Subsocial and aggregating behaviour in Southeast Asian treehoppers (Homoptera: Membracidae: Centrotinae)

ULRICH EKKEHARD STEGMANN and KARL EDUARD LINSENMAIR*

University of Würzburg, Biozentrum, Zoologie III, Am Hubland, 97074 Würzburg, Germany

Abstract: Maternal care within the treehopper subfamily Centrotinae has been considered a rare trait. We present observations on maternal care and nymphal behaviour made in 16 rain forest plots in Peninsular Malaysia and Sabah, Borneo, from 1996 to 1998. Females of 11 Centrotinae morphospecies from the tribes Centrocharesini (*Centrochares* Stål), Gargarini (*Ebhul* Distant), and Hypsaucheniini (*Gigantorhabdus* Schmidt, *Hybandoides* Distant, *Pyrgauchenia* Breddin, *Pyrgonota* Stål) produced egg clutches and guarded them. Maternal care was restricted to egg-guarding in all species. *Pyrgonota ?bulbosa* Buckton eggs hatched successively over a couple of days and females deserted their clutches when most, but not all, 1st instar nymphs had hatched. Nymphs of egg-guarding species lived gregariously and/or by subaggregating, as did some non-guarding species. *Leptobelus dama* Germar, *Gargara semibrunnea* Funkhouser, and two *Tricentrus* Stål spp. were solitary as nymphs and adults.

INTRODUCTION

Two forms of social behaviour occur in many species of New World treehoppers: subsociality and/or gregariousness (reviewed in Wood, 1993). Subsociality is taken, here, to involve postovipositional parental care improving offspring fitness (Tallamy & Wood, 1986), and gregariousness implies group living due to mutual attraction rather than mating or clumped resources (Eickwort, 1981). Gregariousness in New World treehoppers is not restricted to subsocial species and group sizes may range from 5 to more than a hundred individuals (Wood, 1993). In some species group-living secures attraction of tending ants that decrease nymphal mortality (Wood, 1982), in others it may be a prerequisite for maternal care. In *Umbonia crassicornis* Amyot and Serville, only groups of nymphs produce vibrational signals in such a fashion as to elicit their mother's defense behaviour (Cocroft, 1996, 1999a, 1999b). In terms of subsociality, maternal investment in nymphs ranges from (i) egg-guarding until hatching (Bristow, 1983) to (ii) care for nymphs until eclosion, including defense of, facilitating feeding for, and maintaining nymphal aggregations (Wood, 1993; Cocroft, 1996, 1999a, 1999b). Egg-guarding reduces egg mortality in New World membracid species with extended maternal care (Wood, 1976a, 1976b, 1977, 1984; Eberhard, 1986).

This paper deals with the puzzling taxonomic distribution of maternal care within the Membracoidea. Mapping maternal care on the available cladograms of the superfamily Membracoidea (Fig 31, Dietrich & Deitz, 1993; Fig. 10, Dietrich et al., 2001) shows its presence (i) in the Centrotinae (a subfamily occurring predominantly in the Old World, its revision pending; McKamey, 1998;

Dietrich et al., 2001), (ii) in New World membracid subfamilies that are both more derived (e.g., Membracinae) and less-derived (e.g., Endoiastinae, Wood, 1984) than the Centrotinae, and (iii) in the sister clade of the Membracidae, the Aetalionidae (Deitz & Dietrich, 1993; Wood, 1993). Although nearly half of the estimated 3100 species of Membracidae belong to the subfamily Centrotinae (Strümpel, 1983; Dietrich et al., 2001), maternal care in this taxon has been regarded as a rare behaviour, because it is known from only eight Centrotinae species (Ushijima & Nagai, 1979; Singh & Sharma, 1980; Kitching, 1987; Ananthasubramanian, 1996; Stegmann et al., 1998). A report from two other Centrotinae species (Hinton, 1977) is contentious (Lamborn, 1914; Kitching, 1974). Given that maternal care is common in both some more and some less-derived New World subfamilies, and is present in the outgroup, why is subsociality nearly absent in the Centrotinae (distributed across a wide range of habitats)?

Considering that even fundamental biological features of most African, East Asian, and Australian treehoppers are entirely unknown (some Indian and European genera are exceptions, e.g. Ananthasubramanian & Ananthakrishnan, 1975b; Ananthasubramanian, 1996 and Müller, 1984, respectively), the answer to the puzzle may simply be rarity of life-history studies in Old World treehoppers. Therefore, we conducted an extensive search for subsocial and aggregating treehoppers in one of the earth's biodiversity hotspots (Mayers et al., 2000): Sundaland, which comprises Peninsular Malaysia and the band of islands stretching from Sumatra to Borneo. Detailed field observations of selected species added to this search.

* Corresponding author. Biozentrum, Zoologie III, Am Hubland, 97074 Würzburg, Germany; e-mail: ke_lins@biozentrum.uni-wuerzburg.de

MATERIALS AND METHODS

Field sampling and identification

Vegetation in 16 primary and secondary rain forests (Table 1) was examined by visual inspection at ground level during four stays (March to May 1996, January 1997, November 1997 to April 1998, and October to December 1998). Teneral adults were recognized by their soft pronota and/or accompanying last instar nymphs within the same aggregation.

Behavioural classifications were:

(1) egg-guarding: non-ovipositing females found on eggs for at least 5 consecutive days;

(2) aggregating: individuals found, at least before disturbance, in one group usually sitting in body contact with their conspecifics;

(3) subaggregating: individuals found in more than one group (if not obviously due to preceding disturbance); or

(4) solitary: individuals found not adjacent to conspecifics, e.g., not more than one per internode.

Membracid voucher specimens were deposited at the Natural History Museum London (Nr. 2000–86). Keys (Goding, 1931; Funkhouser, 1951) and the NHM-collection were used for species identifications. The tribal classification follows McKamey (1998) and Dietrich et al. (2001). *Pyrgauchenia biuni, P. pendleburyi* and *P. tristaniopsis* are new species described elsewhere (Stegmann et al., in press). Ant morphospecies were determined by Carsten Brühl (CB) and deposited in the entomological collection of the University of Würzburg.

Reproductive biology of selected species

To estimate time of egg development in *Ebhul* near *notatum* Funkhouser sp. 2, *Centrochares ?horrifica* Westwood, and *Hybandoides ?horizontalis* Distant host plants were checked at varying intervals. The time of egg development was estimated as the number of days between first sighting of an egg clutch (same twig not checked previously) and first sighting of 1st instar nymphs or last control. Thus, for each egg clutch of a given species, one minimal and one maximal number of days was obtained. As best available approximations, the largest

minimal time and the shortest maximal development time found for one species are presented (Table 3).

To investigate egg-guarding, egg development, egg hatching, and nymphal development in *Pyrgonota ?bulbosa* Buckton, every fourth day (= measurement error) the number of nymphs was counted (per stage and cohort) and the presence or absence of the guarding female was recorded. Egg-guarding was defined as lasting from start of oviposition and onset of egg hatch, respectively, to last sighting of the female on eggs (Table 4). The number of 1st instar nymphs per cohort documented the hatching process (Table 4, Fig. 1). The time of egg development was estimated as the number of days between first sighting of an egg clutch (same twig found without clutch four days earlier) and the first sighting of 1st instar nymphs (Table 5). Time of nymphal development was estimated per cohort as the number of days between first sighting of nymphs of a given stage and first sighting of nymphs of the next stage in each case (Table 5).

RESULTS

Subsociality

Females of 11 morphospecies from the tribes Centrocharesini, Gargarini, and Hypsaucheniini produced egg clutches and guarded them (Table 2). Females straddled their egg clutches and were not found to leave egg clutches before egg hatch. Therefore, time of egg development indicated time of egg-guarding and was investigated where feasible. Egg-guarding between one and four weeks depending on species was inferred in this fashion (Table 3). Note that egg-guarding in species observed for only one day was unlikely to be mistaken for a pause during continued oviposition, because female straddling behaviour in those species did not differ from that of species under repeated observation (Table 2). Also, not a single female was found ovipositing.

A field study revealed details of maternal care in *Pyrgonota ?bulbosa*. Egg-guarding in this species lasted 36–40 days following oviposition (Table 4). After onset

TABLE 1. Study locations and their elevations (E) in West-Malaysia (WM) and Sabah from 1996-98. Site specific searching efforts are given to explain why some species (being infrequent, restricted in distribution etc.) might be missing in Table 2. Here, searching time is narrowly defined as the time actually spent examining vegetation previously not checked (T), i.e. excluding repeated observations of the same plant specimen, on-the-spot observations for > 5 min, and transportation time.

Location	E (m a.s.l.)	T (hrs.)
Ulu Gombak Field Studies Centre, Selangor (WM); 3°17'N, 101°44'E	250–400	14
Genting Highlands, Selangor/Pahang (WM); 3°22'N, 101°44'E	600–1700	10
Cameron Highlands, Perak/Pahang (WM); 4°30'N, 101°23'E	1500–2000	10
Pasoh Forest Reserve, Negeri Sembilan (WM); 2°55'N, 102°18'E	200	12
Sepilok Forest Reserve, Sabah; 5°53'N, 117°57'E	250	26
Labuk Road Forest Reserve, Sabah; 5°53'N, 117°54'E	300	2
Sukau, Kinabatangan River, Sabah; 5°31'N, 118°16'E	120	12
Gomantong Caves, Sabah; 5°32'N, 118°10'E	150	4
Keningau, Sabah; 5°17'N, 116°12'E	750	1
Deramakot, Telupid, Sabah; 5°30'N, 117°30'E	300	1
Tambunan, Sabah; 5°42'N, 116°22'E	950	3
Rafflesia Forest Reserve, Sabah; 5°43'N, 116°20'E	1300	3
Pulau Gaya, Sabah; 5°59'N, 116°1'E	50	2
Poring Hot Springs, Kinabalu National Park, Sabah; 6°3'N, 116°41'E	450–1100	40
Sayap, Kinabalu National Park, Sabah; 6°10'N, 116°35'E	1000	3
Headquarters, Kinabalu National Park, Sabah; 6°0'N, 116°33'E	1150–3500	70

TABLE 2. Subsocial and aggregating behaviour in Malaysian Centrotinae. Egg-guarding was present (Y) or not found (N). Nymphs aggregated (A), subaggregated (B) or were solitary (S). Sample sizes ranged from N ≥ 5 (= 5–9), N ≥ 10 (= 10–19), N ≥ 20 (= 20–49), N ≥ 50 (= 50–99), to N ≥ 100. Sample sizes do not necessarily reflect densities but, rather, searching effort. Guarding females observed on one day only are indicated by an asterisk (Y*). *Pyrgauchenia* spp. nov. are described in Stegmann et al. (in press). Note that *Tricentrus* Stål is a junior synonym of *Centrotoscelus* Funkhouser (McKamey 1998); however, eight morphospecies were closer to *Centrotoscelus* Funkhouser spp. than to *Tricentrus* Stål and are, therefore, indexed by a C (*Tricentrus* Stål spp[C]); subaggregating nymphs only occurred in the latter.

Tribe	Morphospecies	Care	Nymphs	N (females)	N (nymphs)
Centrocharesini	*Centrochares ?horrifica* Westfood	Y	A	≥ 10	≥ 20
Centrotypini	*Centrotypus* Stål sp. *2*	N	?	≥ 5	-
	Centrotypus Stål sp. *3*	N	?	≥ 10	-
Gargarini	*Ebhul* near *notatum* Funkhouser sp. *2*	Y	A	≥ 5	≥ 50
	Ebhul ?varium Walker	N	A	≥ 10	≥ 20
	Gargara Amyot & Serville sp. *3*	N	?	≥ 5	-
	Gargara Amyot & Serville sp. *7*	N	?	≥ 5	-
	Gargara near *citrea* Distant	N	?	≥ 5	-
	Gargara semibrunnea Funkhouser	?	S	-	≥ 10
Hypsaucheniini	*Gigantorhabdus enderleini* Schmidt	Y	A, B	≥ 50	≥ 100
	Hybandoides ?horizontalis Distant	Y	A, B	≥ 20	≥ 100
	Pyrgauchenia Breddin sp.	Y*	?	1	-
	Pyrgauchenia biuni sp. nov.	Y*	A, B	≥ 10	≥ 20
	Pyrgauchenia ?brevinota Funkhouser	Y*	A, B	≥ 10	≥ 10
	Pyrgauchenia colorata Distant	Y*	A, B	≥ 10	≥ 10
	Pyrgauchenia pendleburyi sp. nov.	Y	A, B	≥ 20	≥ 100
	Pyrgauchenia tristaniopsis sp. nov.	Y	A, B	≥ 100	≥ 100
	Pyrgonota ?bulbosa Buckton	Y	A, B	≥ 20	≥ 100
Leptocentrini	*Leptocentrus ?jacobsoni* Funkhouser sp. *4*	N	B	≥ 10	≥ 5
	Telingana Distant sp. *2*	N	?	≥ 5	-
	Telingana Distant sp. *3*	N	?	≥ 10	-
	Telingana Distant sp. *4*	N	?	≥ 5	-
Micreunini	*Leptobelus dama* Germar	N	S	≥ 5	≥ 5
Tricentrini	*Sipylus dilatatus* Walker	N	?	≥ 10	-
	Tricentrus nigrofrontis Funkhouser	N	B	≥ 10	≥ 20
	Tricentrus Stål sp. *2*[C]	N	?	≥ 5	-
	Tricentrus Stål sp. *5*[C]	N	B	≥ 5	≥ 100
	Tricentrus Stål sp. *6*[C]	N	?	≥ 5	-
	Tricentrus Stål sp. *7*[C]	?	B	-	≥ 10
	Tricentrus Stål sp. *8*[C]	N	?	≥ 5	-
	Tricentrus Stål sp. *9*[C]	N	B	≥ 10	≥ 100
	Tricentrus Stål sp. *11*[C]	?	B	-	≥ 50
	Tricentrus Stål sp. *20*[C]	N	?	≥ 5	-
	Tricentrus Stål sp. *13*	N	S	≥ 10	≥ 5
	Tricentrus Stål sp. *17*	?	S	-	≥ 5
Centrotinae, INCERTAE SEDIS	*Dingkana* Goding sp. *1*	N	?	≥ 5	-

of egg hatch, females remained for 7–11 days on the clutch, while 1st instar nymphs started gathering 1–10 centimeters from the clutch. The presence of this post-hatch egg-guarding behaviour was confirmed by independent estimates of egg development which took 26–31 days (Table 5), as compared with 36–40 days of egg-guarding. In an attempt to explain this behaviour, the process of 1st instar hatching was quantified and nymphal development time was estimated. 1st instar nymphs hatched asynchronously from a given clutch (Fig. 1) with the maximum number of 1st instars per cohort counted 9–10 days after hatching had started (Table 4). Some eggs

TABLE 3. Egg development of three Centrotinae treehoppers and the number of ant morphospecies tending their nymphal aggregations (field observations on *Piper aduncum* L., Piperaceae, at Ulu Gombak, see Table 1; *P. aduncum* is a South American species introduced to Malaysia, see Carrick, 1968). Egg development times are approximations (see Methods); the estimate from a laboratory culture of *Centrochares ?horrifica* (*) is based on daily controls (reared on *P. aduncum* at 28° C).

	Ebhul near *notatum* sp. 2	*Centrochares ?horrifica*	*Hybandoides ?horizontalis*
Egg development [days] (Min.–Max., *N*)	4–19, *3*	11–18, *7* *(Med = 9, N = 3)	28–27 (sic), *10*
Ant morphospecies	*Dolichoderus* Lund CB-2, and 3	*Camponotus* Mayr CB-1, and 3	*Camponotus* Mayr CB-1, 2, and 3
		Crematogaster Lund CB-6	*Plagiolepis* Mayr CB-1
		Oecophylla smaragdina Fabricius	*Technomyrmex* Mayr CB-2
			Polyrhachis Swainson & Schuchardt CB-3

TABLE 4. Egg-guarding (days) and egg hatching in *Pyrgonota ?bulbosa* (field observations on *Tristaniopsis clementis* (Merr.) Wilson & Waterhouse, Myrtaceae, at Kinabalu Headquarters, see Table 1). Note that egg-guarding since onset of egg hatch and time from onset of egg hatch to maximum number of 1st instar nymphs counted per cohort (Days to 1st instar Max) lasted a similar number of days. Values are given as intervals to account for measurement errors (see Methods).

	Egg-guarding (since oviposition)	Egg-guarding (since hatching)	Days to 1st instar Max
Median (days)	35.5–39.5	7–11	9–10
Minimum	31–35	1–5	4–6
Maximum	43–47	13–17	13–15
N (cohorts)	4	4	6

still hatched later as determined by direct examination of clutches. 1st instar numbers began to decline ten to twelve days after onset of egg hatch (Fig. 1). This was probably due to moulting, since 1st instars took 7–11 days to develop (Table 5). Thus, the time when females deserted their clutches (7–11 days after onset of egg hatch) coincided with the maximum number of 1st instars present

(9–10) and with the moult of 1st instars that had hatched first (7–11).

In all species, maternal care was restricted to egg-guarding. In no species were females found to stay with, to defend or to interact with nymphs (or predators). Rarely was a female found off its hatched clutch while still on the same twig with its nymphs. In these rare instances, the female flew or walked off when lightly touched with a pen.

Aggregating behaviour

Nymphs of all egg-guarding species lived in aggregations, whereas *Ebhul ?varium* Walker was the only non-guarding species to live gregariously as nymphs (Table 2). Gregariousness in these species was common to all nymphal stages and to most teneral adults, but was never found in mature adults. Altough more than one mature adult on one twig was found regularly in *Dingkana* Goding sp. 1 (males and non-guarding females on aerial roots of the undetermined host plant), these "groups" were not regarded as aggregations, because adults varied greatly in individual distances from each other (but were at least their body width or length apart). "Groups" of egg-guarding mature females of Hypsaucheniini-species were only occasionally seen (up to 14 of a given species in a row, ≥ 4 mm apart) and, therefore, were not regarded as generally aggregating.

Because aggregating may help nymphs to attract mutualistic ant partners, we investigated ant presence in two selected aggregating species (Table 3). Ants were present for 24h in two (of 4) nymphal *C. ?horrifica*- and in 17 (of 21) *H. ?horizontalis*-aggregations. In one *C. ?horrifica*- and in 3 *H. ?horizontalis*-aggregations ants were also present during the 24h period, but during daytime a different species was present than at night (*C. ?horrifica*: day: *Camponotus* Mayr CB-3, night: *Camponotus*-CB-1; *H. ?horizontalis*: *Camponotus*-CB-3/*Camponotus*-CB-1 and *Polyrhachis* Swainson & Schuchardt CB-3/*Technomyrmex* Mayr CB-2, respectively). For a given aggregation, this diurnal replacement pattern was stable for at least 5 consecutive days. Among the ants engaging in diurnal replacement, only *Camponotus*-CB-1 tended other aggregations for 24 hrs. There was just one aggregation
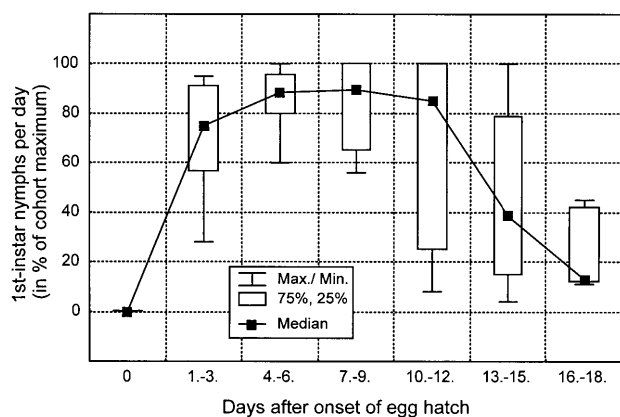

Fig. 1. Hatching of 1st instar nymphs of *Pyrgonota ?bulbosa* estimated from 6 cohorts (field observations as in Table 4). Days were standardized among cohorts by defining the day of egg hatch (= first sighting of 1st instar nymphs in a cohort) as day 1 for every cohort (intervals account for measurement error, see Methods). The dependent variable is the median of 1st instar numbers derived from counting them on the same day in all the six cohorts. To simplify comparisons among cohorts, 1st instar numbers on a given day in one cohort are expressed as percentage of the maximum number of nymphs that was ever counted in that cohort on a single day (maximum numbers were N = 36, 68, 51, 57, 54, 80 nymphs per cohort, respectively).

TABLE 5. Estimated times of development (days) for eggs and four nymphal stages of *Pyrgonota ?bulbosa* (field observations as in Table 4). Values are given as intervals to account for measurement error (see Methods). No estimates for the last (fifth) instar nymph were obtained.

	Eggs	1st instars	2nd instars	3rd instars	4th instars
Median (days)	26–31	6.5–10.5	7.25–11.25	6.5–10.5	12–16
Minimum	20–24	2–6	5–9	5–9	
Maximum	32–36	12–17	9.5–13.5	8–13	
N (cohorts)	8	6	6	2	1

in both *C. ?horrifica* and *H. ?horizontalis* that was tended by ants exclusively during daytime.

Subaggregating behaviour of nymphs was found in *Leptocentrus ?jacobsoni* Funkhouser sp. 4, *Tricentrus nigrofrontis* Funkhouser, and in all those *Tricentrus* Stål spp.[C] (i.e., morphospecies more similar to *Centrotoscelus* Funkhouser than to *Tricentrus* Stål as based on the NHM-collection; the former is considered a junior synonym of the latter, McKamey, 1998) in which nymphal behaviour could be determined (Table 2). Nymphal Hypsaucheniini cohorts occasionally subaggregated by splitting up into several groups without an obvious disturbance prior to dispersal. Solitary nymphs were restricted to *Leptobelus dama* Germar, *Gargara semibrunnea* Funkhouser, and two *Tricentrus* Stål spp. (Table 2).

DISCUSSION

Subsociality in Old World treehoppers has been regarded as an exceptional event. So far, only *Gigantorhabdus enderleini* Schmidt (Ushijima & Nagai, 1979; Stegmann et al., 1998), a *Terentius* Stål sp. (Kitching, 1987), and six *Oxyrhachis* Germar spp. (Singh & Sharma, 1980; Ananthasubramanian, 1996) were known to be subsocial. Hinton's (1977) references do not support his report of two subsocial Centrotinae: One does not mention female behaviour (Kitching, 1974) and the other describes clutch association during oviposition (Lamborn, 1914). In this study, however, maternal care has been confirmed in 11 species from three Old World Centrotinae tribes (Centrocharesini, Gargarini, and Hypsaucheniini). Accordingly, the picture of its general rarity in Old World treehoppers, if taken without further qualifications, reflects a sampling artifact and needs a correction: in one tribe, at least, maternal care seems to be ubiquitous (9 in 9 Hypsaucheniini spp. examined). Further studies may reveal that subsociality is common also in some other tribes, e.g., in the Centrocharesini. Although somewhat speculative at the moment, subsociality within the Old World treehoppers may turn out to be distributed as it is in the New World treehoppers, i.e., a conservative trait within tribes but not within subfamilies.

Maternal care in all species was restricted to egg-guarding. This is surprising, because maternal care in New World treehoppers often involves some care of nymphs (reviewed in Wood, 1993). The observed low level of care in Old World Centrotinae may be explained

by a high degree of iteroparity (relative to New World treehoppers), if the extent of insect maternal care is, indeed, negatively correlated with the degree of iteroparity, as suggested by Tallamy & Brown (1999). Although data on reproductive cycles of Old World Centrotinae are generally lacking, iteroparity may explain the termination of egg-guarding in *Pyrgonota ?bulbosa*: Females guarded eggs until most, but not all, eggs were hatched, suggesting a trade-off between continued guarding and the production of another egg clutch.

Maternal care cannot be excluded in species whose females were not found on eggs in this study (which may be an artifact of small sample sizes; the spatial scattering of eggs, which precludes guarding, was not observed) but there is circumstancial evidence for its absence. First, guarding females were not found although, in confirmed guarding species, they always were among the first 5 adults sighted (possibly because guarding attracted more tending ants which made them more conspicuous). Second, non-guarding may be a genus-level character, because Indian *Leptocentrus* Stål spp., *Telingana* Distant spp., *Tricentrus* Stål spp., and *Gargara* Amyot & Serville spp., do not provide care either (Ananthasubramanian & Ananthakrishnan, 1975a, 1975b).

Because maternal care is restricted to egg-guarding in the species studied here, their nymphal aggregations cannot be linked to maternal care as in *Umbonia crassicornis* (Cocroft, 1996, 1999a, 1999b). Protection by ants may be a better explanation for nymphal aggregations: most aggregations were tended by ants for 24h and, as in *Enchenopa binotata* Say (Wood, 1982), larger aggregation size may attract more ants which reduce mortality rates.

REFERENCES

ANANTHASUBRAMANIAN K.S. 1996: Homoptera, Membracidae. In Director Zool. Surv. India (ed.) *Fauna of India*. Madras, 238 pp.

ANANTHASUBRAMANIAN K.S. & ANANTHAKRISHNAN T.N. 1975a: Taxonomic, biological and ecological studies of some Indian membracids (Insecta: Homoptera) - Part I. *Rec. Zool. Surv. India* **68**: 161–272.

ANANTHASUBRAMANIAN K.S. & ANANTHAKRISHNAN T.N. 1975b: Taxonomic, biological and ecological studies on some Indian membracids - Part II. *Rec. Zool. Surv. India* **68**: 305–340.

BRISTOW C.M. 1983: Treehoppers transfer parental care to ants: a new benefit of mutualism. *Science* **220**: 532–533.

CARRICK J. 1968: A further note on Piper aduncum L. *Malayan Nat. J.* **21**: 63–64.

COCROFT R.B. 1996: Insect vibrational defence signals. *Nature* **382**: 679–680.

COCROFT R.B. 1999a: Offspring-parent communication in a subsocial treehopper (Hemiptera: Membracidae: Umbonia crassicornis). *Behaviour* **136**: 1–21.

COCROFT R.B. 1999b: Parent-offspring communication in response to predators in a subsocial treehopper (Hemiptera: Membracidae: Umbonia crassicornis). *Ethology* **105**: 553–568.

DEITZ L.L. & DIETRICH C.H. 1993: Superfamily Membracoidea (Homoptera: Auchenorrhyncha). I. Introduction and revised classification with new family-group taxa. *Syst. Entomol.* **18**: 287–296.

DIETRICH C.H. & DEITZ L.L. 1993: Superfamily Membracoidea (Homoptera: Auchenorrhyncha). II. Cladistic analysis and conclusions. *Syst. Entomol.* **18**: 297–311.

DIETRICH C.H., MCKAMEY S.H. & DEITZ L.L. 2001: Morphology-based phylogeny of the treehopper family Membracidae (Hemiptera: Cicadomorpha: Membracoidea). *Syst. Entomol.* **26**: 213–239.

EBERHARD W.G. 1986: Possible mutualism between females of the subsocial membracid Polyglypta dispar (Homoptera). *Behav. Ecol. Sociobiol.* **19**: 447–453.

EICKWORT G.C. 1981: Presocial insects. In Hermann H.R. (ed.) *Social Insects*. Academic Press, New York etc., 199–280 pp.

FUNKHOUSER W.D. 1951: Homoptera Fam. Membracidae. In Wytsman P. (ed.) *Genera Insectorum*. Fasc. 208. Brussels, Belgium, pp. 1–383.

GODING F.W. 1931: Classification of the Old World Membracidae. *J. New York Entomol. Soc.* **39**: 299–313.

HINTON H.E. 1977: Subsocial behaviour and biology of some Mexican membracid bugs. *Ecol. Entomol.* **2**: 61–79.

KITCHING R.L. 1974: The immature stages of Sextus virescens (Fairmaire) (Homoptera: Membracidae). *J. Aust. Entomol. Soc.* **13**: 55–60.

KITCHING R.L. 1987: Aspects of the natural history of the Lycaenid butterfly Allotinus major in Sulawesi. *J. Nat. Hist.* **21**: 535–544.

LAMBORN W.A. 1914: On the relationship between certain West African insects, especially ants, Lycaenidae and Homoptera. *Trans. Roy. Entomol. Soc. London.* **1913**: 436–498, 1 pl.

MCKAMEY S.H. 1998: Taxonomic catalogue of the Membracoidea (exclusive of leafhoppers): Supplement to Fascicle I – Membracidae of the General Catalogue of the Hemiptera. *Mem. Amer. Entomol. Inst.* **60**: 1–377.

MÜLLER H.J. 1984: Zur Entwicklung und Lebensweise der Larven der Dornzikade Centrotus cornutus (L.) (Homoptera: Auchenorrhyncha: Membracidae) unter besonderer Berücksichtigung der Kotschleuder. *Zool. Jb. Abt. Anat. Ontog. Tiere.* **111**: 385–399.

MYERS N., MITTERMEIER R.A., MITTERMEIER C.G., DA FONSECA G.A.B. & KENT J. 2000: Biodiversity hotspots for conservation priorities. *Nature* **403**: 853–858.

SINGH S. & SHARMA S.K. 1980: Maternal care in Oxyrhachis tarandus Fabr. (Membracidae: Homoptera). *J. Bombay Nat. Hist. Soc.* **77**: 156–157.

STEGMANN U.E., KESSLER H., SOFIAN M., BIN LAKIM M. & LINSENMAIR K.E. 1998: Natural history of the treehopper Gigantorhabdus enderleini. *Malayan Nat. J.* **52**: 241–250.

STEGMANN U.E., WEBB M. & LINSENMAIR K.E. 2002: New species, synonymies, and life-histories of the Southeast Asian treehopper genus Pyrgauchenia Breddin (Homoptera: Membracidae: Centrotinae). *J. Nat. Hist.* **36**: 279–303.

STRÜMPEL H. 1983: Homoptera (Pflanzensauger). In Fischer M. (ed.), *Handbuch der Zoologie, Part 28*. Walter de Gruyter, Berlin etc., 222 pp.

TALLAMY D.W. & BROWN W.P. 1999: Semelparity and the evolution of maternal care in insects. *Anim. Behav.* **57**: 727–730.

TALLAMY D.W. & WOOD T.K. 1986: Convergence patterns in subsocial insects. *Annu. Rev. Entomol.* **31**: 369–390.

USHIJIMA K. & NAGAI S. 1979: Some notes on the life history of Gigantorhabdus enderleini Schmidt in Borneo (Hemiptera: Membracidae). *Trans. Shikoku Entomol. Soc.* **14**: 191–194.

WOOD T.K. 1976a: Alarm behavior of brooding female Umbonia crassicornis (Homoptera: Membracidae). *Ann. Entomol. Soc. Amer.* **69**: 340–344.

WOOD T.K. 1976b: Biology and presocial behavior of Platycotis vittata (Homoptera: Membracidae). *Ann. Entomol. Soc. Amer.* **69**: 807–811.

WOOD T.K. 1977: Role of parent females and attendant ants in the maturation of the treehopper, Entylia bactriana (Homoptera: Membracidae). *Sociobiology* **2**: 257–272.

WOOD T.K. 1982: Ant-attended nymphal aggregations in the Enchenopa binotata complex (Homoptera: Membracidae). *Ann. Entomol. Soc. Amer.* **75**: 649–653.

WOOD T.K. 1984: Life history patterns of tropical Membracids (Homoptera: Membracidae). *Sociobiology* **8**: 299–344.

WOOD T.K. 1993: Diversity in the New World Membracidae. *Annu. Rev. Entomol.* **38**: 409–435.