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Social behaviour and life history of membracine treehoppers

CHUNG-PING LIN

Department of Entomology, Cornell University, Ithaca, NY, USA and Department of Life Science, Center for Tropical Ecology and Biodiversity, Tunghai University, Taichung, Taiwan

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Abstract

Social behaviour in the form of parental care is widespread among insects but the evolutionary histories of these traits are poorly known due to the lack of detailed life history data and reliable phylogenies. Treehoppers (Hemiptera: Membracidae) provide some of the best studied examples of parental care in insects in which maternal care involving egg guarding occurs frequently. The Membracinae exhibit the entire range of social behaviour found in the treehoppers, ranging from asocial solitary individuals, nymphal or adult aggregations, to highly developed maternal care with parent–offspring communication. Within the subfamily, subsocial behaviour occurs in at least four of the five tribes. The Aconophorini and Hoplophorionini are uniformly subsocial, but the Membracini is a mixture of subsocial and gregarious species. The Hypsoprorini contains both solitary and gregarious species. Accessory secretions are used by many treehoppers to cover egg masses inserted into plant tissue while oviposition on plant surfaces is restricted to a few species. Presumed aposematic colouration of nymphs and teneral adults appears to be restricted to gregarious and subsocial taxa. Ant mutualism is widespread among membracine treehoppers and may play an important role in the evolutionary development of subsocial behaviour. The life history information provides a basis for comparative analyses of maternal care evolution and its correlation with ant mutualism in membracine treehoppers. The results show that there is a strong phylogenetic component to the evolution of maternal care in membracine treehoppers, and provide the first quantitative evidence of correlated evolution of maternal care and ant mutualism in treehoppers. Further research on natural history, particularly of the tropical fauna, will be necessary to better understand the evolution of social behaviour and life history in treehoppers.

Keywords: *Aggregation, ant mutualism, aposematism, egg guarding, maternal care, Membracidae, Membracinae, oviposition, pronotum, vibrational communication*

Introduction

Insect social systems exhibit a great diversity ranging from solitary or asocial individuals, parent–offspring interactions of subsocial insects, to highly complex eusocial societies (Wilson 1971). The study of insect social evolution has traditionally focused on the eusocial Hymenoptera (ants, bees, and wasps) and Isoptera (termites). Extensive natural history

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Correspondence: Chung-Ping Lin, Department of Life Science, Center for Tropical Ecology and Biodiversity, Tunghai University, No. 181, Sec. 3, Taichung-Kan Road, Taichung, Taiwan 40704. Email: treehops@thu.edu.tw

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observations, empirical and theoretical studies, and phylogenetic analyses of these two insect groups have contributed greatly to our understanding of insect social evolution. However, the evolutionary histories of most subsocial insects are less known even though parental care is widespread in at least 47 families of 13 insect orders (Eickwort 1981; Choe and Crespi 1997). Reasons for the paucity of such comparative studies include the lack of detailed life history data and reliable phylogenies. Behavioural and life history data of less-studied insects is often difficult to retrieve from the literature and valuable ecological information collected during fieldwork is frequently not published. Reviews on behaviour and life history of subsocial insects are therefore useful in order to make new information available, lead to future research directions, and provide a basis for comparative phylogenetic analyses.

Treehoppers (Hemiptera: Membracidae) provide some of the best-studied examples of parental care in insects, but the first suggestions that female treehoppers provide parental care were met with skepticism. The observation of Murtfeldt (1887) on *Entylia sinuata* is the first account of maternal care in treehoppers. The pioneering work by Haviland (1925) on the natural history of treehoppers in the tropical lowlands of Guyana provides details that suggest subsociality in Membracidae. Although she never used the terms egg guarding or maternal care, her observations and that of Beamer (1930) on *Platycotis vittata* supported Murtfeldt's (1887) recognition of maternal care in treehoppers. Nevertheless, Funkhouser (1950), who had published extensively on the distribution, taxonomy, and host plants of treehoppers, never accepted these observations. It was only the detailed field studies on Neotropical treehoppers by Wood (1974, 1976a, 1977a, 1978, 1983, 1984) and on several Mexican species by Hinton (1977) that confirmed the existence of maternal care in treehoppers.

Natural history studies of treehoppers were highly biased toward the New World fauna. The majority of the Old World treehoppers are still poorly known except for some species in South East Asia (Stegmann et al. 1998, 2002; Stegmann and Linsenmair 2002a, 2002b; Lin 2003), India (Ananthasubramanian 1996), and China (Yuan and Chou 2002). The aim of this paper is to provide an update on the social behaviour and life history characteristics of treehoppers based on literature and unpublished data from colleagues and myself. It focuses on the relatively well-studied New World subfamily Membracinae. In combination with existing phylogenies (Lin et al. 2004), my goal is to provide a basis for further comparative analyses of maternal care evolution and its correlation with life history traits in membracine treehoppers.

Biology of treehoppers

Generalized life history

Treehoppers are phytophagous insects with piercing and sucking stylets used to feed on the phloem of woody or herbaceous plants. A recent study suggests that treehoppers may also feed on the xylem (H. Shugart and R. B. Cocroft, unpublished data). Nymphs in some species apparently feed on parenchyma (Kiss and Chau 1984). Treehoppers, like most hemipterans, have midgut filter chambers that allow extraction of nutrients (primarily amino acids and carbohydrates) from plant sap. Excess fluid containing nutrients is excreted in the form of honeydew, which in many treehoppers is collected by social hymenopterans such as ants, meliponine bees, and wasps (Way 1963; Fritz 1982) (Figure 1C).

All life stages of treehoppers are associated with their host plants. Females insert eggs into various parts of host-plant tissues with their rigid and elongated ovipositors. Eggs may also be laid on the surface of the plant tissue (Figure 1A). Egg masses are frequently covered with waxy substances from accessory glands (Figure 1A, G). In temperate North America, treehopper nymphs usually go through five nymphal instars prior to adulthood.

The mating biology of most treehoppers is poorly known. However, studies showed females of *Enchenopa binotata* and *Umbonia crassicornis* are monogamous (Wood 1974, 1993b) but females of *Platycotis vittata* can mate up to five times with sperm precedence by the last male (Wood et al. 1984). Mating among siblings is known in a few subsocial species (Wood and Dowell 1984; Eberhard 1986; Masters 1989). Sex ratios in some subsocial species are female biased at eclosion (Wood and Dowell 1984, 1985; Miyazaki and Buzzi 1985; Masters 1989).

In temperate North America, most solitary treehoppers are univoltine and overwinter as eggs. Gregarious species such as *Vanduzea arquata* are bivoltine and overwinter as eggs. Subsocial species such as *Entylia*, *Platycotis*, and *Publibia* overwinter as adults (Wood 1993a). Among tropical taxa, multivoltinism is common but is influenced by elevation and seasonality of habitats and host plants. In tropical lowland wet forests, most gregarious and subsocial treehoppers appear to be multivoltine but there is a trend toward univoltinism at higher elevations and in seasonally dry habitats (Wood and Olmstead 1984). Natural history studies for presumed solitary species is limited but collecting data and museum specimens suggest they are multivoltine in humid lowland forests and seasonally restricted in dry habitats or high elevations (T. K. Wood, personal communication).

Pronotum and vibrational communication

Plant-borne, vibrational signals play a role in many aspects of the biology of treehoppers, including mate attraction (Hunt 1993, 1994; Cocroft 2001; Rodríguez et al. 2004), communication between females and their offspring (Cocroft 1996, 1999a, 1999b, 2002), and communication among individuals in aggregations (Cocroft 2001, 2003). The possibility that variation in pronotal architecture is important in the production of vibrational signals is not supported by comparative evidence. For example, species in the *Enchenopa binotata* complex have very similar pronotal architecture, but produce signals that differ quantitatively (Rodriguez et al. 2004; R. B. Cocroft and R. E. Hunt, unpublished data). The expanded, air-filled cavity in some pronota has a superficial resemblance to resonating structures such as the larynx of howler monkeys. However, because treehoppers communicate by means of substrate-borne vibrations rather than airborne sound, the two structures cannot have an analogous function (R. B. Cocroft, personal communication). Cocroft et al. (2000) showed that a treehopper's body resting on its legs behaves as a mass-and-spring system in response to substrate vibration. They also showed that the motion of the body differed depending on the direction of propagation of the substrate-borne signal, providing a potential source of directional information for signal localization. However, this mechanical directionality does not appear to depend on the presence of a pronotum, since it was retained in insects from which most of the pronotum had been removed (Cocroft et al. 2000). Although these observations do not support a role for the pronotum in vibrational communication, the question will only be settled by direct behavioural experiments.

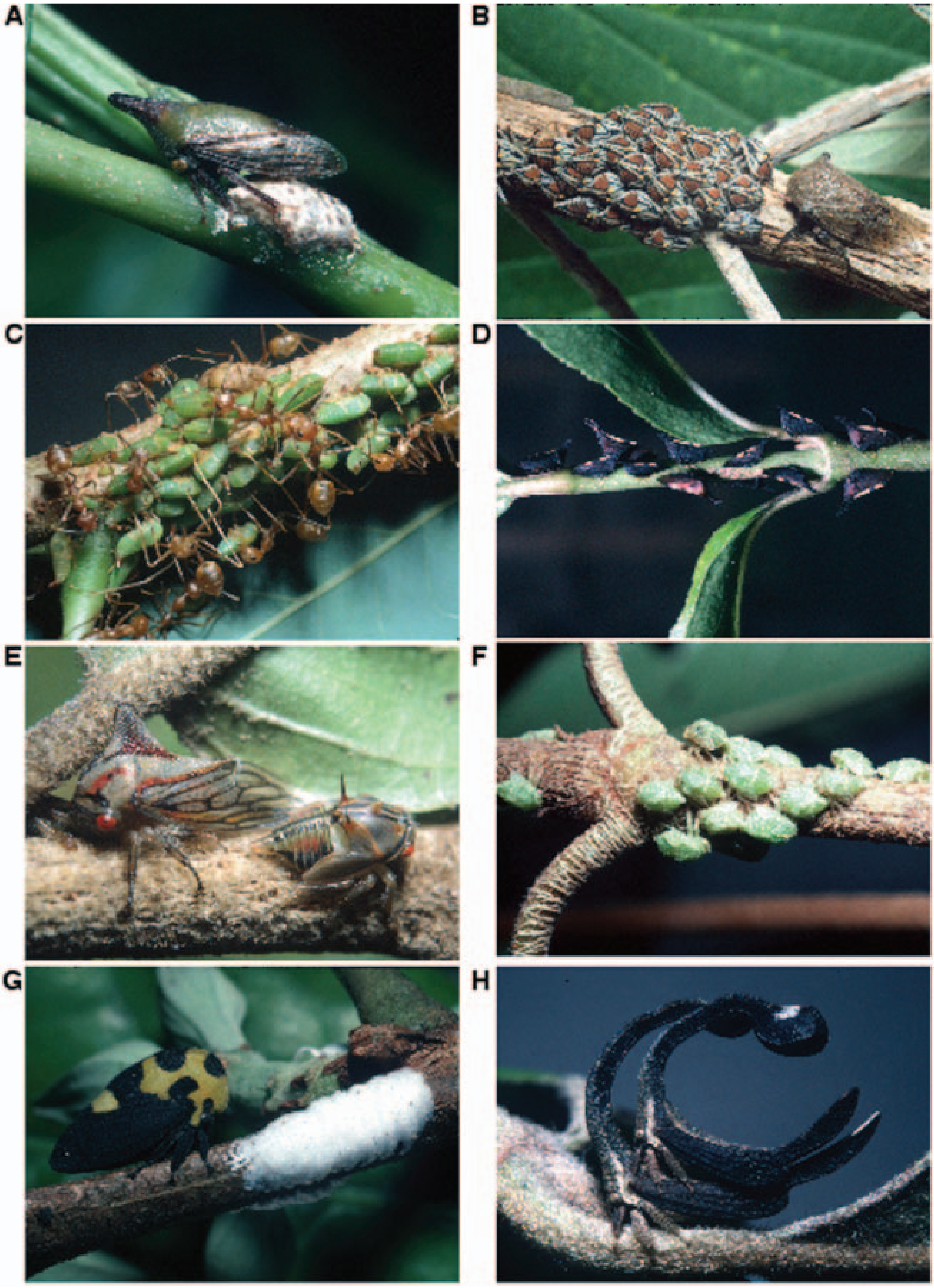

Figure 1. Social behaviour and life history characteristics of treehoppers. (A) Egg-guarding behaviour of *Guayaquila* (Aconophorini), eggs are deposited on the surface of the stem and covered by accessory secretion, Volcan, Panama, 2000; (B) a nymphal aggregation of *Metcalfiella nigrihumera* (Hoplophorionini) guarded by a

Social behaviour and life history characteristics

Variations in social behaviour

Social interactions in treehoppers can be classified into three broad categories: (1) solitary, (2) nymph or adult aggregations, and (3) subsocial behaviour with various degrees of maternal care. Subsocial behaviour is defined as ''postovipositional parental behaviour that promotes the survival, growth, and development of offspring'' (Tallamy and Wood 1986). This definition does not include the female's accessory gland secretion such as egg froth which is deposited postovipositionally, but nevertheless is important for the survival of eggs. These behavioural categories represent subdivisions of a continuum. For example, social behaviour can vary among life stages of a single species: some species currently recognized as solitary based on adult behaviour are found as nymphal aggregations of two to three individuals. Behaviour sometimes can be variable even within a single life stage: treehoppers such as *Publilia* modify their maternal behaviour depending on the availability of ants (Bristow 1983; Billick et al. 2001). A further challenge in assigning behavioural characteristics to discrete categories is that the necessary detailed comparative natural history observations are often not available. With these caveats, I discuss species within these three large categories.

Solitary. Solitary species are those that do not form groups of two or more individuals (excluding mating pairs) spatially clumped on branches, petioles, or flower inflorescences. The majority of temperate North American treehoppers are in this category (Wood 1993a). Natural history studies such as those of Loye (1982, 1987), as well as years of collecting by colleagues, suggest that this generalization is probably true, at least for the Smiliini (T. K. Wood, personal communication). In the tropics, most recognized solitary treehoppers are cryptically coloured, fast flying and not often encountered as adults. However, some tropical treehoppers that were once considered solitary, such as *Notocera*, have subsequently been found to form large ant-tended nymphal aggregations (Lin 2003; T. K. Wood, personal communication for *Notocera* spp.).

Aggregations. The term aggregation is defined by Eickwort (1981) as being ''any group of individuals of the same species, comprised of more than a mated pair that has gathered in the same place'' (Figure 1B–D, F). The primary functions of aggregation in treehoppers were thought to include feeding facilitation, predation diffusion, and attracting ants (see *Ant mutualism* below) (Wood 1993a). However, among these hypotheses only the function of ant attraction was experimentally demonstrated (McEvoy 1979; Wood 1982a; Cushman and Whitham 1989). At least four types of aggregations can be found in treehoppers, each of which is initiated by female ovipositional behaviour. (1) Aggregations of nymphal siblings with a mixed age structure result from the oviposition of egg clutches on the same

female, the sclerotized adult is cryptic dark brown and nymphs have aposematic colouration, Podocarpus National Park, Zamora, Ecuador, 2001; (C) an ant-tended adult and nymphal aggregation of *Gargara* (Centrotinae), Los Banos, Philippines, 2000; (D) an adult aggregation of *Enchenopa binotata* (Membracini), Newark, DE, USA, 1997; (E) aposematic colouration of a teneral adult and nymph of *Platycotis vittata* (Hoplophorionini), La Maralla National Park, Honduras, 2001; (F) cryptic colouration of *Ochropepla* (Hoplophorionini) nymphs, females deposit white waxy secretion encircling the stem, Trinidad, Honduras, 2001; (G) waxy egg froth of *Membracis mexicana* (Membracini), Guatemala City, Guatemala, 1999; (H) a *Cladonota* (Hypsoprorini) male (top) courting a female (bottom), adults are solitary except during mating, San Jose de Rio Tinto, Honduras, 2001. Photographs by C.-P. Lin.

branches over time by a single female. (2) Aggregations of nymphs of the same species resulting from collective oviposition by several females on the same branches at different times. Because when development of over-wintering eggs depends on them being embedded within the plant tissue, in temperate species such as *Enchenopa binotata* egg hatching is synchronized with host-plant phenology and nymphs are uniform in age (Wood and Keese 1990). Nevertheless, nymphs from the spring generations of a temperate species, *Vanduzea arquata*, are synchronized in age whereas the age of summer generations is less uniform (R. B. Cocroft, personal observation for *Vanduzea arquata*) (3) Parent–offspring aggregations in which nymphs can be uniform in age structure depending on whether they are semelparous (deposit their entire reproductive complement in one clutch) or iteroparous (deposit their reproductive potential over a period of time into several egg masses). (4) Mixed-species adult and nymphal aggregations, which go beyond Eickwort's criteria but are nonetheless important to the evolution of ant mutualism in treehoppers.

Subsocial behaviour. Subsocial behaviour in treehoppers is mainly in the form of maternal care of eggs and nymphs (Figure 1A, B). Egg guarding is defined as a female remaining on top of her egg mass for a period of time after oviposition. The body of the female is used as a physical shield to protect eggs against predators or parasitoids. Most females display egg-guarding behaviour that includes body contact with egg masses (Beamer 1930; Wood 1974, 1976b). Females of most subsocial species guard eggs without leaving the egg masses. However, the duration and extent of egg guarding varies among species (Bristow 1983, 1984; Olmstead and Wood 1990; Stegmann and Linsenmair 2002a, 2002b). In some species the female extends the guarding behaviour until offspring reach the adult stage.

Female facilitation of nymphal feeding may involve modifing branches to make food resources accessible to nymphs (Wood 1974, 1976b). When early instars cannot penetrate the epidermis of host plant tissues with their stylets, the female makes a series of feeding slits around the stem with her ovipositor to create sites where they can feed. This may create a nutrient sink near the wounded area similar to that produced by other Hemipterans such as aphids (Way and Cammell 1970; Kidd 1977). Wounding leaf midribs between the petiole and the egg mass by female *Entylia* may trap nutrients within the leaf or prevent the influx of host-plant defense chemicals (Wood 1977b). Females of some subsocial species exhibit anti-predator behaviours including aggressive movements toward predators, leg kicking, wing fanning with audible buzzing, and rapid twisting motions of the body. Maternal anti-predator behaviours can be triggered by visual stimuli, alarm pheromones released from injured nymphs, or vibrational signals from gregarious nymphs (Nault et al. 1974; Wood 1976a, 1983; Cocroft 1996).

Cooperative care and brood mutualism

Cooperative brood care by females is common in subsocial hymenopterans and possibly in Blattodea, Passalidae (Coleoptera), and Thysanoptera (Choe and Crespi 1997). This type of maternal care is undocumented in treehoppers. However, it is not unusual to find two or more egg-guarding females in close proximity (2–3 cm) of each other on a stem or leaf midrib. There is no empirical evidence of fitness accrual to these females but there are several possibilities such as increasing group size of feeding nymphs to attract ants or creating a nutrient sink. Brood mutualism (egg dumping) occurs in the Neotropical *Polyglypta costata* (as *P. dispar*) (Eberhard 1986). Females guard eggs deposited by other females but insert their own eggs into the mass. Females may desert egg masses that are adopted by other females (Eberhard 1986). This behaviour may also occur in *Publilia* (Bristow 1983; Zink 2003a) and *Entylia* (Wood 1977b; Olmstead and Wood 1990). Egg dumping may be beneficial to both egg-dumping and -receiving females if it dilutes predation (Zink 2003b) and increases the probability of ant mutualism. In the absence of ants, egg-dumping females may minimize the cost of egg guarding and increase reproductive success by depositing additional dispersed clutches of eggs throughout the host plant (Eberhard 1986).

Ovipositional biology

Treehoppers may disperse eggs within and between host plants, or over their life span. This ovipositional behaviour was hypothesized to minimize the risks of predation and parasitism that might result from egg clumping (Funkhouser 1917; Dennis 1961; Simons 1962; Loye 1982, 1987). Females of many subsocial species (Aconophorini and Hoplophorionini) have semelparous reproduction and deposit over 100 eggs in a single clutch. Other subsocial (Polyglyptini) or gregarious (Membracini) species appear to be iteroparous, depositing eggs either into a single clutch or several masses over days or weeks. Another type of oviposition involves interaction with ants. Females of *Enchenopa binotata* are attracted to froth extracts that contain ovipositional stimulants and deposit eggs into branches that already have egg masses (Wood 1982a). The result is that multiple females lay eggs on the same branch with multiple clusters of egg masses. This ovipositional behaviour results in large nymphal aggregations, increasing the probability of ant mutualism (Wood 1982a).

Plant defensive responses (resins, latex, or secondary plant chemicals) to ovipositional wounds are potentially a strong mortality factor. Oviposition on plant surfaces by some treehoppers may allow a broader host range since eggs will not be subject to the plant's wound response (Wood 1993a). For eggs deposited on the plant surface, secretions from the female's accessory glands may serve as a protective barrier against desiccation, predators, parasitoids, or fungal infection. When eggs are inserted into plant tissue, additional secretions (egg froths) are used by treehoppers to cover ovipositional wounds in the plant and may increase the survival of eggs by impeding the plant's wound responses. The composition of accessory secretions is known only for the *Enchenopa binotata*. It contains mainly lipids and proteins, and was shown to enhance the survival of over-wintered eggs inserted into plant tissues (Wood 1968). Some treehoppers use accessory secretions to encircle the plant tissue around and below the egg mass. The function of these secretions is unknown but may provide protection against insect predators. However, ants bypass these secretions with ease (Haviland 1925).

Ant mutualism

Ants are dominant eusocial organisms in tropical lowland ecosystems (Hölldobler and Wilson 1990). In addition to extra-floral nectar, honeydew produced by Hemipterans and other insects provides an important nutrient resource for tropical ant communities. Although other Hymenopterans such as bees and wasps are associated with treehoppers, interactions with ants are the most pervasive (Figure 1C). In the Amazonian rainforest canopy, treehoppers are often tended by a single ant colony that is generally the most locally dominant ant (Bluthgen et al. 2000). In addition to protection, treehoppers gain a benefit from ant attendance by increased feeding rates resulting in a greater developmental rate, adult size, and survivorship (Morales 2000; Morales and Beal 2006). Nevertheless, ants sometimes turn aggressive and prey on nymphs (T. K. Wood, personal communication). A recent study shows that ant attendance also affected treehopper stoichiometry (Kay et al. 2004). Treehoppers (*Publilia modesta*) tended by ants (*Formica obscuripes*) contained lower nitrogen concentrations than those without ants (Kay et al. 2004).

Unlike insects such as some species of Lycaenid butterfly larvae that form obligate relationships with ants (Pierce et al. 2002), most treehopper–ant relationships appear to be facultative relative to ant species (Wood 1993a; Lin 2003). Nevertheless, further research on natural history, particularly of the tropical fauna, will be necessary to understand the degree (facultative or obligate) and relationships (range from mutualism to parasitism) of ant association in treehoppers.

Ant mutualism may be a source of selection in favour of gregarious habits in treehoppers (Wood 1977b, 1979, 1982b; McEvoy 1979; Fritz 1982; Kay et al. 2004). Aggregational size (Wood 1982a; Cushman and Whitham 1989) and distance from the ant colony (McEvoy 1979) influence the initial discovery by ants and the persistence of ant attendance. In North America, ants are attracted to larger *E. binotata* nymphal aggregations (Wood 1982a). In temperate *Publilia modesta* interacting with *Formica altipetens*, larger nymphal aggregations benefited from ant mutualism more than smaller ones (Cushman and Whitham 1989). Experiments showed that intraspecific competition for mutualistic ants varies temporally (between years) and that the resulting negative effects of competition (increase in predation and decrease in survival) are density-dependent (Cushman and Whitham 1991; Del-Claro and Oliveira 2000). Temporal variability among years was shown to be much more important than spatial variability among sites in generating conditionality in the mutualism between treehoppers, *Publilia modesta*, and ants, *Formica obscuripes* (Billick and Tonkel 2003).

Ant-constructed shelters

Ant-constructed shelters are an indication of how valuable hemipteran honeydew is to ants (Anderson and McShea 2001). In the tropical lowland forests, nymphs and adults of single or mixed treehopper species are often enclosed in soil–fibre shelters constructed by ants (Lamborn 1914; Wood 1984; McKamey 1992; Lin 2003). Temperate *Entylia* and *Publilia* are occasionally found in ant shelters on stems and leaves of herbaceous plants (T. K. Wood, personal communication for *E. bactriana* and *P. concava*). The size and shape of shelters varies but they usually contain holes for entry by ants. Ant shelters probably reduce movement of the treehoppers and presumably act as a protection from parasites and predators. However, the shelters may also be effective against competition with other ant colonies for honeydew (Way 1963). A given treehopper species can be found in and out of ant shelters, suggesting a facultative association of ant shelters. However, this hypothesis needs to be tested by further natural history studies.

Aposematic and cryptic colouration

Nymphs and teneral adults that form aggregations are sometimes conspicuous in colouration (Lin 2003), presumably providing aposematic displays to vertebrate predators (Figure 1B, E). In the Hoplophorionini, nymphs of *Ochropepla* and *Potnia* appear cryptic (Figure 1F for an *Ochropepla* nymphal aggregation), matching the colour of woody stems or flowers while those of *Alchisme*, *Metcalfiella*, *Platycotis*, *Ramosella*, *Stalotypa*, and *Umbonia* are aposematic (McKamey and Deitz 1991, 1996; Lin 2003). Teneral adults of *Metcalfiella*, *Platycotis*, *Ramosella*, *Stalotypa*, and *Umbonia* are aposematic but those of *Alchisme*, *Ochropepla*, and *Potnia* appear cryptic (McKamey and Deitz 1991, 1996; Lin 2003). Mature sclerotized adults in all these genera are cryptic. Nymphs in other subsocial taxa such as *Aconophora* (Dietrich and Deitz 1991), *Antianthe* (Hinton 1997; Lin 2003), *Gigantorhabdus* (Stegmann et al. 1998), *Hybandoides*, and *Pyrgauchenia* (Stegmann et al. 2002a, 2002b; Lin 2003) appear to be aposematic. This presumably aposematic colouration appears to be restricted to subsocial and aggregational taxa (Lin 2003). Many solitary treehoppers tend to be cryptic with colouration matching their hosts in both nymph and adult stage (Lin 2003).

Changes in colouration of the pronotum during different developmental stages also suggest the cryptic and aposematic functions (Wood 1993a). For example, *Platycotis vittata*, which is often found on oaks (*Quercus*), has presumably aposematic colouration of white with red longitudinal stripes as gregarious teneral adults (Wood 1975b, 1976b; Lin 2003). During this stage they are unpalatable to *Anolis* lizards (Wood 1975b, 1976b). The insects change colour to a cryptic brown and become palatable when they mature and are ready to disperse (Wood 1976b). After dispersal, the cryptic brown colouration may provide protection for solitary individuals during mating and maternal care against vertebrate predators such as birds or lizards (Wood 1975b, 1976b).

Behaviour and life history in Membracinae

There are nearly 3100 described species in the treehopper family Membracidae, which is classified into 12 subfamilies (McKamey 1998). The New World subfamily Membracinae has a mostly Neotropical distribution, with the highest generic and species diversity in the tropical regions of Central America and northern South America on the eastern slope of the Andes (Wood 1993a). The Membracinae consists of five tribes (Aconophorini, Hoplophorionini, Hypsoprorini, Membracini, and Talipedini), 38 genera, and 448 described species (Metcalf and Wade 1965; Deitz 1975; McKamey 1998). Behavioural and ecological characteristics are broadly concordant with presumed tribal relationships but variations exist among genera and species (Wood 1984, 1993a; Lin 2003). Below I review the data on the behaviour and life history among genera and species. Table I presents a brief overview of these characters.

Aconophorini

All Aconophorini for which life history data are available have maternal care where females guard eggs and remain with nymphal aggregations for varying periods of time (Hinton 1977; Wood 1978, 1984; Dietrich and Deitz 1991). In all three genera, eggs are deposited on the surface of stems or midribs of leaves and covered with accessory gland secretions (Wood 1984; Dietrich and Deitz 1991; Lin 2003) (Figure 1A). Maternal anti-predator behaviour has been observed in many species and involves leg kicking, wing buzzing and rapidly twisting body motions. Females and nymphs in *Calloconophora* have an alarm or escape behaviour in response to predators (Wood 1984). When disturbed, females fly off and nymphs disperse. Females of *Calloconophora caliginosa* have the ability to relocate their eggs and re-aggregate with nymphs within several hours, whereas females in *Aconophora* and *Guayaquila* are unable to relocate their offspring (Wood 1978, 1984). In addition to egg and nymphal guarding, females of some *Aconophora* deposit a sticky white secretion that encircles the stem below the egg masses (Dietrich and Deitz 1991). Females of some *Aconophora* prior to oviposition make a series of shallow longitudinal slits with their

Table I. Social behaviour and life history characteristics of the Membracinae

Tribe	Genus	No. of species	Social behaviour[a]	Ant mutualism[a]	Ovipositional site[a]	Ovipositional method[a]	Accessory secretion[a]	Reference
Aconophorini	*Aconophora*	13	Subsocial (8)	Yes (8)	Stem (2)/leaf petiole (1)/midrib of leaf (1)	Surface (4)	Waxy (4)	Hinton 1977; Wood 1984; Dietrich and Deitz 1991; Lin 2003
	Calloconophora	17	Subsocial (3)	No (3)	Stem (2)/leaf petiole (2)	Surface (3)	Waxy (3)	Haviland 1925; Wood 1978, 1984; Dietrich and Deitz 1991; Lin 2003
	Guayaquila	22	Subsocial (11)	Yes (11)	Stem (7)	Surface (7)	Waxy (7)	Marcus 1950; Hood 1952; Wood 1984; Letourneau and Choe 1987; Dietrich and Deitz 1991; Loye 1992; Lin 2003
Hoplophorionini	*Alchisme*	24	Subsocial (5)	No (5)	Woody stem (1)/ midrib of leaf (1)/ herbaceous plants (2)	Insertion (4)	Thin (3)	Wood 1984; McKamey and Deitz 1996; Lin 2003
	Metcalfiella	26	Subsocial (7)	No (7)	Young stem (1)/ woody stem (1)	Insertion (7)	Thin (2)	Wood 1984; McKamey and Deitz 1991, 1996; Lin 2003
	Ochropepla	4	Subsocial (3)	No (3)	Young stem (1)/ midrib of leaf (1)	Insertion (4)	Thin (2)	Wood 1984; McKamey and Deitz 1996; Lin 2003
	Platycotis	9	Subsocial (4)	No (4)	Woody stem (4)	Insertion (4)	Thin (3)	Wood 1976; Zak 1984; McKamey and Deitz 1996; Lin 2003
	Potnia	13	Subsocial (6)	No (6)	Woody stem (1)/ young stem (1)	Insertion (4)	Waxy (1)	Ballou 1936; Wood 1984; McKamey and Deitz 1996; Lin 2003
	Ramosella	2	Subsocial (1)	No (1)	Young stem (1)	Insertion (1)	Thin (1)	Dozier 1931; McKamey and Deitz 1996; Lin 2003
	Stalotypa	2	Subsocial (1)	No (1)	Woody stem (1)	Insertion (1)	Thin (1)	Lin 2003
	Stirpis	1	?	?	?	?	?	McKamey and Deitz 1996
	Turrialbia	1	?	?	?	?	?	McKamey and Deitz 1996
	Umbonia	13	Subsocial (5)	No (5)	Young (1)/woody stem (3)	Insertion (4)	Thin (4)	Butcher 1953; Ekkens 1972; Wood 1984; Masters 1989; Lin 2003
Hypsoprorini	*Cladonota*	46	Solitary adults (2)/ gregarious nymphs (2)	No (1)/ sporadic (1)	?	?	?	Wood 1984; Loye 1992; Lin 2003
	Hypsoprora	20	Solitary adults (1)/ gregarious adults (1)	No (2)	?	?	?	Wood 1984; Lin 2003; R. B. Cocroft, personal communication
	Hypsoprorachis	3	Solitary adults (1)	No (1)	?	?	?	Lin 2003
	Jibarita	1	?	?	?	?	?	
	Notocera	17	Solitary adults (1)/ gregarious nymphs (1)	Yes (2)	?	?	?	Wood 1984; Loye 1992; Lin 2003
	Philya	12	Solitary adults (2)/ gregarious adults and nymphs (1)	No (2)	?	?	?	Lin 2003; R. Dowell, personal communication
	Scalmophorus	2	?	?	?	?	?	

Table I. Continued.

Tribe	Genus	No. of species	Social behaviour[a]	Ant mutualism[a]	Ovipositional site[a]	Ovipositional method[a]	Accessory secretion[a]	Reference
Membracini	*Bolbonota*	19	Gregarious (10)	Yes (10)	Surface of a woody stem (4)/surface of plant tissue (3)	Surface (8)	Waxy (8)	Haviland 1925; Wood 1984; Loye 1992; Lin 2003
	Bolbonotodes	1	?	?	?	?	?	
	Campylenchia	5	Gregarious (3)	Yes (3)	Young stem (1)/ underside of leaf	Insertion (2)	Waxy (2)	Funkhouser 1917; da Costa Lima 1942; Kopp and Yonke 1973; Loye 1992; Wood 1984; Lin 2003
	Enchenopa	24	Gregarious (6)	Yes (6)	Young stem (4)/ apical meristem (1)	Insertion (6)	Waxy (6)	Wood 1984, 1993b; Lin 2003
	Enchophyllum	15	Gregarious (5)	Yes (2)/no (1)	Leaf (1)	Surface (1)	Waxy (1)	Wood 1984; Lin 2003; R. B. Cocroft, personal communication
	Erechtia	32	Subsocial (3)	Yes (3)	Flower inflorescence (1)/stem (2)	Insertion (3)	Waxy (3)	Haviland 1925; Wood 1984; Lin 2003
	Eunusa	1	Subsocial (1)	Yes (1)	Stem (1)/ant shelter (1)	Surface (1)	Waxy (1)	Wood 1984; McKamey 1992
	Folicarina	1	?	?	?	?	?	
	Havilandia	2	Subsocial (1)	Yes (1)	Young stem (1)	Insertion (1)	Waxy (1)	Haviland 1925
	Kronides	4	Gregarious (1)	?	Herbaceous stem (1)	Insertion (1)	Waxy (1)	Torres 1949
	Leioscyta	27	Subsocial (1)/ gregarious (1)	Yes (1)	Young stem (1)/ midrib of leaf (1)	Insertion (1)	Waxy (2)	Haviland 1925; Hinton 1977; Wood 1984; Strumpel 1986; Lin 2003
	Lewdeitzia	1	?	?	?	?	?	
	Membracis	48	Gregarious (12)	Yes (12)	Young stem (2)/ woody stem (2)/ surface of plant (1)/ midrib of leaf (1)	Insertion (1)/ surface (1)	Waxy (12)	Wood 1984; Miyazaki and Buzzi 1985; Lin 2003
	Paragara	2	?	?	?	?	?	
	Phyllotropis	6	?	?	?	?	?	
	Tritropidia	5	Subsocial (2)	Yes (2)	Stem (2)	Insertion (2)	Waxy (2)	Haviland 1925; T. K. Wood, personal communication
	Tylopelta	3	Gregarious (2)	Yes (2)	Herbaceous stem (2)	Insertion (2)	Waxy (2)	Wood 1984; Lin 2003; R. B. Cocroft, personal communication
Talipedini	*Trinarea*	3	Subsocial (1)	Yes (1)	?	?	?	McKamey and Deitz 1996

[a] Numbers in parentheses indicate the number of species exhibiting the life history characteristic; ?, unknown.

ovipositors to facilitate the adherence of egg masses to the plant surface (Dietrich and Deitz 1991). Nymphs of all Aconophorini exhibit presumably aposematic colouration of red or black stripes and white wax bands while adults are cryptic brown (Dietrich and Deitz 1991; Lin 2003). Ants and *Trigona* bees frequently visit *Aconophora* and *Guayaquila* (Wood 1984; Dietrich and Deitz 1991; Lin 2003). There are no reports of ant mutualism in *Calloconophora*, although nymphal aggregations are sometimes attended by *Parachartergus* wasps (Wood 1984; R. B. Cocroft, personal communication for *C. pinguis*).

Hoplophorionini

This tribe contains 10 genera, most of them occurring in montane and submontane forests at higher elevations and latitudes (McKamey and Deitz 1996). Eight of the 10 genera in the tribe are known to exhibit maternal care (Wood 1984; McKamey and Deitz 1996; Lin 2003) (Figure 1B); the other two genera are known only from museum specimens. Unlike the Aconophorini, eggs are deposited in one mass into stems or midribs of leaves and covered by a relatively thin layer of accessory secretion, which breaks down within a few days after oviposition. *Alchisme* and some *Ochropepla* insert their eggs into the veins of leaves (Wood 1984; McKamey and Deitz 1996; Lin 2003), while *Metcalfiella*, *Platycotis*, *Potnia*, *Ramosella*, *Stalotypa*, and *Umbonia* insert their eggs in woody tissue near the apical meristem of young shoots (Wood 1984; McKamey and Deitz 1996; Lin 2003). Aggressive behaviours of females (Wood 1974, 1975b, 1976a, 1976b) include wing fanning and kicking with the metathoracic legs when confronted by potential predators. In addition to alarm pheromones released by injured nymphs and visual stimuli (Wood 1976a), reciprocal plant-borne vibrational signals emitted by both aggregated nymphs of *Umbonia crassicornis* and their mothers provide defense against predators (Cocroft 1996, 1999a, 1999b). Females of *U. crassicornis* maintain offspring aggregations by tapping the dispersing nymphs on the back with their front tarsi (Wood 1983). They successfully defend the offspring against reduviids, syrphid larvae, and coccinellids by directed aggressive movements (Wood 1976a). Females of *U. crassicornis* and *U. spinosa* also defend offspring against wasps (*Pseudopolybia compressa*), which, in some localities, are their major predators (Cocroft 1996, 2002). Females of *Stalotypa fairmairii* were observed to stop wandering nymphs from leaving the aggregation with their front legs, as in *Umbonia* (Lin 2003).

Females of all genera with known biology except *Ochropepla* puncture their host's bark with their ovipositors adjacent to the egg mass where newly emerged nymphs feed (Wood 1974, 1976b, 1984; McKamey and Deitz 1996; Lin 2003). These feeding slits are usually arranged in a crossing diagonal pattern as in *Umbonia crassicornis* (Wood 1974), *Platycotis vittata* (Wood 1976b), and *Ramosella thalli* (Lin 2003). In contrast, in *Metcalfiella* (McKamey and Deitz 1996) and *Stalotypa fairmairii* (Lin 2003), the slits are arranged in a random pattern. Females of *Ochropepla pallens* have been observed to deposit a ring of secretion around the branch (Figure 1F) similar to that produced by some *Aconophora* (Wood 1984; Lin 2003). The Hoplophorionini have never been found interacting with ants or other hymenopterans (but see a doubtful report by Loye (1992) for *Potnia gladiator* and *P. brevicornis* (as *P. granadensis*)) (McKamey and Deitz 1996). This report cannot be confirmed by extensive observations of these species in Panama (R. B. Cocroft, personal communication for *P. brevicornis*; T. K. Wood, personal communication for *P. gladiator*). Within the Hoplophorionini, nymphs of *Ochropepla* and *Potnia* appear cryptic (Figure 1F; Lin 2003), matching the colour of woody stems or flowers while those of *Alchisme*, *Metcalfiella*, *Platycotis*, *Ramosella*, *Stalotypa*, and *Umbonia* are aposematic (Lin 2003)

(Figure 1B). Teneral adults of *Metcalfiella*, *Platycotis*, *Ramosella*, *Stalotypa*, and *Umbonia* are aposematic (Figure 1E) but those of *Alchisme*, *Ochropepla*, and *Potnia* appear cryptic (Lin 2003). Mature sclerotized adults in all these genera are cryptic (Wood 1984; McKamey and Deitz 1996; Lin 2003).

Hypsoprorini

There are seven genera recognized in the Hypsoprorini. This poorly studied tribe includes a mixture of life histories (Wood 1984; Lin 2003). Adults of *Philya* are usually found as solitary individuals (Wood 1984; Lin 2003). Adults and nymphs of *Philya* sp. were collected on shrubs from dry habitat of tropical highlands in Ecuador without ant attendance (Lin 2003), but were found on a single stem of the host plant. *Philya* sp. forms adult and nymphal aggregations of 3–10 or more on *Baccharis* (Asteraceae) in California but the presence of maternal care and ant attendance is uncertain (R. Dowell, personal communication for *Philya* sp.). *Notocera* forms ant-tended nymphal aggregations but adults are solitary (Wood 1984; Lin 2003). *Hypsoprora* occurs in small mixed-species ant-tended adult aggregations (Lin 2003) or as solitary adults (R. B. Cocroft, personal communication. for *Hypsoprora* sp.). Presumed nymphs of *Hypsoprora* are solitary or in ant-tended aggregations of one or two individuals (Lin 2003). Nymphs of *Cladonota* occur in ant-tended aggregations of three to four individuals (Wood 1984) or as solitary individuals (R. B. Cocroft, personal communication for *Cladonota* sp.) and are solitary as adults. Nymphs of Hypsoprorini are cryptic, as are adults (Lin 2003), which resemble the tendrils of vines (some *Cladonota*, Figure 1H) or are covered with stripes or blocks of wax (some *Cladonota*, *Hypsoprora*, and *Notocera*). Oviposition behaviour is unknown for any Hypsoprorini. No natural history information is available for the remaining three genera, *Hypsoprorachis*, *Jibarita*, and *Scalmophorus*.

Membracini

This is the most diverse tribe within the subfamily, containing 17 genera with a mixture of subsocial and gregarious species. Observations by Haviland (1925) and Hinton (1977) suggest that *Bolbonota*, *Campylenchia*, *Enchenopa*, and *Membracis* exhibit maternal care, but these observations were probably made while females were ovipositing and have not been confirmed by subsequent observations (Wood 1984; Lin 2003).

Gregarious genera. *Bolbonota* are among the most frequently encountered treehoppers in the Neotropical lowland wet forests. There are 19 named species, but with a few exceptions most are not easily distinguished morphologically. However, their small size and the black oval shape of the pronotum, resembling caterpillar faeces, make them distinct from the rest of the tribe. Females of *B. inconspicua* cover egg clusters with a sticky white secretion, as do females of *B. pictipennis*; the former deposit eggs on the surface of inflorescences, while the latter deposit eggs on the surface of woody stems (Wood 1984). Nymphs of *Bolbonota* are covered with white wax. Both nymphs and adults form aggregations and are tended by ants (Lin 2003). Haviland (1925) described females of *B. aspidistrae* sitting on eggs until they hatched but this observation requires further confirmation. *Bolbonotodes* is a monotypic genus occurring in Mexico; adults resemble seeds (Poulton 1903).

The temperate *Campylenchia latipes* overwinters as eggs deposited near the base (sometimes in dead stems) of herbaceous host plants such as *Solidago* (T. K. Wood, personal communication for *C. latipes*), although Funkhouser (1917) suggested they overwinter as adults in Central New York. Nymphs of *C. latipes* are ant-tended in the spring (Funkhouser 1917; Kopp and Yonke 1973). Females of a tropical species, *C. hastata*, insert their eggs in multiple clusters into twigs and cover them with wax-like secretions (Wood 1984). Nymphs of *C. hastata* form aggregations, and both nymphs and adults are tended by ants (R. B. Cocroft, personal communication for *C. hastata*). da Costa Lima (1942) observed a *Campylenchia* from Brazil inserting eggs into the stem of a plant and covering them with a waxy secretion. Strands of the secretion were laid down in a V-shape pattern similar to that of some North American *Enchenopa* species. Unlike other Membracini, nymphs of *Campylenchia* are not covered with white wax secretion but rather are cryptic green or brown (Lin 2003). Mature adults are, in general, cryptic, ranging from light to dark brown or black.

The genus *Enchenopa* is a large group with many species. Females of *Enchenopa ferruginea* deposit clusters of eggs into the young meristematic plant tissue (Wood 1984). Ant-tended nymph and adult aggregations occur in *E. binotata*, *E. gladius*, and *E. ignidorsum* (Wood 1984). In *E. gladius*, aggregations are found on the apical meristems of *Cecropia*. Aggregations of *E. ignidorsum* are found on the underside of leaves or on flower inflorescences of *Cassia*. The North American *E. binotata* complex (Figure 1D) comprises nine cryptic species associated with eight plant genera distributed among six plant families (Wood 1993b). Detailed life histories are known for seven of the nine extant species except those from *Juglans cinerea* and *Carya*. All of these univoltine species overwinter as eggs inserted into plant tissue and covered with white wax secretions. Nymphs are usually found in ant-tended aggregations because females commonly deposit eggs in multiple clusters on the same branch (Wood 1982a). Although reported by Hinton (1977), no egg-guarding behaviour is found in this complex.

Enchophyllum dubium and *E. melaleucum* form ant-tended nymphal and adult aggregations on *Acalypha diversifolia* (Wood 1984; R. B. Cocroft, personal communication for *E. melaleucum*) while other *Enchophyllum* in the highlands of Panama are not tended by ants (Lin 2003). Eggs of *E. melaleucum* were deposited on the surface of the leaf and covered with a shiny, translucent white secretion similar to that of *Enchenopa binotata* on *Cercis canadensis* (R. B. Cocroft, personal communication for *E. melaleucum*). *Kronides* is a southern South American genus occurring in Argentina, Brazil, Paraguay, and Uruguay. *Kronides incumbens* feeds on the herbaceous plant *Eryngium eburneum* (Apiaceae) in the lowlands of Argentina (Torres 1949). Females of this species deposit multiple clusters of egg masses inserted into plant stems and covered with waxy secretion arranged in a shape similar to some *Campylenchia* and *Enchenopa* (inferred from drawings; Torres 1949). *Leioscyta* is a widespread genus with a reduced pronotal shape. They are small (~0.4 cm) and commonly found on herbaceous plants in lowland forests. *Leioscyta nitida* forms nymphal and adult aggregations on the underside of leaves (Wood 1984). Eggs of *L. spiralis* are embedded in a brown waxy secretion with white spiral secretions encircling the twig (Haviland 1925; Hinton 1977). Nymphs of *L. spiralis* are covered with white waxy secretion (Strumpel 1986).

Membracis is one of the most extraordinary treehoppers with an enlarged, laterally flattened pronotum (Figure 1G). The shape of the pronotum in *Membracis* may mimic the Neotropical leaf-cutting ants (*Atta*) which carry leaves held above their body (Lin 2003). Nymphs of *Cymbomorpha* (Darninae) have a similar appearance (Poulton 1903; Lin 2003). *Membracis* can form large nymphal and adult aggregations of up to hundreds of individuals on one small herbaceous plant (Lin 2003). Like other Membracini, nymphs are usually covered with white wax secretions and some have thin red or black stripes (Lin 2003). Both

M. fuscata and *M. mexicana* form ant-tended nymphal and adult aggregations (Wood 1984; Lin 2003). Females of *M. mexicana* deposit eggs into young shoots of *Coffea* and *Calliandra* and later cover them with white waxy froth (Wood 1984; Lin 2003). Females of *M. dorsata* lay eggs, along with accessory secretions, on the surface of plants (Miyazaki and Buzzi 1985). Nymphs of *M. dorsata* in Panama form aggregations but they are occasionally ant-tended (R. B. Cocroft, personal communication for *M. dorsata*). Females of *Tylopelta gibbera* (as *T. americana*) deposit wax over eggs inserted into stems of herbaceous plants and nymphs are ant-tended (Wood 1984). Females of this species oviposit communally in Panama, but singly in Missouri, USA (R. B. Cocroft, personal communication for *T. gibbera*).

Subsocial genera. Females of *Erechtia* guard eggs but do not make ovipositional slits to facilitate nymphal feeding. *Erechtia sallaei* in Costa Rica insert their eggs into the stem leading to the flower, which develops a cup-shaped structure on its surface as a result of expansion of the developing eggs (Wood 1984). Females sit on eggs, and may remain or fly off when disturbed; females that are removed from eggs do not return (Wood 1984). Females with nymphs react to disturbance with wing fanning and aggressive body movements; however, Wood (1984) observed that these behaviours did not occur when attending wasps or ants were present. *Erechtia abbreviata* (as *Tropidocyta bulbosa*) from Guyana deposit eggs into the stem of plants, which then form a cup-shaped structure like those of *E. sallaei* (Haviland 1925).

Unlike *Erechtia*, the degree of maternal care in *Eunusa*, *Havilandia*, and *Tritropidia* is unknown. The eggs of *Eunusa concolor* from Guyana and south-east Venezuela are deposited on the ceilings of ant shelters or on the surface of plant stems covered by frothy secretion similar to other Membracini (McKamey 1992). *Eunusa concolor* (as *Trachytalis isabellina*) from Panama are also found in shelters constructed by ants (Wood 1984). Adults and nymphs of *E. concolor* are found together in the shelters made by *Azteca* ants on *Vismia* (McKamey 1992). Nymphs are covered with a white waxy secretion. *Eunusa concolor* females sit on top of egg masses, but the extent of maternal care is not clear. *Havilandia pruinosa* (as *Tropidoscyta pruinosa*) females sit on top of eggs, and produce white spiral secretions on twigs and leaves in the vicinity of the egg mass (Haviland 1925). Eggs are inserted into stems, covered with wax secretions. The nymphs are covered with white waxy secretions. *Tritropidia bifenestrata* (as *Enchenopa bifenestrata*) females insert eggs into plant tissue, deposit a brown scale-like secretion over the egg mass, and sit on top of the eggs after oviposition is completed (Haviland 1925). *Tritropidia* sp. females from Brazil sit on top of egg masses, often in mixed-species and ant-tended aggregations (T. K. Wood, personal communication). Within the Membracini, life histories of remaining genera, *Folicarina*, *Lewdeitzia*, *Paragara*, and *Phyllotropis* are unknown.

Talipedini

This tribe contains only one genus, *Trinarea*, which was elevated to tribal rank (Deitz 1975) and has maternal care similar to that of the Hoplophorionini (McKamey 1996).

Conclusions

For group-living insects such as membracine treehoppers, the life history traits (social behaviour, ant mutualism, ovipositional biology, and aposematic colouration) represent interesting adaptations for their success in tropical environments. Among these traits, maternal care and ovipositional methods (surface versus insertion oviposition) appear to be most consistent within genera and tribes, whereas gregariousness and ant mutualism vary most at the generic level, and in some cases even within a species depending on the life stages (nymphs versus adults), locality, and elevations. Maternal care occurs in at least four of the five tribes. The Aconophorini and Hoplophorionini are uniformly subsocial which suggests that the evolution of maternal care is more or less phylogenetically constrained within these two lineages. On the other hand, the Membracini is a mixture of subsocial and gregarious species, indicating that among these treehoppers this trait is much more labile (phylogenetically conservative). Maternal facilitation of nymphal feeding is restricted to the tribe Hoplophorionini which suggests that this trait is likely to be a unique adaptation for the lineage (absent in all other treehoppers known so far). This behaviour may be historically associated with the evolution of maternal care without ant attendance in this group.

Many insects use warning colouration to signal their unpalatability to potential predators (Cott 1940; Guilford 1990). Similar to other gregarious insects such as Lepidoptera (Rettenmeyer 1970; Edmunds 1974), nymphs of gregarious treehoppers often exhibit aposematic colouration. Within membracine treehoppers, aposematic colouration of nymphs and teneral adults appears to be restricted to gregarious and subsocial species in Aconophorini and Hoplophorionini. Neverthless, there are gregarious nymphs showing cryptic colouration such as those of *Alchisme*, *Ochropepla*, and *Potnia*. There is evidence suggesting that the aposematic nymphs of membracine treehoppers are unpalatable to vertebrate predators (Wood 1977a). Thus, the aposematic treehopper nymph is presumed to serve as a warning colouration that signals such unpalatability. However, the evolutionary history of nymphal aposematism in membracids, and whether it was historically associated with nymphal gregariousness or other ecological factors, are unknown. Two hypotheses have been proposed to account for the correlated evolution between aposematism and gregariousness of insects in general. Cott (1940) proposed that gregariousness evolved to enhance the effect of aposematism, which presumes that gregariousness evolves after the aposematism. Fisher (1930) proposed the kin selection hypothesis that aposematism evolved in a group of closely related individuals, which predicts that gregariousness precedes the evolution of aposematism. Therefore, if nymphal aposematism and gregariousness were evolutionarily associated in membracine treehoppers, it would be important to establish the temporal sequences of these two traits in their evolutionary histories to distinguish between these two hypotheses.

The life history characteristics reviewed in this study provide a basis for recent comparative analyses of maternal care evolution and its correlation with life history traits in membracine treehoppers (Lin 2003; Lin et al. 2004). Given the widespread occurrence of maternal care within the subfamily, this trait is estimated to have fewer than three origins and fewer than two losses (Lin et al. 2004). The results show that there is a strong phylogenetic component to the evolution of maternal care, and that the evolution of social behaviour in treehoppers may not be as evolutionarily labile as previously thought (reviewed in Tallamy and Schaefer 1997). These results confirm the notion that maternal care arose independently multiple times throughout insects and that it rarely reverses to no maternal care (Wilson 1971; Eickwort 1981; Tallamy and Wood 1986).

Current views of how ecology influences the evolution of insect sociality emphasize the importance of ecological factors such as predation and food resources (Wilson 1971; Alexander 1974; Eickwort 1981; see Choe and Crespi 1997 for a phylogenetic perspective).

The comparative phylogenetic analysis of membracine treehoppers and their life history traits suggests that interspecific interactions such as ant mutualisms can also favour an increase in social complexity (i.e. solitary, gregariousness, and maternal care) (Lin 2003). The study provides the first quantitative evidence of correlated evolution of maternal care and ant mutualism in treehoppers. The results also indicate that the origin of maternal care without ant attendance (such as species in the Hoplophorionini) may represent an evolutionary end-point (Lin 2003). However, to what extent the origins and evolutionary transitions of these life history traits are related to each other, and how important the ecological factors such as predation and host plants (food resources) as selection forces in the historical development of these traits in treehoppers are as a whole, require further comparative research with additional taxa and a more complete picture of trait distribution among treehoppers.

Despite the recent progress of morphological and molecular analyses of treehopper phylogenies and biogeographies (Cryan et al. 2000, 2004; Dietrich et al. 2001; Lin and Wood 2002; Lin 2003; Lin et al. 2004; Wallace and Deitz 2004, 2006), our knowledge of the ecology and evolution of life history traits in treehoppers is still limited due to inadequate research of basic biology for most taxa. Further detailed and long-term research of the natural history (similar to that of Stegmann and Linsenmair 2002b), particularly for the understudied tropical fauna, will be necessary to better understand the evolution of life history in treehoppers.

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