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Morfogeneza dróg wyprowadzających układu płciowego wszy *Pediculus humanus* L. *(Anoplura)*

Морфогенез выводных путей половой системы у вши *Pediculus humanus* L. *(Anoplura)*

On the Morphogenesis of the Genital Efferent System in *Pediculus humanus* L. *(Anoplura)**

[Pl. LXXX—LXXXV]

CONTENTS

I. Introduction 2
II. Material and methods 5
III. Observations 5
The female 6
The male 19
IV. Discussion 30
1. Uropods 31
2. The question of paired origin of ectodermal ducts 36
3. Further development of the efferent system 39
a. The time and succession of appearance of its elements . 39
b. Female efferent ducts 41
c. The ovipositor 42
d. Male efferent ducts 43
e. Copulatory apparatus 44

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4. Musculature 46
  a. Muscles in the female 47
  b. Muscles in the male 48
5. Morphological changes in the sternal plate 50
6. Migration of the genital opening 51
Summary 52

I. INTRODUCTION

The morphological examinations of the imagines of lice *(Anoplura)*, begun by SWAMMERDAM and continued by later researches, suggested a number of questions, the answers to which should be sought in the ontogenetically earlier stages. Detailed investigation in some branches of the morphology of insects, and neglect of certain others resulted in the present exceedingly scanty volume of literature, concerning the ontogenetic development of lice *(Anoplura)*. Only the outline of their embryonic development has been investigated (MELNIKOV 1869, GRIMM 1870, SCHÖLZEL 1937) although to some fragments more detailed studies have been devoted (PATAY 1941, YOUNG 1953, PIOTROWSKI 1953 and 1957). Also some gametogenetic processes in Anoplura have been studied, mainly on the material taken from imagines, or from the last instar nymph (FOOT 1919, DONCASTER & CANNON 1920, RIES 1932, RIES & VAN WEEL 1934, HINDLE & PONTECORVO 1942, BAYREUTHER 1955 and others).

The literature, concerning the morphogenetic processes in the ontogenesis of *Mallophaga* is as scanty. One must quote SCHÖLZEL'S work (see above), STRINDBERG'S (1916, the anatomy of the last instar nymph), and also some works of a more cytologic character, concerned with gametogenesis (RIES 1932, PERROT 1933, SCHOLL 1955 and others) and, besides, as in the case of Anoplura, some remarks in the literature dealing with systematics (e. g. BLAGOVESHCHENSKI 1956), or with symbionts (e. g. RIES 1931).

As one may notice, the period of post-embryonic life in *Anoplura* has been hitherto almost entirely overlooked. Even the problems connected with the interpretation of copulatory apparatus, so important an organ for *Anoplura* systematics, did not inspire any investigations on the ontogenetic importance of structures observed in imagines, which cause controversial opinions.

The structure of the copulatory apparatus in *Anoplura* and *Mallophaga* (often included into the group of *Phthiraptera*) is different from that of other insects. Although in many other groups of insects the structure of this apparatus in imago does not seem to be just a simple reflection of phylogenetic connections (GUSTAFSON 1950), the way of its formation during the ontogenesis of lice may considerably contribute to explain the homology not only of *Anoplura* and *Mallophaga* but also of other insects. Theresa CLAY, the eminent investigator of *Mallophaga* had to give up the correct terminology in the glossary of genital parts of insects (1956) in the section enclosing *Phthiraptera*, because of the lack of research on the subject, and she could employ only previously used terms.

The development of the genital efferent system in insects is best investigated in the groups, occupying the leading positions in the phylogeny: in *Amphibiotica*, *Orthopteroidea* and *Blattoidea*. The works of authors such as WHEELER (1893), HEYMONS (1891), SUMIŃSKI (1917), GEORGE (1929), NEL (1929), BECKER (1932), ELSE (1934), ROONWAL (1936), QADRI (1940), GUPTA (1950) and others contributed to it. Of heterometabolic insects, *Hemiptera* have also been investigated. The literature concerning *Homoptera* includes the works of GEORGE (1929) and METCALFE (1932) and BOCHEŃSKA'S research (1939) on the anatomy of the first instar larva of *Porphyrophora polonica* CKLL. The fact, that GUPTA (1951), describing the development of the efferent system in *Dysdercus cingulatus* FABR. could quote but two of his predecessors proves how limited the scope of investigations was. The development of genital efferent system in *Psocoptera* has been till the present time, utterly unkown.

The development of the efferent system in *Anoplura* has not been investigated till now, and NUSBAUM'S work (1882) on the development of these organs in the representatives of *Mallophaga*, namely in *Lipeurus bacilus* and *Goniocotes hologaster*, is the only one. This work was of a great theoretical importance, as it stated for the first time in literature, that a part of genital efferent ducts in insects originate from the mesoderm, and the rest — from ectoderm. This discovery made this work very important in world literature, and it certainly encouraged other authors to investigate various groups of insects with the exception of *Mallophaga* and *Anoplura*, which for a long time have been considered as more or less related.

The work of NUSBAUM, mentioned above, contains also a conclusion on the paired formation of ectodermal parts of efferent system in insects, and on their transformation into the final form of unpaired ducts during ontogenetic development. Such formulation is contrary to the opinions of almost all later investigators of ontogenesis of other insect groups. So it may seem useful to compare the descriptive part of NUSBAUM'S work with the picture of the development of the genital efferent system in *Pediculus humanus* L.

As the insects related to *Anoplura* have been investigated only on a rather limited scale, one must make use of the facts, known from phylogenetically remote groups of insects in order to explain the phenomena, observed in the development of *Pediculus humanus* L. It seems that such a method, especially when applied to the earlier stages of development of investigated organs, may prevent too partial conclusions, which may be very important in investigating a species characterised by such a specific type of development, as *Pediculus humanus* L.

It has become a custom, generally accepted in literature, that the investigations on the development of the genital efferent system in insects are conducted with a complete exclusion of topographic relations with other systems. Such a method does not grant the correct reading of the anatomic details of a young organism, and it would not be acceptable while working on such specifically changed species as *Pediculus humanus* L. So also other systems, besides the efferent genital system, have been included in the investigation — especially the skeleton muscles. Unfortunately it was not possible to include the nervous system in the present study, as the separate ganglions of the abdominal nervous chain reunite early in lice, and shortly after the revolution of the embryo withdraw completely from the abdomen.

On the question of the names of species quoted in the present work, I want to stress that in some original works they have not been given in full, i. e. the author's name was omitted. I have tried to complete these terms, as far as possible, according to the present requirements, giving the names in brackets and with an interrogation mark.

II. MATERIAL AND METHODS

The material came from the breeding of *Pediculus humanus corporis* and from occasional catches of *Pediculus humanus capitis*, and it was treated with the usual methods applied in insect embryology and histology. HENNING'S, CARNOY'S, RATH'S CHAMPY'S, FLEMMING'S and SANFELICE'S solutions were used for fixing. Hematoxylin (acording to EHRLICH and to HEIDENHAIN), eosin and azan were used for staining and the preparations in toto were fixed without staining, or fuchsine was used after KOH treatment. Celoidin-paraffine method to APATHY was used for embedding, as the method proposed by MURRAY did not prove satisfactory.

III. OBSERVATIONS

Discussing homology, one must take into account both the way and the site where the rudiments of the given organs appeared. As far as I know, the process of reduction of the number of abdominal segments to that characteristic for imago has not, till now, been investigated in *Anoplura*, so the number of the abdominal segments and their succession has not been fixed. Taking into account both the tendency to avoid the inconvenient counting of the segments from the rear (the last one, last but one etc.) and the necessity of keeping to the proposed subject, one had to resign the ontogenetic establishing of the successive numbers of genital segments, and to base on the more recent studies on imagines. The segmentation of the abdomen in imago of the species *Pediculus humanus* L. is rather clearly visible in comparison with the rest of the body, although in females it is less evident than in the males. The sclerotized paratergal plates and the furrows between them permit to observe seven abdominal segments. Taking into account the less visible structures and the fact, that the abdomen of the *Hoplopleura* genus is composed of nine clearly visible segments one may assume with FERRIS (1951) the number nine is characteristic for all *Anoplura*. On the abdomen of the first instar nymph of *Pediculus humanus* L. only the last three segments are externally clearly pronounced. We may observe, however, a quantitative and topographic resemblance of the spiracles and dorsoventral muscle bundles, allowing one to infer that the nymph has, like the imago nine abdominal segments. Although such establishing of the successive number of the segment to which the investigated element belongs cannot be absolutely certain, the analogy with other insects makes it fairly probable.

The female

The embryo

24 hours before hatching, or at the moment, when the embryo has passed 3/4 of its development period, one may observe two ovaries on the sections of abdomen: each is composed of five ovarioles, situated closely together in the third and fourth abdominal segments, approximately in the sagittal plane, between the intestine and the bundles of dorsoventral muscles, located metamerically. The separate ovarioles are about 35 μ long, and are differentiated into three parts: the middle, in which the cytoplasm is distinctly basophilic, and the top and base — with the acidophilic plasm. The top part, with the cells characterized by small nuclei, becomes narrower and passes into the long threadlike terminal filament. All the filaments of one ovary meet and unite in the anterior part of the abdomen. The middle part of the ovariole is built of numerous large cells. It was not yet possible to see the follicular epithelium. The basic parts of the ovarioles unite into one solid cord, and its course could be followed up to the sixth abdominal segment. I did not find mesodermal ampullae at that stage, although celoidin — parrafine method was used,

which prevents loosing the little fragments of the section. The ectodermal rudiments of genital efferent ducts were also missing.

First instar nymph.

50 hours after hatching, i. e. about the middle of the first instar, the first unpaired invagination of the ventral hypoderm is seen in the genital region. It appears in the middle line in the posterior part of the seventh segment, so it is topographically corresponding to what is called oviducal invagination in other insects. On the sections from that period it is only over ten μ deep, and is situated between the alimentary canal and the abdominal muscles of the seventh segment. Every five of these muscles form „muscle plate" („Muskelplatte"), situated internally in relation to dorsoventral muscles.

After another 12 hours the further unpaired invagination of hypoderm appears between the eighth and nineth segments, which is termed spermathecal invagination in insects. It is a tube, which is growing fast towards the front in the space limited dorsally by the alimentary canal, and from the sides by the longitudinal ventral muscles of the eighth segment, which are collected into „muscle plates", as in the seventh segment.

On the sections of the specimens about 75 hours old (pl. LXXX, fig. 1) one may notice that the spermathecal invagination has grown towards the front, towards the seventh segment. In my material I did not find preparations, which would show the moment of the meeting of both the hypodermal invaginations, but in the older preparations only one spermathecal invagination is seen. The ectodermal elements are further situated very close to the hypoderm and are formed of similar monolayered epithelium. Its cells are smaller than those of the hypoderm, which might have resulted from intense divisions.

In the posterior part of the VII segment, between the two ventral „muscle plates", the two oviducal ampullae are situated thus, that their narrowed ends are pushed under the corresponding group of muscles, where they pass into a solid cord, which is directed to the gonad of the respective side of the body on the other side of the „muscle plate". It seems these cords are of mesodermal origin, whose growth was begun while still in the embryo.

In the end phase of the first instar, i. e. about 85 hours after hatching, the spermathecal invagination is a tube about 70 μ long, flattened dorsoventrally, and bent towards the sternal plate near the orifice, which is closed with the cuticle, covering the body.

First moulting

The first moulting was beginning after four days of post-embryonic development in the material used in the present investigations.

The two ampullae, resembling narrow cones, forming an obtuse angle, and separated by the anterior portion of the hypodermal invagination, are situated thus that their bases adhere to the walls of the invagination, and their narrow parts are oblique and directed externally. The lumen appears in the oviducts, from the ampulla towards the ovary. The oviducts pass under the ventral muscles of the VII segment.

A pair of symmetrical buds (pl. LXXXIV, fig. 18) is growing posteriorly to the plane uniting the ampullae into the lumen of the hypodermal invagination, from its ventro-lateral wall. They increase in size and they direct towards the posterior part of the body, as two parallel processes. There are mesodermal cells in their basal parts. On the cross section it looks as if a massive shelf were growing from either side into the lumen of the spermathecal invagination, leaning partly against the lateral parts of the ventral walls of the invagination. The further development shows that these „shelves" are the buds of uropods which are, in my opinion, the ovipositor valves.

The comparison of tangential and cross sections shows that the hypoderm is a low epithelium with fairly large nuclei, which is a little less basophilic than the ectodermal rudiments of genital efferent ducts. The epithelium of these genital invagination contains the middle height cells with oval nuclei. Spindle-shaped cells whose staining properties differ distinctly from the epithelium, showing the characteristicts of the elements of mesodermal origin, start to group around the anterior part of hypodermal invagination.

Second instar nymph (pl. LXXX, fig. 2)

This period begins with the considerable growth of the parts formed before. Numerous mitotic divisions in their cells indicate it. Those rudiments constitute now an anatomical loaf-shaped entity, and they spread from the anterior part of the VII segment, where the ampullae are situated, to the posterior part of the VIII segment, with the small genital orifice covered with cuticle. The compactness of ectodermal rudiments is clearly seen especially on the sagittal and transversal sections, and is probably connected with the anatomical relations of that part of the abdomen.

The oviduct joins the ampullae from the ventral side, obliquely from the front and side. It is lined with a cubical epithelium with large, round nuclei. One could not see the muscular layer, applying the azan method one could only discover the delicate tunica propria.

Ampullae are growing considerably and assume the shape of cups. They grow mainly towards the front and the middle, and because of that one may observe the shifting of the ampullae in front of the hypodermal invagination, where they meet in the middle plane of the segment. During the next two days the adherent walls of the two ampullae become one multilayered wall.

In connection with the general growth of the nymph one may also observe the growing of the hypodermal invagination. One may notice besides a gradual enlargement of the invagination directed dorsally, proceeding posteriorly, visible on the cross section. Also the elements of the ovipositor are growing. They are now strong, cylindrical, parallel processes with a large basis and rounded ends, directed towards the posterior part of the abdomen, and slightly towards the dorsum. They are covered with columnar epithelium, common for the anterior part of the hypodermal invagination. The posterior wall of the invagination is built of only a thin layer of flat epithelial cells. The anterior part of the hypodermal invagination is surrounded by spindle-shaped cells with feebly stainable plasma and small, strongly basophilic nuclei. These cells are transversely placed in relation to the long axis of the invagination, and are grouped in especially large numbers on its ventral side and anteriorly to the basis of the ovipositor. It is an early stage of formation of the uterine muscles, when no fibrils are yet visible. Independent of this, the ventral muscles of the VII and VIII segments are situated on both sides of the hypodermal invagination.

Second moulting

The seventh and the eighth abdominal segments are ring-shaped, and the ninth segment is a hemispherical formation, ending the abdomen. The paratergal plates of the seventh and eighth segments are characterized by darker natural pigmentation and a considerable rigidity. On the azan-stained sections they are composed of a thin, blue-stainable endocuticular layer, and a thick, redstainable exocuticle. As in male nymphs, only small fragments of the cuticle between the segments are formed exclusively of chitin endocuticle, and so are very elastic. The remaining cuticle, covering the genital segments, is formed of blue-staining endocuticle and of orange exocuticle of the same thickness, and is moderately elastic.

The skeleton musculature is composed of the following muscles, marked in Fig. 3 by numbers, given here in brackets: Along the tergal plate of VII and VIII segments five identical muscles are situated on either side (pl. LXXX, fig. 3, No. 1 and 2). They are lying in one plane in each segment, and form a compact group, working probably as one muscle, and hence termed sometimes as a „muscle plate". They are dorsal internal muscles.

Along the dorsal edge of paratergal plates a delicate, paired, dorsal external muscle is situated in the VII and VIII segments (3 and 4 respectively).

Ventral muscles lie near the sternal plate of the VII and VIII segments — also in the shape of 5 bundles on either side (5 and 6). At that stage the skeleton muscles show usually the structure, typical of the striated muscles of insects: a thin layer of sarcoplasma with distinctly elongated nuclei is covering a bundle of striated fibrils. Only the microscopic picture of ventral muscles of the VIII segment is different: they are not placed in one plane, they have pycnotic nuclei and obliterated striation; they are weakened and do not correspond to the concept of the muscle plate. On the side of each segment, in the semi-circle bow, formed by tracheal trunc connecting the neighbouring spiracles, the dorsoventral lateral internal muscles are situated. And so on the border of VI and VII segments one can see the group, composed of three strong, parallel muscles (7). On the border of VII and VIII segments three muscles weaker than the former are situated (8), and on the border of VIII and IX segments there are two parallel dorsoventral muscles (9).

Besides the VII and IX segments possess the lateral internal muscles, which appear only once in the complex of genital segments: in the VII segment — the dorsoventral muscle (10), which is inserted on the dorsal side externally to the dorsal external muscle of the VII segment (3), and on the ventral side — behind and outside to the insertions of dorsoventral muscles, which are lying on the border of VI and VII segments (7). In the IX segment, on both sides of the rectum, the following muscles are situated: three delicate, dorsoventral muscles (11) and two groups of muscles probably functionally connected with the anus. One must include here dorsoventral muscle fibres (12), lying in the narrowed part of the IX segment, and two muscles, passing in the approximately transversal plane from the lateral wall of the segment obliquely towards the front, to the rectum (17).

The genital segments are also equipped with the lateral external muscles. In the VII and VIII segments the lateral external lower muscles are visible (13 and 14 respectively). Their anterior insertions are situated in the furrows between the paratergal plates, dividing the VI and VII, or the VII and the VIII segments, and the posterior insertions — in the lateral part of the respective sternal plate; the lower muscle of the VII segment (13) is inserted to the sternal plate between the lateral internal muscles „7“ and „10“.

The seventh segment has also the paired lateral external upper muscle (15), situated between the furrow on the border of paratergal plates of VI and VII segments (at the level of the spiracles) and the posterior part of the VII tergal plate where it touches the paratergal plate.

In the VIII abdominal segment two parrallel muscles (16) are situated, passing obliquely towards the exterior so that their dorsal insertions lie in the paratergal plate externally to the external tergal muscles of the VIII segment (4) and the muscles reach to the sternal plate behind the lateral internal muscle „8“, internally to lateral external muscle of the VIII segment (14).

In the V segment the ovarioles join the oviduct. Some preparations show there a hardly visible dilation; maybe it is just an impression caused by joining of several ducts into one. In this period the chamber begins to be formed, which Ries (1931) called „Ovarialampulle“, with the bacteria which will infect the eggs, shifting that way.

The border between the former ampulla and the oviduct is anatomically and histologically precise: on a very short space the cubical epithelium of the oviduct passes into the columnar epithelium of the ampulla.

The septum dividing the ampullae disappears. This process starts in the posterior, on the ventral side, and slowly proceeds towards the front. Thus the lumina of both ampullae, i. e. of both oviducts, connect.

The hypodermal invagination is further anatomically different, but one may observe the progressing differentiation into the anterior (uterine) and posterior (vaginal) portions. The anterior portion, formed of columnar epithelium, is abundantly furnished with muscles. One may distinguish two layers of finely striated muscles: the inner, thick layer of circular muscles (mm. constrictores uteri) and the outer, thin layer of oblique muscles, descending down (mm. retractores uteri). The anterior part of the invagination is growing intensely, and pressing, against the joined ampullae, flattening them and pushing them partly into the VI abdominal segment. The posterior, vaginal part of the invagination has, as before, a thin wall without muscles. In some preparations a delicate cuticular lining is visible in it.

The ovipositor valves are protruding on the border of the anterior and posterior parts of the hypodermal invagination. If one may judge by the skeleton muscles, it is the border of the VII and VIII segments. The valves are covered with epithelium and contain many spindle-shaped cells.

In the ectodermal rudiments the plasma is further strongly basophilic, which distinctly differentiates it from the hypoderm.

Third instar nymph. (pl. LXXX, fig. 4).

The anterior part of each oviduct starts to dilate (pl. LXXXIV, fig. 15), acquiring a flask-like shape. This process includes longer and longer parts of the oviduct as the nymph is growing, and at last the whole part lined with cubical epithelium is dilated. According to Ries (1931) the causes of this phenomenon should be sought in the processes, connected with the acquisition of the symbionts into the oviduct tissue. I have sketched this process biefly here only for the sake of completeness of the picture — Ries' work contains the rest.

The first stage of the changes is manifesting itself by thickening of the epithelial layer. It is further built of a single layer of cells, but the height of the cells grows 3-fold. This results in the thickening of the ovary on the outside, and slightly diminishes its lumen. The plasma of these cylindrical cells shows numerous, small, acidophilic granules. The distinctly oval nuclei are situated more or less in the middle of the cell height in the beginning, and later on, the lower part of the cells elongates considerably and the nuclei are found in the upper part of the cells, at the end of the third nymphal stage, as the distance between them and the free cell surface remains the same. At the same time the symbionts penetrate into the oviduct cells, and the infected layer is covered by epithelium from the inside and from the outside, which causes a further narrowing of the oviduct lumen.

The part of the oviduct, formed from the connection of the ampullae, no longer shows any traces of its „double" origin, and it is a duct, the middle part of which is slightly concave towards the ventral side, and its remaining short, lateral parts are geniculately bent anteriorly. Its posterior protrudes on both sides of the uterus, forming a rudiment of so called „accessory glands" (pl. LXXXIV, fig. 16). Although this evagination is developing fast and ramifying, it is not histologically different from the oviduct from which it is growing.

The analysis of the skeleton muscles shows the lack of the ventral muscles of the VII segment, and the shifting of the anterior insertions of analogous muscles of the VIII segment anteriorly, as if on the territory of the VII segment. The lateral muscles do not show such shifting. The differentation of the hypodermal invagination into the uterine and the vaginal portions is further proceeding. The uterus is situated in the VII and VIII segments, and it is a straight tube, whose cross section shows an elipsoid lumen. Its walls are furnished with strong muscles, m. constrictor uteri and m. retractor uteri.

The vagina is by half larger than the uterus and more flattened. The genital opening, though further covered by the cuticle, becomes larger and looks like a fissure across the body between the bundles of lateral muscles of the left and the right side. The growing of the genital opening is accompanied by the further uncovering of the ovipositor, the basis of which only is sticking in the ventral wall of the invagination, and the rest is protruding freely in the lumen of the genital opening. The posterior insertion of the ventral VIII segment muscle (pl. LXXX, LXXXI, fig. 3, 6) is now in the wall of the vagina, above the genital opening.

Third moulting

Where the oviducts touch the uterus they are separated from it by a wall, which in its thinnest area is a single layer of cells.

The rudiments of the so called „accessory glands“ are growing and ramifying, acquiring, in the anatomical sense, the shape of a three-fold tubular gland on either side of the body. The histologic structure of this „gland“ is, however, similar to the neighbouring parts of the oviduct. Not very high epithelial cells are filled with granules and contain large nuclei with nucleoli, which may give evidence of their secretory function.

In some specimens the uterus is S-shaped, bent towards the dorsum, maybe as a result of a considerable elongation. The uterine wall (pl. LXXXIV, fig. 17) is creased and is covered by a layer of elastic chitin which is pale-blue stainable by azan method. M. retractor uteri is inserted to the anterior ridge of the VII sternal plate.

The large vagina (pl. LXXXIV, fig. 18) is a rectangular bag with distinctly stiff walls. Its dorsal wall is draped into two longitudinal folds, on which small denticles appear. A trough is thus formed, to which the end, strongly sclerotized part of the penis probably reaches. This trough gradually disappears in the IX segment, and thus the dorsal wall of the vagina passes gradually into the IX sternal plate.

When one compares the pictures of different stages of the third moulting, one may follow the protruding of the ovipositor from the vagina. In the initial stage its base is deep inside the vagina, at the end of the third instar the distal parts of the valves appear in the genital opening, and now the ventral wall of the vagina turns outside in such a way that not only the whole ovipositor is protruding from the opening and shifting to the ventral surface of the body, but a fold called a „lip“ is formed, which prolongs the VIII sternal plate posteriorly. The „lip“ does not contain any muscle insertions. The protruding valves are flat, almost triangular and directed posteriorly with their narrower ends.

As the vagina and the genital opening are growing, one may observe the part of the VIII sternal plate being drawn into the vagina. The ventral muscle of the VIII segment (pl. LXXX, LXXXI, fig. 3, 6), which was lying along the lateral walls of the vagina at the end of the III nymphal period, is now on its dorsal wall. One can term it a musculus retractor dorsalis vaginae, as BLAGOVESHCHENSKI proposed such a term for an analogous muscle in *Mallophaga*. The lateral muscles of the VIII segment are lying now close by the lateral walls of the vagina; the lateral external muscle, designed with no 16 in the fig. 3 and inserted now with its one end on the border of the tergal and paratergal plates, and with the other on the sclerite of the VIII sternal plate, seems to play an especially important role.

The cuticle, lining the vagina passes gradually into the layer covering the surface of the body. A stronger sclerotization of both the central part of the VIII sternal plate appear, thanks to which a large sclerite is formed, called a genital plate by FERRIS, and that of the valves, especially in their externoposterior part..

The young imago

The last, or the IX segment of the abdomen in the female has a deep incision posteriorly, and inside the cleft the anus is situated, slightly shifted dorsally. The remaining genital segments are ring-shaped, with well marked paratergal plates and spiracles. A large sclerite is still visible in the ventral wall of the VIII segment (pl. LXXXI, fig. 5), and a „lip“, under which the small, flat, triangular ovipositor valves are situated. The valves arise from the sternite and are not connected with it by a joint. It may indicate a rudimentary character of the ovipositor in the *Anoplura*.

The skeleton musculature of the VIII and IX abdominal segments does not undergo any essential changes since the period of the second moulting, and is characteristic of the imago (pl. LXXXI, fig. 6): I did not succeed in finding but two lateral internal muscles from the border of the VIII and IX segments (see pl. LXXX, fig. 3, pl. LXXXII, 9). The skeleton muscles of the VII segment do show, however, considerable changes. On the border of the VI and VII segments only two lateral internal muscles (pl. LXXXI, fig. 6, 7) are seen, and not three, as before. It may indicate the partial connection of two muscles, for on some preparations one of the discussed muscles is twofold. In the VII segment of the imago also the lateral external upper muscle (see pl. LXXXI, fig. 3, pl. LXXXIV, 15) and the ventral muscles (see pl. LXXX, LXXXI, fig. 3,5) are missing. The anterior insertions of the ventral muscles of the VIII segment (pl. LXXXI, fig. 5, 6), however, lie on the line, connecting VII spiracles, so it is shifted anteriorly. The considerable distance between the anterior insertion of the ventral muscles of the VIII segment and the nearest analogous muscles (i. e. those of the VI segment) seems to exclude the possibility of the former VII and VIII segment muscles having connected into one bundle. The posterior insertion of ventral muscles of the VIII segment lies in the dorsal wall of the vagina, anteriorly to the dorsoventral muscles of the IX segment (pl. LXXXI, fig. 5, pl. LXXXII, fig. 11).

The filaments of the ovary meet in the III abdominal segment. In the ovarioles one may find different stages of the ovogenesis, described by Ries (1932). The ovarioles meet in the „Ovarialampulla“ in the posterior part of the VI segment. Both the oviducts are now directed towards each other on a slightly curved line, and they join the uterus in the anterior part of the VII segment. Unlike Ries, I did not observe the presence of any cuticular lining in the oviducts, even when using the microscope with a phase contrast. So called accessory glands extend from the lateral parts of the VI segment to the posterior part of the VIII segment. The division into the oviduct and so called accessory gland has but anatomical character, and is not based on function or histologic structure. Both in the oviduct and in the glands the pavement epithelium with large nuclei, placed centrally and the cytoplasm full of granules are seen. It proves the secretory activity of the cells, the more so as the uniform secretion products fill the lumen of so called „accessory glands“ and the oviducts, while it is not visible in the „Ovarial ampulla“. All this suggests that so called „accessory glands“ are but pockets of the oviduct, increasing its secretory activity through the augmentation of the active surface.

The uterus is tube-shaped, slightly curved and provided with strong, circular m. constrictor uteri, and it is connected by m. retractor uteri with the anterior border of the VII sternal plate in its central part. The uterus is lined with cuticle, and golded into regular, deep, longitudinal furrows. The uterine muscles show slight striation, and differ from the skeleton muscles also by the abundance of sarcoplasm and the presence of comparatively large and numerous nuclei.

The vagina, being a large, flat pouch, slightly concave laterally, occupies a considerable part of the VIII segment. Its external orifice is almost as large as the base of the IX segment. The vagina is lined with a two-layer cuticle with denticles and spines. The ventral ridge of the vagina orifice, or of the secondary genital opening is formed by a slightly heart-shaped „lip“, reaching under the IX sternal plate approximately to the line of insertions of dorsoventral muscles (pl. LXXXI, fig. 5).

The vagina is provided with the strong m. retractor dorsalis vaginae, and a much weaker m. retractor ventralis vaginae, which extends from the ventral wall of the vagina externally and posteriorly towards the VIII sternal plate.

Table 1

Terminology applied in the descriptions of female efferent system in the lice

		„Ovarial-ampulle“	oviduct		orifice of the „accessory glands“	uterus	vagina	gonopods-ovipositor valves
			proximal portion	distal portion				
Pediculus	Landois 1865	uterus				vagina		Klappen
	Pavlovski 1908	„cupola“ (in Russian)	oviductus	uterus	vagina			
	Müller 1915	Tuben			uterus		vagina	Vaginalpalpen
	Nuttall 1917					uterus	vagina	gonopods
Phthirus	Landois 1864	uterus				vagina		Klappen
Haematopinus	Ströbelt 1883	tubae		uterus bicornis	vagina			
	Florence 1921	oviductus				uterus	vagina	gonopods
	Blagoveshchenski 1956			uterus bicornis			vagina	
Anoplura	Ferris 1951	oviducts				uterus	vagina	
Phthiraptera	Ries 1931	Ovarial-ampulle	Ovidukt			Vagina		
	Clay 1956						genital chamber	gonapophyses

The male

The embryo

24 hours prior to hatching the male embryo of *Pediculus humanus* L. has in the third and fourth segments a paired, bilobed testicle, approaching „8“ in shape. From the narrow strip, dividing the testicle lobes, a solid cord is growing out. Roundish spermatogonies, about 4 μ in diameter, and so much larger than the remaining cellular elements of the testicle, constitute their main mass. The nuclei of the spermatogonies are not large at that time, and the cytoplasm is basophilic. Single intersticial cells appear occasionally between the spermatogonies, one could not notice, however, any anastomoses, connecting them into a stroma. More small mesodermal type cells are grouped around the narrow strip between the lobes and at the top of each lobe, from which a ligament is growing, which disappears among the large cells of the fat body. Staining by azan method shows the presence of a subtle tunica propria, of probably acellular structure.

The cord, arising from the narrow strip between the testicle lobes, has a cellular structure, and is thick in its initial portion, and then it narrows and remains about 3 μ in diameter. It could be observed through the VI abdominal segment. No ampullae were found. In the hatching embryo the rudiments of the ectodermal part of the efferent system are missing.

First instar nymph

The intersegmental membranes between the VII and VIII and or the VIII and IX segments are clearly visible still in the non-fed nymph 30 hours old. The fold of the intersegmental membrane is reaching deeply enough into the precedent segment especially on the ventral side. Similarly in the female nymphs, „muscle plates“ composed of five identical longitudinal muscles are situated near the ventral and the dorsal walls of the segments. On the border of the VII and VIII segments, between the alimentary canal and the ventral muscles two small vesicles are situated. Their walls are built of cells with round nuclei, which are smaller than the hypodermal cells and less readily stainable. They are mesodermal ampullae.

As during the following hours the folds of the intersegmental membrane are straightening, the abdomen of the nymph increases in size, and the borders between the segments become obliterated.

About 50 hours after the post-embryonic life had started, an unpaired hypodermal invagination appears between the VIII and IX segments, which is growing anteriorly in the medial line of the segment, slightly above the layer of ventral muscles. The epithelium of the invagination, which is called a genital pouch, does not differ at that time from the hypoderm surrounding it, and it flattens only later.

After three and a half days post-embryonic development the ampulla is an egg-shaped, though dorsoventrally flattened vesicle, whose narrower end is directed obliquely externally and posteriorly, and passes into a solid cord. This cord is still as thin as it was in the embryo, which makes observing it on the same specimen difficult. The fragments of the cord, observed on different specimens, and related to its anatomical position and further development indicate, that it is a still solid vas deferens. It passes under the ventral muscle of the VIII segment (pl. LXXXI, fig. 7), although the ampulla is situated in the posterior part of the VII segment. On cross sections the columnar epithelium, building the wall of the ampulla is lower than the hypoderm, and composed of small, readily stainable cells, some of which are just dividing.

The genital pouch reaches to the anterior ridge of the VIII sternal plate, and is situated closer to the ventral wall of the body, than the ampullae. At the end stage of the first instar the anterior part of the dorsal pouch wall thickens (pl. LXXXIV, fig. 15).

The anus is situated at the top of the abdomen.

First moulting

The ampullae are growing and are situated now in the VII segment; they are cucumber-shaped and are lying parallelly, obliquely between the intestine loop and anterior portion of the genital pouch.

The dorsal wall of the genital pouch is built of columnar epithelium. On cross sections one may observe a furrow, appearing in it and dividing the hitherto uniform vault in the median line. Two band are thus formed, and each of them is shaped like a rectangular trough with rounded corners, concave dorsally. Over each epithelial band, or inside the trough, loose cells of mesodermal character are gathering. The discussed bands will be subsequently termed uropods.

The epithelium remains low in the ventral wall of the genital pouch and at its orifice.

In the posterior part of the genital pouch, in its ventral wall, the cells begin to divide intensively, and after a short time two small, finger-like processes start growing into the lumen of the pouch. They are symmetrical, slightly inclined towards each other, and situated close to the orifice of the genital pouch.

Second instar nymph (pl. LXXXI, fig. 8)

Vasa deferentia slightly thicken and gradually a lumen is formed inside them starting from the ampulla towards the testicle. The ampullae will be further referred to as seminal vesicles. The spacious mid-gut is pushing the seminal vesicles between so called rectal glands and the trunk of trachea, which connects the VII and VIII segment spiracles. The seminal vesicles further lie parallelly to each other, with their proximal portion directed dorsally; they are cylindrical and closed at both ends. The vas deferens joins the seminal vesicle subterminally, obliquely from the posterior and ventral side. Histologically the vesicle wall remains uniform throughout: the cylindrical epithelium, almost twice higher than the hypoderm, is covered on the outside with a thin layer of very flat connective tissue cells.

The antero-dorsal part of the genital pouch wall is growing considerably both in thickness and extent so that the uropods, divided by furrow, are hanging deep, towards the ventral wall of the pouch. As a result of this the lumen of the anterior part of the genital pouch assumes on cross sections the shape of a large „W“. About the middle of the furrow a small, tubular rudiment of the ejaculatory duct is protruding. The uropods disappear anteriorly to it, passing gradually into the wall of the genital pouch; the distal parts of the uropods hitherto separate fuse building a V-shaped formation.

The ejaculatory duct is growing anteriorly along the seminal vesicles, and after two days it approaches their ends. Already in an early phase of the invagination of the ejaculatory duct, its ectodermal epithelium, composed of one layer of cells begins to be covered by loose mesodermal elements, which constitute the rudiment of circular muscles.

A little later the posterior part of the genital pouch invaginates into the IX segment, beginning the migratory process of the genital opening.

At the same time the ventral processes of the genital pouch wall grow slightly (pl. LXXXIV, fig. 16). The ventral muscles of the VIII segment end beneath them.

Under the genital pouch a group of spindle-shaped cells with their long axes parallel to the long axis of the genital pouch are situated symmetrically on both sides. It is the rudiment of muscles, serving to push forward the basal plate, which are termed by NUTTALL „mm. protractores of the basal plate“.

The anus is placed subterminally, slightly shifted dorsally.

Second moulting

The genital segments of that period resemble those of a female, i. e. the VII and VIII segments are ring-shaped, and the IX is a hemispherical formation, ending the abdomen. Paratergal plates of the VII and VIII segments are characterized by darker pigmentation and a comparative rigidity. The remaining cuticle, covering the genital segments is elastic enough and seems to be characterized by uniform thickness in the preparations treated in toto with carbol-fuchsine; only in the azan-stained sections, some small areas in the furrows between the segments are observable, where the chitin endocuticle is not covered with a more rigid exocuticle.

These are the skeleton muscles, marked in pl. LXXXII, fig. 9 with numbers, given in brackets:

Under the tergal plate, five symmetrical muscles are seen on both sides, which are called the dorsal internal muscles of the VII and VIII segments (pl. LXXXII, fig. 9, pl. LXXX, fig. 1, 2).

They are placed in one plane, and they form a compact group in any segment, which probably is working together and hence sometimes termed a „muscle plate“ (Muskelplatte).

On the border of the tergal and paratergal plates there is an also paired, though much weaker dorsal external muscle in the VII and VIII segments (3 and 4 respectively).

The ventral muscles lie closely to the sternal plates of the VII and VIII segments, as five paired bundles, like the dorsal ones (5 and 6).

The lateral internal muscles lie metamerically on the sides of the abdomen, divided from the gut by the trunk of the trachea, connecting the neighbouring spiracles. As the posterior abdominal segments are growing smaller and smaller, the lateral muscles are becoming weaker. A group, composed of three strong muscles, lies on the border of the VI and VII segments (7); also three muscles are visible on the border of the VII and VIII segments (8). They are, however, thinner than the former. Two weak muscles on the border of the VIII and IX segments (9) are the last group.

In the VII segment one more muscle strong enough is to be found: it is a paired, dorsoventral muscle (10), whose insertions are situated externally to the dorsal external muscle of the VII segment (3), and posteriorly to the lateral internal muscle of the border of the VI and VII segments (7).

The paired, lateral, external muscles are to be found in the VII and VIII segments (11 and 12). They are inserted on the side of the body, in the furrow between the paratergal plates VI and VII and or VII and VIII, and are directed obliquely posteriorly towards the sternal plate, where they insert on the external part of this plate. The later insertions lie behind those of the lateral internal muscles, and in the case of the lateral external muscle of the VII segment (11) — between the insertions of the lateral muscles of the VII segment (7 and 10).

The vasa deferentia form a loop and adhere to the tracheae, pass externally to the testicles towards the dorsoventral muscles, and further between them and the gut posteriorly, up to the ventral muscle of the VIII segment and then they turn back towards the middle of the body and anteriorly. On the cross sections epithelium is seen in the walls of the vasa deferentia, and also not numerous, but distinct muscle fibres (usually 2—3 on one section) ranged along the vasa.

The seminal vesicles, parallel to each other, are tube-shaped and placed obliquely: their proximal portions, bent dorsally, connect with the vasa deferentia in the posterior part of the VII segment, and the distal portions reach the anterior border of the same segment. Touching each other, the vesicles are, however, separate formations. Numerous mitotic divisions prove their intense growth.

The blind ejaculatory duct is connected with the seminal vesicles on their internal side. At that time the duct is a long, curved tube with a lumen of more or less the same diameter on all its length. Its walls are built of a layer of columnar epithelium, and a comparatively weak layer of circular muscles. The duct is prolonged by a small cone with a canal inside, directed towards the lumen of the genital pouch, which is the bud of the penis.

The penis is growing between the uropods, situated closely near each other, which permits to assume that they take part in the formation of the penis, and to consider the remaining part of the uropods as parameres.

The dorsal wall of the genital pouch is growing rapidly. It is anatomically manifested by further invagination of the vault into its lumen and by its folding, and histologically — by numerous divisions in the epithelial cells. On the dorsal side of the ectodermal rudiment loose, spindle-shaped, though not very long, less readily stainable than the epithelium, mesoderm cells are gathering.

The ventral processes of the genital pouch do not show any pronounced changes. Only in some preparations we see the uropods to be less readily fixable and stainable.

The genital pouch reaches deep posteriorly, halfway between the IX paratergal plate and the end of the body. Also the ventral muscles of the VIII segment (pl. LXXXI, LXXXII, fig. 9, 6) are reaching as far, and are inserted to the sternal plate at the level of the genital pouch orifice. In my material I have not found any specimens with the genital opening more shifted posteriorly. Lateral internal muscles (9) are situated, as before, on the border of the VIII and IX paratergal plates, symmetrically on both sides of the alimentary canal. The observed shifting of the posterior insertions of ventral muscles may prove the posterior growth of the middle part of the VIII sternal plate.

Third instar nymph

Vasa deferentia are about 8 μ thick, and their lumen is about 2 μ in diameter, so they are much thinner than the rest of the efferent ducts, and they are built of epithelium and a delicate muscular layer with few fibres.

A considerable growth of the seminal vesicles, both in diameter and in length causes their not having enough space under the gut; they are shifted sideways, stretching from the middle of the VII segment to the anterior part of the VI segment. On the cross sections the growth in thickness manifests itself mainly by the growth of the lumen of the vesicles; the high cylindrical epithelium with oval nuclei and the muscular layer only thicken a little. The histologic structure of the vesicles is uniform for their entire length, and the blind portion situated before the connection with the vas deferens is not in any way differentiated.

The ejaculatory duct runs parallelly to the seminal vesicles, between them and the alimentary canal, and joins the seminal vesicles. The wall of the ejaculatory duct is built of two layers of approximately the same thickness: the inner epithelial layer, thinner than the epithelium of seminal vesicles, and the outer muscular layer.

Further folding of the dorsal wall of the genital pouch causes the appearence of the future eversible, intumescent part of the penis which is called vesica penis. The sections from that period show that the penis is hanging down as a short tube, hooklike bent dorsally, in the bifurcation of the parameres (pl. LXXXIV, fig. 17). The efferent duct does not run in the penis axis, but closer to its dorsal wall. Hence on the sections the penis has a thick ventral wall, built of high cylindrical epithelium, and a thin dorsal wall of small cells characteristic for pavement epithelium. The ejaculatory duct, equipped with long, spindle-shaped muscle cells, whose striation is becoming visible penetrates into the basal part of the penis. The distal part of the duct with the orifice at the apex of the penis is completely deprived of muscles. An unpaired fold is growing on the dorsal side of the penis, approximately in the middle of its length. I did not succeed in following its development, besides stating, that the imago does not possess it.

The parameres are further increasing in size, and their profile on cross sections becomes more complicated because of the formation of denticles on their posterior part.

At the same time a paired fold appears in the young nymph III in the lateral walls of the genital pouch, which gradually divides it into two parts: dorsal and ventral, in the transversal plane. At the end of this nymphal period the ventral part, already completely cut off, and strongly flattened, is producing cuticle. A kneading-trough shaped formation is built of chitin walls. The trough walls begin to stick together, starting from the sides, forming a stiff basal plate; at its bottom there remain parts proving its two-layer origin. Sclerotization, including especially the lateral ridges of the plate is also observed. The ridges are now translucent as two dark lines in the preparations in toto.

As the dorsal part of the genital pouch is folding more and more, it gives rise to vesica penis.

The orifice of the genital pouch, or the secondary genital opening is covered with cuticle on the dorsal side of the abdomen. A paired muscle is inserted into the anterior pouch wall, not far from its orifice; in earlier stages of ontogenesis it was the ventral muscle of the VIII segment (see pl. LXXXII, LXXXI, fig. 10, 6): the vas deferens is winding around it. Such topography of the discussed muscle, which remains in the imago, means, that the IX sternal plate to which the muscle is inserted has been shifted to the dorsal side of the abdomen, and designs its participation in building of the genital chamber. The tergal and paratergal plates of the VIII and IX segments are not shifted, which may be proved by the topography of the dorsal muscles of the VIII segment and that of the lateral internal muscles from the border of the VIII and IX tergal plates (pl. LXXXII, fig. 10, 9).

The processes of the ventral wall of the genital pouch have disappeared. It is possible, that during the rapid growth of the skeleton elements after the second moulting the pouch has been distended, and the processes disappeared through straightening of the folds.

The secretion of the cuticle by the epithelium of the ectodermal rudiments begins from the penis.

The striation is hardly visible in the muscles of ectodermal rudiments of the efferent system, but the anatomical differentiation is already very distinct. The muscles pushing forward the basal plate (in NUTTALL'S terminology: mm. protractores of the basal plate) form two group of numerous fibres, placed symmetrically in relation to the medial line from the anterior ridge of the basal plate to the VIII sternal plate where it is dorsally bent.

The retracting muscles (mm. retractores) of the basal plate connect its anterior part with the border of the VII and VIII segments, and are directed anteriorly and exteriorly from the basal plate, fan-like.

Above the anterior part of the basal plate elongated mesodermal cells are loosely situated. Their placement indicates, that they are rudiments of the m. retractor vesicae penis.

The anus is situated dorsally in the part, termed in the present work as IX tergum.

Third moulting

Every seminal vesicle assumes the shape of an „S“, disfigured thus, that it does no longer lie in one plane: the proximal part lies near the dorsal wall of the abdomen, in the middle of the VII segment, and the distal — close to the ventral wall, in the anterior part of the VI segment. When azan stained, all the cells of the epithelium of seminal vesicles show the presence of numerous granulations, red-stainable, like the nuclei. It is the initial period of the secretory activity of seminal vesicles, when their lumen in cross sections remains still empty.

The ejaculatory duct is narrowing towards its distal part. Especially its proximal part assumes the faculty of contractability in a considerable degree: the lining epithelium forms six longitudinal folds, and as a result the lumen of the duct looks like a six-pointed star, and moreover the layer of circular muscles is thicker than the epithelium. The part of the ejaculatory duct, lying inside the copulatory organ has less muscles.

The basal plate is a flat trough, shaped like an oblong rectangle, and lies on the ventral side of the penis, parallelly to the VII and VIII sternal plates. As far as the azan method can show, the sclerotization of its lateral ridges has proceeded as far as in the paratergal plates and in the ventral part of the parameres, but the remaining part of the basal plate stains like exocuticula in the sternal plates.

Richly folded, chitin vesica penis, which is partly covered with tubercles and denticles, or forms some stiffening elements, called statumen penis, and the distal part, termed penis, covered with a thin layer of chitin, form the proper intromittent organ. One end of the retracting muscle (m. retractor vesicae penis) is inserted inside the vesica, and its other end — into the dorsal surface of the basal plate.

The parameres are „V“ — shaped, with the opening directed anteriorly so, that the „arms“ embrace the penis; their proximal ends are inserted into the walls of the genital chamber. Their connection with the basal plate is mobile, and the sharp distal end of the parameres is a little protruding over the abdominal surface from the genital chamber. The parameres have undergone a considerable sclerotization and are, moreover, covered with denticles, especially on their externo-ventral surface.

The young imago

The VII segment in the male is the last ring-shaped one. Its size approaches that of the VI segment preceding it which is, like it, deprived of the ventral muscles. The posterior two abdominal segments differ considerably both from the remaining ones and from each other. The tergal and paratergal plates of the VIII and IX segments are shorter by half than in the precedent segments; in the IX segment the paratergal plates are still clearly visible though without the spiracles, and the tergum includes the anus. The topography of the dorsal and lateral muscles remains in the VII and VIII segments the same as in the period of the second moulting but one can observe some changes in the ventral muscles. The paired retracting muscle of the genital chamber (m. retractor) which corresponds to the ventral muscle of the VIII segment, is inserted into the anterior wall of the genital chamber and extends along the sides of the copulatory organ to the anterior part of the VIII sternal plate (pl. LXXXII, fig. 11, pl. LXXXI, fig. 6). The successive stages of dislocation of skeleton muscles of the VIII segment show, that the sternal plate of the VIII segment reaches deep beyond the IX paratergal plates, up to the dorsal side of the abdomen, and it is possible that it reaches even to the posterior wall of the genital chamber. Sagittal sections show, that the sternal plate of the VIII segment is densely folded which, together with the cuticular semicircular element, situated in the transversal plane, possibly affords this segment necessary elasticity and strength.

Above the alimentary canal, in the IV, V and VI segments lie paired testicles, each of them composed of tow heart-shaped lobes, directed to each other with their large bases. Thin vasa deferentia grow out of them; they go around the muscle retracting the genital chamber and are joined to the seminal vesicles. The walls of the vasa are built of a monolayered epithelium, a basic membrane and a delicate muscular layer, whose fibres are ranged along a loose spiral line.

The seminal vesicles (pl. LXXXII, fig. 12) are situated near each other in the VI and VII segments. Their secretory activity is seen, because more or less spread granulations are present in the epithelial cells, and some colloid in the lumen of the vesicles. This colloid stains differently in different parts of the vesicle thus dividing its content into two and sometimes even 3 sections. The histologic structure is an argument for the division into two parts, separated by the orifice of the vas deferens, and corresponding to the proper seminal vesicle and the accessory gland (Pavlovski, 1908).

The proper seminal vesicle is lined with columnar epithelium with oval nuclei, and the accessory gland, which I propose to term glandula appendicularis, is characterized by a much lower epithelium and large, round nuclei.

The copulatory apparatus is composed of the basal plate, the proper intromittent organ and the parameres. In resting position the basal plate reaches at least to the anterior part of the VII segment. Here (pl. LXXXV, fig. 24) the muscles protracting the plate are inserted to it; several dozens of their fibres lie under the plate and are inserted in the VIII sternal plate in its dorsally bent part. The muscles retracting the basal plate connect its lateral parts with the borders of the VI and VII sternal plates.

The copulatory organ is placed in the trough formed by the basal plate so, that only its small anterior part of this plate is vacant. Here m. retractor vesicae penis is inserted. The wall of the vesica penis is built of leather-like chitin, and covered with numerous small denticles and tubercles. The penis, curved like a hook and sclerotized, is lying between the arms of parameres and, as seen on the sections, the thin-walled portion of the ejaculatory duct penetrates it up to the apex.

The parameres are lying in the line, being a prolongation of the basal plate towards the posterior part of the abdomen, and their base is inserted into the anterior part of the genital chamber, forming a simple joint with the basal plate (a sort of hinge joint). On the cross sections the sharp end of the parameres is anchor-shaped. I did not find any muscles connecting the parameres with other skeleton elements. One can infer than the parameres perform but passive movements. Numerous muscle cells, connecting the parts of the parameres differing in the thickness of the cuticle have, however, been found in the sections through the parameres (pl. LXXXV, fig. 23). It seems they make the parameres more flexible and, at the same time, may explain why some specimens of lice, fixed in toto, had bent parameres: it is possible that the improper fixing of those muscles was the cause.

IV. DISCUSSION

The development of the male and female genital efferent systems in the lice *Pediculus humanus* L. described here differs considerably on the first sight from analogical processes, known in other insect groups. The conviction that the basic characteristics should be similar for both sexes and should in certain respect correspond to the morphogenetic processes in both sexes (pl. LXXXIII, fig. 13) is the starting point for the attempt

Table 2

Terminology applied in the descriptions of male efferent system in the lice

<table>
<tr><th></th><th></th><th>vesicula seminalis</th><th>glandula appendicularis</th><th>vesica penis</th><th>statumen penis</th><th>penis s. str.</th><th>basal plate</th><th>parameres</th></tr>
<tr><td rowspan="5">*Pediculus*</td><td>Landois 1865</td><td colspan="2">Schleimorgan</td><td>Präputium</td><td></td><td colspan="3">Penis</td></tr>
<tr><td>Pavlovski 1908</td><td>glandula appendicularis</td><td>glandula appendicularis accessoria</td><td>praeputium</td><td></td><td colspan="3">penis</td></tr>
<tr><td>Müller 1915</td><td>Schleimorgan</td><td>glandula appendicularis accessoria</td><td>Penissack</td><td></td><td>zapfenartiger Auswuchs</td><td>Basalplatte</td><td>penis</td></tr>
<tr><td>Nuttal 1917</td><td colspan="2"></td><td>vesica penis</td><td>statumen penis</td><td>penis</td><td>basal plate</td><td>dilator</td></tr>
<tr><td>Ferris 1935</td><td colspan="2"></td><td>vesica penis</td><td>statumen penis</td><td>penis</td><td>basal plate</td><td>pseudopenis</td></tr>
<tr><td rowspan="2">*Phthirus*</td><td>Landois 1864</td><td colspan="2">Schleimorgan</td><td>Präputium</td><td></td><td colspan="3">Penis</td></tr>
<tr><td>Pavlovski 1923</td><td>glandula appendicularis</td><td>glandula appendicularis accessoria</td><td colspan="5"></td></tr>
<tr><td rowspan="2">*Haematopinus*</td><td>Ströbelt 1883</td><td colspan="2">mucus organs</td><td colspan="2"></td><td colspan="3">penis</td></tr>
<tr><td>Florence 1921</td><td colspan="2">seminal vesicles</td><td>vesica penis</td><td></td><td>penis</td><td>basal plate</td><td>parameres</td></tr>
<tr><td rowspan="2">*Anoplura*</td><td>Ewing 1932</td><td colspan="2"></td><td>internal sac</td><td>anterior endomere</td><td>penis</td><td>basal plate</td><td>*Pediculus:* ventral endomere
Haematop.: paramere</td></tr>
<tr><td>Ferris 1951</td><td>vesicula seminalis</td><td></td><td>aedeagus</td><td>statumen penis</td><td>penis</td><td>basal apodeme = genital apodeme</td><td>pseudopenis a. parameres</td></tr>
<tr><td rowspan="2">*Phthiraptera*</td><td>Mjöberg 1910</td><td colspan="2"></td><td>Präputialsack</td><td></td><td>penis</td><td>Basalplatte</td><td>Parameren</td></tr>
<tr><td>Clay 1956</td><td colspan="2"></td><td>genital sac</td><td>statumen penis</td><td>penis</td><td>basal apodeme</td><td>endomere (= pseudopenis) a. paramere</td></tr>
</table>

Acta Zoologica nr 13, po str. 30.

at some interpretation, made here. This does not mean the homologisation of the male and female systems, for which the material gathered in the present work does not supply sufficient data.

1. Uropods

In the first instar nymph of *Pediculus humanus* — of both sexes, a pair of processes appears in the anterior part of the deep hypodermal invagination, on the side directed towards the ampullae of the respective efferent ducts. They are growing into the lumen of the invagination and are directed posteriorly. Mesoderm penetrates into these processes already in the initial phase of their development in both sexes. Thus those processes have the character of uropods both in males and females. In both sexes the hypoderm invaginations begin behind the VIII segment, and in females the invagination is formed of two separate invaginations (behind the VII and behind the VIII segments), and in the males no such process has been observed. Moreover, another pair of processes appears transitorily in the males. This may prove the existance of a reduced segment, situated between the subsequent VIII and IX abdominal segments. So the male genital opening would be shifted from the border of the VIII and IX segments to the border of the IX and X segments, or to the position normal in insects, and such as is found in the imagines of many *Mallophaga* (*Gliricola* sp. — see Blagoveshchenski, 1956; *Bovicola caprae* Gurlt, *Eomenacanthus stramineus* Uchida, *Trimenopon hispidum* Burm. — see Schmutz, 1955). One might infer from the above, that also in some *Mallophaga* the segments fuse during ontogenesis. The situation of the male genital opening behind the VIII abdominal segment in *Columbicola columbae* Ewing and *Menopon* sp. (Schmutz, Blagoveshchenski) might serve as an example. In the lice such a fusion of the segments probably occurs shortly after the revolution of the embryo, as the topography of the tracheal trunks and that of the dorsoventral muscles is fixed at the moment of the formation of spiracles (Strindberg, 1916, gives the same data concerning the tracheae in *Mallophaga*).

Further, the formation of uropods in lice merits attention. It has been known (Imms, 1931) that in the males the uropods are often connected with the rudiments of the genital pouch, but the succession of appearance of both those elements and the plane in which the rudiments of the uropods are appearing, differ. In the *Hymenoptera* males (D'Rozario, 1942) one may observe a variety of those connections. And so e. g. in *Polemon liparae* (Giraud?) *Prosopis krieschbaumeri* (FörST.?) and *Pteromalus liparae*, the processi appear first, and then the invagination between them, and in *Vespula germanica* (F.?), *Apis mellifica* L. and *Cephus pygmaeus* (L.?) the hypoderm invaginates before the processi appear. Also in *Tribolium castaneum* Herbs. (*Coleoptera*, Srivastava 1953) the invagination appears first. In the light of those examples the processes arising in the anterior part of the genital pouch in the males of *Pediculus humanus* L. are a phenomenon typical for insects.

It is different with the processes of the hypodermal pouch in females. One mentioned above that they might be considered uropods. Nuttall (1917) did not observe their part in copulation, their situation, however, at the orifice of the vagina allows us to ascribe to them at least some role in lying eggs. A similar idea occured to Qadri (1948) as well, when he was studying the anatomy of *Haematopinus tuberculatus* Burm. Those uropods would be the ovipositor valves, belonging ontogenetically to the IX segment (as they appear in the pouch growing behind the VIII sternum and then they lie under the „lip", behind the posterior insertion of the ventral muscles of the VIII segment). However, both the way they are formed (deep inside the hypodermal invagination, and from its walls) and their further development (protruding outside, with the simultaneous formation of the small „lip") are quite different in the lice, than in other insects; namely, the elements of the ovipositor are usually formed of the corresponding sternites on the ventral surface of the abdomen (*Locusta migratoria migratorioides* Reiche & Frm. — Roonwal 1936; *Xiphidium* sp. and *Blatta* sp. — Wheeler 1893; *Tylopsis liliifolia* Fabr.-Becker 1932; *Blattaria* — Gupta, 1950; *Dysdercus cingulatus* Fabr. — Gupta 1951; *Harmolita graminicola* Gir. — *Hymenoptera* — James 1928, and others). The ovipositor is formed in the ventral wall also in those species, in which the ontogenetic development leads to its reduction in the imagines (*Plecoptera*: *Nemoura variegata* Oliv. and *Amphinemoura* sp. — Qadri 1940; *Siphonaptera*: *Nosopsyllus fasciatus* Bosc.- Sharif 1937). Some *Hymenoptera* show slightly different process in the formation of the ovipositor (D'Rozario 1942): In the lower *Symphyta* the buds are formed in postembryonic life on the surface of the segment, and then they plunge into the hypodermal pouches, termed „peripodial cavities" by Imms (1938, according to D'Rozario). In the higher *Symphyta* the ovipositor elements are formed already in the embryo, as outgrowths of the „peripodial cavites". Fig. 6 given by D'Rozario shows that each valve is surrounded by a peripodial cavity. Thus the ovipositor in lice is a rudimentary organ, and is formed in the way unknown in the females of other insects.

According to the classic descriptions of Wheeler (1893) and Else (1934), in the males of *Xiphidium* sp. and *Melanoplus differentialis* (Thomas?) *(Orthoptera)* the ampullae penetrate into the appendages of the same segment, and then both the ampullae and the appendages are shifted anteriorly, together with the invaginating sternum. One can trace the migration in the course of vas deferens, which runs from the testes to the ejaculatory duct by a circular way, through one of the posterior segments of the abdomen, and e. g. in *Orthoptera* (Snodgrass 1941, after Gustafson 1950) it winds round the cercal nerve. Strindberg (1916) examining the course of vas deferens in the nymph *Gliricola* sp. *(Mallophaga)* approaching maturity, noticed also that „turning back to the front", and Schmutz (1955) confirmed this for the imagines of some other biting lice. As I have shown, in the first instar nymph of *Pediculus humanus* L. the vas deferens loops round the ventral muscle of the VIII segment and so it remains, proving the migration of the ampullae to the front. One must stress that in the female the analogous duct, i. e. the oviduct liberates itself in the connection with the reduction of skeleton muscles in the III instar, and thus the traces showing that the ampulla belonged to a particular segment are obliterated.

The above observations, made by Wheeler and Else, the proper interpretation of the phenomena, observed by Nusbaum (1882) in the biting lice *Lipeurus bacilus* and *Goniocotes* *hologaster* (see the question of paired origin of ectodermal ducts) and the fact that in the embryo of *Pediculus humanus* L. the solid mesodermal cords lie initially laterally to the alimentary canal, and only later their distal portions turn towards the middle, where they end with ampullae, permit one to suppose with some probability that in the lice also the migration of the ampullae towards the medial plane of the abdomen takes place. It is difficult to say, in what degree that migration in the lice is a recapitulation of the still more primitive relations than those observed in the *Orthoptera*. GEORGE (1929), at any rate, observed the growing together of both oviducts near the border between the VII and VIII abdominal segments in *Agrion* sp. *(Odonata)*, and SHAROV (1953) saw the same phenomenon in *Lepisma saccharinum* L. *(Thysanura)*.

It is true that migration and neighbourhood of both the ampullae and the appendages are seen in *Pediculus humanus* L., the ampullae, however, and the corresponding appendages belong to different segments. In the first and second instar nymphs the oviducts pass under the ventral muscle of the VII segment, and so the ampullae belong to the same segment, and the corresponding appendages — at least to the VIII segment. Analogically, the vasa deferentia are looping around the ventral muscles of the VIII segment, so, unlike appendages, the ampullae in the male do not belong to the IX segment. It would be difficult to state if such condition is a sufficient argument for GUSTAFSON'S theory (1950) which says, that the parameres and valves in insects come from hypodermal vesicles, situated on the ventral side of the abdomen in *Thysanura*, and are connected with the body cavity. These vesicles or sacs are eversible and may be drawn in by special muscles inserted in the sternum. It seems that it is rather a result of advanced migrations (of both the uropods and the ampullae) which are necessary, as the number of segments has been reduced to nine, and is, perhaps, connected with doubts stressed more and more often, as to the full homology of genital organs in *Orthoptera* with the rest of higher insects. One stress e. g. (QADRI 1940, DUPUIS 1950) that in the males the organs immediately connected with copulating and joined with mesodermal ducts, or so called euphallic organs (organes euphalliques, DUPUIS 1950) are budding as a pair of processes. Then in *Orthoptera* these processes divide in the transversal plane, providing the dorsal and ventral lobes of the penis, and in higher insects those processes divide in the sagittal plane into parameres situated externally, and the internally placed rudiments of the penis. And it is so in the case of *Pediculus humanus* L. Of course the fact that such is the case in the majority of the orders of both holo- and heterometabolic insects, allows us to suppose that this group is non-homogenous. A part of holometabolic insects, e. g. *Diptera* (ABUL-NASR 1950) is characterized by a rather complicated development of euphallic organs: besides the invagination of the ejaculatory duct a separate penis invagination appears and develops into a flaccid, threadlike penis tube. The latter is strenghtened by a sheath, which is formed of the intersegmental membrane and eversible in some species. On the other hand the females of *Diptera* species, examined by ABUL-NASR had no trace of the ovipositor at the genital opening. Other holometabolic insects, e. g. *Hymenoptera* (D'ROZARIO 1942) are characterized by a comparatively simple way of developing the euphallic organs: at most the buds of parameres divide into the external and internal parts.

The development of the efferent system in insects more closely related to *Phthiraptera* has been known only in fragments. From the descriptions, given by GEORGE (1929, *Philaenus leucophthalmus* L.) METCALFE (1932, *Philaenus spumarius* L.) and SINGH-PRUTHI (1924, *Idiocerus* sp.) one may infer that *Homoptera* begin to differ from *Heteroptera* and the lice in an early stage of ontogenesis. The young male nymph of *Philaenus spumarius* L. has 10 abdominal segments and the rudiments of not only euphallic, but also those of pseudophallic organs (organes pseudophalliques, DUPUIS 1950) in the shape of a subgenital plate. The lice after hatching have 9 abdominal segments, and the possible rudiments of pseudophallic organs in the form of posterior outgrowths of the genital pouch disappear already still in the nymph, and probably fuse with the sternum. Discussing the development of *Naucoris cimicoides* L. *(Heteroptera)*, RAWAT (1939) stressed the lack of rudiments corresponding to the subgenital plate in the *Homoptera*. It seems, however, that this author did not follow carefully the development of the parameres. As a result one may only suppose that the „parameres" appearing in the imago of *Naucoris cimicoides* L. are ontogenetically derived from the same uropods as the penis. The young nymph *Naucoris cimicoides* L., having 11 visible abdominal segments, produces the rudiments of the male genital organs on the border of the IX and X segments, so the case is similar to that of lice, assuming that the second pair of outgrowths in their genital pouch are remainders of a reduced segment.

2. The question of paired origin of ectodermal ducts

The ectodermal portions of the female (uterus and vagina) and male (ejaculatory duct) efferent ducts are unpaired formations in *Pediculus humanus* L. This is in accordance with Nusbaum's observations (1882) on the development of *Lipeurus bacilus* and *Goniocotes hologaster*, as far as the ejaculatory duct is concerned. The rudiments of the female ectodermal ducts in *Mallophaga* are, however, paired according to Nusbaum. A stricter comparison of the descriptive part of Nusbaum's work with the material discussed in the present work concerning the development of *Pediculus humanus* L. and supported by a clearly pronounced general resemblance of the ontogenesis of *Mallophaga* and *Anoplura*, make Nusbaum's arguments somewhat doubtful. He writes, e. g. about the female on p. 641: „Dann entstehen in dem vorderen Teile dieses Keimes, wie beim Männchen, zwei paarige, ganz geschlossene Höhlungen (der künftige Uterus)...". And further: „Dann atrophirt die Scheidewand zwischen den zwei vorderen Höhlen, und auch die Scheidewand zwischen den zwei vorderen und der hinteren Höhle. Auf diese Weise kommt der Uterus mit der Vagina in Verbindung". One can see from the above that „uterus", as Nusbaum understands this term, corresponds actually to the ampullae, and „vagina" — to the uterus and vagina together. Such terminology was, by the way, used in Nusbaum's time (see Table 1). Also in the male efferent ducts Nusbaum noticed two anterior cavities, being rudiments of two tubules of the „pyriform body" which corresponds to the seminal vesicles in biting lice (Schmutz 1955). So also in the males the cavities correspond to the ampullae. As Nusbaum writes, the part of the genital rudiment situated behind the ampullae gives rise to the following formations, proceeding from the front to the back: 1) the unpaired ejaculatory duct, 2) the pair of solid processes fusing to form the unpaired penis, the lumen of which connects subsequently with that of the ejaculatory duct, 3) the pair of solid lateral processes.

Nusbaum, however, did not notice the invagination of the unpaired hypodermal pouches, which are the rudiments of the ectodermal part of efferent ducts in males and females. Hence, considering the ampullae as derived from the ectoderm, he described their connecting into a horsehoof-shaped rudiment. It seems, that one should rather speak of the migration of the ampullae towards the centre. According to Nusbaum, the anterior part of the said rudiment is developed in the females into so called uterus (or into the distal portions of the paired oviducts), and the posterior part elongates, forming the so called vagina. In comparison with my observations in *Pediculus humanus* L., this would mean the growing of the young rudiment of the „vagina" from the anterior towards the posterior part of the abdomen, so in the opposite direction as it is the case with lice and other insects. This inaccuracy of observations, which was probably caused by the fact that Nusbaum was working on a particularly difficult object (small *Mallophaga*), caused a faulty, as it seems, assumption, that the unpaired ectodermal ducts are of paired origin. One must stress that, according to Nusbaum, both the ejaculatory duct and the vagina develop in the similar way: the paired rudiments fuse and after some time, one of the said ducts arises from the middle part as an unpaired invagination.

Nusbaum names only the „uterus", penis, receptaculum seminis and unpaired gland as unpaired ducts, whose rudiments were paired in ontogenesis (p. 642). As I have shown above, the „uterus" actually corresponds to the ampullae, generally considered at present as paired, though of mesodermal origin. On the other hand the ectodermal female efferent ducts (termed „vagina" by Nusbaum) have unpaired rudiments. Both Nusbaum's work and the investigations on a number of species of *Orthoptera* (QADRI 1940, GUPTA 1950), *Odonata* (GEORGE 1929), *Homoptera* (GEORGE 1929, METCALFE 1932) and *Heteroptera* (RAWAT 1939, GUPTA 1951) share this opinion. The case is similar with *Pediculus humanus* L. with only one difference: the oviducal and spermathecal invaginations appear in the ontogenesis, and the hypodermal invagination for the accessory gland is missing.

Examining the development of the penis in the lice, I have not found any paired rudiments, anatomically separated, which would fuse to form the unpaired penis during the ontogenesis. One may rather observe in *Pediculus humanus* L. the growing of walls, surrounding the orifice of the ejaculatory duct in the form of a thick-walled tube, directed towards the lumen of the genital pouch. The paired origin of the penis in the lice results from the fact that it grows from the bases of two uropods, situated closely to each other and comparatively large at that time, and that one finds in the insects varying degrees of revealing the pairedness of the penis rudiments during ontogenesis, even in the same order. And thus e. g. among the *Homoptera*, *Philaenus spumarius* L. (METCALFE 1932, Table 27, Fig. 10) shows clearly paired rudiments of the penis, and in *Idiocerus* sp. (SINGH-PRUTHI 1924) this pairedness is as obliterated as in *Pediculus humanus* L. Also in the group *Mallophaga*, related to lice, namely in *Lipeurus bacilus* and *Goniocotes hologaster*, NUSBAUM (1882) had found clearly paired, solid rudiments of the penis.

Receptaculum seminis and the unpaired gland mentioned by NUSBAUM constitute, strictly speaking, but additional elements of the proper efferent ducts. They are altogether missing in *Pediculus humanus* L. during ontogenesis, but in the species where they appear at all, they have unpaired rudiments.

And so it results from NUSBAUM'S and my own investigations that one might speak only of paired origin of the ampullae and the penis. It seems, however, that NUSBAUM'S conclusion about paired origin of the ectodermal genital ducts in *Mallophaga* and in insects in general has not been confirmed even by the facts, which he himself had quoted.

3. Further development of the efferent system

a. The time and succession of appearance of its elements

The information on the appearance of the efferent duct rudiments in the *Anoplura* was missing in the literature till now. The only newer work, embracing, in outline, the whole embryonic development of the lice (and that of *Mallophaga* as well), namely SCHÖLZEL'S work (1937) states that the gonads do not appear in the embryos of both these groups, and that probably this happens in postembryonic life. Hence one may analogically infer about the mesodermal efferent ducts. BLAGOVESHCHENSKI (1956), on the other hand states, in his work on the role of the genital system in *Mallophaga* for their systematics, that the newly hatched female nymphs of *Menacanthus cornutus* SCHÖM. and *Cyclogaster heterographus* N. possess already the gonads, composed of five ovarioles and the mesodermal oviduct rudiments. The author does not mention the possible rudiments of ectodermal parts. The fact that I have found in the embryo of *Pediculus humanus* L. the gonads (ovaries, composed of five clearly differentiated ovarioles, or bi-lobed testicles) and a solid mesodermal efferent duct, while the ectodermal rudiments were missing, is in complete accordance with BLAGOVESHCHENSKI'S view.

Psocoptera and *Hemiptera* have been long considered as related to *Phthiraptera*. Unfortunately, the development of efferent ducts in *Psocoptera* is utterly unknown. The only more recent work on their embryonic development (GOSS 1952 and 1953) shows also the development of the gonads, but does not mention rudiments of any sexual efferent ducts. In the *Hemiptera* the solid mesodermal ducts appear in the embryo, and the ectodermal rudiments begin to form (so it seems) only in the period of hatching. This fact would explain why one writes about the solid mesodermal cords and one does not mention the ectodermal rudiments in the works on the embryonic development (e. g. of *Rhodnius prolixus* STAL.- MELLANBY 1937); hence the investigators who have limited their researches to following the postembryonic development either have found but a little thickening of the hypoderm (Rawat, 1937, in *Naucoris cimicoides* L., and Bocheńska, 1939, in *Porphyrophora polonica*) in the newly-hatched nymphs, or they have not found it at all (George, 1929, in *Philaenus leucophthalmus*, and Gupta, 1951, in *Dysdercus cingulatus*).

The lack of ectodermal rudiments and the existence of the solid mesodermal ducts in the period of hatching is also characteristic for the ontogenesis of some *Orthopteroidea* and *Blattoidea* (Heymons 1891, Wheeler 1893, Qadri 1940). Thanks to Roonwal's work it is, however, known that in the *Locusta migratoria* the embryos of both sexes are furnished with the rudiments of the main elements of the efferent system in the hatching period: they possess gonads with the solid efferent ducts and, besides, the respective ectodermal rudiments. In the female embryos of *Locusta migratoria* one can then see three small invaginations of the hypoderm (oviducal, spermathecal and that of accessory gland) and two pairs of ovipositor valves (the third one appears in postembryonic life), and in the male embryos — one pair of appendages formed from the fusion of the uropods of the X and IX segments and, between them, the invagination of the ejaculatory duct.

And thus *Locusta migratoria* and the males of *Melanoplus differentialis* (Thomas?) (the females have not yet been described) occupy a rather exceptional place among the heterometabolic insects. *Pediculus humanus* L., on the other hand, may be a representative of a more general phenomenon, namely, that only the mesodermal ducts are differentiated in the embryo.

Also in newly hatched larvae of many holometabolic insects a varying degree of development of the genital efferent system is observed. Hirschler's classic work (1909) on the embryonic development of *Donacia crassipes* L. *(Coleoptera)* does not say anything on the appearance of the ectodermal rudiments of efferent ducts. It would coincide with Wray's (1937) observation, that in *Calandra callosa* Oliv. *(Coleoptera)* the larvae are hatching without those rudiments, and so do the larvae of some *Symphyta* (*Hymenoptera*, see D'Rozario 1942) and *Trichoptera* (Dodson 1935). Kessel (1939) did not find any ectodermal duct rudiments in the embryos of fleas *(Siphonaptera)*. The larvae of *Rhagolitis pomonella* (*Diptera*, Dean

1942) are hatching without either mesodermal or ectodermal ducts, and such a state persists, according to METCALFE (1932) in the ontogenesis of *Gastroidea polygoni* L. *(Coleoptera)* still in a fully grown larva. The difficulties, connected nowadays with the comparison of the development stages of holometabolic and heterometabolic insects are, however, speaking for a more cautious interpretation of these phenomena.

As the amount of works concerned with the ontogenesis of the genital efferent system in higher heterometabolic insects was small, it was difficult to find much comparative data concerning the succession of appearance of the hypoderm invaginations in the genital segments of the female. According to my own observations in *Pediculus humanus* L., as in *Naucoris cimicoides* L. (RAWAT 1939) and in *Dysdercus cingulatus* FABR. (GUPTA 1951), first the oviducal invagination appears behind the VII segment, and later the spermathecal one, behind the VIII segment. Besides in *Dysdercus cingulatus* FABR. an invagination of the accessory gland is formed behind the IX segment. The spermatheca does not develop in *Pediculus humanus* L., hence fig. 45 in the paper of KEILIN & NUTTALL (1930) requires correction.

b. Female efferent ducts

In the insects the uterus, formed from an unpaired rudiment, connects anteriorly with paired oviducts. In the simplest case the paired oviducts open independently straight into the uterus. In that case the oviducts in the imago are purely mesodermal. It is so, according to my observations, in *Pediculus humanus* L. The similar conditions are found in many other insects e. g. in *Orthopteroidea* and *Blattoidea* (QADRI 1940, GUPTA 1950), in some *Odonata* (GEORGE 1929) and further in *Philaenus leucophthalmus* (*Homoptera*, GEORGE 1929) and in *Naucoris cimicoides* (*Heteroptera*, RAWAT 1939). One should cease to use the term *uterus bicornis* for those cases (see Table 1).

It is possible that the origin of the definitive oviducts is not identical in the insects, if in the species related to the above mentioned a mixed, ecto-mesodermal character of the discussed ducts had been stated, e. g. in *Phyllodromia supellectilium* SERV. (*Blattaria*, GUPTA 1950), in the family *Gryllidae* (GUPTA,

1950) in *Philaenus spumarius* L. (*Homoptera*, METCALFE 1932) and others. In RIES' opinion (1931) one should include here also *Mallophaga*.

The anterior portion of each paired oviduct of the third instar nymph is transformed in *Pediculus humanus* L., as in other *Anoplura*, into the „Ovarialampulle" (RIES 1931). That organ is developed by the enlargement of the oviduct cells, infected with symbionts, and the subsequent covering of the infected layer with epithelium, inside and outside. It does not seem that this process should basically differ in the *Mallophaga* and *Anoplura*, so one should verify RIES' observation, that in *Mallophaga* „Ovarialampulle" is formed by a dilation of the solid mesodermal cord, caused by the penetration of symbionts. In the same work on the symbiosis in *Mallophaga* and in *Anoplura* RIES expressed an opinion that the paired oviducts of the *Anoplura* are of ectodermal character. The material given in the present work seems to exclude such and interpretation.

The authors, describing the anatomy of the female genital system in *Anoplura*, distinguish so called accessory glands. As I have already shown, in *Pediculus humanus* L. they do not differ from the oviduct either histologically or functionally. Also in *Haematopinus tuberculatus* BURM. imagines the histological structure of the oviducts and the so called accessory glands is identical. Thus further maintenance of the term „accessory glands" seems superfluous. One should rather speak of the oviduct pocket enlarging the active surface of this organ.

c. The ovipositor

Imagines of many insect species possess uropods situated usually on the VIII and IX sternum, differently termed (gonapophyses, gonopods, valves), which play the role of an ovipositor. The ovipositor is composed of three pairs of valves, e. g. in *Orthoptera* s. str. (QADRI 1940). In some *Dermaptera* it is composed of only two pairs of valves, and in *Forficula* sp. they are altogether missing in the ontogenesis (QADRI 1940). One may then suppose that the only pair of uropods, which appears in some *Anoplura* behind the VIII sternum is a rudimentary ovipositor. The development of this organ in *Pediculus humanus* L., presented here, from the moment of its appearance to complete formation fully permits such an interpretation.

The development of the ovipositor in lice recalls to some extent the process, observed in *Hydroporus ferrugineus* Steph. (Heberdey 1931) in the formation of sclerites („Vulvarsklerite“). It does not, however, seem sufficient to consider the ovipositor in the lice a modified Vulvarsklerit.

The valves in *Pediculus humanus* L. appear as medially situated evagination of the sternal plate. Hence Kéler's interpretation (1938) must cause some doubts: he supposed that the valves in *Mallophaga* were of pleural origin. His opinion was grounded only on the examination of the imagines.

d. Male efferent ducts.

Vasa deferentia and the seminal vesicles in *Pediculus humanus* L. seem to derive entirely from the mesoderm. In that respect *Pediculus humanus* L. shows similarity to some *Amphibiotica*, *Orthopteroidea* and *Blattoidea* (Wheeler 1893, Else 1934, Qadri 1940) and to *Naucoris cimicoides* L. (*Heteroptera*, Rawat 1939).

The ejaculatory duct is bifurcated in many other insects and, as a result, the vasa deferentia in the imago are of mixed, ectomesodermal origin. Such is the case with many *Coleoptera* (Metcalfe 1932, Srivastava 1953) and in *Nosopsyllus fasciatus* Bosc. (*Siphonaptera*, Sharif 1937). Vas deferens, however, like the oviduct, may probably be derived from one or another germ layer even in comparatively closely related groups, for D'Rozario (1942) stated the incidence of both forms in *Hymenoptera*. Similarly in *Homoptera* Singh-Pruthi (1924) and Metcalfe (1932) held an opinion that the vasa deferentia of the imago had a mixed character, and George (1929) thought they were of mesodermal origin. The origin of the efferent ducts in the *Diptera* seems even less clear: Bodenstein (1950) states that both internal and external component parts are formed of the same imaginal disc.

The ejaculatory duct was but sporadically described as derived from two separate rudiments. And so e. g. Mehta (1933) found in *Pieris rapae* L. *(Lepidoptera)* paired invagination in the anterior wall of the genital pouch and a small cavity on the apex of the penis. The former subsequently develops into the anterior portion of the ejaculatory duct deprived of chitin, and the cavity on the penis apex lined with cuticle deepens till it connects with the anterior portion of the ejaculatory duct. The ejaculatory duct in *Pediculus humanus* L. arises of a single rudiment, growing into the body, as in the case with almost all described insects. Together with the growing penis its thin-walled part without the muscles, which has been overlooked in the descriptions of the development of male efferent ducts in other insects, is elongating in the direction opposite, than the muscular part of the ejaculatory duct. The non-muscular portion of the ejaculatory duct has been known from the anatomy of *Haematopinus tuberculatus* BURM., and in the *Heteroptera* imagines termed ductus seminis. In the male louse this duct in the resting position is loosely wound and long enough, as the penis pushing forward does not, as it seems, cause the shifting of the muscular ejaculatory duct and of seminal vesicles, connected with it.

e. Copulatory apparatus

From the moment when the penis appears, the processes lying externally to it and derived from the same uropods, are termed parameres in the present work. The parameres in such a sense have been known from the investigations on the ontogenesis of *Dermaptera* (QADRI 1940), *Hemiptera* (GEORGE 1929, METCALFE 1932, RAWAT 1939), *Siphonaptera* (SHARIF 1937), *Hymenoptera* (D'ROZARIO 1942), and others. NUSBAUM (1882) noticed that in the posterior part of the genital rudiment in *Mallophaga*, two lateral solid processes appear and develop into the „seitliche, akzessorische Stücke des Penis“. The comparison with the louse *Pediculus humanus* L. suggests a supposition that those processes are the rudiments of the parameres, whose existence in the imagines of the *Lipeuridae* was confirmed by MJÖBERG (1910).

The rudiments of the parameres are of paired origin in *Pediculus humanus* L., and their distal ends fuse already in the period when the penis separates: a secondary, unpaired, V-shaped formation is thus created. It is placed so, that its arms embrace the penis, and its sharp end is posteriorly directed.

Such a state persists in the imago. As the process of the parameres development in lice was unknown, they were given different names in imagines (see Table 2) most frequently stressing the function of clasping of both partners, or of the dilation of the vagina. The former of these functions — contrary to NUTTALL'S opinion (1917) — seems to be the most important one, on the anatomical background of *Pediculus humanus* L., and in connection with the characteristic position during copulation (the abdomina of the partners raised upwards vertically). Such a position is favoured in the males by the system composed of the specifically shaped VIII sternum, the walls of the genital chamber, the strong protractors of the basal plate, the basal plate itself and the parameres joined by a mobile connection with it and with the wall of the genital chamber. In the female the muscles of the VIII segment, and the sclerite in the sternal plate play an important role, as the male's parameres hook on the female's body above it.

From the investigations on the morphology of the imagines EWING (1932) inferred that the parameres in *Pediculus humanus* L. are reduced to small sclerites, appearing on the wall of the vesica penis and termed today statumen penis, together with its other chitin elements. EWING, however, considered the proper parameres as chitinized outgrowths of vesica penis and called them endomeres. In the light of the investigations presented here, EWING'S opinion should be corrected, the more so that in another species of *Anoplura*, namely in *Haematopinus tuberculatus* BURM., EWING has found V-shaped parameres.

In the initial stage of development, the penis of the lice is much smaller, than the rudiments of the parameres. GEORGE'S opinion (1929) that parameres may be the processes of the penis, cannot be supported.

The investigators were hitherto interested mainly in the question of the paired origin of the copulatory apparatus, and the ontogenetic development of the penis has been described only to such extent as it related to the question of the origin of the parameres. Hence the data on the differentiation of the component parts of the penis in heterometabolic insects are missing in the available literature. The anatomical description of a male „not yet sexually mature" of *Gyropus* sp. *(Mallo-*

phaga), given by Strindberg (1916), illustrates a certain stage, but does not add much to the knowledge of the postembryonic development of the copulatory apparatus in this insect.

The penis of *Pediculus humanus* L., arising from the basis of the gonopods, assumes in a short time a hook-like shape, characteristic for the imago. In the base of such a rudiment a circular fold — vesica penis — is formed, and much later the walls of the vesica penis become partly strongly sclerotized, forming a complex of small stiffening elements (statumen penis). In that period also the distal part of the penis becomes strongly sclerotized. Judging from Cumming's work (1916), the anatomy of the penis in the imagines of some *Mallophaga* (e. g. *Goniodes meleagridis*) is very similar. One should then consider, whether terming the distal, sclerotized part of the penis in both *Mallophaga* and *Anoplura* a „pseudopenis", after Cummings, is correct.

In the period when only vesica penis is formed, the genital pouch divides by a paired fold, invaginating from both sides into its lumen. The folds connect in the transversal plane and divide the genital pouch into two parts: dorsal and ventral. The penis is situated in the former, much larger one; the ventral part has been termed by Strindberg a „pocket of the basal plate" (Basalplattensack). The internal surface of this pocket, strongly flattened dorsoventrally, covers with cuticle. The basal plate is formed of the dorsal and ventral layers of the cuticle, sticking together. It is also interesting that the rudiments of the muscles, protracting the basal plate appear as paired formations still before the separation of the pocket of the basal plate.

4. Musculature

Many authors have discussed the abdominal musculature of the *Anoplura* imagines e. g. Landois (1865), Ströbelt (1883), Pavlovski (1908), Müller (1915), Nuttall (1917) and Ewing (1932), but nothing has been said about the muscles of the nymphs. The situation with the *Mallophaga* is similar: Blagoveshchenski (1937) described only the muscles of the imago of *Gyropus ovalis* N. In the present work the muscles of the ectodermal parts of the efferent system and the skeleton muscles in three posterior abdominal segments of the nymphs have been described.

It appears that from the beginning of postembryonic life the muscles, especially those of the last abdominal segment, are different in both sexes, namely distinctly much weaker in the male. So, the IX segment in the male is, in the respect of muscles, prepared for reduction, which is to take place in the third moulting, already in such an early stage of development.

In general the topography of the skeleton muscles of the genital segments in *Pediculus humanus* L. persists without major changes throughout the nymphal period. Only some few skeleton muscles undergo a dislocation and start to serve the copulatory apparatus.

a. Muscles in the female

At the time, when the ectodermal genital rudiments are appearing, the first nymph is furnished with the longitudinal ventral and dorsal muscles of the VI, VII and VIII segments, placed symmetrically on both sides of the medial plane. During the second moulting the ventral muscles of the VII segment disappear, and at the same time the anterior insertions of the analogous muscles of the VIII segment are shifted anteriorly, approximately up to the line connecting the spiracles of the VII segment. Thanks to these processes the oviduct is liberated from under the muscle, which hitherto connected it with the VII segment, and the border of the VIII sternum is shifted anteriorly, which causes the change of shape of this sternum. The figures given by GUPTA (1950) concerning *Orthopteroidea*, showing the anatomical relations in the first and third instar nymphs of *Gryllodes sigillatus* WALK. and in the first instar nymph of *Schistocerca gregaria* FÖRSK., indicate that the oviduct is situated under the ventral muscle also in those cases. Fig. 1 from the same author's work on *Dysdercus cingulatus* FABR. (1951) shows the possibility of persistence of such a situation in the imago of this heteropterous insect. FORD (1923) has made similar observations in *Orthopteroidea*.

The ventral muscle of the VIII segment is being included in the copulatory organ of the female and corresponds to the muscle described in the louse imago by Nuttall (1917) and by Blagoveshchenski (1931) in *Mallophaga* under the term of m. retractor dorsalis vaginae. Probably the earlier authors also observed this muscle (Landois 1865, and Pavlovski 1908 — in *Pediculus humanus* L., and Ströbelt 1883 in *Haematopinus tenuirostris* Burm.). Ford (1923) stated that, in *Orthopteroidea*, the genital system of the female imago makes use of some skeleton muscles.

Among the muscles of the uterus itself and of the vagina mm. constrictores uteri, mm. retractores uteri and mm. retractores ventrales vaginae have been observed.

So the scheme of the musculature of the female efferent ducts in *Pediculus humanus* L. corresponds with small changes to that presented by Nuttall (1917) for lice and is very similar to what Blagoveshchenski (1931) has found in *Gyropus ovalis* N. imago *(Mallophaga)*: m. retractor dorsalis vaginae connects the anteriorly protruding part of the VIII sternal plate with the dorsal wall of the vagina near the border of the VIII and IX segments; m. retractor uteri extends between the lateral walls of the uterus and the VII sternum, and m. retractor ventralis vaginae — from the ventrolateral wall of the vagina to the VIII sternal plate. The mm. dilatatores vaginae, noticed in *Gyropus ovalis* are missing in *Pediculus humanus* L. All the muscles of the female genital ducts are derived from mesodermal elements, which accompany the developing ducts, and not from dislocation of the skeleton muscles, with the sole exception of the m. retractor dorsalis vaginae. Also the histologic structure of these muscles indicates it.

b. Muscles in the male

In the first instar nymph, during the period when the ectodermal rudiments are appearing, the longitudinal ventral and dorsal muscles of the VI, VII and VIII abdominal segments, situated symmetrically in relation to the medial line are clearly visible. As the copulatory apparatus is growing posteriorly, the muscles of the VI and VII segments are disappearing on the ventral side, while the dorsal ones remain. As the border between the VIII and IX sternum is shifting to the dorsal side of the abdomen, the longitudinal ventral muscles of the VIII segment are being included in the copulatory apparatus. It is now inserting to the anterior wall of the genital chamber, which should for that reason be recognized as the IX sternum. This muscles, together with others retractors, contribute to retracting of the copulatory apparatus and corresponds, as it seems, to what NUTTALL (1917) described as m. flexor of the dilator in lice, and BLAGOVESHCHENSKI (1931) as mm. retractores of the genital chamber in *Gyropus ovalis* N. I am inclined to retain this term, correcting only the information found in literature, concerning the anterior insertion of this muscle: it is situated in the anterior part of the VIII sternal plate, on the sides of the copulatory apparatus.

Among the proper muscles of the male copulatory apparatus the following muscles, mentioned by NUTTALL have been found in *Pediculus humanus* L.: mm. protractores of the basal plate, mm. retractores vesicae penis, and mm. retractores of the basal plate. The similar conditions are found in the biting louse *Gyropus ovalis* (BLAGOVESHCHENSKI, 1931).

All the muscles of the male copulatory apparatus, with the exception of mm. retractores of the genital chamber are formed during the postembryonic life in connection with the developing copulatory apparatus, and differ histologically from the neighbouring skeleton muscles. So in lice the muscles serving to protracting the copulatory apparatus (mm. protractores) are not formed by dislocation, during ontogenesis, of the respective skeleton muscles, as in the case with some *Orthoptera*, accoring to FORD (1923), who drew such an opinion from comparative investigations on imagines.

Contrary to MÜLLER'S opinion (1915) which has not hitherto been corrected, the male of *Pediculus humanus* L. has no ventral muscles in the VI abdominal segment. EWING'S proposal (1932) to apply the term „muscles for flexing endomere“ for m. retractor vesicae penis does not seem well grounded. Apart from discussing the term „endomere“ here (which, as I have shown speaking of the development of the copulatory apparatus, corresponds to the parameres), one must state that the muscle in case is not inserted to the parameres. The change of position of the parameres, the flexing, in *Pediculus humanus* L. is done passively, during the protraction of the copulatory apparatus. The flexing is a result of mutual shifting of the basal plate and the wall of the genital chamber, connected with the parameres. Moreover, NUTTALL had already proposed the term „m. flexor of the dilator“ (where „dilator“ designates the parameres), the term was to be applied, however, to some other muscle.

5. Morphological changes in the sternal plate

The migration of the uropods towards the front is a well known phenomenon in the development of the male efferent system, e. g. in *Orthopteroidea* (WHEELER 1893, ELSE 1934, QADRI 1940), *Siphonaptera* (SHARIF 1937) and in others, and it is anatomically connected with the invagination of the genital pouch, as in the case with *Pediculus humanus* L. In *Melanoplus differentialis* (THOMAS?) (ELSE 1934, p. 594) the invagination occupies the whole width of the X segment. In many insects, however, the genital pouch invaginates in the middle of the width of the segment so that the orifice of the pouch is very small. The authors describing the development of the efferent system usually overlook its topographic connections with the skeleton muscles of the genital segments. The present work shows that the ventral muscles of the VIII abdominal segment in lice extend between the anterior edge of the VIII segment and the anterior edge of the IX segment, i. e. according to the insect pattern (see SNODGRASS 1935). The posterior insertion of those muscles in the louse nymphs lies at the level of the orifice of the genital invagination, both in the male and female nymphs, and it is shifted simultaneously with this orifice; the dorsoventral lateral muscles are not visibly shifted. That means that only a narrow, medially located stripe of the IX sternal plate participates in the formation of the genital pouch. Such a state persists in the ontogenesis of the males of *Pediculus humanus* L., in the females, however, the development of the vagina requires a secondary invagination of the lateral parts of the VIII sternal plate during the last moulting.

The shape of the sternal plates in the genital region also changes. Till the third moulting period the anterior and posterior segment borders are marked by the lines connecting the respective furrows between the neighbouring paratergal plates. The topography of the skeleton musculature and the distribution of the setae on the ventral side of the louse abdomen indicate that those lines are approximately straight. In the third instar nymphs, and especially during the third moulting one may, however, observe the insertions of certain muscles shifting far behind the drawn borders. The comparative morphology assumes that the insertions of the muscles are fixed, so the occuring changes should be considered as a proof of the changes of the sternum shape. The borders, thus drawn, of the genital segments, and especially the border between the VII and VIII sternum in the female and that between the VIII and IX sternum in the male, do not correspond to the distribution of the setae on the ventral surface of the body. My own observations and the data obtained from literature (e. g. Ferris 1951) agree that the distribution of the setae would suggest the „rectangular“ shape of the sternum. In many Arthropods the distribution of the setae is considered an important topographic mark in the case of displacements. If such should be the case, the situation in *Pediculus humanus* L. described here would cause some difficulties in interpretation. It is possible that the discrepancy between the shifting of the muscle insertions and the stability of the setae distribution may be partly explained by the fact that only the medial part of the sternum is elongated, while the lateral parts with the insertions of the respective dorsoventral muscles do not show any dislocations in postembryonic life. It is also possible that the discrepancy, discussed here, partly belongs to the category of differences between the external and internal segmentation of the body, and, being but a secondary one, does not exclude the proposed interpretation, presented here.

6. Migration of the genital opening

In the louse males (pl. LXXXIII, fig. 14) one observe the migration of the genital opening from the ventral, to the dorsal side of the body during ontogenesis. The observation of the muscle topography in the successive instar nymphs has, however, shown that the relative situation of the genital opening does not undergo any change and remains between the VIII and IX sternum. That lack of migration of the genital opening in the males is a common phenomenon in insects (GUSTAFSON 1950). That is why one should with some reservations accept BLAGOVESHCHENSKI'S information (1956) stating that the male ectodermal ducts in *Columbicola* sp. *(Mallophaga)* are formed in the IV abdominal segment.

In the female ontogenesis, however, the posterior shifting of the genital opening of some one or two segments is a rule. It usually occurs by fusion of the hypodermal invaginations, formed in the successive segments, and the subsequent disappearance of the opening already superfluous. In the case of *Dysdercus cingulatus* (*Heteroptera*, GUPTA 1951) the gonopore migrates thus from its initial position behind the VII sternum to the IX sternum. As this process is progressing, the initially independent orifice of the spermatheca and that of the accessory gland migrate to the wall of the common oviduct. In the ontogenetic development of *Philaenus spumarius (Homoptera)* METCALFE observed (1932) the migration of the gonopore from the VII to the VIII segment, RAWAT (1939) noticed the same in *Naucoris cimicoides*, and myself in *Pediculus humanus* L. In *Philaenus spumarius*, however, the accessory gland arises and remains active, having its orifice behind the IX sternum, while in the remaining two species no such gland appears.

The gonopore in the *Trichoptera* (DODSON 1935) and in *Siphonaptera* (*Nosopsyllus fasciatus* BOSC., SHARIF 1937) migrates towards the posterior in a different way: a median hypodermal thickening is formed between the genital opening and its new site, and the opening is gradually shifted to its new position.

SUMMARY

1. Body and head lice *Pediculus humanus* L. were investigated. The genital efferent system and the skeleton musculature of the genital segments were examined using the methods generally applied in insect embryology and histology.

2. Paired gonads were found in the embryo (ovary composed of five ovarioles, or bi-lobed testicles), as well as solid mesodermal cords, constituting rudiments of the efferent ducts. Thus the oviducts, the vasa deferentia and seminal vesicles of the imago are of mesodermal origin.

3. In the first instar nymph, unpaired hypodermal invaginations appear in the females behind the VII and behind the VIII segments (oviducal and spermathecal invaginations), which connect early into one invagination , and in the males — behind the VIII segment (genital pouch).

4. Deep inside the hypodermal invagination, on the side directed towards the ampullae a pair of processes is formed in both sexes, into which the mesoderm penetrates. The author considers them uropods.

5. In the males another pair of processes appears transitorily in the hypodermal invagination. They may be a remainder of reduced segment. If this is indeed the case, the genital opening in the males would be situated in the position normal for insects, i. e. behind the IX sternum.

6. The uropods of the female lice develop into the genital appendages, which the author considers a rudimentary ovipositor. This way of ovipositor formation characteristic for lice has not been known in other insects till now.

7. Parameres and the penis develop from uropods in the males.

8. The parameres are paired and their distal parts fuse very early, building a V-shaped formation.

9. The paired origin of the penis in lice may be understood only as growing from the basis of two uropods. Vesica penis in the form of a circular fold, the basal plate, and the small stiffening formations (statumen penis) appear successively during the ontogenetic development of the penis. Its proper musculature is developing at the same time.

10. The vasa deferentia in the first instar nymph are forming a loop around the ventral muscles of the VIII segment and they remain there, which proves the anterior migration of the ampullae. In the female the oviducts are liberated from under the ventral muscles in connection with the reduction of the skeleton muscles in the third instar nymph.

11. Ampullae and the corresponding appendages belong to the different segments in *Pediculus humanus* L., which may be the result of advanced dislocations, necessary because of the reduction of the abdominal segments to the number of nine.

12. The ventral skeleton muscles of the VIII abdominal segment are included into the copulatory apparatus in postembryonic life, and they act as muscles retracting the genital chamber in the male and as *m.* retractor dorsalis vaginae in the female.

13. In the ontogenesis of the male *Pediculus humanus* L. the genital opening migrates from ventral to dorsal side of the abdomen, without changing its relative position between the VIII and IX segments. The female genital opening migrates posteriorly to the next segment; it is a result of fusion of the respective hypodermal invaginations.

Abbreviations: amp — ampullae, dej — ejaculatory duct gd — accessory gland, k — hypodermal invagination, m — lateral muscles of the VIII segment, oa — „Ovarialampulle“, ovd — oviduct, p — penis, pa — parameres, ut — uterus, us — rudimentary uropods, u — uropods, vag — vagina, vd — vas deferens, vsem — seminal vesicles, w — „lip“.

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STRESZCZENIE

Rozwój płciowego układu wyprowadzającego owadów poznany był lepiej jedynie w grupach, zajmujących kluczową pozycję w rodowodzie *(Amphibiotica*, *Orthopteroidea* i *Blattoidea)*; w pozostałych grupach owadów był słabo poznany (np. u *Mallophaga* — jedynie z pracy Nusbauma, 1882) lub, jak u *Anoplura*, dotąd nie opracowany.

Autor objął badaniem wszy odzieżowe i głowowe *Pediculus humanus* L. i opracował drogi wyprowadzające układu płciowego oraz umięśnienie szkieletowe segmentów płciowych, używając metod powszechnie stosowanych w embriologii i histologii owadów.

W zarodku można było znaleźć parzyste gonady (jajnik złożony z 5 cewek wzgl. dwupłatowe jądro) oraz lite pasma mezodermalne biegnące od gonad ku tyłowi. Spostrzeżenie to pozwala sprostować cytowaną dotąd w literaturze opinię Schölzela (1937), jakoby w zarodku *Anoplura* i *Mallophaga* gonady i ich przewody jeszcze się nie wyodrębniały, i jakoby następowało to u wszy dopiero w życiu pozarodkowym. Dalszy los litych pasm mezodermalnych wskazuje, że jajowody, nasieniowody i pęcherzyki nasienne postaci dorosłej są elementami mezodermalnego pochodzenia.

W okresie I nimfy, u obu płci pojawiają się w okolicy płciowej nieparzyste, hypodermalne wpuklenia. Jeżeli przyjąć za Ferrisem (1951), że odwłok wszy składa się z 9 segmentów, to wspomniane wpuklenia pojawiają się u samic za VII i za VIII segmentem i wcześnie łączą się w jedno wpuklenie z ujściem za VIII segmentem. Jest to więc proces przebiegający podobnie jak u innych owadów i prowadzący do zlania się wpuklenia jajowodowego ze spermatekalnym. Natomiast u samców nieparzyste wpuklenie powstaje za VIII segmentem, a więc w miejscu dla owadów nie typowym.

Głęboko we wpukleniu hypodermy, po stronie zwróconej ku mezodermalnym ampułkom, tworzy się u obu płci para wyrostków, do których wnika mezoderma. Autor uważa je za uropody. U samców, we wpukleniu hypodermalnym pojawia się przejściowo druga para wyrostków. Być może jest to ślad zredukowanego segmentu; w takim przypadku płciowy otwór męski znalazłby się za IX segmentem, a więc na pozycji dla owadów normalnej i takiej, na jakiej mieści się on u imagines wielu *Mallophaga*.

Uropody samic wszy przekształcają się stopniowo w przydatki płciowe, będące jak się wydaje, szczątkowym pokładełkiem. Sposób jego tworzenia się, a mianowicie zawiązywanie się głęboko we wpukleniu hypodermy i późniejsze wysuwanie się na zewnątrz z jednoczesnym pojawianiem się tzw. wargi, przebiega u wszy odmiennie niż u innych owadów. Z uropodów samców wszy powstają paramery i penis.

Paramery zakładają się parzyście i bardzo wcześnie zrastają się w nieparzysty twór kształtu rzymskiej piątki („V“).

Parzystość zawiązków prącia u wszy może być rozumiana jedynie jako wyrastanie prącia z podstawy dwóch paramerów. W rozwoju ontogenetycznym prącia pojawia się wpierw stożek, przebity przewodem wytryskowym, i prędko przybiera haczykowaty kształt charakterystyczny dla końcowej części prącia postaci dorosłej. Następnie pojawia się okrężny fałd, stanowiący zawiązek części pęczniejącej (vesica penis). Ściany tej części podlegają miejscami silnej sklerotyzacji, wykształcając zespół drobnych elementów usztywniających (statumen penis). W tym okresie następuje również silna chitynizacja końcowego odcinka prącia. Jednocześnie kieszeń płciowa dzieli się na 2 piętra: grzbietowe i brzuszne. W grzbietowym, znacznie obszerniejszym, mieści się penis, a piętro brzuszne wytworzy płytkę bazalną. W tym okresie rozwija się też umięśnienie własne aparatu kopulacyjnego.

W I nimfie nasieniowód owija się dookoła brzusznego mięśnia podłużnego VIII segmentu i tak już pozostaje, świadcząc o migracji ampułek do przodu. Analogiczny przewód samicy, tzn. jajowód, w związku z redukcją umięśnienia szkieletowego III nimfy wyswobadza się, zacierając ślad przynależności ampułki do określonego segmentu.

Ampułki i odpowiadające im odnóża należą u *Pediculus humanus* L. do różnych segmentów. Trudno powiedzieć, czy taki stan rzeczy jest dostatecznym argumentem na korzyść teorii Gustafsona (1950). Wydaje się raczej, że jest to u wszy rezultatem daleko posuniętych przemieszczeń zarówno uropodów, jak i ampułek, koniecznych wobec zmniejszenia ilości segmentów do dziewięciu, i być może wiąże się z coraz częściej podnoszonymi wątpliwościami co do pełnej homologii narządów płciowych *Orthoptera* z resztą wyższych owadów.

Ektodermalne odcinki przewodów wyprowadzających żeńskich (uterus i vagina) oraz męskich (ductus ejaculatorius) zakładają się u *Pediculus humanus* L. nieparzyście. W odniesieniu do przewodu wytryskowego zgadza się to z obserwacjami, jakie poczynił Nusbaum (1882) nad rozwojem *Mallophaga*, natomiast ektodermalne drogi żeńskie, zdaniem Nusbauma, zakładają się tam parzyście. Bliższe porównanie opisowej części pracy Nusbauma z przedstawionym w niniejszej pracy materiałem faktycznym dotyczącym *Pediculus humanus* L., poparte zaznaczającym się wyraźnie podobieństwem całej ontogenezy *Mallophaga* i *Anoplura*, nasuwa wątpliwości co do słuszności argumentów Nusbauma.

Jednocześnie z rozwojem elementów ektodermalnych kształtuje się też umięśnienie, i to zarówno umięśnienie własne ektodermalnych części dróg wyprowadzających układu płciowego, jak i umięśnienie szkieletowe końcowych segmentów odwłoka. Na specjalną uwagę zasługuje przemieszczanie się u obu płci brzusznych mięśni VIII segmentu. Rezultatem tego procesu jest włączenie mięśni szkieletowych VIII segmentu w obręb aparatu kopulacyjnego: u samca dawne szkieletowe mięśnie brzuszne VIII segmentu działają jako mięśnie wciągające przedsionek płciowy, a u samicy — jako retractores dorsales vaginae. Boczne mięśnie szkieletowe nie podlegają takim przemieszczeniom.

Zachowanie się umięśnienia szkieletowego w ontogenezie ułatwia poprawną interpretację zmian, jakim podlegają w tym czasie końcowe dwa segmenty odwłoka wszy. U samców VIII płytka sternalna wydłuża się i sięga u imago aż na grzbietową stronę ciała, IX tergum jest niewielkie i kończy się tuż za odbytem, a IX sternum — co najmniej w znacznej części — buduje przedsionek płciowy postaci dorosłej. Otwór płciowy męski przesuwa się co prawda z brzusznej na grzbietową stronę ciała, jednak nie zmienia się przy tym jego względne położenie na granicy VIII i IX segmentu. Żeński otwór płciowy mieści się po brzusznej stronie odwłoka, między VIII i IX segmentem, a IX płytka sternalna bierze pewien udział w budowaniu sklepienia pochwy.

Autor stosuje terminologię wynikającą z rozwoju ontogenetycznego, a dla jasności obrazu zestawia ją w 2 tabelach z tą, która dotyczy narządów płciowych dorosłych postaci *Phthiraptera*. Praca podaje też niektóre szczegóły, nieznane dotąd w anatomii i histologii wszy ludzkiej.

РЕЗЮМЕ

Развитие выводной половой системы у насекомых сравнительно хорошо изучено было только у групп, занимающих исходное место в системе (*Amphibiotica, Orthopteroidea* и *Blattoidea*); у остальных групп было слабо изучено (к. н. у *Mallophaga*, исключительно по работе Nusbaumа, 1882) или, как например у *Anoplura*, вовсе не было обработано.

Автор исследовал вши: платяную и головную *Pediculus humanus* L. и разработал выводные пути половой системы, а также мышечную систему половых сегментов, применяя при этом методы, обычно употребляемые в эмбриологии и гистологии насекомых.

В зародыше найдены были парные гонады (яичники, сложенные из пяти каналов или двудольные семенники) и сплошные мезодермальные тяжа, проходящие от гонад по направлению к заду. Наблюдение это позволяет исправить цитированное до настоящего времени мнение Schölzela (1937), утверждавшего, что в зародыше *Anoplura* и *Mallophaga* гонады и их каналы еще не обособляются и что у вшей это обособление наступает лишь в позднейшей фазе развития. Дальнейшее развитие сплошных мезодермальных каналов показывает, что яйцеводы, семяпроводы и семенные пузырьки у зрелых особей, это элементы мезодермального происхождения.

В период первой нимфы, у обоего пола появляются в половой окрестности гиподермальные впячения. Если принять, следуя за Ferrisom (1951), что брюшко вши состоит из 9 сегментов, то вышеупомянутые впячения появляются у самки за седьмым и за восьмым сегментами. Оба эти впячения очень рано сливаются в одно впячения с исходным за восьмым сегментом. Процесс этот проходит подобно, как и у других насекомых. Ведет он к слиянию яйцеводного впячения со сперматекальным. У самцов непарное впячения появляется за восьмым сегментом, значит, в месте, нетипичным для насекомых.

Глубоко в гиподермальном впячении, по стороне, обращенной к мезодермальным ампулам, образуется у обоего пола пара выпячений, куда проникает мезодерма. Автор считает, что это уроподы. У самцов в гиподермальном впячении появляется временно другая пара выпячении. Возможно, что это след редуцированного сегмента; в таком случае половое отверстие у самца находилосьбы на девятом сегменте, т. е. в таком месте, которое является нормальным для насекомых и на котором оно находится у многих зрелых особей *Mallophaga*.

Уроподы самок вши постепенно превращаются в половые придатки, которые, кажется представляют собой рудиментарный яйцеклад. Способ его возникновения, а именно: зарождение глубоко в гиподермалном впячении и позднее выдвигание наружу с одновременным появлением т. н. губы, пробегает у вши иначе, чем у других насекомых. Уроподы самца превращаются в парамеры и пенис.

Парамеры образуются попарно и очень рано сростаются в непарное образование в форме римской пятерки („V“).

Образование пениса из парных зачатков надо понимать, как вырастание его из основания двух парамеров. В онтогенетическом развитии пениса, сперва образуется конус, пробитый семеизвергательным каналом и скоро принимает форму крючка, характерную для концевой части пениса у зрелой особи. Далее появляется окружной фалд, составляющий зачаток разбухающей части *(vesica penis)*. Стенки этой части в некоторых местах сильно склеротизируются, образуя комплекс мелких элементов, придающих твердость пенису *(statumen penis)*. В этом периоде проявляется также сильная хитинизация концевой части пениса. Одновременно с этим, половой карман *(genital chamber)* разделяется на два яруса: спинной и брюшной. В спинном, более обширном ярусе помещается пенис, а брюшной ярус образует базальную плитку. В этом периоде развивается также мышечная система генитального аппарата.

У первой нимфы, семяпровод обвивается около продольной брюшной мышцы восьмого сегмента и так остается, свидетельствуя о миграции ампул вперед. Аналогичный канал у самки, то есть яйцевод, в связи с редукцией мышечной системы скелета у третьей нимфы, освобождается и затирает при этом след принадлежности ампулы к вышеописанному сегменту.

Ампулы и соответствующие им конечности принадлежат у *Pediculus humanus* L. к разным сегментам. Трудно сказать, насколько такое положение является достаточным аргументом в пользу теории Gustafsona (1950). Вернее, что у вши это будет результатом далеко поступивших перемещений уроподов и ампул, перемещений 1, необходимых по причине уменьшенного числа сегментов до девяти. Вероятно, это стоит в связи со все чаще выдвигаемым сомнением относительно полного соответствия половых органов *Orthoptera* с таковыми у остальных высших насекомых.

Эктодермальные части выводных путей у самок *(uterus* и *vagina)* и у самцов *(ductus ejaculatorius)* образуются у *Pediculus humanus* L. непарно. По отношении к семеизвергательному каналу, это согласно с наблюдениями, сделанными Nusbaumom (1882) над развитием *Mallophaga*, тогда как женские эктодермальные пути, по мнению Nusbauma, основываются попарно. Более подробное сравнение текста Nusbauma с представленным в настоящей работе фактическим материалом, касающимся *Pediculus humanus* L. поддержанного отчетливо зарисовывающимся сходством целого онтогенеза *Mallophaga* и *Anoplura* выдвигает сомнения относительно правильности утверждений Nusbauma.

Одновременно с развитием элементов эктодермы, образуетса и мускулатура, не только эктодермальных частей половых выводных путей, но и мускулатура скелета концевых сегментов брюшка. Особенно следует обратить внимание на перемещение у обоего пола брюшных мускулов восьмого сегмента. Результатом этого процесса является присоединение скелетовых мышц восьмого сегмента к области генитального аппарата: у самца, прежние скелетовые, брюшные мышцы восьмого сегмента действуют, как мышцы втягивающие половое атричм; у самки действуют они, как *retractores dorsales vaginae*. Боковые мышцы не подвержены такому перемещению.

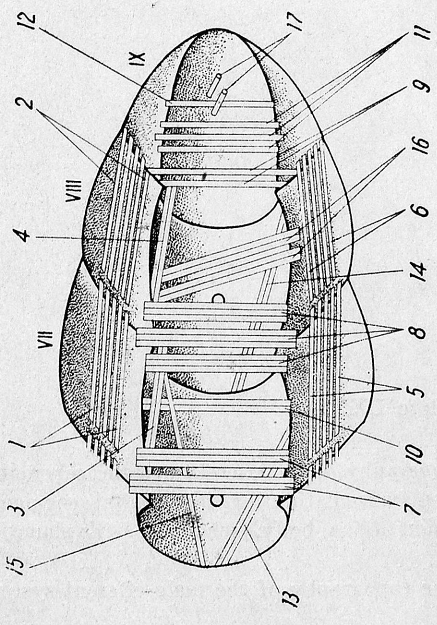
Сохранение скелетовой мышечной системы в онтогенезе облегчает правильное толкование перемен, каким подвергаются в это время два концевых сегмента брюшка вши. У самцов восьмая стернальная пластинка вытягивается и доходит у зрелой особи до спинной стороны тела; девятое тергум небольшое, оно кончается непосредственно за анальным отверстием, а девятое стернум, по крайней мере в бóльшей части, образует переднюю часть полового аппарата взрослой особи. Хотя половое отверстие у самца перемещается с брюшной стороны тела на спинную, однако не изменяется его относительное положение на границе между восьмым и девятым сегментом. Женское половое отверстие помещается на брюшной стороне тела между восьмым и девятым сегментом, а девятая стернальная пластинка принимает известное участие при образовании свода влагалища.

Автор употребляет терминологию, вытекающую из онтогенетического развития и для бóльшей ясности сопоставляет ее в 2 таблицах с той, которая относится к половым органам взрослых особей *Phthiraptera*. В настоящей работе приведены некоторые подробности, неизвестные до настоящего времени в анатомии и гистологии *Pediculus humanus* L.

PLATES

Plate LXXX

Fig. 1. First instar nymph. The topography of the female efferent system, schematic.
Fig. 2. Second instar nymph. The topography of the female efferent system, schematic.
Fig. 3. Female nymph. Skeleton musculature of the genital segments during the second moulting. The view from the inside of the body, schematic. (Explanation in the text).
Fig. 4. Third instar nymph. The topography of the female efferent system, schematic.



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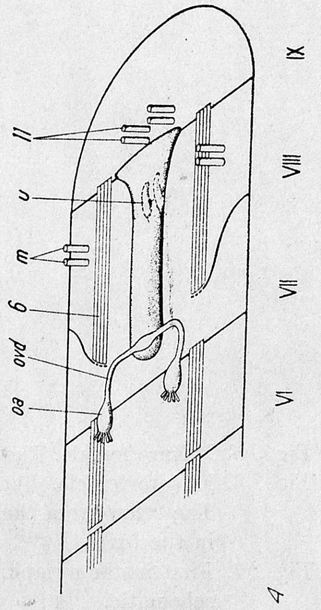

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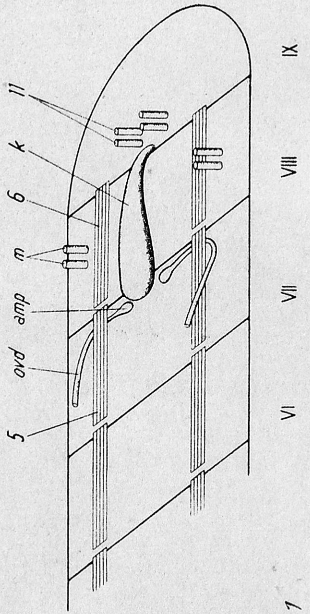

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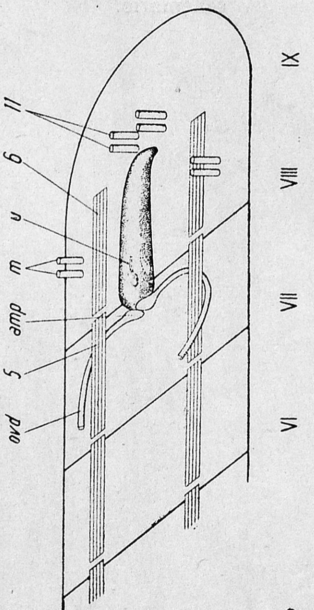

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Auctor del.
F. Piotrowski

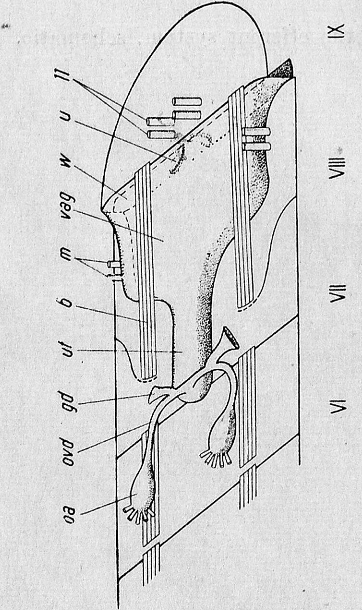
Plate LXXXI

Fig. 5. Mature female. The topography of the efferent system, schematic.

Fig. 6. Mature female. Skeleton musculature of the genital segments. The view from the inside of the body, schematic. (Explanation in the text)

Fig. 7. First instar nymph. The topography of the male efferent system, schematic.

Fig. 8. Second instar nymph. The topography of the male efferent system, schematic.



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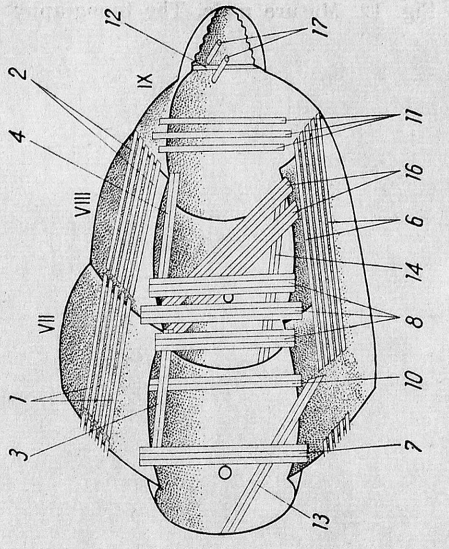

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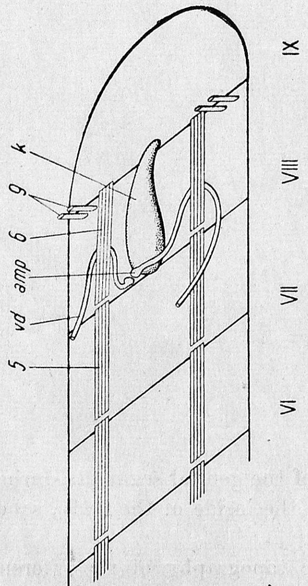

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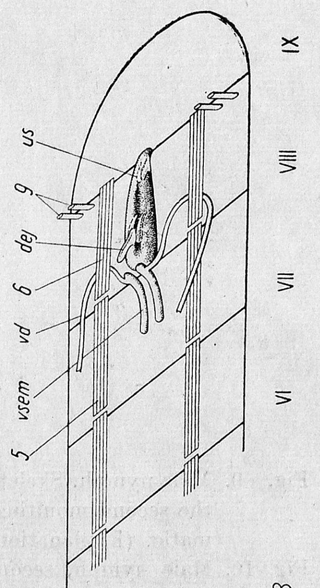

8

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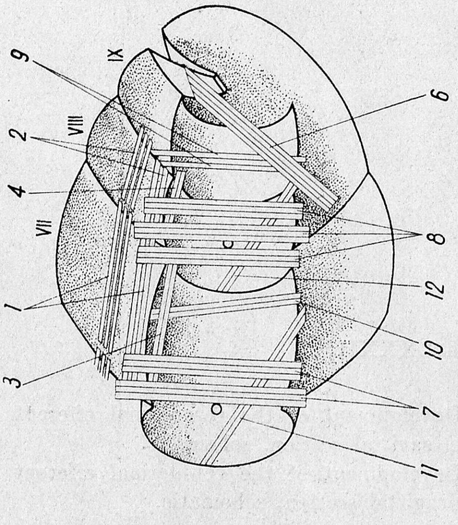
Plate LXXXII

Fig. 9. Male nymph. Skeleton musculature of the genital segments during the second moulting. The view from the inside of the body, schematic. (Explanation in the text).

Fig. 10. Male nymph, second moulting. The topography of the efferent system, schematic.

Fig. 11. Mature male. Skeleton musculature of the genital segments. The view from the inside of the body, schematic. (Explanation in the text).

Fig. 12. Mature male. The topography of the efferent system, schematic.



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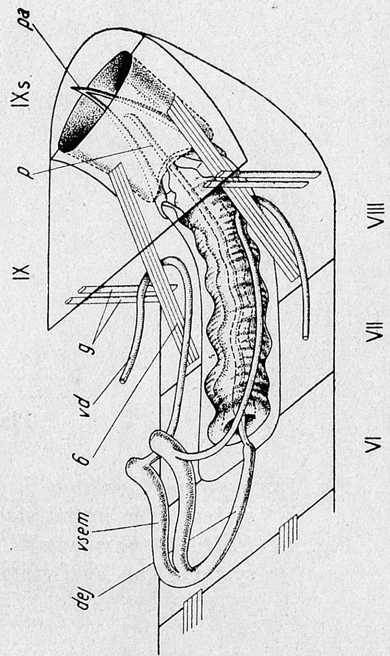

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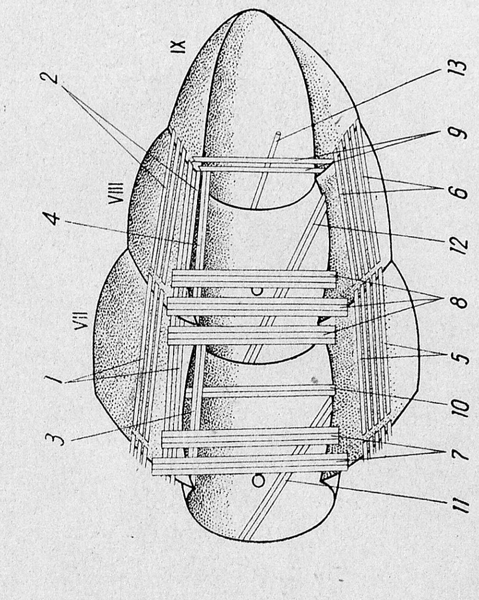

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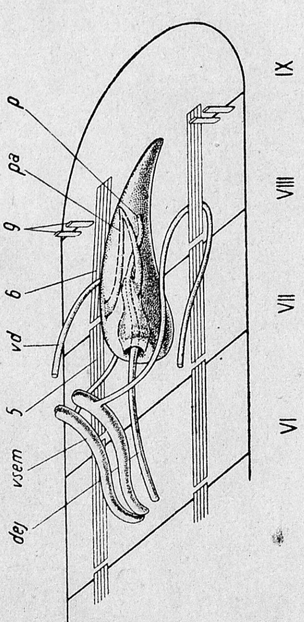

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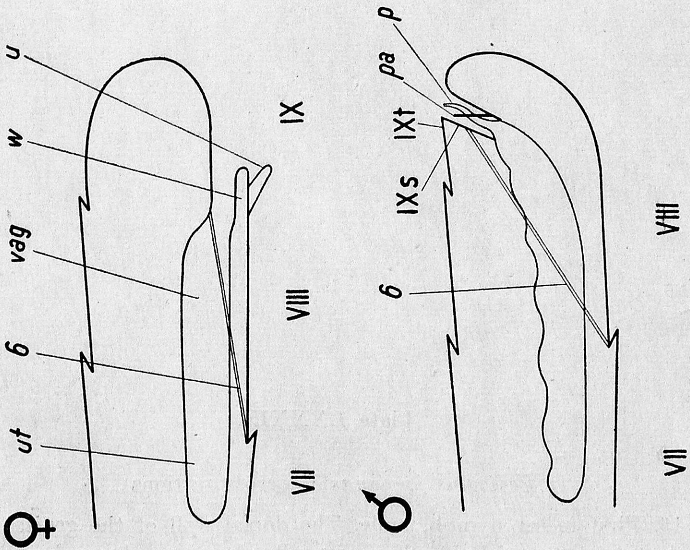
Plate LXXXIII

Fig. 13. *Pediculus humanus* L. Development of the ectodermal efferent system. The initial stage, sagittal section, schematic.

Fig. 14. *Pediculus humanus* L. Development of the ectodermal efferent system. The final stage, sagittal section, schematic.



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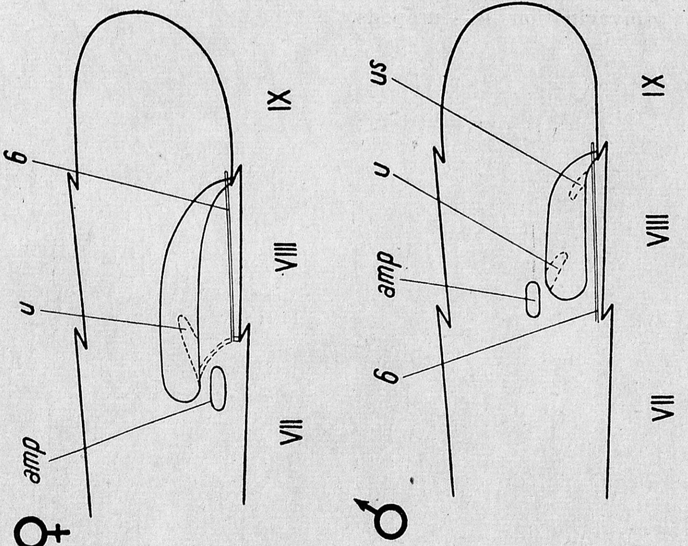

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Plate LXXXIV

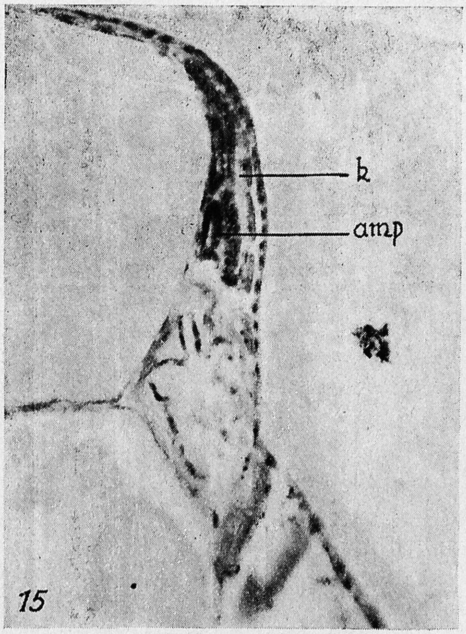
Pediculus humanus L., cross sections

Fig. 15. First instar nymph, male. The dorsal wall of the genital pouch begins to thicken. *amp* — ampulla, *k* — genital pouch.

Fig. 16. Second instar nymph, male. Rudimentary uropods (*us*) in their maximum length. *k* — genital pouch.

Fig. 17. Third instar nymph, male. *dej* — ejaculatory duct, *mb* muscles protracting the basal plate, *p* — penis, *pa* — parameres.

Fig. 18. First instar nymph, female. *amp* — ampulla, *k* — hypodermal invagination, *u* — uropods.



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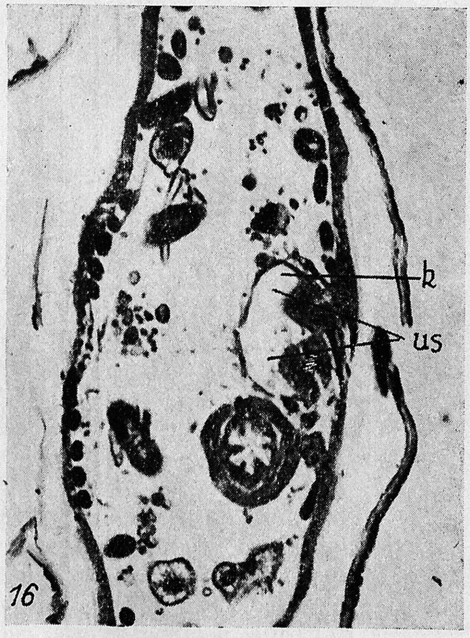

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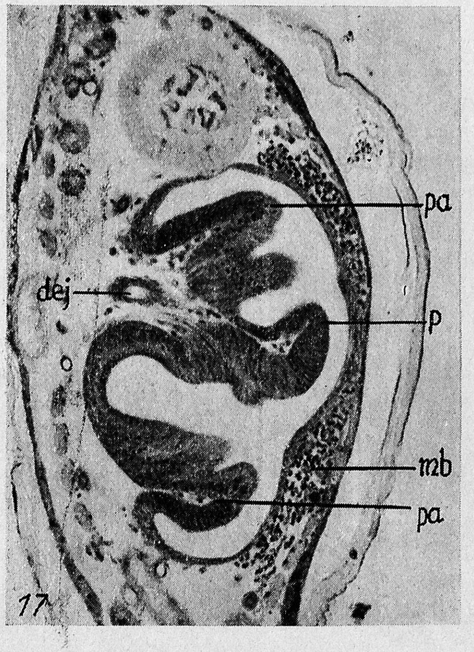

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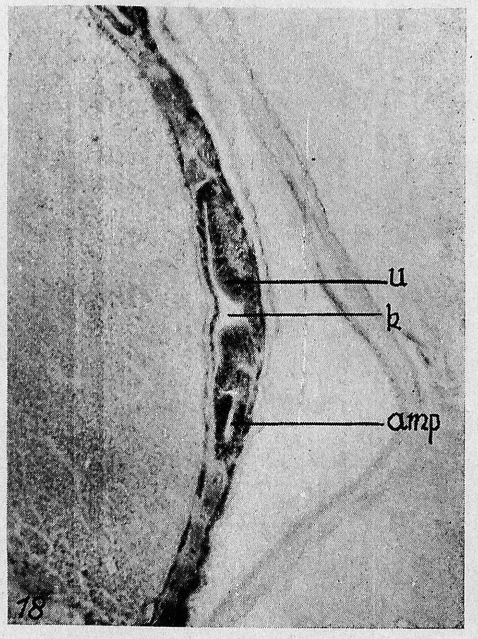

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Plate LXXXV

Pediculus humanus L., cross sections

Fig. 19. Third instar nymph, female. The paired oviducts (*ovd*) after fusion, „Ovarialampulla“ (*oa*) begins to be formed.

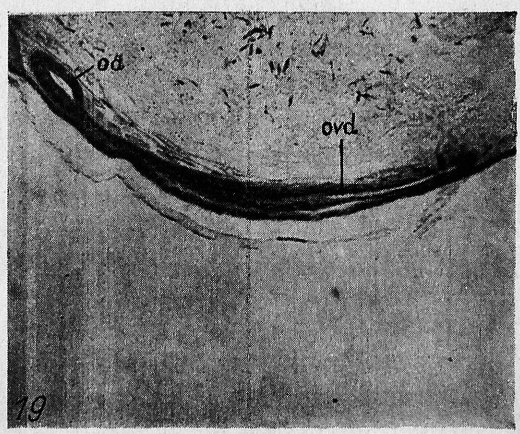
Fig. 20. Third instar nymph, female. *gd* — oviduct pocket („accessory gland“, *ut* — anterior portion of the uterus.

Fig. 21. Third moulting, female. *mc* — m. constrictor uteri, *ut* — uterus.

Fig. 22. Third moulting, female. *vag* — vagina.

Fig. 23. Third moulting, male. *mb* — muscles protracting the basal plate, *mg* — muscles retracting the genital chamber, *mp* — muscles within the parameres, *p* — penis.

Fig. 24. Young male, transversal section. *mb* — muscles protracting the basal plate, *mr* — muscles retracting the basal plate, *mv* — muscles retracting the vesica penis, *vp* — vesica penis.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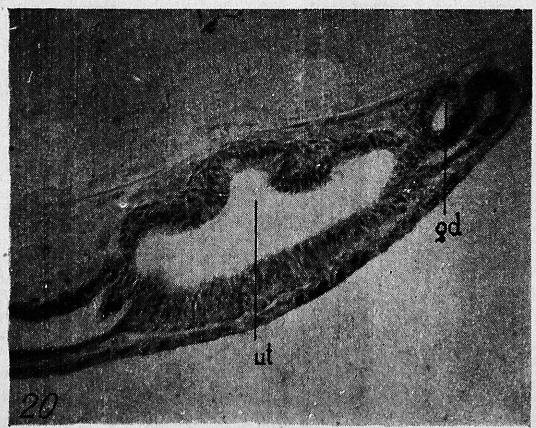
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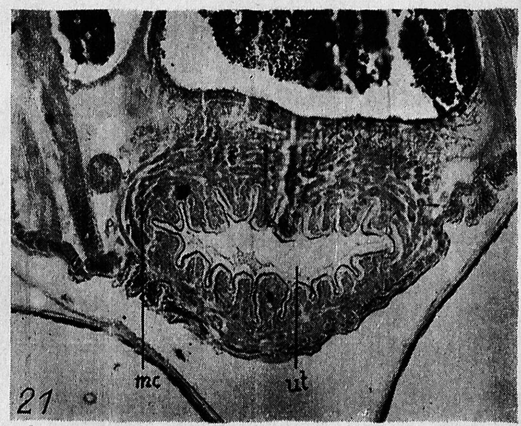
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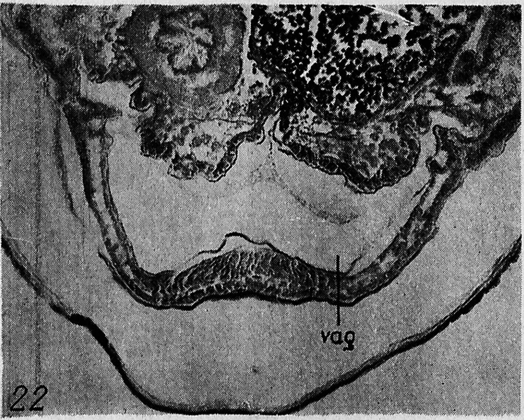
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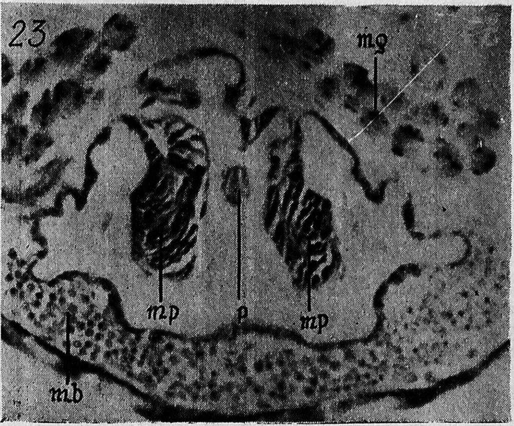
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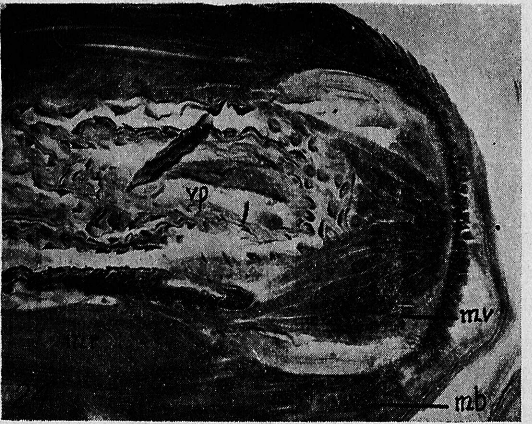

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