BIOLOGICAL CONTROL OF THE EUCALYPT BORERS, *PHORACANTHA SEMIPUNCTATA* (FABRICIUS) AND *P. RECURVA* NEWMAN (COLEOPTERA: CERAMBYCIDAE) IN SOUTH AFRICA

by

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DECLARATION

I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

Judy A. Moore

December 2003

ABSTRACT

The losses incurred to by the South African hardwood industry because of damage caused by the larvae of the Australian eucalyptus borers *Phoracantha semipunctata* (Fabricius) and *P. recurva* Newman (Coleoptera: Cerambycidae) were countered by the introduction of various biological control agents. *Megalyra fasciipennis* Westwood (Hymenoptera: Ichneumonidae), restricted to the southwestern Cape for nearly 91 years after its probable establishment in 1910, is a specialist pupal parasitoid achieving a parasitism level of up to 52.5 %. It has an activity peak in early spring, which coincides with the pupation of a large percentage of its hosts that had overwintered as larvae. The average length of the ovipositor of *M. fasciipennis* (42.71 ± 5.33 mm S.D.) was longer than the average tunnel length (31.34 ± 11.85 mm S.D.) to the pupal chamber of *Phoracantha* spp. within the log despite variations in the thicknesses of the eucalypt stems. Stem thickness therefore did not adversely affect the level of parasitism. *Megalyra fasciipennis* adults are diurnal, with activity largely determined by temperature. Over 70 % were active between 25 °C and 34 °C, the minimum threshold for activity being 16 °C. Optimum temperature for oviposition was 30 °C. Males became active before the females and maximum oviposition occurred between 10h00 and 15h00.

In 1993, a host specific egg parasitoid, *Avetianella longoi* Siscaro (Hymenoptera: Encyrtidae), was introduced for the control of *Phoracantha* spp. A total of 7791 *A. longoi* adults and 80 parasitised eggs were released around Cape Town between 1993 and 1995 before establishment was confirmed. Dispersal was monitored annually and was

determined to occur at a rate of 50 km/year. By 1998 *A. longoi* had dispersed 300 km north of Cape Town to Lutzville and 270 km east to Riversdal. Subsequent to a satellite release in Knysna during 1994, it has been established 40 km from this release site, at Plettenberg Bay. The parasitoid has also bridged a 10 km expanse of ocean to establish on Robben Island, immediately off the west coast of Cape Town. *Avetianella longoi* has a preference for the eggs of *P. semipunctata,* which is the most likely cause for the decline in the population of *P. semipunctata.* However, *P. recurva* remains relatively unaffected. Average parasitism of *Phoracantha* spp. eggs by *A. longoi* was 59.4 %.

An undescribed *Cleonymus* sp. (Hymenoptera: Pteromalidae) of unknown origin (the genus being widely distributed on several continents), was discovered in the Cape Peninsula parasitising late instar larvae of *P. semipunctata* and *P. recurva.* This ectoparasitoid lays its eggs (mean number per larva = 20.3 ± 15.2 S.D.) through the bark into the host chamber after the host has been paralysed. The host is entirely consumed and pupation takes place in the chamber with wasps emerging in the ratio of 1 male : 3 females. Although uncommon in the field, mass rearing of these wasps in culture was easily accomplished and a consignment was released in the Tzaneen district in 1993, where it was confirmed to have become established in 1996. Bark thickness constraints on the effectiveness of this parasitoid as a biological control agent because it's short ovipositor restricts the wasp to certain eucalypt species or trees with thin bark.

The introduction into South Africa in 1995 and attempted establishment of the larval parasitoids, *Syngaster lepidus* Brullé (Hymenoptera: Braconidae), *Jarra phoracantha*

Marsh & Austin (Hymenoptera: Braconidae) and *J. maculipennis* Marsh & Austin proved unsuccessful in the Western Cape. However, the former two species were established in the Tzaneen district and their recruitment for release in the Western Cape should be considered.

The present guild of biological control agents has been insufficient to give the required control. In the absence of biological control agents, intraspecific competition amongst host larvae is the major mortality factor. Although high levels of mortality are achieved as a result of parasitism despite the biological constraints of the parasitoids (e.g. the narrow activity peak of *A. longoi* and the restriction of *Cleonymus* sp. to thin barked eucalypts), their combined parasitism has succeeded in reducing the competition between host larvae, resulting in fewer yet larger host beetles emerging. The introduction of additional viable agents to assist in the biocontrol of *Phoracantha* spp. is required.

UITTREKSEL

Die verliese wat die Suid-Afrikaanse hardehoutbedryf ly as gevolg van skade veroorsaak deur die bloekomboorders *Phoracantha semipunctata* en *P. recurva* (Coleoptera: Cerambycidae), is bekamp deur die invoer van verskeie biologiese beheeragente. *Megalyra fasciipennis* Westwood (Hymenoptera: Ichneumonidae), beperk tot die Suidwes-Kaap vir byna 91 jaar nadat dit waarskynlik in 1910 daar gevestig is, is 'n spesialis papieparasitoïd wat 'n parasitismevlak van tot 52.5% bereik. Dit het 'n aktiwiteitspiek in die vroeë lente wat saamval met die papievorming van baie gasheerlarwes wat oorwinter het. Die gemiddelde lengte van die eierboor van *M. fasciipennis* (42.71 ± 5.33 mm S.A.) was langer as die gemiddelde tonnellengte (31.34 ± 11.85 mm S.A.) na die papieholte van die gasheer binne in die hout, ten spyte van die variasie in die dikte van die bloekomstamme. Stamdikte het dus nie 'n nadelige uitwerking op die vlak van parasitisme nie. Volwassenes van *M. fasciipennis* is bedags aktief en aktiwiteit word hoofsaaklik deur temperatuur bepaal. Meer as 70% was tussen 25 °C en 34 °C aktief, met 16 °C as die minimum drumpel vir aktiwiteit. Mannetjies het voor die wyfies aktief geword en maksimum eierlegging het tussen 10h00 en 15h00 plaasgevind.

In 1993 is die gasheerspesifieke eierparasitoïd *Avetianella longoi* Siscaro (Hymenoptera: Encyrtidae) vir die beheer van *Phoracantha* spp. ingevoer. Van 1993 tot 1995 is 7791 volwassenes van *A. longoi* en 80 geparasiteerde eiers rondom Kaapstad vrygelaat en dis vasgestel dat die spesies gevestig het. Die verspreiding daarvan is jaarliks gemonitor en

dis vasgestel dat dit teen 50 km per jaar plaasvind. Teen 1998 het dit versprei tot 300km noord van Kaapstad na Lutzville en 270 km oos na Riversdal. Na 'n satelliet-loslating by Knysna in 1994 het dit 40 km verder by Plettenbergbaai gevestig. Die parasitoïd het ook 10 km van die oseaan oorgesteek om op Robbeneiland, wes van Kaapstad te vestig. *Avetianella longoi* gee voorkeur aan die eiers van *P. semipunctata* en dis waarskynlik die rede vir die afname in die getalle van hierdie spesies, maar *P.recurva* word relatief min beïnvloed. Die gemiddelde graad van parasitisme van *Phoracantha* spp. was 59.4%.

Dit is gevind dat 'n onbeskryfde *Cleonymus* sp. (Hymenoptera: Pteromalidae) van onbekende oorsprong (die genus kom wyd verspreid in verskeie vastelande voor) die laat instar larwes van *P. semipunctata* en *P. recurva* parasiteer. Hierdie ektoparasitoïd lê sy eiers (gemiddeld 20.3 ± 15.2 S.A.) in die gasheerholte nadat die gasheer eers verlam is. Die gasheer word heeltemal opgevreet en pupering vind plaas in die holte plaas. Volwassenes kom uit in verhoudingvan drie mannetjies tot een wyfie. Alhoewel skaars in die natuur, kan hierdie wesp maklik in massa geteel word. 'n Besending is in die Tzaneen distrik vrygestel en in 1996 is vasgestel dat hulle gevestig het. Basdikte is 'n beperkende faktor in die gebruik van hierdie parasitoïd as effektiewe beheeragent vir biologiese beheer omdat die kort lengte van die eierboor die wesp sal beperk tot bloekomsoorte met dun bas.

Die invoer na Suid-Afrika in 1995 en vestiging van die larwale parasitoïde *Syngaster lepidus* Brullé (Hymenoptera: Braconidae), *J. phoracantha* Marsh & Austin (Hymenoptera: Braconidae) en *J. maculipennis* Marsh & Austin was onsuksesvol in die

Wes-Kaap. Die twee spesies is egter in die distrik Tzaneen gevestig en versameling met die oog op loslating in die Wes-Kaap behoort oorweeg te word.

Die huidige gilde van biologiese beheer-agente is onvoldoende om die vereiste graad van beheer te verskaf. In die afwesigheid van biologiese beheer-agente is intraspesifieke kompetisie tussen gasheerlarwes die belangrikste mortaliteitfaktor. Alhoewel hoë vlakke van mortaliteit as gevolg van parasitisme bereik word, ten spyte van die biologiese beperkings van die parasitoïde (bv. die kort aktiwiteitspiek van *A. longoi* en die beperking van *Cleonymus* tot bloekoms met dun bas), het die gekombineerde parasitisme daarin geslaag om die kompetisie tussen gasheerlarwes te verlaag, met die gevolg dat minder maar groter gasheerkewers verskyn het. Dit is dus nodig dat addisionele organismes gevestig word om by te dra tot die biologiese beheer van *Phoracantha* spp.

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Female *Phoracantha semipunctata* beetle

CHAPTER ONE

INTRODUCTION

1.1 Species and origin

Two species of Eucalypt longhorned borer beetles of the genus *Phoracantha* (Coleoptera: Cerambycidae) occur in South Africa, viz. *P. semipunctata* (Fabricius) and *P. recurva* Newman. They are native to Australia, along with 38 other *Phoracantha* species (Wang 1995) and were most probably inadvertently introduced by ship from Australia into South Africa in railway sleepers around the turn of the century (Lounsbury 1917). *Phoracantha semipunctata* was first reported in South Africa in Wolseley in the Western Cape in 1906.

In Australia, *P. semipunctata* and *P. recurva* are only incidental pests of mainly drought-stressed eucalypts and of trees from other closely-related Myrtaceae genera such as *Syncarpia* and *Angophora* (Duffy 1963; Moore 1963), as well as those which have been felled (Austin *et al.* 1994). Although the *Phoracantha* genus is mainly distributed in southern Australia, *P. semipunctata* and *P. recurva* are the two most widely distributed of the 40 species, occurring throughout Australia in all six biogeographic subregions. This wide distribution and consequent adaptation to different climatic zones supports the observation that these two species are more likely than the other species to find their way to and become established on other continents (Wang *et al.* 1999).

1.2 Distribution

Phoracantha semipunctata is already widespread in several continents. This includes its relatively recent arrival in countries in South America: Chile (Jayawickrama *et al.* 1993), Argentina, Uruguay and Brazil (Berti-Filho *et al.* 1995) and North America (Scriven *et al.* 1986). It has also been recorded from East Africa: Moçambique (Veiga Ferreira 1964), Malawi (Powell 1978), Zambia (Löyttyniemi 1983); from the Mediterranean Basin: Turkey (Acatay 1959), Italy (Tassi 1970; Romano & Carapezza 1975), Portugal (Way *et al.* 1992; Araujo 1990), Spain (Cymorek 1984; González Tirado 1992; Saiz de Omenaca & Rodríguez 1991), Morocco (Haddan *et al.* 1988; El-Yousfi 1992), the Canary Islands (Estevez 1988) and Israel (Bytinski-Salz & Neumark 1952; Spetter 1963) where the only major natural enemy is the Syrian woodpecker (Mendel 1984). *Phoracantha semipunctata* has also been recorded in Europe (Piras *et al.* 1970; Lepesme 1950). *Phoracantha* spp. were not recorded in *Eucalyptus* woodlots in Thailand (Hutcharern & Sabhasri 1985), in India (Thakur 1988) nor in the USSR (Orlinskii *et al.* 1991).

Phoracantha recurva was first discovered in South Africa in 1937 at Brakpan in Gauteng Province where it was identified as a separate species to that of *P. semipunctata* (Drinkwater 1975). *Phoracantha semipunctata* and *P. recurva* are distributed throughout South Africa where *Eucalyptus* spp. occur. The distribution of the two species may have been greatly accelerated by the transportation of infested firewood by rail over great distances. In contrast to the handling of timber, the bark of firewood is not stripped and is consequently more likely to become infested with *Phoracantha* larvae.

1.3 Local hosts

In South Africa, a list of 48 tree species, mostly belonging to the genus *Eucalyptus* (Drinkwater 1975), has been compiled as hosts for the two *Phoracantha* species (Van den Berg 1979). Both *Phoracantha* species are attracted to the odours emanating from most species of felled or stressed eucalypts (Paiva *et al.* 1993), which they then select for oviposition. Although *Eucalyptus grandis, E. saligna*, *E. diversicolor*, *E. paniculata* and *E. maculata* are especially attractive to the beetles, healthy eucalypts remain immune from attack (Drinkwater 1975). Adult cerambycid beetles show a marked predilection for the host in which they had fed as larvae (Linsley 1959). *Eucalyptus* species that are resistant to attack by *Phoracantha* spp. are those that are most tolerant of drought in Australia, for example *E. camaldulensis* & *E. cladocalyx* (Hanks *et al.* 1995c; Poynton 1960). Bark moisture content also plays a critical role in resistance of *Eucalyptus* against colonisation by *Phoracantha* larvae (Hanks *et al.* 1991). Oviposition behaviour of the adult beetles could also contribute to restrictions of the host range of *P. semipunctata* to *Eucalyptus* species (Hanks *et al.* 1995b).

1.4 Oviposition

Phoracantha recurva and *P. semipunctata* favour different oviposition sites on a chosen *Eucalyptus* tree. *Phoracantha recurva* has been observed to lay eggs mostly under smooth loose bark on the upper section of the main trunk and branches. *Phoracantha semipunctata* beetles, on the other hand, prefer to deposit their eggs under generally rougher bark on the trunk and branches of the lower section of the tree. This results in

the larvae feeding on the cambium and inner bark on the lower section of the tree and thus starving the entire tree of nutrients. It is for this reason that *P. semipunctata* larvae cause more deaths of trees than *P. recurva*.

1.5 Biology

Phoracantha spp. have up to three generations per year (Mendel *et al.* 1984; Scriven *et al.* 1986). Adult *Phoracantha* spp. beetles lived for several months and laid an average of 29 eggs per batch (n = 94, S.D. = 16.87) in protected places beneath loose bark and especially where the main branches fork from the stem. The larvae hatch within 4 - 10 days. Larval development varies from 70 – 180 days (Scriven *et al.* 1986) when they fed superficially beneath the bark, later tunneling deep into the heartwood to pupate in excavated cells. The pupal stage lasted between 10 and 20 days (Scriven *et al.* 1986). In this study the adults emerged and laid eggs from about September to April, though they were generally active for most of the year including the winter months. This is in agreement with the observations of Winstanley (1985) in South Africa in winter rainfall areas.

1.6 Damage

The structural damage to *Eucalyptus* timber and poles by *Phoracantha* spp. is mainly caused to the sap- and heartwood. This occurs once the emerged larvae have fed under the bark until they reach the final instar which then bores through to the core of drought-stressed or freshly-felled *Eucalyptus* tree to pupate (Annecke & Moran 1982), hence weakening the wood and lowering the quality of the wood commercially. Large numbers

of *Phoracantha* larvae can cause damage to the xylem to such an extent that the timber is no longer marketable. The tunnels made by final instar *Phoracantha* larvae provide an ideal route through the sapwood to the heartwood for wood-destroying agents such as pathogens, fungi and termites. Because such holes weaken the timber, power transmission poles can not have more than five *Phoracantha*-made holes in any one metre length of pole, according to the South African Bureau of Standards, No. 753 & 754 (Drinkwater 1975). In May 1993, 35 % of *Eucalyptus* saw logs in South Africa were rejected because of *Phoracantha* damage, resulting in a loss of R5,6 million to the timber industry (De Laborde & Atkinson 1993). The potential losses of eucalypts because of *Phoracantha* spp. Borer damage are, however, extremely difficult to differentiate from losses caused by drought (De Laborde & Atkinson 1993). Once drought stressed trees are invaded by *Phoracantha* borers they rarely recover. The losses to the timber industry have necessitated steps to curb the beetle numbers and dispersal into uncolonised areas.

1.7 Control

Several early silvicultural methods that were used to prevent damage to eucalypt logs by *Phoracantha* beetles are still in practice today. For example, in the production of poles, the standard control method is to strip bark from newly felled trees to eliminate potential oviposition sites, but this is very labour intensive (Tooke 1936). Other control methods include the prompt utilization of infested wood and the selective planting of suitably resistant *Eucalyptus* species in specific climatic regions (Tooke 1936). The prospect for chemical control is limited because *Phoracantha* spp. adults hide under loose bark and in cracks in stems during the day. The destructive larval stage occurs beneath the bark and

within the sapwood of felled or stressed *Eucalyptus* trees (Winstanley 1985) but remains unaffected even by systematic insecticides (Ali *et al.* 1989; Paine *et al.* 1995) which may not be translocated around the tree because of possible drought and xylem damage. Biological control offers an environmentally safer, more promising and cost effective alternative. South Africa experiences periodic droughts which favour *Phoracantha* attacks, therefore a long term program was launched to neutralize *Phoracantha* damage by importing biological control agents.

Several unsuccessful attempts at the biological control of *P. semipunctata* and *P. recurva* have been made in South Africa since their first appearance in 1906 (Tooke 1936). Hymenopteran parasitoids of the family Megalyridae were introduced to Cape Town from New South Wales, Australia in 1910 as biological control agents but all attempts to rear them failed (Webb 1974). The parasitoids either escaped from the laboratories or were discarded because in 1962 adult *Megalyra fasciipennis* Westwood were recovered from logs infested with *Phoracantha* spp. in Durbanville, Western Cape (Gess 1964). Lounsbury (1917) recorded that braconid parasitoids were imported from Australia in 1915, but that all attempts to breed them in South Africa failed. No further details were recorded. In 1968 consignments of the most promising of the braconid larval parasitoid species, *Syngaster lepidus* Brullé were received from Australia (Drinkwater 1973) together with specimens of two other larval parasitoids, *Callibracon* (*Bracon*) *capitator* (F). and a *Doryctes* sp. (possibly *Jarra maculipennis* or *J. phoracantha* – see Austin *et al.* 1994). Consignments of up to 2500 pupae and adult *S. lepidus* were sent from Australia over the next two years and were reared for release in South Africa (Moore 1972).

Difficulties in maintaining the parasitoid culture or mass rearing these wasps resulted in the remaining 78 individuals of *S. lepidus* being released in 1971 (Drinkwater 1973) but there is no record of them having become established (Annecke & Moran 1982).

1.8 Aims of the present study

This investigation deals with the assessment of the established parasitoid species, *M. fasciipennis* and *Cleonymus* sp. as biological control agents and the introduction, mass rearing, release and establishment of the egg parasitoid *Avetianella longoi* and of the larval parasitoids, *Jarra phoracantha*, *J. maculipennis*, and *Syngaster lepidus*. Successive monitoring of the dispersal of the parasitoids from their release sites and the subsequent collection and manual dispersal of parasitoids from established breeding sites to new sites was implemented. A final assessment was made of the effectiveness of the present complex of parasitoid species as biological control agents of *Phoracantha* with suggestions to improve the level of control achieved thus far.

***Phoracantha* spp. eggs laid under *Eucalyptus* bark**

***Phoracantha* spp. breeding container with egg trap strips taped to glass lid**

CHAPTER TWO

MEGALYRA FASCIIPENNIS, PUPAL PARASITOID OF *PHORACANTHA* SPP.

2.1 Introduction

Megalyra fasciipennis Westwood (Hymenoptera: Ichneumonidae) originates from Australia (Froggatt 1907; Austin *et al.* 1994) where it has been recorded as a larval parasitoid of several species of *Phoracantha,* including *P. semipunctata* and *P. recurva* (Froggatt 1906). It is the most common and widespread of the Australian megalyrids, being widely distributed in both summer and winter rainfall regions in its native Australia along the eastern and southeastern coasts, in southwestern Australia and Tasmania (Austin *et al.* 1994) (Fig. 1). This widespread distribution and similarity to climatic conditions in South Africa holds promise for its establishment in southern African eucalypt production areas. Species of two genera of indigenous megalyrids have been recorded from South Africa, *Dinaspis* and *Megalyridia*, which are probably parasitic in the larvae of xylophagous beetles (Scholtz & Holm 1985; Hedqvist 1951; Waterston 1922). One megalyrid is reported from neighbouring Madagascar (Hedqvist 1967) and three from South America (Shaw 1987).

In 1982, two female *M. fasciipennis* wasps were discovered in Lebanon Plantation (34°12'S, 19°07'E), Western Cape Province and during the years a few more females were sighted and captured. At the beginning of 1993, 44 male and 31 female *M. fasciipennis* emerged from *Eucalyptus* logs collected in Tokai Plantation (34°03'S, 18°25'E). Subsequently, during the summer months of 1994 to 1999, many more specimens of both

sexes were found in the Cape Town area, some as far as Wolseley (33°24'S, 19°12'E) (200 km NE of Cape Town).

Fig. 1. Distribution of *Megalyra fasciipennis* in Australia (after Shaw 1990; Austin *et al.* 1994)

The biology of *Megalyra fasciipennis* was assessed in this study. The potential of this natural enemy in the control of the two South African *Phoracantha* species was also evaluated. Very few studies on the biology of this parasitoid have been carried out in Australia (Rodd 1951) and none in South Africa. This information is necessary for assessing its potential as a biological control agent of the two *Phoracantha* species.

2.2 Materials and Methods

2.2.1 Distribution

The distribution of *M. fasciipennis* was assessed from observations of adults occurring on felled *Eucalyptus* spp. logs in plantations throughout the Western Cape during the peak ovipositing season between the years 1992 and 1999.

A consignment of 60 wasps (26 males and 34 females) was sent to Mpumalanga in 1993 for release in the *Eucalyptus* plantations in the Tzaneen district (23°50'S, 30°09'E) in an attempt to physically distribute and establish *M. fasciipennis* over a wider area.

2.2.2 Confirmation as pupal parasitoid

To confirm them as pupal parasitoids, observations were made of oviposition behaviour of captured *M. fasciipennis* females released on infested *Eucalyptus* spp. logs collected in Tokai Plantation and placed in a large gauze-covered cage.

2.2.3 Percentage parasitism by *Megalyra fasciipennis*

To determine percentage parasitism, logs infested with *Phoracantha* spp. were collected from Tokai Plantation every two weeks throughout the year, and left in a culture room at room temperature to allow for host or parasitoid emergence. The total number of each emerging species was recorded and compared.

At the same time, sections of *Phoracantha*-infested logs exposed to *M. fasciipennis* female wasps were split open using an axe and the pupal chambers were examined for

their contents. Total numbers of parasitoid larvae or pupae were compared to the total number of hosts recorded out of a total of 48 pupal chambers exposed.

2.2.4 Seasonal activity peaks and sex ratio

To determine seasonal activity peaks and the sex ratios of *M. fasciipennis* as well as the same of *P. semipunctata* and *P. recurva* in South Africa, logs from clearfelled *E. diversicolor* F. Mueller (Karri) windbreaks within Tokai Plantation were transferred to laboratory cages once the majority of *Phoracantha* spp. had pupated. Adult *M. fasciipennis, P. semipunctata* and *P. recurva* emerging in these cages were recorded daily. Weekly counts of beetles and wasps collected from felled trees by hand directly into containers were made at the original site in Tokai Plantation between 1992 and 1999. These two data sets were combined.

During a study of the *Eucalyptus* defoliating tortoise beetle, *Trachymela tincticollis* (Blackburn), from September 1983 to March 1991 (Tribe & Cillié 1997), sticky traps were set to monitor insect activity within a stand of *Eucalyptus gomphocephala* A. DC. trees at Kommetjie. *Megalyra fasciipennis* wasps found to be caught on these sticky traps were recorded (Table 1). The sticky traps consisted of three sets of 4-vaned gauze intercept traps, each 580 mm long and 570 mm high, mounted on a pole at 2 m, 4 m and 6 m and coated with Plantex (sticky ant barrier) on both sides. The pole was attached to a fulcrum so that it could be lowered like a boom. The number, direction, height and date at which the wasps were caught were recorded, as well as the daily temperatures and rainfall.

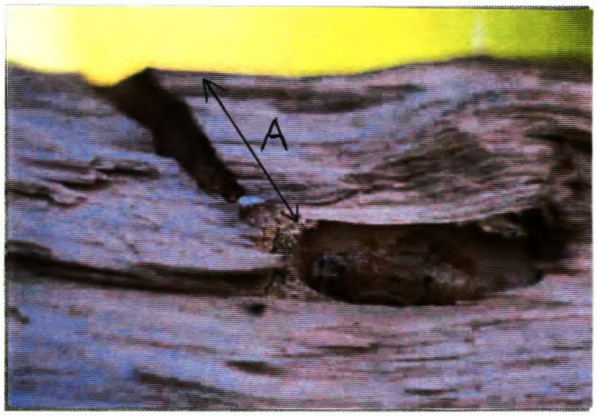
2.2.5 Comparison of body to ovipositor length and pupal chamber tunnel length

Successful parasitism of woodboring insects can sometimes be limited by the thickness of the bark in relation to the length of the ovipositor of the parasitoid (see Tribe & Kfir 2001), particularly in the case of larval and pupal parasioids. Similarly, the effectiveness of *M. fasciipennis* as a pupal parasitoid biological control agent would be influenced by the variable depths at which *Phoracantha* spp. pupate in the logs and the number of host pupae that were out of reach of the ovipositor of the wasp. Hence, the length of the female ovipositor compared to the length of the tunnel to the host pupal chamber was measured. The ratio of the ovipositor lengths in relation to the length of the body of the female wasps was also calculated. To determine whether there was sexual dimorphism with regard to size, the body lengths of male wasps were also measured.

Measurements were made using a vernier caliper on live wasp specimens which were held between two glass plates. Throughout the summer season of 1998/1999, all emerging *M. fasciipennis* female wasps in both the laboratory and in the field were caught and the ratio between body and ovipositor lengths was measured.

Sections of *Phoracantha*-infested logs were split open and measurements of all available tunnel lengths to their respective *Phoracantha* pupal chambers were taken to find a possible comparison between the length of the tunnel to the pupal chamber (A) and the length of the female *M. fasciipennis* ovipositor (Fig. 2).

Fig. 2. A *Eucalyptus* log which has been split open showing the *Phoracantha* sp. larval tunnel and pupal chamber containing a *Phoracantha* sp. pupa



2.2.6 Differences in daily activity peaks between male and female *M. fasciipennis* wasps

Further investigations into the oviposition behaviour of *M. fasciipennis* were carried out in a large room-sized gauze-covered cage in which heavily *Phoracantha*-infested field-collected *Eucalyptus* logs were leaned against stands so that the maximum surface area was exposed to the wasps. Oviposition was allowed by exposing the logs, from which loose bark had been stripped to reveal frass-plugged openings of the *Phoracantha* pupal chambers, to *M. fasciipennis* wasps which emerged naturally from logs parasitised during the previous season. The onset and duration of oviposition by individual wasps was recorded together with the temperature at the time of oviposition. Ovipositing females were individually marked on the thorax with dots of paint and the same colour code was painted on the wood beside the *Phoracantha* tunnel leading to the host pupal chamber where oviposition had just occurred. In this way individual wasps could be continually followed and the history of interactions of the parasitoids with their hosts could be recorded. If a female was observed to partially drill her ovipositor through the frass plug, and then withdraw it immediately, this was recorded separately as it was presumed oviposition had not taken place due to unfavourable conditions or an obstruction. The thin 'crystal' layer which is often found deposited within the frass at the pupal chamber entrance, presumably by the final instar larva, may form a physical barrier to the ovipositor.

To determine when oviposition occurred and if this was influenced by temperature, the number of ovipositing wasps was recorded during October 1998 together with the

ambient temperature, both within and outside this gauze-covered cage, at 15 minute intervals from 07:00 until 18:00 on seven days. In addition, the number of active male and female wasps (i.e. those patrolling the log, flying or ovipositing) was recorded at the end of each 15 minute interval, together with those which had left the logs and had moved onto the netting before seeking shelter for the night.

2.3 Results

2.3.1 Distribution

At present *M. fasciipennis* appears to be restricted to the southwestern Cape where it has been for the last 37 years or perhaps even as long as 91 years, based on findings of Gess (1964) and Webb (1974) respectively. None have been recovered from the one satellite release site in the *Eucalyptus* plantations in the Tzaneen district to date, and their establishment there cannot be confirmed. During these studies no indigenous megalyrids were encountered.

2.3.2 Confirmation as pupal parasitoid

Although *M. fasciipennis* was described as a larval parasitoid in previous publications (Froggatt 1906; Hacker 1913; Webb 1974; Austin *et al.* 1994), it was found to be a pupal parasitoid of *Phoracantha* spp. in this study (Moore 1993).

A plug of frass filling the tunnel to the pupal chamber was deposited by the *Phoracantha* final stage larva before pupation. It formed a barrier which protected the otherwise vulnerable pupa within. After locating an occupied pupal chamber, each *M. fasciipennis*

female moved away from the tunnel to a distance equivalent to the length of her ovipositor before moving backwards while 'drilling' her ovipositor through the frass plug towards the pupal chamber. As an ectoparasitoid, an egg would be oviposited within the chamber external to the host pupa, whereas the egg would be ovipositied within the host pupae if *M. fasciipennis* were an endoparasitoid. In both cases, the length of the ovipositor in relation to the depth at which the host had pupated would be crucial for successful parasitism.

Records from 48 *Phoracantha* spp. pupal chambers revealed 11 *M. fasciipennis* pupae or exuviae. Inside one particular chamber, the exuvia of a pupa from which a female *M. fasciipennis* wasp had emerged was found, with the highly coiled ovipositor skin attached. Also present in the chamber from which this wasp emerged, were 25 pure white fecal pellets which indicated that the wasp larva was probably an idiobiont parasitoid (Shaw 1990). There was no wasp cocoon present, as expected for an insect that is protected within an enclosed chamber. There was also evidence of only one wasp parasitoid having emerged, confirming Rodd's (1951) observations of only a single parasitoid per host pupa. *Megalyra fasciipennis* eggs laid on the 26 and 28 January all developed into pupae by the 22 March indicating a total developmental period to adulthood of about 55 days. Unfortunately, logs were only split open once *M. fasciipennis* had pupated, thus missing the completely unstudied parasitoid egg and early larval stages in the *Phoracantha* pupal chamber.

2.3.3 Percent parasitism by *Megalyra fasciipennis*

Percentage parasitism of *Phoracantha* spp. by *M. fasciipennis* from December 1992 until April 1994, as determined from emergences in the laboratory from logs collected in Tokai Plantation, was 52.5 % (55 *P. semipunctata* + 51 *P. recurva* : 117 *M. fasciipennis*). Field collected logs split open in February 1998 revealed 37 chambers containing unparasitised *Phoracantha* pupae and 11 containing *M.fasciipennis* pupae or exuviae, i.e. 22.9 % parasitism. Percentage parasitism of *M. fasciipennis* at different tunnel length intervals showed varying degrees of parasitism (Fig. 3), but 71 % parasitism of pupae resulted from tunnel depths of 11 to 20 mm, which was much higher than parasitism rates at other tunnel lengths. Empty pupal chambers where frass no longer occurred in the tunnel leading to the pupal chamber, were disregarded because it could not be ascertained whether a beetle or a parasitoid had emerged from the chambers.

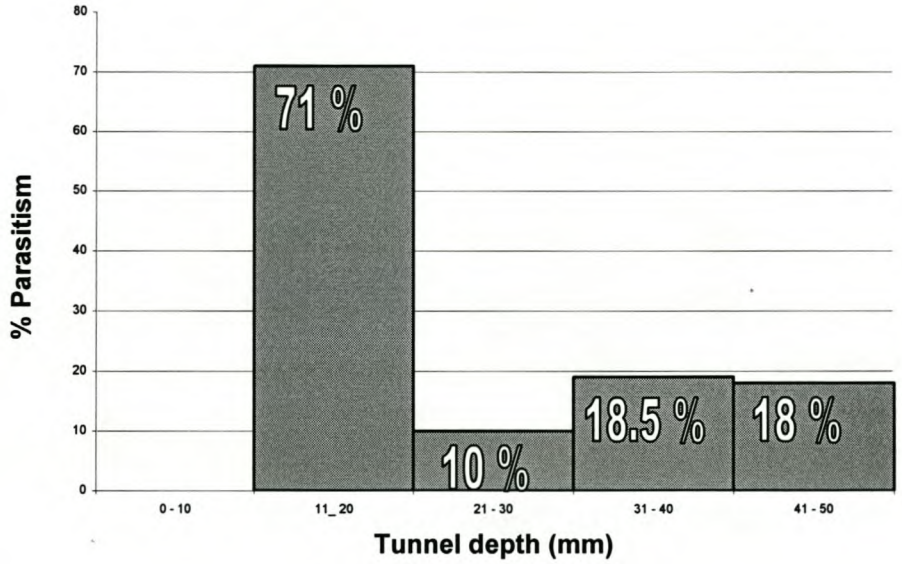


Fig 3. Percentage parasitism of *Megalyra fasciipennis* at varying tunnel depths

2.3.4 Seasonal activity peaks and sex ratio

Phoracantha spp. beetles (collected weekly from logs in laboratory cages at room temperature) were present throughout the year, although there was a distinct spring and a distinct summer activity peak beginning in late August and ending in March (Fig 4). After completing the pupal chamber, many larvae overwintered and only pupated in spring (Duffy 1963). The activity of *M. fasciipennis* was synchronized with that of the pupal stage of its host, the numbers of which peaked in spring (August – October). A distinct decline in numbers of especially *Phoracantha recurva* was recorded around week 45 after the initial peak in spring (Fig. 4). This coincided with the parasitism of *Phoracantha* spp. pupae by *M. fasciipennis* in early spring (week 39-42) before a

resurgence in host numbers around week 49 because of the decline of parasitoid numbers around week 45. The sex ratio calculated from the emerging *M. fasciipennis* wasps was 1 ♀: 1.06 ♂.

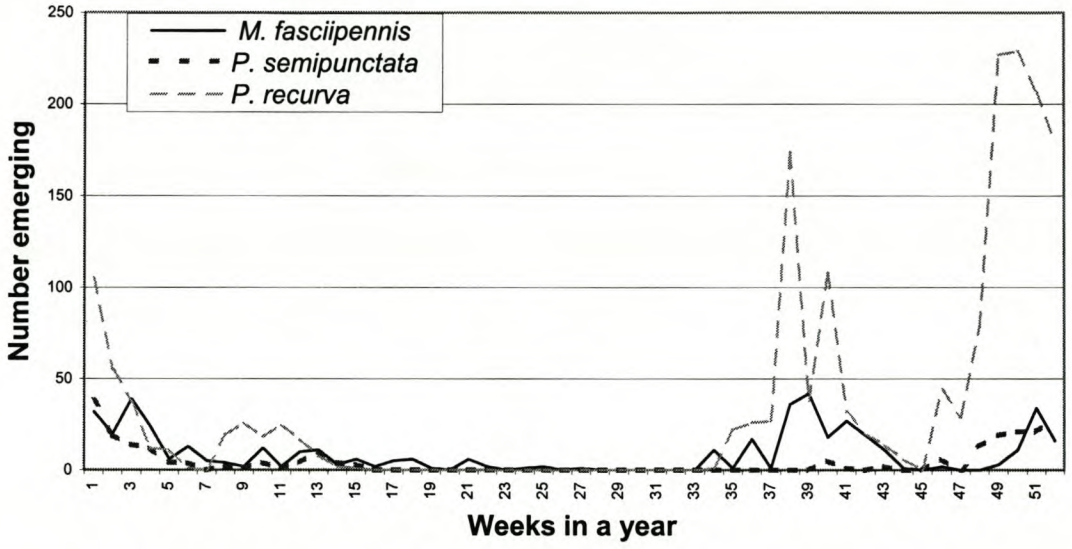


Fig. 4. Weekly emergence of *P. semipunctata* and *P. recurva* beetles in relation to that of the pupal parasitoid *M. fasciipennis* from field collected logs (data for six years combined)

No male *M. fasciipennis* wasps were captured on the sticky traps set for the monitoring of the *Eucalyptus* defoliating tortoise beetle, *Trachymela tincticollis*, probably because the wasps tend to remain on the logs where they mated with emerging virgin females (see section 2.3.6). A small number of female parasitoids were captured on the sticky traps only during the summer months, November to March. This small sample indicated that the females showed no pattern for heights as would be expected when searching for hosts in standing trees (Table 1).

Table 1. *Megalyra fasciipennis* adults caught on 4-vaned sticky traps set at three different heights in a copse of *E. gomphocephala* trees at Kommetjie between September 1983 and March 1991

Date	Number	Height and direction on trap
02/03/1989	2 females	Middle (EN) and bottom (SE)
16/11/1989	1 female	Top (WS)
08/02/1990	1 female	Top (WN)
15/02/1990	1 female	Bottom (NE)
21/02/1991	1 female	Top (WS)
28/02/1991	1 female	Middle (NW)

2.3.5 Comparison of body to ovipositor length and pupal chamber tunnel length

The mean length of the male *M. fasciipennis* wasp was 14.18 (± 1.99 mm S.D., n = 142), as compared to the average female body length of 15.85 (± 1.87 mm S.D., n = 150). This showed that female *M. fasciipennis* wasps were generally slightly larger than their male counterparts. The length of the ovipositor ranged from 28 to 52 mm, with a mean of 42.71 (± 5.33 mm S.D., n = 140) and the mean ratio of body length to ovipositor length was 1 : 2.69 (the ovipositor was almost three times as long as the body).

The tunnel length from the surface of the log to the entrance of the pupal chamber ranged from 7 to 50 mm with a mean of 31.11 ± 11.85 mm S.D. (n = 46). The highest level of parasitism by *M. fasciipennis* occurred at the tunnel length interval of 11 to 20 mm (Fig. 3.). The mean ratio of *Phoracantha* pupal tunnel length in relation to *M. fasciipennis* ovipositor length was 1 : 1.36.

2.3.6 Differences in daily activitiy between male and female *M. fasciipennis* wasps

Both male and female *M. fasciipennis* wasps were mainly active during the summer months from September to April (Fig. 4) and their daily activity was largely determined by temperature. Over 70 % of the wasps were active between ambient temperatures of 25 °C and 34 °C, thus showing a strong correlation with temperature (R = 0.88, n = 56). The temperature at peak wasp activity (13.7 %) was 30 °C (Fig. 5).

Mated *M. fasciipennis* females oviposited continuously and regularly during the day with most activity taking place when temperatures were favourable, i.e. 26 °C to 35 °C (Fig. 6), provided that sufficient *Phoracantha* pupae were available. One female made a maximum of nine attempts (which may or may not have been successful) to oviposit in one day. The duration of oviposition, from the commencement of the ovipositor drilling through the frass-plug blocking the entrance to the host pupal chamber until its withdrawal, was variable, ranging from 5 to 85 minutes with an average time of 22.9 ± 16.94 min. S.D. (n = 63).

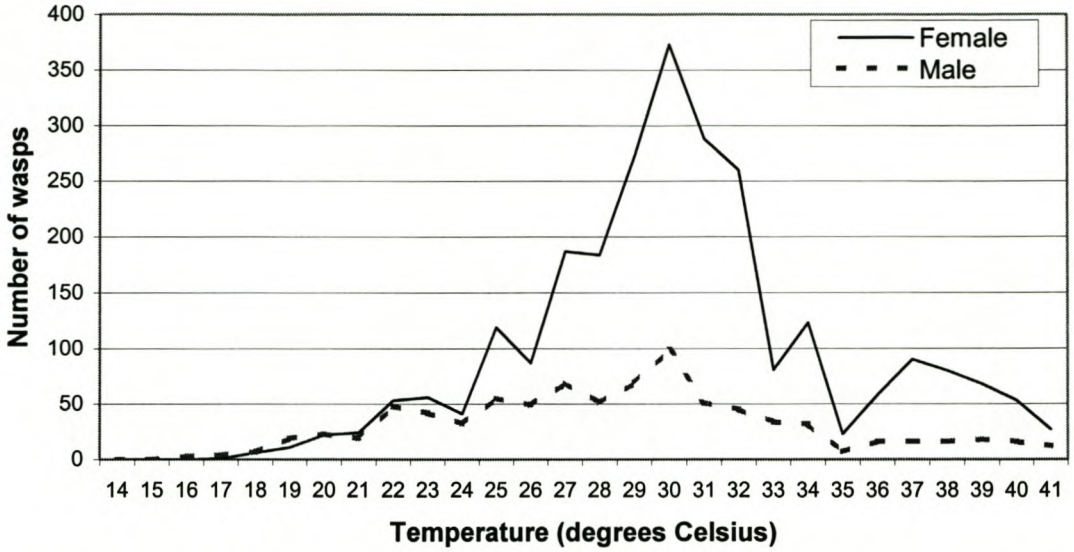


Fig. 5. Frequency of the number of active male and female *M. fasciipennis* wasps in relation to ambient temperature (combined over seven days)

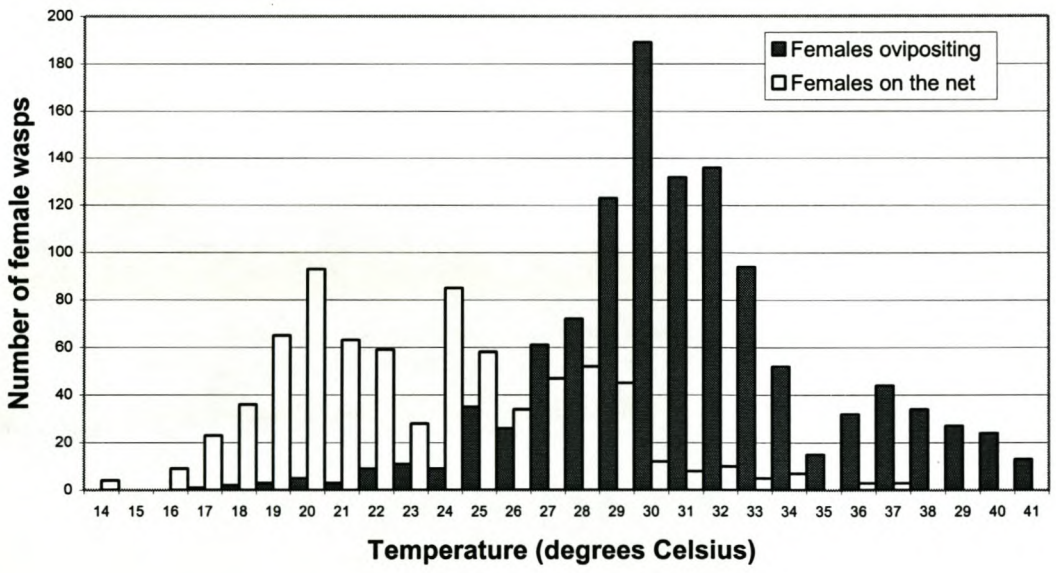


Fig. 6. Number of female *M. fasciipennis* wasps ovipositing or resting on the net in relation to temperature (combined over seven days)

On a diurnal scale, males emerged from their hiding places (usually empty *Phoracantha* tunnels) and reached a peak in numbers of active males at 09h00 after which there was a steady decline in activity (Fig. 7). Almost 64 % of male activity occurred between 08h00 and 12h00, a period of 4 hours. In contrast 64 % of female activity took place between 10h00 and 15h00, a period of 5 hours (Fig. 7). Male wasps became active when the temperature reached 16 °C (Fig. 5). They patrolled the logs until they detected tenneral females emerging from pupal chambers. Mating then took place. Although the large cage contained both eucalypt and *Pinus radiata* D. Don logs, both male and female *M. fasciipennis* only visited the dry eucalypt logs. A male would chase away other intruding males around the tunnel opening where a female wasp was about to emerge. Once a female had mated, she departed from the log.

Daily temperatures when males were active ranged from 16 °C in the morning, with their activity peaking at 30 °C at around 14h00, and dropping to a minimum at 19 °C in the late afternoon (Fig. 5 & 7). In contrast, females became active in the morning at a minimum of 17 to 18 °C. Female activity reached a peak at 30 °C at around 14h00, and ceased below 16 °C in the late afternoon. The earliest oviposition occurred at 07h30 on the hottest of the seven days during which behaviour was monitored, at a temperature of 21 °C, and the latest at 19h00 at 20 °C (Figs 8). However, on a cooler day, oviposition was first observed to occur at 19 °C at 09h45 and the last ended with the temperature at 16 °C at 18h30. Maximum oviposition occurred at temperatures between 27 and 34 °C and between 10h00 and 15h00. Females tended to rest on the net near the top of the cage early in the mornings when temperatures were cooler. By 10h30 all females had left the

net and were active or ovipositing on the logs again (Figs 8). At the end of the day when the temperature dropped below 20 °C, males went into hiding long before the females (60 to 225 minutes earlier). Around 15h00 or when temperatures dropped to below 18 °C, the females would leave the logs and settle on the net again for a minimum of 30 minutes before concealing themselves for the night high in the cage wherever they could. Males would go directly into hiding once activity ceased.

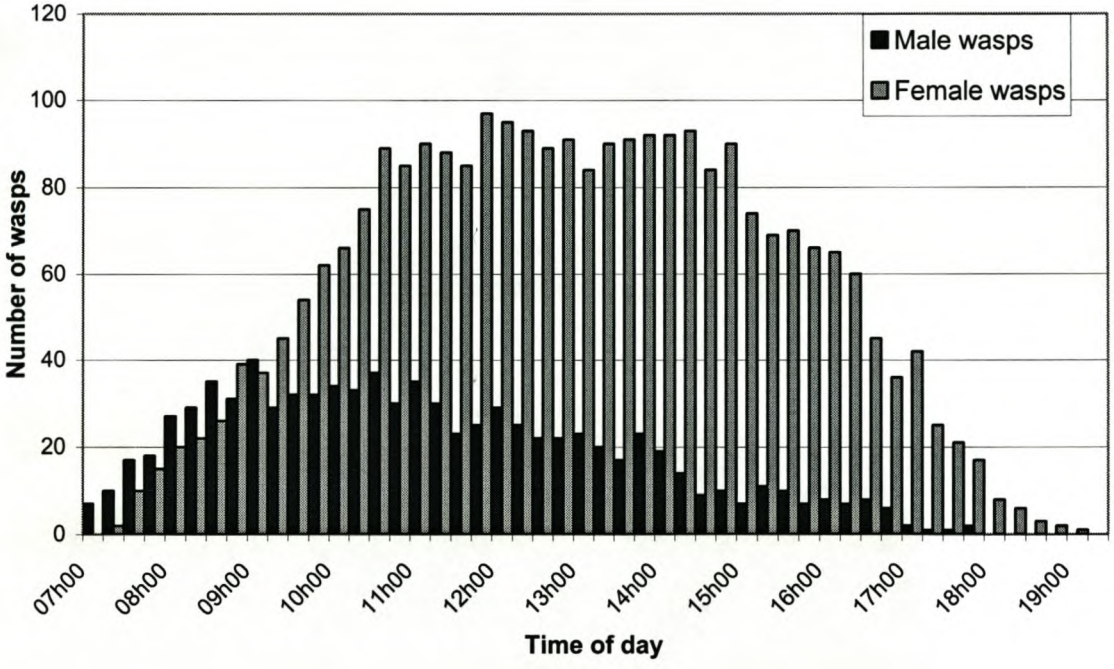


Fig. 7. Number of active male and female *M. fasciipennis* wasps in relation to time of day (combined over seven days)

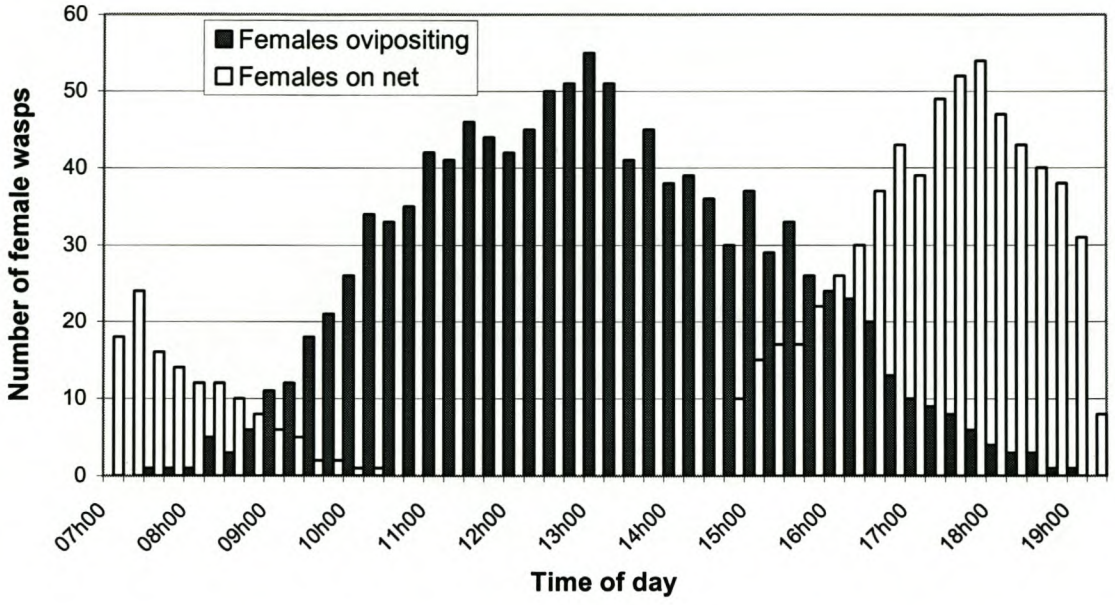


Fig. 8. Number of female *M. fasciipennis* wasps ovipositing or resting on the net in relation to the time of day

2.4 Discussion

2.4.1 Distribution

Megalyra fasciipennis is K-selected and hence a specialist parasitoid, i.e. with a low reproductive rate, a long life-cycle, a high survival rate and a low dispersal rate (Force 1972). Its impact or distribution over the shorter term is therefore not expected to be widespread or dramatic.

2.4.2 Confirmation as pupal parasitoid

Previous publications described *M. fasciipennis* as a larval parasitoid and not a pupal parasitoid as proved in this study. This perhaps helps to explain the failure of Webb

(1974) to rear *Megalyra* sp. (most probably *M. fasciipennis*) which had presumably been presented with a culture of host larvae to parasitise. The presence of an ovipositor three times the body length of the female parasitoid as well as observations on oviposition behaviour, are indicators that the host is in its pupal stage when being parasitised. All larval stages of *Phoracantha* spp. feed beneath the *Eucalyptus* bark until the final larval stage when they burrow into the heartwood to pupate (Drinkwater 1973). Should *M. fasciipennis* have been a larval parasitoid, it would need a much shorter ovipositor to enable it to bore through the thickness of the bark immediately above the host larva, such as occurs in the larval parasitoids *Syngaster lepidus, Jarra phoracantha* and *Jarra maculipennis*.

2.4.3 Percent parasitism by *Megalyra fasciipennis*

An accurate assessment of percent parasitism of *Phoracantha* spp. by *M. fasciipennis* can be made by monitoring populations of both species emerging from collected *Eucalyptus* logs monthly throughout the year. Unfortunately, due to the general limited availability of the parasitoid, levels of parasitism were assessed using the split-open log method only in summer when *M. fasciipennis* numbers were at their peak. Emergence data of host and parasitoids from field-collected logs allowed for the assessment of parasitism levels throughout the year. Hence discrepancies occurred within the results between the two methods.

2.4.4 Seasonal activity peaks and sex ratio

During the summers of 1993 and 1994, high numbers of *M. fasciipennis* were recorded, coinciding with increased logging activity. The increase in availability of breeding resource for the beetles and resulting increase in numbers of parasitoids, suggested that *M. fasciipennis* responds to its host's abundance in a density dependent way.

In spring, numbers of especially *Phoracantha recurva* beetles increased at the same time as *M. fasciipennis* wasp numbers increased (Fig. 4). Because this was the time at which the *M. fasciipennis* parasitised the beetle pupae, further emergences of *Phoracantha* spp. beetles were restricted, so in the following weeks, numbers of beetles emerging declined. The numbers of emerging parasitoids also decreased, and this may have been due to fewer host pupae being available for *M. fasciipennis* females to parasitise. During the following weeks of summer, numbers of emerging *Phoracantha* beetles of both species escalated again, and this may have been due to fewer parasitoids present to curb *Phoracantha* populations.

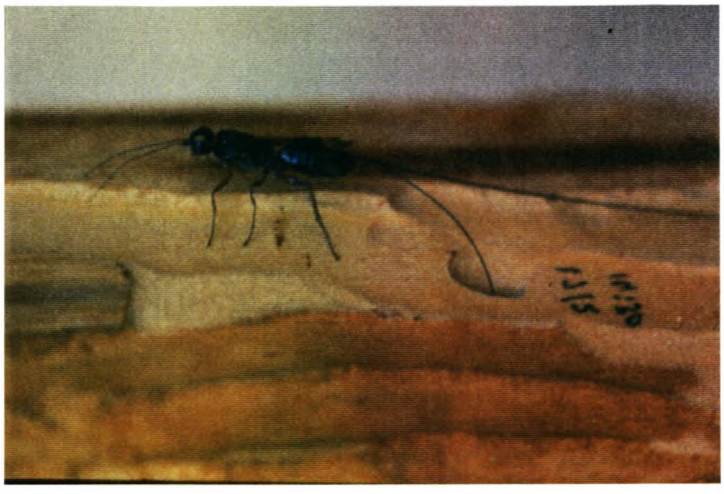
2.4.5 Comparison of body to ovipositor length and pupal chamber tunnel length

Froggatt (1906) noted that the body size of megalyrid wasps was variable within the species. This was confirmed with *M. fasciipennis* in this study. The mean ratio of *Phoracantha* pupal tunnel length in relation to *M. fasciipennis* ovipositor length was 1 : 1.36. This indicated that ovipositor length allows the females to lay their eggs beside the pupa rather than within the frass-filled tunnel. Therefore, *M. fasciipennis* wasps should have no difficulty parasitising most *Phoracantha* pupae.

2.4.6 Differences in daily activity peaks between male and female *Megalyra fasciipennis* wasps

Daily activity records over a period of seven days revealed there were distinct differences in activities and activity peaks between male and female *M. fasciipennis*. Activity of both male and female wasps was greatly influenced by temperature, with activity in both instances peaking at the same temperature, 30 °C.

When female *M. fasciipennis* wasps were in the process of oviposition they were exposed for a considerable length of time on the surface of the log and were therefore vulnerable to predation. Wilson & Clark (1977) showed that harvester termites, *Hodotermes mossambicus* (Hagen), in South Africa were active primarily when predatory birds were not foraging. The birds were active in the morning and late afternoon with a lull during the heat of the day. It was at this time that the termites emerged, in temperatures of up to 44 °C. This might also explain why maximum oviposition by *M. fasciipennis* took place during the hottest time of day when most predators were inactive.



***Megalyra fasciipennis* female ovipositing**

***Megalyra fasciipennis* female ovipositing through a crack in the bark**

CHAPTER THREE

AVETIANELLA LONGOI, EGG PARASITOID OF *PHORACANTHA* SPP.

3.1 Introduction

In the search for effective biocontrol agents of *Phoracantha* spp., the presence of egg parasitoids was investigated. *Phoracantha* eggs are laid under loose bark of dead or dying trees, or within crevices in the bark. There are 40 species of *Phoracantha* in Australia (Wang 1995), all of which lay their eggs on Myrtaceae, especially *Eucalyptus.* *Phoracantha* spp. eggs are deposited in batches of 10 to 110; with a maximum of 300 eggs laid by a single captive female being recorded (Duffy 1963).

Cillié & Tribe (1991) devised a trap to monitor the production of eggs laid by *Phoracantha* spp. and used it as a means to locate egg parasitoids. The trap consisted of standard-sized (± 12 cm x 7 cm) pieces of sloughed bark that were attached to the stem of a newly felled *Eucalyptus* tree using two drawing pins. The eggs laid under these traps could be removed directly and easily. Wang (pers. comm.), using this trapping method, discovered *Avetianella longoi* (Coleoptera: Encyrtidae) in south-eastern Australia (Melbourne and Ballarat) on eggs of *P. semipunctata* in 1992. *Avetianella longoi* was also recovered from the eggs of other cerambycids, *Coptocerus aberrans* (Newman) and *Epithora dorsalis* (Macleay) in Australia (Austin *et al.* 1994).

The genus *Avetianella* Trjapitzin was previously known from only three described and several undescribed species from Holarctic, Neotropical and Oriental regions. Each

Avetianella species had previously been reared from the eggs of cerambycid and scolytid hosts (Austin *et al.* 1994). *Avetianella longoi* was described from Italy and Portugal, emerging from the eggs of *P. semipunctata* (Siscaro 1992). It was probably accidentally introduced into those countries together with its host. Evidence suggests that it is of Australian origin (Siscaro 1992).

Avetianella longoi was imported from Australia into California, USA early in 1993 as a biological control agent of *P. semipunctata* to counter unacceptable losses of *Eucalyptus* trees (Hanks *et al.* 1995a, 1996). From there it was also imported into South Africa early in 1993 as part of this study. The genus *Avetianella* is host specific and only parasitises the eggs of *Phoracantha* spp. and a few related cerambycid species which attack *Eucalyptus* (J.G. Millar, pers. comm.; Q. Wang, pers. comm). This was confirmed in limited host preference trials with eggs from the indigenous cerambycid, *Zamium bimaculatum* (Fabricius), which also lays its eggs on *Eucalyptus* logs, and from the exotic curculionid *Neodiplogrammus quadrivittatus* (Oliver) (F. Kirsten, pers. comm). The results were negative and the parasitoids appear to be specific to the *Phoracantha*/habitat complex (F. Kirsten, pers. comm).

The biology of *A. longoi* was studied after its introduction into California, U.S.A. (Hanks, *et al.* 1995a). With the introduction of the egg parasitoid into South Africa, comparative studies were undertaken on its survival and reproductive requirements under South African climatic conditions. Host preference trials as well as longevity and fecundity of *A.longoi* wasps were studied.

Post-release monitoring, such as percentage parasitism of the parasitoid on *Phoracantha* spp. eggs in the field, and dispersal were measured to determine whether or not *A. longoi* would be a successful biocontrol agent of *Phoracantha* species in South Africa.

3.2 Material and Methods

3.2.1 Mass rearing

A culture of *Phoracantha* beetles was maintained in wooden containers measuring 100 cm x 70 cm x 70 cm, each with a hinged side-door and a glass upper surface. Fresh flowers of *Eucalyptus ficifolia* F. Muell., placed in vials of water, provided beetles with pollen and nectar for feeding. In order to extend the adult life of the beetles, additional sugar-water, rather than distilled water (Hanks *et al.* 1993), was supplied as a nectar substitute in 5 cm long glass vials with a cotton-wool wick.

A strip of brown wrapping paper, 8 cm wide and 40 cm long, was folded lengthwise until an 8 x 8 cm layered square was formed. This was then attached to the upper glass surface of the wooden container using two pieces of masking tape. Six such squares were attached to each container. *Phoracantha* females oviposited between the paper layers. They could easily be collected by cutting out the paper base to which the egg-batches were attached.

In general, as host eggs increased in age, they declined in suitability for parasitoid development (Luhring *et al.* 2000) so only fresh host eggs were supplied to the

parasitoids. The fresh egg batches were then either exposed to *A. longoi* parasitoids or allowed to hatch to maintain a *Phoracantha* culture.

When exposed to parasitoids, a small, damp paintbrush was used to place usually five male and five female *A. longoi* wasps in a 10 cm long glass vial with a gauze lid, together with three to four batches of fresh *Phoracantha* spp. eggs for 24 hours. After four to seven days, any beetle larvae that hatched were removed before they could damage the parasitised eggs. These newly emerged larvae were inoculated into freshly felled *Eucalyptus* logs by cutting 5 cm strips at intervals along the length of the log with a penknife, then slightly lifting the flap of thin, moist wood and bark from the log. About 20 larvae were placed in each strip using a damp paintbrush (Haddan *et al.* 1995). Care was taken not to damage the larvae with the release of the flap. The larvae then fed and developed normally and produced adults that were used for egg production.

After 18 to 30 days *A. longoi* adults emerged from the parasitised *Phoracantha* eggs. They were removed from the vial using a damp paintbrush and placed in another glass vial with a gauze lid, and fed with a honey and water mixture before being released or used for further mass rearing of the parasitoids.

3.2.2 Host preferences

The ratio of *Phoracantha semipunctata* to *P. recurva* populations was monitored before the introduction of *A. longoi* into South Africa and this was continued after the latter had

become established to compare the effectiveness of *A. longoi* as a biological control agent of the two *Phoracantha* species.

In the summer months of 1992 to 1994, before the introduction of *A. longoi* into South Africa, trap trees were felled at fortnightly intervals throughout the summer seasons in Tokai Plantation, to coincide with the peak active periods of both *Phoracantha* species. The felled trees were left on site to attract ovipositing *Phoracantha* beetles. After a month, the infested logs were collected and placed in a sealed holding room until all adult beetles of *P. semipunctata* and *P. recurva* had emerged. The emerging *Phoracantha* beetles were collected daily and the species and sex ratio was recorded. Similar recordings were performed in 1998/1999 after the establishment of *A. longoi* was confirmed.

3.2.3 Longevity and fecundity

The longevity of *A. longoi* was determined at two temperature regimes, viz. a constant temperature of 25 °C and at room temperature (11 to 24 °C) during July/August 1993. Parasitised *Phoracantha* egg batches collected from under bark in the field or from paper oviposition traps (described in section 3.2.2) in containers of *Phoracantha* beetles in the laboratory, were placed in 10 cm glass vials with gauze lids for ventilation until the wasps emerged. Each newly emerged wasp was removed from the vial using a damp paintbrush, and was placed in a separate glass vial with a gauze lid. The wasp was fed with a small drop of honey and water mixture which was smeared daily in a thin line on the inside of the vial. The age at which the wasp died was recorded.

To determine the age at which *A. longoi* wasps are at their most fertile, newly emerged mated females were placed separately in glass vials containing a drop of a mixture of honey and water on which they fed. Each wasp from a varying numbers of female wasps 1, 2, 4 and 8 days old was exposed individually to the available batches of fresh host eggs which had been placed in each respective vial. Two days later, each wasp was removed from its respective vial using a damp paintbrush. The potentially parasitised *Phoracantha* egg batches remained in their respective vials for about two weeks until emergence of the resulting *A. longoi* wasps which were removed from each vial and their numbers were recorded. The mean number of *A. longoi* emerging from parasitised *Phoracantha* eggs was determined for each of the four age groups and expressed as a percentage of the total number of original host eggs that each wasp had been exposed to.

3.2.4 Percentage parasitism

To determine the percentage parasitism of *Phoracantha* eggs by *A. longoi* in the field, *Eucalyptus diversicolor* trees were felled in Tokai Plantation and at Morning Star (33°44'S 18°31'E) throughout the summer season of 1996/1997. Additional bark and leaves were stapled onto the stem or branches to provide additional oviposition sites. The trees were left for a week to allow *Phoracantha* females to oviposit within crevices and under loose bark, and to allow *A. longoi* parasitoids to discover the fresh eggs and to parasitise them. All batches of *Phoracantha* eggs were then removed from each log, using a penknife, and placed in 10 cm long glass vials with gauze-covered lids. The number of egg batches, as well as the number of eggs per batch, were recorded.

Each emerging *Phoracantha* larva was recorded and removed immediately to prevent it from devouring sibling eggs. The percentage parasitism was determined from the ratio of the numbers of *A. longoi* wasps emerging in relation to beetle larvae. The number of collapsed *Phoracantha* spp. eggs was also recorded.

Large logs left in the field remained attractive to *Phoracantha* beetles for several weeks and could be sampled repeatedly to determine percentage parasitism.

3.2.5 Release of *Avetianella longoi* parasitoids

After its introduction into South Africa in this study, *A. longoi* was successfully mass-reared and released in large numbers in *Eucalyptus* plantations at Tzaneen, Mpumalanga Province, as well as at various sites in the Western Cape, particularly within the Cape Peninsula. Releases were made at sites with *Eucalyptus* trees that were likely to have freshly laid *Phoracantha* spp. eggs readily available. Trees were also felled at intervals to attract beetles and encourage them to oviposit. A *Eucalyptus* fire-break belt within the SAFCOL Tokai Plantation close to Cape Town was chosen as the primary release site for *A. longoi* wasps. The first release of 200 wasps took place in May 1993. Since *A. longoi* larvae overwinter inside parasitised *Phoracantha* eggs (Longo *et al.* 1993) the culture was maintained in the laboratory until November when releases recommenced.

Different *Eucalyptus* compartments within Tokai Plantation were used as release sites. Regular releases of between 30 and 500 wasps were made at irregular intervals until the

beginning of April 1994, by which time a total of 6041 *A. longoi* wasps and 80 parasitised *Phoracantha* eggs had been released. Apart from Tokai Plantation, other release sites included *Eucalyptus* firebreaks at Lion's Head, Llandudno and Elsenburg (Stellenbosch), resulting in a total of 7791 wasps released in the Cape Peninsula. One satellite release of 220 wasps was made near Knysna in February 1994 in Buffelsnek Plantation (33°55'S, 23°09'E).

3.2.6 Rate of dispersal

Avetianella longoi wasps were initially released only in the Cape Peninsula and surroundings so that the rate of dispersal could be monitored. Once *A. longoi* was established in the Western Cape, annual surveys were carried out from 1994, during the summer months when *A. longoi* was active, to monitor its rate of dispersal. Patches of *Eucalyptus* trees were inspected along the main routes radiating from Cape Town. All freshly broken branches of *Eucalyptus* trees along the routes were inspected to determine the presence or absence of *A. longoi*. By lifting loose bark, yellow and turgid *Phoracantha* eggs, in the absence of any visible *A. longoi* wasps, were removed and placed in gauze-lidded glass vials and taken back to the laboratory. Eggs blackened by the developing *A. longoi* pupae which were visible through the translucent chorion, were recorded as being parasitised. Parasitism was confirmed when *A. longoi* wasps emerged.

3.3 Results

3.3.1 Mass rearing

A total of 7791 *A. longoi* wasps of both sexes were reared in the laboratory and finally released along with 80 parasitised *Phoracantha* spp. eggs at various sites in the Western Cape, between the years 1993 and 1995. Once they had become established in the field in 1995, mass rearing of *A. longoi* in the laboratory ceased.

3.3.2 Host preferences

Emergences of *Phoracantha* beetles recorded in the summer months of 1992 through 1994 before *A. longoi* was released, showed a slight dominance in *P. semipunctata* populations, viz. 1.07 *P. semipuncata* : 1 *P. recurva* (n = 103). This was in sharp contrast to the ratio of beetles which emerged from trap logs collected from a *Eucalyptus* fire-belt in Tokai Plantation in 1998/99 after the release of *A. longoi,* which showed a distinct dominance in the numbers of *P. recurva* compared to *P. semipunctata*, namely 10.21 : 1 (n = 1943) (Fig. 9). This large- decrease in the proportion of *P. semipunctata* indicated possible successful biological control of this *Phoracantha* species, through the introduction, release and establishment of *A. longoi* in 1993 and 1994.

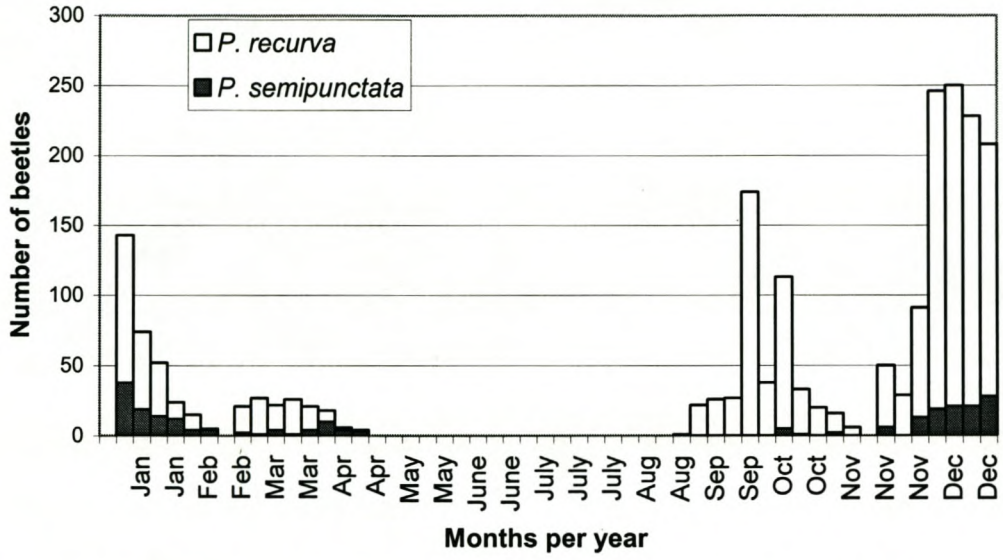


Fig. 9. The combined emergences over six years of *P. semipunctata* and *P. recurva* beetles from field collected logs

3.3.3 Longevity and fecundity

The mean longevity of *A. longoi* wasps in this study was 20.2 ± 4.66 days S.D. (n = 5) at 25 °C and 26.2 ± 7.26 days S.D. (n = 5) at room temperature. Of the four age groups, the eight day old *A. longoi* were the most prolific egg layers. An average of 20 eggs out of 34 were parasitised (59 %) though there was really very little difference in parasitism rates between the ages (Table 2).

Table 2. Percentage parasitism of fresh *Phoracantha* spp. eggs exposed to mated *A. longoi* females of varying ages

Age of female *A. longoi* wasps (days)	Number of female *A. longoi*	Mean no. of fresh *Phoracantha* eggs provided per wasp	Mean no. of *Phoracantha* eggs parasitised per wasp	Percentage parasitism (%)
1	18	85	38	45
2	15	84	44	52
4	15	84	48	57
8	5	34	20	59

3.3.4 Percentage parasitism

Avetianella longoi has a main activity period of about 60 days between January and March with the peak activity in the second week of February (54 % of wasps, n = 460) which coincided with the main activity peak of *P. semipunctata*. In the Western Cape, between November 1995 and March 1996, 46.6 % of the *Phoracantha* egg batches collected at Morning Star, 25 km north of Cape Town, contained parasitised eggs. The average percentage parasitism of eggs within those parasitised egg batches was 62.8 % (n = 74 batches). However, in the same areas during the 1996/1997 season, the percentage parasitism averaged 13.5 % with a large number of collapsed eggs i.e eggs probed and pierced by the wasp's ovipositor, but where oviposition has not taken place (Fig. 10). In Tokai Plantation, the total number of parasitised egg batches was 46.2 % during the 1995/1996 season. The average percentage parasitism of *Phoracantha* eggs within the parasitised batches was 55.9 % (n = 122 batches). Under laboratory conditions, 49.6 % of the batches of eggs were parasitised between September 1995 and January 1996 (a period

before the *A. longoi* field population activity peak in February). Within the parasitised egg batches, 42.2 % (n = 119) of the eggs were parasitised. Very early in the season in October 2000, it was still possible to achieve a parasitism rate of 25.68 % (n = 42) in the laboratory.

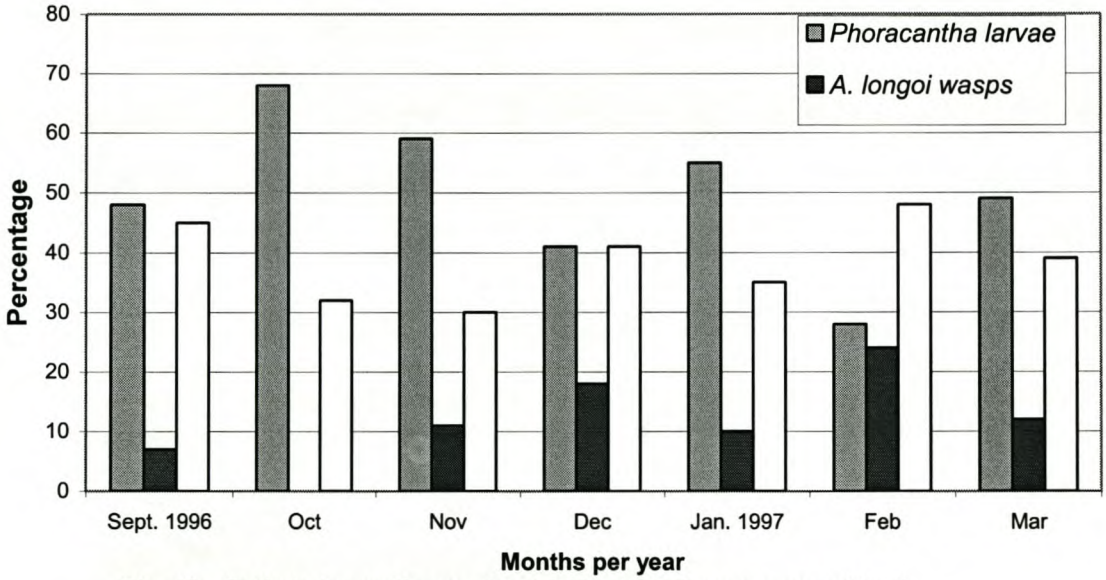


Fig. 10. Ratio between the number of *Phoracantha* eggs parasitised, unparasitised and collapsed from combined samples collected at Tokai and Morning Star from September 1996 to March 1997

Under field conditions, one parasitoid usually emerged from each host egg. However, an over-abundance of parasitoids on a batch of eggs resulted in superparasitism. From two to as many as five wasps emerged from single *Phoracantha* eggs. Hanks *et al.* (1996) obtained similar results in California. These wasps were noticeably smaller than those emerging singly from a host egg.

3.3.5 Release of *Avetianella longoi* parasitoids

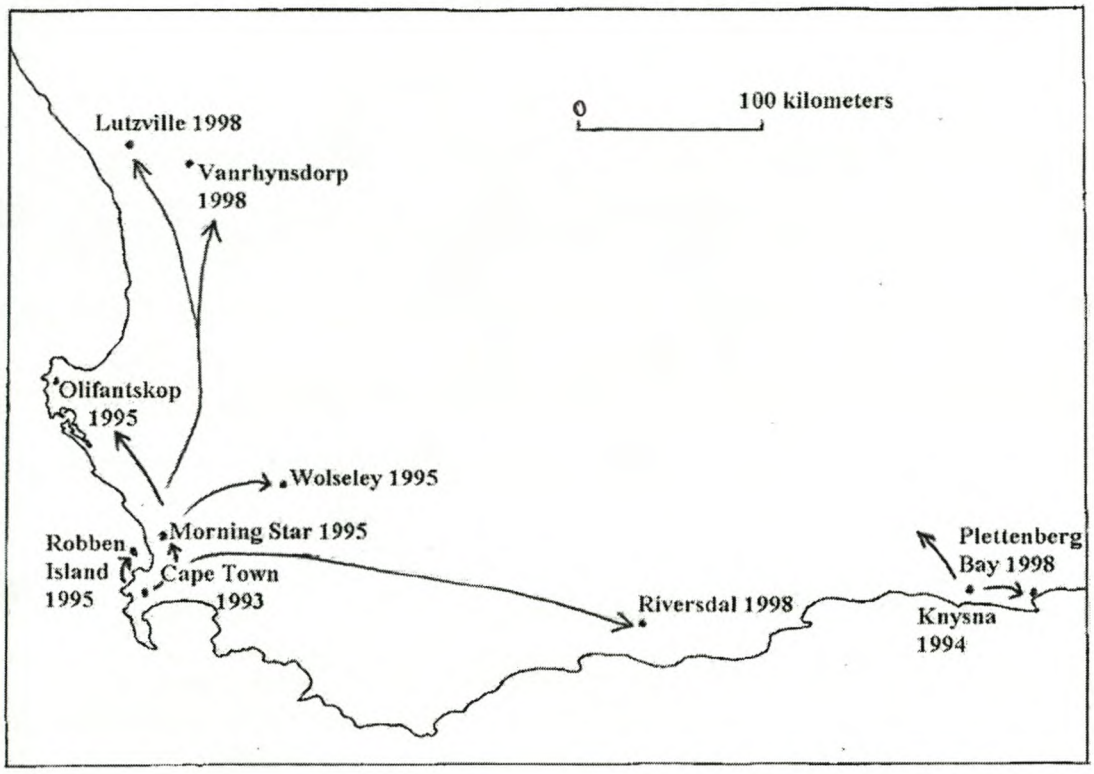
The establishment of *A. longoi* was confirmed in February 1994 when many parasitised eggs were recovered in the Tokai Plantation close to the release sites. Further parasitised eggs were found in April 1994. However, final proof that *A. longoi* wasps were able to overwinter was confirmed when parasitised eggs were recovered in Tokai Plantation in January 1995 at the peak of the summer season.

Besides Tokai Plantation, parasitoids were eventually recovered from all release sites around the Peninsula. However, in 1998, at the time of sampling, *A. longoi* was not recovered from the Knysna site.

3.3.6 Rate of dispersal

Avetianella longoi wasps were found on Robben Island 10 km off the shore of Cape Town in 1995, in Lutzville (31°33'S, 30°27'E) 300 km north of Cape Town, and Plettenberg Bay (34°03'S, 23°22'E) 450 km east of Cape Town in 1998 (Fig. 11). *Avetianella longoi* also established in the Tzaneen area (F. Kirsten, pers. comm.), from consignments of parasitoids sent to that area from the Western Cape in 1993.

Fig. 11. Dispersal map of *Avetianella longoi* after its release in the Cape Peninsula in 1993 and Knysna in 1994



3.4 Discussion

3.4.1 Mass rearing

Phoracantha beetles of both species were easily reared in the laboratory using the methods described, hence fresh *Phoracantha* eggs were readily available for parasitism by *A. longoi* for mass rearing. *Avetianella longoi* wasps were easily reared in large numbers for release due to the multivoltine nature of *A. longoi*, as well as superparasitism when there was a shortage of available host eggs and up to 5 parasitoids could be produced per host egg. However, during the winter months, despite of a temperature

controlled culture room, *Phoracantha* egg production declined as did *A. longoi* parasitism, so fewer parasitoids were available for mass rearing or release.

3.4.2 Host preferences

Besides the narrow activity peak of *A. longoi*, there are other factors inherent in the biology of the two beetle species which accentuated the differentiation in ratios of their respective population numbers. *Phoracantha recurva* is geographically sympatric and shares host species with *P. semipunctata* in Australia, which suggests an intrinsic degree of differentiation between the two species. Luhring *et al.* (2000) found that *Phoracantha recurva* egg masses had significantly more eggs per mass (36.4 ± 3.4 S.D.) than *P. semipunctata* (26.2 ± 3.6 S.D.). *Avetianella longoi* parasitised significantly fewer *P. recurva* eggs per mass (11.4 % ± 2.6 S.D.) than those of *P. semipunctata* (30.3 % ± 6.9 S.D.). When presented with host eggs of all ages, *A. longoi* preferred those of *P. semipunctata* to those of *P. recurva*. *Phoracantha semipunctata* eggs are also more suitable hosts than *P. recurva* eggs for the development of *A. longoi* (Luhring *et al.* 2000). The combination of these factors would explain the difference in ratio between the two *Phoracantha* species before introduction (1993 – 1994) and after establishment (1998 – 1999) of *A. longoi*.

3.4.3 Longevity and fecundity

The mean longevity of *A. longoi* wasps in this study was 20 days, similar to results in California where it was recorded that each *A. longoi* wasp laid up to 250 eggs during her adult life (Paine *et al.* 1995).

Fertility results showed that for mass rearing purposes, the exposure of *Phoracantha* eggs to *A. longoi* wasps which were a week old, would be most suitable. This may be to allow the female time to mate and mature.

3.4.4 Percentage parasitism

Fluctuations in parasitism rates between successive seasons may be attributed to the sampling method employed. The egg batches collected in the field were of variable age (up to one week old) and hence many of them would not have been exposed long enough to allow for them to be detected and parasitised by *A. longoi* females. The eventual parasitism rate could be expected to have been higher.

Not all oviposition probes made by *A. longoi* wasps resulted in an egg being deposited. Such probes may have resulted in the puncturing *Phoracantha* spp. eggs from which neither host nor parasitoid would emerge. This was observed most frequently when there was intraspecific competition by the parasitoids for a limited number of host eggs resulting in superparasitism. During oviposition, parasitoids may inject chemical substances that halt development of the host (Luhring *et al.* 2000). Punctured eggs are

still advantageous to biocontrol as the host larvae are prevented from developing. However, no parasitoids emerge from these eggs.

3.4.5 Release of *Avetianella longoi* parasitoids

The ability to mass-rear *A. longoi* wasps in large numbers in the laboratory for release, may have contributed to this parasitoid becoming established relatively easily. Climatic conditions comparable to those in the country of origin, Australia, also must have had a strong impact on *A. longoi* becoming established.

The relatively small numbers of *A. longoi* released at Knysna, probably resulted in the parasitoid not establishing, or that low parasitoid numbers made sampling and monitoring difficult and that those wasps that established could easily have been bypassed.

3.4.6 Rate of dispersal

Avetianella longoi wasps dispersed much faster northwards than eastwards of Cape Town. This was possibly due to the strong prevailing south-easterly winds common to the western Cape. Wind dispersal would also explain the presence of *A. longoi* on Robben Island. Owing to the semi-desert conditions further north towards the border of Namibia, *Eucalyptus* trees become more scarce, thus hindering further dispersal of the wasp in this direction. However, the continual availability of *Eucalyptus* trees along the south and eastern coast of South Africa, enabled the parasitoid to disperse easily. The wasps are expected to disperse further inland, eastwards and northwards into Kwazulu-Natal and the Free State.

Establishment of *A. longoi* in the northern highveld, from consignments released in Tzaneen in 1993 was very rapid and, because of the many contiguous *Eucalyptus* plantations, coupled with the recent drought during that time, the availability of numerous host eggs was ensured (F. Kirsten, pers. comm). From this area, the parasitoids are expected to disperse southwards, eventually meeting up with those dispersing northwards from the areas of the original releases around Cape Town and Knysna.

3.5 Establishment of *Avetianella longoi* in Uruguay and Chile

The success achieved with the introduction of *A. longoi* into South Africa led to wasps and parasitised eggs being introduced into both Uruguay and Chile. This entailed taking the parasitoids to these countries, setting up mass rearing cultures, teaching technicians various methods, selecting suitable release sites, and releasing the first batch of parasitoids from quarantine. *Phoracantha semipunctata* was recorded as a pest of *Eucalyptus grandis* plantations in Uruguay in 1988. On the request of Nora Telechea of Dirección Forestal in Montevideo, approximately 400 *A. longoi* wasps and many more parasitised *Phoracantha* spp. eggs were taken to Uruguay in January 1998 and placed in quarantine where mass rearing commenced immediately. From the beetles collected for egg production, *P. recurva* was identified and recorded for the first time in Uruguay.

The release of the first progeny of *A. longoi* consisted of 50 wasps released into a plantation of 10 year old *E. grandis* trees outside Montevideo. Further releases of emerged wasps were made continuously in two selected sites until the end of the season.

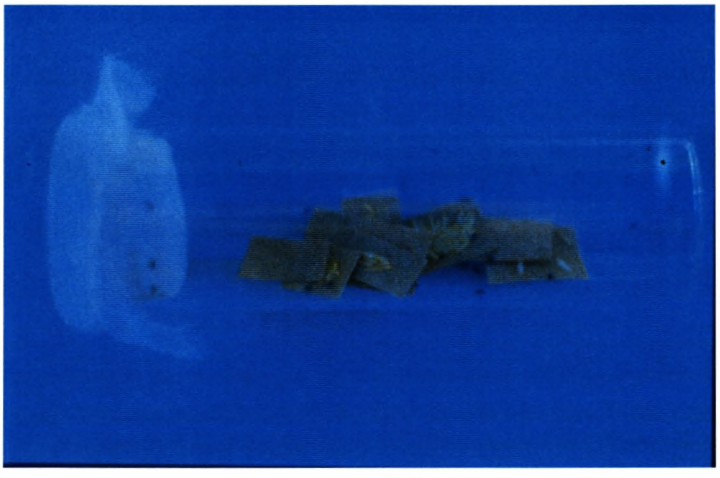
In January 1998, *A. longoi* was confirmed to have become established in Uruguay (N. Telechea, pers. comm.).

Following a visit to South Africa by three Chilean entomologists in January 1998, a biological control program using *A. longoi* was initiated against *Phoracantha* spp. in Chile. Almost 500 *A. longoi* wasps and parasitised *Phoracantha* spp. eggs were taken to Santiago, Chile in February 2000 on behalf of CPF (Controladora de Plagas Forestales) and SAG (Servicio Agrícola y Ganadero).

Three release sites consisting of stands of *Eucalyptus globulus* Labill. were chosen in the Parque Metropolitano de Santiago where high numbers of both *P. semipunctata* and *P. recurva* were known to occur. The first release of about 200 *A. longoi* wasps was made in this region as well as twenty kilometres south of Los Angeles de Chile, in an *E. globulus* plantation. At the latter site, only *P. semipunctata* was known to occur, as *P. recurva* had still not been detected outside the Santiago metropolitan area (M. Beeche, pers. comm.). A consignment of *A. longoi* wasps was flown from the SAG laboratories in Santiago to the CPF laboratories at Los Angeles de Chile where a culture was to be kept and releases made periodically. *Avetianella longoi* was confirmed to have become established in Chile the following season, in 2001 (M. Beeche, pers. comm.).

Austin *et al.* (1994) suggested that the unidentified egg parasitoid species (Drinkwater 1975) that was introduced into South Africa from Australia in 1910 but failed to become established, was possibly *A. longoi*. However, the ease with which *A. longoi* was reared

and established in South Africa, Chile and Uruguay suggests that the unidentified parasitoid was not *A. longoi*. This indicates that possibly another parasitoid of *P. semipunctata* eggs may still exist.



Tiny *Avetianella longoi* wasps ovipositing on *Phoracantha* spp. eggs in a glass vial

CHAPTER FOUR

LARVAL PARASITOIDS AS BIOCONTROL AGENTS OF *PHORACANTHA* SPP.

4.1 *Cleonymus* sp.

An undescribed *Cleonymus* species (Hymenoptera: Pteromalidae) was first discovered in Cape Town in 1993. Sixteen parasitoid pupae were found in the larval tunnels of *Phoracantha* spp. hosts, surrounding a shrivelled *Phoracantha* larva in a *Eucalyptus* log. A year later, large numbers of *Cleonymus* wasps were discovered emerging from field-collected logs containing *Phoracantha* larvae in a temperature-regulated room (24 °C) in Cape Town during the winter. Nothing was known about the biology of this parasitoid. The discovery of *Cleonymus* sp. presented an opportunity to make observations on the oviposition behaviour and biology of this wasp.

The origin of *Cleonymus* sp. is unknown. Bouçek (1988) reported that *Cleonymus* spp. had only been reported as primary parasitoids of coleopterous larvae in Australia. However, other *Cleonymus* spp. occur in Malaysia, Japan and Cuba where they parasitise bees and wasps. Of the eleven *Cleonymus* spp. described by Austin *et al.* (1994) from Australia, only one had been reared from the galleries of *P. semipunctata*. Later, Austin & Dangerfield (1997) recorded another *Cleonymus* species from *Phoracantha*-infested logs. Host species of the other *Cleonymus* spp have not been recorded, but several species have been reared as hyperparasitoids associated with braconid parasitoids of

Phoracantha spp (Moore 1963). The *Cleonymus* sp. reported on in this study does not occur in large numbers in the field, nor do numbers appear to be increasing, therefore it is probably an indigenous species that has switched from an indigenous host to the *Phoracantha* borers. However, it is also possible that it is an unidentified exotic *Cleonymus* species, originating from Australia.

The pupae of *Cleonymus* sp. that were initially collected from a shrivelled *Phoracantha* larval host, were kept in a vial with a gauze-covered lid for ventilation until emergence of the adult wasps. These specimens were preserved in 70 % alcohol and sent to the National Collection of Insects in Pretoria where they were identified to be the undescribed *Cleonymus* sp. Latreille (O.C. Neser, pers. comm.).

Wasps emerging from field-collected *Eucalyptus* logs in a temperature-controlled culture room (24 °C) were collected and also sent to Pretoria where they were identified and determined to be the same species of *Cleonymus*.

A survey was carried out to establish the occurrence of *Cleonymus* in the field by felling trees in Tokai Plantation, allowing oviposition and infestation by *Phoracantha* species. The logs were left until *Phoracantha* larvae had advanced to a late or final instar. This could be detected by the slight loosening and lifting of bark immediately above the larval tunnels. This bark was stripped from the logs to expose host larvae and determine the proportion that were parasitised by *Cleonymus* sp and hence shrivelled.

Although *Cleonymus* sp. has been encountered only rarely in the field, and only as pupae surrounding shrivelled larval hosts, over 80 % parasitism occurred in the *Phoracantha* culture when they were accidentally brought into the culture room in field-collected logs. At a temperature of 24 °C and surrounded by numerous hosts, *Cleonymus* sp. was able to multiply rapidly.

Cleonymus sp. in all life-stages have only been found in the field on *Phoracantha* spp. in *Eucalyptus* logs during the summer months and have only been recorded from the Cape Peninsula. Because *Cleonymus* sp. rarely occur in the field, they are unlikely to be a key parasitoid in the biological control of *Phoracantha* spp.

All of the *Cleonymus* wasps that emerged in the temperature-controlled culture room were collected and examined under a binocular microscope to determine the sex ratio and record the sexual dimorphism. The natural sex ratio recorded from the progeny emerging from this study was 1 male : 3 females (n = 139). This ratio may, however, not be entirely accurate for *Cleonymus* sp. as it is has only been calculated from a single sample of specimens that were collected daily when they emerged from *Phoracantha* infested logs in a culture room. It may have been more accurate to count the *Cleonymus* wasps immediately following emergence from each host *Phoracantha* larva in the larval tunnels. This would have removed the possible sampling bias of more females, as specimens were collected only after flying to a window of the culture room. Females may be more attracted to light than males, because in nature they may need to disperse in search of new oviposition sites, which males would not be required to do. Hence males

may remain near the logs to mate with emerging females and would not be attracted to a light trap.

Sexual dimorphism was apparent, particularly in the shape of the abdomen, where the last abdominal sternum is apically compressed in the male. In addition, the male *Cleonymus* sp. were generally about two-thirds (± 4 mm) the size of the females (± 6 mm). Sexual dimorphism was also apparent in the structure of the antennae of *Cleonymus* sp. Female antennae were yellow except for the final segment which was black, whereas male antennae were completely black. The legs of female wasps were yellow, whereas the males had black femora.

To study the oviposition behaviour of *Cleonymus* sp., adult wasps were reared in July from infested *Phoracantha* larvae that were maintained at a constant temperature of 24 °C. Braconid wasps appear to locate hosts of borer Coleoptera by vibrational cues associated with larval feeding (Hanks *et al.* 2001) rather than through host-produced chemicals. *Cleonymus* sp. appears to conform to this behaviour. *Cleonymus* females showed an increased interest in small sections (approximately 2 cm^2) of logs containing *Phoracantha* larvae (noted by the female repeatedly walking over the area and tapping vigorously with her antennae). She was confined *in situ* above that spot. This was achieved by placing a glass microscope slide over the wasp on top of 10 mm raised Prestik-adhesive barriers surrounding the wasp and attached to the bark surface. Confined in this way the oviposition behaviour of the female *Cleonymus* wasp was recorded.

The number of eggs laid was determined by lifting the bark at the site of oviposition with the aid of a penknife, to reveal the paralysed *Phoracantha* larva surrounded by the eggs of the parasitoid. The thickness of the bark through which oviposition occurred was measured and the number of oviposition holes through the bark above each parasitised *Phoracantha* larva was recorded. The number of times a host was stung by the *Cleonymus* female (as revealed by the bruised circular marks on the pale host larva) was recorded, as well as the duration of each developmental stage of the parasitoid.

Cleonymus sp. oviposited through *Eucalyptus* bark ranging in thickness from 0.5 to 3.5 mm after 'drilling' from directly above the *Phoracantha* larva. The duration of oviposition was only a few minutes and between one and five oviposition holes were drilled through the bark. The circular sting marks, which varied in number, were observed on different parts of the larva. The larva was presumably stung and paralysed prior to the eggs being deposited. Eggs of *Cleonymus* sp., varying in number from 3 to 45 (mean = 20.33 ± 15.29 S.D., n = 9), were deposited around the paralysed body of the *Phoracantha* larval host. Due to intraspecific competition, only as many of the resulting parasitoid larvae as would be sustained by the nutrients of the host larva would survive. This resulted in more parasitoid wasps emerging from larger hosts. This was confirmed by the varying numbers of *Cleonymus* pupae found around a parasitised *Phoracantha* larva, and the lack of much variation in the sizes of the pupae removed from different host larvae.

Cleonymus sp. eggs hatched after five days and the larvae fed by attaching themselves to the exterior of the host larva, typical of ectoparasitoid behaviour. The average duration from pupation until adult emergence of *Cleonymus* sp. was 28.5 ± 0.7 days S.D. (n = 2). The pupae varied in size from 3.9 mm to 6.0 mm with a mean of 5.0 mm (n = 32). Longevity from emergence until death varied from 7 to 19 days (mean = 8.55 days ± 3.97 S.D., n = 9). *Cleonymus* sp. was only observed to parasitise late or final-instar *Phoracantha* larvae in South Africa.

The size of the *Cleonymus* sp. wasp and its short ovipositor may restrict oviposition by these wasps to *Phoracantha* larvae in thin-barked *Eucalyptus* species. Thin bark also allows for easier detection of the larva by the parasitoid through vibrational cues.

A consignment of wasps of both sexes from the 1993 *Cleonymus* sp. culture, were sent to Tzaneen (23°50'S, 30°09'E) where they were released in a *Eucalyptus* plantation. In 1996, a wasp recovered from a log in Tzaneen was identified as the same undescribed *Cleonymus* species from Cape Town (F. Kirsten, pers. comm.). This specimen was presumed to have been the progeny of the original consignment of *Cleonymus* sp. wasps sent from Cape Town in 1993. No follow-up survey has been undertaken since then to ascertain its establishment.

4.2 Attempts to introduce *Syngaster lepidus*, *Jarra phoracantha* and *Jarra maculipennis*

Previous to this study, attempts at biological control of *Phoracantha* spp. in South Africa had concentrated on the importation of larval parasitoid species, several of which had been successfully reared but none of which had become established (Drinkwater 1973; Webb 1974).

In 1969 an attempt at biological control was made by importing the braconid larval parasitoids *Syngaster lepidus* Brullé, *Callibracon capitator* (Fabricius) and *Doryctes* sp. into South Africa (Webb 1974). The braconid species that parasitise *P. semipunctata* larvae are all idiobiont parasitoids (Paine *et al.* 2000). Ovipositing female wasps inject a paralysing venom into the host larvae prior to oviposition, halting further growth or feeding and immobilising the larva (Hanks *et al.* 2001). Of these introduced braconids only *S. lepidus*, a solitary ectoparasitic species, was eventually released but failed to become established in South Africa (Drinkwater 1973).

Syngaster lepidus along with *Callibracon limbatus* (Brullé) were reared as the dominant parasitoids of *P. semipunctata* in south-eastern Australia (Austin *et al.* 1994) and *S. lepidus* was regarded as the best candidate for biological control from studies conducted in the laboratory in California (Hanks *et al.* 2001). According to Austin *et al.* (1994), the so-called *Doryctes* sp. imported originally into South Africa was probably either *Jarra phoracantha* Marsh & Austin or *J. maculipennis* Marsh & Austin. For this reason, a second attempt was made in 1995 to reintroduce *S. lepidus*, together with the additional

gregarious larval ectoparasitoid species, *J. phoracantha* and *J. maculipennis*, into South Africa. These consignments were despatched as pupae from California where they had recently been imported and, on arrival, were placed in quarantine at the Plant Protection Research Institute in Pretoria.

After sufficient wasps had emerged to create a culture for mass release in the northern parts of South Africa, the remainder of the pupae were sent to Rosebank, Cape Town, to establish a culture for mass rearing and eventual release in the southernmost regions. This consignment of pupae resulted in the emergence of 29 *S. lepidus*, 37 *J. maculipennis* and 67 *J. phoracantha* adults. However, the sex ratio of *S. lepidus* and *J. phoracantha* wasps which emerged was strongly male biased at Rosebank, yet those sent to Sabie in the north contained more females that oviposited readily on *Phoracantha* larvae in logs presented to them.

The sex ratio of emerging *J. maculipennis* wasps was 1 male : 1 female. Temperature, humidity or host larvae of the incorrect size or age at oviposition influenced the sex ratio of the resulting parasitoid progeny (J.G. Millar, pers. comm.). In California, USA, Joyce *et al.* (2002) observed a significant relationship among the sizes of *P. recurva* and *P. semipuncata* hosts and the sex ratio of emerging parasitoids.

Parasitised 2-week-old beetle larvae of both *Phoracantha* species produced only male *S. lepidus* progeny, whereas older larval hosts produced increasing proportions of female parasitoids (up to 80 % females from 5-week-old hosts). Male and female parasitoid

sizes increased with increasing host size, females being consistently larger than males in all age classes for both host species. Large females were shown to have a higher reproductive rate than smaller females and could search for hosts over longer distances, whereas the size of males had no influence on the number of matings (Joyce *et al.* 2002).

Once the consignment of larval parasitoids had arrived at the Rosebank station of Plant Protection Research Institute in Cape Town, mass rearing facilities had to be established in the laboratories for the release of as many parasitoids of all three species as possible to contribute to the biocontrol of *Phoracantha semipunctata* and *P. recurva* in South Africa.

To achieve this, freshly cut logs of *Eucalyptus diversicolor*, cut in sections of approximately 50 cm were inoculated with newly-hatched *Phoracantha* larvae to maintain a *Phoracantha* culture for the mass rearing of larval parasitoids. The log sections were allowed to dehydrate sufficiently for two days so that *Phoracantha* larvae would not become water-logged, after which the ends were sealed with melted Paraffin wax to retain the remaining moisture to ensure full development of the larvae.

The logs were placed on two wooden blocks within wooden containers with a glass upper surface, each measuring 100 cm x 70 cm x 70 cm, thus allowing a maximum surface area for oviposition by the parasitoid. These containers were kept in a temperature-controlled culture room at a constant 25 °C during the day (07h30 – 16h00) but with the thermostat switched off at night, allowing temperatures to drop. *Phoracantha* spp. larvae that were

two to five weeks old were selected for parasitism because this is the optimal larval size to obtain the correct sex ratio of *S. lepidus* and *Jarra* spp.

Once the consignments of *J. phoracantha*, *J. maculipennis* and *S. lepidus* wasps had emerged from the consignment of pupae in quarantine, they were placed in their respective containers to oviposit. The parasitoids were allowed seven days to successfully parasitise their host larvae in the containers before being removed. *Eucalyptus diversicolor* was chosen as a suitable thin-barked host for *Phoracantha* larvae to allow for the ovipositor of the larval parasitoids to penetrate the bark and still access the larval host and paralyse it before oviposition. Hanks *et al.* (2001) found that parasitism of eucalypt borers was greatest if bark was less than 17 mm thick and at its lowest under bark over 25 mm thick.

Despite favourable laboratory conditions, no oviposition on host larvae was observed by wasps of any of the three parasitoid species, including *J. maculipennis* which had a relatively high number of females in the population. No progeny was produced by the three parasitoid species from the *Phoracantha*-infested logs. Eventually, only adult *P. semipunctata* and *P. recurva* emerged from these logs. No explanation for this failure can be offered except for the male bias in the relatively small populations of *S. lepidus* and *J. phoracantha*.

In Sabie, the logs on which the parasitoids were observed to oviposit were placed in a *Eucalyptus* plantation to allow the wasps to emerge and become established naturally.

Syngaster lepidus and *J. phoracantha* are reported to have become established in Mpumalanga but *J. maculipennis* has not since been recovered (Kirsten 2001).

***Cleonymus* sp. larvae feeding on a dessicated *Phoracantha* spp. larva**

***Cleonymus* sp. female ovipositing**

CHAPTER FIVE

OTHER POTENTIAL BIOLOGICAL CONTROL AGENTS

Australia has 40 *Phoracantha* species and many closely related cerambycid species, many of which are controlled by a vast array of natural enemies. For example, many natural enemies are associated with *P. semipunctata* and *P. recurva*, two species which have been thoroughly investigated because of their worldwide economic importance. Apart from the biological control agents of *Phoracantha* spp. that have been deliberately introduced into South Africa for this purpose and were previously discussed, various other parasitoid species have been recorded (Table 3), including *Cleonymus* sp. which is probably indigenous to South Africa.

A species of egg parasitoid (Encyrtidae) introduced into South Africa from Australia in 1910 (Lounsbury1917) has not since been collected in South Africa (Drinkwater 1975) but it is unlikely to have been *A. longoi*. Several indigenous South African parasitoid species have also been recorded parasitising the larvae of *Phoracantha* spp. Drinkwater (1973) refers to the indigenous braconid, *Iphiaulax* sp., and chalcid, *Tanycoryphus sulcifrons* Cam., which both emerged from logs containing *Phoracantha* spp. larvae. No mention or observation of either species has been made since. In September 1990 an unidentified wasp emerged from *Phoracantha*-infested logs from Tokai. Several cocoons were subsequently found at the end of *Phoracantha* larval tunnels, two of which contained the bodies of these parasitic wasps (± 20 mm long), indicating that they are larval parasitoids.

In Morocco, *Platystasius transversus* (Thomson) (Platygasteridae), indigenous to that country, was recorded successfully parasitising eggs of *P. semipunctata* which has become established there (Fraval & Haddan 1988). The larval parasitoid, *Helcostizus rufiscutum* Cushman (Hymenoptera: Ichneumonidae), indigenous to California USA was found to have a parasitism rate of up to 81 % of *P. semipunctata* larvae in that country (Hanks *et al.* 1997).

Unlike the egg parasitoid *A. longoi*, larval parasitoids do not appear to discriminate between *P. semipunctata* and *P. recurva* (J.G. Millar, pers. comm.). A large number of larval parasitoid species of *P. semipunctata* and *P. recurva* have been recorded in Australia (Table 3) but limited ecological information on them is available. All these species will not be equally effective as biological control agents and this was evident in south-eastern Australia where *S. lepidus* and *C. limbatus* were the dominant parasitoid species in one area (Austin *et al.* 1994) whereas *S. lepidus* and *Jarra* spp. dominated in another area (Paine *et al.* 2000). *Phoracantha semipunctata* and *P. recurva* have an extensive distribution range throughout Australia and there may be both resource partitioning amongst the parasitoid species and the dominant species could vary between biomes.

Eucalyptus species differ throughout the range of *P. semipunctata* and *P. recurva*. The trees are adapted to regional ecological influences (such as thick bark on trees prone to waterlogging and frequent fires) and show a varying ability to withstand drought.

Although turgor pressure plays a critical role in the susceptibility of a tree to borers, kino gum reaction does not appear to play an important role, at least in the initial defence against the borers (Hanks *et al.* 1991). Besides ecological influences, resource partitioning could be influenced by the thickness of the bark of the tree in which the *Phoracantha* host occurs, the length of the ovipositor of the parasitoid as well as a preference for larval hosts of specific sizes. For example, *C. limbatus* tended to dominate in logs that contained large larvae, whereas *S. lepidus* were more abundant in logs with small larvae, suggesting that the two parasitoid species exploit host larvae differently (Hanks *et al.* 2001). Resource partitioning amongst the *Jarra* species occurs where the two species with the shorter ovipositors, *J. maculipennis* and *J. painei* Austin & Dangerfield, parasitised larvae under thinner bark than did *J. phoracantha* (Paine *et al.* 2000). The only tachinid parasitoid of *Phoracantha* spp. recorded to date has been *Trichostylum curryi* sp. nov. in Australia (Barraclough 1992).

Drinkwater (1973) lists various indigenous and Australian predatory beetles of *Phoracantha* larvae, none of which have been assessed for host specificity. Predatory beetles are usually polyphagus, being attracted primarily directly to the host rather than to the chemical cues released by eucalypts. For this reason they are unlikely to be suitable as potential biological control agents. Predation by ants on *Phoracantha* spp. eggs was recorded in Portugal (Way *et al.* 1992). Similiarly, the invasive Argentine ant, *Linepithema humile* (Mayr), was observed to prey on *Phoracantha* spp. eggs during this study.

Mites were found infesting *Phoracantha* spp. eggs in the laboratory. These mites were either *Pyemotes ventricosus* (Newport), previously found infesting *Phoracantha* spp. eggs in South Africa by Drinkwater in 1973, or *Pyemotes tritici* found on *P. semipunctata* in California, USA (Hanks *et al.* 1992). Another unknown species of mite was found in relatively large numbers on the dorsal surfaces of the prothorax, as well as dorso-laterally on both elytra of the adult *Phoracantha* beetles in South Africa. These mites however, did not appear to have a detrimental affect on the beetles and could be merely phoretic.

During the dissection of the ovaries of *Phoracantha* spp. beetles in 1993, nematodes were recorded for the first time infesting the abdomens of two specimens. These nematodes had live bacteria associated with them and may be bacterial feeders, as several such nematode species are known (A. Swart, pers. comm.). However, bacterial feeders are usually found outside and not within the body of the host. A sample of these nematodes was sent to the National Collection of Insects, P.P.R.I., Pretoria for identification but it was not possible to identify them to even family level, because all of the nematode specimens were juveniles. Any possible detrimental effect of the nematodes on the beetles was not apparent prior to the beetles being killed for an unrelated investigation. No further *Phoracantha* specimens were infested by nematodes during subsequent dissections.

Phoracantha adults of both species often died prematurely in the laboratories at Plant Protection Research Institute in Rosebank, Cape Town. Dissections indicated this to occasionally be the result of a pathogen, due to distinct symptoms such as the softening

of the beetle exoskeleton and disintegration at the joints, combined with a strong, sickly-sweet odour emitted shortly after the death of the beetle. Posthumous dissections showed that the abdomen contents had become liquified into a brown substance. This disease was only observed under laboratory conditions and was probably introduced with field-collected beetles. This pathogen was not identified.

A mammalian predator of *Phoracantha* spp. larvae was recorded in Tokai Plantation in Cape Town. This predator was never positively identified but was presumably the commonly occurring small grey mongoose, *Galerella pulverulenta* (Wagner), judging from the spoor left behind (e.g. scratches and bites found in the bark along the full length of *Eucalyptus* logs from felled trees). This behaviour was observed over a period of several months during which almost 90 % of the *Phoracantha* larvae had been eaten. However, mongoose damage appears to be very localized as very little damage was observed elsewhere. The release of a defensive chemical secretion (phoracanthol) from the metasternal gland of the adult *P. semipunctata* when molested (Moore & Brown 1972) and the stridulation by *Phoracantha* spp. when handled, are probably deterrents to both avian and mammalian predators.

Table 3. Recorded natural insect enemies of *Phoracantha* spp.

Species	Family	Origin	Stage	Reference
**Avetianella longoi* Siscaro	Encyrtidae	Australia	Egg	Siscaro 1992
Platystasius transversus (Thomson)	Platygasteridae	Morocco	Egg	Fraval & Hadden 1974
Hymenopterous sp.	Encyrtidae	Australia	Egg	Webb 1974
**Syngaster lepidus* Brullé	Braconidae	Australia	Larva	Austin *et al.* 1994
**Jarra phoracantha* Marsh & Austin	Braconidae	Australia	Larva	Austin *et al.* 1994
**Jarra maculipennis* Marsh & Austin	Braconidae	Australia	Larva	Austin *et al.* 1994
Jarra bicolor Marsh & Austin	Braconidae	Australia	Larva	Austin *et al.* 1994
Jarra painei Austin & Dangerfield 1997	Braconidae	Australia	Larva	Austin & Dangerfield 1997
Callibracon capitator (Fabricius)	Braconidae	Australia	Larva	Moore 1963
Callibracon limbatus (Brullé)	Braconidae	Australia	Larva	Hanks *et al.* 2001
Callibracon flaviceps mackayensis (Turner)	Braconidae	Australia	Larva	Austin *et al.* 1994
Callibracon moorei Quicke & Austin	Braconidae	Australia	Larva	Austin *et al.* 1994
**Cleonymus* sp. Latreille (in S.Africa)	Pteromalidae	Unknown	Larva	O.C. Neser, 1996
Cleonymus sp. (in Australia)	Pteromalidae	Australia	Larva	Austin *et al.* 1994
Helcostizus rufiscutum Cushman	Ichneumonidae	California	Larva	Hanks *et al.* 1997
Xorides australiensis (Széplegeti)	Ichneumonidae	Australia	Larva	Austin & Dangerfield 1997
Acanthodoryctes tomentosus (Szépligeti)	Braconidae	Australia	Larva	Austin *et al.* 1994
Trichiohelcon phoracanthae (Froggatt)	Braconidae	Australia	Larva	Austin *et al.* 1994
**Iphiaulax* sp.	Braconidae	South Africa	Larva	Drinkwater 1973
**Tanycoryphus sulcifrons* Cam.	Chalcidae	South Africa	Larva	Drinkwater 1973
**Megalyra fasciipennis* Westwood	Ichneumonidae	Australia	Pupa	Gess 1964
Trogodendron fasciculatum Schreibers	Cleridae	Australia	?	Drinkwater 1973

Trichiohelcon phoracanthae (Froggatt)	Braconidae	Australia	Larva	Austin *et al.* 1994
Cleonymus spp. (in Australia)	Pteromalidae	Australia	Larva	Austin *et al.* 1994; Austin & Dangerfield 1997
Trichostylum curryi Barraclough	Tachinidae	Australia	Larva	Barraclough 1992
?*Platytainia* sp.	Tachinidae	Australia	Larva	Moore 1972

Iphiaulax phoracanthae Froggatt = *Trichiohelcon phoracanthae* (Froggatt)
Iphiaulax rubiceps Froggatt = *Syngaster lepidus* Brullé
Iphiaulax morleyi Froggatt = *Acanthodoryctes tomentosus*

* introduced/present in South Africa

***Syngaster lepidus* female - larval parasitoid of *Phoracantha* spp.**

CHAPTER SIX

DISCUSSION AND CONCLUSION

6.1 Discussion

The behaviour and life cycle of *Phoracantha* spp. together with the relatively low value of the crop does not render these borers conducive to chemical control. The crepuscular adults hide under loose bark during the day and lay eggs in crevices or under bark scales. The most damaging stage in the life cycle is the larval stage, which is also the most protected, occurring entirely within the timber itself. All stages of the life cycle of the beetle may be found throughout the year, although distinctive peaks occur in spring. The life cycle can be as short as three months or longer than a year. Hence a single insecticide spray would not be entirely effective while repeated sprays would not be cost effective. Trials in California to determine the efficacy and economics of four systemic insecticides against *P. semipunctata* showed that this was not acceptable in terms of control and cost (Ali, *et al.* 1989).

Vigorously growing eucalypt trees are not susceptible to colonisation by *Phoracantha* spp. Therefore the selection of the *Eucalyptus* species that are best adapted to particular sites will ensure vigorous growth and resistance to insects and pathogens. Colonisation of trees by beetles may also be influenced by the availability of oviposition sites, which may vary between *Eucalyptus* species depending on, for example, whether the bark is smooth or rough and persistent (Powell 1978). It was possible to greatly increase the number of eggs laid on smooth-barked *E. diversicolor* logs by adding additional

oviposition sites through attaching pieces of sloughed bark to the log with staples. Hanks *et al.* (1995b) suggested that beetle oviposition behaviour could restrict the host range of *P. semipunctata* to *Eucalyptus* species.

Resistance of living trees is strongly affected by environmental factors. In particular, lower moisture availability affecting bark moisture content, even for brief periods, predisposes *Eucalyptus* trees to attack (Hanks *et al.* 1991). Southern Africa experiences periodic droughts and fires, resulting in stressed trees, and this leads to upsurges in beetle numbers due to increased breeding resources. It is therefore important that the endemic population is kept as low as possible by removal of all potential oviposition sites. The long established practice of immediately debarking trees felled for poles works on this principle and should be maintained.

Biological control of *Phoracantha* spp. appears to potentially provide the most effective means of control. This was recognized shortly after the first discovery of *P. semipunctata* beetles in 1906 when several parasitoids were introduced (Lounsbury 1917). This attempt at biological control proved unsuccessful, as did the second attempt of establishing larval parasitoids by Drinkwater in 1968. Similar attempts with larval parasitoids introduced for the control of *P. semipunctata* also failed in Israel (Mendel *et al.* 1984).

The pupal parasitoid *Megalyra fasciipennis* had until now been underestimated as an effective biological control agent. A parasitism rate of up to 52.5 % was recorded in this

study. Temperature played an important role in the seasonal and daily activities of the wasp, which were confined to the summer months, which coincided with the peak availability of host pupae. However, the distribution of this specialist species is presently limited to the south-western Cape, a winter rainfall area, although an attempt was made to establish it in the Tzaneen district, a summer rainfall area. Further investigations are necessary to confirm its establishment in the latter locality.

The larval parasitoid *Cleonymus* sp. has not been a successful biological control agent because it remains rare, although mass rearing under laboratory conditions has proved highly successful. The origin of this undescribed species is unknown and *Phoracantha* spp. may therefore not be its natural host. For this reason *Cleonymus* sp. would, at this stage, not be considered for introduction to other parts of the world as a biological control agent, although it was introduced and has become established in the Tzaneen district of South Africa (F. Kirsten, pers. comm.).

The egg parasitoid, *Avetianella longoi*, is highly successful as a biological control agent, not only in the rate of parasitism achieved, but also in its ability to disperse readily, its ability to exist in unpredictable environments and its high reproduction rate. However, the activity peak of *A. longoi* is confined mainly to one month, February. *Phoracantha* spp. oviposition occurs practically uninterrupted from March to November and eggs are deposited in batches of 10 to 110, with a single captive female laying about 300 eggs (Duffy 1963). Chararas *et al.* (1971) recorded a mean of 180 eggs per female and Powell (1982) estimated an egg density of 1776/m² in Zambia. Each *A. longoi* wasp lays

up to 250 eggs during her 20 day adult life (Paine *et al.* 1995). Despite the high parasitism rate achieved in South Africa, the narrow activity peak of *A. longoi* limits the effectiveness of this parasitoid. Furthermore, it has a definite preference for one of the *Phoracantha* species, i.e. *P. semipunctata.*

In Australia, *A. longoi* to date has only been recorded from the south-eastern regions, but the possibility of discovering a much wider gene pool of *A. longoi* in other parts of Australia is likely, as its *Phoracantha* host occurs throughout the continent. These *A. longoi* strains could be recruited and introduced into South Africa to complement the strain already introduced and established. However, the possibility of recruiting a new parasitoid species is likely from areas where *A. longoi* is not found to occur in Australia.

The rearing and establishment of the larval parasitoids, *Syngaster lepidus, Jarra phoracantha* and *J. maculipennis*, have proved to be problematic in South Africa, as was similarly experienced in various other parts of the world where they had been introduced (L.M.Hanks, pers. comm.). In 2001, *Syngaster lepidus* and *J. phoracantha* were finally established in Tzaneen (Kirsten 2001). Their effectiveness as biological control agents and their rate of dispersal from this area remains to be ascertained.

Age-specific life-table data of *P. semipunctata* in Malawi showed that most mortality occurred in the larval stage in that country and that the major mortality factor was intraspecific competition (Powell 1982). In South Africa severe overcrowding led to a reduction in population density from one generation to the next, to a reduction in beetle

size and to a shift in the sex ratio in favour of males. This situation arose because *Phoracantha* spp. arrived in South Africa without its natural enemies. Unfortunately, the present complex of parasitoid species has not achieved the required level of control. This is because the number of hosts destroyed has merely reduced the intraspecific competition, thus allowing the surviving larvae more resources on which to develop, ultimately resulting in larger beetles laying a larger number of eggs. Population sizes of *Phoracantha* species in Australia are much smaller than in South Africa, which indicates the presence of a large cohort of natural enemies. This has been confirmed in the published literature (see Table 3) and many more parasitoid species may yet be discovered.

6.2 Conclusion

In monospecific plantation forestry, biological control is most effective when it is combined with forest hygiene and the production of healthy trees as a result of correct site and species selection. The present control through biological means has not give the required level of protection. One reason for this is that the parasitoid species are still localized in certain areas and have yet to disperse throughout the *Eucalyptus*-growing regions of the country. Once this has been done, a reassessment should be made of the level of parasitism, followed by the selection and introduction of other agents. Special care should be taken that no hyperparasitoids, including facultative hyperparasitoids, are introduced which could negate the effectiveness of the present complement of parasitoid species already established. Previous investigations into possible parasitoid species focused on the more widespread *P. semipunctata*. More focus on the procurement of

additional parasitoid species for *P. recurva* should take priority in light of the upsurge in the numbers of these borers.

REFERENCES

ACATAY, A. 1959. *Phoracantha semipunctata* Fabr. in der Türkey. *Anzeiger für Schädlingskunde* **32**(1): 4 – 5.

ALI, A.D., BARETTE, B.R & GARCIA, J.M. 1989. Efficiency and economics of selected systematic insecticides for control of Eucalyptus borer *Phoracantha semipunctata* (F.). *California Forestry Note* 101(iii): 7.

ANNECKE, D.P. & MORAN, V.C. 1982. *Insects and mites of cultivated plants in South Africa*. Butterworth, Durban, pp. 318.

AUSTIN, A.D., QUICKE, D.L.J., MARSH, P.M. 1994. The hymenopterous parasitoids of eucalypt longicorn beetles, *Phoracantha* spp. (Coleoptera: Cerambycidae) in Australia. *Bulletin of Entomological Research* **84**: 145 - 174.

AUSTIN, A.D. & DANGERFIELD, P.C. 1997. A new species of *Jarra* Marsh & Austin (Hymenoptera: Braconidae) with comments on other parasitoids associated with the eucalypt longicorn *Phoracantha semipunctata* (F.) (Coleoptera: Cerambycidae). *Australian Journal of Entomology* **36**: 327 – 331.

BARRACLOUGH, D.A. 1992. The systematics of the Australasian Dexiini (Diptera: Tachinidae: Dexiinae) with revisions of endemic genera. *Invertebrate Taxonomy* **6**: 1127 – 1371.

BERTI-FILHO, E., CERIGNONI, J.A. & SOUZA JUNIOR, C.N. 1995. First record of *Phoracantha semipunctata* (Fabricius, 1775) (Coleoptera, Cerambycidae) in the state of Sao Paulo. *Revista de Agricultura (Piracicaba)* **70**: 16 – 40.

BOUÇEK, Z. 1988. *Australian Chalcidoidea (Hymenoptera). A Biosystematic Revision of Genera of Fourteen Families, with a Reclassification of Species*. C.A.B. International, Wallingford, pp. 832.

BYTINSKI-SALZ, H. & NEUMARK, S. 1952. The eucalyptus borer (*Phoracantha semipunctata* F.) in Israel. *Transactions of the IXth International Congress of Entomology* (1952) **1**: 696 – 699.

CHARARAS, C., COURTOIS, J.E., LE FAY, A. & THUILLIER, A. 1971. Biologie, évolution et nutrition de *Phoracantha semipunctata* F. Coléoptère Cerambycidae spécifique des *Eucalyptus*. *Comptes Rendus des séances de la Societe de Biologie* **165**: 1565 – 1568.

CILLIÉ, J.J. & TRIBE, G.D. 1991. A method for monitoring egg production by the *Eucalyptus* borer, *Phoracantha semipunctata* (Fab.) (Cerambycidae). *South African Forestry Journal* **157**: 24 – 26.

CYMOREK, S. 1984. Note and Literature survey on the "Eucalyptus-borer" *Phoracantha semipunctata* F. (Col.: Cerambycidae), a pest inbetween forest and wood. *The International Research Group on Wood Preservation*. Paper prepared for the Fourteenth Meeting, Queensland, Australia, May 1983.

DE LABORDE, R.M. & ATKINSON, P. 1993. Estimates of the costs of potential losses from infestations of common forestry pests. *ICFR Annual Research Report*, pp. 179.

DRINKWATER, T.W. 1973. 'n Vergelykende morfologiese en bio-ekologiese studie van *Phoracantha semipunctata* (Fab.) en *P. recurva* Newman. M.Sc. thesis, University of Pretoria, Pretoria.

DRINKWATER, T.W. 1975. The present pest status of Eucalyptus borers *Phoracantha* spp. in South Africa. *Proceedings of the Ist Congress of the Entomological Society of South Africa* **1**: 119 – 129.

DUFFY, E.A.J. 1963. *A monograph of the immature stages of Australasian timber beetles (Cerambycidae)*. British Museum (Natural History).

EL-YOUSFI, M. 1992. Possibilities of control of *Phoracantha semipunctata* (F.) by selection of *Eucalyptus* species. *Boletin de Sanidad Vegetal, Plagas* **18**: 735 – 743.

ESTEVEZ, M.A.P. 1988. First record of *Phoracantha semipunctata* (Fabricius, 1775) (Col.: Cerambycidae), in the Canary Islands. *Boletin de la Asociacion Espanola de Entomologia* **2**: 367.

FORCE, D.C. 1972. r- and K- strategists in endemic host-parasitoid communities. *Bulletin of the Entomological Society of America* **18**: 135 – 137.

FRAVAL, A. & HADDAN, M. 1988. *Platystasius transverses* (Hym.: Platygasteridae) parasitoïde oophage de *Phoracantha semipunctata* (Col.: Cerambycidae), au Maroc. *Entomophaga* **33**: 381 – 382.

FROGGATT, W.W. 1906. Notes on the hymenopterous genus *Megalyra* Westwood, with descriptions of new species. *Proceedings of the Linnaean Society of New South Wales* **31**: 399 – 407.

FROGGATT, W.W. 1907. *Australian Insects*. William Brooks & Company Ltd. Sydney.

GESS, F.W. 1964. The discovery of a parasite of the *Phoracantha* beetle (Coleoptera: Cerambycidae) in the Western Cape. *Journal of the Entomological Society of Southern Africa* **27**: 152.

GONZÁLEZ TIRADO, L. 1992. Estudio sobre integrales térmicas de *Phoracantha semipunctata* Fab. (Col: Cerambycidae), insecto perforador del género *Eucalyptus*, en Huelva (España). *Boletin de Sanidad Vegetal, Plagas* **18**: 529 – 545.

HACKER, H. 1913. Some observations of the biology of Stephanidae and Megalyridae (Hymenoptera). *The Australian Zoologist* **11**: 341 – 346.

HADDAN, M., KADIRI, Z.A. & MAATOUF, N. 1995. Premier essai d'elevage au laboratoire des adultes de *Phoracantha semipunctata* (F.) (Coleoptere, Cerambycidae). *Annales Recherche Forestière au Maroc* **28**: 85 – 90.

HADDAN, M., FRAVAL, A. & THÉVENOT, M. 1988. Ennemis naturels de *Phoracantha semipunctata* (F.) (Col., Cerambycidae), ravageur xylophage des *Eucalyptus* au Maroc. *Bulletin de l' Institut Scientifique, Rabat* **12**: 167 – 170.

HANKS, L.M., CAMPBELL, C., PAINE, T.D. & MILLAR, J.G. 1997. Host range expansion of *Helcostizus rufiscutum* Cushman (Hymenoptera: Ichneumonidae) to *Phoracantha semipunctata* Fabr. (Coleoptera: Cerambycidae) in California. *Pan-Pacific Entomologist* **73**(3): 190 – 191.

HANKS, L.M., GOULD, J.R., PAINE, T.D., MILLAR, J.G., WANG, Q. 1995a. Biology and host relations of *Avetianella longoi* (Hymenoptera: Encyrtidae), an egg parasitoid of the eucalyptus longhorned borer (Coleoptera: Cerambycidae). *Annals of the Entomological Society of America* **88**: 666 – 671.

HANKS, L.M., McELFRESH, J.S., MILLAR, J.G. & PAINE, T.D. 1992. Control of the Straw Itch Mite (Acari: Pyemotidae) with sulfur in an insect rearing facility. *Journal of Economic Entomology* **85**: 683 – 686.

HANKS, L.M., McELFRESH, J.S., MILLAR, J.G. & PAINE, T.D. 1993. *Phoracantha semipunctata* (Coleoptera: Cerambycidae), a serious pest of *Eucalyptus* in California: biology and laboratory-rearing procedures. *Annals of the Entomological Society of America* **86**: 96 – 102.

HANKS, L.M., MILLAR, J.G. & PAINE, T.D. 1995b. Biological constraints on host-range expansion by the wood-boring beetle *Phoracantha semipunctata* (Coleoptera: Cerambycidae). *Annals of the Entomological Society of America* **88**: 183 – 188.

HANKS, L.M., MILLAR, J.G., PAINE, T.D., WANG, Q. & PAINE, E.O. 2001. Patterns of host utilization by two parasitoids (Hymenoptera: Braconidae) of the eucalyptus longhorned borer (Coleoptera: Cerambycidae). *Biological Control* **21**: 152 – 159.

HANKS, L.M., PAINE, T.D. & MILLAR, J.G. 1991. Mechanisms of resistance in *Eucalyptus* against larvae of the eucalyptus longhorned borer (Coleoptera: Cerambycidae). *Environmental Entomology* **20**: 1583 – 1588.

HANKS, L.M., PAINE, T.D. & MILLAR, J.G. 1996. Tiny wasp helps protect eucalypts from eucalyptus longhorned borer. *California Agriculture* **50:** 14 – 16.

HANKS, L.M., PAINE, T.D., MILLAR, J.G. & HOM, J.L. 1995c. Variation among *Eucalyptus* species in resistance to eucalyptus longhorned borer in Southern California. *Entomologia Experimentalis et Applicata* **74**: 185 – 194.

HEDQVIST, K-J. 1951. *South African Animal Life. Results of the Lund University Expedition in 1950 – 1951.* Ed: Bertil Hanström – Per Brinck & Gustav Rudebeck. Vol. VI Almqvist & Wiksell, Stockholm: pp 485 – 490.

HEDQVIST, K-J. 1967. Notes on Megalyridae [Hymenoptera: Ichneumonoidea] and description of New Species from Madagascar. *Annales de la Societe Entomologique de France* (N.S.) **3**: 239 – 246.

HUTCHARERN, C. & SABHASRI, B. 1985. Insect pests of *Eucalyptus camaldulensis* Dehn. in the community woodlot in Thailand. *Zeitschrift für Angewandte Entomologie* **99**: 170 – 174.

JAYAWICKRAMA, K.J.S., SCHLATTER, V.J.E. & ESCOBAR, R. 1993. Eucalypt plantation forestry in Chile. *Australian Forestry* **56**: 179 – 192.

JOYCE, A.L., MILLAR, J.G., PAINE, T.D. & HANKS, L.M. 2002. The effect of host size on the sex ratio of *Syngaster lepidus*, a parasitoid of Eucalyptus longhorned borers (*Phoracantha* spp.). *Biological Control* **24**: 207 – 213.

KIRSTEN, J.F. 2001. Biological control of the eucalyptus borers, *Phoracantha semipunctata* and *P. recurva*, in the summer-rainfall forestry regions of South Africa: establishment of two larval parasitoids, *Syngaster lepidus* and *Jarra phoracantha*. *Proceedings of the 13th Entomological Congress, Entomological Society of Southern Africa*, Pietermaritzburg, 2 – 5 July 2001. p 34.

LEPESME, P. 1950. Sur la dispersion par l'homme et acclimation de quelques Phoracanthini. In: *Longicornia-Etudes et notes sur les Longicornes* **1**: 577 – 579 Lechevalier, Paris.

LINSLEY, E.G. 1959. Ecology of Cerambycidae. *Annual Review of Entomology* **4**: 99 – 138.

LONGO, S., PALMERI, V. & SOMMARIVA, D. 1993. Sull'attività di *Avetianella longoi* ooparassitoide di *Phoracantha semipunctata* nell'Italia meridionale. *Redia*, LXXVI, n.1 1993: 223 – 239.

LÖYTTYNIEMI, K. 1983. Flight pattern and voltinism of *Phoracantha* beetles (Coleoptera, Cerambycidae) in a semihumid tropical climate in Zambia. *Annales Entomologici Fennici.* **49**: 49 – 53.

LOUNSBURY, C.P. 1917. The *Phoracantha* beetle. A borer pest of *Eucalyptus* trees. *Bulletin of Division of Entomology, Department of South Africa, Local Series* **24**: 1 – 10, 2 figs.

LUHRING, K.A., PAINE, T.D., MILLAR, J.G. & HANKS, L.M. 2000. Suitability of the eggs of two species of eucalyptus longhorned borers (*Phoracantha recurva* and *P. semipunctata*) as hosts for the encyrtid parasitoid *Avetianella longoi. Biological Control* **19**: 95 – 104.

MENDEL, Z. 1984. Natural control of the eucalyptus borer, *Phoracantha semipunctata* (F.) (Coleoptera: Cerambycidae) by the Syrian woodpecker. *Bulletin of Entomological Research* **74**: 121 – 127.

MOORE, B.P. & BROWN, W.V. 1972. The chemistry of the metasternal gland secretion of the common eucalypt longicorn, *Phoracantha semipunctata* (Coleoptera: Cerambycidae). *Australian Journal of Chemistry* **25**: 591 – 598.

MOORE, J.A. 1993. Rediscovery and releases of parasitoid of Eucalyptus borer. *Plant Protection News* **33**: 4, 7.

MOORE, K.M. 1963. Observations on some Australian forest insects. 15. Some mortality factors of *Phoracantha semipunctata* (F.) (Coleoptera: Cerambycidae). *Proceedings of the Linnaean Society of New South Wales* **88**: 221 – 229.

MOORE, K.M. 1972. Observations on some Australian forest insects. 25. Additional information on some parasites and predators of longicorns (Cerambycidae, Phoracanthini). *The Australian Zoologist* **17**: 26 – 29.

ORLINSKII, A.D., SHAKHRAMANOV, I.K. MUKHANOV, S.YU. & MASLYAKOV, V.YU. 1991. Potential quarantine forest pests in the USSR. *Zashchita Rastenii* **11**: 37 – 41.

PAINE, T.D., MILLAR, J.G. & HANKS, L.M. 1995. Integrated program protects trees from eucalyptus longhorned borer. *California Agriculture* **49**: 34 – 37.

PAINE, T.D., PAINE, E.O., HANKS, L.M. & MILLAR, J.G. 2000. Resource partitioning among parasitoids (Hymenoptera: Braconidae) of *Phoracantha semipunctata* in their native range. *Biological Control* **19**: 223 – 231.

PAIVA, M.R., MATEUS, E. & FARRALL, M.H. 1993. Chemical ecology of *Phoracantha semipunctata* (Col., Cerambycidae): Potential role in *Eucalyptus* pest management. *IOBC wprs Bulletin; Insect Pheromones* **16**: 72 – 76.

PIRAS, L., CONTINI, C. & PISANO, P. 1970. Sulla introduzione in Europa di un Cerambicide australiano parassita di Eucalyptus: *Phoracantha semipunctata* Fab. (Coleoptera, Cerambycidae). *Bolletin Sociedad Entomologica Italiana* **102**: 58 – 63.

POWELL, W. 1978. Colonisation of twelve species of *Eucalyptus* by *Phoracantha semipunctata* (F.) (Coleoptera: Cerambycidae) in Malawi. *Bulletin of Entomological Research* **68**: 621 – 626.

POWELL, W. 1982. Age-specific life-table data for the Eucalyptus boring beetle, *Phoracantha semipunctata* (F.) (Coleoptera: Cerambycidae), in Malawi. *Bulletin of Entomological Research* **72**: 645 – 653.

POYNTON, R.J. 1960. Notes on exotic forest trees in South Africa. *Government Printer, Pretoria. Bulletin No.* **38**: 166.

RODD, N.W. 1951. Some observations on the biology of Stephanidae and Megalyridae (Hymenoptera). *The Australian Zoologist* **11**: 341 – 346.

ROMANO, F.P. & CARAPEZZA, A. 1975. Sulla presenza de *Phoracantha semipunctata* F. in Sicilia (Coleoptera, Cerambycidae). *Bolletin Sociedad Entomologica Italiana* **107**: 91 – 92.

SAIZ DE OMENACA, J.A. & RODRÍGUEZ, J.A. 1991. Presence of *Phoracantha semipunctata* Fabr. on *Eucalyptus globulus* Labill. in Cantabria (Spain). *Boletin de Sanidad Vegetal, Plagas* **17**: 417 – 422.

SCHOLTZ, C.H. & HOLM, E. 1985. *Insects of Southern Africa*. Butterworths, Durban, pp. 402.

SCRIVEN, G.T., REEVES, E.L. & LUCK, R.F., 1986. Beetle from Australia threatens eucalyptus. *California Agriculture* **40**: 4 – 6.

SHAW, S.R. 1987. Three new Megalyrids from South America (Hymenoptera: Megalyridae). *Psyche* **94**: 189 – 199.

SHAW, S.R. 1990. A Taxonomic Revision of the Long-tailed wasps of the Genus *Megalyra* Westwood (Hymenoptera: Megalyridae). *Invertebrate Taxonomy* **3**: 1005 – 1052.

SISCARO, G. 1992. *Avetianella longoi* sp. n. (Hymenoptera Encyrtidae) egg parasitoid of *Phoracantha semipunctata* F. (Coleoptera Cerambycidae). *Bolletino di Zoologia Agrariae di Bachicoltura*, Ser. II **24**: 205 – 212.

SPETTER, E. 1963. Protection of green eucalypt logs against *Phoracantha semipunctata* Fabr. *Contributions on Eucalypts in Israel* **11**: 49 – 51.

TASSI, F. 1970. Un Longicorne australiano per la prima volta in Italia (Col. Cerambycidae). *Bollettino dell'Associazione Romana di Entomologia* **24**: 69 – 71.

THAKUR, M.L. 1988. Principal insect pests of *Eucalyptus* in India and their management. *Indian Journal of Entomology* **50**: 39 – 44.

TOOKE, F.G.C. 1936. The *Phoracantha* beetle: Insects injurious to forest and shade trees. *Bulletin of the Department of Agriculture of South Africa* **142**: 33 – 39.

TRIBE, G.D. & CILLIÉ, J.J. 1997. Biology of the Australian tortoise beetle *Trachymela tincticollis* (Blackburn) (Chrysomelidae: Chrysomelini: Paropsina), a defoliator of *Eucalyptus* (Myrtaceae), in South Africa. *African Entomology* **5**: 109 – 123.

TRIBE, G.D. & KFIR, R. 2001. The establishment of *Dendrosoter caenopachoides* (Hymenoptera: Braconidae) introduced into South Africa for the biological control of *Orthotomicus erosus* (Coleoptera: Scolytidae), with additional notes on *D.* sp. nr. *labdacus*. *African Entomology* **9**(2): 195 – 198.

VAN DEN BERG, M.A. 1979. Research on forest and timber insects in South Africa since 1899. *Phytophylactica* **11**: 69 – 78.

VEIGA FERREIRA, G.D.A. 1964. Tribo *Phoracantha* Lacordaire. Longicórnios de Mocambique. *I. Revista de Entomologia de Moçambique* **7**(2): 625 – 639.

WANG, Q. 1995. A taxonomic revision of the Australian genus *Phoracantha* Newman (Coleoptera: Cerambycidae). *Invertebrate Taxonomy* **9**: 865 – 958.

WANG, Q., THORNTON, I.W.B. & NEW, T.R. 1999. A cladistic analysis of the Phoracanthine genus *Phoracantha* Newman (Coleoptera: Cerambycidae: Cerambycinae), with discussion of biogeographic distribution and pest status. *Annals of the Entomological Society of America* 92: 631 – 638.

WATERSTON, J. 1922. A new family of Hymenoptera from South Africa. *Annals and Magazine of Natural History* **9**: 418 – 420.

WAY, M.J., CAMMELL, M.E. & PAIVA, M.R. 1992. Studies on egg predation by ants (Hymenoptera: Formicidae) especially on the eucalyptus borer *Phoracantha semipunctata* (Coleoptera: Cerambycidae) in Portugal. *Bulletin of Entomological Research* **82**: 425 – 432.

WEBB, D. van V. 1974. Forest and timber entomology in the Republic of South Africa. *Entomology Memoir No. 34*. Department of Agricultural Technical Services, Pretoria.

WILSON, D.S. & CLARK, A.B. 1977. Above ground predator defence in the harvester termite, *Hodotermes mossambicus* (Hagen). *Journal of the Entomological Society of Southern Africa* **40:** 271 – 282.

WINSTANLEY, J.K. 1985. The *Eucalyptus* borers *Phoracantha semipunctata* F. and *P. recurva* (Cerambycidae: Coleoptera). *Pests and Diseases of South African Forests and Timber*. Department of Environmental Affairs, Pamphlet 273: p 5. .