

Part 1.3

Diaphragm

Definitions

Diaphragm

The membrane, including its sclerotised parts, that closes off the end abdomen and through which the aedeagus is protruded during copulation. It is connected peripherally to the VT-Ring and valvae and centrally to the aedeagus.

Juxta

A sclerotised plate in the anteroventral portion of the diaphragm. It is usually attached anteriorly to the dorsal lamina of the saccus/vinculum, laterally to the internal lamina of the saccular bases and posterodorsally to the manica.

Transtilla

A sclerotised band or plate in the diaphragm immediately posterodorsal to the aedeagus. It may be composed of costal and anellar components. The costal component is continuous with the base of the valval costa. The anellar component is in the dorsal or dorsolateral margin of the anellus.

Manica

The more extensible component of the diaphragm connecting the structures comprising the anellus to the aedeagus. It allows for protrusion of the aedeagus during copulation.



Figure 1: *Panolis flammea* (Pine Beauty). Left - genitalia with aedeagus in situ. Right - central area with aedeagus removed

Anellus

The diaphragmatic structures immediately surrounding the aedeagus. The anellus is not a discrete genital structure. It is formed from parts of the juxta and transtilla and the membrane connecting them.

1) Introduction

The diaphragm has two functional regions^a: an anterior/ventral region, supporting the aedeagus, with copulatory function; and a posterior/dorsal region with excretory function, in which the anal tube emerges.

In species with a gnathos (which is absent in all Noctuoidea), this marks the division between the copulatory and excretory functional regions. In species without a gnathos, the dividing line is somewhat arbitrary (but is posterior/dorsal to the transtilla and anterior/ventral to the anal tube).

Because of its close association with the tegumen the anal tube (and the excretory functional region of the diaphragm) is covered in part 1 dealing with the VT-ring. Only the copulatory functional region of the diaphragm will be considered in the remainder of part 3.

The dominant sclerotisations around the aedeagus are the **juxta** which supports it ventrally and the **transtilla** which supports it dorsally; one or both of these structures may extend to support the aedeagus laterally. The **anellus** usually consists of sclerotised components of the juxta and transtilla connected by hyaline parts of the diaphragm. It usually has a generally rigid structure (compared with the manica), but there is usually some degree of flexibility^b. In some species the sclerotised components are fused together so that the anellus forms a completely rigid ring; or the sclerotised components may be rudimentary so that the anellus is largely hyaline.

The more extensible component of the diaphragm is termed the **manica**^c. The manica is a cylindrical sheath attached to the aedeagus medially, and attached to or merged with the anellus peripherally. It is usually a folded membrane and allows protrusion of the aedeagus during copulation. The manica may be ornamented in various ways, most often by simple stippling with sclerotin, but the ornamentation can be quite elaborate especially in Family: **Geometridae**.

The peripheral attachments of the diaphragm to the VT-ring are as follows: posterodorsally it is attached to the ventral edge of the tegumen, laterally to the base of the internal laminae of the valvae between the costa and the free margin of the sacculus. Attachment to the remainder of the base of the sacculus is more complex and variable, largely due to variation in the degree of connection of the sacculi to each other. Where the sacculi are strongly apposed the effective anteroventral edge of the diaphragm may be at the base of the free edge of the sacculus. Where a clear hyaline membrane separates the bases of the sacculi, the effective anteroventral margin of the diaphragm is continuous with the dorsal lamina of the saccus. In the former case, the structures of the diaphragm are impossible to display in their natural position, as it is necessary to divide the membrane connecting the sacculi to fully expose the juxta. In *Panolis flammea*, (Fig. 1), the sacculi are widely separated and the diaphragmatic structures can be seen in a fairly natural position.

Diaphragmatic structures can be difficult to display well in a standard slide preparation. The act of removing the aedeagus often disrupts the anellus; if the aedeagus is not removed the diaphragmatic structures are obscured by it. Even if the structures can be preserved during dissection, in a set specimen the sacculi often overlay the juxta and the juxta often overlays the transtilla.

Fig. 2 shows the diaphragmatic structures of *Orthosia gracilis*

- The set specimen presents the juxta and transtilla reasonably well and shows their size and position relative to other genital structures; but part of the juxta is obscured by the sacculi and the costal component of the transtilla cannot be seen clearly.
- The dorsal view shows the natural position of the transtilla; its division into costal and anellar components and how the anellar component forms a distinct anterior border to the anellus in its dorsal half.
- The dorsal view also gives some idea of the division of the diaphragm into copulatory and excretory functional regions.
- Note that the aedeagus enters the anellus between the juxta and the transtilla and the anal tube enters the tegumen between the transtilla and the dorsal arc of the tegumen.

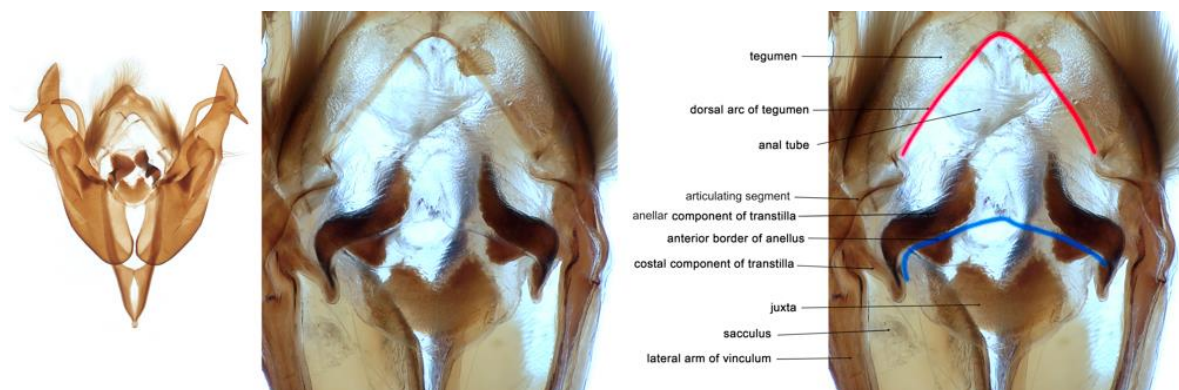


Figure 2: *Orthosia gracilis* (Powdered Quaker). Left - set specimen with aedeagus removed. Right - dorsal view of diaphragm in natural position with aedeagus removed

Diachrysia chrysitis (fig. 3)

The manica is sometimes almost entirely clear hyaline, as in *Orthosia gracilis*, but more often it is stippled with sclerotin and shows some clusters of small setae. Sometimes the ornamentation is more marked: in *Diachrysia chrysitis* the whole manica is densely set with short fine spines. This species also shows the following features:

- The juxta is a very large, fairly flat, ~oval plate
- There is an intersaccular sclerite connecting the sacculi which also has a sclerotised connection to the anterior edge of the juxta.
- The costal component of the transtilla is narrow and flimsy compared with the anellar component

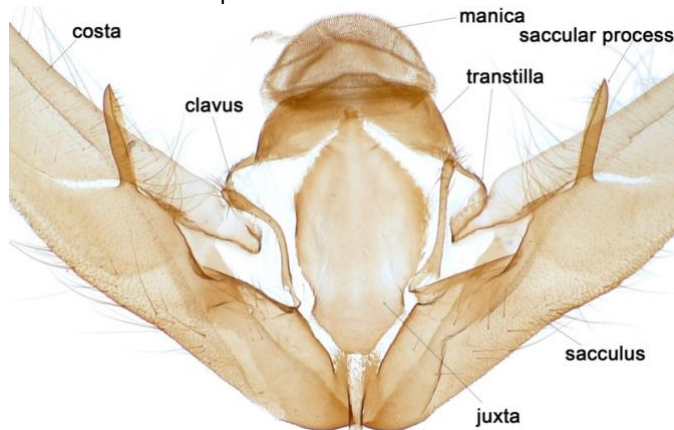


Figure 3: *Diachrysia chrysitis* (Burnished Brass) valvae, juxta and transtilla, detached from VT ring

Fig. 4 shows a typical arrangement of the anellus

- The juxta is a simple well-sclerotised anteroventral plate
- The anterolateral angles of the juxta have a strong hyaline connection to the bases of the internal laminae of the sacculi
- The lateral edges of the juxta are connected to the transtilla by a hyaline portion of the diaphragm
- The posterior edge of the juxta is continuous with the ventral surface of the manica
- The transtilla is strongly attached to the base of the costa (in this case to a carina)
- The transtilla extends medially and then turns posteriorly to strengthen the dorsolateral surfaces of the base of the manica
- The manica is a hyaline membrane stippled with sclerotin

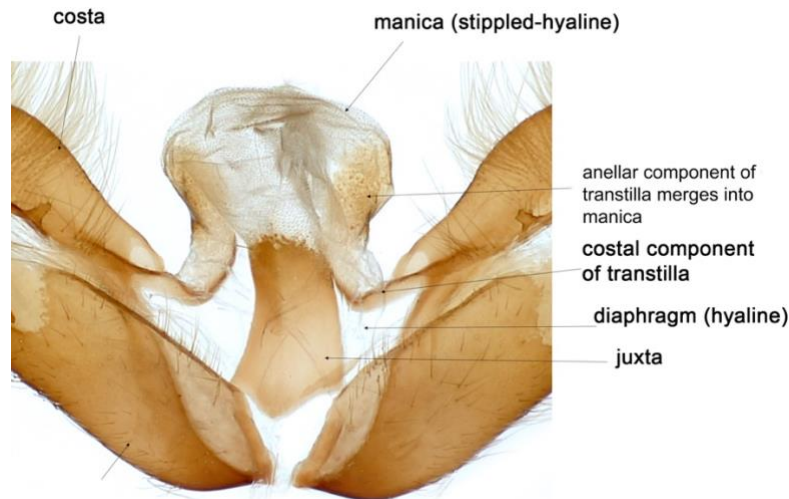


Figure 4: *Calophasia lunula* (Toadflax Brocade) detached valvae and anellus

In figure 5 (*Agrochola lychnidis*) the juxta and transtilla along with part of the manica have been dissected. They were detached as a cylinder, which has been opened on one side and laid flat, they remain attached to each other on the other side by a clear hyaline membrane (which is why the juxta is seen at an angle). The figure demonstrates the following variations seen in this species:

- The clear hyaline membrane attaching the juxta to the sacculus is stronger than the sclerotised sacculus. It can be very difficult to separate the juxta without pulling off part of its saccular attachment
- The transtilla has no costal component
- The anellar component of the transtilla is a well-sclerotised plate anteriorly, but posteriorly the sclerotization becomes diffuse and merges into the stippled-hyaline part of the manica
- The fine sparse setae are a typical ornamentation of the manica in Family: Noctuidae

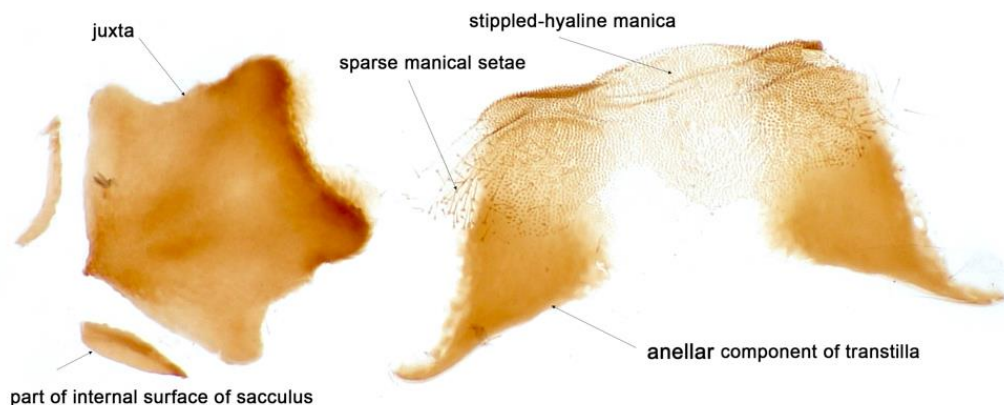


Figure 5: *Agrochola lychnidis* (Beaded Chestnut) detached juxta and transtilla

^a Scoble (1992) and Klots (1979) divided the diaphragm into three functional regions dorsal/posterior, central, and ventral/anterior, the central of which they termed the anellus. Scoble defined the "anellus" as the part "which folds around the aedeagus" and placed the juxta in the ventral/anterior region. This does not make good sense to me as the usual function of the juxta is clearly as a support for the aedeagus and its structure often extends into the anellus.

^b There is a case for regarding the manica as a component part of the anellus. As noted above these structures, as defined here, merge into each other. Over the course of writing this section I have changed my mind several times around this decision. For now I have concluded that it is most useful to regard the anellus as a relatively rigid base for the more flexible manica to attach to.

^c Klots (1979) defined the manica as the part of the anellus attached to the aedeagus: "Medially where perforated by the emerging penis, the diaphragm is doubly folded around this organ to form an eversible cone, the anellus. The innermost layer of this, which fastens around the penis at the zone, is the manica". It doesn't make sense to me that only the innermost layer of the double fold should be termed the manica – when the aedeagus is protruded, the folds disappear.

Pierce altered his definition of the juxta between publications. In his work on Noctuidae (1909) he seems to indicate the whole support through which the aedeagus is protruded and emphasises its connection to the articulation of the valvae (ie base of the costa and dorsal to the aedeagus). In his work on Geometridae (1914) the juxta is clearly a plate on the ventral side of the aedeagus.

2) The Juxta in Family: Noctuidae

The essential function of the juxta is to provide a support on the ventral side of the aedeagus. Its anterior or lateral edges are more or less strongly attached to the internal laminae of the bases of the sacculi and/or to the dorsal lamina of the saccus/vinculum. Its posterior edge may be distinct and mark a junction between anellus and manica; or the posterior margin may be more diffuse and merge into the ventral surface of the manica.

In the Noctuidae the juxta is usually a discrete plate with hyaline attachments, such that it could be dissected and presented separately, if it is necessary to see it well. Its (hyaline) attachments to the base of the sacculus may be stronger than the structure of the sacculus, such that care needs to be taken not to pull off part of the sacculus along with the juxta. The range of variation in size and shape of the juxta in the Family: Noctuidae is almost such that each species has a unique juxtal form.

The Noctuid juxta most often has an anterior edge that diverges posteriorly from a midline point, the two diverging anterior sides being connected to the internal surface of the bases of the sacculi. The lateral edges are variable in detail but often converge to some extent posteriorly. The posterior edge has two common types – notched or produced. In the notched type the notch accommodates the ventral side of the aedeagus, and there is a well-defined posterior edge to the juxta to which the ventral portion of the manica is attached. In the produced type a midline extension merges with and strengthens the manica on the ventral side of the aedeagus. Some typical examples are shown in figures 6 & 7 below.

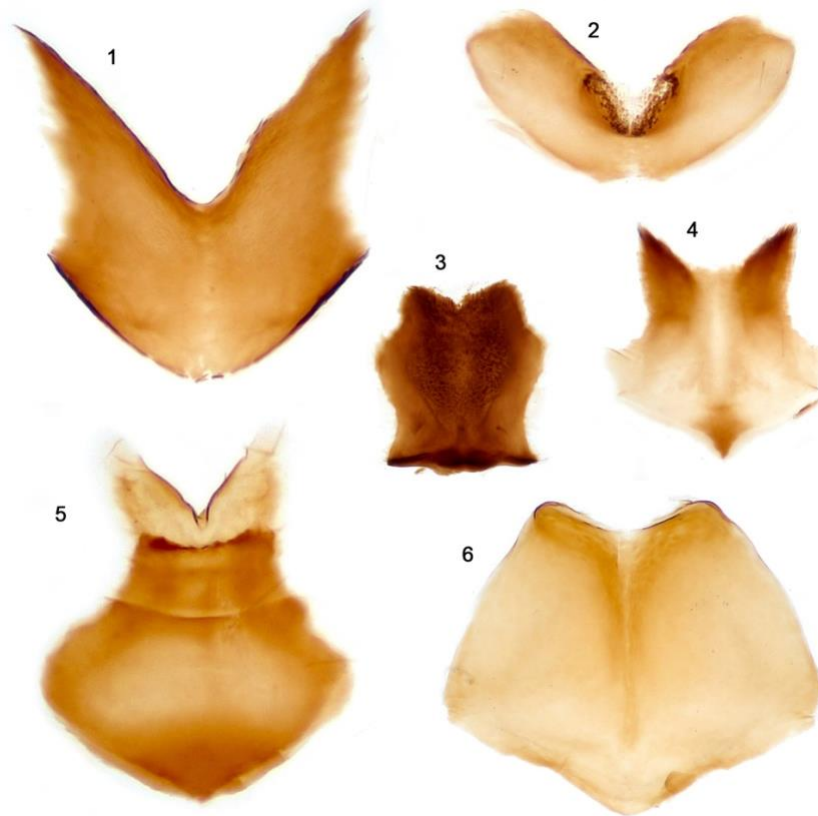


Figure 6: Noctuid juxtas with a notched posterior edge. 1:*Hada plebeja*, 2:*Eugnorisma glareosa*, 3:*Xylena vetusta*, 4:*Apamea monoglypha*, 5:*Amphipoea fucosa*, 6:*Noctua comes*

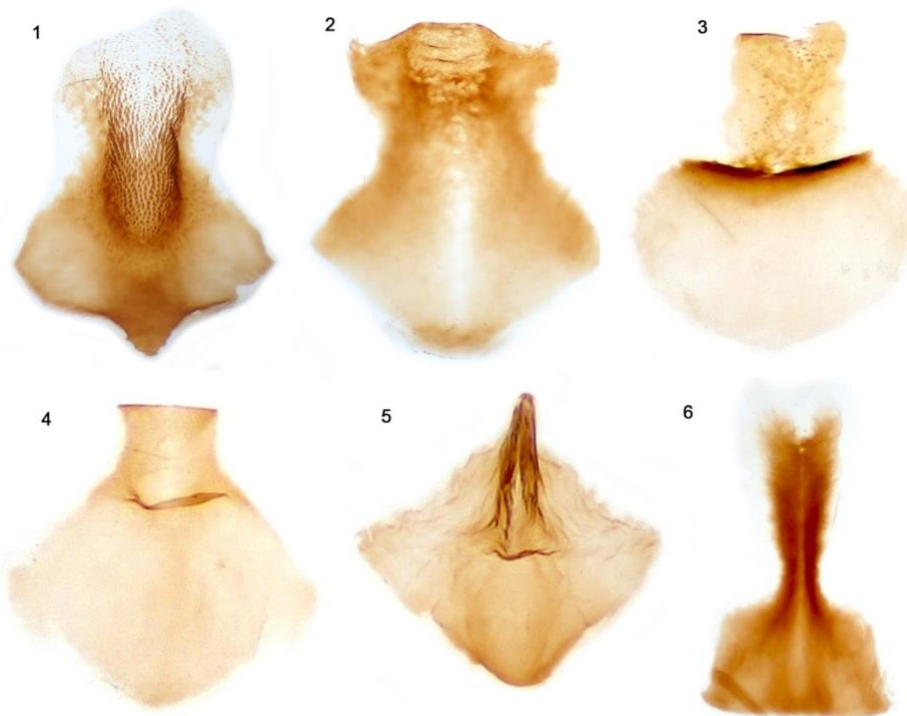


Figure 7: Noctuid juxtas with a produced posterior edge. 1:*Tholera decimalis*, 2:*Hydraecia micacea*, 3:*Mesapamea secalis*, 4:*Nyctobrya muralis*, 5:*Diarsia mendica*, 6:*Lithophane socia*

In fig. 8 images 1-3 show simple juxtas of various shapes in which the posterior edge is neither notched or produced.

Panolis flammea (fig. 8.4) has a complex juxta in which a shallow bowl-like plate, concave posteriorly, is produced posteriorly into the anellus at its posterior edge and is pleated at its anterior ventral edge – from the broad bowl the ventral edge turns posteriorly, narrows to a dome and then folds anteriorly continuing to narrow to a blunt anterior point.

Arenostola phragmitidis (fig 8.5) has a horseshoe-shaped juxta, concave posteriorly, the arms of which are strongly sclerotised and finely serrate.

In *Leucania comma* the juxta is formed of two separate sclerotised plates connected by a hyaline membrane; the anterior plate is cap-shaped with convex anterior and posterior edges; the posterior plate has a notched posterior edge.



Figure 8: Noctuid juxtas of other types. 1:*Calophasia lunula*, 2:*Tiliacea aurago*, 3:*Anarta trifolii*, 4:*Panolis flammea*, 5:*Arenostola phragmitidis*, 6:*Leucania comma*

3) The Transtilla in Family: Noctuidae

The essential function of the transtilla is to provide a support on the dorsal side of the aedeagus. The Noctuid transtilla is usually formed of two connected parts, which I have termed "costal" and "anellar". The costal part extends medially from the costa, is often weak and may be absent; when present it nearly always has a continuous sclerotised connection to the anellar part. The anellar part typically follows a sinuate course, dorsally then medially often forming a distinct anterior border to the dorsal half of the anellus (best seen in dorsal view – see fig. 2), before turning posteriorly and merging into the manica. The right and left anellar parts of the transtilla are usually separated in the dorsal midline by a hyaline gap. In some species the transtilla is reduced to just a smudge of sclerotisation in the dorsolateral part of the manica (e.g. *Anarta trifolii*, *Nyctobrya muralis*); in some it extends laterally and ventrally to connect to the juxta and in a few Noctuids the two sides of the manical component unite in the midline to form a substantial dorsal plate. Some of the range of variation of the transtilla can be seen in the images above and in the valval illustrations in Part 2. Two less typical examples are shown in figures 9 and 10 below.

In *Orthosia cerasi* (fig. 9) the transtilla is elaborated into a well-sclerotised plate that surrounds the aedeagus in all except its ventral 60°; the costal and anellar components are less distinct from each other than in most Noctuidae and the two sides are firmly fused in the dorsal midline; the posterior edge of the sclerotization has a fairly sharply demarcated junction with the stippled-hyaline membrane of the manica.



Figure 9: *Orthosia cerasi* (Common Quaker) left – anellus, centre – transtilla, right – juxta

In *Orthosia gothica* (fig. 10) the anellar component of the transtilla has a pair of long curved posterior processes with serrate apical margins; the juxta and transtilla are fused to form a complete sclerotised ring.

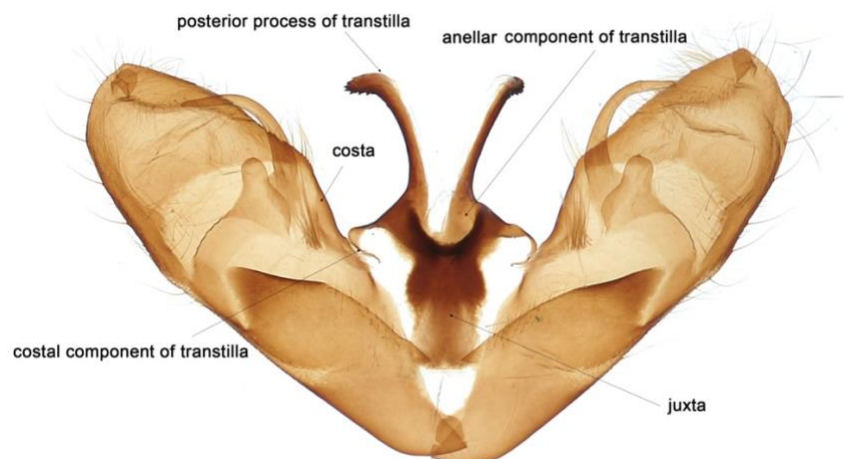


Figure 10: *Orthosia gothica* (Hebrew Character) valvae and anellus

It is notable that the transtilla in the three *Orthosia* species presented here (figs, 2,9&10) are quite different from each other.

Pierce (1914) regarded the transtilla as a structure derived from A10. He defined it as a "cross-bar uniting the costae of the valvae". I think that this usual connection to the costa makes it more likely to be derived from A9 and the definition he provided describes a limited subset of transtillae of a type not seen in the Noctuidae.

4) The Manica in Family: Noctuidae



The manica is the extensible component of the diaphragm that connects it to the aedeagus. It generally has a well-supported basal attachment to the anellus (to the juxta ventrally and to the transtilla dorsally), with one or other of these structures also providing support laterally in many species. The manica is a largely hyaline membrane, often stippled with sclerotin (figs 3,4&9) and ornamented with patches of fine setae (figs 5, 8.4). Further ornamentation is unusual in the Noctuidae – e.g. *Oligia fasciuncula* which has cornutus-like spines attached to the manica at its connection to the aedeagus (fig.11).

Figure 11: *Oligia fasciuncula* (Middle-barred Minor) aedeagus