ENTOMOLOGY.—The oviposition habits of the Eucharidae (Hymenoptera). 1 Curtis P. Clausen, U. S. Bureau of Entomology and Plant Quarantine.

The Eucharidae are a family of small wasps that are parasitic upon the mature larvae and the pupae of ants. This limitation in host preferences to a single family or superfamily, whichever status is given to the group, is in sharp contrast to the wide host range of related families of the Chalcidoidea. The family is world-wide in distribution but is encountered most frequently in the Tropics. The adults are black. metallic blue, or green, often with the thorax distinctively sculptured. and many species have the scutellum variously modified, in may species it being produced into a conspicuous bifurcate process that may extend beyond the tip of the abdomen. Not only are they conspicuous and often weird in form, but the habits and relationships of these insects to their hosts are so unusual and varied as to be outstanding, even in an order in which the most diverse adaptations to the parasitic mode of life are found.

The first studies on the biology and habits of the Eucharidae were by Wheeler (1907), who found several species of Orasema associated with ants of the genera Pheidole and Solenopsis in Texas and Colorado. He reared several successive "broods" of O. viridis Ashm.² upon Pheidole instabilis Emery and described and figured the larval instars

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 According to A. B. Gahan, the species here referred to is probably Orasema wheeleri
 Wheeler and not the true viridis Ashm. (See Proc. U. S. Nat. Mus. 88: 459. 1940.)

and the pupa. Oviposition was not observed nor were the eggs found, yet so certain was he that these must be placed directly upon the ant pupae that he described in some detail the manner in which the female was presumed to accomplish this act. The conclusions reached were entirely logical on the basis of what was then known regarding the habits of parasitic insects.

A few years later H. S. Smith (1912) presented a detailed account of the biology of Perilampus hyalinus Say, of the family Perilampidae, which is closely allied taxonomically to the Eucharidae. Here again the act of oviposition and the egg were not seen, but the first instar larva proved to be identical in general characters with that of Orasema. These planidia (dimunitive wanderers) differed from other known parasitic hymenopterous larvae in the possession of a fusiform body and a highly sclerotized and darkened integument. Because of the form and habits of the planidium of Perilampus. Smith was convinced that oviposition did not take place directly in or on the host, and he believed that the eggs were more probably deposited upon the food plant in the vicinity of a colony of hosts. In discussing Wheeler's observations on Orasema he pointed out the similarity in form and habits of the larvae with those of Perilampus and suggested the probability that oviposition takes place entirely outside the ant nest. Smith was able later (1917) to verify the leaf-ovipositing habit in P. chrysopae Cwfd., and this discovery served to stimulate interest in the habits of the two families.

The first discovery of the oviposition habits of a species of Eucharidae was purely accidental. During the course of a study of the insect fauna of wild cotton in Arizona, Pierce and Morrill (1914) chanced to observe two females of Chalcura arizonensis Cwfd. with their ovipositors inserted in apparently healthy blossom squares of this plant. Upon later examination these squares were found to contain masses of minute eggs immediately beneath the points of insertion of the ovipositors. This record was entirely overlooked by later workers, and it was not until the writer's account of the habits of (Schizaspidia) Stilbula tenuicornis (Ashm.), published in 1923, that the plant-oviposition habit became generally known. Since that time observations have been made upon the oviposition habits of 7 additional genera and 12 species occurring in various parts of the world,³ and several other in-

³ The writer is indebted to A. B. Gahan, of the U. S. Bureau of Entomology and Plant Quarantine, for the determination of species and for the descriptions of those that have proved to be new (Proc. U. S. Nat. Mus. 88: 425–458. 1940). In a forthcoming publication (*Entomophagous insects*, New York) a short account is given of the biology and habits of the family. At the time of submission of the manuscript the names of

vestigators have added to our knowledge of this subject, so that it is now possible to present an account of several of the principal oviposition habits of the family. In every instance it has been found that the eggs are deposited entirely apart from the host, that the association with plants for this purpose is obligatory, and that a wide range exists with respect to the manner of deposition of the eggs and the part of the plant on or in which they are placed.

As an aid to others who may be interested in studying the habits of the family, it may be mentioned that the oviposition habits can be readily and quickly determined by observations on females in the field. They oviposit almost immediately after leaving the ant nest and, because of their limited and relatively slow flight, can be followed until they alight upon the plant that is to receive their eggs. The elapsed time from emergence to oviposition is usually less than 1 hour. Botanical gardens provide exceptional opportunites for the study of the Eucharidae, as the variety of plants grown there insures that some will be present that are suitable for oviposition by such species as may occur in that locality. Also, the ant population is usually relatively high and of many species. The Botanical Garden at Peradeniya, Ceylon, was especially fruitful and yielded three species in abundance during a short visit there in February 1930.

OVIPOSITION PLANTS

In Table 1 are given the species of which the habits are known and the plant or plants with which each one is associated for oviposition. The records are based on the author's observations unless otherwise indicated.

PART OF PLANT UTILIZED FOR OVIPOSITION

The part of the plant utilized for oviposition varies with the species and may be the overwintering buds, opening flower buds, stems of blossom clusters, seed pods, or leaves. The variations in habit, in relation to the part of the plant that serves to receive the eggs, are here discussed under the following headings:

1. In overwintering buds. The single species that is definitely known to pass the winter in the egg stage is *Stilbula tenuicornis* of Japan and Chosen, which places its eggs in the overwintering buds of mulberry (Fig. 1) and, to a lesser extent, in those of chestnut, oak, birch, and

Gahan's new species were not available, and several were referred to under the generic name only. These are now assigned as follows: Psilogaster sp. from Malaya = P. antennatus Gahan; Parapsilogaster sp. from Ceylon = P. laeviceps Gahan; Eucharis sp. from Chosen = E. scutellaris Gahan; and Schizaspidia sp. from Malaya = S. antennata Gahan.

TABLE 1.—OVIPOSITION PLANTS OF THE EUCHARIDAE

Species	Plant	State or Country	Authority
Chalcura arizonensis Cwfd Chalcura deprivata (Walk.)	Thurberia thespessioides. Artocarpus integrifolia, Codiaeum, Cordia myza.	Arizona Ceylon	Pierce & Morrill, 1914.
Kapala foveatella Gir	Ceouna oroccutau. Chiricidalium, Lencana alanca	Philippine Islands	Ishii, 1932.
Kapala furcata (F.)	Mikania micrantha, a species of the Amarantha-	Panama	,
Kapala terminalis Ashm	Tragia volubilis, Casearia spinescens. Tragia volubilis	Cuba	
Losbanos urchancoi Ishii. Orasema aenea Gahan	Celtis philippinensis, Leucaena glauca. Ilex paraguayensis.	Philippine Islands Argentina	Ishii, 1932. A.A. Ogloblin (Gahan,
Orasema coloradensis Wheeler	Stylosanthes biflora, Ceanothus americanus. Casearia spinescens.	Virginia Cuba	1940).
Parapsilogaster laeviceps Gahan. Parapsilogaster montanus Gir.	Artocarpus integrifolia. Sandricum koetiane	Ceylon Philippine Islands	Ishii 1932
Psilogaster antennatus Gahan	Mangifera indica, Erythrina sp. Eucania Medinella	Federated Malay States	
Schizaspidia convergens (Walk.) Stillnila cuniformis Rossi	Artocarps, integration. Press hierarchides var sminnlosa	Ceylon France	Parker 1937
Stilbula manipurensis (Clausen)	Flamingia latifolia.	India	
···· (·······························	Betula 8p., Monis alla	Do.	
	Cladrastis amurensis var. floribunda. Quercus mongolica.	Do. Chosen	

Cladrastis amurensis var. floribunda (Clausen, 1923). The entire quota of eggs of the female, numbering approximately 1,000, is deposited within the interior of the bud at one insertion of the ovipositor.

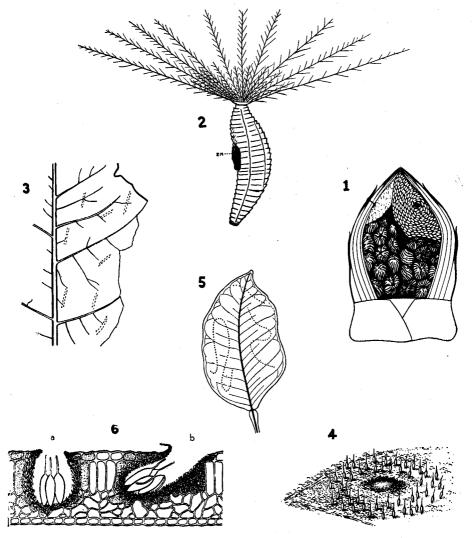


Fig. 1.—A mulberry flower bud cut away to show two egg masses of Stilbula tenuicornis (Ashm.). Fig. 2.—A seed, with fully expanded plumes, of Picris hieracioides var. spinulosa bearing a mass of eggs (E.M.) of Stilbula cyniformis Rossi (from Parker, 1937). Fig. 3.—A portion of a leaf showing, on its under side, the paired rows of oviposition scars of Losbanos uichancoi Ishii (from Ishii, 1932). Fig. 4.—A group of eggs of Psilogaster antennatus Gahan upon the leaf surface surrounding a freshly deposited egg of Selenothrips rubrocinctus. Fig. 5.—A fleshy leaf showing the serpentine lines of oviposition scars of Schizaspidia antennata Gahan. Fig. 6.—A diagrammatic section through a fleshy leaf showing (a) a group of three eggs of Parapsilogaster laeviceps Gahan and (b) a group of four eggs of Schizaspidia antennata Gahan in their characteristic position resulting from the insertion of the curved ovipositor at a sharp angle to the leaf surface.

These eggs remain therein until the following spring, when the buds expand and the great majority of egg masses fall to the ground with the bud scales. A portion of the buds die, however, and the scales draw apart somewhat, thus permitting the escape of the larvae, which hatch from the eggs during July and early in August.

2. In expanding leaf and flower buds. A number of species, representing several genera, utilize the expanding leaf and flower buds of various plants for oviposition. Eucharis scutellaris of Chosen, which oviposits in those of a trailing vine of the genus Cebatha, may even deposit her eggs in fully opened blossoms. Less than 50 eggs are placed in the center of each one, and consequently each female visits a considerable number of blossoms before oviposition is complete. Kapala furcata oviposits similarly in the flower buds of another vine, of the genus Mikania, and of an undetermined species of Amaranthaceae. A colony of this parasite was found inhabiting the small plot of open ground immediately in front of the main laboratory building on Barro Colorado Island, Panama Canal Zone.

Chalcura arizonensis deposits its eggs in the blossoms of wild cotton in Arizona, while C. deprivata of Ceylon does so in the leaf buds of jak fruit, though some individuals were seen to utilize the expanding flower buds of croton and Cordia. Stilbula manipurensis of Assam places its eggs in masses beneath one of the outer scales of the large, loosely formed buds of Flamingia (Clausen, 1928). Schizaspidia convergens deposits them in clusters of a few hundred beneath the outer scales of leaf buds, and occasionally in the flower buds also, of jak fruit in Ceylon, and usually high up in the tree. Buds containing egg masses can frequently be recognized by the presence of a curled ribbon or thread of white congealed sap, several millimeters in length, at the point penetrated by the ovipositor. In all these species the incubation period is relatively short, covering not more than two weeks, but before hatching takes place the bud scales and petals fall to the ground and carry the great majority of eggs with them.

3. In seed receptacles. Parker (1937) describes the oviposition of Stilbula cyniformis in the seed heads of a small composite plant of the genus Picris in southern France. The eggs are deposited en masse among the bracts or adhering to the outer layer of seeds. As the seed head opens the plumes of each seed expand and the seed, with its burden of eggs (Fig. 2), is blown away. Inasmuch as oviposition takes place only during August, it is possible that this species, like S. tenuicornis, passes the winter in the egg stage. After completion of oviposition the female often dies with her ovipositor still inserted in the seed receptacle.

4. In incisions in leaf tissue. The females of Schizaspidia antennata, the commonest of the eucharid species observed at Kuala Lumpur, Federated Malay States, usually deposit their eggs in pairs, but at times in groups of three or four, in incisions in the under sides of the fleshy leaves of Eugenia, Medinella, etc. These punctures are evenly spaced about 1 millimeter apart and are made in serpentine rows over the leaf (Figs. 5, 6, b). When the trees are in bloom oviposition is frequently in the fleshy stems of the blossom clusters rather than in the leaves. Parapsilogaster laeviceps shows a pronounced preference for the half-grown leaves of jak fruit, the eggs are laid singly in incisions on the under side, usually near the leaf margin, and the incisions are made somewhat at random rather than in rows.

In July 1932 J. C. Bridwell showed the writer a colony of Orasema coloradensis at Barcroft, Va., that was restricted to a very limited area along a railroad right-of-way and bordering a wooded area. The females were seen to be ovipositing in the younger leaves of the smallleaf pencil-flower, Stylosanthes biflora, and also occasionally beneath the bud scales of the large-leaf Jersey tea, Ceanothus americanus (determinations by Dr. S. F. Blake). In the pencil-flower the eggs are placed singly or in pairs in incisions in the under sides of the younger leaves. between the parallel veins. While there may be several punctures in a row, yet because of the small size of the leaf any distinct linear or serpentine arrangement of the punctures is prevented. An elongate area of leaf-tissue about the puncture becomes discolored and dies. In the limited area inhabited by this colony practically every leaf of the pencil-flower contained one or more eggs, and the numerous areas of dead tissue gave the plants the appearance of being diseased. O. smithi oviposits in the same way, but this species is distinctive in that it oviposits only in the upper sides of the leaves and limits itself to those within 2 feet of the ground. Kapala terminalis likewise oviposits in the upper rather than the lower sides of the leaves.

Ishii (1932) describes the somewhat similar leaf-ovipositing habits of two species from the Philippine Islands. The females of Kapala foveatella place one to four eggs in each incision in the lower sides of the leaves of Gliricidia and Leucaena. The oviposition punctures made by Losbanos uichancoi on the under sides of the leaves of Celtis and Leucaena occur in two short parallel rows, each row comprising five to ten punctures. This oviposition in a double rather than in a single row, as is the habit of other species, is an interesting variation, but unfortunately the author does not describe the manner in which it is accomplished. His illustration (Fig. 3) indicates that the two rows of eggs are

deposited simultaneously, the ovipositor apparently being inserted alternately right and left as the female moves forward.

- 5. At random on leaf surface. This oviposition habit was first observed by Ishii in the case of Parapsilogaster montanus at Los Banos, Philippine Islands. The eggs are deposited horizontally on the under sides of the leaves of Sandricum and Premna, and, when abundant, they give a white, powdery appearance to the leaf surface. A species of Kapala found in Cuba, and not distinguishable in the adult stage from K. terminalis, oviposits in the same way upon the leaves of Tragia volubilis. A female normally deposits her entire quota of eggs upon a single leaf, and each of these may bear many thousands of eggs. She walks about very slowly over the leaf, tapping its surface rapidly with the tip of the ovipositor, and one or two eggs are extruded each time. Leaves bearing fully incubated eggs appear as if covered with a fungous growth, the slender egg stalks resembling hyphae and the deep amber-colored egg bodies the conidia. These species, and Psilogaster antennatus, are among the very few Chalcidoidea that deposit eggs of the stalked type in such a position that they are completely exposed.
- 6. Upon leaf surface associated with thrips eggs. One of the most striking and highly specialized adaptations in oviposition in the Eucharidae was observed in the Malayan Psilogaster antennatus, which was collected in some numbers in January 1930 near Kuala Lampur. The eggs are placed vertically, regularly spaced and in numbers up to 100, in the immediate vicinity of a freshly deposited thrips egg (Fig. 4). Under cage conditions oviposition could not be secured in the absence of these eggs, and the relationship appears to be obligatory. The thrips species concerned, Selenothrips rubrocinctus (Giard), was found commonly only on mango and Erythrina foliage. The thrips female partially inserts the egg in an incision in the under side of the leaf and covers it with a mass of excrement. The female parasite is attracted to the egg itself rather than to excrementous covering. The parasite's association with the foliage of the two trees mentioned is believed to be incidental and it very probably will be found to frequent any type of plant which bears an infestation of Selenothrips. The presumed ant host of Psilogaster is not known, so it is impossible to give any convincing explanation of this association with thrips. Several species of the genus have been reared from Myrmecia and Pheidole, so there is little basis for believing in any radical departure in host preferences. The association with thrips undoubtedly relates to phoresy, as the eggs hatch simultaneously with those of the carrier and the planidia attach themselves to the young thrips larva as soon

as it emerges from the egg and are carried about until the first molt of the latter. Were the thrips attended by ants, or carried into their nests, the relationship would serve a definite and obvious purpose, but such is not the case.

The number of species for which information is available regarding their oviposition habits is still too small to warrant any generalizations, and in all probability other and perhaps radical departures from those discussed will be found. In examining the data given in the preceding paragraphs it is seen that there is little uniformity in habit even among species of a genus. Parapsilogaster laeviceps places its eggs in incisions in leaf tissue, whereas P. montanus deposits them at random on the leaf surface. Kapala foveatella and K. terminalis oviposit in leaf tissue, K. furcata in the expanding blossom buds of a vine, and an undetermined species of Kapala places its eggs loosely upon the leaf surface. Stilbula tenuicornis oviposits in overwintering leaf and flower buds, S. manipurensis in expanding flower buds, and S. cyniformis in seed receptacles. The three species of Orasema are, however, consistent in placing their eggs in incisions in leaves.

MANNER OF OVIPOSITION

The species of Stilbula, Kapala, Eucharis, Chalcura, and Schiza-spidia that deposit their eggs in buds or seed receptacles have a uniform manner of oviposition. The female penetrates the scales or covering by a downward thrust of the ovipositor, and full penetration of a bud with heavy scales may require 5 minutes or more. In no instance has a female been seen to insert the ovipositor between the scales.

Two distinct methods of oviposition are found among the species that oviposit in leaf tissue. Parapsilogaster laeviceps (Fig. 6, a) and Orasema coloradensis merely puncture the leaf tissue by a perpendicular thrust of the straight ovipositor, and consequently the perforation in the epidermis is found at the center of an area of dead tissue, which, within a few days, becomes about 1 millimeter in diameter. Schizaspidia antennata, however, has a much heavier ovipositor, which is distinctly curved downward, so that when it is lowered preparatory to oviposition the tip is directed forward. Insertion into the leaf is consequently effected by a forward pull rather than by a backward or downward thrust. After being inserted to the proper depth in the fleshy leaf tissue, it is swung from side to side through an arc of about 45°, with the base held stationary. This results in the formation of a fan-shaped recess within the leaf, in which two to four eggs are placed (Fig. 6, b). On leaves in which eggs have been deposited several days

previously the area of dead tissue is almost entirely posterior to the surface incision.

It has been mentioned that Schizaspidia antennata oviposits also in the heavy fleshy stems of the flower clusters of certain trees. At these times it often happens that the eggs are deposited externally rather than embedded in the stems. The tissues of the stem are very soft and tender and offer very little resistance to the ovipositor. It is inserted transversely to the axis of the stem but, because of its curvature, the tip breaks through the surface farther on, thus making a double perforation of the epidermis such as is done with a curved surgeon's needle. The eggs are then extruded from the ovipositor and only the slender anterior stalks remain embedded in the puncture.

Orasema smithi inserts the ovipositor in the same way as Schizaspidia antennata, and its incisions are readily recognized by the triangular form of the surface puncture. The single egg deposited at each insertion is found at the anterior end of the cavity rather than at the center.

The female of *Psilogaster antennatus* makes a very minute puncture in the epidermis of the mango leaf and embeds the pointed posterior tip of the egg therein so that it is firmly held in an erect position, with the anterior stalk turgid and straight.

The form of the incision and the cavity produced in the plant tissue are thus seen to differ among species and they permit of provisional recognition in the field. An examination of the ovipositors of the females often gives a clue to the manner and place of oviposition. A heavy curved ovipositor points to oviposition in succulent leaves and stems whereas one which is long, straight, and slender indicates that the eggs are probably placed in buds or seed pods.

SUITABILITY OF DIFFERENT PLANTS FOR OVIPOSITION

The suitability or otherwise of a plant for oviposition by Eucharidae appears to be governed mainly by the physical qualities of the part in which the eggs are placed, rather than by definite attraction. Stilbula tenuicornis, a bud-ovipositing species, favors mulberry in northern Japan, but it also oviposits to a lesser extent in chestnut, birch, and Cladrastis, while in Chosen it was seen to do so in the buds of oak. These buds have certain qualities in common. The scales, while firm, are not too hard for penetration by the ovipositor, the interior of the bud has at least a small amount of free space in which the eggs may be placed, and the sap is nonresinous. The adults of this species are present in the field for only about three weeks each year, and they

consequently are limited in oviposition to such trees as have their buds fully formed at that time. The same requirements are encountered among other species, such as *S. cyniformis*, which oviposit in seed receptacles.

Among the leaf-ovipositing species, those that insert the eggs in incisions in the tissue restrict themselves to plants having leaves with certain physical qualities. When one surface is punctured the wound must remain permanently open to permit of the later escape of the larvae. This rules out the plants that exude appreciable amounts of sap from leaf wounds. Plants with rather fleshy and smooth leaves, such as Artocarpus, Citrus, and Codiaeum, are most frequently chosen. The two leaf-ovipositing species observed in Ceylon, representing the genera Parapsilogaster and Chalcura, both deposit the great bulk of their eggs in Artocarpus. Orasema smithi and Kapala terminalis, which were found in the same habitat at Hoyo Colorado, Cuba, both oviposit in the leaves of Casearia. O. coloradensis, however, chooses the small and very delicate leaves of Stylosanthes. The collection notes of C. F. Baker, given by Gahan in his discussion of O. wheeleri Wheeler, show three collections on separate dates on Eriogonum at Fort Collins, Colorado. It is quite possible that the females were ovipositing in the leaves of that plant.

In the temperate regions, where the various species apparently have only a single generation each year and the adults are present for only a very short period, the number of plant species that serve for oviposition is at a minimum and a single one may suffice. That chosen in one locality may differ from the one favored in another. Some of the tropical Eucharidae, most of which are assumed to have overlapping generations throughout the year, may change their oviposition plants with the seasons. This is of most probable occurrence among those that oviposit in buds, particularly flower buds, and seed receptacles.

The above generalization regarding the factors influencing the choice of plants for oviposition apparently does not hold true with species that deposit their eggs in expanding flower buds, and some, at least, exhibit a strong response to what is apparently an odor stimulus. The most striking example of such a reaction was observed in *Eucharis scutellaris*, which places its eggs in the flower buds of *Cebatha orbiculata*. A sprig of this vine held near an ant nest from which *Eucharis* is emerging will attract all females in the vicinity within a few minutes. If shaken off they immediately return to the buds and cling to them tenaciously. The males, however, are not attracted to these buds.

Only two species are known to deposit their eggs at random on the leaf surface, but in these instances the plants favored for oviposition have leaves with a hairless and glossy under surface.

RATE OF OVIPOSITION

The total egg capacity of the females of the Eucharidae ranges from a minimum of about 1,000 to a maximum of 10,000 or more. The eggs are very minute, seldom exceeding 0.2 mm in length even in the larger species, and those of the smaller species may not exceed 0.1 mm. The smaller total given above is for Stilbula tenuicornis, which deposits the entire lot en masse in a bud during an elapsed time averaging 20 minutes. This is at the rate of one egg a second, and consequently they must flow from the ovipositor in virtually an unbroken stream during this period. Where the parasite population is high, as in one locality near Koiwai, Japan, several of these masses are deposited in each bud, and one rather sparse mulberry bush 7 feet in height was estimated to contain 4,320,000 eggs. One bud was found to contain 24 egg masses. Because of the limited space available in the bud a high pressure must be exerted by the later females in forcing their eggs into the bud, and instances were seen where previously deposited eggs had been forced out through the older ovipositor puncture holes in the bud scales. The most striking illustration of such pressure was observed in S. manipurensis. One Flamingia bud showed a "ribbon" of eggs 2.5 mm in length and 1.0 mm in width that had been forced out from beneath the margin of a bud scale at a distance of 2 mm from the point of insertion of the ovipositor.

An undetermined species of Kapala from Cuba, which deposits its eggs at random on the leaf surface, has an exceedingly high egg capacity. One female deposited a total of approximately 10,000 eggs during a period of six hours. While the rapidity of deposition does not equal that of Stilbula, yet the total is much greater. Parker (1937) mentions the possibility of the production of 10,000 to 15,000 eggs by each female of Stilbula cyniformis.

In general it is the habit of the species that deposit their eggs en masse to complete oviposition the day of emergence from the host nest, and this appears to be true also of those that place them at random on the surface of leaves. Those that insert them singly or in small groups in leaf tissue are more deliberate in their oviposition activities and this may extend over one week or more. The number of eggs deposited each day is consequently only a few hundred, though a female of *Schizaspidia antennata* was seen to make 10 to 12 insertions of the

ovipositor a minute, which represents a deposition of about 30 eggs during that period. In other species, however, the interval between insertions is much longer.

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