

THE ASTERACEAE OF NORTHWESTERN PICO ZUNIL, A CLOUD FOREST IN WESTERN GUATEMALA

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Abstract: From 2003 to 2005, 46 genera and 96 species of native Asteraceae were collected on the northwestern slopes of Pico Zunil, a montane cloud forest habitat in southwestern Guatemala. Combining the present survey with past collections, a total of 56 genera and 126 species of Asteraceae have been reported from Pico Zunil, five of which are naturalized Old World species. In the present study, the Heliantheae contains the greatest number of native species (29). The most diverse genus is *Ageratina* (Eupatorieae, 9 species). Species richness of native Asteraceae measured along an elevational gradient ranged from a low of 16 species at 3400–3542 m to a high of 68 species at 2300–2699 m, where human land use most actively affects cloud forest habitat. Of the plants collected, *Ageratina rivularis* and *Verbesina sousae* were new species records for Guatemala. Six more species were new records for the Department of Quetzaltenango: *Ageratina pichinchensis*, *A. prunellaeifolia*, *A. saxorum*, *Koanophyllum coulteri*, *Stevia triflora*, and *Telanthophora cobanensis*. In addition, 16 of the 96 native species collected are known only from the western montane departments of Guatemala and the montane regions of southern Chiapas, Mexico. We provide a base of information against which future studies can measure temporal changes in presence of species such as may accompany environmental changes resulting from human activities and/or climate change.

Keywords: Asteraceae, cloud forest, Guatemala, species richness.

INTRODUCTION

Cloud forests, more accurately referred to as *tropical montane cloud forests* (Bruijnzeel and Veneklaas, 1998; Still et al., 1999; Lawton et al., 2001), are high-elevation ecosystems with high levels of biodiversity located in the sub-tropical middle latitudes, including portions of Central America, South America, Africa, and Southeast Asia (Hamilton et al., 1995). The general physiognomy of cloud forest vegetation is characterized more by its dense understory than by overstory characters or species composition, which vary considerably. In Mexico, tree ferns are perhaps the best plant indicator of cloud forest ecosystems (Leopold, 1950). In much of the tropics, cloud forests occur where mountains force trade winds to rise above the condensation level where orographic cloud formation occurs (Lawton et al., 2001). Thus, even during the dry season, cloud forests receive water in the

form of mist (low-intensity windblown precipitation) or cloud water (non-precipitating droplets deposited on vegetation; Pounds et al., 1999).

Guatemala has the highest plant diversity of all the Central American nations, with over 8000 species reported (Steyermark, 1950). Cloud forests in Guatemala are found both in the Sierra de las Minas in the east and on the slopes of the volcanic belt where they are most prevalent on slopes facing the Pacific Ocean (Steyermark, 1950; Fig. 1). The volcanic belt of Guatemala is characterized by two distinct seasons: a rainy season extending from May to November, followed by a dry season that ends in April. During the dry season, cloud forests are inundated daily with fog or mist.

The Asteraceae has been extensively collected in the highlands of western Guatemala. A floristic survey specifically of the Asteraceae has not been conducted on Pico

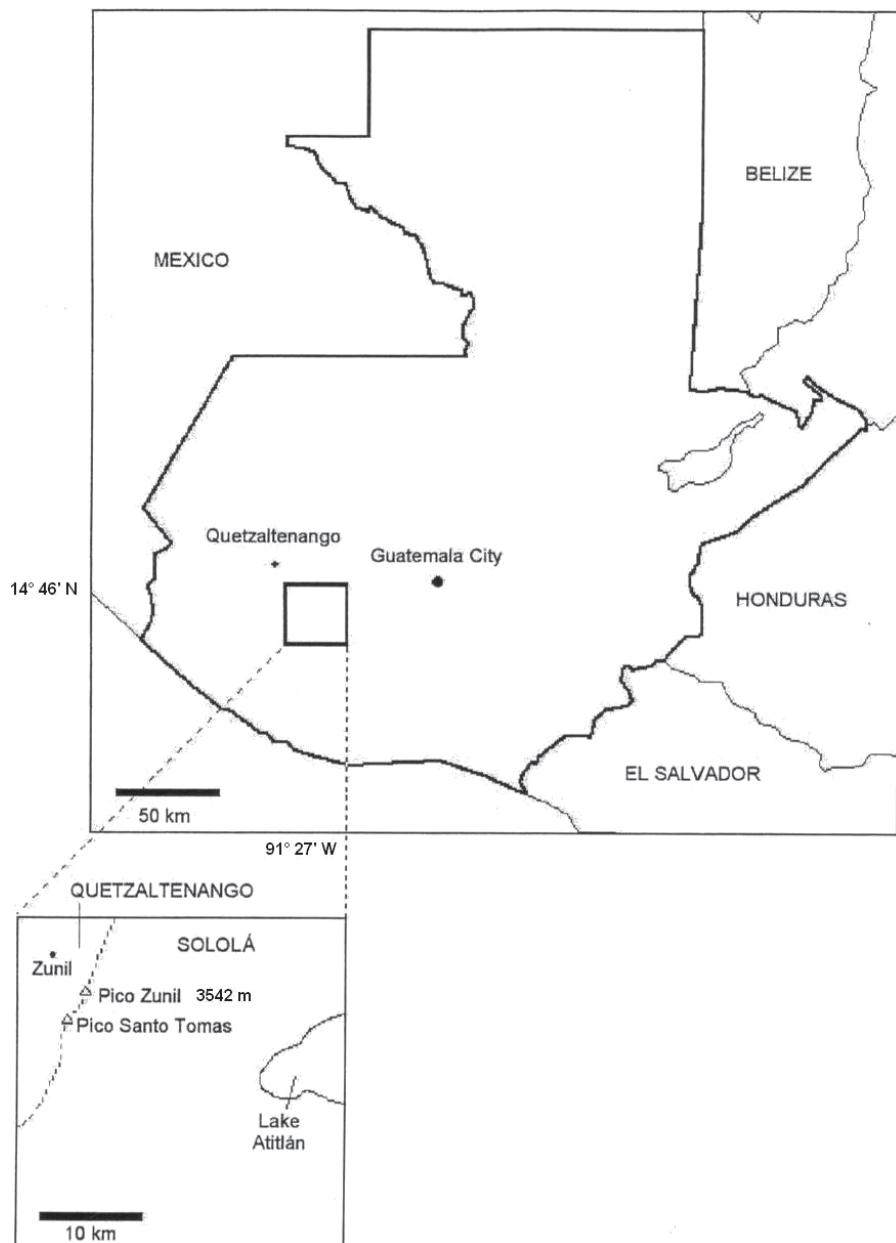


FIG. 1. Study site location in Guatemala. Pico Zunil is located on the border between the departments of Quetzaltenango and Sololá.

Zunil. This study was conducted primarily to fill this gap and to acquire preliminary data for a floristic survey of Pico Zunil that will eventually include all vascular plants and bryophytes. An understanding of the present diversity of this threatened cloud

forest ecosystem may illustrate the impacts of human land use practices and climate change and, therefore, may embolden conservation efforts at Pico Zunil and other cloud forest sites throughout Mexico and Central America.

GEOLOGICAL AND BOTANICAL HISTORY. The volcanoes in western Guatemala are of Pleistocene origin (Steyermark, 1950) and three remain active, continuing to erupt today. Pico Zunil has been mistakenly referred to as one of these volcanic mountains (Almeda, 1993; Anderson, 1908). It and the Zunil Ridge, which form the Sierra Chuatroj including Pico Santo Tomas, are related to volcanic activity only in that they are derived from sloping and horizontal Tertiary tuffs, lavas, and tuffaceous sediments from past volcanic activity (Williams, 1960; Gall, 1983). Fumaroles lie on fractures that cut an eroded fault scarp through the Sierra Chuatroj.

Plants in the highlands of western Guatemala have been studied since the late 1890s. In 1895 and 1896 the naturalist Edward William Nelson made plant collections in western Guatemala, including at Pico Zunil (Breedlove, 1981). In late 1905 and early 1906, the mycologist William Ashbrook Kellerman collected plants on volcanoes adjacent to the Sierra Chuatroj including Volcán Santa María, Cerro Quemado, and Volcán Atitlán. In 1934, the ornithologist Alexander Skutch visited Pico Zunil and recorded plants collected at that time (Nash and Williams, 1976; Skutch, 1979).

The *Flora of Guatemala* project commenced in the late 1930s under the direction of Paul Standley and Julian Steyermark of the Field Museum of Natural History in Chicago. Their work resulted in extensive collections on the montane regions of Guatemala and throughout the country from 1939 to 1941, including Asteraceae collections on Pico Zunil (Nash and Williams, 1976). These collections are housed at the Field Museum of Natural History in Chicago (F). Dennis Breedlove and Frank Almeda, of the California Academy of Sciences, visited Pico Zunil in 1986 and collected, and later described, a new tree species, *Stanmarkia spectabilis* Almeda (Melastomataceae; Almeda, 1993). Records do not show, however, that any collections of

Asteraceae were made by Breedlove and Almeda.

CLOUD FORESTS TODAY. Cloud forest and humid *Pinus-Quercus* forest were once abundant in the Guatemalan highlands. Currently, the majority of these ecosystems are restricted to steep or remote slopes at higher elevations, including the volcanoes, because agricultural land use has lead to extensive deforestation of accessible locations (Veblen, 1978; Howell and Webb, 1995). Now, even these tropical forest remnants, including tropical montane cloud forests of western Guatemala, are disappearing rapidly (Veblen, 1978; Hamilton et al., 1995). Deforestation was occurring throughout Guatemala prior to 1930; acceleration of extensive highland deforestation in Guatemala was first documented in the 1940s (Veblen, 1977). According to field notes at the Field Museum of Natural History in Chicago, Standley witnessed deforestation on the northwest slopes of Pico Zunil in January of 1941.

Climate change has been implicated as a cause for a decrease in habitat and diversity across the earth (McCarty, 2001). Research conducted at the Monteverde Cloud Forest Preserve in Costa Rica has established a link between deforestation, climate change, and either the movement of species from lower elevations to locations higher up the mountainsides, or, in some cases, the local extirpation of higher elevation cloud forest taxa (Pounds et al., 1999; Still et al., 1999; Lawton et al., 2001). Among other findings, research conducted at the Monteverde Cloud Forest determined that orographic cloud formation now occurs higher in the atmosphere than it once did, resulting in the fog passing over the mountain tops and thereby altering water availability to plants and animals at the highest elevations (Pounds et al., 1999; Still et al., 1999; Lawton et al., 2001).

ASTERACEAE. The Asteraceae (Compositae) is the largest plant family, with approximately 1,535 genera and at least 23,000 species worldwide (Bremer, 1994; Pruski and



FIG. 2. *Rojasianthe superba*. Tribe: Heliantheae. Known only from three departments in the western Guatemalan highlands and Chiapas, Mexico. Head 0.25 normal size.

Sancho, 2004). Recently, the Asteraceae has been divided into 17 tribes (Bremer, 1994); current phylogenetic evidence suggests that as many as 31 tribes may be recognized (Panero and Funk, 2002). Growth forms within the Asteraceae include annual, biennial, and perennial herbs, vines, shrubs, trees, lianas, and a small number of epiphytes. Pollen evidence indicates that the Asteraceae has a long evolutionary history in Central America with the family showing an explosion in diversity during the Miocene (Raven and Axelrod, 1974). In addition, topography (Kessler, 2002), geographic isolation, and optimal growth conditions led to the evolution of a particularly large number of Asteraceae in the montane regions of Guatemala and Mexico. In Mexico, the Asteraceae has been used as a target group for conservation based on the high number of endemic taxa found in that country, especially in the states of Chiapas and Oaxaca (Villaseñor et al., 1998).

In addition to being the most species-rich plant family in the montane regions of Latin America, the Asteraceae represents one of the most conspicuous floral elements (Nash and Williams, 1976; Villaseñor et al. 1998; Strother, 1999; Kessler, 2002). For example, in the Bolivian Andes, the Asteraceae, while found to be distributed at all elevations, has its highest values of species



FIG. 3. *Roldana gilgii*. Tribe: Senecioneae. Known only from the western Guatemalan highlands and Chiapas, Mexico. Plant 0.25 normal size.

richness and endemism between 2000–3000 m elevation (Kessler, 2002).

Eleven tribes of Asteraceae were collected by the *Flora of Guatemala* project, all of which have representatives in the montane regions, many of which are known only from relatively restricted distributions (Nash and Williams, 1976; see Figs. 2, 3). The volcanic belt in western Guatemala was found to be especially high in Asteraceae diversity with the greatest number of species occurring in Eupatorieae, Heliantheae, and Senecioneae (Nash and Williams, 1976; Véliz Pérez et al., 2001). The flora of Guatemala has a noticeable southern Mexican influence; most of the genera found in Guatemala are also found in Mexico (Steyermark, 1950).

METHODS

SITE DESCRIPTION. The study was conducted at Pico Zunil ($14^{\circ} 46' N$; $91^{\circ} 27' W$), a mountain with a peak elevation of 3,542 meters (Williams, 1960; Gall, 1983). The study site, Pico Zunil, was selected because the northwestern slopes support cloud forest habitat, are accessible, and have previously been reported to be rich in Asteraceae diversity (Nash and Williams, 1976). The peak is part of the Sierra Chuatroj range formed by the Zunil ridge that extends from south to north perpendicular to the Pacific coast between the departments of Quetzaltenango and Sololá (Fig. 1). The Sierra Chuatroj, located be-

tween Rio Samalá to the west and Rio Nahualá to the east, is part of a volcanic belt that extends 120 km from south of Guatemala City to the Mexican border. At 2800 m, the annual temperature of the highland regions of western Guatemala averages 11°C with 130–250 centimeters of annual precipitation (Véliz Pérez et al., 2001). Climate data specifically from 1700 m elevation on Volcán Acatenango, located 68 kilometers southeast of Pico Zunil, indicates an average annual temperature of 18°C (Véliz Pérez, 2000). During the dry season, there is a daily influx of fog from the Pacific Ocean that shrouds Pico Zunil in mist.

FIELD WORK AND SPECIMEN IDENTIFICATION. Collections were focused on the Asteraceae because the Asteraceae is a morphologically diverse group filling multiple ecological niches. In preparation for field collecting and comparative analysis, Asteraceae specimens at the Field Museum of Natural History in Chicago were surveyed, focusing on those collected for the *Flora of Guatemala* project (Nash and Williams, 1976). Specifically, specimens were surveyed that were collected at and above 1300 meters in the departments of Quetzaltenango and Sololá. These were species most likely to be found at Pico Zunil.

We collected Asteraceae on Pico Zunil in December 2003, January, May, and December, 2004, and January and May, 2005, dates when most of the Asteraceae were flowering. Collections were made along roadsides and trails and up to 100 m off trails on the northwestern slopes of Pico Zunil. Northwestern slopes were selected because they were more accessible than other slopes and because they supported a greater number of habitats. Collections were also made on the peak and to the southwest of the peak along the ridge between Pico Zunil and Pico Santo Tomás. At each collection site, habitat and site information were collected including dominant tree species, GPS coordinates, and elevation. Woody species and herbs other than Asteraceae were collected, identified at the University

of San Carlos, and deposited at the herbarium in Guatemala City (BIGU).

Sampling locations were separated into five elevational bands. The first elevational band (2000 to 2299 m) consisted of dense forest with rocky outcrops. It included the hot springs at Aguas Amargas, the road leading up to the hot springs, and trails at and above the hot springs. Based on specimens we collected and on personal observations in the field, the principal Asteraceae in this band were *Ageratum rugosum*, *Alloispermum integrifolium*, *Fleischmannia pycnocephalooides*, *Montanoa pteropoda*, *Piptothrix areolaris*, *Tagetes sororia*, and *Vernonia arborescens*. Principal trees of this elevational band included *Billia hippocastanum*, *Bocconia arborea*, *Leandra subseriata*, *Oreopanax xalapensis*, *Podachaenium eminens*, *Urera caracasana*, and *Wigandia urens*. Shrubs included *Justicia aurea* f. *erythrina*, *Monocheatum subtriplinervium*, and *Tibouchina longisepala* and common herbs were represented by *Heterocentron subtriplinervium*, *Nasa triphylla* subsp. *rudis*, and *Salvia purpurea*.

The second elevational band (2300 to 2699 m) consisted of dense forest with rocky outcrops and sulfur fumaroles. This band included the hot springs at Fuentes Georginas, the road leading up to the hot springs, and trails at and above the hot springs. It also included the dirt road above the community known as Aldea Chuimucubal. Significant habitat loss due to human land use is prevalent at this elevational band. From 2300 to 2699 m, common Asteraceae included *Alloispermum integrifolium*, *Bidens chrysanthemifolia*, *B. holwayi*, *Dahlia imperialis*, *Fleischmannia pycnocephalooides*, *Montanoa pteropoda*, *Piptothrix areolaris*, *Poda chaenium eminens*, *Rojasianthe superba*, *Roldana gilgii*, *Sigesbeckia jorullensis*, and *Verbesina apuleura*. In this elevational band, predominant tree species were *Alnus acuminata*, *Billia hippocastanum*, *Bocconia arborea*, *Carpinus caroliniana* var. *tropicalis*, *Chiranthodendron pentadactylon*, *Fuchsia arboreascens*, *Leandra subseriata*, *Miconia tacanen-*

sis, *Oreopanax xalapensis*, *Pinus ayacahuite*, *Rondeletia cordata*, *Saurauia oreophila*, *S. subalpina*, *Stanmarkia spectabilis*, and *Wigandia urens*. Predominant shrubs were *Coriaria thymifolia*, *Gaultheria erecta*, *Mono-chaetum deppeanum*, *Rondeletia strigosa*, and *Tibouchina longisepala* with herbs represented by *Lobelia laxiflora*, *Passiflora membranacea*, *Salvia holwayi*, and *S. purpurea*.

The third elevational band (2700 to 2999 m) consisted of dense forest with relatively few rocky outcrops. From 2700 to 2999 m, common Asteraceae included *Baccharis vaccinioides*, *Bidens holwayi*, *Fleischmannia pycnocephaloidea*, *Montanoa pteropoda*, *Rojasianthe superba*, *Roldana gilgii*, and *Verbesina apuleura*. Common trees were *Alnus acuminata*, *Chiranthodendron pentadactylon*, *Cupressus lusitanica*, *Fuchsia arborescens*, and *Saurauia subalpina*, and common shrubs were *Fuchsia cordifolia*, *Lycianthes quichensis*, and *Philadelphus myrtoides*. Common herbs were *Crusea coccinea*, *Eryngium cymosum*, and *Valeriana clematitis*.

The fourth elevational band (3000 and 3399 m) consisted of dense forest, open meadows, and rocky outcrops. From 3000 to 3399 m, common Asteraceae included *Archibaccharis corymbosa*, *Baccharis vaccinioides*, *Senecio rhyacophilus*, *S. warszewiczii*, *Stevia polycephala*, and *Verbesina hypoglauca*. Common trees were *Abies guatemalensis*, *Alnus acuminata*, *Arbutus xalapensis*, *Bocconia vulcanica*, *Cupressus lusitanica*, and *Oreopanax echinops*. Common shrubs were represented by *Ceanothus caeruleus*, *Lycianthes quichensis*, and *Rubus trilobus*. Common herbs were *Acaena elongata*, *Arracacia atropurpurea*, *A. donnell-smithii*, *Bomarea acutifolia*, *Castilleja integrifolia*, *Cunila polyantha*, *Lobelia aguana*, and *Lupinus montanus*.

The fifth elevational band (3400 to 3542 m) consisted of elfin forest and frost woodland (Beard, 1944) with rocky outcrops and sparsely distributed, stunted trees. From 3400 m to the peak at 3542 m, common Asteraceae included *Baccharis vaccinioides*, *Bidens triplinervia*, *Osbertia stolonifera*, *Oxylobus glanduliferus*, *Senecio warszewiczii*, and

Stevia polycephala. At this, the highest elevation, tree species were *Alnus firmifolia*, *Buddleja megalocephala*, and *Pinus hartwegii*. Shrubs included *Berberis vulgaris*, *Holodiscus argenteus*, *Pernettya ciliata*, and *Symporicarpos microphyllus*. Herbs were *Castilleja integrifolia*, *Penstemon gentianoides*, *Polystichum speciosissimum*, and *Stipa ichu*.

Collections were partially dried in the field and then transported to the herbarium at the University of San Carlos in Guatemala City where they were completely dried and fumigated to control insect and fungal growth. Specimens were tentatively identified in Guatemala and then sent to the University of Nebraska at Omaha and the Field Museum of Natural History in Chicago for further identification. In Chicago, Michael Dillon assisted with specimen identification.

The taxonomy of some of the genera collected is not resolved. For example, considerable molecular research is required to elucidate relationships within *Ageratina*, *Archibaccharis*, *Baccharis*, *Bartlettina*, *Gnaphalium*, *Hymenostephium*, *Roldana*, *Schistocarpha*, *Stevia*, *Telanthophora*, and *Vernonia* (Bremer, 1994). Also, the Eupatoreiae (King and Robinson, 1987) and the Senecioneae (Robinson and Brettell, 1975; Barkley, 1985; Barkley et al., 1996) require a complete monographic revision incorporating molecular analysis because the evolutionary relationships within these groups have been addressed only morphologically. Because of the expertise required to identify taxa of the Eupatoreiae, all specimens of the Eupatoreiae were sent to Harold Robinson of the Smithsonian Institution in Washington, D.C., for his determinations. Specimens of *Schistocarpha* were sent to Billie Turner of the University of Texas at Austin for verification.

A full set of specimens was deposited at the University of San Carlos of Guatemala Biology Herbarium (BIGU). Subsets of collections were deposited at the California Academy of Sciences (CAS), the Field Museum of Natural History in Chicago

(F), the Missouri Botanical Garden (MO), the New York Botanical Garden (NY), the Smithsonian Institution (US), The University of Texas at Austin (TEX), and the University of Nebraska at Omaha (OMA). Distribution of specimens is indicated in the annotated checklist.

ANALYSIS

Native species of Asteraceae on Pico Zunil were listed both by elevation and as a comparison to previous collections based on specimens observed at the Field Museum of Natural History. The majority of the vouchers examined were collected by Paul Standley and Julian Steyermark for the *Flora of Guatemala* project. By comparing our collection with past collections, we were able to infer changes in species richness of Asteraceae over time. Elevation data were not accurately represented in past collections, thus a comparison by elevation was not possible. Differences in collecting procedures between the present and past studies further complicated inferences about temporal changes in species richness.

RESULTS

COLLECTIONS: 1895–2005. From 2003 to 2005, 46 genera and 96 species of native Asteraceae were collected during four visits to Pico Zunil, resulting in two new species records for Guatemala and nine new records for the Department of Quetzaltenango (Table 1). Five of the Asteraceae collected were introduced species from the Old World that have become naturalized throughout North America: *Cotula australis*, *Hypochaeris glabra*, *Senecio vulgaris*, *Sonchus oleraceus*, and *Taraxacum officinale* (Table 2). Of the 96 native species of Asteraceae collected, 16, or 16.5% are known only from the Guatemalan highlands, Chiapas, Mexico, El Salvador, and northern Honduras (Table 1). These results compare to 44 genera and 75 species of native Asteraceae recorded from vouchers reported from Pico Zunil for the

Flora of Guatemala project (Nash and Williams, 1976; Table 2).

DISCUSSION

The Asteraceae identified in this study provide both data from a point in time for the flora of Pico Zunil and a more comprehensive baseline against which future comparisons can be made. Of the 126 species of Asteraceae collected from 2003 to 2005, 50 had not been collected previously from Pico Zunil, including 3 exotic, Old World species. Thirty other Asteraceae were collected previously but not in the present study. The most likely explanation for the greater number of species collected at Pico Zunil during 2003–2005 was the greater time spent collecting. During the five trips to the site, over 50 days were spent in the field compared to an estimated seven days spent by previous investigators during their visits to the site. Some newly reported taxa were collected in habitats disturbed by anthropogenic land use practices, which may not have been as prevalent in the past. The absence 30 species from the present study may be a consequence of sampling, which excluded epiphytic Asteraceae and lianas, such as *Pentacalia* (Senecioneae) and *Mikania* (Eupatorieae), which were present in the area but not included in the collections. Land use changes or changes in climate also may have played a role in the local extirpation of some species of Asteraceae.

Data from the present study will allow elevational and other more refined comparisons with future studies. For example, the number and distribution of native Asteraceae found in the present study at 2300–2699 m, the elevation at which most human disturbance occurs, will provide an important base against which to infer the impact of such continued anthropogenic activities. On a broader scale, comparisons between the present and future studies may show changes in the elevational distribution of either the number of Asteraceae taxa or the occurrence of particular taxa at particular elevations. Such comparisons could hint at

TABLE 1. Elevational distribution of native Asteraceae on the northwestern slope and peak of Pico Zunil, Guatemala, based only on collections made during 2003 to 2005. Old World naturalized species are not included.

Species	Elevation (meters)				
	2000–2299	2300–2699	2700–2999	3000–3399	3400–3542
SPECIES RICHNESS	29	68	27	35	16
TAXA					
<i>Ageratina helenae</i>	X	X			
<i>Ageratum corymbosum</i>	X	X			
<i>Alloispermum integrifolium</i>	X	X			
<i>Baccharis serraefolia</i>	X				
<i>Baccharis trinervis</i>	X				
<i>Bidens squarrosa</i>	X	X			
<i>Conyza Canadensis</i>	X				
<i>Coreopsis mutica</i> var. <i>microcephala</i>	X				
<i>Dahlia imperialis</i>	X	X		X	
<i>Erechtites valerianaefolius</i>	X	X			
<i>Erigeron karvinskianus</i>	X	X			
<i>Fleischmannia pycnocephaloidea</i>	X	X	X	X	
<i>Galinsoga cilata</i>	X	X			
<i>Gnaphalium brachyphyllum</i> ^I	X	X			X
<i>Hymenostephium cordatum</i>	X	X			
<i>Koanophyllum coulteri</i> ^{II}	X				
<i>Montanoa pteropoda</i> ^I	X	X		X	
<i>Peteravenia phoenicolepis</i>	X				
<i>Peteravenia schultzii</i>	X				
<i>Piptothrix areolaris</i>	X	X			
<i>Polymnia maculata</i> var. <i>maculata</i>	X				
<i>Rojasianthe superba</i> ^I	X	X		X	
<i>Salmea scandens</i>	X	X			
<i>Simsia amplexicaulis</i>	X				
<i>Stevia lucida</i> var. <i>oaxacana</i>	X				
<i>Tagetes sororia</i>	X	X			
<i>Tithonia longiradiata</i>	X				
<i>Verbesina turbacensis</i>	X				
<i>Vernonia arborescens</i>	X		X		
<i>Acmella repens</i>		X			
<i>Ageratina mairetiana</i>		X		X	
<i>Ageratina pazcuarensis</i>		X		X	
<i>Ageratina prunellifolia</i> ^{II}		X			
<i>Ageratina saxorum</i> ^I		X			
<i>Ageratina subinclusa</i>		X			X
<i>Alepidocline annua</i>		X			
<i>Archibaccharis asperifolia</i>		X			
<i>Archibaccharis blakeana</i>		X			
<i>Archibaccharis flexilis</i>		X			
<i>Archibaccharis schiedeana</i>		X			
<i>Baccharis salicifolia</i>		X			
<i>Bartlettina ornata</i> ^{I, II}		X			
<i>Bidens bicolor</i>		X		X	
<i>Bidens chrysanthemifolia</i>		X	X		X
<i>Bidens holwayi</i> ^I		X	X		X

TABLE 1. continued.

Species	Elevation (meters)				
	2000–2299	2300–2699	2700–2999	3000–3399	3400–3542
<i>Conyza apurensis</i>	X		X		
<i>Conyza bonariensis</i>	X				X
<i>Gamochaeta Americana</i>	X				
<i>Gnaphalium salicifolium</i>	X			X	
<i>Gnaphalium semiamplexicaule</i>	X		X		X
<i>Gnaphalium viscosum</i>	X				
<i>Hieracium irazuense</i>	X				X
<i>Jaegeria hirta</i>	X				
<i>Montanoa hexagona</i>	X				
<i>Podachaenium eminens</i>	X				
<i>Polymnia maculata</i> var. <i>adenotricha</i>	X				
<i>Roldana gilgii</i> ^I	X		X	X	
<i>Roldana heterogama</i>	X			X	X
<i>Roldana jurgensemii</i>	X			X	
<i>Roldana schaffneri</i>	X				
<i>Sabazia pinetorum</i> ^{I,II}	X				
<i>Schistocarpha platyphylla</i>	X			X	
<i>Senecio doratophyllus</i>	X		X		
<i>Sigesbeckia jorullensis</i>	X			X	
<i>Squamopappus skutchii</i>	X				
<i>Stevia polyccephala</i> var. <i>polyccephala</i>	X			X	X
<i>Stevia triflora</i> ^{II}	X		X		X
<i>Tagetes foetidissima</i>	X		X		
<i>Telanthophora cobanensis</i> ^{II}	X				
<i>Verbesina apaura</i> ^I	X		X	X	
<i>Verbesina holwayi</i> ^I	X		X		
<i>Ageratina rivalis</i> ^{II,III}			X	X	X
<i>Baccharis vaccinioides</i>			X	X	X
<i>Gnaphalium greenmanii</i>	X				
<i>Gnaphalium liebmansi</i> var. <i>monticola</i>	X		X		X
<i>Roldana acutangula</i> ^I	X		X		
<i>Roldana aschenborniana</i>	X		X		
<i>Senecio godmanii</i>			X	X	
<i>Senecio rhyacophilus</i> ^{I,II}			X	X	X
<i>Stevia incognita</i>			X		
<i>Stevia jorullensis</i>			X		
<i>Verbesina sousae</i> ^{II,III}			X		
<i>Ageratina caeciliae</i> ^I					X
<i>Ageratina pichinchensis</i>					X
<i>Ageratina zuniliana</i> ^I					X
<i>Archibaccharis corymbosa</i> ^I					X
<i>Cirsium subcoriaceum</i>				X	X
<i>Cosmos caudatus</i> ^{II}				X	
<i>Dahlia australis</i>				X	
<i>Oxylobus glanduliferus</i>				X	X
<i>Roldana barba-johannis</i>				X	
<i>Senecio warszewiczii</i> ^I				X	X
<i>Stevia microchaeta</i>				X	
<i>Tridax procumbens</i>				X	

TABLE 1. continued.

Species	Elevation (meters)				
	2000–2299	2300–2699	2700–2999	3000–3399	3400–3542
<i>Verbesina hypoglauca</i>				X	X
<i>Bidens triplinervia</i>				X	
<i>Senecio callosus</i>				X	

^I Species known only from the highlands of western Guatemala, southern Chiapas, Mexico, El Salvador, and northern Honduras.

^{II} New department records for Quetzaltenango.

^{III} New country records for Guatemala.

TABLE 2. Present and past collections of Asteraceae on Pico Zunil, Guatemala, including naturalized, Old World species.

Taxa	Collection Dates	
	Present Study (2003–2005)	Past Studies ^I
SPECIES RICHNESS	101	72
<i>Acmella filipes</i> var. <i>parvifolia</i>		X
<i>Acmella repens</i>	X	X
<i>Ageratina caeciliae</i>	X	
<i>Ageratina helenae</i>	X	X
<i>Ageratina mairetiana</i>	X	
<i>Ageratina pazcuarensis</i>	X	X
<i>Ageratina pichinchensis</i>	X	
<i>Ageratina prunellifolia</i>	X	
<i>Ageratina rivalis</i>	X	
<i>Ageratina saxorum</i>	X	
<i>Ageratina subinclusa</i>	X	
<i>Ageratina zuniliana</i>	X	X
<i>Ageratum corymbosum</i>	X	X
<i>Alepidocline annua</i>	X	X
<i>Alloispermum integrifolium</i>	X	X
<i>Archibaccharis asperifolia</i>	X	
<i>Archibaccharis blakeana</i>	X	X
<i>Archibaccharis corymbosa</i>	X	
<i>Archibaccharis flexilis</i>	X	
<i>Archibaccharis schiedeana</i>	X	
<i>Baccharis salicifolia</i>	X	
<i>Baccharis serraefolia</i>	X	X
<i>Baccharis trinervis</i>	X	
<i>Baccharis vaccinioides</i>	X	X
<i>Barkleyanthus salicifolius</i>		X
<i>Bartlettina luxii</i>		X
<i>Bartlettina ornata</i>	X	
<i>Bartlettina pinabatensis</i>		X
<i>Bidens bicolor</i>	X	
<i>Bidens chrysanthemifolia</i>	X	X
<i>Bidens holwayi</i>	X	X
<i>Bidens odorata</i>		X
<i>Bidens ostruthioides</i>		X

TABLE 2. continued.

Taxa	Collection Dates	
	Present Study (2003–2005)	Past Studies ^I
<i>Bidens squarrosa</i>	X	
<i>Bidens triplinervia</i>	X	X
<i>Cirsium radicans</i>		X
<i>Cirsium subcordiaceum</i>	X	X
<i>Conyza apurensis</i>	X	
<i>Conyza bonariensis</i>	X	
<i>Conyza canadensis</i>	X	X
<i>Conyza coronopifolia</i>		X
<i>Conyza sophiifolia</i>		X
<i>Coreopsis mutica</i> var. <i>microcephala</i>	X	X
<i>Cosmos caudatus</i>	X	
<i>Cotula australis</i> ^{II}	X	
<i>Critoniadelphus nubigenus</i>		X
<i>Dahlia australis</i>	X	
<i>Dahlia imperialis</i>	X	X
<i>Erechtites valerianaefolius</i>	X	
<i>Erigeron karvinskianus</i>	X	X
<i>Fleischmannia pycnocephaloidea</i>	X	X
<i>Galinsoga ciliata</i>	X	
<i>Gamochaeta Americana</i>	X	
<i>Gamochaeta pensylvanica</i>		X
<i>Gamochaeta purpurea</i>		X
<i>Gnaphalium brachyphyllum</i>	X	X
<i>Gnaphalium brachypterum</i>		X
<i>Gnaphalium greenmanii</i>	X	
<i>Gnaphalium liebmansi</i> var. <i>monticola</i>	X	
<i>Gnaphalium salicifolium</i>	X	
<i>Gnaphalium semiamplexicaule</i>	X	X
<i>Gnaphalium viscosum</i>	X	
<i>Hieracium guatemalense</i>		X
<i>Hieracium irazuense</i>	X	
<i>Hymenostephium cordatum</i>	X	X
<i>Hypochaeris glabra</i> ^{II}	X	
<i>Jaegeria hirta</i>	X	X
<i>Koanophyllum coulteri</i>	X	
<i>Montanoa hexagona</i>	X	
<i>Montanoa pteropoda</i>	X	X
<i>Neomirandea araliifolia</i>		X
<i>Osbertia stolonifera</i>	X	
<i>Oteiza ruacophila</i>		X
<i>Oxylobus glanduliferus</i>	X	
<i>Peteravenia phoenicolepis</i>	X	X
<i>Peteravenia schultzii</i>	X	X
<i>Piptothrix areolaris</i>	X	X
<i>Podachaenium eminens</i>	X	X
<i>Polymnia maculata</i> var. <i>adentricha</i>	X	
<i>Polymnia maculata</i> var. <i>maculata</i>	X	X
<i>Rojasianthe superba</i>	X	X
<i>Roldana acutangula</i>	X	X

TABLE 2. continued.

Taxa	Collection Dates	
	Present Study (2003–2005)	Past Studies ^I
<i>Roldana aschenborniana</i>	X	
<i>Roldana barba-johannis</i>	X	X
<i>Roldana gilgii</i>	X	X
<i>Roldana heterogama</i>	X	X
<i>Roldana jurgensenii</i>	X	X
<i>Roldana petasites</i>		X
<i>Roldana schaffneri</i>	X	
<i>Sabazia pinetorum</i>	X	
<i>Salmea scandens</i>	X	X
<i>Schistocarpha platyphylla</i>	X	X
<i>Senecio callosus</i>	X	X
<i>Senecio doratophyllum</i>	X	X
<i>Senecio godmani</i>	X	X
<i>Senecio rhyacophilus</i>	X	
<i>Senecio vulgaris</i> ^{II}	X	
<i>Senecio warszewiczii</i>	X	X
<i>Sigesbeckia jorullensis</i>	X	X
<i>Simsia amplexicaulis</i>	X	X
<i>Sinclairia discolor</i>		X
<i>Sinclairia sublobata</i>		X
<i>Sonchus oleraceus</i> ^{II}	X	X
<i>Squamopappus skutchii</i>	X	X
<i>Stevia incognita</i>	X	
<i>Stevia jorullensis</i>	X	
<i>Stevia lucida</i> var. <i>oaxacana</i>	X	X
<i>Stevia microchaeta</i>	X	
<i>Stevia ovata</i> var. <i>ovata</i>		X
<i>Stevia polyccephala</i> var. <i>polyccephala</i>	X	X
<i>Stevia triflora</i>	X	
<i>Tagetes foetidissima</i>	X	
<i>Tagetes sororia</i>	X	X
<i>Tagetes tenuifolia</i>		X
<i>Taraxacum officinale</i> ^{II}	X	X
<i>Telanthophora cobanensis</i>	X	
<i>Tithonia longiradiata</i>	X	X
<i>Tridax procumbens</i>	X	
<i>Trixis inula</i>		X
<i>Verbesina apaura</i>	X	
<i>Verbesina holwayi</i>	X	
<i>Verbesina hypoglauca</i>	X	X
<i>Verbesina sousae</i>	X	
<i>Verbesina tubracensis</i>	X	X
<i>Vernonia arborescens</i>	X	X
<i>Vernonia leiocarpa</i>		X
<i>Vernonia salvinae</i>		X

^I Past studies = Specimens collected prior to 1960 and examined by Nash and Williams for the Flora of Guatemala project at the Field Museum of Natural History herbarium (F).

^{II} Naturalized, Old World species.

plant responses to widespread changes in global conditions, such as might occur with global warming.

To incorporate best present and future studies for the purpose of assessing temporal changes in Asteraceae, future studies must involve ongoing, joint efforts by conservation-focused organizations and federal or local government agencies. Such cooperation will also facilitate development of a more thorough biodiversity inventory of the volcanic belt and associated cloud forest ecosystems, as well as encourage the Guatemalan government to work more closely with conservation groups to protect regions whose native plant communities are threatened.

ANNOTATED CHECKLIST

To date, of 56 genera and 126 species of Asteraceae have been recorded from Pico Zunil (Table 2). These species are treated in the following annotated checklist, which includes specimens from both the recent field collections of Asteraceae made for this study and specimens of Asteraceae examined at the Field Museum in Chicago.

The Annotated Checklist briefly describes the specimens of Asteraceae collected on Pico Zunil, is ordered alphabetically by tribe and by genus within each tribe. The w³TROPICOS website (Solomon, 1996) and the *Flora of Guatemala (Asteraceae)* (Nash and Williams, 1976) were used to provide the most current species nomenclature. Names of the Eupatorieae are those used by H. Robinson (King & Robinson, 1987).

Collection numbers are Quedensley's unless otherwise indicated. The location of the specimens as of August, 2006, is given. Designations for herbaria follow Index Herbariorum (Holmgren et al., 1990); the Field Museum of Natural History in Chicago (F), the Missouri Botanical Garden (MO), the New York Botanical Garden (NY), the Smithsonian Institution (US), the University of Nebraska at Omaha (OMA), the University of San Carlos of Guatemala Biology Herbarium (BIGU), and the University of Texas at Austin (TEX). The elevation indicated is based either on the elevation where specimens were collected for this study or, for specimens examined at the Field Museum of Natural History, extrapolated from specimens with sufficiently accurate label information.

Taxa known only from the highland departments of western Guatemala and the southern highlands of Chiapas, Mexico, are so noted. The departments of Guatemala are listed in alphabetical order, the countries of Central America are listed from north to

south, and the countries of South America are listed in alphabetical order. Old World distributions are not included. Locations of type specimens and citations of authorities can be found at the w³TROPICOS website (Solomon, 1996).

Anthemideae

The Anthemideae contains 109 genera and approximately 1740 species (Bremer, 1994). It is distributed mostly throughout temperate and arctic regions. Only one naturalized species from the Anthemideae is reported from Pico Zunil.

Cotula australis (Sieber ex Spreng.) Hook. f.; 2300–2699 m; 761 (BIGU, F), 1698 (BIGU, TEX); Old World species reported from United States, Mexico, Argentina, Bolivia, Colombia, Ecuador, Peru; exotic.

Astereae

The Astereae is the second most species-rich tribe worldwide with approximately 170 genera and 3000 species (Bremer, 1994). It is most abundant in northern temperate regions and *Baccharis* and *Archibaccharis* form a major part of the floral element in the Guatemalan highlands. *Baccharis vaccinioides* is perhaps the most ubiquitous shrub or small tree on the high mountains in Guatemala and was collected more than any other species of Asteraceae during this study. *Baccharis* and *Conyzia* contain weedy species that may be indicators of anthropogenic disturbance.

Archibaccharis asperifolia (Benth.) S. F. Blake; 2300–2699 m; 1681 (BIGU, F); Alta Verapaz, Baja Verapaz, Chimaltenango, Guatemala, Huehuetenango, Progreso, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Sololá, Suchitepéquez, Totonicapán, Zacapa, and Central Mexico, Honduras, northern Nicaragua.

Archibaccharis blakeana Standl. & Steyermark; 2300–2699 m; 512 (BIGU, F); L. O. Williams et al. 22998 (F); Chimaltenango, Guatemala, Quetzaltenango, Sacatepéquez, and Chiapas, Mexico.

Archibaccharis corymbosa (Donn. Sm.) S. F. Blake; 3000–3399 m; 2510 (BIGU, F), 2590 (BIGU, OMA); Known only from Chimaltenango, Huehuetenango, Quetzaltenango, Sacatepéquez, San Marcos, Totonicapán and Chiapas, Mexico.

Archibaccharis flexilis S. F. Blake; 2300–2699 m; 1855 (BIGU, F); Alta Verapaz, Chimaltenango, Quetzaltenango, Sacatepéquez, San Marcos, Sololá, Suchitepéquez, Totonicapán, and Mexico, El Salvador, Honduras, Nicaragua, Costa Rica.

Archibaccharis schiedeana (Benth.) J. D. Jackson; 2300–2699 m; 1715 (BIGU, F, TEX), 1692 (BIGU, TEX); Alta Verapaz, Baja Verapaz, Chimaltenango, Chiquimula, Guatemala, Huehuetenango, Jalapa, Jutiapa, Quetzaltenango, Quiché, Sacatepéquez, Santa Rosa, and southern Mexico, El Salvador, Honduras, Nicaragua, Costa Rica, Panama.

Baccharis salicifolia (Ruiz & Pav.) Pers.; 2300–2699 m; 1838 (BIGU, F); Alta Verapaz, Baja Verapaz, Chimaltenango, Chiquimula, Escuintla, Guatemala, Huehuetenango, Izabal, Jalapa, Jutiapa, Progreso,

Quetzaltenango, Sacatepéquez, San Marcos, Santa Rosa, Sololá, Zacapa, and southwestern United States, Mexico, Belize, El Salvador, Honduras, Nicaragua, South America.

Baccharis serratifolia DC.; 2000–2299 m; 1773 (BIGU, F), L. O. Williams 14308 (F); Alta Verapaz, Baja Verapaz, Chimaltenango, Escuintla, Guatemala, Huehuetenango, Jalapa, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Sololá, Totonicapán, and southern Mexico, El Salvador, Honduras, Nicaragua.

Baccharis trinervis (Lam.) Pers.; 2000–2299 m; 1883 (BIGU, F); Alta Verapaz, Baja Verapaz, Chimaltenango, Escuintla, Guatemala, Huehuetenango, Izabal, Jalapa, Jutiapa, Petén, Quetzaltenango, Quiché, Sacatepéquez, Santa Rosa, Sololá, Suchitepéquez, Zacapa, and central Mexico, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, tropical South America.

Baccharis vaccinioides Kunth; 2000–2299 m, 2700–2999 m, 3000–3399 m, 3400–3542 m; 646 (BIGU, F), 2614 (BIGU, OMA), 581, 775, 1834, 2580 (BIGU, TEX), Standley 83242 (F); Chimaltenango, Guatemala, Huehuetenango, Jalapa, Progreso, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Sololá, Totonicapán, Zacapa, and Chiapas, Mexico, El Salvador, Honduras.

Conyza apurensis Kunth; 2300–2699 m, 2700–2999 m; 770 (BIGU, OMA, TEX), 776 (BIGU, F, MO), 1790 (BIGU, TEX); Alta Verapaz, Guatemala, Izabal, Jalapa, Jutiapa, Petén, Progreso, Quetzaltenango, Quiché, Retalhuleu, Sacatepéquez, Santa Rosa, Totonicapán, Zacapa, and Mexico, Belize, El Salvador, Honduras, Nicaragua, Panama, Ecuador, Peru, Venezuela, West Indies.

Conyza bonariensis (L.) Cronquist; 2300–2699 m, 3400–3542 m; 677 (BIGU, OMA), 707 (BIGU, F), 764, 2537 (BIGU, TEX); southern United States, Mexico, Central America, South America.

Conyza canadensis (L.) Cronquist; 2000–2299 m; 1747 (BIGU, F), Standley 83245 (F), Steyermark 34995 (F); Alta Verapaz, Baja Verapaz, Chimaltenango, Guatemala, Huehuetenango, Izabal, Jalapa, Petén, Quetzaltenango, Sacatepéquez, San Marcos, Santa Rosa, Sololá, and United States, Mexico, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, South America, Caribbean.

Conyza coronopifolia Kunth; 2000–2299 m; Standley 83187 (F); Alta Verapaz, Chimaltenango, Guatemala, Huehuetenango, Quetzaltenango, Quiché, San Marcos, Sololá, and central and southern Mexico, El Salvador, Honduras, Costa Rica, Argentina, Ecuador.

Conyza sophiifolia Kunth; 2000–2299 m, 2300–2699 m; Standley 67309, 83217, 83923 (F), Steyermark 34470 (F); Chimaltenango, Chiquimula, Guatemala, Huehuetenango, Jalapa, Progreso, Quetzaltenango, Sacatepéquez, San Marcos, Sololá, Totonicapán, and southwestern United States, Mexico, El Salvador, Honduras, Argentina, Bolivia, Colombia, Ecuador.

Erigeron karvinskianus DC.; 2000–2299 m, 2300–2699 m; 543 (BIGU, CAS, F, NY), 621 (BIGU, TEX), 1690 (BIGU, MO, TEX), 1768 (BIGU, OMA), Standley 83169, 83925, 85767 (F), Steyermark 34486 (F); Chimaltenango, Chiquimula, Guatemala, Huehuetenango, Jalapa, Quetzaltenango, Quiché, Retalhuleu, Sacatepéquez, San Marcos, Santa Rosa, Sololá, Suchitepéquez, Totonicapán, and Mexico, El Salvador, Honduras, Nicaragua, South America, Caribbean.

Obertia stolonifera (DC.) Greene; 3400–3542 m; 711 (F, BIGU); Chimaltenango, Huehuetenango, Quetzaltenango, San Marcos, Sacatepéquez, Sololá, Totonicapán, and central and southern Mexico.

Cardueae

Formerly the Cynareae, this tribe contains the thistles. Worldwide, the Cardueae includes 83 genera and 2500 species (Bremer, 1994). Only *Cirsium* is present in Guatemala.

Cirsium radians Benth.; 2300–2699 m; Standley 85947, 85764 (F); known only from Alta Verapaz, Chimaltenango, Huehuetenango, Quetzaltenango, San Marcos, Totonicapán.

Cirsium subcoriaceum (Less.) Sch. Bip.; 2300–2699 m, 3000–3399 m, 3400–3542 m; 582 (BIGU, F), 2568 (BIGU, TEX), Standley 83316, 85737 (F); Alta Verapaz, Chimaltenango, Guatemala, Huehuetenango, Jalapa, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Santa Rosa, Sololá, Totonicapán, Zacapa, and Mexico, El Salvador, Honduras, Nicaragua, Costa Rica, Panama.

Eupatorieae

The Eupatorieae has 170 genera and approximately 2400 species worldwide (Bremer, 1994). It accounts for 10% of the species in the Asteraceae and one of every 150 flowering plants, including a major portion of the Asteraceae in the Neotropics (King and Robinson, 1987). In Latin America, the Eupatorieae is represented by annual and perennial herbs, vines, shrubs, and small trees. In Guatemala, members of the Eupatorieae occur in various habitats. Most are found at elevations above 1800 m, where a definite wet-dry climate regimen occurs. One hundred forty-one species of Eupatorieae were reported from Guatemala by Nash and Williams (1976). Harold Robinson of the Smithsonian Institution determined our collections of the Eupatorieae.

Eupatorium sensu lato, with over 600 species worldwide, is concentrated in the Neotropics (Nash and Williams, 1976). *Eupatorium* has been segregated into smaller genera by King and Robinson (1987). The most common genus of Eupatorieae in Guatemala, *Ageratina*, is the largest and most diverse genus in the Oxylobinae (King and Robinson, 1987). The Eupatorieae is still poorly understood in Latin America and requires a thorough systematic revision.

Ageratina caeciliae (B. L. Rob.) King & H. Rob.; 2700–2999 m; 2612A (BIGU, MO, TEX, US); known only from in montane cloud forests of Chimaltenango,

Quetzaltenango, Sololá, Totonicapán, and Chiapas, Mexico.

Ageratina helenae King & H. Rob.; 2000–2299 m, 2300–2699 m; 501 (BIGU, MO, TEX, US), 1797 (US), Standley 65492, 67376, 83306, 85956 (F); Chimaltenango, Guatemala, Quetzaltenango, San Marcos, Santa Rosa, Suchitepéquez, and El Salvador, Honduras, Nicaragua, Costa Rica.

Ageratina mairetiana (DC.) King & H. Rob.; 2300–2699 m, 2700–2999 m; 1832, 2641 (BIGU, US), 1991 (BIGU, TEX, US); Alta Verapaz, Baja Verapaz, Chimaltenango, Guatemala, Huehuetenango, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Santa Rosa, Sololá, Totonicapán, central and southern Mexico, El Salvador.

Ageratina pazcuarensis (Kunth) King & H. Rob.; 2300–2699 m, 2700–2999 m; 502 (BIGU, MO, TEX, US), 1826 (BIGU, MO, US), Standley 67398, 84808, 85739 (F); Alta Verapaz, Baja Verapaz, Chimaltenango, Huehuetenango, Jalapa, Quetzaltenango, San Marcos, Sololá, Totonicapán, and central and southern Mexico, Honduras.

Ageratina pichinchensis (Kunth) King & H. Rob.; 3000–3399 m; 2601 (BIGU, TEX, US); Alta Verapaz, Baja Verapaz, Chimaltenango, Guatemala, Huehuetenango, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Santa Rosa, Suchitepéquez, Totonicapán, and central and southern Mexico, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru.

Ageratina prunellifolia (Kunth) King & H. Rob.; 2300–2699 m; 1706 (BIGU, TEX, US), 1701 (BIGU, US); Huehuetenango, Jutiapa, Quetzaltenango, Sacatepéquez, central and southern Mexico, Ecuador. New record for Quetzaltenango.

Ageratina rivalis (Greenm.) King & H. Rob.; 2700–2999 m, 3000–3399 m, 3400–3542 m; 724, 1724 (BIGU, US), 2618 (BIGU, TEX, US); Quetzaltenango, and central and southern Mexico. New record for Guatemala.

Ageratina saxorum (Standl. & Steyer.) King & H. Rob.; 2300–2699 m; 1716 (BIGU, US); known only from the highlands of Huehuetenango, Quetzaltenango, San Marcos. Southern Chiapas, Mexico. New record for Quetzaltenango.

Ageratina subinclusa (Klatt) King & H. Rob.; 2300–2699 m, 3000–3399 m; 737 (BIGU, MO, US), 2515 (BIGU, TEX, US), 533, 1845 (BIGU, US); Chimaltenango, Huehuetenango, Quetzaltenango, Totonicapán, and central and southern Mexico. New record for Quetzaltenango.

Ageratina zuniliana (Standl. & Steyer.) King and H. Rob.; 3000–3399 m; 560 (BIGU, TEX, US), 2514A, 2637 (BIGU, US), Steyermark 34744, 34905 (F); known only from Pico Zunil and Pico Santo Tomas, Quetzaltenango.

Ageratum corymbosum Zuccagni ex Pers.; 2000–2299 m, 2300–2699 m; 542, 1702 (BIGU, CAS, NY, OMA, US), 1702 (BIGU, TEX, US), 1775 (BIGU, US),

L. O. Williams et al. 23011 (F); Alta Verapaz, Baja Verapaz, Chimaltenango, Chiquimula, Escuintla, Guatemala, Huehuetenango, Izabal, Jalapa, Jutiapa, Petén, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Santa Rosa, Suchitepéquez, Zacapa, and Mexico, El Salvador, Honduras, Nicaragua, Costa Rica.

Bartlettina luxii (B. L. Rob.) King & H. Rob.; Standley 67454 (F); Alta Verapaz, Baja Verapaz, Chimaltenango, Jalapa, Progreso, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Sololá; and southern Mexico, El Salvador.

Bartlettina ornata King & H. Rob.; 2300–2699 m; 519 (BIGU, TEX, US), 2533 (BIGU, US); known only from Chimaltenango, Quetzaltenango, and Honduras. New record for Quetzaltenango.

Bartlettina pinabensis (B. L. Rob.) King & H. Rob.; Standley 67391, 85869 (F); known only from Quetzaltenango, San Marcos, and Chiapas, Mexico.

Critoniadelphus nubigenus (Benth.) King & H. Rob.; Steyermark 34690 (F); Alta Verapaz, Chimaltenango, Chiquimula, Guatemala, Jalapa, Quetzaltenango, Quiché, San Marcos, Suchitepéquez, Zacapa, and southern Mexico, El Salvador, Honduras.

Fleischmannia pycnocephaloidea (B. L. Rob.) King & H. Rob.; 2000–2299 m, 2300–2699 m, 2700–2999 m, 3000–3399 m; 1829 (BIGU, CAS, US), 520, 1816, 2602 (BIGU, MO, US), 2551 (BIGU, NY, TEX, US), 1766, 1854, 1990, 2630 (BIGU, US), Standley 67384, 83948 (F); Chimaltenango, Guatemala, Huehuetenango, Sacatepéquez, Sololá, Totonicapán, and Chiapas, Mexico, Honduras.

Koanophyllum coulteri (B. L. Rob.) King & H. Rob.; 2000–2299 m; 1875 (BIGU, US); Alta Verapaz, Baja Verapaz, Guatemala, Izabal, Progreso, Quetzaltenango, Sololá, Suchitepéquez, Zacapa, and Chiapas, Mexico, El Salvador, Honduras. New record for Quetzaltenango.

Neomirandeaa araliifolia (Less.) King & H. Rob.; Standley 85972 (F). Alta Verapaz, Chimaltenango, Izabal, Petén, Progreso, Quetzaltenango, San Marcos, Suchitepéquez, and southern Mexico, Belize, Honduras, Nicaragua, Costa Rica, Panama.

Oxylobus glanduliferus (Sch. Bip.) Gray; 3000–3399 m, 3400–3542 m; 588 (BIGU, F), 2607 (BIGU, OMA), 716 (BIGU, TEX); Huehuetenango, Quetzaltenango, San Marcos, Totonicapán, and southern Mexico, Venezuela.

Peteravenia phoenicolepis (B. L. Rob.) King & H. Rob.; 2000–2299 m; 1778 (BIGU, US), Standley 65410, 85872 (F), L. O. Williams, Molina, and Williams 23012 (F); Chimaltenango, Huehuetenango, Progreso, Quetzaltenango, Quiché, Sacatepéquez, Sololá, Zacapa, and southern Mexico, Honduras.

Peteravenia schultzii (Schnittsp.) King & H. Rob.; 2000–2299 m; 2592 (BIGU, US), Standley 65385, 83325 (F); Alta Verapaz, Baja Verapaz, Chimaltenango, Escuintla, Guatemala, Huehueten-

nango, Retalhuleu, Sacatepéquez, Sololá, and central and southern Mexico, El Salvador, Honduras, Costa Rica.

Piptothrix areolaris (DC.) King & H. Rob.; 2000–2299 m, 2300–2699 m; 1684 (BIGU, TEX, US), 548, 1765 (BIGU, US); Alta Verapaz, Baja Verapaz, Chimaltenango, Guatemala, Huehuetenango, Jalapa, Quetzaltenango, Quiché, Sacatepéquez, Sololá, Zacapa, and southern Mexico.

Stevia incognita Grashoff; 2700–2999 m; 1722 (BIGU, US); Chimaltenango, Guatemala, Huehuetenango, Jalapa, Progreso, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Totonicapán, and Mexico, Honduras, Colombia, Venezuela.

Stevia jorullensis Kunth; 2700–2999 m; 536 (BIGU, US); Guatemala, Huehuetenango, Quetzaltenango, Sololá, Totonicapán, and Mexico.

Stevia lucida Lag. var. *oaxacana* (DC.) Grashoff; 2000–2299 m, 2300–2699 m; 1750 (BIGU, US), Standley 85780 (F); Chimaltenango, Huehuetenango, Quetzaltenango, Quiché, and southern Mexico, Costa Rica, Panama, Colombia, Venezuela.

Stevia microchaeta Sch. Bip.; 3000–3399 m; 2603, 2608 (BIGU, US), 2641 (US); Quetzaltenango, San Marcos, and southern Mexico.

Stevia ovata Willd. var. *ovata*; 2000–2299 m; Standley 83882 (F); Alta Verapaz, Baja Verapaz, Chimaltenango, Guatemala, Huehuetenango, Jutiapa, Quetzaltenango, Sacatepéquez, San Marcos, Sololá, Zacapa, and central and southern Mexico, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, Venezuela.

Stevia polyccephala Bertol. var. *polyccephala*; 2300–2699 m, 3000–3399 m, 3400–3542 m; 651 (BIGU, MO, US), 551 (BIGU, TEX, US), 1730, 1844, 2508, 2581, 2613 (BIGU, US), Standley 67324, 67388 (F); Chimaltenango, Guatemala, Huehuetenango, Quetzaltenango, Sacatepéquez, San Marcos, Sololá, Suchitepéquez, Totonicapán, and southern Mexico.

Stevia triflora DC.; 2300–2699 m, 2700–2999 m, 3400–3542 m; 537 (BIGU, TEX, US), 1811, 1851, 2572 (BIGU, US); Alta Verapaz, Chimaltenango, Chiquimula, Guatemala, Quetzaltenango, Huehuetenango, and central and southern Mexico, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru. New record for Quetzaltenango.

Gnaphalieae

The Gnaphalieae, formerly placed within the Inuleae, has more than 180 genera and 2000 species. It has a worldwide distribution; it is most diverse in South America and Australia (Bremer, 1994). Most of the members of the Gnaphalieae are herbs found in montane regions. *Gnaphalium* is the largest and most widespread genus in Guatemala.

Gamochaeta americana (Mill.) Wedd.; 2300–2699 m; 504 (BIGU, F, NY), 2520 (BIGU, OMA), 2573 (BIGU, TEX); Alta Verapaz, Baja Verapaz, Chimaltenango, Chiquimula, Guatemala, Huehuetenango, Jalapa, Progreso, Quetzaltenango, Quiché, Retalhuleu,

Sacatepéquez, San Marcos, Sololá, Totonicapán, and British Columbia, southeastern United States, Mexico, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, South America.

Gamochaeta pensylvanica (Willd.) Cabrera; 2000–2299 m, 2300–2699 m; Standley 67322, 83241 (F); Guatemala, Jalapa, Quetzaltenango, and southern United States, El Salvador, Honduras, Costa Rica, Panama, Argentina, Bolivia, Ecuador, Paraguay, Caribbean.

Gamochaeta purpurea (L.) Cabrera; 2000–2299 m, 2300–2699 m, 3400–3542 m; Standley 67314, 85788 (F), Steyermark 34849 (F); Quetzaltenango, and southeastern United States, South America.

Gnaphalium brachyphyllum Greenm.; 2000–2299 m, 2300–2699 m, 3400–3542 m; 622 (BIGU, F, MO), 1769 (BIGU, OMA), 1689, 2579 (BIGU, TEX), Standley 84809 (F); known only from Chimaltenango, Quetzaltenango, Quiché, San Marcos, Sololá, Totonicapán.

Gnaphalium brachypterum DC.; 2000–2299 m, 2300–2699 m; Standley 67416, 83873 (F); Alta Verapaz, Baja Verapaz, Chimaltenango, Guatemala, Huehuetenango, Jalapa, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Totonicapán; and central and southern Mexico, El Salvador, Honduras, Nicaragua, Costa Rica, Panama.

Gnaphalium greenmanii S. F. Blake; 2700–2999 m; 2549 (BIGU, F); Baja Verapaz, Chimaltenango, Escuintla, Huehuetenango, Jalapa, Quetzaltenango, Zacapa, and Mexico, Honduras.

Gnaphalium liebmannii Sch. Bip. ex Klatt var. *monticola* (McVaugh) D. L. Nash; 2700–2999 m, 3000–3399 m, 3400–3542 m; 2588 (BIGU, CAS, MO, TEX), 2584 (BIGU, F), 1718 (BIGU, OMA); Chimaltenango, Huehuetenango, Progreso, Quetzaltenango, Sacatepéquez, San Marcos, Sololá, Totonicapán, and Mexico, Costa Rica.

Gnaphalium salicifolium (Bertol.) Sch. Bip.; 2300–2699 m, 3000–3399 m; 561 (BIGU, F, MO), 2509 (BIGU, TEX); Chimaltenango, Guatemala, Huehuetenango, Progreso, Quetzaltenango, Quiché, Retalhuleu, Sacatepéquez, San Marcos, Sololá, Totonicapán, and southern Mexico, Costa Rica.

Gnaphalium semiamplexicaule DC.; 2300–2699 m, 2700–2999 m, 3000–3399 m; 1709 (BIGU, F), 503 (BIGU, MO, NY, OMA), 1821 (BIGU, TEX), Standley 83273 (F); Alta Verapaz, Baja Verapaz, Chimaltenango, Chiquimula, Escuintla, Guatemala, Huehuetenango, Jalapa, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Totonicapán, Zacapa, and Mexico, Belize, El Salvador, Nicaragua.

Gnaphalium viscosum Kunth; 2300–2699 m; 1857 (BIGU, F); Chimaltenango, Chiquimula, Guatemala, Huehuetenango, Jalapa, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Totonicapán, Zacapa, and Texas, Mexico, Honduras.

Helenieae

The Helenieae is found primarily at lower and middle elevations in Guatemala. In the treatment by

Panero and Funk (2002) *Tagetes* was been treated as belonging in a separate tribe, the Tageteae.

Tagetes foetidissima DC.; 2300–2699 m, 2700–2999 m; 538 (BIGU, F, MO), 1700 (BIGU, OMA), 1726 (BIGU, TEX); Chimaltenango, Guatemala, Jalapa, Quetzaltenango, Quiché, San Marcos, Sololá, and central and southern Mexico, El Salvador, Costa Rica.

Tagetes sororia Standl. & Steyermark; 2000–2299 m, 2300–2699 m; 1749 (BIGU, F), 1705 (BIGU, OMA), 1850 (BIGU; TEX), Standley 83319, 83240 (F); Totonicapán, Huehuetenango, Quetzaltenango, San Marcos, and Chiapas, Mexico.

Tagetes tenuifolia Cav.; 2000–2299 m; Standley 83207 (F); Alta Verapaz, Baja Verapaz, Chimaltenango, Escuintla, Guatemala, Huehuetenango, Jalapa, Jutiapa, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Santa Rosa, Sololá, Suchitepéquez, Totonicapán, and Mexico, El Salvador, Honduras, Nicaragua, Costa Rica.

Heliantheae

Worldwide, the Heliantheae comprises 189 genera and approximately 2500 species, making it the third largest tribe with respect to species diversity (Bremer, 1994). It includes the typical sunflowers with radiate heads. Most genera and species are found in North America and South America, particularly in Mexico (Bremer, 1994). In Guatemala, the Heliantheae is the largest tribe (67 genera) most of which occur in the highlands. The Heliantheae has been split into multiple tribes (Panero and Funk, 2002).

The Heliantheae includes some larger trees and shrubs that are common in the montane regions of Guatemala. In December and January, *Bidens*, *Montanoa*, *Podachaenium*, and *Verbesina* paint the mountainsides white and yellow.

Acmella filipes (Greenm.) R. K. Jansen var. ***parvifolia*** (Benth.) R. K. Jansen; 2300–2699 m; Standley 85789 (F); Quetzaltenango, and Honduras, Nicaragua.

Acmella repens (Walter) Rich.; 2000–2299 m, 2300–2699 m; 508 (BIGU, F, MO), 1680 (BIGU, TEX), Standley 65290, 67331, 83218, 83268 (F); Alta Verapaz, Baja Verapaz, Chimaltenango, Guatemala, Huehuetenango, Jalapa, Jutiapa, Petén, Progreso, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Santa Rosa, Zacapa, and southeastern United States, Mexico, El Salvador, Costa Rica, Panama, northwestern South America.

Alepidocline annua S. F. Blake; 2000–2299 m, 2300–2699 m; 1786 (BIGU, F), 2565 (BIGU, TEX), Standley 83877 (F), Steyermark 34692 (F); known only from Chimaltenango, Huehuetenango, Quetzaltenango, Sacatepéquez, San Marcos, Sololá, Totonicapán, and Chiapas, Mexico.

Alloispermum integrifolium (DC.) H. Rob.; 2000–2299 m, 2300–2699 m; 547 (BIGU, F, MO), 1880 (BIGU, OMA), 672, 678, 1686, 1760 (BIGU, TEX), Standley 83952 (F), L. O. Williams et al. 23035 (F); Alta Verapaz, Chimaltenango, Guatemala, Huehuetenango, Jalapa, Petén, Progreso, Quetzaltenango,

Quiché, Sacatepéquez, San Marcos, Santa Rosa, Sololá, Suchitepéquez, and central and southern Mexico, El Salvador, Honduras, Nicaragua.

Bidens bicolor Greenm.; 2300–2699 m, 2700–2999 m; 1719 (BIGU, F, OMA); 1849 (BIGU, TEX); Baja Verapaz, Chimaltenango, Guatemala, Jalapa, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Sololá, Totonicapán, and Chiapas and Oaxaca, Mexico.

Bidens chrysanthemifolia (Kunth) Sherff; 2000–2299 m, 2300–2699 m, 2700–2999 m, 3000–3399 m; 2517 (BIGU, F), 544 (BIGU, NY), 765, 1711 (BIGU, TEX), Standley 83220, 85784 (F), Steyermark 34474 (F); Baja Verapaz, Chimaltenango, Guatemala, Huehuetenango, Jalapa, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Sololá, and central and southern Mexico, El Salvador, Nicaragua.

Bidens holwayi Sherff & S. F. Blake; 2300–2699 m, 2700–2999 m, 3000–3399 m; 511 (BIGU, CAS, F, NY), 2517 (F), 1733 (BIGU, OMA), 1713, 1823 (BIGU, TEX), Steyermark 34954 (F); known only from Guatemala, Huehuetenango, Quetzaltenango, San Marcos, Sololá.

Bidens odorata Cav.; 2000–2299 m; Standley 83260 (F), Steyermark 34455 (F); Chimaltenango, Guatemala, Huehuetenango, Quetzaltenango, Sacatepéquez, Santa Rosa, Sololá, Totonicapán, and southeastern United States, Mexico, Colombia, Bolivia, Ecuador, Peru.

Bidens ostruthioides (DC.) Sch. Bip.; Steyermark 34743 (F); Chimaltenango, Huehuetenango, Jalapa, Quetzaltenango, Quiché, San Marcos, Sololá, Totonicapán, and central and southern Mexico, Costa Rica, Panama.

Bidens squarrosa Kunth; 2000–2299 m, 2300–2699 m; 1770 (BIGU, F), 1879B (BIGU, MO, OMA), 668 (BIGU, TEX); Alta Verapaz, Baja Verapaz, Chimaltenango, Chiquimula, Escuintla, Guatemala, Huehuetenango, Izabal, Jalapa, Jutiapa, Petén, Quetzaltenango, Quiché, Retalhuleu, Sacatepéquez, Santa Rosa, Sololá, Suchitepéquez, and Mexico, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, South America.

Bidens triplinervia Kunth; 3400–3542 m; 714 (BIGU, CAS, F, NY), 2574 (BIGU, MO, OMA, TEX), Steyermark 34678, 34838 (F); Chimaltenango, Guatemala, Huehuetenango, Quetzaltenango, Sacatepéquez, Totonicapán, and Mexico, Costa Rica, Panama, Bolivia, Ecuador, Peru.

Coreopsis mutica DC. var. ***microcephala*** D. J. Crawford; 2000–2299 m; 1774 (BIGU, F), Standley 83226 (F), L. O. Williams et al. 14297 (F); Alta Verapaz, Baja Verapaz, Chimaltenango, Chiquimula, Escuintla, Guatemala, Huehuetenango, Jalapa, Progreso, Quetzaltenango, Quiché, Sacatepéquez, Sololá, Zacapa, and Chiapas, Mexico, El Salvador, Honduras.

Cosmos caudatus Kunth; 3000–3399 m; 2626 (BIGU, F, TEX); Chiquimula, Escuintla, Guatemala, Jutiapa, Izabal, Petén, Quetzaltenango, Retalhuleu, Santa Rosa, and Mexico, Belize, Honduras, Nicaragua,

Costa Rica, Panama, Colombia, Bolivia, Ecuador, Peru, Caribbean. New record for Quetzaltenango.

Dahlia australis (Sherff) Sorenson; 3000–3399 m; 2511 (BIGU, F); Huehuetenango, Quetzaltenango, Quiché, Sololá, Totonicapán, and central and southern Mexico. New record for Quetzaltenango.

Dahlia imperialis Roezl ex Ortgies; 2000–2299 m, 2300–2699 m, 2700–2999 m, 3000–3399 m; 766, 1752 (BIGU, F), 1996 (BIGU, TEX), Standley 67468 (F), Steyermark 34676 (F);

Alta Verapaz, Chimaltenango, Chiquimula, Guatemala, Huehuetenango, Jalapa, Jutiapa, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Santa Rosa, Sololá, Totonicapán, and Mexico, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Bolivia, Colombia.

Galinsoga ciliata (Raf.) S. F. Blake; 2000–2299 m, 2300–2699 m; 1762 (BIGU, F), 2521 (BIGU, TEX); Alta Verapaz, Chimaltenango, Chiquimula, Escuintla, Guatemala, Huehuetenango, Jalapa, Jutiapa, Progreso, Quetzaltenango, Quiché, Retalhuleu, Sacatepéquez, Santa Rosa, Sololá, Suchitepéquez, Totonicapán, Zacapa, and United States, Mexico, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Argentina, Caribbean.

Hymenostephium cordatum (Hook. & Arn.) S. F. Blake; 2000–2299 m, 2300–2699 m; 571 (BIGU, F, MO), 2593 (BIGU, NY, OMA), 1776 (BIGU, TEX), Standley 65350, 65400 (F); Alta Verapaz, Baja Verapaz, Chimaltenango, Chiquimula, Escuintla, Guatemala, Huehuetenango, Jalapa, Quetzaltenango, Quiché, Retalhuleu, Sacatepéquez, San Marcos, Santa Rosa, Sololá, Suchitepéquez, and Chiapas, Mexico, El Salvador, Honduras, Costa Rica, Panama, South America.

Jaegeria hirta (Lag.) Less.; 2000–2299 m, 2300–2699 m; 505 (BIGU, F, MO, NY), 1710 (BIGU, MO, TEX), 1791 (BIGU, OMA), 1793 (BIGU, TEX), Standley 83333 (F); Alta Verapaz, Baja Verapaz, Chimaltenango, Escuintla, Guatemala, Huehuetenango, Izabal, Jalapa, Progreso, Quetzaltenango, Quiché, Retalhuleu, Sacatepéquez, San Marcos, Santa Rosa, Sololá, Suchitepéquez, Totonicapán, Zacapa, and Mexico, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, western South America.

Montanoa hexagona B. L. Rob. & Greenm.; 2300–2699 m; 1782 (BIGU, F); Alta Verapaz, Chimaltenango, Guatemala, Huehuetenango, Jalapa, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Santa Rosa, Sololá, and Mexico, El Salvador, Honduras, Nicaragua, Costa Rica.

Montanoa pteropoda S. F. Blake; 2000–2299 m, 2300–2699 m, 2700–2999 m; 523 (BIGU, F, MO, NY), 1813 (BIGU, OMA), 1745 (BIGU, TEX), Standley 83232, 84806 (F), Steyermark 34492, 34608 (F); Chimaltenango, Guatemala, Huehuetenango, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Santa Rosa, Sololá, Totonicapán, and Chiapas, Mexico, El Salvador.

Oteiza ruacophila (Donn. Sm.) Fay; Steyermark 34721 (F); known only from Chimaltenango, Quetz-

tenango, Sacatepéquez, San Marcos, Totonicapán, and Honduras.

Podachaenium eminens (Lag.) Sch. Bip.; 2300–2699 m; 666 (BIGU, F, MO, TEX), Standley 85804 (F), Steyermark 34584 (F); Alta Verapaz, Chimaltenango, Guatemala, Jalapa, Petén, Progreso, Quetzaltenango, Retalhuleu, Sacatepéquez, San Marcos, Santa Rosa, Sololá, Suchitepéquez, Totonicapán, and Mexico, Belize, El Salvador, Honduras, Nicaragua, Costa Rica.

Polymnia maculata Cav. var. *adenotricha* S. F. Blake; 769 (BIGU, F); 2300–2699 m; Guatemala, Jalapa, Quetzaltenango, Santa Rosa, Totonicapán, southern Mexico, Honduras, Costa Rica.

Polymnia maculata Cav. var. *maculata*; 1746 (BIGU, TEX), Steyermark 34483 (F). 2000–2299 m; Quetzaltenango, Quiché, Retalhuleu, and Chiapas, Mexico, Belize, Honduras, Nicaragua, Panama.

Rojasianthe superba Standl. & Steyermark; 2000–2299 m, 2300–2699 m, 2700–2999 m; 656 (BIGU, F, TEX), 1874 (BIGU, TEX), Standley 67400, 85894 (F); known only from Huehuetenango, Quetzaltenango, San Marcos, and Chiapas, Mexico (Fig. 2).

Sabazia pinetorum S. F. Blake; 2300–2699 m; 771 (BIGU, F); known only from Huehuetenango, Quetzaltenango, Quiché, and Chiapas, Mexico. New record for Quetzaltenango.

Salmea scandens (L.) DC.; 2000–2299 m, 2300–2699 m; 1714 (BIGU, CAS, OMA), 570 (BIGU, F), 1863 (BIGU, F, MO), 518 (BIGU, MO, NY, TEX), Standley 65332 (F).

Alta Verapaz, Baja Verapaz, Chimaltenango, Chiquimula, Escuintla, Guatemala, Huehuetenango, Izabal, Petén, Quetzaltenango, Quiché, Retalhuleu, Sacatepéquez, San Marcos, Santa Rosa, Sololá, Suchitepéquez, and Mexico, Belize, El Salvador, Honduras, Panama, Bolivia, Ecuador, Peru, Caribbean.

Schistocarpha platyphylla Greenm.; 2000–2299 m, 2300–2699 m, 3000–3399 m; 727 (BIGU, OMA), 540 (BIGU, OMA, TEX), 772 (BIGU, NY), 2512, 2513, 2519, 2544, 2611, 2622 (BIGU, TEX), Standley 65369, 83270, 85901 (F), Steyermark 34622, 35105 (F); Chimaltenango, Escuintla, Quetzaltenango, Retalhuleu, Sacatepéquez, San Marcos, Suchitepéquez, Totonicapán, and Oaxaca and Chiapas, Mexico, El Salvador.

Sigesbeckia jorullensis Kunth; 2000–2299 m, 2300–2699 m; 3000–3399 m; 1707 (BIGU, F), 506 (BIGU, MO, NY, OMA), 2604 (BIGU, TEX), Standley 67434, 83369 (F); Chimaltenango, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Sololá, Totonicapán, and central and southern Mexico, Costa Rica, Panama, Bolivia, Colombia, Ecuador, Peru, Caribbean.

Simsia amplexicaulis (Cav.) Pers.; 2000–2299 m; 1877B (BIGU, F, TEX), Standley 83164, 85789a (F); Chimaltenango, Guatemala, Huehuetenango, Jalapa, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Sololá, and Mexico, Honduras.

Squamopappus skutchii (S. F. Blake) R. K. Jansen, N. A. Harriman & Urbatsch; 2000–2299 m, 2300–2699 m; 513 (BIGU, F, TEX), 1703 (BIGU, OMA), Standley 67387, 67397, 83314 (F); Chimaltenango, Huehuetenango, Quetzaltenango, Quiché, San Marcos, Sololá, Totonicapán, and Chiapas, Mexico.

Tithonia longiradiata (Bertol.) S. F. Blake; 2000–2299 m; Standley 83946, 84811, 85779 (F); Alta Verapaz, Baja Verapaz, Chimaltenango, Huehuetenango, Jalapa, Jutiapa, Petén, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Sololá, Suchitepéquez, Zacapa, and Mexico, El Salvador, Honduras, Nicaragua, Costa Rica, Panama.

Tridax procumbens L.; 3000–3399 m; 2606 (BIGU, F, MO, TEX); Alta Verapaz, Chimaltenango, Escuintla, Guatemala, Izabal, Jutiapa, Petén, Quetzaltenango, Quiché, Retalhuleu, Sacatepéquez, San Marcos, Santa Rosa, Suchitepéquez, Zacapa, and United States (Florida), Mexico, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Argentina, Bolivia, Colombia, Ecuador, Peru, Venezuela, Caribbean.

Verbesina apaura S. F. Blake; 2300–2699 m, 2700–2999 m, 3000–3399 m; 535 (BIGU, CAS, F), 541 (BIGU, MO, NY), 1721 (BIGU, TEX); known only from Chimaltenango, Guatemala, Progreso, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Sololá, Totonicapán, and Chiapas, Mexico, Honduras.

Verbesina holwayi B. L. Rob.; 2300–2699 m, 2700–2999 m; 1827 (BIGU, F), 507 (BIGU, MO, OMA), 2552 (BIGU, TEX); known only from Huehuetenango, Quetzaltenango.

Verbesina hypoglauca Sch. Bip. ex Klatt; 3000–3399 m, 3400–3542 m; 554 (BIGU, CAS, F), 577 (BIGU, MO, TEX), 1997 (BIGU, NY, TEX), 2617 (BIGU, OMA), 644, 718 (BIGU, TEX), Steyermark 34796 (F); Chimaltenango, Guatemala, Huehuetenango, Quetzaltenango, San Marcos, Sololá, Totonicapán, and central and southern Mexico.

Verbesina sousae Fay; 2700–2999 m; 668 (BIGU, F); Quetzaltenango, and Chiapas and Oaxaca, Mexico. New record for Guatemala.

Verbesina turbacencis Kunth; 2000–2299 m; 1741 (BIGU, TEX), 1878B (BIGU, F, OMA), Standley 83184, 85773 (F); Alta Verapaz, Chimaltenango, Chiquimula, Guatemala, Huehuetenango, Izabal, Jalapa, Jutiapa, Quetzaltenango, Retalhuleu, Sacatepéquez, San Marcos, Santa Rosa, Sololá, and Chiapas, Mexico, Belize, El Salvador, Honduras, Costa Rica, Nicaragua, Panama, Colombia, Venezuela

Cichorieae

Formerly the Lactuceae, most species in the Cichorieae have milky latex. The Cichorieae comprises 98 genera and more than 1500 species with centers of distribution in Europe and North America (Bremer, 1994). In Guatemala, some species are exotic and naturalized from the Old World. *Hieracium*, the largest native genus in Guatemala, is abundant in the highlands.

Hieracium guatemalense Standl. & Steyermark; 34860 (F); known only from Huehuetenango, Quetzaltenango, San Marcos, Zacapa.

Hieracium irazuense Benth.; 2300–2699 m, 3400–3542 m; 620 (BIGU, F), 549 (BIGU, MO, TEX), 2529, 2575 (BIGU, TEX); Chimaltenango, Guatemala, Huehuetenango, Jalapa, Progreso, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Sololá, Totonicapán, and Chiapas, Mexico, El Salvador, Honduras, Nicaragua, Costa Rica, Panama.

Hypochoeris glabra L.; 2300–2699 m, 3400–3542 m; 546 (BIGU, F), 705 (BIGU, TEX); Guatemala, Quetzaltenango, San Marcos, Sololá, Totonicapán. Naturalized throughout North and South America; exotic.

Sonchus oleraceus L.; 2000–2299 m, 2300–2699 m, 3000–3399 m; 545 (BIGU, F), 584 (BIGU, MO, TEX), 1708 (BIGU, OMA), Standley 67404 (F), Steyermark 34425, 34680 (F); Alta Verapaz, Chimaltenango, Escuintla, Guatemala, Huehuetenango, Jalapa, Petén, Quetzaltenango, Sacatepéquez, San Marcos, Santa Rosa, Sololá, Totonicapán, Zacapa, and United States, Mexico to Panama, South America; exotic.

Taraxacum officinale Wigg.; 2000–2299 m, 2300–2699 m; 763 (BIGU, F), Standley 83208, 83382, 85795 (F); Alta Verapaz, Chimaltenango, Guatemala, Huehuetenango, Jalapa, Quetzaltenango, Sacatepéquez, San Marcos, Totonicapán. Naturalized throughout North America, Central America, South America; exotic.

Liabeae

The Liabeae is one of the smaller and taxonomically better known tribes of the Asteraceae (Bremer, 1994). Formerly placed within Vernonieae, members of the Liabeae are mainly Andean in distribution with most of the species occurring in Peru and Ecuador. In Guatemala, the tribe includes perennial herbs, terrestrial and epiphytic shrubs, and trees. All are characterized by opposite leaves, distinguishing them from Guatemalan Vernonieae.

Sinclairia discolor Hook. & Arn.; 2000–2299 m; J. R. S. 1800 (F); Alta Verapaz, Progreso, Guatemala, Quetzaltenango, Sacatepéquez; San Marcos, and southern Mexico, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, Panama.

Sinclairia sublobata (B. L. Rob.) Rydb.; 2000–2299 m; Standley 84801 (F); Alta Verapaz, Baja Verapaz, Chimaltenango, Chiquimula, Guatemala, Quetzaltenango, Retalhuleu, Sacatepéquez, Santa Rosa, Sololá, Zacapa, and southern Mexico, El Salvador, Honduras, Nicaragua.

Mutisiae

The Mutisiae has 76 genera and approximately 970 species. It is more common in the New World than elsewhere (Bremer, 1994). Only one species has been reported from Pico Zunil.

Trixis inula Crantz; 2000–2299 m; E. W. Nelson 3696 (F), Standley 83182, 84821 (F); Alta Verapaz, Baja Verapaz, Chimaltenango, Chiquimula, Escuintla, Gu-

temala, Huehuetenango, Jutiapa, Petén, Progreso, Quetzaltenango, Quiché, Retalhuleu, Sacatepéquez, Santa Rosa, Sololá, Zacapa, and Texas, Mexico, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Peru, Venezuela, Jamaica.

Senecioneae

In number of species, the Senecioneae is the largest tribe with more than 3000 species in 120 genera that are distributed globally with prominent concentrations in Central America and South America, tropical and southern Africa, and central and eastern Asia (Bremer, 1994). Some groups within the *Senecio sensu lato* group in Latin America have been revised (Barkley, 1985; Barkley et al., 1996).

In Guatemala, *Roldana* is the most diverse genus of Senecioneae; it includes mostly shrubs and trees that are a characteristic component of the highlands. Turner (2005) revised *Roldana* from Mexico.

Barkleyanthus salicifolius (Kunth) H. Rob. & Brettell; 2000–2299 m; *Standley* 83185 (F); Baja Verapaz, Chimaltenango, Escuintla, Guatemala, Huehuetenango, Jalapa, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Totonicapán, and Mexico, El Salvador.

Erechtites valerianifolius (Link ex Spreng.) DC.; 2000–2299 m, 2300–2699 m; 528 (BIGU, F, MO), 1888 (BIGU, TEX); Alta Verapaz, Chimaltenango, Guatemala, Huehuetenango, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Sololá, Zacapa, and southern Mexico, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, tropical South America.

Roldana acutangula (Bertol.) H. Rob. & Brettell; 2300–2699 m, 2700–2999 m, 3400–3542 m; 729, 2554 (BIGU, F), 1817 (BIGU, MO, TEX), *Standley* 67334, 67483 (F); known only from Chimaltenango, Huehuetenango, Quetzaltenango, San Marcos, Totonicapán, and Chiapas, Mexico.

Roldana aschenborniana (Schauer) H. Rob. & Brettell; 2700–2999 m, 3000–3399 m; 1717 (BIGU, F), 2621 (BIGU, OMA), 2504 (BIGU, TEX); Chimaltenango, Jalapa, Quetzaltenango, Sacatepéquez, and Mexico.

Roldana barba-johannis (DC.) H. Rob. & Brettell; 3000–3399 m; 2609 (BIGU, F), *Steyermark* 34889 (F); Chimaltenango, Huehuetenango, Progreso, Sacatepéquez, Sololá, and Mexico.

Roldana gilgii (Greenm.) H. Rob. & Brettell; 2300–2699 m, 2700–2999 m, 3000–3399 m; 525 (BIGU, CAS, OMA), 667 (BIGU, F), 2589 (BIGU, MO, TEX), 1725, 1842, 1847, 2531 (BIGU, TEX), *Standley* 67378 (F), *Steyermark* 34596 (F); known only Chimaltenango, Guatemala, Quetzaltenango, Quiché, San Marcos, Sololá, Suchitepéquez, Totonicapán, and Chiapas, Mexico (Fig. 3).

Roldana heterogama (Benth.) H. Rob. & Brettell; 2300–2699 m, 3000–3399 m, 3400–3542 m; 586, 713 (BIGU, F), 534 (BIGU, MO, OMA), 2624 (BIGU, TEX), *Standley* 67453, 85837 (F); Chimaltenango, Guatemala, Huehuetenango, Quetzaltenango, Quiché,

Sacatepéquez, San Marcos, Sololá, Totonicapán, and Chiapas, Mexico, Costa Rica, Panama.

Roldana jurgensenii (Hemsl.) H. Rob. & Brettell; 2300–2699 m, 3000–3399 m; 2639 (BIGU, F), 526 (BIGU, MO, TEX), 2623 (BIGU, OMA), 1995 (BIGU, TEX), *Standley* 67368, 84955a (F); Chimaltenango, Huehuetenango, Progreso, Quetzaltenango, Quiché, San Marcos, Sololá, Suchitepéquez, Totonicapán, and southern Mexico, El Salvador, Honduras.

Roldana petasitis (Sims) H. Rob. & Brettell; 2000–2299 m, 2300–2699 m; *Standley* 65377, 83178, 84804, 85734 (F), *Steyermark* 34595 (F); Alta Verapaz, Baja Verapaz, Chimaltenango, Escuintla, Guatemala, Huehuetenango, Jutiapa, Progreso, Quetzaltenango, Sacatepéquez, San Marcos, Santa Rosa, Sololá, Totonicapán, Zacapa, and Chiapas, Mexico, El Salvador, Honduras, Nicaragua.

Roldana schaffneri (Sch. Bip. Ex Klatt) H. Rob. & Brettell; 2300–2699 m; 2561 (BIGU, F, TEX); Alta Verapaz, Baja Verapaz, Chimaltenango, Guatemala, Huehuetenango, Jalapa, Progreso, Quetzaltenango, Quiché, Retalhuleu, Sacatepéquez, Santa Rosa, Sololá, Suchitepéquez, Zacapa, and El Salvador, Honduras, Nicaragua, Costa Rica, Panama.

Senecio callosus Sch. Bip.; 3000–3399 m, 3400–3542 m; 2570 (BIGU, F), *Steyermark* 34900 (F); Chimaltenango, Huehuetenango, Quetzaltenango, Sacatepéquez, San Marcos, Sololá, Totonicapán, and Mexico.

Senecio doratophyllus Benth.; 2300–2699 m, 2700–2999 m; 1720 (BIGU, F), 1812, 1837 (BIGU, TEX), *Standley* 67369, 85692 (F); Chimaltenango, Huehuetenango, Jalapa, Progreso, Quetzaltenango, Quiché, Sacatepéquez, San Marcos, Sololá, Suchitepéquez, Totonicapán, and Chiapas, Mexico, Honduras.

Senecio godmanii Hemsl.; 2700–2999 m, 3000–3399 m; 578, 1723 (BIGU, F), 645 (BIGU, MO, TEX), 2620 (BIGU, TEX); Guatemala, Huehuetenango, Quetzaltenango, Sacatepéquez, and Mexico.

Senecio rhyacophilus Greenm.; 2700–2999 m, 3000–3399 m; 2583 (BIGU, F), 2591 (BIGU, MO, OMA), 2629 (BIGU, TEX); known only from Huehuetenango, Quetzaltenango, Quiché, Sacatepéquez. New record for Quetzaltenango.

Senecio vulgaris L.; 2300–2699 m; 2516 (BIGU, F); reported only from Quetzaltenango, but expected in all departments. Naturalized throughout the New World; exotic.

Senecio warszewiczii Braun & Bouché; 2300–2699 m, 3000–3399 m, 3400–3542 m; 721, 2585 (BIGU, F), 2577 (BIGU, MO, TEX), 720 (BIGU, OMA), 1820, 2600 (BIGU, TEX), *Standley* 67405, 85760 (F); known only from Chimaltenango, Guatemala, Huehuetenango, Quetzaltenango, San Marcos, Sololá, Totonicapán, and Volcán Tacana, Chiapas, Mexico.

Telanthophora cobanensis (Coul.) H. Rob. & Brettell; 2300–2699 m; 1784 (BIGU, F); Alta Verapaz, Baja Verapaz, Chimaltenango, Huehuetenango, Progreso, Quetzaltenango, San Marcos, Sololá, Suchitepé-

quez, and Chiapas, Mexico, El Salvador, Honduras. New record for Quetzaltenango.

Vernonieae

The Vernonieae is most prevalent from the middle elevations to the lowland regions of Guatemala, where it is represented by herbs, shrubs, and trees characterized by alternate leaves. In Guatemala, *Vernonia* is by far the most diverse with 19 indigenous species.

Vernonia arborescens (L.) Sw.; 2000–2299 m, 2300–2699 m; 1759 (BIGU, F), 2540 (BIGU, TEX), E. W. Nelson 3691 (F), Steyermark 34965 (F); Chimaltenango, Chiquimula, Guatemala, Quetzaltenango, Sacatepéquez, Santa Rosa, and southern Mexico, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Bolivia, Ecuador, Peru, Venezuela, Antilles.

Vernonia leiocarpa DC.; Standley 83233 (F); Alta Verapaz, Baja Verapaz, Chimaltenango, Chiquimula, Guatemala, Huehuetenango, Jalapa, Jutiapa, Quetzaltenango, Sacatepéquez, San Marcos, Santa Rosa, Sololá, Totonicapán, Zacapa, and Chiapas, Mexico, Belize, El Salvador, Honduras, Nicaragua.

Vernonia salvinae Hemsl.; Skutch 953 (F); Quetzaltenango, Quiché, San Marcos, and southern Mexico.

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LITERATURE CITED

- Almeda, F. 1993. *Stanmarkia*, a new genus of Melastomataceae from the volcanic highlands of western Guatemala and adjacent Mexico. *Brittonia* 45: 187–203.
- Anderson, T. 1908. The volcanoes of Guatemala. *The Geog. J.* 31: 473–491.
- Barkley, T. M. 1985. Infrageneric groups in *Senecio*, s.l., and *Cacalia*, s.l. (Asteraceae: Senecioneae) in Mexico and Central America. *Brittonia* 37: 211–218.
- , B. L. Clark, and A. M. Funston. 1996. The segregate genera of *Senecio sensu lato* and *Cacalia sensu lato* (Asteraceae: Senecioneae) in Mexico and Central America. Pp. 613–620 in *Compositae: Systematics. Proceedings of the International Compositae Conference*, eds. D. J. N. Hind and H. J. Beentje, Kew: Royal Botanic Garden.
- Beard, J. S. 1944. Climax vegetation in tropical America. *Ecology* 25: 127–158.
- Breedlove, D. E. 1981. Introduction to the flora of Chiapas. Pp. 1–35 in *Flora of Chiapas. Part 1. San Francisco, California*: California Academy of Sciences.

- Bremer, K.** 1994. *Asteraceae: Cladistics and Classification*. Portland, Oregon: Timber Press.
- Bruijnzeel, L. A. and E. J. Veneklaas.** 1998. Climatic conditions and tropical montane forest productivity: The fog has not lifted yet. *Ecology* 79: 3–9.
- Gall, F.** 1983. *Diccionario Geográfico de Guatemala, de la letra Q a la S. Compilación critica. Tomo III*. Instituto Geográfico Nacional.
- Hamilton, L. S., J. O. Juvnik, and F. N. Scatena.** 1995. *Tropical Montane Cloud Forests*. New York: Springer-Verlag.
- Holmgren, P. K., N. H. Holmgren, and W. Keukens.** 1990. *Index Herbariorum. Part I. The Herbaria of the World*. Eighth Ed. Utrecht, The Netherlands: New York Botanical Garden.
- Howell, S. N. G. and S. Webb.** 1995. *A Guide to the Birds of Mexico and Northern Central America*. Oxford: Oxford University Press.
- Kessler, M.** 2002. The elevational gradient of Andean plant endemism: Varying influences of taxon-specific traits and topography at different taxonomic levels. *J. Biogeogr.* 29: 1159–1165.
- King, R. M. and H. Robinson.** 1987. *The Genera of the Eupatorieae (Asteraceae)*. Monographs in Systematic Botany 22. St. Louis, Missouri: Missouri Botanical Garden Press.
- Lawton, R. O., U. S. Nair, R. A. Pielke Sr., and R. M. Welch.** 2001. Climatic impact of tropical lowland deforestation on nearby montane cloud forests. *Science* 294: 584–587.
- Leopold, A. S.** 1950. Vegetation zones in Mexico. *Ecology* 31: 507–518.
- McCarty, J. P.** 2001. Ecological consequences of recent climate change. *Cons. Biol.* 15: 320–331.
- Nash, D. L. and L. O. Williams.** 1976. Flora of Guatemala: Asteraceae. *Fieldiana, Bot.* 24(12): 1–603.
- Panero, J. L. and V. A. Funk.** 2002. Toward a phylogenetic subfamilial classification for the Compositae (Asteraceae). *Proc. Biol. Soc. Washington* 115: 909–922.
- Pounds, J. A., M. P. L. Fogden, and J. H. Campbell.** 1999. Biological response to climate change on a tropical mountain. *Nature* 398: 611–615.
- Pruski, J. F. and G. Sancho.** 2004. Asteraceae, Pp. 33–39 in *Flowering Plants of the Neotropics*, eds. N. Smith, S. A. Mori, A. Henderson, D. W. Stevenson, & S. V. Heald, Princeton, New Jersey: Princeton University Press.
- Raven, P. H. and D. I. Axelrod.** 1974. Angiosperm biogeography and past continental movements. *Ann. Missouri Bot. Gard.* 61: 539–657.
- Robinson, H. and R. Bretell.** 1975. Studies in the Senecioneae (Asteraceae). *Phytologia* 27: 402–439.
- Solomon, J.** 1996. TROPICOS: An example of linked specimen and taxon databases. Pp. 1–8 in *Workshop on Application of Information Systems on Botanical Inventory*. Taipei: Institute of Botany, Academia Sinica.
- Skutch, A. F.** 1979. *The Imperative Call*. Gainesville, Florida: University Presses of Florida.
- Steyermark, J. A.** 1950. Flora of Guatemala. *Ecology* 31: 368–372.
- Still, C. J., P. N. Foster, and S. H. Schneider.** 1999. Simulating the effects of climate change on tropical montane cloud forests. *Nature* 398: 608–610.
- Strother, J. L.** 1999. Compositae-Heliantheae S. L. *Flora of Chiapas, Part 5*. San Francisco: California Academy of Sciences.
- Turner, B. L.** 2005. A recension of the Mexican species of *Roldana* (Asteraceae: Senecioneae). *Phytologia* 87: 204–263.
- Veblen, T. T.** 1977. The urgent need for forest conservation in highland Guatemala. *Biological Cons.* 9: 141–154.
- . 1978. Forest preservation in the western highlands of Guatemala. *Geog. Rev.* 4: 417–434.
- Véliz Pérez, M. E.** 2000. La vegetación del volcán de Acatenango, Guatemala. *Revista de Ciencia y Tecnología [Universidad de San Carlos de Guatemala]* 5: 3–168.
- , N. R. G. Pérez, M. G. V. Gil, and R. L. Soberanis. 2001. La vegetación montaña de Guatemala. *Revista de Ciencia y Tecnología [Universidad de San Carlos de Guatemala]* 6: 3–61.
- Villaseñor, J. L., G. Ibarra, and D. Ocaña.** 1998. Strategies for the conservation of Asteraceae in Mexico. *Cons. Biol.* 12: 1066–1075.
- Williams, H.** 1960. Volcanic history of the Guatemalan highlands. *University of California Pub. Geol. Sci.* 38: 1–86.