11. Structure of the Alimentary Canal of the Stick-Insect, Bacillus rossii Fabr.; with a Note on the Parthenogenesis of this Species. By ALFRED E. CAMERON, M.A., B.Sc., Fullerton Scholar of the University of Aberdeen and Research Student in the University of Manchester *

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(Plates XXVIII. – XXX.†)

Introductory.

The following description of Bacillus rossii, a species of the Phasmatidae, is translated from Girard’s ‘Traité Élémentaire d’Entomologie’ (p. 100) (Paris, 1879).

“The genus Bacillus is of special interest, as it includes the only species of Phasmid known to occur in Europe; this is Bacillus rossii Fabr., green, greyish green, or brownish red, with integument either smooth or bearing slight projections, antennae composed of 12 to 23 segments, with a dorsal ridge, with slender legs angularly striated, the anterior pair very long, the two posterior pairs of femora tridentate below. The male is from 45 to 55 mm. long, the female from 58 to 108 mm. The species is native to South Europe and North Africa, and was discovered by Rossi in the gardens and heaths of Tuscany; it is common on the green hedgerows bordering water-filled ditches; it is found also in Dalmatia and in Istria. Near the town of Pola this motionless Phasmid occurs on the Montpellier rock-rose; but so great is its resemblance to the twigs among which it lives that it is very difficult of recognition; its enemies, besides parasitic larvae, are the Praying Mantis and the Green Lizard. A smaller race of Bacillus rossii exists with antennae of 12 segments, thorax bearing minute prominences, the female 54 to 67 mm. in length, of which several authors make a distinct species under the name of B. gallicus Charp., B. granulatus Brunné, found in Greece at the time of the French expedition, also in Andalusia (Rambur), in North Africa, in the South-East and South-West of France, at Nice, at Cannes, at Hyères, near Toulon. In the early spring the insects may be captured by shaking the bushes over an open umbrella, when there fall into it both adults which have hibernated and larvae in various stages of development; the larvae being more delicate than the adults preserve badly when collected, becoming twisted and folded. The species is said to be found in isolated examples as far north as Orleans.

* Communicated by Professor Sydney J. Hicksok, F.R.S., F.Z.S.
† For explanation of the Plates see p. 182.
ALIMENTARY CANAL OF BACILLUS ROSSII.
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the Old World, and it has a wide distribution, occurring in Europe, Africa, East Indies, Ceylon, Java, China, Sandwich Islands, Australia, Island of Hanoa, and New Zealand."

In the course of the present year several English collectors have had in their possession specimens which were observed to deposit their ova during the months of February, March, and April, and the hatching of the ova began in the latter part of June. It is highly probable that this insect, alien to the British fauna, made its entrance into this country along with fruit-cargoes and nursery-stock imported from France. There is not much chance of its becoming established here since, being accustomed to mild temperatures, it fares rather badly under the changeable conditions of the English climate. In captivity they require close attention; but by supplying them regularly with fresh food-plants and by keeping the temperature of their surroundings at about average house-temperature they appear to thrive. Under these conditions they are quite healthy, and the mortality is very low.

Note on Parthenogenesis.

A very curious phenomenon in connection with the reproduction of Bacillus rossii may be worthy of note. Although my specimens were in the third generation reckoning from the first generation in captivity, no male had been observed, and perhaps parthenogenesis had been the normal method of reproduction previous to this, as my observations were necessarily limited by the fact that I had no record of the generations preceding the first one in captivity. Von Baehr (1907) records that in 1903 he received specimens of B. rossii which belonged at least to the seventh parthenogenetic generation, being descendants of a half-grown female captured in Dalmatia in 1896. But the latter, he says, may itself have arisen from an ovum parthenogenetically produced, so that in all probability it was not the first in the ancestral line to produce ova which had not been fertilised by the sperm.

These facts seem to lend support to the supposition that the female of B. rossii can dispense with the male altogether and that virgin, rather than sexual reproduction is the normal method adopted by this insect of perpetuating its race. We cannot state with any degree of confidence why the insect has betaken itself to the parthenogenetic production of eggs, but that advantages accrue we are tolerably certain. In cases where, owing to some cause or other, there is a scarcity of males, the method would be a decided acquisition, since the great majority of the more prevalent females would stand a very poor chance of ever meeting a male and of the consequent enjoyment of sexual intercourse.

I think that it is open to make the hypothesis that both sexes of B. rossii originally existed in equal numbers. Owing to some cause with which we are not acquainted, the males began to
diminish so that the dominant female, in order to safeguard the species against utter extirpation, began to reproduce parthenogenetically. We must understand that the process has been a very gradual one, proceeding slowly throughout several centuries, the male finally becoming almost extinct.

Another interesting question intimately connected with the subject of parthenogenesis may be asked. Why does the female produce ova from which only females arise? While I offer no suggestion, I may be permitted to allude to the same phenomenon which occurs regularly in many of the Cynipidae or Gall-flies. The male of *Cynips kollari*, the maker of the marble-gall of the oak, has never been observed, although many entomologists have given this species their close attention, and it is now generally believed that it does not exist, but that parthenogenetic reproduction is the only method of preserving the species.

The following is quoted from Adler and Straton's 'Alternating Generations' (Oxford, 1894).

"It would appear that in *Cynips kollari* the sexual generation is wholly subordinated to the asexual, and in *Rhodites rosea*, which forms the pretty Bedeguar galls on the rose-tree, the process is still going on, and the males are becoming functionless and extinct. ... It is difficult to believe that the agamous (or asexual) can be the primitive form; or that the perfectly formed sexual organs could have been evolved unless the sexual had been the earlier generation."

Alimentary Canal.

While at the Royal College of Science, London, in the beginning of 1911, it was suggested to me that the alimentary canal of *Bacillus rossii* would repay careful observation. The material at hand I subsequently worked up in the Zoological Department of Manchester University, and I here take the opportunity of expressing my indebtedness to Professor Hickson as well as to Mr. Mangan for many timely hints.

In the Orthoptera viewed as a whole the alimentary canal shows a very uniform structure; but in the various families there are many secondary differences, sometimes even in the same family, necessitating special description. The gizzard is important in the Orthoptera, and there are diverse degrees of complication in its chitinous armour. The intestinal ceca vary greatly in number, there being eight in Mantidae and Blattidae, six in Acridiidae, and one pair of lateral ceca in Locustidae and Gryllidae. The diverse variations of structure in the gizzard, its different degrees of complexity added especially to the presence or absence of intestinal ceca, suggested to Bordini (1897) a method of dividing the Orthoptera into two large groups:

1. The Acolotasia, or Orthoptera without intestinal ceca;
2. The Colotasia, or Orthoptera with intestinal ceca more or less numerous.
The Malpighian tubes in all Orthoptera except the Forficulidae are very numerous, and are generally grouped in six bundles opening at the summit of six tubercles, as in the Locustidae and Blattidae. In all the Gryllidae, on the contrary, the Malpighian tubes are arranged in a single bundle opening into the dilated extremity of an unpaired excretory canal. Very characteristic is the presence of a "ciliated border" (un revêtement cilié) projecting from the cells of the mid-intestine and lateral appendages.

The alimentary canal of *B. rossii* is divided into three parts, as in all arthropods.

1. Fore-gut, ectodermic, corresponding to the stomodæum, and comprising the mouth, pharynx, oesophagus, and crop (Pl. XXVIII. fig. 1); the gizzard is absent.

2. Mid-gut, endodermic, corresponding to the mesenteron, beginning posterior to the crop and ending at the insertion of the Malpighian tubes. The lateral ceca, generally developed from the anterior part of the mid-gut, are rudimentary in *B. rossii* (fig. 1).

3. Hind-gut, ectodermic, corresponding to the proctodæum, beginning at the insertion of the Malpighian tubes and including small intestine and rectum (fig. 1).

In many respects the alimentary canal is peculiar, and the main features which contribute to its uniqueness may be tabulated as follows:

1. The rectilineal shape of the gut, there being no convolutions of the posterior region (fig. 1).

2. The complete absence of the gizzard.

3. The rudimentary nature of the mid-gut digestive ceca (figs. 1 & 3, C).

4. The presence of numerous peculiar conical tubular organs on the posterior position of the mid-gut (fig. 1, Ta.).

In preparing sections for histological examination of the gut various stains were employed. Grenacher's haematoxylin was especially good in the differentiation of chitin, while Heidenhain's iron-haematoxylin proved very effective where epithelium was concerned. Professor Hickson's brazilin stain and borax carmine were also used to advantage. To get the best results the gut required rather careful treatment, and in the matter of a fixing agent I found that Schaudinn's fluid was all that could be desired.

It is generally accepted that the mid-gut of insects is endodermic in its origin, but in the case of *B. rossii* Heymons (1897) demonstrated that it was really ectodermic, being developed from two epithelial outgrowths of the stomodæum and proctodæum which surround the yolk and become united. This manner of formation, he maintains, may be found to hold good for all Phasmodæae.
The fore-gut up to and including the crop is of rather simple structure. As a rule the histological structure of the insect alimentary canal is always the same: on a layer composed of muscular and connective tissue there rests an epithelium which secretes a strong chitinous lining. This cuticle is raised into straight longitudinal ridges which bear numerous minute horny denticleations. The pharynx of *B. rossii* (fig. 1, Ph.) is very short and is lodged in the posterior cephalic region, the oesophagus (fig. 1, OE.) occupying the elongated prothorax and passing insensibly into the somewhat dilated crop (fig. 1, Cr.) in the region of the mesothorax. Lastly, the crop joins the mid-gut (fig. 1, Gm.) in the region of the metathorax, and, indeed, the internal wall of the crop is telescoped into the cavity of the mid-gut as a cone-shaped prolongation (Rüssel). But in addition to what may be called the primary direct extension of the crop (Pl. XXIX. fig. 5, Ov₁ and Ov₂a) there is also a secondary indirect extension (fig. 5, Ov₂ and Ov₂a). The chitinogenous epithelial cells of the wall of the crop extend backward into the mid-gut for a short distance as far as the point A denoted in the figure. They then become folded back on themselves up to the point B, and turning once more form the long dorsal prolongation which reaches a comparatively long way into the mid-gut. At C the cells are again reflected, and finally at D join with the larger epithelial cells of the mid-gut. The chitinous cuticle lining the prolongations is continuous with that of the crop. From fig. 5 it will be observed that the extensions are not symmetrical but are much more pronounced dorsally than ventrally. This unsymmetrical arrangement is known to occur only in the few Phasmids in which the alimentary canal has been investigated, and the exact reason of the greater development of the dorsal lamina is not known. In the larvae of *Chironomus* the oesophageal telescoping is uniform and symmetrical, and I believe that this is the case with the majority of insects where the telescoping occurs.

Heymons (1897) gives it as his opinion that the elongate dorsal lamina (Verschlussklappe) functions as a closing-valve, preventing the back-flow of digested food from the mid- to the fore-gut. But Sinéty (1901) does not agree with this interpretation, as he is convinced that if the direction of the food-current were to be reversed this flap would be overcome by the pressure. The bundles of circular muscle surrounding the anterior part of the mid-gut would be quite effective in checking the reversed food-current if any such occurred.

The mid-gut of *B. rossii* is divided into two distinct parts, of which the anterior is characterised by very prominent transverse folds (Pl. XXVIII. fig. 1, Gm₁; fig. 3, Gm₂; Pl. XXIX. fig. 5); while the posterior (fig. 1, Gm₃), besides being narrower, is easily distinguished by the presence on its external walls of numerous (about 50) conical, tubular organs (fig. 1, Ta.).

In all Orthoptera as before stated, except the Phasmidæ, the surface of the mid-intestine is enlarged by diverticula of various

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