

Evolution of Cicadomorpha (Insecta, Hemiptera)

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Abstract

Cicadomorpha (Cicadoidea, Cercopoidea and Membracoidea) are one of the dominant groups of plant-feeding insects, as evidenced by their extraordinary diversity and ubiquity in habitats ranging from tropical rainforest to tundra. Improvements on our knowledge of the phylogeny of these insects, based on cladistic analysis of morphological and molecular data and study of the fossil record, provide the opportunity to examine the possible factors that led to their diversification. Factors influencing early divergences among major lineages apparently included shifts in life history strategies, including a transition from subterranean or cryptic to arboreal nymphal stage, shifts in feeding strategy (xylem to phloem or parenchyma), and the acquisition of various morphological adaptations (crypsis, jumping hind legs, specialized grooming structures). Although most modern families presently are distributed worldwide, global plate tectonics undoubtedly contributed to diversification at the level of subfamily

and tribe. The origins of some family-group taxa may also have coincided with shifts in feeding or courtship strategies, or the colonization of novel habitats (e.g., grasslands, deserts). The origins of genera and species, in many cases, can be attributed to shifts in habitat and host plant association, as well as smaller scale biogeographic vicariance. Many aspects of cicadomorphan evolution remain poorly understood. These include phenomena such as the coexistence of many closely related species on the same host plant and the diversity of bizarre pronotal modifications found among Membracidae. Such questions are best addressed by further ecological and behavioral study, as well as phylogenetic analysis.

Key words: cicada, spittlebug, leafhopper, treehopper, adaptation, evolution.

Introduction

Cicadomorpha, comprising modern cicadas (Cicadoidea), spittlebugs (Cercopoidea), leafhoppers and treehoppers (Membracoidea, *sensu lato*), is by far the most speciose and phylogenetically diverse infraorder of Hemiptera and comprises a substantial proportion (perhaps 6-10%) of the fauna of plant-feeding insects. These insects have inhabited Earth for at least 280 million years (SHCHERBAKOV 1996) and, therefore, have evolved coincidentally with the major lineages of plants, the development of complex terrestrial ecosystems, the mass extinctions at the Permian-Triassic and Cretaceous-Tertiary boundaries, the break-up of Pangea and countless smaller-scale geologic events that have shaped the present-day terrestrial realm. Today cicadomorphans are ubiquitous in terrestrial habitats from equatorial rainforests to the tundra and from sea level to the high mountains, wherever vascular plants can be found. The approximately 30,000 described species have been classified into over 5,000 genera and 13 families. Recent sampling in rainforest canopies suggests that the true number of extant cicadomorph species may be ten times higher (HODKINSON & CASSON 1991, Dietrich unpublished).

Evidence from various sources may contribute to an understanding of how cicadomorphans were able to achieve their status as one of the dominant groups of insect herbivores. Phylogenetic studies of modern taxa help elucidate the relationships among lineages and their relative ages, and provide a framework for studying the evolution of various adaptations. Studies of the fossil record provide a means to correlate the timing of the origin and diversification of various lineages with the geological events that shaped our planet, reveal trends in the evolution of the morphological traits, and provide information on the ancient environments in which these insects evolved. Studies of the behavior, physiology, and ecology of modern Cicadomorpha also provide crucial information relevant to our understanding of the adaptations that contributed to their evolutionary success and the means by which closely related species are able to coexist within the same habitats.

This paper reviews the current state of knowledge of cicadomorph phylogenetic relationships and suggests some possible factors that contributed to the origin and diversification of the various lineages. Synthesizing the wealth of biological information available in the vast literature on Cicadomorpha and viewing this information within a phylogenetic context is no easy task and this paper is by no means an exhaustive review. Given our still rudimentary knowledge of cicadomorph phylogenetic relationships and the difficulty of testing adaptive hypotheses within a single lineage (MITTER *et al.* 1988), the evolutionary scenarios presented here are largely speculative. Nevertheless, by briefly summarizing current knowledge and theories of the evolution of the group, I hope to highlight gaps in our understanding and topics deserving of further investigation.

Origin of Major Cicadomorph Lineages

As for most insect groups, the fossil record of Cicadomorpha is extremely fragmentary (BEKKER-MIGDISOVA 1962, HAMILTON 1992, SHCHERBAKOV 1996); thus reconstructions of cicadomorph evolution based on fossils remain highly speculative. Most fossils consist of wing impressions, but the few whole-body fossils known, scattered across the geologic time scale from the Permian to the Tertiary, provide vital clues regarding the diversity of morphological forms through time and the timing of the acquisition of certain key innovations. Fossil taxa relevant to our understanding of Cicadomorpha phylogeny continue to be discovered and described, particularly faunas from the Cretaceous (e.g., HAMILTON 1990, 1992) and Tertiary (DIETRICH & VEGA 1995, SZWEDO & GEBICKI 1998, SZWEDO & KULICKA 1999), when many modern families and genera apparently arose. SHCHERBAKOV (1992, 1996, and this volume) reviewed the fossil evidence pertaining to the evolution of Auchenorrhyncha.

The fossil record indicates that by the middle Permian, Cicadomorpha (*sensu lato*—a paraphyletic assemblage; SHCHERBAKOV 1996) were already one of the dominant groups of insect herbivores. These early cica-

domorphans resembled modern leafhoppers in having well developed jumping abilities. Nymphs associated with these fossil taxa were bizarre biscuitlike creatures that were probably sessile. The apparently explosive diversification of these early hemipterans may have been facilitated by their ability to exploit a novel food resource due to the acquisition of piercing-sucking mouthparts, although such

with an inflated frontoclypeus, presumably indicating a shift to feeding on xylem. The acquisition of enlarged cibarial dilator muscles enabled this group (Clypeata, sensu SHCHERBAKOV 1996 = Cicadomorpha, sensu stricto) to exploit a new food resource and may have facilitated the diversification of this lineage into what are now recognized as the three modern cicadomorphan superfamilies: Cica-

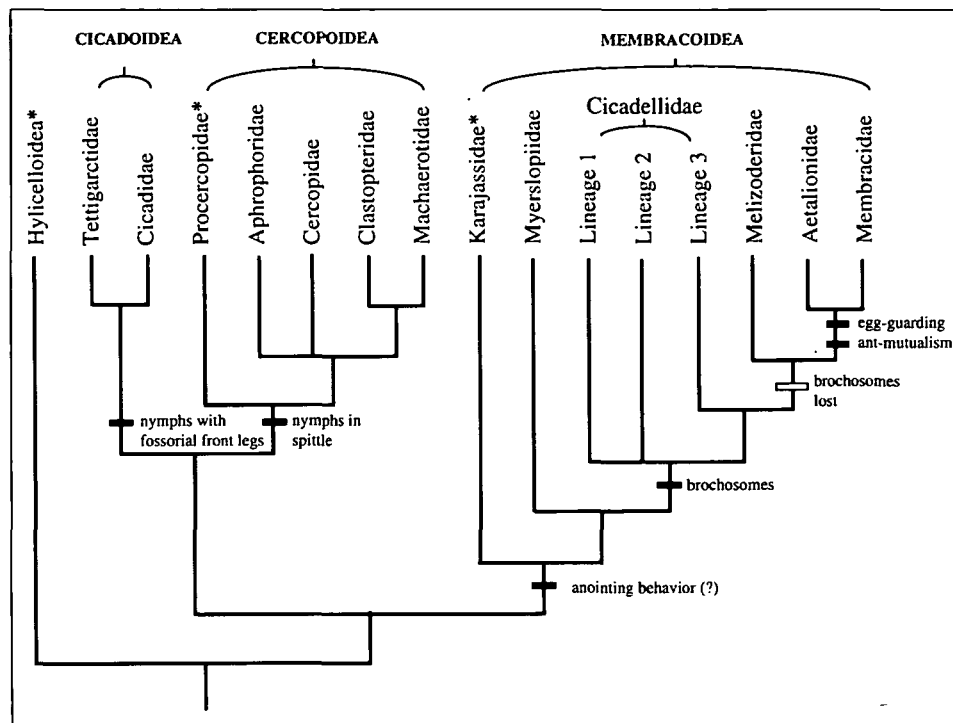


Fig. 1: Provisional estimate of phylogenetic relationships among the major lineages of Cicadomorpha based on information from DIETRICH & DEFTZ (1993), DIETRICH (1999), DIETRICH et al. (2001a, b), HAMILTON (1999), MOULDS (1999), RAKITOV (1998) and SHCHERBAKOV (1996). First occurrences of some possible key innovations are indicated (see text for discussion). Extinct taxa are indicated by an asterisk. Lineages 1-3 of Cicadellidae are defined as follows: Lineage 1 includes Cicadellinae (in part), Makilingiinae, Phereurhininae, Tinterominae, Signoretinae, Phlogisinae, Nirvaninae, Coelidiinae, Typhlocybinae; Lineage 2—Euacanthellinae, Aphrodinae, Xestocephalinae, Acostemminae, Neobalinae, Stegelytrinae, Mukariinae, Penthimiinae, Selenocephalinae, Deltocephalinae, Koebelinae, Arrugadinae, Drakensbergeninae; Lineage 3—Hylicinae, Austroagalloidinae, Ulopinae, Agalliinae, Megophthalminae, Adelungiinae, Evansiolinae, Macropsinae, Tartessinae, Nioniinae, Idiocerinae, Eurymelinae, Ledrinae, Iassininae, Scarinae. Lineage 3 is paraphyletic with respect to the clade Melizoderidae+Aetalionidae+Membracidae. Errhomeninae (placed as a tribe of Cicadellinae by OMAN et al. (1990)) is of uncertain position. Tettigarctidae may be paraphyletic with respect to Cicadidae. Aphrophoridae or Cercopidae may be paraphyletic with respect to the remaining Cercopoidea. According to SHCHERBAKOV (1996), Hylicelloidea gave rise to the extant Cicadomorpha and the extant Cercopoidea are probably derived from Procercopidae.

mouthparts are also known in some Carboniferous-age Paleodictyoptera (LABANDEIRA & PHILLIPS 1996). Early radiations in Hemiptera apparently involved modification of the wing and leg morphology to provide improved jumping and flying capabilities. Because most of the fossil material from the Permian consists of wing impressions, other morphological modifications remain poorly documented. Apparently, these early cicadomorphans retained a primitive head structure, similar to that of modern psyllids, in which the frontovertex extended well onto the face and the clypeus was relatively small. The mass extinction that corresponded to the Permian-Triassic boundary resulted in the loss of several major lineages of vascular plants and, apparently, a substantial loss of diversity in Cicadomorpha as well. Nevertheless, the Triassic saw the advent of the first cicadomorphans

doidea (cicadas), Cercopoidea (spittlebugs), and Membracoidea (leafhoppers and treehoppers).

Several studies have attempted to assess the phylogenetic relationships among the major lineages of Hemiptera (sensu lato) using cladistic analysis of 18S ribosomal DNA sequences from extant taxa (WHEELER et al. 1993, von DOHLEN & MORAN 1995, CAMPBELL et al. 1995, SORENSEN et al. 1995, OUVREARD et al. 2000). Results of these studies are in substantial agreement with paleontological evidence, particularly regarding the monophyly of the extant superfamilies and the paraphyly of Homoptera with respect to Heteroptera. Nevertheless, all of the molecular phylogenetic studies to date have suffered from sparse taxon sampling, equivocal rooting of the resulting trees, and poor resolution of certain relationships. For example, although

these analyses indicate that Auchenorrhyncha gave rise to Heteroptera + Coleorrhyncha, it is not clear whether this lineage is a sister group of Fulgoromorpha or of Cicadomorpha. Attempts to reconstruct the phylogeny of the major lineages of Cicadomorpha based on morphological data (e.g., HAMILTON 1981, 1999, EMELJANOV 1987, SHCHERBAKOV 1996, YOSHIZAWA & SAIGUSA 2001) have yielded conflicting results. A more stable and comprehensive phylogenetic framework, incorporating representatives of relict cicadomorphan lineages such as Myerslopiidae and Tettigarctidae, and combining morphological and molecular data, is needed before various alternative evolutionary scenarios may be tested for Cicadomorpha as a whole. The tree diagram in Fig. 1 represents a consensus phylogenetic estimate for Cicadomorpha (sensu stricto) based on my interpretation of the available morphological and molecular evidence.

Diversification of Families, Genera, and Species

Cicadoidea

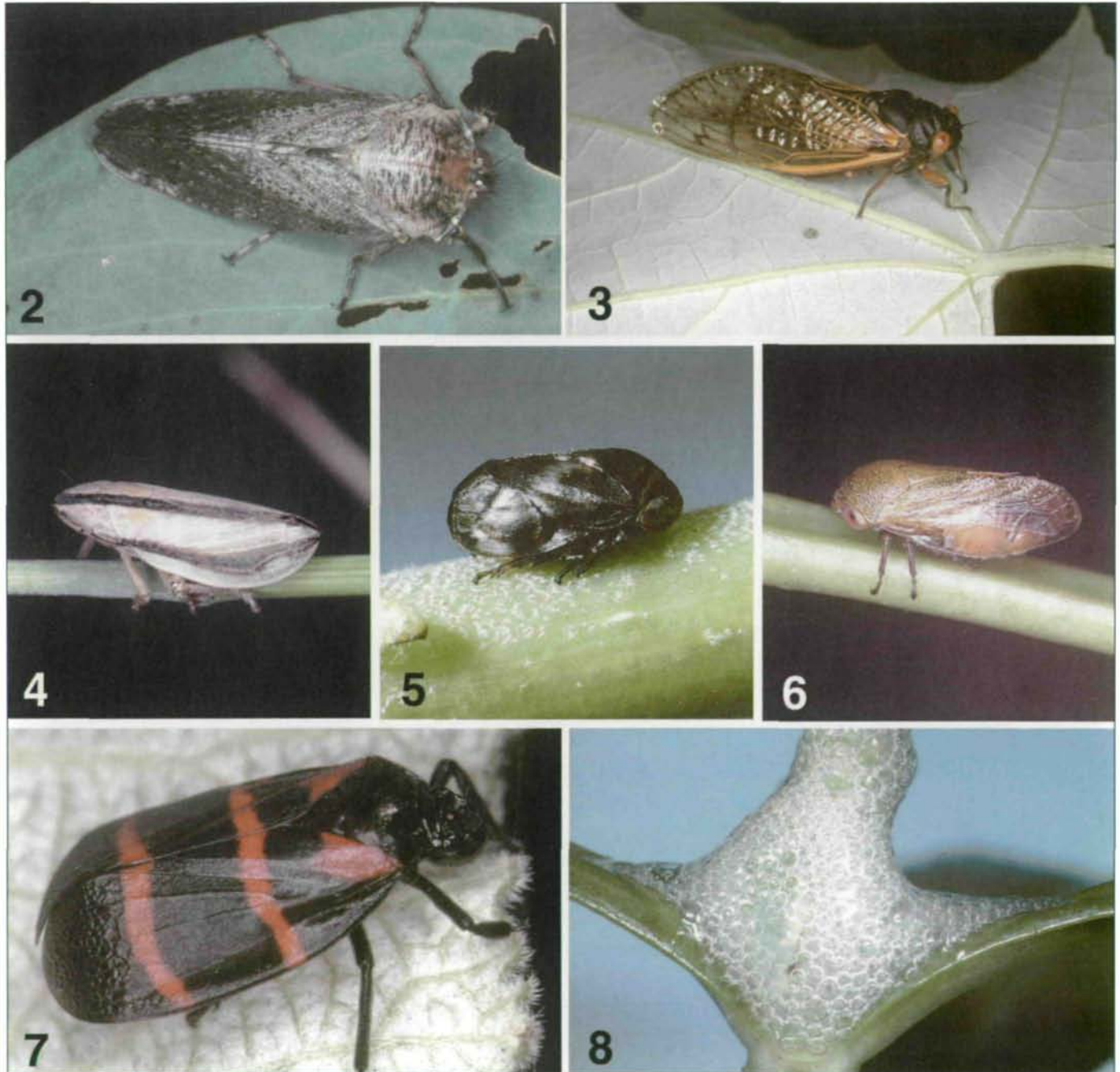
Based on the fossil record, Cicadoidea apparently arose during the late Triassic or early Jurassic. Mesozoic cicadas previously placed in an extinct family (Cicadoprosobolidae) are now considered to belong to Tettigarctidae (BEKKER-MIGDISOVA 1962, SHCHERBAKOV 1996), a family presently represented by two relict southern Australian species (Fig. 2). Cicadidae (sensu lato, Fig. 3) are first recorded from the Paleocene (BEKKER-MIGDISOVA 1962). Phylogenetic studies of modern cicada genera and species, ongoing during the past 30 years, have yielded many insights into the factors that influenced the diversification of this group. A comprehensive morphology-based phylogenetic analysis of the family-group taxa is underway and the higher classification will be revised in the near future (MOULDS 1999). Nevertheless, the restricted distributions of certain currently recognized family-group taxa suggest that continental drift played a role in their origin and diversification. Tribes and subfamilies also tend to differ from one another in certain behavioral strategies. For example, in some tribes (e.g., Platyleurini) searching during courtship is done primarily by females; the males are sedentary and usual-

ly have very loud, persistent calls that facilitate the attraction of females over greater distances. In other groups (e.g., Tettigomyiini), the males have shorter, quieter calls and actively seek out the females, some of which are flightless (VILLET 1999). These alternative strategies may have evolved in conjunction with alternative predator avoidance strategies and possible tradeoffs between mobility and fecundity. Various authors (reviewed by MOULDS 1990) have noted that species of cicadas are often associated with particular habitats or host plants. Thus diversification in some groups probably resulted from host or habitat shifts. Cicadas are especially diverse in desert environments, where they are often active at ambient temperatures that would kill other insects. Recent physiological studies (TOOLSON & HADLEY 1987, TOOLSON 1987, TOOLSON & TOOLSON 1991, SANBORN et al. 1992) have shown that some cicadas are facultatively endothermic, alternatively warming themselves through shivering movements of the flight and/or tymbal muscles and cooling themselves by releasing excess water through pores on the thorax. This enables these insects to remain active at temperature extremes that would induce torpor in other insects. Unfortunately, such physiological adaptations have so far been documented in only a few species and, thus, their distribution among various cicada lineages remains unknown. Moreover, phylogenetic studies have so far been performed on only a few groups. Thus, the extent to which such physiological adaptations facilitated cicada diversification needs further investigation.

Cladistic biogeographic studies on cicadas, particularly in the Indo-Pacific region, indicate patterns of diversification strongly correlated with geographical vicariance (DUFFELS 1986, de BOER 1995, DUFFELS & de BOER 1996). For example, the main speciation events in a cladogram for the tribe Chlorocystini correspond with the hypothesized sequence of fragmentation of the Outer Melanesian island arc, and its incorporation into present-day New Guinea (de BOER 1995). Speciation within the endemic New Zealand genus *Maoricicada* appears to have coincided with the invasion of various montane regions following Pleistocene glaciation (BUCKLEY et al. 1997).

The apparently unique life history strategy of the North American periodical cicada genus *Magicicada* (Fig. 3) deserves special mention. By acquiring an attenuated life-cycle, emerging only every 13 or 17 years, these cicadas mitigate the effects of predation through mass emergences that overwhelm the ability of local predator populations to utilize them as a food resource (KARBAN 1982). Pre-

dators become satiated long before the population of cicadas becomes depleted, ensuring that many cicadas remain to reproduce. Research is ongoing on the factors that contributed to the diversification of *Magicicada* into the seven species and 15 allochronic broods currently recognized (reviewed by SIMON 1988, MARSHALL 2001). Geographic and temporal isolation as well as reproductive character dis-



Figs 2-8:

Cicadoidea and Cercopoidea: (2) *Tettigarcta crinita* DISTANT (Tettigarctidae) — cicadas in this family are nearly indistinguishable from Mesozoic fossil taxa; (3) *Magicicada cassini* (FISHER) (Cicadidae), a periodical cicada from eastern North America; (4) *Paraphilaenus parallelus* (STEARNS) (Aphrophoridae); (5) *Clastoptera obtusa* (SAY) (Clastopteridae); (6) *Pectinariophyes reticulata* (SPÄNGBERG) (Macherotidae); (7) *Tomaspis* sp. (Cercopidae); (8) spittle mass made by nymph of *Philaenus spumarius* (L.) (Aphrophoridae).

placement have all been proposed as speciation mechanisms in this genus (ALEXANDER & MOORE 1962, LLOYD & DYBAS 1966a, b, SIMON 1988, MARTIN & SIMON 1988) and recent population genetic studies have provided support for these mechanisms (MARSHALL & COOLEY 2000, SIMON et al. 2000).

Cercopoidea

Of the three major lineages of Cicadomorpha, Cercopoidea is the least studied phylogenetically. No comprehensive phylogenetic analysis of the superfamily has ever been attempted and only a few cladistic analyses of genera and tribes have been published (e.g., LIANG 1998). Thus, the factors that influenced spittlebug diversification remain unclear. Cercopoidea first appear in the fossil record during the Jurassic. Diversification at the family level apparently occurred during the Cretaceous and Tertiary (BEKKER-MIGDISOVA 1962). The four currently recognized families, Aphrophoridae (Fig. 4), Cercopidae (Fig. 7), Clastopteridae (Fig. 5), and Machaerotidae (Fig. 6), exhibit some differences in behavior and habitat preference. Cercopidae (sensu stricto) occur largely in grasslands and nymphs of most species apparently feed on grass roots. Nymphs of the other three families generally occur on aboveground parts of their hosts. In Aphrophoridae, Cercopidae, and Clastopteridae, nymphs live within spittle masses (Fig. 8). In Machaerotidae, nymphs live immersed in fluid within calcareous tubes cemented to their host plant. These differences suggest that the origins of some major lineages of Cercopoidea involved shifts in habitat and physiology.

THOMPSON (1994) summarized the still rather sparse knowledge of host plant and ecological associations among Cercopoidea, noting that at least three of the four families, although having broad host ranges overall, exhibit statistically significant preferences for particular groups of plants. With the possible exception of Machaerotidae, spittlebugs exhibit a strong preference for nitrogen-fixing plants. Interestingly however, different cercopoid families apparently prefer different groups of such plants. Aphrophoridae exhibit a strong preference for legumes, particularly

those genera and species in which fixed nitrogen is transported in the xylem as amino acids or amides. In contrast, fabaceous plant taxa with xylem containing ureide nitrogen compounds appear to be avoided by these insects. Clastopteridae prefer actinorhizal plants (i.e., those associated with the root-nodule symbiont *Frankia*). Cercopidae exhibit a strong preference for associative nitrogen fixing grasses (which lack true mycorrhizae but grow in loose association with nitrogen-fixing fungi and bacteria). These preferences appear to be confirmed by the large number of cases of native spittlebugs that have become pests of introduced or native legumes, or actinorhizal plants like *Casuarina* (THOMPSON 1994). Such correlations between feeding preference and taxonomic affiliation suggest that shifts in feeding preference may have been involved in the divergence of the major lineages of Cercopoidea. Such shifts presumably involved acquisition of a suite of traits including specialized oviposition behaviors and modification of the flora of endosymbionts to accommodate differences in the chemical composition of the xylem sap of their host plants. A robust phylogenetic framework for the superfamily is needed before the roles of such shifts can be rigorously tested.

As in other cicadomorphans, many cercopoid subfamilies, tribes, genera, and species are apparently limited not only in their geographic ranges (METCALF 1961, 1962) but also in their host plants and habitats (HAMILTON 1982). Thus geographic vicariance and host and habitat shifts presumably played a role in their diversification. In the absence of phylogenetic studies, however, the relative importance of these factors in the origin of spittlebug lineages remains unknown.

Membracoidea

Comprising approximately 25,000 described species placed in 3,500 genera, 150 tribes, 50 subfamilies, and 5 extant families (DEITZ & DIETRICH 1993, HAMILTON 1999), Membracoidea is by far the largest and most phyletically diverse of the extant cicadomorphan superfamilies (Figs 10-21). The ecology and bionomics of Membracoidea have been studied intensively due to their considerable econo-

shift to parenchyma feeding in Typhlocybae. Membracoid nymphs feeding exposed on leaves and twigs faced a new set of challenges, including increased exposure to predators and more extreme fluctuations in environmental (particularly microhabitat) conditions. Different lineages have met these challenges in myriad ways. To avoid predation, some rely on camouflage or mimicry (reviewed by Mejdalani et al., this volume), some on agility, others on defensive morphological armature (EKKENS 1972), and still others on mutualistic associations with aggressive social hymenopterans (WOOD 1984). In some groups, particularly Membracidae, different strategies are employed by adults and immatures; thus selection led to greater divergence between the adult and nymphal body forms (e.g., Fig. 20).

Cladistic analyses of the major membracoid lineages indicate that some life history traits are phylogenetically conservative, suggesting that their acquisition coincided with the origins of major lineages. For example, with the exception of Eurymelinae (*sensu stricto*, EVANS 1931), ant-mutualism appears to be rare among leafhoppers, occurring sporadically within a few other subfamilies (e.g., Idioceirinae, Macropsinae, Deltocephalinae; DIETRICH & MCKAMEY 1990). In contrast, ant-mutualism is common in the treehopper families Aetalionidae (Fig. 15) and Membracidae, and is often associated with parental care (egg guarding, Figs 14, 18) and gregarious behavior (WOOD 1984). Among treehoppers, ant-mutualism and parental care are plesiomorphic traits (Fig. 9), occurring nearly universally in Aetalionidae and in the most plesiomorphic membracid subfamily Endoiastinae (Dietrich et al. 2001b). Most other membracid subfamilies (Stegaspidae, Centrotinae, Heteronotinae, Membracinae, Darninae, and Smiliinae) contain at least some ant-mutualistic species and ant-mutualism appears to occur universally within some tribes, e.g., Amastrini and Tragopini. The behavior of the most plesiomorphic treehoppers, Melizoderidae (sister group of Aetalionidae + Membracidae; endemic to Chile; Fig. 13), has not been studied, but the morphology of melizoderid nymphs indicates that they are adapted for crypsis and may not be ant-mutualistic (DIETRICH & DEITZ 1993). The widespread occur-

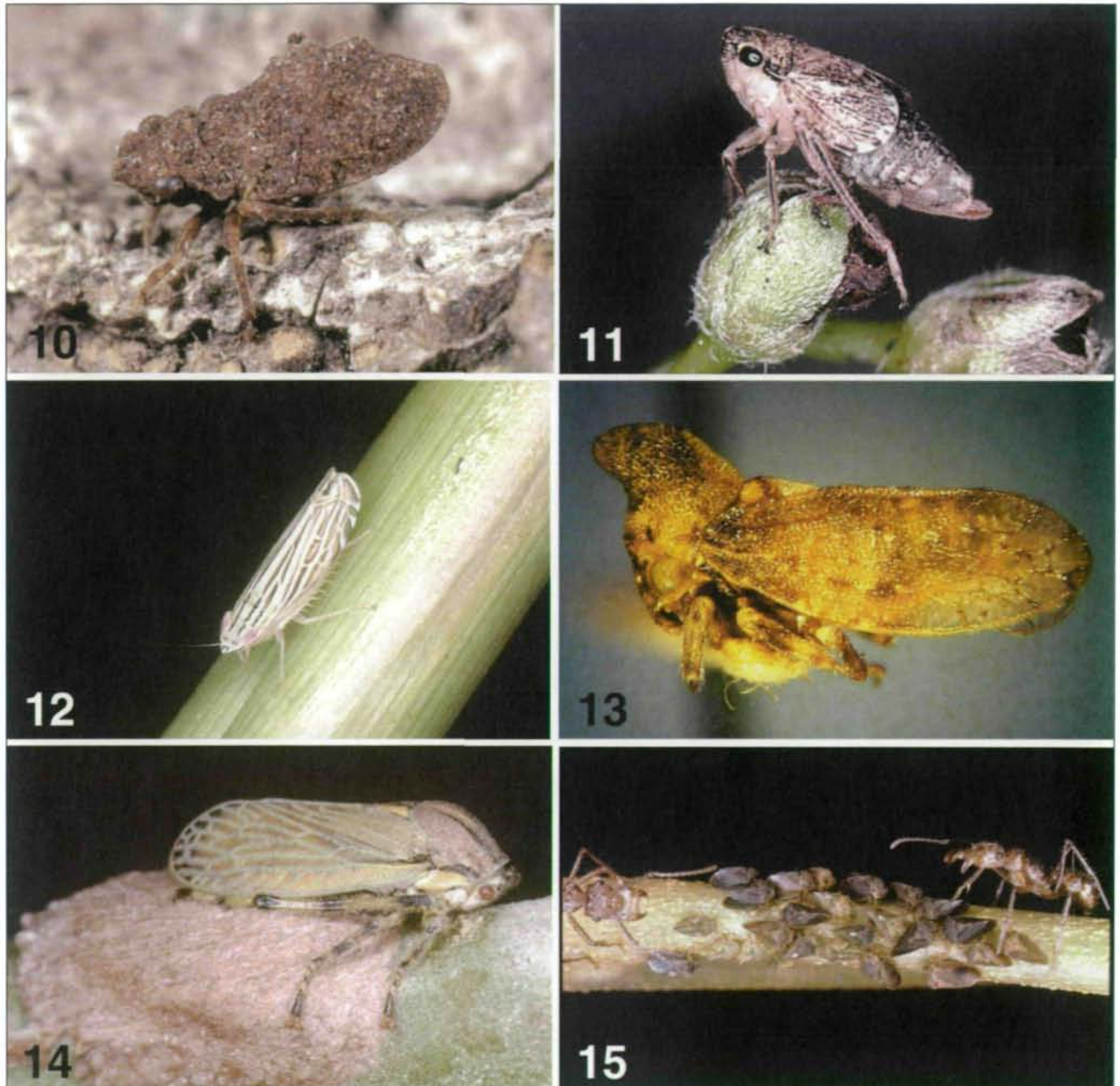
rence of ant-mutualism and parental care among aetalionids and membracids suggests that acquisition of these behaviors coincided with the origin of the treehopper lineage that now comprises the vast majority of species. Phylogenetic analysis of Membracidae indicates that ant-mutualistic behavior became sporadic or, more rarely, was completely lost in various treehopper lineages (e.g., Stegaspidae, Nicomiinae, Darninae, Ceresini, Smiliini). In some, e.g., Stegaspidae and Darninae, the nymphs became solitary and acquired crypsis-enhancing morphological features (Dietrich et al. 2001b). In others, e.g., Aconophorini (Fig. 18) and Hophlophorionini, complex parental care behaviors provided alternative means for protecting nymphal aggregations (DIETRICH & DEITZ 1991; MCKAMEY & DEITZ 1996).

Acquisition of such alternative defensive strategies may account for at least some of the major divergences within Membracoidea but they alone do not explain why there are so many species of leafhoppers and treehoppers. Data on host associations, geographic range, and habitats, coupled with phylogenetic analyses at the genus and species level within several groups suggest numerous scenarios that might account for recent divergences within membracoid genera. Estimates of the phylogeny of Cicadellidae based on morphology (DIETRICH 1999) and DNA sequences (DIETRICH et al. 2001a) indicate that one of the major lineages of leafhoppers (comprising Deltocephalinae and several other subfamilies) comprises species largely associated with semiarid or arid habitats (particularly grasslands). Thus, a habitat shift from forests to grasslands may have coincided with the origin of this lineage. Other major membracoid lineages exhibit a wide variety of host and habitat preferences, suggesting more complex patterns of evolutionary diversification.

Because host and habitat associations are often fairly conservative within genera of Membracoidea, biogeographic vicariance has often been invoked to explain recent speciation events. In *Errhomus*, a genus of large, flight-limited leafhoppers endemic to northwestern North America, partitioning of the range of the host plant (*Balsamorhiza*)

appears to have resulted, in part, from vicariant processes associated with glaciation and river capture in the Columbia River basin (OMAN 1987, HAMILTON & ZACK 1999). Phylogeographic studies incorporating mitochondrial DNA sequence data are needed to test such hypotheses which, thus far, have been based on morphological and geological data alone.

Studies of several groups of grass- and sedge-feeding deltocephaline leafhoppers indicate that host plant shifts were involved in the diversification of individual genera and species. DIETRICH et al. (1997) found that several clades of *Flexamia* species (Fig. 12) were associated with particular grass genera or species. Similar patterns appear in *Athysanella*, a large genus of mostly flightless leafhoppers (HICKS



Figs 10-15:

Membracoidea: (10) *Myerslopiia chilensis* NIELSON (Myerslopiidae) — myerslopiids, restricted to Chile and New Zealand, are thought to be a sister group to the lineage comprising the remaining families of Membracoidea; (11) *Hylaius oregonensis* (BAKER) (Cicadellidae: Errhomeninae); (12) *Flexamia grammica* (BALL) (Cicadellidae: Deltocephalinae), a grass-specialist leafhopper; (13) *Llanquihuea pilosa* LINNAVUORI & DELONG (Melizoderidae) — melizoderids, restricted to Chile, are thought to be the sister group of the lineage comprising the remaining two treehopper families Aetalionidae and Membracidae; (14) a female *Aetalion reticulatum* (L.) (Aetalionidae: Aetalioninae) guarding an egg mass; (15) ant-attended aggregation of *Tropidaspis* sp. (Aetalionidae: Biturritiinae).

et al. 1988, WHITCOMB et al. 1986). Plesiomorphic species of *Dalbulus* specialize on *Tripasacum* spp., but shifts to feeding on *Zea* spp. occurred independently in two lineages (TRIPLEHORN & NAULT 1985, DIETRICH et al. 1998). Within such host-associated lineages, closely related species tend to be allo- or parapatric, suggesting that host shifts followed by biogeographic partitioning of the host range could account for much of the diversification within the genus. Diversification of *Limotettix* (*sensu lato*) may have involved a combination of host and habitat shifts (e.g., among various kinds of wetlands and wetland plants; HAMILTON 1994).

In the above mentioned genera, host plant shifts occurred mostly among closely related plant species (e.g., grasses). In other membracoid genera, different species specialize on unrelated plants that differ substantially in their phenologies. WOOD's (1992 and refs.) extensive studies of one such group, the *Enchenopa binotata* species complex of North American treehoppers, have revealed patterns of diversification consistent with a sympatric speciation model. Isolation of new host-associated *Enchenopa* lineages may have been mediated by the phenological differences among their various host plants, resulting in asynchronous development and temporal isolation of populations within a small geographic area. In the *E. binotata* complex such a process has apparently given rise to at least seven biological species. Similar mechanisms may explain diversification within some lineages of typhlocybina and deltocephalina leafhoppers, where numerous cryptic, host-specialist species have been discovered among specimens of what were once thought to be single polyphagous species (e.g., DELONG 1931, ROSS 1957a, 1965, HEPNER 1966, KLEIN & GAFNY 1999).

Although a combination of host and habitat shifts may suffice to explain the diversification of many membracoid genera and species, the present geographic ranges of many closely related species overlap substantially and it is not uncommon to find congeneric species occupying the same habitats feeding on the same host plant. For example, HEPNER (1976) noted that as many as 100 *Erythroneu-*

ra species may occur together on the same plant. ROSS (1957b, 1958) suggested that many such species have identical niches, an apparent contradiction of Gause's Law. But MCCLURE & PRICE (1975, 1976) demonstrated that, at least in sympatric sycamore-feeding *Erythroneura* species, competition can be severe. Their experiments indicated that a combination of biogeographic and microhabitat partitioning may reduce interspecific competition and facilitate coexistence among the species whose ranges overlap. Other groups of closely related, coexisting leafhopper and treehopper species (e.g., the oak-feeding *Cyrtolobus* generic group of North American treehoppers), appear to show similar patterns. Phylogenetic studies of some such groups are underway (e.g., WOOD et al., pers. comm.).

Character displacement has also been invoked to explain the coexistence of closely related species in the same habitat (e.g., HAMILTON 1998, 2000). Studies of acoustic courtship signals (e.g., HEADY et al. 1986, HUNT 1994, TISHECKIN 1998, 2000a, b) and the extensive divergence in male genitalia, particularly in leafhoppers, appear to confirm the role of sexual selection in reinforcing barriers to interbreeding among congeners. Indeed, within most membracoid genera, other aspects of the morphology are highly conservative, although multivariate morphometric analysis of „external“ structures (e.g., WOOD & PESEK 1992, DIETRICH & POOLEY 1994) may be capable of distinguishing species in some groups. Divergence associated with the most recent speciation events in Membracoidea is often manifested in subtle physiological, ecological, and behavioral differences, in the absence of substantial modification of the morphology, and many cryptic species undoubtedly await discovery.

The Membracid Pronotum: An Evolutionary Enigma

One aspect of cicadomorph evolution that continues to defy explanation is the extreme divergence in pronotal shape observed among genera of Membracidae (Figs 16-21). Early observers (e.g., POULTON 1891, MANN 1912) suggested that these insects

mimic various parts of their host plants (thorns, seeds, bark, etc.) or venomous insects (ants, wasps). HAVILAND (1926), in addition to providing evidence of crypsis and mimicry in some species, suggested that some strikingly patterned species are aposematic. WOOD (1975) confirmed that two North American species exhibit aposematic coloration. Haviland also suggested that the spiny pronot-

al projections of many species deter vertebrate predators, and this hypothesis has received some support by observations of later workers (e.g., EKKENS 1972; WOOD 1975). FUNKHOUSER (1951), while noting the possible adaptive significance of some pronotal shapes, suggested that the pronotum of many species lacked adaptive significance and attributed the diversity of bizarre forms to orthogenesis (i.e., evo-



Figs 16-21:

Membracidae: (16) a member of the *Enchenopa binotata* (SAY) species complex of the eastern U.S.A.; (17) *Cladonota* sp., Guyana; (18) female *Aconophora* sp. guarding eggs and nymphs, Peru; the bands of sticky secretion coating the stem on either side of the egg mass apparently deter predators and parasitoids—note the trapped wasp on the left; (19) *Bocydium globulare* (F.), Guyana; (20) *Heteronotus* sp. from Ecuador; the strikingly marked adult of this species contrasts sharply with the cryptic nymph (exuviae at lower right); (21) *Telamona extrema* BALL, eastern U.S.A.

lution along a progressive line independent of natural selection). STRÜMPEL (1972) refined this idea by demonstrating that differences in pronotal shape among species in some genera may be explained by simple allometric growth models. More recently, WOOD & MORRIS (1974) noting the presence of numerous sensory pits on the membracid pronotum and suggested that the expansion of the pronotum may have been an adaptive response to selection for increased sensory surfaces or evaporative surfaces for dispersal of pheromones.

Another possible function of the expanded pronotum is suggested by recent physiological studies of thermoregulation in cicadas (see Cicadoidea, above). Some cicada species, when subjected to high ambient temperatures, cool themselves by releasing excess water through pores on the thorax and abdomen. If similar cooling mechanisms are present in the related Membracidae, then selection may have favored pronota with larger, pitted surface areas to provide greater efficiency in heat transfer. This possible physiological function of the enlarged membracid pronotum merits investigation. Membracidae achieve their greatest diversity in tropical rainforests, savannas, and deserts, environments where, given their tendency to be active during the day, they may be subjected to extreme heat. Improved thermoregulatory efficiency provided by the enlarged pronotum may have facilitated diversification in treehoppers by giving them a selective advantage in such environments, enabling them to engage in courtship activity during midday when many of their predators are inactive.

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