

## A MECHANISM FOR MOVEMENT OF EGGS ALONG INSECT OVIPOSITORS

A. D. AUSTIN and T. O. BROWNING

The University of Adelaide, Waite Agricultural Research Institute, Glen Osmond 5064, South Australia

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**Abstract**—This paper aims to describe in detail the mechanism by which eggs are moved along the length of the ovipositor of insects. A series of posteriorly orientated scales, located along the inside of the ovipositor valves, catch the surface of the egg as it emerges from the oviduct and move it along the ovipositor as the valves oscillate back and forth. The morphology of ovipositor scales is examined by scanning electron microscopy, and is compared for 22 species in 20 Families of insects. The mechanism is also confirmed by direct manipulation of the ovipositor of an anaesthetized insect. Ovipositor scales vary in length from 1 to 30  $\mu\text{m}$  and can be spine-like, comb-like or scale-like in structure in different species. Caddis-flies (Trichoptera) were the only group examined which did not possess ovipositor scales. One species, *Philanisus plebeius* Walker, has longitudinal ridges along the inside surface of its ovipositor valves. The lack of ovipositor scales in the caddis-fly species examined in this study is discussed in relation to their behaviour and possible oviposition sites.

**Index descriptors** (in addition to those in title): Ovipositor scales, ovipositional behaviour, functional morphology, sensory sensilla, insect egg, scanning electron microscopy.

### INTRODUCTION

THE GENITALIA of insects have been widely studied, especially in relation to the morphology and homology of structures, between different Orders (Snodgrass, 1931, 1933, 1935; D'Rozario, 1942; Michener, 1944; Scudder, 1961a,b, 1964; Smith, 1969; Matsuda, 1976; also see Scudder, 1971 for review). The morphology of the reproductive system and ovipositor has been described for many insects, but most completely for the Hymenoptera (Snodgrass, 1931, 1933; Abbott, 1934, 1935; Hanna, 1934; Bender, 1943; King, 1962; King and Copland, 1969; Copland and King, 1971a,b, 1972a,b,c; Copland *et al.*, 1973; Copland, 1976).

Recently, attention has been paid to the ultrastructure of the reproductive system of insects, especially to the accessory glands and sensory system. Among other possible functions, some accessory glands probably provide lubricants to assist the passage of an egg through the oviduct and ovipositor (Salt, 1965; Wilkes, 1965; Rotherham, 1967; Rafai and King, 1972). The fine structure of the sense organs on the ovipositor valves has been examined by several authors (King and Fordy, 1970; Hawke *et al.*, 1973). Some sensory structures on the ovipositor of insects are strongly implicated in the discrimination of hosts and oviposition sites (Wylie, 1965; Arthur *et al.*, 1969; Fischer and Ganesalingam, 1970; King and Rafai, 1970; Hays and Vinson, 1971).

Authors such as Snodgrass (1931, 1933); Scudder (1961a,b); King and Ratcliffe (1969); Smith (1970) and Copland (1976) have shown that the operation of the insect ovipositor is complex, and that it works in a similar way in all groups, even though in some species both the structure and behaviour have become modified and specialized for particular hosts or oviposition sites.

The ovipositor is formed by the elongation of the genital valves, derived from abdominal segments 8 and 9. The valves are held together by a complicated interlocking mechanism, which allows them to slide back and forth on one another (Snodgrass, 1933; King, 1962; King *et al.*, 1968; King and Copland, 1969; Smith, 1970; Askew, 1971; Copland *et al.*, 1973). This movement provides the functional basis for piercing a host, plant tissue or soil. Few authors, however, have realized that this movement may also explain how an egg is moved along the shaft of the ovipositor. Severin (1935) and Smith (1970) briefly describe a system whereby posteriorly orientated scales, on the inside of the valves, act as a "linear ratchet" and produce unidirectional movement of an egg along the ovipositor. King and Ratcliffe (1969) and Copland *et al.* (1973) mention the presence of pectines or spines on the ovipositors of chalcidoid wasps, which they say are responsible for the movement of an egg along the ovipositor. Hawke *et al.* (1973), in their study of the sense organs of the ovipositor of the wasp *Orgilus lepidus* Muesebeck, present a micrograph which clearly shows scales in the ovipositor.

In this report we show that in most insect ovipositors there are scales on the inner surface of the valves. We also show that the morphology of these differs substantially among Families and Orders of insects. Direct mechanical manipulation of anaesthetized crickets, *Teleogryllus commodus* (Walker), provides strong evidence that these scales are indeed responsible for egg movement. The taxonomic designation of species used in this investigation can be found in Table 1.

We use the term "scales" for these structures because they are continuous with the cuticular surface of the ovipositor valves. Although previous authors have referred to them as ctenidia, pectines, spines and teeth, we feel it is more useful to refer to them as scales, as this term allows for the variation in their morphology among different groups of insects. In some species the ovipositor scales are highly modified; they can be spine-like, or scale-like.

#### MATERIALS AND METHODS

Specimens representing 22 species in 20 Families of insects were used in this study (Table 1). At least 3 individuals of each species were examined. Live material was collected from the field, killed with ethyl acetate vapour and dissected in Ringer's solution (Ephrussi and Beadle, 1936). Specimens were then washed, and dried in a desiccator or critical point-dried (Nemanic, 1972). Observations on the general anatomy of the ovipositor, reproductive system and eggs were made where possible during the course of dissections. Museum specimens were softened in cold 10% potassium hydroxide for 2–6 hr, dissected, washed and dried.

All material was mounted on aluminium holders and coated (10 nm) with carbon and (20–40 nm) with gold–palladium. Some specimens were sputter-coated (20 nm) with gold, while others were examined uncoated. Material was examined at accelerating voltages between 10 and 30 kV, using an ETEC Autoscan Scanning Electron Microscope (SEM) and a JOEL JEM Electron Microscope, fitted with a scanning attachment.

The eggs of the cricket *T. commodus* were also examined by SEM. Eggs from this species could be easily obtained, because gravid females would readily oviposit into damp cottonwool or a dish of water in the laboratory. Either fresh and uncoated, or fixed, coated eggs were used to examine the external surface of the chorion. Eggs were fixed in F.A.A. (Formalin 5 : Glacial Acetic Acid 1 : Alcohol 25 : H<sub>2</sub>O 20) for 6 hr and then prepared as above.

TABLE 1. SPECIES EXAMINED IN THIS STUDY, LISTING THEIR OVIPOSITION SITES AND NUMBER OF OVIPOSITOR SCALE TYPES

Species examined	Number of types of ovipositor scales	Oviposition site
<b>Coleoptera</b>		
<i>Cybister tripunctatus</i> Oliver (Dytiscidae)	1	Stems of aquatic plants (Britton, 1970; McKeown, 1942)
Unknown genus (Gyrinidae)	0	?
<b>Homoptera</b>		
<i>Melampsalta</i> sp. (Cicadidae)	3	Twigs and branches of trees (McKeown, 1942; Woodward <i>et al.</i> , 1970)
<i>Cyclochila</i> sp. (Cicadidae)	3	
<i>Eurymelops rubrovittata</i> Amyot and Serville (Eurymelidae)	2	Branches of eucalypt trees (McKeown, 1942)
<i>Sextius</i> sp. (Membracidae)	1	Bark of trees (McKeown, 1942)
<i>Scolypopa australis</i> (Walker) (Ricaniidae)	1	Dead twigs of various trees (Fletcher, 1979)
<b>Hymenoptera</b>		
<i>Bracon</i> sp. (Braconidae)	1	Insect host (Riek, 1970)
<i>Brachymeria</i> sp. (Chalcididae)	1	Lepidopteran pupae (Riek, 1970)
<i>Lissopimpla excelsa</i> (Costa) (Ichneumonidae)	1	Lepidopteran larvae (McKeown, 1942; Riek, 1970)
<i>Rhyssa</i> sp. (Ichneumonidae)	1	Sawfly larvae, through the bark of trees (Riek, 1970)
<i>Megalyra</i> sp.? (Megalyridae)	1	Coleopteran larvae, through the frass plug of beetle galleries (Riek, 1970)
Unknown genus (Proctotrupidae)	1	?
<i>Ceratobaeus</i> sp. (Scelionidae)	1	Eggs of spiders (Riek, 1970)
<i>Sirex juvenis</i> Linnaeus (Siricidae)	2	Trunk of pine trees (Riek, 1970)
<i>Perga dorsalis</i> Leach (Tenthredinidae)	2	Trunk of eucalypt trees (Riek, 1970)
<b>Orthoptera</b>		
<i>Hadrogyllacris</i> sp. (Gryllacrididae)	1	Soil ?
<i>Teleogryllus commodus</i> (Walker) (Gryllidae)	3	Heavy clay soils (Browning, 1954)
<i>Caedicia</i> sp. (Tettigoniidae)	3	Twigs and leaves (McKeown, 1942)
<b>Trichoptera</b>		
<i>Ecnomina irrorata</i> Kimmins (Ecnomidae)	0	?
<i>Philaniscus plebeius</i> Walker (Philaniscidae)	0	Coelom of starfish (Anderson and Lawson-Kerr, 1977); calcareous algal beds (Leader and Bedford 1979)
<i>Moruya charadra</i> Neboiss (Rhyacophilidae)	0	?

Specimens of *T. commodus* were also used to test the proposed mechanism for egg movement. Females were anaesthetized with carbon dioxide and partly dissected so that the posterior end of the oviduct was exposed. Eggs were then squeezed along the oviduct with forceps until they reached the proximal end of the ovipositor. The alternate movements of the ovipositor valves were simulated by moving them back and forth with fine forceps.

Sections of the ovipositor of *T. commodus* were cut to gain information on the epithelial layer responsible for the production of ovipositor scales. Ovipositors of female nymphs and newly moulted adults were dissected in F.A.A. and left 24 hr, then dehydrated. Specimens were embedded in 58°C m.p. wax, then longitudinal and transverse sections were cut at 7–10 µm and stained with Mayer's Haemalum or Heidenhain's Iron Haematoxylin.

## OBSERVATIONS

The morphology and arrangement of ovipositor scales are described below for representatives of 5 insect Orders and 20 different Families.

*Coleoptera*

The scales of *Cybister tripunctatus* (Dytiscidae) (Fig. 1) are spine-like and vary in length from 4 to 30  $\mu\text{m}$ . They are sparsely distributed towards the lateral margins of the ovipositor valves (approx. 30  $\mu\text{m}$  apart) and are denser towards the centre (3–5  $\mu\text{m}$  apart). Short spines are evenly spaced and found over the whole surface of each valve, while larger spines are concentrated in the midline.

An unidentified grylinid beetle was examined and found to have a very short, blunt ovipositor, but no recognizable scales could be distinguished.

*Homoptera*

The scale morphology of Homoptera is diverse and differs substantially among Families.

The scales of *Scolypopa australis* (Ricaniidae) (Fig. 2) are small and spine-like (approx. 1–2  $\mu\text{m}$  long), and appear to be evenly distributed over the surface of the valves (5–20  $\mu\text{m}$  apart).

*Sextius* sp. (Membracidae) (Fig. 3) has scales that are spine-like, 2  $\mu\text{m}$  long and form regular oblique rows on the inside of the ovipositor valves. There are 16–18 spines per 10  $\mu\text{m}$  along a row, and rows are evenly spaced at 3  $\mu\text{m}$  apart.

*Eurymelops rubrovittata* (Eurymelidae) (Fig. 4) possess 2 distinct types of scales. At the edges of each valve are large curved plates that are partially divided into closely packed spines along their posterior edge. These plates are 10–20  $\mu\text{m}$  wide and approx. 10  $\mu\text{m}$  long. The majority of the valvular surface has rows of scales that are obliquely orientated to the ovipositor. Each scale is 10–15  $\mu\text{m}$  long and has up to 20 spines (1–3  $\mu\text{m}$  long) along its posterior border. At the lateral margin of the valves there appears to be a continuum between the 2 types of scales; where small scales gradually appear more elongate and curved.

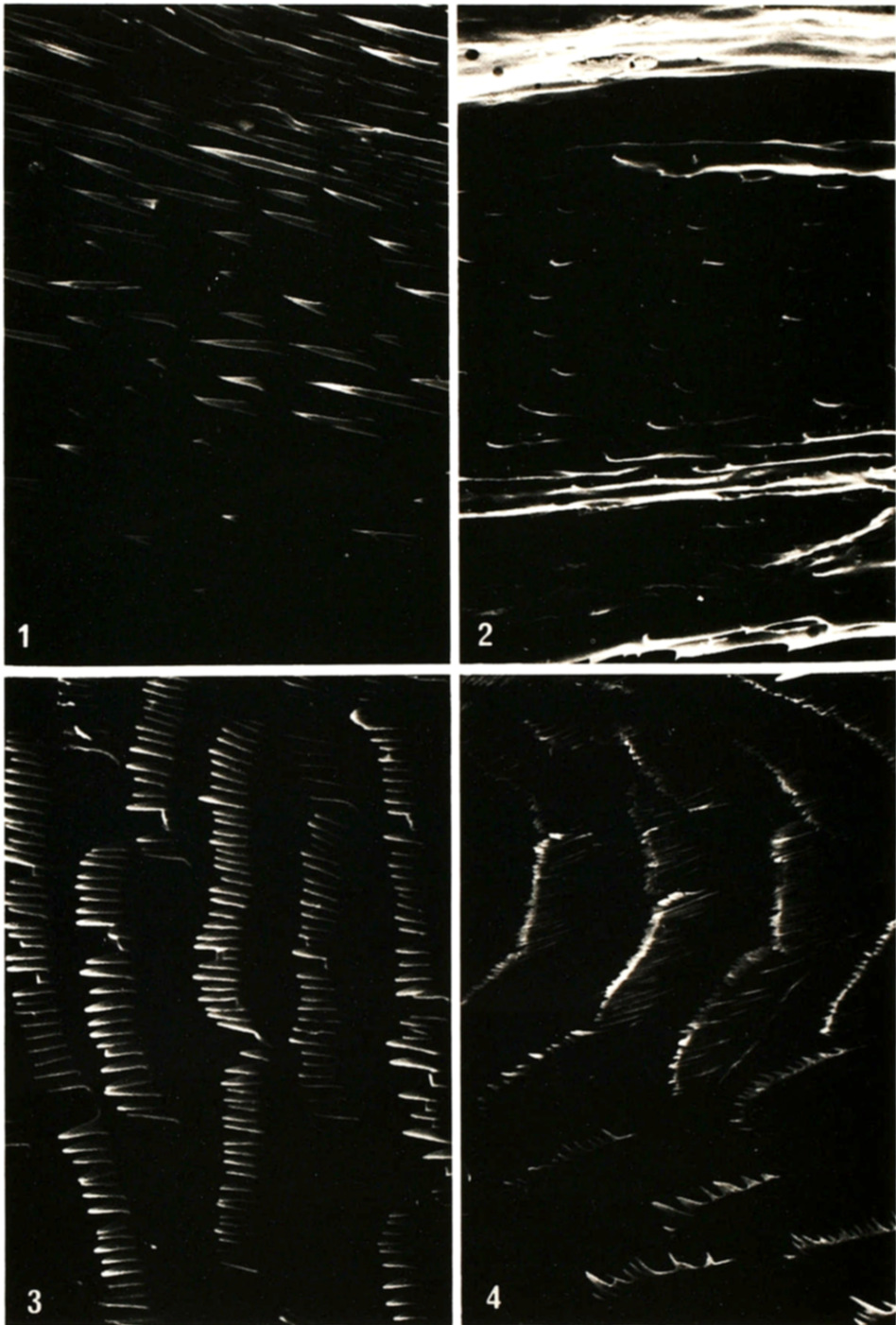
The scales of *Melampsalta* sp. and *Cyclochila* sp. (Cicadidae) (Figs. 5,6) are the most structurally diverse of the homopterans examined. Specimens of the 2 genera examined showed no differences in the types and arrangement of their scales. Both plate-like and spine-like scales are present, each forming longitudinal rows along the inside of the valves. Scales in rows towards the centre of each valve are small (2–4  $\mu\text{m}$  long) and are 2–5  $\mu\text{m}$  apart. They have even, curved edges. Between each longitudinal row of the above scales is a row of spine-like scales. These are 3  $\mu\text{m}$  long, form ill-defined perpendicular rows, and have from 4 to 10 spines along their posterior edges. Scales near the lateral margins are large (8–10  $\mu\text{m}$  long) and overlap with each other. These scales have a row of short spines along their posterior edges.

*Hymenoptera*

The scales on the ovipositor valves of Hymenoptera are single and spine-like, or divided into groups of spines. No plate-like scales were present in any species examined, but the arrangement and form of scales varied substantially.

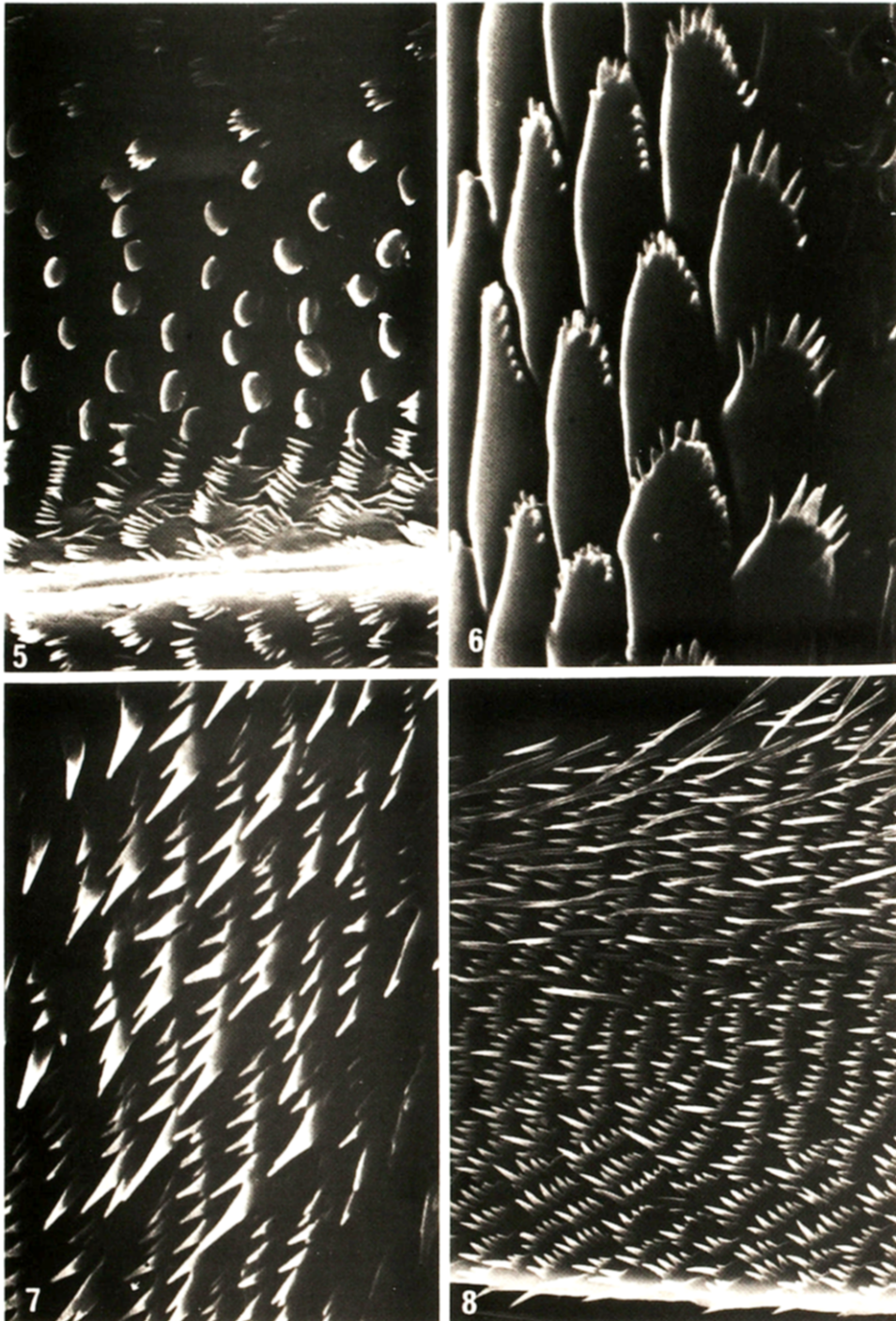
*Sirex juvencus* (Siricidae) (Fig. 7) possesses diagonal rows of short, stout scales. These rows are formed from smaller groups of 5–10 spines, with a single large bifid spine at one end. Spines vary in length from 1 to 8  $\mu\text{m}$ .





FIGS. 1–4. Scanning electron micrographs (SEM) of inside surface of ovipositor valves, showing ovipositor scales. (1) *Cybister tripunctatus* (Coleoptera : Dytiscidae).  $\times 680$ . (2) *Scolypopa australis* (Homoptera : Ricaniidae).  $\times 650$ . (3) *Sextius* sp. (Homoptera : Membracidae).  $\times 2,850$ . (4) *Eurymelops rubrovittata* (Homoptera : Eurymelidae).  $\times 1,450$ .

*Perga dorsalis* (Tenthredinidae) (Fig. 8) has close compact rows of spine-like scales that cover most of the surface area of each valve. Spines form 2 size classes. Most are 2–8  $\mu\text{m}$  long, while some are 15–20  $\mu\text{m}$  long; the latter are found only in the midline of each valve.



FIGS. 5–8. Captions on p. 99.

The scales of *Enura exigue* (Smith) (Tenthredinidae) (Smith, 1970) differ from those of *Perga*. In this species scales form transverse rows of short spines, approx. 8  $\mu\text{m}$  in length, and are similar to the arrangement in the proctotrupid examined in this study (Fig. 13).

*Megalyra* sp. (Megalyridae) (Fig. 9) has scales that form groups of 2–5 spines. Spines vary in length from 1 to 3  $\mu\text{m}$ . The inside surface of the ovipositor valves is rough in texture, except in the midline where the scales are most numerous. There is a central, longitudinal row of regularly arranged scales, with scattered groups in the adjacent areas.

*Rhyssa* sp. and *Lissopimpla excelsa* (Ichneumonidae) (Fig. 10) did not differ in their arrangement and type of scales. Both genera possess diagonal rows of spine-like scales. Each scale consists of 4–15 spines, the latter varying from 1 to 3  $\mu\text{m}$  in length.

*Bracon* sp. (Braconidae) (Fig. 11) has a longitudinal row of spine-like scales along the inside of each valve. Each row is approx. 5  $\mu\text{m}$  wide and is composed of closely compact spines that are 1–2  $\mu\text{m}$  long.

*Brachymeria* sp. (Chalcididae) (Fig. 12) also has longitudinal rows of spine-like scales. Each row is 10–15  $\mu\text{m}$  wide and composed of 2–5- $\mu\text{m}$  long spines.

An unknown genus of Proctotrupidae (Fig. 13) was found to have a regular array of transverse rows of spine-like scales. Each row is 10–25  $\mu\text{m}$  wide and comprised of 1–1.5- $\mu\text{m}$  long spines. Rows are approx. 10  $\mu\text{m}$  apart.

*Ceratobaeus* sp. (Scelionidae) (Fig. 14) has a total body length of 1.5 mm. It has spine-like scales randomly arranged on the inside of the ovipositor valves, except near the distal end, where they occur in groups of 3 and 4. Scales are very small (0.5–1.5  $\mu\text{m}$ ), but not when compared with the size of the ovipositor, which is only 6–8  $\mu\text{m}$  in diameter.

### Orthoptera

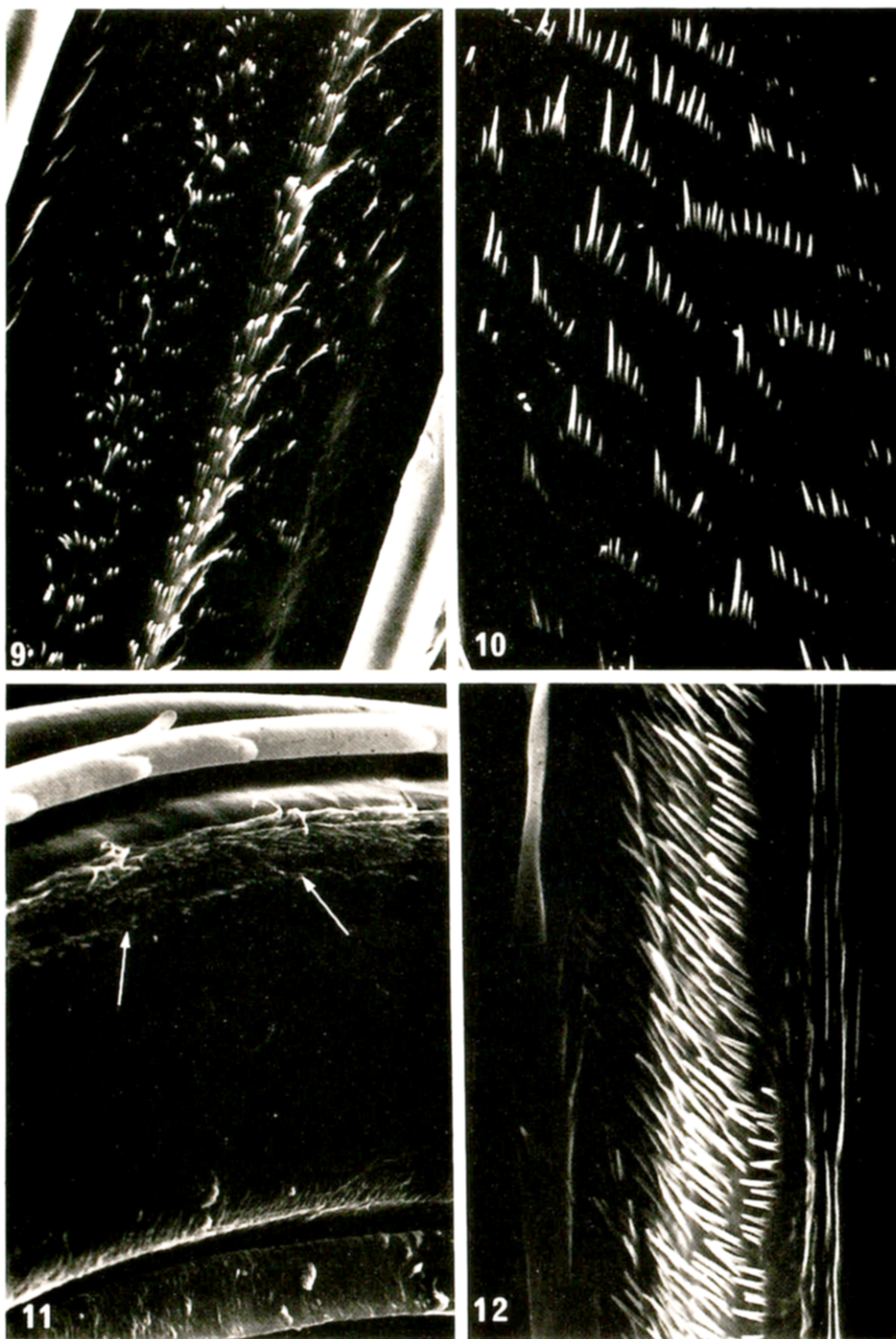
The scales of *T. commodus* (Gryllidae) and *Hadrogryllacris* sp. (Gryllacrididae) are very similar in shape and arrangement. Both possess overlapping plate-like scales that are approx. 5  $\mu\text{m}$  wide and 7–10  $\mu\text{m}$  long. Those on the ovipositor of *T. commodus* (Fig. 15) form compact rows in the central region (Fig. 16), but are randomly arranged towards the lateral margins of each valve. In this species at least, scales appear on the ovipositor only at the last moult, and are not present on the ovipositor of any nymphal instars. Those of *Hadrogryllacris* sp. are randomly arranged over the whole surface of each valve (Fig. 17). The latter species also has central longitudinal bands on each valve, where the scales are flat and their edges flush with the surface. It is only along the lateral margins, where the posterior edges of scales are raised above the surface of the valve, that effective contact can be made with an egg. Also the lateral margins on adjacent valves form a longitudinal ridge, which protrudes into the egg canal. These squeeze the egg, making contact with the scales even more effective. From the description provided by Severin (1935) the scales of *Gryllus assimilis* (Fabricius) are like those of *T. commodus*.

*Caedicia* sp. (Tettigoniidae) (Figs. 18–20) possesses 3 distinct types of scales that are found in different locations on the inside of the valves. The ventral valves are covered with overlapping, elongate scales. These are 15–20  $\mu\text{m}$  long and 5–10  $\mu\text{m}$  wide at their base.

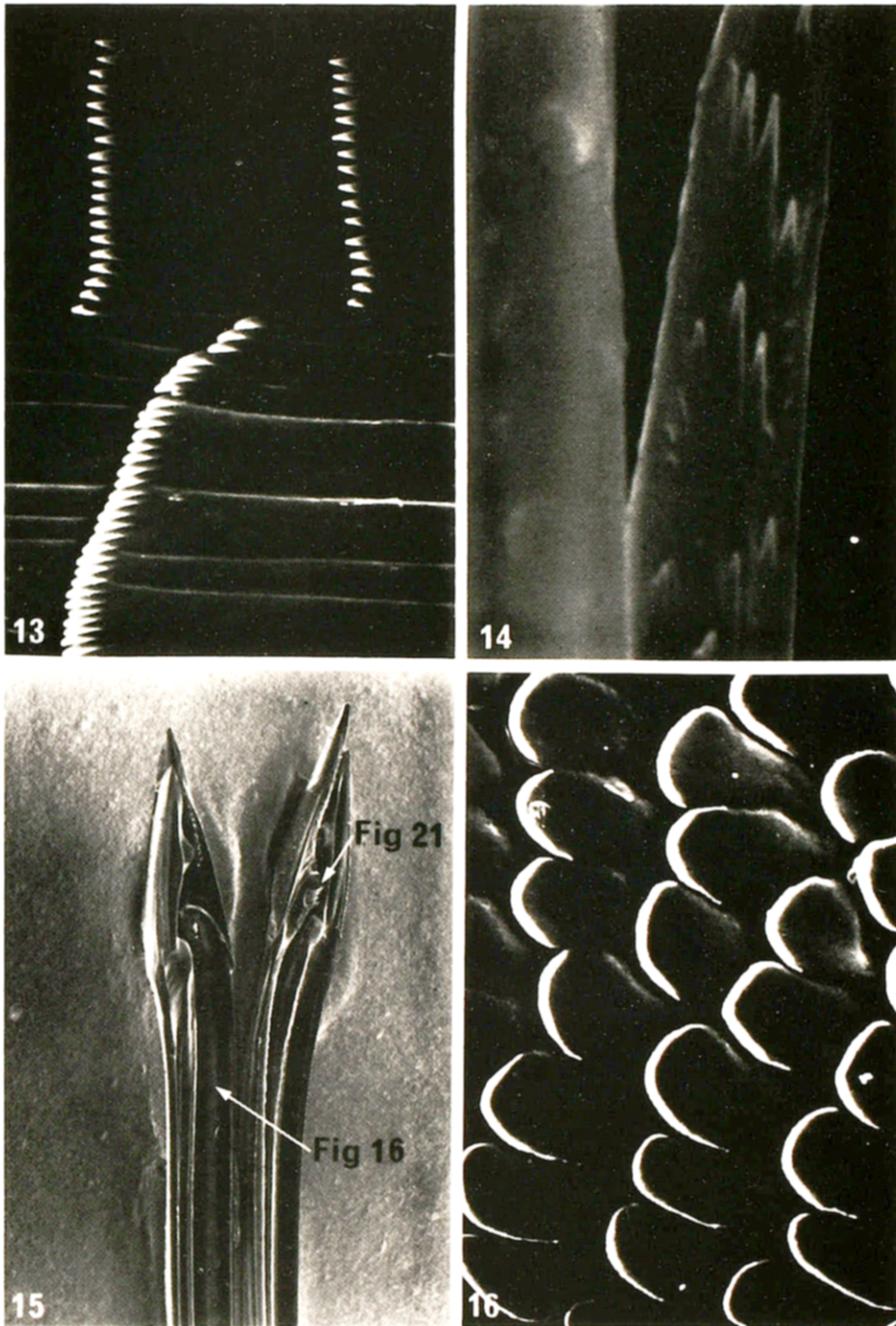
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FIGS. 5–8. SEM of inside surface of ovipositor valves, showing ovipositor scales. (5) *Melampsalta* sp. (Homoptera : Cicadidae), central region of valve.  $\times 1,550$ . (6) *Melampsalta* sp., lateral margin of valve.  $\times 3,200$ . (7) *Sirex juvencus* (Hymenoptera : Siricidae).  $\times 1,650$ . (8) *Perga dorsalis* (Hymenoptera : Tenthredinidae).  $\times 860$ .





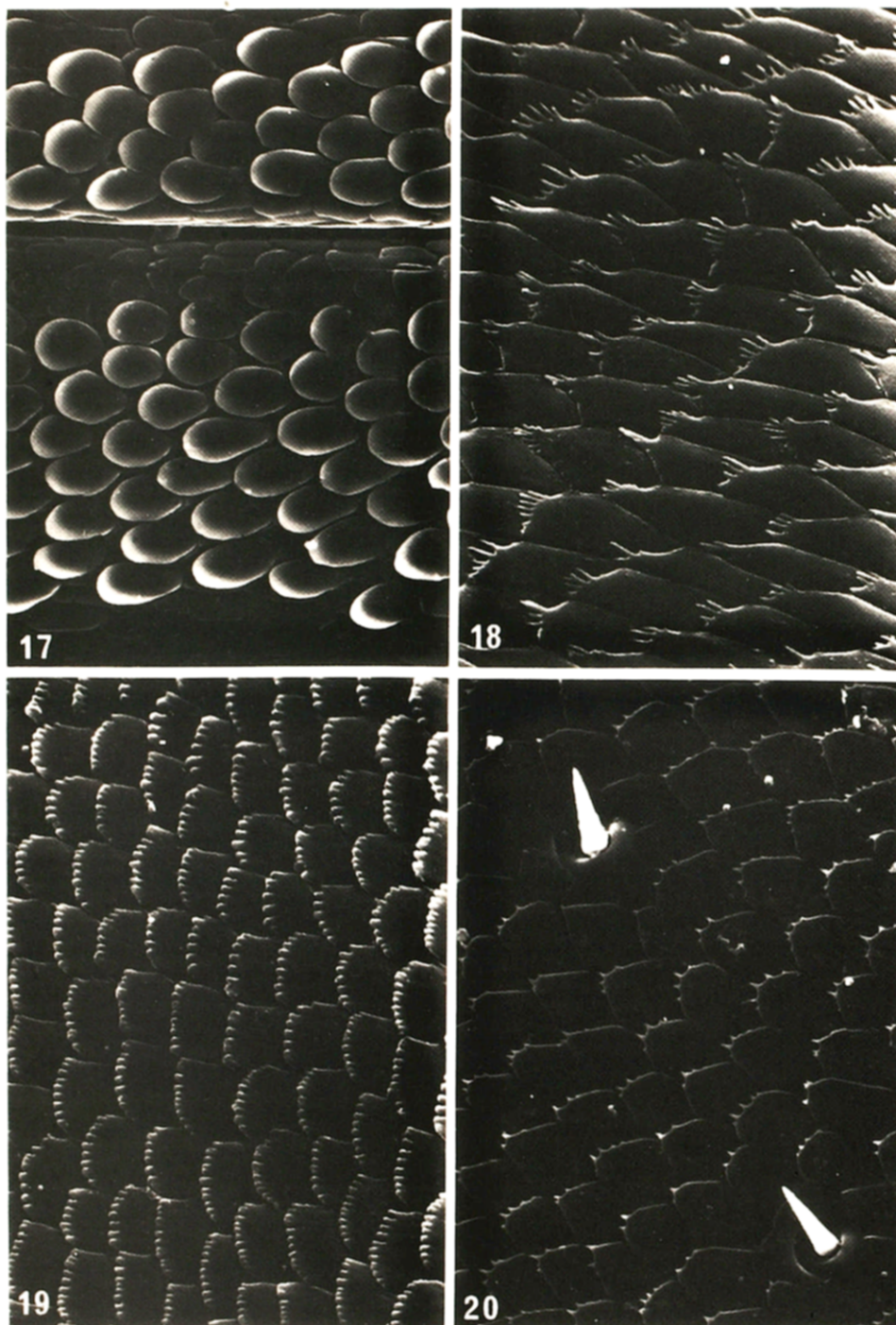
FIGS. 9–12. SEM of inside surface of ovipositor valves, showing ovipositor scales. (9) *Megalyra* sp. (Hymenoptera : Megalyridae).  $\times 1,200$ . (10) *Lissopimpla excelsa* (Hymenoptera : Ichneumonidae).  $\times 1,350$ . (11) *Bracon* sp. (Hymenoptera : Braconidae).  $\times 1,750$ , ovipositor scales arrowed. (12) *Brachymeria* sp. (Hymenoptera : Chalcididae).  $\times 1,750$ .



FIGS. 13, 14, 16. SEM of inside surface of ovipositor valves, showing ovipositor scales. (13) Unidentified proctotrupid (Hymenoptera : Proctotrupidae).  $\times 4,050$ . (14) *Ceratobaeus* sp. (Hymenoptera : Scelionidae).  $\times 11,800$ . (16) *Teleogryllus commodus* (Orthoptera : Gryllidae).  $\times 2,450$ .

FIG. 15. SEM of inside surface of 2 halves of ovipositor of *T. commodus* ( $\times 35$ ) showing position of Figs. 16 and 21.





FIGS. 17–20. SEM of inside surface of ovipositor valves, showing ovipositor scales. (17) *Hadrogryllacris* sp. (Orthoptera : Gryllacrididae).  $\times 570$ . (18) *Caedicia* sp. (Orthoptera : Tettigoniidae), ventral valve.  $\times 1,000$ . (19) *Caedicia* sp., inner ovipositor valve.  $\times 1,000$ . (20) *Caedicia* sp., dorsal valve showing sensilla.  $\times 860$ .

The posterior apex of each scale has from 1 to 8 spines protruding from it (Fig. 18). The central region of the ovipositor, the inner ovipositor valves, is covered with overlapping scales that are approx. 8  $\mu\text{m}$  wide and long. These scales are square and have a serrated posterior border (Fig. 19). The dorsal valves are covered with overlapping scales. These are 8–10  $\mu\text{m}$  long and 8–10  $\mu\text{m}$  wide at their bases. The posterior margin of each scale is either pointed or rounded and has several small projecting teeth (Fig. 20). The dorsal valves of *Caedicia* sp. also have, scattered along their length, a number of short sensilla. These are 10–16  $\mu\text{m}$  long and are at least 80  $\mu\text{m}$  apart.

The valves of *T. commodus* also have similar sensilla, but in this species they are only 5–8  $\mu\text{m}$  long and 200–300  $\mu\text{m}$  apart. *T. commodus* also has a group of 8 large sensilla at the distal end on the inside of the dorsal valves. These are 60–95  $\mu\text{m}$  in length (Fig. 21). It is likely that the small sensilla along the inside of the valves provide information on the progressive position of an egg as it moves down the length of the ovipositor. The large sensilla at the distal end of the egg canal may then signal when an egg is expelled, so that another can be introduced into the proximal end of the ovipositor.

The outer surface of the distal end of the ovipositor of *T. commodus* (Fig. 22) is also covered with scales (Fig. 23). However, these are oriented in the opposite direction to those on the inside surface of the egg canal. These outer scales probably prevent backward movement of the shaft and therefore help with penetration and in holding the ovipositor in the soil, while an individual lays its eggs. Other insects, notably hymenopterans, also possess such scales or spines on the outer surface of the ovipositor tip (Copland and King, 1972a,b,c).

#### *Trichoptera*

The internal surface of the ovipositor of 3 species of caddis-fly was examined, but no scales were observed in any of these. The valves of *Moruya charadra* (Rhyacophilidae) and *Ecnomina irrorata* (Ecnomidae) are completely smooth, while those of *Philanisus plebeius* (Philanisidae) have a series of small, longitudinal ridges (Fig. 24). These ridges are less than 1  $\mu\text{m}$  in height and width, and are about 5  $\mu\text{m}$  apart. No clear explanation can be provided for the absence of ovipositor scales in this group. Very little is known of the ovipositional behaviour and sites of the above species (see Discussion).

#### *Oviposition*

The backward and forward movement of the valves of the ovipositor of *T. commodus* can be shown to result in the movement of an egg posteriorly. A female *T. commodus* was anaesthetized with carbon dioxide and eggs were squeezed along the oviduct until they were at the proximal opening of the egg canal. If the valves of the ovipositor were moved back and forth, using fine forceps, it was possible to move an egg the full length of the ovipositor in only a few seconds. This was repeated many times on different female crickets with the same results. Close observation of female crickets ovipositing showed that penetration of the ovipositor is accomplished by alternate backward and forward movement of the lateral valves. Thus, there is evidence that this mechanism is responsible both for penetration of the ovipositor and for the movement of the egg.

Examination of the surface of freshly laid eggs of *T. commodus* did not reveal any impression of the scales of the ovipositor on the surface of the chorion.

Transverse and longitudinal sections cut through the ovipositor of newly moulted adult *T. commodus* reveal that one epithelial cell is responsible for the formation of each ovipositor scale. The scales of this species therefore represent Type 3 in the classification of cuticular protuberances by Richards and Richards (1979).

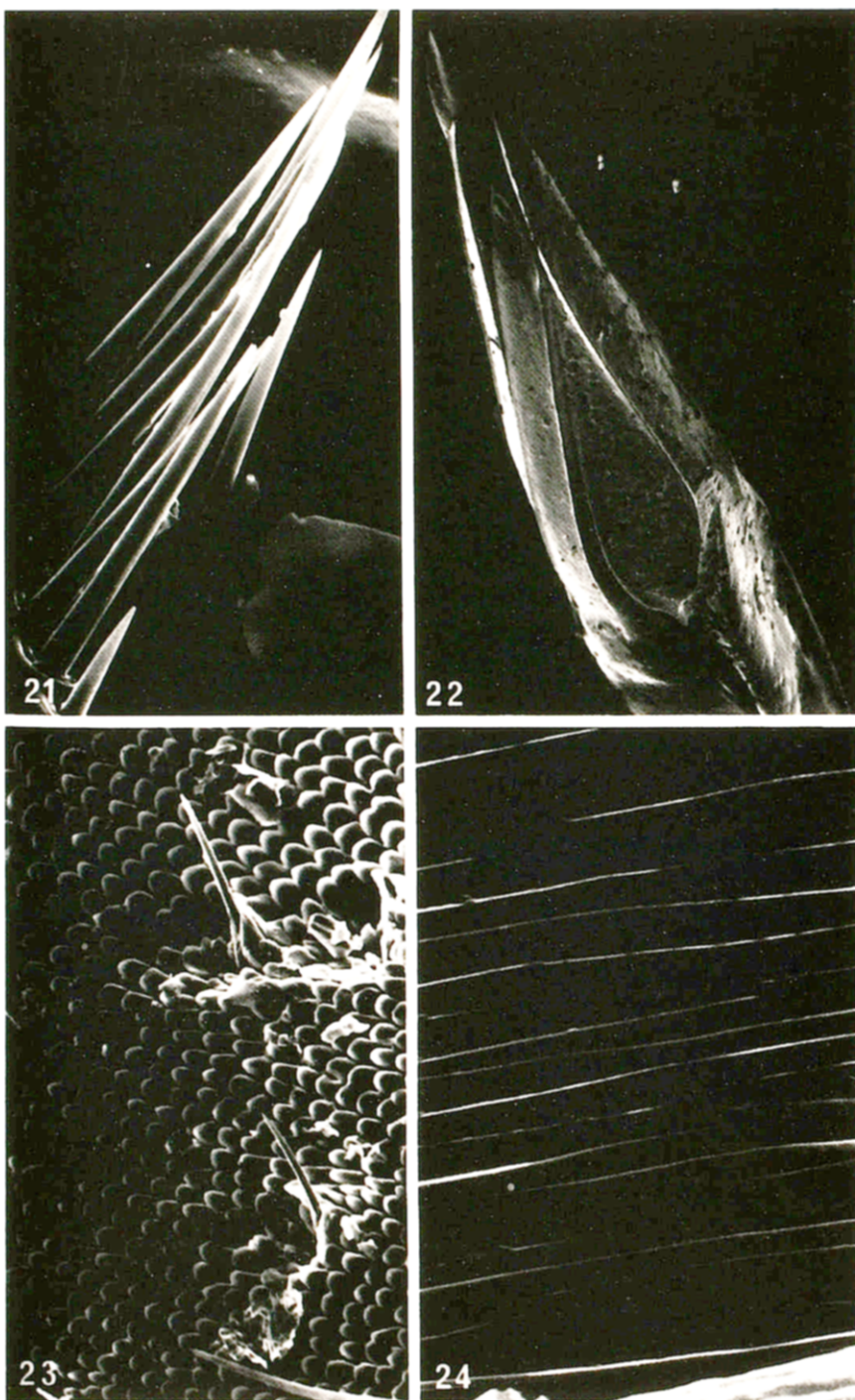


FIG. 21. SEM of large sensilla on inside surface of distal end of ovipositor of *Teleogryllus commodus*.  
× 570.

FIGS. 22, 23. SEM of outside distal end of ovipositor of *T. commodus* (22). × 57. (23). × 860.  
FIG. 24. SEM of inside surface of ovipositor valve of *Philanisus plebeius* (Trichoptera : Philanisidae).  
× 1,900.



## DISCUSSION

The possession of scales on the inside of the ovipositor valves of insects provides a simple yet efficient mechanism for the movement of eggs along the ovipositor. Ovipositors have evolved in several Orders and many Families of insects, yet their basic structure and mode of operation vary little among groups.

Considerable advantage must be conferred on species that can adequately protect their eggs or utilize different oviposition locations. Most insect ovipositors penetrate into clay, bark, leaves, or an insect host by using the sliding-coupled movement of the valves. The same movements are also used to move the egg along the length of the ovipositor. Presumably these 2 aspects of oviposition have evolved together. Homopteran insects also utilize sliding-coupled movements of the paired elements of the mouthparts (the feeding stylets) as the basis for penetration and feeding in plant tissues (Miles, 1958; Pollard, 1970, 1972).

Ovipositor scales vary in structure and arrangement among insect groups. Orthoptera and Homoptera generally possess plate-like scales, while Hymenoptera and one species of Coleoptera have spine-like scales. Although only one coleopteran (a dytiscid), of 2 species examined, was found to possess ovipositor scales, this may be general for at least dytiscids, as members of the family are known to have well-developed and functional ovipositors (Jackson, 1958, 1960). These general structural types may be related to the size of eggs and also indirectly to the ovipositional site (see Table 1). Most orthopteran and homopteran insects have comparatively large eggs that are laid into soil, clay, or vegetation (leaves or branches). In these cases, once a hole has been formed by the ovipositor it may not take much effort to move an egg the length of the egg canal. For these reasons the ovipositor scales may only need to be plate-like and not of a spine-like structure, to hold and move an egg. In the Hymenoptera, the majority of which are parasitic, there has probably been substantial selective advantage in not injuring a host at oviposition. If this is so, certainly the ovipositor could not be very large in diameter, and oviposition may need to be as rapid as possible. Small diameter ovipositors, where the valves are closely interlocked and prevented from expanding laterally (Tiegs, 1922; King, 1962; Smith, 1970) result in the egg being drastically deformed as it travels the length of the ovipositor (Fulton, 1933; King *et al.*, 1968). In this case, spine-like scales may facilitate the movement of the egg, which is greatly elongated and under substantial pressure.

In orthopteran and homopteran insects, the dorsal and ventral valves are certainly closely interlocked, but movement between the 2 halves of the ovipositor is possible. However, when the ovipositor is surrounded by soil or plant tissue, the valves may not be able to move apart, and then the egg would be deformed to some degree (Severin, 1935). It is not necessary for an egg to be squeezed by the valves to produce movement, as shown by *T. commodus*, which will readily oviposit into a dish of water.

Scales or spines have also been reported on the inside surface of the oviduct in some Hymenoptera (King and Copland, 1969; King and Ratcliffe, 1969; Copland and King, 1971a, 1972a,c). These have been described as aiding the movement of an egg along the oviduct and orienting it correctly at the proximal end of the egg canal. The above authors have shown that at least some secretions from the accessory reproductive glands probably function as lubricants to assist egg movement. These may be critical in reducing friction when the egg is drastically compressed.

With the evolution of such a mechanism to transport an egg, there may have been

considerable advantage in modifying an egg's structure to some degree. Certainly many Hymenoptera have pedicellate eggs, which are elongated and have a thin chorionic tail to act as a recess to accommodate the yolk as they are squeezed through the egg canal (Fulton, 1933; King *et al.*, 1968). Many species have eggs with surface sculpturing, such as spines and pits (King *et al.*, 1968; Askew, 1971); these structures may provide a rough surface that is easier for the scales to grip. However, such structures are not necessary for the mechanism to operate, as many insects have eggs with smooth chorions. Also surface sculpturing on eggs may play a more important role in respiration, adhesion or protection from host encapsulation, by acting to help retain secretions from accessory glands.

The only groups that appear so far to provide an exception, by possessing ovipositor but not scales, are some genera of caddis-flies. Of the 3 genera examined in this study, no information is available on their ovipositional behaviour (A. Neboiss, personal communication) and the site of egg deposition is known only for one species. The eggs of the marine caddis-fly, *Philanisus plebeius*, have been recorded from the body cavity of starfish (Anderson *et al.*, 1976; Anderson and Lawson-Kerr, 1977). These authors suggest that *P. plebeius* uses its ovipositor to penetrate the body wall of starfish, by probing through the surface of shallow water at low tide. Previously, Leader (1976) and Riek (1976) proposed that this species deposited its eggs in coralline tuft. More recently this has been confirmed for *P. plebeius* in New Zealand (Leader and Bedford, 1979). Until detailed observations on the ovipositional behaviour of *P. plebeius* are carried out the actual mechanics and method of oviposition will remain unknown.

Dissection of specimens of *Philanisus*, *Moruya* and *Ecnomina* reveals that ovipositors in these genera differ somewhat from those of other insects. The dorsal valves appear to be partly fused (see figures in Riek, 1976 and Neboiss, 1977). However, the ventral valves, in *Moruya* at least, are divided and have a sliding-interlocked arrangement. None of these genera has a serrated cutting edge on the distal end of the ovipositor, a structure which is characteristic of species that use their ovipositor to penetrate a host or plant tissue.

Possibly the ovipositor in some caddis-fly species is not used in the conventional manner, but rather as a probe to break the surface of water, so that a deposited egg will sink to the bottom sediments of a pond, rather than float on the surface and be open to predation. However, this does not explain the recorded oviposition sites of *Philanisus*. Study of these caddis-flies is important of a general understanding of the mechanics of insect oviposition is to be achieved.

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