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A revision of *Solanum thelopodium* species group (section *Anthoresis* sensu Seithe, pro parte): Solanaceae

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CONTENTS

SYNOPSIS. The *Solanum thelopodium* species group, as delimited here, includes three species of slender, wand-like shrubs of primary rainforest in Amazonia and northern South America. All of the species inhabit the dark forest understory, and two of the three occur exclusively in Amazonia. Two new species are described, *S. monarchostemon* of Amazonian Colombia, Ecuador and Peru, and *S. dimorphandrum* of N. and W. coastal Colombia and adjacent Panama. The group is defined by an unusual zygomorphic androecium, which is not found anywhere else in the genus *Solanum*. The nomenclature and morphology of the group is examined in detail, with particular emphasis on the unusual androecium and seeds. Although the phylogenetic position of the group is not known at present, it is possibly related to sections *Pachyphylla*, *Cyphomandropsis* and *Allophyllum* of *Solanum* subgenus *Solanum*.

INTRODUCTION

Despite being one of the five or six largest genera of flowering plants, *Solanum* L. (Solanaceae) has been the focus for relatively little monographic work (see D'Arcy, 1991). 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*. Taxonomic research effort has been concentrated on groups of economic importance, such as potatoes, tomatoes, nightshades, and selected groups of the spiny solanums (see Knapp, 1989; Knapp & Helgason, 1997 for references). As part of an ongoing research program into the taxonomy and phylogeny of non-spiny solanums (see Knapp, 1986, 1989, 1991*a*; Knapp & Helgason, 1997) I have investigated the unusual, primarily rainforest species allied to *S. thelopodium* Sendtn. The group, whose members are characterized by a ternately branched, terminal inflorescence and markedly dimorphic anthers, consists of just three species, and is morphologically very different from any other group of solanums. I have called this group the *Solanum thelopodium* species group, following the convention of Whalen (1984) for recognition of infrageneric groups in *Solanum*. 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. This is the first study to define species limits in the *S. thelopodium* species group and to examine its phylogenetic position within the larger scope of *Solanum*.

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, Archaesolanum, Lyciosolanum* and *Potatoe* – D'Arcy, 1972, see Table 1). Taxonomy of non-spiny solanums has long been confused, and there is considerable disagreement as to the circumscription of monophyletic groups within that portion of the genus (Bohs & Olmstead, 1997; Olmstead & Palmer, 1997). For a detailed history of the taxonomy of *Solanum* both before and after Dunal (1852) see Knapp (1989, 1991*a*) 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* (Child) Bohs (Bohs, 1990), the genus *Cyphomandra* (Bohs, 1994; now with all epithets transferred to *Solanum*, see Bohs, 1995), and *Solanum* section *Pteroidea* Dunal (Knapp & Helgason, 1997).

Since its description by Otto Sendtner in 1846, *Solanum thelopodium* has been enigmatic. Morphologically very distinct from other non-spiny solanums (see below), it has been placed in section *Anthoresis* (Dunal) Bitter by the only two authors to specifically consider it, Dunal (1852) and Seithe (1962). The great early twentieth century solanologist Georg Bitter thought *S. thelopodium* was distinct enough to merit generic rank, but although he annotated herbarium sheets accordingly (e.g. *Ule* 5691 in HBG), he never published the name.

In his group (grad. ambig.) *Anthoresis*, Dunal included 77 species of solanums with terminal and later lateral inflorescences and terminal poricidal anthers where the pores were oval ['Racemi, corymbi, cymae vel paniculae terminales, dein laterales. Antherarum pori antici ovales magni, nonunquam minuti orbiculares.']. Included in the group were species of currently recognized sections *Geminata* (G. Don) Walp., *Afrosolanum* Bitter, *Madagascarienses* Bitter, *Lepidotum* Seithe, *Brevantherum* Seithe, members of the *Solanum nitidum* species group, and some members of subgenus *Leptostemonum*. Although Dunal included *S. thelopodium* in his group *Anthoresis*, he had never seen a specimen and went entirely on Sendtner's description. Seithe (1962) lectotypified section *Anthoresis* with *Solanum cervantesii* Lag. (= *Solanum pubigerum* Dunal) and defined the group as shrubs and subshrubs with entire leaves, terminal or lateral inflorescences and uniseriate or branched trichomes. Species she included in the group were various members of the *Solanum sessile* species group (section *Geminata* s.s., see Knapp, 1991*a*, *b*), members of the *Solanum nitidum* species group (see Knapp, 1989), members of section *Holophylla* (G. Don) Walp. s.s. (see below) and *Solanum thelopodium*. Gilli (1970) followed Seithe's system almost exactly, using section *Anthoresis*, but never listed any component species in his groups, so the utility of his classification is limited. His section *Anthoresis* is defined largely on geography, as being composed of species from Central and South America. Danert (1970) correctly realized that section *Holophylla* was the correct sectional name for the group containing Seithe's lectotype species, *S. cervantesii*, but did not specifically mention *S. thelopodium* in his description and delimitation of the group. His concept of section *Holophylla* is essentially the same as that of Seithe, but he mentions that the species are grouped together for convenience, and perhaps belong to several different groups. D'Arcy (1972) superfluously lectotypified both section *Anthoresis* and section *Holophylla* with *Solanum pulverulentum* Pers. (= *S. nitidum* Ruiz & Pav.: see Knapp, 1989), thereby confusing the situation somewhat. However, since Seithe's lectotypification has priority,

Table 1 Traditional classification of *Solanum* (after D'Arcy, 1972).

Subgenus	Characters	Sections included by D'Arcy, 1972	Monophyly: Bohs & Olmstead, 1997
Solanum	stout anthers, simple hairs, no spines	*Solanum*, *Afrosolanum* Bitter, *Benderanum* Bitter, *Chamaesarachidium* Bitter, *Episarcophyllum* Bitter, *Gonatotrichum* Bitter, *Leiodendra* (=*Geminata*) Dunal, *Lemurisolanum* Bitter, *Lysiphellos* (Bitter) Seithe, *Macronesiotes* Bitter, *Quadrangulare* Bitter	no
Bassovia	stout anthers, simple hairs, pinnate leaves, axillary inflorescences, pointed fruits	*Pteroidea* Dunal, *Herpystichum* Bitter, *Herposolanum* Bitter,	not included in analysis
Brevantherum	stout anthers, entire leaves, dendritic or stellate hairs	*Brevantherum* Seithe, *Extensum* D'Arcy, *Holophylla* (G. Don) Walp., *Lepidotum* Seithe, *Pseudocapsicum* Bitter	no
Potatoe	scandent species, pinnnate leaves with interstitial leaflets, lateral pendulous inflorescences, articulated pedicels	*Petota* Dumort., *Anarrhichomenum* Bitter, *Basarthrum* (Bitter) Bitter, *Dulcamara* Dumort., *Jasminosolanum* Seithe, *Neolycopersicon* Corr., *Normania* (Lowe) Bitter, *Regmandra* (Dunal) Ugent, *Rhynchantherum* Bitter	no
Leptostemonum The 'spiny solanums'	tapering anthers, stellate hairs, often spines	see Whalen, 1984	no
Lyciosolanum	stout anthers, rotate flowers, elongate filaments (South Africa)	*Lyciosolanum* Bitter	not included in analysis
Archaesolanum	stout anthers, rotate flowers, aneuploid chromosome numbers (Australia)	*Archaesolanum* Danert	yes

Fig. 1 Habitats of the *Solanum thelopodium* species group. A. Tahuampa or flooded forest, B. Non-flooded forest. Both from Peru. Loreto: Yanamono, Rio Amazonas between Indiana and mouth of Rio Napo.

we must now regard section *Holophylla* (see discussion in Knapp, 1989) as including only those species related to *Solanum cervantesii* (= *S. pubigerum* Dunal). *Solanum thelopodium* has always been an afterthought in all of the previous systems, as its morphology is so apparently aberrant and specimens are so few. The species, nor its two very close relatives described here, has not been included in any of the recent DNA phylogenies of the genus *Solanum* (Olmstead & Palmer, 1991; Bohs & Olmstead, 1997; Olmstead & Palmer, 1997).

MORPHOLOGY AND NATURAL HISTORY

Habitats

Plants of the *Solanum thelopodium* species group are generally found in or around primary forest. *Solanum thelopodium* itself is usually recorded as occurring in periodically flooded forest – igapó or tahuampa – and is occasionally recorded as being weedy at the edges of clearings. Where I have collected *S. thelopodium* and *S. monarchostemon* growing sympatrically (Yanamono, Dept. Loreto, Peru), they occupy different habitat types: *S. thelopodium* in the sunny clearings in the tahuampa and *S. monarchostemon* in the understory of primary forest (see Fig. 1A, B). Label data from specimens collected in the Ecuadorian Amazon indicate this is also the case there (*Brandbyge* et al. 33209, *S. thelopodium*; *Brandbyge* et al. 33192, *S. monarchostemon*).

Stems

The single-stemmed growth habit of plants of the *Solanum thelopodium* species group is unusual in *Solanum*. The plants are occasionally described as branching, but label data usually mention the wand-like stems characteristic of this group. Some specimens have been collected with their roots, and these are enlarged, thickened and very woody (see Fig. 2). These sorts of tap-roots appear to be more common in *S. thelopodium*, and may be related to growing in periodically flooded forests.

In all *Solanum* species the young stem is monopodial with the leaves arranged in a 2/5 phyllotaxic spiral. When a given stem begins its reproductive stage, sympodial growth begins (Danert, 1958, 1967; Child, 1979, 1991; Bell & Dines, 1995). Every inflorescence is developmentally terminal and shoot continuation and elongation is initiated in the axil of the leaf subtending the inflorescence. Monochasial growth patterns result from a single lateral continuation of shoot growth, while a dichasial growth pattern results from a double lateral continuation (see Fig. 3). In general, a given species is either monochasial or dichasial (see Knapp, 1989), but occasionally both growth patterns occur on a single plant (Bell & Dines, 1995). The determining factor for pattern expression appears to be the dormancy of axillary buds in a given sympodial unit. Sympodial units in *Solanum* consist of leaves along each shoot terminating in an inflorescence, and can vary from plurifoliate (members of sections *Brevantherum*, *Holophylla*, the *S. nitidum* species group) to unifoliate (section *Pteroidea*, some species groups in section *Geminata*). The sympodial units in the *S. thelopodium* species group appear to be plurifoliate, with the most common number of leaves between inflorescences being three. However, most plants bear only a single inflorescence and thus consist of a single plurifoliate sympodial unit.

Leaves

The leaves of members of the *S. thelopodium* species group are usually clustered at the top of the stem (see Figs 2, 7, 8, 10). They are simple, entire and elliptic to obovate in outline. Leaf size is variable both within species and within single plants. The texture is membranous, and some specimens have extremely thin leaves, particularly those from forest understory habitats. Both *S. thelopodium* and *S.*

Fig. 2 Enlarged woody root or underground stem of *Solanum thelopodium* (*S.F. Smith* et al. 533, Madre de Dios, Peru).

Fig. 3 Sympodial growth patterns in *Solanum*. A. Dichasial growth, B. Monochasial growth.

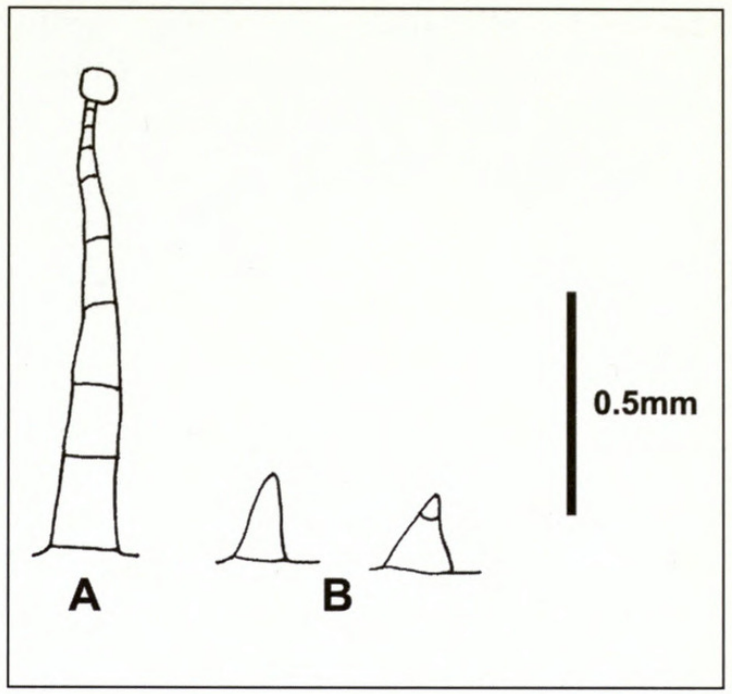

Fig. 4 Trichome types in the *Solanum thelopodium* species group. A. Long, uniseriate trichomes of *S. monarchostemon*, B. Papillate trichomes found in all species.

monarchostemon occasionally have purple or deep burgundy-red leaf undersides. This is also common in section *Pteroidea* (the *S. mite* species group, see Knapp & Helgason, 1997) and may be related to deep forest habitat, although in section *Pteroidea* populations are often dimorphic for the character.

No herbivorous insects have been observed or reported feeding on members of the *Solanum thelopodium* group (Brown, 1987; Drummond & Brown, 1987; Beccaloni, 1995), although ithomiine butterflies (Nymphalidae: Ithomiinae) commonly lay their eggs on similar understory solanums (see Knapp & Helgason, 1997). Damage on leaves of herbarium specimens however is consistent with ithomiine larval feeding, and a few specimens have the damage characteristic of feeding by chrysomelid (Coleoptera: Chrysomelidae) beetles (see Knapp, 1986 for details).

Inflorescences

Inflorescences of the *Solanum thelopodium* species group are scorpioid cymes with the flowers arranged in two rows along the inflorescence axis. This inflorescence type is common to all *Solanum* species and is variously misinterpreted as a raceme or panicle (Dunal, 1852). In the *S. thelopodium* species group the inflorescence is always either bifurcate or ternate with an elongate, erect and rather stout peduncle. The two or three branches all arise from a single point, so the entire structure has an unusual umbrella-like appearance. Other non-spiny solanums with branched inflorescences generally have branches arising all along the length (*S. sessile* species group, see Knapp, 1991*a*; *S. nitidum* species group, see Knapp, 1989) or at irregular intervals on all sides of the axis (e.g. *S. terminale* Bitter of section *Afrosolanum* Bitter).

In the *Solanum thelopodium* species group, pedicel scars are present to the bases of the branches, with occasionally a single scar in the fork; flowers are never borne on the erect peduncle. The pedicels are articulated at the base and do not leave pegs (section *Pachyphylla*, see Bohs, 1994), sleeves (*S. nitidum* species group, see Knapp, 1989), 'platforms' (section *Holophylla* s.s., see Knapp, 1989) or other such prominent scars. In any given inflorescence only one flower per branch is open at a time, but each branch may bear up to 100 flowers over its lifespan. Pubescence of the inflorescence generally parallels that of the leaves, but in *S. monarchostemon*, the inflorescence is usually more densely pubescent than the leaves and is the most reliable place to look for trichomes.

Trichomes

Trichome morphology traditionally has been used extensively in *Solanum* taxonomy and can be a rich source of useful characters (Seithe, 1962; Roe, 1971; Seithe, 1979; Edmonds, 1982; Seithe & Anderson, 1982; Whalen, 1984; Knapp, 1989, 1991*b*). Trichomes in the *S. thelopodium* species group are exclusively simple and uniseriate, varying between single-celled papillate trichomes (all three species) to multicellular, long, white, sometimes glandular, trichomes (*S. monarchostemon*). In *S. monarchostemon*, trichome density varies considerably, but there are always some long, white uniseriate trichomes (see Fig. 4) present on the inflorescence and leaf uppersides. On the leaf uppersides of *S. monarchostemon* the trichomes are present only on the lamina, while on the leaf undersides, they are present only along the veins. Specimens from the provinces of Pastaza and Sucumbíos in eastern Ecuador have inflorescence trichomes with glandular tips; the gland appears to be a single cell and usually dries a reddish brown.

Flowers

In most species of *Solanum* the flowers are actinomorphic and pentamerous. The calyx is synsepalous and the corolla sympetalous, with a very short floral tube. Members of the *S. thelopodium* species group are unusual in the genus in having markedly zygomorphic flowers, with the zygomorphy largely due to the dimorphic anthers. In the group, the calyx lobes are deltate to quadrate. Calyx pubescence parallels that of the rest of the inflorescence, but in some collections of *S. monarchostemon*, the calyx is the most densely pubescent part of the reproductive axis. The corolla is pentamerous, and lobed nearly to the base. The corolla lobes are very narrowly triangular-attenuate, and have markedly cucullate tips. Mature buds just before anthesis are curved at the tips, reflecting this corolla lobe shape. The corolla is either pink or greenish white: plants of

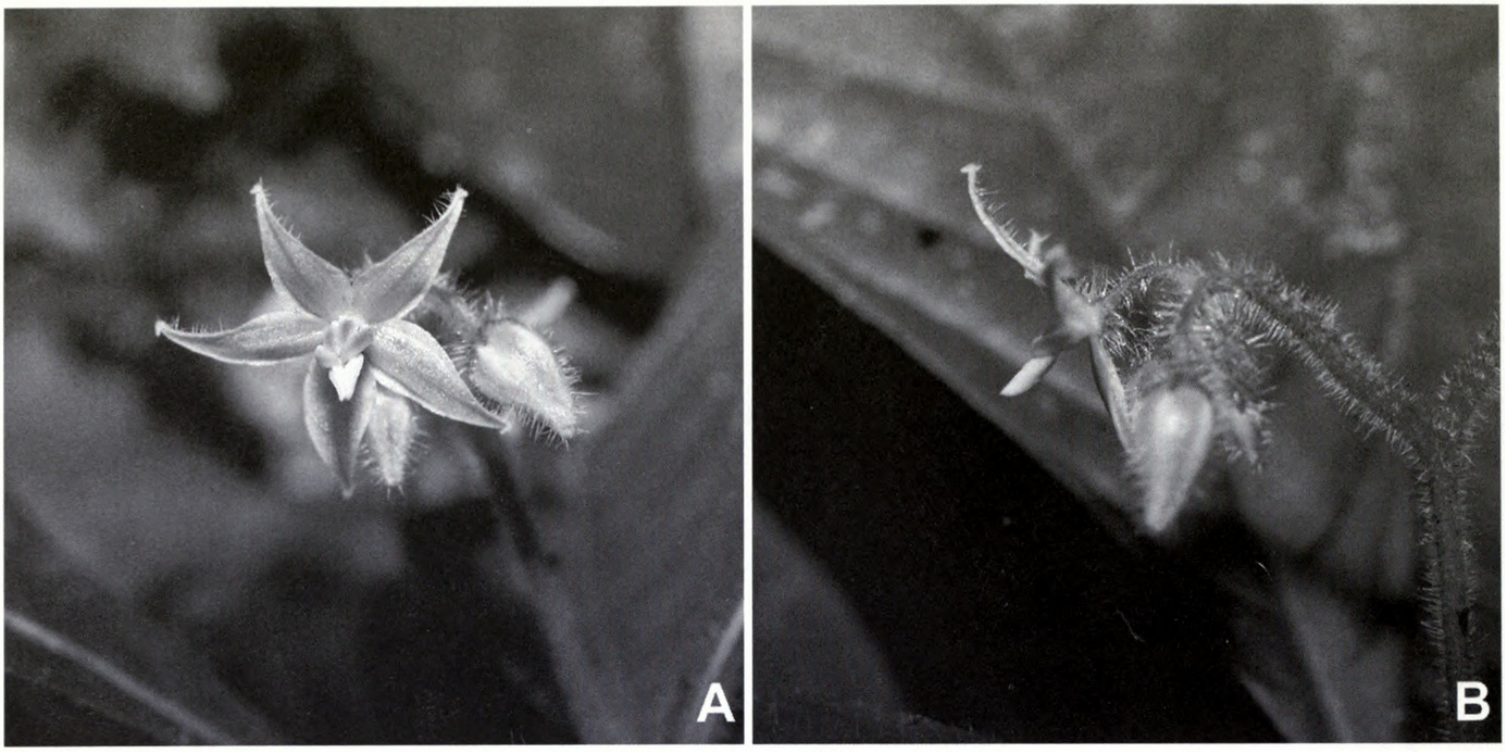

Fig. 5 Flowers of the *Solanum thelopodium* species group. A. *S. monarchostemon* front view, B. *S. monarchostemon*, side view (both *Knapp* 6606, Loreto, Peru).

S. thelopodium tend to more often have pinkish corollas, while those of *S. monarchostemon* and *S. dimorphandrum* tend to have white or greenish white corollas. Colour polymorphism, however, probably exists in all three species (only recorded in *S. thelopodium* and *S. monarchostemon*).

In all three species of the *Solanum thelopodium* group the corolla is nodding at anthesis. The corolla lobes are planar, but the pedicel is deflexed such that the plane of the corolla is at approximately 45° from horizontal (see Fig. 5). The pedicel becomes erect in fruit (Fig. 8, also see below).

The androecium is the most unusual feature of members of the *Solanum thelopodium* species group, and is found nowhere else in non-spiny solanums. In general, the androecium in non-spiny solanums is remarkably uniform, but some use has been made of relatively small differences in pore size and shape and union of filaments (Knapp, 1986; Barboza & Hunziker, 1991). These minor characters, however, can vary considerably between plants of the same species (Knapp, 1986). Some spiny solanums have strongly zygomorphic flowers with markedly dimorphic anthers (section *Androceras*, see Whalen, 1979; *S. tridynamum* Dunal), and some non-spiny solanums have one anther slightly longer than the rest (*S. pensile* Sendtn., *S. wendlandii* Hook.f.), but the situation in the *S. thelopodium* species group is unique in non-spiny solanums. Individual anthers can be classified as one of three types which I have characterized in the species descriptions as long anthers (one only), medium anthers (a pair) and short anthers (a pair). In living plants the anthers are always arranged with the long anther lowermost, the medium anthers next in sequence and the short anthers uppermost (see Figs 5, 8). The anthers thus closely invest the style, which is held in the connective groove of the long anther (see below). The two pairs of anthers (medium and short) are morphologically like those of other non-spiny solanums: ellipsoid in shape, they are poricidally dehiscent with ovate, terminal pores. Unlike other species of non-spiny solanums, however, the pores do not markedly elongate to slits with age, but remain round. The connective of these four anthers is somewhat prolonged at the tip, forming an apiculus which can be as long as 0.5 mm in some individuals. In any individual flower the medium pair of anthers is usually somewhat longer and larger than the short pair, but within a species, measurements overlap completely (see species descriptions). The difference in appearance is almost entirely due to filament length. Filaments on the medium pair are longer than those of the short pair (see Fig. 8). The filament of the long anther is even longer, and is usually almost twice as long as the filaments of the short anther pair. The long anther is somewhat different morphologically from the others. It is larger than the other four, triangular in shape with an elongate tip and wide base (see Fig. 8), slightly paler yellow, and has an unusual membranous connective, wider than the two thecae, in which the style is held at anthesis. The pores at the tips are rounded and extremely small, and the connective is somewhat pointed and prolonged at the tip beyond the pores.

The flowers of all species of *Solanum* are buzz pollinated by bees (Buchmann, 1983): the anthers are tightly grasped by the bee who vibrates her indirect flight muscles, causing pollen to be released in a cloud and deposited on the underside of the thorax and abdomen. In solanums with isomorphic anthers the bee's body is positioned directly over the centre of the anther cone, and the anthers are all manipulated in a similar way. In those taxa with dimorphic anthers, such as members of *Solanum* section *Androceras* (i.e. *S. rostratum* Dunal and relatives), the long anther is differently coloured (usually flushed with purple) and is not manipulated by the bee, who vibrates and 'milks' the cone of four anthers (Bowers, 1975; Whalen, 1979). In section *Androceras*, the long anther functions in pollination while the other anthers are largely the source of 'feeding pollen' for visiting bees. I have not seen flower visitors to any of these species, nor are any reported on labels or in the literature, so how this anther arrangement functions in pollination in the *S. thelopodium* species group is not known. The paler colour of the long anther, coupled

with the tight connivence of the other four in a cone suggests a similar mechanism to that found in the spiny solanums is operating, however.

The ovary is bilocular, conical and glabrous. The style is glabrous, slightly curved, and at anthesis held in the groove of the connective of the large anther. The stigma is flattened and somewhat capitate, and not particularly large. Members of the *Solanum thelopodium* species group do not appear to ever bear short-styled flowers, unlike many groups of non-spiny solanums (see Knapp, 1986; Whalen & Costich, 1986; Knapp & Helgason, 1997). Pollen grains for the group are not known at present, but are being investigated as part of a wider study on anther morphology in the non-spiny solanums. They are likely, however, to be tricolporate with a granular exine as are all other members of the genus *Solanum* (Anderson, 1977; Punt & Monna-Brands, 1980; Bohs, 1994; Knapp et al., 1998).

Fruits and seeds

The most common fruit type in *Solanum* is a berry, although other modified fruit types are found, particularly in Australia (Symon, 1979). Members of the *S. thelopodium* species group all have smooth berries that remain green at maturity. *Solanum thelopodium* and *S. monarchostemon* have globose berries, while *S. dimorphandrum* has ellipsoid berries. Some specimens of *S. thelopodium* have somewhat ellipsoid immature berries, but at maturity the berries are globose. The pointed apex of berries of *S. dimorphandrum* is seed-bearing, rather than being sterile as is often the case in the apiculate berries of section *Pteroidea* (see Knapp & Helgason, 1997). Berries of members of the *S. thelopodium* species group have distinctive dark green stripes when mature, usually four stripes at right angles to one another. The pericarp of berries of all three species is extremely thin when mature, and in dry material quite brittle. At maturity the fruits are held erect on thickened pedicels, but when immature the fruits are nodding as were the flowers (see above). Nothing is known about fruit and seed dispersal in this group, but the soft berries on erect pedicels that remain green at maturity suggest either bats or small mammals as dispersal agents.

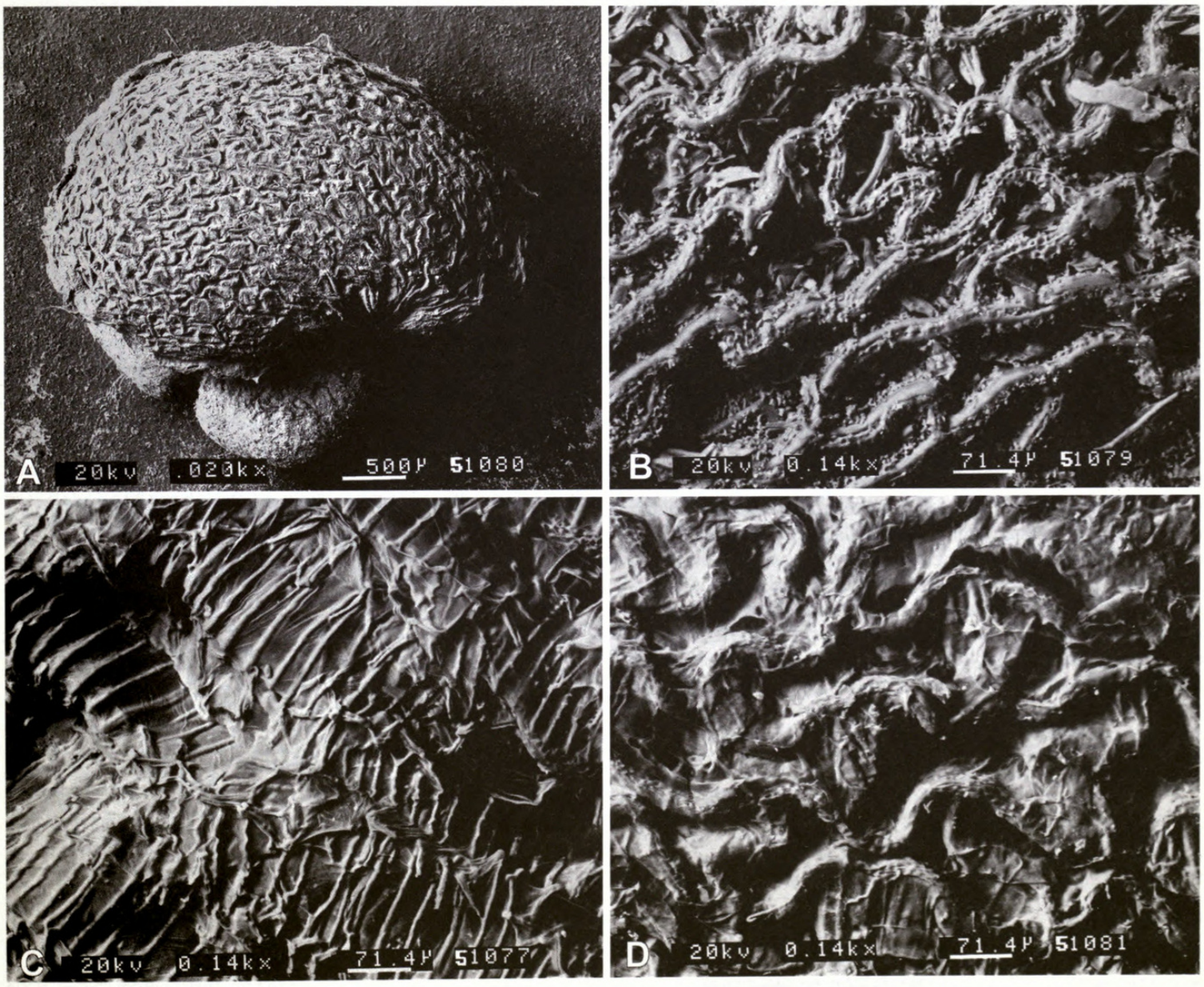

Fig. 6 Seeds of the *Solanum thelopodium* species group. A. Whole seed of *S. dimorphandrum* (*Forero* et al. 4071), B. Sinuate cells (outer testa removed) of *S. monarchostemon* (*Palacios & Neill* 649), C. Outer testal wall with conspicuous and regular thickenings ('comb-like') of *S. monarchostemon* (*Gentry* et al. 54613), D. Outer testal wall lacking conspicuous and regular thickenings of *S. dimorphandrum* (*Forero* et al. 4071).

Seed morphology has proved useful in *Solanum* taxonomy (Edmonds, 1983; Lester & Durrands, 1984; Bohs, 1994; Knapp & Helgason, 1997) and patterns of testal wall thickenings and cell shape are quite variable in the genus. All three members of the *S. thelopodium* species group have relatively few seeds per fruit (5–20). Some other non-spiny solanum groups, such as some species groups of section *Geminata*, also have few seeds per fruit, but many other solanums have large numbers of seeds in each berry (i.e. most spiny solanums, the members of section *Solanum*, the potatoes, tomatoes and their relatives, members of section *Pachyphylla,* etc.).

All three species of the group have reddish brown seeds that are reniform in outline and somewhat ovoid, rather than being markedly flattened as are many other *Solanum* seeds. The fine structure of seeds has been useful for resolving the relationships among species where morphological characters exhibit complex and overlapping 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, washed in distilled water and air dried, and photographed using a ISI ABT-55 low vacuum scanning electron microscope. The lateral cell walls of these seeds do not consist of 'hairs' (see Souèges, 1907; Lester & Durrands, 1984; Edmonds, 1983; Bohs, 1994; Knapp & Helgason, 1997), but are thickened and in all three species the cells are sinuate in outline (see Fig. 6). In *S. thelopodium* and *S. monarchostemon*, but not in *S. dimorphandrum*, the outer testal wall has conspicuous, regularly spaced comb-like thickenings (see Fig. 6), which disappear with vigorous seed cleaning and thus would probably not survive enzymatic digestion.

RELATIONSHIPS

Relationships of the group within *Solanum*

Solanum thelopodium and its relatives are superficially so morphologically different from other members of the genus *Solanum* that a new genus was proposed (but never published) for them by Georg Bitter in the early years of this century (Bitter, in litt.). These differences, particularly in the structure of the androecium, are clearly autoapomorphic, and although indicating the monophyly of this small group, tell us nothing about its relationships to the rest of *Solanum*. Sendtner (1846), Dunal (1852), and Seithe (1962) by placing *S. thelopodium* in groups containing other species with branched, terminal or lateral inflorescences, clearly felt that its affinities lay with these taxa. The taxa placed in section *Anthoresis* (= *Holophylla*) are now considered to be members of various other groups, all of which may have some relationship to the *S. thelopodium* species group (see Table 2 for a list of putative sister groups of the *S. thelopodium* species group). Other groups of solanums which may be related to the members of the *S. thelopodium* species group are sections *Pachyphylla* (ex *Cyphomandra*), *Cyphomandropsis* and *Allophyllum*, all of which have variously modified androecia (see Bohs, 1989, 1994). None of the taxa of the *S. thelopodium* species group have been included in DNA phylogenies of *Solanum*, and potential sister taxa fall into two separate clades (see Bohs & Olmstead, 1997). Future analyses of anatomy, morphology (Knapp, in prep.) and DNA sequences (Bohs, pers. comm.) will certainly shed light on the placement of this unusual group in *Solanum*.

Table 2 Possible sister groups for the *Solanum thelopodium* species group.

Group or section	Shared characters
section *Allophylla*	tightly connivent anthers, woody habit
section *Pachyphylla*	tightly connivent anthers, modified connective
section *Geminata* (*S. sessile* species group)	woody habit, pseudoterminal branched inflorescences
section *Cyphomandropsis*	woody habit, tightly connivent anthers, enlarged rootstocks
section *Holophylla* s.s.	woody habit, branched inflorescences

Relationships of the species

Within the group, *Solanum thelopodium* and *S. monarchostemon* share a number of morphological characters (globose fruit at maturity, seeds with striate outer testal wall, small flowers), perhaps indicating they are sister taxa, more closely related to each other than either is to *S. dimorphandrum*. The long, white, uniseriate trichomes (occasionally gland-tipped) of *S. monarchostemon* are autapomorphic in the group, as are the ellipsoid fruits of *S. dimorphandrum*. Rigorous cladistic analysis of the relationships of these three species is more appropriately done in the wider context of the entire genus *Solanum*, where appropriate hypotheses can be made concerning character polarity within and among other lineages in the genus.

TAXONOMIC TREATMENT

Key to selected groups of non-spiny solanums (woody plants, shrubs or subshrubs)

1 Inflorescences appearing axillary or in branch forks 2

Inflorescences appearing lateral or leaf-opposed 4

2 Plants small trees or shrubs, branching in a complex crown; inflorescences in branch forks; anthers with an enlarged, thickened connective ..... **Solanum** section **Pachyphylla** (genus **Cyphomandra**)

Plants wand-like, shrubs, vines, or herbaceous; inflorescences only in leaf axils; anthers without an enlarged, thickened connective 3

3 Trailing herbs, rooting at the nodes, inflorescences with a single flower; fruit with smooth surfaces ..... **Solanum** section **Herpystichum**

Upright herbs, slender shrubs or vines, inflorescences many (up to 30)-flowered; fruit smooth or rugose ..... **Solanum** section **Pteroidea**

4 Inflorescences internodal 5

Inflorescences leaf-opposed or terminal 7

5 Flowers small, the anthers not markedly connivent, oblong, with large pores; fruits with thin pericarp, stone cells usually present ..... **Solanum** section **Solanum**

Flowers larger, the anthers tightly connivent, tapered distally, with small pores; fruits with pericarp various, often green at maturity, stone cells usually absent 6

6 Inflorescences unbranched; fruit often laterally compressed ..... **Solanum** section **Allophyllum**

Inflorescences branched; fruit not laterally compressed ..... **Solanum** section **Cyphomandropsis**

7 Pedicel scars flush with the rachis ..... **Solanum thelopodium** species group

Pedicel scars variously raised 8

8 Pedicel scars in sleeves ..... **Solanum nitidum** species group

Pedicel scars on platforms ..... **Solanum** section **Holophylla** s.s.

The *Solanum thelopodium* species group

Solanum grad. ambig. *Anthoresis* Dunal in A. DC., *Prodr.* **13**(1): 29, 95 (1852), pro parte, excluding lectotype species. Lectotype species: *Solanum cervantesii* Lag. (Seithe, 1962); superfluous lectotype species: *Solanum pulverulentum* Pers. (D'Arcy, 1972).

Solanum section *Anthoresis* (Dunal) Bitter in *Bot. Jb.* **54**: 489 (1917), excluding lectotype species. Lectotype species: *Solanum cervantesii* Lag. (Seithe, 1962); superfluous lectotype species: *Solanum pulverulentum* Pers. (D'Arcy, 1972).

Shrubs or slender herbs, usually single-stemmed, 0.2–1(–1.5–2) m tall; pubescence of papillate or uniseriate simple trichomes; stems monochasial. *Sympodial units* plurifoliate, the number of leaves per unit extremely variable, the inflorescences usually terminal and with no further lateral growth. *Leaves* elliptic to obovate, glabrous or pubescent with simple, uniseriate trichomes above and beneath. *Inflorescences* terminal or pseudoterminal, bifurcate or ternate, the branches all arising from a single point, papillate or pubescent with usually uniseriate trichomes like those of the leaves, the peduncle stout, usually longer than the branches; pedicels at anthesis white or greenish white, deflexed; buds elliptic when young, later strongly curved and pointed, variously pubescent; *calyx* tube usually conical, the lobes minutely deltoid or long-triangular and acuminate; *corolla* white, greenish white, occasionally pink, or tinged with purple, membranous, lobed nearly to the base, the lobes planar at anthesis, narrowly triangular, the tips and margins of the lobes usually densely papillate, the tips cucullate; *anthers* strongly unequal, one pair on short filaments, one pair on medium length filaments, the anthers of these anther pairs elliptic to obovate, the fifth anther much larger than the rest, with a broad flattened connective, yellow or orangish yellow, all anthers poricidal at the tips, the pores not elongating to slits; *ovary* glabrous; *style* curved and sitting in the groove formed by the connective of the large anther, glabrous; *stigma* capitate or restricted to the unexpanded tip of the style. *Berries* globose or somewhat ellipsoid, bi-locular, usually green or yellowish green at maturity, often with four distinct green lines or blotches from tip to base; *fruiting pedicels* erect, usually thicker at the apex; *seeds* flattened- to ovoid-reniform without incrassate margins, the lateral seed coat walls lignified, the outer testa walls with or without regular, comb-like thickenings. *Chromosome number*: not known for any of the three species.

This revision is based on herbarium specimens and field observations. Taxa in the *Solanum thelopodium* species group are extremely rare and poorly collected and I have cited every herbarium specimen I have seen. The species are delimited on morphological grounds, with ecological and geographical differences being taken into account where appropriate.

Photographs of type specimens are cited in the recommended manner (see Knapp, 1989, 1991*a*; Knapp & Helgason, 1997), 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 (!). I have seen all non-type specimens cited in the species accounts, unless otherwise indicated.

Key to species of the *Solanum thelopodium* species group

1. Plants with at least some long, white uniseriate trichomes (to 3 mm long) on the inflorescences; leaves pubescent above ..... 2. **S. monarchostemon**

   Plants with no long, white uniseriate trichomes on the inflorescences, the pubescence of short, papillate trichomes; leaves glabrous above 2

2. Fruit ellipsoid; outer testal cell walls not markedly or regularly striate; NW South America and Panama ..... 1. **S. dimorphandrum**

   Fruit globose; outer testal cell walls markedly and regularly striate; Amazonia, often in flooded forests ..... 3. **S. thelopodium**

1. **Solanum dimorphandrum** S. Knapp, **sp. nov.** Type: Colombia, Magadalena, Sierra Nevada de Santa Marta, Valparaiso, '4500 ft.', 28 February 1899, *H.H. Smith* 1190 (NY!-holotype; GH!, K!, MO!, US!-isotypes).

Fig. 7

Solanum anceps of D'Arcy, 1974['1973'] not of Ruiz & Pavón.

Species *Solanum thelopodium* Sentdner affinis, sed floribus grandibus, baccis ellipsoidalibus, cellulis testaceis non striis, differt.

Suffruticose *herbs* to *shrubs*, 0.5–1.5(–2) m, single-stemmed; stems glabrous; bark reddish brown. *Leaves* 11.5–45 × 4.5–20 cm, elliptic to ovate, with 7–10(–16) pairs of primary veins, glabrous on both surfaces or with very sparsely scattered uniseriate trichomes on the lamina above, not on the veins, papillate on the veins beneath; base abruptly attenuate; apex acuminate; petiole 0.9–2.5 cm. *Inflorescence* 2 or 3 times branched, minutely papillate, the peduncle 2–10 cm, the branches 1.5–8 cm, with a single flower open at a time, but with up to 100 scars, the scars beginning at the fork. *Buds* elliptic, becoming pointed before anthesis. *Pedicels* 0.9–1 cm, papillate, deflexed. *Flowers* with the calyx tube conical to flattened, *c.* 1 mm, the lobes broadly deltate, 0.5–1 mm, densely to sparsely papillate, without an apical tuft of trichomes; corolla green or white, 1.5–2 cm in diameter, lobed nearly to the base, the lobes planar at anthesis, 8–9 mm, narrowly triangular, the tip markedly cucullate, densely papillate on tips and margins; filament tube absent; long anther 3–5 × *c.* 1 mm, the filament *c.* 1.5 mm; middle anther pair 3–3.5 × *c.* 1 mm, the filaments *c.* 1 mm; small anther pair 2.5–3.5 × *c.* 1 mm, the filaments *c.* 0.5 mm; ovary conical, glabrous; style 4–7 mm, glabrous, the stigma minutely flattened capitate. *Fruit* ellipsoid, 1.6–1.9 × 1–1.2 cm, green with four darker stripes, smooth, the pericarp thin and brittle when dry; fruiting pedicel 1.2–1.4 cm, erect. *Seeds* 10–15 per fruit, 4–6 mm long, pale tan or reddish, flattened reniform, the testal cells sinuate in outline, without regularly striate outer cell walls, the thickenings, if present, irregular and sparse.

COMMON NAMES AND USES. Colombia, Bolivar: 'raicilla de agua' (*Pennell* 4204).

DISTRIBUTION. In low to mid elevation forests on the northern and western coasts of Colombia and adjacent Panama, 0–1000(–1750) m. (Fig. 8).

SPECIMENS EXAMINED.

PANAMA. Darien: 10 km NE of Jaque, headwaters of Río Pavaroandó, 1400 ft, 31 January 1981, *D'Arcy & Sytsma* 14515 (MO); Boca de Pavaroandó on Sambú River, 1911, *Pittier* 5585 (F); Cerro Pirre, just S. of Pirre, 10–20 July 1977, *Folsom* 4524 (MO); vicinity of Cerro Tacaruna summit camp, 1500–1750 m, 31 January 1975, *Gentry & Mori* 14041 (MO). **San Blas**: SE of Puerto Obaldia, 18 August 1971, *Croat* 16769 (MO).

COLOMBIA. Antioquia: Parque Nacional Natural Las Orquideas, sector

Fig. 7 Holotype of *Solanum dimorphandrum* (*Smith* 1190, Magdalena, Colombia).

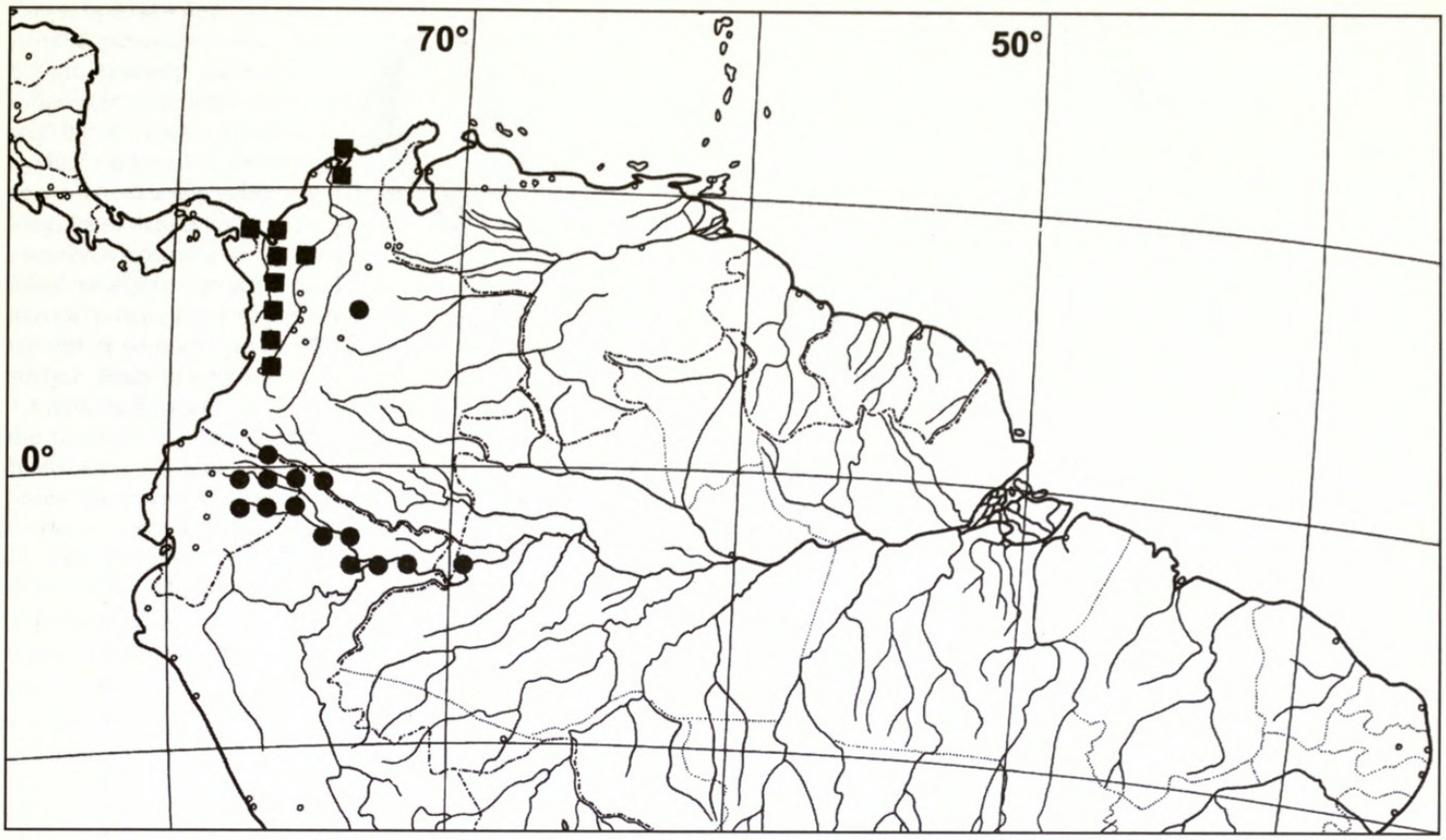

Fig. 8 Distribution of *Solanum dimorphandrum* (squares) and *S. monarchostemon* (circles).

Venados arriba, L. bank of Río Venados, 1110–1240 m, 6°34'N, 76°19'W, 27 July 1988, *Cogollo* et al. 3536 (MO); Chigorodo, 40 km S. of Turbo, *c.* 50 m, 22 May 1945, *Haught* 4702 (NY, US); Quebrada Mercedes, E. of Turbo, *c.* 75 m, 14 July 1946, *Haught* 4963 (US × 2); road to sea near Villa Arteaga, 150 m, 4–8 August 1947, *Hodge* 7075 (US); Mun. de Carepa, 2 km N. of Carepa, grounds of ICA at Tulenapa, 20 m, 7°52'N, 76°42'W, 25 March 1987, *Zarucchi* et al. 4994A (MO). **Bolivar**: Boca Verde, on Río Sinu, 100–300 m, 13–14 February 1918, *Pennell* 4204 (NY). **Chocó**: Mun. de Quibdó, Corregimiento de Guayabal, Río Hugon, *c.* 80 m, 12 September 1976, *Forero & Jaramillo* 2795 (MO, NY); Río San Juan drainage, small hill in front of Palestrina, 30–40 m, 4°10'N, 77°10'W, 26 March 1979, *Forero* et al. 4071 (MO); Río Atrato, between Loma del Sapo & Bocas de Guayabal, about 20 mins upriver from Quibdó by motorboat, 40 m, 23 June 1983, *Forero* et al. 9450 (MO); Río Taparal off Río San Juan, 100 ft, 24 August 1962, *Hugh-Jones* 329 (K); S. of Río Condoto, between Quebrada Guarapo & Mandinga, 120–180 m, 22, 28 April 1939, *Killip* 35131 (US). **Magdalena**: Sierra Nevada de Santa Marta, above Finca Reflejo, Quebrada La Sierna, 1500–1800 m, *c.* 10°59'N, 74°01'W, 6 September 1962, *Kirkbride* 2122 (NY); Sierra Nevada de Santa Marta, below Las Nubes, 4250 ft, May 1899, *Smith* 1722 (K, NY). **Valle de Cauca**: Mun. Buenaventura, region of Bajo Calima, along road between Buenaventura & Malaga, at km 51.3, *c.* 100 m, 4°09'N, 77°11'W, 27 February 1990, *Croat* 71005 (MO); Cordillera Occidental, banks of Río Calima, El Cairo, between Darien & Mediacanoa, 1650–1750 m, 6, 7 January 1943, *Cuatrecasas* 13928 (F); Cordillera Occidental, W. slopes, drainage of Río Sanquininí, L. bank, La Laguna, 1250–1400 m, 10–20 December 1942, *Cuatrecasas* 15689 (F).

Solanum dimorphandrum differs from both *S. monarchostemon* and *S. thelopodium* in its larger, apparently more fleshy, flowers and in its ellipsoidal berries. Like *S. thelopodium*, the leaves are glabrous or with merely papillate trichomes. *Solanum dimorphandrum* tends to grow at slightly higher elevations than the other two taxa, and is only found north and west of the Andes rather than in the Amazon basin.

Specimens of *Solanum dimorphandrum* form the basis for the report of *S. anceps* Ruiz & Pav. from Panama (D'Arcy, 1974, but see Knapp & Helgason, 1997). *Solanum anceps*, a member of section *Pteroidea* (*S. mite* species group), is a similar simple-leaved forest subshrub, but has axillary inflorescences bearing minute flowers with a regular, radially symmetrical androecium and wrinkled, turbinate fruits (see Knapp & Helgason, 1997).

2. **Solanum monarchostemon** S. Knapp, **sp. nov.** Type: Ecuador, Pastaza, Puyo, Comunidad Santa Cecilia, Villano, 380 m, 1°30'S, 77°27'W, 1 May 1992, *Palacios* 10117 (QCNE!-holotype; MO!-isotype).
Fig. 9.

Species *Solanum thelopodium* Sendtner affinis, sed foliis supra et inflorescentiis pubescentibus, trichomatibus longiusculus simplicibus uniseriatibus albis, bacca minoribus differt.

Herbs to small *shrubs*, 0.5–1.3 m, single-stemmed; stems densely pubescent when young with uniseriate white trichomes, 0.5–2 mm, later glabrescent; bark brown. *Leaves* 9–25 × 4–10 cm, elliptic, with 8–13 pairs of primary veins, pubescent above with scattered 4–5-celled, white, uniseriate trichomes 1–2 mm long on the veins and lamina, densely to sparsely pubescent beneath with 4–7-celled, white, uniseriate trichomes 1–2 mm long, only along the veins, not on the lamina, the trichomes denser on the new growth, mixed with papillate trichomes on new growth, occasionally uniseriate trichomes glandular, the gland a single cell. *Inflorescence* 2 or 3 times branched from a single point, densely or more rarely sparsely pubescent with mixed papillate trichomes and uniseriate, white trichomes 1–3 mm long, these occasionally gland-tipped, the gland a single cell, the peduncle 4–9 cm, the branches 1–3 cm, each branch with a single

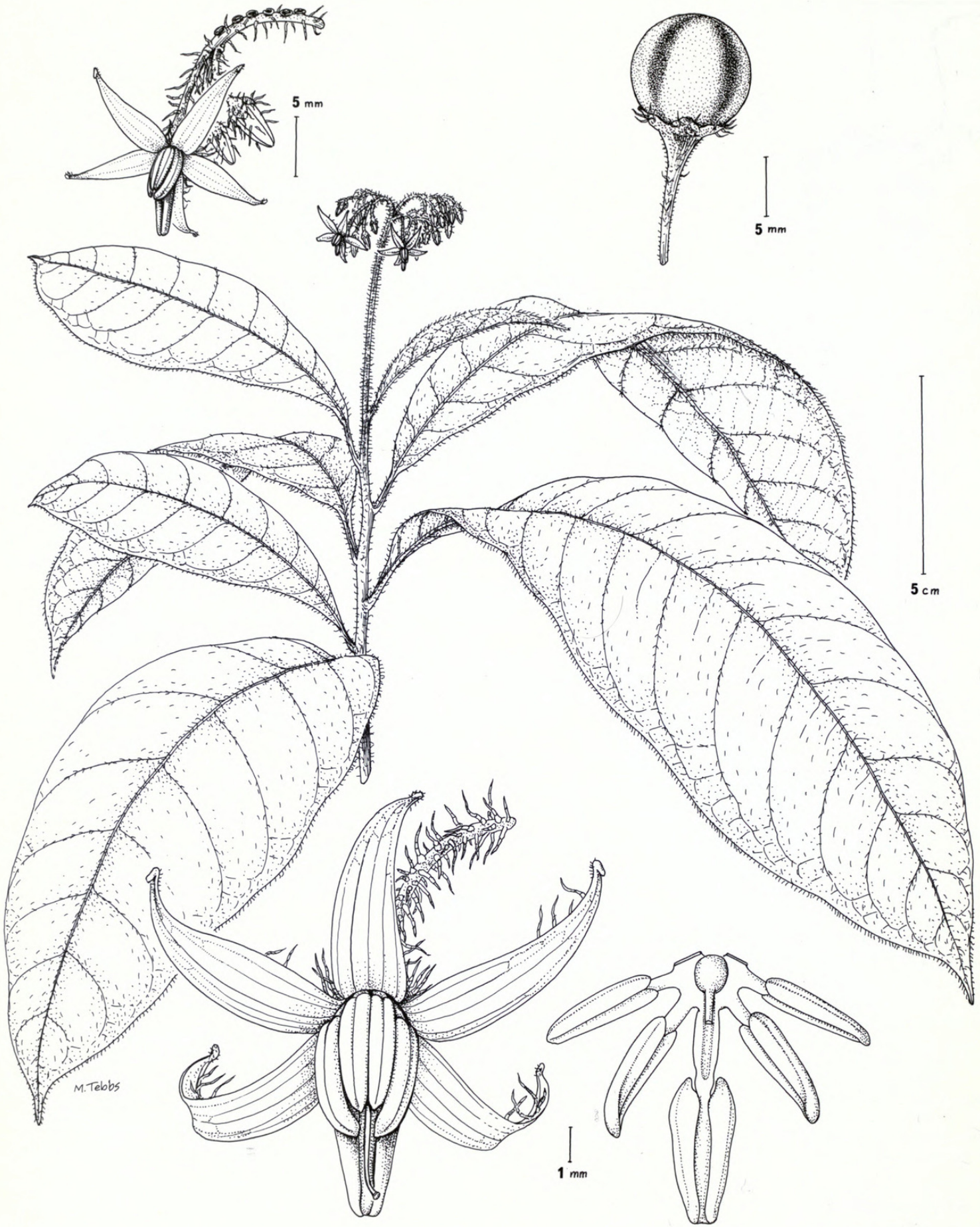

Fig. 9 *Solanum monarchostemon* (based on *Palacios* 10117 (QCNE), Pastaza, Ecuador; fruit (immature) from *Luteyn* et al. 8703 (NY)); flower details based on spirit collections of *Holm-Nielsen* et al. 19867, 20178 (AAU).

flower open at a time, but with up to 100 scars on each branch. *Buds* pointed, pubescent with uniseriate white trichomes. *Pedicels* (3–)5–8 mm, sparsely pubescent with uniseriate trichomes like the inflorescence or with only papillate trichomes, deflexed. *Flowers* with the calyx tube conical, 0.5–1 mm, the lobes deltate with lighter hyaline margins, 1–1.5 mm, without a distinct apical tuft of trichomes, sparsely to densely pubescent with uniseriate trichomes 0.5–2 mm long, these denser along the midline of each lobe; corolla white to greenish white, occasionally purplish tinged, 1.2–1.6 cm in diameter, lobed nearly to the base, the lobes planar at anthesis, 6–9 mm, narrowly triangular with pointed, strongly cucullate tips, papillate at the tips or with scattered uniseriate white trichomes on the abaxial surface; filament tube minute, *c.* 0.1–0.2 mm; long anther 4–4.5 × *c.* 1.5 mm, the filament 1–1.5 mm; middle anther pair 3–3.5 × *c.* 1 mm, the filaments *c.* 1 mm; small anther pair 2.5–3 × *c.* 1 mm, the filaments *c.* 0.5 mm; ovary conical, glabrous; style 5–6 mm, glabrous, the stigma flattened capitate. *Fruit* globose, 0.8–1.4 cm in diameter, green with four darker stripes, smooth, the pericarp thin and brittle when dry; fruiting pedicel 0.8–1.8 cm, erect, or slightly deflexed from the weight of the fruit. *Seeds* 5–10(–15) per fruit, 3–3.5 mm long, pale tan or reddish, flattened to ovate-reniform, the testa cells sinuate in outline, with markedly and regularly striate outer cell walls.

COMMON NAMES AND USES. Ecuador, Sucumbíos, Cofán, 'Saomatëye'hue', Secoya, 'aiquë'je' (*Jaramillo & Coello* 2748); Peru, Loreto, Secoya, 'yanse mat yna' (*King* 472), 'manucari' (*Williams* 709).

DISTRIBUTION. In Amazonian Colombia, Peru and Ecuador, usually growing in *terra firme* (non-flooded) forests, 100–450(–1300) m. Fig. 8.

SPECIMENS EXAMINED.

COLOMBIA. Amazonas: Parque Nacional Natural Amacayacu, Quebrada de Agua Pudre, *c.* 1.5 km NE of outlet to Río Amacayacu, 200–220 m, 3°47'N, 70°15'W, 15 November 1991, *Pipoly* 16210 (MO). **Boyacá**: 130 miles N. of Bogotá, 3500–4000 ft, 2 March 1933, *Lawrance* 643 (K, NY).

ECUADOR. Napo: Añangu, S. bank of Río Napo 95 km downstream from Coca, 300 m, 0°32'S, 76°23'W, 19 June–4 July 1985, *Balslev* et al. 60545 (AAU), 11–28 April 1986, *Balslev* et al. 62224, 62357 (AAU); Parque Nacional Yasuni, pozo petrolero Daimi 2, 200 m, 0°55'S, 76°11'W, 26 May–8 June 1988, *Cerón & Hurtado* 4111 (QCNE, MO); Canton Aguarico, PN Yasuní, lagunas de Garza Cocha, 200 m, 1°01'S, 75°47'W, 22 September 1988, *Cerón & Gallo* 5049 (MO); 1.1 km E. of Río Conejo on road to Lago Agrio, *c.* 340 m, 31 March 1972, *Dwyer & MacBryde* 9787 (MO); Río Yasuni, *c.* 60 km upriver from Nuevo Rocafuerte, 13 September 1977, *Foster* 3620 (F); Río Coca, 3–4 km from the mouth, *c.* 350 m, 11 February 1974, *Harling & Andersson* 11897 (MO); Río Yasuní, 3–4 km from Río Napo, 260 m, 0°57'S, 75°25'W, 25 August 1979, *Holm-Nielsen* et al. 19867 (AAU); 3 km E. of village of Huamaní, N. of Hollin-Loreto road on trail, 1200 m, 0°43'S, 77°36'W, 17 September 1988, *Hurtado & Alvarado* 255 (MO); Nuevo Rocafuerte, SE of town, trail to Río Braga, 200–230 m, 1 March 1981, *Jaramillo & Coello* 4484, 4487 (AAU); Añangu, NW corner of Parque Nacional Yasuní, *c.* 300 m, 0°32'S, 76°22–23'W, 1–30 October 1983, *Korning & Thomsen* 47055, 47072 (AAU); Añangu, Río Napo, 260–350 m, 9–10 March 1983, *Lawesson* et al. 39367 (AAU); Armenia Viejo at Río Napo, *c.* 12 km SW of Coca (Puerto Francisco de Orellana), 12 January 1973, *Lugo S.* 2642 (MO); PN Yasuní, Anango, 0°30'S, 76°25'W, 15 July 1982, *Luteyn* et al. 8703 (NY); Orellana, road to Pozos Gacela, Gacela 2, 250 m, 0°30'S, 77°08'W, 8 August 1993, *Palacios* 11038 (MO, QCNE). **Pastaza**: Lorocachi, 3 km S. of military camp, 200 m, 1°38'S, 75°58'W, 23 May 1980, *Brandbyge & Asanza C.* 30663 (AAU); Ceilán, pica from Ceilán to Río Coconaco on N. side of Río Curaray, 200 m, 1°36'S, 75°40'W, 6 June 1980, *Brandbyge & Asanza c.* 31653 (AAU); Río Curaray, S. bank, vicinity of Laguna Garzayacu, 250 m, 1°29'S, 76°39'W, 20–26 August 1985, *Palacios & Neill* 649 (MO). **Sucumbíos**: Reserva del Batallon de la Selva No. 55 (Putumayo), *c.* 200 m, 0°05'N, 75°52'W, August 1980, *Andrade* 33059 (AAU); Río Wai si ayá, 5 km upstream from outlet in Río Aguarico, 300 m, 0°15'S, 76°21'W, 6 August 1981, *Brandbyge* et al. 33192 (AAU), 10 August 1981, *Brandbyge* et al. 33367 (AAU); Limoncocha on Río Napo, 300 m, 4 March 1974, *Drummond* 7315 (MO); Limoncocha, hunting trail W. of settlement, 243 m, 25 September 1977, *Foster* 3843 (F); Río Jivino, Limoncocha, 13–15 March 1968, *Harling* et al. 7738 (MO); Río Aguarico, E. of Destacamento Zancudo, 310 m, 0°34'S, 75°29'W, 29 August 1979, *Holm-Nielsen* et al. 20178 (AAU); Río Aguarico, SE of Destacamento Largato Cocha, 290 m, 0°10'S, 75°16'W, 30 August 1979, *Holm-Nielsen* et al. 20274 (AAU); union of Río Eno & Río Aguarico, 3–4 km before Secoya village, L. bank of Río Eno, 3 July 1980, *Jaramillo & Coello* 2748 (NY); Río Aguarico, *c.* 5 km S. of Lago Agrio, 7 November 1973, *Lugo S.* 3240 (MO); Reserva Faunistica Cuyabeno, Río Aguarico, Zancudo, behind military camp, 230 m, 0°29'S, 75°32'W, 25 September 1991, *Palacios* et al. 7609 (QCNE); Reserva Cuyabeno, banks of Río Aguarico, Cofán community of Zabalo, 230 m, 0°22'S, 75°45'W, 21 November 1991, *Palacios* et al. 9430 (MO, QCNE); Río Aguarico, town of Dureno, *c.* 1500 ft, 1 August 1974, *Plowman* et al. 4018 (GH, K).

PERU. Loreto: Río Gueppi, tributary of Río Putumayo, N.-most tip of Peru on border with Ecuador, *c.* 200 m, 15 May 1978, *Gentry* et al. 21886, 21934 (F); Yanamono, Explorama tourist camp between Indiana & mouth of Río Napo, 130 m, 3°28'S, 72°48'W, 18 February 1981, *Gentry* et al. 31383 (MO), *c.* 120 m, 23 March 1982, *Gentry* et al. 36673 (MO), *c.* 130 m, 25 June 1982, *Gentry* et al. 37156 (F, MO), 25 July 1982, *Gentry & Alfaro* 37959 (MO), 3°28'S, 72°50'W, 27–28 December 1982, *Gentry & Emmons* 38704 (MO), 28 June 1983, *Gentry & Vásquez* 42285 (MO); Explorama Inn, 1 km S. of Indiana, Río Amazonas, 130 m, 3°30'S, 73°01'W, 17 June 1986, *Gentry* et al. 54613 (MO); Explorama Inn, *c.* 2 km S. of Indiana on Río Amazonas, 130 m, 3°30'S, 73°02'W, 15 February 1987, *Gentry* et al. 55946 (MO); Explorer's Inn near Indiana, Río Amazonas below Iquitos, 130 m, 3°30'S, 73°03'W, 15 February 1989, *Gentry* et al. 65795 (MO, NY); Explorama Lodge Tourist Camp, Yanamono, far end of Bushmaster trail, halfway between Indiana & mouth of Río Napo, 140 m, 3°28'S, 72°50'W, 5 January 1991, *Gentry* et al. 72167 (MO); Explorama Lodge Tourist Camp, Yanamono, halfway between Indiana & mouth of Río Napo, 130 m, 3°28'S, 72°50'W, 7 January 1991, *Gentry* et al. 72213 (MO); Explorama Lodge, Yanamono, 130 m, 3°28'S, 72°50'W, 11 June 1992, *Gentry* et al. 77492 (MO); environs of Río Santa Maria, trail one hour E. of Secoya village of Vencedor, 4 hours by outboard from mouth of Río Santa Maria, *c.* 1°10'S, 74°44'W, *c.* 100 m, 12 May 1982, *King* 472 (F); Yanamono, Explorama Tourist Camp on Río Amazonas between Indiana & mouth of Río Napo, *c.* 80 km NE of Iquitos, *c.* 100 m, 3°28'S, 72°48'W, 23–27 July 1984, *Knapp* 6606 (BH, K, US, USM); Indiana, Reserva Explorama (Yanamono), 25 km NE of Iquitos, along Río Amazonas, perimeter trail along S. limit, 110 m, 3°30'S, 72°50'W, 27 September 1990, *Pipoly* et al. 12532 (MO); Explornapo camp, inventario MacArthur, near Sucusari, along Río Napo, 100–140 m, 3°20'S, 72°55'W, 3 March 1991, *Pipoly* et al. 14178 (MO); Río Nanay, Chiriara, *c.* 100 m, 21 February 1969, *Plowman* 2548 (GH); Río Ampiyacu, Pebas & vicinity, *c.* 3°10'S, 71°49'W, 1 April 1977, *Plowman* et al. 6539 (GH); Indiana, Yanamono, Explorama Lodge, 106 m, 3°30'S, 72°50'W, 25 June 1984, *Vásquez* et al. 5120 (MO), 16 May 1989, *Vásquez* et al. 12154 (MO), 29 June 1991, *Vásquez & Jaramillo* 16925 (MO); Explornapo Camp, Río Sucusari, 140 m, 3°15'S, 72°54'W, 25 July 1991, *Vásquez & Grández* 17457 (MO); lower Río Nanay, between Río Nanay & Río Napo, 6 June 1929, *Williams* 709 (F); Pebas on the Amazon River, 24 July 1929, *Williams* 1679 (F).

Solanum monarchostemon is sympatric with *S. thelopodium* over nearly its entire range, but does occur higher in the Andean foothills than the latter species. Label data indicate that where they occur together, *S. monarchostemon* occurs in upland, non-inundated forest, while *S. thelopodium* occurs in flooded forests (see above). I have chosen to recognize *S. monarchostemon* at the specific level due to the apparently complete distinguishability of the two sets of plants. Even where *S. thelopodium* and *S. monarchostemon* grow together in the same locality (Yanomono, Peru; Yasuní, Ecuador), no intermediate pubescence types seem to occur. I have seen no mixed collections of the two taxa, again indicative of their apparent distinctness to field collectors. More detailed demographic and populational studies of both taxa in areas where they co-occur may shed light on these differences.

3. **Solanum thelopodium** Sendtn. in Mart., *Fl. Brasiliensis* **10**: 46 (1846). Type: Brazil, Amazonas, 'in sylvis ad lacum Teffé, prope Rio Catual, prov. Rio Negro', November, *Martius* 2903 (M!-lectotype, designated here [F neg. 6545-F, G, GH, NY, US]).

Fig. 10

Wand-like *shrubs*, 0.5–1(–2) m, usually single-stemmed; stems glabrous, drying dark; bark brown. *Leaves* 11–30(–45) × 4.1–16 cm, elliptic to obovate, usually very thin and membranous, with 12–13 pairs of primary veins, glabrous on both surfaces or with a few scattered papillae along the veins beneath; apex abruptly acuminate; base attenuate; petiole (0.6–)1–2.5 cm. *Inflorescences* 2–3 times branched from a single point, glabrous or papillate with short trichomes less than 0.5 mm long, the trichomes at most 3-celled and never glandular, the peduncle 2.7–5 cm, the branches 0.5–4 cm, each branch with a single flower open at a time, but with up to 50 scars on each branch. *Buds* elliptic when young, later markedly pointed and somewhat curved. *Pedicels* 5–6 mm, glabrous, nodding. *Flowers* with the calyx tube conical to somewhat flattened, 1–1.5(–2) mm, the lobes deltate to apiculate-deltate to somewhat quadrate, 0.5–1 mm, glabrous or minutely papillose, the apicula with minute trichomes in a tuft at the tip; corolla usually purplish or pink, occasionally white or greenish, 1.5–2 cm in diameter, lobed nearly to the base, the lobes planar at anthesis, 8–9 mm, narrowly triangular with cucullate and papillate tips; filament tube minute, *c.* 0–0.5 mm; long anther 5–7 × 1–2 mm, the filaments 2–2.5 mm; middle anther pair 3.5–4.5 × *c.* 1–1.5 mm, the filaments 0.5–1 mm; small anther pair 2.5–4 × *c.* 1–1.5 mm, the filaments 1–1.5 mm; ovary conical, glabrous; style 8–9 mm, glabrous, gradually widening towards the stigma, the stigma flattened-capitate. *Fruit* globose, 1–1.5 cm in diameter, green with darker stripes and mottlings, smooth, the pericarp thin and brittle when dry; fruiting pedicel 1.0–1.3 cm, erect. *Seeds* (5–)10–20 per fruit, 3–4 mm long, pale tan or reddish, flattened to ovate-reniform, the testa cells elongate, sinuate in outline, with markedly and regularly striate outer cell walls.

COMMON NAMES AND USES. Peru, Loreto, 'ocuerilla' (*Ayala* 3112); 'sacha congompe' (*Martin* et al. 1617 – decoction of fresh leaves applied to skin for itching); Brazil, Rondonia, 'capança' (*Prance* et al. 8715).

DISTRIBUTION. Amazonia in Colombia, Ecuador, Peru, Bolivia and Brazil, usually in flooded forest (*igapó* or *tahuampa*), but occasionally in *terra firme* forests, 100–450(–1300) m. Fig. 11.

SPECIMENS EXAMINED.

COLOMBIA. Amazonas: Boiauassú River, *c.* 100 m, November 1945, *Schultes* 6787 (F, US); Atacuari River, *c.* 100 m, 24 October 1946, *Schultes & Black* 8565 (GH, US). **Putumayo**: Santa Rosa del Río Guamaes, *c.* 300 m, 2 December 1968, *Plowman* 2100 (GH).

ECUADOR. Napo: San Pablo de los Secoyas, 2–5 km W. of the village, 300 m, 0°15'S, 77°21'W, 5 August 1980, *Brandbyge* et al. 32489 (AAU); Río Wai si ayá, 1 km upstream from outlet in Río Aguarico, 300 m, 0°15'S, 76°21'W, 6 August 1981, *Brandbyge* et al. 33209 (AAU); Cantón Archidona, Hollin-Loreto road, between Avila & Loreto, 450 m, 0°43'S, 77°19'W, 24 November 1989, *Cerón* 7767 (MO, QCNE); Cantón La Joya de los Sachas, Pompeya, carretera MAXUS km 3.9–5.2, 250 m, 0°25'S, 76°37'W, 14–15 December 1992, *Gudiño* et al. 2181 (QCNE); Communa San Isla, Río Napo, *c.* 3 km E. of Añangu, along Río Garza Cocha, 260 m, 0°29'S, 76°21'W, 8–9 July 1983, *Lawesson* et al. 39821 (AAU); Santa Rosa at Río Napo, 28 April 1972, *Lugo S.* 1999 (MO); Río Bueno, tributary of Río Suno, 4–5 km N. of Santa Rosa, 7 May 1972, *Lugo S.* 2168 (MO); Coca (Puerto Francisco de Orellana), 17 January 1973, *Lugo S.* 2812 (MO); Las Sachas, Coca (Puerto Francisco de Orellana)-Lago Agrio road, 30–40 km E. of Coca, 13 February 1973, *Lugo S.* 3372 (MO). **Sucumbíos**: Cantón El Chaco, Río Granadillo, INECEL camp Codo Alto, 1300 m, 0°08'S, 77°28'W, 13–15 September 1990, *Palacios* 5634 (QCNE).

PERU. Sin. loc., *Matthews* s.n. (K). **Huánuco**: Finca Panguana, 1 hr walk from Llullapichis on Río Pachitea, on Río Llullapichis, 25 January–15 February 1975, *Dressler* 4934 (MO); Prov. Leoncio Prado, Tingo Maria, Jardin Botánico, Avenida Pimental 358, 670 m, 7 December 1981, *Plowman & Ramirez R.* 11192 (F, MO); Prov. Pachitea, Bosque Nacional Iparia, along Río Pachitea near Miel de Abeja camp, 1 km above Tournevista & *c.* 2 km above confluence with Río Ucayali, 300–400 m, 28 February 1967, *Schunke V.* 1694 (F), 10 October 1967, *Schunke V.* 2201 (F), 16 October 1967, *Schunke V.* 2231 (F). **Loreto**: Río Afayacu, 10 hrs downriver from Iquitos, 14 December 1980, *Ayala* et al. 2926 (MO, NY × 2); 28 de julio-Río Itaya, 100 m, 25 February 1981, *Ayala* 3112 (F, MO, NY); Padre Isla, in front of Iquitos, 120 m, 27 February 1978, *Díaz & Jaramillo* 3 (MO); old Punchana-Nanay road, 5 km N. of Iquitos, 120 m, 27 October 1964, *Dodson* 2863 (MO); Rio Amazonas, 2 hrs upriver from Iquitos by 40 h.p. launch, 14 July 1967, *Martin* et al. 1617 (US); vicinity of Iquitos, 1977, *Revilla* 2622 (MO); Sanagal, R. bank of Río Itaya, 1 hr from Iquitos in motorboat, near Yanayaco, 120 m, 4°10'S, 73°20'W, 9 August 1980, *Vásquez* et al. 409 (MO, NY); Prov. Requena, Cocha Apucate, Río Ucayali near Pto. Peru, *c.* 170 m, 5°15'S, 74°10'W, 5 December 1980, *Vásquez & Jaramillo* 904 (MO); Prov. Alto Amazonas, Andoas, L. bank of Río Pastaza, Campamento OXI, *c.* 210 m, 2°55'S, 76°25'W, 6 June 1981, *Vásquez & Jaramillo* 1982 (MO); Padre Isla, Cocha Pastor, 116 m, 3°45'S, 73°10'W, 29 October 1981, *Vásquez* 2685 (MO); Prov. Maynas, Alpahuayo, Estación IIAP, 14 November 1984, *Vásquez* et al. 5695 (MO, NY); Iquito, Caserio Nuevo Jerusalen, Isla Iquitos, 106 m, 3°45'S, 73°15'W, 12 January 1989, *Vásquez & Jaramillo* 11516 (MO); Iquitos, Allpahuayo, experiment station of the Instituto de Investigaciones de la Amazonia Peruana (IIAP), 150–180 m, 4°10'S, 73°30'W, 20 January 1991, *Vásquez* 15889 (MO); Las Amazonas, Explornapo camp, Sucusari, cocha Shimigay, 140 m, 3°15'S, 72°54'W, 26 June 1991, *Vásquez* et al. 16859 (MO); along Río Itaya, 14 May 1929, *Williams* 248 (F); Caballo-Cocha on Amazon River, 9 August 1929, *Williams* 2281, 2312 (F); La Victoria on Amazon River, 23 August 1929, *Williams* 2744 (F), 5 September 1929, *Williams* 3110 (F). **Madre de Dios**: Prov. Tambopata, *c.* 30 air km or 70–80 river km SSW of Puerto Maldonado at effluence of Río La Torre (Río D'Orbigny)/Río Tambopata, SE bank, Tambopata nature reserve, *c.* 260 m, 12°49'S, 69°17'W, 3 May 1980, *Barbour* 5117 (MO); Tambopata Reserved Zone, 5.1 km down main trail for Explorer's Inn, near Laguna Cocococha, 12°50'S, 69°17'W, 6 March 1988, *Bell & Wiser* 88–10 (US); Tambopata Reserved Zone, near Laguna Chica, 12°50'S, 69°17'W, 15 March 1988, *Bell* et al. 88–192 (US); Río Alto Madre de Dios, near chacra of Sr. Carpio, halfway between Shintuya & Manuy, 10–11 August, 1974, *Foster* et al. 3213 (F): prov. Manu, Río Palotoa (Río Pantiacolla of maps), tributary of Río Alto Madre de Dios NW of Shintuya, 500 m, 26–28 August 1978, *Foster & Terborgh* 6709 (F); Pakitsa, entrance to Manu park, 360 m, 26 October 1979, *Gentry* et al. 27258 (MO); Prov. Tambopata, Cuzco Amazonico, 15 km ENE of Puerto Maldonado, 200 m, 12°35'S, 69°05'W, 12 December 1989, *Gentry* et al. 68604 (MO); Prov. Manu, Manu Park, Cocha Cashu uplands, 400 m, 11°45'S, 71°00'W, 18 August 1986, *Núñez* 5768 (MO, NY), 13 September 1986, *Núñez* 6120 (MO, NY); Explorer's Inn, near confluence of Río Tambopata & Río La Torre, 39 km SW of Puerto Maldonado, 12°50'S, 69°20'W, 3 October 1985, *Smith* et al. 533 (US); Prov. Tambopata, Cuzco Amazonico Inn, 200 m, 12°29'S, 69°03'W, 20 January 1991, *Timaná & Smith* 1294 (MO), 17 November 1991, *Timaná* 3252 (MO), 22 February 1992, *Timaná* 3717 (MO). **San Martín**: Prov. Mariscal Caceres, mouth of Río Mishollo, L. bank of Río Huallaga, 5 February 1971, *Schunke V.* 4701 (F); Quebrada Cañuto, near chacra of Lizardo Aliaga, Dtto. Tochache Nuevo, 500 m, 7 May 1979, *Schunke V.* 10930 (MO).

BOLIVIA. Sin. loc., *Rusby* 836 (NY). **Beni**: Prov. Trinidad, vicinity of Puerto Almacen, 50 m, 22 July 1992, *Rueda* 826 (MO); Prov. Ballivian, Estancia Conquista, 56 km E. of the Río Maniqui on road to Trinidad, then 4 km N. to forest island, 250 m, 14°47'S, 66°24'W, 8 November 1985, *Solomon* 14615 (MO). **La Paz**: Rurrenabaque, 1000 ft, 28 March 1921, *Cardenas* 1874 (NY). **Pando**: Prov. Nicolas Suarez, near Puerto Rico, banks of Río Tahuamanu, 26 January 1983, *Fernández Casas & Susanna* 8491 (NY). **Santa Cruz**: Prov. Ichilo, along Río Saguayo, Parque Nacional Amboro, *c.* 5 miles N. of entrance to Río Saguayo into first Andean foothills, 350 m, *c.* 17°37'S, 63°43'W, 21 January 1988, *Nee* 36031 (NY); Prov. Ichilo, PN Amboro, *c.* 5 km SE of the Río Surutu, along Río Pitasama, 400 m, 17°40'S, 63°36'W, 31 August 1985, *Solomon* 14190 (MO).

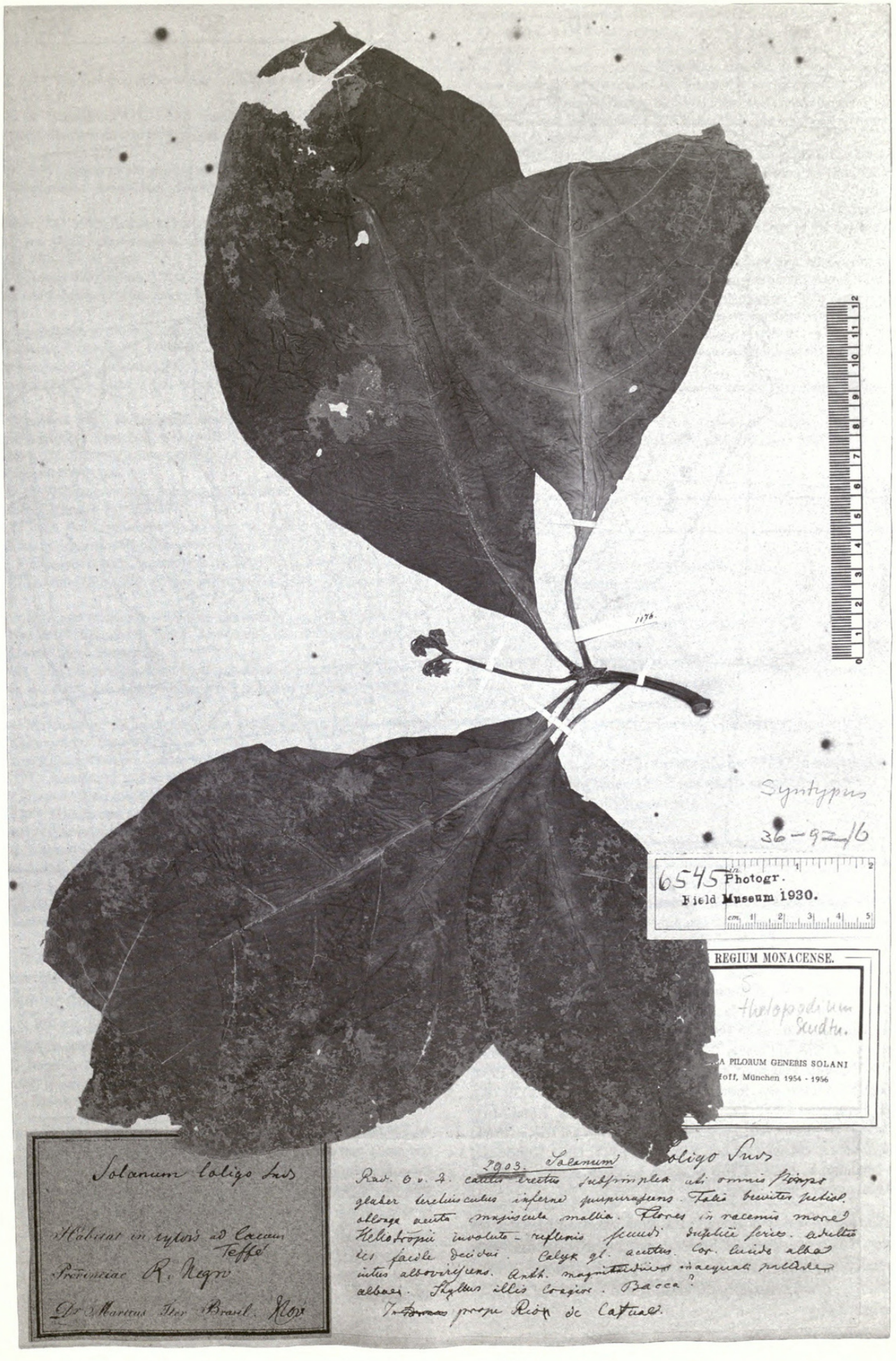

Fig. 10 Lectotype of *Solanum thelopodium* (*Martius* 2903, Amazonas, Brazil).

Fig. 11 Distribution of *Solanum thelopodium*.

BRAZIL. Acre: Mun. Tarauacá, vicinity of Tarauacá, 13 September 1968, *Prance* et al. 7242 (NY), 23 September 1968, *Prance* et al. 7490 (NY); Mun. Sena Madureira, E. of Rio Iaco, 10 km above Sena Madureira, 4 October 1968, *Prance* et al. 7823 (NY). **Amazonas**: near mouth of Rio Embira, tributary of Rio Tarauaca, 7°30'S, 70°15'W, 26 January 1933, *Krukoff* 4998 (NY); Mun. Manicore, near Bella Vista, 8–11 September 1934, *Krukoff* 6020 (NY); Pamirí dos Ramos, October 1850, *Spruce* 1129 (K); Marory, Juruá, September 1900, *Ule* 5206 (HBG); Rio Juruá, Juruá Miry, July 1901, *Ule* 5691 (B [destroyed: F neg. 2814, F, G, GH, NY], HBG). **Pará**: sin. loc., 1826, *Siber* s.n. (M [Morton neg. 8750 F, GH, NY, US]). **Rondônia**: basin of Rio Madeira, E. bank of Rio Madeira between Abuña & Penha Colorado, 20 November 1968, *Prance* et al. 8715 (NY).

Solanum thelopodium tends to grow in flooded forest, rather than on the *terra firme*. It also occurs much lower down on the Rio Amazonas than its partially sympatric relative, *S. monarchostemon*. Flower colour in *S. thelopodium* is usually pinkish, while flowers of *S. monarchostemon* are always greenish white. Label data indicate, however, that *S. thelopodium* does sometimes have greenish flowers. This colour polymorphism is common in the spiny solanums, but less so in the non-spiny part of the genus (see Knapp, 1989 for some exceptions).

The thick woody tap-root of *Solanum thelopodium* (see Fig. 2) may be related to its flooded forest habitat. Plants submerged during the wet season probably die back, resprouting as the water recedes during the dry season and flowering and fruiting in a short space of time.

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EXSICCATAE

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Hugh-Jones, C. 329 (dimorphandrum).
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Jaramillo, J. & Coello, F. 2748 (monarchostemon); 4484 (monarchostemon); 4487 (monarchostemon).
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King, S.R. 472 (monarchostemon).
Kirkbride, J.A. 2122 (dimorphandrum).
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Nee, M. 36031 (thelopodium).
Núñez, P. 5768 (thelopodium); 6120 (thelopodium).
Palacios, W. 5634 (thelopodium); 10117 (monarchostemon); 11038 (monarchostemon).
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Pennell, F.W. 4204 (dimorphandrum).
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Plowman, T. 2100 (thelopodium); 2548 (monarchostemon).
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Plowman, T. et al. 4018 (monarchostemon); 6539 (monarchostemon).
Prance, G.T. et al. 7242 (thelopodium); 7490 (thelopodium); 7823 (thelopodium); 8715 (thelopodium).
Revilla, J. 2622 (thelopodium).
Rueda, R. 826 (thelopodium).
Rusby, H.H. 836 (thelopodium).
Schultes, R.E. 6787 (thelopodium).
Schultes, R.E. & Black, G.A. 8565 (thelopodium).
Schunke V., J. 1694 (thelopodium); 2201 (thelopodium); 2231 (thelopodium); 4701 (thelopodium); 10930 (thelopodium).
Siber s.n. (thelopodium).
Smith, H.H. 1190 (dimorphandrum); 1722 (dimorphandrum).
Smith, S.F. et al. 533 (thelopodium).
Solomon, J. 14190 (thelopodium); 14615 (thelopodium).
Spruce, R. 1129 (thelopodium).
Timaná, M. 3252 (thelopodium); 3717 (thelopodium).
Timaná, M. & Smith, P. 1294 (thelopodium).
Ule, E. 5206 (thelopodium); 5691 (thelopodium).
Vásquez, R. 2685 (thelopodium); 15889 (thelopodium).
Vásquez, R. & Grández, C. 17457 (monarchostemon).
Vásquez, R. & Jaramillo, N. 904 (thelopodium); 1982 (thelopodium); 11516 (thelopodium); 16925 (monarchostemon).
Vásquez, R. et al. 409 (thelopodium); 5120 (monarchostemon); 5965 (thelopodium);12154 (monarchostemon); 16859 (thelopodium).
Williams, Ll. 248 (thelopodium); 709 (monarchostemon); 1679 (monarchostemon); 2281 (thelopodium); 2312 (thelopodium); 2744 (thelopodium); 3110 (thelopodium).
Zarucchi, J. et al. 4994A (dimorphandrum).

INDEX