MORPHOLOGY AND MECHANICS OF THE OVIPOSITOR SYSTEM OF *CERATOBAEUS* ASHMEAD (HYMENOPTERA : SCELIONIDAE) AND RELATED GENERA

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Abstract—This paper aims to describe the ovipositor system of *Ceratobaeus* spp. (Hymenoptera : Scelionidae), which is unlike that known for nearly all other parasitic Hymenoptera. It is invaginated into the body cavity and is detached from the terminal segments of the metasoma (gaster). It is contained within a sclerotized membranous tube and is connected to the posterior metasoma only by elongated muscles and apodemes. However, the ovipositor of *Ceratobaeus* appears to operate in essentially the same manner as has been described for other insects. A model for the mechanics of ovipositor movement, including extension and retraction from the body cavity, is proposed. Observations on ovipositional behaviour and morphology of the system provide support for the proposed model. Closely related genera (*Idris*, *Hickmanella* and *Baeus*) have ovipositor systems that are very similar in structure to *Ceratobaeus*. Only *Odontacolus* has an ovipositor that differs substantially from the previous genera, although it is also thought to be closely related to this group. The anatomy, mechanics, and evolution of the hymenopteran ovipositor are discussed in the light of the present study.

Index descriptors (in addition to those in title): Ovipositional behaviour, muscle, apodeme, functional morphology, insect egg, *Hickmanella*, *Idris*, *Odontacolus*, *Baeus*.

INTRODUCTION

THE OVIPOSITORS of parasitic Hymenoptera are primarily used to deposit an egg into or onto a host. Accessibility of the host may be affected by any structure, such as a cocoon, within which it resides. Secondly, ovipositors function as stinging devices in some species (Snodgrass, 1956). Presumably its morphological diversity is related to that of the substrata, which it has to penetrate. Different species must oviposit through soil, wood, leaves, various types of puparia and egg cases, and in the case of hyperparasites, insect tissue.

The anatomy and mechanics of the insect ovipositor have been well studied. Snodgrass (1931, 1933, 1935), Scudder (1961a,b, 1971) and Smith (1969, 1970) have shown that the morphology and operation of the insect ovipositor is complex, and that it works in a similar way in all groups. Recently, Austin and Browning (1981) have confirmed this by showing that nearly all insects that possess an ovipositor have posteriorly orientated scales located along the inside of the ovipositor valves. These scales act as a "linear ratchet", which moves eggs along the ovipositor when the valves slide back and forth.

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The structure of the ovipositor in different species of parasitic Hymenoptera varies both in length and its arrangement with the terminal metasomal segments. The ovipositor is usually very fine and would probably be damaged if it simply protruded from the posterior end of the body. As a consequence, it is protected in many species when it is not being used for oviposition (Scudder, 1971). Ichneumonids and braconids usually hold the ovipositor in a specialized sheath formed from the gonoplags (Snodgrass, 1933; Askew, 1971). Other species have the terminal segments and ovipositor partly invaginated either into or under the metasoma. Many chalcidoids are known to display this arrangement (King and Copland, 1969; Copland and King, 1971a). The ovipositor of the Aphelinidae is partly held within the body cavity and is extended by the terminal segments which rotate outwards, using a hinge mechanism between the ovipositor and the most posterior tergum (Copland, 1976).

In this study, the ovipositor of *Ceratobaeus masneri* sp. nov. (see below) is examined in detail, and supporting information is presented for some related species and genera. All are parasitoids of the eggs of spiders (Masner, 1976). The ovipositor of this group is completely invaginated into the body cavity and is detached from the terminal metasomal segments. The proximal end is connected to these segments only by elongated muscle bands and a semi sclerotized membranous tube, the latter separating the ovipositor from the haemocoel. The apodemes of the terminal segments are also greatly elongated and extend into the body cavity for at least half the length of the ovipositor. The ovipositors of *Ceratobaeus* and *Odontacolus* are longer than in related genera as they extend into the hollow horn-like process of the 1st metasomal tergum. Such horns (Figs. 4–6) are common in several scelionid genera and some platygasterids (e.g. *Inostemma*) (Askew, 1971; Baumann, 1938; Masner, 1976), and this structure undoubtedly represents an

FIG. 1. Scanning electron micrograph (SEM) of distal end of ovipositor of *Ceratobaeus masneri*. Scale = 10 µm.

FIG. 2. SEM of proximal end of ovipositor of *Ceratobaeus masneri*, after being treated with potassium hydroxide to remove soft tissues. Scale = 10 µm. a = valves of ovipositor; b = sensory hairs on gonoplags; c = gonoplags; d = ramus of the 1st gonapophysis (outer surface); e = ramus of the 2nd gonapophysis (inner surface); f = gonangulum; g = quadrate plate; h = 2nd gonocoxa; i = membranous tube of ovipositor.

FIG. 3. SEM of ovipositor and inside ventral surface of metasoma of *Ceratobaeus masneri*, after being treated with potassium hydroxide. Scale = 10 μ m. j = ovipositor shaft; k = apodemes; S = metasomal sternum; T = metasomal tergum.

FIG. 4. SEM of ♀ *Odontacolus* sp. (wings removed); dorsolateral view of mesosoma and T1 showing horn with compressed sides. Scale = 100 μ m.

FIG. 5. SEM of the dorsal surface of *Ceratobaeus masneri* (wings removed). Scale = 100 μ m.

FIG. 6. SEM of dorsal surface of *Ceratobaeus cuspidicornutus* (wings removed). Scale = 100 μ m.

adaptation to increase the length of the invaginated ovipositor. Other parasitic Hymenoptera, as far as is known, neither have the ovipositor completely invaginated into the metasoma nor have it detached from the terminal segments.

In the following section, the morphology of the ovipositor and associated structures, including the reproductive system of *C. masneri*, is described, and a model is put forward to explain the mechanics of ovipositor movement. Information to support the model is presented from observations on the behaviour of ovipositing wasps and from the morphology of the system. This work is compared with that published for other Hymenoptera, and general aspects of ovipositor mechanics are discussed.

The terminology of Scudder (1961b, 1964) is usually adopted when referring to parts of the ovipositor and associated structures. Alternative schemes have been proposed by various authors (Snodgrass, 1931, 1933; Smith, 1969, 1970; Copland and King, 1971a,b, 1972a,b,c) but that of Scudder has been most widely used and is adopted here. However, some confusion may arise from the terms used to number segments of the abdomen. The 1st abdominal segment (propodeum) of parasitic Hymenoptera is fused to the thorax, so that the remainder of the abdomen is referred to as the metasoma or gaster. The ovipositor is then derived from the 8th and 9th abdominal segments (Scudder, 1971) or alternatively, the 7th and 8th metasomal segments. The abbreviations T and S are used for the terms tergum and sternum e.g. T7 means the tergum of the 7th metasomal segment or alternatively, the 8th abdominal segment.

Most of the species of *Ceratobaeus* in this study are new and are presently being described by the author. The specific names used are therefore manuscript names only. They have been adopted here so that they can be referred to directly in later papers, and to eliminate the necessity for a numbering system e.g. *Ceratobaeus* sp. 1, 2, etc.

MATERIALS AND METHODS

The morphology of the cuticular parts was determined from observation of cleared slide-mounted material and from scanning electron microscopy (SEM). The anatomy of the reproductive system and the musculature of the ovipositor was described from dissected fresh specimens, stained whole-mounted specimens, and wax-embedded and epoxy-resin-embedded sections.

Fresh specimens were partly dissected under saline using fine tungsten wire needles (Pantin, 1946). These needles were produced by etching the end of tungsten wire to a point in molten sodium nitrate. Specimens were placed in 10% potassium hydroxide (2–6 hr at 40°C) to dissolve away all soft tissues, washed in 70% ethanol and dehydrated in 100% ethanol (2 changes, 15 min each), then either transferred to clove oil (12–24 hr) to be cleared and mounted on slides using Canada Balsam or SIRA mountant, or dried in a desiccator (24 hr) and prepared for SEM examination (see Austin and Browning, 1981). Some specimens were critical-point dried in liquid carbon dioxide (Nemanic, 1972) and then treated as for air-dried specimens.

Material for whole-mount preparations was dissected in Ringer's Solution using tungsten needles, washed and mounted unstained on microscope slides in Ringer's, then partly squashed under large coverslips. Others were dissected, fixed in formol acetic acid (FAA) (Austin and Browning, 1981: 6 hr), washed in 70% ethanol, hydrated in an ethanol series, stained with Mayer's Haemalum or Borax Carmine (1–5 min), and dehydrated and mounted as for potassium hydroxide treated material.

Pharate adults (18–20-day old, reared at 25°C) only were used for wax-embedded sectioning, as individuals of this age were not heavily sclerotized, yet the ovipositor and its associated musculature and the reproductive system were well developed. The cuticle of later stages is very thick relative to the size of the insects and sectioning caused the cuticular wall to shatter, causing internal structures to become distorted. Pharate adults were dissected from parasitized host eggs; they were fixed in FAA (24 hr), dehydrated, embedded in 60°C m.p. wax, sectioned at 7–10 µm, stained with Mayer's Haemalum or Heidenhain's Iron Haematoxylin, and mounted on slides using Eukitt's Mountant.

Adult wasps were fixed in 3% glutaraldehyde in 0.2 M sodium cacodylate (pH 7.2), washed in buffer and dehydrated in an ethanol series, transferred to Spurr's Medium (Spurr, 1969) (24–36 hr; 3 changes), embedded, and sectioned at 0.5–1.0 µm using a Sorvall Porter Blum MT2P Ultramicrotome. Sections were stained with Toluidine blue (10 sec at 80°C).

OBSERVATIONS AND RESULTS

General morphology of the female metasoma

The metasoma (gaster) of *C. masneri* is dorsoventrally flattened and comprises 7 terga and 6 sterna (Fig. 5). The laterotergites (pleurites) are closely attached to the sterna and are represented as narrow impressed plates, hidden by the terga in dorsal view. They are weakly sclerotized and stretch to accommodate the additional volume of the ovaries when females are gravid.

The first tergum (T1) is expanded dorsally into a short hollow horn which is continuous with the haemocoel. The first 3 segments are large and comprise approximately three-quarters of the length of the metasoma, so that the posterior segments are quite short. There is one extra dorsal sclerite (T7) which forms a small terminal triangular plate.

Terminal segments and internal apodemes

T7 and S6 form the dorsal and ventral posterior sclerites of the metasoma. Leaf-shaped pygostyles are situated in small lateral depressions on each side of T7. Each has one or more long hairs which are believed to be sensory in function.

The inner surfaces of T7 and S6 are divided by narrow transverse ridges. These ridges form the attachment points for intersegmental membranes, that join these plates to the preceding sclerites (T6 and S5) and to each other. The intersegmental membranes contain the haemocoel and also provide some freedom of movement between sclerites, which allows for expansion and contraction of the body wall.

Behind these ridges, T7 and S6 extend anteriorly into the body cavity, to form 2 large flat plates which almost reach the anterior margins of T5 and S5 respectively. They also form the subgenital plate (S6) and supragenital plate (T7) for the ovipositor (Fig. 8). Their anterior margins are extended to form 3 greatly elongated apodemes; 2 dorsolateral apodemes from T7, and one ventromedial apodeme from S6. They are formed from long cuticular extensions and extend almost to the level of the anterior margin of T3, the medial apodeme being slightly shorter than the lateral ones (Figs. 3, 8). They are semi-rigid and spring back to a longitudinal position when flexed laterally. The anterior end of each apodeme is flattened and curved, forming a surface for the attachment of muscles.

The ovipositor

The ovipositor is formed from 3 valves (stylets) (Fig. 1), interlocked for most of their length by a tongue and groove arrangement, which prevents the valves from pulling apart, but allows them to oscillate back and forth on each other. This movement, combined with the spine-like scales along the inner surface of the valves (Fig. 14, in Austin and Browning, 1981), provides the mechanism for eggs to be moved along the length of the ovipositor.

The 2 ventral valves (1st gonapophyses) are separate but interlock with the dorsal valve (fused 2nd gonapophyses). As the ventral valves are not fused they are able to open slightly to accommodate the large diameter of an egg as it passes down the length of the ovipositor.

The ovipositor is approximately 760 μm long, and is slightly longer than the metasoma (720 μm); it curves dorsally into the recess of the horn on T1. The ovipositor shaft is extremely narrow; it is only 4.5 μm wide, 30 μm from the distal end. The ovipositor becomes wider proximally but is never more than 10 μm wide.

FIG. 7. Light microscope micrograph of ovipositor, reproductive and digestive systems, after being dissected from a fresh specimen of *Ceratobaeus masneri*. Scale = 100 μ m. a = accessory gland; b = membranous tube; c = ovipositor protractor muscle; d = ovipositor retractor muscle (broken); e = common oviduct; f = apodeme; g = ovaries; h = midgut; i = malpighian tubules; j = hindgut; T7 = 7th metasomal tergum.

FIGS. 8–10. Plan view of metasoma showing relative lengths of apodemes, ovipositor and gonoplags (membranous tube not included; ovipositor and gonoplags displaced laterally. N.B. ovipositor is longer than metasoma as it normally curves into horn). (8) *Ceratobaeus masneri*. a = border of sterna; b = lateral apodeme; c = medial apodeme; d = subgenital plate (S6); e = supragenital plate (T7); f = ovipositor shaft; g = gonoplag. (9) *Ceratobaeus cuspidicornutus*. (10) *Baeus* sp. Scales = 100 μ m.

The outer surface of the tip of the ovipositor possesses the characteristic teeth or barbs, present in most parasitic Hymenoptera (Fig. 1) (Copland and King, 1971a, 1972a,b). They presumably help to cut into the oviposition site, and then hold the shaft in place. No sensory structures could be identified on the outside surface of the ovipositor of *C. masneri*. Sensory pits and hairs have been recognized in other parasitoids (e.g. Copland and King, 1971a, 1972a; Hawke *et al.*, 1973), and these have been shown to be involved in host selection (Hays and Vinson, 1971; Vinson, 1975). In *C. masneri* this function is probably served by sensilla on the antennae, gonoplags, or inner surface of the valves.

The ovipositor, which fits between the subgenital plate (S6) and supragenital plate (T7), is held inside the body cavity, but is separated from the haemocoel by a greatly elongated

tubular recess formed from a lightly sclerotized but flexible part of the integument (Figs. 3, 7, 14, 15). This tube collapses when the ovipositor is extended from the body, prior to oviposition. It is proposed that this semi-membranous tube is homologous with the intersegmental membrane between segments 8 and 9 in other insects. This hypothesis is supported by the fact that the membrane (referred to hereafter as the "membranous tube") is attached distally to the inner surface of T7 and S6 (abdominal segment 8), and is attached proximally to the anterior end of the ovipositor, part of which represents the highly modified remnants of abdominal segment 9 (see below).

The gonoplags (3rd valvulae or ovipositor sheath) lie beside the ovipositor shaft and are attached to the wall of the membranous tube (Fig. 14). They are extended with the ovipositor, which is supported or braced by them during oviposition. The gonoplags are usually formed from outgrowths of segment 9 (Scudder, 1971), but in *C. masneri* they are clearly separated from this segment. The distal end of each gonoplac has 3 long sensory hairs (10–15 μm in length), seated in small depressions (Fig. 1).

The proximal end of the ovipositor is formed from a complex array of sclerites and muscles that work to produce the oscillating movements of the valves. The 1st and 2nd gonapophyses give rise to paired rami on each side, which are interlocked and curved dorsally (Fig. 2). The rami of the 1st gonapophyses are connected to the gonangula (Scudder, 1957, 1971) (the 1st gonocoxae being absent in Hymenoptera); the gonangula, in turn, are fused dorsally to the quadrate plates (abdominal segment 9), and are hinged ventrally to the 2nd gonocoxae. The 2nd gonocoxae are attached anteriorly to the rami of the 2nd gonapophyses, the latter being fused for most of their length, but divided proximally to form the rami. The 2nd gonocoxae form 2 prominent arms that are expanded apically into curved flanges, and act as the attachment surfaces for muscles. The shapes of the above sclerites differ from those in other Hymenoptera, but the basic plan and mechanics appear to be the same. The sclerites, which form the proximal end of the ovipositor are extremely compact. They are only 50 μm wide and 160 μm long from the anterior surface to the ends of the 2nd gonocoxae.

Musculature and mechanics of the ovipositor

There appear to be 2 separate sets of muscles involved in the control of the ovipositor. The 1st set produces the rapid oscillation of the valves, as a consequence of the rocking motion of the gonangula on the 2nd gonocoxae. This in turn causes the rami to slide back and forth (oscillate) over each other (see Snodgrass, 1956; Scudder, 1971). This backwards and forwards movement is responsible for cutting into the oviposition site, as well as movement of eggs along the ovipositor shaft (Austin and Browning, 1981). The retractor muscles that bring about this movement are attached between the arms of the 2nd gonocoxae and the quadrate plates. Protractor muscles could not be found in any preparation of *C. masneri*, but they are probably located on the inside of the quadrate plates, running from them to the rami of the 2nd gonapophyses. These muscles could be hidden within the complex arrangement of sclerites that make up the proximal end of the ovipositor. If so, the difficulty of sectioning this part of the ovipositor would preclude their identification.

The retractor and protractor muscles operate antagonistically to rock the gonangula on their hinges with the 2nd gonocoxae, causing the rami of the 1st gonapophyses to be pulled and pushed over the rami of the 2nd gonapophyses (Scudder, 1971). Occasionally, in preparations where live specimens were dissected in hypertonic saline, the retractor

muscles spontaneously contracted and relaxed rapidly, causing the ovipositor valves to oscillate back and forth.

A second set of muscles is also associated with the ovipositor of *C. masneri*. This comprises bands of muscle attached from the proximal end of the ovipositor to the inner surfaces of T7 and S6 (abdominal segment 8) referred to hereafter as "ovipositor retractor muscles" (Figs. 7, 11, 14), and another series of muscles attached from the proximal end of the ovipositor to the tips of the 3 elongated apodemes ("ovipositor retractor muscles"). These muscles are believed to be responsible for extension and retraction of the ovipositor from the body (see discussion below).

The origin of these muscles is unclear, but it is likely that both the ovipositor protractor and retractor muscles are derived from intersegmental muscles between abdominal segments 8 and 9, their function changed due to the unique elongation and invaginated nature of the system.

Ovipositional behaviour

C. masneri searches for the silk nests of its host spider (*Clubiona robusta* L. Koch) under the bark of eucalypt trees. Once a nest is located the wasp enters and inspects the surface of the eggs with its antennae. If the eggs are suitable (i.e. not too old and not previously parasitized) oviposition commences. The wasp stands on an adjacent egg, facing away from the target egg, and extends its ovipositor fully to penetrate the latter. During this process the antennae remain motionless, while the head and pronotum together move backwards and forwards from the rest of the body, at a rate of approximately once per sec. The time taken from orientation of the body to withdrawal of the ovipositor is 45–90 sec (60 observations). The ovipositor is often only partly retracted before being extended to penetrate another egg. It can be orientated approximately 20° away from the longitudinal line of the body, but always remains perfectly straight. If the wasp cannot successfully reach another egg by reorientating the ovipositor alone, then the whole body is moved to achieve alignment with the next egg.

A model for ovipositor extension and retraction

Using the morphological, anatomical and behavioural information described above, the following descriptive model is put forward to explain the extension and retraction of the ovipositor in *C. masneri*.

1. The main ovipositor protractor muscles act to collapse the membranous tube and extend the ovipositor and gonoplags (Figs. 11, 14); the latter are extended passively from the body, together with the final section of the ovipositor.
2. Partial contraction of different combinations of the ovipositor retractor muscles allows the ovipositor to be orientated away from the longitudinal line of the metasoma.
3. Retraction of the ovipositor is achieved by the combined contraction of the ovipositor retractor muscles and the elasticity (spring) of the apodemes that are flexed during ovipositor extension, or by changes in hydrostatic or haemolymph pressure in the body cavity.
4. The muscle system responsible for extension and retraction of the ovipositor operates antagonistically.
5. When the ovipositor is withdrawn into the body cavity, it is held there clamped between T7 and S6.

FIG. 11. Stylized diagram showing probable changes in lengths of muscles and the position of ovipositor, when latter is extended and retracted (membranous tube not included). a = gonocoxae; b = ovipositor retractor muscle; c = ovipositor protractor muscle; d = lateral apodeme; e = medial apodeme; f = ovipositor shaft; g = subgenital plate (S6); h = supragenital plate (T7).

FIGS. 12, 13. Plan view of metasoma showing relative lengths of apodemes, ovipositor and gonoplags. (12) *Idris* and *Hickmanella* spp. (13) *Odontacolus* sp. See Fig. 8 for captions to structures in Figs. 12, 13. Scales = 100 μ m.

Discussion of the model

Sections of individuals with partly extended ovipositors indicate that the ovipositor protractor muscles are responsible for extension of the ovipositor and that the membranous tube surrounding the ovipositor does indeed collapse as the latter is extended (point 1 of the model) (Fig. 11). These sections also show that the gonoplags are not extended until the proximal end of the ovipositor reaches the anterior end of the gonoplags. The latter are then presumably pushed out as the ovipositor is pulled down further by the ovipositor protractor muscles. Conversely, the gonoplags are not withdrawn until the distal end of the ovipositor reaches that of the gonoplags. This process is also confirmed by observation of ovipositing wasps (Austin, 1982).

The only muscles identified that could possibly orientate the ovipositor (point 2) are the ovipositor retractor muscles. Presumably slight contraction of these muscles, singly or in pairs, pulls the ovipositor towards the side of the contraction, thereby allowing the ovipositor to be orientated in that direction.

FIG. 14. Dorsal view of metasoma of *Ceratobaeus masneri* showing muscle system of ovipositor and position of ovaries and oviduct.

FIG. 15. Lateral view of metasoma of *Ceratobaeus masneri* showing ovipositor in invaginated membranous tube (N.B. muscles and apodemes not shown). Scale = 10 μ m. a = border of terga; b = 2nd gonocoxa; c = ovipositor shaft; d = membranous tube; e = lateral apodeme (N.B. medial apodeme hidden by ovipositor and muscle); f = gonoplac; g = supragenital plate (T7); h = retractor muscle responsible for oscillation of ovipositor valves; i = ovipositor protractor muscle; j = ovipositor retractor muscle; k = oviduct; l = ovary.

The present understanding of ovipositor retraction is incomplete (point 3). Contraction of the ovipositor retractor muscles can only bring the ovipositor to the level of the anterior end of the apodemes, i.e. only about 75% of the ovipositor would then be withdrawn.

Retraction of the remaining 25% may be achieved in either of 2 ways. Elasticity of the apodemes may produce a spring effect when they are flexed, causing the ovipositor to be pushed above the level of the apodemes. There is, however, little evidence for this hypothesis. Alternatively, lowering the hydrostatic pressure in the body cavity may draw the ovipositor completely into its tube. This hypothesis is supported by observation of female *C. masneri*, which shows they flex the pronotum in and out during oviposition and ovipositor retraction. Such movements may cause changes in the volume of the body cavity, thereby changing the hydrostatic pressure. This mechanism could be assisted by muscle contraction, or alternate clamping of the ovipositor between the supragenital (T7) and subgenital (S6) plates, to stop it from being accidentally extended when tergal pressure increases. This is similar to the mechanism proposed for stylet (mouth parts) retraction in some bugs (Miles, 1958; Pollard, 1970, 1972). The clamp would also hold the ovipositor in its resting position, when it has been completely withdrawn into the body (point 5). Sectioned material shows that the musculature between T7 and S6 could operate to clamp these plates together but there is no other information to show a clamp mechanism actually exists.

More information is needed if the mechanics of ovipositor retraction in *C. masneri* are to be better understood. It is necessary to fix and section wasps with their ovipositors in varying degrees of retraction, in order to determine which muscles, if any, are involved in this process. So far this has not proved possible. Ovipositing females were killed using a variety of fixatives and other agents, yet in nearly all cases they fully retracted their ovipositors before they died. In fact, it appears that *C. masneri* retracts its ovipositor in response to any disturbance, e.g. loud noise, air turbulence or rapid changes in air temperature. Occasionally wasps partly extended their ovipositors when they were dropped into FAA fixative. These specimens provided much of the information that has been presented in this section.

There is some evidence to suggest that the ovipositor protractor and retractor muscles act antagonistically (point 4); that is to say that contraction of one set of muscles inhibits contraction of the other set. This would be necessary to prevent these muscles from contracting against each other. Ovipositor responses can be assumed to require integration of information about host acceptance from sensilla on the gonopods, ovipositor or antennae (leading to extension of the ovipositor), and information on release of an egg from stretch receptors in the ovaries or oviducts (leading to retraction of the ovipositor).

When the ventral nerve cord of *C. masneri* is cut at a point between the mesosoma and metasoma, the ovipositor is immediately extended for 23% of its length ($\bar{x} = 23.1\%$, ± 0.62 S.D., $n = 20$). This places the proximal end of the ovipositor in a position almost level with the lateral apodemes. It is proposed that this position represents the equilibrium point for the ovipositor, when both retractor and protractor muscles contract simultaneously and therefore against each other, i.e. antagonistic contraction is prevented in some way.

Possibly these muscles are of the supercontracting type. For the previous model to work it is necessary that at least the main ovipositor protractor muscles contract approximately 90% of their resting length, to extend the ovipositor fully. Measurement of wasps fixed with their ovipositors partly extended, indicates that these muscles can contract by at least 50% of their resting length, hence suggesting their supercontractile nature (Osborne, 1967).

Anatomy of the reproductive system

The reproductive system of *C. masneri* is similar to that of other parasitic Hymenoptera (e.g. Bender, 1943; Copland and King, 1971a,b, 1972a,b,c; Copland *et al.*, 1973) except that the common oviduct is greatly elongated; it can thus follow the movements of the ovipositor without being stretched (Figs. 7, 14). There are 2 accessory glands attached to the common oviduct. One of these probably functions as a lubricating gland that coats eggs with a mucous secretion to assist their passage along the ovipositor (Rafai and King, 1972). The spermatheca joins the base of the common oviduct, just before the latter divides into the lateral oviducts. The lateral oviducts are relatively short and expand distally to join the ovaries. Most of the volume of the metasomal cavity is occupied by the ovaries (Fig. 14). When mature they each contain 30–35 greatly elongated eggs (Fig. 7); 250–350 μm long and 30–40 μm wide. They are much larger in diameter than the ovipositor (5–10 μm) and are therefore drastically deformed as they travel the length of the egg canal. In parasitic Hymenoptera that possess this type of egg, the chorionic tail acts as a recess to accommodate the yolk as the egg is deformed between the valves of the ovipositor (Fulton, 1933, King *et al.*, 1968).

During copulation, the membranous tube of the ovipositor also functions as a vagina and receives the aedeagus. Seminal fluid must be taken in at the opening of the oviduct at the base of the proximal end of the ovipositor, and then passed to the spermatheca for storage prior to fertilization.

Comparative morphology of the ovipositor system for related species and genera

Examination of 30 species in the genera *Ceratobaeus* (12), *Idris* (10), *Hickmanella* (2) and *Baeus* (6) show them to have the same basic plan for the ovipositor system as *C. masneri*. Some structures vary in shape and size compared with the latter species, but their function can still be explained in terms of the proposed model for ovipositor movement.

Species of *Ceratobaeus* that have an extremely elongated metasoma and horn (e.g. *C. cuspicornutus* sp. nov., Figs. 6, 9) simply display comparable elongation of the apodemes and components of the ovipositor. The relative lengths of the apodemes compared with those of the ovipositors of all species examined are very similar to the ratio measured for *C. masneri*, and may therefore represent a ratio that is critical to the mechanics of ovipositor extension and retraction. In those species with very long apodemes, the lateral ones are fused basally but divide into lateral arms apically. Some species have the medial apodeme longer than the lateral ones (e.g. *C. clubionus* sp. nov.). Also the 2nd gonocoxae and supragenital plate (T7) vary in shape and length between some species. For example, these structures are more elongated in *C. lamponae* (Hickman) compared with *C. masneri*, even though the metasomas of these 2 species are approximately the same length.

The only difference found in species of *Idris* and *Hickmanella* (Fig. 12) compared with *Ceratobaeus*, is that ovipositors in the former 2 genera are much shorter ($\frac{1}{2}$ – $\frac{3}{4}$ the length of the metasoma) and are accompanied by shorter apodemes. No species examined had the ovipositor as long as in any *Ceratobaeus* species. Members of the genus *Baeus* are morphologically quite distinct from the previous genera yet they also have an ovipositor system similar to that found in *C. masneri* (Fig. 10).

Species of *Odontacolus*, however, appear to have an ovipositor that differs substantially from that described for the previous genera. The ovipositor is approximately twice the length of the metasoma, looping back on itself in the broad apical end of the metasomal horn (Fig. 13). Therefore, when it is retracted, the proximal end lies near the

base of T7 and S6, and not in the apical end of the horn, as in *Ceratobaeus*. This arrangement explains why in *Odontacolus*, the horn is compressed at the sides and broadly rounded apically (Fig. 4), for this shape would protect the shaft of the ovipositor from possible damage by preventing it from being bent at an acute angle. There are 3 apodemes present, similar to the configuration in *C. masneri*, but they extend at least to the base of the horn in *Odontacolus*. No information could be obtained on the muscular system or arrangement of the sclerites at the proximal end of the ovipositor. *Odontacolus* species are rare; only 2 preserved specimens were available for study. However, the mechanics of the ovipositor system in this genus cannot yet be explained in terms of the proposed model. At this stage it is not possible to put forward any sound alternatives. Until more is known about the morphology and musculature of the ovipositor in *Odontacolus* its operation will remain obscure.

DISCUSSION

The ovipositor has evolved independently in many insect families, and yet the fact that the mechanics of its operation are much the same in each of them strongly indicates that it has evolved from a basic plan. The evolution of the insect ovipositor has been the subject of many investigations, mostly using information on its comparative morphology, although some workers have considered functional aspects.

The majority of studies on the ovipositor system of Hymenoptera has utilized large species, e.g. Apidae (Snodgrass, 1933, 1935, 1956; Smith, 1970), Formicidae (Robertson, 1968), Ichneumonoidea (Snodgrass, 1933, 1935; Bender, 1943), Scolioidea (Robertson, 1968; Smith, 1970), Symphyta (Snodgrass, 1933, 1935). This bias towards such species is doubtless because they are easier to study. Work by Copland and King (1971a,b, 1972a,b,c) on members of various families of Chalcidoidea represent the only substantial studies on smaller wasps.

This study, and that by Austin and Browning (1981), have shown that the ovipositor of *Ceratobaeus* operates in the same way as that described for other insects: oscillating movements of the valves are responsible for penetration into a host and movement of an egg along the ovipositor. All components of the ovipositor are homologous with those described by previous authors (Snodgrass, 1931, 1933, 1956; Scudder, 1961a,b, 1964, 1971; Smith, 1969, 1970), even though those in *Ceratobaeus* vary in shape and/or position.

In insects that possess an unprotected ovipositor, the structure is heavily sclerotized and is used to penetrate hard substrata to reach an oviposition site. Some orthopterans, hemipterans and ichneumonids have an ovipositor of this type. However, in most parasitic Hymenoptera the ovipositor is a thin structure, a small diameter having probably evolved to reduce possible injury to the host. Such ovipositors are fragile structures that require protection when not being used. In most species protection is afforded by the development of an ovipositor sheath or partial invagination of the ovipositor into or under the metasoma.

The ovipositor system of *Ceratobaeus* is highly modified and differs from most other Hymenoptera in that it is completely invaginated into the body cavity and is not directly connected to the terminal or pregenital segments. This arrangement, however, can be seen simply as a different solution to the problem of protecting a fragile ovipositor, for in *Ceratobaeus* and related genera it is completely surrounded by the metasoma when it is not being used. Its evolution has undoubtedly depended on the development of a system

to extend and retract the ovipositor from this deep recess, and by mechanics which are completely independent of the oscillating movements of the valves. The tube surrounding the ovipositor is believed to be derived from the intersegmental membrane between abdominal segments 8 and 9. Extension of the ovipositor is probably achieved by protractor muscles derived from the intersegmental muscles between these same 2 segments. However, the mechanism for retraction is not fully understood. Contraction of the associated musculature (ovipositor retractor muscles) alone cannot be responsible for the complete retraction of the ovipositor. Two hypotheses for alternative mechanisms are proposed. These are: (1) muscle contraction in conjunction with flexure of the apodemes and (2) changes in tergal pressure of the body cavity, possibly assisted by alternate clamping of the terminal segments against the ovipositor. So far there is little information to support or reject the above hypotheses. More detailed study will be required if the mechanics of ovipositor retraction in *Ceratobaeus* is to be adequately explained.

Of the scelionid genera that are most closely related to *Ceratobaeus*, *Idris*, *Hickmanella* and *Baeus* all have the same basic plan for the anatomy of the ovipositor and associated structures. Only *Odontacolus* possess an ovipositor differing from that described for *Ceratobaeus*. There is some evidence to suggest that the morphology of the ovipositor system is of some systematic value and that it could be used to clarify the supergeneric classification of Scelionidae (Masner, 1976; personal communication L. Masner). If this is the case then the present information would indicate that *Odontacolus* is more distantly related to *Ceratobaeus* than the other 3 genera examined. However, no detailed studies have been made on the ovipositor system of other scelionid genera and so the systematic value of this structure therefore remains obscure.

The morphology of the ovipositor must be closely linked to selective advantages derived from the exploitation of particular hosts, and must be related to the rather high degree of host specificity found in the parasitic Hymenoptera. Some evidence from the host relationships of the Scelionidae supports this hypothesis (Austin, 1982; personal communication L. Masner). Differences in the structure of the ovipositor most probably reflect particular features of respective host groups (e.g. spiders, orthopterans, hemipterans, embiids, etc.) utilized by different scelionid genera or tribes. If this can be demonstrated in the future then ovipositor morphology could be used to predict the likely host groups, or at least ovipositional sites, of scelionids for which hosts remain unknown.

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