Systematic Botany (1993), 18(2): pp. 209–217

Synonymy within Wild Potatoes (*Solanum* sect. *Petota*: Solanaceae): The Case of *Solanum andreanum*

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ABSTRACT. This study reduces five names to synonymy of *Solanum andreanum*, a variable taxon distributed from southern Colombia to central Ecuador. Two of the five names here united are recognized in Hawkes's latest taxonomic treatment in 1990, and one name was published after that treatment. The species have been distributed among five separate taxonomic series. We believe that this synonymy is only one example of a much larger problem of synonymy in sect. *Petota*.

Solanum L. sect. *Petota* Dumort., the potato and its wild relatives, is taxonomically difficult. This economically important and widespread group (Nebraska to southcentral Chile) has attracted the attention of many taxonomists with various taxonomic philosophies. Hawkes (1990) documents 531 validly published basionyms in the group, plus 67 nomina dubia or nomina nuda, and subsequent transfers to other ranks raise the number of names to 664. Since an earlier monograph by Correll (1962), 176 new taxa have been described, 140 of these by C. Ochoa (adding to his 26 species and varieties published before 1962), including 77 new varietal or form names of Bolivian cultivated species (Ochoa 1988). The latest taxonomic treatment by Hawkes (1990) recognizes 232 species.

This study reduces five names to synonymy of *S. andreanum* Baker, a variable taxon distributed from southern Colombia to central Ecuador. The reduction was unexpected because Hawkes (1990) recognizes two of the five names here united, *S. cyanophyllum* Correll and *S. suffrutescens* Correll (Hawkes 1990 synonymizes *S. baezense* Ochoa and *S. pichinchense* Bitter and Sodiro under *S. andreanum*). *Solanum serratoris* Ochoa was published after this book's release. Also, taxonomists have placed the species among five separate taxonomic series (Table 1).

MATERIALS AND METHODS

This taxonomic treatment is based on the study of descriptions of type material, field work throughout Ecuador from April 13–July 1, 1991, and throughout Colombia from July 1–August 24, 1992. As the locality data permitted, we visited the type localities of all taxa here studied. We used the following geographic references to map localities: Paynter and Traylor (1977); Instituto Geográfico Agustín Codazzi (1980); the 1:50,000 scale Ecuadorian topographic maps from the Instituto Geográfico Militar (dates vary by map); the Instituto Geográfico Militar "Indice Toponímico de la República del Ecuador (anonymous, undated), Tomo I (A-B), Tomo II (C), Tomo III (CH-D), Tomo IV (E-F), Tomo V (G-K), Tomo VI (L), Tomo VII (M-O), Tomo VIII (P-Q) (the others are not yet published); the 1:100,000 and/or 1:200,000 scale Colombian topographic maps from the Instituto Geográfico Agustin Codazzi (dates vary by map; coverage for Colombia is incomplete); the Colombian department maps from the Instituto Geográfico Agustin Codazzi (dates vary by map, scale varies from 1:200,000–1:500,000); and the U.S. Department of Interior, Gazetteers of Colombia and Ecuador (anonymous, undated).

Characters separating *S. andreanum* and its synonyms were determined from the original descriptions, supplemented by data from Correll (1962) or Hawkes (1990). Graphical plots of these comparisons are presented in Fig. 1. Field and herbarium observations and duplicate collections were made to document intrapopulational variation of both immature and mature plants, because some synonyms are based on immature material. We compared these variants

TABLE 1. Hypotheses of series affiliations of the species names here placed in synonymy under *Solanum andreanum*.

	Series			
	Author			
Species names	Correll 1962	Ochoa 1981, 1983, 1990a	Hawkes 1990	Gorbatenko 1989
S. andreanum	*Bukasoviana* (as "Transaequatorialia")	*Tuberosa*	*Tuberosa*	*Bukasoviana*
S. baezense		*Conicibaccata*	*Tuberosa* (as a synonym of *S. andreanum*)	
S. cyanophyllum	*Piurana*		*Piurana*	*Piurana*
S. pichinchense	*Bukasoviana* (as "Transaequatorialia")	*Conicibaccata*	*Tuberosa* (as a synonym of *S. andreanum*)	*Bukasoviana*
S. serratoris		*Tuberosa*		
S. suffrutescens	*Ingifolia*		*Tuberosa*	*Ingifolia*

to the types and to the characters plotted on Figure 1. Herbarium vouchers are deposited at COL, QCA, US, WIS, the Inter-Regional Potato Introduction Station (PTIS); The Instituto Nacional de Investigaciones Agropecuarias, Santa Catalina Station, Ecuador (INIAP); and the International Potato Center in Lima, Peru (CIP). Detailed reports of the expedition are on file at the Inter-Regional Potato Introduction Station at Sturgeon Bay, Wisconsin; the U.S.D.A., ARS Germplasm Services Laboratory in Beltsville, Maryland; the International Board for Plant Genetic Resources Offices in Cali, Colombia and Rome, Italy; the International Potato Center in Lima, Peru; the Instituto Colombiano Agropecuario (ICA), Tibaitatá station; and INIAP. Germplasm samples are deposited at ICA and INIAP, and will be deposited at IR-1 after passage through U.S. Quarantine.

RESULTS

***Variability in* Solanum andreanum.** No comparisons have been made by previous workers in the original descriptions of the names here placed in synonymy with *S. andreanum*. All descriptions were made from single collections, and only *S. andreanum* has had additional collections later identified to this species (Correll 1962). Subsequent comparisons of synonyms in comprehensive treatments (Correll 1962; Gorbatenko 1989; Hawkes 1990) have been precluded by placement of the synonyms in different series (Table 1), as the morphological character states distinguishing many series are vague (see below).

Many characters in *S. andreanum* are highly variable. Characters highlighted by Correll (1962) in the descriptions of *S. andreanum* or its synonyms are the following: 1. Leaves blue abaxially have partly characterized *S. cyanophyllum* (Correll 1962). This trait frequently varies within populations, however, with colors ranging from green to blue (e.g., *Spooner et al. 5014, 5079, 5125b, 5152, 5153, 5156*). 2. Suffrutescent stems have partly characterized *S. suffrutescens* (Correll 1962), but suffrutescent stems do not occur in *S. andreanum*. The type of *S. suffrutescens* lacks the base of the plant, and Correll (1961, 1962) described this characteristic based solely on field notes of another collector. Stem bases may become somewhat woody later in the season, but do not persist. 3. Asymmetrical calyces have been used to partly characterize *S. cyanophyllum* and *S. suffrutescens* by Correll (1961, 1962), but he recognizes intraspecific polymorphism for this trait within *S. andreanum*. This character frequently varies within populations, often on individual plants. 4. Hawkes (1990) places *S. cyanophyllum* in series *Piurana* Hawkes because of the shiny leaves on the type, but there is great variation in leaf pubescence in *S. andreanum*, with shiny, scarcely-pubescent leaves and non-shiny pubescent leaves occurring within populations (e.g., *Spooner et al. 5014; Spooner et al. 5125b*).

A comparison of the characters used to describe the species (Fig. 1) illustrates the follow-

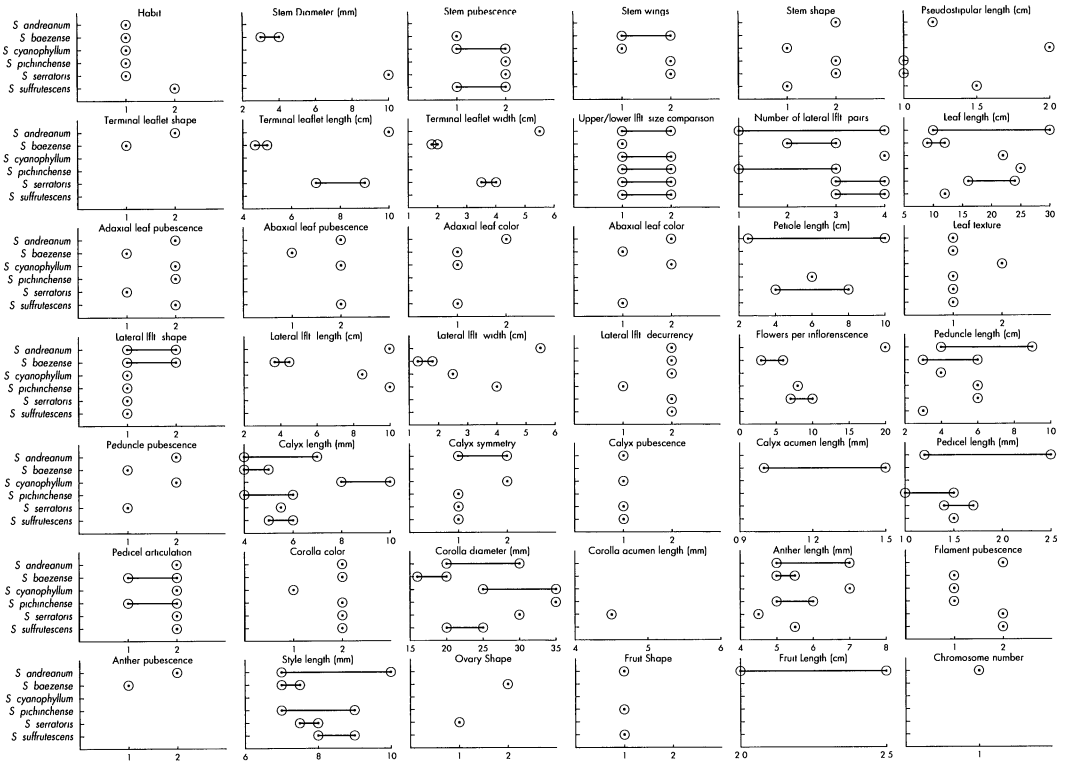

FIG. 1. Quantitative and qualitative characters distinguishing *Solanum andreanum* and the names here placed into synonymy as determined from the original descriptions, supplemented by descriptions from Correll (1962) and Hawkes (1990). Ranges are plotted if provided, but descriptions often state "up to [range of character state]" and only this upper limit is then plotted. Lack of parallel descriptions precluded an entire data set. Character states for quantitative characters follow. Habit: 1. herbaceous, 2. suffrutescent. Stem pubescence: 1. glabrous, 2. puberulent. Stem wings: 1. absent, 2. present. Stem shape: 1. terete, 2. angular. Terminal leaflet shape: 1. elliptic to lanceolate, 2. broadly elliptic to obovate. Lateral leaflet size comparison: 1. lateral leaflets subequal in size, 2. lateral leaflets decreasing in size from apex to base of leaf. Adaxial leaf pubescence: 1. subglabrous to sparsely pubescent, 2. scattered coarse hairs. Abaxial leaf pubescence: 1. glabrous, 2. puberulent. Adaxial leaf color: 1. green, 2. green to blue. Abaxial leaf color: 1. green, 2. green to blue. Leaf texture: 1. herbaceous, 2. subcoriacoeus. Lateral leaflet shape: 1. lanceolate, 2. ovate. Lateral leaflet decurrency: 1. leaflets not decurrent, 2. leaflets decurrent. Peduncle pubescence: 1. glabrous, 2. puberulent. Calyx symmetry: 1. symmetrical, 2. asymmetrical. Calyx pubescence: 1. glabrous, 2. subglabrous to pilose. Pedicel articulation: 1. articulate at middle, 2. articulate above middle. Corolla color: 1. white mottled with lavender, 2. blue to purple. Filament pubescence: 1. glabrous, 2. puberulent. Anther pubescence: 1. glabrous, 2. puberulent. Ovary shape: 1. spherical, 2. conical. Fruit shape: 1. spherical to ovoid. Chromosome number: 1. $2n = 24$ [a count of $2n = 48$ is provided by Ochoa (1981) for *S. pichinchense*, a name we here synonymize with *S. andreanum*, see text].

ing differences among the synonyms: 1. Many qualitative differences determined from the species descriptions are minor (e.g., minor degrees of pubescence of various organs, stem shape, pedicel articulation). 2. *Solanum andreanum* encompassed a greater range of variability (or upper limit, as this was frequently the only number cited, see Fig. 1) than the synonyms. This greater variability attributed to *S. andreanum* reflected the greater specimen data base assigned to this species (Correll 1962). The only quantitative characters used in the descriptions of the synonyms found to exceed that of *S. andreanum* were pseudostipular leaf length (longer in *S. cyanophyllum* and *S. suffrutescens*), calyx length (longer in *S. cyanophyllum*), and

corolla diameter (wider in *S. cyanophyllum* and *S. pichinchense*; see Fig. 1). An examination of the type of *S. cyanophyllum*, however, shows that measurements attributed to this species were in error, for the pseudostipular length is 17, not 20 mm long; the calyx is up to 7 mm long, not 10 mm long; and the upper limit of corolla diam. is 26 mm, not 33 mm. Larger pseudostipular leaf lengths in our collections have ranged up to 25 mm (*Spooner et al. 5125b*), and corolla diam. up to 35 mm (*Spooner et al. 5079*). 4. Conical ovaries were used by Ochoa (1983) partly to characterize *S. baezense*, but the type has developing fruits that are spherical (see Discussion).

We recognize the following synonymy based on our documentation of lack of major differences between the types, and our newly documented understanding of intraspecific variability of characters from throughout the range of *S. andreanum*.

Taxonomic Treatment

SOLANUM ANDREANUM Baker, J. Linn. Soc., Bot., 20: 498. 1884.—TYPE: Colombia, Nariño [not Cauca as in Correll 1962], between La Unión and Meneses, in high river valley, 2400 m, 29 Apr 1878, *E. E. André 2873 p.p.* (holotype: K!, photo: LL!, the herbarium of the Inter-Regional Potato Introduction Station, Sturgeon Bay, WI [PTIS]!; isotype: NY, photo: LL!).

Solanum pichinchense Bitter & Sodiro, Repert. Spec. Nov. Regni Veg. 10: 533. 1912.—TYPE: Ecuador, Pichincha, Mt. Pichincha near Chinguy, Aug 1871, *A. Sodiro 114/6* (holotype: B, destroyed; neotype here chosen: photo of holotype at F!).

Solanum cyanophyllum Correll, Wrightia 2: 180. 1961.—TYPE: Ecuador, Bolívar, below San Jacinto de la Unión, cleared forest, 2300 m, 15 Aug 1939, *E. Asplund 8325* (holotype: S!, photo: F! PTIS!).

Solanum suffrutescens Correll, Wrightia 2: 183. 1961.—TYPE: Ecuador, Bolívar, road between La Magdalena and Balzapampa, 2800 m, 30 Apr 1942, *O. Haught 3289* (holotype: US, photo: F!).

Solanum baezense Ochoa, Phytologia 54: 391. 1983.—TYPE: Ecuador, Napo, near Baeza, 1200 m, Jan 1979, *L. Besse, K. Tan & J. Halton 50* (holotype: F; isotype: SEL!, photo: PTIS!).

Solanum serratoris Ochoa, Amer. Potato J. 67: 381. 1990.—TYPE: Ecuador, Morona-Pastaza [Morona-Santiago], between Laguna Atillo and Macas, 2500 m, 15 May 1989, *M. Hermann 321* (holotype: personal herbarium of C. M. Ochoa; isotype: US!, photo: PTIS!).

Stems 0.2–3 m long, simple to highly branched, terete to angular, unwinged or with straight to wavy wings up to 1 mm wide, up to 1 cm wide at base, green to purple, glabrous to pubescent; tubers spherical to ovoid, up to 3 cm long, with white to light cream skin and flesh; leaves odd-pinnate, 8–33 cm long, 6–20 cm wide, with 0–8 interjected leaflets up to 3 cm long and 2 cm wide; rachis usually unwinged or with wings up to 3 mm wide; leaves 2–4-jugate, green and scarcely short-puberulent to strigose above, green to dark purple and glabrous to pubescent below; lateral leaflets subequal in size except a usually greatly reduced basal pair, or lateral leaflets decreasing in size from apex to base, sessile to petiolate, with petiolules to 9 cm long, leaflets often decurrent on basiscopic side, elliptic to lanceolate to broadly ovate, 3–10 cm long, 10–45 mm wide, obliquely rounded to attenuate at apex, cuneate to rounded at base, margins entire to finely denticulate, glabrous to pubescent; terminal leaflet usually nearly the same size and shape as laterals or larger and more ovate, petiole to 2 cm long or leaflet decurrent on basiscopic side; pseudostipular leaves semiovate to lanceolate, to 2.5 cm long; inflorescence pseudoterminal, a cymose panicle, flowers 3–20; peduncles 3–20 cm long, glabrous to puberulent, simple or branched above; pedicels 5–25 mm long, glabrous to puberulent, articulate from the middle to above the middle; calyx 4–7 mm long, green to deep purple, glabrous to puberulent, lobed at about the middle, symmetrical with 5 equal lobes or bilobed, with 2–4 lobes grouped together, apices linear to acuminate; corolla rotate to rotate-pentagonal, 15–35 mm in diam., usually deep purple, but occasionally pink or rarely whitish; anthers lanceolate, 5–7 mm long, glabrous to pubescent; filaments 1–2 mm long, glabrous to puberulent, ovary spherical to rarely conical, green to deep purple, style slender, 7–9 mm long, glabrous to papillose below, stigma slender to capitate; fruit spherical to spherical-ovoid, 10–15 mm in diam., 10–18 mm long; $2n = 24$ (Correll 1962; Ochoa 1981; Hanneman and Bamberg 1986; Hawkes 1990).

Phenology. Flowering from April through July.

Distribution (Fig. 2). Southern Colombia, south to central Ecuador; in moist areas along roadsides and in recently cleared forests; 1980–3000 m.

Additional specimens examined. COLOMBIA. **Dept. Nariño:** 1.7 km E of La Victoria town square on road to San Jorge, 0°42'N, 77°34'W, 2450 m, 9 Jul 1992, *Castillo et al. 1223* (CIP, COL, PTIS); 3.7 km E of La Victoria town square on road to San Jorge, 0°42'N, 77°33'W, 2450 m, 9 Jul 1992, *Castillo et al. 1224* (CIP, COL, PTIS); 5.4 km E of La Victoria town square on road to San Jorge, 0°42'N, 77°32'W, 2440 m, 9 Jul 1992, *Castillo et al. 1225* (CIP, COL, PTIS); 7.4 km E of La Victoria town square on road to San Jorge, 0°42'N, 77°31'W, 2380 m, 9 Jul 1992, *Castillo et al. 1226* (CIP, COL, PTIS); above San Jorge, 0°42'N, 77°30'W, 2300 m, 9 Jul 1992, *Castillo et al. 1228* (CIP, COL, PTIS); new road connecting Pasto–Buesaco Road (at km 13) to main road from Pasto-Popayán, ca 1 km from main road, 1°15'N, 77°15'W, 2750m, Jul 11, 1992, *Castillo et al. 1231* (CIP, COL, PTIS); Finca El Rosal, 18–19 km NE of Pasto on road to Buesaco, ca 3 km walk upstream in Quebrada El Rosal, 1°17'N, 77°13'W, 2910 m, *Castillo et al. 1232* (CIP, COL, PTIS); Finca El Rosal, 18–19 km NE of Pasto on road to Buesaco, 0.5 km walk upstream in Quebrada El Rosal, 1°17'N, 77°14'W, 2840 m, *Castillo et al. 1233* (CIP, COL, PTIS); 18 km from Pasto on road to La Unión, seepage slope along wooded stream, 2900 m, 7 Apr 1958, *Correll & Estrada Co487* (LL); 18–19 km from Pasto on road to La Unión, Meneses, in a quebrada, 2900 m, 27 Jul 1948, *Hawkes 230a* (US); 18–19 km from Pasto on road to La Unión, Meneses, 27 Jul 1948, *Hawkes 230b* (US). **Dept. Putumayo:** 21.6 km E of border with Nariño Dept., 1.8 km W of town square of Santiago, just E of Río Espinayaco, 1°08'N, 77°00'W, 2180 m, *Castillo et al. 1233* (CIP, COL, PTIS); valley of Sibundoy, 2225–2300 m, *Schultes & Mardoquero Villarreal 7639* (COL); road between Sibundoy and Mocoa, below Mocoa, near the statue of the Virgin, s.d., *Gutiérrez et al. S8* (LL); on brushy slope 1.5 km E of Santiago on road to San Francisco, 2200 m, 8 Apr 1958, *Correll & Estrada Co490* (LL); edge of drainage ditch 2 km E of Santiago, 2200 m, 8 Apr 1958, *Correll & Estrada Co491* (LL).

ECUADOR. **Prov. Bolívar:** in Quebrada Lauszi, ca 1 km E of road from La Magdalena to Balzapampa, 1°39'S, 79°06'W, 2820 m, 12 May 1991, *Spooner et al. 5072* (INIAP, PTIS, QCA); Cochapampa, on farm of Segundo Arevalo, 100 m W of road from La Magdalena to Balzapampa, 6.5 km SW of junction of dirt roads on S side of La Magdalena, 1°40'S, 79°06'W, 2830 m, 12 May 1991, *Spooner et al. 5074* (CIP, INIAP, PTIS, US, QCA); Tundaloma, on road from La Magdalena to Balzapampa, 10.3 km S of junction of dirt roads on S side of La Magdalena, 1°41'S, 79°06'W, 2760 m, 12 May 1991,

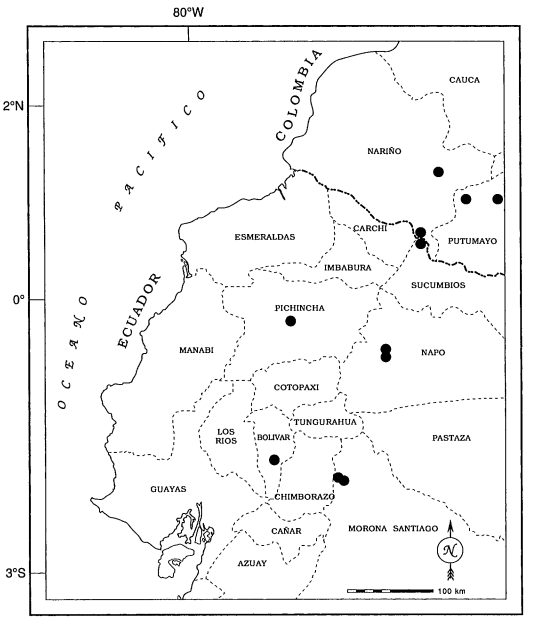

FIG. 2. Distribution of *Solanum andreanum.*

Spooner et al. 5075 (CIP, INIAP, PTIS, QCA, US, WIS); Gualazay, on farm of Medardo Marino, 12.8 km SW of junction of road to La Magdalena, 1°42'S, 79°07'W, 2620 m, 6 Jun 1991, *Spooner et al. 5131* (CIP, INIAP, PTIS, QCA, US, WIS); on W-facing slopes of Cerro Parca Urcu, ca. 150 m uphill of road, just N (by air) of Tundaloma, 1°40'S, 79°07'W, 2790 m, 7 Jun 1991, *Spooner et al. 5132* (CIP, INIAP, PTIS, QCA, US, WIS); on Loma Churchi, by road to antennas of IETEL station, near Tambo de Gobierno, 1°42'S, 79°05'W, 2950–3000 m, 7 Jun 1991, *Spooner et al. 5133* (CIP, INIAP, PTIS, QCA, US); Hacienda El Tambo, at Tambo de Gobierno, just off Cochapampa–San Miguel Road, 1°42'S, 79°05'W, 3140 m, 7 Jun 1991, *Spooner et al. 5134* (INIAP, PTIS). **Prov. Morona-Santiago:** at Sañay, 16 km NW of San Vincente, on old footpath on S side of Río Upano, on way to San Vicente and Nueve de Octubre, 2°10'S, 78°25'W, 2650 m, 9 Jun 1991, *Spooner et al. 5152* (CIP, INIAP, PTIS, QCA, US, WIS); 10 km NW of San Vicente, on old footpath on S side of Río Upano, on way to San Vicente and Nueve de Octubre, 2°10'S, 78°24'W, 2550 m, 20 Jun 1991, *Spooner et al. 5155* (INIAP, PTIS); 300 m W of Río San Francisco, ca 7 km E of San Vicente, on San Vicente to Nueve de Octubre footpath, 2°12'S, 78°23'W, 2350 m, 20 Jun 1991, *Spooner et al. 5157* (CIP, INIAP, PTIS, QCA, US, WIS). **Prov. Napo:** ca. 2 hr walk W of Baeza–Tena Road, on S side of Río Bermejo, on farm of José Guaranda Guambi, in Nueva Andalucía de Bermejo, 0°32'S, 77°55'W, 2100 m, 2 Jun 1991, *Spooner et al. 5126* (CIP, INIAP, PTIS, QCA, US, WIS); near trail to antennas on S side of Baeza, ca 1 km (by air) SSW of center of

town, 0°27'S, 77°53'W, 2170–2220 m, 2 Jun 1991, *Spooner et al. 5127* (CIP, INIAP, PTIS, QCA, US, WIS); Cordillera Guacamayo, slope toward Urcusiqui, 27 Oct 1939, *Asplund 9563* (LL—photo of specimen at S); 10.0 km SE of bridge over Río Cosanga in the town of Cosanga, in the Cordillera de los Huacamayos [Guacamayo], in the headwaters of Río Urcusiqui, 0°37'S, 77°49'W, 2200 m, 27 Jun 1991, *Spooner et al. 5159* (CIP, INIAP, PTIS). **Prov. Pichincha:** 7.8 km SW of Chiriboga, along roadside, next to fish hatchery, by Hacienda San Martín, 0°15'S, 78°47'W, 1980 m, 24 Apr 1991, *Spooner et al. 5014* (CIP, INIAP, PTIS, QCA, US, WIS); 2.1 km N of Hacienda San Martín, 5.7 km SW of Chiriboga, 0°14'S, 78°47'W, 2070 m, 1 Jun 1991, *Spooner et al. 5125b* (CIP, INIAP, PTIS, QCA, US, WIS). **Prov. Sucumbíos:** 0.5–1.9 km W of Santa Barbara on road to El Carmelo, 0°39'N, 77°32'W, 2610–2650 m, 24 May 1991, *Spooner et al. 5101* (CIP, INIAP, PTIS, QCA, US, WIS); along new road to El Calvario, 5.0 km E of town square of Santa Barbara, 0°39'N, 77°30'W, 2700 m, 24 May 1991, *Spooner et al. 5102* (CIP, INIAP, PTIS, QCA, US, WIS).

Type localities. We visited the type localities of the names here placed in synonymy with *S. andreanum* to the precision allowed by the locality data.

Solanum andreanum. "Between La Unión and Meneses, in high river valley, 2400 m" is an unspecific locality. Meneses is the name of a general region about 30 km (by air) south-southwest of La Unión incorporating the site of *Castillo et al. 1232, 1233; Correll & Estrada Co487;* and *Hawkes 230a, 230b.* These collections, therefore, may be at or near the type locality.

Solanum pichinchense. "Mt. Pichincha near Chinguy" is ambiguous, because Chinguy does not appear in any of our available references or maps. A close match is "Quebrada [valley] Chinguil" at 0°13'S, 78°39'W, located on the southern slopes of Mt. Pichincha. We could not find *S. andreanum* there, but our collection *5014* of *S. andreanum* is just to the southwest of Mt. Pichincha. C. M. Ochoa indicated (by letter) that "Chinguy" is a misspelling for "Unguy," and is a place name on Mt. Pichincha east of Quito, but this locality also is not listed on our references or maps. Our collections on Mt. Pichincha east of Quito (*Spooner et al. 5019, 5022, 5023* and *Spooner & López 5024*) are all of *S. tuquerrense* Hawkes. The type of *S. pichinchense* has fruits that are spherical to spherical-ovoid at maturity and leaves that match the range of variability we recognize for *S. andreanum.*

Solanum cyanophyllum / *S. suffrutescens.* The type localities of *S. cyanophyllum* and *S. suffrutescens* probably are very close to each other. The published type locality of *S. cyanophyllum* is ambiguous because no "San Jacinto de la Unión" appears in our references. A close match is "Loma San Jacinto" at 78°59'W, 1°51'S, but this is in the adjacent province of Chimborazo. C. M. Ochoa (pers. comm.) indicates that "San Jacinto de la Unión" is a local place name just west of La Magdalena on the road to Balzapampa, near the location of our collection *5072* of *S. andreanum* in Bolívar Province. This locality is within 3 km (by air) of our collection *5074,* collected at a place that is an almost exact match for the type locality for *S. suffrutescens.*

Solanum baezense. "Near Baeza, 1200 m" is ambiguous because Baeza is at 1900 m, and 1200 m is more than 50 km (by air) to the northeast of Baeza, along the road to Reventador in Napo Province. We collected *5127* on the north side of Baeza at 2170–2200 m, and it is probable that "1200 m" is a transcription error for 2200 m, or a reading taken from a maladjusted altimeter.

Solanum serratoris. Laguna Atillo and Macas are 50 km apart (by air) and the western part of the transect currently is reached along an old footpath between Laguna Atillo and Nueve de Octubre. Fortunately, Elias Guadalupe, who accompanied Miguel Hermann when the type first was collected, also served as our guide and led us to the exact type locality where we collected *Spooner et al. 5157.*

Discussion

Causes of This Synonymy. The proliferation of names for *S. andreanum* has arisen from three types of errors. First, decisions were based on inaccurate information. For example, Ochoa (1981) maintains *S. pichinchense* as distinct from *S. andreanum* because he interprets the former to be a member of series *Conicibaccata* Bitter, characterized by conical fruits. The type, however, exhibits fruits that are spherical to spherical-ovoid at maturity, and leaves that match *S. andreanum.* He also states that *S. pichinchense* is a tetraploid ($2n = 48$), whereas *S. andreanum* is diploid. Unfortunately, he cites no voucher, and it is likely that he has confused *S. pichinchense* with *S. tuquerrense,* a tetraploid, common in many places on Mt. Pichincha. Ochoa (1990a) described *S. serratoris* as having "no close affinities with any other tuber-bearing species," although it is synonymous with *S. andreanum,* as

is *S. baezense*, a species he also described from a type locality about 160 km (by air) south of *S. serratoris*.

The second error has been the use of immature material for descriptions, despite the importance of mature fruits as taxonomic characters. Our observations show that some plants of *S. andreanum* (e.g., *Spooner et al. 5014, 5075*) have ovaries spherical to conical, but that all fruits mature as spherical to spherical-ovoid shapes. Ochoa (1983) described *S. baezense* from an immature specimen, and placed it in series *Conicibaccata*, although the type has spherical developing fruits. *Solanum cyanophyllum* and *S. serratoris* also were described from immature material, and yet these species were described as distinct and assigned to series *Tuberosa*.

The third error has been the application of a topological species concept required by the few (or single) collections available for each previous study. *Solanum cyanophyllum* was characterized partly by scarcely pubescent leaves purple on the abaxial side, and *S. suffrutescens* by a combination of suffrutescent stems and bilobed calyces. We document variability in these characters above. Also highly variable is plant height and leaf size.

Solanum andreanum probably encompasses more putative species than those listed here. The 531 basionyms in sect. *Petota*, with types scattered throughout the world's herbaria, take this problem beyond the scope of this study. Our experience with *S. andreanum* and other species in sect. *Petota* suggests that such overdescription of species occurs elsewhere in the group. Extended field studies, including visits to all of the type localities, collections of data from mature material, and documentation of intrapopulational variability, will result in further reduction in the number of species within sect. *Petota* and better circumscription of taxa recognized.

Series Differences. We make no determination here regarding the affiliation of *S. andreanum* to series (Table 1). The diverse affiliations of *S. andreanum* and its synonyms to various series, however, illustrates an important aspect of the series concept in sect. *Petota*. Many series in sect. *Petota* are poorly characterized by vague or overlapping character states, or are partly defined by geographic criteria or ploidy levels. There is much disagreement among authors regarding series boundaries and interrelationships throughout the group (Spooner and Sytsma 1992; Spooner and van den Berg 1992). This disagreement is evident in the diverse series affiliations of *S. andreanum* and its synonyms (Table 1). Ochoa (1962, 1990b) and Hawkes (1990) maintain a broad concept for series *Tuberosa* (Rydb.) Hawkes, whereas Correll (1962) and Gorbatenko (1989) split series *Tuberosa* into many smaller series, including series *Bukasoviana* Gorbatenko (=series *Transaequatorialia*). Correll (1962) and Gorbatenko (1989) rely heavily on geographic criteria to distinguish these subdivisions of series *Tuberosa*, and the morphological differences between these series are not clear. Correll (1962), Ochoa (1962), Gorbatenko (1989), and Hawkes (1990) principally define series *Ingifolia* Ochoa by its winged rachises and stems, but Hawkes (1990) does not interpret the occasionally winged rachises or stems of *S. andreanum* to be sufficient for inclusion of *S. andreanum* into this series. Correll (1962) is vague regarding his concept of series *Piurana*, and states "This series, probably more than any of the others, may be considered as a catchall. Paradoxically, its component species are held together not so much by their similarity as by their differences." Gorbatenko (1989) and Hawkes (1990) focus on the shiny, subcoriaceous leaves and other characters for series *Piurana*, and Hawkes (1990) states "there still seems to be some possible intergrading [of series *Piurana*] with series *Tuberosa* in southern Peru, whilst further research may perhaps reveal the presence of synonymity between certain species."

Economic Value of This Study. The major potato of commerce, *Solanum tuberosum* L., is one of the most important food crops on earth. In recent years, potatoes have returned 1.5–2.5 billion dollars annually to U.S. growers. The potato is even more important in other countries, as the U.S. grows only 6% of the world's crop (Lucier et al. 1991). The wild species of *Solanum* sect. *Petota* have proven to be of tremendous economic value to improve the disease resistance, environmental tolerance, and agronomic traits of the world's major potato varieties (Hanneman 1989; Ross 1986). Currently, 15 wild species have entered the parentage of the European and North American varieties (Plaisted and Hoopes 1989), and the wild species are used in major breeding programs for many developing countries (International Potato Center 1991). Besides their value in breeding programs,

the wild species are frequently used for basic research. Since 1950, the wild species germplasm of the Inter-Regional Potato Introduction Project alone has been used in programs resulting in more than 1100 published research papers and 175 completed masters and doctoral theses on the biochemistry, cytogenetics, entomology, food science, genetics, horticulture, nematology, pathology, physiology, and taxonomy of *Solanum* sect. *Petota* (Spooner and Bamberg 1991).

The development of an accurate classification of *Solanum* sect. *Petota* is of tremendous practical importance for the utilization of the wild species germplasm. It takes 8–15 yr from the initiation of a breeding program to a commercial variety release (Plucknett et al. 1987). An accurate knowledge of species boundaries and interrelationships, therefore, can save much time and money by allowing breeders to choose or avoid new germplasm based on prior breeding results. The taxonomic errors engendered by the synonymy of *S. andreanum* and the recognition of paraphyletic series (Spooner and Sytsma 1992) confuse our understanding of previously published accounts and complicate the choice of materials in breeding programs. Harlan (1992) uses the taxonomic confusion in *Solanum* sect. *Petota* as an illustrative example of the failure of taxonomy to serve breeders. Careful taxonomic studies are needed to define more completely the taxonomic and genetic resources of wild potatoes. Continuing studies will build upon the work of past taxonomists, reduce the conflicts of different treatments, and make potato taxonomy a servant to the users of the wild potato species.

Germplasm as (true) seed of *S. andreanum* was collected from the following numbers cited above: (from Ecuador) *Spooner et al. 5014, 5075, 5101, 5102, 5125, 5126, 5127, 5133, 5152, 5153, 5155, 5156, 5157;* (from Colombia) *Castillo et al. 1223, 1224, 1225, 1226, 1228, 1232, 1233.* The Ecuadorian collections will be available in late 1993 and the Colombian collections in early 1995 from the Inter-Regional Potato Introduction Project after passage through U.S. Quarantine and subsequent increase at Sturgeon Bay, Wisconsin.

ACKNOWLEDGMENTS. We thank Henry Shands and Calvin Sperling of the U.S.D.A., ARS, and Armando Okada of IBPGR for funding the collections; Jack Hawkes and Carlos Ochoa for locality data; Benjamin Øllgaard and staff at the Universidad Católica, and Santiago Díaz and staff at the Herbario Nacional Colombiano for use of herbarium facilities; Danilo Sánchez and Luis Rodríguez of INIAP, and Iván Artunduaga of ICA for facilities to extract seed and maintain germplasm in the greenhouse; Guillermo Albornoz, Paul Birdsall, Jaime Estrella, Elías Guadalupe, Francisco Muñoz, Ramón Pineda, Ricardo Rodríguez, César Tapia, and José Velasquez for advice or help in the field; George White and John Bamberg for help in importing herbarium and germplasm collections into the United States; Andrew Wynn Rouse for artwork; and William D'Arcy, Paul Fryxell, Robert Kowal, Jack Hawkes, and Carlos Ochoa for advice on an earlier draft of the manuscript (although Hawkes and Ochoa do not agree with all of our taxonomic conclusions).

LITERATURE CITED

CORRELL, D. S. 1961. New species and some nomenclatural changes in section *Tuberarium* of *Solanum*. Wrightia 2: 169–197.

———. 1962. The potato and its wild relatives. Contributions from Texas Research Foundation, Botanical Studies 4: 1–606.

GORBATENKO, L. E. 1989. Conspectus of the system of section *Petota* Dumort. of the genus *Solanum* L. from South America. Trudy po prikladnoj botanike, genetike i selekcii 126: 92–108 (in Russian).

HANNEMAN, R. E., JR. 1989. The potato germplasm resource. American Potato Journal 66: 655–667.

——— and J. B. BAMBERG. 1986. Inventory of tuber-bearing *Solanum* species. Wisconsin Agricultural Experiment Station Bulletin 533: 1–216.

HARLAN, J. R. 1992. *Crops and man*, 2nd ed. Madison, Wisconsin: American Society of Agronomy, Inc. and Crop Science of America, Inc.

HAWKES, J. G. 1990. *The potato: Evolution, biodiversity and genetic resources.* Washington, D.C.: Smithsonian Institution Press.

INSTITUTO GEOGRÁFICO AGUSTÍN CODAZZI. 1980. *Diccionario geográfico de Colombia*, 2nd ed. *Tomo I (A-LL), Tomo II (M-Z).* Bogotá, Colombia: Instituto Geográfico Agustín Codazzi.

INTERNATIONAL POTATO CENTER. 1991. *Annual report CIP 1991.* Lima, Peru: International Potato Center

LUCIER, G., A. BUDGE, C. PLUMMER, and C. SPURGEON. 1991. U.S. potato statistics, 1949-1989. United States Department of Agriculture, Statistical Bulletin 829: 1–127.

OCHOA, C. M. 1962. *Los Solanum tuberíferos silvestres del Perú (Secc. Tuberarium, Sub-secc. Hyperbasarthrum).* Lima, Peru: Publ. by the author.

———. 1981. Colombian tuber bearing Solanums in the *Conicibaccata* series. Phytologia 49: 484–487.

———. 1983. A new taxon and name changes in *Solanum* (sect. *Petota*). Phytologia 54: 391–392.

———. 1988. New Bolivian taxa of *Solanum* (sect. *Petota*). Phytologia 57: 315–324.

———. 1990a. *Solanum serratoris*: A new wild Ecuadorian potato species. American Potato Journal 67: 381–383.

———. 1990b. *The potatoes of South America: Bolivia.* Cambridge: Cambridge Univ. Press.

PAYNTER, R. A., JR. and M. A. TRAYLOR, JR. 1977. Ornithological gazetteer of Ecuador. Cambridge: Bird Department, Museum of Comparative Zoology, Harvard University.

PLAISTED, R. L. and R. W. HOOPES. 1989. The past record and future prospects for the use of exotic potato germplasm. American Potato Journal 66: 603–627.

PLUCKNETT, D. L., N. J. H. SMITH, J. T. WILLIAMS, and N. M. ANISHETTY. 1987. *Gene banks and the world's food.* Princeton, New Jersey: Princeton Univ. Press.

ROSS, H. 1986. *Potato breeding—Problems and perspectives.* Berlin: Paul Parey.

SPOONER, D. M. and J. B. BAMBERG. 1991. The Inter-Regional Potato Introduction Project (IR-1), U.S. center for potato germplasm. Diversity 7(4): 32–35.

——— and K. J. SYTSMA. 1992. Examination of series relationships of Mexican and Central American wild potatoes (*Solanum* sect. *Petota*): Evidence from chloroplast DNA restriction site variation. Systematic Botany 17: 432–448.

——— and R. G. VAN DEN BERG. 1992. An analysis of recent taxonomic concepts in wild potatoes (*Solanum* sect. *Petota*). Genetic Resources and Crop Evolution 39: 23–37.