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 106 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 Corhylolini and twig borers in the Bothrocternini. 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 (59%) were ambiguously beetles (which feed on ecotrophic
fungi in galleries); phloem-feeders (21.7%) and pith-feeding twig borers (15.7%) were also
abundant. The high percentage of ambiguously beetles is similar to that found in tropical rain
forest in Mexico and other humid tropical areas in the Old and New World. Most ambiguously
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 ecotrophic 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 dis-
tinctive habitat not previously studied. In addition
to listing the species present we analyze their biog-
ecropy and biogeography and compare these patterns
to those of other communities in Mexico.

Mesic montane forest (sensus 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 tempera-
tures without extremes of hot or cold. The most
important factor common to these areas is the fre-
quent occurrence of logs and mists, which reduce
the amount of incident insolation and evapotrans-
piration. This forest type forms an altitudinal trans-
ition 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 cen-
tral Mexico and Central America. Small isolated
patches of mesic montane forest occur in almost
all mountain ranges in Mexico, but the largest con-
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 & Fegulhon 1986a) and Valley of Mexico (Atkinson & Fegulhon 1985a) study areas from which comparative data are taken are also shown.

A continuous 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, Cacaoztintla, Coatepec, Emiliano Zapata, Naolino, and San Andrés, an area of approximately 700 km² (approximate coordinates: 19°26'-19°39'N; 96°31'-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 1,100-1,800 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 (Moest 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 1990), 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 (Usambara, Tanzania [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 cavets 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 Platypodidae 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 Cortylini with 14 genera and 48 species, nearly 50% of the total. Within this group, most genera and species were ambrosia beetles in the subtribe Cortylina, notably Monarthrum (11 species) and Cortylus (9 species). The Cortylini are an important 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), Cryptalini (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., Hylophini, Phloeotribini, and Dryocoetini), and those that predominate in particular sites (e.g., Scolytiini, 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 montane forest in the vicinities of Xalapa, Veracruz, Mexico

<table>
<thead>
<tr>
<th>Affinitya</th>
<th>No. of genera</th>
<th>Genera</th>
</tr>
</thead>
<tbody>
<tr>
<td>Holartic</td>
<td>2</td>
<td>Hylesinus, Pitypsythorusb</td>
</tr>
<tr>
<td>Neartic</td>
<td>2</td>
<td>Gnathotrichus, Pseudopityphorus</td>
</tr>
<tr>
<td>Neotropical</td>
<td>11</td>
<td>Bothroterius, Scytostylus, Hylcocerus, Thynnus, Dryocoetoidea, Arazia, Corvisia, Mieracini, Phloeocoleus, Gnathotrichus, Tricola, Amphicranis, Microstylus, Monarchrhim, Cortylus, Cortylectus, Cortylecanus</td>
</tr>
<tr>
<td>Lowland</td>
<td>6</td>
<td>Bothroteriusrus, Scytostylus, Hylcocerus, Thynnus, Dryocoetoidea, Arazia, Corvisia, Mieracini, Phloeocoleus, Gnathotrichus, Tricola, Amphicranis, Microstylus, Monarchrhim, Cortylus, Cortylectus, Cortylecanus</td>
</tr>
<tr>
<td>Upland</td>
<td>11</td>
<td>Bothroteriusrus, Scytostylus, Hylcocerus, Thynnus, Dryocoetoidea, Arazia, Corvisia, Mieracini, Phloeocoleus, Gnathotrichus, Tricola, Amphicranis, Microstylus, Monarchrhim, Cortylus, Cortylectus, Cortylecanus</td>
</tr>
<tr>
<td>Widespread</td>
<td>5</td>
<td>Charanaeus, Chaetophorinae, Pseudothysanidae, Dendrocanthus, Siegenius</td>
</tr>
<tr>
<td>Circumtropical</td>
<td>5</td>
<td>Ambrosiodmus, Xyleborus, Xyleborinus, Hypohenemus, Platypus</td>
</tr>
<tr>
<td>Other</td>
<td>3</td>
<td>Xyleborinus, Micrandrus, Scolytus</td>
</tr>
</tbody>
</table>

a Based on Wood (1960b) and personal observations.
b Greatest species richness in Neartic 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 Xyleborinus 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 Tomocerini, Phloeosinini, Mieracini, and Pityophthorina. On the other hand some groups, particularly the Bothroterini and the Cortylinae, 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 Hypohenemus 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 (Schell 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 neartic and holartic 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 Bolacosternini (Enchusius) and Cortylinae (Cortylvus, Monarchrhim, Tricola, and Amphicranus). Although there were relatively few species present in the Xalapa area, the genera Xylechus (Tomocerini) and Phloeocoleus (Mieracini) 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 Cortylvus 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): Cortylvus spinifer Schwarz is a widespread lowland species, C. fuscus Bland-
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 circumtropical 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. Halfifer (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 socolytid phylogeny and biogeography is insufficient to reach any conclusions in this regard.

The descriptive biogeographical data presented here suggest that the socolytid fauna associated with
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 highland 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 1967]). 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 neartic 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 neartic 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 (xylomycopephagy). 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 (mycophagous). A much smaller number of species feeds directly on sapwood of their hosts (xylephagy). 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 *Conetinus* (Bothrosternini), 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 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 Corthlini, but the Platypodidae and Xyleborini are much better represented in lowland rain forest (Fig. 2) whereas the Corthlini 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 corthline 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, Pseudophasmas*) rather than in lowland tropical forest. Phloem-feeding genera such as *Scolytodes, Scolytus*, and *Arapus*, 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

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**Table 2. Feeding habits and degree of host specificity of 106 species of Scolytidae and Platypodidae in mesic montane forest in the vicinity of Xalapa, Veracruz, Mexico**

<table>
<thead>
<tr>
<th>Degree of specificity</th>
<th>Feeding habit&lt;sup&gt;a&lt;/sup&gt;</th>
<th>P</th>
<th>XM</th>
<th>X</th>
<th>H</th>
<th>M</th>
<th>S</th>
<th>μ</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Monophagy</td>
<td></td>
<td>14</td>
<td>6</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
<td>25</td>
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<tr>
<td>Oligophagy</td>
<td></td>
<td>5</td>
<td>2</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
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<td>11</td>
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<td>Polyphagy</td>
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<td>14</td>
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<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>12</td>
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<tr>
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<td>56</td>
<td>8</td>
<td>16</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>108</td>
</tr>
</tbody>
</table>

<sup>a</sup>Values are number of species. P, phloemphagy; XM, xylomycopephagy; X, xylephagy; M, mycophagy; H, hemipterphagy; S, spermatophagy; ? unknown.
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 host defenses, principally latexes and resins. Specificity of host defenses has probably acted to maintain host specificity on the part of associated phylophages. Ambrosia beetles, on the other hand, make their tunnels in the sapwood, 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 communities. 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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References Cited

Atkinson, T. H., E. Martinez F., E. Saucedo C. & A. Burgos S. 1986a. Scolytidae y Platypodidae (Co-
leoptera) asociados a selva baja caducifolia y comunidades derivadas en el estado de Morelos, México. Folia Entomol. Mex. 69: 41–82.


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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. phloophagous; x, xylphilophagous; s, spermatophagous) 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 single 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**


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


5. *Platypus* sp. 2 (xm, mg, po). Dist. unknown. Xalapa, *Helicocarpus* 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**

**Hylesiniinae**

**Hylesini**

6. *Hylesinus casearis* 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.

**Tomineini**


**Bothrosterni**


9. *Cnesius costulatus* Blandford (m, mg, po). Mexico (Oaxaca, Veracruz*) to Colombia. San Andrs, *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. *Cnesius degener* Wood (m, mg, po). Mexico (Veracruz, Oaxaca). Naoulineo, *Sechium edule* (Jacq.) Swartz***, F-120.


12. *Cnesius 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-51, La Joya, *Rosa sp.***, S-906. Also reported from Xalapa by Wood (1982).

13. *Cnesius equiurai* Wood (m, mg, mo). Mexico (Puebla, Veracruz*). Coacoazintla, F-18; El Castillo, *Croton* sp.***, F-100; Jilotepec, C. sp., S-926.

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


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


**Phloeotribinae**

19. *Phloeotribus denissus* 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 prunif 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. capulii
(Cav.) McVauh, F-104; Banderilla, P. serotina
var. capulii, F-114.

Phloeosini
21. Chramesus chapuisi LeConte (p, mg, ol).
Eastern U.S. and Mexico (San Luis Potosí, Vera-
cruz*). Xalapa, Rhamnus capraefolia***, F-58;
Naolinco, F-123; Coacoatzintla, F-147. Gallery lon-
gitudinal, 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. anneanticus (Wood).
Collected in dry branches (1-2.5 cm diam); gal-
leries in xylem, longitudinal, occasionally forked.

Hypoborini
24. Chaetophloeus struthanti Wood (x, mg, ol).
Mexico (Jalisco, Puebla, Veracruz, Oaxaca). Ban-
derilla, Psittacanthus schiedeanus (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 sap-
wood; transverse, biramous. This species is gener-
ally associated with leguminous hosts (Wood 1982).

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

Micreini
27. Hyllocerus atkinsoni Wood (x, bg, ol). Mexico
(known only from Xalapa). El Castillo, Acacia pen-
natula (Schlecht. & Cham.) Benth., S-917; Ban-
derilla, Leucaena pumolenta (Schlecht.) Benth.,
F-96. Found in small branches 5 cm diam. Gallery
similar to that of Micraceus ovatus described below.
28. Micraceus festivus Wood (x, bg, po). Mexico
(Veracruz*) to Honduras. Coatepec, Inga sp., S-902.
29. Micraceus ignator 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. Micraceus ovatus Wood (x, bg, ?). Mexico
(Puebla, Veracruz*). Xalapa, F-47; F-127; Ban-
derilla, F-115. The gallery consists of a short en-
trance tunnel bored directly into wood, which per-
pendicularly joins a biramous, longitudinal tunnel
at a depth of about 5 mm. At both extremes of the
longitudinal portion of the gallery, females con-
struct a “Y” 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. ameri-
cana, F-118; Banderilla, P. americana, F-132; Coa-
coatzintla, P. americana, F-186. Found in material
ranging from 0.5-15 cm diam. Galleries longitudi-
nal, biramous, eggs deposited in niches.
32. Pseudohysanoes contrarius Wood (p, bg,
ol). Mexico (Puebla, Veracruz*). Banderilla, Pho-
radendron calycatum Tre,***, F-98; P. fulca-
tum***, 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.
33. Pseudohysanoes simbratius Le Conte (x, bg, po).
Eastern U.S. and Mexico (Durango, Hidalgo, Ta-
Gallery similar to that described of Micraceus ova-
tus.

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,
Sohxothium edule, F-190. Galleries axial, biramous;
entrances in nodes of cucurbit vine.

Xyleborini
37. Ambrosiodmus coffeicus (Schell) (xm, ipg,
po). Mexico* (Veracruz), Northern South Amer-
onica Xalapa, 16-VIII-83, 1360 m, Quercus sp., F-33; Helicotarus appendiculatus, F-46; F-55; Quercus sp., F-62, Q. sp., F-64. Collected in material ranging from 4–20 cm diam.
38. Ambrosiodmus fuscus Wood (xm, ipv. no? 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.
40. Ambrosiodmus rusticus (Wood) (xm, ipv. po). Mexico (Morelos, Puebla, Veracruz, Chiapas). Xalapa, Quercus sp., F-33; F-34; F-50; F-110; Banderilla, Ficus elastica, F-113. In material from 2–8 cm diam.
41. Coptoborus pseudotenuis (Schedl) (xm, ipv. po). Southeastern Mexico to Venezuela and Brazil. Xalapa, F-69; Consolapa, Acacia pennatula, F-79.
42. Coptoborus vesatorius (Schedl) (xm, ipv. po). Mexico (Veracruz) to Argentina. Vista Hermosa, Inga sp.
43. Dryococloides caespitosa (Eichhoff) (xm, ipv. 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. Xyleborus gracilis (Eichhoff) (xm, ipv. po). U.S. (Florida), Mexico (Veracruz, Oaxaca, Campeche) to Venezuela. Xalapa, Quercus sp., F-63.
46. Xyleborus discrepans Eggers (xm, ipv. po). Mexico (Veracruz) to Cagayan and Peru. Vista Hermosa, Inga sp., S-713.
47. Xyleborus ferrugineus (Fabricius) (xm, ipv. po). U.S., Mexico, to Argentina, Africa, Hawaii, Micronesia. Xalapa, Quercus sp., F-15; F-16; Helicotarus sp., F-24; F-38; F-39; F-53; Quercus sp., F-110.
49. Xyleborus imbellis Blandford (xm, ipv. po). Mexico (Veracruz) to El Salvador. Vista Hermosa, Inga sp., S-713.
50. Xyleborus posticus Eichhoff (xm, ipv. po). Southeastern Mexico to Brazil. Xalapa, Helicotarus sp., F-24; Cupressus lindleyi Klotzsch, F-66; Leucaena pulcherrima, F-70; Ficus elastica, F-105; F-128; Banderilla, Erithrina americana Mill., F-94.
51. Xyleborus squamulatus Eichhoff (xm, ipv. 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 volubilus (Fabricius, 1775) (xm, ipv. po. U.S. (Florida), Mexico to Argentina, Old World Tropics. Xalapa, Leucaena pulcherrima, F-70; El Castillo, Acacia pennatula, S-917.

Cryptahalinii
54. Hypathemus eradicatus (Panzer) (m, ipv. po). Southeast U.S. to Argentina, Old World Tropics. El Castillo, F-12; S-915; Xalapa, F-149; Coatepec, Inga sp., S-902.
55. Hypathemus erectus Le Conte (m, ipv. po). U.S. (Texas) to Honduras and Venezuela, Cuba, Africa. El Castillo, F-12; S-920; Xalapa, Vittis sp., F-71; Inga vera, F-106; Olite, Persea americana, F-116.
56. Hypathemus eruditus Westwood (p-h, ipv. 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; Jalotepc, Inga sp., F-81; El Castillo, S-920.
57. Hypathemus interstitialis Hopkins (m, ipv. po). Eastern U.S. and Central America, and Jamaica. Xalapa, F-71; Struthanthus sp., F-89; Tithonia sp., F-110; Coatepec, Inga sp., S-920; El Castillo, S-920.

Corythini: Pityophthorina
61. Araptus aztecus Wood, 1971 (p, bg, ol). Mexico (Nayarit, San Luis Potosi, Veracruz, Campeche). Xalapa, Nectandra sp., F-22; F-56; Quercus sp., S-155. Collected in stems 4–15 cm diam. Galleries transverse, bireamous; each with one male and two females. This is the first report of bireamous in this genus. Known from Lauraceae (Nectandra sp., Atkinson & Equihua 1985c; Licaria pecki (J. M. Johnston) Kosterm., Estrada & Atkinson 1987, the record from Quercus may represent an "accidental host" (i.e., one in which breeding does not occur).
63. Araptus deyrollei (Blandford) (s, ipv. ?). Mexico (Veracruz). Collected in dry fruits of milkweed vine.


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.


**Corythulinii:** Corythulina


81. *Corythlus 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 elata*, F-113; *F. elata*, F-131; Olite, *Persea americana***, F-116; Plan de Sechloc, *Alnus jorulensis* HBE***, F-117; Coatpec, F-139; Naolinco, Q. 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 harems polygyne has also been reported for *Corythlus colombianus* Hopkins (Nord 1972).

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

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

84. *Corythlus 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.


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


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

90. *Gnathotrichus obscurus* Wood (xm, mg, po). Mexico (Tuxpan, Puebla, Veracruz*). Xalapa, F-7; *Quercus* sp., F-83; Q. sp., F-110; F-129.

91. *Gnathotrupes tibiaberculatus* Blandford (xm,


94. Microcorhylus vicinus Wood (xm, mg, po). Mexico (Veracruz*, Oaxaca, Chiapas). Acajete, Miconia glaberrima***, F-90; 5 km al Oeste de Acajete, S-892; 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. vescus, often in very small host material (<1 cm diam).


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

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


101. Monarthrum pennatum (Scheidl) (xm, hpg, po). Mexico (Nayarit, Veracruz) to Colombia and Venezuela. Banderilla, Quercus laurina***, F-37; Ficus elastica***, F-113; F-135; 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 Scheidl (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.


105. Monarthrum xalapensis Wood (xm, hpg, mo). 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.


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