

## Comparative Notes on Adaptations for Viviparity Shown by *Dyscritomyia* (Calliphoridae, Diptera) of Hawaii, and *Glossina* (Glossinidae, Diptera)

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Bequaert (1954), discussing viviparity in higher flies, mentioned the observation by D.E. Hardy that larvae of an advanced stage were produced by females of certain Calliphoridae native to Hawaii. Since viviparity has evolved several times in unrelated stocks of higher flies, it is possible, by using comparative methods, to infer which features of these flies have to do with viviparity, and which features derive more or less unaltered from the respective ancestral oviparous stocks.

Thanks to the generous co-operation of Dr. D.E. Hardy, the opportunity arose to examine living specimens of viviparous Hawaiian calliphorids, and the present paper records certain observations made on these specimens.

### MATERIALS AND METHODS

The following notes and drawings are based on specimens sent from Hawaii; it is clear that various species are involved, even in samples taken from a single locality on a single date. It is therefore necessary to treat these notes as applying to unidentified species of Hawaiian native calliphorids.

Flies were dissected in saline in the fresh state, and also examined after maceration in 5% potassium hydroxide. For the naming of parts the usage of Graham-Smith (1939) has been followed for paraphallus, hypophallus, parameres, spine and anal tergum. The term phallosome refers to the male intromittent organ bearing the male gonopore, without regard to homologies.

*External male genitalia* (Fig. 1): The elements usually to be found in calliphorids are present. The paraphalli do not have prominent slender apices. The hypophallus is serrated. The male orifice appears to be at the end of the phallosome. The phallosome is flanked by a pair of large posterior parameres. Anterior parameres are short. The spine at the base of the phallosome is about as long as the posterior paramere. The anal tergum has a pair of prominent flaps at the ventral-lateral margins: there is no homologue to this in *Calliphora* or *Lucilia*, but comparable appendages are to be seen for example in *Xenocalliphora* (*Ptilonesia*) *auronotata* (Macquart) (Kurahashi, 1971, see his Figs. 3 and 4). It is possible that these flaps are a specialization of the male genitalia to cope with the lack

of long extrusible female ovipositor to grip during mating, but in the absence of direct observations on the mating of these flies, this can only be mentioned as a possibility.

*Internal male organs* (Figs. 1, 2 and 3): The internal reproductive system of the male is that of a main-line calliphorid. The two testes are ovoid, slightly longer than wide, covered with pale orange pigment. The pigment disappears when the specimen is stored in 70% alcohol. The vasa deferentia are narrow and colourless, joining with the anterior end of the ejaculatory duct. Attached to the same junction are the two colourless accessory glands. These are sausage shaped, not as long as the vasa, and filled with an almost clear colourless secretion. The accessory glands are slightly deflected to the left hand side of the animal, i.e., they are not symmetrically disposed one to the left, one to the right (Fig. 2). The point of union of the vasa lies immediately beneath the rectum. The ejaculatory duct passes posteriorly, looping left to right over the rectum as it does so, to reach the ejaculatory bulb or pump which lies just to the

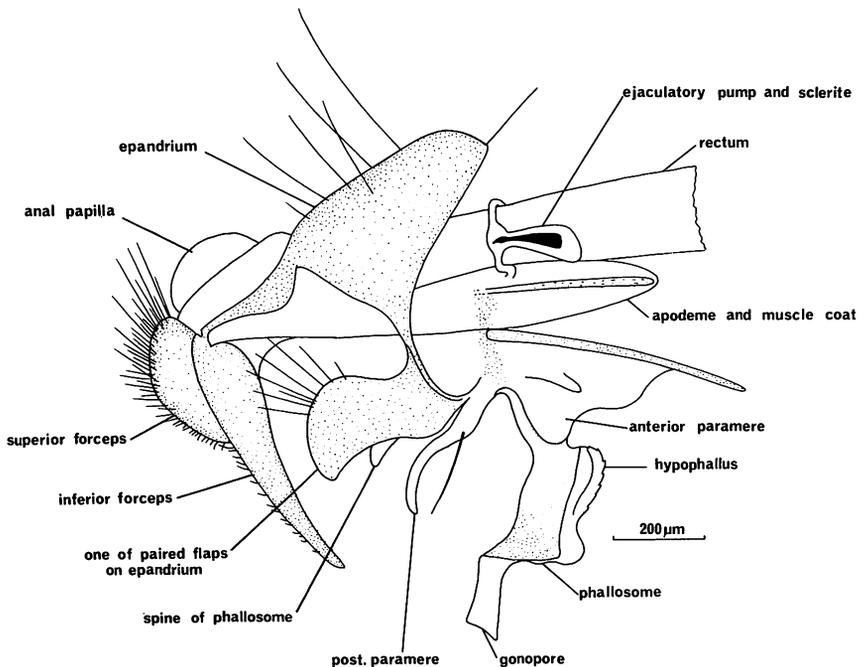


FIG. 1. Lateral view of male genitalia and ejaculatory pump.

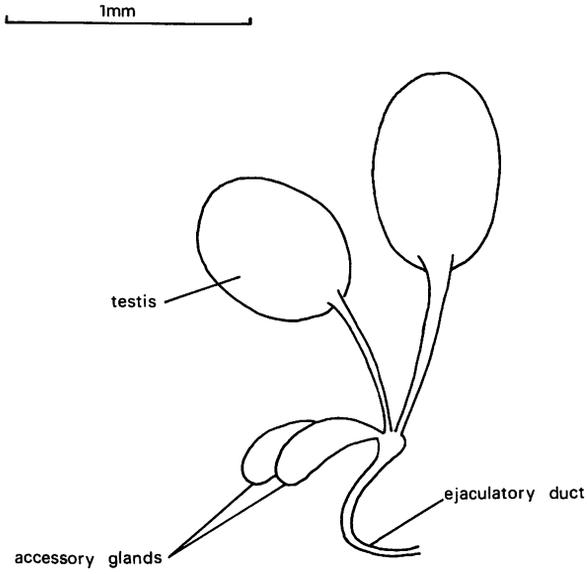


FIG. 2. Rectum and male reproductive system.

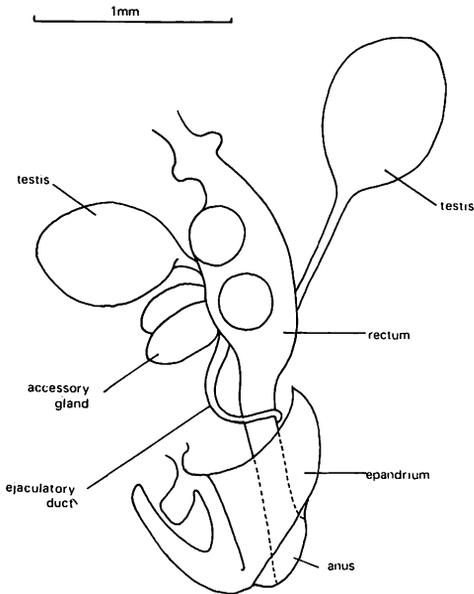


FIG. 3. Male reproductive system.

right of the rectum. The final section of the ejaculatory duct from the pump to the phallosome brings the ejaculatory duct into the mid-line again. The duct therefore follows a 360° clockwise path around the rectum (one imagines the fly being viewed from behind as this course of the ejaculatory duct is followed). The genitalia are therefore of the circumversion type, as is normal for Calliphoridae.

*Female reproductive system:* The female reproductive system is highly adapted for macrolarviparity, but not apparently for adenotrophic viviparity. The ovaries are reduced to two ovarioles in each ovary (Fig. 4). The tracheal supply to the ovaries is very rich (Fig. 5). The ovaries develop a single very large ovum at a time. An ovum measured almost 2.0 mm, and was far from mature at that stage (Fig. 6). In another fly, a recently ovulated egg measured 2.4 x 1.4 x 1.2 mm. (Fig. 7). A virgin female on dissection showed that one of the ovarioles in the left ovary had progressed furthest in oocyte growth, and this ovary presumably would have delivered the first egg to the uterus (Fig. 5). It is not known if this is generally true for these calliphorids: however in *Glossina* it is known that the right ovary normally develops the first ovum (Mellanby H, 1937). The common oviduct leads to a very large "uterus." This is also richly supplied with tracheae. There are three black spermathecae of normal appearance (*Glossina* has two only). There is a pair of accessory glands which are simple sausage-shaped organs, not branched and not greatly different in appearance from the corresponding organs in *Lucilia* and *Calliphora*. These glands are filled with a clear colorless fluid. There is nothing to suggest that these glands have any nutritive function. The uterus leads to the vulva through a greatly abbreviated larvipositor (Fig. 8). There are only seven sternites before the vulva, unlike *Calliphora* and *Lucilia* in which there are eight.

*The Larva:* The observations on larvae have been sparse. The following features of the recently deposited larva are worth mentioning however.

1. The mouthparts of the larva are well developed.
2. Anterior, as well as posterior, spiracles are present.
3. The posterior end of the larva does not show any supernumerary stigmata. The posterior spiracles comprise two slits each: the larva is presumably second instar.
4. A living expelled larva measured about 4.0 mm. long by 1.5 mm. wide.

However, these observations must be treated with reserve. In no case is the whole life history of a native Hawaiian calliphorid known. It is just possible that these larvae which have been observed in specimen tubes have been prematurely aborted, and that in nature a further instar might persist in the uterus of the female, though this is thought to be quite unlikely.

Since there is no evidence of any feeding by the larva within the

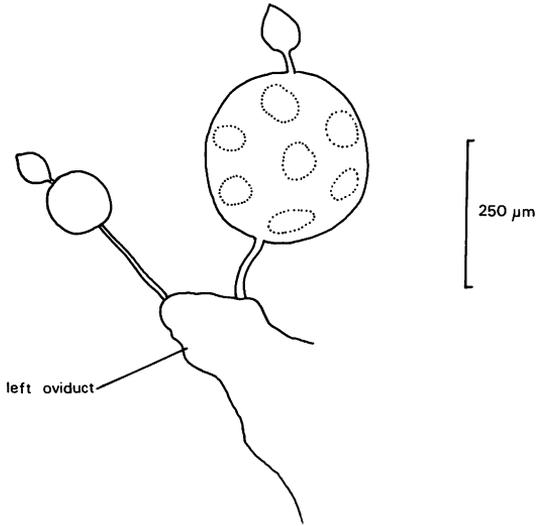


FIG. 4. The two ovarioles dissected from an ovary of a virgin female Hawaiian calliphorid.

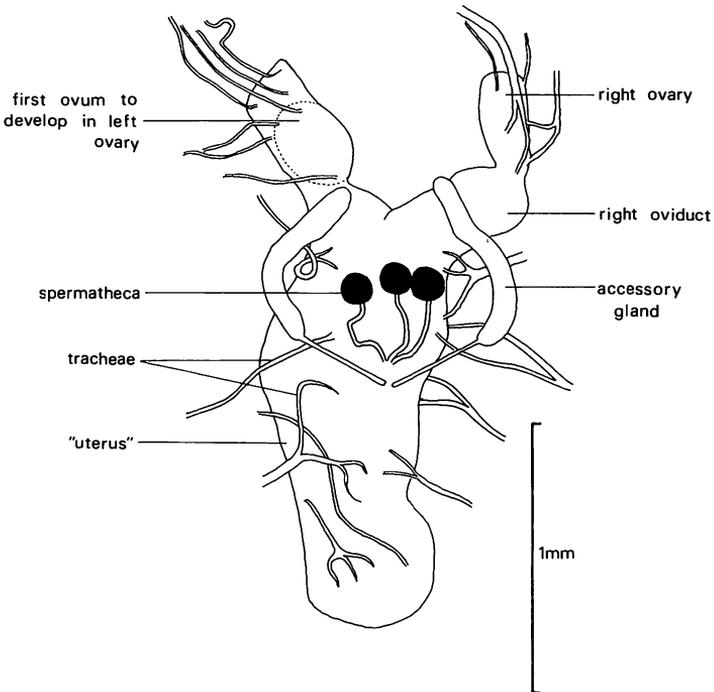


FIG. 5. Virgin female reproductive system (not all the tracheal system is shown).

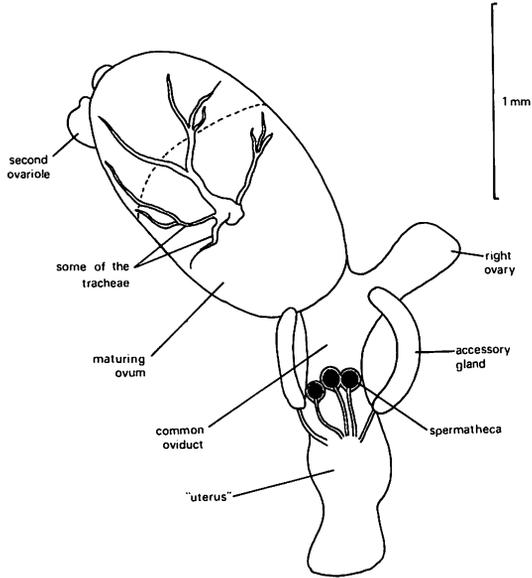


FIG. 6. Female reproductive system, showing a large but immature egg in the left ovary.

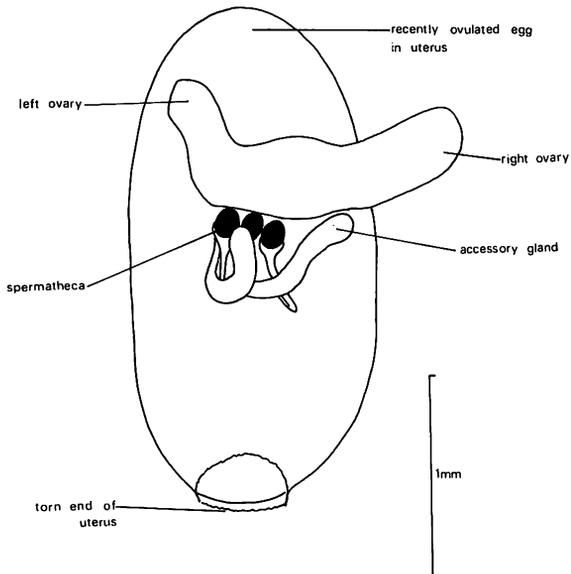


FIG. 7. Female reproductive system, showing a recently ovulated egg in the uterus.

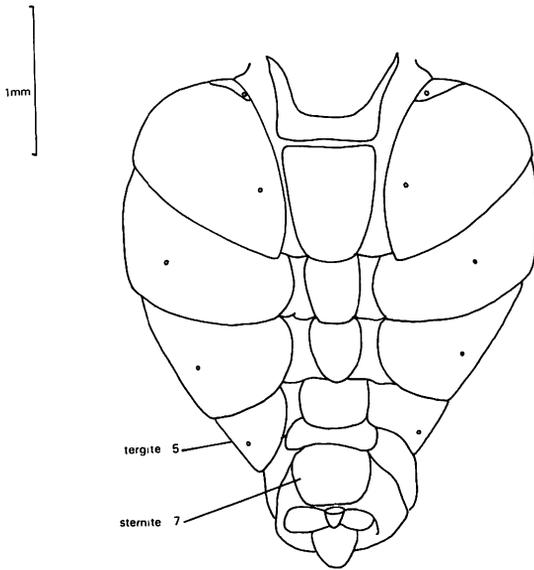


FIG. 8. Female abdomen, ventral view.

uterus, the larva presumably has a free living stage during which it attains its final size before pupation. It is not known if this free living stage is saprophytic or parasitic. A living larva did not feed on fresh liver it was offered, but another did take in a small quantity of defibrinated horse blood. This latter larva though dead on examination was found to have moulted to the third instar. The stage resembles a typical calliphorid third instar larva, without special resemblances to the larva of *Glossina*. Observations of this missing section of the life history might be of considerable interest, and perhaps indicate the selective pressures which have been operating on these flies leading to the adoption of macrolarviparity. Since the egg of the Hawaiian calliphorids is very large and the female accessory glands are unmodified, there are no grounds for supposing that any real intra-uterine growth takes place. The expelled larvae were certainly larger than the ovulated egg previously mentioned, but the difference could be, and probably was, due to the greater water content of the larvae.

#### DISCUSSION

Larviparity has evolved independently on many occasions within the higher Diptera. The best studied case is that of the tsetse fly (*Glossina*), the larva of which does not feed on any external substrate, but is nurtured to maturity within the body of the mother fly. The fully grown

larva is expelled from the female and pupates in loose soil within about an hour. The female internal anatomy is highly modified to support the growing larva. Only one ovum at a time is ovulated, each ovary is reduced to two ovarioles (Saunders, 1960) and the female accessory glands have become nutritive organs serving the needs of the larva. Fossil specimens of this genus are known from the Florissant shales of Colorado (Oligocene) (Cockerell, 1907) and one is fully justified in assuming that these flies must have had a life-history similar to that of extant forms. Macrolarviparity in this genus must therefore have been established at least as long ago as the Oligocene (Pollock, 1971). Externally the narrow ovipositor characteristic of most oviparous higher flies has become suppressed in *Glossina*, to enable the much larger larvae to escape from the female. In turn, the male genitalia have become highly modified to maintain their grip on the truncated female abdomen.

The main reason why this study was undertaken was to see what parallels of morphology were shown by the macrolarviparous calliphorid *Dyscritomyia*, and the quite unrelated tsetse flies. The similarities between the two groups of flies are as follows:

1. The ovaries in both are reduced to two ovarioles per ovary.
2. The large eggs are produced one at a time.
3. The posterior part of the female tract is modified as a uterus.
4. A very extensible ovipositor is lacking.

The differences are as follows:

1. The female accessory glands of *Glossina* are highly modified as nutritive organs; the corresponding organs of the Hawaiian calliphorids appear to be unspecialized.
2. The larva as deposited by *Glossina* is mature, and pupates almost at once; the larva deposited by these calliphorids appears to be equipped for an independent existence of longer duration, though what form this existence takes has yet to be discovered. The third instar larval morphology of the Hawaiian calliphorid resembles that of a normal calliphorid, and does not have posterior bolster-like swellings bearing supernumerary stigmata after the fashion of *Glossina* larvae.
3. The external genitalia of the male are relatively unmodified from the usual calliphorid type, with the exception of the lateral-ventral flaps of the anal tergum. No convergent resemblances to *Glossina* are to be seen.
4. The internal male reproductive system is no different from that of a main-line calliphorid; again there is no convergence towards *Glossina*.

Consequently, the adoption of macrolarviparity by these Hawaiian calliphorids can be seen as a relatively very recent phenomenon, and

while it has affected the female reproductive system very greatly, the male structure has been modified hardly at all. Indeed, although the larviparity of *Sarcophaga* is of a less extreme type than that of the calliphorids described here (several larvae at a time are produced by *Sarcophaga* females), the male genitalia have been much more profoundly modified as a result (Pollock, 1972) than have the genitalia of the Hawaiian calliphorids. It is not clear to what extent this dissimilarity of modifications of the male can be attributed to (a) the length of time for which the respective flies have reproduced viviparously (sarcophagids have surely done so for much longer than the Hawaiian calliphorids), or to (b) the respective ecological circumstances and differing opportunities for competition between males for mating partners.

It is to be hoped that the biology of these interesting macro-larviparous Hawaiian calliphorids will be investigated in more detail by those workers in a position to do so: it would be valuable to have information about the mating stance and about the ecology of the final larval stage. It is the larval ecology which probably holds the key to our understanding of what selective pressures have been at work promoting the rapid and profound modification to the female reproductive system seen in *Dyscritomyia*.

#### ACKNOWLEDGEMENTS

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