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BIOLOGY OF SOME JAPANESE AND
CHONSENSE GRUB PARASITES
(SCOLIIDAE)

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INTRODUCTION

In the course of the investigations upon the natural enemies of the Japanese beetle (*Popillia japonica* Newm.) in the Far East during the period from 1920 to 1928, inclusive, occasion arose to study the habits of a considerable number of species of Scoliidæ parasitic upon the grubs of this and other Scarabæidæ, representing the subfamilies Rutelinae and Melolonthinae. For comparative purposes only those from Japan and Chosen (Korea) are dealt with in this bulletin, though occasional notes are given upon certain Chinese and Indian species. Among those treated the genera *Scolia* and *Campsomeris* are represented by a single species each, and the remaining 15 species are of the genus *Tiphia*. Several of the Japanese and Chosenese species occur also in China and were studied there by H. A. Jaynes from 1924 to 1926, inclusive.

The taxonomic determinations of all the species of *Tiphia* dealt with herein, with the exception of three previously described by S. A. Rohwer, have been made by H. W. Allen and H. A. Jaynes. Their recent publication (1)¹ deals with practically all the species encountered in the investigations in Japan, Chosen, China, and

¹ Italic numbers in parentheses refer to Literature Cited, p. 25.

India, and the greater proportion of them have been described as new in the article cited.

The principal points dealt with in this comparative study are the host relationships, the life cycle, the food habits of the adults, the position and manner of placement of the egg upon the host body, and the type of cocoon. Notes are also given upon such of the natural enemies of the family as have been encountered.

HOST RELATIONSHIPS

All the scoliid species studied have been found to be parasitic upon scarabaeid grubs of the subfamilies Melolonthinae and Rutelinae. In the list below are given the species and their recorded hosts. The records on some of these host species are based on field observations and thus represent the normal host relationship of the parasites, whereas the records on the remaining grub species are from insectary experiments and indicate suitability for development only, with the possibility that some may properly belong to the first group.

Species	Hosts
<i>Scolia japonica</i> Smith-----	<i>Anomala sieversi</i> Heyd. ²
<i>Campsomeris annulata</i> Fab-----	{ <i>Phyllophaga diomphalia</i> Bates. ²
	{ <i>Anomala</i> sp. ²
	{ <i>Popillia</i> spp.
<i>Tiphia agilis</i> Smith-----	{ <i>Serica orientalis</i> Mots. ²
	{ <i>Serica</i> sp.
<i>Tiphia asericæ</i> A. and J-----	<i>Serica</i> spp. ²
<i>Tiphia bicarinata</i> Cam-----	{ <i>Anomala sieversi</i> Heyd. ²
	{ <i>Phyllopertha pubicollis</i> Waterh.
<i>Tiphia biseculata</i> A. and J-----	<i>Anomala</i> sp. ²
	{ <i>Anomala sieversi</i> Heyd. ²
<i>Tiphia brevilincata</i> A. and J-----	{ <i>Phyllopertha pubicollis</i> Waterh. ²
	{ <i>Popillia mutans</i> Newman.
	{ <i>Anomala sieversi</i> Heyd. ²
<i>Tiphia koreana</i> Roh-----	{ <i>Popillia atrocoerulea</i> Bates.
	{ <i>Phyllopertha pubicollis</i> Waterh.
<i>Tiphia malayana</i> Cam-----	<i>Serica</i> spp. ²
<i>Tiphia notopolita alleni</i> Roberts (11)---	{ <i>Phyllopertha conspurcata</i> Har. ²
	{ <i>Phyllopertha pallidipennis</i> Reitt.
<i>Tiphia ovidorsalis</i> A. and J-----	<i>Serica</i> sp. ²
<i>Tiphia ovinigris</i> A. and J-----	<i>Phyllophaga</i> sp. ²
<i>Tiphia phyllophagæ</i> A. and J-----	{ <i>Phyllophaga diomphalia</i> Bates. ²
	{ <i>Phyllophaga</i> sp. ²
<i>Tiphia popillivora</i> Roh-----	{ <i>Popillia japonica</i> Newman. ² (Japan.)
	{ <i>Popillia atrocoerulea</i> Bates. ² (Chosen.)
	{ <i>Popillia castanoptera</i> Hope. ² (Chosen.)
	{ <i>Popillia formosana</i> Arrow. ² (Chjna.)
<i>Tiphia tegitiplaga</i> A. and J-----	<i>Anomala</i> sp. ²
<i>Tiphia totopunctata</i> A. and J-----	{ <i>Anomala sieversi</i> Heyd. ²
	{ <i>Phyllopertha pubicollis</i> Waterh.
<i>Tiphia vernalis</i> Roh-----	{ <i>Popillia castanoptera</i> Hope. ²
	{ <i>Anomala</i> sp.
	{ <i>Phyllopertha</i> sp.

² From field observation.

In view of the wide distribution of *Scolia japonica* (fig. 1), as compared with that of its known host, it is evident that other species, and possibly other genera as well, are attacked in addition to *Anomala sieversi*, of which there is a single record. The larger Scoliidæ, represented by *Scolia* and *Campsomeris*, appear to be more general in their choice of hosts than is *Tiphia*. *Campsomeris annulata* (fig. 2), of wide distribution throughout the Far East, is found in Chosen parasitic upon *Phyllophaga diomphalia* and *Anomala* sp. and will develop very readily upon *Popillia* spp. under laboratory conditions; in fact, it has occasionally been found upon this genus in the field.

In the genus *Tiphia* the number of species with known host records is sufficiently great to permit of some conclusion being drawn regarding the general host relationships of the group. It may be stated that the species of *Tiphia* are, in general, generic rather than specific in their choice of hosts. Specificity in this respect has been



FIGURE 1.—*Scolia japonica*, female. $\times 2.7$

claimed for many species, but investigations indicate that this is only regional and not absolute. Thus *Tiphia popilliavora* (fig. 3) is specific upon *Popillia japonica* in northern Japan, owing primarily to the lack of other representatives of the host genus in that country. The parasite, however, occurs in Chosen and China, whereas *P. japonica* does not occur on the Asiatic mainland, where the hosts are *P. castanoptera*, *P. atrocoerulea*, *P. formosana*, and other members of the genus. In any given locality it confines itself almost exclusively to a single host species, even though others of apparently equal suitability are present. *T. popilliavora* will develop quite readily upon *Phyllopertha* grubs under laboratory conditions.

It is rather noteworthy that a considerable number of species of *Tiphia* will oviposit and develop readily upon *Phyllopertha* grubs in the laboratory. Practically every species tested in this respect, which had as its normal host either *Anomala* or *Popillia*, would

transfer and develop readily on grubs of this genus. In contrast to this was the reaction of the several Phyllophaga parasites of this genus under similar conditions. From the very few eggs that these species were induced to deposit on grubs of other genera not a single larva developed beyond the primary stage.

The stage of development at which the host larva is attacked is of importance from the point of view of parasite development and increase. *Scolia* and *Campsomeris* confine themselves quite strictly to the final larval stage of the host, but this does not hold true in the case of many species of *Tiphia*. It has been noted that several species parasitic upon *Phyllophaga* normally attack the intermediate rather than the final stage, and this has been observed in the case of *T. notopolita alleni*. *T. popilliavora* in northern Japan also oviposits indiscriminately upon the last two host stages. At the time when the adults of this species are in the field (the middle of August

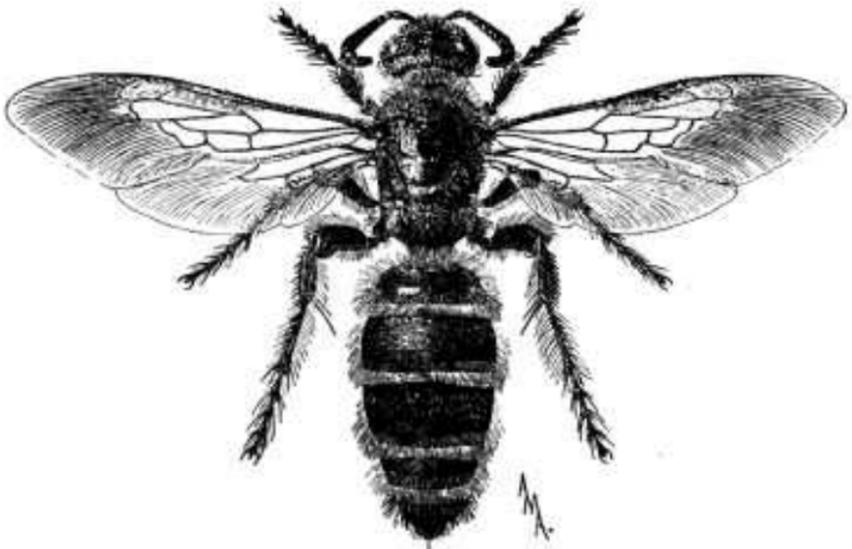


FIGURE 2.—*Campsomeris annulata*, female. $\times 3.5$

to the middle of September) in northern Japan the host is represented by two generations of grubs in the soil, this condition being due to a partial 2-year cycle. Thus, both fully mature grubs from eggs of the preceding season and first and second stage ones of the current generation are found in good numbers. Both the mature forms and those of the early second stage are attacked, apparently without any marked preference being shown between them. The cocoons resulting from development on the very small, immature grubs are often less than 3 mm. in length, much resembling an average sized *Apanteles* cocoon, and a great proportion of them never yield adult wasps.

THE LIFE CYCLE

NUMBER OF GENERATIONS

The life cycles of the Scoliidae are markedly affected by climatic conditions—far more so in fact than are those of many other para-

sitic groups. In the Tropics, unless activity is inhibited during a portion of the year by high temperatures and exceptionally low humidity, resulting in a period of acstivation, breeding goes on continuously throughout the year, and from three to six generations may be produced. In countries in the Temperate Zone, such as Japan and Chosen, this number is considerably reduced. Here *Scolia japonica* has, questionably, a single generation each year, while *Campsomeris annulata* has two, and possibly three. Of the 15 species of *Tiphia* listed herein, 11 have a single generation each year, while *biseculata* and *tegitiplaga* have two. This latter case is due to their occurring in a locality having an exceptionally short and mild winter and a very sandy soil, the latter factor being responsible

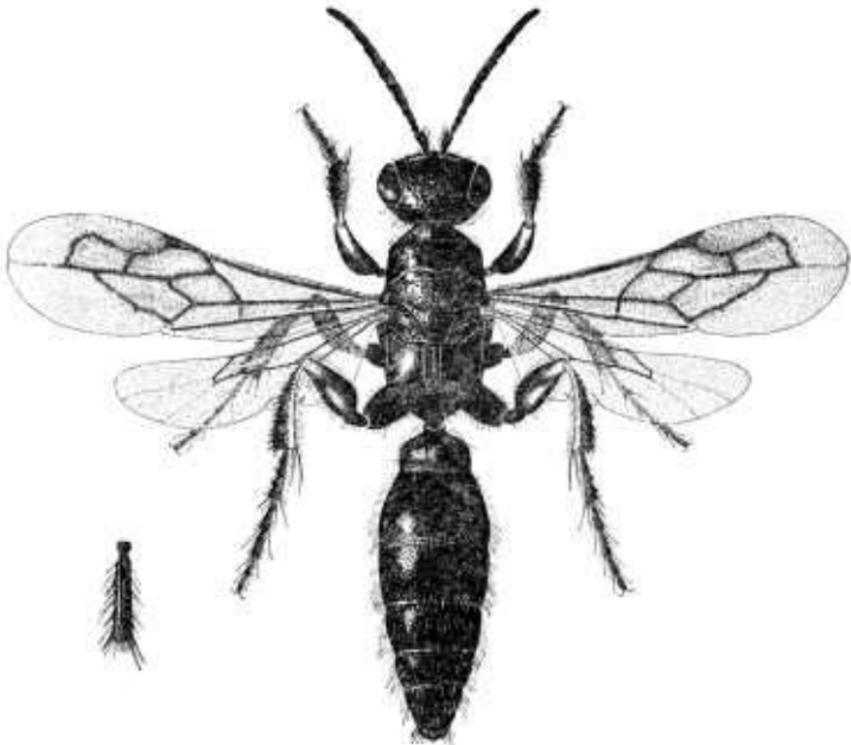


FIGURE 3.—*Tiphia popilliavora*, female. $\times 7.3$

for an earlier emergence in the spring and longer-continued growth in the fall than is the case in heavy soils. *T. ovinigris* and *T. phyllophagae*, both parasitic upon *Phyllophaga* grubs, apparently have a 2-year cycle to accommodate themselves to a corresponding cycle in the host.

LENGTH OF THE EGG STAGE

Within the family the duration of the egg stage ranges from 1 to 6 days under optimum summer conditions, with *Tiphia* in general having a longer incubation period than *Scolia* or *Campsomeris*. The above period may be extended to 10 or 15 days in the case of *Tiphia* breeding under lower temperature conditions. In the insectary breeding work with the species occurring in late fall it was found

that development was almost entirely inhibited, and consequently it was necessary to provide heating facilities to raise the temperature sufficiently to bring them to hatching and to carry on the development to the maturity of the larva.

The minimum period of incubation of *Scolia japonica* was found to be 1 day and that of *Campsomeris annulata* 2½ days. Of the species of *Tiphia* ovipositing in May the eggs of *vernalis* hatched in 13 days (7 days in June) and of *malayana* in 10 to 11 days. In June, July, and August, the period of maximum temperatures and high humidity, the time of hatching ranged from 3 days in the case of *asericae* and *bicarinata*, and 3 to 4 days in *agilis*, *brevilineata*, and *ovidorsalis* to 5 or 6 days with *totopunctata*. Eggs of *T. biseculata* required 4 days in the spring generation (June) and 5 days in the fall brood (September). The eggs of *T. popilliavora* hatched in 3 days at Suigen, Chosen, in late August, in 5 days at Yokohama in the same month, in 8 to 11 days in northern Japan in late August and September, and, as a maximum, in 10 to 14 days in Chosen during early October. Of the remaining fall species *notopolita alleni* required 4 or 5 days in September, *phyllophagae* and *ovinigris* 5 or 6 days in the same month, and *tegitiplaga* 7 days in the latter part of that month. Eggs from late emerging *T. koreana* females also required 5 to 6 days for incubation in September. It is thus seen that there is a considerable uniformity among the different species occurring at the various seasons of the year, and that the longer incubation recorded for many species is attributable directly to temperature influences rather than being a constant species characteristic. This point is brought out particularly well in the case of *T. popilliavora* in the various localities in which it is found, the duration of the stage ranging from 3 to 14 days, due solely to variations in temperature.

LENGTH OF THE LARVAL STAGE

The variation in the duration of the active larval stage, from the time of hatching to the formation of the cocoon, is similar in extent to that found in the incubation period. In *Scolia japonica* and *Campsomeris annulata* this stage is very short, covering only 4 days for the former and 5 days for the latter species under optimum summer conditions. Among *Tiphia*, *vernalis* and *malayana* require 20 to 25 and 21 to 22 days, respectively, at the end of May, under the relatively high temperatures then prevailing. In June, July, and August *asericae* larvae matured in 10 to 12 days, *ovidorsalis* in 11 to 14 days, *agilis* in 12 to 13 days, *biseculata* in 18 days in June (30 in late September), *brevilineata* in 12 to 15 days, *totopunctata* in 18 to 20 days, *bicarinata* in 12 to 20 days (late August and early September), and *koreana* in 18 to 20 days. Of those developing in September *notopolita alleni* required 15 to 17 days (18 to 19 in early October), *phyllophagae* 17 to 21 days, *ovinigris* about 18 days, and *tegitiplaga* 21 days. *T. popilliavora* attained the cocoon stage in 11 or 12 days in Chosen in early September but required 30 days or more in October and early November, whereas at Koiwai, in northern Japan, from 18 to 30 days were required during September, under temperature conditions approximating those of Chosen a month later.

TIME PASSED IN THE COCOON

So far as known, all Scoliidae in the temperate regions pass the winter within the cocoon, though this may be as a mature resting larva, a pupa, or a fully developed adult. *Scolia japonica* hibernates in the mature larval stage, while *Campsomeris* is largely in the pupal form, though there is some evidence to indicate that in certain southern localities a portion of the adult females of the latter carry through the winter. In the summer generations of the species having this habit, the period from the formation of the cocoon to the emergence of the adult comprises a minimum of three weeks.

Among the *Tiphia* having a single generation annually, approximately 10½ months of each year is passed within the cocoon. Of those species regarding which the winter stage is definitely known, *asericae*, *malayana*, and *vernalis* are found as adults, whereas *bicarinata*, *brevilineata*, *koreana*, *notopolita*

alleni, *phyllophagae*, *popilliavora*, *tegitiplaga*, and *totopunctata* hibernate as mature larvae. Of the three first-named species some of the late-developing individuals may pass the winter in the advanced pupal stage. In general it may be said that the spring-emerging species pass the winter in the adult stage in the cocoon, and that the summer and fall species do so as mature larvae. The first group would comprise those species that might be expected to produce a second brood under somewhat more favorable temperature conditions.

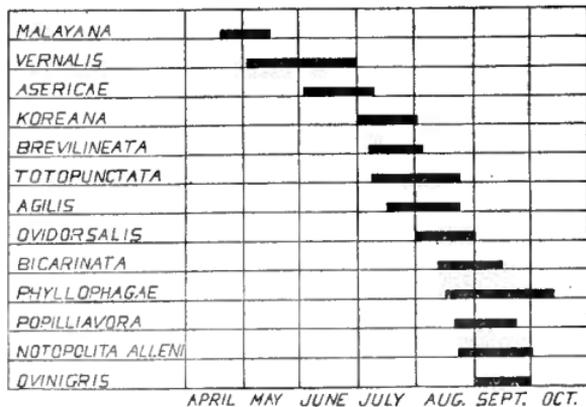


FIGURE 4.—Seasonal appearance of adults of *Tiphia* in Chosen

LENGTH OF ADULT LIFE

The larger Scoliidae, such as *Scolia* and *Campsomeris*, have a considerably longer period of adult life than does *Tiphia*, and this may extend over several months. Williams (13, p. 59) records a female of *Scolia manilae* Ashm. living nearly four months under insectary conditions, while the average of a series was 49 days.

Under normal field conditions the average length of life of *Tiphia* females is from 3 to 4 weeks, though this can be prolonged considerably under insectary conditions by withholding the opportunity for oviposition. Among the different species there is a considerable variation in the length of the period during which they may be found in the field. This shorter period on the part of some is not due to a shorter individual life, but rather to a greater uniformity in the time of emergence of some species than of others.

In Figure 4 there is shown, for comparative purposes, the period of adult occurrence of all the species of *Tiphia* studied at Suigen,

Chosen, the observations having all been made in the one general locality. Conditions being identical for all species, there is greater significance in the variations between them than would be the case were the data secured in widely separated sections with diverse factors influencing them.

FEEDING HABITS OF ADULTS

In all the species studied the general habit is for the females to feed for about three hours during the morning or at midday and then to spend the remainder of the day either resting in the soil or beneath vegetation on the surface, or in the search for host grubs for oviposition. The time of day at which they feed most extensively varies somewhat with the species. *T. popilliavora* in northern Japan was out in greatest numbers from 10 a. m. until 1 p. m., whereas *T. matura* A. and J. in India was to be found in numbers only from 8 to 11 a. m. The males generally appear slightly earlier in the morning than do the females and persist until about the middle of the afternoon. Some authors have noted a tendency on the part of the males of *Scolia*, *Campsomeris*, *Dielis*, and *Elis* to swarm at night, a habit not noticed with the *Tiphia* males.

The food materials required by the adult Scoliidae are derived from three general sources: (1) The exudations or secretions of aphids, scale insects, and various other Homoptera, these occurring particularly upon pine, oak, chestnut, etc.; (2) the blossoms of certain plants, especially of the Umbelliferae and Polygonaceae; and (3) nectar from various glands associated with foliage. The writers have observed *Scolia* and *Campsomeris* feeding only at blossoms, whereas *Tiphia* is represented as feeding at all these sources. Illingworth (10) records *Discolia soror* Smith as feeding very extensively upon the secretions of leaf hoppers on corn. In Table 1 are given the sources of food supply of the species dealt with, the *Tiphia* being listed in the order of their appearance during the season.

TABLE 1.—Sources of food supply of the adults of the various species of Scoliidae listed as occurring in Japan and Chosen

Species	Time of occurrence	Honeydew from—	Blossoms	Nectar glands
<i>Scolia japonica</i>	May to September.....	Various.....	
<i>Campsomeris annulata</i>	All season.....	do.....	
<i>Tiphia malayana</i>	Late April to middle of May.....	Aphids.....	Forsythia.....	
<i>Tiphia vernalis</i>	May to June.....	Aphids, bugs.....	do.....	
<i>Tiphia tegutiplaga</i> (I).....	Late May to June.....	Aphids.....	
<i>Tiphia biseculata</i> (I).....	June.....	do.....	
<i>Tiphia asericæ</i>	do.....	Aphids, bugs.....	
<i>Tiphia koreana</i>	July to early August.....	do.....	Various.....	
<i>Tiphia brevitineata</i>	July to middle of August.....	do.....	
<i>Tiphia totopunctata</i>	Early July to late August.....	do.....	
<i>Tiphia agilis</i>	Middle of July to late August.....	Aphids.....	Various.....	
<i>Tiphia ovidorsalis</i>	August.....	Aphids, bugs.....	
<i>Tiphia bicarinata</i>	August to middle of September.....	Umbelliferae.....	
<i>Tiphia phyllophagæ</i>	Middle of August to early October.....	Seseli, Fagopyrum.....	
<i>Tiphia popilliavora</i>	Middle of August to September.....	Various.....	Polygonum
<i>Tiphia notopolita alleni</i>	Late August to September.....	Seseli.....	
<i>Tiphia biseculata</i> (II).....	do.....	Aphids.....	Fagopyrum.....	Sweetpotato
<i>Tiphia tegutiplaga</i> (II).....	do.....	Do.
<i>Tiphia orinigris</i>	September.....	Umbelliferae.....	

Table 1 shows that the spring species of *Tiphia* confine their feeding almost exclusively to the liquid secretions of aphids and other bugs, with the exception of some *malayana* and *vernalis* feeding at Forsythia blossoms; that those appearing during midsummer feed either upon such secretions or at blossoms, though seldom both; and that the fall species are quite largely restricted to blossoms and nectar glands. The two species occurring at Miho, Japan, which have two generations a year, feed in the spring upon insect secretions and in the fall at the nectar glands of sweetpotato. The second generation of *biseculata*, however, has been noted to feed quite extensively upon aphid secretions upon pine.

The probable explanation of this seasonal change in feeding habit is that the insect secretions represent the favored food of the group, and that these aphids, scales, and bugs are particularly abundant during the early part of the season. They decrease in number by midsummer and are usually relatively scarce during the fall months. In this latter part of the season a much greater variety of flowering plants is available than during the spring.

The wasps are evidently attracted to their source of food by odor, and they usually feed in the general vicinity of the breeding grounds. A notable exception to this latter generalization is the case of *Tiphia matura* in India, which species was found to travel several miles, and to a considerably higher elevation, to the aphid-infested plants at which it fed, and then to return to the locality of origin for oviposition. In northern Japan *T. popilliavora* feeds at the blossoms and nectar glands of various plants, notably Polygonum, when growing on waste land situated at opposite sides of the breeding grounds. The females were always found in far greater numbers on the side of the field from which the wind was blowing.

In the utilization of Scoliidae in the natural control of Scarabaeidae the provision of an adequate supply of food plants, in the case of the blossom and nectar feeding species, would seem to be essential for attaining the desired results. The dispersion of the parasite can follow that of the host only so long as this condition is met, and large areas may be heavily infested with grubs and yet be practically immune from parasite attack, not because of any ineffectiveness of the parasites themselves but owing to the absence of their food supply. This condition seldom occurs in an area where there is any amount of waste land, as this connotes variety in vegetation, but is most likely to occur in relation to such Scarabaeidae as develop in cultivated soil and where a large area is under intensive cultivation for a single crop, which itself neither provides food for the adult *Tiphia* nor harbors insect species which do so.

Certain species of *Tiphia* have, in the adult stage, developed a slight tendency toward an entomophagous habit. This is shown in the case of *T. popilliavora*, the female of which, at the time of oviposition and immediately after the laying of the egg, often grasps a leg between her mandibles and bites upon it until a puncture is made or the leg entirely bitten off, after which she feeds upon the body fluids exuding from the wound. Field-collected grubs often show this type of injury, and the wound at times serves as a point of entrance for disease-producing organisms.

OVIPOSITION

It has not been possible to observe closely the sequence of events incident to oviposition by *Scolia* and *Campsomeris*, and these can only be surmised from the conditions observed when the cells containing ovipositing females are opened. In stinging, the parasite female faces in the same direction as the host grub, and dorsally of it, and the abdomen is then curved diagonally beneath the body so that the tip reaches the mid-ventral area of the thoracic segments. The stinging takes place near this point, and paralysis is effected through action upon one or more of the thoracic nerve ganglia. The sting is inserted several times and with considerable pressure. Illingworth (10, p. 35) states that *Campsomeris radula* Fab. attacks the grub by first seizing a mandible in her jaws and then inserting the sting, first in front of the anterior coxa and then in the throat.

Judging from the flaccid, extended condition of the grub body after oviposition by these parasites it would appear that a considerable kneading of the ventral surface must take place following stinging, though this has not been actually observed. Williams (13, p. 56), in describing the act of oviposition, does not mention this kneading in the case of *Scolia manilae*. With all species, the inert body of the host is left lying on its back.

PARALYSIS OF THE HOST

The influence of the sting of the various Scoliidae upon the host ranges from the complete and permanent paralysis effected by some of the larger genera to a very temporary immobility by *Tiphia*. All *Scolia* and *Campsomeris* known to the writers permanently paralyze the host grub, though this is not always complete, as in some instances a certain degree of disordered movement of the legs may be observed. In no case has complete or even partial recovery been noted. According to various authors the genera *Elis* and *Dielis* similarly paralyze the host grubs, as does also the South American genus *Pterombus* studied by Williams (14, p. 149).

The sting of *Tiphia* and the effect of the poison injected into the wound are much less severe than with the foregoing genera, resulting in a temporary and often incomplete paralysis lasting only 10 to 15 minutes in some species and extending to 30 minutes or slightly longer in others. While mobility is regained in a comparatively short time yet the full effects of the sting do not disappear for many hours, the more lasting effect being evident in a weakness in the abdominal region. No species of this genus is known to paralyze its prey permanently.

MANNER OF OVIPOSITION

In the case of both *Scolia japonica* and *Campsomeris annulata* the egg is placed upon the ventral surface of the body with its own ventral surface facing caudad, and with the posterior end lightly adhering to the derm of the host. From this position it would appear that during the actual deposition of the egg the body of the parasite female must lie parallel with that of the host, and facing caudad, rather than coiled transversely about it. This position dur-

ing the course of oviposition is not common to all members of these genera, for Illingworth (10, Pl. 4) shows the concave (ventral) surface of the egg of *C. radula* facing cephalad, and consequently the female parasite must face in the same direction as the host during the act of oviposition.

With respect to the genus *Tiphia*, the manner of oviposition of *T. popilliavora* has been described in some detail in a previous publication (4) and may be taken as representative of the group. By the use of a large gelatin capsule as a substitute for the soil cell of the grub the entire process of oviposition takes place very readily and can be closely observed under the binocular. The female approaches the grub from the rear, brings her head near to that of the host, and then lowers the abdomen diagonally behind and around the legs to effect stinging in the ventral mid-thoracic region. This stinging may be repeated many times, or until the grub becomes quiescent. Turning about, the female now devotes several minutes to a thorough kneading of the ventral surface of the abdomen with her mandibles. As a result, the body becomes flaccid and the abdomen relaxed and extended as compared with its normal turgid and curved condition. This accomplished, the parasite then grasps with her mandibles a fold of skin just above the lateral margin of the fifth or sixth abdominal segment, at the same time extending the body transversely across the dorsum of the host and bringing the abdomen across the ventral surface from the opposite side, thus forming almost a complete ring, the tip of the abdomen then being situated just beneath the head. The last abdominal segment of *Tiphia* bears at its extremity a roughened pygidium, and this is applied to the suture between the two segments and moved rapidly backwards and forwards for several minutes. The effect of this action is to broaden the groove for the reception of the egg and to wear away to a certain extent the integument of the body at this point, thus permitting its ready perforation by the young larva later. This extensive rasping of the integument is largely responsible for the rarity with which two or more eggs or larvae are found upon a single host grub. There is evidenced no disinclination whatever to oviposit upon a host already bearing an egg or young larva, but where these already occur they are, in most species, almost invariably broken or rubbed off before the succeeding egg is laid. This fresh egg is usually placed one segment in front of, or behind, the position of the earlier egg, rather than in the same suture. Grubs found in the field often bear a number of oviposition scars, though usually only the one egg, whereas in the laboratory instances have been observed of oviposition at least a dozen times upon the same grub, as evidenced by the two rows of oviposition scars in the intersegmental grooves between the second and successive segments to the eighth.

In several species this habit of rubbing off or destroying the eggs previously laid is not nearly so pronounced, and instances have been noted of grubs bearing as many as six fresh eggs upon the abdomen. This duplicate oviposition is particularly noticeable in the case of *T. bicarinata*.

The kneading of the body of the host is not habitual with all species of the genus; in fact, *popilliavora* seems to represent the extreme development of the habit. Those species that oviposit dor-

sally upon the thorax dispense with it entirely, and it is considerably reduced in extent in the case of such species as place their eggs ventrally on the anterior half of the body.

The normal habit of all Scoliidae is to locate the host grub in its cell in the soil, or in exceptional cases in plant tissue, sting it immediately, deposit the egg on the body, and then leave it in the same location in which it was first found. With some of the larger genera, however, the quiescent grub is buried deeply in the soil in a cell excavated by the female parasite, and the egg is then placed on it. This is particularly true of *Scolia*, and to a lesser extent of *Campsomeris*. During their feeding period the host grubs are quite near the soil surface, whereas those parasitized may be buried several feet deep, dependent on the physical condition of the soil. It is due to this habit of the females, of burying their prey, that cocoons of the above two genera are observed only in small numbers in the field, even though the number of adults present indicates their occurrence in abundance. No instance is known of *Tiphia* burying its host grub deeper than the normal feeding or resting cell, and the female always leaves the grub immediately after oviposition without any effort to modify the conditions under which it lies.

Although the habit of the family is to search out the host in its feeding cell or chamber, yet instances are known of various species, or, more exactly, individuals of various species, attacking their prey on the exposed surface of the ground and then burying it before oviposition, a manner identical with that of many of the other hunting wasps which store their cells with adult insects or larvae of various kinds. Gosse (9, p. 120) in Alabama, in 1859, recorded having seen a female *Scolia quadrimaculata* Fab. dragging a large lamellicorn grub along the surface of the ground to bury it. Ferton (7, p. 409) observed *Myzine andrei* Ferton in North Africa hunting a tenebrionid larva over the ground, and then stinging and burying it. In Illinois, Forbes (8, p. 472) noted *Tiphia* doing likewise with *Phyllophaga* grubs. In the present investigations this habit has been noted in the case of only a single species, *T. biseculata*, in Japan. In the particular locality in which this species occurs abundantly the soil is very sandy, and during heavy rains the *Anomala* grubs often come to the surface and wander about for a time. This is presumably due to the collapse of their soil cells. The females of *T. biseculata* become active very shortly after the rain ceases and may then be observed attacking the grubs which they find above ground.

POSITION OF THE EGG

The point of placement of the egg on the body of the host is quite constant among the individuals of any given species, but varies greatly between species and genera. In conjunction with this specificity in position another factor, the direction of the egg (that is, whether the anterior pole is directed towards the lateral margin or the median line of the body of the host) is of value. In Table 2 the direction and position of the eggs of the 17 treated species are given, the respective positions being also illustrated in Figure 5.

TABLE 2.—Location and direction of the egg as placed by the various species of Japanese and Chosenese Scolitidae listed

Species	Position of egg			Direction of egg
	Dorsal	Ventral	Lateral	
<i>Scolia japonica</i>		A4		V
<i>Campsomeris annulata</i>		A3		V
<i>Tiphia tegitiplaga</i>	T2-3			L
<i>Tiphia koreana</i>	T3			M
<i>Tiphia ovidorealis</i>	T3			M
<i>Tiphia totopunctata</i>	T3			M
<i>Tiphia biseculata</i>		T3-A1		L
<i>Tiphia phyllophagae</i>		T3-A1		L
<i>Tiphia vernalis</i>		T3-A1		L
<i>Tiphia agilis</i>		A3-4		L
<i>Tiphia bicarinata</i>		A3-4		L
<i>Tiphia brevilineata</i>		A3-4		L
<i>Tiphia malayana</i>		A3-4		L
<i>Tiphia ovinigrie</i>		A4-5		L
<i>Tiphia popilliavora</i>		A5-6, 6-7		M
<i>Tiphia notopolita alleni</i>		A7-8		L
<i>Tiphia asericae</i>			A7-8	M

Explanation of symbols:—T, on thorax; A, on abdomen; the numerals representing the respective segments of the body divisions. L, anterior pole of egg directed toward side of body; M, anterior pole directed toward the median line; V, vertical, with the posterior pole adhering to the host body.

In *Scolia japonica* and *Campsomeris annulata* the egg stands vertically upon its posterior end on the body of the host, and always on one of the middle abdominal segments. In respect to the former genus several writers have asserted that it is the anterior end that

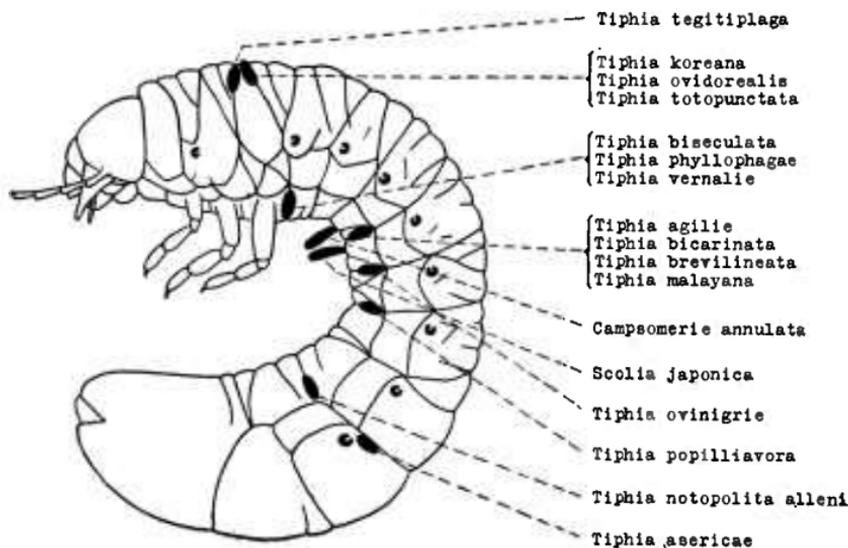


FIGURE 5.—Position of the egg upon the host grub of 17 species of Japanese and Chosenese Scolitidae

adheres to the host derm, but it is difficult to perceive how this reversal of position of the egg could be accomplished by the parasite.

The writers have not had the opportunity to observe the oviposition habits of *Elis* and *Dielis*. Box (2) has studied three species of the latter genus and found that the egg in each case was placed verti-

cally, while with *Elis xanthonotus* Roh. it was in a horizontal and transverse position. Davis (5) noted with *E. 5-cincta* Fab. that it was placed horizontally and diagonally across the body.

In *Tiphia* the egg always lies flat on the body, transversely in one of the segmental or intersegmental grooves. The greater number of species seem to fall into three general groups on the basis of egg placement, as follows:

(1) Egg placed dorsally in one of the grooves of the third thoracic segment and only slightly to one side of the median line. In this case the anterior pole of the egg is directed medially.

(2) Egg placed ventrally in the intersegmental groove between the third thoracic and the first abdominal segments, with the anterior pole directed laterad.

(3) Egg placed ventrally between the third and fourth abdominal segments, with the anterior pole directed laterad.

Of those depositing their eggs ventrally only a single species, *T. popilliavora*, has the anterior pole directed toward the median line, while *T. asericæ*, which places its egg laterally just above the ninth spiracle, also has the pole directed medially.

This position of the anterior pole of the egg seems to be due to the length of the *Tiphia* female in relation to the circumference of the host body at the point at which the egg is laid. In those species in which the body of the parasite is of sufficient length to extend across the dorsum and then across the ventral surface as well, thus forming almost a complete ring, the anterior pole of the egg will be directed medially. If, however, it is too short for this and extends only to the side of the venter opposite the head of the female parasite the egg pole will consequently be directed laterad. With those species which oviposit dorsally on the thorax the body of the parasite extends first across the thorax of the host ventrally, rather than dorsally.

The egg position given for the various species is not absolutely constant, and many instances have been noted of eggs being placed one segment in front of, or behind, the normal position. It is not implied that the positions given in Table 2 are the only ones taken advantage of by the different species of *Tiphia*. Other species are known that oviposit upon the second thoracic segment dorsally, and between the second and third ventrally, the egg thus being found between the coxæ of the last two pairs of legs; and it is probable that species will eventually be found which represent among them every intersegmental position between the first and the eighth abdominal segments. In *popilliavora* the normal egg position on the grubs of *Popillia japonica* in Japan, and in China on other *Popillia*, is between the fifth and sixth abdominal segments ventrally, whereas in Chosen, on *P. atrocoerulea* and *P. castanoptera*, it is largely between the sixth and seventh, only about one-third being between the fifth and sixth.

NUMBER OF EGGS

No complete oviposition records were secured for *Scolia japonica* or *Campsomeris annulata*, but general observations indicate that their reproductive potential somewhat exceeds that of the various species of *Tiphia* in the same region.

Williams (13, p. 58) records *Scolia manilae* as depositing a maximum of 52 eggs during a period of 79 days, and Illingworth (10, p. 33) in Australia secured 84 and 95, respectively, from two females of *Campsomeris tasmaniensis* Sauss., with the general average for the series under observation slightly more than one egg per day. The rate of oviposition of these genera is about the same as that in *Tiphia* but extends over a considerably longer period of time.

Among the *Tiphia* which have been tested sufficiently to give an idea of their normal capacity for oviposition it has been found that 40 eggs represent approximately the general maximum. Of the three species that have been reared very extensively in the insectary, *popilliavora* in Japan deposited an average of nearly 2 eggs per day during the oviposition period, whereas *vernalis* in Chosen and *matura* in India averaged only 1 in two days, these representing the extremes of the genus in this respect. Under field conditions it is probable that this difference in rate is not so great, that mentioned being possibly due more to a difference in adaptability of the various species to the insectary conditions provided. In the breeding cages the greatest number of eggs secured from a single female in one day was 6, this being from *T. bicarinata*. Under forcing conditions in gelatin capsules a female of *popilliavora* was induced to deposit 8 eggs during a period of six hours.

A notable exception to the above-mentioned average capacity for oviposition is that of the Chinese race of *popilliavora* studied by H. A. Jaynes at Penniu. In the investigations of 1925 a series of 46 females yielded an average of 54.9 eggs each, while one of them produced the very exceptional total of 115. This is in marked contrast to the results secured with the Japanese and Chosenese races, the general average of these being approximately doubled. These observations, in conjunction with various published reports by other authors, indicate that the reproductive potential of the tropical and subtropical forms is considerably greater than that of those species occurring in the more temperate regions.

D'Emmerez (6) presents figures for *Elis* and *Tiphia* in Mauritius which differ markedly from those above mentioned. In the case of *Elis rufa* Lep. he states that, in captivity, host larvae are normally parasitized by twos, at intervals of from six to eight days, and this conclusion was corroborated by field observations. His examination of the reproductive systems of the females showed one mature egg in each oviduct, while those still in the ovaries were of markedly smaller size. With *Tiphia parallela* Smith the normal egg capacity is said to be approximately 70, with the same rate and intervals between depositions as given for *E. rufa*. Such periodicity in oviposition has not been noted in any of the 35 or more scoliid species studied in the course of the writers' investigations.

HOST MORTALITY THROUGH MECHANICAL INJURY

In the larger Scoliidae particularly the reproductive potential of the species does not necessarily indicate the maximum host mortality that may be attained. The permanent paralysis and consequent death of the grub are brought about in a variable proportion of cases by *Scolia*, *Campsomeris*, and others, without oviposition, and from the point of view of natural control this factor represents

an added value. With some known parasitic Hymenoptera the number of hosts thus destroyed is far greater than that caused by the feeding of the progeny. In the laboratory the proportion destroyed in this way by *Scolia* and *Campsomeris* is large, but this is difficult of determination in the field. That it does occur under normal conditions is unquestionable, as grubs very evidently paralyzed by species of one of these genera have been found in the field. In his report on the parasites of scarabaeid grubs in Queensland Illingworth, who worked with the larger species (10, p. 25), states that the females of *Scoliidae* often paralyze a much greater number of grubs than actually receive eggs.

This factor is of much less importance in *Tiphia*, where recovery from the effects of the sting is complete, and the mortality effected, aside from that due to normal larval development, is very limited. Such of these as may die without being successfully parasitized do so as a result of the entrance of disease organisms at feeding punctures rather than of direct mechanical injury. This point has been discussed under the feeding habits of the adults.

THE IMMATURE STAGES

THE EGG

The eggs of *Scolia* and *Campsomeris* are quite similar in size and form. Those of average-sized species measure 2 to 4 mm. in length, with the maximum width, near the anterior end, approximately one-fourth to one-third of the length, and with both poles smoothly rounded. The ventral side is straight or very slightly concave, with the dorsum somewhat arched. The eggs at first are a translucent white but become somewhat yellowish or cream-colored towards the end of the incubation period.

In *Tiphia* there is likewise very little diversification either in size or form, the eggs of the largest species being about 2 mm. in length and 0.7 mm. in width, with the dorsum slightly convex and the ventral line nearly straight. In the smallest species studied the egg is approximately half the above length. The chorion is, in general, considerably heavier than in *Scolia* or *Campsomeris*. The one distinguishing character among the eggs of this genus is the color, and this is of very limited application. In the great majority of species the egg is white when laid but quickly assumes an amber tint of varying depth, owing largely to the drying out and oxidation of the mucilaginous material which envelops it and by means of which it adheres to the integument of the host. A further slight darkening in color occurs as incubation proceeds. The extreme in egg color is represented by *ovinigris* and *phyllophagae*, the only two species in the series parasitic upon *Phyllophaga*, in which it is nearly black. Intermediate in the color range are the eggs of *agilis*, *notopolita alleni*, and *totopunctata*, which are brownish black, and of *asericae*, which are a dark gray towards the end of the incubation period.

Among the different species of *Tiphia* there is a considerable variation in the firmness with which the eggs are fastened to the host body, and in some species apparently the amount or degree of adhesiveness of the material used is much greater than in others. In the case of *biseculata* and *asericae* a great deal of difficulty was experi-

enced in the breeding work owing to the high percentage of eggs which were rubbed off. A similar condition was noted in several other species, and this was in marked contrast to the relatively high percentage of development secured with *phyllophagae*, *popilliavora*, and *vernalis*. The position of the egg on the body of the host offers no indication of the probable loss from this cause, as that of *biseculata* is placed between the last thoracic and the first abdominal segments, a relatively protected position, whereas those placed dorsally on the thorax would seem to be most exposed to injury and loss, yet this was not reflected in the breeding results or indicated by field observations. The latter revealed, through the presence of oviposition "scars" (the dried, amber-colored adhesive material which remains on the host integument when the egg is removed), that much the greater loss usually occurs among those species which place the egg in the mid-ventral region.

HATCHING

In *Scolia japonica* and *Campsomeris annulata* hatching is accomplished by a median and irregularly longitudinal splitting of the chorion over the head and the thoracic segments. The fore part of the body of the young larva then emerges from the opening and is bent ventrally until the head comes in contact with the host body, at which point the feeding puncture is made. This mode of emergence from the egg gives a constant position for the feeding puncture with respect to the parasite egg, it being always on the median ventral line of the host body one segment caudad of that on which the egg is situated. In such other species and genera as place the egg with its ventral surface facing cephalad, this feeding position would be on the segment in front of, rather than behind, the egg.

In the hatching of the egg of *Tiphia* the median split of the chorion also occurs over the head and thoracic segments, and this portion of the larval body is then extruded slightly forward and the feeding puncture immediately made. As feeding progresses and the body enlarges, the split extends dorsally nearly to the posterior end, the caudal segments being entirely freed before the end of the primary stage. The cast shell then remains as a pad beneath the body of the larva, adhering both to it and to the integument of the host.

THE LARVA

FEEDING HABITS

The feeding habits of *Scolia* and *Campsomeris* larvae differ markedly from those of *Tiphia* in several respects. In the former two genera a very noticeable feeding puncture is made, and the head of the first-stage larva becomes imbedded in the body of the host. As development progresses not only the head but the thoracic segments as well are within the body. To permit of this, or as a result of it, the thoracic segments are considerably elongated and much narrower than the abdomen. By the time the larva attains the last instar the aperture in the host derm is slightly less than 2 mm. in diameter, and an appreciable quantity of body fluids exudes from the

wound and appears as a ring about the "neck" of the parasite larva. In the early larval stages feeding is in the anterior portions of the host body, and the exposed abdomen of the parasite consequently lies diagonally on that of the host and is directed somewhat caudad. In the final larval stage feeding is completed in the posterior portions of the host body, and the entire contents are consumed, though none of the integument is eaten.

In view of the grossness of the feeding habits of these two genera, resulting in a very large wound and in the constant exudation of body fluids at this point, it is surprising that putrefaction does not set in before the completion of feeding. With a mechanical injury producing such a wound, decay would be evidenced very quickly, but there is no trace of it in the parasitized grubs. The very short feeding period guards against this contingency to a certain extent. It has not been possible to distinguish the point at which complete paralysis ceases and death takes place, but this is believed to be about the middle of the feeding period of the parasite.

Illingworth (10, p. 35) states that the larva of *Campsomeris radula*, when disturbed just prior to pupation, ejects water from the tip of the abdomen to a distance of 6 inches or more. Box (2, p. 317) states that those of the larger Scoliidae in general have this habit. In the writers' investigations, however, this has not been noted to occur in *S. japonica* or *C. annulata*.

In *Tiphia* the manner of feeding corresponds more nearly to a true parasitic habit than does the qualified predatory habit of *Scolia* and *Campsomeris*. In the first four larval stages feeding is entirely suctorial, and the puncture is consequently of such minute size that when the larva is removed from the host body there is no exudation of fluids from the wound. The body of the larva in all stages is of normal form, widest in the mid-abdominal region, and with no appreciable narrowing or elongation of the thoracic segments.

In the last larval stage feeding by suctorial action gives way to the direct use of the mandibles, and the normal habit of all species is to consume not only the entire body contents but also the integument, with the exception of the head, legs, and at times a portion of the thorax.

During the early stages the body of the *Tiphia* larva lies transversely on that of the host. In those species in which the egg is placed ventrally near the lateral margin, and with the anterior pole directed toward the margin of the host body, the body of the parasite larva extends across the venter, whereas in the case of those which place the egg with the pole directed toward the median line the posterior portion of the parasite body curves over the lateral margin and extends dorsally.

NUMBER OF LARVAL INSTARS

In *Scolia* and *Campsomeris* there are four larval instars, and the three cast skins do not remain attached in a fixed position to the bodies of the succeeding instars or to that of the host. In contrast to this there are five stages in *Tiphia*, and the eggshell and the four cast skins remain in leaflike form adhering to the ventral side of the following stages. The eggshell, which forms a part of the ventral

pad, still adheres to, the integument of the host, and the mandibles of each of the exuvia remain imbedded in their respective feeding punctures. Molting is effected by a longitudinal dorsal split over the thorax and abdomen, and the head, upon being extruded from the old skin, is extended slightly forward of the previous position, and a new feeding puncture is made. In figure 6 is shown diagrammatically a fifth-instar *Tiphia* larva with the four cast skins and the eggshell outlined beneath, and also a separate feeding puncture for each stage, as represented by the regularly spaced heads of the exuvia.

The mandibles of *Scolia japonica*, *Campsomeris annulata*, and *Tiphia koreana* are illustrated in Figure 7, and the differences shown serve as a ready means of distinguishing between larvae of these three genera.

Those of *Scolia* and *Campsomeris* have three large teeth and are quite similar in general form, except that in *Scolia* the front tooth is proportionately somewhat larger and the grooves between the teeth are V-shaped, whereas in *Campsomeris* these grooves are narrower and the sides very nearly parallel. In *Tiphia* the three large teeth are also present, the first broader and larger than the remaining two, which are subequal with the grooves broadly V-shaped. The one ready character which distinguishes the mandibles of this genus from those of *Scolia* and *Campsomeris* is the possession of an additional small tooth at the

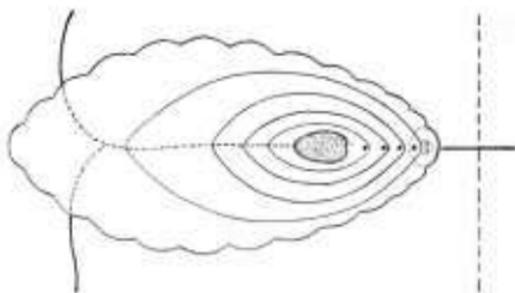


FIGURE 6.—Diagrammatic representation of the position of the successive larval stages of *Tiphia* in situ upon the host, showing the mouth parts remaining in the old feeding punctures. Largest outline represents the fifth and last larval stage

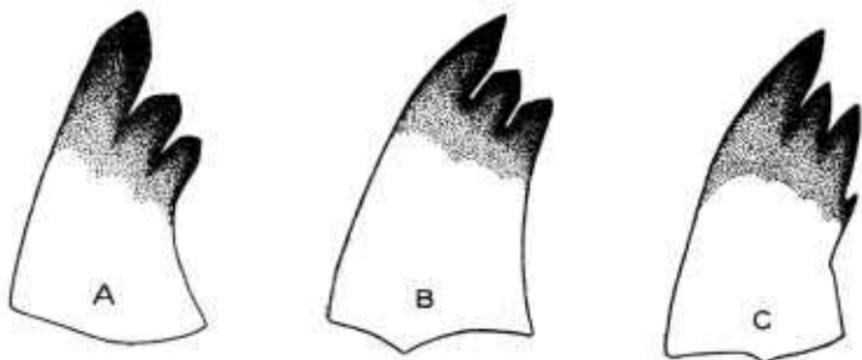


FIGURE 7.—Mandibles of mature scold larvae: A, *Scolia japonica*; B, *Campsomeris annulata*; C, *Tiphia koreana*

basal margin of the third of the main teeth. This varies somewhat in size according to the species but has been noted in all the species studied.

THE COCOON

In *Scolia japonica* the cocoon is broadly oval in form, the posterior end only slightly narrower than the anterior, and both evenly

rounded. It is dark brown with a somewhat glazed surface and lacks any loose covering of silk on the outside. That of *Campsomeris annulata* is of the same general form, reddish brown, and enveloped in a fairly heavy mass of silken strands, giving it a pronounced woolly appearance. The cocoon wall is comparatively delicate.

The *Tiphia* cocoon is quite distinct from those of the other genera in that, whereas the anterior end is broad and smoothly rounded, the posterior end is much narrowed and drawn out to a distinct point. The cocoon wall is very dense and compact, with a highly glazed surface inside, and surrounding it is a mass of silken strands of varying extent, forming either a loosely woven fluffy covering or separated into one or more thin and distinct envelopes. In *agilis*, *biseculata*, *notopolita alleni*, *ovidorsalis*, *phyllophagae*, *popilliavora*, *tegitiplaga*, and *vernalis* this covering is loose and fluffy, and not separable into distinct layers. This is true also of *asericae* and *malayana*, but there is much less of the covering. In *brevilineata*, *koreana*, and *totopunctata* the envelopes are quite distinct. *Tiphia brevilineata* has a cocoon quite different from that of the other species in that it is heavy and parchmentlike, with the surface appearing uneven but somewhat glazed and lacking almost entirely the loose outer strands of silk. Except in form it is thus more nearly comparable to the cocoon of *Scolia* than to the typical *Tiphia* cocoon.

The color of the cocoons in the genus *Tiphia* ranges from tan to a deep brown, those of the smaller species being in general the lighter colored. The color has been found to be due, in part at least, to the composition of the soil in which it is spun, as in a number of instances noted larvae that have been forced to form the cocoon in glass containers or paper cones free from soil produce nearly white cocoons.

In *Scolia* and *Campsomeris* the meconium is discharged in liquid form and is absorbed by the cocoon, considerably discoloring it in irregular patches. There is no trace of a solid meconial pad at the base of the cocoon, and only the cast skins of the larva and pupa may be found in the cocoon upon examination after the emergence of the adult. *Tiphia* forms a very compact meconial pad pressed down into the narrow tip of the cocoon with the upper surface, if somewhat concave, fitting rather closely about the tip of the abdomen of the pupa.

MANNER OF EMERGENCE FROM THE COCOON

The adults of *Scolia japonica* and *Campsomeris annulata* effect emergence from the cocoon by cutting a relatively large circular cap from the anterior end, the plane of the opening being at right angles to the longitudinal axis of the cocoon. All *Tiphia* adults emerge through a hole of irregular outline eaten out at one side of the cocoon near the anterior end, this being barely large enough to permit of the passage of the body.

According to Box (2, p. 318) all *Dielis* emerge by cutting a neat lid from the anterior end, whereas *Elis*, according to Davis (5) and Box, has the same manner of emergence as *Tiphia*.

The emergence holes of secondary parasites may at times be mistaken for those of the scoliid itself. The *Bombyliidae* remove a circular cap from the anterior end of the cocoon, but this can be recog-

nized by the fact that the edges are always quite ragged, on account of the cuts being made by the rasping of the head crown of the pupa, rather than a smooth cut with the mandibles as in *Scolia* and *Campsomeris*. The *Rhipiphoridae* cut away a similar cap, and cocoons from which these have emerged can be distinguished only by an examination of the larval remains contained in them. With *Perilampus* the hole is in the same position as that of *Tiphia*, but usually larger and more irregular in outline. Cocoons of *Tiphia* from which *Mutillidae* have emerged require an examination of the contents for verification, the holes being of similar form, size, and position.

PARTHENOGENESIS

No extended experiments have been made with the Japanese and Chosenese *Scoliidae* with respect to parthenogenesis, as the entire stock of reared cocoons of the principal species studied was forwarded to the United States for colonization purposes. The existence of this mode of reproduction has been demonstrated in some species of the family and its occurrence denied in others. Davis (5) states that it does not occur in *Elis 5-cincta* Fab., though unmated females will sting grubs. According to Illingworth (10) *Campsomeris radula* produces largely males when unmated, though also a few females, and he states that in general a smaller number of eggs is laid by such females. The production of both sexes of progeny by unmated females, even in the disproportionate numbers given, is a very unusual occurrence in the parasitic Hymenoptera. The customary result is the production of males only, or, in a relatively few instances, of females only.

NATURAL ENEMIES

In the course of the investigations on the *Scoliidae* in Japan and Chosen, it was not possible to make extended field collections of cocoons for the rearing of such parasites as might be contained in them. This difficulty was due to the intensive cultivation practiced in these countries, as a result of which very little waste land was available in which diggings could be made. Ten natural enemies, as shown in Table 3, have been noted, of which *Palarus saishiuensis* Okamoto was found in Chosen and the remaining species in Assam, India.

This wasp, *P. saishiuensis*, is one of the hunting wasps which stores its nest largely with adult Apidae, Sphecidae, and *Scoliidae*. The species is known to be well distributed in Chosen and in the island of Saishiu (Quelpart), but has not been recorded from Japan. A general account of the habits of this insect has been published by one of the writers (12).

The female wasps are found most commonly during August and September. Their burrows are invariably situated in rather heavy clay soil, the surface somewhat sloping, and with little or no vegetation upon it. In Figure 8 is shown a section of a typical burrow with the enlarged cell at the bottom, in which the victims are placed and the egg deposited among them. The burrow extends for a distance of from 8 to 12 inches into the soil and at an angle of about 40° from the horizontal. The slope of the burrow is not continuous

but is broken from two to four times by a short diversion after each of which the general trend is resumed. When the excavation of the nest is complete, the mouth of the burrow is filled and covered with sand and dust.

TABLE 3.—*Insect enemies of the scoliid parasites found in Chosen and in India*

Parasite	Family	Scoliid host
Hymenoptera:		
<i>Palarus saishiuensis</i> Okam.....	Sphecidae.....	<i>Tiphia</i> spp.
<i>Mutilla stephani</i> Magr.....	Mutillidae.....	<i>Tiphia matura</i> A. and J.
<i>Mutilla</i> sp., near <i>antennata</i> Sm.....	do.....	<i>Tiphia</i> sp.
<i>Perilampus</i> sp.....	Perilampidae.....	<i>Tiphia pullivora</i> A. and J.
Coleoptera:		
<i>Maerosaigon pusillum</i> Gerst.....	Rhipiphoridae.....	{ <i>Tiphia matura</i> A. and J. <i>Tiphia pullivora</i> A. and J.
Diptera:		
<i>Hyperalonia oenomaus</i> Rond.....	Bombyliidae.....	{ <i>Scolia</i> sp. <i>Campsomeris</i> sp. <i>Tiphia</i> sp.
<i>Ezoprosopa siphio</i> Ald.....	do.....	<i>Tiphia pullivora</i> A. and J.
<i>Aphobantus clauseni</i> Ald.....	do.....	Do.
<i>Aphobantus seriatus</i> Ald.....	do.....	Do.
Nematode:		
<i>Eomeremis tenuissima</i> Cobb.....	{ <i>Tiphia matura</i> A. and J. <i>Tiphia pullivora</i> A. and J.

The search for wasps with which to stock the nest takes place largely during the middle of the day. The actual capture and stinging has not been observed, but numerous females were noted bringing the paralyzed prey to the burrow. It is deposited near the entrance of the burrow, and the female then leaves it and scrapes away the sand and dust from the entrance with her forelegs. She descends into the burrow, then turns about and comes to the surface, after which she seizes the prey by the thorax and drags it into the burrow. (Fig. 8, inset.) It appears probable that each burrow is completed and stocked the same day it is started, and successive returns of the female with freshly captured prey were seen to occur at intervals of 5 to 10 minutes.

In nine completed nests, which were excavated and the contents recorded, 73 paralyzed wasps were found, with 14 as the maximum in one cell. By families the numbers of individuals were as follows:

Scoliidae.....	48 (<i>Tiphia</i> only).
Apidae.....	21 (5 or more species).
Sphecidae.....	2 (<i>Oxybelus</i> , <i>Cerceris</i>).
Mirmosidae.....	1 (<i>Mirmosa</i>).
Ichneumonidae.....	1.

From the foregoing list it will be seen that the greater proportion of the victims of this wasp are *Tiphia*, the remainder being largely various Apidae approximating *Tiphia* in size. It is evident that the numerical abundance of a hunting wasp such as this could affect decidedly the efficiency of such of these scarabaeid parasites as are of suitable size and occur during the latter part of the summer. The injurious effect is accentuated by the fact that by far the greater proportion of the wasps killed are females.

Only an occasional specimen of *Mutilla* was secured from the cocoons of *Tiphia matura* collected in India. An examination of the contents of these parasitized cocoons showed that development

of the parasite had been completed upon the mature *Tiphia* larvae. The mandibles of the last-stage mutillid larva are larger and differ markedly in form from those of any of the Scoliidae. Emergence from the cocoon is effected through a rather irregular hole near the anterior end, very similar to that of the host though possibly somewhat smaller.

Among the thousands of cocoons of *Tiphia pullivora* and others collected in India and shipped to the United States during the period from 1925 to 1927, inclusive, several each year yielded adults of *Perilampus* sp. A number of those retained in India were isolated prior to emergence and the contents later examined. The form of the mandibles of the larva showed the cocoons to be unquestionably those of *Tiphia*. The cast skins of the *Perilampus*

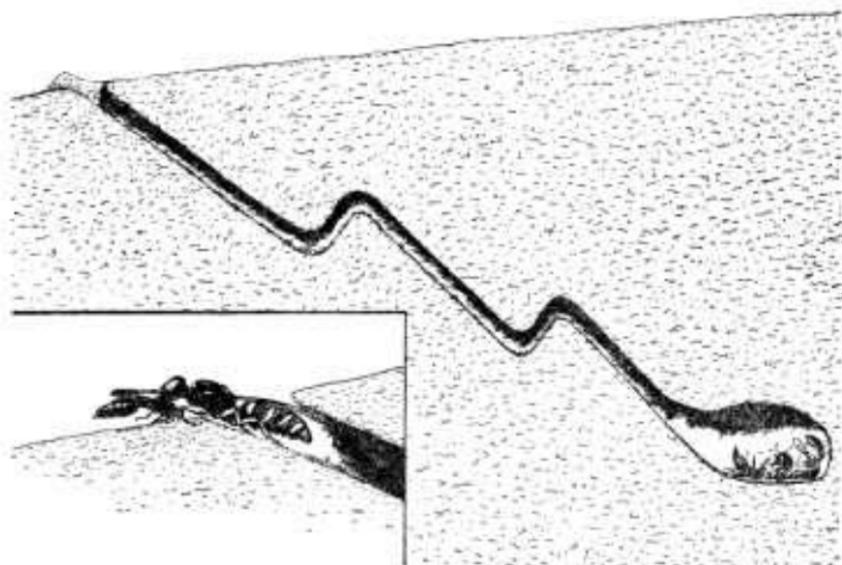


FIGURE 8.—The burrow of *Palarus saishiuensis*, showing the rearing chamber at the bottom, $\times \frac{1}{2}$; and (inset) a female dragging her prey into the mouth of the burrow, natural size

planidia were found still attached to the cast larval skin of the host, though development had been completed upon the pupae.

It is not considered that *Perilampus* is a normal parasite of *Tiphia* but rather that these few instances represent stray planidia which in some manner had gained access to the host larvae, either in the feeding stage or after the formation of the cocoons and once there were able to develop to maturity upon them. The diversity in the previously known hosts of *Perilampus* is so great that development upon *Tiphia* is not at all surprising, but the manner of reaching these larvae in the soil is difficult to explain.

The smaller *Tiphia* species in India are quite generally, and often fairly heavily, attacked by rhipiphorid parasites. One lot of 250 cocoons of *Tiphia pullivora* collected during July at Shillong was found upon examination to contain 1 mature larva, 6 pupae, and 64 adults of *Macrosaigon pusillum* Gerst.³, this representing a para-

³ Determined by E. A. Chaptn.

sitization of 28.4 per cent. In the case of this parasite the *Tiphia* hosts are killed in the mature larval stage, and the adults of the parasite emerge slightly earlier than would those of the host. Emergence is effected by cutting away a neat cap from the anterior end of the cocoon.

The life history of this group of beetles in the rôle of parasites in scoliid cocoons has not been studied, and there is considerable doubt as to the exact manner in which the primary larvae gain access to the host. Neither is it known whether it is the immature larval form upon the scarabaeid grub which is first attacked or the mature form within the cocoon. General observations indicate a mode of development somewhat similar to that of *Hyperalonia* and some other Bombyliidae.

Among the females of *M. pusillum* there is an unusual range of color forms, some being entirely black, others with red thorax, and finally some with both the thorax and abdomen red.

All four species of Bombyliidae listed in Table 3 were reared from isolated cocoons. The species present in the field in greatest numbers was *Hyperalonia oenomaus*, which effected each year a parasitization of 50 to 60 per cent of the cocoons of a large red-legged *Tiphia* which itself attacks *Anomala diomphalia*. An account of the life history of this parasite has been published by the senior writer in an earlier paper (3). In brief it may be stated that the adult flies appear in the field immediately after the period covered by the host adults, the eggs are presumably deposited upon the surface of the ground, and the young larvae find their way into the cocoons and develop as external parasites of the resting larvae. The active feeding period covers 10 to 15 days. There is a single generation each year, and the winter is passed in the mature larval stage within the host cocoon.

A small proportion of the cocoons of *Tiphia pullivora* and *T. matura* which had been collected for rearing purposes were found to yield instead a species of nematode, which has been described by N. A. Cobb as *Eomermis tenuissima*. These emerged from the cocoons early in July, this being only shortly after the formation of the cocoon of *T. matura* and immediately preceding the normal time of emergence of *T. pullivora*.

SUMMARY

All the scoliid species studied have been found to be parasitic on scarabaeid grubs of the subfamilies Melolonthinae and Rutelinae.

The food substances required by the adults come from three general sources—(1) the secretions of aphids, scales, and various other Homoptera, (2) certain plant blossoms, and (3) nectar from various glands associated with foliage. The dispersion of the parasite can therefore follow that of the host only so far as the range of its particular food supply extends.

On the basis of the writers' investigations upon the Scoliidae parasitic upon scarabaeid grubs, and supported by published data of other writers, the following general habits may be given for the different genera under discussion:

(1) In *Scolia*, *Campsomeris*, *Dielis*, and *Elis* there is a marked tendency toward swarming of the males at night. This habit has not been noted in *Tiphia*.

(2) Paralysis of the host is permanent in the case of *Scolia*, *Campsomeris*, *Dielis*, and *Elis*, and only temporary in *Tiphia*. In the first four genera the host grub is usually buried more deeply in the soil than its normal feeding level.

(3) In *Scolia*, *Campsomeris*, and *Dielis*, the egg is placed perpendicularly upon the ventral surface of the abdomen of the host, whereas in *Elis* it lies horizontally and diagonally in the same general region. In *Tiphia* it is placed transversely in a segmental or intersegmental groove, and either dorsally on the thorax or ventrally between any two body segments. The egg position varies with the species but is constant for each.

(4) In *Seolia* and *Campsomeris* and, to a modified extent, in *Dielis* and *Elis* the anterior portions of the body of the larva are thrust into the feeding puncture, whereas in *Tiphia* feeding is suctorial. In *Seolia* and *Campsomeris* no portion of the integument is eaten, whereas the *Tiphia* larva consumes all but the head and the more heavily chitinized portions of the thorax following the completion of feeding upon the body fluids.

(5) The cocoons of *Scolia*, *Campsomeris*, *Dielis*, and *Elis* are smoothly rounded at both ends, as contrasted with the very pointed posterior end of that of *Tiphia*.

(6) The solid meconial pad is absent in the cocoons of *Scolia* and *Campsomeris*, but present in that of *Tiphia*.

(7) In *Scolia*, *Campsomeris*, and *Dielis* emergence from the cocoon is effected by cutting away a circular cap at the anterior end, whereas in *Elis* and *Tiphia* an irregular hole of much smaller size is eaten out at one side near the anterior end.

An account is given of the natural enemies of the Scoliidae encountered during the course of the investigations in the various countries.

Of the Hymenoptera, *Palarus saishiuensis*, a sphecid wasp studied in Chosen, stores its nests with adult *Tiphia* and certain other wasps of similar size. Two species of *Mutilla* and one of *Perilampus* were reared from the cocoons of *Tiphia* in India, though in very small numbers.

The rhipiphorid beetle *Macrosaigon pusillum* was found quite frequently in the cocoons of *T. pullivora* in India.

Four species of bombyliid flies are listed as having been reared from the cocoons of either *Scolia*, *Campsomeris*, or *Tiphia* in India. *Hyperalonia oenomaus* is the only one of these occurring in large numbers, and each year it parasitized from 50 to 65 per cent of the overwintering cocoons of an undetermined species of *Tiphia*.

The nematode *Eomermis tenuissima* was reared occasionally during the summer from cocoons of *Tiphia pullivora* and *T. matura*.

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