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TAXONOMIC, BIOLOGICAL AND ECOLOGICAL STUDIES ON SOME INDIAN MEMBRACIDS PART—II

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BIOLOGICAL STUDIES

(*a*) *Mating and oviposition.*—Mating in the various species studied here, never appears to be seasonal and occurs throughout the year. Generally copulation takes place during the warmer hours of the day. While in most species mating begins soon after the insects attain maturity, in species of *Leptocentrus*, *Oxyrhachis* and *Otinotus* mating was observed a day or two after the sexes attained maturity. Species of *Gargara*, *Tricentrus* and *Coccosterphus* were observed to mate 3-7 days after the last moult. In *Tricentrus pilosus* in spite of very careful observations copulation could not be noticed. In all species of *Oxyrhachis*, and *Otinotus oneratus* often two or more males congregate around a female prior to mating. The position assumed in mating is such that the opposite sexes face away from each other. Sluggish forms like *Oxyrhachis rufescens*, *Oxyrhachis tarandus* and *Otinotus oneratus* are not easily distracted when disturbed and never get detached even when they are dislodged, while the more active forms such as *Otinotus indicatus*, species of *Leptocentrus* and *Coccosterphus* get disengaged at the slightest disturbance. In *Oxyrhachis tarandus*, *O. rufescens* and *Otinotus oneratus* mating lasts for an hour or two, but actual field observations show that these sluggish forms if undisturbed, remain in copula for hours together. The duration of copulation for *Coccosterphus tuberculatus*, *C. minutus*, *Leptocentrus taurus* and *Gargara mixta* was timed 20-35, 5-15, 10-15 and 35-50 minutes respectively.

The majority of local species prefer the bark of twigs which are one or two years old, for oviposition. This is the usual location for all species of *Oxyrhachis*, *Otinotus*, some species of *Leptocentrus* and *Tricentrus*. Some species like *Leptocentrus moringae* and *L. bauhiniae* choose tender twigs which may be punctured to the extent of being broken off. *Leptocentrus taurus* can successfully oviposit on young as well as woody twigs. *Oxyrhachis tarandus*, *O. rufescens* and *Leptocentrus taurus* often deposit the eggs in punctures produced on the slender twiners of weak-stemmed plants. Midribs and petioles are the preferred sites of oviposition in *Gargara albitarsis* and *Coccosterphus minutus*, while the leaf axils are preferred by *Telingana consobrina* and *Gargara malabarica*. Some species regularly oviposit on the peduncles or pedicels of flowers while some polyphagous species often do so. For instance, *Telingana nigroalata*, *Coccosterphus paludatus* and *C. tuberculatus* always choose peduncles. *Otinotus oneratus* which normally lays eggs on twigs of one or two years old, has also been noted to oviposit on the peduncles of *Cestrum diurnum*. The species inhabiting herbaceous or semiwoody annuals or biennials invariably oviposit on the basal part of the main stem as illustrated by *Tricentrus albomaculatus*—a monophagous species found on *Datura fastuosa*. It is interesting to note a few species such as *Leptocentrus rhizophagus* ovipositing, as a rule, on slender free-hanging prop roots of *Ficus bengalensis*. *Tricentrus pilosus*, on the other hand, lays eggs on prop roots as well as on young twigs of *Thespesia populnea* and the choice appears to depend on the season. (vide Table 1). The peculiar instance of oviposition in the roots or on the base of the stem below the surface of the ground reported for *Thelia bimaculata* and *Stictocephala festina* by Funkhouser (1916, 1917) has, however, no parallel among the species studied presently.

The nature of the oviposition slit varies. In many instances, the slit appears to be nearly straight and narrow made by an oblique thrust of the ovipositor. The eggs are inserted in the slit arranged in a single slanting row ; the slit soon closes by the springing back of the bark, leaving but a streak superficially. *Leptocentrus moringae*, *Tricentrus pilosus* and many species of *Gargara* illustrate this type of oviposition. In another type of oviposition observed in *Leptocentrus taurus*, *L. bauhiniae*, *L. nigra* and *L. mangiferae* two crescentic slits are made side by side and a single or double row of eggs are deposited; the slit never closes and often remains as a deep elliptical scar for a long time; should this type of ovipotion occur in a tender twiner or herbaceous stem, the injury causes the stem to break off. Rarely as in *Gargara madrasensis* the slit takes the form of a more or less shallow excavation, never reaching the stele. In some cases, the punctures are superficial extending only to the endodermis with the result that the eggs are not entirely hidden, the tips plainly projecting out. This is illustrated by *Otinotus oneratus* and many of the species of *Oxyrhachis*. In the latter genus, the eggs are arranged in a palmate manner, the opposite rows converging at one end and diverging at the other. In *Oxyrhachis brevicornutus* the eggs are arranged in two rows and the egg mass covered by a viscid substance. In *Otinotus oneratus* the eggs are laid in irregular clusters often one row being partially or entirely overlapped by another. In some species such as *Gargara albitarsis* and *Telingana consobrina* the eggs are laid singly.

The number of eggs in each egg mass varies even within the species. The data for all the species taken during the present studies with regard to the number of eggs in one mass are presented in Table 1.

There are mainly two types of movement of ovipositor in the act of oviposition. In the first type exemplified by all the species of *Tricentrus*, *Gargara*, *Coccosterphus* and *Telingana* the female raises her abdomen as high as possible, unsheaths the ovipositor which is held at right angles to the abdomen and slowly pushed into the bark. In this perpendicular thrust, the ovipositor which bends up and down several times due to the resistance offered by the bark and wood, progresses steadily backwards until it turns almost parallel to the body and the eggs are laid in the slit after which the ovipositor is withdrawn. In *Leptocentrus*, besides the main slit a shallow supplementary slit is made. In the

TABLE 1

Oviposition habits and duration of egg stage.

Name of the membracid species	Minimum No. of eggs in each mass.	Maximum No. of eggs in each mass.	Oviposition site on host.	Duration of egg stage in days
Oxyrhachis rufescens	30	270	Twig of one or two years old slender twiners	7–10
O. tarandus	48	240	,, ,,	7–12
O. minusculus	40	160	,, ,,	6–10
O. krusadiensis	120	160	,, ,,	—
O. uncatus	96	140	,, ,,	—
O. brevicornutus	18	22	,, ,,	—
Leptocentrus taurus	18	27	Young and woody twigs	6–14
L. leucaspis	8	17	Woody branches	8–14
L. bajulans	7	16	,, ,,	5– 9
L. varicornis	18	28	,, ,,	10–15
L. bauhiniae	10	22	Tender twigs	10–15
L. moringae	18	27	Tip of young twigs	10–15
L. mangifarae	5	15	Woody twigs	7–13
L. major	7	16	,, ,,	10–12
L. nigra	5	15	,, ,,	10–14
L. rhizophagus	4	20	Prop roots of Banyan tree	8–10
Otinotus oneratus	3	16	Young or old twigs	7–13
O. mimicus	3	8	,, ,,	—
O. indicatus	6	18	Main trunk of shrubs or two year old twigs of trees	8–11
O.obliquus	4	10	,, ,,	—
Telingana nigroalata	16	40	Peduncles of flowers	—
T. consobrina	1	—	Axil of leaflet	—
Tricentres pilosus	8	20	Prop roots of Banyan tree	9–16
T. decornis	4	8	Young twigs	7– 9
T. albomaculatus	5	15	Basal part of Datura stem	6–11
T. purpureus	6	8	Young twigs	8–14
T. congestus	4	8	Woody twigs	10–13
Gargara mixta	5	18	Tip of twig	7–10
G. extrema	6	18	,, ,,	5–10
G. malabarica	5	8	Leaf axils	7–12
G. albitarsis	1	—	Petioles	6– 9
G. madrasensis	4	8	Young twigs	6– 9
G. rustica	6	20	,, ,,	8–10
Coccosterphus minutus	6	10	Midrib of leaf	5– 7
C. paludatus	6	10	Peduncle of flower or fruit	9–15
C. tuberculatus	4	6	,, ,,	7–12

second type observed in the species of *Oxyrhachis* and *Otinotus*, the ovipositor is held at an angle to the abdomen and thrust obliquely into the bark. It is withdrawn after anchoring each egg in the host tissue and reinserted for the next egg. Some species having high fecundity lay eggs in slits which are very close to each other in the same twig, for instance, in *Gargara mixta* 31-32 egg masses have been deposited within a distance of one inch, in *Otinotus oneratus* 37-98, while *Leptocentrus leucaspis* lays 55-70 egg masses within the same space and this is the case for many other species also.

The ovipositor has sharp saw-like edge for lacerating the host tissue while making the egg slits. A comparison of the ovipositors of many of the species suggests a correlation between the length of this structure and the mechanics of oviposition. It is not unusual for some smaller species to possess comparatively longer and more powerful ovipositors. For example, *Coccosterphus minutus*, *Gargara madrasensis*, *Parayasa maculosa* and *Tricentrus albomaculatus* all of which are small species have relatively long ovipositors enabling them to anchor the eggs deep within the bark.

The eggs of all the species examined are more or less identical in shape, being elongate, with a slight curvature on lateral margins. In most cases, the eggs are shining white with a smooth vitreous chorion. The basal part of the egg is invariably rounded while the tip may either be simple as in the majority of species or slightly drawn out to give a club-like appearance to the egg as in *Leptocentrus leucaspis*. According to Lefroy (1909) the egg of *Oxyrhachis tarandus* has a sharp bent spine at one end which is embedded in the tissue of the host plant. In the present studies, in spite of examining a large number of eggs of this species no such spine was noticed and it appears to be absent in other species of *Oxyrhachis* as well. The eggs of *Oxyrhachis rufescens*, the largest in size found locally, measures 0.9-1.1 mm. long and 0.25-0.3 mm. wide at the maximum diameter. The smallest eggs are those of *Coccosterphus minutus* and *Gargara madrasensis* measuring 0.55-0.6 mm. long and 0.16-0.2 mm. wide. Before hatching, the eggs of all species show an increase in size, the colour in many cases turning to yellowish or light fuscous.

(*b*) *Duration of egg stage*.—The duration of egg stage differs in the different species as shown in the Table 2. A minimum of 5 days and a maximum of 16 days have been noted for incubation. Even within the same species the difference in the incubation period appears to be spectacular during the various seasons of the year due to the effects of the physical factors such as temperature and moisture. However, eggs laid at the same time show variations relating to hatching though the environmental factors are identical. The reason for such a differential rate of embryonic development is not known.

The duration of each instar varies for the different species and even for the individuals hatching from a single egg mass. In general it is found that the duration of the first instar is greater than the succeeding three instars, while the fifth instar has the maximum duration as shown in Table 2.

(*c*) *Hatching*.—Hatching occurs invariably during the early hours of morning when the surrounding temperature is low. Prior to hatching, the egg slightly enlarges and stands conspicuously apart from the neighbouringe ggs. During hatching, the hatching membrane enclosing the embryo breaks up and the chorion splits near the upper end. Then the egg-cap is forced upwards by the cranial tubercules and the head of the nymph projects out. The nymph exhibits rhythmic to and fro movements of its body for working its way out. For a few minutes the insect stands on its anal segment which is still inside the hatching membrane. As soon as it gets a foothold, it pulls the terminal part of the abdomen out of the shell, slowly moves apart and rests for sometime. The whole process of hatching requires from 15 minutes to one hour in the different species.

(*d*) *Ecdysis.*—The region where the ecdysial splitting first appears differs in the different genera. Some species require a firm foothold on the substratum, while others can moult without attachment. In the fifth instar moulting can be easily observed in view of its larger size.

TABLE 2

Duration of nymphal stages in membracids.

Name of species	First instar	Second instar	Third instar	Fourth instar	Fifth instar	Total No. of days
Oxyrhachis tarandus	8	6	6	3	10	33
O.rufescens	5	4	5	5	11	30
O.minusculus	5	3	4	4	8	24
O.krusadiensis	8	6	3	3	10	30
O.uncatus	8	5	4	4	8	29
O.brevicornutus	10	3	4	4	9	30
Telingana nigroalata	8	5	4	5	12	34
T.consobrina	6	4	4	5	9	28
Leptocentrus taurus	5	3	3	4	10	25
L.rhizophagus	6	4	5	5	9	29
L.leucaspis	6	4	4	4	11	29
L.bajulans	5	4	6	6	7	28
L.varicornis	4	3	4	4	10	25
L.moringae	7	4	5	4	9	29
L.mangiferae	7	5	4	4	9	29
L.bauhiniae	5	4	3	3	8	23
L.nigra	9	6	5	5	9	34
L.major	8	6	4	4	10	32
Otinotus oneratus	7	5	5	4	8	29
O.mimicus	6	3	3	3	8	23
O.indicatus	9	3	5	4	10	31
O.obliquus	10	3	3	3	7	26
Tricentrus pilosus	8	4	5	5	9	31
T.albomaculatus	7	3	3	3	6	22
T.purpureus	10	6	5	4	10	35
T.decornis	7	4	3	4	7	27
T.congestus	8	5	4	4	9	30
Gargara mixta	4	5	4	3	7	23
G.extrema	5	5	4	3	7	24
G.rustica	4	3	3	3	8	21
G.malabarica	5	4	3	4	7	23
G.madrasensis	4	3	3	4	7	21
G.albitarsis	5	4	3	3	8	23
Parayasa maculosa	7	3	4	3	9	26
Coccosterphus minutus	5	3	3	3	8	22
C.tuberculatus	6	4	4	5	12	31
C.paludatus	7	6	4	4	13	34

In all species of *Leptocentrus* the nymph attaches to the twig by the first two pairs of legs; the splitting commences from the middle of vertex and extends over the thorax, legs, wings and abdomen; the head emerges through the split followed by the other regions of the body. In all the species of *Coccosterphus* and *Gargara* the nymphsattach to the substratum by all the legs; in *Tricentrus albomaculatus* only the forelegs are attached. In all the above examples, the moulted skins or exuviae have been found to be perfect and useful for the study of the chaetotaxy. In *Oxyrhachis* and *Otinotus*, the nymph is not attached; splitting starts over the thorax followed by the head, legs and abdomen; the exuvium is much torn, parts of it being found attached to the legs of the insect for sometime. Soon after moulting, the various regions of the body become swollen. The new exoskeleton is pale yellowish white, turning to the normal colour in a few hours. The time taken for moulting varies not only in the different species but in the individuals of the same species. The minimum period noted for the process is 10 minutes for *Coccosterphus paludatus* and the greatest is fortyfive minutes for *Leptocentrus rhizophagus*. If the insects are subjected to any mechanical injuries or if the twig of the host plant happens to dry up during the period of moulting, the adults become abnormal, exhibiting unusual twists in the pronotal processes and the wings appear crumpled.

(*e*) *Host Preference*.—Most of the local species of membracids show host specificity to a remarkable extent. Certain species of plants, although occurring in abundance throughout the year, are notably free from membracids. For instance, all plants of the families, *Cucurbitaceae*, *Oleaceae*, *Asclepiadaceae*, *Apocyanaceae*, *Acanthaceae*, *Meliaceae* and *Labiatae* are decidedly avoided by membracids, while *Leguminosae*, the acacias in particular, *Compositae*, *Rubiaceae*, *Solanaceae*, *Myrtaceae* and *Rhamnaceae* are among those most preferred by these insects. The monophagous membracids exhibit absolute host specificity; some which are oligophagous choose closely related plants often belonging to the same family, while others appear to be polyphagous extending their range over a wider variety of plants (Table 3). Monophagous species include *Leptocentrus mangiferae* found only on *Mangifera indica*, *Leptocentrus bauhiniae* on *Bauhinia tomentosa* and *Tricentrus albomaculatus* on *Datura fastuosa*. In a few instances, as Funkhouser (1917) states, the association between the membracid and the host is so specific that a knowledge of the one is sufficient for a recognition of the other. Thus, *Leptocentrus moringae* not only confines itself to *Moringa moringa* but is the only species ever found on this host. *Oxyrhachis rufescens* is notable for its oligophagous habit being found only on the leguminous plants (Table 4), while *Oxyrhachis tarandus*, though found mostly on Leguminosae, is often encountered on *Casurina* and *Morinda tinctoria*. *Leptocentrus taurus* and *Otinotus oneratus* are decidedly polyphagous. *Otinotus oneratus* has so far been recorded from forty host species from South India and the range may be undoubtedly wider (Table 5); some of these plants such as *Prosopis spicigera*, *Cestrum diurnum* and *Zizyphus jujuba* are much preferred.

That membracids are capable of rhizophagous habit, a fact hitherto unrecorded, has been established beyond doubt in the course of the present studies. Four species, *Leptocentrus rhizophagus*, *Coccosterphus paludatus*, *Otinotus oneratus* and *Tricentrus pilosus*—are regularly met with on the slender free-hanging prop roots of *Ficus bengalensis* where oviposition as well as feeding of nymphs and adults have been observed. Strangely enough, none of these membracids have any tendency to feed on the leafy shoots of the banyan tree.

It has been observed that while the majority of the local species utilize specific host plants for oviposition and feeding, a few species choose a particular host for oviposition and feeding during their nymphal period, the adults swarming over and feeding on almost all plants of the locality. Thus, *Telingana nigroalata*, a species common in the

TABLE 3

Host plants of the Indian Membracids.

Oxyrhachis tarandus	Acacia arabica, Prosopis spicigera, Cassia sp. Peltophorum sp. Caesalpinia coriaria, Sesbania grandiflora, Erythrina indica.
O. rufescens	vide Table 7.
O. minusculus	Casuarina equisetifolia.
O. uncatus	Prosopis spicigera.
O. krusadiensis	Prosopis spicigera, Cassia sp.
O. brevicornutus	Prosopis spicigera.
Leptocentrus taurus	Acacia arabica, A. melanoxylon, Albizzia lebbec, Tamarindus indica, Capparis sepiaria Zizyphus jujuba, Vernonia cinerea, Artabotrys odoratissimus, Erythrina indica, Crataeva religiosa, Ipomaea biloba, Hibiscus rosasinensis, Thespesia populnea, Feronia elephantum, Anacardium occidentale, Cyamopsis tetragonoloba, Bauhinia tomentosa, B. purpurea, Casuarina equisetifolia, Solanum torvum, S.melongena, Eranthimum sp.
L. mangiferae	Mangifera indica.
L. major	Michaelia champaka.
L. bajulans	Casuarina equisetifolia.
L. leucaspis	Terminalia cadappa, Pongamia glabra.
L. varicornis	Zizyphus jujuba.
L. rhizophagus	Prop roots of Ficus bengalensis.
L. nigra	Phyllanthus sp.
L. bauhiniae	Bauhinia tomentosa.
Tricentrus pilosus	Prop roots of Ficus bengalensis, Thespesia populnea.
T. decornis	Eugenia caryophyllata, Lagerstroemia sp., Cryptostegia sp.
T. albomaculatus	Datura fastuosa.
T. congestus	Vernonia cinerea.
T. purpureus	Polygonum sp.
Gargara mixta	Lagerstroemia sp., Syzygium jambolanum.
G. rustica	Zizyphus jujuba.
G. madrasensis	Cestrum diurnum, Caesalpinia pulcherrima, Tecoma sp.
G. albitarsis	Tecoma grandiflora.
G. malabarica	Phyllanthus emblica.
G. extrema	Solanum melongena, Zizyphus oenoplia, Capsicum frutescens, Solanum torvum.
Otinotus oneratus	vide Table 8.
O. mimicus	Artocarpus integrifolia.
O. indicatus	Thespesai populnea, Syzygium jambolanum, Tecoma sp.
O. obliquus	Trewia nudiflora, Phyllanthus sp., Premna latifolia.
Coccosterphus minutus	Prosopis spicigera, Cestrum diurnum, Tecoma stans, Vernonia cinerea, Acalypha sp.
C. paludatus	Bauhinia tomentosa, Cestrum diurnum, Lawsonia alba, prop roots of Ficus bengalensis.
C. tuberculatus	Phyllanthus emblica, Morinda tinctoria.
Parayasa maculosa	Cestrum aurantiacum, Acacia melanoxylon.
Telingana nigroalata	Agapanthus umbellatus.
T. consobrina	Aspidium sp.

Kodaikanal hills and sporadic on plains, oviposits on *Agapanthus umbellatus* in the months of March and April; the nymphs feed on the same plant. Emergence of adults occurring during the first and second weeks of June is associated with swarming; subsequently they are found on almost all plants such as *Prunus salicina*, *Acacia auriculiformis*, *Juniperus virginiana*, *Spiraea corymbosa*, *Erythrina cristogalli*, *Cestrumaurantiacum*, and on ferns. Such instances often lead to false conclusions regarding the real host plant of the species.

TABLE 4

Host plants of Oxyrhachis rufescens.

Name of leguminous host plant	Subfamily	Period of occurrence
Acacia arabica	Mimoseae	Throughout the year
A. melanoxylon	,,	Sporadic
A. auriculiformis	,,	,,
Prosopis spicigera	,,	Throughout the year
P. juliflora	,,	,,
Enterolobium saman	,,	September to November
Pithecolobium dulce	,,	Throughout the year
Mimosa sp.	,,	Sporadic and rare
Parkia biglandulosa	,,	,,
Delonix regia	Caesalpiniaceae	July to September
Caesalpinia coriaria	,,	,,
C. pulcherrima	,,	September to December
Cassia fistula	,,	August to December
Cassia sp.	,,	,,
Peltophorum sp.	,,	Rare
Tamarindus indicus	,,	August to December
Bauhinia tomentosa	,,	Rare
B. purpurea	,,	September to November
B. variegata	,,	,,
Parkinsonia aculeata	,,	Rare and sporadic
Crotalaria juncea	Papilionaceae	September to December
C. verrucosa	,,	,,
Erythrina indica	,,	April to June
Butea frondosa	,,	August to November
Sesbania aegyptiaca	,,	Rare and sporadic
Pterocarpus marsupium	,,	,,

It is interesting to note that in South India *Otinotus oneratus* which is very common on a variety of unrelated host plants, is conspicuous by its absence on *Datura fastuosa.* However, the same species reported from North India by Behura (1951, 1956) is stated to prefer *Datura fastuosa* wherever this plant occurs. In the present studies, attempts at rearing this membracid to maturity on *Datura fastuosa* has so far been met with failure. Although no attempt has been made towards a chemical analysis in the present studies, it seems probable that there might be subtle biochemical differences between the host species of the two regions to cause the distinction.

The species whose host plants have been studied appear to have all stages of one or more broods passed through on the same host plant, unlike some American species which are stated by Funkhouser (1917) to require two hosts, one for the feeding of nymphs and the other for the adults to oviposit, the former host being usually herbaceous and succulent, while the latter being woody shrubs or trees. However, certain local species deliberately change their host after completing one or two generations although there is apparently no morphological difference on the host to induce such a behaviour. For instance, *Coccosterphus paludatus* feeds and breeds on *Bauhinia purpurea* from June to September completing two generations, migrating thereafter to *Cestrum diurnum*, *Tecoma stans* and *Lawsonia alba* or taking to a rhizophagous habit on *Ficus bengalensis.*

(*f*) *Communal life*.—While some species of membracids occur solitarily on their host plants, others are decidedly gregarious. Many of the species of *Oxyrhachis* are gregarious though *brevicornutus* forms an exception. In all the strictly solitary species, the eggs are laid either singly or in clusters wide apart and the nymphs immediately on hatching

TABLE 5

Host plants of Otinotus oneratus in the vicinity of Madras.

Name of plant	Family	Period of infestation
Prosopis spicigera	Mimoseae	Throughout the year
P. juliflora	,,	,,
Acacia arabica	,,	,,
Cestrum diurnum	Solanaceae	,,
Zizyphus jujuba	Rhamnaceae	April to December
Z. oenoplia	,,	,,
Bauhinia variegata	Caesalpiniaceae	September to December
B. purpurea	,,	,,
Erythrina indica	Papilionaceae	June to August
Capparis sepiaria	Capparidaceae	April to June
Cassia angustifolia	Caesalpiniaceae	June to September
Cassia fistula	,,	,,
Cassia marginata	,,	,,
Caesalpinia pulcherrima	,,	Sporadic
C. coriaria	,,	,,
Peltophorum sp.	,,	,,
Psidium guajava	Myrtaceae	August to October
Tamarindus indicus	Caesalpiniaceae	November to March
Pongamia glabra	Papilionaceae	Rare and sporadic
Butea frondosa	,,	,,
Sesbania grandiflora	,,	,,
Crotalaria sp.	,,	October-November
Crataeva religiosa	Capparidaceae	April to June
Cadaba indica	,,	,,
Enterolobium saman	Mimoseae	Rare and sporadic
Pithecolobium dulce	,,	October to January
Aegle marmelos	Rutaceae	Sporadic
Feronia elephantum	,,	,,
Morinda tinctoria	Rubiaceae	December to January
Morinda citrifolia	,,	,,
Moringa moringa	Moringaceae	Rare and sporadic
Thespesia populnea	Malvaceae	December to January
Lagerstroemia Flosreginae	Lythraceae	September to January
Terminalia catappa	Combretaceae	September to November
Anona squamosa	Anonaceae	Sporadic
Solanum torvum	Solanaceae	November to January
S. lycopersicum	,,	,,
Prop roots of Ficus bengalensis	Urticaceae	October to December

exhibit a tendency to move along the twigs and become solitary. Some species like *Coccosterphus tuberculatus* are gregarious during their nymphal stages but remain solitarily as adults. Conversely, the adults of a few membracids, for instance, *Leptocentrus moringae* are found in groups on the twigs of *Moringa* while their nymphs are solitary, each occupying a leaf axil. In some, like *Leptocentrus rhizophagus*, the first instar nymphs are gregarious and the later stages are found to be solitary. In a few species, the nymphs appear to be subgregarious, being found in small groups of 5 or 6 individuals.

Gregarious habit in both nymphal and adult stages is observed in many species such as *Oxyrhachis krusadiensis*, *Oxyrhachis uncatus*, *Oxyrhachis minusculus*, *Gargara mixta*, etc. though these species are not observed to live with other species. On the other hand, sometimes the same host plant lodges two gregarious species, the individuals of both the species crowding together and mingling with each other very closely; such close harmony is noticed in *Oxyrhachis tarandus* and *Otinotus oneratus* on *Prosopis spicigera*. The egg masses of these two species are very often laid so close to each other that the egg slits of one species become partially overlapped by the other. In general, the greagarious species happen to be highly prolific and they lay egg masses in close proximity, the nymphs as well as adults showing very little tendency towards migration with the result that several generations are passed through on the same plant, often on the same twig. Nymphs of two species often mingle with each other while the adults are prone to be solitary. Thus, the nymphs of *Gargara rustica* and *Coccosterphus paludatus* live gregariously on *Bauhinia;* the latter species is also found associated with *Tricentrus pilosus* on the prop roots of Banyan. Rarely, an individual nymph of a solitary species has been observed in the midst of a gregarious one. In a few instances, two species which are normally solitary on different host plants live gregariously if they happen to find themselves on the

TABLE 6

Species of Membracid	Type of solitary and communal life
Coccosterphus minutus Gargara albitarsis Tricentrus pilosus Otinotus indicatus Otinotus obliquus Oxyrhachis brevicornutus Telingana consobrina Leptocentrus varicornis Leptocentrus bajulans Leptocentrus nigra Leptocentrus mangiferae	Species entirely solitary as both nymphs and adults.
Leptocentrus moringae Telingana nigroalata	Species gregarious as adults but solitary as nymphs.
Coccosterphus tuberculatus	Species solitary as adults but gregarious as nymphs.
Leptocentrus rhizophagus	Species gregarious in the first instar, but solitary thereafter.
Oxyrhachis krusadiensis Oxyrhachis uncatus Oxyrhachis minusculus Gargara mixta Gargara malabarica	Species gregarious as both nymphs and adults, but not living with other species.
Oxyrhachis tarandus Oxyrhachis rufescens Otinotus oneratus	Gregarious species living with other gregarious species as both nymphs and adults.
Gargara rustica Coccosterphus paludatus Tricentrus pilosus	Species living with other gregarious species as nymphs, but not as adults.
Tricentrus albomaculatus Leptocentrus taurus	Species solitary on different hosts, but living together on the same host.
Leptocentrus bauhiniae	Species found solitarily as nymphs in the midst of another gregarious species.
Leptocentrus taurus Leptocentrus leucaspis	Subgregarious species found in small groups of five or six as nymphs.

same host plant. The various types of communal life observed in local species are summarised in Table 6.

(g) *Attendance by Ants.*—That many membracids are attended by ants for the sake of their anal secretion, the so-called 'honey-dew' is well known. In fact, in many instances the hiding places of the membracids are easily located by following the tract of marching ants. As stated earlier, interesting accounts on this subject have been furnished by many workers. The association, though common, is undoubtedly not as indispensable and obligatory as the strict symbiotic relation between ants and some other insects.

Many of the local species of membracids are attended by one or more species of ants, the exceptions so far noted being *Coccosterphus minutus, Telingana consobrina, Parayasa maculosa, Tricentrus purpureus, Otinotus mimicus, Oxyrhachis brevicornutus* and *Gargara madrasensis* (Table 7).

TABLE 7

Membracid species and their attending ants.

Membracid species	Attending ants
Oxyrhachis tarandus	Camponotus compressus
Oxyrhachis rufescens	Camponotus sericeus, C. compressus
Oxyrhachis uncatus	Camponotus compressus
Oxyrhachis minusculus	Crematogaster sp.
Oxyrhachis brevicornutus	——
Oxyrhachis krusadiensis	Oecophylla smaragdina.
Leptocentrus taurus	Camponotus compressus
Leptocentrus leucaspis	Paratrechina longicornis
Leptocentrus rhizophagus	Camponotus compressus, Myrmecaria brunnea. Crematogaster sp. and Meranoplus bicolor.
Leptocentrus moringae	Crematogaster sp.
Leptocentrus bauhiniae	Anoplolepis longipes, Camponotus compressus
Leptocentrus mangiferae	Camponotus compressus
Leptocentrus major	Camponotus compressus
Leptocentrus varicornis	Camponotus compressus
Leptocentrus bajulans	Camponotus compressus
Otinotus oneratus	Camponotus compressus, Crematogaster sp.
Otinotus mimicus	——
Otinotus indicatus	Paratrechina longicornis
Otinotus obliquus	Paratrechina longicornis
Tricentrus albomaculatus	Solenopsis geminata var. rufa.
Tricentrus pilosus	Camponotus compressus, C. sericeus
Tricentrus decornis	Camponotus compressus
Tricentrus congestus	Camponotus compressus
Tricentrus purpureus	——
Gargara mixta	Camponotus compressus
Gargara extrema	Camponotus compressus
Gargara malabarica	Anoplolepis longipes
Gargara madrasensis	——
Gargara albitarsis	Crematogaster sp.
Gargara rustica	Anoplolepis longipes, Crematogaster sp.
Coccosterphus minutus	——
Coccosterphus paludatus	Crematogaster sp.
Coccosterphus tuberculatus	Crematogaster sp.
Telingana nigroalata	Camponotus sp.
Telingana consobrina	——
Parayasa maculosa	——

The commonest species of ant that is found attending on the majority of membracids in this locality is undoubtedly *Camponotus compressus*, a large black species found throughout India. However, the allied species, *Camponotus sericeus*, is somewhat rare and found attending regularly on *Oxyrhachis rufescens* during the rainy months of September to November, and sporadically on *Tricentrus pilosus*. Other species of ants recorded from this locality are as follows: *Crematogaster* sp. a small shining black ant resting in tree trunks and attending regularly on *Coccosterphus tuberculatus*, *Coccosterphus paludatus* and often on other species as well; this ant has the peculiar habit of turning up its abdomen when excited; *Oecophylla smaragdina*, the red tree ant, attends on *Oxyrhachis krusadiensis*, while *Anoplolepis longipes*, a smaller reddish species visits *Leptocentrus bauhiniae* and *Gargara rustica*, both these species of ants being noted for their virulent nature. *Myrmicaria brunnea* and *Meranoplus bicolor* characterised by backwardly directed prothoracic spines are found associated with *Leptocentrus rhizophagus*. *Solenopsis geminata* var. *rufa*, a small brown-ant nesting on the ground near trees attends on *Tricentrus albomaculatus*; *Paratrachina longicornis*, a very small species attends in large numbers on *Leptocentrus leucaspis* and *Otinotus indicatus* (vide Table 7).

Funkhouser (1917, 1951), in his admirable account on this subject, has mentioned that one of the unsolved problems in connection with the mutual relationship between ants and membracids is that while some species are attended by ants, others are found unattended although there are apparently no morphological or anatomical differences to cause the distinction. He further states that nymphs of the species unattended by ants show the same extended anal tube as do the nymphs of those that secrete the fluid. Observations made in the course of the present studies have clearly revealed that species without eversible anal tubes never secrete the honey dew to the extent of attracting ants. For instance, *Coccosterphus minutus*, a species collected from different localities in South India, is not attended by ants in any of the localities; hundreds of nymphs of this species which have been examined in their natural habitat, on plants kept indoors, and specimens mounted on Balsam, have not been found to have eversible anal tubes; on the other hand, the two other species—*C. tuberculatus* and *C. paludatus*—whose nymphs have eversible anal tubes are invariably attended by ants of the genus *Crematogaster*. Thus, there appears a definite relation between the possession of an eversible anal tube and attendance by ants.

Another factor deciding the association of ants with membracids is the altitude at which the membracid is situated. For instance, in the present studies, *Telingana nigroalata* recorded from Kodaikanal Hills at an elevation of 5000′ is unattended by ants though this species occurs in numbers sufficiently large to be attracted by ants. The same species collected from plains has been found to be associated with *Camponotus* sp. This difference appears to be evidently due to scarcity of ants in Hill Stations.

As a rule, each species of membracid in a particular locality is attended by the same species of ants throughout the year. Exceptionally, the attendance of ants appears to be seasonal. For instance, *Camponotus compressus* attends on *Oxyrhachis rufescens* for the major part of the year, but during the rainy season the species is attended by *C. sericeus*. In the same manner, *Leptocentrus bauhiniae* is attended by *C. compressus* throughout the year while *Anoplolepis longipes* attends on the same membracid during the rainy months of September to December. The most noteworthy example, however, is *Leptocentrus rhizophagus* found on prop roots of *Ficus bengalensis* which has been observed to be attended by as many as four species of ants—*Camponotus compressus*, *Myrmicaria brunnea*, *Crematogaster* sp. and *Meranoplus bicolor*—in the months of August, September and October; during the other months this membracid is attended by two species of ants, *C. compressus* and *Crematogaster* sp.

It is also noteworthy that a particular species of ant attending on a particular membracid species in one locality is not very often associated with the same species of membracid in other localities. In the present studies, *Leptocentrus taurus* has been found to be attended by *C. compressus* throughout S. India, while the same species is reported by Misra (1923) to be attended by *Oecophylla smaragdina* in North India. This difference could be attributed only to chance proximity as stated by Capener (1962) and Haviland (1925).

In all the instances noted here, the ants caress the nymphs as well as the adults for the honey dew; however, in *Tricentrus pilosus* only the nymphs are attended. Further, the behaviour of the ant towards the membracid is not uniform in all the cases studied, the pattern being more or less definite for each of the attending species of ant. Some species of ants care only for the honey dew while others extend their solicitude to a greater degree. For instance, *Camponotus compressus* merely derives honey-dew from *Oxyrhachis rufescens* while *C. sericeus*, a seasonal attendant on the same species has been observed to drive the nymphs along the host plant in such a way as to harbour each nymph in a leaf axil. The ants also drive the sluggish adults of *O. rufescens* from one branch to another by nibbling their tegmina, preventing the deposition of eggs in the same localised spot of the host plant. They also consume the moulted skin of their "cattle" The behaviour of *Camponotus compressus* towards *Oxyrhachis rufescens* whcih has been observed cerefully is as follows: The worker ant applies its mouth close to the anal orifice of the larva whereupon the anal tube fringed with circlets of sensory hairs is moderately everted with a drop of liquid at the tip. If, however, the nymph does not emit the honey-dew the ant strokes it with its antennae at the anal tube. When the liquid exudes, the ant presses its jaws into the drop, grips it and moves away. If the nymph fails to respond to the coaxing of the ant, it bites at the sensory hairs of the anal tube and sometimes even thrusts its jaws into the anal tube but does no injury otherwise. In indoor experiments where nymphs have been reared on their host plants, the ants exhibit the same pattern of behaviour but the dying or dead nymphs are most often consumed by the ants. The behaviour of the ant to the intruder is noteworthy. When the twig containing a membracid colony is touched, the smaller worker minors drop down to the ground probably to warn the soldiers of the approach of any enemy. But the bigger worker minors and soldiers present on the twig keep moving excitedly round their "cattle" If the nymphs are touched with a needle, the nearer soldier or worker darts forward, catches the needle with its powerful mandibles and bites it viciously; other ants in the neighbourhood follow to help it and try to reach parts of the body of the intruder. They fight tenaciously, unless one shakes them off with a jerk of the needle.

The behaviour of *Oecophylla smaragdina* attending on *Oxyrhachis krusadiensis* is of interest. The worker ants enclose and shelter the membracid nymphs of all stages in cobwebby nests constructed by folding the edges of leaves and webbing them together by salivary threads secreted by the ant larvae which are held by the workers between their mandibles and carried to the site of nest construction. When the nymphs become adults, the ants lets them out of the nest so that adults of this membracid species have not been encountered within the nests. The worker ants also keep a fierce watch over their "cattle".—At the slightest disturbance, large numbers of workers drop down to the ground excitedly and climb the body of the intruder. In the meanwhile the nest is surrounded by many workers ready to attack the intruder and also to repair the nest should it be damaged. The bite of this ant is most virulent and painful.

In many instances, close observations have revealed dense aggregations of ants at the cephalic end of the membracids the significance of which remains obscure. Often, groups of ants have been noticed to collect at spots previously occupied by membracid larvae appearing as if feeling on the congealed coagulated anal secretion left by the latter.

The advantages derived by the membracids from the symbiotic relationship with ants in nature are obvious. The ants keep away many of the predators such as spiders, lady bird beetles, riduviid bugs, etc. Further, according to Hood (1952) the expulsion of the anal secretion through the caressing of ants enables the membracids to reduce the pressure with which the plant sap enters the gut. In the absence of ants, the nymphs have to eliminate the honey dew by forcible extrusion. This theory has its own value considering the enormous quantity of the anal secretion expelled by many membracid nymphs and their constant association with ants.

Rice (1893) is of the opinion that disturbance by ants delays metamorphosis in *Entylia sinuata*, while Branch (1913) dealing with the biology of the same species states that in the absence of ants the nymphs fail to moult successfully and die before maturity. The results of rearing experiments conducted in the course of the present studies on local species never support the views of Branch and Rice since nymphs of all species that are normally attended by ants in their natural habitat successfully moulted and metamorphosed into adults irrespective of the presence or absence of ants. Likewise, the feeding habits of the membracids are in no way affected in spite of large numbers of ants swarming over them. The egg-laying process, however, is reported by Mishra (1923) to be affected. Dealing with the relation of *Oxyrhachis tarandus* and *Camponotus compressus* he states: "The ants, at times, are so persistent in their demands for honey dew, that the egg-laying females have been observed to postpone egg-laying to attend to their demand for the supply of the viscid fluid" Present observations on the same species never support this view since the membracids are apparently oblivious of the presence of ants and carry on their functions with equal serenity whether ants are present or not.

No reference has so far been made in literature about the association of membracids with insects other than ants except for Müller (1873, 1874) and Anonymous (1874) and also the interesting account given by Hood (1952) on the relationship of two species of bees—*Trigona hyalinata* var. *branneri* Ckll. and *T pallida* Latr.—with the membracid *Aconophora* sp. at Brazil. The notable feature in this case is that the same membracid colony is stated to be attended by the bees and ants. While the bees are diurnal attendants, the ants, a subspecies of *Camponotus* (*Myrmoturba*) *substitutus* Emery, is stated to be exclusively a nocturnal visitor. Further, each bee is stated to have "its own limited territory of exploitation, for if all the bees are removed from a group of nymphs in the morning, no other bees will take their places during the day" In the course of the present studies, where dense aggregations of *Oxyrhachis tarandus* and *O. rufescens* occur, a dipteran fly of the family Locheidae, identified as *Silba* sp. has been observed as a sporadic visitor. Usually the fly frequents the spots of twigs on the host plant previously occupied by membracid population and appears to dissolve and consume the congealed mass of expelled anal fluid left behind by the nymphs. At times, however, it frequents the nymphs when the latter are found unattended for a while by the ants; the fly caresses the nymphs, licks up the honey-drop and quickly moves away. This fly, which is an exclusive diurnal visitor, appears to be active at first but becomes rather sedate probably under the influence of the honey dew.

Although the camponotine ants guard the membracid nymphs keeping away the intruders from the territory of their exploitation, a beetle of the family Anthicidae identified as *Formicomus* nr. *semiopacus* which mimics the ants in form and action has been noticed to contact nymphs of *heptocentrus taurus* on *Ipomaea biloba*. This bettle mingles freely among the ants. Its behaviour towards the membracid nymphs in the act of caressing for getting the honey dew is identical to that of ants, and it appears to derive most of its food in this manner. Usually four or five beetles are crowded round each nymph. When disturbed, the beetle very often falls down suddenly just like ants do. sometimes, the beetle feigns death on falling to the ground, or sticks on to the host plant of the membracid, hiding itself and remaining quiet. When one attempts to catch the beetle from its hiding place, it runs with great agility.

(*h*) *Protective coloration and mimicry*.—The characteristic colour patterns of the nymphs-brown, green and grey-blend very perfectly with those of the leaves and bark of the host plants affording them excellent protection. For instance, the nymphs of *Coccosterphus minutus* which occupy the terminal parts of the tender twigs of *Prosopis spicigera* closely resemble the tiny unfolding leaves. The extraordinarily long pronotal anterior process of the fifth instar nymph of *Leptocentrus varicornis* strikingly stimulates the shape and colour of the stipular spines of its host plant, *Zizyphus jujuba*. Nymphs of *Tricentrus pilosus*, *T congestus*, *Otinotus oneratus* and *O. obliquus* with their extreme dorso-ventrally flattened bodies remain closely adpressed to their host plants and escape the attention of even the most careful observer. In some cases the dorsal protuberances closely resemble the irregular surface of bark both in colour and texture.

While the nymphs of all species are cryptically coloured, the adults of most of the local species such as *Otinotus*, *Leptocentrus* and *Oxyrhachis* with their characteristic pronotal processes, are most conspicuous on their host plants. However, *Coccosterphus tuberculatus* with its black or rusty brown colour, and oval shape resembles most effectively the small undeveloped dry fruits of its host plant, *Morinda tinctoria.* The light brown colour of *C. paludatus* matches so perfectly with the colour of the prop roots of *Ficus bengalensis* and the twig of *Lawsonia alba* as to make it inconspicuous.

(*i*) *Ecological factors.*—Physical factors of the environment such as temperature and moisture have been found to have a decided effect on the embryonic development and duration of nymphal stages in the various species of membracids. These factors also play an important role in the population density of the species. Though all the local species appear to be influenced by the environmental factors, detailed observations in laboratory and field records were made only on *Otinotus oneratus* since this species, besides being gregarious, is available throughout the year on several host plants and it can also be reared with the least difficulty; the eggs of this species are only partially embedded in the bark so that actual counting and exact times of hatching could be made. The observations were made for 12 months commencing from April, 1964, and the results with regards to variations in the durations of egg-stage and nymphal period are tabulated (Table 8).

TABLE 8

Duration of egg stage and nymphal stage of Otinotus oneratus *recorded during the year* 1964-'65.

Months	Max. temp. C.	Rainfall in mm.	R.H. %	Egg stage in days	Nym-phal stage	Total No. of days for life-cycle	Average in days
April	35.9	—	62	10—12	30—34	40—46	43
May	39.1	1.6	58	10—14	28—32	38—46	42
June	36.9	27.3	59	9—14	24—30	33—44	38½
July	34.3	104.6	71	9—12	22—27	31—39	35
August	33.2	193.2	76	8—10	22—26	30—36	33
Sept.	32.1	130.9	77	8—10	22—26	30—36	33
Oct.	32.7	144.0	78	7—9	24—28	31—37	34
Nov.	28.7	735.0	86	12—15	29—36	41—51	46
Dec.	28.3	24.8	78	12—15	28—33	40—48	44
Jan.	28.7	0.9	74	10—12	28—34	38—46	42
Feb.	30.1	9.2	79	7—9	22—26	29—35	32
March	31.8	—	75	7—9	23—29	30—38	34

It would appear from the table that the months of November, December and January are marked by lower temperatures, while April, May and June are characterised by high temperatures, lower relative humidity and almost complete lack of moisture. On the other hand, the months of February, March, August, September and October are noted for moderate temperature and moisture due to occasional rainfalls as well as high relative humidity. Under these ideal conditions the duration of egg-stage was found to range from 7 to 10 days; the duration of nymphal period, likewise, was found to be shorter, ranging from 32-34 days.

The upper limits of 15 days and 36 days respectively for the egg-stage and the nymphal stage noted against the month of November are obviously due to the combined effect of low temperature and excessive rainfall soaking the eggs and bringing about delayed hatching; however, under such conditions egg mortality is insignificant since the eggs are laid high up from ground level and this situation precludes the possibility of the eggs being damaged.

Egg masses kept in test tubes free from moisture never hatch out within the normal time; such eggs when supplied with a little amount of moisture by keeping them on a wet blotting paper, hatch overnight. While this shows that moisture is absolutely essential, presence of too much of water is detrimental. Nymphal development also requires moisture; nymphs reared in the laboratory by keeping them on twigs of host plants dipped in water, congregate towards the bases of twigs. An optimum moisture is indispensable for normal moulting, especially for the last nymphal instar which, when kept on drying twigs take a longer time for moulting; often, the adults emerging from such nymphs present irregularities such as abnormal asymmetrical horns and impaired crippled wings.

Humidity also appears to have some influence on hatching and nymphal development. As indicated in the Table, the months of April to June are characterised by low relative humidity besides lack of moisture, and these conditions not only delay hatching to a considerrble extent, but also retard nymphal development. It may be infeared that the factors entering into the life history of *Otinotus oneratus* are rather complex; two or more factors combine to alter the rate of metabolism which, in turn, accelerates or retards either the embryonic or the nymphal development or both.

(*j*) *Natural Enemies.*—Incidence of parasitism in membracids has been reported by many workers though very few attempts have hitherto been made to make a detailed study. Funkhouser (1951) has stated "A detailed study of egg parasitism by chalcids has been made by the writer for an African species, and which is to appear as a separate report. " However, the report referred to never appears to have been published anywhere! As early as 1886, Jack noted egg parasitism in *Ceresa bubalus*. Ashmead (1888) found *Trichogramma seresarum* attacking the eggs of *Ceresa bubalus*. Funkhouser (1915) was able to rear the same species from *Vanduzea arquata*. Regarding mymarid parasites, Haviland (1925) made mention of an unidentified species and the mode of parasitization. Hodgkiss (1910) reported *Polynema striaticorne* from *Ceresa bubalus* but it was Balduf (1928) who worked out in detail the life history of this parasite. Yothers (1934) made a passing reference to the eulophid parasite, *Tetrastichus* sp. attacking the eggs of *Stictocephala inermis*.

References to the hymenopterous and dipteran parasites attacking the nymphs of membracids have been made by Matausch (1911) and Funkhouser (1951) though the larvae could not be reared to maturity. Nevertheless, it was stated by Matausch (1911) that the parasitic larvae caused castration on the host. Kornhauser (1917, 1919) was successful in rearing to maturity *Aphelopus theliae*, a dryinid nymphal parasite of *Thelia bimaculata* and discussed at length the effects of parasitism on the host. This was followed by contributions from Meisenheimer (1930) on the same topic. More recently, Capener (1962) has brought to light the occurrence of a hymenopterous genus, *Prionomastix* on the nymph of *Oxyrhachis latipes*, and a dipteron, *Dorilas* sp. parasitising the nymphs of an *Oxyrhachis* sp.

Membracids have been found to be prone to stylopisation in their adult stage and studies in this direction have been made by Subramaniam (1927, 1932) on *Indoxenos membraciphagum*), and Panda and Behura (1956) on *Indoxenos* sp. parasitising *Otinotus oneratus* in India. Jordan (1953) reported a strepsipteran parasite on *Stictocephala inermis* while Capener (1962), recording the incidence of stylopisation in *Oxyrhachis imperialis*, states that the stylopised adults, as far as could be judged, suffered only inconvenience.

Besides entomophagous parasites, several predators of membracids are on record. Observations made in this direction by Wildermuth (1915), Funkhouser (1917), Beal (1918), Mc Atee (1918, 1932), Knowlton and Harmston (1941, 1946) and Aldous (1942) indicate that insectivorous birds occasionally prey upon membracids as a regular routine or accidentally, the nymphs being preferred to the adults. Apart from birds, other predators such as spiders, asilids and mantids have been stated to catch membracid nymphs occasionally (Bromley, 1914), Funkhouser (1951). Acarines were reported to feed on membracid eggs (Wildermuth, 1915, Funkhouser, 1917, Yothers, 1934). Reinhard (1925) observed the wasp *Hoplisus costalis* hunting after tree hoppers. Capener (1912) states that nymphs and adults form the prey of a wasp of the genus *Gorytes*.

In the course of the present studies, the eggs of several species of membracids were found parasitised by 10 species of hymenopterous parasites as recorded below. These are of interest as they are recorded for the first time as parasitic on the respective species of membracids.

**PARASITE SPECIES*	*FAMILY*
Gonatocerus sp.	Mymaridae
Gonatocerus narayani (Subba Rao & Kaur)	,,
Lymnaenon sp.	,,
Aphelinoidea sp.	Trichogrammatidae
Ufens sp.	,,
Tumidiclava sp.	,,
Centrodora sp.	Eulophidae
Aphytis sp.	,,
Azotus sp.	,,
Chartocerus sp.	Thysanidae

*Dr. B. D. Burks who examined and determined the parasites states that the specimens not named to species are probably undescribed.

A notable feature in many of these parasites is the lack of absolute host specificity; for instance, the eggs of *Oxyrhachis rufescens* are parasitised by three different species namely, *Gonatocerus* sp., *Aphelinoidea* sp. and *Centrodora* sp., all of which are also capable of attacking the eggs of *Otinotus oneratus*. The incidence of parasitism on the various species of membracids studied here is given in Table 9.

The bionomics of these parasites have been studied along with brief descriptions of their immature stages adopting the methods mentioned earlier, and the degree of infestation by *Gonatocerus* sp., *Aphelinoidea* sp. and *Centrodora* sp. on the eggs of *Oxyrhachis rufescens* and *Otinotus oneratus* was analysed.

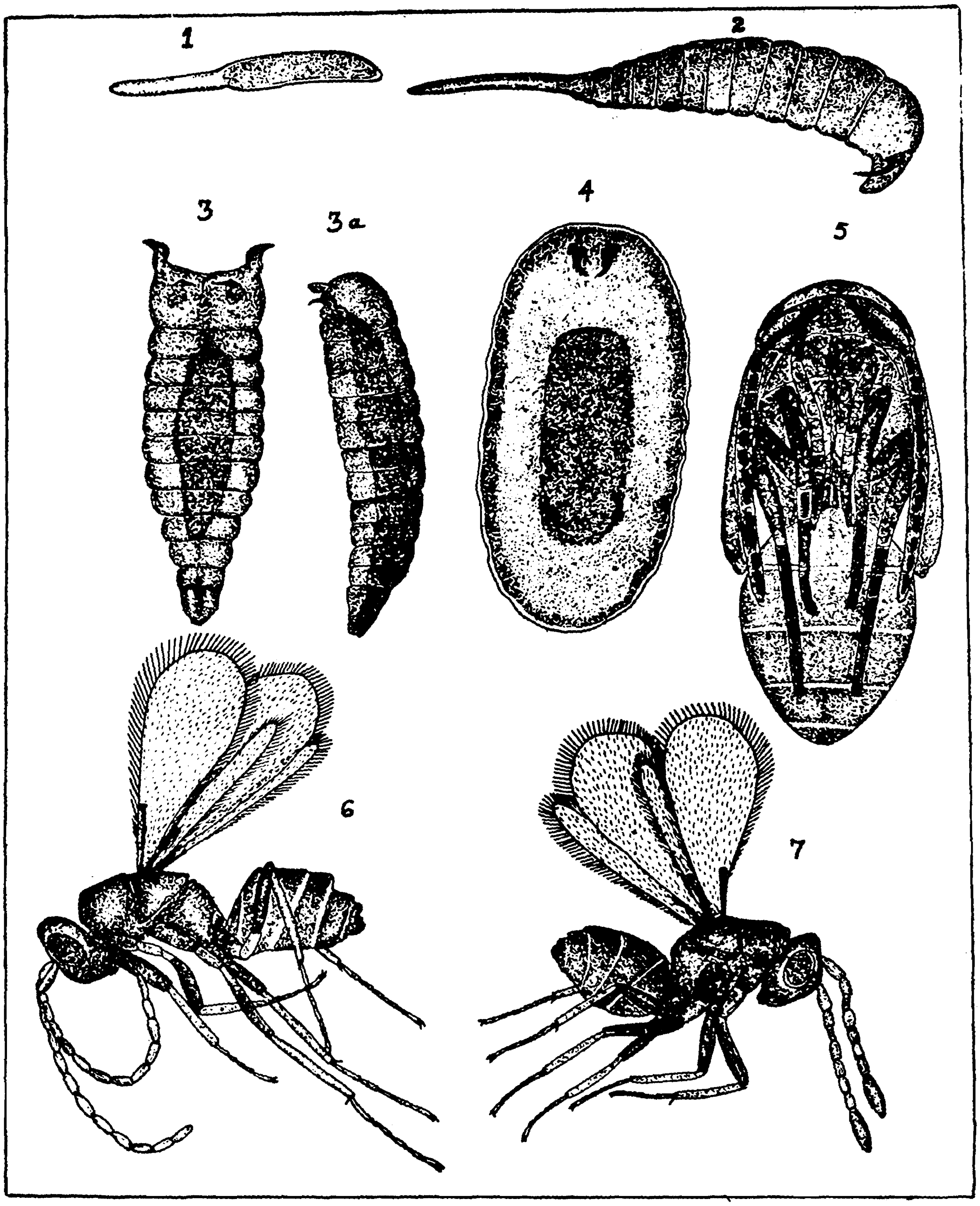
Gonatocerus sp.

(Text-fig. 1)

Egg, 0.240 mm. long, stalked; stalk 0.056 mm. long, nearly one-third the length of main body; main body 0.179 mm. long, elongate oval with a delicate flexure towards the middle; chorion smooth, lacking sculpture. Duration of egg stage is about one day. First instar, just slightly larger than egg, 0.35 mm. long, mymariform, but devoid of setae, body elongate, spindle-shaped; head followed by ten segments; caudal end attenuated, drawn out into a tapering structure; integument thin and translucent recalling the condition of *Lymnaenon effusi* described by *Bakkendorf* (1934); mandibles prominent, feebly chitinised, movable, capable of closing upon one another; tail about one-third of body length; duration about two days. Second instar, 0.8 mm. long, tail almost disappeared; segmentation indistinct; cephalic end broader with a pair of conical processes, caudal end smoothly rounded; duration about a day. Third instar, 0.95 mm. long, sacciform, filling snugly the entire cavity of host egg; mandibles chitinised and projecting out; immobile; duration 2-2½ days. Pupa, 0.95 mm. long, exarate, colour at first light yellow, gradually turning to black; duration 7-10 days.

The parasitised membracid eggs are readily recognisable by the colour changes they show, associated with the developmental phases of the immature stages; such eggs first become yellow; then the chorion shows white and black hues; subsequently the black colour becomes more pronounced as the pupal stage is reached. It may be mentioned here that eggs of *Ceresa bubalus* parasitised by *Polynema striaticorne* are stated to exhibit a similar colour change (Balduf, 1928) due to the deposition of a black pigment in the vitelline membrane of the host egg.

Adults exhibit sexual dimorphism, the males being about two-thirds as long as the females; male antenna 13-segmented, longer than body, all antennal segments equal in length; female antenna 11-segmented, shorter, segments 3-6 very short, terminal segment longest and club-shaped; specimens reared from *Oxyrhachis rufescens* and *Otinotus oneratus* at Madras have antennal segments 3-6 very much compressed, broader than long and similar to each other, segments 7-10 indentical; all segments uniformly light brown. Specimens reared from *Oxyrhachis krusadiensis* have a different antennal structure in female, the 3rd and 4th segments smallest and similar, 5th segment much longer than 3rd and equal to 2nd and 7th; 6th segment slightly longer than 4th; 8th segment longer than 6th but shorter than 7th and 9th; coloration of 1st and 2nd antennal segments yellowish, rest dark brown. Dr. B. R. Subba Rao who examined these two types of specimens is of the opinion that they would prove to be distinct species.



Text-fig. 1. *Gonatocerus* sp.

1. Egg. 2. First instar larva. 3. Second instar dorsal view. 3a. Second instar view. 4. Mature larva. 5. Pupa. 6, Adult male. 7. Adult female.

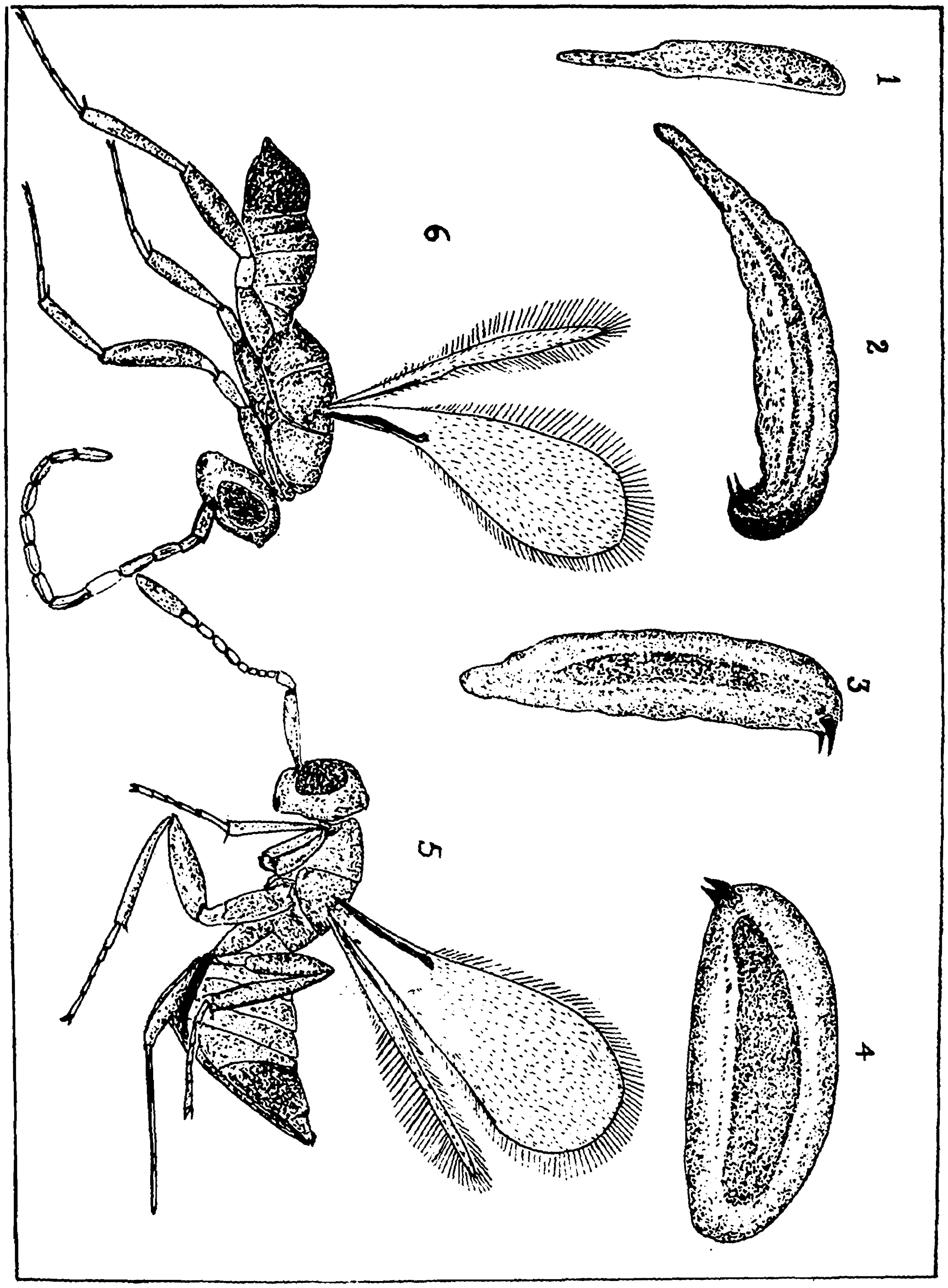
TABLE 9

Incidence of parasitism in the South Indian Membracidae.

Name of membracid	Gonatocerus sp.	G. narayani	Lymnaenon sp.	Apheli-noidea sp.	Ufens sp.	Tumidiclava sp.	Centrodora sp.	Aphytis sp.	Azotus sp.	Chartocerus sp.
Oxyrhachis tarandus	+			+			+			
O. rufescens	+			+			+			
O. krusadiensis	+			+			+			
O. minusculus				+			+			
O. uncatus	+			+			+			
Leptocentrus taurus					+			+		
L. leucaspis		+			+		+		+	
L. rhizophagus								+		
L. varicornis		+								
L. bauhiniae						+				
L. bajulans		+			+					
L. nigra					+					
L. moringae					+				+	
Telingana nigroalata							+		+	
Otinotus oneratus	+			+			+			
Tricentrus pilosus		+								
T. albomaculatus		+		+						
Gargara mixta		+	+							
G. extrema		+		+						+
G. rustica		+	+							+
Coccosterphus minutus			+							+
C. tuberculatus			+							
C. paludatus			+							

Gonatocerus narayani (Subba Rao & Kaur)

(Text-fig. 2)



Text-fig. 2. *Gonatocerus narayani* (Subba Rao and Kaur)

1. Egg. 2. First instar. 3. Second instar. 4. Third instar. 5. Adult female. 6. Adult male.

This species attacks several species of *Leptocentrus*, *Tricentrus* and *Gargara*.

Egg similar to that of *Gonatocerus* sp. but smaller, 0.19 mm. long. First instar, 0.25 mm. long, intermediate between mymariform and sacciform types; body elongate, segmentation obtcure; tail short, cylindrical; mandibles prominent, turned downwards and backwards. Second instar, 0.35 mm. long; body elongate-oblong, caudal end short, broadly rounded; mandibles mobile. Third instar, 0.50 mm. long, robust, sac-like, slightly arched, mandibles short, conically pointed, rigid. Pupa, similar to that of *Gonatocerus* sp. Adults sexually dimorphic; male about two-thirds as long as female with 13-segmented antennae; female with antennal segments 3-6 longer than wide, 7-10 identical.

Lymnaenon sp.

(Text-fig. 3)

A very small mymarid parasitising *Gargara mixta* and *G. rustica*. Egg, 0.18 mm. long, stalked, stalk slender, straight, 0.08 mm. long, body of egg elongate-oval, slightly longer than stalk, translucent. First instar, 0.2 mm. long; modified from typical mymariform larva, body devoid of bristles; head with a pair of blunt lobes and sharp mandibles; anterior one-third of body broader with faint indications of segmentation; posterior two-thirds gradually tapering to tail which is more than one-fourth the body length. Second instar, 0.45 mm. long, typically sacciform. Pupa, 0.7 mm. long, similar to that of *Gonatocerus* sp.

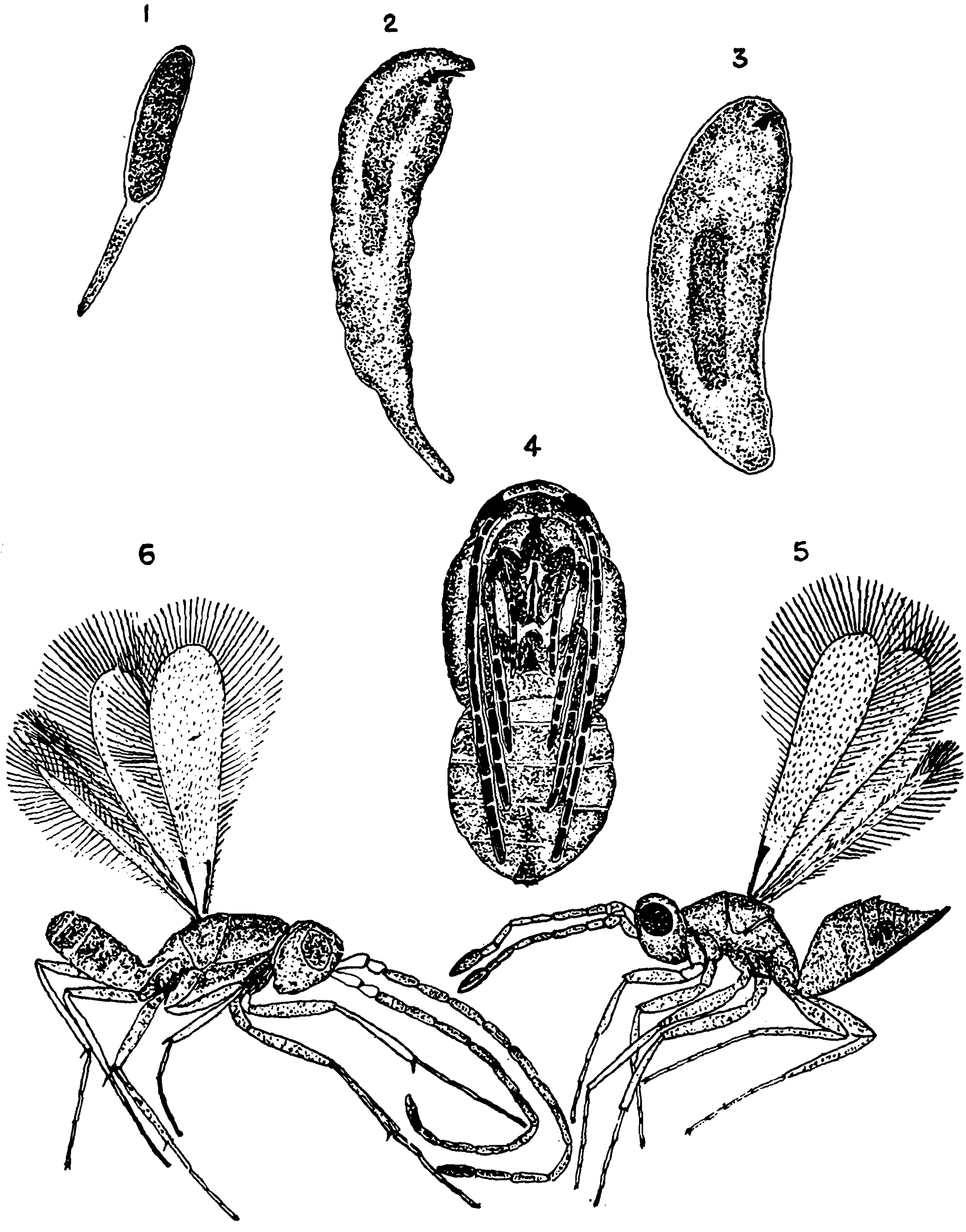
Adults sexually dimorphic, female with posterior end of abdomen tapering, ovipositor half as long as abdomen, antennae 9-segmented, shorter than body; in the male, abdomen shaded with black, posterior end broadly rounded, antennae 13-segmented, about one and three-fourth times longer than body.

Aphelinoidea sp.

(Text-fig. 4, I–VIII)

This trichogrammatid parasite is recorded for the first time as parasitising membracid eggs capable of developing in the eggs of many species of *Oxyrhachis*, all the local species of *Coccosterphus* and in the eggs of *Otinotus oneratus*.

Egg, 0.19 mm. long, maximum width 0.05 mm., stalked, stalk about one-fourth as long as main body, 0.05 mm. long; main body of egg elliptical; chorion smooth. First instar, 0.29 mm. long, sacciform; mandibles prominent, unchitinised, directed upwards; a pair of small fleshy lobes visible at the base of mandibles. Second instar, 0.40 mm. long, similar to preceding stage, Mature larva, 0.95 mm. long, robust, segmented; head distinct, mandibles turned upwards. Prepupa, 0.95 mm. long, body irregular, anterior region more or less segmented;



Text-fig. 3. *Lymnaenon* sp.

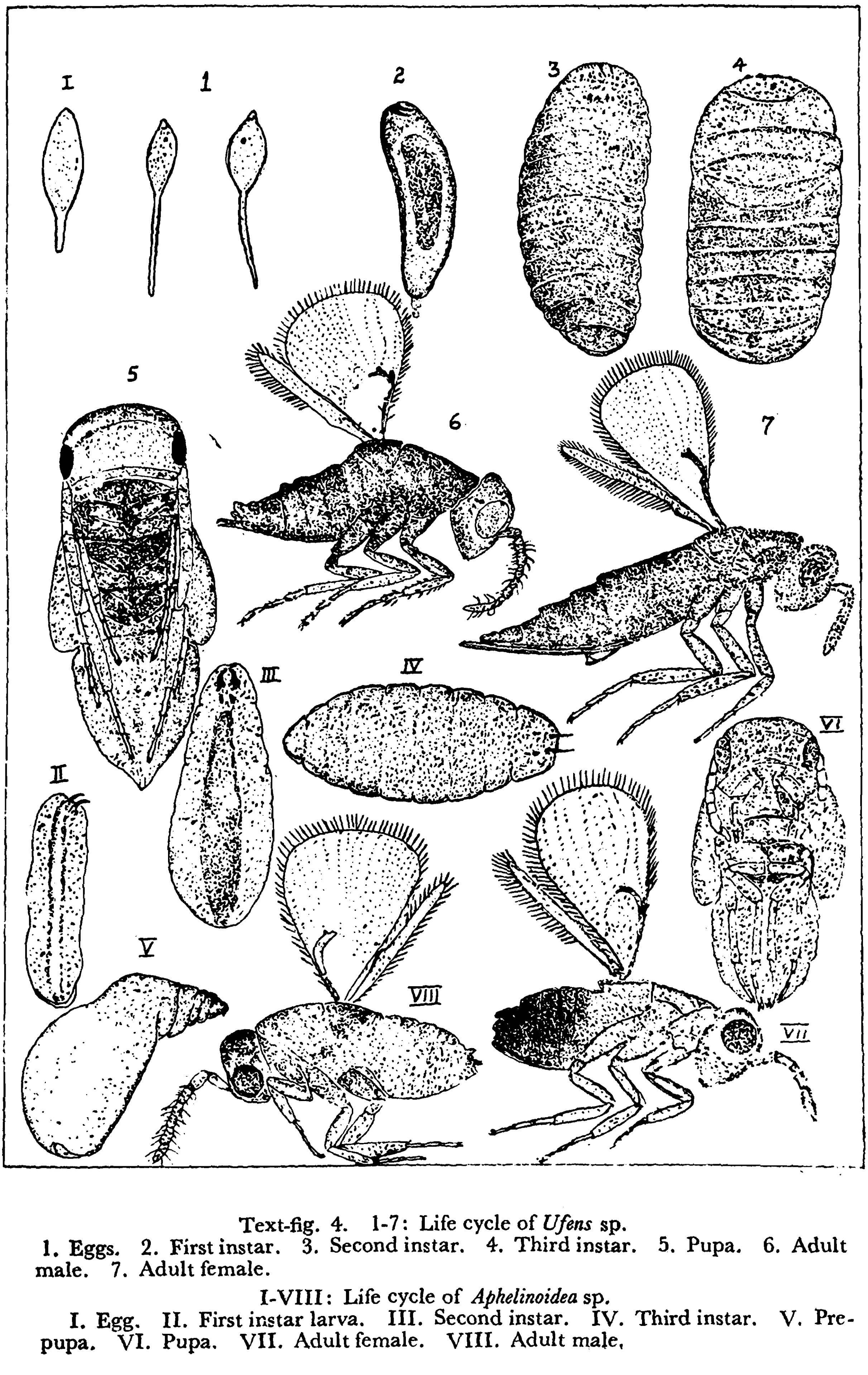
1. Egg. 2. First instar. 3. Second instar. 4. Pupa, ventral view. 5. Adult female. 6. Adult male.

mandibles apparently absent. Pupa, 0.80 mm. long, exarate, at first translucent, subsequently turning to black.

Adults small, measuring 0.85-1.2 mm. long; female with antennae less hairy; male with highly hairy antennae.

Ufens sp.

(Text-fig. 4, 1–7)



Text-fig. 4. 1-7: Life cycle of *Ufens* sp.

1. Eggs. 2. First instar. 3. Second instar. 4. Third instar. 5. Pupa. 6. Adult male. 7. Adult female.

I-VIII: Life cycle of *Aphelinoidea* sp.

I. Egg. II. First instar larva. III. Second instar. IV. Third instar. V. Prepupa. VI. Pupa. VII. Adult female. VIII. Adult male.

Although recorded as an egg parasite of Cicadellid eggs (Clausen, 1940) this trichogrammatid has not hitherto been known to parasitize membracid eggs. The eggs of various species of *Leptocentrus* are attacked by this species.

Egg, 0.27 mm. long, stalked, stalk 0.180 mm. long, slender, flexible, gradually tapering; body of egg 0.084 mm. long, 0.046 mm. wide, broadest at middle and produced into a conical papilla-like outgrowth at the opercular end. First instar, 0.45 mm. long, elongate, unsegmented, caudal end produced as a small tail; mandibles small, more or less chitinised and mobile. Second instar, twice as long as first instar (0.85 mm.), distinctly 13-segmented, mandibles reduced, caudal process absent. Third instar, 1.0 mm. long, segments appearing rather compressed with uneven margins, mandibles inconspicuous; larva motionless, filling the lumen of host egg. Pupa, 1.2 mm. long, similar to that of *Aphelinoidea* sp.

Adults exhibit sexual dimorphism as in *Aphelinoidea* sp.

Tumidiclava sp.

This trichogrammatid which is smaller than *Ufens* sp. has been recorded only from the eggs of *Leptocentrus bauhiniae*.

Egg, 0.18 mm. long, stalked, stalk about one-fourth the main body of egg and very rigid; main body of egg elongate oval with sides parallel. First instar, 0.25 mm. long, sacciform, pale white, caudal process absent; mandibles distinct and movable. Second instar, 0.38 mm. long, rubust, faintly segmented, with undulate margins, mandibles very short. Pupa 0.8 mm. long, similar to that of *Ufens* sp.

Adults, 0.9-1.1 mm. long; similar to *Ufens* sp. but forewings shaded with black.

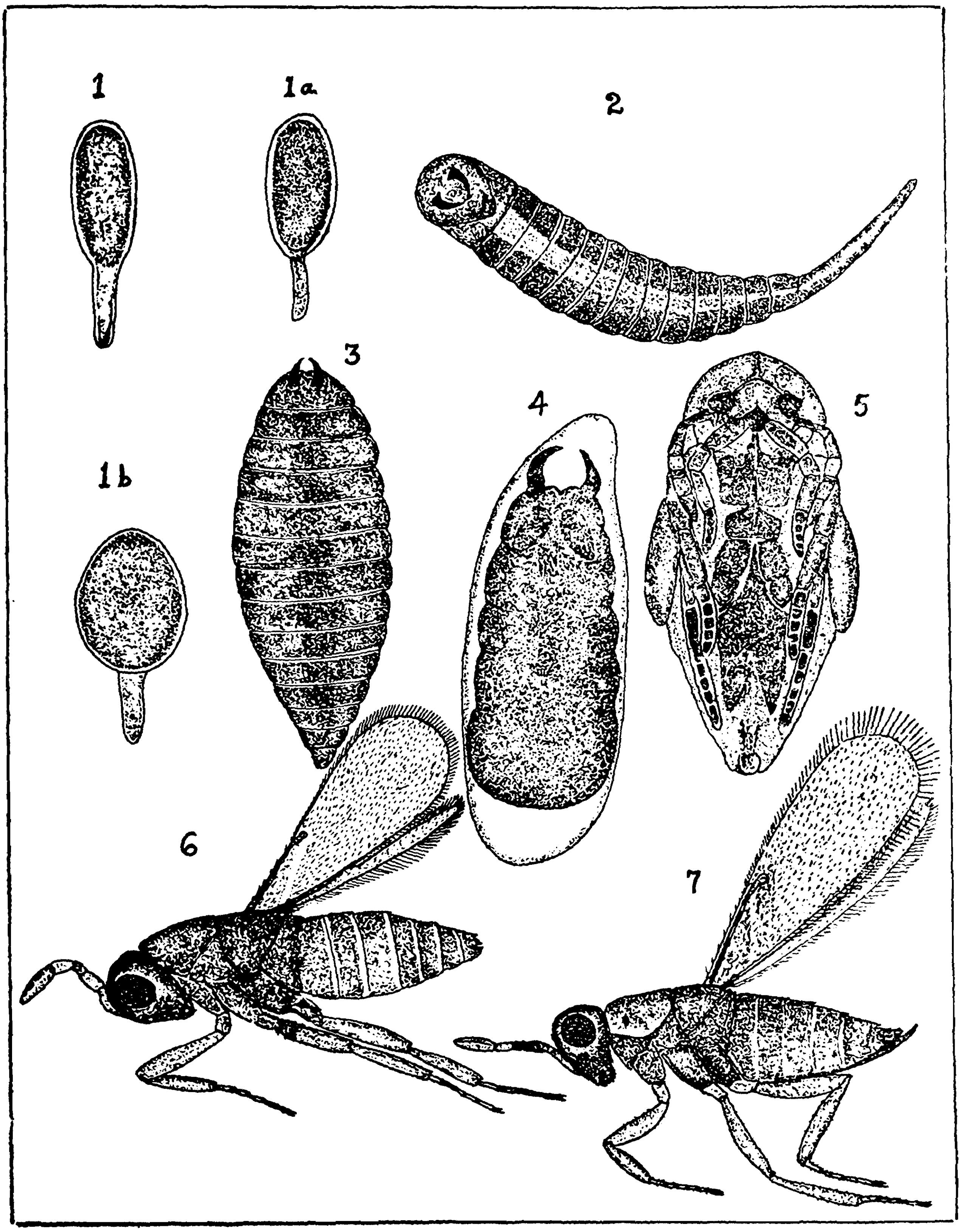
Centrodora sp.

(Text-fig. 5)

Although not recorded so far as parasitizing membracid eggs, species of *Centrodora* have been known to attack other groups of insects. *Centrodora speciosissima* (Girault) is recorded as parasitic on the cecidomyiids; *C. xiphidii* Perk. parasitises the eggs of a locustid, *Xiphidium varipenne* Swezy while *C. cicadae* Silv. develops in the eggs of *Cicada plebeja* Scop. (Clausen, 1940).

Egg, 0.20 mm. long, stalked, main body of egg elongate oval, 0.15 mm. long, stalk robust, 0.05 mm. long; chorion lacking sculpturing. Dissection of ovary revealed only two mature eggs in each ovary in almost all specimens; in one specimen, an exceptionally large egg was noticed. First instar, 0.25 mm. long, caudate; body distinctly segmented, tail about one-fourth as long as body; mandibles short and turned to each other. Second instar, 0.5 mm. long; tail reduced, larva tending towards hymenopteriform; posterior end broadly rounded;

mandibles strongly chitinised and protruding out. Third instar, 0.75 mm. long, segmentation almost obliterated, larva tending towards sacciform; mandibles extraordinarily prominent. Pupa, 0.8 mm. long; flattened dorsoventrally; jet black in colour.



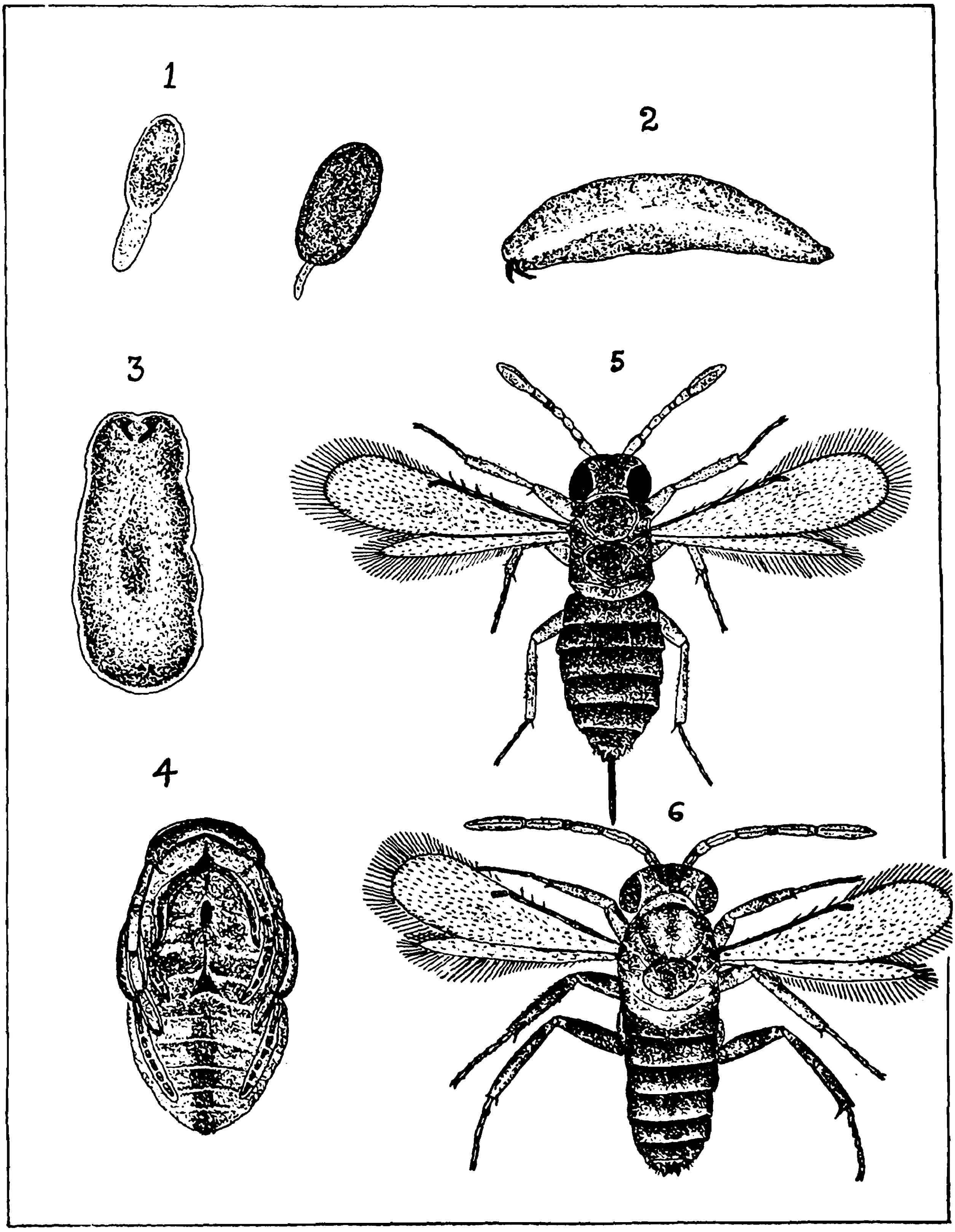
Text-fig. 5. *Centrodora* sp.

1. Ovarian egg. 1a. Egg during incubation. 1b. Abnormal egg. 2. First instar. 3. Second instar. 4. Mature larva. 5. Pupa, ventral view. 6. Adult male. 7. Adult female.

Adult, female 1.2-1.3 mm. long, ovipositor extending a little beyond abdomen; male 1.0-1.1 mm. long.

Aphytis sp.

(Text-fig. 6)



Text-fig. 6. *Aphytis* sp.

1. Ovarian egg. 1a. Egg during incubation. 2. First instar. 3. Second instar. 4. Pupa. 5. Adult female. 6. Adult male.

This eulophid is found to parasitize *Leptocentrus leucaspis* and *L. bajulans*.

Egg, 0.14 mm. long; segmentation almost obscure, body slightly arched in the middle, caudal process absent; mandibles recurved. Second instar, 0.75 mm. long; nearly similar to that of *Centrodora* sp. Pupa, 0.9 mm. long, dark brown, similar to that of *Centrodora* sp.

Adults, exhibiting sexual dimorphism in the antennal structure and abdominal terminalia.

Azotus sp.

This eulophid species is of special interest since it develops as a primary egg parasite of *Leptocentrus rhizophagus*, *L. nigra* and *L. moringae* and as a hyperparasite of *Ufens* sp. The egg and immature stages of *Azotus* sp. are similar to those of *Aphytis* sp. The pupal period, however, is comparatively shorter.

Chartocerus sp.

(Text-fig. 7)

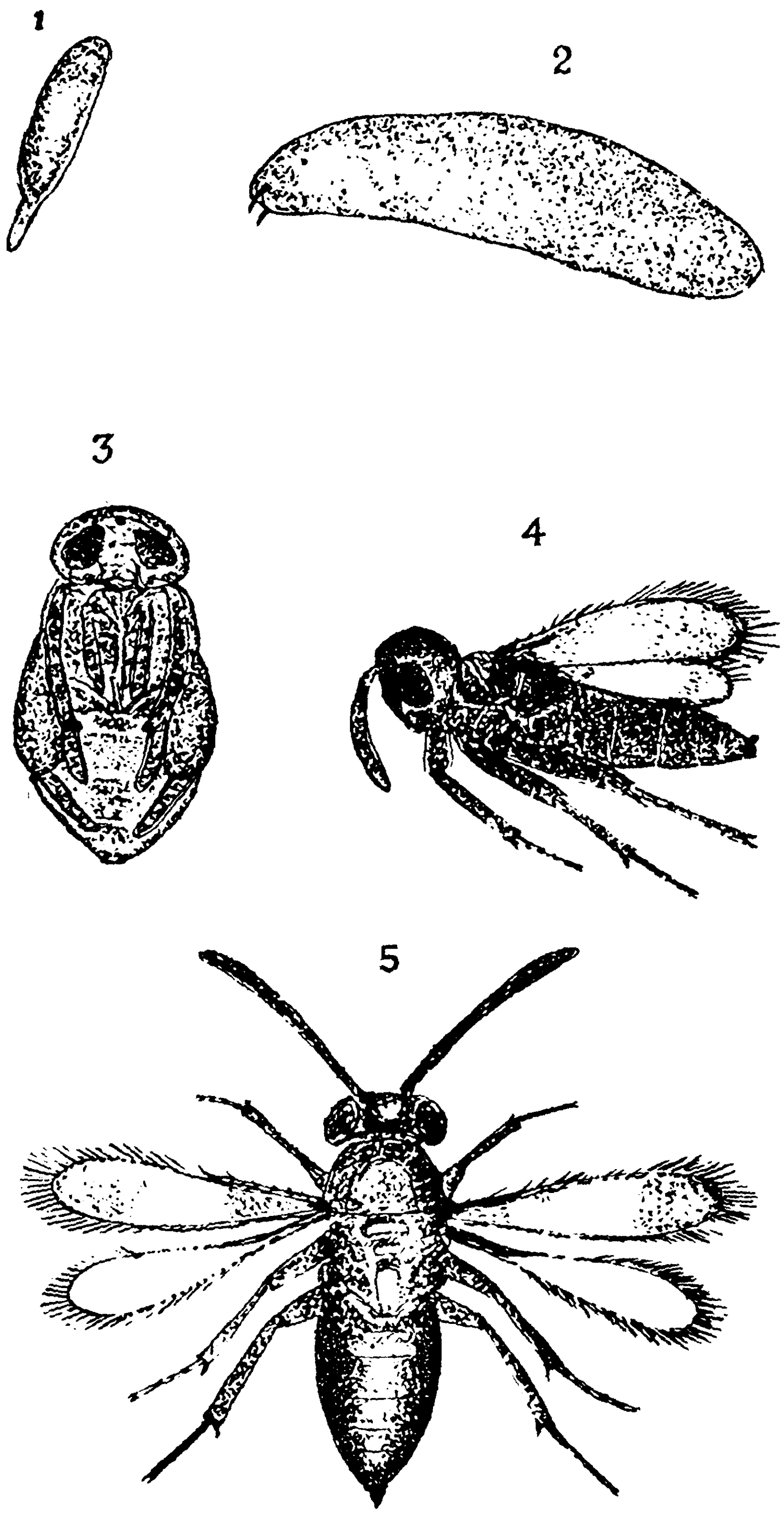
This thysanid parasite is rather rare in its incidence as an egg parasite and recorded from two species of *Gargara*—*G. extrema* and *G. rustica*—and *Coccosterphus tuberculatus*.

Egg, 0.19 mm. long, stalked, elongate-oval, slightly arched, lacking sculpture; stalk short and rigid, 0.05 mm. long. First instar, 0.22 mm. long, elongate, without any traces of segmentation, mandibles pointed; second instar similar to preceding stage, sacciform, mandibles more prominent. Pupa as in *Centrodora* sp.

Adults are very small, 0.75-1.0 mm. long, black, shining, both the sexes somewhat similar in size.

Degree of infestation:

Twigs containing large numbers of egg masses of *Oxyrhachis rufescens* and *Otinotus oneratus* on the host plant, *Prosopis spicigera*, located within the College campus were cut and each twig kept in test tubes loosely plugged with cotton. Since the eggs of these two membracid species are only partially embedded in the bark projecting out for the most part, it was possible to count the number of eggs in each mass. On the emergence of *Gonatocerus* sp., *Aphelinoidea* sp. and *Centrodora* sp. from their hosts, the number of each species was counted, From these data the percentage of parasitization by each species during the different months was calculated for the two host species. The nature of emergence holes is distinct in these 3 species of parasites (large rounded hole near the exposed end of host egg in *Gonatocerus* sp., small rounded hole either at the pole or at the side of host egg in *Aphelinoidea* sp., irregular hole at the exposed end of host egg in *Centrodora* sp.) making it possible to presume the species of parasite that might have emerged even if some egg masses contained such emergence holes at the time of their collection.



Text-fig, 7. *Chartocerus* sp.
1. Egg. 2. First instar. 3. Pupa. 4. Adult male. 5. Adult female.

The twigs containing egg masses were kept moist so that young ones could emerge from unparasitized eggs. The numbers and percentage of eggs parasitized, number of young ones emerged and number

TABLE 10

Duration of life-cycle and sex-ratio of the parasites.

Parasite	Larval period	Pupal period	Total number of days for completing life-cycle			Sex-ratio Female: Male
			Min. No. of days	Max No. of days	Average No. of days	
Gonatocerus sp.	3–4	7–10	12	15	13	5:2
G. narayani	4–5	8–13	15	21	18	3:1
Lymnaenon sp.	2–3	7–9	11	13	12	3:1
Aphelinoidea sp.	2–3	11–16	15	20	18	3:1
Ufens sp.	3–4	10–25	15	30	25	2:1
Tumidiclava sp.	2–3	6–10	10	14	12	5:2
Centrodora sp.	4–5	11–19	17	25	21	3:1
Aphytis sp.	4–5	14–19	20	25	22	3:2
Azotus sp.	3–5	6–9	12	15	14	3:2
Chartocerus sp.	5–7	14–18	22	26	24	1:1

and percentage of egg mortality due to factors other than parasitism are tabulated (Tables 11 & 12).

Incidence of stylopisation appears to be extremely rare as far as the present observations on South Indian membracids have revealed. Only one species, *Leptocentrus taurus*, a very common polyphagous membracid was found to be parasitized by an unidentified strepsipteran. Each stylopised individual had one to three large, oval, nodular outgrowths invariably located at the sides of the abdomen. Since only very few individuals have so far been known to be parasitized, a detailed study was not possible. All the same the incidence is of interest in view of some stylopised membracids appearing normal, while others show abnormalities in the disposition of the pronotal processes (Text-fig. 8). Closer examination of the parasitized individuals revealed that those which suffer abnormal pronotal development present a somewhat shrunken ochraceous appearance without complete skin pigmentation. It is therefore inferred that attack by strepsiptearn parasites on the membracids which have just emerged from the last nymphal skin when complete chitinisation is not effected, brings about structural deformities; adults in which the exoskeleton has become fully chitinised are not apparently affected.

However, more work is needed to determine whether the traumatic variations mentioned above are either merely accidental and teratologcal in nature coincident with the strepsipteran attack, or really parasite-induced.

TABLE 11

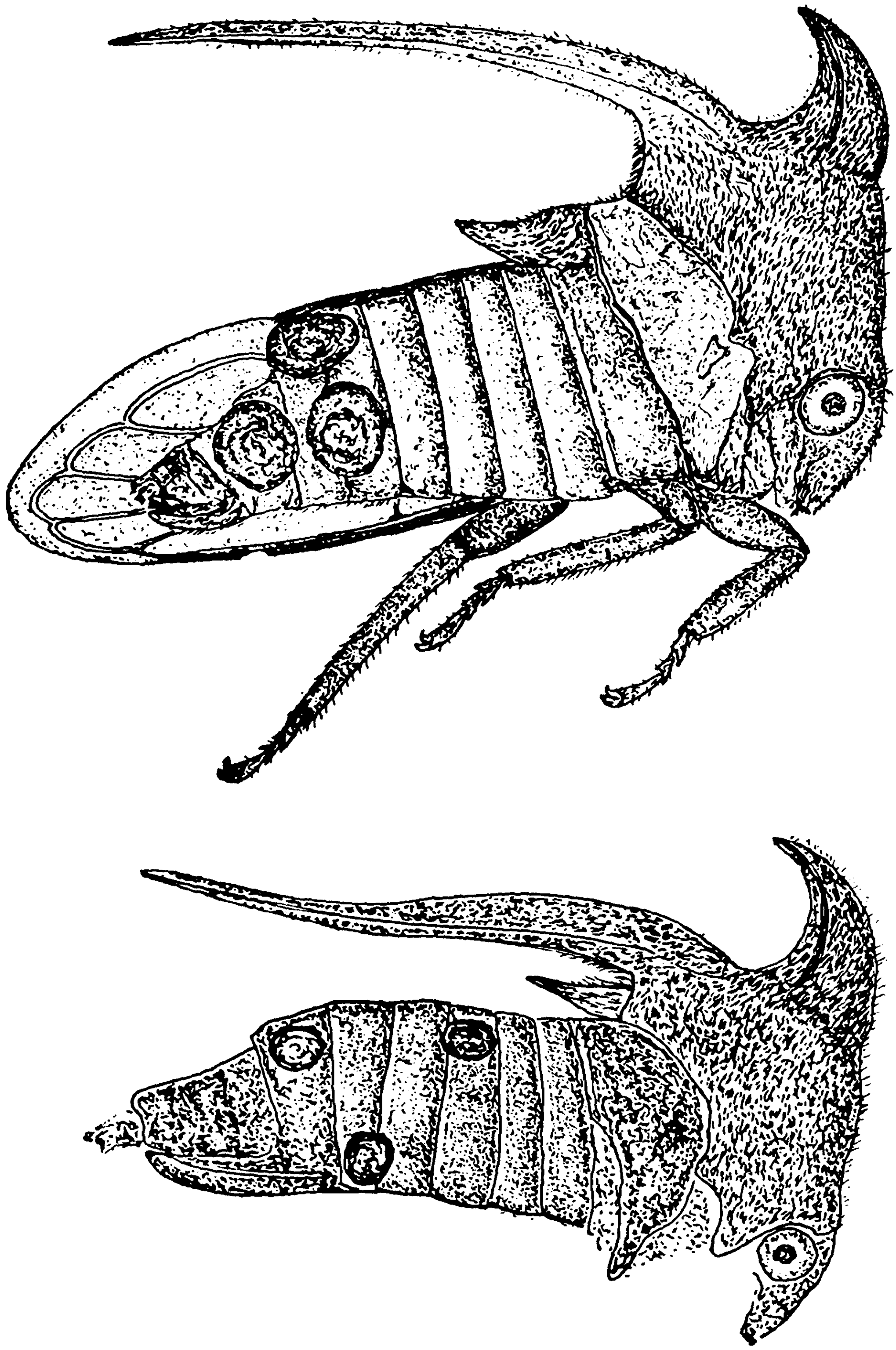
Egg mortality in Oxyrhachis rufescens.

Months	Max. Temp. in °C	Rainfall in mm	Humidity %	Total No. of eggs	No. of eggs parasitized by			Percentage of eggs parasitized by			Total No. of parasitized eggs
					Gonatocerus sp.	Aphelinoidea sp.	Centrodora sp.	Gonatocerus sp.	Aphelinoidea sp.	Centrodora sp.	
1966											
Jan.	28.4	24.2	85	310	12	24	30	3.9	7.7	9.7	66
Feb.	29.9	—	87	295	14	26	25	4.7	8.8	8.5	65
March	34.1	—	75	400	19	28	51	4.75	7.0	12.7	98
April	33.7	0.8	76	250	12	25	17	4.8	10.0	6.8	54
May	37.9	81.7	64	240	10	18	31	4.16	7.5	12.9	59
June	35.5	65.5	71	315	8	30	21	2.54	9.52	6.7	59
July	34.3	102.7	73	390	13	25	62	3.3	6.4	16.0	100
Aug.	33.8	190.2	79	268	9	7	43	3.6	2.6	16.0	59
Sept.	31.8	223.6	81	301	11	24	26	3.65	8.0	8.6	61
Oct.	30.6	230.3	82	330	15	28	18	4.54	8.5	5.45	61
Nov.	30.0	556.3	85	275	12	8	20	4.36	2.9	7.27	40
Dec.	28.3	112.6	81	370	16	22	36	4.32	6.0	9.73	74
1967											
Jan.	28.7	4.3	83	392	17	33	38	4.3	8.4	9.7	88
Feb.	30.5	—	85	504	16	39	52	3.17	7.7	10.3	107
March	31.5	20.3	79	390	18	41	32	4.6	10.5	8.2	91
April	34.1	0.5	76	364	18	32	24	5.0	8.8	6.6	74
May	36.0	92.7	69	394	16	32	6	4.0	8.0	1.6	54
June	35.7	91.6	68	402	7	31	13	1.7	7.7	3.2	51
July	34.1	82.1	71	378	16	24	18	4.2	6.5	4.7	58
Aug.	33.1	259.3	78	384	21	25	12	5.4	6.5	3.1	58
Sept.	33.5	36.9	79	361	18	18	43	5.0	5.0	11.9	79
Oct.	31.1	159.6	82	492	25	45	30	5.0	9.0	6.0	100
Nov.	28.8	128.8	76	480	26	50	26	5.4	10.4	5.4	102
Dec.	28.5	303.7	82	452	21	20	11	4.6	4.4	2.5	52

TABLE 12

Egg mortality in Otinous oneratus.

Months	Total percentage of egg mortality due to parasites	Total No. of eggs	Numbers of eggs parasitized by			Percentage of eggs parasitized by			Total No. of parasitized eggs	Total percentage mortality due to parasites
			Gonatocerus	Apheli-noidea	Centrodora	Gonatocerus	Apheli-noidea	Centrodora		
1966										
Jan.	21.3	331	—	10	69	—	3.0	20.8	79	23.8
Feb.	22.0	291	16	12	43	5.5	4.1	14.4	71	24.0
March	24.0	253	—	6	44	—	2.4	17.4	50	19.8
April	21.6	315	7	23	30	2.2	7.3	9.5	60	19.0
May	24.5	209	—	8	27	—	3.8	13.0	35	16.8
June	18.9	322	—	21	38	—	6.5	11.8	59	18.3
July	23.0	265	—	20	12	—	7.5	4.5	32	12.0
Aug.	22.0	370	—	24	30	—	6.5	8.1	54	14.6
Sept.	20.3	427	—	33	50	—	7.7	11.7	83	19.4
Oct.	18.5	297	8	12	50	2.7	4.0	16.8	70	23.5
Nov.	14.2	224	—	21	40	—	9.4	17.8	61	27.2
Dec.	20.0	246	—	26	45	—	10.6	18.0	71	28.6
1967										
Jan.	22.2	270	17	13	37	6.3	5.0	13.7	67	25.0
Feb.	21.1	439	9	26	61	2.0	6.0	14.0	96	22.0
March	23.3	389	—	41	45	—	10.4	11.6	86	22.0
April	20.4	495	—	20	60	—	4.0	12.1	80	16.1
May	13.6	316	7	15	29	2.2	4.7	9.2	51	16.1
June	12.6	269	4	20	41	1.5	7.4	15.2	65	24.1
July	15.4	300	—	18	21	—	6.0	7.0	39	13.0
Aug.	15.0	410	—	20	27	—	4.8	9.0	47	13.8
Sept.	21.9	255	—	18	33	—	7.0	13.0	51	20.0
Oct.	20.0	320	8	21	51	2.5	6.5	16.0	80	25.0
Nov.	21.2	324	14	33	50	4.3	10.2	15.4	97	29.9
Dec.	11.5	340	—	32	56	—	9.5	16.5	88	26.0



Text-fig. 8. Stylopised *Leptocentrus taurus*, showing abnormal development of posterior process; abdomen bearing galls left by the strepsipteran parasites.

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