On the male, in addition to the hypopygium, there are hairy plates just in front of it called the hectors. The hypopygium and the hectors are used by the male to hold onto the end of the female's abdomen during mating. When mating starts, the male unfolds the hypopygium revealing the superior and inferior claspers and the penis (or aedeagus). The hypopygium can be unfolded and examined under a dissecting microscope, especially for looking at the superior claspers, in the way shown in **Figure 1.11**.

1.3. INTERNAL ANATOMY

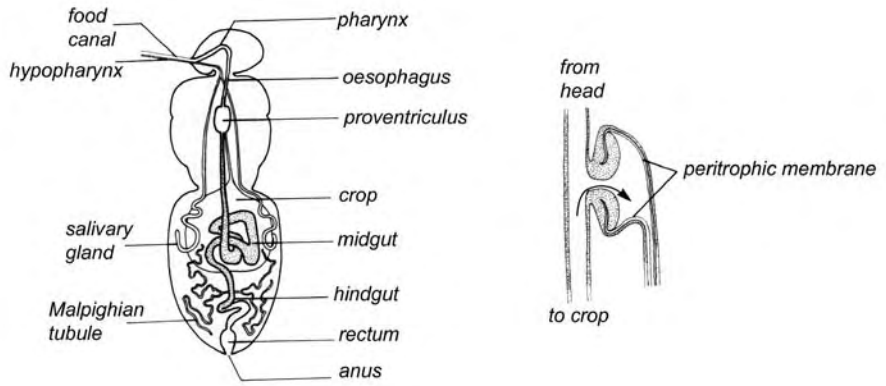
The tsetse fly has two salivary glands that stretch through from the abdomen, through the thorax and head to the proboscis into which they open into the hypopharynx (**Figure 1.13**). The salivary glands produce saliva containing an anticoagulant, preventing the blood of the host from clotting whilst the fly feeds. The glands are very transparent small tubes that can be difficult to see without a microscope but they may be important to recognize as they are the site for development of *Trypanosoma brucei*-complex trypanosomes, which can infect livestock and cause sleeping sickness in humans.

1.3.1. Organs Associated with Feeding and Digestion

When a tsetse fly feeds, it first disengages the proboscis from the maxillary palps and lowers it to the hosts' skin. Using the labellar teeth it then penetrates the skin and cuts small blood capillaries. Blood from these capillaries forms a small pool under the skin and is sucked up through the proboscis by means of a muscular pump in the pharynx. The blood is mixed with saliva from the hypopharynx and then passes down the oesophagus into the muscular proventriculus. Most of the blood continues on from the proventriculus into the crop where it is stored temporarily before being passed back up into the proventriculus

FIGURE 1.13

(left) Digestive system of the tsetse fly, and (right) the internal structure of the proventriculus with arrow showing the route that the blood makes to get from the crop to the midgut



Source: FAO 1982a

and then to the midgut, where digestion takes place. The crop is a thin, membranous sac, capable of expanding to fill the abdomen with a blood meal. A thin sleeve of chitin, called the peritrophic membrane is formed by the proventriculus and encloses the blood meal as it passes from the proventriculus to the midgut. The peritrophic membrane grows continually and is a significant feature in regard to the development of *T. brucei*-complex trypanosomes. In the midgut, water is rapidly removed from the blood meal so that the fly is able to fly normally again. Digested blood, now dark brown, passes into the hindgut and the waste faeces pass out of the rectum through the anus.

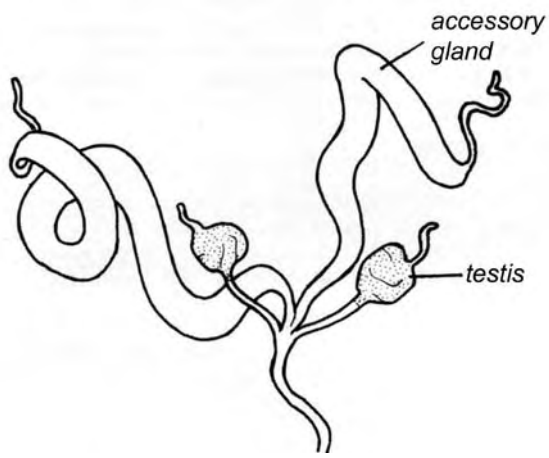
Trypanosomes develop in the proboscis, midgut and salivary glands and therefore it is important to recognize these structures for dissection and examination to determine trypanosome infection rates of tsetse.

1.3.2. Reproductive System

The unusual (for insects) life cycle of the tsetse fly is a very significant feature with regards to control or eradication of the fly and therefore requires a good understanding by those involved in tsetse population management, especially in circumstances involving the release of sterile males. Knowledge of the reproductive system is also essential for a good understanding of this process.

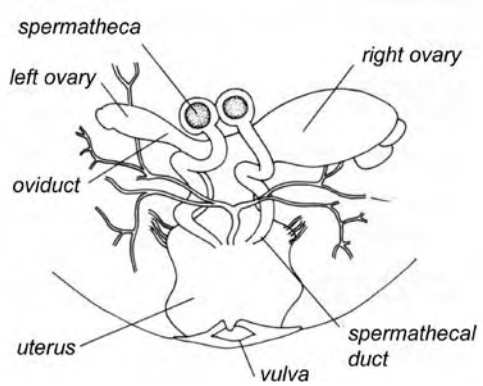
The external male genitalia have already been briefly described. The internal system, in the posterior part of the abdomen, consists of a pair of testes, which are coiled tubes producing and storing sperm, and covered by an orange/brown substance (**Figure 1.14**). Accompanying the testes is a pair of accessory glands which are long, whitish organs with glands producing secretions, which form a bag (spermatophore) containing sperm which is passed into the female's uterus during mating.

FIGURE 1.14
Drawing of internal reproductive organs of a male tsetse fly



Source: FAO 1982a

FIGURE 1.15
(left) Diagram of the reproductive system of a female tsetse fly, and (right) photo showing the spermathecae filled with sperm, the internal left follicle as the next in ovulation sequence, and an egg *in utero*



Source: FAO 1982a

PHOTO: M. VREYSEN

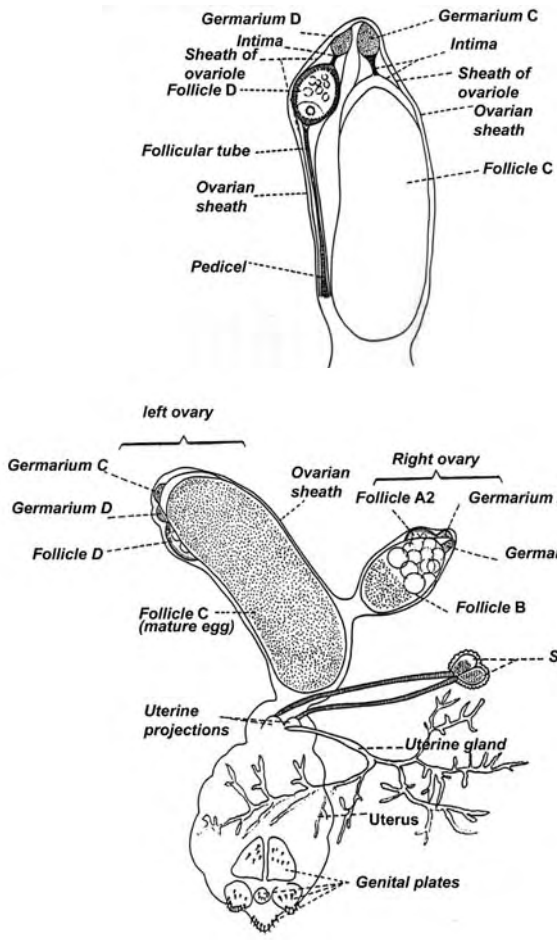
The female reproductive system (**Figure 1.15,** and **Figure 1.16**) consists of a pair of ovaries in which eggs develop. Each ovary has two ovarioles, so the female has a total of four ovarioles. The oocytes mature separately and in a regular sequence, so that only one egg is passed into the uterus at a time. The eggs pass from the ovary to the uterus through a pair of oviducts; these muscular tubes squeeze the mature egg down to where they join as a common oviduct and then into the uterus.

When the female fly is mated and the sperm-containing spermatophore is passed into the females' uterus, the sperm is stored by the female in a pair of spermathecae. These spherical, golden-brown organs store all the sperm from the male and this can last the female for the whole of its reproductive life so it never needs to mate again. Each time a mature egg passes into the female's uterus a small quantity of sperm passes down the spermathecal ducts from the spermathecae into the uterus where one sperm fertilizes the egg. After mating, the spermatophore is expelled from the uterus.

The uterus is a stretchable bag that holds the egg, and the subsequently developing larva as it grows, inside it is a soft sticky "carpet" called the choriothete, on the ventral surface where the egg is held after it enters the uterus. The choriothete is believed to play a role in breaking the membrane ("eggshell") or chorion, when the first stage larva hatches from the egg. There is a branched milk gland or uterine gland in the female's abdomen, which leads into the uterus and which produces a secretion "milk" that nourishes the developing larva within the uterus. Finally, there is an opening at the tip of the abdomen called the vulva, through which the larva is expelled when it is mature.

The sequential nature of the production of eggs, and the fact that as a mature egg bursts out of the membrane surrounding it (called a follicle), leaving a broken piece of tissue behind (a follicular relic), provides a means of ageing female tsetse flies fairly accurately, although this is a delicate dissection, described in 3.2.5.

FIGURE 1.16
(upper) The entire reproductive system, and (lower) detail of the left ovary of a 20-day-old female *Glossina tachinoides*



Source: Itard 1966

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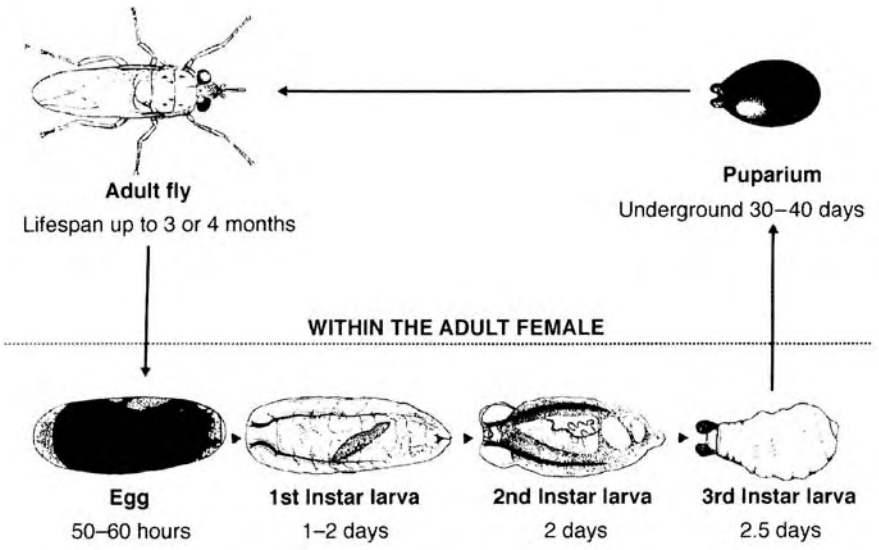
1.4. LIFE CYCLE

The life cycle of tsetse flies, shown diagrammatically in **Figure 1.17**, differs from many other insects as it produces one offspring, deposited as a 3rd instar larva approximately every nine days. The egg stage up to the 3rd instar larva is kept and nourished in the uterus of the adult female. Female tsetse flies mate shortly after emergence; females looking for a first blood meal may encounter a swarm of males (usually older) (in the *morsitans* group of tsetse) looking for females to mate with. The male lands on the back of the female (**Figure 1.18**), unfolds the hypopygium and clasps the female with the inferior and

FIGURE 1.17
Life cycle of the tsetse fly, *Glossina* spp.



Source: Leak 1998

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superior claspers. Mating can last a considerable time; up to one or two hours, and during this process the sperm in a spermatophore are passed into the females' uterus in the region where the spermathecal duct enters it, through the penis as described above. The sperm then pass up into the spermathecae for storage for the rest of the females' life. The mature egg is fertilized as it passes into the uterus and develops for approximately four days (embryogenesis) until a first instar larva is ready to emerge. The 1st instar larva breaks out of the chorion with an egg tooth and grows as it is nourished by milk gland secretions in the uterus until it is ready to moult to a 2nd instar larva after about one day. The 2nd instar larva grows and develops rapidly, showing segmentation and development of posterior spiracles and white swellings, that are developing polypneustic lobes, both of which are for respiration. This stage lasts for about two days and *G. morsitans* larvae will grow to about 4.5 mm during this time. The 2nd instar then moults to a 3rd instar larva, the last stage of larval development. In this stage the polypneustic lobes become black or dark brown. This stage lasts a further two days and the larva of *G. morsitans* reaches a length of 6–7 mm. Sometimes if a fly is stressed, for example if it is caught in a trap, the larva is aborted and passes out of the vulva before it is mature. Otherwise, the female deposits the mature 3rd stage larva in a suitable site where it will quickly burrow a few centimetres into soft sandy soil and form a puparium (equivalent of a pupa). The larva becomes barrel shaped and darkens as it changes, after an hour or two, into a pupa, and then has a hard brown case on the outside which is called a puparium.

FIGURE 1.18
Mating tsetse

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In the puparium metamorphosis to the adult will take place over a period of approximately 30 days (4–5 weeks) and then the adult will break out from the puparium and will struggle to the soil surface. The crumpled adult expands its wings and body and is known as a teneral fly until it has taken its first blood meal. Approximate durations have been given throughout this description because the development times can vary according to the ambient temperature and environmental conditions.

Tsetse flies have a very slow reproductive rate compared with many other insects; closer to that of a small mammal, so at a temperature of 25°C a female will produce a mature larva once every 9–10 days except for the first one which may be deposited 18–20 days after the emergence of its mother as an adult. This slow reproductive rate should theoretically make control or eradication easier.

1.5. IDENTIFICATION OF TSETSE FLIES

It is essential to know the species of tsetse fly present in an area considered for AW–IPM. Different tsetse species have different habitat preferences and behavioural differences that need to be taken into account when planning their control or eradication. When SIT is considered as part of an integrated approach, the target species or subspecies have to be reared.

Tsetse flies are two-winged flies of the Order Diptera, Family Glossinidae, which has a single genus – *Glossina*. Within this genus, there are three subgenera, *morsitans* (Glossina),