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SYSTEMATICS OF COBAEA (POLEMONIACEAE)

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ABSTRACT. A revision of the neotropical genus *Cobaea* (Polemoniaceae), based on herbarium studies, SEM studies of pollen morphology, and field observations, is presented. Within the family, *Cobaea* is well defined by six unique characters: a scandent habit; pinnately compound leaves with the terminal leaflet modified as a tendril; very large, campanulate corollas; nearly free calyx segments; septicidally dehiscent capsules; and very large (102–233 μm), pantoporate, reticulate pollen grains. Traditionally the genus has been divided into three sections, sect. *Aschersoniophila*, sect. *Cobaea* (=*Eucobaea*), and sect. *Rosenbergia*. Based on morphological data presented here, as well as recent molecular data, sect. *Aschersoniophila* is included in sect. *Rosenbergia*; some species of sect. *Cobaea* are transferred to sect. *Rosenbergia*; and two new monotypic sections are proposed: sect. *Pachysepalae* (*C. pachysepala*) and sect. *Triovulatae* (*C. minor*). Section *Cobaea* is mainly Mexican, with one species occurring in the Andes; section *Pachysepalae* is restricted to southern Mexico and Guatemala; section *Rosenbergia* is widespread in the neotropics; and section *Triovulatae* is restricted to central Mexico, Costa Rica, and Panama. A taxonomic treatment of the 18 species, including descriptions, keys, and several illustrations is rendered. Six species are lectotypified.

INTRODUCTION

Cobaea, a neotropical genus of 18 species, is the least studied genus in the otherwise well-known Polemoniaceae, mainly because of its rarity and tropical distribution. It is well defined by a number of characters found in no other genera of the family, including a scandent habit; pinnately compound leaves with the terminal leaflet modified as a tendril; nearly free calyx segments; very large, campanulate corollas; septicidally dehiscent capsules; and very large (102–223 μm), pantoporate, reticulate pollen. The genus is notable because of its striking diversity in floral morphology (Fig. 1). The species of *Cobaea* are distributed from Peru to northern Mexico and typically occur in montane cloud forests.

Because of its many morphological differences from the remainder of the Polemoniaceae, the placement of the genus has been controversial. It was originally described as a member of the Bignoniaceae by Cavanilles (1791) and placed there by de Jussieu (1810) as well. Persoon (1805) placed the genus in the Convolvulaceae. It was first included in the Polemoniaceae by Ventenat (1794). The monotypic Cobaeaceae was erected by D. Don (1824), who recognized its relationship with the Polemoniaceae. Later, Dumortier (1829), G. Don (1838), Hutchinson (1969, 1973), R. Dahlgren (1975, 1980; G. Dahlgren 1989), and Takhtajan (1987) also recognized the Cobaeaceae; Hutchinson and Dumortier aligned it with the Bignoniaceae, and G. Don, Dahlgren, and Takhtajan with the Polemoniaceae. When included in the Polemoniaceae, *Cobaea* has usually been placed in the monotypic tribe Cobaeeae Meisner.

Recent studies by several workers have provided data that clarify the position of *Cobaea*. Based on sequence data from both the ITS region of nuclear ribosomal DNA (Baldwin et al. 1995; Porter 1997) and the chloroplast genes *ndh*F (Prather, Jansen &
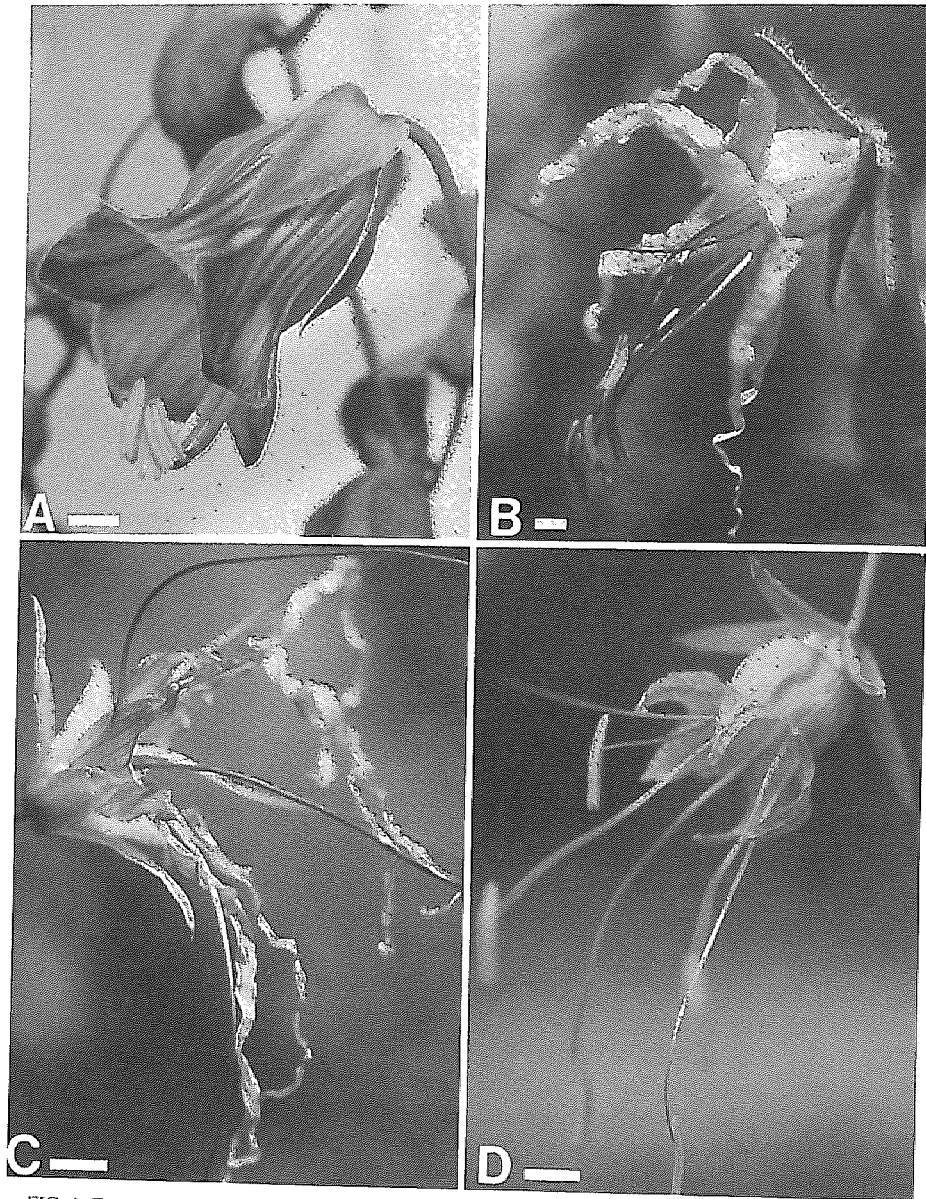
FIG. 1. Examples of floral diversity in *Cobaea*. A. *C. trianae* (*Panero & Clark 3024*, TEX). B. *C. aschersoniana* (*Prather 1577*, TEX). C. *C. gracilis* (*Prather 1576*, TEX). D. *C. lutea* (*Prather 1080b*, TEX). Scale: bar = 1 cm.

Ferguson, unpubl.) and *mat*K (Steele & Vilgalys 1994; Johnson et al. 1996), *Cobaea* is placed with confidence in the Polemoniaceae. Weaker evidence is supplied by wood anatomy (Carlquist et al. 1984). The similarities of the genus to some members of Convolvulaceae and Bignoniaceae are superficial and probably represent convergent evolution of the scandent habit and floral and fruit morphology. The genus is very distinct from

all other members of the Polemoniaceae, but the character states that make it so are derived within the family.

Cobaea is the only genus in the Polemoniaceae that is widespread in mesic, tropical-montane environments, typically montane cloud forests. Narrow endemism is high within the genus; most species are known from only a few closely spaced populations. My field observations, discussions with other collectors, and information from herbarium labels, indicate that populations consist typically of only a few individuals. Even the most widespread taxa, *C. lutea* and *C. pringlei*, are never common; they exist in either isolated populations or small clumps of populations scattered over their ranges. Given the unabated destruction of tropical habitats, the localized distributions of the species, and their small population sizes, most of the species are threatened with extinction.

Cobaea scandens, commonly called the cup and saucer vine, is widely cultivated as an ornamental, and *C. pringlei* is apparently in limited cultivation in northern Mexico. Three additional species, *C. lutea*, *C. penduliflora*, and *C. stipularis*, were once cultivated in greenhouses in Great Britain and other western European countries, but their cultivation has not continued outside of botanical gardens. The leaves of *C. scandens* are used medicinally as a cough suppressant (García R. 1988; de la Rosa 1983).

The present treatment is based on herbarium studies, SEM studies of pollen morphology, and field observations. Field observations were made in Costa Rica (March 1995), Guatemala (December 1991–January 1992, December 1993–January 1994), Mexico (December 1991, January 1992, October 1992, April 1993, October 1993), Panama (February–March 1995), and Venezuela (March–April 1995). For a complete list of species collected by me, see the Index to Numbered Collections.

Several important morphological characters that have been previously overlooked are discussed, and some that have been misinterpreted are clarified. Previous workers often had access to only a very limited number of specimens and were not able to appreciate fully the amount of intraspecific variation. I saw many more specimens than any previous student of *Cobaea*, and as a consequence the descriptions provided herein are more comprehensive than those of previous authors, and several species boundaries are better understood. Several names were found to be synonyms, including one that was reduced to synonymy for the first time. Six species are lectotypified in this treatment.

The previous sectional classification, based solely on floral and inflorescence characters, circumscribed sections that were not well differentiated. This broad-based treatment, in combination with a phylogenetic analysis based on sequences of the internal transcribed spacer (ITS) region of nuclear ribosomal DNA (Prather & Jansen 1998), suggests new sectional alignments that are presented here.

GENERIC RELATIONSHIPS OF COBAEA

Meisner (1839), Bentham (1876), Baillon (1890), Peter (1891), Brand (1907), and Grant (1959) placed *Cobaea* in a monotypic subfamily or tribe because of its many unique characters. Typically the tribe Cobaeeae has been placed near the Cantueae Peter, which consists of the Andean endemic genera *Cantua* Juss. and *Huthia* Brand. Grant (1959) and Brand (1907) suggested a close relationship between *Cobaea*, *Cantua*, and *Huthia* based on embryological characters (Brand 1907), floral vascularization (Dawson 1936), and two morphological characters, attachment of the stamens near the base of the corolla tube and broadly winged seeds.

Other workers have placed *Cobaea* and *Polemonium* L. in the same tribe (Reichenbach 1837; Wherry 1940, 1945), because they share pinnately compound leaves. This placement seems untenable when other characters and recent molecular data (Steele & Vilgalys 1994; Baldwin et al. 1995; Porter 1997; Prather, Jansen & Ferguson, unpubl.) are considered.

A close relationship between *Cantua* and *Cobaea* is suggested by data from *matK* (Steele & Vilgalys 1994; Johnson et al. 1996), ITS (Baldwin et al. 1995; Porter 1997), and *ndhF* sequences (Prather, Jansen & Ferguson, unpubl.), but a closer relationship between *Cobaea* and *Bonplandia* Cav. is suggested by the *ndhF* and *matK* data sets. The phylogeny based on ITS and the first *matK* study (Steele & Vilgalys 1994) are unresolved or have weakly supported branches in this portion of the tree, so that the relationship between *Cobaea* and *Bonplandia* is neither supported nor rejected. Early workers failed to suggest a close relationship between *Cobaea* and *Bonplandia*, but Grant (1959) agreed that *Bonplandia*, *Cantua*, *Cobaea*, *Huthia*, and *Loeselia* L. are possibly more closely related to each other than to the remainder of the family.

Cobaea and *Bonplandia* each have a number of derived character states in the family, and morphology offers little information that suggests that they are closely related, although there are few morphological characters that strongly suggest a relationship between either genus and any other member of the family. Two morphological characters provide weak evidence of a relationship between *Cobaea* and *Bonplandia*. First, *Bonplandia*, *Cobaea*, *Huthia*, and one species of *Cantua* (*C. bicolor* Lem.) have axillary cymes, a character that distinguishes them from the remainder of *Cantua*. Second, *Bonplandia* and *Cobaea minor* have a single ovule in each of the three locules. Uniovulate locules are unique among the taxa here discussed, and because *C. minor* is sister group to the remainder of *Cobaea* (Prather & Jansen 1998), this character state may represent a synapomorphy for *Bonplandia* and the common ancestor of *Cobaea*. In terms of biogeographic history, *Bonplandia* and *Cobaea* share a probable origin in Central Mexico (Grant 1959, see below), whereas *Cantua* and *Huthia* are entirely Andean.

TAXONOMIC HISTORY

The genus *Cobaea* was first proposed by Cavanilles (1791) in honor of the Jesuit priest and naturalist Barnabas Cobo. Cavanilles described *C. scandens* from plants cultivated at the Royal Botanic Gardens in Madrid, which had been grown from seed collected from plants growing near Mexico City (Cavanilles 1791). During the next 60 years three additional species, *C. lutea*, *C. minor*, and *C. stipularis*, were described.

In 1856 Oersted described a new genus, *Rosenbergia*, based on *R. gracilis* Oerst., that was clearly allied to *Cobaea*, but which he believed to be distinct because of its elongated, linear corolla lobes (Oersted 1856). Two years later Karsten described another species of *Rosenbergia*, *R. penduliflora* Karst. from Venezuela in his *Flora Colombiana* (Karsten 1858). J. D. Hooker (1869) was the first to recognize that the two genera were not distinct when he transferred *R. penduliflora* to *Cobaea*. This arrangement has been followed by all later workers.

During the late 19th and early 20th centuries five treatments of *Cobaea* were published: Hemsley (1880), Peter (1891), Brand (1907), House (1908), and Standley (1914). Hemsley (1880) provided brief descriptions of all the known taxa and described two additional species. After Hemsley's treatment was published, *C. triflora* was described. In

Peter's (1891) treatment of *Cobaea* for Engler and Prantl's *Die natürlichen Pflanzenfamilien* he constructed two sections in the genus, sect. *Eucobaea* (=sect. *Cobaea*) and sect. *Rosenbergia*, but four species were overlooked and omitted from his treatment. Brand (1904) described *C. aschersoniana* and sect. *Aschersoniophila* and later treated the entire genus (Brand 1907).

House (1908) described *C. pringlei* and provided a key to the known species. In this treatment he claimed that the name *Cobaea* is invalid, because it was used by Necker in 1790 to refer to a group of plants now included in *Lonicera* (Caprifoliaceae). He therefore transferred all of the species to *Rosenbergia*. Standley (1914) determined that the rank of *Cobaea* Necker was never clearly established, and that the name was not published in combination with any specific epithet and was therefore illegitimate at the generic rank. Thus, he retained the name *Cobaea* for the genus here discussed. Wilson and Bullock (1957) proposed to conserve *Cobaea* Cav. over *Cobaea* Necker, believing that the latter did have priority. The edition of the *International Code of Botanical Nomenclature* ("Montreal Code"; Lanjouw et al. 1961) adopted at the 9th International Botanical Congress rejects the names published by Necker in his *Elementa Botanica* (1790) and negated the need to conserve *Cobaea* Cav.

In Standley's (1914) revision, the most recent, 18 species were recognized, seven described as new. Unfortunately he saw no specimens of five of the species that he included in his revision and only a few specimens of the remaining species. Upon examination of more abundant material, permitting an evaluation of intraspecific variation, I have determined that five of the species described by Standley do not merit recognition. Of these, three had subsequently been reduced in rank to forms (Gibson 1968). Forms are not recognized in the current treatment, and thus all five names are placed in synonymy. Seven new species have been described since 1914, *C. aequatoriensis*, *C. flava*, *C. lasseri*, *C. paneroi*, *C. rotundiflora*, *C. skutchii*, and *C. steyermarkii*. The names *C. lasseri* and *C. steyermarkii* were superfluous when published. The latest additions (Prather 1996) bring the number of recognized species again to 18.

The sectional arrangement of Peter (1891) and Brand (1904, 1907) was followed by House (1908) and Grant (1959), but Standley (1914) did not divide the genus into sections. Sectional classification is more fully discussed below.

MORPHOLOGY

Unless noted otherwise, references to sectional classification refer to the arrangement proposed herein.

Habit. Cobaea is a genus of perennial, and possibly some annual, herbaceous or woody vines. The herbaceous species tend to grow in drier habitats than the woody species, but only rarely in deciduous or semi-deciduous forests. It is unknown whether the herbaceous plants are annual or perennial. Asplund (1954), however, suggested that *C. aequatoriensis* was suffrutescent in nature and had evidently grown back from its rootstock after being cut.

In some of the liana-like species the slender branches often dangle directly from the canopy and are not attached to any support structure except in the uppermost portions of the branches. This condition arises because the plants attach only by tendrils to their support structures; as they age the leaves and tendrils die, thus all that remains for support is

the upper foliose portions of the plant. Other species have only been found climbing upon shrubs or small trees or even scrambling over herbaceous vegetation.

Roots. The roots of *Cobaea* species are fibrous, and the older, larger roots of those species examined (*C. pringlei, C. scandens, C. stipularis*) are furnished with small (up to 2 cm in diameter), white tubers scattered along their length.

Stems. Even those species that become woody have very slender lower stems, seldom reaching more than 3 cm in diameter, although this may be exceeded in cultivation. Most species branch infrequently, except near the apex of the stems where several actively growing branches usually occur. The lateral branches tend to die after only one season, or more quickly if the tendrils fail to attach to some support structure. Some species (*C. pringlei, C. pachysepala*, and *C. gracilis*) have been observed to produce runner- or rhizome-like branches that become buried under litter and produce occasional adventitious roots. Rhizomes may prove to be very common in the genus when careful observations of other species can be made. The stem anatomy of *C. scandens* is discussed by Carlquist et al. (1984).

Leaves. The leaves of *Cobaea* are alternate, pinnately compound, and the terminal leaflet is modified as a tendril. The petioles and petiolules are short and have a narrow channel on the upper surface, which is often lined with minute trichomes. Most species have three pairs of subequal, opposite or subopposite leaflets. Venation is pinnate. The leaflets are mucronate and ciliate with minute multicellular trichomes. Sometimes the leaflets are pubescent along the veins of the abaxial surface. The leaflets of most species are elliptic to ovate. The lowermost pair is often modified in some way; they are sometimes long-ciliate basally, about half as long as the upper pairs, or constricted in the middle of the blade with an auriculate base.

The tendrils, unique in the family, are very long (up to 20 cm on large leaves), much branched, and have rigid bifurcate hooks at each of the tips. The hooks are similar in appearance to the mucros of the leaflet tips and are derived from them. The tendrils attach primarily by means of the hooks, but sometimes the tendril tips wrap around the supporting structure. The tendril coils along its entire length, even in the portions not wrapped around the object, drawing the vine nearer to its supporting structure.

Vestiture. All trichomes of *Cobaea* are "chain-like" (Grant 1959), referring to the tendency of the cells to become flattened as they dry, but typically in a plane different from the cells above and below, producing an effect similar to the links of a chain. Often the trichomes reach 5 mm or more in length, as those near the base of the stamens of nearly all species do. Along the margins of the leaflets, as well as the channel of the petioles, the trichomes are often less than 1 mm long. The trichomes are often glandular-tipped, but the distinction is not always clear, because the tip sometimes detaches as it dries.

Many species of *Cobaea* have villous nodes. Nearly all species have leaflets ciliate with minute trichomes. In a few species the veins of the abaxial leaf surface are puberulent or even villous. The base of the lowermost leaflet pairs of many species is ciliate with long trichomes.

A pubescence pattern similar to that found in the leaflets is found in the calyces, where nearly all species are ciliate with minute trichomes, and a few are ciliate with long trichomes as well. Both types of trichomes are often found on the external surface of the
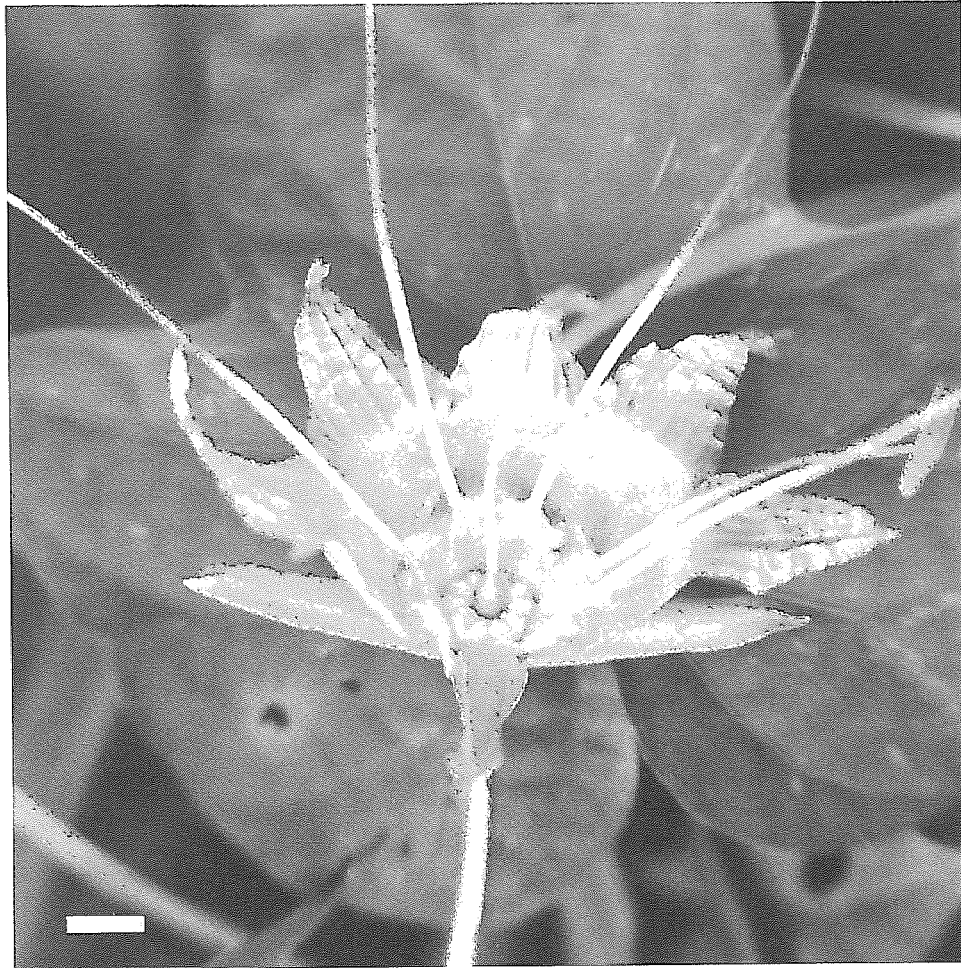
FIG. 2. A flower of *Cobaea lutea* (*Prather 1080b*, TEX) opened to show the internal structures. The lobed structure in the center of the flower is the nectary above which the ovary is positioned. A ring of long trichomes is present on the corolla at the point of filament attachment. Scale: bar = 1 cm.

corolla. When present, longer trichomes are mostly found near the base of the tube, whereas the shorter trichomes are typically more abundant near the apex of the lobes.

In all species, except *C. minor*, there is a ring of long trichomes near the point of stamen attachment on the internal surface of the corolla (Fig. 2). The trichomes occur in a continuous zone 0.5 cm wide or less around the corolla. This vestiture pattern is often called an annulus. In some species the annulus appears as a single line of trichomes. The trichomes extend from the corolla up the filament as far as 1 cm beyond the point at which it separates from the corolla. The position of the annulus corresponds to a constriction of the corolla tube. In one species, *C. pachysepala*, there is a patch of long trichomes near the apex of the filaments.
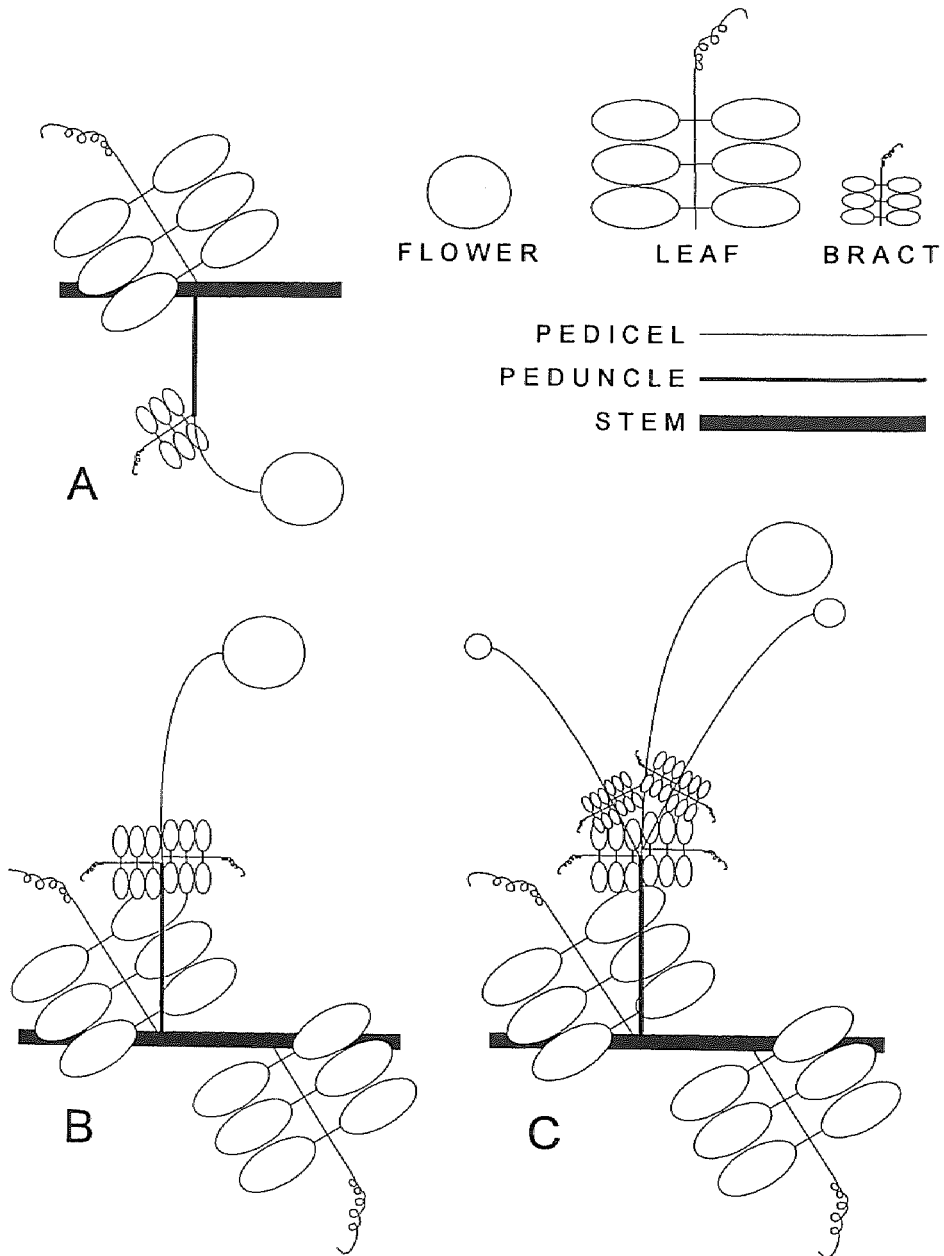
FIG. 3. Diagrammatic representation of inflorescence architecture in *Cobaea*. A. The single-bracted, pendulous, and one-flowered inflorescence of *C. minor*. B. An erect, double-bracted, one-flowered inflorescence. C. A compound inflorescence of three flowers and several bracts.

Inflorescence. The inflorescence is a dichasial cyme of 1 to several flowers subtended by a pair of subopposite foliaceous bracts, except in *C. minor*, which has only a single bract. Diagrammatic representations are shown in Fig. 3. The bract(s) may be either fully expanded, resembling typical leaves, or much reduced in size but maintaining all the typical leaf characters (i.e., 4–8 leaflets and a terminal tendril). When rudimentary, the bracts often senesce and are abscised before anthesis, as is often the case when the inflorescence is reduced to a solitary flower.

The literature reports of pendulous inflorescences in the species of sect. *Rosenbergia* and sect. *Aschersoniophila* are incorrect (e.g., W. J. Hooker 1840; J. D. Hooker 1869; Brand 1907; Standley 1914). This is especially unfortunate because this character has been used in sectional classification (Brand 1907; Grant 1959) and even nomenclature (hence the epithet 'penduliflora'). All of the species of *Cobaea*, except *C. flava*, *C. paneroi*, and *C. triflora*, have been collected by me or by colleagues, and the inflorescence positions are now known with certainty. The position of the bracts and the angle and curvature at the base and apex of the pedicel of *C. flava*, *C. paneroi*, and *C. triflora* imply that these three species have erect inflorescences. Field observations in Panama confirmed that the inflorescence of *C. minor* is pendulous, and the pedicels are shorter than 4.5 cm. The inflorescence of all other species is erect, and the pedicels are longer than 8.0 cm (Fig. 3).

Calyx. In *Cobaea* the calyx segments are united basally for less than 1/10 their length, unlike in other members of the Polemoniaceae, which have segments that are united for considerably more of their length. The calyx of *C. scandens* has been reported as fused for up to half its length (e.g., Standley 1914), but it is in fact only adherent and not connate. The calyx segments of *C. scandens* are circular to broadly ovate, whereas the segments of all other species are deltate to lanceolate.

The adaxial calyx surface of nearly all species is puberulent, especially near the margins. In *C. pachysepala* the zone of pubescence is reduced to less than 1 mm, whereas in most other species the zone is much broader. Many species have ciliate calyx margins, and the calyces of *C. aschersoniana* and *C. rotundiflora* are densely villous abaxially. The calyx of most species is membranous or chartaceous, but in *C. pachysepala* it is coriaceous.

Corolla. Much of the striking floral morphological variation within *Cobaea* is due to corolla form (Fig. 1), which has been a subject of interest to several workers (Behrens 1880; Brand 1904; Asplund 1954; Grant 1959; Grant & Grant 1965; Prather 1995; Prather & Jansen 1998). The corollas of most species are green, but sometimes are purplish red or pink, white, or yellow. When green, the flowers are often suffused with one of the other tints. The corolla tubes vary in length from about 2 to 7 cm long, and are funnelform or campanulate. The tubes are constricted near the base, at the point where the stamens are no longer adnate. Sometimes they are also constricted at the apex of the tube, in which case the tube is urceolate (Fig. 1B, D).

The lobes vary from 1–6 cm long. The shape of the lobes is remarkably variable, ranging from very broadly ovate to long-linear (Fig. 1). In *C. aschersoniana* and some specimens of *C. lutea* the tips are linear and the basal part of the lobes are ovate. The lobes of *C. lutea* vary from deltate to linear. Often the lobes are mucronate and sometimes they are clawed. The extremes in corolla morphology are represented by *C. stipularis* with a long tube (44–64 mm) and short, broadly ovate lobes (16–23 mm long) and *C. gracilis* (Fig. 1C) with a short tube (12–19 mm long) and long, linear lobes (29–60 mm).

If the lobes are ovate or round the corolla is imbricate in bud. In species with narrower lobes the corollas are valvate in bud. In three species, *C. aequatoriensis*, *C. gracilis*, and *C. penduliflora*, the lobes are so narrow that they are not in contact along their edges, even in bud, and in *C. aschersoniana* and *C. lutea* the lobes are in contact only near the base. In all species of sect. *Rosenbergia* the corollas are wrinkled in bud just before anthesis. In some species they flatten as they expand, but in others the corolla maintains this undulate appearance throughout its development (Figs. 1B, C).

The texture of the corollas of most species is membranous when dry. In *C. flava* and *C. minor* the corollas are so thin that they are transparent in dried specimens. The species of sect. *Cobaea* and sect. *Pachysepalae* have thickened corollas that are firm and sometimes approach a brittle texture, even when fresh.

The corollas form a receptacle for nectar at their base, referred to here as a "nectar chamber." The nectar chamber is formed by the constriction of the corolla near the base, accompanied by an annulus on the internal surface, enclosing the five very large nectary glands (Fig. 2), which are located just above the receptacle and below the ovary. The trichomes probably function in restricting access to the nectar and in reducing evaporation.

Androecium. The five stamens have filaments that vary in length from about 20 to 100 mm. In species of sect. *Cobaea*, sect. *Pachysepalae*, and sect. *Triovulatae*, as the upper filaments become free from the corolla, they angle sharply down to the ventral side of the corolla and present the introrse anthers near the basal portion of the orifice (Fig. 4A). In these species the filament is sharply curved at the tip.

In some species of sect. *Rosenbergia* the position of the anthers is similar to that described above, but this placement is achieved by a constant slight decline in the slope of the upper filaments, so that they do not extend ventrally along the corolla, but rather, their tips meet in the ventral side of the orifice, presenting the introrse anthers (Fig. 4B). In these species the anthers are attached to the filaments so that the filament is not so sharply curved at the tip.

In other species of sect. *Rosenbergia*, such as *C. lutea* and *C. skutchii*, the filaments protrude directly from the corolla, and the anther attachment is versatile (Fig. 4C). Three species, *C. aequatoriensis*, *C. gracilis*, and *C. penduliflora*, have filaments that are reflexed from the corolla. In these species the filaments are attached in a spiral fashion, and the anther attachment is versatile (Figs. 4D, E).

Gynoecium. The ovary is tricarpellate and glabrous. Placentation is axile, and the septa are thickened and fleshy, so that the three septa fuse into a large triangular septal column, and the ovules are attached on the flat surfaces (Figs. 5, 6). The slender style is from 28 to 127 mm long.

Two distinct types of stigma are found among the species (Fig. 7). The first, hereafter referred to as "type I stigmas," are found among the species of sect. *Cobaea*, sect. *Pachysepalae*, and sect. *Triovulatae*, as well as *Bonplandia* and *Cantua*. These stigmas occur on style branches that are broad, flattened, and are composed of long papillae only on the adaxial surfaces of the style branches (Fig. 7A, B). "Type II stigmas" are unique to sect. *Rosenbergia*; these occur on terete style branches and are composed of short papillae that cover nearly the entire surface of the style branches (Fig. 7C, D).
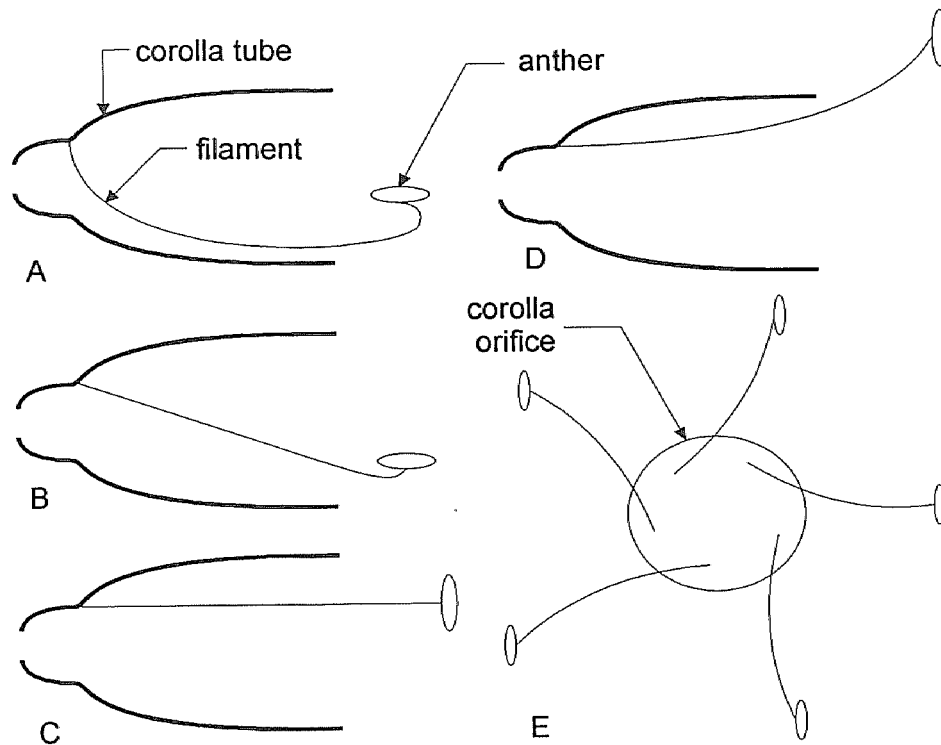
FIG. 4. Diagrammatic representation of stamen positions in *Cobaea*. A–D, side view; E, front view. In A–D only one upper stamen is represented for simplicity. A. Filament extending along the ventral portion of the corolla and sharply curved at the base and apex, presenting the introrse anthers at the base of the floral orifice. B. Filament extending along the ventral portion of the corolla, but not sharply curved at the base and apex, presenting the introrse anthers in base of the floral orifice. C. Filament, with versatile anther, emergent from the corolla. D. Filament, with versatile anther, reflexed from the corolla. E. Same arrangement as in D, but in front view and with all five stamens, illustrating the spiral arrangement.

Fruit. The fruit is a septicidal capsule (Fig. 6). The flat seeds lie overlapping, between the outer wall and the septal column (Figs. 5, 6). The septal column shrinks and dries as the fruit matures, pulling away from the outer wall. At maturity, the dried filamentous placentae are several millimeters long and remain visible. The capsules remain attached to the pedicels, the outer walls separate at the septa and reflex or simply separate, exposing the winged seeds (Fig. 6), which are dispersed short distances by wind. The outer walls of the capsules of *C. scandens* are thickened.

Seeds. The number of seeds per fruit varies from 1 to about 45. The seeds are very large (1–2 cm long), flat, and broadly winged (Fig. 6). The apical seed in most capsules is shaped slightly differently from the remaining seeds. It has a long-acuminate apex that reflects the shape of the capsule apex. The remaining seeds are apically acute or rounded. The seeds of some species have trichomes that are very broad and flatten when dried, resembling scales (Fig. 8). The development of the cytoskeleton of these trichomes has been
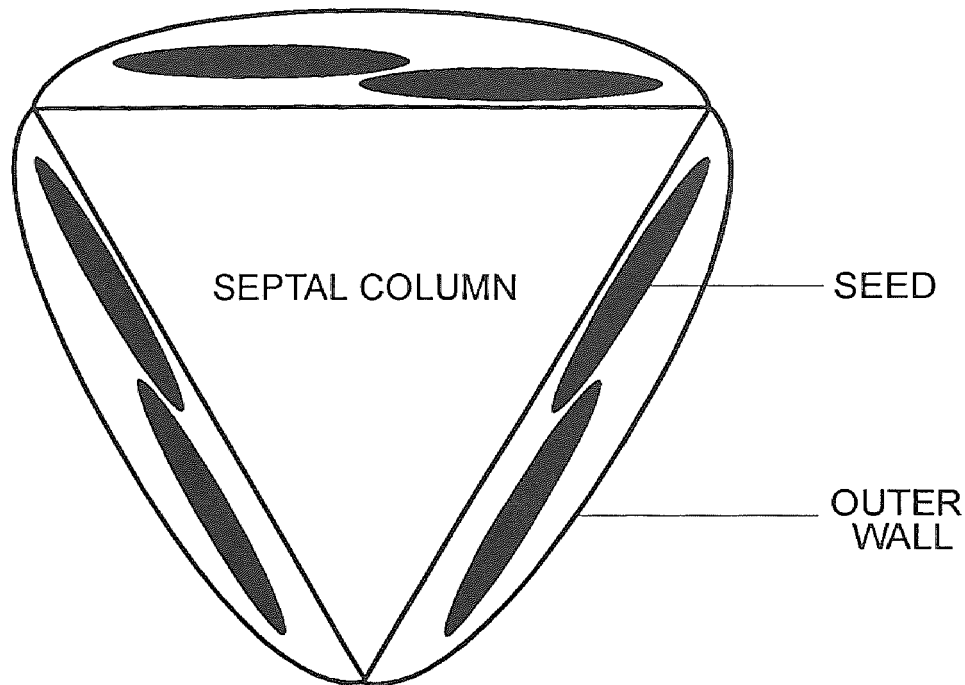
FIG. 5. Diagram of a cross section of a *Cobaea* capsule showing the septal column and position of the seeds.

studied in *C. scandens* by Quader et al. (1986). Like the seeds of many genera in the Polemoniaceae, the seeds of *Cobaea* become mucilaginous when wet.

Seedlings. The seedlings of *Cobaea* have opposite, simple, ovate, and entire cotyledons. The first set of true leaves are also opposite, and have an unmodified terminal leaflet (i.e., are without a tendril). The seedlings of most species examined (*C. lutea*, *C. pachysepala*, *C. penduliflora*, *C. rotundiflora*, *C. scandens*, *C. stipularis*, *C. trianae*, and *C. skutchii*) are epigeous and the cotyledons are sessile, whereas the seedlings of *C. pringlei* are hypogeous and the cotyledons have long petioles.

POLLEN MORPHOLOGY

Pollen morphology of *Cobaea* has been briefly discussed by Erdtman (1952), Stuchlik (1967a, 1967b), Taylor and Levin (1975), and Ludlow-Wiechers (1982), mainly in the context of generic comparisons, and none of their studies is comprehensive. The pollen of *Cobaea* is very large, reticulate, pantoporate, microbaculate, and has three porate lumina adjacent to each aporate lumen; it is unique within the Polemoniaceae.

The pollen of *Cobaea* is most similar to that of *Phlox* L. and *Gymnosteris* Greene, but differs from these in its size, symmetry, and the details of its surface sculpturing. The pollen of *Cobaea* ranges in size from 102 to 233 μm, whereas that of *Phlox* ranges from 22 to 56 μm, and that of *Gymnosteris* from 25 to 32 μm (Stuchlik 1967a). *Phlox* and *Gymnosteris* have no discernible pattern in the number of aporate lumina adjacent to porate
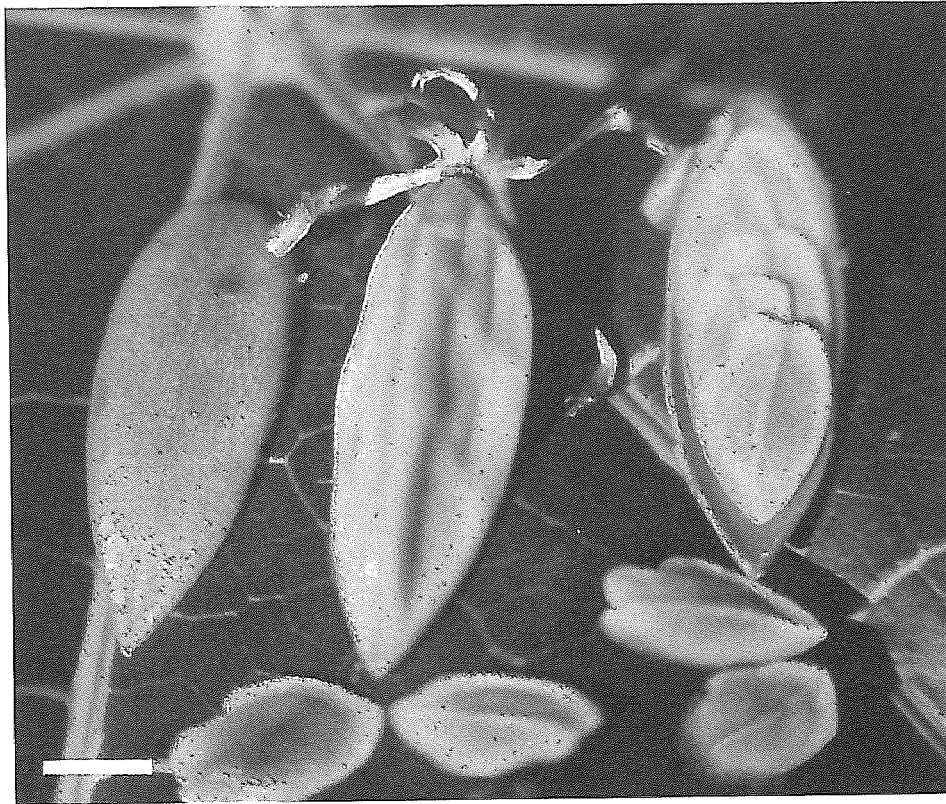
FIG. 6. Immature fruit and seeds of *C. lutea* (*Prather 1080b*, TEX). Segment of outer wall on left, thickened septal column with attached calyx in center, and segment of outer wall with seeds on right. A few seeds are below. Scale: bar = 1 mm.

lumina, lack microbacula, but are furnished with a "micromesh" (sensu Stuchlik 1967a), which *Cobaea* lacks.

Materials and methods. All samples were removed from herbarium specimens (Appendix 1). Two unopened anthers were removed from a single bud that appeared to be in a stage just pre-anthesis and were combined as one sample. Each pollen sample was acetolysed according to the procedures of Adams and Morton (1972), except that maceration and critical point drying were omitted. After the final wash each sample was suspended in about 10 ml distilled water by vortexing, and poured onto a small plastic petri dish. The petri dish was placed on a 45°C slide warmer until the water had evaporated, leaving the grains distributed over the surface of the petri dish. The grains were stored in the petri dishes until used.

Samples were mounted for scanning electron microscopy (SEM) by carefully touching a standard aluminum microscope stub, the surface of which was covered with double-sided tape, to the pollen grains. The specimens were coated with a mixture of 60%
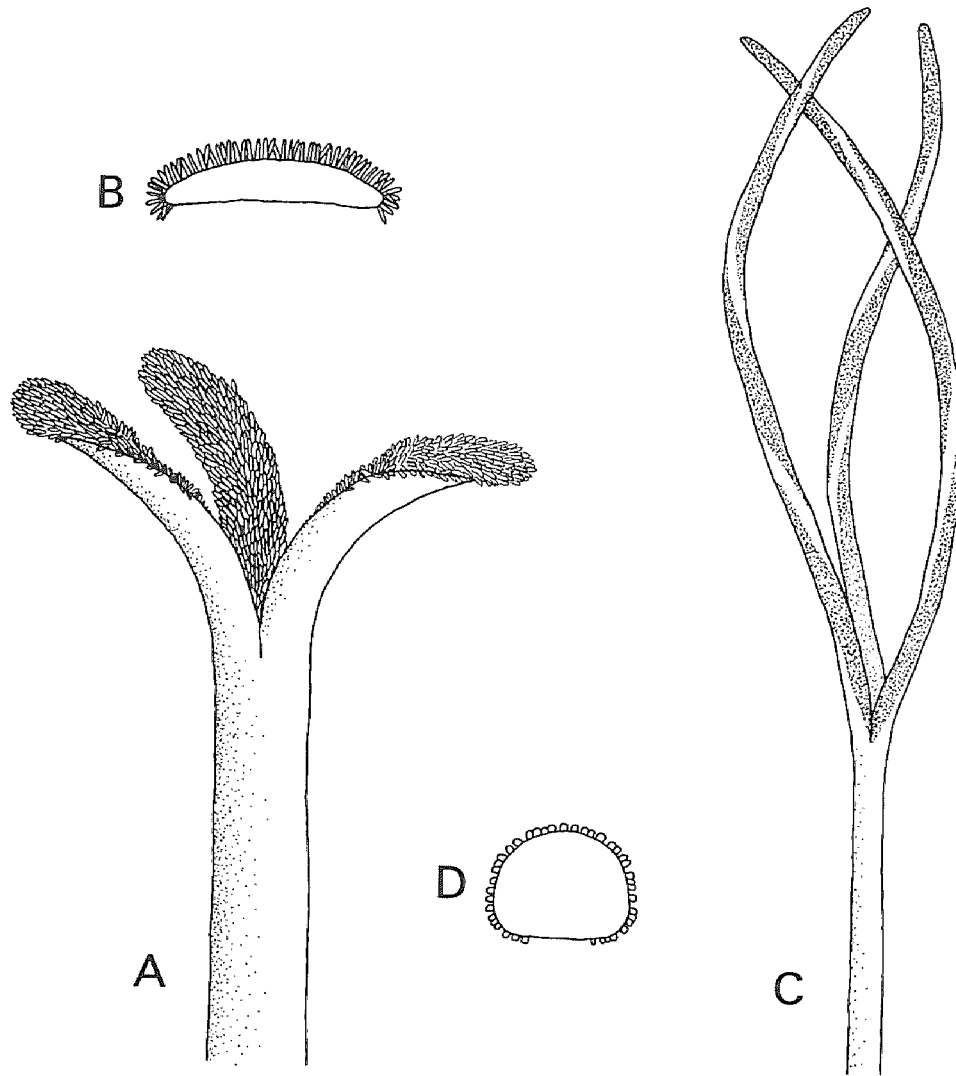
FIG. 7. Stigma morphology of *Cobaea* species. A. Type I stigma. B. Cross section of style branch of Type I stigma. C. Type II stigma. D. Cross section of style branch of Type II stigma.

palladium and 40% gold, and were examined using a Phillips 515 scanning electron microscope in the Cell Research Center at the University of Texas, Austin.

Diameters of the grains, aporate and porate lumina, and pores were measured in water using an ocular micrometer, calibrated with a stage micrometer, on a light microscope at 40× magnification. The ratio of aporate lumen to porate lumen diameters was calculated as the average of individual ratios over each species. At least 20 acetolysed pollen grains were removed from the petri dish and placed in water on a concave slide; a cover slip was carefully added. Any crushed grains, or grains that were apparently teratological, were not examined in this study.
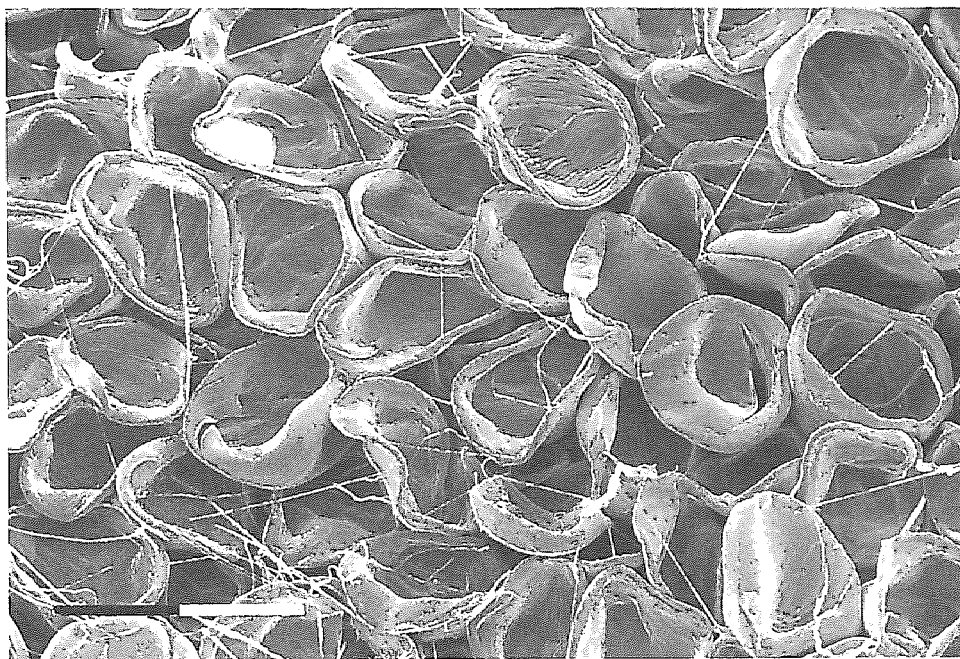
FIG. 8. SEM micrograph of the seed trichomes of *Cobaea scandens* (*Prather 1582*, TEX). Scale: bar = 0.1 mm.

Results and discussion. All references to sectional classification follow the arrangement proposed herein. The pollen grains of *Cobaea* species are spheroidal, with a reticulate sexine, and are quite large (species means from 112 to 195 µm in diameter). The smallest grains measured (102 µm, *C. stipularis*) are less than half the size of the largest (233 µm, *C. rotundiflora*). The winding or linear muri are supported by bacula. In *C. minor*, and to a lesser extent *C. paneroi*, the muri are raised at the junctions where they merge with other muri.

The grains are pantoporate, and each aporate lumen is adjacent to three porate lumina. The average aporate lumen of the species varies from 18 to 28 µm in diameter, the porate lumina average from 15 to 28 µm in diameter, and the pores average from 8 to 16 µm in diameter. The ratio of the diameter of the aporate lumina to the porate lumina varies among taxa from 0.9 to 1.4. The species with smaller mean grain diameters tend to have higher ratios, whereas the species with larger grain diameters tend to have lower ratios. Exceptions exist, such as *C. minor*, which has a small grain diameter (120 µm) and a low ratio (1.0), or conversely *C. triflora*, which as a large grain diameter and a relative high ratio (1.3).

The lumina are provided with thread-like or club-shaped microbacula, though in some taxa these are reduced to granules or are rarely absent (Table 1, Figs. 9–11). In general the microbacula are reduced or absent in species with smaller grain diameters, though they are short in both *C. flava* and *C. triflora*, and both species have relatively large pollen grains.

TABLE 1. Pollen measurements of *Cobaea*. The mean is in parentheses, and the minimum and maximum value are on either side. All measurements are diameters reported in μm. At least 20 grains were measured per sample.

	Grain	Aporate lumen	Porate lumen	Pore	Microbacula	Aporate/ porate
Sect. *Triovulatae*						
C. *minor*	113 (120) 127	16 (19) 25	16 (19) 24	9 (12) 16	short	1.0
Sect. *Cobaea*						
C. *pringlei*	104 (129) 151	18 (24) 31	16 (20) 25	11 (14) 18	granular	1.2
C. *stipularis*	102 (116) 133	16 (22) 28	14 (17) 21	8 (10) 16	granular	1.3
C. *trianae*	107 (112) 116	15 (22) 25	12 (15) 19	7 (8) 10	granular	1.4
C. *biaurita*	142 (152) 161	22 (26) 32	15 (22) 28	10 (15) 20	granular	1.2
C. *scandens*	107 (119) 133	18 (25) 31	16 (20) 24	10 (13) 22	granular	1.3
C. *paneroi*	112 (121) 131	18 (24) 32	14 (20) 25	10 (11) 13	granular	1.3
Sect. *Pachysepalae*						
C. *pachysepala*	161 (172) 184	16 (23) 27	20 (23) 25	13 (14) 17	granular	1.0
Sect. *Rosenbergia*						
C. *skutchii*	128 (140) 145	15 (18) 21	15 (17) 22	7 (8) 10	long	1.0
C. *aschersoniana*	155 (170) 188	22 (26) 32	20 (26) 33	8 (11) 14	long	1.0
C. *gracilis*	154 (165) 172	18 (24) 30	21 (28) 34	9 (11) 13	long	0.9
C. *penduliflora*	184 (193) 206	22 (26) 32	22 (27) 33	12 (15) 25	long	1.0
C. *aequatoriensis*	118 (130) 137	12 (19) 25	16 (19) 24	7 (8) 10	long	1.0
C. *flava*	133 (141) 147	18 (22) 28	17 (20) 24	9 (10) 12	short	1.1
C. *campanulata*	169 (194) 209	21 (28) 35	16 (25) 31	11 (14) 16	long	1.1
C. *lutea*	151 (160) 167	18 (21) 26	16 (20) 24	9 (10) 12	long	1.1
C. *rotundiflora*	135 (195) 233	14 (25) 32	16 (25) 36	7 (16) 21	long	1.0
C. *triflora*	147 (160) 172	17 (21) 25	12 (16) 20	8 (9) 11	short	1.3

The pollen morphology of *Cobaea* species has important implications for sectional classification. These implications and general agreement with morphological and molecular evidence are further discussed below.

POLLINATION AND BREEDING SYSTEMS

It has been suggested that the considerable variation in floral morphology of *Cobaea* is explained by adaptation for specific pollinators (Grant 1961; Grant & Grant 1965). Very little is known about pollination in the genus, however, despite the fact that pollination is perhaps better understood in the Polemoniaceae than in any other angiosperm family (Grant & Grant 1965).

The pollination systems of only five species of *Cobaea* have been previously documented in the literature, and they are remarkably divergent: autogamy in *C. lutea*; chiropterophily (bat pollination) in *C. aschersoniana* (Ippolito & Suarez 1998), *C. scandens*, and *C. trianae*; and phalaenophily (moth pollination) in *C. penduliflora* (reviewed in Grant & Grant 1965). Vogel (1969) confirmed Grant's supposition that *C. scandens* was bat pollinated, and Knudsen and Tollsten (1995), who studied the chemistry of scent in several bat-pollinated plants including *C. scandens*, suggested that hummingbirds may also play a role in pollination. Additionally, hummingbird visitation has been casually reported (i.e., on herbarium labels) for three species (*C. aschersoniana, Poppleton s.n., Jan*
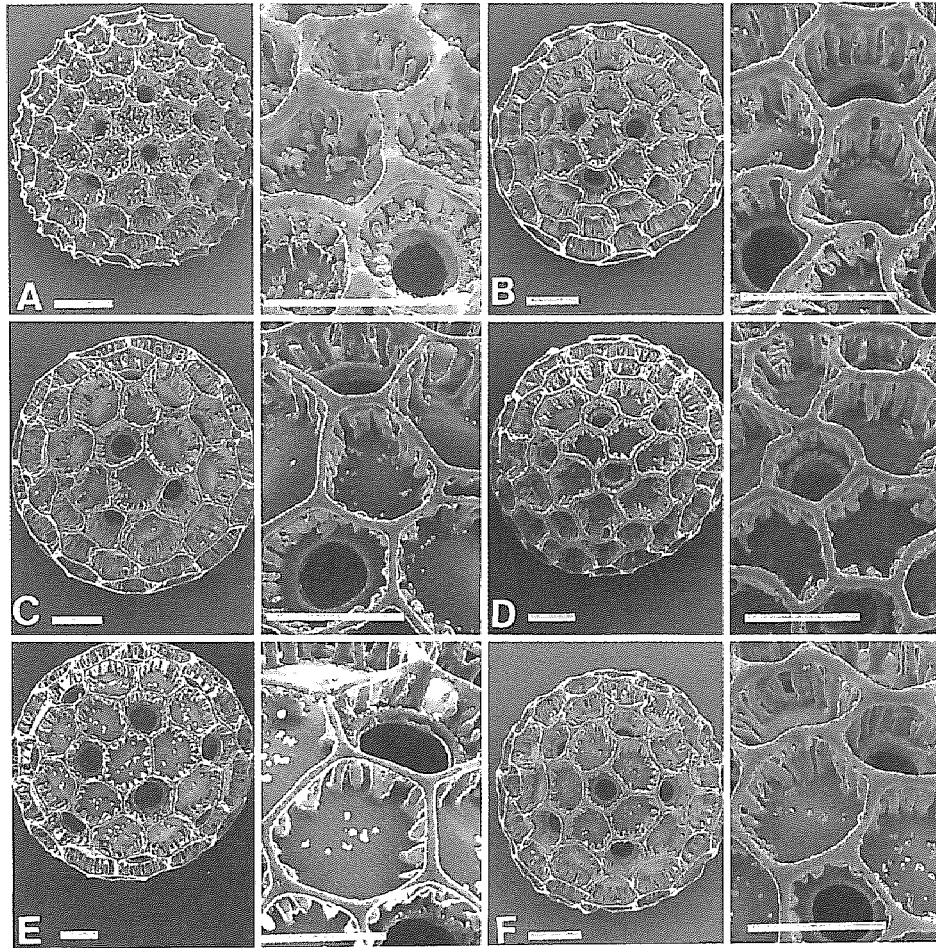
FIG. 9. SEM micrographs of the pollen of *Cobaea*. A. *C. minor* (*Almeda & Nakai 3496*, CAS). B. *C. pringlei* (*Roe & Roe 2178*, WIS). C. *C. stipularis* (*Barrie & Atkinson 931*, TEX). D. *C. trianae* (*Panero & Clark 3044*, TEX). E. *C. biaurita* (*Clarke 293*, DH). F. *C. scandens* (*Benítez de Rojas 1480*, F). Scale: bar = 20 μm.

1974; *C. campanulata*, *Panero & Clark 2998*; and *C. minor*, *Folsom et al. 7125*), and I observed hummingbirds visiting *C. skutchii* in Guatemala (*Prather 1527*, TEX). Finally, Ippolito and Suarez (1998) reported that hummingbirds and bees visit *C. aschersoniana*, but apparently neither were effective pollinators. When pollination systems of the various species are better known, these studies will allow a test of the degree of correlation between floral morphology and pollination systems, and will provide the foundation for studies of the evolution of pollination systems of *Cobaea*.

Cobaea scandens has been reported as self-incompatible (Behrens 1880; Grant & Grant 1965). *Cobaea penduliflora* had much reduced fruit set when selfed compared to that when crossed (Ernst 1880), which led Grant and Grant (1965) to conclude that it was also self-incompatible, though this conclusion seems questionable. On the other hand,
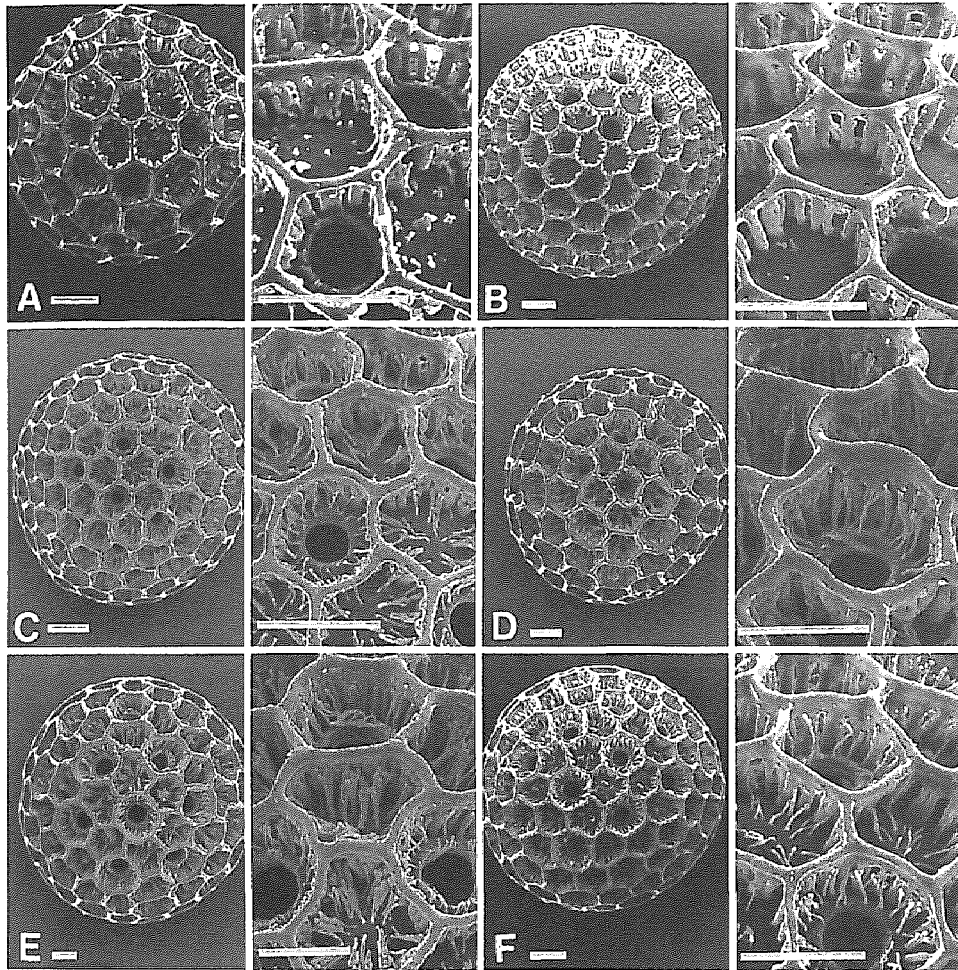
FIG. 10. SEM micrographs of the pollen of *Cobaea*. A. *C. paneroi* (*Hernández 3332*, MEXU). B. *C. pachysepala* (*Breedlove 42780*, CAS). C. *C. skutchii* (*Standley 85652*, F). D. *C. aschersoniana* (*Bangham s. n.*, A). E. *C. gracilis* (*Almeda & Nakai 3517*, CAS). F. *C. penduliflora* (*Haught 2880*, US). Scale: bar = 20 μm.

C. lutea has been reported as self-compatible (Ross 1898), and based on indirect evidence, Ippolito and Suarez (1998) concluded that *C. aschersoniana* is also self-compatible.

Several taxa were grown in the greenhouses at the University of Texas and preliminary studies of breeding systems were performed, consisting mainly of self-pollinations. From sect. *Cobaea*, *C. pringlei*, *C. scandens*, and *C. stipularis* were examined. All three species had flowers that lasted at least 72 hr, and were strongly protandrous. Two or three anthers dehisced at the beginning of anthesis, usually the evening of the first day, and the remainder dehisced the next evening. The style branches separated and reflexed the following evening.

Preliminary self-pollinations suggested that these species were indeed self-incompatible. When self pollen from freshly opened anthers (taken, of necessity, from a different
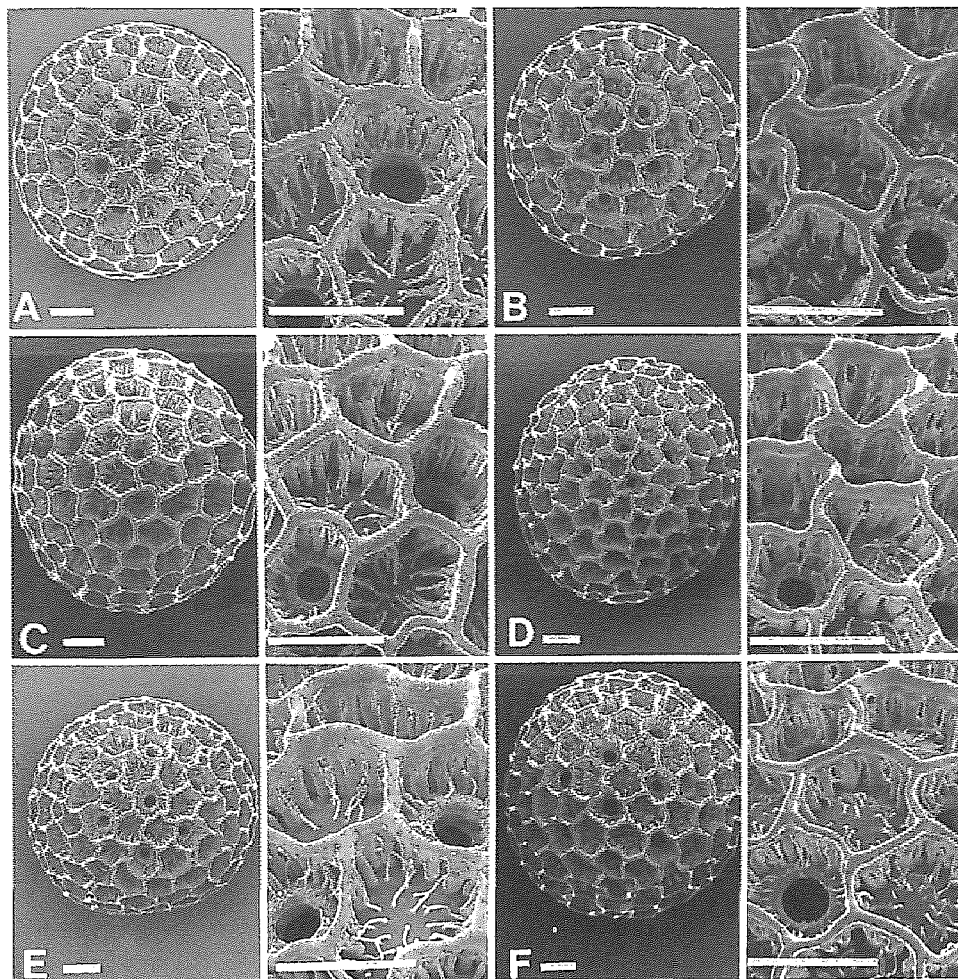
FIG. 11. SEM micrographs of the pollen of *Cobaea*. A. *C. aequatoriensis* (*Panero & Clark 2918*, TEX). B. *C. flava* (*Gentry & Díaz 58300*, MO). C. *C. campanulata* (*Panero & Clark 2998*, TEX). D. *C. lutea* (*Woytkowski 7330*, MO). E. *C. rotundiflora* (*Prather 960*, TEX). F. *C. triflora* (*Williams et al. 40363*, F). Scale: bar = 20 μm.

flower of the same plant), however, was placed on the receptive stigmas of third-day flowers, over 95% of the flowers developed fruits (Appendix 2). This suggests that pollen grains of these species have very short viability (<24 hr). A minimum of 50 flowers on at least two plants of each species were self-pollinated in this fashion. Thus it was determined that all the species of sect. *Cobaea* examined were self-compatible.

Two species of sect. *Rosenbergia*, *C. lutea* and *C. rotundiflora*, were also examined. These plants were self-compatible and self-pollinating (Appendix 2). Over 95% of unmanipulated flowers set fruit on three plants of *C. rotundiflora* and over 75% of unmanipulated flowers set fruit on 15 plants of *C. lutea*. Five flowers of both species were bagged and all of these flowers set fruit. These flowers were not protandrous; at least two anthers dehisced at the beginning of anthesis. At the same time stigmas were also presented.

Flowers in which pollen was placed on the stigmas at the beginning of anthesis produced seeds, demonstrating that the stigmas were receptive at this time.

These preliminary data suggest strongly that the five species studied are all self-compatible, contrary to the literature reports of self-incompatibility in *C. scandens*. The short viability of the pollen in *C. scandens* may have misled Behrens (1880) and Grant and Grant (1965). An interesting result of the short viability is that the three species of sect. *Cobaea* studied are not autogamous (i.e., do not undergo intraflower pollination) even though anther and stigma placement are very close, and pollen may be transferred within an individual flower. The species of sect. *Cobaea* studied require a pollen vector but geitonogamy (interflower pollination on an individual plant) is not prohibited.

TAXONOMIC CATEGORIES

Major morphological discontinuities in conjunction with distinct, or nearly distinct, geographical distributions are used to distinguish species herein. Morphological considerations are given primary importance. If, however, morphological differences are unaccompanied by geographical separation, the differences are viewed more critically in an effort to eliminate errors due to intraspecific variation. There are no populations or series of populations to which the category of variety or subspecies could be usefully applied; therefore, these categories are not used here.

Species may intergrade at their common boundary, but the amount of intergradation should be minimal and the number of individuals and populations affected few. If intergradation occurs gradually over a sizable portion of the range then the two taxa would be considered varieties of one species. *Cobaea lutea* is a highly variable species, and the variants have been formally recognized by previous workers. The morphological differences are minor, however, if compared to morphological differences between most sets of species, and recognizing the variants would require a cumbersome and potentially useless taxonomy.

PHYLOGENY AND CLASSIFICATION

Prior to the recent publication of the phylogeny of Prather and Jansen (1998) there was little discussion of relationships among the species of *Cobaea*. A few authors mentioned morphologically similar species in protologues and speculated on relationships between the taxa under consideration, most notably Standley (1914), Asplund (1954), and Prather (1996), but there were no comprehensive discussions available.

TRADITIONAL CLASSIFICATION

The most recent classification is the synopsis presented in Grant (1959), which was based on that of Brand (1907). Prather (1996) described three new species and placed each of them in sect. *Cobaea*. Grant's (1959) classification is presented in Fig. 12, with the additions of Prather (1996). Four of the species included in Grant (1959) are reduced to synonymy here, *C. lasseri* and *C. viorna* from sect. *Cobaea*, and *C. hookeriana* and *C. panamensis* from sect. *Rosenbergia*.

The sectional classification of Brand (1907) and Grant (1959) was based on three characters: inflorescence position (erect vs. pendent), corolla lobe shape, and stamen

position. Following Grant (1959), sect. *Cobaea* was defined by erect inflorescences, ovate or orbicular corolla lobes lacking caudate tips (scandens type), and stamens equal to or longer than the corolla lobes. Section *Rosenbergia* was defined by pendent inflorescences, linear corolla lobes with caudate tips (gracilis type), and stamens usually longer than the corolla lobes. Finally, sect. *Aschersoniophila* was defined by pendent inflorescences, corolla lobes with ovate bases and long narrow tips (aschersoniana type), and stamens about as long as the corolla lobes. Because corolla lobes of the aschersoniana type have the wide base of the scandens type and the elongate tips of the gracilis type, *C. aschersoniana* has been described as "intermediate" (House 1908; Standley 1914) between sect. *Cobaea* and sect. *Rosenbergia*.

Problems arise when trying to classify species, because inflorescence position, corolla shape, and stamen length cannot be used reliably to distinguish sections. Each character has been either misreported in the literature or is too variable to be reliable (Prather & Jansen 1998, and species descriptions presented here). Inflorescence position of many taxa has been misreported, and all of the species reported to have pendulous inflorescences in the literature actually have erect inflorescences, including *C. penduliflora*. Furthermore, *C. minor*, which has been inferred to have erect inflorescences, is the only species of *Cobaea* that has pendulous inflorescences.

Corolla lobe shape corresponds more closely to the traditional classification than either of the other characters. Corolla lobe shape has been treated as a qualitative character, and in all but one species that treatment is probably justified. In *C. lutea*, however, populations of individuals with either scandens type or aschersoniana type corolla lobes exist, and the lobes of some populations are intermediate between the two types. This variation underscores the underlying quantitative nature of the character. The corolla lobe forms observed in *C. lutea* span the variation observed in both sect. *Cobaea*, where it has been traditionally placed, and in sect. *Aschersoniophila*.

None of the character states of corolla shape can be used to circumscribe a monophyletic group (Prather & Jansen 1998). Furthermore, the two derived character states, aschersoniana and gracilis type corollas, each arose twice (Prather & Jansen 1998), presumably because corolla shape is an evolutionarily labile character. Because the extremes of the types are so different it is hard to imagine that such homoplasy occurs; however, homoplasy through reversal, parallelism, or ancestral polymorphism and lineage sorting seems more plausible when considering that the corolla lobes of *C. aschersoniana* are intermediate between the other two types, and that the corolla lobes of *C. lutea* are polymorphic for two types.

Stamen length is of little use in classification, because it has been applied in a rather vague way and, more generally, because it is quantitative and variable in nature. Following Grant (1959), sect. *Cobaea* included species with "stamens equaling or longer than the corolla lobes," sect. *Rosenbergia* included those species with "stamens usually longer, sometimes shorter than corolla lobes," and the species of sect. *Aschersoniophila* were said to have "stamens about equaling corolla lobes." The ambiguity in application of this character was probably due to the paucity of specimens available for examination. The stamens of most species are about as long as the corollas, but because there is so much infraspecific variation the character lacks any value in sectional classification.

The inconsistencies cited above, together with a better understanding of morphological variation, suggest that the traditional classification might be improved upon. Furthermore, the molecular phylogeny (Prather & Jansen 1998) and several morphological
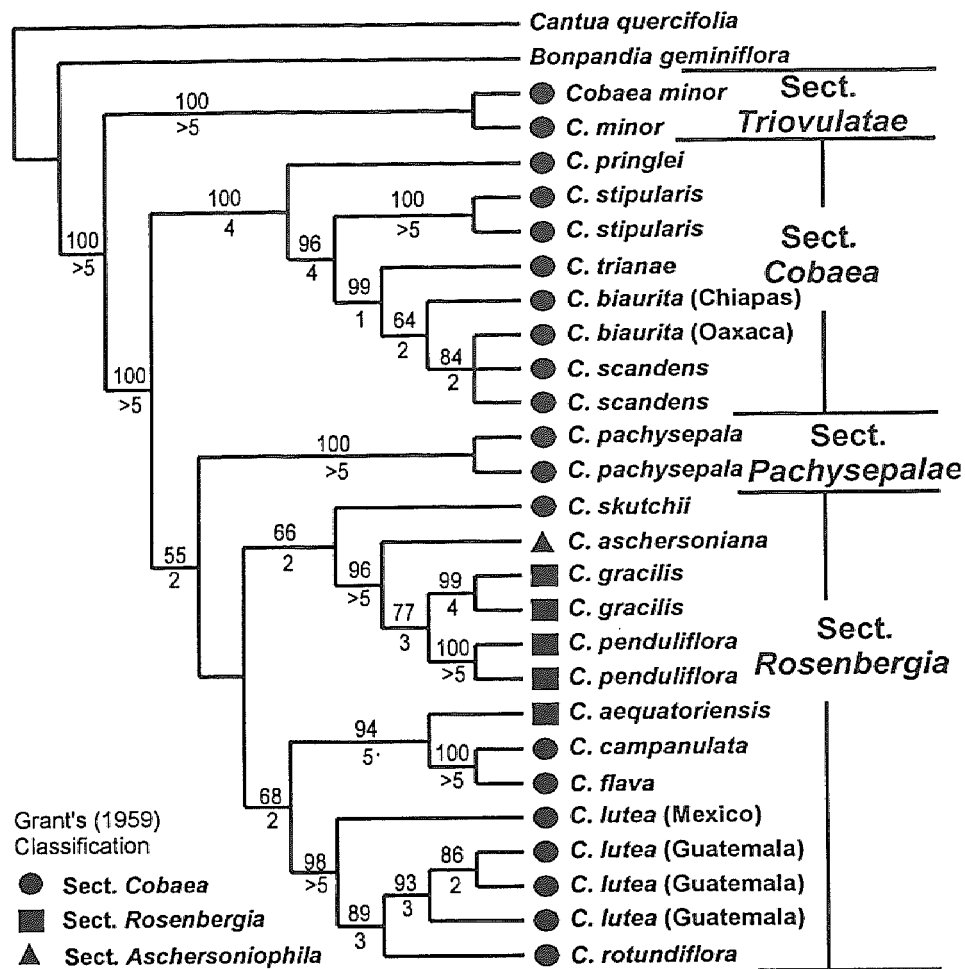
FIG. 12. Strict consensus of the six most-parsimonious trees (length = 558 steps; CI, excluding uninformative characters = 0.688; RI = 0.875) generated from parsimony analyses. Numbers above branches are bootstrap values; numbers below are decay values. The revised sectional classification is shown on the far right. Four samples that had identical sequences to conspecific samples are omitted from the figure. Details are presented in Prather and Jansen (1998).

characters, such as pollen (Prather 1994) and stigma morphology (Prather 1995, 1996), suggest that the traditional sections are not monophyletic. My goal is to evaluate the ITS phylogeny in the context of morphological and palynological characters, and to propose a new classification based on all the available evidence. Many of these characters were first discussed in earlier works such as Standley (1914) and Grant (1959), and these works provided the foundation for my studies. Additionally, I discuss here some newly explored characters. My objective is that the emended sections established below are both monophyletic and taxonomically useful units.

Molecular Phylogeny

A phylogeny of *Cobaea* based on sequences of the ITS1 and ITS2 regions of nuclear ribosomal DNA of 16 of the 18 species of *Cobaea* was presented by Prather and Jansen (1998). *Cobaea paneroi* and *C. triflora* were not included because of a lack of suitable plant material; their placement is discussed below. *Cantua* and *Bonplandia* were chosen for use as outgroups based on phylogenetic analyses of DNA sequences of *ndhF* (Prather et al. 1996; Prather, Ferguson & Jansen, unpubl.), *matK* (Steele & Vilgalys 1994; Johnson et al. 1996), and ITS (Baldwin et al. 1995; Porter 1997). Six most-parsimonious trees (length = 558 steps, CI excluding uninformative characters = 0.688, RI = 0.875) were produced. Support for most branches, evaluated by bootstrap and decay analyses, was quite strong. Insertion/deletion events provide further support for some clades. There are two unresolved nodes in the strict consensus tree (Fig. 12), and one of the unresolved nodes is among samples of one species. The discussion below is based on the report of Prather and Jansen (1998).

With only two exceptions conspecific samples formed monophyletic groupings, and in most cases the sequences were identical or nearly so. Samples of *C. biaurita* were paraphyletic to the two samples of *C. scandens*, and those of *C. lutea* were paraphyletic to the single sample of *C. rotundiflora*. Interestingly, these two species occur in two different biogeographic regions, and the sample(s) from one region appeared as sister group to a different species from that same region, rather than appearing as sister group to the conspecific sample from a different region (Fig. 12). Both instances apparently center on the Isthmus of Tehuantepec. Several hypotheses might account for these results, such as ancestral polymorphism and lineage sorting, hybridization and introgression, speciation without morphological differentiation, or paraphyly of one species to another. Unfortunately we are unable to distinguish among these hypotheses given the data at hand.

Based on the ITS phylogeny the only traditional section of *Cobaea* that is monophyletic is the monotypic sect. *Aschersoniophila*, which is monophyletic by definition. Section *Cobaea* is paraphyletic to sect. *Rosenbergia* and sect. *Aschersoniophila*, while sect. *Rosenbergia* is polyphyletic (Fig. 12).

Revised Sectional Classification

Section *Triovulatae*: *Cobaea minor* is sister group to the rest of the genus based on the ITS phylogeny, and this relationship is strongly supported by both the bootstrap (100%) and decay (>5) analyses. *Cobaea minor* is perhaps the most distinctive taxon in the genus, and the large number of unique characters (see below) justifies segregating *C. minor* from the remainder of sect. *Cobaea*, where it was formerly placed, to the newly erected, monotypic sect. *Triovulatae*.

Cobaea minor is the only species with pendulous inflorescences, a single inflorescence bract, pedicels less than 4.5 cm long, and uniovulate locules. All other species have erect inflorescences, two or more inflorescence bracts, pedicels longer than 8.0 cm, and multiovulate locules. Furthermore, *C. minor* is the only species with scandens type corollas to have lobes that are longer than the tube.

The pollen of *C. minor* is unique in the genus in having raised muri junctions where the walls of the lumina meet (Fig. 9A), although the muri of *C. paneroi* (Fig. 10A) approach those of *C. minor* in this regard. Furthermore, the grains are furnished with microbacula, which have capitate apices larger than those of any other species. The short microbacula are similar in length only to those of *C. flava* and *C. triflora*. The last two

species are herein placed in sect. *Rosenbergia* (see below); the remainder of the species in that section have long microbacula. The species of sections *Cobaea* and *Pachysepalae* have granular microbacula or lack microbacula altogether.

Because I am considering both morphology and phylogeny in my revised sectional classification, it is interesting to identify synapomorphic or autapomorphic character states for several key clades or monotypic sections. Pendent inflorescences, a character state not otherwise found among the species of *Cobaea* nor the outgroup taxa, is the only clearly autapomorphic character state for *C. minor*. The raised muri junctions might also be autapomorphic, but because the pollen of the outgroups lacks muri altogether, this character cannot be polarized and the derived state cannot be established. Two or more inflorescence bracts and pedicels longer than 8.0 cm are synapomorphic character states for all of the species of *Cobaea*, except *C. minor*.

Section *Cobaea*: Another well-supported clade (100% bootstrap and decay value of 4) includes *C. pringlei, C. stipularis, C. biaurita, C. trianae,* and *C. scandens*. The last is the type of the genus. These species are morphologically very similar and in some cases are difficult to distinguish. *Cobaea pachysepala* is also very similar to these species, but is not placed in the same clade in the ITS phylogeny and differs in a few morphological and palynological characters (see below). The five taxa cited plus *C. paneroi* are here treated as the emended sect. *Cobaea*. *Cobaea paneroi*, which was not sampled in the molecular analysis, is included because its erect inflorescences, chartaceous calyx segments, rounded corolla lobes, type I stigmas, filaments that are villous only at the base, and its pollen morphology all indicate that it is best placed here.

This section is difficult to define by any single character though the species do share a unique combination of floral characters. The species of sect. *Cobaea* have chartaceous calyx segments, whereas the calyx segments of the species in sect. *Triovulatae* are membranous and those of the species in sect. *Pachysepalae* are coriaceous. The calyx segments of the species of sect. *Rosenbergia* are either membranous or chartaceous, but the species of sect. *Cobaea* can be distinguished from all the species of sect. *Rosenbergia* by their stigmas; species in sect. *Cobaea* have type I stigmas but species in sect. *Rosenbergia* have type II stigmas (Fig. 7). The inflorescences of the species of sect. *Cobaea* are erect, which also distinguishes them from the species of sect. *Triovulatae*. The species of sect. *Cobaea* can be further distinguished from the species of sect. *Pachysepalae* by their filaments (see below).

The species of sect. *Cobaea* have small pollen grains (mean diameter <130 μm; except *C. biaurita*, mean = 152 μm), like those of the species of sect. *Triovulatae*; all other species of *Cobaea* have pollen grains that are at least 130 μm in diameter. The unique microbacula (Erdtman 1952) are reduced or absent in the species of sect. *Cobaea* and the species of sect. *Pachysepalae*, whereas they are well developed in all remaining species. Finally, the ratio of aporate to porate lumina diameter is 1.2 or greater in all species of sect. *Cobaea*, whereas it is 1.1 or less in all other species of *Cobaea*, except in *C. triflora* (1.3).

From a phylogenetic perspective it is difficult to establish any synapomorphy for sect. *Cobaea*. All of the character states that are used to define the section occur in species outside of the section, thus the section is only identifiable by a combination of character states, except one character state, inrolled corolla lobe margins. The corolla lobes of the species assigned to sect. *Cobaea* all have slightly inrolled margins. This character cannot be observed on pressed specimens and must be carefully observed even on living

material. The ratio of aporate to porate lumina diameter of 1.2 or greater is apparently independently derived in *C. triflora* (sect. *Rosenbergia*) but otherwise is unique to sect. *Cobaea*.

Section *Pachysepalae*: *Cobaea pachysepala* is the sister group to the remaining nine species of *Cobaea*. This placement was not strongly supported (55% bootstrap, decay value of 2), although further support was provided by a 1 base pair deletion shared by those nine species and *C. pachysepala* (Prather & Jansen 1998). On the other hand, *C. pachysepala* has many characters in common with the members of sect. *Cobaea*. If *C. pachysepala* were included in sect. *Rosenbergia* there would be no morphological characters that could be considered synapomorphic for the broader group. If *C. pachysepala* were included in sect. *Cobaea* with morphologically similar species, then the molecular evidence would suggest, albeit weakly, that sect. *Cobaea* would not be monophyletic. A solution then, is to create a second monotypic section, sect. *Pachysepalae* to accommodate *C. pachysepala*.

This arrangement can be justified because *C. pachysepala* has several unique features. As the epithet suggests the calyx segments of *C. pachysepala* are coriaceous, whereas those of all other species are chartaceous or membranous. Furthermore, the calyx segments are furnished with a dense band of puberulence (0.5–2.0 mm wide) on the adaxial surface near the margin. Some other species have pubescence on the adaxial surface of the calyx segments but never in such a dense, well-defined zone and not usually so close to the margin. Finally, the filaments of *C. pachysepala* are villous at the base and about 1–2 cm below the apex, while those of all other species are pubescent at the base only.

The pollen of *C. pachysepala* has no unique features, instead sharing some character states with members of sect. *Cobaea* and other states with species of sect. *Rosenbergia*. Like the species of sect. *Cobaea*, its microbacula are reduced to small granular structures, whereas in the species of the other sections the microbacula are filamentous. The pollen is similar to that of species of sect. *Rosenbergia* (Table 1) in both grain diameter and the aporate to porate lumen ratio.

The filament pubescence and calyx characters mentioned above are autapomorphies for sect. *Pachysepalae*. Acute or acuminate corolla lobe apices could be considered synapomorphic for sect. *Pachysepalae* plus sect. *Rosenbergia* (as defined below), except that this character state has apparently reversed in *C. flava*, *C. campanulata*, and probably *C. triflora*. The large pollen grain diameter could also be considered synapomorphic for sect. *Pachysepalae* and sect. *Rosenbergia* together, except that this character state has apparently been independently derived in *C. biaurita*. The only unambiguous synapomorphy then is the one base pair deletion in the ITS sequence at position 95 (Prather & Jansen 1998). A molecular synapomorphy, while providing support to the classification, is unfortunately of no use in field identification or keys.

Section *Rosenbergia*: Nine species, including all of the species previously placed in sect. *Aschersoniophila* (*C. aschersoniana*) and sect. *Rosenbergia* (*C. aequatoriensis*, *C. gracilis*, and *C. penduliflora*), plus five previously placed in sect. *Cobaea* (*C. campanulata*, *C. flava*, *C. lutea*, *C. rotundiflora*, and *C. skutchii*), form a strongly supported clade (100% bootstrap and decay value of >5). These taxa share unique morphological and palynological characteristics. Because of the morphological differences mentioned below and their congruence with the ITS phylogeny, these taxa are all included in the emended sect. *Rosenbergia*. This circumscription is much broader than in earlier treatments. The

emended circumscription is adopted, because the species that are traditionally included in sect. *Rosenbergia* do not form a monophyletic clade (Fig. 12), and because there is strong support for the monophyly of the broadened section.

These taxa all have corolla lobes that are wrinkled in bud, and in the species with gracilis or aschersoniana type corollas the lobes are typically wrinkled throughout flowering. All other species of *Cobaea* have corolla lobes that are concave, but not wrinkled, in bud. This character, however, is not often apparent, especially on herbarium specimens, which often lack flower buds. A more striking feature that can be used to distinguish the species of this section are the type II stigmas (discussed above, Fig. 7). The outgroups and the remainder of *Cobaea* species have type I stigmas.

The pollen of these species have filamentous microbacula without expanded capitate apices, which distinguishes the pollen of the species of sect. *Rosenbergia* from all other species of *Cobaea*. The apices of the microbacula of the species of sect. *Triovulatae* are capitate, and the microbacula of the species of sect. *Cobaea* and sect. *Pachysepalae* are granular or absent. Furthermore, the microbacula of the species of sect. *Rosenbergia* (except in *C. triflora* and *C. flava*) are long, but those of the species of sect. *Triovulatae* are short.

Type II stigmas and corolla lobes that are wrinkled in bud are synapomorphic for the species of sect. *Rosenbergia*. The long microbacula might also be considered synapomorphic with a reversal for *C. flava* and possibly for *C. triflora*.

Cobaea triflora was not included in the molecular analysis but can be placed in the emended sect. *Rosenbergia* with some confidence, because it has type II stigmas and corolla lobes that are wrinkled in bud. In most pollen characteristics it is similar to other species of sect. *Rosenbergia*, but the microbacula are somewhat short, similar to those of *C. minor*. The pollen of the latter species, however, has capitate microbacula whereas that of *C. triflora* lacks the capitula. The ratio of aporate to porate lumen size is similar to that of the species of sect. *Cobaea* (Table 1). Regardless of pollen that is in some ways atypical of the section, I conclude from the type II stigmas, corolla lobes that are wrinkled in bud, and pollen size, that *C. triflora* is best placed in sect. *Rosenbergia*.

BIOGEOGRAPHY AND SPECIATION

Cobaea occurs mainly in mid- to high-elevation habitats in Mexico, Central America, and northwestern South America. Grant (1959) partitioned the generic distributions of the Polemoniaceae into 17 regions within which many species reached their limits of distribution. He noted that *Cobaea* is distributed over three of these regions: The Andes (3 species), the Mexican Highland (3 species), and Central America and Venezuela (13 species). I present here a biogeographic hypothesis of *Cobaea*, and have delimited four biogeographic areas that are more narrowly defined than Grant's regions, but based on the same criteria. Each of these regions is separated from the others by a low-lying area from which *Cobaea* is absent. This delimitation appears to be more useful than Grant's for purposes of discussion of biogeographic patterns within *Cobaea*.

I define the Mexican Highland in the same way as Grant, the region from the Isthmus of Tehuantepec to the northern limits of the Sierra Madre. Seven species occur there (*C. biaurita*, *C. lutea*, *C. minor*, *C. paneroi*, *C. pringlei*, *C. stipularis*, and *C. scandens*). Three of these have disjunct populations outside of this region: *C. biaurita* in Chiapas, *C. lutea* in northern Central America and South America, and *C. minor* in southern Central America.

I have divided Grant's "Central America and Venezuela" region into two areas: Northern Central America (El Salvador, Guatemala, Honduras, and the Mexican state of Chiapas), and southern Central America (Costa Rica and Panama). I include Venezuela in my South American region. Northern Central America contains four species that are endemic to that region: *C. pachysepala, C. rotundiflora, C. skutchii,* and *C. triflora,* as well as disjunct populations of *C. biaurita* and *C. lutea.* There are three species in southern Central America: two endemic to that region (*C. aschersoniana* and *C. gracilis*) and disjunct populations of *C. minor.*

The remaining region that Grant proposed and discussed is the "Andes." I refer to this area simply as South America, because only *C. trianae* is truly Andean; the other species occur in low- to mid-elevational areas. In South America, however, *Cobaea* is found only in the northern and northwestern areas. There are six species that occur there, five endemics (*C. aequatoriensis, C. campanulata, C. flava, C. penduliflora,* and *C. trianae*) and disjunct populations of *C. lutea.*

I hypothesize that long-distance dispersal and subsequent differentiation of isolated populations has been an important speciation mechanism in *Cobaea.* This seems reasonable, because most species of *Cobaea* occur in montane cloud forests at relatively high elevations, and it is highly unlikely that this habitat was ever continuous between North and South America. Even in glacial times the low-lying areas that separate the regions delimited here probably did not provide the types of habitat suitable for *Cobaea* or other montane plant species (Simpson & Neff 1985).

For one group of species, *C. aequatoriensis, C. campanulata, C. flava, C. lutea, C. rotundiflora,* and *C. triflora,* allopatric speciation via geographical partitioning may be as likely as long-distance dispersal and subsequent differentiation. These species of sect. *Rosenbergia* occur at lower elevations than do most other species. They are found in Pacific mountain ranges in three of the four biogeographic regions (the Mexican Highlands, northern Central America, and South America), and one of the species occurs in all three of these regions (*C. lutea*). These facts suggest that allopatric speciation may account for the distribution pattern observed within this group of taxa.

Allopatric speciation may have also played an important role in speciation events within the biogeographic regions as well. For example, sect. *Cobaea* occurs mainly in the Mexican Highland. Its taxa are very similar morphologically and many are poorly differentiated from one another molecularly (Prather 1995). One hypothesis that could account for this pattern is that these species are of relatively recent origin, perhaps dating from the Pleistocene. The common ancestor of these species might have been widespread at lower elevations during glacial periods, and during the subsequent interglacial warming the populations may have become subdivided as they migrated to higher elevations. Speciation might then have occurred following geographic isolation. This could account for all of the speciation events within the section, except for the event that led to *C. trianae* in South America.

The biogeographic regions have been mapped onto the phylogeny and the biogeographic history of the genus was reconstructed. Parsimony was used as the criterion for mapping the biogeographic regions on the internal nodes and branches of the ITS tree (Fig. 13). If dispersal is in fact responsible for the spread of the species from one biogeographic region to another, then the scenario presented here represents the minimal number of migratory events in the history of *Cobaea.*

According to this phylogenetic hypothesis, *Cobaea* probably originated in the Mexican Highlands. Interestingly, Grant (1959) suggested that the family Polemoniaceae

probably had its origins in the same area. He based his conclusions on the geological, climatological, and vegetational history of the New World, as well as his interpretation of the evolutionary history of the family.

From its origin in Mexico, *Cobaea* appears to have undergone four migrations (Fig. 13). Two of these represent disjunctions of extant taxa: *C. minor* to southern Central America and *C. biaurita* to northern Central America. The ancestor of *C. trianae* migrated a considerable distance to western South America. Finally, the data suggest that the ancestor of sect. *Pachysepalae* and sect. *Rosenbergia* migrated to northern Central America.

From its origin in northern Central America, members of sect. *Rosenbergia* have apparently migrated three times (Fig. 13). Disjunct populations of *C. lutea* represent a migratory event to the Mexican Highlands. The common ancestor of *C. aequatoriensis*, *C. campanulata*, and *C. flava* migrated to South America. The third migration from northern Central America occurred to southern Central America, representing the common ancestor of *C. aschersoniana*, *C. gracilis*, and *C. penduliflora*. Finally, the migration of the ancestor of *C. penduliflora* to South America represents the only migration from southern Central America.

Nearly all of these migratory events occurred between adjacent areas, as logic would suggest. There are three exceptions: The migration of the disjunct populations of *C. minor* from the Mexican Highlands to southern Central America; and two migrations to South America, one from the Mexican Highlands (the ancestor of *C. trianae*) and the other from northern Central America (the common ancestor of *C. aequatoriensis*, *C. campanulata*, and *C. flava*).

TAXONOMY

Cobaea Cavanilles, Icon. 1: 11. 1791.—TYPE: *Cobaea scandens* Cavanilles.

    Rosenbergia Oersted, Vidensk. Meddel. Dansk. Naturhist. Foren. Kjøbenhavn 1856: 30. 1856.—Type: *Rosenbergia gracilis* Oersted [=*Cobaea gracilis* (Oersted) Hemsley].

Vines, stems woody or herbaceous, to 25 m long. Leaves alternate, pinnately compound, the terminal leaflet modified into a branched tendril, each branch terminated with two claws; leaflets 4–8, usually 6, broad, short-petioluled, opposite or subopposite, membranous to chartaceous, glabrous or variously pubescent, mucronate, abaxial surface often glaucous, either equilateral or inequilateral. Inflorescence a dichasial cyme of 1–5 flowers, subtended by a pair of subopposite foliaceous bracts, or rarely a single bract, that are sometimes reduced or abscised at maturity. Calyx segments 5, essentially free, mucronate, usually green, persistent, sometimes ciliate, glabrous or variously pubescent abaxially, usually with a band of tomentulose trichomes near the margin adaxially. Corolla green, yellow, white, or purple, sometimes greenish at the beginning of anthesis and turning pink or purple with age, often suffused with pink, purple, or red, rarely striped, actinomorphic, glabrous or variously pubescent externally, villous internally near stamen insertion; tube usually campanulate, constricted near the base forming a receptacle for nectar, lobes 5, depressed-ovate to linear, nearly always reflexed. Stamens 5, inserted near the base of the tube; filaments villous at insertion and rarely near the apex; anthers usually exserted, dorsifixed, often sagittate. Ovary superior, inserted on a large five-lobed nectary disk, tricarpellate, trilocular, ovate, glabrous but
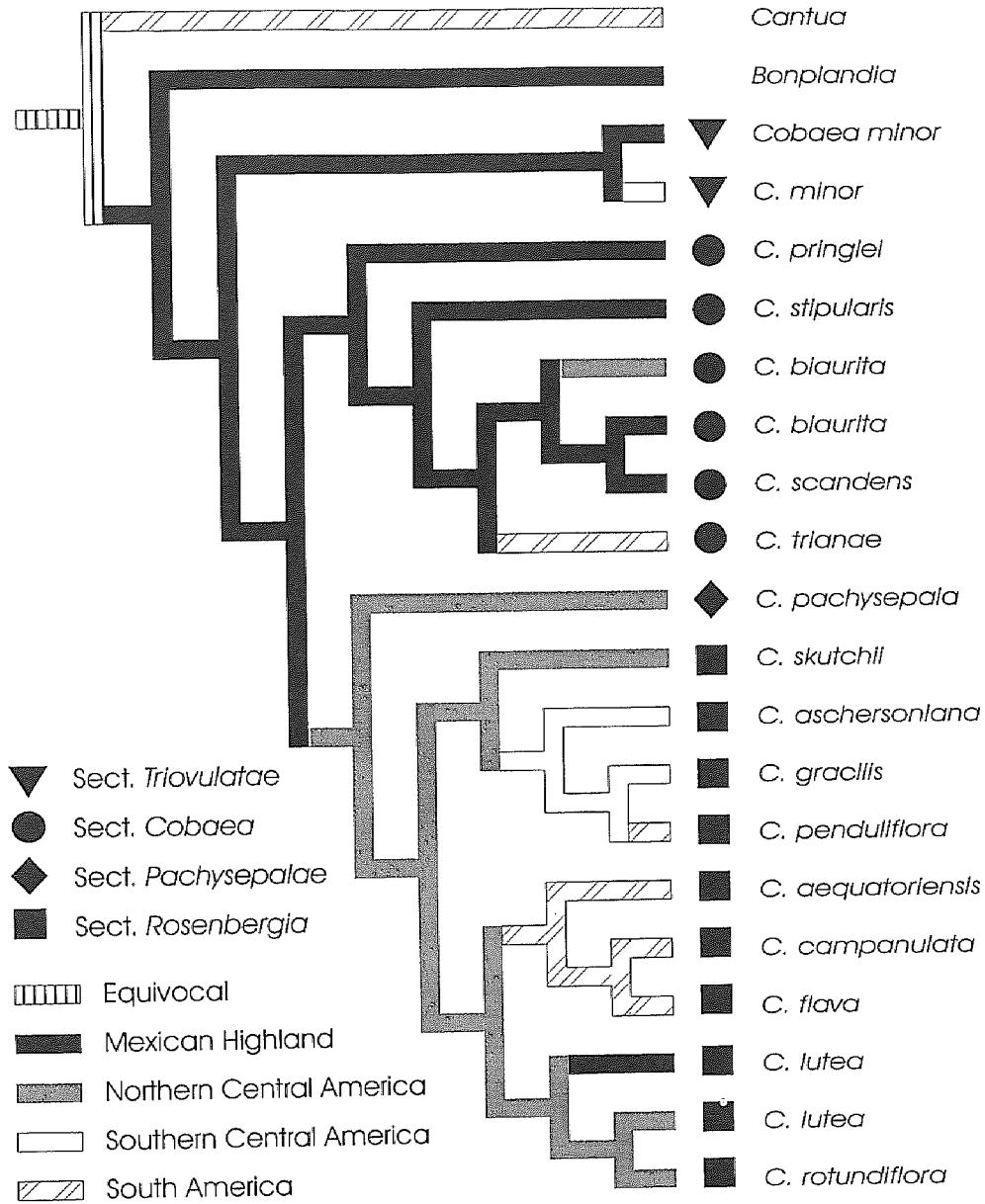
FIG. 13. Simplified phylogeny based on the ITS analysis showing the hypothesized biogeographic history of *Cobaea*. Duplicate samples of taxa are not shown.

often minutely puncticulate, septa thickened and fused into a central column which is triangular in cross section; style slender, glabrous, exserted from the tube, style branches 3, flattened, reflexed, never twisted, with rounded apices, stigma of long papillae covering only the adaxial surface (type I stigmas), or style branches terete,

spreading in an irregular fashion but not reflexed, usually twisted, with acute apices, stigma of short papillae covering nearly the entire surface (type II stigmas). Capsule usually exceeding the calyx, septicidal, elliptic to narrowly elliptic, each locule single- to several-seeded; seeds 1–45, flat, ovate to broadly ovate, usually broadly winged. Base chromosome number: $x = 26$?

KEY TO THE SECTIONS AND SPECIES OF COBAEA

1. Style branches flattened, reflexed, not twisted, their apices rounded, papillae long, on adaxial surface only (type I stigmas; Fig. 7A, B).
    2. Inflorescence pendulous, with a single bract that is often rudimentary; corolla tubes 15–23 mm long; locules with a single ovule.   *Cobaea* sect. *Triovulatae*; 1. *C. minor.*
    2. Inflorescence erect, with at least two bracts that are sometimes rudimentary; corolla tubes 29–65 mm long; locules with two or more ovules in each.
        3. Filaments villous about 1–2 cm below the apex and at the base; calyx coriaceous; corolla lobes sharply acute to acuminate.   *Cobaea* sect. *Pachysepalae*; 8. *C. pachysepala.*
        3. Filaments glabrous except at the base; calyx chartaceous; corolla lobes rounded or broadly acute.   *Cobaea* sect. *Cobaea.*
            4. Leaves green, not suffused with purple; corolla usually white at anthesis, rarely suffused with purple, narrowly campanulate.   2. *C. pringlei.*
            4. Leaves purple or suffused with purple, especially below; corolla greenish white, greenish yellow, or purple, not purely white, nearly always suffused with pink or purple, broadly campanulate.
                5. Leaves purple, lowermost leaflet pair reduced in length to less than half that of the upper pairs, resembling a stipule; seeds without scale-like trichomes.   3. *C. stipularis.*
                5. Leaves green, suffused with purple, lowermost leaflet pair equal to or only slightly shorter than the upper pairs; seeds with scale-like trichomes.
                    6. Apices of calyx lobes rounded to emarginate or rarely broadly acute; calyx (16–) 19–32 mm wide, circular to very broadly ovate in outline.   6. *C. scandens.*
                    6. Apices of calyx lobes attenuate to acute to long-acuminate; calyx 7–18 mm wide, lanceolate to deltate to ovate in outline.
                        7. Lobes of calyx acuminate; style 40–45 mm long; filaments adnate basally for 3–5 mm.   7. *C. paneroi.*
                        7. Lobes of calyx attenuate to acute; style 47–80 mm long; filaments adnate basally for (3–) 5–10 mm.
                            8. Base of lowermost leaflet pair cordate to truncate; style branches 2–3 mm long; seeds 22–28 mm long; Andes.   4. *C. trianae.*
                            8. Base of lowermost leaflet pair unequally auriculate; style branches 3–6 mm long; seeds 16–22 mm long; Mexico.   5. *C. biaurita.*
1. Style branches terete, spreading in an irregular fashion but not simply reflexed, usually twisted, their apices acute, papillae short, covering nearly the entire surface (type II stigmas; Fig. 7C, D).
                                                                        Cobaea sect. *Rosenbergia.*
    9. Corolla lobes imbricate (but sometimes only slightly so), less than twice as long as the tube.
        10. Corolla lobes ovate, broadly ovate, or deltate, apex rounded to acute; stamens 55 mm long or less.
            11. Calyx margin undulate; filaments emergent.   9. *C. skutchii.*
            11. Calyx margin flat; filaments positioned ventrally.
                12. Calyx segments 8–12 mm wide; corolla lobes deltate, their apices acute.   17. *C. rotundiflora.*
                12. Calyx segments 4–7 mm wide; corolla lobes ovate or broadly ovate, their apices rounded.
                    13. Pedicels 10.5–16.0 cm long, filaments adnate basally for 8–14 mm.   14. *C. flava.*
                    13. Pedicels 19–28 cm long, filaments adnate basally for 3–7 mm.
                        14. Stems glabrous; corolla lobes 11–19 mm long; Ecuador.   15. *C. campanulata.*
                        14. Stems puberulent, at least at the nodes; corolla lobes 8–11 mm long; Guatemala.
                                                                        18. *C. triflora.*

10. Corolla lobes basally broad but narrowing to an acuminate or linear apex; stamens, at least
    some of them, 58 mm long, or longer.
    15. Stems, pedicels, and calyx villous; corolla lobes (27–) 38–59 mm long.   10. *C. aschersoniana.*
    15. Stems, pedicels, and calyx glabrous to puberulent, never villous, though the calyx some-
    times long-ciliate; corolla lobes 13–30 mm long.   16. *C. lutea.*
9. Corolla lobes never imbricate, more than twice as long as the tube.
    16. Pedicel villous; calyx densely long-ciliate.   13. *C. aequatoriensis.*
    16. Pedicel glabrous to puberulent; but never villous; calyx glabrous or sparsely ciliate.
        17. Lowermost leaflet pair not ciliate basally; anthers 8–11 mm long; Central America.
            11. *C. gracilis.*
        17. Lowermost leaflet pair ciliate basally; anthers 11–15 mm long; South America.
            12. *C. penduliflora.*

Cobaea section **Triovulatae** Prather, sect. nov.—TYPE: *Cobaea minor* M. Martens &
    Galeotti.

Inflorescentia pendens, pedicelli 1.5–4.5 cm longi. Lobi corollae perlate ovati vel cir-
culares tubum superantes. Ovarium ovulo singulari in quoque loculo.

Inflorescence pendent, with only a single bract; pedicels 1.5–4.5 cm long. Calyx seg-
ments membranous, puberulent or nearly glabrous near the margin adaxially, zone of pu-
berulence broader than 2.0 mm. Corolla lobes very broadly ovate to circular, longer than
the tube, apices rounded to broadly emarginate. Filaments pubescent only at the base.
Style branches flattened, reflexed, not twisted, with rounded apices; papillae long, cover-
ing only the adaxial surface (type I stigmas). Ovary with one ovule per locule.

Cobaea sect. *Triovulatae* is monotypic, composed of only *C. minor*. *Cobaea minor*
has been placed in sect. *Cobaea* by all other workers, but that section, as defined here, is
not easily modified to include the species. *Cobaea minor* is sufficiently different from all
others to warrant its own section, and if *C. minor* is included in sect. *Cobaea*, then sect.
Cobaea becomes paraphyletic (Fig. 12).

The sectional name was chosen to emphasize that the three locules each contain a sin-
gle ovule, a condition unique to this section.

1. Cobaea minor M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 12(2): 276.
    1845. *Rosenbergia minor* (M. Martens & Galeotti) House, Muhlenbergia 4: 24.
    1908.—TYPE: MEXICO. Veracruz: Volcán Orizaba, 3000 m, Nov–Apr 1840, *Ga-
    leotti 1447* (lectotype, here designated: BR!; isolectotypes: BR-2! G! US! W!;
    photo of G specimen: F! MO! MICH! RSA!).

Stems slender, woody, glabrous or rarely pubescent. Leaves green, sometimes suf-
fused with purple, with 6 or 8 leaflets; rachis 26–60 mm long, pubescent along the chan-
nel or sometimes glabrous; petiolules 1.5–8.0 mm long, pubescent along the channel or
sometimes glabrous; blades 24–41 (–65) mm long, 9–18 mm wide, glabrous or rarely
sparsely pubescent, margins minutely ciliate; upper and middle leaflet pairs elliptic,
base acuminate to rounded, apex acute to acuminate; basal pair similar to upper pairs,
but the margins long-ciliate with a few trichomes basally. Inflorescence of 1 flower;
bract usually poorly developed, sometimes fully expanded or abscised at maturity, with
6–8 leaflets. Peduncles 0.7–3.9 cm long, glabrous or pubescent with long trichomes.
Pedicels 1.5–4.5 cm long, glabrous or pubescent with long trichomes, not coiled in fruit.
Calyx segments 18–29 mm long, 4–8 mm wide, green, sometimes suffused with purple,

membranous, ovate, apex acute to acuminate, margins plane, ciliate with minute trichomes and sometimes with occasional long trichomes near the base, puberulent near the margin, sometimes approaching glabrous adaxially, glabrous abaxially. Corollas white or whitish blue with purple nectar-guides in the tube, membranous, glabrous externally, glabrous except for the annulus of short trichomes internally; tube 15–23 mm long, 17–24 mm wide, shallowly campanulate, widest at the apex; lobes (14–) 20–22 mm long, usually longer than the tube, (14–) 17–22 mm wide, very broadly ovate to circular, apex rounded to broadly emarginate, not inrolled at the margin, imbricate, not wrinkled in bud. Filaments 31–42 mm long, adnate basally for 3–4 mm, positioned ventrally, bent basally, sharply curved at the apex, neither becoming undulate or coiling after dehiscence; anthers 2.0–3.5 mm long, 1.0–2.0 mm wide, yellow, elliptic, curved in bud, not twisted after dehiscence, introrse. Styles 34–41 mm long; style branches 1.0–2.0 mm long, flattened, papillae long, occurring on the adaxial surface only (type I stigmas). Fruit 12–18 mm long, emaculate. Seeds 1–3 per fruit, 9–11 mm long, 5–7 mm wide, lacking scales; wings ca. 1 mm wide. Chromosome number unknown. Figs. 9A, 14.

Phenology. Collected in flower and fruit sporadically throughout the year, but mainly from November to April.

Distribution (Fig. 15). Mexico (Veracruz), Costa Rica, and Panama; cloud forests and forested slopes of volcanoes; 2000–3000 m.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** VERACRUZ: Mpio. Acajete, Barranca Cuesta del Vaquero, zona del Alto Pixquiac, *Cházaro & Camarillo 3948* (WIS); Pic Orizaba, *Liebmann 6601* (BR, F, US); Orizaba, *Liebmann 6612* (A, G, MO-2, NY); Orizaba, *Müller 1674* (NY-2, W).

Costa Rica. ALAJUELA: Volcán de Poás, *Endrés s.n.* (W).—CARTAGO: Volcán Irazú, about 7–8 km beyond the entrance to the Parque Nacional and about 5 km beyond the turnoff to Hacienda Coliblanco, *Almeda & Nakai 3763* (CAS); Volcán Irazú and Volcán Turrialba, remnant montane forest patches along the road from Pacayas to Hacienda Central, *Barringer et al. 2228* (F); forêts du Turrialba, *Pittier 887* (BM, BR, US); forêts du Volcán de Turrialba, *Pittier 13075* (BM, F, G-2, GH, MICH, NY, US-3); region of La Esperanza, southern slope of Volcán de Irazú, *Standley 35362* (US); Coli Blanco de Pacayas, *Wercklé 16681* (G).—SAN JOSÉ: camino nuevo de La Estrella a Copey, *Valerio 1033* (BR, F). **Panama.** BOCAS DEL TORO: Upper Río Colubre, *Gómez 21941* (BM, MO).—CHIRIQUÍ: about 8 km W of Cerro Punta in the vicinity of Las Nubes, *Almeda & Nakai 3496* (CAS, MO); Alto Respinga and above, *D'Arcy 9945* (MO); Alto Respinga, above Cerro Punta, *D'Arcy 10708* (MO); just below last climb in Alto Respinga, *D'Arcy 12144* (MO); road between Paseo Respinga and Guadaloupe, *D'Arcy et al. 12875* (MO); N side of Cerro Pavón on Paseo Respinga, *D'Arcy et al. 12937* (MO); forest remnant of Las Cumbres, ca. 1 mi from road near Cerro Punta Dairy, *D'Arcy et al. 13159* (MO); above Cerro Punta, *Folsom et al. 2126* (MO); above Guadeloupe, on private land of Castro Raúl, *Folsom et al. 7125* (BM, MO); path above Cerro Punta to Boquete, *Hamilton & Stockwell 3342* (MO); 6 km E of Cerro Punta, Paso de Respinga area, *Hammel 1536* (BM, MO); E of Cerro Punta roadside W of Paso Respinga below ridgetop, *Hammel et al. 6656* (MO); above Guadeloupe at STRI cabin, *McPherson 9368* (BM, MO); 1 km below ridge on road from Cerro Punta to Alto Respinga, *Prather 1575* (TEX).

Cobaea minor is the sister taxon to the remainder of the genus and is morphologically different from all other species. It is easily distinguished by numerous characters, including its triovulate ovary, pendulous inflorescence with a single bract, and short pedicels.

There are three sheets of the type collection, *Galeotti 1447*, at BR, where the types of Martens and Galeotti are housed. All three sheets are annotated "C. minor nob." although it is unclear who made the annotations. On one sheet the flower is displayed so that the corolla tube and lobes as well as the stamens are evident. This sheet is chosen
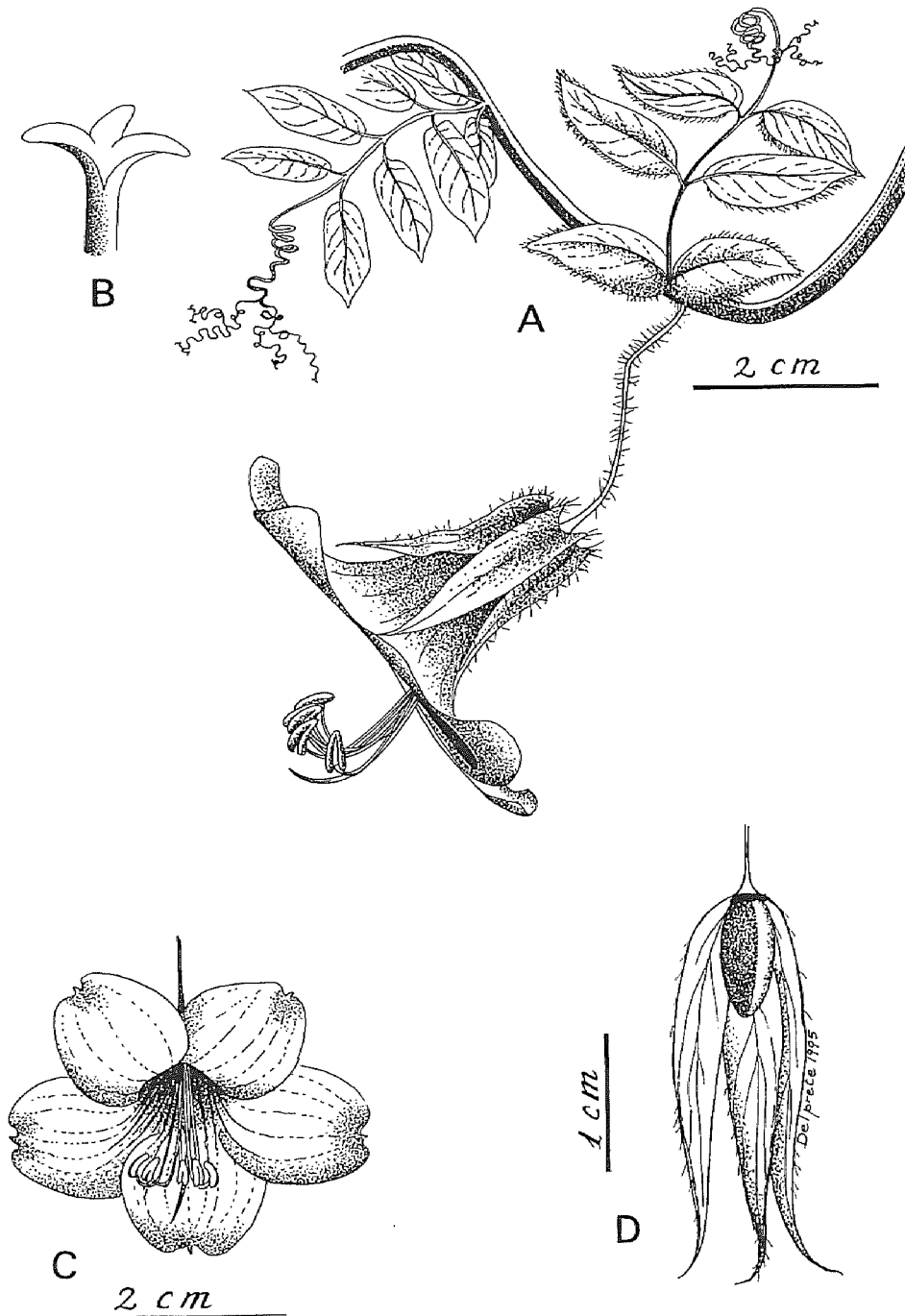
FIG. 14. *Cobaea minor*. A. Portion of habit and side view of flower. B. Upper portion of style and style branches. C. Front view of flower. D. Capsule and surrounding calyx (2 segments removed). (Drawn from field-taken photographs of *Prather 1575*, TEX.)
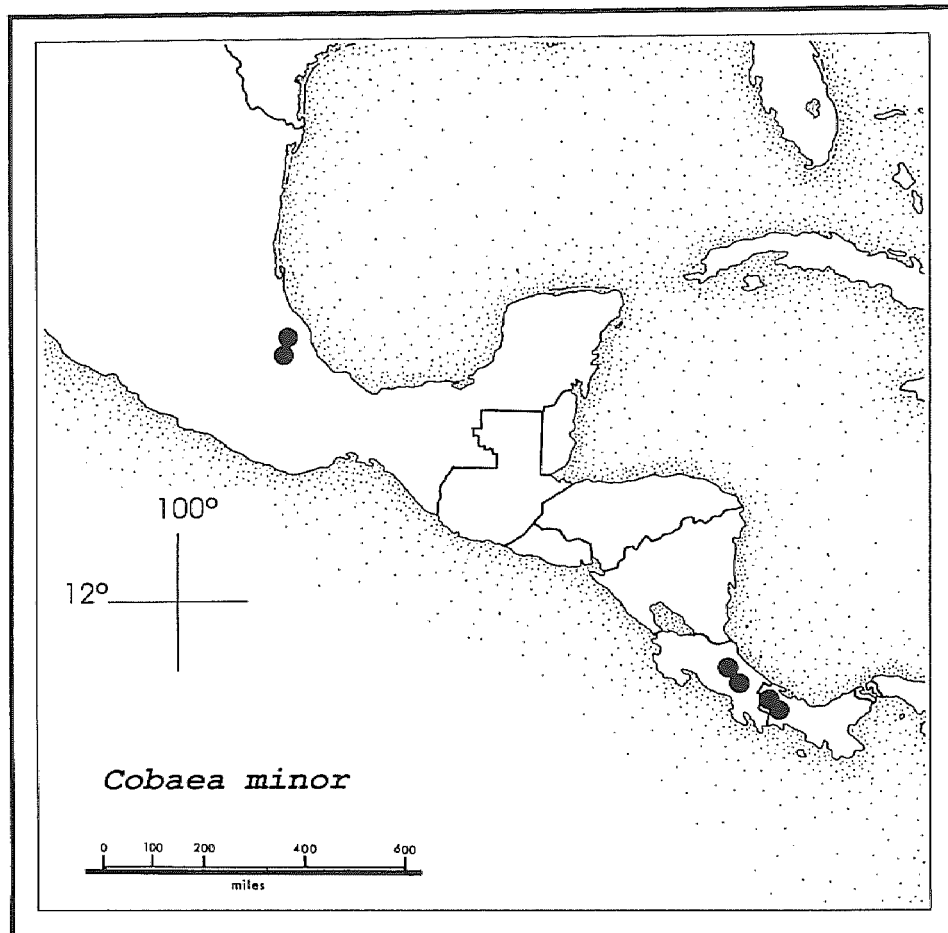
FIG. 15. Distribution of *Cobaea minor*.

as the lectotype and can be distinguished from the other sheets by the lack of any locality information.

Cobaea section Cobaea.

> *Cobaea* section *Eucobaea* Peter in Engler and Prantl, Nat. Pflanzenfam. IV(3a): 44. 1891.

Inflorescence erect, with at least two bracts; pedicels 7–23 cm long. Calyx segments chartaceous, variously pubescent adaxially, zone of pubescence broader than 2.0 mm. Corolla lobes broadly ovate to depressed-ovate, shorter than the tube, apices rounded to broadly acute. Filaments villous only at the base. Style branches flattened, reflexed, not twisted, with rounded apices; papillae long, covering only the adaxial surface (type I stigmas). Ovary with 2–15 ovules per locule.

The circumscription of sect. *Cobaea* given here is narrower than that of other authors (Peter 1891; Brand 1907; Grant 1959), making the group more cohesive and

monophyletic. Only *C. scandens* and its close relatives are included. Five species are Mexican and one is Andean.

2. Cobaea pringlei (House) Standley, Contr. U.S. Natl. Herb. 17: 457. 1914. *Rosenbergia pringlei* House, Muhlenbergia 4: 24. 1908.—TYPE: MEXICO. Nuevo León: Sierra Madre near Monterrey, 29 Aug 1903, *Pringle 11901* (lectotype, here designated: GH!; isolectotypes: GH! MICH! US-2!).

Stems slender, woody, glabrous. Leaves green, with 6 leaflets; rachis 29–65 mm long, glabrous or sparsely pubescent along the channel; petiolules 2–8 mm long, glabrous or pubescent along the channel; blades 30–92 mm long, 11–49 mm wide, glabrous or puberulent along abaxial veins, margins glabrous or minutely ciliate; upper and middle leaflet pairs obovate to elliptic, base acute to rounded, apex rounded to acute, rarely acuminate; basal pair elliptic to lanceolate, base unequally auriculate, the margins not long-ciliate. Inflorescence of 1–2 (–3) flowers; bracts fully expanded or sometimes only partly so, with 6 leaflets. Peduncles 1.5–9.5 cm long, glabrous. Pedicels 7.5–20.5 cm long, glabrous, tightly curved at the apex in fruit. Calyx segments 22–45 mm long, 8–18 mm wide, green, chartaceous, ovate, apex acute, margins plane, glabrous or minutely ciliate, puberulent in a broad zone near the margin adaxially, glabrous abaxially. Corollas white, rarely purple-hued with age, chartaceous, lobes puberulent externally, especially near the apex, glabrous except for the long-villous annulus internally; tube 41–65 mm long, 31–45 mm wide, narrowly campanulate, widest at the apex; lobes 12–23 mm long, much shorter than the tube, 20–32 mm wide, very broadly ovate to depressed-ovate, apex rounded, inrolled at the margin, imbricate, not wrinkled in bud. Filaments (45–) 62–75 mm long, adnate basally for 8–16 mm, positioned ventrally, bent basally, sharply curved at the apex, becoming undulate after dehiscence; anthers 8.5–11.0 (–14.0) mm long, 1.5–3.0 mm wide, yellow, lanceolate, straight in bud, curved but not twisted after dehiscence, introrse. Styles 52–75 mm long; style branches 2–5 mm long, flattened, papillae long, occurring on the adaxial surface only (type I stigmas). Fruit 53–68 mm long, maculate. Seeds 25–35 per fruit, 19–21 mm long, 12–14 mm wide, lacking scales; wings 2–3 mm wide. Chromosome number unknown. Fig. 9B.

Illustration. Standley (1914: plate 31).

Phenology. Collected in flower from July to November, and in fruit from July to October.

Distribution (Fig. 16). Mexico (Guanajuato, Nuevo León, Querétaro, San Luis Potosí, and Tamaulipas); oak or oak-pine woodlands in montane cloud forests; 1800–2500 m.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** GUANAJUATO: Mpio. Xichú, Agua Zarca del Pinal, *Santillán I. 467* (IEB).—NUEVO LEÓN: Mpio. Zaragoza, Cerro El Viejo, *Hinton et al. 22453* (TEX), *23217* (TEX), *23469* (TEX); Mpio. Zaragoza, Potreritos, *Hinton et al. 24881* (TEX); Chipinque Mesa, Monterrey, *Kenoyer 192* (F, MO); San Isidro, camino a Cola de Caballo, Villa de Santiago, 18 Sep 1982, *Ledezma s.n.* (MEXU); Taxus canyon; steep canyon on road above Horsetail Falls going W through Sierra Madre Oriental, Sep 1983, *L. Lowrey s.n.* (TEX); Dulces Nombres, and just E of border into Tamaulipas, *Meyer & Rogers 2745* (BM, BR, G, GH, MO); Mpio. Montemorelos, trail from La Trinidad to Sierra de la Cebolla, *Muller 2876* (GH, LL, MICH, UC, US); Mpio. Zaragoza, Cañada La Tinaja, between Rancho La Encantada and Cerro La Pena, *Patterson 5715* (TEX); Mpio. Montemorelos, 6 km SE of La Trinidad, in La Sierra Cebolla, just W of the precipice "El Butano," *Patterson 6114* (TEX); Mpio. Montemorelos, 6 km SE of La Trinidad below the precipice "El Butano," *Patterson 6394* (TEX); Mpio. Montemorelos, trail up Sierra Cebolla from La Trinidad, *Patterson 7159* (RSA, TEX); Monterrey, Chipinque, on mountain below Chipinque motel, *Peterson 1260* (TEX); along the trails above the city park at Chipinque Mesa (adjacent to Chipinque Motel), near Monterey, *Prather 1300* (TEX); 8 mi W of
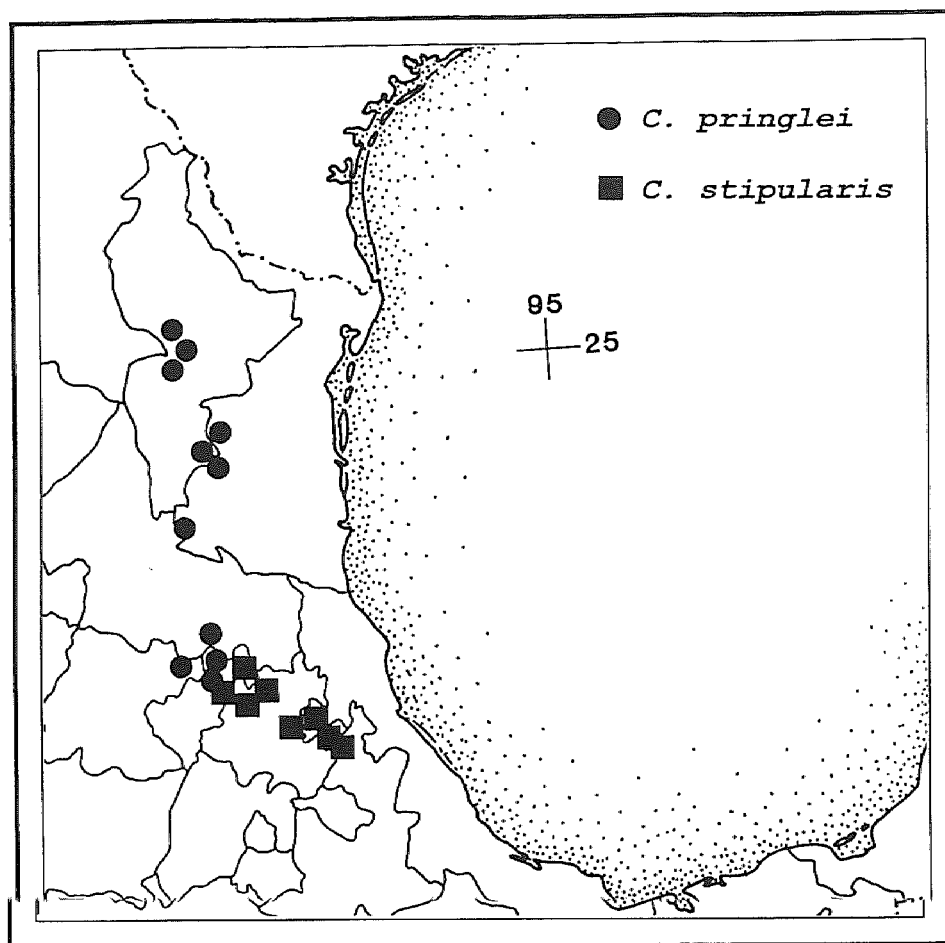
FIG. 16. Distribution of *Cobaea pringlei* and *C. stipularis*.

Horsetail Falls on road to Laguna de Sánchez, 1.7 mi E of La Cienega, *Reeves 6112* (RSA, TEX); mirador, near Monterrey, *Roybal 655* (US); at branch of road near Chipinque, Monterrey, *Smith M648* (TEX); moist canyon N of La Trinidad, on road from Potrero Redondo, *Soule 3287* (TEX); Mpio. Zaragoza, 9 km S de Zaragoza, camino a la Encantada, *Torres C. et al. 1110* (MEXU); Chipinque Mesa on mountain SW of Monterrey, *Turner 15622* (TEX).—QUERÉTARO: Mpio. Pinal de Amoles, ca. 5 km de El Llano, camino a San Pedro Escanela, *Carranza 887* (IEB); Mpio. Arroyo Seco, 1 km N de El Tepozán, *Carranza 1184* (IEB-2, MEXU); ca. de El Llano, 12 km al NE de Pinal de Amoles, sobre la carretera a Jalpan, *Rzedowski 45236* (IEB, MEXU, TEX); Mpio. Jalpan, 1–2 km al Poniente de San Isidro, La Parada, *Servín 426* (IEB); Mpio. Pinal Amoles, entre El Ranchito y El Llano, *Zamudio 9581* (IEB).—SAN LUIS POTOSÍ: 22 km W of Santa Catarina on Hwy 86 at Km 49, *Roe & Roe 2178* (LL, MICH, RSA, WIS).—TAMAULIPAS: 32 km E of Tula along road to Ocampo, *Breedlove & Anderson 63684* (CAS); near abandoned barium mine on ridge W of Rancho del Cielo, 8 km NW of Gómez Farías, *Gilbert 41* (TEX); Mpio. Hidaglo–Pto. Purificación, 58–59 km W del Barretal, *Gonzales M. 6368* (MEXU); Mpio. Hidalgo, Puerto Purificación, *Hinton et al. 24530* (TEX); camino del Encino hacia Rancho del Cielo, Gómez Farías, *Marroquin 4060* (MO); Mpio. Tula, 7 km de Tula por el camino hacia Ocampo, *Martínez 1590b* (MO); Mpio. Hidalgo, along road to Dulces Nombres, Nuevo León, 1.0 road mi N of Los Caballos towards Cañada El Mimbre, 16.0 road mi from the lowermost crossing of arroyo El Mimbre, *Mayfield 2083* (TEX-3); Cima de Sierra Madre Oriental, S de Alta Cumbres, carretera 101, *McDonald 878* (MEXU); Rancho del Cielo above Gómez Farías, *Patterson 7391* (TEX); trail in the Cañón de Tableta and road to Gómez Farías from

Rancho del Cielo, *Sharp et al. 52306* (GH, MEXU); Gómez Farías, area Rancho del Cielo, ca. La Perra, *Richardson 858* (NY, TEX); Mpio. Gómez Farías, Sierra de Guatemala, *Sullivan 725* (TEX); Gómez Farías, area Rancho del Cielo, La Joya, Sep 1967, *Webster s.n.* (TEX); Mpio. Gómez Farías, 4 km NW de Gómez Farías, *Yáñez 425* (MO).

Cobaea pringlei is the sister taxon to the remainder of sect. *Cobaea*. It is morphologically most similar to *C. biaurita* and *C. trianae,* but it can be distinguished from both by its narrowly campanulate, white corollas (v. broadly campanulate greenish or yellowish white corollas that usually turn pink or purple with age); its leaves, which are rarely purple-tinted (v. leaves always purple-tinted, especially abaxially); and its seeds, which lack scale-like trichomes (v. seeds with scale-like trichomes). Additionally, the basal leaflet pairs of *C. pringlei* and *C. biaurita* have enlarged auriculate leaf bases that are absent in *C. trianae,* and they both have seeds that are shorter (19–21 mm in *C. pringlei* and 16–22 mm in *C. biaurita,* compared to 22–28 mm in *C. trianae*). The length of the style branches can be used to separate *C. biaurita* (3–6 mm) from *C. trianae* (2–3 mm), but the length of the branches of *C. pringlei* overlaps with both taxa (2–5 mm).

The differences between *C. pringlei* and *C. stipularis* sometimes break down in Guanajuato and Querétaro, and specimens of *C. pringlei* with purple corollas, reminiscent of *C. biaurita,* have been collected from that region. Rzedowski et al. (1995) placed *C. biaurita* in synonymy under *C. stipularis,* in part because of these confounding specimens from Guanajuato and Querétaro; I believe they are better included in *C. pringlei* and have cited them above. The pattern of variation in specimens from this region may be a result of hybridization between the *C. pringlei* and *C. stipularis,* and further work is needed to fully resolve this issue. The three species are maintained in this treatment, because they can be distinguished throughout most of their ranges.

Only one collection (*Pringle 11901*), is cited in the protologue; however, there are two sheets of the type collection at GH where House worked. Neither sheet was annotated by House, thus lectotypification is required. Both sheets have ample material, but one sheet has two flowers and the constriction of the corolla at the apex of the nectar chamber is evident in one of those. Since this character was discussed by House, and because this specimen has more flowering material, it is selected as the lectotype.

3. **Cobaea stipularis** Bentham, Pl. hartw. 45. 1840. *Rosenbergia stipularis* (Bentham) House, Muhlenbergia 4: 23. 1908.—TYPE: MEXICO. Hidalgo: near San Cornelio, [1836–40], *Hartweg 344* (holotype: K!; isotype: W!).

Stems slender, woody, glabrous. Leaves purple, with 6 leaflets; rachis 38–63 (–78) mm long, glabrous; petiolules 3–8 mm long, glabrous; blades 39–107 mm long, (18–) 27–39 mm wide, glabrous, margins glabrous or minutely ciliate; upper and middle leaflet pairs elliptic, base acute to rounded, apex usually acuminate, rarely acute; basal pair deltate to very broadly ovate, reduced in length to less than half that of the upper pairs, each resembling a stipule, unequally auriculate, the margins not long-ciliate. Inflorescence a solitary flower; bracts fully expanded or sometimes only partly so, with 2–4 leaflets, one of the upper pair rudimentary. Peduncles 0.5–2.5 cm long, glabrous. Pedicels 7.8–17.5 cm long, glabrous, tightly curved at the apex in fruit. Calyx segments 30–49 mm long, 16–21 mm wide, green with purple maculations throughout, chartaceous, ovate, apex acute, margins plane, glabrous, puberulent throughout adaxially, especially along the midvein, glabrous abaxially. Corollas greenish white or white, suffused with pink, chartaceous,

lobes puberulent externally, especially near the apex, occasional long-villous trichomes basally, glabrous except for the long-villous annulus internally; tube 44–62 mm long, 44–56 mm wide, campanulate, widest at the apex; lobes 16–23 mm long, much shorter than the tube, 27–39 mm wide, depressed-ovate, apex rounded or rarely broadly acute, inrolled at the margin, imbricate, not wrinkled in bud. Filaments 55–65 mm long, adnate basally for 10–20 mm, positioned ventrally, bent basally, sharply curved at the apex, becoming undulate after dehiscence; anthers 10.0–13.5 mm long, 1.5–2.5 mm wide, yellow, lanceolate, straight in bud, not twisted after dehiscence, introrse. Styles 50–65 mm long; style branches 2.0–3.5 mm long, flattened, papillae long, occurring on the adaxial surface only (type I stigmas). Fruit 59–79 mm long, sometimes maculate. Seeds 35–45 per fruit, 18–21 mm long, 7–13 mm wide, lacking scales; wings 2–6 mm wide. Chromosome number unknown. Fig. 9C.

Illustration. Lindley (1841: tab. 25).

Phenology. Collected in flower and fruit from May to January.

Distribution (Fig. 16). Mexico (Hidalgo and adjacent parts of Querétaro and Veracruz); oak-pine-sweetgum forests; 1450–2300 m.

ADDITIONAL SPECIMENS EXAMINED. **Mexico.** HIDALGO: Hwy 85, 23 mi SW of SLP-Hgo border, ca. 20 mi NE of Jacala, *Anderson & Anderson 4660* (MICH); Mpio. Tenango de Doria, 2 km W of Tenango de Doria on the road Metepec, *Barrie 931* (MEXU, TEX); 7.2 km SW of Tlanchinol on Hwy 105, *Bartholomew 3424* (CAS); E slope of Cerro del Estribo above Tenango de Doria along road from Metepec, *Breedlove 69452* (CAS); Mpio. La Misión, NE of Jacala, *Breedlove & Almeda 59389* (CAS, MO, US); Mpio. Zacualtipán, 2.5 km NE of Zacualtipán on road to Soyatla, *Breedlove & Almeda 59432* (CAS, US); Mpio. Tenango de Doria, 8–11 km SW of Tenango de Doria, *Breedlove & Almeda 59546* (CAS); Zimapán, *Coulter 928* (GH, K); along Hwy 85 between Tamazunchale and Jacala, 37 mi SW of Tamazunchale near Palomas, *Croat 39323* (MO); along Hwy 105 between Molango and Mezquititlán, 1.0 mi N jct. road to Tizapán, *Daniel 407* (CAS, MICH); Molango a 5 km del Pueblo, *Delgado S. & Hernández 77* (MEXU); Mpio. Tenango de Doria, El Cirio, 8 km E de Tenango de Doria, *Hernández M. 7325* (IEB, MEXU, MO, RSA); Mpio. Tenango de Doria, 25 km E de Metepec, hacia Tenango de Doria, *Hernández M. & Hernández V. 4740* (MEXU, UC); 2.6 mi S on Mex 105 from its jct. with Mex 105 to Ontonga, 6.2 mi N of Ixtlahuaco, *Jones et al. 5561* (NY, TEX); barranca below Honey Station, Trinidad, 5 Sep 1906 *Lozano s.n.* (CAS, MICH, US); ca. de Tenango de Doria, *Miranda 3723* (MEXU); Mpio. Calnali, between Chalma and Ahuacatlán on road from Molango to Calnali, *Moore 3011* (GH); vicinity of Zacualtipán, *Moore 3176* (GH); 29.1 km NE of Jacala on Rte 85 en route to Tamazunchale, *Prather 924* (TEX); 34.6 km N of Jacala along Rte 85, N of Zimapán, *Prather 926* (TEX); same locality, flowering voucher grown in University of Texas greenhouse, *Prather 1271* (TEX); Barranca Trinidad (barranca near Honey Station), *Pringle 13433* (CAS, GH, MICH-2, TEX, US-2); 1 km de la desviación a Sta. Mónica por la carr. Alumbres–Tianguistengo, *Torres C. & Hernández 3059* (MEXU); about 17 mi S of Chapulhuacán, 6.5 mi S of Santa Ana on Hwy 85 to Zimapán, *Woodruff 393* (TEX).—QUERÉTARO: Mpio. Landa, La Alberquilla, ca. 2 km al S de La Florida, *González 670* (IEB); Mpio. Landa, 2 km al NE de El Rincón, *Rubio 811* (IEB); Mpio. Jalpan, 3–4 km al Oriente de La Parada, *Servín 304* (IEB).—VERACRUZ: Mpio. Huayacocotla, Potrero Seco, camino al Río Tenantitla, *Ballesteros & Calzada 241* (IEB); Mpio. Las Minas, Vereda de Rinconada a Cruz Blanca subiendo por la carretera, *Durán E. & Burgos 381* (IEB); El Paraje, Huayacocotla, *Hernández M. & Trigos 809* (DS, F, MEXU, NY); Mpio. Huayacocotla, 3 km SW of Huayacocotla along road to Palo Bendito, *Nee & Diggs 25196* (F); Mpio. Huayacocotla, Sierra Madre Oriental, entre Helechales y Los Ocotes, *Vargas & Castañares 345* (CAS).

Cobaea stipularis is the sister taxon to a clade composed of *C. biaurita*, *C. trianae*, and *C. scandens*. It is very similar to all of these species but can easily be distinguished by its purple leaves (on healthy plants), its basal leaflets, which are less than half the length of the upper pairs, and the scattered purple maculations on its calyx lobes. The remaining three species have leaves that are green or green suffused with purple, but never entirely purple, basal leaflets nearly equal in length to the upper pairs, and green calyx

segments that may have purple margins or veins but never scattered maculations similar to those of *C. stipularis*.

4. Cobaea trianae Hemsley, Garden (London 1871–1927) 17: 353. 1880 (*'trianaei'*). *Rosenbergia trianaei* (Hemsley) House, Muhlenbergia 4: 24. 1908.—TYPE: COLOMBIA. Tolima: "near Ibaque on the Quindiu," Jun 1836, *Purdie s.n.* (lectotype, here designated: K!).

Stems slender, woody, glabrous or puberulent at the nodes. Leaves green, suffused with purple, with 6 leaflets; rachis 38–67 mm long, puberulent along the channel; petiolules 6–9 mm long, puberulent along the channel; blades (37–) 60–106 mm long, 18–41 mm wide, glabrous or puberulent abaxially along veins, margins minutely ciliate; upper and middle leaflet pairs elliptic to ovate, base acute to rounded, apex acuminate or rarely acute; basal pair elliptic to ovate, base slightly cordate to truncate, the margins not long-ciliate. Inflorescence a solitary flower, rarely 2; bracts fully to partly expanded or sometimes abscised at maturity, with 6 leaflets. Peduncles (2.0–) 4.7–8.0 cm long, glabrous or puberulent basally. Pedicels 11–22 cm long, glabrous or puberulent basally, tightly curved at the apex in fruit. Calyx segments 27–50 mm long, 8–18 mm wide, green, chartaceous, lanceolate to ovate, apex acute, margins plane, glabrous or minutely ciliate, puberulent adaxially in a broad zone near the margin, glabrous abaxially. Corollas greenish white turning pink or purple with age, chartaceous, puberulent at the very tips of the lobes or rarely glabrous externally, glabrous except for the long-villous annulus internally; tube 30–47 mm long, 29–45 mm wide, campanulate, widest at the apex; lobes 14–18 (–27) mm long, shorter than the tube, 18–33 mm wide, depressed-ovate to broadly depressed-ovate, apex rounded or rarely broadly acute, inrolled at the margin, imbricate, not wrinkled in bud. Filaments 45–68 mm long, adnate basally for 5–10 mm, positioned ventrally, bent basally, sharply curved at the apex, becoming undulate after dehiscence; anthers 7–13 mm long, 2–3 mm wide, yellow or purple, lanceolate, straight in bud, not twisted after dehiscence, introrse. Styles 46–66 mm long; style branches 2–3 mm long, flattened, papillae long, occurring on the adaxial surface only (type I stigmas). Fruit 40–63 mm long, maculate. Seeds 10–36 per fruit, 22–28 mm long, 10–13 mm wide, furnished with scales; wings 2–5 mm wide. Chromosome number unknown. Figs. 1A, 9D.

Additional illustrations. Brand (1907: fig. 7B); Grant and Grant (1965: fig. 43).

Phenology. Collected in flower and fruit from June to August and December to February.

Distribution (Fig. 17). Colombia, Ecuador, and Venezuela; along streams or canyon walls in Andean cloud forests; 1600–3300 m.

ADDITIONAL SPECIMENS EXAMINED. **Colombia.** ANTIOQUIA: without date, *Jervise s.n.* (K).—BOGOTÁ: without specific locality, *Triana 2180* (BM, BR, G, NY, W); Páramo de Almaguer, el Arracachal, *Triana 3825* (BM-2).—CALDAS: N of Pereira, Cordillera Central, *Pennell 10175* (US).—CAUCA: main hwy Pasto–Popayán, 2 km S of Rosas, *Stein & McDade 3214* (MO).—CUNDINAMARCA: Cordillera Oriental, Sierra de Subia, 6.6 km N of Cumaca along road to Viotá, *Barclay et al. 3520* (US); 18 km E of La Mesa, *Gentry 15161* (MO); Santandercito, quebrada Los Cristales, *Uribe U. 1250* (US).—TOLIMA: Without specific locality and date, *Goudot s.n.* (K).—Department unknown: *Triana 167* (BR, K); *Mutis 4706* (US). **Ecuador.** CARCHI: entre Paja Blanca y El Cucho, *Acosta Solís 10530* (F).—IMBABURA: Cordillera Oriental, along trail between Mariano Acosta and Guanopamba, *Drew E–256* (US); vía Mariano Acosta–Palmira–Tambo–Nueva América, Nueva América–Río Pisque–Cruce a Potrerillos, *Jaramillo et al. 1657* (AAU, QCNE); vía Mariano Acosta–Palmira–Tambo–Nueva

América "Nueva América–Río Pisque–Cruce a Potrerillos," *Jaramillo et al 1681* (AAU); Cuicocha–Apuela road, Km 28, *Jørgensen & Vive 56081* (QCNE); vicinity of Apuela, *Madison & Coleman 2303* (GH); 1.6 km SE of Mariano Acosta main square on road to Guanopamba, ca. the point where the road to La Florida and Guanopamba splits, *Panero & Clark 3024* (CAS, F, K, MEXU, MO, NY, QCA, QCNE, TEX, US); 60.4 km W of Otavalo on road to Selva Alegre, *Panero & Clark 3044* (MEXU, QCA, QCNE, TEX, US); San Francisco de Sigsipamba, Sector San Vicente, *Tipaz et al. 1621* (TEX).—PICHINCHA: Rd. Quito–Mindo, 20 km W of Nono, *Buhlin et al. 1129* (S); road Quito–Mindo, near Cotocollao, *Harling 11139* (GB); Haspunjo, *Holmgren & Heilborn 691* (S); at Sierra between Nono and Nanegalito, *Lægaard 51801* (QCNE); 9 km W of Calacalí on new road to Nanegalito, *Molau & Eriksen 2180* (AAU, GB); along road Nanegalito–Quito, *van der Werff et al. 12336* (MO, QCNE).—Province unknown: Prope Panchi [?], *André 1668* (K); prope Nono [?], *Sodiro s.n.* (G). **Venezuela.** TÁCHIRA: Carretera La Grita–Pueblo Hondo, 4 km S de Pueblo Hondo, o sea 16 km NE de La Grita, en borde de la vía, *Bunting 11671* (NY).

Cobaea trianae is the sister taxon to a clade composed of *C. biaurita* and *C. scandens*. From *C. scandens* it can easily be distinguished by its lanceolate to ovate calyx lobes with acute apices and the base of its lowermost leaflets, which are acuminate to truncate. *Cobaea scandens* has circular to very broadly ovate calyces with rounded or emarginate apices and enlarged auriculate bases on its lowermost leaflet pairs. See the discussion under *C. pringlei* (no. 2) for distinctions from *C. biaurita* and *C. pringlei*.

The four collections cited by Hemsley in the protologue (*Goudot s.n.*, *Jervise s.n.*, *Purdie s.n.*, and *Triana 167*) are all extant at Kew. The Triana collection has no mature
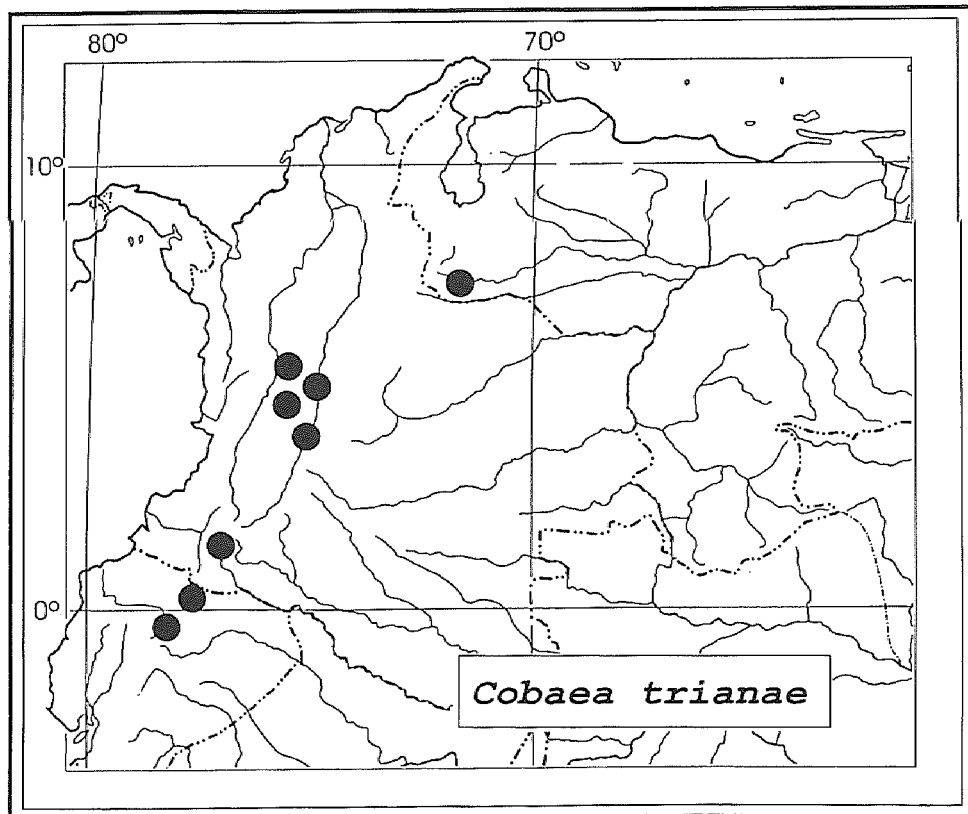

FIG. 17. Distribution of *Cobaea trianae*.

flowers and thus was not selected as the lectotype. Of the remaining three collections, the Purdie collection is the most complete and has been well preserved; thus it is selected as the lectotype. Hemsley did not give the collection number of the Triana collection in the protologue, which has led to confusion. Various duplicates of *Triana 2180*, a different collection of *C. trianae*, deposited in B (now destroyed; photos F! MO!), BM!, BR!, and NY! have been treated as types; however, the Triana specimen seen by Hemsley is clearly marked "167," and I have seen no duplicates of this collection.

5. **Cobaea biaurita** Standley, Contr. U.S. Natl. Herb. 17: 457. 1914.—TYPE: MEXICO. Chiapas: near Túmbala, 4000–5500 ft, 20 Oct 1895, *Nelson 3363* (holotype: US!).

Stems slender, woody, glabrous. Leaves green suffused with purple and often with purple veins abaxially, with 6 leaflets; rachis 35–72 mm long, glabrous or puberulent along the channel; petiolules 4–10 mm long, glabrous or puberulent along the channel; blades 48–97 (–132) mm long, 14–50 mm wide, glabrous or rarely sparsely puberulent along veins, the margins usually minutely ciliate, sometimes glabrous; upper and middle leaflet pairs elliptic-ovate to elliptic to elliptic-obovate, base acuminate to truncate, apex acuminate to long-acuminate; basal pair elliptic, unequally auriculate or rarely rounded, the margins not long-ciliate. Inflorescence of 1–3 flowers; bracts fully to partly expanded, or sometimes abscised at maturity, with 6 leaflets. Peduncles 1.5–8.0 cm long, glabrous. Pedicels 11.5–23.0 cm long, glabrous, tightly curved at the apex in fruit. Calyx segments 26–39 mm long, 7–18 mm wide, green, chartaceous, deltate to deltate-ovate, or rarely lanceolate, apex acute to sharply acute, margin glabrous to minutely ciliate, puberulent in a broad zone near the margin adaxially, glabrous abaxially. Corollas greenish white or greenish yellow, often turning pink or purple with age, chartaceous, lobes puberulent externally, especially near the apex, glabrous except for the long-villous annulus and occasional long trichomes near the base internally; tube 36–48 mm long, 36–48 mm wide, campanulate, widest at the apex; lobes 16–29 mm long, much shorter than the tube, 23–34 mm wide, depressed-ovate to broadly depressed-ovate, apex rounded to broadly acute, inrolled at the margin, imbricate, not wrinkled in bud. Filaments 62–75 mm long, adnate basally for 5–10 mm, positioned ventrally, bent basally, sharply curved at the apex, becoming undulate after dehiscence; anthers 9–13 mm long, 2–3 mm wide, yellow to yellowish purple, lanceolate, straight in bud, not twisted after dehiscence but sometimes curved, introrse. Styles (47–) 55–80 mm long; style branches 3–6 mm long, flattened, papillae long, occurring on the adaxial surface only (type I stigmas). Fruit 50–72 mm long, maculate. Seeds 25–35 per fruit, 16–22 mm long, 10–14 mm wide, furnished with scales; wings 1–3 mm wide. Chromosome number unknown. Fig. 9E.

Illustration. Standley (1914: plate 30).

Phenology. Flowering and fruiting specimens have been collected in Oaxaca year-round, in Chiapas from August to February.

Distribution (Fig. 18). Mexico (Chiapas and Oaxaca); at the base of bluffs and along ridges in oak-dominated cloud forests; 2000–3500 m.

ADDITIONAL SPECIMENS EXAMINED. Mexico. CHIAPAS: Mpio. Jitotol, ca. 7 mi N of Jitotol on a side road to an oil well, *Breedlove 15413* (DS, F, LL, MICH, NY); ca. 12 km N of Jitotol along a side road to an oil well, *Breedlove 19955* (DS); Mpio. Rayón, in the Selva Negra, 10 km above the Rayón Mezcalapa along the