

DIVERSITY IN THE NEW WORLD MEMBRACIDAE

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INTRODUCTION

Perhaps the greatest puzzle for entomologists is understanding the relationship between perceived patterns of an insect group's diversity and the ecological/evolutionary processes that generate them. In poorly studied families such as the Membracidae (Homoptera), the relatively small size of the taxon should facilitate synthesis of information, but this process is offset by major gaps in basic life-history information. In this review, I attempt to identify morphological, geographical, behavioral, ecological, taxonomic, and life-history patterns that characterize the extant New World membracid (treehopper) fauna. Recognition of these patterns may provide insight into the processes that promoted phylogenetic divergences in the family and will enhance our understanding of the forces contributing to insect biodiversity in general. Inferred cause and effect in the multivariate interactions, outlined below, can only be taken as proposed hypotheses. These, of course, will require rigorous testing in the future.

The Metcalf & Wade catalog (77, 78) details the membracid literature up to 1956 (29), while two other excellent bibliographies (28, 29) cover the more recent literature. Because space here is limited, only recent and selected references from these bibliographies are cited; nevertheless, I owe a great debt to workers not cited in this review.

PRONOTUM

The most characteristic morphological structure of the Membracidae is the exaggerated pronotum (27, 50, 112). This structure, which is expanded dorsally, takes on a bewildering array of forms (Figure 1). Pronotal shapes

span the range from simple streamlined structures covering the thorax and abdomen to elaborate and intricate dorsally expanded structures. The visual impact of brilliant, highly contrasted pronotal coloration causes both field and laboratory biologists to question why the Membracidae would have evolved such structures (88).

The function of the pronotum is still somewhat of a mystery. Some authors

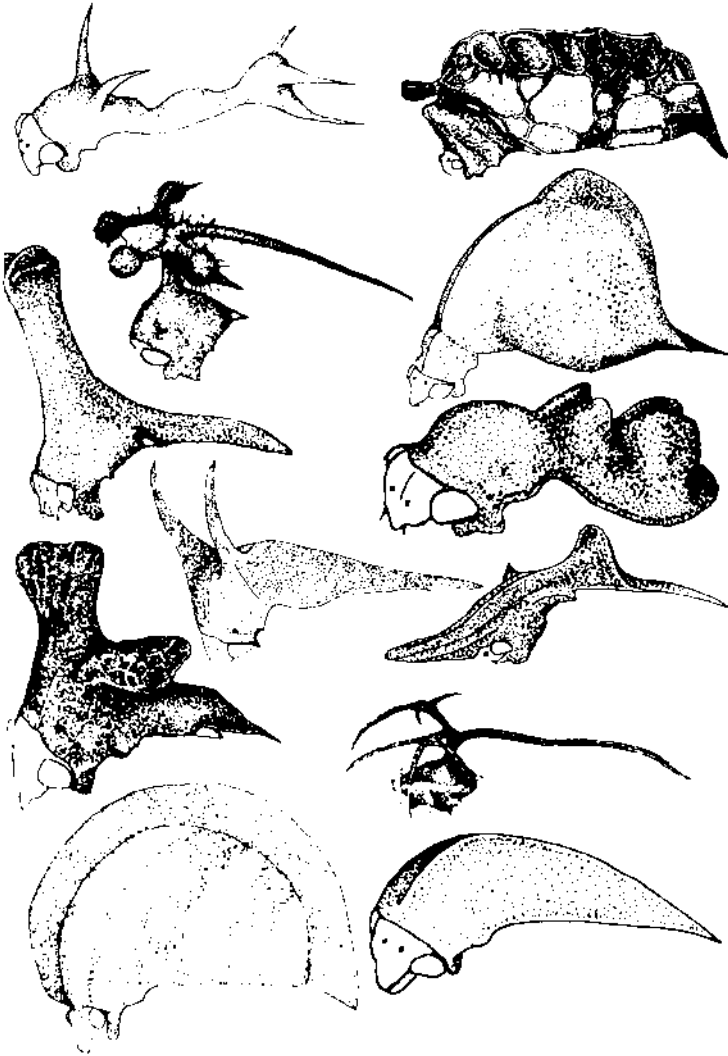


Figure 1 Line drawings of membracid pronota, supplied by Dr. Lewis Deitz at North Carolina State University, Raleigh, N.C.

(18, 69, 88, 101, 102) have speculated about a crypsis function; although this idea is appealing, it lacks experimental evidence. Determining whether apparent cryptic pronotal shape and color reduce visually oriented predation on membracids will require an experimental approach similar to those developed for other organisms such as moths (38, 39). There is evidence, however, for a defensive function of the pronotum in several treehopper species. The pronotum in *Anchistrotus* sp. detaches when individuals are disturbed (9, 70, 112), presumably permitting them to escape from predators. Because of the combination of bad taste and the sharp physical attributes of their pronotum, *Umbonia crassicornis* and *Platycotis vittata* are unacceptable prey to *Anolis* lizards (125, 129). However, these lizards consume many other treehopper species (125).

The purported lack of any physiological function led to the early belief that the pronotum was a product of orthogenesis and was the insect equivalent to the antlers of the Irish elk (47, 50, 102). However, articulating setae over deep conical pronotal pits (147), along with the presence of tracheae, nerves, and neurosecretory tissue (124), suggest a variety of potential physiological functions. One untested hypothesis is that the pronotum serves a sensory function, and the exaggerated dorsal expansions are the result of selection to increase the sensory surface area (147). Another untested hypothesis is that the pronotum may be a dispersal site of sex pheromones. As with many Hemiptera with defensive glands, with Membracidae, increased surface area could facilitate dispersal of volatiles. Although treehopper sex pheromones have not been demonstrated, the hypothesis is attractive because it could help to explain why females have larger pronotal surfaces than males; females prior to mating move to sunny exposed surfaces of twigs or leaves, perhaps facilitating dispersion of pheromones; and males during pre-mating courtship spend considerable time on the lateral surface of the female pronotum (68, 123, 127, 142, 145).

Although the shape of the pronotum is the most striking feature of most membracid species, the structure has been the source of taxonomic confusion (151). Early attempts to use pronotal shape to define higher levels of classification have failed, in part, because shape could not be precisely quantified or measured. Currently, successful membracid classification (27) avoids pronotal shape. At the species level, however, pronotal shape and color are often the most diagnostic features.

The lack of appreciation of extensive pronotal polymorphism in some groups of membracids has led to several taxonomic problems. Most workers have recognized that sexual size dimorphism occurs but failed to recognize that in some genera, such as *Umbonia*, sexual differences in pronotal shape (74, 123) are of the magnitude used to classify new species. *Platycotis vittata* provides a classic example of taxonomic misinterpretation (22) of pronotal

shape and color. This species was described as four species based on permutations of two pronotal features (two color patterns and the presence/absence of a frontal horn). What these character permutations represent are a combination of sexual, seasonal, geographic, and maturational forms. The color dimorphism is a function of age; young adults have one color pattern for three to four weeks but eventually change to the other pattern (127).

The presence or absence of the frontal horn is more complicated in *P. vittata*. Overwintered females raise a brood in the spring, and their offspring rear one in the fall. In most northern areas of this treehopper's distribution, female offspring raised in the spring have a frontal horn while males do not. The offspring of the horned females, raised in the fall, are hornless regardless of sex (127). This pattern is not consistent throughout the geographic range of *P. vittata*. In parts of Florida, both males and females have the frontal horn, and there seems to be no seasonal effect on the character (75). I have observed similar polymorphism in *Platycotis tuberculata*, which indicates the pattern may be a generic trait. The genetic mechanisms and the selective pressures promoting this kind of polymorphism are unknown.

Other observations (18, 69) suggest that pronotal morphs in other genera may have been described as separate species. In contrast to species being incorrectly split into more than one are the numerous species names that have been incorrectly synonymized (29a) because pronotal variants could not be distinguished by discrete characters. In general, the lack of tools for quantifying pronotal shape has left us with inadequate verbal descriptions for identification (151) and over- or underestimates of species diversity.

Pronotal shape and patterns of sexual dimorphism and polymorphism appear to be consistent generic and species characteristics that could be of considerable phylogenetic use and may aid in the understanding of geographic patterns of intraspecific variation. The problem is how to reliably quantify pronotal shape for use in identification and phylogenetic inference. One morphometric approach (32) is to make linear size measurements and use them in discriminant function analyses to identify females in sibling species complexes. Although there is a shape component, this approach works well when the species being considered differ both in size and pronotal shape. Recently, workers (30, 31, 73) defined several pronotal features that broadly reflect pronotal shape and coded these as multistate characters. Although this approach has appeal for traditional cladistic analyses, quantitative definitions of shape may lend greater precision to comparative studies of pronotal form.

An alternative attempt to define pronotal shape (151) involves tracing the lateral outline of the pronotum with a digitizer to generate x,y coordinates, which are then normalized and standardized. From these data, angles and two-dimensional distances between analogous reference points can be calculated as well as two-dimensional estimates of actual pronotal area and

perimeter. A large number of variables reflecting pronotal shape and size can be generated in minutes for individual specimens. As with traditional morphometric analyses (32), discriminate functions derived from these variables have good predictive value for identification. This method (151) has been used to discriminate among 16 groups in the Smiliini, for which pronotal shape and size were traditionally used to define genera. One drawback of the approach is that these variables are difficult to use directly for phylogenetic inference when using cladistic methods. However, correlations among variables can be statistically removed and reduced to distance measures to infer relationships. This process reveals the progression of pronotal shapes representing a pronotal morphocline. Determining if this type of morphocline is a reasonable initial approximation of phylogeny will require a paired comparison of this technique to traditional cladistic analysis.

PATTERNS

New World Taxonomic Diversity

Among the more important pieces of work following the Metcalf & Wade catalog (77, 78) was the higher classification of the New World Membracidae by Deitz (27). Up to that time, the higher classification was in a state of flux consisting of anywhere from 2 to 10 subfamilies-(27, 50, 112). By careful selection of discrete characters and by avoiding pronotal shape, Deitz organized 189 genera into 7 subfamilies and 27 tribes. Throughout this review, I use the Deitz (27) subfamily and tribal arrangements.

Cladistic analysis of the New World treehoppers (C. H. Dietrich, S. H. McKamey & L. L. Deitz, personal communication; Dietrich & Deitz, personal communication) suggests that the subfamilies Stegaspidinae, Centrotinae, and Nessorhininae were the earliest derived membracid lineages, and that the Membracinae, Heteronotinae, Darninae, and Smiliinae were derived more recently. Although the relationships among the subfamilies are not fixed, the subfamilies Smiliinae and Membracinae appear to be genetically more derived.

Analysis of subfamily taxonomic diversity shows some interesting patterns. Of the approximately 1600 New World species (77, 78; references in 28, 29), 6% are in the Stegaspidinae, 4% in the Centrotinae, 3% in the Nessorhininae, 28% in the Membracinae, 6% in the Heteronotinae, 8% in the Darninae, and 44% in the Smiliinae. The relatively low number in the Centrotinae is surprising because in Africa over 260 species belong to this and a closely related subfamily (17). Thus, the four more-derived subfamilies (Membracinae, Heteronotinae, Darninae, Smiliinae) account for approximately 86% of the present New World taxonomic diversity. Within each of the derived subfamilies, some tribes and genera have apparently undergone rather extensive radiation while others have not.

Geographic Regionalism

It has long been recognized that the world's membracid fauna is highly regionalized (50, 78, 112). The primitive subfamily Centrotinae and its relatives are distributed in most of the earth's biogeographic regions (78, 112). Geographic richness of the Centrotinae, in descending order, are those of the Afrotropical (17), Oriental (India), Malaysian, Nearctic, Neotropical, and Australian regions (78). Europe, Siberia, and North China are very poorly represented, while no species are known from Scandinavia or Iceland (50), and none are native to New Zealand (28).

The Nearctic, Caribbean, and Neotropical treehopper fauna is endemic to the New World region. With the exception of the buffalo treehopper introduced into Europe (61) and five species of Old World *Orthobelus* (27, 78) (which may be misplaced), no other species or genera exist in both the Old and New Worlds. The only subfamily with a worldwide distribution is the primitive subfamily Centrotinae (27, 50, 112).

New World Geographic Patterns of Diversity

Although a detailed analysis is not possible here, there is evidence of New World geographic regionalism at the subfamily, tribal, and generic levels. Colombia, Ecuador, Peru, and the Guianas have the richest faunas in terms of subfamilies, tribes, genera, and species (148). In comparison, all of North America (north of Mexico) with approximately 307 species has 40 to 60 fewer species than does Colombia and is comparatively depauperate in terms of subfamilies, tribes, and genera (148).

Latitudinal analysis (148) indicates that with increasing latitude from the equator, species richness declines until central Mexico is reached and then increases, particularly in eastern North America. Part of the explanation for this pattern is that the number of tribes and genera declines as latitude increases, but north of Central Mexico one tribe that has undergone extensive generic and species radiation dominates. With some exceptions, the treehopper fauna north of central Mexico is largely endemic to that region. In contrast, the Andean treehopper fauna (20, 93–100) appears to be more similar to that of Brazil, Central America, and southern South America (78; references cited in 28, 29).

The best example of regional treehopper endemism is that of the West Indies. In 1985, only 26 genera with 64 species were reported from that region; of these, 76% of the species and 54% of the genera are endemic (90). Subsequent description of new species (91) and the inclusion of the genus *Stegaspis* (78) brings the level of endemism to 90%. Endemism may be higher, because three species may have been introduced. About 83% of the endemic

species are in the primitive subfamilies Centrotinae and Nessorhininae. At the subfamily and tribal levels, Mexico and North America have more in common with the West Indies than does northern South America (90). The complete absence of Darninae and Heteronotinae (90), the low frequency of Membracinae and Smilliinae (78), and the high level of endemism of primitive subfamilies implies that the West Indian treehopper fauna has been isolated for a considerable period of time.

Although the geologic details are open to debate (33), when South America and Africa separated, the Proto-Antilles began to shift during the late Mesozoic to become the Greater Antilles of the West Indies (33, 103). Although fossil Cicadelloidea are known from the Paleozoic and Mesozoic eras, no pre-Tertiary membracid fossils have been confirmed, suggesting subfamily differentiation occurred during Tertiary isolation (41) beginning about 65 mya. The almost exclusive distribution of the Nessorhininae, the high level of Centrotinae endemism, and the presence of the Stegaspidae in the West Indies suggests these groups may be pre-Tertiary in origin and became isolated during the Tertiary as the Proto-Antilles shifted. Unfortunately, the Centrotinae has not been analyzed, so neither the number of tribes nor the relationships of the New World tribes within the subfamily are known. If the New World Centrotinae are relatively derived, this would support the contention that their differentiation and the remaining New World subfamilies occurred with the separation of South America and Africa. That Eurasia and North America share only the subfamily Centrotinae (but no tribes) supports the contention that this vicariant event initiated New World subfamily radiation. Although during the last 5 my south-to-north dispersal certainly has occurred, as indicated by faunal similarities of Central and South America, Tertiary isolation may have been a major factor contributing to present-day geographic regionalization of membracid subfamilies, tribes, and genera.

LIFE HISTORY SYNDROMES

Although isolation and limited recent dispersal may account for restricted extant generic distributions, other factors may also contribute to regionalization and radiation. The variety of membracid life-history styles and biologies are equal to or greater than that in any other group of Homoptera (131, 135). Some species are solitary both as nymphs and adults, while others have highly developed subsocial behavior. Various life histories and behaviors form a continuum between these extremes. Superimposed on the continuum are mutualistic interactions with ants, bees, and wasps that appear to modify life histories, behaviors, and perhaps morphology, as well as to restrict geographic distributions (86).

Maternal Care

Within the Membracidae proper and more primitive related families are three major types of sociality (131). Maternal care in its simplest form (paternal care has never been reported in the family) consists of females sitting on eggs until they hatch (54–56, 123, 127, 128, 130, 135, 139). In some cases, the presence of females on eggs is essential to reduce the effects of predation (34, 35, 126), but this practice appears to be less effective in reducing parasitism (35). In tribes such as the Hoplophorionini, maternal care is extended beyond egg guarding to aggressive protection of offspring and to behaviors that alter the host plant to facilitate nymphal feeding (6, 34, 73, 123, 126, 127). In other genera, such as the *Calloconophora*, females do not modify the host to facilitate feeding but do actively maintain offspring aggregations. Mothers and offspring move together within the plant to feed on meristematic tissue (130). In those species with extended maternal care, the presence of the female is essential to the survival of offspring (35, 71, 126, 127, 135).

Within the superfamily Membracoidea, egg guarding occurs in the primitive Aetalionidae (14, 42, 54, 67, 135) and Biturritiidae (40). Although not very common, it occurs in the Old World membracid subfamilies Centrotinae (55) and Oxyrhachinae (108). By far, maternal egg guarding is more frequent in the New World Membracidae in which it is known in four of the seven subfamilies (104, 131, 135). Determining whether or not the absence of egg guarding in the Stegaspidinae, Nessorhininae, and Darninae is a sampling artifact requires further field work. Within the two more-derived subfamilies, egg guarding occurs in four of the six tribes of Membracinae and in four of the nine tribes of Smiliinae (135). Recent reviews (36, 115, 133) discuss the factors that may have promoted sub- and presocial behavior in insects.

Maternal care is often complicated by mutualistic interactions with ants and other Hymenoptera (10, 19, 63, 67, 105, 135). In the Hoplophorionini, in which six of the seven genera are known to practice extended maternal care, no species is known to have interactions with mutualists (135). In contrast, of the three genera of Aconophorini with egg guarding, no *Calloconophora* and *Aconophora* have ever been reported to interact with ants, while in the remaining genera, many species are ant attended (31, 135). Within the Polyglyptini, 10 of the 24 genera have some type of maternal care, and 5 of these interact with ant mutualists (135).

Although the cause and effect of ant interactions cannot be distinguished at present, interactions with ants appear to dramatically affect the nature of maternal care. At present, only two North Temperate species have been examined in detail. In the univoltine *Publilia reticulata*, overwintering females deposit eggs in masses. Once nymphs are ant attended, females desert

offspring to deposit a new clutch on nearby plants (10). In contrast, the bivoltine *Emylia bactriana* appears to have a different strategy (87, 128). In the spring, females move into patches of herbaceous plants from their overwintering sites and begin to deposit eggs into masses. If not attended by ants, females may deposit only a few eggs in a mass and then desert (87). Once females find or are located by ants, however, they deposit many eggs into a mass over several days and desert relatively rarely. By the time the eggs hatch, most females have died, presumably because of old age, but ants maintain and protect the aggregations of nymphs.

In contrast, the pattern of oviposition by second-brood *E. bactriana* females is quite different. Unlike their mothers, these females are attended by ants as soon as they begin to deposit eggs and most remain near their offspring for their entire lifespan (87, 128). The dichotomy between generations in oviposition behavior appears to be related to the predictability of ant mutualists (see below). When oviposition begins in the early spring, the dispersion of ants within a host patch is relatively unpredictable. However, by the time oviposition begins in the second generation, ants have been in the patch for several months and females either locate or become located by ants rapidly. The survival of second brood offspring is higher when both parent female and ants are present than when only one of them is present (128).

Aggregation and Mutualism

In most species with some sort of maternal care, nymphal and adult aggregations most often comprise siblings. Sometimes aggregations, which consist of offspring from two to three females, may occur on a single branch or leaf because of philopatry (35), especially in subsocial species (35, 135, 140). However, many genera, belonging to a variety of subfamilies and tribes, that lack maternal care form nymphal aggregations consisting of offspring from several females. These aggregations are the result of female oviposition behaviors and attractants that cluster eggs (131). In the *Enchenopa binotata* complex, hundreds of egg masses from many females are deposited on single branches over a three-month period (134). Because females die in late fall, there is no possibility of maternal care of eggs throughout the winter nor of offspring during the following spring. Although the details differ somewhat, similar kinds of aggregations are characteristic of *Vanduzee* spp. (49), *Thelia bimaculata* (48), and *Notocera*, *Campylenchia*, and *Tylopelta* spp. (135), to name a few. In fact, in those tribes lacking maternal care, some (but not all) genera form these kinds of nymphal aggregations. One characteristic of these aggregating species is that nymphal aggregations are seldom found without mutualists, which most frequently are ants.

Perhaps the most bizarre twist to ant mutualism is the occurrence of mixed-species, ant-attended nymphal aggregations. The species compositions

do not appear to follow any obligatory pattern, but they usually involve species with some type of maternal care or simple aggregating behavior. However, sometimes nymphs from species that are solitary as nymphs or adults are found in aggregations of other treehoppers (37, 99, 116, 135). Most often these mixed-species aggregations are relatively small (under 40 nymphs) and are found in lowland wet tropical habitats, but mixed species aggregations do occur in temperate regions. In southern Ohio, single giant ragweed leaves frequently have several females of *Entylia* and *Publilia* spp. on egg masses along with hundreds of first-instar nymphs. Within a week or two, extensive nymphal feeding turns leaves yellow, and nymphs, parent females, and ants disperse to other leaves on the plant. Within upper treehopper-density limits, most individual host plants and host patches do not appear to represent a nutrient limitation. What does seem to be a limiting factor in temperate climates is the persistent attendance of enough ant mutualists to protect nymphs (discussed below).

Ant-plant mutualisms are relatively common (7, 15), and numerous studies clearly demonstrate that ant mutualism results in increased survival of membracid nymphs (25, 44, 76, 128, 134). Thus, any female behavior that increases the probability that offspring will be ant attended will increase her fitness. Researchers have empirically (110) and theoretically (24) explored the effects of aggregation size (25, 134), number of attendant ants, and distance from the ant colony (72, 118); the effectiveness of various ant species in providing nymphal protection; fitness effects on the host plant (16, 45, 84); treehoppers as pseudo-extrafloral nectaries (8, 62); and the role plant quality may play in attracting ant mutualists (24). Recent evidence suggests that after females establish aggregations of eggs (in the absence of a priori information on ant spatial dispersion), the resulting nymphal aggregations may be involved in conditional intraspecific competition for ant mutualists (26). In general, larger aggregations are more competitive than smaller ones, but this observation is somewhat situation-dependent and is not consistent over years (26). This kind of intraspecific competition depends on relatively high treehopper densities within restricted host patches and is most often encountered in temperate ant-attended treehoppers that feed on herbaceous patchy plants (11, 12, 25, 76, 87, 128). Cushman & Whitham (26) suggest consistent competition of this sort should favor females that (a) deposit large clutches of eggs, (b) distribute eggs to minimize the number of neighboring plants with nymphs, and (c) maximize the potential of ant attendance through selection of nutritionally high-quality plants, which results in more attractive honeydew, or by selecting host plants closer to ant colonies.

To extend the Cushman & Whitham (26) argument to habitats and years when ant mutualists are not limited, the positive effect of nymphal aggregation size in attracting ants could explain why mixed-treehopper species aggrega-

tions occur. If two treehopper species are not abundant within a plant or patch, as is often characteristic of lowland wet tropical habitats (135), the combined fecundity of females may create nymphal aggregation sizes sufficient to maintain ant attendance with a fitness benefit to both. However, some mixed- and single-species aggregations could be the result of the transport of females or nymphs by ants (99). Ample evidence indicates that tropical and temperate conspecific ovipositing females do lay large or multiple egg masses together on the same plant or branch (1, 134, 135) before they or their offspring are located by mutualists. The persistent yearly colonization of one tree and not others supports the argument that females either do not leave (132) or that they locate trees in close proximity to ant colonies (134). Whether treehoppers manipulate ants or the converse may depend on the treehopper and ant species involved and where the interaction is occurring.

Solitary Life Histories

Solitary life-history patterns are perhaps the most difficult to define (131). In many genera, nymphs are found as single individuals in leaf axils, buds, or flowers. Sometimes small clusters of 5 to 10 nymphs occur that are probably the result of oviposition by a single female (37). Under certain circumstances, species I would define as solitary (131) appear to be aggregated on isolated trees or on suckers from harvested trees (119). Solitary nymphs are sometimes attended by ants (37, 135). Although there are no studies on the nature of these interactions, my experience suggests that the mutualistic interaction is somewhat fortuitous. Often, when these nymphs are ant attended, careful examination of the nearby branches or leaves will turn up ant-attended scales, aphids, or galls. This type of life history is characteristic of all but two genera of Smiliini (151), a tribe constituting 46% of the treehopper fauna north of central Mexico (148).

Solitary nymphs appear to be characteristic of all the tribes in the Darninae; most tribes in the Nessorhininae, Centrotinae, Stegaspidae, Heteronotinae; and four tribes in the Smiliinae. In most of these groups, asociality is an implied life history trait based on the fact that neither nymphs nor adults have been collected in aggregations.

Geographic Patterns of Sociality

Geographically, groups with egg guarding and extended maternal care are not uniformly distributed over the New World. In America north of Mexico, with the exclusion of two introduced species (74, 123, 151), only six genera (10, 31, 55, 75, 127, 128) in three subfamilies have some type of maternal care. Only three of these are essentially pan U.S. while three are restricted to the American Southwest (78). In contrast, southern Mexico, Central America,

and northern South America are rich in subfamilies, tribes, and genera with maternal care (86, 131, 135).

In some cases, maternal care appears to be a tribal characteristic (31, 73, 131, 135), while in other tribes it may be restricted to specific genera or species (55, 104, 135). About 61% of the species in a lowland wet Central American habitat exhibit some kind of sociality, and overall, 64% of the species collected interact with ants (135). Estimates across altitudes in Colombia indicate that approximately 61% of the species are either subsocial or interact with ants (86). In contrast, only about 4% of the North American fauna are subsocial or interact with ants (135). In Colombia, the proportion of treehopper species estimated to be associated with ants decreases with increasing altitude (86), probably because of the limited availability of ants at higher altitudes (57–59). In contrast, the proportion of subsocial species that do not interact with ants increases as altitude increases, but the proportion of presumed solitary species (39% of the total fauna) remains constant over the elevational gradient (86). In North America, approximately 96% of the treehopper fauna can be classified as solitary (135).

Mating Biology

In some subsocial treehoppers, adult-sibling aggregations play a role in mating. Mating in some species occurs among siblings (35, 71) while in others, older males from other aggregations are attracted to aggregations containing virgin females (140). *Umbonia crassicornis* females mate only once for several hours, and within a day or two deposit their entire complement of eggs (123). In contrast, *Platycotis vittata* females can mate up to five times under caged conditions (145). Unlike *U. crassicornis* females, *P. vittata* females when mated are devoid of eggs and store sperm for over a month before oviposition (145). This summer reproductive diapause is related to the physiological condition of their host plant and can be terminated by altering host plant quality (58a). Under normal field conditions, females cannot delay mating until the host plant is acceptable for oviposition because most males die before that time. Multiple mating in this species can be viewed as a mechanism to maintain a fresh supply of sperm during the period of reproductive arrest. It also could be a mechanism to promote mating with males with demonstrated longevity. In this subsocial species, where female longevity is critical to successful offspring rearing, sperm precedence may ensure that the last and oldest male to mate will be the parent. As might be predicted if this were the case, males apparently attempt to assure paternity through extremely long mating times ranging from 8 h to several days depending on the season (127, 145). Multiple mating also occurs in *Polyglypta dispar* (35). In comparison, females in the *Enchenopa binotata* complex mate

only once for about an hour and a half. Depending on the species, oviposition begins a week or two after mating but continues for several months (142).

Oviposition Habits

As with many insects (46), treehoppers vary considerably in terms of how oviposition is distributed within a female's lifespan. Many egg-guarding species are semelparous; females deposit their entire reproductive complement in one clutch within a 24 hour period (123, 127). Other egg-guarding species deposit their entire reproductive potential over a period of time into a single or several egg masses and are moderately iteroparous (35, 87). All of the Hoplophorionini and Aconophorini (23, 71, 123, 127, 135) appear to deposit their entire clutch within a day, while at least some Polyglyptini (10, 35, 128) apparently spread oviposition over several days, depositing eggs into either a single or several masses.

Moderate iteroparity in one egg-guarding species has led to mutualism between females (35). This case represents an intermediate step to extreme iteroparity and aggregations of ovipositing females in the *Enchenopa binotata* species complex. In this species complex, oviposition within a host plant over a two- to three-month period is not random but rather is restricted to relatively few branches within the host (even though alternative oviposition sites are available). Within-host-plant aggregations of egg masses are the result of ovipositional attractants. As discussed earlier, egg-mass aggregations ensure that the resulting nymphal aggregations are large enough to attract ants quickly and persistently (134). Obviously, high treehopper density affects plant health, but beneath these limits, nymphal survival and hence female fitness is a positive function of aggregation size (25, 26, 134). However, there may be some costs of aggregating eggs in terms of egg parasitism (35, 137). Many species that aggregate eggs or are subsocial have egg parasitoids (1, 35, 73, 106, 137) who may inflict high egg mortality (1, 23, 35, 73).

Most Membracidae insert their eggs into plant tissue; however, species of Aconophorini, some genera of Membracini, and some primitive membracoid families are exceptions (42, 54). Within the subfamily Membracinae, all the Aconophorini (31, 135) deposit their eggs in masses on plant surfaces. The masses are held together by copious accessory secretions. In contrast, all of the Hoplophorionini (73, 135) insert their eggs deep into plant tissue and cover them with modest amounts of accessory secretions that seem to break down within a couple of days. In the Membracini, both of these types of oviposition, plus a third, occur. In one genus (without maternal care), eggs encased in accessory secretions are deposited on plant surfaces, a behavior similar to that of the Aconophorini, while two other genera (with maternal care) exhibit oviposition behaviors and egg coverings similar to those of the Hoplophorionini (135). The genus *Membracis* also contains species that

deposit their eggs in masses on the surface of plants (80, 81) and others that insert them into plant tissue (135). Throughout the genus, egg masses are covered with waxy secretions and there is no maternal care. In other Mebracini genera lacking maternal care (134, 135, 150), eggs are merely inserted into the plant tissue and covered with large amounts of accessory secretions.

Voltinism and Seasonality

Voltinism and the degree to which intraspecific life histories are synchronized differs with treehopper genera, level of sociality, and geographic distribution. Tropical and semitropical species with extended maternal care are multivoltine with no seasonal synchronization of life-history timing. Females on eggs and nymphs, adult aggregations, and solitary pre mating adults are usually found at the same time on or near the same tree (71, 123, 131, 135).

Temperate North American bivoltine species with and without extended maternal egg guarding are fairly seasonally synchronized within a habitat. However, there is often within-habitat variation in age of nymphs within a generation that may be a host-plant effect on development time or the result of differences in sexual maturation of their overwintering mothers in the spring (58a, 87, 127, 128). Over the geographic range, life-history timing is asynchronous as a function of elevation, latitude, and longitude (58a). North American multivoltine, ant-attended, aggregating species with no maternal egg guarding hatch relatively synchronously on their only host in the early spring. This early synchronization is only loosely maintained during the four summer generations (49). Many temperate solitary, univoltine species that apparently insert their eggs in buds or adjacent plant tissue and are restricted to *Quercus*, have synchronized spring egg hatch, and very short life histories (151).

These North American examples suggest that voltinism is a generic trait that is not strictly determined by (although it is limited by) climate. In lowland wet tropical habitats, collecting records (116, 135) suggest that aggregating and subsocial genera are multivoltine. In tropical, seasonally dry habitats, subsocial/aggregating genera such as *Umbonia*, which utilize semievergreen or evergreen hosts, are multivoltine (135). Although the data for presumed solitary species are weak, they indicate multiple generations in lowland wet habitats but seasonally restricted voltinism in dry habitats (121, 122, 135). The effect of increasing elevation in tropical regions on treehopper voltinism is not particularly clear. Subsocial genera appear to maintain multivoltine life histories around 1500 m (71, 135). At higher elevations, subsocial and ant-attended aggregating species appear to decline in richness (86), and collecting records become more seasonally restricted, suggesting a trend toward univoltinism in some genera (95, 96, 98).

Host-Plant Specialization

Although the Membracidae are commonly called treehoppers, various groups use herbaceous as well as woody plants. Variation in host-plant specialization is rather extensive, ranging from monophagy to polyphagy on 23 host genera in several plant families (1, 3–5, 31). In treehopper genera for which we have reliable host-plant data, complicated patterns of host-plant use potentially reflect treehopper taxonomic affinities, geography, sociality, and voltinism. A host specialist is defined here as a species restricted to a single host species throughout its geographic range. Progressively less specialized are treehopper genera or species that use plants in a single genus [these treehoppers are often local specialists (43)], several related genera, a single family, and two or more plant families.

Monophagy is characteristic of species in the *Enchenopa binotata* complex (132, 136, 138), *Vanduzeeia arquata* (49), and *Thelia bimaculata* (48). The genus *Cyrtolobus* is restricted to *Quercus*, but some species use only the subgenus *Erythobalanus* while others use *Quercus* (= *Leucobalanus*) (151). *Platycotis vittata*, although restricted to *Quercus*, utilizes both subgenera (58a, 75, 127). *Umbonia crassicornis* throughout its geographic range utilizes hosts in at least nine different genera of legumes (74, 135). Extreme levels of host generalization are found in *Bolbonota*, *Guayaquila*, and *Calloconophora* (3–5, 31, 135), for which two or more plant families have been recorded for some species.

The majority (84%) of North Temperate treehoppers are estimated to be monophagous or restricted to a plant genus (135, 148). Although there are exceptions (109), four patterns generally characterize temperate host-plant specialization: (a) solitary genera with highly synchronized univoltine life histories, deciduous hosts, and high taxonomic generic diversity (151); (b) nymphal-aggregating genera with highly synchronized life histories, deciduous hosts, and moderate generic diversity (132, 134, 138, 141–144, 149); (c) subsocial/aggregating genera with bivoltine/multivoltine, relatively unsynchronized life histories and low generic diversity (48, 49, 60, 127); and (d) solitary, univoltine/bivoltine genera with unsynchronized life histories, possible alteration between herbaceous and woody plants, and low to moderate generic diversity (79, 83, 85, 105, 117).

In contrast, when polyphagy is defined as using two or more plant species or genera over the entire geographic range, the majority of subsocial and aggregating Central and South American species appear to be polyphagous (31, 135). In general, the host records for solitary species suggest more limited host ranges (135), but this may be an artifact of inadequate sampling for these groups. Some subsocial genera such as *Metcalfiella* and *Umbonia* appear to be more restricted in host utilization patterns at higher elevations

(71, 73, 135), but this restriction occurs primarily at the host generic or family level.

Surface ovipositors appear to be host-plant generalists (3–5, 31, 135). At least for some, host lists include plants that when wounded exude resins or latex. Host lists for tropical treehoppers that insert their eggs into plant tissue, to my knowledge, do not contain plants that produce resins or latex when wounded. One could hypothesize that surface oviposition permits a greater range of host-plant utilization than does insertion of eggs into plant tissue. Even with short egg incubation times characteristic of tropical treehoppers (1, 80, 81), plant-wounding responses, especially for resin/latex producers, are probably sufficiently rapid to completely encase and kill eggs inserted into the plant before they hatch. Plant responses to ovipositional wounds in general (2), even in temperate climates, may be fast enough that plant callus can cover and kill eggs (111) that are dormant within the plant tissue for several months. Plant responses to wounds in geographic regions where plant growth is not seasonally arrested could be a powerful selective pressure favoring short egg incubation times, surface oviposition, and multivoltinism.

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Morphological Correlates Associated with Maternal Egg Guarding

Although the factors promoting body size and sexual dimorphism have not been explored in the Membracidae, there appears to be some relationship between sociality, voltinism, mutualism, host specialization, and geography.

Large female body size and sharp lateral pronotal horns appear to be associated with some genera with extended maternal care in the Hophophorionini (73, 123, 127, 135). Species in this tribe are semelparous, oviposit eggs into plant tissue, and modify the host to provide feeding access to offspring. Also, mothers actively defend offspring. Females are sufficiently large to cover the egg mass (73, 123, 127), providing passive protection of eggs, and removal from masses requires considerable force because the long prothoracic and metathoracic legs, a tribal characteristic (27), are used to encircle the branch. Females also use their long legs to maintain offspring aggregations (73, 123, 127). The sharp lateral and dorsal horns in combination with the acute posterior process make females unacceptable prey to naive *Anolis*. When their spines are removed, they are acceptable prey (125). Large body size also enhances the ability of females to drive off invertebrate predators (35, 126). Clearly, the fitness benefits of extended maternal care favor large body size and pronotal defense but may increase development time, restricting the number of generations that can be achieved within a year.

This type of limitation may directly influence geographic distribution and the kinds of host plants utilized. In the case of *Umbonia crassicornis*, the hosts utilized are semievergreen and evergreen leguminous trees restricted to frost-free habitats permitting multivoltinism (74, 135).

The combination of climate and plant physiology appears to impose a bivoltine life history (145) on *Platycotis vittata*, a species restricted to *Quercus* and geographic regions with mild winters (58a, 78). In terms of the North American fauna, the overwhelming majority of species overwinter as eggs inserted into plant tissue (135). Thus, winter temperatures may geographically limit subsocial options (115); relatively short growing seasons may favor shorter nymphal development times and a reduction in body size in solitary and subsocial species.

Morphological Correlates Associated with Ant Mutualism

Mutualistic interactions with ants may favor a reduction in female body size and reduction in the dorsal expansion of the pronotum both in aggregating species and those with maternal egg guarding. Females in genera such as *Entylia* and *Publilia* are small, semi-iteroparous, and cannot completely cover their egg masses (except early in oviposition). They are also not generally as aggressive to potential predators (128) as are species that do not interact with ants (35, 126). Female fitness in these groups is directly related to persistent ant mutualistic interactions (128).

The pervasive occurrence of ant mutualism among the Homoptera (118) and the Membracidae suggests ants may have played a major role in the evolution of the group. The midgut filter chamber occurs in almost all Homoptera (41) and probably developed as an adaptation for removing excess water in plant sap to concentrate nutrients (21, 113). In aphids that have a midgut filter chamber, it is inefficient in extracting amino nitrogen (21) and carbohydrate from plant sap, and these compounds are excreted as honeydew. In this sense, the midgut filter chamber may be the ultimate adaptation permitting ant mutualism as a mechanism to reduce predation by ants (64–66). An extensive Tertiary fauna of ants (120) certainly could have favored treehopper adaptations to reduce the risk of predation by ants. One of the evolutionary costs of mutualism may be the diversion of nutrient resources by means of the filter chamber away from body size into a mechanism to reduce ant predation. This may be a partial explanation of why adult females are ant attended in some species and not in others. In some extant species, females are persistently ant attended during oviposition and when on egg masses (128, 135). The semi-iteroparous mode of egg deposition may ultimately be explained by trade offs between egg production and the establishment of mutualism. The formicine ants often associated with treehoppers are relatively aggressive to potential treehopper predators. The

aggressive nature of these ants may have been the selective pressure favoring the relative inactivity of nymphs except when disturbed by potential predators (82) and the comparatively inactive defense of offspring by females (128). When aggregations are disturbed and/or when adult treehoppers make rapid movements, ants may attack the treehoppers, suggesting a fine line between mutualism and predation.

The obvious prediction, if this scenario is true, is that species with this sort of life history should be small both in terms of body size and defensive pronotal characteristics and restricted to habitats, geographic regions, and climates where ant abundance is predictable. Small body size should favor, in turn, relatively short generation times that in hospitable climates lead to multivoltinism. As noted earlier, ant-attended treehopper species are essentially the norm in tropical regions below ~1500 m (86). In tribes where maternal care occurs both with and without ants, females in genera that do not interact with ants appear on the whole to be larger than those that do (31). In fact, cladistic analysis of the Aconophorini (30) suggests that genera that interact with ants are more plesiomorphic and generally smaller.

Relationships of Morphology, Life History Patterns, and Diversity

If the factors discussed in this review have played an evolutionary role in promoting diversity, there should be some congruence with morphological patterns. Only one North Temperate tribe (Smilliini) has been examined in this context, permitting an initial test of this prediction. The 22 genera in the tribe exhibit the following life history characteristics (151): One genus, *Antianthe*, is subsocial, multivoltine, tropical, restricted to the Solanaceae, and contains six species. Another genus, *Thelia*, is bivoltine and temperate, and nymphal aggregations are ant attended. The adults are solitary, and at least one of the two species is monophagous. The remainder of the genera are univoltine, temperate, and solitary; exhibit various levels of host specialization at the generic level; and vary in species diversity. Pronotal shape analysis (without actual size) indicates that (a) genera ($N = 5$) with highly rounded elevated pronota form a separate group. At the base of this group was the subsocial genus *Antianthe* with pronotal lateral horns. Diversity is low in these genera (one to six species per genus). Regression analysis showed that this group is an isometric series that differs from the remaining genera. (b) The first to diverge in the other lineage group was the bivoltine, nymphal-aggregating genus *Thelia* with extreme monophagy, large body and pronotal size (adult females are not ant attended), and low diversity. (c) Subsequent divergence of univoltine, solitary genera followed a progressive reduction in female body and pronotal size, a decrease in host-plant families and genera utilized, and increased diversity. Although the shape analysis was not

cladistic, the basal groups are those predicted. The most derived genus was *Cyrtolobus*, which has extremely short, synchronized, univoltine life histories. Its host specialization is restricted to *Quercus* subgenera, and it is the most diverse ($N = 44$ species) of the tribe. The selective factors encouraging the comparatively small body size associated with this treehopper genus could have resulted from a seasonally nutritionally limited host (*Quercus*) that favored short univoltine life histories (151).

Speciation Mechanisms

One clue that may help to explain cladogenesis at the generic level comes from the North American *Enchenopa binotata* species complex (51–53, 89, 132, 136–138, 141, 142). Experimental work has demonstrated that this complex consists of nine sympatric species that are reproductively isolated by asynchronous mating periods induced by differences in host-plant phenology. Each of these species is univoltine, is monophagous, and has critical life-history stages that are synchronous on a given host species. Synchronization of life histories is a direct result of inserting dormant eggs into the vascular tissue of the host plant. Egg dormancy is broken in the spring when eggs absorb water from the sap of their deciduous hosts. The consequence of a shift to a novel host, which differs in branch water content in the spring is an alteration of egg maturation schedules that ultimately result in asynchronous mating periods (146, 149). The evidence to date suggests that alterations in plant-induced life-history timing in conjunction with fitness costs imposed by novel host plants has led to host-plant specialization and speciation.

This mechanism of divergence requires restrictive life-history characteristics and climatic conditions. In addition to intrinsic genetic variation to permit host shifts, essential requisites are univoltinism, insertion of eggs into plant vascular tissue of deciduous hosts, highly synchronized life histories, females that mate once, and low vagility. Only areas that have climates with dramatic seasonality (such as temperate North America), high elevations, or seasonally dry tropical regions may be conducive to the development of univoltine life histories for this sort of sympatric host-race formation.

In North America, aside from *Enchenopa*, only 12 genera appear to have the requisites for this mode of speciation. In eastern North America, many species in these genera are sympatric (78), are host-plant specialists, and are species rich (151). North American genera that do not meet these life-history requisites (e.g. *Vanduzee*, *Platycotis*, *Thelia*, *Entylia*) have low taxonomic diversity. In these genera, within-habitat life-history asynchrony apparently imposed by the phylogenetic constraints of bivoltinism or multivoltinism, sociality, body size, and host-plant factors appears to have impeded shifts to novel host plants that would promote sympatric divergence. Although some

species in these genera are host-plant specialists, divergence in North America appears to be related to geographic isolation.

At present, species diversity in large tropical genera [e.g. *Membracis* (78), *Amastris* (13), *Sphongophorus* (78), *Guayaguila* (31)] is difficult to explain. Many species in these genera appear to be geographically and altitudinally restricted, indicating some variation of an allopatric model. According to our current understanding of their distributions and biologies, they do not conform to a host-specialization model of speciation.

Summary of Trends and Hypotheses

Life histories and behaviors evolve in response to selective pressures that increase individual fitness. Changes that permit exploitation of new resources or geographic regions may result in subsequent radiation. On the other hand, changes that enhance fitness on specific resources or under specific climatic conditions may restrict geographic distributions, consequently impeding radiation and speciation. Within the Membracidae, both mechanisms appear to be determinants of present geographic patterns of generic and species richness.

The single cosmopolitan subfamily Centrotinae, in terms of genera and species, is most abundant in tropical or semitropical habitats and have apparently not undergone extensive dispersal or radiation in temperate regions or high-elevation habitats in either the Old or New World (78). This observation suggests that the New World Membracidae originated in part of tropical Gondwanaland and became isolated as Africa and South America separated. Within the New World, groups with distributions in the Proto-Antilles and adjacent areas became isolated with the formation of the West Indies. The remarkable radiation that has occurred since the isolation of the ancestral treehopper faunas, divergence deemed sufficient for subfamily differentiation (27), suggests that membracids speciate rapidly. Old World subfamily comparisons indicate that a tropical or semitropical habitat is ancestral and temperate or high elevation habitats are more derived.

Tropical Old World Centrotinae and Oxyrhachinae have the following biological characteristics (1):

1. Most species form nymphal or adult aggregations.
2. The majority of species are ant attended, either as aggregations or as solitary nymphs.
3. Mixed-species aggregations are ant attended.
4. The majority of species appear to be polyphagous, while some are strictly monophagous.
5. The majority of host plants are semievergreen or evergreen.
6. Multivoltinism appears to be the rule, with little seasonal effects and short egg incubation times (less than 15 days).

7. The majority of species insert their eggs into plant tissue, but one species only partially embeds eggs into the plant.
8. All but one species do not cover eggs with accessory secretions.
9. Some species aggregate eggs within masses and on single branches; others oviposit single or small clusters of eggs throughout their host plant.
10. Species that aggregate egg masses have a fairly extensive egg parasitoid fauna, resulting in high levels of mortality.
11. Maternal care within the two subfamilies is very limited (55, 188).

The above characteristics, except in the few species with maternal care, would be a reasonable summary of the more derived New World tropical Membracidae discussed here.

The similarity in biology of the primitive Old World and the more derived New World Membracidae could be the result of ecological convergence or reflect shared traits that represent generalized ancestral patterns that were molded by selective pressures to achieve the high level of geographic, morphological, and biological diversity of the New World Membracidae. Regardless of how one interprets the biological similarities between Old and New World tropical Membracidae, the effect of New World temperate climates has resulted in major shifts from the shared pattern.

I have suggested (133, 135) the following to explain New World biological diversity. The high incidence of polyphagy, use of semievergreen or evergreen hosts, sociality, ant mutualism, multivoltinism, and the lack of dramatic seasonality appear to promote asynchronous life histories in lowland wet tropical habitats. Under these conditions, it is difficult to imagine speciation occurring except through some kind of geographic isolation. Such isolation is suggested by surveys, in which overall generic richness is high while intrageneric diversity is relatively low within a habitat. Examination of locality records of many genera of tropical treehoppers suggests a general pattern of geographic disjunction (78).

In contrast, temperate North American treehoppers in general share the opposite characteristics. Univoltinism and inserting dormant eggs into the tissues of deciduous hosts appear to be major adaptations to minimize the mortality effects of winter and assure life-history coordination with seasonally available plant-derived nutrients. In some genera, these characteristics are associated with high generic richness, seasonal life-history synchronization, host-plant specialization, and sympatric distributions.

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