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### THE MALE GENITAL ARMATURE IN THE ORDER ANOPLURA, OR SUCKING LICE.

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Only in very recent years has the value of the male genital armature in taxonomic work on the Anoplura been appreciated. In 1907 Pawlowsky made studies of the genital structures of the males by sectioning specimens. But it was not until 1910 that there was any extended comparative account given. In that year Mjöberg published his very extensive studies in which he figured and described many of the chief features of the hard parts for several species of sucking lice. He was the first to employ some of the terms largely used today for the more conspicuous parts, such as the basal plate, parameres and the preputial sack.

Cummings (1916) very accurately figured and described the hard parts of the male genitalia of various *Linognathus* species and worked out what he considered to be homologies with the genital parts as found in the males of biting lice. He gave an accurate account of the finer inner chitinous structures and in naming these introduced such terms as endomere, telomere and hypomere.

Nuttall (1916) was the first to work out the complete gross morphology and the functions of the genital parts for a single sucking louse species. This he did for one of the sucking lice of man, *Pediculus humanus* Linnaeus. Nuttall made dissections of the parts in order to show muscle attachments and the relationships of the soft tissues, and he studied the process of copulation in living specimens.

Ferris in his more recent taxonomic papers has drawn the hard genital parts for the males of many species, using Mjöberg's terminology for the basal plate and parameres.

Notwithstanding the various valuable contributions of these workers we find that for many species of sucking lice the structure and relationships of the finer parts of the genitalia have not been described or figured, and the homologies of these parts have not been ascertained.

In the following account of the male genital armature of the sucking lice an attempt is made to present a logical exposition of the structure and function of the parts as they are known in certain characteristic species, to make a start in homologizing the parts, and to synonymize the technical names as applied. A particular effort has been made to homologize the types found in the Pediculidae with those of other families.

#### GENERAL PLAN OF THE MALE COPULATORY APPARATUS.

The male genital armature (Fig. 1) and most of the genital apparatus of sucking lice lie in and are developed from an inpocketing of the posterior wall (genital cavity) of what is usually called the last abdominal segment. The hard parts—rods, plates and tube-like structures—are developed almost entirely from a continuation of this wall in the form of an eversible sac, the internal sac, which at its inner end is continuous with the ductus ejaculatorius. At this junction of the internal sac with the end of the ductus ejaculatorius, in most species a penis has been developed which is supported by one or more sclerotized rods or strips. From the floor of the internal sac and also from the floor of the genital cavity there is developed a sclerotization known as the basal plate, which is usually a large conspicuous structure. It serves as a base for the movement and attachment of many of the other parts. At its distal end it bears a pair of hinged, forceps-like appendages, the parameres.

In some species there are no other sclerotized parts, yet in most species sclerotizations of parts of the internal sac are observed. These are present in various forms and have been called by Cummings and others endomeres. It is in regard to the position, structure and relationships of these endomeres and their various parts that we are in need of most information to-day. The endomeres doubtless frequently function to give rigidity to the internal sac when the latter is protruded. They evidently at times serve for the muscle attachment of retractor muscles of the sac; again the distal endomeres frequently engage

the parameres and help the latter structures to function more properly. The proximal, or anterior, endomeres may articulate with the parameres or the rods of basal plate, or they may engage the penis near or at its base. It is suggested in this paper that the endomeres be named according to their fundamental positions in relation to the internal sac as: anterodorsal, posterodorsal, or ventral (Fig. 1). If the anterodorsal and posterodorsal are united the term dorsal or holodorsal may be applied. Where the ventral endomeres shift their position so

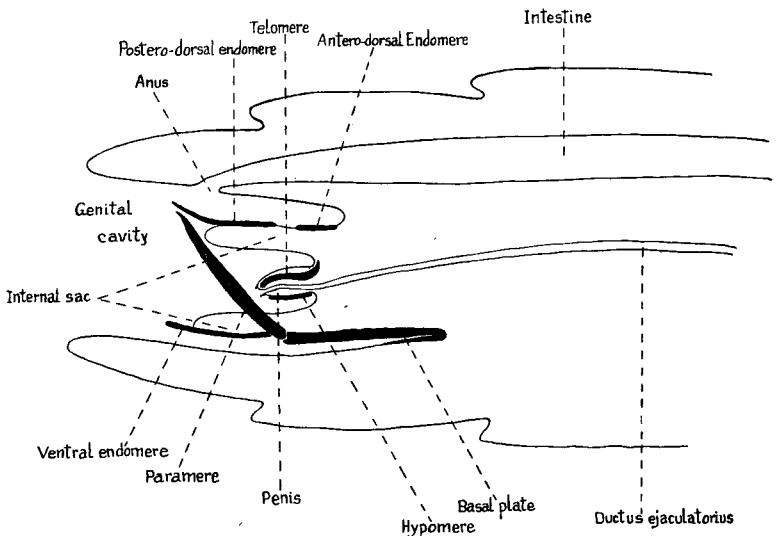


FIG. 1. Paramedian section of last three segments of abdomen of a male sucking louse, illustrating parts of genitalia and their relationships. (Diagrammatic).

that they lie between the parameres, they may be called the posterior endomeres, unless posterodorsal ones are present. The ventral, or posterior, endomere in some species hinges on the parameres.

These different structures of the male genitalia of sucking lice have their counterparts in similar structures in the genitalia of biting lice (Fig. 2), as has well been demonstrated by Cummings. If, indeed, the two groups of lice have had a common origin homologous structures should exist in the male genital armatures of both. It is more probable, however, that the biting and sucking lice had independent origins, but both from psocid-like ancestors.

## COMPARATIVE MORPHOLOGY AND COMPONENT PARTS.

The genital cavity (Fig. 1) is usually almost or quite filled by the male genitalia. At the top of this cavity is an opening, the anus.

The *basal plate* (Fig. 1) is more commonly a plate-like structure with its lateral margins thickened into rods (Figs. 3, 6, 7 and 9). In some species only the rods are present, and in others there are no lateral marginal thickenings (Fig. 4).

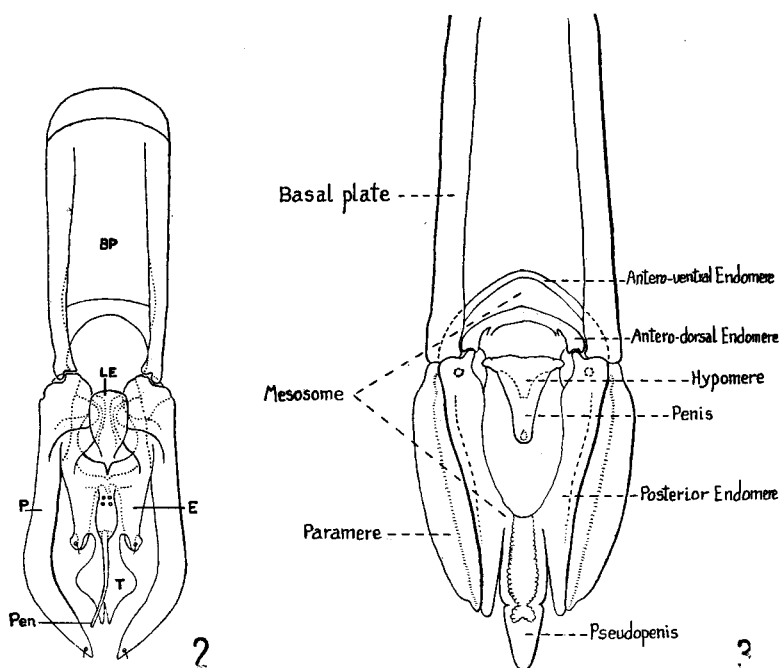


FIG. 2. The genital armature of a biting louse (*Philopterus acanthus* (Giebel) ); *B P*, basal plate; *L E*, lower endomere; *P*, paramere; *E*, endomere; *Pen.*, penis; *T*, telomere. (Figure and terminology after Cummings.)

FIG. 3. Dorsal view of male genital armature of *Phthirpediculus propithecii* Ewing.

As shown by Cummings (1916) the basal plate, in some of the biting lice at least, is formed from both the floor of the genital cavity and that of the internal sac (Fig. 1). The basal plate is probably the same structure as the phalliger of Crampton (1918) found in certain of the more generalized groups of insects.

The basal plate carries above it the internal sac and its parts, when the latter are withdrawn into the body. It has

hinged to its distal end, probably in all species, the parameres (Figs. 1, 2, etc.). In addition, the ventral or posterior endomere may hinge to the end of the basal plate, as in *Phthirpediculus propithecii* Ewing (Fig. 3).

Nuttall (1916) has shown that in *Pediculus humanus* Linnaeus the upper anterior portion of the basal plate serves as a place of origin for numerous muscle fibers that retract the internal sac. I have demonstrated by dissection the presence of these muscle fibers in *Haematopinus tuberculatus* (Burmeister) (Fig. 6), in which species the floor of the sac is sclerotized, a large ventral endomere being present. In this case the muscles may serve to flex the ventral endomere rather than to retract the sac.

The *parameres* (Figs. 1, 3, etc.) are hinged to the lateral distal portion of the basal plate at the ends of the rods. They may be free and clasper-like, or may be united with the ventral endomere for their entire length.

In the Pediculidae the parameres articulate on their inner side with the well developed endomeres and in the genus *Pediculus* are evidently greatly reduced, serving only as small sclerotized pieces between the large endomeres and the basal plate (Fig. 9, *Dil.* 1. sp.).

The *internal sac* (Fig. 1), called by Mjöberg the "preputial sack," by Cummings the "mesosome" and by Nuttall the "vesica penis" (Fig. 9, *V. pen.*), is probably a structure homologous in relationship and function with the internal sac of beetles. The eupenis, or praeputium, of Crampton (1918) is probably the same structure, which is found in many of the more generalized insects. The fundamental relationships of the internal sac have already been stated. It should be added that in many species the inner surface of the sac when withdrawn is studded with minute prickles (Fig. 9). These prickles point backward when the sac is withdrawn in the body, but when it is protruded, as in copulation, they then lie on the outside of the sac and point in the reverse direction. Doubtless they serve to engage the wall of the vagina when the sac is dilated and hold the penis in its inserted position until the semen has been discharged through the ductus ejaculatorius.

The *penis* is a protuberance or tube at the opening of the ductus ejaculatorius. Its base is continuous with the wall of the sac at the latter's apex. Usually one or more rods or strips

are present in the wall of the penis. In some species, as in *Pedicinus rhesi* Fahrenholz, the penis is a long sclerotized tube (Fig. 8). In *Pediculus* species the penis is joined at its base to a sclerotized rod called by Nuttall the *statumen penis* (Fig. 9, *St. pen.*). Some species appear to be without a penis, and in several species it is a minute structure.

The *telomeres* (Fig. 1) are chitinous rods or strips on the sides of the penis. They are probably more commonly united so as to form a tube.

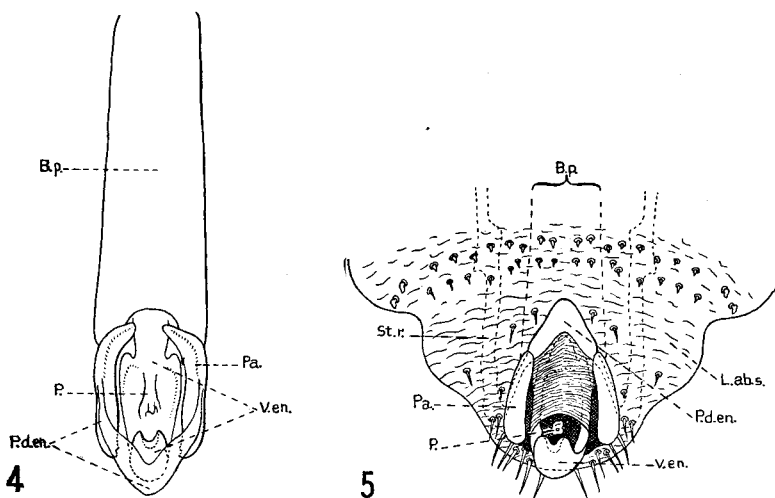


FIG. 4. Genital armature of male of *Echinophthirius phocae* (Lucas), from above, in retracted position. *B. p.*, basal plate; *P.*, penis; *Pa.*, paramere; *P. d. en.*, posterodorsal endomere; *V. en.*, ventral endomere.

FIG. 5. Tip of abdomen of male of *Echinophthirius phocae*, from above, showing the genitalia partly protruded. *B. p.*, basal plate; *L. ab. s.*, last abdominal segment; *P.*, penis; *Pa.*, paramere; *P. d. en.*, posterodorsal endomere; *st. r.*, sternal rod; *V. en.*, ventral endomere.

The *hypomere* (Fig. 1) is a small sclerotized strip on the ventral surface of the penis. In *Phthirpediculus propithecii* Ewing (Fig. 3) it is well developed. In most species this structure is either lacking or united with the telomeres to form the tube and base of the penis.

The *ventral endomeres* (Figs. 1, 4 and 5) represent the sclerotization of the lower part of the internal sac distal to the ventral plate. They are usually united, forming a structure most diverse in form and evidently of a varying function. From the standpoint of the distinction of species this structure

is, in the opinion of the writer, the most important of all, but unfortunately it is scarcely mentioned in any of the existing descriptions of sucking lice; and, with possibly a few exceptions, it has not been carefully drawn or studied. Sometimes this structure is divided, being represented by a pair of ventrolateral rods, but in nearly all instances it is a single, more or less U-shaped or V-shaped structure (Fig. 5, *V. en.*), which usually lies below the parameres and is entirely free from the latter.

In the more specialized species, in the ungulate and primate infesting lice, the ventral endomere engages or is articulated to the parameres; in which cases it is found that frequently they come to lie inside instead of below the parameres as they do in *Phthirpediculus propithecii* Ewing. In *Pediculus humanus* Linnaeus this endomere becomes terminal (Fig. 9, *Dil.*) and is used, as Nuttall has observed, to dilate the vagina of the female before the insertion of the sac and penis.

The *anterodorsal endomere* (Figs. 1 and 3) usually is a sclerotic band that lies near the base of the internal sac above. It is lacking in many species and in some apparently is fused with other sclerotized structures. In *Phthirpediculus propithecii* Ewing (Fig. 3) it is arch-like and is hinged to the bases of the posterior endomere.

The *posterodorsal endomere* (Figs. 1, 4 and 5, *P. d. en.*), frequently absent, is a well developed structure in *Echinophthirius phocae* (Lucas) (Figs. 4 and 5, *P. d. en.*) where it is remarkably similar in structure to, and probably has the same function as, the posterior endomere in *Pediculus humanus* Linnaeus.

Mjöberg (1910) has probably noticed and described this structure, but if so he does not give its proper relationship. More probably his "extra chitinous support" included both the posterodorsal and the ventral endomeres which in specimens with protruding genitalia are seen to be quite different (Fig. 5).

In *Echinophthirius phocae* (Lucas) the posterodorsal endomere (Figs. 4 and 5, *P. d. en.*) is a conspicuous arched chitinous structure which engages the parameres dorsally. When the genitalia are withdrawn into the body, this sclerite extends backward beyond both the parameres and the ventral endomere, in fact, the ventral endomere ends in a broad curved hook which lies inside the bend of the posterodorsal endomere.

### THE GENITAL ARMATURE IN THE GENUS HAEMATOPINUS LEACH.

The genital apparatus of the type species of *Haematopinus*, *H. suis* (Linnaeus), has been well figured and described by Mjöberg (1910) and by Miss Florence (1921). It is of a very simple, and doubtless degenerate type. The parameres are short stubs, and the internal sac is without endomeres. Except

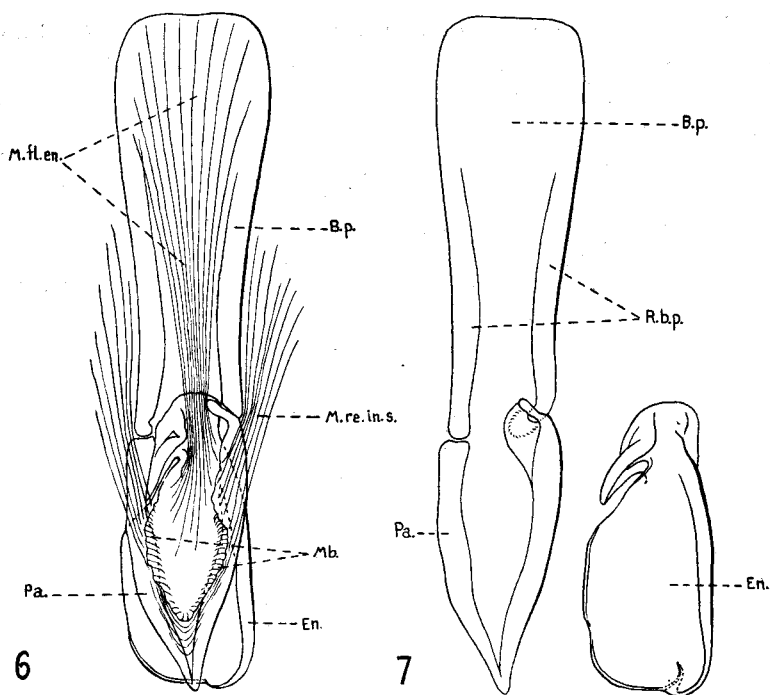


FIG. 6. Dorsal view of male genital armature of *Haematopinus tuberculatus* with most of vesica penis and ductus ejaculatorius removed to show muscle attachments. *B. p.*, basal plate; *En.*, endomere; *Mb.*, membrane; *M. fl. en.*, muscle for flexing endomere; *M. re. in. s.*, retractor muscle *in situ*; *P. a.*, parameres.

FIG. 7. Same as Figure 6 except all soft tissue has been removed and hard parts disarticulated. *R. b. p.*, rods of basal plate.

for the basal plate, the penis is the only well developed sclerotized structure in the whole genital apparatus.

Being familiar with the structures in *Haematopinus suis* (Linnaeus), the writer was much surprised upon dissecting the male genital armature of *Haematopinus tuberculatus* (Bur-

meister) to find a type (Figs. 6 and 7) entirely different and remarkable in that all sclerotized parts are asymmetrical.

In *Haematopinus tuberculatus* (Burmeister) the parameres (Figs. 6 and 7, *Pa.*) are very large and conspicuous. They unite at their tips so as to form a single V-shaped structure. The right paramere is longer than the left and is expanded and perforated at its base where it articulates with a projecting knob of the right rod of the basal plate (Fig. 7). Below the parameres there is a very large, asymmetrical endomere, which is shaped much like a scoop (Fig. 7, *En.*). It has a strong carina on its right margin and a large, backwardly pointed hook on the left side near the base.

By dissection it was easy to demonstrate the attachments of the two chief sets of muscles. One of these sets (Fig. 6, *m. fl. en.*) arises from the upper side of the basal plate along about the first one-third of its length and is inserted chiefly, if not entirely, into the upper surface of the large, flat endomere. Its function appears to be the flexing of the endomere. These muscles are the same as Nuttall's retractor muscles of the vesica penis in *Pediculus humanus* Linnaeus. In this species, which lacks the ventral endomere, the muscles are inserted, according to Nuttall, into the wall of the vesica itself. The action of these muscles, Nuttall states, is to return the vesica to its resting position. A similar action may be effected in the case of *Haematopinus tuberculatus* (Burmeister) during certain stages of the process of retraction of the vesica. The chief action of this muscle would seem, however, to be the flexing of the ventral endomere itself.

Very powerful muscles (Fig. 6, *M. re. in. s.*) arise on either side of the ventral plate from the conspicuous abdominal sternal plate of this species and attach chiefly to the wall of the internal sac. They probably not only retract the internal sac but the whole copulatory apparatus, as their origin from the sternal plate would seem to indicate. They may be concerned in flexing the parameres during the later stage of the protrusion of the genitalia.

The male apparatus of *Haematopinus eurysternus* (Nitzsch) was examined. It is of the same type and arrangement as in *Haematopinus tuberculatus* (Burmeister), but differs in having a rather well developed penis, and in having the parameres and endomere of a different shape.

The presence of large, well developed and apparently functional parameres in these two bovine-inhabiting species, as well as a large endomere, is of much significance as such conditions are not found in the swine-infesting species, *H. suis*.

#### THE HOMOLGY OF PARTS OF THE MALE GENITAL ARMATURE OF *PEDICULUS HUMANUS* LINNAEUS.

Nuttall (1916) in his excellent paper on "The Copulatory Apparatus and the Process of Copulation in *Pediculus humanus*," gives a detailed account of the male genital armature in this man-infesting louse. One question which he did not definitely settle was the homology of three of the sclerotized parts. These three he called the dilator (Fig. 9, *Dil.*), the lateral spur of dilator (Fig. 9, *Dil. l. sp.*) and the statumen penis (Fig. 9, *St. pen.*).

Speaking of the first two of these structures Nuttall states (p. 299): "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."

Soon after the present writer discovered the new genus *Phthirpediculus* and its single species, *propitheci*, on the skins of a lemur, *Propithecus edwardsi*, it occurred to him that in this species, which represented a genus more generalized than, but clearly related to, *Pediculus*, the genital armature would possibly give a clue to homologizing the parts of the armature in *Pediculus humanus* Linnaeus. Hence the armature was studied and drawn (Fig. 3).

When the parameres and posterior endomeres of *Phthirpediculus propitheci* Ewing were examined it was noted that both these structures were hinged to the rods of the basal plate. This unusual condition was further matched by another—the parameres engaged the endomeres for their entire length. However, when the type of armature found in *Phthirpediculus* was compared with such primitive and generalized types as are found in rodent-infesting species, it was observed that the types are very similar except for the two unusual conditions just noted.

Thus far it appeared that, not only had no light been thrown upon the possibility of homologizing the parts in *Pediculus*

*humanus* Linnaeus, but an attempt to do so, using alone the armature of *Phthirpediculus* as a basis, would be positively misleading. In the monkey-infesting genus *Pedicinus*, however, it was observed that in *Pedicinus rhesi* Fahrenholz the key to the solution had been found. In this species the genital armature of the male (Fig. 8) gives an excellent intergrade between that of *Phthirpediculus* and *Pediculus*.

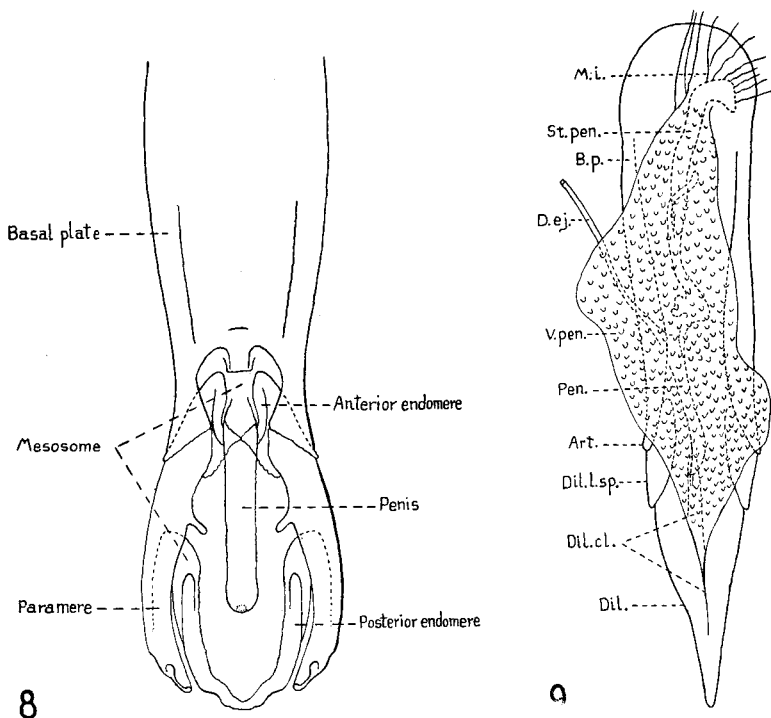


FIG. 8. Dorsal view of genital armature of male of *Pedicinus rhesi* Fahrenholz, *in situ*, with parts labeled.

FIG. 9. Dorsal view of male genital armature of *Pediculus humanus* Linnaeus. *Art.*, articulation; *B. p.*, basal plate; *Dil.*, dilator; *Dil. cl.*, cleft in dilator; *Dil. l. sp.*, lateral spur on dilator; *D. ej.*, ductus ejaculatorius; *M. i.*, muscular insertions in chitin; *Pen.*, penis; *St. pen.*, statumen penis; *V. pen.*, vesica penis. (Drawing and terminology after Nuttall.)

In *Pedicinus rhesi* Fahrenholz the parameres are large, with freely projecting arms, and doubtless perform their usual functions. The posterior endomere is well developed, of much the same shape as in *Pediculus humanus* Linnaeus, and firmly engages the parameres ventrally near their middle (Fig. 8).

An examination of the muscles show their attachments to be similar to those of *Pediculus humanus* Linnaeus. That the inner structures in *Pedicinus rhesi* Fahrenholz (Fig. 8) are the same as the dilator of *Pediculus humanus* Linnaeus there can be but little doubt, as this structure arises from, or rather engages, the parameres distal to their bases. That this structure in *Pedicinus rhesi* Fahrenholz should be regarded as the ventral endomere is shown by its position ventral to the parameres and its relation to the internal sac and its muscle attachment. The presence of the long, free arms of the lateral sclerites in *Pedicinus rhesi* Fahrenholz, together with their attachment to the ends of rods of basal plate as well as some other relationships, shows them to be the true parameres, parameres which bear the ventral endomeres, just as Nuttall's "lateral spurs of dilator" do; hence it is evident that these spurs are the real parameres as Nuttall suggested, and that his dilator is in reality the fused endomeres, or more specifically, the fused ventral endomeres.

The *statumen penis* (Fig. 9, *St. pen.*) of Nuttall likewise may be homologized by comparison with the genital armatures in *Phthirpediculus* and *Pedicinus*. The *statumen penis* (Fig. 9, *St. pen.*) is a long, irregular chitinous strip which supports the penis. In *Pedicinus* there is a much larger piece which is articulated with the parameres at the latter's bases. This structure (Fig. 8) is an anterior endomere. Turning to *Phthirpediculus* we find that there is both a dorsal and a ventral anterior endomere, each of which articulates with the enlarged bases of the parameres (Fig. 3). The anterior endomere of *Pedicinus*, therefore, appears to represent the fused antero-dorsal and anteroventral endomeres. From this fused structure in *Pedicinus* probably was developed the *statumen penis* of *Pediculus*.

A large series of *Pediculus* forms from American monkeys of the genus *Ateles* was examined to see if in any there was to be found a different type of genital armature from that of *Pediculus humanus* Linnaeus. In no instance was any significant difference noted. This appears no less than remarkable when we consider that all of these monkey-infesting species had pleural plates quite different from those of *Pediculus humanus* Linnaeus.

## SUMMARY.

1. The work of Cummings and Nuttall has been taken as a basis for the extension of our knowledge in regard to the types of the male genital armature in the Anoplura.

2. In the main the terminology of Cummings has been adopted, but some new terms are introduced.

3. A rather remarkable asymmetrical type of genital armature is studied and described for the first time.

4. By studying types of lice from rodents, lemurs, and monkeys the parts of the male genital armature of the human louse, *Pediculus humanus* Linnaeus, have been homologized.

5. In the male genital armature of *Pediculus* species the "lateral spurs of dilator" of Nuttall become the parameres, the "dilator" becomes the fused ventral endomeres, and the "statumen penis" becomes the anterior endomere.

6. The genital armature of American monkey-infesting species of *Pediculus* not only is of the same type as is found in the man-infesting forms, but it does not vary sufficiently to be of value in specific differentiation.

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