RHINGIA CAMPESTRIS MEIGEN (DIPT., SYRPHIDAE): AN ACCOUNT OF ITS LIFE-HISTORY AND DESCRIPTIONS OF THE EARLY STAGES.

BY R. L. COE.

The genus *Rhingia* is represented in Britain only by *campestris* Mg. and *rostrata* L., the former a common and widely distributed species, the latter apparently rare. Species belonging to the genus occur in many parts of the world, but no early stages of any have hitherto been described.

Réaumur (1738: 300) stated that a fly, which was evidently a *Rhingia* from his figures, was found in a box containing cow-dung in which he was breeding various larvae. He failed, however, to find any trace of the empty puparium or of Syrphid larvae or puparia. Panzer (1805: 22) remarks of *rostrata*, 'Habitat frequens ruri pecoribus admodum molesta.' Schiner (1862: 326) notes that the females of *Rhingia* are sometimes found in great masses around fresh cow-dung, on which they probably deposit their larvae (sic). Lundbeck (1916: 392), after quoting Réaumur, says of *campestris*, 'The larvae are therefore believed to live in cow-dung; I think, however, this rather doubtful, for it would be strange that in this case the larva or pupa to so common a species was not known.' Dorsman (1920: 339) concludes an article upon the adult of *rostrata* with the erroneous statement, 'The larvae of *Rhingia* should be sought on the leaves of plants, which are damaged by plant-lice (Aphidae). They feed on the tiny creatures, which they attack and suck out.' In other instances authors have either quoted Réaumur's remarks or stated categorically that flies of the genus *Rhingia* breed in cow-dung, without furnishing any confirmatory evidence.

In the summer of 1940 I succeeded in obtaining eggs from females in captivity, but the larvae hatching from these failed to feed up in various media. At an earlier date (1939: 227) I had expressed in print my disbelief that the larvae feed in cow-dung, basing this conclusion on the fact that a favourite haunt of *Rhingia* where I frequently collect is situated at some distance from meadows where cattle occur. Collin (1941: 66) drew attention to a brief statement that had been made by Thomson (1937: 304) in a paper dealing with the biology of various Anthomyiidae, to the effect that he had observed females of *campestris* depositing masses of eggs on the underside of clover leaves and blades of grass overhanging cow-dung, and that the young larvae drop on to the hard surface skin of the dung, and burrow into a suitable fissure or crack. In the light of this observation, I again took up the study of the biology of the species, with the result that the life-history was followed through

and the early stages of a species of the genus *Rhingia* are now for the first time described.

The Life-History.

Except in the case of females engaged in ovipositing, the adults of *campestris* are most commonly found flying around low vegetation at the borders of woodlands and meadows, where they are particularly attracted by the flowers of ground-ivy (*Nepeta hederacea* (L.) Trev.) and red campion (*Lychnis dioica* L.). They are fond of resting on leaves of docks and other low plants, and I have often observed the males on the leaves of small trees. In 1941 (which had a late spring), the adults first appeared a few weeks later than in most years. The species was abundant at Chelsham, Surrey, from the middle of June until early July, after which only occasional specimens were seen until the adults of the second brood appeared during the first week in August. The complete life-cycle was studied of the second brood of adults, which pass their early stages during the summer months.

On June 15th eggs were first discovered, deposited in masses along the under-surface of leaves of grasses, clovers, ground-ivy and self-heal overhanging fresh 'pats' of ox-dung in a large meadow where bullocks were grazing. Dung selected for egg-laying was usually in parts of the meadow exposed to the full heat of the sun. It was noted that when no leaves actually overhung dung the female *Rhingia* hovered above it momentarily, but did not deposit eggs. At no time have I observed numbers of females engaged in egg-laying at a single dung-cake. Details were noted of the manner of oviposition. In one instance the fly settled on the under-surface of an overhanging clover-leaf, rapidly deposited 86 eggs, then flew to an adjacent leaf where 16 more eggs were deposited, and finally 6 eggs were laid on another leaf. Thus an aggregate of 108 eggs were deposited. Although this female alighted on other clover-leaves over the same dung-cake and went through the motions of oviposition, no further eggs were deposited and the fly flew off, having been under observation for about five minutes. The eggs are deposited side by side in close batches of a few to a hundred or more, sometimes in more than one layer. They are lightly cemented by the flat side to the leaf or blade of grass. Occasionally a single egg is found. The adults of the spring brood of *campestris* ceased egg-laying at the beginning of July.

The young larvae commence to emerge 24-72 hours after the eggs are deposited, according to prevailing temperatures. All the

larvae from a single batch of 36 eggs hatched out within an hour of the appearance of the first larva. The young larva pushes against the micropylar end of the egg until a longitudinal breach is made, and this split gradually extends along the dorsal (convex) surface for about two-thirds of the length until the larva is able to creep out. The whole operation takes about a minute. By the time the eggs have hatched a firm greyish crust has formed on the surface of the dung, and the larvae creep down to it when the leaf is touching or drop through the inch or so that may intervene. On reaching the surface of the dung the larvae immediately search for a crevice through which they enter. The newly-emerged larvae progress with a looping gait resembling that of aphidophagous Syrphid larvae, head dipped to surface as posterior is rapidly drawn up, and fleshy antennae extended. Eggs were kept in a petri dish, and it was noted that the young larvae hatching from these died within a few minutes if prevented from reaching the moist dung. Having reached the moist dung, the larvae remain stationary until fully grown. There are three larval instars. Six to eight days after hatching (*i.e.* on the larva attaining the third stage) the segmental spines have developed and minute particles of the dung cling to these formidable appendages, the larva becoming so closely coated with fragments that the only exposed part is the tip of the posterior respiratory process. Although a hundred or more *campestris* larvae may occur in a single dropping, the most patient and methodical search is necessary in order to discover them. In this respect a most striking contrast is afforded by the conspicuous whitish larvae of various Anthomyiidae, which are active in the dung, and to whose smooth integument dung-particles do not adhere. Growth of the *campestris* larvae is rapid. It was observed that well-formed dung-cakes (in which alone the larvae occur) normally become completely dried up during the hot summer weather in a period varying from two to three weeks. The drying and settling of the dung eventually brings the fully fed larvae practically to ground-level, whence they work their way into the closely matted tangle of grass roots and stems and pass into a prepupal period. During this time, which in the summer brood lasts from three to four weeks or more, the larvae take no food, lying quiescent with the head segments withdrawn. The integument remains soft, however, until shortly before pupation, and if the larva is gently rolled between the finger and thumb the head segments are slowly extruded and then rapidly withdrawn. On one occasion prepupal larvae were removed from their resting-place amongst grass roots and placed on the ground above; in a

short time they had worked down into the roots again, the powerful segmental spines doubtless facilitating their progress. The dung-coated prepupal larvae resemble fragments of earth, and in their obscure situation are even more difficult to detect than when in the dung-cake. The baked condition of the ground in midsummer renders study even more difficult, and intensive searching for an aggregate of thirty hours over a period of ten days was rewarded eventually by the discovery of three prepupal larvae. Towards the end of the prepupal period the larva gradually contracts and becomes rounded out dorsally and anteriorly, the head segments being shifted downwards to the ventral plane. The skin then hardens, and the puparium is thus formed.

Three or four days afterwards, the pair of pupal respiratory cornua thrust through weakened areas of the integument. The pupal stage in the summer brood lasts from about nine to twelve days. In 1941 the adults of the summer brood began to emerge at the beginning of August, and the species was abundant again by the 15th of that month, when females were commonly observed ovipositing. The time of appearance of the second brood of adults was approximately the same in the two preceding years, when the flies occurred until the middle of September in the same locality. In 1941 egg-laying had ceased by the second week in September. Almost fully-developed larvae were found in partly-dried dung on October 1st, and it appears probable that the larvae pass the winter in the torpid, prepupal condition, becoming pupae in the spring.

Horse-droppings were abundant in the meadow at Chelsham where the observations were made, but no *campestris* larvae were found in that material, and an examination of leaves of plants overhanging it did not result in the discovery of eggs. Immature larvae were placed in horse-dung, human excrement, and in various kinds of decaying vegetable matter, but they failed to develop. It seems not unlikely that ox-dung may be the sole pabulum of *campestris* larvae.

Descriptions of the Early Stages.

The Egg.

The egg (figs. 1, 2) averages 1·25 mm. in length and ·40 mm. in diameter at broadest part. Its shape (fig. 1) is subcylindrical, elongate-oval, somewhat narrower and rather truncate at the micropylar end, rounded at the other, convex above, flattened below. Colour whitish when freshly deposited, changing to grey shortly before emergence of larva. Under high magnification, the sculpturing (fig. 2) is seen to consist of a fine whitish reticulation distinctly raised above greyish channels, both areas being subequal in width. The elevations are longitudinally arranged, wavy in places, obliquely denticulated, and extend over the entire surface of the chorion, many of the denticulations uniting to form the complete pattern of a raised network. This type of ornamentation is common in the aphidophagous species of Syrphidae, but Metcalf (1916: 249 and 253) describes the eggs of the saprophagous Syrphid species *Tropidia quadrata* Say and *Syritta pipiens* L. (the larvae of which are short-tailed as in the present species) as having the sculpturing divided into small raised polygonal areas, intersected with parallel-sided channels, the latter forming a fine dark depressed network over the surface of the egg.

The Larva.

First stage larva (figs. 3, 4).—Identical with the third stage larva except in the following respects. Length 2 mm. on hatching. Body less tapering towards the extremities and less arched. Colour whitish. Antennae more prominent, anterior spiracles not easily distinguished. Mouth-hood poorly developed, floor of the pharyngeal chamber whitish, weakly striated. Segmental spines lacking, these being replaced by small papillae, which occupy the same positions on the segments. The twelfth segment lacks the two lateral pairs, however. Posterior respiratory process (figs. 3 and 4) proportionately longer, whitish on almost the basal half, then brownish, constricted near the base and again just beyond the middle; component tubes narrowly divided at the extreme tip. The separated stigmal plates (fig. 4) present a very different appearance. The circular plates cannot be traced, while the spiracular openings (fig. 4a) of each stigmal plate are completely joined, forming an almost simple opening extending around the outer part. Both stigmal plates bear a peculiar rounded nodule dorsally near the margin, and have a somewhat convoluted surface.

Second stage larva.—Attained two days after emergence. Length, newly-moulted, 4·25 mm. Colour whitish. Complete fusion of the posterior respiratory tubes has taken place, the circular plates are visible, and the posterior spiracular openings have assumed the form found in the third stage larva. The mouthparts are fully developed, and the anterior spiracles may be seen without difficulty. Otherwise identical with first stage larva.

Third stage larva (figs. 5-10).—Attained six to eight days after emergence. Length, newly-moulted, 9·25 mm. Length, mature, 11-12 mm.; greatest width (in region of ninth segment), 4 mm.; greatest height (in region of ninth segment), 3·75 mm. Body (fig. 5) almost cylindrical, narrowing somewhat towards the extremities, slightly flattened ventrally. Colour greyish-white. First four segments differentiated from those succeeding by a slight constriction, so as to form the globose false-head characteristic of Metcalf's (1916: 210) 'filth-inhabiting' type of Syrphid larva. Composed of the normal twelve segments, the first segment only indicated from the dorsal view by the projecting antennae, fifth to eleventh subequal in length, second, third, fourth and twelfth shorter and subequal. Fifth to tenth segments each rather clearly indicated dorsally and ventrally by three transverse ridges of the body-wall, which merge into a single prominence laterally. Prolegs so vestigial as to be indistinguishable from the transverse folds of the body-wall. The false-head has fourteen longitudinal furrows evenly arranged around it, except on the mid-dorsal and mid-ventral lines. Situated at the extreme anterior margin of the dorsum of the third (prothoracic) segment, slightly dorsad of the second longitudinal furrow from the median line, one at either side, are the minute, light brownish anterior respiratory cornua (figs. 5b and 7), which are provided towards the apex with a kidney-shaped spiracular opening. The first (anterior head) segment bears in front the pair of small, forwardly directed antennae or sensory organs (fig. 5a), each commencing in a rather coniform, fleshy prominence, from which project, side by

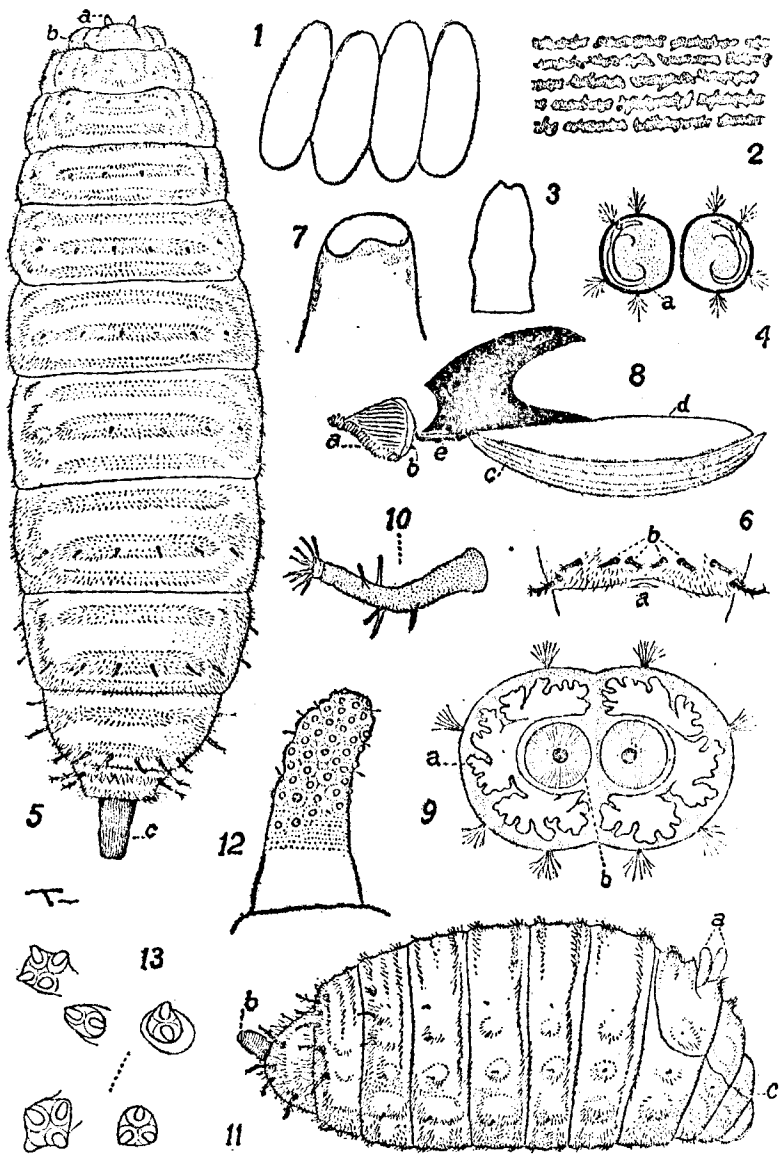
side, two minute, rounded, nodular structures, unequal in size and very lightly chitinized. On the same segment, ventrad of the antennae is the mouth-opening, its hood brownish and (thus viewed in situ) in shape like a horse-shoe. Immediately in front of the mouth-opening there is a small, transverse fleshy pad bearing about twenty rather strong, backwardly directed brownish spinules, and at either side a large, rounded, fleshy prominence of the second (posterior head) segment.

By dissection, the bucco-pharyngeal armature (fig. 8) is found to conform to the general pattern of other saprophagous Cyclorrhaphous larvae (Keilin, 1930: 175). The strongly sclerotized vertical plates of the basal pharyngeal sclerite are short and broad; the pharyngeal chamber leading to the oesophagus is elongate-oval, its floor being lined with nine lightly sclerotized longitudinal ribs (fig. 8c). These ribs bear dorsally for their entire length a pair of outwardly disposed closely set fringes, with the exception of the outermost rib at either side, which bears a single inner fringe; they are bounded laterally by a smooth, scarcely sclerotized flange (fig. 8d), which is narrowly separated from the main structure except towards the base, the whole being enclosed in the membraneous casing of the chamber. In several preparations the ribs appear somewhat wavy, but this results from shrinkage, and they are actually almost straight. The basal sclerite terminates anteriorly in a pair of slender rods joined towards the tips by a broad, shield-shaped plate, which is shortly indented at either side in front. Parallel to these, external and slightly inferior, is a pair of short lateral processes (the intermediate sclerite) (fig. 8e), which bend slightly outwards at their tips and are connected ventrally about half-way along by a narrow bridge. Attached by membrane to the two pairs of projections is the mouth-hood (fig. 8a), a delicately constructed, lightly sclerotized filter. It consists of two laterally situated lobes, which, viewed in profile, are roughly triangular in shape, longitudinally barred except at the base, incurved above and below; each lobe bears ventrally a delicate, membraneous, outwardly disposed flange, the bars of which run almost transversely. A pair of small sclerotized structures that appear to be degenerate mouth-hooklets (fig. 8b) are lightly attached to the smooth base of each lobe in a ventral and rather median position.

The anus (fig. 6a) is a small, inconspicuous transverse slit on the venter of the eleventh segment (immediately caudad in a single example is a small, somewhat asymmetrical, roughly circular, sclerotized area, but such does not occur in other equally developed larvae and the feature is evidently aberrant). The rectal gills (the extrusible set of finger-like sacs attached by muscles internally to the body-wall on either side of the anus) are poorly developed, and their number is uncertain. The posterior respiratory process (figs. 5c and 9) consists of two laterally placed, completely fused tubes, and is short and rigid, projecting about 1 mm. from the end of the twelfth segment. It is reddish-brown, strongly sclerotized and polished, tapering from the broad base to the truncate tip, and is semi-transparent, the two large, narrowly separated, tracheal trunks being visible throughout its length. There is a slight constriction just beyond the middle. At the apex it bears the stigmal plates (fig. 9), one at either side; semi-circular in shape, each bears three spiracular openings (fig. 9a), the two sets being somewhat dissimilar in pattern. The spiracular openings are elaborately denticulated as in the saprophagous Syrphid species *Tropidia quadrata* Say and *Syritta pipiens* L. described by Metcalf (1916) and Heiss (1938), but are larger than in those species; each bears from ten to sixteen short, rounded denticles of various sizes, and the three in each set are broadly connected one to another at the base. Partly enclosed by the spiracular openings, and slightly raised above their level, are the pair of weakly sclerotized circular plates (fig. 9b), which

occupy a median position on each stigmal plate; each is ornamented with about sixty fine lines, radiating from the darkly pigmented centre, so that the resemblance is to the inverted pileus of a mushroom. The inter-spiracular ornamentation consists of four pairs of palmately arranged, but not plumose, hairs, some of them branched; the hairs in each spray number five or six, and all are united at the extreme base.

The depressed areas of the body-wall are covered evenly with minute, suberect, simple or bifurcated, straight or curved, brownish spinules, the elevated areas with stronger, considerably larger, brownish spinules. The latter set is accordingly arranged longitudinally on the false-head, except on the mid-dorsal and mid-ventral lines, and thereafter transversely except at the sides of segments. Both sets of integumental vestiture slightly, but steadily and distinctly, increase in size from the anterior to the posterior extremities of the body-wall. The segmental spines are clearly seen on the fourth and succeeding segments, and on segments five to ten occupy the median transverse ridge. They are remarkable in numbering fourteen on the fourth segment and sixteen on segments five to eleven instead of the normal twelve hitherto found on segments in larvae of Syrphidae. Metcalf (1913: 18) states that there are typically twelve segmental spines (or hairs) in Syrphid larvae, while Heiss (1938: 11) maintains that this character distinguishes the larvae of Syrphidae from those of all other Cyclorrhaphous families with the single exception of *Microdon*, 'in which it is not possible to distinguish any segmentation and in which segmental spines appear to be missing as well.' On segments four to eleven, commencing at the mid-dorsal line and proceeding outward, it is easy to distinguish the six transverse pairs designated by Metcalf (1913: 18) as the median, dorsal, dorso-lateral, lateral, posterior ventro-lateral and the anterior ventro-lateral spines. In *campestris* there are two additional ventral pairs (fig. 6b), an inner ventral and an outer ventral, on segments five to eleven, and on segment four one additional pair (the inner ventral). The eight pairs of spines are arranged in a transverse row, except for the posterior ventro-lateral and anterior ventro-lateral pairs, which are placed slightly more forward in their respective positions than the remainder. The twelfth (terminal) segment has only six pairs of spines, of which four pairs are on the venter; the latter comprise two anterior pairs near the sides, one posterior pair in a slightly more median position than the inner of the anterior pairs, and one pair midway along the segment still nearer the median line. The remaining two pairs occur laterally, side by side, the dorsum of the segment being devoid of spines. No fleshy papillae are present on the terminal segments. The segmental spines (fig. 10) are single. Their position in this type of Syrphid larva is usually occupied by a clump of three or four fine flexible hairs, all arising together. The spines arise direct from the integument and are nowhere carried on papillae. They are rigid, brownish, more or less strongly sclerotized, and become longer on succeeding segments; those on the eleventh and twelfth segments are curved in an anterior direction, the remainder straight. They taper steadily from the stoutish base to the truncate tip, which is surmounted by a circlet of four to twelve tapering filaments of various lengths, more or less horizontally outspread. The spines on segments four to nine have a smooth base, not exceeding in length the longer filaments, while those on segment ten have a corrugated base, longer than the filaments. On segment eleven the spines are more heavily sclerotized, and the corrugations are developed into pointed spikes, numbering five or six, which jut out around the lower three-quarters of the base. On segment twelve the spines are larger, often reaching a length of ·75 mm., and are still more heavily sclerotized, while the spikes around



Rhingia campestris Mg.

FIGS. 1–13.—1, outline of eggs, ×15, dorsal view; 2, small area of chorion of egg; 3, outline of posterior respiratory process of first-stage larva, dorsal view; 4, same, end view, showing the two stigmal plates (a, spiracular opening); 5, mature third-stage larva, ×9, dorsal view (a, antenna; b, anterior larval respiratory cornu; c, posterior respiratory process); 6, eleventh segment of third-stage larva, ventral view (a, anal opening; b, ventral (additional) segmental spines); 7, anterior respiratory cornu of third-stage larva, showing terminal spiracular opening; 8, bucco-pharyngeal armature of third-stage larva, lateral view (a, mouth-hood; b, rudimentary mouth-hooklet; c, longitudinal ribs of pharyngeal chamber; d, flange; e, intermediate sclerite); 9, posterior respiratory process of third-stage larva, end view, showing the two stigmal plates (a, spiracular opening; b, circular plate); 10, segmental spine from twelfth segment of third-stage larva; 11, puparium, ×9, lateral view (a, pupal respiratory cornua; b, larval posterior respiratory process; c, operculum (indicated by lines); 12, pupal respiratory cornu; 13, group of nodules from pupal respiratory cornu, showing papillae with terminal openings.

the basal part are longer, stouter and number from six to eight. The filaments of spines on segments ten to twelve are more horizontally outspread than those on preceding segments, which are mainly inclined upward; they are fewer on the spines of last two segments.

The Puparium.

The puparium (figs. 11-13) is pale brown in colour. Average length (inclusive of larval posterior respiratory process, which is 1 mm. long), 7·75 mm.; greatest width (in region of seventh segment), 3·50 mm.; greatest height (in region of seventh segment), 3 mm. Outline (fig. 11), elongate-oval, somewhat narrowed and globose anteriorly, evenly tapering caudad of seventh segment to less than one-third of greatest width at base of posterior respiratory process. In side-view, ventral line almost straight to middle of tenth segment, thence gradually elevated to posterior end. The segmentation is clearly defined for the most part, the integumental vestiture and segmental spines remaining as in the larva, although somewhat shrivelled and distorted. The second head segment is situated at the anterior extremity of the puparium, at the commencement of the ventral line, and is closely applied around the first head segment, which is completely introverted so that the antennae and mouth-opening of the larva are not visible. The larval anterior spiracles are inconspicuous. The pair of short pupal respiratory cornua (figs. 11a and 12) occupy a dorsal position immediately cephalad and laterad of the median segmental spines on the fifth segment, that is, just cephalad of the median transverse ridge of that segment. They are divergent, somewhat strongly curved in a posterior direction, yellowish-brown, cylindrical, sclerotized and rather polished. Each measures about ·5 mm. in length, and they are about ·75 mm. apart. They are moderately stout and taper slightly from the base to the rounded tip, towards which there are a few fine scattered hairs; the distal two-thirds is studded with a hundred or more minute dark brownish nodules except anteriorly towards the inner face, where they occur only near the tip. In several puparia examined the part devoid of nodules is semi-transparent so that the large tracheal tube can be seen to its termination near the tip of the cornu. Under high magnification, the plane surface of each cornu is found to be ornamented with a fine paler reticulation, and each nodule (fig. 13) to consist of two to four elevations, each with a narrowly oval inwardly directed terminal opening. Horizontal branches of the main tracheal trunk lead to the sets of elevations. The larval posterior respiratory process (fig. 11b) is slightly to considerably upturned. The operculum (fig. 11c) consists of the usual dorsal, crescentic piece (the fifth larval segment) bearing the pupal respiratory cornua, and immediately anterior to this a scallop-shell shaped piece (the third and fourth larval segments). The second head segment remains attached to the floor of the puparium, and within may be seen, slightly caudad, the decumbent bucco-pharyngeal armature of the larva with the attached mouth-hood and introverted first head segment.

Acknowledgment.

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Summary.

The life-history of *Rhingia campestris* Meigen is described. The species is bi-voltine in the British Isles, and the larval stage is passed in ox-dung as it lies in the fields. The external, and some part of the internal, morphology of the early stages is described.

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November 9th, 1941.

Gonia fasciata Mg. (*Dipt., Tachinidae*) *at Ashford, Kent.*—For the last two years this fly has appeared in considerable numbers in some rough sheep pasture and on the golf links adjoining my house. I first came across it on March 16th, 1941, while digging in my garden. A female suddenly appeared in the earth which I had just turned over; judging from its appearance it had probably just emerged. A week or so later a fair number were on the wing, and my last record for that year was on May 5th. This year, 1942, I did not see it until March 25th, when I took a pair *in cop.* in my garden; thereafter they seemed even more plentiful than in the preceding year. I have noticed that all my specimens taken in April and May have the lower margins of the wings badly frayed, and I think that so far as this locality is concerned the last week in March is the most favourable collecting period. The flight of *fasciata* is rather slow and faltering and it rarely rises more than a foot or so above the ground. I have watched females for quite a long time in the hope of coming upon some clue to their breeding habits, but entirely without success. Both sexes appear to spend most of their time resting on the sunny side of hummocks of dead grass.—G. Waller, 'Taunton Dene,' Sandyhurst Lane, Ashford, Kent: *May 6th*, 1942.

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