

A Revision of the Genus *Polylepis*  
(Rosaceae: Sanguisorbeae)

*Beryl B. Simpson*



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## A B S T R A C T

Simpson, Beryl B. Revision of the Genus *Polylepis* (Rosaceae: Sanguisorbeae). *Smithsonian Contributions to Botany*, number 43, 62 pages, 39 figures, 1979.— Species of *Polylepis* are shrubs or trees native to the mid- and high-elevation tropical Andes. Some species of *Polylepis* form woodlands growing well above normal treeline within grass and scrub associations at elevations over 5000 m. Consequently, *Polylepis* appears to be the highest natural occurring arborescent angiosperm genus in the world. The physiological basis allowing such high altitude growth is not understood, but evidence indicates that woodlands at these elevations are restricted to microsites where ecological conditions are similar to those of lower altitudes. The genus is distinct from other rosaceous members of the tribe Sanguisorbeae and is interpreted here as consisting of three species groups that appear to have spread independently north and south along the Andean chain. Because of the patchy distributions of populations and disturbances by man, species are often polytopic. As a result, numerous forms have been described as distinct taxa in the past. In addition, hybridization appears to occur between species making circumscription of some taxa difficult. In this revision, evidence from studies of gross morphology, leaflet anatomy, pollen morphology, and field observations of the autecology of various populations were used to ascertain the number of species within the genus and their relationships to one another. Data from these sources indicate that *Polylepis* should be considered as consisting of 15 species, one of which is first described in this treatment. A key for the identification of the species is provided. Each species is illustrated, discussed, and its modern distribution mapped.

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# Contents

	<i>Page</i>
Introduction .....	1
Acknowledgments .....	2
Previous Treatments of the Genus .....	2
Species Groups and Relationships of the Genus .....	3
Morphological Characters .....	4
Habit .....	4
Bark .....	4
Branching Pattern and Leaf Arrangement .....	6
Stipule Sheaths .....	6
Trichome and Vestiture Types .....	6
Leaves and Leaflets .....	7
Leaf Anatomy .....	8
Inflorescences and Flowers .....	12
Pollen Morphology .....	14
Fruits .....	14
Geographical Distribution .....	14
Ecology .....	15
<i>Polylepis</i> Ruiz and Pavon .....	17
Key to the Species of <i>Polylepis</i> .....	18
1. <i>Polylepis multijuga</i> Pilger .....	19
2. <i>Polylepis lanuginosa</i> Humboldt, Bonpland, and Kunth .....	21
3. <i>Polylepis hieronymi</i> Pilger .....	23
4. <i>Polylepis pauta</i> Hieronymus .....	27
5. <i>Polylepis sericea</i> Weddell .....	28
6. <i>Polylepis subsericans</i> Macbride .....	31
7. <i>Polylepis pepeii</i> , new species .....	32
8. <i>Polylepis reticulata</i> Hieronymus .....	33
9. <i>Polylepis weberbaueri</i> Pilger .....	37
10. <i>Polylepis quadrijuga</i> Bitter .....	40
11. <i>Polylepis besserii</i> Hieronymus .....	42
12. <i>Polylepis tomentella</i> Weddell .....	46
13. <i>Polylepis incana</i> Humboldt, Bonpland and Kunth .....	50
14. <i>Polylepis racemosa</i> Ruiz and Pavon .....	53
15. <i>Polylepis australis</i> Bitter .....	56
Literature Cited .....	60
Index .....	62



# A Revision of the Genus *Polylepis* (Rosaceae: Sanguisorbeae)

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## Introduction

Above elevations of 3500 m in the tropical Andes, vegetation usually consists of various forms of low grass and scrub paramo or puna. Woody elements are scarce at such elevations in terms of both numbers of species and individuals. Yet, one arborescent genus, *Polylepis*, is found throughout the high tropical Andes. Although some members of the genus are components of the upper montane forest, others occur in woodlands at elevations as high as 5200 m, completely surrounded by puna vegetation and well isolated from any other type of forest. The presence of true trees growing at such altitudes is rare anywhere in the world and consequently *Polylepis* ranks with the conifers of the Himalayan Mountains as the highest natural occurring trees. The deep red-colored bark and contrasting dark green leaves of *Polylepis* trees makes them even more noticeable in the often bleak paramo or puna landscapes. On close examination the bark can be seen to be composed of almost an infinite number of parchment-thin layers. The name *Polylepis* is, in fact, derived from the Greek words *poly* (many) plus *lepis* (layers), referring to the shredding, multi-layered bark that is common to all species of the genus.

The physiological tolerances allowing growth at these elevations and the prehuman, natural distribution of *Polylepis* have been the subjects of consid-

erable debate, but evidence indicates that even before severe decimation by man, high elevation trees of *Polylepis* were limited in their distribution by the presence of specialized microhabitats.

In addition to its uniqueness as an inhabitant of extremely high elevations, *Polylepis* has played an important role in the culture of various Andean Indian groups by providing building material and firewood (Hueck, 1972; Pulgar, 1967). As pointed out by Koepcke (1961), the woodlands themselves constitute a distinctive habitat for other organisms. A monotypic bird genus, *Oreomanes*, is completely restricted to *Polylepis* woods, providing the only case of an avian genus limited in distribution to a single plant genus. It is likely that other endemic faunal elements will be found in the future.

Taxonomically, the genus belongs within the Rosaceae to the subfamily Rosoideae, tribe Sanguisorbeae (Focke, 1888; Robertson, 1974 a,b,c). Although similar in various morphological traits to *Acaena* Linnaeus and *Margyricarpus* Ruiz & Pavon (including *Tetraglochin* Poeppig), the genus is a natural one and quite distinct from all other members of the family. However, the spotty distribution of most species (caused by both natural and human factors) has resulted in much interpopulational variation. In the past, local populations were often described as a distinct taxa (varieties, subspecies, or even species). Of the previously described taxa, only 15 are considered here to represent meaningful biological entities. A new species from Peru and Bolivia is described. In the determination of

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these taxa, I have used habitat data, gross morphology, leaf anatomy, and palynology; chromosome counts were unsuccessfully attempted. Because of the specialized environmental conditions required by *Polylepis* and its arborescent, long-lived habit, no crossing experiments were undertaken.

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#### Previous Treatments of the Genus

Unlike most Andean genera, *Polylepis* has no generic synonyms even though it occurs in six different countries. This lack of synonyms seems attributable to its early and complete description by Ruiz and Pavon (1794) and the distinctiveness of the group from other members of the Rosaceae. In addition, all of the subsequently described taxa, with the exception of *Acaena ochreatea* Weddell (placed here in *P. sericea* Weddell), were originally correctly described as members of the genus. The un-complicated generic taxonomy contrasts, however, with the infrageneric taxonomic situation. Variation within species, the patchy distribution of most taxa, and the poor systematic treatments of earlier botanists have tended to produce infrageneric confusion.

Subsequent to the original circumscription of *Polylepis* and the description of a single species,

*P. racemosa* (Ruiz & Pavon, 1798), Humboldt, Bonpland, and Kunth (1824) described three additional species: *P. incana*, *P. lanuginosa*, and *P. villosa*. The last of these is considered here as a synonym. Weddell (1861), in his compilation of Andean plants added three more species (*P. tomentella*, *P. sericea*, and "*Acaena*" *ochreatea*) as well as two varieties of earlier described species. His interpretation of *P. lanuginosa* and his variety, *P. lanuginosa*  $\beta$  *microphylla*, both appear to be misunderstandings of the true *P. lanuginosa* and of the nature of a set of small-leaved specimens that are considered here as belonging to *P. weberbaueri*. Hieronymus (1895 and 1896) described five species of *Polylepis* from northern South America, which he found among the collections of Lehmann (*P. lehmannii*) and Stübel (*P. besseri*, *P. reticulata*, *P. stuebelii*, and *P. pauti*). In 1906 Pilger described five more species (*P. hieronymi*, *P. albicans*, *P. weberbaueri*, *P. multijuga*, and *P. serrata*) from Weberbauer's Peruvian specimens sent to the museum at Berlin.

The only study of the genus as a whole, that of Bitter (1911b), did little to further understanding of the group. Bitter's typological concept (Mayr, 1957) and his treatment of aberrant individuals rather than distinctive populations as varieties (Mayr, 1959) led to such taxonomic fragmentation that it became practically impossible to identify new collections. In all, Bitter described in his monograph 13 of the 33 species he recognized, as well as nine subspecies and 18 varieties. For one species, *Polylepis incana*, he circumscribed nine infraspecific taxa. Later, in 1913, Bitter described a new variety of *Polylepis australis* (*P. australis* var. *tucumanica*) with four new subvarieties. This small group of isolated populations in southern Bolivia and northern Argentina, earlier described as *P. australis* by Bitter, had already been split into several varieties (as varieties of *P. racemosa*) by O. Kuntze (1898), and Bitter had added four more in his 1911 monograph. Few of Bitter's taxa are retained here. It is fortunate that there are photographs of the types of the Berlin Herbarium, which was destroyed in part during World War II (the Rosaceae being one of the casualties), because it allows an assessment of Bitter's species that might otherwise have been totally impossible. Unfortunately, there are no isotypes or photographs of many of his varieties and subspecies. In these cases, I have relied on de-

scriptions and locality data as guides to their placement.

After Bitter's treatments, only five new taxa (*Polylepis subintegrifolia*, *P. subsericans*, *P. quin-diensis*, *P. boyacensis*, and *P. cocuyensis*) were added. An examination of the type material and the range of variation present in previously described species indicates only one of these (*P. subsericans*) is actually distinct.

### Species Groups and Relationships of the Genus

In his monograph, Bitter (1911b) arranged the species of *Polylepis* into two sections and 11 "groups" of species. Six of the groups were given formal names, but Bitter never indicated whether he considered the groups to be subsections or series.

Bitter's arrangement of the species of *Polylepis* is shown in Table 1. Table 2 shows the infrageneric groupings proposed here. Although there has been much reduction in the number of recognized species and some rearrangement, the species groups or complexes recognized here agree to some extent with Bitter's sections except that his section *Gymnopodae* is split into two. None of the groupings proposed here are given formal recognition. The genus is such a tightly knit unit, well isolated from other genera in the Sanguisorbeae, and has so few species, that formal recognition of subgeneric groups seems unduly complex. Instead, I have placed all of the members of Bitter's section *Dendracaena* into a group called the *sericea* group and split the section *Gymnopodae* into the *reticulata* group and the *incana* complex. The last is called a complex be-

TABLE 1.—Alignment of *Polylepis* species according to Bitter (1911b)

Section	Group	Bitter's species	Present treatment				
<i>Dendracaena</i>	<i>Plurijugae</i>	<i>P. multijuga</i>	<i>P. multijuga</i>				
	<i>Annulatipilosae</i>	<i>P. serrata</i>	}	<i>P. pauta</i>			
		<i>P. pauta</i>					
		<i>P. annulatipilosa</i>					
		<i>P. ochreatea</i>					
		<i>P. Stuebeli</i>					
	unnamed	<i>P. hypargyrea</i>	}	<i>P. sericea</i>			
		<i>P. sericea</i>					
	<i>Latifoliolatae</i>	<i>P. albicans</i>	}	<i>P. lanuginosa</i>			
	unnamed	<i>P. coriacea</i>					
		<i>P. Lehmannii</i>					
<i>Subtustomentosae</i>	<i>P. lanuginosa</i>	}	<i>P. hieronymi</i>				
unnamed	<i>P. hypoleuca</i>						
	<i>Gymnopodae</i>	<i>P. Hieronymi</i>	}	<i>P. quadrijuga</i>			
<i>Supranitidae</i>		<i>P. microphylla</i>					
unnamed	<i>Supranitidae</i>	<i>P. Weberbaueri</i>	}	<i>P. reticulata</i>			
		<i>P. quadrijuga</i>					
		<i>P. reticulata</i>					
		<i>P. nitida</i>					
		<i>P. brachyphylla</i>					
	unnamed	<i>P. australis</i>	}	<i>P. australis</i>			
		<i>P. racemosa</i>					
		<i>P. villosa</i>					
		<i>P. Besseri</i>					
		<i>Paucijugae</i>			<i>P. triacontandra</i>	}	<i>P. besseri</i>
					<i>P. Crista-galli</i>		
<i>P. tenuiruga</i>							
<i>P. subquinquefolia</i>							
<i>P. rugulosa</i>							
unnamed	<i>P. pallidistigma</i>	}	<i>P. incana</i>				
	<i>P. incana</i>						
	<i>P. tomentella</i>						
	<i>P. tarpacana</i>						

TABLE 2.—Species groups of *Polylepis* proposed in this treatment

<i>sericea</i> group	<i>reticulata</i> group	<i>incana</i> complex
<i>P. multijuga</i>	<i>P. reticulata</i>	<i>P. racemosa</i>
<i>P. lanuginosa</i>	<i>P. weberbaueri</i>	<i>P. incana</i>
<i>P. hieronymi</i>	<i>P. quadrijuga</i>	<i>P. besseri</i>
<i>P. pauta</i>		<i>P. tomentella</i>
<i>P. sericea</i>		<i>P. australis</i>
<i>P. pepeii</i>		

cause of the blurred specific boundaries and the indication of hybridization of many of the taxa within it.

The *sericea* group includes those species with leaves usually containing many pairs of leaflets, sericeous trichomes on the underleaf surfaces and stipule sheaths. Both *P. multijuga* and *P. hieronymi* have shaggy trichomes on the under surfaces of the leaflets but have sericeous stipule sheaths and numerous pairs of leaflets. The one most discrepant element in the group, *P. subsericans*, forms a connecting link with the *incana* complex. The trichomes of this species are minutely strigose rather than truly sericeous and are mixed with glandular multicellular trichomes characteristic of the *incana* complex. However, because some populations of *P. sericea* (former *P. albicans*) approach this type of vestiture, I have included *P. subsericans* in the *sericea* group.

All species placed in the *reticulata* group have nitid, emarginate leaflets with pannose under leaflet surfaces. The three species in the group are closely related to one another. Their link to other members of the genus appears to be via *P. lanuginosa*. It is probable that the group was derived from an ancestral stock similar to that leading to the modern *P. lanuginosa* and related taxa within the *sericea* group.

Members of the *incana* complex have variable numbers of pairs of leaflets, but often only one. The leaflet lower surface usually has glandular trichomes often mixed with a lanose vestiture and, in the case of *P. racemosa*, with scattered, shaggy trichomes. Individuals of *P. australis* with glabrous leaflets represent one extreme in this group and plants of *P. besseri* with densely lanose leaves constitute another extreme type.

Bitter (1911b) extensively discussed the relationship of *Polylepis* to *Acaena* section *Elongata*. Particularly members of the *sericea* group (*P. multijuga* and *P. pauta*) share characters of multipinnate

leaves and long, densely flowered racemes with members of this section of *Acaena*. Bitter argued for a derivation of *Polylepis* from an *Acaena*-like ancestor rather than the reverse. He based this conclusion on *Polylepis* being more restricted in distribution than *Acaena* and an inhabitant of more specialized habitats. Species of *Acaena* occur in South America, New Guinea, Hawaii, and North America, whereas *Polylepis* is restricted to the Andes. Various other authors, while not commenting on the affinities of *Polylepis*, have placed *Polylepis* next to *Margyricarpus* (including *Tetraglochin*) (cf. Focke, 1888) and more distant from *Acaena*. Hutchinson (1967) placed *Polylepis* between *Leucosidea*, which it resembles in many vegetative and floral characters, and *Tetraglochin* in his tribe Poterieae (=Sanguisorbeae), but he made no statements as to the reasons for his alignment. On the basis of gross and pollen morphology, *Polylepis* appears quite similar to *Acaena* and slightly less similar to *Margyricarpus*. Since the generic relationships of this group of Sanguisorbeae are being investigated by Dr. Werner Rauh of Heidelberg, I have not attempted to assess the alignment of genera within the tribe.

### Morphological Characters

**HABIT.**—All species of *Polylepis* are trees or shrubs ranging in height from 1 to 27 m (Figure 1b–d). Although not absolute, there is a loose correlation of habit with habitat. All of the tropical taxa that grow at relatively low elevations (e.g., *P. multijuga*, *P. pauta*) are tall trees (Tosi 1960), whereas many of the species growing at elevations of 3800 m and above are short trees or shrubs. Both *P. besseri* and *P. pepeii*, which reach elevations over 4000 m, are shrubby, but *P. tomentella*, observed at 5200 m on Volcan Sajama, Bolivia, retains an arborescent habit even at this altitude. In some cases, the presence of shrubby individuals in a population has been caused by the activities of man or domesticated grazing animals, which prune trees and cause the formation of multistemmed individuals through destruction of the apical meristem.

**BARK.**—The bark of *Polylepis* consists of numerous layers of thin, dark red exfoliating sheets (Figure 1a). In some cases, the layered bark can be over an inch thick. All of the larger branches have similar shredding bark. No measurements of tempera-

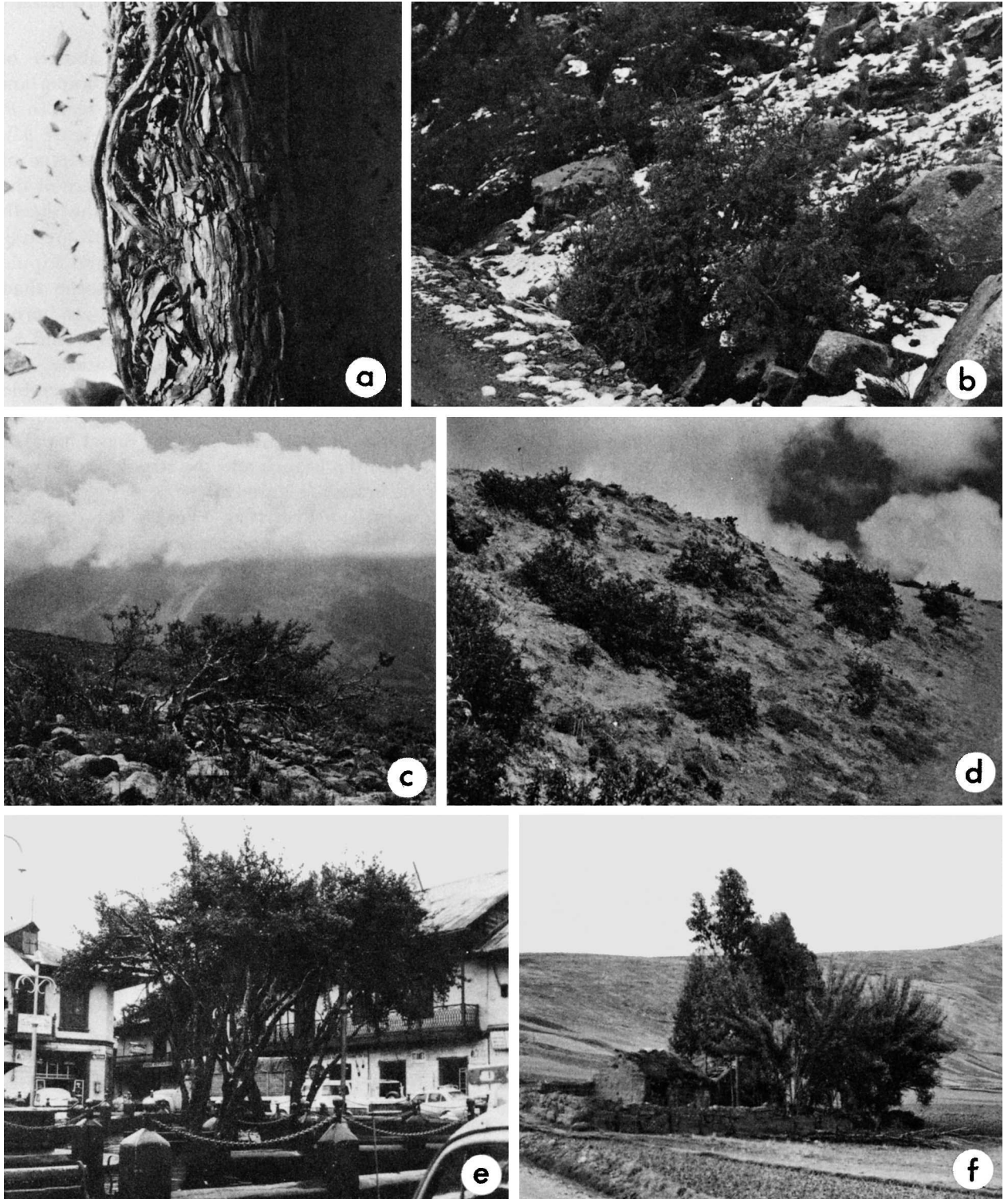


FIGURE 1.—Growth forms and habitats of *Polylepsis* species: *a*, trunk of a small tree of *P. tomentella* with the layered, shredding bark characteristic of all species of the genus; *b*, shrubby growth form of *P. besseri* growing in Chapare, Cochabamba, Bolivia; *c*, tree growth form of *P. besseri*, Volcan Chachani, Arequipa, Peru; *d*, shrubby plants of *P. weberbaueri*, Cañar, Ecuador; *e*, trees of *P. racemosa* planted in the plaza of Cerro de Pasco, Peru; *f*, cultivated group of trees of *P. racemosa* around a house, near Tingo Pacha, Junin, Peru.

tures under the bark relative to the ambient air temperatures have been made, but it would seem that the bark serves as an insulation from both the nightly frosts and the intense diurnal irradiation. Temperature readings have been made of plants in Afroalpine habitats. Hedberg (1964) showed that loose stem coverings such as overlapping scales, mats of trichomes, or persistent leaf bases insulated the interior of arborescent plants from extremes of heat or cold.

**BRANCHING PATTERN AND LEAF ARRANGEMENT.**—Perhaps, in part because of the harsh environment in which many species of *Polylepis* grow, trees tend to have twisted, crooked stems and branches. Contorted growth is often associated with windy, cold, or arid habitats. The angular pattern of the branches is due primarily, however, to the way in which the trees branch and the leaves are borne. Growth is sympodial with repeated sympodial branching. The lateral branches show a "flush" type of growth with long, often naked branch segments and the leaves congested at the branch tips (Figure 2a, c). The leaves are borne alternately but often appear whorled because of their congestion (e.g., Figure 2b). The spurts in growth indicated by the long leafless branch segments probably occur in the short southern summer when temperatures are warm and rainfall is relatively high (a typical pattern in most *Polylepis* habitats). Species that occur in the upper portions of the montane rainforest have less pronounced growth flushes than those of high elevations. Bitter (1911b) noted the tendency of the "less specialized" species to have a more even dispersion of leaves along the branches than the more "advanced" species. Extremes can be seen in *P. multiflora* (Figure 8) and *P. pepeii* (Figure 20).

For taxonomic purposes, therefore, the amount of congestion of the leaves can be used in combination with other characters to discriminate between taxa. The amount of crowding of the leaves near the branch tips is variable within most species, however, and is not as incisive a character as Bitter (1911b) indicated.

**STIPULE SHEATHS.**—Each leaf has a pair of stipules fused around the branch forming a sheath. The congestion of the leaves results in a pattern of stacked, inverted cones due to the overlapping of the stipule sheaths (Figure 2a). On the top of the sheaths on either side of the petiole there are often

projections, or spurs. The presence or absence of these spurs, their size, and vestiture are important taxonomic characters. Extremes can be seen in *P. multijuga* (Figure 8) and in *P. incana* (Figure 34). In addition, the presence or absence and type of trichomes extending along the upper surface of the leaf petiole onto the inner surface of the sheath and projecting from the top of the sheath are useful for separating species. Young leaves and stipule sheaths tend to be much more pubescent than older, mature leaves. Since inflorescences are borne in the axils of leaves, and young leaves would be particularly sensitive to cold air temperatures, this dense pubescence would serve to insulate vulnerable tissues. When the leaves are shed, the petiole up to the point of attachment of the basal pair of leaflets from the branch and the stipule sheath persist on the branch (Figure 2a).

**TRICHOME AND VESTITURE TYPES.**—The type and placement of trichomes on various surfaces and the resultant appearance of the surface (vestiture) of the plant parts (especially the stipule sheaths, leaflets, and fruits) are important taxonomic characters in *Polylepis*. Unfortunately, uses of various terms are not consistently employed by various authors. Bitter (1911b) divided the trichomes found throughout the genus into two principal types: *capilli resiniferi* or *capilli pulverulenti* and *pili*. The first included most multicellular trichomes (usually glandular) and the second the various types of single-celled trichomes or trichomes with one or two basal cells. In this treatment, the first types of trichomes are simply referred to as multicellular trichomes and designated as glandular if they appear to contain, or have secreted, resin. The single-celled trichomes or those with a long terminal cell subtended by one or two small cells can vary from short to long, curled to straight. On various surfaces, they appear downy, woolly, shaggy, rough, or silky. Throughout this treatment, the following usages for vestiture types have been employed.

**Barbate:** with a tuft of long, curled trichomes; usually used for trichomes on the apices of the anther sacs.

**Hispid:** with long, straight, stiff, upright trichomes.

**Lanose:** with long, twisted, interwoven trichomes producing a coarse, woolly effect.

**Pannose:** with short, twisted, very matted trichomes producing a feltlike appearance.

**Pilose:** with short, weak, thin, twisted trichomes; variable in density.

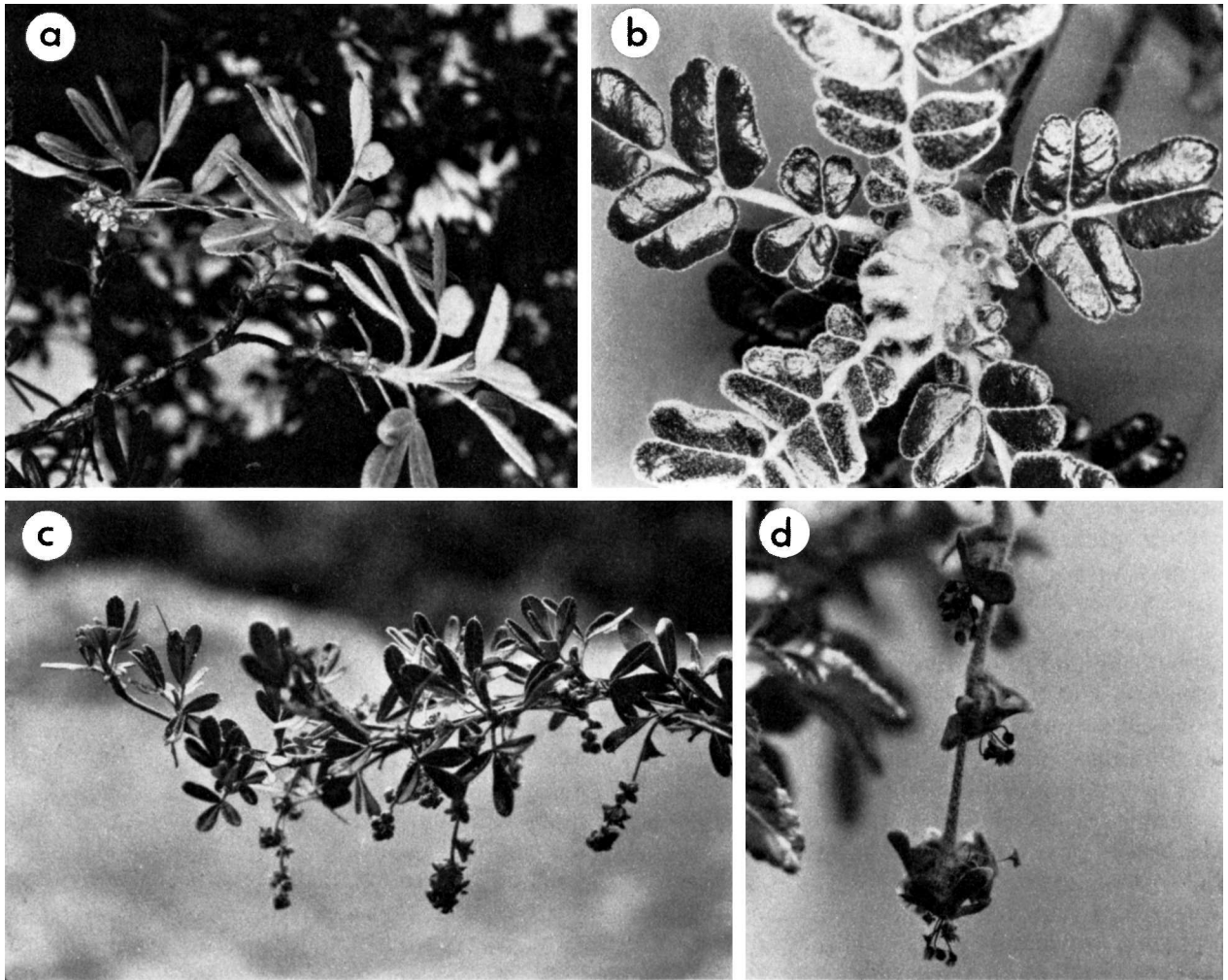


FIGURE 2.—Branching and flowering patterns of *Polylepis* species: *a*, congestion of leaves of *P. racemosa* at the branch tips with persistent petioles surmounting the stipule sheaths of dehiscent leaves; *b*, young leaves at the tips of branches of *P. weberbaueri* appear almost whorled because of the congestion; *c*, branch of *P. incana* with pendant inflorescences; *d*, an inflorescence of *P. besseri* showing the spreading stigma in the lower rear right flower and the hairy anthers on the exposed long-filamented stamens.

Puberulous: with very short, curved trichomes closely packed and producing a downy appearance.

Sericeous: with straight, long trichomes lying flat on the surface and presenting a silky surface.

Strigose: with straight, rather stiff trichomes appressed to the surface and producing a rough appearance.

Tomentose: covered with long, straight trichomes, the trichomes upright and consequently not producing a silky surface; usually used here for trichomes on the apices of the anther sacs.

Villous: with long (over 1 mm), weak, twisted, shaggy trichomes giving a loosely tangled appearance.

LEAVES AND LEAFLETS.—All species of *Polylepis* have compound, imparipinnate leaves, but the number of pairs of leaflets varies within and between species. Within a range of one or two pairs, the number of leaflets is a useful character for distinguishing between species or species groups. Of greater taxonomic utility, however, are the size, shape, thickness, and vestiture of the leaflets. Since the flowers have no modifications for animal pollinators (see below), there are relatively few floral

characters that can be used to distinguish species. Consequently, leaf and leaflet characters take on primary importance for the identification of taxa.

The arrangement of the leaflets and the position from the terminal leaflet of the largest pair of leaflets determine the shape of the leaf. In species with one pair of leaflets, the outline of the leaf is usually rhombic. Depending upon the position of the largest pair, the leaf can be trullate to obrullate in taxa with more than one leaflet pair (Figure 14).

Various taxa differ from one another in the type and amount of trichome coverage of the rachis and the appearance of the top surface of the rachis where the leaflets are attached. The rachis can be tomentose, villous, lanose, sericeous, pilose, or glandular. Often glandular trichomes are mixed with some type of single-celled trichome. Bitter (1911b) often used the presence of glandular trichomes as the basis for the circumscription of a variety (i.e., *P. microphylla* var. *polyarthrotricha*). Within a population, however, individuals vary in the amount of such trichomes. Nevertheless, some species such as *P. tomentella* or *P. incana* often have a preponderance of glandular trichomes that helps to distinguish them from other similar taxa.

The vestiture of the point of leaflet attachment is distinctive in some species of *Polylepis* although the density of trichomes and the amount of glandular trichomes present at this point is often variable within a species. Most taxa have some sort of a hispid vestiture appearing as a tuft of trichomes (e.g., Figure 8c), but leaves of *P. weberbaueri* have no differentiated trichomes on this part of the rachis or only a band of dark, glandular trichomes (Figure 24e). The glandular trichomes present at the point of leaflet attachment often secrete resin, which produces a crust of red or orange material.

The most important taxonomic characters for distinguishing species of *Polylepis* are provided by the leaflets. Leaflet characters are often correlated with others, such as the length of the inflorescence or protuberance type on the fruits, and present the most visible characters for distinguishing taxa. Useful characters include the shape of the outline, the size of the leaflet, the apex type, the aspect of the base, and the vestiture. Most members of the *sericea* group have ovate, entire, or serrate leaflets with acute or obtuse apices. Members of the *reticulata* group have elliptic or almost orbicular leaflets strongly emarginate at the apex. Leaflets of the

*incana* complex are obovate, crenate, and attenuate at the base.

The vestiture of the under leaflet surfaces, and to some extent of the upper leaflet surfaces, is very species specific, although the density of trichomes can often vary within a species. Members of the *sericea* group, for example, usually have long, silky trichomes on the under leaflet surface, but the pattern of the location of the trichomes varies from one species to another (Figure 3). In the *reticulata* group, all taxa have matted, feltlike trichomes on the under leaflet surface but differ in the presence or absence of a second type of trichome. The species of the *incana* complex all have, to some extent, small glandular trichomes, which secrete a yellowish resin, dispersed on the under surfaces.

The appearance of the upper leaflet surface provides an additional character for the separation of taxa. The surface can be nitid, rugose, dull, or variously puberulous (Figure 4).

LEAF ANATOMY.—In his monograph (1911b), Bitter emphasized the importance of the internal structure of the leaves for systematic purposes. Since Bitter tended strictly to apply a typological method and apparently examined only one or a few leaves of each of his narrowly defined taxa, the anatomy of the leaves appeared to be quite constant within a taxon. We have examined the anatomy of leaves of populations of every species, including all of the forms that would have been given specific status by Bitter. While it is true that there are modifications of the internal leaf structure that correlate with the varying habitats of the different taxa, there is too much variation within one species (Figure 5) and too much overlap between species (particularly species of the same species group) to make leaflet anatomy a practical way of distinguishing between taxa.

Basically, the leaves of all species are built on a plan of dorsiventral arrangement of cells, with the epidermis and palisade layer on the adaxial surface and the spongy tissue on the abaxial surface (Figure 4a). In different species, there are modifications that include an increase in the thickness of the cuticle (Figure 5), smaller and more regularly arranged epidermal cells, a more tightly packed series of palisade layers (Figure 6), reduction of the spongy tissue, and an invagination of the lower leaf surface so as to produce stomatal crypts (Figures 4d, 6). In almost all species there are bundle sheaths with

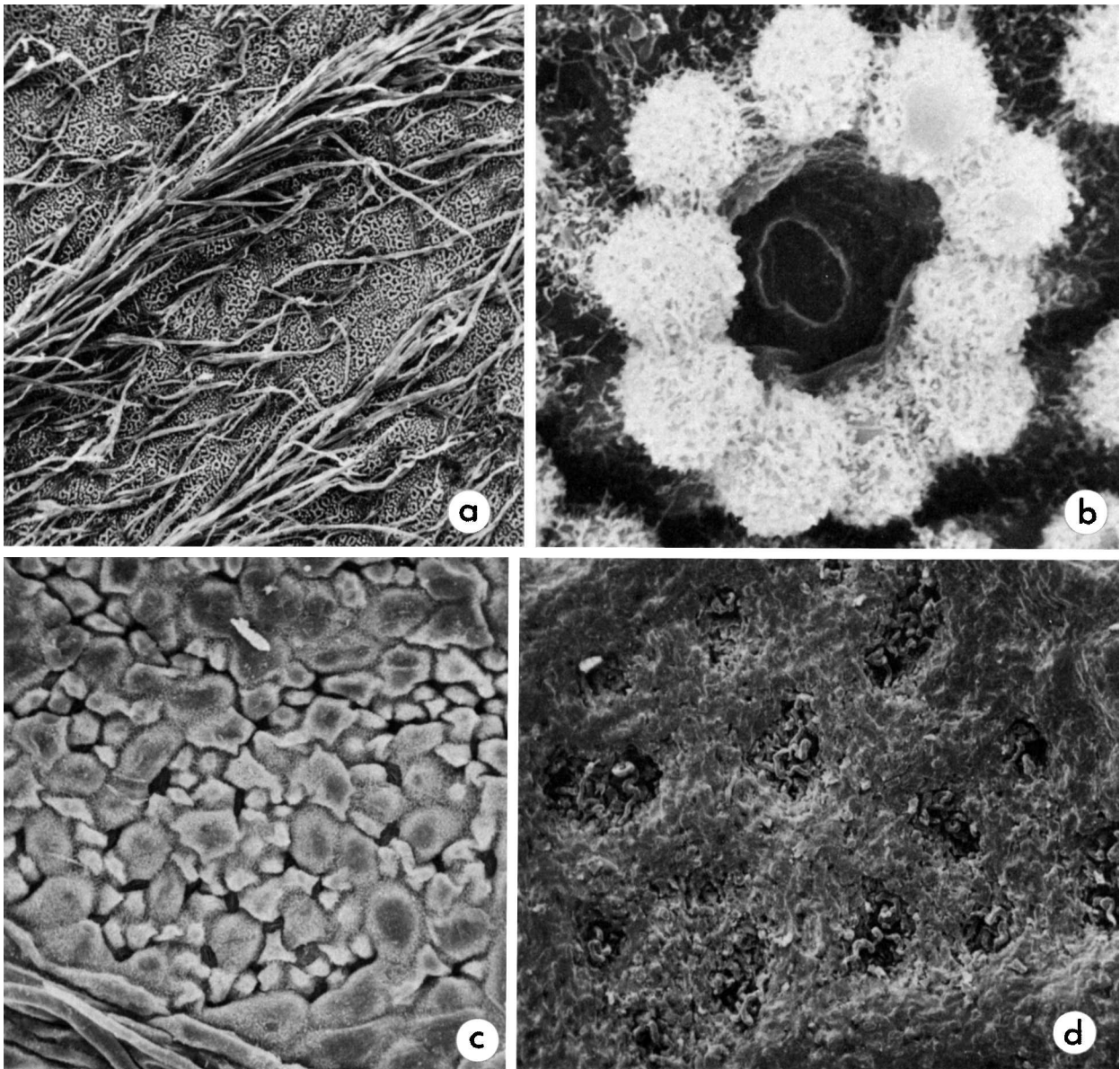


FIGURE 3.—Leaflet surfaces of *Polylepis* species: *a*, underleaf surface of *P. pauta* with trichomes restricted to the veins and stomates sunken in the areas appearing as circles ( $\times 50$ ); *b*, a stomate from 3*a* ( $\times 2500$ ) showing the papillose subsidiary cells; *c*, underleaf of *P. pepeii* from which the trichomes have been scraped away and on which the stomates are deeply sunken and surrounded by irregular subsidiary cells ( $\times 300$ ); *d*, underleaf surface of *P. racemosa*, with accessible trichomes scraped away revealing the depressions (stomatal crypts) in which the stomates are sunken ( $\times 100$ ).

extensions. Usually there are rhomboid crystals throughout the cells of the bundle sheath extensions (Figures 4*b*, 5*b*, *d*, 6*b*), but their arrangement is variable within leaflets from the same leaf.

Many of the features associated with the leaflets

are adaptations to the physiological drought with which many taxa are faced (Openheimer, 1960). In the species that grow at the upper parts of the moist ceja de la montana, xeromorphic adaptations are less pronounced. All of the members of the *sericea*

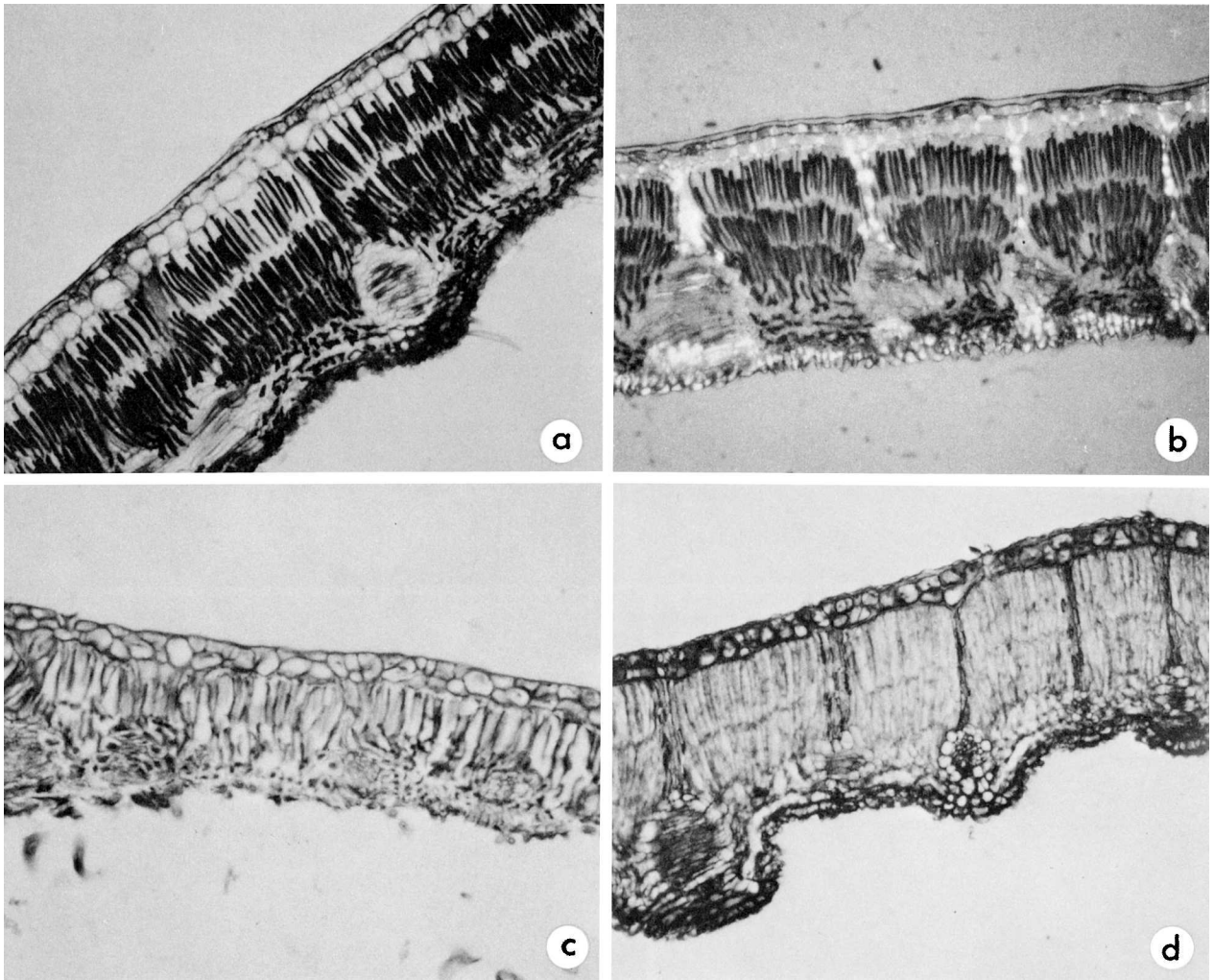


FIGURE 4.— Leaflet cross sections of *Polylepis* species (all  $\times 105$ ): *a*, *P. sericea* (*sericea* group) under normal light microscopy showing the dorsiventral arrangement of the leaflet cells with a thin epidermis, a 2- or 3-layered palisade layer and a small amount of spongy tissue; *b*, another leaflet of *P. sericea* viewed under polarized light revealing the crystals in the cells of the bundle sheath extensions; *c*, *P. multijuga* (*sericea* group) with its irregular epidermis and rather loosely organized palisade layer; *d*, *P. tomentella* (*incana* complex) with an invaginated under-leaflet surface and prominent bundle sheath extensions.

species group have comparatively mesomorphic leaves. The leaflets are large and thin relative to their surface area (Figure 4*a, b, c*). The cuticle is thin. The under surface of the leaflet is flat, although usually covered, at least in part, with trichomes. The cells of the epidermis and palisade layers are not tightly compacted although they can be quite regular (Figure 4*a, b*). Other species also found at lower elevations and/or generally found in relatively mesic habitats (e.g., *P. australis*, *P. hieronymi*) have

similar leaflet anatomies. Species found at higher elevations and in drier habitats show a progression of specializations. The cuticle becomes markedly thicker (Figure 5), the leaflet becomes thicker relative to its surface area (Figure 5), the epidermal layers become more compact, more regular, and composed of smaller cells (Figures 4*d*, 6). In addition, the undersurface of the leaflets of these taxa has invaginations known as stomatal crypts in which the majority of the stomates occur (Figure

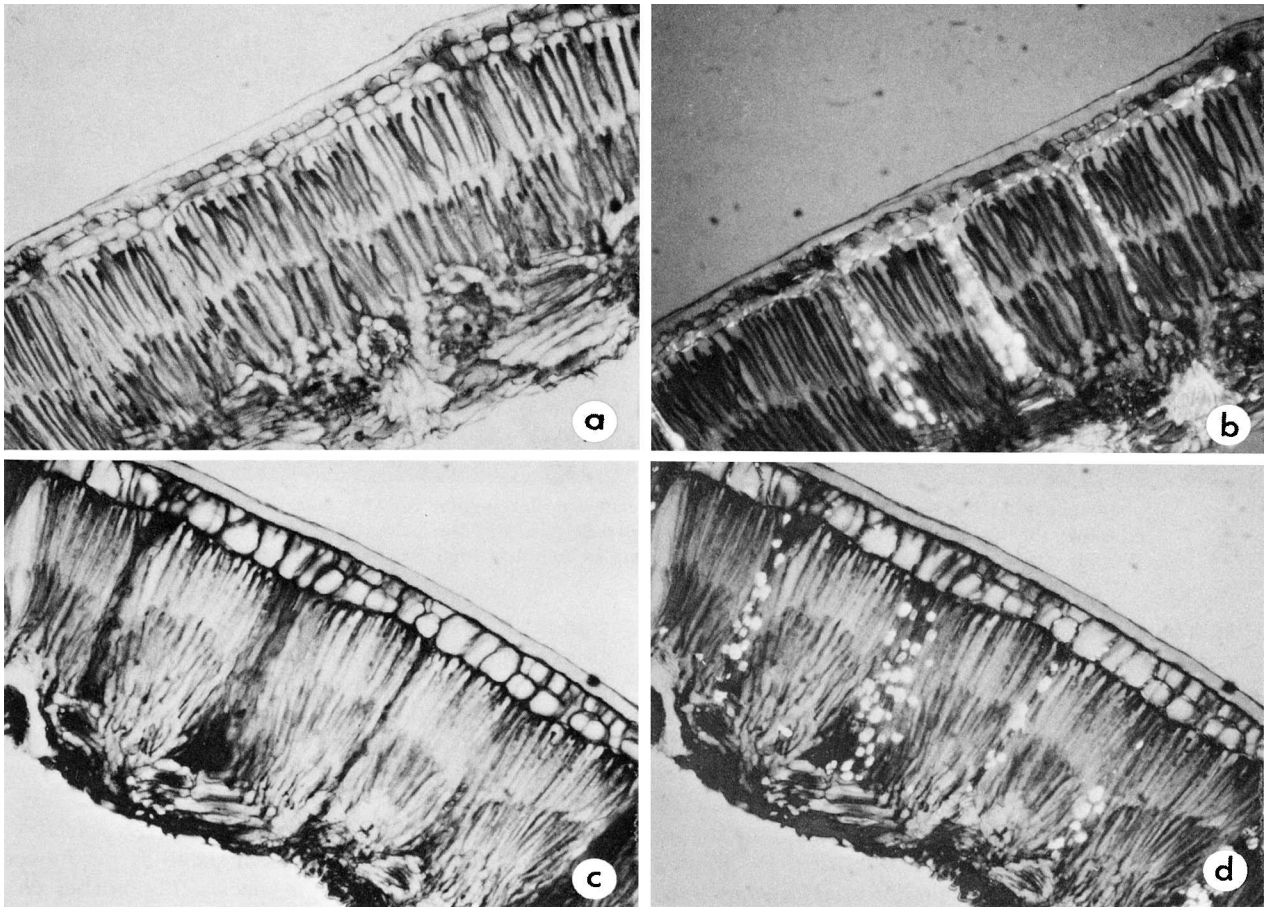


FIGURE 5.—Cross sections of the leaflets of *Polylepis reticulata* ( $\times 105$ ), showing the intraspecific variability in the number of cell layers of the epidermis and the thick cuticle characteristic of members of the *reticulata* group: *a*, *b*, the same leaflet under regular light (*a*) and polarized light (*b*) with a 2-layered upper epidermis; *c*, *d*, another leaflet under regular (*a*) and polarized (*b*) light with an epidermis primarily one cell layer thick.

3*d*). Stomates are often sunken (Figure 3*c*) and/or surrounded by papillose subsidiary cells (Figure 3*b*). The dense covering of trichomes or resin on the under leaf surfaces help prevent desiccation when the stomates are closed.

Bitter (1911*b*) remarked on the groups of cells now known as bundle sheath extensions. He called these cells "pillar cells" and ascribed a supportive function to them. Under the microscope, these bundle sheath extensions do look like pillars of buildings (Figure 4*d*), but more recent investigations have ascribed other functions to them. It now ap-

pears that these cells serve to conduct water to the epidermis (Wylie, 1951), rather than to serve as supports, but the fact that the walls of these cells are often thickened might indeed provide some strengthening for the leaflets. In an environment with almost daily freezing and thawing, leaf cells must be subjected to repeated and severe physical stress. Crystals are commonly found in these cells in a variety of plants throughout the angiosperms (Fahn, 1974). In a few species such as *P. reticulata* and *P. weberbaueri*, raphites are found scattered in the cells of the spongy layer.

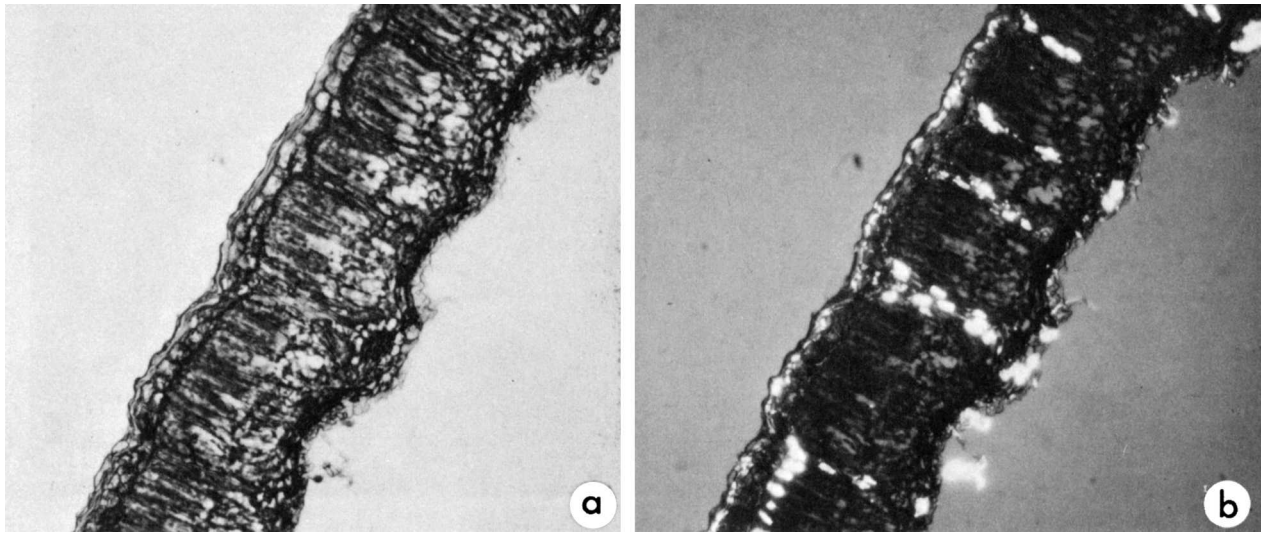


FIGURE 6.—Cross sections of *Polylepis bessei* leaflets under regular (a) and polarized (b) light show the invaginated lower epidermis, the small cell size, and the packed arrangement of the cells characteristic of members of the *incana* complex found at high elevations ( $\times 105$ ).

**INFLORESCENCES AND FLOWERS.**—The flowers of all species of the genus are borne on inflorescences. In most cases the inflorescences are long enough to hang pendantly (Figure 2c), but in the westernmost populations of *P. tomentella* and in at least one population of *P. pepeii*, the inflorescence is so reduced that it remains almost hidden in the leaf axil. Such an extreme reduction (Figure 31) contrasts with the very long racemes of *P. multijuga* (Figure 8). It appears that the single-flowered racemes represent a reduction that resulted from selection against exposed flowers at extremely high elevations. Although not investigated in Andean regions, Hedberg (1964) showed that it was common for Afroalpine plants to nestle the flowers in a “protective” bed of leaves and trichomes. The reduced inflorescences of *Polylepis* are surrounded by densely pubescent young leaves and stipule sheaths.

In the species with pendant inflorescences, the flowers are borne regularly along the rachis or clustered toward the terminal end. All flowers are subtended by a bract. The flowers themselves are reduced and have many features associated with wind pollination (Whitehead, 1969). These include: the absence of petals, green rather than colored sepals, an absence of scent or nectar, numerous anthers with long filaments, abundant, dry pollen, a large, spreading, fimbriate stigma (e.g., Figure 2d), pinnately compound leaves and the growth of trees in

stands. The reduced inflorescences of some populations might seem ill-adapted for wind pollination, but the reduction must represent a compromise between overexposure of vulnerable pollen mother cells and adaptations to wind pollination. Species with reduced inflorescences normally grow in very windy areas.

The number of stamens is exceedingly variable, even within a species. Counts of six to 24 per flower have been made for a single species. The anther sacs are often red or purple and always have trichomes on part or all of the surface. The presence of antheridial trichomes was considered by Bitter (1911b) to be a major character separating *Polylepis* from *Acaena*. The trichomes are single celled, straight or curled, and most commonly restricted to, or most dense on, the apex of the sacs.

The flowers of all species examined are strongly protogynous, which suggests that the trichomes of the anthers serve to insulate the developing pollen grains while the flower is slightly open and the stigma receptive (Figure 26e). After a period of time, the flowers open fully, the anthers dehisce longitudinally (Figure 26d) and the stigma withers. As the pollen is shed, the anther sacs curl in such a way as to turn the anthers “inside out.” The trichomes are consequently “inside” the anther at the end of anthesis (Figure 2d). Although protogyny would tend to increase outcrossing, the flowers mature

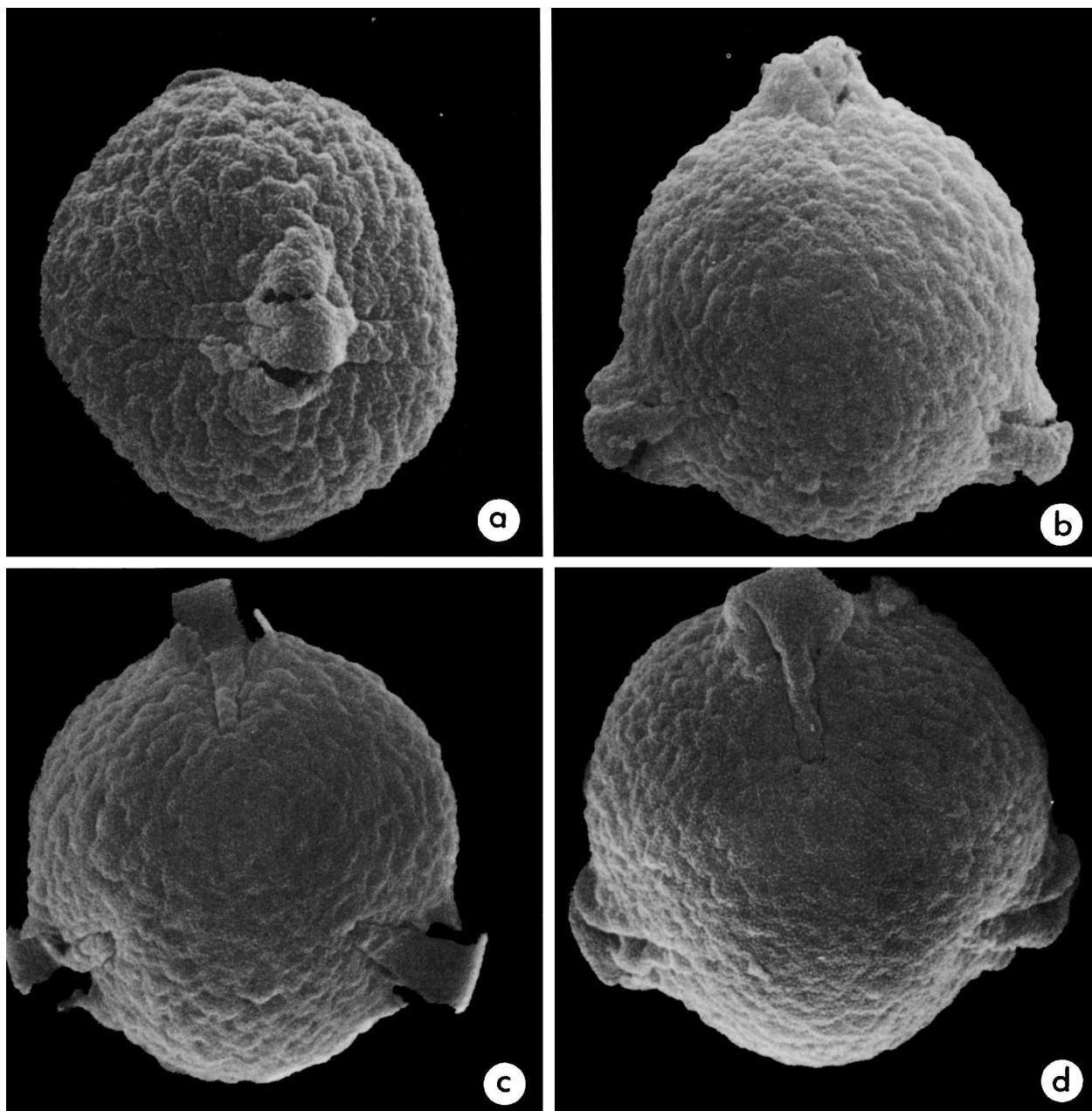


FIGURE 7.—Pollen of *Polylepis* species shows the uniformity of pollen within the genus and the similarity of pollen of related members of the Sangisorbeae: a, *P. besseri*, equatorial view ( $\times 2100$ ), *Simpson 8570* (US); b, *P. besseri*, polar view ( $\times 2200$ ); c, *P. incana*, polar view ( $\times 2100$ ), *Simpson 8544* (US); d, *Margyricarpus pinnatus* ( $\times 2200$ ).

sequentially from the base to the tip of the inflorescence and inflorescences mature at different times within a tree. Consequently, unless physiologically prevented, self-pollination could easily occur.

The ovary is sunken in a surrounding floral cup from which the stigma protrudes. The base of the style, where it emerges from the floral cup, often bears a ring of trichomes appearing as a tuft after

the style has withered. In a few species, trichomes extend up the style. Bitter (1911b) described several varieties on the basis of the presence of these trichomes continuing up the style; however, the character is variable within populations of several species.

**POLLEN MORPHOLOGY** (description provided by Joan W. Nowicke).—We have examined the pollen of all species of *Polylepis* recognized here by scanning electron and light microscopy following preparation by acetolysis (Erdtman, 1952). Figure 7a–c shows two representative grains. The survey indicated no significant differences between species in exine morphology. In addition, widths of pollen grains (10 per sample, four samples per species) were recorded from acetolyzed grains of four species. No significant differences were found in size. In fact as illustrated by Figure 7d, pollen of *Margyri-carpus* and *Acaena* is also exceedingly similar to that of *Polylepis*. Not only would it be impossible to separate taxa of *Polylepis* from one another using pollen, but it would also be difficult to separate *Polylepis* from closely related genera on the basis of pollen alone. It is possible to distinguish between *Polylepis* and *Acaena* pollen only by using extremely high magnification (van der Hammen, pers. comm.).

The pollen of *Polylepis* can be described in the following way: Monads, isopolar, more or less spheroidal to slightly oblate in shape; (the following description of the apertures assumes that the long axis is perpendicular to the equator of the grain) 58–76 $\mu$  wide, 3-colporate, the limits of the endo-aperture obscure, the colpus (ectoaperture?) completely covered by a pontopericulum, the pontopericulum and adjacent sexine protruding at the equator to form a pouchlike extension; the nexine about equal to the sexine in thickness; the tectum slightly undulate to slightly rugose, the surface microechinate, the echinae evenly distributed.

**FRUITS.**—The fruits of *Polylepis* are actually achenes composed of the floral cup fused to the ovary. Fruits of all species are indehiscent and one seeded. The surface of the fruit of different species has ridges, knobs, spines, or wings. There are no definite sites for the placement of these different types of protuberances that appear irregularly over the surface. The type of protuberance, wings versus spines, or knobs versus wings, is useful for distinguishing between species.

Bitter (1911b) asserted that the fruits of all species must be wind dispersed because members of the genus are trees and are thus too tall for animals (presumably mammals) to brush against. However, the elaboration of spines on the fruits of many taxa (e.g., Figure 12e) would argue for animal dispersal although wind dispersal undoubtedly predominates in *P. australis* (Figure 38). Numerous birds forage or live in *Polylepis* trees and it is possible that they disperse fruits caught in their feathers. There are no records of birds eating *Polylepis* fruits.

### Geographical Distribution

Except for one series of populations, *Polylepis* is confined to the tropical South American Andes. Species range from northern Venezuela to northern Chile and adjacent Argentina. One group of extra-tropical populations is distributed in the mountains of northwestern Argentina. Although many species grow at extremely high elevations (4000 to over 5000 m) in habitats that became available for colonization only at the end of the Tertiary (Simpson, 1975, 1979), several other taxa grow at much lower elevations (to 1800 m). The occurrence of species at relatively low altitudes mixed with montane forest elements indicates that components of the genus could have been present in western South America in the Miocene or even earlier. Radiation and specialization appear to have occurred northward and southward from the vicinity of northern Peru and to higher elevations.

Bitter's (1911b) statement that the highest number of species occurs in Colombia, Ecuador, and Peru was based on a count of his numerous artificial species. Using the taxa recognized here, the concentration of species is in Ecuador/Peru. In the mountains of these two countries, both low elevation, unspecialized, and high elevation, specialized, taxa occur. Since these groups of species are not closely related to one another, it appears that there have been several waves of north-south colonization along the Andean chain and differentiation has not been vertical at points along the Cordillera.

Geographical distributions of any particular species are practically impossible to determine with precision for several reasons. First, because of the high elevations and specialized microhabitats in which species occur, collections are few and tend to be concentrated in accessible areas such as Mérida

(Venezuela), Pichincha (Ecuador), central Perú, and northern Argentina. In addition, and of more serious consequence, trees of most species have been cut by man since prehistoric times for firewood or building materials. With the recent reexpansion of human populations in the high central Andes, cutting has accelerated. In contrast to this destruction of natural *Polylepis* populations is the tendency for Andean peoples to plant or shelter trees near houses or settlements. These two factors combine to produce an apparent distribution pattern that may bear little or no relationship to the original distribution of a species. In the mapping of distributions in this treatment, I have used specimen and literature data combined with personal observations. Since many are old collections (pre-1850), however, current distributions may now differ from those indicated for the various species.

### Ecology

Without doubt, many species of *Polylepis* possess some of the most unique autecological and synecological relationships of any angiosperm. While taxa that grow at relatively low elevations (e.g., members of the upper montane forest such as *P. multijuga*, *P. pauta*, and *P. hieronymi*) may have no more specialized adaptations than many other montane forest trees, those species forming woodlands at elevations between 4000 and 5200 m must possess a suite of specializations that allow them to withstand the peculiar conditions of these altitudes. In addition to formidable elevations, the highest habitats also tend to be semiarid since they occur on the western Cordillera of the central Andes, where mean annual rainfall averages between 200 and 500 mm. Moreover, tropical areas above 3600 m exhibit extreme variation in diurnal temperatures. Night temperatures are often below freezing throughout the year while midday temperatures are often 10–12°C higher. This kind of climatic regime causes the soil below about the top 30 cms to remain a constant 2–5°C (or lower) all year (Walter and Medina, 1969). In addition there is no period during the year in which plants can become truly dormant. Instead, they remain active (some are drought deciduous) all year, but under exceedingly harsh conditions. Theoretically, the daily freezing temperatures, the inability of roots to absorb nutrients below the uppermost soil levels that are heated

during the day, and the presence of a constant, drying wind should preclude tree growth. The occurrence of woodlands at elevations up to 5200 m therefore presents a physiological problem. Explanations for the distribution patterns of *Polylepis* have been advanced by several workers.

The classic studies of Andean geography are those of Carl Troll (see Troll, 1959 for references). In many of his expositions, Troll specifically discussed *Polylepis*. In all cases concerning species found within the puna zone or at the upper limits of the ceja (montane cloud forest), Troll considered *Polylepis* woodlands a distinctive type of vegetation different from true ceja, interandean scrub, or puna grassland. The ability of *Polylepis* to grow above the montane forest could, in Troll's opinion, be explained by the presence of microclimatic phenomena that produce "lower elevation" conditions. Such phenomena include the formation of cloud layers, especially at night, on some slopes and along low drainage areas, which prevent nighttime freezing of the soil.

In his discussions of Peruvian vegetation, Rauh (1950a,b) also indicated that *Polylepis* grows in specific elevational belts on west-facing slopes of (primarily) the Eastern Cordillera of Peru. Pulgar (1967) described *Polylepis* as a natural inhabitant of only his *suní* region. This geographical province is confined to eastern and western facing slopes between 3500 and 4000 m and contains no large, flat valleys. Within this zone *Polylepis* is prevalent along water courses. While lamenting the fact that there is no active reforestation of *quiñuales* (*Polylepis* woodlands) where they have been cut, Pulgar (1967:92) cited the custom ("almost a superstition") practiced by the Altiplano Indians of never cutting down an old *Polylepis* tree but merely exploiting the branches. In his discussion of the *puna* region (defined as the treeless flat plateau at 4000 to 4800 m), he mentioned the presence of *Polylepis* but asserted that individual trees in this zone had been purposefully or inadvertently planted by man. He gave an example of the robust growth of *Polylepis* trees within the town and around houses of Cerro de Pasco (Figure 1e) as an example of the former. In the latter case, trees near houses have resulted from sprouting of branches that were brought from lower regions and which were able to grow when sheltered by huts and walls (Figure 1f).

In contrast to all of these views is the hypothesis

of Ellenberg (1958a,b) that the high Andean puna, particularly that of the Altiplano of southern Peru and Bolivia, is a manmade grassland which was originally covered by evergreen tree or shrubland. The dominant woody taxa of these natural woodlands would have been *Polylepis*, *Buddleia*, *Puya raimondii*, and species of *Chuquiraga*. To support this hypothesis, Ellenberg first drew a parallel with the Mediterranean region of Europe, which he claimed has a similar climate to that of the puna and the vegetation of which has been shown to have been caused by man. He cited examples of *Eucalyptus* trees growing successfully at elevations of about 4000 m in the puna. He argued against the restriction of *Polylepis* to slopes with special microclimatic conditions by citing an example of a few trees he saw growing on a level area. The absence of trees anywhere in abundance except on "inaccessible" slopes is attributable, in his opinion, to the cutting of trees for firewood, the clearing of woodlands for pastureland, and the destruction of seedlings by domesticated animals in all other areas. He considered the apparent natural and integrated vegetation of the puna simply the result of immigration and establishment of grasses and forbes from the few prehuman tree-free areas over the last 400 years.

While Ellenberg's hypothesis cannot yet be disproved, it appears less likely than a hypothesis of natural localization of woodlands of *Polylepis* with an additional reduction due to human influence. As pointed out by Walter and Medina (1969), trees with a root system over a few centimeters deep cannot normally grow at very high elevations because of the inability of roots to penetrate or absorb water from soil that is between 0° and 4° C. Special situations are necessary to modify the usual prohibitive conditions. Walter and Medina (1969) proposed that *Polylepis* in Venezuela grows in rock areas where the crevices between the rocks allow warm air to reach considerable depths and hence allow root penetration and function as low as one meter or more. Recently, Smith (1977) tested this suggestion by planting seedlings of *P. sericea* (the native species) in open paramo and sheltered rocky areas at 3600 m in Mérida, Venezuela. No seedling survived one year in exposed areas. Seven trees (14%) planted in rocky areas were surviving at the time of the report (one year after planting).

It is obvious that an enormous amount of decimation and vegetative change has been caused by man

in the high central Andes, but Ellenberg's arguments are untenable on several other grounds. His examples are, for the most part, taken from artificial situations. *Eucalyptus* is an introduced genus in South America and the trees growing at high elevations have been carefully nurtured and protected. His comparison with the Mediterranean region is misleading in view of the enormous differences in climate. Despite the similarities in mean annual rainfall and mean annual temperature (the two parameters he gives) between the two areas (Walter et al., 1975), the dispersion of the precipitation and the annual versus diurnal temperature patterns are completely different. Around the Mediterranean, most of the precipitation falls in the winter and the area is typically temperate in that summers are warm and winters cool or cold. In the puna, rainfall is primarily during the southern summer. At any given hour of the day at a locality on the Altiplano, temperature is practically constant throughout the year, while within any one day there is as much as a 12°C temperature difference. Bliss (1956) has pointed out that there are great physiological differences between arctic and alpine plants (i.e., latitude and altitude vegetation types with similar physiognomies), even though they are similar in visual aspect.

Descriptions of many botanists and geographers who have worked in the Andes (Jameson, 1845; Hertzog, 1923; Weberbauer, 1945; Troll, 1959; Hueck, 1972) clearly indicate that *Polylepis* woodlands are, in the opinions of the authors, a specialized type of vegetation restricted to certain areas such as rocky slopes, river courses, valley bottoms, or slopes normally covered by cloud banks. Koepcke (1961) particularly opposed Ellenberg's views. He logically pointed out that many areas (such as shown in his fig. 59 and in Troll, 1959, figs. 17 and 19) are accessible to man but still have flourishing *Polylepis* woodlands. He interpreted the survival of trees around houses on the Altiplano not as an indication of their ability to grow naturally at these elevations, but rather as a duplication by man of the normal specialized microhabitat conditions (i.e., protection from the wind, relatively warm soil conditions and, usually, increased water availability) of areas in which they naturally occur.

The only studies that shed any light on the possible paleohistory of *Polylepis* are those of van der Hammen and colleagues (van der Hammen, 1974

and references therein) in Colombia. Because *Polylepis* species are all wind pollinated, pollen cores provide a comparatively accurate record of their history in a given area. Cores from the Sabana de Bogotá and Laguna Fuquen, Colombia, spanning almost three million years provide such a record. The core at Bogotá clearly shows the first appearance of *Polylepis* in the area at about 600,000 years ago. Since that time, the fluctuating climates of the Pleistocene caused expansions and contractions of local *Polylepis* populations. During a warm wet period (about 30,000 years ago), the area from which the pollen cores were taken was dominated by *Polylepis* woodlands. Shortly afterward, as conditions became colder, low paramo elements became more abundant until, in drier periods, from 21,000 years ago, trees were so rare that essentially no grains appear in the cores. In the latest cores from Fuquen (10,820 YBP to present), the climate was warmer, but *Polylepis* never regained dominance, in part, perhaps, because the climate was already dry but also because of cutting and burning by man. Nevertheless, it is obvious that even at the low elevation (2650 m) of Bogotá, the distribution of *Polylepis* fluctuated during the Pleistocene and that a complete coverage of this high Andean area by woodlands was an uncommon event and has not occurred since 30,000 YBP—long before the active influence of man.

In addition to ecological arguments, it is hard to explain the differentiation of distinct taxa on the Eastern and Western Cordilleras as well as north-south along the Andean chain if there were a continuous woodland of *Polylepis* covering the mountains. Under circumstances of a more or less continuous cover, clinal variation should, at most, develop. However, until the physiology of *Polylepis* is more completely understood and the microclimatic conditions of the areas in which it now occurs more thoroughly investigated, the question of the potential distributional limits of the genus will remain unsettled. In any case, it will be impossible ever to know with certainty the natural prehuman distribution of the genus.

### *Polylepis* Ruiz and Pavon

*Polylepis* Ruiz and Pavon, 1794:80, Icon 15. [Type-species: *Polylepis racemosa*.]

Deciduous or evergreen trees or shrubs, 1–27 m tall. Bark of the trunk and larger branches deep red, many layered, the layers thin and exfoliating. Branching repeatedly sympodial with long, often bare branch segments and leaves slightly to strongly congested at the tips of branches. Leaves alternate, imparipinnate with 1–9 pairs of leaflets, the first to the third pair from the apex the largest, rhombic, trullate or obrullate in outline, 0.8–9.1 cm wide, 2–19 cm long, rachises sericeous, villous, with scattered twisted trichomes, glandular or glabrescent; point of leaflet attachment with a tuft of straight or twisted long trichomes, a ring of glandular trichomes, or both; stipules fused around the branches forming a sheath; the sheath with spurs on either side of, or sloping away from, the petiole, abaxial surface sericeous, villous, pubescent, glandular or glabrescent, apex with long trichomes often projecting from the inner surface. Leaflets lanceolate, ovate, oblong, or obovate in outline, 0.2–1.7 cm wide, 0.6–3.7 cm long, margins entire, revolute, crenate or serrate, apex acute, obtuse, emarginate or tridentate, base unequally cordate or attenuate; upper surface glabrous, glabrescent, minutely sericeous, hispidulous or with scattered multicellular trichomes (often most dense in the midvein depression); lower surface sericeous, minutely sericeous, hispidulous, villous, pannose or glandular, often with glandular trichomes mixed with another type, sometimes with a pannose covering under another layer. Inflorescences upright or pendant to 36 cm long, bearing 1 to over 60 flowers, the flowers closely packed or spaced along the rachis; floral bracts lanceolate to ovate, to 3 mm long, scarious to variously covered with trichomes; rachis sericeous, villous, pilose, pannose, glabrescent, or glandular. Flowers perfect (perhaps functionally female in some plants due to abortion of the anthers), 0.4–1.0 cm wide, sepals 3 or 4, lanceolate to ovate in outline, sericeous, villous, pilose or glandular on the outer face, sometimes pannose on the tips of the inner surface, persistent; stamens (4?) 6–36, basifixed, inserted on the floral cup at the base of the style; tomentose or barbate on the anther sacs, longitudinally dehiscent; style villous or hispid at the base, occasionally villous along most of the style; stigma peltate, orbicular, flat, expanded, fimbriate; ovary inferior, rarely protruding from the floral cup; carpel 1, ovule 1, pendulous. Fruit an achene, cylindrical, fusiform, turbinate or globose, variously

adorned with protuberances, spines, or wings, body and protuberances sericeous, pilose, lanose, villous, with scattered irregular single-celled or multicelled trichomes, glandular or glabrescent, from 0.2–1.4 cm wide including protuberances, 0.2–1.3 cm long. Seed

pendulous, the testa membranous and the cotyledons flat or slightly convex.

DISTRIBUTION.—In the Andes at elevations of 1800–5200 m from Venezuela in the state of Lara south to Tarapacá, Chile, and Córdoba, Argentina.

### Key to the Species of *Polyopsis*

1. Undersurface of leaflets covered with shiny, silky trichomes, the sericeous trichomes sometimes most prominent on the veins; or covered with dense, straight, short, appressed trichomes, or with long (> 2 mm) shaggy trichomes sometimes covering a shorter layer, not glabrous.
2. Undersurface of leaflets with silky trichomes or short, straight, dense, appressed trichomes.
  3. Trichomes very silky and covering entire under leaf surface, long, dense.
    4. Pubescence silvery or whitish; leaflets ovate or elliptic; apex obtuse .....5. *P. sericea*
    4. Pubescence golden red or white; leaflets obovate or broadly oblong; apex emarginate .....2. *P. lanuginosa*
  3. Trichomes confined to, or most prominent on, the veins of the undersurface of leaflets or short, straight, appressed, and overlying a lower layer of very short, matted trichomes.
    5. Leaves with 4–9 pairs of leaflets; leaflets acute or obtuse at the apex, ovate, oblong or lanceolate, margins serrate .....4. *P. pautia*
    5. Leaves with 1–3 pairs of leaflets; leaflets emarginate at the apex, obovate or narrowly oblong, margins entire.
      6. Undersurface of leaflets dull with short, appressed, straight trichomes over entire surface and overlying a layer of short, twisted trichomes; leaflets robust, yellowish margins crenate toward the apex; fruit more or less cylindrical with irregularly flattened spines .....6. *P. subsericans*
      6. Undersurface of leaflets shiny with short, silky trichomes, often most conspicuous on the veins and leaf margins; leaflets thin, green, margins entire, fruit elongate, slightly twisted, knobbed around the middle .....7. *P. pepeii*
2. Undersurface of leaflets with loose, shaggy, long (> 2 mm) trichomes that can cover shorter twisted or multicellular glandular trichomes.
  7. Leaves with 6–8 pairs of leaflets; inflorescences 17–36 cm long, flowers numerous, usually over 20 per inflorescence, densely packed; stipule sheaths strongly spurred .....1. *P. multijuga*
  7. Leaves with 3–4 pairs of leaflets; inflorescences 3–12 cm long, flowers fewer than 20 (occasionally 24) scattered; stipule sheaths lacking true spurs (although trichomes at the apex can produce the impression of a pointed spur).
    8. Stipule sheaths with prominent long, silky, white trichomes on the outer surface extending down the internode; leaves with 3–4 pairs of leaflets; undersurface of leaflets densely covered with shaggy white scattered trichomes .....3. *P. hieronymi*
    8. Stipule sheaths sparsely villous on the outer surface and with long twisted trichomes projecting at the apex from the inner face near the petiole; leaves with 1–3 pairs of leaflets; undersurface of leaflets sparsely covered with shaggy fulvous trichomes originating from the veins and with scattered glandular trichomes or protuberances .....14. *P. racemosa*
1. Undersurface of leaflets covered with dense, short (< 2 mm), twisted, matted, feltlike, white or yellowish trichomes or with scattered, short (< 2 mm) twisted, 1-celled trichomes, the short trichomes never covered by longer trichomes, but in cases often mixed with multicellular glandular trichomes, or glabrous.
9. Undersurface of leaflets lacking scattered yellow, multicellular glandular trichomes, pan-nose or lanulose, not glabrous; plants of Colombia and Ecuador or northern Peru.
  10. Revolute leaflet margins and undersurface of leaflet apex with short, straight trichomes distinctive from the pan-nose covering of most of the undersurface of the leaflet; leaves with 2–3 pairs of leaflets .....8. *P. reticulata*
  10. Revolute leaflet margins and undersurface of the leaflet apex without a distinctive type of trichome; leaves with 3–5 pairs of leaflets.

11. Upper surface of leaflets very nitid, when young covered with long, shaggy white trichomes; stipule sheaths with acute spurs, inflorescences 5.8–14 cm long with 8–18 flowers; fruits with flattened spines; small trees or shrubs (less than 2 m tall) of southern Ecuador and northern Peru .....9. *P. weberbaueri*
11. Upper surface of leaflets rugose or slightly nitid, occasionally with scattered long trichomes; young leaflets without conspicuous white trichomes; stipule sheaths obtuse at the apex; inflorescences 2.1–5.4 cm long with 3–7 flowers; fruits with thin, terete spines; trees 5–8 m tall of Colombia and Ecuador ....10. *P. quadrifuga*
9. Undersurface of leaflets with yellow multicellular glandular trichomes and resinous exudate mixed with short matted trichomes, or glabrous; plants of Ecuador, Peru, Bolivia, or Argentina.
12. Undersurface of leaflets glabrous.
13. Fruits strongly winged, the wings as wide as the body of the fruit; leaflets broadly lanceolate, almost serrate .....15. *P. australis*
13. Fruits with irregular ridges, narrow wings, or spines; leaflets obovate or oblong, crenate or entire.
14. Fruit with irregular ridges, sometimes flattened into narrow wings; plants of Bolivia .....12. *P. tomentella*
14. Fruit spiny; plants of Colombia, Ecuador or Peru.
15. Apex of leaflets obtuse or acute, leaflet shape elliptic to narrowly ovate, fruits with knobs or stout spines .....5. *P. sericea*
15. Apex of leaflets emarginate, leaflet shape broadly ovate, fruits with irregular thin spines .....10. *P. quadrifuga*
12. Undersurface of leaflets with short matted trichomes, glandular trichomes, or both.
16. Undersurface of leaflets with dense, matted trichomes usually mixed with glandular trichomes most prominent on the veins and leaf margins; plants of southern Peru, Bolivia, northern Chile, and northern Argentina.
17. Undersurface of leaflets with matted gray or white trichomes; stipule sheaths pubescent; fruit with spines prominent at the apex and projected upward, sometimes flattened at the base .....11. *P. besseri*
17. Undersurface of leaflets with a dense covering of matted white or yellowish trichomes; stipule sheaths with glandular trichomes at the apex, glabrous below; fruits with short, irregularly positioned blunt spines or blunt spines flattened and coalesced into a narrow, wavy wing extending the length of the fruit .....12. *P. tomentella*
16. Undersurface of leaflets with sparse, scattered trichomes and irregularly scattered yellow glandular trichomes; plants of Ecuador and central Peru .....13. *P. incana*

### 1. *Polylepis multijuga* Pilger

*Polylepis multijuga* Pilger, 1906:536. [Type collection: at Chugar near Hualgayoc, Cajamarca, Peru, 2700–3000 m, May 1904, *Weberbauer 4098*. Type destroyed, isotypes WRS�, G!]

Trees 4–15 m tall. Leaves only slightly congested at the ends of the branches (Figure 8a), imparipinnate with 6–8 pairs of leaflets, obtrullate in outline, 6.4–9.1 cm wide, 12.2–19.5 cm long; rachises lanose, point of leaflet attachment (Figure 8c) with a tuft of long, straight trichomes (some with stalked basal cells) mixed with small, clavate, multicellular glandular trichomes; stipular sheaths acute at the apex with spurs reaching 1 cm in length, densely sericeous on the outer surface. Leaflets broadly lanceolate or ovate in outline, second or third pair from

the terminal leaflet the largest, one of this pair 1.1–1.7 cm wide and 3.0–3.6 cm long; margins serrate; apex acute, base unequally cordate; upper leaf surface sparsely villous in the midvein depression; lower surface densely lanose with individual trichomes 1–2 cm long (Figure 8b). Inflorescences pendant, 17.3–36.0 cm long, bearing numerous (often more than 45) flowers; floral bracts small, sericeous on the outer surface; rachises sericeous. Flowers perfect, 0.4–0.8 cm in diameter (Figure 8d); sepals 3 or 4, ovate, lanose on the outer surface; stamens 5–16, circular in outline, tomentose; style hispid at the base. Fruit more or less fusiform, sericeous, with irregular spines up to 4 mm long (Figure 8e), sometimes with long trichomes on the spines, 0.6–1.1 cm wide including spines and 0.3–1.0 cm long.

DISTRIBUTION.—Northern Peru in the provinces

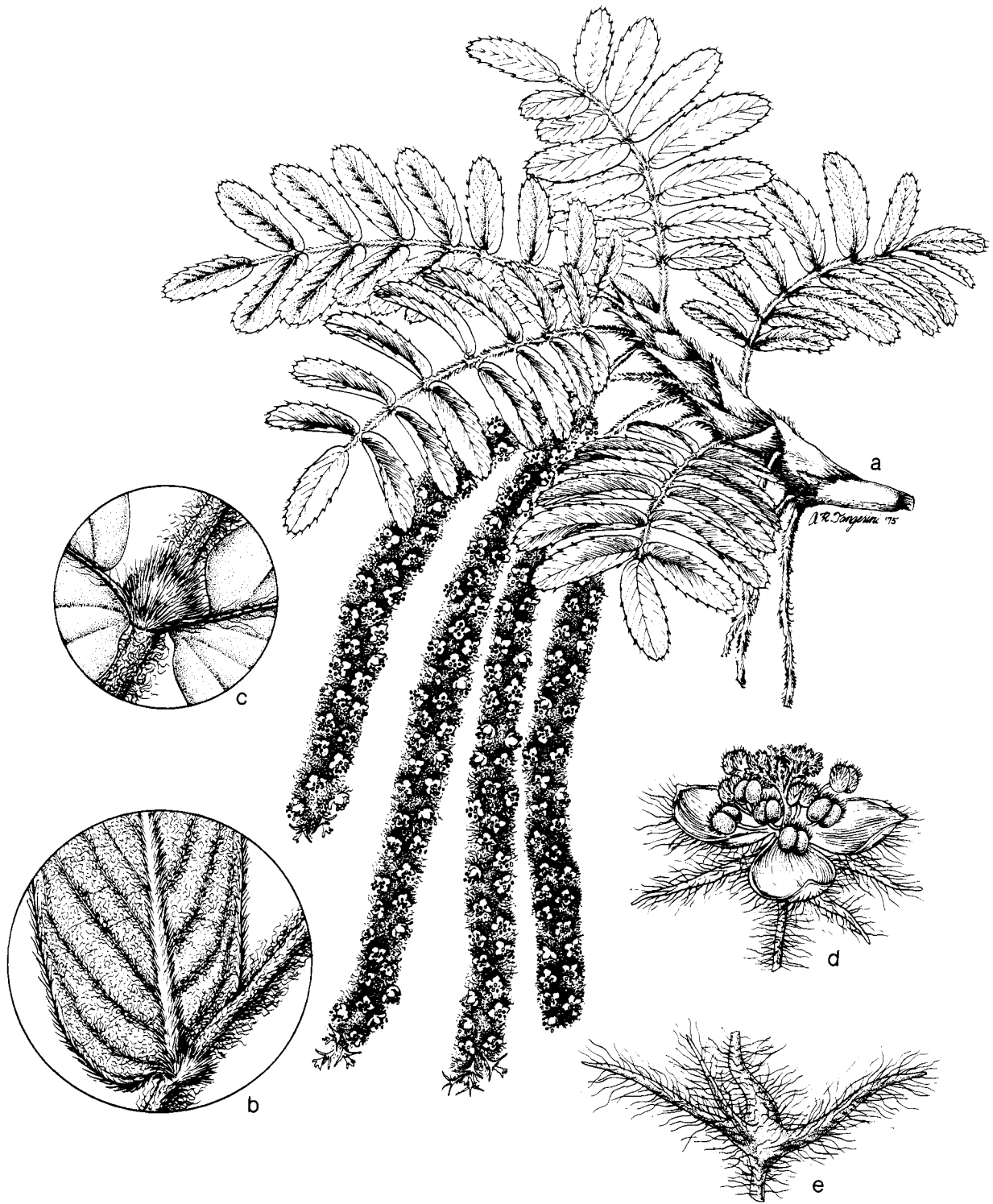


FIGURE 8.—*Polylepis multijuga*: a, branch ( $\times 0.5$ ); b, undersurface of leaflet ( $\times 3$ ); c, point of leaflet attachment ( $\times 6$ ); d, flower ( $\times 6$ ); e, fruit ( $\times 6$ ).

of Amazonas and Cajamarca (Figure 9). Flowers recorded in May, July, and from September to December.

COMMON NAME.—Quiñua.

USES.—The red heartwood is reported to be used for furniture manufacture.

REPRESENTATIVE SPECIMENS EXAMINED.—PERU. AMAZONAS: Chacapoyas, *Matthews s.n.* (K). CAJAMARACA: Hualgayoc, Hacienda Taulis, 13 km beyond Palmito Junction toward La Playa, 2900 m, 2 Sep 1964, *Hutchison & Bismark 6463* (F, MO, NY, P, UC), 3200 m, 15 Oct 1954, *Rauh & Hirsch P2249* (NY).

DISCUSSION.—In the small restricted area of northern Peru in which it grows, *Polylepis multijuga* occurs as low as 2500 m mixed with species of tree ferns, *Podocarpus*, *Chusquea* and *Berberis*, its branches often covered with *Tillandsia* and epiphytic orchids. Bitter considered this species to be the most primitive of the genus. Numerous characters involving morphology, anatomy, and ecology seem to reinforce this conclusion. The leaves are large, thin, and reminiscent of those of some species of *Acaena*. The inflorescences are large and pendulous, presumably the ancestral type for the genus. The

fruits, like those of all of the members of this species group, and species of *Acaena*, are spiny and appear to be dispersed by animals. More advanced taxa have become increasingly dependent on wind as a dispersal agent. Finally, the species is an integral member of the upper montane rainforest (ceja de la montana), rather than a fringe species or one that grows completely isolated from the montane forest in the higher elevations.

The species most similar to *Polylepis multijuga*, *P. pauta*, can be distinguished from it by several leaf characters. The leaves of *P. multijuga* are larger than these of *P. pauta*, the lower surfaces are covered by wooly rather than silky hairs, and the trichomes at the point of leaflet attachment often have multicelled bases. In addition, the apices of the stipule sheaths of *P. multijuga* are larger and more rounded than those of *P. pauta* and the inflorescences, in the specimens I have seen, are much larger, both in length and in the number of flowers they bear. This species differs from *P. lanuginosa* in having more numerous leaflets, obtuse rather than emarginate leaflet apices, and a lanose rather than sericeous under leaflet covering.

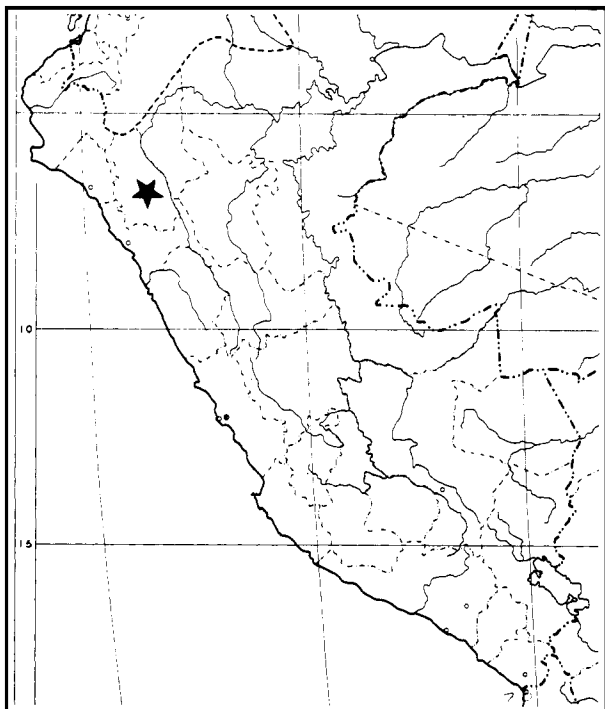


FIGURE 9.—Collection localities of *Polylepis multijuga*.

## 2. *Polylepis lanuginosa* Humboldt, Bonpland, and Kunth

*Polylepis lanuginosa* Humboldt, Bonpland, and Kunth, 1824: 228. [Type collection: near Calpi, Chimborazo, Ecuador, June, *Bonpland 2191*. Holotype P!, isotype P!]

*Polylepis lehmannii* Hieronymus, 1895:29. [Type collection: west of Cuenca, Azuay, Ecuador, *Lehmann 6487*. Type destroyed, Rockefeller photograph no. 3387, types of the Berlin Herbarium, isotypes GH! NY!]

*Polylepis coriacea* Bitter, 1911b:603. [Type collection: Valley of Pangor, Ecuador, *Spruce s.n.* Holotype W!]

Small trees (?) to 4 m tall. Leaves fairly congested at the ends of the branches, imparipinnate with 2–3 pairs of leaflets (Figure 10a), obovate in outline, 2.9–4.2 cm wide, 4.5–7.2 cm long; rachises villous; point of leaf attachment with a small tuft of long straight trichomes; stipular sheath with acute, densely sericeous spurs, the hairs red gold in color. Leaflets (Figure 10a) obovate or oblong in outline, first or second pair from the apex the largest, one of this pair 0.9–1.4 cm wide, 2.0–3.1 cm long; margins crenate or revolute; apex emarginate; base unequally cordate, upper leaf surface rugose or dull, sometimes with trichomes scattered in the vein de-



FIGURE 10.—*Polylepis lanuginosa*: a, branch ( $\times 0.5$ ); b, lower leaflet surface at point of leaflet attachment ( $\times 3$ ); c, flower ( $\times 6$ ); d, fruit ( $\times 6$ ).

pressions; undersurface densely sericeous, the trichomes white or golden red, often with a covering of short wooly trichomes under the silky hairs. Inflorescences (Figure 10a) pendant, sometimes branched, 0.9–4.4 cm long, bearing 4 to 20 flowers; floral bracts lanceolate, sericeo-lanose; rachises lanose. Flowers (Figure 10c) perfect, about 0.7 mm in diameter, sepals 4, ovate, outer surface villous; stamens about 12, lanose at the apex; base of style hispid, lower part villous. Fruit (Figure 10d) fusiform, irregularly spined, the spines flattened or thin, usually villous, body of the fruit pilose; 0.5–0.9 cm wide including spines, 0.3–0.6 cm long.

**DISTRIBUTION.**—Apparently restricted to central and southern Ecuador in the provinces of Chimborazo, Azuay, and Cañar (Figure 11). Flowering recorded April to June.

**COMMON NAME.**—Quiñal.

**USES.**—None specifically reported.

**REPRESENTATIVE SPECIMENS EXAMINED.**—ECUADOR. AZUAY: west of Patul, 3 km between Huahualcay and Rio Patul below Pasas de Pinglion, 2670–3275 m, 19 May 1943, *Steyermark 52599* (F). CAÑAR: between Tambo and Suscal, north rim of the valley of the Rio de Cañar, 2000–3000 m, 23 Apr 1945, *Giler 2773* (F, K, NY); Cañar, 15 Sep 1918, *Rose & Rose 23789* (NY, US).

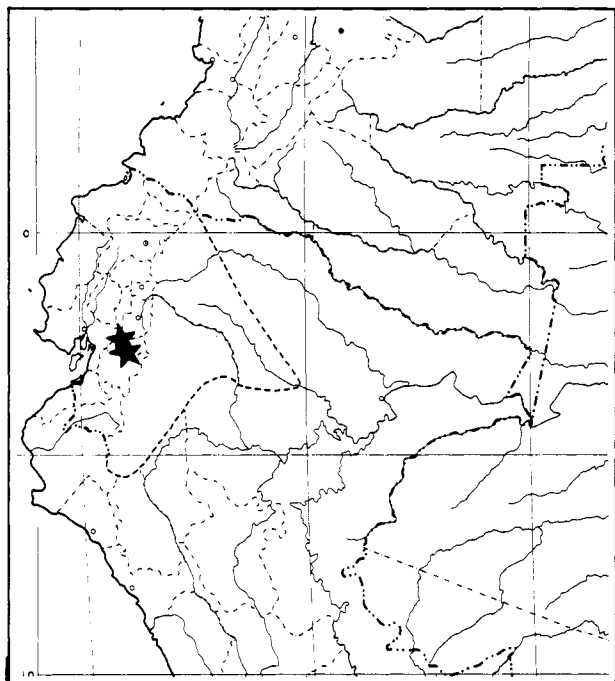


FIGURE 11.—Collection localities of *Polylepis lanuginosa*.

**DISCUSSION.**—Although similar in many morphological characters and probably derived from *Polylepis multijuga*, *P. lanuginosa* differs from it and all other members of the genus in its possession of branched inflorescences. In addition to this character, it differs from *P. multijuga* in leaflet pubescence, leaflet shape, and vestiture of the point of leaf attachment. The leaflets of *P. lanuginosa* are emarginate, the upper surface is rugose, the lower surface has a mixture of short wooly trichomes overlain by dense silky hairs. Leaflets of *P. multijuga* are acute, the upper surface flat, and the lower surface densely lanose. The point of leaflet attachment in the former is a small tuft of straight trichomes and in the latter a ring of glandular hairs mixed with long straight trichomes. The two species also have fruit differences: *P. multijuga* has terete spines on the fruit and *P. lanuginosa* has flattened spines.

There has been some confusion in the characterization of this taxon attributable in part to the specimens cited by Weddell in the *Chloris Andina*. Weddell's brief verbal description could be applied to many members of the genus, but he cites two specimens, neither of which belong with the type cited by Humboldt, Bonpland, and Kunth. Weddell's first specimen was the one he presumably considered the "true" *P. lanuginosa*; the second specimen corresponds to the variety  $\beta$  *microphylla*. Bitter correctly realized that neither of these specimens corresponded to the original *P. lanuginosa* and consequently made the first specimen the type of his new species, *P. quadrijuga*, and the second the type of *P. microphylla*. Nevertheless, Weddell's older application of the name *P. lanuginosa* was followed by many botanists and has often been misapplied to specimens of *P. quadrijuga* or *P. weberbaueri*.

### 3. *Polylepis hieronymi* Pilger

*Polylepis hieronymi* Pilger, 1906:535. [Type collection: Salinas, Cuesta de Pollo, Valle del Tambo, Bolivia, June 1873, *Lorentz & Hieronymus 938a*. Type destroyed, Rockefeller photograph no. 3355, types of the Berlin Herbarium at NY.]  
*Polylepis racemosa*  $\beta$  *hypoleuca* Weddell, 1861:238. [Type collection: between the cities of Tarija and San Luis, Tarija, Bolivia, Jul–Aug. 1846, *Weddell 4607*. Lectotype P!]  
*Polylepis racemosa* var. *albotomentella* O. Kuntze, 1898:77. [Type collection: Sierra de Córdoba, Los Gigantes, Córdoba, Argentina, *Kurtz 6926*. Isotypes NY!]  
*Polylepis hypoleuca* (Weddell) Bitter, 1911b:607. [Type col-

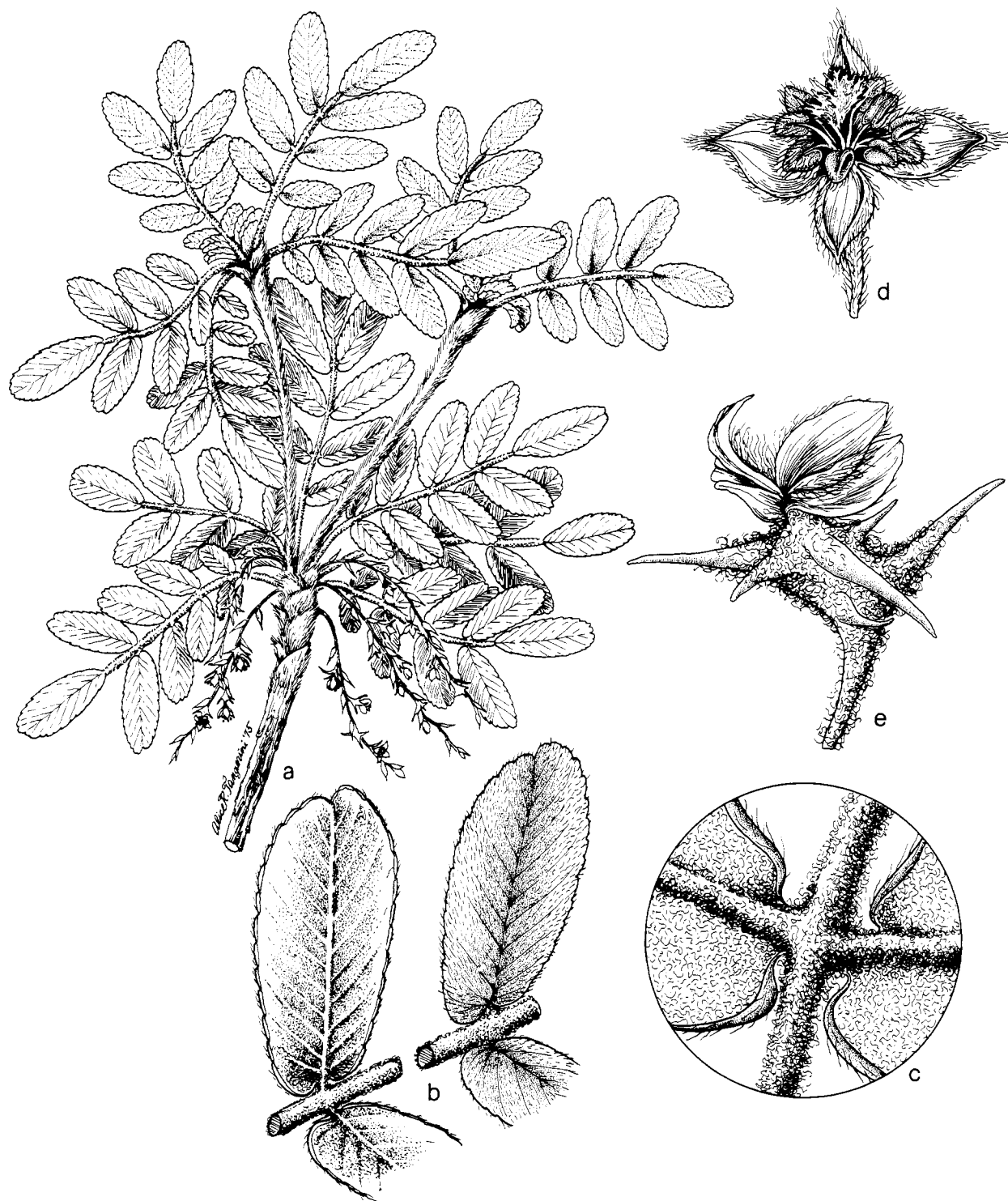


FIGURE 12.—*Polylepis hieronymi*: a, branch ( $\times 0.5$ ); b, upper (right) and lower (left) leaflet surfaces ( $\times 3$ ); c, lower leaflet surface at point of leaflet attachment ( $\times 6$ ); d, flower ( $\times 6$ ); e, fruit ( $\times 6$ ).

lection: based on the same type as *P. racemosa*  $\beta$  *hypoleuca* Weddell.]

*Polylepis hieronymi* var. *dolicholopha* Bitter, 1911b:609. [An illegitimate name since it includes the type of the species and, under the present *International Code of Botanical Nomenclature*, the correct name must be *P. hieronymi* var. *hieronymi*.]

*Polylepis hieronymi* var. *saltensis* Bitter, 1911b:609. [Type collection: near Pampa Grande, the pass "El Alizar," Salta, Argentina, 2400–2600 m, 1900, *Nelson 1258f*. Holotype S!]

*Polylepis australis* var. *bijuga* Bitter, 1911b:624. [An illegitimate name, based on the type of *P. racemosa* var. *albomentella* O. Kuntze.]

Small trees to 3 m tall. Leaves (Figure 12a) congested at the ends of the branches, imparipinnate with 3 to 4 pairs of leaflets; obtrullate in outline; variable in size, from 1.9–5.2 cm wide and 2.9–9.7 cm long; rachises sericeolano; point of leaflet attachment with a band of small, dark-colored multicellular glandular trichomes, appearing as a dark ring around the rachis or seemingly undifferentiated from the rest of the rachis but with small glandular trichomes under the lanose covering, sometimes with a few long trichomes with one or two basal cells; stipular sheaths usually sloping away (downward) from the leaf petiole but sometimes with a slight shoulder, without spurs but sometimes appearing spurred because of the projection of long trichomes on the abaxial surface, sericeous on the outer face with the long, white silky hairs sometimes extending down the internode. Leaflets (Figure 12a) ovate in outline, the first pair below the terminal leaflet the largest, one of this pair 0.5–1.2 cm wide and 1.2–3.2 cm long; margins crenate, apex obtuse; base attenuate or cordate, the pairs of leaflets often slightly

obliquely positioned so as not to appear paired, terminal leaflet petiolate; upper surfaces (Figure 12b) rugose, usually sparsely villous; lower surfaces (Figure 12b) densely lanose with long, twisted trichomes. Inflorescences pendant, 4.9–12 cm long, bearing 8–24 flowers; floral bracts conspicuous but small, to 1 mm, strigose on the outer surface; rachises tomentose. Flowers (Figure 12d) perfect, 0.6–0.9 cm in diameter; sepals 4 (sometimes 3), oval, sericeous on the outer face; stamens 9–13, orbicular, upper half with a dense beard of straight, yellow or white trichomes; stigma spreading; point of style attachment slightly hispid. Fruit (Figure 12e) almost cylindrical with long, sometimes hooked, spines; body of fruit tomentose, spines occasionally tomentose, 0.3–0.9 cm wide including spines, 0.5–1.0 cm long.

**DISTRIBUTION.**—Southern Bolivia (Tarija) and northern Argentina on the upper slopes of the Eastern Andes (Figure 13). Flowering recorded in March, June, July, August, and September.

**COMMON NAME.**—Queñoa.

**USES.**—None specifically reported.

**REPRESENTATIVE SPECIMENS EXAMINED.**—BOLIVIA. Valle del Tambo, Salinas, 10 Jun 1873, *Lorentz & Hieronymus 938* (G, NY, S). TARIJA: O'Connor; Quebrada de Canaletas, between Tarija and Entre Rios, 2300 m, 15 Jul 1954, *Meyer 18213* (LIL); without precise locality, Mar 1890, *Bang 769* (F, GH, MO, NY, US). ARGENTINA. JUJUY: Estacion Volcán, Tiraxi, 2300 m, 27 Jan 1927 *Castillon 388* (LIL); *Tumbaya, Volcán*, 3000 m, 13 Feb 1927, *Venturi 9002* (US). SALTA: Dept. Guachipas Pampa Grande, lomas del Zapallar, 1810 m, 1 Sep 1949, *Hueck 260* (LIL).

**DISCUSSION.**—Collections of *Polylepis hieronymi* are scarce despite the statement by Hueck (1972) that this species is a very common tree forming a ceja of the woodlands at the upper reaches of the Eastern Cordillera. An examination of the few available specimens indicates that different trees vary in leaf size. The Jujuy, Argentina, specimens I have examined have the smallest leaves, whereas those from Salta have the largest.

On the basis of the long, relatively unmatted, cottony pubescence of the under leaflet surface, the presence of clavate multicellular glandular trichomes at the point of leaflet attachment, and the large, narrowly spined fruits, *P. hieronymi* would appear to belong to the *P. sericea* group. The two species, while similar in some respects can, how-

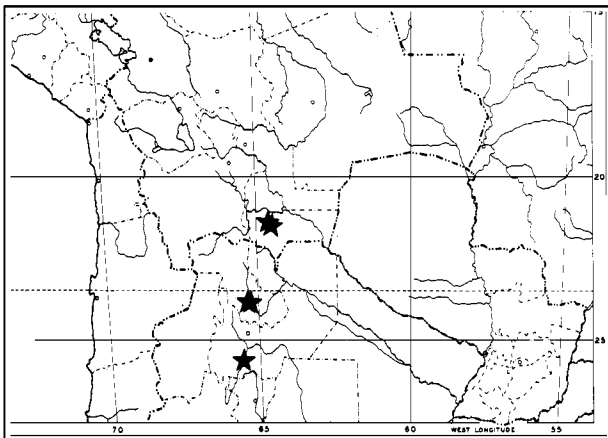


FIGURE 13.—Collection localities of *Polylepis hieronymi*.

ever, easily be told apart. Unlike *P. multiflora*, there are no spurs on the stipule sheaths of *P. hieronymi*. The leaves of *P. multijuga* also have many more pairs of leaflets and there are many more flowers per inflorescence than in *P. hieronymi*. The exceedingly narrow fruit and sometimes hooked,

rather than straight, spines on the fruit of *P. hieronymi* seem unique in the genus. Bitter (1911b) pointed out the similarity of the hooked spines of this species to the glochids of some *Acaena* species, but it is doubtful if there is any homology in the structures. The spiny rather than alate fruits and

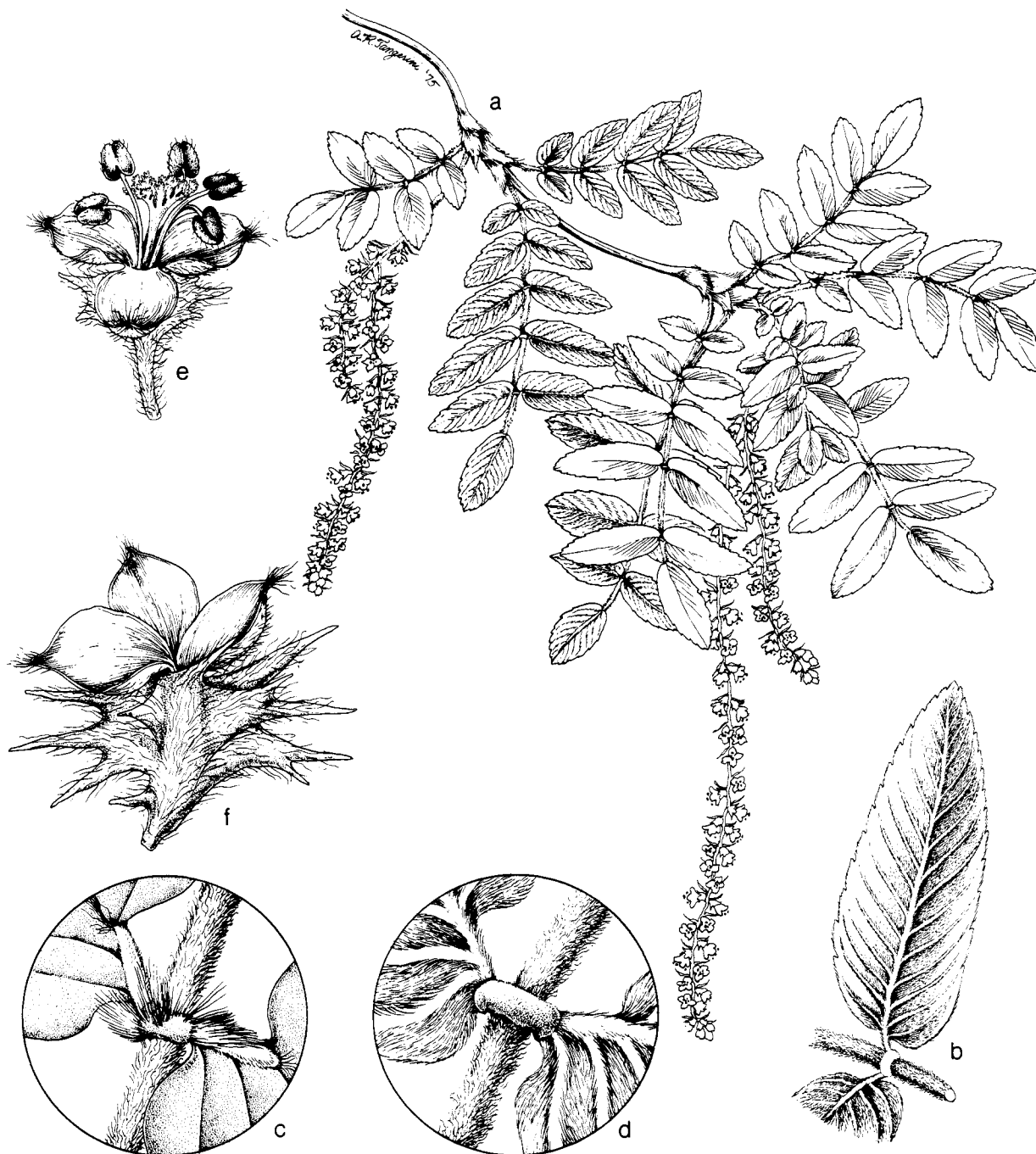


FIGURE 14.—*Polylepis pauta*: a, branch ( $\times 0.5$ ); b, underleaflet surface ( $\times 2$ ); c, point of leaflet attachment, upper surface ( $\times 6$ ); d, point of leaflet attachment, lower surface ( $\times 6$ ); e, flower ( $\times 6$ ); f, fruit ( $\times 6$ ).

the densely sericeous stipule sheaths distinguish this species from *P. besseri* and *P. racemosa*.

#### 4. *Polylepis pauta* Hieronymus

*Polylepis pauta* Hieronymus, 1896:313. [Type collection: Corredor Machai, Ecuador, 3900 m, 1871, *Stübel 232a*. Type destroyed, Rockefeller photograph no. 3390, types of the Berlin Herbarium at GH, NY.]

*Polylepis serrata* Pilger, 1906:536. [Type collection: Huamatics, southeast of Monzón, Huánuco, Peru, 3400–3500 m, 1903, *Weberbauer 3354*. Type destroyed, Rockefeller photograph no. 3394, types of the Berlin Herbarium at GH, NY, U.S.]

*Polylepis serrata* var. *psilantha* Bitter, 1911b:593. [An illegitimate name since the original circumscription includes the type of the species.]

*Polylepis serrata* var. *paricipila* Bitter, 1911b:593. [Type collection: Convención, Yanamanche, between Cuzco and Santa Ana, Cuzco, Peru, 3500–3800 m, *Weberbauer 4854*. Type destroyed, isotype WRSL.]

*Polylepis annulatifilosa* Bitter, 1911b:596. [Type collection: Andes of Quito, Pichincha, Ecuador, *Jameson 16*. Lectotype W!, isotypes G! GH!]

Trees (2) 5–27 m tall. Leaves slightly congested at the ends of the branches, imparipinnate with 4–9 pairs of leaflets (Figure 14a), obtrullate in outline, 2.4–6.6 cm wide and 3.4–11.7 cm long; rachises lanose; point of leaflet attachment hispid on the upper surface, the long (to 3 mm) trichomes (Figure 14c) usually mixed with multicellular, glandular trichomes and resinous exudate; stipular sheaths red brown, sericeous on the outer face. Leaflets (Figure 14b) ovate, acute at the apex, oblong or lanceolate in outline, second pair from the terminal leaflet usually the largest, one of this pair 0.6–1.4 cm wide and 0.8–3.3 cm long; margins serrate; apex acute; base unequally cordate; upper leaflet surface glabrous or slightly tomentose, particularly in the midvein depression; lower surface sericeous with the white or gold trichomes completely restricted to, or most conspicuous on, the veins. Inflorescences pendant, 6–21 cm long, bearing 16 to over 60 flowers; floral bracts conspicuous, pilose on the outer surfaces; rachises sericeous. Flowers (Figure 14e) perfect except possibly for some plants from Peru (Cuzco), which appear to be male sterile, 0.3–0.6 cm in diameter; sepals 3 or 4, ovate, green, outer surface sericeous; stamens 5–12, red, sericeous; stigma expanded, style hispid at the base. Fruit (Figure 14f) irregularly shaped, rhomboid to cylindrical with numerous, unequal, glabrous to villous, thin spines, 0.3–1.4 cm wide including spines, 0.3–1.2 cm long.

**DISTRIBUTION.**—From north-central Ecuador (Pinchincha) to southern Peru (Cuzco), primarily in the eastern Andes (Figure 15). Flowering and fruiting recorded in February, May, July, August, September, and December.

**COMMON NAMES.**—Pauta, quiñual, queña, queuña.

**USES.**—None recorded.

**REPRESENTATIVE SPECIMENS EXAMINED.**—ECUADOR. NAPO: Mount Guamani, 4000 m, 22 Sep 1939, *Asplund 8767* (S). PERU. SAN MARTIN: Huallaga, Valley of the Rio Cipisoncho, 30 km above Jucusbamba, 7°55'S, 77°10'W, 3600 m, 22 Aug 1965, *Hamilton & Holligan 149* (K, S). Cuzco: Paucartambo, Chacapampa, 1800–2000 m, Dec 1950, *no collector 9909* (MO); Urubamba Valley, Torontoy, 1 May 1915, *Bingham 557* (US); Quispicnachi, Marcapata, 15–16 Feb 1929, *Weberbauer 7803* (BM, F, G, GH, K, NY, US); Convención, Panticalla, 3800 m, Jul 1949, *Marin 7608* (UC, US). APURIMAC: Cordillera Salcantyl, 3600 m, 30 May 1969, *no collector T1467* (NY).

**DISCUSSION.**—Like *Polylepis multijuga*, *P. pauta* exhibits many unspecialized characters such as the size of the plants (large trees), thin, large, and numerous leaflets and long inflorescences with numer-

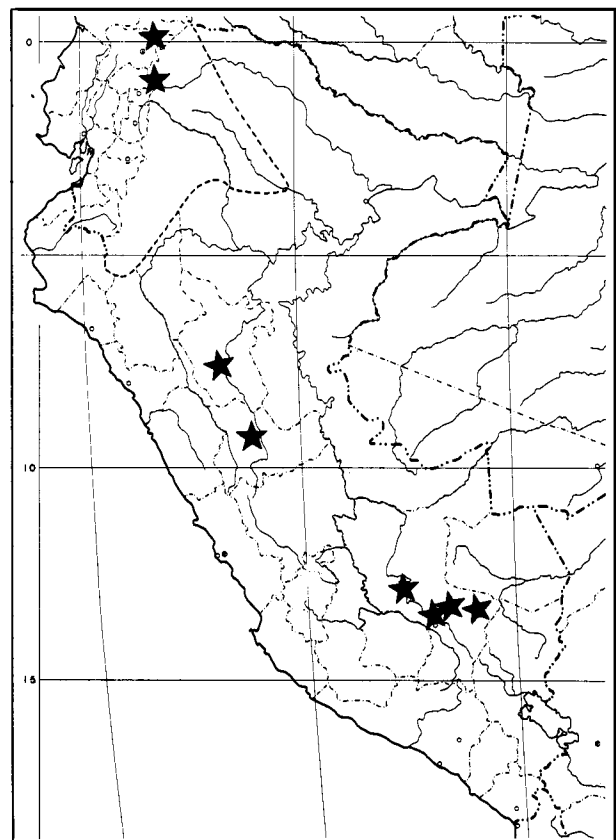


FIGURE 15.—Collection localities of *Polylepis pauta*.

ous flowers. This species appears to grow in relatively mesic habitats, usually mixed with, or at the upper edge of, the montane forest. Specimens have been collected as low as 1800 m, the lowest elevation recorded for any species of the genus within the tropics.

Morphologically, *Polylepis pauta* is intermediate in many characters between *P. multijuga* and *P. lanuginosa* on the one hand and *P. sericea* on the other. It differs from the former two taxa by having smaller leaves and inflorescences, a reduced pubescence on the sheaths and rachises of the leaves and on the inflorescences and a restriction of the pubescence on the underleaf surfaces to the veins. Although very similar in almost all characters to *P. sericea*, the sympatry of *P. pauta* with *P. sericea* (on Volcan Pichincha, Ecuador, and in the Urubamba Valley, Torontoy, Peru) with no intermediates indicates the two are distinct taxa. The two species can be distinguished by the differences in leaf margins (serrate in *P. pauta*) and the fruit morphology (fruit body thinner and the spines thinner and longer in *P. pauta* than in *P. sericea*).

### 5. *Polylepis sericea* Weddell

*Polylepis sericea* Weddell, 1861:238. [Type collection: Sierra Nevada, Mérida, Venezuela, 11,000 ft (3500 m), June 1847, Funck & Schlim 1546. Lectotype P! isotype G!]

*Acaena ochreatea* Weddell, 1861:240. [Type collection: Andes around Quito, west slopes of Pichincha, Pichincha, Ecuador, 12,000 ft (3600 m), April to May 1856, Jameson 73. Lectotype P! isotypes G! GH!]

*Polylepis Stuebelii* Hieronymus, 1896:313. [Type collection: western slope of Mt. Quilindaña near Bambasacha, Ecuador, 3700 m, Stübel 204. Type destroyed, Rockefeller photograph no. 3395, types of the Berlin Herbarium at NY.]

*Polylepis albicans* Pilger, 1906:535. [Type collection: Cordillera Blanca above Caraz, Ancash, Peru, June 1903, Weberbauer 3229. Type destroyed, Rockefeller photograph no. 3383, types of the Berlin Herbarium at GH, NY.]

*Polylepis ochreatea* (Weddell) Bitter, 1911a:5.

*Polylepis ochreatea* var. *integra* Bitter, 1911b:598, fig. 4. [Type collection: Volcan Mojanda, Ecuador, 3000–4000 m, Sodiro s.n. Holotype FI, not seen, possible isotype W!]

*Polylepis hypargyrea* Bitter, 1911b:600, taf. 5. [Type collection: Sierra Nevada, Páramo de la Culata, Venezuela, December, Moritz 1120. Type destroyed, Rockefeller photograph no. 17985, types of the Berlin Herbarium at GH.]

*Polylepis subintegra* Benoist, 1934:326. [Type collection: western slopes of Mt. Pichincha, Taurichupa, Pichincha, Ecuador, 4000 m, 28 Nov 1930, Benoist 3356. Lectotype P!]

*Polylepis quindensis* Cuatrecasas, 1941:343. [Type collection: Central Cordillera, Nevado del Ruiz, western slope of

macizo del Quindio, Caldas, Colombia, 3400–3500 m, 5 May 1940, Cuatrecasas 9327. Holotype US! isotype US!]

Deciduous trees (2) 5–15 m tall. Leaves slightly congested at the ends of the branches (Figure 16a), imparipinnate with 2–6 pairs of leaflets obovate in outline, 2.5–5.9 cm wide, 2.4–11.9 cm long; rachises slightly tomentose, point of leaf attachment hispid or with a ring of multicellular glandular trichomes and resinous exudate, or both; stipular sheaths spurred or truncate at the apex, outer surface and top sericeous. Leaflets elliptic or ovate in outline, second pair from the terminal leaflet the largest, one of this pair from 0.5–1.1 cm wide and 1.4–3.8 cm long; margins entire or slightly serrate; apex acute or obtuse; base unequally cordate; terminal leaflet petiolate; upper surface glabrous, lightly sericeous, or hispidulous; lower surface with a dense layer of gray, white, or gold silky trichomes (Figure 16b, c), but occasionally almost glabrous. Inflorescences pendant, 3–18 cm long, bearing 8–35 flowers; floral bracts conspicuous, green or orange, scarious; rachises tomentose. Flowers perfect, 0.5–1 cm in diameter; sepals 3–5, oval, green, outer surface sericeous (Figure 16d); stamens 6–16, purple or deep red brown, covered with long white trichomes; base of style hispid. Fruit irregularly shaped, more or less turbinate, pilose, with a wide variety of knobs and stout spines (Figure 16e), 0.2–0.7 cm wide including protuberances, 0.2–0.8 cm long.

DISTRIBUTION.—Scattered in populations from Venezuela in the state of Lara along the Andes to Central Bolivia in the province of La Paz (Figure 17). Flowering recorded every month except December.

COMMON NAMES.—Coloradito, keshua, quiñua, quiñual, quiñar, quinhuar, queuña.

USES.—In Peru an infusion made from the bark was used to counteract colic.

REPRESENTATIVE SPECIMENS EXAMINED.—VENEZUELA. LARA: Western slope of the Paramo del Jabon, 3100–3400 m, 2 Nov 1969, Cuatrecasas, Ruiz-Teran & Lopez-Figueiras 28216 (US); Cordillera de Norte, Páramo de Mucuruba, Quebrada de los Colorados, Cueva de los Colorados, 3900 m, 20 Oct 1969, Cuatrecasas, Ruiz-Teran & Lopez-Figueiras 28145 (US). MÉRIDA: Laguna Mucubaji, above Los Apartaderos, 3625–3655 m, 21 Jul 1944, Steyermark 57513 (F, NY); Páramos de Laguna Grande, 21 Jan 1929, Pittier 13253 (A, F, G, MO, NY, US); Laguna Negra, 20 Mar 1951, Gines 2210 (US), Sierra Nevada de Santo Domingo, NW slope, Laguna Negra, 3600–3700 m, 21 Sep 1952, Humbert 26443 (P, S, US); 67 km northeast of Mérida along the road to Barinas, 3500 m, 19 Nov 1963,



FIGURE 16.—*Polylepis sericea*: a, branch ( $\times 0.5$ ); b, lower leaflet surface ( $\times 3$ ); c, point of leaflet attachment, lower surface ( $\times 4$ ); d, flower ( $\times 6$ ); e, fruit ( $\times 6$ ).

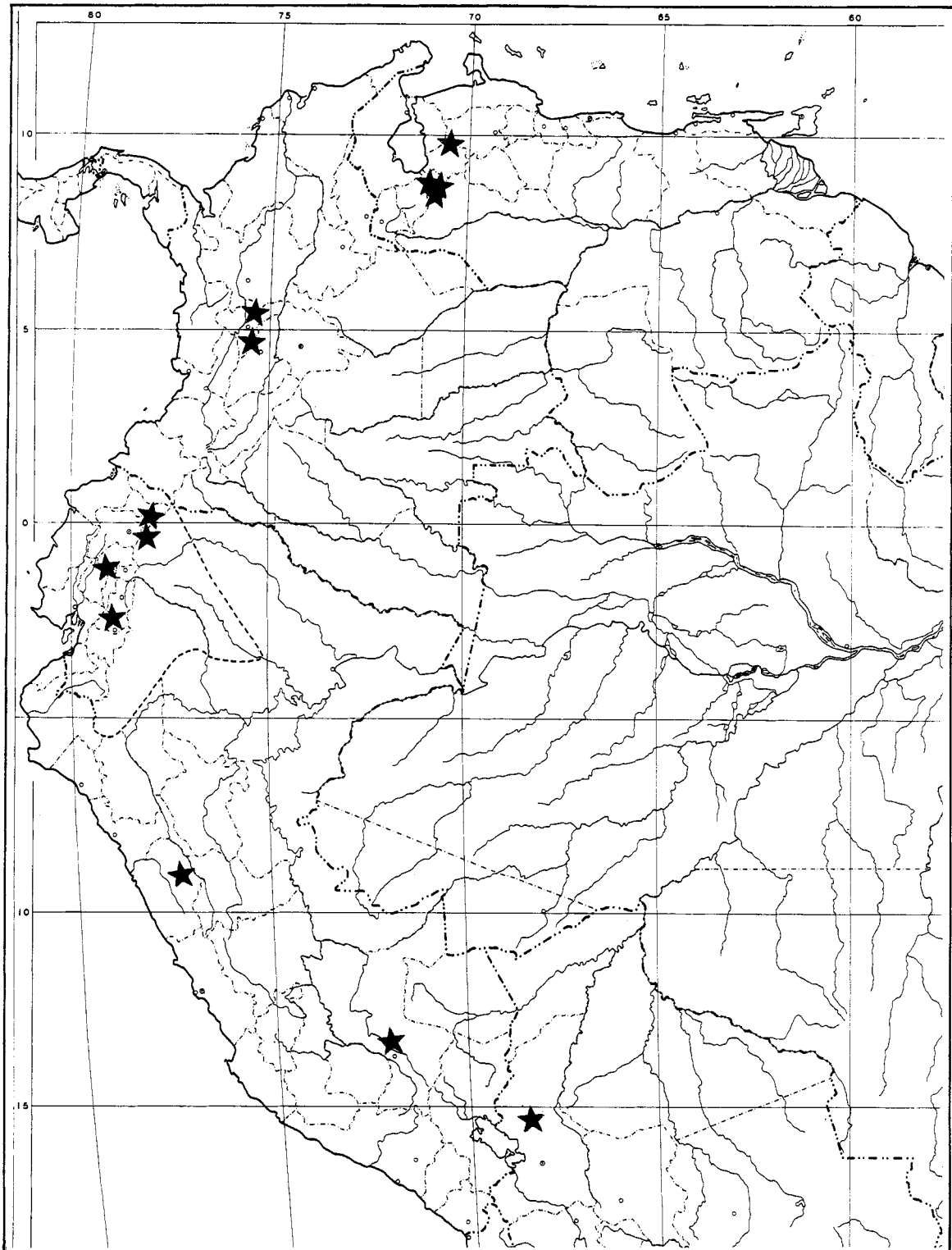


FIGURE 17.—Collection localities of *Polylepis sericea*.

*Breteler 3344* (NY); Sierra Nevada above Mérida, 3900 m, 2 Mar 1939, *Alston 6803* (BM, US); Quebrada El Yoyo, 3880 m, 12 Apr 1930, *Gehriger 73* (A, F, MO, NY, UC, US); Sierra Nevada de Santo Domingo, Laguna de Los Pastos, 3800 m, 17 Oct 1969, *Cuatrecasas, Ruiz-Teran & Lopez-Figueiras 28121* (US); Páramo Piedras Blancas, 4000 m, 27 Mar 1945, *Jahn 403* (US); "Mérida," 3900–4000 m, 13 Jul 1953, *Beruordi 608* (NY); Mérida, Nov 1958, *Schreider s.n.* (K). COLOMBIA. ANTIOQUIA: Vulgo, Páramo de Kerveyo, 4000 m, 1851–1857, *Triana 1866* (G). CALDAS: Cordillera Central, head of the river Otún, páramos between Laguna del Mosquito and Plan del Vilar, 3650–3750 m, 26 Nov 1946, *Cuatrecasas 23257* (F, P, US), southeast of Ruiz, El Aprisco, 3500–3600 m, 5 May 1940, *Cuatrecasas 9327* (US), Páramo del Quindio, 4200–4400 m, 15–20 Aug 1922, *Pennell & Hazen 9912* (GH, K, NY); high valleys near Solamina, 3000 m, Sep 1945, *Tomas 2428* (US). NARIÑO: Yacuanquer, north of Yacuanquer, 4 Jan 1943, *Garganta 472* (F). ECUADOR. CARACHI: above Tufiño, 4000 m, 23 Jul 1955, *Asplund 17037* (S). PICHINCHA: Chaparro de Sebritana, 3400–3500 m, 15 Jul 1944, *Solis 8379* (F); western slopes of Volcan Cayambe, 3900 m, 27 Jul 1967, *Sparre 17789* (S); Páramo de Guamani, slope toward Papallacta, 3900 m, 31 Oct 1955, *Asplund 18244* (S); northwest slope of Mt. Corazón, 3300 m, 27 Jul 1955, *Asplund 17103* (S), 3000 m, 22 Jun 1876, *Andre 3735* (K, NY); west of Pichincha, 12 Jul 1931, *Benoist 4549* (P, S); western slope of Pichincha, 12,000 ft, *Jameson 16* (G). NAPO: Paso de Guamani about 4 km east of pass on road to Papallacta, 3 Mar 1967, *Sparre 15029* (S). CHIMBORAZO: Cordillera Oriental, sotobosque de Cubilliri, Hcda. Alas, 3350–3500 m, 1 Mar 1944, *Solis 7524* (F). CAÑAR: Cañar, 15 Sep 1918, *Rose & Rose 23789* (NY, US). PERU. ANCASH: Carhuas, Cordillera Blanca, above Vicos, 3600 m, 11 Mar 1964, *Hutchison & Wright 4325* (F, MO, NY, UC, US). CUZCO: Urubamba Valley, Torontoy, May 1915, *Heller 2183* (US); Lucumayo Valley, 2600 m, 18 Jan 1915, *Cook & Gilbert 1280* (US). BOLIVA. LA PAZ: between Sorata and Mapiiri, Fola, Aug 1933, *Cardenas 1102* (NY); Murillo, 8 km after Palca on the road to Iquico, 4000 m, *Vuilleumier 342* (GH).

DISCUSSION.—The geographical distribution of *Polylepis sericea* spans the greatest latitude of any species in the genus, but populations (at least at the present time) are discontinuous along a north-south Andean axis. Correspondingly, the species consists of a series of relatively pronounced forms, many of which have been described as distinct taxa. However, examination of a large number of specimens from throughout the range shows that plants similar to a form characteristic of one area frequently occur in a population from another part of the range.

The form upon which the name *Polylepis sericea* was based occurs predominantly in Venezuela and has elliptic leaflets that are glabrous above and densely covered beneath with silvery, silky trichomes. Similar plants are common in Ecuador (Pichincha). In Venezuela, however, there are also

plants with almost entirely glabrous leaves. In fact, the amount, length, and color of the pubescence on the undersurface of the leaflets varies greatly throughout the range. In Colombia, the trichomes of the lower leaflet surfaces tend to be slightly shorter than those most commonly found in Venezuela, while in Ecuador plants from Corazón, and in Peru plants from Caraz, have pronounced pubescence on the upper leaflet surfaces as well, similar to that of *P. subsericans*.

There is also some variation in the shape of the top of the stipule sheaths. Most populations have spurs on either side of the leaf petiole but some specimens from Pichincha have the spurs so reduced as to make the top of the stipule sheath appear flat.

Morphologically, *Polylepis sericea* is most similar to *P. pauta* and the two share most characters. The two differ in that the pubescence of the underside of the leaflets of *P. sericea* usually covers the entire surface and thus appears as a solid layer of silky hairs. The trichomes of the underleaflet surfaces of *P. pauta* on the other hand are always much more conspicuous on, or restricted to, the veins. In addition, the leaflets of *P. pauta* are more ovate and larger than those of *P. sericea* and generally have serrate rather than entire margins.

## 6. *Polylepis subsericans* Macbride

*Polylepis subsericans* Macbride, 1934:367. [Type collection: Huamanga, Hacienda Totorabamba, Ayacucho, Peru, 3500–3600 m, May 1910, *Weberbauer 5487*. Holotype F!, isotype F!]

*Polylepis incana* var. *flavipila* Bitter, 1911b:640. [Type collection: Castro-Virreyna, western slopes of the Andes above Pisco, Huancavelica, Peru, 3900–4000 m, May 1910, *Weberbauer 5433*. Type destroyed at Berlin, Isotypes F! GH! US!]

Trees to 8 m tall. Leaves congested at the ends of the branches, imparipinnate with 1 pair of leaflets; trullate in outline, 1.7–3.3 cm wide, 3.1–3.4 cm long; rachises pilose with scattered multicellular glandular trichomes; point of leaflet attachment (Figure 18b) with a small tuft of long, straight, single-celled trichomes; stipular sheaths sloping away from the petiole, appressed hispid on the upper portion and the outer face. Leaflets obovate in outline, 0.5–0.7 cm wide, 1.7–2.0 cm long, margins slightly revolute, more or less entire or slightly crenate toward the tip, apex slightly emarginate

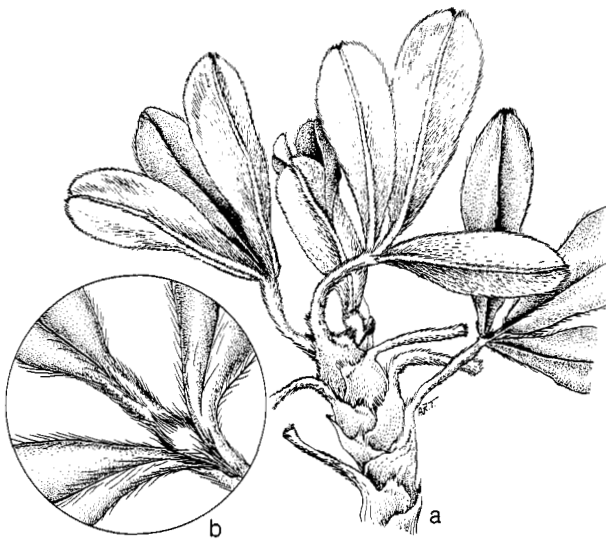


FIGURE 18.—*Polylepis subsericans*: a, branch tip ( $\times 1.5$ ); b, point of leaflet attachment, upper surface ( $\times 6$ ).

with the trichomes from the lower surface projecting into the notch, upper surface dull, sparsely pilose; lower surface (Figure 18a) densely hispid, the trichomes covering a lower layer of short, twisted, several-celled trichomes. Inflorescences pendant, 3–4 cm long, bearing about 3 or 4 flowers; floral bracts lanceolate, pilose on the outer surface; rachises pilose. Flowers perfect, about 0.8 cm in diameter, sepals 4, ovate, outer surface pilose with multicellular glandular trichomes extending to the tips on the inner face; stamens 12 or 13, purple, covered with long, straight white trichomes; base of style sparsely sericeous. Fruit more or less cylindrical in outline with irregularly flattened spines; mature fruit not seen.

**DISTRIBUTION.**—Central Peru in the provinces of Ayacucho and Huancavelica (Figure 19). Flowering recorded only from the month of May.

**COMMON NAMES.**—None specifically reported.

**USES.**—None specifically reported.

**REPRESENTATIVE SPECIMENS EXAMINED.**—The only collections seen are those listed as the type of the species and its synonym (Figure 19).

**DISCUSSION.**—Although originally described as a variety of *Polylepis incana* by Bitter, *P. subsericans* appears to be more closely related to members of the *sericea* group than to the *incana* complex. Presumably Bitter placed the taxon within *P. incana* because of the single pair of leaflets and the yellow-

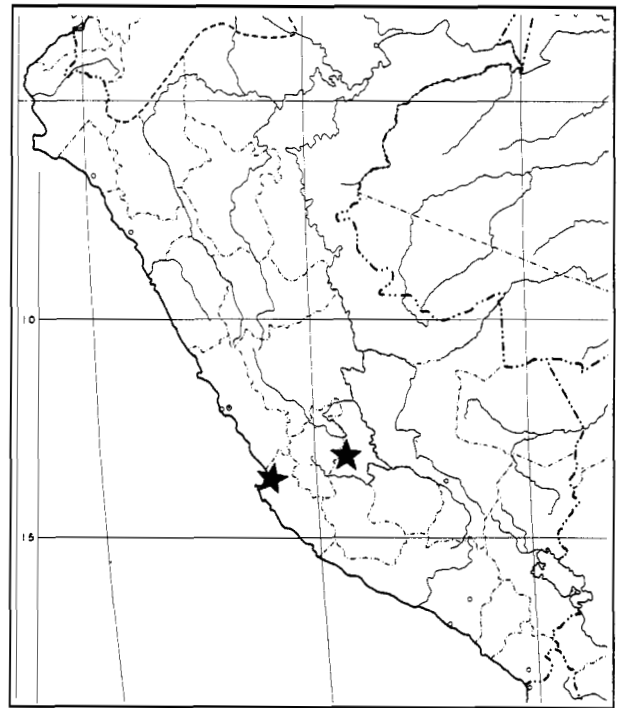


FIGURE 19.—Collection localities of *Polylepis subsericans*.

ish cast of the leaflets due to a resinous exudate from the glandular trichomes. However, the dense, straight trichomes covering the under surface of the leaflets are, as pointed out by Macbride, more similar to those of populations of *P. sericea*. As in the case of *P. pepeii*, *P. subsericans* would seem to have arisen from an isolate of an ancestral stock similar to *P. sericea*.

Because of the coarse, appressed covering of straight trichomes on the leaflets and the single pair of leaflets, this taxon is easily distinguished from other members of the genus.

### 7. *Polylepis pepeii*, new species

**TYPE COLLECTION.**—Chapare, Cochabamba, Bolivia, 77 km after Chapare on the road to Todos Santos, 4200 m, 4 Jan 1968, *Vuilleumier 465* (Holotype US! Isotypes GH! P!).

Frutex nanus. Folia imparipinnata; foliola unijugata ad trijugata; foliolium obovatum ad oblongum, apice emarginatum vel tridentatum, base inequale attentuatum, margine integrum; supra breviter sericeum subtus breviter sericeum apprime secus margines et nervos. Racemi pauciflori. Flores

perfecti, staminibus (4) 10–12, apice barbatis. Fructus fusiformis leviter tortilis, nodosus vel spinulosus ad medium.

ETYMOLOGY.—This species is named for Jose Cuatrecasas, called Don Pepe by his contemporaries, who has devoted his life to further an understanding of the flora and phytogeography of the tropical Andes.

Shrubs to 1.5 m tall. Leaves very congested with the area of overlapping stipule sheaths swollen (Figure 20a), imparipinnate, with 1–3 pairs of leaflets, obtrullate in outline, 1.0–2.4 cm wide, 0.8–2.8 cm long; rachises glabrescent or with variable amounts of short, straight, white, single-celled, appressed trichomes; point of leaflet attachment (Figure 20c) with a ring of short, straight, single-celled trichomes; stipule sheaths with short, obtuse spurs on either side of the petiole, outer face glabrescent to strigose. Leaflets oblong to obovate, second pair from the top the largest if more than one pair is present, one of this pair 0.2–0.4 cm wide, 0.6–1.2 cm long, margins entire, ciliate, apex emarginate or tridentate due to a projection of the midvein, base unequally attenuate; upper surface sparsely to densely covered with short, appressed, straight single-celled trichomes; lower surfaces (Figure 20b) minutely sericeous, the trichomes often most conspicuous on the veins and margins. Inflorescences upright or pendant, to 4 cm long, bearing 1–4 flowers; floral bracts lanceolate, to 3 mm long, outer surface strigose; rachises densely covered with similar trichomes. Flowers (Figure 20d) perfect, sepals 3 or 4, lanceolate to ovate, outer surface covered with short, straight, appressed trichomes; stamens (4?) 10–12, anthers circular, tomentose at the apex; base of style sparsely hispid or glabrous. Fruit (Figure 20e) fusiform, often slightly twisted, with an irregular number of blunt protuberances or spines around the middle, 0.2–0.3 cm wide including protuberances, up to 0.7 cm long.

DISTRIBUTION.—Southeastern Peru in Cochabamba south along the Eastern Cordillera to Bolivia in the province of Cochabamba (Figure 21). Flowers recorded in July and January.

COMMON NAMES.—None specifically reported.

USES.—None specifically reported.

REPRESENTATIVE SPECIMENS EXAMINED.—PERU. CUZCO: Piñasnoij, Panticalla Pass, 3600 m, 15 Jul 1915, *Cook & Gilbert 1837* (US); Arma, 4350 m, July 1915, *Bingham 2068*.

BOLIVIA. Cordillera Real, Alaska Mine, 13,700 ft, 1–4 Mar 1926, *Tate s.n.* (NY).

DISCUSSION.—Although collections are sparse, *Polylepis pepeii* appears to have a fairly large distributional range along the Eastern Cordillera from southern Peru to central Bolivia. My own collections (*Vuilleumier 465*) and those of Cook and Gilbert indicate that the species grows above the cloud forest on the east facing slopes. While Cook and Gilbert do not actually mention the habitat of the species, one of their specimens is covered with lichens and Spanish moss.

On morphological grounds, *Polylepis pepeii* is placed in the *sericea* species group. The type collection, with three pairs of leaflets and with trichomes predominantly on the veins and leaf margins of the underleaf surface, appears similar to small-leaved individuals of *P. sericea* from Volcan Pichincha, Ecuador. The collection from Peru has only one pair of leaflets, reduced inflorescences, and more dense covering of trichomes on the underleaflet surfaces. Despite these similarities to *P. sericea*, *P. pepeii* constitutes one of the most distinctive species in the genus. Plants are true shrubs, not dwarfed trees, the fruit is elongate, twisted and knobbed around the center. The tendency for the leaflet apex to appear tridentate through projection of the midvein is also unique in the genus.

### 8. *Polylepis reticulata* Hieronymus

*Polylepis reticulata* Hieronymus, 1896:312. [Type collection: near Las Calderas de Pasachoa and Rumiñahui, Pichincha, Ecuador, *Stübel 20a*. Type destroyed, Rockefeller photograph no. 3393, types of the Berlin Herbarium at GH, NY.] *Polylepis nitida* Bitter, 1911b:615, fig. 9, taf. 7. [Type collection: Minza at Volcan Tungurahua, Tungurahua, Ecuador, 3600 m, *Stübel 287*. Type destroyed, Rockefeller photograph no. 3388, types of the Berlin Herbarium at GH, NY.] *Polylepis brachyphylla* Bitter, 1911b:616, fig. 10 taf. 8. [Type collection: lower region of the páramos between Chimborazo and Guaranda, Chimborazo, Ecuador, 4 Nov 1856, *Remy s.n.* Holotype P! isotype P!]

Trees 4–8 m tall. Leaves congested at the ends of the branches (Figure 22a), imparipinnate with 2–3 pairs of leaflets, oblanceolate in outline, 1.8–3.5 cm wide, 2.0–5.0 cm long; rachises lanose; point of leaflet attachment (Figure 22c, d) with a small tuft of silky trichomes on the upper side or pilose with small multicellular, stacked glandular trichomes forming an annulus around the rachis; stipular



FIGURE 20.—*Polylepis pepeii*: a, branch ( $\times 0.5$ ); b, leaf, lower surface ( $\times 3$ ); c, point of leaflet attachment, upper surface ( $\times 12.5$ ); d, flower (with stamens missing) ( $\times 4.5$ ); e, fruit ( $\times 4.5$ ).

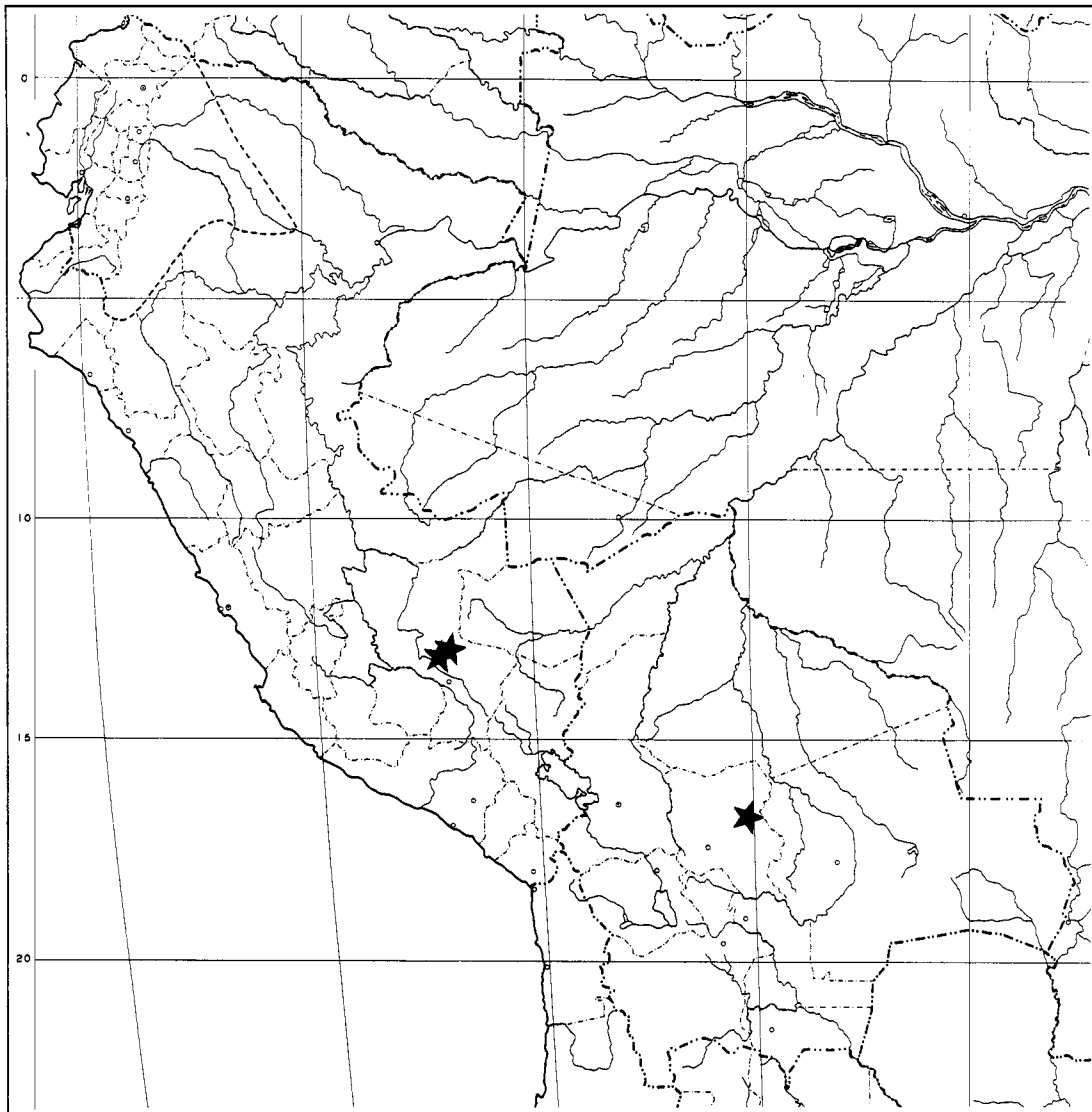


FIGURE 21.—Collection localities of *Polylepis pepeii*.

sheaths with short spurs, outer surface glabrescent to shortly lanose, with various amounts of long, straight trichomes projecting from the underside above the apex. Leaflets oblong or oblanceolate in outline, first or second pair from the terminal leaflet the largest, one of this pair 0.4–0.9 cm wide, 1.2–2.1 cm long, margins revolute, sometimes crenate, the edges of the revolute leaf margins and the apices of the underside with a rim of rather long, straight, appressed trichomes, apex strongly emarginate, base unequally cordate, terminal leaflet petiolate; upper surfaces nitid, sometimes with a few scattered long

white trichomes primarily in the depression of the midvein; lower surface pannose (Figure 22*d*). Inflorescences pendant, 2.0–12 cm long, bearing 3–7 flowers; floral bracts ovate, orange, usually scarios and glabrous but occasionally outer surfaces pilose. Flower (Figure 22*f*) perfect, 0.6–0.7 cm in diameter; sepals (3) 4, ovate, outer surface densely lanulose; stamens 6–17, globose in outline, the anthers tomentose, particularly at the junction of the anther sacs and along the edges of the anther sacs; base of style villous. Fruit (Figure 22*e*) globose, adorned with irregular, flattened spines, the spines with scattered

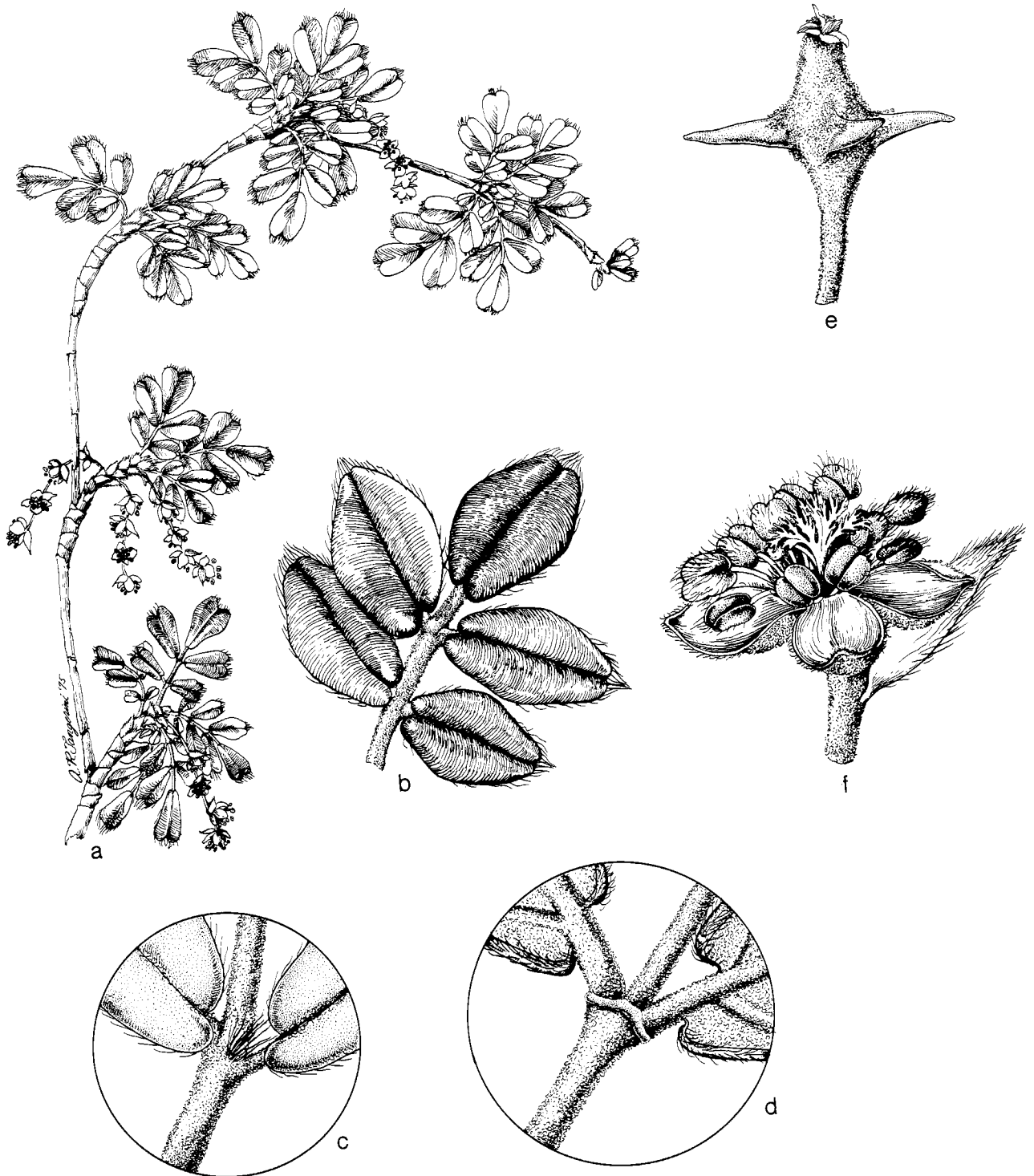


FIGURE 22.—*Polylepis reticulata*: a, branch ( $\times 0.5$ ); b, leaf, upper surface ( $\times 1.5$ ); c, point of leaflet attachment, upper surface ( $\times 6$ ); d, point of leaflet attachment, lower surface ( $\times 6$ ); e, fruit ( $\times 6$ ); f, flower ( $\times 6$ ).

trichomes, the body of the fruit densely lanose, 0.2–0.8 cm wide including spines, 0.3–0.9 cm long.

**DISTRIBUTION.**—Central to southern Ecuador, primarily in the Eastern Cordillera (Figure 23). Flowers recorded in September, November, December, and May.

**COMMON NAMES.**—Quiñua, quinoar, yagual.

**USES.**—None specifically reported.

**REPRESENTATIVE SPECIMENS EXAMINED.**—**ECUADOR.** PICHINCHA: Quito, 1845, *Jameson 204* (G, W); Imbabura, 4000–4300 m, 5 May 1957, *Hirsch E113* (NY). TUNGURAHUA: Mount Caruhuayrayo, 4200 m, 22 Aug 1939, *Asplund 8464* (S); Alta de Passa, 3500 m, 28 Oct 1944, *Solis 8736* (F); southwest slopes of Tungurahua, below páramo of Minza, 3400 m, 14 Apr 1939, *Pentland & Summers 420* (F, US). CHIMBORAZO: Chimborazo, 4000 m, 4 Jul 1846, *Andre 3933* (F, US); Eastern Cordillera of Riobamba, 3200 m, *Rimbach s.n.* (K); woods of Eastern Cordillera, Riobamba, 3400 m, December, *Rimbach 156* (GH, P, US); *ibid 498* (S); Azuay: along the Rio Matadero west of Cuenca, 10,000–10,500 ft, 3 Mar 1945, *Camp 2000* (GH, MO, NY). WITHOUT PRECISE LOCALITY: Eastern Cordillera, *Rimbach 26* (A, F); *ibid*, 3000–3400 m, May 1930, *Rimbach 14* (A, F, GH, NY, US).

**DISCUSSION.**—From accounts by collectors, *Polylepis reticulata* is the most common tree on the relatively humid slopes of the Ecuadorian Andes at the upper reaches of the montane forest. It appears to grow primarily in the cloud forest, but is also found isolated from true forest in valleys and along ridges. In general, the species exhibits a constant morphology throughout its range. The only variant popula-

tions appear to be near Cañar. Plants from this region resemble *P. weberbaueri* more than those farther east.

The most conspicuous feature of this species (which it shares with *P. weberbaueri* and, to a lesser extent, with *P. quadrijuga*) is the shiny upper surface and emarginate apex of the leaflets. *Polylepis reticulata* and *P. weberbaueri* differ in the pubescence of the stipule sheaths and the underleaflet surfaces. The former has silky trichomes on the outer face of the stipule sheaths and along the revolute margins of the leaflets. The latter has a dense woolly covering on both parts and thus no differentiated trichomes along the leaf margins. Although further collections may show these two taxa to be conspecific, I have kept them distinct because of the apparent consistent differences in morphology and the differences in habitat. It is possible that *P. weberbaueri* is derived from *P. reticulata* and represents a taxon that evolved adaptations toward drier conditions following colonization from the more moist eastern slopes.

### 9. *Polylepis weberbaueri* Pilger

*Polylepis weberbaueri* Pilger, 1906:535. [Type collection: from Yanganuco to Yungay, Ancash, Peru, 3700–3800 m, 16 Jun 1903, *Weberbauer 3287*. Type destroyed, Rockefeller photograph no. 3399, types of the Berlin Herbarium at GH, NY.]

*Polylepis lanuginosa* Humboldt, Bonpland & Kunth,  $\beta$  *microphylla* Weddell, 1861:238. [Type collection: Chimborazo, Chimborazo, Ecuador, *Bonpland 3141*. Holotype P! isotypes A! F!]

*Polylepis microphylla* (Weddell) Bitter, 1911b:611. [Based on *P. lanuginosa*  $\beta$  *microphylla* Weddell.]

*Polylepis microphylla* var. *polyarthrotricha* Bitter, 1911b:612. [Locality not specified, *Goudot 1*. Holotype W!]

Shrubs or small trees to 1.5 m tall. Leaves very congested at the end of branches, sometimes producing an appearance of a whorled arrangement (Figure 24a) imparipinnate with 3–5 pairs of leaflets, obtrullate in outline, 0.9–2.4 cm wide and 1.5–5.0 cm long; rachises densely lanose or lanose with dark red glandular trichomes; point of leaflet attachment (Figure 24e) with a tuft of matted multicellular glandular trichomes; stipule sheaths with short obtuse spurs, outer surface glabrous with long, straight silky trichomes protruding from the under-surface. Leaflets (Figure 24b) ovate to obovate in outline, first (rarely second) pair from the apex the

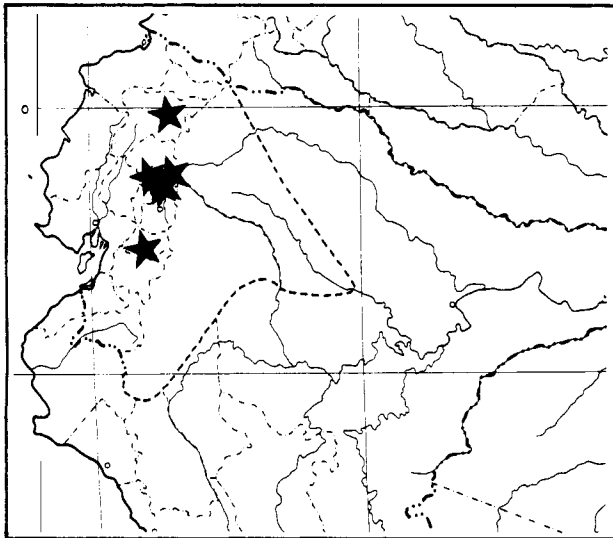


FIGURE 23.—Collection localities of *Polylepis reticulata*.

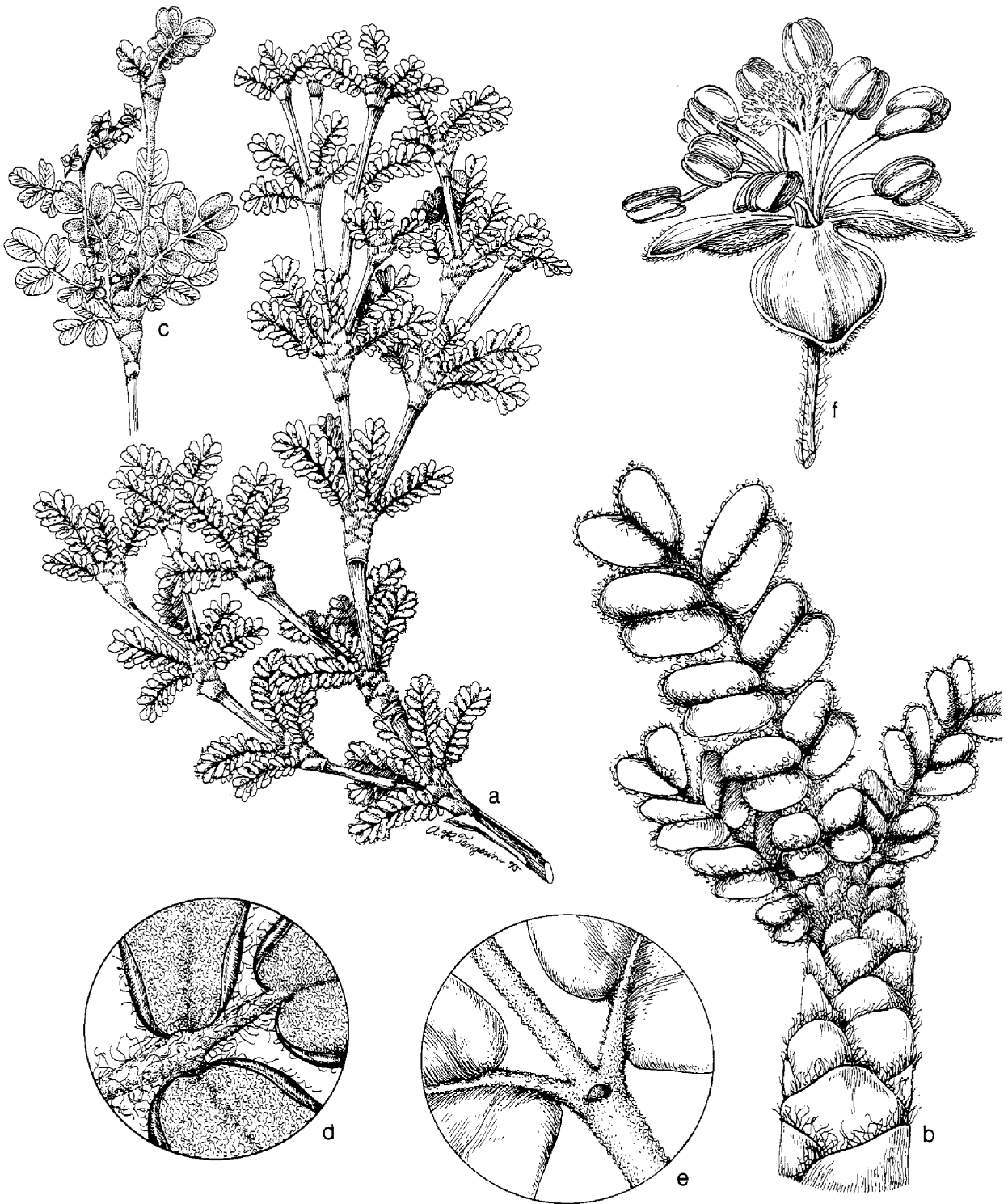


FIGURE 24.—*Polylepis weberbaueri*: a, a young branch tip ( $\times 0.5$ ); b, cluster of young leaves, upper surface ( $\times 3$ ); c, cluster of older leaves ( $\times 0.5$ ); d, underleaflet surface ( $\times 6$ ); e, point of leaflet attachment, upper surface ( $\times 6$ ); f, flower ( $\times 6$ ).

largest, one of this pair 0.4–0.9 cm wide, 0.4–1.6 cm long, margin revolute, apex strongly emarginate, base unequally cordate; upper leaf surface (Figure 24c, d) nitid, rugose, or pilose, particularly in the depression of the midvein; lower surface pannose. Inflorescences pendant, 2.1–5.4 cm long, bearing 3–7 flowers clustered at the terminal end; floral bracts small, 0.1–0.2 cm long, lanose or scarious; rachises lanose. Flowers (Figure 24f) perfect, 0.4–0.6 cm in diameter; sepals four, ovate, sericeo-lanose on the outer surface; stamens 6–16, purple, locules barbate to glabrous, base of the style villous. Fruit globose in outline, irregularly spined, the spines flattened, body of the fruit and spines shortly villous; about 0.29–0.57 cm wide including spines, 0.31–0.65 cm long.

**DISTRIBUTION.**—Central Ecuador in the Province of Pinchincha south to northern Peru in the Department of Ancash, primarily on dry slopes of the Andes (Figure 25). Flowering recorded in September, November, and December.

**COMMON NAMES.**—Queñuar, quiñual.

**USES.**—None reported.

**REPRESENTATIVE SPECIMENS EXAMINED.**—ECUADOR. PICHINCHA: Andes of Quito, 1855, *Couthouy s.n.* (GH). CHIM-

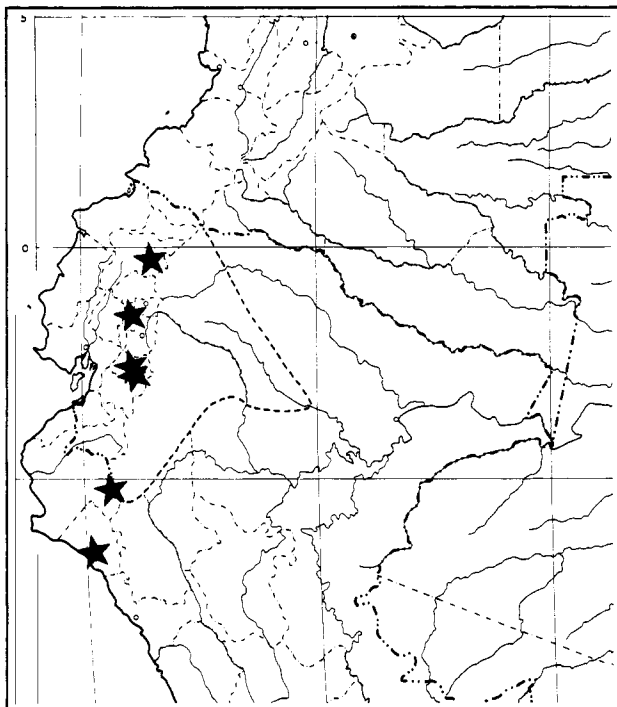


FIGURE 25.—Collection localities of *Polylepis weberbaueri*.

BORAZO: Chimborazo, 12000 ft, Dec 1846, *Jameson 523* (BM, G); eastern side of Chimborazo, 10 Nov 1845, *Jameson 25* (K); border with Cañar (western escarpment) near El Tambo, 10,000–11,500 ft, 6–9 Jul 1845, *Camp 4088* (F, NY). CAÑAR: Cañar, 16 Sep 1918, *Rose, Pachano & Rose 23792* (GH, NY), vicinity of Cañar, 15 Sep 1918, *Rose 22722* (NY, US), *ibid*, 16 Sep 1918, *Rose & Rose 22733* (NY); "Ecuador," Dec 1890, *Sodirol 421* (G, Herb DC). PERU. PIURA: Huancabamba, on the road to Huancabamba just below the summit, 38 km above Canchaque, 3120 m, 13 Sep 1964, *Hutchison & Wright 6578* (F, GH, MO, NY, P, UC). CAJAMARCA: Huambos, 2000 m, 11 Sep 1956, *Soukup 4457* (F, US). ANCASH: Cordillera Blanca, Quebrada Tangamico, 30 Jul 1959, without collector *P1970* (NY).

**DISCUSSION.**—In many respects, *Polylepis weberbaueri* appears to be the ecological equivalent in the drier Ecuadorian Cordillera of *P. reticulata*. It is probable that *P. weberbaueri* is derived from *P. reticulata* following an establishment of a population on the western chain. In areas of apparent sympatry near Cañar, Ecuador, specimens intermediate in morphology could be interpreted as hybrids between the two taxa. Although this hybridization might suggest that *P. weberbaueri* is only a geographic variant of *P. reticulata*, consistent character complexes over extensive geographical areas indicate that the two should be considered as independent, but closely related, species. The two can be distinguished most easily on the basis of the vestiture of the underleaflet surfaces and the stipule sheaths. The lower leaflet surface of *P. reticulata* is lanose over most of the surface, but distinctly sericeous along the slightly revolute leaflet margins. The entire underleaflet surface of *P. weberbaueri* is lanose and the leaf margins glabrous (Figure 24d). In addition, the exterior surface of the stipule sheaths are sericeous in *P. reticulata* and lanose in *P. weberbaueri*.

Included within this taxon are populations originally described as a variety of *Polylepis lanuginosa* (*P. lanuginosa*  $\beta$  *microphylla* Weddell) and subsequently as *P. microphylla* by Bitter (Figure 24a). In our collections in southern Ecuador (*Simpson 8532*) on the slopes of mountains near Cañar, we found plants that have mature, lower leaves characteristic of *P. weberbaueri* and young, upper leaves like those of the specimens placed in *P. microphylla* (Figure 24c). In both "*P. microphylla*" and the branch tips of our specimens from Cañar, the "paired" leaflets are often somewhat skewed so as to appear alternately arranged on the rachis. All of the specimens

that have been previously referred to *P. microphylla* are sterile, precluding the use of flowers or fruits as a taxonomic guide. Until further evidence indicates otherwise, the small-leaved form would seem most logically placed in synonymy with *P. weberbaueri*. In addition to the typical variety, Bitter circumscribed a second variety, *P. microphylla* var. *polyarthrotricha*, which he considered to merit separation on the basis of its possession of dark red multicellular glandular trichomes on the leaf rachis and underleaf surfaces. He recognized (and listed) intermediate forms between the purely lanose type and the lanose-glandular type. Since a gradation of glandular trichome density exists within the populations from Chimborazo, formal recognition of a separate variety seems unnecessary. In all of the specimens of the species examined, at least a small cluster of glandular trichomes exists at the point of leaflet attachment.

### 10. *Polylepis quadrijuga* Bitter

*Polylepis quadrijuga* Bitter, 1911b:613, taf. 6. [Type collection: Cordillera Oriental, Páramos de Bogotá, Muzo, Cundinamarca, Colombia, May 1844, Goudot s.n. Holotype P!]

*Polylepis boyacensis* Cuatrecasas, 1941:343, figs. 13, 14. [Type collection: Cordillera Oriental, Páramo de Santa Rosita between Belén and Susacón, Boyacá, Colombia, 3300–3400 m, 3 Aug 1940, J. Cuatrecasas 10374. Holotype P!, isotype US!]

*Polylepis cocuyensis* Killip & Cuatrecasas.—Cuatrecasas, 1942:33, fig. 19. [Type collection: Nevado del Cocuy in the Quebrada of San Paulino, El Morrón, Boyacá, Colombia, 3800 m, 11 Sep 1938, J. Cuatrecasas 1405. Holotype US! isotype P!]

Tree 5–8 m tall. Leaves (Figure 26a) only slightly congested at the ends of the branches, imparipinnate with 3–5 pairs of leaflets, obovate in outline, 2.6–4.5 cm wide and 3.8–9.4 cm long; rachises densely lanose; point of leaflet attachment (Figure 26c) with a distinct zone of glandular trichomes and resinous exudate; stipulate sheaths with acute spurs, outer surface lanose, with long, straight trichomes emerging from the inside surface at the apex. Leaflets (Figure 26b) ovate to obovate in outline, second or third pair from the apex the largest, one of this pair 0.6–1.3 cm wide and 1.3–2.4 cm long; margins entire or slightly crenate; apex emarginate with long straight trichomes visible in the indentation; base unequally cordate; upper leaflet surface rugose

or nitid, sometimes with scattered long trichomes; lower leaflet surface densely pannose or lanulose. Inflorescences pendant, 5.8–14 cm long, bearing 8–18 flowers; floral bracts lanceolate, exterior surface lanose rachises sericeous. Flowers (Figure 26d) perfect, 0.6–0.7 cm in diameter, sepals 4 or 5, oval in outline, outer surface lanose; stamens 8–20, globose, covered with long, curled trichomes, especially at the apex; base of style villous. Fruit (Figure 26f) globose, covered with irregularly positioned long, thin spines, the spines glabrous or lanose, body of the fruit lanose, 0.3–0.7 cm wide including spines and 0.2–0.7 cm long.

**DISTRIBUTION.**—Colombia in the provinces of Santander, Boyacá, and Cundinamarca (Figure 27). Flowers recorded in May, August, and September.

**COMMON NAMES.**—None recorded.

**USES.**—None recorded.

**REPRESENTATIVE SPECIMENS EXAMINED.**—COLOMBIA. SANTANDÉR: Eastern Cordillera, Páramo de las Coloradas, above La Baja, 3900–4100 m, 27 Jan 1927, Killip & Smith 18470 (A, GH, NY, US); Páramo de la Rusia, 3300–3500 m, 4 Aug 1940, Cuatrecasas 19428 (F, US). BOYACÁ: Nevado del Cocuy, Valle de la Cueva, 3700 m, 10 Sep 1938, Cuatrecasas 1294 (US); Valle de Cocuy, southwest slopes, 3100–3750 m, 8 Sep 1938, Cuatrecasas 1259 (F, US); Chorreo de San Paulino, 3750 m, 10 Sep 1938, Cuatrecasas 1355 (F, US); valley of Río del Corallites, 4000 m, 9 Jun 1957, Grubb, Curry, Fernandez-Perez 755 (K, US); Valle de las Lagunillas, 4000 m, 13 Sep 1957, Grubb, Curry, Fernandez-Perez 839 (US); Páramo de la Rusia near La Opera along the road between Duitama and Charata, 3643 m, 20 Aug 1953, Langenheim 3518 (UC, US); Avenida de Penas Negras (Buenos Aires), 3550 m, 11 Sep 1969, Cuatrecasas & Rodriguez 27741 (US); Güican, Hoya del Río Tabor, in the direction of Ritacuba, 3530–3370 m, 18 Sep 1969, Rodriguez & Cuatrecasas 27834 (US). CUNDINAMARCA: Macizo de Bogotá, eastern slopes of Páramo de Chisaca, Quebrada de Santa Rosa, 3300–3350 m, 16 Sep 1961, Cuatrecasas & Jaramilla 25999 (US).

**DISCUSSION.**—Although isolated far north of similar members of the *Polylepis sericea* species group, *P. quadrijuga* exhibits many characters that indicate its close affinity with *P. lanuginosa*. These include the densely sericeo-lanose stipule sheaths, the large, multiflowered racemes and the presence of multicellular glandular trichomes with a large terminal cell at the point of leaflet intersection. In herbaria the two taxa have often been confused with each other, but they can be distinguished on the basis of several characters. The pubescence of the undersurface of the leaflets is sericeous in *P. lanuginosa* and lanose in *P. quadrijuga*. The latter

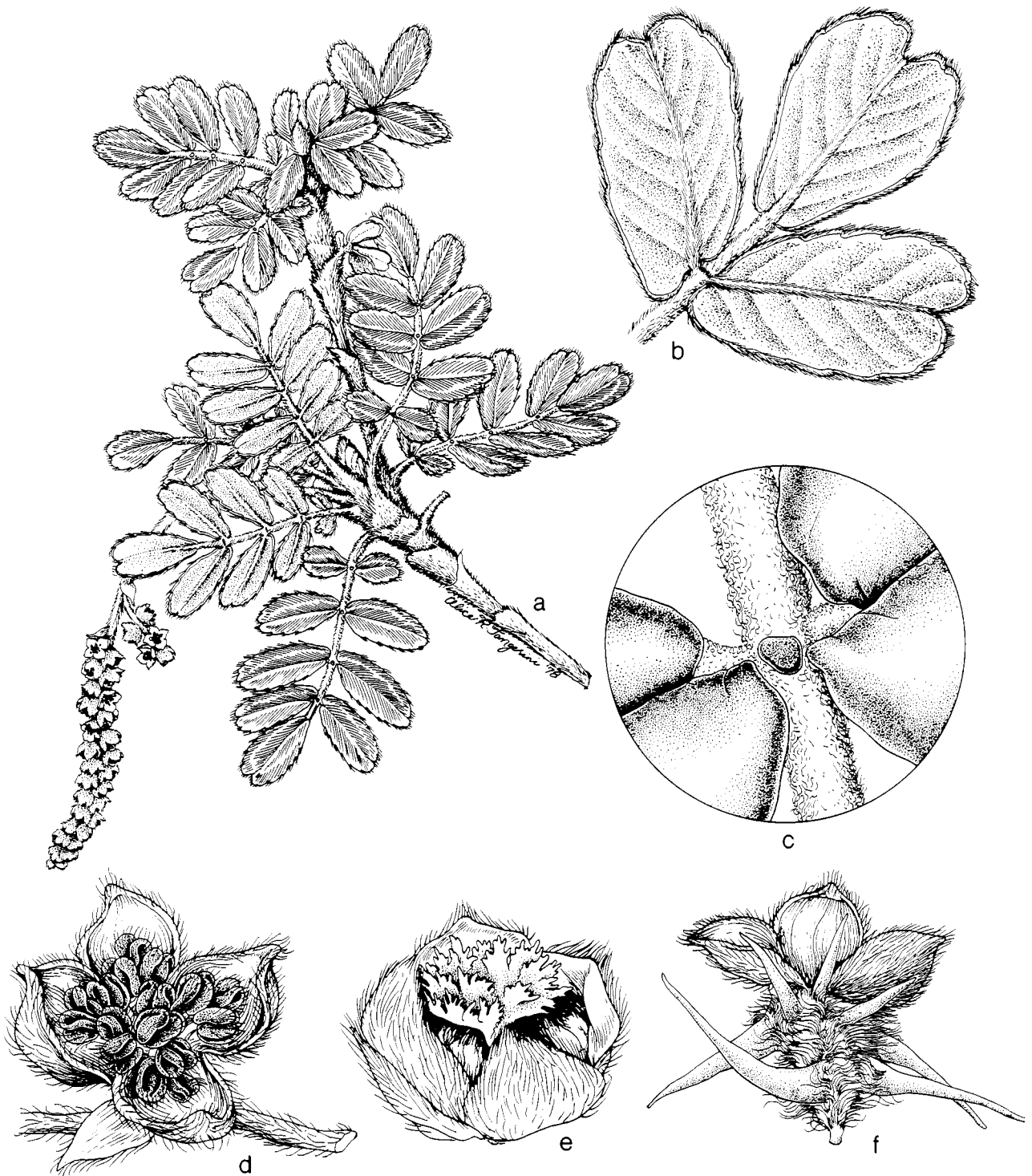


FIGURE 26.—*Polylepis quadrijuga*: a, branch ( $\times 0.5$ ); b, undersurface of leaflets ( $\times 3$ ); c, point of leaflet attachment, upper surface ( $\times 6$ ); d, e, flowers ( $\times 6$ ); f, fruit ( $\times 6$ ).

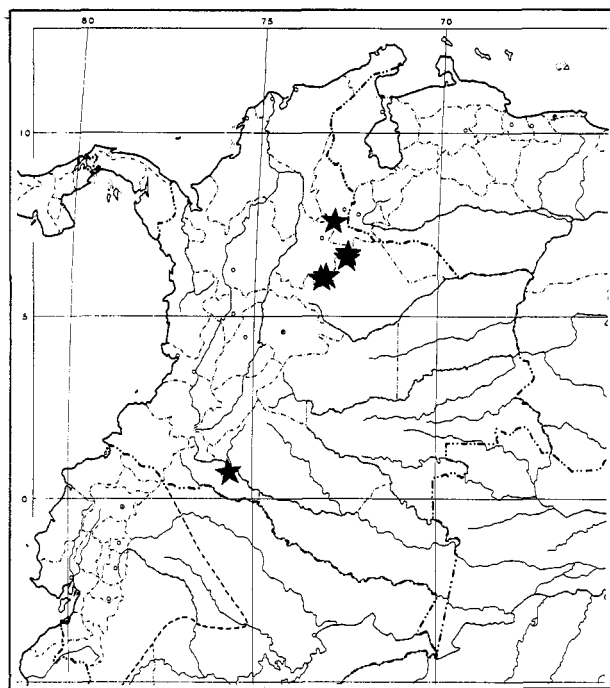


FIGURE 27.—Collection localities of *Polylepis quadrijuga*.

lacks any long, single-celled trichomes at the point of leaflet intersection, whereas the former has these mixed with the glandular trichomes. Presumably *P. quadrijuga* has differentiated from a northern isolated population of *P. lanuginosa* or resulted from establishment of a population from a southern propagule with subsequent differentiation.

The habitat of this species is humid, often boggy páramos or along streams, where trees can form dense stands at elevations as high as 4000 m.

## 11. *Polylepis besseri* Hieronymus

*Polylepis besseri* Hieronymus, 1896:312 [Type collection: Capi, Bolivia, Mar 1890, *Bang* 769. Lectotype G! isotypes GH! MO! NY! US! W!]

*Polylepis racemosa* var. *tomentosa* O. Kuntze, 1898:77 [Type collection: between Challa and Tapacari, Cochabamba, Bolivia, 3600–4600 m, 18 Mar 1892, *Lorentz & Hieronymus s.n.* Type destroyed at Berlin, isotypes NY! UC! US!]

*Polylepis racemosa* var. *lanata* O. Kuntze, 1898:77. [Type collection: Tunari, Bolivia, 3000–4000 m, *Kuntze s.n.* Type destroyed at Berlin, isotype NY!]

*Polylepis besseri* var. *abbreviata* Bitter, 1911b:628. [Illegitimate name since it was based on *P. racemosa* var. *tomentosa* O. Kuntze.]

*Polylepis besseri* var. *longipedicellata* Bitter, 1911b:629. [Type

collection: Puna of Mizque, Cochabamba, Bolivia, *d'Orbigny s.n.* Holotype G!, isotypes NY! US!]

*Polylepis triacontandra* Bitter, 1911b:630. [Type collection: Larecaja near Sorata, Cochipata, La Paz, Bolivia, 3300 m, 9 Oct 1818, *Mandon* 674. Lectotype G!, isotypes NY! P! S! US!]

*Polylepis crista-galli* Bitter, 1911b:633. [Type collection: Tucumilla, Tarija, Bolivia, 2500 m, *Fiebrig* 2020. Lectotype G!, isotypes A! P!]

*Polylepis crista-galli* var. *longiracemosa* Bitter 1911b:634. [Type collection: Pinos, between Tarija and San Luis, Tarija, Bolivia, 2500–2700 m, 1 Mar 1903. *Fries* 1296. Holotype S!]

*Polylepis tenuiruga* Bitter, 1911b:635. [Type collection: "Chile" without precise locality, *Besser s.n.* Type destroyed at Berlin, Rockefeller photograph no. 3397, types of the Berlin Herbarium at GH, NY.]

*Polylepis subquinquefolia* Bitter, 1911b:636. [Type collection: Sandia above Coyoeno, Puno, Peru, 3600 m, *Weberbauer* 931. Type destroyed at Berlin, Rockefeller photograph no. 3391, types of the Berlin Herbarium at GH, NY.]

*Polylepis rugulosa* Bitter, 1911b:639. [Type collection: Pampa behind train station, Arequipa to Puno line, Arequipa, Peru, 3800 m, *Weberbauer* 4881. Type destroyed at Berlin, isotype WRAT.]

*Polylepis incana* ssp. *subtusalbida* Bitter, 1911b:640. [Type collection: Cuesta de Duraznillos, Bolivia, 2400–2600 m, Dec 1907, *Hertzog* 712. Holotype WRSL.]

*Polylepis incana* ssp. *incarum* Bitter, 1911b:643. [Type collection: Lago Titicaca, Isla del Sol, near Challa, Bolivia, *Seller* 148. Holotype B!]

*Polylepis incana* ssp. *brachypoda* Bitter, 1911b:644. [Type collection: Lago Titicaca, Isla del Sol, near Challa, Bolivia, *Seller* 148a. Type not seen, possibly destroyed at Berlin.]

*Polylepis pallidistigma* Bitter, 1911b:645. [Type collection: Azangaro, Munani, Puno, Peru, 3650 m, *Weberbauer* 1369. Type destroyed at Berlin, isotype WRAT.]

Trees 1–8 m tall. Leaves congested at the ends of the branches, imparipinnate with 1–3 pairs of leaflets (Figures 28a, 29a); rhombic or obtrullate in outline, 1.4–4.9 cm wide, 1.8–7.9 cm long, rachises densely lanose mixed with glandular trichomes; point of leaflet attachment (Figures 28b, 29b) with a small tuft of yellowish or white trichomes; stipule sheaths with a slight shoulder or sloping away from the petiole, densely pubescent at the base. Leaflets broadly obovate to almost orbicular, first pair from the apex the largest, one of this pair 0.5–1.5 cm wide, 0.9–3.4 cm long; margins crenate or more or less entire, often revolute, apex obtuse or emarginate, base abrupt, unequal; upper surface dull, often rugose, sometimes with scattered twisted trichomes; lower surface (Figure 28c, 29b) pannose or lanose, the vestiture white, often with glandular trichomes very dense along the veins and leaflet margins, occa-

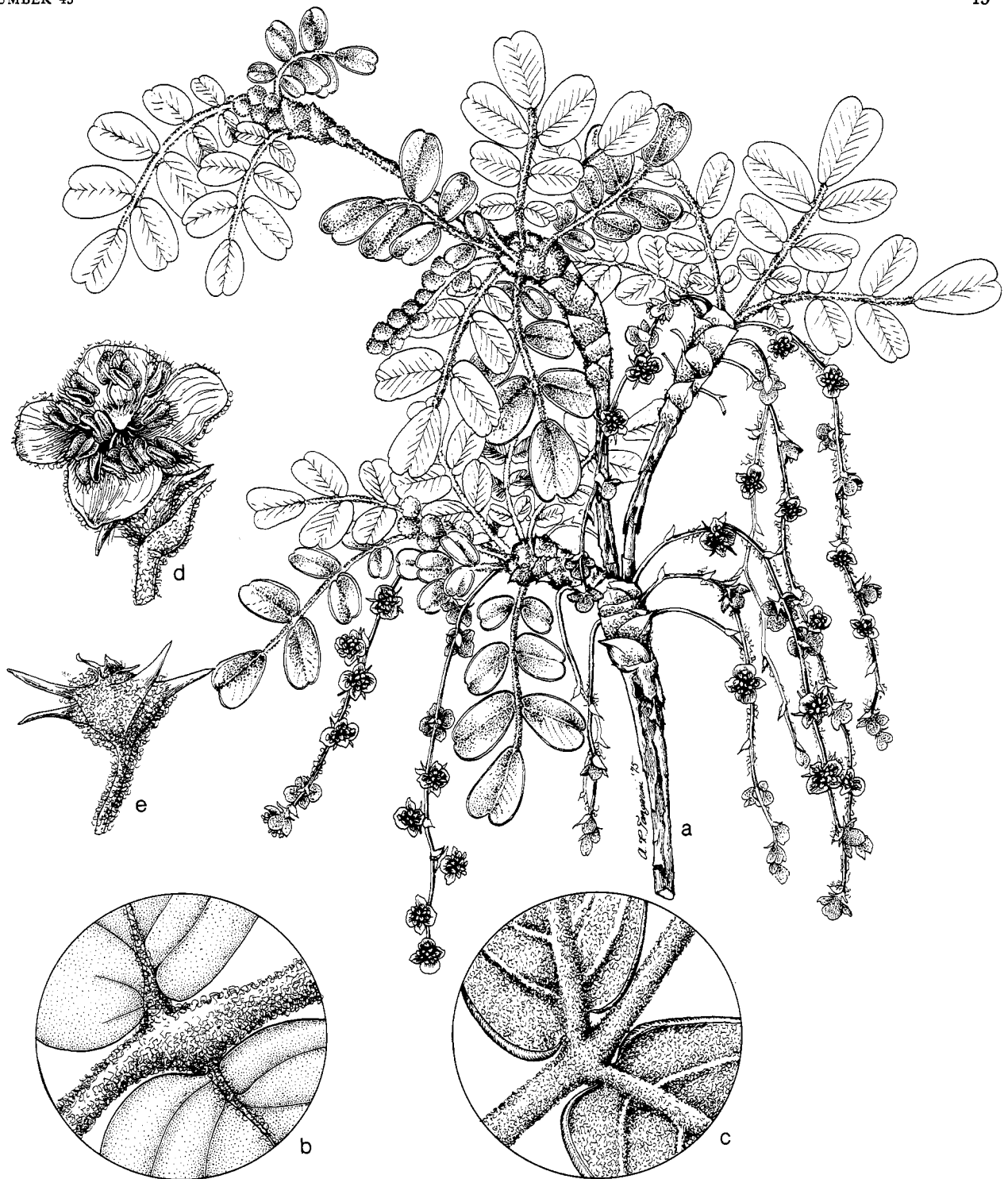


FIGURE 28.—*Polylepis besseri* from Colomi, Bolivia: *a*, branch ( $\times 0.5$ ); *b*, point of leaflet attachment, upper surface ( $\times 3$ ); *c*, point of leaflet attachment, lower surface ( $\times 3$ ); *d*, flower ( $\times 3$ ); *e*, fruit ( $\times 3$ ).

sionally glabrescent. Inflorescence pendant (or more or less upright if very short), 3.0–11.0 cm long, bearing 3–12 flowers; floral bracts lanceolate, glandular on the outer surface; rachises glabrescent with scattered glandular trichomes or lightly lanose. Flowers (Figure 28*d*, 29*c*) perfect, 0.9–1.0 cm in diameter; sepals 3–4, ovate, shortly lanose on the outer surface and on the tips of the inner surface, outer surface often with variable amounts of glandular trichomes; stamens up to 24 (12–24) per flower, anthers orbicular, tomentose at the apex; base of style white tomentose. Fruit (Figure 28*e*, 29*d*) very turbinate, with variable numbers and placement of flattened spines often coalesced into a spiny wing, body of fruit and spines densely lanose; 0.2–0.9 cm wide including protuberances, 0.4–1.3 cm long.

**DISTRIBUTION.**—Southern Peru from Moqueque and Cuzco south to Arequipa and Puno (the Besser specimen label “Chile” was probably collected in Tacna, Peru) and in Bolivia in the provinces of La Paz, Cochabamba, Oruro, Chuquisaca, and Tarija (Figure 30). Flowers recorded in January to June and October and November.

**COMMON NAME.**—Queñua.

**USES.**—None specifically reported.

**REPRESENTATIVE SPECIMENS EXAMINED.**—PERU. CUZCO: 3 km east of Cuzco, valleys and open slopes, 3600 m, 1 Oct 1936, *West 8053* (GH, MO, UC); Cuzco, 3540 m, 19 May 1958, *Infantes 5649* (P); Kavia, *Infantes 6228* (P); near Cuzco, 3300–3800 m, 19–21 May 1958, *Humbert 30526* (P); without locality, 1839–1940, *Gay s.n.* (GH). MOQUEGUA: Cordillera above Torata, 3900–4000 m, 14–15 Feb 1925, *Weberbauer 7470* (BM, F, G, S, US). TACNA: 4 km north of Torata, 3840 m, 27 Jan 1952, *Pearson 33* (F, UC). PUNO: Volcan Chachani, ca. 4000 m, 16 Jan 1977, *Simpson 8570* (US); *ibid.*, *Rauh P556* (NY); *ibid.*, 4000–4200 m, 14 Apr 1925, *Pennell 13295* (F, GH, US); Sihuata, La Cumbre between Arquipa and Puno, 2600–4000 m, 13 Nov 1947, *Ferreyra 2594* (GH, UC, US); between Lake Salina and Arequipa, 13,000 ft, 7 Feb 1943, *Sandeman 3816* (F, K); Prov. Carabaya, between Macusani and Nuñoa, 4000 m, 29 Feb 1948, *Vargas 7139* (MO); Puno, 2 Jan 1920, *Shepard 150* (GH, NY). BOLIVIA. LA PAZ: Dept. La Paz, 3840 m, Mar 1910, *Buchtien 4243* (GH, NY); Titicaca, *d'Orbigny s.n.* (P). COCHABAMBA: Chapare, Quebrada de Colomi, 11,500 ft, *E. K. Balls B6244* (BM, K, UC, US); Colomi, 12,200 ft, *Brooke 5075* (F, NY); Abra de Colomi, 3450 m, 20 Jan 1929, *Steinbach 9869* (F, GH, K, MO, S); *ibid.*, Feb 1947, *Cardenas 3906* (S, US); *ibid.*, Jan 1949, *Cardenas 4333* (US); Prov. Cochabamba, Liriuni, 24 Feb 1950, *Krapovichas & Fuchs 6690* (LIL); 100 mi northwest of Cochabamba across the Tunari Range, Choro, 11,000 ft, 18 Jan 1950, *Brooke 5984* (F, NY); Prov. Quillacollo, 4 km after Cochabamba on the road to Morochata, 5 Jan 1968, *Vuilleumier 468* (GH, P, US); 81 miles out of Cochabamba on the road to Santa Cruz, 13 Nov 1959,

*Maguire & Maguire 4482* (GH, K, NY, US). CHUQUISACA: Guerraloma, 2800 m, May 1958, *Cardenas 5724* (US).

**DISCUSSION.**—Without doubt, *Polylepis besseri* is comprised of the most polymorphic and confusing set of populations of any of the species of the genus. The same confusion I experienced in the treatment of these populations is evident in the treatments of earlier workers. Several specimens described as varieties of *Polylepis racemosa* by Otto Kuntze (1898) are included here and were transferred to components of this species by Bitter (1911*b*). In the original description of the species by Hieronymus, several collections were cited from various parts of Bolivia. Bitter specifically stated that Hieronymus' species was an unnatural one containing more than one species and he separated part of the collections out at *P. tenuiruga*. Another specimen annotated by Hieronymus as belonging to *P. besseri* was made the type of *P. crista-galli* by Bitter. In addition, Bitter described several other species on the basis of one or two collections. Even within the collections designated as the types of his various species, however, there is tremendous variation. The specimen labeled “Type” of *P. triacandra* has leaflets over 3 cm long, whereas other specimens from the same collection have leaflets about 1 cm long. A large series of collections by various botanists from Colomi, Bolivia, has several herbarium names indicating that the collectors considered describing other new species.

While final resolution of this series of populations must wait until more collections are made in the Eastern Bolivian mountains, the treatment proposed here is the only logical one possible with the material now present in herbaria. The assignment of the various populations to a series of species as proposed by Bitter makes no sense in the light of the number of intermediate populations and variation within populations. Within a population, the greatest amount of variation is in the size of the leaflets and the density of the trichomes on the underleaflet surfaces. Between populations, the variation is in amount of crenation or revolution of the leaflet margins, the amount of rugosity of the upper leaflet surface, the extent of the glandular trichomes on the veins of the underleaflet surfaces and the amount of coalescence of the spines of the fruits to form spiny wings. All of these characters can vary to some extent, however, within a population.

Morphologically, *Polylepis besseri* most closely

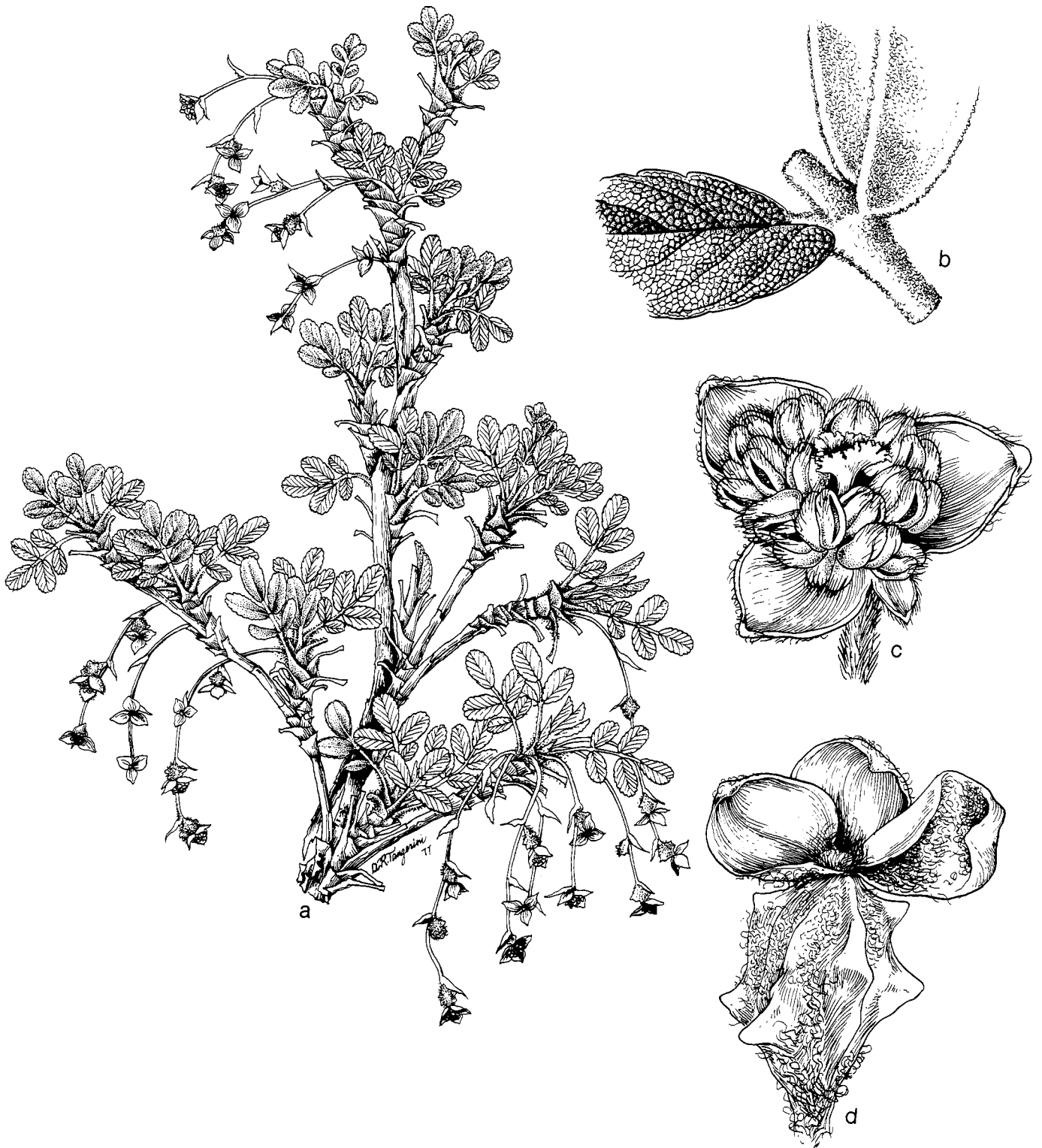


FIGURE 29.—*Polylepis besseri* from Chachani, Peru: a, branch ( $\times 0.5$ ); b, point of leaflet attachment with one leaf turned to show lower surface ( $\times 6$ ); c, flower ( $\times 6$ ); d, fruit ( $\times 6$ ).

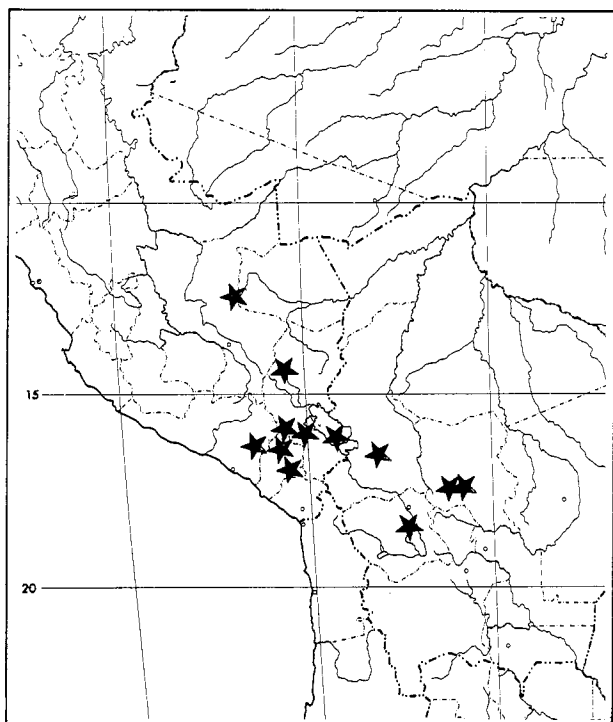


FIGURE 30.—Collection localities of *Polylepis besseri*.

approaches *P. tomentella*, but the latter never has the dense pure white covering of the underleaflet surfaces that is so common in *P. besseri*. In addition, the fruits of *P. tomentella* are ridged or irregularly winged, whereas those of *P. besseri* have flattened spines projecting upward at the apex of the fruit or coalesced into spined wings irregularly placed on the fruit. The stipule sheaths of *P. besseri* are almost always pubescent and those of *P. tomentella* glabrescent or glandular.

## 12. *Polylepis tomentella* Weddell

*Polylepis tomentella* Weddell, 1861:237, taf. 78. [Type collection: Chuquisaca, Cinti, Bolivia, Jan 1846, Weddell 3927. Lectotype P! isotype P!]

*Polylepis tarapacana* Philippi, 1891:21. [Type collection: near Caña, Tarapacá, Chile, 3900 m, Philippi s.n. Lectotype SGO, isotypes GH! SGO.]

*Polylepis tomentella* var. *pilosior* Bitter, 1911b:647. [Type collection: Chuquisaca, Cinti, Bolivia, Jan 1846, Weddell 3947 (in part). Holotype P!]

*Polylepis tomentella* ssp. *pentaphylla* Bitter, 1911b:648. [Type collection: Laguna Tres Cruces, Jujuy, Argentina, Dec 1900 to Feb 1901, Clarin 11688. Holotype S!]

*Polylepis tomentella* ssp. *tetragona* Bitter, 1911b:649. [Type collection: Salinas Grande near Jujuy, Jujuy, Argentina,

3500 m, Hauthal 141. Type not seen, apparently destroyed at Berlin.]

*Polylepis tomentella* ssp. *dentatilata* Bitter, 1911b:650. [Type collection: in a valley between Chorolque and Tacna, Potosí, Bolivia, 3600–3800 m, Hauthal 117. Type not seen, apparently destroyed at Berlin.]

*Polylepis tarapacana* var. *multisquama* Bitter, 1911b:654. [Type collection: Tarapacá, Chile, Philippi s.n. B, apparently destroyed. Probably an illegitimate name since it was based on a Philippi specimen that was most likely part of the type collection of *P. tarapacana*.]

*Polylepis tarapacana* var. *sajamensis* Bitter, 1911b:654. [Type collection: Sajama, Oruro, Bolivia, 4500 m, Stübel 1. Type not seen, probably destroyed at Berlin. Cited by Bitter as a unicate.]

*Polylepis tarapacana* var. *brevifilamentosa* Bitter, 1911b:654. [Type collection: near the Bolivian province of Oruro, Tacna, Peru, Stübel 112. Type not seen, apparently destroyed at Berlin.]

*Polylepis tarapacana* var. *pynoloph*a Bitter, 1911b:654. [Type collection: between La Paz and Tacna, Bolivia, 12,300–13,400 ft, 1838, Pentland s.n. Holotype P!]

Small trees 1–4 m tall. Leaves congested at the ends of the branches or continuously borne all along the branches, composed of 1 (occasionally 2) pair of leaflets (Figures 31a, 32a), trullate in outline, 0.8–3.9 cm wide, 1.9–2.4 cm long, rachises glabrous or covered on the abaxial side with glandular trichomes and long, white, single-celled trichomes, point of leaflet attachment sericeous; stipule sheaths with a slight shoulder at the apex or sloping downward, glabrous at the bottom of the outer surface, the top of the outer surface often with glandular trichomes, and with long trichomes projecting from the inside upper sheath surface (Figures 31b, 32b). Leaflets ovate to obovate, 0.3–0.6 cm wide and 0.7–2.0 cm long, variable in thickness, margins entire to crenate, apex obtuse, base unequal; upper surface glabrous, dull green or yellowish green (Figures 31c, 32c); lower surface variable, densely pilose, often with glandular multicellular trichomes giving the surface a matted, yellow appearance or glabrescent with scattered glandular protuberances. Inflorescences upright or pendant; if upright, bearing 1 or 2 flowers, if pendant, with 1–8 flowers, 0.1–5.1 cm long; floral bracts hidden or lanceolate, denticulate, about 2 mm long, sparsely covered with glandular trichomes; rachises glabrescent with appressed, twisted trichomes mixed with glandular protuberances and resin. Flowers (Figures 31d, 32d) perfect, 0.4–0.6 cm in diameter, sepals 3, ovate, sometimes adnate at the base, green, outer surface with twisted white trichomes and glandular pro-

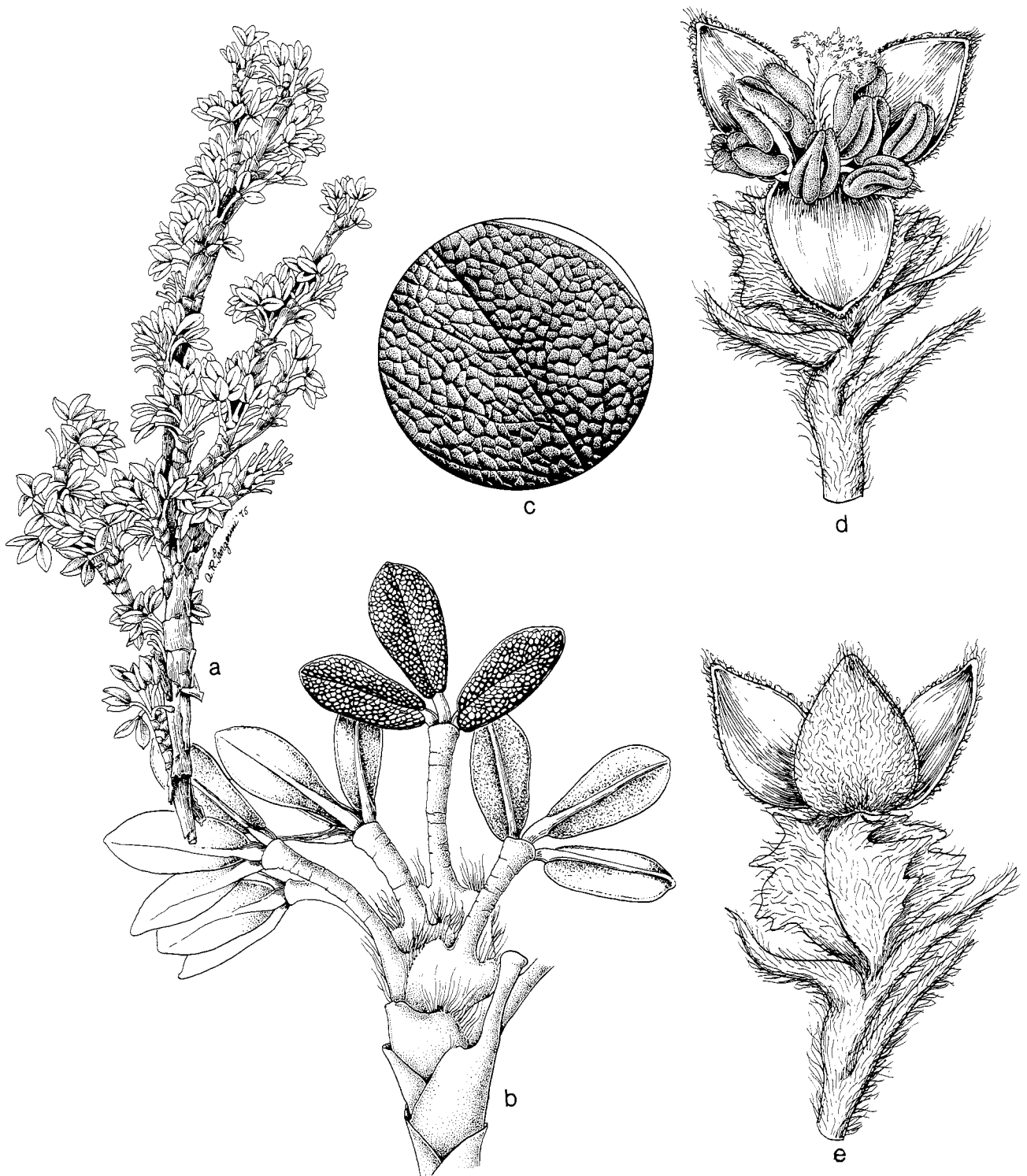


FIGURE 31.—*Polylepis tomentella* from Volcan Sajama, Bolivia: *a*, branch ( $\times 0.5$ ); *b*, cluster of leaves ( $\times 3$ ); *c*, upper leaflet surface ( $\times 12.5$ ); *d*, flower ( $\times 6$ ); *e*, fruit ( $\times 6$ ).

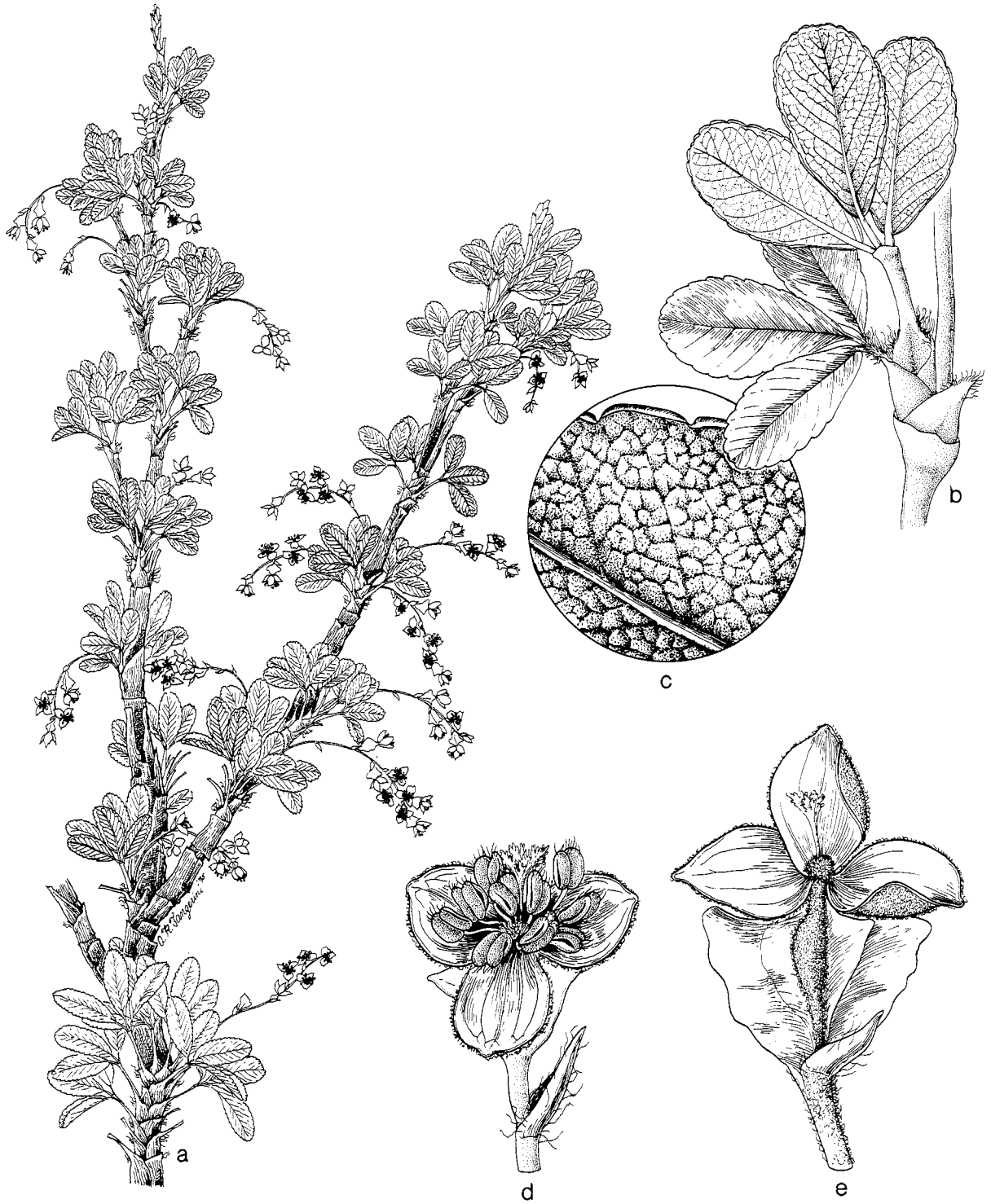


FIGURE 32.—*Polylepis tomentella* from Cochabamba, Bolivia: *a*, branch ( $\times 0.5$ ); *b*, cluster of leaves ( $\times 3$ ); *c*, upper leaflet surface ( $\times 12.5$ ); *d*, flower ( $\times 6$ ); *e*, fruit ( $\times 6$ ).

tuberances, stamens 6-14, ovoid, red, tomentose at the apex; base of style hispid. Fruit turbinate, with 3-4 ridges, the ridges sometimes expanded into wings with entire or toothed margins or merely with a few knobs, body of the fruit with twisted trichomes (Figures 31e, 32e), 0.2-0.78 cm wide, including ridges, 0.3-0.9 cm long.

**DISTRIBUTION.**—Southern Peru from Tacna to Puno southward to northern Chile in the province of Tarapacá and across western and central Bolivia to northern Argentina in the province of Jujuy (Figure 33). Flowering recorded in July, October, and December to March.

**COMMON NAME.**—Queñoa.

**USES.**—None specifically described, but personally observed to be used as firewood.

**REPRESENTATIVE SPECIMENS EXAMINED.**—PERU. PUNO: Santa Rosa, 50 miles south-southwest of Llave, 4600 m, 25 Jul 1946, O. Pearson 16 (US). TACNA: Cordillera de Tacora, Chulunquaiani, Weddell s.n. (P); Tacora, Chislluma, 4500 m, Apr 1926, Werdermann 1143 (A, BM, F, G, GH, K, MO, NY, UC, US). BOLIVIA. ORURO: Province Carangas around the base of Volcan Sajama, 4350 m, 18 Oct 1967, Vuilleumier 316

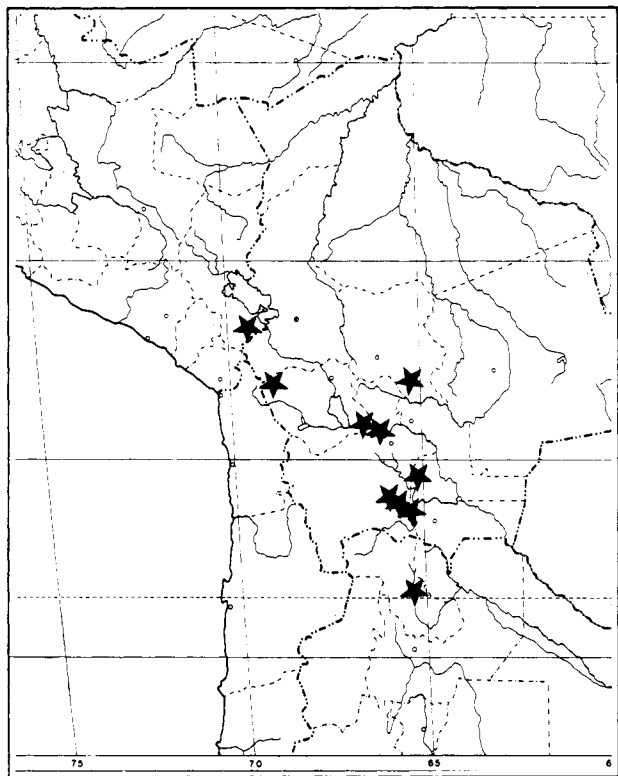


FIGURE 33.—Collection localities of *Polylepis tomentella*.

(GH, US); Challapata, 4000 m, 1 Apr 1921, *Asplund 6169* and *6170* (US). POTOSÍ: Province Frias, 39 km northwest of Potosí on the road to Challapata, 3680 m, 14 Dec 1967, *Vuilleumier 450* (GH, US); Province Chichas, near Quechisla on the road to Chonolque, 3600 m, Dec 1931, *Cardenas 24* (GH); Province Sud Chichas, Mina Isca Isca above the village of La Torre north of Tupiza, 3875-3880 m, 2 Dec 1967, *Vuilleumier 402* (GH, US); near Santa Barbara on the road from Quechisla, 4200 m, 22 Feb 1936, *West 6110* (GH, MO, UC). COCHABAMBA: Mizque, *D'Orbigny 495* (P); between Monte Punco and Siberia, 3500 m, 28 Jan 1958, *Meyer 20335* (LIL). CHUQUISACA: Province Nor Cinti, along the road between Camargo and San Lucas, 3300 m, 10 Dec 1967, *Vuilleumier 427* (GH, US); Quebrada Honda, 3100 m, 28 Mar 1934, *Hammarlund 395* (S). ARGENTINA. JUJUY: Humahuaca, Mina Aguilar, 4500 m, 16 Mar 1953, *Sleumer 3375* (S).

**DISCUSSION.**—Included here within *Polylepis tomentella* are essentially all of the forms originally included in the taxon by Weddell. Bitter considered Weddell's taxon to be an artificial assembly of at least two distinct species, and he consequently recognized both *P. tomentella* and *P. tarapacana*, a species described by Philippi. In his treatment, Bitter effectively typified *P. tomentella* by excluding all of the specimens cited by Weddell except Weddell's own collection from Cinti, Bolivia. Consequently, the specimens cited by Weddell from Tacna fall within the circumscription of *P. tarapacana* if it is recognized. In addition to the treatment of *P. tomentella* as two species, Bitter also erected numerous subspecific taxa within both species. Despite his fragmentation of the entire complex, however, he stated that an examination of more specimens might eventually show *P. tomentella* and *P. tarapacana* to be conspecific. My examination of a variety of specimens, including numerous personal collections from western Bolivia, indicates that this is indeed the case. While it is true that populations from Tarapacá, Chile, and adjacent Bolivia look very different from those in Cochabamba, Bolivia, there is a gradual transition from west to east across the altiplano with no populations that appear as "hybrids." If it were not for the clinal change exhibited by the populations across Bolivia, the eastern and western forms could be considered separate taxa. In the west, plants have reduced thick leaflets with almost entire margins and densely pubescent underleaf surfaces (with a large number of glandular trichomes mixed with tightly twisted, short trichomes). Eastward in Bo-

livia toward Oruro and southward toward Jujuy, Argentina, the leaves become larger, more crenate, and thinner. Especially in central Bolivia, the pubescence of the underside of the leaves becomes less dense. In Cochabamba, the leaflets are quite thin, almost glabrous, and very crenate. In addition, the inflorescences are longer and bear more flowers in the eastern populations than in those in the west. All of these morphological changes from west to east appear to be related to the changes in environmental conditions. Populations in the west are at 4000–5200 m elevations in extremely arid areas. Eastward across the altiplano, the elevation is lower and the rainfall higher. Morphological characteristics of the westernmost populations are common features of desert trees, which become less pronounced as aridity decreases.

Not only does it seem to be most meaningful to consider *P. tomentella* and *P. tarapacana* as one taxon, but it also seems unnecessary to retain the subspecific taxa Bitter erected. In general, the characters that separate these subspecies and varieties are the number of pairs of leaflets, the amount of dentation of the leaflet margins, and number of fruit ridges. All of these characters are variable within populations of many species of the genus and not even consistent within the collections designated as types of these subspecific entities by Bitter.

A more difficult problem with *Polylepis tomentella* lies in an assessment of its affinity with *P. besseri* and *P. incana*, particularly in central and southern Bolivia. In eastern Bolivia, populations of *P. tomentella* are very similar to those of *P. incana*. Both species in this region normally have three leaflets, crenate leaflet margins, glabrous or sparsely pubescent under leaflet surfaces, and few-flowered racemes. The fruits of both usually have irregular wings. It is possible that the two taxa approach each other morphologically because of the similarity of the habitats in which they occur. Since this is the only area where the two species come into contact, it is also possible that they are forms of one species that replace each other geographically. The morphological characters that can best separate the two as treated here are the pubescence of the underleaflet surfaces and the shape of the leaflet. In *P. incana*, the leaflets are long, rather narrow, and distinctly oblanceolate, where in *P. tomentella* they are broader and often more ovate. The underleaf surfaces of *P. incana* have a dusky yellow cast, whereas

those of populations of *P. tomentella* in areas of sympatry (Cochabamba, Bolivia) do not. *Polylepis tomentella* in western Bolivia does have yellowish underleaflet surfaces, but in these populations the leaflets are very thick and have a dense covering of twisted white trichomes mixed with the yellow glandular trichomes. These two characters represent the most easily described of a set of features that gives the foliage of *P. incana* a very different aspect from that of *P. tomentella*. The two are, however, sometimes difficult to distinguish from each other.

In eastern Peru, there are also some specimens that indicate that *Polylepis tomentella* might hybridize with *P. besseri* (e.g., Meyer 20335). Such specimens have crenate, nonmarginate leaflets like *P. tomentella*, but the characteristic densely wooly pubescence of *P. besseri*. The two are usually separated ecologically with *P. besseri*, inhabiting the moist eastern slopes and *P. tomentella* the interior drier regions. In the valley around Cochabamba, the two could naturally meet or have been brought into close proximity by man.

### 13. *Polylepis incana* Humboldt, Bonpland, and Kunth

*Polylepis incana* Humboldt, Bonpland, and Kunth, 1824:227. [Type collection: Los Pastos, Guachucal along the Rio Blanco, Ecuador, 9684 ft, Dec, Bonpland 2191. Holotype P!, isotype P!]

*Polylepis incana* var. *villosistyla* Bitter, 1911b:642. [Type collection: El Altar, Ecuador, Meyer 177. Type not seen, presumed destroyed at Berlin.]

Trees 5–8 m tall. Leaves congested at the ends of branches (Figure 34a), imparipinnate with one pair of leaflets, trullate in outline, 1.4–3.9 cm wide, 1.9–6.4 cm long; rachises with short, twisted trichomes and small, multicellular glandular trichomes mixed with resinous exudate; point of leaflet attachment (Figure 34c) with a small tuft of long, curled trichomes; stipular sheaths sloping away from the petiole, outer surface with glandular trichomes and resinous exudate; inner basal part of petiole and inside of the top of the sheath villous. Leaflets obovate in outline, 0.4–1.4 cm wide (0.5), 1.2–4.0 cm long, margins crenate, apex obtuse to slightly emarginate, base attenuate; upper leaflet surface glabrous; lower surface (Figure 34b) densely covered with short, twisted, irregular multicellular trichomes mixed with resinous exudate and often with sparse,

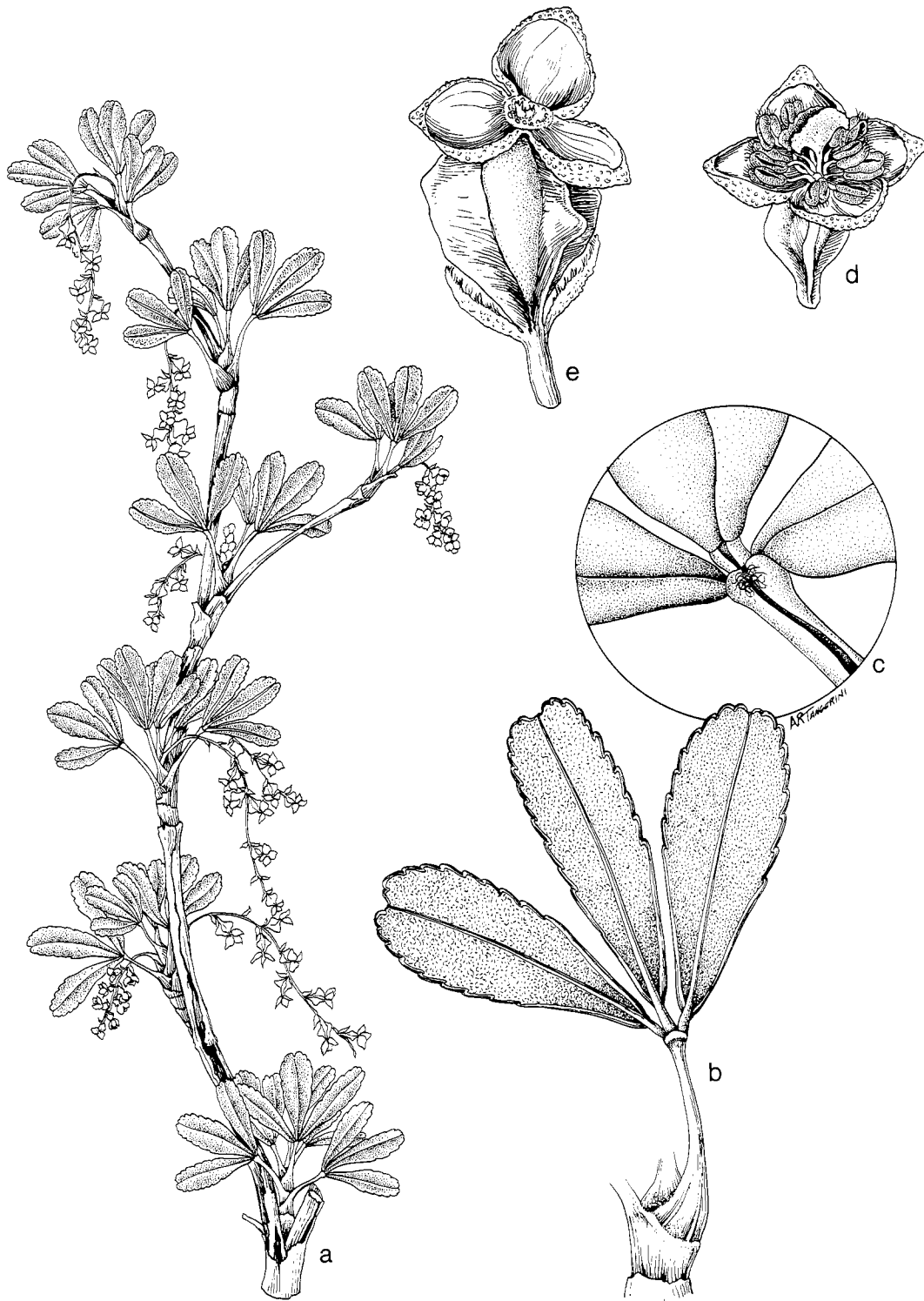


FIGURE 34.—*Polylepis incana*: a, branch ( $\times 0.5$ ); b, leaf from underside ( $\times 1.5$ ); c, point of leaflet attachment, upper surface ( $\times 6$ ); d, fruit ( $\times 6$ ); e, flower ( $\times 6$ ).

bent, long, single-celled trichomes. Inflorescences pendant, 2–7 cm long, bearing 3–10 flowers; floral bracts to 3 mm long, narrowly lanceolate, glabrous or pilose on the outer surface; rachises with glandular trichomes and exudate. Flowers (Figure 34*d*) perfect, 0.3–0.7 cm in diameter; sepals 3 (4), ovate, outer surface covered with appressed small multicellular trichomes; stamens 8–24, anthers orbicular, barbate; base of style villous. Fruit (Figure 34*e*) turbinate to fusiform, irregularly ridged and/or winged with pointed wings, 0.2–0.7 cm wide, including wings, 0.2–0.5 cm long.

**DISTRIBUTION.**—Central Ecuador in Pichincha to southern Peru in the Department of Cuzco (Figure 35). Flowering recorded in January, May, June, and August to November.

**COMMON NAMES.**—Quiñuar, quiñual, quenuina, cceuna, manzanita, qqueuna.

**USES.**—The wood is used by Indians to manufac-

ture instruments for cultivation, for house construction, and as firewood. Recently man has used the wood in construction of mining shafts at high elevations. Tannin extracted from the branches is used for tanning.

**REPRESENTATIVE SPECIMENS EXAMINED.**—ECUADOR. PICHINCHA: Quito, 1845, *Jameson 17* (G, W); Volcan Iliniza, northern slopes, 4000 m, 19 Apr 1969, *Sparre 15625* (S); El Chaupi on the road to Volcan Iliniza, 3300 m, 29 Apr 1967, *Sparre 15644* (S); between Pifo and Papallacta, Jan 1955, *Fagerlind & Wibom s.n.* (S). COTOPAXI: railroad station Cotopaxi, 3400 m, 26 May 1939, *Asplund 6476* (G, S, US). TUNGURAHUA: vicinity of Ambato, 24–28 Aug 1918, *Rose & Rose 22397* (GH, NY). AZUAY: between Molleturo and Toredor, 2590–3900 m, 14 Jun 1943, *Steyermark 53038* (F, NY). PERU. ANCASH: Cordillera Raura, 4300 m, *Rauh & Hirsh 22.754* (NY); Chiklin, 28 Oct 1927, *Sawada P83* (F). HUANUCO: Llata, 7000 ft, 21 Aug 1922, *Macbride & Featherstone 2249* (F, G, GH, S, US). PASCO: near Oyon, Rio Huaura, 3800 m, 29 Nov 1964, *Koepcke 1861bd* (UC); below Cerro de Pasco on the road to Ambo, 24 Nov 1945, *Seibert 2202* (MO, US); between Cerro de Pasco and La Quiñua, 5 km along the highway above La Quiñua, 3600 m, 21 Jun 1940, *Asplund 11847* (G, S, US). CUZCO: Pisac, 3500–3600 m, 1 May 1925, *Pennell 13731* (F, GH); 3 km east of Cuzco, 3600 m, 1 Oct 1936, *West 8053* (GH, MO, UC); Paucartambo Valley, Chatica, 3800 m, Aug 1926, *Herrera 1129* (F, US).

**DISCUSSION.**—Undoubtedly *Polylepis incana* has been the most misapplied epithet in the genus. It has been used for almost any specimen with a single pair of leaflets as well as for most specimens for which a name was not readily apparent. Part of the problem is that *P. incana* forms the center of a complex of species, many of which appear to hybridize in central Peru. An additional element of confusion was introduced by Bitter's treatment of the taxon. Bitter never mentioned Bonpland's type of the species under any of his subspecific taxa, and it thus appears possible that he was actually not certain as to the correct typification of the name. Nevertheless, he circumscribed three varieties and six subspecies within *P. incana*. As correctly pointed out by Macbride (1934:367), many of the varieties and subspecies are elements that belong within *P. racemosa*. These include *P. incana* ssp. *micranthera*, *P. incana* var. *connectens*, *P. incana* subsp. *icosandra* and *P. incana* var. *primovestita*. The type of Bitter's *P. incana* var. *primovestita* is the same as the type of *P. racemosa* of Ruiz and Pavon. The variety *P. incana* var. *flavipila* was the basis on which Macbride erected his new species, *P. subsericans*. Several other of Bitter's infraspecific taxa, *P. incana* var. *incarum*, *P. incana* ssp. *subtusalbida*, and *P.*

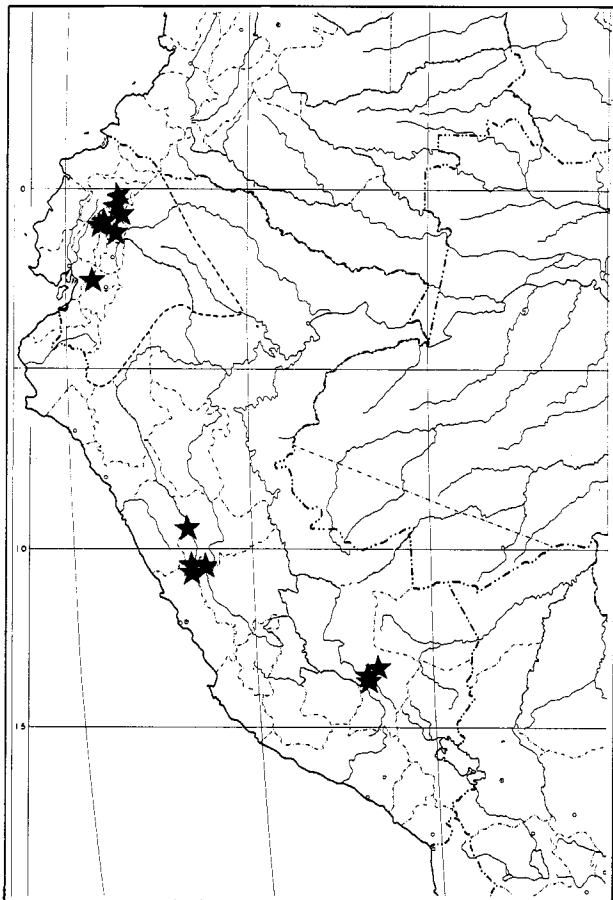


FIGURE 35.—Collection localities of *Polylepis incana*.

*incana* ssp. *brachypoda* belong within *P. besseri*. The only one of Bitter's varieties or subspecies that truly appears to belong to *P. incana* is *P. incana* var. *villosistyla*, but it is not considered here to merit varietal status. While this assignment of Bitter's subspecific taxa appears to be correct, absolute certainty is impossible because most of the types of his taxa were apparently destroyed at Berlin.

As circumscribed here, *Polylepis incana* includes only those individuals with three leaflets having short pilose vestiture on the underleaflet surfaces, usually mixed with multicellular glandular trichomes and resin. Individuals with shaggy, villous underleaflet surfaces are referred to *P. racemosa* and those with a panose covering to *P. besseri*. In central Peru, however, especially in the Pampa de Junín, intermediate specimens do occur. It is probable that human planting of this taxon with *P. racemosa* has fostered hybridization. Personal observations indicate that populations include trees with an upright, narrow branching pattern as well as some with an expanded crown. Intermediate specimens have also been seen from La Libertad, Peru. Under natural circumstances it appears that *P. incana* was distributed from Ecuador to south-central Peru on the dry slopes of the Andes (west-facing slopes of the Eastern Cordillera and east-facing slopes of the Western Cordillera), whereas *P. racemosa* inhabited upper valleys of rivers on the Western Cordillera and the central valleys of Peru from Huanuco.

In Cochabamba, *Polylepis incana* and *P. tomentella* are very similar morphologically. The difference in leaflet pubescence serves to distinguish the two: *P. tomentella* in this region often has glabrous underleaflet surfaces, whereas *P. incana* has pilose, yellowish underleaflet surfaces. Still farther south, either *P. besseri* or *P. rugulosa* replaces *P. incana*. The dense, tomentose (pannose) covering of the undersurface of the leaflets of these two taxa is never found in *P. incana*.

#### 14. *Polylepis racemosa* Ruiz and Pavon

*Polylepis racemosa* Ruiz and Pavon, 1798:139. [Type collection: Caxamarquilla and Pillao, Peru, Ruiz s.n. Holotype P! isotype G!]

*Polylepis villosa* Humboldt, Bonpland, and Kunth, 1824:228. [Type collection: Caxamarca, Peru, 8784 ft. Aug, Bonpland 3685. Holotype P! isotype P!]

*Polylepis incana* ssp. *icosandra* Bitter, 1911b:641. [Type of collection: Cajatambo, between Tallenga and Piscapaccha, Ancash, Peru, Weberbauer 2886. Type not seen, presumably destroyed at Berlin.]

*Polylepis incana* ssp. *micranthera* Bitter, 1911b:642. [Type collection: Sierra, Caxamarquilla, Huanuco, Peru, without collector. Holotype W!]

*Polylepis incana* var. *primovestita* Bitter, 1911b:645. [Type of collection: Caxamarquilla, Peru, Ruiz s.n. An illegitimate name since the same collection is the type of *P. racemosa*.]

*Polylepis incana* var. *connectens* Bitter, 1911b:645. [Type collection: in the mountains of Huanuco, Peru, Haenke s.n. Holotype PR.]

Trees 4–15 m tall. Leaves congested at the ends of the branches (Figure 36a), imparipinnate with 1–3 pairs of leaflets; rhomboid to obovate in outline, 2.3–5.0 cm wide and 3.5–8.8 cm long, rachises villous, especially along a line on the upper surface near the base of the leaf and extending into the inside of the stipule sheath; point of leaflet attachment (Figure 36c) with a tuft of long white, straight trichomes; stipular sheaths with a slight shoulder or sloping away from the petiole, glabrous on the outer surface but with long trichomes protruding at the apex from the inside surface. Leaflets obovate to almost oblong in outline, second pair from the terminal leaflet the largest when present, a leaflet of this pair from 0.7–0.6 cm wide and 2.1–3.7 cm long, margins crenate, especially at the apex, apex slightly to deeply emarginate, base attenuate or unequal; upper leaflet surface glabrous, dark green, sometimes with scattered trichomes in the midvein depression; lower surface (Figure 36b) with long, shaggy trichomes inserted on the veins but loosely covering the entire undersurface, these trichomes mixed with a variable number of short, twisted, several-celled, often glandular trichomes. Inflorescences pendant, 4.0–11 cm long, bearing 3–11 flowers; floral bracts lanceolate, to 3 mm long, scarious; rachises with scattered, curled trichomes. Flowers (Figure 36d) perfect, 0.9–1.0 cm in diameter, sepals 4, ovate, outer surface villous especially at the tips, pilose on the tips of the inner surface, often with intermixed several-celled glandular trichomes, stamens 10–20, anthers orbicular, barbate; style often enlarged near the base due to projection of the ovary from the floral cup, villous at the point of projection. Fruit turbinate (Figure 36e) with 4–5 irregular, flattened wings projecting into a point at the top, body of the fruit covered with curled, white trichomes mixed with glandular multicellular tri-

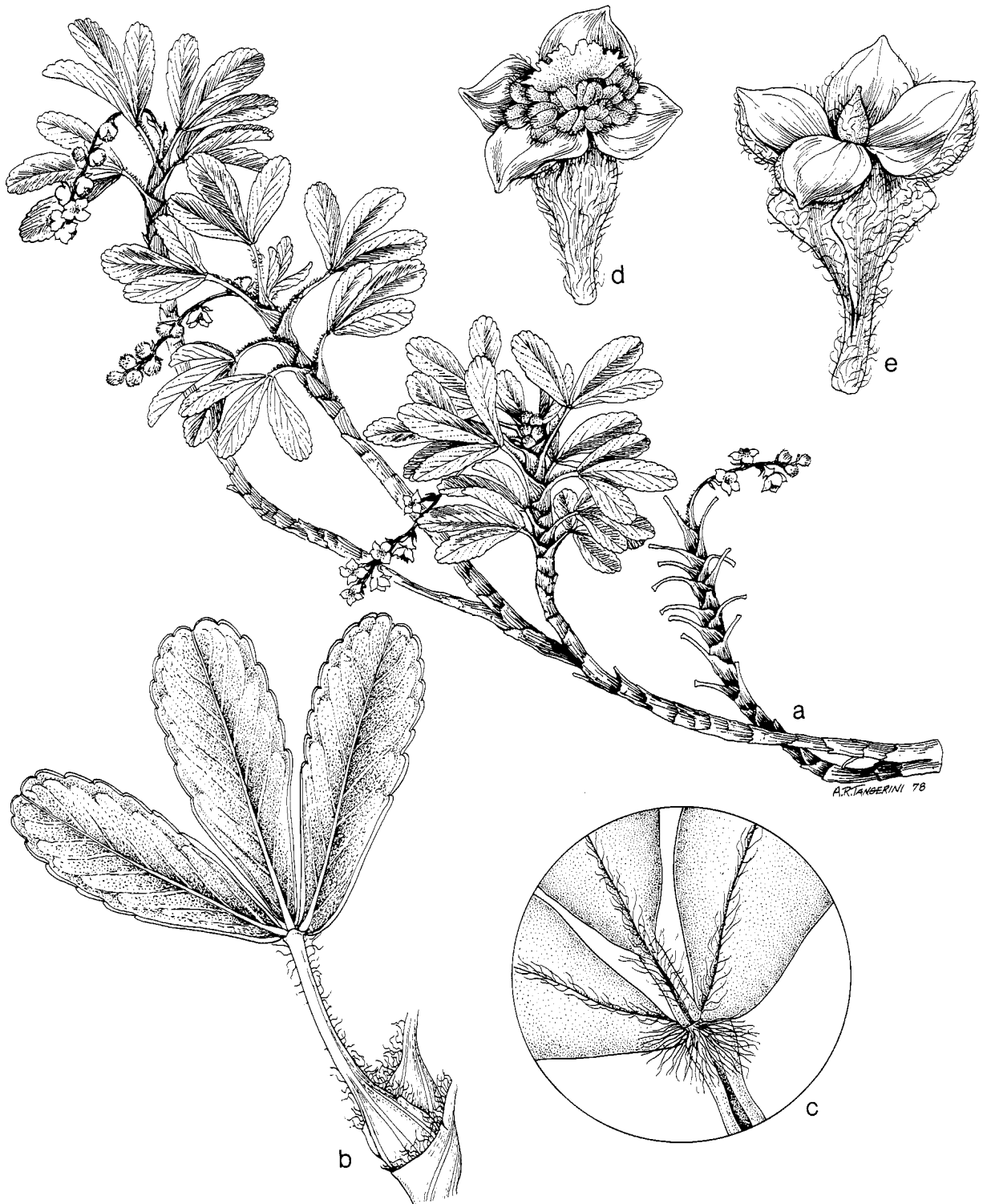


FIGURE 36.—*Polylepis racemosa*: a, branch ( $\times 0.5$ ); b, leaf from the underside ( $\times 1.5$ ); c, point of leaflet attachment, upper surface ( $\times 6$ ); d, flower ( $\times 4.5$ ); e, fruit (4.5).

chomes, 0.2–0.9 cm wide including wings, 0.3–0.8 cm long.

**DISTRIBUTION.**—Northern Peru in the Province of La Libertad and in humid heads of valley on the western slopes of the Peruvian Cordillera south to Lima and in central Peru from Huanuco across the Pampa de Junín to Huancayo (Figure 37). Flowers recorded November to February, April, May, June, and August.

**COMMON NAME.**—Quiñuar.

**USES.**—As an ornamental and as firewood.

**REPRESENTATIVE SPECIMENS EXAMINED.**—PERU. LA LIBERTAD: Province Santiago de Chuco, above Cachicadan toward the top of hills north of Cachicadan, 2900 m, 25 Nov 1938, *Stork & Horton 9972* (F, G, UC), *ibid*, 3100–3250 m, 8 Jun 1953, *Lopez 0983* (US). HUÁNUCO: near Cerro de Pasco, 12,000 ft, 4 Feb 1927, *Kanehira 5* (F); Province Huánuco, km 321 on Route 3 north of Quiñua, 11 Jan 1977, *Simpson 8554* (US). LIMA: Rio Blanco, 3000–3500 m, 15–17 Apr 1929, *Killip & Smith 21745* (F, GH, NY, US); Province Huarochiri, Rio Blanco, 4 Jun 1940, *Asplund 11374* (G, S, US); *ibid*, Infiernillo, 3400 m, 3 Jun 1940, *Asplund 11343* (G, NY, P, S, US); km 111 on Route 20A between Lima and La Oroya, 12 Jan 1977, *Simpson 8559* (US). JUNÍN: Province Cerro, between La Quiñua and Huariaca, Estación La Aurora, 3300 m, 24 Jun 1940, *Asplund 11944* (G, S, US); Tarma, 3300–3500 m, 20–22 Apr 1929, *Killip & Smith 21899* (F, GH, NY, US); Tarma, Ayabamba, 1944, *Soukup 2536* (F, US); between Tarma and Oroya, climbing to the summit, 29 Jun 1948, *Ferreyra 3792*

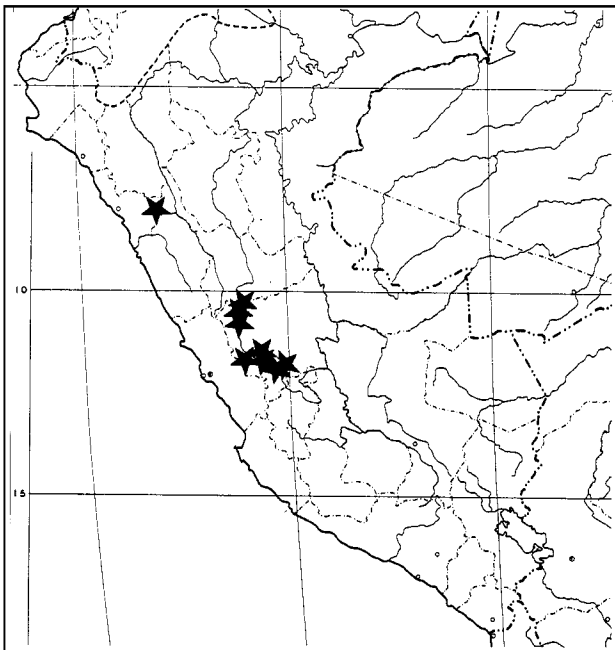


FIGURE 37.—Collection localities of *Polylepis racemosa*.

(US); Province Jauja, Parco between Jauja and Oroya, 3200–3300 m, Nov 1947, *Ferreyra 2833* (US); Huancayo, Pampas Valley, 3300 m, 24 May 1948, *Anderson 695* (US); *ibid*, Concepcion, 10,800 ft, Jul 1945, *Sauleman 4921* (K).

**DISCUSSION.**—This type-species of the genus described by Ruiz and Pavon was redescribed 26 years later by Humboldt, Bonpland, and Kunth as *Polylepis villosa*, but the type specimens of the two taxa are practically identical and come from the same area. Of the two names, *P. villosa* has been most frequently used and, next to *P. incana*, is the name given to most of the specimens that fall within the *incana* complex. Since Bitter's monograph, the name *P. racemosa* has tended to be given to specimens with more than one pair of leaflets and *P. villosa* to those with one pair. The type specimens of both names, however, have only one pair. The collections of Killip and Smith (21745) from Rio Blanco above Lima show that within one population, plants can have leaves with one, two, or three pairs of leaflets. An extreme morphological type with large leaflets in three pairs is seen in the collection of Asplund (11374), which probably came from a particularly favorable environment (planted?). The leaflets of these specimens are quite glabrous—a character often found when water is abundant. The flowers are also large and numerous. The major part of the range of *P. racemosa* (as outlined in Pulgar, 1967) is in the valley of the Río Montaro and across the Pampa de Junín in central Peru. Enormous populations cover the broad, flat valley from Cerro de Pasco to Huancayo. In addition, populations occur down to Huánuco, down the valleys toward Lima and southward toward Cuzco. More than any other species, this taxon is cited as being planted and used as an ornamental by man. The trees around Cerro de Pasco have all been planted. *Polylepis incana*, also much planted, has been collected from the same area. Cerro de Pasco is at a higher elevation, and more exposed, than areas where *P. racemosa* normally grows. Because of this influence of human activities, it is difficult to determine the natural distribution of *P. racemosa*, but it seems safe to infer that it is a natural inhabitant of the Montaro River valley. It is possibly because of man's influence that hybrids with *P. incana* occur. *Polylepis incana* tends to be a species of drier regions, growing from Ecuador south on the eastern side of the Western Cordillera of Peru. If artificially watered, *P. racemosa* could grow in these areas. In southern

Peru where *P. rugulosa* is the native species, similar overlap may occur due to human planting of *P. racemosa*.

Morphologically, *P. racemosa* differs from *P. incana* in the size of the leaflets and the pubescence of the underleaflet surface. The former has leaflets 2.7–4 cm long, whereas in the latter the leaves range from 1.2 to 4 cm but usually shorter than 2.7 cm. The underleaf surfaces of *P. incana* have a relatively sparse covering of yellow glandular protuberances or trichomes and the upper leaf surfaces are often dull and yellowish. The leaflets of *P. racemosa* are green above and have villous trichomes on the veins of the lower leaflet surfaces. In some populations, *P. racemosa* has emarginate leaflets. Possible hybrids include specimens from Huancayo (*Hodge 6221*) and La Libertad (*Stork & Horton 9972*).

### 15. *Polylepis australis* Bitter

- Polylepis australis* Bitter, 1911b:619. [Type collection: Sierra Santa Barbara, Jujuy, Argentina, 2500 m, 11 Jul 1901, *Fries 264*. Lectotype S!, isotype US!]
- Polylepis racemosa* var. *glabra* O. Kuntze, 1898:77. [Type collection: Sierra de Córdoba, Córdoba, Argentina, *Schnyder s.n.* Type presumably destroyed at Berlin, possible isotype NY!]
- Polylepis racemosa* var. *glabrescens* O. Kuntze, 1898:77. [Type collection: Ciénaga, Catamarca, Argentina, *Lorentz 310*. Type destroyed at Berlin, collection duplicate at NY!]
- Polylepis racemosa* var. *albotomentella* O. Kuntze, 1898:77. [Type collection: Los Gigantes, Córdoba, Argentina, *F. Kurtz*, not seen, presumably destroyed at Berlin.]
- Polylepis racemosa* var. *pubescens* O. Kuntze, 1898:77. [Type collection: Cuesta de Copina, Sierra de Achala, Córdoba, Argentina, *Hieronymus s.n.* Type not seen, presumably destroyed at Berlin, collection duplicates at BM! G! K! NY!; specimen at G! annotated by Bitter.]
- Polylepis racemosa* var. *subresinosa* O. Kuntze, 1898:77. [Type collection: Cuesta de Copina, Sierra de Achala, Córdoba, Argentina, *Hieronymus s.n.* Type not seen, presumably destroyed at Berlin, collection duplicate at G!]
- Polylepis racemosa* var. *pubinervia* O. Kuntze, 1898:77. [Type collection: Cerro Champaqui, Argentina. *Kurtz s.n.* Type not seen, presumably destroyed at Berlin.]
- Polylepis racemosa* var. *fuscotomentella* O. Kuntze, 1898:77. [Type collection: Oyada, Argentina, *Lorentz 442*. Type not seen, presumably destroyed at Berlin.]
- Polylepis australis* var. *glabra* (O. Kuntze) Bitter, 1911b:622.
- Polylepis australis* var. *glabrescens* (O. Kuntze *pro parte*) Bitter, 1911b:623.
- Polylepis australis* var. *subcalva* Bitter, 1911b:623. [Type collection: Ciénaga, Catamarca, Argentina, *Lorentz 310 pro parte*. Type presumably destroyed at Berlin, collection duplicate at NY!]

- Polylepis australis* var. *oblanceolata* Bitter, 1911b:623. [An illegitimate name since Bitter cites *P. racemosa* var. *pubescens* as a synonym.]
- Polylepis australis* var. *latifoliolata* Bitter, 1911b:624. [Type collection: north of the Cuesta de Copina, Córdoba, Argentina, *Hieronymus s.n.* Type not seen, presumably destroyed at Berlin.]
- Polylepis australis* var. *fuscitomentella* (O. Kuntze) Bitter, 1911b:625.
- Polylepis australis* var. *crenulata* Bitter, 1911b:625. [Type collection: Sierra Santa Barbara, Jujuy, Argentina, 2500 m, 11 Jul 1901, *Fries 264*. Holotype S!]
- Polylepis australis* var. *tucumanica* Bitter, 1913b:478. [Type collection: Canada del Muñoz, Tafi de Valle, Tucumán, Argentina, *Castillon 22523*. Lectotype destroyed at Berlin, Isotype G!]
- Polylepis australis* var. *tucumanica* subvar. *majuscula* Bitter, 1913:478. [Type collection: La Quenoa, Tucumán, Argentina, 2600 m, 11 Mar 1912, *Lillo 11257*. Type not seen, presumably destroyed at Berlin.]
- Polylepis australis* var. *tucumanica* subvar. *latifrons* Bitter, 1913:479. [Type collection: Canada del Muñoz, Tafi del Valle, Tucumán, Argentina, *Castillon s.n.* Type destroyed at Berlin, Isotype LIL!]
- Polylepis australia* var. *tucumanica* subvar. *gracilescens* Bitter, 1913:479. [Type collection: Angostura, Tafi del Valle, Tucumán, Argentina, *Castillon s.n.* Type presumably destroyed at Berlin, Isotype G!]
- Polylepis australis* var. *tucumanica* subvar. *breviuscula* Bitter, 1913:479. [Type collection: La Ciénaga, Tucumán, Argentina, 2500 m, 19 Dec 1908, *Lillo 8767*. Type not seen, presumably destroyed at Berlin, isotype G!]

Trees 1.5–10 m tall, Leaves very congested at the ends of branches with the area of overlapping stipule sheaths swollen (Figure 38a); leaves composed of (1) 2–3 pairs of leaflets, obtrullate in outline, 1.8–5.3 cm wide, 2.0–7.2 cm long; rachises glabrescent to densely glandular; point of leaflet attachment with a tuft of long white trichomes (Figure 38b); stipule sheaths glabrescent, glandular or pilose on the outer surface and with long straight trichomes projecting from the inside surface near the petiole. Leaflets broadly lanceolate, obovate, first or second pair from the terminal leaflet the largest, one of this pair 0.3–1.5 cm wide, 1.0–4.0 cm long; margins crenate, sometimes ciliate, apex obtuse, base unequally abrupt or attenuate; upper surface glabrescent with a few scattered, twisted trichomes, glabrous or densely glandular (Figure 38b); lower surface glabrous, glabrescent, glandular or with scattered, appressed straight trichomes (Figure 38b). Inflorescence pendant, 1.8–7.3 cm long, bearing 2–12 flowers, floral bracts lanceolate, scarious, sparsely glandular, 3–6 mm long, rachises with scattered

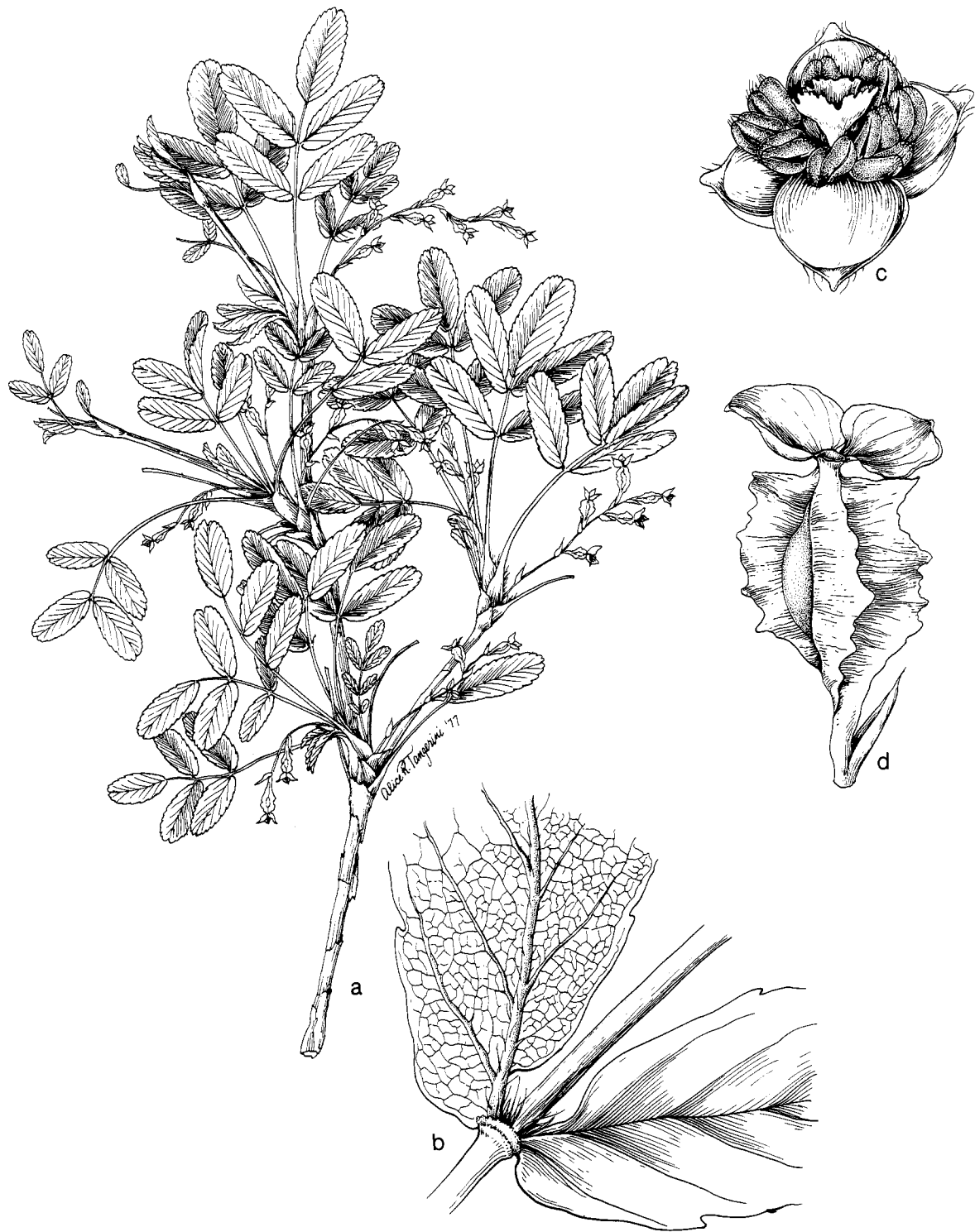


FIGURE 38.—*Polylepis australis*: a, branch ( $\times 0.5$ ); b, point of leaflet attachment, upper surface ( $\times 3$ ); c, flower ( $\times 6$ ); d, fruit ( $\times 6$ ).

glandular trichomes and resin. Flowers (Figure 38c) perfect, 0.7–1.0 cm in diameter, sepals 3 or 4, ovate, outer surface glandular or pilose, stamens 8–16, anthers with a tuft of straight trichomes at the apex; base of style glabrous or with a few straight trichomes. Fruit (Figure 38d) turbinate, winged, the wings irregular and pronounced, 0.2–0.6 cm wide including wings, 0.2–0.9 cm long.

**DISTRIBUTION.**—Northern Argentina in the Provinces of Jujuy, Salta, Catamarca, Tucumán, and Córdoba (Figure 39). Flowering recorded June, July, October to April.

**COMMON NAMES.**—Tabaquillo, queñoa, queñua, queñura.

**USES.**—The wood is used for the manufacture of farming implements.

**REPRESENTATIVE SPECIMENS EXAMINED.**—**ARGENTINA.** **SALTA:** Dept. Santa Victoria, Santa Victoria, 2385 m, 28 Jan 1942, Meyer 4604 (UC); ibid Rodeo Pampa, 3000 m, Jan 1943, Meyer 4876 (F, LIL, UC); between Guachipas and Pampa Grande, 9 Jan 1961, Meyer 21861 (LIL); Dept. La Candelaria, Cuesta occidental, Sierra del Castilloyo, 2000 m, 7 Nov 1931, Schreiter 6639 (LIL, S. UC). **JUJUY:** Laguna de Yala, 13 Jan 1970, Meyer, Legname & Koyama 126 (LIL). **CATAMARCA:**

Dept. Andalgalá, Los Queñoales, above the Mesaco de las Rosas, 15 Jan 1952, Sleumer 2245 (US); Andalgalá, 1800 m, 12 Mar 1915, Jørgensen 1455 (GH, MO, US). **TUCUMÁN:** Dept. Chicligasta, La Estancia los Pavos, 2000 m, 13 Dec 1925, Venturi 3990 (MO, S, US); ibid, 22 Nov 1926, Venturi 4591 (F, GH, UC, US); Saladillo, 1000 m, 18 May 1948, Meyer 14063 (MO, W); Dept. Trancas, Pie a la Cuesta, 21 Apr 1926, Venturi 4553 (A, S); Dept. Tafi, Cumbre de Anfama toward La Aguadita, 26 Oct 1934, Schreier 9814 (S, US); La Ciénaga to Tafi del Valle, 2000–2500 m, 15 Jun 1923, Schreiter 34590 (A, US); La Ciénaga, 2700 m, 6 Oct 1924, Schreiter 89339 (US); Tafi del Valle, 24 Sep 1949, Palacios, Barkley, Balegno 194r106 (MO, S); Cumbre Anfama, 2700 m, 20 Nov 1927, Venturi 5497, (A, MO, S); Quebrada Chada del Neunoy, 23 Mar 1944, Lourteig 553 (A, US); Quebrada de los Glisus, Jan 1912, Castillon 89344 (US); San Jose, Chaquevil, 2650 m, 4 Jan 1953, Petersen & Hjerting 876 (S); Dept. Burroayaco, Cerro del Campo, 2500 m, 30 Dec 1928, Venturi 9171 (BM, US); El Saldillo, 12 Sep 1916, Jørgensen 71 (GH, US); La Queñua, 3000 m, 27 Jan 1933, Parodi 10732 (GH); Laguna del Tesoro, 18 Oct 1969, Legame & Vaca 374V (LIL). **CÓRDOBA:** Dept. Calmuchita, Cerro Champaqui, 2600 m, 14 Mar 1952, Krapovichkas 7690 (LIL); ibid, without date, Kurtz 6842 (NY); Dept. San Alberto, Mina Clatro, 11 Nov 1952, Krapovichkas 7747 (LIL); Dept. Punilla, la barranca de the rio Yuspe, 1780 m, Dec 1949, Meyer & Sleumer 15627 (B); Sierra Grande (Achala), 13–15 Jan 1876, Hieronymus 317 (F, US); Pampa de Achala, 2200 m, 13 Dec 1945, Hunziker 1398 (MO.)

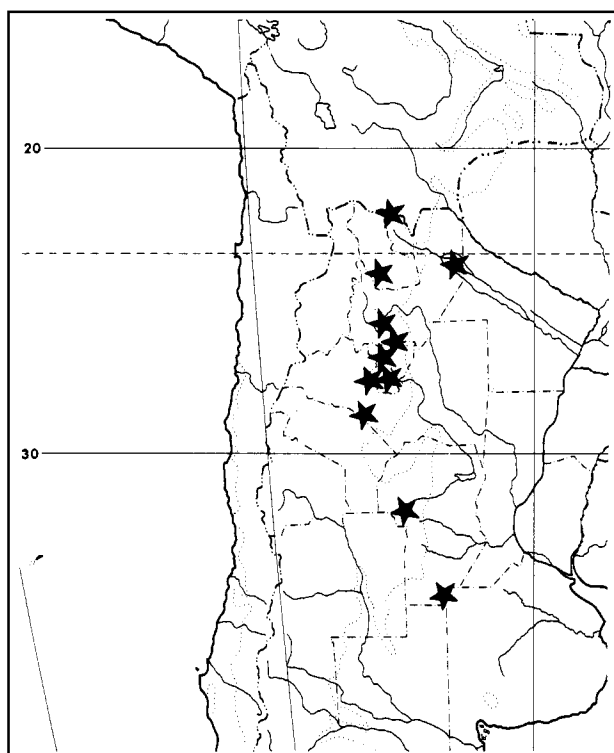


FIGURE 39.—Collection localities of *Polylepis australis*.

**DISCUSSION.**—Because of its isolated geographical position in northern Argentina, *Polylepis australis* is a convenient unit for circumscription. As indicated by numerous authors (Bitter, 1911b, Zardini, 1973), it may be only a geographically isolated form of either *P. racemosa* or *P. tomentella*. Otto Kuntze (1898) described as varieties of *P. racemosa* many populations that have been placed in *P. australis* by Bitter (1911b) and subsequent workers. In morphology, plants from populations included within *P. australis* are distinct enough to be easily recognized. In general, the fruits of this species are more winged than those of any other in the genus. In addition, the leaflets are usually glabrous or glabrescent; however, there is enormous variation within and between populations. Plants even within a population can have leaflets varying from small to large and glabrous to densely glandular. This variability has, unfortunately, been the cause of a taxonomic muddle in the treatment of the species.

When Bitter described *Polylepis australis* (1911b), he neglected to cite any specimens that could be associated directly with the specific epithet. Instead, after the description of the species, he gave a general distributional range and proceeded to circumscribe eight varieties. Bitter did not name a variety *P.*

*australis* var. *australis* nor did he indicate which of the varieties he would consider to contain the type of the species. In choosing a lectotype, I have chosen the only variety for which there is an extant holotype. The type of this variety thus becomes the type of the species. Further complications in the taxonomy of the species arise because Bitter used different specimens of the same collections as types of some of his varieties (e.g., *Lorentz 310*, *Hieronymus s.n.*). Since the actual specimens used by Bitter were destroyed at Berlin, and since he obviously considered the collections to be polytypic, it is impossible to refer duplicates of these collections to his various varieties. While the descriptions of the varieties might provide some clue as to his designation of particular specimens, there is so much variation that designating parts of the collections not

seen by Bitter would be potentially misleading. Also there is no apparent need to recognize subspecific taxa, and I have merely given the types as Bitter listed them and made no attempt to designate lectotypes from the isotypes.

A similar situation pertains in the case of *Polylepis australis* var. *tucumanica* and its subvarieties described by Bitter in 1913. The description of the variety has no specimens associated with it; however, there are extant isotypes of the collections that he cited for the various subvarieties. One of these is designated here as the lectotype of the variety *tucumanica*. Still, as in the case of the other varieties of the species described by Bitter, there appears to be no justification for the retention of this variety or its subvarieties.

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# Index

(Synonyms in italics)

- Acaena ochreatea*, 28  
*Polylepsis albicans*, 28  
  *annulatipilosa*, 27  
  australis, 56  
  australis var. *bijuga*, 23  
  australis var. *crenulata*, 56  
  australis var. *fuscitomentella*, 56  
  australis var. *glabra*, 56  
  australis var. *glabrescens*, 56  
  australis var. *latifoliolata*, 56  
  australis var. *oblanceolata*, 56  
  australis var. *subcalva*, 56  
  australis var. *tucumanica*, 56  
  australis var. *tucumanica* subvar. *breviuscula*, 56  
  australis var. *tucumanica* subvar. *gracilescens*, 56  
  australis var. *tucumanica* subvar. *latifrons*, 56  
  australis var. *tucumanica* subvar. *majuscula*, 56  
  besseri, 42  
  besseri var. *abbreviata*, 42  
  besseri var. *longipedicellata*, 42  
  boyacensis, 40  
  brachyphylla, 33  
  cocuyensis, 40  
  coriacea, 21  
  crista-galli, 42  
  crista-galli var. *longiracemosa*, 42  
  hieronymi, 23  
  hieronymi var. *dolicholopha*, 23  
  hieronymi var. *saltensis*, 23  
  hypargyrea, 28  
  hypoleuca, 23  
  incana, 50  
  incana ssp. *brachypoda*, 42  
  incana var. *connectens*, 53  
  incana var. *flavipila*, 31  
  incana ssp. *icosandra*, 53  
  incana ssp. *incarum*, 42  
  incana ssp. *micranthera*, 53  
  incana var. *primovestita*, 53  
  incana ssp. *subtusalbida*, 42  
  incana var. *villosistyla*, 40  
  lanuginosa, 21  
  lanuginosa  $\beta$  *microphylla*, 37  
  lehmannii, 21  
  microphylla, 37  
  microphylla var. *polyarthrotricha*, 37  
  multijuga, 19  
  nitida, 33  
  ochreatea, 28  
  ochreatea var. *integra*, 28  
  pallidistigma, 42  
  pauta, 27  
  pepei, 32  
  quadrijuga, 40  
  quindiensis, 28  
  racemosa, 53  
  racemosa var. *abbreviata*, 42  
  racemosa var. *albotomentella*, 23  
  racemosa var. *fuscotomentella*, 56  
  racemosa var. *glabra*, 56  
  racemosa var. *glabrescens*, 56  
  racemosa  $\beta$  *hypoleuca*, 23  
  racemosa var. *lanata*, 42  
  racemosa var. *pubescens*, 56  
  racemosa var. *pubinervia*, 56  
  racemosa var. *subresinosa*, 56  
  racemosa var. *tomentosa*, 42  
  reticulata, 33  
  rugulosa, 42  
  sericea, 28  
  serrata, 27  
  serrata var. *parcipila*, 27  
  serrata var. *psilantha*, 27  
  stuebelii, 28  
  subintegra, 28  
  subquinquefolia, 42  
  subsericans, 31  
  tarapacana, 46  
  tarapacana var. *brevifilamentosa*, 46  
  tarapacana var. *multisquama*, 46  
  tarapacana var. *pycnolopha*, 46  
  tarapacana var. *sajamensis*, 46  
  tenuiruga, 42  
  tomentella, 46  
  tomentella *dentatialata*, 46  
  tomentella ssp. *pentaphylla*, 46  
  tomentella var. *pilosior*, 46  
  tomentella ssp. *tetragona*, 46  
  triacontandra, 42  
  villosa, 53  
  weberbaueri, 37