than those of the *S. ternatum* species group. Anthers are poricidal at the tips (as in all solanums, e.g. Barboza & Hunziker, 1991) and the pore lengthens to a slit with age (see Barboza & Hunziker, 1991; Endress, 1996). Flowers of *Solanum* species are usually 'buzz-pollinated' by bees (vibratile pollination) (Buchmann, 1983; Knapp 1986a, b; Bohs, 1994). One of us (S.K.) has seen meliponiine bees (probably the genus *Melipona*) visiting the flowers of *S. uleanum* in San Martín, Peru, but flower visitors to other species have not been observed or recorded in the literature. The conical ovary is bilocular with axile placentation and there are from few (*S. savanillense*) to many ovules (*S. ternatum*). The style is straight, glabrous, papillose to densely pubescent, and usually is exerted from the anther cone. In some species however (*S. conicum*, *S. mite*, *S. anceps*) short-styled flowers do occur in most inflorescences (see Fig. 4). Whether this is indicative of a derived andromonoecious breeding system (Whalen & Costich, 1986; Knapp et al., in press) is not known. The stigma on long-styled flowers is generally small and capitate, and in live plants often bright green. Stigmas of short-styled flowers are poorly developed, as is common in other species of *Solanum* (see Whalen & Costich, 1986). Pollen grains of members of section *Pterioidea* are tricolporate with a granular exine as are all other members of the genus *Solanum* (Anderson, 1977; Punt & Monna-Brands, 1980; Bohs, 1994).

Fruits

Fruits of members of section *Pterioidea* are unusual in *Solanum*.

Fruits in *Solanum* are generally smooth globose berries, but in section *Pterioidea* they are globose to pointed apically and smooth to markedly rugose or warty (see Fig. 5). A few other isolated species of *Solanum* have variously conic berries (*S. capsiciforme* (Domin) G.T.S. Baylis, *S. nigricans* M. Martens & Galeotti, *S. aligerum* Schldl., members of section *Petota* series *Conicibaccata* Bitter, and some members of section *Cyphomandra*), but none of them has the markedly rugose surface found in the berries of section *Pterioidea*. Pointed berries in section *Pterioidea* are of two kinds: conic, where the apex is full of seeds, and apiculate, where the apex is empty of seeds and is prolonged into an occasionally elongate beak. *Solanum trizygum*, *S. chamaepolybotryon*, *S. savanillense*, and *S. conicum* all have conic fruits. *Solanum uleanum*, this group's closest relative, has a round fruit with a truncate apex empty of seeds that is conspicuously membranous and flattened in dried specimens. In the other species, the fruits are basically globose to ovoid, and often apiculate, varying from slightly apiculate in immature berries of *S. mite* to long-pointed in *S. anceps*. In *S. anceps*, variants in fruit shape are geographically coherent, suggesting that there may be discrete morphological clusters within the species as currently delimited. All fruits within section *Pterioidea* are green, and held erect in most species. An exception to this is *S. mite*, where fruits are nodding at maturity. Fruits and seeds provide many of the best characters for distinguishing species in this group. The identification of non-fruited specimens of some taxa is difficult, and collectors are urged to record fruit characteristics in field notes.

Nothing is known about the fruit or seed dispersal in *Solanum* section *Pterioidea*. All species produce green fruits that remain green at maturity, although mature fruits are quite soft and juicy. *Solanum trizygum* fruits (observed by S.K. in Monteverde, Costa Rica) apparently fall to the forest floor rather than being taken by birds or bats as is so common in other *Solanum* species. It is possible that they are eaten and thus dispersed by small ground-dwelling rodents. Fruits of the herbaceous species may be too close to the ground to be taken by bats, but those of the climbing species may be dispersed by bats. Mature fruits of *S. trizygum* smell strongly of wintergreen, but this has not been observed or noted by collectors for any other species in the section.

Seeds

The seeds of members of section *Pterioidea* are typical for *Solanum* and essentially reniform in outline. They differ however from the more typical solanum seed in being plump and somewhat ellipsoid (ovoid-reniform) rather than flattened. As in most of the studied species of *Solanum* the lateral epidermal cell walls are thickened and lignified (Souèges, 1907; Lester & Durrands, 1984; Edmonds, 1983; Bohs, 1994). Seed colour is not uniform in section *Pterioidea*. Seeds of the species in the *S. mite* species group tend towards greenish brown, whereas the *S. ternatum* species group has reddish to orange-brown seeds. Seed colours have been coded as they appear in dried specimens, but in the case of the three or four taxa that have only one specimen with mature seed, this should be treated with some caution. Seed colour is an inconsistent character in the phylogenetic analysis (see p. 43) and is occasionally dependent on whether or not the specimen has been air-dried, dried over very hot driers or preserved in alcohol before drying.

The fine structure of seeds has been useful for resolving the relationships among species where morphological characters exhibit complex patterns of variation. In Solanaceae, lateral cell wall structure can be seen after enzymatic digestion of the outer cell wall (Lester & Durrands, 1984). In order to examine cell wall structures, seeds were collected from herbarium specimens (BM, F, GH, MO,

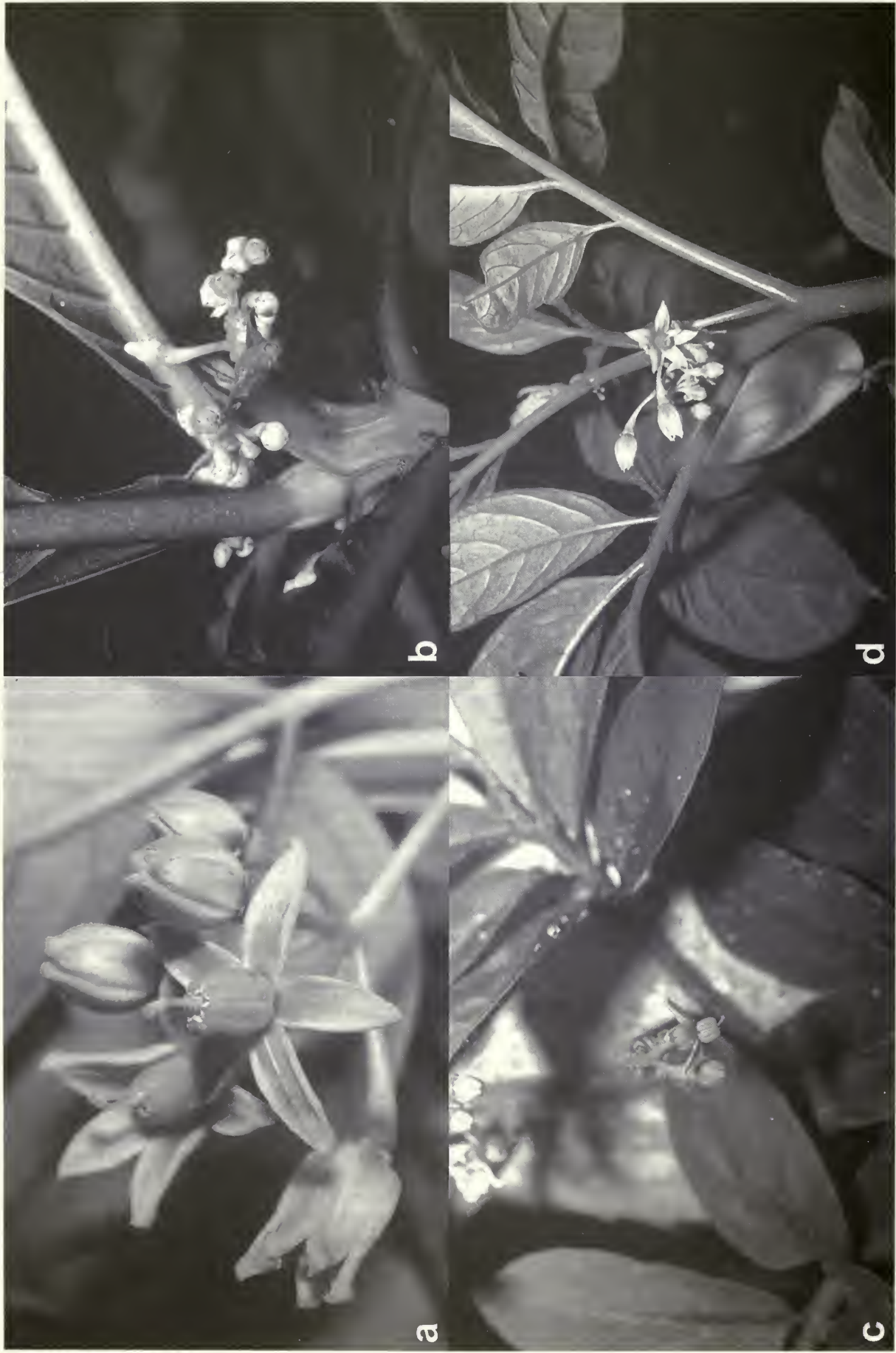


Fig. 4 a) *S. iernatum* (Knapp & Mallet 6626, Pasco, Peru), b) *S. angustialatum* (Knapp & Mallet 8567, San Martín, Peru), c) *S. uleanum* (Knapp & Mallet 6524, San Martín, Peru), d) *S. savanillense* (Knapp et al. 9045, Loja, Ecuador).



Fig. 5 a) *S. mite* (Knapp 8012, San Martín, Peru), b) *S. savanillense* (Knapp et al. 9044, Loja, Ecuador), c) *S. anceps* (Knapp & Mallet 6396, Cuzco, Peru), d) *S. angustialatum* (Knapp & Mallet 8567, San Martín, Peru).

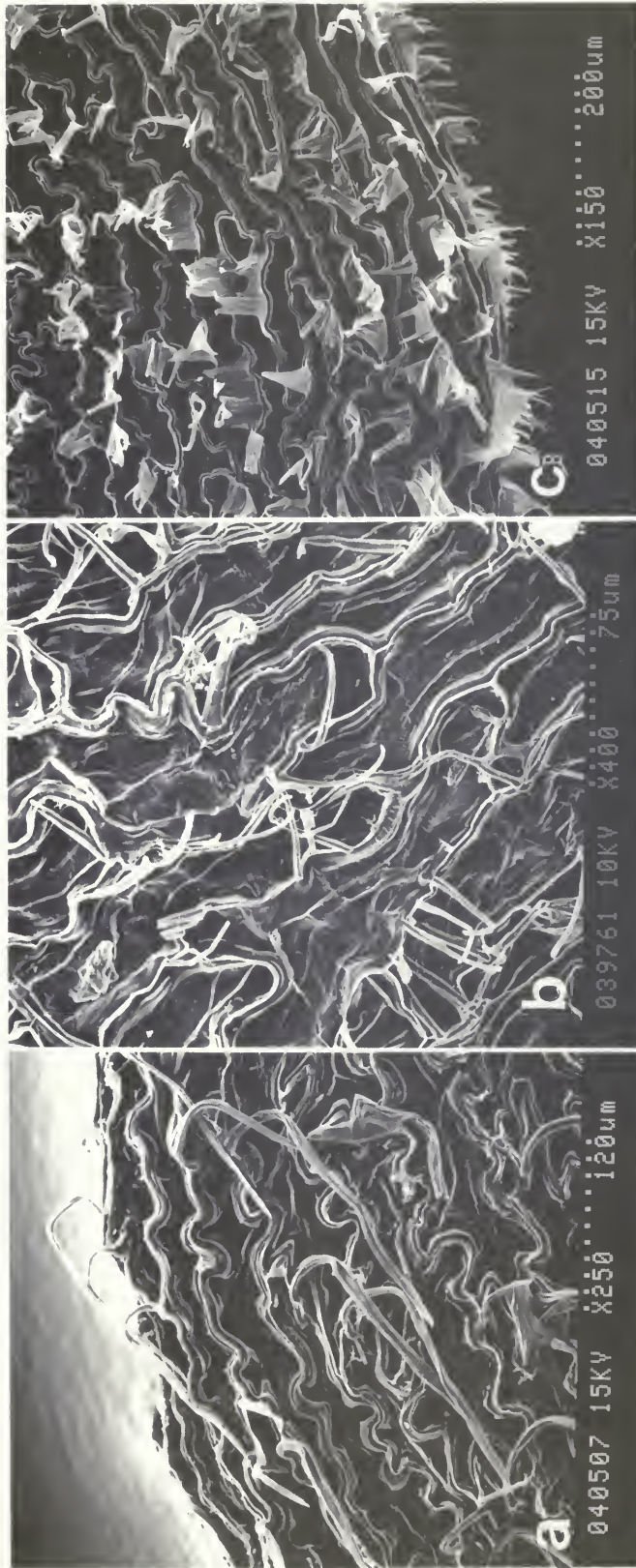


Fig. 6 a, b) Digested testa of *S. incurvum* (Gentry et al. 30871, MO), c) Digested testa of *S. ternatum* (Solomon 8791, MO).



Fig. 7 a) Digested testa of *S. savanillense* (Knapp et al. 9044, QCNE), b) Digested testa of *S. conicum* (Plowman & Davis 4806, GH), c) Digested testa of *S. conicum*, close-up (Knapp & Mallet 6452, F), d) Digested testa of *S. anceps* (Franco et al. 1876, MO).

NY) and washed in a 20% v/v solution of sodium hypochlorite. They were then incubated in a 1% w/v solution of Driselase (SIGMA) in Sorensen's buffer at pH 5.5 for 24 hrs at 30°C. Prepared seeds were washed in distilled water, air dried, and mounted on aluminium stubs using epoxy resin. These were then coated in a Gold-Palladium mixture, and photographed using a Hitachi S-2500 scanning electron microscope.

The most striking feature of the seed structures revealed by enzymatic digestion is the absence in eight of the ten taxa of projections from the cell wall thickenings (Fig. 7). Of the few species of *Solanum* that have been treated, to our knowledge, in this way, none have been found within the genus that have the combination of thickened walls without projections (see e.g. Edmonds, 1983; Knapp, 1991a). Two species have projections from the thickened walls, *S. incurvum* (hair-like, Fig. 6a) and *S. ternatum* (flap-like, Fig. 6b), both species with larger flowers. There also appears to be variation among the species in cell size, though this would have to be confirmed using additional samples. In *S. anceps*, *S. mite*, and *S. trizygum* (the only species for which samples were available from more than one specimen) cell size, shape, and structure is consistent within a species and over a wide geographic range. The other striking character of the seed coat is the highly convoluted cell shape in most taxa (Fig. 7). This may be unusual even within the family, where most specimens analysed have cells that have a more or less regular shape, even where the cell walls are sinuous, e.g. *S. ternatum* (Fig. 6c). Seed coat characters shown in the SEM study are congruent with other seed and fruit characters, and provide many of the supporting characters for the two species group clades revealed by the cladistic analysis (see p. 43). It cannot be said with certainty, however, whether these are plesiomorphic or a synapomorphic characters without a more comprehensive investigation of this character throughout the genus.

CLADISTICS

Few explicit morphologically based cladistic treatments for groups of *Solanum* exist. Increased interest in the use of molecular characters has meant an increase in the use of parsimony analyses, but to date only a few groups of solanums have been studied (Knapp, 1989, 1991b; Spooner et al., 1993). In part the difficulty in attempting character analyses in *Solanum* lies in its extreme diversity and in the choice of appropriate outgroups. Choosing a range of outgroups (Watrous & Wheeler, 1981) has been thought to increase the likelihood of obtaining an accurately rooted tree. Recent work, however (Nixon & Carpenter, 1993), has shown that multiple outgroups perform no better at 'polarizing' ingroup nodes, but that multiple outgroups might improve inference.

Character coding and tree construction

Most of the characters used in the analysis are binary, and were polarized with reference to the outgroup, the *S. nudum* species group (see below). Most characters are self-explanatory but details on the variation and distribution of morphological characteristics in the species of section *Pterioidea* can be found in the section on morphology. Table 4 lists the characters used and their states and the data matrix is presented in Table 5.

The cladistic analyses were undertaken using the computer programme HENNIG86 (Farris, 1988) using the *ie** option (implicit enumeration) with all characters unordered. The ensemble consistency index (CI) is a measure of consistency in the entire data set with respect to the fit of characters to the tree. When the fit of a character

Table 4 Character set used in the HENNIG86 analysis of *Solanum* section *Pterioidea*.

0.	Corolla diameter: >10 mm = 0; 5–10 mm = 1; <5 mm = 2
1.	Corolla texture: papery = 0; fleshy = 1
2.	Number of flowers per inflorescence: few (<40) = 0; many (>40) = 1
3.	Bud shape: globose = 1; elliptic = 0
4.	Corolla in bud: exserted = 0; +/- included = 1
5.	Calyx lobe shape: deltate = 0; quadrate = 1
6.	Apex of calyx lobes: rounded = 0; apiculate = 1
7.	Corolla tube: long (the corolla divided only 1/2–3/4 of the way to the base) = 0; short (divided almost to base) = 1
8.	Corolla lobes at anthesis: planar or nearly so = 0; strongly reflexed = 1
9.	Seed shape: flattened-reniform = 0; ovoid-reniform = 1
10.	Seed number per berry: many (>60) = 0; few (<60) = 1
11.	Seed colour: brown = 0; reddish = 1; green to green-brown = 2
12.	Projections from testal cell walls: present = 0; absent = 1
13.	Projections from testal cell walls: hair-like = 0; flap-like = 1; absent = 2
14.	Testal cell shape: regular = 0; convoluted = 1
15.	Cell wall sinuosity: 1.6–2 mm = 0; 2–3 mm = 1; 3–4 mm = 2
16.	Fruit shape: round = 1; conic = 0
17.	Fruit apex: rounded = 0; elongate = 1
18.	Fruit texture: smooth = 0; rugose = 1
19.	Mature fruit position: nodding = 0; erect = 1
20.	Leaf shape: simple = 0; deeply divided (pinnate, pinnatifid or ternate) = 1
21.	Leaf texture: fleshy = 0; membranous = 1
22.	Leaf petioles: not winged = 0; winged = 1
23.	Plant habit: erect = 0; climbing = 1
24.	Pedicle scars: flush with rachis surface = 0; raised = 1

Table 5 Data matrix used in HENNIG86 analysis of *Solanum* section *Pterioidea*.

	11111	11111	22222
	01234	56789	01234 56789 01234
<i>nudum</i>	10010	00001	20000 11000 01101
<i>ternatum</i>	01000	11000	00010 01001 10010
<i>incurvum</i>	00000	00000	01000 11010 01011
<i>anceps</i>	11010	00111	12121 11110 01001
<i>angustialatum</i>	21111	00011	12121 11110 01101
<i>chamaepolybotryon</i>	10010	00111	1??11 110?1 10101
<i>conicum</i>	20000	01111	10121 10011 11011
<i>mite</i>	11110	00111	10121 11001 11101
<i>savanillense</i>	20000	01101	12121 00011 11101
<i>trizygum</i>	10010	00111	12121 10011 11001
<i>uleanum</i>	10100	11101	10121 01111 11111

is perfect (with no parallelisms or reversals) then the consistency index is 1. The ensemble retention index (RI) is the fraction of apparent synapomorphy in all characters retained as synapomorphies on the tree (Farris, 1989). The *Solanum nudum* species group (section *Geminata*) was selected as the outgroup as its species are of somewhat generalized morphology and are thought to be basal among non-spiny solanums (Bohs, pers. comm.; Knapp, 1989, 1991b). *Cyphomandra* was initially also used, but produced very low resolution in the tree, especially with unordered characters. This reflects the difficulty in classifying *Cyphomandra* and perhaps its problematic position in the genus *Solanum* (Bohs, 1994; also see below).

The analysis produced three most parsimonious trees of length = 55 steps, CI = 0.52 and RI = 0.52, one of which has exactly the same topology as the strict consensus tree (Fig. 8). The other two tree topologies differed in the placement of *Solanum mite* relative to the rest of the *mite* clade: in the first *S. mite* was basal to the clade (*mite* + [*chamaepolybotryon* + the rest]), while in the second *S. mite* and

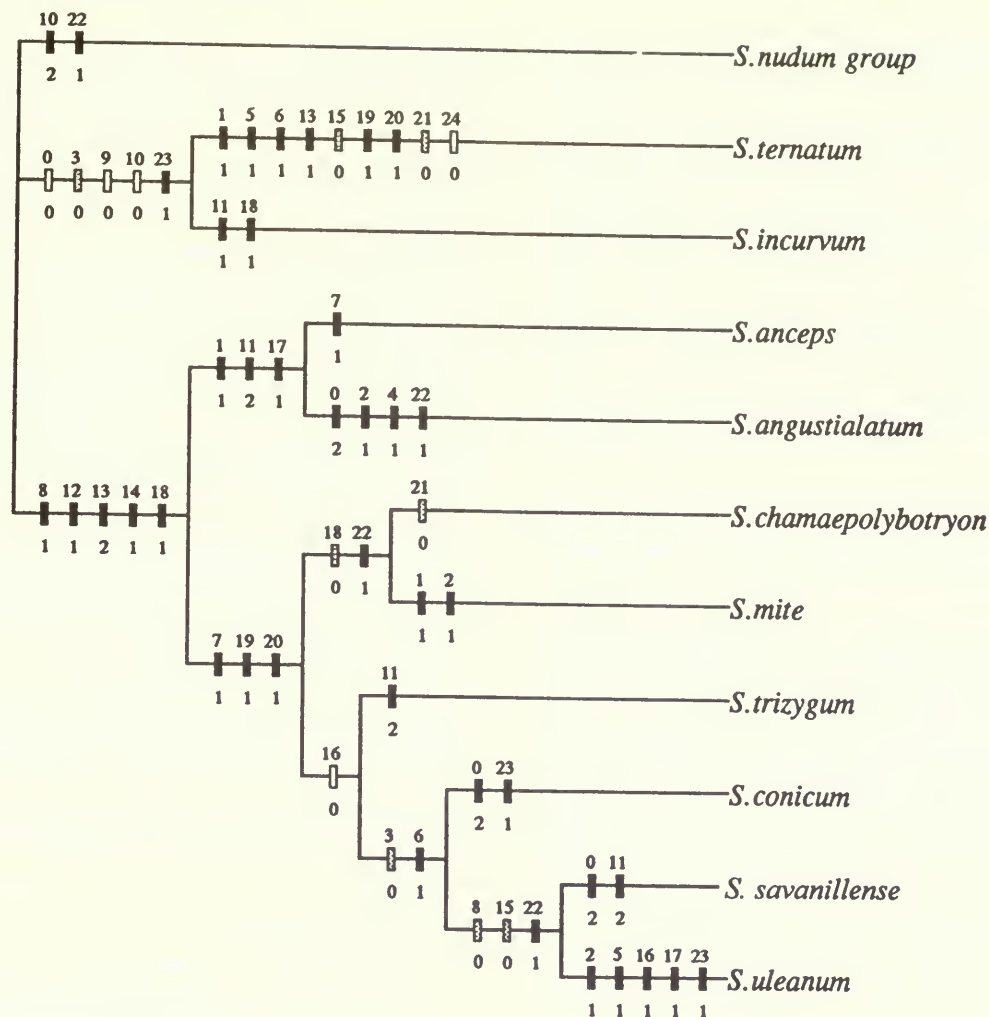


Fig. 8 Cladogram of *Solanum* section *Pterioidea*. L = 55, CI = 0.52, RI = 0.52. For characters marked on the branches of the cladogram: unshaded marks indicate synapomorphies, stippled marks indicate reversals and parallelisms (homoplasy), and solid marks non-homoplastic synapomorphies.

S. chamaepolybotryon were sister to the rest of the clade ([*mite* + *chamaepolybotryon*] + [the rest]). Analysis of the changes in each character suggest strongly that these tree topologies are largely defined by the suite of seed characters (see Fig. 8), with the exception of seed colour. These characters separate the *ternatum-incurvum* clade, whose members have small 'hairy' seeds and many seeded fruits, from the *S. mite* species group, whose members have ovoid-reniform seeds without projections and fewer seeds per fruit. This shows clearly that pinnate leaves are a derived character of the group, and that it has arisen twice, once in the *S. mite* species group, and once in *S. ternatum*. The simple-leaved taxa do not form a separate clade. These trees provide clear support for the treatment of section *Pterioidea* as two distinct monophyletic species groups (see Table 6), and we suggest that in any treatments of the genus *Solanum* at a group level, these clades should be treated as separate monophyletic groups. Section *Pterioidea* as a whole is clearly not a monophyletic group (see p. 32) and although treated as a unit for the purposes of this monograph, should not be lumped in further cladistic analyses. It may be that other taxa, if included in the analysis, would be placed as sister groups to either of these clades – a possibility hinted at by the very low resolution of the tree when *S. diploconos* (Mart.) Bohs (as *Cyphomandra*) was used as an outgroup, and confirmed by the fact that when added to the matrix presented here, it was the sister taxon to *S. ternatum*, with *S. incurvum* basal to the clade.

Table 6 Classification of *Solanum* section *Pterioidea*.

<i>Solanum ternatum</i> species group
<i>S. ternatum</i> Ruiz & Pav.
<i>S. incurvum</i> Ruiz & Pav.
<i>Solanum mite</i> species group
<i>Solanum anceps</i> clade
<i>S. anceps</i> Ruiz & Pav.
<i>S. angustialatum</i> Bitter
<i>Solanum mite</i> clade
<i>S. mite</i> Ruiz & Pav.
<i>S. chamaepolybotryon</i> Bitter
<i>S. trizygum</i> Bitter
<i>S. conicum</i> Ruiz & Pav.
<i>S. savanillense</i> Bitter
<i>S. uleanum</i> Bitter

Classification

We prefer not to assign ranks or formal names to the groups found in these analyses until further cladistic studies are done more widely in the genus *Solanum*. The monophyletic clades identified here, however, have been given informal species group names (following the convention of Whalen, 1984) and their classification is summarized in Table 6. Groups of equal 'rank' are indented equally and the sequencing convention (Nelson, 1974; Forey, 1992) has been used.

TAXONOMIC TREATMENT

Solanum section **Pteroidea** Dunal, *Hist. nat. Solanum*: 43 (1813).

Lectotype species: *Solanum mite* Ruiz & Pav. (D'Arcy, 1972).

Bassovia Aubl., *Hist. pl. Guiane* 1: 217, t. 5 (1775). Lectotype species: *Solanum sylvaticum* (Aubl.) Bitter [basionym *Bassovia sylvatica* Aubl.] (= *Solanum anceps* Ruiz & Pav.) (D'Arcy, 1972).

Solanum grad. ambig. *Polybotryon* Dunal in DC., *Prodr.* 13(1): 28, 66 (1852), pro parte. Lectotype species: *Solanum mite* Ruiz & Pav. (D'Arcy, 1972).

Solanum section *Polybotryon* Bitter in *Reprim nov. Spec. Regni veg.* 11: 469 (1912). Lectotype species: *Solanum mite* Ruiz & Pav. (D'Arcy, 1972).

Solanum subgenus *Bassovia* (Aubl.) Bitter in *Reprim nov. Spec. Regni veg.* 17: 329 (1920/1?). Lectotype species: *Solanum sylvaticum* (Aubl.) Bitter [basionym *Bassovia sylvatica* Aubl.] (= *Solanum anceps* Ruiz & Pav.) (Bitter, 1921).

Slender wand-like shrubs, herbs or woody high-climbing lianas; young stems and leaves pubescent or glabrous, the trichomes if present simple and uniseriate. Leaves simple or pinnate (pinnatisect), fleshy or membranous, often very dark green in live plants, leaf undersides often dark purple or reddish. Inflorescence a scorpioid cyme borne in the axil of the leaf, unbranched, usually bearing 5–30 flowers; pedicel scars not raised. Buds usually rounded to ellipsoid, strongly exerted from the minute calyx tube. Flowers sympetalous, stellate, the tube very short; corolla 5–20 mm in diameter, fleshy or membranous, in the *S. ternatum* species group the lobes planar at anthesis and usually cucullate, in the *S. mite* species group the lobes usually reflexed at anthesis, sometimes strongly so; stamens five, the anthers poricidal at the tips, with age splitting longitudinally, bright yellow. Fruit a berry, usually green or yellowish green when mature, globose with a smooth surface (*S. incurvum*, *S. ternatum*, *S. mite*) or variously conical with a rugose surface; fruiting pedicel nodding or erect. Seeds flattened-reniform, many per fruit (*S. ternatum*, *S. incurvum*) or ovoid-reniform and few per fruit.

Section *Pteroidea*, as here delimited, consists of ten species in two monophyletic clades (see p. 43). The clades are both kept in the section (s.l.) at this time for convenience, despite some doubt as to their degree of relatedness. The *S. ternatum* clade, consisting of *S. incurvum* and *S. ternatum*, has large, lilac or pinkish flowers and globose fruits with many, small, flattened seeds, while the larger *S. mite* clade, consisting of *S. anceps*, *S. angustialatum*, *S. chamaepolybotryon*, *S. conicum*, *S. mite*, *S. savanillense*, *S. trizygam*, and *S. uleanum*, has smaller, usually greenish flowers, and (with the exception of *S. mite*) conical fruits with unusual rugose surfaces, the fruits having a few, ovoid, often bright green, seeds. These rugose fruits are unique in *Solanum*. The section has been accorded subgeneric status by many previous authors (Bitter, 1921; Seithe, 1962; Danert, 1967; D'Arcy, 1972, 1991), on the basis of its extreme morphological difference from the rest of *Solanum*. We feel, however, that until phylogenetic relationships in *Solanum* are much more clearly resolved, the group (as two clades) should be recognized only at the sectional level.

This monograph is based on herbarium specimens and the extensive field observations of the senior author. The species are delimited on morphological grounds, with geographical and ecological preferences being taken into account where appropriate. More than half of the published names of this species group have as a result, been

placed in synonymy. Most of these are synonyms of the two most widely distributed species, *S. mite* and *S. anceps*. *Solanum mite* is relatively homogeneous (excluding variation in pubescence) over its range, whereas *S. anceps* has a number of forms that are somewhat geographically coherent. This variation is described in the species account. Section *Pteroidea* is a poorly collected group, and the material on which many of these descriptions are based is somewhat limited.

A general comment here on the lectotypification, particularly of Ruiz & Pavón names, will save repetition in the species accounts. We have lectotypified all of these names using specimens from MA matched, if possible, to plates in *Flora peruviana et chilensis* (Ruiz & Pavón, 1799). In most cases the choice was straightforward, but when not, we have chosen the best specimen. Other lectotypes have been chosen with an eye to the wide distribution of isolectotypes. When this was not possible, the best preserved specimen was selected. Any lectotype not directly attributed to another author is designated by us here.

Photographs of type specimens are cited in the recommended manner (see Knapp, 1989, 1991a), with the negative number cited in square brackets. Herbaria in possession of prints of that negative are also included in the brackets. Copies of these negatives are generally available from the institutions where they are housed: F for F negatives and US for Morton negatives.

Herbaria are cited using the acronyms in *Index herbariorum* (Holmgren et al., 1990) and types seen are indicated by an exclamation mark (!). All non-type specimens cited in the species accounts have been seen by the authors, unless otherwise indicated.

Key to selected groups of Neotropical non-spiny solanums

- 1 Inflorescences axillary 2
 Inflorescences lateral or leaf-opposed 4
- 2 Plants small trees or shrubs, branching in a complex crown; inflorescences in branch forks; anthers with an enlarged connective
 **Cyphomandra** (*Solanum* section **Cyphomandra**)
 Plants wand-like, shrubs, vines, or herbaceous; inflorescences only in leaf axils; anthers without an enlarged connective 3
- 3 Trailing herbs, rooting at the nodes, inflorescences with a single flower; fruit with smooth surfaces **Solanum** section **Herpystichum**
 Herbs (not trailing), slender shrubs or vines, inflorescences with more than one flower, usually with up to 30 flowers; fruit smooth or rugose **Solanum** section **Pteroidea**
- 4 Inflorescences internodal; fruit brightly coloured, with thin pericarp **Solanum** section **Solanum**
 Inflorescences leaf-opposed or variously terminal; fruit green at maturity, the pericarp not thin **Solanum** section **Geminata**

Key to species of *Solanum* section *Pteroidea*

- 1 Leaves simple 2
 Leaves variously pinnate 4
- 2 Climbing herbs; flowers 1.2–1.4 cm in diameter, purplish; fruit globose, the surface smooth; seeds many per fruit (>50) 1. **S. incurvum**
 Terrestrial herbs or weak subshrubs; flowers 0.4–0.7 cm in diameter, white or greenish white; fruit ovoid, beaked, the surface rugose; seeds few per fruit (usually 10–40) 3
- 3 Stem prominently winged; style densely pubescent along its entire length. San Martín, Peru 4. **S. angustialatum**

- Stem smooth, terete, not winged; style glabrous or at most papillate in the lower 2/3. Widespread 3. *S. anceps*
- 4 Climbing herbs or woody vines 5
Terrestrial herbs or wand-like shrubs, occasionally in large colonies 6
- 5 Woody vines, the basal stems often to several cm in diameter; flowers 1.6–2 cm in diameter, the petals planar, fleshy, cucullate; fruit globose, the surface smooth. 2. *S. ternatum*
Herbaceous vines; flowers 0.6–1 cm in diameter, the petals strongly reflexed, not fleshy or markedly cucullate; fruit conical, the surface rugose. 10. *S. uleanum*
- 6 Leaves with 5 or fewer leaflets, the leaflets usually obovate, especially the terminal 7
Leaves usually with more than 5 pairs of leaflets, the lateral leaflets lanceolate to elliptic, the terminal leaflet similar in shape, not markedly obovate 10
- 7 Leaves pubescent on the veins and lamina on both surfaces 8
Leaves glabrous on lamina, occasionally pubescent along the veins and rachis 9
- 8 Fruit conical; leaf pubescence denser adaxially 8. *S. savanillense*
Fruit globose, smooth; leaves equally pubescent on both surfaces. 7. *S. mite*
9. Fruit conical, the surface rugose; leaves fleshy; plants very small and rooting along the stem 5. *S. chamaepolybotryon*
Fruit globose or at most apically pointed, the surface smooth; leaves membranous; plants often woody at the base and up to 1 m tall 8. *S. mite*
- 10 Flowers 5–6 mm in diameter, the petals strongly reflexed at anthesis; fruit globose, smooth 8. *S. mite*
Flowers 9–13 mm in diameter, the petals usually planar or only slightly reflexed at anthesis; fruit conical, rugose 11
- 11 Flowers > 10 mm in diameter; leaflets long-petiolulate, the petiolule 3–17 mm; leaves densely pubescent in a groove along the adaxial side of the rachis 6. *S. conicum*
Flowers < 10 mm in diameter; leaflets short-petiolulate, the petiolule c. 1 mm long; leaves only sparsely pubescent if at all and then only with a few scattered trichomes abaxially 9. *S. trizygum*

The *Solanum ternatum* species group

1. *Solanum incurvum* Ruiz & Pav., *Fl. peruv.* 2: 34, fig. 154b (1799). Type: Peru, Huánuco, Muña, August, September, Ruiz & Pavón s.n. (MA!-lectotype [F neg. 29716, F!]). Fig. 9.

Climbing herb, up to 2 m in length at maturity, often trailing along the forest floor. *Stems* c. 8 mm in diameter, minutely to densely pubescent with simple uniseriate trichomes 0.3–1.0 mm long. *Leaves* simple, 6–20 × 3–9 cm, elliptic to ovate, with c. (5)6–7 pairs of primary veins, glabrous to somewhat densely pubescent with simple uniseriate trichomes, denser along the veins both abaxially and adaxially, the base acuminate, the apex acute; petiole 1.5–9 cm long, glabrous to pubescent with simple uniseriate trichomes, glabrate. *Inflorescence* to 12 cm long, axillary, 1–3 inflorescences per leaf axil, bearing 3–6 open flowers at a time, with up to 12 scars, glabrous to sparsely pubescent with simple uniseriate trichomes. *Buds* rounded, becoming ellipsoid, strongly exserted from the calyx tube. *Pedicels* at anthesis 0.8–1.8 cm long, 1–2 mm in diameter, quite soft and lax,

pendent, glabrous to sparsely pubescent like the rest of the inflorescence. *Flowers* with the calyx tube c. 0.5 mm long, conical, the sides very straight, the lobes 1–2 × 1–2 mm, acute to slightly obtuse and spreading, glabrous to sparsely pubescent with a few scattered uniseriate trichomes; corolla 12–14 mm in diameter, reddish violet to purple, the tube c. 2 mm long, the lobes 5–6 mm long, planar to very slightly reflexed, sparsely pubescent abaxially, the tips minutely papillate; anthers 3–4 × 1–1.2 mm; free portion of the filaments minute, the filament tube minute; ovary globose to bottle-shaped, glabrous; style c. 6 mm long, straight, glabrous; stigma minutely capitate. *Fruit* a globose (somewhat conical when immature) berry, 1–1.3 × 1–1.3 cm, green at maturity, drying black, the surface smooth; fruiting pedicel 1–1.5 cm long, nodding. *Seeds* c. 80–100 per fruit, 1–2 mm, flattened-reniform, orange-brown; epidermal cells regular, rectangular, with long hair-like projections, especially at the margins.

COMMON NAMES AND USES. None recorded.

DISTRIBUTION. Eastern slopes of the Andes from S. Ecuador to S. Peru, montane forest and forest edges, 1540–3000 m. (Fig. 10).

SPECIMENS EXAMINED

ECUADOR. *Morona-Santiago*: 9–10 km SE of San Juan Bosco, 1540–1600 m, 27 January 1981, Gentry et al. 30871 (MO).

PERU. *Huancavelica*: Choimacota Valley, Huanta, 2800–2900 m, 28 February 1926, *Weberbauer* 7570 (F, MOL). *Huánuco*: Playapampa, 2750 m, 16 June 1923, *Macbride* 4491 (F). *Pasco*: Oxapampa, trail to summit of Cordillera Yanachaga via Río San Daniel, 3000 m, 75°27'W, 10°23'S, 13 July 1984, *Smith* 7756 (MO, USM); Oxapampa. Río San Alberto valley E. of Oxapampa, 2700 m, 75°22'W, 10°27'S, 26 July 1984, *Smith* & *Poetel* 8069 (MO). *San Martín*: Valley of Río Apisoncho, 30 km above Jucusbamba, 2800 m, 77°10'W, 7°55'S, 6 August 1965, *Hamilton* & *Holligan* 1069 (K).

Solanum incurvum is one of the most poorly collected species in section *Pterioidea*. It grows at the highest elevations, and is apparently not at all common where it occurs. Considerable variation in pubescence exists among the few specimens examined, which apparently is not correlated with elevation or any other discernible ecological factor. Like its close relative, *S. ternatum*, it is reported to have lilac flowers, but variation for flower colour may exist.

2. *Solanum ternatum* Ruiz & Pav., *Fl. peruv.* 2: 38, fig. 162b (1799). Type: Peru, Huánuco, Cuchero, June, July, Ruiz & Pavón s.n. (MA!-holotype; B, destroyed [F neg. 2639, F!, MO], F!-isotypes). Figs 4a, 11.

Solanum diffusum Ruiz & Pav., *Fl. peruv.* 2: 37, fig. 161b (1799). Type: Peru, Huánuco, sin loc., June, July, August, Ruiz & Pavón s.n. (MA!-holotype, fragment F!). F neg. 12996 is of an obvious isotype of *Solanum diffusum*, but some confusion exists as to the labelling: prints with negative number 12296 (F!, MO!, NY!) are said to have been taken at B, but photographs without a negative number of the same sheet (F!, GH!, US!) are said to have been taken at MA.

Solanum semievectum Bitter in *Reprrium nov. Spec. Regni veg.* 11: 542 (1913). Type: Peru, sin loc., *Poeppig* s.n. (B-holotype, destroyed [F neg. 2638 – F!]).

Solanum moritzianum Bitter in *Reprrium nov. Spec. Regni veg.* 11: 565 (1913). Type: 'Nouvelle Grenade', either Venezuela or Colombia, sin loc., December 1852, *Moritz* 1028 (P-lectotype [F neg. 39192, G!, US!]; BM!, HBG!, K!, P [Morton neg. 8357, F!, GH!, US!]).

Solanum feddei Bitter in *Reprrium nov. Spec. Regni veg.* 12: 67



Fig. 9 *S. incurvum*. Habit: Gentry et al. 30871 (MO). Inflorescence: Hamilton & Holligan 1069 (K).

(1913). Type: Peru, Huánuco, Muña, May 1863, Pearce s.n. (K!-holotype).

Solanum dendrophilum Bitter in *Reprrium nov. Spec. Regni veg.* **12**: 143 (1913). Type: Peru, San Martín, Cerro Campana, Spruce 4385 (K!-holotype; K!-isotype).

Solanum semiscandens Bitter in *Reprrium nov. Spec. Regni veg.* **12**: 142 (1913). Type: Peru, Huánuco, Muña, 10–11000 ft, May 1863, Pearce s.n. (K!-holotype).

Solanum subquinatum Bitter in *Reprrium nov. Spec. Regni veg.* **12**: 144 (1913). Type: Peru, Amazonas, Chachapoyas, 1835, Matthews s.n. (BM!-lectotype; K!-isotype).

Solanum diffusum subsp. *miozygum* Bitter in *Bot. Jb.* **54**: (Beibl. 119): 14 (1916). Type: Peru, Pasco, valley of Río Pozuzo, tributary of Río Palcazu, 9°46'–9°50'S, 2200 m, 1909–1914, Weberbauer 6783 (B-holotype, destroyed; MOL!-lectotype; F!-isotype).

Solanum diffusum var. *miozygum* (Bitter) J.F. Macbr. in *Publ. Field Mus. (Bot.)* **8**: 111 (1930). Basionym: *Solanum diffusum* subsp. *miozygum* Bitter.

Woody, high climbing vine, to 6–7 m (or more) long. Stems c. 0.5 cm in diameter, quite stout and woody at the base and somewhat four-



Fig. 10 Distribution of *S. incurvum*.

lobed, greenish, not conspicuously white-lenticellate, glabrous to sparsely to densely (type of *S. dendrophilum*) pubescent with simple, uniseriate trichomes 2–3 mm long, these drying white and cateniforme. *Leaves* pinnate, 9–15 × 8–12 cm, ternate or with 2–4 pairs of leaflets, somewhat fleshy, pubescent with scattered to dense simple uniseriate trichomes along the veins abaxially, glabrous to densely pubescent adaxially, the trichomes 5–10-celled, *c.* 2–3 mm long; petiole 2–6 cm long; lateral leaflets 2–6 × 1–3 cm, lanceolate or narrowly elliptic to elliptic or obovate, if the leaf more than ternate the leaflets usually narrower, with 4–6 pairs of primary veins, the base attenuate, oblique, enlarged basiscopically, the apex acute; petiolule 0.5–1 cm; basal leaflets smaller than the laterals if the leaf more than ternate; terminal leaflet 2–10 × 1–3 cm, slightly more obovate, the base attenuate, the apex acute to occasionally acuminate; petiolule *c.* 0.5 cm. *Inflorescence* axillary, 1.5–6 cm long, bearing flowers only in the distal 1/3, simple, occasionally 2 per axil, with 2–4 flowers open at a time, the pedicel scars raised, widely spaced, up to 24 per inflorescence. *Buds* elliptic, *c.* 6 × 3 mm, strongly exerted from the calyx tube. *Pedicels* at anthesis 1–1.3 cm long, *c.* 0.5 mm in diameter, erect to horizontal. *Flowers* with the calyx tube very open, almost flat, *c.* 2 mm long, the lobes 1.5–2 × 2 mm, quadrate with a distinct apical lobe, glabrous to sparsely pubescent with simple uniseriate trichomes like the rest of the plant; corolla 16–20 mm in diameter, white to greenish to pink, lobed *c.* 3/4 of the way to the base, the lobes cucullate, planar at anthesis,

minutely papillate at the tips and along the margins; anthers 4–5 × *c.* 2 mm, slightly sagittate at the base, poricidal at the tips; free portion of the filaments *c.* 0.5 mm long, the filament tube absent; *ovary* conical, glabrous; style *c.* 8 mm long, glabrous; stigma capitate to clavate. *Fruit* a globose to slightly apically pointed, green berry, 1–1.2 cm in diameter, 1–1.5 cm long, the surface smooth; fruiting pedicel 1.5–1.7 cm long, fleshy, *c.* 2 mm in diameter at the apex, pendent. *Seeds* 80–140 per berry, 1.2–2 × 1.2–1.8 mm, flattened, almost round, reddish brown; epidermal cells more or less regular, with flap-like thickenings.

COMMON NAMES AND USES. None recorded.

DISTRIBUTION. Tropical wet forest to humid cloud forest, in deep shade or forest edges from 100–2800 m. In the Andean region from Colombia and Venezuela to Bolivia. (Fig. 12).

SPECIMENS EXAMINED

COLOMBIA. **Cundinamarca:** Municipio de San Bernardo; Vereda Santa Marta, alrededores de la Laguna La Chorrera, 2300–2350 m, 20 July 1981, Díaz P. & Melief 2952 (MO). **Huila:** Finca Merenberg, E. of Volcán Purace, near Cauca border, 2300 m, 76°02'W, 2°16'S, 3 April 1986, Gentry et al. 53970 (MO); Finca Merenberg, border with Cauca, E. of Leticia, 2300 m, 76°12'W, 2°16'S, 08 July 1984, Gentry et al. 47779 (MO). **Magdalena:** Alrededores de Yerbabuena, 2000 m, 26 January 1959, Romero Castañeda 7067 (AAU); Sierra Nevada de Santa Marta, Sierra del Libano, Las Nubes, 1898–1901, Smith 1162 (BM, BR, F, MA, MO, NY, US, W, WIS). **Norte de**



Fig. 11 *S. ternatum*. Habit: Killip & Smith 20235 (GH). Juvenile foliage and flowers: Knapp & Mallet 6626 (US). Fruits: Zaruma et al. 21A (QCNE).

Santander: Pica-Pica Valley, above Tapatá (N. of Toledo), 2100–2400 m, 1 March 1927, Killip & Smith 20235 (GH, US).

VENEZUELA. Aragua: E. of Colonia Tovar, 7500 ft, 8 April 1854, Fendler 1017 (GOET). **Miranda:** Colonia Tovar, 1800–2000 m, December 1924, Allart 335 (US).

ECUADOR. Napo: Carretera Hollín-Loreto, km 25, Centro Challuayacu, en trocha hacia la zona del Guagua Sumaco, 1230 m, 77°40'W, 00°43'S, 10

November 1988, Hurtado & Alvarado 1121 (MO); Carretera Hollín-Loreto, km 40–50, alrededores de la comunidad Huamaní y del Río Pucuno, 1200 m, 77°36'W, 00°43'S, 10 October 1988, Hurtado 625 (MO). **Pastaza:** Capitaine Chiriboga, Río Pastaza, vicinity of army base, 235 m, 76°49'W, 2°32'S, 21 July 1988, Lewis et al. 13771 (QCNE); 2 km al NE de Mera, Hacienda San Antonio del Barón von Humboldt, 1100 m, 78°06'W, 01°27'S, 18 March 1985, Zaruma et al. 21A (AAU, MO, QCNE). **Zamora-Chinchipe:**



Fig. 12 Distribution of *S. ternatum*.

Road from Loja to Zamora, 14 July 1986, *D'Arcy* 16506 (MO); Río Nangaritzu, Pachicutza, camino al hito de Pachicutza, 900–1000 m, 78°07'W, 4°07'S, 18 October 1991, *Palacios* et al. 8188 (QCNE).

PERU. **Amazonas:** Prov. Chachapoyas, 1836, *Matthew* s.n. (BM, K); hills NW of Pomacocha, 2300–2700 m, 19 June 1962, *Wurdack* 940 (K, US); between Molinopampa & Mendoza, 10 km E. of Molinopampa, 2400 m, 23 February 1978, *Wasshausen & Encarnación* 998 (US); Mendoza, 1600 m, 2 September 1963, *Woytkowski* 8265 (MO); Bagua, Cordillera Colán SE of La Peca, 2280–2400 m, 7 October 1978, *Barbour* 3829 (MO), 1800–1870 m, 17 October 1978, *Barbour* 4160 (MO). **Cajamarca:** Cuchero, *Dombey* s.n. (P [n.v., Morton neg. 8354, F!, MO!, US!]); San Andrés de Cutervo, sobre la ruta a las grutas, al N. de San Andrés, 2250 m, 25 June 1989, *Sánchez Vega* 4895 (F). **Cusco:** Dto. Camanti, Maniri, 8 km W. de Quincemil, a los margenes de la quebrada Garrote, 720 m, 70°48'W, 13°17'S, 20 July 1990, *Timaná & Aste* 692 (MO); along Río Pillahuata, 2300–2400 m, 3 May 1925, *Pennell* 14012 (F); Río Mapitunuari, c. half way from Luisiana and Río Apurímac to camp 1, 800–900 m, 73°42'W, 12°39'S, 15 June 1968, *Dudley* 10152 (F). **Huánuco:** Muña, trail to Tambo de Vaca, 2440 m, 5 June 1923, *Macbride* 427 (G, F); Huacachi, estación near Muña, 1980 m, 20 May 1923, *Macbride* 4698 (F); Muña, May 1863, *Pearce* 135 (BM); Divisoria, 1600 m, 10 September 1946, *Woytkowski* 34512 (F, MO); Rupa Rupa, Calpar Bella, Cueva de los Huarñños (margen izquierda del Río Monzón), 700–900 m, 29 June 1976, *Schunke* V. 9440 (GH, MO); La Divisora, Cordillera Azul near border with Ucayali, 1620–1760 m, 75°48'W, 9°05'S, 10 August 1980, *Gentry* et al. 29558 (MO); Pachitea, Codo de Pozuzo, alluvial fan flood plain of Río Pozuzo after it emerges from mountains, trail S. of settlement to main river, 450 m, 75°25'W, 9°40'S, 21 October 1982, *Foster* 9355 (MO); Dto. Hermilio Valdizán, La Divisoria, road from Pumahuasi to La Cumbre, 1600–1660 m, 26 June 1978, *Plowman & Schunke* V. 7394 (MO); Prov. Huánuco, km 452 of Lima-Tingo María road, 2500 m, 2 June 1981 *Young & Sullivan* 570 (MO); Prov. Leoncio Prado, road between Tingo María and Pucallpa, km 35, 1500 m, 75°48'W, 9°10'S, 3 June

1981, *Sullivan & Young* 1154 (MO); Muña, 1000–1100 m, 1863, *Pearce* 144 (BM). **Junín:** Huatsiroke, 1800 m, 21 February 1960, *Woytkowski* 5543 (F, MO); Prov. Tarma, Agua Dulce, 1900 m, 5 March 1948, *Woytkowski* 35416 (F, G, MO, US); San Gaván, August 1854, *Lechler* 2440 (G, P [n.v. Morton neg. 8252, F, GH, US]); Pichis trail, Dos de Mayo, 1700–1900 m, 2 July 1929, *Killip & Smith* 25811 (US). **Pasco:** San Juan de Cacazu, km 36 on Villa Rica-Pto. Bermúdez road, trail behind colegio, 950 m, 75°10'W, 10°38'S, 13 August 1984, *Knapp & Mallet* 6626 (BH, K, US); Oxapampa-Cerro de Pasco road, La Suiza to San Gotardo, 2100–2650 m, 75°35'W, 11°38'S, 19 May 1983, *Smith* 4104 (MO); Río San Alberto valley E. of Oxapampa, slopes of Cordillera Yanachaga, 2400 m, 75°22'W, 10°34'S, 23 July 1984, *Smith & Pretel* 7968 (MO); El Tunqui Alto, 57 km from Oxapampa, 1700 m, 75°30'W, 10°15'S, 14 May 1982, *Smith* et al. 1569 (MO); Oxapampa, trail to summit of Cordillera Yanachaga via Río San Daniel, 2400 m, 75°27'W, 10°23'S, 19 July 1984, *Smith* et al. 7933 (MO). **San Martín:** Valley of Río Apisoncho, 30 km above Jucusbamba, 2800 m, 77°10'W, 07°55'S, 8 August 1965, *Hamilton & Holligan* 1078 (K); Zepelacio, near Moyabamba, 1100 m, June 1934, *Klug* 3665 (A, BM, GH, K, MO, US). **Ucayali:** Río Chino al W. del Restaurant Acapulco, 100–1100 m, 5 June 1976, *Schunke* V. 9144 (MO); La Divisoria cerca a Río Chino, 1400–1600 m, 12 June 1976, *Schunke* V. 9241 (MO).

BOLIVIA. **La Paz:** Prov. Nor Yungas, Serranía de Bella Vista, 16 km N. of Carrasco (37 km N. of Caranavi) on road to Palos Blancos, 1500 m, 67°34'W, 15°35'S, 31 October 1984, *Solomon & Nee* 12704 (M, MO); Prov. Sur Yungas, along road 7.0–9.4 km NE of (above) Huancané, 2286–2499 m, 67°32'W, 16°20'S, 17 May 1990, *Luteyn & Dorr* 13699 (NY); Prov. Nor Yungas, 4.6 km NE (below) Chuspipata on road to Yolosa, 2800 m, 67°47'W, 16°17'S, 8 March 1984, *Solomon & Stein* 11681 (MO); Prov. Nor Yungas, 13.7 km NW of San Pedro on road through Inchuara-Mejillones, and along trail to 12 de Octubre, 1500 m, 67°37'W, 15°58'S, 12 February 1983, *Solomon* 9584 (MO); Hacienda Casana sobre el camino a Tipuani,



Fig. 13 *S. anceps*. Habit: Allard 22077 (US), (inset circle) *S. angustialatum* stem from Knapp & Mallet 8567 (F).

1400 m, 15 October 1922, *Buchtien* 7462 (US); Prov. Sud Yungas, Huancané (cerca Chulumani) 8 kms, 2450 m, 31 October 1981, *Beck* 4881 (F); Prov. Nor Yungas, 4.6 km below Yolosa, then 19.1 km on road up the Río Huar-inilla, 1700 m, 67°53'W, 16°12'S, 12 November 1982, *Solomon* 8791 (MO).

Solanum ternatum can be a very large woody liana, with lower stems up to 2 cm in diameter. In cross-section these woody stems are in the shape of an '8'. Like many of the members of the section, considerable variation in pubescence exists within the species, with densely pubescent specimens having been described as *S. dendrophilum*. The degree of fleshiness of the leaves of *S. ternatum* has also led to the description of many synonyms, but this character is unrelated to geography or habitat, and seems to vary at random throughout the range of the species. Polymorphism in flower colour is common throughout the species range, and unlike members of the *S. mite* species group, purple flower colour does not co-occur with purple leaf undersides (see *S. anceps* and *S. savanillense*).

The *Solanum mite* species group

3. *Solanum anceps* Ruiz & Pav., *Fl. peruv.* 2: 36, fig. 149a (1799).

Type: Peru, Huánuco, Cuchero, July, August, *Ruiz & Pavón* s.n. (MA!-holotype [F neg. 29722, F!, GH!, MO!, US!]).

Figs 5c, 13.

Bassovia sylvatica Aubl., *Hist. pl. Guiane* 1: 217, fig. 75 (1775).

Type: French Guiana, *Aublet* s.n. (BM!-lectotype).

Solanum bassovia Dunal in Poir., *Encycl. suppl.* 3: 754 (1814);

Solan. syn.: 22 (1816). *nom. nov.* for *Bassovia sylvatica* Aublet.

Solanum aubletii Pulle, *Enum. vasc. pl. Surinam*: 411, fig. 16 (1906). *nom. nov.* for *Bassovia sylvatica* Aubl.

Solanum conjungens Bitter in *Reprrium nov. Spec. Regni veg.* 11: 12 (1912). Type: Ecuador, Tungurahua, prope Baños, September 1892, *Sodirol* 114/61 (B-holotype, destroyed [F neg. 2656, F!, G!, GH!, MO!, NY!]); possible lectotype to be found in the Sodirol herbarium in Ecuador which is held privately in the monastery where he was resident).

Solanum hederiradiculum Bitter in *Reprrium nov. Spec. Regni veg.* 11: 12 (1912). Type: Peru, Loreto, Yurimaguas, August 1902, *Ule* 6276 (B-holotype, destroyed [F neg. 2608, F!, G!, GH!, MO!, US!]; HBG!-lectotype).

Solanum theobromophyllum Bitter in *Reprrium nov. Spec. Regni veg.* 11: 472 (1912). Type: Brazil, Amazonas, Rio Jurua, Cachoeira Miry, May 1901, *Ule* 5490 (W!-holotype; G!, HBG!-isotypes).

Solanum theobromophyllum var. *procerius* Bitter in *Reprrium nov. Spec. Regni veg.* 12: 145 (1913). Type: Brazil, Acre, Estella, 1912, *Ule* s.n. (no herbarium cited). Bitter cited no herbarium when he described this variety, and specifically cited the date of the collection as 1912. However, a *Ule* collection (at G!, K!) labelled 'Rio Acre, Seringal Auristella, E. Ule 9735' could be type material. The sheet at G is dated March 1911 and the K sheet is dated April 1911. In the 1913 publication, Bitter cited many K collections, but the K sheet is only annotated '*Solanum theobromophyllum*' in Bitter's hand and dated 1914. The location of the type of this variety remains obscure.

Solanum sylvaticum (Aubl.) Bitter in *Reprrium nov. Spec. Regni veg.* 17: 330 (1921). non *Solanum sylvaticum* Dunal, *Solan. syn.*: 24. (1816). (= *Lycianthes sylvatica* (Dunal) Bitter, a synonym of *Lycianthes geminata* (Vahl) Bitter).

Slender, single-stemmed shrub, to 2 m tall. Stems c. 4 mm in diameter, green, conspicuously white-lenticellate, glabrous to minutely red-papillate on new growth to densely pubescent with simple uniseriate trichomes c. 0.5 mm long. Leaves simple, 12–45

× (3–)5–15 cm, very variable in size, elliptic to obovate, with 10–15 pairs of primary veins, glabrous to densely pubescent with simple uniseriate trichomes c. 0.5–1 mm long, these soon deciduous on the lamina and remaining only sparsely along the veins, the base acute to attenuate (truncate in isolated populations near Iquitos), the apex acute to acuminate; petiole 1–5 cm long. Inflorescence axillary, 1–3 cm long, c. 2–4 per axil, simple, bearing flowers c. 1 cm from the base, with 3–4 flowers open at a time, c. 40–60 pedicel scars, glabrous or if the plant pubescent then with scattered uniseriate trichomes. Buds globose, c. 2 mm in diameter, c. 1/2 included in the calyx tube. Pedicels at anthesis 5–7 mm long, c. 0.5 mm in diameter, nodding. Flowers with the calyx tube c. 1 mm long, broadly conical, the lobes broadly deltate, 0.5–1 × 1–1.5 mm, glabrous or sparsely pubescent with uniseriate trichomes; corolla white, 5–7 mm in diameter, lobed nearly to the base, the lobes reflexed at anthesis, densely papillose at the tips and along the margins; anthers 1.5–2 × c. 1 mm, poricidal at the tips, free portion of the filaments c. 0.05 mm, the filament tube c. 0.05 mm; ovary conical, glabrous; style 4–5 mm long, minutely papillate in lower 2/3 or glabrous; stigma clavate. Fruit a conical, green berry, 1–1.2 cm in diameter, 1–2.3 cm long, the beak 2–8 mm, occasionally breaking off and appearing absent, the surface rugose, the raised portions white; fruiting pedicel 0.8–1.8 cm long, erect. Seeds 2–3.5 × 1.5–2.2 mm, greenish brown, flattened, round to ovoid-reniform, c. 40 seeds per fruit; epidermal cells highly sinuous and irregular, with anticlinal thickenings but without projections.

COMMON NAMES AND USES. Peru: 'ullcu panga' (*Williams* 7322).

DISTRIBUTION. Colombia to Bolivia and into Brazil, from 100–nearly 3000 m, in a wide range of wet forest habitats. (Fig. 14).

SPECIMENS EXAMINED

COLOMBIA. sin loc. *Goudot* 136 (K). **Antioquia:** 8 km S. of Angostura on road to Represa Miraflores, c. 6°50'N, 75°18'W, 2000 m, 8 February 1986, *Stein & Cogollo* 3394 (MO). **Boyacá:** 130 miles NW of Bogotá, 3000 ft, 29 September 1932, *Lawrance* 345 (MO); 130 miles N. of Bogotá, 3500 ft, 3 March 1933, *Lawrance* 645 (GH). **Meta:** Sierra de la Macarena, Cano Entrada, 550 m, 23 January 1950, *Philipson* et al. 2205 (BM, GH); Guamal Municipio, 9 March 1987, *Quiñones* 1045 (MO). **Putumayo:** Orito, Río Calderas, 300–400 m, 11 December 1968, *Plowman* 2129 (GH). **Valle:** Cerca a Morales-Cauca, 8 October 1968, *Espinal T. & Ramos* 2943 (CUVC, F); vereda La Bella, finca Miranda, 1830 m, 25 January 1983, *Franco* et al. 1876 (MO); Cerro La Horqueta (San Antonio), Cordillera Occidental vertiente oriental, c. km 17 de carretera Cali-Buenaventura, 2050 m, 25 November 1983, *Silverstone-Sopkin* 1487 (MO), 1910 m, 6 January 1986, *Silverstone-Sopkin & Rodríguez* 2095 (MO).

GUYANA. Southern Pakaraima Mountains, escarpment to foot of Kopinang Falls, 2750 ft, 2 September 1961, *Maguire* et al. 46080A (NY); Upper Mazaruni River basin, NE side of Mt. Ayanganna, 800–900 m, 1 August 1960, *Tillett* et al. 44971 (NY).

SURINAM. Nassau Mountains, Marowijne River, forested slopes and summit of plateau A, 430 m, 31 December 1954, *Cowan & Lindeman* 39020 (NY); Lely Mts, SW plateaus, along E. road on plateau 1, 550–710 m, 29 September 1975, *Lindeman* et al. 535 (C, F, K, MO, NY, WIS); *Wilhelmina* gebergte, Frederick Top, 2.5 km SE of Juliana Top, 500 m, 56°30'–6°34'W, 3°36'–3°41'N, 31 July 1963, *Maguire* et al. 54407 (NY).

FRENCH GUIANA. Regina region, E. plateau of Montague Torte, 11 km WNW of Approvague River, 200–450 m, 52°22'W, 4°18'N, 17 June 1988, *Feuillet* et al. 10178 (NY); Mt. Tortue, 11 km WNW of Approvague river, along the road, 200–450 m, 52°22'W, 4°18'N, 16 June 1988, *Feuillet* et al. 10230 (NY); Saül, Mont Galbao, 17 October 1984, *de Foresta* 656 (NY); pente NE des Monts Galbao, 10 km au SW de Saül, 500–600 m, 11 March 1975, *de Granville* 2374 (MO, NY); ancienne piste de Saül a Belizon, entre Eau Claire et St. Eloi, 21 August 1981, *de Granville* 4944 (MO); Saül, trace ORSTROM vers les monts Galbao, sur la Montagne Liane, 19 July 1976, *de Granville* B5339 (MO); Haut Camopi – Mont Belvedere, 7 December 1984,



Fig. 14 Distribution of *S. anceps* (circles) and *S. angustialatum* (star in circle).

de Granville 7165 (NY); Montagne Bellevue de l'Inini, ext. SW versant NW, 550 m, 15 August 1985, *de Granville* 7502 (NY, US); Montagne Bellevue de l'Inini, zone centrale, 700–750 m, 20 August 1985, *de Granville* 7686 (NY); Mont Galbao, secteur E, 600 m, 53°17'W, 3°36'N, 15 January 1986, *de Granville* et al. 8704 (NY); Camp 4, Monpé Soula-Bassin du Hoaut-Marouini, 5 km a l'Oest, 180 m, 54°04'W, 2°39'N, 3 September 1987, *de Granville* et al. 9975 (NY); Mont Atachi Bacca – region de l'Inini, centre du plateau sommital, camp IV, 780 m, 53°55'W, 3°33'N, 21 January 1989, *de Granville* et al. 10842 (NY); sin. loc., 1859, *Leprieur* s.n. (G); Saül, Batard d'Eau, 15 September 1978, *Prévost* 304 (MO); Crique Cacao – bassin de la Haute Camopi, 54°12'W, 2°20'N, 10 May 1987, *Prévost & Sabatier* 2422 (NY); Saül region, trail to Crique Limonade, S. of airfield at Saül, 200–210 m, 53°12'W, 3°36'N, 10 November 1986, *Skog* et al. 7380 (NY, US).

ECUADOR. Morona-Santiago: Taisha, c. 5 km NNW of the military camp, 500 m, 77°30'W, 2°23'S, 14 June 1980, *Brandbyge & Asanza* C. 31824 (AAU, NY); Taisha, 3–4 km ESE of the military camp, 450 m, 77°30'W, 2°23'S, 15 June 1980, *Brandbyge & Asanza* C. 31873 (AAU, NY); Taisha, 8–10 km NNW of military camp, 650–700 m, 77°31'W, 2°21'S, 16 June 1980, *Brandbyge & Asanza* C. 31927 (AAU); Pumpuentza, SSW of village, 250 m, 77°20'W, 2°25'S, 29 June 1980, *Brandbyge & Asanza* C. 32365 (AAU, NY); end of road construction into Cordillera del Condor from Guisme, 12 km past Río Zamora, 900 m, 78°27'W, 3°37'S, *Brandbyge & Balslev* 42280 (AAU); along Río Metzera grande on Hacienda Sangay (plantation of Compañía Ecuatoriana del Té C.A.) near Palora, c. 950 m, 77°58'W, 1°40'S, 15 February 1984, *Knapp & Mallet* 6279 (BH, K, QCA, QCNE, US); along new road Méndez-Morona, km 55–62, 800 m, 23 August 1989, *van der Werff & Gudiño* 11400 (MO, QCNE); pozo petrolero Garza de TENNECO, c. 35 km NE de Montalvo, 260 m, 76°42'W, 1°49'S, 2–12 July 1989, *Zak & Espinoza* 4358 (QCNE), *Zak & Espinoza* 4629 (MO, NY, QCNE). **Napo:** Estación de INIAP, San Carlos, 6 km SE de Los Sachas, 250 m, 19 April 1985, *Baker & Trushell* 6099 (NY); Comunidad de Chiro Isla, on Río Napo, 200–275 m, 75°52'30'W,

0°36'06'S, 15 April 1990, *Bensman* 148 (MO); Estación Biológica Jatun Sacha, Río Napo, 8 km al E. de Misahualli, 450 m, 77°36'W, 1°04'S, 22 October 1988, *Cerón M. & Iguago* 5430 (MO, NY, QCNE), 400 m, 10 August 1989, *Cerón M.* 7378 (MO, NY, QCNE); Cerro Antisana, 2 miles SE of Borja, 5700 ft, 3 August 1960, *Grubb* et al. 1210 (K); via Hollín-Loreto, entre Río Guamani y Río Pucuno, km 40, 1200 m, 12 December 1987, *Palacios* 2222 (MO, NY, QCNE). **Pastaza:** Hacienda San Antonio del Barón von Humboldt, 2 km al NE de Mera, 1300 m, 78°06'W, 1°27'S, 27 February–19 March 1985, *Baker* et al. 5651 (NY); Lorocachi, 2–4 km SSE of military camp, 200 m, 75°58'W, 1°38'S, 24 May 1980, *Brandbyge & Asanza* C. 30829 (AAU, NY); Ceilán, path from Ceilán to Río Cononaco on S. side of Río Curaray, 200 m, 75°40'W, 1°36'S, 7 June 1980, *Brandbyge & Asanza* C. 31783 (AAU, F, MO); along road between Puyo & Macas at km 19 S. of Puyo, 1200 m, 77°53'W, 1°37'S, 9 October 1980, *Croat* 50575 (MO); pozo petrolero Moretecocha de ARCO, 75 km al E. de Puyo, 580 m, 77°25'W, 1°34'S, 4–21 October 1990, *Gudiño* et al. 1008 (MO, NY, QCNE); 17 km N. of Palora, c. 2 km N. of Tashapi (Río Pastaza crossing), 46 km S. of Puyo on Puyo-Palora road, c. 900 m, 77°52'W, 1°42'S, 17 February 1984, *Knapp & Mallet* 6303 (BH, QCA, QCNE, US); Kapasí (Amuntai), Río Pastaza, 235 m, 76°48'W, 2°31'S, 14–20 July 1988, *Lewis* et al. 13738 (QCNE); Capitaine Chiriboga, Río Pastaza, vicinity of army base, 235 m, 76°49'W, 2°32'S, 25–29 July 1988, *Lewis* et al. 13898 (QCNE); pozo petrolero Villano 2, 100 m del Río Lliquino, 360 m, 77°27'W, 1°29'S, 24 July 1992, *Palacios* 10299 (QCNE); vicinity of Puyo, 750–1000 m, August 1939, *Skutch* 4466 (K); pozo petrolero Villano 2 de ARCO, entre los ríos Iquino y Villano, 350 m, 77°27'W, 1°29'S, *Tirado* et al. 189 (QCNE). **Sucumbíos:** Along road from Puerto Carmen de Putumayo, (on Colombian frontier) and Lago Agrio, vicinity of Tarapoa, 76 km E. of Lago Agrio, 240 m, 76°23'W, 0°07'S, 27 April 1984, *Croat* 58622 (MO, NY); 4.2–7.5 km W. of Lago Agrio, near Lago Agrio-Baeza road, c. 340 m, 31 March 1972, *MacBryde & Dwyer* 1367 (MO, US). **Tungurahua:** Along Río Topo (Río Toro on maps) above village of Río Negro, on Baños-Mera road,

1200–1400 m, 78°13'W, 1°22'S, 22 January 1984, *Knapp & Mallet* 6183 (BH, QCA, QCNE); **Zamora-Chinchipe:** Above Valladolid on road to Yangana, 2300 m, 1 February 1985, *Harling & Andersson* 21373 (GB, NY); Parque Nacional Podocarpus, Quebrada San Francisco, along Loja-Zamora road, 2040–2250 m, 79°05'W, 3°58'S, 23 June 1988, *Øllgaard* 74954 (AAU, QCNE).

PERU. San Gaván, August 1854, *Lechler* 2464 (K); Casapi, *Matthews* 1967 (K); **Amazonas:** Alrededor de la comunidad Kusu, Río Numpatkin, 1100–1300 ft, 10 March 1973, *Kayap* 536 (MO); Quebrada Huampami lugar Tsaesim, 7200 ft, 4 April 1973, *Kayap* 575 (MO); Huampami, 800–850 ft, 29 July 1974, *Kayap* 1347 (M); Bongara, 4 km N. of Pomacochas on road to Rioja, trail down gorge to W. of road, 2150–2200 m, 77°22'W, 5°40'S, 2 June 1986, *Knapp et al.* 7506 (MO); Bongará, Shillac, N. by trail from Pedro Ruiz, 2300 m, 78°01'W, 5°49'S, 31 August–2 September 1983, *Smith & Vásquez* S. 4899 (MO, NY); Bongara, Sipabamba, Shilla, c. 1850–1900 m, 6 May 1981, *Young & Eisenberg* 375 (F, MO, NY). **Cajamarca:** Cutervo, San Andrés de Cutervo, carretera entre San Andrés y Santo Tomás, km 15 a 20, 15 March 1989, *Díaz & Beltrán* 3335 (NY); Colasay, 2500 m, 30 October 1961, *Woytkowski* 7000 (MO). **Cusco:** Atalaya, near junction of Río Carbon & Río Alto Madre de Dios, 31 July 1973, *Foster* 2411 (K, MO); Limonchayoc, c. 1 km from Cuzco-Pto. Maldonado road at Huayhumbe, c. 16 km E. of Quincemil, 400–500 m, 70°40'W, 13°15'S, 25–26 April 1984, *Knapp & Mallet* 6396 (BH, US, USM); Kosñipata, Quitacalzon (Quebrada Sta. Alicia, c. km 163 Lucre-Paucartambo-Shintuya road, 1100–1200 m, 71°15'W, 13°07'S, 11 May 1984, *Knapp & Mallet* 6427 (BH, US, USM); near Pilcopata, road from Pilcopata to Patria, 6 February 1975, *Plowman & Davis* 5006 (GH); Kosñipata valley, Río Tono, first foothill ridge on road N. of Patria, 750–850 m, 71°12'W, 13°07'S, 27 November 1985, *Wachter* 81 (F). **Huánuco:** Tingo María, valley of Río Huallaga, c. 7000 ft, 11–14 July 1937, *Belshaw* 3089 (US); Tingo María-Pucallpa, 1510 m, 15°WNW, 5 January 1971, *Ellenberg* 3889 (MO); Pachitea, Codo de Pozuzo, floodplain of Río Pozuzo after emerges from mountains, trail N. of settlement to Río Mashoca, 500 m, 75°25'W, 9°37'S, 19 October 1982, *Foster* 9298 (MO); La Divisoria, Tingo María-Pucallpa, near Loreto border, 1150–1350 m, 29 March 1977, *Gentry et al.* 18876 (F, MO); Río Huallaga canyon below Río Santo Domingo, c. 4000 ft, 3 June 1923, *Macbride* 4243 (F); Leoncio Prado, Dist. Emilio Valdizan, along old road to La Divisoria, 1380 m, 16 April 1976, *Plowman* 5906 (GH); Cuchero, 1830, *Poeppig* s.n. (K, W), 1625 (W); Pampayaco, October 1829, *Poeppig* 1469 (F, W); between Acomayo & Carpish Divide, 8500 ft, October 1945, *Sandeman* 5270 (K); Bosque Nacional de Iparia, a lo largo del Río Pachitea cerca del campamento Miel de Abeja, 1 km arriba de Tournevista o unos 20 kms arriba de la confluencia con el Río Ucayali, 300–400 m, 26 December 1966, *Schunke V.* 1414 (F, MO); Bosque Nacional de Iparia, a lo largo del Río Pachitea cerca del campamento Miel de Abeja, 1 km arriba de Tournevista o unos 20 kms arriba de la confluencia con el Río Ucayali, W. de caserío La Paz, 23 May 1967, *Schunke V.* 1981 (F, GH, K); Calpar Bella, cueva de las Huarñinos, margen izquierda del Río Monzón, 700–900 m, 29 July 1976, *Schunke V.* 9454 (MO); E. de Tingo María, cerca al Cerro Quemado, 672–800 m, 21 February 1978, *Schunke V.* 9914 (MO), 2 May 1978, *Schunke V.* 10108 (MO); Divisoria, 1700 m, 26 September 1946, *Woytkowski et al.* 560 (F). **Junín:** E. of Quimiri bridge, near La Merced, 800–1300 m, 1–3 June 1929, *Killip & Smith* 23939 (F, NY, US); Puerto Yessup, c. 400 m, 10–12 July 1929, *Killip & Smith* 26221 (US), *Killip & Smith* 26239 (NY, US). **Loreto:** Río Tigre, caserío Nuevo Canaan, Lago Lamas Tipishca, 15 December 1979, *Ayala et al.* 2543 (MO, NY); Peña Negra, 25 km SW of Iquitos, 1 August 1972, *Croat* 18651 (F, MO, NY); Mishana, Río Nanay, c. 130 m, 20 September 1978, *Díaz & Jaramillo* 576 (MO); Jenaro Herrera, margen derecha Río Ucayali, 2 September 1982, *Encarnación* 26268 (MO, US); Jenaro Herrera, Río Ucayali, 7 December 1977, *Gentry et al.* 21185 (MO); Andoas, Río Pastaza near Ecuador border, 210 m, 76°28'W, 2°48'S, 15 August 1980, *Gentry et al.* 29790 (MO); Iquitos, c. 100 m, 2–8 August 1929, *Killip & Smith* 27329 (F, NY, US); Soledad on Río Itaya, c. 110 m, 20–22 September 1929, *Killip & Smith* 29584 (F, MA, NY, US); Yurimaguas, lower Río Huallaga, c. 135 m, 22 August–2 September 1929, *Killip & Smith* 29076 (NY, US); San Antonio, on Río Itaya, c. 110 m, 18 September 1929, *Killip & Smith* 29420 (NY, US), *Killip & Smith* 29493 (F, NY, US); Balsapuerto, c. 220 m, January 1933, *Klug* 2864 (F, NY, US); Gamitanacocha, Río Mazán, 100–125 m, 18 February 1935, *Schunke V.* 280 (F, GH, NY, US); Santa María de Nanay, NW del Río Nanay, 130 m, 27 February 1968, *Schunke V.* 2432 (F); Alpahuayo, field station of IIAP, c. 26 km along Iquitos-Nauta road, 130 m,

23 August 1988, *van der Werff et al.* 10219 (MO, NY); Jenaro Herrera, c. 170 m, 73°45'W, 4°50'S, 3 July 1981, *Vásquez et al.* 2151 (MO); carretera Nauta-Iquitos, c. 150 m, 73°45'W, 4°29'S, 17 July 1981, *Vásquez* 2243 (MO); Pto. Almendras, 122 m, 73°15'W, 3°45'S, 19 October 1981, *Vásquez & Jaramillo* 2584 (MO), 7 December 1982, *Vásquez & Jaramillo* 3499 (MO); Recreo, Manatí, 110 m, 72°50'W, 3°42'S, 17 October 1983, *Vásquez & Jaramillo* 4475 (AAU, MO, NY); Nauta, 160 m, 73°35'W, 4°32'S, 3 June 1984, *Vásquez & Jaramillo* 5097 (F, MO, NY); Pto. Almendras, Río Nanay, 122 m, 73°25'W, 3°48'S, 15 August 1984, *Vásquez & Jaramillo* 5471 (MO, NY); Alpahuayo, estación IIAP, 150 m, 73°30'W, 4°10'S, 6 June 1985, *Vásquez et al.* 6559 (MO); Iquitos, Puerto Almendras-Río Nanay, 122 m, 73°25'W, 3°45'S, 29 December 1986, *Vásquez & Jaramillo* 8680 (MO); Iquitos, Puerto Almendras, 122 m, 73°25'W, 3°48'S, 11 April 1988, *Vásquez & Jaramillo* 10533 (MO); Iquitos, km 4 carretera Iquitos-Nauta, terrenos de CRI, 150 m, 73°20'W, 4°10'S, 14 March 1989, *Vásquez et al.* 11923 (MO, NY); La Victoria on the Amazon River, 6 September 1929, *Williams* 3137 (F). **Madre de Dios:** Parque Nacional de Manú, Cocha Cashu Biological Station, c. 400 m, 71°22'W, 11°52'S, 24 September 1982, *Emmons* 81 (MO), 13 October 1982, *Emmons* 132 (MO), 12 November 1982, *Emmons* 146 (MO); Cocha Cashu, vicinity ox-bow lake of Río Manú, between Panagua & Tayakame, 17–24 August 1974, *Foster et al.* 3312 (F); Río Manu, Cocha Cashu station, 400 m, 9 February 1977, *Foster & Terborgh* 6071 (F), 14 March 1977, *Foster & Terborgh* 6222 (F); Aguas Calientes, across and downriver from Shintuya on Río Alto Madre de Dios, 400–500 m, 71°15'W, 12°40'S, 13 May 1984, *Knapp & Mallet* 6436 (BH, K, US, USM); Manu park, Cocha Cashu uplands, 400 m, 71°04'W, 11°45'S, 18 August 1986, *Núñez* 5770 (MO); Tambopata, Cuzco Amazonico tourist lodge, 69°03'W, 12°33'S, 20 May 1989, *Núñez & Phillips* 10464 (MO). **Pasco:** Pichis valley, Santa Rosa de Chivis, Río Nochos, 9 km SW of Puerto Bermudez on new highway, 300–400 m, 74°58'W, 10°20'S, 7 September 1982, *Foster* 8592 (MO); Pichis valley, San Matías ridge, 10–12 km SW of Puerto Bermudez above Santa Rosa de Chivis trail to Loma Linda, 1000 m, 75°00'W, 10°20'S, 29 September 1982, *Foster et al.* 8969 (MO); Misericordia trail, Lanturachi-Santa Barbara, 2300–3300 m, 75°40'W, 10°20'S, 3 July 1985, *Foster et al.* 10481 (F, NY); San Juan de Cacazu, km 36 of Villa Rica-Pto. Bermúdez road, along Río Chivis, c. 950 m, 75°10'W, 10°38'S, 14 August 1984, *Knapp & Mallet* 6629 (BH, US, USM); km 15 of Palcazu road, km 73 Villa Rica-Isozacín-Pto. Mairo, along Río Palcazu, c. 380 m, 75°10'W, 10°21'S, 17–18 August 1984, *Knapp & Mallet* 6639 (BH, K, MO, NY, US, USM), *Knapp & Mallet* 6644 (BH, K, US, USM), km 28 Repartition-Isozacín, km 86 Villa Rica-Isozacín-Pto. Mairo, along Río La Raya near Amuesha community of Laguna, c. 350 m, 75°10'W, 10°20'S, 22–23 August 1984, *Knapp & Mallet* 6655 (BH, US, USM); Isozacín, forests near PEPP (Proyecto Especial Pichis-Palcazu) camp, Río Isozacín, tributary of Río Palcazu, c. 320 m, 75°13'W, 10°12'S, 27 August 1984, *Knapp & Mallet* 6658 (BH, K, US, USM); Palcazu valley, Río San José in the Río Chucurras drainage, 400–500 m, 75°20'W, 10°09'S, 14 May 1983, *Smith* 4035 (MO); 5 km SE of Oxapampa, 1850 m, 75°23'W, 10°36'S, 24 December 1983, *Smith* 5346 (MO); around Villa Rica, 1400 m, 26 February 1986, *van der Werff et al.* 8281 (MO, NY); Isozacín, 7 October 1984, *Whalen & Salick* 862 (BH, NY). **San Martín:** Tingo María, 625–1100 m, 30 October 1949–19 February 1950, *Allard* 20850 (F); Boquerón pass, 92 km from Tingo María on highway to Pucallpa, c. 400 m, 16 December 1949–5 January 1950, *Allard* 22077, 22116 (US); Tingo María, 625–1100 m, 30 October 1949–19 February 1950, *Allard* 22522 (US); along road between Tocache Nuevo & Juanjuf, c. 965 km N. of Tocache Nuevo, 84 km S. of Juanjuf, 14.1 km beyond bridge over Río Pulcache, c. 600 m, 76°40'W, 7°41'S, 8 April 1984, *Croat* 58022A (MO); along Tocache Nuevo-Juanjuf road, valley of Río Huallaga, 5 km S. of Cachaco, 42 km N. of Tocache Nuevo, 330 m, 76°38'W, 7°58'S, 8 April 1984, *Croat* 58041 (MO); Venceremos, near Amazonas border, km 291 on Rioja-Pomacocha road, 1850 m, 77°40'W, 5°45'S, 11 February 1984, *Gentry et al.* 45399 (MO); Zepelacio, near Moyobamba, c. 1100 m, August 1934, *Klug* 3757 (BM, F, GH, K, MO, NY, WIS); Cuñumbuque-Sisas road, c. 1 hr driving time from Cuñumbuque, c. 1/3 of way to Sisas, c. 850 m, 76°39'W, 6°35'S, 5 June 1984, *Knapp & Mallet* 6476 (BH, K, MO, NY, US, USM); km 436 of Carretera Marginal, c. 10–15 km E. of Naranjo, 180 km W. of Tarapoto, c. 850 m, 77°20'W, 5°53'S, 2 July 1984, *Knapp & Mallet* 6555 (BH, F, K, MO, NY, US, USM); Cataratas de Ahuashiyacu, km 15 of Tarapoto-Yurimaguas road, 700 m, 76°21'W, 6°28'S, 29 July 1986, *Knapp* 7857 (MO, USM); Río Cañuto, Curarelândia, property of J. Schunke V. near km 23 of Tochache Nuevo-Puerto Pizana road, 475 m, 76°36'W, 8°06'S, 19 December 1981, *Plowman &*

Schunke V. 11509 (F, MO, NY); Tocache Nuevo, Quebrada Huaquisha, margen derecha del Río Huallaga, 19 February 1970, *Schunke* V. 3813 (F, G, N, Y, US); San Juan de Pacayzapa, al E. del Puente (carretera a Moyobamba), 900 m, 7 April 1973, *Schunke* V. 5864 (F, NY, US); Quebrada Luís Salas, 5 km NE de Puerto Pizana, 350–370 m, 1 August 1973, *Schunke* V. 6612 (C, MO); Quebrada de Huaquisha, margen derecha del Río Huallaga, 400–450 m, 3 July 1974, *Schunke* V. 7143 (C, MO); camino a Shunté, E. de Puente de Palo Blanco, 500–800 m, 14 July 1974, *Schunke* V. 7394 (MO); E. del Puente del Río Uchiza, 400 m, 24 July 1974, *Schunke* V. 7745 (MO); camino al Roque, 3–4 km de San Juan de Pacayzapa, 1000–1050 m, 3 July 1977, *Schunke* V. 9765 (MO); Cerro Campana, November 1855, *Spruce* 4377 (K, W); San Roque, 1350–1500 m, 6 January 1930, *Williams* 6929 (F), 12 January 1930, *Williams* 7322 (F), 3 February 1930, *Williams* 7689 (F). **Ucayali:** Bosque Nacional von Humboldt, km 86 Pucallpa-Tingo María road, 270 m, 75°00'W, 8°40'S, 8 August 1980, *Gentry & Horna* 29521 (MO); Bosque Nacional von Humboldt, km 86 Pucallpa-Tingo María road, 270 m, 75°00'W, 8°40'S, 6 February 1981, *Gentry* et al. 31046 (MO); Bosque Nacional von Humboldt, km 88 Pucallpa-Tingo María road, 270 m, 75°02'W, 8°45'S, 15 March 1982, *Gentry* et al. 36396 (MO); Río Chino al W. del Restuarant Acapulco, 1000–1100 m, 6 June 1976, *Schunke* V. 9165 (MO); Bosque Nacional de Iparia, a lo largo del Río Ucayali cerca del pueblo de Iparia, unos 80 km arriba del confluencia con el Río Pachitea, 27 August 1968, *Schunke* V. 2712 (F, G, NY, US); Cinchona, carretera antigua a Pucallpa, 1200–1300 m, 9 May 1978, *Schunke* V. 10139 (F, MO); Bosque Nacional von Humboldt, km 86 Pucallpa-Tingo María road, Arboretum, 330 m, 75°05'W, 8°45'S, 4 April 1982, *Smith* et al. 1184 (MO); Bosque Nacional A.V. Humboldt, 74°45'W, 8°40'S, 1 March 1983, *Vásquez* 3876 (MO, NY); Bosque Nacional von Humboldt, Quebrada Tahuahillo, c. 200 m, 20 June 1981, *Young* 967 (MO).

BOLIVIA. sin loc., *Bang* 2513 (NY), *Bang* 2526 (F, GH, K, NY, US); Espirito Santo, 1891, *Bang* 1210 (NY). **Beni:** Prov. Ballivián, Serranía de Pilon Lajas, 15.8 km N. of the bridge over the Río Quiquibey on road to San Borja, 1100 m, 67°11'W, 15°24'S, 19 November 1985, *Solomon* 14806 (MO). **Cochabamba:** Prov. Chapare, along road from Cochabamba to Villa Tunari, N. of Cochabamba, 20 November 1980, *Croat* 51262 (MO); **La Paz:** Nor Yungas, Coroico-Yolosa, subiendo el Río San Juan a 10 kms, 2100 m, 1 April 1982, *Beck* 7498 (F); San Carlos, Mapiri region, 850 m, 26 January 1927, *Buchtien* 1287 (G, GH, US); Mapiri region, San Carlos, bei Sarampijuni, 600 m, 31 December 1926, *Buchtien* 1288 (US); Mapiri region, San Carlos, 850 m, 11 December 1926, *Buchtien* 1289 (NY, US); Hacienda Casana sobre el camino a Tipuani, 1400 m, 13 December 1922, *Buchtien* 7470 (US); Prov. Inquisivi, N. of Cajuata between Turculi & Loma Linda, 1970 m, 67°15'W, 16°49'S, 26 December 1989, *Dorr* et al. 6816 (AAU, NY); Prov. Sud Yungas, Yanacachi, 2200 m, 3 January 1981, *Lieberman* 262 (F); Yungas, 6000 ft, 1885, *Rusby* 766 (NY); Prov. Nor Yungas, 4.6 km below Yolosa, then 19.1 km on road up Río Huarinilla, 1700 m, 67°53'W, 16°12'S, 12 November 1982, *Solomon* 8821 (MO, NY); Prov. Nor Yungas, Serranía de Bella Vista, 16 km N. of Carrasco, 37 km N. of Caranavi on road to Palos Blancos, 1500 m, 67°34'W, 15°35'S, 31 October 1984, *Solomon & Nee* 12674 (MO); Prov. Larecaja, 19 km al SW de Guanay por el camino a Tipuani, 1200 m, 67°59'W, 15°34'S, 23 January 1988, *Solomon* 17675 (NY). **Pando:** Prov. Nicolás Suárez, en la zona de Campoana, junto a la barraca San José, hacia las riberas del Narueda, 290 m, 15 January 1983, *Fernández Casas & Susanna* 8299 (MO, NY).

BRAZIL. **Acre:** Rio Branco, 33 km NNE of Rio Branco on road to Porto Acre (AC-10) then several km E. on Ramal de Canindê, 67°37'W, 9°45'S, 18–28 July 1989, *Daly* et al. 6118 (NY); Placido de Castro, Seringal Triunfo, c. 17 km WNW of Plácido de Castro on road to Rio Branco (AC-040), c. 67°15'W, 10°19'S, 30 July–1 August 1989, *Daly* et al. 6133 (NY); 45 km from Rio Branco on Rio Branco-Brasileia road, 2 October 1980, *Lowrie* et al. 331 (K, NY); 40 km from Rio Branco on Rio Branco-Santa Rosa road, 8 October 1980, *Lowrie* et al. 441 (NY); Rio Jurua between Mundurucus & Tatajuba, 13 May 1971, *Maas* et al. P12903 (NY); Rio Branco, proxima a Colônia Penal, 10 July 1965, *Pires* 10062 (US); km 18 road Cruzeiro do Sul to Japiim, 26 October 1966, *Prance* et al. 2833 (NY); Rio Moa 8 km above Cachoiera Grande, 27 April 1971, *Prance* et al. 12573 (NY). **Amazonas:** E. bank of Rio Madeira, 1 km N. of Humaitá, 2 December 1966, *Prance* et al. 3541 (NY). **Amapá:** Rio Oiopoque, 1 km W. of Cachoiera Utussansain, near frontier with French Guiana, 52°55'W, 2°08'N, 8 September 1960, *Irwin* et al. 48077 (NY). **Mato Grosso:** source of the Jatuarana River, Machado River region, December 1931, *Krukoff* 1599 (G, NY). **Rondonia:** São Lourenço cassiterite mine,

c. 20 km NW of Rio Madeira across from Mutumparaná, c. 7 km N. of S. Lourenço on road to A Macisa mine, 15 July 1979, *Calderon* et al. 2855 (K, US); Presidente Medici, BR 364 (Cuiabá-Porto Vello, km 300, estrada para Alvorada do Oeste, km 24, linha 110, 62°63'W, 11°12'S, 28 June 1984, *Cid* et al. 4829 (K, NY, US); Rio Javari, behind Estirão de Equador, 10 August 1973, *Lleras* et al. P17286 (NY); c. 2 km E. of Mineração at Campo Novo, 300 m, 63°55'W, 10°34'S, 22 April 1987, *Nee* 34977 (K, NY, US).

Solanum anceps is one of the most widespread and variable of the species of section *Pterioidea*. It is basically an Amazonian lowland species, but is found in the Andes in Peru and Bolivia up to elevations of about 2000 m. There is little discernible difference between the high elevation and low elevation forms of *S. anceps* as so often occurs in other groups of *Solanum* (see Knapp, 1986a, 1991a). Considerable geographical variation in pubescence exists within *S. anceps*, with some densely hairy populations being found throughout the species range. New leaves are always more densely pubescent than mature leaves and there may be a developmental or genetic component to pubescence in *S. anceps*. Leaf size also varies a great deal in *S. anceps*, with some leaves attaining very large sizes in shady habitats. Purple leaf undersides are common in *S. anceps* and are noted on many herbarium labels. Unlike in *S. savanillense*, the purple colour of leaves is not also found in flowers (see discussion of *S. savanillense*). The senior author has seen plants with and without purple leaves growing side by side, so perhaps there is a genetic rather than environmental cause for this characteristic.

In lowland Peru (departments of Loreto & Ucayali), a series of specimens appear quite distinct. These plants (given a manuscript name honouring A.C. Smith by C.V. Morton) have longer petioles, more truncate leaf bases, and somewhat more pointed fruits, but a series of well-marked intermediates occur and thus we prefer to retain this variant within *S. anceps*. Some specimens from Bolivia have more strongly decurrent leaf bases than those from farther north, but again, a complete range of intermediates exist. The degree to which these forms are reproductively isolated and may be in the process of speciation or differentiation is worth further study. Other characters, such as DNA sequence or leaf chemistry, may differ in concert with the morphological ones observed here.

4. *Solanum angustialatum* Bitter in *Reprim nov. Spec. Regni veg.* 11: 471 (1912). Type: Peru, San Martín, near Tarapoto, *Spruce* 4849 (W!-holotype [F neg. 33045, F!, MO!, US!]; BR!, G!, K!-isotypes).

Figs 4b, 5d, 13.

Small single-stemmed *shrub or herb*, to c. 1 m tall. *Stems* c. 5 mm in diameter, completely glabrous, green or purple, conspicuously white-lenticellate, conspicuously winged, the wing c. 4 mm wide and often purple, the internodes usually short. *Leaves* simple, 13–35 × 4–15 cm, elliptic, with 18–20 pairs of primary veins, completely glabrous, occasionally purple abaxially, the base narrowing c. 1–3 cm from the stem to a winged petiole, the apex acuminate, occasionally abruptly; petiole 1–3 cm, strongly winged, the wings continuing onto the stem. *Inflorescence* axillary, 1–3 cm long, occasionally 2 per axil, simple, with c. 2–3 flowers at a time, c. 30 pedicel scars, minutely papillate. *Buds* globose, 1.5–2 mm in diameter, exserted from the calyx tube. *Pedicels* at anthesis 7–8 mm long, c. 0.5 mm in diameter, horizontal with a marked kink, so the flowers are nodding. *Flowers* with the calyx tube 0.5–1 mm long, broadly conical, the lobes c. 0.5 × 1 mm, broadly deltate to rounded, glabrous; corolla white, 4–5 mm in diameter, lobed nearly 3/4 of the way to the base, nodding at anthesis, the lobes very strongly reflexed at anthesis, densely papillate on both surfaces; anthers c. 2 × 1.5 mm, poricidal at the tips, free

portion of the filaments less than 0.05 mm, the filament tube absent; ovary conical, densely red-papillose; style 2–3 mm long, densely white-pubescent with white papillae *c.* 0.05 mm long along its entire length; stigma clavate, often markedly bifid. *Fruit* a conical, green berry, *c.* 1 cm in diameter, 1.5–2 cm long, the beak 2–4 mm long, the surface rugose, the raised portions white; fruiting pedicel 7–8 mm long, erect, enlarged at the apex. *Seeds* 2–3.5 × 1.5–2.2 mm, greenish brown, flattened-round to ovoid-reniform, *c.* 20 seeds per fruit; epidermal cells highly sinuous and irregular, with anticlinal thickenings but without projections.

COMMON NAMES AND USES. None recorded.

DISTRIBUTION. Middle elevation premontane forests in NE Peru, 700–1200 m, only known from the Maynesian Andes (see Spruce, 1908). (Fig. 14).

SPECIMENS EXAMINED

PERU. San Martín: Trail to television antenna, Cerro de la Escalera, km 17.5 of Tarapoto-Yurimaguas road (2.5 km N. of Cataratas de Ahuashiyacu), 850–1200 m, 76°21'W, 6°27'S, 7 September 1986, *Knapp* 8277 (MO, USM); Cataratas de Ahuashiyacu, km 15 Tarapoto-Yurimaguas road, 700 m, 76°21'W, 6°29'S, 19 August 1986, *Knapp & Alcorn* 7792 (MO, USM); trail to television antenna, Cerro de La Escalera, km 17.5 of Tarapoto-Yurimaguas road (2.5 km N. of Cataratas de Ahuashiyacu), 850–1200 m, 76°21'W, 6°27'S, 7 August 1986, *Knapp* 7905 (F, MO, NY, USM); trail to television antenna, Cerro de La Escalera, km 17.5 of Tarapoto-Yurimaguas road (2.5 km N. of Cataratas de Ahuashiyacu), 1200 m, 76°21'W, 6°27'S, 24 January 1987, *Knapp & Mallet* 8567 (K, MO, NY, US, USM).

Solanum angustialatum is only known from the area above Tarapoto (Departamento San Martín, Peru) in wet premontane forest. It is sympatric with *S. anceps* and is perhaps derived from that species. The eastern slopes of the Andes are an area of very high diversity, with many species of extremely local distribution. The type of *S. angustialatum* was collected by Spruce in what he called the Maynesian Andes (Spruce, 1908), an isolated chain running between approximately Pucallpa (Ucayali) and Bagua on the Río Marañón (Departamento Amazonas). Many of the plants collected by Spruce were only known from their types until recent collecting in the area of Tarapoto and the mountains behind it (S.K. in 1986) added substantially to holdings of these plants. Further collecting in other parts of this small but quite distinct mountain range may reveal range extensions for many of these apparent narrow endemics.

The broadly winged stem of *S. angustialatum* is sometimes difficult to see on herbarium specimens, but the strongly decurrent leaves are quite distinctive and unlike those occurring in *S. anceps*.

5. ***Solanum chamaepolybotryon*** Bitter in *Reprim nov. Spec. Regni veg.* **11**: 471 (1912). Type: Peru, San Martín, prope Tarapoto, 1855–56, *Spruce* 4432 (W!-holotype [F neg. 33057, F!, G!, MO!, US!]; K!-isotype).

Small fleshy *herb*, 10–30 cm tall. Stems slender, glabrous or with a few simple uniseriate trichomes in a distinct line along one side, not conspicuously lenticellate, green or purplish. *Leaves* pinnate, *c.* 20 × 10 cm, elliptic to obovate, with *c.* 2 pairs of leaflets, glabrous or pubescent with simple uniseriate trichomes *c.* 0.5 mm long, along the veins, rachis and petiole; petiole *c.* 3 cm long; lateral leaflets 3.5–7 × 1–2.5 cm, with *c.* 5 pairs of primary veins, the base attenuate, the apex acute to acuminate; petiolule *c.* 0.5 cm, lightly winged; basal leaflets equal to the laterals in size and shape; terminal leaflet more obovate, 4.5–8.5 × 1–2.5 cm, the base long-attenuate onto the rachis, the apex acuminate; petiolule 0.5–1 cm long, often winged and not differentiated from the rachis. *Inflorescence* axillary, 0.5–1 cm long, simple, bearing flowers only at the tip, with *c.* 2 flowers open at a time, *c.* 5

scars, glabrous. *Buds* globose, *c.* 1 mm in diameter, exerted from the calyx tube. *Pedicels* at anthesis 3–5 mm long, filiform, horizontal or nodding. *Flowers* with the calyx tube conical, 0.5–1 mm long, the lobes 0.5–1 × 0.5–1 mm, deltate, glabrous or with a few scattered simple, uniseriate trichomes; corolla greenish yellow or purple, 7–8 mm in diameter, lobed nearly to the base, the lobes reflexed (?) at anthesis, minutely papillate at the tips and along the margins; anthers *c.* 1.5 × 0.5 mm, poricidal at the tips, the free portion of the filaments *c.* 0.5 mm long, the filament tube *c.* 0.5 mm long; ovary conical, glabrous; style 2–2.5 mm long, glabrous; stigma minutely capitate. *Fruit* (immature) a conical, green berry, *c.* 4 mm in diameter, *c.* 1 cm long, the beak *c.* 3 mm long, surface unknown, but appearing somewhat rugose; fruiting pedicel *c.* 1 cm long, erect. *Seeds* not seen.

COMMON NAMES AND USES. None recorded.

DISTRIBUTION. In N. Peru in the Maynesian Andes of Spruce (Spruce, 1908). (Fig. 15).

SPECIMENS EXAMINED

PERU. San Martín: Rioja, near km 398 of Carretera Marginal between Pomacochas & Rioja, trail to Quebrada Venceremos and Río Serranoyacu, 1300–1400 m, 10 July 1984, *Knapp & Mallet* 6590 (BH, K, US, USM).

Solanum chamaepolybotryon is the most diminutive species of the *S. mite* species group and apparently only grows as a small, fleshy herb in middle elevation cloud forest in NE Peru. It has only been collected a few times, but is apparently clonal and grows in large groups (*Knapp & Mallet* 6590). This species also occurs in the Maynesian Andes of Spruce (1908, see discussion under *S. angustialatum*) and may be derived from the more widespread *S. mite* or *S. conicum*.

6. ***Solanum conicum*** Ruiz & Pav., *Fl. peruv.* **2**: 88, fig. 162b (1799).

Type: Peru, Huánuco, Chinchao et Cuchero, August, September, *Ruiz & Pavón* s.n. (MA!-lectotype; B [F neg 2602, F!, G!, GH!, MO!, NY!] destroyed, F!-isolectotypes).

Figs 2a, 16.

Solanum alatibaccatum Bitter in *Reprim nov. Spec. Regni veg.* **12**: 68 (1913). Type: Ecuador, Loja, Palandra, 22 October 1906, *André* s.n. (K!-holotype).

Erect or climbing (scrambling) *herb*, to 2 m in length (height). *Stems* *c.* 0.5 cm in diameter, glabrous, greenish, conspicuously white-lenticellate when dry. *Leaves* (10–)15–25(–38) × (6–)12–17(–20) cm, pinnate, elliptic, with (3–)4–5(–9) pairs of leaflets, often unevenly paired and not perfectly opposite, glabrous abaxially, densely pubescent adaxially along the midribs of the leaflets and extending to the rachis, a few scattered trichomes on the lamina, the trichomes *c.* 0.25 mm long, simple, uniseriate, composed of 5–6 cells, drying white; petiole 2–9 cm long; rachis densely pubescent adaxially in a groove with simple uniseriate trichomes *c.* 0.25 mm long; lateral leaflets 6–12 × 1–2.8 cm, lanceolate to narrowly elliptic, with 8–9 pairs of veins, the base truncate, somewhat oblique, the apex long-acuminate, petiolule 0.3–1.5 cm; basal pair of leaflets markedly smaller than the laterals, 1.5–6 × 0.7–2 cm, lanceolate to narrowly elliptic, the base truncate, oblique, the apex long acuminate, petiolule 0.3–1.7 cm; terminal leaflet 7–12 × 1.2–3 cm, elliptic, the base truncate to acute and somewhat decurrent onto the rachis, the apex long acuminate, petiolule 0.3–1.5 cm long. *Inflorescence* 0.7–2.5 cm long, simple or occasionally once-branched, with 3–6 flowers open at a time, with *c.* 10–16 scars, finely and densely pubescent with simple uniseriate trichomes less than 0.25 mm long or with whitish papillae. *Buds* *c.* 0.5 mm in diameter, globose to obovate, exerted from the calyx tube. *Pedicel* at anthesis 0.5–0.8 cm long, *c.*

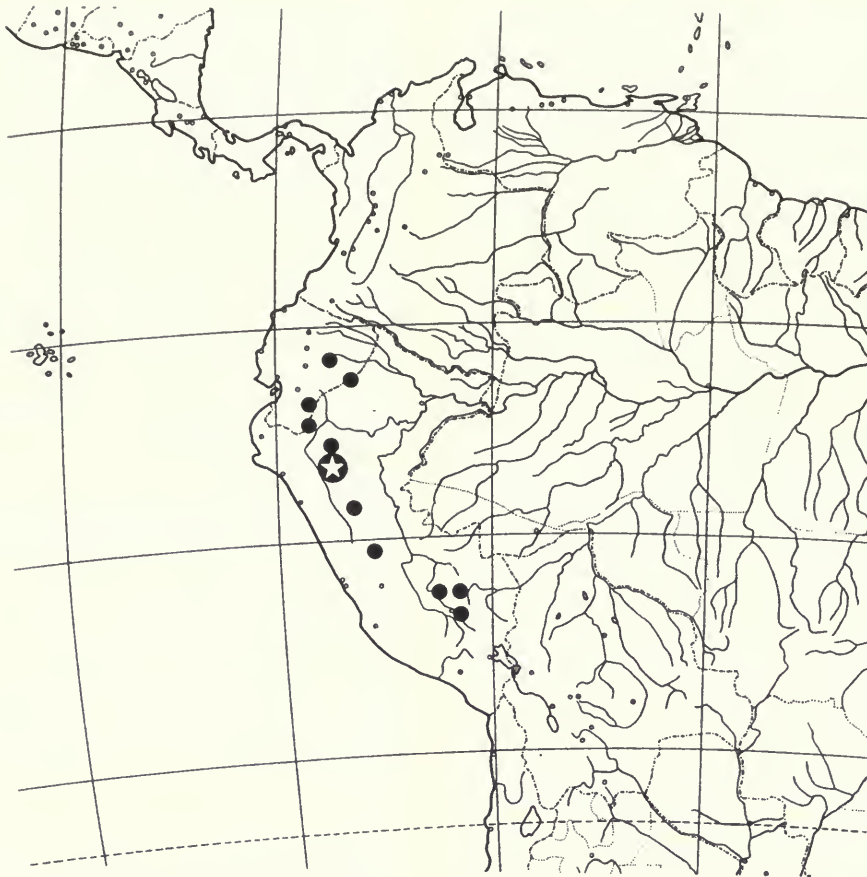


Fig. 15 Distribution of *S. chamaepolybotryon* (star in circle) and *S. conicum* (circles).

0.5 mm in diameter, nodding, finely pubescent like the rest of the inflorescence. *Flowers* with the calyx tube 0.5–1 mm long, conical, the lobes 0.5–1 × c. 0.5 mm, broadly deltate to triangular with an apical projection, papillate to finely pubescent like the rest of the inflorescence; corolla 10–13 mm in diameter, greenish white to white, lobed nearly to the base, the lobes more or less reflexed at anthesis, densely papillate at the tips and margins; anthers c. 2 × 1.5 mm, poricidal at the tips, free portion of the filaments 1–1.5 mm long, the filament tube absent; ovary conical, glabrous; style c. 5 mm long, glabrous; stigma minutely capitate. *Fruit* a long-conical, sharply pointed, green berry, 1.5–1.8 × c. 1 cm, the surface rugose, the rugosities white; fruiting pedicel 0.8–1 cm long, horizontal or nodding. *Seeds* c. 2.0 × 2.0 mm, flattened-round, brown, c. 40 seeds per fruit; epidermal cells sinuous and irregular, with anticlinal thickenings but without projections.

COMMON NAMES AND USES. Ecuador: 'palu rugu' (*Shemluck* 303—stems and leaves as a tea for snakebite).

DISTRIBUTION. Premontane and montane forests, 200–2000 m, S. Ecuador to SE Peru. (Fig. 15).

SPECIMENS EXAMINED

ECUADOR. Pastaza: Kapawí (Amuntai), Río Pastaza, 235 m, 76°48'W, 2°31'S, 14–20 July 1988, *Lewis* et al. 13646 (QCNE); village of Río Chico (8 km from Puyo), near chacra of Reuben Santi, 3 km from village, 1000 m, 21 July 1980, *Shemluck* 303 (F). **Zamora-Chinchipe:** Nangaritzá, Cantón Shaimé, en la unión de los Ríos Nangaritzá & Numpatakaimé, 1000 m, 78°40'W, 4°20'S, 7 December 1990, *Palacios* 6607 (QCNE); hill about 1 km upstream from Shaimé along Río Nangaritzá, 900–1100 m, 16 February

1994, *van der Werff* et al. 13122 (BM).

PERU. Amazonas: Prov. Bongará, Yambrasbamba, 1860–2000 m, 2 March 1967, *Tillet* 673–226 (GH). **Ayacucho:** Estrella, between Huanta & Río Apurímac, c. 500 m, 8, 14 May 1929, *Killip & Smith* 23055 (NY, US). **Cusco:** Paucartambo, vicinity of village of Pilcopata along Río Pilcopata, 700–800 m, 71°10'W, 13°05'S, 10 May 1984, *Knapp & Mallet* 6425 (BH, G, GH, K, NY, US, USM); along Río Carbón near Atalaya, junction of Río Carbón & Río Alto Madre de Dios, 500–600 m, 71°07'W, 13°00'S, 15 May 1984, *Knapp & Mallet* 6452 (BH, K, US, USM); Kosñipata, Quitacalzon (Quebrada Sta. Alicia), c. km 163 of Lucre-Paucartambo-Shintuya road, 1100–1200 m, 71°15'W, 13°07'S, 16 May 1984, *Knapp & Mallet* 6456 (BH, K, US, USM); La Convención, Valle de Santa Ana, above Quillabamba, 5800 ft, 20 January 1975, *Plowman & Davis* 4806 (GH). **Huánuco:** Huacachi, estación near Muña, 1980 m, 20 May 1923, *Macbride* 4134 (F); cumbre de Divisoria, 1600 m, 20 May 1978, *Schunke* v. 10185 (MO). **Madre de Dios:** Manú, Aguas Calientes, across and downriver from Shintuya on Río Alto Madre de Dios, 400–500 m, 71°15'W, 12°40'S, 13 May 1984, *Knapp & Mallet* 6435 (BH, K, US, USM). **Pasco:** Oxapampa, Iscozacín, forests near PEPP (Proyecto Especial Pichis-Palcazu) camp, Río Iscozacín, tributary of the Río Palcazu, 320 m, 75°13'W, 10°12'S, 27 August 1984, *Knapp & Mallet* 6664 (G, K, MO, NY, US); Oxapampa, trail from Río Iscozacín to Ameusha community of Villa America, Río Palcazu Valley, 340 m, 75°15'W, 10°12'S, 31 August 1984, *Knapp & Salick* 6667 (US); 5 km SE of Oxapampa, Oswaldo Müller property, 1850 m, 75°23'W, 10°36'S, 9 December 1982, *Smith* 2905 (NY), 23 May 1983, *Smith* 4170 (K, NY); surroundings of Oxapampa, 1800 m, 4 March 1986, *van der Werff* et al. 8357 (MO, NY); San Juan de Cacazu, km 36 of Villa Rica-Pto. Bermudez road, along Río Chivis, 950 m, 75°10'W, 10°38'S, 14 August 1984, *Knapp & Mallet* 6631 (BH, K, US, USM). **San Martín:** Prov. Rioja, km 436 of Carretera Marginal, c. 10–15 km E. of Naranjo, 180 km W. of Tarapoto, 850 m, 77°20'W, 5°53'S, 2 July 1984, *Knapp & Mallet* 6553 (F, K, US, USM).



Fig. 16 *S. conicum*. Habit: Smith 4170 (NY) and Knapp & Mallet 6456 (K). Fruit: Smith 4170 (NY).

Solanum conicum is superficially very similar to *S. mite* in the vegetative state. Differences include the larger numbers of lanceolate to elliptic (rather than obovate) leaflets with long petiolules, its habit of becoming scandent and rooting along the stem, and its very conical fruit with a pointed apex and rugose surface texture. Leaflets are more elliptic than those of either *S. uleanum* or *S. mite*, and generally have strongly oblique, somewhat truncate bases. *Solanum conicum* can be confused with larger leaved specimens of *S. uleanum*, but the leaflets are not so decurrent on the rachis nor so rounded looking as those of the latter. In southern Peru *S. conicum* more closely resembles *S. mite* than in other parts of its range and non-fruiting specimens are hard to tell apart. Like most of the other species in section *Pterioidea* great variation in pubescence occurs throughout the species range, with some very densely specimens occurring in all areas.

7. *Solanum mite* Ruiz & Pav., *Fl. peruv.* 2: 38, fig. 163a (1799). Type: Peru, Junín, Pozuzo et Chinchao, August, September. Ruiz & Pavón s.n. (MA!-lectotype; B-isolectotype [F neg. 2625 -F!]). Figs 5a, 17.

Solanum pteleifolium Sendtn. in Mart., *Fl. bras.* 10: 15 (1846). Type: Brazil, Amazonas, trajectu Puraque-Goara, R. Negro, June–October, Martius s.n. (M!-lectotype [F neg. 6538 - F!, NY!, US!]; M!-isolectotypes). The original spelling *pteleaefolium* is correctable under Article 60.8 of the *Code* (Greuter et al., 1994) to *pteleifolium*.

Solanum mite subsp. *hexazygum* Bitter in *Reprum nov. Spec. Regni veg.* 11: 10 (1912). Type: Bolivia, La Paz, San Carlos bei Mapiri, 15°S, 700 m, August 1909, Buchtien 1438 (US!-lectotype; NY!-isotype). Bitter cited two herbaria in his original description – Herb. Buchtein, now housed at US and Herb. Vratisl. (either WRSL or BRA, both of which Bitter could have visited) from which we have not been able to obtain a specimen.

Solanum quinquefoliolatum Bitter in *Reprum nov. Spec. Regni veg.* 11: 11 (1912). Type: Brazil, Amazonas, Marary, Rio Jurua, Ule 5201 (B-syntype, destroyed; G!-lectotype [F neg. 23148, F!, MO!, NY!, US!]).

Solanum huallagense Bitter in *Reprum nov. Spec. Regni veg.* 12: 138 (1913). Type: Peru, Loreto, Yurimaguas, Rio Huallaga, May 1885, Spruce 3882 (K!-lectotype; BM!, BR!, W! [F neg. 33079, G!, MO!, US!]-isolectotypes). In the original description of this species, Bitter cites specimens at K, BM, and W. The sheet at K, selected here at the lectotype, is from the first set of Spruce's collections and is annotated in Bitter's hand.

Solanum apiculatibaccatum Bitter in *Reprum nov. Spec. Regni veg.* 12: 141 (1913). Type: Brazil, Acre, Cobija, January 1912, Ule 9731 (No herbarium cited by Bitter, but F neg. 2705 [F!, G!, GH!]) is of a sheet at B that is now no longer extant which may perhaps have been the type).

Small single-stemmed *shrub* to 1 m tall, often growing in large colonies in open places. *Stems* c. 1 cm in diameter, green, white-lenticellate, very woody at the base, when dry usually hollow, extremely variable in pubescence, from glabrous to densely pubescent with simple uniseriate trichomes 1–1.5 mm long, these drying white and cateniforme. *Leaves* pinnate, 10–50 × 7–25 cm, elliptic to obovate, with 2–5 pairs of leaflets, the leaflets not always perfectly opposite, the pubescence reflecting that of the entire plant, glabrous to densely pubescent both adaxially and abaxially with simple uniseriate trichomes on the veins and the lamina, the trichomes 1–2 mm long, white, leaves glabrescent with age, but not markedly so, leaves rarely purple abaxially; petiole 5–15 cm long; lateral leaflets

elliptic to obovate, 7.5–15 × 2–3 cm, with c. 12–14 pairs of primary veins, the base attenuate, markedly oblique and enlarged basiscopically, the apex acute to acuminate; petiolule 2–3 mm; basal leaflets usually somewhat smaller than the laterals, but similar in shape; terminal leaflet obovate, usually much wider than the laterals, 9–15 × 3.5–8(–10) cm, the base attenuate, usually winged and decurrent onto the rachis, the apex acute to acuminate; petiolule winged onto the rachis. *Inflorescence* axillary, 0.5–5 cm, 1–8 arising from an axil, occasionally once-branched, bearing 5–10 flowers at anthesis, with up to 100 scars, pubescence as the rest of the plant, glabrous to densely pubescent. *Buds* globose, c. 2 × 2 mm, exerted from the calyx tube. *Pedicels* at anthesis 4–6 mm long, filiform, nodding. *Flowers* with the calyx tube 1–1.5 mm, broadly conical, abruptly narrowing to the pedicel, the lobes 1–1.5 × c. 1 mm, deltate, glabrous to sparsely pubescent with simple uniseriate trichomes like the rest of the inflorescence; corolla 5–6 mm in diameter, greenish white, lobed nearly to the base, the lobes strongly reflexed at anthesis, the tips and margins minutely papillate, occasionally in pubescent plants with a few simple uniseriate trichomes abaxially; anthers 1–1.5 × 1–1.5 mm, poricidal at the tips, papillose abaxially, the free portion of the filaments 0.5–1 mm long, the filament tube 0.05 mm; ovary conical, glabrous; style 3–4 mm long, glabrous or minutely papillose in the lower half, some flowers short-styled and the style included in the anther cone; stigma capitate to slightly clavate. *Fruit* a globose, occasionally somewhat apically pointed, green berry, 0.8–1.2 cm in diameter, 1–1.2 cm long, the surface smooth; fruiting pedicel 0.8–1 cm long, nodding. *Seeds* 2.3–3.0 × 1.6–2.3 mm, ovoid-reniform, brown, 35–60 seeds per fruit; epidermal cells sinuous and irregular, with anticlinal thickenings but without projections.

COMMON NAMES AND USES. Peru: 'arco sacha blanco' (Martin et al. 1619).

DISTRIBUTION. Throughout the Amazon basin from Colombia and the E. slopes of the Andes in Peru and Bolivia to the mouth of the Amazon in Brazil, from nearly sea level to 1500 m (Fig. 18).

SPECIMENS EXAMINED

COLOMBIA. Putumayo: Selva higrofila entre Quebrada de la Hormiga y San Antonio de Güamaes, 330 m, 18 December 1940, Cuatrecasas 11151 (US); Río Caqueta, downriver from Puerto Limón, 300–350 m, 20 December 1968, Plowman 2185 (GH).

ECUADOR. Napo: Estación Biológica Jatun Sacha, 450 m, 77°36'W, 1°04'S, 24 August 1988, Cerón & Cerón 4604 (MO, NY, QCNE); Estación Biológica Jatun Sacha, Río Napo, 8 km al E. de Misahualli, 400 m, 77°36'W, 1°04'S, 11–14 April 1989, Céron 6389 (MO, NY, QCNE); Reserva Faunística Cuyabeno, Río Aguariico, Zancudo detras del Campamento militar, 230 m, 75°32'W, 0°29'S, 25 September 1991, Palacios et al. 7684 (QCNE); Estación Biológica Jatun Sacha, S. floodplain of Río Napo, 375–400 m, 77°36'–37'W, 1°04'S, 30 July 1990, Webster 28483 (QCNE). **Pastaza:** Lorocachi, pica a Lagatococha a 1 hora siguiendo margen derecha del Río Curaray, 200 m, 75°59'W, 1°39'S, 1 June 1980, Jaramillo et al. 31719 (AAU, F, NY). **Zamora-Chinchipe:** Taisha, 1500 ft, 5 February 1962, Cazalet & Pennington 7676 (B); Shaime, at junction of Río Nangaritz & Río Numpatakai, 100–1080 m, 78°42'W, 4°22'S, 7 December 1990, Øllgaard 98451 (AAU, QCNE).

PERU. Amazonas: Bagua, Cordillera Colan SE of Peca, 7500–7900 ft, 7 October 1978, Barbour 3831 (MO); trail E. from La Peca into Serrania de Bagua, 100–1400 m, 15 June 1978, Gentry et al. 23086 (F, MO); Bongara, c. 7 km above Pedro Ruiz on road to Pomacochas, c. 1500 m, 77°57'W, 5°58'S, 3 July 1984, Knapp & Mallet 6561 (BH, US, USM); 8 km above Pedro Ruiz (Jazan) on road to Pomacochas, 1500–1600 m, 77°53'W, 5°55'S, 3 June 1986, Knapp & Alcorn 7541 (C, MO, USM). **Huánuco:** Tingo María, 625–1100 m, 30 October 1949–19 February 1950, Allard 20481 (F, US); Tingo María, 7 July 1940, Asplund 12043 (US); highway Tingo María-La Oroya, 15.5 km W. of Tingo María, March 1977, Boeke 1200 (NY); at Río Huallaga at Tingo María, 4 October 1972, Croat 21039 (F, GH, MO); on route 16, near km 39



Fig. 17 *S. mite*. Habit: Knapp et al. 6324 (K), Buchtien 1249 (US). Fruit: Knapp & Mallet 7027 (NY).

N. of Tingo María, Cordillera Azul, 10 November 1975, *Davidson* 3487 (F); Hda. Shapigilla, cerca a Tingo María, 700–800 m, 10 August 1946, *Ferreya* 880 (GH, US, USM), 25 February 1947, *Ferreya* 1575 (NY, US, USM); Tulumayo, entre Tingo María y Divisoria, carretera Huánuco-Pucallpa, 600–700 m, 5 August 1947, *Ferreya* 2138 (US, USM); Pachitea, Codo de Pozoso, floodplain of Río Pozoso as it emerges from the mountains, 450 m, 75°25'W, 9°40'S, 16 October 1982, *Foster* 9198 (NY); Tingo María, forest reserve behind University, 780–900 m, 28 March 1977, *Gentry & Daly* 18773 (F); Tingo María, c. 600 m, 1 June 1977, *Hart* 596 (A); Muña, c. 7000 ft, 23 May–4 June 1923, *Macbride* 4001 (F); R. bank of Río Huallaga near Cayumba, 790 m, 20 October 1936, *Mexia* 8326a (GH, K); Jardín Botánico de Tingo María, Vda. Pimentel 358, 670 m, 8 December 1981, *Plozman & Ramírez* R. 11212 (F, K); Tingo María, February 1944, *Soukup* 2210 (US); Bosque Nacional de Iparia, a lo largo del Río Pachitea cerca del campamento Miel de Abeja, 1 km arriba del pueblo de Tournevista o unos 20 km arriba de la confluencia con el Río Ucayali, 300–400 m, 28 November 1966, *Schunke* V. 1280 (US); 10 km downstream from Tingo María, 630 m, 30 October 1938, *Stork & Horton* 9536 (F, K). **Junín:** valley of Río Ulcumayo, 4–10 km W. of San Ramón, 800–1100 m, 31 November 1962, *Illis & Illis* 284 (K, NY, WIS); Chanchamayo, 14 October 1863, *Isern* 2241 (F); La Merced, c. 700 m, 29 May–4 June 1929, *Killip & Smith* 23561, 24066 (F, NY, US); Río Paucartambo valley, near Perene bridge, 700 m, 19 June 1929, *Killip & Smith* 25331 (F, GH, US); Pichis trail, 625 m, 28 June–8 July 1929, *Killip & Smith* 26140 (NY, US); Chanchamayo, along Río Colorado, N. bank, W. of Puente Colorado, 12 km N. of La Merced, c. 850 m, 22 March 1984, *Knapp* et al. 6324 (BH, F, GH, K, NY, US, USM); La Merced, c. 2000 ft, 10–24 August 1923, *Macbride* 5267 (F); La Merced, 2500 ft, August 1945, *Sandeman* 5043 (K); 2 km W. of San Ramón, along river, 8 October 1984, *Whalen & Salick* 864 (BH, NY, USM). **Loreto:** Yurimaguas-Tarapoto road, 15 km SW of Yurimaguas, 180 m, 76°13'W, 5°59'S, 10 October 1985, *Gentry* et al. 52221 (MO); Explorama Tourist Camp Yanamono, halfway between Indiana and mouth of Río Napo, 120 m, 72°50'W, 3°28'S, 20 February 1988, *Gentry* et al. 61713 (NY); Yurimaguas, lower Río Huallaga, c. 135 m, 23 August–7 September 1929, *Killip & Smith* 27614 (BM, F, NY, US); Puerto Arturo, lower Río Huallaga below Yurimaguas, c. 135 m, 24–25 August 1929, *Killip & Smith* 27760 (F, NY, US); between Yurimaguas & Balsapuerto, lower Río Huallaga basin, 135–150 m, 26–31 August 1929, *Killip & Smith* 28108 (NY, US); Balsapuerto, c. 220 m, January 1933, *Klug* 2872 (A, BM, F, G, GH, K, MO, NY, US); Yanamono, Explorama Tourist Camp on Río Amazonas between Indiana & mouth of Río Napo, c. 80 km N. of Iquitos, c. 100 m, 72°48'W, 3°28'S, 22 July 1984, *Knapp* 6592 (BH, K, US, USM); Iquitos and vicinity, along Río Amazonas, July 1967, *Martinet* et al. 1619 (K); Isla Escabino near Santa María, c. 100 m, 14 March 1974, *McDaniel & Rimachi* Y. 18383 (IBE, US), 1 July 1974, *McDaniel & Rimachi* Y. 18903 (IBE, NY); Río Amazonas, Isla Rondña, opposite Leticia, 18 March 1977, *Plozman* et al. 6401 (GH); carretera Iquitos a Santa María, 6 September 1973, *Rimachi* Y. 507 (F, IBE, US); Isla Iquitos, Santa Martha, 18 February 1974, *Rimachi* Y. 876 (IBE, NY, US); Yanamono, campamento Explorama lodgel, 106 m, 72°50'W, 3°30'S, 17 April 1985, *Vásquez & Jaramillo* 6370 (MO), 10 October 1986, *Vásquez & Jaramillo* 8287 (MO, NY); Iquitos, Buena Suerte, Río Itaya, 130 m, 73°30'W, 4°10'S, 15 November 1986, *Vásquez & Jaramillo* 8362 (F, NY); Indiana, Yanamono, 106 m, 72°50'W, 3°30'S, 19 February 1989, *Vásquez & Jaramillo* 11699 (NY); La Victoria on the Amazon River, August–September 1929, *Williams* 2829, 2923 (F); Fortaleza, Yurimaguas, lower Río Huallaga, 155–210 m, October–November 1929, *Williams* 4264 (F); Sapoto-yacu, Santa Rosa, lower Río Huallaga, 155–210 m, October–November 1929, *Williams* 4905 (F); Puerto Arturo, Yurimaguas, lower Río Huallaga, 155–210 m, October–November 1929, *Williams* 5351 (F). **Madre de Dios:** Tambopata, c. 30 air km or 70–80 river km SSW of Puerto Maldonado at Río La Torre (Río d'Orbigny)/Río Tambopata (SE Bank), Tambopata Nature Reserve, c. 260 m, 69°17'W, 12°49'S, 16 April 1980, *Barbour* 4800 (MO), 31 May 1980, *Barbour* 5461 (F); Tambopata Reserved Zone, 5.1 km down main trail from Explorer's Inn, near Laguna Cocococha, 69°17'W, 12°50'S, 6 March 1988, *Bell & Wiser* 88-8 (NY, US); primary floodplain of Río La Torre, La Torre trail in Tambopata Reserved Zone, 69°17'W, 12°50'S, 7 March 1988, *Bell & Wiser* 88-40 (AAU, G, US); Tambopata, 280 m, 69°18'W, 12°50'S, 26 February 1984, *Gentry* et al. 46254 (MO); Río Tambopata, near Puerto Maldonado, 280 m, 9 November 1986, *Núñez* 6473 (F, NY); Cuzco Amazonico, trail 1, 15 km NE of Puerto

Maldonado, 200 m, 69°03'W, 12°33'S, 27 May 1989, *Núñez* et al. 10555 (MO); Explorer's Inn at confluence of Río Tambopata & Río La Torre, 39 km SW of Puerto Maldonado, Río La Torre trail, 69°20'W, 12°50'S, 22 September 1984, *Smith & Shuler* 177 (F, US), 13 October 1985, *Smith* et al. 713 (K, NY, US), 17 October 1985, *Smith* et al. 788 (NY, US); Explorer's Inn, near the confluence of Río Tambopata & Río La Torre, 39 km SW of Pto. Maldonado, Laguna Chica trail, 69°20'W, 2°50'S, 17 January 1989, *Smith* et al. 1355 (NY, US); Tambopata Wildlife Reserve, 30 km S. of Puerto Maldonado, 260 m, 69°17'W, 12°15'S, 11 October 1984, *Young & Stratton* 24 (NY); Tambopata Reserve, junction Río Tambopata & Río La Torre, 250 m, 16 March 1981, *Young* 126 (NY), 18 March 1981, *Young* 134 (F, NY). **Pasco:** Eneñas-Alto Yurinaki-La Florida road, c. 9 km E. of Villa Rica, 1250–1400 m, 75°15'W, 10°50'S, 12 August 1984, *Knapp & Mallet* 6623 (BH, K, NY, US); c. 1 km from division of Villa Rica-Pto. Bermúdez road and Villa Rica-Palcazu road, on Palcazu branch, along small tributary to Río Cacazu, c. 500 m, 75°10'W, 10°30'S, 15 August 1984, *Knapp & Mallet* 6632 (BH, K, NY, US); Pozuzo, c. 2000 ft, 20–22 June 1923, *Macbride* 4676 (F). **San Martín:** Vicinity of Uchisa, 17–18 July 1937, *Belshaw* 3109 (GH, US); Pueblo Mantención, property of Hernan Ortiz, c. 10 km S. of Tocache Nuevo, 400–700 m, 26 April 1983, *Bohs & Schunke* V. 2168 (F, GH); Tocache Nuevo, Río de la Plata, 550–600 m, 76°25'W, 8°10'S, 2 November 1980, *Croat* 51014 (F, MO); along road between Tarapoto & Moyobamba, c. 10 km NW of Tabalosos, c. 500 m, 76°43'W, 6°15'S, 7 November 1980, *Croat* 51156 (MO); Zepelacio, near Moyobamba, c. 1100 m, June 1934, *Klug* 3686 (A, BM, F, GH, K, MO, NY, US); Juanjui, Alto Río Huallaga, 400–800 m, February 1936, *Klug* 4252 (BM, F, GH, K, NY, US); on road between Cuñumbuque & Sisas, c. 1 hr driving time from Cuñumbuque, 1/3 of way to Sisas, c. 850 m, 76°39'W, 6°35'S, 5 June 1984, *Knapp* et al. 6473 (BH, K, US, USM); c. 5 km N. of Tarapoto along Río Shilcayo, c. 400 m, 76°22'W, 6°30'S, 7 June 1984, *Knapp & Mallet* 6484 (BH, F, K, NY, US), *Knapp & Mallet* 6486 (BH, K, US, USM); km 28 of Tarapoto-Yurimaguas road, 650 m, 76°15'W, 6°25'S, 20 June 1984, *Knapp & Mallet* 6526 (BH, K, US, USM); Lamas, c. km 62 of Tarapoto-Yurimaguas road, along Río Yuracyacu, c. 260 m, 76°18'W, 6°18'S, 23 June 1984, *Knapp & Mallet* 6538 (BH, K, MO, NY, US, USM); km 436 of carretera Marginal, c. 10–15 km E. of Naranjo, 180 km W. of Tarapoto, c. 850 m, 77°20'W, 5°53'S, 2 July 1984, *Knapp & Mallet* 6554 (BH, F, K, US, USM); Naranjal, trail to Jorge Chavez, km 85 of Tarapoto-Yurimaguas road, c. 200 m, 76°17'W, 6°15'S, 2 April 1986, *Knapp & Mallet* 6931 (AAU, F, MO, NY, USM); 5–15 km E. of Shapaja on road to Chazuta, 200–300 m, 76°10'W, 6°36'S, 9 April 1986, *Knapp & Mallet* 7027 (NY, USM), *Knapp & Mallet* 7033 (MO, NY, USM), *Knapp & Mallet* 7036 (MO, NY, USM); Toma del Shilcayo, along Río Shilcayo N. of Tarapoto, 380–400 m, 76°22'W, 6°30'S, 14 April 1986, *Knapp & Mallet* 7065 (NY, USM), *Knapp & Mallet* 7068 (MO, USM); Convento, trail to Tioyacu & Neuvo Lamas (then to Río Shanusi), km 68 of Tarapoto-Yurimaguas road, c. 200 m, 76°17'W, 6°16'S, 19 April 1986, *Knapp & Mallet* 7086 (NY, USM), *Knapp & Mallet* 7087 (F, NY, USM), 24 April 1986, *Knapp & Mallet* 7212 (F, MO, NY, USM), 26 April 1986, *Knapp* et al. 7218 (MO, NY, USM); trail to Boca Toma del Shilcayo, along Río Shilcayo N. of Tarapoto, 400 m, 76°22'W, 6°30'S, 20–21 May 1986, *Knapp & Alcorn* 7331 (F, USM), *Knapp & Alcorn* 7332 (MO, NY, USM), 12 August 1986, *Knapp* 8012 (MO, NY, USM); km 54 of Tarapoto-Yurimaguas road, 350 m, 76°18'W, 6°23'S, 3 September 1986, *Knapp* 8264 (MO, NY, USM); Caserío El Progreso, km 30 of Tarapoto-Yurimaguas road, 700 m, 76°19'W, 6°25'5"S, 25 September 1986, *Knapp & Mallet* 8440 (MO, NY, USM); San Juan de Pacayzapa, E. del puente (carretera a Moyobamba), 900 m, 5 April 1973, *Schunke* V. 5837 (K, NY, US); camino a Roque, 8 km de San Juan de Pacayzapa, 800–900 m, 2 May 1973, *Schunke* V. 6169 (F, NY, US); Quebrada de Santiago, al E. de Puerto Pizana, 350–380 m, 29 July 1973, *Schunke* V. 6507 (C); Quebrada de Santa Rosa de Cahiyacu, carretera a Progreso, 500–700 m, 19 July 1974, *Schunke* V. 7595 (F, G, MO, NY, US); Pucayacu, Tarapoto, 750 m, 11 December 1929, *Williams* 6045 (F); San Roque, 1350–1500 m, 6 January 1930, *Williams* 6956 (F), 7 January 1930, *Williams* 7035 (F). **Ucayali:** Becerro Isla, abajo de Jenaro Herrera, 17 November 1981, *Spichiger & Encarnación* 1065 (G, MO, NY); Cordillera Azul, km 15 on Tingo María-Pucallpa road, dirt road near Puente Pumahuasi, 700 m, 5 June 1981, *Young & Sullivan* 715 (F, NY, USM).

BOLIVIA. sin loc., *Bang* 2248 (GH, NY, US). **Cochabamba:** Villa Tunari 34 kms hacia Cochabamba, 670 m, 25 November 1981, *Beck* 7361 (F, NY); Prov. Chapare, Todos Santos, 300 m, 22 October 1966, *Steinbach*

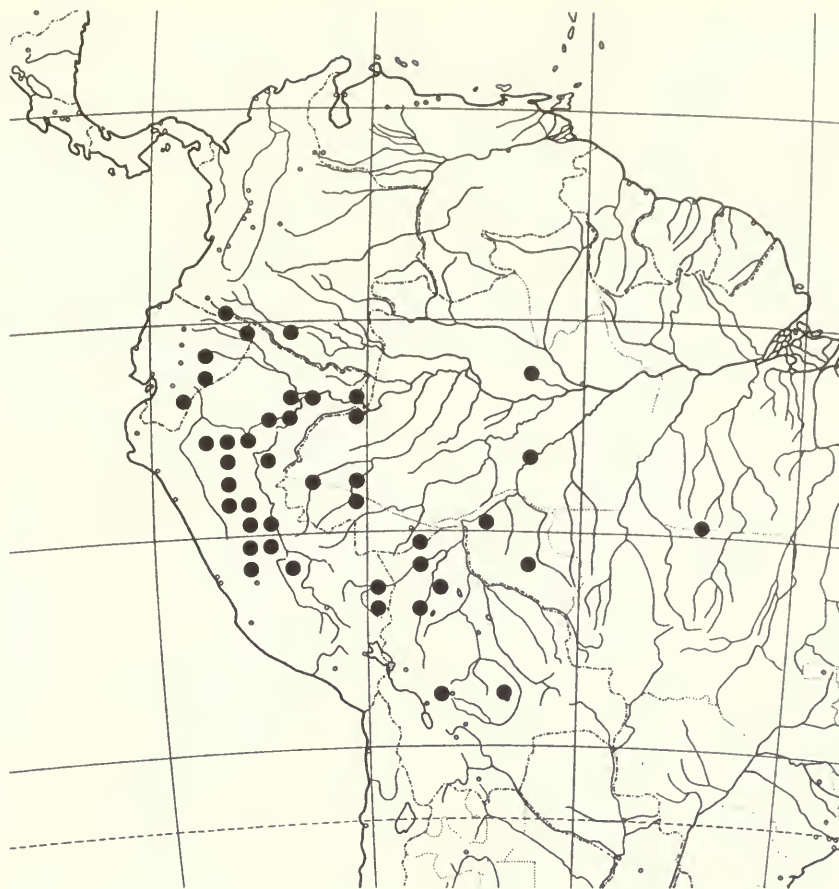


Fig. 18 Distribution of *S. mite*.

424 (F, NY, WIS); Locotal, Prov. Chapare, 1500 m, 2 February 1929, *Steinbach* 9020 (GH). **La Paz:** Rurrenabaque, 1000 ft, 25 November 1921, *Cárdenas* 1168, 2046 (NY); Mapiiri region, San Carlos, 600 m, 18 December 1926, *Buchtien* 1249 (NY, US); San Carlos, Mapiiri, 700 m, 15°S, 3 August 1907, *Buchtien* 1438 (NY, US); Bopi Rover, 3000 ft, 11 October 1922, *Rusby* 578 (NY); Guanai, 2000 ft, May 1886, *Rusby* 800 (NY); near La Paz, 10,000 ft, April 1885, *Rusby* 813 (NY-left-hand specimen). **Pando:** along Río Madre de Dios, upstream and from 22 km WSW of Florencia, 135 m, 67°34'W, 11°30'S, 23 August 1985, *Nee* 31504 (NY); Loma Alta, Río Madre de Dios, 110 m, 65°58'W, 10°47'S, 18 June 1987, *Solomon* 17159 (NY). **Santa Cruz:** Prov. Ichilo, Buena Vista, 370 m, 63°40'W, 17°27'S, 2 August 1987, *Nee* 35480 (NY); Estancia San Rafael de Amboro, 1 km W. toward Río Surutu, 15 km SSE of Buena Vista, 375 m, 63°37'W, 17°35'S, 29 July 1987, *Nee* et al. 35433 (NY); Parque Nacional Amboro, along Río Saguayo, 1 km NE of entrance into first Andean foothills, 400 m, 63°43'W, 17°39'S, 21 January 1988, *Nee* 36036 (NY); c. 3–4 km S. of San Rafael & 0.5 km N. of San Salvador, 11 km by air SW of Villa German Busch, 600–650 m, 63°56'W, 17°29'S, 19 November 1988, *Nee & Saldias* P. 36888 (NY); SW side of Buena Vista, 360 m, 63°40'W, 17°28'S, 15 December 1988, *Nee* 37200 (NY); Parque Nacional Amboro, along Río Saguayo, 1.5–3 km NE of entrance into first Andean foothills, 375 m, 63°43'W, 17°38–39'S, 21 December 1988, *Nee* 37315 (NY); Parque Nacional Amboro, along Río Saguayo, slopes along Quebrada Yapoje, above confluence with Río Saguayo, 400 m, 63°44'W, 17°34'S, 13 December 1989, *Nee* 38119 (NY); Parque Nacional Amboro, along Río Isama (Río Pitasama on maps), 450 m, 63°37'W, 17°41'S, 12 October 1990, *Nee* 39259 (NY); Parque Nacional Amboro, 5 km SWS of Buena Vista, W. side of Río Surutu, 320 m, 63°40'30"W, 17°29'30"S, 20 October 1990, *Nee* 39355 (NY); Parque Nacional Amboro, W. side of Río Surutu, 2 km NE of El Carmen on trail to river crossing, 320 m, 63°41'W, 17°31'S, 29 October 1990, *Nee* 39570 (NY); E. side of Río Yapacani at junction with Río Surutu, 0.5 km upstream and S. from highway bridge over Río Yapacani at Villa Yapacani, 285 m, 63°50'W,

17°24'S, 30 October 1990, *Nee* 39603 (NY); Río Surutu, 400 m, 1 July 1924, *Steinbach* 6080 (A).

BRAZIL: **Acre:** *Maas* et al. P12838 (NY); Cruzeiro do Sul, Rio Juruá, Rio Moa, 29 October 1966, *Prance* et al. 2955 (NY, US, WIS); opposite Cruzeiro do Sul, N. bank of Rio Juruá, 27 October 1966, *Prance* et al. 2908 (K, NY, US, WIS); Santa Maria de Marmellos, Madeira, *Ule* 6922 (HBG, B[destroyed, syntype of *S. quinquefoliolatum*]). **Amazonas:** near mouth of Rio Embira, tributary of Rio Tarauaca, 70°15'W, 7°30'S, 3 June 1933, *Krukoff* 4642 (A, NY); Rio Solimões & Rio Javari, Ilha Aramaçá, opposite Tabatinga, 23 July 1973, *Prance* et al. 16698 (NY). **Pará:** estrada Santarém-Cuiabá (BR 163) km 780 de Cuiabá, 430 m, 54°54'W, 9°22'S, 29 May 1983, *Silva* 159 (MO, NY, US). **Rondônia:** Costa Marques, Chapada dos Pareis, dist. Alto Floresta, estrada P-56, km 17, 62°63'W, 11°12'S, 15 June 1984, *Cid* et al. 4568 (NY); E, bank of Rio Madeira near junction of Rio Abuña, 21 July 1968, *Prance* et al. 6236 (NY).

Solanum mite is the most common of the species of section *Pteroides*, forming large thickets in treefall gaps in the primary and secondary forest and along streams and roads in partial shade. Like *S. anceps*, it is basically an Amazonian species, but unlike *S. anceps*, *S. mite* occurs only in the southern part of the Amazon basin, not extending far north of the N. bank of the Rio Amazonas. *Solanum mite* is superficially similar to both *S. conicum* and *S. uleanum*, but can be differentiated easily from those species by its rounded fruit, pendent at maturity. *Solanum mite* can be hard to distinguish from *S. conicum* in flower, but the latter generally has larger flowers with petals held planar at anthesis, while *S. mite* has tiny ones with reflexed petals. Other differences from *S. conicum* are discussed with that species. Numbers of leaflets and size of leaves are extremely variable in *S. mite*, but leaflet shape is consistently obovate, with the terminal leaflet usually much larger and more enlarged in the distal



Fig. 19 *S. savanillense*. Habit, flowers, and fruit: Madsen & Elleman 75239, Madsen 85749, 85898 (AAU).

third. The type specimen of *S. pteleifolium* (Martius s.n.) has ternate leaves with very large, broad leaflets. There exists however a range of intermediates in both leaflet numbers and size: Maas et al. P12838 from Acre, Brazil and Plowman et al. 6401 from near Leticia on the Colombia/Peru border approach Martius's collection in their broader leaflets, but given the range of variability in *S. mite*, we prefer to take a broad concept of the species. Many of the minor variants have been described as separate species by Bitter (see synonymy), but the range of variation in *S. mite* as recognized here encompasses all of these.

Huge variability in leaf pubescence of collections made by one of us (S.K.) in Departamento San Martín, Peru, shows that pubescence

density and occurrence is quite variable within populations of *S. mite*. In these collections, made in the Tarapoto area in 1986, no differences in phenology or other ecological characteristics were observed, and no morphological differences other than pubescence were seen. The nature of inheritance of this character is not known, but is likely to be relatively simple.

8. *Solanum savanillense* Bitter in *Reprim nov. Spec. Regni veg.* 12: 66 (1912). Type: Ecuador, Zamora-Chinchipec, Tambo de Savanilla, 18 December 1876, André 4565 (K!-holotype). Figs 4d, 5b, 19.



Fig. 20 Distribution of *S. savanillense* (star in circle) and *S. trizygum* (circles).

Slender, wand-like *shrub* to 1.2 m tall. *Stems* c. 7 mm in diameter, fleshy and somewhat translucent, completely glabrous or with a few scattered uniseriate trichomes near the somewhat swollen nodes, the nodes occasionally dark purple, usually the stems green without conspicuous lenticels when dry. *Leaves* 10–17 × 7–16 cm, pinnate, with 1–2 pairs of leaflets, occasionally purple abaxially, sparsely pubescent abaxially with simple uniseriate trichomes c. 0.5 mm long, 4–5-celled, these denser along the veins, more densely pubescent adaxially, the trichomes c. 1 mm long and 8–10-celled; petiole 3.5–4 cm long; rachis of leaf minutely winged, sparsely pubescent with simple, uniseriate trichomes c. 0.05 mm long; lateral leaflets obovate, 10–12.5 × 3–5.5 cm, the base attenuate, the apex acuminate; petiolule 0.5–0.8 cm long; basal leaflets obovate, smaller, 5–10.5 × 1.7–4.2 cm, the lamina often narrower on the adaxial side of the leaflet, the blade attenuate, the apex acuminate; petiolule c. 0.5 cm; terminal leaflet obovate, broader than any of the laterals, 6–16 × 3–7 cm, the base attenuate, the apex acuminate; petiolule c. 1 cm long. *Inflorescence* 1–3 cm long, simple, up to 3 rachis arising from a single leaf axil, bearing flowers only in the distal half, with only 1 or 2 flowers open at a time, but with c. 10–15 scars, sparsely pubescent with simple, uniseriate trichomes like those of the leaves. *Buds* c. 0.5 cm in diameter, globose to ovate, strongly exserted from the calyx tube. *Pedicels* at anthesis 0.5–0.7 cm long, c. 0.5 mm in diameter, nodding, glabrous or minutely pubescent. *Flowers* with the calyx tube 1.5–2 mm long, conical, the lobes c. 0.5–1 × 0.5 mm, deltate, splitting irregularly at the sinuses, with a prominent terminal projection, sparsely pubescent with trichomes like those of the inflorescence, the trichomes denser on the tip of the lobes; corolla 10–12 mm in diameter, white or purple (see discussion), lobed nearly to the base, the lobes planar at anthesis, densely papillate at the tips and margins; anthers 2.5–3 × c. 1 mm, poricidal at the tips, free portion of the filaments c. 0.5 mm long, the filament tube

minute; ovary conical, glabrous; style 5–6 mm long, densely short-pubescent in the lower half; stigma clavate. *Fruit* an elongate, conical green berry, 1–2 × c. 1 cm, the surface lightly rugose; fruiting pedicel 1–1.2 cm long, erect. *Seeds* c. 3.0 × 2.5 mm, ovoid-reniform, bright green, c. 20 per fruit; epidermal cells highly sinuous and irregular, with anticlinal thickenings but without projections.

COMMON NAMES AND USES. None recorded.

DISTRIBUTION. *S.* Ecuador in cloud forest, from 2300–3000 m. (Fig. 20).

SPECIMENS EXAMINED

ECUADOR. *Loja:* Sin loc., 1876, *André* K694 (K); Parque Nacional Podocarpus, Nudo de Cajanuma; sendero del Centro de Información a las Lagunas del Compadre, 2830–2880 m, 21 November 1990, *Gavilanes* et al. 381 (AAU); Parque Nacional Podocarpus, Cajanuma, trail to El Mirador, 2800–3200 m, 4°07'S, 79°10'W, 20 October 1994, *Knapp* et al. 9044, 9045 (QCNE); Parque Nacional Podocarpus, above Nudo de Cajanuma around Centro de Información, 2800–3000 m, 79°10'W, 4°05'S, 6 September 1988, *Madsen & Elleman* 75238 (AAU, LOJA); Parque Nacional Podocarpus, above Nudo de Cajanuma around Centro de Información, 2800–3000 m, 79°10'W, 4°05'S, 6 September 1988, *Madsen & Elleman* 75239 (AAU); Parque Nacional Podocarpus, E. of Nudo de Cajanuma, just N. of Centro de Información, 2900 m, 79°10'W, 4°05'S, 31 January 1989, *Madsen* 85749 (AAU, LOJA, QCNE); Parque Nacional Podocarpus, above Nudo de Cajanuma around Centro de Información, 2800–3000 m, 79°10'W, 04°05'S, 14 May 1988, *Øllgaard* et al. 74105 (AAU); Parque Nacional Podocarpus, at Cajanuma, S. of Loja, at Centro de Información, 2900 m, 79°10'W, 4°05'S, 31 May 1988, *Øllgaard* 74539 (AAU, LOJA); Parque Nacional Podocarpus, E. of Nudo de Cajanuma, trail E. of Centro de Información, to crest on trail to Lagunas de Compadre, 2850–3050 m, 79°10'W, 4°05'S, 7 June 1988, *Øllgaard* 74630 (AAU, LOJA). **Zamora-Chinchipe:** Pass between Loja and Zamora and along trail toward Zamora, 2360–2800 m, 29 July 1982, *Clemants* et al. 2252 (NY); Parque Nacional Podocarpus, road Loja-Zamora, just E. of pass, 2800 m, 79°07'W, 3°58'S, 15 March 1989, *Madsen* 85898 (AAU).

Solanum savanillense is superficially similar to many of the other pinnate-leaved members of section *Pterioidea*. It can be distinguished easily, however, by its larger flowers, more elliptic, slightly less rugose fruits and its tall stature. This last character is impossible to ascertain from herbarium sheets, but in the field *S. savanillense* is quite distinct from *S. mite* or *S. conicum*, the only other members of this group to attain such sizes. The leaves of *S. savanillense* are more pubescent adaxially than abaxially, the reverse of the pattern in other members of the group. In 5-foliolate leaves of *S. savanillense*, the basal pair of leaflets is conspicuously smaller than the other pair, a characteristic not found elsewhere in the section.

In Parque Nacional Podocarpus in southern Ecuador *S. savanillense* is polymorphic for both flower and stem colour but the leaves are monomorphic. In populations collected ascending the Nudo de Cajanuma, groups of plants were either green-stemmed and white-flowered or with purple nodes and purple flowers. Leaf undersides of neither morph were purple as occurs in *S. anceps* (see discussion under that species), perhaps indicating that the colour variation in *S. savanillense* is purely genetic in origin. *Solanum savanillense* grows in the primary forest understory in deep shade.

Bitter, in describing *S. savanillense*, stated that the type was collected in Costa Rica. André never collected in Costa Rica, but was in southern Ecuador in December of 1876. The type specimen does not bear any annotation stating Costa Rica, so it is likely that Bitter made a mistake in transcribing label data or just confused the localities of specimens he saw at K. André's locality Tambo de Savanilla probably corresponds to the present-day village of Sabanilla in the province of Zamora-Chinchipe or to the pass on the Loja to Zamora road (3°38'S, 79°05'W), which lies within the Parque Nacional Podocarpus. In Ecuador, *nudo* means a pass and *tambo* a stopping place, usually a small town.

9. ***Solanum trizygum*** Bitter in *Reprum nov. Spec. Regni veg. 11*: 470 (1912). Type: Venezuela, Distrito Federal, Colonia Tovar, Moritz 1644 (B-holotype, destroyed [F neg. 2702, F!, G!, GH!, MO!, NY!, US!, WIS!], fragment at F!; HBG!-lectotype; BM!, HBG!-isolectotypes). A Moritz collection (BM!, F!, GH!, W [F neg. 33118, F!, MO!, US!, WIS!]) distributed from W could also be type material, but as it is labelled 'Colombia, leg. Moritz' we have excluded it from consideration.

Fig. 21.

Solanum fraxinellum Bitter in *Reprum nov. Spec. Regni veg. 11*: 469 (1912). Type: Mexico, Veracruz, prope Mirador, 3000–3800 ft, Sartorius s.n. (W!-holotype [F neg. 33075, F!, G!]; G!-isotype [Morton neg. 8516, F!, GH!, NY!]).

Solanum trizygum var. *tetrazygum* Bitter in *Reprum nov. Spec. Regni veg. 11*: 471 (1912). Type: Venezuela, sin loc., 27 June 1891, Eggers 13223 (C!-holotype).

Solanum quinquejugum Bitter in *Reprum nov. Spec. Regni veg. 11*: 564 (1912). Type: Mexico, Puebla, Teziutlán, July 1866, Hahn s.n. (P!-holotype [F neg. 39200, G!]).

Solanum pittieri Bitter in *Reprum nov. Spec. Regni veg. 12*: 66 (1912). Type: Costa Rica, Heredia, Alto del Roble, 2000 m, 1888, Pittier 18 (G!-holotype).

Somewhat woody shrub to 1 m. *Stems* c. 5 mm in diameter, usually bright green and fleshy, completely glabrous, but occasionally with sparse reddish papillae (when dry) or simple uniseriate trichomes scattered near the nodes. *Leaves* 10–40 × 5–10 cm, pinnate, elliptic, with 3–6 (most commonly 4) pairs of leaflets, glabrous or minutely papillose adaxially, occasionally with a few uniseriate trichomes along the veins abaxially, occasionally purple abaxially and along the rachis; petiole 2–5 cm long; lateral leaflets lanceolate to elliptic,

4–15(–25) × 2–4 cm, with 6–8 pairs of primary veins, the base attenuate, only very occasionally oblique, the apex acuminate; petiolule 0.1 cm long; basal leaflets either equal to the laterals or somewhat smaller; terminal leaflet similar in shape to the laterals, 6–20 × 3–6 cm, the base attenuate, the apex acuminate; petiolule c. 1 cm or less. *Inflorescence* axillary, 1–4(–9) cm long, simple, c. 2–4 arising from a single axil, bearing 2–3 flowers at a time, with 20–30 pedicel scars, glabrous or minutely papillate at the tip. *Buds* elliptic, the calyx strongly 5-ridged (in dry specimens) in early bud, c. 3 × 2 mm, strongly exerted from the calyx tube. *Pedicels* at anthesis 1–1.5 cm, c. 0.5 mm in diameter at the tip, nodding. *Flowers* with the calyx tube 1–1.5 mm, open-conical, the lobes deltate to broadly triangular, 0.5–1 × 0.5–1 mm, glabrous; corolla 9–10 mm, greenish white or white, lobed nearly to the base, the lobes reflexed at anthesis, minutely papillose at the margins and tips; anthers 2–2.5 × 1–1.5 mm, poricidal at the tips, the free portion of the filaments 0.5–1 mm long, the filament tube absent; ovary conical, glabrous; style 5–6 mm long, minutely papillose in the lower half; stigma minutely capitate, occasionally somewhat clavate. *Fruit* a conical, green berry, the beak not abruptly narrowed, c. 1–1.2 cm in diameter, 1.2–2.5 cm long, the surface rugose, the raised portions white, when ripe smelling distinctly of wintergreen; fruiting pedicels 1.5–2 mm long, c. 3 mm in diameter at the apex, erect. *Seeds* 3.0 × 2.0–2.5 mm, ovoid-reniform to elliptic, greenish brown, c. 40 seeds per fruit; epidermal cells sinuous and irregular, with anticlinal thickenings but without projections.

COMMON NAMES AND USES. Guatemala: 'candelaria' (*Steyermark* 33815, 35135, 37209, 37732, 48735, 51729); Venezuela: 'ajicillo' (*Berry* 1926).

DISTRIBUTION. Montane and premontane forest from Mexico to the Cordillera de la Costa in Venezuela, absent from the Andes, from c. 600–3200 m. (Fig. 20).

SPECIMENS EXAMINED

MEXICO. ?Totalcingo (Chinantla) Montes, 914 m, June 184?, *Galeotti* 1165 (BR). **Chiapas:** Mun. La Concordia, El Triunfo Reserve, trail WSW from Palo Gordo towards Finca Catarina, 1850 m, 15°40'N, 92°51'W, 25 February 1990, *Hampshire* et al. 697 (BM). **Oaxaca:** Cerro Mirador, 15 km al NNW de Valle Nacional, 1000–1200 m, 96°22'W, 17°93'N, 16 October 1992, *del Castillo* 1520 (BM); Cerro Mirador, 15 km al NNW de Valle Nacional, 1000–1200 m, 96°22'W, 17°53'N, 27 April 1993, *Manríquez* et al. 3819 (BM).

GUATEMALA. **Alta Verapaz:** Mountains along road between Tactic & the divide on road to the Tamahú, 1500–1600 m, 1 May 1941, *Standley* 90563 (F); **Baja Verapaz:** Niño Perdido in San Jose road, N. 6 km, bordering Arroyo El Caracol, 24 May 1977, *Lundell* & *Contreras* 20973 (F, MO); mountain of Purulhá between La Unión & Purulhá, 1600 m, 1 October 1972, *Molina R. & Molina* 27734 (F). **Huehuetenango:** Vicinity of Maxbal, about 17 miles N. of Barillas, Sierra de los Cuchumatanes, 1500 m, 15 July 1942, *Steyermark* 48735 (F); Cerro Negro, 2 miles E. of Las Palmas, Sierra de los Cuchumatanes, 1600–2000 m, 31 August 1942, *Steyermark* 51729 (F); **Quezaltenango:** Along old road between Finca Pirineos and Patzún, 1200–1400 m, 9 February 1941, *Standley* 86711 (F); lower S. facing slopes of Volcán Santa María, between Finca Pirineos and Los Positos, between Santa María de Jesús and Calahuaché, 1300–1500 m, 8 January 1940, *Steyermark* 33815 (F); W. slopes of Volcán Zunil, opposite Santa María de Jesús, 1500 m, 21 January 1940, *Steyermark* 35135 (F). **San Marcos:** 1 mile above Africa, c. 3.3 miles above Finca Armenia above San Rafael, 1600 m, 13 July 1977, *Croat* 40937 (NY); Finca Vergel, near Rodeo, 900 m, 15 March 1939, *Standley* 68905 (F); above Finca El Porvenir on 'Todos Santos Chiquitos', lower S. facing slopes of Volcán Tajumulco, 1300–1500 m, 7 March 1940, *Steyermark* 37209 (F); Between Finca El Porvenir and Loma Corona, 9 miles NW of El Porvenir, SW-facing slopes of Volcán Tajumulco, 1300–2000 m, 14 March 1940, *Steyermark* 37732 (F).

HONDURAS. **Santa Barbara:** 10 kms W. de Lago Yojoa, 1500–2000 m, 88°05'W, 14°55'N, 28 April 1973, *Clewell* & *Hazlett* 3859 (MO).



Fig. 21 *S. trizygum*. Habit: Skutch 3166 (A). Fruit: Lent 2788 (F).

COSTA RICA. Alajuela: La Palma de San Ramón, 1300 m, 23 October 1922, *Brenes* 3719 (F, NY); San Antonio de San Ramón, 850 m, 15 July 1927, *Brenes* 5625 (F); Cerro de La Muralla de San Ramón (El Socorro), 2 September 1927, *Brenes* 5704 (F); Santiago de San Ramón, 1150 m, 29 July 1937, *Brenes* 22613 (F); Cordillera Central, 7 miles N. of Carrizal, between Volcán Poas & Volcán Barba, 1850 m, 25 May 1976, *Croat* 35489 (MO); Monteverde, Cordillera de Tilarán, Reserva Vert. Atlántico, 1500–1580 m, 14 December 1976, *Dryer* 1069 (F); above Río Gorrini, Bajos del Toro, 1550 m, 84°18'W, 10°13'N, 20 January 1974, *Lent* 3776 (MO); region of Zarcero, 1680 m, 29 September 1937, *Smith* A456 (F); Pueblo Nuevo, Cantón San Carlos, 1100 m, 15 April 1939, *Smith* 1900 (F); Stefano Ruíz, Cantón Llano Barito, 1650 m, 9 June 1941, *Smith* 2750 (F). **Cartago:** Near El Copey, in cloud forest area, Cordillera de Talamanca, 1800 m, 23 April 1949, *Allen* 16520 (F); hillside overlooking Río Grande de Orosí about 3 km SE of Tapantí, 1400 m, 16 April 1967, *Lent* 822 (F); Tausito, 1400 m, 83°46'W, 10°46'N, 16 February 1974, *Lent* 3819 (F); 12 km S. of Turrialba by air, 4 km SE of Pejibaye along Río Gato, 700 m, 83°42'W, 9°48'N, 16 April 1983, *Liesner* 14374 (MO). **Guacacaste:** SW slopes of Volcán Rincón de la Vieja & Volcán Santa María above the trail from Hda. Guachipelin, 1000 m, 85°21'W, 10°48'N, 30 July 1971, *Burger & Pohl* 7809 (F, MO). **Heredia:** Río Vueltas (upper Río Patria) on E. slope of Volcán Barba on the Caribbean side, 1900 m, 84°04'W, 10°06'N, 1 April 1973, *Gentry & Burger* 2863 (F, MO, NY); Braulio Carrillo Park, Zuruquí, 1700–2000 m, March 1983, *Gómez* 20172 (MO); Finca La Selva, the OTS field station on the Río Puerto Viejo just E. of its junction with the Río Sarapiquí, along Q. El Sura between arboretum and station, 9 March 1980, *Hammel* 7983 (F, MO); Alto de Roble, 2000 m, May 1888, *Pittier* 18 (G); Vara Blanca de Sarapiquí, N. slope of Central Cordillera, 1500–1750 m, July–September 1937, *Skutch* 3166 (A, GH, K, MO, NY); Vara Blanca de Sarapiquí, N. slope of Central Cordillera, 1615 m, February 1938, *Skutch* 3614 (A, K, MO, NY); Cerro de las Caricias, N. of San Isidro, 2000–2400 m, 11 March 1926, *Standley & Valerio* 51987 (F); along the W. fork of the upper Río Parí Blanco beyond the road terminus of Calle Zurquí, 18 March 1974, *Utley & Utley* 701 (F). **Limón:** Cordillera de Talamanca, Atlantic slope, canyon of the Río Siní, 1800–1900 m, 82°59'W, 9°13'N, 15 September 1984, *Davidse & Herrera Ch.* 29142 (MO). **Puntarenas:** Las Tablas, Río Cotoncito, 10 December 1983, *Chacon* et al. 1811 (MO); Monteverde, Cordillera de Tilarán, 1520–1580 m, 12 February 1977, *Dryer* 1194 (F); about 2 km SE of Monteverde, on the Pacific watershed, 1500–1550 m, 84°48'W, 10°18'N, 18 March 1973, *Gentry & Burger* 2721 (F, MO); on and near the Continental Divide about 2–5 km E. & SE of Monteverde, 1580–1700 m, 10°18'N, 84°46'W, 17 March 1973, *Gentry & Burger* 2731 (F); Monteverde Cloud Forest Reserve, Cordillera de Tilarán (Pacific slope), 1500–1620 m, 20 January 1984, *Linhart* 155 (MO), 31 May 1985, *Pounds* 501 (MO), 13 July 1984, *Pounds* 274 (MO), 26 March 1984, *Pounds* 196 (MO). **San José:** Along the Río Para Blanca (Pacific drainage), Cerros de Zuruquí, 1600–1800 m, 10°03'N, 84°01'W, 6 February 1977, *Burger* et al. 10250 (F); Cordillera de Talamanca; Chirripó massif, Pacific slope, place along trail known as Abra, 2500 m, 2 April 1969, *Davidse & Pohl* 1529 (F); near Río Honduras, 1150 m, 83°59'W, 10°04'N, 12 August 1972, *Lent* 2788 (F); vicinity of El General, 880 m, August 1936, *Skutch* 2789 (GH, K, MO, NY), 1035 m, February 1939, *Skutch* 4147 (K, MO, NY); vicinity of Santa María de Dota, 1500–1800 m, 26 December 1925, *Standley & Valerio* 44055 (F); Alto de la Palma on Finca Porvenir, c. 5 km N. of San Jerónimo, 1500 m, 18 August 1975, *Utley & Utley* 2902 (F, MO); Cordillera de Talamanca, about 25 km N. of San Isidro de El General along Pan American Highway, 3200 m, 29 January 1965, *Williams* et al. 25580 (F).

PANAMA. Bocas del Toro: Róballo trail, N. slopes of Cerro Horqueta, 1830–2130 m, 5 August 1947, *Allen* 4953 (F, G, MO); vicinity of Fortuna Dam, 1300–1400 m, 6 February 1987, *Bohs & McPherson* 2307 (GH); 7.2 miles beyond Campamento Chami (12+12 miles from Río San Felix), 1500 m, 20 June 1986, *D'Arcy* 16328 (MO), *D'Arcy* 16343 (MO); Chiriquí border along Continental Divide on Carretera del Oleoducto c. 1 km N. of Quebrada Arena, IHRE Fortuna Hydroelectric project, 1150 m, 8°46'N, 82°12'W, 11 May 1982, *Knapp* 5064 (MO). **Chiriquí:** Along road in vicinity of branch in road to Cerro Colorado and Escopeta; above Río San Felix near town of San Felix (c. 13 miles N. of Río San Felix Bridge), 800–1200 m, 15 March 1976, *Croat* 33456 (MO); vicinity of Monte Azul, 1.4 miles N. of Entre Ríos, on E. slopes of Cerro Punta, 3 miles by road from town of Cerro Punta, 2250 m, 25 November 1979, *Croat* 48589 (MO); along road between Guacala and

Fortuna Dam site, 10.1 miles NW of Los Planes de Hornito, 1250 m, 8°45'N, 82°17'W, 10 April 1980, *Croat* 50031 (MO); edge of Laguna de Volcán, 9 August 1972, *D'Arcy & D'Arcy* 6606 (GH, MO); road from Nueva California and Río Serano c. 9 miles from Río Chiriquí Viejo, 1370 m, 7 April 1979, *D'Arcy* et al. 12988 (MO); between Palo Alto and top of ridge (divide) near Cerro Pate Macho, above Río Palo Alto, 1640–2160 m, 18 March 1979, *D'Arcy* et al. 12647 (MO), *D'Arcy* 12672 (MO); Bajo Chorro, Boquete District, 1830 m, 6 February 1938, *Davidson* 63 (F, MO); Boquete, Finca Collins, 1520 m, 7 August 1967, *Dwyer & Hayden* 7661 (MO), *Dwyer & Hayden* 7670 (MO); Cerro Colorado, Bocas Road, 1500 m, 17 February 1977, *Folsom & Collins* 1765 (MO); slope of hill above camp at Fortuna Dam site, 1400–1500 m, 14 September 1977, *Folsom* et al. 5486 (MO); along trail from end of Río Palo Alto road to Chiriquí border with Bocas del Toro Province near peak of Cerro Pate Macho, 2070 m, 20 November 1978, *Hammel* 5804 (BM, MO, NY); 9 miles from Río Chiriquí Viejo bridge near Nueva California on road to Río Sereno, 7 April 1979, *Hammel* et al. 6848 (MO); trail from Paso Respingo to Bajo Chorro, Cerro Punta to Boquete, 2225 m, 13 April 1979, *Hammel* et al. 7030 (MO); 1 km N. of Fortuna Lake, 1200 m, 82°13'W, 8°45'N, 3 March 1985, *Hampshire & Whiteford* 286 (BM); c. 0.5 km E. of Cerro Pate Macho, headwaters of Río Palo Alto, 1800–2100 m, 82°21'W, 8°47'N, 12 November 1981, *Knapp* et al. 2108 (BM, NY); trail to Cerro Pate Macho, headwaters of Río Palo Alto, above Palo Alto, 1700–2100 m, 82°22'W, 8°47'N, 15 March 1982, *Knapp* et al. 4260 (MO); Finca Collins, c. km 9.5 on the Quiel road above Boquete, 1830 m, 15 May 1971, *Proctor* 31944 (F); 6 miles above Cerro Punta on the Boquete Trail, 2300 m, 7 March 1974, *Tyson* 7144 (MO). **Coclé:** 2 miles N. of Cerro Pilón, 900 m, 16 March 1973, *Liesner* 724 (MO, F). **Veraguas:** E. side of mountain (Cerro Tute) W. of Escuela (Primer Básica, formerly Agrícola) Alto de Piedra, c. 5 miles NW of Santa Fé, 760–850 m, 10 September 1982, *D'Arcy* 15003 (MO).

VENEZUELA. sin. loc., November 1875, *André* K693 (K); sin. loc., *Moritz* s.n. (US). **Aragua:** Rancho Grande, pica detrás del Hotel, Parque Nacional 'H. Pittier', May 1962, *Agostini* 48 (US); prope coloniam Tovar, 1854, *Fendler* 1016 (BR, G, GH, NY); Parque Nacional between Rancho Grande & Dos Riitos, 900 m, 19 May 1943, *Killip & Lasser* 37758 (A, US); Parque Nacional 'Henri Pittier' (Rancho Grande), trail to Pico Guacomayo, behind station, 1100–1400 m, 67°42'W, 10°21'N, 27 October 1984, *Knapp & Mallet* 6852 (BH, MY, US, VEN); Parque Nacional Henri Pittier, Rancho Grande, trail to Toma, 1300 m, 4 October 1968, *Plowman* 1931 (GH, K); Rancho Grande, Parque Nacional H. Pittier, 3 February 1968, *Walter & Walter* 472 (B); in the forest of Rancho Grande, Parc Nacional, 1000 m, 1 December 1938, *Williams & Alston* 139 (BM, NY), *Williams* 10743 (F). **Carabobo:** Along Río San Gián, al S. de Borburata, arriba de la Plant Eléctrica, entre Los Tanques y La Toma, 750 m, 27 March 1966, *Steyermark & Steyermark* 95161 (F). **Distrito Federal:** ?Galipan, 1846, *Linden* 128 (G); Bosque de Cachuca, above Caracas, 1200–1800 m, 9 May 1913, *Pittier* 6145 (US); Chacarito Gorge, around Caracas, 800–1000 m, 8 May 1921, *Pittier* 9508 (GH, NY, US); Cachuca wood, 1200–1300 m, 22 January 1922, *Pittier* 10092 (GH, US, NY); Cerro Naiguatá, laderas pendientes de lado del March que miran hacia el N. arriba del pueblo de Naiguatá, vecinidad de Quebrada Frontina, 5 km al SW de los tanques de la Electricidad de Caracas (Cocuizal), 900–1100 m, 2 November 1963, *Steyermark* 91851 (F); Agua Negra, or above Caracas, 1500 m, December 1939, *Williams* 13624 (F). **Falcón:** Arriba de La Chapa, Sierra de San Luis, 1100 m, 18 January 1979, *Flora Falcón* 210 (WIS); Sierra San Luis, ridges around Hotel Parador, c. 7 km S. of Curimagua, 1300–1350 m, 69°35'W, 11°10'N, 28 September 1984, *Knapp & Mallet* 6685 (BH, K, MY, VEN); Distrito Bolívar, Sierra de San Luis, Cerro Galicia, around TV antenna at summit, 1500 m, 11°11'N, 69°42'W, 29 March 1984, *Plowman* et al. 13440 (F, NY); Sierra de San Luis, vicinity of Hotel Parador, S. of La Tabla, 1450 m, 16 July 1967, *Steyermark* 98915 (US); Sierra San Luis, arriba del Hotel Parador, 1500 m, 25 August 1978, *Wingfield & van der Werff* 6574 (WIS). **Miranda:** Quebrada de las Comadres, near las Mostazas, 1100 m, November 1924, *Allart* 255 (NY); Campo Experimental Padrón – Estación Experimental de Caucagua, 15 km al E. de Caucagua, 40 m, 22 January 1976, *Berry* 1926 (F); Dto Paz Castillo, Municipio Reyes Cueta, Los Guayabitos, 1300–1490 m, 10°21'16"N, 66°38'36"W, 11 December 1987, *Castillo & Bocaranda F.* 2694 (MO); Quebrada de las Comadres near las Mostazas, 1100 m, November 1924, *Pittier* 255 (G); Parque Nacional de Guatopo, headwaters of Río Grande, from Quebrada San Antonio to Fila de

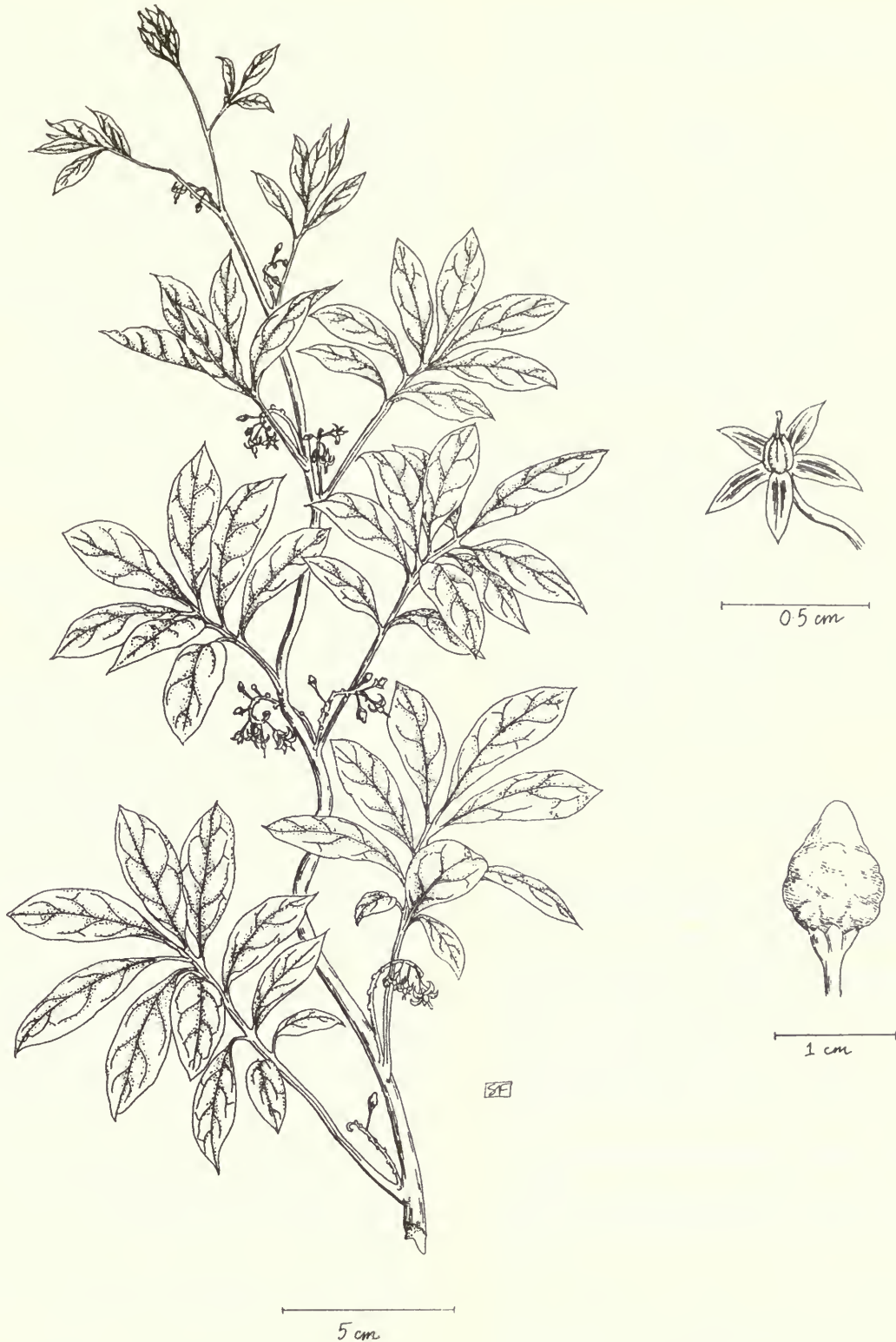


Fig. 22 *S. uleanum*. Habit: Knapp & Mallet 6524 (K), Schunke V. 3898 (MO). Fruit: Schunke V. 5431 (MO).

Río Grande, between Santa Teresa and Alatragraco de Orituco, 6.5 km from Rancharía Mi Querencia, 600–700 m, 27 November 1961, *Steyermark* 90105 (US). **Monagas:** El Páramo, NE of Las Delicias, NE of Caripe, 1200–1450 m, 13 April 1945, *Steyermark* 62034 (F). **Sucre:** Península de Paria, en el camino entre Los Pocitos de Santa Isabel a Roma, 10–15 km NW of Irapa,

700–1060 m, 13 July 1972, *Dumont* et al. VE-7649 (NY); Península de Paria, Cumbre La Estrella, W. of Manacal (turnoff 13.2 km W. of Irapa) N. of El Paujil, 800–850 m, 62°41'W, 10°40'N, 17 October 1984, *Knapp & Mallet* 6771 (BH, F, K, MY, US, VEN); Península de Paria, a lo largo de la Quebrada Nivardo, afluente de Río Caverna, afluente de Río Oscuro arriba de Mundo

Nuevo W. de Cerro de Humo, 700–750 m, 7 August 1966, *Steyermark & Rabe* 96140 (B. NY, US); Peninsula de Paria, cloud forest in tributary headwaters of Río Cumaná, SW of Cerro de Humo, vicinity of Manacal, 15 km (by air) NW of Irapa, 800 m, 62°39'W, 10°41'N, 29 November 1979, *Steyermark & Liesner* 120698 (NY).

Solanum trizygamum is superficially similar to *S. conicum* of the eastern Amazon, and is very closely related to that species (see Fig. 8). It differs from *S. conicum* in its more lanceolate leaflets that are very shortly petiolate or sessile, and its more elongate fruit. The fruit of *S. trizygamum* also resembles that of *S. savanillense*, but is longer and has a more pronounced beak. *Solanum trizygamum* is quite common locally in the cloud forests of Central America.

The distribution pattern of *S. trizygamum*, occurring in Central America and in the cordillera de la Costa in Venezuela, is quite common in angiosperms (see Knapp, 1991b). This may be indicative of some dispersal in the past, but alternatively may support geological hypotheses linking the Cordillera de la Costa with the Pacific plate (see Knapp, 1991b for a discussion).

10. *Solanum uleanum* Bitter in *Reprim nov. Spec. Regni veg.* **12**: 139, pl. I (1913). Type: Brazil, Acre, Rio Acre, Porto Carlos, February 1911, *Ule* s.n. (B-syntype, destroyed; G!-lectotype). Both of the syntypes (*Ule* s.n. from Porto Carlos and *Ule* s.n. from San Francisco) cited by Bitter were destroyed at B. The collection from Porto Carlos is represented in the herbarium at G by a duplicate annotated in Bitter's hand that matches the plate accompanying the original description. The second syntype, *Ule* s.n. collected in June 1911 at San Francisco may be the same specimen as the type of var. *unipedunculatum* below. The numbering and dating of Ule's collections is occasionally somewhat confused.

Figs 2b, 4c, 22.

Solanum uleanum var. *unipedunculatum* Bitter in *Reprim nov. Spec. Regni veg.* **12**: 140 (1913). Type: Brazil, Acre, San Francisco, May 1911, *Ule* 9756 (B holotype?, destroyed; K!-lectotype).

Solanum uleanum var. *gracilescens* Bitter in *Reprim nov. Spec. Regni veg.* **12**: 141 (1913). Type: Peru, San Martín, Cerro Campana, December 1855, *Spruce* 4462 (K!-holotype).

Creeping herb, often tightly adhering to tree trunks and fallen logs, attaining up to 6 or 7 m in length. *Stems* c. 5 mm in diameter, copiously rooting at and between the nodes, pale greenish white, sparsely to densely pubescent with simple, uniseriate 5–6-celled trichomes 0.5–1 mm long, drying cateniforme. *Leaves* 3–15 × 2.5–10 cm, pinnate, elliptic, with 3–7 pairs of leaflets, the petiole 0.8–6 cm long; rachis of leaf minutely winged, especially between the terminal leaflet and the ultimate pair, sparsely to densely pubescent with trichomes like those of the stem; lateral leaflets elliptic, 1.5–6 × 0.4–2 cm, sparsely to densely pubescent with simple uniseriate trichomes like those of the stems, these denser adaxially, especially along the veins, the base attenuate, winged onto the rachis, petiolule c. 2 mm long, the apex obtuse to rounded; basal pair of leaflets smaller than the laterals, the apex more rounded; terminal leaflet equal in size to the laterals, elliptic to obovate, strongly winged onto the rachis. *Inflorescence* 1–10 cm long, axillary, occasionally 2–3 separate rachis arising from a single axil, occasionally branched, with 3–4 open flowers at a time, with up to 100 scars unevenly spaced c. 0.5 mm apart, sparsely to densely pubescent with simple uniseriate trichomes 0.5–1 mm long, drying white. *Buds* c. 3 mm in diameter, globose soon becoming ellipsoid, strongly exserted from the minute calyx tube. *Pedicels* at anthesis 0.5–0.7 cm long, filiform, nodding, sparsely pubescent like the rest of the inflorescence.

Flowers with the calyx tube c. 0.5 mm long, conical, the lobes 0.5 × 0.5–0.75 mm, quadrate with an apical projection, sparsely to densely pubescent with simple uniseriate trichomes, these denser on the apical projection; corolla 6–10 mm in diameter, greenish white, lobed nearly to the base, the lobes somewhat cucullate and slightly reflexed at anthesis, minutely papillose at the tips and along the margins; anthers 1.5–2.5 × 1–1.2 mm, poricidal at the tips, the pores lengthening to slits, free portion of the filaments c. 0.5 mm long, the filament tube minute and glabrous; ovary glabrous, conical; style 3–4 mm long, straight, densely long-papillose in the lower 1/2; stigma capitate. *Fruit* a conical, green berry, 1–1.2 × 1.5–1.6 cm, the beak c. 5 mm long and not containing seeds, truncate at the tip; fruiting pedicel 0.8–1 cm long, hanging. *Seeds* c. 20 per berry, 3–3.5 × 1.5–2.5 mm ovoid-reniform, greyish green to grey-brown; epidermal cell walls sinuous, thickened but without projections.

COMMON NAMES AND USES. 'pupu huasca' (*Kohn* 1102 – used medicinally by mother to prevent bleeding from umbilical cord of baby), 'yana barabacha panga' (*Shemluck & Ness* 174 – mashed leaves applied to wound like hydrogen peroxide, juice also used [Quechua]), 'ofa kibi' (*Vickers* 143 – remedy for diarrhoea, plant crushed and mixed with water [Cofan]), 'ahi anta ikó' (*Vickers* 273 – for stomach ache [Siona]).

DISTRIBUTION. Eastern slopes of the Andes from central Ecuador to central Peru, from 200–1200 m elevation, usually growing in primary forest or at the edges of clearings (Fig. 23).

SPECIMENS EXAMINED

ECUADOR. **Napo:** Parque Nacional Yasuní, Pozo petrolero Daimi 2, 200 m, 76°11'W, 00°55'S, 26 May 1988, *Cerón & Hurtado* 4057 (MO, NY, QCNE); Carretera Hollín-Loreto-Coca, km 40, entre Río Guamaní y Río Pucuno, 1200 m, 77°00'W, 00°40'S, 11 December 1987, *Neill* et al. 8107 (MO, NY), *Cerón* 2931 (MO, NY), *Palacios* 2219 (MO); Cantón Tena, Río Blanco community, headwaters of Río Huambuno, 6 km NNW of Ahuano, 440 m, 77°40'W, 01°00'S, 19 February 1990, *Kohn* 1102 (QCNE). **Pastaza:** Río Chicó, affluent of Río Pastaza, village of Río Chicó and vicinity, c. 10 km S. of Puyo, 3 km S. of Tarqui, 1000 m, 77°55'W, 01°03'S, August 1979, *Shemluck & Ness* 174 (F). **Sucumbíos:** Río Aguarico, Shushufindi, 23 February 1975, *Vickers* 143 (F); Shushufindi, 18 July 1979, *Vickers* 273 (F); San Pablo de los Secoyas, 300 m, 76°21'W, 00°15'S, 4 August 1981, *Brandbyge* et al. 32965 (AAU).

PERU. **Amazonas:** Pongo de Manseriche, Río Santiago & Río Marañón, c. 77°30'W, anno 1924, *Tessmann* 3890 (G, NY). **Huánuco:** Pachitea, Codo de Pozuzo, alluvial fan floodplain of Río Pozuzo after it emerges from mountains, trail to NW behind settlement, 450 m, 75°25'W, 9°40'S, 18 October 1982, *Foster* 9269 (MO); camino a Ayamiría a 2 km de Miel de Abeja, 300–400 m, 20 January 1967, *Schunke* V. 1538 (F); Bosque Nacional de Iparia, a lo largo del Río Pachitea cerca del Campamento Miel de Abeja, 1 km arriba del pueblo de Tournevista o unos 20 km arriba del confluencia con el Río Ucayali, 300–400 m, 28 February 1968, *Schunke* V. 1696 (F, GH, K, NY, US). **Loreto:** Prov. Coronel Portillo, Padre Abad, Granja del Sr Barrera, NE de la chacra de César Vela (Aguaytia), 295 m, 22 October 1972, *Schunke* V. 5431 (MO, WIS). **Pasco:** Oxapampa, km 28 Repartición-Isozacín (km 86 Villa Rica-Isozacín-Pto. Mairo), Río La Raya near Ameusha community of Laguna, 350 m, 75°10'W, 10°20'S, 22 August 1984, *Knapp & Mallet* 6654 (K, NY, US, USM); Oxapampa, trail from Río Isozacín to Ameusha community of Villa América, Río Palcazu Valley, 340 m, 75°15'W, 10°12'S, 31 August 1984, *Knapp & Salick* 6669 (K, US, USM); Oxapampa, km 15 of Palcazu road, (km 73 Villa Rica-Isozacín-Pt. Mairo) along Río Palcazu, 380 m, 75°10'W, 10°21'S, 17 August 1984, *Knapp & Mallet* 6645 (BH, US, USM). **San Martín:** San Martín, km 28 of Tarapoto-Yurimaguas road, 650 m, 76°15'W, 6°25'S, 20 June 1984, *Knapp & Mallet* 6524 (F, K, MO, NY, US, USM); km 28 of Tarapoto-Yurimaguas road, 750–800 m, 76°19'W, 6°27'S, 23 September 1986, *Knapp & Mallet* 8394 (MO); Quebrada de Ishichimi cerca a Tocache, 400 m, 12 March 1978, *Schunke* V. 10020 (MO); road by Río Tocache, Dto Tocache Nuevo, 12 April 1970, *Schunke* V. 3898 (F, G, NY); al W. del Vivero del Instituto Agropecuario de



Fig. 23 Distribution of *S. uleanum*.

Tocache, 400 m, 10 November 1969, *Schunke* V. 3602, (F, NY, US); Cerro Monte, nr. Tarapoto, 1855, *Spruce* 4462 (K). **Ucayali:** Trail from Quebrada Shesha, (tributary of Río Abujao) to base of Cerro Las Cachoeiras, c. 70 km NE of Pucallpa, 300–400 m, 73°55'W, 8°02'S, 24 June 1987, *Gentry & Diaz* 58484 (MO, USM).

Solanum uleanum is certainly one of the most beautiful of the species of section *Pterioidea*. Its small size and peculiar (but found elsewhere in the section, see *S. anceps*) creeping habit make it conspicuously different from the other pinnate-leaved species. Even so, it can be difficult to distinguish on the herbarium sheet. *Solanum uleanum* differs from *S. conicum* and *S. mite* (both of which are sympatric with *S. uleanum*) in its more rounded, smaller leaflets which are more winged onto the rachis (i.e. without a petiolule) than in other pinnate species and greenish flowers. Fruiting specimens of *S. uleanum* are very rare, but its fruit, with an elongate non-seed-bearing beak is distinctive.

As with almost all other members of the section, *Solanum uleanum* possesses great variability in pubescence density. The type specimen (a photograph in the original publication and the lectotype at G) is densely hairy, while other collections are almost glabrous. There appear to be no environmental factors influencing this, but more detailed field studies could help clarify the situation. *Solanum uleanum* often grows up trees at the edge of gaps or clearings in the forest, and individuals growing in the deep shade of the understory have much thinner, more membranous leaves.

EXCLUDED SPECIES

1. ***Solanum cormanthum*** Vell. (synonym of *S. caavurana* Vell. = section *Geminata* (G. Don) Walp.)
2. ***Solanum lacteum*** Vell. (affinities and identification unknown, no type specimen exists and plate in Vellozo resembles no known species of *Solanum*)
3. ***Solanum laurinum*** Dunal (synonym of *S. decorticans* Sendtn. = section *Lysiphellos* Bitter)
4. ***Solanum loxophyllum*** Bitter (= section *Anarrhicomenum* Bitter)
5. ***Solanum marantifolium*** Bitter (= section *Geminata* (G. Don) Walp.)
6. ***Solanum pentaphyllum*** Bitter (= section *Herpystichum* Bitter)
7. ***Solanum robustifrons*** Bitter (= section *Geminata* (G. Don) Walp.)

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EXSICCATAE

- Agostini, G.* 48 (trizygmum).
Allard, H.A. 6236 (mite); 20481 (mite); 20850 (anceps); 22077 (anceps); 22116 (anceps); 22522 (anceps).
Allart, A. 255 (trizygmum); 335 (ternatum).
Allen, P.H. 4953 (trizygmum); 16520 (trizygmum).
André, E. s.n. (conicum); K693 (trizygmum); K694 (savanillense); 4565 (savanillense).
Asplund, E. 12043 (mite).
Aublet, J.B.C.F. s.n. (anceps).
Ayala, F. et al. 2543 (anceps).
Baker & Trushell 6099 (anceps).
Baker et al. 5651 (anceps).
Bang, M. 2248 (mite); 2513 (anceps); 2526 (anceps).
Barbour, P. 3831 (mite); 3829 (ternatum); 4160 (ternatum); 4800 (mite); 5461 (mite).
Beck, St.G. 4881 (ternatum); 7361 (mite); 7498 (anceps).
Bell, D. & Wiser, S. 88-8 (mite); 88-40 (mite).
Belshaw, C.M. 3089 (anceps); 3109 (mite).
Bensman, R. 148 (anceps).
Berry, P.E. 1926 (trizygmum).
Boeke, J.D. 1200 (mite).
Bohs, L. & McPherson, G. 2307 (trizygmum).
Bohs, L. & Schunke V, J. 2168 (mite).
Brandbyge, J. & Asanza C., E. 30829 (anceps); 31783 (anceps); 31824 (anceps); 31873 (anceps); 31927 (anceps); 32365 (anceps).
Brandbyge, J. & Balslev, H. 42280 (anceps).
Brandbyge, J. et al. 32965 (uleanum).
Brenes, A.M. 3719 (trizygmum); 5625 (trizygmum); 5704 (trizygmum); 22613 (trizygmum).
Britton, N.L. & Rusby, H.H. 1210 (anceps); 2513 (anceps); 2526 (anceps).
Buchtien, O. 1249 (mite); 1287 (anceps); 1288 (anceps); 1289 (anceps); 1438 (mite); 7462 (ternatum); 7470 (anceps).
Burger, W.C. & Pohl, R.W. 7809 (trizygmum).
Burger, W.C. et al. 10250 (trizygmum).
Calderón, C.E. et al. 2855 (anceps).
Cardenas, M. 1168 (mite); 2046 (mite).
Castillo, A & Bocaranda, F. 2694 (trizygmum).
Castillo, M. del 1520 (trizygmum).
Cazalet, P.C.D. & Pennington, T.D. 7676 (mite).
Cerón, C.E. 2931 (uleanum); 7378 (anceps); 6389 (mite).
Cerón, C.E. & Cerón, M. 4604 (mite).
Cerón, C. E. & Hurtado, F. 4057 (uleanum).
Cerón, C.E. & Iguago, C. 5430 (anceps).
Chacon, I.A. et al. 1811 (trizygmum).
Cid, A.C. et al. 4568 (mite); 4829 (anceps).
Clemants, S.E. et al. 2252 (savanillense).
Clewell, A. & Hazlett, D. 3859 (trizygmum).
Cowan, R.S. & Lindeman, J.C. 39020 (anceps).
Croat, T.B. 18651 (anceps); 21039 (mite); 33456 (trizygmum); 35489 (trizygmum); 40937 (trizygmum); 48589 (trizygmum); 50031 (trizygmum); 50575 (anceps); 51014 (mite); 51156 (mite); 51262 (anceps); 58022A (anceps); 58041 (anceps); 58622 (anceps);
Cuatrecasas, J. 813 (mite).
D'Arcy, W.G. 12672 (trizygmum); 15003 (trizygmum); 16328 (trizygmum); 16343 (trizygmum); 16506 (ternatum).
D'Arcy, W.G. & D'Arcy, J.J. 6606 (trizygmum).
D'Arcy, W.G. et al. 12647 (trizygmum); 12988 (trizygmum).
Daly, D.C. et al. 6118 (anceps); 6133 (anceps).
Davidse, G. & Herrera Ch., G. 29142 (trizygmum).
Davidse, G & Pohl, R.W. 1529 (trizygmum).
Davidson, C. 3487 (mite).
Davidson, M.E. 63 (trizygmum).
Díaz, C. & Beltrán, 3335 (anceps).
Díaz, C. & Jaramillo, N. 576 (anceps).
Díaz, P. & Melief, B. 2952 (ternatum).
Dombey, P. s.n. (ternatum).
Dorr, L.J. et al. 6816 (anceps).
Dryer, V.J. 1069 (trizygmum); 1194 (trizygmum).
Dudley, T.R. 10152 (ternatum).
Dumont, K. et al. VE-7649 (trizygmum).
Dwyer, J.D. & Hayden, M.V. 7661 (trizygmum); 7670 (trizygmum).
Egger, H.F.A. Baron von 13223 (trizygmum).
Ellenburgh, H. 3889 (anceps).
Emmons, L. 81 (anceps); 132 (anceps); 146 (anceps).
Encarnación, F. 26268 (anceps).
Espinal T., S. & Ramos, J. 2943 (anceps).
Fendler, A. 1016 (trizygmum); 1017 (ternatum).
Fernández C., J. 8299 (anceps).
Ferreyra, R. 800 (mite); 1575 (mite); 2138 (mite).
Feuillet, C. et al. 10178 (anceps); 10230 (anceps).
Flora Falcón 210 (trizygmum).
Folsom, J.P. & Collins, L. 1765 (trizygmum).
Folsom, J.P. et al. 5486 (trizygmum).
Foresta, H. de. H.F 656 (anceps).
Foster, R.B. 2411 (anceps); 8592 (anceps); 9198 (mite); 9269 (uleanum); 9298 (anceps). 9355 (ternatum).
Foster, R.B. & Terborgh, J. 6071 (anceps); 6222 (anceps).
Foster, R.B. et al. 3312 (anceps); 8969 (anceps); 10481 (anceps).
Franco, P. et al. 1876 (anceps).
Galeotti, H. 1165 (trizygmum).
Gavilanes et al. 381 (savanillense).
Gentry, A. 31046 (anceps).
Gentry, A. & Daly, D. 18773 (mite).
Gentry, A. & Diaz, C. 58484 (uleanum).
Gentry, A. & Horna, M. 29521 (anceps).
Gentry, A. et al. 18876 (anceps); 21185 (anceps); 23086 (mite); 29558 (ternatum); 29790 (anceps); 30871 (incurvum); 36396 (anceps); 45399 (anceps); 46254 (mite); 47779 (ternatum); 53970 (ternatum); 61713 (mite).
Gentry, J.L. & Burger, W.C. 2721 (trizygmum); 2731 (trizygmum); 2863 (trizygmum).
Gómez, L.D. 20172 (trizygmum);
Goudot 136 (anceps).
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