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HOST ACCEPTANCE TRIALS OF PARASITOIDS FROM INDIAN *PARATACHARDINA LOBATA* (HEMIPTERA: KERRIIDAE) ON THE INVASIVE LOBATE LAC SCALE IN FLORIDA

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ABSTRACT

The invasive lobate lac scale identified as *Paratachardina lobata* (Chamberlin) (Hemiptera: Keriidae), native to southern India and Sri Lanka, is a severe threat to native and economic plants in southern Florida. In an attempt to find appropriate control against the invasive scale, 3 parasitoid species associated with *P. lobata* in its native southern India were tested in host acceptance trials in quarantine. *Ooencyrtus kerriae* Hayat (Encyrtidae) and *Coccophagus parlobatae* Hayat (Aphelinidae) drill their ovipositor through the rigid lac covering of the scale, whereas *Aprostocetus bangaloricus* Narendran (Eulophidae) oviposits into the anal pore of the scale. Despite this apparent oviposition behavior, their reproduction on lobate lac scale in these tests failed. *Ooencyrtus kerriae* and *C. parlobatae* yielded insignificant numbers of offspring and *A. bangaloricus* did not reproduce on lobate lac scale in Florida. To investigate the lack of offspring, scales were dissected 2 months after parasitoid oviposition. No parasitoid development to the larval stage was recorded in the scales, but round blood cell accumulations were found, which appeared to be encapsulations of parasitoid eggs. These findings indicate a strong immune response of the invasive scale to the tested parasitoids. The unsuitability of the invasive lac scale as a host for these parasitoids suggests that the invasive lobate lac scale and the Indian *P. lobata* differ physiologically. Additional surveys are needed to find a better matching form of the invasive lobate lac scale in order to obtain more suitable parasitoids for the control of this serious pest in Florida.

Key Words: Eulophidae, Aphelinidae, Encyrtidae, biological control, host suitability, immune response

RESUMEN

La escama lobulada de laca invasora identificada como *Paratachardina lobata* (Chamberlin) (Hemiptera: Keriidae) y nativa del sur de la India y Sri Lanka, es una amenaza seria a las plantas nativas y económicas en el sur de la Florida. En un esfuerzo para encontrar un control apropriado contra esta escama invasora, 3 especies de parasitoides asociados con *P. lobata* que provienen de su región nativa al sur de la India fueron evaluados en pruebas de aceptación de hospedero en quarentena. *Ooencyrtus kerriae* Hayat (Encyrtidae) y *Coccophagus parlobatae* Hayat (Aphelinidae) barrenan sus ovipositores por la cubierta rigida de la escama laca, mientras que *Aprostocetus bangaloricus* Narendran (Eulophidae) oviposita en el poro anal de la escama. A pesar de este aparente comportamiento de oviposición, las pruebas mostraron que no pudieron reproducirse sobre la escama lobulada de laca. *Ooencyrtus kerriae* y *C. parlobatae* rendieron numeros de progenies insignificativos y *A. bangaloricus* no pudo reproducirse sobre la escama lobulada de laca en la Florida. Para investigar la falta de progenie, las escamas fueron disecadas 2 meses después de la oviposición de los parasitoides. No se registro el desarrollo de parasitoide hasta el estadio de la larva en las escamas, pero se encontraron acumulaciones de celulas redondas de sangre, que aparecieron ser encapsulaciones de los huevos de parasitoides. Estos hallazgos indican una respuesta inmunólogica fuerte de la escama invasora hacia los parasitoides evaluados. La inadecuada habilidad de la escama de laca invasora como un hospedero de estos tres parasitoides indica que la escama lobulada de laca invasora y la *P. lobata* en la India son fisiológicamente diferentes. Se necesita realizar sondeos adicionales para encontrar la forma de escama mas suceptible de la escama lobulada de laca invasora para obtener parasitoides mas apropiados para el control de esta plaga seria en la Florida.

The lobate lac scale is a highly invasive insect, which is a severe threat to native and economic plants in Florida (Howard et al. 2002; Pemberton 2003a). The invasive scale was identified as *Paratachardina lobata* (Chamberlin) (Hemiptera: Kerriidae), a highly polyphagous scale (Varshney 1992), native to southern India and Sri Lanka (Varshney 1976). In its native area it is controlled

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by various antagonists such as Neuroptera, Lepidoptera, and chalcidoid wasps (Varshney 1976). Today in Florida the lobate lac scale attacks over 300 plant species (Howard et al. in press). To protect the susceptible native and economic plants in Florida and the Bahamas from this pest, biological control is urgently needed. Only 2 parasitoid species have been isolated from the lobate lac scale in Florida: *Ammonoencyrtus carolinensis* (Meyer) (n. comb.) and an unnamed *Metaphycus* sp., both of which are encyrtids (Howard & Pemberton 2003; Schauff 2005). The rate of parasitism is extremely low with only about 1% of scales with emergence holes (Pemberton 2003b), too low to provide population regulation. In India, research on antagonists of lac insects has focused on predaceous Lepidoptera and parasitoids that are pests of *Kerria lacca* (Kerr) (Narayanan 1962; Varshney 1976; Subbarayudu & Maheswahar 1998), a species cultivated to produce shellac. Some of these parasitoids also attack *P. lobata* (Pemberton 2003b). Two biological control approaches were initiated (Pemberton 2003a). One was to determine whether parasitoids associated with *K. lacca*, especially species recorded from *P. lobata*, would attack the lobate lac scale in Florida. Parasitoids of *K. lacca*, including some known from *P. lobata* were discovered in Thailand and imported to Florida for evaluation against the invasive lobate lac scale (Pemberton et al. 2006). These parasitoids neither oriented to nor attacked the lobate lac scale. The second approach has been to try to locate parasitoids on *P. lobata* from its native India and Sri Lanka.

During Mar 2004, an intensive survey for *P. lobata* was made in the type localities for the insect in Sri Lanka, in Peridenyia, Kandy and other locations, but no *Paratachardina* scales were found (Pemberton unpublished).

In Aug 2005, *P. lobata* was located at different sites in southern India (Schroer & Pemberton, unpublished data). Following the discovery of these *P. lobata* populations, a program was developed to make periodic collections of *P. lobata* to discover and assess its parasitoids with the goal of finding promising species with biological control potential. The scale was collected bimonthly from 14 different field sites between 11° and 13° latitude in the area of Bangalore in Karnataka and Coimbatore in Tamil Nadu. Four parasitoid species were associated with *P. lobata*. *Marietta leopardina* Motschulsky (Aphelinidae), previously recorded to be a hyperparasitoid of chalcidoid wasps (Noyes 2003; Hayat et al. 2003), was found to be a primary parasitoid on *P. lobata*. *Coccophagus parlobatae* Hayat (Aphelinidae) was found as a secondary parasitoid of the scale. Two primary parasitoids were found, neither of which has been recorded as a hyperparasitoid. *Ooencyrtus kerriae* Hayat (Encyrtidae) develops gregariously, while *Aprostocetus bangaloricus* (Eulophidae) is a solitary parasitoid. In the present study the host finding behavior and abilities of the 3 latter parasitoids to successfully parasitize the invasive lobate lac scale were examined. *Marietta leopardina* was excluded from the studies due to low occurrence and knowledge of its nature as a hyperparasitoid.

Materials and Methods

Insect and Plant Sources

Parasitoid wasps from the field collections made in southern India were used for the experiments (Schroer & Pemberton, unpublished data). Immature wasps, developing in *P. lobata* on cut twigs of *Pongamia pinnata* (L.) Pierre (Fabaceae), were shipped bimonthly from India, double packed in jute in a polystyrene box with cooling packs, to our Ft. Lauderdale, Florida, quarantine laboratory. The consignments took an average of 5 d, during which the temperatures within the boxes ranged from 16 to 30°C (WatchDog datalogger series 100, Spectrum Technologies, Plainfield, IL). The adult wasps were used in the tests within 3 d of emergence, which occurred during the first 3 weeks after arrival of the parasitized *P. lobata* in the laboratory.

Coco plum seedlings (*Chrysobalanus icaco* L.) infested with the invasive lobate lac scale were used to observe the host finding behavior. The seedlings were grown in potting soil (Atlas Peat & Soil, Inc., Boynton Beach, FL) in 4 × 21-cm plastic planting cones (Stuewe & Sons, Inc., Corvallis, OR). Fifty plant seedlings in cones were cultivated in a flow tray holding >5 cm level water supplied with soluble fertilizer (Peters Professional, Spectrum Group Div. of United Industries Corp., St. Louise, MO). To induce lobate lac scale infestations, these seedlings were placed beneath heavily infested shrubs in Secret Woods County Park, Broward Co., FL to allow crawlers to access and settle on the seedlings (Pemberton et al. 2006). After an exposure period of 4 months, when seedlings were infested with both immature and mature lobate lac scale, they were used for parasitoid observation and oviposition tests.

For the parasitoid acceptance tests, other host plants of lobate lac scale were used including coco plum, wax myrtle (*Myrica cerifera* (L.)), yaupon holly (*Ilex vomitoria* Ait.), myrsine (*Rapanea guianensis* Aubl.) and white indigo berry (*Randia aculeata* L.). These plants, grown in 3-gallon pots and fertilized with Osmocote (Scotts Company LCC, Marysville, OH), were infested with the lobate lac scale in the same manner as plum seedlings. After 4 months of exposure, 5 plants were randomly picked and the numbers of *P. lobata* was estimated on each. Plants used in the parasitoid acceptance trials were infested with a mean of 4 (±2) lobate lac scales per cm^2.

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Observations of Parasitoid Host Finding and Oviposition

For observation tests experimental chambers were required that confined the wasps with the infested seedlings in a small area that allowed a view from every angle. Small, rectangular glass boxes were built with 3 microscope glass slides (75 × 25 mm) joined with a fourth side of transparent plastic to create a rectangular shaped box (78 × 26 mm^2). Holes were cut into the plastic and sealed with micromesh gauze (300 µm mesh). The holes were used for air circulation and placement of wasps into the boxes. The observation boxes were put over lobate lac scale infested coco plum seedlings (growing in the cones), which were manually defoliated to allow an unobstructed view. After placement over the seedling, the ends of the boxes were sealed with sponges which were taped to the plastic parts of the boxes. Female parasitoid wasps were introduced (a) individually, in groups of 2 or 4 wasps of (b) the same species or (c) different species. Wasp behavior was observed with a stereo dissecting microscope for about 2 h, recording periods for host finding behavior and oviposition. The length of the oviposition period was measured for 5 individual wasps of each species. The time required for ovipositor penetration was measured from the time when a favorable host was contacted to the time when the ovipositor completely penetrated the lac covering the scale. After observations the parasitoids were removed and used for rearing tests. The scales which were penetrated by ovipositors were marked and plants were stored in water trays for 2 months. After this time scales were dissected to examine parasitoid development.

Acceptance and Rearing Trials

Host plants in 3-gallon pots infested with lobate lac scale were covered with 10 × 58-cm Plexiglas cylinders (Pemberton et al. 2006). The tops of these cylinders and two 28.3 cm^2 round holes were covered with micromesh gauze to ensure air circulation. Two round holes (12.6 cm^2) with rubber stopper plugs served as openings to insert an aspirator for the introduction of wasps and capture of adult offspring. Test wasps were released into separate cylinders according to their species. The numbers of released wasps and their sex ratios (Table 1) were determined by adult parasitoid emergence from lobate lac scale collections made in India (Schroer & Pemberton, unpublished data). The gender was not determined for all tested aphelinid individuals because the small amount of sexual dimorphism made determining gender difficult until distinguishing morphological characteristics were better understood. Subsequent gender determinations indicated the sex ratio for *C. parlobatae* was 16 ♀: 1 ♂ (n = 402) (Schroer & Pemberton, unpublished data). We assume that the sex ratios of the wasps used in the tests was similarly female biased but the actual numbers of males and females used is uncertain. Test cylinders were kept at 23° to 26°C and 65% RH in a greenhouse with natural sun light. Offspring were readily detected and collected inside the mesh tops of the cylinders because of their movement to the tops due to their attraction to the brighter light. Emerging wasp progeny were collected with an aspirator and examined under a dissecting microscope to determine their identities and gender. The cylinders were monitored regularly for emerging wasps for 6 months after the first test wasps were introduced. The lobate lac scales on the plants in the cylinders were then examined to identify the individual hosts of emerging wasps. The acceptance and rearing trials were replicated 3 to 7 times for each species. Scale host plants varied because of availability and scale colony development. The numbers of test cylinders and tested host plants are indicated in Table 1.

TABLE 1. NUMBER OF FEMALES AND MALE PARASITOIDS USED IN ACCEPTANCE TESTS OF THE INVASIVE LOBATE LAC SCALE ON DIFFERENT HOST PLANTS. THE NUMBER OF ADULTS INTRODUCED INTO THE CYLINDERS WAS THE NUMBER EMERGING FROM *PARATACHARDINA LOBATA* COLLECTIONS MADE IN SOUTHERN INDIA. LOBATE LAC SCALE HOST PLANTS USED WERE *CHRYSOBALANUS ICACO*, *ILEX VOMITORIA*, *MYRICA CERIFERA*, *RANDIA ACULEATA* OR *RAPANEA GUINENSIS*.

	Number of wasps ♀ (+♂) released per host plant						
Parasitoid species	*C. icaco*	*C. icaco*	*I. vomitoria*	*I. vomitoria*	*R. aculeata*	*M. cerifera*[1]/ *R. guinensis*[2]	*C. icaco*
Aprostocetus bangaloricus	30 (+12)	22 (+25)	48 (+41)	5 (+4)	15 (+10)	13 (+19)[1]	8 (+0)
Coccophagus parlobatae	25*	13*	23*	25*	44*	58 (+8)[1]	
Ooencyrtus kerriae	12 (+0)	6 (+0)	5 (+5)	31 (+18)	20 (+3)	5 (+6)[2]	

*The number of males and females was not determined due to inability to determine the gender in the Aphelinidae.

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Scale Dissection and Microscopic Analysis

Two months after parasitoid exposure, marked scales which experienced oviposition were carefully removed from the coco plum seedlings. Scales which were not exposed to parasitoids were dissected as a control. Ten control scales and 3 scales receiving apparent oviposition for each parasitoid species were dissected. After removal from the seedlings the scales were put into 70% alcohol and then mounted on slides following Williams & Granara de Willink (1992). In order to remove the lac covering, scales were first submerged into 10% potassium hydroxide for 1 d. The soft bodies of the scales were stained with Double Stain (BioQuip Products, Inc., Rancho Dominguez, CA). Mounted scales were examined and measured with a compound microscope at up to 400×.

Data Analysis

In order to compare the ability of parasitoid species to oviposit and parasitize the lobate lac scale, the length of time required to penetrate the lobate lac scale with the ovipositor, and the reproductive rates (number of offspring per test cylinder) were compared. The mean penetration time for 5 individual wasps of each species was recorded as well as the mean number of offspring, counting wasp releases per test cylinder as replicates for each species. Means of the times required to penetrate the scales were analyzed by the Tukey test of ANOVA; the number of offspring was analyzed with the Kruskal-Wallis *H* test (SPSS 10.0, SPSS, Inc., Chicago, IL). The significant levels were at 5%.

Results

Observations of Parasitoid Host Finding and Oviposition

To find a favorable host and penetrate it with the ovipositor involved a learning progress for females of each observed species. Inexperienced females searched their habitat for up to 95 min. However, experienced wasps could find their hosts in seconds. Certain scales were preferred by the parasitoids, while others were not. *Coccophagus parlobatae* females preferred second or early third instars, while *O. kerriae* and *A. bangaloricus* attacked older scales of adult size. Scales previously penetrated by other wasps of the same or different species were preferred by *A. bangaloricus* females. When females found attractive hosts they palpated the scales' surface with their antennae and pivoted on them until they found the best positions for penetration, which was distinct for each species. *Coccophagus parlobatae* and *O. kerriae* females pressed their ovipositors with great effort through the rigid lac covering. *Coccophagus parlobatae* females drilled the ovipositor through the side of the lac, holding on to the scale with their hind-legs, while *O. kerriae* penetrated the lac dorsally. Both species took about 15 min to penetrate the lac, 14.6 ± 6.1 and 16.6 ± 5.2 min, respectively (n = 5). In contrast to these 2 species, *A. bangaloricus* inserted its ovipositor into the anal pore on the dorsal surface of the scale. Penetration into the lobate lac scales by this wasp took only 1.1 ±0.8 min (n = 5), which is significantly faster than *C. parlobatae* and *O. kerriae* (F = 16.424; df = 2, 12; $P \geq 0.002$). *Aprostocetus bangaloricus* palpated the scales with their antennae to locate the anal pore and with the hypoygium sensed the anal orifice in the lac before they pushed the ovipositor inside. After a successful penetration and apparent oviposition, the wasps of all species moved to find other hosts. *Coccophagus parlobatae* was the only species observed to host-feed on lobate lac scale usually on second instar scales. Host-feeding involved penetration and then feeding at the penetration injury and lasted up to 15 min. Penetration and host-feeding were repeated several times for up to 65 min at the same scale.

Acceptance and Rearing of Parasitoid Wasps

No progeny were obtained from tested *A. bangaloricus* (Table 2). *Ooencyrtus kerriae* produced progeny about 2 months after test female wasp introductions, but a mean offspring of only 3 wasps per test cylinder was obtained (Table 2). The mean time from the test wasp release to produce adult progeny was 76 d, most of which was developmental time because the test wasps were short lived. *Ooencyrtus kerriae* progeny were obtained in 2 tests, both of which were conducted with coco plum as the host plants. In one test, 12 females were introduced and 2 progeny were produced. In the other test, 6 females were introduced and 19 progeny were produced. All progeny were males, presumably haploid offspring due to arrhenotokous parthenogenesis. Host scales held multiple emergence holes, indicating gregarious development of the parasitoids. In 4 other tests, both females and males were introduced together in cylinders (Table 1) but no offspring were obtained.

Coccophagus parlobatae produced an average of 2 wasps per test cylinder but only 8 total wasps emerged, 7 in 1 cylinder with white indigo berry as a host plant and 1 wasp emerged in another cylinder from coco plum as a host plant. The mean time to progeny emergence was 90 d on average. Six emergence holes were detected, 2 in lobate lac scales and 3 in false armored scales (Conchaspididae). Dissections of these 6 parasitized scales disclosed 5 with remains of other parasitic wasp species, indicating secondary parasitism. Only 1 single lobate lac scale was found with an emergence hole without parasitoid remains, thus indicating facultative primary parasitism. The num-

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TABLE 2. REPRODUCTION RATES OF INDIAN PARASITOIDS OF *PARATACHARDINA LOBATA* IN ACCEPTANCE TESTS WITH THE INVASIVE LOBATE LAC SCALE IN FLORIDA. N = THE NUMBER OF REARING CYLINDER REPLICATIONS FOR EACH PARASITOID SPECIES. PARASITOID OFFSPRING PER REARING CYLINDER ARE MEAN NUMBERS ACROSS ALL CYLINDERS FOR THAT SPECIES. PERIOD OF EMERGENCE IS THE MEAN TIME IN DAYS FROM THE TIME OF ADULT INTRODUCTION TO THE TIME OF EMERGENCE OF OFFSPRING.

Parasitoid species	*N*	Parasitoid offspring ± SD	Period to emergence (d) ± SD
Ooencyrtus kerriae	6	3.5 ± 7.6 a	76.5 ± 11.6 (n = 21)
Coccophagus parlobatae	6	1.6 ± 3 a	90.2 ± 25.5 (n = 18)
Aprostocetus bangaloricus	7	0 a	0

Means within a column followed by the same letter do not differ significantly according to Kruskal-Wallis H test at $P < 0.05$.

bers of offspring produced by *C. parlobatae* and *O. kerriae* were quite low; their mean production of offspring did not significantly differ from the absence of offspring in *A. bangaloricus* ($\chi^2 = 3.85$; $df = 3$; $P = 0.278$).

Scale Dissection and Microscopic Analysis

Every mature scale which experienced apparent parasitoid oviposition, regardless of the parasitoid species (n = 3 per species), exhibited round, red-stained patches, measuring 40 to 120 µm across, usually containing a smaller oval-shaped area of 10 to 20 µm in length (Fig. 1). These red-stained patches appear to be blood cell accumulations which have encapsulated the parasitoid eggs. No parasitoid larvae were observed in any of the dissected scales regardless of exposed parasitoid species, suggesting highly efficient encapsulation. Dissections of immature scales, used by *C. parlobatae* for host-feeding (n = 3), and control scales (n = 10) did not reveal any blood cell accumulations.

DISCUSSION

The present study may have been limited by the low number of available wasps. Pemberton et al. (2006) isolated hundreds of parasitoids from the con-familial *K. lacca* scale. The smaller number of parasitoids isolated from *P. lobata* was presumably due to the relatively smaller size of this scale compared to *K. lacca*.

Despite the small number of available parasitoids, close observations on the oviposition behavior of parasitoid species produced better insights into their relationship to the invasive lobate lac scale. *Coccophagus parlobatae* was isolated as a secondary parasitoid of *P. lobata* (Schroer & Pemberton, unpublished data) but in the present study, it was found to host feed and oviposit in unparasitized lobate lac scales, indicating primary parasitism. However, *C. parlobatae* preferred to parasitize a scale of another family, which appeared randomly in much smaller numbers than lobate lac scale in the test cylinders; hence this species is not host specific and thus has no potential for biological control. *Aprostocetus bangaloricus* showed the highest behavioral adaptation to *P. lobata*. Penetration of the ovipositor into the anal pore required less time and energy than for the other parasitoids to penetrate the scales. The oviposition behavior, however, did not lead to offspring. This negative result might be due to the low number of available wasps, but 6 replicates containing wasps of both sexes were conducted with *A. bangaloricus* and 4 for *O. kerriae*. Individuals of *C. parlobatae* were not determined by sex, but more than 20 individuals in each of 5 replicates were tested suggesting that both sexes were probably present even though the sex ratio is female biased.

Microscopic observations of attacked scales revealed an immune defense against the parasitoid eggs. Initiated by external wounding or introduction of an alien object such as an egg into the hemoceol, hemocytes can agglomerate, which normally do not spread or clump (Strand & Pech 1995). Salt (1963) described the immune response of mealybug species (Hemiptera: Pseudococcidae) to parasitoid attacks as the development of 50 to 250-µm agglomerations of blood cells and distinct melanised layers around developing parasitoids. Our dissection results showed similar reactions. Attacked scales produced blood cell agglomerations which encapsulated parasitoid eggs and prohibited hatch and larval development. Blumberg (1997) reported parasitoid encapsulation in Coccoidea ranging from 0 to 100%. Variations were due to host and parasitoid species, quality and age of the scale, the scales' origin or strain, and conditions for parasitism such as host plant, temperature, and mode of parasitism. Complete encapsulation of all parasitoid eggs was reported for the encyrtids *Metaphycus flavus* Howard attacking 2 different soft scale species *Leptomastix dactylopii* Howard and *L. epona* (Walker) on the citrus mealybug *Pseudococcus citri* Risso (Pseudococcidae) (Blumberg & Van Driesche 2001).

The microscopic dissections in the present study were carried out on scales which were grown on coco plum seedlings. None of the apparent parasitoid ovipositions yielded any development to larvae. However, coco plums as host plants in the rearing trials yielded parasitoid offspring on 2 oc-

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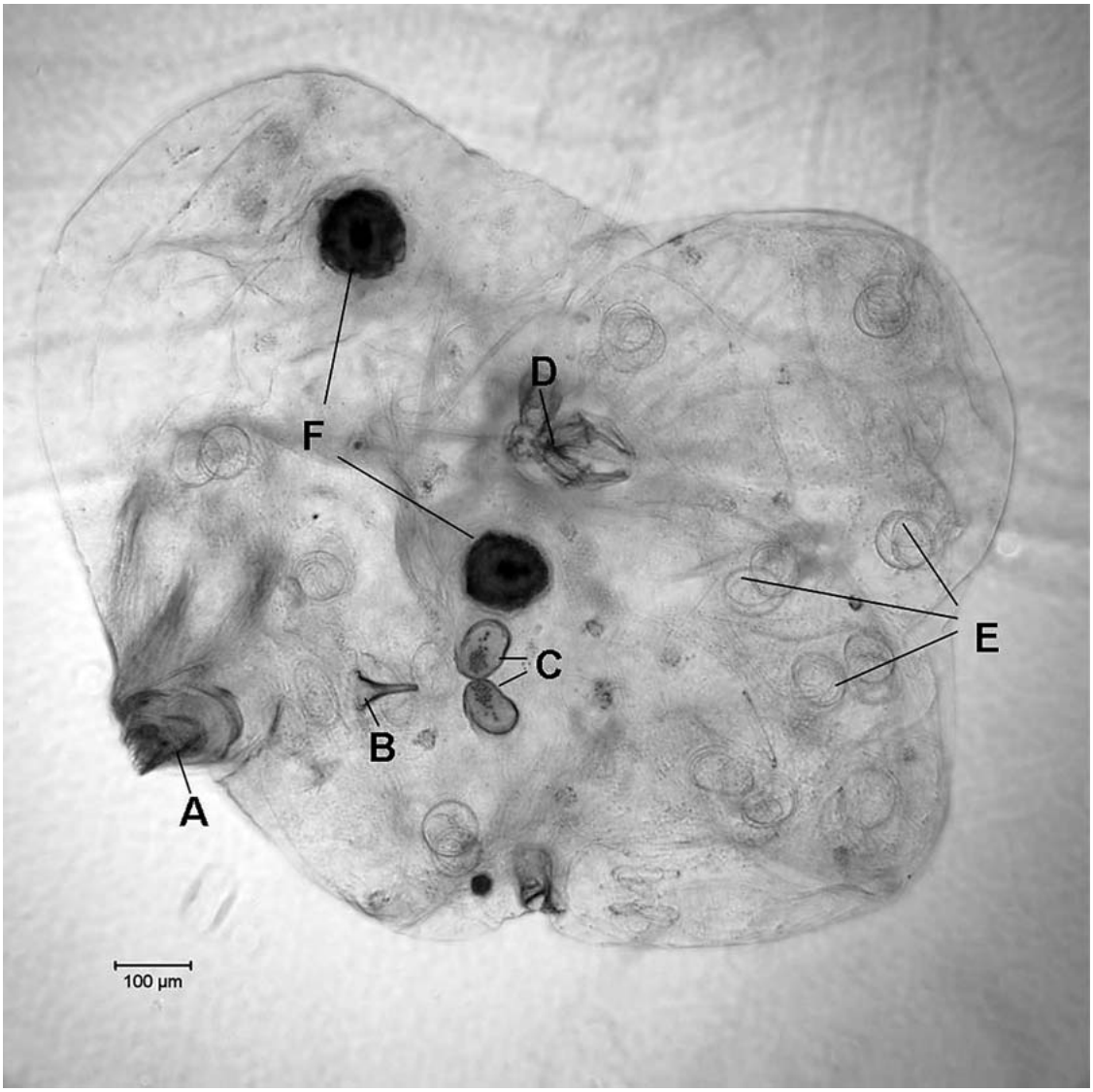


Fig. 1. Soft body of a lobate lac scale female at 400× magnification, showing the anal pore (A), the dorsal spine (B), brachial plates (C), mouthparts (D), developing offspring (E) and blood cell accumulations due to parasitoid oviposition (F).

casions. Hence, the choice of the host plants might not have had an impact on parasitoid development, but the immune defense of the scales was overcome occasionally by the parasitoids.

The suitability of a host involves co-evolution of the parasitoid to develop modes of parasitism which can overcome the specific defensive reaction of the host. Parasitoid mechanisms may include placement of the egg to avoid host tissue with strong defensive reactions or actively using specific factors to disguise the alien tissue or diminish the host's chemical defensive reaction (Strand & Pech 1995). Host-feeding by *C. parlobatae* did not cause any blood cell accumulation, presumably due to the lack of a defense mechanism in younger instars. Hence, a parasitoid which attacked younger instars might be able to avoid the strong immune response. Attempts by some parasitoids to overcome mature scales' immune response were observed in this study. Despite its solitary development, *A. bangaloricus* was observed to repeatedly oviposit into the same scale and was attracted to hosts experiencing prior oviposition. Many parasitoids mark the host while ovipositing with pheromones to prevent further parasitization of the same host, but in some cases

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these pheromones attract con-specific parasitoids (Vinson 1976). This behavior produces multiple egg clutches inside the host scale, which more effectively resist the host insects' immune responses (Rosenheim & Hongkham 1996). The few *O. kerriae* adults which emerged from lobate lac scales developed gregariously with about 4 siblings per scale, suggesting that the scale's immune response might have been overwhelmed by the greater number of eggs. Similar behavior was reported for the parasitoid *Anagyrus kamaly* Moursi which superparasitized the hibiscus mealybug *Maconellicoccus hirsutus* (Green) to overcome the strong immune response of older instars, which provide better conditions for parasitoid development (Sagarra et al. 2000). Arrhenotokous parthenogenesis was the only mode of progeny production of *O. kerriae*. We therefore reason that unmated *O. kerriae* females in our study may have laid higher number of unfertilized eggs into single scales than mated females, resulting in successful production of male progeny.

In future work this suggestion needs to be investigated. *Ooencyrtus kerriae* was first isolated from *K. lacca* (Hayat et al. 2003), which might produce large numbers of offspring of this parasitoid. We would like to expose the invasive scale to larger numbers of *O. kerriae* and the cultivated *K. lacca* may be a possible source. Despite suitable oviposition behavior and parasitoid attempts to overcome defensive reactions of the host, the immune response of the invasive scale was rarely successfully negotiated. We therefore must conclude that the parasitoids isolated from *P. lobata* might not have co-evolved with the invasive lobate lac scale. Morphological and molecular comparisons between the invasive lobate lac scale from Florida and *P. lobata* from India are urgently needed to better understand the degree of difference in these species, which may help explain the poor success rate of *P. lobata* parasitoids on the invasive lobate lac scale. Better adapted forms of these parasitoids or undiscovered species are needed for the control of the invasive lobate lac scale.

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