

Biogeography and Biology of Bark and Ambrosia Beetles (Coleoptera: Scolytidae and Platypodidae) of a Mesic Montane Forest in Mexico, with an Annotated Checklist of Species

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ABSTRACT We found 103 species in 33 genera of Scolytidae and five species in one genus of Platypodidae in mesic montane forest in the region of Xalapa, Veracruz, Mexico. The most distinctive elements of the fauna are the large numbers of species of ambrosia beetles in the tribe Corthylini and twig borers in the Bothrosternini. Neotropical genera, especially those typical of upland areas, formed the largest portion of the fauna. Most species in these genera are restricted to montane habitats of Mexico and Central America. Because mesic montane forest is transitional between highland temperate forests and lowland tropical forests in central Mexico, some mixing occurs and both areas contribute to the fauna. Nonetheless, the scolytid fauna includes a large component restricted to this forest type. This faunal element is derived from montane Central America, has penetrated into Mexico in favorable habitats, and is historically distinct from the predominantly South American scolytid fauna of lowland rain forest and the western North American-Mexican Plateau fauna of highland temperate forests. Most species (52%) were ambrosia beetles (which feed on ectosymbiotic fungi in galleries); phloem-feeders (21.7%) and pith-feeding twig borers (15.7%) were also abundant. The high percentage of ambrosia beetles is similar to that found in tropical rain forest in Mexico and other humid tropical areas in the Old and New World. Most ambrosia beetles and twig borers in the Xalapa fauna were extremely polyphagous, whereas most phloem-feeders were strongly monophagous. This relationship between host substrate and degree of specificity is similar to patterns observed in local scolytid faunas in temperate as well as tropical communities.

KEY WORDS Insecta, Coleoptera, ecology, biogeography

BARK AND ambrosia beetles (Scolytidae and Platypodidae) are small beetles that breed in living, dying, or recently killed woody tissue. They are among the first insects to invade cut, fallen, or injured hosts. Some species cause the death of all or part of their hosts. Most feed on phloem (bark beetles in the strict sense) or ectosymbiotic fungi that grow in their tunnels (ambrosia beetles). Others feed directly on wood, pith of twigs and small branches, seeds and fruits, or on herbaceous hosts (Wood 1982). The degree of host specificity is generally related to feeding habit in most areas, phloem-feeders showing a high degree of specificity and ambrosia-feeders showing a very low degree of specificity (Beaver 1979; Atkinson & Equihua 1986a,b). Recent studies in Mexico have focused on Scolytidae and Platypodidae of highland temperate communities (Atkinson & Equihua 1985a, Atkinson et al. 1986b), tropical deciduous forest (Atkinson & Equihua 1986b, Equihua & Atkinson 1986, Atkinson et al. 1986a), and lowland rain for-

est (Atkinson & Equihua 1986a). Here we examine the scolytid fauna of mesic montane forest, a distinctive habitat not previously studied. In addition to listing the species present we analyze their biogeography and biology and compare these patterns to those of other communities in Mexico.

Mesic montane forest (sensu Rzedowski [1978], deciduous forest of Gómez [1973], cloud forest of many authors) is found at intermediate elevations of seaward-facing cordilleras in Mexico. Altitudinal ranges vary considerably according to latitude and local topography. Areas supporting mesic montane forests are characterized by high precipitation (1,000-3,000 mm/yr) and cool average temperatures without extremes of hot or cold. The most important factor common to these areas is the frequent occurrence of fogs and mists, which reduce the amount of incident insolation and evapotranspiration. This forest type forms an altitudinal transition between temperate forests of pine, oak, and fir that are characteristic of colder, drier areas in Mexico, and lowland tropical forests, principally rain forest, which require a warmer climate in central Mexico and Central America. Small isolated patches of mesic montane forest occur in almost all mountain ranges in Mexico, but the largest con-

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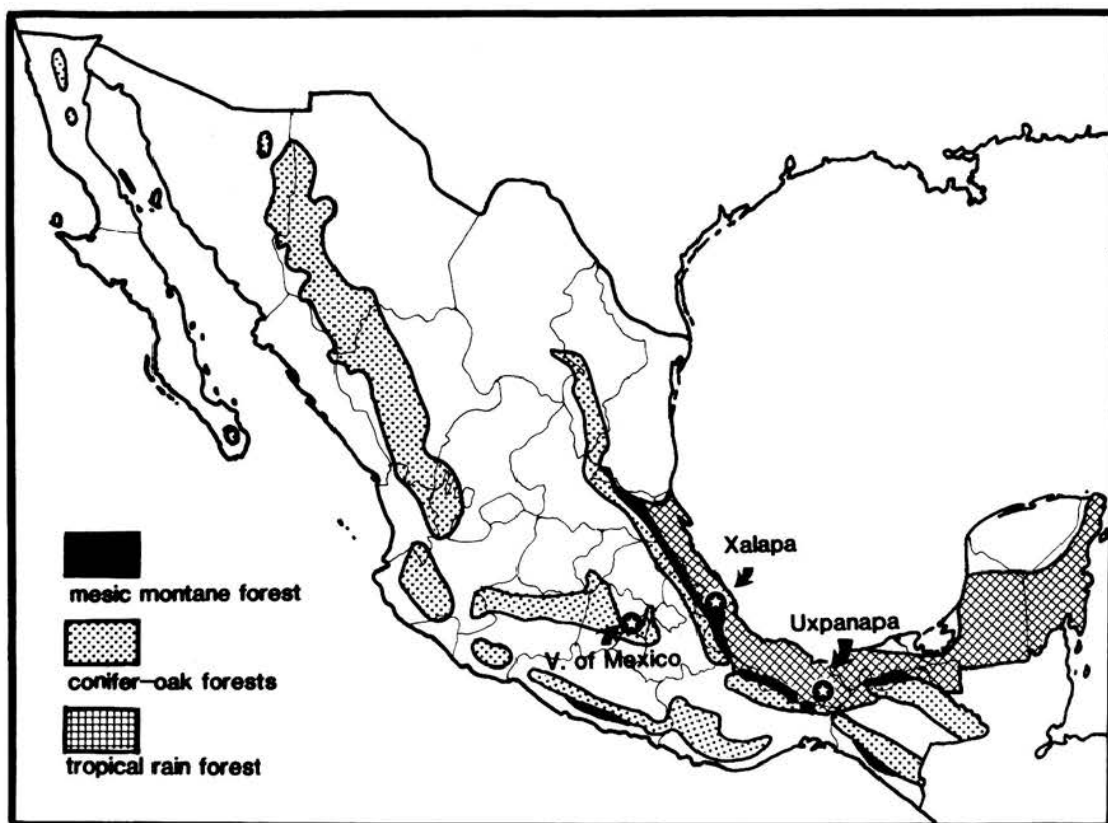


Fig. 1. Map of study area in the vicinity of Xalapa, Veracruz, Mexico, showing distribution in Mexico of mesic montane forest, highland temperate conifer-oak associations (from Rzedowski 1978), and tropical rain forest. Locations of the Uxpanapa (Atkinson & Equihua 1986a) and Valley of Mexico (Atkinson & Equihua 1985a) study areas from which comparative data are taken are also shown.

tinuous area is located in a narrow band on the eastward-facing slopes of the Sierra Madre Oriental from Oaxaca to southern Tamaulipas. Another large area occurs in the southern state of Chiapas that is continuous with similar forests of Guatemala, Honduras, El Salvador, and northern Nicaragua (Rzedowski 1978).

Methods

Xalapa is situated in the center of the state of Veracruz on the eastern slopes of the Sierra Madre Oriental (Fig. 1). Our collecting was confined to areas originally covered by mesic montane forest in the immediate vicinity of Xalapa including all or part of the municipalities of Xalapa, Banderilla, Acajete, Coacoatzintla, Coatepec, Emiliano Zapata, Naolinco, and San Andrés, an area of approximately 700 km² (approximate coordinates: 19°26'–19°39'N; 96°51'–97°01'W). Much of the original forest cover has been destroyed and largely replaced with coffee plantations with shade provided by leguminous trees. Elevations range from 1,100–1,600 m. The climate is cool and moist with rainfall throughout the year, ranging from 1,400–1,800

mm/yr within the study area and with a mean annual temperature of 18.1°C (14.8°C in the coldest month, 20.4°C in the hottest) (Zola Baez 1980). Elevations rise sharply to the west and the predominant vegetation changes to pine-oak forest. In the east elevation drops abruptly and the vegetation changes to tropical subdeciduous and deciduous forests.

This study is based primarily on our field collections over a 2-yr period during which the senior author was resident in Xalapa. Most collections were made in naturally infested host material, but we also cut branches or trunks of plant species of particular interest in an attempt to attract insects (i.e., those known or suspected to have host-specific associates). We also used pitfall traps baited with 70% ethanol, a known attractant for many species of ambrosia beetles (Moeck 1970, Bustamante & Atkinson 1984). Our collecting was guided by a working list of species known to occur in nearby areas with similar climate and vegetation, knowledge of specific host associations in other areas, a local floral checklist (Zola Baez 1980), and extensive field experience with bark and ambrosia beetles. Host plants were identified by the herbaria of the Universidad

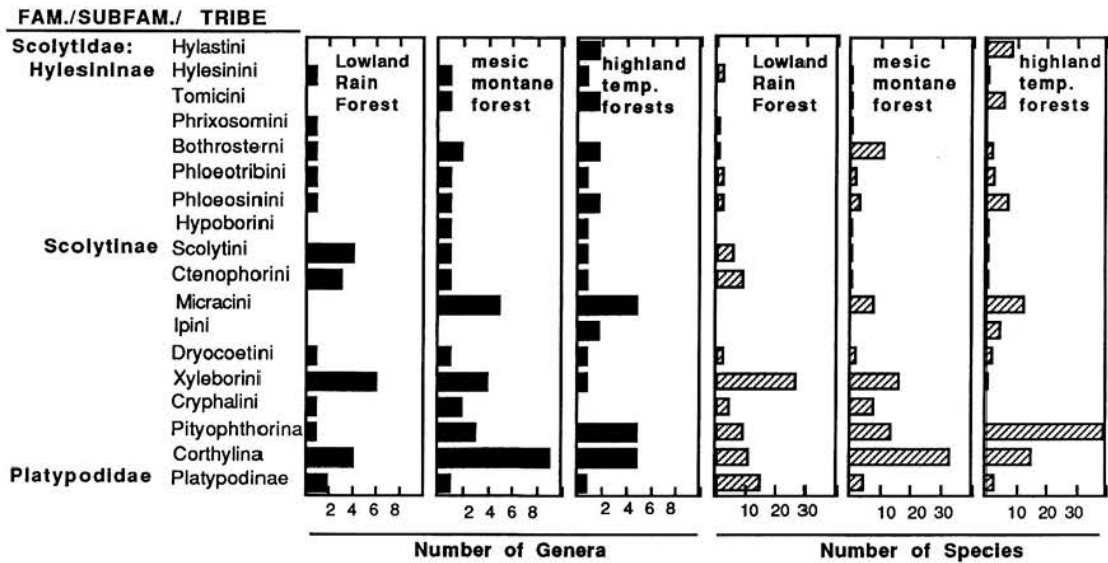


Fig. 2. Taxonomic comparison of the faunas of Scolytidae and Platypodidae of mesic montane forest at Xalapa, Veracruz, lowland rain forest (Uxpanapa, Mexico [Atkinson & Equihua 1986a]), and highland temperate forests (Valley of Mexico [Atkinson & Equihua 1985a]).

Veracruzana and of the Instituto Nacional de Investigaciones sobre Recursos Bióticos. Insects were identified by the junior author with confirmations in some cases by S. L. Wood (Brigham Young University, Provo, Utah) and D. E. Bright (Biosystematics Research Institute, Ottawa, Ontario). Voucher specimens from this study are deposited in the insect collection of the Colegio de Postgraduados, Chapingo, Mexico and in the Florida State Collection of Arthropods, Gainesville.

We made extensive observations on the biology of species collected, emphasizing host plants and degree of host specificity, feeding habits, and mating habits. Feeding habits were determined by direct observation of boring activities of adults and larvae. Host specificity was inferred from our collections, related studies (e.g., Atkinson & Equihua 1986a,b), and a critical review of available literature. Mating systems were inferred by gallery architecture (with attention to caveats mentioned by Kirkendall [1983]), number and sex of adults present, and supporting evidence in the literature, but are not analyzed in this paper.

Results and Discussion

Taxonomic Composition. We found 103 species in 33 genera of Scolytidae and five species in one genus of Platypodidae (including 2 species reported from the area but not collected in this study). Ten of these were previously undescribed, 10 unknown from Mexico, and 34 unreported from the state of Veracruz. A complete list of species collected with host plants, biological notes, and distributions is given as an appendix. The Platypod-

idae are closely related to the Scolytidae (Wood 1982, 1986b) and are maintained as separate families principally for traditional reasons. For the sake of simplicity "scolytids" means "scolytids and platypodids" throughout the discussion. The numbers of genera and species from the Xalapa region are shown graphically by tribe in Fig. 2. The most speciose group in the fauna is the Corthylini with 14 genera and 48 species, nearly 50% of the total. Within this group, most genera and species were ambrosia beetles in the subtribe Corthylina, notably *Monarthrum* (11 species) and *Corthylus* (9 species). The Corthylini are an important to dominant component of most New World scolytid assemblages, but species of the phloem-feeding subtribe Pityophthorina are generally better represented in cooler and drier areas (Atkinson & Equihua 1985a, 1986b; Atkinson et al. 1986a,b; Deyrup & Atkinson 1987). Other well-represented tribes include the Bothrosternini (11 species), Xyleborini (16 species), Cryphalini (8 species), and Micracini (8 species).

Also shown in Fig. 2 for comparative purposes are the taxonomic profiles of numbers of genera and species for a lowland rain forest site (Atkinson & Equihua 1986a) and for a site with highland temperate forests (oak, pine-oak, pine-fir [Atkinson & Equihua 1985a]), both in central Mexico. At first glance these profiles are somewhat confusing, but tribes basically can be divided into those that are of similar importance in all areas (e.g., Hylesinini, Phloeotribini, and Dryocoetini), and those that are predominate in particular sites (e.g., Scolytini, Ipini, Bothrosternini, and Hylastini). Only the latter groups offer any insight into the faunal relationships among areas.

Table 1. Biogeographic affinities of genera of Scolytidae and Platypodidae from mesic montane forest in the vicinity of Xalapa, Veracruz, Mexico

Affinity ^a	No. of genera	Genera
Holarctic	2	<i>Hylesinus</i> , <i>Pityophthorus</i> ^b
Nearctic	2	<i>Gnathotrichus</i> , <i>Pseudopityophthorus</i>
Neotropical:		
Lowland	6	<i>Bothrosternus</i> , <i>Scolytodes</i> , <i>Hylocurus</i> , <i>Thysanoes</i> , <i>Dryocoetoides</i> , <i>Araptus</i>
Upland	11	<i>Cnesinus</i> , <i>Micracis</i> , <i>Phloeocleptus</i> , <i>Gnathotrupes</i> , <i>Tricolus</i> , <i>Amphicranus</i> , <i>Microcorthylus</i> , <i>Monarthrum</i> , <i>Corthylus</i> , <i>Corthycyclon</i> , <i>Corthylocurus</i>
Wide-spread	5	<i>Chramesus</i> , <i>Chaetophloeus</i> , <i>Pseudothysanoes</i> , <i>Dendrocranulus</i> , <i>Stegomerus</i>
Circum-tropical	5	<i>Ambrosiodmus</i> , <i>Xyleborus</i> , <i>Xyleborinus</i> , <i>Hypothenemus</i> , <i>Platypus</i>
Other	3	<i>Xylechinus</i> , ^c <i>Phloeotribus</i> , ^d <i>Scolytus</i> ^d

^a Based on Wood (1986b) and personal observations.

^b Greatest species richness in Nearctic realm.

^c All continents, including Australia.

^d Widespread in temperate and tropical North and South America and in temperate Eurasia.

Because mesic montane forest is altitudinally transitional between highland temperate forests (principally pine-oak forest) and lowland rain forest (evergreen and subdeciduous tropical forests) (Rzedowski 1978), one might expect its scolytid fauna to be largely a mixture, or "average" of the faunas at either extreme of the continuum. To a limited extent this is the case. The Xyleborini and Platypodidae are best represented in lowland rain forest, less so in mesic montane forest, and even less in highland temperate forests. The reverse is true of the Tomicini, Phloeosinini, Micracini, and Pityophthorina. On the other hand some groups, particularly the Bothrosternini and the Corthylina, are prevalent in mesic montane forests and notably less important towards either end of the altitudinal gradient. The apparent predominance of the Cryphalini in mesic montane forest is more related to the number of species of *Hypothenemus* associated with disturbed habitats than to any large scale taxonomic pattern.

Biogeography. The broad affinities of the genera found in the Xalapa area are shown in Table 1 and Fig. 3. *Biogeographic affinity* refers to the large scale region in which the greatest proliferation of species occurs for a given genus. More than 60% of the genera from the Xalapa area are exclusively or predominantly neotropical. Although our knowledge of the biogeography of the neotropical fauna is limited, some genera clearly are best represented in either lowland or upland sites and others are well represented across a broad range of neotropical habitats. The separation of neotropical genera into lowland, upland, and widespread groups is based primarily on their distribution in Mexico and Central America (Schedl 1940, 1972; Wood

1982; Atkinson & Equihua 1985a,b,c, 1986a; Atkinson et al. 1986a,b; Equihua & Atkinson 1986, 1987; Estrada & Atkinson in press), not on their occurrence or richness in the specific sites compared here. Most of the neotropical genera found in the Xalapa area are those with greatest diversity in upland, montane habitats. This contrasts strongly with the generic affinities of the scolytid fauna of a lowland rain forest site (Fig. 3) also preponderantly neotropical, but dominated by genera with greatest diversity in lowland areas. In an area characterized by highland temperate forests (Fig. 3), the neotropical element is much less important, particularly with respect to lowland genera.

As is true of the taxonomic composition of the fauna, a visual comparison of the profiles in Fig. 3 suggests that the fauna of mesic montane forest is in part a mixture of the faunas of the highland temperate forests and lowland tropical forests. This is indicated by the presence of nearctic and holarctic elements shared with highland forests and conversely by the decrease in relative abundance of lowland neotropical and circumtropical genera with increasing altitude. The most distinctive element of mesic montane forest is that of upland neotropical genera. Specifically, these are in the Bothrosternini (*Cnesinus*) and Corthylina (*Corthylus*, *Monarthrum*, *Tricolus*, and *Amphicranus*). Although there were relatively few species present in the Xalapa area, the genera *Xylechinus* (Tomicini) and *Phloeocleptus* (Micracini) are both essentially restricted to mesic montane forest in Mexico and Central America.

A tabulation of distributional patterns of species found in the Xalapa area, as well as those in a lowland rain forest site and highland temperate forest site, is shown in Fig. 4. The basic divisions used here are lowland tropical, upland tropical, and temperate, which loosely correspond to zones of hot, cool, and cold climates, or low, intermediate, and high altitudes, respectively. These categories follow vegetation patterns (e.g., Rzedowski 1978). The category "local" includes those species known only from the respective study areas. Some of these may be narrow endemics in the usual sense, but most are probably more widely distributed but simply have not been collected elsewhere in other parts of Mexico. A given species is assigned to a category and subcategory based on its overall distribution, not its presence or absence in a given site. Lowland tropical species in mesic montane forest and highland temperate forests, for example, were not necessarily found in the particular lowland rain forest site used here for comparison. The categories used at the species level do not correspond with those used for genera. For example, the genus *Corthylus* is treated here as an upland neotropical genus (in the sense of Fig. 3) because most species are found in montane environments in the Neotropics. Individual species, however, have different patterns (in the sense of Fig. 4): *Corthylus spinifer* Schwarz is a widespread lowland species, *C. fuscus* Bland-

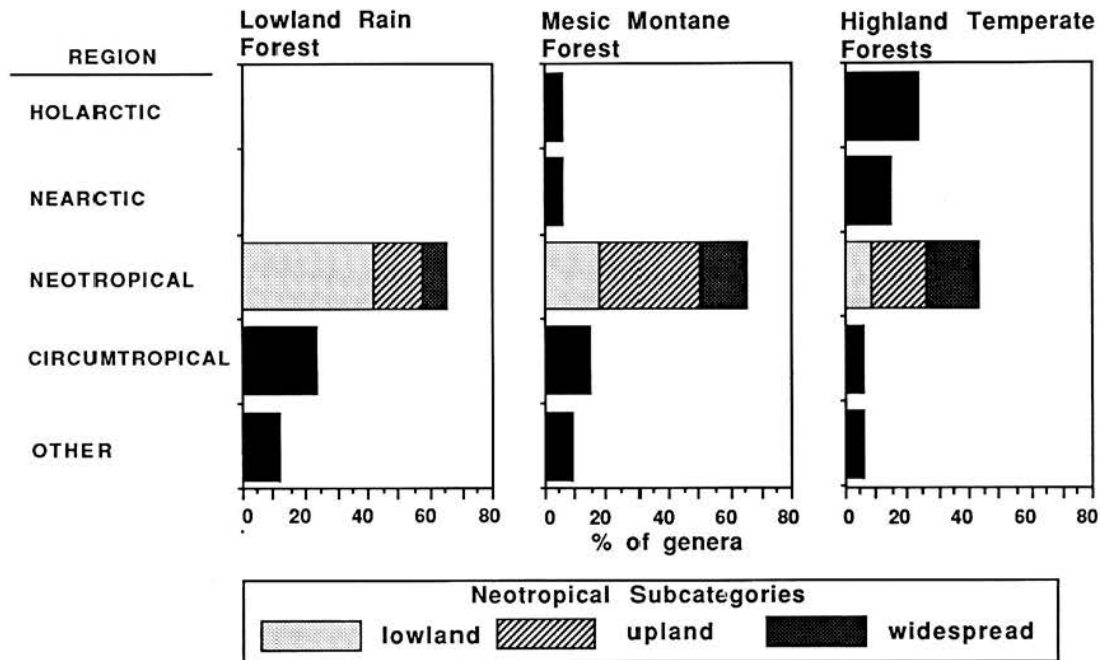


Fig. 3. Comparison of biogeographic affinities of genera of Scolytidae and Platypodidae of mesic montane forest at Xalapa, Veracruz, lowland rain forest (Uxpanapa, Mexico [Atkinson & Equihua 1986a]), and highland temperate forests (Valley of Mexico [Atkinson & Equihua 1985a]).

ford is restricted to the temperate highlands of Mexico and Guatemala, and *C. flagellifer* Blandford is found throughout central and southern Mexico in cool habitats at intermediate elevations. All are found in the Xalapa region.

All the species present in the lowland rain forest site are found only in lowland tropical areas. The largest subcategory, "widespread," includes species that range into southern South America, the Antilles, and the southeastern United States. Large numbers of species are also found southward into northern South America and Central America. By contrast, relatively few of these species are restricted to Mexico. In general, the fauna of lowland rain forest in Mexico consists of wide-ranging neotropical species belonging to neotropical and circum-tropical genera, many of which reach their northern distributional limits in southeastern Mexico (Atkinson & Equihua 1986a). This pattern is very similar to that of the flora of rain forests in Mexico (Rzedowski 1978, Gomez 1973). Similarly, most species found in the highland temperate site are found only in temperate areas. The breakdown into subcategories is fundamentally different from that of lowland rain forest in that most species are restricted to the Mexican Plateau (in the broad sense, including the southwestern United States) or are widely distributed in western North America. Again, the faunal pattern mirrors the distribution of plant communities, as most highland plant communities in central Mexico are similar in taxonomic composition and physiognomy to those of the highlands of the western United States (Rzedowski 1978).

In contrast to the communities on either extreme of the ecological gradient, the fauna of mesic montane forest includes species with a wide variety of distributional patterns. As was true for comparisons of taxonomic composition and biogeographic affinities of genera, visual comparison of the profiles in Fig. 4 indicates some blending, with a slight bias toward lowland species. The relative proportions of different subcategories within the lowland tropical category for mesic montane forest are roughly similar to those for lowland rain forest. The same is true for the temperate category with respect to highland temperate forests. This suggests that the lowland tropical and temperate species found in mesic montane forest are representative subsets of the larger faunas of the two extremes of the gradient. The distinctive element of mesic montane forest consists of upland tropical species. Most of these have very local distributions and are largely restricted to the mountains of Mexico and Central America. This is very different from the compositions of lowland rain forest and highland temperate forest which mostly contain wide-ranging representatives of a South American or Western North American fauna, respectively. Halffter (1987) indicated that there are many vicariant species pairs of insects shared between the moist highlands of eastern Mexico and the mountains of Nuclear Central America. Current knowledge of scolytid phylogeny and biogeography is insufficient to reach any conclusions in this regard.

The descriptive biogeographical data presented here suggest that the scolytid fauna associated with

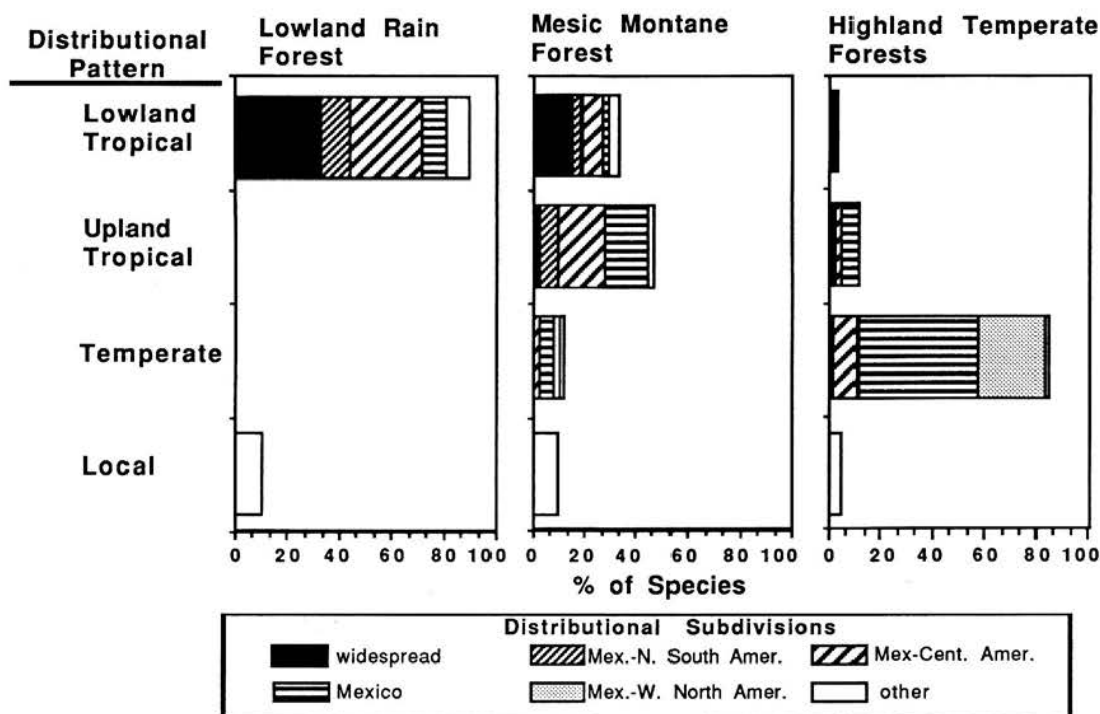


Fig. 4. Comparison of distributional patterns of species of Scolytidae and Platypodidae of mesic montane forest at Xalapa, Veracruz, lowland rain forest (Uxpanapa, Mexico [Atkinson & Equihua 1986a]), and highland temperate forests (Valley of Mexico [Atkinson & Equihua 1985a]).

mesic montane forest can be separated into three components: wide-ranging lowland tropical species which are able to tolerate cooler climates; temperate species, most of which are widely distributed in the Mexican Plateau–western United States; and species belonging to groups that are most prolific in upland tropical habitats and are restricted to Mesoamerican upland areas. Given the current incomplete state of knowledge of scolytid phylogeny (there are no resolved phylogenies for any genus or tribe) and the lack of information on distributional patterns in South America, it is impossible to reach any strong conclusions about the origin of this mesic montane element in the Scolytidae. Nonetheless, some speculative suggestions are proposed based on geological evidence and distributional patterns of other groups of organisms.

The wide distributions of the first group, species in the lowland rain forest fauna (including the more limited numbers which are also found in the mesic montane forest), suggest that the majority of these dispersed from South America into suitable lowland humid habitats along a continuous dispersal route with little or no differentiation after the relatively recent closure of the Isthmus of Panama (Coney 1982). This is the most widely accepted scenario for the current distribution of rain forest plants in Mexico and Central America (Raven & Axelrod 1974, Gentry 1982, Rzedowski 1978). The genera and species of scolytids found in the high-

land temperate forests in central Mexico, the second group, are widely distributed in western North America or derived from formerly widespread taxa. This is similar to the pattern presented for other insect groups (Halffter 1987) and for temperate plants (Rzedowski 1978, Graham 1973, Furlow 1987). The current fragmentation of the highland temperate forests in Mexico and the southwestern United States results from the retreat of a more widespread flora and fauna to more restricted montane areas following unfavorable climatic changes (e.g., increasingly xeric conditions [Graham 1973, Furlow 1987]). The breakup of the nearctic flora and fauna in Mexico and the southwestern United States has resulted in extensive speciation because of vicariance and possibly to subsequent dispersals. This scenario would explain the more geographically restricted ranges of temperate highland species by comparison with the wide distributions of lowland tropical species.

The third group, those genera characteristic of mesic montane forest, has apparently dispersed northwards from South America, independently of the lowland fauna, along the discontinuous Mesoamerican highlands, which are separated by several important lowland barriers, some of which might not have been barriers during periods of cooler climate (e.g., Graham 1973). This would explain the greater geographic restriction of species in this group, and the strong affinities to montane

Central America. The lack of species in common with the Andean region probably results from there never having been any highland connection between the Andes and montane Central America. Halffter (1987) stated that the Mesoamerican distribution pattern in insects resulted from migration and subsequent radiation and dispersal of lowland tropical and nearctic elements that colonized the highlands of Nuclear Central America and that there is little indication of Andean affinities. Although some scolytid groups might fit Halffter's paradigm, current distributional patterns of typically mesic montane genera suggest that these are most closely related to Andean groups that have undergone a secondary radiation in montane Mesoamerica, similar to patterns observed in many plant taxa (Gentry 1982).

Graham (1973) has pointed out the strong floristic similarities between the mesic hardwood forests of the mountains of eastern Mexico and of temperate eastern North America, particularly in canopy and understory trees. He suggested that this might be the result of a relatively recent connection between these disjunct areas during a period of cooler, moister climate in the southwestern United States, which permitted the southward movement of plants. Furlow (1987) suggests that this similarity is based on the differential extinction of an older, wider-ranging flora, from most of the southwestern United States and mountains of western Mexico. Although there are some scolytid species common to both areas or forming vicariant pairs, most of these are also distributed in other parts of Mexico and the United States. Certainly, there is no similarity between the scolytid faunas comparable to that of the floras. Most of the existing similarity is probably due to northward dispersal of neotropical and circumtropical taxa into the southeastern United States rather than to southward dispersal of nearctic taxa. This is the opposite of the floristic pattern.

Biology. Most species present are ambrosia beetles (Table 2). These beetles feed on ectosymbiotic fungi which they introduce into their tunnels and cultivate in the wood of their hosts (xylomycetophagy). Phloem-feeders, true bark beetles in the ecological sense, are next in number of species, followed by those species which bore into the pith of twigs and small branches (myelophagy). A much smaller number of species feeds directly on sapwood of their hosts (xylophagy). In all areas whose scolytid faunas have been studied, most species are either phloem-feeders or ambrosia-feeders and the Xalapa fauna is not unusual in this regard (Fig. 5). The large number of pith-feeding species is unusual. Most of these are species of *Cnesinus* (Bothrostermini), a genus which is most speciose in upland neotropical areas. With respect to the relative balance of phloem-feeders and ambrosia-feeders, the mesic montane fauna more nearly resembles that of lowland rain forest than it does that of highland temperate forests. The high proportion

Table 2. Feeding habits and degree of host specificity of 108 species of Scolytidae and Platypodidae in mesic montane forest in the vicinity of Xalapa, Veracruz, Mexico

Degree of specificity	Feeding habit ^a							Total
	P	XM	X	H	M	S	?	
Monophagy	14	6	2	1	2	—	—	25
Oligophagy	5	2	2	2	—	—	—	11
Polyphagy	2	42	2	—	14	—	—	60
Unknown	2	6	2	—	—	1	1	12
Total	23	56	8	8	16	1	1	108

^a Values are number of species. P, phloeophagy; XM, xylomycetophagy; X, xylophagy; M, myelophagy; H, herbiphagy; S, spermatophagy; ?, unknown.

of ambrosia beetles in both habitats is probably related to the constant, high ambient humidity which is favorable to the growth of the ectosymbiotic fungi (Atkinson & Equihua 1986a). The apparent ecological similarity obscures important taxonomic differences. In both areas most ambrosia beetles belong to the Platypodidae, Xyleborini, and Corthylini, but the Platypodidae and Xyleborini are much better represented in lowland rain forest (Fig. 2) whereas the Corthylini are best represented in mesic montane forest. Most species of Xyleborini and Platypodidae collected in the Xalapa area were also collected at the lowland rain forest site or are known from similar sites. Virtually no corthyline ambrosia beetles were common to the two sites, even though many of the same genera were represented. Most phloem-feeding species are in the genera best represented in highland temperate forests (e.g., *Pityophthorus*, *Pseudopityophthorus*, *Pseudothysanoes*) rather than in lowland tropical forest. Phloem-feeding genera such as *Scolytodes*, *Scolytus*, and *Araptus*, all conspicuous elements of the lowland neotropical fauna, are poorly represented in the mesic montane fauna.

For purposes of this discussion, species which are restricted to hosts in a single genus are considered monophagous, those found in a single family are considered oligophagous, and those which breed in unrelated hosts in different families are considered polyphagous. Strict monophagy (i.e., restriction to a single host species) is relatively uncommon among scolytids. Most species will breed in several or all congeneric hosts when more than one species of potential host occurs locally. Difficulties in accurate identification of dead trees and branches in which most collections are made makes a more precise breakdown of host-specificity classes impractical.

There is a strong relationship between feeding habits and degree of host specificity (Table 2). Phloem-feeding species tend to be strongly host-specific (at least at the genus level), while ambrosia-feeders and pith-feeders tend to be very polyphagous. This pattern is similar to that in other temperate and tropical areas (Beaver 1979; Atkinson & Equihua 1986a,b; Deyrup & Atkinson 1987; Estrada & Atkinson in press). Phloem-feeding scolytids feed directly on living or moribund tissues

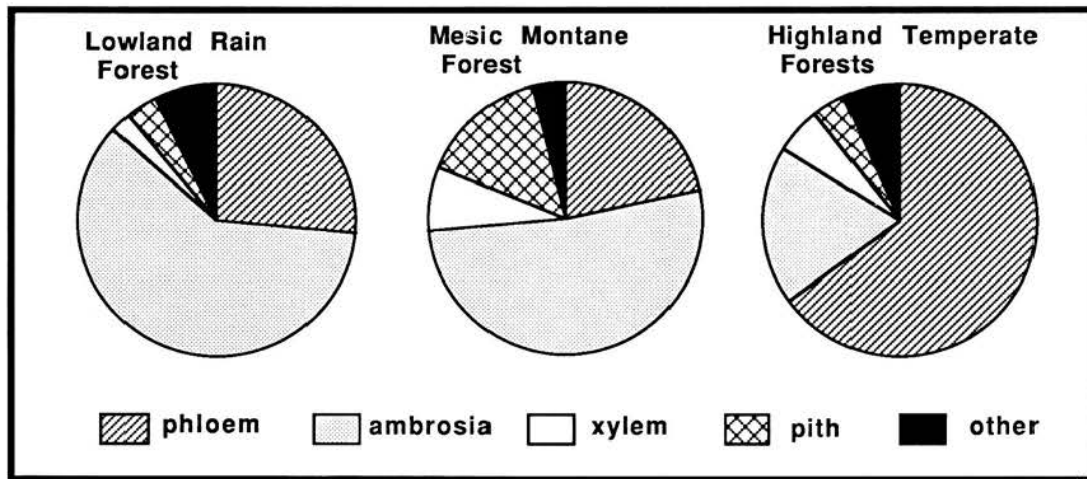


Fig. 5. Comparison of feeding habits of Scolytidae and Platypodidae of mesic montane forest at Xalapa, Veracruz, lowland rain forest (Uxpanapa, Mexico [Atkinson & Equihua 1986a]), and highland temperate forests (Valley of Mexico [Atkinson & Equihua 1985a]).

and are exposed to active host defenses, principally latexes and resins. Specificity of host defenses has probably acted to maintain host specificity on the part of associated phloeophages. Ambrosia beetles, on the other hand, make their tunnels in the sapwood and, less commonly, in the heartwood, mostly composed of dead cells without active defenses. In addition, they do not actually feed directly on the wood, but on their fungal associates. Apparently these fungal symbionts are polyphagous and probably mediate the effects of toxic allelochemicals which might be present in host tissues. Polyphagy in pith-feeding scolytids suggests that the pith of the hosts they breed in is not strongly defended.

A very noticeable aspect of the relationship between the scolytid fauna and the flora in mesic montane forest is that most woody plants do not have host-specific associates. Although host-specialists are few in number with respect to the available plant diversity, host generalist ambrosia beetles and pith borers are ubiquitous. Virtually no twig, branch, or tree dies, falls, or is cut in this community without prompt attack by several of these species. Beaver (1979) and Atkinson & Equihua (1986a) have suggested that low specificity (i.e., relative scarcity of host specialists) among rain forest scolytids in the New and Old World tropics may be related to the very high diversity of these forests, with the consequent rarity of individuals of a given potential host species. Mesic montane forest in Xalapa and other parts of Mexico is more diverse floristically than most highland temperate forests, but not nearly so diverse as humid lowland tropical forests. Atkinson & Equihua (1986b) observed that most host-specific scolytids in dry tropical forest are associated with resinous or lactiferous hosts. A subjective impression of mesic montane forest in Mexico is that resinous and lactiferous hosts are less common than in other plant com-

munities. Ten of the 25 monophages found in the Xalapa region were associated with oaks. Although oaks do not produce resin or latex, they are the dominant forest trees locally. This suggests that both host abundance and host characteristics may be important in understanding scolytid-plant interactions at the species and community level.

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Appendix

This checklist is based mostly on collections made by the authors and collaborators (Armando Equihua M., in particular). The following information is included for each species: valid name, feeding habit (p, phloeophagous; xm, xylomycetophagous; x, xylophagous; m, myelophagous; h, herbiphagous; s, spermatophagous: terms from Wood [1982]), reproductive system (mg, monogynous; bg, bigynous; pg, polygynous; ipg, inbred polygynous: terms from Kirkendall [1983]), degree of host specificity (mo, monophagous; ol, oligophagous; po, polyphagous;

?, unknown: defined in text) and geographic distribution. Distributions are taken from Atkinson & Equihua (1985a,b,c, 1986a), Atkinson et al. (1986a,b), Equihua & Atkinson (1986, 1987), Estrada & Atkinson (1989), Schedl (1940, 1972), and Wood (1982). Locality, host plant, collection number (not present in all cases; prefix "F" indicates collections by F. A. Noguera, prefix "S" indicates collections by T.H.A.) are included for each record; data are grouped by locality, which is not repeated. Records are separated by semicolons. Species reported for the first time from the state of Veracruz are indicated by an asterisk in the distribution; new

records for Mexico are indicated by a double asterisk. Significant new host records are indicated by a triple asterisk. Comments are included on some species when these represent significant new information. Descriptive terms for galleries follow Wood (1982). Subfamilies and tribes are arranged according to Wood (1986b); genera and species are ordered alphabetically.

Platypodidae

1. *Platypus excisus* Chapuis (xm, mg, ol). Lowland Mexico to Brazil. Xalapa, *Citrus sinensis* (L.) Osbeck, F-43; F-107; *Rhamnus capraefolia* Schlecht., F-58; Jilotepec, *Inga vera* Willd., F-75; Briones, *I. sp.*, F-80; Coatepec, *I. sp.*, S-903; Vista Hermosa, *I. sp.* For the most part this species limits its attacks to leguminous hosts (Atkinson & Equihua 1986a, Atkinson et al. 1986a, Equihua & Atkinson 1986). Collected in material from 5–70 cm diam.

2. *Platypus godmani* Blandford (xm, mg, po). Lowland Mexico (Veracruz), Guatemala. Xalapa, *Heliocarpus appendiculatus* Turcz., F-42. Also known from the Uxpanapa region from several unrelated hosts (as *Platypus sp. 1*, Atkinson & Equihua 1986a).

3. *Platypus segnis* Chapuis (xm, mg, po). Mexico* to Brazil. Xalapa, *Heliocarpus sp.*, F-24; *Ficus elastica* Roxb. ex Hornem., F-105. Collected in branches and trunks from 9–30 cm.

4. *Platypus sp. 1* (xm, mg, ?). Dist. unknown. Xalapa, *Quercus sp.*, F-15.

5. *Platypus sp. 2* (xm, mg, po). Dist. unknown. Xalapa, *Heliocarpus sp.*, F-24; *H. sp.*, F-23; *H. sp.*, F-68. This species has also been collected from Oaxaca (as *Platypus sp. 4*, Atkinson & Equihua 1986a) and Morelos (as *Platypus sp.*, Atkinson et al. 1986a) from a variety of unrelated hosts.

Scolytidae Hylesininae

Hylesinini

6. *Hylesinus caseariae* Wood (p, mg, mo?). Mexico (known only from Xalapa area). Acajete, *Casearia sp.*, F-92. Recently initiated attacks were observed in the phloem of small branches (1.5–3 cm diam). Although Wood's description (1986a) contrasts this species exclusively with *H. californicus* (Swaine), it most nearly resembles *H. guatemalensis* Wood, from which it differs only slightly.

Tomicini

7. *Xylechinus marmoratus* Blandford (p, mg, mo). Mexico**, (Veracruz), Guatemala. Xalapa, *Oreopanax xalapensis* (HBK) Decne. & Planchon***, F-154. Collected in branches, 2–5 cm diam. Gallery transverse, biramous, with clearly marked egg niches.

Bothrostermini

8. *Bothrostermus foveatus* (Blackman) (xm, ? males unknown, po). Mexico (Veracruz, Oaxaca), Costa Rica. El Castillo, S-920.

9. *Cnesinus costulatus* Blandford (m, mg, po). Mexico (Oaxaca, Veracruz*) to Colombia. San Andrés, *Persea americana* Mill., F-87; Xalapa, *P. americana*, F-111; Olite, *P. americana*, F-116; Banderilla, *P. americana*, F-132. The galleries of all species of this genus collected in this study were similar. The galleries are axial, within the pith of twigs, vines, and small branches, extending to both sides of the entrance.

10. *Cnesinus degener* Wood (m, mg, po). Mexico (Veracruz, Oaxaca). Naolinco, *Sechium edule* (Jacq.) Swartz***, F-120.

11. *Cnesinus electinus* Wood (m, mg, mo). Mexico (Jalisco, Veracruz*). Olite, *Persea americana*, F-116.

12. *Cnesinus elegans* Blandford (m, mg, po). Mexico (Puebla, Veracruz) to Panama. Xalapa, *Struthanthus sp.****, F-112; F-125; *Vitis sp.****, F-71; Briones, *Inga sp.****, F-81; La Joya, *Rosa sp.****, S-906. Also reported from Xalapa by Wood (1982).

13. *Cnesinus equihuai* Wood (m, mg, mo). Mexico (Puebla, Veracruz*). Coacoatzintla, F-13; El Castillo, *Croton sp.****, F-109; Jilotepec, *C. sp.*, S-926.

14. *Cnesinus gracilis* Blandford (m, mg, po). Mexico** (Veracruz), Honduras to Colombia. Xalapa, F-71; *Persea americana****, F-111; *Struthanthus sp.****, F-112.

15. *Cnesinus myelitis* Wood (m, mg, po). Mexico (Puebla, Veracruz*) to Panama. Olite, *Persea americana****, F-116.

16. *Cnesinus noguerae* Atkinson 1989 (m, mg, po). Mexico (known only from Xalapa and Tuxpan, Veracruz). Xalapa, *Psittacanthus sp.*, F-77.

17. *Cnesinus pullus* Wood (m, mg, mo). Mexico** (Veracruz), Guatemala to Panama. Xalapa, F-4; *Persea americana****, F-111; Olite, *P. americana*, F-116.

18. *Cnesinus punctatus* Blandford (m, mg, po). Mexico (Puebla, Veracruz*) to Panama. Olite, *Persea americana****, F-116.

Phloeotribini

19. *Phloeotribus demessus* Blandford (p, bg, mo). Mexico (Chihuahua, Jalisco, Veracruz) to Panama. Xalapa, *Croton sp.*, F-59. Collected in trunk of dead tree (10 cm diam). Galleries were longitudinal and biramous, rather than transverse as reported by other authors (Wood 1982, Kirkendall 1984, Atkinson & Equihua 1985b). Generally each branch was occupied by a female, with a single male in the entrance. This is the first report of bigyny in this genus. The discrepancy in observations by different authors may be due to behavioral differences in local populations, unusual conditions when we

or they collected this species, or morphologically indistinguishable species.

20. *Phloeotribus pruni* Wood (p, mg, mo). Western U.S. and Mexico (Chihuahua to Veracruz* and Chiapas). Xalapa, *Prunus persica* (L.) Batsch., F-27; *P. persica*, F-40; Piletas, *P. serotina* var. *capuli* (Cav.) McVaugh, F-104; Banderilla, *P. serotina* var. *capuli*, F-114.

Phloeosinini

21. *Chramesus chapuisii* LeConte (p, mg, ol). Eastern U.S. and Mexico (San Luis Potosí, Veracruz*). Xalapa, *Rhamnus capraefolia****, F-58; Naolinco, F-123; Coacoatzintla, F-147. Gallery longitudinal, uniramous.

22. *Chramesus rotundatus* (Chapuis) (x, mg, mo). Mexico** (Veracruz) and Northern South America. Xalapa, F-21; *Inga vera****, F-106; Jilotepec, F-76; Coatepec, *I. sp.*, F-81; *I. sp.*, F-150; Briones, *I. sp.*, F-83. Galleries longitudinal, biramous, in sapwood. One branch was usually more developed than the other in most galleries.

23. *Chramesus xalapae* Atkinson 1989 (x, mg, ?). Mexico (known only from Xalapa). Xalapa, F-65. Undescribed species near *C. annectans* (Wood). Collected in dry branches (1–2.5 cm diam); galleries in xylem, longitudinal, occasionally forked.

Hypoborini

24. *Chaetophloeus struthanthi* Wood (x, mg, ol). Mexico (Jalisco, Puebla, Veracruz, Oaxaca). Banderilla, *Psittacanthus schiedeana* (Cham. & Schlecht.) Blume***, F-97; Piletas, *Struthanthus deppeanus* (Cham. & Schlecht.) Blume***, F-103. Galleries in wood, usually longitudinal, uniramous. Occasionally biramous galleries were observed, but with one arm longer than the other.

Scolytinae

Scolytini

25. *Scolytus dimidiatus* Chapuis (p, bg, ol). Mexico (Veracruz) to Venezuela and Cuba. Xalapa, *Rhamnus capraefolia****, F-58; Naolinco, F-123; Coacoatzintla, F-147. Collected in material from 3–8 cm diam. Galleries in phloem, but scoring sapwood; transverse, biramous. This species is generally associated with leguminous hosts (Wood 1982).

Ctenophorini

26. *Scolytodes maurus* (Blandford) (h, mg, mo). Mexico (Veracruz, Oaxaca, Campeche), Panama and Venezuela. Coatepec, petioles of *Cecropia* sp., S-909. In spongy pith at base of fallen petioles.

Micracini

27. *Hylocurus atkinsoni* Wood (x, bg, ol). Mexico (known only from Xalapa). El Castillo, *Acacia pen-*

natula (Schlecht. & Cham.) Benth., S-917; Banderilla, *Leucaena pulverulenta* (Schlecht.) Benth., F-96. Found in small branches 3 cm diam. Gallery similar to that of *Micracis ovatus* described below.

28. *Micracis festivus* Wood (x, bg, po). Mexico (Veracruz*) to Honduras. Coatepec, *Inga* sp., S-902.

29. *Micracis lignator* Blackman, 1928 (x, bg, mo). US (Arizona), Mexico (Nuevo Leon, Durango to Veracruz*, Oaxaca and Guerrero). Naolinco, F-122. Gallery similar to that of *M. ovatus*. Found in small branches 1–3 cm diam.

30. *Micracis ovatus* Wood (x, bg, ?). Mexico (Puebla, Veracruz*). Xalapa, F-47; F-127; Banderilla, F-115. The gallery consists of a short entrance tunnel bored directly into wood, which perpendicularly joins a biramous, longitudinal tunnel at a depth of about 5 mm. At both extremes of the longitudinal portion of the gallery, females construct "V" shaped oviposition galleries. The entire system resembles two "Y's" joined at the bases with a total of four egg galleries. Eggs are deposited in individual niches.

31. *Phloeocleptus caudatus* Wood (p, bg, mo). Mexico (Puebla, Veracruz*). Xalapa, F-78; *Persea americana*, F-111; San Andres, *P. americana*, F-87; Olite, *P. americana*, F-116; Naolinco, *P. americana*, F-118; Banderilla, *P. americana*, F-132; Coacoatzintla, *P. americana*, F-136. Found in material ranging from 0.5–15 cm diam. Galleries longitudinal, biramous, eggs deposited in niches.

32. *Pseudothysanoes contrarius* Wood (p, bg, ol). Mexico (Veracruz*, Chiapas). El Castillo, *Inga* sp.***, F-9; *Acacia pennatula****, S-907; Consolapa, *A. pennatula*, F-73; Briones, *Inga* sp., F-81. Galleries longitudinal, biramous. Egg galleries filled with frass; eggs packed in frass in gallery, not in niches. Collected in material from 3–10 cm diam.

33. *Pseudothysanoes fimbriatus* Wood (p, bg, mo). Mexico (Puebla, Veracruz*). Banderilla, *Phoradendron calyculatum* Trel.***, F-98; *P. falcatum****, F-99; 5 km al Oeste de Acajete, *P. sp.*, S-893. Found in material <1 cm diam; gallery similar to that of *P. contrarius*.

34. *Thysanoes fimbriicornis* Le Conte (x, bg, po). Eastern U.S. and Mexico (Durango, Hidalgo, Tamaulipas, Veracruz). El Castillo, *Cestrum* sp., S-916. Gallery similar to that described of *Micracis ovatus*.

Dryocoetini

35. *Dendrocranulus macilentus* (Blandford) (h?, mg?, ol?). Mexico (Veracruz), Costa Rica. Reported from Xalapa by Wood (1982).

36. *Dendrocranulus mexicanus* Wood (h, mg, ol?). Mexico (known only from Xalapa). Naolinco, *Secchium edule*, F-120. Galleries axial, biramous; entrances in nodes of cucurbit vine.

Xyleborini

37. *Ambrosiodmus coffeicus* (Schedl) (xm, ipg, po). Mexico** (Veracruz), Northern South Amer-

ica. Xalapa, 16-VIII-83, 1360 m, *Quercus* sp., F-33; *Heliocarpus appendiculatus*, F-46; F-55; *Quercus* sp., F-62; *Q.* sp., F-64. Collected in material ranging from 4–20 cm diam.

38. *Ambrosiodmus ferus* Wood (xm, ipg, mo?). Mexico (known only from Xalapa). Xalapa, *Quercus* sp., F-33; *Q.* sp., F-110; F-155. In branches, 2–8 cm diam. Treated here as monophagous although more hosts are probably used.

39. *Ambrosiodmus rugicollis* (Blandford) (xm, ipg, po). Mexico (Puebla, Veracruz), Guatemala. Xalapa, *Quercus* sp., F-33; F-155. In branches, 3–8 cm diam.

40. *Ambrosiodmus rusticus* (Wood) (xm, ipg, po). Mexico (Morelos, Puebla, Veracruz*, Chiapas). Xalapa, *Quercus* sp., P-33; F-34; F-50; F-110; Banderilla, *Ficus elastica*, F-113. In material from 2–8 cm diam.

41. *Coptoborus pseudotenius* (Schedl) (xm, ipg, po). Southeastern Mexico to Venezuela and Brazil. Xalapa, F-69; Consolapa, *Acacia pennatula*, F-79.

42. *Coptoborus vespatorius* (Schedl) (xm, ipg, po). Mexico (Veracruz) to Argentina. Vista Hermosa, *Inga* sp.

43. *Dryocoetoides capucinus* (Eichhoff) (xm, ipg, po). Lowland Mexico to Peru and Brazil. Xalapa, F-1; F-28; F-38; F-47; *Leucaena* sp., F-85; Coatepec, *Acacia pennatula*, F-79; F-138; Briones, *Inga* sp., F-83; *I.* sp., F-81. In branches 2–5 cm diam.

44. *Xyleborinus gracilis* (Eichhoff) (xm, ipg, po). U.S. (Florida), Mexico (Veracruz, Oaxaca, Campeche) to Venezuela. Xalapa, *Quercus* sp., F-63.

45. *Xyleborus affinis* Eichhoff (xm, ipg, po). Eastern U.S. to Argentina, Old World Tropics. Xalapa, *Leucaena pulverulenta*, F-41; *L. pulverulenta*, F-44; Briones, *Inga vera*, F-82.

46. *Xyleborus discretus* Eggers (xm, ipg, po). Mexico (Veracruz) to Cayenne and Peru. Vista Hermosa, *Inga* sp., S-713.

47. *Xyleborus ferrugineus* (Fabricius) (xm, ipg, po). U.S., Mexico, to Argentina, Africa, Hawaii, Micronesia. Xalapa, *Quercus* sp., F-15; F-16; *Heliocarpus* sp., F-24; F-38; F-39; F-53; *Quercus* sp., F-110.

48. *Xyleborus horridus* Eichhoff (xm, ipg, po). U.S. (Texas), Mexico (Tamaulipas, Veracruz, Campeche), Guatemala. Vista Hermosa; *Inga* sp., S-713.

49. *Xyleborus imbellis* Blandford (xm, ipg, po). Mexico (Veracruz) to El Salvador. Vista Hermosa, *Inga* sp., S-713.

50. *Xyleborus posticus* Eichhoff (xm, ipg, po). Southeastern Mexico to Brazil. Xalapa, *Heliocarpus* sp., F-24; *Cupressus lindleyi* Klotzsch., F-66; *Leucaena pulverulenta*, F-70; *Ficus elastica*, F-105; F-128; Banderilla, *Erythrina americana* Mill., F-94.

51. *Xyleborus squamulatus* Eichhoff (xm, ipg, po?). Mexico (Veracruz*, Chiapas) to Brazil. Xalapa, pitfall trap with ethanol, F-144; pitfall trap with ethanol, F-151. No hosts have been reported for this species but it is probably polyphagous like other members of the genus.

52. *Xyleborus volvulus* (Fabricius, 1775) (xm, ipg, po). U.S. (Florida), Mexico to Argentina, Old World Tropics. Xalapa, *Leucaena pulverulenta*, F-70; El Castillo, *Acacia pennatula*, S-917.

Cryphalini

53. *Hypothenemus californicus* Hopkins (p-h, ipg, po). Southeastern U.S., lowland Mexico, Africa. El Castillo, *Phoradendron* sp., S-915.

54. *Hypothenemus crudiae* (Panzer) (m, ipg, po). Southeast U.S. to Argentina, Old World Tropics. El Castillo, F-12; S-915; Xalapa, F-149; Coatepec, *Inga* sp., S-902.

55. *Hypothenemus erectus* Le Conte (m, ipg, po). U.S. (Texas) to Honduras and Venezuela, Cuba, Africa. El Castillo, F-12; S-920; Xalapa, *Vitis* sp., F-71; *Inga vera*, F-106; Olite, *Persea americana*, F-116.

56. *Hypothenemus eruditus* Westwood (p-h, ipg, po). Southern U.S. to Argentina, Cosmopolitan. Xalapa, *Prunus persica*, F-27; *Rhus radicans* L., F-101; F-149; *Rhus radicans*, F-156; El Castillo, S-916; Jilotepec, S-926.

57. *Hypothenemus interstitialis* (Hopkins) (m, ipg, po). Eastern U.S., Mexico, Central America, and Jamaica. Xalapa, F-71; *Struthanthus* sp., F-89; *Tithonia* sp., F-140; Coatepec, *Inga* sp., F-81; El Castillo, S-920.

58. *Hypothenemus seriatus* (Eichhoff) (m, ipg, po). Southeastern U.S. to Brazil, Old World Tropics. Coacoatzintla, F-14.

59. *Hypothenemus squamosus* (Hopkins, 1915) (m, ipg, po). U.S. (Florida), Mexico (Colima, Tamaulipas, Veracruz) and Cuba. El Castillo, *Phoradendron* sp., S-915.

60. *Stegomerus mexicanus* Wood, 1967 (p, mg, ?). Mexico (Michoacan, Puebla, Veracruz*). Xalapa, *Passiflora* sp.***, F-126. Collected in stems 1-cm diam. Galleries in phloem, generally longitudinal, biramous.

Corthylini: Pityophthorina

61. *Araptus aztecus* Wood, 1971 (p, bg, ol). Mexico (Nayarit, San Luis Potosí, Veracruz*, Campeche). Xalapa, *Nectandra* sp., F-22; F-56; *Quercus* sp.**, F-60. Collected in stems 4–15 cm diam. Galleries transverse, biramous; each with one male and two females. This is the first report of bigyny in this genus. Known from Lauraceae (*Nectandra* sp., Atkinson & Equihua 1985c; *Licaria peckii* (I. M. Johnston) Kosterm., Estrada & Atkinson 1987, the record from *Quercus* may represent an "accidental host" (i.e., one in which breeding does not occur).

62. *Araptus confinis* (Blandford) (? , ? , ?). Mexico (Veracruz) to Guatemala. Reported from Xalapa by Wood (1982).

63. *Araptus deyrollei* (Blandford) (s, hpg, ?) Mexico (Veracruz*) to Honduras. Coacoatzintla, *Gonolobus* sp.***, F-148. Collected in dry fruits of milkweed vine.

64. *Araptus tabogae* (Blackman) (m, ?, po). Mexico (Jalisco, Veracruz, Campeche) *Gonolobus* sp., F-145. In stems of milkweed vine.

65. *Pityophthorus alni* Blackman (p, hpg, mo). Mexico (Hidalgo, Puebla, Veracruz). Naolinco, *Alnus acuminata****, S-929; Also reported from Xalapa by Wood (1982) in alder.

66. *Pityophthorus atomus* Wood (p, hpg, ol). Mexico (Veracruz to Oaxaca). Xalapa, *Tithonia* sp.***, F-130; *T.* sp., F-140; *Vernonia* sp.***, F-143. Found in phloem of 1–2 cm diam stems of wood compositae.

67. *Pityophthorus hyllocuroides* Wood (p, hpg, mo). Mexico (Hidalgo, Veracruz*). Xalapa, *Tithonia* sp.***, F-130; *T.* sp., F-140. Found in phloem of 1–2 cm diam stems of woody compositae.

68. *Pityophthorus paulus* Wood (p, hpg, mo). Mexico (Chihuahua to Veracruz and Chiapas). El Castillo, F-67; S-918; Le Estanzuela, S-294. Breeds in branches of composite shrubs of the genus *Senecio* (Atkinson & Equihua 1985a,c; Atkinson et al. 1986a).

69. *Pityophthorus tutulus* Bright (p, hpg, mo). Mexico (known only from Xalapa). Xalapa, *Rhus radicans*, F-100. Found in small stems 0.5 cm diam of poison ivy vines. Gallery radial; up to four females per male.

70. *Pseudopityophthorus granulifer* Wood (p, mg, mo). Mexico (Veracruz*, Chiapas) to Honduras. Xalapa, *Quercus* sp., FANM-49; Naolinco, *Q.* sp., F-121; El Castillo, S-919.

71. *Pseudopityophthorus opacicollis* Blackman (p, mg, mo). U.S. (Arizona) to Mexico (Nuevo Leon and Durango to Veracruz* and Chiapas). El Castillo, *Quercus* sp., F-11; *Q.* sp., S-919.

72. *Pseudopityophthorus singularis* Wood (p, mg, mo). Mexico (Veracruz to Chiapas). Xalapa, *Quercus* sp., F-17; F-54; Banderilla, *Q.* sp., F-35; El Castillo, *Q.* sp., F-35; *Q.* sp., S-919.

73. *Pseudopityophthorus virilis* Wood (p, mg, mo). Mexico (Hidalgo, Veracruz). Piletas, F-93. Found in oaks (Wood 1982, Atkinson & Equihua 1985c).

74. *Pseudopityophthorus xalapae* Wood (p, mg, mo). Mexico (known only from Xalapa). Xalapa, F-3; F-30; *Quercus* sp., F-33; F-34; Banderilla, F-36; *Q.* sp., F-95. Found in 2–15 cm diam host material. Galleries transverse, biramous, made by a single mated pair.

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75. *Amphicranus brevipennis* Blandford (xm, ?, po?). Mexico** (Veracruz), Guatemala, Costa Rica. Vista Hermosa, *Inga* sp.***, S-713.

76. *Amphicranus filiformis* Blandford (xm, mg, po). Mexico (Guerrero, Veracruz*, Chiapas). Banderilla, *Quercus laurina*H&B***, F-37; Xalapa, F-53. Gallery circular, following growth rings.

77. *Amphicranus stenodermus* Schedl (xm, mg, po). Mexico (Nayarit, Veracruz). Xalapa, *Leucaena pulverulenta****, F-45; *Quercus* sp.***, F-110.

78. *Amphicranus* sp. (undescribed) (xm, ?, ?). Mexico (known only from Xalapa). Xalapa, *Leucaena pulverulenta*, F-45.

79. *Corthylyclon aztecum* (Bright) (xm, mg, po). Mexico (Puebla, Veracruz*) to Costa Rica. Acajete, *Miconia glaberrima* (Schlecht.) Naud.***, F-90.

80. *Corthylocurus mexicanus* (Schedl) (xm, mg, po). Mexico (Veracruz) to Panama. Acajete, *Miconia glaberrima****, FANM-90. Reported from Xalapa by Wood (1982).

81. *Corthylus comatus* Blandford (xm, mg, po). Mexico (Puebla, Veracruz*) to Panama. Xalapa, F-8; F-84; pitfall trap with ethanol, F-144; pitfall trap with ethanol, F-146; pitfall trap with ethanol, F-151; F-155; pitfall trap with ethanol, F-142; Banderilla, *Ficus elastica****, F-113; *F. elastica*, F-131; Olite, *Persea americana****, F-116; Plan de Sedeño, *Alnus jorullensis* HBK***, F-117; Coatepec, F-139; Naolinco, *A.* sp., S-929. Generally galleries of this species were circular, following growth rings of hosts, extending on either side of the entrance tunnel and were made by a single mated pair. Several galleries were found with up to three circular branches leading off the entrance tunnel, each with a female inside it, but with a single male guarding the common entrance. Occasional harem polygyny has also been reported for *Corthylus columbianus* Hopkins (Nord 1972).

82. *Corthylus consimilis* Wood (xm, mg, po). Mexico (Puebla, Veracruz*). Xalapa, F-19; pitfall trap with ethanol, F-86.

83. *Corthylus flagellifer* Blandford (xm, mg, po). Mexico (Nayarit, Veracruz) to Guatemala. Xalapa, *Leucaena pulverulenta****, F-41; pitfall trap with ethanol, F-146; Briones, *Inga* sp.***, F-81; Coatepec, F-139.

84. *Corthylus fuscus* Blandford (xm, mg, po). Mexico (Distrito Federal Mexico, Veracruz*) to El Salvador. Xalapa, pitfall trap with ethanol, F-86; pitfall trap with ethanol, F-142; pitfall trap with ethanol, F-146.

85. *Corthylus sentus* Wood (xm, mg, po). Mexico** (Veracruz), Guatemala, Costa Rica. La Joya, *Rosa* sp.***, S-906.

86. *Corthylus senticosus* Wood (xm, mg, ?). Mexico (known only from Xalapa). Xalapa, *Psittacanthus schiedianus*, F-77.

87. *Corthylus spinifer* Schwarz (xm, mg, po). Florida, Antilles, lowland Mexico to Brazil. Coatepec, *Inga* sp., F-81. Wood (personal communication) has indicated that this name is a junior synonym of *C. papulans* Eichhoff.

88. *Corthylus suturifer* Schedl (xm, mg, po). Mexico (Veracruz). Coatepec, *Inga* sp.***, F-81.

89. *Corthylus* sp. (undescribed) (xm, mg, ?). Mexico (known only from Xalapa). Xalapa, F-52; San Andres, *Cnidoscopus* sp., F-88. Gallery circular, typical of genus.

90. *Gnathotrichus obscurus* Wood (xm, mg, mo). Mexico (Tlaxcala, Puebla, Veracruz*). Xalapa, F-7; *Quercus* sp., F-63; *Q.* sp., F-110; F-129.

91. *Gnathotrupes bituberculatus* Blandford (xm,

mg, ?). Mexico** (Veracruz), Guatemala. Coatepec, *Inga* sp.***, S-903.

92. *Microcorthylus demissus* Wood (xm, mg, po). Mexico (Puebla, Veracruz*), Costa Rica. Banderilla, F-8; Xalapa, F-38; *Vitis* sp.***, F-71.

93. *Microcorthylus vesus* Wood (xm, mg, po). Mexico (Puebla, Veracruz), Guatemala. Xalapa, F-29; F-55; Olite, *Persea americana****, F-116. Gallery circular following growth rings with larval "cradles" above and below, similar to those of most species of *Corthylus*.

94. *Microcorthylus vicinus* Wood (xm, mg, po). Mexico (Veracruz*, Oaxaca, Chiapas). Acajete, *Miconia glaberrima****, F-90; 5 km al Oeste de Acajete, Banderilla, F-115; Coatepec, F-138; Coacoatzintla, F-135; *Persea americana****, F-136; Xalapa, F-141; La Joya, *Phoradendron****, S-907. Gallery similar to that of *M. vesus*, often in very small host material (<1 cm diam).

95. *Monarthrum corditicum* Wood (xm, hpg, mo). Mexico (Puebla, Hidalgo, Veracruz*). Banderilla, *Quercus laurina****, F-37.

96. *Monarthrum egenum* Blandford (xm, hpg, ol). Mexico (Puebla, Veracruz), Guatemala to Brazil, Vista Hermosa, *Inga* sp.***, Coatepec, *Inga* sp., S-913. This species breeds only in leguminous hosts (Wood 1982; Atkinson & Equihua, 1985c, 1986a).

97. *Monarthrum laterale* (Eichhoff, 1869) (xm, hpg, po). Mexico (Michoacan, Puebla, Veracruz*) to Venezuela. Banderilla, F-133.

98. *Monarthrum lobatum* (Ferrari) (xm, hpg, po). Mexico** (Veracruz) and Guatemala to Venezuela. Xalapa, *Leucaena pulverulenta*, F-41.

99. *Monarthrum luctuosum* (Blandford) (xm, hpg, po). Mexico (Puebla, Veracruz*) to Guatemala. Xalapa, *Leucaena pulverulenta****, F-45; *Quercus* sp., F-110; pitfall trap with ethanol, F-144.

100. *Monarthrum morsum* Wood (xm, hpg, mo). Mexico** (Veracruz), Costa Rica. Xalapa, *Quercus* sp., F-32; *Q.* sp., F-110; F-53; F-19; Banderilla, *Q. laurina****, F-37.

101. *Monarthrum pennatum* (Schedl) (xm, hpg, po). Mexico (Nayarit, Veracruz) to Colombia and Venezuela. Banderilla, *Quercus laurina****, F-37; *Ficus elastica****, F-113; F-133; Xalapa, *Leucaena pulverulenta****, F-41; *L. pulverulenta*, F-44; *L. pulverulenta*, F-70; *L. pulverulenta*, F-45; Naolinco, *Persea americana*, F-118; Coacoatzintla, F-135.

102. *Monarthrum robustum* Schedl (xm, hpg, po). Mexico (Veracruz), Costa Rica and Trinidad. Xalapa, F-19; *Leucaena pulverulenta****, F-41; *L. pulverulenta*, F-45; F-49; *L. pulverulenta*, F-70.

103. *Monarthrum tetradontium* Wood (xm, hpg, mo). Mexico (Jalisco, Morelos, Veracruz*). Xalapa, *Quercus* sp.***, F-32.

104. *Monarthrum validum* (Ferrari) (xm, hpg, mo). Mexico (Puebla, Veracruz), Costa Rica. Xalapa, *Quercus* sp., F-32.

105. *Monarthrum xalapensis* Wood (xm, hpg, ?) Mexico (known only from Xalapa). Xalapa, F-58; *Quercus* sp., F-110.

106. *Tricolus nodifer* Blandford (xm, mg, po). Mexico (Veracruz), Guatemala, Costa Rica. Xalapa, F-5; pitfall trap with ethanol, F-142; pitfall trap with ethanol, F-146.

107. *Tricolus ovicollis* Blandford (xm, mg, po). Mexico (Puebla, Veracruz*), Costa Rica. Acajete, *Miconia glaberrima****, F-90.

108. *Tricolus senex* Schedl (xm, mg, po). Mexico** (Veracruz), Costa Rica to Brazil. Xalapa, F-71; *Miconia glaberrima****, F-153.