

AN ABSTRACT OF THE THESIS OF

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Title: Systematics and Host Associations of Ormyrus Species (Hymenoptera: Chalcidoidea)

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The genus Ormyrus has a worldwide distribution and comprises about sixty recognized species. The higher taxonomic relationships of the genus are uncertain, as evidenced by its placement in the families Ormyridae, Pteromalidae, or Torymidae. Here, the genus is described in detail and a preliminary catalog of the world species is provided.

The Nearctic species of Ormyrus have never been revised and the original descriptions are inadequate for separating species. Fifteen species have been described from the Nearctic, but two were previously synonymized. After examining all type material and over 8000 additional specimens, I consider nine species to be valid and relegate five to junior synonymy. The nine recognized species are redescribed. With the description of seven new species, the genus now comprises sixteen Nearctic species; a key is provided for separating these species. Certain characters such as color and size were found to be quite variable in some species. Surface sculpture, as documented through the use of SEM, proved especially useful in separating species.

Thirteen of the sixteen Nearctic species may be associated exclusively with cynipid galls on oaks. Host records from specimen labels are summarized in tables, one

of which includes an updated list of all Nearctic oak cynipids. Twig galls harbor several oligophagous species of Ormyrus, many leaf galls just a single polyphagous species, and "apple" galls usually none. Other hosts of Nearctic species include cynipid galls on Rosaceae and a pteromalid gall on blueberry. In other parts of the world, dipteran and chalcidoid galls may be important hosts.

Distributional patterns of Nearctic Ormyrus species are compared with those of host cynipids and oaks.

Systematics and Host Associations of  
Ormyrus Species (Hymenoptera: Chalcidoidea)

by

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Jim Whitfield, and Jim Zimmerman. I am also grateful to the numerous curators who sent me specimens. Nearly everyone I have travelled with in the last four years deserves thanks for help in collecting galls; Lin Bennett, Jim DiGiulio, and Jeff Schultz deserve special mention. I wish to thank Ray Gagne for identifying cecidomyiid hosts of African material collected by Jim DiGiulio.

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## PREFACE

The present research has a history more varied than most. At the University of Minnesota I did my Master of Science research on rice water weevils associated with wild rice. I applied to OSU with no clear research goals, and therefore when Dick Clarke took me on, I initiated my doctoral research on potato leaf roll virus transmission by the green peach aphid. This research ended when Dick left. At this point I became a student of Jeff Miller and began working on parasitoids of oak pit scale. Repeated exposure to oaks diverted my attention to cynipid galls and their parasitoids. At the same time, I was taking Mycology courses from Bill Denison and becoming enthralled by the diversity of fungi inhabiting oak twigs. I attempted to combine these sundry interests by presenting to my committee a research proposal to study the community ecology of everything that lives on oak twigs.

It soon became obvious that, while a good idea, a complete community ecology of oak twigs was too much for one person. I had anticipated cynipid twig galls to be the easy part of the study and naively believed that I could identify the chalcidoid associates myself. I thus sent my list of chalcidoid species to Eric Grissell at the USNM, who responded simply, "I don't know what to make of your list". Although keys exist for most of the genera, Eric was only willing to comment on Torymus, the genus he revised. Realizing now that credible species determinations were not possible in most genera, I began to question an ecological study that rested on such a flimsy taxonomic foundation. One genus not included in my list was Ormyrus, since no keys existed for the North American species. I therefore decided that by revising this genus I could at least contribute to future ecological studies such as the one I had originally envisioned.

I realize now, that in revising a genus, one is confronted directly with fundamental questions, like what is a species. In this revision of the Nearctic species of Ormyrus, I have attempted to be conservative in recognition of species. Examination of extensive series of reared specimens has convinced me that considerable intra-specific variation is possible in some species of this genus. I have therefore proposed synonymies where morphological differences seemed attributable to intra-specific variation. There are of course still problems that I have not been able to solve and these are indicated in the appropriate places.

Systematics and Host Associations of Ormyrus Species  
(Hymenoptera:Chalcidoidea)

CHAPTER 1. INTRODUCTION

The genus Ormyrus Westwood (Hymenoptera: Chalcidoidea) has a worldwide distribution. There are presently about 60 recognized species, including 23 species from the Palearctic, 13 from the Nearctic, 12 from sub-Saharan Africa, 5 from Australia, 2 from India, 1 from the Philippines, and 1 from South America. Only O. orientalis Walker is presently recorded from more than one region (India and Palearctic) but further studies may reveal that other species are widespread. The number of species reported from the Palearctic likely includes some that will ultimately be synonymized. With the present study the total for the Nearctic is 16 described species.

What is now recognized as the superfamily Chalcidoidea was first distinguished as a separate group of Hymenoptera by Dalman (1820), as the family Pteromalini. Latreille (1825) referred to this group as the tribe Chalcidites. In 1832 Westwood described several new genera in the family Chalcididae, including Ormyrus for the new species O. punctiger. Foerster (1856) placed Ormyrus in the family Ormyroidae; subsequently, Walker (1871) recognized the family Ormyridae. Thomson (1875) placed Ormyrus as a subtribe of the tribe Toryminae and Ashmead (1904) as the subfamily Ormyrinae of the family Torymidae. More recently, the family Ormyridae has been recognized by Muesebeck et al. (1951), Nikolskaya (1952), Peck (1963), Peck et al. (1964), Graham (1969), and Yoshimoto (1984). Riek (1970) placed Ormyrus as a subfamily of the Pteromalidae, a placement followed by the latest Hymenopteran catalog for North America (Krombein et

al. 1979). Boucek has placed Ormyrus in Ormyridae (Boucek 1969), Torymidae (Boucek et al. 1981), and most recently, again in Ormyridae (Boucek 1986).

Six genera have been synonymized previously with Ormyrus. Monobaeus and Tribaeus were described by Foerster (1860), based on differences in antennal formulae, but both genera were synonymized with Ormyrus by Mayr (1904). Although these synonymies have been accepted by later workers (e.g. Nikol'skaya 1952, Boucek et al. 1981, Zerova 1985) and are accepted in the present study, Monobaeus and Tribaeus have been recognized as distinct genera in several publications: Erdos (1946), Peck et al. (1964), Krombein et al. (1979), and Sellenschlo and Wall (1984). Four other generic synonymies are more widely accepted: Periglyphus Boheman, Siphonura Nees, Cyrtosoma Perris, and Wania Risbec. Since Mayr's (1904) revision, several new species of Ormyrus have been described and additional keys to the Palearctic species of Ormyrus have been published: Hoffmeyer (1931), Erdos (1946), Nikolskaya (1952), Zerova (1978 and 1985), Sellenschlo and Wall (1984). None of these publications however, treat all of the recognized Palearctic species.

Ormyrus appears to be taxonomically isolated from other Chalcidoidea. The only closely related genus is Ormyrulus, which was recently described from a new species associated with a cecidomyiid gall in India (Boucek 1986). The relationship of these two genera to other Chalcidoidea is uncertain, as evidenced by previous placements of Ormyrus in Ormyridae, Pteromalidae, and Torymidae. Understanding of higher level relationships must begin with an evaluation of evidence supporting the hypothesized monophyly of Ormyrus + Ormyrulus. Such evidence consists of derived character states shared by all species of the group under consideration, but absent elsewhere in the Chalcidoidea (i.e. synapomorphies, see Hennig 1966). Character analysis is, in turn, dependent

on studies that elucidate the limits of species. Revisionary study of Ormyrus has been limited to Palearctic species (Mayr 1904) and therefore such studies of species from other regions are needed before comprehensive character analyses can be done.

In the absence of revisionary studies it is impossible to compile reliable data on host associations, other than host records given in the original descriptions. Sellenschlo and Wall (1984) compiled known host associations of several Palearctic species of Ormyrus but compilations from other regions are lacking. Where hosts are known, species of Ormyrus are parasitoids (primary and/or hyperparasitoids) in plant galls elicited by species of Hymenoptera (Chalcidoidea and Cynipidae) and Diptera (Agromyzidae, Cecidomyiidae, and Tephritidae). I report in this study the first records of Ormyrus from seeds, where the hosts may be phytophagous Chalcidoidea. Detailed knowledge about the immature stages of Ormyrus species is virtually non-existent. Triggerson (1914) illustrated the egg of a Nearctic species (probably O. labotus Walker) and Parker (1924) illustrated the larval spiracle of a Palearctic species (undetermined species). I have not encountered any other references to the immature stages of Ormyrus species.

The major objectives of my research are to provide a revision of the Nearctic species of Ormyrus and to summarize the host records. Fifteen species have been described from the Nearctic, two of which were relegated to junior synonymy by Burks (1964, 1975). The first Nearctic species was described by Walker in 1843; the last species to be described from the Nearctic were by Girault in 1917. The majority of species were described by Ashmead (seven species) and Girault (four species). Single species were described by Fitch (1859), Provancher (1887), and Fullaway (1912). Most of the original descriptions consist of generic characters and variable



characters (e.g. color and size), and are thus useless in separating species. In this study I recognize nine of the previously described species as valid and relegate five to junior synonymy. The nine previously described species are redescribed and seven new species are described.

NOTE: The new names used in the following pages are manuscript names that are not available until published.

In addition to revising the Nearctic species and summarizing host records for these species, I will provide a detailed description of the genus and a preliminary catalog of the non-Nearctic species. A summary of known host associations of the non-Nearctic species is presented, including some new records from labels of specimens I examined. Finally, I compare biogeographic patterns in Nearctic Ormyrus, cynipid, and oak species. It is hoped that the present study will facilitate further study at the world level.

## CHAPTER 2. MATERIAL, METHODS, AND TERMS

The present study began in 1982 with local collecting of cynipid galls. In 1983, loans of Nearctic material were requested from as many sources as possible and examination of this material began later that year. In 1985, I visited the Canadian National Collection in Ottawa, the Kinsey collection at the American Museum of Natural History in New York City, and the U.S. National Museum in Washington, D.C. (the latter contains the majority of type material). Throughout this period extensive personal collecting was continued.

## A. MATERIAL EXAMINED

I have examined all type specimens of Nearctic Ormyrus species plus an additional 8200 specimens from the Nearctic and 1200 from other parts of the world. Specimens were borrowed from the following museums; the acronyms are used in the species descriptions (chapter 4) and elsewhere to indicate where specimens are deposited.

- AMNH: American Museum of Natural History, New York, NY  
(M. Favreau)
- ANS: Academy of Natural Sciences, Philadelphia, PA  
(D. Azuma)
- BM: Bishop Museum, Honolulu, HA (G.M. Nishida)
- BMNH: British Museum (Natural History), London (J. Noyes)
- CAS: California Academy of Sciences, San Francisco  
(W.J. Pulawski)
- CM: Carnegie Museum of Natural History, Pittsburgh, PA  
(J. Rawlins)
- CNC: Canadian National Collection, Ottawa  
(C.M. Yoshimoto and G. Gibson)

CSC: California State Collection of Arthropods,  
Sacramento (M.S. Wasbauer)

CSU: Colorado State University, Fort Collins  
(W.D. Fronk)

CU: Cornell University, Ithaca, NY (Q.D. Wheeler)

FSC: Florida State Collection of Arthropods, Gainesville  
(L.A. Stange)

INH: Illinois Natural History Survey, Urbana (D.W. Webb)

ISU: Iowa State University, Ames (A. Ward)

KIEV: Inst. Zool., Ukrainian SSR Acad. Science, Kiev  
(M. Zerova)

KSU: Kansas State University, Manhattan (H.S. Blocker)

LA: Natural History Museum of Los Angeles County, CA  
(R.R. Snelling)

LU: Laval University, Quebec (J.M. Perron)

MCZ: Museum of Comparative Zoology, Harvard Univ.,  
Cambridge, MA (H.W. Levi)

OHSU: Ohio State University, Columbus (C.A. Triplehorn)

OKSU: Oklahoma State University, Stillwater (W.A. Drew)

ORSU: Oregon State University, Systematic Entomology  
Laboratory, Corvallis (J.D. Lattin)

QM: Queensland Museum, Brisbane, Australia (E.C. Dahms)

REM: Rutgers Entomological Museum, New Brunswick, NJ  
(G.W. Wolfe)

ROM: Royal Ontario Museum, Toronto (D.C. Darling)

TAM: Texas A & M University, College Station  
(R.A. Wharton)

UA: University of Arizona, Tucson (C.A. Olson)

UC: University of Connecticut, Storrs (J.E. O'Donnell)

UCB: Univ. of California, Berkeley (L.E. Caltagirone)

UCD: University of California, Davis (R.O. Schuster)

UCR: University of California, Riverside (S.I. Frommer)

UG: University of Georgia, Athens (C.L. Smith)

UI: University of Idaho, Moscow (J.B. Johnson)

- UK: Snow Ent. Mus., University of Kansas, Lawrence  
(R.W. Brooks)
- UMA: University of Massachusetts, Amherst (G.J. Couch)
- UMIC: University of Michigan, Ann Arbor (M.F. O'Brien)
- UMIS: University of Missouri, Columbia (R.L. Blinn)
- USNM: United States National Museum, Washington, D.C.  
(E.E. Grissell)
- USU: Utah State University, Logan (G.E. Bohart)
- UT: University of Texas, Austin, Breland collection  
(L. Gilbert)
- UW: University of Wisconsin, Madison (S. Krauth)
- VP: Virginia Polytechnic Institute & State Univ.,  
Blacksburg (M. Kosztarab)
- WSU: Washington State University, Pullman (R.S. Zack)

Specimens were also obtained from several personal collection: Charles Dailey (Sierra College, Rocklin, CA), Jim DiGiulio (Oregon State University, Corvallis), Jeff Halstead (California State University, Fresno), John Huber (Biosystematic Research Institute, Ottawa), James Johnson (University of Idaho, Moscow), John LaSalle (University of California, Riverside), Joel Shorthouse and Al Ritchie (Laurentian University, Sudbury, Ontario), Jan Washburn and Jim Whitfield (University of California, Berkeley), Jim Zimmerman (University of New Mexico, Las Cruces).

## B. MORPHOLOGY: METHODS AND TERMS

Most of the observations for the species descriptions were made with a dissecting microscope at 105x magnification using a fiber optic illuminator with a plastic drawing film placed between the light source and the specimen (to reduce glare). Measurements were done at 70x magnification on ten females (if available) of each species. Specimens were selected from different hosts and geographic locations. Measurements were converted to ratios commonly employed in chalcidoid systematics (Graham 1969, Grissell 1976) and the results are presented as ranges. Ranges in total body length are given in millimeters, with the specific measurement of the holotype (HT) given in parenthesis. Some of the ratios used here are probably subject to allometric variation (see Janzon 1986), but detailed morphometric studies were beyond the scope of my study.

Female and male specimens of eight Nearctic species and one Palearctic species (*O. papaveris*) were partially cleared in nearly boiling lactophenol, dissected, and mounted in Hoyer's solution on slides for examination with a phase contrast, compound microscope (430x magnification). Genitalia did not differ among species, a result consistent with observations in other chalcidoid taxa (e.g. Domenichini 1953, Grissell 1976). A few species showed slight differences in mouthparts, i.e. glossa, prementum, stipes.

Morphological terms follow common useage (Graham 1969, Grissell 1974, Richards 1977) except "prepectus" is used instead of "postspiracular sclerite" (Gibson 1985); the following terms and acronyms are used (see figs. 37-39, chapter 4):

## HEAD

EH = eye height

F1-F11 = antennal flagellar segments 1-11 = annelli  
(annular segments) + funicle + clava (club).

Funicular segments may be elongate (longer than wide), quadrate (as long as wide), or transverse (wider than long).

frons width = distance between compound eyes, measured across the upper scrobe.

IMD = intermalar distance = distance across oral fossa, between malar grooves.

lower face = area of head below antennal toruli and between malar grooves.

MD = malar distance, length along malar groove, from lower margin of eye to oral fossa.

median frons = area immediately anterior to median ocellus.

OOL = length of ocular-ocellar line.

POL = postocellar line, distance between posterior ocelli.

MESOSOMA = thorax + propodeum

panels = area of propodeum between spiracular sulcus and median area (latter often bounded by submedian carinae).

## METASOMA

T1-T7 = metasomal tergites 1-7 = abdominal segments 3-9.

Surface sculpture of the median frons, mesoscutum (only in certain non-Nearctic species), scutellum, hind coxa, and the metasomal tergites is described in detail. Scanning electron photomicrographs (Amray 1000 A) are used to document surface sculpture and standardized terms (see Eady 1968, Harris 1979) are used in the descriptions:

imbricate = like shingles on a roof or scales on a fish.

interstice = a space between two lines.

foveate = pitted, used here to refer to the

characteristic pits on T3-T5 of most Ormyrus species  
(T3-T4 in males).

punctate = with fine, impressed points or punctures.

punctulate = diminutive of punctate.

crenulate = refers to the metasomal (T3-T5) sculpture  
characteristic of most Ormyrus species; crenulate is  
used rather than crenate since the former was  
illustrated by Eady (1968) using Ormyrus; crenulate  
border refers to the entire toothed band on  
a tergite and cusp refers to a single tooth.

reticulate = net-like.

carinate = keeled (e.g. the median longitudinal carina  
on T3-T5 of females in most Nearctic species).

ecarinate = not keeled.

strigate = with narrow, parallel lines (raised in the  
case of Ormyrus); may be arranged transversely,  
longitudinally, or diagonally.

strigulate = minutely strigate.

## C. BIOLOGICAL INFORMATION: METHODS

All Nearctic records of distribution, flight times (dates on non-reared material), and host associations are compiled from labels of specimens that I examined in the course of the revisionary study. Several new distribution and host records for non-Nearctic species were also obtained in this manner. Because of the small quantity of non-Nearctic material examined, I had to rely on published records (species descriptions; also, Sellenschlo and Wall 1984) in summarizing hosts of non-Nearctic species. Host records listed in compilations such as that of Fulmek (1968) were not used, since many of these need verification.

Many of the host records were obtained from specimens reared by cynipid researchers such as Alfred Kinsey (AMNH and UT), Lewis Weld (USNM), and more recently, Charles Dailey (Sierra Community College, Rocklin, Calif.), Joel Shorthouse and Al Ritchie (Laurentian Univ., Sudbury, Ontario), Jan Washburn (Univ. Calif., Berkeley) and Jim Zimmerman (New Mexico State Univ., Las Cruces). Although about 80% of the 8200 Nearctic specimens I examined bear labels indicating that they were reared, many of the specimens are insufficiently labelled, for example "ex oak gall". Others had Hopkins numbers which could not be traced. Since I could not find the appropriate Hopkins numbers in the files at the USNM, I recorded numbers directly from the cynipid collection; in several instances I was able to match them with numbers on Ormyrus specimens. I have excluded many records where the locality or host plant is inconsistent with the cynipid species. Some of Kinsey's names could not be correlated with current names and had to be excluded.

I have attempted to fill gaps in the rearing records through personal collecting in all parts of the U.S. In August 1983 cynipid galls were collected from Gambel oak



in Utah and Colorado and from bur oak in South Dakota and Minnesota. In April 1985, galls were collected from several oak species in southeastern Arizona. From August through October of 1985 an extensive trip was made from Oregon to the east coast and back, encompassing 32 states and 11,000 miles. On this trip numerous oaks were sampled, especially in Mississippi, western Texas, and southern New Mexico; cynipid galls also were collected from composites (Asteraceae), including Lactuca (Connecticut, Iowa, and Minnesota), Prenanthes (Michigan), and Silphium (Iowa, Minnesota, and Nebraska). Several trips were made to the Siskiyou Mountains of southern Oregon where galls were collected from canyon live oak, sadler oak, and chinkapin. Throughout the period of this investigation numerous collections of cynipid galls were made from local Quercus garryana Dougl. ex Hook., Potentilla gracilis Dougl., Rosa spp., and Rubus parviflorus Nutt. Various plant seeds and galls formed by insects other than cynipids were also collected in attempts to obtain Ormyrus from previously unreported hosts.

## CHAPTER 3. THE FAMILY ORMYRIDAE

The genus Ormyrus has been and still is placed in three different families by different authors (see chapter 1), i.e. in the subfamily Ormyrinae of the Pteromalidae or Torymidae, or in Ormyridae. For reasons presented below, it seems most prudent at the present time to place Ormyrus in Ormyridae. The only other genus of Ormyridae recognized here is the monotypic Ormyrulus (Boucek 1986). Although Monobaeus and Tribaeus are still recognized in some recent publications (e.g. Krombein et al. 1979, Sollenschlo & Wall 1984), both Boucek (in Boucek et al. 1981) and the results of my research support Mayr's (1904) synonymizing these genera with Ormyrus. Both genera were originally separated from Ormyrus on the basis of one character: number of annelli in the antenna. Other genera of Chalcidoidea have been separated on the basis of the ratio of number of annelli to number of funicular segments, i.e. 1-7, 2-6, or 3-5. In Ormyrus however, these character states vary continuously rather than discretely between species, and I have also observed some intraspecific variation.

## A. RELATIONSHIPS OF ORMYRIDAE

Possible synapomorphies defining Ormyridae include the following: structure of the labrum (see illustrations in Domenichini, 1969), mesosoma weakly sculptured (mesopleuron mostly shiny, mesoscutum and scutellum predominantly imbricate with shiny interstices), metasoma coarsely sculptured (foveate and crenulate) and heavily sclerotized, hind tibia with two apical spurs (of unequal length) that are thick and curved. These characters need to be examined in a wider range of Ormyrus species and compared with a wider range of Chalcidoidea. Some of these characters may have functional significance. The hind tibial spurs for instance probably are used in grooming behavior. The metasomal foveae would appear to be functionally significant given the detailed ultrastructure consisting of small holes around the perimeter of each fovea (pers. observ.).

Ormyridae shares with most Torymidae the following character states: enlarged hind coxa which tends to be triangular in cross-section, postmarginal and stigmal veins of forewing short with respect to the marginal vein. Ormyrids share certain genitalic characters with torymids of the subfamily Megastigminae (DiGiulio 1983): sculpture of stylet sheath, shape of fulcral plate, and in males, shape of cuspis (the latter also shared with Idarnes in the Sycophaginae). Megastigminae however, differ from other torymids and ormyrids by having two instead of three teeth on the digitus of the male genitalia (DiGiulio 1983). Megastigmine and ormyrid larvae are also quite similar, although these similarities are shared with some pteromalids (Parker 1924). Adult ormyrids however lack the exerted ovipositor and exerted pygostyles of Torymidae, character states that may be synapomorphies for Torymidae.

Pteromalidae as presently "defined" (e.g. Graham

1969) is undoubtedly para- or polyphyletic. Chalcedectinae and Cleonyminae for example share apomorphic character states with Eupelmidae (Gibson 1986); removing these subfamilies still leaves Pteromalidae without synapomorphies, or even defining characters. Thus, placing Ormyrus in Pteromalidae cannot be justified at this time.

I have seen two series of specimens (USNM) from South America that seem to be intermediate between Ormyridae and Pteromalidae. One series (5 females, 2 males) bears labels reading, "Huamampinto specimens from Peru, Chuguiraga spinosa" (presumably from galls). The other series (2 females, 2 males) bears labels reading, "From galls in twigs of Moquinea polymorpha, Pelotas Brazil" (presumably the plant is Moquinia polymorpha). Both plants are members of the tribe Mutisieae of the family Asteraceae (composites), but the only gall recorded from these plants is a mite gall on Moquinia polymorpha DC. (Houard 1933). These specimens differ from Ormyrus in the following character states: dark-brown to black color with less metallic reflections, hind coxa only partially enlarged, metasomal tergites slightly less sclerotized and lacking characteristic sculpture of Ormyridae. Specimens from Moquinia have hind tibial spurs as in Ormyridae, but specimens from Chuguiraga have the hind tibial spurs long, thin, and only slightly curved. Both series of specimens have a reduced prepectus, reduced notauli, and wing venation as in Ormyridae. These specimens also appear to share similarities with Brachyscelidiphagninae, such as Hemadas nubilipennis (Ashmead). Future research on the higher level relationships of Ormyridae should include more extensive examination of South American pteromalids related to the North American Hemadas which forms galls on Vaccinium (a plant genus with many species in the Andes Mountains). What is perhaps most needed at this point is more extensive collecting in South America, especially

rearing of galls.

B. DESCRIPTION OF THE GENUS ORMYRUS WESTWOODGENUS ORMYRUS Westwood

Ormyrus Westwood, 1832: 127

Type-species: Ormyrus punctiger Westwood.

Monotypic.

Periglyphus Boheman, 1833: 378

Type-species: Periglyphus gastris Boheman.

Monotypic.

Siphonura Nees, 1834: 81

Type-species: Siphonura variolosa Nees.

Desig. by Gahan and Fagan 1923.

Cyrtosoma Perris, 1840: 96

Type-species: Cyrtosoma papaveris Perris.

Monotypic.

Monobaeus Foerster, 1860: 95

Type-species: Monobaeus cingulatus Foerster.

Desig. by Ashmead 1904.

Tribaeus Foerster, 1860: 95

Type-species: Tribaeus punctulatus Foerster.

Monotypic.

Wania Risbec, 1951: 294

Type-species: Wania ornata Risbec. Monotypic.

Diagnosis--All described species of Ormyrus probably have large foveae on metasomal tergites 3-5 in females and T3-T4 in males. In some species however, the foveae are always concealed beneath the preceding tergite. The latter resemble some pteromalids but can be distinguished (in both sexes) by the presence of an occipital carina, the reduced notauli, the enlarged hind coxae, the short stigmal and postmarginal veins relative to the marginal vein, and the heavily sclerotized metasoma. The best single character separating all species of Ormyrus from all other Chalcidoidea is the presence of two stout,

curved spurs at the apex of the hind tibia.

Boucek (1986) described Ormyrulus gibbus (reared from cecidomyiid galls on mango) primarily on the basis of the carinate ridge separating the vertex from the occiput (the true occipital carina, which is present in all Ormyrus, is said to be absent). The posterior ocelli are very close to the eyes, a character state that may be correlated to the preceding character according to Boucek. Ormyrulus lacks crenulate borders on the metasomal tergites (as do some Ormyrus species), but foveae and curved hind tibial spurs are present as in Ormyrus.

Description--Total body length ranges from 1 to 7 mm. Color usually metallic blue or green, sometimes metallic bronze or violet, sometimes nonmetallic yellow-brown, rarely black; coxae same color as body; antennal flagellum brown, tarsi pale yellow (apical segment often darker); body usually with white procumbent setae, sometimes with black erect setae.

HEAD: both punctate and strigate, often obscured; apex of clypeus usually straight and entire (rarely emarginate), lower face usually strigate (lines radiating from clypeus); malar sulcus present; eye height  $0.7x$  head height; scrobe ecarinate, shallow, shiny (top part often weakly sculptured); vertex transversely strigate; occipital carina present. Mandibles bidentate, outer tooth acute, inner tooth broad with apical edge straight. Antennal toruli situated slightly above ventral margin of eye; antennal formula 1-1-1-7-3, 1-1-2-6-3, or 1-1-3-5-3 (1-1-2-6-3 most common); scape length usually  $0.8-0.9x$  eye height; clava with sutures slightly asymmetric.

MESOSOMA: sculpture usually weak, mesopleuron almost totally shiny, scutum usually imbricate to transversely strigate with shiny interstices (often reticulate at base, adjacent to scutellum), scutellum strigate to imbricate to reticulate usually with shiny interstices; pronotum almost

as wide as scutum, length  $0.4 \times$  length of scutum, ecarinate and rounded anteriorly; prepectus reduced, partially concealed by latero-posterior edge of pronotum; notauli usually visible but shallow, sometimes absent; width of scutellum at base  $0.5-0.6 \times$  greatest width; scutellum length subequal to length of scutum, without frenal groove but demarcation visible on side of scutellum; pleural sulcus faint, mesepisternum continuous with sternum but junction marked by a line, mesepimeron not divided into upper and lower parts; propodeum transverse (width about  $4-5 \times$  length along midline), usually quite shiny (rarely more heavily sculptured), callus setose, spiracle slightly oval and nearly touching anterior margin, spiracular sulcus usually faint but deep in some species, nucha poorly developed, median area often bordered by two submedian carinae. Forewings ciliate, with postmarginal (R1) and stigmal veins very short (stigmal vein usually less than postmarginal vein), marginal vein (R1)  $0.5-0.6 \times$  submarginal vein (Sc+R); costal cell asetose above, and with a row of setae below which may be complete or incomplete; basal vein, cubital vein (Cula; below basal cell, M+Cul), and medial vein indicated by rows of setae. Hindwings with 3 hamuli on anterior margin. All tarsi 5-segmented with first segment longest and each succeeding segment shorter than preceding except fifth (which is subequal to 3 + 4); tarsal claws usually lobed; foretibia with a slender, curved spine at apex and calcar on first tarsal segment; middle tibia with a long, slender, straight spine at apex; hind coxae greatly enlarged, length equals twice width, subtriangular in cross section; hind tibia with row of spines along outer edge and with two stout, curved spurs at apex, longest one greater than half the length of the first tarsomere.

METASOMA: heavily sclerotized; petiole very reduced (usually not visible); base of T1 shiny, except for concave area anterior-medially that is weakly sculptured;



apex of T1 usually straight, rarely somewhat emarginate, weakly sculptured in all Nearctic species but shiny in some Palearctic species; T2 almost completely covered by T1; T3-T5 usually densely foveate anteriorly (in one species group foveae are always concealed by preceding tergite), imbricate to punctulate posteriorly, anterior part of tergite sometimes raised above posterior part and usually demarcated by a crenulate border (with or without cusps); pygostyles not exerted, with 3 long bristles and 2 short bristles.

Variation--In several species that are normally metallic colored, occasional specimens can be totally yellow-brown. Some species show geographic variation in color and many species are more yellowish in Florida (perhaps a function of temperature).

Several characters vary with the size of the specimen. Smaller specimens often have more clavate antennae with more quadrate funicular segments (also observed in Torymus, Grissell 1974). Smaller specimens sometimes have fewer setae in the wing and usually have a relatively shorter metasoma (the last tergite is often noticeably stouter).

Males tend to be more setose than females. Shape and sculpture of the metasoma in males is more uniform among species and is therefore less useful in separating species. There is greater intra-specific variation in the female metasoma than in the male metasoma: females apparently have greater mobility between tergites (probably related to oviposition) and thus metasomal shape varies with degree of contraction. For this reason, the species group characterized by concealed foveae is most easily recognized in males. In males of most species the antennal scape and flagellum are shorter than in the female. In a few species the male scape is noticeably different in shape from that of the female.

Distribution--- Ormyrus has a worldwide distribution, occurring on all continents except Antarctica. I have seen specimens (BM, unplaced species) from Vanuatu (New Hebrides), Samoa, and the Solomon Islands but not from New Zealand or Hawaii. In the Northern Hemisphere, I have seen O. rosae from as far north as Yellowknife in the Northwest Territories of Canada. The distribution of the genus can be hypothesized through knowledge of host associations (chapter 5). In North America, Ormyrus is most abundant where there are oaks (Quercus spp.) and indeed specimens are seldom collected in general sweep samples unless oaks are swept. In lowland tropics the genus can be found in figs (Ficus) as well as on many other host plants.

C. CATALOG OF THE NON-NEARCTIC SPECIES OF ORMYRUS

The following is a preliminary catalog of the world species of Ormyrus (Nearctic species are given in chapter 4) which summarizes information about type specimens and previously proposed synonymies. Museums holding type specimens are given where known (see chapter 2 for acronyms). In this catalog, HT = holotype and LT = lectotype.

aerosus Foerster

Ormyrus aerosus Foerster, 1860: 104.

Female, Germany.

australiensis Girault

Ormyrus australiensis Girault, 1915: 309.

Female, Australia (Queensland), QM.

australis Risbec

Ormyrus australis Risbec, 1957: 355. Males,

Madagascar.

bicarinatus Girault

Ormyrus bicarinatus Girault, 1915: 309.

Female, Australia (Queensland), QM.

bicoloripes Girault

Ormyrus bicoloripes Girault, 1915: 309.

Female, Australia (Queensland), QM.

brasiliensis Ashmead

Ormyrus brasiliensis Ashmead, 1904: 401.

Female, Brazil (Chapada), USNM.

bucharicus Zerova

Ormyrus bucharicus Zerova, 1985: 11.

Females (HT), male, USSR (Uzbekistan),

ex Urophora repeteki on Cousinia hamade; KIEV.

carinativentris Girault, 1915:309

Ormyrus carinativentris Girault, 1915: 309.

Female, Australia (Queensland), QM.

chevalieri (Risbec)Monobaeus chevalieri Risbec, 1955b: 569.

Females, Chad, ex root gall.

cingulatus (Foerster)Monobaeus cingulatus Foerster, 1860: 96.

Female, Germany.

cosmozonus FoersterOrmyrus cosmozonus Foerster, 1860: 98.

Female, Germany

decaryi (Risbec)Tribaeus decaryi Risbec, 1955a: 177.

Females, males, Madagascar.

destefanii MayrOrmyrus destefanii Mayr, 1904: 566.

Female, Sicily.

diffinis (Fonscolombe)Cynips diffinis Fonscolombe, 1832: 287.

Male

Siphonura punctulata Ratzeburg, 1848: 151.Female?, Germany, ex Xestophanes potentillae.

Synon. Mayr 1904.

Ormyrus caeruleus Walker, 1850: 127.

Female, Germany, BMNH. Synon. Mayr 1904.

Tribaeus punctulatus Foerster, 1860: 94.

Females, males, Germany. Synon. Mayr 1904.

eugeniae RisbecOrmyrus eugeniae Risbec, 1955a: 176.Female, Madagascar, ex twig gall on Eugenia sp.flavipes BoucekOrmyrus flavipes Boucek et al., 1981: 226.

Females (HT), males, Zimbabwe,

ex Ficus burkei, BMNH.

flavitibialis Yasumatsu & Kamijo

Ormyrus flavitibialis Yasumatsu & Kamijo, 1979: 103.

Females (HT), males, Japan, ex Trichagalma serratae on Quercus serrata, Kyushu Univ.

gratiosus (Foerster)

Monobaeus gratiosus Foerster, 1860: 97.

Female, Germany.

halimodendri Zerova

Ormyrus halimodendri Zerova, 1985: 14.

Females (HT), USSR (Turkmenistan); KIEV.

harongae (Risbec)

Wania harongae Risbec, 1952: 321.

Females, Madagascar, ex stem galls on Haronga sp., Paris MNHN.

indicus

Monobaeus indicus Ahmad, 1946: 7

Males (HT), India, ex Lepidoptera larva?

laccatus Zerova

Ormyrus laccatus Zerova, 1985: 17.

Females (HT), USSR (Turkmenistan); KIEV.

lanatus Zerova

Ormyrus lanatus Zerova, 1985: 13.

Females (HT), males, USSR (Kazakhstan), ex Asiodiplosis palpata on Anabasis aphylla, KIEV.

langlandi Girault

Ormyrus langlandi Girault, 1920: 2 (in Gordh et al, 1979: 159). Female, Australia (Queensland), QM.

longicornis Boucek

Ormyrus longicornis Boucek, 1969: 42.

Females (HT), males, Bulgaria, Prague Nat. Mus.

nitidulus (Fabricius)

Chalcis nitidula Fabricius, 1804: 163.

Female, North Africa ("Batbaria"),  
Copenhagen Univ. Mus. LT: Boucek 1977.

Cynips tubulosa Fonscolombe, 1832: 290.

Female?, France, ex Cynips argentea.

Synon. Boucek 1977.

Ormyrus nigrocyaneus Walker, 1833: 140.

Male. Synon. with O. tubulosa Dalla Torre 1898.

Siphonura variolosa Nees, 1834: 82 & 421.

Females, males, Europe.

Synon. with O. tubulosa Mayr 1904.

Siphonura chalybea Ratzeburg, 1844: 207.

Females, males, Germany, Cynips globuli.

Synon. with O. tubulosa Mayr 1904.

Siphonura Schmidtii Nees, 1851: 52.

Females, males, Italy. Synon. with O. tubulosa  
Mayr 1904.

Ormyrus violaceus Foerster, 1860: 105.

Female?, Germany. Synon. with O. tubulosa  
Mayr 1904.

orientalis Walker

Ormyrus orientalis Walker, 1871: 68.

Female, Sri Lanka, BMNH. LT: Boucek 1977.

Ormyrus hungaricus Erdos, 1946: 79.

Synon. Boucek 1977

Ormyrus peninsularis Mani & Kaul, 1972: 328.

Females (HT), males, India (Agra). Synon. ?

ornatus (Risbec)

Wania ornata Risbec, 1951: 294.

Females, Senegal.

papaveris (Perris)

Cyrtosoma papaveris Perris, 1840: 96.

Females, males, France, ex Aylax papaveris

parvulus Zerova

Ormyrus parvulus Zerova, 1985: 15. Females (HT),  
males, USSR (Elton Lake), ex Anabasis salsa, KIEV.

philippinensis Hedqvist

Ormyrus philippinensis Hedqvist, 1968: 162.

Female (HT), Philippines; Zool. Mus. Copenhagen.

punctiger Westwood, 1832:127

Ormyrus punctiger Westwood, 1832: 127.

Females, males, Europe.

Periglyphus gastris Boheman, 1833: 379.

Females, males, Europe. Synon. Dalla Torre 1898.

Siphonura brevicauda Nees, 1834: 83 & 421.

Females, males, Germany?. Synon. Dalla Torre 1898.

Siphonura sericea Nees, 1834: 83.

Females, males, Germany. Synon. Mayr 1904.

Siphonura viridiaenea Ratzeburg, 1844: 207.

Male, Germany, Cynips curator. Synon. Mayr 1904.

Siphonura cyanosthetus Walker, 1847: 227.

Female, Austria. Synon. Mayr 1904.

Ormyrus viridanus Foerster, 1860: 100.

Female, Germany? Synon. Mayr 1904.

Ormyrus prodigus Foerster, 1860: 101.

Female, Germany. Synon. Mayr 1904.

Ormyrus placidus Foerster, 1860: 103.

Female, Germany. Synon. Mayr 1904.

Ormyrus aeneicinctus Rondani, 1877: 191.

Female, Italy, Andricus conglomeratus.

Synon. Mayr 1904. LT: Boucek 1974.

Ormyrus blandus Foerster, 1860:104.

Female, Germany. Synon. Mayr 1904.

Siphonura gallae quercus Dufour, 1864: 214.

Females, males, France. Synon. Mayr 1904.

Ormyrus badius Stefani, 1898: 257. Synon.?

rufimanus Mayr

Ormyrus punctiger var. rufimanus Mayr, 1904: 579.

Females, males, Germany, ex Rubus & Potentilla.

salmanticus Nieves-Aldrey

Ormyrus salmanticus Nieves-Aldrey, 1984: 120.

Females (HT), males, Spain, ex Aulacidea subterminalis on Hieracium pilosellae.

sculptilis Crosby

Ormyrus sculptilis Crosby, 1909: 83.

Females, males, Malawi, ex Asphondylia terminaliae & unknown Agromyzina galls on Flueggea obovata stems, Cornell Univ. N.Y. LT: Boucek et al. 1981.

silvae Girault

Ormyrus silvae Girault, 1925: 93.

Female, Australia, ex Moreton Bay fig, QM.

similis Zerova

Ormyrus similis Zerova, 1985: 15. Female,

USSR (Uzbekistan), ex Haloxylonomyia gigas; KIEV.

speculifer Erdos

Ormyrus speculifer Erdos, 1946: 79.

Female, Hungary?

striatus Cameron

Ormyrus striatus Cameron, 1907: 223.

Male, South Africa, "bred from galls".

LT: Boucek et al. 1981.

subconicus Boucek

Ormyrus subconicus Boucek et al., 1981: 228.

Females (HT), males, Zimbabwe, ex Ficus burkei, BMNH.

versicolor Foerster

Ormyrus versicolor Foerster, 1860: 102.

Female, Germany.

wachtli Mayr

Ormyrus wachtli Mayr, 1904: 569.

Females, males, Europe.

watshami Boucek

Ormyrus watshami Boucek et al., 1981: 224.

Females (HT), males, Zimbabwe, ex Ficus burkei, BMNH.



D. SPECIES GROUPS OF ORMYRUS

Boucek (Boucek et al. 1981) has discussed three species groups of Ormyrus: species lacking a median longitudinal carina on the metasoma, species with a single carina, and species with a double carina (to me it looks more like a groove). Although this character is useful in constructing keys to species, my observations suggest that several metasomal characters are quite variable in female specimens. Some species have a very weak single carina, which is sometimes difficult to distinguish from species lacking a carina; similarly, a weak double carina may look like a single carina.

Nonetheless, species with a double median carina appear to be quite distinct and are thus far unknown from the New World. In this species group Boucek (Boucek et al. 1981) included O. eugeniae (from unknown galls on Eugenia), O. orientalis (primarily from tephritid galls), O. ornatus (host unknown), and O. striatus ("bred from galls"). Ormyrus orientalis appears to be quite widespread: I have seen specimens from South Africa (CNC, USU), the Philippines (BM), and Japan (UCR). There is a series of specimens (CNC, 11 females) collected in South Africa (Transvaal, Guernsey Farm, 19-31 Dec. 1985; M. Sanborne, S. & J. Peck colls.) that appear to belong to this species group but differ from O. orientalis by the more elongate hind tibial spurs and first tarsomere, a much more horizontal propodeum, and smaller more irregular foveae and lack of a distinct crenulate border on T3-T5. These character states may be plesiomorphic (ancestral) with respect to O. orientalis (the only other species in this species group that I have observed).

I propose consideration of another species group characterized by a relatively shiny mesoscutum with modified setation. This group has the mesoscutum (and often the scutellum) transversely strigate (as opposed to

imbricate), with extensive shiny interstices; setae tend to be fewer in number, longer, and more erect than in other species of Ormyrus. All species have the funicular segments of the antenna transverse, although this condition is present in other Ormyrus species. Species in this group may also share similar hosts: all species for which rearing records exist are from figs (e.g. O. silvae and O. watshami). Not all Ormyrus species reared from figs however, are members of this species group. I have seen one specimen of this species group (USNM; reared from Ficus benjamina in Hong Kong) that has a carinate vertex approaching that described for Ormyrus gibbus by Boucek (1986).

The Palearctic Ormyrus graciosus, O. papaveris, O. salmanticus, and O. wachtli share similar hosts (cynipids of the tribe Aulacini, see chapter 5) and a similar morphology (metasomal foveae always concealed, even in males). The hosts of O. decaryi (from South Africa) and O. longicornis (Europe) are unknown, but these two species are morphologically close to the above species and both may be synonymous with the Australian O. langlandi (Boucek, pers. comm.). Ormyrus longicornis appears to be quite widespread: I have seen specimens from South Africa (CNC), India (ORSU), and Laos (BM) that may belong to this species. This species group is not known from the Nearctic, although O. tenuis has the foveae mostly concealed. Further study is needed to determine whether these species constitute a natural group.

Recognition of monophyletic groups within Ormyridae will require more detailed character analyses on a wide range of species. Although presence of foveae is derived, it is possible that these have become secondarily reduced in some species. Many derived character states represent losses or reductions, and are therefore less likely to be synapomorphies: reduction of the second and third

flagellomeres of the antenna (all species have Fl reduced, i.e. annular), reduction in setation of the body and wings, reduction of notauli on the mesoscutum. Further study is needed to polarize sculptural characters, which may then prove useful in delimiting monophyletic groups. Finally, characters not included here should be examined in greater detail, notably the mouthparts. I found the prementum of O. unifasciatipennis to be basally emarginate, as opposed to non-emarginate in the other species I examined. Mouthparts of O. papaveris (the only Palearctic species dissected) were more setose than other species examined.

CHAPTER 4. REVISION OF THE NEARCTIC SPECIES OF ORMYRUS

The Nearctic species of Ormyrus have never been revised and, consequently, separation of species has been impossible. In this revision I recognize 16 species, 7 of which are new, and propose 5 new synonymies. The new synonymies are all with O. labotus Walker, a species which, as defined here, includes about 50% of the 8200 specimens I examined. Ormyrus rosae, which accounts for 20% of the specimens, is not easily distinguished from O. labotus. Specimens from cynipid galls on composites (Asteraceae) are similar to O. labotus and O. rosae but I hesitate to place these specimens until more detailed studies can be done. A small series of specimens (11 females, 3 males; ORSU) collected from oaks in the southwest appear to represent a new species, but their description is deferred until more material can be obtained.

The following key is best used with female specimens, except the last couplet where males are needed. This key can be used with male specimens except where there are metasomal characters; that is, males can be used in all couplets except the first. The three species encompassed by the first couplet are, however, quite distinctive (scutellar sculpture, basal cell of forewing) and are also scarce in most collections.

A. KEY TO THE NEARCTIC SPECIES OF ORMYRUS

1. Metasomal tergites 3-5 (T3-T5) punctulate posteriorly, crenulate border without elongate cusps (fig. 14)....2
  - T3-T5 imbricate posteriorly, crenulate border with cusps (fig. 15).....4
2. Basal cell of forewing asetose (fig. 39); propodeum with spiracular sulcus deep (fig. 10); scutellum reticulate (fig. 1)..... acylus
  - Basal cell of forewing setose (figs. 26 & 27); propodeum with spiracular sulcus shallow; scutellum strigate.....3
3. Scutellum transversely strigate (fig. 4); antenna usually with 1 annellus; basal cell of forewing with less than 5 setae, speculum present..... hegeli
  - Scutellum diagonally-longitudinally strigate to imbricate (fig. 5); antenna with 2 annelli; basal cell of forewing with more than 5 setae, speculum absent..... setosus
4. Forewing usually with dark spot (fig. 28); if faint, then costal cell with row of setae incomplete and apex of scutellum not extending beyond metanotum (fig. 30).....5
  - Forewing without dark spot; costal cell with row of setae complete (fig. 39); apex of scutellum extending beyond metanotum (fig. 31).....7
5. Hind coxa transversely strigate (fig. 12; foveae on T5 concealed)..... thymus
  - Hind coxa reticulate; foveae on T5 exposed.....6
6. Femora orange; T6 not upturned (fig. 33)..... unimaculatipennis
  - Femora metallic blue-green; T6 upturned (fig. 34)..... unifasciatipennis

7. Head in dorsal view subquadrate (fig. 35); mesosoma narrow, length = 1.5-1.6 width.....8
- Head in dorsal view transverse (fig. 36); mesosoma wide, length = 1.3-1.4 width.....9
8. Antennal flagellum clavate; propodeum diagonal (fig. 32); T3-T5 with foveae evident..... turio
- Antennal flagellum filiform; propodeum vertical (fig. 31); T3-T5 with foveae mostly concealed by preceding tergite..... tenuis
9. Scutellum shiny, transversely strigate (fig. 8); median frons regularly strigulate (fig. 9); forewing with 1-3 setae in apex of basal cell (fig. 29)..... venustus
- Scutellum diagonally strigate or reticulate; median frons irregularly strigulate; forewing with basal cell aetose, or if setose, setae not restricted to apex.....10
10. Hind coxa strigate (fig. 11).....11
- Hind coxa reticulate (fig. 13).....13
11. Antenna with 1 annellus, funicular segments mostly transverse (wider than long)..... crassus
- Antenna with 2 annelli, funicular segments elongate (longer than wide).....12
12. Metasoma blue, hind femora orange; forewing with speculum reduced (fig. 25)..... dryorhizoxeni
- Metasoma and hind femora yellow-brown; forewing with speculum present, not reduced..... vacciniicola
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B. DESCRIPTIONS OF NEARCTIC SPECIES OF ORMYRUS

Presented here are descriptions of 7 new species and redescriptions of 9 previously described species. All species are known from both sexes except O. unimaculatipennis, in which males are unknown. Host records exist for all species except O. tenuis, O. thymus, and O. unimaculatipennis.

Ormyrus acylus new species

(figs. 1, 10, 14, 16, 40)

Type locality--Lincoln, California, U.S.A.

Type material--Holotype (Female, USNM, donated by C. Dailey) bears the following labels: "3 mi. E Lincoln, Placer Co. Cal., VI-21 1969, "Quercus wislizeni A. D.C.", "Callirhytis milleri Weld, det. C. Dailey", "C. Dailey No.1056". Paratypes (17 females; BMNH, CNC, KIEV, ORSU, USNM; donated by C. Dailey): same data as holotype.

(Note: a specimen of this species from the USNM bears a label reading "Ormyrus elasmoides Girault type"; this name was never published and is therefore not a valid name.)

Other material examined--CANADA (1 female): Ontario (Constance Bay). USA (43 females, 15 males): Arizona (Graham, Maricopa), California (Contra Costa, Marin, Placer, Santa Clara, Tulare, Yolo), Florida (Duval, Franklin, Marion), Iowa, Michigan (Manistee, Midland), Missouri (Butler), Mississippi, New Mexico (Hidalgo), New York (Monroe), North Carolina (Durham), Pennsylvania, Texas (Brewster, Jeff Davis), Wisconsin (Vernon). MEXICO (3 females): Sonora. Specimens are deposited in: CAS, CNC, INH, ISU, ORSU, ROM, UI, USNM, UW.

Etymology--A noun in apposition, from the Latin, for acorn, with reference to the most common host association.

Diagnosis--The propodeum in O. acylus is unique; no other Nearctic species has a deep spiracular sulcus bordered laterally by a carina on the callus (fig. 10; best viewed from behind). Like O. hegeli and O.



setosus this species has punctulate (as opposed to imbricate) sculpture posterior to the crenulate borders of metasomal tergites 3-5 (fig. 14); O. acylus can be distinguished by the asetose basal cell of the forewing, the reticulate scutellum (fig. 1), and the deep spiracular sulcus on the propodeum.

Distribution--Ormyrus acylus has been collected in eastern North America from Ontario to Florida to Wisconsin, Iowa, Missouri, and Texas; it has also been collected in the southwest, i.e. New Mexico, Arizona, California (north to Marin Co.), and Mexico (Sonora)--see fig 40. Thus far O. acylus has not been collected from oaks in Colorado, Utah, and the Pacific Northwest. Records of flight time are from early June to late September.

Host Associations--Ormyrus acylus appears to be primarily associated with cynipid galls in acorns: specimens from Ontario (Canada) to Sonora (Mexico) bear labels reading "ex acorn" or "ex stone gall in acorn". The only specific record is Callirhytis milleri (sexual generation of C. flora Weld) in California. Three specimens (USNM, Hopkins No. 13651i) reared from C. quercusoperator (O.S.) may be from the asexual generation acorn gall although the rearing dates (late June to late July) leave this questionable. There are fewer records from other types of oak galls: Andricus cinnamomeus Ashmead (bud gall) in Florida and Callirhytis tumifica (O.S.) (leaf gall, no location given).

Description--

Female--Length, 2.5-6.0mm (holotype 4.0mm). Color variable (see below). Holotype, blue-green, including scape (basal part yellow), tegula, and femora; tibiae yellow-brown; metasomal tergites blue anteriorly and black posteriorly. Forewing immaculate.

Head--Width 2.1-2.3x length and 1.3-1.4x height; IMD 2.0-2.3x MD; EH 2.1-2.3x MD; frons width 1.1x EH; POL

2.1-3.2x OOL; lower face with punctures evident; median frons irregularly strigulate. Antennal flagellum subfiliform, F1 and F2 annular, funicular segments slightly elongate to quadrate.

Mesosoma--Length 1.4x width; dorsum with procumbent brown to white setae; notauli present but shallow, scutum imbricate-strigate; scutellum length 1.1-1.2x width, reticulate (fig. 1), apex extending beyond metanotum (markedly elongate in large specimens). Propodeum perpendicular to ventral scutellum; spiracular sulcus usually deep, as wide as spiracle, and bordered laterally by a carina on the callus (fig. 10); panels strigate-reticulate; submedian carinae parallel, median area weakly reticulate to heavily sculptured. Forewing with row of setae in costal cell sometimes incomplete; basal cell asetose; speculum present, usually closed below by cubital vein; postmarginal vein longer than stigmal vein. Hind coxa reticulate to partially strigate.

Metasoma--Length 1.1-1.7x head + mesosoma, moderately compressed; posterior edge of T1 straight; T3-T5 (fig. 14) slightly carinate, foveate anteriorly, foveae deep and with small diameter, crenulate border imbricate and elevated, cusps reduced to absent, punctulate posteriorly, posterior margins straight; T6 upturned; T7 length subequal to height.

Male--Antennal scape flattened and clavate (fig. 16), funicular segments slightly elongate

Variation--The scutellar apex, spiracular sulcus, and carina on the callus vary considerably in the extent of their development; however, only 5 out of 81 specimens I examined lacked a distinctive spiracular sulcus. Color variation is quite pronounced in this species and displays a geographic pattern: specimens from California and Arizona are darker and more blue (see above) whereas specimens from eastern North America tend to be green, with scape, tegula, femora, and metasoma quite yellow;

specimens from Florida have the head and mesosoma bronze-violet, with even more yellowish metasoma and femora.

Ormyrus crassus new species

(figs. 2, 41)

Type locality--Mariana, Florida, U.S.A.

Type material--Holotype (female, USNM) bears the following labels: "Hopkins U.S. 15632f" (Dryocosmus favus), "reared Oct. 21-19", "Quercus catesbae", "Mariana Fla", "L.H. Weld collector". Paratypes (15 females, 2 males; USNM): same data as holotype.

Other material examined--U.S.A. (9 females, 1 male): Arkansas (Garland), Florida (Jackson, Sarasota, Volusia), New York (Suffolk), Pennsylvania (Philadelphia), South Carolina. Specimens are deposited in: AMNH, CNC, FSC, ORSU, USNM, UW.

Etymology--From the Latin for thick or stout, with reference to the stout antenna and relatively stout metasoma.

Diagnosis--This species, like O. hegeli, appears to have only one anellus in the antenna (i.e. length of F2 is subequal to F3). Ormyrus crassus can be distinguished by the transverse funicular segments of the antenna, the coarsely imbricate scutellum (fig. 2), the slightly strigate hind coxa, and the imbricate sculpture posterior to the crenulate border on the metasomal tergites. Color and sculpture of the scutellum and hind coxa are similar to O. dryorhizoxeni, but the latter has elongate funicle segments and the frenulum of the forewing is usually reduced.

Distribution--Records are from Arkansas, Florida, New York (Long Island), Pennsylvania, and South Carolina (fig. 41). Records of flight time include dates between May 25 and November 3.

Host associations-- Dryocosmus favus Beutenmueller, a cynipid root gall on red oaks, is the only known host.

Description--

Female--Length 2.5-4.3mm (holotype 3.9mm). Color blue-green, often with slight bronze; tegula brown; scape,

femora, and tibiae yellow (hind femur with some blue).  
Forewing immaculate.

Head--Width 2.2-2.3x length and 1.3-1.4x height; IMD 1.7-1.9x MD; EH 2.0-2.3x MD; frons width 1.1-1.2x EH; POL 2.3-2.5x OOL; lower face with punctures inconspicuous; median frons irregularly strigulate. Antennal flagellum moderately clavate, F1 annular; length of F2 subequal to F3, wider distally; funicle segments quadrate proximally, transverse distally.

Mesosoma--Length 1.3-1.4x width; dorsum with procumbent white setae; notauli indicated by faint line, scutum imbricate-strigate; scutellum length 1.2-1.3x width, coarsely imbricate (fig. 2), apex extending beyond metanotum. Propodeum somewhat diagonal (visible in dorsal view, as in fig. 32), spiracular sulcus inconspicuous, panels strongly diagonally strigate to reticulate, submedian carinae parallel, median area coarsely sculptured. Forewing with row of setae in costal cell complete; basal cell asetose; speculum present but slightly reduced, closed below by medial and cubital veins; postmarginal vein longer than stigmal vein. Hind coxa diagonally strigate.

Metasoma--Length 1.3-1.4x head + mesosoma, stout, slightly compressed; posterior edge of T1 straight; T3-T5 carinate, foveate anteriorly, foveae deep, crenulate border imbricate and only slightly elevated, cusp length slightly greater than intercusp distance, imbricate posteriorly, posterior margins straight; T6 hardly upturned, parallel to dorsum of T5; T7 length subequal to height.

Male--Scape with edges parallel; F2 may be anelliform, funicular segments quadrate. Forewing with speculum more reduced than in female.

Ormyrus distinctus Fullaway

(figs. 13, 17, 24, 42)

Ormyrus distinctus Fullaway 1912:276

Type locality--California, U.S.A.

Type Material--This species was described from one female specimen, which is now located in the LA collection and bears the following labels: "L.S. Jr. U.", "Lot 497", "sub 5". The specimen is missing the apical portions of both antennae, both hind tarsi, and the left hind tibia. According to the original description, this specimen was reared "from strawberry gall on Quercus dumosa from which no gall-flies were bred"; the most strawberry-like gall on this oak is the asexual generation gall of Antron quercusechinus (O.S), a gall from which I have seen 20 other specimens of O. distinctus.

Material examined--U.S.A. (296 females, 225 males): California (Alameda, Amador, Colusa, Contra Costa, El Dorado, Fresno, Lake, Los Angeles, Marin, Mendocino, Napa, Nevada, Placer, Riverside, Sacramento, San Bernardino, San Joaquin, San Luis Obispo, Santa Barbara, Santa Clara, Siskiyou, Sonoma, Tehama, Tulare, Yolo), Oregon (Benton, Curry, Douglas, Jackson, Jefferson, Josephine, Klamath, Lane, Wasco, Washington), Washington (Klickitat). Specimens are deposited in: AMNH, BMNH, CAS, CM, CNC, CSC, CU, FSC, KIEV, LA, MCZ, OHSU, ORSU, ROM, UCB, UCD, UCR, UI, UK, USNM, USU.

Diagnosis--Ormyrus distinctus can be distinguished by the absence of a longitudinal median carina on the metasomal tergites and by the relatively shiny propodeum (submedian carinae usually very weak). Other Nearctic species having the metasomal carina weak or absent are O. tenuis and O. turio, both of which have a more quadrate head (viewed from above), a narrower mesosoma, and distinctive antennae. O. thymus, O. unifasciatipennis, and O. unimaculatipennis also have

the metasomal carina weak or absent but these species have a gap in the row of setae in the costal cell, lack a scutellar shelf, and usually have a large infuscate spot on the forewing. Larger specimens of O. distinctus have the forewing with a linear stigmal vein surrounded by slight infuscation and with the basal cell setose (fig. 24).

Distribution--Ormyrus distinctus appears to be confined to the Pacific coast of North America (fig. 42). Most of the records of flight time are between mid May and the end of October; there is one record from mid April.

Host associations--Ormyrus distinctus is restricted to cynipid oak galls and is primarily associated with detachable twig galls and detachable leaf galls that become hard: Andricus brunneus Fullaway, A. crystallinus Bassett, A. fullawayi Beutenmueller, A. kingi Bassett, A. lasius (Ashmead), Antron douglasii (Ashmead), A. quercusechinus (O.S.), Besbicus multipunctatus (Beutenmueller), Disholcaspis corallina (Bassett), D. mellifica Weld, D. plumbella Kinsey, D. simulata Kinsey, D. washingtonensis (Gillette), Heteroecus melanoderma Kinsey, H. pacificus (Ashmead), H. sanctaeclarae (Fullaway), Sphaeroterus trimaculosum (M. & C.), Xanthoterus clavuloides (Kinsey), X. teres Weld. There are also a few records from swollen twig galls (Andricus chrysolepidicola (Ashmead), Callirhytis perdens (Kinsey), Dryocosmus asymmetricus (Kinsey)) and bud galls (Andricus opertus (Weld) and sexual generation galls of Antron quercusechinus), gall types in which other species of Ormyrus may occur. Ormyrus distinctus appears to be the only Ormyrus species present in all types of galls on Quercus sadleriana and Chrysolepis chrysophylla (chinkapin).

Description--

Female--1.6-5.3mm (holotype 3.6mm). Color green-blue, including scape (sometimes yellow basally), tegula, and

femora; tibiae yellow, hind tibia often yellow-orange, dark brown at distal tip, sometimes entirely dark with traces of green. Forewing immaculate, sometimes (in larger specimens, but not in the holotype) slightly darkened around stigmal vein.

Head--Width 2.0-2.1x length and 1.3x height; IMD 1.9-2.2x MD; EH 2.6-2.9x MD; frons width 1.0-1.1x EH; POL 3.4-4.0x OOL; lower face with punctures faint; median frons irregularly strigulate. Antennal flagellum subfiliform, F1 and F2 annular, funicular segments slightly elongate

Mesosoma--Length 1.3x width; dorsum with procumbent white setae; notauli inconspicuous, scutum imbricate-strigate; scutellum length 1.1x width, diagonally strigate, apex extending beyond metanotum. Propodeum perpendicular to ventral scutellum, spiracular sulcus inconspicuous, panels weakly strigate diagonally and quite shiny, submedian carinae parallel and very weak, median area shiny. Forewing (fig. 24) with row of setae in costal cell complete; basal cell setose in larger specimens and aetose in smaller specimens (holotype with 1 seta); speculum present and usually closed below by cubital vein, medial vein nearly complete; postmarginal vein longer than stigmal vein. Hind coxa reticulate (fig. 13).

Metasoma--Length 1.1-1.8x head + mesosoma, moderately compressed in larger specimens, subcylindrical in smaller specimens (including holotype); posterior edge of T1 straight; T3-T5 ecarinate, foveate anteriorly, foveae deep (at least in larger specimens), crenulate border imbricate and slightly elevated, cusp length subequal to intercusp distance in larger specimens (more reduced in smaller specimens), imbricate posteriorly, posterior margins straight; T6 upturned; T7 length subequal to height in larger specimens or less than height in smaller specimens.

Male--Scape with edges parallel (fig. 17); funicular



segments quadrate to slightly elongate.

Variation-- Ormyrus distinctus shows considerable variation in size which is correlated to the size of the host gall. Smaller specimens often have an asetose basal cell, a less distinctive stigmal vein, and relatively shorter metasoma. The largest and smallest specimens might appear to be separate species but intermediate sized individuals (such as those reared from Antron species and Andricus kingi, and including the type specimen) demonstrate a continuum between the two extremes. The most aberrant specimens are those reared from Neuroteras sadlerensis and cynipid galls on chinkapin, hosts which are more or less geographically isolated in the Klamath Ranges of southwestern Oregon and northwestern California (see chapter 6). Although I am placing them as O. distinctus their status needs further investigation.

Ormyrus dryorhizoxeni Ashmead

(figs. 3, 11, 15, 25, 43)

Ormyrus dryorhizoxeni Ashmead, 1885:xiv

Type locality--Jacksonville, Florida, U.S.A.

Type material--According to the original description, this species was described from 22 female specimens reared from Dryorhizoxenus floridanus Ashmead (= Belonocnema treatae Mayr). However, I could locate only eight specimens in the USNM collection. One of these is here designated LECTOTYPE and it bears the following labels: "Jacksonville, Fla", "Type No. 2890 U.S.N.M.", "Collection Ashmead". The lectotype is in good condition except the apical portions of both antennae are missing. Two of the paralectotypes are from Jacksonville and five are from St. Nicholas, Florida.

Other material examined--U.S.A. (325 females, 131 males): Arizona (Coconino), Arkansas (Bradley, Washington), California (Marin, Santa Clara), Colorado (Custer), Florida (Alachua, Duval, Franklin, Jackson, Marion, Nassau, Volusia), Georgia (Bulloch, Floyd, Jefferson, Tift), Maryland (Prince George), Mississippi (Chickasaw, Holmes, Jackson, Lowndes, Panola, Pearl River), Missouri (Shannon), Nevada (Clark), New Jersey (Cape May, Middlesex), New Mexico (Lincoln), North Carolina (Bertie, Carteret, Columbus, Cumberland, Dare), Oklahoma (Oklahoma), South Carolina (Florence), Tennessee (Grundy, Shelby), Texas (Anderson, Travis), Utah (Box Elder, Davis), Virginia (Arlington, Northhampton). Mexico (1 female, 2 males): Chiapas, Tamaulipas. Specimens are deposited in: AMNH, ANS, CAS, CNC, CU, FSC, INH, OKSU, ORSU, ROM, TAM, UK, USNM, UT.

Diagnosis--Ormyrus dryorhizoxeni is readily distinguished from all other Nearctic species by the generally blue body color contrasting with orange-yellow

femora; most other species have metallic femora, especially the hind femora), elongate funicular segments, reticulate-striate hind coxae (fig. 11), reduced speculum in forewing (fig. 25).

Distribution--Ormyrus dryorhizoxeni has been most commonly collected in the southeastern states, New Jersey to Florida to Missouri and Texas (fig. 43). There are a few records from the southwest: Arizona, California, Colorado, Nevada, and Utah; these specimens differ somewhat from typical southeastern forms (see below). There are few records of flight time since the vast majority of specimens were reared; records are between May 13 and October 27.

Host associations--Ormyrus dryorhizoxeni is restricted to various cynipid galls on oaks. It has more records from root galls than any other species of Ormyrus: Belonocnema treatae Mayr, Disholcaspis acetabula Weld, D. terrestris Weld, Dryocosmus favus Beutenmueller, and Holocynips hartmani (Weld). Ormyrus dryorhizoxeni is also frequently associated with twig galls: Disholcaspis colorado (Gillette), D. quercusvirens (Ashmead), D. spongiosa (Karsch), Dryocosmus imbricariae (Ashmead), and Neuroterus quercusbatatus (Fitch). Kinsey reared over 200 specimens from bud galls of Andricus quercusfoliatus (Ashmead); the only records from leaf galls include Andricus pattoni (Bassett), Belonocnema kinseyi Weld, and Callirhytis infuscata (Ashmead).

#### Description--

Female--Length, 2.4-5.9mm (holotype 4.1mm). Color blue (holotype) to sometimes green; scape, tegula, femora, and tibiae yellow; hind femur yellow orange sometimes with a trace of blue. Forewing immaculate, often slightly darkened around stigmal vein, whole wing sometimes faintly darkened.

Head--Width 2.3-2.5x length and 1.4x height; IMD

2.0-2.3x MD; EH 2.0-2.5x MD; frons width 1.1x EH; POL 2.4-3.5x OOL; lower face with punctures inconspicuous; median frons irregularly strigulate. Antennal flagellum subfiliform, F1 and F2 annular, funicular segments elongate.

Mesosoma--Length 1.3-1.4x width; dorsum with procumbent white setae; notauli inconspicuous, scutum imbricate-strigate; scutellum length 1.2-1.3x width, imbricate-diagonally strigate (fig. 3), apex extending beyond metanotum. Propodeum perpendicular to ventral scutellum, spiracular sulcus inconspicuous, panels diagonally strigate, submedian carinae parallel, median area shiny. Forewing (fig. 25) with row of setae in costal cell complete; basal cell usually aetose; speculum usually very reduced and closed below by medial and cubital veins; postmarginal vein longer than stigmal vein. Hind coxa diagonally strigate, becoming reticulate in central area (fig. 11).

Metasoma--Length 1.5-1.9x head + mesosoma, moderately compressed; posterior edge of T1 straight; T3-T5 (fig. 15) carinate, foveate anteriorly, foveae deep, crenulate border shiny and slightly elevated, cusp length subequal to intercusp distance, imbricate posteriorly, posterior margins straight; T6 upturned; T7 length subequal to height.

Male--Scape with edges parallel, as in female; funicular segments quite elongate.

Variation--Specimens from the southwest have the forewing with the speculum better developed (fewer setae) and are often more bronze (less blue) colored. However the elongate antennal segments, strigate hind coxa, and shiny crenulate border suggest that these specimens are best placed in O. dryorhizoxeni, pending further investigation.

Ormyrus hegeli (Girault)

(figs. 4, 18, 26, 44)

Monobaeus hegeli Girault 1917:106

Type locality--Michigan, U.S.A.

Type material--This species was described from one female specimen, which bears the following labels: "Mich", "C.P. Gillette, 857", "female type 20230" (the original description reads: "Type: Catalogue No. 20239, U.S.N.M."). An antenna is mounted on a slide (not seen).

Other material examined--U.S.A. (44 females, 25 males): Arizona (Coconino, Navajo, Santa Cruz, Yavapai), California (Colussa, Shasta, Tehama), Colorado (El Paso), Connecticut (Fairfield), Florida (Alachua, Duval, Polk), Michigan (Ingham), Missouri (Shelby), New Jersey (Camden), New Mexico (Catron, Socorro), New York (Bronx), Texas (Dallas), Utah (Davis, Washington). MEXICO (34 females, 14 males): Chiapas, Chihuahua, Durango, Oaxaca. Specimens are deposited in: AMNH, ANS, CNC, CSU, CU, FSC, OHSU, ORSU, ROM, UCD, UMIS, USNM, UT.

Diagnosis--Like O. crassus, O. hegeli has the second flagellar segment nearly as long as the third segment, thus appearing to have 1 anellus and 7 funicle segments in most specimens. Metasomal tergites 3-5 have crenulate borders with cusps reduced and with punctulate sculpture posteriorly, as in O. acylus and O. setosus; O. hegeli can be distinguished by the transversely strigate scutellum (fig. 4).

Distribution--Ormyrus hegeli has been collected in the eastern states (Connecticut and Florida to Michigan, Missouri, and Texas) as well as in Colorado, Utah, New Mexico, Arizona, California (north to Shasta Co.), and Mexico (south to Oaxaca)--see fig. 44. Most records are from the southwestern states and Mexico. There are very few records of flight time since most of the material was reared; records include April to October.

Host associations--Most of the records for O. hegeli are from cynipid galls on oak twigs. The best documented host records are Andricus ruginosus Bassett and A. wheeleri Beutenmueller; both galls are large woody stem swellings. There are single records from Amphibolips quercuscinerea (Ashmead), Disholcaspis mammilana Weld, D. pedunculoides Weld, and D. quercusmamma (Walsh). From Mexican oaks, Kinsey reared specimens from "globulus", "mellana", "mellaria", "peredurus", and "tecturn".

Description--

Female--Length, 3.0-5.5mm (holotype 3.6mm). Dark colored, mostly bronze-violet with some green; antennal scape, tegula and femora dark green; tibiae dark brown to green. Forewing immaculate.

Head--Width 2.2-2.3x length and 1.3-1.4x height; IMD 1.9-2.0x MD; EH 2.1-2.4x MD; frons width 1.1x EH; POL 2.4-3.6x OOL; lower face with punctures faint; median frons irregularly strigulate. Antennal flagellum subfiliform, F1 annular, F2 usually subequal to F3 (rarely annular), funicular segments slightly elongate to quadrate.

Mesosoma--Length 1.4x width; dorsum with procumbent white setae; notauli inconspicuous, scutum imbricate-strigate; scutellum length 1.1-1.2x width, transversely strigate with lines strong and shiny interstices reduced (fig. 4), apex extending beyond metanotum. Propodeum perpendicular to ventral scutellum, spiracular sulcus inconspicuous, panels diagonally strigate, submedian carinae diverging posteriorly, median area coarsely sculptured. Forewing (fig. 26) with row of setae in costal cell complete; basal cell usually with 1-3 setae; speculum present, closed below by medial and cubital veins; postmarginal vein longer than stigmal vein. Hind coxa reticulate.

Metasoma--Length 1.3-1.6x head + mesosoma, moderately

compressed; posterior edge of T1 straight; T3-T5 carinate, foveate anteriorly, foveae deep, crenulate border imbricate and elevated, cusps reduced, punctulate posteriorly, posterior margins straight; T6 upturned; T7 length subequal to height.

Male--Scape noticeably emarginate (fig. 18), funicular segments quadrate.

Variation--Color is fairly uniform although I have seen two specimens from Florida which have the scape, tegula, femora, and tibiae yellow. Although the scutellum is usually transversely strigate, in specimens reared from Andricus ruginosus the scutellum is reticulate.

O. labotus Walker

(figs. 19, 45)

Ormyrus labotus Walker, 1843: 148Pteromalus Querci-pilulae Fitch, 1859: 819 NEW SYNONYMYOrmyrus quercus Ashmead, 1886: 128 NEW SYNONYMYOrmyrus andricus Ashmead, 1886: 128Ormyrus brunneipes Provancher, 1887:198 NEW SYNONYMYOrmyrus ventricosus Ashmead, 1887: 189 NEW SYNONYMYOrmyrus minutus Ashmead, 1887: 189 NEW SYNONYMY

Type locality--St. John's Bluff, Florida, U.S.A.

Type material-- O. labotus: The type series, one female and two males (only one examined), is in the BMNH collection. The female (labelled: "1479a") was designated lectotype by Burks (1975) and it is in good condition except the hind tarsi are missing. The one paralectotype I examined (labelled: "1479c") is another species, O. reticulatus n.sp., according to my interpretation. O. quercipilulae: This species was described from a single female. The holotype is attached to a gall of Acraspis pezomachoides (O.S.) and bears the following labels: "Fitch's Type", "From Fitch's Collection", "Type No 1835 USNM". O. quercus: This species was described from eight specimens (six females, two males). One of the females is here designated LECTOTYPE; it is point mounted, in good condition, and bears the following labels: "Jacksonville Fla", "5/2/81 batatoides" (= Callirhytis quercusbatatoides), "Type No 41107 USNM". O. andricus: This species was described from one female and was synonymized with O. labotus by Burks (1975). According to the original description, the type specimen was reared from Andricus difficilis Ashmead ms. (= Callirhytis). O. brunneipes: This species was described from a single female (located in the LU collection); label data are given in Burks (1963). O. ventricosus: According to the original description, this species was "described



from specimens reared from Andricus ventricosus B., and an undescribed oak gall sent by Mr. Brodie". The description itself appears to be based on one male which was all I found; it is labelled: "5-86", "17", "Type No 41106 USNM". This species was synonymized with O. brunneipes by Burks (1963). O. minutus: According to the original description, this species was described from "numerous specimens reared from oak gall Neuroterus laurifoliae Ashm." (an unplaced cynipid in Krombein et al 1979, type lost). I found thirteen specimens (two females, eleven males) in the USNM collection. One of the males is here designated LECTOTYPE; it is point mounted with two other males and one eupelmid (!) on the same pin (lectotype is second from top) and bears the label: "Cotype No 41105".

Other material examined--CANADA (21 females, 21 males): Nova Scotia (Halifax), Ontario (Hamilton, Ottawa, Welland), Quebec (Cap Rouge, Luskville Falls). U.S.A. (2323 females, 1783 males): Arkansas (Hempstead, Prairie, St. Francis), Colorado (El Paso, Fremont, Garfield, Ouray), Connecticut (Fairfield, New Haven, Tolland), Florida (Alachua, Duval, Franklin, Marion, Volusia), Georgia (Floyd, Hart, Monroe, Peach), Illinois (Champaign, Cook, Jo Daviess, Marshall), Indiana (Greene, Marion, Monroe, Owen, Ripley, Tippecanoe, Vanderburgh, Warrick), Iowa (Allamakee, Woodbury), Kansas (Cherokee, Riley), Kentucky (Bell, Christian, Fayette, Marion, Union), Louisiana (Jackson, St. Tammany), Maine (Hancock), Maryland (Carroll, Prince Georges), Massachusetts (Essex, Hampden, Middlesex), Michigan (Allegan, Washtenaw), Minnesota (Fillmore, Ramsey, Rice, Yellow Medicine), Mississippi (Alcorn, Chickasaw, Clarke, Hinds, Kemper, Lowndes, Marshall, Panola, Pearl River, Wayne), Missouri (Boone, Butler, Franklin, Greene, Iron, Mississippi, Shannon, Shelby, Wayne), New Jersey (Camden, Gloucester, Middlesex), New Mexico, New York (Rockland, Saratoga,

Tompkins), North Carolina (Columbus, Henderson), North Dakota (Cass), Ohio (Allen, Gallia, Morgan, Ross, Scroto, Summit), Oklahoma (Grady, Payne), Pennsylvania (Allegheny, Cambria, Crawford, Dauphin, Lebanon, Somerset, Westmoreland), South Carolina (Berkeley, Florence), South Dakota (Lincoln), Tennessee (Claiborne, Hamilton, Monroe, Shelby), Texas (Bexar, Brazos, Chambers, Dallas, Fort Bend, Harris, Travis, Waller, Wharton, Wheeler), Utah (Box Elder, Davis, Salt Lake, Sevier, Washington), Virginia (Arlington, Fairfax, Rockingham), West Virginia, Wisconsin (Brown, Columbia, Fond du Lac, Iowa, Marathon, Monroe, Portage, Walworth). MEXICO (62 females, 88 males): Coahuila, Nuevo Leon, Tamaulipas. Specimens are deposited in AMNH, ANS, CM, CNC, CSU, CU, FSC, INH, ISU, KSU, MCZ, OHSU, OKSU, ORSU, REM, ROM, TAM, UA, UC, UCD, UCR, UG, UI, UK, UMA, UMIC, UMIS, USNM, UT, UW, VP, WSU.

Diagnosis--Ormyrus labotus is very close to O. rosae, the females being particularly difficult to distinguish. Ormyrus labotus males usually have the antennal scape noticeably emarginate (fig. 19) whereas in O. rosae the scape is like the female (parallel sided). Females differ from O. rosae in having the sculpture of the upper head with more shiny interstices, the metasoma usually more metallic (less brown), and the foveae often somewhat removed from the crenulate border.

Distribution--This species is the most abundant Ormyrus species in oak galls in eastern North America. It also occurs in the Rocky Mountain states and in the southwest and Mexico, but is absent from the Pacific coast states (only reared specimens are included in the distribution map, fig. 45). Records of flight time are from March through December.

Host associations--Ormyrus labotus occurs in a wide variety of cynipid galls on oak (see Table 5, chapter 5) and has more recorded hosts (65 cynipid species) than any other Nearctic Ormyrus species. The majority of records

are from leaf galls, especially woolly leaf galls; this species appears to be relatively less common in acorn, root, and twig galls.

Description--

Female--Length 1.6-4.6mm (holotype 2.0mm). Color usually green-blue; scape and tibiae yellow; femora usually with green-blue (especially hind femur) but often quite yellow. Forewing immaculate.

Head--Width 2.1-2.2x length and 1.3x height; IMD 1.5-1.9x MD; EH 2.0-2.5x MD; frons width 1.0-1.1x EH; POL 3.3-3.9x OOL; lower face with punctures faint; median frons irregularly strigulate. Antennal flagellum usually subfiliform, F1 and F2 annular, funicular segments slightly elongate, sometimes quadrate.

Mesosoma--Length 1.3-1.4x width; dorsally with procumbent white setae; notauli usually inconspicuous; scutum imbricate-strigate; scutellum length 1.1-1.2x width, diagonally strigate, apex extending beyond metanotum. Propodeum perpendicular to ventral scutellum, spiracular sulcus inconspicuous, panels weakly diagonally strigate, submedian carinae parallel, median area mostly shiny. Forewing with row of setae in costal cell usually complete; basal cell asetose; speculum present, usually closed below by cubital setae; postmarginal vein longer than stigmal vein. Hind coxa usually reticulate.

Metasoma--Length 1.3-2.0x head + mesosoma, moderately compressed to subcylindrical; posterior edge of T1 straight; T3-T5 carinate, foveate anteriorly, foveae quite deep to shallow, crenulate border imbricate and slightly elevated, cusp length subequal to intercusp distance, imbricate posteriorly, posterior margins straight; T6 upturned; T7 length usually subequal to height, sometimes more elongate.

Male--Scape usually emarginate on one side (fig. 19), funicular segments quadrate.

Variation--Much of the variation is size related (e.g.

relatively longer metasoma in larger specimens). The male scape is sometimes not noticeably emarginate (e.g. specimens reared from Andricus quercuslanigera (Ashmead), A. quercuspetiolicola (Bassett), and Belonocnema kinseyi Weld). As defined here, O. labotus is the most polyphagous and abundant species of Ormyrus in North America and thus morphological variation is expected. Although the flagellar segments of the antennae are usually elongate, a series of specimens (USNM) reared from Callirhytis cornigera (Osten Sacken) have quadrate flagellar segments. There is also variation in the relative proximity of the metasomal foveae to the crenulate border.

Discussion--Despite the variation displayed by this species, I found no consistent or discrete differences with which to separate variant specimens and for this reason I propose the above synonymies. I view these synonymies as a tentative convenience pending further study of both this species and O. rosae. Females of these two species are very difficult to separate and since the lectotype was not from a reared series, it is quite possible that O. rosae should be synonymized with O. labotus. In this case, specimens reared from oak galls and having an emarginate scape in males (here called O. labotus) would become O. quercipilulae --assuming that the importance I attribute to the male scape is justified. It is disconcerting that O. labotus specimens reared from a few oak galls have males with non-emarginate scapes (this includes the type series of O. quercus). Perhaps O. rosae occasionally occurs in oak galls, or possibly O. rosae and O. labotus (as defined here) are one species, or a complex of sibling species. A more detailed analysis of this complex is required and should include Palearctic species such as O. punctiger and O. rufimanus (neither of which has an emarginate male scape).

Ormyrus reticulatus new species

(figs. 20, 46)

Type locality--Paradise Key, Florida, U.S.A.

Type material--Holotype (female, USNM) bears the following labels: "Hopkins U.S. 10781v" (Callirhytis quercusbatatoides), "reared Feb., Mar. 1919", "Quercus virginiana", "Paradise Key Fla", "H S Barber collector". Paratypes (5 females, 3 males; USNM): same data as holotype.

Other material examined--CANADA (1 female): British Columbia (Victoria). U.S.A. (57 females, 20 males): California (Colusa, Contra Costa, Napa, Santa Clara, Tuolumne), Colorado (El Paso, Pueblo), Florida (Alachua, Duval, Hernando, Leon, Monroe, Pinellas, Putnam), Louisiana (Washington), New Mexico (Roosevelt), South Dakota (Lincoln), Texas (Dallas), Utah (Davis, Washington), Virginia (Arlington). Specimens are deposited in: AMNH, CM, CNC, FSC, ORSU, UCB, UCD, UK, USNM.

Etymology--From the Latin for netlike, with reference to the sculpture of the scutellum.

Diagnosis--Ormyrus reticulatus resembles O. labotus and O. rosae but can be distinguished by the reticulate scutellum (as in fig. 1) and more sculptured propodeum. Some O. labotus and O. rosae may have the scutellum slightly reticulate but the shiny interstices are more extensive and the lines are more diagonally (as opposed to transversely). Like O. rosae, the male scape is not emarginate.

Distribution--This species, although uncommon in collections, appears to have a broad distribution across North America, from Virginia and Florida to British Columbia and California (fig. 46); there are more specimens from Florida than any other state. No records exist from the northeast. The only records of flight time

are from Florida and include the months from October through March.

Host associations--Ormyrus reticulatus appears to be primarily associated with cynipid twig galls on oaks. The host records are further restricted to just two types of twig galls: woody stem swellings (Andricus chrysolepidicola (Ashmead), Callirhytis frequens (Gillette), and C. quercusbatatoides (Ashmead)) and detachable twig galls formed by Disholcaspis eldoradensis (Beutenmueller), D. pernicioso (Bassett), D. prehensa Weld, D. quercusmamma (Walsh), and D. simulata Kinsey. There are two records from unidentified acorn galls (unspecified oak in Texas and Quercus palustris Muenchh. in Virginia).

Description--

Female--Length 2.4-4.6mm (holotype 3.8mm). Color varies from bronze-violet with yellow scape and femora (Florida specimens) to green-blue, including scape, tegula, and femora; tibiae yellow-brown. Forewing immaculate.

Head--Width 2.1-2.3x length and 1.3-1.4x height; IMD 1.7-2.0x MD; EH 2.1-2.5x MD; frons width 1.1x EH; POL 2.5-3.1 OOL; lower face with punctures inconspicuous; median frons irregularly strigulate. Antenna flagellum subfiliform, F1 and F2 annular, funicular segments slightly elongate.

Mesosoma--Length 1.3x width; with procumbent white setae on dorsum; notauli indicated by faint line or inconspicuous; scutum imbricate-strigate; scutellum length 1.1-1.2x width, reticulate (lines quite transverse), apex extending beyond metanotum. Propodeum perpendicular to ventral scutellum, spiracular sulcus inconspicuous, panels diagonally strigate, submedian carinae parallel, median area coarsely sculptured. Forewing with row of setae in costal cell complete; basal cell asetose; speculum present, closed below by cubital vein; postmarginal vein

longer than stigmal vein. Hind coxa reticulate.

Metasoma--Length 1.3-1.8x head + mesosoma, moderately compressed; posterior edge of T1 straight; T3-T5 carinate, foveate anteriorly, foveae deep, crenulate border imbricate and elevated, cusp length subequal to intercusp distance, imbricate posteriorly, posterior margins straight; T6 upturned; T7 length subequal to height.

Male--Scape with edges parallel (fig. 20); funicular segments slightly elongate to quadrate.

Variation--Specimens from Florida are mostly bronze colored and the metasoma is often longer. Two specimens from New Mexico (Roosevelt Co.; JZ) have the length of the head relatively small with respect to width. West coast specimens have more strigate hind coxae.

Discussion--One of the hosts, Callirhytis quercusbatatoides, is the same host recorded for the type series of O. quercus (here synonymized with O. labotus). Like O. reticulatus, males of O. quercus have a non-emarginate scape, but types of the latter have the scutellum diagonally strigate and the median part of the propodeum shiny.

O. rosae Ashmead

(fig. 47)

Ormyrus rosae Ashmead, 1885: xiv

Type locality--Jacksonville, Florida, U.S.A.

Type material--According to the original description, this species was described from "specimens bred 1881 from gall Rhodites ignota O.S." (= Diplolepis ignota). I found two females in the USNM collection, one of which is here designated LECTOTYPE; it bears the following labels: "Jacksonville Fla", "Type No 2891 U.S.N.M.", "July 81, Rose gall".

Other material examined--CANADA (239 females, 150 males): Alberta, British Columbia, Northwest Territories (Yellowknife), Ontario, Quebec, Saskatchewan. U.S.A. (619 females, 368 males): Arizona (Coconino), Arkansas (Washington), California (Contra Costa, Marin, Nevada, Placer, Riverside, Sacramento, Santa Clara, Solano, Sutter, Tulare, Yolo), Colorado (Clear Creek), Connecticut (New Haven), Delaware, Florida (Duval), Georgia (Clarke, Monroe), Idaho (Gooding, Kootenai, Latah, Oneida), Illinois (Cook), Indiana (Monroe, Posey), Kansas (Rice, Riley), Maine (Washington), Maryland (Anne Arundel, Prince George), Massachusetts (Barnstable, Middlesex), Michigan (Kalamazoo, Livingston, Malcomb, Midland, Washington), Minnesota, Missouri (Boone, Pike), Montana, Nevada (Washoe), New Hampshire (Merrimack, Rockingham), New Jersey (Burlington, Cumberland, Middlesex, Ocean, Union), New York (Bronx, Greene, Nassau, Rockland, Tompkins), North Carolina (Cumberland, Wake), Ohio (Cuyahoga, Franklin, Green, Licking, Richland, Sandusky, Stark), Oregon (Benton, Jackson, Marion, Wasco), Pennsylvania (Dauphin, Fulton, Montgomery, Philadelphia), South Carolina (Greenville), Tennessee (Monroe), Texas (Bastrop, Patricio), Utah (San Juan), Virginia (Arlington, Fairfax, Frederick, Montgomery, New Kent), Washington (King, San



Juan Island, Skagit, Thurston, Whitman), Washington D.C., West Virginia (Barbour, Clay), Wyoming (Johnson, Uinta). Specimens are deposited in AMNH, ANS, CAS, CM, CNC, CSC, CU, FSC, INH, ISU, KSU, LA, MCZ, OHSU, ORSU, REM, ROM, TAM, UA, UCB, UCD, UCR, UG, UI, UK, UMA, UMIC, UMIS, USNM, USU, UT, UW, VP, WSU; extensive reared material from galls of Diplolepis spp. are deposited at Laurentian University, Sudbury, Ontario.

Diagnosis--Ormyrus rosae differs from O. labotus by the parallel sided scape in the male (as opposed to a sexually dimorphic, emarginate scape). Ormyrus rosae females often have more crowded sculpture on the upper head (fewer shiny interstices), and a more brownish metasoma with foveae nearly always adjacent to the crenulate border. Because some male O. labotus specimens lack a noticeably emarginate scape, host data is often necessary for positive identification of O. rosae. In the west, where O. labotus is absent, O. rosae is more readily identifiable.

Geographic distribution-- Ormyrus rosae occurs across North America (fig. 47) and extends farther north (Yellow Knife, Northwest Territories) and higher in elevation than any other North American species. There are no records from Mexico. Records of flight time are from April through October.

Host associations--This species is associated with cynipid galls on species of Rosa, Rubus, and Potentilla (Rosaceae). Specific records are given in table 5 (chapter 5); there are a few records from the introduced Diplolepis rosae (L.) but I have not been able to verify this. Specimens representing a second Ormyrus species from pteromalid galls (Hemadas nubilipennis) on Vaccinium (Ericaceae) appear to be O. rosae.

Description--

Female--Length 1.6-4.5mm (holotype 3.0mm). Color blue-green, sometimes including parts of femora, nearly

always with some brown visible in metasoma; scape, femora, and tibiae yellow; hind femur varies from yellow (holotype) to blue-green. Forewing immaculate.

Head--Width 2.2x length and 1.3x height; IMD 1.5-1.8x MD; EH 2.0-2.2x MD; frons width 1.1-1.2x EH; POL 2.5-2.8x OOL; lower face strigate with punctures usually inconspicuous; median frons irregularly strigulate. Antennal flagellum subfiliform, F1 and F2 annular, funicular segments usually slightly elongate to quadrate (see under variation).

Mesosoma--Length 1.3-1.4x width; dorsally with procumbent white setae; notauli inconspicuous; scutum imbricate-strigate; scutellum length 1.2x width, diagonally strigate, apex extending beyond metanotum. Propodeum perpendicular to ventral scutellum, spiracular sulci inconspicuous, panels weakly diagonally strigate, submedian carinae parallel, median area shiny. Forewing with row of setae in costal cell usually complete; basal cell asetose; speculum present, usually closed below by cubital vein; postmarginal vein longer than stigmal vein. Hind coxa reticulate.

Metasoma--Length 1.3-1.9x head + mesosoma, subcylindrical to moderately compressed; posterior edge of T1 straight; T3-T5 carinate, foveate anteriorly, foveae fairly deep, crenulate border imbricate and barely elevated, cusp length subequal to intercusp distance, imbricate posteriorly, posterior edge straight; T6 upturned; T7 length subequal to height.

Male--Scape parallel sided (not noticeably emarginate).

Variation--Specimens reared from Potentilla and western Rubus (Diastrophus kincaidii Gillette) have the antennal flagellum very slender with funicular segments elongate, whereas specimens from eastern Rubus (Diastrophus cuscutaeformis O.S. and D. nebulosus O.S.) have the flagellum quite stout with funicular segments quadrate. Specimens from Rosa and Vaccinium usually have

the flagellum intermediate between these two extremes and therefore I am considering these all one species. Female specimens from Vaccinium have an elongate, compressed metasoma as in O. vacciniicola --perhaps due either to effects of host on parasitoid morphology or to hybridization.

Discussion--see O. labotus.

Ormyrus setosus new species

(figs. 5, 21, 27, 48)

Type Locality--Idyllwild, California, U.S.A.

Type material--Holotype (female, USNM) bears the following labels: "Hopkins U.S. 15641a", "Reared June 25.23", "Quercus chrysolepis", "Idyllwild Calif", "L.H. Weld collector". Paratypes (4 females, 6 males; USNM): same data as holotype.

Other material examined--U.S.A. (27 females, 12 males): California (Placer, Riverside, San Bernardino, Solano, Tulare). Specimens are deposited in: CNC, LA, OHSU, ORSU, UCD, UCR, USNM.

Etymology--From the Latin, with reference to the setose body and wings.

Diagnosis--Females of O. setosus can be separated from all other Nearctic species by the following characters: last metasomal tergite very elongate, dorsum of head and thorax with erect black setae (rather than procumbent white setae), very setose forewings (more setose than in any other Nearctic species, fig. 27), and metasomal tergites 3-5 with cusps reduced and punctulate posteriorly. Males can be distinguished by the very setose forewings.

Distribution--Ormyrus setosus is known only from southern and central California (fig.48). There are few records of flight time; early and late records include April and October, respectively.

Host associations--The only host record is from the unisexual generation gall of Callirhytis quercuspomiformis (Bassett), a large detachable twig gall. Since this cynipid species does not occur on Quercus chrysolepis Liebm., records (holotype and paratypes) from unspecified galls on this oak indicate that there is another host.

Description--

Female--Length, 3.5-6.0mm (holotype 4.5mm). Color

green-blue (with traces of bronze and violet), including scape (basal part yellow) and femora; tegula and tibiae yellow; hind tibia often black apically. Head and mesosoma more setose than other species. Forewing immaculate, slightly darkened around stigmal vein.

Head--Width 2.4-2.5x length and 1.4-1.5x height; IMD 2.1-2.3x MD; EH 2.5-2.9x MD; frons width 1.1x EH; POL 2.3-2.5x OOL; lower face with punctures evident; median frons irregularly strigulate. Antennal flagellum subfiliform, F1 and F2 annular, funicular segments slightly elongate.

Mesosoma--Length 1.4x width; dorsum with semi-erect dark setae; notauli present, scutum imbricate-strigate; scutellum length 1.1x width, imbricate-diagonally strigate (fig. 5), apex extending beyond metanotum. Propodeum perpendicular to ventral scutellum, spiracular sulcus inconspicuous, panels diagonally strigate, submedian carinae weak and subparallel, median area weakly sculptured to shiny. Forewing (fig. 27) with row of setae in costal cell complete; basal cell very setose; speculum absent, median and cubital veins complete; postmarginal vein longer than stigmal vein. Hind coxa transversely strigate.

Metasoma--Length 1.5-2.1x head + mesosoma, very compressed; posterior edge of T1 slightly emarginate; T3-T5 carinate, foveate anteriorly, foveae deep and with small diameter, crenulate border imbricate and elevated, cusps reduced to absent, punctulate posteriorly, posterior margins straight; T6 upturned; T7 length greater than height.

Male--Scape with edges parallel (fig. 21); funicular segments slightly elongate.

Ormyrus tenuis new species

(figs. 35, 49)

Type locality--Archuleta Co., Colorado, U.S.A.

Type material--Holotype (female, USNM) bears the following labels: "Colo. Archuleta, Low. Piedra Cpg., San Juan Nat.For., 21 Aug 83 Hanson" (Lower Piedra Campground, swept from Quercus gambelii). Paratypes (3 females; USNM): same data as holotype.

Other material examined--CANADA (5 females, 1 male): Ontario (Ottawa). U.S.A. (10 females, 2 males): Arizona (Cochise), Colorado (Huerfano), Michigan (Midland), New Mexico (Lincoln), New York (Erie), Ohio (Tuscarawas), West Virginia. Specimens are deposited in: CAS, CNC, OHSU, ORSU, UK, USNM.

Etymology--From the Latin, for thin, with reference to the shape of the antennal flagellum and mesosoma.

Diagnosis--This species has a quadrate head (dorsal view) and narrow mesosoma as in O. turio (fig. 35) but it can be separated from the latter by the filiform antennal flagellum (vs clavate), the more vertical propodeum (fig. 31), and the usually concealed foveae on metasomal tergites 3-5; this is the only Nearctic species in which foveae are often concealed even in males.

Distribution--Ormyrus tenuis has been collected in the southwest and the east, from Arizona and Colorado to Ontario and West Virginia (fig. 49). Records of flight time include dates between May 25 and September 17.

Host associations--Although there are no host records, most specimens were swept from oak; morphological similarity to O. turio (thick head, narrow mesosoma) and paucity of specimens suggest that the host may be cynipid galls embedded in oak twigs.

## Description--

Female--Length 1.8-3.0mm (holotype 2.7mm). Color green, including femora and usually tegula; metasoma predominantly dark brown-black (with traces of green);

scape and tibiae brown. Forewing immaculate.

Head--Width 1.8x length and 1.2-1.3x height; IMD 1.5-1.9x MD; EH 2.1-2.3x MD; frons width subequal to EH; POL 3.3-3.7x OOL; lower face with punctures faint; median frons irregularly strigulate. Antennal flagellum filiform and slender, F1 and F2 annular, funicular segments elongate.

Mesosoma--Length 1.5-1.6x width; dorsum with procumbent white setae; scutum and scutellum noticeably flattened in lateral view; notauli evident but shallow; scutum imbricate-strigate; scutellum length 1.1-1.3x width, transversely-diagonally strigate, apex extending beyond metanotum. Propodeum more or less perpendicular to ventral scutellum, spiracular sulcus inconspicuous, panels diagonally strigate to reticulate, submedian carinae parallel, median area weakly sculptured. Forewing with row of setae in costal cell usually incomplete; basal cell asetose; speculum present and open below; postmarginal vein longer than stigmal vein. Hind coxa reticulate.

Metasoma--Length 1.4-1.6x head + mesosoma, moderately compressed; posterior edge of T1 slightly emarginate; T3-T5 weakly carinate to ecarinate, foveae concealed by preceding tergite, crenulate border imbricate and only slightly elevated, cusp length less than intercusp distance, imbricate posteriorly, posterior margins slightly emarginate; T6 only slightly upturned; T7 length subequal to height.

Male--Scape with edges parallel; funicular segments slightly elongate. Metasomal foveae usually concealed.

Ormyrus thymus Girault

(figs. 12, 30, 50)

Girault, 1917:87

Type locality--Mountain View, California, U.S.A.

Type material--This species was described from one female specimen, which bears the following labels: "Mtn View Cal", "Ehrhorn Lot 2", "27", "Type No. 20976" (USNM). The specimen is embedded in glue, concealing the antennae and hind coxae.

Other material examined--U.S.A. (3 females, 1 male): Florida (Putnam), Georgia. MEXICO (4 females): Tamaulipas. BELIZE (1 female). Specimens are deposited in: CNC, ORSU, USNM.

Diagnosis--Ormyrus thymus, like O. unifasciatipennis and O. unimaculatipennis, has the forewing with a large infusate spot and the row of setae in the costal cell incomplete, and the scutellum seldom extending beyond the metanotum (fig. 30). Ormyrus thymus can be distinguished by the strigate (rather than reticulate) hind coxa (fig. 12) and by the absence of exposed foveae on T5.

Distribution--The type was collected in southern California but all other specimens were collected in the Southeast (Georgia, Florida, Mexico, and Belize). The only records of flight time are December 24 and February 21 in Florida.

Host associations-- The only record is one specimen (USNM) from seeds of Bucida cucides (Combretaceae) in Belize (26 June 1970, Matthews).

## Description--

Female--Length 1.9-2.2mm (holotype 2.2mm). Color varies from entirely light brown with dark brown metasoma (Florida and Georgia specimens, including holotype) to blue-green including scape (except basal part), tegula, and femora, with dark brown metasoma and tibiae (Mexico



and Honduras). Forewing usually with large infusate area below marginal vein, with setae in this area longer.

Head--Width 2.1x length and 1.3x height; IMD 1.7-2.0x MD; EH 2.4-2.6x MD; frons width subequal to EH; POL 3.0-3.7x OOL; lower face with punctures inconspicuous; median frons regularly and transversely strigulate. Antennal flagellum clavate, F1 and F2 annular, funicular segments slightly elongate to quadrate proximally, transverse distally.

Mesosoma--Length 1.3x width; dorsum with procumbent white setae; notauli absent, scutum imbricate-strigate; scutellum length 1.1x width, transversely-diagonally strigate, apex not extending beyond metanotum (fig. 30) Propodeum perpendicular to ventral scutellum, spiracular sulcus inconspicuous, panels weakly diagonally strigate, submedian carinae parallel, median area quite shiny. Forewing with row of setae in costal cell incomplete; basal cell aetose; speculum present, open below; postmarginal vein subequal to stigmal vein. Hind coxa transversely strigate (fig. 12).

Metasoma--Length 1.1-1.3x head + mesosoma, subcylindrical; posterior edge of T1 straight; T3-T5 weakly carinate to ecarinate, crenulate border weakly imbricate and barely elevated, cusp length less than intercusp distance, imbricate-shiny posteriorly, posterior margins straight; T3-T4 foveate anteriorly, foveae shallow; T5 with foveae always concealed; T6 upturned; T7 length subequal to or less than height.

Male--Scape widest in middle; funicular segments mostly transverse.

Variation--Color varies considerably (see above).

Discussion--The distribution suggests that what I am calling O. thymus is actually a new species and that O. thymus may be synonymous with O. unifasciatipennis. More collecting and reexamination of the type (including removal of glue from hind coxae) are necessary to

determine whether this is the case.

Ormyrus turio new species

(figs. 32, 35, 51)

Type locality--Corvallis, Oregon, U.S.A.

Type material--Holotype (female, USNM) bears the following label: "OR Benton Co., Corvallis, 23 June 1981, Paul Hanson". Paratypes (17 females, 8 males; BMNH, CNC, KIEV, ORSU, USNM): same data as holotype except dates are 23 May, 6 June, 11 June, 15 June, 3 July, 9 July, 12 July, 4 August, 13 August, 16 August, 16 September.

Other material examined--U.S.A. (28 females, 19 males): California (Madera, San Diego, Santa Clara, Yolo), Oregon (Benton, Marion). Specimens are deposited in: CNC, FSC, LA, ORSU, UCD, UCR, UK, USNM.

Etymology--A noun in apposition, from the Latin, for branch or twig, with reference to the host association of this species.

Diagnosis--This species resembles O. tenuis in its general habitus: quadrate head (viewed from above) and elongate, narrow mesosoma (fig. 35). Ormyrus turio can be distinguished by its clavate antennal flagellum, well developed metasomal foveae, and propodeum more diagonal than in other Nearctic species (fig. 32).

Distribution--Ormyrus turio has been collected only in California and Oregon (fig. 51), but probably occurs in Washington and southern British Columbia as well. In Oregon, I have recorded flight times ranging from May 23 to October 5; in California there is one record from November 11 and one from December 24.

Host associations--I have reared this species from the cynipid, Bassettia ligni Kinsey, in twigs of Quercus garryana Dougl. ex Hook. Although there are no other host records, O. turio probably occurs in similar galls (cells hidden under bark) of other cynipid species; it may be restricted to this type of gall, thus accounting for the paucity of specimens.

Description--

Female--Length 2.1-3.4mm (holotype 2.9mm). Color dark green-blue, including femora; scape, tegula, and tibiae dark brown; scape more or less yellow basally. Forewing immaculate.

Head--Width 1.9-2.0x length and 1.2x height; IMD 1.7-1.8x MD; EH 2.0-2.3x MD; frons width 1.1x EH; POL 3.3x OOL; lower face with punctures faint; median frons irregularly strigulate. Antennal flagellum clavate, F1 and F2 annular, funicular segments slightly elongate proximally to quadrate distally.

Mesosoma--Length 1.5-1.6x width; dorsum with procumbent white setae; scutum and scutellum noticeably flattened in lateral view; notauli inconspicuous, scutum imbricate-strigate; scutellum length 1.2-1.4x width, transversely to diagonally strigate, apex extending beyond metanotum. Propodeum quite convex and diagonal to ventral scutellum (completely visible from dorsal view, fig. 32), spiracular sulcus inconspicuous, panels diagonally strigate to reticulate, submedian carinae close together and often converging anteriorly, median area weakly sculptured. Forewing with row of setae in costal cell usually complete; basal cell aetose; speculum present, usually open below; postmarginal vein longer than stigmal vein. Hind coxa reticulate.

Metasoma--Length 1.3-1.5x head + mesosoma, moderately compressed; posterior edge of T1 straight; T3-T5 with weakly carinate to ecarinate, foveate anteriorly, foveae shallow, crenulate border imbricate and only slightly elevated, cusp length less than intercusp distance, imbricate posteriorly, posterior margins straight; T6 only slightly upturned; T7 length subequal to height.

Male--Scape with edges parallel; funicular segments quadrate proximally to transverse distally.

Ormyrus unifasciatipennis Girault

(figs. 6, 22, 28, 30, 34, 52)

Girault 1917:87

Type locality--Los Angeles Co., California, U.S.A.

Type material--This species was described from one female specimen, which bears the following labels: "July", "Los Angeles Co. Cal.", "Type No. 20975 U.S.N.M.". The original description indicates that the collector was Coquillett.

Other material examined--CANADA (2 females, 3 males): Ontario (Toronto), Quebec (Cap-Rouge, Luskville Falls). U.S.A. (70 females, 25 males): Arizona (Cochise, Pima, Santa Cruz), California (Alameda, Contra Costa, El Dorado, Fresno, Los Angeles, Marin, Sacramento, San Mateo, Santa Clara, Tulare, Yolo), Florida (Liberty), Massachusetts (Hampden), Minnesota (Lac Qui Parle), New Jersey (Ocean), New Mexico (Dona Ana, Hidalgo, Lincoln, Otero), New York (Saratoga), Ohio (Tuscarawas), Oregon (Benton, Lane, Wasco), Texas (Brewster), Utah (Utah), Wisconsin (Clark, La Crosse, Vernon). MEXICO (1 female, 1 male): Chihuahua, Nayarit. Specimens deposited in: AMNH, CAS, CNC, CU, FSC, LA, OHSU, ORSU, ROM, UCB, UCD, UCR, UG, UI, UK, USNM, UW.

Diagnosis--Like O. unimaculatipennis, this species has a reticulate hind coxa, and the forewing with a large infuscate spot and an incomplete row of setae in the costal cell (fig. 28). Ormyrus unifasciatipennis however has the hind femur blue-green (rather than yellow-orange) and T6 upturned (fig. 34).

Distribution--Ormyrus unifasciatipennis is apparently distributed across North America from Oregon, California, Utah and Mexico (Chihuahua) to Quebec and Florida (fig. 52). Records of flight time are between April 26 and November 4.

Host associations--There are very few host records for this species; the few that exist include asexual

generation galls of Andricus opertus (Weld), A. wiltzae Fullaway and Neuroterus saltatorius (Edwards). There are also records from an unidentified acorn cup gall on Quercus prinoides Willd. (USNM, Hopkins # 2406c), an unidentified bud gall on Q. lobata Nee (JHA), and an unidentified twig gall (cells hidden under bark) on Q. alba L. (ROM).

Description--

Female--Length 1.3-2.8mm (holotype 2.0mm). Color blue-green, including tegula and femora; scape yellow or green (partially green in holotype); tibiae brown, sometimes with some green. Forewing usually with large infuscate area below marginal vein, with setae in this area longer.

Head--Width 1.3x 2.1x length and height; IMD 1.7-2.0x MD; EH 2.3-2.6x MD; frons width subequal to EH; POL 3.7-4.0x OOL; lower with punctures faint; median frons regularly and transversely strigulate. Antennal flagellum clavate, F1 and F2 annular, funicular segments slightly elongate, quadrate apically.

Mesosoma--Length 1.3x width; dorsum with procumbent white setae; notauli absent, scutum imbricate-strigate; scutellum length 1.1x width, transversely-diagonally strigate (fig. 6), apex not extending beyond metanotum (fig. 30). Propodeum perpendicular to ventral scutellum, spiracular sulcus inconspicuous, panels weakly diagonally strigate, submedian carinae parallel and weak, median area shiny. Forewing (fig. 28) with row of setae in costal cell incomplete; basal cell asetose; speculum present, open below; postmarginal vein longer than stigmal vein. Hind coxa reticulate.

Metasoma--Length 1.3-1.5x head + mesosoma, subcylindrical; posterior edge of T1 straight; T3-T5 weakly carinate to ecarinate, foveate anteriorly, foveae shallow, crenulate border usually weakly imbricate and barely elevated, cusp length less than intercusp distance,

imbricate posteriorly, posterior margins straight; T6 upturned (fig. 34); T7 length subequal to or less than height.

Male--Scape with edges parallel (fig. 22); funicular segments quadrate.

Ormyrus unimaculatipennis Girault

(Figs. 33, 53)

Girault 1916:342

Type locality--Louisiana, USA.

Type material--This species was described from one female specimen, which bears the following labels: "Loui", "2553", "Collection C.F. Baker", "20327" (USNM).

Other material examined--U.S.A. (3 females): California (Solano, Tulare). Specimens are deposited in CNC, ORSU, USNM (donated by J. Halstead and J. Johnson).

Diagnosis--Ormyrus unimaculatipennis is most similar to O. unifasciatipennis; both have infusate forewings, an incomplete row of setae in the costal cell, and reticulate hind coxae. Ormyrus unimaculatipennis can be distinguished by the yellow-orange (rather than blue-green) femora contrasting with dark tibiae (a color combination that is unique among Nearctic Ormyrus species) and by T6 which is not upturned (fig. 33)

Distribution--Ormyrus unimaculatipennis is known only from California and Louisiana (fig. 53). Records of flight time include June 2 and October 8.

Host associations-- Unknown; label data on specimens indicate areas where oaks are present.

Description--

Female--Length 2.6-3.1mm (holotype 3.1mm). Color green-blue, including tegula, with metasoma dark brown-black; scape yellow proximally, dark colored distally; femora yellow-orange, tibiae brown. Forewing usually with large infusate area below marginal vein, with setae in this area longer.

Head--Width 2.1-2.2x length and 1.3x height; IMD 1.7x MD; EH 2.3x MD; frons width subequal to EH; POL 3.8-4.0x OOL; lower face with punctures faint; median frons regularly and transversely strigulate. Antennal flagellum clavate, F1 and F2 annular, funicular segments slightly



elongate proximally, quadrate to transverse distally.

Mesosoma--Length 1.3x width; dorsum with procumbent white setae; notauli absent, scutum imbricate-strigate; scutellum length 1.1x width, transversely-diagonally strigate, apex extending only slightly beyond metanotum. Propodeum perpendicular to ventral scutellum, spiracular sulcus inconspicuous, panels weakly diagonally strigate, submedian carinae parallel and weak, median area quite shiny. Forewing with row of setae in costal cell incomplete; basal cell asetose; speculum present, open below; postmarginal vein longer than stigmal vein. Hind coxa reticulate.

Metasoma--Length 1.3-1.4x head + mesosoma, subcylindrical; posterior edge of T1 straight; T3-T5 weakly carinate to ecarinate, foveate anteriorly, foveae shallow, crenulate border shiny and barely elevated, cusp length less than intercusp distance, imbricate posteriorly, posterior margins straight; T6 not upturned, producing a bluntly pointed metasomal apex (fig. 33); T7 length less than height.

Male--Unknown.

Ormyrus vacciniicola Ashmead

(figs. 7, 54)

Ormyrus vacciniicola Ashmead 1887:189

Type locality--Toronto, Ontario, Canada.

Type material--According to the original description, this species was described from three female specimens, "sent by Mr. Wm. Brodie, and reared from the cynipidous gall Solenozopheria vaccinii Ashm." (now known to be the pteromalid, Hemadas nubilipennis (Ashm.)). One of the specimens is here designated LECTOTYPE; it bears the following labels: "16-86", "1-1-6", "34", "Paratype No. 2889".

Other material examined--CANADA (65 females, 229

males): New Brunswick (Kouchibouguac N.P.), Ontario (Constance Bay, Marmora, Ottawa, Oxford Mills, Penetang, St. Lawrence Islands N.P.), Quebec (Quyon). U.S.A. (18 females, 24 males): Illinois, Indiana, Maine (Cumberland), Massachusetts (Essex), Michigan (Manistee), New York (Suffolk), South Carolina (Oconee). Specimens are deposited in: AMNH, ANS, CNC, FSC, INH, OHSU, ORSU, ROM, UCR, USNM.

Diagnosis-- This species can be separated from all other Ormyrus species by its unique habitus and color: body elongate, slender, and compressed; mesosoma blue-black, metasoma and legs generally yellowish. Further characters distinguishing this species are the strigate hind coxa and the elongate funicular segments of the antenna.

Distribution--Ormyrus vacciniicola has been collected in the northeastern provinces and states: from Ontario and Quebec to South Carolina and Illinois (fig. 54). Its distribution probably parallels that of its host gall on Vaccinium. Records of flight time are limited to July through mid September.

Host associations--Ormyrus vacciniicola appears to be primarily restricted to galls on blueberry (Vaccinium angustifolium and other species?) elicited by Hemadas nubilipennis (Ashmead) (Pteromalidae: Brachyscelidiphaginae). There is a small series (CNC) reared from cynipid galls on strawberry (Fragaria) in Ottawa, Canada. I have also seen a single male specimen (INH) reared from sumac seed in Illinois. Although I did not obtain specimens from sumac seed that I reared (from Nebraska and Oregon), the record seems credible since it was accompanied by Idiomacromerus (Torymidae), a known parasite of Eurytoma in sumac seed.

Description--

Female--Length 1.7-3.8mm (holotype 2.9mm). Color yellowish, especially legs and metasoma; head and mesosoma

blue-black to brownish. Forewing immaculate.

Head--Width 2.2-2.3x length and 1.3-1.4x height; IMD 1.7-2.0x MD; EH 2.3-2.6x MD; frons width 1.1x EH; POL 2.2-2.6x OOL; lower face with punctures inconspicuous; median frons irregularly strigulate. Antennal flagellum filiform, F1 and F2 annular, funicular segments elongate.

Mesosoma--Length 1.3-1.4x width; dorsum with procumbent white setae; notauli absent; scutum shiny, strigate-imbricate; scutellum length 1.1x width, diagonally strigate (fig. 7), apex extending beyond metanotum. Propodeum perpendicular to ventral scutellum, spiracular sulcus inconspicuous, panels weakly diagonally strigate, submedian carinae parallel, median area shiny. Forewing with row of setae in costal cell complete; basal cell asetose; speculum present, cubital vein complete, medial vein nearly complete; postmarginal vein longer than stigmal vein. Hind coxa diagonally strigate.

Metasoma--Length 1.4-2.0x head + mesosoma, very compressed; posterior edge of T1 straight; T3-T5 carinate, foveate anteriorly, foveae shallow, crenulate border imbricate to shiny and elevated, cusp length less than intercusp distance, imbricate posteriorly, posterior margins straight; T6 upturned; T7 length usually greater than height.

Male--Scape with edges parallel; funicular segments slightly elongate.

Variation--Specimens (CNC) from galls of Diastrophus fragariae on strawberry have the last tergite of the metasoma very stout and the hind coxa less strigate.

Ormyrus venustus new species

(figs. 8, 9, 23, 29, 55)

Type locality--Rocklin, California, U.S.A.

Type material--Holotype (female; donated by CD to USNM) bears the following labels: "Rocklin Calif., Placer Co., em. V-31 1969", "Quercus wislizenii", "emerged from gall of *C. congregata* Ashm.", "C. Dailey No. 1125". Paratypes (10 females, 6 males; BMNH, CNC, KIEV, ORSU, USNM; donated by C. Dailey): same data as holotype.

Material examined--CANADA (1 female, 4 males): Ontario (Ancaster). U.S.A. (334 females, 217 males): Arizona (Cochise, Coconino, Graham, Navajo, Pima, Pinal, Santa Cruz, Yavapai), California (Alameda, Contra Costa, Fresno, Kern, Los Angeles, Marin, Mariposa, Mendocino, Napa, Placer, Riverside, Sacramento, San Diego, San Joaquin, San Luis Obispo, Santa Barbara, Santa Clara, Tulare, Yolo), Colorado (Custer, Douglas, El Paso), Maryland, Massachusetts (Hampden, Middlesex), New Mexico (Bernalillo, Grant, Guadalupe, Hidalgo, Lincoln, Socorro, Torrance), New York (Tompkins), Oregon (Benton, Curry, Josephine, Lane, Wasco, Washington), Texas (Brewster, Culberson, Presidio, Travis, Ward), Utah (Davis, Salt Lake, Utah), Washington (Klickitat). MEXICO (134 females, 70 males): Chiapas, Chihuahua, Durango, Hidalgo, Nuevo Leon, Oaxaca, Tamaulipas). GUATAMALA (3 females, 3 males). COSTA RICA (8 females, 7 males). Specimens are deposited in: AMNH, CAS, CNC, CU, FSC, LA, OHSU, ORSU, REM, ROM, TAM, UA, UCB, UCD, UCR, UI, UK, USNM, UT.

Etymology--From the Latin, like Venus, beautiful.

Diagnosis--Like *O. acylus*, *O. hegeli*, and *O. setosus*, eastern specimens of this species have reduced cusps on the crenulate borders of tergites 3-5; *O. venustus* can be distinguished by the imbricate (rather than punctulate) sculpture posterior to the crenulate borders. The most diagnostic characters are the upper frons (in front of the anterior ocellus, fig. 9) and

scutellum (fig. 8), both of which are transversely strigate with extensive shiny interstices. Only O. thymus, O. unifasciatipennis, and O. unimaculatipennis approach this type of sculpture. O. venustus however has 2-3 setae in the apex of the basal cell of the forewing (fig. 29).

Distribution--Ormyrus venustus has been collected from Ontario to Costa Rica to Oregon and Washington (fig. 55), and is probably present wherever there are oaks. It has been much more frequently collected from the western and southwestern states than from the eastern states. This species is represented by more Central American specimens than any other species treated here. In Oregon I have collected this species in flight from early May through early October; there is one record from Tampico, Mexico, on December 29 (taken at a blacklight!).

Host associations--Ormyrus venustus is associated with cynipid galls on oaks where it occurs in a variety of gall types, most notably in bud, catkin, and leaf galls. The only host records from eastern North America are Andricus quercuspetiolicola (Bassett) (according to the Hopkins No.; the label however, reads "A. quercussingularis") and Belonocnema kinseyi Weld, both leaf galls. In the southwest and the west coast states this species occurs in acorn galls of Disholcaspis pedunculoides Weld and Callirytis eldoradensis (Beutenmueller), bud galls of Andricus opertus (Weld), catkin galls of Callirhytis congregata (Ashmead) and Neuroterus floricomus Weld, and leaf galls of Andricus atrimentus Kinsey, A. fullawayi Beutenmueller, A. opertus, A. pilula Bassett, A. sulfureus (Weld), A. tecturnarum Kinsey, C. flora Weld, Dros amphora (Weld), N. washingtonensis Beutenmueller, and X. pulchripenne (Ashmead); it occurs in twig galls of Andricus chrysolepidicola (Ashmead), A. wiltzae Fullaway, Disholcaspis rubens (Gillette), D. sulcata (Ashmead),

Dryocosmus coxii (Bassett), Neuroteras varians Kinsey, and Xanthoteras eburneum (Bassett). Kinsey reared nearly a hundred specimens from "emoryi" on "Quercus repanda" in Mexico (Pachuca, Hidalgo). There are many more Kinsey records from Mexico but the identities of the cynipids and oaks are questionable. The only records from Guatamala are from "mexicana" on "Q. chestnut" and "Q. pilicaulis". A series reared from the introduced Plagiotrochus suberi Weld (twig gall) on cork oak in California indicates a recent host acquisition. The small size of O. venustus with respect to some of the host cynipids (e.g. Disholcaspis spp.) suggests that it may actually be associated with inquiline cynipids in these cases.

Description--

Female--Length, 1.2-5.6mm (holotype 2.4mm). Color dark blue, including scape, tegula, femora, and tibiae. Forewing immaculate.

Head--Width 2.1-2.4x length and 1.3-1.4x height; IMD 1.6-2.0x MD; EH 2.3-2.7x MD; frons width 1.0-1.1x EH; POL 2.7-3.7x OOL; lower face with punctures faint; median frons regularly and transversely strigulate, continuing laterally to inner orbit (fig. 9). Antennal flagellum subfiliform, F1 and F2 annular, funicular segments slightly elongate to quadrate.

Mesosoma--Length 1.3-1.4x width; dorsum with procumbent white setae; notauli inconspicuous, scutum imbricate-strigate; scutellum length 1.1x width, transversely strigate with extensive shiny interstices (fig. 8), apex extending slightly beyond metanotum. Propodeum perpendicular to ventral scutellum, spiracular sulcus inconspicuous, panels diagonally strigate, submedian carinae parallel, median area shiny. Forewing (fig. 29) with row of setae in costal cell complete; basal cell setose apically; speculum present, medial vein nearly complete and deflected anteriorly, cubital vein

incomplete; postmarginal vein longer than stigmal vein.  
Hind coxa reticulate.

Metasoma--Length 1.2-2.0x head + mesosoma, moderately compressed; posterior edge of T1 entire; T3-T5 carinate, foveate anteriorly, foveae fairly deep, crenulate border imbricate and only slightly elevated, cusps reduced, imbricate posteriorly, posterior margins straight; T6 upturned; T7 length slightly greater than height

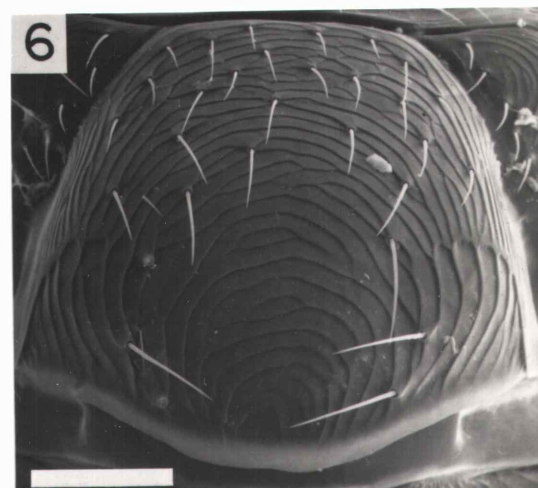
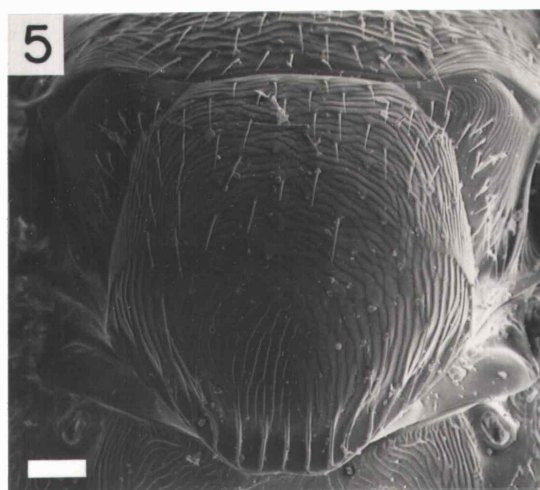
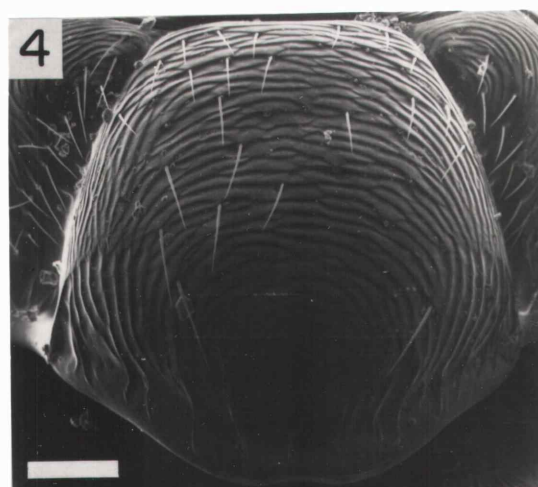
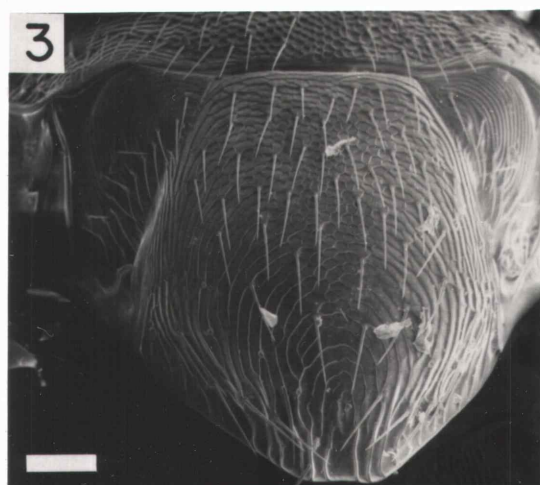
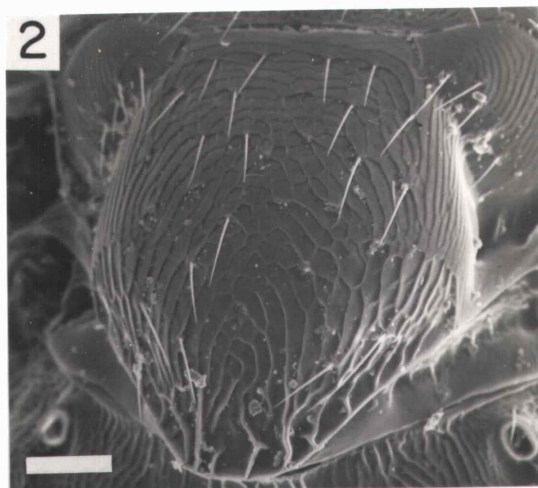
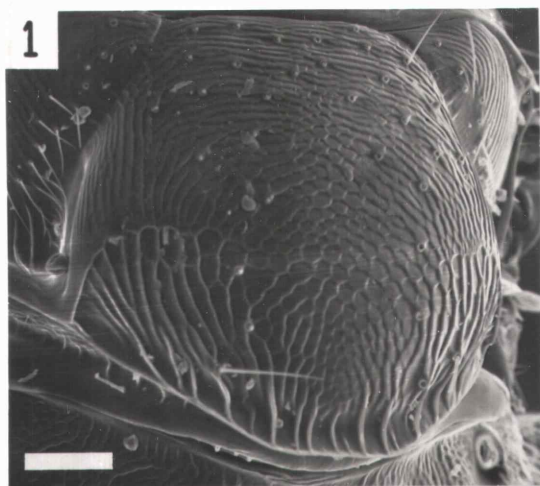
Male--Scape with edges almost parallel, wider in middle (fig. 23); funicular segments quadrate.

Variation--Specimens from the eastern states have tergites 3-5 with cusps virtually absent from the crenulate borders whereas specimens from west coast states have cusps evident. Eastern specimens also tend to have the entire metasoma more elongate and the tibiae are usually more yellow. Although these may eventually prove to be distinct species, I consider them here as one species because of intermediate specimens from the southwest; also, eastern and western specimens share similar sculpture, wing setation, and body color distinct from other species.

Figures 1-6  
(bar = 0.1mm)

- Figure 1. O. acylus scutellum
- Figure 2. O. crassus scutellum
- Figure 3. O. dryorhizoxeni scutellum
- Figure 4. O. hegeli scutellum
- Figure 5. O. setosus scutellum
- Figure 6. O. unifasciatipennis scutellum





Figures 1-6

Figures 7-13  
(bar = 0.1mm)

Figure 7. O. vacciniicola scutellum

Figure 8. O. venustus scutellum

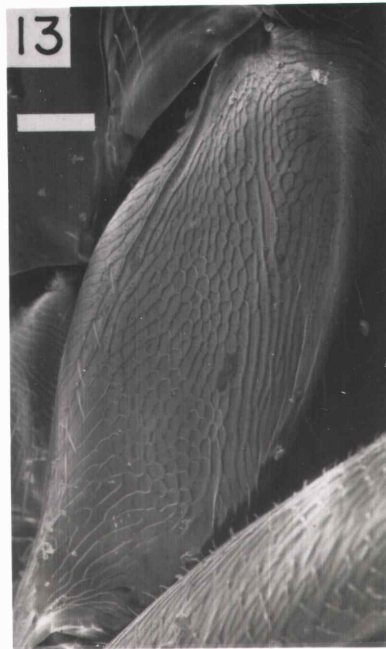
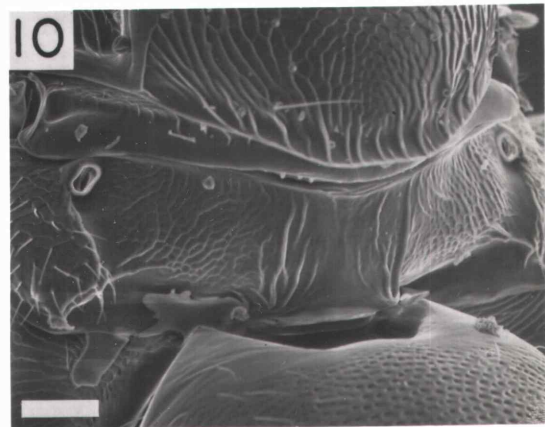
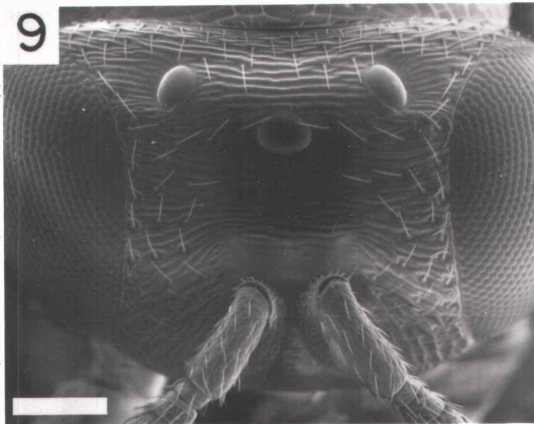
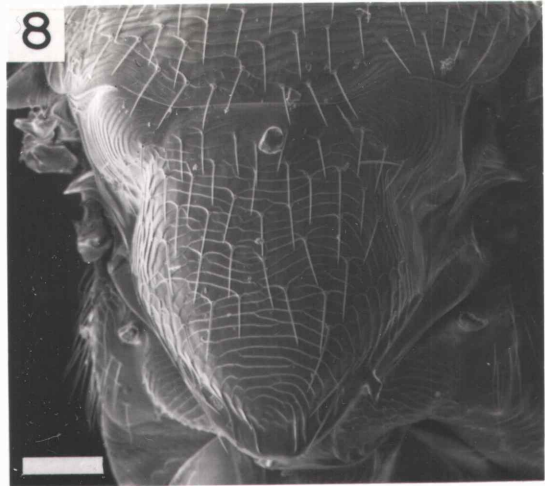
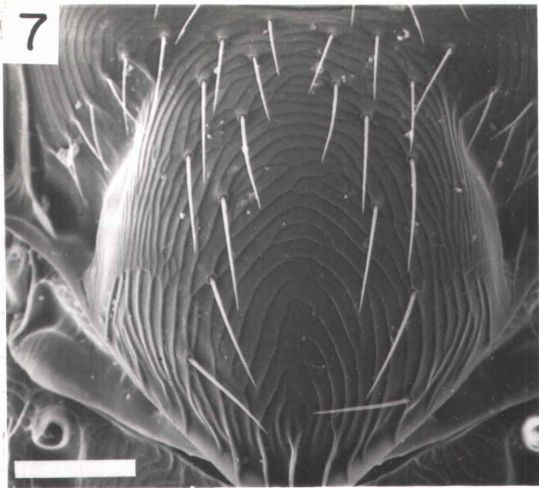
Figure 9. O. venustus median frons

Figure 10. O. acylus propodeum

Figure 11. O. dryorhizoxeni hind coxa

Figure 12. O. thymus hind coxa

Figure 13. O. distinctus hind coxa



Figures 7-13

## Figures 14-23

(bar = 0.1mm)

Figure 14. O. acylus metasomal tergite 4

Figure 15. O. dryorhizoxeni metasomal tergite 4

Figure 16. O. acylus male scape

Figure 17. O. distinctus male scape

Figure 18. O. hegeli male scape

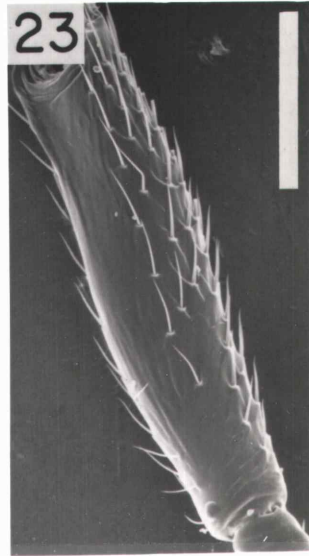
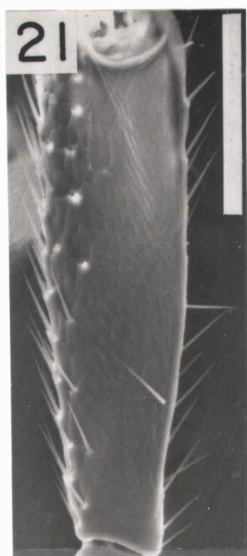
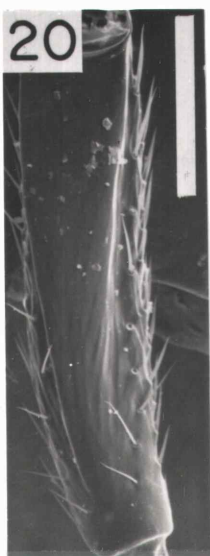
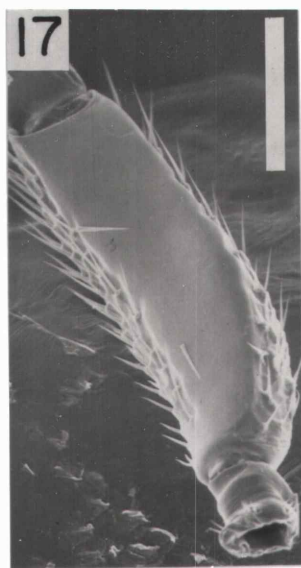
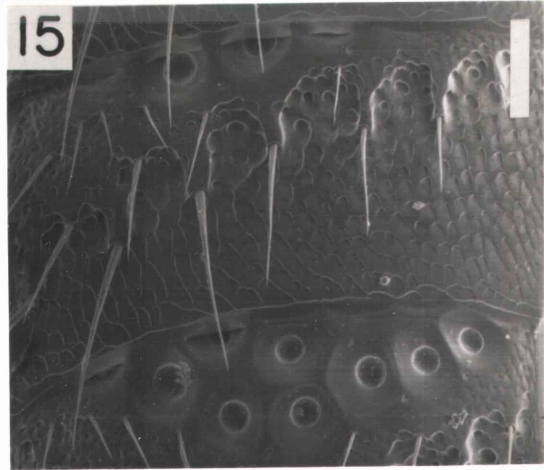
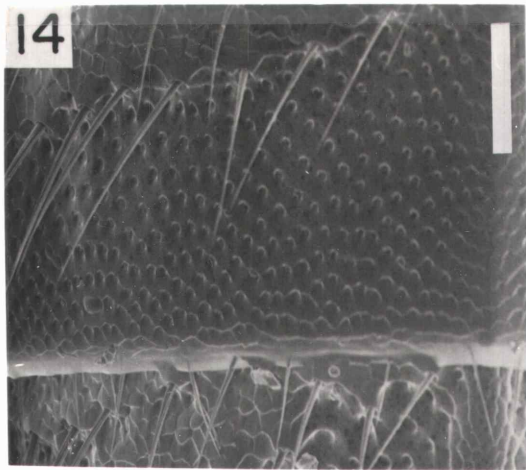
Figure 19. O. labotus male scape

Figure 20. O. reticulatus male scape

Figure 21. O. setosus male scape

Figure 22. O. unifasciatipennis male scape

Figure 23. O. venustus male scape



Figures 14-23

## Figures 24-29.

Figure 24. O. distinctus forewing

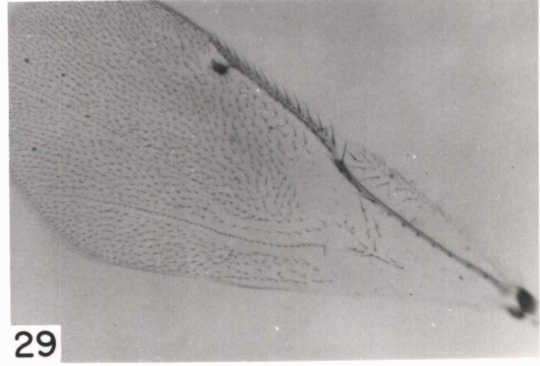
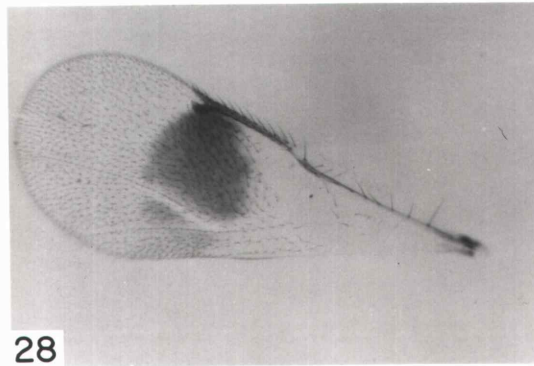
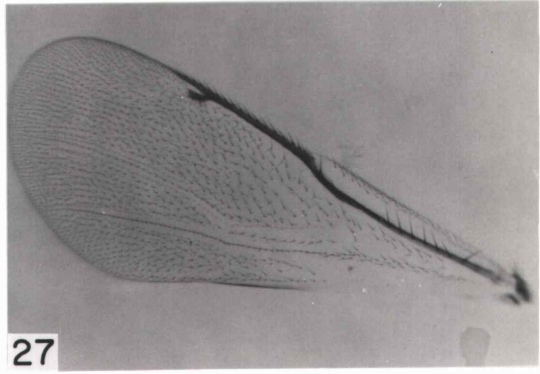
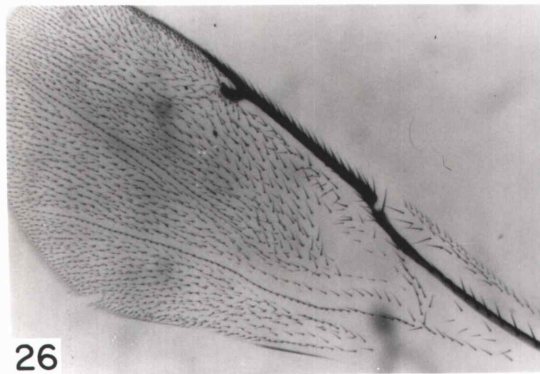
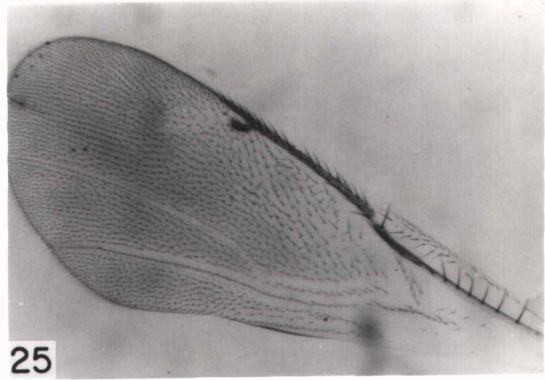
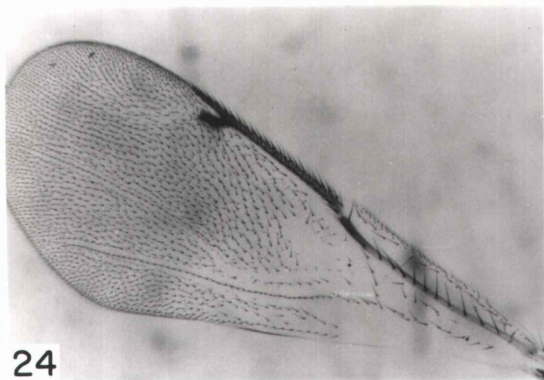
Figure 25. O. dryorhizoxeni forewing

Figure 26. O. hegeli forewing

Figure 27. O. setosus forewing

Figure 28. O. unifasciatipennis forewing

Figure 29. O. venustus forewing

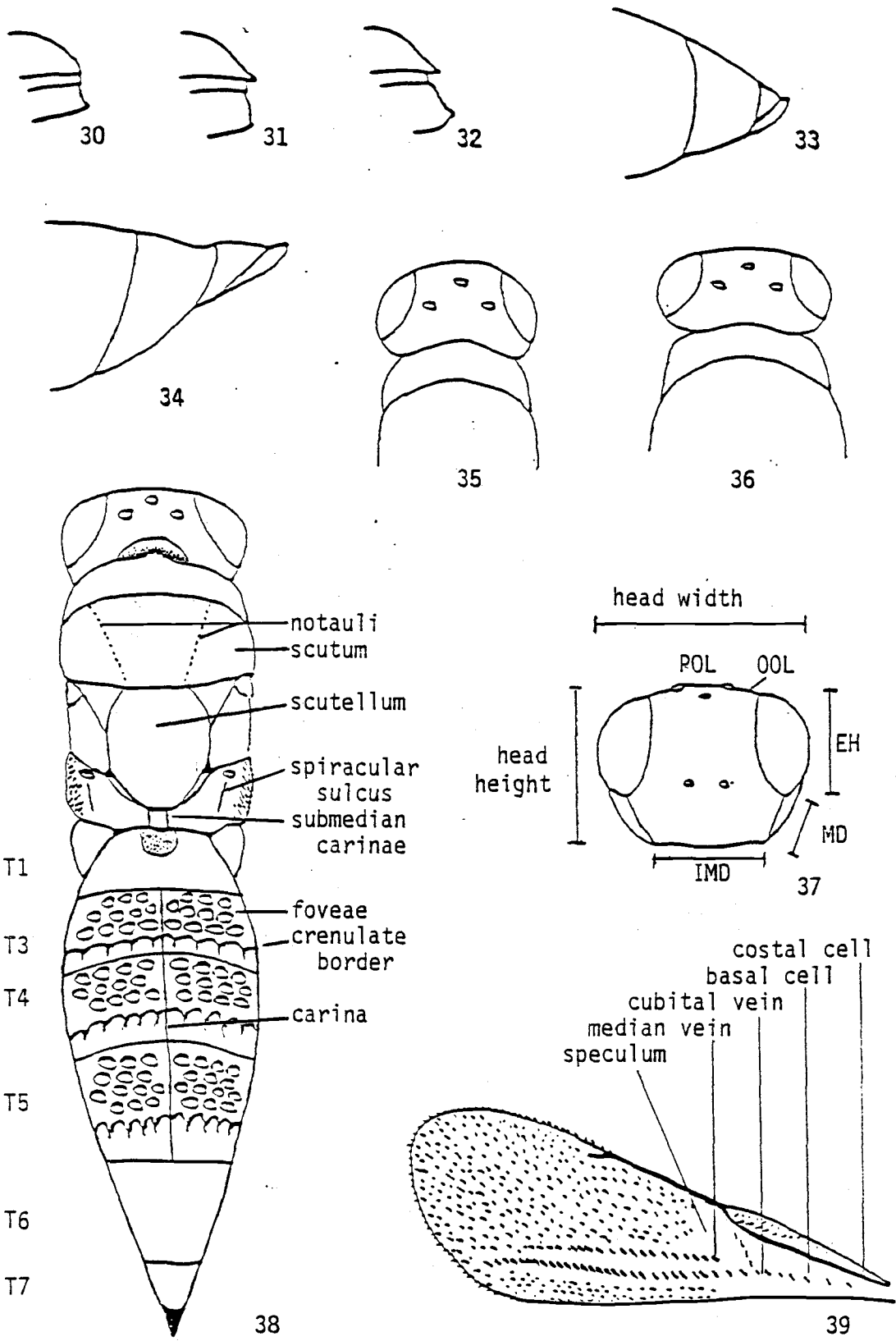


Figures 24-29

## Figures 30-39

- Figure 30. O. thymus and O. unifasciatipennis  
profile of scutellum and propodeum
- Figure 31. Usual profile of scutellum and propodeum
- Figure 32. O. turio profile of scutellum and propodeum
- Figure 33. O. unimaculatipennis metasomal apex
- Figure 34. O. unifasciatipennis metasomal apex
- Figure 35. O. tenuis and O. turio head and mesosoma
- Figure 36. Usual head and mesosoma
- Figure 37. Frontal view of head: terminology
- Figure 38. Dorsal view of body: terminology
- Figure 39. Forewing: terminology





Figures 30-39.

CHAPTER 5. HOST ASSOCIATIONS OF ORMYRUS SPECIES

Galls on terrestrial plants are elicited by various bacteria, fungi, nematodes, mites, and insects. Insect gall-formers include species of Thysanoptera, Hemiptera (primarily Homoptera-Sternorhyncha), Coleoptera (primarily Curculionidae), Lepidoptera (primarily Nepticulidae), Diptera (Agromyzidae, Cecidomyiidae, Chloropidae, Fergusonidae, Tephritidae), and Hymenoptera (Chalcidoidea, Cynipidae, Tenthredinidae) (Mani 1964). In addition to the gall-former, a gall may be occupied by various other gall associates. These associates may be carnivorous (primary parasitoids and hyperparasitoids) or phytophagous (i.e. inquilines, which feed on gall tissue), or sometimes, both. The most common associates of insect galls in general are species of Chalcidoidea, a superfamily which is thus unique in that it includes both gall-formers and gall-parasitoids.

Several chalcidoid genera (e.g. Eurytoma, Tetrastichus, Torymus) are associated with a wide range of insect galls while other genera are more restricted. Ormyrus appears to be restricted to galls formed by Diptera (Agromyzidae, Cecidomyiidae, and Tephritidae), Chalcidoidea, and Cynipidae. The exact trophic relationship of Ormyrus within a gall is unknown for most species. Hyperparasitism (parasitoid of another gall parasitoid) is reported in O. orientalis and O. flavipes (see below) but it is not known whether hyperparasitism is ever obligatory. Many of the Ormyrus species associated with cynipid galls may be facultative hyperparasitoids. Whether any species feed partially or totally on gall tissue (i.e. as inquilines) is unknown.

In this chapter I will summarize what is known about the host associations of Ormyrus species in various parts of the world. The emphasis will be upon Nearctic species

associated with cynipid galls on oaks since these associations are the best documented and are the subject of my taxonomic revision.

A. DIPTERA AS HOSTS OF ORMYRUS

There are probably more species of gall-formers in Diptera than in any other insect order (Felt 1940). Cecidomyiidae, in particular, is the most speciose and widespread family of gall-formers. Ormyrus is one of the least-often-recorded associates of dipteran galls, at least in the Holarctic, where most of the research has occurred. More extensive collecting in tropical areas may yield many more records of Ormyrus from galls formed by Diptera.

Published records of Ormyrus from dipteran galls are presently restricted to species in Africa and the Palearctic. Ormyrus orientalis is widely distributed throughout much of the Old World (absent from Australia) and has been recorded from more dipteran galls (mostly tephritid) than any other species of Ormyrus (see Table 1). In galls formed by Tephritis stictica Loew on Otanthus maritimus (Smith) (Asteraceae), O. orientalis is reported to be a hyperparasitoid on the primary parasitoid Eurytoma tristis Mayr (Rivosecchi 1958). There are also records of O. orientalis from cynipid galls in Europe (Sellenschlo and Wall, 1984) but these records should perhaps be verified.

Zerova (1985) has recently described three new species of Ormyrus from cecidomyiid galls on Chenopodiaceae in arid areas of the USSR as well as one species from a tephritid gall on Cousinia (Asteraceae)--see Table 1. Ormyrus punctiger is reported from an agromyzid gall on Rubus (Rosaceae) but this species is primarily associated with cynipid galls on European oaks.

In Africa, where a smaller percentage of the galls have been studied, Ormyrus is known to occur in several dipteran galls (Table 1). Crosby (1909) described Ormyrus

sculptilis from cecidomyiid and agromyzid galls on Flueggea (Euphorbiaceae) in Malawi and also reported an undetermined species of Ormyrus from a dipteran stem gall on Dalbergia (Fabaceae). Specimens of Ormyrus were recently reared from two cecidomyiid galls in Cameroon: galls of Schizomyia sp. on Ceiba (Bombacaceae) and galls of Resseliella sp. on an unknown plant growing at 900 meters on Mt. Cameroon (DiGiulio, pers. comm.).

There are no published records of Ormyrus from dipteran galls in the Nearctic. The only label data I have seen indicating dipteran hosts are 32 specimens of O. labotus reared from cecidomyiid galls on oak (all collected in the eastern U.S. by Kinsey). Since O. labotus is primarily associated with cynipid galls on oaks, these records from cecidomyiid galls on the same host plant need verification.

Because Palearctic species of Ormyrus have been recently described from cecidomyiid galls on Chenopodiaceae, I reared a few cecidomyiid galls on Sarcobatus (collected in south-central Oregon) but obtained no Ormyrus. I have also reared various other cecidomyiid and tephritid galls in Oregon but these efforts have not produced Ormyrus. Further study is necessary to determine whether Ormyrus is actually absent from all Nearctic dipteran galls.

B. PHYTOPHAGOUS CHALCIDOIDEA AS HOSTS OF ORMYRUS

Chalcidoidea and Cynipidae are the only groups of gall-formers which are derived from carnivorous (parasitoid) ancestors. Unlike Cynipidae, phytophagy in Chalcidoidea is polyphyletic, and therefore phytophagous species are often closely related to parasitoid species (usually parasitoids in galls). For this reason it is often difficult to determine whether a particular species is a gall-former or an associate of another gall-former; hence, knowledge of which Chalcidoidea are actually phytophagous is incomplete. Chalcidoidea also differ from Cynipidae in that some phytophagous species feed in seeds with no apparent gall formation.

The majority of phytophagous chalcidoid species belong to Brachyscelidiphaginae (Pteromalidae), Epichrysommalinae (Pteromalidae), Eurytominae (Eurytomidae), Tanaostigmatidae (sometimes placed in Eupelmidae), and Megastigminae (Torymidae). There are very few records of Ormyrus from galls of Pteromalidae and Eurytomidae and no records from galls of Tanaostigmatidae and Torymidae. In the Nearctic, O. vacciniicola and O. rosae occur in galls formed by the brachyscelidiphagine, Hemadas nubilipennis (Ashmead), on Vaccinium (blueberry). The Brachyscelidiphaginae occur predominantly in the southern hemisphere: the species on blueberry in eastern North America is the only species recorded from the Holarctic. In Australia, where this subfamily constitutes a major group of gall-formers, the only record of Ormyrus from a brachyscelidiphagine gall is from a gall on Casuarina (see Table 1).

Closely related to the Brachyscelidiphaginae is the Epichrysomallinae, species of which are thought to be mostly gall-formers in fruits of Ficus (Moraceae). Ormyrus species reared from figs (Table 1) may be associated indirectly with these pteromalids rather than

with the fig wasp pollinators (Agaonidae): O. flavipes was observed attacking Syceurytoma ficus Boucek (Eurytomidae), which is presumably parasitic on one of the gall-forming epichrysomallines (Boucek et al. 1981). Since there are about 1000 species of Ficus distributed throughout the tropics and subtropics, figs probably are major hosts for Ormyrus species in these areas.

The only other records of Ormyrus from phytophagous Chalcidoidea are from Eurytominae. An undetermined species of Ormyrus occurs in a gall on Eremocitrus in Australia, a gall presumably formed by Eurytoma fellis Girault. I have seen one specimen of O. vacciniicola which bears a label reading, "Grays's Siding, Ill. Iss.5.25.27; ex seed of sumach" [sic]. Phytophagous eurytomids (Eurytoma spp.) are known to occur in seeds of sumac (Rhus spp.) and this Ormyrus specimen was accompanied by the torymid, Idiomacromerus bimaculipennis Crawford, which is a known parasitoid of eurytomids in sumac seed. In an attempt to confirm this isolated record I reared thousands of eurytomids from sumac seeds from Nebraska and eastern Oregon but no Ormyrus were obtained. I have also reared smaller quantities (hundreds) of eurytomid-infested seeds of Ceanothus, various Umbelliferae, and Juniperus from Oregon, but again no Ormyrus were obtained.

There are a few records of Ormyrus from seeds which may harbor phytophagous chalcidoids, although none are presently known. One specimen of O. thymus bears a label, "Belize Hond., seeds of Bucida cucides " (Combretaceae). Mite galls are known from the fruits of Bucida (Houard 1933) but no Chalcidoidea have been reported from the seeds; further study is needed to determine the exact host of O. thymus . I have also seen one specimen of Ormyrus (species undetermined) with a label indicating that it was reared from seeds of Ardisia (Myrsinaceae) in Java, but again, no chalcidoids are

reported from seeds of this genus. Specimens from Agropyrum seed (Table 1) are in poor condition, but what remains looks like Ormyrus.

Among the most common chalcidoid galls in the Holarctic are those of Tetramesa (Eurytominae) in grass stems. Boucek (Boucek et al. 1981) suggested that Ormyrus may occur in grass stems but thus far I have seen no Ormyrus from my limited rearing of eurytomid-infested grass stems in Oregon. Tanaostigmatid galls on woody legumes in the southwestern U.S. are known to harbor several parasitic chalcidoid genera which are also present in cynipid galls, but no Ormyrus have yet been found (LaSalle, pers. comm.). I have also reared tanaostigmatid galls (about 50 galls from Arizona), but no Ormyrus were obtained.

It is probable that species of Ormyrus are more prevalent in chalcidoid galls than is indicated by existing records. Phytophagous Chalcidoidea are so poorly known that at present there is not even an adequate survey of which taxa are phytophagous. Since Gahan's (1922) survey, many additional phytophagous species have been discovered (e.g. LaSalle 1984) and a few species included in his list are now known to be parasitoids. There have also been several changes in nomenclature and classification. Thus, a revised survey of phytophagous Chalcidoidea is needed to facilitate the search for additional hosts of Ormyrus.



C. CYNIPIDAE AS HOSTS OF ORMYRUS

Gall-forming Cynipidae probably constitute a monophyletic group (Ritchie, pers. comm.). Species in one lineage have lost the ability to initiate galls and instead are inquilines (rarely parasitoids) in galls of other cynipids. Although cynipids have a worldwide distribution, only four genera are reported from the southern hemisphere (Weld 1952): Thrasorus in Australia, Eschatocerus and Myrtopsen in South America, and Rhoophilus in South Africa. There is some evidence for the first three genera being inquilines in chalcidoid galls but the habits of Rhoophilus in galls on Rhus (Anacardiaceae) apparently are unknown. In the Holarctic, cynipids constitute one of the most speciose groups of gall-forming insects, with the majority of species (80-90%) forming galls on oaks (Fagaceae, primarily Quercus). The remaining species form galls primarily on certain species of Rosaceae and Asteraceae; a few species in the Palearctic are gall-formers on Lamiaceae, Valerianaceae, Papaveraceae, and Aceraceae.

Host data are available for 13 of the 16 Nearctic species of Ormyrus treated here, and 12 of these are associated with cynipid galls--11 on oaks and one on Rosaceae (the other species is primarily associated with brachyscelidiphagine galls on blueberry; see Table 5). Among the three species for which hosts are unknown, O. tenuis has been swept from oaks and is therefore probably associated with cynipid galls on oaks. Ormyrus unimaculatipennis may also be associated with oak galls but the evidence is meager; the only record for O. thymus is one specimen reared from seeds of Bucida (see above). The following discussion includes a brief examination of Ormyrus records from cynipids on Asteraceae and Rosaceae followed by a more detailed examination of records from cynipids on Nearctic oaks.

Among the Ormyrus species associated with cynipid galls on plants other than Fagaceae and Rosaceae, there is an interesting contrast between the Nearctic and Palearctic. Members of the plesiomorphic (and probably paraphyletic) cynipid tribe, Aulacini, form galls on Aceraceae, Asteraceae, Lamiaceae, Papaveraceae, and Valerianaceae in the Palearctic. Five of the six Palearctic Ormyrus species reported from these cynipid galls (Table 2) share a similar morphology (lack of exposed foveae on the metasoma) and belong to a species group that is apparently absent from the Nearctic. Galls on Centaurea (Asteraceae) are hosts for three species of Ormyrus : O. cingulatus is apparently restricted to Centaurea ; O. graciosus is primarily associated with Centaurea, but also with Potentilla (Rosaceae); O. wachtli is associated with Centaurea and Salvia (Lamiaceae). Ormyrus papaveris is restricted to galls on Papaver and O. salmanticus was recently described from galls on Hieracium (Nieves-Aldrey 1984). This species group of Ormyrus is absent from the Nearctic, where cynipids of the tribe Aulacini are less diverse. Nearctic Aulacini are confined to Asteraceae (Table 2) and are hosts for two species of Ormyrus which are morphologically very close to O. labotus and O. rosae (on oaks and Rosaceae, respectively). Further study is needed to determine the species placement of Ormyrus reared from cynipid galls on Nearctic Asteraceae.

There are a few isolated records of Nearctic Ormyrus specimens similar to those from cynipids on Asteraceae but having labels indicating they were reared from plants not known to host cynipids. A series of twelve specimens bear labels reading: "L.I. from galls on dry stem of Primrose 6.20.04" (presumably L.I. is an abbreviation for Long Island), nine specimens with labels reading "ex Cicutu gall, B.C." (I have not been able to find galls or records of galls on this plant), one specimen with a label

reading: "L.I. 5.10.04 from stems of aster", and one specimen labelled "ex goldenrod gall, Livernois Mich." It is possible that the host plants were incorrectly identified and therefore I consider the above records questionable, and in need of further study.

The species of Ormyrus associated with cynipid galls on Rosaceae are quite similar in the Nearctic and the Palearctic, perhaps reflecting the more northern distributions of these plants. O. rosae occurs in cynipid galls on Potentilla , Rosa , and Rubus while O. rufimanus occurs only on Potentilla and Rubus (Table 2). Although O. rosae is present in most Nearctic cynipid galls on Rosa, Ormyrus appears to be largely absent from Palearctic rose galls (there is no mention of Ormyrus in the studies of Blair 1945; Nieves Aldrey 1980, 1983; Nordlander 1973; Schroeder 1967). The only record of Ormyrus in Palearctic rose galls is O. nitidulus , a species which is primarily associated with oak galls.

Ormyrus rosae reared from Rubus galls in eastern North America differ morphologically from typical O. rosae, such as those from Rubus parviflorus Nutt. in the West and Rosa galls across the continent (see chapter 4). Ormyrus from eastern Rubus galls may represent an undescribed species but for now I include them under O. rosae , pending further study. As mentioned previously, the pteromalid gall on Vaccinium in eastern North America harbors two species of Ormyrus : O. vacciniicola and another species that appears to be intermediate between typical O. rosae and those present in eastern Rubus galls. Interestingly, the only Ormyrus from galls on Fragaria (Rosaceae) are specimens (CNC, collected in Ottawa) which are morphologically intermediate between O. vacciniicola and O. rosae ; perhaps these specimens indicate hybridization between the two species or effects of host gall on Ormyrus morphology.

As mentioned above, the majority of Nearctic Ormyrus

species are exclusively associated with cynipid galls on oaks. There are presently more Ormyrus species described from cynipid oak galls in the Nearctic than in the Palearctic, 11 (possibly 13) vs 4, respectively. Askew (1961) illustrated food webs stemming from 38 cynipid oak galls in England, but Ormyrus is present in only one--that of Biorhiza pallida (Oliv.). Sellenschlo and Wall (1984) however, record numerous oak gall hosts for O. nitidulus and O. punctiger in Europe.

In North America, Brookfield (1972) found Ormyrus (all specimens I saw are O. labotus ) to be the most widely distributed parasitoid in cynipid galls on Quercus rubra L. Ormyrus was the only parasitoid reared from galls of Callirhytis quercusoperator (O.S.). Brookfield (1972) suggests that the widespread occurrence of Ormyrus may result from its intermediate length ovipositor housed in an elongate, conical metasoma. The results of my research confirm the polyphagy of certain species such as O. labotus, and also demonstrate the widespread occurrence of the genus in Nearctic oak galls (Table 3).

Most cynipid species associated with oaks undergo cyclical parthenogenesis, alternating between one asexual (unisexual) and one sexual (bisexual) generation each year, and usually forming two totally different galls on the same species of oak. Both generations are known for only a small number of species. Of the 483 cynipid species listed in Table 3, 35 are known from both generations, 363 from the asexual generation only, and 85 from the sexual generation only. I have recorded as asexual those species for which males were not listed in Krombein et al. (1979). In addition, I have attempted to verify the identity of the generation by consulting the taxonomic literature; only in the case of Amphibolips acuminata Ashmead was there a deviation from Krombein et al. (1979): Weld (1926) described males for this species.

Knowledge of alternate generations in cynipids is incomplete and much basic research is needed.

Table 3 includes all North American cynipid species associated with oaks, even those without Ormyrus records, for the following reasons. First, listing cynipid species which lack Ormyrus records will draw attention to those galls which need further rearing. Second, several new species and new alternate generations have been described subsequent to the compilation of the latest hymenopteran catalog (Krombein et al. 1979) and incorporating these changes here may facilitate future research. I have also attempted to incorporate changes in oak nomenclature (Dorr and Nixon 1985, Kartesz and Kartesz 1980) although accurate oak records will require recollection from problematic oak species (c.f. Hardin 1979, Dorr and Nixon 1985) and recently described oak species (Johnson and Abrahamson 1982, Nixon and Steele 1981).

Weld (1957, 1959, 1960) categorized cynipid galls according to plant part (bud, flower, fruit, leaf, root, stem) and gall characteristics (detachable vs internal, etc.). Some oak galls defy categorization: sexual generation galls of Andricus chrysolepidicola (Ashmead), A. crystallinus Bassett, and A. gigas Kinsey occur on both leaves and catkins; some root galls such as Bassettia floridana Ashmead and Neuroterus contortus (Weld) can also occur in stems above ground. Despite their arbitrary nature, Weld's gall types are adopted here (with slight modifications) to facilitate comparison of host gall characteristics and patterns in associated species of Ormyrus.

Of the 483 species of cynipids listed in Table 3, 122 (25.3%) have Ormyrus records. There are 22 cynipid species having records of two Ormyrus species and three cynipid species having records of three Ormyrus species each. Eliminating records documented by only one or two specimens (as possible errors in rearing) leaves seven

cynipid species having records of two Ormyrus species. In some cases where two different sized species of Ormyrus have been reared from the same gall, it is possible that one species is attacking an inquiline cynipid while the other is attacking the gall-forming cynipid (as recorded in Disholcaspis californica Burnett by Burnett, 1977, but not recorded here). The two species of Ormyrus I reared from D. simulata Kinsey, however, are represented by large specimens, suggesting that they both attack the gall-former.

There appear to be some differences in the number of Ormyrus records from different gall types (Table 4). Of the gall types represented by more than 15 cynipid species, the percentage of species with Ormyrus records are as follows: twig swelling on older growth, 55.6%; leaf parenchyma swelling, 35.3%; detachable twig gall, 33.8%; leaf midrib or petiole swelling, 26.3%; detachable leaf gall, 26.2%; detachable leaf "apple", 21.2%; bud gall, 16.4%; root gall, 15.8%; leaf pustules, 11.8%. These percentages reveal at least two patterns. First, inconspicuous galls (such as bud galls and leaf pustules) and galls which are difficult to collect (root galls) have the fewest records, perhaps indicating lack of collecting. Second, twig galls in general seem to have both more Ormyrus records and more species of Ormyrus. Galls formed by species of Disholcaspis (mostly detachable twig galls) are particularly rich in Ormyrus species. The polyphagous O. labotus is relatively uncommon in these galls (except perhaps as parasitoids of inquiline cynipids), suggesting that this type of gall requires specialized parasitoids.

The only known host of O. setosus is the large detachable twig gall of Callirhytis quercuspomiformis (Bassett). Ormyrus turio (and possibly O. tenuis, see chapter 4) may be restricted to galls consisting of individual cells embedded in twigs. Ormyrus acylus

appears to be primarily, although not exclusively, associated with acorn galls, especially "stone galls" in the nut. Species from root galls include O. crassus (in one particular root gall) and O. dryorhizoxeni (in several root galls as well as other galls). Species of Ormyrus occurring in bud galls and catkin galls are mostly the same species which occur in various leaf galls.

In the east, the extremely polyphagous O. labotus is especially abundant in detachable, wooly leaf galls, such as Andricus ignotus (Bassett), A. pattoni (Bassett), and A. quercuslanigera (Ashmead). In the west, O. distinctus and O. venustus together occupy the same range of gall types occupied by O. labotus in the east (O. venustus occurs in both regions but is much less common in the east). Ormyrus distinctus typically occurs in twig galls and those detachable leaf galls resembling detachable twig galls in tissue toughness (e.g. Andricus kingi Bassett, Antron spp., Xanthoteras spp.). Ormyrus venustus, on the other hand, is more common in softer leaf galls (e.g. pustules, midrib and parenchyma swellings). The sexual generation gall of Neuroterus sadlerensis Weld is very similar to that of N. washingtonensis Beutenmueller (both are leaf parenchyma swellings) and might be expected to share the same species of Ormyrus, namely O. venustus. Nonetheless, I have reared only O. distinctus from N. sadlerensis. These specimens are quite morphologically distinct from the rest of the species, but are similar to specimens from galls on chinkapin (see chapter 7).

The absence of Ormyrus from a gall (Table 3) may reflect biological reality or it may indicate that insufficient quantities have been reared. True absence is indicated for the conspicuous "apple" galls (detachable leaf and twig galls), which have a central cell surrounded by radiating fibers which attach to the outer wall. Although Ormyrus species are mostly absent from the apple

galls of Atrusca, Besbicus, and Trichoteras, parasitoid Torymus species are recorded from several of these galls (Grissell 1976).

Some large detachable twig galls may harbor specialized Ormyrus (see above) while others apparently harbor no Ormyrus, for example Andricus quercuscalifornicus (Bassett). This gall has been reared extensively but the only parasitoids I have seen are species of Tetrastichus and Torymus. Preliminary evidence suggests that Andricus quercuscalifornicus may have deleted the sexual generation from its life cycle (Charles Dailey, per. comm.). The reason for the absence of Ormyrus from Andricus quercuscalifornicus may be related to phenology. This gall begins developing in late winter and may be too large by the time Ormyrus begins flying in the spring.

Because sexual generation galls are usually more ephemeral than asexual generation galls, the former might be expected to have fewer Ormyrus records than the latter. For example, among bud galls, there are no records of Ormyrus from sexual generation bud galls of Besbicus mirabilis (Kinsey), but there are numerous records of Ormyrus from asexual generation bud galls of Andricus opertus (Weld). Nonetheless, the number of Ormyrus records from sexual generation galls and asexual generation galls are comparable: 29 of the 120 (24.2%) sexual galls and 100 of the 406 (24.6%) asexual galls have Ormyrus records. Some of the less ephemeral sexual generation galls, such as Neuroterus washingtonensis, harbor numerous parasitoids including Ormyrus. This particular gall is many-celled (as opposed to single-celled) thereby providing a clumped resource for parasitoids to attack and researchers to collect. There are Ormyrus records from both generations of seven cynipid species; in all but two of these the same species of Ormyrus attacks both generations. The exceptions are



Callirhytis flora Weld and C. quercusoperator (O.S.), where acorn galls are attacked by O. acylus.

The exact feeding habits of Ormyrus species in oak galls are poorly understood. There are a few references to Ormyrus species acting both as primary parasitoids and hyperparasitoids (Brookfield 1972; Washburn & Cornell 1979, 1981). Although Ormyrus is widespread in cynipid galls, individuals often are few in number--consistent evidence that Ormyrus may frequently be hyperparasitic. Thus, in Nearctic oak galls, Ormyrus seems to occupy the position occupied by Mesopolobus (Pteromalidae) in Palearctic oak galls (see Askew, 1961).

Table 1. Ormyrus hosts: Diptera and phytophagous Chalcidoidea. Gall-formers: A = Agromyzidae, C = Cecidomyiidae, Ch = Chalcidoidea, T = Tephritidae; ? = uncertain. Distribution: Afr = Africa, Aus = Australia, N = Nearctic, P = Palearctic. References: Ormyrus records are from species descriptions (see chapter 3) or Sellenschlo and Wall (1984) unless otherwise noted; unpublished records are indicated by acronyms for collections (see chapter 2), followed by the number of specimens seen.

PLANT	GALL-FORMER	ORMYRUS SP. DISTRIBUTION REFERENCE
<u>ANACARDIACEAE</u>		
<u>Mangifera</u>		
<u>M. indica</u>	<u>Procontarinia matteiana</u> C	<u>Ormyrus gibbus</u> India
<u>Rhus</u>		
<u>R. sp.</u> (sumac)	seed Ch	<u>vacciniicola</u> N INH, 1
<u>ASTERACEAE (COMPOSITAE)</u>		
<u>Carduus</u>		
<u>C. hamulosus</u>	T?	<u>orientalis</u> P USNM, 1
<u>Centaurea</u>		
<u>C. maculosa</u>	T?	<u>orientalis</u> P USNM, 7
<u>C. pannonica</u>	T	<u>orientalis</u> P
<u>C. sadleriana</u>	T	<u>orientalis</u> P
<u>C. solstitialis</u>	T?	<u>orientalis</u> P USNM, 2
<u>Cirsium</u>		
<u>C. arvense</u>	<u>Urophora cardui</u> T	<u>orientalis</u> P CNC, 1
<u>Cousinia</u>		
<u>C. hamade</u>	<u>Urophora repetiki</u> T	<u>bucharicus</u> P
<u>Microlonchus</u>		
<u>M. salmanticus</u>	T	<u>orientalis</u> P Aldrey 1984
<u>Moquinea</u>		
<u>M. polymorpha</u>	unknown	sp. Brazil USNM, 4
<u>Otanthus</u>		
<u>O. maritimus</u>	<u>Tephritis stictica</u> T	<u>orientalis</u> P Rivosecchi 1958

Table 1 continued

PLANT	GALL-FORMER	ORMYRUS SP. DISTRIBUTION REFERENCE
<u>Wedelia</u> <u>W. biflora</u>	T?	<u>orientalis</u> Malaya USNM, 2
BOMBACACEAE		
<u>Ceiba</u> <u>C. pentandra</u>	<u>Schizomyia</u> C	sp. Afr DiGiulio, 1
CAPPARIDACEAE		
<u>Apopophyllum</u>	unknown	sp. Aus Riek 1970
CASUARINACEAE		
<u>Casuarina</u> <u>C. sp.</u>	<u>Lisseurytoma</u> ? Ch	sp. Aus Riek 1970
CHENOPODIACEAE		
<u>Anabasis</u> <u>A. aphylla</u>	<u>Asiodiplosis</u> <u>palpata</u> C	<u>lanatus</u> P
<u>A. salsa</u>	C	<u>parvulus</u> P
?	<u>Haloxylonomyia</u> <u>gigas</u> C	<u>similis</u> P
CLUSIACEAE (GUTTIFERAE)		
<u>Harungana</u> <u>H. sp.</u>	stem gall	<u>harongae</u> Afr
COMBRETACEAE		
<u>Bucida</u> <u>B. cucides</u>	seeds	<u>thymus</u> Belize USNM, 1
ERICACEAE		
<u>Vaccinium</u> <u>V. spp.</u>	<u>Hemadas</u> <u>nubilipennis</u> Ch	<u>vacciniicola</u> N CNC 10, INH 6, OHSU 5, UCR 13, USNM 14 <u>rosae</u> N CM 2, CNC 16, OHSU 5, REM 10, UCR 16, USNM 71

Table 1 continued

PLANT	GALL-FORMER	ORMYRUS SP. DISTRIBUTION REFERENCE
<u>EUPHORBIACEAE</u>		
<u>Flueggea</u>		
<u>F. obovata</u>	<u>Asphondylia</u> <u>terminalia</u> C	<u>sculptilis</u> Afr
<u>F. obovata</u>	A	<u>sculptilis</u> Afr
<u>FABACEAE (LEGUMINOSAE)</u>		
<u>Dalbergia</u>		
<u>D. melanoxyylon</u>	Diptera stem gall	sp. Afr Crosby 1909
<u>FAGACEAE</u>		
<u>Quercus</u>		
<u>Q. spp.</u>	C	<u>labotus</u> N UT, 32
<u>MALVACEAE</u>		
<u>Abutilon ?</u>		
<u>A. sp.</u>	<u>Hexomyza</u> <u>abutilonicaulis</u> A	<u>orientalis</u> Pakistan USNM, 10
<u>MORACEAE</u>		
<u>Ficus</u>		
<u>F. burkei</u>	Ch	<u>flavipes</u> Afr
<u>F. burkei</u>	Ch	<u>subconicus</u> Afr
<u>F. burkei</u>	Ch	<u>watshami</u> Afr
<u>F. lepriurii</u>	leaf gall	sp. Afr DiGiulio, 2
<u>F. macrophylla</u>	Ch	<u>silviae</u> Aus Dahms 1986
<u>MYRSINACEAE</u>		
<u>Ardisia</u>		
<u>A. attenuata</u>	seed	sp. Java USNM, 1
<u>MYRTACEAE</u>		
<u>Eugenia</u>		
<u>E. sp.</u>	stem gall	<u>eugeniae</u> Afr
<u>Melaleuca</u>		
<u>M. sp.</u>	unknown	sp. Aus Riek 1970

Table 1 continued

PLANT	GALL-FORMER	ORMYRUS SP. DISTRIBUTION REFERENCE
POACEAE		
<u>Agropyrum</u>		
<u>A. trichophorum</u>	seed	sp. USSR-Tashkent USNM, 2
ROSACEAE		
<u>Rubus</u>		
<u>R. spp.</u>	<u>Agromyza rubi</u> A	<u>punctiger</u> P
RUTACEAE		
<u>Eremocitrus</u>		
<u>E. sp.</u>	<u>Eurytoma fellis</u> ? Ch	sp. Aus Riek 1970

Table 2. ORMYRUS HOSTS: NON-OAK CYNIPIDS. Nearctic records (N) are from label data associated with specimens I examined; Palearctic records (P) are from Sellenschlo & Wall (1984) and Nieves-Aldrey (1984); \* = introduced.

PLANT	GALL-FORMER	ORMYRUS SP. DISTRIBUTION
ASTERACEAE (COMPOSITAE)		
<u>Centaurea</u>		
<u>C. jacea</u>	<u>Phanacis centaureae</u>	<u>wachtli</u> P
<u>C. rhenana</u>	<u>Phanacis centaureae</u>	<u>wachtli</u> P
<u>C. sadleriana</u>	<u>Isocolus rogenhoferi</u>	<u>cingulatus</u> P <u>gratiosus</u> P
<u>C. sadleriana</u>	<u>Isocolus scabiosae</u>	<u>cingulatus</u> P <u>gratiosus</u> P
<u>C. scabiosae</u>	<u>Isocolus rogenhoferi</u>	<u>cingulatus</u> P <u>gratiosus</u> P
<u>C. scabiosae</u>	<u>Isocolus scabiosae</u>	<u>cingulatus</u> P <u>gratiosus</u> P
<u>C. stenolepis</u>	<u>Phanacis centaureae</u>	<u>wachtli</u> P
<u>Hieracium</u>		
<u>H. pilosellae</u> P	<u>Aulacidea subterminalis</u>	<u>salmanticus</u>
<u>Hypochoeris</u>		
<u>H. radicata</u>	<u>Phanacis hypochaeridis</u>	sp. *N
<u>Lactuca</u> spp.	<u>Aulacidea</u> spp.	sp. N
<u>Prenanthes</u> sp.	<u>Aulacidea nabali</u>	sp. N
<u>Silphium</u>		
<u>S. laciniatum</u>	<u>Antistrophus rufus</u> ?	sp. N
LAMIACEAE (LABIATEAE)		
<u>Salvia</u>		
<u>S. officinalis</u>	<u>Aylax salviae</u>	<u>wachtli</u> P <u>diffinis</u> P
<u>S. silvestris</u>	<u>Aylax salviae</u>	<u>wachtli</u> P <u>diffinis</u> P
PAPAVERACEAE		
<u>Papaver</u>		
<u>P. dubium</u>	<u>Aylax papaveris</u>	<u>papaveris</u> P
<u>P. rhoeas</u>	<u>Aylax papaveris</u>	<u>papaveris</u> P

Table 2 continued

PLANT	GALL-FORMER	ORMYRUS SP. DISTRIBUTION
ROSACEAE		
<u>Fragaria</u>		
<u>F. virginiana</u>	<u>Diastrophus fragariae</u>	<u>vacciniicola</u>
N		
<u>Potentilla</u>		
<u>P. gracilis</u>	<u>Diastrophus fusiformans</u>	<u>rosae</u> N
<u>P. reptans</u>	<u>Xestophanes potentillae</u>	<u>diffinis</u> P
		<u>rufimanus</u> P
<u>P. spp.</u>	<u>Diastrophus mayri</u>	<u>gratiosus</u> P
		<u>rufimanus</u> P
<u>Rosa</u>		
<u>R. canina</u>	<u>Diplolepis rosae</u>	<u>nididulus</u> P
<u>R. spp.</u>	<u>Diplolepis spp.</u>	<u>rosae</u> N
<u>Rubus</u>		
<u>R. parviflorus</u>	<u>Diastrophus kincaidii</u>	<u>rosae</u> N
<u>R. spp.</u>	<u>Diastrophus rubi</u>	<u>orientalis</u> P
		<u>rufimanus</u> P
<u>R. spp.</u>	<u>Diastrophus spp.</u>	<u>rosae?</u> N

Table 3. ORMYRUS HOSTS: NEARCTIC OAK CYNIPIDS.

REFERENCES are given for changes subsequent to Krombein et al. (1979) and are listed (in parentheses) after the relevant cynipid species: 1 & 2 = Burnett (1974 & 1977), 3 & 4 = Dailey (1969 & 1977), 5 = Dailey & Menke (1980), 6 = Dailey et al. (1974), 7-10 = Dailey & Sprenger (1973a & b, 1977, 1983), 11 = Evans (1972), 12 = Lyon (1984); \* = personal observation.

## GENERATIONS

A = Asexual

S = Sexual

## GALL TYPES

a = acorn galls

1 = leaf galls

1 = cell(s) in cup  
fibers

1 = detachable, radiating

2 = large, attached to cup

2 = detachable, other

3 = "pip", attached to cup

3 = prolongation of vein

4 = stone gall in nut

4 = pustules

5 = midrib or petiole swelling

b = bud galls

6 = parenchyma swelling

7 = integral, free-rolling cell

8 = integral, wooly

c = catkin galls

1 = swelling of axis

2 = large, several-celled

t = twig galls

3 = small one-celled  
fibers

1 = detachable, radiating

2 = detachable, other

r = root galls

3 = swelling, new growth

4 = swelling, older growth

5 = cell, little swelling

## HOST OAKS

ER = eastern red oaks

SR = southwestern red oaks

EW = eastern white oaks

SW = southwestern white oaks

P = Protobalanus

WR = western red oaks

(canyon live)

WW = western white oaks

abbreviations of oak species: agr=agrifolia, alb=alba, ari=arizonica, bic=bicololr, buc=buckleyi, cha=chapmani, coc=coccinea, dou=douglasia, dum=dumosa, dur=durata, emo=emoryi, eng=engelmanni, fal=falcata, gam=gambelii, gar=garryana, gri=grisea, hav=havardii hyp=hypoleucoides, ili=ilicifolia, imb=imbricariae, inc=incana, kel=kelloggii, lac=laceyi, lae=laevis, lau=laurifolia, lob=lobata, lyr=lyrata, mac=macrocarpa, marg=margaretta, mari=marilandica, mic=michauxi, muh=muhlenberbia, myr=myrtifolia, nig=nigra, obl=oblongifolia, pal=palustris, phe=phellos, pro=prinoides, pru=prinus, pum=pumila, rub=rubra, rug=rugosa, sad=sadleriana, shu=sumardii, ste=stellata, tou=toumeyii, tur=turbinella, vel=velutina, vir=virginiana, wis=wislezenii.



Table 3 continued

## CYNIPID GENUS

species: generation, gall-type, host oaks Ormyrus sp.  
# specimens

ACRASPIS

<u>alaria</u> A,1-2,SW:gam	<u>labotus</u> 7
<u>arida</u> A,1-2,SW:gri	
<u>bandero</u> A,1-2,SW:gam	
<u>conica</u> A,1-2,SW:gri	
<u>echini</u> A,1-2,EW:bic	
<u>erinacei</u> A,1-2,EW:alb	<u>labotus</u> 60
S,b	
<u>gemula</u> A,1-2,EW:alb mic muh pro	<u>labotus</u> 8
S,b	<u>labotus</u> 4
<u>hibrida</u> A,1-2,SW:alb	
<u>hirtior</u> A,1-2,SW:gam?	
<u>inflata</u> A,1-2,EW:alb	
<u>longicornis</u> S,t-5,EW:ste	
<u>macrocarpae</u> A,1-2,EW:mac	<u>labotus</u> 39
<u>pezomachoides</u> A,1-2,EW:alb SW?	<u>labotus</u> 105
S,b	
<u>prinoides</u> A,1-2,EW:pro	<u>labotus</u> 13
<u>quercushirta</u> A,1-2,EW:cha mac mic pru	<u>labotus</u> 71
SW:gam	
<u>ulterior</u> A,1-2,SW:gam	
<u>villosa</u> A,1-2,EW:mac SW:ari gri gam	<u>labotus</u> 5

ADLERIA

<u>arizonica</u> A,1-2,SW:ari
<u>dimorpha</u> A,1-2,EW:alb mac
<u>flavicollis</u> A,1-2,EW?
<u>nigricens</u> A,1-2,EW:bic
<u>quercusstrobilana</u> A,t-2,EW:bic mac
<u>vacciniiformis</u> A,1-2,EW:ste
<u>weldi</u> A,1-2,EW:alb

AMPHIBOLIPS

<u>acuminata</u> S,t-2,ER:fal inc	
<u>arcuata</u> A,t-1,ER?	
<u>confluenta</u> A,1-1,ER	
<u>cookii</u> A,b,ER:rub	
<u>gainesi</u> A,a-2,ER:lau (mari)	<u>labotus</u> 1
<u>globulus</u> A,b,ER:mari (fal)	<u>dryorhizoxeni</u> 1
<u>globus</u> A,b,ER:pal	
S,b	
<u>gumia</u> A,t-2,SR:emo hyp	
<u>melanocera</u> S,b,ER:nig	

Table 3 continued

## CYNIPID GENUS

species: generation, gall-type, host oaks Ormyrus sp.  
# specimens

<u>murata</u> A,b,ER:inc lau myr pum	
<u>nigra</u> A,t-2,SR:emo hyp	
<u>nubilipennis</u> S,1-1,ER	<u>labotus</u> 1
<u>quercuscinerea</u> A,t-1,ER:inc	<u>hegeli</u> 1
<u>quercuscitriformis</u> A,b,ER:phe	
<u>quercuscoelebs</u> S,1-3,ER:coc	<u>labotus</u> 2
<u>quercusfuliginosa</u> A,a-2,ER:lau	
<u>quercusilicifoliae</u> S,1-3,ER:ili	
<u>quercusinanis</u> A,1-1,ER:rub	
<u>quercusjuglans</u> A,a-2,ER	
<u>quercusracemaria</u> A,1-1,ER:lau	
<u>quercusspongifica</u> A,1-1,ER:coc mari vel	<u>labotus</u> 3
<u>spinosa</u> A,b,ER:lau	
<u>tinctoriae</u> A,b,ER:coc vel	<u>labotus</u> 2
<u>trizonata</u> S,t-2,SR:emo hyp	
 <u>ANDRICUS</u>	
<u>aciculatus</u> A,t-2,EW:ste	
<u>albicomus</u> A,1-2,WW:gar	
<u>albobalani</u> A,a-1,WW:dou dum lob	
<u>atrimentus</u> (8) A,1-2,WW:dou S,1-4	<u>venustus</u> 1
<u>bakkeri</u> (12) A,1-2,WW:dum	
<u>biconicus</u> A,1-2,EW:ste	
<u>bracteatus</u> A,t-3,SW:ari obl rug tou	
<u>brunneus</u> A,1-2,WW:dou dum gar lob	<u>distinctus</u> 6
<u>caepula</u> A,1-2,SW:ari obl tur	
<u>capillatus</u> A,1-2,EW:alb	
<u>cellularius</u> A,b,SW:"undulata"	
<u>chico</u> A,b,WW:lob	
<u>chinquapin</u> S,1-3,EW:albbic pro	
<u>chrysobalani</u> A,a-1,P	
<u>chrysolepidicola</u> A,t-4,WW:dou dum gar lob	<u>distinctus</u> 4
	<u>reticulatus</u> 1
	<u>venustus</u> 3
	S,1-2
<u>cinnamomeus</u> A,b,EW:cha	<u>acylus</u> 5
	<u>labotus</u> 1
<u>confertus</u> A,1-2,WW:lob	
<u>coortus</u> A,b,WW:dou dum	
<u>coronus</u> A,t-2,ER:pal phe	<u>labotus</u> 1
<u>costatus</u> A,a-2,SW:gam tur	
<u>crassicornis</u> A,t-2,?	

Table 3 continued

## CYNIPID GENUS

species: generation, gall-type, host oaks Ormyrus sp.  
# specimens

<u>crenatus</u> = <u>gigas</u> (7)	
<u>crystallinus</u> A,1-2,WW:dou dum gar S,1-2	<u>distinctus</u> 4
<u>deciduatus</u> A,b,EW:bic	
<u>discalis</u> A,1-2,SW:tur	
<u>disularis</u> A,1-2,WW:gar	
<u>ellipsoidalis</u> A,b,ER:fal pal	
<u>femoratus</u> A,1-1,ER:lau phe	
<u>fimbrialis</u> = <u>opertus</u> (11)	
<u>flavohirtus</u> A,b,EW:bic	
<u>foliaformis</u> S,1-5,EW:alb bic mac	
<u>formosalis</u> A,t-2,SR:emo	
<u>fullawayi</u> A,1-2,WW:lob	<u>distinctus</u> 5 <u>venustus</u> 18
<u>furnessulus</u> A,t-2,SW:ari obl	
<u>gigas</u> (7) A,1-2,WW:dou dum S,1-2	
<u>howertoni</u> A,t-3,SW:tur	
<u>ignotus</u> A,1-2,EW:bic mac	<u>labotus</u> 749
<u>incertus</u> A,a-1,EW:bic	
<u>incognitus</u> A,?,EW:ste	
<u>indistinctus</u> A,t-2,EW:alb	
<u>kingi</u> A,1-2,WW:dou dum gar lob	<u>distinctus</u> 37
<u>lasius</u> A,1-2,P	<u>distinctus</u> 3
<u>mamillaformis</u> A,b,EW:alb	
<u>maxwelli</u> S,t-2,?	
<u>mendocinensis</u> A,r,Lithocarpus	
<u>montezuma</u> A,t-4,SW:ari obl rug tou	
<u>multicostatus</u> A,b,SW:tur	
<u>murtfeldtae</u> S,b,EW:ste	
<u>occultatus</u> A,b,WW:dou dum lob	
<u>opertus</u> (11) A,b,WW:dou gar lob	<u>distinctus</u> 2 <u>unifasciatipennis</u> 1 <u>venustus</u> 12 <u>venustus</u> 3
S,1-3	
<u>parmula</u> A,1-2,WW:dou dum eng gar lob	
<u>pattersonae</u> to <u>Liadora</u> (11)	
<u>pattoni</u> A,1-2,EW:ste	<u>dryorhizoxeni</u> 50 <u>labotus</u> 699 <u>venustus</u> 1
<u>pilula</u> S,1-4,SW:gam	
<u>pilularis</u> S,1-4,SW:ari gam obl rug tou tur	
<u>pisiformis</u> A,b,EW:alb bic	
<u>prescotti</u> A,a-3,SW:ari gam obl rug tur	
<u>projectus</u> A,b,P	

Table 3 continued

## CYNIPID GENUS

species: generation, gall-type, host oaks Ormyrus sp.  
# specimens

<u>pulchellus</u> A,?,EW:pro	
<u>quercuscalifornicus</u> A,t-2,WW:dou dum eng gar lob	
<u>quercusflocci</u> A,1-2,EW:alb	<u>labotus</u> 37
<u>quercusfoliatus</u> A,b,EW:vir	<u>dryorhizoxeni</u> 221
	<u>labotus</u> 1
<u>quercusformosus</u> A,t-2,ER:coc inc mari phe rub	
<u>quercuslanigera</u> A,1-2,EW:vir	<u>labotus</u> 219
<u>quercusostensackenii</u> S,1-1,ER:pal coc	<u>labotus</u> 1
<u>quercuspetiolicola</u> S,1-5,EW	<u>labotus</u> 63
	<u>venustus</u> 3
<u>quercussingularis</u> S,1-1,ER:rub	<u>labotus</u> 2
<u>quercusutriculus</u> S,1-4,EW:alb cha ste	
<u>reniformis</u> A,t-2,P	
<u>reticulatus</u> A,1-5,SW:ari gam obl rug tou tur	
	WW:eng (12)
<u>rhizoxenus</u> A,t-4,SW:rug	
<u>robustus</u> A,1-2,EW:ste	
<u>rugatus</u> A,1-2,EW:lyr	
<u>ruginosus</u> A,t-4,SW:gam	<u>hegeli</u> 9
<u>scutella</u> A,1-2,SW:gam tur	
<u>spectabilis</u> A,t-4,P	
<u>spicatus</u> A,t-2,SW:ari obl tou	
<u>splendens</u> A,1-2,SW:gri tur	
<u>stellaris</u> A,1-2,WW:dou gar	
<u>stellulus</u> (1) A,1-2,WW:dum	
<u>stramineus</u> A,t-2,SW:obl	
<u>stropus</u> A,b,EW:ste	
<u>sulfureus</u> A,1-2,SW:ari obl	<u>venustus</u> 4
<u>tecturnarum</u> A,1-2,SW:ari gam obl tou tur	<u>labotus</u> 2
	<u>venustus</u> 15
<u>tenuicornis</u> A,1-2,SW:ari	
<u>toumey</u> A,t-3,SW:tou tur	
<u>truckeensis</u> A,t-2,P	
<u>tubalis</u> A,t-2,SW:ari obl	
<u>tubularius</u> A,t-5,SW:tur	
<u>verensis</u> A,b,WW:dum gar	
<u>vernus</u> A,b,ER:ili	
<u>wheeleri</u> A,t-4,SW:ari obl tou tur	<u>hegeli</u> 10
	<u>venustus</u> 1
<u>wiltzae</u> A,t-3,WW:dum lob	<u>unifasciatipennis</u> 1
	<u>venustus</u> 3

Table 3 continued

## CYNIPID GENUS

species: generation, gall-type, host oaks Ormyrus sp.  
# specimens

ANTRON

acraspiformis A,1-2,SW:tur tou  
clavula to Xanthoteras (5)  
douglasii A,1-2,WW:dou dum lob distinctus 21  
S,b  
dumosae A,1-2,WW:dum  
magdalenae A,1-2,SW:tur  
pileus S,t-2,SW:tur  
plumbeum A,1-2,SW:ari obl tou  
quercusechinus A,1-2,WW:dou dum distinctus 20  
venustus 1  
S,b distinctus 1  
quercusnubila A,1-2,SW:ari obl ret tou tur  
russum A,1-2,SW:ari obl

ATRUSCA

aggregata A,t-2,SW:ari obl tou  
bella A,1-1,SW:ari obl rug tou tur  
brevipennata A,1-1,SW:gam tur  
capronae A,1-1,SW:tur  
catena A,1-1,SW:gri  
cava A,1-1,EW:sin  
clivorum A,1-1,EW:ste  
congesta A,1-1,SW:gri  
cubitalis A,1-1,SW:gam  
pupoides A,1-1,SW:gri  
quercuscentricola A,1-1,EW:ste  
simulatrix A,1-1,SW:ari gam gri obl  
strians A,1-1,EW:ste  
subnigra A,1-1,SW:gri  
vanescens A,1-1,SW:gri

BASSETTIA

aquaticae A,t-5,ER:nig  
ceropteroides A,t-5,ER:vel  
floridana A,r,EW:cha pro?  
gemmae A,t-5,?  
herberti A,t-5,WR:agr kel wis  
ligni A,t-5,WW:dou dum gar lob turio 12  
S,1-4  
pallida A,t-5,?  
quercuscatesbaei S,t-5,ER:lae  
tenuana A,r,SW:gam tur

Table 3 continued

## CYNIPID GENUS

species: generation, gall-type, host oaks Ormyrus sp.  
# specimens

BELONOCNEMAkinseyi A, 1-2, EW:virdryorhizoxeni 2labotus 47venustus 7quercusvirens A, 1-2, EW:virtreatae S, r, EW:virdryorhizoxeni 22BESBICUSconspicuus A, 1-2, WW:dou lobheldae A, 1-2, WW:lobindictus A, 1-1, WW:douleachii A, 1-1, WW:garmaculosus A, 1-1, WW:dummirabilis A, 1-1, WW:gar

S, b

multipunctatus A, 1-1, WW:doudistinctus 3tritior A, 1-1, WW:dum durCALLIRHYTISapicalis A, r, WR:agr kel wisattigua A, 1-2, ER:bucattractans (3) S, b, WR:agr kel wisbalanacea A, a-3, ER:palbalanaspis A, a-3, ER:maribalanella A, a-2, SR:emobalanoides A, a-3, ER:velbalanopsis A, a-3, ER:maribalanosa A, a-3, ER:cocbipapillata S, 1-6, ER:iliblastophaga A, c-3, ER:inccarmelensis A, a-3, WR:agr kel wiscedros (9) A, t-2, Pcedrosensis (9) A, t-2, Pcistella A, a-3, SR:emo hypclarkei A, c-3, ER:iliclavula A?, t-4, EW:albcongregata A, c-1, WR:agr wislabotus 3distinctus 1venustus 50labotus 48cornigera A, t-4, ERcorrugis A, a-4, ER:velcressoni A, b, EW:stecrypta = quercusmedullae (5)cryptica A, b, ER:myrdifficilis A, t-2, ER:myr nig phe

Table 3 continued

## CYNIPID GENUS

species: generation, gall-type, host oaks Ormyrus sp.  
# specimens

<u>eldoradensis</u> (6) A,b,WR:agr kel wis S,a-1	<u>distinctus</u> 1 <u>venustus</u> 1
<u>electrea</u> A,a-4,EW:pru	
<u>ellipsoïda</u> A,r,EW:bic	
<u>elliptica</u> A,r,EW:alb	
<u>elongata</u> A,t-5,EW:bre ste	<u>labotus</u> 3
<u>excavata</u> A,t-2,ER:rub	
<u>exigua</u> S,c-3,EW:ste	
<u>favosa</u> S,l-6,ER:pal vel	<u>labotus</u> 6
<u>flavipes</u> S,l-5,EW:mac	<u>labotus</u> 2
<u>flora</u> (6) A,l-5,WR:agr wis S,a-4	<u>distinctus</u> 1 <u>venustus</u> 17 <u>acylus</u> 22
<u>florensîs</u> S,c-3,ER:mari	
<u>floridana</u> S,t-4,EW:cha ste	
<u>floripara</u> S,c-3,WR:agr	
<u>frequens</u> A,t-4,SW:gam hav	<u>reticulatus</u> 7
<u>fructicola</u> A,a-4,ER:ili mari vel	
<u>fructuosa</u> A,a-4,ER	
<u>fulva</u> A,r,P	
<u>furva</u> A,l-2,ER:nig pal	
<u>gallaestriatae</u> A,b,ER:coc pal rub vel	<u>labotus</u> 1
<u>gemmiformis</u> A,b,EW:alb	
<u>glandulus</u> A,a-1,EW:pro	
<u>glomerosa</u> A,b,ER:coc	
<u>hopkinsi</u> A,a-3,ER:imb	
<u>infuscata</u> A,l-2,ER:lae	<u>dryorhizoxeni</u> 5 <u>labotus</u> 2
<u>intersita</u> A,?,EW:alb	
<u>juvenca</u> A,l-2,SWari gam obl rug tur	
<u>lanata</u> A,l-2,ER:coc rub	<u>labotus</u> 37
<u>lapillula</u> A,a-4,EW:bic	
<u>lentiformis</u> (12) A,b,WR:agr	
<u>lupana</u> S,l-5,SR:emo hyp	
<u>marginata</u> A,r,ER:coc	
<u>medularis</u> S,t-4,ER:coc vel	
<u>middletoni</u> A,a-3,ER:phe	
<u>milleri</u> = <u>flora</u> (Dailey et al 1974)	
<u>morrisoni</u> S,l-5,?	
<u>myrtifoliae</u> S,c-3,ER:myr	
<u>oblata</u> A,b,ER:coc fal	
<u>obtusilobae</u> A,?,EW:ste	
<u>ovata</u> A,r,ER:buc inc lae myr	

Table 3 continued

## CYNIPID GENUS

species: generation, gall-type, host oaks Ormyrus sp.  
# specimens

<u>parva</u> S, c-2, ER: imb	
<u>parvifoliae</u> S?, 1-5, EW: cha	
<u>parvula</u> A, ?, ER: ili	
<u>patiens</u> = <u>parvula</u> ?	
<u>pedunculata</u> S, 1-3, ER: coc rub	<u>labotus</u> 2
<u>perdens</u> A, t-4, WR: agr kel wis	<u>distinctus</u> 6
<u>perditor</u> A, a-3, ER: ili	
<u>perfoveata</u> (6) S, 1-6, WR: agr kel wis	
<u>perobscura</u> A, ?, ER: vel	
<u>perplexa</u> A, 1-2, ?	
<u>perrugosa</u> A, r, EW: alb	
<u>petrina</u> A, a-4, SR: hyp	
<u>petrosa</u> A, a-4, ER: inc	
<u>pigra</u> A, 1-5, ER: coc vel	
<u>piperoides</u> A, 1-2, ER	
<u>protobalanus</u> (9) A, a-4, P	
<u>pulchra</u> S, c-2, ER: rub vel	<u>labotus</u> 5
<u>quercifoliae</u> S, 1-7, ER: lae	
<u>quercusagrifoliae</u> A, 1-2, WR: agr kel wis S, 1-4	
<u>quercusbatatoides</u> A, t-4, EW: vir	<u>reticulatus</u> 10
<u>quercusclavigera</u> A, t-4, ER: lau	
<u>quercusconfusa</u> A, 1-7, ER: lau	
<u>quercusfutilis</u> A, r, EW: alb pru S, 1-6	<u>labotus</u> 11
<u>quercusgemmaria</u> A, t-2, ER	<u>labotus</u> 3
<u>quercusmedullae</u> A, t-4, ER: inc	<u>labotus</u> 1
<u>quercusmodesta</u> A, 1-6, ER: rub vel (mar)	<u>labotus</u> 12
<u>quercusnigrae</u> S, 1-5, ER: mar	
<u>quercusoperator</u> A, a-3, ER S, c-1	<u>acylus</u> 3 <u>labotus</u> 46
<u>quercusphellos</u> A, t-5, ER: phe	
<u>quercuspomiformis</u> A, t-2, WR: agr wis S, 1-2	<u>distinctus</u> 3 <u>setosus</u> 32
<u>quercuspunctata</u> A, t-4, ER: coc pal vel	<u>labotus</u> 10
<u>quercusrugosa</u> S, 1-6, ER: imb lau phe	
<u>quercusscitula</u> S, t-3, ER: coc vel	<u>labotus</u> 12
<u>quercussimilis</u> S, t-4, ER	<u>labotus</u> 3
<u>quercussuttonii</u> A, t-4, WR: agr kel wis S, 1-4	
<u>quercusturnerii</u> A, c-1, ER: nig	
<u>quercusventricosa</u> A, t-2, ER: ili imb phe	
<u>rubida</u> A, r, ER: coc rub	



Table 3 continued

## CYNIPID GENUS

species: generation, gall-type, host oaks Ormyrus sp.  
# specimens

<u>rugulosa</u> A,b,ER:rub vel	
<u>seminator</u> A,t-2,WW:alb	<u>labotus</u> 11
<u>seminosa</u> A,t-4,ER:coc pal	
<u>serricornis</u> A,1-2,WR:agr wis S,c-3	
<u>tuberosa</u> S,t-5,ER:ili	
<u>tubicola</u> A,1-2,EW:ste	<u>labotus</u> 32
<u>tumifica</u> S,1-5,ER:rub vel	<u>acylus</u> 1 <u>labotus</u> 22
<u>uvellae</u> = <u>attractans</u> (3)	
<u>vaccinii</u> A,1-5,EW:ste	<u>labotus</u> 15
DISHOLCASPIS	
<u>acetabula</u> A,r,SW:gam rug tou tur	<u>dryorhizoxeni</u> 3
<u>bassetti</u> A,t-2,EW:bic mac	
<u>brevinota</u> A,r,EW:sin	
<u>californica</u> (2) A,t-2,WW:dou dum tur	
<u>canescens</u> A,t-2,WW:dou dum lob	
<u>chrysolepidis</u> A,t-2,P	
<u>cinerosa</u> A,t-2,EW:vir S,b	<u>labotus</u> 1
<u>colorado</u> A,t-2,SW:gam?	<u>dryorhizoxeni</u> 19
<u>conalis</u> A,t-2,WW:gar	
<u>corallina</u> A,t-2,WW:dou	<u>distinctus</u> 1
<u>eldoradensis</u> (11) A,t-2,WW:dum gar lob S,b	<u>reticulatus</u> 2
<u>edura</u> A,t-2,SW:ari obl rug	
<u>fungiformis</u> A,t-2,EW:vir	
<u>globosa</u> A,r,EW:alb	
<u>heynei</u> A,t-2,EW?	
<u>lacuna</u> A,r,SW:gam	
<u>mamillana</u> A,t-2,WW:dou	<u>hegeli</u> 1
<u>mellifica</u> A,t-2,WW:gar	<u>distinctus</u> 7
<u>pattersoni</u> A,t-2,EW:sin	
<u>pedunculoides</u> A,a-2,SW:ari obl tur	<u>hegeli</u> 1 <u>venustus</u> 1 <u>reticulatus</u> 1
<u>perniciosa</u> A,t-2,SW:gam	
<u>persimilis</u> A,t-2,EW?	
<u>plumbella</u> A,t-2,WW:dum dur tur	<u>distinctus</u> 13
<u>prehensa</u> A,t-2,WW:dum	<u>reticulatus</u> 1
<u>pruniformis</u> A,t-2,EW:lac sin (ste?)	
<u>quercusglobulus</u> A,t-2,EW:alb pro pru	
<u>quercusmamma</u> A,t-2,EW:bic mac	<u>hegeli</u> 1 <u>reticulatus</u> 2

Table 3 continued

## CYNIPID GENUS

species: generation, gall-type, host oaks Ormyrus sp.  
# specimens

<u>quercusomnivora</u> A, t-2, EW: cha	
<u>quercussuccinipes</u> A, t-2, EW: vir	
<u>quercusvirens</u> A, t-2, EW: vir	<u>dryorhizoxeni</u> 1
<u>rubens</u> A, t-2, SW: ari gam obl rug tou tur	<u>venustus</u> 4
<u>sileri</u> A, t-2, SW: gam?	
<u>simulata</u> A, t-2, WW: dou dum gar	<u>distinctus</u> 2
	<u>reticulatus</u> 1
<u>spissa</u> A, t-2, SW: ari hav rug tur	
<u>spongiosa</u> A, t-2, EW: cha ste	<u>dryorhizoxeni</u> 38
	<u>labotus</u> 6
<u>sulcata</u> A, 1-2, SW: ari obl pun rug tou tur	<u>venustus</u> 2
<u>terrestris</u> A, r, EW: marg ste	<u>dryorhizoxeni</u> 3
<u>truckeensis</u> to <u>Andricus</u> (5)	
<u>washingtonensis</u> A, t-2, WW: dou dum dur gar	<u>distinctus</u> 9

## DROS

<u>amphora</u> A, 1-2, SW: ari obl	<u>venustus</u> 10
<u>atrimentum</u> to <u>Andricus</u> (8)	
<u>pedicellatum</u> S, 1-3, WW: dou gar	
<u>sessile</u> A, 1-2, SW: ari obl	
<u>viscidum</u> A, 1-2, SW: obl	

## DRYOCOSMUS

<u>albidus</u> A, 1-2, ER: coc vel	
<u>asymmetricus</u> A, t-4, P	<u>distinctus</u> 1
<u>attractans</u> to <u>Callirhytis</u> (3)	
<u>castanopsidis</u> A, c, <u>Chrysolepis</u>	
<u>cinereae</u> S, 1-7, ER	
<u>coxii</u> A, t-4, SR: emo hyp	<u>venustus</u> 4
<u>deciduus</u> A, 1-2, ER: rub vel	
<u>dubiosus</u> A, 1-2, WR: agr wis	
S, c-3	
<u>favus</u> A, r, ER	<u>crassus</u> 19
	<u>dryorhizoxeni</u> 1
<u>floridensis</u> A, t-2, ER	
<u>gigas</u> to <u>Andricus</u> (7)	
<u>imbricariae</u> A, t-2, ER	<u>dryorhizoxeni</u> 1
<u>kuriphilus</u> A, b, <u>Castanea</u> (introduced)	<u>labotus</u> 7
<u>minusculus</u> A, 1-2, WR: agr	
<u>quercuslaurifoliae</u> S, 1-7, ER: lau nig	
<u>quercusnotha</u> S, 1-7, ER	<u>labotus</u> 2
<u>quercuspalustris</u> S, 1-7, ER	<u>labotus</u> 30
<u>rileyi</u> A, 1-2, ER	

Table 3 continued

## CYNIPID GENUS

species: generation, gall-type, host oaks Ormyrus sp.  
# specimens

EUMAYRIAeldoradensis to Callirhytis (6)floridana S,r,ERinvisa A,t-5,ER:myrlongipennis S,t-5,ER:lauHETEROECUSchrysolepidis A,t-2,Pcrescentus (12) S,l-4,Pdasydactyli A,t-2,P

S,l-4

devorus (12) S,l-4,Periophora A,t-2,P?flavens A,l-6,Pfragilis (10) A,t-2,Plyoni (10) A,t-2,Pmalus A,t-2,Pmelanoderma A,t-2,Ppacificus A,t-2,P

S,l-2

sanctaeclarae A,t-2,Pdistinctus 1distinctus 9distinctus 3HOLOCYNIPSbadia A,r,EW:alb bic cha mac pru stehartmani A,r,Phumicola A,r,WR:agr kel wismaxima A,r,EW:alb bic mac prudryorhizoxeni 1LIODORAapiarium A,l-2,EW:albclarkei S,b,EW:alb stecomata S,l-4,EW:albpattersonae (11) A,l-2,WW:dou dum gar lob

S,l-2

LOXAULUSashmeadi A,t-5,robur (introduced)atrior (4) A,t-5,WW:lobbeutenmuelleri A,l-2,ER:rubboharti (10) A,t-5,Pbrunneus A,t-5,Pferrugineus A,?,?humilis A,r,EW:cha steillinoisensis A,r,EW:maclabotus 1

Table 3 continued

## CYNIPID GENUS

species: generation, gall-type, host oaks Ormyrus sp.  
# specimens

maculipennis A, t-4, ?  
pattersoni A, r, EW: vir  
quercusmammula S, t-4, EW: alb labotus 1  
tenuis A, r, SW: gam x tur  
trizonalis A, a-4, P  
S, t-2  
vaccinii A, t-5, ?

## NEUROTERUS

affinis S, b, EW: pro  
argentatus A, l-2, SW: gam obl  
bassettii S, l-4, EW: alb  
chrysolepis (12) A, t-5, P  
clarkeae S, l-4, EW: alb  
clavensis A, t-3, SW: gam tur  
cockerelli A, l-2, SW: gam?  
congregatus S, b, SW: gam?  
consimilis A, t-4, EW: alb  
contortus A, r, EW: sin  
S, t-4  
cupulae A, a-1, WW: lob  
distortus S, t-5, EW: bic  
dubius S, ?, EW?  
engelmanni A, l-4, WW: eng  
escharensis A, t-5, EW: bic  
evanescens S, c-1, EW: sin  
evolutus A, t-5, WW: dou lob (= washingtonensis?)  
exiguissimus A, l-8, EW: alb  
exiguus S, c-1, EW: ste labotus 46  
floccosus A, l-8, EW: bic labotus 4  
floricola S, c-3, WW: dou  
floricomus S, c-1, SW: obl rug tou venustus 1  
florulentus S, c-3, WW: dum lob  
fragilis S, l-6, WW: dou dum  
fugiens S, l-6, EW: mac  
gillettei S, l-5, EW: ste  
howertoni A, l-4, SW: ari obl  
lamellae A, l-5, SW: tur  
minutus S, b, EW: alb  
niger A, l-6, EW: mac sin ste vir SW: ari gri  
S, l-4  
noxiosus A, t-4, EW: bic  
S, l-6  
pallidus S, c-3, EW: bic

Table 3 continued

## CYNIPID GENUS

species: generation, gall-type, host oaks Ormyrus sp.  
# specimens

<u>papillosus</u> S, 1-6, EW: bic	
<u>perminimus</u> S, 1-6, EW: alb	
<u>quercicola</u> S, 1-5, SW: gam?	
<u>quercusbatatus</u> A, t-4, EW: alb pru	<u>dryorhizoxeni</u> 2
	<u>labotus</u> 15
	S, t-3
<u>quercusirregularis</u> S, 1-6, EW: sin ste	<u>labotus</u> 6
<u>quercusmajalis</u> S, 1-2, EW: alb	
<u>quercusminutissimus</u> A, 1-8, EW: vir	
<u>quercusrileyi</u> S, t-2, EW: muh pro pru	
<u>quercusverrucarum</u> A, 1-8, EW: bre cha mac ste	<u>labotus</u> 17
<u>sadlerensis</u> A (NR), t-5, WW: sad	<u>distinctus</u> 3
	S, 1-6
	<u>distinctus</u> 62
<u>saltarius</u> A, 1-2, EW: mac	
<u>saltatorius</u> A, 1-2, EW: ste vir SW: ariz	
	WW: dou gar lob
	<u>unifasciatipennis</u> 2
	S, 1-4
<u>tantulus</u> A, 1-2, EW: alb	
<u>tectus</u> A, 1-5?, EW: pro	
	S, t-5
<u>umbilicatus</u> A, 1-6, EW: bic	
<u>varians</u> A, t-3, WW: dou lob	<u>venustus</u> 7
<u>vernus</u> A, 1-5, EW: mac	
<u>vesicula</u> S, b, EW: alb ste	
<u>virgens</u> S, t-5, SW: ari gam tur	
<u>washingtonensis</u> (11) A, t-5, WW: gar	<u>venustus</u> 3
	S, 1-6
	<u>venustus</u> 24
<u>ODONTOCYNIPS</u>	
<u>nebulosa</u> A, r, EW: ste	
<u>PARACRASPIS</u>	
<u>guadaloupenis</u> A, 1-2, P	<u>distinctus</u> 1
<u>insolens</u> A, 1-2, P	
<u>patelloides</u> A, 1-2, P	
<u>PHILONIX</u>	
<u>fulvicollis</u> A, 1-2, EW: alb cha mac	<u>labotus</u> 69
<u>gigas</u> A, 1-2, EW: lyr	
<u>insulensis</u> A, 1-2, EW: mac & SW: gam	
<u>lanaeglobuli</u> A, 1-2, EW: mic	
<u>latigenae</u> A, 1-2, SW: gam	
<u>nigra</u> A, 1-2, EW: alb	<u>labotus</u> 2
<u>nigricollis</u> A, ?, EW?	
<u>pallipes</u> S, b, EW: alb (= <u>fulvicollis</u> ?)	

Table 3 continued

## CYNIPID GENUS

species: generation, gall-type, host oaks Ormyrus sp.  
# specimens

PHYLLOTERAScupella A, 1-2, SW:ari obl rug turrubinum A, 1-2, EW:albsigma A, 1-2, EW:albPLAGIOTROCHUSsuberi A, t-5, suber (introduced)venustus 9SPHAEROTERAScaepuliforme A, r, ERcarolina A, 1-2, EW:alb stemelleum A, 1-2, EW:alb cha min? sin steocala S, r, EW:charydbergiana A, 1-2, SW:rydbergiana?texanum A, 1-2, ?trimaculosum A, 1-2, WW:dou dum gar lob distinctus 3unicum A, 1-2, EW:steTRICHOTERASburnetti (10) A, 1-5, Pcalifornicum A, 1-2, WW:dou dumcoquilletti A, 1-1, Pfrondeum A, b, Pperfulvum A, 1-2, Protundula A, 1-2, Ptubifaciens A, 1-2, WW:garvacciniifoliae A, 1-1, PTRISOLENIELLAbrevicornis A, b, EW:albenigma A, r, ER:buc lae myr rubbignelli A, ?, ?saltata A, b, ER:inc falXANTHOTERASclavuloides (5) A, 1-2, WW:lobdistinctus 8eburneum A, t-2, SW:gam rug turlabotus 2venustus 1emoryi A, 1-1, ?fumosum S, r, SW: gam rug turmediocre A, r, SW:turobconicum = pulchellum (5)ornatum S, 1-5, EW:sinpolitum A, 1-1, EW:cha stedryorhizoxeni 1labotus 20

Table 3 continued

## CYNIPID GENUS

species: generation, gall-type, host oaks Ormyrus sp.  
# specimens

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<u>pulchellum</u> S,r,WW:dou gar	
<u>pulchripenne</u> A,1-1,SW:ari obl rug tou tur	<u>venustus</u> 20
<u>pumiliventre</u> S,r,SW:gam?	
<u>quercusforticorne</u> A,t-2,EW:alb	<u>labotus</u> 132
<u>radicola</u> S,r,EW:alb	
(= X. <u>quercusforticorne</u> ?)	
<u>teres</u> A,1-2,WW:dum gar	<u>distinctus</u> 3

## XYSTOTERAS

nigrum A,1-2,EW:alb  
poculum A,1-2,EW:alb  
volutellae A,1-2,EW:mac

## ZOPHEROTERAS

compressum A,1-2,ER:rub  
cuneatum A,1-2,EW:alb  
guttatum A,1-2,ER:pal  
hubbardi A,1-2,ER:coc vel  
sphaerula A,1-2,ER:rub  
vaccinii A,1-2,EW:ste

## UNDESCRIBED CYNIPIDS

a-1, <u>Chrysolepis</u>	<u>distinctus</u> 16
b,P	<u>distinctus</u> 3
1-3,P (Weld 1957, fig.99)	<u>distinctus</u> 3
1-7, <u>Chrysolepis</u> (Weld 1957, p.34)	<u>distinctus</u> 11
t-3,WW:dou,dum,gar (Weld 1957, "terminal club like clavula")	<u>distinctus</u> 18
t-5, <u>Chrysolepis</u> (= 1-7?)	<u>distinctus</u> 26

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Table 4. Nearctic Ormyrus records for various oak gall types. A = asexual generation, S = sexual generation.

GALL TYPE---# Cynipid species	
Cynipid species (generation)	<u>Ormyrus</u> sp. # specimens
ACORN GALLS, cells in cup---6	
<u>Callirhytis</u> <u>eldoradensis</u> (S)	<u>distinctus</u> 1 <u>venustus</u> 1
ACORN GALLS, large, attached to cup---6	
<u>Amphibolips</u> <u>gainesi</u> (A)	<u>labotus</u> 1
<u>Disholcaspis</u> <u>pedunculoides</u> (A)	<u>hegeli</u> 1 <u>venustus</u> 1
ACORN GALLS, "pip", attached to cup---12	
<u>Callirhytis</u> <u>quercusoperator</u> (A)	<u>acylus</u> 3
ACORN GALLS, stone gall in nut---10	
<u>Callirhytis</u> <u>flora</u> (S)	<u>acylus</u> 22
BUD GALLS---54	
<u>Acraspis</u> <u>gemula</u> (S)	<u>labotus</u> 4
<u>Amphibolips</u> <u>globulus</u> (A)	<u>dryorhizoxeni</u> 1
<u>Amphibolips</u> <u>tinctoriae</u> (A)	<u>labotus</u> 2
<u>Andricus</u> <u>cinnamomeus</u> (A)	<u>acylus</u> 5 <u>labotus</u> 1
<u>Andricus</u> <u>opertus</u> (A)	<u>distinctus</u> 2 <u>unifasciatipennis</u> 1 <u>venustus</u> 12
<u>Andricus</u> <u>quercusfoliatus</u> (A)	<u>dryorhizoxeni</u> 221 <u>labotus</u> 1
<u>Antron</u> <u>quercusechinus</u> (S)	<u>distinctus</u> 1
<u>Callirhytis</u> <u>gallaestriatae</u> (A)	<u>labotus</u> 1
<u>Dryocosmus</u> <u>kuriphilus</u> (A)	<u>labotus</u> 7
CATKIN GALLS, swelling of axis---6	
<u>Callirhytis</u> <u>congregata</u> (A)	<u>distinctus</u> 1 <u>venustus</u> 50
<u>Callirhytis</u> <u>quercusoperator</u> (S)	<u>labotus</u> 46
<u>Neuroterus</u> <u>exiguus</u> (S)	<u>labotus</u> 46
<u>Neuroterus</u> <u>floricomus</u> (S)	<u>venustus</u> 1
CATKIN GALLS, large, several-celled---2	
<u>Callirhytis</u> <u>pulchra</u> (S)	<u>labotus</u> 5
CATKIN GALLS, small, one-celled---11	NO RECORDS



Table 4 continued

GALL TYPE---# Cynipid species Cynipid species (generation)	<u>Ormyrus</u> sp. # specimens
LEAF GALLS, detachable, with radiating fibers---33	
<u>Amphibolips nubilipennis</u> (S)	<u>labotus</u> 1
<u>Amphibolips quercusspongifica</u> (A)	<u>labotus</u> 3
<u>Andricus quercusostensackenii</u> (S)	<u>labotus</u> 1
<u>Andricus quercussingularis</u> (S)	<u>labotus</u> 2
<u>Besbicus multipunctatus</u> (A)	<u>distinctus</u> 3
<u>Xanthoteras politum</u> (A)	<u>dryorhizoxeni</u> 1
	<u>labotus</u> 20
<u>Xanthoteras pulchripenne</u> (A)	<u>venustus</u> 20
LEAF GALLS, detachable, other---130	
<u>Acraspis alaria</u> (A)	<u>labotus</u> 7
<u>Acraspis erinacei</u> (A)	<u>labotus</u> 60
<u>Acraspis gemula</u> (A)	<u>labotus</u> 8
<u>Acraspis macrocarpae</u> (A)	<u>labotus</u> 39
<u>Acraspis pezomachoides</u> (A)	<u>labotus</u> 105
<u>Acraspis prinoides</u> (A)	<u>labotus</u> 13
<u>Acraspis quercushirta</u> (A)	<u>labotus</u> 71
<u>Acraspis villosa</u> (A)	<u>labotus</u> 5
<u>Andricus brunneus</u> (A)	<u>distinctus</u> 6
<u>Andricus crystallinus</u> (A)	<u>distinctus</u> 4
<u>Andricus fullawayi</u> (A)	<u>distinctus</u> 5
	<u>venustus</u> 18
<u>Andricus ignotus</u> (A)	<u>labotus</u> 749
<u>Andricus kingi</u> (A)	<u>distinctus</u> 37
<u>Andricus lasius</u> (A)	<u>distinctus</u> 3
<u>Andricus pattoni</u> (A)	<u>dryorhizoxeni</u> 50
	<u>labotus</u> 699
<u>Andricus quercusflocci</u> (A)	<u>labotus</u> 37
<u>Andricus quercuslanigera</u> (A)	<u>labotus</u> 219
<u>Andricus sulfureus</u> (A)	<u>venustus</u> 4
<u>Andricus tecturnarum</u> (A)	<u>labotus</u> 2
	<u>venustus</u> 15
<u>Antron douglasii</u> (A)	<u>distinctus</u> 21
<u>Antron quercusechinus</u> (A)	<u>distinctus</u> 20
	<u>venustus</u> 1
<u>Belonocnema kinseyi</u> (A)	<u>dryorhizoxeni</u> 2
	<u>labotus</u> 47
	<u>venustus</u> 7
<u>Callirhytis infuscata</u> (A)	<u>dryorhizoxeni</u> 5
	<u>labotus</u> 2
<u>Callirhytis lanata</u> (A)	<u>labotus</u> 37
<u>Callirhytis tubicola</u> (A)	<u>labotus</u> 32
<u>Disholcaspis sulcata</u> (A)	<u>venustus</u> 2

Table 4 contiued

GALL TYPE---# Cynipid species Cynipid species (generation)	<u>Ormyrus sp.</u> # specimens
<u>Dros amphora</u> (A)	<u>venustus</u> 10
<u>Neuroterus saltatorius</u> (A) 2	<u>unifasciatipennis</u>
<u>Paracraspis guadaloupensis</u> (A)	<u>distinctus</u> 1
<u>Philonix fulvicollis</u> (A)	<u>labotus</u> 69
<u>Philonix nigra</u> (A)	<u>labotus</u> 2
<u>Sphaeroterus trimaculosum</u> (A)	<u>distinctus</u> 3
<u>Xanthoterus clavuloides</u> (A)	<u>distinctus</u> 8
<u>Xanthoterus teres</u> (A)	<u>distinctus</u> 3
LEAF GALLS, prolongation of vein---6	
<u>Amphibolips quercuscoelebs</u> (S)	<u>labotus</u> 2
<u>Andricus opertus</u> (S)	<u>venustus</u> 3
<u>Callirhytis pedunculata</u> (S)	<u>labotus</u> 2
LEAF GALLS, pustules, spring---17	
<u>Andricus atrimentus</u> (S)	<u>venustus</u> 1
<u>Andricus pilula</u> (S)	<u>venustus</u> 1
LEAF GALLS, midrib or petiole swelling---18	
<u>Andricus quercuspetiolicola</u> (S)	<u>labotus</u> 63 <u>venustus</u> 3
<u>Callirhytis flavipes</u> (S)	<u>labotus</u> 2
<u>Callirhytis flora</u> (A)	<u>distinctus</u> 1 <u>venustus</u> 17
<u>Callirhytis tumifica</u> (S)	<u>acylus</u> 1 <u>labotus</u> 22
<u>Callirhytis vaccinii</u> (A)	<u>labotus</u> 15
LEAF GALLS, parenchyma swelling---17	
<u>Callirhytis favosa</u> (S)	<u>labotus</u> 6
<u>Callirhytis quercusfutilis</u> (S)	<u>labotus</u> 11
<u>Callirhytis quercusmodesta</u> (A)	<u>labotus</u> 12
<u>Neuroterus quercusirregularis</u> (S)	<u>labotus</u> 6
<u>Neuroterus sadlerensis</u> (S)	<u>distinctus</u> 62
<u>Neuroterus washingtonensis</u> (S)	<u>venustus</u> 24
LEAF GALLS, integral, free-rolling cell---6	
<u>Dryocosmus quercusnotha</u> (S)	<u>labotus</u> 2
<u>Dryocosmus quercuspalustris</u> (S)	<u>labotus</u> 30
LEAF GALLS, integral, wooly, fall---4	
<u>Neuroterus floccosus</u> (A)	<u>labotus</u> 4
<u>Neuroterus quercusverrucarum</u> (A)	<u>labotus</u> 17

Table 4 contiued

GALL TYPE---# Cynipid species Cynipid species (generation)	<u>Ormyrus</u> sp. # specimens
ROOT GALLS---38	
<u>Belonocnema</u> <u>treatae</u> (S)	<u>dryorhizoxeni</u> 22
<u>Disholcaspis</u> <u>acetabula</u> (A)	<u>dryorhizoxeni</u> 3
<u>Disholcaspis</u> <u>terrestris</u> (A)	<u>dryorhizoxeni</u> 3
<u>Dryocosmus</u> <u>favus</u> (A)	<u>crassus</u> 19
	<u>dryorhizoxeni</u> 1
<u>Holocynips</u> <u>hartmani</u> (A)	<u>dryorhizoxeni</u> 1
<u>Loxaulus</u> <u>humilis</u> (A)	<u>labotus</u> 1
TWIG GALLS, detachable, radiating fibers---3	
<u>Amphibolips</u> <u>quercuscinerea</u> (A)	<u>hegeli</u> 1
TWIG GALLS, detachable, other---74	
<u>Andricus</u> <u>coronus</u> (A)	<u>labotus</u> 1
<u>Callirhytis</u> <u>quercusgemmaria</u> (A)	<u>labotus</u> 3
<u>Callirhytis</u> <u>quercuspomiformis</u> (A)	<u>distinctus</u> 3
	<u>setosus</u> 32
<u>Callirhytis</u> <u>seminator</u> (A)	<u>labotus</u> 11
<u>Disholcaspis</u> <u>cinerosa</u> (A)	<u>labotus</u> 1
<u>Disholcaspis</u> <u>colorado</u> (A)	<u>dryorhizoxeni</u> 19
<u>Disholcaspis</u> <u>corallina</u> (A)	<u>distinctus</u> 1
<u>Disholcaspis</u> <u>eldoradensis</u> (A)	<u>reticulatus</u> 2
<u>Disholcaspis</u> <u>mamillana</u> (A)	<u>hegeli</u> 1
<u>Disholcaspis</u> <u>mellifica</u> (A)	<u>distinctus</u> 7
<u>Disholcaspis</u> <u>perniciosa</u> (A)	<u>reticulatus</u> 1
<u>Disholcaspis</u> <u>plumbella</u> (A)	<u>distinctus</u> 13
<u>Disholcaspis</u> <u>prehensa</u> (A)	<u>reticulatus</u> 1
<u>Disholcaspis</u> <u>quercusmamma</u> (A)	<u>hegeli</u> 1
	<u>reticulatus</u> 2
<u>Disholcaspis</u> <u>quercusvirens</u> (A)	<u>dryorhizoxeni</u> 1
<u>Disholcaspis</u> <u>rubens</u> (A)	<u>venustus</u> 4
<u>Disholcaspis</u> <u>simulata</u> (A)	<u>distinctus</u> 2
	<u>reticulatus</u> 1
<u>Disholcaspis</u> <u>spongiosa</u> (A)	<u>dryorhizoxeni</u> 38
	<u>labotus</u> 6
<u>Disholcaspis</u> <u>washingtonensis</u> (A)	<u>distinctus</u> 9
<u>Dryocosmus</u> <u>imbricariae</u> (A)	<u>dryorhizoxeni</u> 1
<u>Heteroecus</u> <u>melanoderma</u> (A)	<u>distinctus</u> 1
<u>Heteroecus</u> <u>pacificus</u> (A)	<u>distinctus</u> 9
<u>Heteroecus</u> <u>sanctaeclarae</u> (A)	<u>distinctus</u> 3
<u>Xanthoteras</u> <u>eburneum</u> (A)	<u>labotus</u> 2
	<u>venustus</u> 1
<u>Xanthoteras</u> <u>quercusforticorne</u> (A)	<u>labotus</u> 132

Table 4 contiued

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GALL TYPE---# Cynipid species Cynipid species (generation)	<u>Ormyrus sp.</u> # specimens
<hr/>	
TWIG GALLS, swelling, new growth---8	
<u>Andricus wiltzae</u> (A)	<u>unifasciatipennis</u>
1	
<u>Callirhytis quercusscitula</u> (S)	<u>venustus</u> 3
<u>Neuroterus varians</u> (A)	<u>labotus</u> 12
	<u>venustus</u> 7
<hr/>	
TWIG GALLS, woody swelling, older growth---27	
<u>Andricus chrysolepidicola</u> (A)	<u>distinctus</u> 4
	<u>reticulatus</u> 1
	<u>venustus</u> 3
<u>Andricus ruginosus</u> (A)	<u>hegeli</u> 9
<u>Andricus wheeleri</u> (A)	<u>hegeli</u> 10
	<u>venustus</u> 1
<u>Callirhytis clavula</u> (A)	<u>labotus</u> 3
<u>Callirhytis cornigera</u> (A)	<u>labotus</u> 48
<u>Callirhytis frequens</u> (A)	<u>reticulatus</u> 7
<u>Callirhytis perdens</u> (A)	<u>distinctus</u> 6
<u>Callirhytis quercusbatatoides</u> (A)	<u>reticulata</u> 10
<u>Callirhytis quercusmedullae</u> (A)	<u>labotus</u> 1
<u>Callirhytis quercuspunctata</u> (A)	<u>labotus</u> 10
<u>Callirhytis quercussimilis</u> (S)	<u>labotus</u> 3
<u>Dryocosmus asymmetricus</u> (A)	<u>distinctus</u> 1
<u>Dryocosmus coxii</u> (A)	<u>venustus</u> 4
<u>Loxaulus quercusmammula</u> (S)	<u>labotus</u> 1
<u>Neuroterus quercusbatatus</u> (A)	<u>dryorhizoxeni</u> 2
	<u>labotus</u> 15
<hr/>	
TWIG GALLS, cells, little swelling---28	
<u>Bassetia ligni</u> (A)	<u>turio</u> 12
<u>Callirhytis elongata</u> (A)	<u>labotus</u> 3
<u>Neuroterus sadlerensis</u> (A)	<u>distinctus</u> 3
<u>Neuroterus washingtonensis</u> (A)	<u>venustus</u> 3
<u>Plagiotrochus suberi</u> (A)	<u>venustus</u> 9

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Table 5. Nearctic species of Ormyrus: Hosts. The generation (see text) is given for oak cynipids, A = asexual, S = sexual.

<u>Ormyrus</u> species	Host (generation) # <u>Ormyrus</u> specimens
<u>acylus</u>	<u>Andricus cinnamomeus</u> (A) 5 <u>Callirhytis flora</u> (S) 22 <u>C. quercusoperator</u> (A) 3 <u>C. tumifica</u> (S) 1
<u>crassus</u>	<u>Dryocosmus favus</u> (A) 19
<u>distinctus</u>	<u>Andricus brunneus</u> (A) 6 <u>A. chrysolepidicola</u> (A) 4 <u>A. crystallinus</u> (A) 4 <u>A. fullawayi</u> (A) 5 <u>A. kingi</u> (A) 37 <u>A. lasius</u> (A) 3 <u>A. opertus</u> (A) 2 <u>Antron douglasii</u> (A) 21 <u>A. quercusechinus</u> (A,S) 20,1 <u>Besbicus multipunctatus</u> (A) 3 <u>Callirhytis congregata</u> (A) 1 <u>C. eldoradensis</u> (S) 1 <u>C. flora</u> (A) 1 <u>C. perdens</u> (A) 6 <u>C. quercuspomiformis</u> (A) 3 <u>Disholcaspis corallina</u> (A) 1 <u>D. mellifica</u> (A) 7 <u>D. plumbella</u> (A) 13 <u>D. simulata</u> (A) 2 <u>D. washingtonensis</u> (A) 9 <u>Dryocosmus asymmetricus</u> (A) 1 <u>Heteroecus melanoderma</u> (A) 1 <u>H. pacificus</u> (A) 9 <u>H. sanctaeclarae</u> (A) 3 <u>Neuroterus sadlerensis</u> (A,S) 3,62 <u>Paracraspis guadaloupensis</u> (A) 1 <u>Sphaeroterus trimaculosum</u> (A) 3 <u>Xanthoterus clavuloides</u> (A) 8 <u>X. teres</u> (A) 3
<u>dryorhizoxeni</u>	<u>Amphibolips globulus</u> (A) 1 <u>Andricus pattoni</u> (A) 50 <u>A. quercusfoliatus</u> (A) 221 <u>Belonocnema kinseyi</u> (A) 2 <u>Belonocnema treatae</u> (S) 22 <u>Callirhytis infuscata</u> (A) 5

Table 5 continued

<u>Ormyrus species</u>	Host (generation) # <u>Ormyrus specimens</u>
	<u>Disholcaspis acetabula</u> (A) 3
	<u>D. colorado</u> (A) 19
	<u>D. quercusvirens</u> (A) 1
	<u>D. spongiosa</u> (A) 38
	<u>D. terrestris</u> (A) 3
	<u>Dryocosmus favus</u> (A) 1
	<u>D. imbricariae</u> (A) 1
	<u>Holocynips hartmani</u> (A) 1
	<u>Neuroterus quercusbatatus</u> (A) 2
	<u>Xanthoteras politum</u> (A) 1
<u>hegeli</u>	<u>Amphibolips quercuscinerea</u> (A) 1
	<u>Andricus ruginosus</u> (A) 9
	<u>A. wheeleri</u> (A) 10
	<u>Disholcaspis mamillana</u> (A) 1
	<u>D. pedunculoides</u> (A) 1
	<u>D. quercusmamma</u> (A) 1
<u>labotus</u>	<u>Acraspis alaria</u> (A) 7
	<u>A. erinacei</u> (A) 60
	<u>A. gemula</u> (A,S) 8,4
	<u>A. macrocarpae</u> (A) 39
	<u>A. pezomachoides</u> (A) 105
	<u>A. prinoides</u> (A) 13
	<u>A. quercushirta</u> (A) 71
	<u>A. villosa</u> (A) 5
	<u>Amphibolips gainesi</u> (A) 1
	<u>A. nubilipennis</u> (S) 1
	<u>A. quercuscoelebs</u> (S) 2
	<u>A. quercusspongifica</u> (A) 3
	<u>A. tinctoriae</u> (A) 2
	<u>Andricus cinnamomeus</u> (A) 1
	<u>A. coronus</u> (A) 1
	<u>A. ignotus</u> (A) 749
	<u>A. pattoni</u> (A) 699
	<u>A. quercusflocci</u> (A) 37
	<u>A. quercusfoliatus</u> (A) 1
	<u>A. quercuslanigera</u> (A) 219
	<u>A. quercusostensackenii</u> (S) 1
	<u>A. quercuspetiolicola</u> (S) 63
	<u>A. quercussingularis</u> (S) 2
	<u>A. tecturnarum</u> (A) 2
	<u>Belonocnema kinseyi</u> (A) 47
	<u>Callirhytis clavula</u> (A) 3
	<u>C. cornigera</u> (A) 48
	<u>C. elongata</u> (A) 3

Table 5 continued

<u>Ormyrus</u> species	Host (generation) # <u>Ormyrus</u> specimens
<u>C. favosa</u> (S)	6
<u>C. flavipes</u> (S)	2
<u>C. gallaestriatae</u> (A)	1
<u>C. infuscata</u> (A)	2
<u>C. lanata</u> (A)	37
<u>C. pedunculata</u> (S)	2
<u>C. pulchra</u> (S)	5
<u>C. quercusfutilis</u> (S)	11
<u>C. quercusgemmaria</u> (A)	3
<u>C. quercusmedullae</u> (A)	1
<u>C. quercusmodesta</u> (A)	12
<u>C. quercusoperator</u> (S)	46
<u>C. quercuspunctata</u> (A)	10
<u>C. quercusscitula</u> (S)	12
<u>C. quercussimilis</u> (S)	3
<u>C. seminator</u> (A)	11
<u>C. tubicola</u> (A)	32
<u>C. tumifica</u> (S)	22
<u>C. vaccinii</u> (A)	15
<u>Disholcaspis cinerosa</u> (A)	1
<u>D. spongiosa</u> (A)	6
<u>Dryocosmus kuriphilus</u> (A)	7
<u>D. quercusnotha</u> (S)	2
<u>D. quercuspalustris</u> (S)	30
<u>Loxaulus humilis</u> (A)	1
<u>L. quercusmammula</u> (S)	1
<u>Neroterus exiguus</u> (S)	46
<u>N. floccosus</u> (A)	4
<u>N. quercusbatatus</u> (A)	15
<u>N. quercusirregularis</u> (S)	6
<u>N. quercusverrucarum</u> (A)	17
<u>Philonix fulvicollis</u> (A)	69
<u>P. nigra</u> (A)	2
<u>Xanthoteras eburneum</u> (A)	2
<u>X. politum</u> (A)	20
<u>X. quercusforticorne</u> (A)	132
<u>reticulatus</u>	
<u>Andricus chrysolepidicola</u> (A)	1
<u>Callirhytis frequens</u> (A)	7
<u>C. quercusbatatoides</u> (A)	10
<u>Disholcaspis eldoradensis</u> (A)	2
<u>D. perniciosa</u> (A)	1
<u>D. prehensa</u> (A)	1
<u>D. quercusmamma</u> (A)	2
<u>D. simulata</u> (A)	1

Table 5 continued

<u>Ormyrus species</u>	Host (generation) # <u>Ormyrus specimens</u>
<u>rosae</u>	<u>Diastrophus cuscutaeformis</u> 57 <u>D. fusiformans</u> 24 <u>D. kincaidii</u> 87 <u>D. nebulosus</u> 267 <u>Diplolepis bicolor</u> 14 <u>D. dichlocera</u> 14 <u>D. fusiformans</u> 10 <u>D. ignota</u> 5 <u>D. inconspicuis</u> 18 <u>D. lens</u> 49 <u>D. nebulosa</u> 36 <u>D. nodulosa</u> 2 <u>D. polita</u> 16 <u>D. radicum</u> 14 <u>D. spinosa</u> 8 <u>D. triforma</u> 26 <u>D. variabilis</u> 4 <u>Hemadas nubilipennis</u> 121 (Pteromalidae)
<u>setosus</u>	<u>Callirhytis quercuspomiformis</u> (A) 32
<u>turio</u>	<u>Bassetia ligni</u> (A) 12
<u>unifasciatipennis</u>	<u>Andricus opertus</u> (A) 1 <u>A. wiltzae</u> (A) 1 <u>N. saltatorius</u> (A) 2
<u>vacciniicola</u>	<u>Diastrophus fragariae</u> 19 <u>Hemadas nubilipennis</u> 51 (Pteromalidae)
<u>venustus</u>	<u>Andricus atrimentus</u> (S) 1 <u>A. chrysolepidicola</u> (A) 3 <u>A. fullawayi</u> (A) 18 <u>A. opertus</u> (A,S) 12,3 <u>A. pilula</u> (S) 1 <u>A. quercuspetiolicola</u> (S) 3 <u>A. sulfureus</u> (A) 4 <u>A. tecturnarum</u> (A) 15 <u>A. wheeleri</u> (A) 1 <u>A. wiltzae</u> (A) 3 <u>Antron quercusechinus</u> (A) 1 <u>Belonocnema kinseyi</u> (A) 7



Table 5 continued

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<u>Ormyrus</u> species	Host (generation) # <u>Ormyrus</u> specimens
<u>Callirhytis congregata</u>	(A) 50
<u>C. eldoradensis</u>	(S) 1
<u>C. flora</u>	(A) 17
<u>Disholcaspis rubens</u>	(A) 4
<u>D. sulcata</u>	(A) 2
<u>Dros amphora</u>	(A) 1
<u>Dryocosmus coxii</u>	(A) 4
<u>Neuroterus floricomus</u>	(S) 1
<u>N. varians</u>	(A) 7
<u>N. washingtonensis</u>	(A,S) 3,24
<u>Plagiotrochus suberi</u>	(A) 9
<u>Xanthoteras eburneum</u>	(A) 1
<u>X. pulchripenne</u>	(A) 20

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CHAPTER 6. BIOGEOGRAPHY OF ORMYRUS, CYNIPID,  
AND OAK SPECIES

Eleven of the 16 Nearctic species of Ormyrus recognized here appear to be exclusively associated with cynipid galls on oaks. Two additional species, O. tenuis and O. unimaculatipennis, also may prove to be exclusive associates of cynipid oak galls, although no reared specimens currently exist. Of these 13 species potentially restricted to oak galls, seven are distributed across North America, at least in the southern states (figs. 40-55). The two most polyphagous species, O. labotus (64 cynipid species) and O. distinctus (29 cynipid species), are not distributed across the continent. Ormyrus labotus, like O. tenuis (host unknown but probably monophagous, see chapter 4), occurs only east of the Cascade and Sierra Nevada Mountains. Ormyrus distinctus, like the monophagous O. setosus and O. turio, occurs only west of the Cascade and Sierra Nevada Mountains. Ormyrus crassus is restricted to the eastern states where the only known host is a root gall. Thus, monophagous species tend to show more restricted distributions, but the converse does not appear to be true for polyphagous species. Instead, widespread species tend to be oligophagous.

Although host specificity with respect to gall structure (and secondarily to cynipid taxa, see chapter 5) has undoubtedly affected distributional patterns in Ormyrus species, some of the patterns may be the result of past geologic-climatic events. Such events would also affect distributional patterns of host cynipid and oak species. For this reason, I shall compare geographic ranges of species at all three trophic levels in an attempt to discover underlying processes.

General hypotheses will be proposed to explain two

particular sets of observations. First, distributional patterns of Ormyrus, cynipid, and oak species all suggest the recognition of three regions within the Nearctic: east, southwest, and west. Nearly all cynipid and oak species are restricted to one of these three regions but only four out of thirteen Ormyrus species are similarly restricted. Second, specimens of O. distinctus from sadler oak and chinkapin are morphologically distinguishable from the rest of the species (chapter 4); this represents the only example of Ormyrus specificity with respect to oak taxa (other Ormyrus show specificity with respect to gall structure). Sadler oak and chinkapin are also interesting because they have fewer cynipid species than most other oaks.

A. HISTORICAL BIOGEOGRAPHY OF THE EASTERN,  
SOUTHWESTERN, AND WESTERN NEARCTIC REGIONS.

Weld (1957, 1959, 1960) divided his cynipid guides into three volumes--Pacific slope, east, and southwest--since most species occur in just one region. Most oak species are also restricted to just one of these regions. The three regions, which are best illustrated by the geographic ranges of the northern most oak species within each region (fig. 56), are bounded by four barriers: the Bering Sea, the Cascade-Sierra Nevada-Peninsular Ranges and its rain shadow, the Great Plains, and the Atlantic Ocean. The oldest barrier is probably the Great Plains area, which was covered by an epicontinental sea in the Cretaceous and became the rain shadow of the rising Rocky Mountains in the early Tertiary. The north Atlantic connection between eastern North America and Europe was severed in the late Eocene (Tiffney 1985). The Beringian connection between western North America and eastern Asia has existed intermittently throughout much of the Cenozoic. The Cascade and Sierra Nevada Mountains represent the most recent barrier (Pliocene).

Although no cynipid or oak species occurs in all three regions, about half of the Ormyrus species do. One explanation for this difference between Ormyrus and cynipid species relates to host specificity. All cynipid species and several genera are restricted to either red, white, or canyon live oak groups (sections Rubrae, Quercus, and Protobalanus, respectively; see Nixon 1984). Species of Ormyrus show no specificity with respect to oak taxa (with one apparent exception that is discussed in the next section). Thus, past climatic fluctuations bringing a red oak species in contact with a white oak

species allows for exchange of Ormyrus species, but not cynipid species.

Certain species of Ormyrus are restricted to just one or two of the three regions. In these cases distributional patterns may be explainable by historical events (geologic-climatic) that have similarly affected distributional patterns of cynipids and oaks (table 6). Such events may have caused splits (vicariance) in Ormyrus lineages. Because phylogenetic analyses have not yet been performed, the only presently known lineage splits are within the species O. acylus and O. venustus (see chapter 4). Although it is tempting to posit a sister group relationship between O. turio and O. tenuis, the similarities (shape of the head and mesosoma) are probably due to convergence (see chapter 4).

Only a few cynipid genera have been sufficiently studied to allow some degree of certainty about monophyletic groups. Kinsey's (1930, 1936) detailed systematic studies of the cynipid genus Cynips (his six subgenera are now considered genera) included phylogenetic maps showing species relationships with respect to geographic distribution. Kinsey (1930) depicted the entire group as originating in Mexico and suggested that the western Nearctic Antron and Besbicus are more closely related to the Palearctic Cynips than they are to the southwestern and eastern Nearctic Acraspis, Atrusca, and Philonix. Further phylogenetic analyses are needed to verify the relationships suggested by Kinsey. If true, such higher level differences between southwestern and western cynipids would seem to suggest a separation predating the rise of the Cascade-Sierra Nevada barrier in the Pliocene, or else rapid speciation since then.

Disholcaspis species are generally thought to be closely related to the Cynips group of genera. Burnett (1977) proposed a new genus name, Weldia (name preoccupied, Dailey pers. comm.), for certain Disholcaspis

species that appear to constitute a monophyletic group, distinct from other species in the genus. Within this group of species, Burnett (1977) presented evidence for a sister group relationship between D. sulcata (Ashmead) on southwestern oaks and the rest of the species on western oaks. Interestingly, plesiomorphic species such as D. sulcata tend to be polyphagous whereas apomorphic species, such as D. conalis Weld and D. corallina (Bassett), tend to be monophagous (Burnett, 1977); this may indicate that within a particular region, cynipid species acquire more host oak species over time.

Current studies in oak systematics (e.g. Nixon 1984) will likely reveal several oak lineages that have split as a result of the same historical events. Quercus garryana Dougl. ex Hook. and Q. gambelii Nutt. for example, appear to be sister species (Nixon pers. comm.), and may have separated in the Pliocene with the rise of the Cascade-Sierra Nevada rain shadow (Tucker & Muller 1958). According to the fossil record, the ancestor of Gambel oak (and presumably Garry oak) was present in the central Rocky Mountains as early as the Oligocene and spread to the western Great Basin in the Miocene (Axelrod & Raven 1985). Another example of possible vicariance is Q. sadleriana R. Br. Campst. and its probable sister species, Q. serrata Thunb. in Japan (Muth 1976), which may have separated in the Miocene with the onset of colder climates in Beringia.

A few cynipid species do occur in more than one region (never in all three) and these may represent recent contacts between host oaks. For example, Acraspis quercushirta (Bassett) is recorded from both Gambel oak (southwest) and bur oak (east, see fig. 56), which may be the result of recent contacts between these two oak species. During a warmer climatic regime 4000-8000 years ago, Gambel oak moved northward and hybridized with bur oak in the Black Hills of South Dakota and Wyoming (Maze

1968). The occurrence of Neuroterus niger Gillette on both southwestern and eastern oaks could be the result of recent contacts farther south. Present day ranges of some eastern oaks in east Texas overlap the ranges of southwestern oaks in west Texas. Kinsey (1930), however, believed that contacts between east and west Texas oaks have been minimal, based on evidence from cynipid distributions.

At least two cynipid species on white oaks, Andricus reticulatus Bassett and Neuroterus saltatorius (Edwards), occur in both the west and southwest (see Lyon 1984), and these may also represent recent contacts between host oaks. Canyon live oak (Q. chrysolepis Liebm.) is one of the few oak species to occur in both the west and the southwest; thus it is not surprising that cynipids restricted to this section of Quercus (about five species) show more trans-regional distributions (see Weld 1957, 1960) than any other group of cynipids.

Although east-west movements of Ormyrus, cynipid, and oak species have been limited by various barriers, the climatic fluctuations accompanying Pleistocene glaciations probably have resulted in considerable north-south movements. For example, during the warmer climatic regime 40000-80000 years ago, Q. turbinella Greene moved northward, leaving hybrids with Gambel oak that remain today as relicts, far north of the present day distribution of Q. turbinella (Cottam et al. 1959, Neilson & Wullstein 1983). These north-south movements, in the absence of appreciable east-west movement, may explain the extensive overlap in Ormyrus and cynipid species between Garry oak and California white oaks, and between Gambel oak and southwestern white oaks. Gambel oak and Garry oak have no cynipid species in common despite the fact that they are sister species.

North-south movements of oaks have not resulted in complete homogeneity between northern and southern parts

of each region. In the western region, Ormyrus acylus, O. dryorhizoxeni, O. hegeli, and O. setosus appear to be absent in the north (in the Willamette Valley of Oregon). Only in the case of O. setosus can host specificity be invoked as an explanation for absence in the north. In the eastern region, host specificity may account for absence of O. crassus in the north, but this requires more study.

In cynipids also, more species appear to be present in the southern part of each region, despite the presence of potential hosts farther north. Some cynipid species reported from Garry oak in California are apparently absent from the same host in Oregon (pers. observ.). Andricus stellaris Weld, Spharoterax trimaculosum (McCracken & Egbert), and Trichoterax tubifaciens (Weld) occur on Garry oak in California and east of the Columbia Gorge, but I have not yet collected these species from the Willamette Valley; this would be a very interesting distributional pattern and should be investigated further. Absence of a cynipid species from part of its potential range does not always involve northern areas. Disholcaspis corallina for example occurs around the margins of the Central Valley of California but is absent from the southwest valley margin, despite the presence of host oaks (Burnett 1977). Patterns of absence of cynipid and Ormyrus species from areas containing potential hosts may be just as illuminating as patterns of presence. Unfortunately, much more intensive collecting is required to document absence than is required to document presence.



## B. ECOLOGICAL BIOGEOGRAPHY OF SADLER OAK AND CHINKAPIN

The only apparent case of Ormyrus specificity with respect to oak taxa is the morphologically deviant form of O. distinctus (see chapter 4) reared from cynipid galls on sadler oak (Q. sadleriana) and chinkapin (Chrysolepis spp.); the exact status of these specimens requires further study. Regardless of their status, the exclusive presence of a unique form of O. distinctus on these two host plants requires explanation.

Biogeographic study of sadler oak and chinkapin, and their cynipid and chalcidoid associates, is especially fertile since it poses questions for both ecological and historical biogeography. Sadler oak and chinkapin have fewer associated cynipid species than do most other oaks, perhaps explainable by small geographic range and taxonomic isolation, respectively. Neither of these explanations is applicable to Ormyrus. Instead, I shall argue that the exclusive presence of a unique form of O. distinctus is due to ecological isolation of sadler oak and chinkapin over long periods of time. The following discussion considers first sadler oak, and then chinkapin.

The predominant theory in contemporary ecological biogeography is based on mathematical models of colonization and extinction rates on islands (for references, see Cornell & Washburn 1979, Cornell 1985, Cornell 1986). Host plants may be regarded as islands for phytophagous insects. The specificity of cynipids with respect to oak taxa is especially amenable to ecological studies addressing the correlation between species richness of parasites (cynipids) and geographic area occupied by the host (oaks). Theoretically, oak species with larger ranges should have more cynipid species. Indeed, in the western Nearctic, geographic range and host taxonomic isolation appear to explain most of the regional

richness variation in oak cynipids (Cornell & Washburn 1979, Cornell 1985).

Quercus durata Jeps. and Q. sadleriana have very small geographic ranges of comparable size, yet the former has fifteen described cynipid species whereas the latter has only two (Cornell & Washburn 1979). I have found only one species on Q. sadleriana whereas Q. durata appears to actually have over twenty species (pers. obs.; Cornell 1985). This disparity in numbers of associated cynipid species between these two oaks has not been addressed.

Quercus sadleriana is a relictual endemic of the western Klamath Ranges (includes the Siskiyou Mnts.) of southwestern Oregon and northwestern California, where it occurs primarily at elevations above 1200 meters (Muth 1976). At this elevation it is spatially and ecologically isolated from most other Fagaceae (except chinkapin); only occasionally does Q. garryana grow in the same vicinity. Quercus turbinella, on the other hand, is restricted to serpentine soils in California (Forde & Faris 1962) and because these soils frequently interdigitate with non-serpentine soils, this species is often spatially close to other white oaks, such as Q. douglasii Hook. & Arn. and Q. dumosa Nutt. (pers. obser., Cornell 1985). There would thus appear to be greater opportunity for Q. durata to receive cynipid species from other white oaks.

Another possible explanation for different numbers of cynipid species on Q. durata and Q. sadleriana, is that the latter is more taxonomically isolated. Sadler oak belongs to the chestnut white oak group, the other species of this group occurring in eastern Asia and eastern North America (Muth 1976). Quercus durata on the other hand may be the sister species of Q. dumosa (Nixon, pers. comm.), which often occurs in the same vicinity as Q. durata.

Yet, the degree of taxonomic isolation of sadler oak from Garry oak may not be sufficient to exclude exchange

of cynipid species. Both oaks are in the white oak group and several other unrelated white oaks have cynipid species in common. Weld (1926) noted the similarity of Neuroterus sadlerensis Weld on sadler oak to N. washingtonensis Beutenmueller on Garry oak. My observations have provided additional evidence of close phyletic relationship between these two cynipid species. I have discovered the previously unknown asexual generation of N. sadlerensis and it is very similar to that of N. washingtonensis. Further study of the genus Neuroterus is needed to determine whether these two species are sister species, or even conspecific.

I have reared Ormyrus from both generations of both species of Neuroterus, although not in large numbers. Only O. distinctus was present in N. sadlerensis galls whereas N. washingtonensis galls contained only O. venustus. On the basis of gall-type (see chapter 5), the sexual generation galls (leaf swelling) would be expected to harbor O. venustus. Yet sexual generation galls of N. sadlerensis have thus far yielded only deviant forms of O. distinctus, like those from chinkapin galls.

The paucity of cynipid species on sadler oak and the presence of a deviant form of O. distinctus may be a result of long-term ecological isolation of the host oak. Sadler oak, like weeping spruce (Picea breweriana S. Wats.), which was a component of the Arcto-Tertiary Geoflora but is now restricted to higher elevations in the western Klamath Ranges. The climate of this area is thought to be more nearly like that of the Miocene and Pliocene than any other part of the region (Raven & Axelrod 1978). Thus sadler oak appears to have been a member of a mixed conifer forest (Arcto-Tertiary Geoflora) that has been isolated by elevation and latitude from other oaks (which are mostly members of the Madro-Tertiary Geoflora). An interesting question remains: did sadler

oak have more cynipid species in the past when it had a wider distribution, has it lost cynipids?

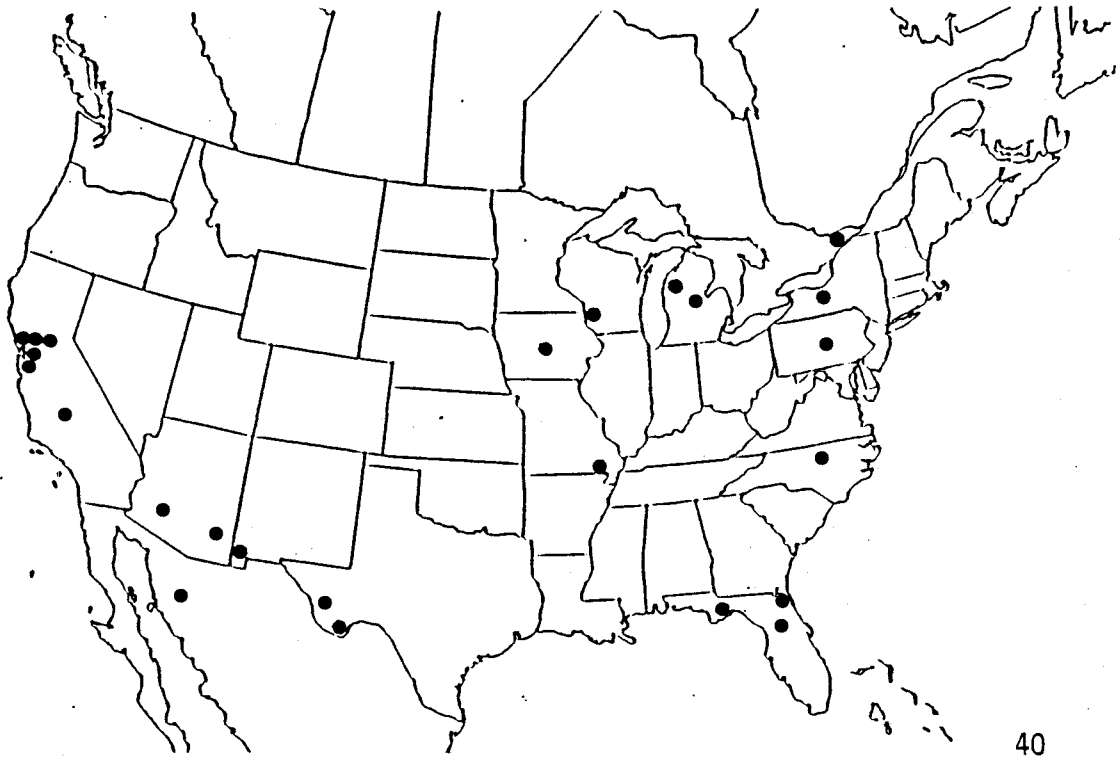
Chinkapin is not restricted to the Klamath Ranges although its distribution centers around this area. Chinkapin, like sadler oak, was a component of the Arcto-Tertiary Geoflora and today generally occurs at elevations above most oaks. The paucity of cynipid species associated with non-Quercus Fagaceae, chinkapin (Chrysolepis) and tanoak (Lithocarpus), has been explained by taxonomic isolation (Cornell & Washburn 1979, Cornell 1985). On chinkapin I have found three undescribed generations representing at least one new species, and Dailey (pers. comm.) has found additional species on tanoak. Despite these recent discoveries, the numbers of cynipids associated with non-Quercus Fagaceae are probably much less than the numbers associated with Quercus species occupying comparable areas. Cynipids associated with chinkapin and tanoak are members of the plesiomorphic genus Dryocosmus and therefore it seems likely that taxonomic isolation may indeed explain the paucity of cynipids on these plants.

The presence of a unique form of O. distinctus on both sadler oak and chinkapin indicates a causal factor common to both host plants, which would seem to exclude geographic range and taxonomic isolation. Both sadler oak and chinkapin have probably been ecologically isolated from other oaks for a long period of time and this may account for the unique Ormyrus association. A prediction emerging from this hypothesis is that similar Ormyrus specimens will be found in galls of tanoak, and perhaps in those of Q. vaccinifolia Kellogg (in the canyon live oak section) growing at higher elevations.

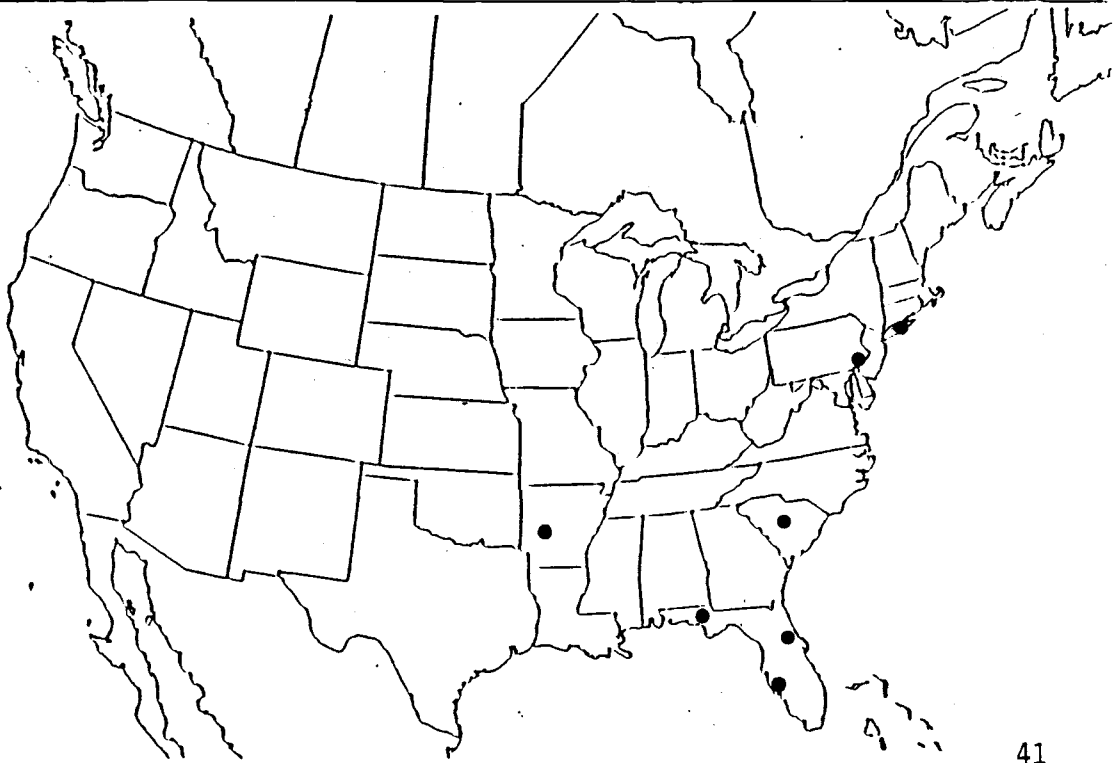
The composition of communities changes over time and the Arcto-Tertiary Geoflora is certainly no exception. Some plant species that grew together in the Miocene and Pliocene do not occur together today and many have become

extinct in the area (often surviving in eastern North America and eastern Asia). Yet many plant species of the Arcto-Tertiary Geoflora probably have occurred together, separated from other communities, for long periods of time. This is suggested not only by the cynipid and Ormyrus associates of sadler oak and chinkapin, but also by congruent vicariance patterns. Sadler oak, chinkapin, tanoak, weeping spruce, vine maple, and several other members of the Arcto-Tertiary Geoflora have their nearest relatives in Asia, indicating that each of these lineages was split by disappearance of the Beringian connection.

Although this discussion has been both cursory and speculative, due largely to lack of phylogenetic studies, it is hoped that the included topics will stimulate further investigation. Historical events invoked here to explain distributional patterns in Ormyrus, cynipid, and oak species should be tested against distributional patterns of other organisms. Comparative ecological and historical studies of oaks, cynipids, and their chalcidoid parasites, done at the world level, show much promise for contributing to understanding of biogeographic processes in general.



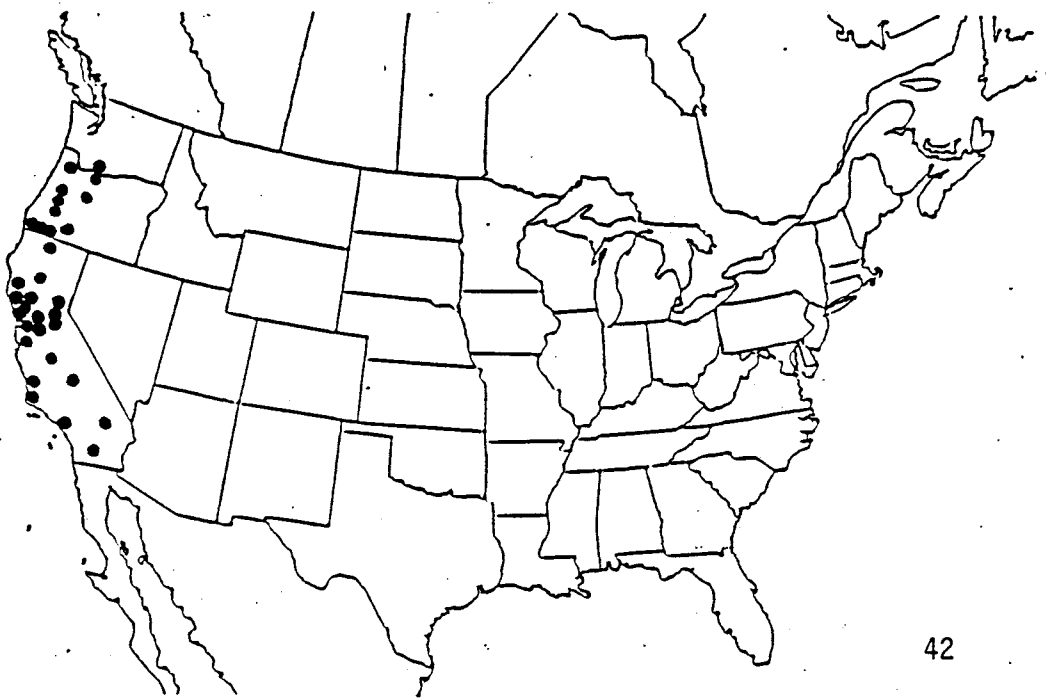
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Figure 40. Distribution of *O. acylus*

Figure 41. Distribution of *O. crassus*



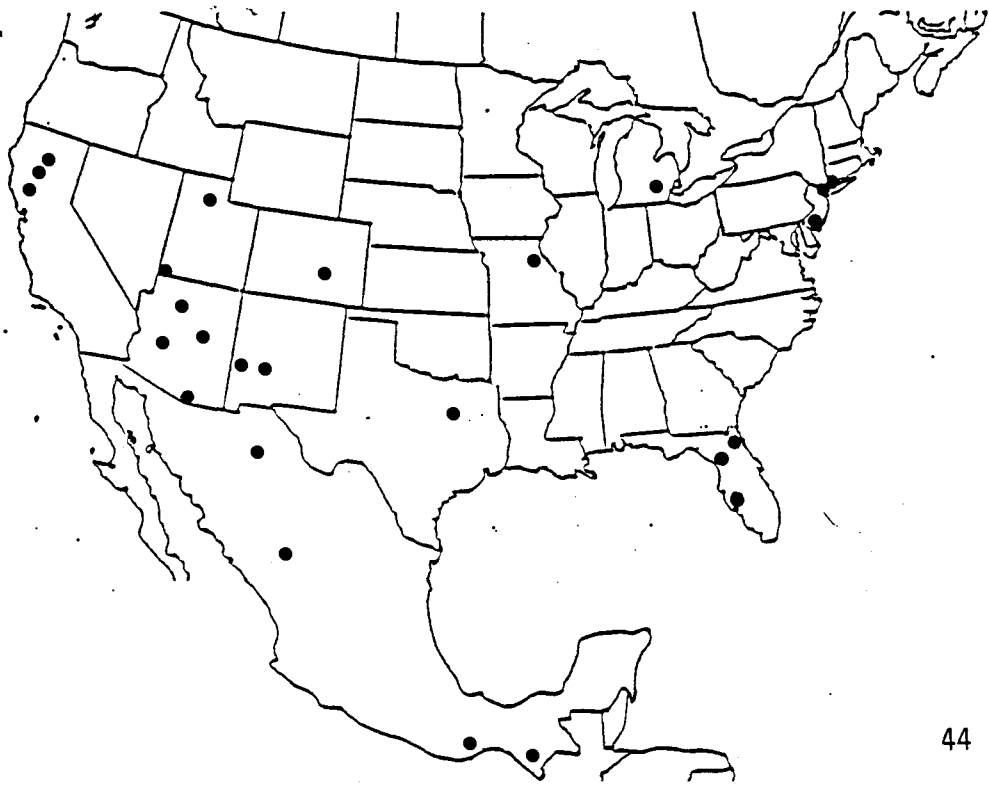
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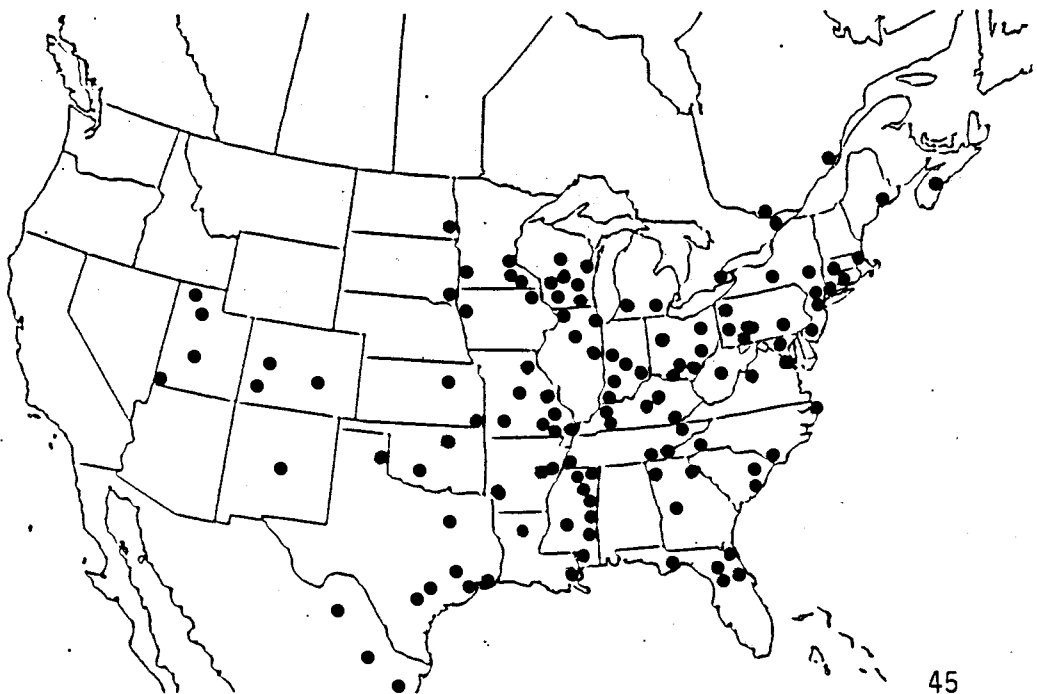
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Figure 42. Distribution of *O. distinctus*

Figure 43. Distribution of *O. dryorhizoxeni*



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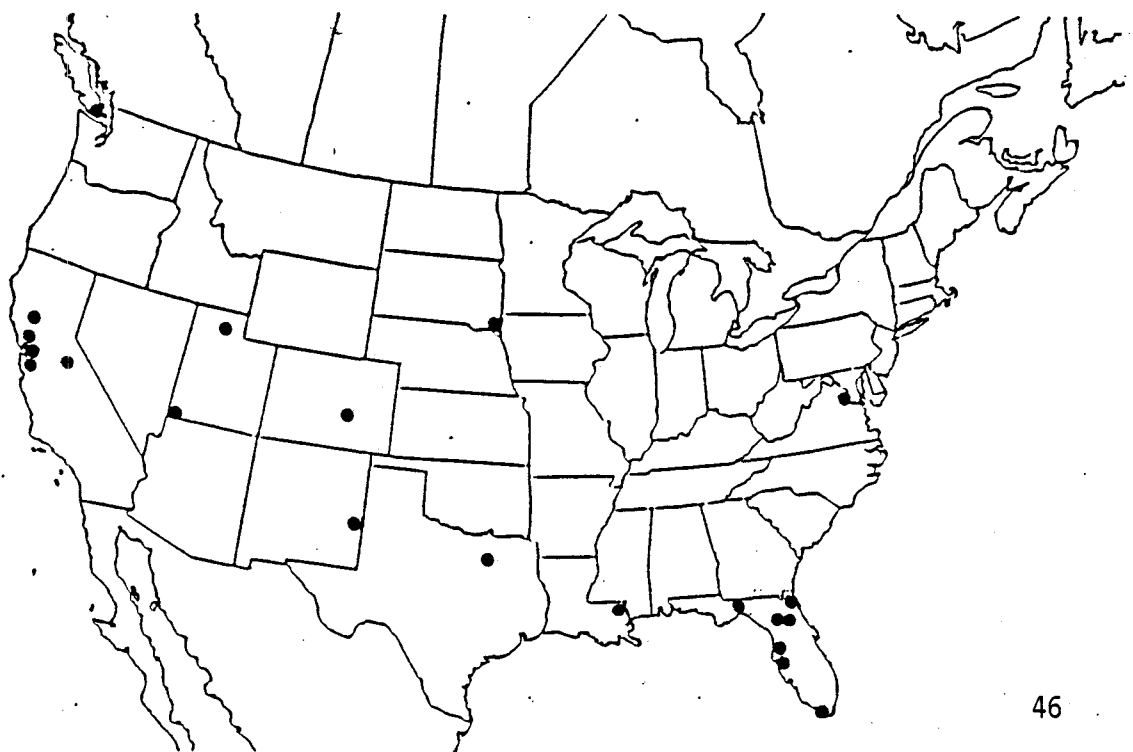


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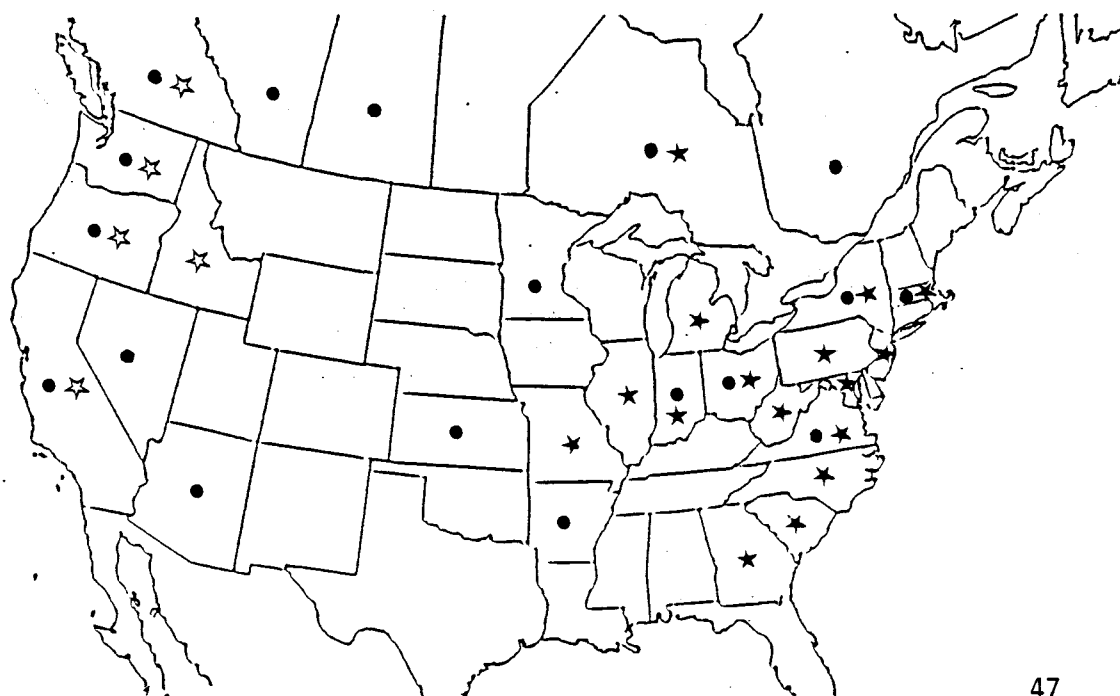
Figure 44. Distribution of *O. hegei*

Figure 45. Distribution of *O. labotus*





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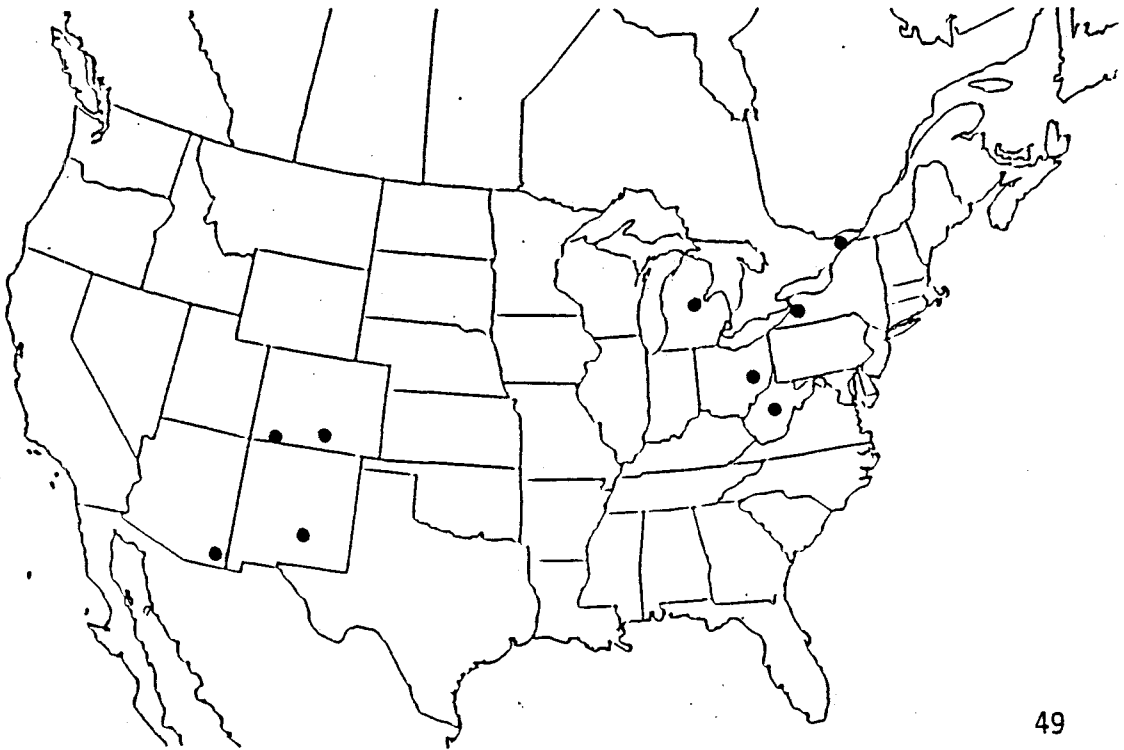
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Figure 46. Distribution of O. reticulatus

Figure 47. Distribution of O. rosae. ● = ex Rosa,  
 ★ = ex eastern Rubus, ☆ = ex western Rubus  
 (only state records are shown).



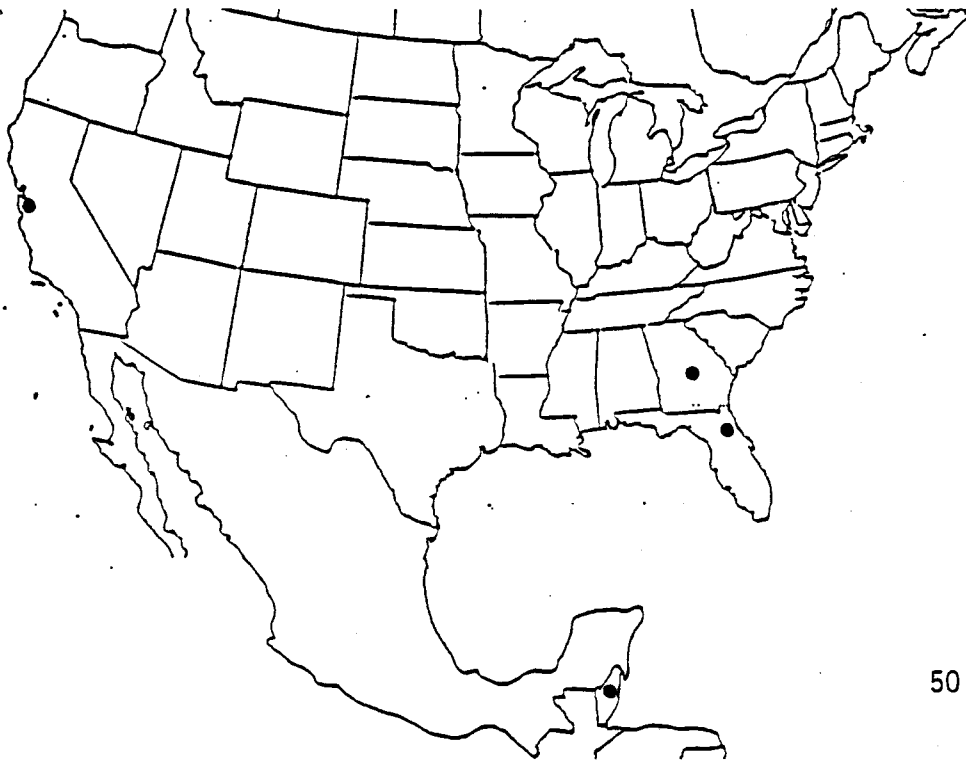
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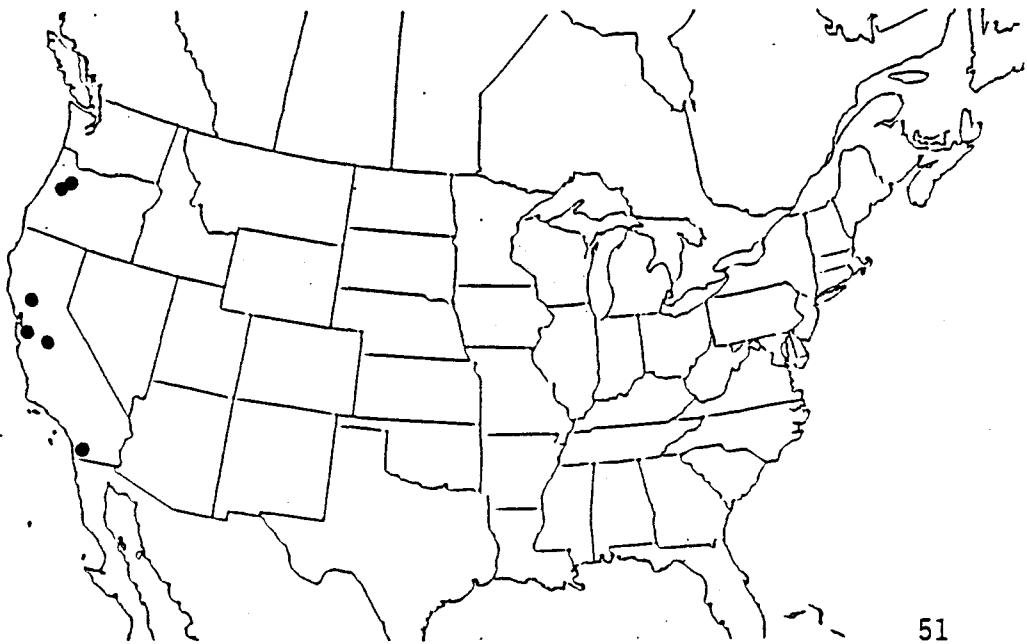
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Figure 48. Distribution of *O. setosus*

Figure 49. Distribution of *O. tenuis*



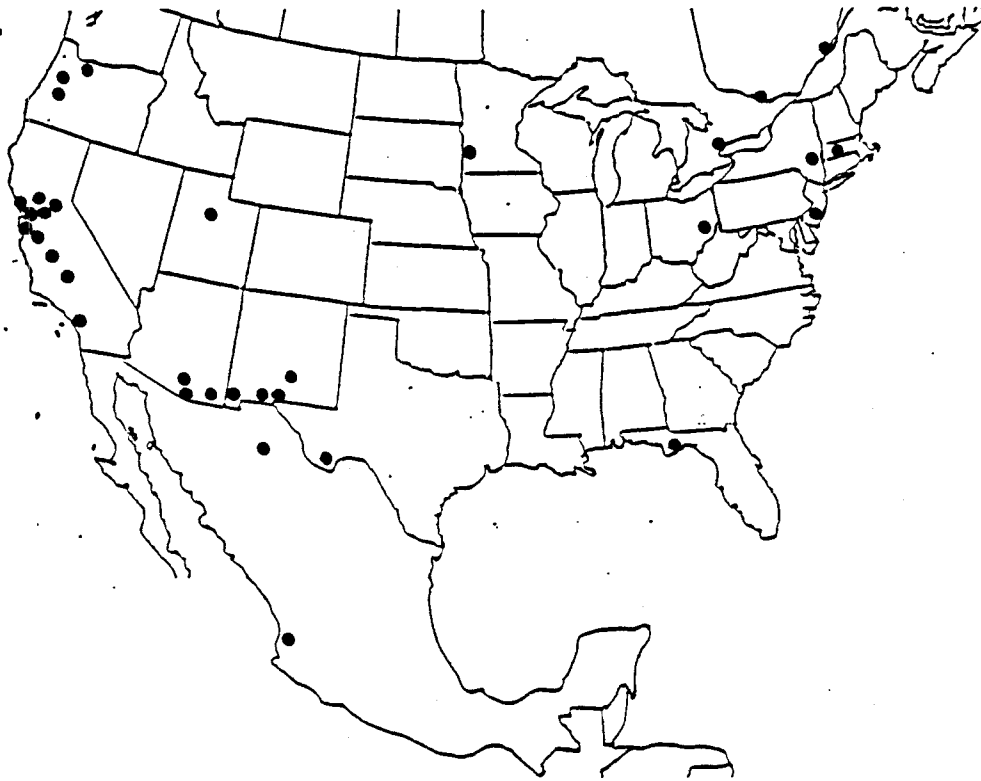
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Figure 50. Distribution of O. thymus

Figure 51. Distribution of O. turio



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Figure 52. Distribution of *O. unifasciatipennis*

Figure 53. Distribution of *O. unimaculatipennis*

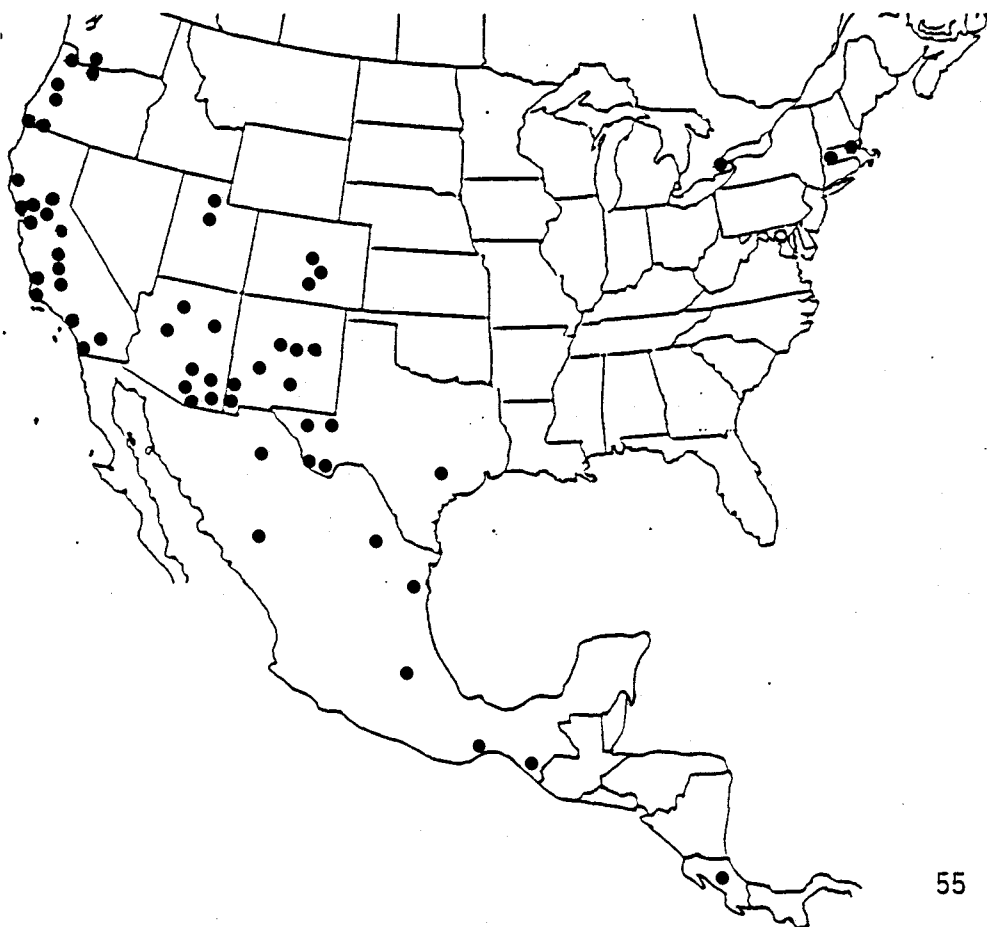
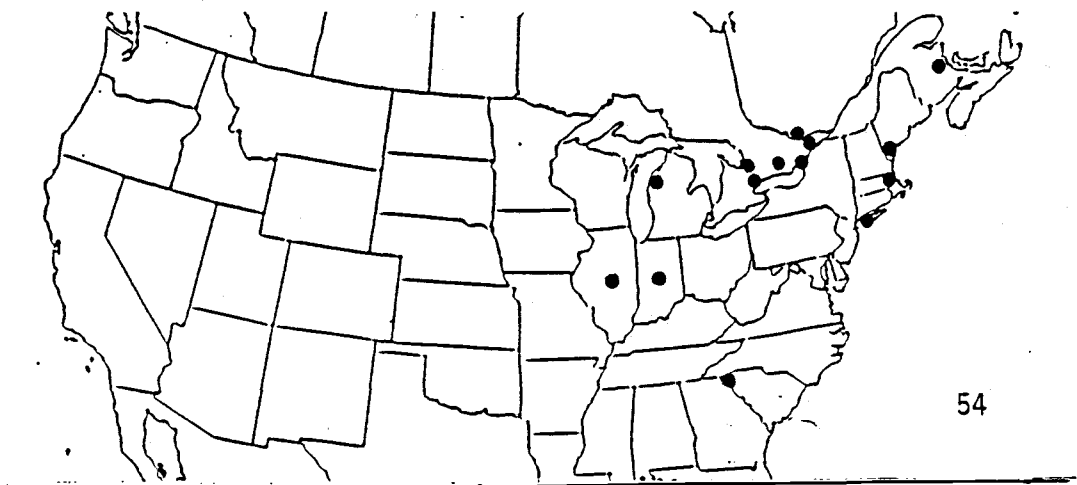


Figure 54. Distribution of *O. vaccinicola*

Figure 55. Distribution of *O. venustus*

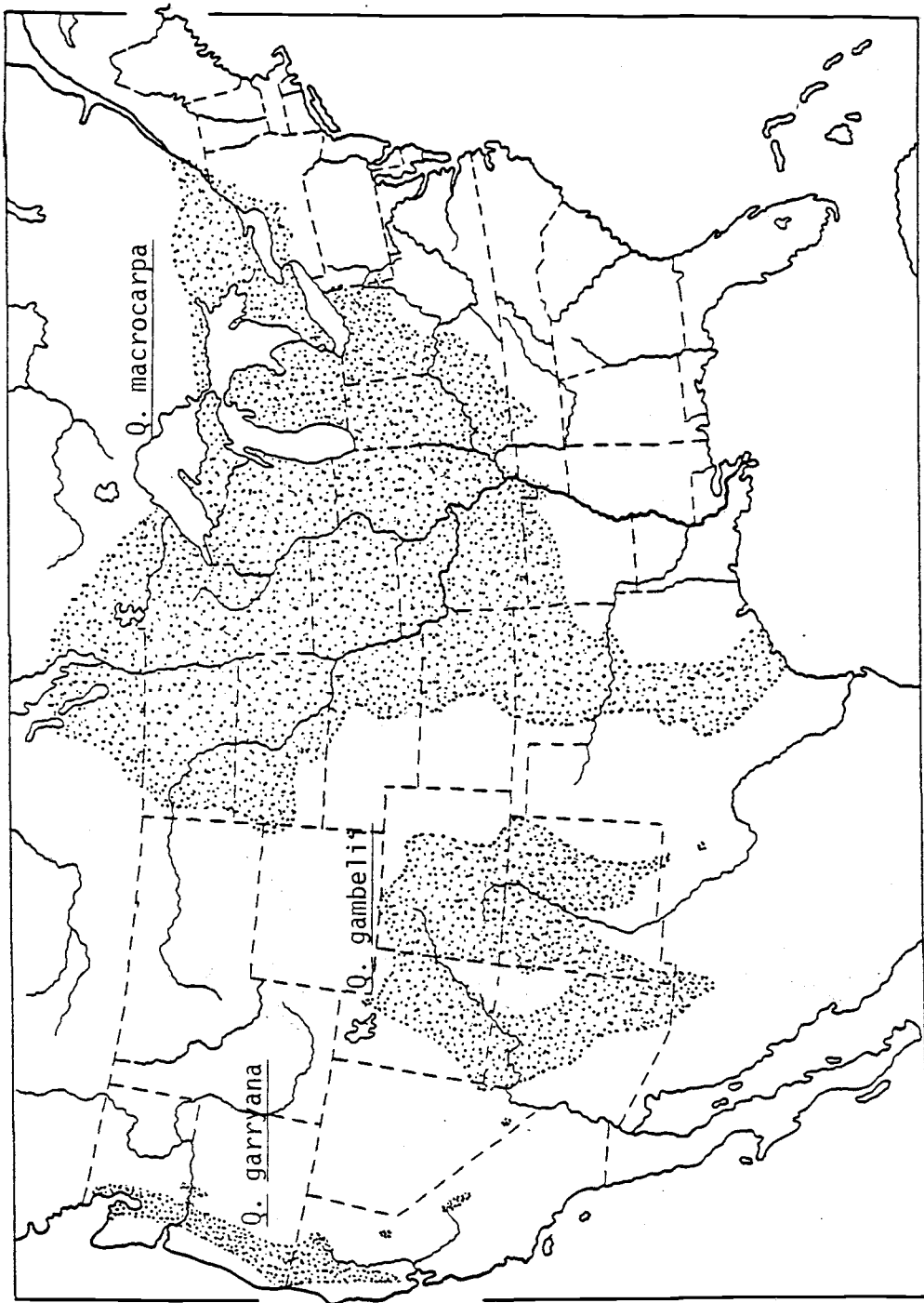


Figure 56. Three Nearctic regions as illustrated by ranges of *Quercus gambelii*, *Q. garryana*, and *Q. macrocarpa*

Table 6. Vicariant distributions of Nearctic oak, cynipid, and Ormyrus species. The three regions (west, southwest, and east) are illustrated in fig. 56; \_\_\_\_\_ = absent; for "Weldia" spp., see text. Each row represents a monophyletic group.

WEST	SOUTHWEST	EAST
OAKS:		
<u>Q. garryana</u>	<u>Q. gambelii</u>	_____
CYNIPIDS:		
<u>Besbicus</u>	_____	_____
<u>Antron</u>	<u>Antron</u>	_____
_____	<u>Acraspis</u>	<u>Acraspis</u>
_____	<u>Atrusca</u>	<u>Atrusca</u>
_____	<u>Philonix</u>	<u>Philonix</u>
<u>Disholcaspis</u> "Weldia" spp.	<u>D. sulcata</u>	_____
ORMYRUS:		
<u>O. distinctus</u>	_____	_____
<u>O. setosus</u>	_____	_____
<u>O. turio</u>	_____	_____
_____	<u>O. labotus</u>	<u>O. labotus</u>
_____	<u>O. tenuis</u>	<u>O. tenuis</u>
_____	_____	<u>O. crassus</u>
<u>O. acylus</u> dark form	dark form	light form
<u>O. venustus</u> stout form	stout form	elongate form

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