PROC. ENTOMOL. SOC. WASH.
101(3), 1999, pp. 640–644

# HYPERPARASITISM BY *ABLERUS CLISIOCAMPAE* ASHMEAD (HYMENOPTERA: APHELINIDAE)

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*Abstract.*—*Ablerus clisiocampae* (Hymenoptera: Aphelinidae) is known as a parasitoid both of diaspidid scale insects and lepidopteran eggs. Although it has been suspected that *A. clisiocampae* is a secondary (hyper) parasitoid of diaspidid scale insects, direct evidence of hyperparasitism has been lacking. We used observation and rearing data from field-collected material to demonstrate hyperparasitism of three species of diaspidid scale insects, and primary parasitism of two species of parasitoid wasps by *A. clisiocampae*. *Ablerus clisiocampae* was found feeding on *Aphytis aonidiae* (Hymenoptera: Aphelinidae) attacking San Jose scale (*Quadraspidiotus perniciosus*) and *Comperiella bifasciata* (Hymenoptera: Encyrtidae) attacking California red scale (*Aonidiella aurantii*) and yellow scale (*A. citrina*). *Ablerus clisiocampae* were associated with pupal *Aphytis aonidiae* and pupal and pharate adult *C. bifasciata*. All *Ablerus clisiocampae* reared for this study were females.

*Key Words:* *Ablerus clisiocampae, Aphytis aonidiae, Comperiella bifasciata,* hyperparasitism, parasitoids, *Quadraspidiotus perniciosus,* San Jose scale, *Aonidiella aurantii,* California red scale, *Aonidiella citrina,* yellow scale

The aphelinid parasitoid *Ablerus clisiocampae* Ashmead has been reared both from lepidopteran eggs and diaspidid scale insect hosts (Darling and Johnson 1984, Polaszek 1991). There has been confusion, however, regarding the exact host relationships exhibited by this species. The genus *Ablerus* has historically been considered largely or exclusively hyperparasitic (Viggiani 1984, 1990), and some authors have assumed that *A. clisiocampae* attacks primary parasitoids of the hosts from which it has been reared (Muma 1959, Hughes 1960, Viggiani 1981). Also, Ehler (1995) found that *A. clisiocampae* was the smallest of a guild of parasitoids associated with obscure scale, *Melanaspis obscura* (Comstock) (Homoptera: Diaspididae), and that its phenology was consistent with a hyperparasitic life history. Although these lines of reasoning are consistent with hyperparasitism, the information required to distinguish between primary and secondary parasitism in this species has not been available to date. Here, we provide direct evidence that *A. clisiocampae* hyperparasitizes primary parasitoids of three armored scale insects (Homoptera: Diaspididae): the San Jose scale, *Quadraspidiotus perniciosus* (Comstock); the California red scale, *Aonidiella aurantii* (Maskell); and the yellow scale, *A. citrina* (Coquillet).

### San Jose Scale System

San Jose scale is a pest of fruit, nut, and ornamental trees. Its most important natural enemy in California is the parasitoid *Aphytis aonidiae* (Mercet) (Hymenoptera: Aphelinidae) (Gulmahamad and DeBach 1978a, Heimpel et al. 1996). *Aphytis aonidiae* lays eggs singly on the external surface of the scale insect under the scale cover, and larvae and pupae develop ectoparasitically (Gulmahamad and DeBach 1978b, Heimpel et al. 1996). We encountered *Ablerus clisiocampae* underneath San Jose scale covers during a study aimed at quantifying parasitism of San Jose scale by *A. aonidiae* on almonds.

We collected 20-cm twig samples from a 4 ha section of an organically managed almond orchard in Sutter County, California, that supported a moderate infestation of San Jose scale (Heimpel et al. 1996). Samples were taken to the laboratory, and scale insects were individually examined at 40×. Each scale insect was noted as being healthy, dead from unknown causes, or parasitized, and the identity and stage of each parasitoid was recorded.

Samples were taken during 1992, 1993 and 1994. Between August and October 1994, we recovered twelve specimens of *Ablerus clisiocampae,* all of which were female. These individuals were discovered as larvae (n = 9) or pupae (n = 3) and reared to adulthood in glass vials. Two of the 9 larvae were observed feeding ectoparasitically on *Aphytis aonidiae* pupae, providing direct evidence of hyperparasitism (Fig. 1a). In both of these cases, remains of the scale insect and the *A. aonidiae* pupa were clearly visible underneath the scale cover. We did not find *A. aonidiae* or scale insect remains associated with the other 10 *Ablerus clisiocampae.* We were unable to classify these cases as either primary or secondary parasitism, and suspect that scale insect and/or *Aphytis* remains were lost during handling of the samples. Scale insects associated with *Ablerus clisiocampae* represented a small fraction of the total number sampled. Between August and October of 1994, we examined 1,462 adult female scale insects, 19.7% of which were parasitized by *Aphytis aonidiae* (GEH and JAR, unpublished data).

### California Red Scale and Yellow Scale System

The California red scale (CRS) and yellow scale are important pests of citrus worldwide, including California. *Comperiella bifasciata* Howard (Hymenoptera: Encyrtidae) is a solitary parasitoid of both CRS and the yellow scale, although it is generally considered to be of secondary importance to *Aphytis melinus* DeBach as a control agent in many citrus growing regions (Flaherty et al. 1973, Blumberg and Luck 1990). *Comperiella bifasciata* is an endoparasitoid, laying one or a few eggs inside the bodies of armored scales (Rosenheim and Hongkham 1996). At most, only one egg survives to adulthood, and many eggs become encapsulated by the host (Blumberg and Luck 1990, Ode and Rosenheim 1998). In a study examining host encapsulation rates in the field, we encountered *Ablerus clisiocampae* along with the remains of *C. bifasciata* pupae and pharate adults that had parasitized both CRS and yellow scale (PJO, unpublished data).

Leaf samples infested with both species of armored scale were collected weekly from an organic mandarin orange grove in Glenn County, California, between June and October 1995. Scales were examined under a dissecting microscope at 40× and their condition was scored as described above for the San Jose scale. When *A. clisiocampae* individuals were found, they were always in association with the remains of *C. bifasciata.* Overall, 2,391 female CRS and yellow scales were examined, 875 of which were parasitized by *C. bifasciata,* and approximately 400 of which were parasitized by *Aphytis* (probably *A. melinus*). *Ablerus clisiocampae* was found to have hyperparasitized *C. bifasciata* in 213 cases;

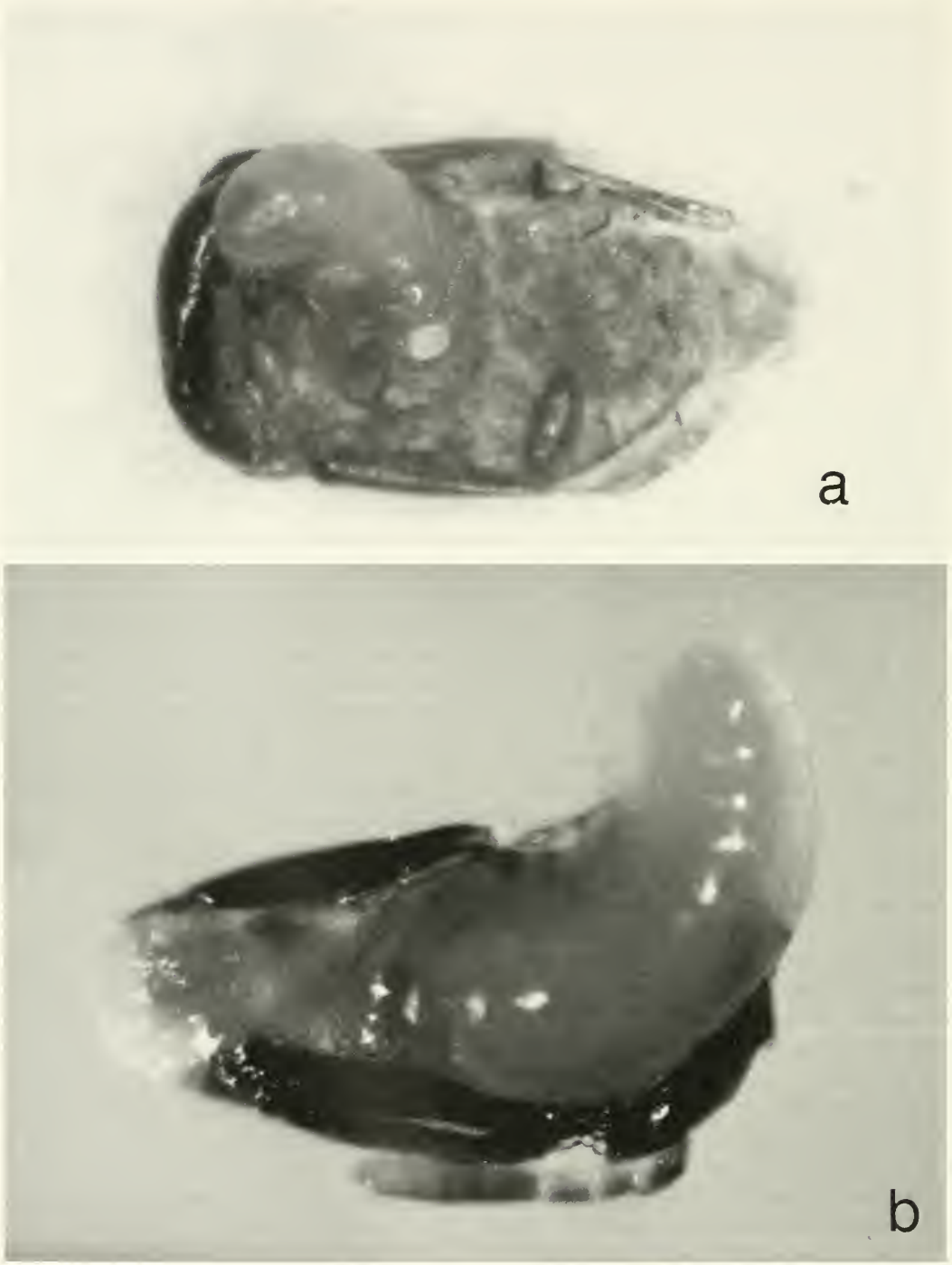


Fig. 1. *Ablerus clisiocampae*. a, Larva feeding on *Aphytis aonidiae* pupa. b, Larva feeding on a female *Comperiella bifasciata* pharate adult.

in 27 of these cases, we clearly saw an *A. clisiocampae* larva feeding ectoparastically on *C. bifasciata* pharate adults (Fig. 1b; PJO, unpublished data). We successfully reared these individuals to adulthood, and all *A. clisiocampae* were females. Voucher specimens of *A. clisiocampae* reared from San Jose scale, CRS and yellow scale have been deposited at the Bohart Insect Museum, University of California, Davis.

## Discussion

Our rearing data and dissections of armored scales with developing parasitoids demonstrate that *A. clisiocampae* develops as an obligate hyperparasitoid. *Ablerus clisiocampae* was observed feeding on the pupae or pharate adults of ectoparasitic and endoparasitic primary parasitoids, and no primary parasitism was observed despite extensive sampling of primary host material.

All of the *Ablerus clisiocampae* individuals that we reared were females. Although female-biased sex ratios are known in this species (Smith and Goyer 1985, Ehler 1995), a complete lack of males has not been reported. An all-female sex ratio in our samples could be explained in at least two ways. First, the populations could be thelytokous. Although thelytoky has not been reported in this species, it is known from a number of chalcidoid species, including aphelinids (Werren 1997). In most of these species, thelytoky is linked to the presence of parthenogenesis-inducing endosymbionts, and can be present in some populations and absent in others (e.g., Stouthamer and Kazmer 1994). Alternatively, the populations of *A. clisiocampae* that we encountered may be heterotrophic, with the males feeding on a non-sampled host. Various forms of heterotrophism are found in the Aphelinidae (Walter 1983), but no evidence for such behavior exists for *A. clisiocampae* because both sexes have been reared from Lepidoptera (Darling and Johnson 1984, Smith and Goyer 1985) and Homoptera (Pinto 1980, Ehler 1995).

## Acknowledgments

Thanks go out to Edward Sills and Richard Johansen for allowing us to use their land for this work. *Aphytis aonidiae* was identified by David Rosen, Department of Entomology, Hebrew University of Jerusalem, Rehovot, Israel, and *Ablerus clisiocampae* was identified by Michael Schauff, USDA Systematic Entomology Laboratory, Washington D.C. We thank Jane Adams and Francisco Hernandez for field and laboratory assistance. For advice on the manuscript, we thank Les Ehler, Brook Murphy, and two anonymous reviewers. This work was supported in part by USDA grant #9202397 to J. A. Rosenheim, a University of California Statewide IPM Project grant to G. E. Heimpel and J. A. Rosenheim, and USDA NRIGCP award #94-37312-0960 to P. J. Ode.

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