The function of some remarkable crane-fly ovipositors.

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1. **Introduction.**

The function of typical ovipositors for superficial deposition of eggs, as found in the majority of crane-flies and of the atypical deep-boring ovipositors with shovel-shaped cerci of the subgenus *Vestiplex* Bezzi and of the *Tipula juncea*-group (= subgenus *Odonatisca* Savchenko 1956) were explained in a previous paper (Hemmingsen, 1956, p. 282 seqq.). Briefly, the function of the cerci (upper or tergal valves) of a typical tipulid (fig. 1) is to open the soil by abduction (opening) of the two valves, whereas the function of the hypovalves (= hypogynal, lower, or sternal valves) is to receive and hold the egg which has been thrown out from the genital orifice, to penetrate into the slit created by the opening of the cerci and there to squeeze out the egg into the substrate. In the deep-boring species the soil-opening function of the cerci has been extended. They have become shovel-shaped, and by alternate abductions and adductions both in the frontal and sagittal planes produce a boring canal in which the eggs are laid. There is no need having any hypovalves to guide the eggs into the soil, and they are accordingly strongly reduced. It is to be expected, on the other hand, that if there were species which (1) laid the eggs on the surface of the substrate or (2) in water, where there would be no need for having the substrate opened, both the cerci and the hypovalves might be re-

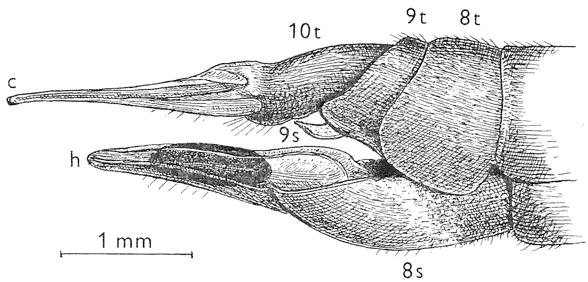

Fig. 1. Ovipositor of *Tipula oleracea* "L. 1758". Cerci slightly lifted. The segment numbers apply to the undoubtedly visible segments. c: cerci; h: hypovalves; s: sternite; t: tergite. Drawn by Mr. H. Bülow-Hansen from preserved specimen. Reproduced from Hemmingsen, 1956, fig. 15 on p. 284.

duced. Perhaps species of the *Tipula fascipennis*-group represent possibility (1); *Tipula saginata,* possibility (2).

We shall in this paper also study some other lines of specialization of ovipositors in tipulids. First we shall study some ovipositors (of *Limoniinae*) which may perhaps represent more original stages; next we shall study representatives of the *T. fascipennis*-group (*T. vernalis* and *T. fascipennis*) and *T. saginata,* in which both the cerci and the hypovalves are reduced; *T. livida* in which not the cerci but the hypovalves are somewhat reduced, possibly representing a stage in the evolution of the deep-boring species; and finally three species of *Cylindrotominae,* in which either the substrate-opening function of the cerci has been modified into cutting slits in the epidermis of leaves by means of sawing movements (*Cylindrotoma distinctissima*); or, movements reminiscent of these sawing movements, though performed during oviposition, have no substrate-opening function (*Diogma glabrata* and *Phalacrocera replicata*).

Unless otherwise stated the actual mechanism of egg extrusion from the ovipositor was studied under the stereomicroscope by holding the wings of a gravid female fly with the left fingers and placing her ovipositor onto wet cotton (cf. fig. 9). In some cases the process could be started, if necessary, by gently pressing the abdomen with a finger or a pair of pincers.

2. *Limoniinae* with egg-guiding lid.

It was demonstrated (Hemmingsen, 1956, p. 285—286) that in some *Tipula* species a small projection above the genital orifice, supposed to be the reduced 9th sternite (see fig. 1), assists the downward pressure of the base or "stalk" of the cerci in guiding the egg in between the hypovalves, and it was mentioned that in some *Limoniinae* this projection is much longer and constitutes a sort of lid to the "hypovalvular boat" in which the egg is led before being squeezed out by the hypovalves into the soil.

Besides in the species already mentioned in the previous paper I have seen the lid in *Limonia (Dicranomyia) chorea* Meigen, *Limonia (Limonia) tripunctata* Fabr. (fig. 2), *Limonia (Metalimnobia) elegans* Zett. and *L. (M.) quadrinotata* Meig. (cf. Tjeder, 1958, p. 143 and figs. 15—17 on p. 149, where for the latter two species and *L. (M.) quadrimaculata* the lid is called vaginal apodeme).

The actual process was studied in *L. (D.) chorea*. The movements accompanying the ejection of the egg into the hypovalvular boat could be seen, though the egg could not be seen, being hidden in the container formed by the hypovalves and the lid. Thereafter the egg was squeezed out by the hypovalves as in other tipulids, with cerci opened.

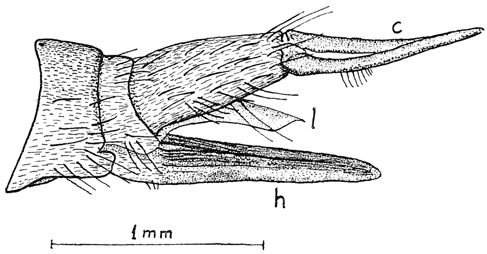

Fig. 2. Ovipositor of *Limonia (Limonia) tripunctata* Fabr. Strødam, beginning of July, 1956. c: cerci; h: hypovalves; l: lid (9th sternite). Drawn by Mr. Kay W. Petersen from the preserved specimen.

In such ovipositors there is no need having the egg pressed into the hypovalvular boat by assistance on the part of the cerci. In the species of *Limonia (Metalimnobia)* above mentioned (and also in *L. (M.) bifasciata* Schrank) the cerci are remarkably short.

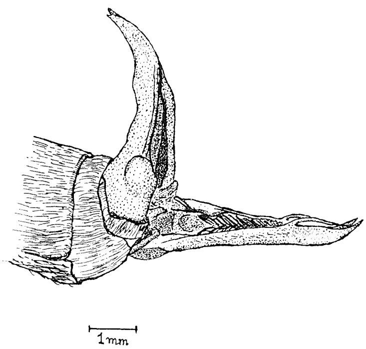

Fig. 3. Ovipositor of *Pedicia (Pedicia) rivosa* L. Strødam, August 1955. The cerci are bent strongly upwards in order to show the hairs at the edge of the "hypovalvular boat". Drawn by Mr. Kay W. Petersen from the preserved specimen.

Some *Limoniinae* have no such lid, e. g. *Epiphragma ocellaris* L., *Limnophila (Elœophila) maculata* Meigen, *Limnophila (Limnophila) punctata* Schrank, and *Pedicia (P.) rivosa* L. But in these four species the upper edge of the hypovalves — at least in part — is provided with hairs which point obliquely inwards-backwards and which — at least in two of these species aided by an inward bending of the edge — constitute a cover, more or less replacing the lid (fig. 3). They are indicated for *Pedicia rivosa* by Grünberg (1910, fig. 64 on p. 60). If one tries to squeeze out the egg, the hairs are seen to hold about it. In all four species the two hypovalves are fused underneath; in the three first mentioned species in the shape of a membrane; in *P. rivosa* along a seam which is visible only below the line of fusion, but not above in the bottom of the "hypovalvular boat".

To the category without lids belongs also *Limnophila (Idioptera) macropteryx* Tjeder (as judged from Tjeder, 1958, p. 133—134, figs. 1—4 on p. 135). According to Tjeder the hypovalves of *L. (I.) macropteryx* are composed of three pairs of "valves". The dorsal pair which on the posterior half of their inner edges have hairs that point obliquely inwards-backwards, correspond to what above was described as an inward bending of the upper edge of the hypovalves. According to Tjeder only the hypovalves form the ovipositor. As, however, in tipulids in general both the cerci and the lid, when present, aid in oviposition, such restriction of the term ovipositor seems unfortunate. It would mean, for instance, that the *Vestiplex* and *Odonatisca* species had no (or rather extremely reduced) ovipositors.

I looked in vain for a lid in one species of *Ptychoptera* and one of *Trichocera*.

3. *Tipula (Lunatipula) vernalis* Meigen.

In this and the following species both the cerci and the hypovalves are reduced (figs. 4—5); and the eggs have a peculiar shape compared with other tipulid eggs (fig. 6). They are black like the eggs of other *Tipulinae*. A rounded edge around the egg divides it into an upper and a lower part. There is a transverse rounded edge on the flatter upper side and a longitudinal rounded keel-like edge on the lower side, the former usually situated about above the highest point of the latter (up and down defined from the position of eggs in the ovipositor). The micropyle (fig. 6) is on the lower side near

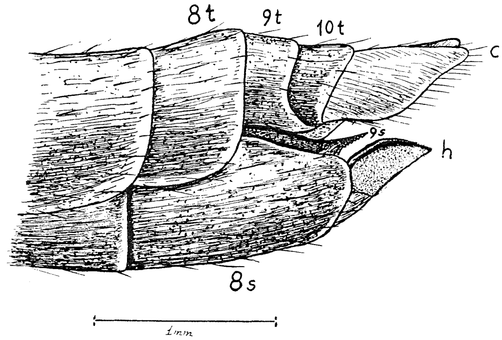

Fig. 4. Ovipositor of *Tipula (Lunatipula) vernalis* Meigen. Collected by the author at Vedersø Klit (dunes), West Jutland, 17—24/VI. 1956. c, cerci; h, hypovalves; s, sternite; t, tergite. Drawn by Mr. O. Dybkjær from the preserved specimen.

the end from which the distance to the transverse keel is shortest (when this distance could at all be ascer-

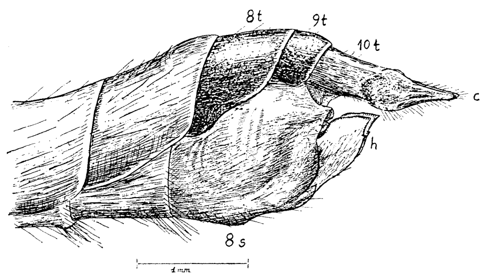

Fig. 5. Ovipositor of *Tipula (Lunatipula) fascipennis* Meigen. c, cerci; h, hypovalves; s, sternite; t, tergite. Drawn by Mr. O. Dybkjær from preserved specimen.

tained to be shorter from one end than from the other). This micropylar end comes out last. Also in an ordinarily shaped tipuline egg the micropyle is on the lower side near the end that comes out last, so that it is easy to homologize the various parts of these keeled eggs with those of ordinarily shaped tipuline eggs. The peculiar shape apparently makes the eggs in question more resistant to shriveling than tipulid eggs of the ordinary shape,

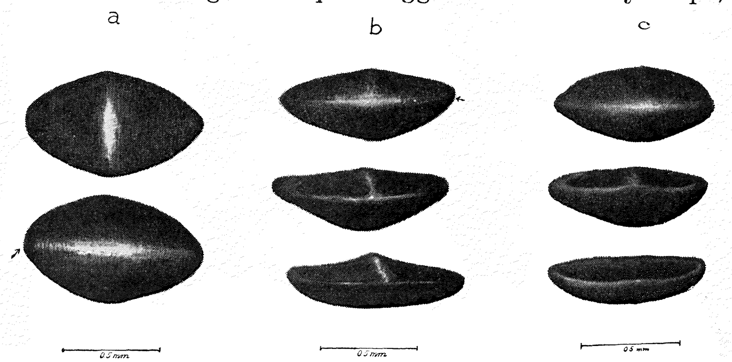

Fig. 6. Eggs of *Tipula (Lunatipula) vernalis* Meigen and *Tipula (Lunatipula) fascipennis* Meigen. Dorsal view: *T. vernalis* in left row (a) above. Ventral view: *T. vernalis* in left row (a) below. Lateral views: *T. vernalis* in middle row (b); *T. fascipennis* in right row (c). The two lower eggs in each of these rows (b and c) are in progressing degrees of desiccation. Arrows point to site of micropyle. Drawn by Mr. O. Dybkjær from preserved eggs.

though as seen in the figure desiccation produces one depression on either side of the transverse (upper) keel and, at least in some *T. vernalis* eggs, two on either side of the longitudinal (lower) keel. In cross section the recently laid egg is approximately triangular, as stated by De Jong (1925, p. 43) for *T. vernalis*.

Fig. 7. Micropylar area of the egg of *Tipula (Lunatipula) vernalis* Meigen.

Drawn by Mr. Kay W. Petersen from preserved egg.

The reduction of the ovipositor and an atypical egg shape characterize also other species of the *Tipula fascipennis*-group. Thus, eggs similar in shape to those here described, though with less pronounced transverse and longitudinal keels, so that the shape approaches that of an oblong lens, are found in *T. (L.) mellea* Schummel and *T. (L.) affinis* Schummel. Eggs of a different shape, more rounded and on one side with a longitudinal depression lined by a wall and reminiscent of the neural groove of a frog embryo, are found in *T.* (*L.*) *truncata* Loew (fig. 8 b), *T.* (*L.*) *trunca* Mannheims and *T.* (*L.*) *caudatula* Loew (fig. 8 c). The micropyle is in the crater-like knob seen at one end of the eggs in the figures. Also the eggs of *T.* (*L.*) *helvola* Loew are of this type (fig. 8 a) though the groove is quite shallow. This species has a reduced ovipositor as in the *T. fascipennis*-group, but does not possess the spines in the

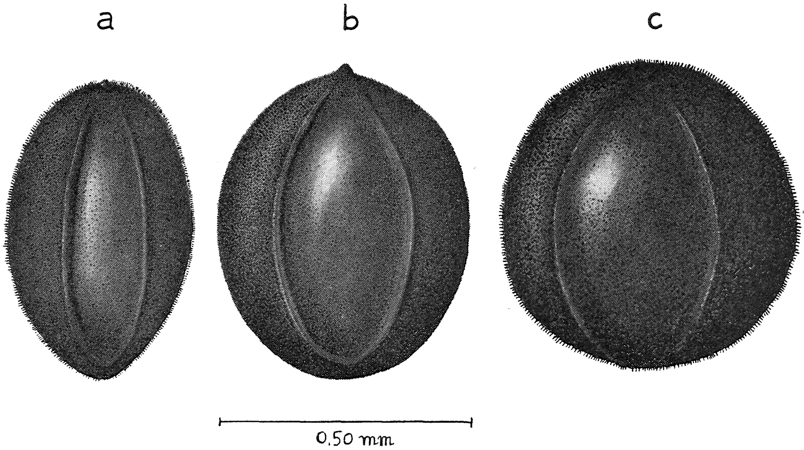

Fig. 8. Eggs of *Tipula* (*Lunatipula*) *helvola* Loew (a), *Tipula* (*Lunatipula*) *truncata* Loew (b), and *Tipula* (*Lunatipula*) *caudatula* Loew (c). As to exaggerated details see text. From preserved flies collected in Greece, June 1952, by Dr. B. Mannheims, Museum Koenig, Bonn, Germany. Drawn by Mr. Kay W. Petersen (a and b) and Mr. Ole Dybkjær (c).

hypopygium characteristic of the group *Spinosae* to which the *T. fascipennis*-group belongs. In fig. 8 the protrusion and distinctness of the wall limiting the groove has been for clearness somewhat exaggerated, especially in a. Furthermore, the closed end of the grove is in many eggs apparently as open (wall-less) as the other end (nearest to the knob). The eggs studied of these non-Danish western-palaearctic species were obtained by dissection of females very kindly presented by Dr. B. Mannheims, Museum Koenig, Bonn.

T. vernalis was very common in a sandy heather (*Calluna vulgaris*) area on Venusberg near Bonn, Germany, 15., 16. and 23. V. and 5. VI. 1953, while only few were seen there 12. VI. 1953. At Vedersø Klit (= dune), West coast of Jutland, it was common on *Salix repens* on the eastern side of the dune ridge about 10.—23. VI. 1956.

When placed in small glasses with sand and with or without small twigs or plants, no pricking in the soil as in ordinary superficially ovipositing species was seen, but the flies shot out the eggs from the ovipositor in all directions so that they came to lie on the sand or on the plants or on the glass wall. The flies thus "ovipositing" were evidently excited: for about 10 seconds restless, then for about 5 seconds completely quiet, then again for about 10 seconds restless, etc. The eggs could be seen in the ovipositor, but whether they were preferably shot out in the restless or in the quiet phase, could not be ascertained. Though this was repeatedly observed in many flies, it is hard to believe that it could be the normal method of oviposition. So female flies were placed in a very large glass container filled up with plant material (earth, dry grass, willow twigs, roots) from the ground below the *Salix repens* bushes. Two of the females penetrated to the bottom, where they behaved like ordinary tipulid females in ovipository mood: probed by inserting the ovipositor down or horizontally in between the material, and also assumed the ordinary tipulid ovipository posture with the abdomen vertical and wings pointing obliquely backwards. But real egg-laying was not seen, nor were any eggs recovered from the sites of probing by pouring saturated $MgSO_4$ over the material and stirring (cf. Hemmingsen, 1952, p. 387).

The actual mechanism of egg extrusion was seen to be as follows. Coming out from the genital opening the egg is brought to rest between the lower and upper valves by a ventrally directed movement of the hypovalves which are somewhat opened to hold it (as in fig. 10). The cerci either do not participate in the movement or a slight upward movement of cerci plus their stalk (10th tergite) is seen. When lying in the ovipositor a smaller or greater part of the egg may be visible from above between the cerci.

At the directly observed extrusions of the egg from the ovipositor, the cerci were opened (abducted) and at the same time moved upwards; that is, in the opposite direction to the bending downwards of the substrate-opening cerci in the typically built ovipositor. The opening of the cerci in *T. vernalis* might seem to be a "rudimentary soil-opening". Their upward movement presumably takes place merely in order to allow the egg to pass. The eggs are squeezed out of the hypovalves. The 9th rudimentary sternite is rather large relative to the hypovalves (see fig. 4) and no doubt serves to guide the egg into the hypovalves. Whether it also contributes to the final extrusion of the egg is uncertain.

To all appearances, then, the cerci do not function as soil- or substrate-openers and are accordingly reduced and fleshy. Also the comparatively reduced state of the hypovalves and the apparent resistance of the eggs to shrivelling suggest oviposition without much insertion into a substrate. A direct observation of the actual natural oviposition is, however, highly desirable.

4. *Tipula (Lunatipula) fascipennis* Meigen.

The species was extremely common at Strødam, North Zealand, in July 1955 and 1956, but I never succeeded in seeing the actual posture of oviposition in nature or in glasses. It was comparatively easy, however, to witness the mechanism of egg extrusion by holding the ovipositor of a gravid female onto wet cotton (fig. 9), if necessary pressing the abdomen gently. The eggs (fig. 6 c) and their position in the ovipositor have been described under *Tipula vernalis*. *In situ* the egg reaches only the cerci-furcature, nearly as the subanal plate, so that it is not visible from above as in *T. vernalis*. And its longitudinal axis which is parallel to the sagittal plane of the fly, is not parallel to the frontal plane with which it forms an angle of perhaps about 45°, the caudal end

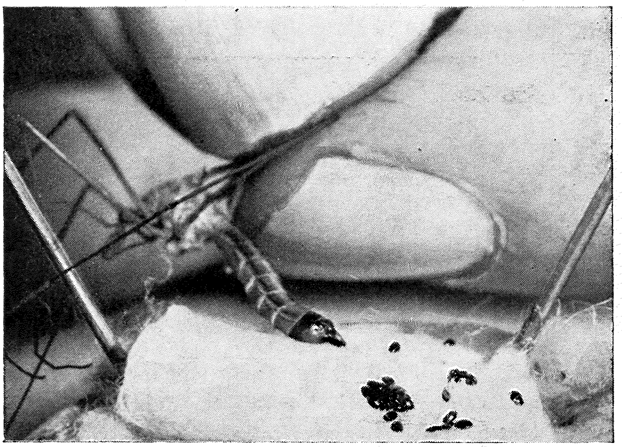

Fig. 9. Studying the mechanism of egg extrusion in *Tipula* (*Lunatipula*) *fascipennis* Meigen by holding the wings between the fingers and placing the ovipositor on wet cotton. Photograph by Mr. A. Nørrevang.

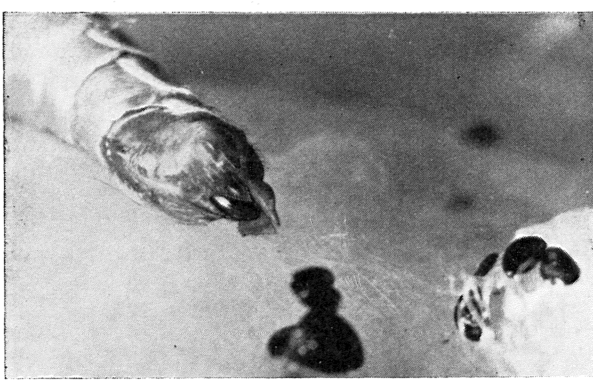

Fig. 10. Ovipositor of *Tipula* (*Lunatipula*) *fascipennis* Meigen seen obliquely from below. The egg is seen between the diverging hypovalves. Photograph by Mr. A. Nørrevang.

pointing upwards. The tip of the rudimentary sternite 9 reaches the transverse keel. From below the egg is distinctly seen between the diverging hypovalves (fig. 10). These also diverge somewhat when there is no egg between them (fig. 5). If cerci, stalk (tergite 10) and the rudimentary sternite 9 are lifted during egg extrusion it is revealed that the egg is squeezed out exclusively by the hypovalves pressing against one another (as in ordinary tipulids). The two cerci do not in any way move relative to one another. But stalk-cerci move a little upwards when the egg is ejected from the genital orifice in between the hypovalves and thereafter a little downwards whereby the egg is aided down between the hypovalves. Also when the egg is squeezed out from the hypovalves the cerci move a little upwards, presumably to create room for the passing egg. By comparison with the process described for *T. vernalis* it will be seen that the opening of the cerci at the extrusion of the egg is not seen in *T. fascipennis* though in other details, for instance the upward movement of cerci, the process of egg extrusion is much the same. Thus, in this species the cerci appear to function still less as soil-openers. And as in *T. vernalis* also the reduced hypovalves and the peculiar type of eggs suggest oviposition without or with little insertion into a substrate. But in both species direct observations in nature appear difficult to attain.

5. ***Tipula saginata*** **Bergroth.**

Along the idyllic stony streams which wind through forest and lead away the water from the rocky hills at Skäralid and at Klöva Hallar in Scania, some species of larger tipulids are associated with the water in early summer. Most of them oviposit at the river side but one is always seen ovipositing in the stream proper, on wet moss on rocks protruding from the stream. This is *Tipula saginata* Bergroth of uncertain subgenus. The ovipositor (fig. 11) reminds by its reduced state of the *T. fascipennis*-group. But the eggs are of such ordinary tipulid shape besides having a particularly well developed terminal filament, that if not by other criteria, as for instance the male hypopygium, it is clear from the eggs even to a non-taxonomist that the species cannot belong to the *T. fascipennis*-group with its peculiar egg shapes. I have seen and caught it 25. V.—14. VI. 1954 and 1956 at Skäralid and Klöva Hallar.

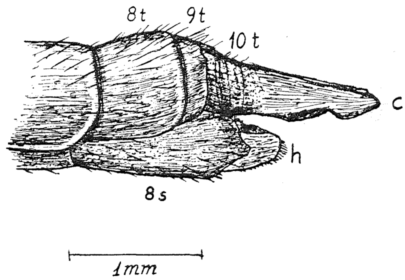

Fig. 11. Ovipositor of *Tipula saginata* Bergroth. c, cerci; h, hypovalves; s, sternite; t, tergite. Drawn by Mr. O. Dybkjær from preserved specimen.

In the early part of its flying period, it may when on wing be confused with *Tipula vittata* Meigen and later with *T. (Acutipula) maxima* Poda. But both these species are seen to oviposit at the beach of the stream or at least in less soaked places preferably not in midstream, whereas *T. saginata* invariably keeps away from the beach proper for oviposition.

A peculiar trait about the *T. saginata* females was that (Skäralid 25. V. 1954) they appeared preferably or sometimes exclusively to fly upstream in search for sites of oviposition. During the whole afternoon now and then a female was seen thus flying upstream, dipping down to the water surface, even where there were minor rapids. When the moss cushion on the side of one of the many protruding stones was hit, she remained there pricking in the moss cushion with the ovipositor.

The actual act of oviposition can be observed through glasses. The flies, unlike certain other tipulids, are not very shy until they discover they are pursued. Then they are very shy and quick. Each ovipository insertion is accompanied by quivering of forelegs and wings, and after each insertion the ovipositor is withdrawn and then thrust backwards-downwards in the air, whereafter the procedure is repeated. The wings are seen to quiver now and then. Judging from the similar behaviour which has been observed at close range in glasses in a number of other superficially ovipositing species (Hemmingsen, 1956, p. 283) the egg might be supposed to be emitted into the ovipositor at this backward movement in the air and to be extruded from the ovipositor at each insertion into the moss. However, in a female of *T. saginata* ovipositing on moss in a glass, the same behaviour was seen but no egg was seen to come out at the backward-downward thrust in the air. Eggs taken from the moss at the site of oviposition could be easily identified, because the chorion of the eggs of this species has a specific microscopic meshy sculpture, reminding of some limoniids and visible as shallow depressions. Besides, I know of no other eggs with terminal filaments which are as large as these.

The mechanism of egg extrusion was studied on wet cotton (cf. fig. 9) by means of a magnifying glass immediately after capture (2 flies at Klöva Hallar 12.—13. VI. 1956; 1, at Skäralid 14. VI. 1956), because flies brought home in glasses like many other species would have laid the eggs during transport. When the egg comes out of the genital orifice the cerci are moved upwards. When in the ovipositor, the egg extends with $^2/_3$ behind the hypovalves which are opened a little to hold about it, while $^1/_3$ extends beyond the ends of the cerci. The egg is laid by being squeezed out of the hypovalves + sternite 9, the cerci being again moved in dorsal direction;

that is, opposite to what is "normal" in most tipulids. They are fused at their base, so there is no question of opening them. If the cerci are held lifted, it is clearly ascertained that they do not participate in the squeezing, while on the other hand their presence is necessary to keep the egg in its position. The egg may be squeezed out a fair distance. The particularly well developed coil of terminal filament comes out first and is fixed by its tip. The large micropyle is near the other end; as usual, at the curved underside of the egg. The part of the coil of filament nearest to the egg is brown, while the distal part is yellowish. If the egg is pulled away from the point of fixation the thread is uncoiled at its egg end, so that the rest of the coil remains at the point of fixation.

The reduced state and function of the ovipositor must be interpreted on the same grounds as for the two preceding species: As the eggs are laid on moss in water, the cerci need not be moved downwards and opened to create in any substrate a passage for the insertion of the hypovalves, and the latter need be only short. The upward movement of the cerci may facilitate for the egg the passage out of the hypovalves.

6. *Tipula (Lunatipula) livida* v. d. Wulp.

A number of females but not so many males of this species were collected in the Bonn area at the end of May 1953 and at Strødam in July 1956 and 1957.

The stalk of the hypovalves is remarkably long and so is the reduced 9th sternite (fig. 12). The hypovalves themselves are reduced so as to consist each of only two tine-like branches, forming a sort of "hay-fork". When in position in the ovipositor, the egg is held between these two forks (fig. 13).

The mechanism of egg extrusion was studied by placing the ovipositor on wet cotton. Segment 8 is rather transparent so that an egg about to be emitted from the genital orifice can be seen through the cuticle already when in the foremost part of the segment. When it gets out it is pressed down between the two forks by the long

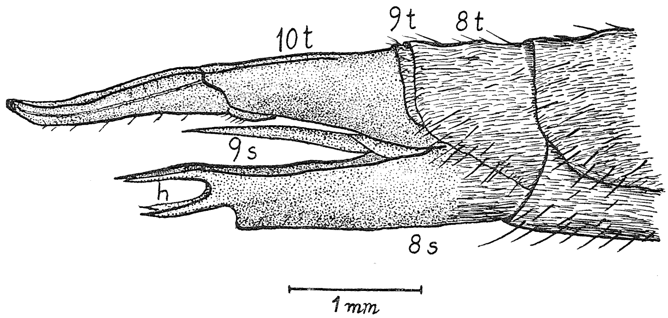

Fig. 12. Ovipositor of *Tipula* (*Lunatipula*) *livida* v. d. Wulp. c, cerci; h, hypovalves; s, sternite; t, tergite. Drawn by Mr. Kay W. Petersen from preserved specimen.

rudimentary sternite 9 and the cerci. Sternite 9 rests on the cephalic, most pointed part of the dorsal, flat side of the egg. The tiny micropyle is on the ventral, most curved side of the egg near its cephalic, most pointed end.

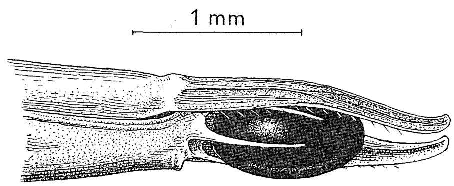

Fig. 13. Ovipositor of *Tipula* (*Lunatipula*) *livida* v. d. Wulp. The fork-like hypovalves hold the egg between them. Drawn by Mr. H. Bülow-Hansen from sketch by the author of dried specimen still holding an egg. Reproduced from Hemmingsen, 1956, fig. 16 on p. 288.

Now, while in most tipulids the egg is squeezed out from its position between the hypovalves by the latter being pressed inwards against one another, such movements, though they can be seen also in this species, are insufficient. If an ovipositor with the egg in its position between the forks is held free in the air, nothing happens. But when the ovipositor is placed on wet cotton the egg is pushed out of the forks by the cerci in the following way. The cerci are opened (abducted) and bent slightly downward, just as in most tipulids when the egg is extruded. Ordinarily the egg extrusion is brought about by the hypovalves pressing inwards towards one another, while the movements of the cerci do not contribute to this. But in *T. livida* the furcature between the bent abducted cerci presses down in front of the egg and by repeated hindward jerks presses it out of the forks. This was seen in both of the two flies studied. In one of them the posterior half of the stalk (tergite 10) with cerci was removed by a cut. Then, every time an egg came out from the genital orifice I had to help it down between the forks by a slight pressure. And it stayed there in spite of the fact that movements of the remaining part of the stalk (tergite 10) and tergite 9 were made just as before the cut, and even when the ovipositor rested on the cotton. That the egg thus could not be laid in the absence of the furcature constituted by stalk and abducted cerci, was established repeatedly in this fly.

As previously established (Hemmingsen, 1956, p. 285) the egg is squeezed out of an ordinary tipulid ovipositor by the hypovalves also in the absence of the cerci or when they are lifted. Also cinematographic pictures reveal that during the bending and opening of the cerci of such an ovipositor with an egg ready to be extruded, the cerci have not been bent so much as to get before the egg when the latter is shot out, so that there can be no question of a sort of aiding the hypovalves in shooting out the egg by any pushing — even of short duration — in the manner seen in *T. livida*.

Flies of *T. livida* (Bonn area, end of May, 1953) placed in sand in glasses oviposited by thrusting the ovipositor hard into it, especially in the wet parts, and eggs were seen in the ovipositor before the thrust, and to have disappeared after it. But the actual mechanism was not seen. The eggs recovered afterwards from the soil were covered all over with tiny soil particles difficult to remove, and it seems possible that detachment of the egg from the thread-like hypovalvular forks may be aided by this surface sticking to the soil.

Flies placed on earth (Strødam, July 1957) were seen sometimes to thrust $^1/_3$ of the abdomen into it, and to withdraw hesitatingly presumably when an egg had been laid. Afterwards the tip of the abdomen was thrust backwards as if to sweep soil over the spot, but this was repeated as the fly moved along, so that it may also serve as preparation of a new oviposition site. When placed on glass balls of sand particle size (ballotini nr. 7; cf. Hemmingsen, 1956, with reference to Agarwala, 1951) in narrower glasses (4 cm in diameter) the flies (2 specimens) would often thrust the abdomen down between ballotini and glass wall to depths from a few mm to maximally 8 mm corresponding to $^1/_4$-$^1/_3$ of the abdomen. Even when then the thrust was made further away from the glass the ovipositor would sometimes reach the glass wall. And in this light transparent substrate the process could be distinctly observed. The cerci were continuously opened and closed during the thrusts, the egg remaining all the time between the hypovalvular forks. It seemed to be difficult for the fly to get rid of the egg, but several times an egg was seen to be pushed out by the cerci in the manner observed on cotton. It thus seems that also during the actual oviposition of *T. livida* in soil the egg is pushed out in the way observed on cotton. The ovipositions were preferably performed towards the evening or in the dark.

Both in structural and in functional respects the oviposition of *T. livida* may be said to be intermediary between (1) the typical superficial oviposition of most tipulids and (2) the deep-boring oviposition in the *Vestiplex* species and the *T. juncea*-group. The cerci are more shovel-shaped than in the former (1) but less so than in the latter (2). The ovipository diggings performed by them are deeper than in the former (1) but not so deep as in the latter (2). The hypovalves are so much reduced relative to the typical ovipositors that, unlike these, they are unable to squeeze out the egg by their own effort. But though they are reduced into forks with tine-like branches they are not so much reduced as in the deep-boring species, and they are still large enough to hold the egg between them.

In several *Vestiplex* species each hypovalve still retains the shape of a tine, in *T. (V.) pallidicosta* Pierre even with a lobe representing the base of a missing second tine, thus being the most *T. livida*-like of them (cf. Mannheims, 1953, fig. 70 on p. 122).

This does not, however, mean necessarily that the *T. livida*-oviposition in all its details actually represents a stage in the evolution of the present-day deep-boring species. These have been thought to show affinities to the subgenus *Oreomyza* rather than to *Lunatipula*. Still Savchenko (1956, p. 130) finds that the *T. juncea*-group (subgenus *Odonatisca* Savchenko) shows special affinities to *Arctotipula* and *Yamatotipula*, and Theowald (1957, p. 296, 302—303) actually suggests close affinities between *Vestiplex*, the *T. juncea*-group, and the *T. livida*-group (and other *Lunatipula* groups).

In another species of the *T. livida*-group, *Tipula* (*Lunatipula*) *lesnei* Pierre 1921, one of the branches of the hypovalvular fork has an extra small branch, and its ovipository mechanism is very much like that of *T. livida* (Hemmingsen, 1958, p. 223 with fig. 10).

In *T.* (*L.*) *circumdata* Siebke 1863 (fig. 14), also of the *T. livida*-group, there is only a slight incision near the end of the hypovalves though they possess ribs that appear likely to correspond to the hypovalvular tines of *T. livida*. In other species of the group the end of the hypovalves is divided into three short tines, shorter in *T.* (*L.*) *urania* Mannheims 1954 and *T.* (*L.*) *erato* Mannheims 1954 from Greece, than in *T.* (*L.*) *bimaculata* Riedel 1913 (cf. Mannheims, 1954, p. 178—179).

7. ***Cylindrotoma distinctissima*** **Meigen.**

Flies of this species were caught at Klöva Hallar, Scania, and at Strødam in June 1954, and at Gurre Aa, Langesø Plantage, North Zealand, 22. VIII. 55.

The oviposition was observed on leaves of *Caltha palustris* placed in glasses. The fly placed herself on the upper side of the leaf and by turning the abdomen 180^0 about its longitudinal axis managed to place the toothed upper side of the cerci against the underside of the leaf near its edge. The forked dorsal appendage, which this species possesses proximally to the cerci, was placed on the upper side of the leaf edge, which was thus pressed between the cerci and the fork. By a special arrangement the process could be observed from below. The cerci, which were kept closely to one another, were then seen to move alternately parallel to one another cutting a slit in the leaf epidermis, the tip of the abdomen thereby moving a little from side to side. The teeth of both edges of the cerci point forwards in the basal half, backwards in the distal half of the cerci, so that each saw operates in either direction. In some cases the cerci were seen to be opened a little before the ovipositor was removed so that the egg could be seen. The egg was covered with a sticky fluid when the ovipositor was withdrawn, and the slit in the leaf epidermis closed. As long as it is moist the egg can easily be removed by bending the edges of the leaf epidermis. There was no attachment as in *Diogma* and *Phalacrocera*. After the slit has become drier the egg gets easily crushed when one tries to remove it, the covering edges of the epidermis sticking to it.

The cutting parallel movements of the cerci are also seen during copulation.

The oviposition of the American *Cylindrotoma splendens* Doane (from Vancouver Island, British Columbia) has been described by Cameron (1918) and that of *C.*

distinctissima Meig. (from Germany) by Lenz (1921) and Peus (1952).

None of these authors have described the alternate parallel movements of the cerci. Cameron (1918, p. 73) writes that "the blades are then moved to and fro". Lenz (1921, p. 131) and Peus (1952, p. 43) believed that the edges of the cerci by being kept narrowly together constituted one single saw.

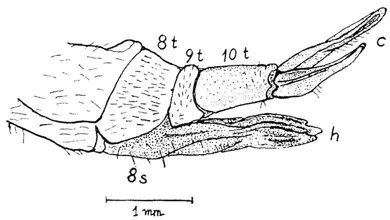

Fig. 14. Ovipositor of *Tipula (Lunatipula) circumdata* Siebke. c, cerci; h, hypovalves; s, sternite; t, tergite. Specimen collected by the author at Schwarzensee, Sölktal, Steiermark (Styria), 28. VIII. 1953. Drawn by Mr. Kay W. Petersen from preserved specimen.

8. *Diogma glabrata* Meigen.

This species was caught at Gurre Aa, Langesø Plantage 28. VIII. 55 and at Strødam 20-21. VII. 57. Female flies were placed in glasses with the moss *Rhytidium squarrosum*. The ovipository behaviour started with the vertically held abdomen being moved forwards in jerks without movements of the cerci. The ovipositor, which was turned backwards, that is in dorsal direction relative to the abdomen more or less perpendicular to the latter, was placed under a leaf so that the upper side of the cerci faced the underside of the leaf. Then the cerci were moved rapidly alternately and parallel to one another. Shortly afterwards the cerci were removed a little from the hypovalves, between which the egg appeared, the cerci moving all the time in the way described. Though the moving cerci rested against the leaf, the egg did not come out between them but behind them. They appeared to hold on to the egg end a little before being withdrawn. The egg was wet and remained on the underside of the leaf. When an egg was torn from the leaf a thready or meshy substance was seen on the egg, where it had stuck, but nothing like the club-like structures found in the *Phalacrocera* eggs (Hemmingsen, 1952, p. 407—408). Already in eggs removed from the fly by dissection a special area is seen on the flat side of the eggs just where at oviposition the egg is to be attached to the leaf. So just as in *Phalacrocera* the attachment of the egg is confined to an area of the egg which has a special structure. The difference in specialization of this area may be correlated with the fact that *D. glabrata* oviposits in air where the evaporation of a sticky fluid may perhaps aid in the attachment, whereas *Ph. replicata* oviposits in water where further attaching structures may be required and are in fact present.

Between the actual ovipositions the flies move about jerkwise between the plants, and it was far from every time when the ovipositor was placed below a leaf that an egg was laid.

The alternate parallel movements of the cerci are also seen during copulation as in *Cylindrotoma distinctissima*.

9. ***Phalacrocera replicata*** L.

Certain details in the oviposition of this species have already been published (Hemmingsen, 1952, p. 404—408). With a special view to studying the cerci during copulation and oviposition, 25 larvae were collected 4. IV. 1958 in the same locality, Gribsø, North Zealand, and copulation and oviposition studied in the emerged flies in glasses. As ascertained in several flies the cerci did not move during copulation as in *Cylindrotoma* and *Diogma*. But at oviposition the cerci are moved in the same way as in these species, both when the flies walked about and oviposited in the submerged moss, and when their ovipositors were placed in wet cotton; that is, alternately and parallel to one another with quick movements. The upper edges of the cerci are placed where the egg is going to be attached, and the egg is squeezed out of the lower valves in an obliquely backward-upward direction, whereby the cerci are opened (presumably by mere pressure) when the egg passes between them. Under the stereomicroscope the pale, sticky area by means of which the egg is attached (cf. 1952, fig. 6 on p. 408) is distinctly visible on the upper side of the egg when it comes out. When the cerci are lifted or removed by cutting, the hypovalves work in exactly the same way as else; occasionally also in the intact fly in the absence of the movements of the cerci. In other words, the alternate parallel movements of the cerci do not serve to assist in the extrusion of the eggs, but may perhaps serve in probing for a site for the eggs.

In all three species of *Cylindrotominae* studied the dorsal edges of the cerci are placed where the egg is going to be attached and it comes out in upward direction between or behind the cerci. The movements of the cerci at oviposition are alike in the three species and no doubt of a similar nature genetically, even though they are present at copulation only in two of the species. Whether in *Diogma* and *Phalacrocera* these movements represent an evolution (preadaptation) toward leaf-cutting or the later stages in a reduction, is difficult to decide.

The same applies to the fact that in *Phalacrocera* the upper edges of the cerci possess rudimentary teeth though the eggs are fixed to the surface of the leaves by a special area, and that there is a short unforked process at the site corresponding to the dorsal fork in *Cylindrotoma*. Thienemann (1919) and Lenz (1921, p. 134—135) are inclined to consider *Diogma, Triogma* and *Phalacrocera* as descendents of *Cylindrotoma.* Alexander (1927, p. 6) is of the opinion that *Diogma* (by him called *Liogma*) and *Triogma* have been derived from an ancestor that was very close to our recent *Cylindrotoma,* and that *Phalacrocera* came off the main stem before or almost coincidently with *Cylindrotoma.* Peus (1952, p. 58) cannot accept the highly specialized *Cylindrotoma* as the more original form, because the direction of evolution among *Tipuliformia* is from moister to drier biotopes; and he is inclined to think that the genera of *Cylindrotominae* have evolved quite independently of one another.

10. Summary.

In some *Limoniinae* sternite 9 is not so much reduced as in most tipulines and functions as a lid to the "boat" constituted by the two hypovalves, between which the egg rests when in the ovipositor. The egg thus gets from the genital opening into this closed chamber without any aid from the cerci or their stalk and without being directly visible from the outside. It is not visible until it has been squeezed out of the ovipositor by the hypovalves.

In other *Limoniinae* the lid in question is absent, but is replaced, so to speak, by inward-backward directed hairs at the upper edge of the hypovalves, which are in addition fused below.

The mechanisms of egg extrusion from the reduced and rather uniform ovipositors of *Tipula* (*Lunatipula*) *vernalis* Meigen, *T.* (*L.*) *fascipennis* Meigen and *T. saginata* Bergroth were found to be much alike. The cerci are bent upward not only at the emission of the egg from the genital opening into the ovipositor but also at the extrusion of the egg from the ovipositor (accompanied by a rudimentary opening (abduction) in *T. vernalis*). In both these phases the upward movement of the cerci seems to be made to better permit the egg to pass. The upward movement at the extrusion of the egg from the ovipositor is the opposite of the downward bending accompanied by opening (abduction) which opens a slit for the egg in the substrate, seen in most tipulids.

In *T. saginata* this reduction in structure and function of the ovipositor is ascribed to the oviposition on moss in running water, where there is no need for any substrate to be opened by the cerci and no need for well-developed hypovalves to insert the egg into it. It is an obvious guess then that the similarly built and functioning reduced ovipositors of *T. vernalis* and *T. fascipennis* are

also adapted to oviposition without much insertion into a substrate, but decisive observations of the actual ovipositions under natural conditions are lacking.

In *Tipula* (*Lunatipula*) *livida* v. d. Wulp and *T.* (*L.*) *lesnei* Pierre the downward bent and opened cerci push out the egg from the forks (reduced tine-like hypovalves) which hold it; that is, in contrast to the function of ordinary tipulid ovipositors, the cerci and not the hypovalves are active in the egg extrusion. This mechanism functions also under natural conditions (more or less deep-boring ovipositions).

The method of oviposition in *T. livida* and *T. lesnei* is considered intermediate between superficial and deep-boring ovipositions both as regards the development of the cerci and their digging, and as regards the partial reduction of the hypovalves into forks.

In *Cylindrotoma distinctissima* Meig. the upper toothed edges of the cerci cut a slit in the epidermis of a leaf by alternate parallel sawing movements. These movements are also seen during the oviposition of *Diogma glabrata* Meig. and *Phalacrocera replicata* L. though the sawing teeth are rudimentary or absent and the eggs are fixed onto the leaf surface by a specially developed sticky area on the upper egg surface. In *C. distinctissima* and *D. glabrata*, but not in *Ph. replicata*, the movements in question are seen also during copulation.

The leaf-cutting function of the cerci in *Cylindrotoma distinctissima* is thought to be, at least formally, a modification of the substrate-opening function of the cerci in typical tipulids. Whether the corresponding movements in *Diogma glabrata* and *Phalacrocera replicata*, where they have no substrate-opening (though, as it seems, a substrate-probing or -finding) function, represent the beginning of an evolution or the later stages in a reduction of an original leaf-cutting, is difficult to decide.

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Denne Bog er i Virkeligheden en Slags Lærebog bygget over de forhaandenværende zoologiske Haandbøger, der jo er Opslagsværker og ikke direkte til at lære. Det betones paa Titelbladets Bagside, at den er autoriseret som Lærebog ved Universiteter og "Højskoler" i Øst-Tyskland. Det vil jo altid bero paa et Skøn, hvor meget man synes, Studenterne "bør vide"; men hvis de tyske zoologiske Studenter kan denne Bog til Examen, saa har de et solidt Grundlag — Anm. vil mene solidere end nødvendigt. Det er godt at have Viden; men det er nyttigere at kunne slaa op, og paa det Punkt svigter Lærebogen; forsaavidt som den ingen Litteraturhenvisninger giver i Teksten, og blot efter hvert Afsnit en ret spartansk Litteraturliste efter Stikord og uden fulde Titler. Man vilde ofte gerne vide: hvor har Du det fra? Men man maa altsaa som Student bygge paa Autoriteten.

En Mængde værdifulde Oplysninger er samlet i Bogen; Lærebogsprincippet gør ganske vist, at Siderne er en urolig Blanding af almindelige Typer og Petit (som Studenten vel kan gaa lettere henover); men tilsammen er en meget stor Viden ført op til den allersidste Tid. Som særlig instruktivt bør maaske Afsnittet om Facetøjet i Indledningen til Lief. 4, Indledningen til samtlige Mandibulata, fremhæves, hvor der er gjort meget fint Rede for baade Øjets Morfologi og Grænserne for dets Anvendelighed. Men talrige andre Afsnit kunde nævnes. At Bogen som Lærebog betragtet er omfattende, vil fremgaa af, at Cheliceraterne fylder 183 Sider, Krebsdyrene 320. Figurerne er desværre ofte omtegnede (hvad der er en Uskik) og det i den af Weber saa yndede Stil med meget sort i; de forekommer mig ikke altid lige anskuelige, og hvor jeg har sammenlignet med Originalfiguren, finder jeg faktisk denne bedre, saaledes f. Ex. Trombicula-Larven p. 626. Men alt i alt er Bogen et værdifuldt Supplement til de almindelige zoologiske Lærebøger, en Slags moderniseret og stærkt udvidet Claus-Grobben, som den, der specialiserer sig, absolut bør gøre sig fortrolig med. Og saa er den utroligt billig.

S. L. Tuxen