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A REVIEW OF THE HIGHER CLASSIFICATION OF THE INQUILINE
GALL WASPS (HYMENOPTERA: CYNIPIDAE) AND A REVISION
OF THE NEARCTIC SPECIES OF *PERICLISTUS* FOERSTER.

by

ALASDAIR JOHN RITCHIE B.S., M.S.

A thesis submitted to
the Faculty of Graduate Studies and Research
in partial fulfilment of

the requirements for the degree of

Doctor of Philosophy

Department of Biology

Carleton University

Ottawa, Ontario

November 23, 1984

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ABSTRACT

The higher classification of the inquilline gall wasps (Hymenoptera: Cynipidae) is reviewed. The inquilline gall wasps live in the galls of other Cynipidae. Eight genera occur in the Nearctic region; these are *Ceroptres* Hartig, *Euceroptres* Ashmead, *Myrtopsen* Rubsaamen, *Periclistus* Foerster, *Saphonecrus* Dalla Torre and Kleffer, *Synergus* Hartig, *Synophromorpha* Ashmead, and *Synophrus* Hartig. Each genus is thoroughly redescribed and a key to the Nearctic genera of inquilline gall wasps is presented. Morphological characters are presented that show most genera are monophyletic taxa. It is suggested that the members of *Synophrus* are not closely related and that *Synophrus* and *Saphonecrus* are specialized members of *Synergus*. Thus, only *Synergus* should be recognized; however, *Synergus* needs to be revised and therefore *Synophrus* and *Saphonecrus* are maintained.

The phylogenetic relationships between the the inquilline and gall forming taxa is determined. Many authors place the inquilline genera in their own subfamily, the Synerginae. Morphological evidence is presented to show the inquillines are a monophyletic group. The closest relative of the inquillines is *Diastrophus* Hartig, a genus of gall inducers on *Rubus* (Rosaceae); hence, recognition of two subfamilies cannot be justified. The relationships between the genera of inquilline Cynipidae are also examined. Three alternative phylogenies are proposed and discussed.

The Nearctic members of the genus *Periclistus* Foerster (Cynipidae) are revised. A generic diagnosis and key to species are presented. Ten species are recognised in North America, six of them new to science: *Periclistus ashmeadi*, *P. cataractans*, *P. fusicolus*, *P. gracilicollis*, *P. vancouverensis*, and *P. weldi*. Four of the seven previously described species are found to be valid; the remaining three species are either placed in synonymy or are transferred to other genera. Host relationships and biological notes are given for each species. Several species of *Periclistus* are polyphagous in their choice of hosts, while others are restricted to a single host. Hence, host relationships cannot be used as an absolute criterion for making taxonomic decisions, although in many cases new host records are indicative of new species.

Information on the taxonomy and biology of the inquiline Cynipidae is scattered throughout the diverse literature. Before these insects can be fully understood, all the previous information must be studied. A synoptic catalogue has been compiled for all species of inquiline gall wasps. The nomenclature and the location of the types (when known) is given for each species. A list of host records for each species is given, as well as a list of inquillines reared from each host gall.

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1. Introduction.

Insect-induced galls are atypical plant growths that represent one of the most complex insect-plant relationships known to science. Galls are a rich, compact source of energy and nutriment and it is therefore not surprising that many other insects have adapted to living in the gall habitat. The galls of each species of gall inducer support an assemblage of associated parasitoids and inquillines (guests) which can be considered a micro-ecosystem. As such, galls can be used to investigate many ecological and evolutionary phenomena, such as community analysis or co-evolution. Before such studies can be undertaken, the systematics of the gall community must be thoroughly understood. The present study is concerned with the systematics of one group of gall inhabitants, the inquilline gall wasps (Hymenoptera: Cynipidae).

The gall community consists of the host plant, the gall inducer, parasitoids, and inquillines. The host plant supplies all photoassimilates used in the construction of the gall. Gall inducers are highly specialized phytophages that feed exclusively on gall tissues; these insects have evolved the ability to induce atypical growth patterns from undifferentiated tissues of the host plant. The mechanism of gall induction has yet to be determined (Meyer and Maresquille 1963). The gall tissues provide a highly nutritious source of food and some degree of protection from the

external environment. Parasitoids are entomophagous insects that feed on the gall inducer or inquillines, although some subsequently feed on the gall tissues (eg. *Eurytoma* sp. (Hymenoptera: Eurytomidae). Inquillines are species that feed on gall tissues, not on the gall inducer. The gall inducer may or may not be affected by the presence of inquillines (Evans 1965, 1967, 1972).

Inquillinism has evolved several different times, usually from within families of gall inducers. The two largest groups of gall formers, the gall midges (Diptera: Cecidomyiidae) and the gall wasps (Hymenoptera: Cynipidae), both contain large numbers of inquillines (Mamaev 1968; Weld 1952b). Inquillinism has also evolved in the weevils (Coleoptera: Curculionidae), thrips (Thysanoptera: Thripidae), and aphids (Homoptera: Eriosomatidae) (Akimoto 1981; Ananthakrishnan 1978; Felt 1940).

All genera of inquilline gall wasps are in need of revision and species concepts that have been applied to this group need to be examined. Before this can be done, the limits of each genus must be adequately defined. Descriptions of inquilline cynipids are scattered throughout the literature and generally do not distinguish between species. The species concepts that have been applied to the inquilline gall wasps are based on our knowledge of the gall inducing taxa.

The purpose of the present study is to review the systematics of the inquilline Cynipidae in an attempt to improve their identification and our understanding of their evolution. A thorough revision of all inquilline species is not feasible at this time; hence, several aspects have been selected to demonstrate the need for further studies. The higher classification of the Nearctic genera of inquilline gall wasps is reviewed (Section 2). Each genus is thoroughly redescribed for a phylogenetic analysis of the evolutionary relationships between the genera. The evolutionary relationship between the inquilline and gall inducing gall wasps is also determined. This provides a framework for future revisions of each genus.

The Nearctic members of *Periclistus* Foerster (Cynipidae) are revised (Section 3). This genus was selected for revision for several reasons. *Periclistus* is a moderately sized genus, the species of which are common in the galls of *Diplolepis* Fourcroy (Cynipidae) on *Rosa* (Rosaceae). A large amount of material from accurately determined host galls was also available; this allowed a detailed study on host relationships, distribution, and morphological variation. The conclusions drawn from this study should be applicable to other genera of inquilline gall wasps.

In addition to the morphological aspects of the study, a catalog of the inquilline Cynipidae has been compiled (Section 4). The catalog gives the nomenclatural history of

each species (Section 4.1). Many species names have been emended arbitrarily, especially in the older literature. These nomenclatural changes have confused the identity of many species. Host relationships and distributional information are presently the most useful data used in determining species, as keys to species are not available; however, host records are generally scattered throughout the diverse literature and there has been no work bringing all the host and distributional records together (Section 4.2). In addition, a list of the inquiline species known from each host gall is presented (Section 4.3).

It is not within the scope of this study to determine the correct higher classification of the Cynipoidea. However, it is desirable to point out some of the shortcomings of the present classification and to propose a preliminary hypothesis for the evolutionary relationships between the "subfamilies and families" of the Cynipoidea (Appendix 1). This is useful in determining the degree of reliability and the polarity of characters. Also, while there are a number of keys to the families and subfamilies of the Cynipoidea, none are easy to use for all taxa or for both sexes. Hence a new key to the families and subfamilies of the Cynipoidea is presented and a short descriptive synopsis of each taxon is given.

1.2. Synopsis of the Cynipoidea and the Cynipidae.

In any systematic study, it is essential to know the closest relatives to the taxon under consideration. This is necessary for two reasons. First, the limits of the group being studied need to be determined; second, characters cannot be polarized in any meaningful manner without this information (Hennig 1966). This often has been satisfactorily resolved by previous studies; however, if the closest relatives are not known, then all members of the next higher taxon must be considered when evaluating characters. Therefore, a knowledge of the Cynipoidea is necessary in order to polarize characters within the Cynipidae.

The Cynipidae are a moderately large family of phytophagous species within the small superfamily Cynipoidea; all other taxa of the superfamily are parasitic. Members of the Cynipoidea can be distinguished from all other Hymenoptera by the following characters: antennae usually filiform, distal antennomeres with rhinaria; forewing venation moderately reduced, with characteristic radial cell, usually without appearance of pterostigma; metasoma laterally compressed (gaster or abdomen of older literature); sternites fused, forming a hypopygium; ovipositor extruding from the end of the metasoma.

The higher classification within the Cynipoidea has not been satisfactorily resolved (Brown 1982). There appear to be approximately 13 natural groups based on biological

characteristics but the relationships between these groups have not been determined. Most authors treat each group as a subfamily (eg. Quinlan 1979; Weld 1952b); however, there is little agreement on the number and composition of families within the Cynipoidea. The current classification of the Cynipoidea is based primarily on biological characteristics, and secondarily on morphological evidence. Unfortunately, there are many important taxa for which the biology is unknown. Also, there are many genera that appear to be intermediate between two or more "subfamilies", which raises doubt about the validity of the current classification. These genera are difficult to place into subfamilies, especially when biological and morphological evidence is contradictory. Males are typically more difficult to determine as most work has been done on female cynipoids.

The most recent work on the world fauna of Cynipoidea is that of Weld (1952b). This work gives keys to genera for all subfamilies. The only other treatment of the world fauna is the monograph by Dalla Torre and Kieffer (1910). More recently, Riek (1971) and Quinlan (1979) have prepared new keys to the families and subfamilies of the Cynipoidea. Both keys have their faults. Riek's key does not work for many males and will not accurately place the inquiline gall formers. Quinlan's key attempts to place males, but utilises many characters that are not present for all taxa. Hence, a new key has been prepared (Appendix 1). The class-

ification proposed by Quinlan (1979) is followed here, but with reservations. Families and subfamilies not found in the Nearctic region are included in the key for the sake of completeness.

The Cynipidae are distinguished from other Cynipoidea by being phytophagous and by the development of a spine on the hypopygium on the female metasoma; a hypopygium is the result of fusion of metasomal tergites into a syntergite. Males are very difficult to identify. Many systematists place the inquillines and the gall formers in separate subfamilies. The inquillines are placed in the Synerginae and the gall formers are placed in the Cynipinae (Ashmead 1896; Burks 1979). This classification is based solely on biological characteristics and has not been substantiated by morphological evidence. The correct placement of the inquillines can be determined by first establishing a framework of higher classification for the gall formers. The inquillines can then be placed in this framework. A discussion of the classification of the gall forming species is also warranted, as the taxonomic concepts that have been applied to the inquillines have been extrapolated from those applied to the gall formers.

There are about 60 genera and 1200 species of gall inducing Cynipidae in the world (Dalla Torre and Kieffer 1910; Weld 1952b; Burks 1979). These gall wasps possess the ability to initiate and sustain gall formation (Rohdtritsch

and Shorthouse 1982). The true gall wasps are very host specific; a given species of gall former usually attacks a single organ (leaf, stem, or root) on a single species or group of closely related species of host plant (Kinsey 1920a-c, 1930, 1936; Weld 1952b; Shorthouse 1982). Exceptions to this rule occur in species which exhibit alternation of generations. In these cases, two organs of a host plant may be galled by different generations of a single species (Evans 1967, 1972; Kinsey 1930, 1936; Lyon 1970). Similarly, a given genus of gall former is usually restricted to a single genus of host plant. Exceptions occur in the more primitive genera (eg. *Aulacidea* Ashmead, *Aylax* Hartig, and *Diastrophus* Hartig) in which two or three genera of host plants may be attacked (Kinsey 1920b). Each species of gall wasp induces a characteristic gall. Cynipid galls are structurally complex and have a consistent external shape; Kuster (1911) termed this type of gall prosoplastic, as opposed to the simpler kataplastic galls of aphids and thrips.

Kinsey (1920c) proposed a phylogenetic higher classification for the gall forming Cynipidae. He recognised three distinct tribes, which were based mainly on gall morphology and host plant relationships; these are: 1) the Aulacini, 2) the Rhoditini, and 3) the Cynipini. Kinsey believed that the Aulacini were the most primitive of the gall formers and were ancestral to the Rhoditini and Cyni-

pini (Fig. 1). Kinsey included six genera in the Aulacini, all of which form rather simple galls on various Compositae, herbaceous plants, and *Rubus* (Rosaceae). With the exception of two species, all members of this tribe form polythalamous stem galls. However, no synapomorphy has been found to unite the genera of the Aulacini. Hence, the Aulacini is based on symplesiomorphy and is a paraphyletic group. Thus, I will refer to these genera as the Aulacine genera.

The Rhoditini is composed of *Diplolepis* Fourcroy (= *Rhodites* Hartig), which induce galls on *Rosa* (Rosaceae). Some authors (Kinsey 1920c; Weld 1952) also include *Eschatocerus* Mayr, a genus of gall inducers on *Acacia* (Legumaceae), in the Rhoditini; however, many morphological characters indicate that this genus belongs to the Cynipini. All organs of the host plant are attacked by various species of *Diplolepis* and the galls are more complex than those of the Aulacine genera. Some species of *Diplolepis* induce polythalamous galls while others induce monothalamous galls (Weld 1957b, 1959, 1960; Shorthouse 1973, 1975).

The Cynipini is composed of all the oak gall formers; these species attack all oaks of *Quercus* spp. (Fagaceae) (except *Dryocosmus castaneaefidis* Beutenmueller which induces galls on *Castanea* spp. (Fagaceae)). All Cynipini form complex galls and most are monothalamous (Kinsey 1930, 1936). There are about 40 genera and 1000 species of oak gall formers (Dalla Torre and Kieffer 1910; Weld 1952b; Burks 1979).

Kinsey (1920c) did not include the Inquilline genera in his analysis except in a table showing the phylogenetic significance of open and closed radial cells. However, in an earlier paper (1920b), he stated that the Inquillines are Figitidae. Thus, he believed that the Inquillines did not belong to the same lineage as the gall wasps.

Kinsey (1920c) provided some morphological data in addition to biological data to support his classification. He also stated which characters were derived and which were primitive. The Rhoditini and Cynipini are clearly monophyletic and are sister groups. Members of both tribes have a narrowed pronotum (median longitudinal line less than one seventh of lateral height), which is a unique synapomorphy within the Cynipoidea. Subsequently, each tribe shows separate apomorphic changes to the hypopygial spine. The Rhoditini are defined by having the hypopygium modified into a "ploughshare", whereas the Cynipini have the hypopygial spine elongated or broadened and usually with long setae. Kinsey's figure on the evolution of the Cynipidae shows a sister group relationship between the Rhoditini + Cynipini and *Diastrophus* (including *Gonaspis*).

Similar systems for the higher classification of the Cynipidae have been proposed Eady and Quinlan (1963), Quinlan (1968), and Weld (1952b). However, the relationships within the Cynipidae must be inferred from their arrangement of genera. All three of these works include the in-

quilline genera. Eady and Quinlan (1963), and later Quinlan (1968), implied that the inquillines are a polyphyletic group (Fig. 2). Weld (1952b) implied that the inquillines form a monophyletic taxon that is the sister group to the gall inducers. (Fig. 3). However, Weld (1952b) needed four different groups of characters to separate the inquillines from the gall inducers, suggesting that the inquillines do not form a monophyletic group.

1.3. Taxonomic concepts

The taxonomic concepts that have been applied to the Cynipidae have been a matter of controversy and this is particularly true for species concepts. Part of the reason for the controversy is due to the nature of the organism under study and part is due to different ideas of various workers.

Most taxonomists utilise the Biological Species Concept for their definition of a species (Scudder 1974). This concept has been stated in various ways, but a widely accepted one is:

"Species are a group of interbreeding natural populations that are reproductively isolated from other such groups." (Mayr 1969: 26).

Kinsey appears to have had a similar concept as he stated:

... our definition of species as populations having access to a common stock of genes." (Kinsey 1936: 26).

Other definitions have been proposed, but most seem to be

variations of the one given above. Implicit in this concept is that members of a species share a common gene pool and that the gene pool is mixed between generations, usually through sexual reproduction.

The most thoroughly studied Cynipidae are the oak and rose gall inducers (the Rhoditini and Cynipini). Species concepts have been based on our knowledge of these species and have been extrapolated to other cynipid taxa. Most oak and rose gall formers are agamic and therefore the Biological Species Concept cannot be applied to these taxa (Scudder 1974). Hence, there is an intrinsic difference between agamic and sexual species and the concepts and trends that are based upon our knowledge of the agamic taxa should not be applied to sexual species.

Three main criteria that have been used in making taxonomic decisions within the Cynipidae are: 1), gall morphology, 2) host-plant relationships, and 3) distribution. Kinsey (1930) correctly argued that gall morphology is dependent on the species of gall former, not the host plant. Subsequent studies on gall developmental morphology have supported this hypothesis (eg. Shorthouse 1975, 1982; Rohfritsch and Shorthouse 1982). Kinsey (1930) stated that only 28% of oak gall formers have multiple host plants and that the alternate hosts are always closely related species. Similarly, only 26% of oak gall formers have very similar galls. Finally, less than 1% of all closely related

oak gall formers occur on the same host plant in the same area (Kinsey 1942). Hence, many species have been described on these criterion without a critical examination of the insect itself. An example is given below.

Weid (1952a) described *Diplolepis lens*, a species that induces lens-shaped galls on *Rosa* in Oregon. A very similar species, *D. roseaeformis* (Cockereil), is widely distributed throughout Eastern North America (Burks 1979). Weid compared *D. lens* to other species already known from Oregon and California, but did not consider that an eastern species could have such a wide distribution. Shorthouse (1975) has examined both species and suggested that they are the same. Many of Kinsey's species are apparently distinguished on the basis of their distribution, as Kinsey's keys (1930, 1936) will not work without such information. There are many other examples of this sort of taxonomy in the literature.

Similar concepts have been applied to the Inquiline Cynipidae. Most previous workers believed that each species of inquiline was restricted to the gall of a single gall former. Exceptions to this rule occur, but 96% of all Nearctic species have been reported from a single host gall (data from Burks 1979). However, 37% of Palearctic Inquillines have multiple hosts and some Palearctic species of *Synergus* have been reared from the galls of up to 25 species of gall inducers (data from Section 4.2)

Recently, it has been shown that a cynipid species can induce several distinct types of gall and that the range of a gall-inducing species (*Diplolepis trifurcata* S. & R.) can be almost transcontinental (Shorthouse and Ritchie 1984). There is little reason to believe that host plant specificity is always as absolute as previously thought. This is not to say that "monophagy" does not occur in the Cynipidae, but rather that it cannot be used as an absolute criterion for the recognition of species. Hence, information from other sources, such as morphological studies, are needed to corroborate biological and zoogeographical data.

Fig. 1. Phylogenetic relationships of some genera of gall inducing Cynipidae as defined by Kinsey (1920c).

Fig. 2. Phylogenetic relationships of some genera of inquiline Cynipidae, as implied by Eady and Quinlan (1963). (I = Inquiline; G = Gall inducer).

Fig. 3. Phylogenetic relationships of some genera of inquiline Cynipidae as implied by Weld (1952b). (I = Inquiline; G = Gall inducer).

2. The Higher Classification of the Inquilline Gall Wasps.

2.1 Introduction

The higher classification of the inquilline gall wasps has never been thoroughly examined. There are no phylogenetic hypotheses available regarding the relationship of the inquillines to the true gall wasps, or to the relationships between the genera of inquillines. Also, it is generally assumed that the inquillines form a monophyletic group, but little evidence has been presented to support this hypothesis. Most authors simply list the genera and species of inquillines, either at the beginning or end of the work, without adding any further information (eg. Dalla Torre and Kieffer 1910). Thus, the only phylogenetic information available is implied, not directly stated. The purpose of the present study is to provide evidence showing: 1) the inquilline gall wasps are a monophyletic group; 2) the phylogenetic relationships between the inquillines and the true gall inducers; and 3) to propose a phylogenetic hypothesis showing the evolutionary relationships between the genera of inquilline gall wasps.

Inquilline gall wasps differ from the true gall wasps in several ways, the most important of which is their biology. Both the inquillines and gall inducers are phytophagous, whereas other members of the superfamily Cynipoidea are parasitic (Weid 1952b). The true gall wasps have the capability to induce galls. The inquillines lack the ability

to induce galls but live in the galls of other gall wasps (Weid 1952b; Shorthouse 1975). The inquillines feed on the gall tissues induced by the gall former and induce individual chambers which appear as galls with the gall (Shorthouse 1982). Such structures have been termed endogalls (Hawkins and Goeden 1982). Although the inquilline never feeds on the gall inducer, the gall inducing larva is frequently killed either by the ovipositing female or by crowding by the inquilline larvae (Evans 1965, 1967, 1972; Weid 1952b; Shorthouse 1975). The tissues of the host gall are often modified by the inquilline, sometimes substantially altering the external appearance of the gall (Evans 1965, 1967, 1972; Shorthouse 1975, 1980).

Members of each genus of inquillines are restricted to attacking galls on only one genus of host plant; however, if more than one genus of gall inducer occurs on a host plant, then each is susceptible to attack by a given genus of inquilline. These data are corroborated with consistent morphological differences. However, the morphological evidence appears to be based on a few key characters; several pairs of genera are separated by the presence or absence of characters (eg. radial cell open vs. closed). Thus, while one genus of such a pair would be defined by a synapomorphy, the other would be defined by symplesiomorphy. Higher taxa should be based on apomorphic characters, not plesiomorphic characters (Hennig 1966; Wiley 1981).

Weld (1952b) recognised 10 genera of Inquilline cynipids: *Ceroptres* Hartig, *Euceroptres* Ashmead, *Myrtopsen* Rubsaamen, *Periclistus* Foerster, *Poncylia* Kieffer, *Rhoophilus* Rubsaamen, *Saphonecrus* Dalla Torre and Kieffer, *Synergus* Hartig, *Synophromorpha* Ashmead, and *Synophrus* Foerster. Members of *Synergus*, *Saphonecrus*, *Ceroptres*, and *Euceroptres* are Inquillines in galls on *Quercus*; the species of *Periclistus* are Inquillines in the galls of *Diplolepis* on *Rosa* and those of *Synophromorpha* are restricted to the galls of *Diastrophus* Hartig on *Rubus*. Members of *Myrtopsen* are Inquillines in the galls of *Tanaostigmodes* (Eupelmidae: Tanaostigmatinae) on *Mimosa* (Legumaceae) (Weld 1926), and from galls on *Eugenia* and *Blepharocalyx* (Myrtaceae) (Diaz 1980). Weld (1952b) tentatively recognised *Poncylia* and *Synophrus* as Inquillines due to their morphological structure; previously, they had been thought of as gall formers on *Quercus*. Weld (1952b) also placed *Rhoophilus* in the Inquilline group due to the morphological similarity to the other Inquillines. *Rhoophilus loewi* Mayr is known from galls on *Rhus* from South Africa; *Poncylia ferruginea* Kieffer had previously been thought to be a gall former on *Quercus* from Europe (Kieffer 1905).

Ratzeburg (1833) described the first species of Inquilline, *Cynips brandtii*. Hartig (1840) was the first to recognise the biological differences between the Inquilline and gall forming Cynipidae. Hartig (1840, 1843) described

Ceroptres, *Synergus*, and *Synophrus* from oak galls, although he thought *Synophrus* was a gall former. Foerster (1869) erected *Periclistus* for the Inquillines of rose galls and *Sapholytus* for those species of *Synergus* with an open radial cell. Mayr (1881) erected *Rhoophilus* for *R. loewii* Mayr, a species from South Africa reared from a gall on *Rhus*. Ashmead (1896) erected *Euceroptres* for *E. prunus* Ashmead, and later (1903) described *Synophromorpha* for *S. salicis* Ashmead. Kieffer (1903) described *Poncyia* for *P. ferruginea* Kieffer, which he thought was a gall former. Dalla Torre and Kieffer (1910) synonymized *Sapholytus* with *Synergus* and erected *Saphonecrus* for those species of *Synergus* with the radial cell open. Rubsaaman (1908) erected *Mytopsen* for *M. mayri* Rubsaaman, an Inquilline in galls on *Mimosa*.

There have been several works on the species of Inquilline Cynipidae. Important works on the Palearctic fauna include Hartig (1840, 1841, 1843), Mayr (1872), Kieffer (1902b), Dalla Torre and Kieffer (1910), Tavares (1920), Ross (1951), and Eady (1952). The Nearctic fauna has been studied by Osten Sacken (1861, 1862, 1863, 1865), Walsh (1864), Ashmead (1885, 1886, 1896, 1899, 1903, 1904), Gillette (1890, 1896), Fullaway (1911), McCracken and Egbert (1922), and Weld (1913, 1926, 1952a).

In the present study, the Nearctic genera of Inquilline Cynipidae are thoroughly redescribed for an analysis of the phylogenetic relationships between the Inquilline genera and also to determine the correct placement of the Inquillines within the Cynipidae. Apomorphic characters are determined by out-group comparison (Watrous and Wheeler 1981); the gall forming Cynipidae was used as a generalized out-group. Characters found useful for phylogenetic analyses also have been surveyed for throughout the Cynipoidea. This allows an assessment of the reliability of the characters being used.

2.2 Morphology and Abbreviations

Morphological terms used here generally follow those of Ritchie and Peters (1981), Nordlander (1982), and Short-house and Ritchie (1984). Additional terms are: 1) median protuberance, a protruding ridge on the frons running between the antennal sockets and the clypeus; 2) subantennal fovea, a depression between the dorsal end of the median protuberance and the antennal socket; 3) subalar triangle, a triangular depression on the mesopleuron below the base of the forewing; 4) supracoxal carina, a carina on the propodeum running between the metacoxal socket to the posterodorsal margin of the mesopleuron; 5) supracoxal tubercle, a tubercle above the metacoxa marking the junction between the supracoxal and subspiracular carinae; 6) subspiracular carina, a carina on the propodeum running ventrally from the spiracular flap to the supracoxal tubercle.

All measurements were made with a calibrated net reticule with the specimen positioned such that both endpoints were in focus. Measurements of antennomeres are of lateral length and do not include the basal insertion (if the antenna is distended, only the cylindrical part of each antennomere is included in the measurement). The lateral ocellar line (LOL), the distance between the anterior ocellus and a posterior ocellus, is measured in terms of the diameter of a posterior ocellus (D). Similar measurements are taken for the posterior ocellar line (POL), the distance between the posterior ocelli, and the oculo-ocellar line (OOL), the distance between a posterior ocellus and an eye. Other measurements are self-explanatory. Scanning Electron Micrographs (SEM's) were taken on a Jeol JSU-U3 scanning electron microscope.

Most characters are readily observable; however, care must be taken in determining the degree of development of the notauli and other mesosomal structures. These must be observed under strong, diffuse light from several different angles. This is especially true when the notauli are complete as creases, not grooves. This is also true for determining the condition of the mesopleuron (smooth or sciculate) and the ventral margin of the subalar triangle (punctopubescent area present or absent). I have distinguished between pubescence and pilosity. Pubescence refers to hairs that are relatively long and sparse, and do not obscure the

surface. Pilosity refers to much shorter, denser, almost felt-like hairs that generally cover the surface.

This study is based on material that is deposited in several major collections (listed below). It is currently impossible to assign species names to most specimens of Inquillines; hence, a list of material examined has not been given for each genus. Nearctic and Palearctic members of Holarctic genera have been examined when necessary.

Museums and Collections Containing Material Examined

- AJR - Collection of A. J. Ritchie, Carleton University.
- AMNH - American Museum of Natural History, New York City, NY. (M. Favreau)
- CNC - Canadian National Collection of Insects and Arachnids, Biosystematics Research Institute, Agriculture Canada, Ottawa, ONT. (C. Yoshimoto)
- CORN - Cornell University, Ithaca, NY. (Q. Wheeler)
- HKT - Collection of H. K. Townes, American Entomological Institute, Ann Arbor, MI.
- JDS - Collection of J. D. Shorthouse, Laurentian University, Sudbury, ONT.
- LHW - Collection of L. H. Weld; Los Angeles City Coll., Los Angeles, CA. (R. Lyon).
- MCZ - Museum of Comparative Zoology, Harvard University, Cambridge, MA. (J. Carpenter).
- USNM - United States National Collection, Smithsonian Institution, Washington, DC. (A. Menke)

2.3 Key to the Nearctic genera of Inquilline Cynipidae.

1. Pronotum narrow (median length less than one seventh of lateral height); hypopygium either ploughshare shaped or with long setae, sometimes elongate or broadened. ex galls on *Acacia*, *Castanea*, *Quercus*, and *Rosa*. Rhoditini and Cynipini
- 1'. Pronotum broad (median length greater than one sixth lateral height); hypopygium poorly developed, without long setae.
 Aulacine genera and Inquillines ... 2
2. T3 expanded reaching or nearly reaching posterior of metasoma; T2 frequently fused with T3; maxillary palps 4 segmented, or with 5 palpomeres with palpomeres 1 and 2 fused. Inquillines ... 3
- 2'. T3 not expanded, not reaching posterior of metasoma; T2 and T3 never fused; maxillary palps 5 segmented. Aulacine genera of Gall formers
3. Proximal hamulus strongly bifid (Fig. 32); T2 and T3 fused in females, separate in males; maxillary palpi 5 segmented, palpomeres 1 and 2 rigidly fused; ex galls on *Rosa* and *Rubus*. 4
- 3'. Proximal hamulus simple or at most weakly bifid; T2 and T3 separate or fused; maxillary palpi with 4 segments. ex galls on *Quercus* and *Mimosa*. 5

4. Mesoscutum smooth or graniculate, with strong anterior setigerous pits (Fig. 24); radial cell open; ventral margin of subalar triangle without a row of conspicuous setigerous punctures (Fig. 25). Eastern North America, Mexico. ex galls on *Rubus*. *Synophromorpha* Ashmead
- 4'. Mesoscutum coriaceous, without strong anterior setigerous pits (Fig. 18); radial cell closed; ventral margin of subalar triangle with a row of conspicuous setigerous punctures (Fig. 19). Holarctic. ex galls on *Rosa*. *Periclistus* Foerster
5. T2 and T3 separate in both sexes. 6
- 5'. T2 and T3 fused in both sexes. 7
6. Pronotum without lateral carinae (Fig. 12); subantennal ridges incomplete (Fig. 4); female T2 and T3 separated by connate suture, T2 with anterior patch of pubescence; Holarctic. ex galls on *Quercus*. *Ceroptres* Hartig
- 6'. Pronotum with well developed lateral carinae (Fig. 14); subantennal ridges absent (Fig. 5); T2 without anterior patch of pubescence; female T2 and T3 separated by oblique suture. Holarctic. ex galls on *Quercus*. *Euceroptres* Ashmead

7. Pronotum with strongly developed lateral carinae (Fig. 16); S2 short and smooth; mesopleuron smooth, groove present (Fig. 16); propodeal carinae bent. Nearctic, Neotropical. ex galls on *Mimosa*. *Myrtopsen* Rubsaamen
- 7'. Pronotum without lateral carinae; S2 expanded ventrally and dorsally, dorsal portion at least partially sulcate (Fig. 30); mesopleuron at least partly striate (Fig. 23), groove absent. Holarctic. ex galls on *Quercus*, *Castanea*. 8
8. Radial cell closed; frontal ridges often present; hind margin of T2+3 frequently excised dorsally; *Synergus* Hartig
- 8'. Radial cell open; frontal ridges usually absent; hind margin of T2+3 not excised. 9
9. S2 entirely sulcate (as in Fig. 30).
. *Saphonecrus* Dalla Torre and Kieffer
- 9'. S2 smooth medially, sulcate laterally (Fig. 31).
. *Synophrus* Hartig

2.4 Description of genera.

Ceroptres Hartig

Figures 4, 12, 13, 28.

Ceroptres Hartig 1840: 186, 197.

Type species: *Ceroptres clavicornis* Hartig. Designated by Foerster 1869.

FEMALE. Length 1.2 - 3.0 mm. Black, rarely rufous; head sometimes rufous, yellow, frequently variegated; antenna and legs usually amber or yellow. Head (Fig. 4) ovoid; radiating striae weak to very weak; median protuberance usually weak, often moderately developed; subantennal ridges often present, incomplete (Nearctic species) to complete (Palearctic species; acc. Tavares 1920); frontal ridges, frontal field absent; clypeus "shield-shaped"; genal carina absent; palpal formula 4-3; antenna with 12-13 antennomeres, rarely 14, usually filiform, rarely weakly clavate. Pronotum with weak transverse rugulae; anterior pilosity present, frequently strong; pronotal plate weakly developed. Mesoscutum (Fig. 12) coriaceous; anterior margin usually evenly arcuate, rarely produced anteriorly; notauli incomplete to complete, never strong, never widened posteriorly; median groove usually absent, never reaching past middle of mesoscutum; lateral lines weak; anterior lines weakly impressed, convergent. Mesoscutellum rugulose to rugose; foveae small and shallow, usually weakly defined, often indistinct; septum weak to absent. Mesopleuron (Fig.

13) usually shining smooth, sometimes with aciculation, very rarely striate; mesopleural groove absent; metapleuron weakly defined, posterior margin arcuate; supracoxal carina usually weak; propodeal pilosity weak or absent; propodeal carinae usually moderately developed, parallel; petiole striate. Metasoma not strongly compressed; S2 (Fig. 26) smooth, crescent shaped; T2 and T3 separate, T2 and T3 covering most of metasoma (dorsal view); T2 with strong lateral pilosity; posterior third of T3 often punctate, posterior margin not excised dorsally. Forewing hyaline, never infuscated, about 1.0 - 1.1 of body length; radial cell closed, length to width ratio = 2.6 - 3.1; areolet usually equilateral, sometimes elongate; proximal hamulus weakly bifid, ectal margins parallel. Tibial spurs weak; tarsal claws strongly toothed.

MALE. Differs from female as follows: length: 1.0 - 3.0 mm; antenna with 14-15 antennomeres, A3 weakly curved and excavated, never expanded distally; pilosity of T2 usually weak, sometimes very weak.

BIOLOGY. All except two species of *Ceroptres* attack the galls of various Cynipidae on *Quercus* spp. *Ceroptres inermis* (Walsh) is known from galls of *Cincticornia pilulae* (Osten Sacken) (Diptera: Cecidomyiidae) (Osten Sacken 1865). *Ceroptres globulus* (Beutenmueller) has been reared from a rose stem gall which was probably a gall of *Diplolepis nodulosa* (Ashmead) that has been modified by *Periclistus*

pinata (Osten Sacken) (see Appendix II for a discussion of *C. globulus*). Host galls that are attacked by *Ceroptres* spp. are usually considerably modified from the normal condition. As far as is known, all species have one generation per year and spend one winter in the gall.

REMARKS. Female members of the genus *Ceroptres* may be recognised by the following characters: head often variegated; T2 and T3 separate, T2 with dense anterior pubescence and dense anterior pilosity; mesoscutellar foveae usually very shallow and indistinct. Males are very similar to male *Periclistus* but can be separated by the following characters: subantennal ridges present, although often weak and incomplete; subalar triangle without row conspicuous setigerous punctures; mesoscutellar fovea usually very shallow and indistinct; T2 usually with well developed anterior pubescent patch; proximal hamulus weakly bifid, ectal margins parallel. Tavares (1920) and Eady and Quinlan (1963) state that European members of *Ceroptres* have the subantennal ridges complete, running from the ventral margin of the antennal sockets to the dorsal margin of the clypeus. These carinae are incomplete in Nearctic specimens that I have examined.

Ceroptres has no strong synapomorphy with the other genera of Inquillines. The weakly bifid hamulus may be a synapomorphy with *Periclistus* + *Synophromorpha*, whereas the reduced number of maxillary palpi (four) and the weakly

developed mesoscutellar fovea suggest a close relationship with the other oak gall inquillines (see Section 2.5). Weld (unpublished) has seen specimens that are intermediate between *Ceroptres* and *Synergus*. In these specimens, T2 + T3 are separate but S2 is expanded and sulcate and the mesopleuron is striate. Weld places these specimens in *Ceroptres*; although I have not seen these specimens, I believe that they support a close relationship between the two genera.

The genus *Ceroptres* is distributed throughout the Holarctic region, with the majority of species described from the Nearctic region. No species are known from either Northern Africa or from Mexico. Tavares (1920) has revised the Iberian species of *Ceroptres*, but omitted one European species. The Nearctic species have never been revised and it is currently impossible to identify any of the Nearctic species. (See Section 4.1 for a list of included species).

Euceroptres Ashmead

Figures 5, 14, 15.

Euceroptres Ashmead 1896: 187.

Type species: *Euceroptres primus* Ashmead. Original designation.

FEMALE. Length: 1.8 - 4.0 mm. Black; antenna beyond scape, legs beyond coxae brown to yellow. Head (Fig. 5) not expanded behind eyes, ovoid; radiating striae, median protuberance absent; frons bulging; subantennal ridges, frontal ridges, frontal field absent; clypeus trapezoidal; genal carina absent; antenna filiform, with 12 - 14 antennomeres. Pronotum often weakly transversely rugulose, anterior pilosity absent; pronotal plate absent, lateral carinae (Fig. 14) well developed (absent in all other genera except *Myrtopsen*). Mesoscutum (Fig. 14) coriaceous with weak to strong transverse rugae; anterior margin evenly arcuate, not produced anteriorly; notauli complete; median groove usually absent; anterior lines weakly impressed; lateral lines weakly impressed; mesoscutellum rugose; foveae shallow and weakly defined; septum distinct, narrow. Mesopleuron (Fig. 15) smooth to weakly aciculate; mesopleural groove absent; metapleuron distinct, posterior margin arcuate; propodeal carinae moderately strong, straight; propodeal pilosity absent; supracoxal carina present, weak; petiole smooth. Metasoma shorter than head plus mesosoma, not compressed laterally; S2 not expanded dorsally and ventrally,

smooth; T2 and T3 not fused, separated by an oblique suture; T2 1.5 - 2.5 length of T3; anterior pilosity absent; posterior margin of T3 not excised; posterior of T3 third frequently punctate; hypopygial spine very weakly developed. Forewing hyaline, about 1.0 - 1.1 of body length; radial cell closed, length to width ratio = 3.0; radius evenly arcuate; areolet equilateral, elongate or absent; proximal hamulus simple. Tibial spurs strongly developed; tarsal claw weakly toothed.

MALE. Differs from female as follows: length 2.4 - 3.9 mm; antenna with 15 - 16 antennomeres; A3 weakly notched, weakly curved, sometimes expanded distally.

BIOLOGY. Members of the genus *Euceroptres* attack various species of Cynipidae inducing galls on *Quercus* spp. There is only one generation per year and the larvae spend one winter in the gall (Weid 1926).

REMARKS. Members of *Euceroptres* can be distinguished from all other Inquilline Cynipidae by the following characters: pronotum truncate, lateral carinae well developed, pronotal plate absent; mesoscutum transversely rugose; T2 and T3 separate in both sexes, posterior margin of T2 oblique. Three species are found in the Nearctic region and a fourth species is known from Japan (Weid 1952b). Ashmead (1896, 1904) described two species; Weid (1926) described two additional species, supplemented the description of Ashmead's species, and gave a key to the four species. (See

Section 4.1 for a list of included species).

The genus *Euceroptres*, while quite distinctive, is difficult to relate to the other genera of Inquillines. The transverse rugulae on the mesonotum and absence of the pronotal plate appear to ally *Euceroptres* with *Synergus*. However, the trapezoidal clypeus, well developed lateral carinae, smooth petiole, and strongly developed metatibial spurs suggest a close relationship with *Myrtopsen*; these characters are also typical of the Figitidae (sensu lato), suggesting that *Euceroptres* and *Myrtopsen* are not closely related to the other genera of Inquillines. At present, however, it seems better to keep these genera in the Cynipidae.

Myrtopsen Rubsaamen

Figures 6, 16, 17.

Myrtopsen Rubsaamen 1908: 136.Type species: *Myrtopsen mayri* Rubsaamen. Monobasic.

FEMALE. Length 1.9 - 2.4 mm. Black; head sometimes dark brown; antenna beyond scape and legs beyond coxae usually brown. Head semilunar (dorsal view), not expanded behind eyes, frons bulging; subantennal ridges, radiating striae, median protuberance, frontal ridges, frontal field absent (Fig. 6); clypeus trapezoidal, lateral margins diverging anteriorly, ventral margin arcuate; genal carina absent; palpal formula 4 - 3; antenna weakly clavate, with 13 antennomeres. Pronotum (Figs. 16, 17) irregularly rugulo-areolate, with strong anterior pilosity; pronotal plate absent, lateral carinae strongly developed. Mesoscutum (Fig. 16) weakly to strongly transversely rugulose, anterior margin evenly arcuate, not produced anteriorly; notauli complete, often greatly widened posteriorly; median groove absent to complete and strong; anterior lines weakly impressed; lateral lines weakly impressed. Mesoscutellum rugose and areolate; foveae well defined, shining smooth; septum broad, distinct. Mesopleuron (Fig. 17) weakly aciculate, mesopleural groove present; metapleuron distinct, posterior margin curved; propodeal carinae strong, divergent ventrally, strongly bent medially, with lateral carinae, convergent dorsally; dorsal surface shining smooth,

glabrous; propodeal pilosity present laterally, absent medially; supracoxal carina very weak to absent; petiole smooth. Mesosoma long as head plus mesosoma; S2 not expanded, smooth; T2 and T3 completely fused and without trace of a suture, covering entire metasoma; anterior pilosity strong, moderately weak pubescence; posterior margin of T2+3 not excised; posterior third of T2+3 punctate; T4 abruptly deflexed; hypopygial spine very weakly developed. Forewing hyaline, about 0.95 of body length; radial cell closed, length to width ratio = 2.5; radius weakly arcuate; areolet absent; proximal hamulus weakly bifid, ectal margins parallel. Tibial spurs strongly developed, tarsal claw weakly toothed.

MALE. Differs from female as follows: Length 2.1 - 2.4 mm; antenna with 14 antennomeres; A3 weakly curved, weakly expanded distally; T2+3 shorter than head plus mesosoma.

BIOLOGY. Species of *Myrtopsen* are inquillines in galls on *Mimosa* (Legumaceae) and *Eugenia* and *Blepharocalyx* (Myrtaceae) (Weid 1926; Diaz 1980). The host gall for *M. mimosae* Weid is caused by a species of *Tanaostigmodes* sp. (Hymenoptera: Eupelmidae, Tanaostigmatinae) on *Mimosa*. Other host gall inducers are unknown but are probably Brachyscelidi-phagine chalcids (Hymenoptera: Pteromalidae). All species have 1 generation per year and spend one winter in the gall (Weid 1926; Diaz 1980). It appears that species of *Myrtopsen* greatly modify their host gall; there are numerous

inquiline larvae in each gall that is attacked.

REMARKS. Members of the genus *Myrtopsen* are easily distinguished from other inquiline Cynipidae by the following characters: head without median protuberence or radiating striae, clypeus trapezoidal; pronotal lateral carinae well developed; mesopleural groove present; propodeal carinae bent; T2+3 fused in both sexes, anterior pubescence sparse, with dense pilosity.

Myrtopsen contains five species that are distributed throughout the New World; four species are Neotropical and one is known from the Southwestern United States. This distribution is unusual, as no other inquiline cynipid is known from the Neotropical region. Weld (1926) described *M. mimosae*, the only Nearctic species; Diaz (1980) has revised the Argentinian species. (See Section 4.1 for a list of included species).

Myrtopsen appears to be a highly apomorphic genus which is easy to diagnose but difficult to relate to the other inquiline Cynipidae. Different characters indicate different, contradictory relationships. All species of *Myrtopsen* have T2+3 fused and have transverse rugulae on the mesoscutum, suggesting a close relationship to *Synergus* + *Saphonecrus* + *Synophrus*. However, the dense pilosity on the anterior of T2+3 and the weakly bifid proximal hamulus suggests a close relationship to *Ceroptres* and *Periclistus*. Furthermore, *Myrtopsen* has a trapezoidal clypeus, well

developed lateral carinae on the pronotum, the petiole is smooth, and the metatibial spurs are well developed; these characters show a close relationship to *Euceroptres* and also a closer relationship to the *Fligitidae* than to the other *Cynipidae*. It seems better to maintain the current status of these genera on the basis of the presence of the hypopygial spine and weakly toothed tarsal claw.

Periclistus Foerster

Figures 7, 18, 19, 29, 32.

Periclistus Foerster 1869: 332, 337.

Type species: *Aylax caninae* Hartig. Original designation.

FEMALE. Length: 1.2 - 3.5 mm. Black; rarely brown or rufopiceus; antenna and legs usually amber, sometimes brown to black. Head (Fig. 7) subquadrate, not expanded behind eyes; radiating striae weak to moderately developed, absent medially; median protuberance present, often strong; subantennal ridges, frontal ridges, frontal field absent; clypeus shield shaped, lateral margins usually distinct and parallel; genal carina absent; palpal formula 5 - 3, maxillary palpomeres 1 and 2 fused; antenna filiform, with 12 antennomeres. Pronotum often with weak posteroventral rugulae; anterior pilosity present, usually strong; pronotal plate present, weakly developed. Mesoscutum (Fig. 18) granulate of coriaceous; anterior margin evenly arcuate or weakly produced anteriorly; notauli complete to almost absent, often expanded in posterior third of mesoscutum; median groove sometimes complete (weak crease in anterior half of mesoscutum), usually incomplete or absent; anterior lines weakly impressed or weakly raised; lateral lines weakly impressed or weak creases. Mesoscutellum rugose to rugo-areolate, never with posterior carina; foveae usually strong, well defined, closed posteriorly, shining smooth

(sometimes with setigerous tubercles); septum strong, usually narrow, sometimes broad. Mesopleuron (Fig. 19) usually shining smooth, sometimes aciculate, usually with dent; subalar triangle with conspicuous row of setigerous punctures (absent in other genera); mesopleural groove absent; metapleuron moderately distinct, posterior margin curved; supracoxal carina weakly to moderately developed; propodeal carinae straight; moderate to strong, usually shagreened and pubescent; propodeal pilosity usually present laterally, frequently present medially; supracoxal carina weak to strong; petiole striate. Metasoma short, not compressed laterally; S2 not expanded dorsally or ventrally, smooth (Fig. 29); T2 and T3 completely fused, sometimes with a trace of suture; anterior pilosity present, moderately strong; posterior margin of T2+3 never excised, often punctate. Forewing hyaline, about 1.0 - 1.1 of body length; radial cell open, length to width ratio = 2.6 - 3.1; areolet equilateral or elongate; proximal hamulus (Fig. 32) strongly bifid, ectal margins divergent. Tibial spurs weakly developed; tarsal claw with well developed toothed.

MALE. Differs from female as follows: length: 1.1 - 3.5 mm; antenna with 14 antennomeres; A3 often strongly notched and curved, sometimes weakly curved; T2 and T3 not fused.

BIOLOGY. Members of *Periclistus* areinquillines in the galls of *Diplolepis* Fourcroy on *Rosa* (Rosaceae). Many species greatly modify the host gall; this is especially true for

leaf galls (Shorthouse 1975). Most stem galls are not modified, at least externally, except the galls of *Diplolepis nodulosa* (Ashmead) and *D. inconspicua* (Dallay and Campbell). These galls are normally monothalms and are slight swellings at or near the tip of a rose twig. When these galls are attacked by *Periclistus* spp. they are greatly expanded and the plant epidermis covering the gall becomes greyish (Dallay and Campbell 1973). Each species of *Periclistus* has a single generation per year.

REMARKS. Members of *Periclistus* can be distinguished from all other inquiline Cynipidae by the following characters: S2 smooth and crescent shaped; genal carina absent; maxillary palp with five palpomeres; ventral margin of subalar triangle with conspicuous row of setigerous punctures; T2+3 fused in female, separate in male; proximal hamulus strongly bifid, ectal margins of points divergent. Members of *Periclistus* are most similar to *Synophromorpha* but differ by the following characters: male A3 often strongly curved, strongly notched, expanded distally; radiating striae usually weaker; mesoscutum coriaceous; notauli usually much weaker anteriorly, not suddenly widened posteriorly; radial cell open; female T2+3 usually without trace of suture.

The Nearctic members of *Periclistus* are revised in Section 3. (See Section 4.1 for a complete list of included species.)

Saphonecrus Dalla Torre and Kieffer

Figures 20, 21.

Saphonecrus Dalla Torre and Kieffer 1910: 605

Type species: *Synergus connatus* Hartig. Original designation.

FEMALE. Length 1.2 - 3.8 mm. Similar to *Synergus* except: frontal ridges absent; antenna with 13 - 14 antennomeres; mesoscutum usually with transverse rugosity, rarely coriaceous or shining smooth; median groove absent; mesoscutellar foveae indistinct, rugulose, forming a crescent shaped depression (Fig. 20); septum very weak to absent; propodeal carinae strong; metasoma never knifelike, usually shorter than head plus mesosoma; T2+3 never excised posteriorly or laterally; radial cell open; tarsal claws simple (Palearctic species) or strongly toothed (Nearctic species).

MALE: Differs from *Synergus* similarly to female except: antennae 15 segmented.

BIOLOGY. Members of *Saphonecrus*, as far as is known, are inquillines in galls on *Quercus* spp. All species appear to be single brooded and emerge after one winter in the gall.

REMARKS. The genus *Saphonecrus* is most similar to *Synergus*, from which it differs by the following characters: radial cell open; head with frontal field but without frontal ridges; foveae indistinct, rugulose, merging together to form a crescent shaped depression. These characters appear to be apomorphic and may define *Saphonecrus* as a monophyle-

tic taxon, probably derived from *Synergus* Section I Mayr. However, this would mean that *Synergus* is defined by symplesiomorphy and therefore would be a paraphyletic assemblage. It appears that *Saphonecrus* is a specialized lineage within *Synergus*, at least as the latter genus is currently understood. Until *Synergus* is thoroughly revised, it is impossible to determine whether *Saphonecrus* should be maintained. Thus, at this time, it seems better to maintain *Saphonecrus* as a valid genus. Weld (1926) has presented a key to the Philippine and some Nearctic species of *Saphonecrus*. (See Section 4.1 for a list of included species).

Synergus Hartig

Figures 8, 22, 23, 30.

Synergus Hartig 1840: 186.

Type species: *Synergus vulgaris* Hartig. Designated by
Foerster 1869.

Sapholytus Foerster 1869: 332, 337; Dalla Torre and Kieffer
1910: 608.

Type species: *Sapholytus apicalis* Hartig. Monobasic.

FEMALE. Length: 1.2 - 7.0 mm. Black, rufous, or yellow, usually variegated; antenna, leg beyond coxae usually brown to yellow, rarely black. Head (Fig. 8) ovoid trapezoidal, genae moderately expanded behind eyes; genal carina strong; radiating striae strong, covering entire frons and ventral half of gena; median protuberance absent to weakly developed; 1-3 frontal ridges present or absent, frontal field present; clypeus indistinct, shield shaped; lateral margins indistinct; palpal formula 4-3; antenna with 13-15 antennomeres, filiform. Pronotum bulging dorsolaterally, dorso-median margin deflexed, posterolateral area weakly and irregularly rugulose to strongly transversely rugulose; anterior pilosity absent; posterior part of pronotal plate absent. Mesoscutum (Fig. 22) with weak to strong transverse rugae, anterior margin produced; notauli usually complete, moderately strong, never abruptly widened in posterior third, rarely incomplete; median groove usually absent, sometime present in posterior third; anterior lines pre-

sent, weakly impressed; lateral lines present, weakly impressed. Mesoscutellum rugulose to rugo-areolate, disc frequently with irregular posterior carina; foveae usually narrowed and often open posteriorly, always opaque, never shining smooth; lateral bars weak; septum weak to moderately strong. Mesopleuron (Fig. 23) aciculate to strongly striate, often smooth dorsally; mesopleural groove absent. Metapleuron distinct, posterior margin usually straight. Propodeal carinae straight, shagreened, often very strong, pubescent, rectangular in cross-section; propodeal pilosity absent; supracoxal carina strong, complete, usually running straight to spiracular flap. Petiole striate or sulcate. Metasoma usually as long as head plus mesosoma, often compressed laterally, sometimes knifelike; S2 (Fig. 30) expanded dorsally and ventrally, dorsal portion sulcate; T2 and T3 completely fused, without trace of a suture, without pilosity, with only a few scattered anterolateral hairs, posterior margin often deeply excised; T3 with posterior third frequently punctate. Forewing hyaline, about 1.0 - 1.1 of body length; radial cell closed, length to width ratio = 2.3 - 3.1; areolet usually elongate, sometimes equilateral or absent. Proximal hamulus simple. Tibial spurs weakly developed; tarsal claws simple, weakly toothed (Palearctic species) or strongly toothed (Nearctic species).

MALE. Differs from female as follows: length 1.0 - 5.1 mm; antenna with 14 - 15 antennomeres; A3 weakly curved, smooth and flattened on eudorsal surface; T2+3 not excavated dorsally; metasoma shorter than head plus mesosoma.

BIOLOGY. Member of *Synergus* attack galls on *Quercus* spp. except for *S. castanopsidis* (Beutenmueller) which is known from the galls of *Dryocosmus castanopsidis* (Beutenmueller) on *Castanea* sp. Also, an unnamed species of *Synergus* from Japan has been reared from galls of *Dryocosmus kuruphillus* Yasumatsu on *Castanea* (Otake et al. 1982). All species are thought to be phytophagous, although Triggerson (1914) reported *Synergus erinacei* Gillette was also entomophagous on the larvae of *Acraspis* (= *Dryophanta*) *erinacei* (Mayr) and associated chalcidoid parasites. The majority of species are single brooded, although many European species have two generations per year (Eady 1952) and some Nearctic species may take up to six years to emerge from the gall (Ritchie, unpublished).

REMARKS. Members of *Synergus* can be distinguished from all other genera of Inquiline gall wasps by the following characters: head usually with frontal field and ridges; mesopleuron longitudinally striate; 82 expanded and sulcate; T2+3 fused without visible suture in both sexes radial cell closed. The Nearctic species of *Synergus* have the tarsal claw strongly toothed, whereas the Palearctic species have simple tarsal claws (Eady and Quinlan 1963; Quinlan 1968).

The simple tarsal claws of the Palearctic species appears to be a secondary loss of the claw.

There are 106 described species of *Synergus* distributed throughout the Holarctic region. Individual species are restricted to either the Palearctic region or the Nearctic region. Currently, it is impossible to identify any Nearctic species of *Synergus* with any degree of certainty. Gillette (1896) revised the 24 Nearctic species known at that time and an additional 29 species have been described since then (Burks 1979). Gillette (1896) divided the Nearctic species of *Synergus* into three sections, based on the number of female antennomeres (13, 14, or 15). Gillette's distinction between sections appears to be one of convenience and has little phylogenetic meaning.

Mayr (1872) divided the European species of *Synergus* into two sections. Section I contains species that have a single generation per year; these species are characterized by frontal ridges being absent and female T2 + 3 at most with a small posterodorsal triangle of punctation (Eady 1952). Species in Section II have two generations per year and are characterized by frontal ridges present and female T2 + 3 having a broad posterior band of punctation (Ross 1951). Section II appears to be defined by synapomorphy while Section I is plesiomorphic. Part of the Palearctic fauna has been studied by Tavares (1920), Ross (1951), Eady (1952), and Wiebes-Rijks (1979); however, the Palearctic

fauna is still poorly known.

The genus *Synergus* is most similar to *Saphonecrus* and *Synophrus*. It differs from both genera by having the radial cell closed. Furthermore, *Saphonecrus* never has frontal ridges and *Synophrus* has the dorsal portion of S2 medially striate. It appears that these characters are plesiomorphic and therefore should not be used to justify the separation of these genera from *Synergus*. Eady and Quinlan (1963) questioned the validity of maintaining *Saphonecrus* but declined to synonymize the two genera.

Synophromorpha Ashmead

Figures 9, 24, 25.

Synophromorpha Ashmead 1903: 145.

Type species: *Synophrus sylvestris* Osten Sacken. Designated here.

FEMALE. Length: 1.2 - 3.5 mm. Black; rarely brown or rufopiceus; antenna and legs usually amber, rarely brown. Head (Fig. 9) subquadrate, not expanded behind eyes; radiating striae often strong laterally, absent medially; median protuberance present, usually strong; frontal field, frontal ridges, subantennal ridges absent; clypeus shield shaped, lateral margins usually distinct and parallel; genal carina absent; palpal formula 5 - 3, maxillary palpo-meres 1 and 2 fused; antenna filiform, with 12 antenno-meres. Pronotum coriaceous; anterior pilosity present, usually strong; pronotal plate present, moderately developed, not expanded laterally. Mesoscutum (Fig. 24) shining smooth to graniculate, with strong setigerous pits anteriorly (absent in other genera); anterior margin produced anteriorly; notauli complete, strong to very strong, usually abruptly expanded in posterior third of mesoscutum; anterior pits present; median groove absent to very short; anterior lines weakly impressed; lateral lines weakly impressed. Mesoscutellum (Fig. 24) rugo-areolate, without well developed posterior carina; foveae strong, large, well defined, closed posteriorly, shining smooth; septum strong, long.

usually narrow. Mesopleuron (Fig. 25) shining smooth to graniculate, usually with dent; mesopleural groove absent. Metapleuron distinct, posterior margin curved; supracoxal carina angulate, strong ventrally, weak dorsally, ventral portion parallel to hind margin of mesoscutum; propodeal carinae straight; moderate to strong, usually shagreened and pubescent; propodeal pilosity usually present laterally, frequently present medially; petiole striate. Metasoma shorter than head plus mesosoma, not compressed laterally; S2 not expanded dorsally or ventrally, smooth; T2 and T3 completely fused, usually with trace of a suture; anterior pilosity present, moderately strong; posterior margin of T2+3 never excised; T2+3 sometimes with small postero-dorsal triangle of punctation. Forewing hyaline, about 1.0 - 1.1 of body length; radial cell open, length to width ratio = 2.6 - 3.1; areolet equilateral or elongate; proximal hamulus strongly bifid, ectal margins divergent (as in Fig. 32). Tibial spurs weakly developed; tarsal claw with well developed tooth.

MALE. Differs from female as follows: length: 1.1 - 3.5 mm; antenna with 14 antennomeres; A3 weakly curved, broadly notched, weakly expanded distally; T2 and T3 not fused.

BIOLOGY. Members of *Synophromorpha* areinquillines in the galls of *Diastrophus* Hartig on *Rubus* (Rosaceae) (Weid 1952a, b); Osten Sacken (1863) has also reared specimens from galls of *Diplolepis ignota* (O. S.) on *Rosa* (Rosaceae).

Osten Sacken (1863) reared *Diastrophus nebulosus* O. S. and *S. sylvestris* (O. S.) from the same gall. Similarly, I have reared *Diastrophus turgidus* Gillette and *S. rubi* Weld from the same gall. Hence, it appears that unlike the species of *Periclistus*, members of *Synophromorpha* do not appear to have a deliterious effect on the host gall inducer. However, the galls of *Diastrophus* spp. are polythalmous and the biology of *Synophromorpha* spp. has not been studied in detail. It is possible that some gall inducing larvae are affected by the presence of the inquiline while others are not.

REMARKS. Members of *Synophromorpha* can be distinguished from all other inquiline Cynipidae by the following characters: mesoscutum smooth to graniculate, with strong anterior setigerous pits; notauli very strong, complete as distinct grooves; maxillary palp with five palpomeres, basal two palpomeres fused; genal carina absent; S2 smooth and crescent shaped; T_2+3 fused in female, separate in male; radial cell open; proximal hamulus strongly bifid, ectal margins of points divergent.

Synophromorpha is most similar to *Periclistus*; the latter genus differs as follows: radial cell closed, the notauli are much weaker; mesoscutum coriaceous, without anterior setigerous pits; pronotal plate more strongly developed. *Synophromorpha* is superficially similar to *Synophrus* and *Saphonecrus* in that the radial cell is open; however, these genera differ as follows: frontal field

present, genal carina^o present, maxillary palpi with four palpomeres, mesoscutum with transverse rugulae, mesopleuron often striate, S2 expanded (dorsally and ventrally), S2 sulcate laterally, and proximal hamulus simple.

Ashmead (1903) erected the genus *Synophromorpha* for *S. salicis*, a species that was supposed to have been reared from a *Diastrophus* gall on *Smilax*. However, a description of *S. salicis* was never published and specimens of *S. salicis* have never been found (Weld 1952a, b; Burks 1979). *Synophromorpha salicis* must be regarded as a nomen nudum and the designation of *S. salicis* as the type-species of *Synophromorpha* cannot be valid. Thus, *Synophromorpha* must be regarded as being described without included species.

Weld³ (1952a) was the first to include species in the genus; he transferred *Synophrus sylvestris* Osten Sacken to *Synophromorpha* and described *S. rubi* and *S. terricola*. I now designate *Synophrus sylvestris* Osten Sacken as the type-species for the genus. This was the first described species and it appears that it was the one on which Weld based his conception of the genus.

The three described members of *Synophromorpha* (*S. rubi*, *S. sylvestris*, and *S. terricola*) are distributed throughout the eastern half of the Nearctic region; no species is known from the Palearctic region. Recently, an undescribed species has been collected in Vera Cruz, Mexico. Previously, the only inquillines known from Mexico were

members of *Synergus* and *Cenoptres*. This species is also interesting in that appears to be the sister species to the remaining species of *Synophromorpha*.

Synophrus Hartig

Figures 10, 11, 26, 27, 31.

Synophrus Hartig 1843: 411.Type species: *Synophrus politus* Hartig. Monotypic.

FEMALE. Differs from *Synergus* as follows. Length: ~~3.5~~ 5.5 mm. Palearctic species: black; antennae, metasoma, coxae, trochanters, femora brown; Nearctic species: variegated yellow, black and brown; antenna, legs beyond coxae brown to amber. Head with 3 incomplete frontal ridges (Nearctic species) (Fig. 10) or absent (Palearctic species) (Fig. 11), frontal field present; antenna filiform, with 13 - 15 antennomeres. Propodeal carinae straight, divergent (Nearctic species) or parallel (Palearctic species), very strong, smooth; supracoxal carina weak, incomplete; subspiracular carina and tubercle absent. S2 (Fig. 31) expanded dorsally and ventrally, dorsal portion striate medially and sulcate laterally; T2 and T3 completely fused, without trace of suture, covering entire dorsal aspect of metasoma, posterior margin not excised. Forewing hyaline, about 0.9 of body length; radial cell open, length to width ratio = 3.3; areolet elongate. Proximal hamulus simple. Tibial spurs weakly developed; tarsal claws simple (Nearctic species) or with a well developed tooth (Palearctic species).

MALE. Differs from female as follows: length 3.5 - 5.5 mm; antenna with 15 antennomeres; A3 weakly curved, flattened and smooth on eudorsal surface, not expanded distally;

metasoma shorter than head plus mesosoma.

BIOLOGY. All species, as far as is known, are inquillines in galls on *Quercus*. The two Palearctic species are single brooded and spend one winter in the gall.

REMARKS. Members of *Synophrus* are recognised by the following combination of characters: 82 expanded dorsally and ventrally, dorsal portion smooth medially; radial cell open. The genus *Synophrus* is most similar to *Synergus* and *Saphonecrus* but differs in the characters given above. Hartig (1843) and most subsequent authors believed that *Synophrus* sp. were true gall inducers. Weld (1952b) believed that these species were inquillines and based his classification on the structure of the prothorax and the metasoma. Three species have been placed in the genus: *S. politus* Hartig, *S. olivieri* Kieffer, and *S. mexicanus* (Gillette). The two former species are known from the Palearctic region whereas *S. mexicanus* is known from the Nearctic region.

The three species of *Synophrus* are a homogeneous assemblage and do not appear to be closely related to each other. Gillette (1896) originally placed *S. mexicanus* in *Synergus* but Weld (1952a) transferred it to *Synophrus* on the basis of the open radial cell. However, *S. mexicanus* appears to be very closely related to several species of *Synergus*; synapomorphies for this relationship are: frontal ridges present, body variegated yellow and black, T2+3 with broad posterior band of punctures. Thus, with the exception

of the open radial cell, *S. mexicanus* would be placed in *Synergus* Section II Mayr. Specimens of *S. politus* Hartig show several similarities to *Synergus* Section I Mayr. Thus, it appears that *Synophrus* is polyphyletic, with the three species representing different lineages within *Synergus*. However, until *Synergus* can be revised, it seems better to maintain the current classification.

FIGURES 4 - 9

Figure 4. *Ceroptres*, anterior view of the head. Note the incomplete subantennal ridges below the antennal sockets and weak radiating striae.

Figure 5. *Euceroptres*, anterior view of the head. Note the trapezoidal clypeus and the absence of radiating striae on the frons.

Figure 6. *Myrtopsen*, anterior view of the head. Note the trapezoidal clypeus and the absence of radiating striae on the frons.

Figure 7. *Periclistus*, anterior view of the head. Note the "shield shaped" clypeus and the distinct radiating striae on the frons are absent medially.

Figure 8. *Synergus*, anterior view of the head. Note the frontal ridges between antennal sockets and ectal margin of posterior ocelli, the "shield shaped" clypeus, and the distinct radiating striae covering the entire frons.

Figure 9. *Synophnomorpha*, anterior view of the head. Note the "shield shaped" clypeus and the very strong radiating striae which are absent medially.

FIGURES 10 - 15.

Figure 10. *Synophrus mexicanus*, anterodorsal view of frons. Note the weak frontal ridges and the distinct frontal depression.

Figure 11. *Synophrus politus*, anterodorsal view of frons. Note the absence of frontal ridges.

Figure 12. *Ceroptres*, dorsal view of mesonotum.

Figure 13. *Ceroptres*, lateral view of mesopleuron.

Figure 14. *Euceroptres*, dorsal view of mesonotum.

Figure 15. *Euceroptres*, lateral view of mesopleuron.

FIGURES 16 - 21.

Figure 16. *Myntopsen*, dorsal view of mesonotum.

Figure 17. *Myntopsen*, lateral view of mesopleuron.

Figure 18. *Periclistus*, dorsal view of mesonotum.

Figure 19. *Periclistus*, lateral view of mesopleuron.

Figure 20. *Saphonecrus*, dorsal view of mesonotum.

Figure 21. *Saphonecrus*, lateral view of mesopleuron.

FIGURES 22 - 27.

Figure 22. *Synergus*, dorsal view of mesonotum.

Figure 23. *Synergus*, lateral view of mesopleuron.

Figure 24. *Synophromorpha*, dorsal view of mesonotum.

Figure 25. *Synophromorpha*, lateral view of mesopleuron.

Figure 26. *Synophrus*, dorsal view of mesonotum.

Figure 27. *Synophrus*, lateral view of mesopleuron.

FIGURES 28 - 32.

Figure 28. *Ceroptres*, lateral view of S2.

Figure 29. *Periclistus*, lateral view of S2.

Figure 30. *Synergus*, lateral view of S2.

Figure 31. *Synophrus*, lateral view of S2.

Figure 32. *Periclistus*, proximal hamulus of hind win.

2.5 Evolution of the Genera of Inquiline Cynipidae.

A phylogenetic analysis of evolutionary relationships between the genera of Inquiline Cynipidae is complicated by two factors. One is that the higher classification of the Cynipoidea has not been satisfactorily determined and hence the sister group to the Cynipidae is not known. Without a well defined sister-group, it is difficult to polarize characters. Secondly, many characters appear to have evolved several different times. These characters tend to confuse any analysis and weaken the reliability of any phylogenetic hypothesis. Similarly, many of the higher taxa within the Cynipoidea are distinguished by autapomorphies; these characters give little information about the relationships between these taxa.

Several authors have suggested different sister groups for the Cynipidae. Eady and Quinlan (1963) suggest that the Eucollidae are the sister group to the Cynipidae. Weld (1952b) placed the Pycnostigmatidae immediately before the Cynipidae, implying a close relationship. Nordlander (1982) believes the Pycnostigmatidae are specialized *Synergus* (Cynipidae) and suggests that the Charipidae are the sister group for the Cynipidae. My preliminary studies indicate that the probable sister group to the Cynipidae is composed of Figitidae and Eucollidae and Charipidae (See Appendix I).

Phylogenetic methods (Cladistics) as defined by Watrous and Wheeler (1981) have been used here but with certain reservations. Unfortunately, characters do not always evolve in clear patterns. Many characters have evolved several times, apparently for a number of reasons (eg. functional adaptation, multiple losses, convergent or parallel evolution). If a character has multiple states in both the in-group and the out-group, it becomes difficult to determine the polarity of the character (ie. plesiomorphic vs. apomorphic) and it becomes necessary to examine other taxa. However, the usefulness of the character has been decreased, as it has been shown to have evolved more than once. Strict phylogenetic considerations would cause this character to be rejected. Many of the characters used here are of this type. Most characters appear in other families of the Cynipoidea and many are relatively simple. However, the lack of more reliable characters means that these weaker characters must be used. This method of analysis is more subjective than more rigorous methods, but is the only means of elucidating evolutionary relationships.

Characters were surveyed throughout the gall inducing Cynipidae and the remaining Cynipoidea. The distribution of characters throughout the gall inducing Cynipidae was used (when possible) in determining apomorphic characters. Characters found useful for determining the phylogenetic relationships between inquiline genera are listed in Table 1;

the distribution of characters within the genera of Inquilline Cynipidae are tabulated in Table 2. These characters were also assessed for a degree of reliability (i.e. number of "independent" occurrences) throughout the Cynipoidea. The distribution of these characters is recorded in Table 3. Very few characters were found to be unique to the Cynipidae and none were unique to all the Inquilline genera. Characters used to define lineages are placed in the text in parentheses and are discussed when necessary. Three alternative phylogenetic hypotheses are depicted in Figures 33, 34, 35.

The Cynipidae can be defined as a monophyletic lineage by two strong synapomorphies: 1) phytophagy (1b); and 2) the presence of the hypopygial spine on the female metasoma (35b). All other members of the Cynipoidea are parasitic and phytophagy occurs only rarely in other related superfamilies (Chalcidoidea, Proctotrupoidea, Ichneumonoidea). Hence, it appears that phytophagy is a derived behavior. The hypopygial spine is found nowhere else in the Hymenoptera and is a unique morphological synapomorphy that can be used to define the Cynipidae. Kinsey's (1920c) hypothesis on the evolutionary relationships of the gall inducing genera of Cynipidae is followed here (Fig. 1).

Several authors (eg. Ashmead 1895, Burks 1979) place the Inquillines in a separate subfamily from the gall inducers. This implies that the Inquillines and gall inducers

are sister groups. Since the survival of the Inquillines are dependant on the gall inducers, one would expect to find Inquillines in the galls of the Aulacine genera, which are the most primitive of the gall inducers. However, Inquillines are found only in the galls of *Diastrophus*, the Rhoditini, and the Cynipini. Hence, biological data indicates that the Inquillines are derived from one of these taxa.

The Rhoditini and Cynipini are sister groups and together form a monophyletic lineage, which is defined by the pronotum being narrowed medially (15b). This character is not found in any Inquilline genus. Hence, the Inquillines cannot be derived from either an oak or a rose gall inducer, although this does not preclude a sister group relationship between the Inquillines and the Rhoditini + Cynipini.

Amongst the gall formers, the sister group to the Rhoditini and Cynipini is *Diastrophus*, a genus of gall inducers on *Rubus* and *Potentilla* (Rosaceae). This is supported by the presence of the toothed tarsal claw (9b) and host plant relationships, as *Rubus* is closely related to *Rose* (both are members of the Rosaceae). Members of *Diastrophus* induce galls of intermediate complexity to those of the Aulacine genera (relatively simple) and of the Rhoditini and Cynipini (relatively complex) (Kinsey 1920c).

Diastrophus and most Inquillines (except *Myrtoseen* and *Euceroptres*) have a shield shaped clypeus (8b); the presence of a trapezoidal clypeus in *Euceroptres* and *Myrtoseen*

is interpreted as a reversal to the plesiomorphic condition. Also, *Diastrophus*, *Periclistus* and *Ceroptres* have a median protuberance on the frons (8b). The Inquillines are also restricted to attacking galls on *Rubus*, *Rosa* and *Quercus*, which mirrors the host plant relationships of *Diastrophus*, the Rhoditini and Cynipini. Radiating striae on the frons (7b,c) also may be a synapomorphy for *Diastrophus* and the Inquillines, but this character also appears in some Aulacine genera, some Eucollidae and some Figitidae. Thus, it appears that Inquillines are derived from a *Diastrophus*-like ancestor.

Monophyly of the inquilline genera is supported by T3 being expanded, reaching or almost reaching the posterodorsal aspect of the metasoma (33b). This character is unique within the Cynipidae but also occurs in the Figitidae and most Eucollidae. Additional morphological evidence is the reduction of maxillary palpi from five to four palpomeres (five in *Periclistus* and *Synophromorpha*, with palpomeres 1 and 2 fused)(11b, c). A reduction of palpomeres also occurs in the Figitidae, Eucollidae and Charipidae; in these families the labial palpi are also reduced to two palpomeres, a condition not found in the Cynipidae.

Relationships between the genera of Inquilline Cynipidae are not clear due to conflicting morphological data. Three phylogenies (Figs. 33, 34, 35) are suggested, depending on which characters are used to make the initial

split in lineages. Phylogeny 1 (Fig. 33) is derived when the bifid hamulus (38b,c) and loss of the pronotal plate (17b) are emphasized. Phylogeny 2 (Fig. 34) gives emphasis to the fusion of female metasomal tergites 2 and 3 (31c). Phylogeny 3 (Fig. 35) stresses the reduction of the numbers of maxillary palpi (11c) and to host plant relationships (3b,c). Subsequent splits in lineages are justified by other characters (indicated on Figures).

Table 1. Characters found useful for determining relationships within the Cynipidae. a = hypothesized plesiomorphic state; b - d = apomorphic states.

NO.	CHARACTER	CHARACTER STATE
1	BIOLOGY:	a = Parasitic. b = Phytophagous.
2	BIOLOGY:	a = Gall inducer. b = Inquiline.
3	HOSTPLANT:	a = Compositae, Herbaceous plants. b = Rosaceae. c = Fagaceae. d = Legumaceae
4	HEAD, SHAPE:	a = Normal. b = Expanded behind eyes.
5	HEAD, FIELD:	a = Absent. b = Present.
6	HEAD, RIDGES:	a = Absent. b = Present.
7	HEAD, STRIAE:	a = Absent. b = Present laterally. c = Entire.
8	HEAD, PROTUBERANCE:	a = Absent. b = Present.
9	CLYPEUS SHAPE:	a = Trapezoidal. b = Wide Shield-shape. c = Narrow.
10	GENAL CARINA:	a = Absent. b = Present.
11	MAXILLARY PALPS:	a = 5 palpomeres. b = 5 Palpomeres, basal 2 fused. c = 4 palpomeres.
12	ANTENNA, ♀:	Number of antennomeres greater than 10.
13	ANTENNA, ♂:	Number of antennomeres greater than 10.
14	A3, ♂:	a = Weakly curved. b = Strongly curved and notched.

Table 1 (cont.). Characters found useful for determining relationships within the Cynipidae. a = hypothesized plesiomorphic state; b - d = apomorphic states.

NO.	CHARACTER	CHARACTER STATE
15	PRONOTUM, L/H:	a = Broad. b = Narrow.
16	PRONOTAL PILOSBITY:	a = Absent. b = Present.
17	PRONOTAL PLATE:	a = Present, not expanded laterally. b = Present, expanded laterally. c = Absent (non-homologous with d) d = Absent (non-homologous with c)
18	MESOSOCUTAL SCULPT.:	a = Transverse rugae absent. b = Transverse rugae present.
19	MESOSOCUTUM, ANTERIOR MARGIN:	a = Arcuate. b = Produced.
20	NOTALLI:	a = Narrow. b = Broad.
21	MESOPLEURON:	a = Smooth. b = Aciculate. c = Striate. d = Rugulose.
22	MESOPLEURAL GROOVE:	a = Absent. b = Present.
23	FOVEAE:	a = Normal, shining. b = Narrowed, opaque. c = Absent.
24	SEPTUM:	a = Strong. b = Weak. c = Absent.
25	METAPLEURON:	a = Curved. b = Straight.
26	PROPODEAL PILOSBITY:	a = Absent. b = Present.
27	PROPODEAL CARINAE:	a = Straight. b = Curved.

Table 1 (cont.). Characters found useful for determining relationships within the Cynipidae. a = hypothesized plesiomorphic state; b - d = apomorphic states.

NO.	CHARACTER	CHARACTER STATE
28	METASOMA:	a = Not compressed laterally. b = Compressed laterally.
29	S2, SCULPT:	a = Smooth. b = Striate. c = Sulcate (at least laterally).
30	S2, LENGTH:	a = Short. b = Expanded.
31	T2, T3, ♀:	a = Separate, connate suture. b = Separate, oblique suture. c = Fused.
32	T2, T3, ♂:	a = Separate. b = Fused.
33	T3, ♀:	a = Not expanded. b = Expanded.
34	T2, PILOSITY:	a = Absent. b = Present, weak. c = Present, strong.
35	HYPOPYGIUM, ♀:	a = Without spine. b = With spine.
36	HYPOPYGIAL SPINE:	a = Weak. b = Ploughshare shaped. c = Strong, with ventral setae.
37	RADIAL CELL:	a = Closed. b = Open, short. c = Open, elongate.
38	HAMULUS:	a = Simple. b = Weakly bifid. c = Strongly bifid.
39	TARSAL CLAW:	a = Absent. b = Present, weak. c = Present, strong. d = Secondarily lost (some species).

Table 2 (cont.). Distribution of characters (from Table 1) throughout the Nearctic genera of Inquiline Cynipidae. (See Table 1 for an explanation of characters).

NO.	GALL INDUCERS (OUT-GROUP)				INQUILINES (IN-GROUP)							
	A U L A C I N E G E N E R A	D I A S T R O P H U S	D I P L O L E P I S	C Y N I P I N I	C E R O P T R E S	P E R I C L I S T U S	S Y N O P H R O M O R P H A	M Y R T O P S E N	E U C E R O P T R E S	S Y N O P H R U S	S Y N E R G U S	S A P H O N E C R U S
26	a	b	a	a	a	b	b	b	a	a	a	a
27	a	a	a	a	a	a	a	b	a	a	a	a
28	a	a	a, b	a, b	a	a	a	a	a	b	b	b
29	a	a	a	a	a, b	a	a	a	a	c	c	c
30	a	a	a	a	a	a	a	a	a	b	b	b
31	a	a	a	a	a	c	c	c	b	c	c	c
32	a	a	a	a	a	a	a	b	a	b	b	b
33	a	a	a	a	b	b	b	b	b	b	b	b
34	a, b	a	a	a	c	b	b	c	a	a	a	a
35	b	b	b	b	b	b	b	b	b	b	b	b
36	a	a	b	c	a	a	a	a	a	a	a	a
37	a, b	b	b	c	a	a	b	a	a	b	a	b
38	a	a	a	a	b	c	c	b	a	a	a	a
39	a	c	d	b-d	c	c	c	b	b	c	c, d	c, d

Table 3. Distribution of characters 1 - 39 (from Table 1) throughout the other families of Cynipoidea. (See Table 1 for an explanation of characters)

NO.	I B A L I D A E	L I O P T E R I D A E	F I G I T I N A E	A N A C H A R I T I N A E	A S P I C E R I N A E	E U C O I L I D A E	C H A R I P I D A E
1	a	a	a	a	a	a	a
2	NA	NA	NA	NA	NA	NA	NA
3	NA	NA	NA	NA	NA	NA	NA
4	b	b	b	b	b	a	a
5	b	a	a	a	a, b	a	a
6	b	a	a	a, b	a, b	a	a
7	a	a	a	a	a	a	a
8	a	a	a	a	a	a	a
9	a	a	a	a	a	a	a
10	b	b	b	a	b	a	a
11	a	a	c	c	c	c	c
12	3	2	3	3	3	3	3
13	4	4	4	4	4	5	3-4
14	a	a	a	a	a	a	a, b
15	a	a	a	a	a	a	a
16	a	a	a, b	a	a	a, b	a
17	a	a	a	a	a	a	a
18	b	a, b	a	a	a	a	a
19	b	b	b	b	b	b	a, b
20	a	a	a, b	a, b	a, b	a	a
21	a	a	a	a	a, b	a, b	a
22	a	a	a	a	a	a, b	a
23	a	a	a	a, b	a	a, b	a, b
24	a	a	a	a	b	a	a, b
25	a	b	a, b	a	a	a, b	a

Table 3 (cont.). Distribution of characters 1 - 39 (from Table 1) throughout the other families of Cynipoidea. (See Table 1 for an explanation of characters)

	I B A L I I D A E	L I O P T E R I D A E	F I G I T I N A E	A N A C H A R I T I N A E	A S P I C E R I N A E	E U C O I L I D A E	C H A R I P I D A E
26	a	a	a	a	a	a	a
27	a	a	a	a	a	a	a
28	a	a, b	a, b	a, b	a, b	b	a
29	a	a, b	a, b	a, b	a, b	a, b	a
30	a	a, b	a, b	b, c	b, c	a, c	a
31	a	a	a	a	a	a, b	a
32	a	a	a	a	a	a, b	a
33	a	a	b	b	b	b	b
34	a	a	a, b	a	a	a, b	a, b
35	a	a	a	a	a	a	a
36	NA	NA	NA	NA	NA	NA	NA
37	a	a, b	a, b	a	a, b	a, b	a, b
38	a	a	a	a	a	a	a
39	a	a	a	a	a	a	a

Fig. 33. Phylogeny 1: possible relationships between the genera of Inquilline Cynipidae. Characters uniting lineages from Tables 1 and 2.

Fig. 34. Phylogeny 2: possible relationships between the genera of Inquilline Cynipidae. Characters uniting lineages from Tables 1 and 2.

Fig. 35. Phylogeny 3: possible relationships between the genera of Inquilline Cynipidae. Characters uniting lineages from Tables 1 and 2.

2

2.6 Discussion and Conclusion.

Although all three phylogenies have some aspects in common, they differ in fundamental ways and have quite different implications. All three phylogenies recognise the close relationship between *Synergus* + *Saphonecrus* + *Synophorus* and also between *Periclistus* + *Synophromorpha*. This is expected, as it has been previously shown that there are very few characters separating these genera. However, the relationship of *Myrtopsen* and *Euceroptres* to the other genera has not been satisfactorily resolved.

Phylogeny 1 (Fig. 33) implies that either T2 and T3 have fused independently in *Periclistus* and the *Synergus* lineage; however, as this is a rather simple character, it is not improbable that this has occurred. The reduction of maxillary palpi in *Ceroptres* and the *Synergus* lineage must have occurred independently. Finally, this hypothesis implies that the plesiomorphic host plant for the Inquillines is *Quercus* and that *Rosa* is the apomorphic host plant. This directly contradicts the polarity of host plant relationships that are shown by the gall inducers (Kinsey 1920c). Since biological data appear to be very important in the systematics of the Cynipoidea, these data must be included in any study on the evolutionary relationships between taxa. Thus, for all these reasons, I do not believe that Phylogeny 1 reflects the actual relationships between the Inquilline genera.

Phylogeny 2 (Fig. 34) assumes the fusion of female metasomal tergites 2 and 3 occurred only once. However, several characters contradict this phylogeny. Phylogeny 2 implies that the bifid hamulus has been lost independently several times. Since this character is relatively simple, it is quite likely that this has occurred. However, the criticisms of Phylogeny 1 regarding host plant relationships and the loss of maxillary palpi also apply to Phylogeny 2.

Phylogeny 3 (Fig. 35) accounts for the observed host plant relationships and also is consistent with the reduction of maxillary palpomeres. However, this hypothesis also implies that female metasomal tergites 2 and 3 have fused independently in *Periclistus* and in the *Synergus* lineage. Similarly, it implies that the bifid hamulus has been gained and then lost. Weld (unpublished) has seen specimens that are intermediate to *Ceroptres* and *Synergus*, giving further support to this relationship. These specimens have all the apomorphic characters of *Synergus* except T2 and T3 are separated by a suture and T2 has an anterior patch of pubescence. Weld placed these specimens in *Ceroptres*; although I have not seen these specimens, I would place them in *Synergus* on the basis of §2 being expanded.

The placement of *Euceroptres* and *Myrtopsen* is problematic. Each genus is quite distinctive yet there are few characters that can be used to relate these genera to the

other Inquillines. Both genera have the clypeus trapezoidal (9a), a character that is plesiomorphic within the Cynipoidea. Also, members of both genera have the hypopygial spine and tarsal claw very weakly developed. Finally, members of both genera have lateral carinae on the pronotum, a character that is more indicative of the Figitidae than of the Cynipidae. These characters indicate that these genera might not be closely related to the other Inquillines. However, each appears to share a number of synapomorphies with some of the other Inquillines. Thus, it is very difficult to determine the relationships of these genera to the other Inquillines.

Euceroptres may be the sister group to *Synergus* + *Synophrus* + *Saphonecrus*, as it shows the following synapomorphies: pronotal plate absent, mesoscutum usually with transverse rugulae, and mesopleuron usually striate. However, this would contradict the direct connection between *Ceroptres* and *Synergus* that is shown by the specimens described by Weld (unpublished). It is possible that if separate T2 and T3 is indeed an apomorphic character, then *Euceroptres* may be the sister group to *Ceroptres*. However, there is little other evidence to support this.

Myrtopsen shares some synapomorphies with *Periclistus* and some with *Synergus*. Like *Periclistus*, *Myrtopsen* has pronotal pilosity (15b), a weakly bifid proximal hamulus, and has anterior pilosity on T2+3; however, like *Synergus*

Myrtopsen has T2+3 fused in males and has transverse rugulae on the mesoscutum.

There are still many unanswered questions regarding the evolutionary relationships between the genera of Inquilline Cynipidae. It is evident that the classification of the Inquillines in a separate subfamily cannot be justified. However, the relationships between the genera of Inquillines are still not totally resolved. This may be due to the lack of knowledge of many species of *Cenoptres* and *Synergus*. Also, the inclusion of Palearctic species and genera may significantly alter the interpretation of evolutionary relationships. However, these studies must wait until some future date. All three phylogenies have their strengths and weaknesses. Phylogeny 1 (Fig. 33) is supported by the most morphological evidence, while Phylogeny 3 (Fig. 35) is most concordant with the biological evidence. I believe that Phylogeny 3 most accurately reflects the actual evolutionary relationships between the Inquilline genera.

2.7 The origin of the Inquilline Cynipidae.

Although the biological differences between Inquillines and gall forming species has long been recognised, little has been said about the origin of Inquillinism. Malyshev (1966) hypothesised that in general, Inquillinism was an intermediate step to parasitism. If this were true, then it follows that the parasitic taxa within the Cynipoidea have descended from the Inquilline Cynipidae. Recently, Rasnitsyn

(1980) and Koenigsmann (1978) have refuted Malyshev's concepts on the evolution of the Hymenoptera. It is therefore unlikely that the parasitic Cynipoidea evolved from the Inquillines.

Shorthouse (1975, 1980) has offered the only concrete hypotheses regarding the evolution of Inquilline Cynipidae. He proposed 2 alternative hypotheses; they are:

1) Inquillines are very primitive gall wasps, just now evolving the capability to induce galls.

OR

2) Inquillines once had the ability to form galls and have now lost it.

Both hypotheses are reasonable and are consistent with what is known about the Cynipidae and about the Inquillines. However, both hypotheses have different implications. The first hypothesis implies that phytophagy has evolved twice within the Cynipidae, while the second hypothesis implies that it has evolved only once. Preliminary studies on the higher classification of the Cynipoidea show that phytophagy is a derived behavior (Appendix 1). Secondly, phytophagy is a rare phenomenon within the "Parasitica" or Microhymenoptera. Both of these facts support Shorthouse's second hypothesis and contradict the first hypothesis.

It is now possible to propose a hypothesis on the origin of Inquillinism. This hypothesis is based on the phylogenetic relationships proposed in Phylogeny 3 and

excludes *Myrtopsen* and *Euceroptres*.

All Cynipidae need undifferentiated plant tissues to complete their development (Rohfritsch and Shorthouse 1982). One source for this is near apical meristem in growing plants. This is the location of most cynipid galls. However, when the local population of gall wasps becomes large, this resource may be limited and result in competition for oviposition sites. Hence, it is likely that there will be multiple ovipositions at the same site; these may be either sequential or simultaneous. This has been observed in *Diastrophus kinkaidii* Gillette on *Rubus parvifloris* (Wangberg 1975; Jones 1983; Lalonde, pers. comm.). There are three possible outcomes of such a behavior. One is that the offspring of only one female survives whereas the offspring of the other females do not. A second possibility is that all offspring survive in a "communal" gall. Neither of these possibilities would lead to inquilineism.

The third possible outcome arises when the multiple ovipositions are sequential and the subsequent eggs hatch in an already developing gall. Many gall formers are known to have some variation in their times of emergence (Shorthouse 1975; Shorthouse and Ritchie 1981; Yasumatsu and Taketani 1967). When there is a limited number of suitable oviposition sites, it is possible that all have been utilized by the time the latter part of the generation emerges. However, there is an alternative source of undifferentiated

tissues; this is the gall tissue induced by the offspring of the earlier emerging adults. In all studies conducted so far, this is the substrate on which the inquillines develop (Shorthouse 1973, 1975, 1980; Taketani and Yasumatsu 1973).

Studies on some gall forming aphids, have shown a similar phenomenon. A significant portion of a population of *Epipemphigus* sp. (Homoptera: Pemphigidae) attempt to usurp the galls of other members of the species (Akoi and Makino 1982). These females actively search and fight for plant tissues that have already been modified by other females. These individuals appear to be inquillines in the galls of other members of their own species. Akimoto (1981) states that *Eriosoma* sp. live in the galls of other species of *Eriosoma*. Similarly, Mamaev (1968) states that at least one gall midge (Diptera: Cecidomyiidae) exists as both a gall former and an inquilline.

A model for the origin of inquillinism can now be proposed. The ancestor of the inquillines was a gall inducer on *Rubus*. At some point in time, some members of this population began to attack galls induced by other members of their own species; this was presumably due to the lack of suitable oviposition sites. This led to a change in behavior from inducing galls in immature plant tissues to inducing galls in gall tissues. Thus, two distinct populations existed; one that continued to induce galls and one that relied on these galls for its own existence.

5

The origin of Inquilinism allowed the exploitation of other galls as hosts. Presumably, these host switches occurred randomly, but it appears that the galls of *Diplolepis* on *Rosa* was the first new habitat. Since *Rosa* is closely related and very similar to *Rubus* and also occurs in similar habitats (Britton and Brown 1913), this is quite possible. It is unclear, at the moment, if the switch to galls on *Quercus* was sequential or independent of the switch to *Rosa*.

3. Revision of the Nearctic Species of *Periclistus* Foerster.

3.1 Introduction.

The species of *Periclistus* Foerster (Hymenoptera: Cynipidae) areinquillines in the galls of *Diplolepis* Fourcroy (Cynipidae) on *Rosa* (Rosaceae). Although unable to initiate gall formation themselves, members of *Periclistus* induce endogalls with their host galls (Shorthouse 1975, 1980; Taketani and Yasumatsu 1973). There is no evidence that *Periclistus* larvae feed on the gall larvae; however, the *Diplolepis* larva is killed by the ovipositing female *Periclistus* (Shorthouse 1975, 1980). The developing *Periclistus* larvae induce additional gall tissues, which frequently results in gross external modification of the host gall. Some galls are modified to the extent that the original host gall cannot be recognised (Dalley and Campbell 1973; Weid 1960).

The genus *Periclistus* is distributed throughout the Holarctic region, although no individual species has a holarctic distribution (Burks 1979; Dalla Torre and Kieffer 1910; Weid 1952b). Seven species from each region are currently placed in *Periclistus*. Foerster (1869) erected *Periclistus* for *Aylax caninae* Hartig, a Palearctic inquilline in the galls of *Diplolepis eglanteriae* (Hartig). Mayr (1881) transferred *Cynips brandtii* Ratzeberg to *Periclistus*; this species is the common inquilline in the Palearctic galls of *D. rosae* (L.). Five additional Palearctic species

of *Periclistus* have been described; these are: *P. capitatus* Belizen (1968), *P. natalis* Taketani and Yasumatsu (1973), *P. quinlani* Taketani and Yasumatsu (1973), *P. rosarum* Dettmer (1924b), and *P. spinosissimae* Dettmer (1924b). Eady and Quinlan (1968) have reviewed the three species in Great Britain. Dalla Torre and Kieffer (1910) proposed a key to world species; however, this appears to have been based on literature descriptions and utilizes unreliable characters.

Seven Nearctic species of *Periclistus* have been described; these are: *P. arefactus* McCracken and Egbert (1922), *P. californicus* Ashmead (1896), *P. piceus* Fullaway (1911), *P. pirate* (Osten Sacken) (1863), *P. semipiceus* (Harris) (1841), and *P. smilacis* Ashmead (1896). These species have never been revised and there is confusion about the identity of many species. Most original descriptions of species are short and lack detail. This has caused many species to be misidentified, which has lead to many erroneous host records being reported in the literature. In this manner, the concepts of the various species have changed.

The species concepts that have been applied to the inquiline Cynipidae also need to be examined. These concepts have been derived from studies on the gall inducing taxa and then have been extrapolated to the inquiline species. Most gall-inducing cynipids have been described on

the basis of a few specimens from a single locality, with great emphasis on gall morphology, host plant relationships, and distribution. Very little attention has been paid to the morphology of the adult insect. This has caused an artificial belief that gall wasps do not exhibit a great deal of morphological or biological variation.

Kinsey (1923, 1930, 1936) attempted to study the morphology of various Cynipidae and has proposed several keys to species which are based on insect morphology. However, the morphological characters he used in his keys were not dichotomously exclusive, and he relied heavily on distributional data. Kinsey has been obliquely criticised by several authors, although there is little in print directly criticising his work. Beutenmueller, in a letter to Kinsey, wrote "... your work is largely synthetic and of no use." (footnote in Kinsey 1930: 317). Weld felt that most gall inducers were not restricted to a single species of host plant, but rather they occurred on groups of closely related host plants. Weld (1952b: 259) stated: "I have never been able to separate the adults of the species that come from galls on different (closely related) host oaks and regard giving variety names to them as superfluous and a needless burdening of the literature."

It is not within the scope of this study to determine the validity of Kinsey's work; however, similar concepts have been applied to the Inquilines. It appears that most

authors believed that most inquilline species are restricted to attacking the galls of a single species of gall inducer. Hence, they believed that new host records for inquillines represented the discovery of new species; such a priori decisions cannot be justified. This does not mean that all inquillines are polyphagous, for as will be subsequently shown, there are several species of *Periclistus* that are restricted to a single host. However, host relationships cannot be used as the sole criterion for species concepts; this sort of biological data must be supported by other evidence, such as external morphology.

The present study on *Periclistus* is the first study of inquilline Cynipidae that is based on large numbers of specimens from throughout North America. The majority of these specimens belong to three important collections. The Shorthouse collection contains large numbers of *Periclistus* reared primarily from leaf galls from Central and Western Canada through Alaska. The Kinsey collection contains material from most of the United States, as does the Weld collection. Not only do these collections contain large amounts of material, but the host galls are accurately identified. Thus, it is possible to account for specific variation and also to examine the question of host gall specificity.

Shorthouse (1975) suggested that each of the six leaf galls he studied was attacked by a different species of *Periclistus*. Shorthouse based his suggestions on identifi-

cations by Dr. C. Yoshimoto (Biosystematics Research Institute, Ottawa, ONT) and Dr. R. Lyon (Los Angeles City College, Los Angeles, CA). Dr. Lyon has possession of the Weld collection of Cynipidae and all of Dr. Weld's notes (Lyon, pers. comm). Weld was the last major worker on the Cynipidae; his notes indicate that he believed that there were approximately 25 species of Nearctic *Periclistus*.

I have used both morphological and biological data in determining the limits of the species. Since I feel that past studies on the gall inducers have overly "split" the actual species, I have taken a rather conservative approach. I would rather "lump" two species under one name than to overly "split" species. Subsequent studies may allow these problems to be resolved and new names can be proposed at that time (see remarks for *P. weldi*). This is an attempt to keep the number of needless names to a minimum. However, when there is doubt about a species that has been previously described, I have tended to give it the benefit of the doubt (see remarks on *P. californicus*).

My operative rule is that specimens that show consistent biological and morphological differences are different species. One corollary to this approach is that species with the same host have greater morphological differences than do species with different biologies. Intraspecific variation was evaluated by examining large numbers of members from individual populations. It was assumed that indi-

viduals reared from the same gall were the same species; characters that varied within these populations were not used in making taxonomic decisions.

Morphological terms are explained in Section 2.2. Complete label data is given for all specimens for new species and for previously described species that are known from less than ten records. Label data for other wide ranging species are summarized. Lectotypes and allolectotypes are designated when necessary.

3.2 The genus Periclistus Foerster.

Periclistus Foerster 1869: 332, 337.

TYPE-SPECIES: *Aylax caninae* Hartig. Original designation.

DIAGNOSIS (see Section 2.4 for a full generic description): head without frontal ridges, frontal field, or genal carinae; frons with median protuberence and lateral radiating striae; female with 12 antennomeres, male with 14 antennomeres; mesoscutum coriaceous, without anterior setigerous pits or well defined complete transverse rugulae (*P. arefactus* has some very short, very weak transverse rugulae); mesopleuron either smooth or aciculate (striate in *P. brandtii*, a Palearctic species); ventral margin of subalar triangle with conspicuous row of setigerous punctures; female metasoma with T2 + T3 fused, male metasoma with T2 + T3 separate; radial cell open; hind wing with proximal hamulus bifid.

Members of *Periclistus* are most similar to *Synophromorpha*, but can be distinguished by the following characters: mesoscutum coriaceous, without conspicuous anterior setigerous punctures; ventral margin of subalar triangle with at least a single row of setigerous punctures; radial cell closed. Species of *Periclistus* have been recorded wherever galls of native *Diplolepis* have been found. Surprisingly, neither genus has been recorded from Mexico.

3. Mesoscutum with weak incomplete transverse rugulae; notauli strongly divergent, arcuate posteriorly (Fig. 38); Rs1 reaching anterior margin of wing near mid-point of radial cell length. ex modified stem galls of *D. inconspicuis*; Western United States. *arefactus* McCracken and Egbert
- 3'. Mesoscutum without transverse rugulae; notauli weakly divergent, straight; Rs1 reaching anterior margin of forewing in basal third of radial cell length. 4
4. Notauli slightly broadened posteriorly, separated by 2.0 times width at posterior margin of mesoscutum (Fig. 40); mesopleuron with narrow ventral pubescent area (Fig. 62). ex galls of *D. polita*. California. *californicus* Ashmead
- 4'. Notauli distinctly broadened posteriorly, separated by 1.0 times width at posterior margin of mesoscutum (Figs. 46, 47); mesopleuron with broad ventral pubescent band (Fig. 71). ex modified stem galls. Oregon, Vancouver Island.
 vancouverensis n. sp.

5. Lateral margin of metanotal fovea shining smooth (as in Fig. 59); pronotum with setigerous tubercles; male A3 strongly notched, expanded distally (as in Fig. 72). ex modified galls of *D. bicolor*, *D. polita*, rarely from modified stem galls. 6
- 5'. Lateral margin of metanotal fovea shagreened (as in Fig. 58); pronotum with setigerous punctures; male A3 weakly notched, weakly expanded distally (Fig. 73). ex modified or unmodified leaf galls. 7
6. Ocelli large: $LOL < 1.0D$, POL and $OOL < 2.0D$; notauli incomplete in females (Fig. 43), complete in males; pronotum shining smooth between setigerous tubercles; ex (modified?) galls of *D. polita*; California, Oregon, "Wyoming & Colorado".
..... *piceus* Fullaway
- 6'. Ocelli small: $LOL > 1.0D$, POL and $OOL > 2.0D$; notauli complete at least as distinct creases (Fig. 45), often as distinct grooves; pronotum coriaceous between setigerous tubercles; ex modified galls of *D. bicolor*, *D. polita*, rarely modified stem galls. North America east of Rocky Mountains, Alaska, northern British Columbia, Yukon Territory.*..... *weldi* n. sp.

7. Notauli arcuate, not widened posteriorly; posterior margin of mesoscutum notched medially, rounded between median notch and posterior of notauli (Figs. 36, 37); gena dimpled, shagreened behind eyes; mesoscutellum sloping posteriorly. ex galls of *D. ignota*, *D. nebulosa*, *D. variabilis*. Transcontinental. *ashmeadi* n. sp.
- 7'. Notauli straight (although divergent), gradually widened posteriorly; posterior margin of mesoscutum straight between median notch (if present) and posterior of notauli; genae not dimpled, strongly coriaceous; mesoscutellum bulbous. 8
8. Female $A_{12} > 1.2 A_{10} + A_{11}$; male $A_{14} > 0.9 A_{12} + A_{13}$. ex unmodified galls of *D. fusiformans*, *D. nodulosa*, *D. triforma*. Transcontinental. *fusicolus* n. sp.
- 8'. Female $A_{12} < 1.1 A_{10} + A_{11}$; male $A_{14} < 0.8 A_{12} + A_{13}$. ex leaf galls. 9

9. Female $A_{12} < 1.0 A_{10} + A_{11}$; gena arcuate below eye; mesocutum without median groove (Fig. 42); female T_{2+3} with narrow band of posterior punctation. ex galls of *D. gracilis*. Alberta, North Dakota, Saskatchewan. *graciliculus* n. sp.
- 9'. Female $A_{12} > 1.0 A_{10} + A_{11}$; gena weakly angulate below eye; mesocutum often with weak, incomplete median groove; female T_{2+3} often with broad band of posterior punctation. ex galls of *D. lens*, *D. rosaefolia*. Transcontinental.
 catenactens n. sp.

3.3 Description of species.

Periclistus arefactus McCracken and Egbert

Figs. 38, 48, 60.

Periclistus arefactus McCracken and Egbert 1922: 62. ♀, ♂.

TYPE: Lectotype, designated here. ♀ (USNM). Labelled: March 1917, Stan U Cal; L. S. Jr U. Lot 568, sub 269; Paratype (yellow label); Beut. coll., rec'd 1939; Lectotype, *Periclistus arefactus* McCracken and Egbert 1896, Ritchie and Shorthouse, 1984.

FEMALE. (Lectotype). Length 2.3 mm. Dark piceous brown; antenna, mandible, tegula, legs except coxal bases, anterior margin of T2+3 amber; coxal bases, anterior two thirds of T2+3 (except anterior margin) dark brown. Head wider than mesosoma; subquadrate, gena expanded below eye; frons weakly shagreened; median protuberance narrow, poorly developed; clypeus indistinct dorsally, protuberant medially; radiating striae moderately weak, reaching antennal sockets and inner orbit of eye; subantennal foveae broad, shallow, indistinct; interocular space 0.83 of eye height, malar space 0.32 of eye height; vertex, ocellar triangle raised; ocelli surrounded by weak, indistinct crescent shaped depression; LOL = 0.8D, POL = 1.5D, OOL = 1.7D. Antenna 1.62 mm; A1-12 (mm): 0.17, 0.08, 0.19, 0.19, 0.19, 0.17, 0.15, 0.15, 0.12, 0.11, 0.10, 0.22; A12 = 1.05 A10 + 11. Pronotum finely coriaceous, without evident punctures or tubercles, posterolateral region rugulose; anterior pilosity absent;

posterior part of plate very weak, lateral margins parallel except strongly curved posterodorsally. Mesoscutum (Fig. 38) flattened posteriorly, shagreened, posterior half with weak transverse rugulae, anterior margin evenly rounded, length 0.93 of width. Notauli incomplete, not reaching middle of mesoscutum, strong, strongly divergent, curved posteriorly; grooves separated by 1.3 times width at posterior margin of mesoscutum; posteroventral margin of groove weakly raised; posterior margin of mesoscutum weakly depressed between grooves, not notched. Median line absent. Anterior lines short, straight, convergent. Lateral lines weak. Mesoscutellum flattened medially, rounded posteriorly, coarsely rugoareolate, shining between rugae, in same plane as posterior of mesoscutum; axilla shagreened; lateral bars broad, weakly depressed; foveae large, triangular, open posteriorly; septum very short, broad, inverted "V" merging with rugosity of disc; lateral shining strip (Fig. 48) gradually broadened posteriorly, posterodorsal extension weakly developed. Mesopleuron (Fig. 60) aciculate anteriorly, ventrally; shining smooth posterodorsally; dent weak; ventral pubescent area moderately broad; subalar triangle weakly pubescent, weakly pilose; ventral margin of subalar triangle weakly sulcate, with narrow anterior punctopubescent area (as in Fig. 68); subalar pit broad. Metapleuron depressed anteriorly, broad; supracoxal carina strong, angulate, ventral portion parallel to posterior

margin of mesopleuron; subspiracular tubercle, carina strong; antespiracular area large, deep, shining smooth. Metanotal lateral foveae weakly pubescent, lateral margin shining smooth (as in Fig. 59). Propodeum without lateral or medial pilosity; propodeal carinae moderately strong, shagreened, setose, slightly divergent. Metasoma shorter than length of head plus mesosoma; T2+3 without visible suture, anterior pubescent patch poorly developed, with weak pilosity; posterodorsal margin with narrow band of fine punctation. Forewing 2.7 mm long; radial cell length 2.9 times width; R weakly arcuate, shorter than Rs1; Rs1 arcuate, joining wing margin at middle of anterior margin of radial cell; Rs2 bent distally (as in Fig. 74); areolet large, slightly elongate, posterior side very weak. Hind wing 1.69 mm long.

MALE. Allolotype differs from lectotype as follows. Length 2.3 mm. Antenna 14 segmented, 2.00 mm long; A1 - 14 (mm): 0.12, 0.07, 0.19, 0.19, 0.19, 0.19, 0.17, 0.16, 0.12, 0.12, 0.11, 0.10, 0.10, 0.17; $A_{14} = 0.85 A_{12} + 13$; A3 strongly curved, deeply notched, strongly expanded distally (as in Fig. 72). Notauli not curved posteriorly. T2 separate from T3, relative lengths 0.42: 0.28; T3 with broad posterodorsal triangle of punctation and narrow posterolateral band of punctation. Forewing 2.5 mm long, hind wing 1.66 mm long.

TYPE MATERIAL. Lectotype, ♀ (USNM), designated here. Labelled: March 1917, Stan U Cal; L. S. Jr. U Lot 598, sub 269; Paratype, *Periclistus arefactus* McCracken and Egbert (yellow label); Lectotype, *Periclistus arefactus* McCracken and Egbert 1922, Ritchie and Shorthouse 1984 (red label). Allotype, ♂ (USNM). Labelled: Palo Alto Cal., April 1917, L. S. Jr. U. Lot 539 sub 269; Paratype (yellow label); Paratype No. 24504 U.S.N.M. (red label); Allotype, *Periclistus arefactus* McCracken and Egbert 1922, Ritchie and Shorthouse 1984 (red label). Paralectotypes: 1 ♀, 2 ♂♂ with same data as lectotype; 4 ♀♀, 3 ♂♂ with same data as allotype.

OTHER MATERIAL EXAMINED. CALIFORNIA: 12 ♀♀, 7 ♂♂ (JDS), Grass Valley, Nevada Co.; 21 ♀♀, 19 ♂♂ (AMNH), Palo Alto; 16 ♀♀, 14 ♂♂ (JDS), Putah Canyon, Yolo Co.; 5 ♀♀, 5 ♂♂ (AMNH), San Jacinto Mtns.

VARIATION. Female length 1.9 - 2.6 mm ($\bar{x} = 2.4 \pm 0.1$ mm, N = 10). Male length 1.4 - 2.5 mm ($\bar{x} = 2.1 \pm 0.1$ mm, N = 10). Fresh specimens black except antenna, mandible, tegula, legs, anterior margin of T2+3 amber; notauli sometimes extending to middle of mesoscutum as weak creases (never complete); mesopleuron sometimes with stronger or weaker aciculation; R rarely joining wing margin nearer base of radial cell.

HOST GALLS. *Diplolepis inconspicuis* Dalley and Campbell, *D. neglecta* (Gillette).

DIAGNOSIS. Vertex strongly shagreened; mesoscutum with weak transverse rugulae; mesopleuron aciculate anterodorsally, striate ventrally; notauli incomplete, usually not reaching middle of mesoscutum, strongly divergent, curved posteriorly in female; median groove absent; anterior lines short, straight, convergent; lateral margin of metanotal fovea smooth; female T2+3 with small posterodorsal triangle of punctation; male A3 strongly curved and expanded distally, deeply notched; Rs1 arcuate, usually meeting anterior wing margin at middle of radial cell.

BIOLOGY. *Periclistus arefactus* attacks the galls of *Diplolepis inconspicuis*, a species of stem gall inducer from California (Dalley and Campbell 1973). *Diplolepis inconspicuis* females emerge in February and March and oviposit into immature buds of *Rosa* spp; immature galls appear shortly thereafter. Adult males and females of *P. arefactus* emerge after of *D. inconspicuis*, mate, and oviposit into the immature galls (Dalley and Campbell 1973). The larvae of *P. arefactus* greatly modify the host gall. The normal gall is monothalamous, slender, fusiform, and reddish; inquiline modified galls are polythalamous, enlarged, oval, and are tan or gray.

Two series of insects have been reared from galls identified by Kinsey as *D. nebulosa*; these are probably the same galls described by Dalley and Campbell (see remarks on this host under *P. californicus*).

REMARKS. *Periclistus arefactus* is most similar to *P. californicus* Ashmead but can be recognised by the characters given above. *Periclistus californicus* has the notauli longer and less divergent, does not have weak transverse rugulae on the mesoscutum, and the sculpturing of the vertex is weaker. Although these species are very similar morphologically, they appear to be distinct biological differences. *Periclistus californicus* apparently attacks leaf galls of *D. polita* (Ashmead) and stem galls induced by *D. californicus*; *P. arefactus* attacks the stem galls of *D. inconspicuis*.

McCracken and Egbert (1922) described *P. arefactus* from a gall that resembled the gall of *Diplolepis arefactus* (Gillet). McCracken and Egbert thought that *D. arefactus* was the true gall inducer and therefore named the inquiline after its host. Dalley and Campbell (1973) have shown that the true host for this species is *D. inconspicuis*, a species closely related to *D. nodulosa* (Ashmead) (Shorthouse and Ritchie 1984). Galls of *D. nodulosa* are similarly modified by *P. pirata* (O. S.).

Periclistus ashmeadi n. sp.

Figs. 36, 37, 49, 61.

FEMALE. (Holotype). Length 2.3 mm. Black; antenna, tegula, legs beyond coxal bases, anterior margin of T2+3 amber; coxal bases, valves of ovipositor brown; posterodorsal region of mesopleuron rufopiceous. Head as wide as mesosoma, subquadrate; frons strongly coriaceous above antennal sockets, weakly coriaceous (almost shining) below antennal sockets, with very fine setigerous punctures; median protuberance weak, poorly defined; clypeus indistinct dorsally, medially protuberant (continuous with median protuberance); radiating striae moderately strong, reaching antennal sockets and inner orbit of eye; subantennal foveae weak and indistinct; interocular space 0.87 of eye height; malar space 0.37 of eye height; vertex, ocellar triangle weakly raised, ocelli surrounded by weak, crescent shaped depression; frons without crease below median ocellus; $LOL = 1.2 D$, $POL = 2.5D$, $OOL = 2.1D$. Antenna 2.01 mm long; A1 - A12 (mm): 0.12, 0.08, 0.17, 0.19, 0.17, 0.17, 0.15, 0.12, 0.12, 0.12, 0.10, 0.25; $A12 = 1.1 A10 + A11$. Pronotum finely coriaceous between setigerous tubercles; anterior pilosity strong; with very weak posterolateral rugosity; posterior part of plate weak, lateral margins weakly curved, convergent, not quite reaching posteromedial margin. Mesoscutum (Fig. 36) weakly arched posteriorly; length 0.76 of width, without fine setigerous punctures, finely coriaceous between punc-

tures. Notauli incomplete, moderately strong, gradually widening posteriorly, not reaching middle of mesoscutum; anterior pits absent; grooves separated by 2.0 times their width at posterior margin of mesoscutum (Fig. 37); posterodorsal margin of notauli not raised; posterior of mesoscutum strongly coriaceous between notauli, posterior margin not notched. Median groove present, very short, not reaching middle of mesoscutum. Anterior lines moderately long, slightly concave, weakly impressed. Lateral lines weak. Mesoscutellum bulbous, densely rugulose, shining between rugae; axilla weakly coriaceous; lateral shining strip with poorly developed posterodorsal extension (Fig. 49); foveae transversely oval, deep, closed posteriorly, shining smooth; septum long, distinct, merging with anterior rugosity of disc. Mesopleuron (Fig. 61) shining smooth, ventral pubescent area broad, subalar triangle sparsely pubescent, moderately pilose; ventral margin straight, without narrow punctopubescent area (as in Fig. 59); subalar pit narrow, deflexed. Metapleuron strongly depressed anteriorly, broad; supracoxal carina strong, angulate; ventral portion parallel to posterior margin of mesopleuron; subspiracular carina and tubercle moderately developed; antespiracular area large, shallow, shining smooth. Metanotal lateral foveae sparsely pubescent; lateral margin shagreened, sculptured. Propodeum with lateral pilosity, without median pilosity; propodeal carinae straight,

strong, weakly divergent, shagreened, pubescent; intracarinai area shining, glabrous except dorsal pilose area. Metasoma less than length of head and mesosoma; T2+3 without visible suture, hind margin with small elongate triangle of punctation; anterior pubescent patch small, anterior pilosity weak. Forewing 2.5 mm long; radial cell distinctly closed, length 2.7 times width; R weakly arcuate, longer than Rs1; Rs1 straight; Rs2 bent medially (as in Fig. 75); areolet large, elongate, posterior side very weak. Hind wing 1.6 mm.

MALE. Allotype differs from holotype as follows: length 1.8 mm; coxae dark brown, remainder of legs brown, antennae amber; malar space 0.36 of eye height; antenna with 14 antennomeres, 2.1 mm long, A1 - 14 (mm): 0.12, 0.08, 0.17, 0.17, 0.17, 0.15, 0.12, 0.12, 0.10, 0.10, 0.10, 0.10, 0.09, 0.19; A3 weakly curved, broadly notched, weakly expanded distally (as in Fig. 75); $A14 = 1.0 A12 + A13$; T2 separate from T3, relative lengths 0.37: 0.33; T3 with large posterodorsal triangle of punctation almost reaching anterior margin, extending ventrally as narrow band; forewing 2.2 mm long, hindwing 1.5 mm long.

TYPE MATERIAL. Holotype, ♀ (CNC No. ____). Labelled: BC, 1/2 ml. e. Kerameos, coll. 10-III-70, Coll. No. 4-70, Lab Reared, J. D. Shorthouse, ex gall of *Diptolepis variabilis* (Bassett); Holotype, *Periclistus ashmeadi* Ritchie & Shorthouse 1984 (red label). Allotype, ♂ (CNC), with same data

as holotype. Paratypes (334 ♀♀, 118 ♂♂). **BRITISH COLUMBIA:** 203 ♀♀, 55 ♂♂ (JDS) with same data as holotype. **NEBRASKA:** 4 ♀♀, 2 ♂♂ (AMNH), Chadron, coll. 17-VIII-29, A. Kinsey, ex gall of *Diplolepis nebulosa*. **ONTARIO:** 3 ♀♀, 1 ♂ (JDS), Manitoulin Is., Providence Bay, coll. 2-X-76, Coll. No. 126-76, J. D. Shorthouse, ex gall of *Diplolepis nebulosa*; 13 ♀♀ (JDS), Bay of Quinte, coll. VI-77, R. Gordinier, ex gall of *Diplolepis ignota*; 59 ♀♀, 39 ♂♂ (JDS), Manitoulin Is., Providence Bay, coll. 10-V-79, Coll. No. 19-79, J. D. Shorthouse, ex gall of *Diplolepis nebulosa*; 3 ♀♀, 2 ♂♂ (AJR), Spanish, coll. 22-V-83, Coll. No. 508-83, R. DeClerck, ex gall of *Diplolepis nebulosa*. **OREGON:** 3 ♀♀, 1 ♂ (AJR), Benton Co., ex *Diplolepis variabilis*, em. 8 Feb. 1983, P. Hanson, ex *Rosa pisocarpa*; 4 ♀♀ (AJR), Benton Co., Corvallis, em. 22 Feb. 1983, P. Hanson, ex *Diplolepis variabilis*, ex *Rosa pisocarpa*. **SASKATCHEWAN:** 1 ♀ (JDS), 15 mi. e. Saskatoon, coll. 3-V-72, Coll. No. 11-72, J. D. Shorthouse, ex gall of *Diplolepis ignota*; 1 ♀ (JDS), 6 mi. w. Aberdeen, coll. 10-V-72, Coll. No. 15-72, J. D. Shorthouse, ex gall of *Diplolepis ignota*; 2 ♀♀, 3 ♂♂ (JDS), 15 mi. e. Saskatoon, coll. 31-V-72, Coll. No. 50-72, J. D. Shorthouse, ex gall of *Diplolepis ignota*; 33 ♀♀, 12 ♂♂ (JDS), Lemsford Ferry, 12 mi. n. Lemsford, coll. 6-IX-72, Coll. 215-72, J. D. Shorthouse, ex gall of *Diplolepis nebulosa*; 7 ♀♀, 1 ♂ (JDS), 1 mi. s. Briercrest, coll. 3-VIII-72, Coll. No. 216-72, J. D. Shorthouse, ex gall of *Diplolepis nebulosa*; 3 ♀♀,

1 ♂ (JDS), 25 mi. e. Saskatoon, coll. 10-IX-72, Coll. No. 221-72, J. D. Shorthouse, ex gall of *Diplolepis ignota*; 5 ♀♀, 1 ♂ (JDS), 8 mi. e. Ardath, coll. 29-IX-72, Coll. No. 241-72, J. D. Shorthouse, ex gall of *Diplolepis ignota*; 1 ♀ (JDS), 4 mi. e. Macrorie, coll. 13-X-72, Coll. No. 242-72, J. D. Shorthouse, ex gall of *Diplolepis ignota*.

VARIATION. Female length 1.8 - 2.4 mm ($\bar{x} = 2.1 \pm 0.2$ mm, $N = 10$); male length 1.5 - 1.9 mm ($\bar{x} = 1.7 \pm 0.1$ mm, $N = 10$). Antennae, legs beyond coxae often yellow; mesopleuron, metasoma sometimes entirely black (specimens from Bay of Quinte, ONT. are yellow-orange due to storage in isopropyl alcohol); female $A_{10} = 1.0 - 1.2$ $A_{10} + A_{11}$; notauli rarely slightly broadened near posterior margin of mesoscutum; median groove sometimes extending anteriorly as distinct line.

HOST GALLS. *Diplolepis ignota* (O. S.), *D. nebulosa* (Bassett), *D. variabilis* (Bassett).

DIAGNOSIS. Notauli incomplete, strongly divergent, ectal and ental margins arcuate; median groove strong, short, posterior margin of mesoscutum distinctly notched; posterior margin of mesoscutum rounded between posterogental margins of notauli and margins of median groove; gena behind eye shagreened, with large dimples.

BIOLOGY. Shorthouse (1975) described the effect of *P. ashmeadi* on the galls of *D. ignota* and *D. nebulosa* from Saskatchewan; his findings are summarized here. Immature galls

of *D. nebulosa* and *D. ignota* appear in mid-summer (July - August); this is relatively late compared to other species of *Diptolepis*. *Periclistus ashmeadi* adults emerge after the appearance of immature host galls, which indicates that the life cycle of *P. ashmeadi* is synchronized with that of their hosts. Ovipositing females puncture and kill the *Diptolepis* larva, similar to other species of *Periclistus*. Unlike other species, eggs are laid on the larval remains, not on the ental wall of the gall chamber. However, there is no evidence that the *Periclistus* larvae feed on the *Diptolepis* larva.

Shorthouse (1975) found that relatively few galls of *D. ignota* were attacked by *Periclistus*; 11.4% of mid-season galls and 5.8% of mature galls contained *Periclistus* larvae. In contrast, 66% of mid-season galls of *D. nebulosa* were attacked by *Periclistus*, although only 13.1% of mature galls contained inquiline larvae. Attacks by entomophagous (parasitic) insects is responsible for the decrease in the percentage of galls inhabited by *Periclistus*. These data suggest that galls of *D. nebulosa* are the normal host for *P. ashmeadi*, while *D. ignota* galls are only occasionally attacked. Relatively low numbers of *Periclistus* larvae are found in each gall (*D. nebulosa* galls: 3.3 ± 3.1 larvae per gall; *D. ignota* galls: 2.9 ± 1.4 larvae per gall).

Periclistus ashmeadi has different effects on the morphology of galls of *D. ignota* and *D. nebulosa*, due in large

part to the differences in the normal galls (unmodified by Inquillines). Both galls are found on the abaxial surface of the leaves of *Rosa* spp., and both galls are usually smaller when attacked by *P. ashmeadi*.

Normal *D. nebulosa* galls are thin walled, monothal-mous, and usually have a distal depression; most galls are single, although a row of adjacent galls may occasionally coalesce. Normal mature *D. nebulosa* galls are circumscribed by a single layer of sclerenchyma cells, initially derived from two sclerenchymous discs. In *Periclistus* modified galls, this layer is not affected; however, an additional layer of sclerenchyma cells is induced. This layer circumscribes the endogalls of each individual *Periclistus* larvae.

Normal galls of *D. ignota* are larger than *D. nebulosa*, and can be either spherical or kidney shaped; the latter form of gall is a coalescing of several individual galls. There is also often a distal depression. The larger size of the gall is due to a very thick layer of cells surrounding the *Diplolepis* larval chamber. Normal mature *D. ignota* galls have two layers of sclerenchyma cells, one just below the epidermis of the gall and one very near the *Diplolepis* larval chamber. When the gall is attacked by *P. ashmeadi*, the ental *Diplolepis* induced sclerenchyma layer does not circumscribe the original *Diplolepis* larval chamber. It is not clear whether the development of this layer

is inhibited by *P. ashmeadi* larvae or whether the sclerenchyma layer degenerates.

Kinsey (1922b) has suggested that *D. ignota* and *D. variabilis* are probably synonyms. Shorthouse (1975) agrees with Kinsey's belief and states that *D. ignota* from Saskatchewan appear to be intermediate between western *D. variabilis* and eastern *D. ignota*. Hence, it is likely that the effects of *P. ashmeadi* on *D. variabilis* galls is similar to those described for *D. ignota* galls.

ETYMOLOGY. This species is named after Dr. W. H. Ashmead for his contributions to our knowledge on the Cynipidae.

REMARKS. *Periclistus ashmeadi* is similar to *P. cataractans*, *P. fusicolus*, and *P. gracilicollis* but can be distinguished by characteristic notauli, posterior margin of the mesoscutum, and sculpturing of the gena behind the eye. The latter three species also have a bulbous mesoscutellum whereas that of *P. ashmeadi* is sloping posteriorly.

Periclistus ashmeadi has an apparently disjunct distribution in that specimens have not been seen from Alberta, although both *D. ignota* and *D. nebulosa* occur in the province (Shorthouse 1975). The few specimens of *Periclistus* from Alberta reared from these hosts belong to other species (*P. pirata*, *P. weldi*). However, this may be a collecting artifact. I expect that *P. ashmeadi* will eventually be found wherever *D. nebulosa* occurs, and possibly throughout the ranges of *D. ignota* and *D. variabilis*.

Periclistus californicus Ashmead

Figs. 40, 50, 62.

Periclistus californicus Ashmead 1896: 188. ♀, ♂.

TYPE: Lectotype, selected here. ♀ (USNM). Labelled: 125 (red letters); Nevada Co., Cal.; Through C. V. Riley; Type, No. 3288, U. S. N. M. (red label); Lectotype, *Periclistus californicus*, Ashmead 1896, Ritchie and Shorthouse, 1984.

FEMALE. (Lectotype). Length 2.2 mm. Very dark piceous brown, almost black; anterior two thirds of T2+3 dark brown; antenna, mandible, tegula, anterior margin of T2+3 dark amber. Head as wide as mesosoma; subquadrate, gena expanded below eye; frons finely coriaceous above antennal sockets, moderately coriaceous below antennal sockets, densely pubescent with few evident punctures; median protuberance narrow, poorly developed; clypeus indistinct dorsally, median portion of epistomal suture absent, very weakly protuberant medially; radiating striae weak, reaching antennal sockets but not inner orbit of eye; subantennal foveae broad, shallow, indistinct; interocular space 0.89 of eye height, malar space 0.43 of eye height; vertex weakly raised; ocellar triangle raised; ocelli surrounded by weak, indistinct crescent shaped depression; LQL = 0.9D, POL = 1.75D, OOL = 2.0D. Antenna 1.82 mm; A1-12 (mm): 0.17, 0.09, 0.19, 0.17, 0.17, 0.17, 0.15, 0.14, 0.14, 0.13, 0.11, 0.19; A12 = 0.79 A10 + 11. Pronotum moderately pubescent,

finely coriaceous, without evident punctures or tubercles, posterolateral region finely rugulose; anterolateral margin weakly pilose; posterior part of plate weak, lateral margins parallel except strongly curved posterodorsally. Mesoscutum (Fig. 40) very weakly arched, anterior margin evenly rounded, length 0.78 of width, with small evident setigerous punctures, weakly coriaceous between punctures. Notauli incomplete, reaching middle of mesoscutum, strong, weakly divergent grooves posteriorly, weak parallel creases anteriorly; grooves separated by 2.0 times width at posterior margin of mesoscutum; posteroental margin of groove very weakly raised, posterior margin of mesoscutum weakly depressed between grooves. Median line absent. Anterior lines moderately long, very weakly impressed, weakly convergent anteriorly, parallel posteriorly. Lateral lines weak. Mesoscutellum weakly flattened medially, rounded posteriorly, densely rugoreticulate, shining between rugae, in same plane as posterior of mesoscutum; axilla weakly rugulose; lateral bars broad, weakly depressed; foveae oval, narrow, closed posteriorly; septum very short, broad, not depressed; lateral shining strip with moderately developed posterodorsal extension (Fig. 50). Mesopleuron (Fig. 62) striate ventrally, weakly aciculate anterodorsally, shining smooth posterodorsally; dent weak; ventral pubescent area narrow; subalar triangle weakly pubescent, weakly pilose; ventral margin of subalar triangle slightly curved, with

narrow anterior punctopubescent area (as in Fig. 68); subalar pit broad. Metapleuron not depressed anteriorly, broad; supracoxal carina moderately developed, angulate, ventral portion not parallel to hind margin of mesopleuron; supracoxal tubercle, subspiracular carina moderately developed; antesp spiracular area large, moderately deep, shining smooth. Metanotal lateral foveae weakly pubescent, lateral margin shining smooth (as in Fig. 59). Propodeum with weak lateral pilosity, median pilosity absent; propodeal carinae strong, shagreened, setose, slightly divergent. Metasoma shorter than length of head plus mesosoma; T2+3 without visible suture, anterior pubescent patch with weak pilosity, posterodorsal margin with small triangular area with fine punctation. Forewing 2.6 mm long; radial cell length 2.9 times width; R weakly arcuate, longer than Rs1; Rs1 straight basally, arcuate distally, moderately oblique to wing margin; Rs2 bent distally (as in Fig. 74); areolet moderately small. Hind wing 1.69 mm long.

MALE. Allotype differs from lectotype as follows. Length 1.6 mm. Black; coxal bases, metasoma piceous brown; legs except coxal bases, antenna amber. Antenna with 14 antennomeres, length 1.83 mm, 0.95 of body length; A1 - 14 (mm): 0.12, 0.08, 0.20, 0.17, 0.17, 0.15, 0.15, 0.12, 0.12, 0.12, 0.12, 0.10, 0.08, 0.13; A3 strongly curved, deeply notched, strongly expanded distally (as in Fig. 72); A14 = 0.72 A12+13. Pronotum more strongly coriaceous. Mesoscutum

flattened posteriorly. Notauli longer, reaching past middle of mesoscutum. T2 separate from T3, relative lengths 0.33: 0.25; T3 with broad posterodorsal triangle of punctation.

TYPE MATERIAL. Lectotype, ♀ (USNM), 125 (red letters), Nevada Co. Cal., Through C. V. Riley, Type No. 3288 U.S.N.M., Lectotype, *Periclistus californicus* Ashmead 1896, Ritchie and Shorthouse 1984 (red label). Paralectotypes: 6 ♀♀, 2 ♂♂ with same labels as lectotype except 3 ♀♀, 1 ♂ missing red U.S.N.M. Type label.

OTHER MATERIAL EXAMINED (all non-type material reared from galls of *D. californica*). CALIFORNIA: 2 ♀♀, 3 ♂♂ (AMNH), Kelseyville; 13 ♀♀, 17 ♂♂ (AMNH), Santa Rosa; 2 ♀♀, 6 ♂♂ (AMNH), Salinas.

VARIATION. Female length 2.1 - 2.4 mm long; head and mesosoma often black, basal half of coxa sometimes brown to dark amber; interocular space 0.82 - 0.93 height of eye, malar space 0.38 - 0.44 eye height; LOL = 0.9 - 1.0D, POL = 1.7 - 1.8D, OOL = 1.8 - 2.0D; clypeus sometimes more distinct dorsally; pronotum, mesoscutum sometimes more strongly coriaceous between punctures, rarely weaker; notauli sometimes extending to middle of mesoscutum as weak creases (never complete); anterior lines sometimes very weak, almost imperceptible; lateral lines often more distinct; mesoscutellum often coriaceous or weakly shagreened between rugulae; septum sometimes absent; mesopleural sculpture often very weak (specimens from *D. californica*); dorsal

portion of ~~supracoxal~~ carina frequently very weak, ventral portion sometimes weak; forewing 2.4-2.8 mm long; radial cell length 2.7-2.9 times width; hind wing 1.6-1.9 mm.

HOSTS GALLS. *Diptolepis californica* (Beut.), *D. polita* (Ashmead).

DIAGNOSIS. Mesopleuron aciculate anterodorsally, usually striate ventrally; notauli incomplete, weakly divergent; median groove absent; anterior lines short, parallel to weakly concave; lateral margin of metanotal fovea smooth; female T2+3 with small posterodorsal triangle of punctation; male A3 strongly curved and expanded distally, deeply notched; Rs1 arcuate.

REMARKS. *Periclistus californicus* is most similar to *P. arefactus* McCracken and Egbert but can be recognised by the characters given above. *Periclistus arefactus* has the notauli shorter and more strongly divergent, has some weak transverse rugulae on the mesoscutum, and the sculpturing of the vertex is stronger.

Ashmead (1896) described *P. californicus* from two series of insects that were sent to him. One series was from California (labelled 125) and the other was from Wyoming and Colorado (labelled 3839). A lectotype has been selected from the Californian series; the series from Colorado and Wyoming are *P. piceus* Fullaway. The morphological differences between *P. californicus* and *P. arefactus* are slight and may not reflect interspecific variation.

Ashmead (1896) reported the host for *P. californicus* as the galls of *D. polita*; however, no other specimens of *P. californicus* have been seen from this host. The only other specimens of *P. californicus* that have been seen were reared from galls of *D. californica*. The specimens reared from *D. californica* galls differ slightly from the type-series in that the aciculation of the mesopleuron is often very weak. The Californian species of *Diplolepis* were not well known when Ashmead described *P. californicus*. Hence, it is possible that the original host determination was incorrect.

Periclistus cataractans n. sp.

Figs. 39, 51, 63.

FEMALE. (Holotype). Length 1.9 mm. Black; proximal antennomeres, tegula, hind coxa brown; legs, mandible except tip, anterior margin of metasoma amber. Head as wide as mesosoma, weakly subquadrate, gena below eye weakly angled; frons weakly coriaceous above antennal sockets, very weakly coriaceous between punctures below antennal sockets, moderately pubescent with small evident punctures; median protuberance strong, narrow, well defined; clypeus distinct dorsally, median portion of epistomal suture weak, strongly protuberant medially; radiating striae moderately strong, reaching inner orbit of eye and antennal socket; subantennal foveae shallow, indistinct; interocular space 0.79 of eye height, malar space 0.31 of eye height; vertex weakly raised; ocellar triangle weakly raised; ocelli not surrounded by weak, indistinct crescent shaped depression; frons with weak crease anterior to median ocellus; $LOL = 1.00$, $POL = 2.30$, $OOL = 1.70$. Antenna 1.60 mm, $A1 - A12$ (mm): 0.12, 0.08, 0.15, 0.17, 0.15, 0.15, 0.13, 0.12, 0.11, 0.11, 0.10, 0.21; $A12 = 1.0 A10 + A11$. Pronotum moderately pubescent, finely coriaceous, with evident punctures; anterolateral margin strongly pilose; posterolateral region without longitudinal rugulae; posterior part of plate very weak, lateral margins weakly convex. Mesoscutum (Fig. 39) strongly arched, anterior margin evenly arcuate; length 0.7

of width, with evident setigerous punctures, punctures small, weakly coriaceous between punctures. Notauli incomplete, reaching middle of mesoscutum, grooves strong, weakly divergent posteriorly, weak creases anteriorly; anterior pits absent; grooves separated by 2.0 times width at posterior margin of mesoscutum; posteroventral margin of groove not raised, posterior of mesoscutum weakly coriaceous, not depressed between grooves; posterior margin of mesoscutum weakly notched. Median groove present, incomplete, not reaching middle of mesoscutum. Anterior lines moderately long, weakly impressed, concave. Lateral lines weak. Mesoscutellum bulbous, finely rugoareolate, shining between rugae, not in same plane as posterior of mesoscutum; axilla weakly coriaceous, sparsely pubescent; lateral bars narrow, depressed; foveae transversely oval, with a few setigerous punctures, posterior margin indistinct; septum distinct, long, narrow; lateral shining strip with well developed posterodorsal extension (Fig. 51). Mesopleuron (Fig. 63) smooth, dent weak; ventral pubescent area broad, subalar triangle densely pubescent, moderately pilose; ventral margin of subalar triangle straight, without narrow puncto-pubescent area anteriorly (as in Fig. 69); subalar pit narrow. Metapleuron strongly depressed anteriorly, with dense ventral patch of pubescence; supracoxal carina, supracoxal tubercle, subspiracular carina absent; antespinal area large, deep, shining smooth. Metanotal lateral

fovea sparsely pubescent, lateral margin shagreened (as in Fig. 58). Propodeum with lateral and median pilosity; propodeal carinae strong, shagreened, sparsely setose, moderately divergent; intracarinial area weakly raised medially, weakly coriaceous, width 2.00 times height. Metasoma less than length of mesosoma plus head; T2+3 without visible suture, anterior pubescent patch moderately large, with moderately strong pilosity, posterior margin with narrow band of fine punctation. Forewing 2.5 mm long, 1.3 of body length; radial cell length 2.8 times width, 0.27 of forewing length; R weakly arcuate, slightly longer than Rs1; Rs1 straight, strongly oblique to wing margin; Rs2 bent medially (as in Fig. 75); areolet large, slightly elongate. Hind wing 1.6 mm long.

MALE. Allotype differs from holotype as follows. Length 1.7 mm. Coxal bases light brown; interocular space 0.78 of eye height; malar space 0.34 of eye height; antenna with 14 antennomeres, 1.63 mm, A1 - A14 (mm): 0.12, 0.08, 0.15, 0.15, 0.15, 0.14, 0.12, 0.12, 0.10, 0.10, 0.09, 0.08, 0.08, 0.15, A3 weakly curved, weakly expanded distally (as in Fig. 73); $A14 = 0.94 A12 + A13$; T2 separate from T3, relative lengths 0.37: 0.29; T2 without posterior band of punctation; T3 with broad posterior band of punctations, punctation not reaching anterior margin of T3.

TYPE MATERIAL. Holotype, ♀ (CNC No. _____), 3 mi. s. Waske-
 siu, P.A.N.P., Sask., Galls coll. 25-V-72, Coll. No. 27-72,
 J. D. Shorthouse, ex gall of *Diplolepis lens* Weld, Det. J.
 D. Shorthouse. Allotype, ♂ (CNC), with same data as holo-
 type. Paratypes (141 ♀♀, 346 ♂♂) (all specimens reared from
 galls of *Diplolepis lens* Weld or *D. roseifolia* (Cocker-
 ell)). ALASKA: 31 ♀♀, 23 ♂♂ (JDS), Fairbanks, University
 grounds, coll. 3-VIII-71, Coll. No. 30-71, J. D. Short-
 house; 2 ♀♀, 2 ♂♂ (JDS), Fairbanks, nr. Airport, coll. 5-
 VIII-71, Coll. No. 32-71, J. D. Shorthouse. ALBERTA: 14 ♀♀,
 3 ♂♂ (JDS), Peace River Block, Dunvegan Bridge, coll. 1-
 VIII-72, Coll. No. 244-72, J. D. Shorthouse; 6 ♀♀, 8 ♂♂
 (JDS), Athabasca, Athabasca River, coll. 2-VIII-72, Coll.
 No. 245-72, J. D. Shorthouse; 4 ♀♀ (JDS), La Biche River,
 Hwy. 63, coll. 2-VIII-72, Coll. No. 252-72, J. D. Short-
 house; 1 ♀ (JDS), 7 mi. s. Smokey Lake, N. Sask. River,
 coll. 3-VIII-72, Coll. No. 147-72, J. D. Shorthouse, ovi-
 positing into gall of *Diplolepis lens* Weld, det. J. D.
 Shorthouse; 1 ♀ (JDS), Lloydminster, coll. 5-VIII-72, J.
 D. Shorthouse, ovipositing into gall of *Diplolepis lens*
 Weld, det. J. D. Shorthouse; 2 ♀♀, 3 ♂♂ (JDS), Cypress
 Hills Prov. Pk., coll. 14-VII-80, J. D. Shorthouse (sweep);
 1 ♀ (JDS), George Lake, coll. 8-VII-69, J. D. Shorthouse
 (sweep). BRITISH COLUMBIA: 1 ♂ (JDS), Alaska Hwy, 29 mi. n.
 Muncho Lake, coll. 31-VII-71, Coll. No. 22-71, J. D. Short-
 house; COLORADO: 9 ♀♀, 2 ♂♂ (AMNH), Aspen, 23-VIII-29,

Rosa, Kinsey coll.; 1 ♀, 3 ♂♂ (AMNH), Ouray, 26-VIII-29, Inq. 10-V-30, Rosa, Kinsey coll.; 2 ♀♀ (USNM) (No locality), C. F. Baker. **MARYLAND**: 1 ♀ (USNM), Cabin John, coll. 21-VII-07, R. M. Fouts. **MASSACHUSETTS**: 1 ♀ (CORN), Woods-hole, coll. 18-VII-19. **MICHIGAN**: 3 ♀♀, 2 ♂♂ (AMNH), Cheboygen, gaff 3-X-27, Rosa, Kinsey coll.. **NEW MEXICO**: 2 ♀♀, 2 ♂♂ (USNM), Beulah, 1900, Rosa. **ONTARIO**: 22 ♀♀ (JDS), Azilda, RR 18, coll. 24-V-7.VI-77, J. D. Shorthouse (sweep); 8 ♀♀, 14 ♂♂ (JDS), Capreol, Hwy 69N, coll. 27-V-31-VI-77, J. D. Shorthouse (sweep); 3 ♀♀, 2 ♂♂ (JDS), 3 mi. s. Little Current, Manitoulin Island, coll. 2-V-78, Coll. No. 103-78, J. D. Shorthouse; 17 ♀♀, 8 ♂♂ (JDS), McClean Mtn. Rd, Manitoulin Is., coll. 10-V-79, Coll. No. 10-79, J. D. Shorthouse; 6 ♀♀ (JDS), 25 mi. w. Sudbury, coll. 25-V-79, Coll. No. 26-79, J. D. Shorthouse; 12 ♀♀, 10 ♂♂ (AJR), Poplar Road to Square Bay, Manitoulin Is., coll. 7-V-81, Coll. No. 703-81, A. J. Ritchie; 11 ♀♀, 9 ♂♂ (AJR), Hwy 17, 30 mi. w. Sudbury, coll. 6-V-82, Coll. No. 509-82, A. J. Ritchie. **SASKATCHEWAN**: 70 ♀♀, 72 ♂♂ (JDS), with same data as holotype; 20 ♀♀, 7 ♂♂ (JDS), P.A. Nat. Pk., W. Park Road, coll. 10-VIII-72, Coll. No. 155-72, J. D. Shorthouse; 19 ♀♀, 5 ♂♂ (JDS), P.A. Nat. Pk., W. Road, Neslin L., coll. 10-VIII-72, Coll. No. 161-72, J. D. Shorthouse; 15 ♀♀, 13 ♂♂ (JDS), P.A. Nat. Pk., 41 mi. from entrance, coll. 10-VIII-72, Coll. No. 182-72, J. D. Shorthouse; 4 ♀♀, 8 ♂♂ (JDS), Otter Rapids, 10 mi. n. Missinipe, coll. 24-VIII-72,

Coll. No. 186-72, J. D. Shorthouse; 4 ♀♀, 12 ♂♂ (JDS),
Waskeieu R. X, Sask. Hwy. 2, coll. 23-VIII-72, Coll. No.
188-72, J. D. Shorthouse; 10 ♀♀, 12 ♂♂ (JDS), 8 mi. s.
LaRonge, coll. 24-VIII-72, Coll. No. 190-72, J. D. Short-
house; 4 ♀♀, 1 ♂ (JDS), 22 mi. w. Flin Flon, Hwy 165, coll.
24-VIII-72, Coll. No. 192-72, J. D. Shorthouse; 19 ♀♀, 10
♂♂ (JDS), 8 mi. n. Smeaton, coll. 25-VIII-72, Coll. No.
193-72, J. D. Shorthouse; 2 ♀♀, 2 ♂♂ (JDS), E. Boundry,
Nipawin Prov. Pk, coll. 25-VIII-72, Coll. No. 199-72, J. D.
Shorthouse; 11 ♀♀, 11 ♂♂ (JDS), 5 mi. w. Langham, coll. 29-
VIII-72, Coll. No. 201-72, J. D. Shorthouse; 17 ♀♀, 14 ♂♂
(JDS), 10 mi. w. Belbutte, coll. 30-VIII-72, Coll. No. 207-
72, J. D. Shorthouse; 28 ♀♀, 50 ♂♂ (JDS), P.A. Nat. Pk.,
Waskeieu R. Bridge, coll. 30-VIII-72, Coll. No. 210-72, J.
D. Shorthouse; 1 ♀, 1 ♂ (JDS), E. Mont Nebo, Small Creek,
coll. 30-VIII-72, Coll. No. 213-72, J. D. Shorthouse; 16
♀♀, 2 ♂♂ (JDS), W. Rosthorn, N. Sask. R., coll. 5-IX-72,
Coll. No. 225-72, J. D. Shorthouse; 7 ♀♀, 10 ♂♂ (JDS), P.A.
Nat. Pk., coll. 23-IX-72, Coll. No. 226-72, J. D. Short-
house; 5 ♀♀, 3 ♂♂ (JDS), Prince Albert N.P., coll. 25-IX-
72, Coll.No. 228-72, J.D. Shorthouse; 2 ♀♀ (JDS), Pike
Lake, coll. 6-X-72, Coll. No. 231-72, J. D. Shorthouse; 8
♀♀, 3 ♂♂ (JDS), Cypress Hills, coll. 8-IX-72, Coll. No.
236-72, J. D. Shorthouse; 20 ♀♀, 3 ♂♂ (JDS), Cypress Hills,
coll. 8-IX-72, Coll. No. 238-72, J. D. Shorthouse; 21 ♀♀, 4
♂♂ (JDS), Nipawin, N. Sask. R., coll. 25-VIII-72, Coll. No.

261-72, J. D. Shorthouse. UTAH: 2 ♀♀, 1 ♂♂ (AMNH), Bountiful, Inq. 16.15.28, gall 9.12.27, Rosa, B. + H. J. Pack coll.. YUKON TERRITORY: 1 ♀, 1 ♂ (JDS), 10 mi. n. Pelly River River Crossing, coll. 17-VIII-71, Coll. No. 52-71, J. D. Shorthouse; 5 ♀♀, 5 ♂♂ (JDS), 55 mi s. Carmacks, roadside Rosa, coll. 18-VIII-71, Coll. No. 54-71, J. D. Shorthouse.

VARIATION. Female length: 1.3 - 2.0 mm. ($\bar{x}$ = 1.7 ± 0.1 mm, N = 10). Male length: 1.3 - 1.8 mm ($\bar{x}$ = 1.6 ± 0.2 mm, N = 10). Western specimens and very small specimens sometimes brown and females usually have a remnant of the suture between T2 and T3; western specimens usually with weak supracoxal carina and subspiracular carina. Specimens from Peace River Block, Alberta, have supracoxal carina strong.

HOST GALLS. *Diplolepis lens* Weld, *D. rosaefolia* (Cockerell).

DIAGNOSIS. Gena weakly angulate below eye; female $A_{12} = 1.0 A_{10} + A_{11}$; male A_3 weakly notched, weakly curved, weakly expanded distally; mesoscutum strongly arched; notauli incomplete; mesoscutellum bulbous, finely rugoreticulate, foveae transversely oval; lateral shining strip with well developed posterodorsal extension; mesopleuron shining smooth; lateral margin of metanotal lateral fovea shagreened; female T2+3 usually with narrow band of fine posterior punctation.

BIOLOGY. Shorthouse (1975) studied the biology of *Periclistus* inhabiting the galls of *Diplolepis* *lens*. Laboratory reared *P. cataractans* emerge approximately two weeks after emergence of the gall inducer. Galls collected from relatively northern localities in Alberta and Saskatchewan yielded *Periclistus* earlier than did those collected from more southerly localities. *Periclistus cataractans* emerges slightly before *P. gracilicollis*. This indicates that *P. cataractans* is closely adapted to the life cycle of its host gall inducer.

Periclistus cataractans primarily attacks galls that are initiated early in the season. Both immature and maturing galls are attacked and early differentiation of the sclerenchyma layer does not appear to prevent *P. cataractans* from attacking maturing galls of *D. lens*. Up to 70% of galls are attacked by *P. cataractans*, although the percentage of galls yielding *Periclistus* is much lower due to subsequent attack by entomophagous insects.

The ovipositing female kills the host *D. lens* larva with her ovipositor. Nutritive cells induced by *D. lens* degenerate and the gall chamber becomes lined with parenchymous cells. Each *P. cataractans* larva becomes surrounded by parenchyma cells, with a subsequent redevelopment of a thick layer of nutritive cells. A secondary layer of sclerenchyma cells forms around each endogall. Unlike the normal gall, in which the sclerenchyma layer is limited to the

dorsal and ventral regions, *Periclistus* modified galls have a complete sclerenchyma layer. *Periclistus cataractans* initiates the lowest number of endogalls (1.4 ± 0.6) per host gall of the six Rose leaf galls studied by Shorthouse (1975). Galls containing only one larva of *P. cataractans* are much smaller than the normal gall, while those with several *Periclistus* larvae are larger.

ETYMOLOGY. The specific epithet refers to the hardening and bumpiness caused by this species on the lens shaped gall.

REMARKS. *Periclistus cataractans* is most similar to *P. fusicolus* and *P. gracillicolus* but differs in the relative length of the distal antennomeres and the shape of the head. *Periclistus fusicolus* has the distal antennomere much longer than in *P. cataractans*, while *P. gracillicolus* has a relatively shorter distal antennomere. *Periclistus gracillicolus* also has arcuate genae below the eye as opposed to the weakly angulate gena in the other two species. These three species, along with *P. ashmeadi*, differ from other leaf gall inhabiting *Periclistus* by having the lateral margin of the metanotal fovea shagreened.

Periclistus fusicolus n. sp.

Figs. 41, 52, 64, 73.

FEMALE. (Holotype). Length 1.8 mm. Black; antenna, tegula, metasoma except anterior margin dark brown; legs, mandibles except tips, anterior margin of metasoma amber. Head as wide as mesosoma, weakly subquadrate, gena below eye weakly angled; frons weakly coriaceous above antennal sockets, smooth between punctures below antennal sockets, moderately pubescent with small evident punctures; median protuberance weak, broad, poorly defined; clypeus distinct dorsally, median portion of epistomal suture weak, weakly protuberant medially; radiating striae weak, reaching inner orbit of eye but not antennal socket; subantennal foveae shallow, indistinct; interocular space 0.83 of eye height, malar space 0.37 of eye height; vertex strongly raised; ocellar triangle weakly raised; ocelli not surrounded by crescent shaped depression; frons with weak crease anterior to median ocellus; $LOL = 1.0D$, $POL = 2.0D$, $OOL = 1.7D$. Antenna 1.48 mm. $A1 - A12$ (mm): 0.12, 0.08, 0.13, 0.13, 0.13, 0.12, 0.12, 0.12, 0.10, 0.09, 0.09, 0.25; $A12 = 1.39 A10 + A11$. Pronotum moderately pubescent, finely coriaceous, with evident punctures; anterior pilosity weak; posterolateral region with longitudinal rugulae; posterior part of plate very weak, lateral margins weakly convex. Mesoscutum (Fig. 41) strongly arched, anterior margin evenly arcuate, length 0.8 of width, with evident setigerous punctures, punctures

small, weakly coriaceous between punctures. Notauli incomplete, not reaching middle of mesoscutum, grooves moderately strong, strongly divergent posteriorly, weak creases anteriorly; anterior pits absent; grooves separated by 2.0 times width at posterior margin of mesoscutum; posteroventral margin of groove not raised, posterior of mesoscutum shining smooth, not depressed between grooves; posterior margin of mesoscutum distinctly notched. Median line present, incomplete, not reaching middle of mesoscutum. Anterior lines moderately long, weakly impressed, concave. Lateral lines distinct, very weak creases. Mesoscutellum bulbous, finely rugoreticulate, shining between rugae, not in same plane as posterior of mesoscutum; axilla weakly coriaceous, sparsely pubescent; lateral bars narrow, depressed; foveae transversely oval, with a few setigerous punctures, closed posteriorly; septum distinct, short, narrow; lateral shining strip with well developed posterodorsal extension (Fig. 52). Mesopleuron (Fig. 64) smooth, dent strong; ventral pubescent area broad; subalar triangle densely pubescent; ventral margin of subalar triangle straight, without narrow punctopubescent area anteriorly (as in Fig. 69); subalar pit narrow. Metapleuron weakly depressed anteriorly; supracoxal carina, supracoxal tubercle, subspiracular carina absent; antespiracular area small, shallow, shining smooth. Metanotal lateral fovea sparsely pubescent, lateral margin shagreened (as in Fig. 58). Propodeum without lat-

eral or median pilosity; propodeal carinae strong, shagreened, sparsely setose, moderately divergent; intracarinial area weakly raised medially, weakly coriaceous, width 1.75 times height. Metasoma shorter than length of head plus mesosoma; T2+3 without visible suture, anterior pubescent patch small, with weak pilosity, posterodorsal margin with narrow band of fine punctation. Forewing 2.1 mm long; radial cell length 3.5 times width; R weakly arcuate, longer than Rs1; Rs1 almost straight basally, strongly arcuate distally, strongly oblique to wing margin; Rs2 bent medially (as in Fig. 75); areolet large, slightly elongate. Hind wing 1.4 mm long.

MALE. Allotype differs from holotype as follows. Length 1.4 mm. Coxal bases dark brown. Interocular space 0.93 of eye height; malar space 0.40 of eye height; antenna with 14 antennomeres, A1 - A14 (mm): 0.10, 0.07, 0.12, 0.12, 0.10, 0.10, 0.10, 0.09, 0.09, 0.09, 0.09, 0.08, 0.08, 0.15, A3 weakly curved, weakly expanded distally (Fig. 73); A14 = $0.94 A_{12} + 13$; T2 separate from T3, relative lengths 0.28: 0.21; T2 without posterior band of punctation; T3 with narrow posterior band of punctations, punctation not reaching anterior margin of T3.

TYPE MATERIAL. Holotype, ♀ (CNC. No. _____), 1 ml. s. Arnprior, ON., coll. 2-V-77, Coll. No. 113-77, J. D. Shorthouse, ex gall of *Diplolepis fusiformis* (Ashmead). Allotype, ♂ (CNC), with same data as holotype. Paratypes (174

99, 162 ♂♂) (all specimens reared from galls of *Diptolepis fusiformans* (Ashmead) except as noted). ALBERTA: 14 ♀♀, 13 ♂♂ (JDS), 8 mi. s. Lethbridge, coll. 16-VI-71, Coll. No. 6-71, J. D. Shorthouse; 2 ♂♂ (JDS), Taber, Taber Prov. Park, coll. 14-X-83, Coll. No. 513-81, Shorthouse & LaLonde, ex unmodified gall of *D. (?) nodulosa* (Ashmead). ARIZONA: 3 ♀♀, 8 ♂♂ (LHW, USNM), Flagstaff, bred from gall 50, 15600. CALIFORNIA: 8 ♀♀, 7 ♂♂ (AMNH), S. Bernadino, gall 31-I-20. COLORADO: 20 ♀♀, 11 ♂♂ (AMNH), Manitou, Inq. spr. 1920, gall 29-IV-20, Rosa, Kinsey coll.; 1 ♀ (USNM), Colorado Springs, bred from gall 50. ONTARIO: 25 ♀♀, 34 ♂♂ (JDS), with same data as holotype; 1 ♀, 1 ♂ (JDS), 6 mi. n. Kagawong, Manitoulin Is., coll. 2-X-76, Coll. No. 133-76, J. D. Shorthouse; 4 ♀♀, 2 ♂♂ (JDS), Manitoulin Is., McClean Mtn. Rd., coll. 2-V-78, Coll. No. 113-78, J. D. Shorthouse; 4 ♀♀, 2 ♂♂ (JDS), Manitoulin Is., McClean Mtn. Rd., coll. 2-V-78, Coll. No. 116-78, J. D. Shorthouse; 21 ♀♀, 1 ♂♂ (JDS), 3 mi. s. Little Current, Manitoulin Is., coll. 10-V-79, Coll. No. 9-79, J. D. Shorthouse; 3 ♀♀, 1 ♂ (JDS), 3 mi. s. Little Current, Manitoulin Is., coll. 10-V-79, Coll. No. 12-79, J. D. Shorthouse; 1 ♂ (AJR), Manitoulin Is., McClean Mtn. Rd., coll. 7-V-81, Coll. No. 722-81, A. J. Ritchie; 2 ♀♀, 2 ♂♂ (AJR), Hwy 6, Goat Is. nr. Manitoulin Is., coll. 26-IX-81, Coll. No. 761-81, A. J. Ritchie; 4 ♀♀, 2 ♂♂ (AJR), Spanish, coll. 22-V-83, Coll. No. 507-83, ex unmodified gall of *D. nodulosa*, R. DeClerck; 1 ♂ (AJR),

Manitoulin Is., McClean Mtn. Rd., coll. 7-V-81, Coll. No. 727-81, A. J. Ritchie; 1 ♀, 4 ♂♂ (AJR), Manitoulin Is., McClean Mtn. Rd., coll. 1-VI-83, Coll. No. 534-83, A. J. Ritchie, 1 ♀, 3 ♂♂ (AJR), Manitoulin Is., 3 mi. s. Maple Pt., coll. 1-VI-83, Coll. No. 536-83, A. J. Ritchie; 2 ♀♀ (AJR), Manitoulin Is., 3 mi. s. Maple Pt., coll. 1-VI-83, Coll. No. 537-83, A. J. Ritchie, 1 ♀, 1 ♂ (AJR), Manitoulin Is., 2 mi. s. Maple Pt., coll. 1-VI-83, Coll. No. 540-83, A. J. Ritchie; 1 ♀ (AJR), Manitoulin Is., 2 mi. s. Maple Pt., coll. 1-VI-83, Coll. No. 544-83, A. J. Ritchie; 1 ♀, Manitoulin Is., Square Bay Beach, coll. 2-VI-83, Coll. No. 568-83, A. J. Ritchie; 6 ♀ (AJR), Manitoulin Is., 1 mi. s. Little Current, coll. 3-VI-83, Coll. No. 578-83, A. J. Ritchie. OREGON: 3 ♂♂ (AJR), Benton Co., on *Rosa pisocarpa*, em. 17 Feb. 1983, P. Hanson. QUEBEC: 4 ♂♂ (JDS), Alouette Is., coll. 4-V-77, Coll. No. 113-77, J. D. Shorthouse. SASKATCHEWAN: 26 ♀♀, 26 ♂♂ (JDS) 15 mi. e. Saskatoon, coll. 10-XI-71, Coll. No. 67-71, J. D. Shorthouse, ex (unmodified?) galls of *Diptolepis trifurcata* Shorthouse and Ritchie or *D. nodulosa*; 4 ♀♀, 3 ♂♂ (JDS), 15 mi. e. Saskatoon, coll. 18-11-72, Coll. No. 3-72, J. D. Shorthouse; 6 ♀♀, 6 ♂♂ (JDS), 15 mi. e. Saskatoon, coll. 10-IV-72, Coll. No. 7-72, J. D. Shorthouse; ex unmodified galls of *D. nodulosa*; 14 ♀♀, 24 ♂♂ (JDS), Hwy 17, 18 km. e. Alta.-Sask. border, coll. 15-IX-81, Coll. No. 503-81, Shorthouse & LaLonde, ex unmodified gall of *D. nodulosa*; UTAH: 1 ♀ (AMNH), Bounti-

ful, gall 12-IX-27, Rosa, B. + H. J. Pack coll..

VARIATION. Female length 1.4 - 1.9 mm. ($\bar{x} = 1.6 \pm 0.2$ mm, $N = 10$). Male length 1.3 - 1.7 mm. ($\bar{x} = 1.4 \pm 0.1$ mm, $N = 10$). Smaller specimens with weaker sculpture. Eastern specimens sometimes have an apparent median line due to a change in mesoscutal sculpture; also, females have T2+3 very rarely without punctures, frequently with narrow band of punctures and an enlarged dorsal triangular area of punctation. Western specimens tend to have the anterior lines less distinctly convex and less distinct than those from Eastern North America. Specimens from Colorado differ from those collected in Ontario as follows: fuscous, anterior half of T2+3 (♀) almost amber; mesoscutum less strongly arched, depressed posteriorly between notauli, notauli sometimes abruptly widened posteriorly; foveae larger, rounder; posterior band of punctation (♀ T2+3, ♂ T3) broad, distinct. Specimens from California are similar to those from Colorado except the foveae are shallow and less distinct, the septum is usually broad and rugulose, and the supracoxal carina is weakly present. The specimen from Utah has stronger sculpturing, a stronger supracoxal carina, and does not have a mesopleural dent.

HOST GALLS. *Diptolepis fusiformis* (Ashmead), *D. nodulosa* (Ashmead), *D. triforce*, Shorthouse and Ritchie.

DIAGNOSIS. Genae weakly angulate below eye; female $A_{12} > 1.2 A_{10} + A_{11}$; male $A_{14} > 0.9 A_{12} + A_{13}$; male A_3 weakly notched, weakly curved, weakly expanded distally; mesoscutum strongly arched; notauli incomplete; mesoscutellum bulbous, finely rugoreticulate, foveae transversely oval; lateral shining strip with well developed posterodorsal extension; mesopleuron shining smooth; lateral margins of metanotal lateral foveae shagreened; female T_{2+3} usually with narrow band of fine posterior punctation.

BIOLOGY. The usual host of *Periclistus fusicolus* are the galls of *Diplolepis fusiformans* (Ashmead) and it appears that other host records are atypical. All three recorded hosts oviposit in immature buds and it is possible that ovipositing *P. fusicolus* females cannot distinguish between the galls of these three species. It is quite likely that the galls of these species appear at different times during the season. Unfortunately, very little is known about the biology of either *D. nodulosa* or *D. fusiformans*. There is no gross modification of the host gall and it is therefore impossible to detect whether a gall of *D. fusiformans* has been attacked by *P. fusicolus*.

ETYMOLOGY. This species is named after its usual host, *Diplolepis fusiformans*.

REMARKS. *Periclistus fusicolus* is very similar to *P. cataractens* and *P. gracilicollis*, but differs primarily in the length of the last antennomere. Both male and female *P.*

fusicolus have the distal antennomere extremely elongated ($\varnothing A12 > 1.2 A10 + A11$; $\sigma A14 > 0.9 A12 + A13$). *Periclistus fusicolus* also differs from *P. gracilicollis* by having the genae slightly angled below the eyes and having a median line on the mesoscutum.

Periclistus fusicolus is apparently an extremely variable species. It is quite likely that the specimens from Arizona and Utah, California, Colorado, and eastern North America represent different subspecies. However, without additional western material, it is difficult to distinguish between local populational differences and true subspecies. Therefore, I leave this decision for the future.

Periclistus gracilicollis n. sp.

Figs. 42, 53, 65:

FEMALE. (Holotype). Length 1.75 mm. Black; posterior half of T2+3 dark piceous brown; anterior half of T2+3 piceous brown; mandible, basal antennomeres dark amber; distal antennomeres, tegula, remainder of legs amber. Head as wide as mesosoma, subtriangular, gena arcuate below eye; vertex moderately coriaceous, with sparse setigerous punctures; frons above antennal sockets moderately coriaceous, weakly coriaceous and sparsely pubescent below antennal sockets; median protuberance well developed, broad; clypeus distinct, protruding medially continuous with ventral portion of median protuberance; radiating striae very weak, just reaching antennal socket and inner orbit of eye; sub-antennal foveae distinct, narrow, shining; malar space 0.29 of eye height; interocular space 0.82 of eye height; vertex, ocellar triangle weakly raised; ocelli surrounded by weak, indistinct crescent shaped depression; LOL = 1.0D, POL = 2.3D, OOL = 1.9D. Antenna 1.32 mm; A1 -A12 (mm): 0.08, 0.06, 0.12, 0.12, 0.12, 0.12, 0.11, 0.11, 0.10, 0.10, 0.08, 0.20; A12 = 1.1 A10 + A11. Pronotum coriaceous, moderately pubescent, posterolateral rugulae absent, without evident punctures or tubercles; anterolateral margin weakly pilose; posterior part of pronotal plate very weak, lateral margins strongly convex, barely reaching posterior margin of pronotum. Mesoscutum (Fig. 42) strongly arched, anterior

margin evenly arcuate, with sparse fine setigerous punctures, punctures small, weakly shagreened between punctures; posterior of mesoscutum between notauli shining and slightly depressed. Notauli incomplete, not quite reaching middle of mesoscutum, grooves strong, straight, divergent; grooves separated by 4.0 times width at posterior margin of mesoscutum; posterior margin of mesoscutum without median notch, not depressed between posterior of notauli. Median line absent. Anterior lines moderately short, very weakly impressed, strongly convex. Lateral lines weak. Mesoscutellum bulbous, finely rugoreticulate, shagreened between rugae, not in same plane as posterior of mesoscutum; axilla weakly rugulose, sparsely pubescent; lateral bars very short, narrow, depressed; foveae transversely oval, shining, closed posteriorly; septum long, not depressed; lateral shining strip with well developed posterodorsal extension (Fig. 53). Mesopleuron (Fig. 65) shining smooth; dent strong; ventral pubescent area narrow; subalar triangle weakly pubescent, weakly pilose; ventral margin of subalar triangle straight, smooth anteriorly (as in Fig. 69); subalar pit broad. Metapleuron depressed anteriorly, narrow; supracoxal carina very weak, straight, not parallel to anterior margin of metapleuron; supracoxal tubercle, subspiracular carina absent; antespiracular area small, shining smooth except for setigerous punctures. Metanotal lateral foveae densely pubescent, lateral margin shagreened

(as in Fig. 58). Propodeum without median or lateral pilosity; propodeal carinae moderately strong, shagreened, straight and slightly divergent; intracarinial area width 1.4 of height. Metasoma shorter than length of head plus mesosoma; T2+3 with trace of suture; anterior pubescent patch moderately strong, pilosity weak; posterodorsal margin with narrow band of fine punctation. Forewing 2.0 mm long; radial cell length 2.75 times width, R very weakly arcuate, longer than Rs1; Rs1 straight, moderately oblique to wing margin; Rs2 bent medially (as in Fig. 75); areolet large, equilateral, anterior and posterior margins weak. Hind wing 1.4 mm long.

MALE. Allotype differs from holotype as follows. Length 1.5 mm; mesosoma dark piceous brown; head slightly wider than mesosoma; antenna with 14 antennomeres, 1.4 mm; A1 - A14 (mm): 0.09, 0.08, 0.13, 0.12, 0.12, 0.12, 0.11, 0.11, 0.09, 0.08, 0.08, 0.8, 0.08, 0.12; A3 weakly curved, broadly notched, not expanded distally (as in Fig. 73); A14 = 0.75 A12 + A13; interocular space 0.76 of eye height; OOL = 1.4D; mesoscutellum more finely rugoreticulate; subalar triangle densely pubescent; supracoxal carina moderately weak; T2 separate from T3, relative lengths 0.27:0.21; T2 with only a few sparse hairs; T3 with broad posterodorsal band of punctations, punctation nearly reaching anterior margin of T3, band narrowing ventrally. Forewing 1.9 mm; radial cell length 3.0 times width; hindwing 1.3 mm.

TYPE MATERIAL. Holotype, ♀ (CNC No. ____). Labelled: Pike Lake Provincial Park, SASK., coll. 6-IX-72, em. spring 1973, Lab reared, Coll. No. 239-72, J. D. Shorthouse, ex gall of *Diplolepis gracilis* (Ashmead). Allotype, ♂ (CNC) with same data as holotype. Paratypes (16 ♀♀, 18 ♂♂) (all specimens reared from galls of *Diplolepis gracilis* (Ashmead)). ALBERTA: 4 ♀♀, 4 ♂♂ (JDS), Whitemud Creek, Edmonton, coll. 6-X-72, em. spring 1973, Coll. No. 229-72, J. D. Shorthouse. NORTH DAKOTA: 5 ♀♀, 4 ♂♂ (JDS), Grand Forks, coll. 15-IX-48, G. C. Wheeler. SASKATCHEWAN: 37 ♀♀, 10 ♂♂ (JDS), with same data as holotype.

VARIATION. Female length 1.4 - 2.0 mm, ($\bar{x} = 1.6 \pm 0.1$ mm, $N = 10$; male length 1.1 - 1.6 mm ($\bar{x} = 1.4 \pm 0.1$ mm, $N = 10$). Specimens from North Dakota tend to be larger than those from Alberta or Saskatchewan; these specimens do not have the mesoscutum as strongly arched and the mesoscutellum does not protrude above the mesoscutum as distinctly. Smaller specimens from all localities show weaker sculpturing and a weaker development of the median ridge and subantennal pits.

HOST GALLS. *Diplolepis gracilis* (Ashmead).

DIAGNOSIS. Genae arcuate below eye; female $A_{12} = 1.0 - 1.1$ $A_{10} + A_{11}$; male $A_{14} 0.75 A_{12} + A_{13}$; male A_3 weakly notched, weakly curved, weakly expanded distally; mesoscutum strongly arched; notauli incomplete; median line absent; mesoscutellum bulbous, finely rugoreticulate, foveae transversely

oval; lateral shining strip with well developed posterodorsal extension; mesopleuron shining smooth; lateral margins of metanotal lateral foveae shagreened; female T2+3 usually with narrow band of fine posterior punctation.

BIOLOGY. *Periclistus gracillicolus* is restricted to attacking the galls of *Diplolepis gracilis* (Ashmead). Shorthouse (1975) examined the biology of *Periclistus* inhabiting the galls of *D. gracilis*; his findings are summarized here. Adult *D. gracilis* emerge in mid-summer and immature galls appear shortly thereafter. Adult *P. gracillicolus* emerge shortly after *D. gracilis* and oviposit into the immature galls. As in the other leaf galls, the *Diplolepis* larva is killed by the ovipositing female *Periclistus* and eggs are laid on the ental surface of the gall chamber.

After hatching, the *Periclistus* larvae commence feeding; this induces additional tissue growth and the *Periclistus* larva becomes enclosed in its own endogall. Normal *D. gracilis* galls have two distinct sclerenchyma layers; there are a pair of well lignified discs, and also a weakly lignified, thick layer that circumscribes the chamber (as in *D. bicolor*). Shorthouse (1975) indicates that the weakly lignified circumscribing layer of sclerenchyma is absent in *Periclistus* modified galls. However, the strongly lignified sclerenchyma discs are expanded to form circumscribing sclerenchyma layer. Each endogall is also surrounded by a layer of strongly lignified sclerenchyma which is

continuous with the outer layer.

Relatively few galls of *D. gracilis* are attacked by *P. gracillicolus*; less than 20% of mid-season and mature galls examined were inhabited by *P. gracillicolus*, the lowest percentage of the six leaf galls studied by Shorthouse (1975). Usually, there is only a single *Periclistus* larva within each *D. gracilis* gall ($N = 1.8 \pm 1.0$); when more than one larva is present, each larva becomes surrounded by its own endogall. Galls of *D. gracilis* attacked by *P. gracillicolus* are smaller than normal galls, in contrast to the effect of *Periclistus* on the size of other host galls. Mature *Periclistus* modified galls are thicker, rounder, and have blunter tubercles than do normal galls; modified galls are also usually red compared to the normal whitish color.

ETYMOLOGY. This species is named after the gall which it inhabits.

REMARKS. *Periclistus gracillicolus* is most similar to *P. cataractans* and *P. fusicolus*, but can be distinguished by the relatively short distal antennomere and by the gena being arcuate below the eye. All three species have the mesoscutum strongly arched, the posterolateral margins of the metanotal lateral fovea coriaceous, and male A3 weakly curved and weakly expanded distally.

Periclistus gracillicolus is the rarest of all the species of *Periclistus*. This is due, in part, to the scarcity of the host gall, and also to the low percentage of

galls attacked by *P. gracillicolus*. The low numbers of specimens collected, and the extreme similarity between *P. gracillicolus* and *P. cataractans* suggests that these may be one species. The observed differences may be host-gall induced and therefore do not reflect specific differences. *Periclistus gracillicolus* may then represent the offspring of *P. cataractans* females that made a mistake in selecting a site for oviposition. Since the galls of *D. lens* and *D. gracilis* are frequently found on the same plant (Shorthouse 1975), this is not improbable. However, until this can be shown experimentally, I believe that *P. gracillicolus* is a valid species.

Periclistus piceus Fullaway

Figs. 43, 54, 70.

Periclistus piceus Fullaway 1911: 374. ♀, ♂.

TYPE: Lectotype, ♀ (CAS), designated here. Labelled:

L. S. Jr. U. Lot 498, sub 2; Lectotype, *Periclistus piceus* Fullaway 1911. Ritchie and Shorthouse 1984 (red label).

FEMALE. (Lectotype). Length 2.3 mm. Dark piceus brown; antenna, tegula, procoxa, anterior two thirds of T2+3 brown; mandible, meso- and metacoxa dark amber; remainder of legs amber. Head wider than mesosoma, subquadrate; gena angled below eye; frons weakly coriaceous above antennal sockets, very weakly coriaceous (almost shining) below antennal sockets, with very fine setigerous punctures; median protuberance weak, poorly defined; clypeus indistinct dorsally, slightly impressed, medially protuberant (continuous with median protuberance); radiating striae moderately strong, reaching antennal socket and inner orbit of eye; subantennal fovea weak, indistinct; interocular space 0.91 of eye height; malar space 0.40 of eye height; vertex, ocellar triangle weakly raised; ocelli surrounded by weak, indistinct crescent shaped depression; LOL = 0.7D, POL = 1.6D, OOL = 1.6D. Antenna 2.01 mm long; A1 - A12 (mm): 0.15, 0.09, 0.19, 0.20, 0.20, 0.19, 0.17, 0.17, 0.15, 0.13, 0.11, 0.26; A12 = 1:1 A10 + A11. Pronotum with fine setigerous tubercles, shining between tubercles, densely pilose along

anterior margin, without posterolateral rugosity; posterior part of plate weak, lateral margins strongly curved, not quite reaching posteromedial margin. Mesoscutum (Fig. 43) strongly arched, somewhat flattened posteriorly and near anterior lines; length 0.86 of width, with fine setigerous punctures, finely coriaceous between punctures. Notauli very strong, gradually widening posteriorly, incomplete, not reaching middle of mesoscutum, straight, strongly divergent; grooves separated by 1.3 times their width at posterior margin of mesoscutum. Median groove very weak crease, complete except absent near posterior margin of mesoscutum. Anterior lines long, close together, not quite reaching middle of mesoscutum, concave, slightly raised. Lateral lines very weak. Mesoscutellum evenly rounded, densely rugulose; axilla shining; lateral shining strip with well developed dorsal extension (Fig. 54); fovea large, deep anteriorly and laterally, shallower posteriorly, gradually merging with anterior rugosity of disc; septum long, distinct, merging with anterior rugosity of disc. Mesopleuron (Fig. 70) shining smooth, ventral pubescent area narrow; subalar triangle weakly pubescent, pilose anteriorly and posteriorly; ventral margin smooth (as in Fig. 69) sulcate; subalar pit narrow, deflexed, Metapleuron depressed anteriorly, broad; supracoxal carina very weak, weakly curved, ventral portion not parallel to posterior margin of mesopleuron; subspiracular carina and tubercle absent;

antespiracular area deep, shining smooth. Metanotal lateral foveae weakly pubescent; lateral margin coriaceous anterior to spiracular flap, shining smooth medially, coriaceous posteriorly. Propodeum with lateral pilosity, without median pilosity; propodeal carinae moderately strong, weakly divergent, straight, shagreened, pubescent; intracarinial area shining, glabrous except dorsal pilose area. Metasoma equal to length of head plus mesosoma; T2+3 without visible suture, hind margin shining smooth; anterior pubescent patch moderately developed, with weak anterior pilosity. Forewing 2.8 mm; radial cell distinctly closed, length 2.8 times width; R weakly arcuate, longer than Rs1; Rs1 straight basally, obliquely angled to wing margin, weakly arcuate distally; Rs2 bent medially (as in Fig. 75); areolet moderately developed, not elongate, posterior side very weak. Hind wing 1.85 mm.

MALE. Allotype differs from lectotype as follows. Length 2.0 mm. Antenna with 14 antennomeres, A1 - A14 (mm): 0.15, 0.08, 0.21, 0.21, 0.19, 0.19, 0.17, 0.17, 0.12, 0.12, 0.12, 0.12, 0.11, 0.18; $A14 = 0.78 A12 + A13$; A3 strongly curved, broadly notched, expanded distally (as in Fig. 72). Interocular space 0.85 eye height, malar space 0.30 eye height; $LOL = 0.5D$, $OOL = 1.4D$. Posterior part of pronotal plate stronger, more distinct. Mesoscutum flattened posteriorly, length = 1.0 times width. Notauli complete, reaching anterior margin as distinct grooves; an-

terior pits present; grooves separated by 2.0 times posterior width at posterior margin of mesoscutum. Median groove strong near posterior margin of mesoscutum, weak crease anteriorly. Anterior lines more widely separated. Mesoscutellar areola weakly developed. Propodeum with median pilosity. Metasoma shorter than head plus mesosoma; T2 separate from T3, relative lengths 0.44: 0.30. T3 with broad posterodorsal triangle of punctation. Forewing 2.7 mm; hind wing 2.0 mm.

TYPE MATERIAL. Lectotype, ♀ (CAS), L. S. Jr. U. Lot 498, sub 2, Paratype (yellow label); Lectotype, *Periclistus piceus* Fullaway, Ritchie and Shorthouse 1984. Paralectotypes: 3 ♀♀, 10 ♂♂ (CAS), with same data as lectotype; 7 ♀♀, 17 ♂♂ (USNM, AMNH, CAS), with same data as lectotype but collected Pt. Arena, Mendocino, CA (1 ♀, 2 ♂♂ also labelled Stanford U., CA).

OTHER MATERIAL EXAMINED (179 ♀♀, 99 ♂♂): remains of 8 specimens (CAS), with same data as lectotype. CALIFORNIA: 10 ♀♀, 16 ♂♂ (JDS), 2 mi. w. Fairfield, Solano Co.; 1 ♀ (LHW), Berkeley; 63 ♀♀, 13 ♂♂ (AMNH), El Toro; 12 ♀♀, 13 ♂♂ (AMNH), Santa Rosa; 18 ♀♀, 5 ♂♂ (AMNH), Albion; 2 ♀♀ (AMNH), Gilroy; 5 ♀♀ (AMNH), Sequoia Nat. Pk. COLORADO: 2 ♀♀, 6 ♂♂ (USNM; Paralectotype, *P. californicus* Ashmead). OREGON: 3 ♀♀, 4 ♂♂ (AJR), St. Marys Peak, 14 mi., Benton Co.; 10 ♀♀, 7 ♂♂ (AJR), Wasco Co.; 11 ♀♀, 1 ♂ (AJR), Corvallis, Benton, Co.; 24 ♀♀, 16 ♂♂ (USNM), Goble. NEV-

ADA: 8 ♀♀, 5 ♂♂ (JDS), Lamotte Cyn., Elko Co.. UTAH: 10 ♀♀, 13 ♂♂ (AMNH), Wellsville.

VARIATION. Females vary as follows: length 2.3 - 2.4 mm; $A_{12} = 1.0 - 1.1 A_{10} + A_{11}$; legs beyond coxae, antennae sometimes amber; anterior lines sometimes weaker, more or less distinctly concave; mesoscutal length 0.86 - 0.91 of width; notauli sometimes longer (never reaching middle of mesoscutum); median groove may be absent near posterior margin of mesoscutum or may reach anterior margin of mesoscutum; supracoxal carina sometimes stronger; forewing 2.8 - 3.0 mm long; radial cell length 2.7 - 2.8 times width. Males vary as follows: length 1.7 - 1.9 mm; $A_{14} = 0.86 - 0.90 A_{12} + 13$; mesoscutal length 0.92 - 0.97 of width; notauli incomplete and median groove absent in one specimen; forewing 2.5 - 2.8 mm; radial cell length 3.0 - 3.2 times width.

HOST GALLS. *Diplolepis polita* (Ashmead).

DIAGNOSIS. Pronotum shining smooth between setigerous tubercles; ocelli large, $LOL \leq 1.0D$, OOL and $POL < 2.0D$; mesopleuron shining smooth except narrow ventral pubescent area; notauli incomplete in female, complete in male; propodeum with lateral and medial pilosity.

REMARKS. *Periclistus piceus* is most similar to *P. weidi* but can be distinguished by the diagnostic characters. Males are extremely difficult to separate, as the notauli are complete in both species, but can be diagnosed by the

larger ocelli. The narrowly separated anterior lines and the flattening of the mesoscutum near the anterior lines are also diagnostic for this species, although these characters are not present in all specimens.

Periclistus piceus was described by Fullaway (1911) from an unknown number of specimens. Ten specimens have been found labelled "Paratype" or "cotype"; the lectotype and allotype have been selected from this material. The California Academy of Sciences (CAS) has an additional 15 intact specimens (and the remains of 8 others) which bear the same lot and sublot numbers. I believe that these also belong to the type series and have therefore labelled them "Paralectotype".

Periclistus piceus appears to be restricted to attacking the galls of *Diplolepis polita* from western North America. Most specimens have been collected west of the Cascade and Sierra Nevada mountains; however, the species is also found in Nevada and "Colorado and Wyoming" (Ashmead 1896). The latter series is part of the type series for *P. californicus* Ashmead but is conspecific with *P. piceus*. Thus, it is likely that *P. piceus* will be found throughout western North America wherever its host, *D. polita*, is found.

Periclistus pirata (Osten Sacken)

Figs. 44, 55, 59, 66, 68, 72, 74.

Aulax pirata Osten Sacken 1863: 42. ♀, ♂.

TYPE: Lectotype, designated here. ♀ (MCZ). Mounted with 4 ♂♂; fourth specimen from top. Labelled: K (circular label); Osten Sacken collection; Type, 13977 (red label); Lectotype, *Aulax pirata*, Osten Sacken 1863, Ritchie and Shorthouse 1984.

Periclistus pirata (O. S.), Mayr 1881: 32.*Periclistus smilacis* Ashmead 1896: 188. ♀, ♂. NEW SYNONYMY.

TYPE: Lectotype, designated here. ♀ (USNM). Labelled: Through C. V. Riley; 86x on *Smilax rotundifolia*; Type, No. 3287, U.S.N.M. (red label); remounted from multiple mount, Ritchie, 1983; Lectotype, *Periclistus smilacis*, Ashmead 1896, Ritchie and Shorthouse, 1984.

FEMALE. (Lectotype). Length 2.5 mm. Black; coxal bases, tips of mandibles dark brown; mandibles except tips, legs amber. Head subquadrate, gena strongly angled below eye; radiating striae strong, reaching inner orbit of eye and antennal socket; median protuberance well developed, narrow; clypeus slightly protuberant medially; interocular space 0.90 of height of eye; malar space 0.40 of height of eye; genae behind eye, frons above antennal sockets, vertex finely shagreened; vertex, ocellar triangle weakly raised, ocelli not surrounded by weak crescent shaped depression;

LOL = 1.3D, POL = 2.5D, OOL = 2.0D; A1-A12 (mm): 0.12, 0.10, 0.18, 0.17, 0.17, 0.17, 0.16, 0.16, 0.13, 0.12, 0.10, 0.21; $A12 = 0.95 A10 + A11$. Pronotum moderately shagreened, ventrolateral area transversely rugulose, moderately pubescent, anterior pilosity well developed. Mesoscutum (Fig. 44) with moderately dense setigerous punctures, shagreened between punctures. Notauli complete, reaching anterior margin of mesoscutum as weak creases, strong and gradually widened posteriorly, weaker anteriorly; anterior pits absent; ental margins separated by 2.0 times posterior width of notauli; posteroental margins of notauli slightly raised, suddenly arcuate near posterior margin of mesoscutum; mesoscutum between raised margins of notauli with a smooth shining area. Anterior lines short straight, moderately impressed, strongly convergent. Lateral lines distinct. Mesoscutellum slightly flattened, in same plane as posterior portion of mesoscutum, coarsely rugoareolate, shagreened between rugae; axillae shagreened, foveae large, deep, shining, triangular, distinctly closed posteriorly; septum a broad inverted "V", rugose, shagreened; lateral bars well developed, aciculate laterally; lateral shining strip gradually broadened posteriorly, without well developed dorsal extension (Fig. 55). Mesopleuron (Fig. 66) finely coriaceous and aciculate, with conspicuous setigerous punctations and rugosity near posteroventral margin; subalar triangle densely pilose; ventral margin of subalar

triangle rugulose, with setigerous punctures (Fig. 68). Metapleuron distinct, trapezoidal; supracoxal carina strong, angulate, ventral portion parallel to posterior margin of mesopleuron; subspiracular carinae, subspiracular tubercle well developed; antespiracular area large, deep, shining smooth. Metanotal lateral foveae sparsely pubescent, lateral margin shining smooth (Fig. 59). Propodeum with lateral and median pilosity; propodeal carinae very strong, square in cross-section, strongly shagreened, moderately pubescent, slightly concave. Metasoma shorter than head plus mesosoma; T2+3 completely fused, without trace of suture, shining smooth, with small triangular patch of fine punctation near posterodorsal margin; anterior pubescent patch large, with well developed pilosity. Forewing 2.7 mm, radial cell length 3.1 times width; radius strongly arcuate, shorter than Rs1; Rs1 arcuate, curving tangentially to wing margin; Rs2 bent distally (Fig. 74); areolet present, equilateral, moderate size, distal margin weak, posterior margin very weak. Hind wing 1.8 mm.

MALE. Allotype differs from lectotype as follows. Length 2.4 mm. Head, mesosoma dark piceous brown. Head slightly wider than mesosoma; subantennal pits distinct; interocular distance 0.86 of eye height; LOL = 1.00, POL = 2.00, OOL = 1.80. Antenna with 14 antennomeres, A1 - A14 (mm): 0.17, 0.10, 0.25, 0.23, 0.21, 0.19, 0.19, 0.17, 0.16, 0.15, 0.13, 0.12, 0.10, 0.17; A3 deeply notched, strongly

bent, expanded distally (Fig. 72); $A_{14} = 0.77 A_{12} + A_{13}$; dorsal portion of supracoxal carina weaker; T2 and T3 separate, relative lengths 0.50: 0.37; T2 with sparse anterior pubescent patch, anterior pilosity absent; T3 with broad posterodorsal triangle of punctation. Forewing 2.9 mm; radial cell length 3.2 times width; hind wing 1.75 mm.

TYPE-MATERIAL. *Periclistus pirata*. Lectotype, designated here. ♀ (MCZ) (Mounted with 4 ♂♂; fourth specimen from top). Labelled: K (circular label), Osten Sacken collection, Type 13977 (red label); Lectotype *Aulax pirata* Osten Sacken 1863, Ritchie and Shorthouse 1984 (red label). Allotype, ♂ (MCZ), top specimen on pin with lectotype. *Periclistus smilacis*. Lectotype, designated here. ♀ (USNM No. 3287), Through C. V. Riley, 86x on *Smilax rotundifolia*. Paralectotypes, *Aulax pirata*: 8 ♀♀, 6 ♂♂, with same data as lectotype. Paralectotypes, *Periclistus smilacis*: 8 ♀♀, 1 ♂ (USNM), with same data as lectotype; 1 ♀, 2 ♂♂ (USNM); labelled 1010, 14-11-1894.

OTHER MATERIAL EXAMINED (1831 ♀♀, 1311 ♂♂). ALBERTA: 79 ♀♀, 36 ♂♂ (JDS), 3 mi. sw. Cherrhill; 34 ♀♀, 24 ♂♂ (JDS, USNM), Edmonton (Whitemud Creek); 31 ♀♀, 31 ♂♂ (JDS), George Lake; 2 ♀♀, 1 ♂ (JDS), 5 mi. s. Hillspring; 12 ♀♀, 6 ♂♂ (JDS), Lethbridge (Indian Battle Park); 43 ♀♀, 19 ♂♂ (JDS), 10 mi. sw. Lethbridge, St. Mary & Oldman Rivers; 46 ♀♀, 17 ♂♂ (JDS), 8 mi. s. Lethbridge; 1 ♀ (JDS), 6 mi. n. Minburn; 68 ♀♀, 49 ♂♂ (JDS), Peace River (Shaftsbury Trail, 4 mi. nw.

Hills); 13 ♀♀, 4 ♂♂ (JDS), Taber, Taber Prov. Pk.; 1 ♀ (AJR), 0.5 mi. e. Writing-on-Stone Prov. Pk.. COLORADO: 76 ♀♀, 16 ♂♂ (AMNH), Aspen; 1 ♂ (USNM), Durango; 18 ♀♀, 11 ♂♂ (AMNH), Manitou; 5 ♀♀, 9 ♂♂ (USNM), West Cliff; 54 ♀♀, 39 ♂♂ (USNM), No locality. DISTRICT OF COLUMBIA: 5 ♀♀ (LHW, USNM), Washington. FLORIDA: 10 ♀♀, 7 ♂♂ (USNM), Jacksonville; 4 ♀♀ (USNM), E. Florida. INDIANA: 27 ♀♀, 33 ♂♂ (AMNH), Bloomington; 30 ♀♀, 30 ♂♂ (AMNH), Howe. MASSACHUSETTS: 1 ♀ (MCZ), Cambridge; 30 ♀♀, 14 ♂♂ (AMNH), Forest Hills. MICHIGAN: 8 ♀♀, 5 ♂♂ (AMNH), Cheboygen; 29 ♀♀, 9 ♂♂ (AMNH), Ionescu Co. (Fire Channel, Ausable River); 15 ♀♀, 10 ♂♂ (AMNH), Mio. MINNESOTA: 3 ♀♀ (USNM), Olmstead Co.; 1 ♀, 1 ♂ (USNM), No Locality. NEW HAMPSHIRE: 2 ♀♀, 2 ♂♂ (AMNH), Hampton. NEW MEXICO: 10 ♀♀, 22 ♂♂ (USNM), Beulah. NEW YORK: 12 ♀♀, 1 ♂ (MCZ), Ausable; 2 ♀♀, 13 ♂♂ (CORN), Ithaca; 1 ♂ (AMNH), Mattituck; 1 ♀, 1 ♂ (USNM), Nyack Co.; 35 ♀♀, 13 ♂♂ (AMNH), 3 Mile Harbor; 39 ♀♀, 12 ♂♂ (AMNH), Schraon River. NOVA SCOTIA: 26 ♀♀, 16 ♂♂ (AMNH), Digby. ONTARIO: 14 ♀♀, 1 ♂ (JDS), 20 mi. w. Dryden; 698 ♀♀, 616 ♂♂ (JDS, AJR), Manitoulin Island (6 mi. nw. Kagawong, 3 mi. s. Little Current, 3 mi. sw. Poplar, Providence Bay, Dominion Bay, Square Bay, McClean Mountain Road, Wolsey Lake Road); 3 ♀♀, 1 ♂ (USNM), Ottawa; 20 ♀♀, 17 ♂♂ (AJR), Spanish; 30 ♀♀, 32 ♂♂ (AJR, JDS), Sudbury (8. Bay Road; Keast Road, Domestic Garden); 29 ♀♀, 22 ♂♂ (AJR), Thunder Bay (Lakehead University, McVickers Creek nr. Brent Park); 7 ♀♀, 12 ♂♂

(USNM), Toronto. QUEBEC: 9 ♀♀, 1 ♂ (CORN), Montreal. SASK-
ATCHEWAN: 40 ♀♀, 64 ♂♂ (JDS), Hwy. 17, 18 km. e. Alta.-
Sask. border; 101 ♀♀, 54 ♂♂ (USNM), Oxbow; 18 ♀♀, 9 ♂♂
(JDS), 10 mi. sw. Park entrance, P.A.N.P.; 1 ♀, 4 ♂♂ (JDS),
3 mi. n. Waskesieu River, P.A.N.P. VIRGINIA: 7 ♀♀, 16 ♂♂
(USNM), Vienna. WISCONSIN: 4 ♀♀, 1 ♂ (USNM), Cranmoore. NO
LOCALITY: 71 ♀♀, 34 ♂♂ (LHW, MCZ, USNM).

VARIATION. Female length 1.5 - 2.9 mm ($\bar{x}$ = 2.5 ± 0.2 mm, N
= 10); male length 1.3 - 2.9 mm. ($\bar{x}$ = 2.1 ± 0.2 mm, N =
10). Black to piceus brown; antennae, coxae amber to brown;
anterior two thirds of T2+3 sometimes dark brown; median
protuberance, radiating striae sometimes less well devel-
oped; intraocular space 0.85 - 0.93 of eye height, malar
space 0.38 - 0.43 of eye height, LOL = 1.0 - 1.2D, POL =
2.0 - 2.2D, OOL = 2.0 - 2.2D; antennae 0.85 - 0.93 of body
length; A12 = 0.9 - 1.0 of A10 + 11; mesoscutum length 0.85
- 0.90 width; anterior of notauli, anterior lines sometimes
weaker; axilla rarely shagreened; dorsal sculpture of meso-
pleuron sometimes weaker; dorsal portion of supracoxal
carina often moderately developed, rarely weak; radial cell
length 2.9 - 3.1 times width; radius sometimes moderately
arcuate.

HOST GALLS. *Diplolepis basseti* (Beutenmueller), *D. bicolor*
(Harris), *D. dichlocera* (Harris), *D. nebulosa* (Bassett), *D.*
neglecta (Gillette), *D. nodulosa* (Ashmead), *D. polita* (Ash-
mead), *D. rosea* (L.), *D. spinosa* (Ashmead), *D. triforma*

Shorthouse and Ritchie, *D. tuberculatrix* (Cockerell), *D. tumida* Weld.

DIAGNOSIS. Anterior lines strongly convergent, straight, short; notauli complete, often reaching anterior margin as distinct grooves, usually abruptly curved at posterior margin of mesoscutum; posteroental margins of notauli raised near posterior margin of mesoscutum; mesopleuron aciculate anteriorly; anterovental margin of subalar triangle rugulose, with setigerous punctures; Rs1 arcuate.

BIOLOGY. There has not been any detailed studies of the biology of this species; all that is known are the various host records. *Periclistus pirate* attacks the galls of several species of *Diplolepis*, although the majority of specimens have been reared from modified galls of *Diplolepis nodulosa* (Beutenmueller). The host records for *D. rosae* and *D. tumida* are doubtful determinations. A short series of specimens from Nova Scotia (AMNH) are labelled "ex *bicolor*, *polita*, or *rosae*"; however, neither of the first two species has been recorded from Nova Scotia (Burks 1979). The records from *D. tumida* are from ovoid polythalamous stem galls from Alberta which most closely agree with the description of *D. tumida*. These galls lack spine, are globular, and the epidermis is reddish; unfortunately, no gall inducers have been reared from these galls, so the determination cannot be verified. The records of *P. pirate* from *D. neglecta* are also doubtful, but for different reasons. Kin-

sey and Ayres (1922) questioned the validity of *Diplolepis neglecta*; they suggested that these galls were actually inquiline modified galls of *D. tuberculatrix*. The records for all other hosts except *D. nodulosa* are each from one or two series of specimens from Alberta or Ontario; it appears that these records represent "accidental" attacks by *P. pirata* on these galls.

Most specimens have been reared from oval polythalmous stem galls which have a gray or tan epidermis; these galls have been described as *Rhodites globulus* by Beutenmueller (1892). In almost all known cases, only inquilines and parasites emerge from this gall (Beutenmueller 1897; Weld 1957; Ritchie unpublished). Beutenmueller (1907) reared a single female *Diplolepis* from the gall of *R. globulus*; he described this specimen as *R. globuloides* and placed *R. globulus* in synonymy under *P. pirata* (O. S.). The holotype of *R. globuloides* has been examined and is a specimen of *D. nodulosa* (Ashmead) (new synonymy). The unique holotype of *R. globulus* belongs to the genus *Ceroptres* (see Appendix II for a discussion of *C. globulus*).

Recently, another specimen of *D. nodulosa* has been reared from this modified gall (Judd, unpublished). This specimen was reared from a gall that only issued the gall inducer and parasites (*Eurytoma* sp., *Habrocytus* sp.) (Yoshimoto, unpublished). These parasites normally attack the larvae of both *Periclistus* and *Diplolepis* (Shorthouse

1975). It is probable that the parasites attacked the *Periclistus* larvae, which allowed the *Diplolepis* larva to survive. This may mean that the ovipositing female *P. pirate* did not puncture (and kill) the *Diplolepis* larva, a behavior found in *Periclistus* attacking many leaf galls (Shorthouse 1975, 1982). It is also possible that puncturing the host larva during oviposition does not immediately kill the host, but that the larva is "crowded out" by the expanding endogalls of the *Periclistus* larvae. Subsequent attack by parasites on the *Periclistus* larvae then could prevent this.

There is also strong circumstantial evidence to support this host relationship. There are nine species of *Diplolepis* on Manitoulin Island (*D. fulgens*, *D. fusiformans*, *D. lens*, *D. nebulosa*, *D. nodulosa*, *D. polita*, *D. rosae*, *D. spinosa*, and *D. triformis*) (Shorthouse, unpublished); *Periclistus* spp. have been reared from identifiable galls of all these species except *D. nodulosa* and *D. rosae*. The latter species is introduced from Europe (Burks 1979) and is found on domestic and feral roses (eg. *R. eglanteriae*, *R. rubiginosa*). *Diplolepis rosae* induces a very distinctive leaf gall, characterized by long mossy filaments covering the exterior. Since the host gall for *P. pirate* is a smooth stem gall, it is highly unlikely that the actual host is *D. rosae*.

Thus, *Diplolepis nodulosa* is left as the only possible host for *P. pirata*. Further evidence to support this relationship lies in the position of the normal and modified galls on the plant. Normal *D. nodulosa* galls usually cause the death of the stem or twig distal to the gall; thus, the galls are found either at the extreme end of the twig or with a little distal growth. Only rarely does the twig survive to grow a great distance distal to the gall. This is the exact location of the modified galls of *P. pirata*.

REMARKS. *Periclistus pirata* is most similar to *P. arefactus* but can be readily distinguished by the complete notauli. *Periclistus pirata*, *P. arefactus*, *P. californicus*, and *P. vancouverensis* can be distinguished from all other Nearctic species of *Periclistus* by the aciculate mesopleuron and the ventral margin of the subalar triangle being rugulose with setigerous punctures.

The identity of this species has been greatly confused; Osten Sacken (1863) described *Aulax pirata* from smooth rounded galls on *Rosa* sp.. Osten Sacken correctly recognized that it was an Inquiline, but did not know the name of the host gall, although he described it as a smooth rounded stem gall. Mayr (1881) transferred the species to *Periclistus*. Ashmead (1885) reared specimens of *Periclistus* from galls of *Diplolepis ignota* in Florida and believed them to be *P. pirata*; these galls superficially meet Osten Sacken's description of the host galls for *P. pirata* but

are leaf galls. Ashmead apparently believed Osten Sacken was mistaken in stating that the host gall was a stem gall. Weld (unpublished) believed that *D. polita* was the true host for *P. pirata*; this determination was followed by Shorthouse (1973, 1975, 1980). Although *P. pirata* has occasionally been reared from these hosts, the majority of specimens belong to other species. Thus, with the exception of the Osten Sacken records (1863, 1865), all published records of *P. pirata* belong to other species.

Ashmead (1896) described *P. smilacis* from two series of specimens reared from the galls of *Diastrophus smilacis* Ashmead on *Smilax rotundifolia* (Liliaceae). This is a very unusual host record as all other *Diastrophus* spp. induce galls on *Rubus* spp. and *Potentilla* spp. (Rosaceae) (Beutenmueller 1909a; Weld 1952b). Since *S. rotundifolia* is frequently a climbing vine and may have spines (Britton and Brown 1913), it is quite likely that the host record is incorrect. An error may also have occurred when the specimens were sent to Ashmead by C.V. Riley.

One series of *P. smilacis* (9 ♀♀ and 1 ♂; labelled 86x on *Smilax rotundifolia*) agrees with Ashmead's description; it is from this series that the lectotype was chosen. This series originally contained 13 specimens (reared 28-IV-1871) (Ashmead 1886) and the females were mounted on multiple points on two cards; however, 3 ♀♀ were missing from the cards and are presumed lost. The multiple points have

been separated, mounted on their own pins, and the labels have been copied; each specimen bears my lectotype or para-lectotype label.

The second series (1 ♀, 2 ♂♂; labelled 1010, 14-11-1894) appear to be abnormal specimens; they differ from the first series as follows; length 1.5 mm, head and mesosoma light brown to brown; vertex without median crease; notauli incomplete; septum not depressed; supracoxal carina not as strong, not parallel to hind margin of mesoscutum. However, although these specimens are much smaller than normal *P. smilacis* and have the coloration and sculpturing much weaker, they also have the mesopleuron weakly aciculate, and have setigerous punctations and very weak rugosity near the ventral margin of the subalar triangle. I believe that these are atypical specimens, ones that for some reason were not able to develop properly. Wiebes-Rijks (1979) has shown that differences in temperature and humidity cause differential development of sculpturing and coloration in *Synergus*.

distinguished from other species with aciculate mesopleurae (*P. arefactus*, *P. californicus*, *P. pirata*) by the posterior of the notauli being relatively close together.

The specimens from Vancouver Island are from a modified stem gall, very similar to the modified galls of *D. inconspicua* and *D. nodulosa*. The modified galls are broad, fusiform (teardrop shaped) and the epidermis is beige-gray. The specimens from Oregon were reared from modified galls of *D. inconspicua* (Hanson, pers. comm.). This agrees with the biology of *P. arefactus* and *P. pirata*, two very similar species. One series of specimens (Junction City, OR) has been reared from the galls of *D. neglecta* (Gillette). Kinsey and Ayres (1922) have questioned the validity of this species of *Diplolepis*, suggesting that these galls are galls of *D. tuberculatrix* (Cockerell) that have been modified by Inquillines. I have not seen galls of *D. neglecta*, therefore cannot comment on this suggestion.

length 0.8 of width, with evident setigerous punctures, punctures small, very weakly coriaceous between punctures. Notauli incomplete, reaching middle of mesoscutum, grooves strong, strongly divergent posteriorly, weak creases anteriorly; anterior pits absent; grooves separated by 1.0 times width at posterior margin of mesoscutum (Fig. 47); posterodorsal margin of groove distinctly raised, posterior of mesoscutum almost smooth, raised between posterior portion of notauli; posterior margin of mesoscutum distinctly notched. Median groove absent. Anterior lines distinct, moderately long, slightly convex. Lateral lines distinct. Mesoscutellum flattened, sloping posteriorly, coarsely rugoareolate, shining between rugae, in same plane as posterior of mesoscutum; axilla weakly coriaceous; lateral bars wide, not depressed; foveae deep, teardrop shaped, closed posteriorly, shining smooth; septum short, broad; lateral shining strip with weakly developed posterodorsal extension (Fig. 56). Mesopleuron (Fig. 71) aciculate anteriorly, smooth posteriorly, dent absent; ventral pubescent area broad, subalar triangle sparsely pubescent, moderately pilose; ventral margin of subalar triangle straight, with narrow punctopubescent area anteriorly (as in Fig. 68); subalar pit narrow. Metapleuron not strongly depressed anteriorly, without dense ventral patch of pubescence; supracoxal carina strong, distinctly angled; supracoxal tubercle, subspiracular carina moderately developed; antespinal area

large, deep, weakly rugulose. Metanotal lateral fovea weakly pubescent, lateral margin shining smooth (as in Fig. 59). Propodeum with lateral pilosity; propodeal carinae strong, shagreened, sparsely setose, moderately divergent. Metasoma less than length of head plus mesosoma; T2+3 with visible suture, anterior pubescent patch small, with weak pilosity, posterodorsal margin with very small triangle of punctation. Forewing 2.88 mm long; radial cell length 3.0 times width; R arcuate, distinctly bent near areolet, as long as Rs1; Rs1 straight basally, arcuate distally; Rs2 bent distally (as in Fig. 74); areolet large, elongate. Hind wing 1.81 mm long.

MALE. Allotype differs from holotype as follows: length 2.0 mm; antennae, legs amber; coxal bases light brown; malar space 0.39 of eye height; antenna with 14 antennomeres, 2.10 mm., A1 - A14 (mm): 0.15, 0.08, 0.21, 0.19, 0.19, 0.19, 0.17, 0.16, 0.15, 0.12, 0.11, 0.11, 0.10, 0.17, A3 strongly curved, strongly notched, expanded distally (as in Fig. 72); $A14 = 0.81 A12 + 13$; T2 separate from T3, relative lengths 0.46; 0.26; T3 with large posterodorsal triangle of punctation, punctation almost reaching anterior margin of T3.

TYPE MATERIAL. Holotype, ♀ (CNC No. _____), 11 mi.s. Nanaimo, Vancouver Is., B.C., coll. 10-III-70, Coll. No. 3-70, J.D. Shorthouse, *Periclistus vancouverensis* Ritchie and Shorthouse (red label). Allotype, ♂ (CNC), with same data

as holotype. Paratypes (160 ♀♀, 99 ♂♂). BRITISH COLUMBIA: 98 ♀♀, 54 ♂♂ (JDS), with same date as holotype; 10 ♀♀, 12 ♂♂ (JDS), 5 m.l.s. Parkesville, Vancouver Is., coll. 7-III-70, Coll. No. 1-70, J.D. Shorthouse. OREGON: 17 ♀♀, 14 ♂♂ (AJR), Benton Co., Corvallis, ex gall on *Rosa pisocarpa*, P. Hanson, em. Jan. - Mar. 1983; 35 ♀♀, 19 ♂♂ (AMNH), Junction city, coll. 4.9.20, ex gall of *neglecta*.

VARIATION. Female length 1.7 - 2.4 mm ($\bar{x}$ = 2.1 ± 0.2 mm, N = 10); male length 1.7 - 2.3 mm ($\bar{x}$ = 1.9 ± 0.2 mm, N = 10). Smaller specimens sometimes dark brown; mesopleuron rarely with weak dent.

HOST GALLS. *D. inconspicuis* D. & C., *D. neglecta* (Gill.).

DIAGNOSIS. Notauli incomplete, broadened posteriorly, posteroventral margins distinctly raised, separated by 1.0 times width at posterior margin of mesoscutum. Mesopleuron aciculate anteriorly, ventral margin of subalar triangle with anterior patch of rugosity; lateral margin of metanotal fovea shining smooth; R distinctly arcuate near areolet.

ETYMOLOGY. The specific epithet is based on the locality of the holotype.

BIOLOGY. Nothing is known about the biology of this species except that it has been reared from modified stem galls.

REMARKS. *Periclistus vancouverensis* has the mesoscutum and notauli similar to that of *P. ashmeadi* but can be distinguished by the the aciculate mesopleuron and shining smooth lateral margin of the metanotal fovea. This species can be

distinguished from other species with aciculate mesopleurae (*P. arefactus*, *P. californicus*, *P. pirata*) by the posterior of the notauli being relatively close together.

The specimens from Vancouver Island are from a modified stem gall, very similar to the modified galls of *D. inconspicuis* and *D. nodulosa*. The modified galls are broad, fusiform (teardrop shaped) and the epidermis is beige-gray. The specimens from Oregon were reared from modified galls of *D. inconspicuis* (Hanson, pers. comm.). This agrees with the biology of *P. arefactus* and *P. pirata*, two very similar species. One series of specimens (Junction City, OR) has been reared from the galls of *D. neglecta* (Gillette). Kinsey and Ayres (1922) have questioned the validity of this species of *Diplolepis*, suggesting that these galls are galls of *D. tuberculatrix* (Cockerell) that have been modified by inquillines. I have not seen galls of *D. neglecta*, therefore cannot comment on this suggestion.

Periclistus weldi n. sp.

Figs. 45, 57, 67, 69.

FEMALE. (Holotype). Length 2.3 mm. Black; antenna, tegula, valves, ovipositor brown; coxae, trochanters, bases of femora dark piceous brown; remainder of legs, anterior margin of T2+3 amber. Head as wide as mesosoma, subquadrate; frons strongly coriaceous above antennal sockets, weakly coriaceous below antennal sockets, with very fine setigerous punctures; median protuberance moderately strong, distinct; clypeus indistinct dorsally, medially protuberant (continuous with median protuberance); radiating striae moderately strong, reaching antennal sockets and inner orbit of eye; subantennal foveae weak, indistinct; interocular space 1.0 of eye height; malar space 0.40 of eye height; vertex, ocellar triangle weakly raised; ocelli surrounded by weak, indistinct crescent shaped depression; $LOL = 1.2D$, $POL = 2.7D$, $OOL = 2.1D$. Antenna 1.91 mm long; $A1 - A12$ (mm): 0.12, 0.08, 0.19, 0.19, 0.17, 0.17, 0.17, 0.15, 0.15, 0.13, 0.13, 0.26; $A12 = 1.0 A10 + A11$. Pronotum with fine setigerous tubercles, weakly coriaceous between setigerous tubercles, with strong anterior pilosity, without posterolateral rugosity; posterior part of plate moderately strong, lateral margins straight except strongly curved posterodorsally. Mesoscutum (Fig. 47) moderately arched, somewhat flattened anteriorly near anterior lines; length 0.62 of width, with fine setigerous punctures, strongly

coriaceous between punctures; notauli very strong, gradually widening posteriorly, complete, strong creases anteriorly; grooves separated by 2.0 times width at posterior margin of mesoscutum; median groove very weak crease, complete. Anterior lines moderately long, not reaching middle of mesoscutum, weakly concave, slightly raised. Lateral lines weak. Mesoscutellum evenly rounded, coarsely rugo-areolate, longer than wide; axilla coriaceous; lateral shining strip gradually broadened posteriorly, with broad, moderately well developed posterodorsal extension (Fig. 57). fovea large, teardrop shaped, deep anteriorly and laterally, shallower posteriorly, gradually merging with anterior rugosity of disc; septum long, shagreened, distinct, merging with anterior rugosity of disc. Mesopleuron (Fig. 67) shining smooth, ventral pubescent area narrow; subalar triangle weakly pubescent, pilose anteriorly and posteriorly, ventral margin with a single row of setigerous punctures, without anterior rugosity, (as in Fig. 69), straight; subalar pit narrow, deflexed. Metapleuron depressed anteriorly, trapezoidal; supracoxal carina very weak, distinctly bent, ventral portion parallel to posterior margin of mesopleuron; subspiracular carina, subspiracular tubercle weakly developed; antespiracular area deep, irregularly rugulose. Metanotal lateral foveae weakly pubescent; lateral margin shining smooth (as in Fig. 59). Propodeum with strong lateral pilosity, weak median pilosity; propo-

deal carinae moderately strong, straight, parallel, shagreened, setose; intracarinial area shining, glabrous except dorsal pilose area. Metasoma equal to length of head plus mesosoma; T2+3 without visible suture, hind margin shining smooth; anterior pubescent patch moderately developed, with weak anterior pilosity. Forewing 2.7 mm; radial cell distinctly closed, length to width ratio = 2.8; R weakly arcuate, longer than Rs1; Rs1 straight basally, obliquely angled to wing margin, weakly arcuate distally; Rs2 bent medially (as in Fig. 75); areolet moderately developed, not elongate, posterior side very weak. Hind wing 1.9 mm.

MALE. Allotype differs from holotype as follows: antenna with 14 antennomeres, 2.1 mm long, A1 - A14 (mm): 0.15, 0.08, 0.22, 0.21, 0.21, 0.17, 0.17, 0.17, 0.15, 0.13, 0.13, 0.12, 0.12, 0.10, 0.18; A3 strongly curved, broadly notched expanded distally (as in Fig. 72); A14 = 0.8 A12 + A13; median groove weaker; T2 separate from T3, relative lengths 0.48: 0.33; forewing 2.6 mm long, 1.1 of body length; hind wing 1.7 mm long.

TYPE MATERIAL. Holotype, ♀ (CNC _____). Labelled: ALTA., 10 mi. s. Lethbridge, St Mary and Oldman Rivers, coll. 12-X-81, Coll. No. 500-81, Shorthouse and LaLonde; ex gall of *Diptolepis bicolor*, det. Shorthouse; *Periclistus weldi* Ritchie and Shorthouse 1984 (red label). Allotype, ♂ (CNC), with same data as holotype. Paratypes (1112 ♀♀, 757 ♂♂). ALASKA (ex gall of *D. polita*): 21 ♀♀, 17 ♂♂ (JDS), Circle

City Hwy, 138 mi. n. Fairbanks, coll. 6-VIII-71, Coll. No. 33-71, J. D. Shorthouse; 3 ♀♀ (JDS), 17 mi. s. Circle City, coll. 6-VIII-71, Coll. No. 35-71, J. D. Shorthouse; 4 ♀♀, 1 ♂ (JDS), Fairbanks, University grounds, coll. 5-VIII-71, Coll. No. 31-71, J. D. Shorthouse; 9 ♀♀ (JDS), Circle City, coll. 5-VIII-71, Coll. No. 34-71, J. D. Shorthouse; 7 ♀♀, 5 ♂♂ (JDS), 25 mi. w. Glennallen, coll. 10-VIII-71, Coll. No. 38-71, J. D. Shorthouse; 3 ♀♀ (JDS), 45 mi. e. Palmer, coll. 11-VIII-71, Coll. No. 39-71, J. D. Shorthouse; 7 ♀♀ (JDS), Taylor Highway, 8 mi. s. Tetlin Junction, coll. 14-VIII-71, Coll. No. 43-71, J. D. Shorthouse; (no host record): 1 ♀ (USNM), Healy, coll. 28-VI-21, Aldrich; 1 ♀ (USNM), Fairbanks, coll. 7-VII-21, Aldrich. **ALBERTA** (ex-gall of *D. bicolor*): 97 ♀♀, 84 ♂♂ (JDS), with same data as holotype; 15 ♀♀, 7 ♂♂ (JDS), sw. Calgary, 25-III-68, J. D. Shorthouse; 8 ♀♀, 12 ♂♂ (JDS), George Lake, J. D. Shorthouse; 18 ♀♀, 11 ♂♂ (JDS), George Lake, coll. VI-69 (swept), J. D. Shorthouse; 2 ♀♀, (JDS), George Lake, coll. 8-V-69, Coll. No. 114-69, J. D. Shorthouse; 1 ♀, (JDS), George Lake, Donald's Road, coll. 17-V-69, Coll. No. 103-69, J. D. Shorthouse; 1 ♀, 1 ♂ (JDS), George Lake, coll. 16-V-69, Coll. No. 111-69, J. D. Shorthouse; 3 ♀♀, (JDS), George Lake, coll. V-69, J. D. Shorthouse; 11 ♀♀, 6 ♂♂ (JDS), 8 mi. s. Lethbridge, coll. 16-VI-71, Coll. No. 7-71, J. D. Shorthouse; 2 ♂♂ (JDS), 8 mi. s. Lethbridge, Plains above St. Mary River, coll. 19-IV-71, J. D. Shorthouse; 15

♀♀ (JDS), 8 mi. s. Lethbridge, near St. Mary River, coll. 19-IV-71, Coll. No. 3-71, J. D. Shorthouse; 1 ♀ (JDS), 8 mi. s. Lethbridge, Russell Ranch River Bottom, coll. 10-IV-71, Coll. No. 2-71, J. D. Shorthouse; 2 ♀♀ (JDS), 8 mi. s. Lethbridge, Russell Ranch River Bottom, coll. 19-IV-71, Coll. No. 4-71, J. D. Shorthouse; 5 ♀♀ (JDS), 20 mi. se. Lethbridge, above Oldman River, coll. 3-III-77, Coll. No. 188-77, J. D. Shorthouse; 2 ♀♀, 1 ♂ (JDS), Lethbridge, Indian Battle Park, coll. 31-XII-69, J. D. Shorthouse; 4 ♀♀, 2 ♂♂ (JDS), Lethbridge, Indian Battle Park, coll. 13-IX-69, Coll. 109-69, J. D. Shorthouse; 105 ♀♀, 38 ♂♂ (JDS), Lethbridge, Indian Battle Park, coll. 31-XII-69, Coll. Nos. 108-69, 112-69, 113-69, 115-69, 116-69, 117-69, 118-69, 119-69, J.D. Shorthouse; 28 ♀♀, 17 ♂♂ (JDS), 5 mi. s. Hillspring, coll. 19-VII-71, Coll. No. 16-71, J. D. Shorthouse; 4 ♀♀, 3 ♂♂ (JDS), Taber, Taber Prov. Park, coll. 14-X-81, Coll. No. 512-81, Shorthouse and LaLonde; (ex gall of *D. ignota*): 6 ♀♀, 5 ♂♂ (JDS), 4 mi. s. Lethbridge, Coulees nr. St. Mary R., coll. 14-III-71, Coll. 1-71, J. D. Shorthouse; 3 ♀♀, 4 ♂♂ (JDS), Lethbridge, coll. 12-IX-69, J. D. Shorthouse; 2 ♀♀, 2 ♂♂ (JDS), George Lake, Fall 1969, J. D. Shorthouse; (ex gall *D. polita*): 2 ♀♀, 1 ♂ (JDS), George Lake, 1968, J. D. Shorthouse; 20 ♀♀, 17 ♂♂, (JDS), George Lake, Fall 1969 - Spring 1970, J. D. Shorthouse; 34 ♀♀ (JDS), George Lake, 22-V-22-VI-69, J. D. Shorthouse; 7 ♀♀, 3 ♂♂ (JDS), Banff, nr. Banff School of Fine Arts, coll. 5-

6-X 81, Coll. No. 501-81, Shorthouse & LaLonde; 2 ♀♀, 2 ♂♂ (JDS), 2 mi. nw. Little Smokey, Hwy. 43, coll. 31-VII-72, Coll. No. 250-72, J. D. Shorthouse; 1 ♀ (JDS), 10 mi. w. Peace River, coll. 14-VI-71, J. D. Shorthouse; 2 ♀♀, 3 ♂♂ (JDS), Peace River, coll. 16-VIII-70, J. D. Shorthouse; 3 ♀♀ (AMNH), Brazen For. Pres., Coalspur, coll. X-26, A. Kinsey; (ex gall of *D. spinosa*): 26 ♀♀, 11 ♂♂ (JDS), 10 mi. sw. Lethbridge, St. Mary & Oldman Rivers, coll. 12-X-81, Coll. No. 506-81, Shorthouse & LaLonde; (no host record): 2 ♀♀ (JDS), 5 mi. e. Hillispring, coll. 19-VII-71, Coll. No. 17-71, J. D. Shorthouse, (ex hairy leaf gall); 1 ♀ (AJR), 0.5 mi. e. Writing-on-Stone Prov. Park, 14-VI-82, G. Gibson. **BRITISH COLUMBIA** (ex gall of *D. polita*): 1 ♀, 1 ♂ (JDS), Alaska Hwy, 5 mi. s. Coal River, coll. 31-VII-71, Coll. No. 24-71, J. D. Shorthouse; 16 ♀♀, 9 ♂♂ (JDS), MP 559 Alcan Hwy, 16 mi. n. Coal River, coll. 19-VIII-71, Coll. No. 60-72, J. D. Shorthouse; (no host record): 1 ♀ (JDS), 1 mi. s. Grand Forks, coll. 17-VII-71, Coll. No. 15-71, J. D. Shorthouse, (ex hairy leaf gall); 1 ♀ (CAS), Victoria, Swazey. **COLORADO** (ex gall of *D. bicolor*): 3 ♀♀ (USNM), Boulder, coll. 5-V-05, Cockerell; 1 ♀ (USNM), West Cliff; 48 ♀♀, 41 ♂♂ (USNM), (No locality), Baker; (ex gall of *D. polita*): 2 ♂♂ (USNM), Custer Co., Cockerell. **KANSAS** (ex gall of *D. bicolor*): 59 ♀♀, 74 ♂♂ (AMNH), Emporia, coll. 21-VIII-36, A. Kinsey. **NEBRASKA** (ex gall of *D. bicolor*): 1 ♀ (USNM), Lincoln, D. B. Whalen. **NEW HAMPSHIRE** (ex gall of

D. bicolor): 2 ♀♀ (USNM). Hampton, coll. 10-V-86, Riley.

NEW MEXICO (ex gall of *D. bicolor*): 16 ♀♀, 13 ♂♂ (USNM); Aztec, coll. 24-29-IV-1899; (no host data): 1 ♀ (AJR), 1.5 mi. w. Alto, Lincoln Co., coll. 25-VIII-82, G. Gibson.

NEW YORK (ex gall of *D. bicolor*): 4 ♀♀ (MCZ, USNM), Nyack, coll. 8-11-1884, Riley.

ONTARIO (ex gall of *D. bicolor*): 15 ♀♀, 12 ♂♂ (JDS), Manitoulin Is., Square Bay, coll. 7-V-76, Coll. No. 31-76, J. D. Shorthouse; 1 ♀, 2 ♂♂ (AJR), Manitoulin Is., 2 mi. s. Maple Pt., coll. 1-VI-83, Coll. No. 543-83, A. J. Ritchie; 7 ♀♀ (AJR), Manitoulin Is., 2 mi. s. Maple Pt., coll. 24-V-82, Coll. No. 513-82, A. J. Ritchie; 54 ♀♀, 8 ♂♂ (AJR), Sudbury, Keast Road, coll. 25-IX-81, Coll. No. 765-81, A. J. Ritchie; (ex gall of *D. polita*): 1 ♂ (AJR), Manitoulin Is., 2 mi. s. Maple Pt., coll. 7-V-81, Coll. No. 725-81, A. J. Ritchie; 24 ♀♀, 20 ♂♂ (JDS), Manitoulin Is., 6 mi. n. Kagawong, coll. 7-V-76, Coll. Nos. 9-76, 33-76, J. D. Shorthouse; 2 ♀♀, 3 ♂♂ (AJR), Manitoulin Is., Providence Bay Beach, coll. 16-VIII-83, Coll. No. 601-83, A. J. Ritchie; 1 ♀, 1 ♂ (AJR), Manitoulin Is., Square Bay Beach, coll. 16-VIII-83, Coll. No. 608-83, A. Ritchie; 3 ♀♀ (AJR), Sudbury, S. Bay Road, coll. 25-IX-81, Coll. no. 758-81, A. J. Ritchie; 8 ♀♀ (AJR), Sudbury, Keast Road, coll. 25-IX-81, Coll. no. 762-81, A. J. Ritchie; 5 ♀♀ (JDS), Finn Rd., 20 mi. w. Sudbury, coll. 30-V-78, Coll. No. 107-78, J. D. Shorthouse; 7 ♀♀ (AJR), 30 mi. w. Sudbury, coll. 16-VIII-83, Coll. No. 629-83, A. J. Ritchie;

(no host record): 3 ♀♀ (JDS), Capreol, coll. 30-V-77, J. D. Shorthouse; 2 ♀♀ (JDS), Sudbury, coll. 17-27-V-77, J. D. Shorthouse; 1 ♀ (AJR), Manitoulin Is., Wolsey Lake Road, coll. 2-VI-83, Coll. No. 546-83, A. J. Ritchie; 2 ♀♀ (JDS), Manitoulin Is., McClean Mtn. Rd., coll. 22-V-78, J. D. Shorthouse; 2 ♀♀ (AJR), 1 km. n. Hwy 17, nr. Fairbanks Prov. Pk., coll. 19-V-82, A. J. Ritchie. **OREGON** (ex gall of *D. dassetti*): 83 ♀♀, 57 ♂♂ (AMNH), Ashland, coll. 4.6.20, A. C. Kinsey. **SASKATCHEWAN** (ex gall of *D. bicolor*): 1 ♀ (JDS), 9 mi. s. Aberdeen, coll. 10-V-72, Coll. No. 13-72, J. D. Shorthouse; 20 ♀♀, 7 ♂♂ (JDS), Cypress Hills, coll. 8-IX-72, Coll. No. 235-72, J. D. Shorthouse; 31 ♀♀, 29 ♂♂ (JDS), Hwy 17, 18 km. e. Alta.-Sask. border, coll. 15-IX-81, Coll. No. 502-82, Shorthouse & LaLonde; 33 ♀♀, 33 ♂♂ (JDS), Saskatchewan Landing, coll. 3-VIII-72, Coll. No. 168-72, J. D. Shorthouse; 11 ♀♀, 3 ♂♂ (JDS), 15 mi. e. Saskatoon, coll. 19-IX-71, Coll. No. 69-71, J. D. Shorthouse; 37 ♀♀, 15 ♂♂ (JDS), 15 mi. e. Saskatoon, coll. 3-V-72, Coll. No. 17-72, J. D. Shorthouse; 14 ♀♀, 15 ♂♂ (JDS), 25 mi. e. Saskatoon, coll. 13-VIII-72, Coll. No. 166-72, J. D. Shorthouse; 4 ♀♀, 23 ♂♂ (JDS), 5 mi. n. Webb, coll. 15-IX-81, Coll. No. 517-81, Shorthouse & LaLonde; (ex gall of *D. ignota*): 1 ♀ (JDS), 10 mi. e. Hanly, coll. 18-V-72, Coll. No. 22-72, J. D. Shorthouse; (ex gall of *D. nebulosa*): 2 ♀♀ (JDS), Saskatchewan Landing, coll. 3-VIII-72, Coll. No. 163-72, J. D. Shorthouse; (ex gall of *D. polita*): 6 ♀♀

(JDS), Cypress Hills, coll. 8-IX-72, Coll. No. 237-72, J. D. Shorthouse; 28 ♀♀, 4 ♂♂ (JDS), P. A. N. P., West Park Station, coll. 10-VIII-72, Coll. No. 154-72, J. D. Shorthouse; 3 ♀♀ (JDS), P.A.N.P., 10 mi. sw. Park entrance, coll. 26-V-72, Coll. No. 42-72, J. D. Shorthouse. **YUKON TERRITORY** (ex gall of *D. polita*): 19 ♀♀, 42 ♂♂ (JDS), Alaska Hwy, 3 mi. nw. Whitmore, coll. 1-VIII-72, Coll. No. 27-71, J. D. Shorthouse; 59 ♀♀, 52 ♂♂ (JDS), 5 mi. e. Dawson City, coll. 16-VIII-71, Coll. No. 48-71, J. D. Shorthouse; 10 ♀♀, 4 ♂♂ (JDS), Alaska Hwy, MP 995, Ashihik Falls Road, coll. 2-VIII-71, Coll. No. 28-71, J. D. Shorthouse; 25 ♀♀, 13 ♂♂ (JDS), 45 mi. n. Pelly River Crossing, coll. 17-VIII-71, Coll. No. 51-71, J. D. Shorthouse; 2 ♀♀ (JDS), Tetlin Junction - Dawson Hwy, 15 mi. e. border, coll. 15-VIII-71, Coll. No. 45-71, J. D. Shorthouse; 2 ♀♀, 1 ♂ (JDS), 62 mi. s. Carmacks, coll. 18-VIII-71, Coll. No. 55-71, J. D. Shorthouse; 32 ♀♀, 36 ♂♂ (JDS), 5 mi. se. Watson Lake, coll. 19-VIII-71, Coll. No. 59-71, J. D. Shorthouse; 19 ♀♀, 9 ♂♂ (JDS), 10 mi. nw. Pelly River Crossing, coll. 17-VIII-71, Coll. No. 61-71, J. D. Shorthouse. **NO LOCALITY** (ex gall of *D. bicolor*): 2 ♀♀, 15 ♂♂ (USNM).

VARIATION. Female length: 2.1 - 2.9 mm ($\bar{x} = 2.5 \pm 0.2$ mm, $N = 10$); male length: 1.7 - 2.7 mm ($\bar{x} = 2.3 \pm 0.2$ mm, $N = 10$). Rarely variegated brown and black or entirely brown (usually very small specimens); antennae, legs beyond coxae

bases often amber, rarely yellow. Anterior of notauli frequently distinct grooves; notauli often not, or slightly broadened posteriorly; anterior lines sometimes strongly convex, sometimes parallel; median line often absent; lateral shining strip sometimes more strongly developed; mesoscutellar areola sometimes more strongly developed, sometimes very weakly developed; Rs1 straight or arcuate basally.

HOST GALLS. *Diplolepis bassetti* (Beut.), *D. bicolor* (Harris), *D. ignota* (O. S.), *D. nebulosa* (Bassett), *D. nodulosa* (Ashmead), *D. spinosa* (Ashmead).

DIAGNOSIS. Ocelli normal sized: LOL > 1.0, POL and OOL > 2.0; pronotum coriaceous between setigerous tubercles; notauli complete, reaching anterior margin of mesoscutum at least as distinct creases; mesoscutellum (Fig. 47) somewhat elongate; septum long, rugulose; foveae large, indistinctly closed posteriorly, often quadrangular.

BIOLOGY. Shorthouse (1975, 1980) has described the biology of *P. weldi* (under the name of *P. pilata*) and its effect on the principle host galls (*D. bicolor*, *D. pilata*); his findings from Alberta and Saskatchewan are summarized here. *Diplolepis bicolor* and *D. pilata* emerge in early summer, earlier than other species of leaf gall inducers. The beginning of the emergence of *P. weldi* occurs slightly before the emergence of *D. bicolor* and *D. pilata*, but continues over a relatively prolonged period. *Periclistus weldi* re-

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males oviposit into all immature stages of *D. bicolor* and *D. polita* galls.

Eggs are layed on the inner surface of the gall chamber. After hatching, the larvae distribute themselves about the inside of the gall and begin feeding on the *Diplolepis* induced tissues. Feeding by *Periclistus* larvae induces the growth of additional tissues and each larva becomes enclosed in its own endogall. The endogalls induced by *P. weldi* almost completely occlude the original larval chamber in *Diplolepis bicolor* galls but not in *D. polita* galls.

Normal *Diplolepis polita* galls have a moderate circumscribing layer of sclerenchyma cells. This layer becomes thicker when the gall is attacked by *P. weldi*. The *Periclistus* larvae also induce a layer of sclerenchyma cells which circumscribes each endogall. Normal *D. bicolor* galls have a very poorly developed sclerenchyma layer; however, when attacked by *Periclistus*, this layer is more readily apparent. An additional, more strongly lignified layer of sclerenchyma cells circumscribes each endogall.

The galls of *D. bicolor* and *D. polita* each have their own characteristic spines; the number of spines and the degree of development of the spines is greatly reduced when the galls are attacked by *P. weldi*. Attack by *Periclistus* also causes the gall to expand in size; modified galls are approximately twice the size of normal galls and can be identified by these characteristics.

ETYMOLOGY. This species is named for Dr. L. H. Weld in honor of his contribution to our knowledge of the Cynipidae.

REMARKS. *Periclistus weldi* is most similar to *P. piceus* but can be recognized by the diagnostic characters. Both species differ from other *Periclistus* from leaf galls by having the lateral margin of the metanotal fovea shining smooth.

Periclistus weldi is a highly variable species and may be a complex of two species, one primarily attacking the galls of *D. polita* and the other usually inhabiting galls of *D. bicolor*. However, no consistent characters were found to separate specimens from the different hosts and I therefore, treat them as one species. The specimens reared from galls of *D. basseti* from Oregon may also represent a different species; however, no characters could be found to distinguish these specimens.

Most specimens reared from *D. polita* are smaller than those from *D. bicolor* and can be characterized as follows: pronotal bridge with larger shining area; notauli complete as distinct grooves, at most only slightly broadened posteriorly; anterior pits usually present; posterior of meso-scutum more strongly arched; R_{4+5} straight basally. Most specimens from *D. bicolor* galls can be characterized as follows: pronotal bridge coriaceous or with small shining area; notauli complete as distinct creases or grooves, usually more distinctly slightly broadened posteriorly;

anterior pits often very weak; posterior of mesoscutum more weakly arched; Rs1 straight or weakly arcuate basally. However, none of these characters are consistent and all exist in various combinations. The resolution of this problem must wait for a future study.

Periclistus weldi has been consistently misidentified as *P. pirata* (O. S.), due in large part to the confusion about the identity of that species. As far as I can tell, all references to *P. pirata* in the literature, except Osten Sacken (1863, 1865) refer to *P. weldi*. Weld identified *P. weldi* as *P. pirata* in his collection; this caused Short-house (1973, 1975, 1980) to refer to this species as *P. pirata*.

FIGURES 36 - 41

Figure 36. *Periclistus ashmeadi*, dorsal view of mesonotum.

Figure 37. *Periclistus ashmeadi*, posterior margin of mesoscutum.

Figure 38. *Periclistus arefactus*, dorsal view of mesonotum.

Figure 39. *Periclistus cataractans*, dorsal view of mesonotum.

Figure 40. *Periclistus californicus*, dorsal view of mesonotum.

Figure 41. *Periclistus fusicolus*, dorsal view of mesonotum.

FIGURES 12 - 17.

Figure 12. *Periclistus gracilicollis*, dorsal view of mesonotum.

Figure 13. *Periclistus piceus*, dorsal view of mesonotum.

Figure 14. *Periclistus pirata*, dorsal view of mesonotum.

Figure 15. *Periclistus weldi*, dorsal view of mesonotum.

Figure 16. *Periclistus vancouverensis*, dorsal view of mesonotum.

Figure 17. *Periclistus vancouverensis*, posterior margin of mesoscutum.

FIGURES 48 - 53

Figure 48. *Periclistus arefactus*, lateral view of meso-scutellum.

Figure 49. *Periclistus ashmeadi*, lateral view of meso-scutellum.

Figure 50. *Periclistus californicus*, lateral view of mesoscutellum.

Figure 51. *Periclistus cataractans*, lateral view of mesoscutellum.

Figure 52. *Periclistus fusicolus*, lateral view of meso-scutellum.

Figure 53. *Periclistus gracilicollis*, lateral view of mesoscutellum.

FIGURES 54 - 59.

Figure 54. *Periclistus piceus*, lateral view of meso-scutellum.

Figure 55. *Periclistus pirata*, lateral view of meso-scutellum.

Figure 56. *Periclistus vancouverensis*, lateral view of mesoscutellum.

Figure 57. *Periclistus weldi*, lateral view of meso-scutellum.

Figure 58. *Periclistus gracilicollis*, lateral margin of metanotum.

Figure 59. *Periclistus pirata*, lateral margin of metanotum.

FIGURES 60 - 65

Figure 60 . *Periclistus arefactus*, lateral view of mesopleuron.

Figure 61. *Periclistus ashmeadi*, lateral view of mesopleuron.

Figure 62. *Periclistus californicus*, lateral view of mesopleuron.

Figure 63. *Periclistus cataractans*, lateral view of mesopleuron.

Figure 64. *Periclistus fusicolus*, lateral view of mesopleuron.

Figure 65. *Periclistus gracilicollis*, lateral view of mesopleuron.

FIGURES 66 - 71

Figure 66. *Periclistus pirata*, lateral view of mesopleuron.

Figure 67. *Periclistus weldi*, lateral view of mesopleuron.

Figure 68. *Periclistus pirata*, anteroventral margin of subalar triangle.

Figure 69. *Periclistus weldi*, anteroventral margin of subalar triangle.

Figure 70. *Periclistus piceus*, lateral view of mesopleuron.

Figure 71. *Periclistus vancouverensis*, lateral view of mesopleuron.

FIGURES 72 - 75.

Figure 72. *Periclistus pirata*, male third antennomere.

Figure 73. *Periclistus fusicolus*, male third antennomere.

Figure 74. *Periclistus pirata*, radial cell.

Figure 75. *Periclistus ashmeadi*, radial cell.

3.4 Evolution of the Nearctic species of *Periclistus*.

In a revision of a genus it is desirable to propose a phylogenetic hypothesis on the evolutionary relationships between the included species. However, when working on the fauna of a particular region, this means that some species of the genus may be excluded. The omission of taxa can cause character polarities to be mis-interpretted, as the origin of the fauna is not known. The regional fauna may have evolved in several ways, each of which has a different effect on phylogenetic hypotheses. It is possible that the fauna has arisen from multiple invasions from an outside source (eg. the Palearctic region). In this case, any phylogenetic hypothesis is likely to be incorrect, for the regional fauna will be polyphyletic. Phylogenetic analysis is most informative when the group being studied is monophyletic (Hennig 1966; Wiley 1981).

The sister group relationship between *Periclistus* and *Synophromorpha* (Section 2.5) implies that *Periclistus* evolved in the Nearctic region. *Synophromorpha* is limited to the Nearctic region, while *Periclistus* is distributed throughout the Holarctic region; this implies that the common ancestor occurred in the Nearctic region. It is therefore unlikely that the Nearctic species of *Periclistus* are derived from multiple invasions from the Palearctic region. It is more probable that *Periclistus* has invaded the Palearctic region one or more times, and thus the

Palaearctic fauna may be polyphyletic. Thus, the Nearctic fauna of *Periclistus* is probably a paraphyletic assemblage.

There are some merits to proposing a phylogenetic hypothesis for the species of a paraphyletic assemblage. Such a hypothesis will have a defined structure; if additional species can be placed within that structure without changing the relationships between the originally included species, then the original hypothesis can be corroborated. Hence, when there is a low probability of a multiple origin of the fauna, it is desirable to propose a phylogenetic hypothesis regardless of whether all species are included in the study. However, the limitations of such a study must always be kept in mind.

The initial hypothesis for the polarity of characters is determined by the comparison of *Periclistus* with *Synophromorpha*; the character state within *Synophromorpha* is assumed to be plesiomorphic. Subsequent hypotheses on character polarity are determined by out-group comparison, as described by Watrous and Wheeler (1981). Very few characters were found to be useful for a phylogenetic analysis of evolutionary relationships between the Nearctic species of *Periclistus*. These characters are listed in Table 4 and their distribution within *Periclistus* is tabulated in Table 5.

The genus *Periclistus* can be divided into two monophyletic species groups (Fig. 76). One group contains those species reared from stem galls (except *P. fusicolus*), while

the other contains the species reared from leaf galls (except possibly *P. californicus*). I see no need to give these groups formal names and will refer to them as the stem gall and leaf gall groups.

The stem gall group contains the following species: *P. arefactus*, *P. californicus*, *P. pirata*, and *P. vancouverensis*. Monophyly of the group is defined by the presence of an area of rugosity with setigerous punctures near the anterior end of the ventral margin of the subalar triangle (Fig. 68). Members of this species group also have the mesopleuron at least partly aciculate and the median protuberance narrow and well developed. These may also be synapomorphies, but are difficult to polarize as they occur in many outside groups. Other diagnostic characters, including host relationships, are generally plesiomorphic.

Periclistus pirata is the most plesiomorphic of these species and also appears to be the most generalized in its biology. Most specimens have been reared from modified galls of *D. nodulosa*, but many have been reared from leaf galls. In all cases, the host gall is highly modified. The relationships between the other three species are unclear, primarily because of the characters used to define the other species are autapomorphies. *Periclistus californicus* differs only marginally from *P. arefactus* (presence or absence of transverse rugulae on the mesoscutum) and these may be the same species. Hence, they are treated a sister

species, even though this is based on overall similarity; strict cladistic analysis would result in a trifurcation here.

The leaf gall species group contains *P. piceus*, *P. weldi*, *P. ashmeadi*, *P. fusicolus*, *P. cataractans*, and *P. gracillicolus*. All of these species except *P. fusicolus* have been reared from leaf galls; association with leaf galls is an apomorphic character. Other synapomorphies for this group are: mesoscutum arched posteriorly, anterior lines long and concave, and vein Rs2 bent medially. *Periclistus piceus* and *P. weldi* are sister species; both species have a relatively elongate mesoscutellum, large mesoscutellar fovea, and the septum is elongate.

The remaining four species are the sister group to *P. piceus* + *P. weldi*; monophyly of this lineage is defined by the sculptured lateral margin of the metanotal fovea and possibly A3 being weakly notched and not expanded distally. Within these four species, *P. cataractans*, *P. gracillicolus*, and *P. fusicolus* are united by the bulbous mesoscutellum. No morphological synapomorphies were found to determine the relationships between these three species; however, the relatively low number of larvae per gall (1-2) may be a biological synapomorphy for *P. cataractans* and *P. gracillicolus* (1-3 for these species; usually greater than 5 for all other species) (data from Shorthouse 1975).

Table 4. Characters showing phylogenetic relationships between the Nearctic species of *Periclistus*. a = hypothesized plesiomorphic character state. b - d = apomorphic character states.

NO	CHARACTER	STATE
1	Host gall	a = Stem galls b = Leaf galls c = Stem gall d = Leaf gall
2	Male A3	a = Strongly notched b = Weakly notched
3	Mesoscutum	a = Flattened posteriorly b = Arched posteriorly
4	Anterior lines	a = Short, straight b = Long, concave
5	Notauli, Female	a = Complete b = Incomplete
6	Notauli, Male	a = Complete b = Incomplete
7	Notauli	a = Not broadened posteriorly b = Broadened posteriorly
8	Mesoscutellum	a = Flattened posteriorly b = Elongate c = Bulbous.
9	Mesopleuron	a = Aciculate b = Smooth
10	Subalar triangle	a = Smooth b = Rugose
11	Metanotum	a = Lateral margin smooth b = Lateral margin aciculate
12	Rs2	a = Straight or bent distally b = Bent medially

Table 5. Distribution of characters throughout the Nearctic species of *Periclistus* (see Table 4 for an explanation of characters). a = hypothesized plesiomorphic character state; b - d = apomorphic character states.

	P I R A T A	A R E F A C T U S	C A L I F O R N I C U S	V A N C O U V E R E N S I S	P I C E U S	W E L D I	A S H M E A D I	F U S I C O L U S	C A T A R A C T A N S	G R A C I C O L U S
1	a	a	b	d	b	b	b	c	b	b
2	a	a	a	a	a	a	b	b	b	b
3	a	a	a	a	b	b	b	b	b	b
4	a	a	a	a	b	b	b	b	b	b
5	a	b	b	b	b	a	b	b	b	b
6	a	b	b	b	a	a	b	b	b	b
7	a	b	b	b	b	b	a	b	b	b
8	a	a	a	a	b	b	a	c	c	c
9	a	a	a	a	b	b	b	b	b	b
10	b	b	b	b	a	a	a	a	a	a
11	a	a	a	a	a	b	b	b	b	b
12	a	a	a	a	b	b	b	b	b	b

Figure 76. Phylogenetic relationships between the Nearctic species of *Periclistus*. Numbers refer to characters in Table 4. * = No synapomorphy found; relationship based on overall similarity.

Figure 77. Possible co-evolutionary relationships between *Periclistus* and *Diplolepis*.

3.5 Evolutionary interaction between *Periclistus* and *Diplolepis*.

The intricate relationship between the Cynipidae and their host plants is conducive to studies on co-evolution (Ström et. al. 1984). The relationship between *Periclistus* and *Diplolepis* offers a similar challenge. One of the first steps in such a study is to examine the phylogenies of both groups involved in the possible co-evolutionary relationship. If the phylogenies mirror each other, then it is possible that some degree of co-evolution has occurred. Unfortunately, the evolutionary relationships within the genus *Diplolepis* are not fully understood and the genus is in need of revision (Shorthouse and Ritchie 1984). However, there are some apparent relationships that have been described or implied. Although these relationships have not been fully explored, they are useful for a preliminary hypothesis of possible co-evolution between *Periclistus* and *Diplolepis*.

Many stem gall formers belong to a monophyletic lineage, although not all stem gall formers belong to this lineage (Shorthouse and Ritchie 1984). Included in this species group, which is defined by a morphological synapomorphy, are the following species: *D. ashmeadi* (Beut.), *D. inconspicua* Dalley and Campbell, *D. nodulosa* (Ashmead), *D. spinosa* (Ashmead), *D. terrigena* Weld, *D. trifurcata* Shorthouse and Ritchie, *D. tuberculatrix* (Cockerell), *D. tumida*

(Bassett), and *D. verna* (Osten Sacken). Although this species group is defined by a synapomorphy, stem gall induction is probably a plesiomorphic character, as the vast majority of Aulacine gall formers induce stem galls.

Periclistus arefactus is known only from the galls of *D. inoconspicuis*, while *P. pirata* has been recorded from many of these hosts. Thus, it appears that plesiomorphic galls are attacked by plesiomorphic inquillines. However, *P. pirata* has also been reared from several other stem and leaf galls. Thus, the co-evolutionary relationship is very loose between these species (diffuse co-evolution of Strong et al. 1983).

Shorthouse (1975) has reported the only detailed descriptions of some leaf galls induced by *Diplolepis*. Similarities in either the external morphology of the gall or the internal morphology of the gall, or in both, suggest the following pairs of leaf gall formers are closely related: *D. polita* and *D. bicolor*; *D. ignota* and *D. nebulosa*; *D. lens* and *D. gracilis* (based on Shorthouse 1975). These data also suggest that *D. gracilis*, *D. lens*, *D. ignota* and *D. nebulosa* are closely related. However, it must be kept in mind that these relationships are intuitive and are not based on firm, morphological evidence. It should also be pointed out that there are several other leaf gall inducing species that have not been considered.

The relationships between these species of *Diplolepis* leaf gall formers loosely mirror the host relationships of the leaf gall group of *Periclistus* (Fig. 77). A single species of *Periclistus* usually attacks the members of only one pair of host species; the exception to this is *P. weldi* which has been reared from four of the six galls studied by Shorthouse. If the relationships between the gall formers is correct, then there appears to be a high correlation between the evolution of the Nearctic species of *Periclistus* and the Nearctic species of *Diplolepis*.

The various types of co-evolution have been discussed by Strong et al. (1983). In the strictest sense, co-evolved taxa are groups of organisms that mutually influence the evolution of each other. They point out that this definition is probably only fulfilled by species that are obligate symbiotes in a mutualistic relationship. All other types of co-evolution are called "diffuse co-evolution". This includes relationships where the evolution of only one member is influenced by the other, such as "species tracking" by parasitoids.

Although the phylogenies of *Periclistus* and *Diplolepis* are in general agreement, I strongly doubt that co-evolution (in its strictest sense) has occurred. I believe that *Periclistus* has been influenced by the evolution of *Diplolepis*, but that the converse is probably not true, although Shorthouse (1975) has shown that attacks by *Periclistus* are

a major cause of mortality of *Diplolepis* larvae. It is more probable that as *Diplolepis* has evolved, more potential host galls have appeared for *Periclistus*. It is reasonable to assume that closely related species of *Diplolepis* are likely to have similar galls and biologies. A species of *Periclistus* that is already adapted to the ancestral gall is likely to encounter the gall of the new species. If the inquiline can become adapted to the new host, then these populations may evolve into a new species.

This is not the only mechanism for speciating within *Periclistus*, as major host shifts also seem to occur. A good example is shown by the host relationships of *P. cataractans*, *P. graciliculus*, and *P. fusicolus*, three very closely related species. *Periclistus cataractans* and *P. graciliculus* are apparently restricted to attacking the galls of two closely related species of *Diplolepis* (*D. lens* and *D. gracilis*); however, the host for *P. fusicolus* is *D. fusiformans*, a stem gall former that does not appear to be closely related to *D. lens* and *D. gracilis*. Similarly, *P. californicus* has apparently shifted from stem galls (the plesiomorphic host) to leaf galls induced by *D. polita*.

3.6 Discussion and Conclusion.

The revision of *Periclistus* had two goals; one was to improve our knowledge of the Nearctic species, while the other was to examine the taxonomic concepts that have been applied to the Inguilline cynipids. Ten species of *Periclistus* are recognised, six of them new to science, and a key to species has been given. The identity of the previously described species has been clarified; this, along with the key to species, will allow accurate determinations in the future.

Many of the species of *Periclistus* have been shown to have extremely large ranges, some being distributed across North America. Hence, distributional data should not be used as a criterion for making taxonomic decisions. Only one species, *P. gracilicollis*, has a fairly restricted range (Alberta, Saskatchewan, North Dakota); however, this may be a collecting artifact due to the apparent rareness of the host gall.

Host relationships also have been shown to be a variable character. Some species are restricted to attacking the galls of a single species of gall inducer, while others are quite catholic in their tastes. Several *Diplolepis* galls are attacked by only one species of *Periclistus*; for these species, host relationships can be used to identify the species of *Periclistus*. However, there are several galls that are attacked by two or more species of *Periclistus*.

tus and several species attack the galls of more than one species of *Diplolepis*. Accurate determinations can only be made from studies of the insect itself. Thus, host relationships cannot be used as an absolute criterion for making taxonomic decisions, although new host records suggest new taxa. These principles should be applied to revisions of other inquiline genera.

Although this study has clarified many of the species in *Periclistus*, there are still several aspects that need to be studied in greater detail. One problem, already alluded to, is a further refinement in species concepts. This will require more material from poorly collected areas such as the south-western United States, California, and particularly Mexico. Most of the material from these regions have been placed in wide ranging species, due to the conservative approach to this study. However, given the pattern of speciation for other Cynipidae (eg. the oak gall formers; Kinsey 1930, 1936), it might be expected that these regions be particularly rich in species of *Periclistus*.

The Palearctic species of *Periclistus* are also in need of revision; of the seven described species, only one (*P. brandtii*) can be easily identified. The remaining six species have been rather nebulously described and the justification for their recognition appears to rest on host relationships and distribution.

This study has shown evidence for some degree of co-evolution between the members of *Periclistus* and the species of *Diplolepis*. However, with the exception of a group of stem gall formers, relationships within *Diplolepis* are still unknown. Further studies on the systematics and evolution of *Diplolepis* are necessary. One reason is to adequately determine the identity and biology of each potential host gall. A thorough understanding of *Diplolepis* is needed before the evolution of *Periclistus* can be completely understood. Without knowing the numbers of potential hosts, and their biologies, further studies on *Periclistus* will be limited. Further studies on *Diplolepis* will also allow a more complete evaluation of the degree of co-evolution between *Diplolepis* and *Periclistus*.

There are several studies on *Periclistus* that should be undertaken in the future. Very little is known about host gall preferences and host acceptability for the species of *Periclistus*. Although we now know that several species are restricted to attacking galls of one species of *Diplolepis*, we do not know why this is so. Presumably each species has a search pattern to look for oviposition sites. Is the observed restriction to a single gall due to a narrow range of host acceptability, or is the single host the only gall that they are likely to encounter? Studies on laboratory colonies of the various host galls might provide some answers to this question. Similarly, do the polyphagous

species have a preferred host? *Periclistus pirata* has been reared from several *Diplolepis* galls; however, the number of specimens reared from stem galls suggests that these may be preferred to leaf galls. Such studies will take a great deal of time and effort, as each component of the host plant - gall inducer - inquiline system presents different problems. The long time between generations means that such a study will have to be part of long term studies. If such a system can be established, it will be a marvelous tool.

4. Catalogue of the Inquilline Cynipidae.

The purpose of this catalogue is to bring together the nomenclatorial and biological information on every species of inquilline gall wasps (Hymenoptera: Cynipidae). The catalogue is divided into three parts. The first part (Section 4.1) includes every name used for inquilline cynipids, gives its status, and also the location of the types when known. The second part (Section 4.2) compiles the biological information on each species of inquilline, giving its distribution, the name of the host gall former, the type of host gall, and the first reference establishing the host relationship. The third section (Section 4.3) lists the inquilline species known from each host. At present, this information is scattered throughout the literature. There is no recent comprehensive work of this sort. Dalla Torre and Kieffer (1910) treated the world species and Weld (1952b) wrote a supplement to Dalla Torre and Kieffer's monograph; however, these works are sufficiently out of date to warrant a new catalogue.

One reason for compiling such a list is that there have been many changes in the way original names have been treated, both by individuals and by the various versions of the International Code of Zoological Nomenclature (ICZN). Prior to the first edition of the ICZN, many early workers used the name of the host plant as the name of new species of gall wasp. They either used the entire name of the host

plant as the specific epithet (eg. *Cynips quercus phellos* Osten Sacken) or hyphenated the host plant name (eg. *Cynips quercus-arbos* Fitch). Some subsequent workers abbreviated the prefix "quercus" (whether hyphenated or alone) to "q."; others described new species with "quercus" abbreviated to "q." (eg. *Cynips q. strobiliana* Osten Sacken). These names are not consistent with binomial nomenclature. Several authors attempted to correct this by dropping the prefix ("quercus" or "q.") entirely or by hyphenating the name, but still credited the species to the original describer. However, these names are unjustified emendations and take their own date and authorship. Similarly, many authors did not believe that descriptions of the gall only, without a description of the gall former, did not constitute a valid description. Thus, these names were treated as nomina nuda and new names were proposed as the insects became known.

The 1948 edition of the ICZN dealt with compound names, ruling that names that included the name of the host plant were consistent with the spirit of binomial nomenclature and that the individual words were to be joined without a hyphen. It also allowed the use of hyphenated names. Subsequently, the 1968 edition of the ICZN rules that hyphenated names are to be emended to a single word without the hyphen. All of these changes have caused many different names to be used in the literature for individual species of gall wasps.

NOMENCLATORIAL CHANGES

Euceroptres futilis (Osten Sacken) n. comb.

Aylax (?) *futilis* Osten Sacken 1861: 51, 64, Weld 1951: 615.

Euceroptres primus Ashmead 1896: 187, Weld 1951: 615.

Weld (1951) synonymized *Aylax* (?) *futilis* Osten Sacken with *Euceroptres primus* Ashmead but recognised *E. primus* as the valid name, perhaps because *E. primus* is the type species for *Euceroptres*. This is not a valid reason for rejecting a senior synonym.

Synergus punctularis Ritchie and Shorthouse. NEW NAME.

Synergus punctatus Dettmer 1924b: 146-147. Preoccupied by Gillette 1896.

Synergus punctatus Dettmer (1924b) is preoccupied by Gillette (1896) and therefore needs renaming. The name *Synergus punctularis* is proposed as a replacement.

Eumayria obliquus (Provancher). N. COMB.

Periclistus obliquus Provancher 1888: 396.

TYPE: Lectotype, +. Selected by Rohwer and Fagan 1916.

Examined.

Provancher (1888) described *Periclistus obliquus* from an unknown Californian gall, however, the lectotype is a true gall former and is a species of *Eumayria*, to which it is hereby transferred.

4.1. Synoptic Catalogue of the Inquilina Cynipidae.

The synoptic catalogue is arranged alphabetically, first by genus and then by species. Junior synonyms are listed chronologically; if a reference follows junior synonym, it is where the synonymy was first recognised. Names that are preceded with an asterisk (*) are either junior synonyms or are unjustified emendations. If a name has been justifiably emended, the pertinent reference is given.

Type material has not been seen for the majority of species in this catalogue and most locations come from the literature. The term "Types" has been used whenever a holotype or lectotype has not been designated and the species is known to be described from more than one specimen. When type material is thought to be in a museum or collection, this has been indicated by a question mark (?) after the acronym for the location. Weld (1952b) states that most of the Mayr collection is in Vienna, the Hartig collection is in Munich, and the Foerster collection is in Berlin. However, many types described by these authors are in other collections, thus the location of type material is only probable. Kieffer returned type material to the people that sent him the material; thus, his types are scattered throughout many museums and no attempt has been made to give the probable location. Also, there is no information on the location of the Walsh collection.

Abbreviations for Museums containing Type Material:

- AMNH - American Museum of Natural History, New York, NY.
- BMNH - British Museum (Natural History), London, England.
- CAS - California Academy of Sciences, San Francisco, CA.
- CMNH - Chicago Museum of Natural History, Chicago, IL.
- CORN - Entomology Department, Cornell University, Ithaca, NY.
- EIHU - Hokaido University, Hokaido, Japan.
- INHS - Illinois Natural History Survey, Illinois Institute
of Natural Resources, Urbana, IL.
- MCZ - Museum of Comparative Zoology, Harvard University,
Cambridge, MA.
- MLPA - Natural History Museum, La Plata, Argentina.
- MUCP - Museum of the University of Coimbra, Lisbon, Portugal.
- NHMM - Natural History Museum, Maastricht, Netherlands.
- PANS - Philadelphia Academy of Natural Sciences, Philadel-
phia, PA.
- PMQ - Public Museum of Quebec, University of Laval, Quebec
City, PQ.
- POM - Entomology Department, Pomona College, Claremont, CA.
- UOKJ - University of Kyoto, Kyoto, Japan.
- USNM - United States National Museum, Washington, DC.
- VIEN - Naturhistorisches Museum, Zool. Abteilung, Vienna,
Austria.
- ZSBS - Zoologische Sammlung des Bayerischen Staates, Mun-
ich, West Germany.

CEROPTRES Hartig

Ceroptres Hartig 1840: 186, 197.

TYPE-SPECIES: *Ceroptres clavicornis* Hartig. Designated
by Foerster 1869.

Ceroptres anator Hartig

Ceroptres anator Hartig 1841: 343. ♀. Europe. Types in
ZSBS?

Aulax (*Ceroptres*) *anator* Hartig, Thomson 1887: 302.

**Ceroptres arbos* Osten Sacken = *Ceroptres quercusarbos* (Fitch)

Ceroptres arbos Osten Sacken 1865: 370. Unjustified
emendation.

Ceroptres catesbaei Ashmead

Ceroptres catesbaei Ashmead 1885: 301. ♀, ♂. FL. Types
in USNM.

Ceroptres cerni Mayr

Ceroptres cerni Mayr 1872: 725-726. ♀, ♂. Austria.
Types in VIEN?

**Ceroptres cicatriculus* (Bassett) sensu Kinsey 1920a: 302.

In *Andricus*.

**Ceroptres citriformis* Ashmead. In *Synergus*.

Ceroptres citriformis Ashmead 1885: 300. ♀, ♂. FL.
Types in USNM. Weld 1922: 26.

Ceroptres clavicornis Hartig

Ceroptres clavicornis Hartig 1840: 197. ♀. Europe.
Types in ZSBS.

Ceroptres confertus (McCracken and Egbert)

Periclistus confertus McCracken and Egbert 1922: 62.

♀. CA. Holotype in CAS.

Ceroptres confertus (McCracken and Egbert), Weld 1944:

2.

**Ceroptres dorsalis* Provancher. In *Synergus*.

Ceroptres dorsalis Provancher 1888: 298. ♀, ♂. CA.

Lectotype in PMQ. Weld 1951: 601.

**Ceroptres ensiger* (Walsh) = *Ceroptres petiolicola* (Osten Sacken)

Amblynotus ensiger Walsh 1864: 487, 496. ♀. Location

of types unknown. Osten Sacken 1865: 369.

**Ceroptres ficus* Osten Sacken = *Ceroptres quercusficus* (Fitch)

Ceroptres ficus Osten Sacken 1865: 368. Unjustified emendation.

Ceroptres frondosae Ashmead

Ceroptres frondosae Ashmead 1896: 186. ♀. MO. Types in USNM.

Ceroptres globulus (Beutenmueller). NEW STATUS. NEW COMB.

Rhodites globulus Beutenmueller 1892: 247. ♀, ♂. NY.

Holotype in AMNH. Beutenmueller 1907: 638.

Ceroptres inermis (Walsh)

Amblynotus inermis Walsh 1864: 498. ♀, ♂. IL. Location of types unknown.

Ceroptres inermis (Walsh), Osten Sacken 1865: 369.

•*Ceroptres japonicus* Ashmead. In *Euceroptres*.

Ceroptres japonicus Ashmead 1904: 78. ♂. Japan. Types
in USNM. Weld 1926: 113.

Ceroptres lanigeræ Ashmead

Ceroptres lanigeræ Ashmead 1885: 301. ♀. FL. Types in
USNM.

Ceroptres melanomerus Hartig

Ceroptres melanomerus Hartig 1841: 343. ♀. Europe.
Types in ZSBS?.

Ceroptres minutissimi Ashmead

Ceroptres minutissimi Ashmead 1885: 301. ♀, ♂. FL.
Types in USNM.

Ceroptres montensis Weld

Ceroptres montensis Weld 1957a: 108. ♀, ♂. CA. Types
in USNM.

Ceroptres niger Fullaway

Ceroptres niger Fullaway 1911: 373. ♀. Type lost.
(Specimen labelled as Type in CAS is an undeter-
mined gall maker; Weld 1952b: 268)

•*Ceroptres obtusilobæ* Ashmead. In *Synergus*.

Ceroptres obtusilobæ Ashmead 1885: 300. ♀. FL. Type
in USNM. Weld 1922: 26.

•*Ceroptres obtusilobæ* (Dalla Torre) = *Ceroptres quercusob-*
tusilobæ (Karsch).

Cynips obtusilobæ Dalla Torre 1893: 47. Unjustified
emendation.

**Ceroptres obtusilobensis* Weld = *Ceroptres quercusobtusilobae* (Karsch)

Ceroptres obtusilobensis Weld 1951: 614. Unnecesary new name.

Ceroptres petiolicola (Osten Sacken)

Amblynotus petiolicola Osten Sacken 1861: 67. ♀. DC. IL. Types in MCZ?

Amblynotus ensiger Walsh 1864: 487, 496. ♀. Location of types unknown. Osten Sacken 1865: 369.

Ceroptres petiolicola (Osten Sacken), Osten Sacken 1865: 369.

**Ceroptres pisum* (Osten Sacken) = *Ceroptres quercuspisum* (Fitch)

Sarothrus? pisum Osten Sacken 1861: 54. Unjustified emendation.

Ceroptres politus Ashmead

Ceroptres politus Ashmead 1896: 23. ♀, ♂. VA. Types in USNM.

**Ceroptres pomiformis* Ashmead. In *Synergus*.

Ceroptres pomiformis Ashmead 1885: 300. ♂. CA. Types in USNM. Weld 1922: 26,

Ceroptres quercusarbores (Fitch)

Cynips Quercus-arbores Fitch 1859(1858): 809. ♂. NY. Location of types unknown.

Cynips q. arbores Osten Sacken 1865: 370. Unjustified emendation.

Ceroptres quercusarbos (Fitch) (cont.)

Ceroptres arbos Osten Sacken 1865: 370. Unjustified emendation.

Ceroptres quercusarbos (Fitch), Burks 1979: 1065.

Ceroptres quercusficus (Fitch)

Cynips Quercus-ficus Fitch 1859(1858): 812. ♀. Location of types unknown.

Cynips q. ficus Osten Sacken 1865: 368. Unjustified emendation.

Ceroptres ficus Osten Sacken 1865: 368. Unjustified emendation.

Ceroptres quercusficus (Fitch), Burks 1979: 1065.

Ceroptres quercusobtusilobae (Karsch)

Diplolepis q. obtusilobae Karsch 1880: 292. ♀. Location of types unknown.

Cynips obtusilobae Dalla Torre 1893: 47. Unjustified emendation.

Ceroptres obtusilobensis Weid 1951: 614. Unnecessary new name.

Ceroptres quercusobtusilobae (Karsch), Burks 1979: 1065.

Ceroptres quercuspisum (Fitch)

Cynips Quercus-pisum Fitch 1859(1858): 818. ♀, ♂. NY. Location of types unknown.

Cynips q. pisum Osten Sacken 1861: 54. Unjustified emendation

Ceroptres quercuspisum (Fitch) (cont.)

Sarothrus? pisum Osten Sacken 1861: 54. Unjustified emendation.

Ceroptres pisum Osten Sacken 1865: 369. Unjustified emendation.

Ceroptres quercuspisum (Fitch), Burks 1979: 1065.

Ceroptres quercustubur (Fitch)

Cynips Quercus-tuber Fitch 1859(1858): 806. ♀, ♂. NY.

Location of types unknown.

Cynips q. tubur Osten Sacken 1865: 370. Unjustified emendation.

Ceroptres tubur Osten Sacken 1865: 370. Unjustified emendation.

Ceroptres quercustuber (Fitch), Burks 1979: 1065.

Ceroptres rufiventris Ashmead

Ceroptres rufiventris Ashmead 1896: 186. ♀, ♂. MO.

Types in USNM.

Ceroptres socialis Hartig

Ceroptres socialis Hartig 1840: 197. ♀, ♂. Europe.

Types in ZSBS?

**Ceroptres succinipedis* Ashmead. In *Synergus*.

Ceroptres succinipedis Ashmead 1885: 200. ♀. FL. Types in USNM. Weld 1922: 26.

**Ceroptres tuber* Osten Sacken = *Ceroptres quercustuber* (Fitch)

Ceroptres tubur Osten Sacken 1865: 370. Unjustified emendation.

**Ceroptres virentis* Ashmead. In *Synergus*.

Ceroptres virentis Ashmead 1885: 300. ♀. FL. Types in
USNM. Weld 1922: 26.

EUCEROPTRES Ashmead

Euceroptres Ashmead 1896: 187.

TYPE-SPECIES: *Euceroptres primus* Ashmead. Monobasic.

Euceroptres futilis (Osten Sacken). N. COMB.

Aylax? futilis Osten Sacken 1861: 51, 64. ♀. FL. Type
in MCZ?. Weld 1951: 615.

Euceroptres primus Ashmead 1896: 187. ♀, ♂. Type in
USNM.

Euceroptres japonicus (Ashmead)

Ceroptres japonicus Ashmead 1904: 78. ♂. Japan. Types
in USNM.

Euceroptres japonicus (Ashmead), Weld 1926: 113.

Euceroptres maritimus Weld

Euceroptres maritimus Weld 1926: 113, 116. ♀, ♂. Holo-
type in USNM.

Euceroptres montanus Weld

Euceroptres montanus Weld 1926: 113, 115. ♀, ♂. Holo-
type in USNM.

**Euceroptres primus* Ashmead = *Euceroptres futilis* (Osten
Sacken). N. STAT.

Euceroptres primus Ashmead 1896: 187. ♀, ♂. Types in
USNM.

MYRTOPSEN Ruebsaamen

Myrtopsen Ruebsaamen 1908: 136.

TYPE-SPECIES: *Myrtopsen mayri* Ruebsaamen. Monobasic.

Myrtopsen luederwaldti Dettmer

Myrtopsen luederwaldti Dettmer 1930: 62-64. ♀, ♂.

Brazil. Types in NHMM.

Myrtopsen mayri Ruebsaamen

Myrtopsen mayri Ruebsaamen 1908: 136-137. ♀. Brazil.

Location of type unknown.

Myrtopsen mimosae Weld

Myrtopsen mimosae Weld 1926: 116. ♀, ♂. AZ. Holotype
in USNM.

Myrtopsen platensis Diaz

Myrtopsen platensis Diaz 1975: 33-36. ♀, ♂. Argentina.
Holotype in MLPA?.

Myrtopsen rodovaioi Dettmer

Myrtopsen rodovaioi Dettmer 1930: 57-61. ♀. Brazil.
Types in NHMM.

PERICLISTUS Foerster

Periclistus Foerster 1869: 332, 337.

TYPE-SPECIES: *Aylax caninae* Hartig. Original designation.

Periclistus arefactus McCracken and Egbert

Periclistus arefactus McCracken and Egbert 1922: 62.

♀, ♂. CA. Holotype in CAS.

Periclistus ashmeadi Ritchie and Shorthouse. N. SP.

Periclistus brandtii (Ratzeburg)

Cynips Brandtii Ratzeburg 1832: 183. Name only.

Cynips Brandtii Ratzeburg in Brandt and Ratzeburg 1833:

151. ♀, ♂. Europe. Location of types unknown.

Aylax brandtii (Ratzeburg), Hartig 1840: 196.

Periclistus brandtii (Ratzeburg), Mayr 1882: 11.

Aulax (*Periclistus*) *brandtii* (Ratzeburg), Thomson 1877: 800.

Periclistus californicus Ashmead

Periclistus californicus Ashmead 1896: 188. ♀, ♂. CA.

Types in USNM.

Periclistus caninae (Hartig)

Aylax caninae Hartig 1840: 196. ♂. Europe. Types in ZSBS?.

Aulax germanus Giraud in Schenck 1863: 134. Dalla Torre and Kieffer 1910: 651.

Periclistus caninae (Hartig), Foerster 1869: 188.

**Periclistus castanopsidis* Beutenmueller. In *Synergus*.

Periclistus castanopsidis Beutenmueller 1918b: 251. ♀.

CA. Cotypes in USNM.

Periclistus cataractans Ritchie and Shorthouse. N. SP.

**Periclistus confertus* McCracken and Egbert. In *Ceroptres*.

Periclistus confertus McCracken and Egbert 1922: 62.

♀. CA. Type in CAS.

Periclistus fusicolus Ritchie and Shorthouse. N. SP.

Periclistus gracilicollis Ritchie and Shorthouse. N. SP.

**Periclistus germanus* (Giraud) = *Periclistus caninae* (Hartig)

Aulax germanus Giraud in Schenck 1863: 134. Dalla Torre
and Kieffer 1910: 651.

Periclistus natalis Taketani and Yasumatsu

Periclistus natalis Taketani and Yasumatsu 1973: 2-4.

♀, ♂. Japan. Types in EIHU.

**Periclistus obliquus* Provancher. In *Eumayria*. N. COMB.

Periclistus obliquus Provancher 1888: 397. ♀, ♂. CA.
Lectotype in PMQ.

Periclistus piceus Fullaway

Periclistus piceus Fullaway 1911: 374. ♀, ♂. CA. Types
in CAS.

Periclistus pirata (Osten Sacken)

Aulax pirata Osten Sacken 1863: 42. ♀, ♂. DC. Lecto-
type in USNM.

Periclistus pirata (Osten Sacken), Beutenmueller 1907:
638.

Periclistus piratus Dalla Torre and Kieffer 1902: 72.
Unjustified emendation.

Periclistus quinlani Taketani and Yasumatsu*Periclistus quinlani* Taketani and Yasumatsu 1973:

2, 4, 5. ♀, ♂. Japan. Types in EIHU.

Periclistus rosarum Dettmer*Periclistus rosarum* Dettmer 1924b: 146. ♀, ♂. Netherlands. Types in NHMM.**Periclistus semipiceus* (Harris) = *Diplolepis semipiceus*
(Harris)*Cynips semipiceus* Harris 1841: 400. ♀?. MA. Lectotype
in MCZ.**Periclistus smilacis* Ashmead = *Periclistus pirata* (O. S.).
N. SYNONYMY.*Periclistus smilacis* Ashmead 1896: 188. ♀, ♂. FL.
Types in USNM.*Periclistus spinosissimae* Dettmer*Periclistus spinosissimae* Dettmer 1924b: 146. ♀, ♂.
Netherlands. Types in NHMM.*Periclistus vancouverensis* Ritchie and Shorthouse. N. SP.*Periclistus weidi* Ritchie and Shorthouse. N. SP.PONCYLIA Kieffer*Poncyia* Kieffer 1903: 87. Monotypic.TYPE-SPECIES: *Poncyia ferruginea* Kieffer. Monotypic.*Poncyia ferruginea* Kieffer*Poncyia ferruginea* Kieffer 1903: 87. ♀. Tangiers.
Location of types unknown.

RHOOPHILLUS Mayr

Rhoophilus Mayr 1881: 22-23.

TYPE-SPECIES: *Rhoophilus loewi* Mayr. Monotypic.

Rhoophilus loewi Mayr

Rhoophilus loewi Mayr 1881: 23. ♀, ♂. South Africa.

Types in VIEN.

SAPHONECRUS Dalla Torre and Kieffer

Saphonecrus Dalla Torre and Kieffer 1910: 605.

TYPE-SPECIES: *Synergus connatus* Hartig. Original designation.

Saphonecrus areolatus Weld

Saphonecrus areolatus Weld 1926: 112. ♀, ♂. Philippines. Holotype in USNM.

Saphonecrus brevicornis (Ashmead)

Synergus brevicornis Ashmead 1896: 189. ♀, ♂. CA. Types in USNM.

Saphonecrus brevicornis (Ashmead), Weld 1952a: 315.

Saphonecrus brevis Weld

Saphonecrus brevis Weld 1926: 109-111. ♀, ♂. AZ, NM. Holotype in USNM.

Saphonecrus connatus (Hartig)

Synergus connatus Hartig 1840: 198. ♀, ♂. Types in ZSBS.

Synergus erythroneurus Hartig, Mayr 1872: 722.

Saphonecrus connatus (Hartig) (cont.)

Synergus (*Sapholytus*) *connatus* (Hartig), Thomson 1877:
798.

Saphonecrus connatus (Hartig), Dalla Torre and Kieffer
1910: 605.

Saphonecrus connatus subspecies *luteipes* Tavares 1920a:
58-60. ♀, ♂. Spain, Portugal. Types in MUCP.

Saphonecrus excisus (Kieffer)

Sapholytus excisus Kieffer 1904: 62. ♀, ♂. Europe.
Location of types unknown.

Saphonecrus excisus (Kieffer), Dalla Torre and Kieffer
1910: 607.

Saphonecrus favanus Weld

Saphonecrus favanus Weld 1944: 1. ♀, ♂. DC, MO. Holo-
type in USNM.

Saphonecrus gemmariae (Ashmead)

Sapholytus gemmariae Ashmead 1885: 297, 302. ♂. Holo-
type in USNM.

Saphonecrus gemmariae (Ashmead), Dalla Torre and Kieff-
er 1910: 607.

Saphonecrus halmi (Mayr)

Sapholytus halmi Mayr 1872: 723. ♀, ♂. Austria. Types
in VIEN?.

Saphonecrus halmi (Mayr), Dalla Torre and Kieffer 1910:
606.

**Saphonecrus kiefferianus* (Tavares) = *Saphonecrus lusitanicus* (Tavares)

Plagiotrochus kiefferianus Tavares 1902: 138 (not Tavares 1901: 48). Dalla Torre and Kieffer 1910: 606.

Saphonecrus lusitanicus (Tavares)

Sapholytus lusitanicus Tavares 1901: 26. ♀, ♂. Portugal. Types in MUCP?.

Plagiotrochus kiefferianus Tavares 1902: 138 (not Tavares 1901: 48). Dalla Torre and Kieffer 1910: 606.

Saphonecrus lusitanicus (Tavares), Dalla Torre and Kieffer 1910: 606.

Saphonecrus lusitanicus subspecies *ater* Tavares 1922: 122. ♀. Portugal. Types in MUCP?.

Saphonecrus serratus Weld

Saphonecrus serratus Weld 1926: 111. ♀, ♂. Philippines. Holotype in USNM.

Saphonecrus undulatus (Mayr)

Sapholytus undulatus Mayr 1872: 723. ♀, ♂. Europe. Types in VIEN?.

Saphonecrus undulatus (Mayr), Dalla Torre and Kieffer 1910: 605.

SYNERGUS Hartig

Synergus Hartig 1840: 186.

TYPE-SPECIES: *Synergus vulgaris* Hartig. Designated by
Foerster 1869.

Sapholytus Foerster 1869: 332, 337, Dalla Torre and Kieffer
1910: 608.

TYPE-SPECIES: *Synergus apicalis* Hartig. Monobasic.

Synergus agrifoliae Ashmead

Synergus agrifoliae Ashmead 1896: 189. ♀, ♂. CA. Types
in USNM.

Synergus maculatus Fullaway 1911: 371. ♀, ♂. CA. Holo-
type in CAS. Weld 1952a: 337.

Synergus obscurus McCracken and Egbert 1922: 57-58. ♀.
CA. Holotype in CAS. Weld 1952a: 337.

Synergus albifaciatus Dettmer

Synergus fasciatus albifaciatus Dettmer 1924b: 148. ♂.
Netherlands. Type in NHMM. Lapsus calamni.

Synergus albifaciatus Dettmer 1924c: 168. Emendation
for *Synergus fasciatus albifasciatus* Dettmer.

**Synergus albinervus* (Vollenhoven) = *Synergus gallaepomi*
formis (Fonscolombe)

Aulax albinervus Vollenhoven 1869: 126. ♀. Europe.
Location of types unknown. Kieffer 1902: 293.

Synergus albipes Hartig

Synergus albipes Hartig 1841: 349. ♀, ♂. Europe. Types
in ZSBS.

Synergus albipes Hartig (cont.)

Synergus erythrocerus Hartig 1841: 349. ♀, ♂. Europe.

Types in ZSBS?. Mayr 1872: 722.

Synergus varius Hartig 1841: 349. ♀, ♂. Europe. Types
in ZSBS? Eady 1952: 151.

Synergus tscheki Mayr 1872: 708. ♀, ♂. Austria. Types
in VIEN?. Eady 1952: 151.

Synergus tristis Mayr 1872: 715. ♀, ♂. Austria. Types
in VIEN?. Eady 1952: 151.

Synergus nervosus Mayr sensu Ross 1951: 92. Eady 1952:
151.

Synergus nervosus form *albipes* Mayr sensu Ross 1951:
91. Eady 1952: 151.

Synergus nervosus form *tristis* Mayr sensu Ross 1951:
93. Eady 1952: 151.

Synergus mutabilis Dettmer, Wiebes-Rijks 1979: 318.

**Synergus albipes* (Walsh) = *Synergus walshii* Gillette

Synophrus albipes Walsh 1861: 479, 496. ♀, ♂. IL.

Location of types unknown. Preoccupied by Hartig
1841: 341.

Synergus apicalis Hartig

Synergus apicalis Hartig 1841: 349. ♂. Europe. Types
in ZSBS?.

Synergus immarginatus Hartig 1841: 348. ♀, ♂. Europe.
Types ZSBS?. Mayr 1872: 705.

Synergus apicalis Hartig (cont.)

Synergus erythrostomus Hartig 1841: 348. ♀, ♂. Europe.

Types in ZSBS?. Mayr 1872: 705.

Sapholytus apicalis (Hartig), Foerster 1869: 338.

Synergus atamiensis Ashmead

Synergus atamiensis Ashmead 1904: 77. ♀. Japan. Holotype in USNM.

Synergus atra Gillette

Synergus atra Gillette 1896: 86. ♀, ♂. CO. Types in USNM.

Synergus atripennis Ashmead

Synergus atripennis Ashmead 1896: 189. ♀. FL. Types in USNM.

Synergus atripes Gillette

Synergus atripes Gillette 1896: 189. ♀, ♂. CO. Types in USNM.

**Synergus australis* Hartig = *Synergus pallicornis* Hartig

Synergus australis Hartig 1843: 414. ♀. Europe. Types in ZSBS?. Mayr 1872: 709.

Synergus basalis Hartig

Synergus basalis Hartig 1840: 198. ♀. Europe. Types in ZSBS?.

Synergus batatoides Ashmead

Synergus batatoides Ashmead 1885: 301. ♀, ♂. FL. Types in USNM.

Synergus bellus McCracken and Egbert

Synergus bellus McCracken and Egbert 1922: 54. ♀, ♂.

CA. Holotype in CAS.

Synergus bicolor Ashmead

Synergus bicolor Ashmead 1885: 297, 302. ♀, ♂. FL.

Types in USNM.

Synergus bipunctatus Hartig

Synergus bipunctatus Hartig 1811: 317. ♀. Europe.

Types in ZSBS?.

**Synergus bispinus* Hartig = *Synergus gallaepomiformis* Fons-
colombe

Synergus bispinus Hartig 1810: 317. ♀. Europe. Types

in ZSBS?. Mayr 1872: 717.

**Synergus brevicornis* Ashmead. In *Saphonecrus*.

Synergus brevicornis Ashmead 1896: 189. ♀, ♂. CA.

Types in USNM. Weld 1952a: 315.

Synergus campanula Osten Sacken

Synergus campanula Osten Sacken 1865: 376. ♀. DC, IL,

NJ, NY. Types in MCZ?.

**Synergus carinatus* Hartig = *Synergus thaumacerus* (Dalman)

Synergus carinatus Hartig 1811: 318. ♀. Europe. Types

in ZSBS?. Mayr 1872: 719.

Synergus carinulatus Dettmer

Synergus carinulatus Dettmer 1924b: 148. ♀, ♂. Nether-

lands. Types in NHMM.

Synergus castanopsidis (Beutenmueller)*Periclistus castanopsidis* Beutenmueller 1918: 251. ♀.

CA. Types in USNM.

Synergus castanopsidis (Beutenmueller), Weld 1926: 112.*Synergus citriformis* (Ashmead)*Ceroptres citriformis* Ashmead 1885: 300. ♀, ♂. FL.

Types in USNM.

Synergus citriformis (Ashmead), Weld 1922: 26.*Synergus clandestinus* Eady*Synergus clandestinus* Eady 1952: 148. ♀, ♂. Figs. 10

a-c, 15, 17. Holotype in BMNH.

Synergus confertus McCracken and Egbert*Synergus confertus* McCracken and Egbert 1922: 55. ♀,

♂. CA. Holotype in CAS.

Synergus coniferae Ashmead*Synergus coniferae* Ashmead 1885: 297, 301. ♀, ♂. FL.

Types in USNM.

**Synergus connatus* Hartig. In *Saphonecrus*.*Synergus connatus* Hartig 1840: 198. ♀, ♂. Europe.

Types in ZSBS?. Dalla Torre and Kieffer 1910: 606.

Synergus crassicornis Hartig*Synergus crassicornis* Hartig 1843: 414. ♂. Europe.

Types in ZSBS?.

Synergus davis (Beutenmueller)*Andricus davis* Beutenmueller 1907a: 463. Figs. 1-6.

♀, ♂. NJ. Types in AMNH.

Synergus davisi (Beutenmueller) (cont.)*Synergus davisi* (Beutenmueller), Weld 1922: 21.*Synergus digressus* McCracken and Egbert*Synergus digressus* McCracken and Egbert 1922: 52. ♀,

♂. CA. Holotype in CAS.

Synergus dimorphus Osten Sacken*Synergus dimorphus* Osten Sacken 1865: 376-377. ♀, ♂.

DC. Types in MCZ?

Synergus distinctus McCracken and Egbert*Synergus distinctus* McCracken and Egbert 1922: 58-59.

♀, ♂. CA. Holotype in CAS.

**Synergus dorsalis* Cameron = *Andricus guatemalensis* Cameron.

NEW SYNONYMY

Synergus dorsalis Cameron 1883: 71. ♀. Guatemala.

Holotype in BMNH.

Synergus dorsalis (Provancher)*Ceroptres dorsalis* Provancher 1888: 298. ♀, ♂. CA.

Lectotype in PMQ.

Synergus dorsalis (Provancher), Weld 1951: 601. (Not

Cameron 1883: 71.

**Synergus dubiosus* Fullaway = *Synergus splendidus* Fullaway*Synergus dubiosus* Fullaway 1911: 372. ♀. CA. Holotype

in CAS.

Synergus dugesi Ashmead*Synergus dugesi* Ashmead 1899: 195. ♀, ♂. Mexico. Types

in USNM.

Synergus duricornis Gillette

Synergus duricornis Gillette 1896: 90, 93. ♀. DE. Types
in USNM.

Synergus erinacei Gillette

Synergus erinacei Gillette 1896: 90, 94. ♀, ♂. IO, NY.
Types in USNM.

**Synergus erythrocerus* Hartig = *Synergus albipes* Hartig

Synergus erythrocerus Hartig 1841: 349. ♀, ♂. Europe.
Types in ZSBS?. Mayr 1872: 722.

**Synergus erythroneurus* Hartig = *Saphonecrus connatus* (Hartig)

Synergus erythroneurus Hartig 1840: 198. ♀, ♂. Europe.
Types in ZSBS?. Dalla Torre and Kieffer 1910: 606.

**Synergus erythrostomus* Hartig = *Synergus apicalis* Hartig

Synergus erythrostomus Hartig 1841: 348. ♀. Europe.
Types in ZSBS?. Mayr 1872: 705.

Synergus evanescens Mayr

Synergus evanescens Mayr 1872: 699. ♀, ♂. Austria.
Types in VIEN?.

Synergus evanescens var. *rubricornis* Tavares 1901: 24.
♀, ♂. Portugal. Types in MUCP?.

Synergus evanescens subspecies *fidelis* Tavares 1920a:
19-20. ♀. Portugal. Types in MUCP.

Synergus evanescens subspecies *tudensis* Tavares 1920a:
20-21. ♀. Spain. Types in MUCP.

Synergus exaratus Hartig

Synergus exaratus Hartig 1841: 348. ♀. Europe. Types
in ZSBS?.

**Synergus facialis* Hartig = *Synergus gallaepomiformis* Fons-
colombe

Synergus facialis Hartig 1840: 199. ♀, ♂. Europe.

Types in ZSBS?. Dalla Torre and Kieffer 1910: 621.

**Synergus faciatus albifasciatus* Dettmer = *Synergus albi-
fasciatus* Dettmer

Synergus faciatus albifasciatus Dettmer 1924b: 148. ♂.

Netherlands. Types in NHMM. Lapsus calamni for
Synergus albifasciatus Dettmer; Dettmer 1924c: 148.

Synergus ficigeræ Ashmead

Synergus ficigeræ Ashmead 1885: 301. ♀, ♂. FL. Types
in USNM.

Synergus filicornis Cameron

Synergus filicornis Cameron 1883: 71. ♀. Guatemala.
Holotype in BMNH.

Synergus furnessiana Weld 1913: 134. Pl. 4, Figs. 8-13.
♀, ♂. MX. Holotype in PANS.

Synergus filicornis Cameron, Weld 1930b: 143.

Synergus flavens McCracken and Egbert

Synergus flavens McCracken and Egbert 1922: 55. ♀. CA.
Holotype in CAS.

**Synergus flavicornis* Hartig = *Synergus pallicornis* Hartig

Synergus flavicornis Hartig 1840: 198. ♀, ♂. Europe.

Types in ZSBS?. Mayr 1872: 709.

Synergus flavipes Hartig

Synergus flavipes Hartig 1843: 413. ♂. Europe. Types

in ZSBS?.

Synergus flavus Kieffer

Synergus flavus Kieffer 1904: 133. ♀, ♂. CA. Location
of types unknown.

Synergus fulvipes Dettmer

Synergus fulvipes Dettmer 1924b: 147. ♀, ♂. Nether-
lands. Types in NHMM.

**Synergus furnessana* Weld = *Synergus filicornis* Cameron

Synergus furnessana Weld 1913: 134. Pl. 4. Figs. 8-13.

♀, ♂. Mexico. Holotype in PANS. Weld 1930b: 143.

Synergus gallaepomiformis (Fonscolombe)

Diptolepis gallae pomiformis Fonscolombe 1832: 118,
195. ♀. Europe. Location of types unknown.

Synergus facialis Hartig 1840: 199. ♀, ♂. Europe.

Types in ZSBS?. Dalla Torre and Kieffer, 1910: 621.

Synergus dispinus Hartig 1840: 347. ♀. Europe. Types

in ZSBS?. Mayr 1872: 717.

Aulax albinervus Vollenhoven 1869: 126. ♀. Europe.

Location of types unknown. Kieffer 1902: 293.

Synergus pomiformis Kieffer 1893: 264 (Not Ashmead

1885: 300). Unjustified emendation.

Synergus gallaepomiformis (Fonscolombe) (cont.)

Synergus gallaepomiformis minimus Kieffer 1902b: 358.

♀, ♂. France. Location of types unknown.

Synergus gallaepomiformis (Fonscolombe), Dalla Torre and Kieffer 1910: 621.

Synergus gallae-pomiformis gallicus Dalla Torre and Kieffer 1910: 622. ♀. France. Location of types unknown.

Synergus vulgaris Hartig 1840: 198. ♀, ♂. Europe. Types in ZSBG?. Ross 1951: 88.

Synergus gallaepyriformis (Olivier)

Diplolepis gallae-pyriformis Olivier 1791: 282. ♀. Europe. Location of types unknown.

Cynips pyriformis Dalla Torre 1893: 76. Unjustified emendation.

Synergus gallaepyriformis (Olivier), Dalla Torre and Kieffer 1910: 627.

Synergus gallaeviscosae (Fairmaire)

Cynips gallaeviscosae Fairmaire 1882: 34. ♀. Europe. Location of types unknown.

Cynips viscosae Dalla Torre 1893: 79. Unjustified emendation.

Synergus gallaeviscosae (Fairmaire), Dalla Torre and Kieffer 1910: 627.

Synergus gallaicus Tavares*Synergus gallaicus* Tavares 1920a: 23-24. Pl. 1. Figs.

24, 25. ♀. Spain. Types in MUCP.

Synergus gallaicus subspecies *annulatus* Tavares 1920a:

25. ♀. Spain. Types in MUCP.

Synergus garryana Gillette*Synergus garryana* Gillette 1893: 110. ♀, ♂. OR, WA.

Types in USNM.

Synergus gifuensis Ashmead*Synergus gifuensis* Ashmead 1904: 78. ♀. Japan. Types

in USNM.

Synergus hakonensis Ashmead*Synergus hakonensis* Ashmead 1904: 78. ♀. Japan. Types

in USNM.

Synergus hayneanus (Ratzeburg)*Cynips Hayneana* Ratzeburg 1832: 154. ♀, ♂. Europe.

Location of types unknown.

Synergus Hayneanus (Ratzeburg), Hartig 1841: 347.*Synergus rugulosus* Hartig 1841: 348. ♀. Europe. Types

in ZSBS? Mayr 1872: 700.

Synergus ibericus Tavares*Synergus ibericus* Tavares 1920a: 21-23. Pl. 1, Figs.

19-23. ♀, ♂. Spain, Portugal. Types in MUCP.

**Synergus immarginatus* Hartig = *Synergus apicalis* Hartig*Synergus immarginatus* Hartig 1841: 348. ♀, ♂. Europe.

Types ZSBS? Mayr 1872: 705.

Synergus incisus Gillette

Synergus incisus Gillette 1896: 90. ♀, ♂. CO. Types in USNM.

Synergus incrassatus Hartig

Synergus incrassatus Hartig 1840: 199. ♂. Europe. Types in ZSBS?.

Synergus inflatus Dettmer

Synergus inflatus Dettmer 1924b: 148-149. ♀, ♂. Netherlands. Types in NHMM.

Synergus insuetus Tavares

Synergus insuetus Tavares 1920a: 27-28. Pl. 1, Figs. 31-35. ♀. Portugal. Types in MUCP.

Synergus japonicus Walker

Synergus japonicus Walker 1874: 309. ♀. Japan. Types in BMNH?.

Synergus jezoensis Uchida and Sakagami

Synergus jezoensis Uchida and Sakagami 1948: 15-17. ♀, ♂. Hokkaido, Japan. Types in EIHU.

**Synergus klugii* Hartig = *Synergus thaumacerus* (Dalmat)

Synergus klugii Hartig 1840: 199. ♀, ♂. Europe. Types in ZSBS?. Mayr 1872: 719.

**Synergus lana* (Ashmead) = *Synergus quercuslana* (Fitch)

Andricus lana Ashmead 1885: 295. Unjustified emendation.

**Synergus lanæ* Dalla Torre = *Synergus quercuslana* (Fitch)

Synergus lanæ Dalla Torre 1893: 111. Unjustified emendation.

Synergus laeviventris (Osten Sacken)

Synophrus? *laeviventris* Osten Sacken 1861: 57. ♀. DC.

Types in MCZ?.

Synergus laeviventris (Osten Sacken), Osten Sacken 1865: 375.

Synergus lignicola (Osten Sacken)

Cynips (*Synerges?*) *lignicola* Osten Sacken 1862: 252.

♀, ♂. DC, IN, MI, NY. Types in MCZ?.

Synergus lignicola (O. S.), Osten Sacken 1865: 374-375.

Synerges rhoditiformis Walsh 1864: 499. ♀, ♂. Location of types unknown. Osten Sacken 1865: 374-375.

Synergus lusitanicus Tavares

Synergus lusitanicus Tavares 1901: 26. ♀. Portugal.

Types in MUCP?.

**Synergus luteus* Hartig = *Synergus thaumacerus* (Dalman)

Synergus luteus Hartig 1840: 199. ♀, ♂. Europe. Types in ZSBS?. Mayr 1872: 719.

**Synergus maculatus* Fullaway = *Synergus agrifoliae* Ashmead

Synergus maculatus Fullaway 1911: 371. ♀, ♂. CA. Holotype in CAS. Weld 1952a: 337.

**Synergus maculatus* Tavares = *Synergus maculosus* Tavares

Synergus maculosus Tavares 1920: 47-49. ♀, ♂. Spain.

Types in MUCP. Preoccupied by Fullaway 1911: 371.

Synergus maculosus Tavares

Synergus maculatus Tavares 1920a: 47-49. Figs. 24-26.

♀, ♂. Spain. Types in MUCP. Preoccupied by Fullaway 1911: 371.

Synergus maculosus Tavares 1925: 96. New name for

Synergus maculatus Tavares 1920a: 47-49.

Synergus magnificus Weld

Synergus magnificus Weld 1957: 107. ♀, ♂. CA. Types in USNM.

Synergus magnus Gillette

Synergus magnus Gillette 1890: 202. ♀. MI. Holotype in INHS.

Synergus medullae Ashmead

Synergus medullae Ashmead 1885: 302. ♀, ♂. FL. Types in USNM.

**Synergus melanopus* Hartig = *Synergus umbraculus* Olivier

Synergus melanopus Hartig 1843: 414. ♀, ♂. Europe.

Types in ZSBS?. Dalla Torre and Kieffer 1910: 615.

Synergus mendax Walsh

Synerges mendax Walsh 1864: 498. ♀. IL. Location of types unknown.

Synergus mendax Walsh, Osten Sacken 1865: 378.

**Synergus mexicanus* Gillette. In *Synophrus*.

Synergus mexicanus Gillette 1896: 90, 96. ♀. NM. Types in USNM. Weld 1952a: 315-316.

Synergus mizunarae Shinji

Synergus mizunarae Shinji 1940a: 258. 258. ♀, ♂. Japan. Location of types unknown.

Synergus multiplicatus Fullaway

Synergus multiplicatus Fullaway 1911: 370. ♀, ♂. CA. Types in CAS.

**Synergus mutabilis* Dettmer = *Synergus albipes* Hartig

Synergus mutabilis Dettmer 1924b: 147. ♀, ♂. Netherlands. Types in NHMM. Wiebes-Rijks 1979: 318.

Synergus nervosus Hartig

Synergus nervosus Hartig 1840: 197. ♀, ♂. Europe. Types in ZSBS?.

Synergus tibialis Hartig 1840: 197/98. ♀, ♂. Europe. Types in ZSBS?. Mayr 1872: 713.

Synergus nigricornis Hartig 1841: 347. ♀. Europe. Types in ZSBS?. Mayr 1872: 713.

Synergus radiatus Mayr 1872: 718-719. ♀, ♂. Austria. Types in VIEN?. Eady 1952: 15.

Synergus tschecki Mayr sensu Ross 1951: 90. Eady 1952: 151.

Synergus tschecki var. *radiatus* Mayr sensu Ross 1951: 89. Eady 1952: 151.

Synergus tristis Mayr sensu Ross 1951: 90. Eady 1952: 151.

Synergus niger Fullaway

Synergus niger Fullaway 1911: 369. ♀, ♂. CA. Types in CAS.

**Synergus nigricornis* Hartig = *Synergus nervosus* Hartig

Synergus nigricornis Hartig 1841: 347. ♀. Europe.

Types in ZSBS?. Mayr 1872: 713.

**Synergus nigripes* Hartig = *Synergus pallicornis* Hartig

Synergus nigripes Hartig 1840. 197. ♀. Europe. Types

in ZSBS?. Mayr 1872: 709.

Synergus nigroornatus McCracken and Egbert

Synergus nigro-ornatus McCracken and Egbert 1922: 57.

♀, ♂. CA. Holotype in CAS.

Synergus nigroornatus McCracken and Egbert, Burks

1979: 1065.

**Synergus obscurus* McCracken and Egbert = *Synergus agrifo*

liae Ashmead

Synergus obscurus McCracken and Egbert 1922: 57-58. ♀.

CA. Holotype in CAS. Weld 1952a: 337.

Synergus obtusilobae (Ashmead)

Ceroptres obtusilobae Ashmead 1885: 300. ♀. FL. Types

in USNM.

Synergus obtusilobae (Ashmead), Weld 1922: 26.

Synergus ochreus Fullaway

Synergus ochreus Fullaway 1911: 368. ♀. CA. Types in

CAS.

Synergus oneratus (Harris)

Cynips oneratus Harris 1841: 398. ♀. MA. Types in MCZ?

Synerges oneratus (Harris), Walsh 1864: 488.

Synergus oneratus (Harris), Osten Sacken 1865: 373.

Synergus oneratus (Harris) (cont.)*Synergus oneratus* var. *coloradensis* Gillette 1896: 90.

♀, ♂. CO. Types in USNM.

**Synergus orientalis* Hartig = ~~*Synergus*~~ *umbraculus* (Olivier)*Synergus orientalis* Hartig 1841: 347. ♀, ♂. Europe.

Types in ZSBS?. Dalla Torre and Kieffer 1910: 615.

Synergus pacificus McCracken and Egbert*Synergus pacificus* McCracken and Egbert 1922: 56. ♀,

♂. CA. Holotype in CAS.

Synergus palliceps Hartig*Synergus palliceps* Hartig 1841: 349. ♂. Europe. Types
in ZSBS?.*Synergus pallidiceps* Dalla Torre 1893: 112. Unjusti-
fied emendation.*Synergus pallicornis* Hartig*Synergus pallicornis* Hartig 1841: 348-349. ♀, ♂. Eur-
ope. Types in ZSBS?.*Synergus australis* Hartig 1843: 414. ♀. Europe. Types
in ZSBS?. Mayr 1872: 709.*Synergus flavicornis* Hartig 1840: 198. ♀, ♂. Europe.
Types in ZSBS?. Mayr 1872: 709.*Synergus nigripes* Hartig 1840: 197. ♀. Europe. Types
in ZSBS?. Mayr 1872: 709.**Synergus pallidiceps* Dalla Torre = *Synergus palliceps* Hartig*Synergus pallidiceps* Dalla Torre 1893: 112. Unjusti-
fied emendation.

Synergus pallidipennis Mayr

Synergus pallidipennis Mayr 1872: 699-700. ♀, ♂. Austria. Types in VIEN?.

**Synergus pallidipes* Dalla Torre = *Synergus pallipes* Hartig

Synergus pallidipes Dalla Torre 1893: 113. Unjustified emendation.

Synergus pallipes Hartig

Synergus pallipes Hartig 1840: 198. ♀, ♂. Europe. Types in ZSBS?.

Synergus pallidipes Dalla Torre 1893: 113. Unjustified emendation

Synergus physoserus Hartig

Synergus physoserus Hartig 1843: 413. ♂. Europe. Types in ZSBS?.

Synergus pomiformis (Ashmead)

Ceroptres pomiformis Ashmead 1885: 300. ♂. CA. Types in USNM.

Synergus pomiformis (Ashmead), Weld 1922: 26.

**Synergus pomiformis* Kieffer = *Synergus gallaepomiformis* (Fonscolombe)

Synergus pomiformis Kieffer 1893: 264 (Not Ashmead 1885: 300). Unjustified emendation.

Synergus profusus McCracken and Egbert

Synergus profusus McCracken and Egbert 1922: 59-60. ♀, ♂. CA. Holotype in CAS.

Synergus punctatus Gillette

Synergus punctatus Gillette 1896: 90, 94. ♀, ♂. CO.

Types in USNM.

**Synergus punctatus* Dettmer = *Synergus punctularis* Ritchie
and Shorthouse

Synergus punctatus Dettmer 1924b: 116-117. ♀, ♂. Netherlands. Types in NHMM. Preoccupied by Gillette
1896: 90, 94.

Synergus punctularis Ritchie and Shorthouse. N. NAME.

Synergus punctatus Dettmer 1924b: 116-117. Preoccupied by Gillette 1896: 90, 94.

**Synergus pyriformis* (Dalla Torre) = *Synergus gallae-pyriformis* (Olivier)

Cynips pyriformis Dalla Torre 1893: 76. Unjustified emendation.

Synergus quercus-lana (Fitch)

Cynips Quercus-lana Fitch 1859(1858): 31. ♀. IO, NY.
Types in USNM.

Andricus lana Ashmead 1885: 295. Unjustified emendation.

Synergus lana (Ashmead), Cresson 1887: 180.

Synergus lanæ Dalla Torre 1893: 111. Unjustified emendation.

Synergus quercus-lana (Fitch), Burks 1979: 1065.

**Synergus radiatus* Mayr = *Synergus nervosus* Hartig

Synergus radiatus Mayr 1872: 718-719. ♀, ♂. Austria.

Types in VIEN?. Eady 1952: 15.

Synergus reinhardi Mayr

Synergus reinhardi Mayr 1872: 698. ♀, ♂. Austria.

Types in VIEN?.

Synergus reniformis McCracken and Egbert

Synergus reniformis McCracken and Egbert 1922: 53. ♀,

♂. CA. Holotype in CAS.

**Synergus rhoditiformis* Walsh = *Synergus lignicola* (Osten Sacken).

Synergus rhoditiformis Walsh 1861: 499. ♀, ♂. Location of types unknown. Osten Sacken 1865: 374-375.

Synergus rotundiventris Mayr

Synergus rotundiventris Mayr 1872: 706. ♀, ♂. Austria.

Types in VIEN?.

Synergus ruficornis Hartig

Synergus ruficornis Hartig 1840: 198. ♀. Europe. Types in ZBMB?.

**Synergus rufipes* (Fonscolombe) = *Synergus umbraculus* (Olivier)

Diplolepis rufipes Fonscolombe 1832: 193. ♀. Europe.

Location of types unknown. Mayr 1872: 695.

**Synergus rugulosus* Hartig = *Synergus hayneanus* (Ratzeburg)

Synergus rugulosus Hartig 1841: 348. ♀. Europe. Types in ZBMB?. Mayr 1872: 700.

Synergus rutulus McCracken and Egbert*Synergus rutulus* McCracken and Egbert 1922: 60. ♀. CA.

Holotype in CAS.

Synergus scaber Hartig*Synergus scaber* Hartig 1856: 268. ♀, ♂. Europe. Types

in Z886?.

Synergus semisulcatus Kieffer*Synergus semisulcatus* Kieffer 1905: 342-343. ♀, ♂.

Europe. Location of types unknown.

Synergus similis Gillette*Synergus similis* Gillette 1896: 90, 92. ♀. CO. Types

in USNM.

**Synergus socialis* Hartig = *Synergus umbraculus* (Olivier)*Synergus socialis* Hartig 1843: 413. ♀, ♂. Europe.

Types in Z886? Mayr 1872: 695.

Synergus splendidus Fullaway*Synergus splendidus* Fullaway 1911: 369. ♀. CA. Holo-

type in CAS.

Synergus dubiosus Fullaway 1911: 372. ♀. CA. Holotype

in CAS. McCracken and Egbert 1922: 51.

Synergus dubiosus Fullaway, Weld 1952b: 263. Holotype

is ♂.

Synergus succinipedis (Ashmead)*Ceroptres succinipedis* Ashmead 1885: 300. ♀. FL. Types

in USNM.

Synergus succinipedis (Ashmead), Weld 1922: 26.

Synergus synophri Kieffer

Synergus synophri Kieffer 1902b: 346. ♂. Algeria. Location of types unknown.

Synergus testaceus (Hartig)

Xystus testaceus Hartig 1841: 352. ♀. Austria. Holotype in ZSBS.

Allotria testacea (Hartig), Hartig 1843: 415.

Synergus testaceus (Hartig), Quinlan 1978: 71.

Synergus thaumacerus (Dalman)

Cynips Thaumacera Dalman 1823: 96. ♂. Europe. Location of types unknown.

Synergus luteus Hartig 1840: 199. ♀, ♂. Europe. Types in ZSBS?. Mayr 1872: 719.

Synergus Klugii Hartig 1840: 199. ♀, ♂. Europe. Types in ZSBS?. Mayr 1872: 719.

Synergus carinatus Hartig 1841: 348. ♀. Europe. Types in ZSBS?. Mayr 1872: 719.

Synergus thaumatocerus Dalla Torre 1893: 114. Unjustified emendation.

**Synergus thaumatocerus* Dalla Torre = *Synergus thaumacerus* (Dalman)

Synergus thaumatocerus Dalla Torre 1893: 114. Unjustified emendation.

**Synergus tibialis* Hartig = *Synergus nervosus* Hartig

Synergus tibialis Hartig 1840: 197-198. ♀, ♂. Europe. Types in ZSBS?. Mayr 1872: 713.

**Synergus tristis* Mayr = *Synergus albipes* Hartig

Synergus tristis Mayr 1872: 715. ♀, ♂. Austria. Types
in VIEN?. Eady 1952: 151.

**Synergus tscheki* Mayr = *Synergus albipes* Hartig

Synergus tscheki Mayr 1872: 708. ♀, ♂. Austria. Types
in VIEN? Eady 1952: 151.

**Synergus tscheki* Mayr sensu Ross 1951: 90 = *Synergus nervosus* Hartig. Eady 1952: 151.

Synergus umbraculus (Olivier)

Diplolepis umbraculus Olivier 1791: 281. ♀. Europe.
Location of types unknown.

Diplolepis gallae-umbraculatae D'Anthoine 1793: 35.
Unjustified emendation.

Diplolepis rufipes Fonscolombe 1832: 193. ♀. Europe.
Location of types unknown. Mayr 1872: 695.

Synergus melanopus Hartig 1843: 414. ♀, ♂. Europe.
Types in ZSBS?. Dalla Torre and Kieffer 1910: 615.

Synergus orientalis Hartig 1841: 347. ♀, ♂. Europe.
Types in ZSBS?. Dalla Torre and Kieffer 1910: 615.

Synergus socialis Hartig 1843: 413. ♀, ♂. Europe.
Types in ZSBS?. Mayr 1872: 695.

Synergus umbraculus (Olivier), Kieffer 1898: 264.

Synergus umbraculus var. *histris* Kieffer 1902: 340-
341. ♀. France. Location of types unknown.

Synergus umbraculus var. *mixta* Kieffer 1902: 342. ♀.
Austria. Location of types unknown.

Synergus umbraculus (Olivier) (cont.)

Synergus umbraculus var. *minor* Kieffer 1902: 342. Europe. Location of types unknown.

Synergus umbraculus subspecies *pseudohistrio* Tavares 1920a: 12. ♀, ♂. Spain. Types in MUCP.

Synergus variabilis Mayr

Synergus variabilis Mayr 1872: 702. ♀, ♂. Austria.

Lectotype (designated by Quinlan 1978: 72-73), in ZSBS.

Synergus varicolor Fullaway

Synergus varicolor Fullaway 1911: 371. ♀, ♂. CA. Types in CAS.

Synergus variegatus McCracken and Egbert

Synergus variegatus McCracken and Egbert 1922: 51. ♀, ♂. CA. Holotype in CAS.

Synergus variolosus Hartig

Synergus variolosus Hartig 1841: 349. ♀. Europe. Types in ZSB9?.

**Synergus varius* Hartig = *Synergus albipes* Hartig

Synergus varius Hartig 1841: 349. ♀, ♂. Europe. Types in ZSB6? Eady 1952: 151.

Synergus villosus Gillette

Synergus villosus Gillette 1890: 202. ♀. MI. Types in INHS.

Synergus virentis (Ashmead)

Ceroptres virentis Ashmead 1885: 300. ♀. FL. Types in USNM.

Synergus virentis (Ashmead), Weld 1922: 26.

**Synergus viscosae* (Dalla Torre) = *Synergus gallaeviscosae* (Fairmaire).

Cynips viscosae Dalla Torre 1893: 79. Unjustified emendation.

**Synergus vulgaris* Hartig = *Synergus gallaepomiformis* (Fonscolombe)

Synergus vulgaris Hartig 1840: 198. ♀, ♂. Europe. Types in ZSBS?.

Synergus walshii Gillette

Synophrus albipes Walsh 1864: 479, 496. ♀, ♂. IL.

Location of types unknown. Preoccupied by Hartig 1841: 344.

~~*Synergus albipes*~~ (Walsh); Osten Sacken 1865: 377-378.

Synergus walshii Gillette 1896: 97. New name for *Synophrus albipes* Walsh.

Synergus xanthocerus Hartig

Synergus xanthocerus Hartig 1841: 350. ♂. Europe. Types in MUN?.

SYNOPHROMORPHA ~~Ashmead~~

Synophromorpha Ashmead 1903: 145.

TYPE-SPECIES: *Synophrus sylvestris* Osten Sacken. Designated here. (Original designation of *S. salicis* Ashmead unjustified).

Synophromorpha rubi Weld

Synophromorpha rubi Weld 1952a: 317. ♀, ♂. IL. Types in USNM.

**Synophromorpha salicis* Ashmead

Synophromorpha salicis Ashmead 1903: 145. NOMEN NUDEM.

Synophromorpha sylvestris (Osten Sacken)

Synophrus sylvestris Osten Sacken 1861: 145. ♀. CT, DC, MI, NJ, NY, ON. Types in MCZ.

Synophromorpha sylvestris (Osten Sacken); Weld 1952a: 316.

Synophromorpha terricola Weld

Synophromorpha terricola Weld 1952a: 316. ♀, ♂. DC, VA. Types in USNM.

SYNOPHRUS Ashmead

Synophrus Hartig 1843: 411.

TYPE-SPECIES: *Synophrus politus* Hartig. Monotypic.

**Synophrus albipes* Walsh = *Synergus walshii* Gillette

Synophrus albipes Walsh 1864: 479, 496. ♀, ♂. IL.

Location of types unknown. Preoccupied by Hartig
1841: 349.

Synophrus mexicanus (Gillette)

Synergus mexicanus Gillette 1896: 90, 96. ♀. NM. Holotype in USNM.

Synophrus mexicanus (Gillette); Weld 1952a: 315-316.

**Synophrus laeviventris* Osten Sacken. In *Synergus*.

Synophrus laeviventris Osten Sacken 1861: 57. ♀. DC.

Types in MCZ?

Synophrus olivieri Kleffer

Synophrus olivieri Kleffer 1898: 375. ♀, ♂. Algeria.

Location of types unknown.

Synophrus politus Hartig

Synophrus politus Hartig 1843: 412. ♀. Types in ZSBS.

Cynips politus Hartig; Kalténbach 1867: 23.

**Synophrus sylvestris* Osten Sacken. In *Synophromorpha*.

Synophrus sylvestris Osten Sacken 1861: 145. ♀. CT,

DC, MI, NJ, NY, NJ, ON. Types in MCZ.

4.2. Host records for Inquilline Cynipidae.LEGEND

G	=	Gall type	AG	=	Agamic Generation
LE	=	Leaf Gall	SX	=	Sexual generation
ST	=	Stem Gall	D	=	Distribution
BU	=	Bud Gall	WP	=	Western Palearctic
AC	=	Acorn Gall	EP	=	Eastern Palearctic
RT	=	Root Gall	WN	=	Western Nearctic
CA	=	Catkin Gall	EN	=	Eastern Nearctic
FL	=	Flower Gall	OR	=	Oriental
S	=	Generation	ET	=	Ethiopian
*	=	New Gall Host Record for Inquilline			
D. T. & K.	=	Dajia Torre and Kieffer			
E. & Q.	=	Eady and Quinlan			
M. & E.	=	McCracken and Egbert			
O. S.	=	Osten Sacken			
R. & S.	=	Ritchie and Shorthouse			
AMNH	=	Specimens in Kinsey Collection, American Museum of Natural History, New York City.			
AJR	=	Specimens in A. J. Ritchie Collection, Carleton University, Ottawa, ONT.			
JDS	=	Specimens in J. D. Shorthouse Collection, Laurentian University, Sudbury, ONT.			
HKT	=	Specimens in H. K. Townes collection, Ann Arbor, MI.			

CEROPTRES

<i>Ceroptres</i> <i>arator</i> Hartig	<i>Adleria</i> <i>calliciformis</i> (Giraud)	WP AG BU	Mayr 1872
	<i>Andricus</i> <i>amblycerus</i> Giraud	AG BU	Fulmek 1968
	<i>Andricus</i> <i>gallae-</i> <i>urnaeformis</i> (Fonsc.)	AG BU	Mayr 1872
	<i>Andricus</i> <i>kollari</i> (Hartig)	AG BU	Mayr 1882
	<i>Andricus</i> <i>lignicola</i> Hartig	AG BU	Mayr 1872
	<i>Andricus</i> <i>lucidus</i> (Hartig)	AG BU	Mayr 1872
	<i>Andricus</i> <i>quadri-</i> <i>lineatus</i> Hartig	AG LE	Wiebes-Rijks 1976
	<i>Andricus</i> <i>quercus-</i> <i>radicis</i> (Fabr.)	SX ST	Hartig 1841
	<i>Andricus</i> <i>quercus-</i> <i>ramuli</i> (L.)	SX CA	Mayr 1872
	<i>Andricus</i> <i>testaceipes</i> (Hartig)	AG BU	Askew 1961
	<i>Cynips</i> <i>conglomerata</i> Giraud	AG BU	Mayr 1872

<i>Ceroptres</i> <i>arator</i> Hartig (cont.)	<i>Cynips</i> <i>divisa</i> Hartig	AG LE Bellizen 1928
	<i>Cynips</i> <i>flosculi</i> Giraud	SX BU Mayr 1872
	<i>Cynips</i> <i>galeata</i> Giraud	AG BU Mayr 1872
	<i>Cynips</i> <i>glutinosa</i> Giraud	AG BU Mayr 1872
	<i>Cynips</i> <i>hungarica</i> Giraud	AG BU Mayr 1872
	<i>Cynips</i> <i>polycera</i> Giraud	AG BU Mayr 1872
	<i>Cynips</i> <i>quercus-</i> <i>folii</i> L.	SX BU Mayr and Fitch 1876
	<i>Neuroterus</i> <i>aprilinus</i> (Giraud)	SX BU Mayr 1872
	<i>Neuroterus</i> <i>quercus-</i> <i>baccarum</i> (L.)	AG LE Kieffer 1905 or SX
<i>Ceroptres</i> <i>catesbaei</i> Ashmead	<i>Bassettia</i> <i>quercus-</i> <i>catesbaei</i> (Ashmead)	EN SX ST Ashmead 1885
<i>Ceroptres</i> <i>cerri</i> Mayr	<i>Andricus</i> <i>circulans</i> Mayr	SX BU Mayr 1872
	<i>Andricus</i> <i>crispator</i> (Tschek)	SX LE Mayr 1872

<i>Ceroptres</i> <i>berri</i> Mayr (cont.)	<i>Andricus</i> <i>luteicornis</i> Kieffer	SX BU Kieffer 1902b
	<i>Andricus</i> <i>multiplicatus</i> Giraud	SX BU Mayr 1872
	<i>Aphelonyx</i> <i>cernicola</i> Giraud	AG ST Mayr 1872
	<i>Neuroterus</i> <i>glandiformis</i> (Giraud)	SX BU Mayr 1872
	<i>Neuroterus</i> <i>macropterus</i> (Hartig)	AG ST Mayr 1872
	<i>Neuroterus</i> <i>quercus-</i> <i>baccarum</i> (L.)	SX LE Tavares 1920
	<i>Plagiotrochus</i> <i>quercus-</i> <i>ilicis</i> (Fabr.)	SX LE Kieffer 1905
<i>Ceroptres</i> <i>clavicornis</i> Hartig	<i>Andricus</i> <i>callidoma</i> Hartig	WP AG BU Foerster 1869
	<i>Andricus</i> <i>giraudianus</i> D. T. & K.	AG CA Kieffer 1902b
	<i>Andricus</i> <i>quercus-</i> <i>radicus</i> (Fabr.)	SX ST Foerster 1869
<i>Ceroptres</i> <i>confertus</i> (M. & E.)	<i>Andricus</i> <i>confertus</i> M. & E.	WN AG LE M. & E. 1922
<i>Ceroptres</i> <i>frondosae</i> Ashmead	<i>Andricus</i> <i>quercus-</i> <i>frondosa</i> (Bassett)	EN ? LE Ashmead 1896

● <i>Ceroptres globulus</i> (Beut.)	<i>Diplolepis nodulosa</i> (Beut.)	EN SX ST	Beutenmueller 1892
<i>Ceroptres inermis</i> (Walsh)	<i>Cincticornia pilulae</i> (O. S.) (Cecidomyiidae)	EN SX LE	Walsh 1864
<i>Ceroptres lanigeræ</i> Ashmead	<i>Andricus quercus-lanigera</i> (Ashmead)	EN AG LE	Ashmead 1885
<i>Ceroptres melanomerus</i> Hartig	?	WP ? ?	
<i>Ceroptres minutissimi</i> Ashmead	<i>Neuroterus quercus-minutissimus</i> (Ashmead)	EN AG LE	Ashmead 1896
<i>Ceroptres montensis</i> Weld	<i>Andricus opertus</i> Weld	WN AG BU	Evans 1972
	<i>Andricus reniformis</i> M. & E.	AG ST	Weld 1957b
	<i>Disholcaspis truckeensis</i> (Ashmead)	AG ST	Weld 1957b
	<i>Neuroterus washingtonensis</i> Beut.	AG ST	Evans 1972
✓ <i>Ceroptres niger</i> Fullaway	<i>Disholcaspis eldoradensis</i> (Beut.)	WN AG ST	Fullaway 1911
<i>Ceroptres petiolicola</i> (O. S.)	<i>Andricus quercus-petiolicola</i> (Bassett)	EN SX LE	O. S. 1861
<i>Ceroptres politus</i> Ashmead	?	EN ? LE	

<i>Ceroptres quercus-arbos</i> (Fitch)	<i>Callirhytis clavula</i> (O. S.)	EN AG ST	O. S. 1865
<i>Ceroptres quercus-ficus</i> (Fitch)	<i>Xanthoteras quercus-forticorne</i> (Walsh)	EN AG ST	O. S. 1861
<i>Ceroptres quercus-obtusilobae</i> (Karsch)	?	EN ? ?	
<i>Ceroptres quercus-pisum</i> (Fitch)	<i>Acraspis pezomachoides</i> (O. S.)	EN AG LE	O. S. 1861
<i>Ceroptres quercus-tubur</i> (Fitch)	<i>Callirhytis clavula</i> (O. S.)	EN AG ST	O. S. 1861
<i>Ceroptres rufiventris</i> Ashmead	<i>Andricus quercus-ostensackeni</i> (Bassett)	EN SX LE	Ashmead 1896
<i>Ceroptres</i> spp.	* <i>Acraspis erinacei</i> (Beut.)	AG LE	AMNH
	* <i>Acraspis macroterpae</i> Bassett	AG LE	AMNH
	* <i>Acraspis quercus-hirta</i> (Bassett)	AG LE	AMNH
	* <i>Acraspis ulterior</i> (Kinsey)	AG LE	AMNH
	* <i>Adleria nigriceps</i> (Gillet)	AG LE	AMNH

Ceroptres spp. (cont.)	* <i>Amphibolips</i> <i>cookii</i> Gillette	AG BU	AMNH
	* <i>Amphibolips</i> <i>quercus-</i> <i>cinerea</i> (Ashmead)	AG ST	AMNH
	* <i>Andricus</i> <i>crystallinus</i> Bassett	AG LE	AMNH
	* <i>Andricus</i> <i>ignotus</i> (Bassett)	AG LE	AMNH
	* <i>Andricus</i> <i>kingi</i> Bassett	? ?	AMNH
	* <i>Andricus</i> <i>murtfeldtae</i> Ashmead	AG BU	AMNH
	* <i>Andricus</i> <i>pattoni</i> (Bassett)	? ?	AMNH
	* <i>Andricus</i> <i>quercus-</i> <i>floccl</i> (Walsh)	AG LE	AMNH
	* <i>Andricus</i> <i>quercus-</i> <i>foliatus</i> (Ashmead)	AG BU	AMNH
	* <i>Andricus</i> <i>tecturnarum</i> Kinsey	AG LE	AMNH
	* <i>Basibicus</i> <i>helgae</i> (Fullaway)	AG LE	AMNH
	* <i>Callirhytis</i> <i>lanata</i> (Gillette)	AG LE	AMNH

Ceroptres spp. (cont.)	* <i>Callirhytis</i> <i>quercus-</i> <i>gemmaria</i> (Ashmead)	? ?	AMNH
		-	
	* <i>Callirhytis</i> <i>quercus-</i> <i>punctatus</i> (Bassett)	AG ST	AMNH
	* <i>Callirhytis</i> <i>quercus-</i> <i>similis</i> (Bassett)	SX ST	AMNH
	* <i>Callirhytis</i> <i>tubicola</i> (O. S.)	AG LE	AMNH
	* <i>Callirhytis</i> <i>tumifica</i> (O. S.)	SX LE	AJR
	* <i>Neuroterus</i> <i>quercicola</i> Dalla Torre	SX LE	AMNH
	* <i>Neuroterus</i> <i>quercus-</i> <i>batatus</i> (Fitch)	AG ST	AMNH
	* <i>Neuroterus</i> <i>quercus-</i> <i>rileyi</i> (Bassett)	AG ST	AMNH
	* <i>Neuroterus</i> <i>quercus-</i> <i>verrucarum</i> (O. S.)	AG LE	AMNH
	* <i>Neuroterus</i> <i>saltatorius</i> (Edwards)	AG LE	AMNH
	* <i>Neuroterus</i> <i>umbilicus</i> Bassett	AG LE	AMNH

<i>Ceroptres</i> spp. (cont.)	* <i>Neuroterus</i> <i>vesicula</i> (Bassett)	SX BU AMNH
	* <i>Philonix</i> <i>fulvicollis</i> Fitch	AG LE AMNH

EUCEROPTRES

<i>Euceroptres</i> <i>futilis</i> (O. S.)	<i>Andricus</i> <i>quercus-</i> <i>petiolicola</i> (Bassett)	EN SX LE O. S. 1861
	<i>Callirhytis</i> <i>quercus-</i> <i>futilis</i> (O. S.)	SX LE O. S. 1861
<i>Euceroptres</i> <i>japonicus</i> Ashmead	?	EP ? ?
<i>Euceroptres</i> <i>maritimus</i> Weld	<i>Callirhytis</i> <i>quercus-</i> <i>suttoni</i> (Bassett)	WN AG ST Weld 1926
<i>Euceroptres</i> <i>montanus</i> Weld	<i>Disholcaspis</i> <i>truckeensis</i> (Ashmead)	WN AG ST Weld 1926

MYRTOPSEN

<i>Myrtopsen</i> <i>leuderwaldti</i> Dettmer	?	NT ? ?
<i>Myrtopsen</i> <i>meyri</i> Ruebsaamen	?	NT ? ?
<i>Myrtopsen</i> <i>mimosae</i> Weld	<i>Tanaostigmodes</i> sp. (Chalcidoidea)	WN SX ? Weld 1926

Myrtopsen platensis Diaz	?	NT ? ?
Myrtopsen rodvalhoi Dettmer	?	NT ? ?

PERICLISTUS

Periclistus arefactus M. & E.	Diplolepis inconspicuis D. & C.	WN SX ST D. & C. 1973
	*Diplolepis neglecta (Gillette)	SX LE AMNH
Periclistus ashmeadi R. & S.	*Diplolepis ignota (O. S.)	WN SX LE AJR, JDS
	*Diplolepis nebulosa (Bassett)	SX LE JDS
	*Diplolepis variabilis (Bassett)	SX LE JDS
Periclistus brandtii (Ratze.)	Diplolepis mayri (Schlecht.)	WP SX ST Kieffer 1902b
	Diplolepis rosae (L.)	WP SX LE Ratzeburg 1832
Periclistus californicus Ashmead	Diplolepis polita (Ashmead)	WN SX LE Ashmead 1986
	*Diplolepis neglecta (Gillette)	SX LE AMNH
Periclistus caninae (Hartig)	Diplolepis centifoliae (Hartig)	WP SX LE Kieffer 1902b

<i>Periclistus</i> <i>caninae</i> (Hartig) (cont.)	<i>Diplolepis</i> <i>eglantariae</i> (Hartig)	SX LE	Kieffer 1902b
	<i>Diplolepis</i> <i>nervosa</i> (Curtis)	SX LE	Fulmek 1968
	<i>Diplolepis</i> <i>rosarum</i> (Giraud)	SX LE	Tavares 1920
	<i>Diplolepis</i> <i>spinosissimae</i> (Giraud)	SX LE	Kieffer 1902b
<i>Periclistus</i> <i>capillatus</i> Belizen	<i>Diplolepis</i> sp.	WP SX ?	Belizen 1968
<i>Periclistus</i> <i>catractans</i> R. & S.	* <i>Diplolepis</i> <i>rosaefolia</i> (Cockerell)	SX LE	JDS AJR
<i>Periclistus</i> <i>fusicolus</i> R. & S.	* <i>Diplolepis</i> <i>fusiformans</i> (Ashmead)	SX ST	AJR JDS AMNH
	* <i>Diplolepis</i> <i>nodulosa</i> (Ashmead)	SX ST	JDS AJR
	* <i>Diplolepis</i> <i>triformis</i> S. & R.	SX ST	JDS AJR
<i>Periclistus</i> <i>graciliculus</i> R. & S.	* <i>Diplolepis</i> <i>gracilis</i> (Ashmead)	SX LE	JDS GCW
<i>Periclistus</i> <i>natalis</i> T. & Y.	<i>Diplolepis</i> <i>japonica</i> (Walker)	EP SX LE	T. & Y. 1973
<i>Periclistus</i> <i>piceus</i> Fullaway	<i>Diplolepis</i> <i>polita</i> (Ashmead)	WN SX LE	Fullaway 1911
<i>Periclistus</i> <i>pirata</i> (O. S.)	* <i>Diplolepis</i> <i>bassetti</i> (Beut.)	EN ST LE	AMNH

<i>Periclistus</i> <i>pirata</i> (O. S.) (cont.)	* <i>Diplolepis</i> <i>dichlocera</i> (Harris)	SX ST	AMNH
	<i>Diplolepis</i> <i>ignota</i> (O. S.)	EN SX LE	O. S. 1863
	* <i>Diplolepis</i> <i>nebulosa</i> (Bassett)	SX LE	JDS
	* <i>Diplolepis</i> <i>neglecta</i> (Gillette)	SX LE	AMNH
	* <i>Diplolepis</i> <i>nodulosa</i> (Ashmead)	SX LE	AJR JDS AMNH
	<i>Diplolepis</i> <i>polita</i> (Ashmead)	SX LE	Shorthouse 1980
	<i>Diplolepis</i> <i>radicum</i> (O. S.)	SX RT	O. S. 1863
	* <i>Diplolepis</i> <i>spinosa</i> (Ashmead)	SX ST	AMNH JDS AJR
	* <i>Diplolepis</i> <i>tumida</i> (Bassett)	SX ST	AMNH JDS
	* <i>Diplolepis</i> <i>tuberculatrix</i> (Cockerell)	SX ST	AMNH
<i>Periclistus</i> <i>quinlani</i> T. & Y.	<i>Diplolepis</i> <i>japonica</i> (Walker)	EP SX LE	T. & Y. 1973
<i>Periclistus</i> <i>rosarum</i> Dettmer	<i>Diplolepis</i> <i>rosarum</i> (Giraud)	WP SX LE	Dettmer 1924b
<i>Periclistus</i> <i>spinosissimae</i> Dettmer	<i>Diplolepis</i> <i>spinosissimae</i> (Giraud)	WP SX LE	Dettmer 1924b

<i>Periclistus</i> <i>vancouver-</i> <i>ensis</i> R. & S.	* <i>Diplolepis</i> <i>neglecta</i> (Gillette)	WN SX ST	AJR JDS
<i>Periclistus</i> <i>weldi</i> R. & S.	* <i>Diplolepis</i> <i>bicolor</i> (Harris)	WN SX LE	AJR JDS
	* <i>Diplolepis</i> <i>ignota</i> (O. S.)	EN SX LE	O. S., 1863
	* <i>Diplolepis</i> <i>nebulosa</i> (Bassett)	SX LE	JDS
	* <i>Diplolepis</i> <i>polita</i> (Ashmead)	WN SX LE	AJR JDS
	* <i>Diplolepis</i> <i>nodulosa</i> (Ashmead)	SX LE	AJR JDS AMNH

PONCYLIA

<i>Poncyia</i> <i>ferruginea</i> Kieffer	?	WP ? ?
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RHOOPHILUS

<i>Rhoophilus</i> <i>loewi</i> Mayr	?	SE ? ?
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SAPHONECRUS

<i>Saphonecrus</i> <i>areolatus</i> Weid	?	OR ? ?	
<i>Saphonecrus</i> <i>brevicornis</i> (Ashmead)	<i>Andricus</i> sp.	WN ? ?	Ashmead 1896
<i>Saphonecrus</i> <i>brevis</i> Weid	<i>Andricus</i> <i>durangensis</i> Beut.	WN ? ST	Weid 1926
	<i>Andricus</i> <i>ruginosus</i> (Basset)	AG ST	Weid 1926
<i>Saphonecrus</i> <i>connatus</i> (Hartig)	<i>Andricus</i> <i>glandulae</i> Hartig	WP AG BU	Hartig 1840
	<i>Andricus</i> <i>inflator</i> Hartig	SX ST	Hartig 1840
	<i>Andricus</i> <i>ostreus</i> (Hartig)	AG LE	Hartig 1840
	<i>Andricus</i> <i>quercus-</i> <i>radicis</i> (Fabr.)	SX ST	Hartig 1840
	<i>Andricus</i> <i>quercus-</i> <i>ramuli</i> (L.)	AG LE	Tavares 1920
	<i>Cynips</i> <i>quercus-</i> <i>folii</i> L.	AG LE	Mayr 1872
<i>Saphonecrus</i> <i>diversus</i> Belizen	?	WP ? ?	
<i>Saphonecrus</i> <i>excisus</i> (Kieffer)	<i>Neuroterus</i> <i>haasi</i> Kieffer	WP AG ST	Kieffer 1904

<i>Saphonecrus favanus</i> Weid	<i>Dryocosmus favius</i> Beut.	EN AG RT	Weid 1944
<i>Saphonecrus gemmariae</i> (Ashmead)	<i>Callirhytis quercus-gemmaria</i> (Ashmead)	EN AG ST	Ashmead 1885
<i>Saphonecrus halmi</i> (Mayr)	<i>Arnoldia cernis</i> Kollar	WP ? LE	Mayr 1872
	<i>Chilasplis nitidus</i> (Giraud)	AG LE	Mayr 1872
	<i>Neuroterus lanuginosus</i> Giraud	AG LE	Mayr 1872
	<i>Neuroterus saliens</i> (Koll.)	AG LE	Mayr 1872
<i>Saphonecrus lusitanicus</i> (Tavares)	<i>Plagiotrochus klefferianus</i> Tavares	WP AG ST	Tavares 1920
<i>Saphonecrus serratus</i> Weid	?	OR ? ?	
<i>Saphonecrus sinicus</i> Belizen	?	WP ? ?	
<i>Saphonecrus undulatus</i> (Mayr)	<i>Aphelonyx cerricola</i> (Giraud)	WP AG ST	Mayr 1872
<i>Saphonecrus</i> spp.	* <i>Andricus furnaceus</i> Kinsey	AG ST	AMNH
	* <i>Andricus peredurus</i> Kinsey	AG ST	AMNH
	* <i>Andricus rhizoxenus</i> (Ashmead)	AG ST	AMNH

SYNERGUS

<i>Synergus</i> <i>agrifoliae</i> Ashmead	<i>Dryocosmus</i> <i>minusculus</i> Weld	WN ? LE Weld 1957
	<i>Neuroterus</i> <i>saltatorius</i> (Edwards)	WN AG LE Burks 1979
<i>Synergus</i> <i>albipes</i> Hartig	<i>Adleria</i> <i>caliciformis</i> (Giraud)	WP AG BU Mayr 1872
	<i>Adleria</i> <i>quercus-</i> <i>calicis</i> (Bgsdf.)	AG BU Mayr 1872
	<i>Andricus</i> <i>amblycerus</i> Giraud	AG BU Mayr 1872
	<i>Andricus</i> <i>callidoma</i> Hartig	AG BU Wiebes-Rijks 1979
	<i>Andricus</i> <i>clementinae</i> (Hartig)	AG BU Mayr 1872
	<i>Andricus</i> <i>corruptrix</i> (Schlect.)	AG BU Wiebes-Rijks 1978
	<i>Andricus</i> <i>curvator</i> Hartig	AG BU Hartig 1811 & SX LE
	<i>Andricus</i> <i>fecundator</i> Hartig	AG BU Mayr 1872
	<i>Andricus</i> <i>galiae-</i> <i>urnaeformis</i> (Fonscolombe)	AG, LE Mayr 1872
	<i>Andricus</i> <i>inflator</i> Hartig	AG BU Hartig 1840

<i>Synergus</i> <i>albipes</i> Hartig (cont.)	<i>Andricus</i> <i>kollar</i> Hartig	AG BU Mayr 1872
	<i>Andricus</i> <i>lignicola</i> Hartig	AG BU Mayr 1872
	<i>Andricus</i> <i>lucidus</i> (Hartig)	AG BU Mayr 1872
	<i>Andricus</i> <i>nudus</i> Adler	AG ST Wiebes-Rijks 1976
	<i>Andricus</i> <i>ostreus</i> (Hartig)	AG BU Mayr 1872
	<i>Andricus</i> <i>quadri-</i> <i>lineatus</i> Hartig	AG LE E. & Q. 1963
	<i>Andricus</i> <i>quercus-</i> <i>ramuli</i> (L.)	AG BU Wiebes-Rijks 1979
	<i>Andricus</i> <i>seminationis</i> Giraud	AG CA Mayr 1872
	<i>Andricus</i> <i>solitarius</i> (Fonsc.)	AG BU Wiebes-Rijks 1979
	<i>Cynips</i> <i>agame</i> Hartig	AG LE Mayr 1872
	<i>Cynips</i> <i>caputmedusae</i> Hartig	AG BU Mayr 1872
	<i>Cynips</i> <i>conglomerata</i> Giraud	AG BU Mayr 1872

<i>Synergus</i> <i>albipes</i> Hartig (cont.)	<i>Cynips</i> <i>coriaria</i> Hartig	AG BU Mayr 1872
	<i>Cynips</i> <i>disticha</i> Hartig	AG LE Mayr 1872
	<i>Cynips</i> <i>divisa</i> Hartig	AG LE Mayr 1872
	<i>Cynips</i> <i>gallae-</i> <i>tinctoriae</i> (Olivier)	AG BU Mayr 1872
	<i>Cynips</i> <i>glutinosa</i> Giraud	AG BU Mayr 1872
	<i>Cynips</i> <i>hungarica</i> Giraud	AG BU Mayr 1872
	<i>Cynips</i> <i>longiventris</i> Hartig	AG LE Wiebes-Rijks 1979
	<i>Cynips</i> <i>polycera</i> Giraud	AG LE Kieffer 1902b
	<i>Cynips</i> <i>quercus-</i> <i>tozae</i> Bosc.	AG BU Mayr 1872
	<i>Cynips</i> <i>quercus-</i> <i>folii</i> L.	AG LE Mayr 1872
	<i>Neuroterus</i> <i>albipes</i> Schenck	AG LE Askew 1961
	<i>Neuroterus</i> <i>numismalis</i> (Fourcroy)	AG LE Mayr 1872 & SX LE

<i>Synergus</i> <i>albipes</i> Hartig (cont.)	<i>Neuroterus</i> <i>quercus-</i> <i>baccarum</i> (L.)	AG LE & SX LE	Hartig 1841
	<i>Neuroterus</i> <i>sallens</i> (Koll.)	AG LE	Marchal 1896
	<i>Neuroterus</i> <i>tricolor</i> Hartig	AG LE & SX LE	Mayr 1872
	<i>Plagiotrochus</i> <i>amenti</i> Tavares	SX CA	Kieffer 1902b
	<i>Trigonaspis</i> <i>megaptera</i> (Panzer)	AG LE	Hartig 1840
	<i>Trigonaspis</i> <i>mendisi</i> Tavares	AG LE	Tavares 1920
	<i>Trigonaspis</i> <i>synaspis</i> (Hartig)	AG BU	Mayr 1872
<i>Synergus</i> <i>albofaciatus</i> Dettmer	<i>Trigonaspis</i> <i>megaptera</i> (Panzer)	WP AG BU & SX LE	Dettmer 1924b
<i>Synergus</i> <i>apicalis</i> Hartig	<i>Andricus</i> <i>amblycerus</i> Giraud	WP AG BU	Mayr 1872
	<i>Andricus</i> <i>fecundator</i> Hartig	AG ST	Mayr 1872
	<i>Andricus</i> <i>lignicola</i> Hartig	AG BU	Mayr 1872
	<i>Andricus</i> <i>quercus-</i> <i>radicis</i> (L.)	SX ST	Hartig 1841

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<i>Synergus</i> <i>apicalis</i> Hartig	<i>Andricus</i> <i>testaceipes</i> Hartig	SX LE	Mayr 1872
	<i>Cynips</i> <i>agama</i> Hartig	AG LE	Briscke 1882
	<i>Cynips</i> <i>conglomerata</i> Giraud	AG ST	Mayr 1872 Mayr 1872
	<i>Cynips</i> <i>longiventris</i> Hartig	AG LE	Briscke 1882
	<i>Neuroterus</i> <i>albipes</i> Schenck	SX LE	Mayr 1872
<i>Synergus</i> <i>atamiensis</i> Ashmead	?	EP ? ?	
<i>Synergus</i> <i>atra</i> Gillette	<i>Disholcaspis</i> <i>rubens</i> (Gillette)	WN AG ST	Gillette 1896
<i>Synergus</i> <i>atripennis</i> Ashmead	<i>Disholcaspis</i> <i>spongiosa</i> (Karsch)	EN AG ST	Ashmead 1896
<i>Synergus</i> <i>atripes</i> Gillette	<i>Atrusca</i> <i>brevipennata</i> (Gillette)	WN AG LE	Gillette 1896
<i>Synergus</i> <i>basalis</i> Hartig	<i>Adenia</i> <i>quercus-</i> <i>calicis</i> (Bgsdf.)	WP AG AC	Hartig 1840
<i>Synergus</i> <i>batatoides</i> Ashmead	<i>Callirhytis</i> <i>quercus-</i> <i>batatoides</i> (Ashmead)	EN AG ST	Ashmead 1885
<i>Synergus</i> <i>bellus</i> M. & E.	?	WN ? ?	

<i>Synergus</i> <i>bicolor</i> Ashmead	<i>Andricus</i> <i>quercus-</i> <i>foliatus</i> (Ashmead)	EN AG BU	Ashmead 1885
<i>Synergus</i> <i>bipunctatus</i> Hartig	?	WP ? ?	
<i>Synergus</i> <i>campanula</i> O. S.	<i>Disholcaspis</i> <i>quercus-</i> <i>globulus</i> (Fitch)	EN AG ST	O. S. 1865
	<i>Disholcaspis</i> <i>quercus-</i> <i>mamma</i> (Walsh)	AG ST	Gillette 1896
	<i>Xanthoteras</i> <i>quercus-</i> <i>forticorne</i> Walsh	AG ST	Gillette 1896
<i>Synergus</i> <i>carinulatus</i> Dettmer	<i>Andricus</i> <i>curvator</i> (Hartig)	WP AG BU & SX LE	Dettmer 1924b
<i>Synergus</i> <i>castanopsidis</i> (Beut.)	<i>Dryocosmus</i> <i>castanopsidis</i> (Beut.)	WN AG FL	Weid 1926
<i>Synergus</i> <i>citriformis</i> (Ashmead)	<i>Amphibolips</i> <i>quercus-</i> <i>citriformis</i> (Ashmead)	EN AG BU	Ashmead 1885
<i>Synergus</i> <i>clandestinus</i> Eady	<i>Andricus</i> <i>legitimus</i> Wiebes-Rijks	WP AG AC	Eady 1952
<i>Synergus</i> <i>confertus</i> M. & E.	<i>Andricus</i> <i>confertus</i> M. & E.	WN AG LE	M. & E. 1922
<i>Synergus</i> <i>coniferae</i> Ashmead	<i>Callirhytis</i> <i>quercus-</i> <i>ventricosa</i> (Bassett)	EN AG ST	Ashmead 1885

<i>Synergus</i> <i>crassicornis</i> Hartig	?	WP ? ?	
<i>Synergus</i> <i>cultratus</i> R. & S.	<i>Andricus</i> <i>guatemalensis</i> (Cameron)	WN AG LE	R. & S. 1984
<i>Synergus</i> <i>davisi</i> (Beut.)	<i>Callirhytis</i> <i>quercus-</i> <i>gemmaria</i> (Ashmead)	EN AG ST	Weid 1922
<i>Synergus</i> <i>digressus</i> M. & E.	<i>Callirhytis</i> sp.	WP ? ST	M. & E. 1922
<i>Synergus</i> <i>dimorphus</i> O. S.	<i>Besbicus</i> <i>multipunctatus</i> (Beut.)	EN AG LE	Fullaway 1911
<i>Synergus</i> <i>distinctus</i> M. & E.	<i>Disholcaspis</i> <i>canescens</i> (Bassett)	WN AG ST	M. & E. 1922
	<i>Disholcaspis</i> <i>washingtonensis</i> (Beut.)	AG ST	AJR
<i>Synergus</i> <i>dorsalis</i> Provancher	?	WN ? ST	Provancher 1888
<i>Synergus</i> <i>dugei</i> Ashmead	<i>Andricus</i> <i>championi</i> (Cameron)	WN AG ST	Ashmead 1899
<i>Synergus</i> <i>duricoria</i> Gillette	<i>Disholcaspis</i> <i>quercusmamma</i> (Walsh)	EN AG ST	Gillette 1896
<i>Synergus</i> <i>erinacei</i> Gillette	<i>Acraspis</i> <i>erinacei</i> (Beut.)	EN AG LE	Gillette 1896
<i>Synergus</i> <i>evanescens</i> Mayr	<i>Adleria</i> <i>quercus-</i> <i>calicis</i> (Bgsdf.)	WP AG AC	Mayr 1872

<i>Synergus evanescens</i> Mayr (cont.)	<i>Andricus curvator</i> Hartig	AG BU & SX LE	Tavares 1920
	<i>Andricus fecundator</i> Hartig	AG CA	Mayr 1872
	<i>Andricus inflator</i> Hartig	SX ST	Askew 1961
	<i>Andricus kollari</i> Hartig	AG BU	Kieffer 1902b
	<i>Andricus mayri</i> (Wachtl.)	AG BU	Kieffer 1902b
	<i>Andricus multiplicatus</i> Giraud	SX LE	Mayr 1872
	<i>Cynips infectoria</i> Hartig	AG BU	D. T. & K. 1910
	<i>Cynips mayri</i> (Kieffer)	AG BU	Kieffer 1902b
	<i>Plagiotrochus burnayi</i> Kieffer	AG AC	Tavares 1920
<i>Synergus exaratus</i> Hartig	?	WP ? ?	
<i>Synergus ficigeræ</i> Ashmead	<i>Disholcaspis quercus-virens</i> (Ashmead)	EN AG ST	Ashmead 1885
<i>Synergus filicornis</i> Cameron	<i>Callirhytis furnessæ</i> Weid	WN SX ST	Weid 1922
<i>Synergus flavens</i> (M. & E.)	<i>Callirhytis serricornis</i> (Kinsey)	WN AG LE	Lyon 1970

<i>Synergus flavens</i> (M. & E.) (cont.)	<i>Heteroecus flavens</i> (M. & E.)	AG LE	M. & E. 1922
<i>Synergus flavicornis</i> Hartig	<i>Cynips agama</i> Hartig	WP AG LE	Hartig 1840
<i>Synergus flavipes</i> Hartig	<i>Neuroterus macropterus</i> Hartig	WP AG ST	Hartig 1840
<i>Synergus flavus</i> Kieffer	<i>Callirhytis quercus-pomiformis</i> (Bassett)	WP AG ST	Kieffer 1904
<i>Synergus fulvipes</i> Dettmer	<i>Andricus curvator</i> (Hartig)	WP AG BU & SX LE	Dettmer 1924b
	<i>Andricus quadri-lineatus</i> Hartig	AG LE	Dettmer 1924b
<i>Synergus gallae-pomiformis</i> (Fonsc.)	<i>Adleria quercus-calicis</i> (Burgsdorf)	WP AG BU	Mayr 1872
	<i>Andricus albopunctatus</i> Schlecht.	AG BU	Mayr 1872
	<i>Andricus callidoma</i> Hartig	AG BU	Askew 1961
	<i>Andricus clementinae</i> (Giraud)	AG BU	Mayr 1872
	<i>Andricus corruptrix</i> (Schlecht.)	AG BU	Wiebes-Rijks 1978
	<i>Andricus curvator</i> Hartig	AG BU & SX LE	Mayr 1872

<i>Synergus</i> <i>gallae-</i> <i>pomiformis</i> (Fonsc.) (cont.)	<i>Andricus</i> <i>fecundator</i> Hartig	AG CA	Hartig 1840
	<i>Andricus</i> <i>gallae-</i> <i>urnaeformis</i> (Fonscolombe)	AG LE	Mayr 1872
	<i>Andricus</i> <i>glandulae</i> Hartig	AG BU	D. T. & K. 1910
	<i>Andricus</i> <i>inflator</i> Hartig	AG BU	Mayr 1872
	<i>Andricus</i> <i>kollar</i> Hartig	AG BU	Askew 1961
	<i>Andricus</i> <i>legitimus</i> Wiebes-Rijks	AG AC	Wiebes-Rijks 1980
	<i>Andricus</i> <i>lignicola</i> Hartig	AG BU	Hartig 1840
	<i>Andricus</i> <i>nudus</i> Adler	AG ST	D. T. & K. 1910
	<i>Andricus</i> <i>ostreus</i> (Hartig)	AG LE	Hartig 1840
	<i>Andricus</i> <i>quadri-</i> <i>lineatus</i> Hartig	AG LE	Askew 1961
	<i>Andricus</i> <i>quercus-</i> <i>corticus</i> (Fabr.)	AG ST	D. T. & K. 1910
	<i>Andricus</i> <i>quercus-</i> <i>radicis</i> (Fabr.)	AG RT & SX ST	Hartig 1840

<i>Synergus</i> <i>gallae-</i> <i>pomiformis</i> (Fonsc.) (cont.)	<i>Andricus</i> <i>quercus-</i> <i>ramuli</i> (L.)	. AG BU Mayr 1872 & SX CA
	<i>Andricus</i> <i>seminationis</i> Giraud	AG CA Mayr 1872
	<i>Andricus</i> <i>solitarius</i> (Fonscolombe)	AG BU Mayr 1872 & SX CA
	<i>Andricus</i> <i>testaceipes</i> Hartig	AG BU Tavares 1920
	<i>Biorhiza</i> <i>pallida</i> Olivier	SX BU Hartig 1840
	<i>Callirhytis</i> <i>glandium</i> (Giraud)	SX AC D. T. & K. 1910
	<i>Cynips</i> <i>caputmedusae</i> Hartig	AG LE Mayr 1872
	<i>Cynips</i> <i>coriaria</i> Hartig	AG ST Kieffer 1902b
	<i>Cynips</i> <i>coronata</i> Giraud	AG BU Kieffer 1902b
	<i>Cynips</i> <i>disticha</i> Hartig	AG LE Hartig 1840
	<i>Cynips</i> <i>divisa</i> Hartig	AG LE Welbes-Rijks 1979
	<i>Cynips</i> <i>gallae-</i> <i>tinctoriae</i> (Olivier)	AG BU Mayr 1872

<i>Synergus</i> <i>gallae-</i> <i>pomiformis</i> (Fonsc.) (cont.)	<i>Cynips</i> <i>glutimosa</i> Giraud	AG ST	Mayr 1872
	<i>Cynips</i> <i>longiventris</i> Hartig	AG BU & SX LE	Askew 1961
	<i>Cynips</i> <i>quercus-</i> <i>folii</i> L.	AG LE & SX BU	Hartig 1840
	<i>Dryocosmus</i> <i>gallae-</i> <i>ramulorum</i> (Fonsc.)	SX ST	Fonscolombe 1832
	<i>Dryocosmus</i> <i>rugosus</i> Kieffer	AG LE	Tavares 1920
	<i>Neuroterus</i> <i>albipes</i> Schenck	AG LE	Wiebes-Rijks 1979
	<i>Neuroterus</i> <i>laniginosus</i> Giraud	AG LE	Kieffer 1902b
	<i>Neuroterus</i> <i>numismalis</i> (Geoffroy)	AG LE	Wiebes-Rijks 1979
	<i>Neuroterus</i> <i>quercus-</i> <i>baccarum</i> (L.)	AG LE & SX LE	Mayr 1872
	<i>Neuroterus</i> <i>tricolor</i> (Hartig)	AG LE & SX LE	Mayr 1872
	<i>Trigonaspis</i> <i>megaptera</i> (Panzer)	AG LE & SX BU	D. T. & K. 1910
<i>Synergus</i> <i>gallae-</i> <i>pyriformis</i> (Olivier)	<i>Andricus</i> <i>callidoma</i> Hartig	WP AG BU	D. T. & K. 1910

<i>Synergus</i> <i>gallae-</i> <i>viscosae</i> (Fairm.)	<i>Cynips</i> <i>mayri</i> (Kieffer)	WP AG BU D. T. & K. 1910
<i>Synergus</i> <i>gallaicus</i> Tavares	<i>Andricus</i> <i>kollar</i> Hartig	WP AG BU Tavares 1920 & SX BU
<i>Synergus</i> <i>garryana</i> Gillette	<i>Bassettia</i> <i>ligni</i> Kinsey	WN SX LE. Evans 1972
	<i>Besbicus</i> <i>mirabilis</i> (Kinsey)	AG LE Evans 1967
	<i>Disholcaspis</i> <i>eldoradensis</i> (Beut.)	AG ST Evans 1972
	<i>Disholcaspis</i> <i>perniciosa</i> (Bassett)	AG ST Gillette 1896
<i>Synergus</i> <i>giftuensis</i> Ashmead	?	EP ? ?
<i>Synergus</i> <i>hayneanus</i> (Retze.)	<i>Andricus</i> <i>kollar</i> (Hartig)	WP AG BU Tavares 1920
	<i>Andricus</i> <i>lignicola</i> (Hartig)	AG BU Mayr 1872
	<i>Cynips</i> <i>coronata</i> Giraud	AG BU Kieffer 1902b
	<i>Cynips</i> <i>gallae-</i> <i>tinctoriae</i> (Olivier)	AG BU Mayr 1872
	<i>Cynips</i> <i>mayri</i> (Kieffer)	AG AC Kieffer 1902b

<i>Synergus haynearius</i> (Retze.) (cont.)	<i>Cynips stefani</i> Kieffer	AG BU Kieffer 1902b
<i>Synergus hakonensis</i> Ashmead	?	EP ? ?
<i>Synergus ibericus</i> Tavares	<i>Andricus kollari</i> (Hartig)	WP AG BU Tavares 1920
<i>Synergus incisus</i> Gillette	<i>Callirhytis frequens</i> (Gillette)	WN AG ST Gillette 1896
<i>Synergus incrassatus</i> Hartig	<i>Andricus krajnovici</i> Tavares	WP AG BU Tavares 1920
	<i>Andricus quercus- conticus</i> (Fairm.)	AG ST Mayr 1872
	<i>Andricus quercus- radicus</i> (L.)	AG RT Mayr 1872
	<i>Andricus rhisomae</i> Hartig	AG ST Kieffer 1902b
	<i>Andricus sieboldi</i> Mayr	AG ST Mayr 1872
	<i>Andricus testaceipes</i> Hartig	AG BU Mayr 1872
<i>Synergus inflatus</i> Dettmer	<i>Trigonaspis megaptera</i> (Panzer)	WP SX BU Dettmer 1924b
<i>Synergus insuetus</i> Tavares	<i>Andricus kollari</i> (Hartig)	WP AG BU Tavares 1920

<i>Synergus japonicus</i> Ashmead	?	EP ? ?
<i>Synergus jezoensis</i> Sakagami	?	EP ? ?
<i>Synergus kinseyi</i> R. & S.	<i>Andricus peredurus</i> Kinsey	EN AG ST R. & S. 1984
<i>Synergus laeviventris</i> (O. S.)	<i>Amphibolips quercus-spongifica</i> (O. S.)	EN AG LE O. S. 1865
	<i>Atrusca quercus-centricola</i> (O. S.)	AG LE O. S. 1861
	<i>Disholcaspis quercus-globulus</i> (Fitch)	AG ST Gillette 1896
	<i>Disholcaspis rubens</i> (Gillette)	AG ST Gillette 1896
<i>Synergus lignicola</i> (O. S.)	<i>Callirhytis cornigera</i> (O. S.)	EN AG ST O. S. 1862
	<i>Callirhytis quercus-punctata</i> (Bassett)	AG ST O. S. 1865
<i>Synergus lusitanicus</i> (Tavares)	<i>Andricus ostreus</i> (Hartig)	WP AG LE Kieffer 1905
<i>Synergus maculosus</i> Tavares	<i>Andricus amenti</i> Giraud	WP AG CA Tavares 1920
<i>Synergus magnificus</i> Weid	<i>Disholcaspis truckeensis</i> (Ashmead)	WN AG ST Weid 1957

<i>Synergus magnus</i> Gillette	<i>Amphibolips cookii</i> Gillette	EN AG BU	Gillette 1896
<i>Synergus medullae</i> Ashmead	<i>Callirhytis quercus-medullae</i> (Ashmead)	EN AG ST	Ashmead 1885
<i>Synergus mendax</i> Walsh	<i>Callirhytis quercus-punctata</i> (Bassett)	EN AG ST	Walsh 1864
<i>Synergus mesoamericanus</i> R. & S.	<i>Andricus</i> sp.	SN ? ST	R. & S. 1984
<i>Synergus mizunarae</i> Shinji	?	EP ? ?	
<i>Synergus multiplicatus</i> Fullaway	<i>Andricus phrysolepidocola</i> (Ashmead)	WN AG ST	Fullaway 1911
<i>Synergus nervosus</i> Hartig	<i>Andricus albopunctatus</i> Schlecht.	WP AG BU	Mayr 1872
	<i>Andricus callidoma</i> Hartig	AG BU	Mayr 1872
	<i>Andricus curvator</i> Hartig	AG BU & SX LE	Hartig 1840
	<i>Andricus corruptrix</i> (Schlecht.)	AG BU	Wiebes-Rijks 1978
	<i>Andricus giraudianus</i> D. T. & K.	AG BU	D. T. & K. 1910
	<i>Andricus glandulae</i> Schenck	AG BU	Hartig 1840

Synergus
nervosus
Hartig
(cont.)

Andricus
inflator
Hartig

AG BU Hartig 1840

Andricus
kollari
Hartig

AG BU Wiebes-Rijks 1978

Andricus
nudus
Adler

AG BU Hartig 1840
& SX CA

Andricus
ostreus
(Hartig)

AG LE Askew 1961

Andricus,
quadri-
lineatus
Hartig

AG CA E. & Q. 1963
& SX BU

Andricus
quercus-
ramuli
(L.)

AG BU Hartig 1840
& SX CA

Andricus
seminationis
Giraud

AG CA Askew 1961

Andricus
solitarius
(Fonscolombe)

AG BU Mayr 1872

Cynips
coronata
Giraud

AG BU Kieffer 1902b

Cynips
disticha
Hartig

SX BU Askew 1961

Cynips
divisa
Hartig

AG LE Askew 1961

Cynips
longiventris
Hartig

AG LE Askew 1961

<i>Synergus nervosus</i> Hartig (cont.)	<i>Cynips quercus-folii</i> L.	AG LE Hartig 1840
	<i>Neuroterus albipes</i> Schenck	AG LE E. & Q. 1963
	<i>Neuroterus numismalis</i> (Fourcroy)	SX BU Tavares 1920
	<i>Neuroterus quercus-baccarum</i> (L.)	AG CA Mayr 1872 & SX LE
	<i>Neuroterus tricolor</i> Hartig	AG LE E. & Q. 1963 & SX LE
	<i>Plagiotrochus quercus-ilicis</i> (Fabr.)	SX LE Kieffer 1902b
	<i>Trigonaspis megaptera</i> (Panzer)	AG LE Hartig 1840
<i>Synergus niger</i> Fullaway	?	WN ? BU
<i>Synergus nigripes</i> Hartig	<i>Callirhytis agama</i> Hartig	WP AG LE Hartig 1840
<i>Synergus nigroornatus</i> M. & E.	<i>Heteroecus pacificus</i> (Ashmead)	WN AG ST M. & E. 1922
<i>Synergus obtusilobae</i> (Ashmead)	?	EN ? ?
<i>Synergus ochreus</i> Fullaway	<i>Callirhytis quercus-pomiformis</i> (Bassett)	WN AG ST Fullaway 1911

<i>Synergus ochreus</i> Fullaway (cont.)	<i>Besbicus multipunctata</i> (Beut.)	AG LE	Fullaway 1911
<i>Synergus oneratus</i> (Harris)	<i>Adleria quercus-strobiliana</i> (O. S.)	WN AG ST	O. S. 1865
	<i>Atrusca brevipennata</i> (Gillette)	AG LE	Gillette 1896
	<i>Disholcaspis eldoradensis</i> (Beut.)	AG ST	M. & E. 1922
	<i>Disholcaspis quercus-globulus</i> (Fitch)	AG ST	O. S. 1861
	<i>Disholcaspis rubens</i> (Gillette)	AG ST	Gillette 1896
<i>Synergus pacificus</i> M. & E.	<i>Andricus opertus</i> Weld	WN AG BU	Evans 1972
	? <i>Antron</i> sp.	AG LE	Evans 1965
	<i>Besbicus mirabilis</i> (Kinsey)	AG LE	Evans 1967
	<i>Disholcaspis</i> sp.	AG LE	Evans 1965
	<i>Heteroecus pacificus</i> (Ashmead)	AG ST	M. & E. 1922
	<i>Neuroterus washingtonensis</i> Beut.	SX ST	Evans 1972
	<i>Liodora</i> sp.	AG LE	Evans 1965
<i>Synergus palliceps</i> Hartig	<i>Andricus curvator</i> Hartig	WP AG BU	Hartig 1840

<i>Synergus pallicornis</i> Hartig	<i>Adleria quercus- calicis</i> (Bgsdf.)	WP AG BU	Mayr 1872
	<i>Andricus callidoma</i> Hartig	AG BU	Tavares 1920
	<i>Andricus corruptrix</i> (Schlect.)	AG BU	Wiebes-Rijks 1978
	<i>Andricus curvator</i> Hartig	AG BU	Wiebes-Rijks 1979
	<i>Andricus kollarl</i> (Hartig)	AG BU	Mayr 1872
	<i>Andricus lignicola</i> (Hartig)	AG BU	Mayr 1872
	<i>Andricus ostreus</i> (Hartig)	AG LE	Tavares 1920
	<i>Cynips agama</i> Hartig	AG LE	Mayr 1872
	<i>Cynips caputmedusae</i> Hartig	AG LE	Mayr 1872
	<i>Cynips conglomerata</i> Giraud	AG ST	Mayr 1872
	<i>Cynips coriaria</i> Hartig	AG ST	Mayr 1872
	<i>Cynips cornifex</i> Hartig	AG LE	Mayr 1872
	<i>Cynips disticha</i> Hartig	AG LE	Mayr 1872

Synergus
pallicornis
Hartig
(cont.)

Cynips
divisa
Hartig

AG LE Mayr 1872

Cynips
gallae-
tinctoriae
(Olivier)

AG BU Mayr 1872

Cynips
glutinosa
Giraud

AG BU Mayr 1872

Cynips
hartigi
Foerster

AG ST Mayr 1872

Cynips
hungarica
Giraud

AG BU Mayr 1872

Cynips
infectoria
Hartig

AG BU Hartig 1843

Cynips
longiventris
Hartig

AG LE Mayr 1872

Cynips
polycera
Giraud

AG LE Mayr 1872

Cynips
quercus-
folia
L.

AG LE Hartig 1840

Cynips
quercus-
tozae
Bosc.

AG AC Mayr 1872

Neuroterus
numismalis
(Fourc.)

SX LE Tavares 1920

Neuroterus
quercus-
baccarum
(L.)

AG LE Wiebes-Rijks 1979

<i>Synergus pallicornis</i> Hartig (cont.)	<i>Trigonaspis synaspis</i> (Hartig)	AG LE Kieffer 1902b
<i>Synergus pallidipennis</i> Mayr	<i>Andricus amblycerus</i> Giraud	WP AG BU Fulmek 1968
	<i>Andricus bocagel</i> Kieffer	WP AG BU Tavares 1920
	<i>Andricus coriaria</i> Hartig	AG ST Mayr 1872
	<i>Andricus kollari</i> Hartig	AG BU D. T. & K. 1910
	<i>Andricus lignicola</i> (Hartig)	AG BU Mayr 1872
	<i>Cynips confica</i> Hartig	AG ST Mayr 1872
	<i>Cynips gallae-tinctoriae</i> (Olivier)	AG ST Mayr 1872
<i>Synergus pallipes</i> Hartig	<i>Andricus nudus</i> Adler	WP AG BU Mayr 1872
	<i>Neuroterus quercus-baccarum</i> (L.)	AG LE D. T. & K. 1910
<i>Synergus physoserus</i> Hartig	<i>Cynips quercus-folii</i> L.	WP AG LE D. T. & K. 1910
	<i>Trigonaspis synaspis</i> (Hartig)	AG LE Mayr 1872

<i>Synergus pomiformis</i> (Ashmead)	<i>Callirhytis quercus-pomiformis</i> (Bassett)	WN AG ST	Ashmead 1885
<i>Synergus profusus</i> M. & E.	<i>Disholcaspis canescens</i> (Bassett)	WN AG ST	M. & E. 1922
<i>Synergus punctatus</i> Gillette	<i>Disholcaspis eldoradensis</i> (Beut.)	WN AG ST	Fullaway 1911
	<i>Disholcaspis perniciosa</i> (Bassett)	AG ST	Gillette 1896
	<i>Disholcaspis rubens</i> (Gillette)	AG ST	Gillette 1896
	<i>Xanthoteras eburneum</i> (Bassett)	AG ST	Gillette 1896
<i>Synergus punctularis</i> R. & S.	<i>Andricus kollari</i> (Hartig)	WP AG BU	Dettmer 1924b
<i>Synergus quercus-lana</i> (Fitch)	<i>Andricus quercus-flocci</i> (Walsh)	EN AG LE	O. S. 1865
<i>Synergus reinhardi</i> Mayr	<i>Adleria caliciformis</i> (Giraud)	WP AG BU	Mayr 1872
	<i>Adleria quercus-calcis</i> (Bgsdf.)	AG BU	Mayr 1872
	<i>Andricus kollari</i> Hartig	AG BU	Mayr 1872
	<i>Andricus lignicola</i> Hartig	AG BU	Wiebes-Rijks 1978

<i>Synergus</i> <i>reinhardi</i> Mayr (cont.)	<i>Cynips</i> <i>caputmedusae</i> Hartig	AG LE Mayr 1872
	<i>Cynips</i> <i>gallae-</i> <i>tinctoriae</i> (Olivier)	AG BU Mayr 1872
	<i>Cynips</i> <i>glutinosa</i> Giraud	AG BU Mayr 1872
	<i>Cynips</i> <i>mitrata</i> Mayr	AG BU D. T. & K. 1910
	<i>Cynips</i> <i>quercus-</i> <i>tozae</i> Bosc.	AG AC Mayr 1872
<i>Synergus</i> <i>reniformis</i> M. & E.	<i>Andricus</i> <i>reniformis</i> M. & E.	WN AG ST M. & E. 1922
<i>Synergus</i> <i>rotundi-</i> <i>ventris</i> Mayr	<i>Andricus</i> <i>bella</i> (Dettmer)	WP AG LE Wiebes-Rijks 1979
	<i>Andricus</i> <i>corruptrix</i> (Schlect.)	AG BU Wiebes-Rijks 1979
	<i>Andricus</i> <i>kollari</i> Hartig	AG BU Wiebes-Rijks 1979
	<i>Andricus</i> <i>quercus-</i> <i>radicis</i> (L.)	AG RT E. & Q. 1963 & SX ST
	<i>Neuroterus</i> <i>macropterus</i> Hartig	AG ST Mayr 1872
<i>Synergus</i> <i>rubricornis</i> Tavares	<i>Andricus</i> <i>gemmae</i> (Giraud)	WP AG BU Tavares 1920

<i>Synergus</i> <i>ruficornis</i> Hartig	<i>Andricus</i> <i>bocagei</i> Tavares	WP AG BU Tavares 1920
	<i>Andricus</i> <i>inflator</i> Hartig	AG BU Hartig 1810
	<i>Andricus</i> <i>ostreus</i> (Hartig)	AG LE Hartig 1810
<i>Synergus</i> <i>rutulus</i> M. & E.	<i>Disholcaspis</i> <i>plumbella</i> Kinsey	WN AG ST M. & E. 1922
<i>Synergus</i> <i>scaber</i> Hartig	<i>Callirhytis</i> <i>picta</i> Hartig	WP AG AC D. T. & K. 1910
<i>Synergus</i> <i>semisulcatus</i> Hartig	?	WP ? LE
<i>Synergus</i> <i>similis</i> Gillette	<i>Atrusca</i> <i>brevipennata</i> (Gillette)	WN AG LE Gillette 1896
<i>Synergus</i> <i>splendidus</i> Fullaway	<i>Callirhytis</i> <i>quercus-</i> <i>pomiformis</i> (Bassett)	WN AG ST M. & E. 1922
<i>Synergus</i> <i>succinipidis</i> (Ashmead)	<i>Disholcaspis</i> <i>quercus-</i> <i>succinipes</i> (Ashmead)	EN AG ST Ashmead 1885
<i>Synergus</i> <i>synophris</i> Kieffer	<i>Synophrus</i> <i>olivieri</i> Kieffer	WP SX BU Kieffer 1905
<i>Synergus</i> <i>testaceus</i> (Hartig)	?	WP ? ?
<i>Synergus</i> <i>thaumacerus</i> Dalman	<i>Andricus</i> <i>curvator</i> Hartig	WP SX BU Kieffer 1905

<i>Synergus</i> <i>thaumacerus</i> Dalman (cont.)	<i>Andricus</i> <i>cydoniae</i> Giraud	SX BU Mayr 1872
	<i>Andricus</i> <i>singulus</i> Mayr	SX BU Mayr 1872
	<i>Andricus</i> <i>gallae-</i> <i>urnaeformis</i> (Fonsc.)	SX LE D. T. & K. 1910
	<i>Aphelonyx</i> <i>cernicola</i> (Giraud)	AG ST Mayr 1872
	<i>Cynips</i> <i>disticha</i> Hartig	AG LE Brischke 1882
	<i>Cynips</i> <i>quercus-</i> <i>folii</i> L.	SX BU Wachtl 1876
	<i>Dryocosmus</i> <i>nervosus</i> (Giraud)	SX LE Mayr 1872
	<i>Neuroterus</i> <i>glandiformis</i> (Giraud)	SX AC Mayr 1872
	<i>Neuroterus</i> <i>quercus-</i> <i>baccarum</i> (L.)	SX BU Kieffer 1902b
	<i>Neuroterus</i> <i>tricolor</i> Hartig	SX BU Mayr 1872
	<i>Trigonaspis</i> <i>megaptera</i> (Panzer)	AG LE Mayr 1872 & SX BU
<i>Synergus</i> <i>umbraculus</i> Olivier	<i>Adleria</i> <i>caliciformis</i> (Giraud)	WP AG BU Mayr 1872

<i>Synergus</i> <i>umbraculus</i> Olivier (cont.) /	<i>Adleria</i> <i>quercus-</i> <i>calicis</i> (Bgsdf.)	AG BU Hartig 1843
	<i>Andricus</i> <i>amblycerus</i> Giraud	AG BU Mayr 1872
	<i>Andricus</i> <i>clementinae</i> (Giraud)	AG BU Mayr 1872
	<i>Andricus</i> <i>fecundator</i> Hartig	AG BU Mayr 1872
	<i>Andricus</i> <i>kollar</i> (Hartig)	AG BU Hartig 1843
	<i>Andricus</i> <i>lignicola</i> (Hartig)	AG BU Mayr 1872
	<i>Andricus</i> <i>lucidus</i> (Hartig)	AG BU Hartig 1843
	<i>Andricus</i> <i>mayri</i> Wachtl	AG BU Kieffer 1902b
	<i>Biorhiza</i> <i>pallida</i> (Olivier)	SX BU Kieffer 1902b
	<i>Cynips</i> <i>caputmedusae</i> Hartig	AG BU Mayr 1872
	<i>Cynips</i> <i>conglomerata</i> Giraud	AG ST Mayr 1872
	<i>Cynips</i> <i>conifica</i> Hartig	AG BU Hartig 1843
	<i>Cynips</i> <i>coriaria</i> Hartig	AG ST Mayr 1872

<i>Synergus</i> <i>umbraculus</i> Olivier (cont.)	<i>Cynips</i> <i>coronata</i> Giraud	AG BU Kieffer 1902b
	<i>Cynips</i> <i>gallae-</i> <i>tinctoriae</i> (Olivier)	AG BU Mayr 1872
	<i>Cynips</i> <i>glutinosa</i> Giraud	AG BU Mayr 1872
	<i>Cynips</i> <i>hungarica</i> Giraud	AG AC Mayr 1872
	<i>Cynips</i> <i>mayri</i> (Kieffer)	AG AC Kieffer 1902b
	<i>Cynips</i> <i>panteli</i> Tavares	AG BU Tavares 1920
	<i>Cynips</i> <i>polycera</i> Giraud	AG BU Mayr 1872
	<i>Cynips</i> <i>quercus-</i> <i>folii</i> L.	AG LE Magretti in Stegano 1904
	<i>Cynips</i> <i>quercus-</i> <i>tozae</i> Bosc.	AG AC Kieffer 1902b
	<i>Trigonaspis</i> <i>megaptera</i> (Panzer)	AG LE Tavares 1920 & SX BU
	<i>Trigonaspis</i> <i>mendisi</i> Tavares	AG LE Tavares 1920
<i>Synergus</i> <i>variabilis</i> Mayr	<i>Andricus</i> <i>grossulariae</i> Giraud	WP SX CA Mayr 1872

<i>Synergus</i> <i>variabilis</i> Mayr (cont.)	<i>Aphelonyx</i> <i>cerricola</i> (Giraud)	AG BU Mayr 1872
	<i>Chilaspis</i> <i>nitidus</i> Giraud	AG LE Mayr 1872
	<i>Dryocosmus</i> <i>cerriphilus</i> Giraud	AG ST Mayr 1872
	<i>Dryomyia</i> <i>circinans</i> Giraud (Cecidomyiidae)	SX LE Mayr 1872
	<i>Neuroterus</i> <i>laniginosus</i> Giraud	AG LE Mayr 1872
	<i>Neuroterus</i> <i>macropterus</i> Hartig	AG ST Mayr 1872
	<i>Synophrus</i> <i>politus</i> Hartig	SX BU Kieffer 1902b
<i>Synergus</i> <i>varicolor</i> Fullaway	<i>Callirhytis</i> <i>quercus-</i> <i>pomiformis</i> (Bassett)	WN AG ST Fullaway 1911
<i>Synergus</i> <i>variegatus</i> M. & E.	<i>Heteroecus</i> <i>pacificus</i> (Ashmead)	WN AG ST M. & E. 1922
<i>Synergus</i> <i>variolosus</i> Hartig	<i>Andricus</i> <i>quercus-</i> <i>radicus</i> (Fabr.)	WP SX ST Hartig 1841
	<i>Andricus</i> <i>quercus-</i> <i>ramuli</i> (L.)	AG LE Hartig 1841
<i>Synergus</i> <i>villosus</i> Gillette	<i>Acraspis</i> <i>villosa</i> (Gillette)	EN AG LE Gillette 1896

<i>Synergus</i> <i>virentis</i> (Ashmead)	<i>Belonocnema</i> <i>quercus-</i> <i>virens</i> (O. S.)	EN AG LE	Ashmead 1885
<i>Synergus</i> <i>walshii</i> Gillette	<i>Andricus</i> <i>quercus-</i> <i>flocchi</i> Walsh	EN AG LE	Gillette 1896
<i>Synergus</i> <i>xanthocerus</i> Hartig	?	WP ? ?	
<i>Synergus</i> sp.	<i>Dryocosmus</i> <i>kunriphillus</i> Yasumatsu	EP ? LE	Otake et. al 1982
<i>Synergus</i> spp.	* <i>Acraspis</i> <i>macrocarpae</i> Bassett	AG LE	AMNH
	* <i>Acraspis</i> <i>pezomachoides</i> (O. S.)	AG LE	AMNH
	* <i>Acraspis</i> <i>quercushirta</i> (Bassett)	AG LE	AMNH
	* <i>Acraspis</i> <i>ulterior</i> (Kinsey)	AG LE	AMNH
	* <i>Amphibolips</i> <i>confluenta</i> (Harris)	AG LE	AMNH
	* <i>Amphibolips</i> <i>gainsei</i> Bassett	AG AC	AMNH
	* <i>Amphibolips</i> <i>melanocera</i> Ashmead	SX BU	AMNH
	* <i>Amphibolips</i> <i>quercus-</i> <i>cinerea</i> (Ashmead)	AG ST	AMNH

Synergus
spp.
(cont.)

* <i>Amphibolips</i> <i>quercus-</i> <i>ilicifoliae</i> (Bassett)	SX LE	AMNH
* <i>Amphibolips</i> <i>quercusinarus</i> (O. S.)	AG LE	AMNH
* <i>Amphibolips</i> <i>trizonata</i> Ashmead	SX ST	AMNH
* <i>Atrusca</i> <i>simulatrix</i> Kinsey	AG LE	AJR
* <i>Disholcaspis</i> <i>simulata</i> Kinsey	AG ST	AJR
* <i>Neuroterus</i> <i>cupulae</i> Kinsey	AG AC	AMNH
* <i>Neuroterus</i> <i>englemanni</i> Kinsey	AG LE	AMNH
* <i>Neuroterus</i> <i>fragilis</i> Bassett	SX LE	AMNH
* <i>Neuroterus</i> <i>niger</i> Gilllette	AG LE	AMNH
* <i>Neuroterus</i> <i>quericola</i> Dalla Torre	SX LE	AMNH
* <i>Neuroterus</i> <i>saltatorius</i> (Edwards)	AG LE	AMNH
* <i>Neuroterus</i> <i>tumba</i> Kinsey	AG LE	AMNH
* <i>Neuroterus</i> <i>varians</i> Kinsey	AG ST	AMNH

SYNOPHROMORPHA

- Synophromorpha* ? WN ? ? AJR
kaulbarsi
 R. & S.
- Synophromorpha Diastrophus* EN SX ST Weld 1952
rubi cuscuthaeformis
 Weld (O. S.)
- Synophromorpha Diplolepis* EN SX LE O. S. 1863
sylvestris ignota
 (O. S.) (O. S.)
- Diastrophus* SX ST O. S. 1865
nebulosus
 O. S.
- Synophromorpha Diastrophus* EN SX ST Weld 1952a
terricola bassetti
 Weld (Beut.) ?
- Diastrophus* SX RT Weld 1952a
radicum
 Bassett
- Synophro-* **Diastrophus* WN SX ST AMNH
morpha *kincaidi*
spp. Gillette
- **Diastrophus* EN SX ST AJR
turgidus
 Bassett

SYNOPHRUS

- Synophrus* ? WN ? ?
mexicanus
 (Gillette)
- Synophrus* ? WP ? BU D. T. & K. 1910
olivieri
 Kleffer
- Synophrus* *Andricus* WP AG BU Hartig 1843
politus inflator
 Hartig Hartig

4.3. Hosts of Inquiline Cynipidae.*ACRASPI* Mayr

<i>A. erinacei</i> (Beut.)	* <i>Ceroptres</i> sp.
* <i>Synergus erinacei</i> Gillette
<i>A. macrocarpae</i>
Bassett	* <i>Ceroptres</i> sp.
* <i>Synergus</i> sp.
<i>A. pezomachoides</i>
(O. S.)	<i>Ceroptres quercuspisum</i>
(Fitch)
* <i>Synergus</i> sp.
<i>A. quercushirta</i>
(Bassett)	* <i>Ceroptres</i> sp.
* <i>Synergus</i> sp.
<i>A. ulterior</i>
(Kinsey)	* <i>Ceroptres</i> sp.
* <i>Synergus</i> sp.
<i>A. villosa</i> (Gillette)	<i>Synergus villosus</i> Gillette

ADLERIA Kinsey

<i>A. caliciformis</i> (Giraud)	<i>Ceroptres arator</i> Hartig
<i>Synergus albipes</i> Hartig
<i>Synergus reinhardi</i> Mayr
<i>Synergus umbraculus</i>
(Olivier)
<i>A. nigricens</i> (Gillette)	* <i>Ceroptres</i> sp.
<i>A. quercuscalicis</i> (Burgsdorf)	<i>Synergus albipes</i> Hartig
<i>Synergus basalis</i> Hartig
<i>Synergus evanescens</i> Mayr
<i>Synergus gallaepomiformis</i>
(Fonsc.)
<i>Synergus pallicornis</i> Hartig
<i>Synergus reinhardi</i> Mayr
<i>Synergus umbraculus</i>
(Olivier)
<i>A. quercusstrobliana</i>
(O. S.)	<i>Synergus oneratus</i> (Harris)

AMPHIBOLIPS Reinhard

<i>A. confluenta</i> (Harris)	<i>Synergus</i> sp.
<i>A. cookii</i> Gillette	* <i>Ceroptres</i> sp. <i>Synergus magnus</i> Gillette
<i>A. gainsei</i> Bassett	* <i>Synergus</i> sp.
<i>A. melanocera</i> Ashmead	* <i>Synergus</i> sp.
<i>A. quercuscinerea</i> (Ashmead)	* <i>Ceroptres</i> sp. * <i>Synergus</i> sp.
<i>A. quercuscitriformis</i> (Ashmead)	<i>Synergus citriformis</i> (Ashmead)
<i>A. quercusilicifoliae</i> (Bassett)	* <i>Synergus</i> sp.
<i>A. quercusinanus</i> (O. S.)	* <i>Synergus</i> sp.
<i>A. quercusspongifica</i> (O. S.)	* <i>Synergus laeviventris</i> (O. S.)
<i>A. trizonata</i> Ashmead	* <i>Synergus</i> sp.

ANDRICUS Hartig

<i>A. albopunctatus</i> Schlect.	* <i>Synergus gallaepomiformis</i> (Fonsc.) <i>Synergus nervosus</i> Hartig
<i>A. amblycerus</i> Giraud	<i>Synergus albipes</i> Hartig <i>Synergus apicalis</i> Hartig <i>Synergus umbraculus</i> (Olivier)
<i>A. bella</i> (Dettmer)	<i>Synergus rotundiventris</i> Hartig
<i>A. bocagei</i> Kieffer	<i>Synergus pallidipennis</i> Mayr <i>Synergus ruficornis</i> Hartig
<i>A. callidoma</i> Hartig	<i>Ceroptres clavicornis</i> Hartig <i>Synergus gallaepyriformis</i> (Olivier)

ANDRICUS Hartig (cont.)

A. callidoma Hartig (cont.)	Synergus nervosus Hartig Synergus pallicornis Hartig
A. championi Cameron	Synergus dugesi Ashmead
A. chrysolepidocola (Ashmead)	Synergus multiplicatus Fullaway
A. circulans Mayr	Ceroptres cerni Mayr
A. clemantinae (Giraud)	Synergus albipes Hartig Synergus gallaepomiformis (Fonsc.) Synergus umbraculus (Olivier)
A. confertus M. & E.	Ceroptres confertus M. & E. Synergus confertus M. & E.
A. conleria Hartig	Synergus pallidipennis Mayr
A. corruptrix (Schlect.)	Synergus albipes Hartig Synergus gallaepomiformis (Fonsc.) Synergus nervosus Hartig Synergus pallicornis Hartig
A. crispator (Tschek)	Ceroptres cerni Mayr
A. crystallinus Bassett	*Ceroptres sp.
A. curvator Hartig	Synergus albipes Hartig Synergus carinulatus Dettmer Synergus evanescens Mayr Synergus fulvipes Dettmer Synergus gallaepomiformis (Fonsc.) Synergus nervosus Hartig Synergus palliceps Hartig Synergus thaumacerus Dalman
A. cydoniae Giraud	Synergus thaumacerus Dalman

ANDRICUS Hartig (cont.)

<i>A. durangensis</i> Beut.	<i>Saphonecrus brevis</i> Weld
<i>A. fecundator</i> (Hartig)	<i>Synergus albipes</i> Hartig <i>Synergus apicalis</i> Hartig <i>Synergus evanescens</i> Mayr <i>Synergus gallaepomiformis</i> (Fonsc.), <i>Synergus umbraculus</i> (Olivier)
<i>A. furnaceus</i> Kinsey	* <i>Saphonecrus</i> sp.
<i>A. gallaeurnaeformis</i> (Fonsc.)	<i>Ceroptres arator</i> Hartig <i>Synergus albipes</i> Hartig <i>Synergus gallaepomiformis</i> (Fonsc.)
<i>A. gemmae</i> (Giraud)	<i>Synergus rubricornis</i> Tavares
<i>A. giraudianus</i> D. T. & K.	<i>Ceroptres clavicornis</i> Hartig <i>Synergus maculosus</i> Tavares <i>Synergus nervosus</i> Hartig
<i>A. glandulae</i> Hartig	<i>Saphonecrus connatus</i> (Hartig) <i>Synergus gallaepomiformis</i> (Fonsc.) <i>Synergus nervosus</i> Hartig
<i>A. grossulariae</i> Giraud	<i>Synergus variabilis</i> Mayr
<i>A. guatemalensis</i> (Cameron)	<i>Synergus cultratus</i> R. & S.
<i>A. ignotus</i> (Bassett)	* <i>Ceroptres</i> sp.
<i>A. inflator</i> Hartig	<i>Saphonecrus connatus</i> (Hartig) <i>Synergus albipes</i> Hartig <i>Synergus evanescens</i> Mayr <i>Synergus gallaepomiformis</i> (Fonsc.) <i>Synergus nervosus</i> Hartig <i>Synergus ruficornis</i> Hartig <i>Synophrus politus</i> Hartig

ANDRICUS Hartig (cont.)

A. kollari (Hartig)	<i>Ceroptres anator</i> Hartig
<i>Synergus albipes</i> Hartig
<i>Synergus evahescens</i> Mayr
<i>Synergus gallaepomiformis</i> (Fonsc.)
<i>Synergus gallaicus</i> Tavares
<i>Synergus hayneanus</i> (Retzeburg)
<i>Synergus ibericus</i> Tavares
<i>Synergus insuetus</i> Tavares
<i>Synergus nervosus</i> Hartig
<i>Synergus pallicornis</i> Hartig
<i>Synergus pallidipennis</i> Mayr
<i>Synergus punctularis</i> R. & S.
<i>Synergus reinhardi</i> Mayr
<i>Synergus umbraculus</i> (Olivier)
A. krajnovici Tavares	<i>Synergus incrassatus</i> Hartig
A. legitimus Wiebes-Rijks	<i>Synergus clandestinus</i> Eady
<i>Synergus gallaepomiformis</i> (Fonsc.)
A. leuticornis Kieffer	<i>Ceroptres cerni</i> Mayr
A. lignicola Hartig	<i>Ceroptres anator</i> Hartig
<i>Synergus albipes</i> Hartig
<i>Synergus apicalis</i> Hartig
<i>Synergus gallaepomiformis</i> (Fonsc.)
<i>Synergus hayneanus</i> (Retze.)
<i>Synergus pallicornis</i> Hartig
<i>Synergus pallidipennis</i> Mayr
<i>Synergus reinhardi</i> Mayr
<i>Synergus umbraculus</i> (Olivier)
A. lucidus (Hartig)	<i>Ceroptres anator</i> Hartig
<i>Synergus albipes</i> Hartig
<i>Synergus umbraculus</i> (Olivier)

ANDRICUS Hartig (cont.)

<i>A. mayri</i> (Wachtl.)	<i>Synergus evanescens</i> Mayr <i>Synergus umbraculus</i> (Olivier)
<i>A. multipunctatus</i> Giraud	<i>Ceroptres cerri</i> Mayr <i>Synergus evanescens</i> Mayr
<i>A. murtfeldtae</i> Ashmead	* <i>Ceroptres</i> sp.
<i>A. nudus</i> Adler	<i>Synergus albipes</i> Hartig <i>Synergus gallaepomiformis</i> (Fonsc.) <i>Synergus nervosus</i> Hartig <i>Synergus pallipes</i> Hartig
<i>A. opertus</i> Weld	<i>Ceroptres montensis</i> Weld <i>Synergus pacificus</i> M. & E.
<i>A. ostreus</i> (Hartig)	<i>Saphonecrus connatus</i> (Hartig) <i>Synergus albipes</i> Hartig <i>Synergus gallaepomiformis</i> (Fonsc.) <i>Synergus lusitanicus</i> (Tavares) <i>Synergus nervosus</i> Hartig <i>Synergus pallicornis</i> Hartig <i>Synergus ruficornis</i> Hartig
<i>A. peredurus</i> Kinsey	* <i>Saphonecrus</i> sp.
<i>A. quercus corticus</i> (Fabricius)	<i>Synergus gallaepomiformis</i> (Fonsc.) <i>Synergus incrassatus</i> Hartig
<i>A. quercus flocci</i> (Walsh)	* <i>Ceroptres</i> sp. <i>Synergus quercusiana</i> (Fitch) <i>Synergus walshii</i> Gillette
<i>A. quercus foliatus</i> (Ashmead)	* <i>Ceroptres</i> sp. <i>Synergus bicolor</i> Ashmead
<i>A. quercus frondosa</i> (Bassett)	<i>Ceroptres frondosae</i> Ashmead

ANDRICUS Hartig (cont.)

<i>A. quercuslanigera</i> (Ashmead)	<i>Ceroptres lanigerae</i> Ashmead
<i>A. quadrilineatus</i> Hartig	<i>Ceroptres arator</i> Hartig <i>Synergus albipes</i> Hartig <i>Synergus fulvipes</i> Dettmer <i>Synergus gallaepomiformis</i> (Fonsc.) <i>Synergus nervosus</i> Hartig
<i>A. quercuspetiolicola</i> (Bassett)	<i>Ceroptres petiolicola</i> (O. S.) <i>Euceroptres ficus</i> (O. S.)
<i>A. quercusostensackeni</i> (Bassett)	<i>Ceroptres rufiventris</i> Ashmead
<i>A. quercusradicis</i> (Fabricius)	<i>Ceroptres arator</i> Hartig <i>Ceroptres clavicornis</i> Hartig <i>Saphonecrus connatus</i> (Hartig) <i>Synergus apicalis</i> Hartig <i>Synergus gallaepomiformis</i> (Fonsc.) <i>Synergus incrassatus</i> Hartig <i>Synergus rotundiventris</i> Mayr <i>Synergus variolosus</i> Hartig
<i>A. quercusramuli</i> (L.)	<i>Ceroptres arator</i> Hartig <i>Saphonecrus connatus</i> (Hartig) <i>Synergus gallaepomiformis</i> (Fonsc.) <i>Synergus nervosus</i> Hartig <i>Synergus variolosus</i> Hartig
<i>A. reniformis</i> M. & E.	<i>Ceroptres montensis</i> Weld <i>Synergus reniformis</i> M. & E.
<i>A. rhisomae</i> Hartig	<i>Synergus incrassatus</i> Hartig
<i>A. rhizoxenus</i> (Ashmead)	* <i>Synergus nervosus</i> Hartig

ANDRICUS Hartig (cont.)

A. sieboldi Mayr	Synergus incrassatus Hartig
A. singulus Mayr	Synergus thaumacerus Dalman
A. solitarius (Fonsc.)	Synergus gallaepomiformis (Fonsc.) Synergus nervosus Hartig
A. sufflator ² Mayr	Synergus thaumacerus Dalman
A. tecturnarum Kinsey	*Ceroptres sp.
A. testaceipes (Hartig)	Ceroptres arator Hartig Synergus apicalis Hartig Synergus gallaepomiformis (Fonsc.) Synergus incrassatus Hartig
Andricus sp.	Saphonecrus brevicornis (Ashmead)

ANTRON Kinsey

?Antron sp.	Synergus pacificus M. & E.
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APHELONYX Mayr

A. cernicola Giraud	Ceroptres cerni Mayr Saphonecrus undulatus (Mayr) Synergus thaumacerus Dalman Synergus variabilis Mayr
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ARNOLDIA

A. cernis Kollar	Saphonecrus haimi (Mayr)
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ATRUSCA Kinsey

A. brevipennata (Gillette)	Synergus atripes Gillette
Synergus oneratus (Harris)
Synergus similis Gillette
A. quercuscentricola
(O. S.)	Synergus laeviventris
(O. S.)
A. simulatrix Kinsey	*Synergus sp.

BASSETTIA Ashmead

B. ligni Kinsey	Synergus garryana
Gillette
B. quercusatesbaei
(Ashmead)	Ceroptres catesbaei
(Ashmead)

BELONOCNEMA Mayr

B. quercusvirens (O. S.)	Synergus virentis
(Ashmead) |
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BESBICUS Kinsey

B. heidiae (Fullaway)	*Ceroptres sp.
B. mirabilis (Kinsey)	Synergus garryana
Gillette
Synergus pacificus
M. & E.
B. multipunctata (Beut.)	Synergus ochreus Fullaway
Synergus dimorphus O. S.

BIORHIZA Westwood

B. pallida (Olivier)	Synergus gallaepomiformis
(Fonsc.)
Synergus umbraculus
(Olivier) |
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CALLIRHYTIS Foerster

<i>C. agama</i> Hartig	<i>Synergus nigripes</i> Hartig
<i>C. ashmeadi</i> D. T. & K.	<i>Synergus dugesii</i> Ashmead
<i>C. clavula</i> (O. S.)	<i>Ceroptres quercusarbus</i> (Fitch)
	<i>Ceroptres quercustubus</i> (Fitch)
<i>C. cornigera</i> (O. S.)	<i>Synergus lignicola</i> (O. S.)
<i>C. frequens</i> (Gillette)	<i>Synergus incisus</i> Gillette
<i>C. furnessae</i> Weld	<i>Synergus filicornis</i> Cameron
* <i>C. glandium</i> (Giraud)	<i>Synergus gallaepomiformis</i> (Fonsc.)
<i>C. lanata</i> (Gillette)	* <i>Ceroptres</i> sp.
<i>C. picta</i> Hartig	<i>Synergus scaber</i> Hartig
<i>C. quercusbatatoides</i> (Ashmead)	<i>Synergus batatoides</i> Ashmead
<i>C. quercusfutilis</i> (Osten Sacken)	<i>Euceroptres futilis</i> (Osten Sacken)
<i>C. quercusgemmaria</i> (Ashmead)	<i>Saphonecrus gemmariae</i> (Ashmead)
	<i>Synergus davisii</i> (Beut.)
<i>C. quercusmedullae</i> (Ashmead)	<i>Synergus medullae</i> Ashmead
<i>C. quercuspomiformis</i> (Bassett)	<i>Synergus flavus</i> Kieffer
	<i>Synergus ochreus</i> Fullaway
	<i>Synergus pomiformis</i> (Ashmead)
	<i>Synergus splendidus</i> Fullaway
	<i>Synergus varicolor</i> Fullaway
<i>C. quercuspunctatus</i> (Bassett)	* <i>Ceroptres</i> sp.
	<i>Synergus lignicola</i> (O. S.)
	<i>Synergus mendax</i> Walsh
<i>C. quercussimilis</i>	* <i>Ceroptres</i> sp.

CALLIRHYTIS Foerster (cont.)

<i>C. quercussuttoni</i> (Bassett)	<i>Euceroptres maritimus</i> Weid
<i>C. quercusventricosa</i> (Bassett)	<i>Synergus coniferæ</i> Ashmead
<i>C. serricornis</i> (Kinsey)	<i>Synergus flavens</i> (M. & E.)
<i>C. tubicola</i> (O. S.)	* <i>Ceroptres</i> sp.
<i>C. tumifica</i> (O. S.)	* <i>Ceroptres</i> sp.
<i>Callirhytis</i> sp.	<i>Synergus digressus</i> M. & E.

CHILASPIS Mayr

<i>C. nitidus</i> (Giraud)	<i>Saphonecrus halmi</i> (Mayr) <i>Synergus variabilis</i> Mayr
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CYNIPS Linneus

<i>C. agama</i> Hartig	<i>Synergus albipes</i> Hartig <i>Synergus apicalis</i> Hartig <i>Synergus flavicornis</i> Hartig <i>Synergus pallicornis</i> Hartig
<i>C. caputmedusæ</i> Hartig	<i>Synergus albipes</i> Hartig <i>Synergus gallæpomiformis</i> (Fonsc.) <i>Synergus pallicornis</i> Hartig <i>Synergus reinhardi</i> Mayr <i>Synergus umbraculus</i> (Olivier)
<i>C. conglomerata</i> Giraud	<i>Ceroptres arator</i> Hartig <i>Synergus albipes</i> Hartig <i>Synergus apicalis</i> Hartig <i>Synergus pallicornis</i> Hartig <i>Synergus umbraculus</i> (Olivier)

CYNIPS Linneus (cont.)

<i>C. conifica</i> Hartig	<i>Synergus pallidipennis</i> Mayr <i>Synergus umbraculus</i> (Olivier)
<i>C. coriaria</i> Hartig	<i>Synergus albipes</i> Hartig <i>Synergus gallaepomiformis</i> (Fonsc.) <i>Synergus pallicornis</i> Hartig <i>Synergus umbraculus</i> (Olivier)
<i>C. cornifex</i> Hartig	<i>Synergus pallicornis</i> Hartig
<i>C. coronata</i> Giraud	<i>Synergus gallaepomiformis</i> (Fonsc.) <i>Synergus hayneanus</i> (Retze.) <i>Synergus nervosus</i> Hartig <i>Synergus umbraculus</i> (Olivier)
<i>C. disticha</i> Hartig	<i>Synergus albipes</i> Hartig <i>Synergus gallaepomiformis</i> (Fonsc.) <i>Synergus nervosus</i> Hartig <i>Synergus pallicornis</i> Hartig <i>Synergus thaumacerus</i> Dalman
<i>C. divisa</i> Hartig	<i>Ceroptres arator</i> Hartig <i>Synergus albipes</i> Hartig <i>Synergus gallaepomiformis</i> (Fonsc.) <i>Synergus nervosus</i> Hartig <i>Synergus pallicornis</i> Hartig
<i>C. flosculi</i> Giraud	<i>Ceroptres arator</i> Hartig
<i>C. galeata</i> Giraud	<i>Ceroptres arator</i> Hartig
<i>C. gallaetinctoriae</i> (Olivier)	<i>Synergus albipes</i> Hartig <i>Synergus gallaepomiformis</i> (Fonsc.) <i>Synergus hayneanus</i> (Retze.)

CYNIPS Linnaeus (cont.)

- C. gallaetinctoriae* (Olivier)
(cont.)
- Synergus pallicornis* Hartig
Synergus pallidipennis Mayr
Synergus reinhardi Mayr
Synergus umbraculus (Olivier)
- C. glutinosa* Giraud
- Ceroptres arator* Hartig
Synergus albipes Hartig
Synergus gallaepomiformis (Fonsc.)
Synergus pallicornis Hartig
Synergus reinhardi Mayr
Synergus umbraculus (Olivier)
- C. hartigi* Foerster
- Synergus pallicornis* Hartig
- C. hungarica* Giraud
- Ceroptres arator* Hartig
Synergus albipes Hartig
Synergus pallicornis Hartig
Synergus umbraculus (Olivier)
- C. infectoria* Hartig
- Synergus evanescens* Mayr
Synergus gallaepomiformis (Fonsc.)
Synergus hayneanus (Retze.)
Synergus pallicornis Hartig
- C. longiventris* Hartig
- Synergus apicalis* Hartig
Synergus gallaepomiformis (Fonsc.)
Synergus nervosus Hartig
Synergus pallicornis Hartig
- C. mayri* (Kieffer)
- Synergus evanescens* Mayr
Synergus gallaeviscosae Fairm.
Synergus reinhardi Mayr
- C. pantelli* Tavares
- Synergus umbraculus* (Olivier)

CYNIPS Linneus (cont.)

C. polycera Giraud

Ceroptres anator Hartig
Synergus albipes Hartig
Synergus pallicornis
 Hartig
Synergus umbraculus
 (Olivier)

C. quercusfolii L.

Ceroptres anator Hartig
Saphonecrus connatus
 (Hartig)
Synergus albipes Hartig
Synergus gallaepomiformis
 (Fonsc.)
Synergus nervosus Hartig
Synergus pallicornis
 Hartig
Synergus physoserus
 Hartig
Synergus thaumacerus
 Dalman
Synergus umbraculus
 (Olivier)

C. quercustozae Bosc.

Synergus albipes Hartig
Synergus pallicornis
 Hartig
Synergus reinhardi Mayr
Synergus umbraculus
 (Olivier)

C. stefani Kleffer

Synergus hayneanus
 (Retze.)

DI ASTROPHUS Hartig

D. basseti (Beut.)

Synophromorpha sylvestris
 (O. S.)
Synophromorpha terricola
 Wied

D. cuscataeformis (O. S.)*Synophromorpha rubi* Wied*D. kincaidi* Gillette**Synophromorpha* sp.*D. nebulosus* O. S.

Synophromorpha sylvestris
 (O. S.)

DI ASTROPHUS Hartig (cont.)

<i>D. radicum</i> Bassett	<i>Synophromorpha terricola</i> Weid
<i>D. smilacis</i> Ashmead	<i>Synophromorpha smilacis</i> Ashmead
<i>D. turgidus</i> Bassett	* <i>Synophromorpha</i> sp.

DIPLOLEPIS Fourcroy

<i>D. bassetti</i> (Beut.)	* <i>Periclistus pirata</i> (O. S.)
<i>D. bicolor</i> (Harris)	<i>Periclistus pirata</i> (O. S.) <i>Periclistus weidi</i> R. & S.
<i>D. californica</i> (Beut.)	* <i>Periclistus californicus</i> Ashmead
<i>D. centifoliae</i> (Hartig)	<i>Periclistus caninae</i> (Hartig)
<i>D. dichlocera</i> (Harris)	* <i>Periclistus pirata</i> (O. S.)
<i>D. eglantariae</i> (Hartig)	<i>Periclistus caninae</i> (Hartig)
<i>D. fusiformans</i> (Ashmead)	* <i>Periclistus fusicolus</i> R. & S.
<i>D. gracilis</i> (Ashmead)	* <i>Periclistus gracilicollis</i> R. & S.
<i>D. ignota</i> (O. S.)	* <i>Periclistus ashmeadi</i> R. & S.
<i>D. inconspicuis</i> D. & C.	<i>Periclistus arefactus</i> M. & E.
<i>D. japonica</i> (Walker)	<i>Periclistus natalis</i> T. & K. <i>Periclistus quiniani</i> T. & K.
<i>D. lens</i> Weid	* <i>Periclistus cataractans</i> R. & S.
<i>D. mayri</i> (Schlect.)	<i>Periclistus brandtii</i> (Ratze.)

DIPLOLEPIS Fourcroy (cont.)

<i>D. nebulosa</i> (Bassett)	* <i>Periclistus ashmeadi</i> R. & S. * <i>Periclistus pirata</i> (O. S.) * <i>Periclistus weidi</i> R. & S.
<i>D. neglecta</i> (Gillette)	* <i>Periclistus anefactus</i> M. & E. * <i>Periclistus pirata</i> (O. S.) * <i>Periclistus vancouverensis</i> R. & S.
<i>D. nervosa</i> (Curtis)	<i>Periclistus caninae</i> (Hartig)
<i>D. polita</i> (Ashmead)	<i>Periclistus californicus</i> Ashmead <i>Periclistus piceus</i> Fullaway * <i>Periclistus pirata</i> (O. S.) * <i>Periclistus weidi</i> R. & S.
<i>D. rosae</i> (L.)	<i>Periclistus brandtii</i> (Retze.)
<i>D. rosaefolii</i> (Cockerell)	* <i>Periclistus cataractans</i> R. & S.
<i>D. rosarum</i> (Giraud)	<i>Periclistus caninae</i> (Hartig) <i>Periclistus rosarum</i> Dettmer
<i>D. spinosa</i> (Ashmead)	* <i>Periclistus pirata</i> (O. S.)
<i>D. spinosissimae</i> (Giraud)	<i>Periclistus caninae</i> (Hartig) <i>Periclistus spinosissimae</i> Dettmer
<i>D. triformis</i> S. & R.	* <i>Periclistus fuscicollis</i> R. & S.
<i>D. tuberculatrix</i> (Cockerell)	* <i>Periclistus pirata</i> (O. S.)
<i>D. tumida</i> (Bassett)	* <i>Periclistus pirata</i> (O. S.)
<i>D. variabilis</i> (Bassett)	* <i>Periclistus ashmeadi</i> R. & S.
<i>Diplolepis</i> sp.	<i>Periclistus capillatus</i> Belizen

DISHOLCASPIIS Dalla Torre and Kieffer

<i>D. canescens</i> (Bassett)	<i>Synergus distinctus</i> M. & E. <i>Synergus profusus</i> M. & E.
<i>D. eidoradensis</i> (Beut.)	<i>Ceroptres niger</i> Fullaway <i>Synergus garryana</i> Gillette <i>Synergus oneratus</i> (Harris) <i>Synergus punctatus</i> Gillette
4 <i>D. perniciosa</i> (Bassett)	<i>Synergus garryana</i> Gillette <i>Synergus punctatus</i> Gillette
<i>D. plumbella</i> Kinsey	<i>Synergus rutulus</i> M. & E.
<i>D. quercusglobulus</i> (Fitch)	<i>Synergus campanula</i> O. S. <i>Synergus oneratus</i> (Harris) <i>Synergus laeviventris</i> (O. S.)
<i>D. quercusmamma</i> (Walsh)	<i>Synergus campanula</i> O. S. <i>Synergus duricornis</i> Gillette
<i>D. quercussuccinipes</i> (Ashmead)	<i>Synergus succinipedis</i> (Ashmead)
<i>D. quercusvirens</i> (Ashmead)	<i>Synergus ficigeræ</i> Ashmead
<i>D. rubens</i> (Gillette)	<i>Synergus atra</i> Gillette <i>Synergus oneratus</i> (Harris) <i>Synergus punctatus</i> Gillette <i>Synergus laeviventris</i> (O. S.)
<i>D. simulata</i> Kinsey	* <i>Synergus</i> sp.
<i>D. spongiosa</i> (Karsch)	<i>Synergus atripennis</i> Ashmead

DISHOLCASPIS Dalla Torre and Kieffer (cont.)

<i>D. truckeeensis</i> (Ashm.)	<i>Euceroptres montanus</i> Weld <i>Ceroptres montensis</i> Weld <i>Synergus magnificus</i> Weld
<i>D. washingtonensis</i> Beutenmueller	* <i>Synergus distinctus</i> M. & E.
<i>D. favus</i> Beut.	<i>Saphonecrus favanus</i> Weld
<i>D. gallaeramulorum</i> (Fonsc.)	<i>Synergus gallaepomiformis</i> (Fonsc.)
<i>D. kuriphilus</i> Yasumatsu	<i>Synergus</i> sp.
<i>D. minusculus</i> Weld	<i>Synergus agrifoliae</i> Ashmead
<i>D. nervosus</i> (Giraud)	<i>Synergus thaumacerus</i> Dalman
<i>D. rugosus</i> Kieffer	<i>Synergus gallaepomiformis</i> (Fonsc.)

HETEROECUS Kinsey

<i>H. pacificus</i> (Ashmead)	<i>Synergus variegatus</i> M. & E.
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LIODORA Foerster

<i>Liodora</i> sp.	<i>Synergus pacificus</i> M. & E.
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NEUROTERUS Hartig.

<i>N. albipes</i> Schenck	<i>Synergus albipes</i> Hartig <i>Synergus apicalis</i> Hartig <i>Synergus nervosus</i> Hartig
<i>N. aprillinus</i> (Giraud)	<i>Ceroptres arator</i> Hartig
<i>N. cupulae</i> Kinsey	* <i>Synergus</i> sp.
<i>N. englemanni</i> Kinsey	* <i>Synergus</i> sp.
<i>N. fragilis</i> Bassett	* <i>Synergus</i> sp.
<i>N. gillettei</i> Bassett	* <i>Ceroptres</i> sp.
<i>N. glandiformis</i> (Giraud)	<i>Ceroptres cerni</i> Mayr <i>Synergus thaumacerus</i> Dalman
<i>N. haasi</i> Kieffer	<i>Saphonecrus excisus</i> (Kieffer)
<i>N. lanuginosus</i> Giraud	<i>Saphonecrus halmi</i> (Mayr) <i>Synergus gallaeopomiformis</i> (Fonsc.) <i>Synergus variabilis</i> Mayr
<i>N. macropterus</i> (Hartig)	<i>Ceroptres cerni</i> Mayr <i>Synergus flavipes</i> Hartig <i>Synergus rotundiventris</i> Mayr <i>Synergus variabilis</i> Mayr
<i>N. niger</i> Gillette	* <i>Synergus</i> sp.
<i>N. numismalis</i> (Fourcroy)	<i>Synergus albipes</i> Hartig <i>Synergus nervosus</i> Hartig <i>Synergus pallicornis</i> Hartig
<i>N. quercicola</i> Dalla Torre	* <i>Ceroptres</i> sp. * <i>Synergus</i> sp.
<i>N. quercusbaccarum</i> (L.)	<i>Ceroptres arator</i> Hartig <i>Ceroptres cerni</i> Mayr <i>Synergus albipes</i> Hartig <i>Synergus gallaeopomiformis</i> (Fonsc.) <i>Synergus nervosus</i> Hartig <i>Synergus pallipes</i> Hartig

NEUROTERUS Hartig (cont.)

<i>N. quercusbaccarum</i> (L.)	<i>Synergus thaumacerus</i> Dalman
<i>N. quercusbatatus</i> (Fitch)	* <i>Ceroptres</i> sp.
<i>N. quercusminutissimus</i> (Ashmead)	<i>Ceroptres minutissimi</i> Ashmead
<i>N. quercusrileyi</i> (Bassett)	* <i>Ceroptres</i> sp.
<i>N. quercusverrucarum</i> (O. S.)	* <i>Ceroptres</i> sp.
<i>N. saliens</i> (Kollar)	<i>Saphonecrus halmi</i> (Mayr) <i>Synergus albipes</i> Hartig
<i>N. saltatorius</i> (Edwards)	* <i>Ceroptres</i> sp. <i>Synergus agrifoliae</i> Ashmead
<i>N. tricolor</i> Hartig	<i>Synergus albipes</i> Hartig <i>Synergus gallaepomiformis</i> (Fonsc.) <i>Synergus nervosus</i> Hartig <i>Synergus thaumacerus</i> Dalman
<i>N. tumba</i> Kinsey	* <i>Synergus</i> sp.
<i>N. umbilicus</i> Bassett	* <i>Ceroptres</i> sp.
<i>N. varians</i> Kinsey	* <i>Synergus</i> sp.
<i>N. vesicula</i> (Bassett)	* <i>Ceroptres</i> sp.
<i>N. washingtonensis</i> Beut.	<i>Ceroptres montensis</i> Weld <i>Synergus pacificus</i> M. & E.

PHILONIX Fitch

<i>P. fulvicollis</i> Fitch	* <i>Ceroptres</i> sp.
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PLAGIOTROCHUS Mayr

<i>P. amenti</i> Tavares	<i>Synergus albipes</i> Hartig
<i>P. burnayi</i> Kieffer	<i>Synergus evanescens</i> Mayr
<i>P. kiefferianus</i> Tavares	<i>Saphonecrus lusitanicus</i> (Tavares)
<i>P. quercusilicis</i> (Fabricius)	<i>Ceroptres cerni</i> Mayr <i>Synergus nervosus</i> Hartig

TRIGONASPIS Hartig

<i>T. megaptera</i> (Panzer)	<i>Synergus albipes</i> Hartig <i>Synergus albofaciatus</i> Dettmer <i>Synergus gallaepomiformis</i> (Fonsc.) <i>Synergus inflatus</i> Dettmer <i>Synergus nervosus</i> Hartig <i>Synergus thaumacerus</i> Dalman <i>Synergus umbraculus</i> (Olivier)
<i>T. mendisi</i> Tavares	<i>Synergus albipes</i> Hartig <i>Synergus umbraculus</i> (Olivier)
<i>T. synaspis</i> (Hartig)	<i>Synergus albipes</i> Hartig <i>Synergus pallicornis</i> Hartig <i>Synergus physoserus</i> Hartig

XANTHOTERAS Ashmead

<i>X. eburneum</i> (Bassett)	<i>Synergus punctatus</i> Gillette
<i>X. quercusforticorne</i> (Walsh)	<i>Ceroptres quercusficus</i> (Fitch) <i>Synergus campanula</i> O. S.

NON CYNIPID HOSTS

<i>Cincticornia pilulae</i> (O. S.) (Diptera: Cecidomyiidae)	<i>Ceroptres inermis</i> (Walsh)
<i>Dryomyia circinans</i> Giraud (Diptera: Cecidomyiidae)	<i>Synergus variabilis</i> Mayr
<i>Tanaostigmoides</i> sp. (Hymenoptera: Pteromalidae)	<i>Mytopsen mimosae</i> Weld

NO KNOWN HOST

Ceroptres japonica Ashmead
Ceroptres melanomerus Hartig
Ceroptres politus Ashmead
Ceroptres quercusobtusilobae (Karsch)
Euceroptres japonicus Ashmead
Mytopsen leuderwaldti Dettmer
Mytopsen mayri Rubsaamen
Mytopsen platensis Diaz
Poncynia ferruginea Kieffer
Rhoophilus loewii Mayr
Saphonecrus areolatus Weld
Saphonecrus diversus Belizen
Saphonecrus serratus Weld
Saphonecrus sinicus Belizen
Synergus atamiensis Ashmead
Synergus bellus M. & E.
Synergus bipunctatus Hartig
Synergus crassicornis Hartig
Synergus dorsalis Provancher
Synergus exaratus Hartig
Synergus gifuensis Ashmead
Synergus hakonensis Ashmead
Synergus japonicus Ashmead
Synergus jezoensis Sakagami
Synergus mizunarae Shinji
Synergus niger Fullaway
Synergus obtusilobae (Karsch)
Synergus semisulcatus Hartig
Synergus testaceus (Hartig)
Synergus xanthocerus Hartig
Synophromorpha kaulbarsi R. & S.
Synophromorpha smilacis Ashmead
Synophrus mexicanus (Gillette)
Synophrus olivieri Kieffer

APPENDIX 1: Superfamily Cynipoidea.

DIAGNOSIS: antennae arising from the middle of the frons, usually filiform, distal antennal segments with rhinaria; forewing venation moderately reduced, with characteristic radial cell, usually without pterostigma; hindwing venation reduced to marginal vein; metasoma laterally compressed, sternites fused into hypopygium, hypopygium frequently with a spine; ovipositor extruding from the end of the metasoma.

KEY TO THE FAMILIES AND SUBFAMILIES OF WORLD CYNIPOIDEA

1. Radial cell 9 times as long as wide; hind basitarsus longer than remaining tarsomeres combined; metasoma knifelike, strongly compressed laterally; large insects, 10-30 mm long. Holarctic and introduced to New Zealand and Tasmania. IBALIIDAE
- 1'. Radial cell 1-6 times as long as wide; hind basitarsus shorter than remaining tarsomeres combined; metasoma not strongly compressed; smaller insects, 1-8 mm. 2
2. Metasomal tergite IV or V largest in lateral view (except in *Xenocynips*, which has a distinct tooth on the underside of the hind femur); moderate sized insects, 4-8 mm. Neotropical, Ethiopian, Oriental, and Nearctic. LIOPTERIDAE ... 3
- 2'. Metasomal tergite I or II largest in lateral view... 5

3. Hind femur with a distinct tooth on underside
3-8 mm. Ethiopian. Obethurellinae
- 3'. Hind femur without tooth. 4
4. Metasoma petiolate, attached to mesosoma high
above base of hind coxae. Neotropical. ... Liopterinae
- 4'. Metasoma not distinctly petiolate, petiole short-
er than wide. Neotropical, Oriental, Nearctic (3
sp.). Mesocynipinae
5. Scutellum with raised "teardrop shaped" plate
head, mesoscutum, and mesopleuron never with rough
sculpture; notauli rarely distinct; minute to
moderate sized insects, 1-8 mm. Worldwide.
..... EUCOILIDAE
- 5'. Scutellum without raised "teardrop shaped" plate;
head, mesoscutum, and mesopleuron often with
rough sculpture. 6
6. Metasomal tergite 1 liguliform; propodeum with
transverse rugulae, somewhat produced posteriorly;
propodeal carinae absent or very weak and weak
median carina present; hind basitarsus usually
with ridges on ental surface; scutellum frequently
with either a spine projecting posteriorly or with
posterior foveae; forewing venation often weakly
pigmented. Worldwide. FIGITIDAE ... Aspiceratinae

- 6'. Metasomal tergite 1 not liguliform; propodeum without transverse rugulae; median propodeal carina usually absent; hind basitarsus not ridged; scutellar spine, if present, projecting posterodorsally; venation of forewing usually strongly pigmented. 7
7. Petiole at least 1.5 times as long as wide in lateral view; head distinctly wider than mesosoma; body wedgeshaped in dorsal view. Worldwide.
 FIGITIDAE ... Anacharitinae
- 7'. Petiole shorter than wide or not apparent; head as wide as or narrower than mesosoma; body not wedgeshaped in dorsal view. 8
8. Pronotum with well developed lateral carinae; mesoscutum smooth except for notauli, never with transverse rugulae, frequently longer than wide, with only a few stout hairs; scutellum sometimes with posterior spine or carina; female hypopygium without spine. Worldwide. FIGITIDAE ... Figitinae
- 7 8'. Pronotal plate weakly developed (except in *Eucenoptres* and *Myrtopsen*, which have the tarsal claws weakly toothed and a weak hypopygial spine); mesoscutum wider than long, smooth or sculptured; mesoscutal pubescence, if present, finer and denser; scutellum never with posterior spine; hypopygium (females) sometimes with spine. 9

9. Head shining smooth, posterior margin of gena without carina; body usually without sculpture (except *Lytoxysta*, which has a distinct genal brush of strong dense pubescence); females without hypopygial spine; males frequently with A4 bent; tibial spur formula often 1-1-1; minute to small insects, 1-3 mm. Worldwide. CHARIPIDAE
- 9'. Head with rough sculpturing, posterior margin of gena often with carina, without genal brush; body with sculpture, although some areas may be smooth; females with hypopygial spine; males never with A4 bent; tibial spur formula 1-2-2; small to moderate insects, 2-8 mm. Worldwide. CYNIPIDAE ...10
10. Female antenna with 20 antennomeres; head oblong in dorsal view, distinctly narrower than mesosoma; clypeus projecting forward. Palearctic (Nepal). Himalocynipinae
- 10'. Female antenna with at most 19 antennomeres; head oval in dorsal view, at most only slightly narrower than mesosoma; clypeus not projecting anteriorly. 11
11. Forewing with pterostigma at base of radial cell; female antenna with 15 antennomeres (male unknown). Australian. Austrocynipinae
- 11'. Forewing without pterostigma at base of radial cell; female antennae with at 12-20 antennomeres. ...12

12. Forewing of normal size; radial cell very reduced, veins very thick and heavily pigmented, giving appearance of pterostigma. Ethiopian, Palearctic (North Africa). Pychostigmatinae
- 12'. Forewing of normal size, brachypterous, or apterous; radial cell normal or only slightly reduced, veins not thickened or heavily pigmented, not with the appearance of a pterostigma. World-wide. Cynipinae

CLASSIFICATION OF THE CYNIPOIDEA

The classification of the Cynipoidea followed here differs from the classification used in all other parts of this study. Previously, I have restricted the Cynipidae to the phytophagous members of the Cynipoidea. This is the normal usage of North American workers (eg. Burks 1979). European workers generally use a wider concept of the Cynipidae, relegating the phytophagous forms to the subfamily Cynipinae. This approach has been used recently by Riek (1971) and Quinlan (1979) and gives a better approximation of the relationships between the higher taxa within the Cynipoidea. The classification of Quinlan (1979) is followed here but with reservations.

IBALIIDAE. The Ibalidae are distinguished from all other Cynipoidea by the extremely long radial cell, the basimetatarsus longer than the remaining metatarsomeres combined, and the metasoma being strongly compressed. These are the largest Cynipoidea known, with some members reaching 30 mm in length. This family contains a single genus, *Ibalia* Latreille, which are parasitic on Siricidae and Syntexidae (Hymenoptera: Symphyta) boring into trees. The family is restricted to the Holarctic region, but has been introduced to New Zealand. Kerrich (1973) revised the species associated with conifers, Maa (1949) revised the eastern Palearctic species, and Weld (1952b) reviewed the Nearctic fauna. There are about 15 described species world-

wide and 7 species in North America.

LIOPTERIDAE. Members of the Liopteridae are distinguished from other Cynipoidea (except the Ibalidae) by the largest metasomal tergite (dorsal view) being T4, T5, or T6. The Liopteridae are divided into three subfamilies: the Liopterinae, the Oberthurellinae, and the Mesocynipinae. The Oberthurellinae are distinguished by the presence of a strong spine on the underside of the metafemur; the Liopterinae have the metasomal petiole distinctly elongate, whereas the Mesocynipinae have the petiole shorter than wide. The biology of the Liopteridae is unknown but circumstantial evidence indicates that some are parasitic on wood boring insects (Coleoptera: Buprestidae; Hymenoptera: Siricidae) (Weid 1952b; Maa 1949). Since Dalla Torre and Kieffer's monograph on the Cynipoidea (1910), there have been several studies of the Liopteridae. Heidecke and Kerrich (1940) revised the Liopterinae and proposed the Mesocynipinae as a new subfamily. Weid (1922) described the Liopteridae of the Oriental region, primarily from the Philippines. Weid (1952b) gives keys to genera and species of the world Mesocynipinae. Recently, Quinlan (1979) revised the Oberthurellinae from the Ethiopian region. The family is primarily tropical in distribution with only three species in two genera (Mesocynipinae) being found north of Mexico. There are 13 genera and 71 described species worldwide.

EUCOILIDAE. The Eucoilidae are the largest family in the Cynipoidea and are parasites of the puparia of Diptera. Members of this family are easily recognised by the characteristic "teardrop shaped" raised plate on the scutellum ("cup" of the older literature). Many species are associated with dung or rotting fruit but the family is not restricted to these habitats. There have been no revisions of the Eucoilidae since Dalla Torre and Kieffer (1910), although Nordlander (1976, 1982) has begun to study this family. The family is found throughout the world and contains about 70 genera and 2000 described species. There are 15 genera and 78 species in North America.

FIGITIDAE. The Figitidae are characterized by having T3 the largest tergite, usually a modification of the scutellum (eg. spines, additional foveae or carinae), female hypopygium without a spine, and the sculpturing of the head and mesosoma is usually strong. The family is traditionally divided into three subfamilies: the Anacharitinae, Aspiceratinae, and Figitinae. The relationships between the subfamilies are unclear and there are several genera that appear to be intermediates between the subfamilies. Both the Aspiceratinae and the Anacharitinae are monophyletic groups based on a number of synapomorphies; however, both the Figitinae and the Figitidae appear to be based on symplesiomorphy and do not appear to be monophyletic. The family is distributed throughout the world and has 30

genera and approximately 250 described species. There are 18 genera and 58 species in North America.

Anacharitinae. The Anacharitinae are characterised by having the metasomal petiole longer than wide, the head distinctly wider than the mesosoma, and the genae with a strong posteroventral carina. The mesoscutellar spine, when present, is directed posterodorsally. Members of this subfamily are parasites of Neuroptera (Hemerobiidae, Chrysopidae).

Aspiceratinae. Members of this subfamily can be recognised by having T2 liguliform and the ental surface of the metatibia having carinae. The metasomal petiole is shorter than wide and the mesoscutal spine, when present, is directed posteriorly. Known host records for the Aspiceratinae indicate that they are parasites of Diptera puparia (Cyclorhapha) and appear to be associated with dung. Quinlan (1979) has revised the Aspiceratinae of the Ethiopian region. Nordlander (1982) has suggested that the Aspiceratinae should be elevated to the family level; however, until the Figitidae are revised, it seems better to maintain its present status.

Figitinae. The Figitinae are distinguished by having the metasomal petiole shorter than wide, T2 not liguliform, ental surface of the metatibia not carinate, gena usually with posteroventral carina, and mesoscutal spine (when present) directed posterodorsally. This subfamily appears to

be a rather heterogeneous assemblage and is best defined as those Figitidae that do not belong to either the Aspiceratinae or the Anacharitinae.

CHARIPIDAE. The Charipidae (= Alloxystidae of some authors) are hyperparasites of Homoptera and Hemiptera; the primary host is usually a chalcidoid or braconid parasite. This family is apparently defined by host association and negative morphological characters (i.e. the lack of sculpture); however, there appear to be several exceptions. For example, species of *Lytoxysta* have a very distinct sculpturing of the mesosoma and appear to be intermediate to the Figitinae and the other Charipidae. Individuals are usually very small (1-3 mm) and thus can be difficult to determine. Hellen (1963) has studied the European fauna and Andrews (1978) has revised the Nearctic fauna. The family is distributed throughout the world and contains about 7 genera and about 200 species. There are 5 genera and 29 species in North America.

CYNIPIDAE. The Cynipidae are phytophagous and either induce galls on various plants or live in the galls of other gall-inducing insects. There is some disagreement about the limits of this family. Most European authors (eg. Quinlan 1979) have a broad concept of the Cynipidae and recognise 4 subfamilies; these are the Himalocynipinae, Austrocynipinae, Pycnostigmatinae, and the Cynipinae. These four subfamilies apparently form a monophyletic taxon. Many North

American authors have a narrower concept of the Cynipidae, limiting the family to the gall inducers and inquillines. This is probably due to the absence of other closely related taxa from the Nearctic region. If the Cynipidae is restricted to the gall inducers and inquillines, then the other subfamilies should be elevated to family rank; however, until the higher classification is resolved, to do so here would be strictly an arbitrary decision and is therefore unwarranted.

Himalocynipinae. Yoshimoto (1970) proposed the subfamily Himalocynipinae in the Figitidae for *Himalocynips vigilis* Yoshimoto from Nepal. Although the biology of *H. vigilis* is unknown, it appears to be morphologically intermediate between the Figitinae and the Cynipinae; it is easily distinguished from both by the forward projecting clypeus and by the antenna having 20 antennomeres. The presence of a distinct hypopygial spine appears to show a closer relationship between *Himalocynips* and other Cynipidae than to the Figitidae; hence, the Himalocynipinae are hereby transferrad to the Cynipidae.

Austrocynipinae. Riek (1971) proposed the subfamily Austrocynipinae in the Cynipidae for *Austrocynips mirabilis* Riek. *Austrocynips* is intermediate between the Mesocynipinae and the Cynipinae and is therefore placed in its own subfamily. It is easily distinguished by the pterostigma in the radial cell of the forewing; the presence of a hypopyg-

ial spine relates *Austrocynips* to the Cynipidae (Riek 1971). It has been reared from seeds of *Auracacia* in Australia.

Pycnostigmatinae. The *Pycnostigmatinae* contains two species, each in its own monotypic genus. The subfamily is restricted to Africa and is distinguished by the distinctive radial cell. The biology of these genera is unknown but it is presumed that these species are inquillines in the galls of other insects. However, the expanded and sulcate petiole and the metasoma having T2 and T3 completely fused suggests that these genera are derived from *Synergus* Hartig (Cynipinae).

Cynipinae. Many female Cynipinae the hypopygial spine extremely well developed; however, males are difficult to determine and it is often impossible to place males to genus. The Cynipidae are restricted to the Holarctic region except for 1 species in South Africa (*Rhoophilus loewi* Kieffer), 8 species in South America (*Myrtopsen* spp., *Plagetrochus suberi* Weld), and 2 species in Australia (*Thra-sorus* spp.). The majority of Cynipidae induce galls on oaks (*Quercus* spp.) or roses (*Rosa* spp.); these species can be recognised by the extremely narrow pronotum (median dorsal length less than one seventh lateral height). Weld (1952b) gives keys to genera of gall inducers and inquillines and gives illustrated lists of the galls of the United States (1957, 1959, 1960). Kinsey (1930, 1936) described and gave keys for the oak gall inducers of North America; however,

these keys are difficult to use and the status of many of Kinsey's "varieties" is unclear. Eady and Quinlan (1963) give illustrated keys to the galls and gall inducers of Britain; Buhr (1965) gives keys to the European fauna. Many oak gall inducers exhibit an alternation of sexual and agamic generations. There are approximately 60 genera and 1200 species throughout the world with 46 genera and 800 species in North America.

Table 6. Explanation of characters used in Table 7. a = hypothesized plesiomorphic character state. b - d = apomorphic character states.

NO	CHARACTER	STATE
1	HEAD, SHAPE:	a = Ovate. b = Expanded below eyes.
2	HEAD, STRIAE:	a = Absent. b = Present laterally. c = Entire.
3	HEAD, PROTUB:	a = Absent. b = Present.
4	HEAD, RIDGES:	a = Absent. b = Present.
5	HEAD, FIELD:	a = Absent. b = Present.
6	MAX PALPS:	N = Number of Palpomeres.
7	LAB PALPS:	N = Number of Palpomeres.
8	CLYPEUS, SHAPE:	a = Trapezoidal. b = Wide Shield. c = Narrow.
9	GENAL MARGIN:	a = Present. b = Absent.
10	ANTENNOMERES, ♀:	Number of antennomeres greater than 10.
11	ANTENNOMERES, ♂:	Number of antennomeres greater than 10.
12	A3, ♂:	a = Weakly curved. b = Strongly curved and notched.
13	PRONOT, PILOSI:	a = Absent. b = Present.
14	PRONOTAL PLATE:	a = Absent. b = Present. c = Strongly developed.
15	PRONOTUM, L/H:	a = Broad. b = Narrow.
16	MESOSCU, SCULP:	a = Coriaceous/Smooth. b = Transverse rugae.

Table 6 (cont.). Explanation of characters used in Table 7. a = hypothesized plesiomorphic character state. b = apomorphic character states.

NO	CHARACTER	STATE
17	MESOSCU, ANTER:	a = Arcuate. b = Produced.
18	NOTAULI:	a = Normal. b = Widened posteriorly.
19	MEDIAN GROOVE:	a = Absent. b = Present.
20	ANTERIOR LINES:	a = Absent. b = Impressed. c = Raised.
21	LATERAL LINES:	a = Absent. b = Impressed. c = Raised.
22	MESOSCU. CAR:	a = Absent. b = Present.
23	FOVEAE:	a = Normal, shining. b = Narrowed, opaque.
24	SEPTUM:	a = Strong. b = Weak, absent.
25	MESOPLEURON:	a = Smooth. b = Aciculate. c = Striate.
26	MESOPLE GROOVE:	a = Absent. b = Present.
27	METAPLEURON:	a = Curved. b = Straight.
28	PROPOD CARINAE:	a = Straight. b = Curved.
29	PROPOD PILOSIT:	a = Absent. b = Present.
30	SUPRACOX CARIN:	a = Absent. b = Present.

Table 6 (cont.). Explanation of characters used in Table 7. a = hypothesized plesiomorphic character state. b - d = apomorphic character states.

<u>NO</u>	<u>CHARACTER</u>	<u>STATE</u>
31	PETIOLE:	a = Striate. b = Smooth.
32	S2, L:	a = Short, crescent shaped. b = Expanded, tubular. c = Petiolate.
33	S2, SCULPT:	a = Smooth. b = Sulcate.
34	T2, T3, ♀:	a = Separate. b = Fused.
35	T2, T3, ♂:	a = Separate. b = Fused.
36	T2, PILOSITY:	a = Absent. b = Present.
37	T3, POST MAR, ♀:	a = Not excised. b = Excised.
38	T3, POST MAR, ♂:	a = Not excised. b = Excised.
39	T3, PUNCTATION:	a = Absent. b = Present.
40	RADIAL CELL:	a = Closed. b = Open.
41	RAD. CELL L/W:	Ratio of length to width.
42	RADIUS:	a = Almost straight. b = Arcuate.
43	RS1:	a = Almost straight. b = Arcuate.
44	AREOLET:	a = Equilateral. b = Elongate. c = Absent.
45	HAMULUS:	a = Simple. b = Bifid.

Table 6 (cont.). Explanation of characters used in Table 7. a = hypothesized plesiomorphic character state. b - d = apomorphic character states.

<u>NO</u>	<u>CHARACTER</u>	<u>STATE</u>
46	TARSAL CLAW:	a = Absent. b = Present.
47	HYPOPYGIUM:	a = Spine absent. b = Spine present.
48	DISTRIBUTION	W = Worldwide, H = Holarctic. N = Nearctic, P = Palearctic. O = Oriental, E = Ethiopian. Nt = Neotropical, A = Australian
49	BIOLOGY	G = Gall inducer. I = Inquiline. P = Parasite.
50	HOST	D = Diptera, H = Hymenoptera. C = Coleoptera. N = Neuroptera, P = Psylloidea.

Table 7. Distribution of characters in the Cynipoidea.

a = hypothesized plesiomorphic character state.

b - d = apomorphic character states. ? = unknown.

NO.	T B A L I N A E	M E S O C Y N I P I N A E	L I O P T E R I N A E	O B E R T H U R E L L I N A E	F I G I T I N A E	A N A C H A R I T I N A E	A S P I C E R I N A E	E U C O I L I N A E	C H A R I I N A E	H I M A L O C Y N I P I N A E	A U S T R O C Y N I P I N A E	C Y N I P I N A E
1	a	a	a	b	a	b	a	b	b	a	a	a-b
2	c	a	a	b	a	a	a	a	a	a	b	a-c
3	a	a	a	a	a	a	a	a	a	a	a	a-b
4	b	b	b	b	b	a	b	a	a	b	a	a-b
5	b	b	b	b	b	a	b	a	a	b	a	a-b
6	5	?	?	?	4	4	4	4	4	?	?	4-5
7	3	?	?	?	c	c	c	c	c	?	?	3
8	a	a	a	a	a	a	a	b	a	a	b	b-c
9	c	?	?	?	c	a	c	a	a	a	b	b
10	3	3	3	3	3	3	3	3	3	10	5	?
11	4	4-5	4	4	4	4	4	5	3-4	NA	NA	?
12	b	a	a	a	c	a	c	a-c	a-b	NA	NA	b-c
13	a	?	?	?	b	a	b	b	b	?	?	?
14	b	c	c	b	c	b	c	c	a-b	b	b	a-b
15	a	a	a	a	a	a	a	a	a	a	a	a-b
16	c	b	b	b	a-b	a	a-b	a	a	b	b	a-b
17	a	?	?	?	a	a	a	a	b	a	a	a-b
18	a	?	?	?	a-b	b	a-b	a	a	a	c	a-b
19	c	?	?	?	b	b	b	a-b	a	b	a	a-b
20	c	?	?	?	b	c	b	a	a	?	a	a-c
21	b	?	?	?	b	a	c	a	a	?	a	a-b
22	b	?	?	?	?	?	?	?	?	?	?	a-b
23	a	?	?	?	a	b	a	a	c	b	c	a-b
24	a	?	?	?	a	a	b	a	c	b	b	a-c
25	b	?	?	?	c	a	a	a	a	?	b	a-b
26	b	?	?	?	c	a	b	a-b	a	?	a	a-b
27	b	?	?	?	b	a	a	a	a	?	?	a-b
28	a	?	?	?	a	a	a	c	a	?	?	a-b
29	a	?	?	?	b	a	b	b	b	?	?	?
30	a	?	?	?	b	a	b	b	a	?	?	a-b
31	a	?	?	?	b	a	b	b	b	?	?	?

Table 7 (cont.). Distribution of characters in the Cynipoidea. a = hypothesized plesiomorphic character state. b - d = apomorphic character states. ? = unknown.

NO.	IBALINAE	MESOCYNIPINAE	LIPTERINAE	OBERTHURELLINAE	FIGITINAE	ANACHARITINAE	ASPICERINAE	EUCOILINAE	CHARIPINAE	HIMALOCYNIPINAE	AUSTROCYNIPINAE	CYNIPINAE
32	a	b	c	c	a-b	b-c	a	a-c	a	a	a	a-b
33	a	b	b	b	a-b	a-b	b	a-b	a	a	a	a-b
34	a	a	a	a-b	a	a	a	b	a-b	a	a	a-b
35	a	a	a	a-b	a	a	a	b	a	NA	NA	a-b
36	a	a	a	a	a-b	a	a	a-b	b	a	a	a-b
37	a	a	a	a	a	a	a	a	a	a	a	a-b
38	a	a	a	a	a	a	a	a	a	NA	NA	a-b
39	a	a	a	a	b	b	b	a	a	a	a	a-b
40	a	a	a	a	a-b	a-b	b	a-b	a-b	b	a	a-b
41	9	3-4	3-4	5-6	2-3	2-3	2-3	2-4	2-3	3	3	3-6
42	b	a	b	a	a	a	a	a	a	b	b	a-b
43	b	b	a	a	a	a	a	a	a	a	?	a-b
44	b	c	c	c	b-c	c	c	a, c	c	c	c	a-c
45	a	a	a	a	a	a	a	a	a	a	a	a-b
46	a	a	a	a	a	a	a	a	a	a	a	a-b
47	a	a	a	a	a	a	a	a	a	b	b	b
48	H	O	Nt	E	W	W	W	W	W	P	A	H
49	P	P?	P?	P?	P	P	P	P	P	1?	1?	G, I
50	H	?	C?	?	D	D	N	D	H	?	?	NA

Figure 78. Preliminary phylogenetic relationships between "subfamilies" of the Cynipoidea.

APPENDIX II: Species not now included in Periclistus.

Ceroptres globulus (Beutenmueller). NEW COMB.

Rhodites globulus Beutenmueller 1892: 274. ♀, ♂.

TYPE: Lectotype, ♀ (AMNH). Designated here. - Labelled:

"Type" (red letters); *Rhodites globulus*, Types
Beut.; Lectotype, *Rhodites globulus* Beutenmueller
1892, Ritchie and Shorthouse 1984 (red label)."

FEMALE. (Lectotype). Length 2.1 mm. Dark rufo-piceous; T2, anterior half of T3 rufo-piceous; femora dark amber; remainder of legs, antennae, tegulae amber. Head as wide as mesosoma, ovate; gena arcuate below eye; frons finely coriaceous above antennal sockets, moderately coriaceous below antennal sockets, weakly pubescent, with few evident punctures; median protuberance very weak, very poorly defined; clypeus not medially protuberant; radiating striae very weak, reaching inner orbit of eye but not antennal sockets; subantennal fovea very weak; indistinct; interocular space 1.0 of eye height, malar space 0.5 of eye height; vertex not raised; ocellar triangle weakly raised; ocelli surrounded by weak, indistinct crescent shaped depression; LOL = 1.3D, POL = 2.5D, OOL = 1.4D. Antenna 1.31 mm, weakly clavate, with 13 antennomeres; A1 - A13 (mm): 0.10, 0.06, 0.13, 0.12, 0.12, 0.12, 0.11, 0.10, 0.08, 0.08, 0.08, 0.07, 0.14; A13 = 0.93 A11 + A12. Pronotum sparsely pubescent, finely coriaceous, without evident punctures or tubercles; anterolateral margin weakly pilose; posterolateral region

without longitudinal rugulae; posterior part of plate moderately strong, lateral margins convex, reaching posterior margin of pronotum. Mesoscutum weakly arched, anterior margin protruding anteriorly; length 0.84 of width, with few evident setigerous punctures, weakly coriaceous between punctures. Notauli incomplete, not reaching middle of mesoscutum, moderately strong, divergent grooves posteriorly, weak creases anteriorly; grooves separated by 4.0 times width at posterior margin of mesoscutum; posterior margin of mesoscutum strongly notched between grooves. Median line present, strong, reaching about one fourth of length of mesoscutum. Anterior lines short, straight, weakly convergent. Lateral lines very short. Mesoscutellum flattened medially, rounded laterally and posteriorly, rugoreticulate, shagreened between rugae, in same plane as posterior of mesoscutum; lateral bars narrow, short; foveae broad, open posteriorly, posterior gradually merging with rugosity of disc; septum very short, broad, not depressed. Mesopleuron with anteromedial longitudinal aciculation; ventral pubescent area narrow; subalar triangle weakly pubescent, weakly pilose; ventral margin of subalar triangle straight, with narrow punctopubescent area anteriorly; subalar pit narrow. Metapleuron not depressed anteriorly, narrow; supracoxal carina, supracoxal tubercle, subspiracular carina absent; antespiracular area large, moderately deep, shining smooth. Metanotal lateral foveae weakly pubescent, lateral

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Thus, *Rhodites globulus* is resurrected from synonymy and is transferred to *Ceroptres*. A series of other specimens labeled *Rhodites globulus* were found in the Museum of Comparative Zoology; these are not part of the type-series and are all specimens of *Periclistus pirata*.

The host gall for *C. globulus* has not been examined, and it is doubtful whether it will ever be found. From the description, it is apparently very similar to a gall of *Diplolepis nodulosa* (Ashmead) that has been highly modified by *Periclistus pirata* (O. S.) (see discussion of *Periclistus pirata*). The host for this species is very unusual, as all other species of *Ceroptres* have been reared from galls on *Quercus*. *Ceroptres globulus* is not simply an aberrant form of *P. pirata* as no other characters agree between the two species.

Diplolepis semipiceus (Harris). N. COMB.

Cynips semipicea Harris 1841: 400. ♀, ♂, gall.

Aulax semipicea (Harris), Osten Sacken, 1863: 366.

Periclistus semipiceus (Harris), Ashmead 1885: 297.

Rhodites fulgens Gillette 1894: 159, Ashmead 1885: 297.

Lytorhodites fulgens (Gillette), Kieffer 1902: 97.

Rhodites semipiceus (Harris), Beutenmueller 1908: 9.

Harris (1841) described *Cynips semipicea* from specimens reared from a root gall on *Rosa* sp. from Massachusetts. Subsequently, Osten Sacken (1863) considered *C.*

semipicea to be an inquiline rather than a gall inducer and suggested that *C. semipicea* belonged to *Aulax*. Ashmead (1885) transferred *C. semipicea* to *Periclistus*.

Beutenmueller (1908) examined the type of *C. semipicea* (MCZ, Cambridge, MA). He recognised that *C. semipicea* was a gall inducer belonging to the genus *Rhodites* and that it was a senior synonym of *R. fulgens* Gillette 1894. Weld (1926) also recognized the synonymy between *C. semipicea* and *R. fulgens*. However, Weld (1951, 1959) later reversed his interpretation of *C. semipicea*; he recognised *Diplolepis fulgens* (Gillette) as the correct name for the gall inducer and *P. semipiceus* (Harris) for an inquiline that was presumed to have been reared from root galls. He gave no reason for his change in opinion.

I have examined the remaining specimen of *Cynips semipicea* Harris, now deposited in the MCZ, and concur with Beutenmueller's interpretation of this species. It belongs to the genus *Diplolepis* Fourcroy, and is apparently conspecific with *D. fulgens* (Gillette). No other type material of *C. semipicea* has been found in the museums likely to contain Harris material (AMNH, PANC, USNM). Thus, *Periclistus semipiceus* must be considered a nomen nudum.

Eumayria obliquus (Provancher) N. COMB.

Periclistus obliquus Provancher 1888: 397. ♀.

TYPE: Lectotype (ULQ), ♀. Selected by Gahan and Rohwer 1917. Labelled 156; 74; *Periclistus obliquus* Prov. (with double red border); Lectotype: *Periclistus obliquus* Provancher, 1594, Gahan and Rohwer '15, Barron '71 (Red); *Eumayria obliquus* (Prov.), Det. A. Ritchie 1983. Examined.

Provancher (1888) described *Periclistus obliquus* from a female sent to him by Coquillett from California; he did not describe the male, the host gall, or any aspects of the biology of the species. Gahan and Rohwer (1917) selected a lectotype, which was examined during the course of a study on *Periclistus* Foerster. The lectotype is not an inquiline (as are the rest of the species of *Periclistus*), but rather a gall inducer belonging to the genus *Eumayria* Ashmead.

Periclistus obliquus is probably a senior synonym of *Eumayria eldoradensis* (Beutenmueller), as it generally agrees with the description of this species. The synonymy will be confirmed when I see authentic specimens of *E. eldoradensis*. Weld (1922) redescribed *Andricus eldoradensis*, described the female and gall, and transferred the species to *Blorhiza*. Weld (1951) later transferred *A. eldoradensis* to *Eumayria*.

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