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Longevity and reproduction in *Apiomorpha* Rübsaamen (Hemiptera: Sternorrhyncha: Coccoidea)

Abstract - Adult females of *Apiomorpha* Rübsaamen are remarkably long-lived (up to five years) and those of most species are able to produce thousands of offspring. Males rarely live more than one year and survive only several days after emerging from their galls. Males and females of the one cohort mature at about the same time despite extreme size differences between the sexes, thereby allowing brother-sister matings. Age to maturity ranges among species from two and a half months to more than 12 months. The longevity of females results in the overlap of generations of females on the one host plant.

Key words: *Apiomorpha*, Eriococcidae, galls, *Eucalyptus*.

INTRODUCTION

Apiomorpha Rübsaamen is an endemic Australian eriococcid in which both males and females induce galls on *Eucalyptus*. Each adult female of *Apiomorpha* is confined within the gall that she initiated when she first began feeding as a first-instar nymph (crawler). Galls of females of *Apiomorpha* each have a chamber in which the insect has limited mobility and is oriented with its head towards the base of the gall and its anal lobes towards the apex. As the gall of a female matures an apical opening forms as plant tissue in the region becomes necrotic. The opening allows elimination of honeydew, mating and the escape of first-instar nymphs (crawlers). Crawlers are the primary dispersers and appear well suited to air-borne dispersal (Cook *et al.*, 2000). There are few reports of the life history of *Apiomorpha* (Short, 1947; Gullan, 1984). Females of *Apiomorpha* have three instars and males have five (Gullan, 1981), thereby conforming to the general pattern in other eriococcids such as *E. coriaceus* Maskell (Patel, 1971), and in dactylopiids (Pérez Guerra & Kosztarab, 1992), asterolecaniids, kermesids (Miller, 1991) and diaspidids (Koteja, 1990).

This study aims to provide information on reproduction, development and adult longevity in *Apiomorpha*, which is unusual among scale insects in having a number of long-lived species.

MATERIALS AND METHODS

Field-collected galls usually were stored in plastic bags (Rob's Long Life Vegetable Bags®) until dissection. Mature females were kept alive in their galls for up to several months at room temperature in gauze-covered containers. A record was kept of the emergence of crawlers from field-collected galls. Crawlers of nine species of *Apiomorpha* were released onto potted eucalypt saplings in either of two ways:

1. The gall of the adult female with crawlers emerging was tied to a potted plant.
2. Crawlers were placed directly on the host using a fine paintbrush.

Cultures were housed in a glasshouse in the Plant Culture Facility (PCF), ANU, on a daily cycle of 26° C days and 12° C nights with natural light. Females of *A. strombylosa* (Tepper) and *A. munita* (Schrader) were housed in a separate glasshouse isolated from conspecific males. Females of *A. spinifer* Froggatt and *A. pharetrata* (Schrader) gall form II also were reared in the absence of males.

Observations were made of crawler settling positions and gall induction generally. The times to maturity were recorded. Adult males were readily discernible within their galls by the presence of the two long apical wax filaments, which are absent in earlier instars. The moult to the adult instar was detected in females by the ejection of the second-instar cuticle from the gall, or destructively by dissecting the gall. Successive generations were marked by tying different coloured cottons on the branch distal to the last settled crawlers and around individual galls of females. The longevity of females also was recorded. Because females remain enclosed within gall tissue, the anal lobes were stimulated with a hair and wriggling was taken as an indication that the female was alive.

RESULTS

Females of most species of *Apiomorpha* were able to produce thousands of offspring over several weeks. The body cavity of gravid females is almost entirely filled with developing embryos. For example, the ovaries containing developing embryos removed from a female of *A. regularis* (Tepper) had a volume of more than 1.2 ml (fully developed embryos are generally $\leq 300\mu\text{m}$ long). *Apiomorpha* is ovoviviparous and nymphs are born fully developed. At birth they are still encased in the chorionic membrane that dries and frees the insect after about 5-30 minutes. The first-instar nymphs usually remain grouped at the base of the gall chamber for up to several days before emerging from the gall. Emergence of crawlers from individual galls may continue for up to three months and not all females within a population reproduce simultaneously. There does not appear to be a seasonal pattern to reproduction in the field (Table 1). Although there appears to be an increase in emergence in spring and summer, this may reflect collection bias. Of those species that were well sampled (Table 1), crawler emergence was recorded from different times throughout the year.

Table 1 - Emergence dates of field-collected crawlers of *Apiomorpha*. Numbers indicate the number of different populations with crawlers emerging that month.

Species ^a	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
<i>A. baeuerleni</i> (Froggatt)	1											
<i>A. sp. nov.</i> "burracoppinensis"										1		
<i>A. calycina</i> (Tepper)									2		1	
<i>A. conica</i> (Froggatt)						1	1		1			
<i>A. densispinosa</i> Gullan									1			
<i>A. dipsaciformis</i> (Froggatt)					1							2
<i>A. duplex</i> (Schrader)	1									1		
<i>A. frenchi</i> Froggatt								1				
<i>A. helmsii</i> Fuller												1
<i>A. sp. nov.</i> "Hervey Range"									1			
<i>A. karschi</i> Rübsaamen	1										1	
<i>A. sp. nov.</i> "lumphead"											1	
<i>A. maliformis</i> Fuller	2	1				1						
<i>A. malleacola</i> Gullan												1
<i>A. minor</i> (Froggatt)	1		1			2	2	1	1			1
<i>A. munita malleensis</i> Gullan				3					2		2	
<i>A. munita tereticornuta</i> Gullan	1		1		1				1		1	
<i>A. munita munita</i> (Schrader)	1			1		1					1	1
<i>A. ovicola</i> (Schrader)		1									1	
<i>A. ovicoloides</i> (Tepper)											2	
<i>A. pharetrata</i> form I	2								1		1	2
<i>A. pharetrata</i> form II	1											
<i>A. pileata</i> northern form				2								
<i>A. pileata</i> southern form	2					1		1	1	1		1
<i>A. regularis</i> (Tepper)						1	1					
<i>A. sp. nov.</i> "rose3"												1
<i>A. sessilis</i> (Froggatt)	2											
<i>A. sloanei</i> (Froggatt)				1	1	1						
<i>A. spinifer</i> Froggatt	1	1							2	1		
<i>A. strombylosa</i> eastern form									3		1	
<i>A. strombylosa</i> western form			1	2	1					1	1	1
<i>A. subconica</i> (Tepper)									1		1	1
<i>A. tepperi</i> Gullan										1		
<i>A. urnalis</i> (Tepper)										1	3	
<i>A. variabilis</i> (Froggatt)												1
<i>A. withersi</i> Froggatt											1	1

^a Code names for undescribed species are not intended for nomenclatural use.

Crawlers wandered over plants for up to seven days before settling on new plant growth or dispersing. Some crawlers display dispersal behaviour of congregating at the tips of plants and are easily dislodged with a puff of air. In many species, each sex preferentially settles on different plant parts (Table 2).

The fastest developing males and females from each cohort reach maturity at about the same time (Table 2). Development to adulthood takes a minimum of about two and a half months in species in which females are small and up to or exceeding nine months for species in which females are large (Table 2). There can be considerable variation within a cohort (Table 2). For example, 12 months after settling, some males of *A. strombylosa* and *A. duplex* (Schrader) were adults whereas others were still second instar-nymphs. Similarly, females from the one cohort of each of *A. munita*

Table 2 - Gall and insect development in *Apiomorpha* under glasshouse conditions. Body lengths are ranges for adult females (from Gullan, 1984).

Species	Body length (mm)	Site of gall induction	Gall enclosure	Ostiole opening	Adult eclosion	Age at first Reproduction	Max. age
<i>Apiomorpha conica</i> females	7-27	stems				12-13 months	>3 years
<i>Apiomorpha duplex</i> females	23-34	stems	3-4 weeks		9-12 months	12 months	3 years
males		stems, leaves	3-4 weeks		9-12 months		1 year
<i>Apiomorpha minor</i> females		stems				10 months	>2 years
males		leaves					
<i>Apiomorpha munita tereticornuta</i> females	5-15	stems	3-4 weeks	6-7 weeks	3-14 months	6 months	5 years
males		galls of females	3-4 weeks	6-7 weeks	3-9 months		<1 year
<i>Apiomorpha pharetrata</i> form I females	4-11	leaves	3-4 weeks		2.5 months	14 months ^a	2.5 years
males		galls of females	3-4 weeks		2.5 months		<1 year
<i>Apiomorpha pileata</i> S form females	11-21	stems	3-4 weeks			15 months	
males		leaves	3-4 weeks				<1 year
<i>Apiomorpha pileata</i> N form females	11-21	stems				15 months	
<i>Apiomorpha regularis</i> females	12-30	stems	3-4 weeks	≥4.5 months	5.5 months	13 months	3 years
males		leaves	3-4 weeks	≥4.5 months	5.5 months		<1 year
<i>Apiomorpha spinifer</i> females	3-9	leaves					>2 years
<i>Apiomorpha strombylosa</i> E form females	10-22	stems	3-4 weeks	≥8 months	9-24 months		5 years
males		stems, leaves	3-4 weeks	≥4.5 months	8-18 months		1.5 years

^a Seven months after mating

tereticornuta Gullan and *A. strombylosa* reached maturity at different times over a 12 month period.

Males of most species did not live longer than one year and adult males survived fewer than five days after emerging from their galls. Although males of most species of *Apiomorpha* are about the same size, the development time varied among species with males reaching maturity at the same time as conspecific females. Males of *A. duplex* and *A. strombylosa* were the longest lived, up to 18 months, corresponding to the long maturation time for females of these species.

Females of *A. m. tereticornuta* Gullan were able to reproduce as young as six months old whereas females of *A. regularis* and *A. pileata* (Schrader) were aged 13 and 15 months respectively at first reproduction despite the presence of adult males at maturity. No females of the four species reared without males reproduced and there was no embryo development in their ovaries.

Some adult females of *A. m. tereticornuta* and *A. strombylosa* survived up to five years under glasshouse conditions. Many females of *A. conica* (Froggatt), *A. duplex* (Schrader), *A. minor* (Froggatt), *A. munita*, *A. regularis* and *A. strombylosa* lived at least three years under glasshouse conditions. In species with small adult females, such as *A. pharetrata* and *A. spinifer*, some females survived at least two and a half years. Adult females (*A. minor*, *A. urnalis* (Tepper), *A. regularis*, *A. maliformis* Fuller, *A. pileata* (Schrader)), still enclosed in their galls, often survived two to three months after being removed from their host. One female of each of *A. minor* and *A. variabilis* (Froggatt) survived five and a half months and two females of *A. maliformis* reproduced nine months after collection. These observations suggest that females may out-live the plant structures on which they occur.

DISCUSSION

Females of most species of *Apiomorpha* are able to produce many more offspring than females of other eriococcids. Typically, eriococcids produce 50 to 100 eggs (Miller, 1991) although some such as *E. coriaceus* may produce between 150 and 280 eggs (Patel, 1971). It is likely that the number of offspring is positively correlated with adult female body size, as it is in coccids (Marotta, 1997). As a consequence of high female fecundity, population size in *Apiomorpha* may expand through the fecundity of individual females, rather than via the reproductive efforts of multiple females as occurs in many other scale insects (e.g., Beardsley & Gonzalez, 1975; Moran & Cobby, 1979).

Reproduction does not appear to be markedly seasonal because crawlers were collected throughout the year. However, there may be seasonality among populations or species that was not detected by the low levels of sampling of most taxa.

Females of *A. munita tereticornuta*, *A. pharetrata* gall form II, *A. spinifer* and *A. strombylosa* reared in the glasshouse did not reproduce in the absence of males and thus reproduction in these species appears to be exclusively sexual. Matings are likely

to occur between siblings on the natal host because they mature at the same time and, in *A. munita*, because males often develop on galls of their sisters. The success of colonies initiated by brother-sister matings in the glasshouse suggests that there is no clear inbreeding depression. The variability in development rates within cohorts, recorded also by Short (1947), may be a mixed reproductive strategy where inbreeding is likely to occur among offspring which develop at the typical (common) rate whereas delayed development may provide an increased opportunity for outcrossing.

Adult females of *Apiomorpha* are long-lived relative to males, and to both sexes of other eriococcids. Older females of *A. m. tereticornuta* were still alive after several successive generations of their offspring had developed and therefore there is an overlap of generations of females on the one host plant. This is contrary to Short's (1947) recording of an annual lifecycle in *A. ovicola* (Schrader) in which females did not live longer than one year. The overlap of generations is unusual among the Coccoidea and provides an opportunity for high levels of inbreeding and for females to manipulate the sex ratio of her offspring over several years.

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