INTRODUCTION

In the fall of 1939 a shipment of a gregarious platygasterid, *Allotropa burrelli* Mues., was received at Moorestown, N. J., from the Yokohama, Japan, station of the Division of Foreign Parasite Introduction, Bureau of Entomology and Plant Quarantine. The primary purpose of the importation was to furnish breeding stock for propagating parasites of this species for release against the Comstock mealybug (*Pseudococcus comstocki* (Kuw.)), which has recently become a serious pest of apple in sections of Virginia, West Virginia, and Ohio.

During the course of the propagation work at Moorestown, from January 1940 to January 1941, the author had an excellent opportunity to make observations on the biology of this species, a member of a very interesting and little-known group. The genus *Allotropa* contains only three other described North American species, *A. convexifrons* Mues. from the Comstock mealybug, *A. utilis* Mues. from *Phenacoccus aceris* (Sign.), and *A. ashmeadi* Mues. from an undetermined mealybug.

A special attempt was made to determine whether polyembryony occurs in this platygasterid. All drawings and observations were made from fresh material dissected in normal salt solution, without special stains or sectioning. Consequently, the precleavage development of the egg was not followed.

THE ADULT

The adult is shining black and approximately 0.8 mm. long. The sexes can be most readily distinguished by differences in the antennae; the male has long, hirsute, moniliform antennae, whereas the female has shorter, sparsely pubescent, and distinctly clavate antennae. The insects are fairly active at room temperatures, although they rarely attempt flight.

At 80°F. adults live on an average but 3 to 5 days. Even at lower temperatures they seldom live more than 10 days.

Males generally begin emerging first and remain on or near the mummies to assist and mate with the females. The eggs are deposited at random in the host’s body cavity, and oviposition begins immediately if hosts are present. After a brief examination, the
female turns about, thrusts her ovipositor backward into the mealybug, and then remains motionless for 5 to 10 seconds, often being dragged along by the host until oviposition is completed. Under favorable conditions the female parasitizes several hosts in quick succession, thereby depositing most of her eggs in a short time—an obvious necessity in view of her short life span.

Mealybug nymphs of all stages are attacked, although preference appears to be shown for those at least half grown. Small hosts are generally able to become nearly mature before being mumified, although the developmental period is somewhat lengthened.

THE EGG AND THE PARASITE BODY

The ovarian eggs are exceedingly small and numerous; they average 0.056 by 0.010 mm. in size (fig. 1, A). From 332 to 784 eggs per female, with an average of 565, have been disclosed by dissection. The ovarian eggs are nearly all mature when the female emerges, although the ovarioles may produce additional ova as deposition proceeds.

After oviposition at 75°–80° F., the deposited egg remains outwardly unchanged for approximately 24 hours. Within the next 12 hours, however, it commences to shorten and becomes more spherical in outline, until after 36 to 48 hours it is perfectly round and measures about 0.025 mm. in diameter (fig. 1, B). At this stage the central body is well defined, either round or oval, and distinctly granular in appearance. It is obviously identical with the "masse vitelloide" of the monembryonic platygasterid Synopeas rhanis Walk., although the embryonic nuclei are not yet apparent. It is surrounded by a circular clear area which is variable in extent (fig. 1, B and C), and outside of that is a ring of gray, semiopaque material which is probably the trophamnion. Eggs in this stage can be distinguished from the fat cells and other of the host contents only by their typical organization. Owing to the quantity of host tissue encountered, it was impossible to identify eggs prior to this stage after they had become spherical in outline.

Intermixed with these eggs are numerous others that have attained the morula stage (fig. 1, D), together with many in the premorula stage (fig. 1, B). All stages are present approximately 2 days after oviposition, owing to individual differences in rate of development. Since the egg begins to increase in size during the morula stage, it is henceforth known as the parasite body. It now averages 0.036 mm. in diameter, and generally contains five or six embryonic nuclei around the central body. It will be noted that the entire embryonic region is slightly off center. The paranucleus was not observed in the temporary unstained mounts used, although on several occasions faint partial outlines of the paranucleus were noted.

After about 2½ days the parasite body enters the early blastula stage (fig. 1, E) and measures approximately 0.045 mm. The paranucleus is now a distinct round to oval-crescentic body located in the wider portion of the trophamnion. The embryonic nuclei vary in number, and each consists of an inner and an outer layer; this double-bodied effect is also frequently noticeable among late morulae.

Figure 1.—Embryonic development of *Allotropa burrelli*: A, Ovarian egg; B and C, premorulae before appearance of embryonic nuclei; D, typical morula; E, early blastula, showing double-bodied embryonic nuclei and paranucleus; F, later blastula; G, late blastula with three paranuclear masses; H, gastrula, showing proliferated cells; I, later embryo undergoing organ and tissue formation; J, advanced embryo within delicate membrane.

About 3 days from oviposition the typical hollow sphere or blastula becomes apparent, generally with a single, large paranucleus in the periphery (fig. 1, F). The parasite body now averages 0.060 mm. in
diameter, and is readily distinguished from the surrounding host bodies.

Figure 2.—Evidences of polyembryony and the larval morphology of *Allotropa burrelli*: A, Larva ready to emerge from degenerate trophamnion; B, twin early morulae within membrane, probably of host origin; C, twin embryos within a single trophamnion—definite evidence of polyembryony; D, mature larva; E, oral structures of larva; F, enlarged maxillary palpus.

During the fourth day the blastula attains its maximum development, with countless small cells surrounding the still faintly discernible
central body (fig. 1, C). The parasite body has become oval and slightly irregular in outline, averaging 0.090 mm. in greatest diameter, and contains from two to five paranuclear masses of various sizes.

In the late blastula and subsequent stages it becomes increasingly difficult to dissect out the entire parasite body, since the fragile trophamnion ruptures very easily.

Although the eggs are deposited free in the host fluids, during their development most, if not all, of them eventually become associated with the mealybug fat bodies. If the fat bodies are carefully teased out and pressed beneath a cover glass, the immature stages are seen adhering to the surface or partially embedded among the fat cells. As growth proceeds and nutriment is extracted by the various trophamnia, the fat bodies become depleted of their contents until, as the embryos approach maturity, all that remains is a tangled mass of host tissues and tracheae. The earliest stage found definitely associated with the fat body was the blastula.

The tendency toward cyst formation in the Platygasteridae by those species that develop in the coelomic fluids has been well demonstrated by Marchal and Leiby and Hill. Other species deposit their eggs in specific organs, such as the brain, ventral nerve cord, or intestine, where nourishment is readily obtained. Although *Allotropa burrelli* does not actually become encysted, its close relation to the host fat body undoubtedly serves the same purpose.

The gastrula stage (fig. 1, H) appears about the fifth day after oviposition. At first a slight indentation on one side is noted, which as it grows deeper gradually becomes filled with a loose mass of proliferated cells. These cells frequently appear late in the blastula stage, and may be involved in the formation of the delicate membrane which subsequently enfolds the embryo, although occasionally they are found within this membrane. The paranuclear masses vary in number and size, and the parasite body is typically irregular in outline, measuring about 0.180 mm. long.

By the following day germ-layer formation is generally complete and organogeny has commenced (fig. 1, I). The parasite body now averages about 0.31 mm., the trophamnion contains a variable number of paranuclear masses, and a delicate, tight-fitting membrane surrounds the embryo. At high magnifications the cells comprising the embryo can be barely distinguished.

The embryo 7 to 8 days old (fig. 1, J) is considerably advanced internally and has begun to exhibit body segmentation; it is now approximately full-sized, and the trophamnion has also attained its maximum development. Henceforth the paranuclear masses become smaller and less distinct and the trophamnion becomes thinner. At this stage the parasite body measures about 0.43 mm. in length, although it varies greatly in shape. Also at this time the host fat bodies have been practically exhausted of their contents, and are nearly obscured by the gelatinous parasite bodies which adhere to one another in shapeless masses. It is extremely difficult to tease them out entire.

Just before eclosion the embryo straightens out, rupturing the inner membrane and bringing the mandibles into contact with the trophamnion. These movements probably combine to effect hatching.

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6 See footnote 5, p. 160.
The mature embryo, or unhatched larva, now averages 0.54 mm. in length (fig. 2, A), the parasite body having increased approximately 24 times in length. The tracheal system, however, rarely becomes filled with air, and thereby clearly distinguishable, until the trophamnion is broken.

According to all available evidence Allo tropa burrelli normally develops monembryologically. Three twin embryos were found out of the hundreds examined. Two of these pairs were identical early morulae (fig. 2, B), and were complete parasite bodies, each with a separate trophamniotic layer, tightly enclosed by a thin membrane possibly of host origin; they may represent twins from a single egg deposited by accident within a fat cell or other host body, or perhaps be the result of two eggs laid simultaneously therein. The third pair (fig. 2, C) was more advanced, and there is no doubt that embryonic fission had actually occurred, since both embryos were surrounded by a single trophamnion. That this phenomenon is either accidental or of rare occurrence is indicated by the finding of only one such individual.

It is possible that twinning sometimes takes place at a very early stage, as has been shown by Leiby and Hill 8 in Platygaster hiemalis Forbes. This could be demonstrated, however, only through a detailed embryological study involving special techniques of staining and sectioning. The present study has at least shown that monembryony is the rule (additional evidence is presented in a subsequent section), and that polyembryony, if it does occur, is of an extremely simple type.

THE LARVA

Eclosion takes place from 8 to 12 days after oviposition, the average being about 9½ days, at 75°–80° F. After the trophamnion is consumed, the various host tissues and organs are attacked, until within 1 to 3 days the larva has doubled in size, average measurements being 1.10 mm. by 0.50 mm. The host is not killed until its inhabitants are approximately half-grown, although it shows little activity after the parasite larvae emerge.

The larva of Allo tropa burrelli (fig. 2, D) is peculiar in several respects. It possesses but one pair of spiracles, situated on the anterolateral regions of segment 1, and is without a posterior commissure. There are 10 well-defined segments in addition to the head, which bears ventrally an unusual and apparently heretofore undescribed series of oral structures (fig. 2, E). The slender, amber-tipped mandibles merge imperceptibly into the head, the tips measuring 0.063 mm. in length; they are capable of only very feeble movement. Between them lies the slitlike oral aperture, which is distinguishable in life by means of the undulating labrum, while immediately adjacent on each side are the maxillary palpi. Each palpus (fig. 2, F) extends slightly outward from the surface, and is tipped with a microscopic dark seta. A series of minute raised protuberances traverse the posterior margin of the head from the palpi to a point near the spiracles, while the salivary duct opens centrally in the region of the anterior commissure.

The ingested food materials are contained within a peritrophic membrane which forms a complete sac. If the larva is carefully

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8 See footnote 7, p. 163.
dissected, this sac floats free as a single unit; it is resilient and will bear considerable pressure beneath a cover glass before bursting.

That cannibalism occurs in *Allotropa burrelli* was proved by the finding of several young larvae impaled upon the mandibles of older individuals. Most of the body contents had been extracted, leaving the prey a shapeless mass distinguishable only by means of the tiny mandibles. Such examples were frequently encountered, particularly where development was uneven, the "stragglers" being eliminated in this manner. Cannibalism is apparently due to chance encounter rather than to aggressive action on the part of the parasite.

As the larvae become full-fed they lie closely packed together within the host derm. After 2 or 3 days each larva has formed about itself a parchmentlike cell or cocoon, which adheres to neighboring cocoons. The host is now rigidly distended into numerous small brownish "blisters." All attempts to locate the source of this cocoon-making material were unsuccessful; it may issue through the prominent salivary duct.

The brown, watery meconium is expelled approximately 2 days after cocoon formation, and wells up around the posterior half of the larva, where it soon hardens into an opaque layer. Larvae at this stage are identical in every respect, including oral structure, to those newly emerged or in the process of eclosion; therefore, only one instar occurs in *Allotropa burrelli*. Both *Platygaster hiemalis* and *P. ornatus* Kieffer have also been shown to have but one instar.

**THE PUPA**

Following a prepupal period of about 2 days, the pupal stage is begun. At first the eyes and then the rest of the pupa become melanized, and just prior to emergence a coal-black color is assumed. The sexes can be distinguished only by microscopic examination of the antennae. The pupal stage ranges from 11 to 16 days, with an average of about 13 days.

**SEX RATIO AND NUMBER OF PARASITES PER HOST**

From the original shipment from Japan, which consisted entirely of field-collected overwintering mummies, on an average 2.7 females to 1 male were obtained. Only 8.3 percent of the mummies produced an excess of males, while those yielding solely males or females were exceedingly scarce. In breeding experiments at Moorestown there were only twice as many females as males.

The material from Japan yielded 11.6 adult parasites per host, as compared with 5.2 from their progeny reared at Moorestown. The average mortality of mature larvae was also lower for the imported material—1.6 as compared with 4.3. It should be stated, however, that parasites received from Japan had been hand-picked and the imperfect and very small individuals removed. Furthermore, a portion of those propagated at Moorestown had entered the prepupal stage before being stored at 42° F. Since they overwinter as mature larvae, other stages cannot withstand low temperatures. It was also found that mealybugs parasitized in the third instar or in the

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early adult female stage produced the greatest number of parasites. If parasitized prior to the third instar, many hosts become mummified before attaining full growth, while those parasitized as full-fed adult females often succeed in laying eggs and can mature few if any *Alloptropha* larvae. Mealybugs parasitized in the first or second instar will frequently produce solitary mummies. The number of adult parasites issuing per host has ranged from 1 to 22.

Hosts of various instars were subjected to a single oviposition by different mated females and immediately dissected to ascertain the number of eggs laid. The number ranged from 1 to 18 eggs per host, with an average of 8.8, but did not seem to depend on the size of the host. Since the number of eggs deposited is approximately equal to the number of larvae that develop, it is obvious that monembryony is the rule.

**LIFE CYCLE**

At temperatures in the range of 75°–80° F. the life cycle generally runs as follows, although frequent variations are found, particularly in the postembryonic stages: Egg (including parasite body) 8.0 to 12.0 days, averaging 9.5 days; larva 5.5 to 7.5 days, averaging 6.5 days; prepupa 1.5 to 2.5 days, averaging 2.0 days; pupa 11.0 to 16.0 days, averaging 13.0 days. Since considerable growth occurs during embryonic development, the incubation period is proportionally long, while the larval feeding period is comparatively short and confined to a single instar.

Mummies containing mature *Alloptropha* larvae can be stored at low temperatures for many months. The material from Japan was collected in October 1939, and upon its receipt at Moorestown was stored at 42° F. According to samples incubated at frequent intervals, emergence was wholly normal until the following June—after at least 7 months under overwintering conditions.

**SUMMARY**

*Alloptropha burrelli* Mues., a gregarious platygasterine parasite of *Pseudococcus comstocki* (Kuw.), was introduced into the United States from Japan in 1939. Propagation of stocks at the Moorestown, N. J., laboratory for release in infested apple orchards afforded an opportunity for a biological study of this parasite.

The adults are small and short lived, and oviposit at random in the host body cavity. There is no preoviposition period. All nymphal stages of mealybugs are attacked, but a preference is shown for those at least half grown. Dissections have disclosed on an average 565 eggs per female.

Development is normally monembryonic, although twinning may rarely occur. The parasite body increases to approximately 24 times its initial length during incubation, nourishment being elaborated by the trophamnion with its paranuclear masses. As development proceeds the parasite body becomes closely associated with the host fat body.

There is but one instar. A single pair of spiracles is located in segment 1, and there is no posterior commissure. The mouth parts are unusual, and there are 10 body segments. The food materials are
contained within a complete peritrophic sac. Supernumerary larvae and embryos are partially eliminated by cannibalistic attack.

The sex ratio has ranged from 2:1 to 3:1, with females predominating. Laboratory-reared material has produced from 1 to 22 parasites per host, with an average of 5.2. Mealybugs parasitized during the first or second stage frequently produce solitary mummies. An average of 8.8 eggs were deposited per host, regardless of size.

The life cycle ranges from 26 to 38 days, with an average of 31 days at 75°–80° F. Growth is most rapid during embryonic development, and the incubation period is nearly five times as long as the larval feeding period. Overwintering occurs as mature larvae, and mummies in that stage will endure prolonged cold storage.
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Because of the imminent paper shortage, attempts are being made to collect old periodicals for pulp. The Committee hopes to enlist the cooperation of subscribers to this Journal in preventing the sacrifice of this type of material to the pulp demand.

Questions concerning the project or concerning the value of particular periodicals should be directed to Wayne M. Hartwell, Executive Assistant to the Committee on Aid to Libraries in War Areas, Rush Rhees Library, University of Rochester, Rochester, New York.