ABSTRACT

Title of Dissertation: Biosystematics and the evolution of gall formation in hackberry psyllids *Pachypsylla* (Insecta: Homoptera: Psylloidea: Psyllidae)

Man-Miao Yang, Doctor of Philosophy, 1995

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This dissertation is a study of the phylogeny and evolutionary biology of gall formation in psyllids of the subfamily Spondyliaspidinae, with particular focus on North American hackberry gallers in the genus *Pachypsylla*. Species in this genus produce a variety of gall types on the leaves, petioles, buds and twigs of their hosts, four species of *Celtis* subgen. *Euceltis* (Ulmaceae). The homogeneity of adult morphology in *Pachypsylla*, contrasted to the great variation in gall morphology and phenology, has led to much difficulty in delimiting species.

Chapter I investigates species limits as related to gall type and host specificity in *Pachypsylla*. Strong differences in allozymes, morphology and life history confirm that leaf, petiole, bud and twig gallers belong to different species or species groups. Different leaf gall morphs probably also represent different species, as evidenced by significant allozyme frequency differences among sympatric pairs of gall morphs, consistent frequency difference between co-occurring morphs across localities, and discrete differences in gall type between progenies of individual females.

Differences in allozymes, female phenology, adult and nymphal coloration, as well as laboratory rearings and field manipulations, show that side cell individuals within two nipple gall types represent an inquiline sibling species (Chapter II).

Chapter III is an analysis of phylogenetic relationships within *Pachypsylla*, based on allozyme, morphological, life history and chromosome characters. Galler populations attacking the same plant tissue form monophyletic groups. The leaf galler morphs are little diverged, and phylogenetic relationships among them are unclear. Populations of inquilines from two different gall types appear closely related; the inquiline appears to be derived from a gall-forming ancestor. Phylogenetic relationships among gallers on different plant parts are consistent with an evolutionary sequence of gall position from leaf to petiole to bud to twig.

Chapter IV is a morphological study of phylogenetic relationships within Spondyliaspidinae. The tribe Pachypsyllini, including *Pachypsylla* and two related *Celtis* feeders, is monophyletic. The tree favors the hypothesis of Burckhardt over that of White and Hodkinson. The distribution of lerp and gall formation is shown to be non-random within Spondyliaspidinae.

Biosystematics and the evolution of gall formation in hackberry psyllids *Pachypsylla* (Homoptera: Psylloidea: Psyllidae)

by

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DEDICATION

To

Adrienne Venables and Life of Uncertainty

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GENERAL INTRODUCTION AND OBJECTIVES

The biology of gall forming insects represents one of the most conspicuous and complicated animal-plant interactions known. Galls have been utilized extensively in medicine, industry, and food for over a thousand years in ancient countries such as India and China. The first scientific report on insect-induced galls was published in the seventeenth century by Malpighi in Italy (Mani, 1992), but most subsequent reports were based on casual observation. In recent decades, however, serious and intensive studies have been undertaken on numerous aspects of galling, including gall morphology and development, physiology and biochemistry of gall tissues, life history, behavior, host specificity and nutritional physiology of gall makers, and also trophic relationships of the complex assemblages of organisms associated with galls (Mani, 1992). Contemporary studies report gall making from seven insect orders with their biology proving remarkably diverse. However, there is still little understanding of the evolutionary origin, adaptive significance, and ecological and evolutionary consequences of gall formation.

This dissertation is a study of the phylogeny and evolutionary biology of gall formation in psyllids of the subfamily Spondyliaspidinae, with particular focus on North American hackberry gallers in the genus *Pachypsylla*.

The Psylloidea (Insecta: Homoptera: Sternorrhyncha) comprises about 2000 species in the world (Hodkinson, 1984). Psyllids feed on a wide range of dicots,

with a few species on monocots (*Juncus*, *Carex* and the palm *Pritchardia*) and conifers (*Pinus*). They are usually narrowly host specific, and species that initially appear to feed on more than one plant family are likely to prove to represent complexes of host specific sibling species (Hodkinson, 1986; Klimaszewski, 1964; Yang et. al, 1986).

Psyllids are sucking insects, feeding primarily on the soluble contents of phloem tissue, though some species attack mesophyll tissues (Woodburn and Lewis, 1973; Hodkinson, 1973, 1984; White, 1970). In Roskam's view (1992), feeding on plant sap offers homopterans extensive opportunities for manipulating host plants, accounting for the repeated evolution of gall formers in this group.

Gall-forming psyllids are broadly distributed across plant taxa and geographical regions. There are at least 350 gall-inducing species (Mani, 1964; Hodkinson, 1984; Dreger-Jauffret and Shorthouse, 1992), constituting more than 15% of all psyllid species. Psyllid gall forms range from simple distortion of plants, such as leaf curling and leaf pit galls, to a highly complex structure, such as the sealed gall of *Schedotrioza* or that of *Trioza magonoliae*, which develops a dehiscent mechanism when mature (Ashmead, 1881; Crawford, 1914; Morgan, 1984). Psyllid galls usually show a high degree of site specificity on their host plant.

The complexity and specificity of ecological relationships in galling psyllids are well illustrated by the North American genus *Pachypsylla*, commonly known as hackberry psyllids. Species in this genus produce a variety of gall types on the

leaves, petioles, buds and twigs of their hosts (Fig.1-1), four species of *Celtis* subgen. *Euceltis* (Ulmaceae), whose geographic distributions are partially overlapping (Fig. 1-2). The homogeneity of adult morphology in *Pachypsylla*, contrasted to the great variation in gall morphology and phenology, has led to much difficulty in delimiting species. Over two dozen specific entities have been named, but the status of most of these is entirely unclear.

Goals

The first goal of this project is to combine electrophoretic, morphological and life history data to determine species limits and phylogenetic relationships in *Pachypsylla*, as a basis for understanding speciation and the evolution of host use and gall formation in this group. The second objective is an analysis of phylogenetic relationships in the subfamily Spondyliaspidinae, with particular focus on the monophyly and phylogenetic position of *Pachypsylla*. The third objective is a comparative analysis of galling and related habits in the subfamily, asking whether several evolutionary patterns suggested by *Pachypsylla* and allied genera reflect broader trends. The literature on spondyliaspidine life history is synthesized, and the distribution of galling and related habits mapped on the morphological phylogeny.

Significance

Over the long term, these and my intended subsequent studies will bear on

several general questions about the nature of evolution in gall formers. The first concerns the role of ecological specialization in speciation. Perhaps more than any other phytophagous insect, gallers meet the broad definition of "parasites" advanced by Price (1980). There are several reasons to suppose that ecologically highly specialized organisms, exemplified by parasites, should have unusually high rates of diversification (Price, 1980; Futuyma and Moreno, 1988). Parasites, including galling psyllids, are typically modified and intimately dependent for survival on only one or a few types of hosts or even parts thereof, which often constitute both food and habitat for the much smaller parasite. They should thus be highly subject to diversifying selection arising from variation within and among host species. Reproductive isolation could result from such selection either directly, *e.g.* through adaptive divergence in phenology (Wood, 1980; Wood and Guttman, 1982; Wood et. al. 1990; Bush, 1969; Prokopy et. al. 1988), or indirectly, through pleiotropy (Maynard Smith, 1966; Ringo, 1977; Futuyma, 1986). Ecological specialization could also promote diversification by reducing competition between incipient species; this is the gist of Mayr's assertion (1976) that "extreme specialization is characteristic in insects and explains their prodigious rate of speciation."

A necessary first step in assessing the role of host adaptation in the speciation of galling psyllids is documentation of the degree and kinds of differences in host use between closely related species. Do nearest relatives differ most prominently in host species, in plant part attacked, or in phenology with

respect to that of the host; or do they instead show great overlap, suggesting that niche specificity is not crucial to speciation? This study of species limits in *Pachypsylla* is one of the first to explicitly address this question for galling insects.

The "specialization-diversification" hypothesis above also makes two broader predictions, which I hope to address in a long-term phylogenetic analysis of psyllids as a whole, for which this project is a first step. First, gall-forming species should show greater specialization in host taxon use than related non-gallers. Second, clades of gallers should be consistently more diverse than closely-related non-galling clades of the same age, *i.e.* their sister groups.

In strong contrast to the "specialization-diversification" hypothesis as applied to "parasites" in the broad sense, an older view holds that ecological specialization particularly as exhibited by parasites is a "dead end" sharply limiting the potential for subsequent evolutionary change or diversification (Futuyma and Moreno, 1988; Moran, 1988). On a broad scale, this hypothesis predicts that evolutionary reversion to free living from galling should be rare, gall formers may shift among host taxa less often than related free-living forms, and gall formers should be <u>less</u> diverse than their non-galling sister groups.

If galling imposes strong constraints on niche shifts, we might also expect that evolutionary transitions to different types of galling habit would occur in small steps (Janson, 1992). This should be reflected in phylogenetic sequences predictable from the probable degree of genetic divergence between habits. For example, it could be predicted that in *Pachypsylla*, leaf blade galling should

represent the ancestral gall position, as leaf feeding is typical of psyllids as a whole; attack of the petiole, bud and twig may represent successively more different and evolutionarily more recent habits. A similar sequence was postulated for leaf, bud and twig gallers in the sawfly subfamily Nematinae (Smith, 1970; Price, 1988, 1992).

On a broader scale, it has been hypothesized that the origin of true gall formation itself may occur in a predictable sequence from other forms of concealed feeding. Thus, construction of a lerp (a cover constructed from hardened honeydew and probably mixed with wax; see Chapter IV) and of partial galls by related species in related genera have been suggested by Hodkinson (1984) as precursors to the enclosed galls formed by *Pachypsylla*.

My phylogenetic analyses test these postulates for *Pachypsylla* and relatives. The comparative study across Spondyliaspidinae and related genera permit a preliminary statistical testing for the generality of such trends, as all of these habits have probably arisen multiple times.

This dissertation is divided into four chapters, each will be a separate publication. The first chapter treats the analyses of species limits within *Pachypsylla*. The second chapter examines the occurrence of multiple individuals within leaf galls, and provides the first demonstration of a gall inquline in psyllids, and discusses the evolution of inquilinism in *Pachypsylla*. The third chapter is a phylogenetic analyses of relationships and the evolution of gall types within

Pachypsylla and the two other genera in Pachypsyllini, based on allozyme and morphological data. The fourth chapter examines phylogeny in the subfamily Spondyliaspidinae, test hypotheses of previous authors including White and Hodkinson (1985), then uses the phylogeny estimate to examine the evolution of galling and lerp formation.

Chapter I.

Species limits as related to gall form and host specificity in hackberry psyllids, *Pachypsylla*

INTRODUCTION

Pachypsylla is one of the most conspicuous gall formers in North America, producing a variety of gall types on the leaves, petioles, buds and twigs of its hosts, *Celtis* subgen. *Euceltis* (Ulmaceae) (Fig. 1-1). The gall types are differentially distributed across four species of *Celtis* whose geographic distributions are partially overlapping (Fig. 1-2). Within the gall makers in the same position in the tree, adult morphology is quite homogeneous but there is great variation in gall morphology, especially among the leaf gall makers. This has led to widely differing views on the number of species in *Pachypsylla*.

This study tests several hypotheses on species limits of *Pachypsylla* as related to galling position, gall shape variation, and host specificity, as a pre-requisite for understanding speciation in this group.

PACHYPSYLLA BACKGROUND

The first described species of what is now considered to be *Pachypsylla* was the petiole gall maker, *Psylla venusta* Osten Sacken. In a short paragraph, Osten Sacken (1861) delineated the shape and seasonal change in texture of petiole galls and mentioned the large body size and dark maculated wings of the adults. Although he treated the insect as *Psylla venusta*, he pointed out that peculiarities of venation and the form of the metasternal spur indicated that it should be placed in a new genus. Riley first described the genus in 1883 and gave a short

description of the gall and nymph. He provided a more extensive description two years later (Riley, 1885) for the genus and three species, *P. venusta*, *P. celtidis-mamma* and *P.* (*Blastophysa*) *celtidis-gemma*.

Twenty-four names (Table 1-1) have been used for species of *Pachypsylla*, based on gall structure, host differences, and adult morphology. The status of many of these entities is uncertain. Of the two recent treatments, Tuthill (1943), who followed Crawford's system (1914), recognized 7 species, while Riemann (1961) in his unpublished dissertation recognized 12 (Table 1-1).

Members of *Pachypsylla* can be divided into four groups based on nymphal and adult morphology and on the position of the galls on the hackberry host. The groups are the petiole gall maker, *Pachypsylla venusta*, leaf-blade gall makers (here after termed simply leaf gall makers), *Pachypsylla* spp., the bud gall maker, *Pachypsylla celtidisgemma*, *P. pallida* & *P. dubia*, and the twig gall maker, *P. celtidisinteneris*.

It is generally accepted that there is only one species of petiole gall maker. Riley (1883) synonymized *P. celtidisgrandis*, which he had described as a new species in his earlier publication (Riley, 1876), with *P. venusta*, and Crawford (1914) synonymized *P. tridentata* (Patch, 1912) with *P. venusta*; their actions left only one eligible name for the petiole gall maker.

Bud and twig gall makers are similar in morphology. Several species of bud and twig gall makers have been named, but these are mostly based on little information. Tuthill (1943) recognized four of these, namely *P. celtidisgemma*, *P.*

celtidisinteneris, *P. dubia* and *P. pallida*. The first two species, *P. celtidisgemma* and *P. celtidisinteneris*, are bud and twig gall makers, respectively. The latter two species were described by Patch (1912) based on specimens in the Cornell collection. They are similar morphologically to the bud gall maker *P. celtidisgemma*, except in forewing pattern. *P. celtidisgemma* has uniformly immaculate wings, whereas the wings of *P. dubia* are densely mottled and those of *P. pallida* are shaded, with a pale streak extending transversely across the forewing. Patch associated only the specimens of *P. dubia* with a *Celtis* gall, while no gall data were indicated for *P. pallida*. Tuthill (1943) identified specimens accompanied by galls from several localities in Arizona and New Mexico as *P. pallida*. These are very densely pubescent bud galls. The subgenus *Blastophysa* was erected by Riley (1885) for *P. celtidisgemma* but was not accepted by most later workers.

The taxonomic situation is most confusing within the leaf gall making complex. At least twelve names have been assigned to the leaf gall makers. Riley looked at gall variations and named many new species based more on the gall rather than on the insect itself in his series of publications (1876-1890) on hackberry galls. He provided a key to three species of *Pachypsylla* based mainly on adult morphology, but gave a key and description to the galls for 9 species and a variety, including 6 new species (Riley, 1890). Mally (1894) studied the biology of hackberry psyllids at Ames, Iowa. Unlike Riley, Mally individually separated galls of variant nipple shapes in pill boxes and reared the adults. Because there

was great variation in adult characters but no constant association of these variants with gall shape and size, he concluded that they were all part of a single variable species. A year later, however, Mally (1895) listed several names that Riley described, such as *P. celtidis-cucurbita*, and *P. celtidis-pubescens* which form different nipple-shaped galls. It is not clear to what extent Mally considered gall variation to be species specific.

Crawford (1914) adopted Mally's skepticism about Riley's species and considered all leaf gallers except the blister gall maker to represent *P. celtidismamma*. From then on, many authors looked at gall shape and/or adult morphology and named new species or synonymized old species (*e.g.* Caldwell, 1938; Tuthill, 1943). Tuthill (1943) in his revision of North American psyllids separated the leaf galling species by body size; he recognized two species, the blister gall maker, *P. celtidisvesicula* (2.5mm or less), and the nipple gall maker, *P. celtidismamma* (3 to 4 mm).

Riemann (1961) reported that there is no variation in chromosome number among leaf gall makers including *P. celtidisasterisca*, *P. celtidispubescens*, *P. celtidismamma*, *P. celtidisvesicula* and five undetermined species, although there is variation among gallers on different plant tissues. Various species of *Pachypsylla* leaf gall makers and the twig galler, *P. celtidisinteneris*, had the same chromosome numbers (2N= 25 ♂ and 26 ♀) as did their closest North American relative, *Tetragonocephala flava*. Both the petiole galler, *P. venusta* (2N= 23 ♂, 24 ♀), and the bud galler, *P. celtidisgemma* (2N= 22 ♂, 22 ♀), had smaller

chromosome numbers. All of these were reported to have an XO sex determination system except *P. celtidisgemma* which was described as having XY.

Riemann's findings, however, did not entirely agree with those of Walton (1960). Four species of *Pachypsylla* from New York were studied by Walton, including three leaf gall makers and a bud galler. Unlike Riemann, Walton found variation between leaf gallers; both *P. celtidismamma* and *P. celtidisvesicula* were reported to have a 2N chromosomal number of 27 in males and 28 in females while *P. celtidiscucurbita* had 2N= 25♂, 26♀. Like Riemann, Walton found fewer chromosomes in the bud gall maker (2N= 21♂, 22♀) than leaf gallers, but he reported a different male chromosome number. Chromosome number variation in *Pachypsylla* remains unclear.

Gallers on different host tissues also differ in which stage overwinters. The leaf gall makers emerge from the gall just before leaf drop in the fall and overwinter as adults. Where the leaf gall makers overwinter is uncertain. Mally (1894) found leaf gall makers in the cracks and crevices of hackberry bark in March 1892 while the weather was still cold in Iowa. Some authors (*e.g.* Tuthill, 1943) reported that psyllids were found in large numbers on screens and frequently became a nuisance in the house in autumn. Most workers (*e.g.* Wells, 1920; Tuthill, 1943) have assumed, without real evidence, that these psyllids overwinter in bark crevices or leaf litter.

The petiole, bud and twig gallers overwinter inside the gall on the tree in the last nymphal instar and emerge the following spring. All *Pachypsylla* nymphs

emerge by sawing their way out of the gall using the spiny chitinized tip of the abdomen.

All species of *Pachypsylla* mate and lay eggs in the spring. However, there are phenological differences among gall types. The petiole gall makers emerge from the gall in very early spring (mid-March to early April in Maryland) as soon as the weather turns warm. If petiole galls are brought into a warm room in the winter, nymphs emerge from the gall and molt to adults several hours later. The leaf gall makers come back to the tree in early spring when the buds begin to swell and are present until the leaves are fully extended (from late March/early April to late May in Maryland). They usually mate and lay eggs on the bud scale or underside of the leaf. In late spring (late May to early June in Maryland), when the year's new twigs are formed but still green, the bud and twig gall makers emerge, mate and lay eggs.

Differential times of occurrence were also observed between different types of leaf gall makers in the National Agricultural Library population. Of the two types of leaf galls which co-exist on this tree, even on the same leaf, nipple galls were formed earlier than star galls.

The petiole galls are always polythalamous or multi-chambered, each chamber confining a single nymph. The bud galls are usually polythalamous but sometimes there is only one individual inside a gall whereas a twig gall always harbors only one individual. Both single and multiple-cell galls are found in most leaf galls except blister galls on *C. occidentalis*. The species status of the

individuals within one gall is discussed in Chapter II.

A final uncertainty concerning species limits in the leaf gallers is the status of populations on different host species. Some species of *Pachypsylla* use several hosts and are widely distributed over the range of subgenus *Euceltis* in the United States, *e.g. P. venusta* and *P. celtidisinteneris*. Others are largely restricted to particular species of *Celtis* (Table 1-2). For example, in the northeastern United States, the hairy nipple gall (*P. celtidismamma*) and the blister gall (*P. celtidisvesicula*) are commonly associated with *C. occidentalis*, while the glabrous nipple gall (probably *P. celtidisglobulus*) and the star gall (*P. celtidisasteriscus*) are usually on *C. tenuifolia*.

Riemann (1961) postulated strict host specificity within two of the leaf gall making groups, the nipple gall group and blister gall group. He named two new species (Table 1-2, new species 1 and 2) comprising the blister gall makers feeding on *Celtis laevigata* and *C. reticulata*, respectively, and restricted the name *P. celtidisvesicula* to blister gallers on *C. occidentalis*. Similarly, he restricted *P. celtidismamma* to the *occidentalis* nipple gall maker, applying the name *P. celtidispubescens* to nipple gall makers on *C. reticulata*, and *P.* sp. (probably *P. celtidiscucurbita* var. "?" Riley) to those on *C. laevigata*. Members of the nipple gall group were distinguished by host and gall shape differences as well as slight dissimilarities of male genitalia. The blister gallers were distinguished by host differences and slight differences in the male genitalia, mainly the head/shaft ratio of the terminal segment of the aedeagus.

Riemann attributed some exceptions to host specificity to hybridization among *Celtis* species. Hybridization and introgression among hosts are not rare. The species of *Euceltis* are very similar to each other, and there has been difficulty in defining species limits (Elias, 1970; Wagner, 1974).

HOST PLANT *CELTIS* BACKGROUND

Celtis belongs to the elm family, Ulmaceae. It consists of about 70-80 species, found in both temperate and tropical regions (Rehder, 1949; Preston, 1961; Correll and Johnston, 1970; Krüssmann, 1976).

Celtis has been used in the manufacture of furniture, as an ornamental plant, as a shade tree in Temperate region (Hough, 1936) and as material for making ropes and papers in Asia. The native American Indians used the fruits as a flavoring for meat or finely pounded the berries and mixed them with parched corn (Gilmore, 1919; p.76). The common hackberry, *C. occidentalis*, has many desirable traits as a shade tree, such as an upright crown with lower branches 8 to 10 feet from the ground, and considerable drought hardiness (Albertson and Weaver, 1945). It is receiving attention in the Great Plains because of the disease problems that have developed in several tall-tree species such as elm (Anderson and Tauer, 1993).

Planchon (1873) divided *Celtis* into four subgenera on the basis of floral morphology and geographic distribution. Two of these occur in North America, *i.e. Euceltis* and *Momesia*. *Euceltis* is distributed in temperate regions of the

northern hemisphere and high mountains of the tropics. *Momesia* is found in tropical and subtropical parts of the western hemisphere.

Five species of *Celtis* are found in North America. The desert hackberry, *C. pallida*, is a member of the subgenus *Momesia*. The remaining four species belong to the subgenus *Euceltis*, namely the common hackberry, *Celtis occidentalis*, the dwarf hackberry, *C. tenuifolia*, the sugar hackberry, *C. laevigata*, and the netleaf hackberry, *C. reticulata*. They support as many as 17 or even more types of insect galls, though these pests seldom kill the tree (Elias, 1970; Wells, 1916). Arthropod galls are so common on hackberries that some field botanists use these galls, *e.g.* witches brooms caused by mites and petiole galls of hackberry psyllids, as a way to identify these deciduous trees in the winter (Wagner, 1974). *Pachypsylla* and the other two genera of the tribe Pachypsyllini feed only on species of *Euceltis*. Apart from *Pachypsylla*, the monotypic North American genus *Tetragonocephala* is known from *C. reticulata* and *C. laevigata*, while *Celtisaspis*, found in China, Japan and Korea, has been reported from *Celtis sinensis* and *C. bungeana*, two of the approximately 26 species of subgenus *Euceltis* in Asia (Rehder, 1949).

Of the host plants of *Pachypsylla*, *Celtis occidentalis* has the widest distribution (Fig. 1-2), occurring mainly in mid-western and north-eastern North America. It is commonly found in rich, moist soil along stream banks or on flood plains (Stephens, 1973) usually in semi-shade areas. *Celtis tenuifolia* has a patchy distribution in the eastern region. It prefers limestone regions, growing upon

rocky bluffs, in rocky woods, and in open glades (Stephens, 1973; Wagner, 1974). Some authors consider *C. tenuifolia* to be a subspecies or variety of *C. occidentalis* (*e.g.* Pepoon, 1927), but most recent researchers have recognized it as a true species (*e.g.* Krüssmann, 1976). Wagner (1974) compared the two species in the Great Lakes region and confirmed the species distinctness of *C. tenuifolia*. He reported that in addition to its "normal" range, which is well below the line of maximum Wisconsin glaciation, this species occupies scattered localities in the Great Lakes region. I also found the distribution of this species to be far broader than depicted by Little (1971, 1976, 1977) (Fig. 1-2). Many populations were found in Maryland, Virginia and Delaware, sometimes closely co-occurring with *C. occidentalis* (*e.g.* at Great Falls, Virginia). The sugar hackberry, *Celtis laevigata*, is a southeastern species while *C. reticulata* is a southwestern species. The distributions of the two species overlap in central Texas and Oklahoma.

Species of *Euceltis* are very difficult to distinguish, because there are many varieties and natural hybrids (Rehder, 1949; Preston, 1961; Stephens, 1973; Krüssmann, 1976). Named varieties tend to be intermediate between species. For example, *C. laevigata* var. *taxana* seems to be intermediate between *C. reticulata* and *C. laevigata* (Sargent, 1922). Thus the taxonomy of *Celtis* is in a confused state and needs revision.

QUESTIONS ADDRESSED and SPECIFIC OBJECTIVES

Complete revision of the *Pachypsylla* species is one long-term aim of my

work, but this goal will take many years. My thesis work has focused on several hypotheses about the nature of species differences in this genus. These include contrasts among gallers on different host tissues, on different host species, and with different gall morphologies and phenologies.

The following specific questions are addressed.

1. Do galls on different plant tissues represent different species?

Nymphs dissected from and adults emerging from leaf, bud, petiole, and twig galls were compared by electrophoresis, to check previous conclusions that they are distinct species, and to gauge the power of allozyme data for separating species in *Pachypsylla*.

2. Are different leaf gall types different species?

The following hypotheses are contrasted:

A. The null hypothesis is that all the leaf gall makers, despite making different gall types, are a single species.

B. Under the "two species hypothesis" of Crawford (1913) and Tuthill (1943), only the blister galler (*P. celtidisvesicula*) is distinct from all other gallers (*P. celtidismamma*).

C. Under the "multiple species hypothesis" of Riley (1876- 1890) and Riemann (1961), there are multiple species (up to seven) of leaf gall makers distinguished by gall shape.

Different types of leaf gallers from different hosts across a wide

geographical area were sampled and analyzed morphologically and electrophoretically. Possible differences in life history were examined, and rearing experiments were conducted to test whether the offspring of an individual female all produce the same gall type, as expected if gall shape is genetically determined and species specific, rather than being determined by, for example, leaf developmental stage.

3. Do *Pachypsylla* of similar gall type on different host species represent different species?

The hypothesis of Riemann (1961), who proposed that blister gall makers on different host species are different species, was tested. Sympatric samples of nymphs and/or adults from *Celtis laevigata* and *C. reticulata* were compared using morphological and allozyme analysis.

MATERIAL AND METHODS

Samples:

Extensive collections of adults from sixteen localities across the United States were obtained in the fall of 1991. Galls were collected by myself and lab colleagues in the greater Washington area and by cooperators in Ohio, Arkansas, Louisiana, Texas and Arizona (Table 1-3 and Fig. 1-3). Galls were collected in the fall before the adults emerged. I sorted the galls by shape into different bags, collected emergent adults from the bags, and froze them at -80°C. Seven gall types, including 3 populations of petiole gall makers, 3 populations of bud gall

makers and 32 populations of leaf gall makers were included in this survey. These samples represented all five leaf gall types. Owing to its rarity and the high parasitism rate in the greater Washington area, the twig gall was not included in this survey of adult. Each type of gall on each host in each locality was treated initially as a separate population. Samples of each population were collected from 1-3 trees. Sample sizes for individual populations ranged from two to 33, with most being 8 or more. For pairwise comparison of 5 sympatric leaf gall types at Great Falls Virginia (GFV), three (blister gall, hairy nipple gall and glabrous nipple galls) of the five gall types were taken from the same tree. The other two gall types were collected from two other separate trees. All these trees are *C. occidentalis* and are located within 0.5 km of each other.

Following the discovery that adults emerging from leaf galls with multiple cells may include both the gall former and inquilines (see Chapter II), a second set of samples, of nymphs, was obtained in the fall of 1992. These individuals were collected by dissecting individual galls from multiple branches of one to five trees. Only individuals from mono-cell galls or from the center cell of multiple cell galls were used to represent each gall type. The sample sizes were 14 to 46 individuals for each population for leaf gall makers, and 4 to 13 per population for other gall makers. Twenty-four populations were examined, including three populations of the petiole gall maker, four populations of glabrous bud gall makers, one population of hairy bud gall maker, one population of twig gall maker and 15 populations, including all five types, of the leaf gall makers (Table 1-3, Fig.

1-4).

For pairwise comparisons of sympatric gall types, three populations with multiple gall types were studied. Three gall types, blister gall, disc gall and glabrous nipple gall, were collected from two trees, both bearing all three gall types in the GFV population. These two trees are ten meters from each other in an open area. The two gall types, blister and hairy nipple gall, from Catoctin Mountain (CMt), Maryland, were from four and three trees, respectively, with two of these trees being sampled for both gall types. All the trees are in the Poplar Grove area within 0.5 km of each other. Both glabrous nipple gall and star gall were found on the same tree in the National Agricultural Library (NAL) and Branchville Road, Berwyn (BB) populations in Maryland. Samples of these are based on a single tree from each locality. The NAL and BB populations are about 5 km apart.

For testing Riemann's hypothesis on host specificity, I made a trip to the Southwest, including Riemann's original localities, in the fall of 1992. Riemann (1961) regarded populations of blister gall makers on *Celtis laevigata* and *C. reticulata* in the southwestern U.S. as separate species. My collecting sites included the following Texas localities: Brackenridge field lab of the University of Texas at Austin; Zilker Park, Austin; and Palmetto State Park, Gonzales. In each locality, samples were collected, dissected and frozen from two or three sets of paired trees of *C. laevigata* and *C. reticulata*, located from 0 to 10 meters apart with no intervening barriers.

Electrophoretic methods:

Allozyme electrophoresis was carried out using cellulose acetate gels, following the methods of Hebert and Beaton (1989) and Easteal and Boussy (1987). The Titan III cellulose acetate gel apparatus from Helena Laboratories was used, with gels measuring 94 x 76 mm. This allowed twelve samples to be run side-by-side at the same time.

Prior to sample preparation, body sizes of each individual was measured using electronic caliper. Frozen individual psyllids were homogenized in 5 μl of distilled water in the sample well, using a glass rod cut from microscope slides. Then, another 0 to 2.5 μl of distilled water, depending on the body size, was added to each well. Up to 13 runs, yielding 16 loci, could be obtained from each individual. However, the PEP-2 locus stain was too light to be read accurately, so this locus is not included in the analyses.

Buffer systems follow Richardson *et al.* (1986). Fifteen loci were resolved by an initial survey of 27 enzyme stains across 11 buffers. The optimal buffers and running conditions for each locus, used in data collection, are given in Table 1-4. Gels were soaked prior to loading in the same buffer as for running. They were run in a refrigerator at 180 volts for 35 to 90 minutes (Table 1-4).

Staining was carried out using an agar overlay, following recipes taken from Hebert and Beaton (1989). The agar was washed away after the gel was sufficiently stained. Gels were then soaked in water for at least half an hour and recorded by drawings, photographs or xeroxing. All gels were preserved dry in

transparent pocket sheets and filed for later reference.

Fourteen loci were recorded for the adults. These plus PEP-1, discovered later, were analyzed for nymphs. Three of the loci were monomorphic in *Pachypsylla*, but the other 12 showed differences among gall types.

Electrophoretic data analysis:

With exceptions to be noted, alleles at each locus were originally designated alphabetically from fast to slow in the adult data and (separately) in the nymphal data for leaf gall makers. The codings for adults and nymphs do not correspond exactly, because the adult were analyzed first, and additional rare alleles were found in nymphs. Moreover, some of the alleles originally recognized at five loci (PGM, ME, PEP-1, MDH-1 and LDH) in some gall makers were subsequently found to consist of two distinct alleles. The new alleles were given new codes, out of alphabetical order (see footnote to Table 1-6).

The fit to Hardy-Weinberg equilibrium was analyzed at each variable locus using the Biosys-1 package of Swofford and Selander (1981). Chi-square contingency table analyses, carried out in Systat 5.2, were used for testing the heterogeneity of allele frequencies for all loci among samples. Alleles for which the expected value was less than five in more than 1/5 of the cells were pooled (Sokal and Rohlf, 1981). Multiple pairwise, *a posteriori*, comparisons were carried out, using the adjusted $\alpha' = 1- (1-\alpha)^{1/k}$ (Sokal and Rholf, 1981, p. 728), where k is the number of comparisons. This value was rounded down to the nearest value

table in Rohlf and Sokal (1969), making the test more conservative.

Life history traits:

The life histories of two leaf gall makers, the glabrous nipple gall and the star gall, in the NAL population were observed closely starting in 1990. I visited the NAL tree every two to four weeks from March to November, 1991, in addition to occassional observations made at various localities between 1990 and 1994. Collected galls were dissected and preserved in alcohol or by freezing. The developmental stages of the insects were recorded for each gall type.

Rearing experiments:

Individual wild-caught females were caged on hackberry seedlings in the lab to determine whether their progenies are always homogeneous in gall type. The sources of insects were two nearby populations in Maryland in which the same two gall types occur. In one, the NAL population, the glabrous nipple gall (LNg) is more abundant than the star gall (LS), whereas in the other, the BB population, the reverse is true. No absolute morphological differences are known between the adults of LNg and LS, but the adults emerging from the two gall types differ in size. To ensure that both gall types were represented in the experiment, adults were sorted into "large" (bigger than 3mm), presumably LNg, and "small" (smaller than 3mm), presumably LS, size classes. Only dark abdomen females were used, to avoid side cell inquilines (see Chapter II). Species distinctness is supported if

siblings always have the same gall type, but progeny from different individuals set up on the same date are different in gall type.

Cylindrical cages (30 cm X 50 cm) were sewn from white polyester fine-mesh organza, incorporating a median belt of transparent mylar (4cm wide, 0.012 mm thick) to permit convenient inspection of the cage contents. These cages were slipped onto branches and tied on with "Stretchrite" round cord elastic at both ends.

Originally, this experiment was intended to be carried out in the field. Numerous cages were set in place in the field before budbreak to exclude natural infestation by adult psyllids. Single females were introduced into the experimental cages when the insects became available, while none were introduced into control cages. However, several weeks into the experiment it was apparent from the numbers of galls in both control and experimental cages that the cages had failed to exclude natural infestation. The field experiment was therefore abandoned, and a reduced version of the original design was added to a lab rearing experiment conducted to investigate the possibility of an inquiline species (see Chapter II).

In the lab experiment, wild-caught females were caged on potted seedlings, three or more years old, during the period when both types of galls are being initiated in the field. The seedlings included both *Celtis tenuifolia* and *C. occidentalis* and also varied in leaf age. The latter had been manipulated to test the possibility that differences in gall morphology are due not to differences in the cecidogen, but to attack of the host during different stages in leaf development.

"Old" (well developed) versus "young" (still-developing) foliage seedlings were produced by covering the plants with plastic bags, placing wet paper towels at the bottom of the bag, keeping the plants in a cold room (2-5°C) starting in late winter, and moving them back to the lab at different times the following spring (1993).

Seedlings were used as their foliage reached the appropriate stage of development. Four sets of cagings were set up, two using females from the NAL population (May 13 and 24), both on *C. tenuifolia*, and the other two with females from the BB population (May 17 and 23), one on *C. tenuifolia* and the other on *C. occidentalis* (see Table 1-9). Four or five seedlings were used each time, for a total of 18. Each seedling received three cages, one containing a large female, another a small female, and the other had no psyllids as a control. (Each seedling also bore three other cages, part of an experiment on inquilines - see Chapter II.) The seedlings were kept near a south-facing window in ambient light. Females were removed and frozen at -80° C ten days after being caged. The type of galls formed within each cage was recorded one month after infestation.

Morphological methods:

Morphological comparisons were conducted using both optical and scanning electron microscopy. Color variation of live insects was recorded immediately after dissection from the gall. Specimens were preserved in a freezer, in alcohol or dry. Specimens were dissected and slide mounted in Canada balsam when

necessary. Both adults and last (5th) instar nymphs were examined. Taxa examined included gall makers from all five type of leaf galls, and petiole, bud and twig galls. Ten to thirty specimens were examined for each gall type and each stage, except that for rare species only 3-7 individuals were used. The specimens inspected for each taxon included 2-7 populations across geographic regions (Table 1-3).

Body sizes of gall makers from petiole, glabrous bud and all five leaf gall types were measured based on electrophoretic samples. The sample size of each gall types were 42 to 99 for leaf gall makers and 14 to 15 for non-leaf gall makers. The body size variation among leaf gall makers was analyzed using Tukey-Kramer methods of multiple comparisons among pairs of means (Sokal and Rohlf, 1981, p. 252).

Specimens for scanning electronic microscopy were sonicated before dehydration. Five treatments of specimen preparation process were compared using 2 individuals each in a preliminary study. In the full process, specimens were pre-treated with glutaradelhyde fixer (4%, 12hrs) and osmium tetroxide (2%, 4hrs), dehydrated in a series of increasing ethanol concentrations (30, 40, 50, 60, 70, 80, 90, 95% each 10 mins and 100% EtOH 1hr), then critical point dried in CO_2 using a "Samdri-780A" critical point dryer. Three other treatments were similar but the pre-treatment of glutaradelhyde and osmium tetroxide was eliminated. Each of these treatments started with different concentrations of ethanol (30-40-50-70-80-90-100%; 70-80-90-95-100% and 70-100%), followed by

critical point drying. The final treatment was air drying alone. Air-dried specimens shrank dramatically and this method was abandoned. No significant differences were found between specimens which were or were not pre-treated with glutaradelhyde and osmium tetroxide. Neither did it matter whether dehydration started with a lower EtOH concentration (30%-) or a higher (70%-). The final procedure adopted was an EtOH series with concentrations of 70-80-90-95-100%, followed by critical point drying. Specimens were then mounted on aluminum stubs with double-sided adhesive tape, sputter coated with gold-palladium using Hummer V and examined with an Amray scanning electronic microscope. Polaroid 4X5 photos (type 55, black and white) were taken. Two to four adults and nymphs of each gall type were examined.

RESULTS

1. Do galls on different plant parts represent different species?

Electrophoretic analyses of the 1991 adult (Table 1-5) and 1992 nymphal (Table 1-6) samples confirm that psyllids that make petiole, bud and twig galls are clearly separate species, from each other and from leaf gallers. There are multiple fixed or nearly fixed allelic differences among these classes of gall types. For example, allele C (adult) or D (nymph) of TPI is fixed in and unique to the petiole gall maker, allele D (adult) or E (nymph) of TPI similarly distinguishes the bud gall makers, and allele D of GPDH and allele C of TPI characterize the twig gall maker (Tables 1-5 and 1-6).

Variations among populations within the glabrous bud galls were minor,

suggesting that it represent a single species (Table 1-7, contrast A00). When the hairy bud gall was added, the differences were significant (Table 1-7, contrast A0). However, five out of the six pairwise X^2 contingency tests of allele frequency between the four bud gall populations in the nymphal data showed no significant differences (Table 1-7, contrasts A1-A6). The only significant pair was between glabrous bud gall from Virginia and hairy bud gall from Oklahoma. Since the two populations were far apart from each other, the geographic variation may contribute to the variation. However, the two types of bud galls, hairy versus glabrous, have some times been regarded as distinct (Crawford, 1914; Tuthill, 1943). Tree building methods usually intermingle these two bud gall types (see Chapter III, Fig. 3-2).

The three geographic populations of petiole gall makers show significant differences in allele frequencies when considered all together (Table 1-7, contrast B0) or pairwisely (Table 1-7, contrasts B1-B3). No morphological differences were found among these populations except that the body color of the last instar nymphs from Arizona is lighter (yellow) than the color (orange) of those from the other two populations.

Gall makers attacking different plant parts are also distinct in morphology. Although the bud and twig gallers are very similar, one can easily distinguish them by body size and wing maculation.

The petiole gall maker has a large body size including wings (ca. 5.5-6.5 mm) compared to the rest of *Pachypsylla*, which range from 1.9 to 4.4 mm (Table

1-8). The forewing of the petiole galler is clear with a few brown maculations, mostly in the apical region (Fig. 1-5). The glabrous and hairy bud gallers are very similar. Both are of moderate size (ca. 3.2 mm). However, while the forewings of the glabrous gall type are uniformly brownish, the hairy type has a lighter brown background with an oblique clear band subapically. The twig galler looks like the bud galler but its body size is bigger (3.5-4 mm) and the brown colored region is restricted to the margin of the distal half of the wing. The leaf gallers range in body size from 1.9 to 4.4 mm. Their wings are uniformly mottled and spotted except for a clear subapical oblique band.

The bud and twig gall makers also have similar life histories. Their adults emerge in late spring and overwinter in the last (5th) nymphal instar. The petiole gall makers also overwinter in the last (5th) nymphal instar but the adults emerge in very early spring. The leaf gall adults emerge in the fall and it is this stage that overwinters.

2. Do the different leaf gall morphs represent different species?

Allozyme evidence

Initial evidence on this question came from the electrophoretic analysis of adults collected in 1991 (Table 1-5). These data suggest that species limits will be harder to determine within the leaf gallers than between these and other gall positions. The Nei genetic distances among leaf gallers are all smaller than 0.1, and there are no fixed or nearly fixed differences (Table 1-5; see also Fig. 3-3 a).

However, there are almost always significant frequency differences between different gall types from a single locality. For example, at Great Falls, Virginia, there are five co-occurring gall types on *Celtis occidentalis*. Three of these types were collected from the same individual tree. At this site, all 10 pairwise comparisons between leaf gall types showed strongly significant differences (Table 1-9, contrasts C1-C10). This suggests that the leaf gall makers do not form a single randomly mating population.

The hypothesis that leaf gall morphs represent separate species would be stronger if one could show consistent frequency differences of particular alleles, in comparisons from different locations. The most consistent differences are those between the blister gall maker and other gall makers. For example, adults show a consistently much higher frequency of the C allele and a lower frequency of allele E in IDH-1 in the blister galler than in other sympatric gall types, in collections at three widely separated localities from the same host, *C. occidentalis* (Table 1-10). A similar trend was seen at the 6PGDH locus.

A difficulty with interpreting the adult data is that in the adult samples, center-, mono- and side-cell individuals are combined. The side cell nymphs actually represent a distinct species (see Chapter II). Their occurrence could either decrease the ability to detect frequency differences between gall types, or produce apparent differences where none exist, depending on the relative frequency of side cells among different gall types. However, removal of adult individuals carrying the allele E (equivalent to allele F in the nymphs) at malic

enzyme, the strongest marker for the side cell nymphs (see Chapter II), had no effect on the conclusions to be drawn from Table 1-10 (contrast set C), suggesting that the differences among gall types are not due to "contamination" by the side cell form.

Direct support for the reality of the patterns seen in the adult data comes from analysis of nymphal collections in 1992, from which inquilines were excluded by using monocell or center cell individuals only. As in adults, the allele frequencies in sympatric gall morphs are generally significantly different. For example, the allele frequencies of the three leaf gall types (disc, blister and glabrous nipple) types sampled from Great Falls, Virginia were significantly different from each other pairwisely (Table 1-9, contrast D1-3), paralleling the adult findings. Similar differences were detected between the two gall types sampled from Catoctin Mountain (Table 1-9, contrast E1), and the other two gall types found in Maryland (BB and NAL) populations (Table 1-9, contrast F1). Concordant with the adult data, the allele frequencies of the blister gallers differed most obviously from other gallers, consistently across localities, in the frequencies of allele D in IDH-1. A similar pattern, though less pronounced and consistent, is found in 6PGDH, as in the adult data.

Life history evidence

Phenological differences were found among co-occurred leaf gall makers in the National Agricultural Library population. Of the two types of leaf galls

which co-exist on this tree, even on the same leaf, nipple galls were formed earlier than star galls (Fig. 1-5). Eggs of glabrous nipple galls were laid earlier in the spring than those of star galls.

Rearing evidence

In 18 of 36 cages set up with single females, three or more leaf galls were found (Table 1-11). None were found in the other 18 cages, presumably because the female either died or was unfertilized at capture. None of the control bags had galls at all. In every cage containing galls, all the galls, necessarily representing progeny of a single female, were of the same type. Seven cages contained nipple galls while eleven had star galls. In 14 of 18 cases, the gall type was that predicted from the size class of the female. Both types of gall were formed on both "old" and "young" foliage class seedlings, and on two seedlings, both types of galls occurred (in separate cages). This suggests that foliage age is not a determinant of gall shape. Progenies of "large" females did not always produce nipple galls, nor did those of "small" size females always produce star galls, suggesting either that 3 mm is not the appropriate recognition criterion, or that the sizes of these gall-formers overlap. However, there is a strong association between the body size and type of galls made (see foot note to Table 1-11 and next section).

Morphological evidence

Morphologically, the leaf gallers are extremely similar to each other, with highly overlapping variation. All the differences I could find were relative, not absolute. However, measurements of adult body size among almost all different pair leaf gall types show significant differences, except those of two types of nipple galls. The galler which is most nearly distinguishable from the others is the blister gall maker. The smaller body size (<2.5mm) of the blister gall maker was used to separate it from the nipple galler (3-4mm) by Crawford (1914) and Tuthill (1943). The male genitalia of the blister galler are also slightly different from those of the others: the male proctiger is less hairy and the forceps are more sharply pointed (Fig. 1-7).

All other gallers are very hard to identify without knowing the gall shape.

3. Do *Pachypsylla* of similar gall type on different host species represent different species?

Allozyme allele frequencies did not differ between blister gall nymphal samples from different localities on the same host species in Texas. The data were therefore pooled to yield a single contrast between the two host species (Table 1-6, populations 10 & 11). There were no significant frequency differences between these populations, either at individual loci or when they were combined (Table 1-9, contrast G1). Thus, there is no evidence of allozyme divergence between sympatric blister gall makers from the two different host species.

Morphological differences between blister gall makers from *C. laevigata*, *C. reticulata* and *C. occidentalis* were also investigated, especially in the male aedeagus, following Riemann (1961). Riemann found the largest differences to lie in the head/shaft ratio of the terminal segment of the aedeagus. He reported ratios of 0.5, 0.25 and 0.38 for blister gallers in Texas and Oklahoma from *C. laevigata*, *C. reticulata*, and *C. occidentalis*, respectively. My measurements on blister galler specimens yielded mean estimates of 0.50, 0.33, and 0.33 for the same ratios. The former two were from Texas and the latter was from Maryland and Virginia. These means are similar to Riemann's except for specimens from *C. reticulata*. The differences between blister gallers from *C. laevigata* and *C. reticulata* in my samples are significantly different from each other (see foot note of Table 1-12). I also measured blister gallers from Arizona, where only *Celtis reticulata* is available. The mean ratio and range are similar to the blister gallers from Texas, though the sample size of Arizona population is small (Table 1-12). No other significant morphological differences between blister gallers from different host plants were found.

DISCUSSION AND CONCLUSIONS

Evidence from morphology, allozymes and life histories strongly confirms that the petiole, bud, twig and leaf gall makers each constitute at least one species distinct from the others.

Within the bud gallers, allozymes show little geographic variation, even

between allopatric gall morphs, which argues against the separate species names, *P. celtidisgemma* Riley (glabrous bud gall) and *P. pallida* Patch (hairy bud gall) advanced for these morphs by some authors. However, the gall morphs are associated with differences in wing pattern and host affiliation. Within the petiole galls, there is significant allozyme differentiation among geographic populations on different hosts. The possibility that allopatric populations of the petiole and bud gallers are specifically distinct remains open.

The members of the leaf gall making complex are very closely related and hard to distinguish. However, several lines of evidence indicate that they are at least partially reproductively isolated, and quite possibly separate species. First, sympatric gall types always show statistically significant differences in allozyme frequencies. In the case of the blister gall, the differences are marked enough, and consistent enough across geography, to argue by themselves for strong reproductive isolation, supporting the hypotheses of Crawford (1914) and Tuthill (1943). Second, the rearing experiment, in demonstrating that gall shape variation between isofemale progenies is both all-or-none and associated with body size, provides evidence at least strongly consistent with a genetic, species-specific basis for that trait. Third, pairs of sympatric gall morphs examined in detail differ substantially in the timing of adult appearance and/or gall formation as well as body size. Though more evidence is needed, it is probable that in addition to the blister galler, the three species named by Riley but synonymized by others (e.g. Crawford, 1914; Tuthill, 1943), *i.e. P. celtidisumbilicus* (disc galler), *P.*

celtidisglobulus (glabrous nipple galler) and *P. celtidisasterisca* (star galler), should be revived.

Allozyme variation between sympatric blister galls from *C. laevigata* and *C. reticulata* is small, which casts doubt on Riemann's hypothesis that blister gallers on different hosts represent different species. In contrast, significant morphometric differences in the male genitalia, corroborating Riemann's observation, seem to support that hypothesis. Since morphometric variation is subject to environmental effects including host differences, however, it is not clear whether the observed differences have a genetic basis. Reciprocal host transplant experiments are needed to answer this question, and the species issue remains in doubt.

Conclusions about the status of several additional described nipple gall makers, including *P. celtidispubescens*, *P. rohweri*, *P. celtidisglobulus*, *P. celtidiscucurbita* and *P. celtidiscucurbita* var."?", can not be made, since they were not included in this study.

Further studies using other techniques and more extensive and intensive geographical sampling are needed to fully resolve the species problem among leaf gall makers. One constraint of the cellulose acetate gel electrophoresis used here is that the small size of the gel does not allow enough migration distance to separate alleles of very similar mobility.

KEY TO SPECIES OF *PACHYPSYLLA* STUDIED

1 Vertex and thoracic dorsum not shining, covered with conspicuous, short stiff pubescence 2

Vertex and thoracic dorsum glabrous, with only sparse, minute pubescence 8

2(1) Body size large (5-6 mm); forewing narrowly rounded at the apex, clear with maculation mainly apically; galls spherical and large (1-3 cm) on petiole, usually polythalamous ..... *venusta* Osten-Saken (petiole gall maker)

Body size small to moderate (2-4 mm); forewing broadly rounded at the apex, mottled and spotted throughout, with a clear subapically oblique band; galls on leaf-blade of various shapes, monothalamous or polythalamous 3

3(2) Female abdomen; male forcep tip roof-like, side margins parallel, straight in lateral view; nymphs found in side cells of other leaf-blade galls; 5th instar nymphs with yellow wing pad ..... *cohabita sp.n* Yang and Riemann (leaf inquiline psyllid)

Female abdomen brown; male forceps in lateral view gradually tapering in apical half, tip pointed, side margins convex; nymphs found in single cell galls or in center cell of multiple-cell galls, 5th instar nymphs with brown wing pad 4

4(3) Gall on the upper side of leaf, raised or convex 5

Gall on the upper side of leaf concave, forming a depression 6

5(4) Galls inconspicuous, blister like, elevated on both upper and under sides of the leaf . . . . . *celtidisvesicula* Riley

(leaf blister gall maker)

Galls rounded, raised on the upper side; star-shaped or flower shaped on the under side . . . . . *celtidisasterisca* Riley

(leaf star gall maker)

6(4) Galls disc-like or button-like, much flattened; upper depression with an outer rim and the central portion slightly raised with a median spine; under side wart-like, with a depression at middle . . . . . *celtidisumbilicus* Riley

(leaf disc gall maker)

Galls nipple-like, much rounded; upper side with depression and under side rounded 7

7(6) Galls glabrous; upper side forming a cup-like depression with an outer rim; under side rounded, nearly as long as wide or wider than length, apple-like, with a central depression . . . . . *celtidisglobulus* Riley

(leaf glabrous nipple gall maker)

Galls pubescent on the apical portion of the under side, but hairs easily rubbed off, giving glabrous appearance; upper side a depression with central spine but no outer rim; under side nipple-like, longer than wide,

without obvious central depression . . . . . *celtidismamma* Riley

(leaf hairy nipple gall maker)

8(1) Pterostigma prominent; wings with a smoky band along the anal and apical margins and extending along veins toward base; galls oblong-oval in shape on one side of the twig, monothalamous . . . . . *celtidisinteneris* Mally

(twig gall maker)

Pterostigma not obvious; forewing homogeneous or maculated not as above; forming irregularly round galls on bud 9

9(8) Forewing uniformly brown; gall glabrous on bud, usually polythalamous . . . . . *celtidisgemma* Riley

(glabrous bud gall maker)

Forewing with light brown in apical half extending to some basal regions; gall densely pubescent on bud, usually polythalamous . . . . . *pallida* Patch

(hairy bud gall maker)

Chapter II

The evolution of inquilinism in hackberry leaf galling psyllids: Are multiple individuals within the same gall conspecific?

INTRODUCTION

The organisms and interactions that occur in a gall are often more diverse than one might expect. A gall very often represents a complex community rather than a microhabitat for a single gall former. Some oak galls, for example, support as many as 22 species of insects (Askew, 1961), comprising the original gall former, inquilines and their parasites. Contemporary studies have shifted emphasis from rearing and identifying the emergent insects of a gall to understanding the ecological relationships of the gall community (Wiebes-Rijks and Shorthouse, 1992) and their evolutionary origin (*e.g.* Ronquist, 1994). However, most such works have focused on major galling groups, *e.g.* Cynipidae (*e.g.* Askew, 1961; Brookfield, 1972; Shorthouse, 1973; Washburn and Cornell, 1979; Abe, 1992) and Cecidomyiidae (*e.g.* Askew and Ruse, 1974; Roskam, 1979, 1986; Roskam and Van Uffelen, 1981; Shorthouse and West, 1986).

Only a few studies have examined the relationships of inhabitants of psyllid galls (*e.g.* Jensen, 1957; Walton, 1960; Moser, 1965; Hodkinson and Flint, 1971) and all concentrated on the natural enemies of the gall formers. No inquilines have been reported in psyllids except Riemann's (1961) observation on hackberry psyllids, *Pachypsylla*, in his unpublished dissertation. Present research tests Riemann's and related hypotheses on the potential inquilinism in *Pachypsylla*, and discusses the evolution of this trait.

BACKGROUND

Gall Inquilines

The term "inquiline" comes from the Latin word *inquilinus* meaning temporary inhabitant or guest (Brown, 1956, pp. 439 & 387) and has been broadly used. For instance, a search of the Life Science Collection on CD-Rom (Cambridge Scientific Abstracts, Bethesda, MD) found 57 papers on "inquilines" between 1982 and 1993. The "inquiline" in these research projects ranged from various kinds of organisms in galls, to social parasites in Hymenoptera (*e.g.* Bourke and Franks, 1991; Reed and Akre, 1983), to crickets (*e.g.* Henderson and Akre, 1986; Bolton, 1986), beetles (*e.g.* Howden and Gill, 1988) and worm lizards (*e.g.* Riley *et al.*, 1986) in ant nests, and to co-occurring fishes in coral reefs (Spiegel, 1980). For the purposes of this study, the term will be restricted to gall inquilines unless otherwise indicated.

While reports of inquilinism are rare in psyllids, inquilines are frequent in other galling groups. Gall inquilines are gall inhabitants that feed on gall tissues, without directly damaging the gall-inducer, but are unable to induce galls themselves independently (Skuhrava *et al.*, 1984; Shorthouse and West, 1986; Shorthouse, 1991; Wiebes-Rijks and Shorthouse, 1992). Although inquilines can be viewed as parasites of gall tissue, their ecological relationship to the original gall former is not clear, and should not be assumed to be parasitic. Meyer (1987, p.177) defined inquilines as "insects living commensally in the gall cortex," implying that they do little harm to the original gall inducer. The inquiline

Synergus pallicornis in galls of the cynipid *Cynips quercusfolii* is an example (Askew, 1961). However, other studies on cynipid galls have demonstrated that inquilines have negative effects on gall inducers by food deprivation, or even by killing the host at an early stage of development of the gall (Evans, 1965, 1967; Shorthouse, 1973, 1980; Washburn and Cornell, 1981). For example, the inquiline *Periclistus* kills the gall former *Diplolepis* at oviposition (Shorthouse, 1980).

In other homopterans, gall inquilines have been reported in the aphids genus *Eriosoma* (Akimoto, 1981, 1988). Akimoto hypothesized that facultative inquilinism is a pre-adaptation for obligate inquilinism. He postulated that the latter arose by dispersal beyond the range of the primary host. This could result in strong selection for invasion of galls formed by related species, if the dispersants could not form their own galls on the available hosts. Subsequent specialization for this habit might preclude the re-acquisition of gall induction, even on re-encounter with the ancestral host.

Occurrence of multiple individuals in *Pachypsylla* leaf galls

The number of nymphs within a single hackberry psyllid gall varies from one to 17 and probably more, depending on the gall type and population. Petiole and bud galls are usually polythalamous, that is, with multiple individuals in the same gall, and each is confined to a separate chamber. Twig galls are usually monothalamous, that is, with only one individual per gall.

The situation in leaf gall makers is more complicated. Usually there is only

one individual inside a gall, but sometimes, particularly in the nipple gall in Maryland and vicinity, there can be multiple individuals, each enclosed in a separate cell. The proportion of multiple-cell galls and the number of cells within one gall vary between gall types and localities.

There are no obvious differences among individuals and cells within the same petiole or bud gall. In contrast, within multiple-cell leaf galls one can generally distinguish between a center cell, presumably the individual that initiated the gall, and one or more "side cells." This distinction raises a series of questions. Are multiple individuals within the same gall conspecific? Does the differentiation between the center and side cells within the same leaf gall suggest that there is more than one species? Do they both contribute to gall production? Do the side cell and center cell individuals differ in performance and survivorship? What are the ecological relationships between the center and side individuals? What is the adaptive significance of having monothalamous or polythalamous galls? If the side cell individual is a true inquiline, how did it evolve? This study was designed to answer some of these questions.

Two interpretations of the species status of side cell individuals within *Pachypsylla* leaf galls have been offered. Moser (1965) observed multiple cells in leaf hairy nipple galls on *Celtis occidentalis* in New York State. He called the side cell a "marginal gall" and considered the side cell nymph to be conspecific with the blister gall nymphs, the only other leaf gall that occurred in that area.

Riemann (1961) found the side cell individuals in several different leaf gall

types in Texas and considered the side cells species to be undescribed. He regarded the side cell nymphs, across different gall types, to be the same species but not conspecific with the various center cell species. He hypothesized that the side cell species was unable to induce a gall and is an inquiline that became incorporated into the gall by feeding next to the gall maker during gall initiation in the spring. He also suggested that the inquiline sometimes killed the gall maker by expanding its own cell too much.

In my initial observations, there were consistent color differences between the fifth instar nymphs from center cells and side cells, especially in wing pad color. The center cell nymph always has darker wing pads, which are usually brown, whereas the side cell nymph always has light colored wing pads, which usually are yellow. The nymphs from mono-cell galls and from center cells within multiple cell galls are either brown in general color with green or red color in the intersegmental membranes while the side cell nymphs are greenish yellow in general body color without differentially colored intersegmental membrane.

Field observations and lab rearing results also suggests that first-instar nymph and adult coloration are associated with cell position, at least in the glabrous nipple gall and the star gall in the Maryland area. Side cell nymphs in the first instar are white, sometimes with dark maculation, and adult females have a green abdomen. Center cell individuals have yellow first instar nymphs and the adult female has a dark abdomen.

These observations indicate that there is considerable variation between

side and center individuals besides the position in the gall and suggest that side cell nymphs may be a different species than center cell nymphs.

QUESTIONS ADDRESSED

Two questions were asked in this study:

1. **What is the nature of side cell individuals within a leaf gall?**

   The following hypotheses are contrasted:

   A. The null hypothesis is that the side and center cell individuals are the same species.

   B. Moser's hypothesis predicts that in multiple cell nipple galls, side cells are "marginal galls" that contain individuals of the co-occurring blister gall maker that have become incorporated into the nipple galls.

   C. Riemann's hypothesis predicts that side cell individuals represent a separate species, that does not have the ability to form its own gall.

2. **Are side cell individuals from different types of leaf galls conspecific?**

   Riemann's hypothesis is that there is only one side cell species regardless of the "host" species. There are two other possible hypotheses 1) that each kind of leaf gall has a separate inquiline species or 2) that the inquiline is the same species as the host.

Samples of side cell individuals from two types of nipple galls, glabrous and

hairy, were examined morphologically and electrophoretically to test these hypotheses. A rearing experiment was designed to test the ability of side cell individuals to induce galling. Dependency of the side cell individuals on the center individual was further investigated by destroying the center individual at different stages of gall initiation.

MATERIALS AND METHODS

Samples for electrophoretic and morphological studies

Center versus side-cell nymphs from the two types of nipple galls in Maryland were compared to each other and to those from single-celled galls of other co-occurring leaf gall types using allozyme, morphological, and life history characters to assess possible species differences.

Nymphs were examined from the hairy nipple gall and glabrous nipple gall from three populations in Maryland in 1992, plus two other types of galls that commonly co-occur with these nipple galls. These included hairy nipple galls and blister galls from Catoctin Mountain (CMt) in northern Maryland (population #1-4 in Table 2-1), and glabrous nipple galls and star galls from both the National Agricultural Library (NAL) population in Beltsville (population #5-8 in Table 2-1) and the Branchville Road (BB) population in Berwyn (population #9-12 in Table 2-1). In both locations, the host is *Celtis tenuifolia*. The NAL population occupies a tree about 12 meters high located beside a small graveyard in the middle of an open lawn. Few seedlings were found near it but there is another tree 3 m high,

500 m from it. The BB population contains many hackberries, from small seedlings to tall trees, in a residential neighborhood. The two populations are about 5 km apart. The CMt population is located at the Poplar Grove campsite in Catoctin Mountain Park where trees and seedlings of *C. occidentalis* are abundant. This population is at about 450 m elevation and about 85 km from the BB and NAL populations.

The sympatric non-nipple gall is the blister gall, which never has multiple cells and often co-occurs with the hairy nipple gall, and the star gall, which often co-occurs with the glabrous nipple gall. Galls were collected in the fall of 1992 and 1993 from at least two trees in BB and CMt and one tree in NAL. I dissected each gall, separated the side cell nymphs from the center cell nymph, and collected the nymphs from mono-cell galls. These nymphs were either frozen for later electrophoretic and morphological studies, or reared in small glass vials to obtain the associated adults for morphological comparisons.

Electrophoretic and morphological methods

Three to twenty-one nymphs from each cell position in each locality were analyzed by electrophoresis (Table 2-1). Five to twenty individuals of each category were examined for the morphological comparison. Electrophoretic, morphological, and data analytical methods are as described in Chapter I. Allozyme frequency data for samples from the same gall type and cell position were combined if they did not differ significantly.

Rearing experiments

Two experiments were conducted in the spring of 1993 to test the inquiline hypotheses. The first experiment tests whether the side cell nymphs can form galls, and also provides further data on color differences between center and side cell individuals. Fertilized females were collected from the NAL and BB populations and confined in cages on hackberry seedlings in the lab. This experiment was carried out at the same time and on the same plants as described in Chapter I.

There were three treatments: 1) cages containing a single brown abdomen female, presumably a center cell individual (these are the same females described in the rearing experiment in Chapter I); 2) cages containing a single green abdomen female, presumably a side cell individual; and 3) cages containing one brown plus one green abdomen female. In treatment 3, both "large" (>3mm) and "small" (<3mm) brown abdomen females were used (in separate replicates), to ensure inclusion of both star and nipple galls, as described in Chapter I. Control bags contained no insects.

Each replicate was reared in a separate bag, but at least one replicate of all treatments and one control were reared simultaneously on the same seedlings. Thus, each seedling had at least six cages, each contain: a single large brown abdomen female, a single small brown abdomen female, a single green abdomen female, a pair consisting of one large brown abdomen plus one green abdomen female, one small brown abdomen plus one green abdomen female, or no psyllid

at all. The number and timing of the replicates set up, shown in Table 2-5, corresponds to that previously described (Table 1-9). Most seedlings used were *C. tenuifolia*, except that one batch of insects was reared on *C. occidentalis* seedlings.

Females were removed from the cages after ten days and frozen at -80°C, and the color of nymphs found was recorded. Gall formation or lack thereof was recorded a month after infestation. Galls were dissected in September to examine cell numbers within each gall.

Riemann's hypotheses predicts that treatment 1 will have yellow nymphs and mono cell galls only, treatment 2 will have white nymphs and no galls, and treatment 3 will have white and yellow nymphs, and both mono cell and multiple cell galls.

Destruction experiment

The second experiment tests the dependency of side cell on center cell nymphs. Aggregates of newly hatched nymphs were located in the field and the center nymph experimentally destroyed. Destruction was conducted under a dissecting microscope fixed on a plastic manipulation and recording platform, which could be either fastened on a tripod or suspended from the shoulders on straps, leaving hands free for dissection and recording. Insect pins were used to pick the center cell nymph out of the leaf.

Treatments were: 1) center cell nymphs destroyed early, *i.e.*, before any nymphs were enclosed in the gall; 2) center cell nymphs destroyed after the center cell individual was enclosed in the gall but the side cell nymphs were still exposed; 3) center cell nymphs destroyed when both the center and side cell nymphs were fully enclosed; 4) control, in which galls in developmental stages corresponding to the first three treatments were left undisturbed. Predictions were that treatment 4 would develop normally, galls of treatment 1 would not develop and side cell nymphs would die, while galls in treatment 2 and 3 might continue their development and side cell nymphs might survive.

Experiments were initiated during four time intervals in late May, in the NAL population. Leaf gallers were abundant, and several nymphal aggregations in different gall development stages could be found even within a single leaf. Each replicate, consisting of two or more treatments, was performed on a single leaf when possible, or otherwise on different leaves on the same twig. The experimental leaves were numbered and marked with blue plastic tape on the twig right below where the petiole attached. The position of each gall on the leaf was sketched on paper when destruction was carried out, and the development (size) of the gall was measured immediately and again two weeks, two months, and four months after destruction. The total number of replications for each treatment, which was determined in part by the difficulty of finding galls in all four developmental stages, ranged from 16 to 30.

Female phenology

To compare the phenology of center versus side cell females, females were collected in the NAL population every five days in spring of 1993, from April 15 to May 15. Females found on the plant were randomly collected from different branches. About 50 to 70 females were collected each time, and the numbers of brown abdomen and green abdomen individuals recorded, to determine the change in proportion of the two morphs over time.

RESULTS

Electrophoretic data

Allozyme frequencies in center cell nymphs from multiple cell galls and nymphs from mono-cell galls of the same gall type in the same population were not significantly different (Table 2-2, contrast A1-A3), so these data were pooled. I also pooled the two populations (NAL and BB) of combined mono and center cell nymphs of glabrous nipple gall makers (Table 2-2, contrast B1), two populations (NAL and BB) mono cell nymphs of star gall makers (Table 2-2, contrast B3), and two populations (NAL and BB) of side cell nymphs from glabrous nipple galls (Table 2-2, contrast B2), for the same reason. There were six populations in all after pooling (Table 2-3).

Within both the glabrous and the hairy nipple gall samples, there are strong frequency differences between side cell nymphs and center cell plus mono cell nymphs (Table 2-4, contrast C1-C2). The most pronounced differences are at the

malic enzyme locus (Table 2-3).

There are also marked differences in frequency between the side cell samples from the hairy nipple gall and sympatric mono cell blister gall (Table 2-4, contrast D1) and between the side cell individuals from the glabrous nipple gall and sympatric mono cell star gall (Table 2-4, contrast D2). Thus, the side cell individuals are not likely to be conspecific with either of these co-occurring gall types.

Allele frequencies in side cell individuals from the two nipple gall types are significantly different from each other (Table 2-4, contrast E1). However, these samples are from populations ~85 km apart, in very different habitats; the degree of differentiation between them is typical of the differences within gall morphs between the same two localities. A distance Wagner tree based on Rogers' distance for the six pooled populations grouped the two side cell taxa from different nipple galls together, rather than with the center cell populations from the same gall (Fig. 2-1a). However, UPGMA analyses did not group the side cell samples taxa with each other or with center cell samples from their respective gall types (Fig. 2-1b; see also Chapter III).

Single female rearing experiment

None of the offspring of the eighteen green abdomen females formed galls, whereas offspring of most brown females caged alone did form galls (Table 2-5). No galls were found in the control bags. The progeny of brown females

caged alone produced only single cell galls. When brown and green abdomen females were caged together, both single and multiple cell galls were formed, except that in the two cages in which the green female died early in the experiment, only single cell galls were formed. The results strongly suggest that the side cell individual is an obligatory inquiline which alone could not induce a gall.

Destruction experiment

Some of the treated leaves were dropped before the last examination, reducing the number of observations in each category at the last stage from 16-30 to 3-13. While galls in which the center nymph was left intact until the third stage mostly completed normal development (>91%, n=23), destruction of the center nymph at any of the three stages resulted in significantly smaller galls than the corresponding control ($p<0.01$, t-test). Gall size is plotted against observation date for each treatment in Figure 2-2. While one may argue that the differences in gall size were due to gall damage when the center individual was destroyed, this explanation is not valid in the cases where the center individual was destroyed at the first stage before it was enclosed by the gall.

None of the inhabitants of the galls that had their center cell destroyed at the first stage survived while their undisturbed controls developed until emergence (Figure 2-2 a). Leaves bearing the controls of the center cell nymphs that were destroyed at the first stage dropped from the tree before the last examination was

performed. In one case a dropped leaf was found on the ground. No measurement of this first control group in the fourth time period was taken (Fig. 2-2 a). However, the leaf found on the ground had three galls and all had obvious psyllid emergence holes (1-3 holes each gall), suggesting that the insects survived until adulthood. Those galls with center cell individuals destroyed at the second and third stages kept developing until the adult stage, though the survivorship was lower (42.8% and 55.6%, respectively) than in their control (86.7% and 100%, respectively) (Figure 2-2, b and c).

Timing of female appearance

Leaf gall maker females were occasionally found in early April, but did not become abundant until mid April. On April 15, 1993, none of the females caught in the field had green abdomens (Figure 2-3). Ten days later (April 25), the proportion of green abdomen females increased to 10% and in the first two weeks of May, it rose and remained around 70%.

Morphological comparison

No clear distinctions in morphology were found between center and side cell individuals, apart from the initial differences observed in coloration of the female abdomen and wing pads of 5th instar nymphs.

DISCUSSION AND CONCLUSIONS

Taken together, the results strongly support the hypothesis that, at least within nipple galls, side cell individuals represent separate species from central cell and mono cell nymphs. The allozyme frequency differences are dramatic, though not absolute, and rule out free interbreeding. They are supported by fixed differences in coloration in two life stages, and by life history differences in female flight time and gall induction ability. Strong allozyme frequency and coloration differences between side cell samples and sympatric blister or star gallers also permit rejection of Moser's (1965) hypothesis that side cells are "marginal" galls overgrown by a nipple gall.

Grouping of the side cell inquiline populations from different nipple gall types in the distance Wagner tree is consistent with the hypothesis that these represent a single inquiline species. However, this finding is sensitive to choice of clustering method and the question needs further study (see Chapter III).

The results of the rearing and destruction experiments fully support Riemann's hypothesis that the side cell individuals are true inquilines. Galls were never formed independently by progeny of side cell females, and side cell nymphs rarely survived in the field if the center cell nymph was removed before the gall was well established. Conversely, galls with side cells were never formed by progenies of center cell females alone; the nymphal habit of feeding next to a gall inducer is presumably unique to the side cell form. As would be expected if the inquiline nymphs need to feed close to already-initiated galls, the phenological

observations also suggests that the side cell females come back to the buds to mate and lay eggs later, on average, than brown abdomen females (Fig. 2-3).

While side cell individuals cannot initiate a gall, whether they subsequently contribute to gall development is not clear. In cynipid galls, the species-specific morphology is sometimes altered by the presence of inquilines (Evans, 1965; Askew, 1984; Meyer, 1987). Although one cannot in general be sure whether there are side cell individuals in a *Pachypsylla* leaf gall without dissection, it is sometimes possible to distinguish mono-cell galls from multiple cell galls by appearance. Especially in the glabrous nipple gall, the mono-cell gall is usually perfectly rounded, while protrusions on the gall margin are sometimes evident, though not always, when side cells are present. This observation, and the fact that the inquilines are enclosed in separate cells, suggests that the side cell individual can modify gall development to some degree.

From what ancestral habit did *Pachypsylla* inquilinism evolve? The inquiline falls well within the leaf gall makers (Fig. 2-1, see also Chapter III), but its exact phylogenetic position is not certain - the differences among leaf gallers are small, with no fixed allelic differences, thus phylogenetic relationships at this level are not well resolved. However, it seems quite clear that the inquiline is derived from an ancestor which made an enclosed gall. The very few other gall inquilines reported in Homoptera also seem to be derived from gall formers (Akimoto, 1988). The same is true for at least some inquilines in other groups, such as cynipid wasps and cecidomyiid flies (Askew, 1984; Ronquist, 1994).

However, it is not yet clear whether all gall inquilines have this origin.

The side cell population represents one of the closest ecological interactions with a congeneric gall-inhabiting species and may offer the opportunity to study the early stages in the evolution of inquilinism. The implication of this discovery for the attempt to delimit species in *Pachypsylla* is that one cannot assume, without inspecting the nymphs, that adults emerging from the same gall are conspecific. This may help explain part of the lasting confusion about species recognition in this genus.

The fitness effects of the *Pachypsylla* inquiline have not yet been measured, but anecdotal evidence suggests a detrimental effect. Riemann (1961) reported that the center cell nymph can be killed by expansion of the side cells.

How common is obligate inquilinism and under what circumstances is the shift to this habit favored? In Homoptera, it appears to be rare, though if homopteran inquilines are typically as similar to their hosts as in *Pachypsylla*, there could be more undiscovered cases. Apart from *Pachypsylla*, the only obligate inquiline that I am aware of is the aphid *Eriosoma yangi*, although a number of aphids seem to be facultatively inquiline, in that fundatrices will invade and take over each others' galls, particularly in cases where the gall forms at some distance from the site of induction. Inquilinism may be substantially more common in some other galling groups. In cynipids, for example, inquilinism seems to have multiple origins and one tribe Aulacini is dominated by this habit, though the monophyly of this tribe has been questioned (Askew, 1984). Recent studies by

Ronquist (1994) supported the hypothesis of the monophyletic origin of cynipid inquilines.

The adaptive origins of inquilinism are unclear. The scenario of the evolution of inquilinism by host shift in *Eriosoma* (Akimoto, 1988) seems doubtful for *Pachypsylla*, given that the inquiline seems to have a broader host plant range than the individual gall forming species. An alternative explanation, not invoking unique historical circumstances, is that inquilinism represents a strategy for avoiding high mortality risk associated with gall initiation. Causes for this might include gall failure due to phenological mismatch with host development, and predation or desiccation during a longer period of exposed feeding. This hypothesis remains to be tested.

Chapter III.

Phylogeny and the evolution of galling position in *Pachypsylla*

INTRODUCTION

In this chapter, I examine phylogenetic relationships within *Pachypsylla*, using electrophoretic and morphological characters. Representatives of the two other genera in the tribe Pachypsyllini are used as outgroups.

A phylogeny is necessary for any attempt to understand the evolutionary origins of galling diversity in *Pachypsylla*. Several questions from previous chapters are examined here. The hypothesis that the various leaf gall types are separate species (Chapter I), supported by significant frequency differences among sympatric samples, would gain support if geographically separate populations of the same morph were grouped together in a phylogeny. The hypothesis that side cell individuals from different leaf gall types in different localities represent a single origin of inquilinism, perhaps a single species (Chapter II), would likewise be strengthened if these populations grouped together. A phylogeny can also help answer such questions as whether the inquiline arose from a galling ancestor, and whether its origin preceded, and could hence have helped bring about, the differentiation of leaf gall morphs.

A fourth question which can be addressed by a phylogeny concerns the evolution of the range of plant parts attacked by different *Pachypsylla* species, the greatest found in any group of closely related psyllids. What was the ancestral galling position, and did the others arise by stepwise shifts to physically adjacent or similar niches? Within an analogous complex of gall forming sawflies in the subfamily Nematinae (Tenthredinidae), it has been suggested that gall formers are

derived from a stock of free-living sawflies with a probable phylogenetic trend from free feeding, to leaf folding, to leaf galling to petiole and bud galling, to shoot galling (Smith, 1970; Price, 1988, 1992). The hypothesis that gall position in *Pachypsylla* follows a similar trend predicts that the leaf gallers should be phylogenetically basal, the petiole galler branches off next, and the bud and twig gallers form the most recent pair of sister groups, as suggested by their morphological and life history similarities.

BACKGROUND

In addition to allozyme and morphological characters, these studies incorporated information on chromosome number reported by Riemann (1966) for various species of *Pachypsylla*, including *P. celtidisasterisca*, *P. celtidispubescens*, *P. celtidismamma*, *P. celtidisvesicula* and five undetermined species, and *Tetragonocephala flava*. Riemann found that most species of *Pachypsylla* (leaf gall makers and twig galler) and *T. flava* have 2N chromosome numbers of 25 ♂ and 26 ♀, and suggested that these represented the ancestral chromosome numbers in these 2 related genera. The lower chromosome numbers in the petiole galler *P. venusta* (2N= 23 ♂, 24 ♀) and the bud galler *P. celtidisgemma* (2N= 22 ♂, 22 ♀) are derived, presumably by chromosome fusion. He further argued that the XY sex mechanism of the latter species was derived from an XO system in an ancestral *Pachypsylla*. The large size of the sex chromosomes suggests that this occurred as the result of the X chromosome fusing with one of the larger

autosomes. In this case the combined X and autosome would become the new X while the homologous autosome would become a Y chromosome.

MATERIAL AND METHODS

Samples and electrophoretic methods:

As described in Chapter I, twenty populations (after pooling) of nymphal samples of *Pachypsylla* were included as ingroups (Table 1-6).

A collecting trip to Asia was made in the summer of 1992 to obtain specimens of the outgroup *Celtisaspis*, purported to be closely related to *Pachypsylla*. Adults and last instar nymphs of the lerp-forming *Celtisaspis beijingana* were collected by me and F. Li in June and July 1992 from Beijing and Shengyang, China. Only the first instar nymphs of *Celtisaspis japonica* were found in Seoul and Daegu, South Korea in August 1992. Since adults and the last instar nymphs were used for electrophoretic analyses in *Pachypsylla*, the first instar nymphal samples from Korea were not included in the electrophoretic analyses. Only the population of *Celtisaspis* from China was used. *Tetragonocephala flava* was collected by C. von Dohlen from Florida Canyon, Arizona in the June of 1993. A total of 22 populations of nymphal samples were then analyzed, including 20 ingroups and 2 outgroups.

Electrophoretic methods were those described in Chapter I. Three of the 15 loci were monomorphic in *Pachypsylla*, but showed differences in the outgroups. The other 12 showed differences among gall types.

Morphological methods:

Characters were observed both under optical and scanning electronic microscopy. The methods were described in Chapter I. Characters were coded numerically. Terminology followed Brown and Hodkinson (1988) in adult morphology and White and Hodkinson (1982) for nymphal morphology.

Fourteen taxa were analyzed, including populations from all four gall position groups and two outgroups (Table 3-1), and from a variety of geographic localities (see Table 1-3). These included eight leaf gall populations, a petiole gall population, two bud gall populations (one each of the glabrous and hairy morphs), and a twig gall population. The leaf gall populations included two types of leaf hairy nipple gallers and their inquilines, the leaf star galler, the leaf disc galler, and two leaf blister gallers.

Thirty-three morphological characters (Table 3-1 and 3-2, characters 1-33) were coded, from both adults and fifth instar nymphs. There are seven head characters, six thorax characters, five and four male and female genitalic characters, respectively. Eleven characters were coded from last instar nymphs. Among the thirty-three characters, four had multiple states, while the others were binary.

Many possible characters were examined but rejected because of highly overlapping variation among taxa. For example, the presence of caudal spurs is an apomorphic character in *Pachypsylla*, but there is considerable variation in their number and arrangement (Figure 3-10), and in many instances there are

differences in these structures between sides of the same specimen. Therefore, this and similar characters were excluded from my analysis.

Chromosome data

Male and female chromosome numbers from Riemann's reports were coded as separate characters (Table 3-1, char. 49-50; Table 3-2, char. 131-132). Both characters were assigned three states, coded as the 2N number minus 20, *e.g.*, the condition 2N=25 is coded as state "5."

Life history data

Three characters encode life history information (Table 3-1, char. 51-52; Table 3-2, char. 133-135). These include number of generations per year (state 1 = univoltine, state 2 = bivoltine or multivoltine), overwintering stage (state 0 = egg, state 1 = nymph, state 2 = adult), and female oviposition time relative to plant development in the spring (state 0 = in very early spring before bud swelling, as in the petiole gall maker; state 1 = between bud swelling and full leaf extension, as in the leaf gall makers; and state 2 = after the new year's twigs are formed - the twig and bud gall makers lay eggs on these twigs or their axillary buds.)

Phylogenetic analyses

(1) Electrophoretic data:

Phylogeny estimation from the electrophoretic data used both distance and discrete character-based methods. Distance analyses employed the distance Wagner and UPGMA routines in Biosys-1 (Swofford and Selander, 1981) using Rogers' distances for both algorithms as well as Nei's distance for UPGMA.

For discrete character analysis, the first approach treated each locus as a character and the alleles as unordered states (Table 3-1, char. 34-48) (Mickevich and Mitter, 1981). For polymorphic loci, all alleles with frequencies of 0.2 or more were assigned as states of that character (locus). When there was more than one such allele, the character was coded as polymorphic (ambiguous) (Table 3-1, char. 34-48). The second approach treated each allele as an independent character scored as present or absent (Table 3-2, char 34-130) (Mickevich and Johnson, 1976). An allele was scored as present in a population if its frequency was 0.05 or greater. A drawback to this coding is that sampling error can result in false scoring. A sample of 30 individuals is necessary to detect an allele with frequency above 0.05 with a probability greater than 0.95 (Swofford and Berlocher, 1987). Only five samples in the data are this large. However, the most variable group is the leaf gall makers, in which sample sizes are relatively large.

(2) Morphological data:

Most parsimonious trees for discrete allozyme characters, morphology and combined characters were generated using PAUP 3.1.1 (Swofford). The random addition sequence option for heuristic search was used in Paup, with replications

set at 1000. Analyses were performed both on equally weighted characters, and following the successive weighting of Farris (1988), using the rescaled consistency index. Unrooted trees were rooted using *C. beijingana* and *T. flava* as the outgroups. A strict consensus tree was calculated when more than one most parsimonious tree was found. Evolution of individual characters was analyzed using MacClade (ver. 3, Maddison and Maddison, 1992).

In the analysis of morphological data, multistate characters were treated both as entirely ordered, and with orderings assigned to four characters (#s 1, 3, 24, and 27) in which a morphocline seemed plausible on inspection.

(3) Combined evidence from morphology, allozyme, karyotype and life history:

While twenty-two populations were scored for allozymes, only 14 populations were scored for morphology. When combining these two data sets, fourteen populations, matched in geographic region to the morphology samples, were extracted from the allozyme data set.

The first approach combined morphological data, allozyme data (with each locus as single character), and the two karyotypic and three life history characters, with all characters unordered. The second approach is similar except that each electrophoretic allele was treated as a separate character, as described above. Both these analyses were also carried out with the karyotype character treated as ordered, that is, with the bud and petiole gallers assumed to share a reduction in chromosome number.

RESULTS

Pachypsylla phylogeny:

(1) Trees based on electrophoretic data:

No matter which coding methods were employed (frequencies or discrete), which genetic distance measures were applied to the frequency data (Nei's or Rogers'), and which grouping methods were used for genetic distances (UPGMA or Distance Wagner), the multiple populations within each galling position group were always joined together (Fig. 3-2 to 3-5). The results confirm that the leaf gall makers, the petiole gall makers, the bud gall makers and the twig gall makers each form a monophyletic group.

Parsimony analysis treating loci as characters yielded unresolved relationships among the four major gall position groups. Under the other two phylogenetic approaches, distance methods using Rogers' distance and parsimony analysis with alleles as characters, the leaf gall makers are the sister group of the other three, and among the latter, the twig galler and the bud galler together are the sister group to the petiole galler. The UPGMA phenograms give a somewhat different picture, with the petiole galler as basal, and the outgroup *Tetragonocephala* falling within *Pachypsylla*, adjacent to the leaf gallers.

Among the leaf gall makers, the genetic distances are very small (Nei's distances < 0.1), which suggests that the leaf gall makers are recently diverged. Relationships within the leaf gallers vary considerably with the type of analysis and cannot be considered well resolved. When loci are used as discrete characters, the

leaf gall makers are completely unresolved. The strongest suggestion of a grouping is the clustering of the blister gallers in both the distance Wagner and UPGMA analyses (Fig. 3-2 and 3-3). This does not hold, however, when alleles are treated as independent presence/absence characters. Similarly, the inquilines from the two types of nipple galls are joined together in most analyses, but not under UPGMA on Nei's distance.

(2) Cladograms based on morphological data:

Three equally parsimonious trees with a length of 45 steps (Fig. 3-6 a-c) were found when all characters were treated as unordered and equally weighted (CI=0.91, RI=0.94). Successive weighting yielded the same results. These trees differ only in an exchange of positions between the leaf star and blister gallers, and resolution of the latter. The strict consensus tree (Fig. 3-6 d) shows unresolved nodes within the leaf gall makers, the only groups recognized being the two inquilines from nipple galls, and these plus the nipple and disc gallers.

Treating the four morphocline characters as ordered also resulted in three trees (length 49, CI=0.84, RI=0.90) and no change of the topology after successive weighting (Fig. 3-7 a-c). Two of these trees were the same as those found with all characters unordered (Fig. 3-7 a and b). The other differs in grouping the petiole gall maker with the leaf gallers (Fig. 3-7 c).

As in the electrophoretic data, populations of the same gall position were always grouped together. The bud and twig gall makers were always grouped

together. The petiole gall maker is grouped either with the twig and bud gallers, or with the leaf gall makers. Two potential apomorphies, which are unambiguous only if the characters are ordered by morphoclines, place the petiole galler with the leaf gallers. One is surface texture of the vertex with deep wrinkles and short setae (character 1, Fig. 3-8 a and b), and the other is surface texture on the genae bumpy with deep wrinkles (character 3, Fig. 3-8). The petiole gallers share four potential apomorphies (in characters 11, 24, 26 and 31) with the bud and twig gall makers, but all are ambiguous, whether or not morphoclines are used.

(3) Trees based on combined evidence from morphology, allozymes, karyotype and life history:

Ten equally parsimonious trees (length = 99, CI = 0.93, RI = 0.93) were found for the combined data under locus-as-character coding for allozymes with all characters unordered and equally weighted. Five trees are found (length = 190, CI = 0.74, RI = 0.77) when alleles-as-characters coding is used instead. These results are not changed when chromosome number is treated as an ordered character. The strict consensuses for these two sets of trees differ from each other only in that the second is more resolved (3-9 a), and differ little from the consensuses for the corresponding analyses of either allozymes or morphology alone (Figs. 3-4, 3-5, 3-6d). In both, the four gall positions are monophyletic, the bud and twig gallers are sister species, and the inquilines are both monophyletic and related more closely to the nipple and disc gallers than to the other leaf

gallers.

DISCUSSION AND CONCLUSIONS

Monophyly and diversity of gall position groups

The results strongly support the monophyly of gall position groups. In all analyses, all populations with the same galling positions were grouped together.

Diversity within the twig, petiole and bud gallers is low. Petiole gall populations from *Celtis occidentalis* (Maryland) and *C. laevigata* (Texas) are grouped to the exclusion of that from *C. reticulata* (Arizona) in analyses of the electrophoretic data that resolve them, but the frequency differences among these are small (see Chapter I). Allozyme variation among geographic populations of bud gallers is non-significant, and the glabrous bud gallers are not grouped to the exclusion of the hairy bud galler, as might have been expected if these are different species (see Chapter I).

Character variation among populations of leaf gallers is somewhat greater, but there is little clear phylogenetic information and the analysis permits few inferences about the species status or relationships among the gall forming morphs. Several analyses group the blister gall populations together, supporting the hypothesis that these constitute a distinct species (see Chapter I), but this does not always happen (Fig. 3-5). The two populations of the glabrous nipple galler, the other morph represented by more than one sample, are never grouped together. Relationships among different morphs vary considerably with data set

and analytical method.

Perhaps the best-supported conclusion within the leaf gall complex is the grouping of the inquilines from two types of nipple galls, seen in all phylogenetic (as opposed to phenetic) analyses of both allozymes and morphology. This finding is at least consistent with there being only a single inquiline species. The position of this inquiline with respect to the true gall formers is unsettled, but it is very clearly inside the leaf galler complex, and undoubtedly evolved from an ancestor that formed an enclosed gall like that of all other extant *Pachypsylla* species. A similar conclusion, of monophyletic origin from a galling ancestor, was reached in a recent phylogenetic study of

a set of cynipid inquilines (Ronquist, 1994).

Evolution of gall position

The phylogenetic results are consistent with, though they do not conclusively support, the hypothesis that evolution shifts in galling position have proceeded between adjacent plant tissues, *i.e.*, from leaf to petiole to bud to twig. In all analyses in which the positions of the twig and bud galler are resolved, these species are sister groups as the hypothesis predicts (despite the contradictory evidence from chromosome number noted by Riemann [1961]). The petiole galler is ambiguously placed in some analyses, grouping with either the leaf galler or the bud and twig gallers. However, the latter placement, predicted by the hypothesis, is always favored in analyses yielding a single resolution. Finally, given the results

of this analysis, plus the fact that all other members of tribe Pachypsyllini (and indeed most psyllids) are leaf feeders, the ancestral galling site in *Pachypsylla* is almost certainly the leaf blade. On any of the trees with full resolution among the four galling positions, assignment of any other ancestral condition requires an instance of parallel evolution in this trait.

Chapter IV.

Phylogenetic relationships of Pachypsyllini in Spondyliaspidinae and evolution of lerp and gall formation in Spondyliaspidinae

INTRODUCTION

This study presents the first quantitative cladistic analyses of psyllid phylogeny. Although some Hennigian cladograms have been published (*e.g.* Hollis, 1976, 1987; Brown and Hodkinson, 1988; Hollis and Broomfield, 1989), these analyses have been limited in scope. The most comprehensive phylogenetic hypothesis yet advanced is that of White and Hodkinson (1985), which included all of the major groups of the Psylloidea. However, since their paper did not use current computer algorithms and did not present a data matrix, there remains confusion and controversy over phylogeny and classification in this group. As a start toward an intended long-term re-analysis of psyllid phylogeny, this study focuses on the systematics of Spondyliaspidinae, with special reference to Pachypsyllini.

There are three objectives in this paper. The first is to test the monophyly of Pachypsyllini and to estimate the phylogenetic relationships of its constituent genera. The second objective is to test hypotheses on the placement of Pachypsyllini within the subfamily Spondyliaspidinae. Genera included in White and Hodkinson's cladogram and related controversial taxa are sampled. The third goal is to look for phylogenetic trends of gall and lerp formation in Spondyliaspidinae by mapping these traits on the phylogeny. Most members of this subfamily exhibit one or both of these forms of concealment in the nymphal stage.

BACKGROUND

Systematics of Pachypsyllini

Pachypsylla and its relatives *Celtisaspis* and *Tetragonocephala* comprise the tribe Pachypsyllini of the Spondyliaspidinae. The monotypic genus *Uhleria* was included in Pachypsyllini by Crawford (1914). However, the description of its type species *Uhleria mira* was based on a single adult specimen for which both genitalia and locality data were missing. Heslop-Harrison (1954) believed it to be introduced from Australia but offered no opinion on its placement. Taylor (1960) treated it as a synonym of the Australian genus *Lasiopsylla*, a member of Spondyliaspidini in Spondyliaspidinae. This species was not included in my study.

Analysis of the works of previous authors suggests that the following characters define the Pachypsyllini: (1) vertex of adults quadrate, flat and large, (2) adult head very strongly deflexed, (3) adult pronotum vertical, (4) dorsal surface of abdomen lacking distinct sclerites in the nymph, (5) circum-anal pore ring of nymph absent (Crawford, 1914; Tuthill, 1943; White and Hodkinson, 1985). However, some of these characters are also shared by other taxa in the Spondyliaspidinae. Therefore, it was not clear initially which characters are synapomorphies for Pachypsyllini.

All three genera of Pachypsyllini feed on *Celtis* subgenus *Euceltis*, and all are concealed feeders in the nymphal stages. Background information on the classification of *Pachypsylla* was given in Chapter I. The systematic and biological background on *Tetragonocephala* and *Celtisaspis* is given here.

(1) *Tetragonocephala*

Crawford (1914) described the new genus *Tatragonocephala* to include the single species *T. flava,* based on a single "male" specimen collected at Brownsville, Texas. Although the species has been collected in many locations, it remains the only included species of *Tetragonocephala.* He placed this genus together with *Pachypsylla* and *Uhleria* in the tribe Pachypsyllini of the Psyllinae. Tuthill (1943) agreed that *Tetragonocephala* is closely related to *Pachypsylla* although it lacks one of the essential characters of Psyllinae, *i.e.,* spines on the basal segment of the metatarsus. He described more specimens from Texas, Arizona, and from Mexico. Tuthill pointed out that the type specimen designated by Crawford was a female rather than a male and designated a male from Brownsville, Texas, as the allotype.

The reason a psyllid expert like Crawford could make such a mistake is that the species has bizarre female genitalia. Unlike most other psyllids, *T. flava* has a rounded dorsal valve instead of a triangular pointed one (Fig. 3-1). The dorsal valve is exaggeratively enlarged and the caudal margin is covered with dense long hairs.

Tuthill also attributed a nymph described by Ferris (1926) to *T. flava.* Ferris reported that the 5th instar nymph was found in small wax cells on leaves of *Celtis reticulata* at Marathon, Texas. No additional biological information was provided until Riemann (1958) found several populations of *Tetragonocephala* in various parts of Texas on both *Celtis reticulata* and *C. laevigata.* He reported that it occurred in waxy cells similar to those described by Ferris. He reared adults

from the nymphs and confirm that they belong to *Tetragonocephala flava*, which he predicted probably has more than one generation, unlike its univoltine relative *Pachypsylla*.

In 1990, an outbreak of *T. flava* occurred in the southern United States on *Celtis laevigata* (R. Brown and J. Moser, personal communication). The population apparently has been reduced to low levels since then. In 1992, a population of *T. flava* was found in Arizona on *C. reticulata*. I reared material from this population in the lab on seedlings of *C. occidentalis* and *C. tenuifolia* at 20-25°C and found that the generation time from egg to adult was about a month, that individuals have varying growth rates and that the generations overlap. They seemed to be able to survive even when plant quality was poor since they persisted even when all the leaves on the host were drying.

(2) *Celtisaspis*

The genus *Celtisaspis* was described by Yang and Li (1982) in China to accommodate seven Asian *Celtis*-feeding psyllids, two of which had been previously assigned to *Pachypsylla*. The first member of *Celtisaspis* was a nymph described by Boselli (1929) from China. It feeds on *Celtis sinensis*, also a member of the subgenus *Euceltis*, and forms both lerps and galls. Miyatake (1968, 1980) subsequently described two species, *Pachypsylla japonica* (=*Celtisaspis japonica*) and *P. usubai* (=*Celtisaspis usubai*), from Japan on *Celtis sinensis* var. *japonica* and gave detailed biological information. Kown (1983) described *P. japonica* from

Korea on the same host. Takagi and Miyatake (1993) later recorded *P. japonica* from *Celtis bungeana jessoensis*, which is also a member of the subgenus *Euceltis*. *Celtisaspis japonica* was the first lerp-forming psyllid known in Japan. It is bivoltine whereas *C. usubai* is univoltine. Both of them overwinter in the egg stage. In *C. japonica* only the first generation forms both lerps (dome-shaped) and galls (horn-like) whereas the second generation forms lerps only. *C. usubai* forms both round lerps and pit galls.

Yang and Li (1982) described five species of *Celtisaspis* from various regions of China. Three of them, namely *C. guizhouana*, *C. zhejiangana*, *C. liaoningana*, form horn-like galls and lerps at the same time. Previous studies reported that *C. sinica* produces slight pit galls and white oyster lerps. *C. beijingana* forms lerps only (Yang and Li, 1982) but my observations suggest that the nymphs also cause deformation of the leaves on which they form lerps. Yang and Li reported the host species of *C. sinica* to be *Celtis sinensis* but did not specify which species of *Celtis* others feed on. During my collecting trip in China, Li and I found *Celtisaspis beijingana* on both *Celtis sinensis* and *C. bungeana*.

Yang and Li considered *Celtisaspis* to be closer to *Tetragonocephala* than *Pachypsylla* since the former two genera have longer genal cones, longer antennae, an indistinct pterostigma, a short rounded female dorsal valve and have the lerp-forming habit. They agreed with Heslop-Harrison (1954) that all three genera should be placed in Spondyliaspidinae rather than Psyllinae.

Systematics of Spondyliaspidinae

The Spondyliaspidinae, later elevated to family rank (White and Hodkinson, 1985), was described by Schwarz (1898) for the Australian lerp-forming genus *Spondyliaspis* but no definition of the subfamily was given. Heslop-Harrison (1949, 1951, 1954, 1958 and 1959) reviewed the higher classification of world psyllids and first properly defined the Spondyliaspidinae. He distinguished them from the Psyllinae by the following characters: bipartite male proctiger; presence of anteoccipital lobes; tubular or quadrate genae that possess a single, large, peg-like seta; stout antennae; and infrequently the presence of meracanthal spurs (Heslop-Harrison, 1958). Thirteen genera were included; they are from Australia, New Zealand, Central and North America and the Indo-Malayan Archipelago (Heslop-Harrison, 1954).

Most authors since Heslop-Harrison have recognized the group, although there has been some dispute on its definition and boundaries. Four subfamilies of Spondyliaspididae were contained in White and Hodkinson's system, namely Arepuniinae, Euphalerinae, Pachypsyllinae and Spondyliaspidinae, based on both nymphal and adult characters. However, these four subfamilies are polyphyletic in their phylogeny (Fig. 4-1). Taylor (1990) transferred the tribe Ctenarytainini from Aphalarinae to the Spondyliaspidinae based on the similarity of adult morphology. Burckhardt (1991) pointed out that some of the clades in White and Hodkinson (1985) were defined by either plesiomorphic or homoplasious characters and required reexamination. He defined Spondyliaspidini, included

Ctenarytaini as a junior synonym and excluded Euphalerini from the Spondyliaspidinae (Table 4-1). His earlier paper (Burckhardt, 1987), based on the structure of larval tarsal arolia, placed the Arepuninae outside of the Spondyliaspidinae in the Aphalaroidinae. These actions left only two tribes in the Spondyliaspidinae, *i.e.* the Spondyliaspidini and the Pachypsyllini. Although Burckhardt (1991) defined Spondyliaspidini and provided constituent genera, he did not define either Spondyliaspidinae or Pachypsyllini in a definitive manner. Thus, a clear phylogenetic definition for this subfamily is needed.

The position of Pachypsyllini within Spondyliaspidinae

From host plants and biogeography, one might question whether Pachypsyllini belong in Spondyliaspidinae. All other Spondyliaspidinae are endemic to the southern Hemisphere, mostly Australia, and feed on Myrtaceae, mostly *Eucalyptus*. Members of Pachypsyllini occur in the Holarctic, and develop on *Celtis* spp. (Ulmaceae).

Recent authors nonetheless agree that Pachypsyllini is correctly placed in Spondyliaspidinae (Klimaszewski, 1964; Loginova, 1964; Becker-Migdisova, 1973; White and Hodkinson, 1985; Burckhardt, 1991). However, there has been no rigorous phylogenetic test of this proposition, and the exact position of the Pachypsyllini in the subfamily is uncertain. White and Hodkinson regarded Pachypsyllini as a sister group to *Phellopsylla*, which is a member of their polyphyletic Euphalerinae within the Spondyliaspididae (=Spondyliaspidinae)

sensu White and Hodkinson. In contrast, Burckhardt (1991) placed Pachypsyllini as the sister group of the Spondyliaspidini, in which he included *Phellopsylla*. Heslop-Harrison (1949) in his discussion of the strong linkages between many animal and plant groups of Australia and Southern America, stated that *Ctenarytaina*, a small genus in Australia, New Zealand and the South Pacific Islands, "has its nearest relatives in the anomalous genera *Pachypsylla* Riley, *Tetragonocephala* Craw. of Central and Southern North America." These hypotheses are tested by reconstruction of the phylogenetic relationships of Pachypsyllini and other Spondyliaspidinae in this study.

Concealed feeding (lerp- and gall-forming) in Spondyliaspidinae

The Pachypsyllini resembles other Spondyliaspidinae in constructing lerps and galls, unlike nearly all other North Temperate psyllids. The majority of psyllids are free-living. However, at least two types of shelter construction by the nymphal stages have evolved, lerp formation and gall induction. These habits illustrate a widespread evolutionary tendency in sternorrhynchous Homoptera and in a number of other insect groups, *i.e.*, the origin of a concealed, immobile way of life from more or less free-living forms.

A lerp is a case constructed from a carbohydrate secretion from the anus of psyllid nymphs (honeydew) which hardens upon exposure to the air (Dobson, 1851; White, 1972). It has been reported that in some psyllids, *e.g. Celtisaspis usubai* and *Macrohomotoma* sp., the lerp is a mixture of anal discharge and wax

filaments which is similar to the test of the armoured scale *Conchaspis* (Takai and Miyatake, 1993). Each lerp is inhabited and constructed by a single nymph and usually occurs on the leaves. The structure of the lerp is constant within species (Morgan, 1984). Most lerps look rather like the shells of a bivalve but some have the appearance of oyster scale insects, and some form a horizontal tube.

Lerps have generally been accorded a protective function, as a barrier against predator and parasite attack, a reflective shield against radiation, or a means of avoiding desiccation (White, 1970). Most lerp formers occur in the dry regions of Australia, feeding on *Eucalyptus*. White (1970) worked on the feeding biology of the lerp-forming *Cardiaspina densitexta* on *Eucalyptus* in Southern Australia, where the relative humidity frequently drops to 10-15% in the summer. He found that the mouthparts of the nymphs are always inserted through a stoma and that there is almost no air movement under the lerp. There is a remarkable increase in humidity from water vapor transpired by the leaf beneath this structure. The high humidity within the lerp increases the probability that the stomata beneath the lerp will stay open, while elsewhere on the leaf they remain closed to reduce transpiration.

Galls are generally interpreted as abnormal growth of plant tissues caused by various organisms that irritate the plant and possibly lead to the production of a growth hormone (Meyer, 1987). Most galls of psyllids are formed by the feeding of the nymphs. Partial galls, such as pit galls or rolled leaf galls, can be distinguished from complete, enclosed galls, which are exemplified by those of

Pachypsylla species. These broad categories of gall types may represent different degrees of evolutionary advancement. The phylogenetic conservatism exemplified in the retention of ancestral concealment forms in the Pachypsyllini may be mirrored in the evolution of gall variation within *Pachypsylla*. In an analogous gall forming group of insects, the sawfly subfamily Nematinae, it has been suggested that gall formers are derived from a stock of *Nematus*-like free-living sawflies, with a probable evolutionary sequence from free feeding, to leaf folding, to leaf galling to petiole and bud galling, to shoot galling (Smith, 1970; Price, 1988, 1992). Evidence consistent with a similar trend in gall position in *Pachypsylla* was presented in Chapter III.

Hodkinson (1984) proposed that Pachypsyllini illustrate another evolutionary trend in the form of psyllid concealment, from lerp construction to gall formation as in *Pachypsylla*. In contrast, Moore (1970), in a phylogenetic study of *Glycaspis* (Spondyliaspidini) hypothesized a sequence in which galls came first then gave rise to flat lerps, to round lerps, to oval lerps, to rectangular lerps, and finally to no lerps. To test the existence and generality of such hypothesized trends, it will be necessary to identify the nearest relatives of Pachypsyllini among the Spondyliaspidinae.

MATERIALS AND METHODS

Sampling of taxa:

Twenty-seven species in 16 genera were analyzed (Tables 4-1, 4-3),

including all three genera of Pachypsyllini. Within *Pachypsylla*, four species representing three major galling position groups were sampled, including a leaf blister gall maker, *P. celtidisvesicula*, a hairy nipple gall maker, *P. celtidismamma*, a petiole gall maker, *P. venusta*, and a glabrous bud gall maker, *P. cletidisgemma*. To estimate major lineages in Spondyliaspidinae, representative genera of the major groups according to White and Hodkinson (1985), as well as other genera included in the subfamily by Burckhardt (1991), were studied (Fig 4-1, Table 4-1). These taxa are *Creiis*, *Spondyliaspis*, *Cardiaspina*, *Glycaspis*, *Colophorina*, *Euphalerus*, *Phellopsylla*, *Retroacizzia*, and *Arepuna sensu* White and Hodkinson (see Table 4-1). The trees were rooted by including representative genera of other subfamilies of Psyllinae, namely, *Trigonon*, *Acizzia*, *Heteropsylla*, *Psylla* and *Russelliana*. One to three species of each genus were sampled. Five to 30 specimens, slide mounted or pinned, were examined, except that for some only 1 to 4 specimens were available (Appendix 4-1). *Phellopsylla* was sampled in order to contrast White and Hodkinson's hypothesis that *Phellopsylla*, placed in their taxon Spondyliaspididae: Euphalarinae, is the sister group to Pachypsyllini, versus Burckhardt's inclusion of *Phellopsylla* in his Spondyliaspidini. Ctenarytainini was included to test White and Hodkinson's (1985) exclusion of this tribe from their Spondyliaspididae, versus Taylor's (1990) and Burckhardt's (1991) inclusion of it in that taxon. Similarly, *Arepuna* (= synonym of *Russeliana*) is included to test White and Hodkinson's inclusion of this genus in Spondyliaspidini, in contrast to Burckhardt's exclusion of the genus from that tribe.

Morphological methods:

Adult and 5th instar nymphal morphological characters were examined in pinned and slide-mounted specimens. Specimens were obtained from material collected by the author and colleagues, from the psyllid collection of U.S. National Museum of Natural History, Smithsonian Institution (USNM) and from loaned specimens (Appendix 4-1). Slides were prepared from dry or deep-frozen specimens which were dissected under the stereomicroscope after treatment with KOH. Parts were slide mounted in Canada Balsam. Some slides borrowed from the Australian National Insect Collection were originally mounted in polyvinyl lactophenol (see Appendix 4-1).

Characters that were used to define groups of Spondyliaspidinae in White and Hodkinson's (1985) cladogram were carefully examined. Most were included in my analyses; however, the treatment is different. White and Hodkinson tend to treat what are logically the alternative states of a single character as independent, presence/absence characters. For instance, their character 71 is "pterostigma reduced" while character 72 is "pterostigma absent or very reduced", each with two states (present and absent). The pterostigma in my analyses was treated as a single character (#13) with two states, "obvious" versus "absent or very reduced." Other similar examples include adult metatarsus segment I with one or no spines (their characters 78 and 79; my character 16) and wing apex shape (their characters 63-65; my character 11).

Forty-five characters were used, including 10 adult head characters, 7 adult

thorax characters, 5 male genitalic characters, 4 female genitalic characters and 19 nymphal characters (Tables 4-2, 4-3). Twenty-eight characters were binary, while the remaining eighteen had multiple states.

Terminology follows Brown and Hodkinson (1988) for adult characters, and White and Hodkinson (1982) for nymphal characters.

Morphological data analyses:

Morphological characters were coded numerically. Polymorphism within a terminal taxon was coded as ambiguity (*e.g.* character 14). In an initial analysis, with all characters unordered and no outgroups specified, the two species of *Russelliana* grouped with the four taxa of Psyllinae. In subsequent analyses, these six taxa were designated as outgroups. Characters were first treated as all unordered and of equal weight. Successive weighting according to the rescaled consistency index was then applied (Farris, 1988). In a separate analysis, transformation series were assigned for multistate characters 3, 4, 5, 6, and 7, as discussed below. Equal weighting was followed by successive weighting as before.

Transformation series were erected only for characters in which a morphocline seemed clearly plausible. Character 3 describes irregular depressions or fovea on the vertex, which are always present in psyllids (Brown and Hodkinson, 1988). Usually these appear as a pair, one on each side of the vertex, with different degree of expression in different taxa, sometimes obvious and sometimes not. In *Trigonon longicornis*, the depression appears as a vertical curve

bearing two pits or indentations on each side. In *Phyllolyma*, three indentations were seen. The number of obvious indentations, which varied from zero to three, was treated as a stepwise transformation series.

In psyllids, the genae are often swollen to form genal processes or cones, which provide useful characters (Brown and Hodkinson 1988). Character 4, which encodes the length of the genal cones compared to the length of the vertex, is treated as a linear transformation series.

Character 5 describes variation in the shape of the occipital foramen, a previously overlooked feature. The apparent shape varies with the viewing angle, but is constant within genera when the head is positioned horizontal to the vertex. Three shape categories were recognized (Fig. 4-2). The apparent intermediacy of type b between types a and c was encoded in the transformation series a-b-c.

The antennae of psyllids show different degrees of modification. Character 6 encodes the length of the antennae standardized by the width of head including eyes, and is treated as a four-state linear transformation series ranging from 0.7 to 2.0.

Most psyllid antennae have ten segments. The basal two segments are usually the shortest and the third the longest. In *Pachypsylla* the tenth segment is the shortest. Character 7 encodes the length of antennal segment X to compared to that of segment I, and is treated as a linear transformation series.

The phylogenetic significance of one character, the apical spines (saltatorial spurs, character 14), might be questioned. The number of these spines is variable

within species, sometimes even within one individual, and there is overlap between species. Hollis (1984), in his revision of Afrotropical Triozidae, did not consider the apical tibial spurs a good phylogenetic character since they have arisen more than once. In contrast, Brown and Hodkinson (1988), in their study of Panamanian psyllids, considered the number and position of these spurs to be an important character in the higher taxonomy of the Psylloidea. White and Hodkinson's analyses divided the number of spines into two groups, more than 6 or less. The same method of coding was used in this study. Despite its variability, this character had a retention index of 0.75, about average. Therefore, it was retained in the analysis.

Phylogenetic reconstruction was carried out first in Hennig86 ver. 1.5 (Farris, 1988) and then in PAUP ver 3.1.1 (Swofford, 1993) based on the parsimony criterion. In PAUP, the random addition sequence option for heuristic search was used, with replications set at 1000. Additional character analyses were performed using MacClade ver. 3 (Maddison and Maddison, 1992).

Life history information, character coding and hypotheses testing:

Relatively little attention has focused on the life history and ecology of the Psylloidea as compared to other sternorrhynchous homopterans such as aphids and scale insects. The relevant literature is widely scattered and has not been comprehensively reviewed. I compiled the available information on the feeding habits for each genus included in the phylogenetic analysis. These data are

presented in Results.

To reconstruct the evolutionary history of concealment forms on the cladogram, the variation in habits must be coded as character states. The best way to do this is not obvious. Therefore, two approaches were taken. The first coding method (Table 4-4, coding 1) is a simplified contrast among three conditions treated as states of a single character, namely, free-living (F or 0), lerp-forming (L or 1), and gall-making (G or 2). This coding is the simplest rendering of the hypothesis of Hodkinson described earlier, in which lerp forming is postulated to be intermediate between free living and full concealment as in galls. Species that do not form galls or lerps, even if they produce ample wax or flocculent, were coded as free-living, and no distinction was made between partial and enclosed galls. *Celtisaspis beijingana*, which forms both lerp and gall, was coded as polymorphic (ambiguous).

The second approach coded lerp-forming and gall-making as independent characters, which seems appropriate because these concealment forms are structurally non-homologous and can be found together in the same species. For gall formation, it is postulated that partial gall-forming (P or 1) is phylogenetically intermediate between enclosed gall-making (G or 2) and no host modification (N or 0) (Table 4-4, coding 2). For lerps, it is postulated that production of abundant wax and honey dew flocculence (W or 1) is an intermediate stage in the evolution of structured lerps (L or 2) from free living (N or 0), defined as production of neither lerp nor flocculence (Table 4-4, coding 3).

To test the hypotheses embodied in them, these codings were superimposed on the phylogeny of Figure 4-3 (tree b), inferred from morphological characters excluding feeding habits, to determine the minimum number of evolutionary changes required by each. The number of steps required under the postulated ordering was contrasted to that under all possible other ordering. These calculations were done using PAUP ver. 3.1.1 (Swofford 1993) and MacClade ver. 3 (Maddison and Maddison 1992).

To test statistically whether there is any phylogenetic component to the distribution of concealment types, a randomization approach was used (Faith and Cranston 1991; Liebherr and Hajek, 1990; Maddison, 1990). The inferred number of independent origins of concealment types was contrasted to a null distribution obtained by 1000 random reassignments of the character states to taxa on the cladogram, generated by the PC Pascal program "MMMAT" (G. Roderick, unpublished). The minimum required number of origins of concealment types (treated as unordered character states) under each randomization was calculated in PAUP.

RESULTS

The phylogenetic relationships

When all characters were treated as unordered, three most parsimonious trees (Figure 4-3) were found, with a length of 124 steps and a consistency index (CI) and retention index (RI) of 0.55 and 0.78, respectively. The same three trees

are found by successive weighting. The strict consensus of these, shown in Figure 4-3 (d), is identical to the Adams and 50% majority rule consensus trees. The three most parsimonious trees differ only in the way the two species of *Creiis* are related to *Cardiaspina*. As in the earlier analysis of Pachypsyllini (Chapter III), relationships among the *Pachypsylla* leaf gall makers are unresolved.

When the five characters (3-7) for which morphocline transformation series were hypothesized were treated as ordered, 164 equally parsimonious trees with a length of 134 steps were found with CI = 0.51 and RI = 0.75. Among these are the three trees found for unordered characters. The strict consensus tree is shown in Figure 4-4. There is considerably less resolution than in the unordered analysis (17 groups resolved versus 24). Ambiguities in addition to those appearing in the unordered analysis include the positions of *Spondyliaspis*, *Euphalerus* sp. and *Acizzia*. Successive weighting reduced the number of trees to ten, all included in the original 164 but none identical to any tree found with unordered characters. Their strict consensus tree is shown Figure 4-5. This tree is nearly as resolved as that for the unordered analysis, except for the position of Spondyliaspis, and disagrees only slightly, in the position of *Euphalerus* sp. A.

Lerp and gall forming biology in the Spondyliaspidinae

The literature search on feeding habits produced the following summary for the genera included in the phylogenetic analysis.

(1) *Pachypsylla* is a North American enclosed gall former, feeding exclusively

feeding on hackberry *Celtis* subgenus *Euceltis*. The plant tissues attacked include the leaf blade, petiole, bud, and twig, each by different species (Osten Sacken, 1861; Riley, 1876-1890; Tuthill, 1943).

(2) *Tetragonocephala* is found in the southern United States and northern Mexico feeding on *Celtis* subgenus *Euceltis*. This monotypic genus forms a round white lerp on the leaves (Crawford, 1914; Riemann, 1958).

(3) *Celtisaspis* is distributed in Asia (Japan, Korea and China) and also infests *Celtis* subgenus *Euceltis*. Nymphs feed on the undersides of hackberry leaves, producing partial (pit or horn-shaped) galls or sometimes just inconspicuous deformation of the leaf, and are always concealed within lerps (Boselli, 1929; Miyatake, 1968, 1980; Yang and Li, 1982; Kwon, 1983).

(4) *Phellopsylla*, originally described as *Thea*, is an Australian *Eucalyptus* feeder. Species of *Phellopsylla* are found under smooth barked eucalypts, feeding on the bark and excreting long white waxy filaments at various levels on the main trunk, usually under pieces of dried bark still loosely attached, up to the terminal branchlets (Taylor, 1990).

(5) *Phyllolyma* is a *Eucalyptus* feeder in Australia, forming white round lerps on the terminal branchlets or bivalve lerps inserted into the margins of the leaves. The white round lerps are unwoven and fragile. In some cases, more than one species may occupy the same site (Morgan, 1984; Taylor, 1990).

(6) *Creiis* forms oyster-shaped lerps on the leaves of *Eucalyptus* in Australia

(Froggatt, 1900; Morgan, 1984).

(7) *Spondyliaspis* forms brown shell-like lerps on *Eucalyptus* leaves in Australia (Morgan, 1984; Carver, 1987)

(8) *Cardiaspina* is one of the most divergent Spondyliaspidinae (Taylor, 1960, 1962). It is an *Eucalyptus* feeder. Different species form various kinds and colors of lerps (Cambell, 1964; Crawford, 1911; Morgan, 1984; Taylor, 1989, 1992; White, 1970).

(9) *Glycaspis* is a large Australian group that forms either lerps or galls on *Eucalyptus*. Moore (1970) divided the genus into three subgenera, of which *Boreioglycaspis* was raised to the generic level by Burckhardt (1991). The remaining subgenera are *Synglycaspis*, which builds round, oval, or rectangular lerps, and *Glycaspis*, which makes galls, flat lerps or round lerps (Moore 1970).

(10) *Ctenarytaina* is an Australian/Asian/Pacific genus. All the known species are free-living, feed on shoots of *Eucalyptus*, and produce viscous globules and flocculent threads. One species, *C. longicauda*, was found feeding among young leaf buds that were still closely folded, and it exuded thin white threads (Morgan 1984; Taylor, 1987; Carver, 1989).

(11) *Colophorina* occurs in Southern Africa on *Cassia petersiana* (Leguminosae). The nymphs are covered with fine wax particles, and live and develop between pairs of unopened leaflets which form a globular pouch (Capener, 1973).

(12) *Euphalerus* is a heterogeneous legume-feeding group found in both the New World and the Old World. Both gall-making and "nest-constructing" (=lerp-forming?) species are found (Russell, 1971).

(13) *Russelliana* (= *Arepuna sensu* White and Hodkinson) is a free-living South American group feeding on Solanaceae (Tuthill, 1959).

(14) *Heteropsylla* is a New World legume-feeding and free-living genus (Crawford, 1914; Beardsley, 1987).

(15) *Acizzia* is a free-living and legume-feeding genus typical of the warmer regions of the Old World, Africa, Arabia, India and Australia (Morgan, 1984; Carver, 1987; Heslop-Harrison, 1949).

(16) *Trigonon* is a small Austral-Oriental genus with unknown feeding habits (Crawford, 1920).

(17) *Psylla s. str.* is a Holarctic genus, members of which are free-living on Betulaceae and Carpinaceae (Crawford, 1914; Hodkinson, 1988).

The evolution of concealed feeding in psyllids

In the first coding method (Table 4-4, coding 1), under which lerps and galls are treated as part of a single transformation series, the predicted ordering, F-L-G, requires 4 steps, the same as does no ordering at all, while the alternatives F-G-L and L-F-G require 7 and 5 steps, respectively. Under all three transformation series as well as no ordering, significantly fewer steps are required than for the same data randomized on the tree ($p<0.0001$).

Under the second coding, galls and lerps were treated independently. For galls, the predicted ordering, N-P-G, requires 3 steps, as does the alternative N-G-P, but the alternative P-N-G requires the minimum possible, 2 steps. Thus, the prediction is not supported. For lerps, the predicted ordering N-W-L requires 6 steps, one more than the alternative N-L-W, which requires 5. For both lerps and galls, significantly fewer transformations are required than under the null hypothesis of independence of phylogeny (randomization test, $p<.05$ and $p<.001$, respectively).

DISCUSSION AND CONCLUSIONS

Phylogenetic relationships

The phylogenetic analyses confirm that the Pachypsyllini are a monophyletic group. *Tetragonocephala* and *Celtisaspis* form a clade which is the sister group to *Pachypsylla*. This result is congruent with White and Hodkinson's (1985) conclusion. However, the characters defining the group are somewhat different. Three characters were presented as defining the Pachypsyllini in White and Hodkinson's phylogeny, namely, anteoccipital lobes absent (their char. 53), rhinarium absent from seg. V (their char. 58), and dorsal surface of abdomen lacking distinct sclerites (their char. 126). The second character is homoplasious and probably plesiomorphic within the Psylloidea (Burckhardt, 1991). The first and third characters are true synapomorphies (characters 10 and 33 in my analyses). In my analysis another character was found that also defines the group,

i.e. the presence of the nymphal trochanters (character 30).

Since the hypothesized morphoclines decreased rather than enhanced tree resolution, presumably because they increased character conflict, I place more credence in the analysis using only unordered characters. The three trees obtained with the latter differed only in the position of the two *Creiis* species; the monophyly of *Creiis* needs further testing. For comparison with White and Hodkinson's results, tree (b) in Figure 4-3, which grouped the two *Creiis* species together, was chosen. This tree differs from White and Hodkinson's (1985) cladogram in many places. The main differences are as follows:

(1) *Phellopsylla* is not the sister group to Pachypsyllini in my analyses. Instead, it and *Phyllolyma* together are the sister group of the rest of Spondyliaspidinae *sensu* Burckhardt and are a group within Spondyliaspidinae *sensu* White and Hodkinson. One character uniting *Phellopsylla* and Pachypsyllini in White and Hodkinson's tree is the bipartite male proctiger. This character is hard to see. Burckhardt (1991) reported that the second segment is present in *Phellopsylla*, but is reduced and membranous. Examination of the specimens available to me yielded no suggestion of the presence of a second segment. Therefore, I coded the proctiger in these groups as unipartite. Changing the coding to bipartite, to agree with Burckhardt's and White and Hodkinson's codings, did not change the results. More observations are needed to determine which coding is correct.

(2) *Euphalerus nidifix* is the sister group to all other Spondyliaspidinae *sensu* White & Hodkinson in my analysis, whereas in White and Hodkinson's cladogram, it is next to *Phellopsylla* and in the middle of the spondyliaspidid clade. *Euphalerus* was a polyphyletic taxon on White and Hodkinson's cladogram; different species of the genus were in different clades of Spondyliaspidinae. Burckhardt (1991) removed Euphalerini *sensu* White and Hodkinson from Spondyliaspidinae since it has a larval tarsal arolium with a pedicel and a visible unguitractor. In my analyses, the arolia and unguitractor are absent in all species above *Colophorina* and *Euphalerus*, whereas all others have them. *Euphalerus* sp. A. *sensu* White and Hodkinson shares more character states, though plesiomorphic, with *Colophorina* than with *E. nidifix*. It is not likely that *Euphalerus* sp. A is congeneric with *E. nidifix*. As suggested by D. Hollis (per. comm.) and White and Hodkinson's tree, *Euphalerus sp. A.* might turn out to be a species of *Colophorina*, although these are not always grouped together.

(3) *Ctenarytaina* branches off above (*Phellopsylla* + *Phyllolyma*), well within the Spondyliaspidinae. It was excluded from the Spondyliaspidinae and placed in Euphyllurinae (Aphalaridae) by White and Hodkinson. This hypothesis is not conclusively ruled out by my study, since no other members of Euphyllurinae were sampled, but my results support instead the views of Taylor (1990) and Burckhardt (1991). Taylor (1990) transferred Ctenarytainini to the Spondyliaspidinae based on the similarity of adult

characters with other spondyliaspidines. He also pointed out that the only significant differences between Ctenarytainini and Spondyliaspidini are the presence of a caudal plate and lanceolate setae in the larvae. Burckhardt (1991) further noted that Ctenarytainini have the spondyliaspidine nymphal aroliumi, *i.e.*, membranous without pedicel and visible unguitractor, and rejected the free-living habit of Ctenarytainini as grounds for removal from Spondyliaspidini, since concealment habits are quite homoplasious.

(4) The relationships within the *Creiis* + *Cardiaspina* + *Glycaspis* + *Spondyliaspis* clade are completely different between my tree and White and Hodkinson's.

My results also cast doubt on the monophyly of Spondyliaspidini *sensu* Burckhardt, part of which forms the sister group to Pachypsyllini. Further sampling of Spondyliaspidini and Ctenarytainini *sensu* White and Hodkinson and Taylor is needed to test this finding.

Heslop-Harrison (1949) suggested that the Australian psyllids originated in part, during early Tertiary times, as immigrants from Antarctica, and in part through. He assigned psyllid fossils of that age from Tasmania, presumably a major corridor between these two continents, to the genus *Ctenarytaina* Ferris and Klyver. The relatively basal position of *Ctenarytaina* in my cladogram of the Spondyliaspididae, a largely Australian group, is consistent with Heslop-Harrison's view.

The evolution of concealed feeding in psyllids

The analysis of concealment habits under coding method #1 supported Hodkinson's postulate that lerps tend to precede galls in spondyliaspidine phylogeny. Within galls and lerps considered separately, however, there is no support for the idea that partial galls or lerps represent a phylogenetically transitional stage from free living. These tests, it must be stressed, are heuristic only. No statistical test was applied, and the data are very incomplete. Outgroup sampling and life history information is sparse, and even within Spondyliaspidinae, numerous genera and species are unrepresented in the analysis.

Despite limited data, however, there is strong support for the more general postulate that concealment forms characterize phylogenetic groups. Thus, we can reject the alternative hypothesis that these features reflect only rapid and variable adaptation to local environmental conditions, appearing and disappearing with no phylogenetic pattern. It will therefore be of interest to look further into possible evolutionary trends in, and consequences of, those habits.

In a survey of gall-inducing families among arthropods, Roskam (1992) distinguished two patterns in the taxonomic distribution and host associations of gallers. In major groups (families) of gall inducers, *e.g.* Cecidomyiidae, most members are gall makers and their host plants include diverse angiosperms. These are likely to have evolved from an ancestor that already possessed the gall-inducing ability in an early period of angiosperm radiation. In contrast, minor galling groups, such as Curculionidae, Tenthredinidae, Cephidae, Gelechiidae,

Tephritidae, and Agromyiidae, have only a few exceptional members making galls. These represent late radiations confined to particular plant genera. In Roskam's view, homopteran and thrips gall inducers are intermediate between these two groups. The numerous galling members are scattered among non-galling ones and across many plant groups. His interpretation is that sap-feeding offers homopterans considerable opportunities for manipulating host plant; as a consequence, gall inducers evolved independently many times from sap feeders, over a long geological time span.

Roskam's explanation seems plausible. Galling psyllids occur in various clades. The phylogenetic pattern may not be demonstrated at higher levels but is evident in closely related groups. Burckhardt (1991) suggested that diversification of Spondyliaspidini may have occurred, together with that of their myrtaceous hosts, during the mid-Eocene. The earliest fossil Psylloidea come from the middle (Handlirsch, 1925; Klimaszewski, 1993a) and upper Jurassic periods (Becker-Migdisova, 1949, 1985). If this is true, Spondyliaspidini is relatively young compared to other major galling insect groups and other psyllid clades. By the Oligocene the eucalypts and acacias became important elements in the vegetation of Australia, which became increasingly arid. Fire resistance probably played an important role in the high diversity of present-day Australian Myrtaceae. In conjunction with host-plant speciation, development of lerp and gall concealment might have furthered spondyliaspidine diversification by protecting them from environmental extremes.

There are many hypotheses on the adaptive value of gall formation. Price *et al.* (1986, 1987) recognized six explanations. These include the "nonadaptive" hypothesis, the "mutual benefit" hypothesis, the "plant protection" hypothesis, the "nutrition" hypothesis, the "microenvironment" hypothesis, and protection from enemies. They rejected the first three hypotheses since galls clearly benefit the gall forming insect, not the plant.

The relative importance of these alternative effects, for psyllid gallers, is unclear. Many studies have suggested that galls do not protect psyllids from natural enemies (Smith, 1970; Askew, 1980; Washburn & Cornell, 1981). They may even increase susceptibility to enemies which seek out aggregations of hosts. The "microenvironment" hypothesis, that galls serve to protect psyllids from climatic extremes such as desiccation, seems plausible, in the absence of evidence to the contrary. There is also evidence consistent with the hypothesis that gall formation improves psyllid nutrition. It has been found that in the nipple galls formed by *Pachypsylla celtidismamma* on *Celtis*, lipid material is abundant basal to the central depression, and carbohydrates are also present (Beisler, 1989; Beisler and Baker, 1992). However, the importance of these supplies to the nymphs has not been studied.

Heslop-Harrison (1949), in his discussion of a free-living species, *Ctenarytaina eucalypti*, and its close association with lerp formers suggested that lerp-making habits may function as a way of surviving in sticky or gummy surroundings. Although *C. eucalypti* is not a lerp maker, it shares many peculiar

structures with true lerp makers. Heslop-Harrison believed that some of these peculiarities are undoubtedly closely associated with the lerp-making habits. This suggests a variant of the microenvironment hypothesis for evolution of lerps, contrasting to avoidance of desiccation, the focus of previous theories. The flocculence or lerp seems to provide a way of carpeting that may serve both functions. In fact, observation of the lerp forming *Celtisaspis* and *Tetragonocephala* found that the lerp actually encloses the nymph even on the under side. If the lerp is formed solely to avoid desiccation or even natural enemies, one would not expect the lerp to cover the underside of the psyllid body beneath the leaf. This feature in Pachypsyllini lerp-formers, not gummy eucalyptus feeders, may be explained as a primitive characteristic maintained from the *Eucalyptus*-feeding ancestors. More careful observations are necessary for testing the hypotheses.

The basal groups of Spondyliaspidinae, *i.e. Ctenarytaina*, *Phellopsylla* and *Phyllolyma*, are either free-living or lerp-forming. The free-living species produce copious amounts of flocculence, and tend to be cryptic. Ctenarytainini live among leaf buds, within rolled leaves caused by spiders or caterpillars, under deserted lerps of Spondyliaspidini, and even inside sawfly leaf mines (Taylor, 1990). *Phellopsylla* hide under bark and cover the space with fair amount of wax (Froggatt, 1990). Even the lerp-forming *Phyllolyma* produce primitive lerps similar to some *Glycaspis* species although it is more like a sugary encrustation than the true lerps of *Cardiaspina* and *Lasiopsylla* (Morgan, 1984; Froggatt, 1990; Taylor, 1990). This suggests that these taxa are intermediate between the free-living and

true lerp-forming groups.

Appendices

Appendix 4-1. Specimens examined* for the Study of Pachypsyllini/ Spondyliaspidinae Phylogeny.

Pachypsyllini Becker-Migdisova
- *Pachypsylla* Riley [see Table 1-3, USNM, MMY]
- *Tetragonocephala* Crawford [10 dry USNM, 20 ♂+♀+n MMY]
- *Celtisaspis* Yang & Li [1 dry USNM, 15 ♂+♀+n MMY, 5 dry FSL]

Spondyliaspidini Schwartz
- *Cardiaspina* Crawford
  - *C. albitexturata* Taylor [2 slds, nymph+♂+♀, DH; 1♂+1♀ dry prtp, USNM]
  - *C. vittaformis* [1 sld, ♂+♀, DB]
- *Creiis* Scott
  - *C. tecta* [1 sld, ♂, DB]
  - *C. longipennis* (Walker) [2♂+2♀ lerps, KLT; ♂+♀+n, 3 slds, ANIC]
- *Glycaspis* Taylor
  - *G. (Glycaspis) baileyi* Moore [1 sld, nymphs+♂+♀, DH; 3♂+3♀ lerps, KLT]
  - *G. (Synglycaspis) aggregata* Moore [1 sld, ♂, DH; 2 slds, ♂+♀, DB]
  - *G. (Synglycaspis) planitecta* [1 sld, ♂, DB]
- *Phellopsylla* Taylor
  - *P.* sp. [2♂+2n, 4 slds (3plvp), ANIC]
  - *P.* sp. [4♀+ many n, in alc, GT]
- *Phyllolyma* Walker
  - *P. (=Cometopsylla) rufa* (Frog.) [2♂, 2 slds, ANIC]
  - *P.* sp. [♂+n, 2 slds (plvp), ANIC]
  - *P.* sp. [a+n, GT]
- *Spondyliaspis* Signoret
  - *S. plicatuloides* (Froggatt) [♂+♀+n, 3 slds, ANIC]

Ctenarytainini White & Hodkinson (1985) = Spondyliaspidinae
- *Ctenarytaina* Ferris & Klyver
  - *C. eucalypti* (Markell) [3 slds (♂,♀,n), DH; 1 sld, nymph, DB; 5 dry, USNM; 2♂, 2 slds (plvp), ANIC]

Others
- *Arepuna* Tuthill = *Russelliana* (Aphalaroidinae)
- *Acizzia* Heslop-Harrison
  - *A. uncatoides* (Ferris and Klyver 1932) [3 slds (♂,♀,n), USNM (Brown's collection)]
- *Colophorina* Capener (Euphalerinae sensu Hollis ms)
  - *C. cassiae* Capener [1 dry (♂), DH]
- *Cometopsylla* Froggatt = *Phyllolyma* (Spondyliaspidinae)

Euphalerus Schwartz (Euphalerinae)

E. sp. A. (=? *Colophorina*) [3 slds (♂,♀,n), DH]

E. nidifex Schwarz 1940 [♂+♀ 117 dry NE, 14 dry NT, lerps+nymphs USNM]

Heteropsylla Crawford 1914

H. texana Crawford 1914 [6+ slds, ♂+♀n, USNM]

Russelliana (syn. Arepuna Tuthill) = Aphalaroidinae

R. adesmiae [4 slds, ♂+♀ prtp, DB]

R. fabianae [4 slds, ♂+♀ prtp, DB]

Trigonon Crawford 1920

T. longicornis (Crawford 1919) [4 dry (3♂,2♀), USNM Tuthill collection]

* Acronyms: 1) prtp: paratypes, slds: slides, dry: pinned specimen; 2) ANIC: Australian National Insect Collection, DB: Daniel Burckhardt, Geneva Museum, DH: David Hollis, National Museum of Natural History, London, FSL: Fasheng Li, Beijing Agricultural University, China, KLT: Keith L. Taylor, CSIRO, MMY: Man-Miao Yang, USNM: U.S. National Muesum of Natural History; YJK: Yong Jung Kwon, South Korea; 3) Biogeographic regions: NE: Neartic, NT: Neatropic, ET: Ethiopian, OR: Oriental, PA: Paleartic, AU: Australian.

Tables and Figures

Table 1-1. Species entities described in *Pachypsylla* (Homoptera: Psylloidea).

SPECIFIC EPITHET	GALL POSITION AND SHAPE	HOST PLANT *CELTIS****	DISTRIBUTION	OVER-WINTER
*celtidismamma**+ (Riley 1876)	leaf mammiform	*occidentalis* (*laevigata*) (*tenuifolia*)	AZ CO CT IA IL ID IN KS MD MN NE NJ NY NC OH OK TX UT VA DC CANADA	adult
celtidispubescens Riley 1890	leaf mammiform	*reticulata* *laevigata*	MS TX OK CO	adult
celtidisglobulus+ Riley 1890	leaf mammiform	sp.	MS MO	adult
celtidiscucurbita Riley 1890	leaf mammiform	sp.	MO IA	adult
celtidiscucurbita var? (Riley 1890)	leaf mammiform	sp.	MO TX	adult
sp. Riemann 1961**+	leaf mammiform	*laevigata*	TX	adult
rohweri Cockerell 1910	leaf mammiform	*reticulata*	CO TX OK	adult
celtidisminute Mally 1894	leaf ?	?	IA KS	adult
celtidisasteriscus+ Riley 1890	leaf star-shaped	*laevigata* *reticulata* *tenuifolia* (*occidentalis*)	MD MS IA OK TX VA MO LA	adult

Table 1-1 (cont.). Species entities described in *Pachypsylla* (Homoptera: Psylloidea).

SPECIFIC EPITHET	GALL POSITION AND SHAPE	HOST PLANT *CELTIS****	DISTRIBUTION	OVER-WINTER
celtidisumbilicus Riley 1890	leaf wart-like depressed at middle	sp.	IA MS MD VA MO AR	adult
*celtidisvesicula**+ Riley 1884	leaf blister-like	*occidentalis* (*reticulata*) (*laevigata*)	AZ CT IL IA KS LA MD MS NE NY OH OK VA	adult
new sp. 1 Riemann 1961**+	leaf blister-like	*laevigata*	TX OK	adult
new sp. 2 Riemann 1961**+	leaf blister-like	*reticulata*	TX NM AZ OK	adult
new sp. 3 Riemann 1961**+	leaf blister-like	*reticulata* *laevigata*	TX	adult
new sp. 4 Riemann 1961**+	leaf variously modified ass. w/ others	*reticulata* *laevigata*	TX	adult
*venusta**+ Osten-Sacken 1861	petiole spherical	*occidentalis* *laevigata* *reticulata* *tenuifolia*	CO CT IA ID KS MD MS NJ NM NC OH TX TN VA	5th instar nymph
tridentata Patch 1912	petiole	sp.	CO	?

Table 1-1 (cont.). Species entities described in *Pachypsylla* (Homoptera: Psylloidea).

SPECIFIC EPITHET	GALL POSITION AND SHAPE	HOST PLANT *CELTIS****	DISTRIBUTION	OVER-WINTER
celtidisgrandis Riley 1876	petiole	?	IA	?
*celtidisgemma**+ Riley 1885	bud irregularly round	*occidetalis* *laevigata* *reticulata* *tenuifolia*	CT IA KS MD MO MS NY NJ OH OK TX VA DC	5th instar nymph
*celtidisinteneris**+ Mally 1894	twig obolong-oval	*occidentalis* *tenuifolia* *laevigata* *reticulata*	MD IA IL OH KS TX VA	5th instar nymph
ungulata Caldwell 1938	twig obolong-oval	sp.	OH	5th instar nymph
*dubia** Patch 1912	?	sp.	TX	?
*pallida** Patch 1912	bud irregularly round covered with dense hairs	*reticulata*	AZ NM TX	?
tropicala Caldwell 1944	?	?	MEXICO	?

* Species recognized by Tuthill (1943).
+ Species recognized by Riemann (1961).
** Unpublished Ph.D. dissertation.
*** Host plants in parantheses are probably erroneous records.

Table 1-2. Synopsis of hackberry psyllid gall types, *Pachypsylla* (Homoptera: Psyllidae), their distribution and association with host species.

GALL TYPES	ASSOCIATED SPECIES NAMES	DISTRIBUTION	ASSOCIATED HOST PLANT*
PETIOLE GALL	*P. venusta* (Osten-Saken 1861) *P. tridentata* Patch 1912 *P. celtidisgrandis* Riley 1876	All over the hosts ranges, northeast to CT, southwest to AZ, UT, southeast to Georgia, northwest to ID.	*C. occidentalis* *C. tenuifolia* *C. laevigata* *C. reticulata*
GLABROUS BUD GALL	*P. celtidisgemma* Riley 1885	Central and eastern U.S.	*C. occidentalis* *C. tenuifolia* *C. laevigata*
HAIRY BUD GALL	*P. pallida* Patch 1912	AZ, NM, OK	*C. reticulata*
TWIG GALL	*P. celtidisinterneris* Mally 1894 *P. ungulata* Caldwell 1938	Reported from central and eastern U.S.	*C. occidentalis* *C. tenuifolia* *C. laevigata* *C. reticulata*
REGULAR BLISTER GALL without upper central spine	*P. celtidisvesicula* Riley 1884	Northeastern U.S., as for *C. occidentalis*	*C. occidentalis*
	new sp. 1 Riemann 1961**	TX	*C. laevigata*
	new sp. 2 Riemann 1961**	TX, NM, AZ, OK	*C. reticulata*
BLISTER GALL with upper central spine	?	LA VA	*C. laevigata* (*C. tenuifolia*)
ROUGH BLISTER GALL without upper central spine	new sp. 3 Riemann 1961**	TX	*C. reticulata* (*C. laevigata*)
DISC GALL	*P. celtidisumbilicus* Riley 1890	MD, VA, AR, MO, IA, MS	*C. occidentalis*

Table 1-2. (cont.) Synopsis of hackberry psyllid gall types, *Pachypsylla* (Homoptera: Psyllidae), their distribution and association with host species.

GALL TYPES	ASSOCIATED SPECIES NAMES	DISTRIBUTION	ASSOCIATED HOST PLANT*
HAIRY NIPPLE GALL	*P. celtidismamma* (Riley 1876)	Widely distributed in eastern North America, north to Ontario, south to NC, east to CT, NY, west to NE, KS, OK.	*C. occidentalis*
	P. rohweri Cockerell 1910	CO, TX, OK	*C. reticulata*
	P. celtidispubescens Riley 1890	Southwestern U. S., e.g. TX, OK, CO, MS.	*C. reticulata*
GLABROUS NIPPLE GALL	*P. celtidisglobulus* Riley 1890	Northeastern U. S., e.g. MD, VA, MO, MS.	*C. tenuifolia*
	P. celtidiscucurbita Riley 1890		
	P. sp. Riemann 1961** (probably= *P. celtidiscucurbita* var. ? Riley 1890)	Southern U.S., e.g. MO, TX.	*C. laevigata*
STAR GALL with upper central spine	*P. celtidisasterisca* Riley 1890	Southern U.S., e.g. TX, MO, LA.	*C. laevigata* *C. reticulata*
STAR GALL without upper central spine	*P. celtidisasterisca* Riley 1890	Northeastern U.S., e.g. MD, VA.	*C. tenuifolia* (*C. occidentalis*)
UNKNOWN	*P. tropicala* Caldwell 1944	Mexico	unknown
	P. dubia Patch 1912	TX	unknown
INQUILINE	new sp. 4 Riemann 1961**	in TX and may be widespread in all gall types except *occidentalis* blister gall.	*C. laevigata* *C. reticulata* *C. occidentalis* *C. tenuifolia*

* host in parentheses = occasional observation.

** based on unpublished dissertation of Riemann (1961). Proposed species here numbered arbitrarily.

Table 1-3. Localities from which samples of populations of different Pachypsylla gall types from various host plants were obtained for protein electrophoretic, life history and morphological studies.

Gall types	Localities sampled[1]	
LEAF STAR GALL (LS)	MD: BB[2,b], NAL[2,b], PG[a], PRP[a], SI[a]	(C. tenuifolia).
	VA: WBP[a]	(C. laevigata);
	GFV[2,a]	(C. occidentalis).
	TX: AUS[a]	(C. laevigata).
LEAF GLABROUS NIPPLE GALL (LNg)	MD: BB[2,b], DEAL[a], NAL[2,b], PRP[a], PG[a], SI[a]	(C. tenuifolia).
	VA: GFV[2,b]	(C. occidentalis);
	WBP[a]	(C. laevigata).
	AR: FAY[a]	(C. occidentalis).
	LA: ALX[a]	(C. laevigata).
LEAF HAIRY NIPPLE GALL (LNh)	MD: BB[a], CMt[2,b]	(C. occidentalis).
	VA: GFV[a]	(C. occidentalis).
	OH: OARDC[2,a]	(C. occidentalis).
	AR: FAY[2,a]	(C. occidentalis).
LEAF DISC GALL (LD)	MD: GFV[2,b]	(C. occidentalis).
	AR: FAY[a]	(C. occidentalis).
LEAF BLISTER GALL (LB)	MD: CMt[2,b]	(C. occidentalis).
	VA: GFV[2,b]	(C. occidentalis).
	OH: BAY[2,b]	(C. occidentalis).
	AR: FAY[a]	(C. occidentalis).
	LA: ALX[a]	(C. laevigata).
	TX: AUS[2,b], BFL[2,c], PMT[2,c], ZKR[2,c]	(C. laevigata).
	BFL[2,c], PMT[2,c], ZKR[2,c]	(C. reticulata).
	AZ: TUC[2,a]	(C. reticulata).
	ID: PCT[c]	(C. occidentalis).
	ND: FRG[c]	(C. occidentalis).

Table 1-3. (cont.)

Gall types	Localities sampled[1]		
PETIOLE GALL (P)	MD:	BB[2,b], SI[2,a]	(C. tenuifolia);
		HUS[2,a]	(C. occidentalis)
	TX:	AUS[2,c]	(C. laevigata).
	AZ:	TUC[2,c]	(C. reticulata)
GLABROUS BUD GALL (Bg)	MD:	BB[c], HUS[2,a], NAL[2,c], PG[a]	(C. tenuifolia).
	VA:	GFV[2,b]	(C. occidentalis).
	LA:	ALX[c]	(C. laevigata).
HAIRY BUD GALL (Bh)	OK:	BSP[2,c]	(C. laevigata?).
TWIG GALL (T)	OK:	BSP[2,c]	(C. laevigata?)

[1] Acronyms for each population used:
MD: BB- Branchville, Berwyn; CMt- Catoctin Mountain Park, Thurmont; DEAL- Broadwater Rd., Churchon; HUS- Hughes Rd, Seneca; NAL- National Agricultural Library, Beltsville; PG- Schoolhouse pond, Upper Marlboro; PRP- Patuxent River Park, Upper Marlboro; SI- Smithsonian Environmental Research Center, Edgewater.
VA: GFV- Great Falls, McLean; WBP- George Washington's Birthplace, Washington Birthplace.
OH: BAY- South Bass Is., Put-in-Bay; OARDC- Ohio Agricultural Research and Development Center, Wooster.
AR: FAY- Fayetteville.
ID: PCT- Pocatello.
ND: FRG- Fargo.
LA: ALX- Cole Street, Alexandria.
OK: BSP- Boiling Spring State Park, Woodward.
TX: AUS- Austin city; BFL- Brackenridge Field Lab of Univ. of Texas at Austin; ZKR- Zilker Park, Austin; PMT- Palmetto Park, Gonzales.
AZ: TUC- Santa Rita Mts, Tucson.

[2] Populations sampled for morphological study.

[a] Only adult samples used for electrophoretic study.
[b] Both adult and nymphal samples used for electrophoretic study.
[c] Only nymphal samples used for electrophoretic study.

Table 1-4. Enzyme loci scored for analysis of *Pachypsylla*.

ENZYME	E. C. #	LOCUS	BUFFER	VOLTAGE	RUN TIME
Fructose-1,6-Diphosphatase	3.1.3.11	FDP	Tris-Citrate 0.1M pH 8.2	180	1 hr
Fumarate Hydratase	4.2.1.2	FUM	Tris-glycine 0.025M pH 8.5	180	1 hr
Glyceraldehyde-3-Phosphate Dehydrogenase	1.2.1.12	G3PDH	Tris-Citrate 0.1M pH 8.2	180	1.5 hr
Glycerol-3-Phosphate Dehydrogenase	1.1.99.5	GPDH	Phosphate 0.02M pH 7.0	180	1 hr
Isocitrate Dehydrogenase	1.1.1.42	IDH-1 IDH-2	Tris-Citrate 0.1M pH 8.2	180	1.5 hr
Lactate Dehydrogenase	1.1.1.27	LDH	Tris-Maleate-EDTA-$MgCl_2$ 0.05M pH 7.8	180	35 min
Malate Dehydrogenase	1.1.1.37	MDH-1	Tris-Maleate 0.015M pH 7.2	180	1.5 hr
		MDH-2	Tris-Maleate-EDTA-$MgCl_2$ 0.05M pH 7.8	180	35 min
Malic enzyme	1.1.1.40	ME	Tris-Maleate 0.05M pH 7.8	180	1.5 hr
Peptidase	3.4.11	PEP-1	Tris-Glycine 0.025M pH 8.5	180	45 min
Phosphoglucomutase	2.7.5.1	PGM	Citrate Phosphate 0.01M pH 6.4	180	1.5 hr
6-phosphogluconate Dehydrogenase	1.1.1.44	6PGDH	Tris-Maleate-EDTA-$MgCl_2$ 0.05M pH 7.8	180	1.5 hr
Phosphoglucose Isomerase	5.3.1.9	PGI	Citrate Phosphate 0.01M pH 6.4	180	1hr 10 min
Triose Phosphate Isomerase	5.3.1.1	TPI	Tris-Citrate 0.1M pH 8.2	180	1 hr

Table 1-5. Allele frequencies of adults from different gall types from 38 populations of Pachypsylla in the United States and one population of Celtisaspis bellingana from Asia. Acronyms for gall types and populations follow table 3.

	Population[a]																				
Locus	1 LWh (GFV)	2 LS (GFV)	3 LD (GFV)	4 LB (GFV)	5 LWg (GFV)	6 LWh (CMt)	7 LB (CMt)	8 LWh (BB)	9 LS (BB)	10 LWg (BB)	11 LS (WAL)	12 LWg (WAL)	13 LS (PRP)	14 LWg (PRP)	15 LS (PG)	16 LWg (PG)	17 LS (SI)	18 LWg (SI)	19 LWg (DEALE)	20 LS (WBP)	21 LWg (WBP)
PGM																					
(N)	25	33	25	26	6	9	11	3	8	12	5	12	8	8	6	8	8	8	8	8	7
A	.000	.000	.000	.019	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.400	.424	.040	.115	.417	.167	.000	.000	.125	.125	.000	.167	.063	.125	.000	.125	.063	.188	.125	.125	.071
C	.000	.000	.020	.000	.000	.000	.000	.000	.063	.000	.000	.000	.000	.000	.000	.063	.000	.000	.000	.000	.143
D	.560	.576	.880	.692	.500	.556	1.000	1.000	.813	.792	1.000	.708	.875	.625	.917	.688	.813	.813	.625	.750	.571
E	.000	.000	.000	.000	.083	.056	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.071
F	.040	.000	.060	.154	.000	.167	.000	.000	.000	.083	.000	.125	.063	.188	.083	.125	.125	.000	.188	.125	.143
G	.000	.000	.000	.019	.000	.056	.000	.000	.000	.000	.000	.000	.000	.063	.000	.000	.000	.000	.063	.000	.000
PGI																					
(N)	19	27	20	20	6	9	12	3	8	12	5	12	8	8	6	8	8	8	8	8	8
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.050	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	.974	1.000	.875	1.000	.667	1.000	1.000	1.000	.813	.917	.900	.917	.938	.938	.583	.938	.625	.813	.938	.813	.813
D	.000	.000	.075	.000	.250	.000	.000	.000	.000	.083	.000	.083	.000	.063	.250	.063	.188	.188	.063	.125	.063
E	.026	.000	.000	.000	.083	.000	.000	.000	.063	.000	.100	.000	.000	.000	.083	.000	.188	.000	.000	.063	.063
F	.000	.000	.000	.000	.000	.000	.000	.000	.125	.000	.000	.000	.063	.000	.083	.000	.000	.000	.000	.000	.063
G	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
GPDH																					
(N)	19	27	20	20	6	9	12	3	8	12	5	12	8	8	6	8	8	8	8	8	8
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.125	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.042	.100	.125	.000	.063	.000	.000	.063	.125	.063	.000	.000
C	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.958	.900	.875	1.000	.938	1.000	1.000	.813	.875	.938	1.000	1.000
D	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
ME																					
(N)	23	32	24	27	8	9	11	3	8	12	5	12	8	8	6	8	8	8	8	8	8
A	.000	.000	.021	.000	.000	.000	.000	.000	.063	.042	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	1.000	1.000	.979	.963	.938	.389	1.000	.833	.813	.833	.800	1.000	.813	1.000	.917	.938	1.000	1.000	1.000	1.000	1.000
D	.000	.000	.000	.000	.000	.000	.000	.167	.063	.042	.000	.000	.000	.000	.083	.063	.000	.000	.000	.000	.000
E	.000	.000	.000	.037	.063	.611	.000	.000	.063	.083	.200	.000	.188	.000	.000	.000	.000	.000	.000	.000	.000
FUM																					
(N)	12	20	13	15	8	9	12	3	8	12	5	12	8	8	6	8	8	8	8	8	8
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	1.000	1.000	1.000	.967	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.917	1.000	1.000	1.000	.938	1.000	.813	1.000	1.000	.938
D	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
E	.000	.000	.000	.033	.000	.000	.000	.000	.000	.000	.000	.083	.000	.000	.000	.063	.000	.000	.000	.000	.063
F	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
G	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.188	.000	.000	.000
FDP																					
(N)	10	23	17	12	6	9	12	3	8	12	5	12	8	8	6	8	8	8	8	8	8
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.500	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
C	.500	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
TPI																					
(N)	7	15	8	8	6	9	12	3	8	12	5	12	8	8	6	8	8	8	8	8	8
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.100	.000	.000	.000	.000	.000	.125	.000	.000	.000	.000
B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.900	1.000	1.000	1.000	1.000	1.000	.875	1.000	1.000	1.000	1.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
O	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
G3PDH																					
(N)	19	27	19	19	6	9	12	3	8	12	5	12	8	8	5	6	8	8	8	8	8
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

	Population*																		
Locus	22 LS (TX)	23 LB (TX)	24 LB (AZ)	25 LNh (AR)	26 LD (AR)	27 LB (AR)	28 LWg (AR)	29 LNh (OARDC)	30 LB (OHBAY)	31 LB (LA)	32 LWg (LA)	33 P (HUS)	34 Bg (HUS)	35 P (SI)	36 P (BB)	37 Bg (GFV)	38 Bg (PG)	39 LRP (CNI)
PGM																		
(N)	12	12	12	8	8	8	6	8	8	8	8	8	9	4	2	4	2	6
A	.000	.000	.000	.000	.125	.000	.167	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.125	.125	.125	.688	.000	.188	.000	.188	.125	.063	.000	.875	.333	.500	.500	.250	.250	.000
C	.083	.000	.083	.000	.000	.000	.083	.000	.000	.000	.000	.000	.000	.500	.500	.125	.250	.083
D	.667	.625	.458	.313	.750	.750	.583	.688	.688	.938	.938	.063	.389	.000	.000	.500	.500	.000
E	.042	.042	.000	.000	.000	.063	.000	.063	.063	.000	.000	.063	.111	.000	.000	.000	.000	.000
F	.083	.208	.125	.000	.000	.000	.167	.063	.125	.000	.063	.000	.167	.000	.000	.125	.000	.917
G	.000	.000	.208	.000	.125	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
PGI																		
(N)	12	12	12	8	7	8	6	7	8	8	8	8	9	4	2	4	2	6
A	.000	.000	.000	.000	.000	.000	.167	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.083	.000	.000	.000	.000	.063	.167	.071	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	.750	.917	1.000	1.000	1.000	.938	.583	.929	1.000	.938	.938	.000	.000	.000	.000	.000	.000	.000
D	.167	.083	.000	.000	.000	.000	.083	.000	.000	.063	.063	.000	.000	.000	.000	.000	.000	.500
E	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.500
G	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000	1.000	1.000	1.000	1.000	1.000	.000
GPDH																		
(N)	12	12	12	8	8	8	6	8	8	8	8	8	9	4	2	4	2	6
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.500	.000	.500	.500	.000	.000	1.000
D	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.500	1.000	.500	.500	1.000	1.000	.000
ME																		
(N)	12	12	12	8	8	8	6	8	8	8	8	8	9	4	2	4	2	6
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.250	.250	1.000	.278	1.000	1.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000
C	.875	.875	.917	1.000	1.000	1.000	1.000	1.000	1.000	.750	.750	.000	.000	.000	.000	.000	.000	.000
D	.000	.042	.042	.000	.000	.000	.000	.000	.000	.000	.000	.000	.111	.000	.000	.500	.500	.000
E	.125	.083	.042	.000	.000	.000	.000	.000	.000	.000	.000	.000	.611	.000	.000	.500	.500	.000
FUM																		
(N)	12	12	12	8	8	8	6	8	8	8	8	8	9	4	2	4	2	6
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000	.000	.000	1.000	1.000	.000
C	.958	.958	.958	.875	.813	1.000	.917	.938	1.000	.750	1.000	.000	.000	.000	.250	.000	.000	.000
D	.042	.000	.000	.000	.000	.000	.000	.063	.000	.125	.000	.250	.000	.375	.500	.000	.000	.000
E	.000	.042	.042	.125	.000	.000	.083	.000	.000	.125	.000	.625	.000	.500	.250	.000	.000	1.000
F	.000	.000	.000	.000	.188	.000	.000	.000	.000	.000	.000	.125	.000	.000	.000	.000	.000	.000
G	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.125	.000	.000	.000	.000
FDP																		
(N)	12	12	12	8	8	8	6	8	8	8	8	6	8	4	2	4	2	6
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000
B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
TPI																		
(N)	12	12	12	8	8	8	6	8	8	8	8	8	9	4	2	4	2	6
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.000	.000	.000	.000	.000	.000	1.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000	.000	1.000	1.000	.000	.000	.000
D	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000	.000	.000	1.000	1.000	.000
G3PDH																		
(N)	12	12	12	8	8	8	6	7	8	8	7	5	6	4	2	4	2	6
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000
B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.000

Table 1-5 (cont.)

	Population*																				
Locus	1 LWh (GFV)	2 LS (GFV)	3 LD (GFV)	4 LB (GFV)	5 LWg (GFV)	6 LWh (CMt)	7 LB (CMt)	8 LWh (BB)	9 LS (BB)	10 LWg (BB)	11 LS (NAL)	12 LWg (NAL)	13 LS (PRP)	14 LWg (PRP)	15 LS (PG)	16 LWg (PG)	17 LS (SI)	18 LWg (SI)	19 LWg (DEALE)	20 LS (WBP)	21 LWg (WBP)
IDH-1																					
(N)	21	29	22	22	8	6	11	3	8	12	5	11	8	8	6	8	8	8	8	8	8
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.190	.362	.023	.068	.063	.000	.000	.000	.125	.000	.200	.000	.000	.000	.250	.000	.188	.000	.063	.188	.000
C	.500	.224	.159	.864	.250	.250	.727	.167	.313	.042	.000	.000	.250	.125	.250	.000	.313	.063	.063	.063	.000
D	.000	.000	.000	.000	.000	.000	.000	.167	.000	.083	.200	.000	.000	.000	.000	.125	.000	.063	.000	.000	.000
E	.310	.414	.795	.045	.625	.667	.273	.667	.500	.875	.600	1.000	.688	.875	.500	.875	.500	.875	.875	.750	1.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
G	.000	.000	.023	.023	.063	.083	.000	.000	.063	.000	.000	.000	.063	.000	.000	.000	.000	.000	.000	.000	.000
IDH-2																					
(N)	23	31	24	19	10	6	11	3	8	12	5	12	8	8	6	8	8	8	8	8	8
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.042	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	.000	.016	.000	.000	.000	.000	.000	.000	.063	.042	.000	.000	.125	.000	.167	.063	.125	.000	.063	.000	.000
D	1.000	.984	1.000	1.000	1.000	.917	1.000	.833	.938	.958	1.000	.917	.875	1.000	.833	.875	.875	1.000	.938	1.000	1.000
E	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.042	.000	.000	.000	.063	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
G	.000	.000	.000	.000	.000	.083	.000	.167	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
H	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
MDH-1																					
(N)	5	13	3	2	3	7	7	3	7	11	5	12	2	2	6	8	8	8	8	8	8
A	.000	.000	.000	.000	.000	.000	.071	.000	.000	.091	.000	.042	.000	.250	.000	.188	.000	.000	.188	.000	.000
B	.000	.038	.167	.500	.000	.214	.429	.000	.214	.045	.100	.208	.000	.250	.000	.125	.063	.063	.063	.000	.125
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.125	.000	.000	.125	.000	.000
D	1.000	.923	.833	.500	1.000	.786	.500	1.000	.786	.818	.900	.667	1.000	.500	1.000	.438	.938	.938	.625	1.000	.875
E	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.125	.000	.000	.000	.000	.000
F	.000	.038	.000	.000	.000	.000	.000	.000	.000	.045	.000	.083	.000	.000	.000	.000	.000	.000	.000	.000	.000
G	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
H	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
I	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
MDH-2																					
(N)	7	12	8	7	6	9	12	3	8	12	5	12	8	8	5	8	8	8	8	8	8
A	.000	.125	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	1.000	.875	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.917	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.083	.000	.000	.000	.000	.000	.000	.000	.000	.000
D	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
G	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
H	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
I	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
6PGDH																					
(N)	10	18	14	9	6	8	5	2	8	9	5	9	8	7	6	8	8	8	8	8	8
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.050	.028	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	.050	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
D	.850	.861	.857	.611	1.000	.938	.500	1.000	1.000	1.000	1.000	1.000	.938	1.000	.833	.938	.938	1.000	1.000	1.000	.938
E	.000	.000	.000	.000	.000	.000	.200	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
F	.000	.056	.071	.222	.000	.000	.300	.000	.000	.000	.000	.000	.063	.000	.167	.000	.000	.000	.000	.000	.063
G	.050	.056	.036	.167	.000	.063	.000	.000	.000	.000	.000	.000	.000	.000	.000	.063	.063	.000	.000	.000	.000
H	.000	.000	.036	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
LDH																					
(N)	23	31	25	24	8	9	12	3	8	12	5	12	8	8	6	8	8	8	8	8	8
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.056	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	.261	.371	.040	.188	.188	.056	.042	.000	.063	.000	.000	.000	.000	.125	.000	.063	.000	.000	.063	.125	.000
D	.500	.500	.880	.604	.750	.778	.792	.833	.750	.875	.900	.958	1.000	.875	.917	.938	.750	.938	.875	.813	.688
E	.174	.081	.060	.146	.063	.000	.083	.167	.000	.042	.000	.000	.000	.000	.000	.000	.000	.063	.000	.063	.063
F	.065	.048	.020	.042	.000	.111	.083	.000	.188	.083	.100	.042	.000	.000	.000	.000	.250	.000	.063	.000	.250
G	.000	.000	.000	.021	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.083	.000	.000	.000	.000	.000	.000

* see table 3 for acronyms for gall types and populations.

	Population*																		
Locus	22 LS (TX)	23 LB (TX)	24 LB (AZ)	25 LWh (AR)	26 LO (AR)	27 LB (AR)	28 LWg (AR)	29 LWh (OARDC)	30 LB (OHBAY)	31 LB (LA)	32 LWg (LA)	33 P (HUS)	34 Bg (HUS)	35 P (SI)	36 P (BB)	37 Bg (GFV)	38 Bg (PG)	39 LRP (CMI)	
IDH-1																			
(N)	12	12	12	8	8	8	6	8	8	8	8	8	9	4	2	4	2	6	
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000	
B	.000	.000	.000	.000	.000	.000	.000	.063	.000	.000	.000	.000	.000	.000	.000	.250	.250	.000	
C	.000	.000	.083	.125	.313	.063	.000	.250	.750	.000	.000	.000	.167	.500	.500	.375	.000	.000	
D	.000	.000	.000	.063	.188	.000	.000	.000	.125	.000	.000	1.000	.000	.500	.500	.250	.250	.000	
E	.958	1.000	.917	.813	.500	.938	1.000	.688	.125	1.000	1.000	.000	.833	.000	.000	.125	.500	.000	
F	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	
G	.042	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	
IDH-2																			
(N)	12	12	12	8	8	8	6	8	8	8	8	8	9	4	2	4	2	6	
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000	
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.063	.000	.000	.000	.000	.000	.000	.000	
D	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.938	.000	.000	.000	.000	.000	.000	.000	
E	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	
F	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000	.000	.000	.000	.000	.000	.000	
G	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.889	1.000	1.000	1.000	1.000	.000	
H	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.111	.000	.000	.000	.000	.000	
MDH-1																			
(N)	12	12	12	8	8	7	6	5	5	5	5	8	9	4	2	4	2	6	
A	.000	.000	.000	.000	.000	.000	.000	.200	.100	.000	.000	.000	.000	.000	.000	.000	.000	.000	
B	.000	.000	.000	.313	.000	.071	.000	.000	.100	.100	.000	.000	.611	.000	.000	1.000	.500	.000	
C	.000	.000	.000	.000	.000	.143	.083	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	
D	.917	1.000	.958	.688	.875	.643	.750	.700	.800	.900	1.000	.688	.389	.500	.000	.000	.500	.000	
E	.000	.000	.000	.000	.000	.071	.083	.100	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	
F	.083	.000	.042	.000	.125	.071	.083	.000	.000	.000	.000	.313	.000	.500	1.000	.000	.000	.000	
G	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	
H	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	
I	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000	
MDH-2																			
(N)	12	12	11	8	8	8	6	6	6	8	8	4	3	4	1	4	2	6	
A	.000	.000	.000	.000	.000	.000	.000	.083	.083	.000	.000	.000	.000	.000	.000	.000	.000	.000	
B	1.000	1.000	.773	1.000	1.000	1.000	1.000	.917	.917	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.000	
C	.000	.000	.227	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	
D	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	
E	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	
F	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	
G	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	
H	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	
I	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000	
6PGDH																			
(N)	12	12	12	8	8	8	6	8	8	7	8	8	9	3	2	4	2	6	
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	
B	.000	.042	.042	.000	.000	.000	.000	.000	.000	.071	.063	.938	.000	.500	1.000	.000	.000	.000	
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.071	.000	.000	.000	.167	.000	.000	.000	.000	
D	.917	.875	.958	.813	.500	.813	.833	.875	.750	.857	.938	.063	.000	.333	.000	.000	.000	.000	
E	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	
F	.083	.083	.000	.188	.063	.188	.167	.125	.125	.000	.000	.000	.000	.000	.000	.000	.000	.000	
G	.000	.000	.000	.000	.250	.000	.000	.000	.125	.000	.000	.000	.000	.000	.000	.000	.000	1.000	
H	.000	.000	.000	.000	.188	.000	.000	.000	.000	.000	.000	.000	1.000	.000	.000	1.000	1.000	.000	
LDH																			
(N)	11	12	12	8	8	8	6	8	8	7	7	2	9	4	2	4	2	6	
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.250	.000	1.000	.500	.000	.000	.000	
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.750	.000	.000	.500	.000	.000	.833	
C	.000	.125	.000	.000	.000	.000	.000	.000	.063	.000	.000	.000	.000	.000	.000	.000	.000	.000	
D	.727	.708	.750	.875	.813	.750	.667	.938	.875	.929	.643	.000	.944	.000	.000	.750	.750	.167	
E	.045	.125	.125	.063	.063	.063	.167	.000	.000	.071	.143	.000	.056	.000	.000	.250	.250	.000	
F	.091	.042	.125	.063	.125	.188	.000	.063	.000	.000	.143	.000	.000	.000	.000	.000	.000	.000	
G	.136	.000	.000	.000	.000	.000	.167	.000	.063	.000	.071	.000	.000	.000	.000	.000	.000	.000	

Table 1-6. Allele frequencies in nymphs from different gall types from 20 populations of Pachypsylla (after pooling) and one population of Tetragonocephala flava from Arizona plus one population of Celtisaspis beijingana from China.

	Population**														
Locus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Galltype	LWh(m+c)	LWh(sd)	LWg(m+c)	LWg(m)	LWg(sd)	LS(m)	LB(m)	LB(m)	LB(m)	LB(m)	LB(m)	LD(m)	P	P	P
Locality	CMt	CMt	NAL+BB	GFV	NAL+BB	NAL+BB	CMt	GFV	OH+ND+ID	TX	TX	GFV	TX	BB	AZ
Host sp.	C.o.	C.o.	C.t.	C.o.	C.t.	C.t.	C.o.	C.o.	C.o.	C.l.	C.r.	C.o.	C.l.	C.t.	C.r.
PGM*															
(N)	30	21	33	12	19	22	18	20	14	44	45	37	8	9	5
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	.017	.000	.000	.083	.000	.000	.000	.000	.000	.000	.000	.027	.000	.000	.000
D	.267	.024	.152	.000	.000	.091	.222	.050	.036	.159	.200	.203	.000	.000	.000
E	.017	.000	.061	.208	.000	.023	.028	.025	.143	.000	.000	.014	.000	.000	.000
F	.583	.786	.697	.500	.895	.864	.639	.750	.571	.739	.711	.689	.000	.000	.000
G	.000	.000	.015	.208	.000	.023	.028	.025	.250	.011	.011	.000	.000	.000	.000
H	.117	.119	.076	.000	.105	.000	.083	.150	.000	.091	.078	.068	.000	.000	.000
I	.000	.071	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
J	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000	1.000	1.000
K	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
L	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
PGI															
(N)	30	21	33	16	19	24	18	22	14	46	45	39	8	9	5
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.011	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.028	.000	.000	.033	.033	.013	.000	.000	.000
C	.950	1.000	.864	.875	1.000	.896	.972	1.000	1.000	.902	.922	.949	.000	.000	.000
D	.000	.000	.045	.000	.000	.000	.000	.000	.000	.011	.000	.000	.000	.000	.000
E	.050	.000	.091	.031	.000	.042	.000	.000	.000	.043	.044	.038	.000	.000	.000
F	.000	.000	.000	.000	.000	.021	.000	.000	.000	.000	.000	.000	.000	.000	.000
G	.000	.000	.000	.094	.000	.042	.000	.000	.000	.000	.000	.000	.000	.000	.000
H	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.125	.000	.000
I	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
J	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.200
K	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.875	1.000	.800
L	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
GPDH															
(N)	23	18	33	16	19	24	17	20	14	46	45	41	9	9	5
A	.000	.000	.000	.000	.000	.083	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.121	.000	.000	.042	.029	.000	.000	.000	.000	.000	.000	.000	.000
C	1.000	1.000	.879	1.000	.974	.875	.971	1.000	1.000	.989	1.000	1.000	.000	.000	.000
D	.000	.000	.000	.000	.026	.000	.000	.000	.000	.011	.000	.000	.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000	1.000	.000
G	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
ME*															
(N)	30	21	39	16	22	27	18	22	14	46	44	41	8	9	5
A	.000	.000	.051	.000	.000	.000	.056	.000	.000	.000	.023	.000	1.000	1.000	1.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
D	.983	.286	.910	1.000	.568	.889	.917	1.000	.857	1.000	.977	.988	.000	.000	.000
E	.000	.119	.000	.000	.023	.037	.000	.000	.000	.000	.000	.000	.000	.000	.000
F	.017	.595	.038	.000	.409	.074	.028	.000	.071	.000	.000	.000	.000	.000	.000
G	.000	.000	.000	.000	.000	.000	.000	.000	.071	.000	.000	.012	.000	.000	.000
H	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
I	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
J	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
K	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
FUM															
(N)	30	21	33	16	19	24	17	20	12	46	45	41	8	9	5
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.015	.031	.000	.000	.000	.000	.000	.065	.000	.012	.000	.000	.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.011	.022	.024	.000	.000	.000
D	.983	.905	.970	.969	1.000	.938	.912	.750	1.000	.891	.911	.963	.000	.111	.000
E	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.011	.000	.125	.389	.800
F	.017	.095	.015	.000	.000	.063	.088	.250	.000	.033	.056	.000	.438	.111	.000
G	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.375	.389	.200
H	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.063	.000	.000
PEP-1*															
(N)	12	12	18	16	12	22	14	22	14	45	45	41	9	9	5
A	.042	.000	.000	.000	.000	.000	.000	.000	.000	.011	.011	.000	.000	.000	.000
B	.333	.250	.083	.156	.083	.114	.000	.000	.000	.022	.022	.280	.889	.333	1.000
C	.583	.625	.806	.750	.917	.886	1.000	1.000	1.000	.922	.922	.610	.111	.667	.000
D	.000	.042	.000	.000	.000	.000	.000	.000	.000	.000	.000	.049	.000	.000	.000
E	.042	.083	.083	.094	.000	.000	.000	.000	.000	.033	.044	.000	.000	.000	.000
F	.000	.000	.028	.000	.000	.000	.000	.000	.000	.011	.000	.061	.000	.000	.000
G	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
H	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
I	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000

Locus	16	17	18	19	20	21	22
Galltype	Bg	Bg	Bg	Bh	T	LRP	LRP
Locality	LA	NAL+BB	VA	OK	OK	AZ	CHI
Host sp.	C.l.	C.t.	C.o.	Cl?	Cl?	Cr	Ca
PGM*							
(N)	4	5	4	12	7	6	10
A	.000	.000	.000	.000	.000	.167	.000
B	.000	.000	.000	.000	.000	.750	.000
C	.000	.000	.000	.042	.000	.083	.100
D	.000	.000	.000	.000	.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000
G	.000	.000	.000	.000	.000	.000	.000
H	.000	.000	.000	.042	.000	.000	.000
I	.000	.000	.000	.000	.000	.000	.000
J	.500	.500	.500	.458	.000	.000	.000
K	.500	.500	.500	.458	1.000	.000	.000
L	.000	.000	.000	.000	.000	.000	.900
PGI							
(N)	6	5	3	12	8	8	8
A	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000
C	.000	.000	.000	.000	.000	.000	.000
D	.000	.000	.000	.000	.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	1.000
G	.000	.000	.000	.000	.188	.000	.000
H	.000	.000	.000	.000	.813	.000	.000
I	.000	.000	.000	.000	.000	.688	.000
J	.917	1.000	1.000	1.000	.000	.313	.000
K	.000	.000	.000	.000	.000	.000	.000
L	.083	.000	.000	.000	.000	.000	.000
GPDH							
(N)	6	5	3	12	8	9	10
A	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000
C	.000	.000	.000	.000	.000	1.000	1.000
D	.000	.000	.000	.000	1.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000
G	1.000	1.000	1.000	1.000	.000	.000	.000
ME*							
(N)	6	5	4	13	9	10	10
A	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.038	.000	1.000	.000
C	.000	.000	.000	.000	.000	.000	1.000
D	.000	.000	.000	.000	.000	.000	.000
E	.000	.000	.000	.038	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000
G	.167	.000	.125	.077	.000	.000	.000
H	.000	.000	.000	.192	1.000	.000	.000
I	.167	.200	.375	.346	.000	.000	.000
J	.083	.100	.250	.154	.000	.000	.000
K	.583	.700	.250	.154	.000	.000	.000
FUM							
(N)	6	5	3	12	8	9	10
A	.000	.000	.000	.000	.063	.000	.000
B	.000	.000	.000	.000	.000	.000	.000
C	1.000	1.000	1.000	.958	.938	.000	.000
D	.000	.000	.000	.000	.000	.111	.000
E	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.042	.000	.889	1.000
G	.000	.000	.000	.000	.000	.000	.000
H	.000	.000	.000	.000	.000	.000	.000
PEP-1*							
(N)	6	5	4	12	8	6	10
A	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000
C	.000	.000	.000	.000	.000	.000	.000
D	.000	.000	.000	.000	.000	.000	.000
E	1.000	1.000	1.000	1.000	.000	.000	.000
F	.000	.000	.000	.000	1.000	.000	.000
G	.000	.000	.000	.000	.000	.000	.900
H	.000	.000	.000	.000	.000	.000	.100
I	.000	.000	.000	.000	.000	1.000	.000

Table 1-6. (cont.)

Locus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Galltype	LNh(m+c)	LNh(sd)	LNg(m+c)	LNg(m)	LNg(sd)	LS(m)	LB(m)	LB(m)	LB(m)	LB(m)	LB(m)	LD(m)	P	P	P
Locality	CNt	CNt	NAL+BB	GFV	NAL+BB	NAL+BB	CNt	GFV	OH+ND+ID	TX	TX	GFV	TX	BB	AZ
Host sp.	C.o.	C.o.	C.t.	C.o.	C.t.	C.t.	C.o.	C.o.	C.o.	C.l.	C.r.	C.o.	C.l.	C.t.	C.r.
FDP															
(N)	23	18	27	4	16	20	8	10	3	46	45	29	9	9	5
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
TPI															
(N)	23	18	27	16	16	16	12	20	8	40	39	37	9	9	5
A	.000	.000	.000	.000	.000	.031	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	1.000	1.000	1.000	1.000	.969	.969	1.000	1.000	1.000	.988	1.000	1.000	.000	.000	.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
D	.000	.000	.000	.000	.000	.000	.000	.000	.000	.013	.000	.000	1.000	1.000	1.000
E	.000	.000	.000	.000	.031	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
G3PDH															
(N)	23	18	27	4	16	22	10	12	6	34	32	29	9	9	5
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
IDH-1															
(N)	30	18	39	16	22	27	18	22	14	42	45	41	9	9	5
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.011	.000	.000	.000	.000
C	.000	.000	.000	.000	.000	.204	.000	.000	.000	.000	.044	.000	.000	.000	.000
D	.233	.389	.103	.000	.023	.204	.972	.932	.786	1.000	.922	.134	1.000	1.000	1.000
E	.767	.611	.872	.875	.932	.500	.028	.068	.000	.000	.000	.756	.000	.000	.000
F	.000	.000	.026	.125	.000	.093	.000	.000	.214	.000	.022	.110	.000	.000	.000
G	.000	.000	.000	.000	.045	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
IDH-2															
(N)	29	21	39	12	22	27	15	5	14	42	42	39	3	7	2
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	.000	.000	.026	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
D	1.000	1.000	.949	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.988	1.000	.000	.000	.000
E	.000	.000	.026	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
G	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.012	.000	1.000	1.000	1.000
MDH-1*															
(N)	28	21	33	16	19	16	13	10	8	38	37	37	9	9	5
A	.000	.000	.061	.000	.000	.063	.000	.000	.000	.000	.014	.000	.000	.000	.000
B	.071	.024	.152	.188	.158	.219	.346	.100	.063	.000	.068	.054	.000	.000	.000
C	.036	.048	.000	.000	.000	.000	.000	.000	.000	.000	.014	.000	.000	.000	.000
D	.875	.405	.742	.813	.632	.719	.654	.900	.750	.934	.824	.892	.333	.222	.400
E	.000	.119	.000	.000	.079	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
F	.018	.381	.030	.000	.079	.000	.000	.000	.188	.066	.081	.054	.000	.000	.000
G	.000	.024	.015	.000	.053	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
H	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
I	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.667	.778	.600
MDH-2															
(N)	26	18	39	14	22	27	14	20	14	46	45	39	8	9	5
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
6PGDH															
(N)	28	21	39	12	22	27	16	18	14	46	45	36	9	9	5
A	.000	.024	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.111	.000
B	.018	.024	.000	.000	.000	.000	.000	.000	.071	.043	.011	.000	.889	.722	1.000
C	.018	.000	.000	.000	.000	.000	.000	.000	.036	.011	.000	.000	.000	.000	.000
D	.839	.952	.987	1.000	.841	.870	.813	.444	.536	.924	.933	.764	.111	.167	.000
E	.000	.000	.000	.000	.068	.019	.031	.278	.000	.000	.000	.000	.000	.000	.000
F	.071	.000	.013	.000	.091	.111	.156	.278	.321	.022	.056	.028	.000	.000	.000
G	.054	.000	.000	.000	.000	.000	.000	.000	.036	.000	.000	.125	.000	.000	.000
H	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.083	.000	.000	.000
LDH*															
(N)	30	21	38	16	22	27	17	20	14	46	43	41	2	2	1
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000	1.000	1.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	.033	.095	.000	.094	.068	.000	.118	.350	.250	.022	.000	.012	.000	.000	.000
D	.833	.881	.868	.813	.932	.833	.824	.575	.500	.826	.849	.988	.000	.000	.000
E	.133	.024	.092	.063	.000	.019	.000	.000	.143	.087	.081	.000	.000	.000	.000
F	.000	.000	.039	.000	.000	.148	.059	.075	.107	.054	.058	.000	.000	.000	.000
G	.000	.000	.000	.031	.000	.000	.000	.000	.000	.011	.000	.000	.000	.000	.000
H	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.012	.000	.000	.000	.000

Population**

Locus	16	17	18	19	20	21	22
Galltype	Bg	Bg	Bg	Bh	T	LRP	LRP
Locality	LA	NAL+BB	VA	OK	OK	AZ	CWI
Host sp.	C.l.	C.t.	C.o.	Cl?	Cl?	Cr	Ca
FDP							
(N)	6	5	3	12	8	5	10
A	.000	.000	.000	.000	.000	.000	1.000
B	1.000	1.000	1.000	1.000	1.000	1.000	.000
TPI							
(N)	6	5	4	13	9	10	10
A	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.500	.000	.000	1.000	1.000
C	.000	.000	.000	.000	1.000	.000	.000
D	.000	.000	.000	.000	.000	.000	.000
E	1.000	1.000	.500	1.000	.000	.000	.000
G3PDH							
(N)	5	4	4	8	8	10	10
A	.000	.000	.000	.000	.000	.000	1.000
B	1.000	1.000	1.000	1.000	1.000	1.000	.000
IDH-1							
(N)	6	5	4	12	9	10	8
A	.000	.000	.000	.000	.000	.000	.375
B	.000	.000	.000	.000	.000	.000	.625
C	.000	.000	.000	.000	.778	.000	.000
D	.000	.000	.000	.000	.000	.000	.000
E	1.000	1.000	1.000	1.000	.000	.000	.000
F	.000	.000	.000	.000	.222	1.000	.000
G	.000	.000	.000	.000	.000	.000	.000
IDH-2							
(N)	5	4	2	5	7	10	10
A	.000	.000	.000	.000	.000	.000	1.000
B	.000	.000	.000	.000	.000	1.000	.000
C	.000	.000	.000	.000	.000	.000	.000
D	.000	.000	.000	.000	.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000
G	1.000	1.000	1.000	1.000	1.000	.000	.000
MDH-1*							
(N)	6	4	4	11	7	6	6
A	.000	.000	.000	.000	.000	.000	.000
B	.167	.250	.125	.045	.000	.000	.000
C	.000	.000	.000	.000	.000	.000	.000
D	.833	.750	.875	.955	.143	.000	.000
E	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000
G	.000	.000	.000	.000	.000	1.000	1.000
H	.000	.000	.000	.000	.857	.000	.000
I	.000	.000	.000	.000	.000	.000	.000
MDH-2							
(N)	6	5	4	12	8	8	8
A	.000	.000	.000	.000	.000	1.000	1.000
B	.000	.000	.000	.000	.000	.000	.000
C	1.000	1.000	1.000	1.000	1.000	.000	.000
6PGDH							
(N)	6	5	4	13	9	10	10
A	.000	.000	.000	.000	.000	.600	.000
B	.000	.000	.000	.000	.000	.350	.000
C	.000	.000	.000	.000	1.000	.050	.000
D	.000	.000	.000	.000	.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.000
F	.250	.000	.000	.000	.000	.000	.000
G	.000	.000	.000	.000	.000	.000	1.000
H	.750	1.000	1.000	1.000	.000	.000	.000
LDH*							
(N)	6	5	3	12	6	8	10
A	.000	.000	.000	.000	.000	.000	.200
B	.000	.000	.000	.000	.000	.000	.800
C	.000	.000	.000	.000	.000	.000	.000
D	1.000	1.000	1.000	1.000	1.000	.938	.000
E	.000	.000	.000	.000	.000	.000	.000
F	.000	.000	.000	.000	.000	.063	.000
G	.000	.000	.000	.000	.000	.000	.000
H	.000	.000	.000	.000	.000	.000	.000

* Mobility of the alleles in these locI does not follow the alphabet exactly. Actual mobility rank from fast to slow: PGM: ABCDEJFKGHIL; ME: AHBCDIEJFK; PEP-1: ABCDEIFGH; MDH-1: ABCDEFHIG; LDH: ABCDIEFGH.

** Population acronyms follow table 1-3. Host plant species following "?" are uncertain in some Oklahoma populations.

Table 1-7. X^2 tests for differences in allele frequency among nymphal populations of bud and petiole gall makers, all loci.

Contrast number	Contrast*	Chi-square	degrees of freedom	Signifi-cance level
A0	all four populations of bud galls (glabrous and hairy types)	59.88	24	***
A00	all three populations of glabrous bud galls	23.35	12	NS
A1	glabrous bud gall (MD) vs. glabrous bud gall (VA)	9.69	4	NS
A2	glabrous bud gall (MD) vs. glabrous bud gall (LA)	4.30	5	NS
A3	glabrous bud gall (MD) vs. hairy bud gall (OK)	11.11	5	NS
A4	glabrous bud gall (VA) vs. glabrous bud gall (LA)	12.6	6	NS
A5	glabrous bud gall (VA) vs. hairy bud gall (OK)	17.3	6	**
A6	glabrous bud gall (LA) vs. hairy bud gall (OK)	15.43	7	NS
B0	all 3 populations of petiole galls	87.42	14	***
B1	petiole gall from MD(BB) vs. TX(BFL)	21.18	6	***
B2	petiole gall from MD(BB) vs. AZ	52.89	7	***
B3	petiole gall from TX(BFL) vs. AZ	38.01	6	***

*: Population acronyms follow table 1-3.
**: $0.01 \leq p \leq 0.05$.
***: $p < 0.005$.
NS: non-significant, $p > 0.05$.

Table 1-8. Body size measurement of *Pachypsylla* gall makers from various gall types. Matrix at the bottom shows pairwise comparisons between means of leaf gall makers using Tukey-Kramer method (Sokal and Rohlf, 1981). The absolute pair average mean differences are given below the diagonal while minimum significant difference (MSD) value are given above the diagonal. Differences larger in absolute value than their MSD value are significant at the 0.05 level and are marked with an asterisk.

Gall types		Non-leaf galler		Leaf galler				
		Petiole gall	Glabrous bud gall	Disc gall	Hairy nipple gall	Glabrous nipple gall	Star gall	Blister gall
Number of individuals		14	15	42	59	54	99	98
Body size	Mean	6.02	3.25	3.83	3.34	3.27	2.98	2.65
	Minimum	5.50	2.90	3.10	2.70	2.70	2.4	1.9
	Maximum	6.40	3.60	4.40	4.10	3.50	3.6	3.3
	Standard Error	0.07	0.06	0.05	0.05	0.03	0.03	0.04
Ranked gall size	Disc gall			-	0.172	0.175	0.158	0.040
	Hairy nipple gall			0.489*	-	0.161	0.140	0.140
	Glabrous nipple gall			0.559*	0.070	-	0.144	0.143
	Star gall			0.85*	0.360*	0.291*	-	0.120
	Blistr gall			1.184*	0.695*	0.625*	0.344*	-

Table 1-9. X^2 tests for allele frequency differences among populations of leaf gall makers, all loci.

Contrast number	Contrast*	Chi-square	degrees of freedom	Significance level
C0	all 5 leaf gall types from GFV (adults)	48.77	8	***
C1	blister vs. hairy nipple gall (GFV)	58.96	14	***
C2	blister vs. glabrous nipple gall (GFV)	280.43	56	***
C3	blister vs. star gall (GFV)	88.05	14	***
C4	blister vs. disc gall (GFV)	78.23	12	***
C5	hairy vs. glabrous nipple gall (GFV)	35.57	11	***
C6	hairy nipple vs. star gall (GFV)	46.16	13	***
C7	hairy nipple vs. disc gall (GFV)	82.74	13	***
C8	glabrous nipple vs. star gall (GFV)	45.00	13	***
C9	glabrous nipple vs. disc gall (GFV)	18.84	7	***
C10	star vs. disc gall (GFV)	78.81	13	***
D0	all 3 leaf gall types from GFV (nymphs)	261.24	24	***
D1	blister vs. glabrous nipple gall (GFV)	107.83	10	***
D2	blister vs. disc gall (GFV)	30.86	10	***
D3	glabrous nipple vs. disc gall (GFV)	200.93	14	***
E1	hairy nipple vs. blister gall (CMt)	86.16	12	***
F1	glabrous nipple vs. star gall (MD)	48.66	17	***
G1	blister galler (TX) on *Celtis laevigata* vs. *Celtis reticulata*	20.95	15	NS

*: Population acronyms follow table 1-3.
***: $p < 0.005$.
NS: non-significant, $p > 0.01$.

Table 1-10. Frequencies of major alleles in IDH-1 in adults (1991 samples) from blister galls versus hairy nipple galls.

Allele	Great Falls Virginia		Catoctin Mt. Maryland		Wooster Ohio	
	Blister	Hairy Nipple	**Blister**	Hairy Nipple	**Blister**	Hairy Nipple
C	**.86**	.50	**.73**	.25	**.75**	.25
E	**.05**	.31	**.27**	.67	**.13**	.69

Table 1-11. Numbers and types of gall formed by progenies of individual females in rearing experiment. One large and one small female were caged on each seedling. Empty cells represent no galls of that type.

PPOPU-LATION *	HOST (DATE OF RELEASE)	SEED-LING #	LARGE SIZE** FEMALE (> 3mm)		SMALL SIZE** FEMALE (< 3mm)	
			NIPPLE GALL	STAR GALL	NIPPLE GALL	STAR GALL
NAL	Celtis tenuifolia (5/13)	1	3			
		2	50			30
		3	8			14
		4	15		29	
		5	14			
	Celtis tenuifolia (5/24)	31				8
		32	9			
		33				8
		34				
BB	Celtis tenuifolia (5/17)	11				
		12				
		13		15		15
		14				6
		15		13		8
	Celtis occidentalis (5/23)	21		10		10
		22				
		23				
		24				

* NAL: National Agricultural Library, Beltsville, Maryland;
BB: Branchville Rd., Berwyn, Maryland.

** Body size revealed strong association with type of gall made (2X2 contingency test, $X^2 = 5.5$, $p < 0.01$).

Table 1-12. Head/shaft ratio of the terminal segment of male aedeagus in blister gall makers of *Pachypsylla* on different hosts.

Host	Number of individuals	Head/shaft ratio			
		Mean	Minimum	Maximum	Standard Error
Celtis laevigata (TX)*	9	0.50	0.35	0.65	0.038
Celtis reticulata (TX)*	12	0.33	0.24	0.44	0.029
Celtis reticulata (AZ)	4	0.33	0.32	0.37	0.028
Celtis occidentalis (MD)	10	0.33	0.31	0.37	0.007

* The ratios between blister gallers from *C. laevigata* and *C. reticulata* from Texas differed from each other significantly (t-test, $t=3.59$, $df=19$, $p < 0.01$).

Table 2-1. Allele frequencies of nymphs from different cell positions within various gall types collected in 1992 and 1993. Acronyms for gall types and populations follow Table 1-3.

	Population											
Gall type	1 LNh	2 LNh	3 LNh	4 LB	5 LNg	6 LNg	7 LNg	8 LS	9 LNg	10 LNg	11 LNg	12 LS
Locality	(CMt)	(CMt)	(CMt)	(CMt)	(NAL)	(NAL)	(NAL)	(NAL)	(BB)	(BB)	(BB)	(BB)
Cell pos.*	momo	center	side	mono	mono	center	side	mono	mono	center	side	mono
PGM												
(N)	16	14	21	18	17	10	13	11	3	3	6	11
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	.031	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
D	.344	.179	.024	.222	.176	.200	.000	.045	.000	.000	.000	.136
E	.031	.000	.000	.028	.088	.000	.000	.000	.167	.000	.000	.045
F	.563	.607	.786	.639	.647	.700	.923	.955	.667	1.000	.833	.773
G	.000	.000	.000	.028	.029	.000	.000	.000	.000	.000	.000	.045
H	.031	.214	.119	.083	.059	.100	.077	.000	.167	.000	.167	.000
I	.000	.000	.071	.000	.000	.000	.000	.000	.000	.000	.000	.000
PGI												
(N)	16	14	21	18	17	10	13	13	3	3	6	11
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.028	.000	.000	.000	.000	.000	.000	.000	.000
C	.938	.964	1.000	.972	.824	.900	1.000	.846	.833	1.000	1.000	.955
D	.000	.000	.000	.000	.088	.000	.000	.000	.000	.000	.000	.000
E	.063	.036	.000	.000	.088	.100	.000	.077	.167	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.045
G	.000	.000	.000	.000	.000	.000	.000	.077	.000	.000	.000	.000
GPDH												
(N)	12	11	18	17	17	10	13	13	3	3	6	11
A	.000	.000	.000	.000	.000	.000	.000	.077	.000	.000	.000	.091
B	.000	.000	.000	.029	.088	.250	.000	.077	.000	.000	.000	.000
C	1.000	1.000	1.000	.971	.912	.750	1.000	.846	1.000	1.000	.917	.909
D	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.083	.000
ME												
(N)	16	14	21	18	20	13	16	16	3	3	6	11
A	.000	.000	.000	.056	.075	.038	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
D	1.000	.964	.286	.917	.900	.885	.531	.844	1.000	1.000	.667	.955
E	.000	.000	.119	.000	.000	.000	.031	.031	.000	.000	.000	.045
F	.000	.036	.595	.028	.025	.077	.438	.125	.000	.000	.333	.000
FUM												
(N)	16	14	21	17	17	10	13	13	3	3	6	11
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.050	.000	.000	.000	.000	.000	.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
D	.969	1.000	.905	.912	.971	.950	1.000	.962	1.000	1.000	1.000	.909
E	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
F	.031	.000	.095	.088	.029	.000	.000	.038	.000	.000	.000	.091
PEP-1												
(N)	7	5	12	14	9	4	7	11	3	2	5	11
A	.000	.100	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.429	.200	.250	.000	.111	.125	.143	.182	.000	.000	.000	.045
C	.571	.600	.625	1.000	.778	.875	.857	.818	.667	1.000	1.000	.955
D	.000	.000	.042	.000	.000	.000	.000	.000	.000	.000	.000	.000
E	.000	.100	.083	.000	.111	.000	.000	.000	.167	.000	.000	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.167	.000	.000	.000
FDP												
(N)	12	11	18	8	14	7	10	11	3	3	6	9
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
TPI												
(N)	12	11	18	12	14	7	10	8	3	3	6	8
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.063
B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.917	.938
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
D	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.083	.000

Table 2-1. (cont.)

	Population											
Gall type	1 LNh	2 LNh	3 LNh	4 LB	5 LNg	6 LNg	7 LNg	8 LS	9 LNg	10 LNg	11 LNg	12 LS
Locality	(CMt)	(CMt)	(CMt)	(CMt)	(NAL)	(NAL)	(NAL)	(NAL)	(BB)	(BB)	(BB)	(BB)
Cell pos.*	momo	center	side	mono	mono	center	side	mono	mono	center	side	mono
G3PDH												
(N)	12	11	18	10	14	7	10	11	3	3	6	11
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
IDH-1												
(N)	16	14	18	18	20	13	16	16	3	3	6	11
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	.000	.000	.000	.000	.000	.000	.000	.188	.000	.000	.000	.227
D	.250	.214	.389	.972	.125	.077	.031	.219	.000	.167	.000	.182
E	.750	.786	.611	.028	.850	.923	.938	.500	.833	.833	.917	.500
F	.000	.000	.000	.000	.025	.000	.000	.094	.167	.000	.000	.091
G	.000	.000	.000	.000	.000	.000	.031	.000	.000	.000	.083	.000
IDH-2												
(N)	16	13	21	15	20	13	16	16	3	3	6	11
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	.000	.000	.000	.000	.000	.077	.000	.000	.000	.000	.000	.000
D	1.000	1.000	1.000	1.000	.950	.923	1.000	1.000	1.000	1.000	1.000	1.000
E	.000	.000	.000	.000	.050	.000	.000	.000	.000	.000	.000	.000
MDH-1												
(N)	15	13	21	13	17	10	13	8	3	3	6	8
A	.000	.000	.000	.000	.059	.100	.000	.000	.000	.000	.000	.125
B	.067	.077	.024	.346	.206	.050	.115	.250	.167	.167	.250	.188
C	.067	.000	.048	.000	.000	.000	.000	.000	.000	.000	.000	.000
D	.867	.885	.405	.654	.735	.750	.654	.750	.833	.667	.583	.688
E	.000	.000	.119	.000	.000	.000	.115	.000	.000	.000	.000	.000
F	.000	.038	.381	.000	.000	.050	.077	.000	.000	.167	.083	.000
G	.000	.000	.024	.000	.000	.050	.038	.000	.000	.000	.083	.000
MDH-2												
(N)	12	14	18	14	20	13	16	16	3	3	6	11
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
6PGDH												
(N)	15	13	21	16	20	13	16	16	3	3	6	11
A	.000	.000	.024	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.033	.000	.024	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	.033	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
D	.867	.808	.952	.813	.975	1.000	.781	.875	1.000	1.000	1.000	.864
E	.000	.000	.000	.031	.000	.000	.094	.031	.000	.000	.000	.000
F	.067	.077	.000	.156	.025	.000	.125	.094	.000	.000	.000	.136
G	.000	.115	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
LDH												
(N)	16	14	21	17	19	13	16	16	3	3	6	11
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	.031	.036	.095	.118	.000	.000	.063	.000	.000	.000	.083	.000
D	.875	.786	.881	.824	.763	.962	.938	.813	1.000	1.000	.917	.864
E	.094	.179	.024	.000	.158	.038	.000	.000	.000	.000	.000	.045
F	.000	.000	.000	.059	.079	.000	.000	.188	.000	.000	.000	.091

* Cell position within an individual gall.

Table 2-2. X^2 tests for allele frequency differences between nymphal populations of leaf gall makers in the same cell positions, all loci.

Contrast number	Contrast*	Chi-square	degrees of freedom	Significance level
A1	Hairy nipple gall: mono vs. center cell (CMt)	6.69	10	NS
A2	Glabrous nipple gall: mono vs. center cell (NAL)	14.90	13	NS
A3	Glabrous nipple gall: mono vs. center cell (BB)	5.60	5	NS
B1	Glabrous nipple gall (mono + center cells): NAL vs. BB	35.69	33	NS
B2	Glabrous nipple gall (side cell): NAL vs. BB	10.28	9	NS
B3	Star gall (mono cell): NAL vs. BB	10.67	11	NS

*: Population acronyms follow table 1-3.
NS: non-significant, $p>0.01$.

Table 2-3. Allele frequencies (after pooling) of nymphs from different cell positions, within various gall types collected in 1992 and 1993. Major allele frequency differences between side cell and center cell nymphs are underlined. Acronyms for gall types and populations follow Table 1-3.

	Population					
Gall type	1 LNh	2 LNh	3 LB	4 LNg	5 LNg	6 LS
Locality	(CMt)	(CMt)	(CMt)	(NAL+BB)	(NAL+BB)	(NAL+BB)
Cell pos.*	m+c	side	mono	m+c	side	mono
PGM						
(N)	30	21	18	33	19	22
C	.017	.000	.000	.000	.000	.000
D	.267	.024	.222	.152	.000	.091
E	.017	.000	.028	.061	.895	.023
F	.583	.786	.639	.697	.000	.864
G	.000	.000	.028	.015	.105	.023
H	.117	.119	.083	.076	.000	.000
I	.000	.071	.000	.000		.000
PGI						
(N)	30	21	18	33	19	24
C	.950	1.000	.972	.864	1.000	.896
D	.000	.000	.000	.045	.000	.000
E	.050	.000	.000	.091	.000	.042
F	.000	.000	.000	.000	.000	.021
G	.000	.000	.000	.000	.000	.042
GPDH						
(N)	23	18	17	33	19	24
A	.000	.000	.000	.000	.000	.083
B	.000	.000	.029	.121	.000	.042
C	1.000	1.000	.971	.879	.974	.875
D	.000	.000	.000	.000	.026	.000
ME						
(N)	30	21	18	39	22	27
A	.000	.000	.056	.051	.000	.000
D	.983	.286	.917	.910	.568	.889
E	.000	.119	.000	.000	.023	.037
F	.017	.595	.028	.038	.409	.074
FUM						
(N)	30	21	17	33	19	24
B	.000	.000	.000	.015	.000	.000
D	.983	.905	.912	.970	1.000	.938
F	.017	.095	.088	.015	.000	.063
PEP-1						
(N)	12	12	14	18	12	22
A	.042	.000	.000	.000	.000	.000
B	.333	.250	.000	.083	.083	.114
C	.583	.625	1.000	.806	.917	.886
D	.000	.042	.000	.000	.000	.000
E	.042	.083	.000	.083	.000	.000
F	.000	.000	.000	.028	.000	.000
FDP						
(N)	23	18	8	27	16	20
A	.000	.000	.000	.000	.000	.000
B	1.000	1.000	1.000	1.000	1.000	1.000
TPI						
(N)	23	18	12	27	16	16
A	.000	.000	.000	.000	.000	.031
B	1.000	1.000	1.000	1.000	.969	.969
E	.000	.000	.000	.000	.031	.000

Table 2-3. (cont.)

	Population					
	1	2	3	4	5	6
Gall type	LNh	LNh	LB	LNg	LNg	LS
Locality	(CMt)	(CMt)	(CMt)	(NAL+BB)	(NAL+BB)	(NAL+BB)
Cell pos.*	m+c	side	mono	m+c	side	mono
G3PDH						
(N)	23	18	10	27	16	22
A	.000	.000	.000	.000	.000	.000
B	1.000	1.000	1.000	1.000	1.000	1.000
IDH-1						
(N)	30	18	18	39	22	27
C	.000	.000	.000	.000	.000	.204
D	.233	.389	.972	.103	.023	.204
E	.767	.611	.028	.872	.932	.500
F	.000	.000	.000	.026	.000	.093
G	.000	.000	.000	.000	.045	.000
IDH-2						
(N)	29	21	15	39	22	27
C	.000	.000	.000	.026	.000	.000
D	1.000	1.000	1.000	.949	1.000	1.000
E	.000	.000	.000	.026	.000	.000
MDH-1						
(N)	28	21	13	33	19	16
A	.000	.000	.000	.061	.000	.063
B	.071	.024	.346	.152	.158	.219
C	.036	.048	.000	.000	.000	.000
D	.875	.405	.654	.742	.632	.719
E	.000	.119	.000	.000	.079	.000
F	.018	.381	.000	.030	.079	.000
G	.000	.024	.000	.015	.053	.000
MDH-2						
(N)	26	18	14	39	22	27
A	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000
C	1.000	1.000	1 .000	1 .000	1 .000	1 .000
6PGDH						
(N)	28	21	16	39	22	27
A	.000	.024	.000	.000	.000	.000
B	.018	.024	.000	.000	.000	.000
C	.018	.000	.000	.000	.000	.000
D	.839	.952	.813	.987	.841	.870
E	.000	.000	.031	.000	.068	.019
F	.071	.000	.156	.013	.091	.111
G	.054	.000	.000	.000	.000	.000
LDH						
(N)	30	21	17	38	22	27
C	.033	.095	.118	.000	.068	.000
D	.833	.881	.824	.868	.932	.833
E	.133	.024	.000	.092	.000	.019
F	.000	.000	.059	.039	.000	.148

* Cell position within an individual gall: m or mono= mono-cell; c= center cell; side= side cell.

Table 2-4. X^2 tests for allele frequency differences between nymphs in different cell positions within the same gall type, side cell nymphs and other co-occurring mono cell gall types, and side cell nymphs from different gall types, all loci.

Contrast number	Contrast*	Chi-square	degrees of freedom	Significance level
C1	Hairy nipple gall (CMt): (mono + center) vs. side cell	87.95	13	***
C2	Glabrous nipple gall (NAL+BB): (mono + center) vs. side cell	63.87	15	***
D1	CMt: Hairy nipple gall (side cell) vs. Blister gall (mono cell)	106.87	16	***
D2	NAL+BB: Glabrous nipple (side cell) vs. Star gall (mono cell)	58.36	14	***
E1	Side cell: Hairy nipple gall vs. Glabrous nipple gall	53.78	13	***

* Population acronyms follow table 1-3.
*** $p < 0.005$.

Table 2-5. Number and kinds of galls formed by progenies of single females in rearing experiments testing for inquilinism of side cell individuals in glabrous nipple gall and star galls from two Maryland populations.

POPULATION*	HOST** (DATE OF RELEASE)	SEEDLING #	BROWN ABDOMEN ♀ (CENTER CELL)		GREEN ABDOMEN ♀ (SIDE CELL)		GREEN+BROWN ABDOMEN ♀♀ (CENTER+SIDE)	
			SINGLE CELL GALL	MULTIPLE CELL GALL	SINGLE CELL GALL	MULTIPLE CELL GALL	SINGLE CELL GALL	MULTIPLE CELL GALL
NAL	*Celtis tenuifolia* (5/13)	1	3					
		2	54				10	6
		3	22				1	14
		4	18				19***	
		5	14					
	Celtis tenuifolia (5/24)	31	8				8	5
		32	6					
		33	7					
		34						
BB	*Celtis tenuifolia* (5/17)	11						
		12						
		13	6				7	5
		14	6				20	18
		15	8				12**	
	Celtis occidentalis (5/23)	21	5				9	6
		22						
		23						
		24						

* NAL: National Agricultural Library, Beltsville, Maryland;
BB: Branchville Rd., Berwin, Maryland.

** C.t.: *Celtis tenuifolia*; C.o.: *C. occidentalis*.

*** Green abdomen female died early in experiment.

Table 3-1. Character matrix for all evidences: morphological characters (1-33); allozyme data (34-48); karyotype (49-50); and life history (51-52) coded from Table 1-6. Each locus is treated as single character.

Pachy4.ALL (alle0.2) 1		1	2	3	4	5	6	7	8	9	10	11	12	13
1	Hairy Nipple Gall (center cell)	3	1	2	1	0	1	0	0	1	1	1	1	1
2	Hairy Nipple Gall (side cell)	3	1	2	1	0	1	0	0	1	1	1	1	1
3	Glabrous Nipple Gall (center ce	3	1	2	1	0	1	0	0	1	1	1	1	1
4	Glabrous Nipple Gall (side cell	3	1	2	1	0	1	0	0	1	1	1	1	1
5	Star Gall (center cell)	3	1	2	1	0	1	0	0	1	1	1	1	1
6	Blister Gall (center cell) MD	3	1	2	1	0	1	0	0	1	1	1	1	1
7	Blister Gall (center cell) TX	3	1	2	1	0	1	0	0	1	1	1	1	1
8	Disc Gall (center cell)	3	1	2	1	0	1	0	0	1	1	1	1	1
9	Petiole Gall	3	1	2	0	0	1	0	1	1	0	2	1	1
10	Glabrous Bud Gall	2	1	1	0	0	1	0	1	1	1	2	1	1
11	Hairy Bud Gall	2	1	1	0	0	1	0	1	1	?	2	1	1
12	Twig Gall	2	1	1	0	0	1	0	1	1	?	2	1	1
13	Tetragonocephala	1	0	0	0	1	0	1	1	0	1	0	0	0
14	Celtisaspis	0	0	0	0	2	0	1	1	0	1	0	0	1

Table 3-1 (cont.).

Pachy4.ALL (alle0.2) 2		14	15	16	17	18	19	20	21	22	23	24	25	26
1	Hairy Nipple Gall (center cell)	1	0	0	1	1	1	0	0	0	0	0	1	1
2	Hairy Nipple Gall (side cell)	1	0	1	1	1	1	0	0	0	0	0	1	1
3	Glabrous Nipple Gall (center ce	1	0	0	1	1	1	0	0	0	0	0	1	1
4	Glabrous Nipple Gall (side cell	1	0	1	1	1	1	0	0	0	0	0	1	1
5	Star Gall (center cell)	1	0	0	0	0	1	0	0	0	0	0	1	1
6	Blister Gall (center cell) MD	0	0	0	1	0	1	0	0	0	0	0	1	1
7	Blister Gall (center cell) TX	0	0	0	1	0	1	0	0	0	0	0	1	1
8	Disc Gall (center cell)	1	0	0	1	1	1	0	0	0	0	0	1	1
9	Petiole Gall	1	1	0	0	1	1	0	0	0	0	1	1	2
10	Glabrous Bud Gall	1	0	0	0	0	1	0	0	1	0	1	1	2
11	Hairy Bud Gall	1	0	0	0	0	1	0	0	1	0	1	1	2
12	Twig Gall	1	0	0	0	0	1	0	0	1	0	1	1	2
13	Tetragonocephala	0	0	0	0	0	0	1	1	0	1	0	0	0
14	Celtisaspis	0	0	0	0	0	0	1	1	0	1	2	0	0

Pachy4.ALL (alle0.2) 3		27	28	29	30	31	32	33	34	35	36	37	38	39
									PGM	PGI	GPDH	ME	FUM	PEP1
1	Hairy Nipple Gall (center cell)	2	0	1	1	0	0	0	D/F	C	C	D	D	B/C
2	Hairy Nipple Gall (side cell)	2	0	1	1	0	0	0	F	C	C	D/F	D	B/C
3	Glabrous Nipple Gall (center ce	2	0	1	1	0	0	0	F	C	C	D	D	C
4	Glabrous Nipple Gall (side cell	2	0	1	1	0	0	0	F	C	C	D/F	D	C
5	Star Gall (center cell)	2	0	1	1	0	0	0	F	C	C	D	D	C
6	Blister Gall (center cell) MD	0	0	1	1	0	0	0	D/F	C	C	D	D	C
7	Blister Gall (center cell) TX	0	0	1	1	0	0	0	D/F	C	C	D	D	C
8	Disc Gall (center cell)	2	0	1	1	0	0	0	D/F	C	C	D	D	B/C
9	Petiole Gall	0	0	1	1	1	1	0	J	K	F	A	E/G	B/C
10	Glabrous Bud Gall	0	1	1	1	1	0	1	J/K	J	G	J/K/Q	C	E
11	Hairy Bud Gall	0	1	1	1	1	0	1	J/K	J	G	Q	C	E
12	Twig Gall	1	1	1	1	1	1	0	K	H	D	H	C	F
13	Tetragonocephala	0	0	0	0	-	-	0	B	J/Q	C	B	F	Q
14	Celtisaspis	0	0	0	0	-	-	0	L	F	C	C	F	G

Table 3-1 (cont.).

Pachy4.ALL (alle0.2) 4		40	41	42	43	44	45	46	47	48	49	50	51	52
		FDP	TPI	G3PDH	IDH1	IDH2	MDH1	MDH2	6PGD	LDH	M-KAR	F-KAR\	voltine	overwi
1	Hairy Nipple Gall (center cell)	B	B	B	D/E	D	D	C	D	D	5	6	1	2
2	Hairy Nipple Gall (side cell)	B	B	B	D/E	D	D/F	C	D	D	5	6	1	2
3	Glabrous Nipple Gall (center ce	B	B	B	E	D	D	C	D	D	5	6	1	2
4	Glabrous Nipple Gall (side cell	B	B	B	E	D	D	C	D	D	?	?	1	2
5	Star Gall (center cell)	B	B	B	C/D/E	D	B/D	C	D	D	?	?	1	2
6	Blister Gall (center cell) MD	B	B	B	D	D	B/D	C	D	D	5	6	1	2
7	Blister Gall (center cell) TX	B	B	B	D	D	D	C	D	D	?	?	1	2
8	Disc Gall (center cell)	B	B	B	E	D	D	C	D	D	?	?	1	2
9	Petiole Gall	B	D	B	D	G	D/Q	C	B	A	3	4	1	1
10	Glabrous Bud Gall	B	B/E	B	E	G	D	C	H	D	2	2	1	1
11	Hairy Bud Gall	B	E	B	E	G	D	C	H	D	?	?	1	1
12	Twig Gall	B	C	B	C/F	G	H	C	C	D	5	6	1	1
13	Tetragonocephala	B	B	B	F	B	G	A	A/B	D	5	6	2	?
14	Celtisaspis	A	B	A	A/B	A	G	A	G	A/B	?	?	1/2	0

Pachy4.ALL (alle0.2) 5		53
		oviposi
1	Hairy Nipple Gall (center cell)	1
2	Hairy Nipple Gall (side cell)	1
3	Glabrous Nipple Gall (center ce	1
4	Glabrous Nipple Gall (side cell	1
5	Star Gall (center cell)	1
6	Blister Gall (center cell) MD	1
7	Blister Gall (center cell) TX	1
8	Disc Gall (center cell)	1
9	Petiole Gall	0
10	Glabrous Bud Gall	2
11	Hairy Bud Gall	2
12	Twig Gall	2
13	Tetragonocephala	?
14	Celtisaspis	?

Table 3-2. Character matrix for all evidences: morphological characters (1-33); allozyme data (34-130); karyotype (131-132); and life history (133-135) coded from Table 1-6. Each allele is treated as single character.

Pachy4.ALL (s.allele) 1		1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	Hairy Nipple Gall (center cell)	3	1	2	1	0	1	0	0	1	1	1	1	1	1
2	Hairy Nipple Gall (side cell)	3	1	2	1	0	1	0	0	1	1	1	1	1	1
3	Glabrous Nipple Gall (center ce	3	1	2	1	0	1	0	0	1	1	1	1	1	1
4	Glabrous NIpple Gall (side cell	3	1	2	1	0	1	0	0	1	1	1	1	1	1
5	Star Gall (center cell)	3	1	2	1	0	1	0	0	1	1	1	1	1	1
6	Blister Gall (center cell) MD	3	1	2	1	0	1	0	0	1	1	1	1	1	0
7	Blister Gall (center cell) TX	3	1	2	1	0	1	0	0	1	1	1	1	1	0
8	Disc Gall (center cell)	3	1	2	1	0	1	0	0	1	1	1	1	1	1
9	Petiole Gall	3	1	2	0	0	1	0	1	1	0	2	1	1	1
10	Glabrous Bud Gall	2	1	1	0	0	1	0	1	1	1	2	1	1	1
11	Hairy Bud Gall	2	1	1	0	0	1	0	1	1	?	2	1	1	1
12	Twig Gall	2	1	1	0	0	1	0	1	1	?	2	1	1	1
13	Tetrogonocephala	1	0	0	0	1	0	1	1	0	0	0	0	0	0
14	Celtisaspis	0	0	0	0	2	0	1	1	0	0	0	0	1	0

Pachy4.ALL (s.allele) 2		15	16	17	18	19	20	21	22	23	24	25	26	27	28
1	Hairy Nipple Gall (center cell)	0	0	1	1	1	0	0	0	0	0	1	1	2	0
2	Hairy Nipple Gall (side cell)	0	1	1	1	1	0	0	0	0	0	1	1	2	0
3	Glabrous Nipple Gall (center ce	0	0	1	1	1	0	0	0	0	0	1	1	2	0
4	Glabrous NIpple Gall (side cell	0	1	1	1	1	0	0	0	0	0	1	1	2	0
5	Star Gall (center cell)	0	0	0	0	1	0	0	0	0	0	1	1	2	0
6	Blister Gall (center cell) MD	0	0	1	0	1	0	0	0	0	0	1	1	0	0
7	Blister Gall (center cell) TX	0	0	1	0	1	0	0	0	0	0	1	1	0	0
8	Disc Gall (center cell)	0	0	1	1	1	0	0	0	0	0	1	1	2	0
9	Petiole Gall	1	0	0	1	1	0	0	0	0	1	1	2	0	0
10	Glabrous Bud Gall	0	0	0	0	1	0	0	1	0	1	1	2	0	1
11	Hairy Bud Gall	0	0	0	0	1	0	0	1	0	1	1	2	0	1
12	Twig Gall	0	0	0	0	1	0	0	1	0	1	1	2	1	1
13	Tetrogonocephala	0	0	0	0	0	1	1	0	1	0	0	0	0	0
14	Celtisaspis	0	0	0	0	0	1	1	0	1	2	0	0	0	0

Table 3-2 (cont.)

Pachy4.ALL (s.allele) 3		29	30	31	32	33	34	35	36	37	38	39	40	41	42
							A-PGM	A-PGM	B-PGM	C-PGM	D-PGM	E-PGM	F-PGM	G-PGM	H-PGM
1	Hairy Nipple Gall (center cell)	1	1	0	0	0	0	0	0	0	1	0	1	0	1
2	Hairy Nipple Gall (side cell)	1	1	0	0	0	0	0	0	0	0	0	1	0	1
3	Glabrous Nipple Gall (center ce	1	1	0	0	0	0	0	0	0	1	0	1	0	1
4	Glabrous NIpple Gall (side cell	1	1	0	0	0	0	0	0	0	0	0	1	0	1
5	Star Gall (center cell)	1	1	0	0	0	0	0	0	0	1	0	1	0	0
6	Blister Gall (center cell) MD	1	1	0	0	0	0	0	0	0	1	0	1	0	1
7	Blister Gall (center cell) TX	1	1	0	0	0	0	0	0	0	1	0	1	0	1
8	Disc Gall (center cell)	1	1	0	0	0	0	0	0	0	1	0	1	0	1
9	Petiole Gall	1	1	1	1	0	0	0	0	0	0	0	0	0	0
10	Glabrous Bud Gall	1	1	1	0	1	0	0	0	0	0	0	0	0	0
11	Hairy Bud Gall	1	1	1	0	1	0	0	0	0	0	0	0	0	0
12	Twig Gall	1	1	1	1	0	0	0	0	0	0	0	0	0	0
13	Tetrogonocephala	0	0	-	-	0	1	1	1	1	0	0	0	0	0
14	Celtisaspis	0	0	-	-	0	0	0	0	1	0	0	0	0	0

Pachy4.ALL (s.allele) 4		43	44	45	46	47	48	49	50	51	52	53	54	55	56
		I-PGM	J-PGM	K-PGM	L-PGM	C-PGI	E-PGI	F-PGI	G-PGI	H-PGI	I-PGI	J-PGI	K-PGI	L-PGI	A-GPDI
1	Hairy Nipple Gall (center cell)	0	0	0	0	1	1	0	0	0	0	0	0	0	0
2	Hairy Nipple Gall (side cell)	1	0	0	0	1	0	0	0	0	0	0	0	0	0
3	Glabrous Nipple Gall (center ce	0	0	0	0	1	0	0	0	0	0	0	0	0	0
4	Glabrous NIpple Gall (side cell	0	0	0	0	1	0	0	0	0	0	0	0	0	0
5	Star Gall (center cell)	0	0	0	0	1	0	0	0	0	0	0	0	0	1
6	Blister Gall (center cell) MD	0	0	0	0	1	0	0	0	0	0	0	0	0	0
7	Blister Gall (center cell) TX	0	0	0	0	1	0	0	0	0	0	0	0	0	0
8	Disc Gall (center cell)	0	0	0	0	1	0	0	0	0	0	0	0	0	0
9	Petiole Gall	0	1	0	0	0	0	0	0	0	0	0	1	0	0
10	Glabrous Bud Gall	0	1	1	0	0	0	0	0	0	0	1	0	0	0
11	Hairy Bud Gall	0	1	1	0	0	0	0	0	0	0	1	0	0	0
12	Twig Gall	0	0	1	0	0	0	0	1	1	0	0	0	0	0
13	Tetrogonocephala	0	0	0	0	0	0	0	0	0	1	1	0	0	0
14	Celtisaspis	0	0	0	1	0	0	1	0	0	0	0	0	0	0

Table 3-2 (cont.)

Pachy4.ALL (s.allele) 5		57	58	59	60	61	62	63	64	65	66	67	68	69	70
		B-GPDH	C-GPDH	D-GPDH	E-GPDH	F-GPDH	G-GPDH	A-ME	B-ME	C-ME	D-ME	E-ME	F-ME	G-ME	H-ME
1	Hairy Nipple Gall (center cell)	0	1	0	0	0	0	0	0	0	1	0	0	0	0
2	Hairy Nipple Gall (side cell)	0	1	0	0	0	0	0	0	0	1	1	1	0	0
3	Glabrous Nipple Gall (center ce	1	1	0	0	0	0	1	0	0	1	0	0	0	0
4	Glabrous NIpple Gall (side cell	0	1	0	0	0	0	0	0	0	1	0	1	0	0
5	Star Gall (center cell)	0	1	0	0	0	0	0	0	0	1	0	1	0	0
6	Blister Gall (center cell) MD	0	1	0	0	0	0	1	0	0	1	0	0	0	0
7	Blister Gall (center cell) TX	0	1	0	0	0	0	0	0	0	1	0	0	0	0
8	Disc Gall (center cell)	0	1	0	0	0	0	0	0	0	1	0	0	0	0
9	Petiole Gall	0	0	0	0	1	0	1	0	0	0	0	0	0	0
10	Glabrous Bud Gall	0	0	0	0	0	1	0	0	0	0	0	0	1	0
11	Hairy Bud Gall	0	0	0	0	0	1	0	0	0	0	0	0	1	1
12	Twig Gall	0	0	1	0	0	0	0	0	0	0	0	0	0	1
13	Tetrogonocephala	0	1	0	0	0	0	0	1	0	0	0	0	0	0
14	Celtisaspis	0	1	0	0	0	0	0	0	1	0	0	0	0	0

Pachy4.ALL (s.allele) 6		71	72	73	74	75	76	77	78	79	80	81	82	83	84
		I-ME	J-ME	K-ME	A-FUM	B-FUM	C-FUM	D-FUM	E-FUM	F-FUM	G-FUM	H-FUM	B-PEP	C-PEP	E-PEP1
1	Hairy Nipple Gall (center cell)	0	0	0	0	0	0	1	0	0	0	0	1	1	0
2	Hairy Nipple Gall (side cell)	0	0	0	0	0	0	1	0	1	0	0	1	1	1
3	Glabrous Nipple Gall (center ce	0	0	0	0	0	0	1	0	0	0	0	1	1	1
4	Glabrous NIpple Gall (side cell	0	0	0	0	0	0	1	0	0	0	0	1	1	0
5	Star Gall (center cell)	0	0	0	0	0	0	1	0	1	0	0	1	1	0
6	Blister Gall (center cell) MD	0	0	0	0	0	0	1	0	1	0	0	0	1	0
7	Blister Gall (center cell) TX	0	0	0	0	0	0	1	0	1	0	0	0	1	0
8	Disc Gall (center cell)	0	0	0	0	0	0	1	0	0	0	0	1	1	0
9	Petiole Gall	0	0	0	0	0	0	1	1	1	1	0	1	1	0
10	Glabrous Bud Gall	1	1	1	0	0	1	0	0	0	0	0	0	0	1
11	Hairy Bud Gall	1	1	1	0	0	1	0	0	0	0	0	0	0	1
12	Twig Gall	0	0	0	1	0	1	0	0	0	0	0	0	0	0
13	Tetrogonocephala	0	0	0	0	0	0	1	0	1	0	0	0	0	0
14	Celtisaspis	0	0	0	0	0	0	0	0	1	0	0	0	0	0

Table 3-2 (cont.)

Pachy4.ALL (s.allele) 7		85	86	87	88	89	90	91	92	93	94	95	96	97	98
		F-PEP1	G-PEP	H-PEP	I-PEP1	A-FDP	B-FDP	B-TPI	C-TPI	D-TPI	E-TPI	A-G3DI	B-G3DI	A-IDH1	B-IDH1
1	Hairy Nipple Gall (center cell)	0	0	0	0	0	1	1	0	0	0	0	1	0	0
2	Hairy Nipple Gall (side cell)	0	0	0	0	0	1	1	0	0	0	0	1	0	0
3	Glabrous Nipple Gall (center ce	0	0	0	0	0	1	1	0	0	0	0	1	0	0
4	Glabrous NIpple Gall (side cell	0	0	0	0	0	1	1	0	0	0	0	1	0	0
5	Star Gall (center cell)	0	0	0	0	0	1	1	0	0	0	0	1	0	0
6	Blister Gall (center cell) MD	0	0	0	0	0	1	1	0	0	0	0	1	0	0
7	Blister Gall (center cell) TX	0	0	0	0	0	1	1	0	0	0	0	1	0	0
8	Disc Gall (center cell)	1	0	0	0	0	1	1	0	0	0	0	1	0	0
9	Petiole Gall	0	0	0	0	0	1	0	0	1	0	0	1	0	0
10	Glabrous Bud Gall	0	0	0	0	0	1	1	0	0	1	0	1	0	0
11	Hairy Bud Gall	0	0	0	0	0	1	0	0	0	1	0	1	0	0
12	Twig Gall	1	0	0	0	0	1	0	1	0	0	0	1	0	0
13	Tetrogonocephala	0	0	0	1	0	1	1	0	0	0	0	1	0	0
14	Celtisaspis	0	1	1	0	1	0	1	0	0	0	1	0	1	1

Pachy4.ALL (s.allele) 8		99	100	101	102	103	104	105	106	107	108	109	110	111	112
		C-IDH1	D-IDH1	E-IDH1	F-IDH1	A-IDH2	B-IDH2	D-IDH2	G-IDH2	A-MDH	B-MDH	D-MDH	E-MDH	F-MDH	G-MDH
1	Hairy Nipple Gall (center cell)	0	1	1	0	0	0	1	0	0	1	1	0	0	0
2	Hairy Nipple Gall (side cell)	0	1	1	0	0	0	1	0	0	0	1	1	1	0
3	Glabrous Nipple Gall (center ce	0	1	1	0	0	0	1	0	1	1	1	0	0	0
4	Glabrous NIpple Gall (side cell	0	0	1	0	0	0	1	0	0	1	1	1	1	1
5	Star Gall (center cell)	1	1	1	1	0	0	1	0	1	1	1	0	0	0
6	Blister Gall (center cell) MD	0	1	0	0	0	0	1	0	0	1	1	0	0	0
7	Blister Gall (center cell) TX	0	1	0	0	0	0	1	0	0	1	1	0	1	0
8	Disc Gall (center cell)	0	1	1	1	0	0	1	0	0	1	1	0	1	0
9	Petiole Gall	0	0	0	0	0	0	0	1	0	0	1	0	0	0
10	Glabrous Bud Gall	0	0	1	0	0	0	0	1	0	1	1	0	0	0
11	Hairy Bud Gall	0	0	1	0	0	0	0	1	0	0	1	0	0	0
12	Twig Gall	1	0	0	1	0	0	0	1	0	0	1	0	0	0
13	Tetrogonocephala	0	0	0	1	0	1	0	0	0	0	0	0	0	1
14	Celtisaspis	0	0	0	0	1	0	0	0	0	0	0	0	0	1

Table 3-2 (cont.)

Pachy4.ALL (s.allele) 9		113	114	115	116	117	118	119	120	121	122	123	124	125	126
		H-MDH	I-MDH	A-MDH	B-MDH	A-6PGI	B-6PGI	C-6PGI	D-6PGI	E-6PGI	F-6PGI	G-6PGI	H-6PGI	A-LDH	B-LDH
1	Hairy Nipple Gall (center cell)	0	0	0	1	0	0	0	1	0	1	1	0	0	0
2	Hairy Nipple Gall (side cell)	0	0	0	1	0	0	0	1	0	0	0	0	0	0
3	Glabrous Nipple Gall (center ce	0	0	0	1	0	0	0	1	0	0	0	0	0	0
4	Glabrous Nipple Gall (side cell	0	0	0	1	0	0	0	1	1	1	0	0	0	0
5	Star Gall (center cell)	0	0	0	1	0	0	0	1	0	1	0	0	0	0
6	Blister Gall (center cell) MD	0	0	0	1	0	0	0	1	0	1	0	0	0	0
7	Blister Gall (center cell) TX	0	0	0	1	0	0	0	1	0	1	0	0	0	0
8	Disc Gall (center cell)	0	0	0	1	0	0	0	1	0	0	1	1	0	0
9	Petiole Gall	0	1	0	1	1	1	0	1	0	0	0	0	1	0
10	Glabrous Bud Gall	0	0	0	1	0	0	0	0	0	0	0	1	0	0
11	Hairy Bud Gall	0	0	0	1	0	0	0	0	0	0	0	1	0	0
12	Twig Gall	1	0	0	1	0	0	1	0	0	0	0	0	0	0
13	Tetrogonocephala	0	0	1	0	1	1	1	0	0	0	0	0	0	0
14	Celtisaspis	0	0	1	0	0	0	0	0	0	0	1	0	1	1

Pachy4.ALL (s.allele) 10		127	128	129	130	131	132	133	134	135
		C-LDH	D-LDH	E-LDH	F-LDH	m-kary	f-kary	voltine	overwi	oviposi
1	Hairy Nipple Gall (center cell)	0	1	1	0	5	6	1	2	1
2	Hairy Nipple Gall (side cell)	1	1	0	0	5	6	1	2	1
3	Glabrous Nipple Gall (center ce	0	1	1	0	5	6	1	2	1
4	Glabrous Nipple Gall (side cell	1	1	0	0	?	?	1	2	1
5	Star Gall (center cell)	0	1	0	1	?	?	1	2	1
6	Blister Gall (center cell) MD	1	1	0	1	5	6	1	2	1
7	Blister Gall (center cell) TX	0	1	1	1	?	?	1	2	1
8	Disc Gall (center cell)	0	1	0	0	?	?	1	2	1
9	Petiole Gall	0	0	0	0	3	4	1	1	0
10	Glabrous Bud Gall	0	1	0	0	2	2	1	1	2
11	Hairy Bud Gall	0	1	0	0	?	?	1	1	2
12	Twig Gall	0	1	0	0	5	6	1	1	2
13	Tetrogonocephala	0	1	0	1	5	6	2	?	?
14	Celtisaspis	0	0	0	0	?	?	1/2	0	?

Table 3-3. List of morphological characters used for *Pachypsylla* phylogenetic study

I. ADULT

HEAD

1. Surface texture of vertex [seen from SEM (Fig. 3-8)]:
   0. rough surface without obvious pattern, with scattered hairs, e.g. *Celtisaspis*,
   1. with small shallow bumps like fish scales, with scattered hairs, e.g. *Tetragonocephala flava*,
   2. with shallow wrinkles and some scattered short setae. e.g. *Pachypsylla* bud galler,
   3. densely and evenly covered with deep wrinkles and short setae, e.g. *Pachypsylla* leaf and petiole gallers.

2. Between vertex and gena [seen from dry specimens]:
   0. gena conical, not forming a flat plane vertical to body, gap between frons and vertex not deep,
   1. frontal part of gena very flat, vertical to the body, forming a grove between vertex and gena.

3. Surface texture of genae [seen from SEM] (Fig. 3-8):
   0. a little rough, e.g. *Tetragonocephala, Celtisaspis*,
   1. smooth in frontal portion and rough on the side, e.g. bud galler,
   2. bumpy, with deep wrinkles, e.g. leaf and petiole gallers.

4. Length of setae on genae:
   0. nearly homogeneous,
   1. apical end of genae with group of significantly longer setae.

5. Length of genae ÷ length of vertex:
   0. $< 1/2$
   1. ≥ 1

6. Antenna length ÷ head width:
   0. > 1.2
   1. ≈ 1.0

7. Thickness of antenna, distal vs. proximal
   0. flagellum of antenna within each segment with similar width between distal and proximal ends,
   1. flagellum of antenna with narrow proximal end and wider distal end, esp. seg. VI to VIII.

THORAX

8. Surface of thoracic dorsum:
   0. covered with conspicuous, short stiff pubescence,
   1. glabrous, shining, often with sparse minute pubescence.

9. Pterostigma
   0. indistinct,
   1. distinct.

10. Hind-coxae, ventral crescentic denticulate patch of nearly crescent shape on outer side above meracanthas [seen under SEM (Fig. 3-11)]:
    0. with some bumps, not pointed,
    1. full with sharply pointed bird-beak-structure.

11. Fan-shaped area in crescent-shaped patch on hind-coxa, [seen under SEM (Fig. 3-11)]:
    0. no obvious groves and ridges.
    1. with a few ridges parallel to each other,
    2. with obvious groves and ridges in fan-like arrangement.

12. Meracanthus, length ÷ width:
    0. > 2.0
    1. 1.0 - 1.5

13. Two black claws on the basal segment of metatarsus
    0. absent,
    1. present.

MALE GENITALIA

14. Male proctiger bipartite, setae on the basal segment in lateral view:
    0. sparsely distributed on apical caudal area, e.g. Leaf blister galler, and outgroups
    1. apical caudal area and caudal margin densely covered.

15. Setae, apical half of basal segment of male proctiger:
    0. mainly on upper caudal side, leaving small portion of lower frontal part without setae,
    1. evenly distributed.

16. Male forceps, in lateral view:
    0. gradually tapering at apically, lateral margins convex, not parallel.
    1. abruptly reduced subapically, lateral margins parallel.

17. Male aedeagus, apex of head of the second segment:
    0. rounded, blunt.
    1. hooked.

18. Second segment of male aedeagus, base of head at joint to basal rod:
    0. forming a sharp angle,
    1. joining smoothly.

FEMALE GENITALIA

19. Paired thumb-like processes, lateral proximal side of female proctiger (Fig. 3-1a):
    0. absent,
    1. present.

20. Shape of female dorsal valve (proctiger):
    0. wide at base, pointed toward the end, triangular shape in lateral view,
    1. short, rounded down, broad at caudal end, pointed toward ventral side.

21. Setae on female proctiger:
    0. setae of homogeneous size evenly distributed,
    1. long thin setae densely covering apex, shorter setae elsewhere, e.g. *Tetrogonocephala, Celtisaspis.*

23. Female circumanal ring, rows of pores
    0. single row,
    1. double row.

II. NYMPH (5th instar)

22. Dorsal surface of head:
    0. lacking conspicuous chitinized areas.
    1. with paired rectangular chitinized bands.

24. Base of nymphal antenna:
    0. very close to margin of head, the antenna extending beyond first segment outside margin of head.
    1. near margin, the entire first segment and part of second segment inside the head margin,
    2. first and second segments inside margin .

25. Trochanter:
    0. absent,
    1. present.

26. Pairs of ventral plates on abdomen anterior to caudal plate:
    0. no plates,
    1. only one pair near the caudal plate,
    2. three pairs, each on a different segment.

27. Abdominal median dorsal plate near caudal plate:
    0. absent,
    1. present, one small irregular plate, e.g. twig galler,
    2. paired small semi-circular plates, e.g. most leaf gallers.

28. Dorsal margin of caudal plate in conjunction with abdomen:
    0. a straight line without median indentation,
    1. a straight line with median indentation, i.e. a small middle area on the margin not chitinized.

29. Caudal plate in ventral view:
    0. a median plate flanked by pair of ventral plates,
    1. entire, except for segmentation, without separate ventral plate.

30. Pointed chitinized caudal spurs:
    0. absent,
    1. present.

31. Central apical spur on pointed chitinized caudal spurs (if present):
    0. sharp pointed,
    1. blunt and/or notched.

32. Apical caudal spurs on strongly chitinized caudal plates:
    0. present in apical two segments only,
    1. present in all three segments.

33. Abdominal caudal spurs:
    0. absent,
    1. present.

Table. 4-1. Classification of Spondyliaspidinae, showing differences between systems of White & Hodkinson and Burckhardt. Asterisks indicate taxa included in my phylogenetic analyses. Underlining indicates taxa whose position has been especially controversial.

WHITE & HODKINSON (1985)	BURCKHARDT (1991)
SPONDYLIASPIDIDAE	
Arepuiinae White & Hodkinson	
Arepuna Tuthill*	=*Russelliana** (APHALAROIDINAE)
Euphalerinae Becker-Migdisova	
Euphalerus Schwarz*	(out of Spondyliaspidinae)
Retroacizzia Heslop-Harrison	(" " ")
?*Pachyparia* Longinova	(" " ")
Phellopsylla Taylor*	
Colphorina Capener*	
Cometopsylla Froggatt*	(= Phyllolyma Walker)
	SPONDYLIASPIDINAE
Pachypsyllinae Becker-Migdisov	Pachypsyllini
Pachypsylla Riley*	*Pachypsylla**
Tetragonocephala Crawford*	*Tetragonocephala**
Pachypsylla japonica Miyatake*	*Celtisaspis* Yang & Li*
Spondyliaspidinae Schwartz	Spondyliaspidini Schwartz
Australopsylla Tuthill & Taylor	*Australopsylla*
	Boreiogycaspis Moore
Cardiaspina Carwford*	*Cardiaspina**
Creiis Scott*	*Creiis**
	Dasypsylla Froggatt
Eucalyptolyma Froggatt	*Eucalyptolyma* Froggatt
	Eurhinocola Crawford
Glycaspis Taylor*	*Glycaspis* Taylor*
Hyalinaspis Taylor	*Hyalinaspis* Taylor
	Kenmooreana Taylor
Lasiopsylla Froggatt	*Lasiopsylla* Froggatt
	Phellopsylla Taylor*
	Phyllolyma Walker*
	Platyobria Taylor
Spondyliaspis Signoret*	*Spondyliaspis* Signoret*
APHALARIDAE	
Ctenarytaininae White & Hodkinson	(to Spondyliaspidini Schwartz), including:
	Agelaeopsylla Taylor
	Anoeconeossa Taylor
	Blastopsylla Taylor
	Cryptoneossa Taylor
Ctenarytaina Ferris & Klyver*	*Ctenarytaina* Ferris & Klyver*
	Eriopsylla Froggatt
	Leptospermonastes Taylor
Syncarpiolyma Froggatt	*Syncarpiolyma* Froggatt
Eurhinocola Crawford	

Table 4-2. List of characters used for Pachypsyllini/Spondyliaspidinae phylogenetic study.

I. ADULT CHARACTERS.

HEAD

1. Vertex: the lowest part of the lower margin, adjacent to gena:
   0. near median ocellus,
   1. near antennal socket,
   2. between ocellus and antennal socket,
   3. margin flat, equally low.

2. Angle between top margin of vertex and median carina:
   0. $\approx$ 90°,
   1. >> 90°.

3. Irregular depressions or fovea on vertex:
   0. not obvious,
   1. one obvious depression,
   2. two apparent depressions,
   3. three apparent depression.

4. Genal cones:
   0. absent.
   1. present, length << 1/2 length of vertex,
   2. present, length about half as long as vertex,
   3. present, subequal to or longer than vertex in length.

5. Shape of occipital foramen, surrounded by the occipital sclerite, when vertex positioned horizontally:
   0. basic shape, dorsal margin straight (Fig. 4-2 a),
   1. similar to a, dorsal margin indented (Fig. 4-2 b),
   2. reverse triangular shape, ventral margin poninted (Fig. 4-2 c).

6. Length of antennae ÷ width of head including eyes:
   0. 1.71 - 2.0,
   1. 1.11-1.69,
   2. $\approx$ 1.0,
   3. < 0.7.

7. Antennal segment X length ÷ segment I length:
   0. $\leq$ 0.6,
   1. 0.61 - 1.0,
   2. > 1.0.

8. Antennal segment width, distal to proximal:
    0. homogeneous,
    1. Widen at distal end within each segment, especially on seg. VI to VIII.

9. Rhinaria:
    0. absent from seg. V,
    1. present on seg. V.

10. Anteoccipital lobes, a usually narrow sclerite between eye and genae/vertex:
    0. present, obvious,
    1. highly reduced or absent.

THORAX

11. Edge of forewing apex:
    0. rounded,
    1. pointed.

12. Forewing:
    0. not elongate with curvy veins not parallel,
    1. very elongate with veins straight and almost parallel:

13. Pterostigma:
    0. present, obvious,
    1. absent or very reduced.

14. Number of spines, thick black saltatorial spurs, at apex of metatibia:
    0. < 6,
    1. ≥ 6.

15. Metatibial basal (genual) spine:
    0. present,
    1. absent.

16. Apical spines on metatarsal segment I:
    0. present,
    1. absent.

17. Meracanthus:
    0. prominent,
    1. absent.

MALE GENITALIA

18. Male proctiger:
    0. unipartite (seg. X and XI of abdomen fused),
    1. bipartite.

19. Male paramere, lateral view:
    0. distal end tapered,
    1. distal end swollen.

20. Male paramere, lateral protruding lobes:
    0. absent ,
    1. present.

21. Male paramere, a line of marginal teeth at terminal end:
    0. absent,
    1. present.

22. Shape of terminal segment of aedeagus, lateral view:
    0. long and narrow with a small head, like a slender rod swollon at one end,
    1. swollen before middle without a slender rod-like part at the base,
    2. dramatically swollen at both ends.

FEMALE GENITALIA

23. Shape of female dorsal valve (proctiger). lateral view:
    0. wide at base, pointed toward the end, tiangular,
    1. wide at base till middle, at apical 1/3 narrow, sharply angled dorsally,
    2. short, rounded down, broad at caudal end, pointed toward vetral side.

24. Setae on female proctiger:
    0. similar in size, evenly distributed,
    1. uneven in size, a group of long setae dorsomedianly, others shorter and evenly distributed in rest area,
    2. long thin setae densely covering the apex, some short setae dorsally.

25. Number of rows of pores on female circumanal area:
    0. single,
    1. double.

26. Shape of female circumanal ring
    0. elliptical/circular,
    1. convoluted.

II. NYMPHS

HEAD

27. Number of nymphal antennal segments:
    0. 10,
    1. 9.

28. Base of nymphal antenna placement:
    0. very close to head margin, only partiall first basal segment cover by head,
    1. partial second segment covered by head,
    2. both the first and second segments covered by head.

THORAX

29. Apical angle of nymphal forewing-pad:
    0. adjacent or exterior to the margin of the hindwing-pad,
    1. interior to the hindwing-pad margin,

30. Trochanter:
    0. absent,
    1. present.

31. Arolium:
    0. triangular,
    1. broad, semi-circular,
    2. highly reduced or absent.

32. Nymphal unguitractor, a central sclerotized rod within arolium:
    0. present, obvious,
    1. absent or very reduced.

ABDOMEN

33. Nymphal abdominal sclerites on dorsal surface:
    0. present, obvious,
    1. highly reduced or lacking distinct sclerite.

34. Nymphal abdominal apex:
    0. smoothly truncate,
    1. pointed.

35. Shape of nymphal abdominal apex, if pointed:
    0. no special structure,
    1. serrate,
    2. with large medial 'teeth'.

36. Nymphal abdominal segments produced laterally as rounded or 'tooth' like projections:
    0. absent,
    1. present.

37. Lateral bulges on the abdomen, coincident with each apparent segment:
    0. absent,
    1. present.

38. Position of anal opening:
    0. ventral,
    1. most posterior point.

39. Circum-anal pore ring (nymphs):
    0. present,
    1. absent.

40. Anal pore field (other than circum-anal ring):
    0. absent,
    1. present.

41. Arrangement of anal pores in field other than circum-anal ring, if present:
    0. entire or broken rings,
    1. small groups.

42. Setal type on nymphal head:
    0. simple setae only,
    1. clavate setae,
    2. capitate setae.

43. Setal type, beside simple setae, on dorsal area of nymphal abdomen:
    0. simple setae only,
    1. clavate setae,
    2. capitate setae.

44. Setal type, beside simple setae, on ventral area of nymphal abdomen:
    0. simple setae only,
    1. lanceolate setae,
    2. rod setae,
    3. capitate setae.

45. Setal type, beside simple setae, on the margin of nymphal abdomen:
    0. simple setae only,
    1. lanceolate setae,
    2. secta setae,
    3. capitate setae.

Table 4-3. Character matrix used in Spondyliaspidinae phylogenetic analyses based on morphological characters.

spon4.data	1	1	2	3	4	5	6	7	8	9	10	11	12	13	14
		vertex	vertex	fovea	genal c	occipita	AL/HW	X/I	ant.	rhinaria	anteoc	wing a	wingsh	pterost	saltator
1	Pachypsylla c-mamma	2	0	1	2	1	2	0	1	0	1	0	0	0	1
2	Pachypsylla c -vesicula	2	0	1	2	1	2	0	1	0	1	0	0	0	1
3	Pachypsylla venusta	2	0	1	2	1	2	0	1	0	1	0	0	0	1
4	Pachypsylla c-gemma	2	0	1	2	0	2	1	1	0	1	0	0	0	1
5	Tetragonocephala flava	3	0	1	2	0	1	1	0	0	1	0	0	0	1
6	Celtisaspis beijingana	3	0	1	3	0	1	0	0	0	1	0	0	0	1
7	Phellopsylla spp.	1	0	3	1	1	1	0	0	0	0	1	0	0	1
8	Phyllolyma rufa	1	0	3	1	1	3	0	1	0	0	1	0	0	0
9	Phyllolyma sp	1	0	3	1	1	3	1	1	0	0	1	0	1	0
10	Creiis tecta	2	0	1	2	1	0	1	0	0	0	0	1	0	1
11	Creiis longipennis	2	0	1	2	1	0	1	0	0	0	0	1	0	1
12	Spondyliaspis plicatuloid	2	0	1	2	1	1	2	0	0	0	0	1	0	1
13	Cardiaspina albitexturata	3	0	1	2	1	2	1	0	0	0	0	1	0	1
14	Cardiaspina vittaformis	3	0	1	2	1	2	1	0	0	0	0	1	0	1
15	Glycaspis baileyi	2	0	1	3	2	0	1	0	1	0	1	1	0	0
16	Glycaspis aggregata	2	0	1	3	2	0	1	0	1	0	1	1	0	0
17	Glycaspis planitecta	2	0	1	3	2	0	1	0	1	0	1	1	0	0
18	Ctenarytaina eucalypti	2	0	1	2	1	2	2	1	0	0	0	1	0	0
19	Colophorina spn	0	0	0	2	0	2	2	0	0	1	0	0	0	0
20	Euphalerus spA	0	0	1	2	0	1	2	0	0	1	0	0	0	0
21	Euphalerus nidifix	0	0	1	2	2	1	2	0	0	0	0	0	0	0
22	Russelliana adesmiae	0	1	0	2	0	1	1	0	0	1	0	0	0	0
23	Russelliana fabiahae	0	1	0	2	0	1	1	0	0	1	0	0	0	1
24	Heteropsylla texana	0	0	0	0	2	0	2	0	0	1	0	0	0	0
25	Acizzia uncatoides	0	1	2	2	2	1	0	0	0	1	0	0	0	0
26	Trigonon longicornis	0	1	2	0	2	0	2	0	0	1	0	0	0	0
27	Psylla alni	0	1	1	2	2	0	1	0	0	1	0	0	0	0

Table 4-3 (cont.).

spon4.data 2		15	16	17	18	19	20	21	22	23	24	25	26	27	28
		genual	metata	meraca	male p	parame	parame	parame	aedeag	female	setae	circum	circum	ant seg	ant pla
1	Pachypsylla c-mamma	1	0	0	1	0	0	0	0	0	0	0	0	0	0
2	Pachypsylla c -vesicula	1	0	0	1	0	0	0	0	0	0	0	0	0	0
3	Pachypsylla venusta	1	0	0	1	0	0	0	0	0	0	0	0	0	1
4	Pachypsylla c-gemma	1	0	0	1	0	0	0	0	0	0	0	0	0	1
5	Tetragonocephala flava	1	1	0	1	0	0	0	0	1	2	1	0	0	0
6	Celtisaspis beijingana	1	0	0	1	0	0	0	0	1	2	1	0	0	2
7	Phellopsylla spp.	1	0	1	0	0	0	0	0	0	0	0	0	1	0
8	Phyllolyma rufa	1	0	1	0	0	0	0	?	?	?	?	?	?	?
9	Phyllolyma sp	1	0	?	0	0	0	0	0	?	?	?	?	1	0
10	Creiis tecta	0	0	1	1	1	0	1	1	?	?	?	?	?	?
11	Creiis longipennis	0	0	1	1	1	0	1	1	0	1	1	0	0	0
12	Spondyliaspis plicatuloid	0	0	1	1	?	?	?	?	0	1	1	1	0	0
13	Cardiaspina albitexturata	0	0	1	1	1	0	1	0	0	0	1	0	0	0
14	Cardiaspina vittaformis	0	0	1	1	1	0	1	0	?	?	?	?	0	0
15	Glycaspis baileyi	0	0	1	1	1	1	0	1	0	0	1	2	0	0
16	Glycaspis aggregata	0	0	1	1	1	1	0	1	0	0	1	2	?	?
17	Glycaspis planitecta	0	0	1	1	1	0	0	1	?	?	?	?	?	?
18	Ctenarytaina eucalypti	1	1	0	1	0	0	0	0	0	0	1	0	0	0
19	Colophorina spn	1	0	0	0	0	0	0	0	?	?	?	?	1	0
20	Euphalerus spA	1	0	0	0	0	0	0	0	0	1	1	0	1	1
21	Euphalerus nidifix	0	0	0	0	0	0	0	0	0	1	1	0	1	2
22	Russelliana adesmiae	0	1	0	0	1	0	0	1	0	1	0	0	?	?
23	Russelliana fabiahae	0	1	0	0	1	0	0	1	0	1	0	0	?	?
24	Heteropsylla texana	0	0	0	0	0	1	0	2	0	0	1	0	1	0
25	Acizzia uncatoides	0	0	0	0	0	1	0	2	0	1	1	0	1	1
26	Trigonon longicornis	0	0	0	0	0	0	0	?	0	1	1	0	?	?
27	Psylla alni	0	0	0	0	1	0	1	0	0	1	1	0	1	1

Table 4-3 (cont.).

spon4.data	3	29	30	31	32	33	34	35	36	37	38	39	40	41	42
		win-pac	trocha	aroliun	unguitr	dorsal	abd spe	pointed	lat. pr	abd lat	anal op	circum-	anal pc	anal pc	head s
1	Pachypsylla c-mamma	0	1	2	1	1	1	2	0	0	1	1	1	1	0
2	Pachypsylla c -vesicula	0	1	2	1	1	1	2	0	0	1	1	1	1	0
3	Pachypsylla venusta	0	1	2	1	1	1	2	0	0	1	1	1	1	0
4	Pachypsylla c-gemma	0	1	2	1	1	1	2	0	0	1	1	1	1	0
5	Tetragonocephala flava	0	1	2	1	1	1	0	0	0	1	1	1	1	0
6	Celtisaspis beijingana	0	1	2	1	1	1	0	0	0	1	1	1	1	0
7	Phellopsylla spp.	0	0	2	1	0	0	-	0	0	1	0	1	?	0
8	Phyllolyma rufa	?	?	?	?	?	?	?	?	?	?	?	?	?	?
9	Phyllolyma sp	0	0	2	1	0	1	0	0	0	1	0	1	1	0
10	Creiis tecta	?	?	?	?	?	?	?	?	?	?	?	?	?	?
11	Creiis longipennis	1	0	2	1	0	1	0	1	1	1	1	1	1	0
12	Spondyliaspis plicatuloid	0	0	2	1	0	1	0	0	0	1	1	0	-	0
13	Cardiaspina albitexturata	1	0	2	1	0	1	0	0	1	1	1	0	-	0
14	Cardiaspina vittaformis	1	0	2	1	0	1	0	0	1	0	1	0	-	0
15	Glycaspis baileyi	0	0	2	1	0	1	0	0	0/1	1	1	1	2	0
16	Glycaspis aggregata	?	?	?	?	?	?	?	?	?	?	?	?	?	?
17	Glycaspis planitecta	?	?	?	?	?	?	?	?	?	?	?	?	?	?
18	Ctenarytaina eucalypti	0	0	2	1	0	0	-	0	0	1	0	1	1	0
19	Colophorina spn	0	0	0	0	0	0	-	0	0	1	0	1	0	0
20	Euphalerus spA	0	0	0	0	0	0	-	0	0	1	0	1	0	0
21	Euphalerus nidifix	0	1	0	0	0	1	1	0	0	1	1	1	0	0
22	Russelliana adesmiae	?	?	?	?	?	?	?	?	?	?	?	?	?	?
23	Russelliana fabiahae	?	?	?	?	?	?	?	?	?	?	?	?	?	?
24	Heteropsylla texana	0	0	1	0	0	0	-	0	0	0	0	0	-	1
25	Acizzia uncatoides	0	0	1	0	0	0	-	0	0	0	0	0	-	2
26	Trigonon longicornis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
27	Psylla alni	0	0	1	0	0	0	-	0	0	1	0	0	-	0

Table 4-3 (cont.).

spon4.data	4	43	44	45
		abd set	abd se	abd set
1	Pachypsylla c-mamma	0	0	0
2	Pachypsylla c -vesicula	0	0	0
3	Pachypsylla venusta	0	0	0
4	Pachypsylla c-gemma	0	0	0
5	Tetragonocephala flava	0	0	0
6	Celtisaspis beijingana	0	0	0
7	Phellopsylla spp.	0	1	1
8	Phyllolyma rufa	?	?	?
9	Phyllolyma sp	0	1	1
10	Creiis tecta	?	?	?
11	Creiis longipennis	0	0	0
12	Spondyliaspis plicatuloid	0	0	0
13	Cardiaspina albitexturata	0	0	0
14	Cardiaspina vittaformis	0	0	0
15	Glycaspis baileyi	0	0	0
16	Glycaspis aggregata	?	?	?
17	Glycaspis planitecta	?	?	?
18	Ctenarytaina eucalypti	0	0	1
19	Colophorina spn	0	0	2
20	Euphalerus spA	0	0	2
21	Euphalerus nidifix	0	0	0
22	Russelliana adesmiae	?	?	?
23	Russelliana fabiahae	?	?	?
24	Heteropsylla texana	1	2	1
25	Acizzia uncatoides	2	3	3
26	Trigonon longicornis	?	?	?
27	Psylla alni	0	0	0

Table 4-4. Summary of concealment types and character states scored for each taxa for the analyses of evolution of gall/lerp formation of Spondyliaspidinae.

Taxa	Coding1	Coding2	Coding3	Summary of concealed biology**
Pachypsylla celtidismamma	2	2	0	G
Pachypsylla celtidivesicula	2	2	0	G
Pachypsylla venusta	2	2	0	G
pachypsylla celtidisgemma	2	2	0	G
Tetragonocephala flava	1	0	2	L
Celtisaspis beijingana	1/2	1	2	L+G(P) or L
Phellopsylla spp.	0	0	1	F (W) [under bark w/ floccuent cover]
Phyllolyma rufa	1	0	2	L
Phyllolyma sp.	1	0	2	L
Creiis tecta	1	0	2	L
Creiis longipennis	1	0	2	L
Spondyliaspis plicatuloides	1	0	2	L
Cardiaspina albitexturata	1	0	2	L
Cardiaspina vittaformis	1	0	2	L
Glycaspis baileyi	1	0	2	L
Glycaspis aggregata	1	0	2	L
Glycaspis planitecta	1	0	2	L
Ctenarytaina eucalypti	0	0	1	F (W)
Colophorina cassiae	0	0	1	F (W) [between pairs of unopene leaflets]
Euphalerus sp. A	?	?	?	unknown
Euphalerus nidifex	1	0	2	L
Russelliana adesmiae	0	0	0	F
Russelliana fabianae	0	0	0	F
Heteropsylla texana	0	0	0	F
Acizzia uncatoides	0	0	0	F
Trigonon longi	?	?	?	unknown
Psylla alni	0	0	0	F

* See text for the details.

** F= free-living; W= wax; L= lerp; P= partial gall (not enclosed); G= enclosed gall; ?= biology unknown; W within parentheses means associate habits with F; notes are enclosed in bracket.

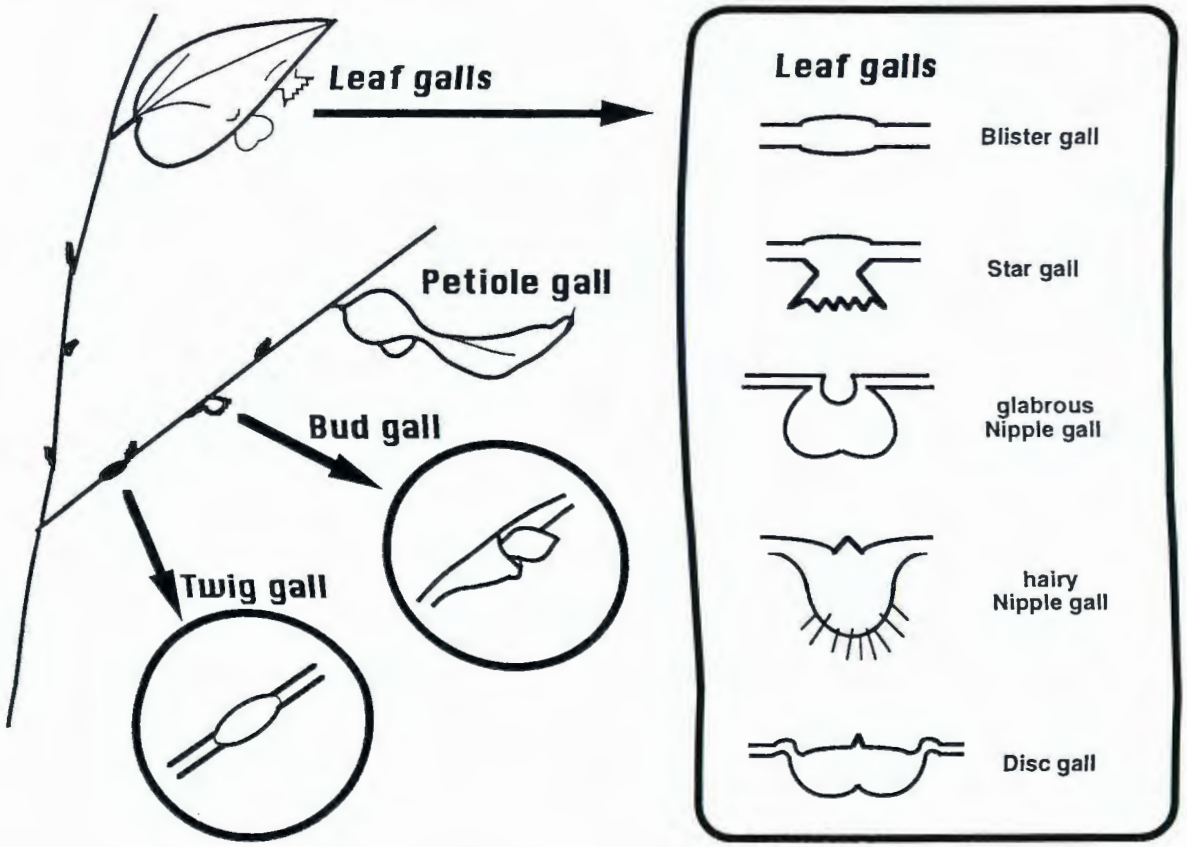

Fig.1-1. Diagrammatic profiles of gall types of hackberry psyllids, *Pachypsylla,* on host plant *Celtis*. There are four major groups according to galling position, i.e., the leaf-blade gall makers, the petiole gall makers, the bud gall makers, and the twig gall makers. Drawings in the box show five major types of leaf galls .

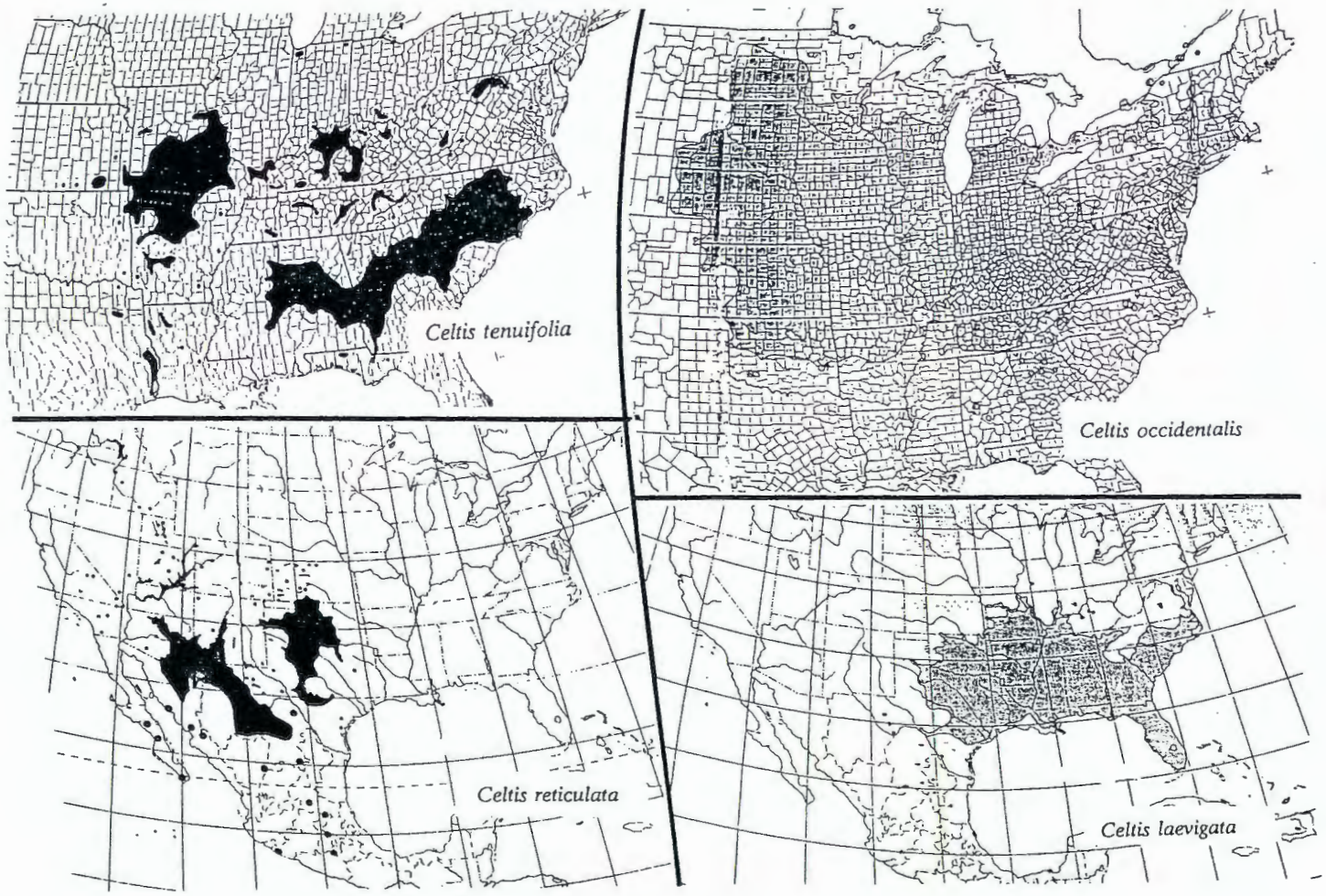

Figure 1-2. Distribution of hosts of the hackberry psyllids, *Pachypsylla* (after Little, 1971, 1976, 1977)

Figure 1-3. Map of United States showing sampling localities for *Pachypsylla* adults. Numbers of populations sampled from each state are indicated.

Figure 1-4. Map of United States showing sampling localities for *Pachypsylla* nymphs. Numbers of populations sampled from each state are indicated.

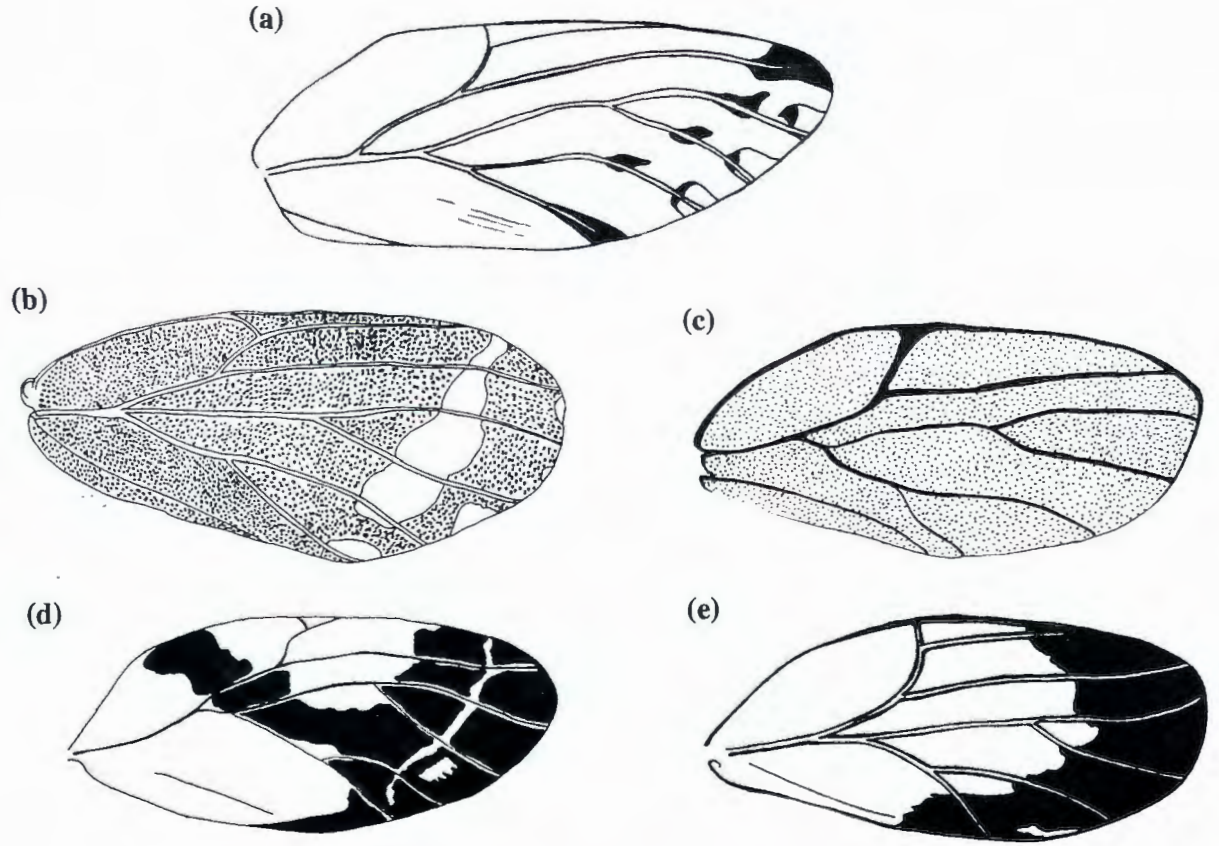

Figure 1-5. Forewing pattern variations of the major galling groups of *Pachypsylla* adults: (a) the petiole gall maker, *P. venusta*; (b) the leaf-blade hairy nipple gall maker, *P. celtidismamma*; (c) the glabrous bud gall maker, *P. celtidisgemma*; (d) the hairy bud gall maker, *P. pallida*; (e) the twig gall maker, *P. celtidisinteneris*. (after Porter)

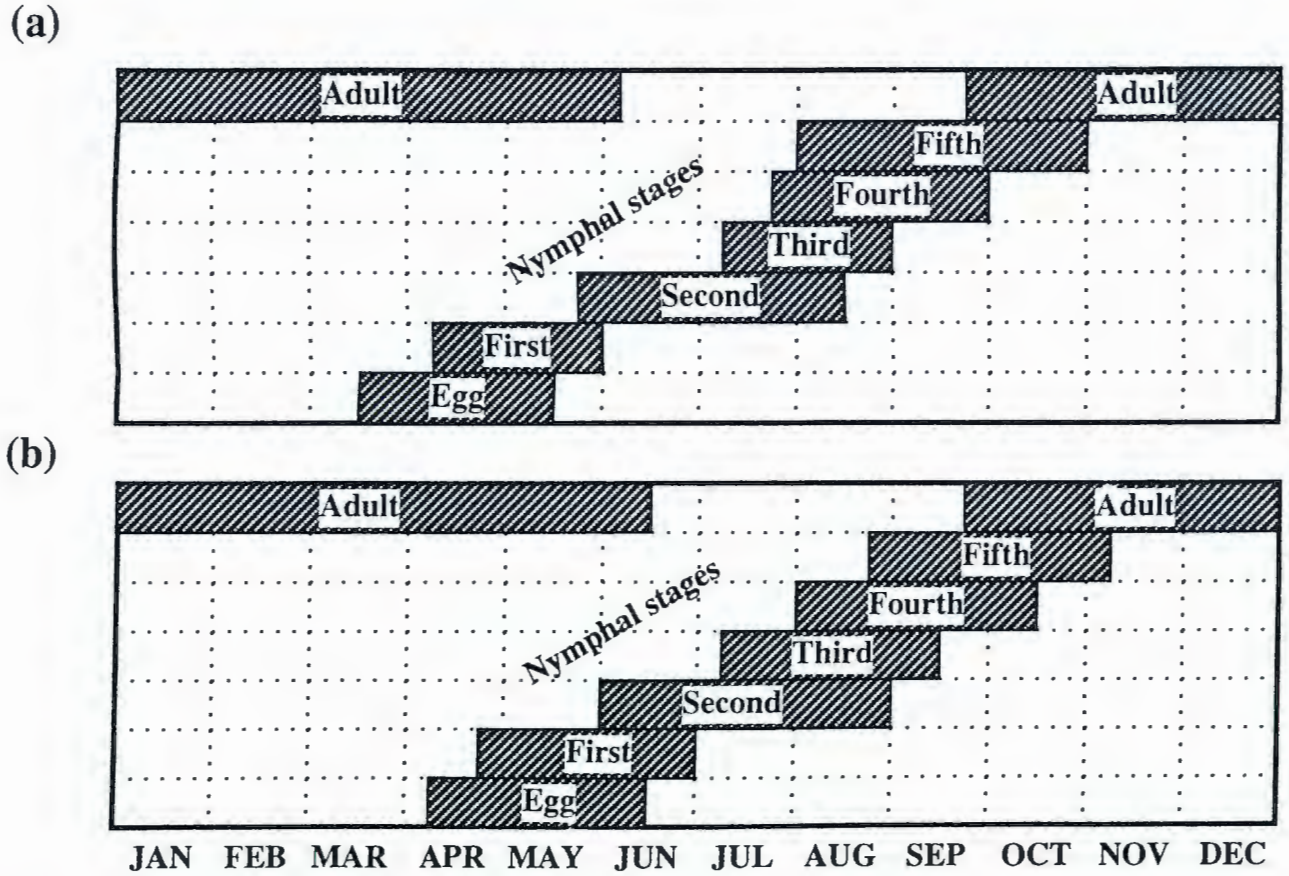

Figure 1-6. Life history of two types of leaf gall makers at National Agricultural Library (NAL) population in Beltsville , Maryland: (a) glabrous nipple gall maker; (b) star gall maker.

(a) Leaf blister gall maker

(b) Leaf disc gall maker

(c) Leaf hairy nipple gall maker

(d) Side cell individual of leaf hairy nipple gall

Figure 1-7. Scanning electron micrographs showing variation of hair density on male proctiger among leaf gall makers: (a) blister gall maker, (b) disc gall maker, (c) hairy nipple gall mkaer, and (d) side cell individual (an inquiline) from hairy nipple gall. P: proctiger; F: forcep.

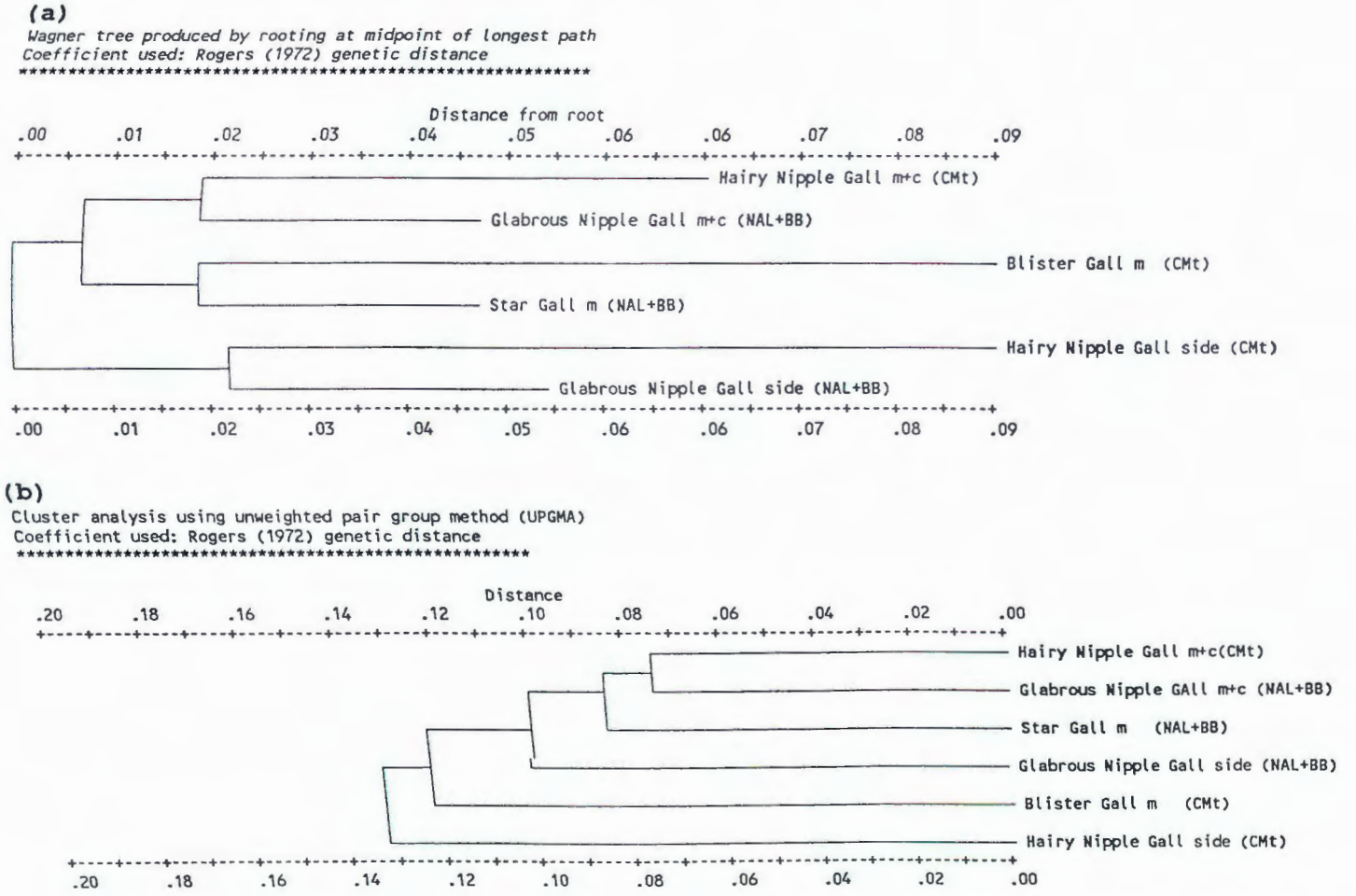

Figure 2-1. Distance Wagner and UPGMA trees, based on Rogers' distance (15 loci), of eight populations of *Pachypsylla* leaf gall nymphs from different gall types and cell positions (m= monocell gall; c= center cell of multiple cell gall; side= side cell of multiple cell gall). Populations are given in parentheses; acronyms follow Table 1-3.

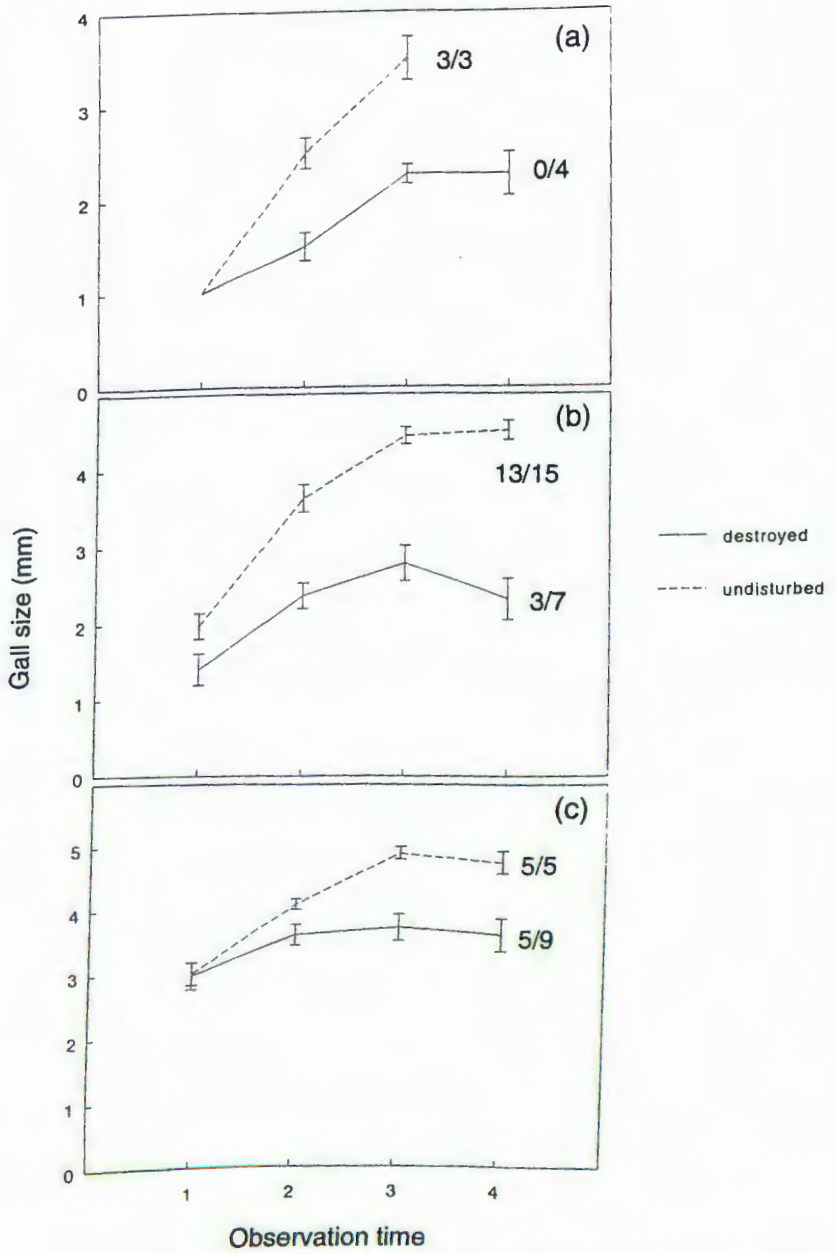

Figure 2-2. Change of gall size through time between treatment (center cell individual destroyed) and control (center cell individual undisturbed). Destruction was conducted at three different times during gall initiation: (a) both center and side cell nymphs exposed, (b) center cell nymph enclosed but side cell nymphs exposed, (c) both center and side cell nymphs enclosed in galls. Observation time 1: time when destruction implemented; Time 2: two weeks after time 1; Time 3: two months after time 1; Time 4: four months after time 1. Number of individual survived out of total observed individuals until emergence is given at time 4.

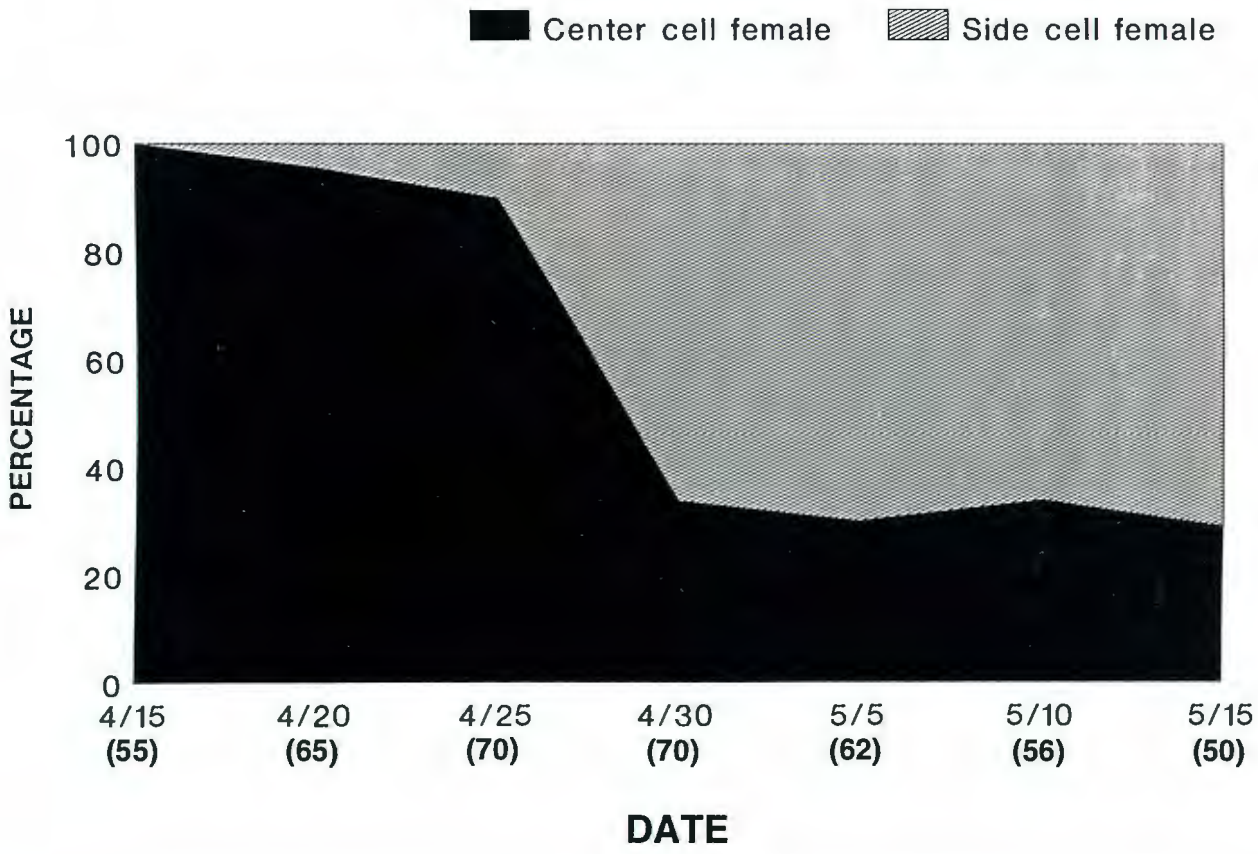

Figure 2-3. Change of proportion of center and side cell females of hackberry leaf gall makers at Beltsville, Md, in the spring of 1993. Numbers in parentheses below each date indicate total number of individuals collected.

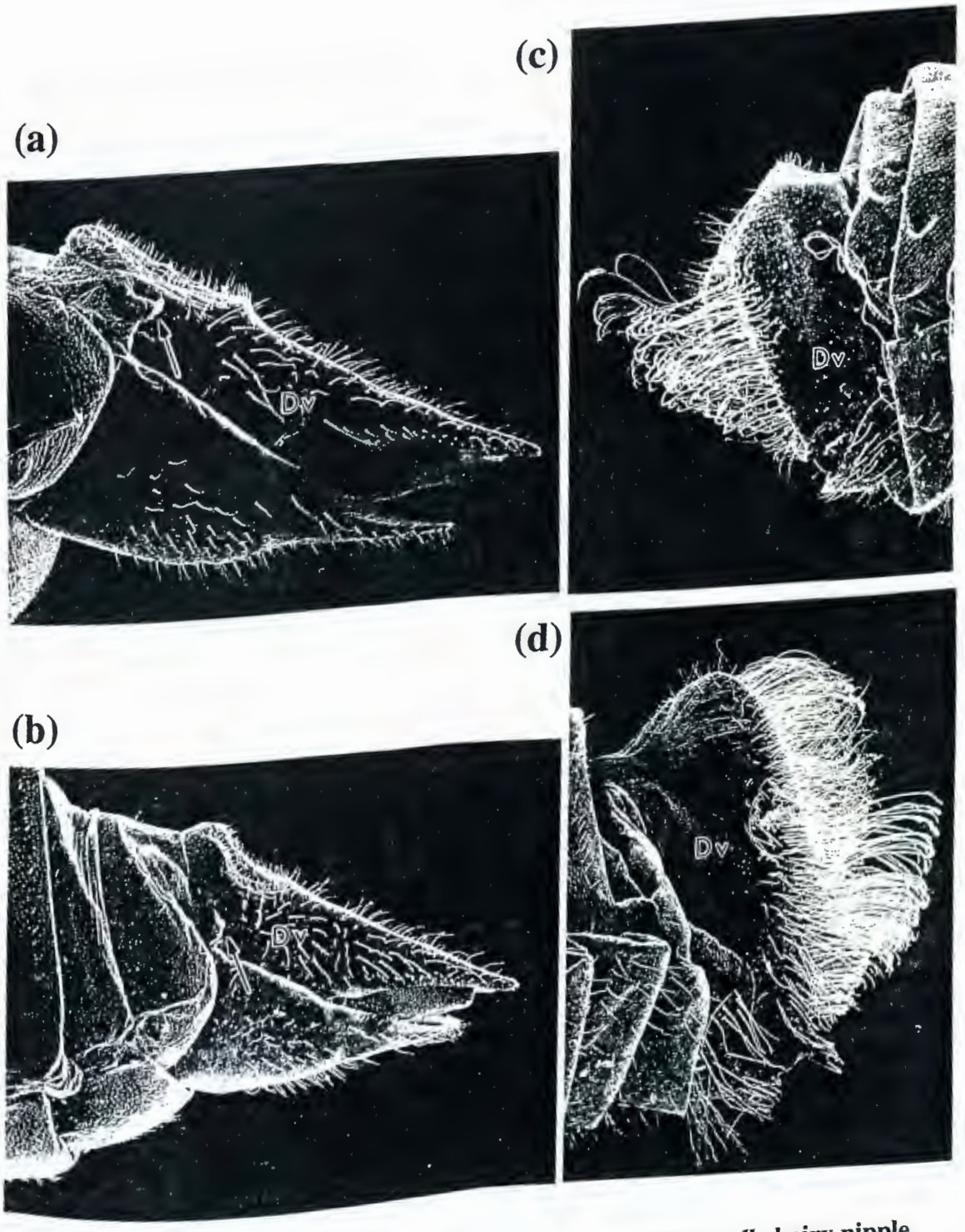

Figure 3-1. Female genitalia of: side cell individual of *Pachypsylla* hairy nipple gall (a), star gall maker(b), *Tetragonocephala flava* (c) and *Celtisaspis beijingana* (d), showing rounded dorsal valve (Dv) in the latter two taxa, and thumb-like process (arrow) in the former two species.

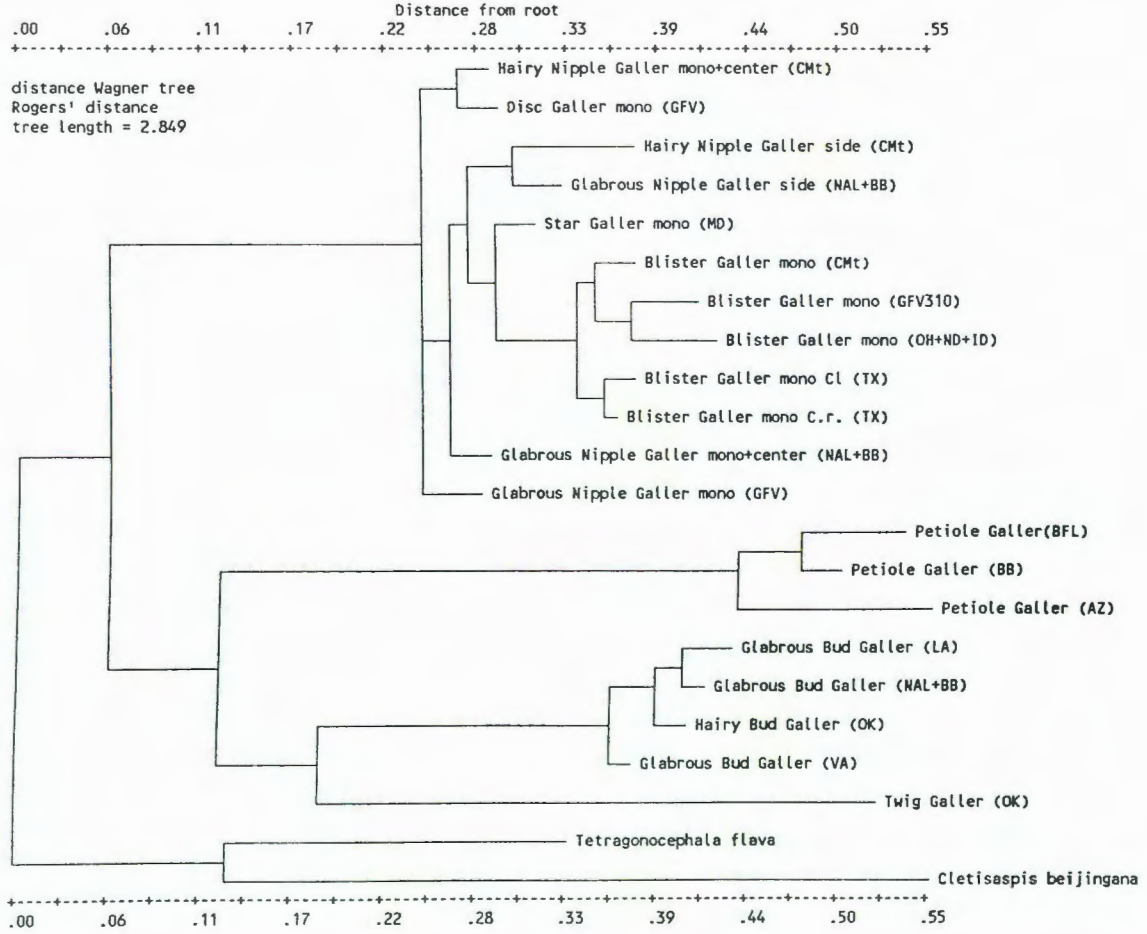

Figure 3-2. Distance Wagner tree of *Pachypsylla* with outgroups *Tetragonocephala flava* and *Celtisaspis beijingana* based on Rogers' genetic distance using allozyme data (15 loci).

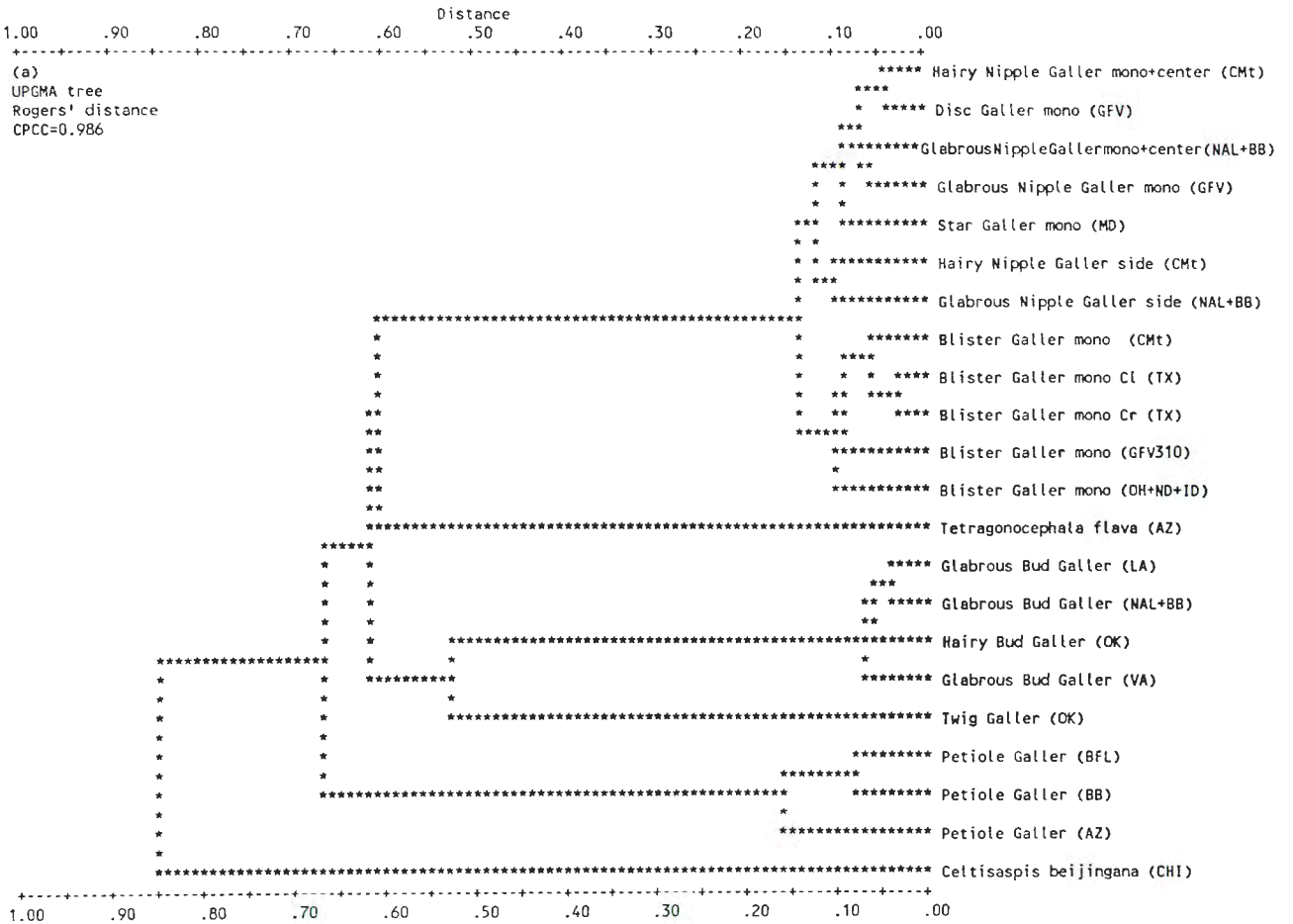

Figure 3-3 (a) UPGMA tree of *Pachypsylla* with outgroups *Tetragonocephala flava* and *Celtisaspis beijingana* based on Rogers' genetic distance using allozyme data (15 loci).

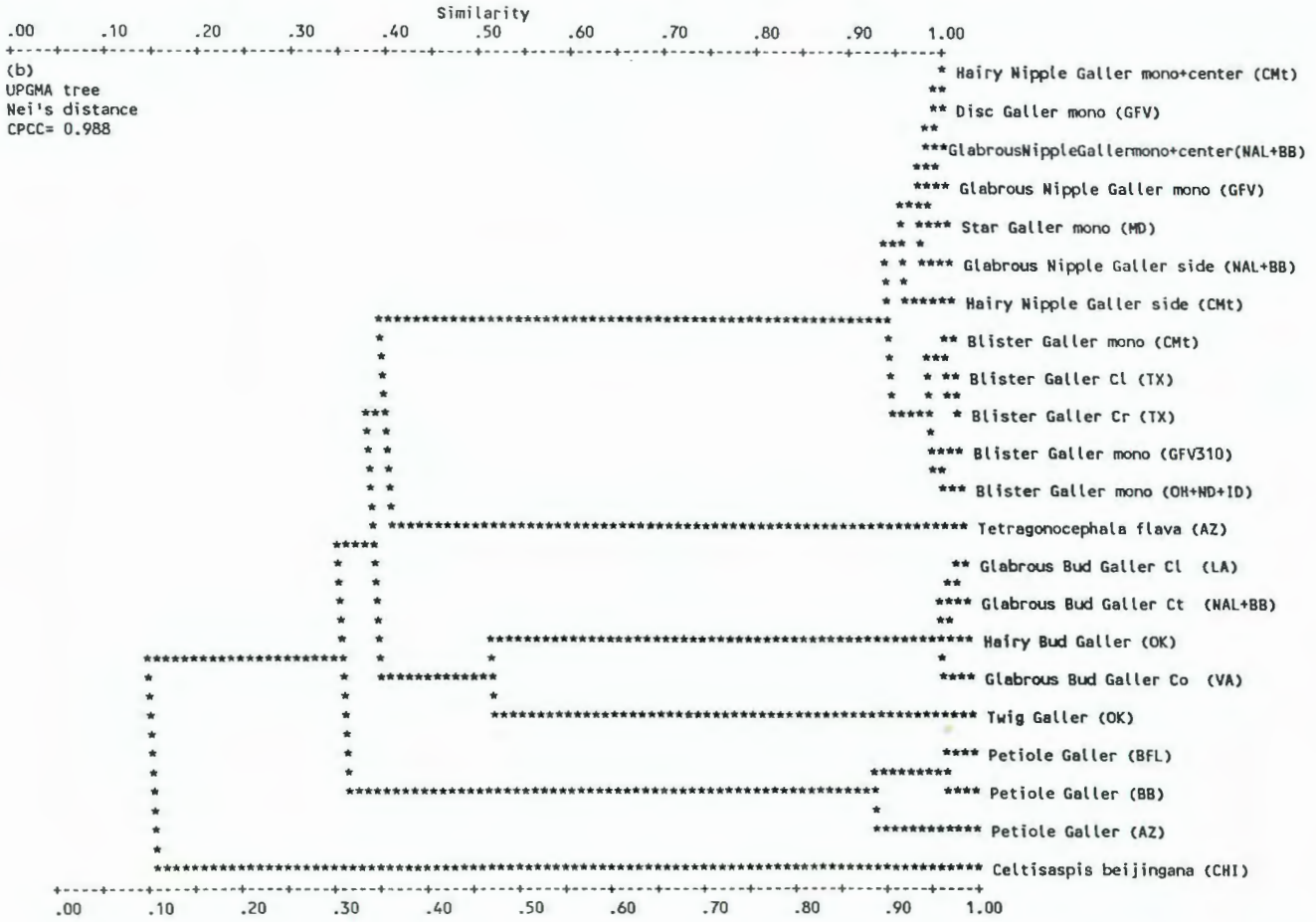

Figure 3-3 (b) UPGMA tree of *Pachypsylla* with outgroups *Tetragonocephala flava* and *Celtisaspis beijingana* based on Nei's genetic distance using allozyme data (15 loci).

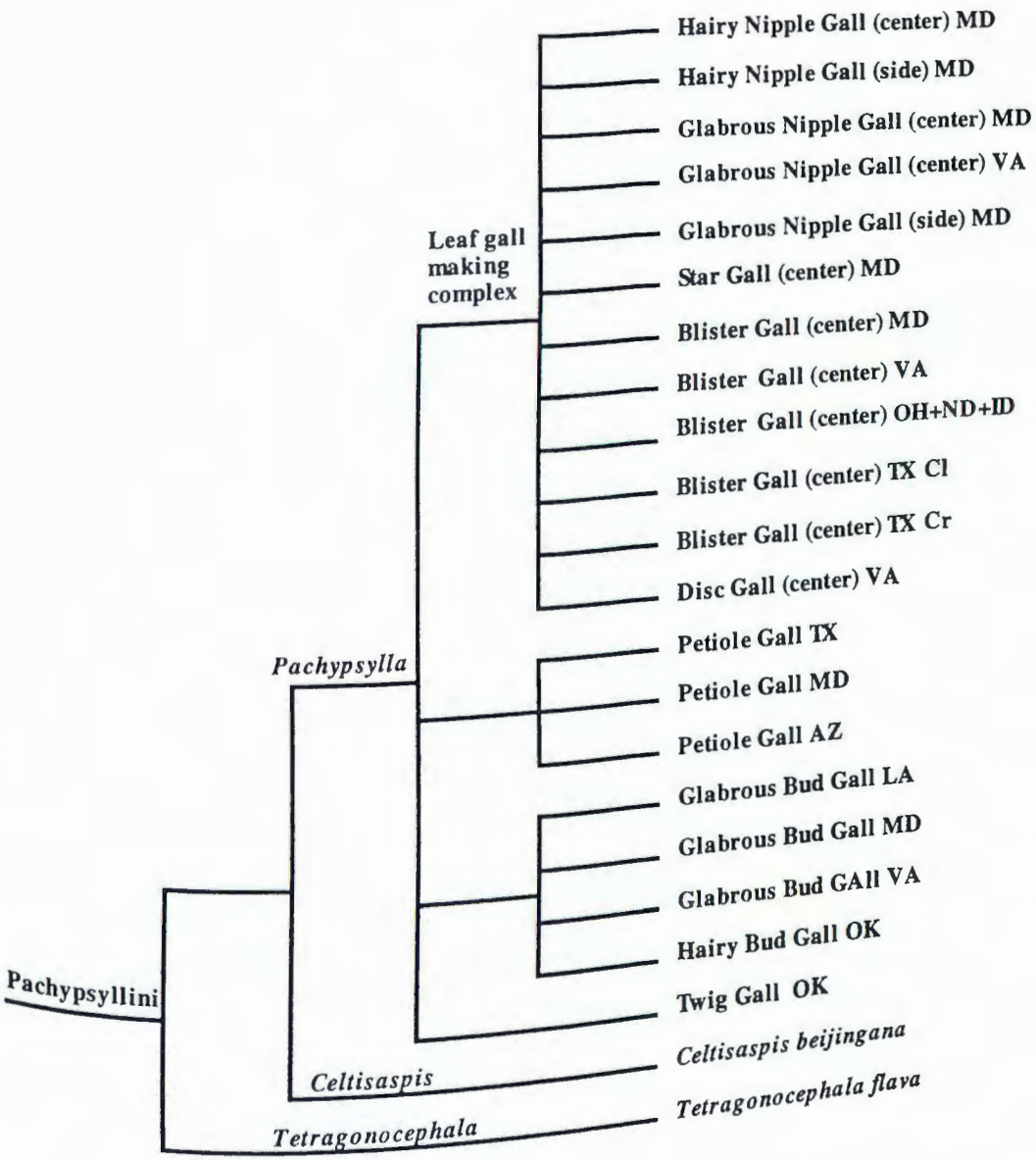

Figure 3-4. Strict consensus of 3400 most parsimonious trees for nymphal allozyme data when loci treated as characters, alleles as discrete character states. Cell position within a gall in parentheses. Cl: *Celtis laevigata*; Cr: *C. reticulata*.

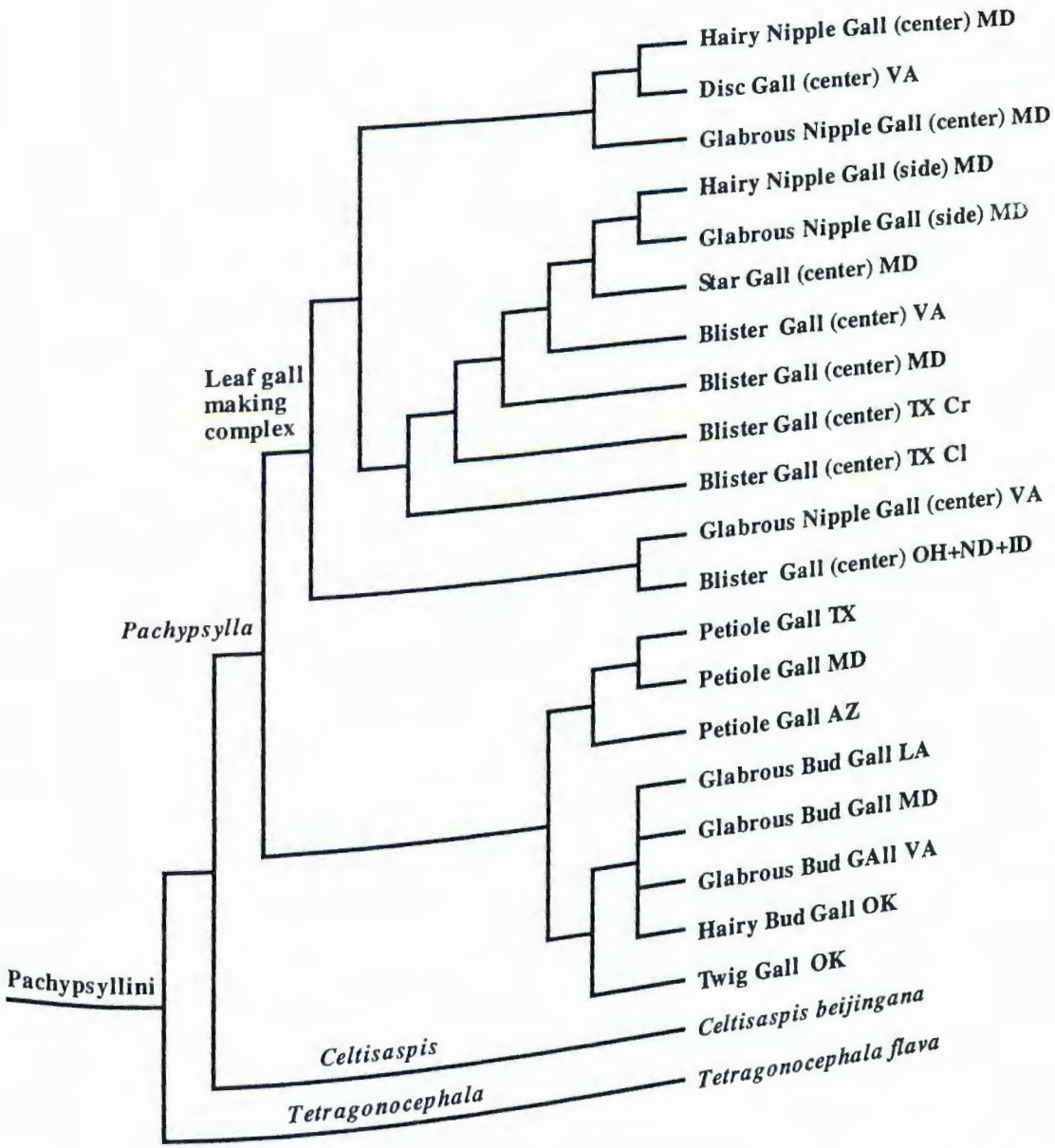

Figure 3-5. Strict consensus of four most parsimonious trees for allozyme data with each allele treated as an independent present/absent character. Cell position within a gall in parentheses. Cl: *Celtis laevigata*; Cr: *C. reticulata*.

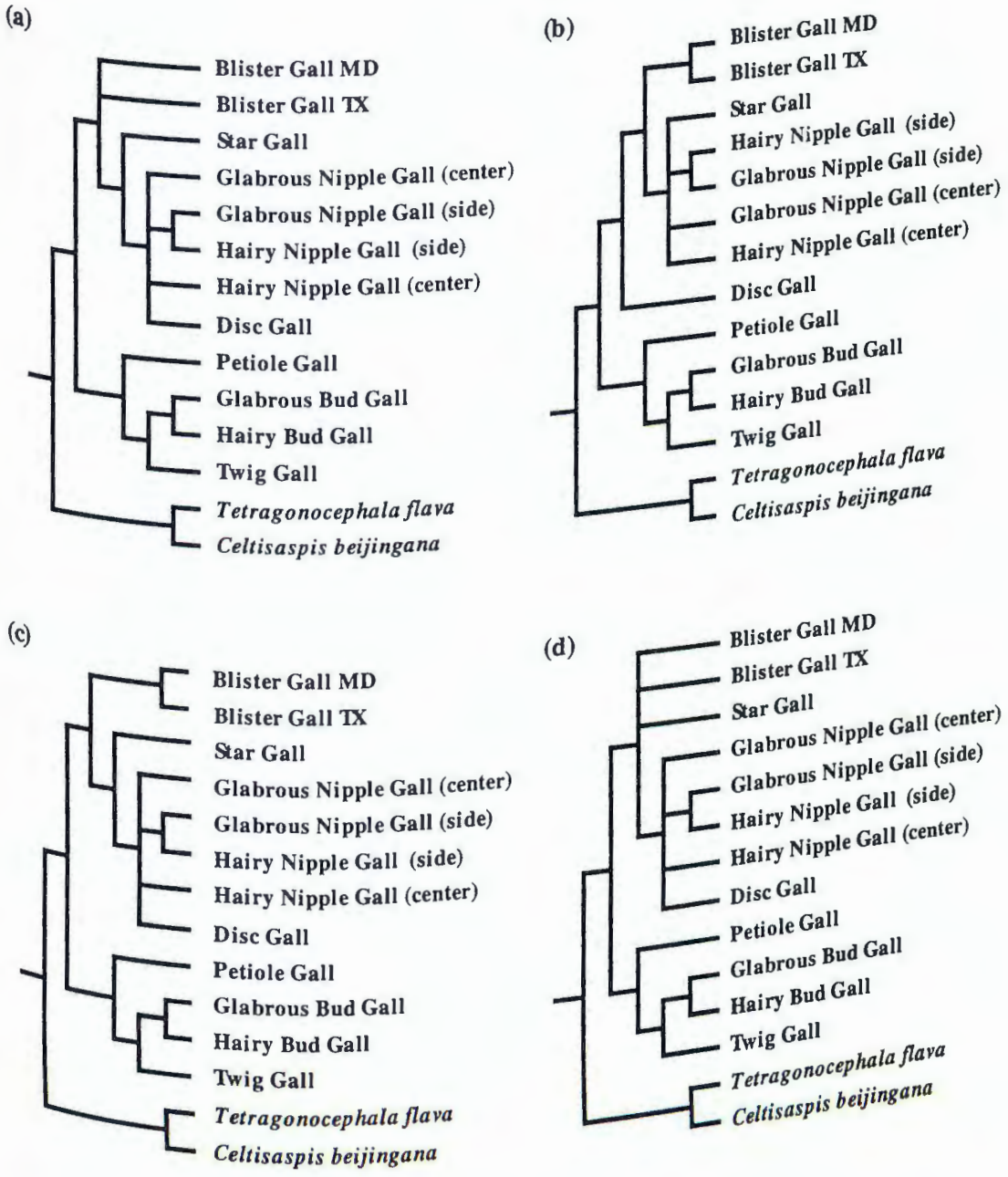

Figure 3-6. Three equally parsimonious trees (a-c) and their strict consensus (d) for *Pachypsylla* based on morphological data with all characters unordered. Cell position in parentheses.

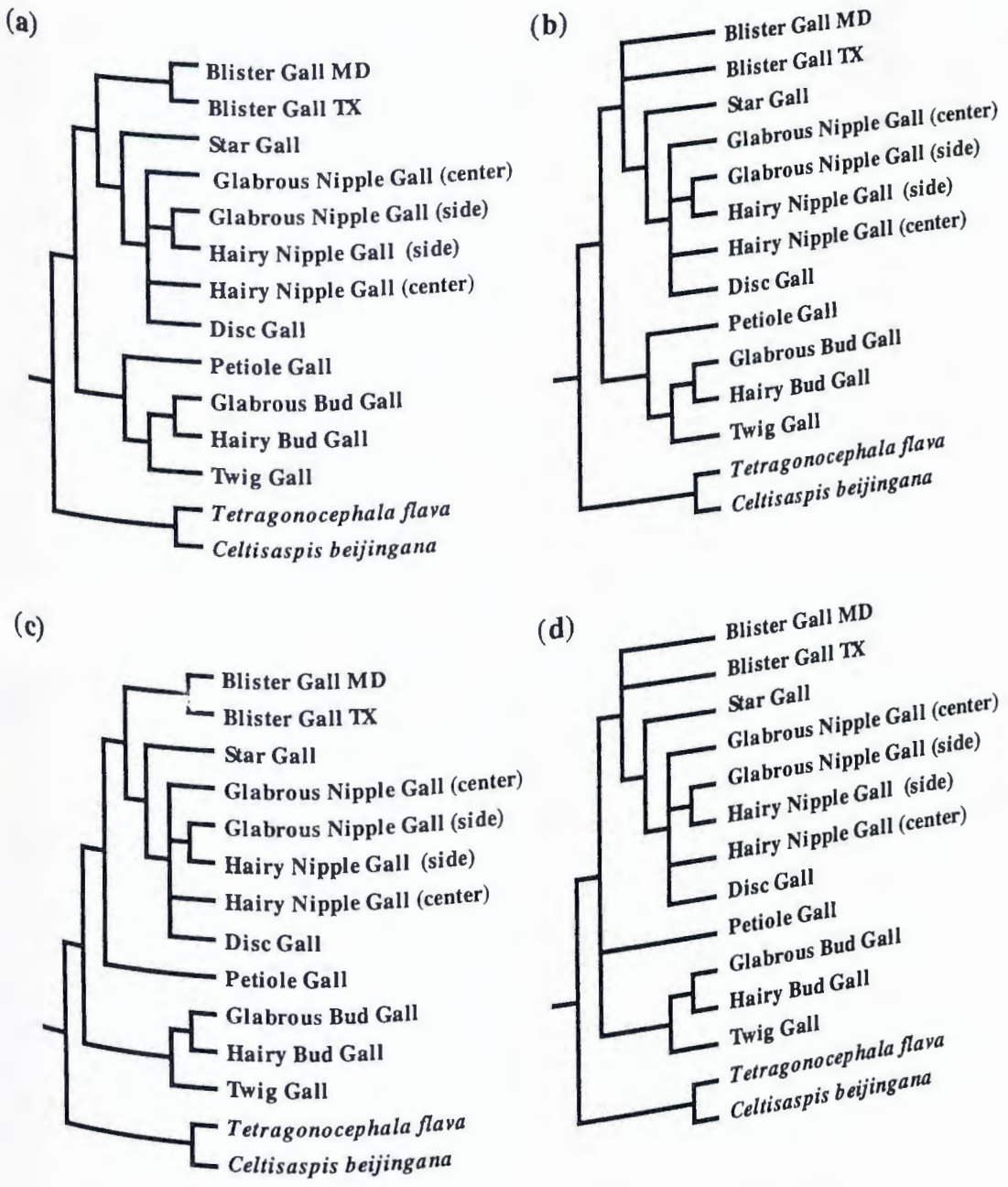

Figure 3-7. Three equally parsimonious trees (a-c) and their strict consensus (d) for *Pachypsylla* morphological data, with all characters ordered. Cell position in parentheses.

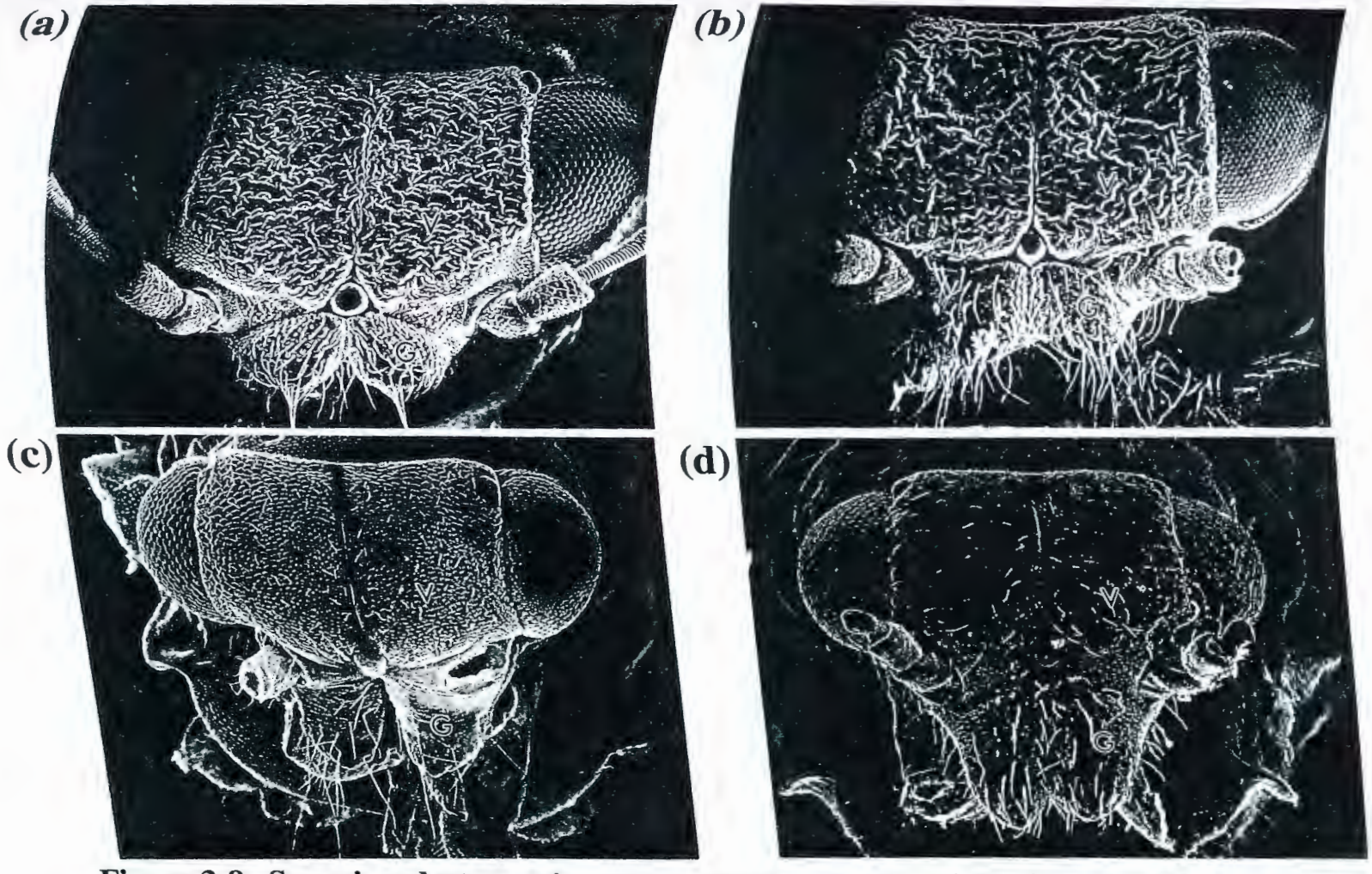

Figure 3-8. Scanning electron micrographs of adult heads: (a) *Pachypsylla* leaf star galler; (b) *Pachypsylla* petiole galler; (c) *Tetragonocephala flava*; (d) *Celtisaspis beijingana*, showing the surface structure of vertex (V) and genae (G).

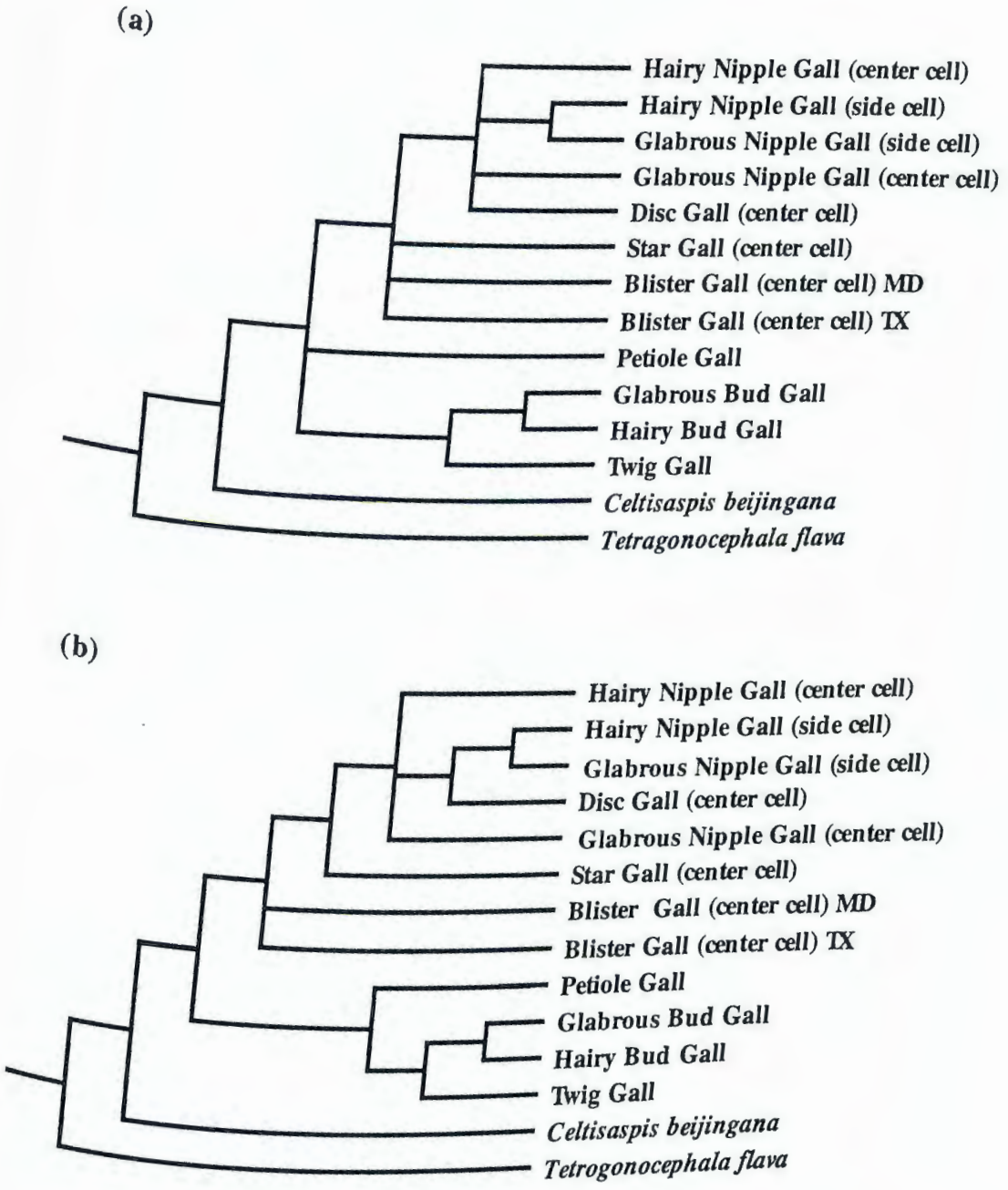

Figure 3-9. Consensus trees for combined morphological, electrophoretic, karyotypic, and life history data: (a) each locus treated as single character (from 10 trees); (b) each allele treated as single character (from 5 trees). Cell position of leaf galls in parentheses.

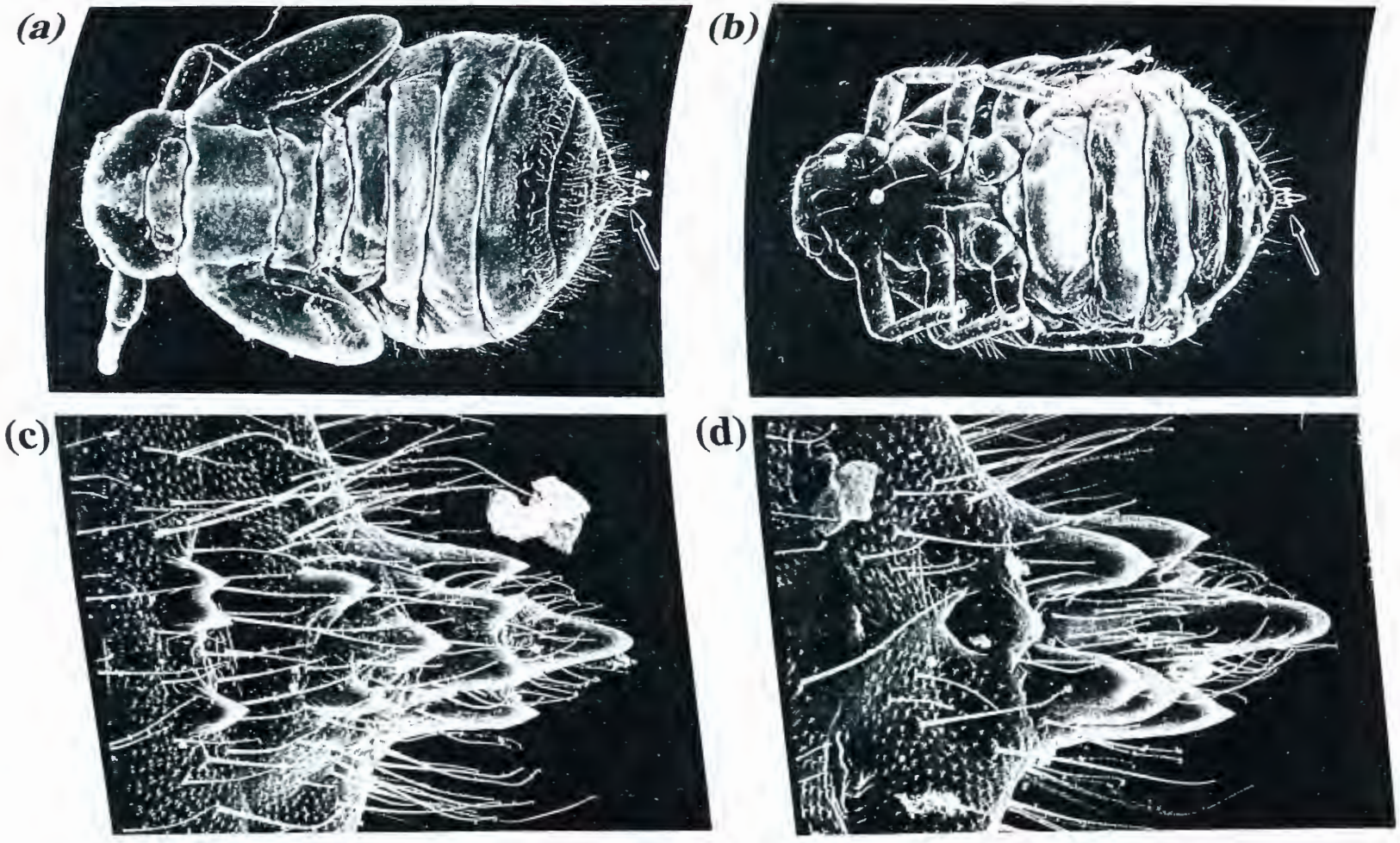

Figure 3-10. Fifth instar nymph of leaf blister gall maker: (a) dorsal view; (b) ventral view; (c) enlargement of caudal spurs (arrow) of (a); (d) enlargement of caudal spurs (arrow) of (b).

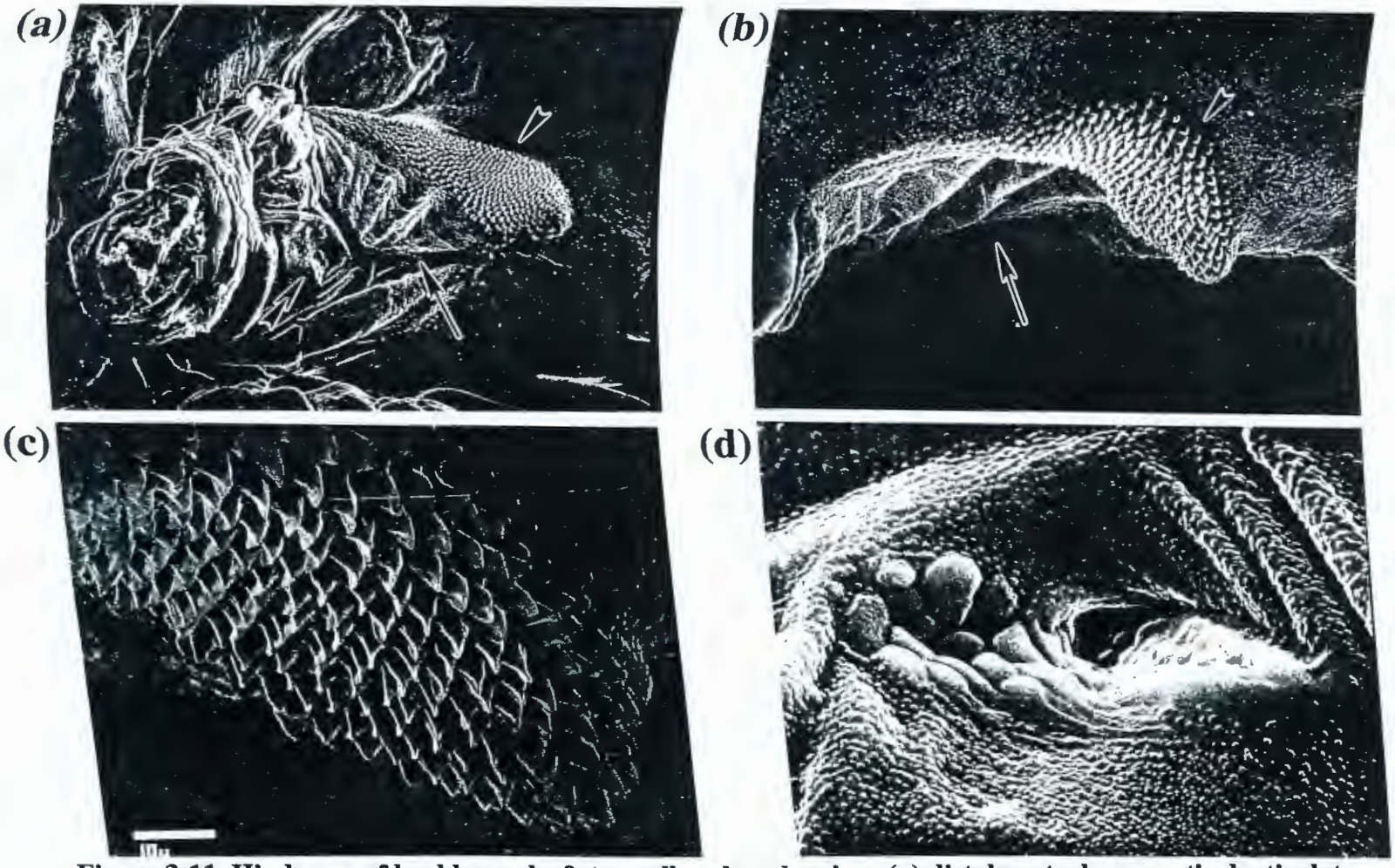

Figure 3-11. Hind coxa of hackberry leaf star gall maker showing: (a) distal ventral crescentic denticulate patch (arrow head) and a fan-shaped area (arrow) near the patch, ventral view; (b) lateral view; (c) enlargement of denticulate patch of (b); (d) enlargement of hole (double arrow head) between fan-shaped area and trochanter (T) of (a).

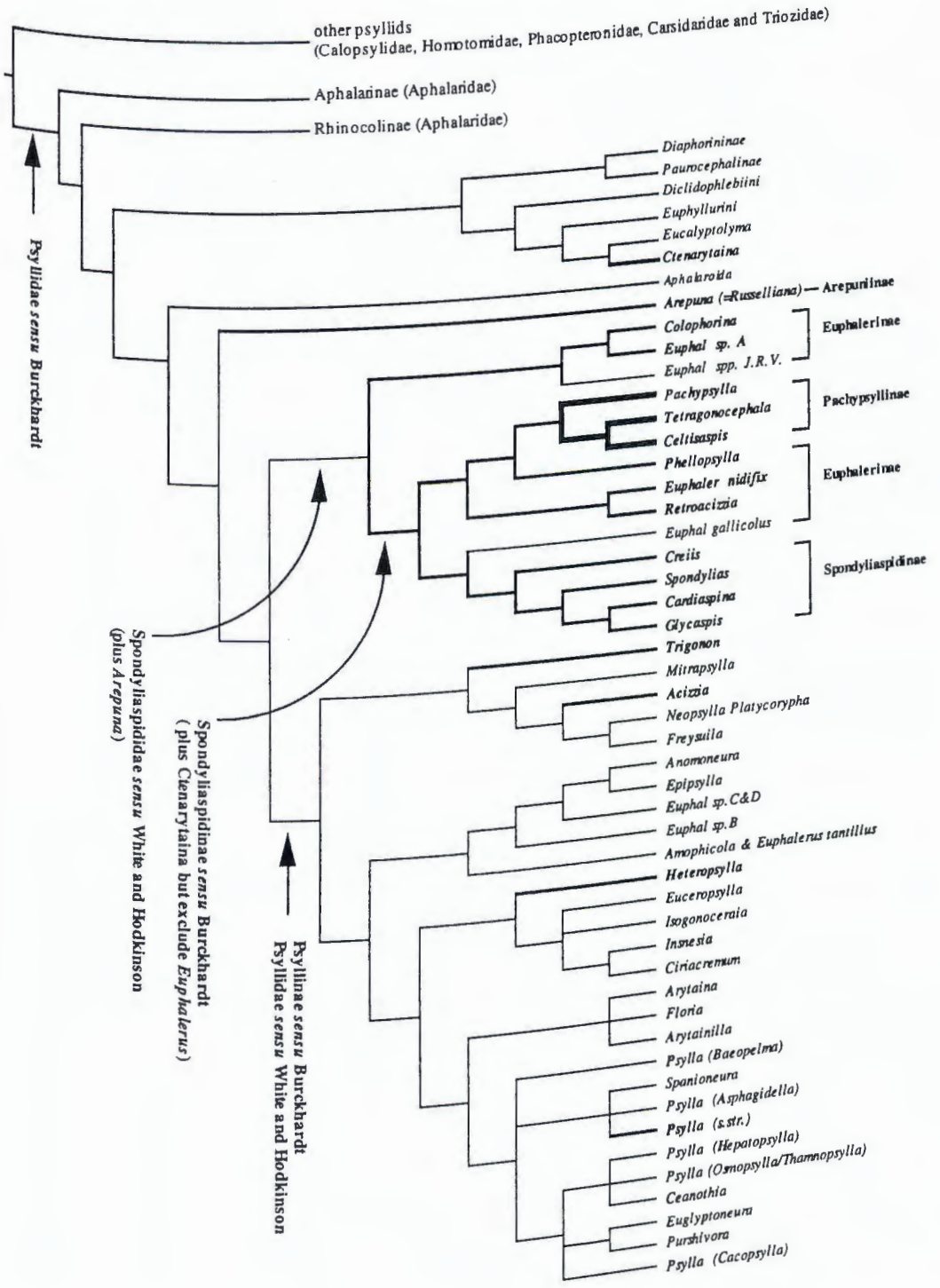

Figure 4-1. Partial phylogeny of Psylloidea after White and Hodkinson (1985). Highlighted taxa indicate those sampled for current study.

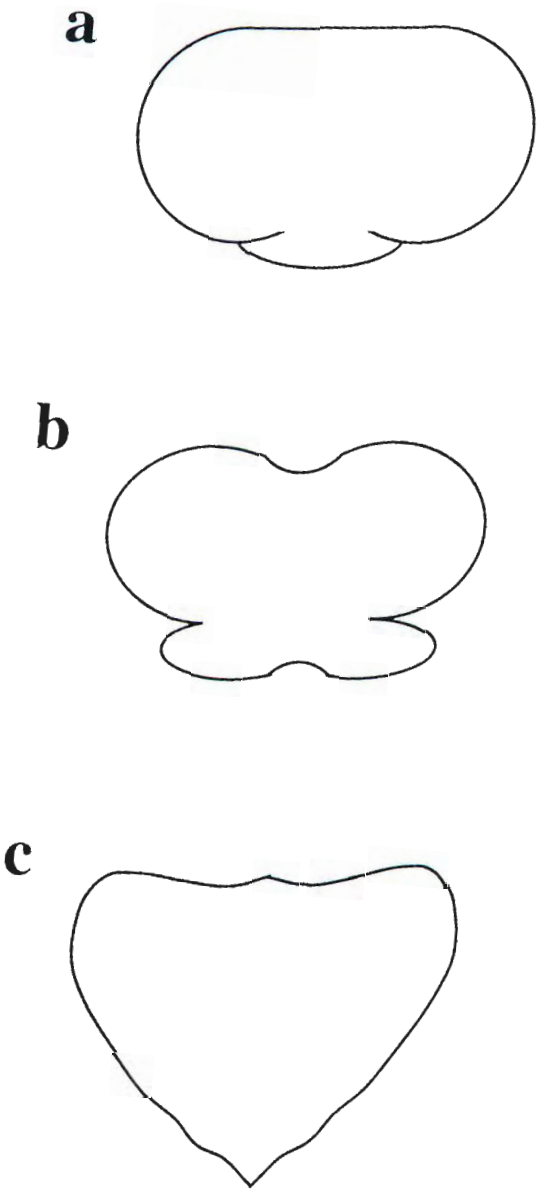

Fig. 4-2. Shapes of occipital foramen.

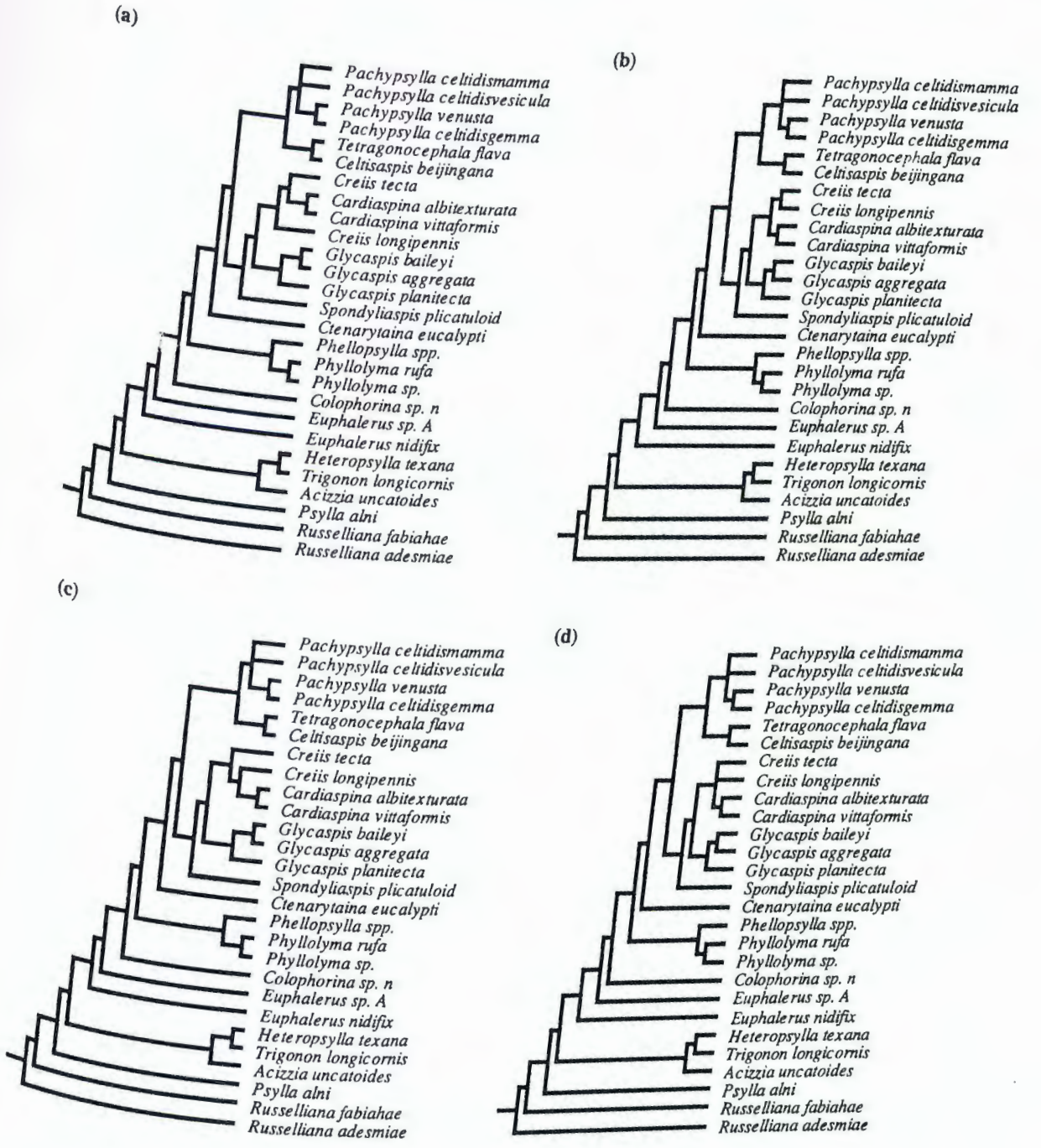

Figure 4-3. Three equally parsimonious trees (a-c) and their strict consensus (d) for Spondyliaspidini based on morphological data with all characters unordered. Same trees found after successive weighting.

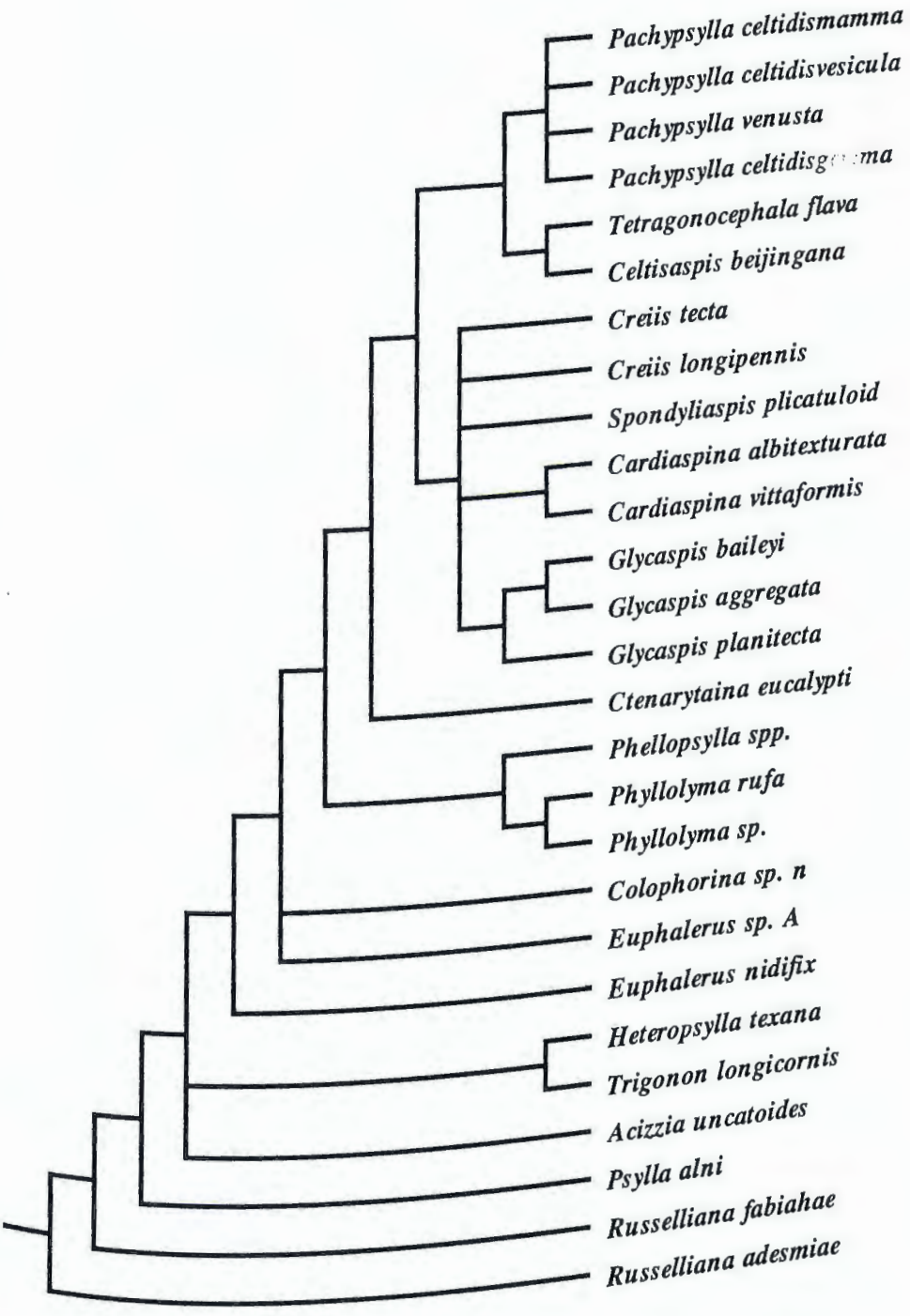

Figure 4-4. Strict consensus of 164 most parsimonious trees for Spondyliaspidinae based on morphological data with some characters (#3-7) ordered and others unordered.

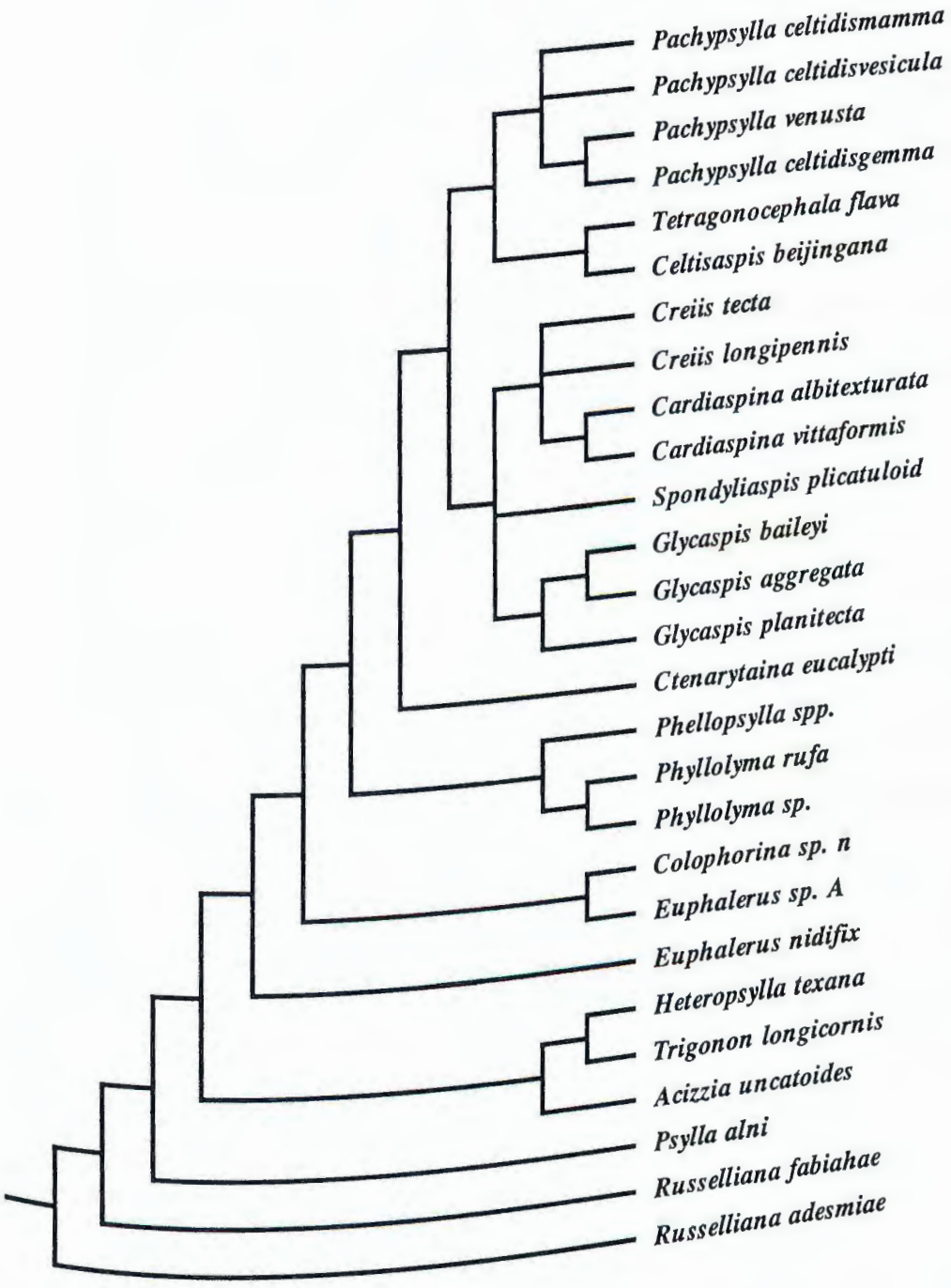

Figure 4-5. Strict consensus of 10 most parsimonious trees for Spondyliaspidinae after successive weighting with some characters (#3-7) ordered and others unordered.

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