THE BIOLOGY AND ECOLOGY OF *CLUBIONA* SPECIES (ARANEAE : CLUBIONIDAE) AND THEIR SCELIONID PARASITOIDS (HYMENOPTERA)

By

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SUMMARY

Spiders of the genus *Clubiona* are abundant under the bark of *Eucalyptus* trees at Mylor, South Australia, specifically *E. viminalis* and *E. leucoxylon*. *Clubiona robusta* L.Koch, the largest species at this location, has up to 9 juvenile instars. It feeds on a variety of insects that are associated with bark; and it constructs a specialized silk chamber in which it moults, overwinters, mates, lays and guards its eggs. Females lay 1-2 eggmasses per season.

Eggs are present in the field for up to 8 months of the year, from August to April. Juveniles hatch, go through 2 moults inside the nest and then disperse. The majority undertake aerial dispersal (ballooning) to reach other trees, but a few remain on the same tree and disperse by walking. Other species of *Clubiona* that coexist in the same habitat have a similar biology to that of *C. robusta*.

Adult *C. robusta* are most abundant in spring and summer, but are present at all times of the year. Generations are not discrete. There is a summer and winter generation, but spiders maturing late in summer can also overwinter to oviposit in the following spring. Mortality occurs in 2 main phases; from parasitism on eggs by *Ceratobaeus masneri* sp.nov. (Scelionidae), and at the time of juvenile dispersal.

C. masneri killed 22-25% of all eggs in the 3 seasons of the study. Although this mortality is high, the very similar results obtained in each season suggest that it may be constant and therefore not important in causing fluctuations in *C. robusta* populations.

Changes in the abundance of this spider are more likely to be caused by differences in mortality at dispersal. Observations in the field indicate that about 60-70% of juveniles die from landing in unfavourable habitats. It is proposed that this species has a Type IV mortality pattern (Slobodkin 1961) (i.e. very high mortality in the early life history stages), and not

Type III (i.e. a constant rate of mortality over all stages) as has been reported for other spiders.

C. robusta guards its eggs and the first 2 instars by attacking intruders that attempt to enter the nest. All intruders larger than 2 mm are killed. Removal of spiders from nests in the field caused almost total mortality of the unguarded eggs. *C. masneri* escaped attack; experimental evidence suggests that this may be due to the small size of this species. It never parasitizes all the eggs in an eggmass. In all observed cases eggs on the periphery were likely to die, whereas those in the centre were protected by being too deep for the ovipositor to reach.

Female *C. robusta* are more common than males in the field, but they occur in equal numbers in laboratory cultures. Behavioural trials show that males are much more aggressive than females and can kill or injure each other. Male aggression is thus believed to result in their low abundance and the biased sex ratio in this species.

Studies on the biology of *C. masneri* show that the larval and pupal stages of the parasitoid develop inside its host. The host is not completely consumed until after the larval-pupal apolysis, i.e. the parasitoid continues to feed while it is a pharate pupa. This phenomenon has not previously been described for any Hymenoptera. Individuals emerge as adults; males emerge prior to females, then wait for the latter and mate with their sibs. A limited amount of outbreeding occurs in the few eggmasses that are attacked by more than one female wasp. Ovarian development of eggs continues for several days after emergence, even though females can successfully oviposit in the interim.

Females of *C. masneri* overwinter as adults under bark and do not feed or resorb their eggs. This species, as with other parasitic Hymenoptera, displays arrhenotokous parthenogenesis and has a sex ratio biased towards the female. They can discriminate between parasitized and unparasitized eggs and also determine when hosts are too old to allow for successful development of their oppspring. Host eggs can be successfully parasitized up to early

germ band stage at 15 and 20°C, but at 25°C development occurs only up to germ disc stage, even though oviposition occurs up to germ band stage. Transfer of parasitized eggs between temperatures indicates that high temperature alone is responsible for unsuccessful development between these stages.

C. masneri and related species show a high degree of host specificity. They usually attack spiders belonging to only one genus and have a 'preference' for one species. They find their hosts by searching for eucalypt trees and then the silk of nests under the bark. Final location and acceptance is probably achieved by recognition of chemicals on the surface of host eggs.

The ovipositor of *C. masneri* is unlike that described for any other Hymenoptera. It is invaginated into the body cavity and is detached from the terminal segments of the metasoma. It is contained within a semi-sclerotized membranous tube, and is connected to the metasoma by elongated muscles and apodemes. A model for the mechanics of ovipositor movement, including extension and retraction of the ovipositor, is proposed.

C. masneri and related species have a horn-like process on their anterior metasoma to accomodate the elongated ovipositor. These species all oviposit through the eggsac wall to reach the eggs inside. Other genera are wingless, have a streamlined body, a short ovipositor, and burrow through the eggsac wall to parasitize their host eggs. These adaptations are related to the thickness and density of the eggsacs produced by spiders in different families. The protection of eggs through their physical isolation by eggsacs, and the adaptations required to penetrate them, are discussed as factors that have contributed to host specificity in scelionid wasps.

The taxonomy of scelionids that attack the eggs of spiders is reviewed to support the biological sections of this study. Keys to genera and species of *Ceratobaeus* are presented, several species are described or redescribed, and *Hickmanella* is erected as a new genus.

DECLARATION

The work presented in this thesis is my own unless otherwise acknowledged, and has not previously been published or submitted to any university for the award of any degree.

The published paper (Appendix 3) written by A.D. Austin and T.O. Browning is included as part of this thesis. The idea for this work was proposed by Browning, but the research conducted towards it and writing of the manuscript was solely my responsibility.

February 1982 A.D. Austin.

ACKNOWLEDGMENTS

Adams (1979) states that a simple bath towel, if used properly, is of great assistance in extricating oneself from 'tricky' situations. Unfortunately, I have found that this item was no use whatsoever in solving any problems during the research conducted for this thesis. It did not suffice as a replacement for a calculator, camera, SEM, or thermistor probe. I had to construct these pieces of equipment myself, from string, cardboard and glue. The only possible scientific function that a towel may perform is as some type of sampling device; however, it did not work for spiders! During this study I have enjoyed (and have hated afterwards) many *Pan Galactic Gargle Blasters* procured from the Edinburgh and British.

My stay in the Department of Entomology (Waite Institute) has been highly rewarding. I have found it friendly, conducive to research and scientifically stimulating.

I wish to sincerely thank my 2 supervisors Professor T.O. Browning and Dr. P.W. Miles for their advice, profitable discussions, suggestions, and critical reading of my thesis.

Discussions with Dr. D.A. Maelzer, Dr. R. Laughlin, Professor H.G. Andrewartha, Professor W.P. Rogers, Mrs. E.H. Lever and fellow postgraduate students, especially Paul and David, helped me to sharpen my ideas and refine some of the techniques I used.

Dr. B.Y. Main and Dr. V.T. Davies identified *Clubiona* and other spiders for me; Dr. G. Gross, Dr. E. Matthews and Dr. P.J.M. Greenslade identified the insect prey of *Clubiona;* Dr. D.E. Symon identified the eucalypt trees that occur at the study site; Dr. L. Masner, Dr. I.D. Galloway and Dr. I.D. Naumann made many useful suggestions in regard to the taxonomic and morphological sections of my work, and lent me many valuable specimens; Dr. K. Bartusek and Mr. R. Miles gave assistance with SEM techniques; Mr. T.W. Hancock suggested appropriate analyses for my data; Mr. N.C. Stewart helped by obtaining many pieces of equipment; the

Library staff (especially Mrs. J. Mount) acquired innumerable interlibrary loans for me; Mr B.A. Palk printed the half-tone and line illustrations; Chroma Colour Pty. Ltd. printed the colour plate; Miss T.R. Siekmann and Mrs. S. Heard typed my thesis. I wish to thank all these people, and others that I may have forgotten.

Finally and most of all I thank Sally for her encouragement, advice and help in every phase of my work.

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CHAPTER 1

INTRODUCTION

Spiders are both abundant and diverse in many terrestrial habitats and have even adapted to some aquatic environments (Forster and Forster 1973). Their success in this regard probably relates to their development of a multitude of uses for the silk they produce. The functions of the silk of spiders has been the subject of many natural history studies, but until recently there have been few attempts to examine the ecology of these animals. The reason for this is unclear, but may be due to the fact that they have not been considered to be of any direct economic importance. Certainly the large body of information available on many insects is due to their being classed as agricultural pests or beneficial as agents of biological control.

Recent studies on the role of spiders in both natural and agricultural habitats indicate that they are efficient predators and important as causes of mortality in many populations of invertebrates (Hagen *et al.* 1976, Riechert 1974a, Turnbull 1973). Thus spiders have come to be used more extensively in both population ecology and community studies. However, most investigations have been carried out on the wellknown orb-weaving araneids and ground-living lycosids (Turnbull 1973). Very few studies have been conducted on the ecology of other hunting spiders, e.g. Clubionidae, Salticidae, Gnaphosidae and Thomisidae, even though these groups are dominant in several habitats, such as in vegetation.

Many aspects of the natural history of these spiders are different from those of araneids and lycosids (Main 1976, Turnbull 1973), and therefore one might expect comparable differences to exist between their ecologies. Confirmation that such differences exist between spiders from different families was indicated prior to this study, when it was found that parasitism by members of the Family Scelionidae (Hymenoptera) was causing apparent high mortality to some hunting spiders. In comparison,

food and weather have emerged as the main factors responsible for limiting populations of araneids and lycosids, though predation and parasitism do occur in some species. Therefore, to determine the extent and nature of the possible differences between these groups of spiders, a study was initiated to examine the biology and ecology of a group of common hunting spiders and their scelionid parasitoids.

A group of coexisting species belonging to the genus *Clubiona*, that inhabit the bark of eucalypt trees, was chosen for the study, as they were readily available, appeared to be abundant at most times of the year, adults could be easily distinguished from each other and from other spiders in the same habitat, and their eggs were parasitized by scelionids.

Initially, the natural history of these spiders is examined, with most work being carried out on one species, *Clubiona robusta* L.Koch. The phenology of this spider is investigated and its behaviour and main causes of mortality are studied, especially in relation to the scelionid parasitoid, *Ceratobaeus masneri* sp.nov. Further, the interactions between this parasitoid and its host are examined, i.e. how it penetrates the nest and eggsac to reach its host eggs; how it overwinters when hosts are not available; how survival is affected in hosts when they are of different ages or at different temperatures; and how it finds and recognizes its host eggs from those of other spiders. These and other aspects of the biology of the scelionid are studied. This information is then compared and discussed in relation to that for other spiders, scelionids and other hymenopteran parasitoids.

This study also provides an opportunity to examine the morphology and mechanics of the ovipositor of *C. masneri* and other scelionids. This structure is of vital importance in the biology of these wasps, as it enables them to lay their eggs into hosts that are hidden or protected behind physical barriers, such as eggsacs. The mechanics of the ovipositor of scelionids and other parasitoids in the Superfamily Proctotrupoidea has

not previously been studied. In fact there have been very few studies on the ovipositor of any microhymenopterans. The present work therefore also investigates whether scelionids have an ovipositor that functions in a similar way to that found in other members of the order Hymenoptera.

In conjunction with information on the comparative anatomy of the ovipositor, the host relationships and degree of host specificity for scelionids that attack the eggs of spiders are examined. Special attention is paid to the ovipositional behaviour and morphological adaptations of these wasps in relation to types of eggsacs and groups of hosts they attack. Such a functional approach in examining host relationships has been attempted for few groups of parasitoids (Askew 1965, Heathwole and Davis 1965, Price 1972, 1975).

Finally, the taxonomy of these scelionids is reviewed, so that genera and species involved in the study can be accurately identified. This section is presented as an appendix chapter, as it is not continuous with the biological parts of this study.

CHAPTER 2

NATURAL HISTORY OF *CLUBIONA* SPECIES

2.1 INTRODUCTION

Surveys in natural vegetation and agricultural systems show that members of the Family Clubionidae comprise a substantial part of the araneid fauna in these habitats (Dondale 1966, Kayashima 1960, Mansour *et al.* 1980a, Palmegren 1972, Toft 1976, 1978, 1979, Whitcomb *et al.* 1963). However, there have been few studies on the biology of this important group of spiders. Most field studies have concentrated on spiders that live on the ground (e.g. Lycosidae) or in aerial webs (e.g. Araneidae), while less attention has been paid to the hunting or vagabond spiders (e.g. Clubionidae, Gnaphosidae, Salticidae and Thomisidae) associated with vegetation. Some species in the latter group have been used in experimental studies in the laboratory (e.g. Jackson 1977a, 1978a, Krafft 1978, Land 1969), but problems with sampling spiders in vegetation and with their taxonomy are probably the main reasons why most workers have selected other spiders for ecological and field studies.

Investigations on the Clubionidae have concentrated on one genus, *Chiracanthium* (Lecaillion 1904, Mansour *et al.* 1980b, 1980c, Peck and Whitcomb 1970), that is predominant in the foliage part of vegetation. Information on the genus *Clubiona* is restricted to a few short reports on aspects of the natural history of some species (Comstock 1940, Duffey 1969, Forster and Forster 1973, Gertsch 1949, Hickman 1967a, Main 1976, Palmegren 1972, Toft 1976, 1979). This genus is found mostly associated with the woody parts of vegetation, but is also found in foliage and on the ground (Forster and Forster 1973). What data is available indicate that *Clubiona* represents a major group of nocturnal predators in many vegetation communities.

In Australia the biology of very few spiders has been examined in detail (Austin and Anderson 1978, Austin and Blest 1979, Humphreys 1976, Main 1957) and several groups, such as Clubionidae and Salticidae, have been totally neglected. There are several habitat-types unique to

Australia and these have undoubtedly been of primary importance in the development of an equally unique and diverse spider fauna (Main 1976, 1981). Among Australian spiders are several groups that are arid adapted and others that are strongly associated with eucalypt trees. Most species of *Eucalyptus* (gum trees) shed their bark annually. This corticating bark drops off some trees almost immediately after being shed, while in other species it remains loosely attached and provides a refuge for many invertebrates. In this respect eucalypts differ markedly from most trees found in the northern hemisphere, which provide very little or no space under their bark and consequently harbour few invertebrate species (but see Duffey 1969 and Turnbull 1960).

Incidental observations prior to this study indicated that the genus *Clubiona* was dominant, compared with other spiders found under the bark of eucalypt trees. These observations also showed that several species of *Clubiona* coexist in this habitat. The aim of this section is to investigate and compare the biology and natural history of these species of *Clubiona*, concentrating on aspects of their reproductive biology, seasonality, growth stages and behaviour. This information is then compared with the few previous studies on clubionids, and those on other hunting spiders, to determine similarities and differences between species from various habitats. This chapter is intended to provide basic information to support the more detailed sections on the ecology and behaviour of *C. robusta* (Chapter 3) and the interaction between *Clubiona* species and their scelionid parasitoids (Chapter 4). The natural history of araneomorph spiders has been adequately reviewed elsewhere (Forster and Forster 1973, Jackson 1978b, Main 1976, Turnbull 1973).

2.2 MATERIALS AND METHODS

2.2.1 Study Site and Climatological Data

The site chosen for this study is located approximately 4 km

south-east of Mylor (25 km south-east of Adelaide), South Australia, at an altitude of 350 m above see level (a.s.l.). It consists of 3 areas of open native forest that originally belonged to a larger forest, that is now divided by 100-400 m of open grazing land. The 3 areas comprise 10 ha of a mature mixed stand of trees, dominated by *Eucalyptus viminalis* Labillardiere and *E. leucoxylon* Mueller (see Boomsma 1972): Area 1 is 7 ha and borders the Onkaparinga River, Area 2 is 1.5 ha and Area 3 is 0.5 ha. All have had their undergrowth cleared and have been previously grazed; however Areas 1 and 3 are presently regenerating. Areas 2 and 3 are on private property, while Area 1 is in the Kuitpo State Forest (administered by the Department of Woods and Forests, South Australian Government). Cattle were occasionally grazed in Area 2 for short periods during the study, but they did not interfere with any trees.

The fire history of the site is relatively unknown, though Area 1 was completely burnt out by a bushfire on 20 February 1980. Fortunately, this had little effect on the study, as long term field work was conducted only in Area 2.

The study site is within a broad region of South Australia that experiences a Mediterranean climate; summers are hot and dry while winters are cool and wet. Although no continuous climatic recordings were taken during the study, occasional measurements indicated that temperature and rainfall at the Mylor site were intermediate between Stirling (500 m a.s.l.; 5 km from the study site) and Strathalbyn (80 m a.s.l.; 22 km from the study site), the 2 closest meteorological stations (Bureau of Meteorology, Commonwealth Government). Data for these stations (1960-80) are summarized in Figures 2.1 and 2.2, to provide an indication of the climate of the region. Rainfall experienced at Mylor is believed to be closer to that of Stirling, and temperatures are probably more similar to those experienced at Strathalbyn. Conditions at these 2 stations for the period of the study (1978-81) were very similar to the overall patterns depicted in Figures 2.1 and 2.2.

Figure 2.1 Mean monthly rainfall, 1960-1980 (mm, $\pm$ 1 S.D.), for the 2 closest meteorological stations to the Mylor study site.

Figure 2.2 Mean daily maxima and minima, 1960-1980 (C^{o}, $\pm$ 1 S.D.), for the 2 closest meteorological stations to the Mylor study site.

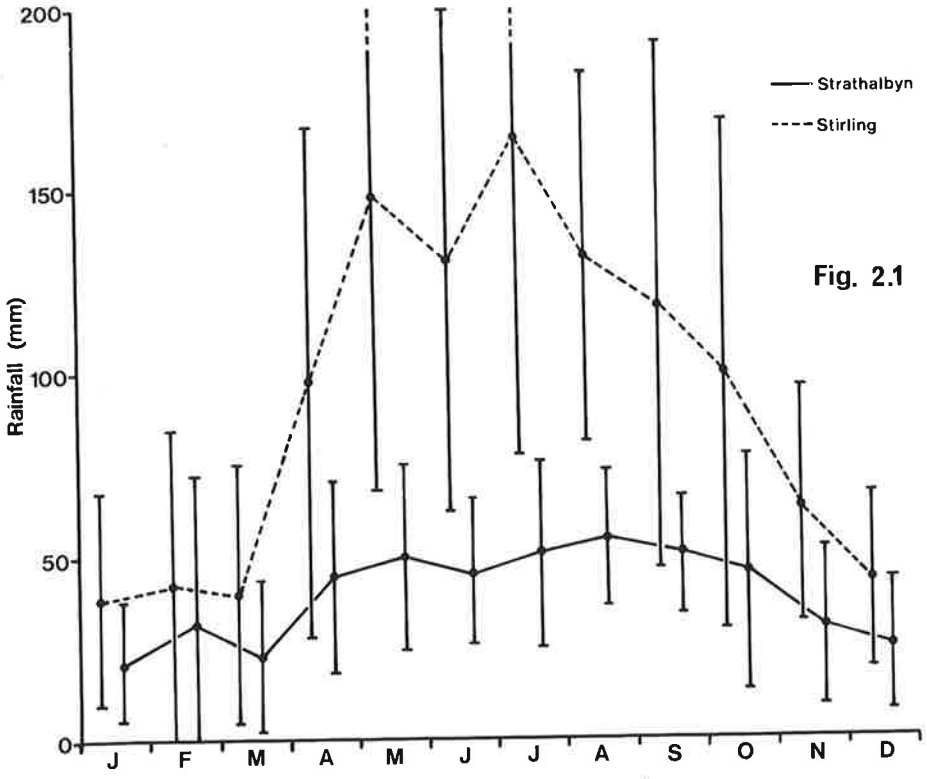
200
150
100
50
0
Rainfall (mm)
Strathalbyn
Stirling
J
F
M
A
M
J
J
A
S
O
N
D

Fig. 2.1

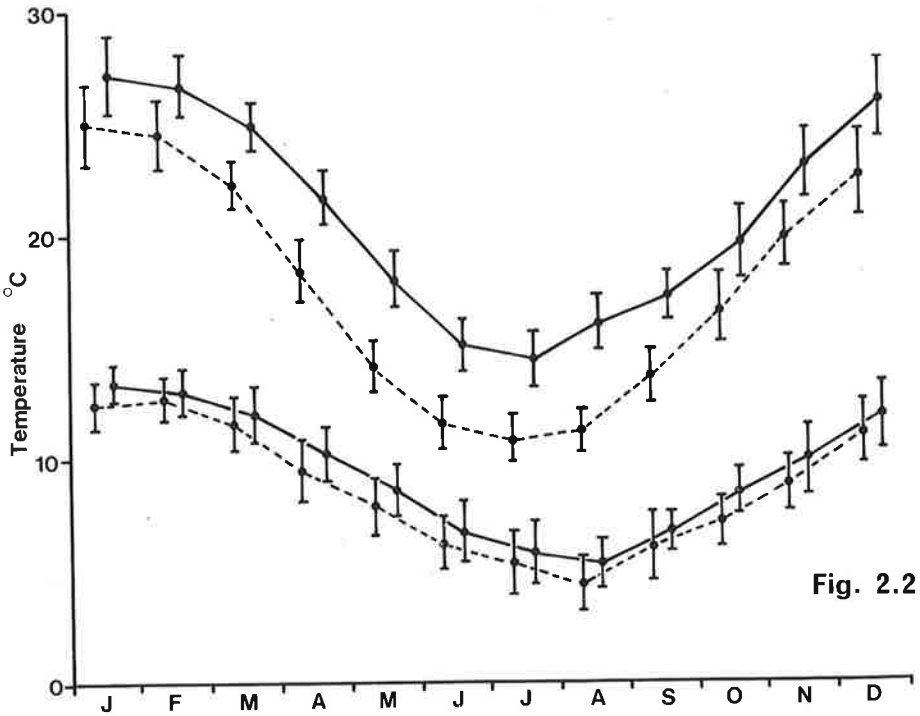
30
20
10
0
Temperature °C
J
F
M
A
M
J
J
A
S
O
N
D

Fig. 2.2

2.2.2 Collecting Techniques

The study site was divided into 2 sections; quantitative monthly samples of spider populations were carried out in Area 2 (see 3.2.1), while collection of spiders and eggs for laboratory studies and some field experiments were conducted in Areas 1 and 3. Spiders were collected from under bark by pulling it from trees and manupulating individuals into glass vials. Spiders were also collected in this manner each month, from December 1978 to July 1981, to assess their reproductive status. Information on habitat preferences, nest morphology and prey species were collected at the same time.

An initial survey of the composition and relative abundance of the spider fauna under bark in the study area (Area 1) was conducted during June 1978. Seven trees 30 cm or more in diameter were randomly chosen and surrounded by galvanized iron pans (60 x 38 x 8 cm), that had been partly filled with water and a small amount of detergent. All the corticating bark from these trees was removed to a height of 2 m (approximately 10 m^2 of trunk area); it was then broken up and spiders were brushed into the pans. These pans also served to collect spiders that attempted to jump away as the bark was disturbed. Trees that were sampled in this survey or for any other reason were not resampled during the study.

2.2.3 Laboratory Cultures

Adult spiders were kept in large plastic containers (15 cm diameter, 15 cm high) with gauze-covered air holes. These were held at 20°C ($\pm$ 1.0°C range), 70% relative humidity and 12L:12D. Glass vials (15 mm diameter) with cottonwool wicks served as water dispensers. Spiders were fed large cockroaches from a laboratory culture, and occasionally pentatomid bugs collected from the field, when the latter were available. Pieces of bark approximately 50 mm^2 were attached to the inside walls of the containers

with adhesive tape, to provide sites for nest construction and oviposition. It was found that the number of eggmasses produced by *Clubiona robusta* was much lower when bark pieces were omitted, ~~compared with when the latter were provided as sites for oviposition~~. *Clubiona cycladata* could not be induced to oviposit readily under these same conditions. The rate of eggmass production for this species was always low and mortality was extremely high, even though the rearing conditions, i.e. temperature, light regime, density of spiders and prey species, were changed several times.

The number and sizes of the instars of *C. robusta* were determined by rearing juvenile spiders through to adults in containers in the laboratory. Third instar spiders were removed from nests and placed in small plastic containers (70 mm diameter, 70 mm high) supplied with water and kept under the same conditions as above. Ten juvenile spiders were placed in each container and the latter were checked every 5 d for moulted exoskeletons and the spiders measured. Instars 3-5 were fed wingless *Drosophila*, lucerne aphids and small cockroaches (< 4 mm in length). Once spiders had reached the sixth instar they were transferred to large containers (15 x 15 cm), reduced in density to 10 per container and fed only adult cockroaches. Once males could be identified they were separated so that a maximum of 2 or 3 were present in each container. Mortality in all instars was high; death at moulting and cannibalism appeared to be the major causes.

2.2.4 Development of Eggs

The embryological development of *C. robusta* was studied by removing 5 eggs from each of 4 eggmasses every 12-24 h, immersing them in liquid paraffin and noting the embryonic stage of each under a stereomicroscope. Liquid paraffin renders the chorion of eggs transparent (Holm 1954), thereby allowing the embryo to be easily observed. Batches of eggs were kept at 4 different temperatures (15°C, ± 1.0 range; 20°C, ± 1.0; 25°C, ± 1.5;

30°C, ± 2.0), to enable examination of the effect of temperature on the duration of individual embryonic stages.

2.3 RESULTS

2.3.1 The Diversity of Spiders Under Bark and the Taxonomy of *Clubiona*

All spiders under the bark of 7 eucalypt trees (see 2.2.1 and 2.2.2) were collected at the beginning of the study to determine the species composition and relative abundance of the fauna present. The corticating bark on these trees can form several layers that are often held together by the webs and nests of spiders. This bark breaks away from the branches and high trunk, but it builds up at the base of trees to a height of 2 m, where it forms an ideal habitat for many invertebrates (Figure 2.4). In the above sample 322 individual spiders were collected, representing 27 species; a further 6 species were collected at the study site at other times during the year. The genus *Clubiona* (Clubionidae) was dominant in the sample and comprised 63% of individuals; with Salticidae (*Breda jovialis* (L.Koch), *Clynotis viduus* (L.Koch), *Servea vestita* (L.Koch) and *Holoplatys* sp. comprising 15%; Gnaphosidae, including *Lampona cylindrata* (L.Koch) and *Hemicloea* sp., contributing 9%, the remaining 13% being made up of 15 species.

There are 4 species of *Clubiona* that coexist under the bark of eucalypt trees at the Mylor study site (Figure 2.3). Two of these species, *Clubiona robusta* L.Koch and *Clubiona cycladata* Simon have been described (see Acknowledgments). The 2 undescribed species were designated Species A and B for the purposes of the study. Studies on the morphology of the adults of these 4 species of *Clubiona* showed that they could be distinguished from each other on differences in their size, shape, colour (Figure 2.3), chelicerae and genitalia. Data for these characters are summarized in Table 2.1 and Figure 2.6. The length of the carapace (dorsal plate of prosoma) was used as an index to the size of spiders, as this measurement

Figure 2.3 Species of *Clubiona* found under bark at Mylor:

a) *C. robusta* (♀)
b) *C. robusta* (♂)
c) *C. cycladata* (♀)
d) *C. cycladata* (♂)
e) *Clubiona* Sp.A (♀)
f) *Clubiona* Sp.B (♀)

Scale: 10 mm

Figure 2.4 *Eucalyptus viminalis* showing a build-up of corticating bark at the base of the trunk.

Figure 2.5 Eggmass of *Clubiona robusta* showing eggs parasitized by *Ceratobaeus masneri* (brown eggs) and unparasitized eggs (white eggs).

Scale: 5 mm

2.3


2.4


2.5

has been shown to provide the most constant estimate (see Jackson 1978b). Total body length was not used as it varies when the opisthosoma distends with feeding and when females become gravid. It was, however, impossible to identify the juvenile instars of these species accurately, until they reached the pentultimate stage. Their genitalia are undeveloped until this stage and colour patterns are variable. Juveniles of *C. robusta* and Species B have an opisthosomal pattern similar to that of adults (see Figure 2.3), but often it is faded and almost indistinguishable, so that these individuals closely resemble juveniles of *C. cycladata* and Species A. The background colour of *C. robusta* and Species B also varies. The red-brown colour of the anterior carapace and chelicerae do not develop until the pentultimate instar, so that the prosoma is usually cream or light brown in colour, though sometimes the lateral margins are olive green. The opisthosoma of these 2 species varies from light brown and purple-brown to pink-brown, behind the dark brown striped pattern. Juveniles of *C. cycladata* and Species A are identical in colour to the adults of *C. cycladata* (uniform light brown), except they lack ventral opisthosomal markings. Voucher specimens of these 4 species of *Clubiona* and the other spiders collected at the study site have been lodged in the Department of Entomology insect collection (Waite Agricultural Research Institute, The University of Adelaide).

The relative abundance of the 4 species at the study site varies considerably. Of the 203 *Clubiona* collected in the sample of 7 trees discussed previously, 72 (35%) were adults or subadults (pentultimate instar) of *C. cycladata*, 28 (14%) were *C. robusta*, 3 (1.5%) were Species A and one (0.5%) was Species B; the remaining 99 (49%) were juveniles and could not be accurately identified to species. Species A and B were therefore considered rare in the sample. This was verified by extensive collecting at different times of the year: only 35 adults of Species A and 17 Species B were collected during the 30 months of field work conducted in the study.

Clubiona Species A

Colour		Anterior carapace and chelicerae dark red-brown, chelicerae sometimes almost black; posterior carapace yellow-brown; opisthosoma light grey to cream, dorsally with single faint longitudinal stripe, sometimes with faint transverse bands posteriorly or faint elongated lateral patches; male identical to female, but longitudinal stripes often absent, and replaced by brown stippled pattern covering dorsal opisthosoma.
Size		Carapace length
	Female:	$\bar{x}$ = 2.44 mm, S.D. $\pm$ 0.21, Range 2.1-2.8 mm, n = 15
	Male:	$\bar{x}$ = 2.44 mm, S.D. $\pm$ 0.24, Range 2.0-2.7 mm, n = 6
		Body length
	Female:	Range 4.9-9.8 mm
	Male:	Range 4.9-7.0 mm
Chelicerae	Female:	1 + 1 (large) + 2 very small promarginal teeth 3 retromarginal teeth
	Male:	2 promarginal teeth Retromarginal ridge (no teeth)

Clubiona Species B

Colour		Identical to *Clubiona robusta*, but with pattern on dorsal opisthosoma slightly darker relative to the background colour.
Size		Carapace length
	Female:	$\bar{x}$ = 3.35 mm, S.D. $\pm$ 0.52, Range 2.8-4.5 mm, n = 9
	Male:	$\bar{x}$ = 3.44 mm, S.D. $\pm$ 0.24, Range 3.1-3.6 mm, n = 5
		Body length
	Female:	Range 7.4-11.2 mm
	Male:	Range 7.8-11.2 mm
Chelicerae	Female:	1 + 1 (large) + 2 very small promarginal teeth 2 retromarginal teeth
	Male:	2 promarginal teeth 4 very small retromarginal teeth

Table 2.1 cont.

Clubiona robusta

Colour		Anterior carapace dark red-brown, chelicerae usually black; posterior carapace and legs yellow-brown; dorsal opisthosoma with dark brown striped pattern dorsally on a light-brown background (Figure 2.3).
Size		Carapace length
	Female:	$\bar{x}$ = 5.13 mm, S.D. $\pm$ 0.39, Range 4.2-5.8 mm, $\underline{n}$ = 32
	Male:	$\bar{x}$ = 4.82 mm, S.D. $\pm$ 0.24, Range 4.3-5.4 mm, n =26
		Body length
	Female:	Range 13.1-17.4 mm
	Male:	Range 12.2-16.5 mm
Chelicerae	Female:	2 promarginal teeth 3 + 1 (very small) retromarginal teeth
	Male:	2 (1 very large) promarginal teeth 2 very small retromarginal teeth

Clubiona cycladata

Colour		Carapace pale brown or light red-brown, chelicerae slightly darker; opisthosoma uniformly cream in colour, sometimes grey or brownish, dorsal pattern absent, but with 3 longitudinal stripes ventrally, 2 triangular brown patches anterior to openings of book-lungs and 2 small transverse stripes anterior to spinnerets.
Size		Carapace length
	Female:	$\bar{x}$ = 2.67 mm, S.D. $\pm$ 0.21, Range 2.3-2.9 mm, $\underline{n}$ = 54
	Male:	$\bar{x}$ = 2.42 mm, S.D. $\pm$ 0.23, Range 2.1-3.1 mm, n = 30
		Body length
	Female:	Range 6.6-7.7. mm
	Male:	Range 7.0-8.7. mm
Chelicerae	Female:	2 (2nd very large) + 5 very small promarginal teeth 2 (small) retromarginal teeth
	Male:	chelicerae extremely elongated, protruding from anterior prosoma

Table 2.1 Morphological characteristics used for the identification of adult *Clubiona* species.

2.3.2 Habitat Preferences

At the Mylor study site the 4 species of *Clubiona* were exclusively found under the corticating back of *E. viminalis* and *E. leucoxylon*. Spiders were predominantly found under the bark at the base of trees, but they also occurred higher up, where the corticating bark had not sloughed off, i.e. mostly where large branches join the main trunk. *Clubiona* species were not found under the bark of dead trees, in logs on the ground or associated with the other species of *Eucalyptus* on the study site, i.e. *E. obliqua* L'Herit.

Incidental observations on the 2 most abundant species of *Clubiona* (*C. robusta* and *C. cycladata*) and other spiders, suggest that the smooth bark of *E. viminalis* and *E. leucoxylon* provides a better surface for the attachment of silk. In the laboratory individuals of *C. robusta* usually constructed nests in the corner of plastic containers rather than on bark pieces from *E. obliqua* (see 2.2.3). The few nests that were constructed on this bark came away easily from the fibrous layers of the latter when touched. However, when bark of *E. viminalis* or *E. leucoxylon* was placed in containers, spiders always constructed well attached nests under it, rather than against the plastic sides of containers.

The bark around the base of *E. viminalis* and *E. leucoxylon* is not uniform. It varies in the number of layers (one layer representing one year's growth), and distribution around the trunk. When the number of layers builds up excessively, they fall off, creating smooth bare patches. Otherwise, they stay attached to each other and to the trunk at places where the bark has not separated completely or where they are stabilized by the silk of spiders. The distribution of these patches and the bark between them appears to be random, but it was not known whether the distribution of *Clubiona* under this bark was biased in any way. To test the null hypothesis that *Clubiona* species do not congregate on one or more sides of trees (facing in a particular direction), all adults of *C. robusta*

Figure 2.6 Genitalia of *Clubiona* species.

Female Genitalia		Male Palp	
a)	*C. robusta*	e)	*C. robusta*
b)	*C. cycladata*	f)	*C. cycladata*
c)	*Clubiona* Sp.A	g)	*Clubiona* Sp.A.
d)	*Clubiona* Sp.B	h)	*Clubiona* Sp.B

Figure 2.7 Longitudinal section through the nest of *C. robusta* (Scale = 10 mm).

Fig. 2.6

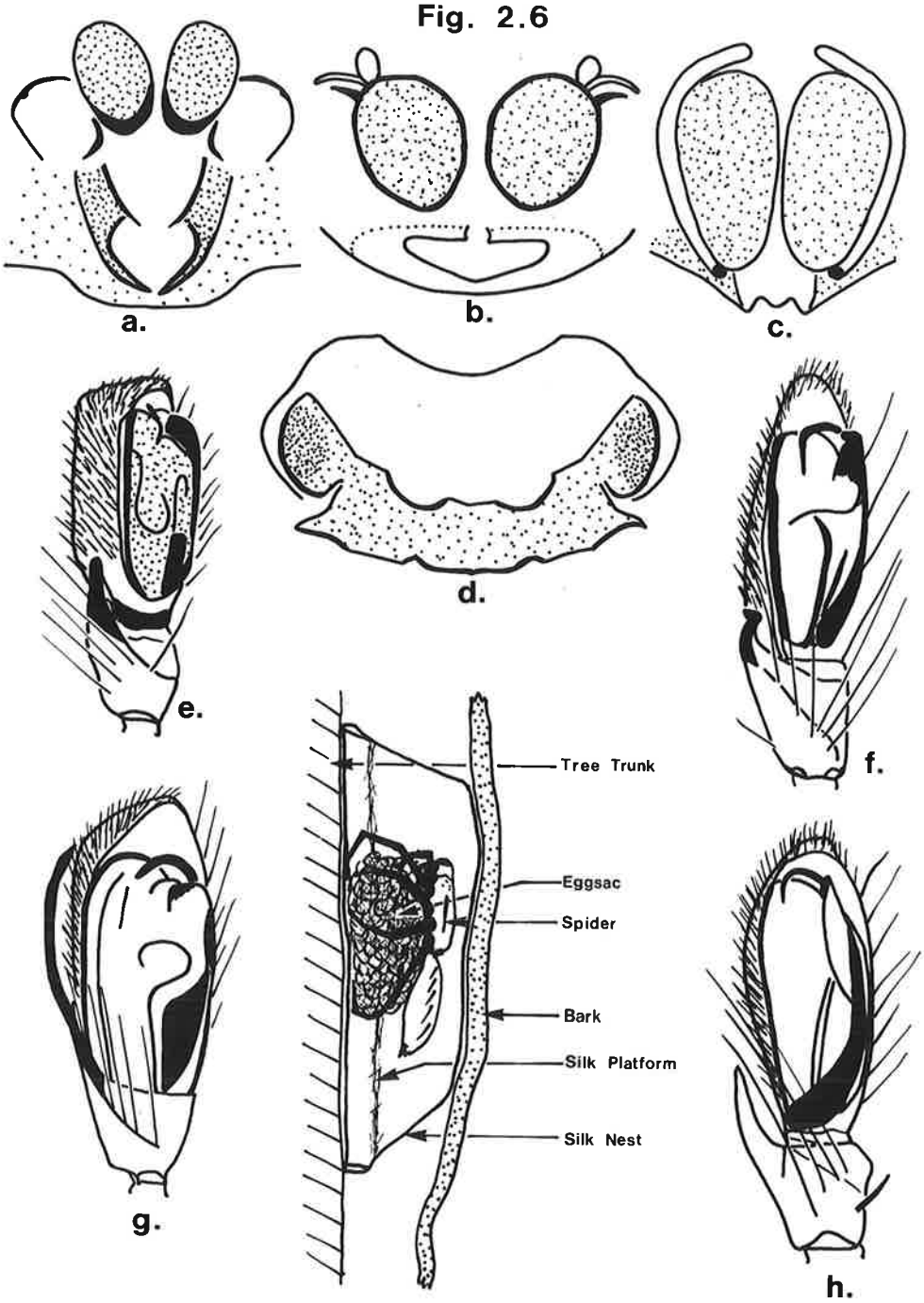
a.
b.
c.
d.
e.
f.
g.
h.
Tree Trunk
Eggsac
Spider
Bark
Silk Platform
Silk Nest

Fig. 2.7

and *C. cycladata* were collected from 5 large trees (approximately 30 cm diameter) to a height of 2 m in February 1980, and their positions (i.e. compass orientation) were recorded. The number of spiders found in each of the 4 compass quadrants (i.e. N., S., E. and W.) were compared against an equal distribution in numbers. These data showed no significant differences for *C. robusta* ($n = 42, \chi^2_1 = 1.62, P > 0.10$) or *C. cycladata* ($n = 122, \chi^2_1 = 3.31, P > 0.05$), indicating that these 2 species are randomly distributed around trees, with respect to direction.

It was also uncertain whether there is any relationship between the size of trees and the number of *Clubiona* that inhabit the bark. This was determined by selecting 58 trees covering the available size range (measured as tree diameter), and comparing the sizes of each with the number of adult *C. robusta* that were collected from under their bark, to a height of 2 m. These data (Figure 2.8) showed a significant correlation ($r = 0.76, t = 8.66, P < 0.005$) between size of trees and number of spiders. A similar trend was evident for *C. cycladata*, but this spider was not systematically collected. Numbers of spiders were not compared with the surface area or amount of corticating bark, because the latter forms a complex and heterogeneous habitat that was not possible to quantify. It was, however, evident that large trees support more corticating bark, because they have a larger surface area of trunk, compared with small trees. Also small trees (mean diameter < 20 cm) have little or no corticating bark that stays attached to the trunk and therefore there are few sites for spiders on these trees.

2.3.3 Prey of *Clubiona*

Prey of *C. robusta* and *C. cycladata* were obtained by collecting spiders that were feeding, or collecting prey remains that had been deposited outside nests by resident spiders after feeding had been completed. This method yielded 75 prey for *C. robusta* and 23 for *C. cycladata*. The main prey groups of *C. robusta* were Hymenoptera, mostly *Camponotus* spp.

Figure 2.8 Relationship between size of trees and number of adult *C. robusta* ($r = 0.76$, $t = 8.66$, d.f. = 56, $P < 0.005$).

Figure 2.9 Relationship between size of female *C. robusta* and number of eggs they produce ($r = 0.81$, $t = 6.71$, d.f. = 23, $P < 0.005$).

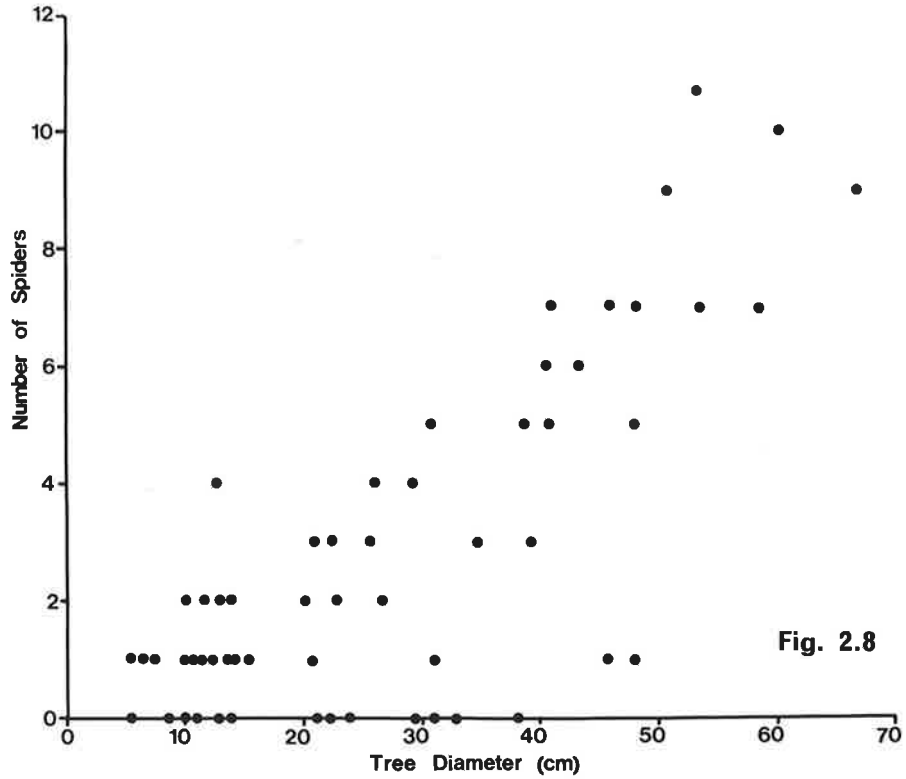
Number of Spiders
0
2
4
6
8
10
12
0
10
20
30
40
50
60
70
Tree Diameter (cm)

Fig. 2.8

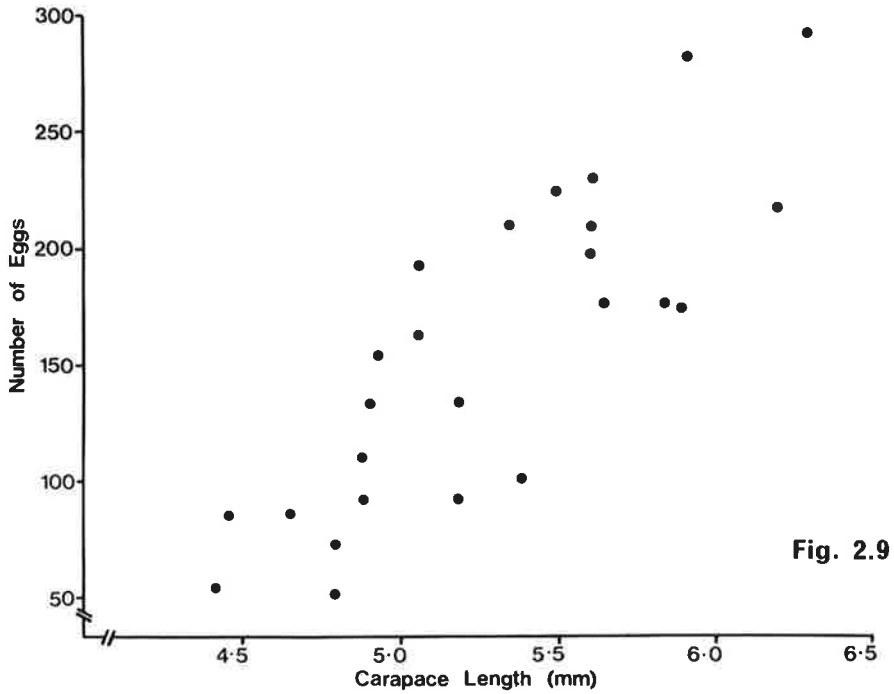
Number of Eggs
50
100
150
200
250
300
4·5
5·0
5·5
6·0
6·5
Carapace Length (mm)

Fig. 2.9

(Formicidae) (n = 26; 35%); Coleoptera (n = 22; 29%); Blattodea, mostly *Laxta granicollis* (Sauss.) (Blaberidae) (n = 12; 16%) and Heteroptera, mostly *Notius depressus* Dallas (Pentatomidae) (n = 11; 15%). The prey of *C. cycladata* mostly comprised the same groups; Blattodea (n = 7), Heteroptera (n = 6), Hymenoptera (n = 4), Araneae (n = 3) and Coleoptera (n = 2). These 2 species of *Clubiona* therefore do not appear to specialize on any one group of prey, but seem to be opportunistic in their feeding habits. The only potential prey that was not well represented was other spiders. These were the most abundant arthropods under bark, yet they comprised only 3% of all prey for both species. Predation on other spiders may be low due to the protection afforded by nests, or alternatively, spiders may be actively avoiding each other. Data from Section 3.3.7 would support the first hypothesis, but no information is available on avoidance behaviour in these or other spiders, and therefore the second hypothesis remains untested.

The null hypothesis that size of prey does not differ for these 2 species, was tested by comparing the mean lengths of the prey caught by each. Bartlett's test (Snedecor and Cochran 1967) demonstrated homogeneity of variances for these data, and a t-test showed a significant difference between the means ($t = 3.30$, d.f. = 96, $P < 0.005$). These 2 species therefore appear to feed on prey of different sizes. Comparison of prey showed that *C. cycladata* feeds predominantly on juvenile stages, while the majority of prey caught by *C. robusta* were adults.

2.3.4 Number of Instars

The number of instars of *C. robusta* was determined by rearing eggs through to adults in the laboratory (see 2.2.3). The majority of females reached maturity at instar 10, but some individuals became adults at the ninth instar. Males matured at instar 7-9. Although the sample sizes of each instar are small (instars 1-4, n = 20; instars 5-10, n = 10),

the range in lengths of the carapace showed little or no overlap (Figure 2.10). Males in the penultimate instar were excluded from the data, so that the size range of other instars was not swamped or distorted. These males were recognized by their slightly elongated chelicerae and swollen, but undeveloped pedipalps. Instars 1 and 2 are non-feeding stages and they take place inside the eggsac and nest. In the laboratory, juveniles first began to emerge from eggsacs and start to feed 17-35 d into the third instar. Emergence of juveniles from the same eggsac then continued for up to 14 d (see 2.3.7). It took 29-38 weeks (at 20°C) to complete development from the egg to adult stage, with males maturing before females.

The null hypotheses that males* and females reared in the laboratory do not differ in mean carapace length from those in the field was tested. Ten males and 10 females were randomly collected in the field and compared with those from the laboratory. Bartlett's test indicated homogeneity of variances among these data, and a t-test disclosed no reason to reject the null hypothesis for females spiders ($t = 1.63$, d.f. = 28, $P > 0.05$). However, males reared in the laboratory ($\bar{x} = 4.56$ mm) were significantly smaller than those collected from the field ($\bar{x} = 4.84$) ($t = 3.03$, d.f. = 28, $P < 0.005$). A possible reason for this was furnished by the observation that males from the laboratory spent long periods in aggressive interactions with each other. The density of males in rearing containers was much higher than of males in the field (see below and 3.3.1), and therefore males in laboratory cultures were probably spending much longer periods in aggressive interactions rather than feeding (see Givens 1978). This may have caused a substantial decrease in feeding time and resulted in the smaller size of these males, even though food was abundant.

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* Hereafter the terms male and female refer to adults, unless otherwise stated.

Figure 2.10 Mean carapace length (mm, ± range), of instars of *C. robusta* reared in the laboratory (n = 20 for instars 1-4, n = 10 for instars 5-10, N.B. pentultimate instar males are excluded - see text).

Figure 2.11 Size classes of *C. cycladata* collected from the field (N.B. pentultimate instar males are excluded - see text; the numbers along the X-axis correspond to the scale on the eyepiece micrometer that was used to measure spiders).

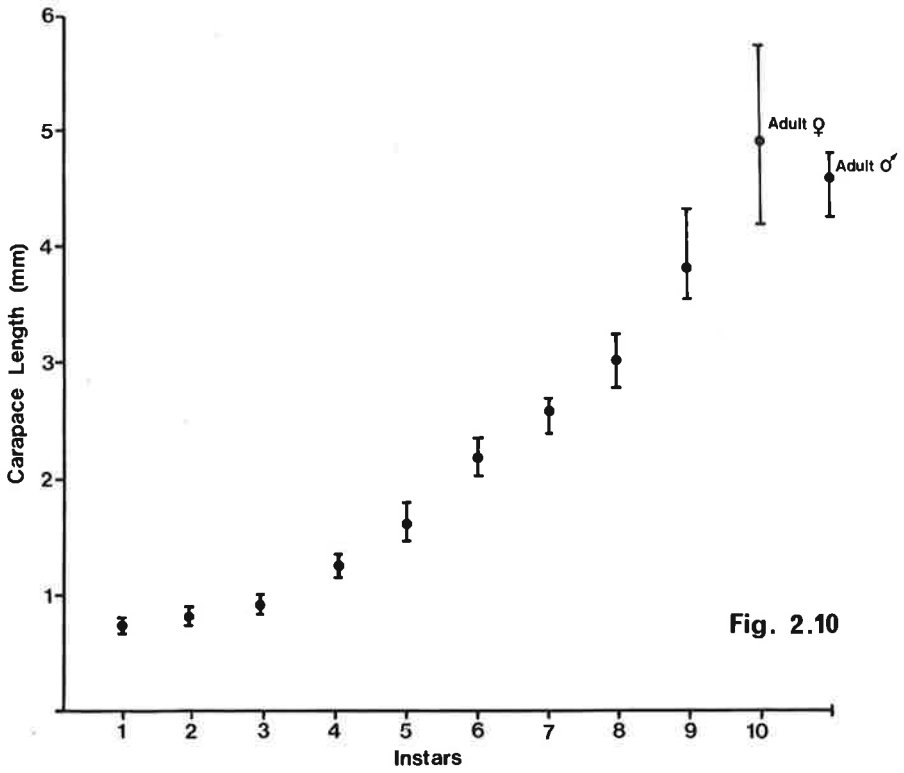


Fig. 2.10

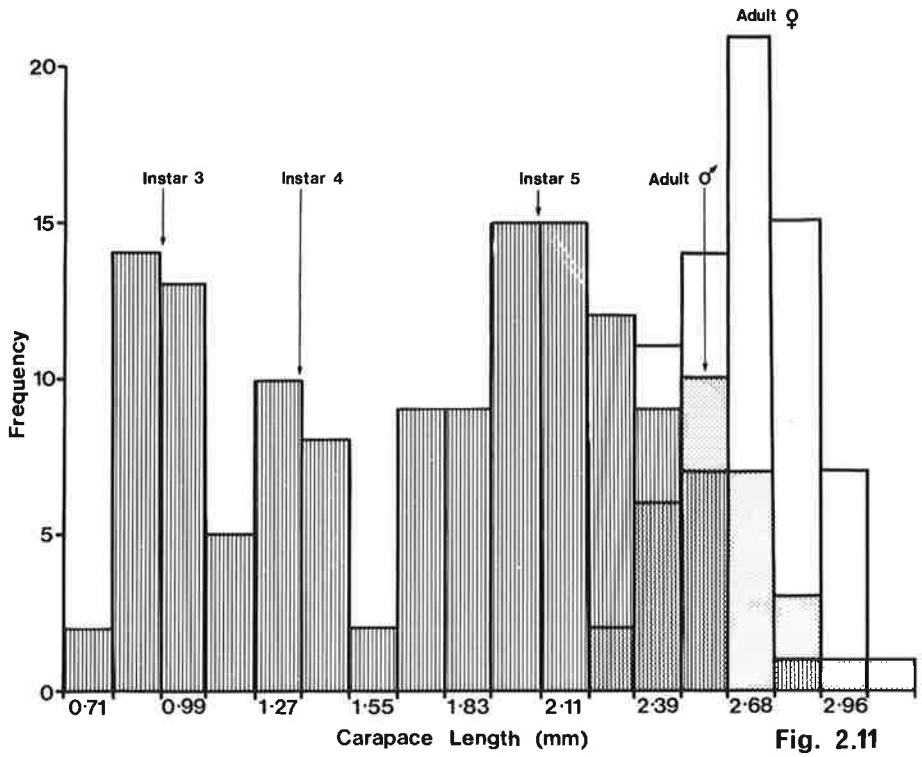


Fig. 2.11

Although few spiders were reared to the adult stage in laboratory cultures, the data available indicate that the ratio of males to females is close to 1:1 or slightly in favour of females. However, collections made in the field for *C. robusta* ($n > 500$) showed that only 30% of adults are males, thus indicating that many more males than females die before or soon after maturity (see 3.3.1).

The number of instars for *C. cycladata* could not be determined from laboratory cultures, due to the difficulty experienced in rearing this species (see 2.2.3). However, juveniles collected from the field (January 1980) (see 2.2.2) were used to obtain an estimate of the number of instars. The dorsal opisthosomal pattern of juveniles of *C. robusta* and Species B were used to recognize and remove these species from the sample, although some individuals with very faint patterns may have been included. Species A and B are rare at the study site (see 2.3.1) and so very few, if any, of these could have been present. In graphing the data for *C. cycladata*, males in the pentultimate instar were again excluded from the sample to prevent them swamping the larger size classes. The frequency distribution for size classes of 131 juveniles and 84 adults were calculated (Figure 2.11). The data show that *C. cycladata* collected from the field have 3 distinct size classes excluding adults, and these probably correspond to instars 3, 4 and 5. Females, therefore, probably have 6 instars while males appear to have 5. Data for instars 1 and 2 are not included as they take place only inside the nest, and therefore would not be collected. Comparison of the size of female Species A and B with the data for *C. robusta* and *C. cycladata* indicates that Species A probably goes through 5 or 6 instars and Species B 7 or 8 instars, assuming the same instars for each species are of similar size.

2.3.5 Nests and Moulting Chambers

The 2 types of silk retreats of clubionid spiders, namely nests and moulting chambers, serve a number of important functions. Nests are

constructed by females for oviposition, mating and overwintering, while moulting chambers are built only by juvenile stages. Moulting chambers vary in size depending on the size of the spiders that construct them, but they are nearly all smaller and have thinner (transparent) walls than nests. These chambers presumably provide protection from predators during the vulnerable moulting stages, when spiders are inactive. Juveniles also spend most of their time in these chambers, once moulting is completed, only leaving them at night to feed. Spiders in various instars were marked with spots of red paint of different shapes to identify individuals (n = 20) (January 1981), to determine their rate of movement. They were released into the same moulting chamber and 15 were recaptured 7 d later. Nine of these juveniles had moved to new sites on the same tree and constructed new chambers, or taken up residence in unoccupied retreats, while the rest had remained in or returned to the same chamber. Some individuals in the first group had constructed new chambers inside the nests or moulting chambers of other larger spiders. Thus, moulting chambers are probably not permanent refuges.

Unlike moulting chambers, the structure of nests varies between species of *Clubiona*. Nests of *C. robusta* have thick opaque walls and are usually circular (30-40 mm diameter, 5-7 mm in depth) or slightly elongated, depending on the shape of the space in which they are constructed. There are 2 entrances at opposite ends of the nest (Figure 2.7). The nests of *C. cycladata* are elongated (25 x 10 mm) and have transparent walls. Species A and B construct very similar nests to those of *C. robusta*, except that the nests of Species A are smaller (15 x 10 x 4 mm). One nest belonging to the latter species was found to have 3, not 2, entrances, equally spaced around the nest.

The nests of the 4 species of *Clubiona* occur together under bark but those of *C. cycladata* and Species A were sometimes found in spaces that

were too small for the nests of *C. robusta* or Species B. Males of all species construct temporary retreats that are similar in structure to but larger than the moulting chambers of juveniles.

Females of all species construct a low silk platform inside their nests on which they oviposit. The thin silk eggsac deposited around the eggs is attached to this platform and holds the ~~former~~ eggs in place. Females remain in the same nest while they have eggs or juveniles. They stop feeding approximately 7 d prior to oviposition and then stay with their eggs and juveniles for up to 3 months, until the latter disperse. Only then do they emerge from the nest to feed. An experiment conducted in the field during January 1981 to determine whether female spiders display any homing behaviour at this time, produced inconclusive results, due to a very low rate of recaptures. It did, however, show that some females return to the same nest, while others construct new nests at different sites before producing a second eggmass.

Observations on spiders in the field indicated that the walls of nests prevented the latter from becoming waterlogged in winter. Also occasional measurements of temperature and humidity (the latter using cobalt thiocyanate paper and a Lovibond Comparator Kit, standardized with various saturated salt solutions (Wilson and Bates 1961)) in the nests of *C. robusta* during summer (January 1981) showed them to be slightly cooler and to have a significantly higher relative humidity by 5-15%, compared with conditions on the outersurface of the bark. Nests may then provide more favourable conditions for eggs and spiders. This may be especially important as female spiders are probably easily stressed during the period in which they stop feeding. The higher humidity in nests may prevent excessive water loss during this critical period for females and also for juveniles (Davies and Edney 1952, Jones 1941, Peck and Whitcomb 1970, Toft 1980). Other functions of nests and eggsacs in relation to protection of eggs and spiders from predators and

parasitoids are discussed in Chapters 3 and 6.

A large number of invertebrates use the nests of *Clubiona* species as a refuge. This fauna, referred to as nest associates (Jackson and Griswold 1979) include the following groups: Acarina, Araneae, Coleoptera, Collembola, Heteroptera, Hymenoptera, Psocoptera and Thysanura. Nests appeared to contain more associates in winter and when they have been vacated by the resident spider. Samples of nests of *C. robusta* and *C. cycladata* ($n > 200$) in summer (February 1980) and winter (July 1980) showed that 42% of nests in summer and 78% of nests in winter were vacant, excluding some conspecific juveniles that had invaded them. Unoccupied nests remain intact for at least one year after they have been vacated, during which time they are inhabited by a greater number of nest associates. After this time nests fall apart, as their walls are gradually destroyed by associates burrowing through them.

2.3.6 Mating Behaviour

The mating behaviour of *Clubiona* species takes place in and around the nest of females. During spring and summer males are found in close proximity to nests of females, or to those in the pentultimate stadium. In August-October 1979 approximately 70% (33 out of 48) of males of *C. robusta* had constructed retreats next to the nests of females, while in April-May 1980 all males ($n = 19$) were found in isolated retreats. In some cases where space is restricted males place their nest in line with that of the female, i.e. orientated entrance to entrance. Males of *C. cycladata* all build retreats above (on top of) those of females, while the few observations on males of Species A and B indicate that they construct retreats in the same position as *C. robusta*.

Only 3 pairs of *C. robusta* and 5 pairs of *C. cycladata* were observed mating in the field during the study. These few cases indicate that mating takes place inside the nest of females at dusk and possibly during the night,

and very soon after the latter have completed their final moult. All females were in the soft post-moulting or teneral stage, and all pairs were in the same mating position, i.e. ventral surfaces opposed and bodies facing in opposite directions (Type 4 position in Forster and Forster 1973). Males mating with teneral females (see Jackson 1978a) is possibly an adaptation to prevent unreceptive females from attacking advancing males. No information was obtained on pre-mating behaviour, but it is unlikely that courtship behaviour in these species is very complex, if it exists at all. Teneral females probably cannot respond to any behavioural signals prior to mating. They are capable of only very slow and restricted movement, and do not respond to being touched with forceps or to being picked up. Other spiders, where females mate outside the teneral period, have complex mating behaviour and this is also thought to reduce predatory tendencies (Jackson 1978a, 1979a, 1980a, Robinson and Robinson 1980).

2.3.7 Eggs, Fecundity, Seasonality and Juveniles

The eggs of *Clubiona* species are cream to yellow in colour and are non-glutinous, i.e. females do not coat their eggs with a secretion that sticks them together, as do spiders in the Family Araneidae; the eggs of *Clubiona* have smooth chorions. The size of eggs of each species vary slightly. Random samples of 10 eggs from 5 separate eggmasses (3 for Species B) showed *C. robusta* to have the largest eggs ($\bar{x}$ = 1.09 mm diameter, $\pm$ 0.02 S.D.), followed by Species B ($\bar{x}$ = 1.05 mm, $\pm$ 0.02 S.D.), *C. cycladata* ($\bar{x}$ = 0.94 mm, $\pm$ 0.02 S.D.), with Species A having the smallest eggs (0.90 mm, $\pm$ 0.01 S.D.). Eggsacs from the field and laboratory culture showed that 3.4% of all eggs of *C. robusta* are infertile.

The number of eggmasses and eggs produced by each species varies. *C. robusta* produces up to 2 eggmasses per season, *C. cycladata* and Species A produce only one, while no information is available for Species B. Eggmasses collected from the field yielded the following

numbers of eggs per mass for each species; *C. robusta* ($\bar{x}$ = 131, ± 47 S.D., n = 72), Species B (range 43-86, n = 3), Species A ($\bar{x}$ = 37, ± 13 S.D., n = 15) and *C. cycladata* ($\bar{x}$ = 26, ± 10 S.D., n = 34). Marked females of *C. robusta* (see 2.3.6) showed that individuals which oviposit early in the season (August-October) can produce a second eggmass before the end of summer. No females were found with 2 separate eggmasses at the same time in a nest. They oviposit, stay with the subsequent juveniles, and then feed after the latter have dispersed, before producing a second eggmass. Although only 5 out of 20 females were successfully recaptured in March (1980) after being marked in September (1979), they all produced 2 eggmasses, thus indicating that the proportion of early maturing spiders that produce a second eggmass is probably very high. Eight of 11 females that had recently moulted (i.e. they had not previously oviposited) were marked in January (1980) and recaptured in April (1980); all of these individuals produced only one eggmass. Some females that mature late in summer, however, overwinter and produce eggmasses at the beginning of the following season (see 3.3.4).

Gravid females of *C. robusta* of widely different sizes, were collected from the field in September-October (1980) (i.e. they had not oviposited that season) to determine whether any relationship existed between size of spiders and number of eggs they produce. The mean time from collection to oviposition for these individuals was 17.5 d (± 12.4 S.D., n = 25). The number of eggs produced was counted and compared with the size of each spider. These data (Figure 2.9) show a strong positive correlation between number of eggs produced and size of spiders ($r = 0.81$, $t = 6.71$, d.f. = 23, $P < 0.005$), and this probably accounts for the large range in sizes of eggmasses encountered in the field.

Observations in the field during the course of the study (3 summer seasons) showed that 3 species at least have extended periods ~~for~~ during which

eggs are present in nests (Figure 2.12). The eggs of *C. robusta* and *C. cycladata* were usually present from August-March inclusive, with eggs of *C. robusta* extending into April during one season. Those of Species A were found from September-April but extended into May for one season. Eggs of this species were not collected in some months, presumably as they are rare compared with those of *C. robusta* and *C. cycladata*. As mean temperatures are relatively low during March-May compared with mid-summer (see Figure 2.2), the development rate of all eggs at this time is slow. The last eggmasses of each season must be produced approximately 30-40 d before these eggs hatch. Only 3 eggmasses of Species B were collected and ~~so~~ there are no data on the ovipositional period of this species ~~were forthcoming~~. Juveniles of these species spend the first 2 instars and part of the third in the eggsac and nest before dispersing. They are found in nests in the field approximately 1-2 months after the first eggmasses are produced and after the last have hatched (Figure 2.12). Dispersal of juveniles occurs throughout the summer from November onwards.

The stimulus that leads to dispersal of juvenile spiders is not known, although temperature and other factors are implicated (Duffey 1956, Legel and Van Wingerdan 1980). Austin and Anderson (1978) suggest that depletion of yolk reserves may also cause them to leave the nest. This hypothesis is supported by Harrington (1978) who has shown that larger juveniles, containing more stored yolk, can survive for longer periods without feeding, compared with smaller individuals. Third instar juveniles of *Clubiona* certainly vary in size and they disperse from nests over an extended period (up to 2 weeks) rather than all at once. This may be a result of individuals exhausting their yolk reserves at different times and then being forced to disperse to find food. Early instars of some spiders have been recorded as feeding on infertile eggs in the same nest (Peck and Whitcomb 1970, Schick 1972, Valerio 1974), however this was never observed for the *Clubiona* species in this study. The first meal of these species is probably taken when prey

Figure 2.12 Time of the year for which eggs and juveniles of *Clubiona* are present in nests. Observations began on December 1978.

Figure 2.13 Effect of temperature on the time taken to reach the main embryonic stages in the eggs of *C. robusta*; measured as a proportion of total developmental time (N.B. changes in the slope of the line between stages is not significant, e.g. between stages 7-8 and 8-9, as the main embryonic stages were chosen only as they were easily recognized; they are not separated by equal developmental times - see Figure 4.4).

Embryonic stages:

1. oviposition
2. blastoderm
3. germ disc
4. germ band (no limbs developed)
5. germ band (limbs half the length of their final size)
6. early inversion
7. s-shaped germ band
8. dorsal closure
9. eclosion

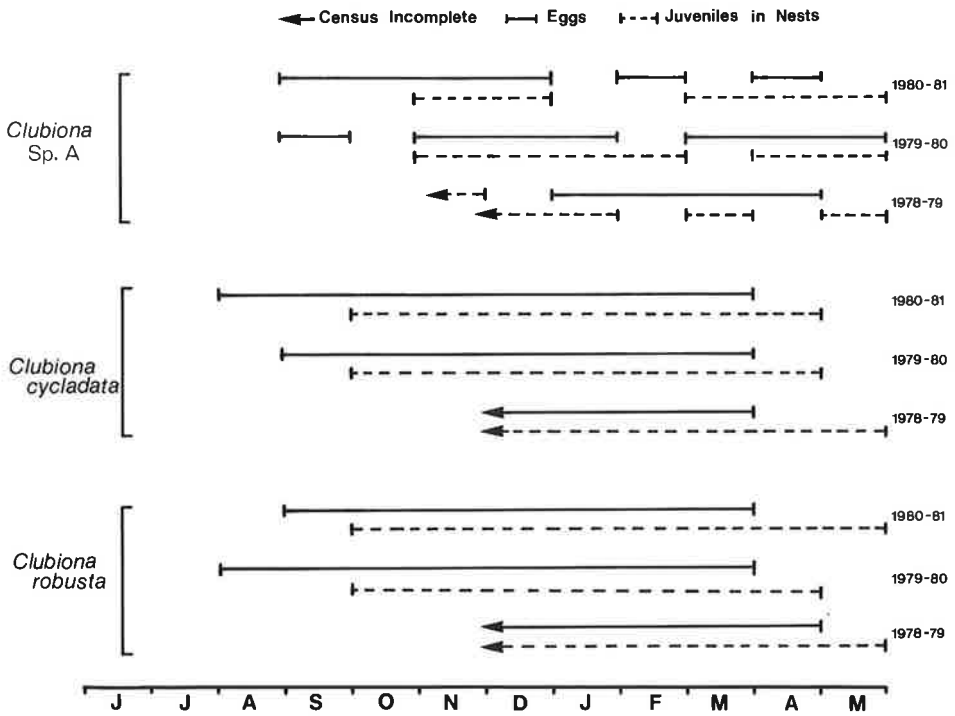


Fig. 2.12

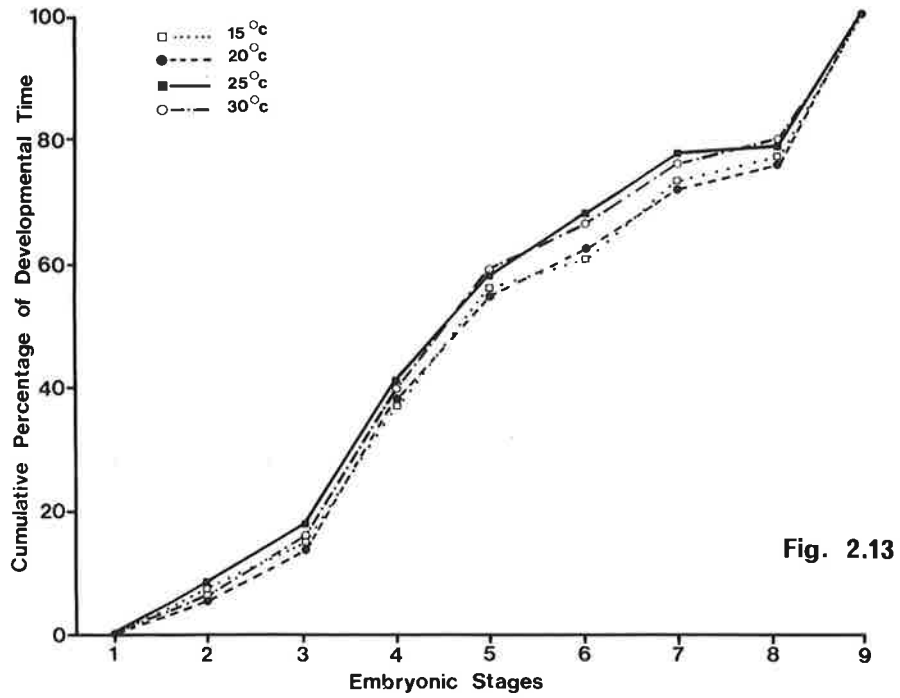


Fig. 2.13

is caught after juveniles have dispersed.

2.3.8 Development of Eggs

The embryological development of *C. robusta* was compared at 4 temperatures: 15, 20, 25 and 30°C. The main embryonic stages were identified (see Anderson 1973, Austin and Anderson 1978, Holm 1954) and their duration timed, so that the effect of temperature on the rate of development of separate stages could be examined. Development time (oviposition to eclosion) decreased with increasing temperature, as would be expected. The mean development time was 6.3 d at 30°C, 8.4 d at 25°C, 13.0 d at 20°C and 26.0 d at 15°C. Comparison of the proportion of time taken to reach each stage with the total development time (Figure 2.13), showed that different temperatures do not affect individual embryonic stages differentially, but rather cause similar changes to the rates of development of each stage as they do to total development time. No variability is given for these data because development times are estimates for the central points of each stage. These stages are not discrete, but are continuous and merge with each other. The eggs of *C. cycladata* showed almost identical development times to *C. robusta*, but individual embryonic stages in the former were not compared.

2.3.9 Causes of Mortality

This section represents a brief summary of the factors that cause mortality in the *Clubiona* species in this study, without attempting to quantify their effect. A more detailed examination of mortality in *C. robusta* is given in Chapter 3.

Comparison of the number of eggs of *C. robusta* with the number that become adults indicates that more than 95% die before they reach maturity. Observations during monthly population surveys showed that mortality is high in the egg and third instar stages. Eggs of *C. robusta*, *C. cycladata*

and Species A are heavily parasitized (10-35%) by scelionid parasitoids (Figure 2.5), while additional but minor predation on eggs of *C. robusta* by ants (*Iridomyrmex* sp.), eulophids (*Tetrastichus* sp.) and chloropid flies (possibly *Gaurax clubionae* Hickman; Hickman 1970), and on *C. cycladata* by pompilids (*Epipompilus* sp.) was also recorded.

The highest mortality in *Clubiona* species, as with many other spiders, probably occurs during dispersal of third instar juveniles. The majority of individuals leave the nest and disperse on the wind (called ballooning), by trailing a silk thread from their spinnerets into a breeze. A minor but unknown proportion of juveniles disperse from the nest without ballooning, and probably stay on the same tree. Difficulties with estimating mortality at this stage were not overcome, as it occurs away from the preferred habitat (i.e. eucalypt trees). Also the inability to accurately distinguish juveniles of different species (see 2.3.1) substantially added to this problem. However, studies on other spiders indicate that mortality during this phase, resulting from juveniles falling into unfavourable habitats, is extremely high (Duffey 1956, Horner 1975, Salmon and Horner 1977, Turnbull 1973, Valerio 1977). Almost no mortality was recorded for instars 1-3 before dispersal. No conspecific individuals or other spiders were found eating eggs or juveniles in nests, as has been observed for *Clubiona* in New Zealand (pers. comm. R.R. Jackson).

Mortality during the post-dispersal stages (instar 4 to the adult stage) was assumed to be low, as very few dead individuals or exoskeletons were found under bark (see 3.3.4). Death at moulting or from cannibalism was not observed in the field, as happened in the laboratory (see 2.2.3), nor did starvation appear to be important, as prey were abundant at all times during the study. No predation by mammals, birds or reptiles was recorded, though it is known for other spiders (Bristowe 1941, Turnbull 1973, pers. comm. A.P. Smith). Predation by the spider *Lampona cylindrata*

(L.Koch) (Gnaphosidae) was observed, however, with 19 *Clubiona* (both adults and juveniles) being recorded as prey. All the latter appeared to be outside their nests when they were taken. *Lampona* and other gnaphosids have been recorded as preying on spiders (Forster and Blest 1979, Hickman 1967a, Jackson 1976), and it is possible that some species in this family may specialize in feeding on spiders. No other spiders in the same habitat were observed to feed on each other, except for 2 records of *C. cycladata* found eating juvenile salticid spiders (see 2.3.3).

Several dead adults of *C. robusta*, *C. cycladata* and Species A found during winter (May-September) were covered with a fungus (*Verticillium* sp.). Attempts to infect healthy spiders with this fungus in the laboratory failed, but it was successfully cultured on freshly killed spiders. Thus, this fungus appears to infect dead spiders only and probably is not the cause of death.

2.4 DISCUSSION

This study has shown that a number of similarities and differences exist in the biology of the *Clubiona* species examined. Firstly, they vary markedly in their relative abundance; *C. robusta* and *C. cycladata* are common at the Mylor study site, while Species A and B are rare. Also, due to differences in body size, they differ correspondingly in number of instars, number of eggs laid, and size of prey caught. However, they show similarities in the types of retreats constructed, time of egg production, type of prey caught, habitat in which they live, and apparently in causes of mortality. These generalizations are based on information obtained on *C. robusta* and *C. cycladata*; only supporting data were forthcoming on the 2 rare species.

At high latitudes *Clubiona* species usually have a biennial life cycle, produce only one generation in that time, and have a short period of egg production of 1-2 months (Toft 1976, 1979). This pattern apparently

varies, as species at lower latitudes are reported as having annual cycles (Almquist 1969, Peck and Whitcomb 1970). The *Clubiona* species in South Australia produce eggs for more than half the year and therefore have overlapping generations. They probably have 1½-2 generations per year, and appear to have annual life cycles. However, some females mature late in summer and overwinter to live for longer than 12 months. Such differences in seasonality and reproductive period are known for many spiders. This has been correlated with climatic conditions at different latitudes, and is also probably related to other factors such as prey availability and local climatic effects. The stage or stages in which spiders overwinter is also related to climate, and is presumably most affected by temperature. Turnbull (1973) states that spiders overwinter in the egg stage, but recent studies show that many spiders overwinter in any stage, but usually as juveniles or adults rather than as eggs. This is certainly the case for *Clubiona* in South Australia and clubionids elsewhere (Mansour *et al.* 1980b, Peck and Whitcomb 1970, Toft 1979). The reason for this discrepancy may be that until recently nearly all detailed studies (reviewed by Turnbull 1973) have been conducted in colder northern hemisphere climates where spiders may tend to overwinter as eggs. In the last 10 years more attention has been paid to tropical and subtropical spiders that overwinter in post-eclosion stages (Robinson and Robinson 1973, 1976), and breed for much longer periods (Austin and Anderson 1978).

The number of instars of different spiders is a function of their size. Species of similar size usually go through a similar number of instars before maturation, as might be expected. Comparison of the number of instars of *Clubiona* in this study with other spiders of approximately the same size range, show that they have between 6 and 9 instars (Jackson 1978b, Mansour *et al.* 1980b, Peck and Whitcomb 1970, Toft 1978), while much

larger spiders have up to 14-16 instars (Humphreys 1976, Robinson and Robinson 1973). These studies show that males usually mature before females, though Mansour *et al.* (1980b) reports the opposite for a species of *Chiracanthium*. Some spiders have both early and late maturing adults (Jackson 1978b, Wise 1976); however, there is no evidence of this for *Clubiona*. Most species show substantial variability in size of the adults, and this is probably the result of individuals going through different numbers of instars before maturation and having different rates of food consumption (Anderson 1978, Enders 1976, Kessler 1970). This variability could explain the wide range in number of eggs produced by spiders of one species. This study and others (Enders 1976, Harrington 1978, Jackson 1978b) have demonstrated a high correlation between size of spiders and the number of eggs they produce. However, *Clubiona* species do not show a great range in the size (diameter) of eggs or a decrease in the number of eggs placed in subsequent batches, as do other spiders (e.g. Anderson 1978, Enders 1976, Jackson 1978b, Mansour *et al.* 1980b). Presumably this is at least partly due to *Clubiona* feeding between the laying of eggmasses, when they may replenish nutrients used in the production of yolk. Spiders that show a reduction in the number of eggs in different eggmasses apparently do not feed between successive ~~subsequent~~ ovipositions.

Most studies on the behaviour of prey capture in spiders have been carried out on web-building species, as their prey are easily collected from webs. Few studies have examined the prey of hunting spiders, and yet families comprising this group are the dominant arthropod predators in several habitats. *Clubiona* in South Australia, as do many other spiders, feed on a diverse array of prey species. Most spiders are opportunistic and take what prey is available at any particular time (e.g. Jackson 1977b, Mansour *et al.* 1980b, Morse 1979). This has led to inaccurate reports that some spiders show distinct preferences for a particular prey, when it is likely that observations have been made over a short period when only one

prey species is abundant (see Turnbull 1973). Some spiders do, however, refrain from attacking distasteful or stinging prey, while this and other studies have shown that spiders of different size attack prey of different sizes (Austin and Blest 1979, Nentwig 1980, Robinson and Robinson 1973). Experimental studies on behavioural discrimination and selection of prey by hunting spiders are required if any detailed understanding of their ecology is to be attained. Only a few spiders have been shown to have a very restricted range of prey species. This can usually be associated with very specialized methods of prey capture, such as the use of chemical attractants by *Mastophora* (Araneidae) and related araneids (Eberhard 1977), or the use of specialized webs, e.g. *Menneus* (Austin and Blest 1979).

Silk retreats (moulting chambers and nests) are constructed by most hunting spiders. They vary considerably in structure both within and between species (Jackson 1979b, Mansour *et al.* 1980b, Peck and Whitcomb 1970), although this study indicates that *Clubiona* species may construct retreats that are comparatively uniform in shape and density of silk. The function of nests has not previously been studied in detail. Data obtained in this study has provided support for the hypothesis put forward by Jackson (1979b), that nests act to protect eggs and/or resident spiders from adverse physical factors, i.e. water logging, high temperatures, low relative humidity. Nests, in conjunction with the guarding behaviour of female spiders, also serve to protect eggs from predators (see 3.3.5). Moulting chambers probably prevent mortality of juveniles during and after ecdysis, although this hypothesis has not been tested. The function of eggsacs has also received scant attention in the past. Many workers have speculated that these structures protect eggs (e.g. Bristowe 1941, 1958, Comstock 1940, Forster and Forster 1973, Main 1976, Robinson, M.H. 1980). Some authors have commented on the apparently camouflaged surface of eggsacs, and yet in nearly all cases the factor(s) from which eggs are being protected are unknown. The function of eggsacs undoubtedly varies between species. There is good evidence to support the hypothesis that for some species the

eggsac protects eggs from harsh physical factors (Austin and Anderson 1978, Levi and Levi 1969, Main 1976, Riechert 1981). Austin and Anderson (1978), however, could not demonstrate this as a function for the eggsac of *Nephila edulis*, although Christenson and Wenzel (1980) have shown that the eggsac of another species in this genus does increase the rate of survival of eggs and juveniles. Hunting spiders such as *Clubiona*, that construct nests, usually have flimsy eggsacs, compared with those of other spiders. In these cases the wall of the nest, rather than that around the eggs, probably provides the barrier to protect the latter from severe physical factors. Eggsacs of these spiders may, therefore, only function to hold the non-glutinous eggs together. The eggsacs of some spiders are manipulated by the female to maintain a favourable temperature for the eggs. This has been reported for theridiids (Norgaard 1956), and more recently for lycosids (Humphreys 1974). Wise (1974) and Robinson, M.H. (1980) have observed spiders that sometimes bury their eggsacs in soil or litter. So far these reports have not been followed by studies to examine the possible function of this behaviour. Eggsacs of some spiders also probably reduce or prevent mortality due to predation and/or parasitism (see 3.3.6 and 3.4).

The early post-eclosion stages of spiders have caused some confusion in regard to the terminology used to describe them (Peck and Whitcomb 1970, Valerio 1974, Whitcomb 1978). At least the first instar of all spiders is inactive and does not feed. Embryological studies (Anderson 1973) have shown that the midgut during this period is incomplete, and therefore feeding may not be possible (Austin and Anderson 1978). This stage of the life history of spiders has been referred to by various terms, e.g. 'prelarvae', 'deutova', 'incomplete stadia', 'postembryos' and 'nymphs' and it is said to occur prior to the 'true' growth instars (Valerio 1974). Some authors have suggested that the true first instar (third instar in this study) begins during the stage when feeding commences. However, incomplete development of the

gut and non-feeding in the first instars is not unique to spiders. It is also known to occur in some hemipteran bugs and other insects (Mukerji and Le Roux 1965, Tostowaryk 1971). Study of these cases has not caused undue confusion nor required the use of new terms to refer to them, and therefore the nomenclature specifically used for the same stages in the development of spiders would seem unnecessary. Furthermore, these stages are presumably subject to the same endocrine events that result in apolysis and ecdysis, as for later instars, and hence they should simply be referred to as Instars 1 and 2, as in this study.

No studies have examined the possible function of the quiescent instars of spiders in detail. Schick (1972) proposes that they may be related to the feeding on infertile eggs in the same nest. However, there are many species for which this type of feeding is unknown, and yet all spiders go through these early inactive stages. Gertsch (1949) questions whether they have any function at all, except that it is difficult to envisage that such a widespread phenomenon has occurred by accident. One possible function that has not been considered is that early eclosion may occur to allow for expansion or growth that would otherwise be impossible when the embryo is tightly packed into a ball. Early hatching, before internal development is completed, may then be an adaptation in groups that possess lecithotrophic eggs.

Study of the biology of spiders has progressed significantly in the past 20 years, from simple descriptions of natural history to quantitative and experimental analyses. However, several areas of araneid biology, including the behaviour of prey capture and prey discrimination, and the functions of early inactive instars, nests and eggsacs, are still neglected. This study has examined these and other areas of the biology of several *Clubiona* species, as a contribution towards a better understanding of clubionids and spiders in general.

CHAPTER 3

ECOLOGY AND BEHAVIOUR OF *CLUBIONA ROBUSTA*

3.1 INTRODUCTION

Spiders have recently found wide appeal in ecological studies, both at the population and community level (see below). As with natural history studies (see 2.1) the majority of investigations have been directed towards ground-living and web-building spiders, especially of the Families Lycosidae and Araneidae. The few studies conducted on the ecology of spiders inhabiting vegetation have investigated possible associations with plants, especially the vertical distribution of spiders (e.g. Enders 1974, LeSar and Unzicker 1978, Muma 1980, Turner and Polis 1979), rather than aspects of their population ecology.

Although there are problems in obtaining accurate estimates of the size and age structure of spider populations (see Turnbull 1973), lycosids and araneids have presented fewer difficulties than other spiders. Quadrat samples, line transects, pitfall traps and visual searching, among others, have been employed as sampling techniques on these spiders with reasonable success (Edgar 1971a, Humphreys 1976, McQueen 1978, Robinson and Robinson 1973, Turnbull 1973, Uetz and Unzicker 1976, Workman 1978). Spiders inhabiting vegetation, especially the foliage of shrubs and trees, have proven very difficult to sample. Some species and instars are more easily collected than others, resulting in over- or under-estimates of the numbers present.

Many ecological studies on spiders have concentrated on prey selectivity, prey consumption and related energetic considerations (e.g. Anderson 1974, Ford 1977a, 1977b, Greenstone and Bennet 1980, Humphreys 1975, 1978, Nentwig 1980, Wise 1979), while fewer studies have examined other factors that limit the size and structure of populations. The direct effect of scarcity of food and adverse weather (temperature and humidity) have emerged as the most important limiting factors for spider populations (Anderson 1974, Dondale and Binns 1977, Kessler 1971, 1973,

Wise 1975, 1979). Some workers have also shown that these factors operate indirectly through the structure (quality) of a habitat, i.e. the site chosen for web or burrow construction (Colebourn 1974, Enders 1977, Riechert 1976, 1978, 1979). The decline in numbers over complete cohorts have been measured for several species but the major factors responsible for this mortality are often not well recognized. Predation, parasitism and mortality at the dispersal stage occur in these species, but their importance compared with other factors is generally not known (Edgar 1971a, 1971b, Humphreys 1976, McQueen 1978, Workman 1978).

The assumptions that spiders display a constant rate of mortality through all age classes (Humphreys 1976, Edgar 1971c, Workman 1978) and that food and weather are the main limiting factors, can be disputed, as they have been based on studies on 2 groups of spiders, the majority of which were lycosids. There is a need to examine the ecology of other types of spiders, as lycosids show unusual characteristics that could have biased the above generalizations. For example, they often have a prolonged maturation time (up to 2 or 3 years); they are well protected in burrows for long periods; and many species do not employ ballooning as a means of dispersal.

The present study examines some aspects of the ecology of one spider, *C. robusta*, that is associated with the bark of eucalypt trees. The relative abundance of this species, the incidence of parasitism and other mortality factors are studied. Also, the importance of overwintering, possible structural and behavioural adaptations to reduce parasitism, and interactions between adult spiders are investigated. This work is then discussed in relation to studies on the ecology and behaviour of other spiders.

3.2 MATERIALS AND METHODS

The general methods and materials used in this section are the same

as those in 2.1, except for the specific techniques that are described below.

3.2.1 Sampling Spiders in the Field

Spiders were sampled in the field (Area 1 of the Mylor study site - see 2.2.1) every month between February 1979 and July 1981 inclusive. Due to the extreme variability in the bark on eucalypt trees, i.e. number of layers, percentage cover and size of trees (see 2.3.1 and 2.3.2), it was not possible to use any technique that was based on a fixed sampling area, as the area of bark could not be measured accurately. Instead, a standard searching time of 2 h was used to overcome this problem. All trees in Area 2 were assigned a number and those to be sampled each time were selected by choosing random numbers ($n \simeq 30$). Trees were then searched by pulling all the loose bark from the trunk to a height of 2 m from the ground, and all adults and subadults (those in the pentultimate instar) of *C. robusta* were collected. The number of trees searched in different months varied, depending on their size, but at least 10 trees were sampled each month. Trees selected but not searched were replaced back into the population of trees that could still be examined in the following samples, while trees that were searched were excluded from the study. To test the reliability of this technique, 4 replicate samples were taken in 4 months at different times of the year. These samples produced ranges in the total number of female spiders caught that were much greater between months than within monthly samples (see Figure 3.1). Also, trees were re-searched on these occasions and virtually no new spiders were located, indicating that all spiders present were being collected.

3.2.2 Mortality of Eggs and Juveniles

The number of eggs parasitized by *Ceratobaeus masneri* was determined by collecting all eggmasses that were found during monthly 2 h sampling periods. Eggmasses were held at 20°C and the number of parasitoids

that emerged was counted. Only eggs older than the mid germ band stage at the time of collection were used to calculate the incidence of parasitism (see 4.3.7). Eggs collected in earlier stages could still have been parasitized if they had been left in the field, and thus their inclusion in samples would have resulted in an under-estimate of the number of eggs parasitized. This method was used for the 1979-80 and 1980-81 seasons (i.e. August-April). Because monthly population samples began in February 1979 the above method could not be used for most of the 1978-79 season. However, an estimate of mortality due to parasitism was obtained by collecting a large number of nests in February-April (1979). Nests formed during that season could easily be recognized because their walls were relatively clean and white. They could not be confused with nests constructed in previous seasons (1977-78 or before), as nests older than one year became discoloured and damaged, i.e. they fall apart due to the activity of nest associates (see 2.3.5). It was possible to determine accurately the number of parasitized and unparasitized eggs in these nests where wasps and spiders had already emerged and dispersed, by counting the brown tanned egg-shells left by parasitoids and the white eggshells remaining after spiders had hatched. Some nests collected in February-April contained wasps in host eggs and unparasitized eggs or juvenile spiders, and so these could be counted directly.

3.2.3 Guarding Behaviour by Female Spiders

Gravid female *C. robusta* were collected from the field, placed in plastic containers, and allowed to construct nests and to oviposit. Non-gravid females were collected in 2 groups. One group was collected 30 d or more prior to the experiment; these were supplied with water but no food. The second group was collected approximately 7 d before the experiment, and were supplied with both food (cockroaches) and water. Some spiders did not construct nests, presumably due to the absence of bark

(see 2.3.2), and so these individuals could not be used in the experiment. The behavioural response of spiders in nests was measured by the time it took them to kill different types and sizes of intruders. Normally the walls of a nest are opaque (see 2.3.5) but when a light source (Schott Mainz 150W fibre-optics lamp at one-quarter intensity) is placed behind a nest, the silhouette of the spider and intruder can be clearly seen. Light intensity was kept at this low level to reduce any effect on the behaviour of spiders. However, tests prior to the experiment, using *Drosophila* and starved spiders, showed the former were killed in approximately the same time (4-30 s) whether containers were illuminated or kept in the dark. Trials with each type of intruder were replicated 10 times. Intruders were pushed through the entrance of a nest using forceps; each trial being stopped after 30 min, unless the intruder was killed before that time. Due to the large number of spiders needed for the experiment, some individuals were used several times. In trials where feeding did not occur spiders were retained and used again, however, replicates for each type of intruder were conducted with 10 different spiders. Subsequent trials with the same spider were always separated by at least 48 h.

3.2.4 Behavioural Interactions Between Adult Spiders

A spider was placed in each end of a perspex tube (3 cm diameter, 15 cm long), divided by a sliding aluminium barrier. They were isolated in these chambers for 15 min before the barriers were removed to allow entrance into the tube. Each trial was conducted until the 2 spiders met and interacted once. As soon as they moved away from each other the trial was stopped. No trials ran for more than 2 min. Twenty-five replicates of each treatment, e.g. female-female, male-male, female-male pairs, were conducted at room temperature (23-28^{o}C). The perspex tube was washed and dried between each trial, to remove any substances left by previous spiders. Spiders used in the experiment were collected from the

field 7-14 d beforehand; all were well fed and provided with water during that period.

3.3 RESULTS

3.3.1 Phenology

Samples of adults and subadults of *C. robusta* were taken monthly for 30 months (see 3.2.1) to determine the population phenology of this species. Juvenile stages could not be studied in this way because they could not be distinguished from the juveniles of other species of *Clubiona* (see 2.3.1). These data (Figure 3.1) show that female spiders were present in the field at all times of the year, but their relative abundance varied. Numbers were highest during the warmer months (September-February) and lowest during the cool months (May-August). Adults and subadults were present in approximately equal numbers during each month. They are combined in Figure 3.1 to highlight ~~this~~ these seasonal differences in abundance.

The number of males collected in monthly samples was much lower than that of females; in fact only 30% of all adults collected were males. Males were not collected in 2 out of 30 months, presumably because they were so rare that they were not detected in the 2 h searching period. However, they showed the same fluctuation in numbers as females, i.e. most abundant in summer, least abundant in winter.

Examination of the phenology of *C. robusta* at Mylor gives rise to 3 main questions; (1) were females that were caught during winter months reaching maturity at regular intervals during that period, or were they overwintering as adults from individuals that were maturing late in summer or early autumn?; (2) what were the main factors causing mortality, and how do they contribute to the seasonal population cycle of *C. robusta*?; and (3) why were males in such low numbers in the field, when the sex ratio in laboratory cultures is close to 1:1 (see 2.3.4)? These questions are

Figure 3.1 Number of adults and subadults of *C. robusta* collected at the Mylor study site in monthly 2 h samples (N.B. bars ≡ ranges in number of female spiders for months in which replicate samples (n = 4) were taken - see 3.2.1).

Figure 3.2 Cumulative percentage of parasitized eggs of *C. robusta* as a function of time (N.B. mean curve fitted by eye).

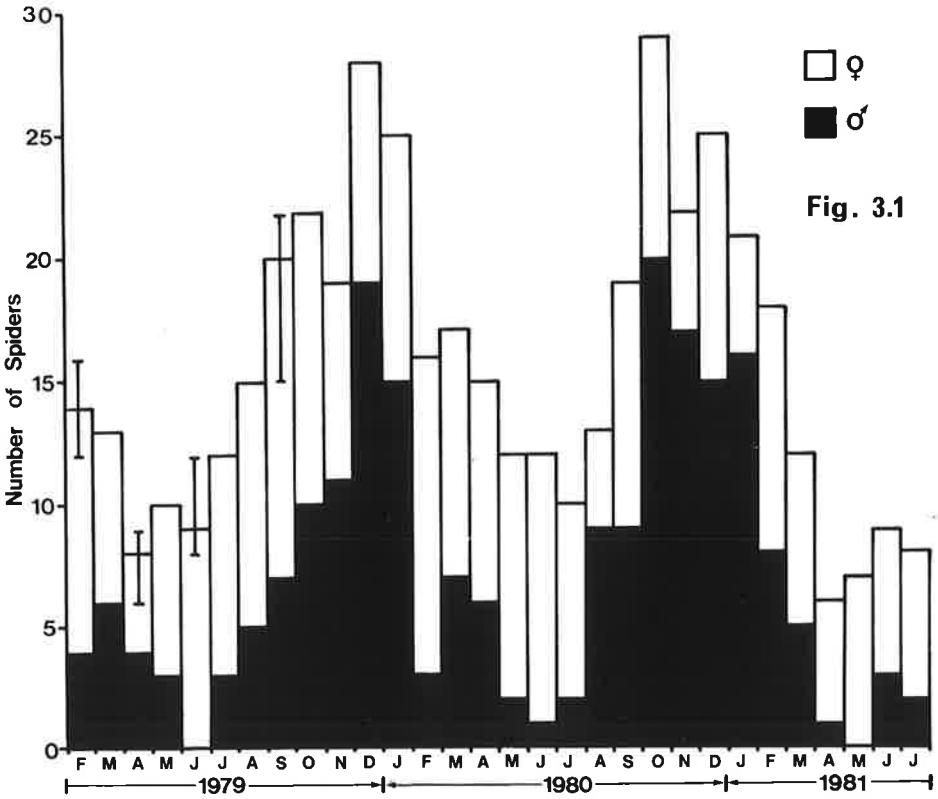

30
25
20
15
10
5
0
Number of Spiders
♀
♂
F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J
1979
1980
1981

Fig. 3.1

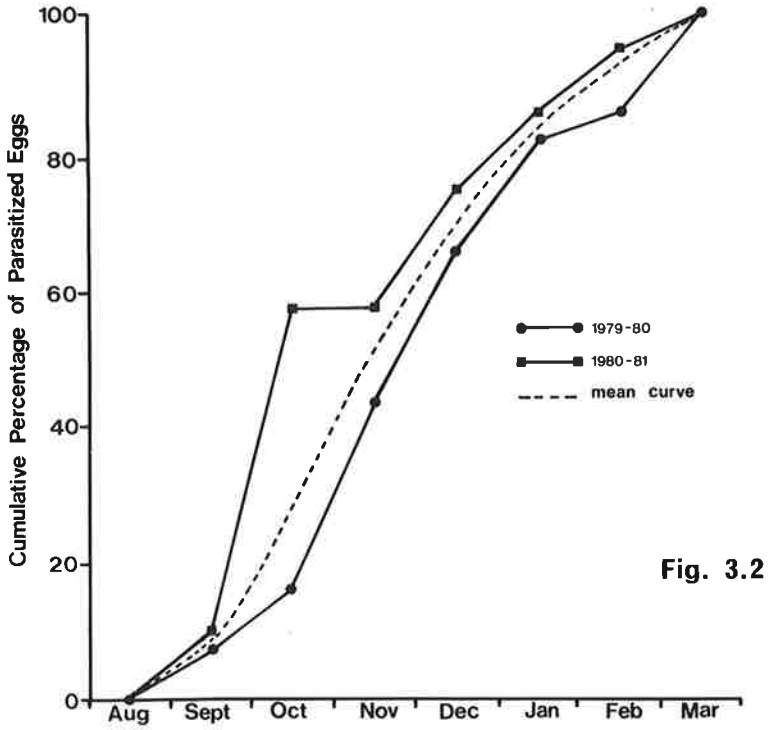

100
80
60
40
20
0
Cumulative Percentage of Parasitized Eggs
1979-80
1980-81
mean curve
Aug
Sept
Oct
Nov
Dec
Jan
Feb
Mar

Fig. 3.2

examined in the following sections.

3.3.2 Overwintering by Adult Females

All females from 3 trees (30 cm diameter) were removed from under the corticating bark with as little disturbance as possible being made to the latter. Ten recently matured females that had been marked with red paint, were then released onto each tree (April 1980). These trees were intensively searched 6 months later (October 1980) and all female *C. robusta* were collected from them. Eleven spiders were located; 6 marked and 5 unmarked. The dried exoskeleton of one marked individual was also collected. The frequency distribution of these spiders was; tree (1) - 5 marked (1 dead), 1 unmarked; tree (2) - 2 marked, 3 unmarked; tree (3) - 0 marked, 1 unmarked. Also, 2 marked and 3 unmarked females had produced eggmasses. It is not known what happened to the 24 marked individuals that were not recaptured. It is possible that there was not enough suitable bark for all spiders to construct nests. Although care was taken when spiders were initially removed, some bark was loosened or pulled away from the trunk. This disturbance could have reduced the number of suitable sites for spiders, and thus have left many exposed to predation, strong wind or other adverse factors.

These data show that females of *C. robusta* can overwinter as adults, and produce eggs in the following spring. Also, some spiders appear to overwinter as juveniles and either reach maturity during that time, or at the beginning of the following season. It is unlikely that these spiders (unmarked females) had emigrated from other trees. Mark-recapture of various stages (see 2.3.5) and other observations on this species indicated that post-dispersal instars do not move between trees, but rather grow to maturity on the tree that ballooning juveniles land on.

3.3.3 Mortality of Eggs and Juvenile Stages

Observations in the field have indicated that mortality of juvenile stages after dispersal has occurred, may be very low. Marking and recapture of individuals has confirmed this for at least the adult and pentultimate stages. By comparison, mortality when juveniles leave the nest and disperse by ballooning is probably extremely high. This has already been discussed (see 2.3.9) and so emphasis here is placed on pre-dispersal stages, i.e. those occurring inside the nest.

Nests collected in the field showed that most mortality of pre-dispersal stages is caused by the scelionid parasitoid *Ceratobaeus masneri*. Samples of nests taken monthly revealed that this parasitoid is active for the whole period that eggs are present in the field, except perhaps for the first month, August (see Table 3.1 and Figure 3.2). These data also show that the incidence of parasitism was high, with approximately 22-25% of all eggs being killed (Table 3.3). Other causes of mortality (see 2.3.9) to the egg stage were very low (Table 3.3). When the frequency of eggmasses is plotted against the percentage of eggs parasitized (Figure 3.3), it is revealed that a high proportion of eggmasses escape parasitism altogether and that the remainder experience a fairly even distribution of mortality from 1 to 99%. The striking similarity between seasons for (1) the total percentage parasitism, and (2) the percentage parasitism for eggmasses that suffered some mortality (Table 3.3 and Figure 3.3), may be explained by the similar shapes of the curves generated from the data presented in Figure 3.3. Given that a large and similar proportion of eggmasses experience no mortality in each season (i.e. approximately 30-40% of eggmasses), and that the incidence of parasitism within eggmasses is evenly distributed over all classes (1-99%), then the mean mortality ($\bar{x}_2$) will always be approximately 50% and the overall mean (including eggmasses with no parasitism) ($\bar{x}_1$) will

Figure 3.3 Frequency of eggmasses of *C. robusta* as a function of the incidence of parasitism by *C. masneri* for 3 consecutive seasons (N.B. $\bar{x}_1$ = mean parasitism including eggmasses that had no mortality; $\bar{x}_2$ = mean parasitism for eggmasses that suffered some mortality, i.e. excluding the zero column).

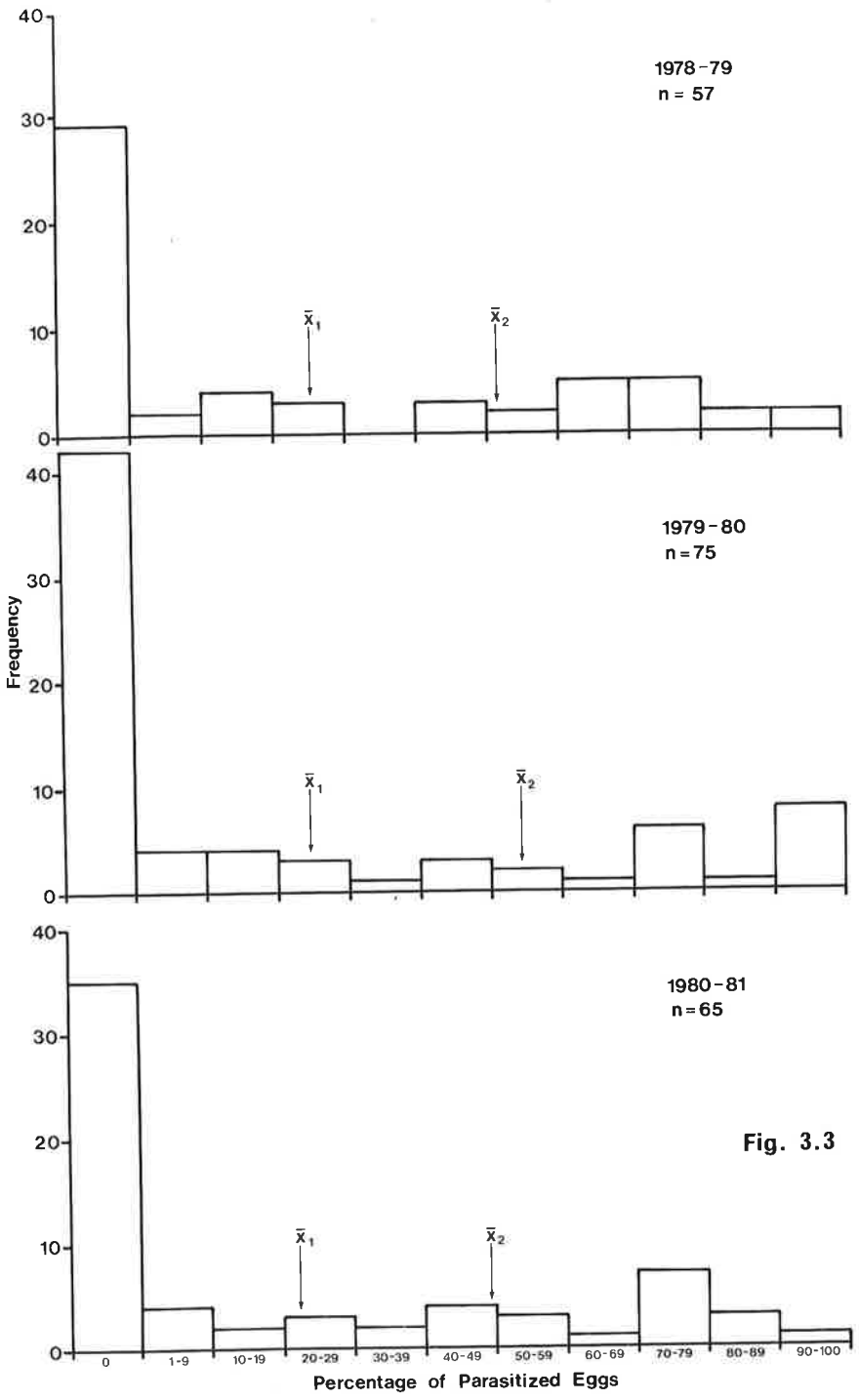

1978-79
n = 57
1979-80
n=75
1980-81
n=65
Frequency
40
30
20
10
0
$\bar{x}_1$
$\bar{x}_2$
0
1-9
10-19
20-29
30-39
40-49
50-59
60-69
70-79
80-89
90-100
Percentage of Parasitized Eggs

Fig. 3.3

1979-80

Month	Number of Eggmasses	Total Number of Eggs	Number of Eggs Parasitized (Number of Eggmasses in Brackets)	Percentage of Eggs Parasitized per Month	Pooled Data
August	2	290	0	0	13.0
September	8	1003	168 (3)	16.8)n=10	
October	14	1834	263 (6)	14.3	27.5
November	11	1634	691 (7)	42.3)n=25	
December	10	1614	573 (6)	35.5	31.7
January	11	1495	413 (6)	27.6)n=21	
February	7	958	67 (1)	7.0	17.4
March	12	1691	394 (4)	23.3)n=19	
Total	75	10519	2569 (33)		

1980-81

August	0	0	0	0	18.1
September	7	945	171 (1)	18.1)n=7	
October	22	2791	899 (13)	32.2	28.6
November	3	462	0	0)n=25	
December	10	1226	311 (4)	25.4	19.8
January	11	1341	196 (6)	14.6)n=21	
February	6	776	193 (4)	24.0	15.5
March	6	876	63 (2)	7.2)n=12	
Total	65	8417	1833 (30)		

Table 3.1 Statistics for the number of eggmasses and eggs of *C. robusta* collected in 2 seasons and the incidence of parasitism by *C. masneri*.

always be about 25%. It is proposed that these conditions are met and fixed by the biology of *C. masneri*, i.e. its fecundity and searching efficiency (see 4.3.8).

Comparisons of the mortality between eggmasses and between months show the variability around means to be high (Tables 3.1 and 3.2). Also, examination of these data for separate months and months pooled together (to increase sample sizes) shows that there is probably a peak in the incidence of parasitism between October and January, i.e. the middle 4 months for which eggs are present in the field. At this time there is also a larger number of eggmasses present in the field. To eliminate bias in the way months were pooled, cumulative mortality was plotted against time (Figure 3.2). The slope of the curve for 2 seasons' data (1979-80 and 1980-81) is steeper over the period October-January, thus supporting the hypothesis that parasitism is more prevalent at this time of year. This presumably comes about from parasitoids locating a different proportion of eggmasses each month, rather than from an increase in the number of eggs parasitized within eggmasses. Inspection of the data in Table 3.1 indicates that a higher proportion of eggmasses may be parasitized during October-January, as compared with August-September and February-March combined. However, the high level of variability and relatively small sample sizes prevent statistical support for this hypothesis. Comparison of the proportion of eggmasses that are attacked at these times of the year show the following differences for the 1979-80 season ($\chi^2_1 = 3.17$, $0.10 > P > 0.05$, $n = 33$) and 1980-81 season ($\chi^2_1 = 0.63$, $P > 0.25$, $n = 30$). It therefore seems likely that differences occur in at least some years. The latter result may be substantially affected by the low number of eggmasses and no parasitism recorded in November 1980. Comparison of the number of eggs parasitized within eggmasses (i.e. expressed as a proportion of the eggs in only those eggmasses that suffered some mortality) for the same periods showed that they did not differ

Month	Number of Eggmasses	Number of Parasitized Eggs ($\bar{x} \pm$ 1 S.D.)	n	Months Pooled ($\bar{x} \pm$ 1 S.D.)		
1978-79						
February	4	63.8±35.1				
March	3	48.2±31.8	9	54.8±30.2		
April	2	46.8±31.5				
Total	9					
1979-80						
September	3	36.5±16.9				
October	6	47.9±35.8	9	44.1±30.1		
November	7	54.6±33.9			n=25	n=8
December	6	61.1±43.6	13	59.0±37.3	53.8	56.4
January	6	48.5±33.3			±35.0	±31.6
February	1	76.1	11	57.5±33.4		
March	4	66.5±38.4				
Total	33					
1980-81						
September	1	87.7				
October	13	51.7±24.6	14	54.2±25.5		
November	0	0			n=23	n=7
December	4	77.0±6.7	4	77.0±6.7	50.7	43.3
January	6	31.1±24.6			±26.5	±35.8
February	4	42.4±39.9	12	33.5±27.8		
March	2	22.9±10.9				
Total	30					

Table 3.2 Incidence of parasitism due to *C. masneri* recorded each month for eggmasses of *C. robusta* that suffered some mortality.

Eggs	1978-79	1979-80	1980-81
Number of eggmasses collected	57	75	65
Number of eggmasses with some eggs parasitized by *C. masneri*	28	33	30
Mean percent parasitism for eggmasses that suffered some mortality due to *C. masneri* (± 1 S.D.)	51.6±28.5	54.4±33.7	49.0±28.5
Mean monthly percent parasitism, August-March (all eggmasses) (± 1 S.D.)	-	20.9±14.2	15.3±12.1
Total percent parasitism (all eggmasses)	25.4	24.4	21.7
Number of eggmasses that suffered mortality due to other factors (see 2.3.9)	-	4	1
Total percent mortality (all eggmasses) due to other factors	-	5.3	1.5
Total percent mortality: All factors	25.4 (+)	28.7	23.2
Juveniles			
Number of nests collected with juvenile stages (instar 3)	28	41	34
Number suffering some mortality	0	1	2
Percent mortality of juveniles for all nests	0	2.4	5.9

Table 3.3 Statistics of mortality at the egg and juvenile stages of *C. robusta* (in nests) for 3 consecutive seasons (N.B. some data are not available for the 1978-79 season because sampling began in February 1979).

significantly in either season (1979-80 $t = 0.19$, d.f. = 31, $P > 0.45$; 1980-81 $t = 0.60$, d.f. = 28, $P > 0.30$).

Collection of nests (outside the 2 h sampling period) that contained third instar juvenile spiders, indicates that mortality of post-eclosion stages (instars 1 - 3 in nests) is extremely low (Table 3.3). Three nests out of a total of 103 sampled over 3 seasons were recorded as experiencing mortality. These had been completely destroyed by the ant *Iridomyrmex* sp.

3.3.4 Population Dynamics and Limiting Factors

The seasonal fluctuations described for the adult population (see 3.3.1) are thought to be the result of several factors. The extended breeding season that is presumably due to prolonged favourable climatic conditions and possibly abundant food, means that eggs are continually being produced for more than 6 months of a year. These conditions allow some spiders to oviposit twice before the winter (see 2.3.7), while others that do not mature until later (i.e. after February), possibly produce one eggmass either side of winter (3.3.2). This pattern of oviposition gives rise to a rapidly maturing summer generation and a separate overlapping generation, that overwinters in both adult and juvenile stages. The larger number of adults present during the summer months probably then results from the combined effect of these 2 generations. Overwintering juveniles will reach maturity from early spring onwards (August-November), causing an increase in the numbers of adults in the population. Also, by this time offspring from the first eggs of that season will be approaching maturity, thus causing a further increase in adults. The following decline in numbers from February onwards occurs after most spiders have oviposited. At this time of year dead females were found in nests. This was not associated with any obvious factor and may simply represent the end of normal life expectancy for part of the population.

As it was not possible to study all stages of *C. robusta* in detail, only a preliminary discussion of likely mortality factors is presented here. A summary of the presumed pattern of mortality is given in Figure 3.4. If this graph accurately reflects what happens to this species in nature, then nearly all mortality occurs at the egg stage due to parasitism, and at the third instar when dispersal occurs. Only the first phase of this mortality pattern has been quantified, while the occurrence of the second phase and subsequent low mortality in post-dispersal stages, is only supported by incidental observations (see 2.3.9). Some appreciation of mortality due to dispersal by ballooning juveniles was gained after the bushfire that burnt out Area 1 of the study site, in February 1980. All invertebrates on trees in this area were killed by the fire, and yet third and fourth instar *Clubiona* were found on them in the following spring (October 1980). These spiders had obviously got there by aerial dispersal, as the closest unburnt trees were over 200 m away. Even under normal conditions trees probably represent very small targets surrounded by a vast area of unfavourable habitat, for airborne juveniles that have no directional control, other than to disperse when conditions are most favourable. This situation must therefore lead to the death of most juveniles at this stage.

Although mortality due to parasitism by *C. masneri* was high during the period of this study, it was also relatively constant between seasons (see 3.3.3). If this situation occurs in all years, then any change in the number of spiders that reach maturity is more likely to occur from differential survival at dispersal. Only minor differences in the number of juveniles surviving dispersal would be needed to affect greatly the number that reach maturity. For example, if there is 95% instead of 99% mortality at the third instar, and no deaths or very few occur after this stage, then 5 times more individuals will become adults. Conversely, increased survival or mortality of the post-dispersal stages will have much less effect on the number of individuals that reach maturity.

Figure 3.4 Pattern of mortality that is presumed to occur in *C. robusta* populations at Mylor (N.B. the solid line represents mortality that has been quantified; the broken line is an estimate of mortality).

Figure 3.5 Patterns of mortality displayed by many animals. Type III represents a constant rate of mortality between stages. Type IV represents very high mortality occuring in the initial life history stages (after Slobodkin 1961).

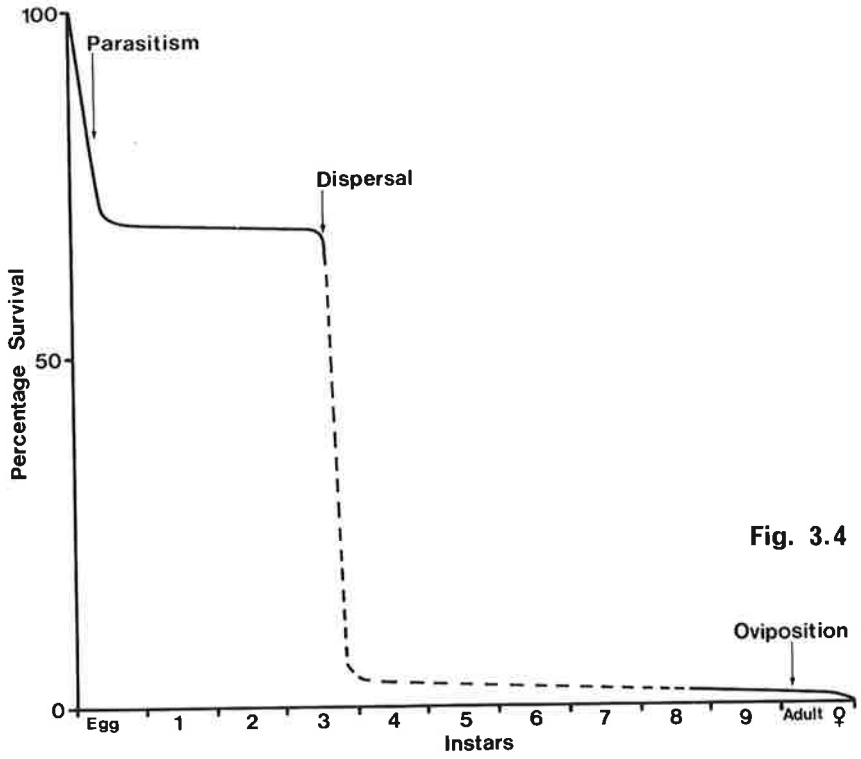

100
Parasitism
Dispersal
Percentage Survival
50
0
Egg
1
2
3
4
5
6
7
8
9
Adult ♀
Instars
Oviposition

Fig. 3.4

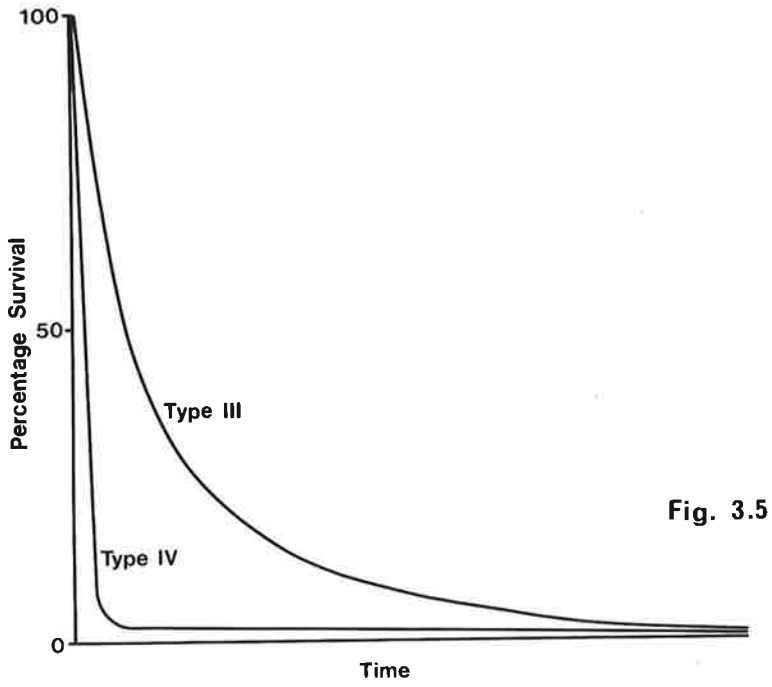

100
Percentage Survival
50
Type III
Type IV
0
Time

Fig. 3.5

Other factors that may limit the population size of this spider appear to be much less important than those discussed above. Climatic conditions during the study were similar to the expected average (see 2.2.1). There is also some evidence to suggest that the silk retreats of clubionids can protect them from at least short periods of extreme conditions (2.3.5). Food was plentiful at all times of the year (2.3.3), and space (suitable bark under which to construct retreats) was abundant, with only a small proportion being utilized at any one time. This assessment is unfortunately based on information from only 2 seasons, and so the potential for these factors to vary and subsequently affect populations of *C. robusta* is unknown.

3.3.5 Guarding Behaviour by Female Spiders

The results from 3.3.3 show that few of the many predators that inhabit bark, with the exception of *C. masneri*, utilize the eggs of *C. robusta*. Many authors (see 3.4) have suggested that the eggsac and apparent guarding behaviour of some spiders act to protect the early stages from predation. This hypothesis would then explain the very low mortality due to ants and other predators, but it does not account for the high incidence of parasitism by *C. masneri*. In this and the following section guarding behaviour by spiders and the effectiveness of the eggsac and eggmass are examined in relation to *C. masneri* and other potential predators.

The null hypothesis that the presence of female spiders with their eggs does not increase the survival of the latter, was tested. Ten nests containing eggs were located in the field during March 1980 and resident spiders were removed. These nests were left for 14 d, and then collected to determine the survival of eggs. Of the 10 eggmasses 8 had been completely destroyed by ants (*Iridomyrmex* sp.). Data for nests collected during the

1979-80 and 1980-81 seasons (see Table 3.3) were used as a control, as most of these nests contained female spiders. In this group only 8 out of 215 nests containing eggs or juveniles had been destroyed by predators other than *C. masneri*. This experiment shows that the presence of female spiders in nests substantially increases the survival of eggs, and that in the absence of this protection the surrounding eggsac is not an effective barrier to predators. In the experimental group above (i.e. female spiders removed from nests) some nests may have been damaged when spiders were removed, thereby possible allowing ants easier access. However, care was taken to reduce such damage and some nests definitely remained intact, so that the results obtained are considered to reflect accurately what could happen under natural conditions.

The behaviour of female spiders was then investigated to determine how they protect their eggs from intruders into the nest, and how *C. masneri* can successfully parasitize eggs. The response of spiders was observed for 8 types of intruders covering a size range of 1-10 mm. Responses were measured as the time it took to kill an intruder (see 3.2.3), and these were compared for 3 groups of spiders, (1) spiders with eggs, (2) spiders without eggs and starved for 30 d, and (3) spiders without eggs that had been well fed prior to the experiment. As females of *C. robusta* stop feeding several days before oviposition and do not emerge from their nests until after juveniles have dispersed, spiders with eggs can be considered to be starved.

Data for this experiment are summarized in Table 3.4. The results for spiders with eggs are very similar to those that had been starved. Spiders in both these groups killed and ate nearly all intruders larger than approximately 2 mm in length. The only major difference was that starved spiders did not kill ants, though they attacked them. Spiders with eggs killed all ants but did not eat them (see below). The fact that spiders

Intruder (length, mm)	Treatment 1 Females with eggs	Treatment 2 Females without eggs, starved for 30 d	Treatment 3 Females without eggs, well fed
Acari < 1.0	0 killed no response	0 killed no response	0 killed no response
Various Scelionidae (other than *C. masneri*) 1.0-1.5	0 killed 3 orient.	0 killed no response	0 killed no response
Ceratobaeus masneri 1.2	0 killed 2 orient.	0 killed no response	0 killed no response
Wingless *Drosophila* 2.0-2.5	10 killed 8.6 s (4-30)	8 killed 53.5 s (3-420) 2 orient. and attacked	0 killed no response
Iridomyrmex sp. (Formicidae) 3.0-5.0	10 killed (none eaten) 15.9 s (2-27)	0 killed 10 orient. and attacked	0 killed 2 orient.
Blatella germanica nymphs 5.0-6.0	10 killed 18.6 s (3-65)	10 killed 4.9 s (2-14)	1 killed (21 min) 5 orient.
Various Araneae (adults) 5.0-7.0	10 killed 115.6 s (6-900)	9 killed 69.4 s (20-250) 1 orient. and attacked	4 killed (2 not eaten) (Range 5-24 min) 6 orient.
Blatella germanica 7.0-10.0	10 killed 19.6 s (3-34)	10 killed 4.9 s (2-17)	2 killed (1 not eaten) (10, 26 min) 6 orient.

Table 3.4 Response of female *C. robusta* to different types and sizes of intruders in nests. Data represent number of intruders killed (n=10 in each cell) and mean time (range) to kill intruders (N.B. 'killed' = killed and eaten, unless otherwise stated; 'orient,' = orientation towards intruder but not attacked; 'attacked' = lunge towards and attempt to bite intruder but not kill it; 'no response' = no apparent behavioural response to presence of an intruder). The maximum duration of each trial was 30 min.

in the latter group ate all other large intruders lends support to the above assumption that they were starved. All intruders less than 2 mm in length, including *C. masneri*, survived in nests for the 30 min duration of each trial. Thus, *C. masneri* appears to escape attack by female spiders due to its small size. This observation explains how *C. masneri* can parasitize the eggs of *C. robusta*, while other larger intruders (predators) such as ants and possibly spiders are excluded. Experiments with the third group, female spiders that had been well fed, showed quite different results. Only 7 out of 50 intruders larger than 2 mm in length were killed and 3 of these were not eaten. The aggressive response of this group was therefore much lower and their tendency to tolerate intruders in the nest was higher, compared with starved spiders.

Observations during this experiment show that the response of the first 2 groups of spiders to intruders (> 2 mm) follows a fixed pattern. When an intruder enters a nest the spider immediately orientates towards it and lunges forward, with chelicerae open and forelegs raised. The intruder is bitten and the spider moves backwards away from it. This can be repeated several times, if the intruder continues to move, otherwise feeding commences. With small intruders such as *Drosophila*, the spider does not back away after the first bite, but immediately starts to feed. During several trials intruders remained motionless as soon as they were placed in nests. On these occasions, spiders would orientate to the initial disturbance, but they would not lunge forward until the intruder moved. Therefore, attack behaviour seems to be elicited only by movement. After feeding is completed the spider pushes any debris (exoskeleton of intruder) out of one of the entrances of the nest. It then inspects the walls of the nest with its forelegs and repairs damage or breaks that may have occurred, before returning to the position of straddling the eggmass. The behavioural sequence described above, up to and including the lunging

stage, could also be elicited by pushing against or plucking the wall of the nest with forceps. From this observation, it is assumed that orientation towards a disturbance is mediated by vibrations transmitted through the nest wall and silk platform on which the spider sits. This assumption is supported by the fact that all spiders rapidly and accurately orientated to disturbances that were outside their visual field, i.e. posterior ventral position.

The only departure from this fixed behavioural sequence was in response to ants (*Iridomyrmex* sp.). Spiders with eggs lunged and killed these intruders but did not feed on them, rather they quickly pushed them out of the nest. Starved spiders (without eggs) lunged at and attempted to bite them, but then immediately backed away. Both these groups spent some time cleaning their forelegs and chelicerae after contacting ants, indicating that the latter are distasteful. Thus, it appears that the guarding behaviour of spiders with eggs is independent of whether or not the intruder is edible.

A final experiment was carried out in which the effect of hunger in spiders with eggs and spiders that had been starved, was compared. Large cockroaches (7-10 mm) were continually placed into nests every 15 min for 5 h (n = 3 in each group). All spiders in both groups became satiated after 2-3 h. Those that did not have eggs refrained from killing intruders after this time. However, females with eggs killed all intruders immediately they were placed in nests, for 5 h until the experiment was terminated. The aggressive response of this species towards possible predators or scavengers is therefore independent of hunger level.

3.3.6 The Function of Eggmass Formation and Eggsacs

The eggsac of *C. robusta* does not prevent the eggs from being eaten by large predators, but it is possible that this structure and the behaviour

of laying eggs into a tight mass, may reduce the level of parasitism by *C. masneri*.

The null hypothesis that the number of eggs parasitized is the same, with or without an eggsac present around the eggmass, was tested. Eggmasses in blastoderm stage containing 140-160 eggs were placed in separate containers at 20°C, and each was exposed to 5 gravid *C. masneri*. The mean percentage of eggs parasitized for the control group (eggsacs intact) was compared after 14 d, with those that had their eggsacs removed (n = 10 in each group). Bartlett's test showed homogeneity of variances and a t-test disclosed no reason to reject the null hypothesis ($t = 0.35$, d.f. = 18, $P > 0.30$). The eggsac around the eggs of *C. robusta* therefore, does not appear to reduce mortality caused by *C. masneri*.

The null hypothesis that the number of eggs that can be parasitized by *C. masneri* is the same, whether eggmasses are left intact or broken up, was tested in a similar way to that above. The percentage of eggs parasitized in the control group (eggmasses intact) was compared with eggmasses that had been broken up (eggsacs were removed in both groups). Bartlett's test indicated heterogeneity of variances and so a Mann-Whitney test was applied to the data. Eggmasses that had been broken up showed significantly higher parasitism ($\bar{x}$ =95.9%) compared with control eggmasses ($\bar{x}$ = 75.1%) ($U = 6.5$, $P < 0.002$, n = 20). Examination of intact eggmasses showed that only eggs in the outer 2 layers had been parasitized, and that eggs at the centre had escaped parasitism. Thus, the formation of eggmasses by *C. robusta* protects at least some eggs (approximately 20%) from parasitism (see 4.3 and 6.3.2).

3.3.7 Aggressive Interaction Between Adult Spiders

Collection of spiders has shown that males are less abundant in nature compared with laboratory cultures (see 2.3.4). Also, it has been

shown that males reared in the laboratory are slightly smaller in size compared with those from the field. Higher densities of males in cultures and a higher rate of aggressive interactions tending to reducing feeding time, has been proposed as an hypothesis to explain this difference in size. In this section the aggressive behaviour of *C. robusta* is explored in detail, to determine whether interactions between males may explain their low numbers in the field. At the same time interactions between the sexes and between different species are examined and compared with the results for males.

Experiments were conducted as described in 3.2.4. Initially several trials were carried out to identify the main phases in the behaviour of individuals when they meet. Ten types of behaviour could be readily identified. These were:

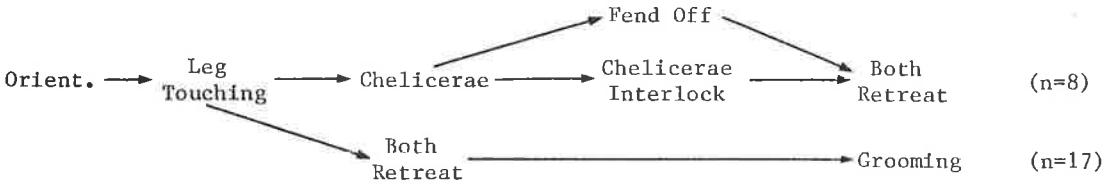
1. Orientation of individuals to face each other (abbreviated to orient. in Figure 3.6).
2. Forelegs raised and touching the other spider (leg touching).
3. Chelicerae open and spider lunges forward (chelicerae).
4. Chelicerae of 2 individuals interlock (chelicerae interlock).
5. Pushing the other individual away with the forelegs (fend off).
6. One individual retreats away from the other (one retreat).
7. Vibrating of the opisthosoma on the substratum by the winner of an encounter (vibrating). This occurred only in conjunction with and after No. 6, and was carried out only by males.
8. Both individuals retreat (both retreat).
9. Cleaning of forelegs and chelicerae for prolonged periods (grooming). This occurred only after No. 8 and is probably an extension of non-aggressive interactions.

10. One individual killed (one killed).

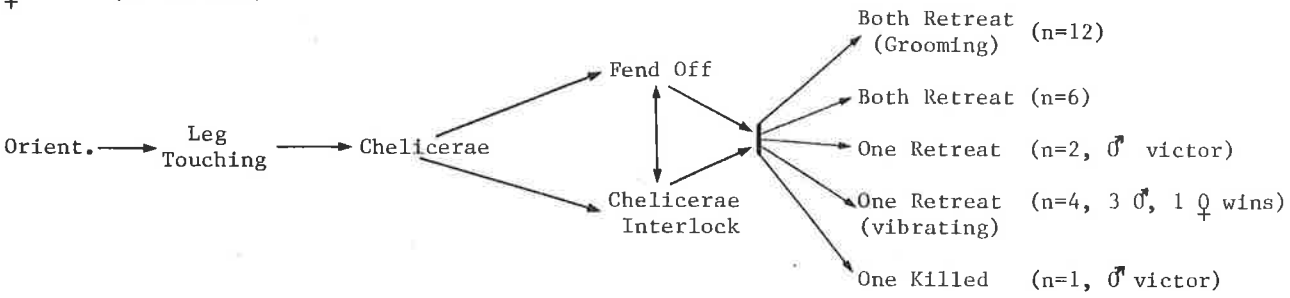
Twenty-five trials were carried out to determine the interactions for the following pairs of spiders:- female-female, female-male and male-male *C. robusta*, female (*C. robusta*) - female (*C. cycladata*), and male (*C. robusta*) - male (*C. cycladata*). The order in which behavioural types occurred and the frequency of the final outcomes are summarized as flow diagrams (Figure 3.6). These data are somewhat simplified to emphasize the main differences between interactions. Relatively subtle differences, such as initial orientation not being complete or difficulty in distinguishing between leg touching and fending off during some trials, are not included in the data presented.

Results for *C. robusta* show that interactions between males are much more aggressive compared with those between females. Male-male interactions led to one individual being killed in 4 out of 25 and one spider retreating in 20 out of 25; while female-female interactions all led to both individuals retreating, after interactions that were much less aggressive. The outcomes of female-male interactions were more similar to those of female-female trials, although the former showed a higher incidence of more overt aggressive behaviour, i.e. one female was killed and one spider (usually the female) retreated in 6 out of 25. Therefore, only interactions involving males resulted in an individual being killed or one retreating to the opposite end of the experimental chamber. The significance of some male spiders (i.e. the winner in an encounter) vibrating their opisthosoma on the substratum, is unclear. Similar behaviour has been reported for other spiders (Jackson 1978a, Riechert 1978), and it seems to occur only in association with aggressive behaviour. Possibly it represents some type of reinforcement behaviour that is transmitted to the loser by vibrations through the substratum (see Jackson 1978b).

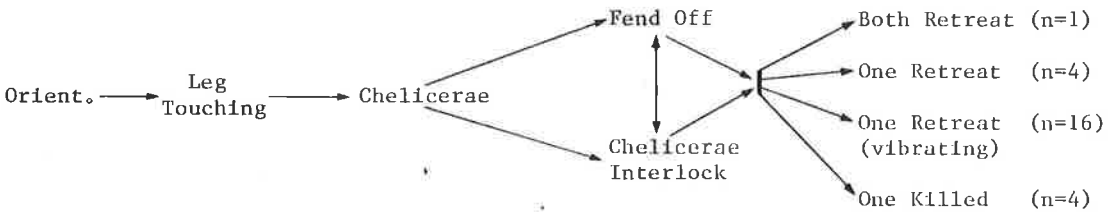
♀ - ♀ (*C. robusta*)



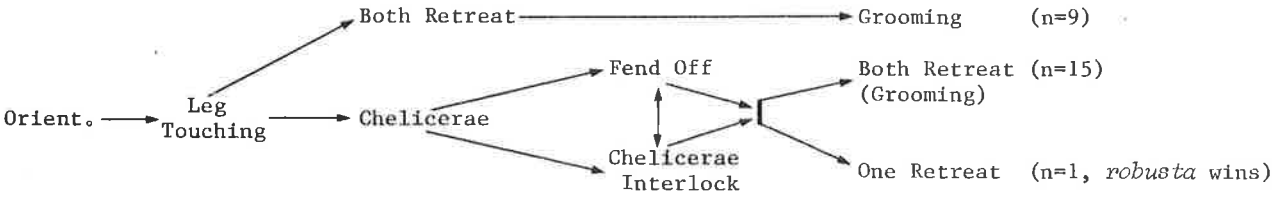
♀ - ♂ (*C. robusta*)



♂ - ♂ (*C. robusta*)



♀ (*C. robusta*) - ♀ (*C. cycladata*)



♂ (*C. robusta*) - ♂ (*C. cycladata*)

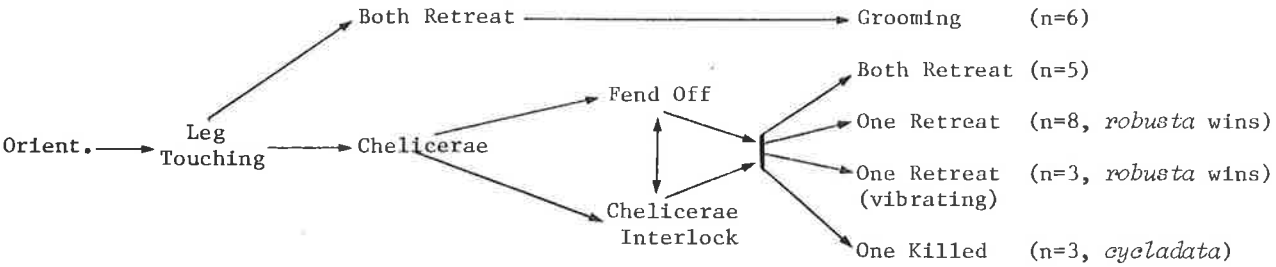


Figure 3.6 Summary of behavioural interactions between sexes and species of *Clubiona*. The frequency of the final outcomes and sex or species that won encounters are given in brackets (N.B. see text for description of each type of behaviour).

Interactions between the 2 species were similar to those between 2 *C. robusta*. Encounters between female *C. robusta* and female *C. cycladata* resulted in both individuals retreating in nearly all cases (24 out of 25), while the behaviour of males showed a much higher level of aggression. Male-male interactions resulted in one spider being killed in 3 out of 25 and one spider retreating in 11 out of 25, with the large species, *C. robusta*, always winning. The results, however, show a signficantly higher number of non-aggressive outcomes, 11 out of 25 (i.e. both retreating), compared with trials involving male-male *C. robusta* (1 out of 25).

These results clearly demonstrate that male-male interactions in a confined space are much more aggressive than those between females. Interactions between males have a much higher probability of one individual being killed or retreating away from the other. Although the conditions under which this experiment was conducted may be relatively artificial compared with the situation in the field, the data at least support the hypothesis that males of *C. robusta* are less abundant than females due to aggressive displacement by the former. Males probably spend significant periods during summer wandering under bark searching for mates. When individuals meet the outcome of the ensuing interaction would seem likely to result in the death or retreat of one individual. If these encounters are frequent the number of males in the population would decrease. However, experiments conducted under field conditions would be required to test the above hypothesis more thoroughly.

In contrast, the data from this experiment for females indicate that they are able to coexist in the field at high densities due to their lack of aggression towards each other. This seems to be the case for interactions between individuals of the same species and individuals of different species. Furthermore, females spend prolonged periods in nests where they are probably well protected, and as a result of which they are unlikely to contact other spiders, whatever their behaviour towards other individuals.

3.4 DISCUSSION

The phenology of spiders, especially that of the adult stage, varies substantially between species. Adults of some species are present throughout the year, but are most abundant during spring and summer (Humphreys 1976, Lubin 1980, Mansour *et al.* 1980b, Toft 1976, 1978, this study); some are present for only part of the year (Edgar 1971c, McQueen 1978, Riechert 1974b, Robinson and Robinson 1973, Vlijm and Kessler-Geschiere 1967, Toft 1976, 1978, Workman 1978); while others are of variable occurrence depending on their location (Jackson 1978b). Generally, no family of spiders can be said to have members showing predominantly one type of phenology, nor is there any correlation with habitat type. However, species in which adults are present at all times of the year tend to have more than one generation per year and occur in warm climates.

In only 3 species of spiders other than *C. robusta*, has the sex ratio of adults been shown to depart significantly from 1:1 (Jackson 1978b, Vlijm and Kessler-Geschiere 1967, McQueen 1978). In all cases it is the males that are least abundant. Jackson (1978a, 1978b, 1980b) has shown that aggression over mates between males of *Phidippus johnsoni* (Salticidae) rarely leads to mortality, but he suggests that males may be more susceptible to predation, and this results in their lower numbers. In the case of *C. robusta*, it is highly likely that inter-male aggression results in a decline in their numbers. The lower death rate due to aggression in *P. johnsoni* possibly results from 2 factors: this spider lives on the ground, and thus males have a much larger area in which to retreat; and aggression in *P. johnsoni* may be more ritualized as salticids have well developed vision. In comparison, *C. robusta* is limited by a relatively small area of bark on one tree, males are very aggressive, and they probably have poorly developed sight (see 2.3.6). It is possible that males of *C. robusta* establish territories on trees or, alternatively, they may simply

remove most other individuals by attempting to kill them when they meet. The possibility of territoriality in *C. robusta* is significant and requires further study, as this behaviour has only been described in detail for one species, *Agelenopsis aperta* (Agelenidae), although it is reported for others (Jackson 1979a). In *A. aperta* territorial behaviour is not related to competition for mates, but rather for the quality of resources, e.g. food and shelter (Riechert 1976, 1978, 1981).

The results of several studies indicate that mortality at the dispersal stage for those species that undertake ballooning (see 2.3.9) is extremely high. Mortality at this stage can be in excess of 90% (Turnbull 1973, Valerio 1977). This mortality is presumed to occur from juveniles falling into unfavourable habitats and not reaching their target habitat, e.g. eucalypt trees in the case of *C. robusta*. Dispersing juveniles all carry large energy reserves in the form of stored yolk. This has been shown to increase survival time and allow larger distances to be covered by juveniles before they starve (Anderson 1978, Turnbull 1973), thus increasing their probability of reaching a favourable habitat.

Although mortality due to predation and parasitism at the early life history stages may be significant, it is not as great as that caused by dispersal. In all studies on spiders mortality due to the former has not been higher than 40% for the whole of a population. This is much lower than for many insects, where levels in excess of 80% mortality due to parasitism on the egg stage alone have been recorded (Fedde 1977, McLaren and Buchanan 1973, Yeargan 1979). Parasitism due to scelionids is by far the most important factor for spiders (see Appendix 1), but other predators or parasitoids cause similar mortality at the early stages in some species, e.g. Ichneumonidae (Edgar 1971b, Kessler and Fokkinga 1973), Sarcophagidae (Diptera) (Lubin 1974), Mantispidae (Neuroptera) (Valerio 1977). Lycosids are the only spiders where significant mortality has been recorded for medium sized (post-dispersal) instars (Humphreys 1976,

McQueen 1978). Mortality of 30-35% due to acrocerid flies, has been reported in these studies. McQueen (1978) also recorded extreme mortality (approaching 100%) at the adult stage due to the activity of pompilid wasps, but in this case all deaths occurred after oviposition, and no effect on the subsequent generation could be demonstrated.

The importance of parasitism and predation in spiders as limiting factors is not clearly understood, even though they can cause relatively high mortality. If nearly all juveniles die at dispersal, any mortality before this stage may have little effect on the number that reach maturity. Even so, any significant decrease in the incidence of parasitism or predation prior to dispersal could result in slightly higher survivorship after this event, as more offspring would reach the dispersal stage. As species that undertake ballooning may suffer very low mortality during post-dispersal stages (Valerio 1977, this study), such increases in survival could greatly increase the number that become adults (see 3.3.4). However, there are no data available to suggest mortality prior to dispersal varies to any degree; in fact, it is relatively constant within the few populations that have been studied.

Comparison of ecological studies on spiders shows that food and weather are important limiting factors (see 3.1), but they may operate almost exclusively at the dispersal stage, as a result of juveniles not reaching a suitable habitat. Predation may also be significant at this stage (Turnbull 1973). The effect of starvation and adverse weather on other stages appears to be negligible for most spiders, but this has not been stressed by previous authors. The exception to this may occur in ground living spiders in desert regions, where flooding can result in death of all adults. However, Riechert (1981) has shown that this mortality has little effect on the subsequent generations of at least one species, as the eggsacs are waterproofed and protect the stages inside. Predation

and parasitism are proposed as significant factors for some spiders (Edgar 1971b, Humphreys 1976, Kessler and Fokkinga 1973). In one species, *Geolycosa domifex*, parasitism of medium-sized juveniles is proposed as the only source of mortality that has the potential for population regulation (McQueen 1978).

The mortality pattern of species that disperse by ballooning (Valerio 1977, see above) provides evidence to refute the suggestion by Humphreys (1976), that all spiders display a Type III survivorship curve (Slobodkin 1961, Figure 3.5). It has not been possible to express survival as a function of time for species that undertake ballooning, as their rate of development for different instars in the field is unknown, and juvenile stages cannot be identified easily. However, if rates of development between instars are similar (and this is not an unrealistic assumption for juveniles - see Humphreys 1976, Jackson 1978b, Peck and Whitcomb 1970, Workman 1978), then the resulting survivorship curve will be more similar to that of Type IV (Figure 3.5), where nearly all mortality occurs during the early life history stages. This type of mortality is well known in many populations of invertebrates and vertebrates (e.g. Aeschlimann 1979, Morris 1963, Moss *et al.* 1981, Watt 1963, White 1978). Type III survivorship may therefore occur only in spiders similar to lycosids where mortality at dispersal is relatively low. Juveniles of most lycosids are dispersed by being transported on the back of their mother. Thus, they are protected from predators and probably experience a more favourable climate, due to the activity pattern of the female, e.g. being nocturnal or remaining in shade during the day. In some cases even a Type IV curve may not accurately represent mortality in those species, such as *Achaearanea tepidariorum* (Valerio 1971, 1977), and *C. robusta*, where mortality follows a biphasic pattern, i.e. parasitism followed by juvenile dispersal. However, even in these cases a Type IV survivorship curve would appear to fit the data

better than that of Type III.

If any of the above predictions, in relation to limiting factors and patterns of mortality, are to be tested for species that disperse by ballooning, then techniques will need to be developed for identifying juvenile stages. Although size classes have met with success for several spiders, this technique is not consistent for many species (Randall 1978).

Guarding behaviour by females to protect the vulnerable egg and juvenile stages is common for many groups of animals. The importance of this strategy in increasing the survival of offspring is well recognized and has been discussed in detail for many animals (Eberhard 1975, Keenleuside 1978, Matthews and Matthews 1978, Wilson 1975 and references). Such behaviour for spiders has been proposed by several authors (e.g. Comstock 1940, Forster and Forster 1973, Gertsch 1949, Main 1976, McCook 1890, Peck and Whitcomb 1970, Turnbull 1973), yet this is the first time that any survival advantage has been demonstrated. The early life history stages of spiders represent a potential and concentrated food source, that would be easily accessible to predators unless it is protected in some way. Lubin (1974) has described guarding behaviour for one species, *Cyrtophora moluccensis*, that responds to predators (Sarcophagidae - Cantrell 1981) attacking its eggs. However, in this case no study was carried out to determine whether this behaviour led to decreased mortality in eggmasses. Females of *C. moluccensis* can recognize eggsacs that have been parasitized by sarcophagids, and respond by cutting them out of the web. The value of such behaviour is unknown (Lubin 1974), but it is possible that it provides some selective advantage by allowing spiders to maximize protection of unaffected eggsacs.

This study has shown that the eggsac of *C. robusta* neither prevents nor reduces parasitism or predation on eggs, although the eggmass itself

allows some eggs at its centre to escape parasitism. The eggmass of spiders has not previously been considered as a structure that could reduce such mortality. The eggsacs of many other spiders are more complex than those of clubionids (see 6.3.3). These probably provide protection against general predators, but they do not prevent mortality by highly specialized parasitoids, such as scelionids. Eggsacs that have relatively thick and dense walls may function to exclude a wide range of predators, such as ants and other spiders. This is supported by the fact that ants are rarely reported as preying on the eggs of spiders (see Brown 1958), although they are by far the most abundant predators in many habitats.

The effectiveness of guarding behaviour, and the structure of eggsacs and eggmasses as factors that may reduce mortality caused by predators and parasitoids, remains unstudied for most spiders. Investigation of these factors for *C. robusta* has resulted in a better understanding of the sources and levels of mortality that can operate at the egg and early juvenile stages of this spider. Similar studies on other species will undoubtedly allow the importance of such adaptations in the ecology of spiders to be assessed in more detail.

CHAPTER 4

THE BIOLOGY OF *CERATOBAEUS MASNERI*

4.1 INTRODUCTION

The biology of scelionid parasitoids has been the subject of many investigations in the past 50 years. Most studies have been on members of only 2 genera, *Telenomus* and *Trissolcus* (synonyms: *Asolcus*, *Microphanurus*). Their study has undoubtedly been fostered to a large degree by the fact that many species parasitize the eggs of economically important lepidopteran and heteropteran pests of crops and forests.

All scelionids display arrhenotokous parthenogenesis, possess a female biased sex ratio, and most have a high fecundity. Many species cause significant mortality to their hosts and several are probably important factors in the regulation of host populations (Agudelo-Silva 1980, Anderson and Kaya 1977, Hokyo and Kiritani 1963, Ryan *et al.* 1981, Ticehurst and Allen 1973). As with other parasitic Hymenoptera, scelionids are well adapted to the biology of their hosts. They possess efficient methods of locating host eggs and the ability to determine the suitability of hosts as sites for successful oviposition, i.e. those suitable for the development of viable offspring (Bosque and Rabinovich 1979, Eberhard 1975, Fedde 1977, Rabb and Bradley 1970, Rabinovich 1970, Wilson 1961). Some species also show specific types of ovipositional behaviour to overcome the various forms of protection displayed by their hosts (Eberhard 1975, Pickford 1964), e.g. when host insects guard their eggs, bury them in soil or conceal them in timber.

Few studies have been carried out on scelionids that attack the eggs of spiders. Spiders are the only arthropods other than insects that are exploited by these parasitoids. One might hypothesize that the substantial differences that exist between the biology of spiders and insects have probably resulted in comparable differences between the scelionids that attack them. However, this is not obvious from the few,

mostly short, studies that have been undertaken on those that parasitize spiders (Brado 1972, Pierce 1942, Valerio 1971, 1973, 1974, 1976), and the hypothesis has remained unexplored.

In this section the biology and ecology of one species of *Ceratobaeus* (*C. masneri*) is studied in detail and supportive information is presented for several other species. Ovipositional behaviour, fecundity, overwintering, host finding and recognition, and the effect of age of eggs and temperature on oviposition are examined. These aspects of the biology of *C. masneri* are compared with those of other scelionids and other egg-parasitoids (e.g. Trichogrammatidae and Mymaridae) and their importance in host-parasitoid interactions are discussed.

4.2 MATERIALS AND METHODS

4.2.1 Culturing Techniques

C. masneri was reared on the eggs of its host *Clubiona robusta*, in small glass vials at 25°C, at about 70% relative humidity, and with free water supplied. Female wasps older than 10 d were used to parasitize host eggs. Only host eggs oviposited in the laboratory and in the blastoderm stage or earlier, were used to maintain the culture. A continual supply of wasps was achieved by keeping parasitized eggs at various temperatures (15-25°C), so that emergence times were staggered. It was also possible to regulate the number of males and females, by separating the sexes as they emerged. Different numbers of either sex could be produced by selectively exposing host eggs to either mated or virgin females.

Other species of *Ceratobaeus* that were used in this study could not be reared in the above manner, due to the difficulty of obtaining host eggs from laboratory cultures (see 2.2.3). In these cases parasitized eggs of various spiders were collected from the field. Emerging wasps were

then retained until they were needed for experiments, by placing them at 15-20°C with a supply of water.

4.2.2 Longevity

The effect of temperature and relative humidity, on the longevity of *C. masneri* was studied. Newly emerged female wasps, reared at 25°C, were placed in glass vials at one of 4 temperatures (10, 15, 20 and 25°C). Two treatments were set up for each temperature: one group had free water supplied and had a relative humidity in vials close to 100%; the other had no water supplied and had a relative humidity of 40-50%. Relative humidities were measured with a Lovibond Comparator Kit (see 3.3.5). Twenty-five wasps were placed in each treatment and temperature; they were examined every 5 d, and the number of wasps that had died was counted. The time taken for 50% and 90% of wasps to die was determined by reading these values from survivorship curves, plotted with the data.

4.2.3 Effect of Age of Host Eggs

Eggmasses of *C. robusta* were reared at 3 different temperatures (15, 20 and 25°C) for different periods, and were then exposed to 5 mature female *C. masneri* for 12 h. Eggmasses were broken up so that maximum parasitism occurred, i.e. no eggs were left unparasitized by being protected at the centre of eggmasses (see 3.3.6). All eggs were allowed to develop until eggs could be identified as being parasitized (see 4.3.2) and then the latter were counted. The embryonic stages of host eggs, after different periods of development, were determined using the method described in 2.2.4 and from the data presented in 2.3.8. Wasps were observed every hour to ascertain whether or not they probed host eggs with their ovipositor.

4.3 RESULTS

4.3.1 Oviposition and its Relationship with Temperature

The ovipositional behaviour of *C. masneri* is similar to that of other scelionids (Bradoo 1972, Eberhard 1975, Wilson 1961). It is described here in detail to complement the work conducted on the mechanics of oviposition in this species (see Chapter 5).

A female wasp on finding a nest of its host, enters via one of the 2 entrances, locates the eggsac (see 3.3.5) and begins to tap the surface rapidly with its antennae. Many eggsacs of *C. robusta* have small openings, where the silk wall is incomplete or has been broken. Wasps use these to gain entrance into the eggsac, and then inspect the surface of the eggs with their antennae. If the eggs have not previously been parasitized (see 4.3.5) and they are not too old (see 4.3.7), oviposition commences. The female orientates its metasoma, the ovipositor and ovipositor sheaths (gonoplacs) are extended for their full length, and the host egg is penetrated. During this process the antennae remain motionless, and the head and pronotum move backwards and forwards, at a rate of approximately once per second (see Sales *et al.* 1978, Wilson 1961). Sometimes the membranous recess, that surrounds the ovipositor in the body cavity (see 5.3.3), partly protrudes between the ovipositor sheaths, as the latter are extended. Each oviposition takes 45-90 s ; the ovipositor is then withdrawn and reorientated towards another egg. The ovipositor is usually not completely withdrawn into the metasoma each time, but rather is retracted for about half its length before being fully extended again.

In cases where wasps cannot gain entrance into the eggsac, they oviposit through the silk wall in the same manner as above. Observations on wasps when they are ovipositing show that the ovipositor can reach eggs only in the outer 2 layers of an eggmass (see 3.3.6); eggs at the centre

are never parasitized. After females commence oviposition they spend little or no time inspecting eggs with their antennae, unless they move to the opposite side of the eggmass or to a new eggsac. Antennal tapping is most pronounced when a potential host eggsac is located for the first time. Initial inspection lasts for approximately 5 min with newly oviposited eggs, but this time increases (5-30 min) with older hosts, until eventually they are rejected by wasps as oviposition sites (see 4.3.7). Once oviposition has commenced, it is possible with some care to place eggs that have already been parasitized or that are too old in the vicinity of a wasp, and it will then sometimes oviposit into host eggs that it would not normally parasitize (see 4.3.7).

Female wasps were found to move over an eggmass in a systematic manner, until nearly all the eggs potentially within the wasp's reach had been parasitized, or until the wasp had depleted its load of eggs. This was achieved by wasps ovipositing into eggs in a small area, then moving onto an adjacent area, and repeating this until the surface of the eggmass had been covered. Such behaviour must optimize the number of eggs that are parasitized, and reduce the chance of superparasitism (see 4.3.5).

The relationship between temperature and oviposition was investigated by exposing 3 eggmasses (containing > 100 eggs) to 5 mature wasps, at various temperatures. All wasps were reared at 25°C (see 4.2.1), and those to be placed at low temperatures were transferred stepwise, by differences of approximately 5°C, spending 3 h at each temperature. The number of parasitized eggs in each mass was counted when they could be recognized as such (see 4.3.2). Eggs were parasitized at all temperatures above 8°C, but wasps were most efficient above 15°C (Figure 4.1). Temperatures below 15°C presumably slow wasps down so that they cannot move around sufficiently to oviposit into all the host eggs available. However, at temperatures above 15°C no such constraints were observed. Comparison of temperature records at locations near the study site (see Figure 2.2),

Figure 4.1 Percentage of host eggs parasitized by *C. masneri* at different temperatures (N.B. n = 3 eggmasses for each temperature, closed circles = means).

Figure 4.2 The timing and range in the main stages of developing *C. masneri*, and the change undergone by host eggs (25°C).

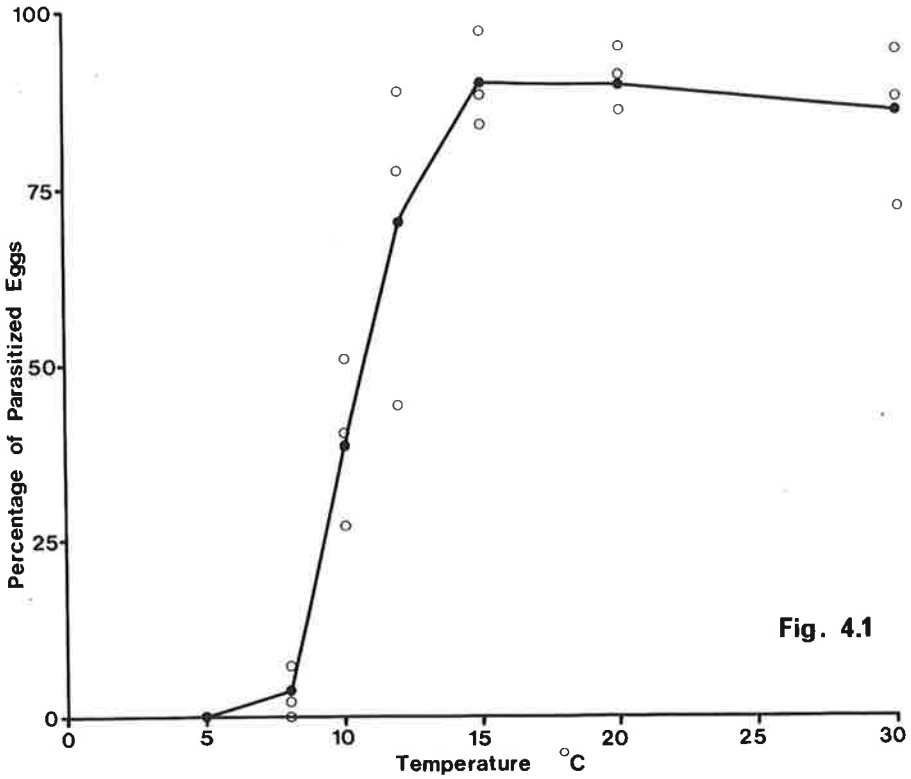

100
75
50
25
0
Percentage of Parasitized Eggs
0
5
10
15
20
25
30
Temperature °C

Fig. 4.1

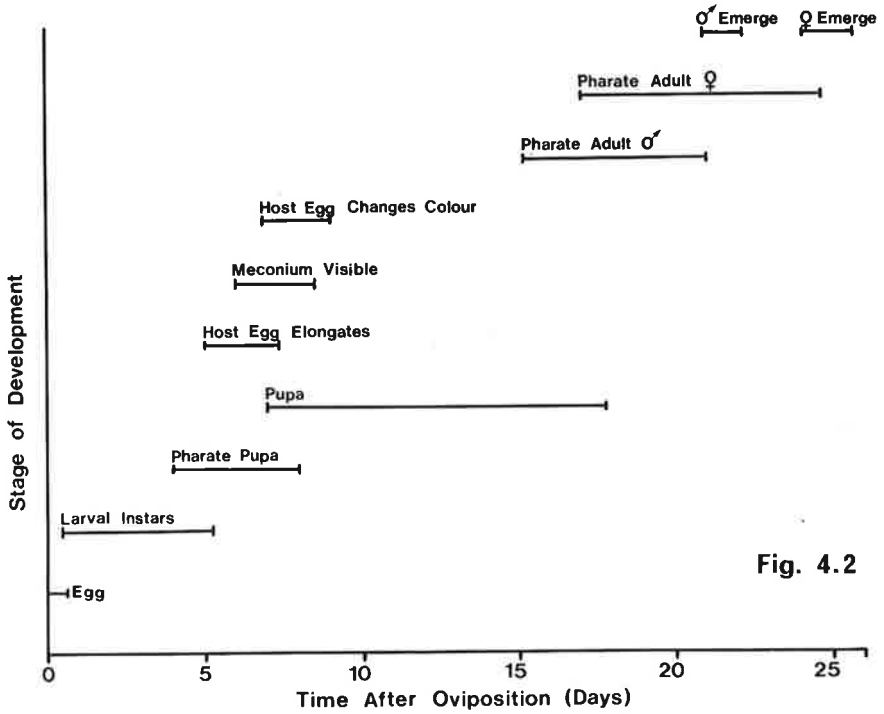

♂ Emerge
♀ Emerge
Pharate Adult ♀
Pharate Adult ♂
Host Egg Changes Colour
Meconium Visible
Host Egg Elongates
Pupa
Pharate Pupa
Larval Instars
Egg
Stage of Development
0
5
10
15
20
25
Time After Oviposition (Days)

Fig. 4.2

with the range of temperatues in the laboratory at which parasitism was greatest, i.e. above 15°C, shows that *C. masneri* can probably parasitize host eggs at almost maximum efficiency, as soon as the latter become available at the beginning of a season (August-September).

4.3.2 Developmental Stages, Developmental Time, Emergence and Mating

Eggs parasitized by *C. masneri* were fixed in alcoholic Bouin, at 12 h intervals from oviposition to emergence of wasps. They were dissected to determine the stage of development, position and number of parasitoids per host. Different stages were stained with Borax Carmine (1-5 min) for ease of identification of each stage.

C. masneri was found to go through 3 larval instars, before entering the pupal stage. Larvae occupied different places in host eggs, when the former were in early stages of development. Once hosts had reached the germ band stage larvae were usually located in the yolk directly below the embryonic tissue. The larval instars are very similar to those described for other scelionids (Bradoo 1972, Clausen 1940, Egwuatu and Taylor 1977, Subba Rao and Chacko 1961). However, it was found that this parasitoid did not completely consume the contents of its host until after larval-pupal apolysis. This means that the parasitoid continues to ingest its host after it has become a pharate pupa (see Hinton 1973). There seems little doubt that this stage was in fact a pupa, as 2 rows of antennal segments were recognized on its ventral surface. This phenomenon has not previously been described within the parasitic Hymenoptera, though Hinton (1958) has described feeding in the pharate pupal stages of other insects.

Host eggs can be recognized as being parasitized when they become distorted in shape, i.e. they become elongated. This becomes more obvious soon after when the chorion hardens and becomes darker (Figure 2.5). Wasps emerge from their hosts as adults and are able to fly and oviposit into new host eggs immediately. A summary of the time spent in each stage

until emergence is presented in Figure 4.2. The data for the duration of the pharate stages are only estimates based on external morphology; no histological study was undertaken to determine the precise time of apolysis. These data also show that males emerge prior to females. The method of emergence is identical to that described for the scelionid *Baeus semilunum* (Vachon 1955). The membranous pupal case is broken by movement of the adult wasp, and it then chews and pushes its way out of the host egg, at the opposite end to the meconium. The hardened chorion of the host egg forms a secondary but more substantial pupal case around that of the wasp.

Differences in the developmental time for males and females at various temperatures in the laboratory, and at different times of the year, are presented in Table 4.1. These data in conjunction with parasitized eggs collected from the field (see Table 3.1), indicate that *C. masneri* can go through 3 or possibly 4 generations in one season (September-March). Also, parasitized eggs and adult wasps reared in the laboratory at different temperatures , relative humidities and under different light regimes, show that this species does not diapause. The fact that female wasps do not resorb their eggs and will readily oviposit into hosts under a range of environmental conditions, supports this conclusion (see 4.3.3).

Observations in the laboratory show that in most cases, mating occurs at the time females emerge. Males emerge several days prior to females and then wait for the latter to chew their way out of the remaining host eggs. Single males will mate with more than one female, and females remain receptive to mating for at least 2 h after emergence. However, mated females removed from males for 12 h were unreceptive to subsequent mating attempts. There was no evidence of males actively guarding unemerged females from other males as has been recorded for other scelionids (Eberhard 1975, Subba Rao and Chacko 1961, Wilson 1961); nor

	Mean Developmental Time (d, ± range)	
A. Laboratory		
Temperature °C (± 0.5°C range)	♀	♂
12	96.0 ± 3.0	88.0 ± 3.0
15	57.0 ± 2.0	53.0 ± 1.5
20	32.0 ± 1.5	29.6 ± 1.0
25	25.5 ± 1.0	22.5 ± 0.5
28	22.7 ± 1.0	21.5 ± 0.5
B. Field		
(date of oviposition)		
10 September 1980	81.0 ± 4.0	-
5 October 1980	69.0 ± 3.0	64.0 ± 3.0
1 January 1981	29.5 ± 1.0	27.0 ± 1.0

Table 4.1 Developmental times for males and females of *C. masneri* at different temperatures in the laboratory (12:12 L/D; 70% R.H.) and at different times of the year in the field.

does *C. masneri* display any pre-copulatory courtship behaviour, as has been observed for some Hymenoptera, e.g. Chalcidoidea (Gordh and DeBach 1978, Van Den Assem *et al.* 1980), Diapriidae (pers. comm. I.D. Naumann). Males simply mount the female from behind, she raises her metasoma and copulation occurs (Vachon 1955). All males died within 3 or 4 d after mating, at 25°C, but survived for a few days longer at temperatures below 20°C.

4.3.3 Fecundity

Preliminary experiments with *C. masneri* showed that females which had just emerged (1 d old) had a much lower fecundity than older individuals (7 d old). The relationship between fecundity and age was therefore investigated, to determine when females carry most eggs.

An eggmass of *C. robusta* containing parasitized eggs was held at 25°C and the wasps allowed to emerge. Ten females were dissected on glass slides every 5 d and the number of fully developed eggs in each individual were counted. Newly emerged females were found to carry some fully developed eggs, but a full complement was not reached until after 10 d (Figure 4.3). (referred to as mature wasps in 4.2.3 and elsewhere). This increase in the number of developed eggs is related to a decrease in the amount of yolk stored in the gut and a reduction in the number of immature eggs with nurse cells. Fully developed eggs in the ovaries of newly emerged wasps were shown to be mature, as these wasps could successfully parasitize hosts. Female *C. masneri* from the above eggmass all died after 50 d. Three wasps examined at Day 48 were found to contain a maximum number of eggs ($\bar{x}$ = 69.3). Similar results were obtained for wasps at 15°C and 118 d old (see 4.3.6) (n = 2, 71 and 67 eggs), and wasps collected from the field in June 1980 ($\bar{x}$ = 75.6, n = 5). Also individuals from the 15°C group, 105 d old, successfully parasitized hosts when they were exposed to the latter. These data

Figure 4.3 Mean number of fully developed eggs in the ovaries of *C. masneri* at different times after emergence from host eggs (N.B. n = 10 for 0-25 d, n = 3 for 48 d, ± 1 S.D.).

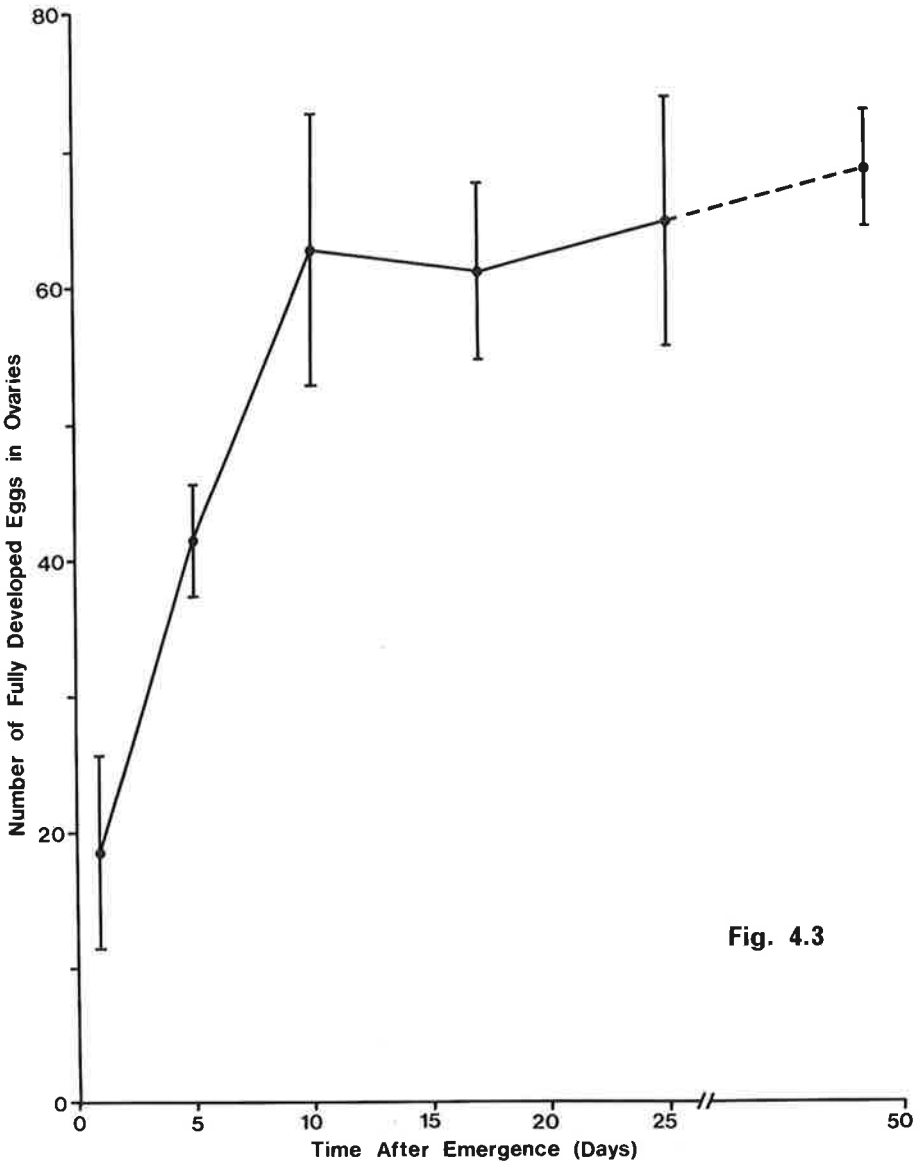

80
60
40
20
0
Number of Fully Developed Eggs in Ovaries
0
5
10
15
20
25
50
Time After Emergence (Days)

Fig. 4.3

indicate that *C. masneri* do not resorb mature eggs when they are overwintering, but rather eggs are retained in the ovaries until they are oviposited or until the wasp dies.

Observations on females in the laboratory indicate that they do not produce a second lot of eggs, but rather die soon after the first lot are laid. In the field dead females were often found inside or on the outer surface of host eggsacs.

4.3.4 Sex Ratio

The sex ratio of 2 species of *Ceratobaeus*, i.e. *C. masneri* and *C. clubionus*, was determined by collecting parasitized eggmasses of their hosts, *Clubiona robusta* and *C. cycladata* respectively, from the field and then rearing all parasitoids through to adults. The sex ratio and distribution of males and females from these eggmasses are given in Table 4.2. These data show that the number of males and females is strongly biased towards the latter, and that the sex ratio between the 2 species is similar. This bias in favour of females indicates that most females are being fertilized before they disperse to find new host eggs. This may be explained by the fact that a large proportion of parasitized eggmasses contain some male wasps. Seventy-five percent of eggmasses parasitized by *C. masneri* and 74% of those attacked by *C. clubionus* contained both males and females, while 7% and 2% respectively, contained only male wasps. Similar results to these were also obtained in the laboratory for eggmasses parasitized by mated females. In this case (n = 20) the majority of females (85%) placed a few male offspring in each eggmass, while eggmasses parasitized by unmated females only produced male offspring. It appears therefore that mated females possess a mechanism for withholding sperm from some eggs, so that males are produced. This situation is not due to a depletion of sperm before all the eggs are oviposited, as single females exposed to 2 eggmasses

A. *Ceratobaeus masneri* (Host - *Clubiona robusta*)

Number of parasitized eggmasses	Sex of Wasps	Total Number of Wasps	Mean Number per Eggmass (± 1 S.D.)
5	♀ only	85	17 ± 6
21	♀ + ♂	1740 ♀, 230 ♂	85 ± 52 ♀ 11 ± 13 ♂
2	♂ only	46	(21 + 25)
28		Total ♀ 1825 Total ♂ 276	
		Sex ratio 6.6 ♀ : 1.0 ♂	

B. *Ceratobaeus clubionus* (Host - *Clubiona cycladata*)

Number of parasitized eggmasses	Sex of Wasps	Total Number of Wasps	Mean Number per Eggmass (± 1 S.D.)
13	♀	78	6 ± 5
39	♀ + ♂	402 ♀, 69 ♂	8 ± 6 ♀ 2 ± 1 ♂
1	♂	11	-
53		Total ♀ 480 Total ♂ 80	
		Sex ratio 6.0 ♀ : 1.0 ♂	

Table 4.2 Sex ratio and frequency of males and females of 2 species of *Ceratobaeus*, reared from eggmasses collected in the field at various times of year.

sequentially will place some male offspring in each batch. The oviposition of some male and female eggs at the same site has been described for other parasitoids (e.g. Abdelrahman 1974, Eberhard 1975, Pickford 1964), but in most cases the production of males is attributed to 'fatigue of the spermatheca', i.e. presumably to a shortage of sperm.

Observations on adult wasps at the time of emergence show that males will readily mate with their sibs and that 5 males is more than enough to fertilize over 80 females. Thus, the placement of some males in eggmasses parasitized by mated females, leads to a high rate of fertilization in the next generation. Also, presumably individuals in eggmasses containing only male wasps, disperse to search for unfertilized females, thereby possibly increasing the number of fertilized females in the population. Dispersing males probably serve an important function in this and other species of parasitoids by providing a source of outbreeding. Non sib-mating is further maintained at moderate levels in *C. masneri*, as approximately 30% of parasitized eggmasses are attacked by more than one female wasp (see 4.3.8).

4.3.5 Superparasitism and Discrimination between Parasitized and Unparasitized Eggs

Three eggmasses were exposed to 5 gravid females of *C. masneri* each for 12 h at 25°C, and eggs were sampled every day until emergence. They were fixed in alcoholic Bouin and later dissected. The number of parasitoids in each egg were counted and their stage of development noted. The frequency of parasitoids in hosts of different ages is given in Table 4.3. The level of superparasitism was found to be 13%, with the number of parasitoids decreasing to one per egg, by the time the pupal stage was reached. Presumably the number of larvae is reduced by cannibalism as has been reported for other parasitic Hymenoptera, including scelionids (Eberhard 1975, Klomp and Teerink 1978). Eggmasses from the field, that

Time after Oviposition (d)	Number of Parasitoids per Host Egg			n
	1	2	3	
0 - 2	41	5	1	47
2 - 6	51	1	0	52
6 - 25	35	0	0	35
		superparasitism		134

Table 4.3 Frequency of superparasitism in host eggs at different times after oviposition by *C. masneri* (25°C).

were known to be recently oviposited, had a similar incidence of superparasitism (16%, n = 87), compared with those parasitized in the laboratory. The incidence of superparasitism is therefore low and probably results from accidental ovipositions. Observations made on ovipositing females showed that occasionally wasps that were attempting to oviposit into one egg accidently would slip the ovipositor into an adjacent egg, and this could be one already parasitized. Such cases occurred when the ovipositor was not correctly orientated to the egg, resulting in the ovipositor being deflected off the target egg and into an egg next to or below the target. This phenomenon has also been described for other scelionids (Wilson 1961) and is proposed as one of the main causes of superparasitism. Superparasitism by *C. masneri* did not appear to cause an increase in the number of male offspring, as occurs in other Hymenoptera (Flanders 1939, Jackson 1966, Schwartz and Gerling 1974). When female wasps were exposed to hosts that had been parasitized for about 6 h or longer, they refrained from probing the latter with their ovipositor. Eggs that had been parasitized for less than 6 h were probed, but later dissection of hosts revealed that oviposition took place only in a few cases. *C. masneri* does not mark the surface of host eggs with its ovipositor after oviposition, as do other scelionids (e.g. Eberhard 1975, Rabb and Bradley 1970, Wilson 1961). Marking in the former species may be undertaken by injecting some factor into the host along with its own egg or, alternatively, the larval parasitoid may cause subtle changes inside the host or to the chorion, that are then detected by other females. The fact that probing into parasitized hosts was observed only in the first few hours after initial parasitism (i.e. the parasitoid's egg would not yet have hatched), lends some support to the latter hypothesis.

4.3.6 Overwintering

Collection of host eggs in the field strongly indicated that *C. masneri* was not overwintering in any juvenile stages inside its host. No parasitized or unparasitized eggs of *C. robusta* (or any other species of *Clubiona*) were found from April - August, during the 3 years of the study. However, female wasps were located on several occasions during this period. Thus, *C. masneri* appears to overwinter only as an adult. The few wasps that were located (n = 15), were found inside nests or old eggsacs of *C. robusta*.

For adult females to overwinter they must survive under bark for at least 90 - 110 d, as this is approximately the period when there are no host eggs available. Climatic conditions at the study site during April - August are cold and wet (see 2.2.1). Measurements of temperature and humidity under bark on 10 different days showed that temperatures never rose above 12°C and relative humidity was nearly always 100%. The longevity of female *C. masneri* was therefore tested under similar conditions in the laboratory, to determine what proportion of wasps could be expected to survive the winter. The experiment was conducted as described in Section 4.2.2.

As expected, wasps survived longest under conditions that were closest to those experienced in the field, i.e. 10°C and 100% relative humidity (Table 4.4). Longevity was greatly reduced at high temperatures and at low relative humidity (40-50%).

The above experiment shows that more than 10% and possibly as many as 50%, of all female wasps that emerge at the beginning of winter, are capable of surviving until the beginning of the following season. Furthermore, wasps that had survived for more than 110 d, had not resorbed any eggs (see 4.3.3), thus indicating that the fecundity of overwintering females is not reduced. Dissection of several wasps during the course of the experiment

Temperature (± range) °C	Access to water	Time taken (d) for 50% and 90% of wasps to die	
		50%	90%
10 ± 1	+ water	89	116
15 ± 1	"	44	113
20 ± 2	"	45	48
25 ± 2	"	27.5	35
10 ± 1	- water	66	77
15 ± 1	"	59	67
20 ± 2	"	23	28
25 ± 2	"	15	18

Table 4.4 Longevity and survival of female *C. masneri* at different temperatures, with and without water supplied (N.B. R.H. with water ≃ 100%, without water = 40-50%; n = 25 in each treatment).

showed that the amount of fat body in the metasoma decreased with time. Females that had recently died were found to contain virtually no fat, and therefore had probably died because their store of nutrients was exhausted.

Reduced longevity at low relative humidities in laboratory experiments was undoubtedly due to loss of water. However, such mortality is unlikely to occur in the field even during summer, as wasps spend most time under bark and in the nests of spiders, where relative humidities are higher than in other habitats (see 2.3.5). Furthermore, *C. masneri* appeared to drink from condensation on the surface of glass vials, and so this species is probably capable of replacing lost body fluid, as need and opportunity arise.

The above results also show that female *C. masneri* do not need to feed to survive the winter. In fact, it is likely that this species does not feed at all, as individuals supplied with food, i.e. 15% sugar solution, honey, yeast paste and chopped raisins, did not attempt to feed, even though they had been starved for 80 d.

4.3.7 Effect of Age of Host Eggs

Preliminary trials aimed at rearing *C. masneri* on its host, at 25°C, showed that female wasps would not attempt to oviposit into eggs that were older than approximately 2 d. Similar observations have also been made on other hymenopteran parasitoids including other scelionids (e.g. Clausen 1940, Eberhard 1975, Fedde 1977, Subba Rao and Chacko 1961, Wilson 1961). Hardening of the chorion may explain how these species are prevented from successfully ovipositing into their hosts (see 4.4). However, the eggs of spiders do not develop a hard surface with age, as do many insect eggs (Anderson 1973, Browning 1967), and therefore this does not provide an explanation for the short period that they are suitable to attack. The effect of age of host eggs was thus investigated, as to possible factors

that determine their suitability for oviposition by *C. masneri*.

The percentage of eggs in various stages of development that contained viable parasitoids, i.e. offspring developed to at least the pupal stage, was determined for 3 different temperatures (see 4.2.3 for methods). At the highest temperature (25°C) eggs became parasitized only when they were less than 1.5 d old, i.e. the first 20% of the total developmental time, but at lower temperatures (15 and 20°C) successful parasitism occurred in eggs that were relatively much older, i.e. for approximately the first 40% of their developmental time. This is shown in Figure 4.4, where the data for the 3 temperatures are plotted on different time scales, so that the stage of development of host eggs can be compared. These data show that the results for 15°C and 20°C are similar; wasps oviposit into eggs in stages up to early germ band stage, where the incidence of parasitism drops to zero. They then refrain from ovipositing into hosts that are older than this stage. The difference in the shape of the 15°C curve is probably due to the effect of low temperatures on the efficiency of oviposition (see 4.3.1), rather than on changes in the suitability of hosts. On one occasion female wasps were induced to oviposit into hosts in early inversion stage at 20°C (open circle on graph), by placing these eggs in the vicinity of wasps ovipositing into eggs in younger stages (see 4.3.1). Some of these eggs developed signs of being parasitized, but later dissection showed that the juvenile parasitoids had not developed past the last larval stage.

At 25°C wasps accept stages approaching early germ band stage, as being suitable for oviposition (open circle on graph), but only in eggs earlier than germ disc stage do offspring develop successfully. Thus, it appears as though high temperature in some way inhibits the development of parasitoids in later stages of their host (i.e. between germ disc and germ band stage), stages that nevertheless allow for successful development at lower temperatures. To test the null hypothesis, that high temperatures

Figure 4.4 Relationship of temperature (± range) and age of host eggs with the incidence of parasitism by *C. masneri* (N.B. curves of best fit were plotted by eye; closed circles indicate successful oviposition, offspring reached at least the pupal stage; open circle at 25°C indicates oviposition occurred but signs of parasitism did not develop; open circle at 20°C indicates parasitoids did not reach the pupal stage).

Embryonic stages of host eggs:

1. oviposition
2. blastoderm
3. germ disc
4. germ band (no limbs developed)
5. germ band (limbs half the length of their final size)
6. early inversion
7. s-shaped germ band
8. eclosion

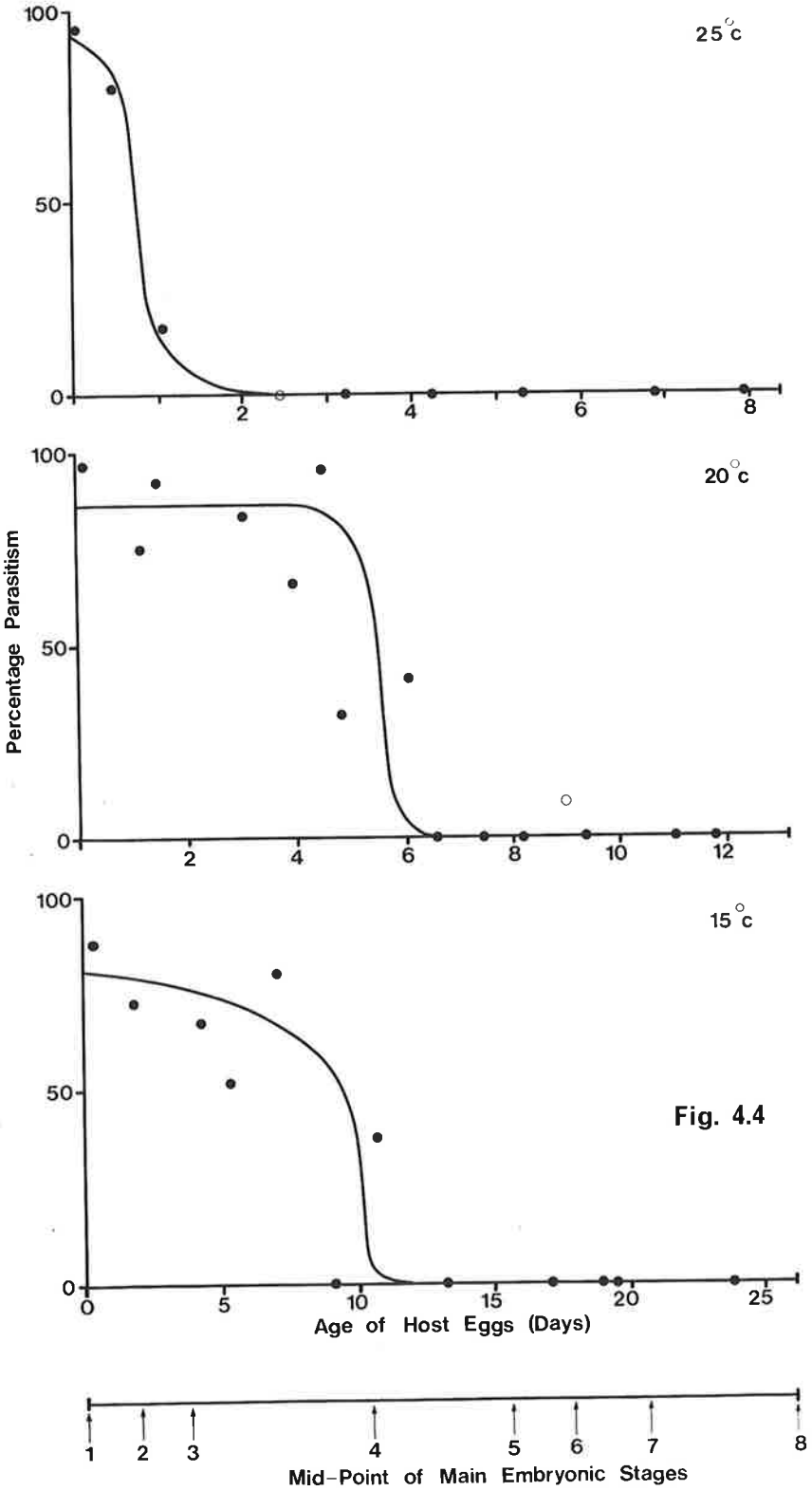

25°c
20°c
15°c
Percentage Parasitism
100
50
0
2
4
6
8
10
12
15
20
25
Age of Host Eggs (Days)
1
2
3
4
5
6
7
8
Mid-Point of Main Embryonic Stages

Fig. 4.4

are not responsible for such mortality, an experiment was set up where wasps where allowed to oviposit into eggs that were in the same stage of development (i.e. midway between the germ disc and early germ band stage), but at 2 temperatures, 20 and 25°C. Each eggmass was then divided (total $n \simeq 100$); one group was transferred to the other temperature while the second group remained at the same temperature to act as the control (see Table 4.5). The results show that in eggs at 25°C (D - Table 4.5), or in eggs transferred to 25°C after oviposition (A), no parasitoids develop. In comparison, at constant 20°C (B), a high proportion of eggs were successfully parasitized (47%), as would be expected from the results presented in Figure 4.4. However, the fact that even some eggs (6%) that were transferred from 25 to 20°C developed signs of parasitism, strongly indicates that high temperature is indeed preventing the normal development of *C. masneri*. Unfortunately these results are confounded, as the transfer of eggs from one temperature to another was itself a cause of mortality, i.e. 34% and 46% of the transferred eggs died, versus 7% and 11% in controls. This interaction therefore probably reduced the number of eggs that would have become parasitized in group C.

The way in which high temperature prevents the development of this parasitoid inside its host is unknown. However, the different rates of development of these organisms may provide some clue. At 25°C the eggs of *C. robusta* take 8.5 d to develop, while *C. masneri* takes 26 d, with the larval and pharate pupal stages taking up the first 8 d. The embryo of the spider may then be able to reach the stage where the parasitoid is prevented from developing, i.e. post early germ band stage (see below), as the former has a faster rate of development. Oviposition must therefore occur before the germ disc stage at 25°C, if the parasitoid is to take over and kill its host. In contrast, at lower temperatures (15 and 20°C) the slower rate of development of both organisms may allow

Temperature at which eggs were reared and oviposition occurred (°C ± range)	Groups (n)	Treatment after oviposition	Results for Host Eggs		
			Number that show signs of developing parasitoids	Number that die with no sign of parasitism	Number that hatch successfully
20 ± 1.0	A. Experimental (50)	25°C	0	17 (34%)	33 (66%)
	B. Control (59)	20°C	28 (47%)	4 (7%)	27 (46%)
25 ± 1.0	C. Experimental (50)	20°C	3 (6%)	23 (46%)	24 (48%)
	D. Control (46)	25°C	0	5 (11%)	41 (89%)

Table 4.5 Results of the experiment to test the effect of transferring host eggs to higher and lower temperatures, after they have been parasitized by *C. masneri*.

the parasitoid enough time to destroy its host, when oviposition has occurred in eggs approaching early germ band stage.

This effect of high temperature is probably a real phenomenon in the field, but its importance in limiting the time eggs are available for parasitism can be questioned. The mean temperature from December - March is about 20°C (see Figure 2.2), and this would indicate that eggs are always available as hosts up to germ band stage. However, periods of warmer weather with means approaching or in excess of 25°C do occur during summer. At these times the relative time for which eggs are suitable must be greatly reduced, but the frequency of such periods probably results in little or no effect on the total number of eggs parasitized over the whole season (September-March).

4.3.8 Host Specificity and Host Finding

Eggs of many species of spiders found under bark in the study site (see 2.3.1) were collected and parasitoids, when present, were reared out in the laboratory. This provided information on the host relationships of the predominant species of scelionids, and on the proportion of eggs that are attacked by the different species. Data on only the 4 scelionids that attack members of *Clubiona* are presented here (Figure 4.5). Each of the scelionid species was allowed access to the eggs of all host species in the laboratory. Mature female wasps were placed in vials with recently oviposited eggmasses (both with and without eggsacs) and observations were made every hour for 16 h. No scelionid was found to probe and oviposit into eggs of species other than those from which it had been reared in the field, thus confirming the host relationships in Figure 4.5. The laboratory data also show that wasps recognize their host(s) in the absence of a surrounding silk eggsac. It seems likely therefore that it is some property, probably on the surface of eggs, that wasps use to recognize hosts from non-hosts.

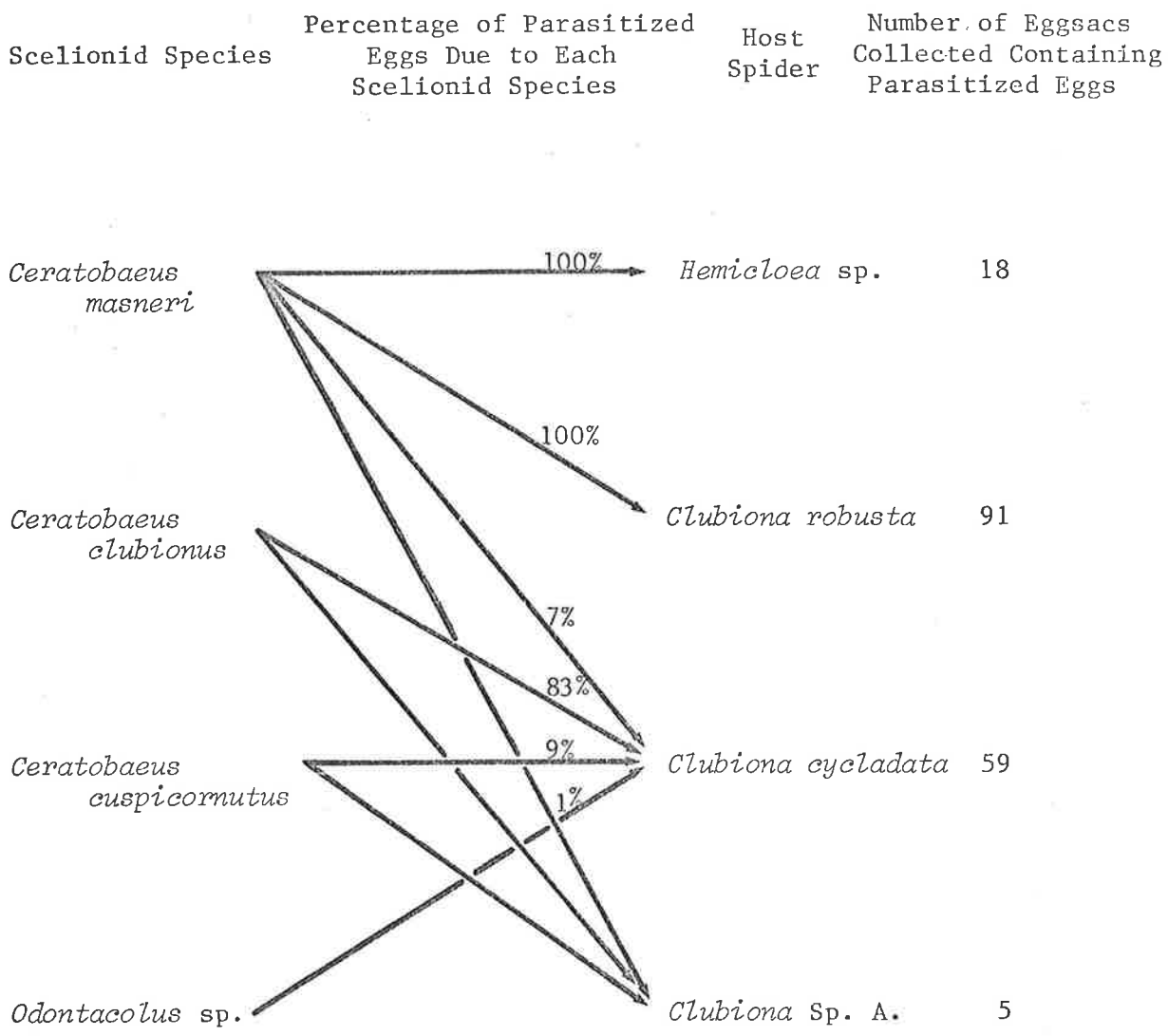


Figure 4.5 Host relationships of scelionids as determined from eggs collected in the field over a 3 year period. The percentage of parasitized eggs of *Clubiona* Sp. A. are omitted as only 5 parasitized eggsacs of this species were found.

The host relationships of these 4 scelionids show that the 3 species of *Ceratobaeus* all attack more than one species of host: *C. clubionus* and *C. cuspicornutus* parasitize the eggs of 2 species of *Clubiona*, *C. masneri* parasitizes all 3 species of *Clubiona*, plus an unrelated spider (*Hemicloea* sp.); while *Odontacolus* sp. attacks only the eggs of one host. Furthermore, *C. masneri* is the only parasitoid of 2 spiders, *C. robusta* and *Hemicloea* sp., while *C. cycladata* is parasitized by all 4 scelionids. Even though these scelionids attack more than one host, each shows a preference for one species; 84% of *C. masneri* from eggs collected in the field came from *C. robusta*, even though the eggs of *C. cycladata* are more abundant, while 93% of *C. clubionus* and 85% of *C. cuspicornutus* were reared from the latter spider. The number of parasitized eggmasses of *Clubiona* Sp. A was too small to allow assessment of the host-parasitoid relationships of this species.

The methods by which the wasps find host eggs was unknown. Females of *C. masneri* were observed to disperse from nests after emergence and mating, and they undoubtedly fly between trees. However, attempts to sample flying wasps using yellow pan-traps filled with water, failed. Either wasps were not attracted to these traps, which seems unlikely as they collected many scelionids, including other species of *Ceratobaeus*, or they were dispersing for only short periods at certain times of the day.

To test the null hypothesis that flying wasps cannot locate eggs associated with substrata other than the bark of trees (e.g. *Eucalyptus viminalis*), nests of *C. robusta* containing female spiders and newly oviposited eggmasses were attached to wooden posts at the same height and near nests on trees, i.e. each post was 1.5 m away from each tree. Two nests were placed on each of 5 trees and 5 posts. Trees with a minimum of bark were chosen; the bark plates were removed and sprayed with 0.1% pyrethrum, as was the surface of trees, to kill any *C. masneri* that were present. The bark was then nailed back into place and the extra

pieces with nests and eggmasses (but no *C. masneri*) were attached 7 d later (November 1980). All nests were collected after 28 d in the field and examined for parasitized eggs. Only nests under bark and on trees were found to contain parasitized eggs (4 out of 10 nests); no eggmasses in nests associated with wooden posts had been parasitized. Parasitized eggs could only have come from wasps flying onto the sprayed trees. These results confirm that *C. masneri* flies between trees, and they also strongly indicate that wasps preferentially search for substrata where host eggs are most likely to be found, i.e. the bark of *E. viminalis*.

Once females locate the correct substratum they appear to search for the silk of spiders, more specifically the nests of *Clubiona*. Individual *Ceratobaeus* collected in the field were found either inside or on the outside of nests. Many of these nests did not contain female spiders or host eggs, and so wasps were presumably using some cue from the silk to locate nests. Wasps were found associated with the nests of both host and non-host species of *Clubiona*. However, when *C. masneri* and *C. clubionus* were left overnight in large containers that contained the nests (but no spiders or eggs) of *C. robusta*, *C. cycladata* and those of 2 species from non-host groups, *Lampona cylindrata* and *Ixeuticus robustus*, the parasitoids were found associated with silk of only the former 2 species. Thus, they can distinguish between the silk of *Clubiona* and that of other spiders.

It appears therefore that these parasitoids find their host(s) by initially searching for the host's habitat; they then switch to searching for the silk nests of the host group, i.e. those of the genus *Clubiona*, and finally use some cue from the surface of eggs to distinguish between host and non-host species.

Work carried out on the fecundity of *C. masneri* (see 4.3.3) shows that each female of this species produces about 65 eggs. However,

approximately 30% of eggmasses of *C. robusta* collected from the field contained more than 80 parasitized eggs, and therefore these must have been located by more than one wasp. A female that locates an eggmass that has already been parasitized will probably not be able to oviposit all her eggs, as available host eggs will become exhausted. If a second eggmass is found, the chances are that it will be unparasitized (see 3.3.3) and so the wasp would be able to oviposit her remaining eggs. This situation may provide an explanation for the apparent even distribution of percentage parasitism of *C. robusta* eggs by *C. masneri* (see Figure 3.3). If the majority of eggmasses are found by one wasp only, then a normal distribution in the number of parasitized eggs would be expected around a mean of approximately 65. However, with some eggmasses being located by more than one wasp, ~~some being located by 2~~ and others having only a few eggs parasitized, as some female wasps will have unloaded most of their eggs elsewhere, a much flatter distribution would occur. In addition, variations in temperature (see 4.3.1 and 4.3.7), the age of female wasps (see 4.3.3) and the age of host eggs (see 4.3.7), must compound this effect by producing even more variability in the number of eggs in single eggmass that are parasitized. Thus, an almost horizontal distribution in the data would occur, as seen in Figure 3.3.

4.4 DISCUSSION

This is the first time that fecundity, host discrimination, overwintering and host specificity have been studied in detail for scelionids that attack the eggs of spiders. It is also a unique study of the biology of a species of *Ceratobaeus*. This work shows that the biology

of *C. masneri* displays a number of similarities and differences, when compared with other scelionids. Some differences between these genera seem to be related to the variety of host groups they exploit.

Ovipositional and preovipositional behaviour is one characteristic that is closely related to the host groups attacked by these parasitoids. Some species of *Scelio* are known to burrow through the soil surface to reach the eggs of their orthopteran hosts (Pickford 1964), while members from other genera are phoretic (Clausen 1940, 1976) and parasitize eggs before the latter are buried, or become too hard, or are covered in protective silk or mucous. *Phanuropsis semiflaviventris* has a very short oviposition time and an extensible metasoma. Both these characteristics enable it to overcome the behaviour of the bug *Antiteuchus tripterus*, that guards its eggs and attacks any predators or parasitoids (Eberhard 1975). The preovipositional behaviour of *C. masneri* is concentrated on penetrating the nest and eggsac around its hosts. All species of *Ceratobaeus* possess an elongated ovipositor that is used to reach the eggs through the silken wall of the eggsac (see Chapters 5 and 6), however, some eggs at the centre of the eggmass always escape parasitism (Bradoo 1972, this study 3.3.6 and 4.3.2). Valerio (1973) has proposed that *Baeus* regulates the number of eggs that it attacks by refraining from ovipositing into about 35% of eggs in each mass. However, the findings of this study indicate that this figure represents the proportion of eggs that would be protected in the centre of the eggmass, and thus the existence of active regulation may be questioned.

The fact that the development of eggs in the ovaries of *C. masneri* progresses for several days before a full complement is reached (see 4.3.3), means that a maximum number of hosts cannot be parasitized until after that time, even though females can oviposit successfully soon after emergence. This phenomenon has been described for only a few other species (Laing

and Caltagirone 1969, Ryan *et al.* 1981, Schell 1943), in which a preovipositional period between adult emergence and oviposition occurs. However, varying degrees of postemergent delay in the development of eggs may be more widespread among scelionids and other parasitic Hymenoptera, especially if it is disguised by the absence of a distinct preovipositional period, such as in *C. masneri*. If this is the case, studies on fecundity using newly emerged females may be inaccurate.

The overwintering stages of many parasitoids have not been identified. Riek (1970) has proposed that *Ceratobaeus* and related genera overwinter inside host eggs. However, several studies (Agudelo-Silva 1980, Bradoo 1972, Hickman 1967b, this study - 4.3.6) indicate that these scelionids do so as free-living adults, without going into diapause. Other egg-parasitoids overwinter in host eggs, either quiescently (López and Morrison 1980) or in diapause (Askew 1971, Birch 1945, Jackson 1963). The longevity of many species, especially *Telenomus* spp., has been investigated, but usually only in the laboratory and at temperatures much higher than would be experienced by wasps during winter. Thus, few of these data can be used to estimate winter survival. The importance of feeding in relation to increasing longevity also varies between species. Several studies (Bradoo 1972, Ticehurst and Allen 1973, Zatyamina and Burkova 1980) have demonstrated increased survival times and fecundity due to feeding, while others show that feeding does not occur in some species (Egwuatu and Taylor 1977, Valerio 1976, this study - 4.3.6).

Nearly all parasitoids that attack the egg stage of their host display 2 distinct types of discrimination in regard to the suitability of the latter as an ovipositional site (Klomp *et al.* 1980, Vinson 1976). They can distinguish parasitized from unparasitized hosts, and also recognize hosts that are too old to allow for successful development of offspring. The way in which parasitoids determine whether or not a host

is already parasitized, varies between species. *Trissolcus*, *Telenomus*, *Trichogramma* and related genera, all mark the surface of their hosts with a water soluble chemical (kairomone) that inhibits subsequent oviposition by conspecific individuals (Askew 1971, Bosque and Rabinovich 1979, Eberhard 1975, Klomp *et al.* 1980, Rabb and Bradley 1970, Salt 1937, 1961, Wilson 1961, see Vinson 1975, 1976 for reviews). This behaviour is said to reduce the incidence of superparasitism, thereby leading to a higher rate of survival. Also it optimizes the chance of finding an unparasitized host, by deterring subsequent wasps from searching the same space (Van Alpen 1980, and above references). However, some variation in this behaviour occurs between species. Several studies have shown that the incidence of successful discrimination by some species increases if the individual has had prior ovipositional experience (Bosque and Rabinovich 1979, Klomp *et al.* 1980, Rabb and Bradley 1970). For one species of *Telenomus*, marking of hosts does not appear to reduce the degree of superparasitism (Gerling and Schwartz 1974). However, this result may be explained if only inexperienced females (wasps that had never oviposited) were used in this study.

Bosque and Rabinovich (1979) point out that surface marking of hosts is almost exclusive to egg-parasitoids, and usually to those that attack exposed hosts, as these parasitoids can readily test the surface with their antennae, i.e. *Telenomus*, *Trissolcus* and *Trichogramma*. Studies on other egg-parasitoids that attack physically protected hosts (e.g. Bradoo 1972, Jackson 1966, Pickford 1964, Valerio 1973) indicate that host discrimination occurs via the extended ovipositor, after it has penetrated the chorion. This is not the case ~~of~~ with *C. masneri* ~~or~~ and some other species (Gerling and Schwartz 1974, Klomp *et al.* 1980, Vinson 1976), that utilize both the antennae and the ovipositor for discrimination, at different times, depending on whether or not the antennae can reach the

surface of the host.

Egg-parasitoids therefore differ substantially in the way they discriminate between parasitized and unparasitized eggs from each other. However, no studies have attempted to determine the origin of the internal marker that wasps detect with their ovipositor, inside a parasitized egg. Two possibilities are; (1) a chemical injected by the previous wasp, or (2) some factor produced by the newly hatched parasitic larva. This study suggests that the second of these alternatives exists in *C. masneri* (see also Vinson 1976), but further work is needed to support this hypothesis.

The second type of discrimination relates to the age of host eggs. Most scelionids, mymarids and trichogrammatids will parasitize only the very early stages of their hosts, i.e. eggs younger than 1 - 3 d (Clausen 1940, Leibee *et al.* 1979, Vinson 1976). In addition, many species show a rapid increase in the rejection of hosts with increasing age of the latter (Eberhard 1975, Klomp *et al.* 1980, Rabinovich 1970, this study - 4.3.7).

The present work shows that *C. masneri* differs from most other egg-parasitoids that have been studied, in that its host remains susceptible to successful parasitism up to a much later stage in its embryonic development. Also, this is the first time that temperature, independent of the age of hosts, has been investigated and has been shown to affect the survival of larval parasitoids. It is proposed that high temperatures (above 25^{o}C) adversely affect the larvae of *C. masneri*, by differentially increasing the rate of development of the host compared with the parasitoid. However, it is not clear what actually causes the death of the larva inside its host egg at these temperatures. Further, it is not known why eggs after early germ band stage are unsuitable for the parasitoid. It may be that embryos at this stage have developed an immune response. This seems unlikely, however, as all embryos that were parasitized died. Also, even the tissues of well-developed arthropod embryos are probably not advanced enough to possess such a response, unlike

those of adults (Salt 1970). Alternatively, late stage embryos may not be suitable, as a greater volume of the egg contains embryonic tissue rather than yolk, and parasitoids may need to ingest mostly yolk to complete development. There is some indirect support for this hypothesis, as larval parasitoids were only found in the yolk part of the egg, never in the embryo itself (see 4.3.2), and the embryonic tissues always appeared to be the last that were ingested, prior to pupation. Similar observations have been made on other parasitoids (Fedde 1977).

The cues used by parasitoids to find their hosts have received much attention (see Lewis *et al.* 1976, Vinson 1975, 1976, Vinson and Iwantsch 1980). In most cases chemicals from the host or some part of the host's habitat are used to locate them. *C. masneri* was found to search preferentially for the trunks of eucalypt trees rather than adjacent habitats. It is probable that it also recognizes the particular species of eucalypts with which its host is associated. Once a tree is located, *C. masneri* searches for the silk nests of its hosts (*Clubiona* spp.) rather than those of other spiders. A chemical factor deposited by the female spider, possibly associated with the silk itself, is likely to be involved. The pattern of host location displayed by this species lends support to the hypothesis that parasitoids follow a heirarchy of cues: as each cue is recognized the area of searching is reduced, and the probability of finding a host increases (see Vinson 1975, 1976). In *C. masneri* at least 2 cues have been identified, i.e. the bark of eucalypt trees and the silk of nests. Possibly a third cue is also received from the surface of host eggs.

Recent studies on scelionids have greatly elucidated their biology. Several of the generalized characteristics proposed by Wilson (1961) for the family now appear to be present in only some genera, e.g. surface marking of eggs, aggression between males over mates and between females

over hosts. The present work on *C. masneri* shows this species to possess a behaviour that is specifically adapted to finding, recognizing and penetrating the nests and eggsacs of its host. These qualities tend to characterize various scelionids and can be related directly to the host groups that these parasitoids utilize.

CHAPTER 5

THE MORPHOLOGY AND MECHANICS OF THE OVIPOSITOR OF *CERATOBAEUS* AND RELATED GENERA

5.1 INTRODUCTION

The ovipositor is primarily used to reach and deposit an egg, either into or onto a host, the latter otherwise presumably being inaccessable to the parasitoid. Secondarily, the ovipositor functions as a stinging device in some species (Snodgrass 1956). Presumably its diversity in morphology is related to the diversity of substrata that the ovipositor has to penetrate. Different species oviposit through soil, wood, leaves, various types of puparia and egg cases, and in the case of hyperparasities, insect tissue, to reach their host.

The anatomy and mechanics of the insect ovipositor have been well studied. Authors such as Scudder (1961a, 1961b, 1971), Smith (1969, 1970) and Snodgrass (1931, 1933, 1935) have shown that the morphology and operation of the insect ovipositor is complex, and that it works in a similar way in all groups. Recently, Austin and Browning (1981)* have confirmed this by showing that nearly all insects possessing an ovipositor have posteriorly orientated scales located along the inside of the ovipositor valves. These scales act as a 'linear ratchet' to move eggs along the ovipositor when the valves move back and forth.

The structure of the ovipositor is most diverse in the parasitic Hymenoptera. It varies between species in length and in its arrangement with the terminal metasomal segments. The ovipositor is usually very fine and would probably be damaged if it simply protruded from the posterior end of the body. Correspondingly, it is protected in many

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* see Appendix 3.

species when it is not being used for oviposition (Scudder 1971). Ichneumonids and braconids usually hold the ovipositor in a specialized sheath formed from the gonoplacs (Askew 1971, Snodgrass 1933). Other species have the terminal segments and ovipositor either partly invaginated into or under the metasoma. Many chalcidoids are known to display this arrangement (Copland and King 1971a, King and Copland 1969). The ovipositor of the Aphelinidae is partly held within the body cavity and is extended by the terminal segments which rotate outwards, using a hinge mechanism between the ovipositor and the most posterior tergite (Copland 1976).

During the course of this study it was possible to examine the ovipositor of *Ceratobaeus masneri* in detail, and to obtain some information on related species. It was found that the ovipositor of these species was unlike that described for any other Hymenoptera. The ovipositor of all *Ceratobaeus* species is completely invaginated into the body cavity and is therefore detached from the terminal metasomal segments. The proximal end is connected to these segments only via elongated muscle bands and a semi-sclerotized membranous tube, the latter separating the ovipositor from the haemocoel. The apodemes of the terminal segments are also greatly elongated and extend into the body cavity for at least half the length of the ovipositor. Other parasitic Hymenoptera, as far as is known, neither have the ovipositor completely invaginated into the metasoma nor have it detached from the terminal segments.

In the following section the morphology of the ovipositor and

associated structures including the reproductive system of *Ceratobaeus* is described, and a model is put forward to explain the mechanics of ovipositor movement. Information to support the model is presented from observations on the behaviour of ovipositing wasps and from the morphology of the system. This work is compared with that published for other Hymenoptera, and general aspects of ovipositor mechanics are discussed.

The terminology of Scudder (1961b, 1964) is usually adopted when referring to parts of the ovipositor and associated structures. Alternative schemes have been proposed by various authors (Snodgrass 1931, 1933, Copland and King 1971a, 1971b, 1972a, 1972b, 1972c, Smith 1969, 1970), but that of Scudder is most widely used. However, some confusion may arise from the terms used to name the terminal segments of the metasoma. The first abdominal segment (propodeum) of parasitic Hymenoptera is fused to the thorax, so that the remainder of the abdomen is referred to as the metasoma or gaster. The ovipositor is derived from the eighth and ninth abdominal segments or alternatively, the seventh and eighth metasomal segments. It is usual to refer to 'metasomal segmentation' in hymenopteran systematics, but often 'abdominal segmentation' is used when referring to structures associated with the ovipositor. To prevent any confusion, both terminologies are used together in describing the ovipositor of *Ceratobaeus*. The abbreviations T and S are used for the terms tergite and sternite, e.g. T7 means the tergite of the seventh metasomal segment or the eighth abdominal segment.

5.2 MATERIALS AND METHODS

The morphology of the cuticular parts was determined from observation of cleared slide-mounted material and from scanning electron microscopy (SEM). The anatomy of the reproductive system and the musculature of the ovipositor was described from dissected fresh specimens, stained whole-mounted specimens, and wax embedded and epoxy resin embedded sections.

Fresh specimens were partly dissected under water using fine tungsten wire needles (Pantin 1946). These needles were produced by etching the end of tungsten wire to a point in molten sodium nitrite. Specimens were placed in 10% potassium hydroxide (2-6 h at 40°C) to dissolve away all soft tissues, washed in 70% ethanol and dehydrated in 100% ethanol (15 min, 2 changes each), then either transferred to clove oil (12-24 h) to be cleared and mounted on slides using Canada Balsam or SIRA mountant, or dried in a desiccator (24 h) and prepared for SEM examination as in Appendix 1.2. Some specimens were critical point dried in liquid carbon dioxide (Nemanic 1972) and then treated as for air-dried specimens.

Material for whole-mount preparations was dissected in Ringer's Solution (Ephrussi and Beadle 1936) using tungsten needles, washed and mounted unstained on microscope slides in Ringer's, then partly squashed under large coverslips. Others were dissected, fixed in FAA (Austin and Browning 1981: 6 h), washed in 70% ethanol, hydrated in an ethanol series, stained with Mayer's Haemalum or Borax Carmine (1-5 min), and dehydrated and mounted as for potassium hydroxide treated material.

Pharate adults (18-20 d old, reared at 25°C) were only used for wax embedded sectioning, as individuals of this age were not heavily sclerotized, yet the ovipositor and its associated musculature and the reproductive system were well developed. The cuticle of later stages is very thick relative to the size of the insects and sectioning caused shattering of the cuticular wall and/or disloding or distortion of internal structures. Pharate adults were dissected from parasitized host eggs; fixed in FAA (24 h), dehydrated, embedded in 60°C m.p. wax, sectioned at 7-10 µm, stained with Mayer's Haemalum or Heidenhain's Iron Haematoxylin, and mounted on slides using Eukitt's Mountant.

Adult wasps were fixed in 3% glutaraldehyde in 0.2M sodium cacodylate (pH 7.2), washed in buffer and dehydrated in an ethanol series, transferred to Spurr's Medium (Spurr 1969) (24-36 h; 3 changes), embedded, and sectioned at 0.5-1.0 µm using a Sorvall Porter Blum MT2P Ultramicrotome. Sections were placed on slides held at 60-100°C and stained with toluene blue (10 s). This procedure eliminated the problem of cuticle shattering, as occurred when sectioning adult wasps embedded in wax.

5.3 RESULTS

5.3.1 General Morphology of the Metasoma of Female *Ceratobaeus masneri*

The metasoma (or gaster) of *C. masneri* is dorsoventrally flattened and comprises 7 tergites and 6 sternites. The laterotergites (or pleurites) are closely attached to the sternites and are represented as narrow impressed plates, that are hidden by the tergites in dorsal view. The laterotergites are weakly sclerotized and stretch to accommodate the additional volume of the ovaries when females are gravid.

The first tergite (T1) is expanded dorsally into a short hollow horn which is continuous with the haemocoel. The first 3 segments are large and comprise approximately three-quarters of the length of the metasoma; the posterior segments are, therefore, quite short. There is one extra dorsal sclerite (T7) which forms a small terminal triangular plate.

5.3.2 Terminal Segments and Internal Apodemes

T7 and S6 form the dorsal and ventral posterior sclerites of the metasoma. Pygostyles are developed on each side of T7. These structures are leaf-shaped and occur in small lateral depressions on T7. They each have one or more long hairs; the latter are believed to be sensory in function.

The inner surfaces of T7 and S6 are divided by narrow transverse ridges. These ridges form the attachment points for intersegmental membranes, that join these plates to the preceding sclerites (T6 and S5) and to each other. The intersegmental membrane acts to contain the haemocoel and provides some movement between sclerites, to allow for expansion and contraction of the body wall.

Behind these ridges, T7 and S6 extend anteriorly into the body cavity, to form 2 large flat plates. These plates almost reach the anterior margin on T5 and S5 respectively. They also form the subgenital plate (S6) and supragenital plate (T7) for the ovipositor (Figure 5.5). The anterior margin of these plates is extended to form 3 greatly elongated apodemes; 2 dorsolateral apodemes from T7, and one ventromedial apodeme from S6. These apodemes are formed from long cuticular extensions; they extend almost to the level of the anterior margin of T3, the medial apodeme being slightly shorter than the lateral

ones (Figures 5.3 and 5.5). They are semi-rigid and spring back to a longtiduinal position if flexed laterally. The anterior end of each apodeme is flattened and curved, forming a surface for the attachment of muscles.

5.3.3 The Ovipositor

The ovipositor is formed from 3 valves (stylets) (Figure 5.1), that are interlocked for most of their length by a tongue and groove arrangement. This prevents the valves from pulling apart, but allows them to oscillate back and forth on each other. This movement, combined with the spine-like scales along the inner surface of the valves (Figure 14, in Austin and Browning 1981), provides the mechanism for eggs to be moved along the length of the ovipositor (see 5.1).

The 2 ventral valves (first gonapophyses) are separate but interlock with the dorsal valve (fused second gonapophyses). As the ventral valves are not fused they are able to open slightly to accommodate the large diameter of an egg as it passes down the length of the ovipositor (see 5.3.6).

The ovipositor is approximately 760 um long, and is slightly longer than the metasoma (720 um) as it curves dorsally into the recess of the horn on T1. The ovipositor shaft is extremely narrow; it measures 4.5 um in width, 30 um from the distal end. The ovipositor becomes wider proximally but is never more than 10 um in width.

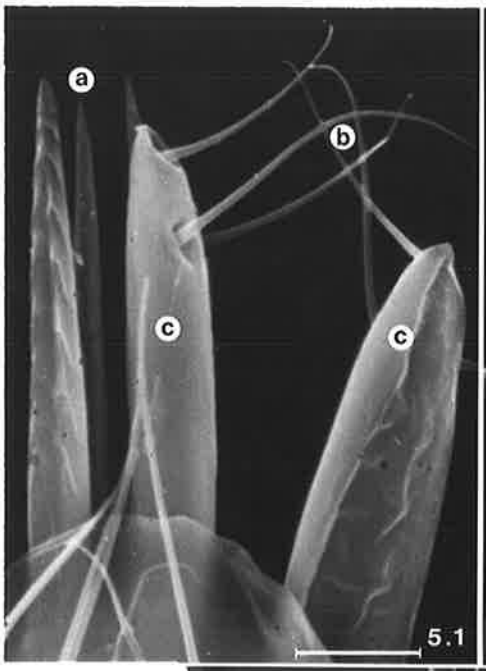
The outer surface of the tip of the ovipositor shows the characteristic teeth or barbs, present in most parasitic Hymenoptera (Figure 5.1) (Copland and King 1971a, 1972a, 1972b). These structures presumably assist in cutting into and then holding the shaft in the oviposition site. No sensory structures could be located on the outside

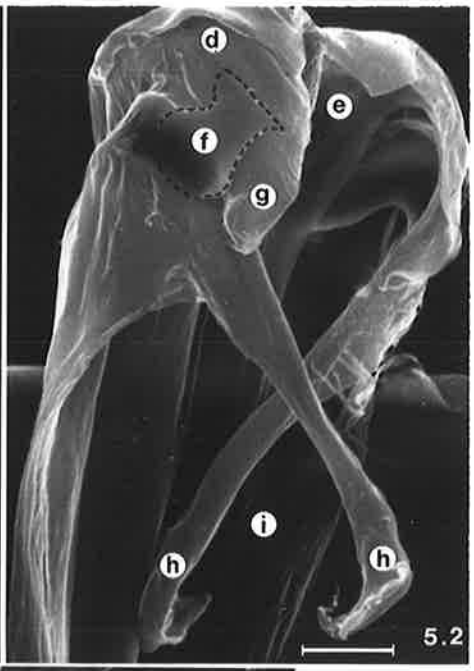
Figure 5.1 Scanning electron micrograph (SEM) of the distal end of the ovipositor of *C. masneri* (Scale = 10 um).

Figure 5.2 SEM of the proximal end of the ovipositor of *C. masneri*, after being treated with potassium hydroxide to remove soft tissues (Scale = 10 um).

Figure 5.3 SEM of the ovipositor and inside ventral surface of the metasoma of *C. masneri*, after being treated with potassium hydroxide (Scale = 10 um).

a) valves of the ovipositor
b) sensory hairs on the gonoplacs
c) gonoplacs
d) ramus of the first gonapophysis (outer surface)
e) ramus of the second gonapophysis (inner surface)
f) gonangulum
g) quadrate plate
h) second gonocoxa
i) membranous ovipositor recess
j) ovipositor shaft
k) apodemes
S = metasomal sternites
T = metasomal tergites


a
b
c
c
5.1


d
e
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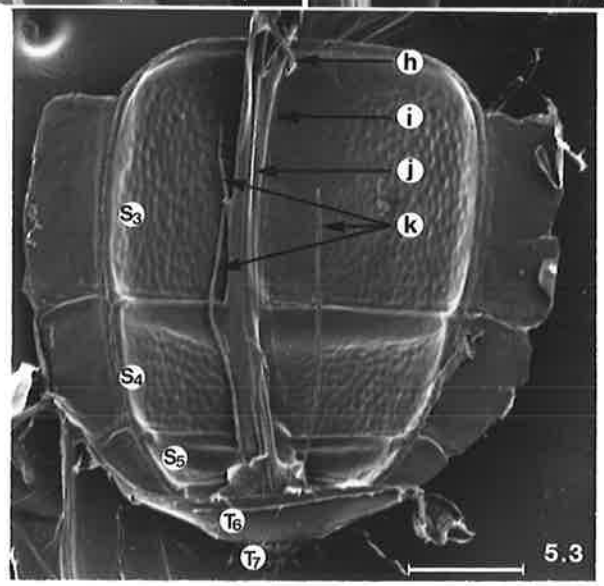
5.2


h
i
j
k
S3
S4
S5
T6
T7
5.3

surface of the ovipositor of *C. masneri*. Sensory pits and hairs have been recognized in other parasitoids (e.g. Copland and King 1971a, 1972a, Hawke *et al.* 1973), and these have been shown to be involved in host selection (Hayes and Vinson 1971, Vinson 1975). In *C. masneri* this function is probably served by sensilla on the antennae, gonoplacs, or inner surface of the valves.

The ovipositor fits between the subgenital plate (S6) and supragenital plate (T7). It is held inside the body cavity, but is separated from the haemocoel by a greatly elongated tubular recess that is formed from a lightly sclerotized, but flexible part of the integument (Figures 5.3 and 5.4). This recess collapses when the ovipositor is extended from the body, prior to oviposition. It is proposed that this semi-membranous recess is homologous to the intersegmental membrane found between segments 8 and 9 in other insects. This hypothesis is supported by the fact that the membrane (referred to hereafter as the ovipositor recess) attaches distally to the inner surface of T7 and S6 (which equals segment 8 of the abdomen), and attaches proximally to the anterior end of the ovipositor, part of which represents the highly modified remnants of segment 9.

The gonoplacs (third valvulae or ovipositor sheath) lie beside the ovipositor shaft and are attached to the wall of the ovipositor recess (Figures 5.4 and 5.5). They are extended with the ovipositor and act to support or brace the latter during oviposition. Usually the gonoplacs are formed from outgrowths of segment 9 (Scudder 1971), but in *C. masneri* they are clearly detached from this segment. The distal end of each gonoplac has 3 long sensory hairs (10-15 um in length), which sit in small depressions (Figure 5.1).

Figure 5.4 Light microscope micrograph of the ovipositor, reproductive and digestive systems, after being dissected from a fresh specimen of *C. masneri* (Scale = 100 µm).

a) accessory gland
b) ovipositor recess
c) protractor muscle
d) retractor muscle (broken)
e) common oviduct
f) apodeme
g) ovaries
h) midgut
i) malpighian tubules
j) hindgut
T_7 = seventh metasomal tergite (supragenital plate)

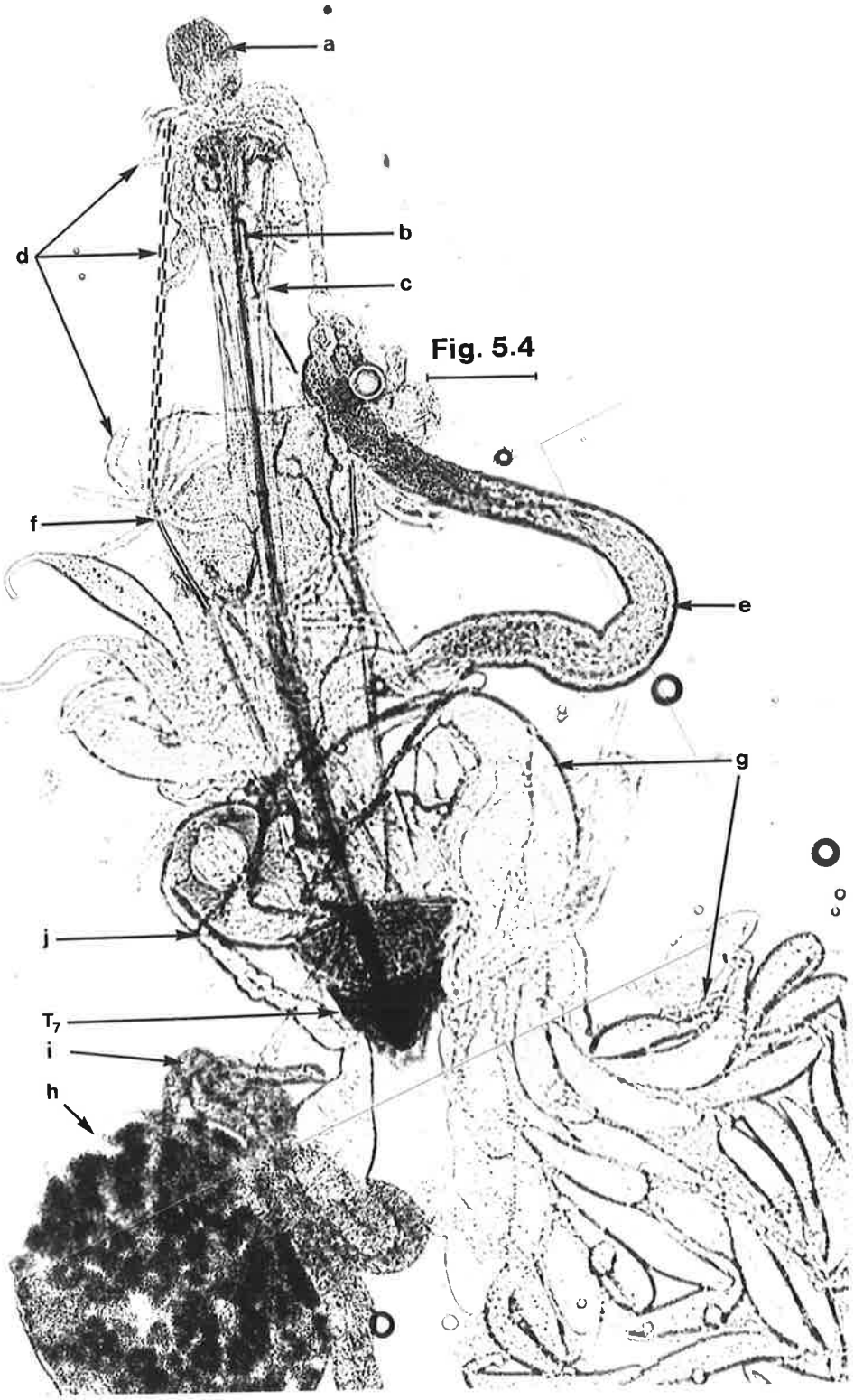


Fig. 5.4

The proximal end of the ovipositor is formed from a complex array of sclerites and muscles that work to produce the oscillating movement of the valves. The first and second gonapophyses give rise to paired rami on each side, which are interlocked and curve dorsally (Figure 5.2). The rami of the first gonapophyses are connected to the gonangula (Scudder 1957, 1971) (the first gonocoxae being absent in Hymenoptera); which in turn are fused dorsally to the quadrate plates (segment 9), and are hinged ventrally to the second gonocoxae. The second gonocoxae are attached anteriorly to the rami of the second gonapophyses, the latter being fused for most of their length, but divided proximally to form the rami. The second gonocoxae form 2 prominent arms that are expanded apically into curved flanges, and act as the attachment surfaces for muscles. The shape of the above sclerites differ from those in other Hymenoptera, but the basic plan and mechanics appear to be the same. The sclerites which form the proximal end of the ovipositor are extremely compact. They are only 50 um wide and 160 um long from the anterior surface to the ends of the second gonocoxae.

5.3.4 Musculature and Mechanics of the Ovipositor

There appear to be 2 separate sets of muscles which are involved in the control of the ovipositor. The first set produce the rapid oscillation of the ovipositor valves (see 5.3.3). This movement is produced by the rocking motion of the gonangula on the second gonocoxae. This in turn causes the rami to slide back and forth (oscillate) over each other (see Scudder 1971, Snodgrass 1956). The retractor muscles that bring about this movement are attached between the arms of the second

gonocoxae and the inner surfaces of the quadrate plate (segment 9). Protractor muscles could not be found in any preparations of *C. masneri*, but they are probably located on the inside of the quadrate plates, running from them to the rami of the second gonapophyses. These muscles are probably hidden within the complex arrangement of sclerites that make up the proximal end of the ovipositor; and, if so, the difficulty of sectioning this part of the ovipositor would have precluded their identification.

The retractor and protractor muscles must operate antagonistically, to rock the gonangula on their hinges with the second gonocoxae, causing the rami of the first gonapophyses to be pulled and pushed over the rami of the second gonapophyses. Occasionally, in preparations where live specimens were dissected in hypertonic saline, the retractor muscles could be made to contract and relax rapidly, causing the ovipositor valves to oscillate back and forth.

A second set of muscles are thought to extend and retract the ovipositor from the body cavity (Figures 5.4 and 5.8). It is likely that these muscles also work antagonistically. Muscles attached from the proximal end of the ovipositor to the inner surfaces of T7 and S6 (segment 8) and from the proximal end to regular positions along the membranous ovipositor recess, probably contract to extend the ovipositor (referred to hereafter as ovipositor protractor muscles). Bands of muscle also attach the proximal end of the ovipositor to the tips of the 3 elongated apodemes. These muscles, referred to as ovipositor retractor muscles, are probably responsible, in part, for retracting the ovipositor and also for orientating it once it is extended.

The origin of the muscles associated with the ovipositor is unclear, but it is likely that both the ovipositor protractor and

retractor muscles are derived from intersegmental muscles between segments 8 and 9, their function changed due to the elongation and invaginated nature of the system.

5.3.5 A Model for Ovipositor Movement

Using the morphological and anatomical information described above, the following descriptive model is put forward to explain the known movements of the ovipositor in *C. masneri*.

The Model

1. The ovipositor is held in a membranous recess within the body cavity when not being used.

2. Contraction of the main protractor muscles collapses the membranous recess and extends the ovipositor and gonoplacs (Figure 5.8); the latter are extended passively from the body, with the final section of the ovipositor.

3. The ovipositor must be fully extended before oviposition can occur.

4. The ovipositor can be partly retracted and extended again when the shaft is being orientated towards another host egg.

5. Partial contraction of different combinations of the retractor muscles allows the ovipositor to be orientated at different angles up to 20^{o}, in reference to the longitudinal line of the metasoma.

6. Alternate contraction of separate protractor and retractor muscles within the proximal end of the ovipositor, produces the oscillating movements of the valves, that are responsible for cutting into the oviposition site and the movement of eggs along the shaft (see 5.3.3).

7. Retraction of the ovipositor is achieved by the combined contraction of the retractor muscles and/or the elasticity (spring) of the apodemes that may be flexed during ovipositor extension, or changes in tergal or haemolymph pressure of the body cavity.

8. The muscle systems, responsible for oscillation of the valves and extension and retraction of the ovipositor, operate antagonistically.

9. When the ovipositor is withdrawn into the body cavity, it is held there clamped between T7 and S6.

This model is supported by a number of observations made on the behaviour of oviposition (see 4.3.1), as well as by the comparative morphology of wasps fixed with ovipositors partly extended. Sections cut of individuals with partly extended ovipositors indicate that the protractor muscles are responsible for extension of the ovipositor and that the membranous recess surrounding the ovipositor does collapse as the latter is extended (point 2 of the model) (Figure 5.8). These sections also show that the gonoplacs are not extended until the proximal end of the ovipositor reaches the anterior end of the gonoplacs. The latter are then presumably pushed out as the ovipositor is pulled down further by the protractor muscles. Conversely, the gonoplacs are not withdrawn until the distal end of the ovipositor reaches that of the gonoplacs. This process, as well as points (3) and (4) of the model, are also confirmed by observation of ovipositing wasps (see 4.3.1).

Orientation of the ovipositor through angles of up to 20^{o} in any direction (point 5), could only be achieved by contraction of muscles attached around the proximal end of the ovipositor. The only muscles recognized in this position are those running from the elongated apodemes.

Unfortunately, it has not been possible to identify their exact attachment points to the ovipositor. Presumably contraction of these muscles, singly or in pairs, pulls the ovipositor towards the side of the contraction, thereby allowing the ovipositor to be orientated in that direction.

The present understanding of ovipositor retraction is incomplete (point 7). Contraction of the retractor muscles can only bring the ovipositor to the level of the anterior end of the apodemes,i.e. only about 75% of the ovipositor would then be withdrawn. Retraction of the remaining 25% may possibly be achieved in either of 2 ways. Elasticity of the apodemes may produce a spring effect when they are flexed, causing the ovipositor to be pushed above the level of the apodemes. There is, however, little evidence for this hypothesis. Alternatively, lowering the tergal or haemolymph pressure in the body cavity may draw the ovipositor completely into its recess. This hypothesis is supported by observation of female *C. masneri*, which shows they flex the pronotum in and out during oviposition and ovipositor retraction. Such movements may cause changes in the volume of the body cavity, thereby changing the tergal pressure. This mechanism could be assisted by muscle contraction, or alternate clamping of the ovipositor between the supragenital (T7) and subgenital (S6) plates, to stop it from being accidentally extended when tergal pressure increases. This is similar to the mechanism proposed for stylet (mouth parts) retraction in some bugs (Miles 1958, Pollard 1970, 1972). The clamp would also hold the ovipositor in its resting position, when it has been completely withdrawn into the body (point 9). Sectioned material shows that the musculature between T7 and S6 could operate to clamp these plates together but there is no other information to show a clamp mechanism actually exists.

More information is needed if the mechanics of ovipositor retraction in *C. masneri* is to be better understood. It is necessary to fix and section wasps with their ovipositors in varying degrees of retraction, to determine which muscles, if any, are involved in this process. So far this has not proved possible. Ovipositing females were killed using a variety of fixatives and other agents, yet in nearly all cases they fully retracted their ovipositors before they died. In fact, it appears that *C. masneri* retracts its ovipositor in response to any disturbance, e.g. loud noise, air turbulence or rapid changes in air temperature. Occasionally wasps partly extended their ovipositors when they were dropped into FAA fixative. These specimens provided much of the information that has been presented in this section.

There is some evidence to suggest that the ovipositor protractor and retractor muscles act antagonistically (point 8); that is to say that contraction of one set of muscles inhibits contraction of the other set. This is necessary to prevent these muscles from contracting against each other. The pathways and transmitter substances for inhibitory and excitatory nerves, innovating somatic muscle in insects, are known and are summarized in Pitman (1971). Both types of nerves interconnect with each other and with the central nervous system (CNS). Their innervation is probably mediated by a number of feedback loops operating through the CNS, e.g. integration of information on host acceptance from sensilla on the gonoplacs, ovipositor or antennae leading to extention of the ovipositor, and information on release of an egg from stretch receptors in the ovaries or oviducts leading to retraction of the ovipositor.

When the ventral nerve cord of *C. masneri* is cut at a point between the mesosoma and metasoma, the ovipositor is immediately extended for 23% of its length ($\bar{x}$ = 23.1%, $\pm$ 0.62 S.D., n = 20). This places the proximal end of the ovipositor in a position almost level with the lateral apodemes. It is proposed that this position represents the equilibrium point for the ovipositor, when both retractor and protractor muscles contract simultaneously. This could be caused by release of inhibition and subsequent depolarization of excitatory nerves, when connections with the CNS are broken. This would then cause contraction of both sets of muscles. The above observation is then compatible with the hypothesis that these muscles operate antagonistically.

It is also likely that these muscles are of the supercontracting type. For the previous model to work it is necessary that at least the main protractor muscles contract approximately 90% of their resting length, to extend the ovipositor fully. Measurement of wasps fixed with their ovipositors partly extended, indicates that these muscles can contract at least 50% of their resting length, hence suggesting their supercontractile nature. Osborne (1967) has described a model for the supercontracting mechanism. He proposes that myosin filaments of a sarcomere penetrate through Z-disc pores and link to actin sites in the adjacent sarcomere, thereby shortening the muscle several fold. This is supported by the identification of perforate Z-discs and filaments penetrating them, in muscles of a number of insects (see Elder 1975). Ultrastructural examination of the protractor muscles in *C. masneri* was beyond the scope of the present work, but such a study would be required to confirm the presence of supercontracting muscles in this species.

Figure 5.5 - 5.7 Plan view of the metasoma showing relative lengths of the apodemes, ovipositor and gonoplacs.

Figure 5.5 *Ceratobaeus masneri*.

a) border of the sternites
b) lateral apodeme
c) median apodeme
d) subgenital plate (S_6)
e) supragenital plate (T_7)
f) ovipositor shaft
g) gonoplac

Figure 5.6 *Ceratobaeus cuspicornutus*.

Figure 5.7 *Baeus* sp.

(Figures 5.5 - 5.7, Scale = 100 *u*m).

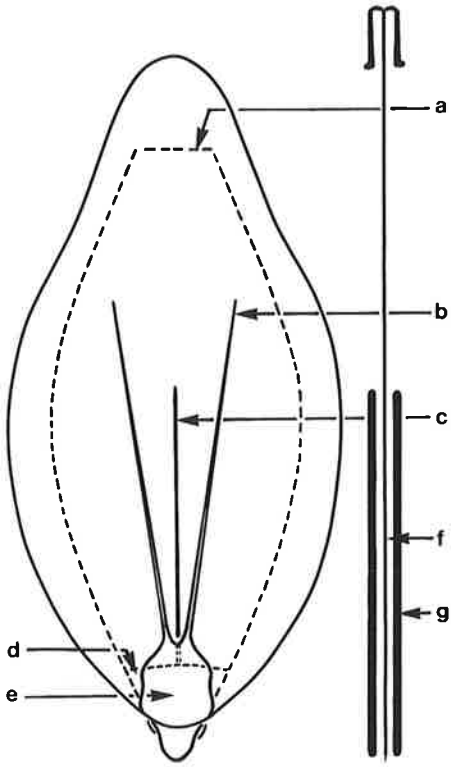


Fig. 5.5

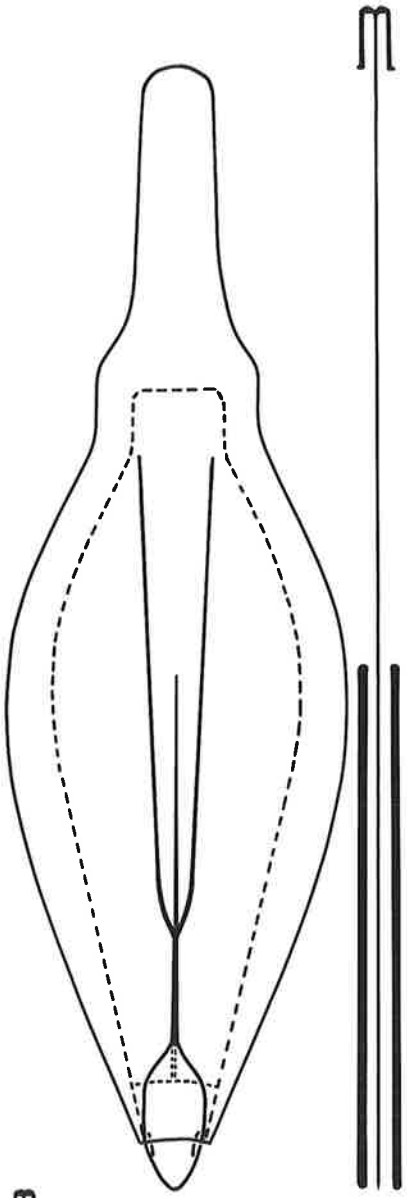


Fig. 5.6

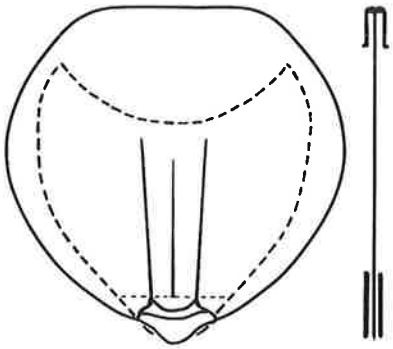


Fig. 5.7

5.3.6 Anatomy of the Reproductive System

The reproductive system of *C. masneri* is similar to that of other parasitic Hymenoptera (e.g. Bender 1943, Copland and King 1971a, 1971b, 1972a, 1972b, 1972c, Copland *et al.* 1973), except poison glands are not developed and the ovipositor does not function as a sting.

The common oviduct is greatly elongated; it can thus follow the movements of the ovipositor without being stretched (Figure 5.4). There are 2 accessory glands attached to the common oviduct. One of these probably functions as a lubricating gland, that coats eggs with a mucous secretion to assist their passage along the ovipositor (Rafai and King 1972). The spermatheca joins the base of the common oviduct, just before the latter divides into the lateral oviducts. The lateral oviducts are relatively short and expand distally to join the ovaries. Most of the contents of the metasomal cavity is occupied by the ovaries. When mature they each contain 30-35 eggs (see 4.3.3). Eggs are greatly elongated (Figure 5.4); 250-350 um long and 30-40 um wide. They are much larger in diameter than the ovipositor (5-10 um) and are therefore drastically deformed as they travel the length of the egg canal. In parasitic Hymenoptera that possess this type of egg, the chorionic tail acts as a recess to accommodate the yolk as the egg is deformed (Fulton 1933, King *et al.* 1968).

During copulation the membranous recess of the ovipositor also functions as a vagina, to receive the male aedaegus. Seminal fluid must be taken in at the opening of the oviduct at the base of the proximal end of the ovipositor, and then passed to the spermatheca for storage prior to fertilization.

5.3.7 Comparative Morphology of the Ovipositor System for Related Species and Genera

Examination of 30 species in the genera *Ceratobaeus* (12), *Idris* (10), *Hickmanella* (2) and *Baeus* (6) show them to have the same basic plan for the ovipositor system as *C. masneri*. Some structures vary in shape and size compared to the latter species, but their function can still be explained in terms of the proposed model for ovipositor movement.

Species of *Ceratobaeus* that have an extremely elongated metasoma and horn (e.g. *C. cuspicornutus* (Figure 5.6), *C. rieki*) simply display comparable elongation of the apodemes and components of the ovipositor. The relative lengths of the apodemes compared with the ovipositor of all species examined are very similar to that measured for *C. masneri*. These lengths may therefore represent a constant, that is critical to the mechanics of ovipositor extension and retraction. In those species that have very long apodemes, the lateral ones are fused basally but divide into lateral arms apically. Some species have the medial apodeme longer than the lateral ones (e.g. *C. clubionus*). Also the second gonocoxae and supragenital plate (T7) vary in shape and length between some species. For example, these structures are more elongate in *C. lamponae* compared with *C. masneri*, even though the metasoma of these 2 species is approximately the same length.

The only difference found in species of *Idris* and *Hickmanella* (Figure 5.9) compared with *Ceratobaeus*, is that the ovipositor in the former 2 genera is much shorter; approximately one half to three-quarters the length of the metasoma. No species examined had the ovipositor as long as in any *Ceratobaeus* species. Members of the genus *Baeus* are morphologically quite different compared with the previous genera (see

Figure 5.8 Diagram showing the probable changes in the lengths of muscles and position of the ovipositor, when the latter is extended and retracted (Scale = 100 μm) (N.B. ovipositor recess not included).

a) gonocoxae
b) retractor muscle
c) protractor muscle
d) lateral apodeme
e) median apodeme
f) ovipositor shaft
g) subgenital plate (S_6)
h) supragenital plate (T_7)

Figures 5.9 and 5.10 Plan view of the metasoma showing relative lengths of the apodemes, ovipositor and gonoplacs.

Figure 5.9 *Idris* and *Hickmanella* (Scale = 100 μm).

Figure 5.10 *Odontacolus* sp. (Scale = 100 μm).

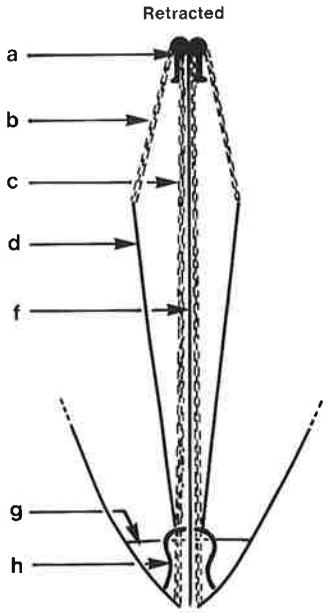
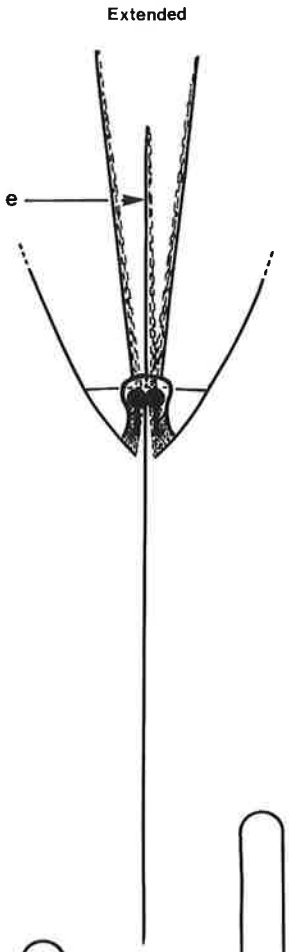


Fig. 5.8



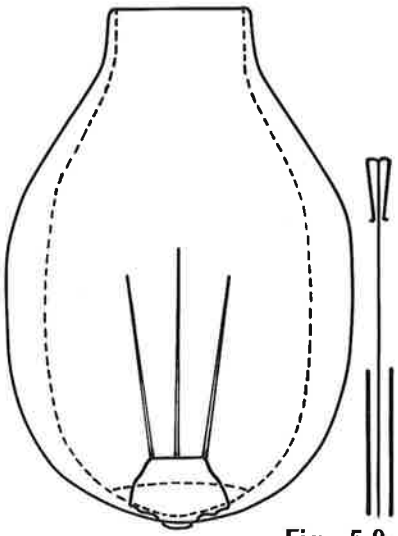


Fig. 5.9

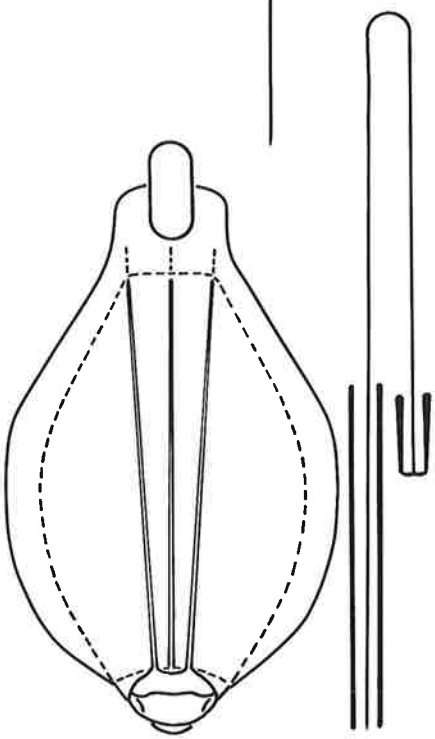


Fig. 5.10

Appendix 1.4), yet they also have an ovipositor system similar to that found in *C. masneri* (Figure 5.7).

Species of *Odontacolus*, however, appear to have an ovipositor system that differs substantially from that described for the previous genera. In this genus the ovipositor is approximately twice the length of the metasoma, as it loops back on itself in the broad apical end of the metasomal horn (Figure 5.10). Therefore, when the ovipositor is retracted, its proximal end lies near the base of T7 and S6, and not in the apical end of the horn, as for *Ceratobaeus*. This arrangement explains the shape of the horn in *Odontacolus*. The horn is compressed at the sides and broadly rounded apically (see Figure A22). This shape presumably protects the shaft of the ovipositor from possible damage, by preventing it from being bent at an acute angle. There are 3 apodemes present, similar to the configuration in *C. masneri*, but they extend to at least the base of the horn in *Odontacolus*. No information could be obtained on the muscular system or arrangement of the sclerites at the proximal end of the ovipositor. *Odontacolus* species are rare; the above information was obtained from only 2 preserved specimens. However, the mechanics of the ovipositor system, as it is known for this genus, cannot be explained in terms of the previously proposed model. At this stage it it not possible to put forward any sound alternatives. Until more detail is known on the morphology and musculature of the ovipositor in this genus, any understanding of its operation will remain obscure.

5.4 DISCUSSION

The ovipositor has evolved independently in many insect families, and yet the fact that the mechanics of its operation are much the same

in each case, strongly indicates that it has evolved from a basic plan that has allowed for the evolution of a common mechanism. The evolution of the insect ovipositor has been the subject of many investigations. These have mostly used information on the comparative morphology of the ovipositor, i.e. homology of its components and study of its ontogenetic development, but some workers have taken functional aspects into account. The present work supports the general hypothesis that the ovipositor has evolved from common structures (probably posterior abdominal appendages) in all groups (see Scudder 1971 for review).

This study has also shown that the ovipositor of *Ceratobaeus* species operates in the same way as that described for other insects, i.e. that the oscillating movements of the valves are responsible for penetration into a host and movement of an egg along the ovipositor. It has been possible to homologize all components of the ovipositor with those previously described (Scudder 1961a, 1961b, 1964, 1971, Smith 1969, 1970, Snodgrass 1931, 1933, 1956), even though those in *Ceratobaeus* may vary in shape and/or position.

In other insects that possess an unprotected ovipositor, the latter is heavily sclerotized and is used to penetrate hard substrata to reach the oviposition site. Some orthopterans, hemipterans and ichneumonids have an ovipositor of this type. However, in most parasitic Hymenoptera the ovipositor is a thin structure. This apparent limit in diameter has probably evolved to prevent or reduce possible injury to hosts. It has resulted in the ovipositor being a fragile structure that requires protection when it is not being used. In most species protection is afforded by the development of an ovipositor sheath or partial invagination of the ovipositor into or under the metasoma, the latter made possible by appropriate modification to the pregenital segments (see 5.1).

The ovipositor system of *Ceratobaeus* is highly modified and differs from all other Hymenoptera in that it is completely invaginated into the body cavity and is not directly connected to the terminal or pregenital segments. This arrangements, however, can be seen as simply a different solution to the problem of protecting a fragile ovipositor. In this case it is completely surrounded by the metasoma when not being used. Its evolution has undoubtedly depended on the development of a system to extend and retract the ovipositor from its recess, the mechanics of which are completely independent of the oscillating movements of the valves. The recess surrounding the ovipositor is believed to be derived from the intersegmental membrane between abdominal segments and 9. Extension of the ovipositor is probably achieved by protractor muscles derived from the intersegmental muscles between these same 2 segments. However, the mechanism for retraction is not fully understood. Contraction of the associated musculature (ovipositor retractor muscles) alone cannot be responsible for the complete retraction of the ovipositor. A number of hypotheses for alternative mechanisms are proposed. These are;(1) muscle contraction in conjunction with flexure of the apodemes produces full retraction; (2) changes in tergal pressure in the body cavity, possibly assisted by muscle contraction, produce retraction, and (3) tergal pressure in conjunction with clamping of the terminal segments fully retracts the ovipositor. So far there is little information to support or reject the above hypotheses. Obviously more detailed study is required if the mechanics of ovipositor retraction in *Ceratobaeus* is to be adequately explained.

Most studies on the ovipositor of Hymenoptera have utilized large species,e.g. Apidae (Smith 1970, Snodgrass 1933, 1935, 1956), Formicidae (Hermann and Blum 1966, Robertson 1968), Ichneumonoidea (Abbott 1934,

Bender 1943, D'Rozario 1940, Fulton 1933, Snodgrass 1933, 1935), Scolioidea (Smith 1970, Robertson 1968), Symphyta (D'Rozario 1940, Snodgrass 1933, 1935). This bias in size probably represents an attempt by the above workers to facilitate easier methods of study. Work by Copland and King (1971a, 1971b, 1972a, 1972b, 1972c) on members of various families of Chalcidoidea represent the only substantial studies on smaller insects. There has been no detailed examination of the ovipositor in Scelionidae or other Proctotrupoidea prior to this work, except for a brief reference in Scudder (1961a) and in systematic studies (Kieffer 1926, Masner 1976). It is therefore not surprising that the unique arrangement of the ovipositor in *Ceratobaeus* has not been described until now.

Of the scelionid genera that are most closely related to *Ceratobaeus*, *Idris*, *Hickmanella* and *Baeus* all have the same basic plan for the anatomy of the ovipositor and associated structures. Only *Odontacolus* possess an ovipositor differing from that described for *Ceratobaeus*. There is some evidence from this study and that of Masner (1976) to suggest that the morphology of the ovipositor system is of some systematic value and that it could be used to clarify the supergeneric classification of Scelionidae. If this is the case then the above information would indicate that *Odontacolus* is more distantly related to *Ceratobaeus* than the other 3 genera examined. However, the morphology of the ovipositor in other scelionid genera is virtually unknown, and therefore the systematic value of this structure remains obscure.

The morphology of the ovipositor must be closely linked to selective advantages concerning the exploitation of particular hosts. To some degree this must also be related to the relatively high degree of host specificity found in the parasitic Hymenoptera. There is some evidence from the Scelionidae to support this hypothesis (see Chapter 6; and pers. comm. L. Masner). Therefore, recognized modifications in

the structure of the ovipositor may reflect the respective host groups (e.g. spiders, orthopterans, hemipterans, embiids, etc.) utilized by different scelionid genera or tribes. If this can be demonstrated, then ovipositor morphology could be used to predict the likely host groups, or at least ovipositional sites, of scelionids for which hosts remain unknown.

CHAPTER 6

HOST RELATIONSHIPS AND HOST SPECIFICITY IN SCELIONID PARASITOIDS OF SPIDERS

6.1 INTRODUCTION

The degree of host specificity displayed by various groups of hymenopteran parasitoids has been the subject of extensive investigations (Askew 1971, Matthews 1974, Nagarkatti and Nagaraja 1977, Peck 1963, Sweetman 1963). Parasitoids can be monophagous - specific to a single species; oligophagous - limited to a group of allied species; or polyphagous - attacking a wide range of hosts (Askew 1971). The evolution of host specificity in parasitoids, however, has not been well studied. Malyshev (1968) suggests that entomophagous hymenopteran parasitoids may have evolved from plant parasitic habits, because many species are attracted to the odour of the food plants of their hosts. Further studies on groups such as Eurytomidae, that contain both phytophagous and entomophagous parasitoids and other completely phytophagous groups (Askew 1975, Cates 1980, Eastop 1973), may lend support to Malyshev's hypothesis.

Most hymenopteran parasitoids have evolved a high degree of host specificity, i.e. most are monophagous or oligophagous. In association with this they display a high level of morphological, behavioural and physiological specialization (Askew 1971, Vinson 1975, 1976, Vinson and Iwantsch 1980), that can in many cases be related to the methods they use to find and oviposit into hosts. However, hosts also have evolved elaborate methods of protection, e.g. formation of puparia and eggsacs, burial in soil and timber (Austin and Browning 1981), violent movement (Matthews 1974), regurgitation of fluid exudates (Hays and Vinson 1971), association with ants and other organisms (Flanders 1947, Way 1963), and encapsulation of parasitoids in the host's haemolymph (Salt 1970, Vinson 1977). Therefore, many host-parasitoid relationships may be best understood as coevolved associations (Vinson 1975).

Apart from a high degree of host specificity at the species level, many groups of hymenopteran parasitoids also display a high level of specificity to broad taxonomic groupings of hosts (referred to as group specificity); for example, as seen in the host relationships of the Family Scelionidae (Table 6.1) (also see Askew 1971, Matthews 1974, Nagarkatti and Nagaraja 1977, Sweetman 1963, for group specificity in other families of parasitoids). In many cases this group specificity shows a hierarchical association. For example, a family of parasitoids may attack hosts from only one insect order; genera may specialise in parasitizing a particular host subfamily or genus, while species may be specific to one or a few closely related host species. In some cases host associations may be more related to a particular habitat, such as the food plant(s) that hosts are found on, or the morphology or surface texture of hosts, rather than the taxonomic relationships of the latter (Askew 1971, Cushman 1926, Kozlov 1970b, Sugonyayev 1966).

It is possible that the same factors responsible for group specificity in parasitoids have also contributed to the development of species specificity. Few studies, however, have examined the possible factors causing restricted host ranges at any taxonomic level. Askew (1968, 1971) and Vinson (1975, 1976) among others, have proposed that competition, haplo-diploid reproduction, the problem of finding patchily distributed hosts, and the effective immune response of some hosts, have led to a high degree of specialization in parasitoids, and thus a high level of host specificity. No workers have made a detailed study of spatial isolation due to physical barriers as a possible factor causing host specificity. Parasitoids that attack hosts which are spatially isolated would require appropriate adaptations to overcome these barriers. Selection for morphological and/or behavioural characters that allow these hosts to be successfully parasitized, would also restrict parasitoids to them, probably for mechanical reasons related to oviposition; while other

Subfamily	Tribe*	Host Group
Scelioninae	Aradophagini**	Aradidae (Heteroptera)
	Baeini	Araneae
	Baryconini	Phaneropterinae (Tettigoniidae)
	Calliscelionini	Tettigoniidae; Gryllidae; Odonata (Clausen 1976)
	Cremastobaeini	unknown
	Doddiellini	unknown
	Embidobiini	Embioptera; Araneae
	Gryonini	Coreidae, Pentatomidae, Scutelleridae, Lygaeidae, Reduviidae, Phymatidae (Heteroptera); Mantidae
	Idrini	Araneae
	Mantibariini	Mantidae
	Neoscelionini†	unknown
	Nixoniini**	unknown
	Platyscelionini	Phaneropterinae (Tettigoniidae)
	Psilanteridini	unknown
	Scelionini	Acrididae; Phymatidae (Heteroptera)
	Sparasionini	Decticinae (Tettigoniidae); Stenopelmatinae (Gryllacrididae)
	Thoronini	Nepidae, Gerridae (Heteroptera)
Teleasinae	Teleasini	Carabidae
	Xenomerini	unknown
Telenominae	Telenomini	Mostly Lepidoptera and Heteroptera; also Diptera and Neuroptera

Table 6.1 Host relationships of the Family Scelionidae (compiled from Galloway 1980, Kozlov 1970a, Masner 1976, 1980).

* Arranged in alphabetical (not phylogentic) order.

** Not recorded from the Australian region.

† New tribe proposed by Kozlov (1981).

parasitoids that lack appropriate adaptations would be excluded from such hosts. Adaptation by parasitoids to spatially isolated hosts would therefore lead to the development of narrow host ranges and speciation (see Askew 1968, Gibbons 1979).

Examination of the importance of spatial isolation of hosts in determining the degree of host specificity in hymenopteran parasitoids may help rationalize the observed host associations of these insects, as well as providing a better understanding of their evolution and systematics. The Family Scelionidae provides an ideal group on which to carry out such a study for several reasons: (1) they all parasitize the same stage of their hosts, viz. the eggs; (2) the taxonomy of the family is reasonably well known in Australia compared with other groups of parasitoids (see Appendix 1, Galloway 1980, Masner 1976, 1980); (3) protective adaptations by their hosts are usually in the form of physical barriers, rather than ones that may be more difficult to analyse, such as the behavioural or immune responses of some larval or adult hosts; (4) they are known to display a high degree of both group specificity (Table 6.1) and species specificity, thereby allowing both these phenomena to be examined.

This section documents the known host records of scelionids that parasitize the eggs of spiders to determine the host associations of this group. Adaptations in these parasitoids related to the methods they use to parasitize their hosts are described, along with differences in the structure of the eggsacs of spiders and the effectiveness of the latter in preventing or reducing parasitism. Finally, information from this work is used to assess the importance of spatial isolation as a factor contributing to host specificity in the Scelionidae, and it is hoped, provide a better understanding of the evolution of host specificity in this family.

6.2 MATERIALS AND METHODS

Host records for the species listed in Appendix 2 were compiled from 3 sources; (1) spiders and eggsacs collected in the field during the study; (2) museum specimens that had host data recorded; and (3) published information. Eggsacs of various spiders were collected in the field and brought back to the laboratory, to determine whether the eggs had been parasitized. If they were parasitized, the eggs were retained and parasitoids reared through to adults (see 4.2.1). Where possible the female spider that produced the eggsac was also collected, to facilitate accurate identification of the latter. Spiders that produce very characteristic eggsacs, e.g. *Argiope*, *Celaenia*, *Araneus* species, could be identified with reasonable certainty by their eggsacs alone. Cases where eggsacs could not be readily identified were excluded from the study.

The generic and family names used for spiders are those considered to be correct in the recent taxonomic literature (CSIRO 1980, Lehtinen 1967, also see Acknowledgements). Therefore some names listed in Appendix 2 are different from those quoted in original references, especially in older papers. Voucher specimens of spiders and eggsacs collected during the study have been deposited in the Department of Entomology insect collection (see 2.3.1).

To determine the method used by parasitoids to reach and oviposit into host eggs, representative species from several genera were released into separate containers, with eggsacs of the same host from which they had been reared. The behaviour of these parasitoids was then observed under a stereomicroscope. Eggsacs used for these observations were always less than 2 d old (held at 20°C) and were produced by female spiders kept in the laboratory. Eggsacs collected from the field were not

used as they could already have been parasitized.

Information on the structure and morphology of eggsacs of host spiders was compiled from material collected in the field, and from published descriptions. The thickness of the wall of various eggsacs was measured under a stereomicroscope after the former had been partly cut open with fine scissors or a razor-blade. The density of silk comprising the wall was estimated from the rigidity and resistance to tearing of the latter. Density estimates were assigned a value on a scale of 1 (least dense) to 5 (most dense).

6.3 OBSERVATIONS AND RESULTS

6.3.1 Host Relationships

The hosts of species in the genera *Aneurobaeus*, *Baeus*, *Mirobaeoides*, *Idris*, *Ceratobaeus*, *Hickmanella*, *Odontacolus*, *Mirobaeus* and *Echthrodesis* are recorded together for the first time (see Appendix 2). Host data for 51 species are presented, 23 being recorded as new. The majority of these records are from Australia (32), with only 19 coming from other zoogeographic regions. Unfortunately, the hosts of many species in the above genera are unknown. Of the 69 described species from Australia (see Appendix 1), only 21 have had their hosts recorded, while only 11 of the many undescribed species recognized by Austin (1981a) have their hosts known.

Examination of these records shows that scelionids display varying degrees of host specificity. Most species (78%) appear to parasitize one host, thus indicating a high level of monophagous specificity. It is possible that some of these species may attack alternative hosts, nevertheless intensive collecting of eggsacs at the Mylor study site should have revealed such relationships for the majority of species if they existed. Some workers (Hickman 1967b, Pierce 1942, this study - 4.3.8) have tested the potential host range of some species, and these studies confirm that the

latter display a high degree of host specificity.

Those scelionids (Appendix 2) that parasitize more than one host species and are therefore not monophagous, display some group specificity. Of the 7 species recorded as having 2 hosts, 5 attack species from the same host genus, while scelionids that parasitize 3 or more hosts show similar associations: *Idris flavicornis* has been reared from eggs belonging to 3 genera in the Family Lycosidae; *Idris saitidus* has been recorded from the Family Salticidae; while *Ceratobaeus masneri* parasitizes 3 species in the genus *Clubiona*, but also attacks one species in a different family, *Hemicloea* sp. (see 4.3.8). *Baeus semilunum* is the only scelionid known to attack hosts that are not closely related: this species has been recorded as parasitizing 4 hosts from 4 different families (Vachon 1955).

When the data in Appendix 2 is condensed and host families are compared with each scelionid genus (Table 6.2), a further level of group specificity is revealed. For example, most *Baeus* species are associated with 3 spider families, i.e. Araneidae, Linyphiidae and Theridiidae (15 out of 18 host records). *Hickmanella* has been recorded only from the Family Salticidae, and although only 2 host species are known, Austin (1981b) indicates that the genus may specialize on hosts from this family.

Although the majority of scelionids are specific to a single host, the eggs of some spiders are parasitized by more than one scelionid species. The eggs of *Stiphidium facetum* are parasitized by at least 2 species, *Mirobaeus pilosus* and *Ceratobaeus flavipes*, in the same habitat in Tasmania (Hickman 1967b). Other spiders are apparently attacked by different scelionids in different parts of their distribution. The eggs of *Breda jovialis* are parasitized by *Hickmanella intrudens* in Tasmania and Victoria, while an unknown species of *Idris* has been recorded from this spider in South Australia. Also, the eggs of *Ixeuticus* species are parasitized by *Idris ixeutici* in Tasmania, Victoria, South Australia and inland New South Wales, while *Ceratobaeus setosus* attack spiders in this genus along the

Scelionid Genus	Host Family	Number of Different Species in Each Family, Parasitized by the Scelionid Genera Listed	Ovipositional Strategy and Number of Species for which this Data is known (see 6.3.3)
Aneurobaeus	Araneidae	1	-
Baeus	Agelenidae	1	
	Araneidae	5	
	Dysderidae	1	
	Linyphiidae	3	inside 3
	Lycosidae	1	
	Theridiidae	7	
Mirobaeoides	Oxyopidae	1	both 1
Echthrodesis	Amaurobiidae	1	-
Mirobaeus	Amaurobiidae	1	-
Ceratobaeus	Amaurobiidae	2	
	Clubionidae	4	outside 6
	Gnaphosidae	3	both 2
	Salticidae	1	
Hickmanella	Salticidae	2	inside 2
Idris	Agelenidae	1	
	Amaurobiidae	1	
	Ctenizidae	1	
	Gnaphosidae	1 (?)	
	Linyphiidae	1 (?)	
	Lycosidae	4	outside 2
	Salticidae	3	inside 6
	Segestriidae	1	
	Tetragnathidae	1	
	Theridiidae	6	
	Thomisidae	1	
	Uloboridae	1	
Odontacolus	Clubionidae	1	outside 1

Table 6.2 Relationships between scelionid genera and host families. (N.B. species recorded from 2 host families are listed twice in the table.)

coasts of Queensland and New South Wales. Unfortunately there is insufficient evidence to indicate whether the parasitoids of *Stiphidium* compete with each other, nor is there enouth evidence to show whether the parasitoids of *Breda* and *Ixeuticus* overlap in their distributions. More detailed study of these spiders and their egg-parasitoids may reveal interesting ecological interactions.

6.3.2 Adaptations of Spiders to Protect their Eggs from Scelionid Parasitoids

This study has examined the importance of several possible adaptations of the spider *C. robusta* in relation to their effectiveness in reducing mortality by scelionids. The eggsac of this species and guarding behaviour by the female do not reduce mortality caused by *C. masneri;* but they do reduce that caused by general predators. Only the formation of eggs into a mass by this spider has been shown to reduce the effect of this scelionid (see 3.3.5 and 3.3.6), as the wasp's ovipositor is long enough to reach eggs only in the first 2 layers.

The proportion of eggs protected by the eggmass must depend on the ratio between the volume and the surface area of the mass, and therefore its shape, the number of eggs it contains and whether or not it is attached to a substratum. This may explain why spiders such as *Breda* and *Holoplatys*, that construct flattened eggmasses (i.e. high surface to volume ratio) containing few eggs (< 50), suffer rates of parasitism often in excess of 90% (observations at the Mylor study site), while other spiders that construct spherical or ovoid eggmasses containing many eggs (> 100), experience rates of parasitism usually well below 80% (e.g. *Clubiona robusta*, also see Kessler and Fokkinga 1973, Lubin 1974, Valerio 1971).

Type and Description of Eggsac	Spider		Thickness of Wall	Density of Wall	References
Type 1 - single layer; thick wall; low density flocculent silk; rarely with debris incorporated into silk wall; often constructed in exposed locations, e.g. attached to vegetation or in web	Araneidae	*Araneus*	7-15 mm	+/++	Livecchi *et al.* 1977 McCook 1890
	"	*Nephila*	10-15 mm	+	Austin and Anderson 1978 Christenson and Wenzel 1980 Robinson and Robinson 1976
	"	*Araeys*			
	"	*Cyclosa*	2 mm	+	Mascord 1970, 1980
	"	*Gasteracantha*			
	Theridiidae	*Achaearanea*	1-1.5 mm	+	-
	"	*Steatoda*	2-3 mm	+	Hickman 1967a
	"	*Theridium*	1-1.5 mm	+	Hickman 1967a; McCook 1890
	Linyphiidae	*Linyphia*	1 mm	+	Wise 1974
	"	*Micryphantes*	-	+ (?)	-
Type 2 - single layer; moderately thin wall; low density but not flocculent silk; eggsac often with debris incorporated into silk wall; usually constructed in sheltered location, sometimes in web or diffuse nest	Amaurobiidae	*Ixeuticus*	1 mm	++	Hickman 1967a
	"	*Stiphidium*	0.5 mm	++	Hickman 1967a
	Gnaphosidae	*Intruda*	1 mm	++	-
	"	*Lampona*	1 mm	++	Mascord 1970
	Many Lycosidae		0.5-1 mm	++	Bristowe 1958; Forster and Forster 1973
Type 3 - single layer; very thin wall; dense silk, reaching texture of fine paper; sometimes with debris incorporated into wall; constructed in various habitats, e.g. under bark or in a web	Clubionidae	*Supunna*	50 µm	+++	Mascord 1980
	Gnaphosidae	*Hemicloea*	0.1 mm	+++	Hickman 1967a
	Most Sparassidae		0.2 mm	+++/++++	Main 1976
	Uloboridae	*Uloborus*	50 µm	+++	Mascord 1970, 1980
	Thomisidae	*Tharpyna*	50 µm	+++	-
Type 4 - single layer; very thin wall; low density silk but not flocculent; usually constructed inside a nest or retreat	Most Clubionidae		50 µm	+/++	Hickman 1967a; this study 2.3
	Some Thomisidae		50 µm	++	-
Type 5 - single layer; thin wall; low density flocculent silk eggsac, incorporated into flocculent lining of nest	Nearly all Salticidae		50 µm	+/++	Austin 1981b; Hickman 1967a; Jackson 1979b
Type 6a - 2 layers; very thin dense outer layer; thick often flocculent silk inner layer; constructed in various locations, e.g. exposed habitats on vegetation, in web, under bark	Araneidae	*Celaenia*	3 mm	+++++	Hickman 1967a; Mascord 1970
	Dinopidae	*Dinopis*	1 mm	+++++	Hickman 1967a; Mascord 1970
	Dolomedidae	*Dolomedes*	1.5-2 mm	++/+++	Forster and Forster 1973
	Some Lycosidae		1 mm	+++	Forster and Forster 1973
Type 6b - as above, but with outer flocculent layer and thin dense inner layer	Theridiidae	*Argyrodes* (e.g. *A. colubrius*)	0.5-1 mm	++++	Mascord 1980
	"	*Euryopis*	0.5-1 mm	+++ (?)	-
	"	*Latrodectus*	2-2.5 mm	++/+++	Hickman 1967a; Main 1976
	Araneidae	*Cyrtophora*	2-3 mm	++++	Lubin 1974, 1980
Type 7a - 3 layers; thin, dense outer layer; spongy silk medial layer; parchment-like inner layer; usually constructed in exposed locations, e.g. in web, on vegetation	Araneidae	*Argiope*	1-2 mm	++++	Gertsch 1949
Type 7b - as above but loose silk outer layer; thin dense medial layer, flocculent silk inner layer	Oxyopidae	*Oxyopes*	1-2 mm	+++/++++	Hickman 1967a

Table 6.3 Summary of types of eggsacs produced by various genera and families of spiders. (Data for thickness and density of eggsac walls are examples only, i.e. species examined in this study: therefore these parameters may not be accurate for all species in a genus. Indices for density of silk are based on a scale of 1(+) to 5(+++++), 5 representing the most dense silk. Measurements were made on the most dense silk for eggsacs with 2 or more layers.)

The construction of eggsacs by spiders, however, still represents what is probably the most widely adopted adaptation within the group to protect their eggs (see 3.4). Eggsacs vary considerably in their structure and morphology, i.e. size, shape, colour, density and thickness of the wall, and number of layers comprising the wall. Scelionids possess morphological and behavioural specializations that are used to penetrate a wide variety of eggsac types (6.3.3), and therefore, a brief examination of the structure of the eggsacs of those species parasitized by scelionids may be useful in the following analysis.

The morphology of eggsacs has been described for many species by several authors (Bristowe 1958, Comstock 1940, Forster and Forster 1973, Hickman 1967a, McCook 1890, Main 1976). No studies pay attention to the thickness and density of the silk from which the wall of an eggsac is constructed, yet it is these characteristics that must determine the success of an eggsac in excluding parasitoids and predators. Eggsacs can be divided into several types (Table 6.3), based on the structure of the wall and whether or not it is constructed inside a nest. Although the summary of types presented in Table 6.3 was compiled from relatively few examples, it shows that there is some association between the structure of eggsacs and the family to which a species belongs. Type 1 eggsacs are mostly constructed by spiders in the Families Araneidae, Theridiidae and Linyphiidae; Type 4 are associated with Clubionidae and some Thomisidae; Type 5 are constructed by Salticidae; while Types 2, 3 and 6 are produced by a wide range of families. Also, the species listed in Table 6.3 do not provide a good indication of the relative proportion of species in a family that construct each type of eggsac, as the sample size is small and biased towards those species listed in Appendix 2.

6.3.3 Adaptations of Scelionids to Penetrate the Eggsacs of Their Hosts

Scelionids display a number of morphological and behavioural

adaptations that are related to the method they use to overcome the physical barrier (eggsac wall) that surrounds the eggs they parasitize. The most obvious adaptation present in this group of parasitoids is the possession of an elongated ovipositor. Species in the genera *Ceratobaeus* and *Odontacolus* have an elongated metasoma and an expanded metasomal horn (see 5.3.7) that form a recess for the internally retracted ovipositor. The ovipositor is therefore longer than the metasoma (not including the horn), and in some species it is almost as long as the body. Ovipositors vary in length between species in this group, from 0.7 mm (*C. flavipes*) to 2.0 mm (*C. rieki*).

Behavioural observations show that scelionids parasitize the eggs of their hosts in either of 2 ways; (1) by burrowing or chewing through the eggsac wall, or (2) by probing through the eggsac wall with their ovipositor. This behaviour has been abbreviated to the 'inside' and 'outside' ovipositional strategies, and are recorded for individual species in Appendix 2 and summarized for genera in Table 6.2. Combining the data further (Table 6.4) shows that the genera that possess an elongated metasoma, a metasomal horn and have an elongated ovipositor (i.e. *Ceratobaeus* and *Odontacolus* - Group 1), all oviposit from outside the wall of their host eggsac (n = 8). Two of these species sometimes enter the eggsac, but never by burrowing through the eggsac wall. They enter only through pre-existing holes that have resulted from damage or incomplete construction by the female spider (see 4.3.1).

Species in genera that do not possess a metasomal horn or elongated metasoma (i.e. *Baeus*, *Mirobaeoides*, *Hickmanella* and *Idris* - Group 2) and therefore have shorter ovipositors (0.2-0.5 mm) than species in Group 1, nearly all burrow through the eggsac wall and then oviposit into the eggs (11 out of 14 species); the 3 remaining species use either the

		Number of Species for which the Ovipositional Strategy is known (see 6.3.3)	
Group 1 -	Genera with metasomal horn		
	Ceratobaeus	6 outside	n = 8
	Odontacolus	2 both	
Group 2 -	Genera without metasomal horn		
	Baeus	11 inside	n = 14
	Mirobaeoides	2 outside	
	Hickmanella	1 both	
	Idris		
			n = 22

Table 6.4 Behaviour of scleionid genera in relation to the method they use to penetrate the eggsacs of their hosts. (N.B. outside = oviposit from outside the eggsac wall; inside = burrow through the eggsac wall and oviposit into eggs from inside the eggsac.)

'outside' strategies or both strategies. Species in Group 2 also possess morphological adaptations that complement this behaviour. Females of *Baeus* and *Mirobaeoides* have squat, rounded and wingless bodies that have a streamlined surface, while many species in *Idris* and *Hickmanella* also have a smooth surface and are dorsoventrally flattened (see Appendix 1). These characteristics have probably evolved to facilitate easier penetration of the eggsac wall, and may prevent individuals from becoming tangled in the silk matrix of the eggsac.

The above analysis of scelionid genera shows that behaviour related to the penetration of eggsacs, is closely correlated with particular morphological adaptations. Further study of these parasitoids may reveal other possible adaptations associated with their ovipositional behaviour. For example, the large range in lengths of ovipositors of *Ceratobaeus* species (see 5.3.7) and the variability in the morphology of their host eggsacs suggests that ovipositor length may be correlated with the thickness of the eggsac wall. Such hypotheses, however, must remain untested until further host records are collected, especially for species with very long ovipositors, such as *C. rieki*.

6.3.4 Eggsacs of Spiders as a Factor Contributing to Host Specificity in Scelionids

The eggsacs of spiders effectively isolate the eggs they contain by providing a physical barrier between them and the outside environment. However, the eggs of a large number of spiders are successfully attacked by various species; members of the family Scelionidae being most important in terms of the amount of mortality they cause (Eason *et al.* 1967; this study - 3.3.3 and 3.4). Nonetheless, some spiders produce structurally complex eggsacs that must be costly to produce in time and energy. This suggests indirectly that the production of eggsacs is of some selective

value to the survival of the eggs and juvenile spiders they contain. The eggsacs of some species take more than 12 h to construct, and females may produce more than one gram of silk per season, much of which is used for the construction of eggsacs (Forster and Forster 1973, Main 1976).

Comparison of information presented in sections 6.3.1, 6.3.2 and 6.3.3 shows that most species in the genera *Baeus* and *Mirobaeoides* parasitize hosts that belong to families that produce thick walled flocculent silk eggsacs (Type 1, Table 6.3) or complex multilayered eggsacs (Types 6 and 7). These eggsacs are constructed mainly by spiders in the Families Araneidae, Linyphiidae, Oxyopidae and Theridiidae, and thus the majority of host records for *Baeus* and *Mirobaeoides* comes from these families (16 out of 19 records - Table 6.2). The thickness and density of Types 1, 6 and 7 eggsacs make it impossible for small parasitoids to oviposit through the wall, and since nearly all scelionids are < 2.0 mm in length, the genera that attack such eggsacs must burrow through them. Winglessness and the rounded shape of females can then be recognized as adaptations to penetrate the eggsacs of spiders in these families.

Ceratobaeus and *Idris* attack hosts in a wide range of araneid families (Table 6.2), however, the latter construct eggsacs of a similar type, i.e. mostly thin walled eggsacs of variable density (Types 2, 3 and 4), although a few *Idris* species attack the eggsacs of theridiids (Type 1 eggsacs). Species in these genera have evolved different solutions to the problem of penetrating the eggsacs around their hosts. *Idris* has a smooth flattened body and burrows through the eggsac wall, while *Ceratobaeus* has an elongated ovipositor and oviposits from outside the eggsac. These 2 genera are also the most speciated of those that attack the eggs of spiders (Austin 1981a), as well as parasitizing hosts in the largest number of spider families.

Behavioural observations (see 4.3.1, 5.3.5) show that the full length of the ovipositor of *Ceratobaeus* species is extended to oviposit into host eggs, and that partial extention never occurs. It has been shown for some ichneumonid species (Gibbons 1979, Heathwole and Davis 1976) that they cannot parasitize hosts closer than the length of their ovipositor, i.e. they cannot penetrate part the way into the substratum around their host, but must use the whole length of the ovipositor. It is not known whether scelionid species with very long ovipositors can attack eggsacs with thin walls, but in view of the above observation this possibility seems unlikely (see also 4.3.1).

Examination of the behaviour, morphology and host relationships of scelionids has indicated that the level of group specificity displayed by them may be explained to a large degree by protection afforded by eggsacs. The genera *Baeus*, *Mirobaeoides*, *Ceratobaeus*, *Idris* and *Hickmanella* show strong associations with particular types of eggsacs, and therefore, also with the spider families that construct them, i.e. group specificity in these scelionids may not to be directly determined by the taxonomy of spiders, but rather by the structure of the eggsacs they produce. This hypothesis is supported by the fact that spider families that are not closely related, but construct similar eggsacs are all parasitized by the same genera of scelionids. For example, the eggs of many spiders in Araneidae, Linyphiidae and Theridiidae and protected by Type 1 eggsacs and are parasitized by *Baeus* and *Mirobaeoides*, although these families are not closely related (Lehtinen 1967).

However, there is no clear connection between the degree of specificity at the species level and the structure of eggsacs. Possibly the host ranges of different species are determined by other factors, such as competition between species, or nutritional and physiological requirements. Certainly the host range of some scelionids (e.g. *Ceratobaeus masneri*), that

attack hosts which construct different types of eggsacs, cannot be explained in terms of the structure of eggsacs. There is, however, insufficient data to exclude the latter as a factor in regard to other species.

Further collection of host records, as well as detailed studies on the biology and ecology of selected species, will be required if a more complete understanding of the factors affecting host specificity in scelionids, especially at the species level, is to be achieved.

6.4 DISCUSSION

The origin of the Family Scelionidae is not clearly understood. Kozlov (1970a) has proposed that it separated from the Diapriidae when an ancestor made the transition from ovipositing through the puparia of dipteran hosts, to ovipositing through the chorion of insect eggs. The eggs of Orthoptera, many of which are approximately the same size, shape and texture as fly puparia, were probably the first hosts of these parasitoids (see Masner 1976). Kozlov (1970a) also suggests that some Diapriidae became secondarily parasitic on insect eggs where the latter were morphologically poorly differentiated from fly puparia. Thus, adaptations to penetrate puparia is probably preadapted ancestors of the Scelionidae and some Diapriidae to oviposit successfully into insect eggs. Scelionids probably radiated quickly into this previously unexploited niche, adapting to different types of eggs that belonged to a wide variety of potential hosts, including the eggs of spiders.

Many groups of parasitoids show a great diversity in the morphology of the ovipositor and associated structures. Members of several scelionid genera, e.g. *Macroteleia*, *Harringtonia*, *Calliscelio*, *Holoteleia*, *Calotelea* and *Probaryconus* (Masner 1980), have an elongated metasoma and/or a dorsal

metasomal horn, similar to that in *Ceratobaeus* and *Odontacolus* (see 5.4). Also, some species of *Inostemma* (Diapriidae) have a dorsal horn (Askew 1971); *Cardiopria* and *Dissoxylabis* (Diapriidae) have a ventral horn extending to the hind coxae (pers. comm. I.D.Naumann) while some Pelecinidae (Askew 1971) and Torymidae (Riek 1970) have an extremely long metasoma. Such structures allow for an elongated ovipositor, and at the same time protect the fragile ovipositor valves (see 5.1).

The length of the ovipositor of some parasitoids has been successfuly correlated with the thickness of the protective barrier around hosts. Askew (1965) has shown that morphs of *Torymus* species with short and long ovipositors are associated with seasonal variations in the thickness of galls around their cynipid hosts. The length of the ovipositor of some ichneumonid species has been related to the depth of their sawfly hosts in tree trunks (Heathwole and Davis 1976, Price 1972). Flanders (1947) proposes that the length and sturdiness of the ovipositor of some *Trichogramma* species can explain their observed host ranges. They are apparently excluded from some potential hosts because the chorion of the latter is too hard, yet they successfully attack such eggs under artificial conditions when the chorion is chemically softened. Tanning or hardening of eggs probably represents an adaptation in many insects at least to restrict the period available for successful oviposition by parasitoids (Askew 1971, Clausen 1940, this study - 4.3.5 and 4.4). Parasitoids therefore display modifications of the ovipositor that in many cases can be directly associated with reaching and penetrating spatially isolated hosts. In conjunction with this, they also show behavioural and chemical specializations that allow them to find and recognize their hosts successfully.

Although the length of the ovipositor is an obvious adaptation to spatially isolated hosts, no previous studies have examined the latter as a factor in the evolution of host specificity of parasitoids. In the few cases where evolutionary trends have been studied (Askew 1971, Gordh 1975, Kozlov 1970a, Matthews 1974, Nagarkatti and Nagaraja 1977, Stary 1981), they are usually based only on a comparison between a group of parasitoids and their corresponding host records. However, when host records are used as an indication of the level of host specificity, the results may not be reliable. Askew (1971) believes that there are probably many inaccuracies in host records due to taxonomic problems with both hosts and parasitoids. He maintains that some parasitoids, which are presently considered to have broad host ranges, actually represent aggregates of oligophagous and monophagous sibling species. Matthews (1974) states that host data are simply not extensive enough, nor are the classification of hosts and parasitoids sufficiently well known, to permit evolutionary conclusions. Examination of host records and their use as a guide to the evolution of host specificity may also fail for more intrinsic reasons. Askew (1971) proposes that some species probably became secondarily polyphagous in their evolutionary history, through the development of favourable attributes that allowed a wider range of hosts to be exploited. He maintains that this process would have led to secondary radiation within higher taxa, subsequently masking original host relationships. In cases where host associations are often complex or confusing, a functional analysis of recognized adaptations related to host finding and oviposition, could help provide some understanding of how such relationships have developed.

All parasitoids that display a high level of host specificity also have been shown to display a correspondingly high degree of specialization (see Vinson 1976, Vinson and Iwantsch 1980). Askew (1971, 1975) states that endoparasitic Hymenoptera have narrower host ranges (i.e. many

monophagous or oligophagous species compared with ectoparasitoids, as adaptations in the former need to be more rigidly defined. Further, Askew maintains that once parasitism or more precisely parasitoidism (Vinson and Iwantsch 1980) is adopted as a life history strategy, some degree of host specificity is inevitable, because characters that increase the probability of survival on a particular host will be selected for, thus leading to specialization and competitively superior species. Jensen (1975) has generalized these ideas to some degree by stating that specialization is the outcome of adaptations for attacking well defended hosts (see 6.1), for since highly specialized parasitoids would be unable to attack hosts for which their specilizations were unsuited. The sophistication of adaptations displayed by parasitoids is only just being realized in many cases. This is exemplified in a series of recent studies (Edson *et al.* 1981, Stoltz *et al.* 1981, Vinson and Iwantsch 1980) which demonstrate that symbiotic viruses associated with the reproductive system of some parasitoids block the immune response of their lepidopteran hosts. Such work poses a number of questions on the role of symbionts in the development of host relationships of parasitoids.

This study has shown that spatial isolation of hosts has probably been a major factor contributing to the degree of group specificity observed in some scelionid parasitoids. In scelionids that attack the eggs of spiders, the specializations they display can be shown to be related to methods for overcoming the protective barriers around their hosts. Studies on other parasitoids also indicate a high degree of specialization to spatially isolated hosts. Detailed examination of these groups may show that spatial isolation has been of general importance in the evolution of host specificity in the parasitic hymenoptera.

CHAPTER 7

GENERAL DISCUSSION

This study has attempted to examine the natural history and population ecology of a common clubionid spider, *Clubiona robusta*, that is found under the bark of *Eucalyptus* trees in South Australia. Emphasis has been placed on the importance of its scelionid parasitoid *Ceratobaeus masneri*, as a source of mortality and a possible factor causing fluctuations in numbers of *C. robusta*.

Each section of this study has its own discussion section, where data are discussed and compared with the published literature. However, it would seem worthwhile to mention here several points that have not been considered previously in detail, and that may be of general interest to workers contemplating similar ecological studies on spiders. In conclusion, aspects of this project that show promise as subjects for future research work are discussed.

In recent years there has been more interest shown in spiders for their importance as predators in natural habitats and as biological control agents of insect pests. In regard to the latter, the data available strongly indicate that spiders cause significant mortality to several species, especially those associated with intensively cultivated crops (e.g. rice, soybeans, cotton, vegetables) and orchards (Bishop 1980, 1981, Dondale 1958, 1966, Hagen *et al.* 1976, Kiritani *et al.* 1972, Le Sar and Unzicker 1978, Mansour *et al.* 1980a, Turnbull 1973, Whitcomb 1967, Whitcomb *et al.* 1963). However, in none of these studies has any detailed assessment of the potential of spiders to control pest populations over even short periods, been attained. At least part of the reason for this situation seems clear. Although these studies have reported spiders as killing a significant proportion of some pest species at a particular time, they suffer from a lack of information on the

biology and ecology of the spiders involved, so that it is impossible to ascertain their impact under variable conditions of weather, pest density, crop management etc. It is thus possible that spiders are not as important as these studies would suggest, or alternatively, their value may have been under-estimated. This situation can only be improved if studies on the basic biology of spiders in agricultural habitats are carried out in parallel with the more general surveys, aimed at assessing the overall impact of these predators.

However, ecological research on spiders is fraught with several difficulties, as this and other studies have found. Several workers (Humphreys 1976, McQueen 1978, Robinson and Robinson 1973, Workman 1978, this study) have shown that it is extremely difficult to determine the causes of mortality for some stages of spiders. In this study it was possible to measure mortality with reasonable levels of accuracy and determine its probable causes for the early stages of the life history that develop inside the nest, and also the pentultimate and adult stages of *C. robusta*. These stages are stationary or move around in a limited space only, and so it was possible to develop appropriate sampling techniques that could be used to monitor their fate in the field. However, no methods could be found to assess the death rate during individual instars, between the dispersal stage and up to the pentultimate instar. Comparison between the number of third instar juveniles prior to their dispersal on the one hand and the number that reach the pentultimate stage on the other, was used to provide a rough estimate of mortality between these stages. It was found that 60-70% of all individuals disappear from the population during this time. The only clue to the causes of death and stage(s) at which it occurs, came from incidental observations. These observations indicate that most of this mortality occurs at the stage of dispersal, as a result of juveniles landing in unfavourable habitats. Death was presumed to occur from exposure, starvation or predation; but there is no direct evidence to show that these are the

real causes of mortality.

This unaccountable mortality appears to be indicative of many studies on invertebrates, especially those on animals that disperse widely or that enter habitats that are difficult to sample, or both. Such mortality has been referred to by various terms, e.g. 'winter kill', 'winter disappearance', 'winter mortality' and 'non-established mortality', and it has been documented for members of many groups, e.g. Coleoptera (Aeschlimann 1979), Lepidoptera (Johnson 1969, Morris 1963, Varley and Gradwell 1965, 1968, Watt 1963), Homoptera (Johnson 1969) and Araneae (Humphreys 1976, McQueen 1978, Turnbull 1973, Valerio 1977). The problem of studying mortality for specific instars makes it difficult to achieve a detailed understanding of the ecology of such species. For example, if changes in the rate of survival at one such stage is largely responsible for fluctuations in the number of adults, as is suspected for *C. robusta*, then it is very difficult to predict the effects of differential survival, because the factors that alter it cannot be studied.

The problem of studying juvenile spiders is further compounded by the fact that it is usually not possible to identify them to species. The established taxonomy of spiders is based on the adults. Species and many genera are distinguished on the structure of the genitalia, which develop only at the pentultimate stage. This situation created difficulties in this study, as it was not possible to separate reliably juveniles of *C. robusta* from those of other species of *Clubiona* that coexist in the same habitat. If one is sampling juvenile spiders in the field to estimate numbers in various stages, a quick and reliable method is needed to identify them. Methods for identification of juveniles have been developed for a few species, but these are unsuited to ecological work, as they require extensive measurements on each individual (see Randall 1978). The excessive handling time required to process even a small number of spiders renders such techniques inappropriate for quantitative field studies.

Identification of juvenile spiders in this study was partly resolved by using colour and body marking to separate species. Also 2 of the 4 species involved appeared to be rare, and so for the purpose of the study it was decided they could be ignored without affecting the accuracy of work conducted on the main species. However, the characters that were used to separate juveniles (colour and markings) were found to be variable and overlap with each other to some extent, so that the problem of identifying juveniles even of the main species was only partially solved.

It is also difficult to distinguish the instar to which juveniles belong for many species. This and other studies (Humphreys 1976, Jackson 1978b, McQueen 1978, Toft 1976, 1979, Valerio 1977, Workman 1978) have used size classes to differentiate instars with reasonable success, but this method does not work for all species because extensive overlap in sizes of instars has been reported for many species (Peck and Whitcomb 1970, Randall 1978, Whitcomb *et al.* 1966).

Thus, workers undertaking studies on the ecology of spiders can expect to spend significant periods unravelling the taxonomic and sampling problems associated with the species on which they choose to work. Turnbull (1973) has stated in relation to spiders:

> *"Consolidation of the scattered taxonomic literature and revisions of higher taxa are essential to ecological progress. Dependence of ecologists on sound taxonomy cannot be overemphasized."*

This situation can only be improved by sponsoring research into the taxonomy and systematics of this important group of invertebrates, as well as developing methods of sampling and following the dispersing juvenile stages.

This study has produced a number of potentially stimulating lines of research that are worthy of attention at some time in the future. Firstly, the role of male aggression in *C. robusta* needs to be examined in the field and the possibility of territoriality investigated, in relation

to the importance of these factors in the regulation of the number of males in populations. *C. robusta* is one of the few spiders that is known to have a biased sex ratio, and it is the only species studied where intraspecific aggression may lead to the death of many individuals. The role of such aggression in the ecology of the species, however, is unclear and thus requires further investigation.

Study of the scelionid parasitoid *C. masneri*, has revealed that it displays a keen ability in choosing host eggs that will allow for the successful development of its offspring. It can distinguish parasitized from unparasitized eggs, determine the age of hosts, and discriminate hosts from non-hosts. Such behaviour is not uncommon in the parasitic Hymenoptera (Vinson 1976) and yet there have been few attempts to examine how the wasps distinguish suitable hosts from those that are unsuitable for oviposition. A detailed examination of the mechanisms by which these parasitoids recognize the state of their hosts, especially in relation to the changes that are undergone by the latter after they have been parasitized and as they age, would provide a better understanding of the interactions between host and parasitoid, both at the ecological and physiological level.

Finally, comparison of the types of eggsacs in spiders and the adaptations in scelionids to penetrate them, has shown that spatial isolation of hosts can explain to some extent the degree of host specificity displayed by these parasitoids. Extension of this approach may be useful in explaining the host relationships of other groups of parasitic Hymenoptera, and thus provide a better understanding of the way such associations may have developed.

APPENDIX 1

THE TAXONOMY OF AUSTRALIAN SCELIONIDAE

THAT PARASITIZE THE EGGS OF SPIDERS

A1.1 INTRODUCTION

This section is not intended to represent a comprehensive revision of the taxonomy of the Scelionidae; rather, it is a brief review of the Australian genera that are known to parasitize the eggs of spiders. *Ceratobaeus* Ashmead is the most important genus in relation to this project. It is therefore treated in more detail, with specific emphasis on descriptions of new species, and rediscriptions of species involved in this study.

The taxonomy of some of the above genera, especially the Australian species, were in a muddle prior to this work. There has been no revision of them since the majority of Australian species were described by Dodd (1914) and Hickman (1967b). It was essential that the problems surrounding these species be solved, so as to prevent any taxonomic confusion that might otherwise have arisen in the biological sections of the project. It is especially important that species be well defined and easily recognized when investigating questions involving the host specificity of these and other parasitoids.

There are 7 genera of Scelionidae in Australia, that have spiders' eggs as their hosts, viz. *Baeus* Haliday, *Idris* Foerster, *Ceratobaeus*, *Odontacolus* Kieffer, *Hickmanella* Austin, *Mirobaeus* Dodd and *Mirobaeoides* Dodd; the last 3 being known only from Australia. The Australian species in these genera have recently been listed and corrected (Austin 1981a); and one new genus has been described, i.e. *Hickmanella* (Austin 1981b). Although published elsewhere, these papers are to be considered as part of this study (see Appendices 4 and 5).

The following information is predominantly new or substantially revised. To reduce repetition references are quoted only for those sections that have been adequately treated by previous authors. The suprageneric classification of Masner (1976) is followed here, i.e. the

Tribes Idrini and Baeini are considered to be part of the Subfamily Scelioninae, and not to represent a separate subfamily as proposed by previous authors (Kieffer 1926, Kozlov 1970a). Revision of the other genera within the Scelioninae has recently been completed by Masner (1976, 1980) and Galloway (1980).

A1.2 MATERIALS AND METHODS

Descriptions of genera and species were compiled using a number of sources. Whole-mounted specimens (glued on cards and pinned) were used to obtain information on colour and general body dimensions. Slide-mounted specimens were used for antennal and wing characteristics. Results from both these methods were compared with specimens viewed under the SEM. The latter method was particularly useful for determining sculpturing patterns and degree of pilosity. Where possible large series of specimens, of both sexes from different localities, were used to determine the degree of intraspecies variability.

Fresh specimens were killed and washed in 70% ethanol (5 min), transferred to 100% ethanol (2 min) and 100% ether (1 min), then placed on a clean glass slide to dry. Museum or dried specimens were softened in 10% ethanol (30 min), then treated as above. During evaporation of the ether, the wings, legs and body hairs spring apart, making these structures easier to see. This technique was found to produce superior specimens compared with material taken from water or alcohol and air dried. Specimens were then mounted on card points, using a minimum of water soluble glue, and viewed under an Olympus Zoom Stereomicroscope. Antennae and wings were fixed in 70% ethanol (1 h), transferred to 90%, 100% ethanol and xylene (10 min , 2 changes each), and mounted on slides using Canada Balsam or SIRA mountant. Specimens for the SEM were washed and dried as above, except that drying was prolonged in a desiccator (24 h), mounted

on specimen holders using electroconductive glue (DAG 915 Silver Paint) or double-sided adhesive tape, coated with 10 nm carbon and 30 nm gold-palladium, and viewed under an ETEC Autoscan SEM, operated at 5 - 20 keV. Some specimens, including all type material, were examined uncoated using the SEM in the Environmental Chamber Mode (Robinson, B.W. 1980).

Live specimens were obtained from the eggs of spiders collected from the field, and were reared out in the laboratory. Other methods used were yellow pan-traps and sweep-netting. Balasate samples borrowed from the Australian National Insect Collection (ANIC), were useful in determining which genera and species inhabit leaf litter. Borrowed material, used in conjunction with that collected during the course of the study, was obtained from the following institutions. The abbreviations are those used in the text: CSIRO, Canberra (ANIC); Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa (CNC); Collection of Dr Lars Huggert, University of Umeå, Sweden (HUG); Queensland Department of Primary Industries, Brisbane (QDPI); Queensland Museum, Brisbane (QM); South Australian Museum, Adelaide (SAM); Department of Entomology, Waite Agricultural Research Institute, Adelaide (WAITE).

Terminology. Most abbreviations and morphological terms used in the following keys and descriptions are defined in Masner (1980). Those that do not appear there are defined below.

A: antennal segment, e.g. A11 = eleventh antennal segment.

Approximated segments: antennal segments which are partly fused; not freely articulated.

Cilia: fine hairs covering the surface of the wings.

Clava: expanded distal segments of the female antennae.

Eyes: compound eyes.

Frontal carina: a narrow vertical ridge on the frons extending from the base of the antennae towards the median ocellus.

Funicle segments: antennal segments between pedicel and clava.

H: height, e.g. L:W:H - ratio of length : width : height.

Horn: metasomal horn - dorsal expansion of the first tergite.

L: length (see H).

Propodeal keel: flange projecting from the posterior propodeum. It is usually horizontal (parallel to the metanotum), sometimes indented medially, and extended laterally and medially into small teeth.

Propodeal laminae: modified keel where the flange is divided medially into two parts. The latter are vertical or oblique, and sometimes produced dorsally into small teeth.

Scutellum: mesoscutellum.

Scutum: mesoscutum.

Sessile: the condition where the metasoma appears to be completely fused onto the mesosoma. The surfaces of the metasoma and mesosoma are usually continuous.

Subsessile: the condition where the metasoma appears to be partly fused onto the mesosoma.

T1: the first tergite of the metasoma (or gaster).

W: width (see H).

A1.3 KEY TO AUSTRALIAN GENERA OF SCELIONIDAE THAT PARASITIZE THE EGGS OF SPIDERS

1. Apterous (wings reduced to tiny residual sclerites) 2

   Macropterous, sometimes brachypterous 4

2(1) Metasoma subsessile; T3 usually longer than T2, sometimes T3 and T2 subequal (Figure A12) ... *Mirobaeus* Dodd (♀)

   Metasoma sessile; T2 much longer than T3; T1 very narrow, sometimes hidden (Figures A13 and 16) 3

Figures A1-A6 Antennae.

Figure A1. ♀ *Baeus*, *Idris* and *Ceratobaeus*
Figure A2. ♂ *Baeus*, *Mirobaeus* and *Mirobaeoides*
Figure A3. ♀ *Mirobaeus* and *Mirobaeoides*
Figure A4. ♂ *Odontacolus*
Figure A5. ♀ *Odontacolus*
Figure A6. ♂ *Idris* and *Ceratobaeus*

Figures A7-A9 Anterior view of head.

Figure A7. *Idris*, *Ceratobaeus* and *Mirobaeus*
Figure A8. *Baeus*
Figure A9. *Odontacolus*

Figures A10 and A11 Forewings.

Figure A10. ♂ *Mirobaeoides*
Figure A11. ♂ *Baeus*

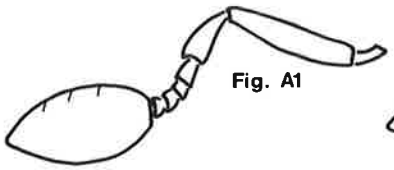


Fig. A1

Fig. A2

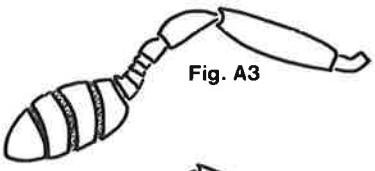


Fig. A3

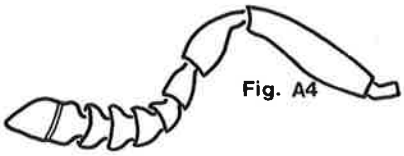


Fig. A4

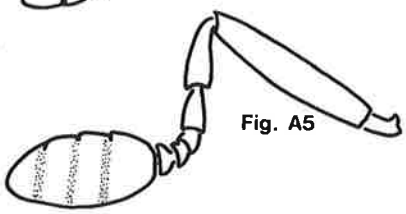


Fig. A5

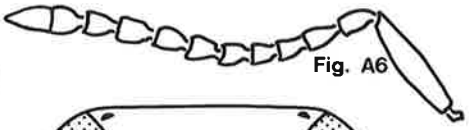


Fig. A6

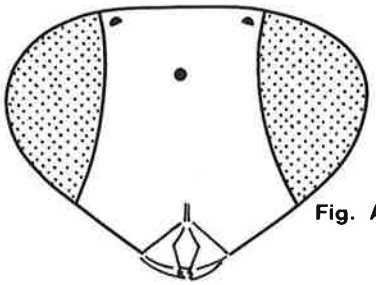


Fig. A7

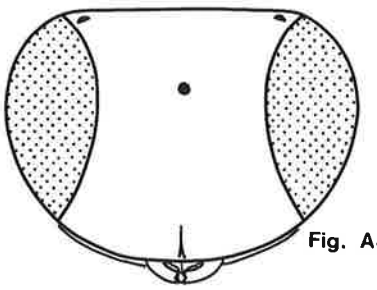


Fig. A8

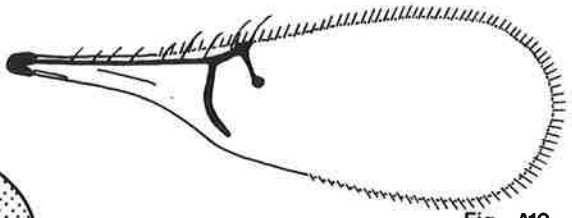


Fig. A10

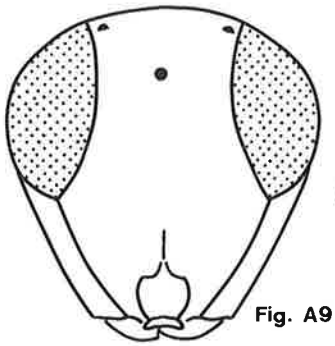


Fig. A9

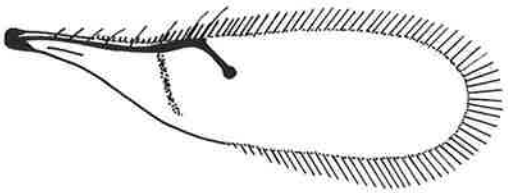


Fig. A11

3(2) Antennae 7-segmented, with 4 funicle segments and unsegmented clavae (Figure A1) ..... *Baeus* Haliday (♀)

Antennae 11-segmented, with 5 funicle segments and 4-segmented clavae (Figure A3) ..... *Mirobaeoides* Dodd (♀)

4(1) Metasoma with T2 distinctly longer than T3; if T2 and T3 subequal, then scutellum strongly arched dorsally 5

Metasoma with T3 distinctly longer than T2; if T3 and T2 subequal, then scutellum not strongly arched dorsally . 6

5(4) Forewings often narrow; basal vein if present never dark, usually faint or faded (Figure A11) .. *Baeus* Haliday (♂)

Forewings of normal width; with very dark distally curving basal vein (Figure A10) ..... *Mirobaeoides* Dodd (♂)

6(4) Head elongated in anterior aspect, long in buccal region (Figure A9); propodeum with 2 long posteriorly pointing spines (Figure A22) (♀ metasoma with large horn, which is compressed from sides) ..... *Odontacolus* Kieffer (♀ and ♂)

Head not elongated in anterior aspect (Figure A7); propodeum without long spines, though sometimes with small teeth (if ♀ metasoma with horn, then horn cylindrical (Figure A46); sometimes flattened apically) 7

7(6) Frons with expanded keel-like carina, reaching to median ocellus; distal venation of forewings blurred (see Appendix 5) ..... *Hickmanella* Austin (♀ and ♂)

Frons with only a small narrow carina at most, rarely reaching to median ocellus; distal venation of forewings clearly delineated 8

8(7) Propodeum, and sometimes metanotum and scutellum, at least flattened or indented, often excavated to form posterior cavity (Figures A41 and 46); propodeal keel divided into 2 diverging or almost vertical laminae, rarely produced

Figure A12 SEM of the whole body of *Mirobaeus* sp., ♀ (dorsal view) (backscattered electron image).

Figures A13-A15 SEM of *Baeus* sp.

Figure A13. ♀, dorsolateral view of whole body.

Figure A14. ♀, lateral view of mesosoma.

Figure A15. ♂, lateral view of whole body, wings removed.

Figures A16 and A17 SEM of *Mirobaeoides* sp.

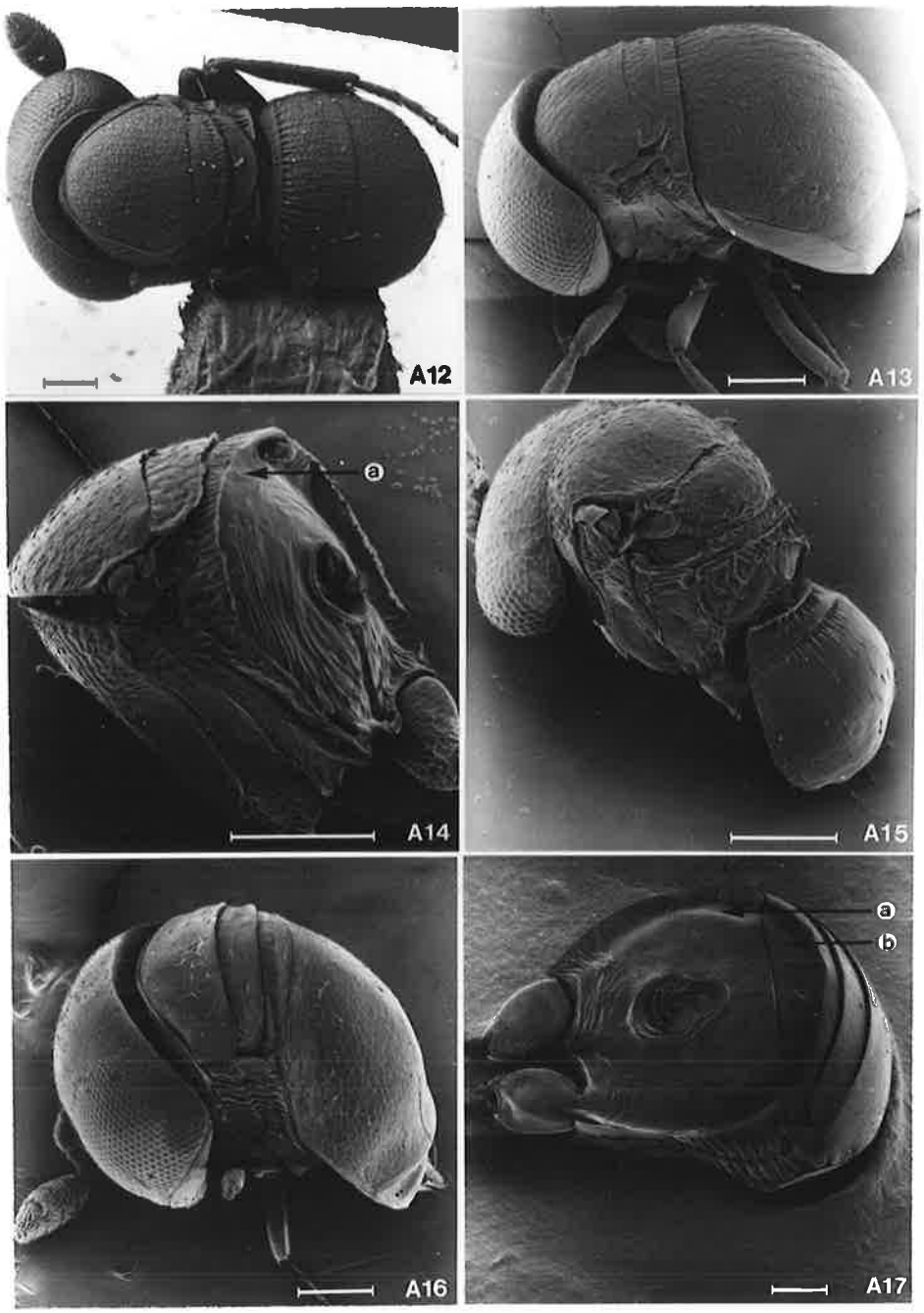
Figure A16. ♀, lateral view of whole body.

Figure A17. ♀, prosteriolateral view of mesosoma.

a) propodeum

b) metanotum

(Figures A12-A17, Scale = 100 µm.)


A12
A13
a
A14
A15
A16
a
b
A17

dorsally into small teeth (♀ with T1 expended into a dorsal hump or cylindrical horn; ♂ with T1 inflected dorsally along anterior margin) .. *Ceratobaeus* Ashmead (♀ and ♂)

Propodeum never flattened, indented or excavated posteriorly (Figure A19); propodeal keel continuous, usually parallel to metanotum; T1 always flat, rarely inflected anteriorly 9

9(8) Antennae 7-segmented, with large unsegmented apical clavae (Figures A1 and 20) ..... *Idris* Foerster (♀)

Antennae 10 to 12-segmented, without clavae 10

10(9) Antennae usually 11 or 12-segmented, rarely 10-segmented; f11 and f12 nearly always approximated (Figure A6) .... *Idris* Foerster (♂)

Antennae 12-segmented; f11 and f12 not approximated but freely articulated (Figure A2) ..... *Mirobaeus* Dodd (♂)

A1.4 REVIEW OF GENERA

The following review of genera was compiled from information obtained when examining over 2,000 Australian specimens, including all holotypes and many undescribed species. Important diagnostic characters and other useful information are presented for each genus. The characters for *Mirobaeus*, *Baeus* and *Mirobaeoides* are listed separately for males and females, as these genera are extremely sexually dimorphic. In all cases, characteristics are listed for males only where they differ from females.

Tribe Embidobiini Kozlov

(Kozlov 1970a, Masner 1976, Masner and Dessart 1972).

In Australia this tribe is represented by 2 genera, *Embidobia* Ashmead and *Mirobaeus* Dodd. Species of *Embidobia* are parasitoids on the eggs of various embiids, and are therefore not treated here (see Kieffer (1926) and Masner (1964, 1976) for discussion of this genus).

Figure A18 SEM of the mesosoma and metasoma of *Mirobaeoides* sp. ♂ (dorsal view).

Figures A19 and A20 SEM of *Idris* sp.

Figure A19. ♀, dorsal view of whole body.

Figure A20. ♀, lateral view of posterior mesosoma and T1.

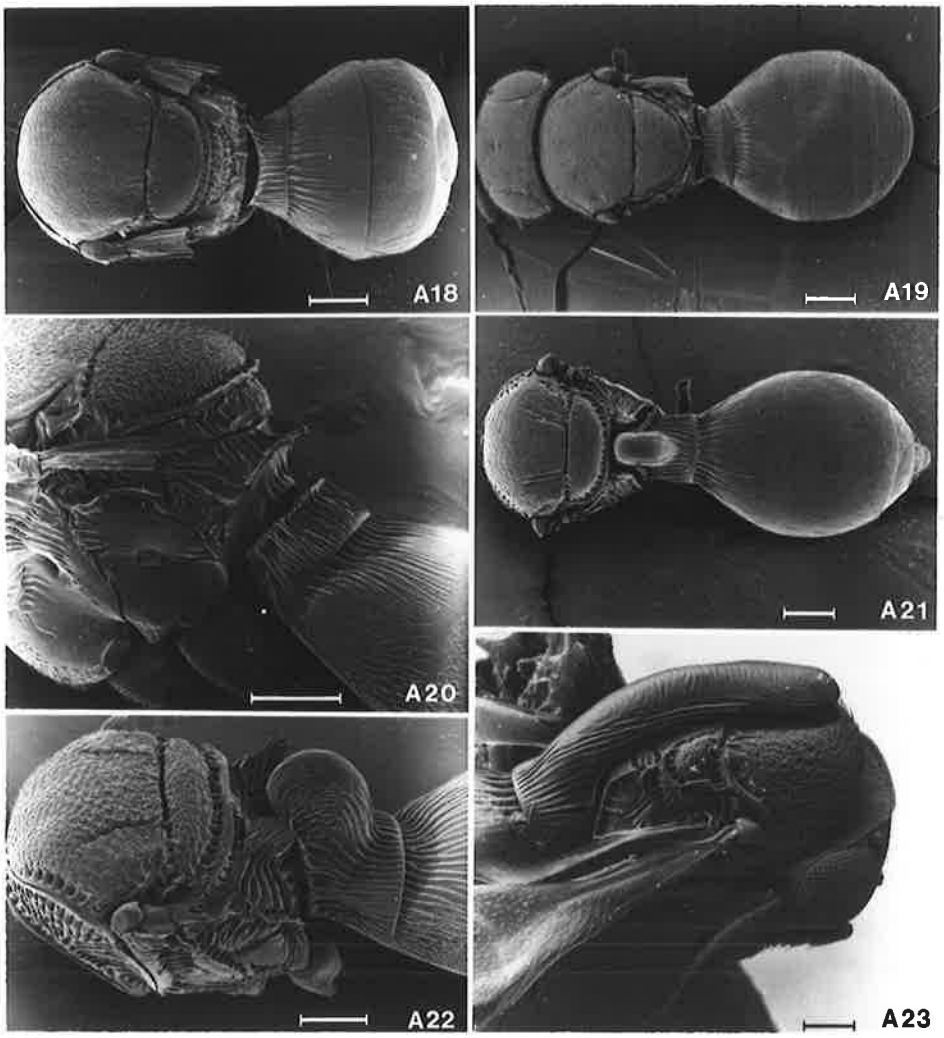
Figures A21 and A22 SEM of *Odontacolus* sp.

Figure A21. ♀, dorsal view of mesosoma and metasoma.

Figure A22. ♀, dorsolateral view of mesosoma and T1.

Figure A23 SEM of *Ceratobaeus mirobilis* Dodd (♀) showing the extremely elongated horn (T1) in this species (backscattered electron image).

(Figures A18 - A23, Scale = 100 μm; wings removed from specimens in Figures A18 - A22.)


A18
A19
A20
A21
A22
A23

A1.4.1 Genus *Mirobaeus* Dodd

Mirobaeus Dodd 1914: 73.

Type-species. *Mirobaeus bicolor* Dodd.

Distribution. Known only from south-eastern Australia, including Tasmania.

Discussion. Dodd's description of this genus was based only on a single female specimen. The male was not recorded until 1967, when Hickman described a new species from Tasmania. He was also able to show that this species parasitizes the eggs of spiders, thereby providing the first host record for the genus (Hickman 1967b). Males of *Mirobaeus* are very similar to those of *Idris*, but they can be separated on antennal segmentation and wing venation. No males have been recorded since the work of Hickman. There are 2 described species in this genus. Dodd's original description of *Mirobaeus* is adequate, but some additional useful characters are listed here and a generic diagnosis for males is provided for the first time.

Generic Description.

♀: head anteriorly, ovoid or subtriangular in shape (Figure A7); frons sometimes slightly depressed; frontal carina usually absent; palpal formula 2-1; antennae 11-segmented, with 5 funicle segments and 4-segmented clavae (Figure A3); notauli absent; scutellum usually much wider than long (expanded posteriorly over metanotum and anterior T1 in one undescribed species); metanotum narrow and horizontal; propodeum unarmed, vertical, usually only seen at posterior lateral corners of mesosoma; apterous; metasoma subsessile, convex dorsally; T1 often transverse; T3 usually the largest tergite (Figure A12), sometimes T3 and T2 subequal.

♂: antennae 12-segmented, A11 and A12 not approximated (Figure A2); scutellum semicircular, not strongly arched dorsally; metanotum narrow and vertical; propodeum visible throughout; propodeal keel parallel to metanotum, angled at corners; wings fully developed; venation not reaching to middle of wing foremargin; metasoma free (not

subsessile) and flattened.

Tribe Baeini Ashmead

(Ashmead 1893, Kozlov 1970a, Masner 1976).

In Australia this tribe is represented by 2 genera, *Baeus* Haliday and *Mirobaeoides* Dodd.

A1.4.2 Genus *Baeus* Haliday

Baeus Haliday 1833: 270.

Hyperbaeus Foerster 1856: 144; Synonymy: Muesebeck 1979: 1160.

Psilobaeus Kieffer 1926: 132; Synonymy: Masner 1965: 67.

Type-species. *Baeus seminulum* Haliday.

Distribution. Recorded throughout Australia and from all other zoogeographical regions (Kieffer 1926, pers. comm. L. Masner, this study).

Discussion. *Baeus* has 2 unique features compared with other scelionids. It is the only genus where the presence or absence of the metanotum and the arrangement of the laterotergites varies between the sexes. In Australia there are 3 described species in this genus. The following brief description of this genus will separate it from all closely related genera.

Generic Description (based on Australian species).

♀: body compact, convex dorsally (Figure A13); frontal carina small; eyes large, continuous with surface of head (Figure A8); occipital carina sharp; palpal formula 1-1; antennae 7-segmented, clavae unsegmented (though sometimes with 3 faint incomplete sutures) (Figure A1); notauli and metanotum absent (Figure A14); scutellum transverse; propodeum narrow and horizontal; apterous; metasoma sessile; T1 hidden by propodeum; T2 the largest tergite; laterotergites excised.

♂: body not convex (Figure A15); eyes slightly bulging from head; antennae 12-segmented. A11 and A12 sometimes approximated (Figure A2); notauli sometimes weakly indicated; scutellum rounded posteriorly, arched

dorsally; metanotum present; propodeum with narrow keel; wings fully developed, forewing with margins near parallel, venation not reaching middle of wing foremargin (Figure A11); metasoma free (not sessile), small and rounded; T1 narrow but visible throughout; laterotergites incised.

A1.4.3 Genus *Mirobaeoides* Dodd

Mirobaeoides Dodd 1914: 74.

Notoscelio Hickman 1967b: 35; Synonymy: Austin 1981a: 90.

Type-species. *Mirobaeoides tasmanicus* Dodd.

Distribution. Known only from eastern Australia, including Tasmania.

Discussion. Dodd misinterpreted several characters when he described this genus. Later authors (Hickman 1967b, Masner 1968, 1976, Masner and Dessart 1972) accepted Dodd's description without examining the type, and this led to the genus being misplaced and described under a separate name (*Notoscelio* Hickman). The problems surrounding *Mirobaeoides* were not solved until the type species was recently re-examined (Austin 1981a). Dodd's description of *Mirobaeoides* was very brief and was only based on the female. Hickman (1967b) recorded males for the first time and provided the first host record. There are 2 described species in the genus. *Mirobaeoides* is redefined and a generic diagnosis is provided for males for the first time.

Generic description.

♀: small frontal carina sometimes present; palpal formula 2-1; eyes continuous with surface of head; occipital carina sharp; antennae 11-segmented, with 5 funicle segments and 4-segmented clavae (Figure A3); notauli absent; scutellum and metanotum narrow, visible dorsally (Figure A17)(scutellum expanded posteriorly over metanotum and anterior T1 in one undescribed species); propodeum only seen laterally; apterous; metasoma sessile; T1 narrow; T2 occupying most of dorsal

surface of metasoma (Figure A16); laterotergites incised.

♂: eyes slightly bulging from head; antennae 12-segmented with A11 and A12 never approximated (Figure A2); notauli prominent; scutellum rounded posteriorly, arched dorsally; propodeum visible dorsally, with narrow curved keel; wings fully developed, forewing ventation not reaching to middle of wing foremargin (Figure A10); basal vein very strong, curved distally; metasoma free (not sessile), small and rounded (Figure A18); T2 usually the largest tergite, sometimes T2 and T3 subequal.

Tribe Idrini Kozlov

(Kozlov 1970a, Masner 1976).

In Australia this tribe is represented by 4 genera; *Idris* Foerster, *Ceratobaeus* Ashmead, *Hickmanella* Austin and *Odontacolus* Kieffer.

A1.4.4 Genus *Idris* Foerster

Idris Foerster 1856: 102, 105.

Acoloides Howard 1890: 269; Synonymy: Masner 1961: 163.

Acolus auctorum nec Foerster; Synonymy: Masner 1961: 163.

Dissacolus Kieffer 1926: 155; Synonymy: Austin 1981a: 85.

Megacolus Priesner 1951: 151; Synonymy: Masner 1961: 163.

Philoplanes Muesebeck and Walkley 1956: 384; Synonymy: Masner 1961: 163.

Pseudobaeus Perkins 1910: 620; Synonymy: Huggert 1979: 7.

Tasmanacolus Hickman 1967b: 30; Synonymy: Masner 1976: 64.

Tasmanibaeus Hickman 1967b: 27; Synonymy: Masner 1976: 64.

Type-species. *Idris flavicornis* Foerster.

Distribution. Recorded throughout Australia and from all other zoogeographical regions (Masner 1976, this study).

Discussion. This genus is relatively well defined (Huggert 1979, Masner 1961, 1964, 1976). It is most closely related to *Ceratobaeus* Ashmead; the latter mainly differing in having T1 developed as a horn

and the propodeum modified to form a recess for this structure. Males of these 2 genera are almost identical, but can be identified on minor differences in the shape of T1 and the propodeum. *Idris* is also similar to *Gryon* Haliday and *Hickmanella*, but differs from these in antennal segmentation, wing venation and arrangement of the metasomal tergites (*Gryon* only). There are 27 described species from Australia in this genus and a large number of undescribed species are known from various collections. The following characters are useful in the diagnosis of this genus.

Generic description (based on Australian species). Frontal carina usually present but small; ♀ antennae 7-segmented, with 4 funicle segments and large unsegmented clavae (Figure A1) (though sometimes with 3 faint incomplete sutures); ♂ antennae 11 or 12-segmented, rarely 10-segmented, last 2 segments approximated (Figure A6); notauli rarely developed; scutellum nearly always rounded posteriorly; propodeum never excavated, keel usually parallel to metanotum, nearly always with lateral and medial teeth; macropterous, rarely brachypterous (♀ only), ventation clear; metasoma usually rounded often constricted anteriorly (Figure A19); T1 flat never expanded dorsally into a hump (Figure A20); T3 the largest tergite.

Genus *Ceratobaeus* Ashmead - treated in detail in section A1.5.

A1.4.5 Genus *Hickmanella* Austin

Hickmanella Austin 1981b: 303.

Type-species. *Hickmanella intrudens* (Hickman).

Distribution. Known only from southeastern Australia, including Tasmania.

Discussion. See Austin (1981b - Appendix 5).

A1.4.6 Genus *Odontacolus* Kieffer

Odontacolus Kieffer 1910: 294.

Ceratobaeoides Dodd 1913: 337; Synonymy: Austin 1981a: 88.

Type-species. *Odontacolus longiceps* Kieffer.

Distribution. Recorded throughout Australia and from the Ethiopian, Neotropical and Oriental regions (Masner 1976, this study).

Discussion. Dodd misinterpreted the Australian species of *Odontacolus* and placed them in *Ceratobaeoides* Dodd. Both Kieffer (1926) and Masner (1976) maintained the latter as a valid genus, as neither worker had examined the type. Dodd, Girault and Hickman confused the matter further by describing a number of species under *Odontacolus* which belonged in *Ceratobaeus* Ashmead. Austin (1981a) was able to clear up the confusion surrounding these genera by synonymizing *Ceratobaeoides* with *Odontacolus* and transferring several species to *Ceratobaeus*. The generic limits of *Odontacolus* are well defined (Masner 1976). It obviously has several characters in common with *Ceratobaeus* but differs substantially in the shape of the head and mesosoma. In Australia *Odontocolus* appears to be predominantly tropical in distribution, with the majority of specimens being collected in north Queensland. There are 3 described species from Australia.

Generic description (based on Australian species). Head elongated in anterior view, long in buccal region, strongly conical towards mandibles (Figure A9); frons flat and shiny, frontal carina small; gena considerably prolonged; occiput well exposed; occipital carina high on head, rounded at corners; ♀ antennae 10-segmented, with 4 funicle segments and 4-segmented clavae (Figure A5); ♂ antennae 8 or 9-segmented, subclavate (Figure A4); notauli often developed; dorsally scutellum rounded or flattened posteriorly, rarely indented; propodeum flattened or slightly excavated, with 2 long posteriorly pointing spines flanking horn (Figure

A22); wings fully developed, venation clear; metasoma wider than mesosoma, constricted anteriorly, rounded posteriorly; expanded into a horn which is compressed laterally; ♂ without horn, but anterior T1 inflected dorsally; T3 the largest metasomal tergite (Figure A21).

A1.5 GENUS *CERATOBAEUS* ASHMEAD

Ceratobaeus Ashmead 1893: 167, 175.

Type-species. *Ceratobaeus cornutus* Ashmead.

Distribution. Recorded throughout Australia and from all other zoogeographical regions (Masner 1976, this study).

Discussion. *Ceratobaeus* is one of the largest scelionid genera, with 29 species known from Australia, including those described as new in this study. *Odontacolus* and *Ceratobaeus* are the only genera in the Idrini where T1 is expanded into a horn. However, the horn is obviously compressed from the sides (not cylindrical) in the former. These genera also differ in antennal segmentation, shape of the head and metasoma, and spination of the propodeum (see Masner (1976) for key and diagnoses). *Ceratobaeus* is also similar to *Idris*, especially males (see discussion under *Idris*). Huggert (1979) proposed that *Ceratobaeus* should be included under *Idris* as a subgenus, but this has since been rejected on the grounds that there are true morphological and biological differences between these genera (Austin 1981a).

Characters found to be important in the diagnosis of species of *Ceratobaeus* include the shape of the antenna, mesosoma and metasoma; body sculpturing and colour; the venation, shape and cilia of the forewing.

The length of the horn in females varies substantially between species. In some the horn is represented as a small hump, while in others it reaches past the scutellum (see Chapters 5 and 6 for discussion on the function of this structure). In association with this structure, the

posterior mesosoma is excavated so that the horn can fit against it. Species with long horns have greater modification to the mesosoma. Males do not have T1 developed into a horn, but rather have a slight dorsal inflection of this tergite. The posterior mesosoma shows some excavation, but never to the degree displayed in females. However, this excavation is always more pronounced in males of species where the female has a long horn (e.g. *C. cuspicornutus* sp.nov.), as compared with species in which the female has only a hump (e.g. *C. clubionus* sp.nov.).

Colour is a useful character and can be used to distinguish species that have prominent markings (i.e. *C. maculatus* Dodd, *C. fasciatus* Dodd and *C. laeviventris* (Dodd)), or light coloured species from dark species. Examination of long series of specimens indicates that colour variation within species is only slight. At most it varies by one or 2 shades, never in gross colour or patterning.

There are 2 species in which the female is brachypterous (*C. leai* Dodd and *C. flavipes* (Hickman)). Although Huggert (1979) has shown that some European species of *Idris* are polymorphic for wing size no such variation is known for Australian *Idris* or any species of *Ceratobaeus*.

Generic Description (based on Australian species). Head usually sub-triangular in shape, not long in buccal region (Figure A7); frontal carina usually present but small; ♀ antennae 7-segmented, with 4 funicle segments and large unsegmented clavae (Figure A1) (though sometimes with 3 faint incomplete sutures); ♂ antennae 12-segmented, A11 and A12 usually approximated (Figure A6); notauli rarely developed; posterior mesosoma in ♀ excavated or indented to form a cavity for reception of metasomal horn (Figure A46); cavity sometimes present in ♂, but less pronounced; propodeum with 2 lateral, near vertical or diverging laminae, sometimes produced dorsally into small teeth; macropterous, rarely brachypterous

(♀ only), venation clear; metasoma elongated in ♀, less so in ♂; T1 expanded into a hump or cylindrical horn in ♀; ♂ without hump or horn, but anterior T1 inflected dorsally; T3 the largest tergite.

The key to species presented here is for females only. It is not yet possible to compile a key to males as only 8 are known for the 29 recorded species. In the following section, 6 species are described as new and 2 are redescribed. The male of *C. setosus* Dodd is recorded for the first time. This species and *C. lamponae* (Hickman) are redescribed as their original descriptions will not reliably distinguish them from other species.

A1.6 PROVISIONAL KEY TO FEMALES OF THE KNOWN AUSTRALIAN SPECIES OF *CERATOBAEUS* ASHMEAD

1. Dorsal scutellum strongly indented or very narrow (Figure A46) .. 2
   Dorsal scutellum never indented, always round or square posteriorly (Figure A56) 15

2(1). Scutum with medial furrow for reception of horn; horn almost reaching to pronotum (Figure A23) 3
   Scutum without furrow; horn not reaching past scutellum, sometimes represented by no more than a hump 4

3(2). Length of metasoma (excluding T1) more than 2x its width; dorsally, dark brown to black ..... *C. elongatus* Dodd
   Length of metasoma (excluding T1) less than 2x its width; dorsal head, mesosoma and horn black, metasoma brown ..... *C. mirabilis* Dodd

4(2). Length of metasoma (excluding T1) more than 2x its width 5
   Length of metasoma (excluding T1) less than 2x its width 8

5(4). Metasoma extremely elongated, more than 4x longer than wide, narrower than mesosoma (Figure A68); (body dark brown to black) ..... *C. rieki* sp.nov.

Figures A24 and A25 Antennae.

Figure A24. ♀, *Ceratobaeus grandis* Dodd.
Figure A25. ♀, *Ceratobaeus leai* Dodd.

Figures A26, A27 and A29 Forewing venation.

Figure A26. ♀, *Ceratobaeus laeviventris* (Dodd).
Figure A27. ♀, *Ceratobaeus longicornutus* Dodd.
Figure A29. ♀, *Ceratobaeus flavios* (Dodd) and *Ceratobaeus flavicorpus* Dodd.

Figure A28 Forewing of *Ceratobaeus fasciatus* Dodd, ♀.

Figures A30 and A31 Dorsal surface of metasomas showing the pattern of dark markings.

Figure A30. ♀, *Ceratobaeus maculatus* Dodd.
Figure A31. ♀, *Ceratobaeus fasciativentris* Dodd.

(Figures A24, A25, A28, A30 and A31, Scale = 100 µm.)

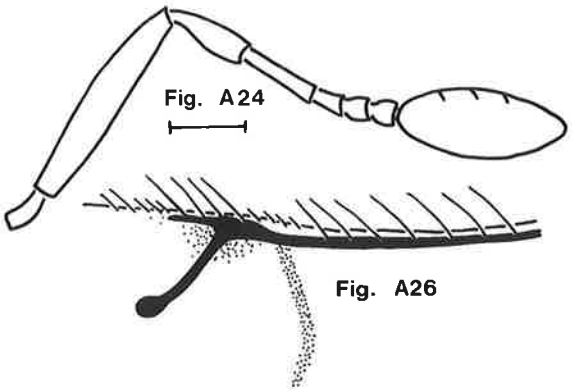


Fig. A24

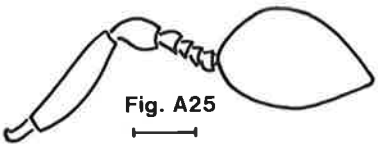


Fig. A25

Fig. A26

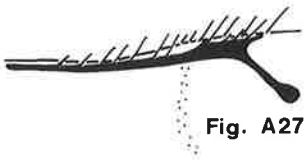


Fig. A27

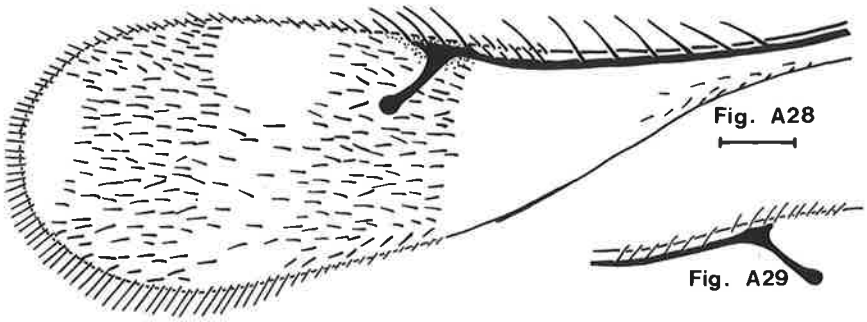


Fig. A28

Fig. A29

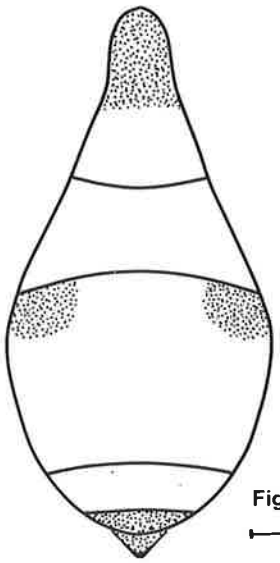


Fig. A30

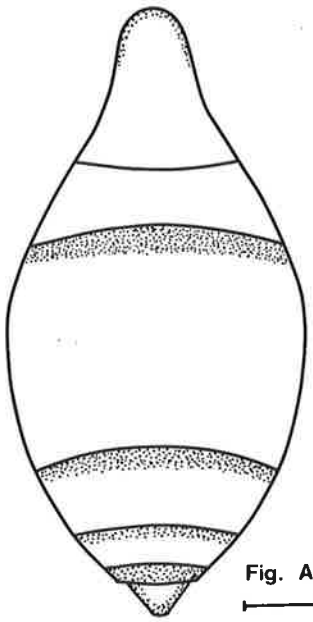


Fig. A31

Metasoma only moderately elongated, 2.5x longer than wide, wider than mesosoma 6

6(5). Dorsally, apical horn flattened and disc-shaped, wider than medial section of horn (Figure A60) ..... *C. platycornutus* sp.nov.

Dorsally, horn gradually tapering to the end, apically rounded or pointed, not flattened 7

7(6). Basal vein present, moderately dark (Figure A38); antennal pedicel L:W (10:4.1) (Figure A32); head, mesosoma and horn black, metasoma dark brown ... *C. cuspicornutus* sp.nov.

Basal vein almost absent, represented by a very faint impression (Figure A27); antennal pedicel L:W (10:4.4); dorsal head, mesosoma and distal 1/3 of horn brown, rest of body yellow ..... *C. longicornutus* Dodd

8(4). Antennal segments, especially A3, greatly elongated; A3 more than 3x longer than wide (Figure A24) 9

Antennal segments not elongated; A3 less than 2x longer than wide 10

9(8). Dorsal head, mesosoma and horn dark brown to black, metasoma light brown ..... *C. varicornis* Dodd

Dorsal head and mesosoma light brown, apical horn black, rest of horn and metasoma yellow .. *C. grandis* Dodd

10(8). Distal 1/2 of forewing with very coarse cilia (Figure A28); metasoma yellow with 2 transverse black bands (horn black, dorsal mesosoma with dark patches) .. *C. fasciatus* Dodd

Forewing uniformly covered with fine cilia; metasoma without black bands; horn and dorsal mesosoma sometimes dark in colour 11

11(10) Brachypterous, forewings not reaching past T1; antennal clavae large and bulbous (Figure A25); (body brown to dark brown) ..... *C. leai* Dodd

Wings fully developed, reaching to posterior metasoma; clavae not bulbous, usually long and pointed 12

12(11). Forewings without marginal fringe of hairs; (body dark brown to black) ..... *C. girault*i Dodd

Forewings with marginal fringe of hairs 13

13(12). Body golden yellow, horn black (basal vein present but faint) ..... *C. flaviventris* Dodd

Body uniformly black or very dark brown 14

14(13). Postmarginal vein absent ..... *C. turneri* (Dodd)

Postmarginal vein long, almost as long as stigmal vein ..... *C. faunas* (Girault)

15(1). Horn long but not curved anteriorly, reaching to level of dorsal scutellum 16

Horn very short, not reaching to level of scutellum 24

16(15). Basal vein very dark, equal to other veins (Figure A69); body covered with dense pilosity (Figures A64 and 65); propodeal laminae with 2 tapering sharply pointed spines; (body black) ..... *C. setosus* Dodd

Basal vein sometimes present, always faint; rarely covered with dense pilosity; spines on propodeal laminae never very sharp, usually rounded or blunt 17

17(16). Dorsal metasoma with 2 black patches laterally and black posterior tip (Figure A30); (horn black, body yellow).. ..... *C. maculatus* Dodd

Metasoma usually uniform in colour, sometimes with dark transverse bands or dark horn, but never with lateral patches 18

18(17). Postmarginal vein at least as long as stigmal vein 19

Postmarginal vein never more than 1/2 length of stigmal vein, usually very short or absent 21

19(18). Apical horn with circular striae (Figure A53 and 54); metasoma moderately elongated (Figure A48), L:W excluding T1 (9:5); (head, mesosoma and horn dark brown to black, metasoma dark brown with a yellow band behind horn, central region of T3 light brown) ..... *C. intrudae* sp.nov.

Apical horn without circular striae, but with punctate sculpturing, metasoma broad, L:W excluding T1 (9:7.5) 20

20(19). Mesosoma and horn lightly punctate; head and mesosoma dark brown to black, metasoma golden yellow, apical horn dark brown ..... *C. australicus* (Dodd)

Mesosoma and horn coarsely punctate (Figures A55 and 56); head, mesosoma and horn black, metasoma dark brown to black ..... *C. lamponae* (Hickman)

21(18). Dorsal mesosoma coarsely punctate; postmarginal vein equal to 1/2 length of stigmal vein (Figure A26); (head, mesosoma and horn dark brown to black, metasoma yellow) .... *C. laeviventris* (Dodd)

Dorsal mesosoma only lightly punctate; postmarginal vein very short or absent (Figure A29) 22

22(21). Dorsoposterior scutellum with small triangular hood projecting over horn; basal vein present but light, body dark brown to black ..... *C. ater* (Hickman)

Scutellum without triangular hood; basal vein absent; body yellow 23

23(22). Metasoma wider than mesosoma; with dark transverse bands at joints of metasomal segments (Figure A31); antennae dark brown, much darker than head ..... *C. fasciativentris* Dodd

Metasoma narrower than mesosoma, uniformly yellow; antennae yellow, same colour as head ..... *C. flavicorpus* Dodd

24(15). Brachypterous, wings not reaching past T1; horn flat and very broad, occupying all of T1 ..... *C. flavipes* (Hickman)

Wings fully developed; horn usually only developed on anterior 3/4 of T1 25

25(24). Postmarginal vein at least 1/2 length of stigmal vein 26

Postmarginal vein very short or absent 28

26(25). Horn represented as an anterior inflection of T1, not rounded dorsally (Figure A41); basal vein present, moderately dark (Figure A47); (head and mesosoma black, metasoma dark brown, posterior T1 and antennae light brown) .... *C. clubionus* sp.nov.

Horn rounded dorsally (Figure A58), basal vein sometimes present but faint (Figure A39) 27

27(26). Body uniformly light yellow ..... *C. parvicornutus* Dodd

Head, mesosoma and horn black, metasoma brown ... *C. masneri* sp.nov.

28(25). Forewing without marginal fringe of hairs ..... *C. flavios* (Dodd)

Marginal fringe of hairs long ..... *C. aureus* Dodd

A1.7 DESCRIPTIONS OF SPECIES OF *CERATOBAEUS* ASHMEAD

A1.7.1 *Ceratobaeus clubionus* sp.nov.

Types.- Holotype ♀ on tag, ANIC, South Australia: 5 km S. of Mylor, 29.iii.79, A.D. Austin, ex egg *Clubiona* sp. (Araneae). Allotype ♂ on tag, ANIC; paratypes 2 ♀♀, 2 ♂♂ gold coated on SEM holders, antennae and wings of 1 ♀ and 1 ♂ on slides, 4 ♀♀, 1 ♂ on tags, ANIC; 4 ♀♀, 1 ♂ on tags, CNC; 4 ♀♀ and 1 ♂ on tags, QDPI; 4 ♀♀, 1 ♂ on tags, SAM; 4 ♀♀, 1 ♂ on tags, WAITE; - all with labels same as holotype.

Other material examined.- South Australia: 6 ♀♀, 2 ♂♂, 15.iii.79; 13 ♀♀, 2 ♂♂, 18.xi.79, 5 km S. of Mylor, A.D. Austin; 7 ♀♀, 1 ♂, Myponga, 4.ii.79, A.D. Austin; 10 ♀♀, 1 ♂, 3.ii.79, 5 ♀♀, 1 ♂, 4.ii.79, Strathalbyn, A.D. Austin, ANIC; 8 ♀♀, 15.iii.79, 15 ♀♀, 1 ♂, 13.iv.79, 5 km S. of Mylor, A.D. Austin, CNC; 4 ♀♀, 1 ♂, 13.ii.79, 5 ♀♀, 9.iii.79, 5 ♀♀, 1 ♂, 25.xi.79, 5 ♀♀, 1 ♂, 7.xii.79, 5 km S. of Mylor, A.D. Austin, QDPI; 5 ♀♀, 1 ♂, 13.iv.79, 12 ♀♀, 2 ♂♂, 20.i.80, 5 km S. of Mylor, A.D. Austin, SAM; 11 ♀♀, 23.i.79, 8 ♀♀, 2 ♂♂, 13.ii.79, 5 km S. of Mylor, A.D. Austin, WAITE.

Female. Length 1.3 - 1.4 mm.

Colour. Head and mesosoma shiny black; antennae and legs light brown, almost yellow; apical clavae and femora slightly darker; metasoma dark brown with lighter margin; posterior T1 and anterior T2 light brown.

Head. L:W:H (6.5:19:14), with punctate sculpturing and fine scattered hairs; dorsally, wider than mesosoma and arched around pronotum (Figure A47); occipital carina sharp; eyes large and hairy; lateral ocelli touching inner margins of eyes (Figure A40); frons slightly curved; anteriorly, head ovoid; occiput arched; eyes separated by 1/2 width of head; frons smooth; frontal carina weakly developed; laterally, gena with sides not quite parallel; antennal scape (A1) L:W (24:5), pedicel (A2) (10:5), A3 (6:4.5), clava (20:10) with 3 faint incomplete sutures (Figure A49).

Mesosoma. Dorsally, with punctate sculpturing and sparse short hairs; pronotum not visible; scutum wider than long, L:W (11:14); notauli absent; scutellum almost semicircular, L:W (5.5:11), posterior margin with wide flange extending over metanotum, slightly inflected medially; metanotum narrow and crenulated; propodeum vertical and smooth, laminae diverging ventrally, extended into 2 small teeth dorsally (Figure A40); legs normal.

Wings. Forewings not quite reaching to posterior margin of metasoma, not particularly broad, L:W (36:13); venation distinct, marginal and postmarginal veins short; stigmal vein long, basal vein present but lighter than other veins; lightly infuscated around apex of stigmal vein; marginal fringe of hairs moderately long (Figure A47).

Metasoma wider than mesosoma, L:W (30:17), sparsely covered with hairs, pointed posteriorly; anterior T1 expanded into large hump, not reaching above propodeum (Figure A41); T1 and T2 with coarse longitudinal striations, T3 with lighter striations (Figure A47); lateral margins of T2-T3 and all T4-T6 with punctate sculpturing.

Figures A32-A37 Antennae.

Figure A32. ♀, *Ceratobaeus cuspicornutus* sp.nov.
Figure A33. ♂, *Ceratobaeus cuspicornutus* sp.nov.
Figure A34. ♀, *Ceratobaeus masneri* sp.nov.
Figure A35. ♂, *Ceratobaeus masneri* sp.nov.
Figure A36. ♀, *Ceratobaeus platycornutus* sp.nov.
Figure A37. ♂, *Ceratobaeus platycornutus* sp.nov.

Figures A38 and A39 Forewings.

Figure A38. ♀, *Ceratobaeus cuspicornutus* sp.nov.
Figure A39. ♀, *Ceratobaeus masneri* sp.nov.

(Figures A32-A39, Scale = 100 µm.)

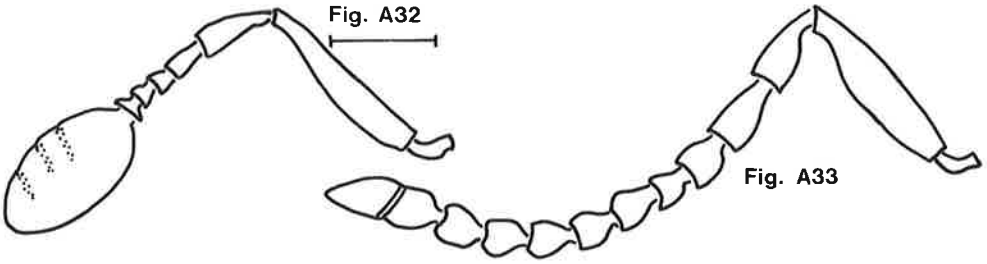


Fig. A32

Fig. A33

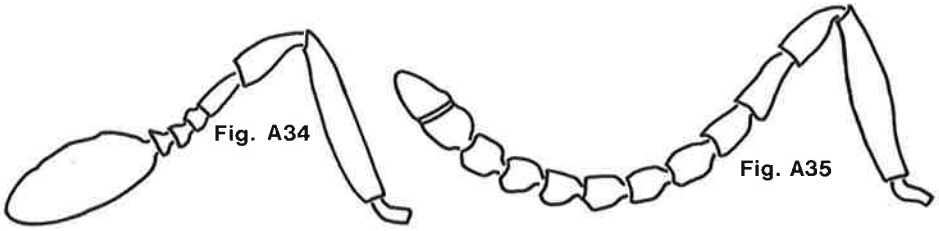


Fig. A34

Fig. A35

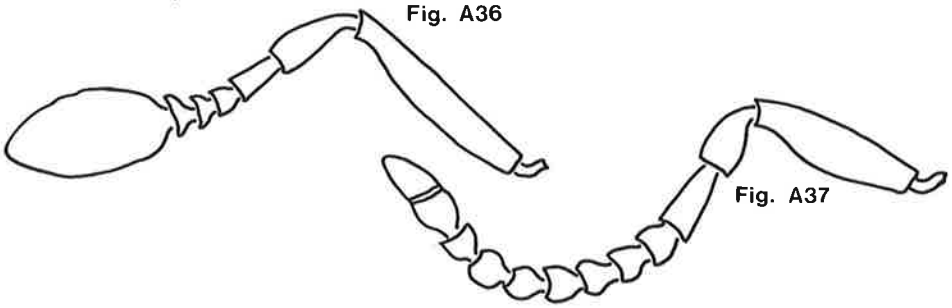


Fig. A36

Fig. A37

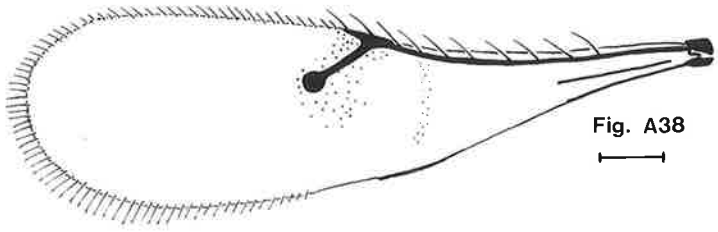


Fig. A38

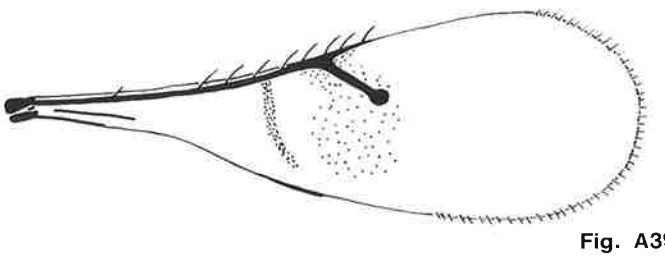


Fig. A39

Male. Differing from female in the following:

Length 1.2 - 1.3 mm; antennae 12-segmented, A11 and A12 approximated (Figure A50); propodeal laminae diverging slightly more than in female; wings reaching well past posterior margin of metasoma; forewing L:W (46:19), marginal fringe of hairs long, venation dark, basal vein darker than in female; metasoma rounded posteriorly, wider than mesosoma, L:W (26:18); anterior T1 inflected dorsally into hump, but not as pronounced as in female (Figure A42).

Note. *C. clubionus* sp.nov. parasitizes the eggs of *Clubiona cycladata* Simon and *C.* Sp.A (Clubionidae); the former spider being common under the bark of eucalypt trees in the Mount Lofty Ranges, South Australia.

A1.7.2 *Ceratobaeus cuspicornutus* sp.nov.

Types.- Holotype ♀ on tag, ANIC. South Australia: 5 km S. of Mylor, 18.ii.79, A.D. Austin, ex egg *Clubiona* sp. (Araneae). Allotype ♂ on tag, ANIC; paratypes 2 ♀♀, 1 ♂ gold coated on SEM holders, antennae and wings of ♂ and 1 ♀ on slides, 2 ♀♀ dissected on slides, 2 ♀♀, 2 ♂♂ on tags, ANIC; 2 ♀♀, 1 ♂ on tags, CNC; 2 ♀♀, 1 ♂ on tags QDPI; 2 ♀♀, 1 ♂ on tags, SAM; 2 ♀♀, 1 ♂ on tags, WAITE - all with labels same as holotype.

Other material examined.- South Australia: 9 ♀♀, 3 ♂♂, 9.iii.79, 10 ♀♀, 13.xi.79, 5 km S. of Mylor, A.D. Austin, ANIC. 4 ♀♀, 2 ♂♂, 5 km S. of Mylor, 15.iii.79, A.D. Austin, CNC; 6 ♀♀, 1 ♂, 5 km S. of Mylor, 13.xi.79, A.D. Austin, QDPI; 5 ♀♀, 2 ♂♂, 5 km S. of Mylor, 9.ix.79, A.D. Austin, SAM; 2 ♀♀, 29.iii.79, 3 ♀♀, 26.iii.78, 5 km S. of Mylor, A.D. Austin, WAITE.

Female. Length 1.50 - 1.75 mm.

Colour. Head and mesosoma black; legs and antennae brown to dark brown; metasomal horn black and shiny; posterior T1 light brown; T2-T7 brown.

Head wider than mesosoma, L:W:H (6:19:15), with punctate sculpturing and short scattered hairs; dorsally, occipital carina sharp; eyes large, with very short hairs; lateral ocelli touching inner margins of eyes; frons slightly curved (Figure A46); anteriorly, head sub-triangular in shape; occiput slightly depressed medially; eyes separated by slightly more than 1/2 width of head; lower frons smooth and shiny;

frontal carina weakly developed; laterally, gena large, margins parallel; antennal scape (A1) L:W (26:5), pedicel (A2) (11.5:4.6), A3 (5:3.5), clava (22:12.3) with 3 faint incomplete sutures (Figure A32).

Mesosoma strongly compressed anterioposteriorly; dorsally, with punctate sculpturing and scattered hairs; pronotum not visible; scutum much wider than long, L:W (9:14); notauli absent; scutellum transverse, L:W (1:10), with posterior fringe of long hairs; scutellum, metanotum and propodeum strongly excavated, sloping away posteriorly towards metasoma (Figures A44 and 46); propodeal laminae parallel, not extended dorsally into small teeth; laterally mesosoma smooth and shiny.

Wings. Forewings not reaching past posterior margin of T4, fairly narrow, L:W (44:13); marginal vein short, stigmal vein long, postmarginal vein less than 1/2 length of stigmal vein, basal vein faint; lightly infuscated at apex of stigmal vein; marginal fringe of hairs moderately long (Figure A38).

Metasoma elongated, L:W including horn (55:17), slightly wider than mesosoma, with scattered hairs; horn long, angled forward into mesosomal cavity, reaching above level of scutellum (Figures A44 and 46); apical horn moderately pointed and smooth; T1-T4 with longitudinal striations; lateral margins of T2-T3 and all T4-T7 with punctate sculpturing; T7 slightly elongated.

Male. Differing from female in the following:

Length 1.35 - 1.50 mm; antennae 12-segmented, A11 and A12 approximated (Figure A33); dorsal mesosoma arched more than in female; scutellum more than 2x wider than long L:W (5:12), posterior margin rounded and inflected medially; posterior mesosoma not excavated but flat, sloping posteriorly towards metasoma; metanotum narrow and crenulated, visible from above; propodeum smooth (Figure A43); propodeal laminae diverging ventrally; wings reaching well past posterior metasoma; forewings moderately broad,

Figures A40-A42 SEM of *Ceratobaeus clubionus* sp.nov.

Figure A40. ♀, lateral view of head and mesosoma.

Figure A41. ♀, dorsolateral view of posterior mesosoma and T1.

Figure A42. ♂, dorsoposterior view of posterior mesosoma and T1.

Figures A43, A44 and A46 SEM of *Ceratobaeus cuspicornutus* sp.nov.

Figure A43. ♂, dorsal view of posterior mesosoma and T1.

Figure A44. ♀, lateral view of mesosoma and horn on T1.

Figure A46. ♀, dorsal view of whole body.

Figure A45 SEM of *Ceratobaeus intrudae* sp.nov., ♂ (lateral view).

(Figures A40-A46, Scale = 100 µm; wings removed from all specimens.)

L:W (55:20); basal vein darker than in female, but still faint compared to submarginal vein, marginal fringe of hairs long; metasoma moderately elongated, rounded posteriorly, L:W (29:16); anterior T1 inflected dorsally (Figure A43); striations reaching to anterior margin of T1.

Note. The specific name *Cuspicornutus* (cuspis in latin, pointed or pointed end; cornutus, horn) refers to the shape of the apical end of the metasomal horn. This species parasitizes the eggs of *Clubiona cycladata* and *C.* Sp.A. (Clubionidae); the former spider being common under the bark of eucalypt trees, in the Mount Lofty Ranges, South Australia. *C. cuspicornutus* sp.nov. is similar to *C. longicornutus* Dodd, but they differ in colour, wing venation and shape of the antennal pedicel (see key to species).

A1.7.3 *Ceratobaeus intrudae* sp.nov.

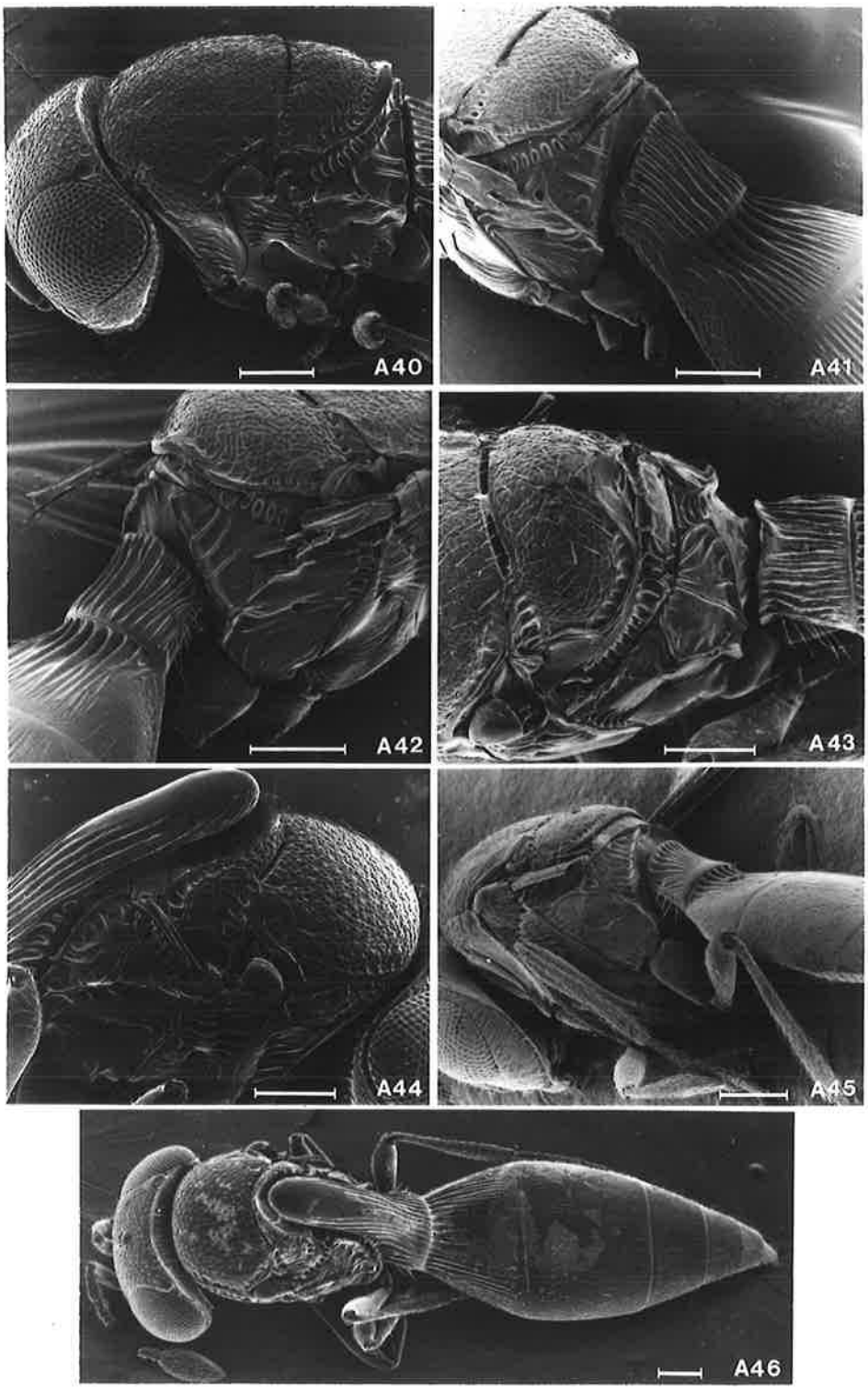
Types.- Holotype ♀ on tag, ANIC, South Australia: Mount Compass 4.ii.79, A.D. Austin, ex egg *Intruda* sp. (Araneae). Allotype ♂ on tag, ANIC; paratypes 1 ♀, 1 ♂ gold coated on SEM holders, antennae and wings on slides, 2 ♀♀, 2 ♂♂ dissected on slides, ANIC; 1 ♀, 1 ♂ on tags, CNC - all with labels same as holotype.

Other material examined.- South Australia: 3 ♀♀, 1 ♂, Bridgewater, 26.iii.79, A.D. Austin, ANIC; 4 ♀♀, 1 ♂, Bridgewater, 26.iii.78, A.D. Austin, SAM.

Female. Length 1.30 - 1.45 mm.

Colour. Head and dorsal mesosoma very dark brown to black; legs, antennae and lateral mesosoma dark brown; metasoma with a light brown band behind horn and a medial brown patch occupying approximately 2/3 of T3, rest of metasoma dark brown to black.

Head wider than mesosoma, not strongly curved around pronotum, with punctate sculpturing and sparse short hairs, L:W:H (7.5:18:13), dorsally, occipital carina sharp; eyes large, covered with short hairs; lateral ocelli touching inner margins of eyes; frons slightly curved; anteriorly, head sub-triangular in shape; occiput flat; eyes separated by more than ½ width of head; frons lightly sculptured; frontal carina well developed, reaching


A40
A41
A42
A43
A44
A45
A46

half way to median ocellus; laterally, gena large, margins almost parallel; antennal scape (A1) L:W (26:5), pedicel (A2) (13:4.7), A3 (6:3.8), clava (25:13) with 3 faint incomplete sutures (Figure A51).

Mesosoma. Dorsally, fairly flat, with punctate sculpturing and scattered hairs; pronotum not visible; scutum wider than long, L:W (10:14.5); notauli absent; scutellum almost semi-circular, L:W (4:11), posterior border crenulated, with a narrow flange (Figure A54); metanotum narrow and crenulated; propodeum vertical and smooth; laminae curving dorsally, extended into 2 small teeth; laterally, mesosoma smooth and shiny; legs normal.

Wings. Forewings narrow, not quite reaching to posterior margin of metasoma, L:W (38:12.5); marginal vein short, stigmal vein long, postmarginal vein as long as stigmal vein, basal vein present but very faint (Figure A48); infuscated around apex of stigmal vein; marginal fringe of hairs short.

Metasoma slightly wider than mesosoma and 2x longer than wide, L:W (32:16), with scattered hairs, pointed posteriorly (Figure A48); horn almost vertical, reaching above level of posterior scutellum, with circular striated sculpturing apically (Figure A53 and 54); T1 behind horn and T2-T3 with longitudinal striations; lateral T2-T3 and all T4-T6 with punctate sculpturing.

Male. Differing from female in the following:

Dorsally, head slightly more curved around pronotum, only slightly wider than mesosoma, L:W:H (7.5:17:13); antennae 12-segmented, A11 and A12 approximated (Figure A52); propodeum not quite vertical, sloping away slightly towards metasoma (Figure A45); propodeal laminae slightly wider than in female; wings reaching well past posterior metasoma; forewing L:W (42:16), marginal fringe of hairs long; metasoma rounded posteriorly, L:W (25:16); anterior T1 strongly inflected dorsally, not reaching above propodeal laminae (Figure A45); without striated or punctate sculpturing, but with longitudinal striations extending to anterior margin.

Figure A47 Dorsal surface of the whole body of *Ceratobaeus clubionus* sp.nov., ♀.

Figure A48 Dorsal surface of the whole body of *Ceratobaeus intrudae* sp.nov., ♀.

Figure A49-A52 Antennae.

Figure A49. ♀, *Ceratobaeus clubionus* sp.nov.
Figure A50. ♂, *Ceratobaeus clubionus* sp.nov.
Figure A51. ♀, *Ceratobaeus intrudae* sp.nov.
Figure A52. ♂, *Ceratobaeus intrudae* sp.nov.

(Figures A47-A52, Scale = 100 µm.)

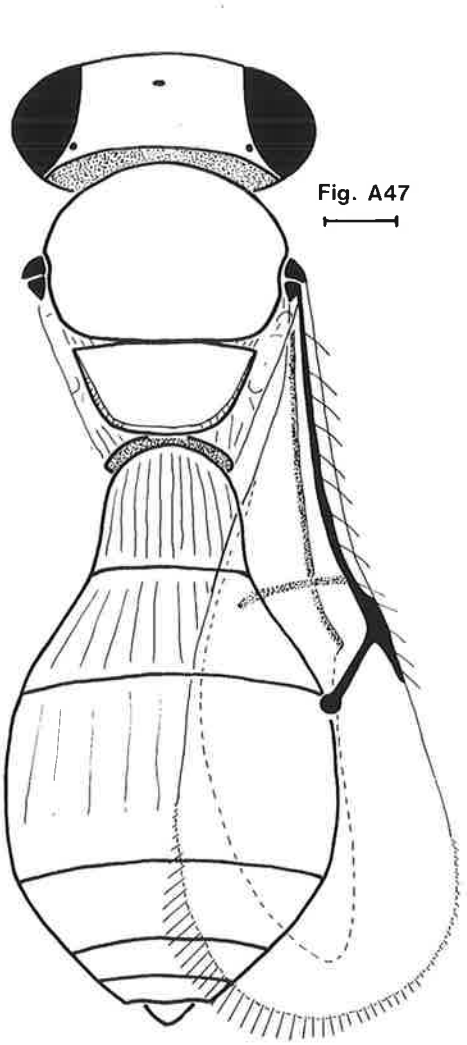


Fig. A47

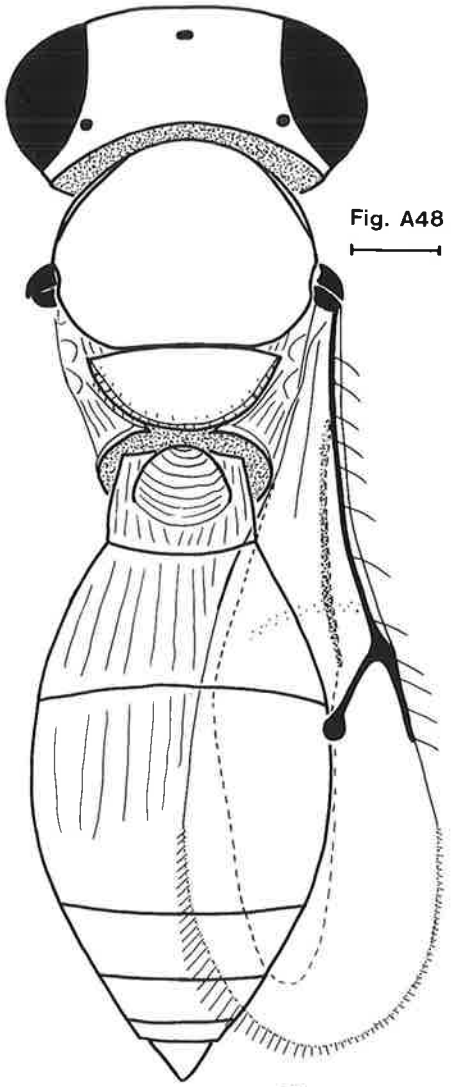


Fig. A48

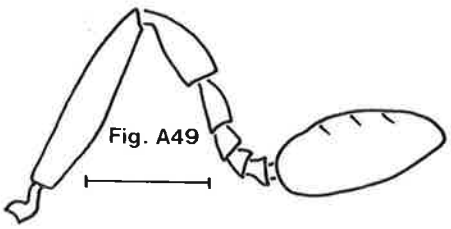


Fig. A49

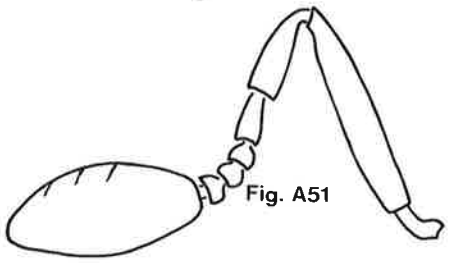


Fig. A51

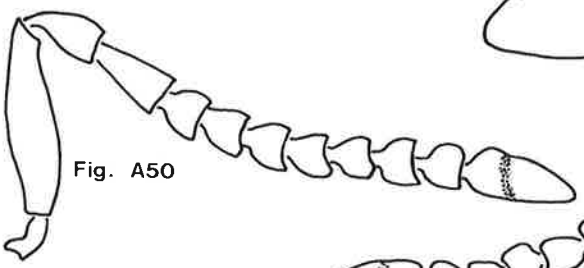


Fig. A50

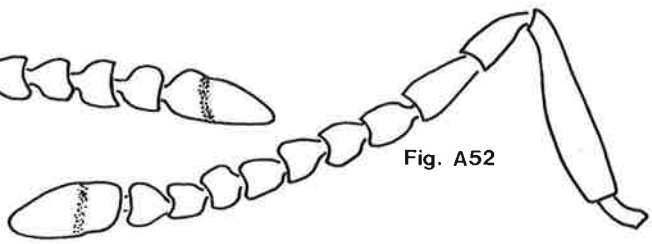


Fig. A52

Note. *C. intrudae* sp.nov. parasitizes the eggs of an unknown species of *Intruda* (Gnaphosidae), the latter being found under the bark of eucalypt trees in the Mount Lofty Ranges, South Australia.

A1.7.4 *Ceratobaeus lamponae* (Hickman) - see figures in Hickman 1967b.

Odontacolus lamponae Hickman 1967b: 18; *Ceratobaeus lamponae* (Hickman), in Masner 1976: 66; Austin 1981a: 84.

Types.- Holotype ♀ on slide, ANIC: Tasmania, Domain, Hobart, 29.xii.66, V.V. Hickman, ex egg *Lampona cylindrata* (L.Koch) (Araneae), paratypes 1 ♀, 2 ♂♂ on same slide as holotype.

Other material examined.- South Australia: 1 ♀, 1 ♂ gold coated on SEM holders, antennae and wings on slides, 11 ♀♀, 2 ♂♂ on tags, 5 km S. of Mylor, 29.iii.79, A.D. Austin, ANIC; 8 ♀♀ and 4 ♂♂, 5 km S. of Mylor, 20.i.80, A.D. Austin, CNC; 11 ♀♀, 1 ♂, 5 km S. of Mylor, 29.iii.79, A.D. Austin, QDPI; 6 ♀♀, 4 ♂♂, 5 km S. of Mylor, 20.i.80, A.D. Austin, SAM; 6 ♀♀, 1 ♂, 5 km S. of Mylor, 14.xii.79, A.D. Austin, WAITE.
Tasmania: 11 ♀♀, 1 ♂, Domain, Hobart, 9.iii.67, V.V. Hickman, ANIC, 11 ♀♀, 3 ♂♂, Domain, Hobart, 29.xii.67, V.V. Hickman, CNC; 1 ♀, Domain, Hobart, 9.iii.67, V.V. Hickman, HUG.

Female. Length 1.60 - 1.85 mm.

Colour. Head, mesosoma and horn shiny black; antennae and metasoma dark brown to black; legs brown.

Head. L:W H (9:22.5:16), with coarse punctate sculpturing, covered with long hairs; dorsally, wider than mesosoma, arched around pronotum; occiput well exposed; occipital carina sharp, moderately angled at corners; eyes large, with long hairs; lateral ocelli touching inner margins of eyes, frons straight; anteriorly, head subtriangular in shape; occiput straight; eyes separated by slightly less than 1/2 width of head; frons flat, with horizontal striae; frontal carina very small; laterally, gena with margins parallel, rounded ventrally; antennal scape (A1) L:W (31:6), pedicel (A2) (13:5.5), A3 (10:4.5), clava (27:12) with 3 faint incomplete sutures.

Mesosoma dorsally, with coarse punctate sculpturing, sparsely covered with long hairs; pronotum visible at anterior lateral corners; scutum wider than long; L:W (13.5:17.5); notauli absent; scutellum 3x wider than long, L:W (4:12), posterior margin straight (Figure A56), fringe

of long hairs projecting over horn often present; metanotum and propodeum flat; metanotum narrow and crenulated; propodeal laminae diverging ventrally, extended dorsally into blunt teeth, legs normal.

Wings. Forewings not quite reaching to posterior margin of metasoma, moderately broad, L:W (73:27), infuscated medially; venation clear and dark; marginal vein short, postmarginal vein as long as stigmal vein, basal vein light; marginal fringe of hairs moderately long.

Metasoma wider than mesosoma, L:W including horn (42:22), covered with long hairs; horn reaching to level of dorsal scutellum, with punctate sculpturing almost scaly in appearance (Figure A55); T1 behind horn and T2-T3 with longitudinal striations, T4-T6 with punctate sculpturing.

Male. Differing from female in the following:

Length. 1.55 - 1.70 mm; antennae 12-segmented, A11 and A12 approximated; dorsally, scutellum more rounded, though slightly flattened posteriorly, 2x wider than long, L:W (6.5:12.5); propodeum flat, almost vertical; propodeal laminae wide, with punctate sculpturing, strongly diverging ventrally, extended into 2 blunt teeth dorsally which almost touch medially (Figure A57); wings reaching well past posterior metasoma; forewing L:W (83:32), well infuscated, marginal fringe of hairs long; metasoma subpedunculate, wider than mesosoma, with scattered long hairs, L:W (35:25); anterior T1 inflected dorsally; T1-T2 and anterior T3 with longitudinal striations, rest of metasoma with punctate sculpturing.

Note. *C. lamponae* (Hickman) parasitizes the eggs of *Lampona cylindrata* (L.Koch) (Gnaphosidae); the latter being widespread throughout Australia. *C. lamponae*, previously only known from Tasmania, is recorded from mainland Australia for the first time. There appears to be some minor geographic variation in this species. Some specimens from Tasmania have the posterior fringe of hairs on the scutellum very short or absent, while mainland specimens always have a very long fringe.

Figures A53 and A54 SEM of *Ceratobaeus intrudae* sp.nov.

Figure A53. ♀, lateral view of posterior mesosoma and T1.

Figure A54. ♀, dorsal view of mesosoma and T1.

Figures A55-A57 SEM of *Ceratobaeus lamponae* (Hickman).

Figure A55. ♀, lateral view of posterior mesosoma and T1.

Figure A56. ♀, dorsal view of mesosoma.

Figure A57. ♂, lateral view of posterior mesosoma and T1.

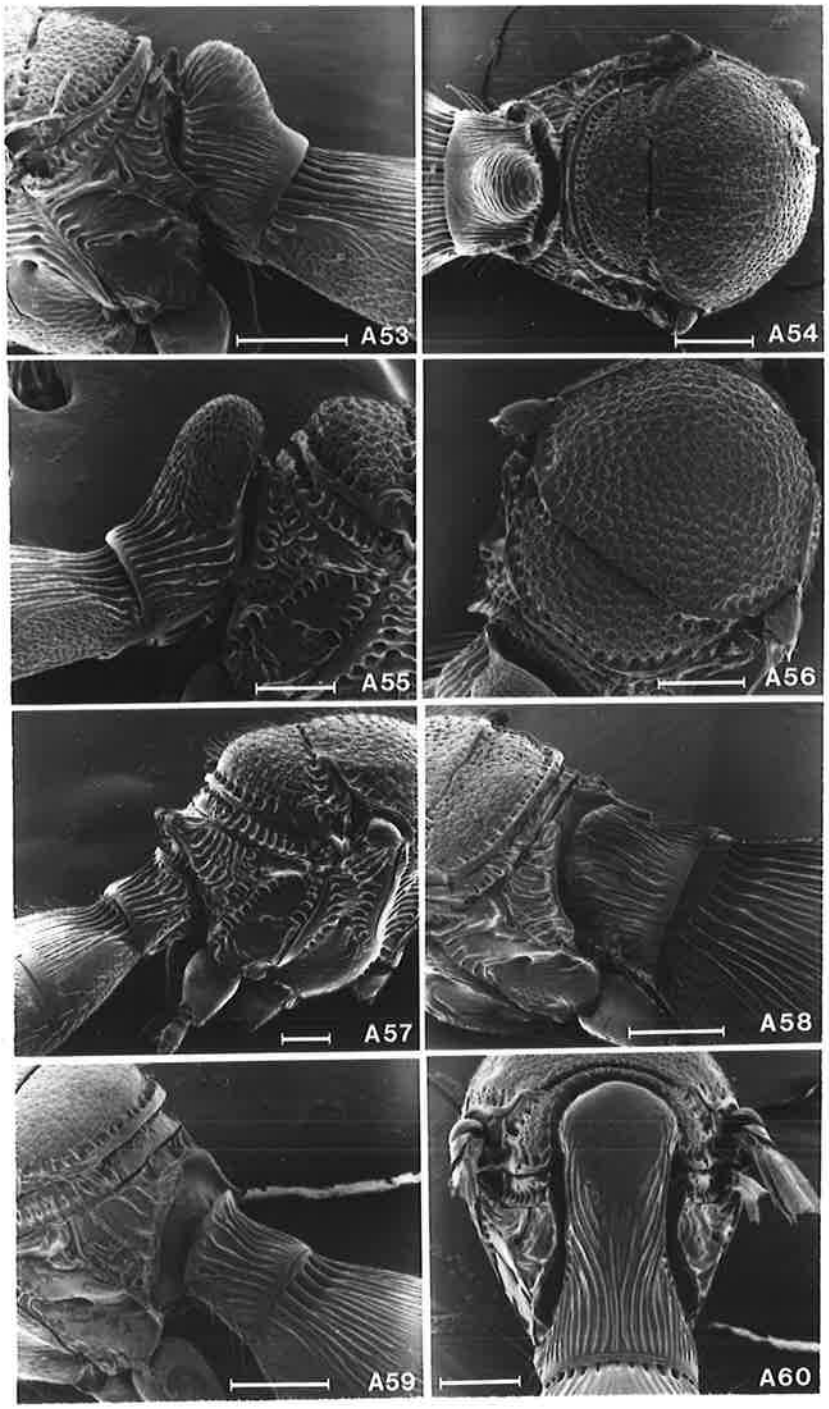
Figures A58 and A59 SEM of *Ceratobaeus masneri* sp.nov.

Figure A58. ♀, dorsolateral view of posterior mesosoma and T1.

Figure A59. ♂, dorsolateral view of posterior mesosoma and T1.

Figure A60 SEM of posterior mesosoma and T1 of *Ceratobaeus platycornutus* sp.nov., ♀ (dorsoposterior view).

(Figures A53-A60, Scale = 100 μm; wings removed from all specimens.)


A53
A54
A55
A56
A57
A58
A59
A60

A1.7.5 *Ceratobaeus masneri* sp.nov.

Types.- Holotype ♀ on tag, ANIC, South Australia: 5 km S. of Mylor, 18.ii.79, A.D. Austin, ex egg *Clubiona* sp. (Araneae). Allotype ♂ on tag, ANIC; paratypes 3 ♀♀, 2 ♂♂ gold coated on SEM holders, antennae and wings of 1 ♀, 1 ♂ on slides, 4 ♀♀, 4 ♂♂ on tags, ANIC; 4 ♀♀, 1 ♂ on tags, CNC; 4 ♀♀, 1 ♂ on tags, QDPI; 4 ♀♀, 1 ♂ on tags, SAM; 4 ♀♀, 1 ♂ on tags, WAITE - all with labels same as holotype.

Other material examined.- Australian Capital Territory: 6 ♀♀, Canberra, 14.i.80, A.D. Austin, ANIC.

South Australia: 13 ♀♀, 20.i.79, ex eggs *Clubiona* sp. (Araneae), 14 ♀♀, 6 ♂♂, 13.xi.79, ex eggs *Hemicloea* sp. (Araneae), 5 km S. of Mylor, A.D. Austin, ANIC; 33 ♀♀, 7 ♂♂, 5 km S. of Mylor, 10.iii.80, A.D. Austin, ex eggs *Hemicloea* sp., CNC; 6 ♀♀, 4 ♂♂, 1.xii.79, 6 ♀♀, 2 ♂♂, 20.i.80, 5 km S. of Mylor, A.D. Austin, QDPI; 6 ♀♀, 5 ♂♂, 5 km S. of Mylor, 17.ii.80, A.D. Austin, SAM; 7 ♀♀, 15.iv.79, 11 ♀♀, 12.viii.79, 5 km S. of Mylor, A.D. Austin, WAITE.

Victoria: 9 ♀♀, 1 ♂, Woorndoo, 26.ix.79, A.D. Austin, SAM.

Female. Length 1.25 - 1.40 mm.

Colour. Head and mesosoma black; antennae and legs brown; metasoma dark brown; T1 light brown, but with apex of horn brown to dark brown.

Head wider than mesosoma, L:W:H (7:18:13), arched around pronotum, with punctate sculpturing and scattered short hairs; dorsally, occipital carina sharp; eyes large and hairy; lateral ocelli touching inner margins of eyes; frons curved; anteriorly, head subtriangular in shape: occiput curved; eyes separated by slightly more than 1/2 width of head; frons smooth; frontal carina weakly developed, reaching half the distance to median ocellus; laterally, gena wide, sides not parallel; antennal scape (A1) L:W (24:5), pedicel (A2) (11:5), A3 (6:3.7), clava (23:10) (Figure A34).

Mesosoma. Dorsally, with punctate sculpturing and scattered hairs; pronotum not visible; scutum wider than long, L:W (9:12); notauli absent; scutellum L:W (4.5:10), rounded posteriorly, with crenulated border, slightly inflected medially (Figure A61); metanotum narrow and crenulated; propodeum vertical and smooth; laminae diverging ventrally and curved dorsally into 2 small teeth; legs normal.

Wings. Forewings just reaching to posterior margin of metasoma, fairly narrow, L:W (40:13); marginal vein short, stigmal vein long,

postmarginal vein approximately 3/4 length of stigmal vein, basal vein present but faint; marginal fringe of hairs short (Figure A39).

Metasoma wider than mesosoma, nearly 2x longer than wide, L:W (35:19), pointed posteriorly (Figure A61), sparsely covered with hairs; T1 expanded into a small dorsal horn, not reaching to level of scutellum (Figure A58); apex of horn with faint punctate sculpturing, sides of horn and rest of T1-T3 with longitudinal striations; lateral margins of T2-T3 and all T4-T6 with punctate sculpturing.

Male. Differing from female in the following:

Length 1.20 - 1.35 mm; antennae 12-segmented, A11 and A12 approximated (Figure A35); hairs on dorsal surface of mesosoma slightly longer than in female; scutellum slightly arched dorsally; wings reaching well past posterior margin of metasoma; forewing L:W (49:18), venation same as female, but with basal vein more obvious, almost as dark as submarginal vein; marginal fringe of hairs long; metasoma rounded posteriorly, L:W (27:16.5); anterior T1 inflected dorsally, only reaching to 1/2 height of propodeum, striations reaching to anterior margin of T1 (Figure A59).

Note. This species is named after Dr Lubomir Masner, whose work on scelionid wasps is well known. *C. masneri* sp.nov. parasitizes the eggs of *Clubiona robusta* L.Koch, *C. cycladata*, *C.* Sp.A. (Clubionidae) and *Hemicloea* sp. (Gnaphosidae). The first 2 spiders are common under the bark of eucalypt trees throughout southeastern Australia. So far *C. masneri* has been collected from locations in South Australia, Victoria and the Australian Capital Territory.

A1.7.6 *Ceratobaeus platycornutus* sp.nov.

Types.- Holotype ♀ on tags, ANIC, Australian Capital Territory: University campus, Canberra, 14.i.80, A.D. Austin, ex egg *Clubiona* sp. (Araneae). Allotype ♂ on tag, ANIC; paratypes 3 ♀♀, 2 ♂♂ gold coated on SEM holders, antennae and wings of 1 ♀ and 1 ♂ on slides, 7 ♀♀, 2 ♂♂ on tags, ANIC; 4 ♀♀, 1 ♂ on tags, CNC; 4 ♀♀, 1 ♂ on tags, QDPI; 4 ♀♀, 1 ♂ on tags, WAITE - all with labels same as holotype.

Other material examined.- Australian Capital Territory: 11 ♀♀ 4 ♂♂, University campus, Canberra, 10.i.80, A.D. Austin, ANIC.

Figure A61 SEM of the whole body of *Ceratobaeus masneri* sp.nov., ♀ (dorsal view).

Figure A62 SEM of the posterior mesosoma and T1 of *Ceratobaeus platycornutus* sp.nov., ♂ (dorsolateral view).

Figure A63 SEM of head, mesosoma and T1 of *Ceratobaeus rieki* sp.nov., ♀ (dorsolateral view).

Figures A64-A67 SEM of *Ceratobaeus setosus* Dodd.

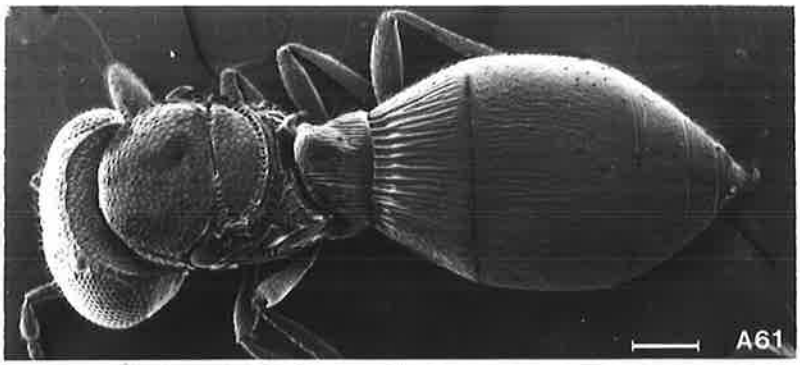
Figure A64. ♀, anterior view of head.

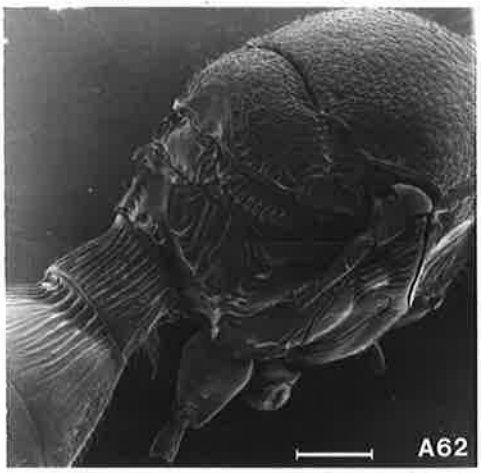
Figure A65. ♀, dorsolateral view of mesosoma.

Figure A66. ♀, lateral view of posterior mesosoma and T1.

Figure A67. ♂, lateral view of posterior mesosoma and T1.

(Figures A61-A67, Scale = 100 μm, wings removed from specimens in Figures A61-A63, A65 and A67.)


A61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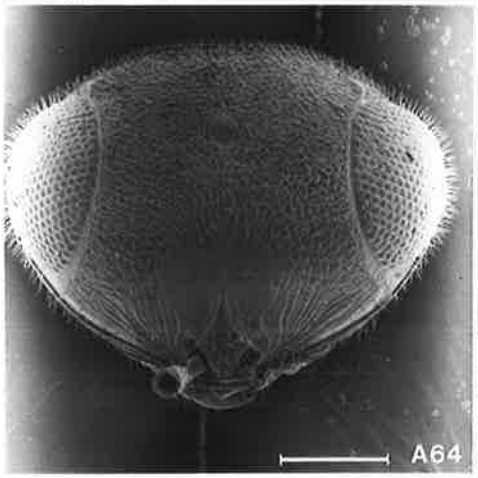
A63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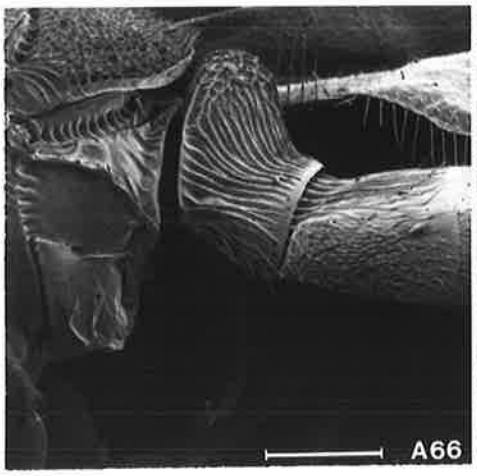
A65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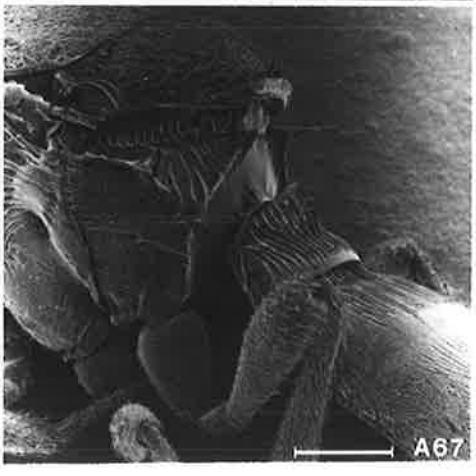
A67

Female. Length 1.75 - 1.85 mm.

Colour. Head, mesosoma and apical horn black; antennae, legs and metasoma dark brown; anterior metasoma behind horn, with a light brown band.

Head wider than mesosoma, L:W:H (7:20:15), arched around pronotum, with punctate sculpturing, sparsely covered with hairs; dorsally, occipital carina sharp; eyes large, with fine hairs; lateral ocelli touching inner margins of eyes; frons curved, anteriorly, head subtriangular in shape; occiput straight; eyes separated by 1/2 width of head; frons lightly punctate; frontal carina very small; laterally, gena wide, sides almost parallel; antennal scape (A1) L:W (30:5.7), pedicel (A2) (13:5.2), A3 (7:4), clava (23:12.5) (Figure A36).

Mesosoma strongly compressed anterioposteriorly; dorsally, with punctate sculpturing and scattered hairs; pronotum not visible; scutum wider than long, L:W (10:15); notauli absent; scutellum transverse, L:W (1:10), scutellum, metanotum and propodeum all strongly indented posteriorly, sloping towards metasoma; propodeal laminae vertical, curved outwards ventrally, without dorsal teeth; legs normal.

Wings. Forewings reaching to posterior margin of T4, fairly narrow, L:W (71:23); lightly infuscated medially; marginal vein short; stigmal vein long, postmarginal vein less than 1/2 length of stigmal vein, basal vein light; marginal fringe of hairs moderately long.

Metasoma elongated, L:W including horn (56:18), wider than mesosoma; horn long, angled anteriorly, closely fitting to mesosoma, reaching above level of scutellum, flattened and disc-shaped apically (Figure A60); T1 including shaft of horn, T2-T4 with longitudinal striations; lateral T2-T4 and all T5-T7 with light punctate sculpturing.

Male. Differing from female in the following:

Length 1.4 - 1.5 mm; antennae and legs yellow; metasoma dark brown to black, with light brown band anteriorly; antennae 12-segmented, A11 and A12 approximated (Figure A37); head not as high, L:W:H (7:20:13.5); scutellum almost semicircular, slightly indented posteriorly; metanotum and propodeum flattened and smooth; propodeal laminae diverging ventrally (Figure A62); wings reaching well past metasoma; forewings broad, L:W (80:31); postmarginal vein not as long as in female, basal vein slightly darker; marginal fringe of hairs long, metasoma not as elongated, L:W (30:20); anterior T1 inflected dorsally; T1-T3 with longitudinal striations; rest of metasoma with light punctate sculpturing.

Note. The specific name *platycornutus* (platys in latin, broad or flat; cornutus, horn) refers to the flattened, disc-shaped apical end of the metasomal horn. This species has been recorded as parasitizing the eggs of *Clubiona* sp. (Clubionidae), under the bark of eucalypt trees, in the Australian Capital Territory. *C. platycornutus* sp.nov. is very similar to *C. cuspicornutus* sp.nov. and *C. longicornutus* Dodd, but differs from these species in the shape of the metasomal horn.

A1.7.7 *Ceratobaeus rieki* sp.nov.

Types.- Holotype ♀ on tag, ANIC. New South Wales: 10 ml E. Trangie, 20.x.49, E.F. Riek. Paratypes, 1 ♀ gold coated on SEM holder (mesosoma missing), wings on slide, 1 ♀ dissected on slide, 13 ♀♀ on tags, ANIC. - all with labels same as holotype.

Female. Length 2.1 - 2.3 mm.

Colour. Head and mesosoma black; antennae dark brown; legs brown; metasoma dark brown to black.

Head. L:W:H (7:20:14.5), with punctate sculpturing, covered with short hairs; dorsally, slightly wider than mesosoma; occiput excavated and arched around pronotum; occipital carina sharp, not angled at corners; eyes large and hairless; lateral ocelli touching inner margins of eyes;

Figure A68 Dorsal surface of the whole body of *Ceratobaeus rieki* sp.nov., ♀.

Figure A69 Dorsal surface of the whole body of *Ceratobaeus setosus* Dodd, ♀.

Figures A70–A72 Antennae.

Figure A70. ♂, *Ceratobaeus setosus* Dodd.
Figure A71. ♀, *Ceratobaeus setosus* Dodd.
Figure A72. ♀, *Ceratobaeus rieki* sp.nov.

(Figures A68–A72, Scale = 100 µm.)

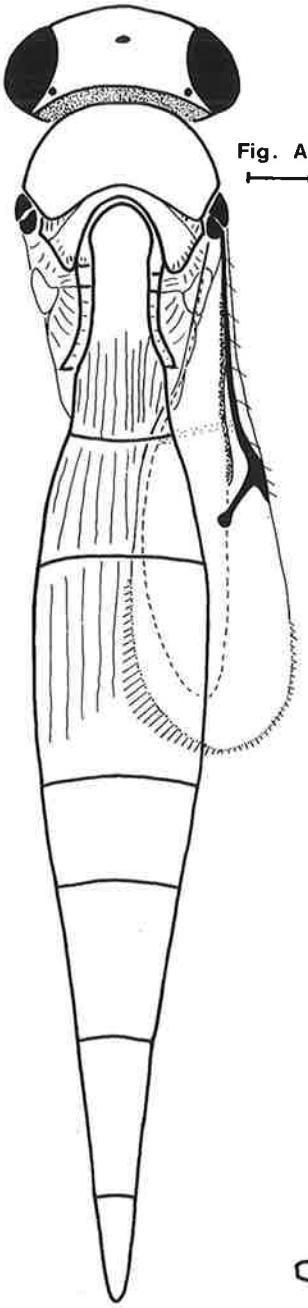

Fig. A68

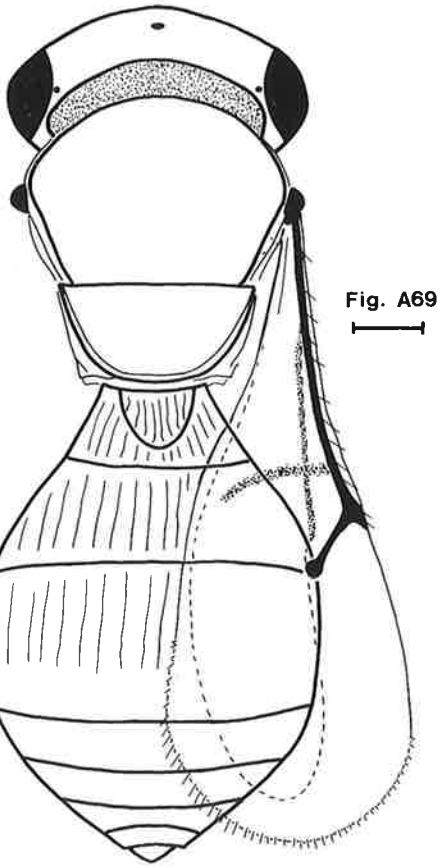

Fig. A69

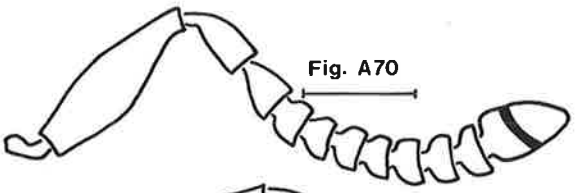

Fig. A70

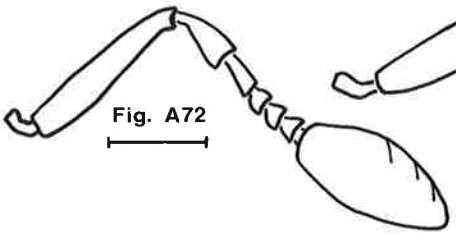

Fig. A72

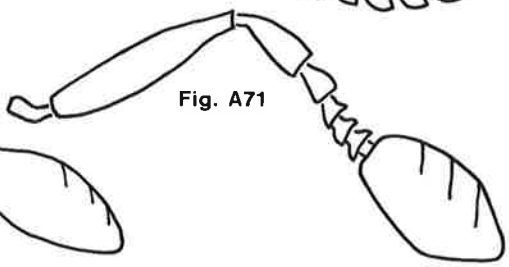

Fig. A71

frons slightly arched; anteriorly, head subtriangular; occiput slightly depressed medially; eyes separated by slightly more than 1/2 width of head; frons smooth; frontal carina not developed; laterally, gena with margins parallel; antennal scape (A1) L:W (28:5.7), pedicel (A2) (11:5), A3 (6:4), clava large, (27:13.5) with 3 faint incomplete sutures (Figure A72).

Mesosoma strongly compressed anterioposteriorly, posterior surface sloping towards metasoma; dorsally, with punctate sculpturing, covered with short hairs; pronotum not visible; scutum 2x wider than long, L:W (8:16); notauli absent; scutellum transverse, L:W (1:10), with posterior fringe of long hairs; scutellum, metanotum and propodeum strongly excavated posteriorly for reception of horn (Figure A63); propodeal laminae vertical, without teeth dorsally; legs normal.

Wings. Forewings fairly narrow, L:W (47:16), not reaching past T3, not infuscated; venation clear; marginal and postmarginal veins short, stigmal vein long, basal vein present but faint; marginal fringe of hairs moderately long (Figure A68).

Metasoma extremely elongated, approximately 4x longer than head and mesosoma combined, 6x longer than wide, L:W (90:15) (Figure A68), covered with short hairs; horn long, strongly arched anteriorly, cylindrical but flattened apically: T1-T3 including shaft of horn with longitudinal striations; lateral margins of T2-T3, and all T4-T7 with punctate sculpturing.

Male. Unknown.

Host. Unknown.

Note. This species is named after its collector, Dr E.F. Riek. It is the largest species of *Ceratobaeus* so far recorded.

A1.7.8 *Ceratobaeus setosus* Dodd

C. setosus Dodd 1914: 65; Kieffer 1926: 142; Austin 1981a: 85.

Type.- Holotype ♀ on tag, head and wings on slide, No. 1966, SAM: Queensland, Gordonvale (Nelson), 29.x.13, A.P. Dodd.

Other material examined.-
New South Wales: 4 ♀♀, 1 ♂ gold coated on SEM holders, wings and antennae of 1 ♀ and 1 ♂ on slides, 1 ♀ dissected on slide, 21 ♀♀, 4 ♂♂ on tags, ANIC; 17 ♀♀, 3 ♂♂, CNC; 2 ♀♀, HUG, Pearl Beach, Jan. 1976, A.D. Austin, ex eggs *Ixeuticus robustus* (L.Koch) (Araneae); 5 ♀♀, 1 ♂, SAM; 5 ♀♀, 1 ♂, WAITE, Caringbah, 12.iii.76, A.D. Austin; 4 ♀♀, 2 ♂♂, Caringbah, 22.iii.76, A.D. Austin, QDPI.
Queensland: 1 ♀, Brisbane, Sept. 1928, A.P. Dodd; 1 ♀, Gogango, Dec. 1928, A.P. Dodd; 1 ♀, Gordonvale, Nov. 1920 (No collector), ANIC; 6 ♀♀, 2 ♂♂, Maleny, 14.vi.73, M.D. (D.A.I.); 1 ♀, 600-700 m Sunday Creek nr Jimna, 28-29.ix.74, I. Naumann, QDPI.

Female Length 1.3 - 1.5 mm.

Colour. Head and mesosoma black; antennae and legs brown to dark brown; dorsal metasoma dark brown to black, ventral surface dark brown.

Head. L:W:H (8.5:19:15), with punctate sculpturing, covered with dense mat of short hairs (Figure A64); dorsally squarish, slightly wider than mesosoma, not strongly excavated posteriorly; occipital carina sharp, not angled at corners; eyes large, covered with hairs; lateral ocelli touching inner margins of eyes; frons almost straight; anteriorly, head subtriangular in shape; occiput arched; eyes separated by more than 1/2 width of head; frons smooth and shiny; frontal carina very short; laterally, gena with margins converging, rounded ventrally: antennal scape (A1) L:W (24:5.8), pedicel (A2) (10:5), A3 (4.5:5), clava (19:11) with 3 faint incomplete sutures (Figure A71).

Mesosoma. Dorsally slightly arched, with punctate sculpturing, covered with dense mat of short hairs (Figure A65); pronotum not visible at anterior lateral corners; scutum not much wider than long, L:W (11:14.5); notauli absent; scutellum semicircular, L:W (5:11), with crenulated posterior border; metanotum narrow and crenulated; posterior surface of propodeum vertical; laminae diverging slightly, extended into 2 small

sharply pointed teeth dorsally (Figure A66); laterally, mesosoma smooth and shiny; legs normal.

Wings. Forewings just reaching posterior margin of metasoma, L:W (38:15.5); marginal and postmarginal veins short, stigmal vein long, basal vein dark; marginal fringe of hairs short (Figure A69).

Metasoma broad and flat, wider than mesosoma, pointed posteriorly (Figure A69), L:W (30:19), covered with dense mat of short hairs; horn vertical, coarsely sculptured apically, just reaching to level of scutellum (Figure A66); T1-T3 with longitudinal striations; lateral margins of T2-T3 and all T4-T6 with punctate sculpturing.

Male. Differing from female in the following:

Length 1.2 - 1.3 mm; antennae and legs light brown; metasoma dark brown; antennae 12-segmented, A4-A11 wider than long, A11 and A12 approximated (Figure A70); posterior mesosoma identical, except propodeal laminae diverging slightly more than in female; forewings long, reaching well past posterior metasoma, L:W (42:16); metasoma broad, slightly wider than mesosoma, rounded posteriorly, L:W (24:18); anterior T1 expanded dorsally into hump, not reaching above propodeum (Figure A67), longitudinal striations reaching to anterior margin; T2-T6 with long scattered hairs.

Note. *C. setosus* has only been collected on the coast of Queensland and New South Wales. In New South Wales this species has been reared from the eggs of *Ixeuticus robustus* (L.Koch) and *I. martius* (Simon) (Amaurobiidae), collected from around buildings and under bark of eucalypt trees. One other species, *Idris ixeutici* (Hickman), has also been recorded as parasitizing the eggs of these 2 spiders in Tasmania, Victoria, inland New South Wales and South Australia.

APPENDIX 2

KNOWN HOSTS OF SCELIONID SPECIES THAT PARASITIZE THE EGGS OF SPIDERS

Known hosts of scelionid species that parasitize the eggs of spiders (see 6.2 and 6.3.1).

Tribe and Genus	Species	Host Species	Family*	Reference**	Ovipositional Strategy (see 6.3.3)
Tribe Baeini					
Aneurobaeus	*A. apterus* Bugion and Popoff	*Argiope aetherea* (Walckenaer)	Araneidae (NA)	Kieffer (1926)	-
		Argiope catenulata Doleschall	"	"	
Baeus	*B. americanus* Howard	*Enoplognatha marmorata* (Hentz)	Theridiidae (NA)	Auten (1925)	-
		Araneus sp. (from *Epeira*)	Araneidae (NA)	Howard (1890)	
			"	Ashmead (1893)	
		Araneus (?) sp. (from *Epeirida*	"	Kieffer (1926)	
	B. castaneus castaneus Kieffer	*Theridium* (?) sp.	Theridiidae (NA)	Kieffer (1926)	
	B. castaneus krygeri Kieffer	*Micryphantes* (?) sp.	Linyphiidae (NA)	Kieffer (1926)	
	B. latrodecti Dozier (synonymy: *B. californicus* in Muesebeck 1979)	*Latrodectus mactans* (Fabricius)	Theridiidae (NA)	Pierce (1938, 1942) Eason *et al.* (1967) Pemberton and Rosa (1940)	inside
	B. rotundiventris Gahan	*Enoplognatha marmorata* (Hentz) (?)	"	Auten (1925)	
	B. semiluvum Haliday	*Dysdera erythrina* (Walckenaer)	Dysderidae (NA)	Vachon (1955)	-
		Tegenaria picta Simon	Agelenidae (NA)	"	
		Micryphantes sp.	Linyphiidae (NA)	"	
		Theridium sp.	Theridiidae (NA)	Kieffer (1926) Vachon (1955)	
	B. achaearaneus Loiácono	*Achaearanea tepidariorum* (C.L. Koch)	"	Valerio (1976)	
	Baeus sp.	*Pardosa* sp.	Lycosidae (NA)	Masner (1976)	-
	Baeus sp.	*Cyrtophora moluccensis* (Dolaschall)	Araneidae (NA)	Lubin (1974)	-
	B. saliens (Hickman)	*Aulacocyba subitanea* (OP. Cambridge) (from *Microctenonyx*)	Linyphiidae (A)	Hickman (1967b)	inside
	Baeus sp.	*Celaenia* sp.	Araneidae (A)	n.r.	-
	Baeus sp.	*Argiope aetherea* (Walckenaer)	"	n.r.	inside
	Baeus sp.	*Araneus* sp.	"	n.r.	-
	Baeus sp.	*Steatoda livens*	Theridiidae (A)	n.r.	-
Mirobaeoides	*M. atra* (Hickman)	*Oxyopes mundulus* L.Koch	Oxyopidae (A)	Hickman (1967b)	both
Tribe Embidobiini					
Echthrodesis	*E. lamoral*: Masner	*Desis formidabilis* (OP. Cambridge)	Amaurobiidae (NA)	Masner (1968, 1976)	-
Mirobaeus	*M. pilosus* Hickman	*Stiphidium facetum* Simon	"	Hickman (1967b)	-
Tribe Idrini					
Ceratobaeus	*C. ater* (Hickman)	*Trite albopilosa* (Keyserling)	Salticidae (A)	Hickman (1967b)	outside
	C. clubionus Austin	*Clubiona cycladata* Simon	Clubionidae (A)	n.r.	outside
		Clubiona Sp.A			(both sometimes)
	C. cuspicornutus Austin	*Clubiona cycladata* Simon	"	n.r.	outside
		Clubiona Sp.A			
	C. flavipes (Hickman)	*Stiphidium facetum* Simon	Amaurobiidae (A)	Hickman (1967b)	-
	C. intrudae Austin	*Intruda* sp.	Gnaphosidae (A)	n.r.	outside
	C. lamponae (Hickman)	*Lampona cylindrata* L.Koch	"	Hickman (1967b)	outside
	C. masneri Austin	*Clubiona robusta* L.Koch	Clubionidae (A)	n.r.	outside
		Clubiona cycladata Simon	"	n.r.	
		Clubiona Sp.A	"	n.r.	
		Hemicloea sp.	Gnaphosidae (A)	n.r.	(both sometimes)
	C. platycornutus Austin	*Clubiona* sp.	Clubionidae (A)	n.r.	outside
	C. setosus Dodd	*Ixeuticus robustus* (L.Koch)	Amaurobiidae (A)	n.r.	outside
		Ixeuticus martius (Simon)	"	n.r.	outside

cont./

(continued) ...

Tribe and Genus	Species	Host Species	Family	References	Ovipositional Strategy (see 6.3.3)
Hickmanella	*H. holoplatysa* Austin	*Holoplatys* sp.	Salticidae (A)	Austin (1981b)	inside
	H. intrudens (Hickman)	*Breda jovialis* (L.Koch)	"	Hickman (1967b), Austin (1981b)	
Idris	*I. flavicornis* Foerster	*Pardosa* spp.	Lycosidae	Kessler and Fokkinga (1973)	-
		Lycosa sp.	"	Huggert (1979)	
		Arctosa perita (Latreille)	"	Kieffer (1926)	
	I. flavoclavatus (Kieffer)	*Segestria senoculata*	Segestriidae (NA)	Huggert (1979)	-
		possibly *Linyphia* sp. (unconfirmed)	Linyphiidae (NA)		
	I. piceiventris (Kieffer)	*Meta segmentata* (Clerek) (unconfirmed)	Tetragnathidae (NA)	Huggert (1979)	-
	I. saitidus (Howard)	*Habrocestum pulex* (Hentz) (from *Saitis*)	Salticidae (NA)	Auten (1925), Howard (1890), Kieffer (1926), Masner (1964), Masner and Muesebeck (1968), Muesebeck (1979)	-
		Phidippus opifex (McCook)	"	Muesebeck (1979), Muesebeck and Masner (1967)	
		Phidippus audax (Hentz) (from *P. mortisans*)	"	Ashmead (1893), Auten (1925)	
	Idris sp.	*Pardosa lapidicina* Emerton	Lycosidae (NA)	Eason *et al.* (1967)	-
	Idris sp.	*Avicosa avida* (Walckenear)	"	Eason *et al.* (1967)	outside
	Idris sp.	*Uloborus* sp.	Uloboridae (NA)	Bradoo (1972)	outside
	Idris sp.	*Agelenopsis potteri* (Blackwell)	Agelenidae (NA)	Harrington (1978)	-
	I. flavipes Dodd	*Theridium* sp.	Theridiidae (A)	n.r.	
	I. helpidis (Hickman)	*Helpis* sp.	Salticidae (A)	Hickman (1967b)	-
	I. ixeutici (Hickman)	*Ixeuticus robustus* (L.Koch)	Amaurobiidae (A)	Hickman (1967b)	inside
		Ixeuticus martius (Simon)	"	Hickman (1967b)	-
	I. niger (Hickman)	*Argoctenus nebulosus* Simon	Ctenidae (A)	Hickman (1967b)	inside
	I. spadix (Hickman)	*Dipoena* sp.	Theridiidae (A)	Hickman (1967b)	-
	I. scutellaris (Dodd)	*Lycosa godeffroyi* (L.Koch)	Lycosidae (A)	n.r.	-
	I. theridii (Hickman)	*Theridium properum* Keyserling	Theridiidae (A)	Hickman (1967b)	-
	Idris sp.	*Argyrodes colubrinus* (Keyserling)	"	n.r.	inside
	Idris sp.	eggsac unknown genus	Gnaphosidae (?)	n.r.	-
	Idris sp.	*Tharpyna* (?) sp.	Thomisidae (A)	n.r.	-
	Idris sp.	*Euryopis* sp.	Theridiidae (A)	n.r.	inside
	Idris sp.	*Breda jovialis* (L.Koch)	Salticidae (A)	n.r.	inside
	Idris sp.	*Theridium* (?) sp.	Theridiidae (A)	n.r.	-
Odontacolus	*Odontacolus*	*Clubiona cycladata* Simon	Clubionidae (A)	n.r.	outside

* (NA) : Record from overseas (not Australian)
(A) : Record from Australia

** n.r. : New record

genus (?) : Genus not accurately determined
species (?) : Genus determined; species unknown or not accurately determined

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