HOW MEGARHYSSA DEPOSITS HER EGGS

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Considering the conspicuous size and form of *Megarhyssa lunator*,[1] it is rather strange that the study of this insect has been neglected. It is true that in 1888 C. V. Riley published in "Insect Life" a very full and interesting account of the biology of *Megarhyssa* (then called *Thalessa*). But Riley's description of the drilling process which accompanies oviposition, although detailed, is superficial; it fails even to mention the action of the plates to which the drilling organ is attached. Mention is made of the "powerful muscles" of the abdomen without giving any evidence that the author was aware of their relationship to the ovipositor.

Henneguy (p. 283) states that: "Les Ephialtes, les Rhyssa, deposent leurs œufs dans les larves des Longicornes qui vivent dans des galeries situees souvent a grande prefondeur a l'interieur du bois." But this tells us nothing of the mechanisms involved. The nearest approach to a solution is found in a paper by Baumann (1924). This, although it deals with an European species, *Thalessa leucographa,* does give a rather careful description of the "Plattenapparates." Through dissection Baumann arrived at the same conclusion I reached through observation of the living insect, namely that: "Den gleichzeitig mit der dorsalen Membran kommt auch die ventral Blasmembran sur Entfaltung so dasz sich der Blase aus einem auszeren dorsalen und einem inneren ventralen Anteil zusammensetzt." The musculature of the organs was not described.

Original Studies

The abdomen of the adult female *Megarhyssa* consists of eight externally visible segments and the propodeum, which, as far

[1] *Megarhyssa* obviously comes from the Greek *megas,* large and *hrysos,* wrinkle. Lunator means "moonlike"; so the English equivalent of the name is "lunar large-wrinkle." This is mentioned because it doubtless refers to the stretching of membranes to be described hereafter.

as this study is concerned, may be ignored. The penultimate segment extends forward on either side in the form of a narrow plate ending just beneath the posterior margin of the sixth segment (Fig. 1). The terminal segment bears corresponding

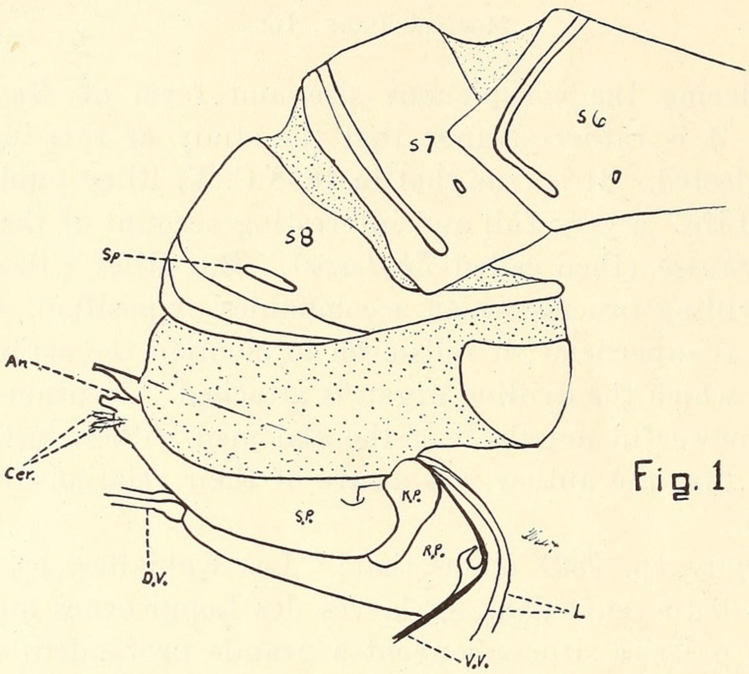

Fig. 1

Figure 1. Right lateral aspect of distal part of abdomen with drilling organ extruded.
An., anus
Cer., cerci
D.V., dorsal valves
V.V., ventral valves
L., lancets
R.P., "runner" plate
K.P., "kidney" plate
S.P., "sled" plate
Sp., spiracle
S6, S7, S8, abdominal segments

lateral extensions which are even larger; suggesting in outline the runner of an old-fashioned "cutter." For this reason I have designated each of these as a "sled plate." Each terminates anteriorly in a horny point which articulates with the plate next anterior. The latter, which excepting for its contiguity with surrounding membranes is free, is more or less reniform. Its long axis is vertical and its convex margin anterior. At its base a hinge joint attaches it to a third and more anterior plate which is runner-shaped, with its recurved anterior in the body cavity. From below this "runner" plate is visible to its posterior angle, at which point the corresponding *dorsal valve* is attached. Anterior to the runner plate is a small plate which, with the corresponding plate on the opposite side of the insect, covers the base of the drilling organ. The relationship of these various parts are best shown in Figure 2.

The drill proper is composed of three parts. Of these the most conspicuous really consists of the two fused *ventral valves.*

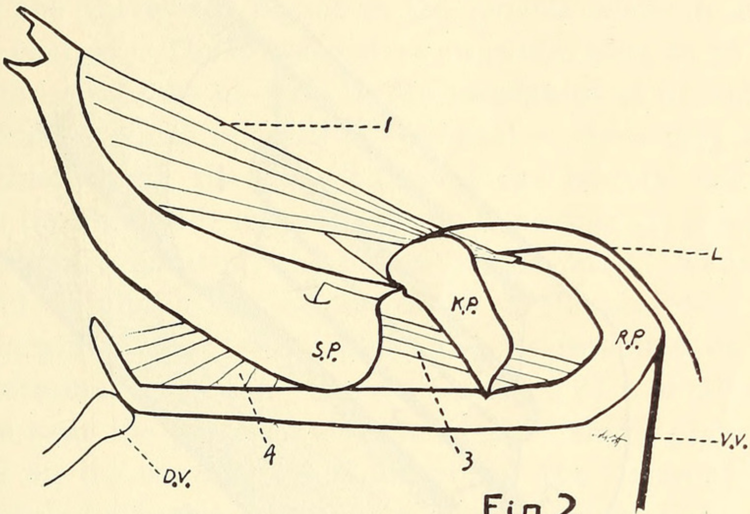

Fig. 2

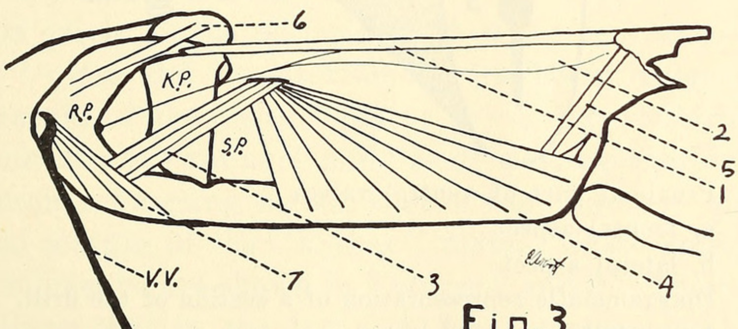

Fig. 3

Figure 2. Right lateral aspect of drilling organs removed from insect. For labels see Figures 1 and 3.

Figure 3. Ental aspect of drilling organs removed from insect.
1, 2, 3, and 6, extensor muscles of lancet
4, retractor muscle of lancet
5, posterior dorso-ventral muscle
7, retractor of ventral valves

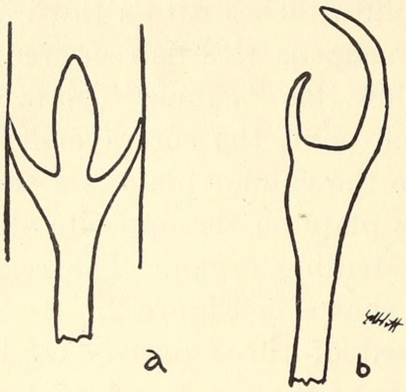

Fig. 4

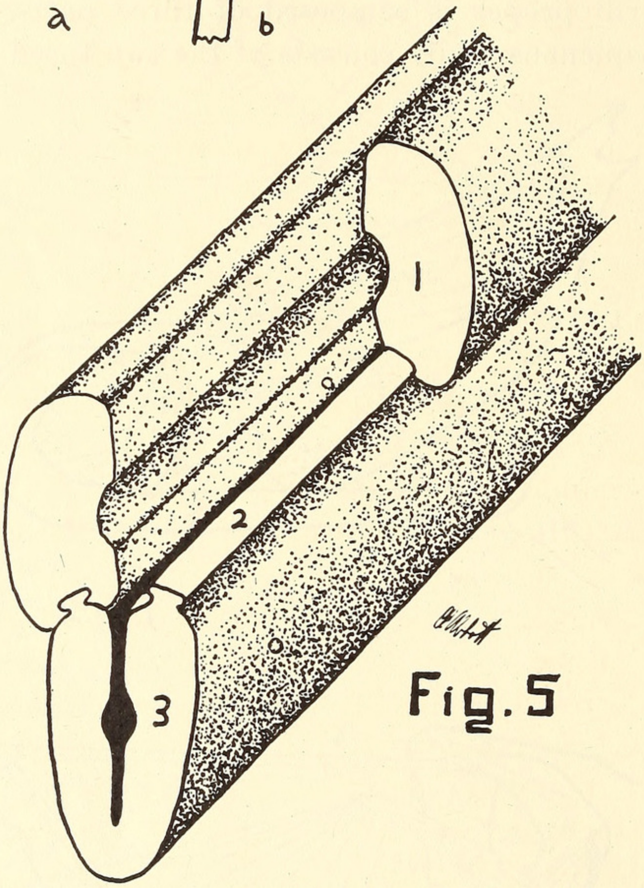

Fig. 5

Figure 4. Proximal part of ventral valves
a, frontal aspect
b, lateral aspect

Figure 5. Diagrammatic representation of a section of the drill.
1, partially retracted lancet
2, T-ridge of ventral valve, upon which lancet rides
3, ventral valve

It is attached to the anterior angle of the "runner" plates. At this point it is trident in form; each lateral extension articulating with the corresponding plate, while the median tine curves inward between them, its convex posterior surface attached by muscles with the basal margins of the plates (Fig. 4). The remaining parts of the drill are the two *lancets,* each of which is attached to the dorsal margin of its corresponding ''kidney'' plate.

The lancets are so closely adherent to the ventral valves that the two are separated with difficulty. Riley was well aware of the reason for this: that each ventral valve is equipped with a T-shaped ridge which fits a corresponding cavity running the length of the lancet (Fig. 5). Riley's one mistake was in assuming that the valves are *dorsal* to the lancets when in actuality they are *ventral.* The dorsal valves or *guides* seem to be sensory in function, and take no part in the mechanics of drilling.

The muscles which operate the ovipositor, since they are concerned chiefly with the functioning of the lancets, are paired. Those on the right side may be seen by removing the penultimate segments and separating the halves of the body. They are as follows (1) a muscle having its origin on the posterior and interior margin of the ''sled'' plate and its insertion on the recurved termination of the ''runner'' plate; (2) a muscle having its origin near the posterior margin of the ''sled'' plate and its insertion on the concave inner margin of the ''runner'' plate; (3) a muscle having its origin on a sloping ridge at the anterior of the ''runner'' plate and its insertion on the ridge near and parallel to the dorsal margin of the ''sled'' plate; (4) a muscle having its origin on the posterior half of the ventral part of the ''runner'' plate and its insertion on the horny ridge near the dorsal margin of the ''sled'' plate; (5) a dorso-ventral muscle which connects the ''runner'' and ''sled'' plates posteriorly; (6) a small muscle connecting the anterior of the ''runner'' plate with the dorsal margin of the ''kidney'' plate. These muscles, with their attachments, are shown in Figures 2 and 3. Their enumeration follows that in the text. A few intersegmental muscles connect the penultimate with the terminal segment.

Observations made on living insects indicate that the ''sled'' and ''runner'' plates describe a rhythmic, lateral motion which rotates the ''kidney'' plate forward and back. The process can be simulated in the dead insect under the binocular magnifier, when it becomes evident that each lancet, since it is attached to the dorsal margin of its corresponding "kidney" plate, is alternately extended and retracted by this action (see Figures 2 and 3). The action of the muscles is as follows: 1, 2, and 3, by drawing the "sled" and "runner" plates together, rotate the "kidney" plate and thus extend the lancet; muscle 6 aids in the process by drawing the "kidney" plate forward; muscle 4, by drawing the "sled" plate *back*, has the opposite effect. The function of muscle 5 seems to be to keep the two larger plates from separating posteriorly. The paired muscles (Figures 2 and 3) attached to the mid-tine of the ventral valves appear to throw the latter forward, thus aiding in the "looping" of the ovipositor.

Since the "runner" plates are attached to each other anteriorly through their articulations with the ventral valves, and since the "sled" plates are merely extensions of the terminal segment, it follows that the degree of extension of either lancet can at no time be very great. Moreover, the action of the plates gives a partial rotation to the whole ovipositor; this, however, may be an advantage.

When about to deposit an egg, the insect elevates her abdomen, looping the ovipositor within the intersegmental membranes, while the two terminal segments are folded against the belly of the abdomen. The plates of the drilling mechanism are forced back into the membranes in an *inverted* position. This inversion is of no consequence to the drilling action, which depends upon the interrelationship of the drill plates and not upon their position with respect to the body of the insect. The exposed portion of the ovipositor, with its distal end directed against the tree, lies throughout most of its length upon the ventral surface of the abdomen. Drilling begins with the alternate action of the lancets. As the instrument penetrates the tree its parts are slowly withdrawn from the body membranes, the drill plates are everted, and the abdomen assumes the position of an inverted U. For a few seconds action is suspended. Then the ovipositor is withdrawn; the actions described above being duplicated in reverse order.

During the "looping" of the ovipositor the ventral membrane is forced in against the dorsal membrane, which in turn is extended dorsally until both membranes become stretched and transparent.

Riley's account is none too clear concerning the way in which the egg passes through the ovipositor. It is probable that the ovum passes through the tube formed by the lancets. Three facts seem to indicate that such is the case: (1) the vagina opens between the lancets, (2) the action of these parts would tend to work the egg through the ovipositor, and (3) eggs are sometimes accidentally extruded between the lancets.

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