

## STUDIES ON PEDICULUS.

I. THE COPULATORY APPARATUS AND THE PROCESS  
OF COPULATION IN *PEDICULUS HUMANUS*.

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*(From the Quick Laboratory, University of Cambridge.)**(With Plates III and IV and 12 Text-figures.)*

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Introduction<sup>1</sup>.

OWING to the active interest now being taken in all that concerns lice and their habits, especially in connection with the war, it seems expedient to forestall a fuller publication, now in preparation, by

<sup>1</sup> I am much indebted to Dr D. Keilin for his very able and friendly assistance in connection with the work upon which this paper is based.

giving an account of the copulatory apparatus and the curious process of copulation in *Pediculus humanus* Linn.<sup>1</sup>

It is remarkable, in view of the mass of literature that has been published on lice, dating from the time of Leeuwenhoek, that the subject of this paper has remained practically untouched. Where it has been approached, it has received scant treatment, and, as we shall see, the structure of the copulatory organs and mechanism of copulation have been misunderstood. This has doubtless been due to but a few casual observations having been made upon the living insects.

We may begin by considering the main differences shown by the sexes in *P. humanus*, for some of them have a direct bearing upon the subject in hand. These differences concern chiefly the general body form, pigmentation, the structure of the legs, what may be visible of the genitalia viewed externally, the distribution of the hairs upon the abdomen, and the abdominal musculature. A number of these points of difference have been dwelt upon by previous authors and they are summarized as follows:

#### CERTAIN ESSENTIAL DIFFERENCES IN THE ANATOMY OF THE SEXES.

(*Exclusive of the generative organs.*)

**The Male.** The *abdomen* of the male is rounded behind, the ventral surface curving dorsally and forward so that the sexual and rectal orifices come to lie dorsally (Text-fig. 3). The anus lies just in front of the sexual orifice; its position is best indicated when the insect defaecates whilst feeding or immediately afterwards. The anus is marked by a minute pit with a small ventrally situated chitinous plate overlapped by a dorsal integumentary fold. Immediately behind the anal plate lies the broad transverse slit forming the sexual aperture from which the

<sup>1</sup> To avoid confusion I append the following Synonymy:

<i>Pediculus humanus</i> Linn. 1758.	
<i>P. capitis</i> de Geer 1778	} lice from head.
<i>P. cervicalis</i> Latreille 1803	
<i>P. consobrinus</i> Piaget 1880	
<i>P. corporis</i> de Geer 1778	} lice from clothes and body.
<i>P. vestimenti</i> Nitzsch 1818	
<i>P. tabescentium</i> Alt 1824	

Most authors recognize what they hold to be two species the head louse and clothes or body louse. These are, however, identical in all points of structure and can no longer be regarded as distinct, though they may show slight biological differences. The studies here recorded have been carried out on so-called "*P. vestimenti*."

dark point of what we shall call the dilator<sup>1</sup> (Plate III) may, or may not, protrude in life or in preserved specimens. Basally is seen the basal plate (internal) upon which the dilator articulates, the same being visible by translucency through the body wall.

The postero-ventral abdominal wall, which is very convex transversely, is traversed by a number of accordion-like folds which allow of considerable extension of its surface (Text-figs. 1, 3). The male is usually smaller than the female, its abdomen is slenderer and more clearly segmented. Although both sexes show variable degrees of *pigmentation*, the male usually shows the deepest coloration. In well pigmented males the abdominal tergites appear as pairs of dark transverse bands, an appearance never seen in the female whose integumentary structure differs in this region. In the male, the *abdominal hairs* are fairly regularly disposed in rows corresponding to the body segments, whereas, in the female, most of the hairs are scattered about irregularly except on the last segments. A very marked sexual difference is observable in the structure of the *first pair of legs* in the male, these being also larger and more powerful than the others.

The *longitudinal abdominal intersegmental muscles* in the male (Text-fig. 3) are very powerful; dorsally, at the base of the abdomen, they fall into line with corresponding muscles arising in the thorax (*M. levator abdominalis* of Müller) and form a continuous chain of five pairs of muscles on each side extending backward to the last segment. The corresponding ventral muscles are confined to the basal part of the abdomen, extending from the thorax backward so as to include only the first four recognizable sternites.

**The Female.** We have already indicated some of the characters of the female in the preceding paragraphs. The abdomen is broader than that of the male and posteriorly it presents a bilobed appearance (Text-fig. 7). The anal aperture lies dorsally between the lobes beneath which is situated the vaginal aperture whose entrance is seen when the insect is viewed from behind or in ventral aspect. When thus viewed, the aperture is seen to be guarded ventrally by two incurved flattened processes, the gonopods, which are fringed with hairs and connected in the middle line by a fold of the integument surrounding a circular space. Anterior to the gonopods, which are more or less pigmented, a darkly chitinized and thickened area marks the region occupied beneath by

<sup>1</sup> We apply the term dilator to the structure described as the parameres by Mjöberg and by Cummings. All writers on *P. humanus* falsely call it the penis (*v. infra*, p. 296).

the vaginal pouch (Text-fig. 6). The first pair of legs, as in the immature stages, do not differ materially in structure from the others.

The arrangement of the longitudinal intersegmental abdominal muscles (Text-fig. 6) differs from that seen in the male. Dorsally there are five pairs of these muscles to each segment, but they are only present beneath the last three penultimate tergites. Ventrally there are corresponding muscles: three pairs (omitting two pairs of more obliquely directed lateral muscles) at the base of the abdomen in continuation of the ventral longitudinal muscles of the thorax, and there are five pairs of muscles situated posteriorly beneath the fifth and sixth segments.

To recapitulate, the great difference in the longitudinal abdominal musculature observable in the two sexes may be summarized as follows:

	Dorsal abdominal muscles are present under segments	Ventral abdominal muscles are present under segments
In the ♂	2, 3, 4, 5, 6, 7, 8	2 + 3, 4, 5, 6
In the ♀	6, 7, 8	2, 3, 5, 6

This arrangement of the musculature was first observed by Landois (1865) in the female and by Müller (1915) in the male; the enumeration of the segments is in accordance with that advanced by Müller.

The significance of some of the structural differences above enumerated will be considered presently.

### HISTORICAL.

Regarding the copulatory organs of the male and female.

#### *The male apparatus.*

The first reference in the literature on lice to the male copulatory apparatus is that of Leeuwenhoek. In the English edition of his works (1807, p. 163) it is stated that he observed some lice in which he found what appeared to be a weapon of defence or hollow sting lying in a groove whence it was protruded when the insect was roughly handled. He conjectured that the "sting" was present in the male only but did not reach a final conclusion on this point. Gaulke (1863, p. 315; cited by Landois) took the organ for an ovipositor which served for laying eggs in the skin, whereas nearly all subsequent writers, including Landois (1865, p. 52), refer to this sting-like organ as the penis. Landois described it as wedge-shaped and flattened, as consisting of a long basal portion and a slightly bent distal portion. The margins are thickened and a slit-like gutter runs from the point back into the basal part. The organ is protruded through a transverse slit situated dorsally upon

the last abdominal segment and appears to be retractile into a tube lying within the body. This tube bears teeth, as does the vagina, the teeth pointing anteriorly. Landois' figure agrees with his description, both being partly right and partly wrong.

Patton and Cragg (1913, p. 540) somewhat vaguely describe the organ as "of a comparatively simple type" consisting of "two pairs of chitinous rods lying in front of each other in the terminal segment of the abdomen and articulated on a moveable joint." The posterior pair of rods converge behind, "are in close contact with one another, and convey the ejaculatory duct to the exterior between their inner surfaces." The musculature is complicated. This description is cryptic and mostly wrong. The authors' "anterior pair of rods" are what is termed the basal plate, the "posterior pair" are the parameres, or what in this paper we term the dilator. The authors apply the name of penis to both of these structures combined.

Pawlowsky (1907, p. 30) illustrates his paper by cross and longitudinal sections of the male which are more enlightening than his text. He does not appear to have understood the mechanism any better than the preceding authors, to have made dissections, or to have studied the living insect. He refers to the teeth upon the "enveloppe de propulsion" which he thinks holds the "penis" in place in the vagina; what he terms the penis are the combined basal plate and dilator. Pawlowsky's figures are good, for he evidently made faithful drawings of what he saw.

Mjöberg (1910, p. 252), although he does not mention *Pediculus*, compared the male copulatory organs in ANOPLURA and MALLOPHAGA. He is the first author who seems to have understood the structure in the allied forms which he studied.

Leaving the testes and vesiculae seminalis aside for future consideration, we find that Mjöberg states that these insects usually possess a copulatory apparatus consisting of (1) a long ductus ejaculatorius, (2) a basal plate (in some AMBLYCERA represented by two long free rods), (3) parameres, either free or more or less fused (probably serving to widen the vulval aperture to allow the copulatory apparatus to enter), (4) a "preputial sack," studded with small chitinous knobs. In ANOPLURA and ICHNOCERA, the male carries the female on his back, introduces the parameres, then everts the preputial sack which bears an apical penis that penetrates into the female. The chitinous knobs upon the sack anchor the organ to the vaginal wall. Copulation appears to last a long time.

We are indebted to Mjöberg (1910, p. 226) for giving us a nomenclature of certain parts of the male copulatory apparatus in ANOPLURA and MALLOPHAGA. To repeat somewhat, these parts are (1) the *basal plate*, articulating distally as a rule with more or less free structures, the ductus ejaculatorius always running dorsally to the plate; (2) the *parameres* (a term taken from Verhoeff, 1903, pp. 113-170 (cited by Mjöberg), who used it in relation to Coleoptera), these being accessory parts articulating upon the distal portion of the basal plate; (3) the *preputial sack* which surrounds the penis and distal portion of the ductus ejaculatorius and appears usually to be attached to the distal part of the basal plate between it and the parameres. Mjöberg supposes that the preputial sack, like the penis, may have originated from the ninth and tenth intersternal cuticle. (In *Haematopinus suis*, Mjöberg noted the great length of the narrow ductus ejaculatorius and its uniform width, but failed to trace it into the penis.)

Müller (1915, pp. 41-43, figs. 24, 25 and plates II, III) describes and figures the male genitalia. Confining ourselves to the copulatory organs, we find that he describes the ejaculatory duct as entering a copulatory apparatus so complicated that "even Pawlowsky did not fathom it." Müller describes it as a deeply invaginated apparatus with chitinous rods, plates, and teeth, but gives no account of these structures. He refers to the parameres (what we call the dilator) as the penis and says that the term "preputial sack" is a misnomer; in his opinion it should be called the "sac interne," following Jeannel's nomenclature applied to beetles<sup>1</sup>. It is clear that Müller did not grasp the significance of the structure as a whole. He gives figures similar to those of Pawlowsky, a longitudinal section of the posterior extremity of the male abdomen, which is accurate but for the relation of the so-called penis to the sack. His interpretation of the function of certain parts is inaccurate. He denies that the sack contains the ductus ejaculatorius (as stated by Pawlowsky) and finds that the duct ends dorsally in the sack. We shall see presently that the duct runs dorsally to the sack when the latter is invaginated, but that it runs inside the sack when it is expelled.

Cummings (1916, p. 257), like Mjöberg, does not deal with *Pediculus*. He adopts Mjöberg's nomenclature of the parts of the male copulatory

<sup>1</sup> *Vide* Sharp, D. and Muir, F. (1912), "The comparative anatomy of the male genitalia in Coleoptera," *Trans. Ent. Soc. London*, p. 603. According to these authors, the sack is evaginated in Coleoptera: it may have spines pointing basally, these preventing its withdrawal while distended. It is clear that the apparatus in beetles, though very different and varied in construction, has points of resemblance, functionally speaking, with that in *Pediculus*.

apparatus and considers that the basal plate is probably derived from two longitudinal apodemes upon whose posterior ends articulate the two parameres. He prefers, however, to call Mjöberg's preputial sack "the mesosome." The large and extrusible end of the latter is said to be continuous with the ductus ejaculatorius, and distally it bears the penis, with frequently a splint on each side called the telomere, and beneath, the hypomere (terms applied, according to Cummings, by Waterston, 1914, *Ann. S. Afric. Museum*, x, 279, to Philopterid forms). At the proximal end are the endomeres, usually strongly chitinized bands or rods, one on each side, supporting the membrane of the sack of which they are only local thickenings. Cummings notes a suture in the middle line of the basal plate.

Judging from the instructive figures whereby Cummings illustrates these structures in different forms (*Linognathus*, *Trichodectes*, *Goniodes*, etc., but not in *Pediculus*) it appears to me that in *Pediculus*, Mjöberg's parameres are the parameres + endomeres of Cummings. Adopting for the moment the nomenclature of Cummings, I believe that in *Pediculus* we have a partial fusion of the endomeres distally and that they exceed the parameres in length, the latter being fused laterally to the endomeres and thus appearing merely as two small points (see Pl. III, figs. 1, 2). Cummings illustrates the extruded preputial sack in three species belonging to different genera, and it is clear that the function of this organ, though it varies in form in different species, is similar to that we shall describe in this paper for *Pediculus*.

Although not wishing to detract from the importance of the contributions of Mjöberg and of Cummings, neither of them afford evidence of these authors having studied the apparatus they describe other than in caustic potash preparations, for only the chitinous structures are referred to. The mechanism of the apparatus therefore remains to be described and an effort to do so is made in this paper.

*The musculature* of the male copulatory apparatus has received scant attention. Except for the protractor muscles which have their origin at the posterior and postero-ventral portion of the body wall and run forward to their insertions upon the margin of the basal plate, the musculature of these parts has not hitherto been understood. In addition to the protractor muscles just mentioned, Landois (1865, pp. 53-54) refers to retractors inserted dorsally upon the plate and arising from the inside of the last segment; he does not state whether they arise dorsally or ventrally upon the segment. Pawlowsky (1907, pls. IV, VI, figs. 19, 29-33) describes circular muscles about the ejaculatory

duct, and retractors running obliquely from the ventral body wall to the dorsal surface of the sack, these being the retractors of the sack (for which we use the term vesica) whose function we shall describe presently. Pawlowsky places the ejaculatory duct within the inverted sack, whereas it runs outside excepting where it traverses it at the base of the penis. Müller (1915), in his illustrations, refers to the "Bulbus Muskulatur des Penis," muscles called the retractors of the vesica in this paper; Müller figures them in a cross section as running dorsally to the basal plate. He states correctly (p. 43) that these muscles are inserted in the folds of the sack, but from the name he gives them it would appear that he did not apprehend their function.

*The female apparatus.*

A survey of the literature shows that the female apparatus has not hitherto been understood. Landois (1865, p. 50) refers to the presence of teeth upon the vaginal wall, these being seen by transparency through the surface of the body. He figures circular, longitudinal and oblique muscles surrounding the vagina (what we term the uterus), but the structure and shape of the vagina and its relation to the uterus escaped him. Pawlowsky (1907, pls. II, III, figs. 4-12) illustrates his paper by figures of cross and longitudinal sections of the female. He evidently made no dissections and his description is inadequate. His figures indicate, however, that the vagina is flattened dorso-ventrally, dentate internally; muscles arising from the ventral surface of the abdomen run backward to attach themselves upon the dorsal surface of the vaginal wall; the proximal half of the ventral wall of the vagina has inserted upon it retractor muscles running obliquely forward to the ventral surface of the body and it is also traversed by a few muscle fibres which he terms sphincter vaginae. These muscles are not to be confused with others surrounding what we term the uterus but which Pawlowsky terms the vagina (he also terms these muscles sphincter vaginae).

Müller (1915, pp. 37-41, figs. 21, 22) gives an accurate figure of the posterior portion of the female abdomen. He terms the gonopods "vaginal palps" and refers to their position as being at the point of transition between the last two abdominal segments. He gives a misleading schematic figure of the female genitalia for he surrounds the uterus by circular fibres only, making it appear bulbous, the vagina being represented as a straight, narrow tube, whereas it is broad, purse-like, and dentate internally. Finally may be mentioned a superficial paper by Peacock (1916, p. 39) who describes the external features of



the female. He asserts that the gonopods serve to hold the penis during copulation, but this appears to be merely an inaccurate assumption on his part, we have failed to discover their ability to grasp any part of the male genitalia.

## THE AUTHOR'S DESCRIPTION OF THE COPULATORY APPARATUS.

### THE MALE APPARATUS.

To obtain a clear conception of the mechanism of the parts, it is best to commence by giving a general description of the apparatus as it appears when fully extruded by the male in the act of copulation.

When a pair in copula are separated forcibly by traction with two pairs of forceps which hold their bodies, the extruded apparatus of the male appears to the naked eye as a large, pale, rounded mass protruding dorsally from the end of the abdomen. If the male is not molested, this mass is presently retracted into its body.

To view the extruded apparatus at leisure, it is necessary to kill the male by a rapid method, either killing the male alone, immediately after its removal from the female, or together with the female with which it is in copula. For this purpose the insects are best killed by immersion in water heated to 70° C. whilst they are held with a pair of forceps.

### General description of the extruded apparatus.

Assuming that a male has been killed immediately after its separation from the female in the manner described, the insect, or the isolated apparatus, may be conveniently studied whilst floating in water. Or, if permanent preparations are desired, the parts may be (1) treated in the usual way with caustic potash and subsequently mounted in balsam, or (2) immediately fixed in Carnoy's solution and stained *in toto*, or (3) sectioned.

*Chitinous structures:* We shall confine our attention in the first instance to the chitinous structures. In a freshly killed male, viewed from behind whilst in water (Text-fig. 1), the apparatus is seen to consist of a thin-walled globular sack (*V. pen.*) supported upon a stem (*V. pen. S.*) issuing from between two darkly chitinized rods (*Dil.*) which are pointed backward and downward; these structures articulate upon what appear to be two dark rods (*B. P.*) which protrude from the last abdominal segment. The greater part of the sack, which measures

0.4–0.7 mm. transversely, is studded over with short chitinous tuberosities or teeth that point outwardly and basally; some areas, as shown in this and succeeding figures, appear finely granular and devoid of teeth. Protruding from the left side of the vesica, and this position appears to be constant, there is a darkly chitinized tubular structure, the penis (*Pen.*). The latter is continuous basally with the walls of the vesica and with a peculiarly shaped rod (*St. pen.*) imbedded in the wall of the sack.

When viewed laterally, as shown in the semi-schematic Text-fig. 2, the relations of some of the chitinous structures enumerated will be more

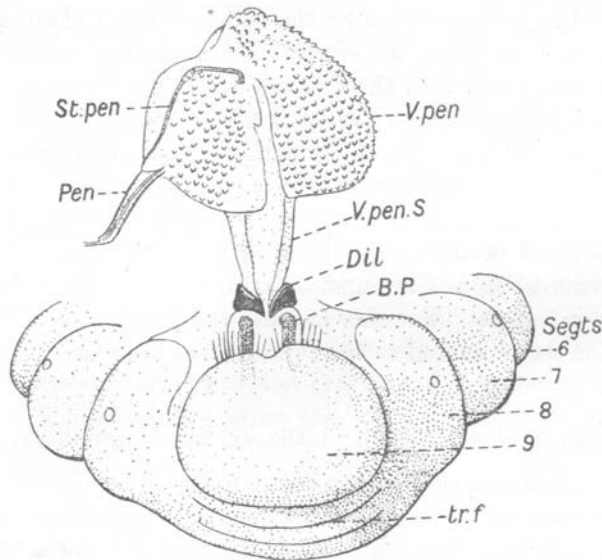


Fig. 1. *Pediculus humanus* ♂. Extruded copulatory apparatus seen from behind in a male forcibly removed from a female whilst in copula and promptly killed.

clearly understood; they are represented in solid black. The sack or vesica is represented by a serrated contour denoting the teeth which project from its surface, it issues from a cleft in the dilator (*Dil.*), the cleft being, however, better seen in subsequent figures. The teeth on the surface of the vesica are omitted for clearness' sake, the *statumen penis* (*St. pen.*) and *penis* (*Pen.*) are represented in black. The structure of the dilator will be best understood by reference to Plate III, figs. 1 and 2, wherein it is shown as it appears when retracted within the body of the male (fig. 1) and when extruded (fig. 2). The dilator is sharply

V-shaped distally, and, when extruded, it is flexed forward and downward so that its point impinges upon the dorsal surface of the male's abdomen.

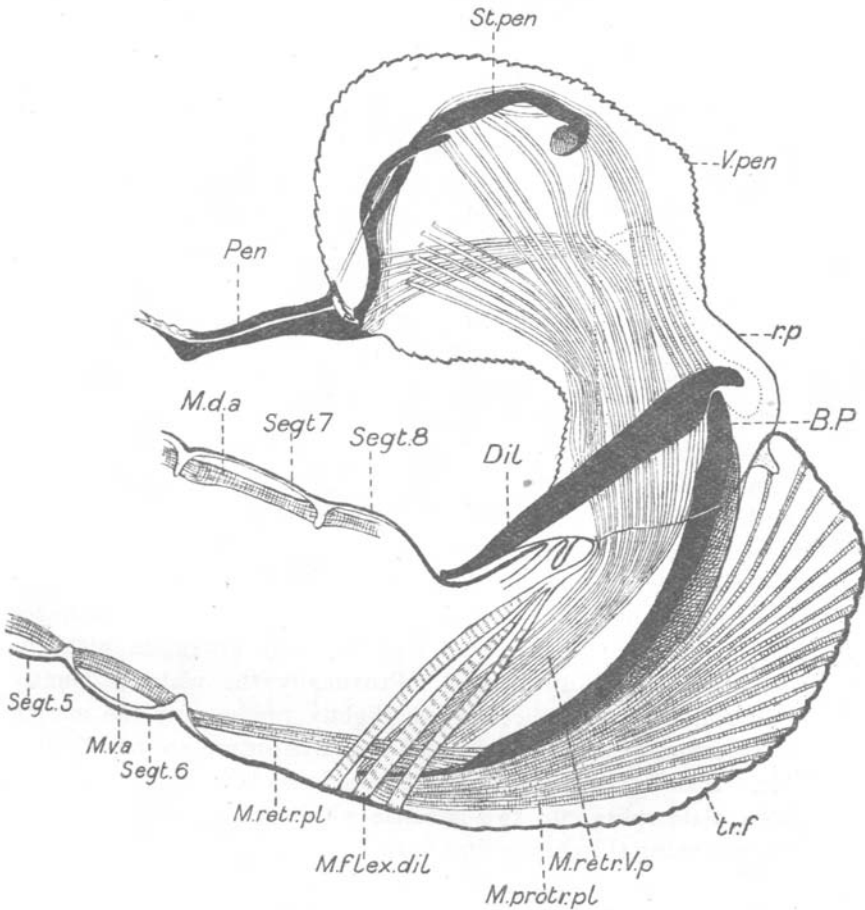


Fig. 2. *Pediculus humanus* ♂. Extruded copulatory apparatus seen from the side. Semi-schematic figure. The extruded parts, drawn from a carmine-stained preparation *in toto*, show the distribution of the muscles in the vesica penis (*V. pen.*): to the walls of the sack, the statumen penis (*St. pen.*) and penis (*Pen.*), the dilator being flexed and impinging upon the dorsal surface of the abdomen. The lower part of the abdomen is schematized from sections and dissections.

We may now consider in greater detail some of the chitinous structures which constitute the apparatus.

The component parts of the apparatus.

The copulatory apparatus of the male, when at rest, is usually completely retracted within the last three abdominal segments (Text-fig. 3). It issues through a large transverse slit upon the dorsal surface of the abdomen immediately behind the anus. The walls of this slit form the beginning of a flattened tube which is continuous with the chitinous exoskeleton. At its deepest point of invagination into the body, the tube folds backward and inward like the partly inverted finger of a mitten, and its walls fuse distally with the chitinous structures of the evertible copulatory organs (see Text-fig. 3 where the post-genital [*p. g. f.*] and pregenital fold, in front of *p. pl.*, are shown).

*The essential parts of the apparatus are:* (1) the *basal plate*, (2) the *dilator* (parameres), (3) the *vesica penis*, including its rib or strut, *statumen penis*, embedded in its wall, (4) the *penis*, and (5) the *ductus ejaculatorius*.

(1) *The basal plate* (Pl. III, figs. 1, 2; Text-figs. 1-4, *B. P.* or *B. Pl.*) is of elongated form, concave dorsally in transverse section, and curving gently in a dorsal direction along its length. It measures 0.75-1.15 mm. in length depending upon the size of the male (the other structures below-mentioned vary correspondingly in size). The basal plate is greatly strengthened laterally by a rod-like thickening on each side which arises gradually and terminates distally in a heavily chitinized rounded extremity. The pair of rounded ends articulate with the dilator which hinges upon them. Proximally the plate is bluntly rounded, thin and almost colourless, slightly rugose near the margin for the insertion of muscles; signs of a median suture are usually discernible. Distally, as is seen in sagittal sections (Text-fig. 3, *B. Pl. cl.*), the basal plate splits into two lamellae which are in continuity with the chitin forming the post-genital fold (Text-fig. 3, *p. g. f.*).

(2) *The dilator* (Pl. III, figs. 1, 2; Text-figs. 1, 2, 4, *Dil.*). Apart from lateral thickenings of the basal plate above described, the dilator constitutes the most heavily chitinized part of the whole apparatus. The structure is composite in origin for it is derived from two if not four chitinous rods (the *parameres* of Mjöberg) which through fusion of their distal extremities into a point have, functionally speaking, become a single V-shaped organ. The two rods diverge basally to their articulations on the basal plate. For purposes of description the name dilator is here preferred, it being more convenient to refer to the structure in the singular. The dilator measures 0.4-0.7 mm. in length. When the

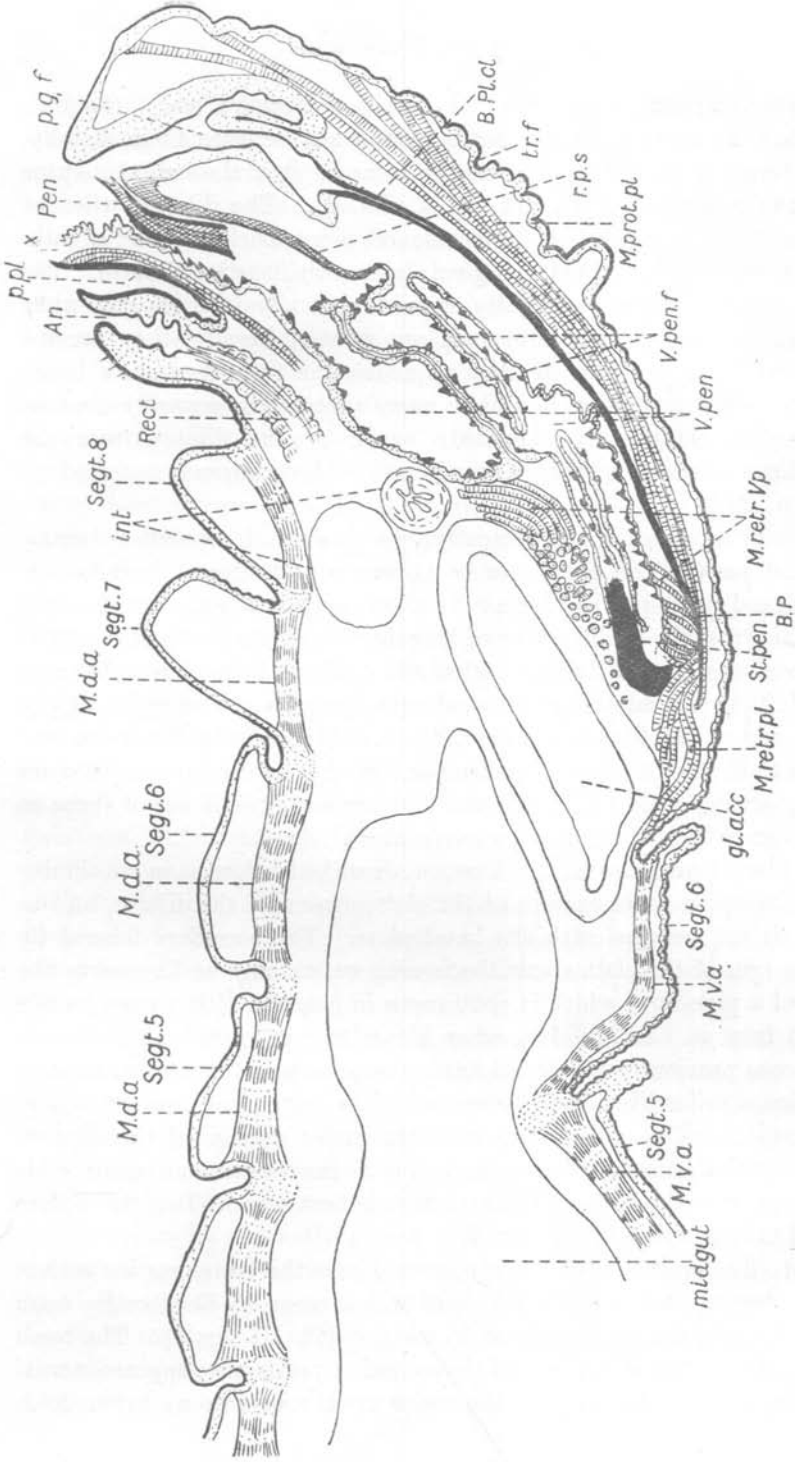


Fig. 3. *Pediculus humanus* ♂. Longitudinal, almost median section of the posterior part of the abdomen in a male whose copulatory apparatus is retracted into the body and at rest. The point of the penis is shown issuing from the inverted vesica, it has been somewhat displaced outwardly in sectioning. The thick chitin of the dilator has been torn away, causing a break in the section at x. Figure slightly schematized.

copulatory apparatus is retracted within the male's body, the rods approach each other leaving but a narrow slit between them distally, the interspace broadens considerably behind; it is through this space that the penis issues (Pl. III, fig. 1, *Dil. cl.*). The dilator, when at rest, as shown in the figure just mentioned, points backward and slightly dorsally within the animal, lying on a plane with the basal plate. The point of the dilator is slightly curved ventrally (the reverse when seen in copula). The dilator rods are stoutest basally, they become flattened dorso-ventrally as they approach the tip; they show longitudinal ridges, and near their bases carry a lateral, backwardly directed spine. The supposedly composite origin of the dilator from the parameres + endomeres of Cummings has been already referred to (*vide p.* 299).

When, as we shall see presently, the process of copulation begins, the first part of the apparatus to appear is the dilator (Text-fig. 5); it is flexed upon the basal plate at about a right angle. At the next stage the vesica is slightly everted and the basal plate protrudes slightly. The pressure exerted by the vesica and penis in being forced through the cleft of the dilator greatly enlarges the cleft. The union at the distal end of the dilator, however, limits the increase in the space, and owing to the shafts becoming flatter and weaker as they progress toward the point they yield to the pressure and become twisted out of shape to a greater or less degree as depicted in Pl. III, fig. 2.

It should be noted that the vesica, described below, is in continuity with the upper inner margin of the cleft portion of the dilator, and to some extent perhaps with the basal plate. The boundary formed by the margin of the cleft about the issuing vesica may be likened to the edge of a pipe-bowl which is continuous in contour with a soap bubble blown from it. In addition, when the dilator is extruded and flexed, what was previously the dorsal having now become the ventral surface, a delicate *collar-like sheath* becomes visible, extending upward out of the genital orifice and fusing with the under surface of the dilator; this sheath forms a tube through which the vesica and penis glide outward from the body. The structure is best seen in Text-fig. 5; see also Text-fig. 2 and Pl. III, fig. 2.

(3) *The vesica penis*, when retracted into the body, carries with it the *statumen penis* and penis, all of which come to lie dorsally upon the hollow of the basal plate as in a spoon (Pl. III, fig. 1). The teeth which stud the outer surface of the extruded vesica now appear internal (Text-fig. 3), and the walls of the vesica are thrown into numerous folds

(*V. pen. f.*) which appear at times very confusing in sections; the teeth are mostly directed toward the genital orifice. When the vesica is extruded it is seen to glide outward upon the basal plate (Pl. III, fig. 2) and the teeth alter their direction as illustrated in the figure. The penis is seen lying within the invaginated vesica, its distal extremity pointing into the cleft in the dilator (Pl. III, fig. 1, *Dil. cl.*), through which it is propelled. The base of the penis is continuous with the *statumen penis*. The latter may be regarded as merely a rod-like thickening of the vesica wall, it shows some variation in appearance and size in different individuals, it measures 0.45–0.70 mm. in length but is difficult to measure because of its curvature. Basally, the *statumen* protrudes more or less from the inverted vesica, at this point it is broad and twisted and shows faintly visible chitinous strands which indicate where muscle fibres are inserted; its shaft is slender and bandlike, about midway it sends off a retrograde flattened branch which curves about it, and distally, near the base of the penis, it shows a large asymmetrical protrusion which is best seen when the parts are isolated (Pl. III, fig. 3). The appearance of the vesica when extruded has already been described.

(4) *The penis* is a tubular structure, darkly chitinized, and tapering to a point, somewhat like that of a quill pen. Its length varies, measuring from 0.24 to 0.32 mm. in the specimens examined. It is broadest basally, where upon its internal surface there are fine granulations and striations where muscles are inserted. Its shaft tapers to about a width of  $20\mu$ , and distally it ends in a fine point or points of very thin colourless chitin. Running through the lumen of the penis and clearly discernible is the ductus ejaculatorius. The penis protrudes from the left side of the evaginated vesica; its chitin is continuous with that of the vesica and *statumen*.

(5) *The ductus ejaculatorius* is a very thin-walled, colourless and structureless tube of remarkably uniform width from near the tip of the penis to where it suddenly becomes muscular near the proximal end of the basal plate. Within the tube of the penis it measures  $5\text{--}6\mu$ , posterior to this it may measure  $7\mu$ , but possibly this slightly increased width may be due to flattening. In dissections of the inverted vesica, the duct can be distinctly traced from the base of the penis directly through the wall of the vesica, along whose dorsal surface it afterwards runs backward to the accessory glands. Basally, its muscular investiture sets in abruptly and rapidly grows in volume, the strong musculature doubtless being essential to force out the spermatic fluid through the long and minute duct. In one specimen the duct measured 1.1 mm. in

length from the base of the penis to where the duct became muscular. The whole course of the duct is best shown in Text-fig. 4, but its position is also shown in Plate III, figs. 1, 2, *D. ej.* It is evident from what has been said that when the vesica is everted the duct follows the penis,

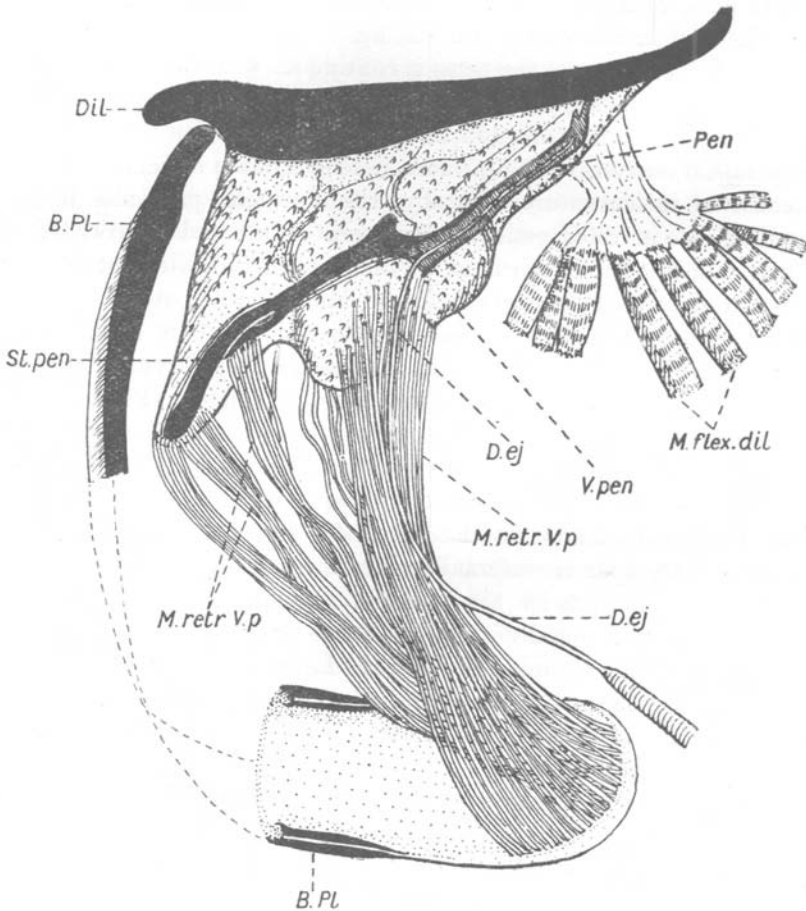


Fig. 4. *Pediculus humanus* ♂. Dissection of the retracted copulatory apparatus. The basal plate is cut across and the muscles running from its base to their insertions in the vesica, etc., are stretched. Figure slightly schematized.

traversing the vesica, where it runs parallel with the fibres of the retractor muscles which stretch outward in the cavity of the sack. The protrusive movement of the basal plate and whole copulatory apparatus, as is seen from sections, also entails a corresponding movement of the accessory glands which lie partly dorsal to the plate.



## Mechanism.

In considering the chitinous structures we have already had to touch upon matters relating to the mechanism but there are other points still to consider, especially the mechanism whereby the apparatus is protruded and retracted.

*The mechanism whereby protrusion is effected.* When the living male is handled, as Leeuwenhoek and apparently no others since have observed, the point of the dilator is protruded to a moderate degree in the course of muscular efforts made by the insect to free itself. This point is the first part of the apparatus to be protruded, and males approaching females may be seen to protrude it intermittently in a similar manner. This movement is effected by a system of parallel muscular fibres, of great length, which arise at the posterior (ventral) part of the abdomen where it curves dorsally, and run forward to their insertions upon the ventral surface of the anterior or rounded end of the basal plate (Text-figs. 2, 3, *M. protr. pl.*). When a male is viewed ventrally, or the parts are dissected out, these protractor muscles are seen to cover the whole ventral surface of the plate, the fibres running parallel to each other, a few fibres running alongside the edge of the plate. When viewed in longitudinal sections the muscles are seen to spread out in a fan-like manner as they approach their points of origin on the wall of the abdomen. This wall, beneath the basal plate, is traversed by numerous creases which permit of considerable extension of the surface and only the deeper creases remain clearly in evidence when the copulatory apparatus is extruded (Text-figs. 1, 2, 3, *tr. f.*).

As the dilator is further extruded it becomes flexed upon the basal plate. This movement is no doubt in the main due to the traction exerted through the collar-like membrane connecting the dilator with underlying structures, mainly a system of powerful flexor muscles (Text-fig. 2, *M. flex. dil.*) which run obliquely backward and upward from the ventral abdominal wall to their insertion in the collar-membrane which serves as a tendon. These muscles do not, however, come into full play until a later stage, for the male starts the process of copulation by inserting the dilator only and it is not until the vesica is fully everted that he depresses the dilator fully by the action of these muscles so that the tip of the dilator rests upon his back. These flexor muscles of the dilator are only shown schematically, as in Text-fig. 2, as three fibres, whereas in Text-fig. 4, drawn from an actual dissection, they are shown torn away from their abdominal attachments and much contracted; the

collar-membrane in which they are inserted is partly torn away and lies external to the inverted vesica.

Following upon a moderate flexing of the dilator, whereby it forms roughly a right angle with the basal plate (Text-fig. 5; Pl. III, fig. 2) a third movement takes place. This movement concerns *the expulsion of the vesica*, and it is due to the flow of coelomic fluid out of the body cavity into the vesica, all of the retractor muscles being the while relaxed. The expulsion of the coelomic fluid which renders the sack turgid, is due to powerful contractions of the trunk muscles whereby the fluid is pressed out of the body into the vesica. It is possible that there are fine muscles present which serve to constrict the channel into the sack

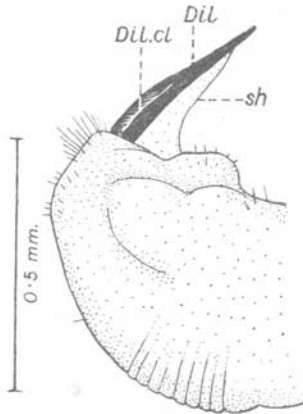


Fig. 5. *Pediculus humanus* ♂. Posterior part of the abdomen, showing the first stage in the protrusion of the copulatory apparatus, when the male attacks the female. Only the dilator protrudes and beneath it is seen the collar-like membrane which forms a sheath for the transit of the vesica, etc. Drawing from preserved specimen.

thus maintaining it erect, but if they exist they still remain to be discovered. It seems likely that there are no such muscles, and that the sack remains inflated once it has been filled with fluid, the turgidity being maintained throughout by the moderately sustained contraction of the muscles which reduce the space for the fluid in the body. When the vesica is fully extruded, the point of the dilator is fully depressed by the flexor muscles already referred to.

In the retracted apparatus (Pl. III, fig. 1), the point of the penis is directed outward toward the cleft in the dilator (*Dil. cl.*), the result being that when the vesica begins to issue (Pl. III, fig. 2, *Pen.*) the point of the penis promptly emerges from the cleft, its point being surrounded

by folds of the issuing vesica. The distortion in the form of the dilator due to pressure from the vesica has already been noted, that this pressure is very considerable is clear; we have one specimen in which a fracture of one of the rods of the dilator distally appears attributable to this cause.

Finally, the whole vesica disappears from the dorsal surface of the basal plate (Text-fig. 2); the neck of the sack is the last part to emerge (when inverted, it lies adjacent to the cleft in the dilator upon the ventral surface of the basal plate); the non-dentate or rugose portion (Text-figs. 2, 3, *r. p. s.*) is clearly seen in longitudinal sections.

*The mechanism whereby retraction is effected.* The *vesical musculature* is shown in Text-figs. 2, 3 and 4, and keeping in mind the description given of the process of expulsion of the vesica we obtain a fairly clear conception of how retraction is effected. To begin with, any pressure which may have been maintained upon the coelomic fluid in the vesica would have to be suspended, the flexor muscles of the dilator and the protractors of the basal plate would have to be successively relaxed. As is well shown in Text-fig. 2, the vesica is supplied with numerous very fine and long muscle fibres which arise around the anterior rounded margin of the basal plate upon its dorsal surface. These muscles run parallel to each other dorsally to the basal plate, and some of them, on entering the vesica, diverge in smaller bundles running respectively to the walls of the vesica, the statumen penis and penis base. The number of fibres is actually larger than figured, some fifty-six fibres having been counted in a cross section of the vesica. It is clear that when these muscles contract they will retract all the parts in which they are inserted, thereby causing the vesica to empty back its coelomic fluid into the body cavity while the vesica gradually becomes invaginated. It is possible that some fibres may give a certain independence of movement to the penis.

In dissections of the retracted copulatory apparatus, the retractor muscles of the vesica form a rounded mass, recalling a heap of string, lying dorsally upon the retracted vesica above the anterior end of the basal plate. In sections, the fibres run in different directions (Text-fig. 3, *M. retr. V. p.*), and from sections alone it would be impossible to explain their mode of action; these muscles constitute the so-called "Bulbus Muskulatur des Penis" of Müller (1915). The best picture of their arrangement is conveyed by Text-fig. 4 which represents a drawing from a dissection of the retracted copulatory apparatus. In this case the basal plate (*B. Pl.*) was cut across and the muscles running from its

base to their insertions were put upon the stretch between two fine needles, and, whilst stretched upon the slide, the preparation was fixed by dropping Carnoy's solution upon it; the specimen was afterwards stained and mounted in balsam.

*The retractor muscles of the basal plate* (Text-figs. 2, 3, *M. retr. pl.*) are relatively few. They arise from the ventral intersegmental fold bounding the seventh abdominal segment anteriorly and pass backward to their insertions laterally near the anterior end of the basal plate; these muscles will serve to retract the plate gently into the body.

*The return of the dilator to its resting position* is due to the relaxation of its flexor muscles and its elastic rebound upon its basal articulation; similarly, as the pressure of the vesica within the cleft lessens, the rebound of the chitin surrounding the cleft causes the lumen of the latter to narrow. When at rest, the axes of the dilator and basal plate fall into line.

*The ductus ejaculatorius* (Text-fig. 4, *D. ej.*) runs between the retractor muscles of the vesica and enters the latter at the base of the penis. The duct is therefore propelled passively with the sack when the latter is extruded, and it is also retracted passively.

Judging from the presence of a few muscle fibres attached to the posterior thickened wall of the pregenital fold (Text-fig. 3, *p. pl.*), these muscles may serve to occlude the lumen of the genital aperture and perhaps aid in the act of defaecation by raising and pushing forward the anal papilla.

#### THE FEMALE APPARATUS.

The structure of the female copulatory apparatus is very much simpler than that of the male. Its position is shown in Text-figs. 6, 7 and 9. It is situated ventrally in the last three segments of the body. The vaginal orifice (Text-figs. 6 and 9, *vag.*) appears as a transverse slit occupying the greater portion of the width of the last segment, and immediately dorsal to it lies the anal orifice (*An.*) between the two terminal lobes of the body. In darkly pigmented specimens, a sharply defined, darkened area of thickened chitin of characteristic form, covers a part of this region ventrally (Text-fig. 6, *v. pl.*), and posterior thereto occur the paired, so-called gonopods which are usually pigmented (Text-figs. 7, 9, *Gon.*). The gonopods are in the form of flat incurved hooks which overlap slightly behind and whose inner concave margins are in continuity anteriorly through a concave fold of the integument; this fold and the inner margins of the hooks, bound a subcircular space

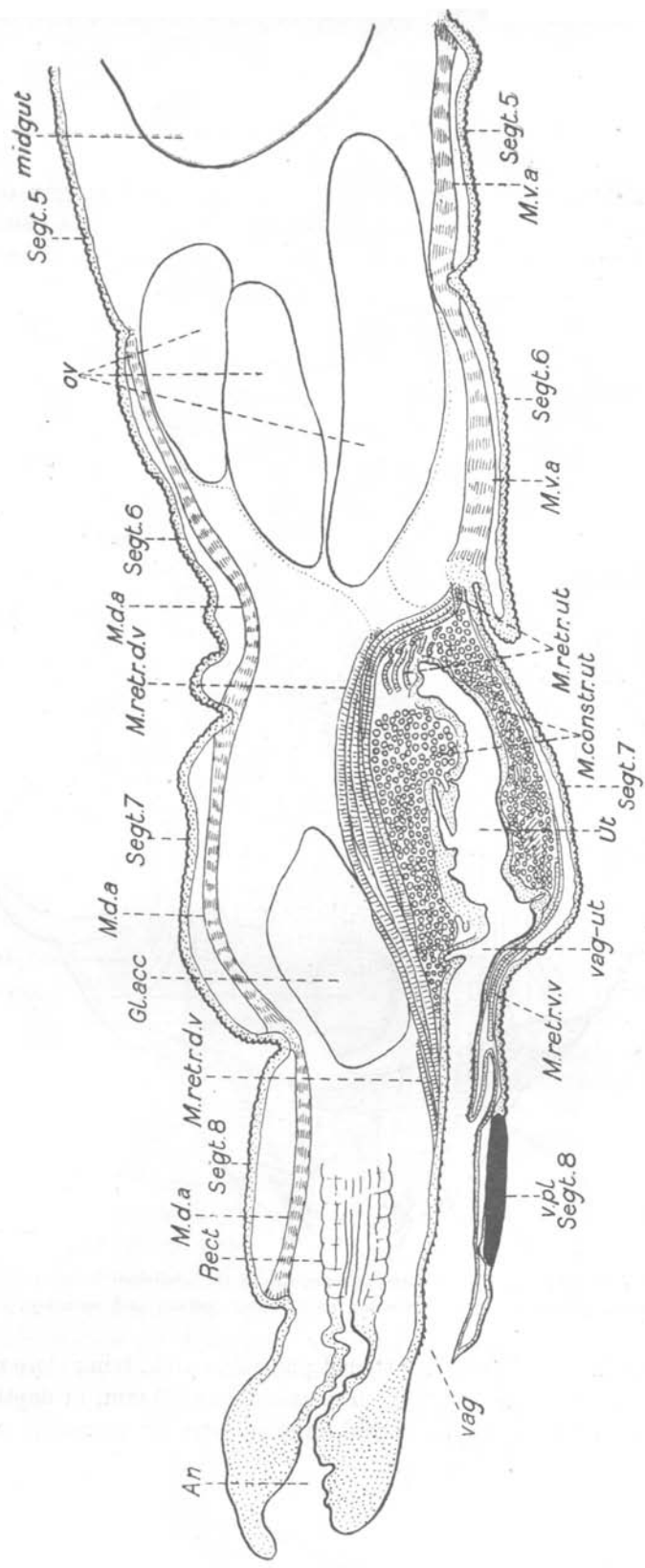


Fig. 6. *Pediculus humanus* ♀. Longitudinal, almost median section of the posterior part of the abdomen. Slightly schematized figure.

leading into the vagina. Projecting from the ventral margin of the vaginal orifice, and visible through the aforesaid space, is a chitinous flap (*v. fl.*) guarding the entrance. Folds of integument on either side of the orifice bear a number of fine long tactile hairs.

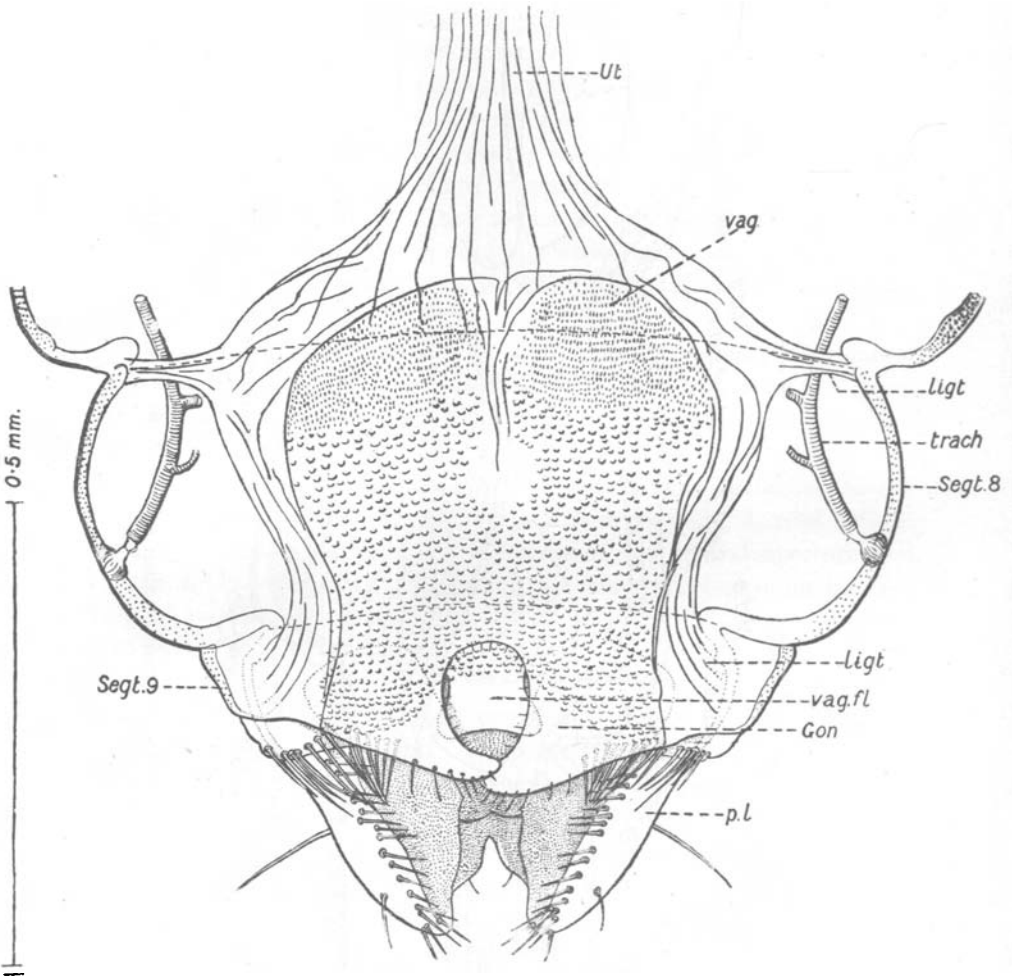


Fig. 7. *Pediculus humanus* ♀. Posterior segments of the abdomen in ventral aspect. Drawing from a specimen treated with caustic potash and mounted.

The vagina consists of a flattened purse-like sack, lying close to the ventral surface of the body; it measures about 0.5 mm. in depth and is covered on its dorsal and ventral inner surfaces by numerous minute

teeth which are directed outwardly (compare Text-figs. 6 and 7). The greater number of these teeth (Text-fig. 8) are semicircular in contour, these measure about  $10\mu$  in width, but at the fundus of the vagina they are long and pointed, measuring about  $10\mu$  in length; the distribution of the two kinds of teeth is sharply defined as shown in the accompanying illustrations (Text-figs. 7, 8). Laterally, chitinous ligaments (*ligts.*) running to the exoskeleton at the intersegmental folds, serve to hold the vagina in place. The vagina at its fundus leads into the uterus

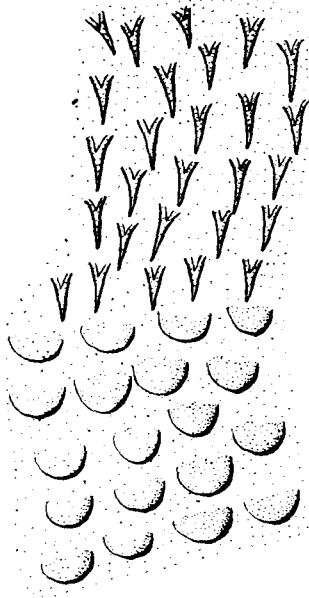


Fig. 8. *Pediculus humanus* ♀. Detail showing the dentition of the vaginal wall where the shape of the teeth changes abruptly as indicated likewise in Fig. 6. The pointed teeth measure  $10\mu$  in length.

(Text-fig. 7, *Ut.*) whose delicate and structureless chitinous lining is thrown into numerous deep convoluted folds allowing of great expansion for the passage of the eggs. The uterus is provided with a powerful musculature consisting, as Landois first showed, of transverse and oblique muscles surrounding its lumen (Text-fig. 6, *M. constr. ut.*); a consideration of the uterus does not, however, enter into the province of this paper.

The structures above enumerated can be seen to a great extent in living specimens, the teeth covering a part of the vaginal wall being visible also by transparency. Text-fig. 7 was drawn from a specimen

treated with caustic potash and mounted in balsam, it therefore only shows the chitinous structures.

Text-fig. 6 illustrates certain muscles that may or may not play a part in copulation: retractor muscles running from the posterior dorsal and ventral surfaces of the vagina (*M. retr. d. v.* and *M. retr. v. v.*) and running forward to their origin in the intersegmental fold bounding the seventh segment anteriorly. The retractor muscles of the uterus (*M. retr. ut.*) may also be noted, these also originate in the above-mentioned intersegmental fold and are more numerous than shown in the section, for they are mostly situated laterally to the median line. All of these muscles doubtless play an important part, together with the constrictors of the uterus, in the expulsion of the eggs. The function of the fine, backwardly directed chitinous teeth protruding from the

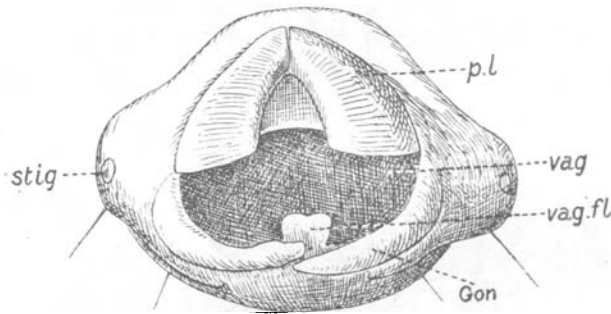


Fig. 9. *Pediculus humanus* ♀. Posterior aspect of a female killed whilst in copula and fixed, the male having subsequently been pulled away. Sketch.

vaginal wall is probably in the main to aid in the expulsion of the eggs, it is difficult to see how they could assist materially in copulation.

In Text-fig. 9 a sketch is given of the posterior aspect of a female which was killed and fixed whilst in copula, the male being subsequently pulled away. The vagina is seen to have been fully dilated by the male copulatory apparatus; the parts are lettered in accordance with the figures previously described.

### THE ACT OF COPULATION.

#### Historical.

The first author to give any information about the process of copulation in *P. humanus* is Warburton (1910, pp. 23-27), who states that he observed a female copulating on the fifth day after ecdysis, after which copulation took place frequently and lasted for hours; he considered



that adults only begin to perform their sexual functions on the fourth to fifth day after ecdysis. He made rough sketches of pairs in copula but never published them. Sikora (VIII, 1915, pp. 523-537) observed that copulation may occur ten hours after ecdysis in lice kept at 35° C. upon man, and personally I have no doubt but that it may take place even sooner. Hase (1915, p. 64, cited by Müller) states that copulation lasts 40-70 minutes or more. Müller (1915, p. 43, and pl. III, fig. 8) is the first author who has illustrated a pair in copula: he gives their relative positions correctly in a coloured figure of a pair killed in copula with chloroform. Whilst he states that the fully extruded "penis sack" occupies the vagina, the teeth being directed outward and backward, his figure is incorrect as it only depicts the dilator entering the vagina. Finally, Hindle, in his unpublished notes made some two years before the outbreak of the present war, records that he observed copulation to occur whilst the insects were feeding, and that couples at times remained in copula for several hours.

The foregoing paragraph sums up all that has hitherto been published regarding the process of copulation. The paper by Müller became known to me through the courtesy of Dr A. E. Shipley, this autumn, after this investigation had been practically completed. Müller's description is, however, misleading, and, as far as I am aware, nobody has hitherto followed the whole process from start to finish or explained the anatomy and functions of the copulatory organs with even an approximate degree of accuracy.

#### THE AUTHOR'S OBSERVATIONS.

As the result of numerous observations made in the course of investigations on *P. humanus*, it has been found that the sexes may copulate at any time but that they do so mostly a few hours after feeding. To observe copulation, the insects require to be kept warm, otherwise they are inactive; a temperature of about 30° C. is suitable for the purpose. The following account is based on notes made immediately after a pair had been observed to enter into copulation, and it may be taken as a typical description of the sexual act. The observation was made with a Zeiss binocular microscope, magnification  $\times 40$ , the tube of the instrument being placed horizontally so that the pair were viewed sideways and in a good light.

The male approached the female from behind whilst she was feeding, her abdomen being well raised behind. The male, with the claws of his

first pair of legs, seized the female's third pair of legs at the bases of the femurs. He then curved his back so that it became concave and closely applied to the body of the female. The female was thereby tilted into a vertical position with her abdomen curving away from the male. This led to the extraordinary position of attack depicted in Text-fig. 10, wherein the female stands as on a tripod consisting of her head and the claws of her forefeet which latter cling to the substratum and prevent

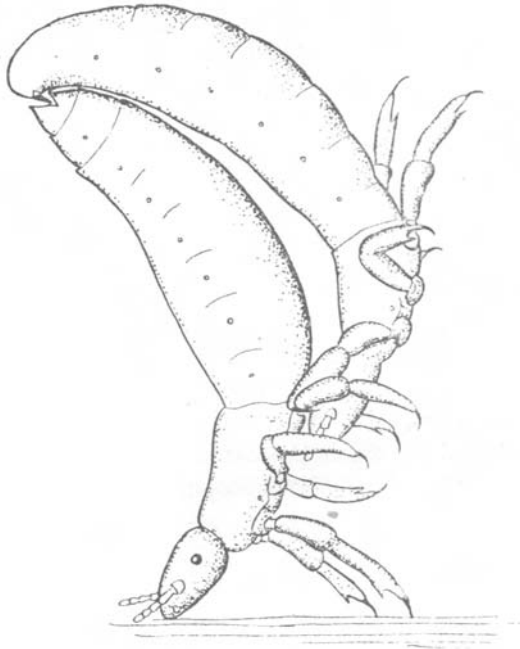


Fig. 10. *Pediculus humanus*. Commencement of copulation, the female stands tripod-wise upon her buccal region and first pair of legs, entirely supporting the weight of the male who grasps her third leg-pair at the base with the claws of his first pair of legs, bends backward and inserts the point of his dilator into the vaginal orifice.

her performing a somersault. The male's whole weight is now supported by the female. The male maintains himself in position solely by his grip on the female's legs and by the slight support afforded from leaning backward against the slanting surface of the female's abdomen. During this time the male's head and antennae appear as if stroking the ventral surface of the female's thorax. The male, having extruded the point of the dilator and flexed that structure upon the basal plate (as in Text-fig. 5), protrudes and retracts it rapidly, but fitfully whilst seeking to

hook it into the vagina. Both sexes defaecate whilst these efforts continue, the amount voided by the female being greatly in excess of that voided by the male. The faeces, or rapidly inspissating masses of the freshly ingested blood are pushed to one side by the dilator as they get in the way, and finally, after a struggle lasting about a couple of minutes, the dilator penetrates the vagina. The dilator now gives the male an additional hold on the female and it is extruded still further and rapidly pushed in and out, whilst penetrating more and more deeply. After some 30-40 strokes, when it has penetrated to its full length, corresponding to the depth of the vagina, the parts are seen to glisten

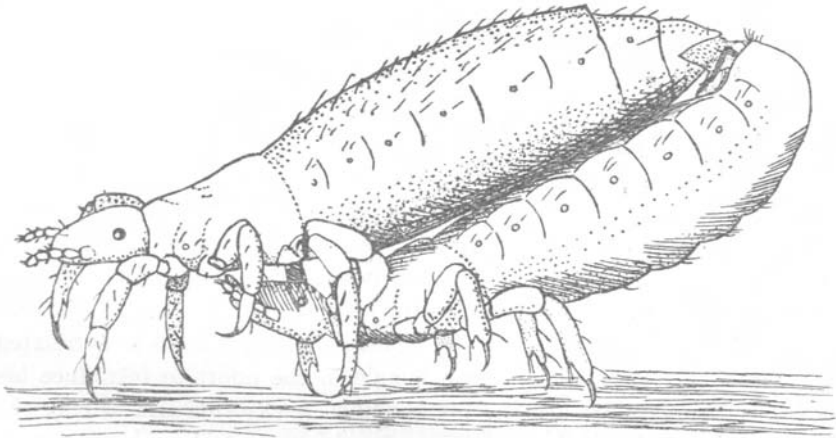


Fig. 11. *Pediculus humanus*. The male having dilated the vagina as shown in Fig. 10, has extruded his vesica with its distal penis into the vagina, and withdrawn the dilator whose point is flexed on his back. He is now firmly anchored by the teeth on the vesica adhering to the walls of the vagina, and the couple walk away to a retreat. This, and the preceding figure were drawn from hasty sketches subsequently amplified from killed specimens.

with secretion. The female's abdomen now suddenly shortens, owing to the last two segments becoming somewhat telescoped, apparently through the forceful efforts of the male. The dilator continues to penetrate deeply for a few strokes, it is then quickly retracted, having been rapidly replaced by the everted vesica. The dilator is immediately flexed downward and out of the way on the male's back, having served its purpose in widening the vagina. At no time do the so-called gonopods appear to come into play as graspers or otherwise. The dilated vesica fills the whole lumen of the vagina which it distends almost to

its own size, a small portion of the basal portion of the sack and the whole of its stem remaining outside the greatly stretched vulva. As soon as the vesica is safely anchored by means of its teeth to the inside of the vagina, the male ceases to strain backward, the female's abdomen again lengthens and the pair drop into a less acrobatic attitude upon their legs as shown in Text-fig. 11, and, united in copula, they retreat beneath a sheltering piece of cloth.

This undoubtedly represents the usual procedure. On one occasion only was a male observed to seize the female by the bases of the second pair of legs. When on cloth and ready to copulate, the females are frequently seen to assume an attitude approximating to that shown in Text-fig. 10, the hind pair of legs and the abdomen being raised almost vertically as if inviting the male to approach and seize her. The pair remain united for a variable time, anywhere from half an hour to several hours. A male which has just ceased to copulate with a female has been seen to clamber on her back, seize her about the body with his six legs, she walking away with him. At other times the male has been seen to copulate again immediately after having abandoned a female.

We may revert here to the differences already noted in the abdominal musculature of the sexes, since in part it bears directly upon the process of copulation. The more powerful dorsal system of longitudinal muscles in the male (compare Text-figs. 3 and 6) appears to be correlated with his ability to overcome the female in the effort to introduce his copulatory organs by arching his abdomen backwards and forcing the dilator forward; doubtless these muscles also serve to keep his abdomen from being unduly pressed downward by the female's weight during copula, especially when the pair move about. The latter suggestion as to the function of these muscles emanates from Müller who was the first to appreciate the differences in the musculature in the sexes.

*The legs as accessory organs of copulation.* Previous authors have noted the form and greater size and especially the powerful claws of the first pair of legs in the male. It is clear that they are more powerful, so as to enable the male, as we have seen, to grasp the female firmly during copulation. There is, however, a corresponding adaptation in the structure of the third pair of legs in the female. But for two drawings of the female by Terzi (in Castellani and Chalmers, 1913, pp. 632-633, figs. 268, 270) the structure appears to have escaped the notice of previous observers; its significance has certainly not been understood hitherto. Although less pronounced in poorly chitinized females, the structure is invariably present. It consists (Text-fig. 12) of a blunt

recurved ventral spur near the base of the femur. This spur serves to facilitate and maintain the grip of the male claw upon the leg.

In conclusion, a glance at Plate IV will serve to recapitulate the main points regarding the structure and interrelations of the copulatory apparatus in both sexes of *Pediculus humanus*. The figure is printed in two colours to differentiate the parts belonging to each sex, black for the male and red for the female. The figure represents a camera lucida drawing of a specimen mounted in balsam and confines itself to the chitinous structures. The terminology of the parts will be found accompanying the other figures described in the text.

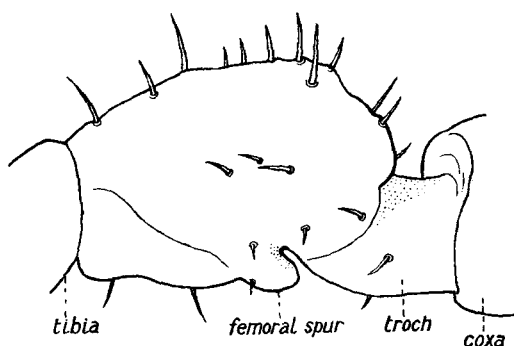


Fig. 12. *Pediculus humanus* ♀. Portion of the third leg, showing the ventral spur upon the femur which aids the male to grasp the female. Camera lucida drawing of the leg in profile.

The manipulations of killing and mounting the insects led to the male relaxing his hold with his claws, and, in consequence, their bodies became somewhat separated, the dorsal surface of the male and ventral surface of the female being uppermost in the illustration. The copulatory apparatus of the male occupies the greater part of the lumen of the vagina, although the male organ has been somewhat retracted. The parts of the male lying within the vagina are stippled and the teeth covering a corresponding area on the surface of the vaginal wall are omitted to avoid confusion. It may be regarded as certain that the vesica fills the whole vagina in life and the presumption is justified that the penis enters the lower part of the uterus. The illustration further elucidates some details in the structure of the male apparatus. Dotted lines indicate the course of the ductus ejaculatorius from above the dorsal plate through the vesica to the tip of the penis, dorsal to the

duct is shown the course of the anus to the rectum which opens immediately in front of the genital aperture.

#### NOTE ON THE NOMENCLATURE OF PARTS.

In the foregoing description I have used some of the terms established by previous authors; most of these require no comment. The names applied to certain muscles are in accordance with their obvious functions as described in this paper. Several structures have been named for convenience of description and a few of these call for remark; namely the terms dilator, vesica penis and statumen penis:

*Dilator*: this term is frequently used to denote the *parameres*, which, through the fusion of their distal extremities into a point constitute, functionally speaking, a single organ. The dilator corresponds to what all writers except Mjöberg and Cummings call the penis or a part of the penis. It is a composite structure whose derivation is discussed on p. 299.

*Penis*: a term confined, in agreement with Mjöberg, to the chitinous tube which projects from the vesica (v. infra).

*Vesica penis*, or simply *vesica*, is a term applied in lieu of "preputial sack" (Mjöberg) and "sac interne" (Jeannel) both of which are misnomers though supposed to be descriptive.

*Statumen penis* is a term applied to the riblike chitinous thickening of the wall of the vesica penis (*Statumen* signifies a concrete object which causes a thing to stand, a support, stay, or prop).

These terms are purely descriptive. In this connection Sharp and Muir (1912, p. 485)<sup>1</sup> may appropriately be quoted, they rightly say in writing of the copulatory organs that it is "premature to establish permanent terms for the parts of the complex genitalia of insects till the various Orders have been more thoroughly examined and compared."

<sup>1</sup> See footnote, p. 298.

**KEY TO THE LETTERING ACCOMPANYING THE ILLUSTRATIONS.**

- An.* = anus.  
*art.* = articulation.  
*B. P.* = basal plate.  
*B. Pl. cl.* = basal plate cleft.  
*D. ej.* = ductus ejaculatorius.  
*Dil.* = dilator (the parameres).  
*Dil. cl.* = cleft in the dilator.  
*Dil. l. sp.* = lateral spur on dilator.  
*Gl. acc.* = accessory gland.  
*Gon.* = gonopod.  
*int.* = intestine.  
*ligt.* = chitinous ligament fixing vagina.  
*M. d. a.* = longitudinal dorsal abdominal muscles.  
*m. i.* = muscular insertions in chitin.  
*M. constr. ut.* = muscles, constrictors of uterus (transverse and oblique).  
*M. flex. dil.* = muscles, flexors of the dilator.  
*M. pro. pl.* = muscles, protractors of basal plate.  
*M. retr. d. v.* = muscles, dorsal retractors of vaginal wall.  
*M. retr. pl.* = muscles, retractors of basal plate.  
*M. retr. ut.* = muscles, retractors of uterus.  
*M. retr. v. p.* = muscles, retractors of vesica penis et al.  
*M. retr. v. v.* = ventral retractors of vaginal wall.  
*M. v. a.* = muscles, longitudinal ventral abdominal muscles.  
*ov.* = ovaries.  
*p. g. f.* = post-genital fold.  
*p. l.* = posterior lobes of ninth segment (♀).  
*p. pl.* = pregenital plate, facing pregenital fold.  
*Pen.* = penis.  
*r. p.* = rugose portion of vesica penis.  
*rect.* = rectum.  
*segt.* = segments of abdomen, numbered sixth to ninth.  
*sh.* = collar-like sheath beneath protruded dilator.  
*St. pen.* = statumen penis.  
*Stig.* = spiracle.  
*trach.* = trachea.  
*tr. f.* = transverse folds of abdominal wall (♂).  
*Ut.* = uterus.  
*V. pen.* = vesica penis.  
*V. pen. f.* = folds of inverted vesica penis.  
*V. pen. st.* = stem of vesica penis.  
*v. p.* = ventral plate over vagina.  
*vag.* = vaginal orifice.  
*vag. fl.* = vaginal flap.  
*vag.-ut.* = vagina ends and uterus begins.  
*x* = break in section, see legend to Text-fig. 3.

## EXPLANATION OF PLATES III AND IV.

## PLATE III.

Copulatory apparatus of *Pediculus humanus* ♂.

- Fig. 1. Apparatus in its retracted state, treated with caustic potash, isolated, and viewed dorsally. The vesica is inverted and most of it lies in the hollow of the basal plate. It contains the penis which points into the cleft of the dilator. The ductus ejaculatorius issues on one side.
- Fig. 2. Apparatus in situ, showing the first stage of extrusion of the vesica penis, the point of the penis appearing through the cleft in the dilator. Caustic potash preparation.
- Fig. 3. Detail of the fully everted vesica penis, showing the penis with the therein contained ductus ejaculatorius, the statumen penis and a portion of the vesica with its strongly chitinized teeth. More highly magnified than the preceding figures to which the accompanying scale applies.

## PLATE IV.

The relations of the ♂ and ♀ apparatus when in copula.

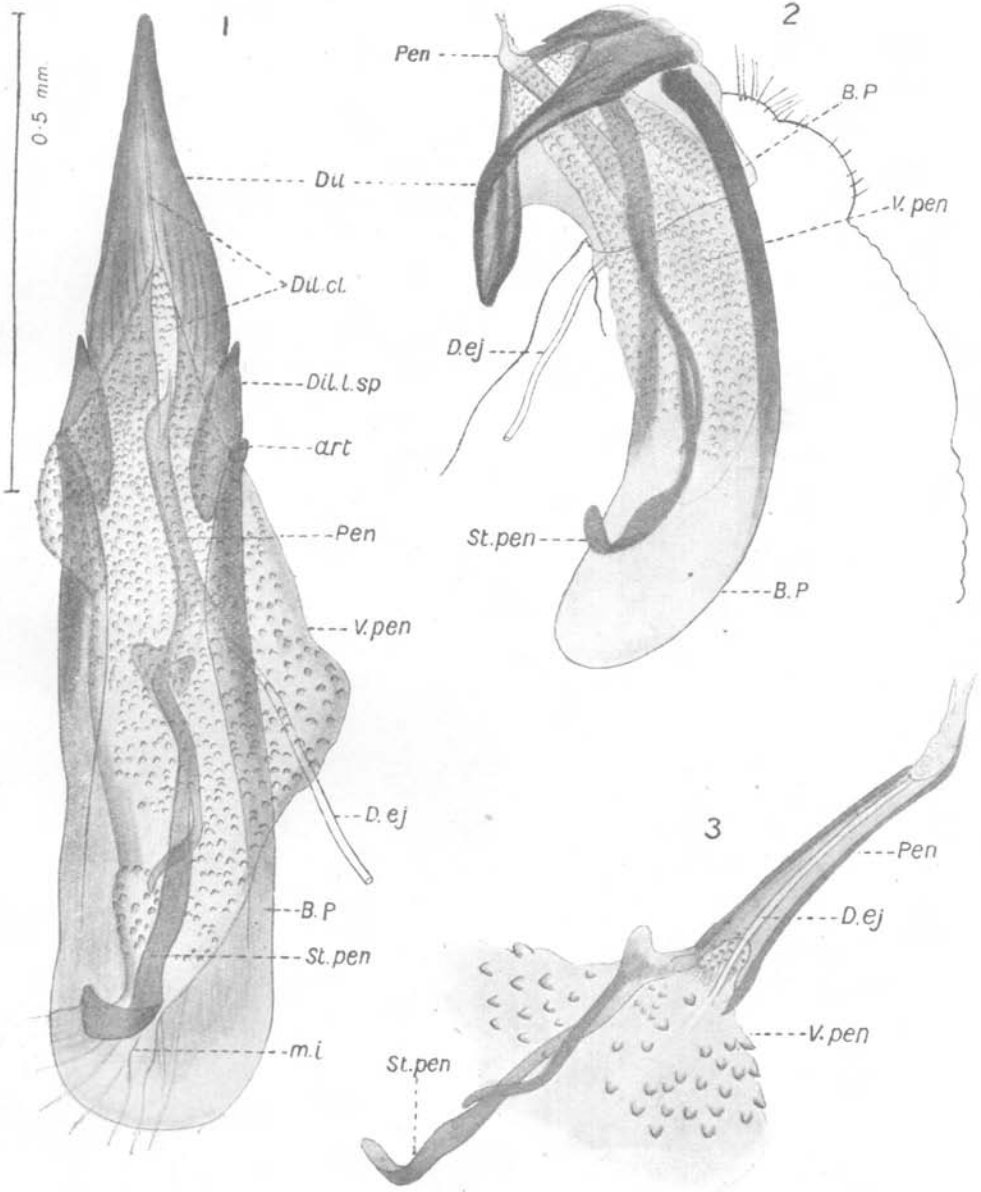
Drawing from mounted specimen of a pair killed in copula; the male parts printed in black, the female parts in red. For nomenclature of parts see preceding figures and text. Specimen treated with caustic potash.

Note all of these figures were drawn by me with the aid of a camera lucida. This remark likewise applies to the text-figures, excepting Nos. 9, 10 and 11.

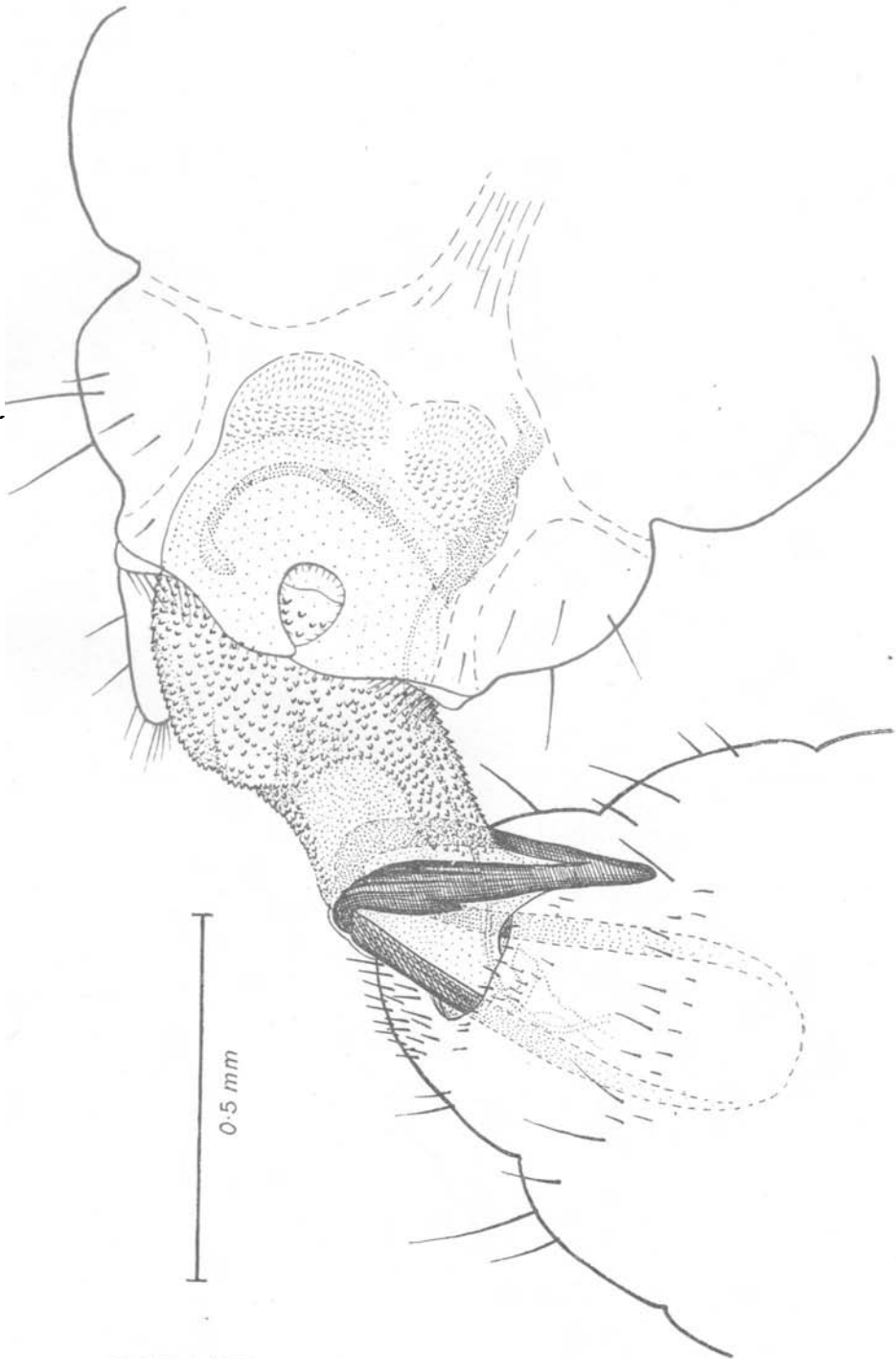
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