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Biological and Systematic Studies of Developmental Stages in *Aphytis* (Hymenoptera: Aphelinidae)

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David Rosen and Avner Eliraz

II. Larval Criteria in the Systematics of *Aphytis*

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III. Meconia as a Possible Systematic Tool in *Aphytis*

Paul DeBach, Mike Rose, and David Rosen

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I. Developmental History of *Aphytis chilensis* Howard

Species of *Aphytis* Howard (Hymenoptera: Aphelinidae) are the most effective natural enemies of armored scale insects (Homoptera: Diaspididae). Their classification, based on the morphology of adult wasps, is difficult. The studies herein were intended to explore the possibility of using morphological characteristics of developmental stages in the systematics of this genus.

The developmental stages of *A. chilensis* Howard, the generotype of *Aphytis*, are described. The ovarian egg is double-bodied, whereas the deposited egg is stalked. The larva passes through three instars, each of which differs markedly in shape and size of the mandibles. First-instar larvae have four pairs of spiracles; the second and third instars have eight pairs, *viz.*, one pair in the mesothoracic segment and one in each of the first seven abdominal segments. The cephalic skeleton, respiratory system, and various integumentary structures of the third-instar larva are described. The morphology of the pupa was studied with light and scanning electron microscopy.

At 28 ± 1° C, egg development takes 2 to 3 days, larval development (including the prepupal period) 10 to 12 days, and pupal development 6 to 7 days. Rearings under various constant temperatures gave the theoretical threshold of development as 14.1° C and a thermal constant of 270.2 day-degrees for the completion of development.

II. Larval Criteria in the Systematics of *Aphytis*

Eggs and larvae of six species of *Aphytis*, representing five of the seven species-groups currently recognized in this genus, were

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Paul DeBach, Mike Rose, and David Rosen

III. Meconia as a Possible Systematic Tool in *Aphytis*

INTRODUCTION

THIS PAPER is the third in a series of biological and systematic investigations of developmental characteristics in the genus *Aphytis* Howard (Hymenoptera: Aphelinidae).

The systematics of *Aphytis* has been based almost entirely on imaginal morphology, which often does not show strong interspecific differences. Other than pupal pigmentation, which has proved useful in certain cases (DeBach, 1959), characteristics of developmental stages have not been utilized as systematic tools in this genus. The first paper in this series (Rosen and Eliraz, 1978) presented the developmental history of the generotype of *Aphytis, A. chilensis* Howard, as a basic background study, and included detailed descriptions of the various developmental stages. The second paper (Eliraz and Rosen, 1978) presented a comparative study of larval characteristics of several species in five species-groups, and the present paper reports the results of a comparative investigation of meconial pellets in several species of *Aphytis*.

In most parasitic Hymenoptera, fecal material accumulates in the midgut throughout the larval feeding period, and is expelled, in the form of a meconium or meconial pellets, only when the blind midgut becomes linked with the proctodaeum prior to pupation (Hagen, 1964). The meconia of numerous parasitic Hymenoptera have been occasionally described, but have not been used much as a diagnostic character for identification or classification. Flanders (1942) briefly discussed the meconia of several species, and concluded that "although larval meconium is of little, if any, value in identifying the species of a genus, it may be of value in the recognition of the species which compose the parasitic fauna of a host in the field." More recently, Viggiani (1969) has shown that the shape of the meconia may be used to separate certain eulophid parasites of leaf-mining insects.

All the known species of *Aphytis* are ectoparasites of armored scale insects, developing externally on the bodies of their hosts beneath the covering scale (Rosen and DeBach, 1976). Their distinctive meconial pellets are very conspicuous under the scale, and have been noted by some of the early workers. Quayle (1910), for instance, described the meconia of *A. chrysomphali* (Mercet) [erroneously recorded by him as *A. diaspidis* (Howard)] as follows:

> "Always accompanying the pupa are from six to ten black or dark brown torpedo like bodies .125 mm. long and .055 mm. broad, which are evacuations from the digestive tract and are expelled by the larva preliminary to pupation."

Similarly, Taylor (1935), in his description of (presumably) the same species, wrote:

> "No excretion occurs until the larva is ready to pupate. The excrement is in the form of small, shiny, black or brown bodies, bluntly pointed at each end—and usually 5 or 6 in number, and uniform in shape. They are deposited inside the scale, round the posterior end of the larva, and are so conspicuous in *Aspidiotus destructor* that they are very useful as a means of detecting the full-grown larvae or pupae *in situ.*"

Surprisingly, at about the same time Carmin and Scheinkin (1934) mistook the meconia of *A. chrysomphali* for eggs. They described the "eggs" of that parasite as "dark brown, somewhat lighter at both edges," and stated:

> "An interesting fact which still awaits its explanation is that infested scales show late in the season besides the pupa of the parasite (always single as far as observed) —a large number of eggs (up to ten or even more) of the parasite lying around the border of the scale under beneath it."

No one to our knowledge has repeated that mistake.

Protected by the covering scale of the parasitized host, the typical meconia of *Aphytis* remain there, unchanged, even long after the parasite has emerged—lasting evidence to the former presence of some species of *Aphytis*. They are readily obtainable by turning the covering scale over, with the aid of a dissecting needle or a fine forceps, under a low-power dissecting microscope. If consistent specific differences could be shown to exist among them, the meconia would conceivably provide a convenient adjunct in the identification of *Aphytis* species.

Although P. H. Timberlake apparently noticed some differences in the structure of the meconia of the *Aphytis* species that he studied at Whittier, California, as early as 1910–1911, namely *A. chrysomphali* and *A. diaspidis,* the information was never published (H. Compere, personal communication, 1972). Most subsequent workers either ignored the meconia, or considered them to be highly variable (e.g., Traboulsi, 1969). The first published attempt to utilize some characteristics of the meconia in the systematics of *Aphytis* was recently made by Yasnosh (1972), who referred mainly to their number, color, general shape and arrangement. However, the detailed morphology of *Aphytis* meconia has remained unexplored.

The present investigation used a scanning electron microscope to study the meconia of several species and strains of *Aphytis,* as well as one species of *Signiphora* Ashmead (Hymenoptera: Signiphoridae), the only other genus known to contain ectoparasites of armored scale insets (see Quezada, DeBach and Rosen, 1973). Included in the study were representatives of all six major species-groups of *Aphytis:* the **vittatus, chilensis, proclia, mytilaspidis, lingnanensis** and **chrysomphali groups** (Rosen and DeBach, 1976)· Only the small, aberrant **funicularis group** (Rosen and DeBach, 1977) was not available for study. Our aim was threefold: 1) to evaluate meconia as a generic character separating *Aphytis* from other parasitic Hymenoptera of similar habits, 2) to assess their potential value for the classification of species-groups within *Aphytis* and 3) to evaluate their usefulness for separating closely-related or sibling *Aphytis* species. We therefore selected seven closely-related members of the **lingnanensis group** (including two biological strains of one species), as well as one member of each of the other groups and one species of *Signiphora.*

MATERIALS AND METHODS

Meconia were collected from identified scale-insect hosts obtained either from insectary cultures of known *Aphytis* species maintained at Riverside, California, or from field samples that had yielded only one species of *Aphytis* or *Signiphora.* They were transferred onto a double-sticky adhesive tape fastened on standard metal targets used in scanning electron microscopy. They were then coated with a 200-Å layer of gold in a JEOL vacuum evaporator, type JEE-4B, and were studied under a JEOL JSM-U3 scanning electron microscope.

The following species and strains

were included in this study:

(a). Genus *Signiphora* Ashmead.

1. *Signiphora flava* Girault: Described from Peru, and as a parasite of "*Aspidiotus camelliae* Signoret" [= *Hemiberlesia rapax* (Comstock)] on *Acacia* in Mexico (Girault, 1913), this species is apparently recorded here for the first time from the United States. Meconia were collected from a sample of the latania scale, *Hemiberlesia lataniae* (Signoret), on English ivy in California.

(b). Genus *Aphytis* Howard.

I. **The vittatus group.**

2. *Aphytis costalimai* (Gomes): A parasite of the Florida red scale, *Chrysomphalus aonidum* (L.), in Brazil (DeBach, 1963). Meconia were collected from samples of that host on citrus in Brazil.

II. **The chilensis group.**

3. *Aphytis chilensis* Howard: A nearly cosmopolitan parasite of the oleander scale, *Aspidiotus nerii* Bouché, and the generotype *Aphytis* (Compere, 1955). Meconia were collected from an insectary culture originally obtained from the oleander scale on English ivy in California, and reared on that host on lemons.

III. **The proclia group.**

4. *Aphytis paramaculicornis* DeBach and Rosen: A parasite of the olive scale, *Parlatoria oleae* (Colvée), introduced from Iran into California and previously recorded as the "Persian strain" of *A. maculicornis* (Masi) (Huffaker, Kennett and Finney, 1962; DeBach and Rosen, 1976*b*). Meconia were collected from an insectary culture originally obtained from the olive scale in California and reared on the latania scale, *Hemiberlesia lataniae* (Signoret), on potatoes.

IV. **The mytilaspidis group.**

5. *Aphytis aonidiae* (Mercet): A parasite of the San Jose scale, *Quadraspidiotus perniciosus* (Comstock), in California (Gulmahamad and DeBach, 1978). Meconia were collected from samples of that host on rose in California.

V. **The lingnanensis group.**

6. *Aphytis lingnanensis* Compere: A complex Oriental species known to include several strains and semi-species (Rao and DeBach, 1969). Two reproductively compatible strains were examined: (i). The original strain, obtained from the California red scale, *Aonidiella aurantii* (Maskell), on citrus in China and introduced into California. (ii). A strain obtained from the snow scale, *Unaspis citri* (Comstock), on citrus in Hong Kong, and introduced into Florida as well as California (DeBach and Rosen, 1976*a*). Meconia were collected from insectary cultures of these strains, reared separately on the oleander scale on lemons.

7. *Aphytis melinus* DeBach: An Oriental parasite of *Aonidiella* spp. introduced into California (DeBach, 1959). Meconia were collected from an insectary culture originally obtained from the yellow scale, *Aonidiella citrina* (Coquillett), and the California red scale in India and Pakistan and reared on the oleander scale on lemons.

8. *Aphytis holoxanthus* DeBach: An oriental parasite of the Florida red scale introduced into Israel, closely related morphologically to *A. melinus* (DeBach, 1960). Meconia were collected from an insectary culture reared on the oleander scale on lemons, originally obtained from the Florida red scale on citrus in Israel.

9. *Aphytis fisheri* DeBach: An Oriental parasite of the California red scale, morphologically nearly indistinguishable from *A. melinus* (DeBach, 1959). Meconia were collected from an insectary culture originally obtained from the California red scale on citrus in Burma, and reared on the oleander scale on lemons.

10. *Aphytis yasumatsui* Azim: An Oriental parasite of the Asiatic red

scale, *Aonidiella taxus* Leonardi, and the bifasciculate scale, *Chrysomphalus bifasciculatus* Ferris. Whereas morphologically this species appears to be more closely related to *A. holoxanthus* than to *A. melinus,* it was found to be completely reproductively isolated from the former, but only partly so from the latter. Meconia were collected from an insectary culture originally obtained from the Asiatic red scale and the bifasciculate scale in Japan, and reared on the California red scale on lemons.

11. *Aphytis africanus* Quednau: A parasite of the California red scale and various native scale insects in South Africa (Quednau, 1964), probably occupying an intermediate position between the **lingnanensis** and **chrysomphali groups.** Meconia were collected from an insectary culture originally obtained from the California red scale on citrus in South Africa, and reared on that host on lemons.

VI. **The chrysomphali group.**

12. *Aphytis chrysomphali* (Mercet): A cosmopolitan, uniparental species (Compere, 1955). Meconia were obtained from an insectary culture, originally obtained from the coconut scale, *Temnaspidiotus destructor* (Signoret), on coconut palm in Tahiti and reared on the California red scale and the oleander scale on lemons. [This was probably the same species recorded by Taylor (1935) from Fiji under that name].

RESULTS AND DISCUSSION

Representative scanning electron micrographs of the meconia of the species in this study are presented in figures 1–33. (The tiny rings apearing on the meconia in some of these figures are wax particles produced by the scale insect host, and should not be confused with the characteristics of the meconia themselves).

All the *Aphytis* species studied produce discrete meconial pellets. By contrast, the meconia of *Signiphora flava* (figs. 1 to 3) adhere to each other, forming irregular chains or clusters. They are also considerably smaller than those of the *Aphytis* species, are irregular in shape, and lack distinctive surface patterns. Thus, the meconia can serve as a reliable generic character, separating *Aphytis* from other parasites of armored scale insects. If evidence of ectoparasitism is seen in a dead, field-collected, scale insect host, the generic status of the parasite can be determined at a glance with the aid of the distinctive meconia.

The meconia of the *Aphytis* species, with the striking exception of *A. chilensis* (figs. 7 to 11), are more or less fusiform, tapering at one or both ends. The species differ from one another mainly in the size and general shape of the meconia, and in the surface patterns or striations on them. Following are brief notes on the various species.

A. costalimai (figs. 4 to 6). The meconia are rather large, elongated, tapering on one end and more rounded on the other, and numerously deeply

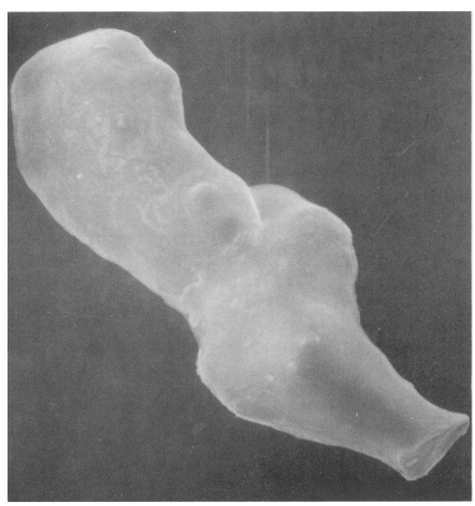

Fig. 1. *Signiphora flava,* two meconia × 800.

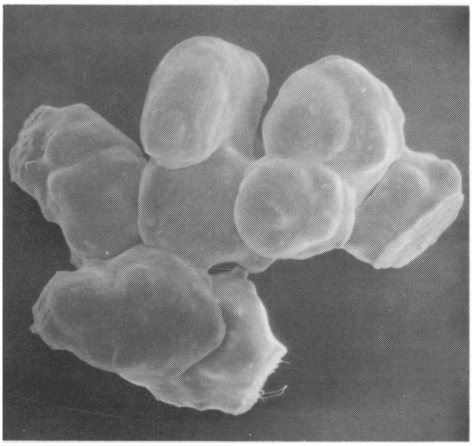

Fig. 2. *Signiphora flava,* meconia × 600.

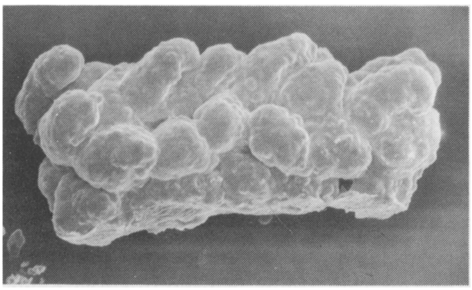

Fig. 3. *Signiphora flava,* meconia × 250.

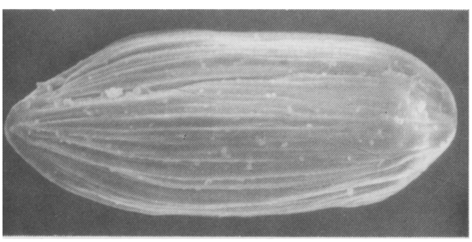

Fig. 4. *Aphytis costalimai,* × 500.

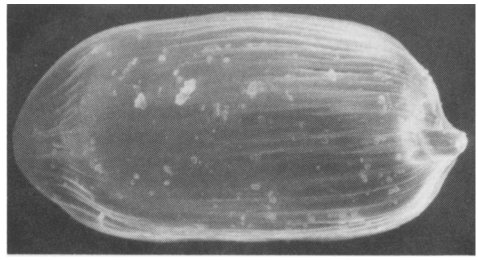

Fig. 5. *Aphytis costalimai,* × 600.

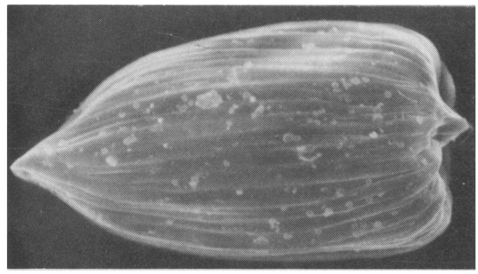

Fig. 6. *Aphytis costalimai,* × 600.

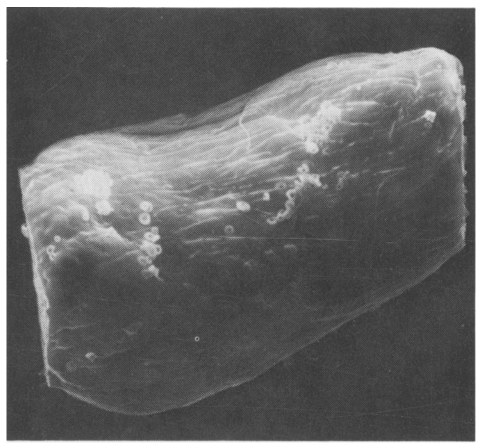

Fig. 7. *Aphytis chilensis,* × 600.

grooved longitudinally. The rounded end appears to be smooth (fig. 5), and sometimes is invaginated (as in fig. 6).

A. chilensis (figs. 7 to 11). Unlike all other species studied, the meconia of *chilensis* are truncated on both ends and are sometimes nearly rectangular (figs. 8, 9) or irregular in shape (fig. 10). They vary considerably in size, and are marked by fine striations which usually do not extend the entire length of the meconia. Most *chilensis* meconia are also grooved longitudinally. Rarely, when viewed from certain angles, they may appear nearly fusiform (fig. 11).

The meconia of *Aphytis* usually lie loose, in a horizontal position, beneath the covering scale of the host. In marked contrast with that pattern, DeBach (unpublished data, 1962) recorded a population of *A. chilensis* parasitizing the oleander scale on *Pittosporum tobira* at the National Garden, Athens, Greece, in which the meconia were arranged vertically in the form of columns surrounding the pupa, at-

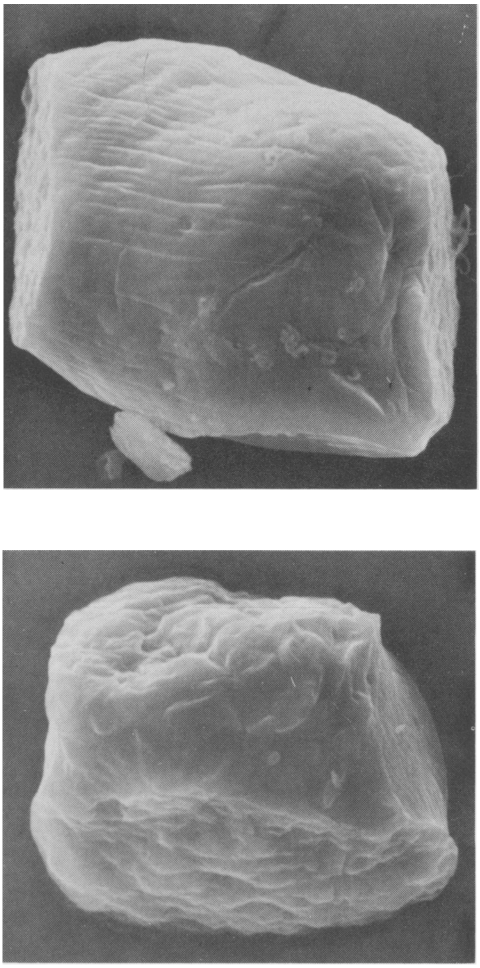

Fig. 9. *Aphytis chilensis,* × 600.

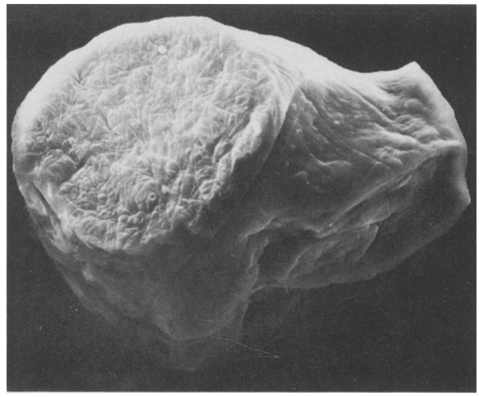

Fig. 10. *Aphytis chilensis,* × 600.

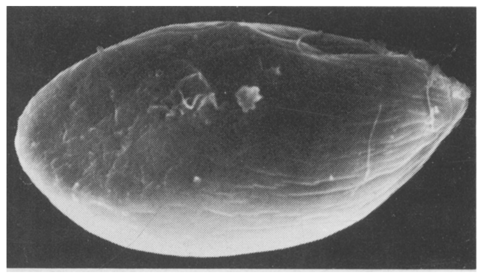

Fig. 11. *Aphytis chilensis,* × 900.

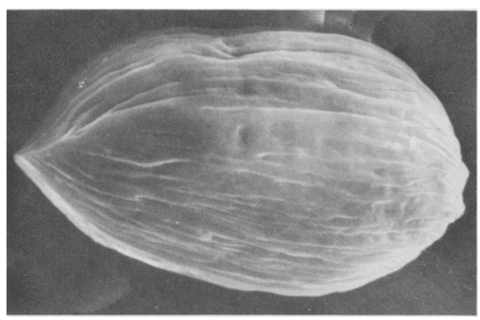

Fig. 12. *Aphytis paramaculicornis,* × 600.

tached ventrally to the substrate and dorsally to the underside of the scale covering. Obviously, such an arrangement is feasible with the truncated meconia of *chilensis,* but is impossible with the fusiform meconia of other *Aphytis* species. Column-like arrangement of the meconia has not been recorded in *A. chilensis* in other countries (see Rosen and Eliraz, 1978), but *chilensis* attacking *Hemiberlesia rapax* (Comstock) was recently observed with a similar meconial arrangement in the field at Riverside (DeBach, unpublished observation). Viggiani (1964) described a similar habit with species of *Kratochviliana* and *Diglyphus* (Hymenoptera: Eulophidae) parasitic upon leaf-mining insects. These species use their meconia to support the walls of the mine, which otherwise tend to collapse.

A. paramaculicornis (figs. 12, 13). The meconia appear to be somewhat smaller than in the two preceding species. They are robust, fusiform and deeply grooved longitudinally their entire length.

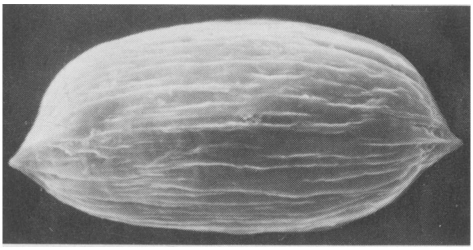

Fig. 13. *Aphytis paramaculicornis*, × 600.

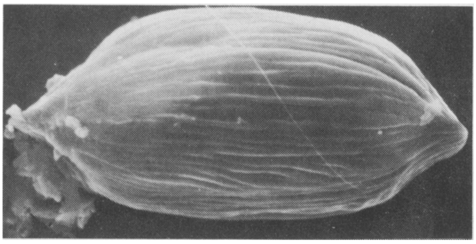

Fig. 14. *Aphytis aonidiae*, × 600.

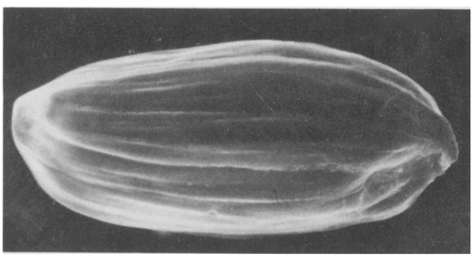

Fig. 15. *Aphytis aonidiae*, × 600.

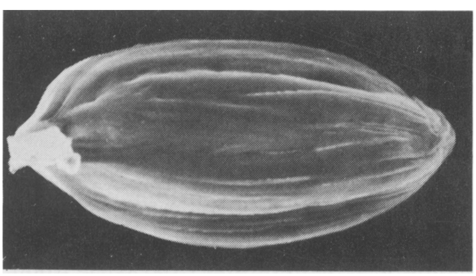

Fig. 16. *Aphytis aonidiae*, × 600.

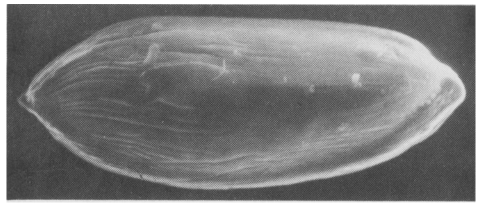

Fig. 17 *Aphytis lingnanensis*, red-scale strain, × 600.

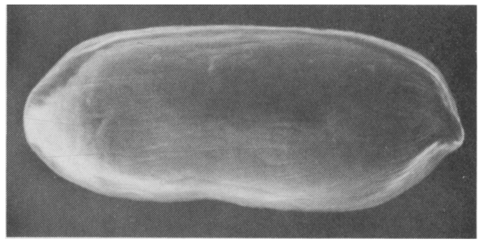

Fig. 18. *Aphytis lingnanensis*, red-scale strain, × 500.

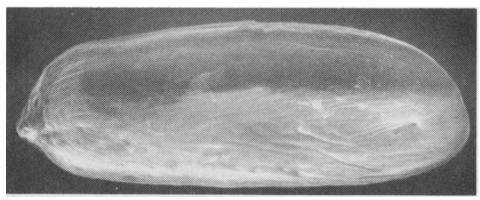

Fig. 19. *Aphytis lingnanensis*, snow-scale strain, × 500.

Fig. 20. *Aphytis lingnanensis*, snow-scale strain, × 500.

A. aonidiae (figs. 14 to 16). The meconia of this species are rather similar to those of *A. paramaculicornis*, although perhaps somewhat smoother. They are rather robust and fusiform with several deep longitudinal grooves.

A. lingnanensis. The "typical" California-red-scale strain (figs. 17, 18) produces elongated, often pearly parallel-sided meconia, mildly tapering on one or both ends, that are considerably smoother than in all the preceding species, and are marked by fine longitudinal striations. The meconia of the snow-scale strain (figs. 19, 20) appear to be somewhat more elongated but essentially similar.

A. melinus (figs. 21, 22). The meconia are less elongated, more spindle-shaped

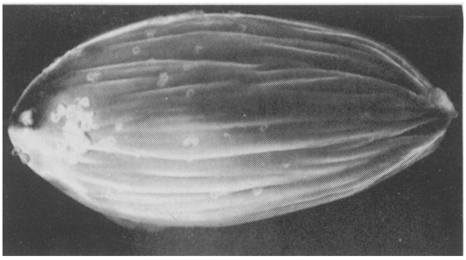

Fig. 21. *Aphytis melinus,* × 600.

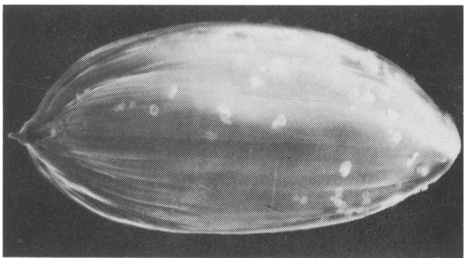

Fig. 22. *Aphytis melinus,* × 600.

Fig. 23. *Aphytis holoxanthus,* × 500.

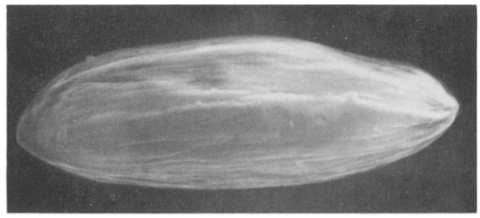

Fig. 24. *Aphytis holoxanthus,* × 500.

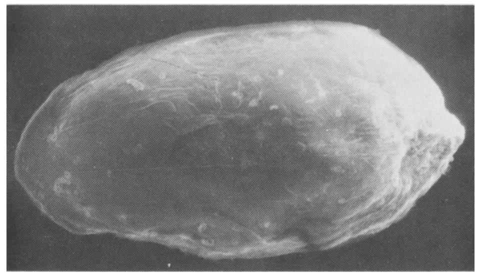

Fig. 25. *Aphytis fisheri,* × 500.

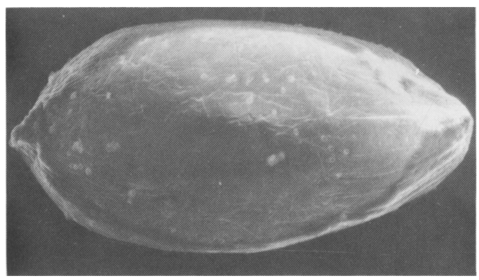

Fig. 26. *Aphytis fisheri,* × 500.

than in *lingnanensis,* not nearly parallel-sided, and noticeably grooved longitudinally.

A. holoxanthus (figs. 23, 24). The meconia of this species differ markedly from those of *melinus* and *lingnanensis.* They are elongated, narrow, but not parallel-sided, and are convoluted as well as grooved longitudinally.

A. fisheri (figs. 25, 26). Although this species is essentially indistinguishable from *melinus* except for pupal pigmentation, it produces strikingly different meconia. They are relatively large, blunt and thick, robust, with only faint indications of some fine longitudinal striation, and an intricate pattern of irregular fine lines.

A. yasumatsui (figs. 27, 28). Although *yasumatsui* is completely reproductively isolated from *holoxanthus* and only partially so from *melinus,* its meconia are much more similar to those of *holoxanthus.* They are longer than those of either other species, pointed at each end, narrow, and deeply grooved longitudinally. Thus, meconial characters in the *melinus - holoxanthus - yasumatsui* complex exhibit much the same affinities as do imaginal and pupal characters.

A. africanus (figs. 29, 30). The meconia are elongated and smoother than in any other species studied, with only faint indications of some longitudinal striation. In a classification based on imaginal morphology, *A. africanus* can be considered to occupy an intermediate position between *lingnanensis* and the **chrysomphali group.** The meconia of

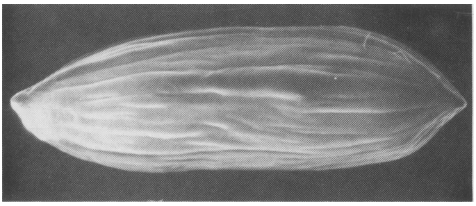

Fig. 27. *Aphytis yasumatsui,* × 500.

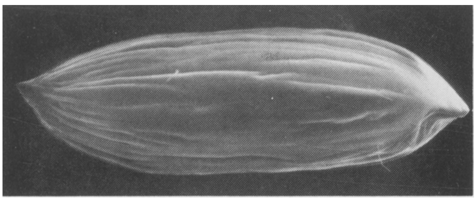

Fig. 28. *Aphytis yasumatsui,* × 500.

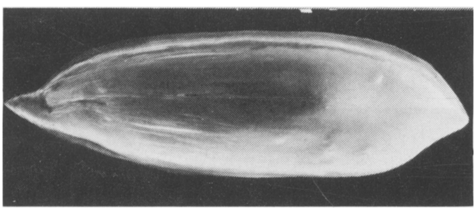

Fig. 29. *Aphytis africanus,* × 600.

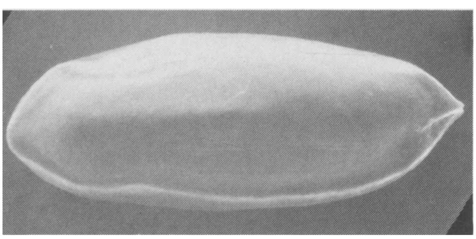

Fig. 30. *Aphytis africanus,* × 600.

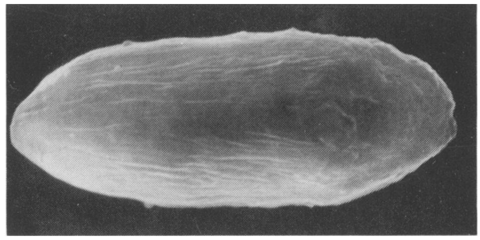

Fig. 31. *Aphytis chrysomphali,* × 600.

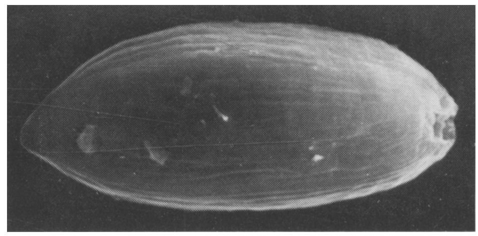

Fig. 32. *Aphytis chrysomphali,* × 600.

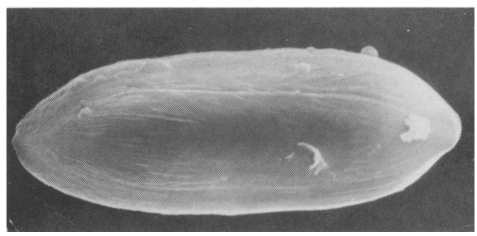

Fig. 33. *Aphytis chrysomphali,* × 600.

this species are indeed rather similar in surface structure to those of *lingnanensis.*

A. chrysomphali (figs. 31 to 33). The meconia are very small, mildly fusiform and rather smooth, with some longitudinal striation.

We would hesitate to generalize on the basis of this preliminary investigation. As pointed out by Rosen and DeBach (1973), one of the pitfalls of scanning electron microscopy is that it tends to over-emphasize individual rather than specific differences. Much more information is required on the extent of intraspecific variation in meconial characters in *Aphytis* before the true taxonomic value can be assessed. Also, more should be known about the possible influence of the host insect and the host plant on the meconia of *Aphytis.*

The meconia do not offer many characters for the taxonomist to work with, and the few available ones are not represented by numerous character states. Nevertheless, in certain cases they seem to be of potential use, such as in the separation of *Aphytis* from *Signiphora.* Their value for the classification of *Aphytis* groups is still uncertain, although there seems to be a trend from coarsely-grooved and convoluted meconia in the more primitive species, to smoother, more finely striated ones in the more advanced members of the genus. Additional representatives of the various species-groups will have to be investigated to test this hypothesis. On the other hand, the meconia appear to be very useful for the identification of particular species (e.g., *chilensis*), and even as a means to help separate certain closely related species complexes of *Aphytis*. Unlike larval characters, which are at best rather impractical (Eliraz and Rosen, 1978), meconial characters may offer a valid diagnostic tool in *Aphytis*, especially if used in combination with the pigmentation of pupae (whenever present) or exuviae, and with data on host specificity. Thus, a combination of biosystematic criteria is available, of which the characteristics of the meconia may constitute a significant part, to complement the conventional systematics of *Aphytis*, which will continue to be based on the morphology of adult specimens.

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