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AN HISTORICAL ACCOUNT OF CASCA SMITHI AND ITS COMPETITOR APHYTIS HOLOXANTHUS, PARASITES OF FLORIDA RED SCALE

by

Dr. S. E. Flanders

Department of Biological Control

University of California

Observations on the Oriental chalcidoid wasps, Casca smithi Compere and Aphytis holoxanthus DeBach, as reported by Professor E. Rivnay in his comprehensive review of the biological control of pests in Israel for the period 1905 to 1965 (Rivnay 1968) are of great interest not only from the standpoint of practical pest control but from the standpoint of ecology in general, Consequently it seems appropriate in this "Festschrift" to review the literature and other available information concerning these 2 parasites, the events lead- ing up to their establishment on the Florida red scale Chrysomphalus aonidum . (Linnaeus) in Israel and their ecological relations with each other.

Observations on Casca smithi

Casca smithi, an endoparasite of Florida red scale, was described by Harold Compere in 1953. However, this parasite had been observed to attack Florida red scale as early as 1906 by George Compere, the father of Harold (Craw 1907; Kotinsky 1906).

The larval instars of Casca develop gregariously in the body cavity of the host, consume its blood and viscera and then emerge as free-living adults, both male and female. Each vacated carcass of the host scale shows "tell-tale" perforations through which the adult Casca emerged (Fig. 1).

The species of the genus Casca are the only endoparasites of the Diaspididae known to develop gregariously. This characteristic was used by the writer (Flanders 1953b) in a composite key to the genera of Aphelinidae. Al- though Casca has been synononized by Novitzky (1961) with the genus Pteroptrix on a purely morphological basis, the writer at the suggestion of H. Compere, will continue to use the name Case a until such time that the type species, Pteroptrix dimidiatus Westwood, is also known to be gregarious in development.

Incidentally, the transfer by Novitzky (1961) of Casca parvipennis Gahan to Howard's genus Bardyli's on the basis of the 8-segmented antennae of the male is probably justified because the female develops as a solitary rather than gregarious endoparasite of the full-grown female of Aspidiotus destructor Signoret (Taylor 1935). However, the supposed Casca male that accompanied

the Casca females sent to Gahan (1927) by Taylor may have been the male of a Prospaltella-like parasite which commonly develops hyperparasitically on the full-fed larva of Casca spp. (Flanders 1967). If such is the case the larval male of C. parvipennis is a primary parasite and not a secondary as stated by Taylor (1935). A reexamination of the supposed paratype males in the U. S. National Museum is in order.

The introduction and establishment of C. smithi in Israel was the direct result of a letter the writer received in August 1955 from I. Cohen of the Citrus Marketing Board of Israel. In this letter, Cohen stated, "... I assume you have read upon your return to Riverside... of our interest in attempting the control of the Florida red scale (Chrysomphalus aonidum) biologically. Your opinion and advice regarding this matter will be greatly appreciated." Fortunately, the writer was able to inform Cohen immediately that in the Hong Kong area the Florida red scale was generally scarce because of parasitization by Casca smithi and an associated species of Aphytis. This information was based on detailed ecological studies made the preceding year (1954) in the native habitat of C. aonidum and its natural enemies. The writer then suggested that S. K. Cheng, who had assisted him on various occasions, would be glad to arrange for the collection and shipment of these effective parasites. It was recommended particularly that Casca be introduced before Aphytis because of the latter's host-mutilation habit. This sequence in the shipments by Cheng, however, was not attained because of collection difficulties, the host being extremely scarce.

Cheng used two methods of collecting prior to May 1957 when examinations of pummelo trees located in Chinese villages revealed the presence of one or several specimens of C. aonidum: (1) the removal of the scale-bearing portions of the tree and their placement in glass containers for parasite emergence, (2) the beating of the foliage surrounding the scales in order that some of the parasite adults, if present thereon, would drop to a white cloth-covered board (45 x 30 x 1/2 cm) held below. Then each parasite if noted soon enough was quickly forced to hop into a glass vial (Fig. 2).

Cheng informed the writer, "I am intending not to collect the scales but to collect the parasites only, so that I can keep the host Florida red scale in the field to trap the parasites that come to lay eggs. Otherwise if I collect the host once from the tree there will be no more host and parasites the next time. It is very, very hard to find a new collecting place...."

The scarcity of C. aonidum in south China was first reported by Muir (1907). He stated that C. aonidum which is so injurious to citrus in most parts of the world occurred there only in small numbers. In 1906 he sent

several lots of leaves and twigs bearing parasitized scales to Hawaii in the hope that the parasite (presumably either Aspidiotiphagus or Aphytis because the multiple emergence holes characteristic of parasitization by Casca were not mentioned) would become established there. Apparently, none survived the trip, there being no record of either their receipt or their release.

In the same year, however, George Compere, temporarily employed by the Government of Western Australia, wrote to Ellwood Cooper of the California State Horticultural Commission on the 6th of August 1906 as follows: "At Macao I secured a palm tree (Cycas) infested with Florida red scale upon which the parasites (Casca) were noticed at work..... and am sending it in the cool room of the Nippon Maru to Mr. Craw (Head of the Division of Entomology, Board of Agriculture and Forestry, Territory of Hawaii)." According to Craw (1907) the parasites were released in Honolulu as they emerged from their hosts on the potted palm as depicted in Fig. 1. Infested fronds from this palm were exhibited by Kotinsky (1906) at a meeting of the Hawaiin Entomological Society. They were then placed in a cage with local plants infested with C. aonidum. The parasite responsible for the 4 to 6 exit holes in each scale was then unknown, Howard (1907) not having at the time described the genus Casca.

It is noteworthy that the first official record of C. aonidum as being present in Hawaii was that of Kotinsky (1910). Casca was not established in Hawaii either as a result of this importation from the Orient or a later one in 1925 (Fullaway 1926). The situation in Hawaii today with respect to C. aonidum and its parasites according to Mabel Chong, Entomologist for the State Department of Agriculture, is as follows (personal communication):

"The Florida red scale is not and never was considered a major pest in Hawaii, although at times it has been quite troublesome on certain types of orchid plants, citrus and other ornamentals such as coconut palms, Pandanus, rose, Strelitzia reginae and others.

"Parasites reared from C. aonidum are as follows:

1. Aphytis chrysomphali (Mercet) introduced from Mexico in 1956.
2. Aspidiotiphagus citrinus (Craw) introduced from China in 1894 (?).
3. Comperiella bifasciata Howard from Japan in 1908.
4. Habrolepis rouxi Compere - a chance immigrant; a single specimen was reared from C. aonidum on a coconut palm leaf in 1956.

"I have not been able to locate any record of Casca smithi Compere. This species failed to become established in Hawaii, unfortunately."

In Java, according to Taylor (1935), Chrysomphalus aonidum (ficus

pallens) on coconut is parasitized by Aspidiotiphagus citrinus, Casca parvipennis, Aphytis chrysomphali, Comperiella bifasciata and Physcus varicornis. Gregarious development occurred only when those species which normally attack small female scales or males oviposited on larger scales. This conclusion apparently was based on the supposed behavior of A. citrinus which although normally solitary in development was frequently gregarious, particularly with C. aonidum, as many as 5 individuals becoming mature in a host individual. Significantly, the occurrence of this habit in the genus Aspidiotiphagus was mistakenly reported once before (Compere 1961), " . . . it is easy to mistake Casca for Aspidiotiphagus. "

It is highly probable that Taylor's rearings of A. citrinus also included Casca smithi. He admittedly lacked the opportunity to study A. citrinus in great detail. However, he reported developmental behavior typical of C. smithi, that is, ". . . each larva when preparing to pupate becomes separated from its neighbor on either side by a delicate transparent septum which extends right across the scale; the scale is thus divided up into a number of small 'cubicles' (membraneous cocoons). Each larva deposits its excrement against the sides of its own cubicle. . . . When the adult parasites emerge, each makes a separate hole through the cuticle of the host and through the covering scale, the septa remaining intact even after all the parasites have emerged. "

The climate of California is not favorable for the continuous development of Florida red scale. It has been seen there only occasionally in nurseries and in greenhouses, despite the accidental importations that must have occurred many times.

Nevertheless, California entomologists, concerned prior to 1949 with the biological control of the California red scale Aonidiella aurantii (Maskell), were interested in obtaining the Casca that attacked the Florida red scale because at that time it was considered to be the same as that known to attack A. aurantii in south China.

This misidentification was not generally known until 1953 (Compere 1953; Flanders 1953a).

However, Silvestri (1928) recognized the Casca on Florida red scale as a distinct species in 1924-25 when he was in south China as an employee of the University of California for the purpose of obtaining the Casca spp. that attack the California red scale. He reported that in China C. aonidum is certainly fairly well-controlled by natural factors among which is "Casca smithi n. sp." In his opinion, C. smithi is ". . . the more effective parasite of Chrysomphalus aonidum in the South as far as the 25° N. L. "

From the standpoint of the California entomologists, Silvestri accomplished the purpose of his exploration by successfully sending to Riverside a sago palm (Cycas revoluta) infested with Casca-parasitized Florida red scale that subsequently yielded 650 adult Casca.

Compere and Smith (1927) reported on the handling of this Casca (subsequently identified as C. smithi) its morphology (Fig. 3) and its biology as follows:

"From the material sent by Silvestri we succeeded in obtaining about 650 living adults. Colonies comprising a total of 378 specimens were liberated on citrus trees infested with red scale, C. aurantii, on the property of the San Joaquin Fruit Company near Tustin, Orange Country. Here arrangements were made with the ranch manager, Mr. C. Newman, to leave the trees unfumigated. A total of 211 specimens were liberated in White Park, Riverside, where there are three large California bay trees, Umbellularia californica, chronically infested with C. aurantii and never sprayed or fumigated. Several small colonies numbering 10 or 12 parasites each were liberated on the property of the Citrus Experiment Station. In addition an effort was made to propagate the parasites in the insectary. In the insectary the species was present for several months working on C. aonidum (Chrysomphalus bifasciculatus Ferris, misidentified) infesting Aspidistra, but later disappeared without ever becoming abundant. As yet the species has not been recovered from the orchards or park where colonies were liberated.

"The following data obtained within the confines of the quarantine room satisfied us that Casca chinensis (C. smithi, misidentified) is essentially a primary parasite and a species which may prove of value if established in California.

"The eggs are elongate-oval, slightly arcuate, with a smooth and semi-transparent chorion and in shape similar to a Coccophagus egg. Eggs of unknown age dissected from a scale measured between 0.13 mm. and 0.14 mm. in length by 0.45 mm. to 0.48 mm. in width. The ovarian eggs are of the same shape as those found in the scale but were slightly smaller in size measuring 0.11 mm. and 0.10 mm. in length by 0.45 mm. and 0.43 mm. in width. Three to six eggs were discovered in each host. When the host is ruptured the eggs of the parasite are expelled with the fluid body contents of the scale. Three scales were dissected and each contained three to six larvae ranging near 0.3 mm. in length. A detailed study of the larva was not made."

Flanders (1953a, 1967) concluded that the larval male of C. smithi does not develop parasitically on its larval and pupal female unlike certain species of other aphelinid genera.

The colonization of C. smithi in California was abortive, not a single progeny being recovered. We know now, of course, that this was inevitable, the parasites being released on an unsuitable host.

However, Compere and Smith (1927) were able under insectary conditions to reproduce a few C. smithi on the Aspidistra scale Chrysomphalus bifasciculatus Ferris but the culture died out within a month or two. Subse-

quently, the writer (Flanders 1953a) reproduced under insectary conditions a female of C. smithi from California red scale. This occurred in 1948 when numerous C. smithi adults emerged at Riverside from a shipment of Florida red scale collected by J. L. Gressitt on the campus of Lingnan University at Canton, China.

These two instances of parasitization of hosts other than C. aonidum represent the "occasional" type of "inadequate" parasitization (Flanders 1953c). C. smithi is the only species of the genus known to be an habitual adequate parasite of C. aonidum.

In Mexico, interest in the biological control of C. aonidum by Casca smithi was such that the writer on April 26, 1957 in answer to an inquiry by Herbert Smith, Entomologist, Entomology Research Branch, U.S. Department of Agriculture, located in Mexico City, wrote as follows:

> "Our Hong Kong collector, Mr. Cheng, has been sending us material off and on since I left there in July, 1954. Mr. Cheng is a school teacher and part-time farmer (his father and sister do the farming). Ostensibly his collecting in the various Chinese villages is to obtain material for his school work. I taught him the 'beating' method of obtaining adult parasites. This is the best method of getting material from citrus in citrus canker areas. Cheng does not scrape for Florida red scale because it is so scarce he does not want to destroy the source of the parasites.....
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> "In 1927 Compere reported Casca smithi under the name C. chinensis as temporarily parasitic in Chrysomphalus aonidum infesting Aspidistra in the insectary. This scale on Aspidistra, however, was subsequently found to be a new species, C. bifasciculatus Ferris, which accounts for the dying out of the C. smithi population. The specific parasite of Chrysomphalus bifasciculatus is the unisexual species, Casca silvestri Comp. Compere, however, was unable to get reproduction in California on this host.
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> "The females of Casca smithi readily oviposit, and the eggs develop. No observations have been made on oviposition of females known to be either unmated or mated. It is possible of course that with C. smithi the unfertilized eggs produce feamles as well as males, and that mating is unnecessary. However, I suspect that the five females that you received from Cheng were mated.

"Casca smithi develops gregariously in Florida red scale. It appears to be a specific parasite of the scale and to effectively control it in China. The sex ratio is about 50:50. Both sexes develop in a single specimen of the scale and will emerge at about the same time; the male, sometimes a day earlier, sometimes a day or two later than the female....

"If you can infest potted cycads, yucca or agave with pure cultures of Florida red scale, you may be able to work out the life history of Casca smithi. I suggest using very light infestations and parasitizing the scales individually, marking the leaf near each scale with a code number in India ink or indelible pencil.

"After the parasites have consumed the body content of the scales each scale can be removed and fastened by a slight trace of honey to the inside of a glass vial. The development of the parasite inside the scale can then be followed under the microscope using transmitted light.

"The first test would be that of ascertaining the sex of progeny produced by a single mated female and a single unmated female. If the unmated female produces no progeny then your troubles begin."

Observations on Aphytis holoxanthus

In Israel the field of colonization of the Florida red scale parasites Casca smithi and Aphytis sp. (the latter subsequently described by Paul DeBach as A. holoxanthus) were made under apparently ideal conditions. The number of A. holoxanthus colonized is unknown since Cheng was unable to distinguish between the various species of Aphytis that inhabit the citrus trees in Hong Kong. Rivnay released a total of 146 adults of Aphytis spp., several at a time, over a period of 4 months (February to May 1956). These probably included more than one species. This possibility became evident during a survery in 1957 of the parasites of diaspidine scale insects infesting citrus in Israel by David Nadel, entomologist of the Citrus Marketing Board (Rivnay 1968). This survey, which was initiated by Nadel's discovery in September, 1957, of the Florida red scale Aphytis on 4 citrus trees growing in a dooryard in Rehovot, revealed the presence of 3 species of the genus Aphytis new to Israel: A. holoxanthus DeBach, parasitizing the Florida red scale Chrysomphalus aonidum (Linneaus); A. coheni De Bach, parasitizing the California red scale Aonidiella aurantii (Maskell); and A. lepidosaphes Compere, parasitizing the purple scale Lepidosaphes beckii(Newman).

Specific identification of the specimens of Aphytis colonized in Israel remains unknown, all of the live adult Aphytis obtained from Hong Kong having been released before being identified. Prior to release, however, certain individuals were observed to oviposit in Florida red scale but there is no record of the identification of their progeny nor of the adults received from Hong Kong that were dead on arrival.

The history of Aphytis holoxanthus, as with many other species of parasites (used in biological control work) began after its importation, colonization and establishment in a new habitat, the recognition of its distinctive morphological characters following the recognition of biological differences (Flanders 1964; Rosen 1965).

The findings by Nadel probably were the first recoveries from colonizations of Aphytis spp. made a year and a half previously by Rivnay at the request of the Citrus Marketing Board, recoveries that presumably were the progenies of adults which had been collected by S. K. Cheng in Hong Kong as they were searching for hosts on the foliage of citrus trees. The Aphytis because of its short life cycle reproduced at a much greater rate than did C. smithi and kept it "submerged" for about 3 years.

Because of the abundance of their hosts the numerical increae of the Aphytis spp. was, of course, astronomical. For a few months high densities of host scales were highly parasitized. This phenomenon when such hosts occur on the leaves and fruits of plants such as citrus that commonly are transported by travelers and tourists over long distances may result in the unintentional translocation of their parasites from region to region in a surprisingly short time. With a newly established parasite species capable of regulating its hosts at a low density as do many species of Aphytis, the period of such translocation would be brief.

Ecological relations of Casca and Aphytis

Casca smithi was discovered in Israel in 1962 (Rosen 1964) 5 years after the recovery of A. holoxanthus. According to Rivnay (1968) the total number of Hong Kong adults colonized was 120, these being released, several at a time, over a period of 5 months ending April, 1957. In this case, contrary to Aphytis, the colonizations occurred on a relatively light infestation of C. aonidum in close proximity to the Agricultural Experiment Station. As with most host-parasite relations it is under such circumstances that the individuals of a host population are most likely to be healthy and eminently suitable for successful parasitization and the factors of environmental resistance fewest. The relative freedom from Aphytis competiton undoubtedly facilitated the reproduction and establishment of C. smithi. It is significant that in south China the existence at low densities of C. smithi, a host-specific parasite, may be characterized by a density of host individuals lower than is the case with A. holoxanthus whose hosts probably include several genera.

Under field conditions in Israel it was inevitable that Casca, if it became established, would eventually actively compete with Aphytis for C. aonidum and that this competition would increase in intensity as the scale population was decimated. Aphytis, within 2 years after its colonization, had reduced the population of C. aonidum in large areas of Israel to non-economic densities. As long as it could find its host readily it continued to be by far the dominant parasite, probably an effect of (1) the period of its life cycle being several days less than that of Casca and (2) its intrinsic superiority.

An ectoparasite such as Aphytis is usually, if not always, the winner when synchronously competing with an endoparasite such as Casca for an individual host, the endoparasite suffering the same fate as its host. The embryo of Casca, however, is less affected by environmental conditions, being immersed in the host's body fluids and less subject to changes in environmental humidity.

At low host densities Aphytis is extrinsically inferior to Casca because it destroys, by host-feeding, hosts that it could use for its progeny. Since the individual Aphytis must host-feed in order to generate its full complement of eggs, it requires during its lifetime more hosts than does the individual Casca. A parasite population in which each individual during its lifetime needs only 1 host, as with Casca, obviously has a greater chance of finding hosts at low host densities than a population of Aphytis.

According to Rivnay (1968, p. 28) this phenomenon is apparently being realized in Israel citrus groves. After pointing out that Casca even to exist in the presence of so effective a competitor as Aphytis, its female must possess a high host-finding capacity, he states thus: "Presumably it has not yet attained its host controlling potential."

It has been pointed out by the writer (Flanders 1965) that a number of parasite species known to effectively control their hosts at low densities are intrinsically inferior to their parasitic competitors. Any fear that the replacement of Aphytis by Casca will have "an ill effect" on the overall biological control of C. aonidum is without foundation. In Hong Kong where it is difficult to find C. aonidum the writer observed both Casca and Aphytis parasitizing a rare infestation on a small isolated citrus plant.

Rivnay (1968) is summing up the situation in Israel 10 years after the establishment of Aphytis and Casca, states "Casca smithi which was scarce became more prominent and in some groves reached about 50% parasitization of the live scales."

The biological control of C. aonidum in Israel by Aphytis during the past 10 years demonstrates Nicholson's (1933) law of population regulation, that is, the action of the regulative factor must be governed by the density of the population regulated. A host-regulative natural enemy in regulating the

density of its host or hosts necessarily regulates its own density. Thus, we see today in Israel the Florida red scale and its parasite Aphytis in a state of "reciprocal balance" (Flanders and Badgley 1963) at a very low equilibrium position (level).

In any given localized habitat, however, the number of adult female parasites to one adult female host may increase so greatly that the host population and consequently the parasite population are temporarily eliminated. In such a case, of course, the habitat is subject to reinvasion by both host and parasite from neighboring localities.

It now appears probable that within a few years Casca smithi because of its extrinsic superiority will replace Aphytis holoxanthus as the most effective natural enemy of Florida red scale in Israel.

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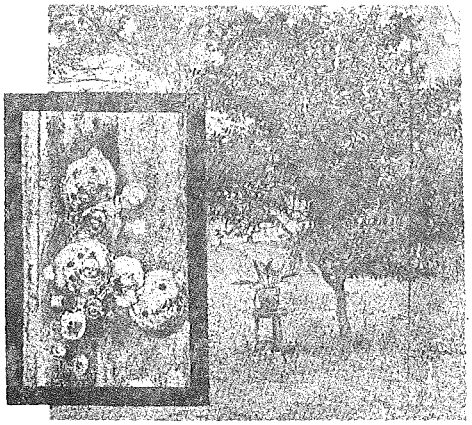

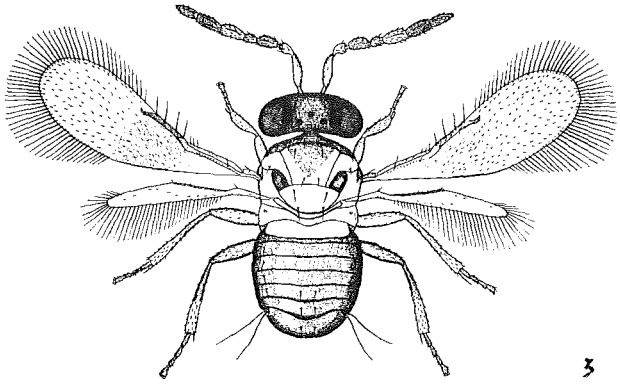

Fig. 1 - The release of Casca smithi in the Government Nursery Hawaii by means of parasitized Florida red scale on a young sago palm. This palm which had been purchased in Macao by G. Compere and sent to Hawaii in the cool room of the "Nippon Maru" in 1906 was repotted and placed on stool under an orange tree well infested with same scale. Inset shows C. aonidum carcasses with exit holes of C. smithi (Craw 1907).

Fig. 2. - A University of California parasite explorer working in Hong Kong (1954) equipped with head magnifier (4X), glass vials (held between lips) and beating board for collecting the microscopic wasp Casca. (The "California parasite explorer" is Prof. F.S.Flanders (Editor)).

Fig. 3 - Casca smithi Compere drawn by H. Compere from specimens reared from Chrysomphalus aonidum collected in the Orient by Silvestri.