

Newer trends in the biosystematics of Membracidae

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Abstract. Membracids, in general, display a very few morphological characters of taxonomic value. Many species exhibit remarkable intraspecific variations, in addition to sexual dimorphism and cornuate polymorphism that makes it difficult to allocate them to their respective taxa, unless a long series of male and female individuals belonging to the same population are available for examination. The male genitalia, although of value in the diagnosis of higher categories of the Membracidae, find limited application at the species level. The nymphal characters, especially those of the fifth immature stage, are very useful in the identification of the species, but nymphal materials are not available except for a few species, and the host plants of many species remain unknown. In recent years, it has become imperative to consider the ecophysiological aspects of these insects for a better and precise understanding of their systematics. The host plant specificity of some species of membracids, the mutual association of a particular species of membracids with a particular species of ants and the parasite-host interaction involving certain chalcidoid egg parasites of membracids are considered with a view to evaluate their role in the membracid taxonomy. The impact of differential reproductive potential in terms of host diversity, the allochronic differences in mating and initiation of oviposition, and the differences in the relative growth patterns with particular reference to the polymorphic species *Oxyrhachis tarandus* (Fabricius) on 5 species is investigated.

Keywords. Membracidae: host-plant specificity; ant-attendance.

1. Introduction

Within the Membracidae relatively few morphological characters of taxonomic value are found at the higher category level (Deitz 1975). Even at the specific level adults of membracids, in general, display a very few morphological characters of systematic importance. Quite a number of species examined from India have been found to exhibit remarkable intraspecific variations added to sexual dimorphism. In view of the conspicuous development of pronotum and its processes, taxonomists have relied mostly upon the disposition and relative development of horns in the classification at generic and specific levels. This has led to misconception and errors in the identification of several species. Funkhouser (1917) stressed on the value of male genitalia in membracid taxonomy, and Caldwell (1949) attempted to revise the North American genera of Ceresini on the basis of male genitalia. However, a review of literature on this subject shows that although recent workers have placed increased emphasis on the genitalia, even the most extensive studies are of narrow scope (Deitz 1975). The male genitalia of membracids, from which so much was expected, have proved unsatisfactory, for although at a tribal level they are distinctive, they have proved so similar in general shape and so variable in microscopic details, that they can only be used as subsidiary characters (Capener 1962). Membracid nymphs display significant morphological characters of taxonomic value (Matausch 1910, 1911; Yothers 1934; Yothers and Allen 1941; Funkhouser 1951; Ananthasubramanian and Ananthakrishnan 1975; Quisenberry *et al* 1978). Nymphal taxonomy has the

added advantage, because the nymphs of even highly polymorphic species are remarkably uniform and monomorphic, displaying characters sufficient to distinguish them from related species. Unfortunately, nymphal materials are not available and are rarely represented in museum collections.

The present study aims at evaluating the role of host-plant specificity, the mutual relationship between a particular species of membracids and a particular species of ants, the ovipositing behaviour, the biogeographical influence on polymorphism and the impact of differential reproductive behaviour in some of the local species of membracids, following the methods of Ananthasubramanian and Ananthakrishnan (1975).

2. Host-plant specificity

The literature referring to hosts adopted by Membracidae from southern India is not extensive, and is confined to the observations made by Ananthasubramanian and Ananthakrishnan (1975) and supplemented afterwards by Ananthasubramanian (1979, 1984). The membracids confine themselves to very definite host plants both for feeding and for oviposition. In many cases the association between the membracid and the host is so characteristic that a knowledge of the one is sufficient for recognition of the other (Funkhouser 1917). In southern India, the more important natural orders of plants harbouring the membracids are Leguminosae, Solanaceae, Rubiaceae, Rhamnaceae and Malvaceae, while they seem to avoid some families such as Euphorbiaceae, Labiatae and Asclepiadaceae, but there are exceptions. It is noteworthy that the membracids avoid almost all the plants of monocotyledons.

Many species such as *Leptocentrus taurus* and *Otinotus oneratus* are decidedly polyphagous being encountered on host-plants belonging to widely different natural orders, while some are oligophagous found on plants belonging to a single natural order. However, it is strictly the monophagous species that exhibit absolute host-plant specificity that have considerable value in the biosystematics of the Membracidae (table 1). *Leptocentrus moringae* not only confines itself to *Moringa oleifera* from September to December, but it is the only species of membracid ever found on this host plant during this period. From June to August this host plant harbours another species, *Gargara hraswa*. It is noteworthy that the same species of host plant does not harbour two different species of membracids belonging to the same genus during the same period. Thus, *Oxyrhachis uncatus*, *O. krusadiensis* and *O. brevicornutus*, all of which appear to be monophagous, occur on *Acacia arabica*, but not at the same time on the same host plant. It is in respect of polymorphic monophagous species (such as *Leptocentrus varicornis* found only on *Zizyphus jujuba*) that a precise understanding of host-plant relationships would be useful in the allocation of the species to their correct taxa. In spite of their significance in the biosystematics of the membracids, the host records of many species are still unknown, because most collectors of membracids adopt beating and sweeping methods applied over wild shrubs and bushes without any consideration to the host plants.

3. Ant-attendance

Many species of membracids are attended by ants for the sake of the so-called honey-dew, an anal secretion of the former eagerly sought for by the latter, and in

Table 1. Host-plant specificity in some membracids from southern India.

Name of membracid	Name of host plant
<i>Oxyrhachis minusculus</i> Anan. and Anan.	<i>Casuarina equisetifolia</i>
<i>O. krusadiensis</i> Anan. and Anan.	<i>Acacia arabica</i>
<i>O. brevicornutus</i> Anan. and Anan.	"
<i>O. uncutus</i> Melichar	"
<i>O. malabaricus</i> Ananthas.	<i>Tamarindus indicus</i>
<i>Lanceonotus cinnamomi</i> Ananthas.	<i>Cinnamomum tamala</i>
<i>Leptocentrus rhizophagus</i> Anan. and Anan.	Prop roots of <i>Ficus bengalensis</i>
	<i>Thespesia populnea</i>
<i>L. bauhiniæ</i> Anan. and Anan.	<i>Bauhinia tomentosa</i>
<i>L. varicornis</i> Anan. and Anan.	<i>Zizyphus jujuba</i>
<i>L. moringæ</i> Anan. and Anan.	<i>Moringa oleifera</i>
<i>L. mangiferae</i> Anan. and Anan.	<i>Mangifera indica</i>
<i>L. bajulans</i> Dist.	<i>Casuarina equisetifolia</i>
<i>L. major</i> Anan. and Anan.	<i>Michaelia champaka</i>
<i>Otinotus mimicus</i> Dist.	<i>Agapanthus umbellatus</i>
<i>Telingana nigroalata</i> Anan. and Anan.	" "
<i>T. consobrina</i> Dist.	" "
<i>Tricentrus spathodei</i> Ananthas.	<i>Spathodea campanulata</i>
<i>T. nobilis</i> Ananthas.	<i>Boerhaavia repens</i>
<i>T. albomaculatus</i> Dist.	<i>Datura fastuosa</i>
<i>T. congestus</i> (Walker)	<i>Vernonia cinerea</i>
<i>T. purpureus</i> Anan. and Anan.	<i>Polygonum</i> sp.
<i>Gargara pellucida</i> Ananthas.	<i>Gymnosporia montana</i>
<i>G. albitarsis</i> Anan. and Anan.	<i>Tecoma stans</i>
<i>G. rustica</i> Anan. and Anan.	<i>Zizyphus jujuba</i>
<i>G. malabarica</i> Anan. and Anan.	<i>Phyllanthus emblica</i>
<i>G. hraswa</i> Ananthas.	<i>Moringa oleifera</i>
<i>Parayasa nigrolimbata</i> Ananthas.	<i>Gymnosporia montana</i>
<i>Coccosterphus tuberculatus</i> Motsch.	<i>Morinda tinctoria</i>

many instances the hiding places of the membracids are easily located by the presence of the attending ants. Since in many instances, a particular species of membracid is always associated with a particular species of ant, a precise knowledge of this trophobial mutualism would be of immense value in the identification of the membracid species involved. The same observations were made by Capener (1962) with reference to the African species of membracids. Each species of membracid in a particular locality is attended by the same species of ant throughout the year. For instance, the common species of gregarious membracid, *Oxyrhachis rufescens*, is regularly attended by the large ants of the species *Camponotus sericeus*, wherever this membracid colony occurs. *Crematogaster* sp., a small shining black ant, regularly attends on *Coccosterphus paludatus* Dist. and *Oecophylla smaragdina*, a ferocious reddish brown ant, attends on *Oxyrhachis krusadiensis* on its host plant, *Acacia arabica*, and on *Anchon ulniforme* Buckton on its host plant, *Cajanus cajan*s. *Anoplolepis longipes*, a smaller reddish species of ant, is associated with *Leptocentrus bauhiniæ* and on *Gargara rustica* on their respective host plants, *Bauhinia tomentosa* and *Z. jujuba*. *Myrmecaria brunnea* and *Meranoplus bicolor*, both characterised by backwardly directed spines, attend on *Leptocentrus rhizophagus* and *L. moringæ* respectively. *Solenopsis germinata* var. *rufa*, a small brown ant nesting on the ground near trees, attends on *Tricentrus albomaculatus* on its host plant, *Datura fastuosa*. Colonies of a

large species of membracid, *Leptocentrus leucaspis*, are attended by a minute species of ant, *Paratrechina longicornis*. In those species of membracids that are multivoltine completing several generations in an year on the same host plant, the ant-attendance is found to be a regular feature. Thus, a knowledge of the host specificity of the membracids and the species of ants attending on them may be used as effective tools in the biosystematics of the membracids.

4. Biogeographical influence on the cornuate polymorphism in *Tricentrus pilosus* and its impact on membracid taxonomy

Ananthasubramanian and Ananthakrishnan (1975) reported the occurrence of cornuate polymorphism in several species of membracids from southern India. Of particular interest is this phenomenon found in *T. pilosus* A and A, an oligophagous species found on the prop roots of *Ficus bengalensis* and on the slender twigs of *Thespesia populnea* in and around Madras. The females of this membracid include 4 different morphs, viz (i) normal horns, (ii) short horns, (iii) vestigial horns and (iv) no horns. Males include 3 different morphs, viz (i) short horns, (ii) reduced horns and (iii) no horns. The frequency of occurrence of the different morphs of this species on its two host-plant species was reported by Ananthasubramanian (1979). Recently, the discovery of geographical races of this species has added new dimensions to the complexity of this species complex (figure 1). Specimens collected from Chedia Tope (Andamans) on *T. populnea* and prop roots of *F. bengalensis* were found to be remarkably uniform and monomorphic, but in both sexes the horns were distinctly longer than those of the females with normal horns collected from Madras, while those collected from Narakkal (Kerala) on the same species of host plants, though monomorphic, showed horns shorter than those of normal females collected from Madras. These observations have led to the conclusion that biogeographical factors should have a decisive role in bringing about phenotypic plasticity within certain limits, and hence great caution has to be exercised in the matter of allocating the different morphs to their correct taxon. Mating experiments performed on the different morphs collected at Madras from their host plants showed the absence of reproductive barrier, but the eggs deposited by such females failed to develop.

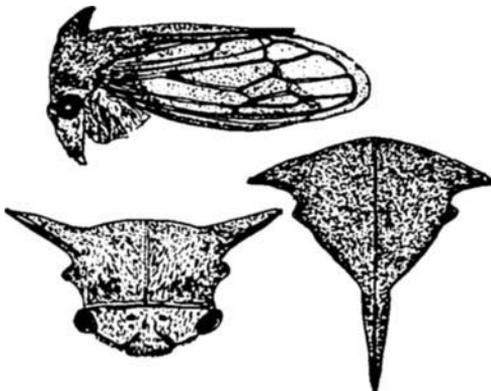


Figure 1. Geographical form of *T. pilosus* from Andamans.

Intercrossing of the morphs from different geographical regions has not been successful due to the difficulty of maintaining the insects alive on holidics.

5. Ovipositing behaviour

Though the eggs of different species of membracids are more or less identical in shape and lack sculpturing of any kind, the ovipositing behaviour is distinctive, constituting reliable parameters in the biosystematics of the family. In all the species of the Subfamily Oxyrhachinae with no known exception, the eggs are deposited on fairly thick twigs and are arranged in a palmate manner, the opposite rows converging at one end and diverging at the other. In fact, this is the pattern of oviposition characteristic of all the species of the only genus *Oxyrhachis*, the different species differing in the number of eggs deposited in each egg mass. Curiously, the egg mass of *O. brevicornutus* is covered by a viscid secretion of the female. In the Subfamily Centrotinae the ovipositing behaviour is much varied. In the Leptocentrini, the eggs are always arranged in straight rows. The oviposition slit, however, varies in the different species of *Leptocentrus*. In *L. taurus* F. for instance, two egg slits are cut by the ovipositor side by side and eggs are deposited in two parallel rows. The oviposition wound does not completely heal up so that a deep elliptical scar is left behind. *L. rhizophagus*, *L. moringae*, *L. bauhiniae* and *L. major* deposit their eggs in a single straight row, and the slit closes by springing back, leaving an extremely narrow streak. The length of this streak which is species-specific, is correlated with the number of eggs laid. In *L. leucaspis*, 55–70 egg slits, each measuring 3–4 mm long, are laid close to each other. In the genus *Otinotus*, exemplified by *O. oneratus* (Walker) the eggs are laid in irregular manner very superficially, and the different rows of eggs overlap to a considerable extent. *Gargara albitarsis* and *Telingana nigroalata* lay their eggs solitarily. *Gargara mixta* and *G. extrema* make numerous short straight or crescentic slits very close to each other; the slits are deep so that the eggs are almost completely enclosed. In the tribe Coccosterphini the ovipositing behaviour differs in different genera. In the genus *Coccosterphus* the egg slits are invariably made in tender twigs of herbs or shrubs, while *Parayasa* invariably oviposits on the herbaceous plants which it inhabits. The egg clusters are short, each containing a small number of 3–5 eggs in the former genus and 5–9 in the latter, and the egg masses are laid far apart. In *Eucoccosterphus* the eggs are laid either on woody twigs or on the peduncles, the egg masses being close to each other, each containing 4–9 eggs.

6. Allochronic shifts in oviposition in the intraspecific variants of the polymorphic species complex, *Oxyrhachis tarandus* (F.)

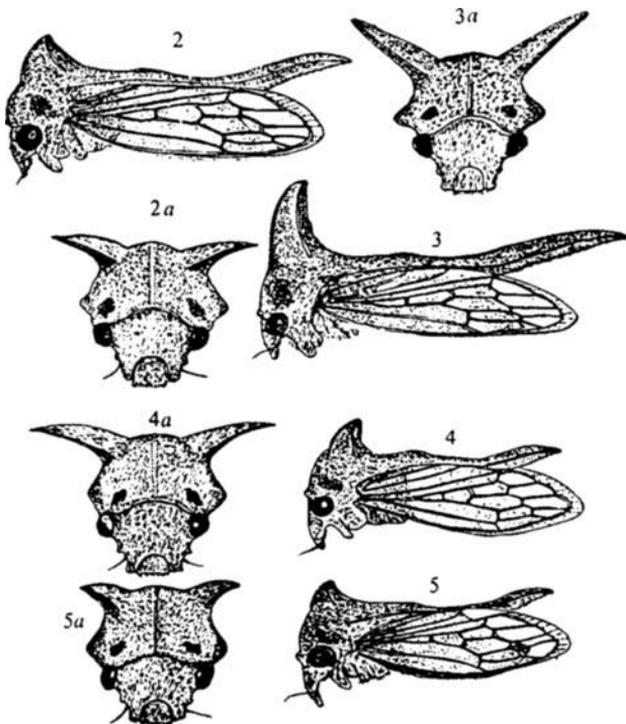
An analysis of the morphometric variations in *O. tarandus* collected from 5 of its host-plant species, viz *Prosopis spicigera*, *A. arabica*, *Pithecolobium dulce*, *Peltophorum ferrugineum* and *Poinciana regia*, disclosed 4 groups of individuals with reference to differences in the degree of development of the suprahumeral horns and the disposition of the posterior process. These 4 groups are: (i) Individuals with moderately developed suprahumeral horns which are less divergent; the posterior process moderately elevated and extending slightly behind the tegmina, (ii) individuals with

suprahumeral horns longer and more divergent than those of group (i) and projecting obliquely upwards; width across tips of horns greater than that of group (i); posterior process moderately elevated as in group (i), but extending well behind the tegmina, (iii) individuals with suprahumeral horns about as long as those of group (ii), but never projecting obliquely upwards, the angles of their carinae being more or less similar to those of group (i); posterior process shorter, less elevated and never reaching the tips of the tegmina, (iv) individuals with suprahumeral horns much reduced; posterior process as in group (iii) (figures 2-5).

The egg masses of these 4 groups of intraspecific variants also showed differences in the number of eggs (table 2). The identification of the egg masses of 4 groups was made possible since the egg masses were guarded by the mothers by sitting on them for hours or for days.

It was also noticed that the initiation and termination of oviposition by the females of the 4 groups do not always occur simultaneously, but vary by several days or weeks. While oviposition has been noticed to occur in the case of group (i) individuals almost throughout the year, it occurs only from August to March in group (ii) individuals. In groups (iii) and (iv) individuals, initiation of oviposition occurs in the first and second (or third) week of October respectively, and the oviposition period extends to only $2\frac{1}{2}$ - $2\frac{3}{4}$ months respectively (table 3).

The frequencies of occurrence of these 4 groups of individuals of *O. tarandus* are also found to differ on its 5 species of host plants analysed. On *P. spicigera* all the 4



Figures 2-5. Cornuate polymorphism in the species complex *O. tarandus*.

Table 2. Morphometric variations in 4 groups of individuals in the species complex of *O. tarandus*.

	Group I		Group II		Group III		Group IV	
	Female	Male	Female	Male	Female	Male	Female	Male
Length from frontal margin to tips of tegmina	8.0	7.4	8.2	7.5	6.8	6.4	6.8	6.5
Length from frontal margin to tip of posterior process	8.5	8.0	9.1	8.9	6.2	6.0	6.2	6.0
Width across tips of supra-humeral horns	4.5	4.2	5.2	3.0	5.2	5.0	4.9	3.5
Width across tips of humeral angles	3.1	2.4	3.3	3.1	3.12	3.0	3.2	3.1
Width across eyes	2.4	2.2	2.4	2.2	2.43	2.3	2.45	2.35
Length of horn	2.4	2.3	2.8	2.5	2.22	2.0	1.05	1.10
Width across bases of horns	1.25	1.19	1.4	1.35	1.2	1.9	1.26	1.9

Numbers indicate the mean value of 5 individuals in each group and in each sex. Measurements are in mm.

Table 3. Number of eggs per egg mass and the allochronic variations in the initiation and termination of oviposition in 4 groups of intraspecific variants in the species complex of *O. tarandus* during 1985-86.

	Group I	Group II	Group III	Group IV
Number of eggs per egg mass	80-112	92-118	63-78	34-40
Initiation of oviposition	2nd week of July	1st week of August	1st week of October	2nd or 3rd week of October
Termination of oviposition	1st week of June	4th week of March	1st week of January	1st week of January
Ovipositing phase	11 months	7 months	3½ months	2½-2¾ months

Table 4. Frequency of occurrence of 4 groups of intraspecific variants in the species complex of *O. tarandus* on 5 of its host plants during the year 1985-86.

	<i>P. spicigera</i>	<i>A. arabica</i>	<i>P. ferrugineum</i>	<i>P. dulce</i>	<i>P. regia</i>
Group I	46-50%	20-25%	—	—	—
Group II	20-25%	40-45%	90-95%	—	7.5%
Group III	20-28%	—	5-10%	70-85%	2.5%
Group IV	10-14%	25-34%	—	15-30%	90%

groups of individuals occur, although group (i) individuals constitute 45-50%. On the other 4 species of host plants, one or two groups of the individuals are absent. Group (iii) individuals are not found on *A. arabica*, groups (i) and (iv) on *P. ferrugineum*, groups (i) and (ii) on *P. dulce*, and group (i) individuals are absent on *P. regia*. On *A. arabica* the frequency of occurrence of group (ii) individuals is higher than the group (i) and group (iv) individuals, while on *P. ferrugineum* group (ii) individuals form 90-95% of the total population. On *P. dulce*, group (iii) individuals form about 85%, while on *P. regia* group (iv) individuals constitute about 90% from November to February, after which these as well as the other groups of individuals disappear since this plant sheds off its leaves (table 4).

7. Discussion

The trophobial mutualism between membracids and ants, apart from its value in the biosystematics of the Membracidae, is significant in the context of evolutionary divergence. According to Wood (1982), ant-attendance on gregarious species of membracids enhances the survival rate of the membracid nymphs. Survival of nymphs varies among trees due to variation in attendance by ants. Variation among individual trees in nymphal survival and ant attendance promotes distinct insect distributions. Such distributions magnify microgeographic disjunct among insect populations on conspecific host-plant species and have facilitated the divergence of the species into a complex of reproductively isolated species, one on each species of the host plant. This concept of genetic differentiation along host plant lines, originally offered to account for the host plant races in the sympatric species complex *Enchenopa binotata* Say by Wood (1980, 1982), Wood and Guttman (1981) and Guttman *et al* (1981) may be extended to account for the differences in the percentage of occurrence of the 4 groups of intraspecific variants of *O. tarandus* on its 5 host-plant species where they are attended by a large number of *C. sericeus*. Further studies in this direction are required to ascertain the role of ants in promoting disjunct insect distributions and sympatric speciation as the ultimate product of evolution.

Allochronic shifts in life-histories or adoption of new host plants by phytophagous insects have been implicated in the formation of host-plant races and reproductive isolation. Bush (1975) suggested that shifts in host plants promoted sympatric divergence in some phytophagous insects. Wood and Guttman (1981, 1982) have presented considerable data to support a sympatric model of speciation in the species complex, *E. binotata* by shifts in host plants. Studies on the origin of insect host-plant races and the evolution of species in certain phytophagous insects by Bush (1969, 1975), Alexander (1968), Tauber and Tauber (1977a,b) and Edmunds and Alstac (1978) show that new host races and species may arise sympatrically. The species

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