A comparative study of the male gentalia in the Pulicoidea (Siphonaptera)

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A comparative study of the male genitalia in the Pulicoidea (Siphonaptera)

by

Thomas Bigelow Cheetham

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GENERAL INTRODUCTION

The purpose of this work is three-fold: First, to clarify our knowledge of the basic structure of the male genitalia in the Siphonaptera through a detailed examination of a representative pulicid species, *Xenopsylla cheopis* (Rothschild, 1903). Second, to present a comparative study of these structures in the Pulicoidea in such a way that it may be of use in the taxonomy of the family, both with regard to identification of known species and in the placement of any species yet to be described. Third, to provide an initial hypothesis as to the phylogeny of the taxa treated, based principally on characters of the male genitalia, which it is hoped, will provide a framework for future hypotheses based on additional comparative data.
MATERIALS AND METHODS

In the course of this work a variety of techniques were used, and in many cases those most satisfactory were not discovered until well into the study. As a result, the material upon which these conclusions is based was prepared by a number of different procedures. Formulae for various procedures, fixatives and stains are outlined in Appendix II.

Histological Sections

Live eggs and pupae of *Xenopsylla cheopis* (Rothschild, 1903) were provided by Dr. William Chamberlain of the USDA ARS at Kerrville, Texas. Eggs were processed following a variation of the method recommended by Zalokar (1971) (see Appendix III). Pupae at several stages of development were removed from their cocoons and most were fixed in Bouin’s Dubosq-Brasil. In most cases the pupae were halved transversely with a razor just posterior to the metathorax to facilitate penetration of the fixative. Several pupae were fixed in various mixtures of glutaraldehyde. Good results were obtained using the heptane/glutaraldehyde procedure of Zalokar. All pupae were stored in fixative until such time as they were embedded. Adults were treated in the same way as the pupae, the majority fixed in Bouin’s, a few in Zalokar’s. The best overall results were
obtained with glutaraldehyde. Later in the study more conventional techniques were used for specimens prepared for transmission electron microscopy (TEM) as described below. These specimens were also then used for light microscopy.

Many adult specimens and nearly all pupae were embedded in a glycolmethacrylate (GMA) water soluble embedding medium (JB-4(TM); Polysciences Inc.). Four to five hours infiltration proved sufficient. Thick sections (2 microns) for light microscopy were cut on a Sorvall Porter-Blum microtome using glass knives. Pupae section easily but adults prove more difficult because of the tough cuticle. In the latter case, the terga and sterna were often removed prior to embedding. Many specimens were cut whole, however, and with sufficient patience this can produce excellent results. In many cases, with pupae as well as adults, the inability of the embedding medium to adhere to the cuticle resulted in the separation of the tissue from the resin. This was only a minor annoyance since the tissue may be transferred to the slide in any case. Sections were floated out on a drop of water to which approximately 1% NaOH has been added, then dried on a plate at 40-50 degrees Celsius. Use of JB-4 precluded the possibility of obtaining serial ribbons, but the advantages over paraffin far outweighed this inconvenience. Sections were arranged serially on the slides in individual drops of water.

Several stains were tried, the most convenient being a
solution of approximately 5% toluidine blue in water. This was applied to the dried sections for a few seconds and rinsed off with water. A simple polychrome stain method was discovered which provided good differentiation between tanned and untanned cuticle, though the results were not always consistent, and the technique resulted in rather low contrast, making photography difficult. Toluidine blue was preferred in pupae, where the enhancement of contrast was particularly necessary. Dried slides were placed for 2-3 minutes in Chatton's Eosin Y/ Light Green (see Appendix III), then passed to acetic acid alcohol for 5 minutes. A bath of absolute ethanol was used to bleach the surrounding embedding medium. Various shades of red and blue were obtained in the cuticular areas, and differential tanning could be detected.

Specimens for TEM were fixed in Karnowsky's Fixative (Glauert, 1975) both with and without the addition of picric acid, in 0.2M phosphate or cacodylate buffer, pH 7.3, for 1-2 hours. The initial fixative was injected into the specimens, both pupae and adults, via micropipettes. After the tissues had hardened somewhat, dissection, where it was performed, was easier than with fresh specimens. After washing in 3 changes of buffer, 15 minutes each, the samples were postfixed in 1% osmium tetroxide in the same buffer. After a further buffer wash, the tissues were dehydrated in acetone and embedded in Medcast(TM) resin. Infiltration of the resin was carried out very slowly in
three stages of 12-18 hours each to assure adequate penetration. Sections were cut on a Reichert Ultramicrotome with a glass or diamond knife and stained with uranyl acetate and lead citrate for 15 minutes each. They were examined with an Hitachi HU11E-1 Electron microscope operated at 50KV.

This last fixation and embedding schedule has been used routinely in later studies, whether for TEM or light microscopy, and is recommended as a general technique if time and resources allow. The only disadvantage is that the range of polychrome stains is restricted by the use of resin embedding media, but toluidine blue gives such excellent contrast and detail that polychrome techniques lose much of their appeal.

Dissections and Whole Mounts

In addition to sectioned material, fixed specimens of X. cheopis, both adults and pupae, were dissected and the genitalia examined whole in a drop of alpha terpineol, which provides a good index of refraction, clears the specimens slightly, and does not evaporate readily. It was found useful to clear fixed tissue in xylene and view it under a binocular microscope, either floating freely in terpineol or mounted permanently in medium. For the examination of muscles it was helpful to halve the animal longitudinally with a razor, clear it in xylene and make a permanent mount. The internal tissues were then easily visible. Occasionally, dissected phallosomes were lightly stained in
Chatton's eosin Y - light green prior to the preparation of permanent mounts. This was helpful in highlighting muscles. For viewing the dorsal, ventral, and caudal aspects of the genitalia, the structures were removed, cleared in xylene, and mounted permanently in the desired position by placing them in a drop of mountant in the gap between two #2 coverslips lying alongside one another on a microscope slide. These were then capped with a #1 slip. Gentle adjustment of the lower slips around the specimen produced the desired orientation.

All specimens other than X. cheopis and Ctenocephalides felis felis (Bouché, 1835) were unavailable live. Most that were obtained had been preserved in 70% ethanol for periods ranging up to 20 years. This preservation proved adequate for the purpose of determining musculature as well as cuticular structure. Such specimens are easily dissected, and for all but the smallest species, the aedeagus was embedded in JB-4 and sectioned as described above. For observation of the whole phallosome, the alcoholic preservation was quite useful. It seems to produce a clarity of the cuticular structures not found with more elaborate fixatives, probably by altering the refractive index of the cuticle. The musculature, though somewhat distorted, maintained its structure and position well. Sectioned material from these specimens took Chatton's stain quite well. One additional advantage to working with specimens preserved in alcohol for long periods of time, is that the structures become quite resilient.
and resistant to damage, thus making microdissection much easier. All dissections were done using a Wild dissecting microscope at the maximum magnification (X50), using minuten pins mounted on wooden sticks, and extra fine forceps, sharpened regularly on emery paper. Fleas which have been preserved in ethanol are best treated by dehydration to absolute ethanol and then immersion in xylene for a few minutes. They then may be placed in permanent mounts. This gives an excellent view of the muscles and cuticle.

Line drawings from permanent mounts were prepared with the use of a slide projector. Light micrographs were made with a Zeiss photomicroscope using Kodak Panatomic-X, except for a few of the low contrast pupae which were photographed with Kodak Technical Pan. A blue-green filter was used on most of the photos of whole, cleared specimens.

Scanning Electron Microscopy

Specimens of *X. cheopis* to be viewed with the scanning electron microscope were fixed in Bouin's and stored in 70% ethanol for periods ranging between 6 months and a year. All other species viewed had been preserved in ethanol as described above. Sonicating the specimens for a few minutes prior to coating results in cleaner cuticle. Some of the samples were left in 100% freon for a week or more, then either air-dried or critical point dried prior to sputter-coating with
gold-palladium. In many cases the specimens were simply dehydrated in absolute ethanol, sonicated for 2-3 minutes, air-dried and coated. The results were comparable in all cases. Whole fleas or dissected portions were placed on wet silver paint or on the sticky side of metal tape attached to the stubs with silver paste or paint. The specimens were viewed with a JEOL scanning microscope operated at various accelerating voltages between 5 and 25KV.
PART I

DEVELOPMENT AND ANATOMY OF THE MALE GENITALIA IN

*Xenopsylla cheopis* (Rothschild, 1903)
INTRODUCTION

The descriptions and remarks which follow have as their goal the explanation of the basic structure of the genitalia of male pulicid fleas. The choice of *X. cheopis* for study was based, initially, on the availability of both immature and adult specimens, but this species proved more than adequate as a reference point for an understanding of the male genitalia of all the pulicoid taxa. While it will be argued in Part II that the Xenopsyllinae are a derived group in some respects, they exhibit the major genitalic characteristics required for a general description, and are perhaps more suitable than other subfamilies for such a description because of their relative simplicity.

It is not a primary aim of this work to detail the development of the genitalia from the larval stage in a complete and exhaustive manner. The investigations undertaken on immature stages were intended to supplement the thorough work of Sharif (1937) and particularly Günther (1961) on the development of the genitalia in other families of fleas, and to describe any differences that were found.

The analysis of the musculature likewise relies heavily on the work of Günther (1961) on non-pulicid fleas, and his briefer treatment of the adult musculature in *Ctenocephalides canis* (Curtis, 1826). Although most of the muscles of the genitalia are described herein for *X. cheopis*, it was not felt necessary to confirm all aspects of Günther's results for this species. Most
attention has been given to those muscles which were expected to be of some use in establishing homologies of the various structures among the pulicids. The internal muscles of the phallosome in particular have not been fully treated since they are very difficult to describe with certainty and are not likely to be subject to much variation. I have, in cases such as this, relied on Günther's interpretations. In every case in which I could compare my results with Günther's he has proven completely correct, and his excellent work made this study immeasurably less tedious. Günther's Latinized terminology and numbering system for the muscles of the larva and adult are used throughout, and a key is provided in Section III. 5.
INTRODUCTORY ANATOMY AND BASIC TERMINOLOGY

(Figs. 1-3)

The following is intended as an initial overview to enable the reader with little or no previous familiarity with flea anatomy, or with little experience with the interpretation of male flea genitalia in particular, to follow the discussion in Part I. Only the basic ground plan of the male genitalia is presented. For additional illustration of the internal organs of Xenopsylla cheopis the reader is referred to Rothschild et al. (1986). The list of terms provided here is not intended to be complete, but rather to illustrate the basic structures. Throughout this study, 'proximal' refers to the direction towards the anterior of the animal as a whole, and 'distal' to the caudal end. The usage should be clear in context.

The terminal abdominal structures of male pulicids are arranged as follows. The seventh tergum and sternum are basically unmodified. The eighth sternum is large and its lateral areas are expanded. The eighth tergum is reduced but bears large spiracular openings which unite dorsally over the PYGIDIAL PLATE. The ninth tergum is reduced externally but may bear a large internal apodeme. The extent of the ninth tergum is a matter of contention. The ninth sternum is well defined and is more or less closely associated with the aedeagus. It is normally telescoped within the confines of the eighth sternum. It appears in lateral view to be composed of proximal and distal
arms. The former lie laterad of the aedeagal base and the latter ventro-laterad of the aedeagus itself. The remainder of the abdomen is composed of the pygidial plate, bearing a median SENSILIJUM dorsally and capped terminally by the ANAL CONE. The cone is comprised of dorsal and ventral sclerites connected laterally by membranous areas. Lying alongside the opening between the anus and the ninth sternite are the lobes of the CLASPERS. The base of the clasper lobes is formed by an internal invagination, the MANUBRIUM. The cavity formed between the ventral anal sclerite and the ninth sternum is lined by the AEDEAGAL POUCH, from which arises the external portion of the PHALLOSOME, the AEDEAGUS. The internal mass of the phallosome is usually greater than that of the aedeagus.

I. The Superstructure

The phallosome itself is divisible for descriptive purposes into three sections: the SUPERSTRUCTURE, the PENIS and PENIS RODS, and the AEDEAGAL SHEATH.

The elements of the superstructure are as follows.

A. The AEDEAGAL APODEME is composed of longitudinally arranged plates referred to as the MEDIAN and LATERAL LAMINAE, which produce an 'M' shaped cross section for the apodeme as a whole.

B. The FULCRUM consists of three processes configured like the prongs of a fork. These are the MEDIAN and the paired
LATERAL FULCRAL LOBES.

C. The CAPSULE fits into the slots formed by the lobes of the fulcrum, leaving a lumen between the median fulcral lobe and the roof, or TECTUM, of the capsule. The lateral walls of the capsule are produced proximally into extensions on which muscles insert. These are the LATERAL SHAFTS OF THE CAPSULE. This structure has been interpreted as a sperm pump.

D. The floor of the capsule lumen is formed proximally by the median fulcral lobe. Distally the latter is fused with a narrow tongue-like structure directed distally. This sclerite is often 'Y' shaped in lateral view and is designated the Y-SCLERITE. The tendons of the muscles which insert on it extend into the proximal portion of the phallosome and are sometimes visible in cleared specimens. This is referred to as the VIRGA DORSALIS.

E. The lumen of the capsule and the cavity below the Y-sclerite both open distally into the SCLEROTIZED INNER TUBE. This bears a ventral expansion known as the VESICLE, which is lined with cuticular hairs. Projecting proximally from the vesicle is the VIRGA VENTRALIS. The latter is rod-like when seen in lateral view, but is a shallow 'U' when seen in cross section.
2. The Penis and Copulatory Rods

The lumen within the phallosome and bounded dorso-laterally by the aedeagal apodeme and ventrally by the virga ventralis is the ENDOPHALLUS. Within this are found two rod-like structures of variable length and shape, one lying more or less above the other. These are the upper and lower PENIS RODS. Above these there is a third structure, usually only faintly discernible in cleared specimens. This is the PENIS. It follows the course of the penis rods and extends from the EJACULATORY BULB to the area below the fulcrum where it ends in the GONOPORE.

3. The Aedeagal Sheath

Surrounding the distal portion of the phallosome and forming its external boundary is the AEDEAGAL SHEATH. This is continuous basally with the aedeagal pouch. Ventrally, an invaginated apodeme is produced inwards to form the APODEMAL ROD. Dorsally the sheath fuses with the wall of the pouch and with the aedeagal apodeme. The distal portion of the sheath forms supporting structures, membranes, and a pair of variously shaped sclerites, the CROCHETS, which lie laterally within the END CHAMBER.
I. LARVAL ANATOMY AND DEVELOPMENT  
(Figs. 5, 6 & 10-13)

The following account is based primarily on Günther (1961) and Sharif (1937), supplemented by serial sections of several larvae of X. cheopis. Detailed studies of larval anatomy and sequential development in X. cheopis were not undertaken, but all available evidence does not reveal major differences between the development of the genitalia of this species, and those studied by Günther.

The general anatomy of the larval flea has been well described by Sharif (1937) and applies in all essentials to that of X. cheopis (Fig. 5).

The genitalic rudiments first become apparent during the transition from the first to the second larval instar in all fleas studied and this is assumed to be the case in X. cheopis (Sharif, 1937; Günther, 1961). They appear ventro-medially as cone-shaped paired cell masses in an invaginated pocket in the area between the ninth and tenth sterna (Figs. 10 & 11).

By the end of the third instar the rudiments have developed externally into paired primary phallic lobes (Günther, after Snodgrass, 1957), which divide longitudinally into median mesomerases and lateral parameres (Fig. 6). The internal portion of the rudiment continues to expand proximally and to form a central lumen. This mass becomes the internal portion of the
phallosome. During early pupal development, the parameres migrate dorsally and lengthen to form conspicuous flaps on the dorso-lateral body wall (Fig. 14). These will become the claspers. The mesomerses fuse dorsally and ventrally to surround the median invagination and produce the aedeagus. Somewhat later than the appearance and separation of the four phallic lobes, the paired lobes which produce the distal arms of the adult ninth sternum arise on the caudal edge of the larval ninth sternum (Fig. 6).

As the mass of cells forming the mesomerses grows, it and the surrounding area undergo apolysis and withdraw from the larval cuticle, and the entire structure withdraws into the body cavity (Fig. 12). The withdrawal of the ventral area surrounding the rudiment causes the ninth segmental ventral longitudinal muscles (M9) to loosen and loop into the body cavity. At this point the genitalic mass lies entirely within the ninth segment of the larval cuticle. Sections seem to indicate that the genitalic mass as a whole develops between the insertions of the ventral longitudinal muscles of segments nine and ten.

In the late third instar there appears a mass of developing ectodermal cells situated near the dorsum of segment ten (Fig. 13). In one specimen available in my material, there is visible a very distinct dorsal invagination. This was not discussed by Sharif or Günther. The fate of these cells is not clear, but appears to be as follows: As the animal sheds the final larval
cuticle and the anal struts are retracted, these cells proliferate to form the terminal cap of the final segment. It is apparently from this cap that both the pygidial plate and at least the dorsal anal sclerite arise.
II. PUPAL ANATOMY AND DEVELOPMENT

(Figs. 7-9 & 14-39)

1. Segmental Structure

By the time of the molt to the pupal stage the parameres have migrated dorsally to a median position on the sides of the abdomen, the ninth sternal lobes are readily apparent, and the cell mass representing the phallosome is large and has come to occupy a significant portion of the abdomen. The eighth sternum has produced two small protuberances in areas seemingly corresponding to the ninth sternal lobes, which develop merely as "forms" for setae on this segment, two within each lobe. Dorsally, two large outgrowths develop from tergum seven which extend caudally beyond the eighth and ninth segmental terga and produce the antepygidial bristles. During the molt to the pupal stage the abdominal segments telescope into one another, producing a marked shortening of the entire body. The eighth and ninth terga are reduced, while the ninth sternum continues to form within the expanding eighth. The general result of this contraction of the terga and expansion of the sterna, accompanied by the rapid expansion of the phallosome, is an enlargement of the ventral portion of the abdomen, directing the long axis of the phallosome upwards (Figs. 8 & 14).

During pupation, the epidermis withdraws from the pupal cuticle and further reorganization occurs, prior to the
sclerotization of the cuticle of the pharate adult. The eighth tergum is reduced further, its position marked largely by the position of the developing spiracles (Fig. 19).

In Ceratophylius gallinae (Schrank, 1803) Günther (1961) found that the so-called apodeme of tergum nine is actually formed by an invagination between segments nine and ten. This structure is very much reduced in X. cheopis, but the anatomy is not inconsistent with his findings. As was noted above, the terminal cap of the tenth, terminal segment produces the pygidial plate and at least the dorsal portion of the anal cone.

2. The Claspers (Figs. 20-23, 28, 29 & 36)

During the pupal stage, the tissues within the parameral lobes, which now lie midway up the abdominal wall, withdraw from the pupal cuticle and connect with the ventro-lateral walls of the pygidial plate and produce the clasper apparatus. Internally an apodeme is invaginated on each side which will be the manubrium in the adult. In the area which forms the dorsal portion of the aedeagal pouch, the clasper lobes are connected by a bridge of tissue. This has been designated the pons parameralis by Günther. This parameral bridge in X. cheopis does not become a distinct structure in the adult, as it does in some species. Latero-distally to the parameral bridge, the external lobes of the clasper develop. There are three lobes in X. cheopis. These lobes, or processes, are designated P1, P2 and
P3. P1 and P2 bear muscle insertions in the adult while P3 is a simple hyaline extension of the base of the manubrium. The basic formation of the three lobes appears to result from the direct separation of the lobes in a fan-like manner.

3. The Phallosome (Figs. 7 & 14-39)

The complexities of the adult phallosome and the details of pupal development tend to obscure the basic topology of the organ which is not at root unduly intricate, as the accompanying schematic diagram will illustrate (Fig. 7).

The dorsal invagination continues to develop inwards and to flatten laterally. This will produce the aedeagal apodeme. Ventrally the membrane forming the ventral, external sheath of the aedeagus grows inwards, and in addition to this, a thin, rod-like invagination develops, which becomes the apodemal rod. The true lumen of the phallosome, the endophallus, opens to the exterior via a single orifice, the phalotremal, which becomes the opening of the inner tube. A dorsal invagination of the endophallus produces the cavity which becomes the capsule, a ventral one produces the vesicle. Proximally, as the phallosome extends inwards, a hollow finger of tissue develops, and this will become the penis, bearing the gonopore of the adult. The penis rods develop along the length of the lumen as evaginations of its lateral walls. The ejaculatory duct extends through the penis to the ejaculatory bulb.
Reduced thus to the essentials, the major structures of the phallosome are comparable with the basic types delineated by Snodgrass (1935, 1946, 1957). The ejaculatory duct traverses the penis (Snodgrass, 1946, p. 46), which lies within the main lumen of the phallosome, the endophallus. The endophallus is bordered ventrally and laterally by the virga ventralis and its dorsal wall is formed by the limits of the muscles of the inner phallosome and more distally by the Y-sclerite. The exterior aperture of the inner tube is properly the phallotreme in Snodgrass' terminology, while the true gonopore opens at the end of the penis. Although Günther would interpret the structure which Snodgrass call the penis as a pseudopenis, and place the gonopore in an ill-defined region in the endophallus, I think it is best to side with Snodgrass. The gonopore is usually defined by him as the opening of the ejaculatory duct. The paired vasa deferentia leading from the ejaculatory bulb to the accessory glands are said by Günther to be ectodermal in origin, and though I can neither confirm nor deny this, the ejaculatory bulb is likely ectodermal, judging by its inner cuticular spines. The ejaculatory duct leads from the bulb, and its opening may be interpreted in accordance with Snodgrass' usual terminology as the gonopore.

In the late pupa, just prior to adult ecdysis, when the cuticular structures of the adult are fully formed, the aedeagus and the lobes of the ninth sternum are extruded and extend beyond
the end of the anus (Fig. 9). This perhaps allows space for the formation and hardening of the complicated and delicate lobes of the distal portion of the aedeagus. The aedeagus and the ends of the ninth sternum are generally retracted after emergence into the confines of the eighth sternum.
III. THE ANATOMY OF THE ADULT MALE GENITALIA

(Figs. 40-83)

The sections which follow include accounts of the major muscles of the claspers and the phallosome. An exhaustive treatment is not intended. The muscles of the internal phallosome are most likely very similar in all fleas, and the details are admirably and exhaustively treated in Günther's work.

1. Pygidial Plate and Anal Sclerites (Figs. 40-44)

The dorsal sclerite which bears the sensillum is the pygidial plate. It appears triangular in lateral view, with the apex directed dorsal. Latero-ventrally it is broadly fused with the base of the clasper apparatus in the area where the manubrium and clasper lobes join. There is a well-defined line of articulation at this junction, suggesting some freedom of movement for the clasper complex as a whole with respect to the plate. Most of the area defined by the margins of the sclerite is occupied by the sensillum. The structure contains 28 circular sensillal pits of equal diameter, and more or less evenly spaced. From each pit, there extends a single long trichobothrium. The areas between the pits are filled with short, stout spines. The trichobothria may be tactile but it has also been suggested that they are high frequency sound detectors (Amrine and Jerabeck).
The anal cone lies ventro-distad of the pygidial plate, and is composed of both a dorsal and ventral sclerite, separated from each other laterally by membrane. The ventral sclerite extends about twice as far proximally as the dorsal, and is continuous with the membrane which forms the dorsal portion of the aedeagal pouch. In some fleas, this area above the base of the aedeagus which stretches between the bases of the clasps apparatus on either side may be more or less sclerotized, forming what Günther calls the pons parameralis, or parameral bridge. This area is membranous in most pulicids, but the bridge itself may be represented by more or less sclerotized projections of the clasps apparatus on either side. These projections Günther calls the processus pontalis, and will be designated here the process of the parameral bridge (Fig. 44).

There is a small muscle bundle on either side of the anal cone, originating on the ventral margin of the sensillum and inserting on the lateral area of the ventral sclerite. Günther has designated this M12 in Ctenocephalides canis. M12 in other families extends from the 9th tergal apodeme to the ventral anal sclerite. M13 unites the dorsal and ventral sclerites in these species. Simplicity would seem to be served by assuming that the anal muscles in X. cheopis and Ctenocephalides correspond to M13, and that it is M12 that has been lost, since the proposed shift in origin is not as great.
2. The Claspers and Sternum Nine (Figs. 40-44)

The external portion of the clasper apparatus consists of three lobes or processes. The lateral and medial setose lobes are designated P1 and P2 respectively. The innermost and least sclerotized lobe (P3) is often invisible in cleared specimens and bears neither setae nor muscles. Both P1 and P2 bear muscle insertions while the inner lobe is closely connected basally to P2 and, with it, to the manubrium. P2 extends inwards in the form of an internal apodeme. The apodemes on either side are connected by a membranous area dorsal to the aedeagus and represent the process of the parameral bridge. The manubrium is a rod-like, invaginated apodeme which comprises the internal portion of the clasping mechanism. Dorso-laterally the manubrium and the lobes come together and connect to the lateral wall of the pygidial plate. This latter thus provides the anchor and support for the whole apparatus.

The muscles which insert on the setose lobes originate on the pygidial plate and the lobes are thus moveable independently of the phallosome. The muscle to the basal area of P1 is M18, and originates on the proximal rim of the pygidium. In the species studied by Günther, this muscle and M20 originate on the invaginated apodeme of the ninth tergum. This apodeme is greatly reduced in \textit{X. cheopis} and the rim on which the muscle inserts is the remnant of it. M20 operates the inner setose lobe, P2, and
arises on the rim of tergum nine as well, although more ventrally.

The manubrium supports three muscle bundles, one distal and two proximal. M23 connects the proximal end of the aedeagal apodeme with an area near the base of P1, lateral to the tergal bridge. M24 connects the proximal end of the aedeagal apodeme to the proximal end of the manubrium, and thus may be able to act in concert with M23 (as well as other abdominal muscles) to evert the aedeagus. The other bundle inserting on the proximal end of the manubrium is M16-17. It runs to the dorso-lateral area of the aedeagal pouch, on the inner side of the base of the manubrium. Although indistinct in *Xenopsylla cheopis*, this region may be enlarged to form a sclerotized connection between the dorso-lateral area of the capsule region (usually near the ribs when these are present), and the base of the manubrium above. Günther has called these structures the "Anhangsplatte". They will be termed here the suspensory sclerites.

It is notable that a third muscle inserting on the proximal end of the manubrium in all four of the species studied by Günther is apparently absent in *X. cheopis*. In some species M15 originates on the dorsal or proximal arm of the ninth sternum. Its function is perhaps performed by the intersegmental muscles of the eighth and ninth sterna.

The ninth sternum in *X. cheopis* is V-shaped in lateral view (Fig. 40). The processes apparent from this perspective are
referred to as the proximal and distal arms. In reality each is composed of two separate lobes and the structure is thus split into four arms. The proximal arms surround the ventral and lateral portions of the aedeagal pouch and come to lie lateral to the base of the manubrium where it joins the pygidial plate. The two apical arms are setose and lie ventro-laterally to the aedeagus.

3. The Phallosome (Figs. 40-42 & 45-82)

A. Outer Musculature (Figs. 40, 45)

The phallosome is by far the most prominent abdominal structure of the male flea. Its size is relatively enormous, occupying perhaps a third or more of the abdominal cavity. The complexity of the cuticular structures is rivaled by that of the extensive musculature of the organ. Apart from the muscles running to the manubrium discussed above, the bulk of the internal portion of the phallosome is surrounded by very distinct muscle sheaths which envelop the penis and penis rods and the dorsal portion of the aedeagal apodeme. There are two separate sheaths surrounding the penis rods. There is a sheath of muscles which connects the apodemal rod with the ventral edge of the lateral laminae on either side. Günther considered these to be separable into internal and external sheets which he designated M27 and M28. On the proximal end of the penis rods is a sheath extending from the longer of the two rods (the lower rod),
ventrally and distally into the inner body of the phallosome. This is M34, the insertion of which is not clear in X. cheopis. In Ctenocephalides canis Günther found it to insert near the junction of the lateral laminae and the lateral fulcral lobes. The lateral laminae in X. cheopis do not fuse with the fulcrum, and M34 likely inserts near their more dorsal fusion with the median lamina. In addition to the manubrium musculature described earlier, the outer surface of the aedeagal apodeme bears M25. This is a fan-shaped bundle extending distally from the outer surface of the lateral lamina to fuse with a similar muscle, M26, which arises from the inner surface of the lateral lamina. Together they form a thin tendon which passes along the outer surface of the inner tube, and inserts on the crochets, or on the membranes surrounding them. M29 is also present as a pair of tendons which insert on the dorso-distal portion of the inner tube on the membrane which forms the boundary between the inner tube and the dorsal and lateral lobes of the aedeagus (Fig. 67).

Transmission electron micrographs show that the muscles of the phallosome are of the microfibrillar type found in insect skeletal muscles generally (Fig. 76).
B. Cuticular Structures

The bulk of the skeletal portion of the phallosome may be conveniently divided for descriptive purposes, into three parts. The penis and penis rods are conveniently treated together. The aedeagal sheath forms the external boundary of the aedeagus proper and bears the crochets and the apodemal rod. The superstructure forms the main skeletal element.

i. The Superstructure (Fig. 62)

The principal parts of the superstructure are the aedeagal apodeme, the fulcrum/capsule complex, the inner tube, vesicle and virga ventralis.

The Aedeagal Apodeme

This structure often appears as a single plate in lateral view (Fig. 46), but actually consists of three laminae, and is thus M-shaped in cross section (Fig. 2 & 54-56). The lateral laminae form the lateral wings of the apodeme, and provide the place of origin for M23, 24, 25, 26, 27, 28 and 29. The median lamina is thickened ventrally at the distal end where it fuses with the fulcrum and forms a support for it. The median lamina is continuous with the lateral and medial fulcral lobes. The lateral laminae curve dorsally to fuse with the median lamina in the area just internal to the membrane of the aedeagal pouch. In transverse sections of the adult, the remnant of the invagination
from which the whole of the apodeme arises is visible as a cavity at the dorsal juncture of the three laminae (Fig. 56). The muscles which insert on the lateral shafts of the capsule (M32), originate along the dorsal internal surface of the median lamina. Electron micrographs of this middle lamina clearly reveal the lamellar structure typical of insect cuticle (Fig. 76).

The Fulcral Region (Figs. 47, 50, 58, 59 & 62-65)

The median and lateral lobes of the fulcrum are continuous with the median lamina of the aedeagal apodeme (Figs. 50 & 65). The lateral lobes are small and weak in comparison to the wide median lobe. The middle lobe is somewhat dome shaped, its dorsal surface forming the floor of the capsule lumen, and ventrally providing space for the Y-sclerite. In lateral aspect it appears tongue shaped. The tectum of the capsule consists of a membranous area fused with the median lobe of the fulcrum proximally, and a more sclerotized dorsal portion, which, seen in lateral view, forms the so-called crescent sclerite (see Discussion, Part II). Ventro-laterally to this sclerite the tectum thickens where its sides fit into the slots formed between the median and lateral lobes of the fulcrum. These thickenings are termed the lateral shafts of the capsule. Onto each of these inserts M32, the tendon of which is often visible in cleared specimens. The proximal end of the capsule is connected by membranes to the walls of the inner tube both laterally and
dorsally. Thus a continuous lumen is formed by the tectum of the capsule, the dorsal surface of the median fulcral lobe and the inner tube.

The Y-sclerite appears as a finger-like projection of the underside of the median lobe when seen in lateral view. In fact, the structure is bifid distally, consisting in effect of two arms with a very thin membrane stretched between them. Transverse sections reveal thin membranes stretching between the distal arms of the structure ventrolaterally to the junction between the inner tube proper and the lateral bulges of the vesicle (Fig. 60). Thus the Y-sclerite and its associated membranes form the boundary between the lumen of the capsule and distal-most portion of the inner tube and the lumen of the endophallus, there being no apparent connection between these spaces elsewhere than at the point just distal to the end of the arms of the Y-sclerite.

The base, or proximal end of the Y-sclerite is equally complex. Though essentially fused with the median fulcral lobe dorsally, and very difficult to dissect apart, it appears as a distinct structure. It lies ventral to the median lobe, and is flanked by it on either side, but free ventrally. In the shape of an inverted 'U' in transverse section (Fig. 58), it bears two proximally projecting lobes which extend on either side of the endophallus. These may be visible in whole mounts as the virga dorsalis. The muscle which connects these shafts to the inner wall of the aedeagal apodeme, and thus operates the Y-sclerite,
is M31. The membrane which forms the ventral boundary of the Y-sclerite continues laterally and ventrally to surround the penis and the penis rods, and is to be regarded as the wall of the endophallus. It is clothed with fine cuticular hairs which project distally. Their size and extent differ among taxa.

In short, the Y-sclerite forms a distal projection of the floor of the capsule lumen, and apparently acts as a sort of valve between the latter and the lumen of the endophallus.

The Sclerotized Inner Tube, Vesicle and Virga Ventralis (Figs. 47, 62, 64 & 66-70)

The sclerotized inner tube and the vesicle together form the ventro-distal portion of the superstructure. The vesicle is the area of attachment for the distal end of the virga ventralis. The lateral walls of the inner tube are strengthened by areas of increased thickness and sclerotization. These may be termed the proximal processes of the inner tube. They articulate with the distal ends of the lateral fulcral lobes in an area just dorsal to the vesicle (Fig. 56). The latter is a spherical enlargement of the ventral area of the inner tube. It lies just dorsal to the ventral membrane of the aedeagal sheath. The lower lip of the vesicle is the insertion point for M30 which originates along the lateral proximal edges of the virga ventralis (Fig. 47). The hirsute distal tip of the latter lies within the lumen of the vesicle, and is supported there by a multitude of hairs which
connect it to the inner wall (Fig. 70). The lumen of the vesicle opens dorsally into the cavity of the inner tube via an opening which is U-shaped viewed from above (Fig. 64).

The distal end of the inner tube is relatively uncomplicated. In lateral view it appears to bear a short tooth-like projection, more or less well developed in various specimens. This is actually a ridge extending along the top of the tube from side to side. Somewhat proximally to this is a smaller ridge which indicates the line of attachment of the membrane connecting the tube to the inner wall of the end chamber. As has been mentioned the dorsal portion bears the insertion for M23. Ventrally, the distal tip bears a pair of lobe-like thickenings between which lies a folded membrane which provides for the expansion of the distal tip thus allowing extrusion of the rod(s) during copulation.

The virga ventralis (Figs. 47, 62, 68 & 69) appears in lateral view as a thin rod-like structure underlying the penis rods. It extends from within the vesicle proximally a distance usually about equal to the length of the aedeagal apodeme. Transverse sections reveal that it is a broadly U-shaped plate underlying the endophallus. At its widest part in the proximal portion of the phallosome, the virga is approximately two-thirds the width of the entire aedeagal apodeme. The musculature described by Günther is almost certainly identical to that in X. cheopis. There are two sets of muscles associated with the
structure, M30 and M33. The former extends from the proximal margins of the virga to the ventral rim of the vesicle. M33 runs from the same area on the virga to the ventro-proximal margin of the lateral laminae. Distally the virga connects with the interior of the vesicle via a curled, spinose knob which lies within the vesicle. It is difficult to tell from TEM micrographs whether the cuticle forming this structure is layered or not, and thus it cannot be decided whether it arises as an invagination or is formed in a manner comparable to that which produces the penis rods.

The relation between the virga ventralis and the ventral and lateral walls of the endophallus is difficult to interpret. Proximally the two are usually quite distinct structures. Distally they apparently fuse. In cleared specimens of most male fleas there are small circular spots visible, usually slightly proximad of the fulcrum area and lying alongside the penis rods. They are highly developed in some species (e.g., *Vermipsylla alakurt*), or may be nearly indiscernible. These are associated with either the virga ventralis or with the lining of the endophallus and are almost certainly trichoid sensilla. Sections of the phallosome of *X. cheopis* did not reveal the anatomy of these tiny structures, but they can be seen in whole mounts. A transverse section of the phallosome of *Hectopsylla psittaci*, a species in which these hairs are quite large, does show their structure to some degree, at least enough to confirm
the presence of what are presumably sensory hairs (Fig. 231). In *H. psittaci* they appear to be outgrowths of the virga ventralis itself. This is also the case in *Pulex irritans*. It would seem most likely that the spiculose lining of the endophallus is the source of these structures, and that it and the virga ventralis are fused distally. This suggests the possibility that the hair-like spines of the vesicle, the trichoid sensilla, and the spines of the endophallus all derive from the same membrane.

ii. The Penis and Penis Rods (Figs. 46, 53, 58-60, & 71-82)

The lower penis rod is the longer of the two. It is comparatively uniform in cross section and has a small and delicate distal tip. Near the distal end the lower rod becomes closely associated with the upper, the latter becoming quite elaborate and variable in cross section, and forming a guide for the smaller rod which fits into a groove in the larger. The distal end of the upper rod is quite large in comparison with other pulicids, and occupies considerable space in the inner tube where it is usually seen to lie. The proximal end of the upper rod is flattened, to provide area for muscle attachment, giving it a spatula-like shape in lateral view.

As was noted earlier, the rods appear to arise during pupal development from the lateral walls of the endophallus and are not formed as invaginations. The nature of the process by which they are laid down is puzzling. The ultrastructure of the rods is
most unique as they are found not to be formed of the layered lamellae typical of insect cuticle, but are amorphous internally, unlike the aedeagal apodeme and the apodemal rod, which are, as has been noted, invaginations (Fig. 75).

The penis itself lies immediately dorsal to the upper rod, appearing to be nearly fused with it along part of its length. That it is not in fact so fused is revealed by the fact that the two easily separate when dissected out. The penis is a soft, untanned organ consisting of a tracheated, cellular interior traversed by a small lumen for the passage of sperm (Figs. 78 & 79). In well-fixed specimens, the dorsal surface of the penis at least partially adheres to the ventral membranes of the internal musculature, at the proximal end of the penis.

More distally the penis does lie freely within the endophallus, the ventral surface of which may be fused with the virga ventralis, as mentioned above. The dorsal surface of the endophallus is formed by a membrane lying under the central muscles of the phallosome and continuous distally with the ventral surface of the Y-sclerite. The endophallic membrane is clothed with fine cuticular hairs directed distally. The penis itself is free of such vestiture. This is in contrast to the opinion of Snodgrass (1946) who thought that the hairs were borne by the penis itself. The penis does have a covering of fleshy, finger-like projections, here called the fringe of the penis (Figs. 30 & 32). The gonopore is not truly terminal, but rather
opens out onto a shelf produced by a distal extension of the penis.

Electron micrographs of the penis in pharate adults show the deposition of cuticle by the microvilli of the epidermal cells along the outer margin (Fig. 80). The cells comprising the penis are simple, and tracheoblasts and tracheoles are concentrated centrally. The gonoduct is apparently lined with a very thin cuticle-like layer (Fig. 79), similar to that which lines the endophallus (Fig. 75).

iii. The Aedeagal Sheath (Figs. 48, 51, 52 & 61)

The sheath is that portion of the phallosome which forms the external boundary of the aedeagus, and should not be confused with the aedeagal pouch from which the aedeagus protrudes. (Note that this usage differs from that used by Rothschild and Traub, 1971. I recommend this nomenclature over theirs since it seems much more descriptive, given the knowledge of the structure revealed in this study.)

Dorsally the sheath consists of the ribs which are continuous with the aedeagal apodeme, which itself develops as an invagination from the aedeagal pouch. The point of demarcation between the sheath and internal aedeagal apodeme, and the membrane of the pouch dorsal to these can easily be distinguished in longitudinal sections, though it is less clearly seen in whole mounts. This connection was first noted by Sharif (1945) in
Ctenocephalides and in those species in which it is sclerotized, it is referred to as the proximal spur.

The ribs extend dorso-laterally on either side of the aedeagus, and are connected to the manubrium via lightly sclerotized areas of membrane. These suspensory sclerites (Anhangsplatte of Günther) are more strongly developed in other species. Both the median proximal spur and the suspensory sclerites are formed by differential tanning of the dorsal areas of the membrane of the aedeagal pouch. Thus the proximal spur may be regarded as a single, median suspensory sclerite.

Laterally and ventrally the sheath is strengthened to form the girdle, from the ventral portion of which arise the ventro-lateral runners. The distal portion of the runner on each side is slightly hook shaped and was termed the pseudo-crochet by Traub (1950). The ribs, the girdle and the runners are connected to form the scaffolding of the sheath, and help to support the distal structures of the end chamber. The areas between the ribs dorsally and between the runners ventrally are membranous.

In the same way that the ribs are closely associated with the aedeagal apodeme, the latter being an invagination alongside the former, so the apodemal rod is closely connected with the ventral portion of the girdle. The apodemal nature of the rod is shown by the presence of an empty inner core running a good portion of its length, as well as by the layered lamellae (Fig. 77).
The girdle, the runners, and the apodemal rod thus form a structural unit which is connected by the membranes of the aedeagal pouch with the ninth sternum, both ventrally and laterally.

To the apical median dorsal lobe are appended the lateral lobes of the aedeagus. These are produced into sclerotized supporting structures which may appear in lateral view to be part of the crochets. The latter are teardrop-shaped in lateral view and lie at the sides of the distal portion of the inner tube within the end chamber. On the inner end of each crochet is inserted the thin tendon of M25-M26, which enters the aedeagus by passing between the ribs and the tectum of the capsule.

The end chamber itself with its various lobes and processes is not rigidly fused with the inner tube; the two structures are joined by a flexible folded membrane.

4. The Internal Organs of Reproduction (Figs. 84-89)

In the larva each testis is composed of four follicles (Wasserburger, 1961), but these degenerate, and in the adult the organs serve as 'seminal vesicles', each containing a number of sperm bundles. Rothschild et al. (1970) state that the testes of *Spilopsyllus cuniculi* (Dale, 1878) are muscular. This has not been observed in *X. cheopis*. The sperm bundles consist of a sheath of 'sustenaculal cells' surrounding the sperm (Rothschild et al., 1970). Spermatogenesis is complete by the latter part of
the pupal stage, although the presence of a testicular plug (Fig. 85), prevents movement of the sperm into the vasa deferentia until some time after eclosion (Rothschild et al., 1970).

The sperm themselves, like those of *Spilopsyllus cuniculi* (Rothschild et al., 1970), *Ctenocephalides* (Baccetti, 1972 and Phillips, 1969) and *Ctenophthalmus p. pseudagyrtes* Baker, 1904 (Cheetham and Lewis, 1987), are unusual among the insects in that the axoneme coils around the central mitochondrial derivative (Figs. 88 & 90). Siphonapteran sperm share this characteristic with the Mecoptera (Phillips, 1969). In addition, both orders lack normal outer ring of nine accessory tubules (Phillips, 1969).

At the distal end of each testis lies the coiled mass of the vasa efferens referred to as the epididymus (Figs. 83-85). The ducts of the vasa deferentia (Fig. 87) unite to form a paired structure which leads into the ejaculatory bulb (Fig. 86).

The ejaculatory bulb itself (Figs. 40 & 86) is surrounded by circular muscle, and is divided into two spherical portions, though the inner lumen is continuous. This lumen is lined with cuticular 'hairs' directed towards the distal end of the bulb, presumably preventing backflow of sperm and seminal fluid. These 'hairs' are most likely acanthae in the sense of Richards and Richards (1969), which is to say they are cuticular structures formed from a single cell, and are thus the same formation as the 'spines' of the proventriculus. Leading from the ejaculatory
bulb is the ejaculatory duct which coils beneath the rods to enter the penis.

5. Comparative List of Adult Genitalic Musculature

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<td>36 inter-endotendonalis</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
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</tr>
<tr>
<td>37 endotendonalis major</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
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</tr>
<tr>
<td>38 minor</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>39 bulbalis</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>40 anularis ducti</td>
<td>+</td>
<td>+</td>
<td>+</td>
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<td>+</td>
</tr>
</tbody>
</table>
The species listed are: 1. *Hystrichopsylla talpae talpae* (Curtis, 1826), 2. *Ctenophthalmus assimilis assimilis* (Taschenburg, 1880), 3. *Ceratophyllum gallinae* (Schrank, 1803), 4. *Ctenocephalides canis* (Curtis, 1826), 5. *Xenopsylla cheopis* (Rothschild, 1903). The first four formed the basis for Günther's (1961) study from which this list is adapted.

6. Notes on Function

Observations of copulating fleas are rare. Many will only mate while on the host, making observation difficult. There are species which do mate off the host, but reports on these concern general behavioral traits. Detailed anatomical discussions are limited mainly to aspects of the operation of the claspers (Humphries, 1967a, 1967b), since internal anatomy is not readily visible. The knowledge we have of the mechanism of the phallosome comes in the main from those rare specimens mounted in copula, and from material sectioned by Dr. Miriam Rothschild. The most complete account of gross behavioral aspects of copulation in Siphonaptera is that of Geigy and Suter (1960), who describe copulation in *X. cheopis*, *Echidnophaga gallinacea* (Westwood, 1875) and *Tunga penetrans* (L., 1758).

Humphries (1967b) has indicated that the anatomy of the claspers is crucial for proper coupling in subspecies of *Ceratophyllum styx* (Rothschild, 1900). In this species, it seems that relatively small differences in clasper shape can prevent
successful copulation, and thus may well serve as a premating isolating mechanism. The extent of the taxa for which this is true is completely unknown. It would seem reasonable to suggest that some species are less dependent on the actual clasping function of the lobes for successful mating, since in many taxa the claspers are apparently less able to clasp than in others. *Xenopsylla* species would seem to have a clasper design less adequate to the task of holding onto the female than, for instance, species of *Pulex* or *Cediopsylla*. The sort of premating isolating mechanism suggested for *Ceratophyllus* would seem less likely.

Various portions of the aedeagus also serve a holding function. In some taxa (*Ctenocephalides, Pulex*) the crochets or pseudocrochets swing outward during copulation and seem to serve to anchor the aedeagus in the female genital opening. The action of the crochets in *Xenopsylla* has not been observed.

The action of the penis rods is inferred from mounted material as well as from sectioned specimens (Holland, 1955; Rothschild, 1964). The larger of the rods forms a guide for the smaller. It is not known whether the large rod ever actually enters the female. The small rod serves to transfer sperm, a few at a time, through the often tortuous path provided by the spermathecal duct of the female to the spermatheca itself or into the lumen of the duct. Sperm have been seen attached to the tip of the small rod in sectioned material of *Spilopsyllus cuniculi*.
Copulation may be prolonged in fleas, and this presumably allows time for several "trips". Each trip would account for the transfer of a small number of sperm.

The delivery of small numbers of sperm to the end of the small rod is accomplished by the capsule, which operates as a pump. Sperm, a few at a time, have been observed in the capsule in sectioned material (Dr. M. Rothschild, Ashton Wold, Peterborough, England; pers. comm.). The delivery of sperm to the capsule occurs when the penis itself is extended to a point near the opening of the Y-sclerite (M. Rothschild, pers. comm.). This elaborate mechanism apparently provides fine control over the delivery of sperm to the female. There is no reason to believe that male fleas are less productive of sperm than other male insects, and thus should have no particular need to conserve them. So little is known about the mating behavior of fleas that speculation on this topic is futile. We do not even know how often males and females copulate, or whether there is any indication of female choice in the selection of the mate. It would also be useful to know how length of copulation time relates to numbers of sperm transferred. In an attempt to determine whether there is any kind of sperm precedence in the biology of flea reproduction, Dr. Rothschild has observed the spermathecae of the females of *Spilopsyllus cuniculi*, and has found that although the sperm tended to align themselves along the strigillae initially, the action of the spermathecal muscle
soon resulted in an apparently thorough mixing of the sperm.

It has been proposed that the complexity of male genitalia found in many groups of animals can be explained as an effect of "sexual selection by female choice" (Eberhard, 1985). On this view, male genitalia may be regarded as functioning in a form of courtship. The elaboration of flea genitalia is certainly suggestive of a stimulatory function at least in some cases.
IV. DISCUSSION

1. Abdominal Segmentation in the Siphonaptera and the Origin of the Male Genitalia: A Review of the Literature

The nature of abdominal segmentation in insects has always been a matter of some dispute. The questions that arise concern the number of segments which are primitively present in the given taxon, and the extent of the limits of these segments in the various stages of development of the given insect. The underlying assumption is that the segments, properly defined, retain a developmental individuality and continuity, and may be regarded as units of development. The problem is thus the methodological one of determining the limits of the segment. Complications may arise involving the possibility of the fusion or elimination of segments or parts thereof. While this may make determinations of anatomy difficult, it does not in principle vitiate the undertaking, though one must always keep in mind the possibility that discrete results may not be attainable in all cases. The difficulties arise primarily because of the radical reorganization of anatomy which takes place during the pupal stage. Traditional techniques of anatomical analysis are rarely unambiguous enough to eliminate the possibility of varied interpretations. It has been shown that in some cases modern cytological techniques can provide very strong evidence that may
be used in such anatomical studies (Struhl, 1981). Perhaps at some future time more adequate techniques will be used to address these questions.

In the Siphonaptera difficulties in interpretation of abdominal segmentation pertain to the segments posterior to the eighth. The anterior abdominal segments in insects are generally unmodified and retain their segmental identity from embryo to adult. The genital segments are often highly modified however, and nowhere more so than in the male flea.

Both Wagner (1932) and Matsuda (1976) have proposed that a twelfth terminal segment is present in the abdomen of adult fleas. This is most unlikely. Kessel (1939) has shown that the embryonic abdomen of fleas from three different families (Pulicidae, Hystrichopsyllidae and Ceratophyllidae) is composed of eleven externally delimited segments, plus a rudimentary and evanescent terminal bud which he calls the telson. This latter, along with the eleventh, is separate only initially, and both soon become telescoped into the tenth (Kessel, 1939). Thus the larvae upon hatching possess ten visible segments. It is also important to note that segments ten and eleven are not 'complete segments' by the standard definition. Both lack coelomic sacs, and eleven lacks paired segmental ganglia. None of the embryonic abdominal segments ever show signs of appendage rudiments. Thus while it is true that embryonic fleas retain vestiges of the primitive eleven insectan abdominal segments, plus the telson,
the last two are only vestiges and fuse with the tenth long before the beginning of the development of the adult anatomy.

Wagner (1932) referred the anal sclerites to the twelfth segment on the basis of an examination of adult anatomy alone. This is a dubious procedure at best, and is certainly so in a group as highly derived as the fleas. In addition, even if there were twelve segments in the larva, a further point may be made, and Sharif quotes Snodgrass to that effect: "Subdivisions of a principle segmental plate or the component sclerites of a major area of sclerotization do not define anatomical areas" (Snodgrass, 1935; p. 71).

Matsuda, marshalling evidence from all other orders, as well as from Kessel's work, agrees with Wagner's conclusions (Matsuda, 1976; pp. 363-372). His argument is rather weak. He first of all accepts the proposition that the twelfth 'segment' apparent in the larva is a true segment and not the telson. in spite of the lack of nearly all the characteristics required for the definition of such a segment. Then, disregarding the complete absence of such a twelfth segment in the larva, says in effect that since there are twelve segments in the embryo, and there are twelve segments in the adult according to Wagner, then the only question outstanding is as to the nature of the transformation of such a segment through metamorphosis. He holds that the anal sclerites are clearly homologous with those in other orders, presumably because they look like they should be, and that since
these are, on his view, referrable to the twelfth segment (disputable in any case), so must be those in fleas. As Sharif points out, while it may be sensible to call the last adult segment a composite of the tenth and the eleventh, there is "nothing... in the organization of the larva, pupa or adult, that would suggest the existence of a twelfth abdominal segment in fleas" (Sharif, 1945). Wagner and Matsuda aside, there is general agreement that the abdomen of larva and adult is composed of ten externally delimited segments, the last being a fusion of the embryonic tenth and eleventh.

In male pulicids the major questions of segmentation concern the extent of the ninth, tenth, and eleventh segments. The eighth segment, though it is modified from the basic structure of the true pregenital segments, has a structure which is quite straightforward. The eighth tergum is much reduced and only occasionally bears an apodeme (as in *Pulex irritans*), but the eighth sternum has expanded to cover the ventral areas of the genitalia almost entirely.

Jordan held that the sensilial plate and the claspers with their various processes all derive from tergum nine, which also contributes to the dorsal anal sclerite. He considered the processes P1 and P2 of Pulicidae to be derived from the "tergal pleurite" of segment nine. The anal sclerites he assigned to segment ten (cited in Rothschild and Traub, 1971).

Wagner's views (cited in Matsuda, 1975) are based on his
belief in twelve abdominal segments as discussed above. This requires the belief that the eleventh is largely or entirely undeveloped (a view shared by Matsuda). The claspers are held to be the appendages of the ninth segment, the tergite of which is either fused with the proximal part of the tenth tergite or with the claspers. The tenth tergite forms the sensillial plate, and the tenth sternite is the 'subpygidial sclerite', which may be absent. Segment eleven is represented by the subanal sclerite which may be fused with the anal sternite. The latter, together with the anal tergite, comprise segment twelve.

Sharif (1945) considers the adult abdomen to consist of ten segments, though the last is a fusion product of the embryonic tenth and eleventh. He refers the sensillial plate and the claspers to tergum nine, and the anal sclerites to the tenth. He expends considerable effort delineating the exact extent of the area covered by the ninth and tenth sterna in the formation of the aedeagus. The tenth sternum is said to extend from the subanal sclerite to the "gonotreme", and the ninth sternite from the latter to the intersegmental boundary with the eighth sternite. Sharif considers the claspers to be structures peculiar to fleas, and to represent neither gonopods, nor apparently, parameres of any sort. The reasoning behind these conclusions is not presented. He remained equivocal in his 1937 paper as to whether the rudiment of the phallic lobes belongs to the ninth or the tenth segment, though later, (Sharif, 1945; p.
he asserts definitely that it belongs to the tenth. Much of his confusion is due to a misinterpretation of the ninth sternum, which he calls the subgenital plate in 1937 and the harpagoones in 1945. While it is true that this structure arises somewhat late in *Xenopsylla cheopis*, it is unquestionably the ninth sternum, displaced forward by the growth of the phallic rudiment.

Snodgrass held that the ninth tergum was greatly reduced in most male fleas, and to the point of obliteration in many, leaving as its trace the antecostal apodeme. Thus segment ten comprises the sensilial plate and anal sclerites as a unit. Contrary to all the views delineated above, the claspers are held to be fused secondarily with the ninth tergum. They are said to arise originally as subdivisions of the primary phallic lobes primitively associated with segment ten, but apparently developing within segment nine in most higher insects (Snodgrass, 1957). The aedeagus is regarded as formed from the fusion of the median lobes of the primary phallic rudiments, and as lying in the intersegmental area between the ninth and tenth sterna.

Though Snodgrass gave attention to the pupal anatomy and Sharif (1937) to the larval, it remained for Günther (1961) to provide a superb, detailed account of the developmental anatomy of the male genitalia, and thus provide a firm basis for understanding the structures and their origins. Günther provided the definitive study of the male genitalia of *Ceratophyllus gallinae* (Ceratophyllidae) and *Hystrichopsylla*
talpae (Hystrichopsyllidae), including the developmental stages in C. gallinae. The studies here undertaken on the development of the genitalia in X. cheopis were intended to determine if any major differences exist between the course of events in the pulicids and that in the ceratophyllids.

Günther came to the following basic conclusions, which agree in all essentials with Snodgrass. According to Günther, there is no question that the rudiments of the primary phallic lobes lie originally in the tenth segment, and that there is in fact an ectodermal opening from the genital pouch which initially lies medially on the tenth sternum distal to the insertion of the ventral longitudinal muscles of this segment. The genitalia as a whole thus arise from the tenth segment, though the primordia are displaced anteriorly early in the third larval instar. The primary phallic lobes give rise to the lateral parameres and the median mesomeres. The parameres migrate dorsally to fuse with tergum ten and form the claspers. While Snodgrass believed the primary phallic lobes to be unrelated to primitive segmental locomotory appendages, Günther claims that the parameres indeed represent the gonopods of segment ten. The paramere in Ceratophyllum gallinae pupae subdivides along the long axis, forming proximal and distal segments. He states that the developing rudiments form as a pair of lobes inside a pouch which is so similar in form to the peripodial pouches which surround rudimentary appendages on the thorax that one can only conclude
they are homologues. Thus he holds that the distal portion of the claspers in non-pulicid fleas is the telomere, and the base of the clasper the basimere. The median lobes of the primary phallic rudiments fuse to form the phallosome, which lies between the sterna of segments nine and ten. The apodeme of tergum nine is produced by an invagination incorporating parts of tergum nine (which may otherwise be indistinguishable) and part of tergum ten. The rest of tergum ten forms the sensilial plate while sternum ten contributes to the invagination which becomes the aedeagal apodeme. Segment eleven is represented in the larva by the anal struts and in the adult by the anal scerites. This assignment is based on muscle homologies.
2. Discussion and Comparison with the Anatomy of Xenopsylla cheopis (Rothschild, 1903)

A. Origin of the Primary Phallic Lobes

As only a few X. cheopis larvae were sectioned during this study, instances of third instars were rare. In the earliest specimens sectioned, the external opening of the primary phallic rudiment is not visible, but the position of the developing cell mass with respect to the muscles and the external segmentation seems consistent with Günther's claim that the rudiment arises in the tenth segment.

In X. cheopis the phallic lobes of the third instar lie caudad of the ventral longitudinal muscles of segment nine (M9 of Günther), which have looped forward into the body cavity as a result of the growth of the lobes coupled with the withdrawal of the epidermis from the larval cuticle. While the lobes appear to lie in the intersegmental space between segments nine and ten, analysis of the serial sections reveals that Günther's findings apply as well to X. cheopis. Laterad of the genitalic rudiment on each side lies a longitudinal muscle (M7) which clearly belongs to segment ten, and which originates along the body wall at a point about midway along the axis of the rudiment. There is nothing in the anatomy of X. cheopis inconsistent with Günther's interpretation, and I am inclined to accept it in spite of the fact that I was not able to observe the original opening of the
rudiment on segment ten myself. Günther also notes that the
rudiments are connected firmly to a narrow portion of the tenth
sternum, anteriorly. I cannot affirm this in X. cheopis.
Snodgrass (1957) believed that the male genitalia of higher
insects arose on segment ten primitively, but have shifted
forward into segment nine, though always occurring behind the
ninth sternum. This is consistent with the anatomy in X.
cheopis.

The further development of the phallosome as described above
for the late larval and pupal stages is consistent in all
essentials with that found by Günther.

8. Major Segmental Limits

Tergum eight is represented in the adult by a tergal plate
and by the spiracles which arch over the pygidium, and tergum
nine is reduced to a very small vestige which consists of the
weak apodeme invaginated around the dorsal proximal edge of the
pygidium. Though the apodeme of the ninth tergum in X. cheopis
is more reduced than in any of the species Günther studied, its
anatomical relationship to other structures is fundamentally the
same.

According to Günther, the proximal portion of the tenth
sternum contributes to the invagination which forms the aedeagal
apodeme. This seems to conform with the pattern in X. cheopis.

This leaves the sensilial plate and the anal sclerites to be
accounted for. The caudal disks which proliferate near the end of each anal strut in the late third instar larva are perhaps a clue to their origin. If as suggested, it is from these that the terminal cap of the pupa grows, then they may give rise to the pygidium and the anal sclerites. The apparent invagination observed in the caudal disk is suggestive of an original sensory function in the ancestral homologues of these cells, and this would be consistent with their development into the pygidium. Given the complete retraction of the anal struts and the apparent competence of the end cap to produce both the sensillum and the anal sclerites, it is probably best to regard the terminal segments of the adult and larval stage as Snodgrass did: a fusion of segments ten and eleven.

C. The Origin of the Claspers

The claspers in *X. cheopis* arise from the lateral lobes of the primary phallic rudiments, designated parameres by Snodgrass (1957), in the same manner as in *Ceratophyllus gallinae*. In *Hystrichopsylla talpae*, Günther found the process to be somewhat different. The primary phallic lobes do not divide, but move dorsally as do the parameres in the other species. They give rise to basal bulges in the midstage pupa, which then move together to form the aedeagus.

In both *Hystrichopsylla* and *Ceratophyllus*, Günther found that the lobes of the claspers (of which there are two in each
species) are formed by subsegmentation along the longitudinal axis of the paramere. In both species, the distal subsegment formed migrates toward the medial surface of the basal lobe and becomes, in the adult, movable by a muscle originating on the latter (M22). This movable process is not present as such in X. cheopis, although it is in other pulicids. There is no homologue to M22. As has been described above, the subsegmentation in X. cheopis is rather different, the lines of fissure being longitudinal rather than perpendicular to the long axis of the paramere.

Based on the subsegmentation observed in the species he studied, Günther has designated the moveable process the telomere and the fixed process the basimere, in accord with his belief that the phallic lobes as a whole are homologous with the primitive abdominal appendages of the tenth segment. This raises two questions. First, are the 'telomeres' homologous within the Siphonaptera, or are those of the Pulicidae unique? Günther assumes that they are homologous across the order when he unhesitatingly declares that P2 of Ctenocephalides is the same structure as the moveable process of the other families. This is probably true, but discussion of this point is deferred until Part II. The fact that the subsegmentation of the parameres in X. cheopis does not agree with that found by Günther is not necessarily contradictory evidence since the claspers in Xenopsylline fleas are probably in a derived state with respect
to the other families, as will be discussed later. The second question concerns possible homologies between segmental locomotory appendages and the parameres. Günther appears to base his conclusion solely on the appearance of the early phallic rudiments, and their resemblance to leg buds. This kind of evidence is indeed appropriate in determining homologies, but it is greatly strengthened by any additional evidence available. There is nothing in the embryology or metamorphosis of fleas which would provide further evidence since abdominal appendage rudiments are entirely absent. Conclusions on this question must be based on studies of other orders of insects. I prefer to remain mute on the subject since I believe that within the Siphonaptera there is not sufficient evidence to decide the question. The lobes of the claspers will therefore be referred to throughout this work merely as such.

There is, further, some question as to whether part of the clasper apparatus in the adult may not be derived from tergal precursors, that is, as to where the "line of fusion" occurs (Smit, 1980). This point also is best treated in Part II since anatomical studies which do not follow cell lineages from the embryonic segmentation are not of sufficient resolution to decide the issue, and results of comparative work must be considered.
V. SUMMARY

The development of the male genitalia of *Xenopsylla cheopis* has been found to be fundamentally in accord with that of *Ceratophyllus gallinae* as described by Günther (1961). It should be noted however that conclusions as to the segmental origins of these structures should be regarded as necessarily provisional since the boundaries of segments and compartments are not easily discerned by traditional methods, no matter how painstaking.

The genitalic rudiments probably arise from the proximo-ventral area of segment ten in the late third larval instar, but shift forward as they enlarge and come to lie entirely within the ninth segment. The anlagen appear externally as a pair of primary phallic lobes ventrally in the area between segments nine and ten. The primary lobes divide, forming median mesomeres and lateral parameres. The former fuse to produce the phallosome, the latter migrate dorsally and produce the claspers which fuse partially with the tenth tergum.

Although Günther found that the moveable process of the clasper in *Ceratophyllus gallinae* arises as a result of a subsegmentation across the long axis of the clasper rudiment, in *X. cheopis* the three clasper lobes arise by the production of fingers lying side by side near the terminus of the lobe. This is likely related to the derived nature of the adult anatomy of
Xenopsylline fleas (see Part II). Thus this in itself could not be used to argue against Günther's claim that the parameres are derived from primitive insectan gonopods. However, I do not believe that any such conclusions can be drawn on the basis of flea anatomy alone. Theories of this sort must be based on comparative studies of all the orders in the class.

The sensilial plate and the anal sclerites probably derive from a cell mass derived from larval segment ten, which in turn is a fusion of embryonic segments ten and eleven.

The aedeagal apodeme and the apodemal rod are true invaginations, while the penis rods develop as internal outgrowths of the wall of the endophallus. The gonopore is borne on the terminus of the penis which lies within the endophallus lumen.

The genitalic anatomy of adult *Xenopsylla cheopis* has been described and illustrated. This knowledge will serve as a groundwork for the comparative study of these structures within the Pulicoidea, which forms the substance of Part II.
PART II

COMPARATIVE ANATOMY OF THE MALE GENITALIA

IN THE PULICOIDEA
INTRODUCTION

There are 204 species and subspecies of pulicoid fleas (Lewis, 1972, Lewis & Lewis, 1985). Two genera, *Nesolagobius* (Archaeopsyllinae) and *Pulicella* (Xenopsyllinae), have been described only from the female, and these are not treated in the following discussion.

The higher classification of the Siphonaptera is complicated by two factors: the great degree of morphological uniformity of the order, and the occurrence of a large measure of parallel and convergent evolution, based largely, it is thought, on the independent acquisition of similar hosts (see e.g., Traub, 1980b). The most reliable single guide to generic grouping among the Siphonaptera has proven to be the male genitalia. It has been suggested by various authors that the genitalia are less likely to be subject to adaptive modifications based on direct environmental factors than are other aspects of the anatomy, and are therefore a useful guide to suprageneric relations (Jordan, 1947; Mardon, 1978; Traub, 1950, 1980a).

The descriptions of the genitalic anatomy given here will provide a complete and consistent reference for workers seeking generic level identification of male pulicids, and should aid in the placement of new taxa. In a few cases, suggestions are made in an effort to standardize anatomical nomenclature in the family. An effort has been made to avoid unnecessary confusion
of nomenclature by the introduction of new terminology.

The higher classification of the group has been disputed. Results of the present study suggest certain alterations in the accepted arrangement of taxa, including the establishment of three new genera, which will be formally established in subsequent publications. On the basis of this comparative study of the male genitalia, the first explicit phylogeny for the group will be presented.

The Pulicoidea is here considered to contain a single family, Pulicidae, which may be divided into seven subfamilies. An explanation of the arrangement used will be discussed in section II. Each group with its constituent genera will be treated in turn. For each subfamily a detailed description and illustrations of a representative species will be provided, followed by less exhaustive discussions of the remaining genera (or species groups in the case of Xenopsylla). Descriptions of selected aspects of the musculature are included for the species selected as representative of the subfamilies. An attempt has been made to depict the principal muscles of the periphallic structures. Muscles of the phallosome are not treated in detail, and only those pertaining to the aedeagal sheath are described.

The anatomical descriptions are followed by comments on function where this is appropriate. Variations within each genus are occasionally treated, but not in the detail appropriate to revisionary work at that level. Anatomical descriptions are not
given in the detail that is required for determinations at the species level. For example, setation which may be important in many genera is only treated in special cases. Emphasis has been given to those major structural features which are felt to have the most bearing on supraspecific classification, and the most important functional roles.

Discussion of interspecific variation within each genus is based upon examination of as many species as were actually available for study. In cases where material was not available, illustrations from the literature have been utilized where possible. In most cases the older literature does not include drawings of the phallosome.

A list of known host associations and zoogeographic distribution for all the genera is provided in Appendix I.
NOTES ON TERMINOLOGY AND MEASUREMENT

Except in those cases where new terms are coined, or where terms are not available therein, the terminology used is that of Rothschild and Traub (1971).

Some of the criteria for descriptions and measurements to be noted are as follows:

'Proximal' will always refer to the cephalic end of the flea, 'distal' to the caudal end. Basal may refer to the base of the structure being described.

The length of the inner tube is taken as the distance from the distal end of the lateral fulcral lobes to the distal tip of the inner tube.

The width of PI is measured at the widest section, whether this is perpendicular to the long axis or not. The length is the longest measure possible, taken from the most proximal articulation. In those species with no such articulation, the measure is from the dorsal attachment of PI.

The length of the "manubrium" is measured from the most proximal articulation of PI, or from the dorsal attachment. This has been chosen as a convenient reference and may not in some cases measure the manubrium proper.

The length of the aedeagal apodeme is measured from the most proximal point of the notch between the lateral and medial fulcral lobes.

The broadest point of the aedeagal apodeme is measured
across the median lamina.

The penis rods are described, somewhat loosely, as curling a certain number of degrees over the long axis of the aedeagal apodeme, a full circle being 360 degrees (see Plate 1, Fig. 3).

The crescent sclerite is a useful landmark, but due to some uncertainty as to the meaning of the term I have chosen to use the term 'tectum' when referring to the dorsal portion of the capsule seen in lateral view (see Discussion).

It should be noted that all measurements are approximate, and are taken in all cases from a single specimen. They are intended as a general guide to the anatomy and not in any sense as data for statistical analysis.
FORMAT FOR THE GENERIC DESCRIPTIONS

This guide is provided for ease of reference in consulting the generic descriptions.

Genus name.
Number of species; brief zoogeography and host associations.
Identification of primary specimen used in the description. LC: Lewis Collection; TC: Traub Collection; BM(NH): British Museum (Natural History).

1. Periphalllic Anatomy:
   Cuticular Structures:
   a. apodeme of 9T
   b. manubrium
   c. Pi:<>() as long as broad; ()X length of manubrium
   d. P2 & P3
   e. parameral bridge
   f. 8T and 8S
   g. 9S
   h. misc.
   Musculature:
   Listed by number

2. Anatomy of Phallosome:
   Cuticular Structures:
   a. aedeagal apodeme
   b. rods, penis and v. v.
   c. capsule/fulcrum
   d. suspensory sclerites/ proximal spur
   e. inner tube and vesicle
   f. aedeagal sheath and crochets
   g. misc.
   Musculature:
   a. M25-26
   b. M29
   c. misc.

3. Notes on Function

5. Comments

6. List of Taxa
I. GENITALIC ANATOMY IN THE PULICOIDEA

1. Descriptions of the Genera

ARCHAEOPSYLLINAE Oudemans, 1909
Plates 28 - 39.

There are five genera of archaeopsylline fleas, four of which are known from both sexes. Male Nesolagobius have not been collected and the genus is not treated here.

Ctenocephalides Stiles and Collins, 1930
Plates 28 - 36.

There are ten species and in this mainly Ethiopian genus, including the common cat flea, C. felis, and the dog flea C. canis. Members of the genus infest a variety of mammalian hosts.

Ctenocephalides orientis (Jordan, 1925)
LC #14892; Nepal.

The following descriptions are based on specimens of C. orientis. Günther (1961) supplied illustrations of C. canis which have been compared with dissections of C. felis felis and C. orientis. The three taxa share identical clasper musculature, and are fundamentally identical in gross structure, though there
are variations in the details.

Periphallic structures: Apodeme of 9T large, well developed, quadrate, bilobed when seen from above not fused with manubrium. Manubrium thin, rod-like, freely articulated with P1, P2 and lateral wall of 10T. P1 large, paddle-shaped, 1.7X as long as broad, 0.7X length of manubrium; Apodeme of P1 small, not noticeable in lateral view, parameral bridge formed of flexible membrane. P2 small, 0.2X as long as P1, elongate triangular in lateral view, lying medioventrally to base of P1; articulates in socket formed by base of P1. 8S unmodified, 8T spur present. 9S free of apodemal rod; proximal arm 9S paddle shaped, well developed, distal arms small, 0.5X as long as aedeagus. Trichoid sensillum lying between bases of P1 and P2.


Phallosome: Detailed descriptions of the cuticular structures and musculature of C. canis are provided by Günther (1961). C. felis felis and C. orientis agree in all essentials
Aedeagal apodeme less than 3.5X as long as broad, 1.2X as long as aedeagus. Median lamina with ventral margin concave, strongly fused with ribs and median fulcral lobe. Lateral laminae well developed, ventral margin straight, thickened, fused broadly with lateral fulcral lobes. Penis rods approximately equal in length, longer than aedeagal apodeme, but not arching over it; upper rod expanded proximally into teardrop shaped plate for muscle insertions. Virga ventralis usually prominent, approximately the length of aedeagal apodeme. Apodema rod strongly developed, nearly as long as penis rods, strongly connected basally with girdle and runners. Capsule/fulcrum area large and well developed; tectum large, arched and well tanned, flexible untanned proximal portion usually visible. Lateral fulcral lobes strong, straight; median lobes with dorsal margin thickened, straight. Y-sclerite large and pointed distally. Lateral areas of floor of capsule clothed with fine hairs. Suspensory sclerites present, but not heavily tanned, articulating with distal portion of ribs, dorsal to distal end of lateral fulcral lobes; connects to manubrium slightly cephalad of base of latter. Inner tube broad, 4x as long as broadest portion, lateral walls forming strongly thickened lateral process which articulates with lateral fulcral arms; terminal half tapering distally, angled dorsally. Vesicle large, strongly margined in lateral view. Aedeagal sheath strongly upturned
distally into median dorsal lobe; supporting structures of sheath clearly visible – ribs, girdle and runners continuous and well connected to apodemal rod forming unitary scaffolding; proximal margin of girdle crossing distal third of capsule; ventral membrane present and circular; lateral lobes of end chamber large, covering wing-like processes supported basally by distal fusion of dorsal and ventral branches of the runners; ventral lobe of aedeagus lying below true crochets which are tri-lobed and surround the distal end of inner tube.

Musculature: M25-26: origin on lateral laminae of aedeagal apodeme, insertion near base of crochet. M29: probably present, insertion near distal end of inner tube on dorsal surface.

Notes on Function

P1 and P2 are independently musculated and can probably move together in a pinching motion. The muscles of the manubrium act to evert or retract the phallosome as a whole. M23 and 24 acting to evert, and M16-17 to retract. M15 acts on the proximal arm of the ninth sternum probably in order to evert the distal arms.

No specimens have been seen in copula, but occasionally alcohol preserved material will provide specimens with the phallosome everted, and inferences can be drawn from these. By means of the contraction of M25-26, aided perhaps by hemolymph
pressure produced by contraction of M27+28 and other muscles of the aedeagal apodeme, the wings are flared laterally by pivoting on the support provided by the union of the dorsal and ventral runners, and press the lateral lobes of the end chamber outwards as well. This probably serves to anchor the aedeagus in the female genital chamber. The ventral lobes are also expanded and may act to further anchor the aedeagus. The crochets may serve as a kind of support and guide for the distal end of the inner tube, through which the rods will be everted. It is not known whether the rods are everted together in life.

Comments

The wing-like structures of the sheath are usually considered to be homologous with the crochets in other taxa (see for example, Traub (1950)). This survey of the pulicid taxa suggests that the true crochets are best understood as sclerites which flank the inner tube and lie within the end chamber. They are musculated by M25-26. The true crochets in Ctenocephalides are not easily seen in cleared specimens mounted laterally, but do serve as supports for the end of the inner tube. They are the structures labelled pseudocrochets by Traub (1950). It will be suggested in the discussion below that the wings in Ctenocephalides are homologues of similar structures in the Xenopsyllinae. These are thought to be secondarily musculated and to be new structures derived from lateral lobes of the
aedeagal sheath. The reinforced portions of the sheath on which the wings pivot are here termed the dorsal and ventral branches of the runners for the sake of simplicity of nomenclature. This broadens the notion of 'runner' somewhat.

This taxon is among the most homogeneous in the Pulicidae. Chaetotaxy aside, there are variations of a minor sort in the shape of the periphallie organs and in the proportions of the primary structures of the phallosome, but the most obvious differences are to be found in the aedeagus itself. Here the form of the dorsal arm, the pseudocrochet, the inner tube and the lateral lobes of the end chamber are species specific.

Taxa:
- *arabicus* (Jordan, 1925)
- *arabicus multispinosis* Smit, 1960
- *brygogi* Beaucornu, 1975
- *canis* (Curtis, 1826)
- *chabaudi* Beaucornu & Bain, 1982
- *connatus* (Jordan, 1925)
- *craterus* (J. & R., 1913)
- *felis damarensis* Jordan, 1936
- *felis felis* (Bouché, 1835)
- *felis strongylus* (Jordan, 1925)
- *orientis* (Jordan, 1925)
- *paradoxuri* Wagner, 1936
- *rosmarus* (Rothschild, 1907)

(NOTE: male *chabaudi* unknown)
The genus is known from two species inhabiting the European and Manchurian subregions of the Palearctic region. They are parasites of hedgehogs.

Archaeopsylla erinacei maura J. & R., 1912

LC #8286; Tunisia.

Periphallie Structures: 9T apodeme strong, dorsal margin concave; bilobed when seen from above; knob-like in lateral view. Manubrium rod-like, connection with 10T and bases of P1 and P2 more or less flexible. P1 large, broadly triangular, 1.75X length of manubrium, 2.0X as long as broad; dorsal margin strongly convex upward; ventral margin strong, bearing hyaline fringe with hairlike projections of variable length. Parameral bridge formed of membranous connection between internal apodemes of P1 on either side. P2 small, knob-like, at medio-basal corner of P1, surrounded by membrane, not cuticular socket. Large trichoid sensillum between bases of P1 and P2, covered with hyaline flap anteriorly. 8T with small spur laterally; 8S well tanned ventrally with inflected area on either side of 8S and phallosome; short hyaline fringe present on lateral margin 8S. 9S connected to apodemal rod via large area of membrane, proximal arms weak, distal arms thin, not as long as aedeagus.

Musculature: Large muscle bundle (unique to this genus and of
uncertain homology), originating on ventral portion BS, insertion near base of manubrium. M22 small but present.

Phallosome: Aedeagal apodeme thin, rodlike overall, 1.4x length of aedeagus, median lamina approx. 1/2 maximum width of capsule area throughout; approx. 12x as long as broad; apical appendage present, upcurved; lateral laminae weak, flared slightly over proximal 2/3 of apodeme, united with median lamina proximally to lateral fulcral arms; Penis rods about equal in length, not flared proximally, similar in size and thickness, curving 90 degrees over aedeagal apodeme. Penis bears ventral sclerite of same length as aedeagal apodeme. Apodemal rod heavy, directly continuous with runners on either side. Capsule area small, compact; lateral fulcral lobes strong, broadly continuous proximally with median lamina and suspensory sclerites; tectum flat. Suspensory sclerites very well developed, connecting with aedeagus near base of aedeagal apodeme at proximal portion of ribs, wide and platelike when seen from above, nearly united over dorsum of phallosome. Inner tube gently tapered and upcurved distally; tip turned ventrally, blunt dorsal tooth present; distal end evidently articulated. Vesicle present, not prominent. Aedeagal sheath narrow, tapering and upturned slightly distally, apex truncate; ribs present, sloping disto-laterally to meet with runners. Runners large and strong, closely appressed ventrally, flanking narrow ventral membrane. Paddle-shaped sclerites, articulated near confluence of runners
and ribs, probably represent crochets. Lateral lobes
ventro-distally pointed. End chamber lined with fine hairs.

Notes on Function

Rothschild (1976) noted that male Archaeopsylla erinacei
(Bouché) are capable of very rapid vibrations of the feathery
fringe of untanned cuticle at the ventral margin of P1. Similar
structures (vexillae) present on the eighth sterna of some
non-pulicid fleas are known to be used to brush the female
sensillum during copulation (Holland, 1955), and it may be
assumed that a similar function is involved here. In the
pulicids, somewhat similar hyaline fringes occur on the ninth
sternum in Actenopsylla and on the eighth sternum of Hoplopsyllus
pectinatus. There is a very slight fringe on the eighth sternum
in Archaeopsylla, though much too short to serve the same
purpose. The mechanism for the production of the vibration
probably involves the action of the unique eighth sternal muscles
inserted at the base of the manubrium. The very highly developed
suspensory sclerites may also assist in providing mechanical
strength for this action, as perhaps does the presence of a
membranous area at the base of P1. These actions may also
explain the presence of M22, the usual function of which is to
move P2 in those fleas with pincing claspers. It is not found in
Ctenocephalides or Xenopsylla and is assumed to be absent in
related genera.
Comments

This small taxon is homogeneous. Distinction at the species level can be seen in the shape of P1, P2, the trichoid sensillum and perhaps the crochet and distal end of the inner tube. At the subspecific level the crochet and the inner tube may be useful.

Taxa:
erinacei erinacei (Bouché, 1835)
erinacei maura J. & R., 1912
sinensis J. & R., 1911

Centetipsylla Jordan, 1925
Plate 39, Fig. 124.

Known from a single species taken in Madagascar where it is a parasite of tenrecs.

Centetipsylla madagascariensis (Rothschild, 1900)

LC #6210; Madagascar

Periphallic Structures: 9T apodeme large, broader than long; lobe of 9T large and strong. Manubrium broadly fused to apodeme at base. P1 2x as long as broad, 0.8X as long as manubrium; six short, stout spines along distal margin; apodeme of P1 small, directed ventromedially. P2 knobbed basally, with long, dorsally directed arm medial to P1. Trichoid sensillum between bases of P1 and P2. Manubrium broadly fused with
pygidial plate. ST well developed with weak lateral spur. SS strongly tanned ventrally, forming support for SS and phallosome, two large spines present on each side. SS probably free of apodemal rod; proximal arm thin and sinuous, distal arm large, elaborate, nearly as long as aedeagus.

Phallosome: Median lamina of aedeagal apodeme approx. 5.3X as long as broad, slightly upcurved proximally, 1.6X as long as aedeagus, lateral laminae indistinct, fusing with fulcrum near base of ribs. Penis rods thin, 1.5X as long as aedeagal apodeme; curving less than 90 degrees over apodeme. Apodemal rod very stout, not as long as penis rods, probably terminating in lateral walls of girdle. Lateral fulcral lobes stout, strongly produced distally; median fulcral lobe strong, hook-like. Tectum small, indistinct. Suspensory sclerites apparently not developed. Inner tube stout with large lumen, slightly decurved apically; vesicle heavily margined in lateral view. Aedeagal sheath very stout, approximately 2X as long as broad at base; runners weak, ribs very large and strong, decurving distally to form wide lateral lobe; area lateral and ventral to vesicle heavily tanned. Crochet very large and heavily tanned, with ringed apical projection, apex of sheath broad and pointed distally.
Aphropsylla Jordan, 1932
Plate 39, Fig. 125.

Both species in the genus are from the Ethiopian region where they are found on hyraxes, civets and various rodents.

Aphropsylla conversa J & R, 1913
Paratype BMNH>; E. Africa.

Periphallic Structures: 9T apodeme strongly developed, dorsal margin concave, lobe upcurved; bilobed when seen from above; slightly longer than manubrium. Manubrium thin, broadly fused basally with 9T apodeme. P1 3X as long as broad, approx. equal in length to manubrium; apodeme P1 short, directed medially. P2 very short, less than 0.2x as long as P1, 2X broader than long. Large trichoid sensillum borne on lobe present between bases of P1 and P2. 8T with spur present, 8S well tanned ventrally, forming support for 9S and phallosome. 9S free of apodemal rod; proximal arm thin, distal arms large, wide, nearly length of aedeagus. Lateral spiculose membrane present between proximal arm of 9S and phallosome, derived from aedeagal pouch.

Phallosome: Median lamina of aedeagal apodeme long and narrow, 12X as long as broad, expanded and upturned proximally, 1.2X as long as aedeagus. Lateral laminae weak and shallow, fusing with fulcrum dorsally to lateral arms. Penis rods similar
in shape and length, curving only slightly beyond aedeagal apodeme. Penis bearing ventral sclerotization over distal 1/2. Apodemal rod well developed, nearly as long as penis rods, fused distally with runners and girdle. Lateral fulcral lobes strong and blunt, broadly fused with median lamina; median fulcral lobe with strong dorsal tongue; tectum flat. Suspensory sclerites large, well developed, strongly curved. Proximal spur appears as small protuberance. Inner tube long, thin, ending well within end chamber; lateral walls articulate with lateral fulcral lobes; distal end with dorsal thickening. Vesicle well developed. Aedeagal sheath more than 2.5X as long as broad at base; ribs well developed, runners strong, broad and continuous with apodemal rod. Girdle developed laterally. Lateral lobes long and broad, continuous with ribs proximally. Lateral wings present, medial to lateral lobes. Crochet large with two projecting fingers.

Comments

Only one specimen of *A. wollastoni* was available. Genitalic differences are very minor, and involve the setation of PI.

**Taxa:**
- *conversa* (J. & R., 1913)
- *wollastoni* (Rothschild, 1908)

*Nesolagobius* J. & R., 1922

Male not known.
There are seven currently recognized genera of xenopsylline fleas. Two species groups (the conformis- and erilli-groups) of Xenopsylla will be raised to the rank of genus in a separate publication. Pulicella is not known from the male and is not considered in the text. A single male of an as yet undescribed genus was discovered in material from the British Museum. With these changes, the subfamily will contain 10 genera. This is the largest subfamily with 99 species, 58 of these belonging to Xenopsylla (s.s.).

Xenopsylla Glinkiewicz, 1907
Plates 40 - 47.

The members of this large taxon are mostly confined to the Ethiopian and Palaearctic Regions. The group has traditionally been divided into eight species groups. The results of the present study have provided reasons for suggesting rearrangements of the taxa including the erection of one species group and the sinking of another. In addition it seems not unlikely that the genus is paraphyletic, and reasons for this will be explained below. Consequently two of the species groups, the erilli- and conformis-groups, are treated separately below. In order to make
the new arrangements clear, two lists are provided. The first, at the end of this section, lists the species according to the group placement suggested here. The second appears as Appendix II, where the species are arranged according to the classification found in Hopkins and Rothschild (1953), with species described since then listed according to the placement in the original descriptions.

In general the periphallic structures of the species in the genus as here defined are broadly comparable, but a great range of variation is found in the structures of the phallosome. The descriptions which follow are based on an examination of all of the 58 species. The nominate species for each group will be presented in some detail here, followed by a brief account of the nature of the group as a whole.

1. Species group: cheopis

Plates: Part I entire, and Part II, plates 40 & 41.

This group contains 15 species, which range from the Ethiopian through the Palaearctic and Oriental to the Australian regions. They are mainly parasites of murids and cricetids. *Xenopsylla cheopis* has been treated at length elsewhere. A brief survey of key features is included below.
Xenopsylla cheopis (Rothschild, 1903)

Lab Reared; Cosmopolitan.

Periphallic Structures: Boundary of 10T with 9T apodeme well marked; 9T apodeme reduced to vanishing. P1 0.45X as long as manubrium, 2.7X as long as broad. Manubrium thin, rod-like, forming base for clasper lobes. P2 mesal to and thinner than P1, subequal in length to P1. P3 hyaline, flap-like, mesal to P2. Parameral bridge membranous, associated with inner apodeme of P2. 8T, 8S unmodified. 9S with weak proximal arms, distal arms thin, flared somewhat distally. Musculature: M15: absent. M16-17: origin, proximal end manubrium, insertion near suspensory sclerites. M18: origin on proximal rim pygidial plate, insertion at base of P1. M20: origin on proximal rim pygidial plate, insertion near process of parameral bridge at base of P2. M23: origin at base of manubrium, insertion on proximal end aedeagal apodeme. M24: origin on proximal end manubrium, insertion on proximal end aedeagal apodeme.

Phallosome: Median lamina 6.5X as long as broad at base, 1.3X length of aedeagus. Penis rods strongly developed, lower rod more expanded proximally and shorter than upper; curling slightly less than 180 degrees over aedeagal apodeme; distal end lower rod expanded. Apodemal rod long, well developed. Median fulcral lobe large, lateral lobes thin, weakly connected to proximal process of inner tube; tectum flat, often collapsed; Y-sclerite bifid viewed from above. Suspensory sclerites weak.
Inner tube and vesicle with large lumen; dorsal apical tooth inner tube small. Aedeagal sheath 1.5X as long as broad at base, scaffolding apparent; crochets small, hook-like, lateral lobes well developed. Musculature: M25-26: origin proximal end lateral laminae, insertion at membranous base of crochets. M29: insertion near apex inner tube.

Comments

The group is divisible into 2 distinct sections. The cheopis-subgroup contains X. acomydis, X. aequisetosa, X. bantorum and X. cheopis. This assemblage is primarily Ethiopian, though X. acomydis is reported from Cyprus, and X. cheopis itself is cosmopolitan. The members of the astia-subgroup are linked with the cheopis-subgroup geographically by X. pestanai, X. versuta and X. nubica, the latter occurring as far east as Afghanistan. Xenopsylla dipodilll is known from Israel, Jordan and Sinai, X. nesokiae from Turkmeniya and Afghanistan. Xenopsylla astia and X. hussaini are endemic to the Oriental region. The remaining species occur in the Australian region.

The periphallic structures in all species in the cheopis-group are fairly uniform. P1 and P2 are small and approximately equal in size, except in X. hussaini where P2 is quite long. P3 is hyaline and lacks setae. The distal arm of 9S is generally simple, and about as long as the aedeagus, except in X. hussaini, where it is rather large.
Xenopsylla cheopis and its closest allies are distinguishable from the others in that they have a very simple inner tube armature, and the inner tube itself is less upturned and narrowed distally. All members of the group except X. cheopis, X. aequisetosa and X. bantorum have a ventral process of the inner tube just distal to the vesicle. In these species the armature of the inner tube tends to be formed of a toothed or ridged crochet which is more or less fused with a sclerite dorsal to the distal end of the inner tube as well as a confusing membranous area associated with the distal ends of the runners. There is also often a thickening of the lateral lobes of the end chamber.

Xenopsylla versuta and X. pestanai in general resemble the cheopis-subgroup and are distinct from the rest of the astia-subgroup in that the latter share high arching ribs with a large supratactal space, and a particularly short aedeagal apodeme.

2. Species group: trispinis

Plate 42, Fig. 130.

There are two species in the group, both parasites of birds in the Ethiopian region.
Xenopsylla trispinis Waterston, 1911.

LC: Transvaal.

Periphallic Structures: ST apodeme absent. P1 subequal in length to P2, slightly broader; P1 0.3X length of manubrium, 2.6X as long as broad. Manubrium long, rod-like, forming base for clasper lobes. P2 4X as long as broad, subequal in length to inner apodeme. P3 flap-like, hyaline distally. Process of parameral bridge formed from internal apodeme of P2. ST, SS unmodified. SS thin, constant breadth, upcurved distally, nearly as long as aedeagus.

Phallosome: Median lamina of aedeagal apodeme much as in X. cheopis, 5X as long as broad at base, 1.2X as long as aedeagus, lateral laminae indistinct. Penis rods large, upper expanded proximally, lower longer; curving 180 degrees over aedeagal apodeme. Apodemal rod well developed. Penis with distinct ventral rod. Median fulcral lobe tongue-like, straight; lateral fulcral lobes with sharp 60 degree angle, dorsal and ventral struts distinct; ventral struts articulate with proximal process of inner tube; tectum large, sinuous. Suspensory sclerites weak, not connected to base of manubrium. Inner tube and vesicle with large lumen, tapering distally as in X. cheopis. Aedeagal sheath at sharper angle to aedeagal apodeme than X. cheopis; runners and ribs prominent, dorsal arm pointed, upcurved; elaborate armature around distal end inner tube, tripartite, lateral lobes present, with heavy ventral margin.
Comments

The group is closest to the astia section of the cheopis-group, but shares characters with both subgroups. The aedeagal apodeme is very like X. cheopis, but the armature of the inner tube places it nearer the astia subgroup. The ventral process of the inner tube, lateral crochets, ventral runner complex and thickening of the lateral lobes of the end chamber are all present and very like those in the cheopis group. In addition, the shape and size of the penis rods, the aedeagal apodeme and the general conformation of the aedeagus itself all strongly suggest this placement.

3. Species group: nilotica.

Plate 42, Fig. 131.

With the additions proposed herein there are 12 Ethiopian species in this group. They are parasites of gerbils.

_Xenopsylla nilotica_ (J. & R., 1908)

LC #12532; Ethiopia.

Periphallic Structures: 9T apodeme absent. Manubrium thin, rod-like. P1 0.3X as long as manubrium, 4X as long as broad. P2 slightly shorter than P1, 1.5X as long as internal apodeme. P3 indistinct. Process of parameral bridge formed from internal apodeme of P2. 8T, 8S unmodified. 9S distal arm large, nearly
as long as aedeagus, free of apodemal rod.

Phallosome: Median lamina long, thin, 11.5X as long as broad at base. 2.1X length of aedeagus; lateral laminae indistinct. Penis rods large, well developed, upper rod expanded proximally, lower rod longer; curving 180 degrees over aedeagal apodeme. Apodemal rod well developed. Penis with distinct ventral rod. Capsule region proportionately smaller than in \textit{X. trispinis}; lateral arms with distinct 60 degree angle; median lobe pointed; tectum straight. Suspensory sclerites absent. Inner tube with strong proximal process, articulating with lateral fulcral lobes; vesicle large with prominent dorsal process; distal end inner tube with dorsal thickening. Aedeagal sheath with runners and ribs prominent; lateral lobes large, continuous with ribs, apex pointed; tripartite crochet apparatus; spiculose membrane of end chamber present.

Comments

This group, as it was then understood, was said to be "unsatisfactory" by Hopkins and Rothschild (1953), and to be closely linked to the \textit{brasiliensis}-group by the presence in the latter of \textit{X. mulleri}, \textit{X. trifaria} and \textit{X. scopulifer}. While \textit{X. scopulifer} clearly belongs in the \textit{brasiliensis}-group the others fall much more naturally within the \textit{nilotica}-group. Hopkins and Rothschild felt that \textit{X. mulleri} and \textit{X. trifaria} may well belong to the \textit{eridos} section of the \textit{cheopis}-group, but it is better to
place them with *X. nilotica* and recognize that the *nilotica*-group as a whole is close to the newly erected *eridos*-group, primarily on the basis of the inner tube armature. In fact, in characters of the phallosome, *X. trifaria* and *X. nilotica* are very closely allied.

The armature of the inner tube in all these species is built on a similar tripartite plan, the basic outline of which can be seen in *X. nilotica*. Most proximally is a ventral sclerite, crescentic or hook-shaped in lateral view. Distal to this is a finger-like lobe, and dorsally, laterad of the inner tube, is a fold which may represent the true crochet. The spiculose membrane of the end chamber lies within the limits of these structures.

The members of this group are distinguished from the *brasiliensis*-group by the lack of suspensory sclerites, the truncate inner tube and the conformation of the armature of the inner tube. The aedeagal apodeme is distinctive, though modified somewhat in *X. nilotica* itself, the ribs and the fulcrum area are different as well, being broader and dorsally arched. The sheath is truncate distally, rather than pointed as in *brasiliensis*-group members.

*Xenopsylla nilotica* and its allies are separable from the *eridos*-group, previously a section of the *cheopis*-group, most obviously by the length of the penis rods, which are hypertrophied in the latter. Members of the *eridos*-group exhibit
a distinctive aedeagal apodeme and fulcral region. *Xenopsylla nilotica* itself might arguably be placed in the *eridos* section. Both groups share similar inner tube armature as well as similar aedeagal sheaths. Other aspects of the phallosome are not obviously distinct. But while *X. nilotica* represents an intermediate anatomy in some respects, the penis rods and fulcral structures do place it within the *nilotica*-group, which might be better designated the *huminis* or *debilis*-group since these species are more characteristic for the group as a whole. It is thus possible that the *nilotica*-group is paraphyletic with respect to the *eridos*-group, but the latter is so easily recognized that it is best to keep them separate.

4. Species group: *eridos*

Plate 42, Fig. 132; Plate 43.

The *eridos*-group as defined here contains eight species which are restricted to southern Africa. They are mostly parasites of gerbils.

*Xenopsylla eridos* (Rothschild, 1904)

LC #15590; S. Africa.

Perifhallic Structures: Not markedly different from *X. cheopis*. ST apodeme absent. Manubrium rod-like. P1 subequal in length to P2. P1 0.3x length of manubrium; less than 3x as long as broad. P3 hyaline. Apodeme of P2 forming process of
parameral bridge. 9T, 8S unmodified. Distal arm 9S thin, as long as aedeagus.

Phallosome: Median lamina of aedeagal apodeme narrow, 7X as long as broad, pointed apically; 2x as long as aedeagus. Lateral laminae hyaline, fused with ribs distally. Penis rods very large, long, curling 360 degrees. Apodemal rod well developed. Lateral fulcral lobes stout, sharply angled. Tectum small, flat. Vesicle large. Suspensory sclerites absent. Inner tube small, tapered distally. Aedeagal sheath upturned and pointed distally; ribs large, broad; runners expanded distally, armature of inner tube tripartite, membrane of endchamber spiculose.

Comments

Members of this group are easily recognized by the long penis rods and the knife-like aedeagal apodeme. Those species in which the penis rods are not greatly elongate still exhibit a broadly circular form which distinguishes them from the less regular arcs of other species in the genus. The ribs in these species do not arch, and extend in a more or less straight path to the latero-ventral area of the sheath. The armature of the inner tube is fundamentally the same tripartite structure as described above for the nilotica-group.

Hopkins and Rothschild (1953) expressed some doubt as to whether X. frayi should be included in the original cheopis-group, but conclude that it is a close relative of X. phyllomae.
This is surely borne out by the genitalic characters.

5. Species group: *brasiiliensis*

Plate 44, Fig. 135.

All of the 17 taxa in this group are from the Ethiopian region, except *X. brasiiliensis* itself, which has become cosmopolitan as a result of human activities. They parasitize a wide range of rodent hosts.

*Xenopsylla brasiiliensis* (Baker, 1904)

LC #6975; Tanganyika.

Periphallic Structures: 9T apodeme absent. Manubrium long, thin. P1 0.4X length of manubrium, with strong setae present marginally. 3.75X as long as broad, with strong setae. P2 long, strong, upcurved apically, 1.3X length of inner apodeme. P3 hyaline. Process of parameral bridge formed from internal apodeme of P2. 8T, 8S unmodified. 9S distal arm large, subequal in length to aedeagus.

Phallosome: Median lamina thin, 11.0X as long as broad at base, 1.7X length of aedeagus; lateral laminae indistinct, fused with ribs dorsal to crescent sclerite. Penis rods not heavy, not curling over aedeagal apodeme; apodemal rod strong basally. Lateral fulcral lobes strong, median lobe heavy, decurved distally, with median dorsal process; tectum small, straight. Proximal spur slightly sclerotized distally. Suspensory
sclerites present. Inner tube with heavily tanned proximal process; dorso-proximal bulge present; vesicle large, hemispherical, strong dorsal process; distal end inner tube tapering, with dorsal notch. Aedeagal sheath with strong girdle, ribs, wide runners; distal end unclear in available material; crochet present, simple; spiculose membrane present on ventral portion of endchamber.

Comments

As suggested by Hopkins and Rothschild (1953), *X. mulleri* and *X. trifaria* do not belong in this group. However, they retained these species on the basis of the shape and origin of the antepygidial bristles, but similar anatomy can be found elsewhere (e.g., in the *hirsuta*-group), and this is thus not a good character to unite the group. They considered these species to be close to the *eridos* section of the *cheopsis*-group, but they are better placed in the *nilotica*-group.

The members of the *brasiliensis*-group are quite distinctive. P2 is long and upturned apically and P1 bears heavy setae. The aedeagal apodeme is blade-like, the inner tube long and tapering, and usually strongly decurved. Suspensory sclerites and/or a proximal spur are present in all members of the group. The aedeagal sheath is pointed distally. All members of the group, with the possible exception of *X. cornigera*, exhibit a spiculose membrane in the endchamber. Most members of the *torta* section
have very large and distinctive lateral crochets. These are particularly large with distal claws in some members of the section (X. bechuane, X. crinita, X. scopulifer, X. torta). In other members of the group these are absent entirely.

6. Species Group: hirsuta

Plate 44, Fig. 136.

There are 6 species in the group, all are Ethiopian, and most parasitize cricetids.

Xenopsylla hirsuta hirsuta Ingram, 1928

LC; Cape Province, S. Africa.

Periphallic Structures: ST apodeme absent. Manubrium very thin and pointed. P1 greatly reduced, 0.3X length of P2. P2 0.3X length of manubrium, 3X as long as broad. P3 as ventral expansion of manubrium. Parameral bridge apparently formed of apodeme of P2, strengthened by internal ridge of base of manubrium (seen to a lesser extent in X. nilotica and X. brasiliensis). ST unmodified, 8S with ventral bulge below 9S. Distal arm 9S large, broad and heavily tanned, subequal in length to aedeagus. Musculature: Inner flange of base of manubrium bears insertion for M23. Flange more developed than in X. cheopis and closer to base of apodeme P2.

Phallosome: Median lamina teardrop shaped, constricted basally, expanded and rounded proximally, 3.5X as long as width
at broadest point, 1.8X as long as aedeagus; lateral laminae large, similar in shape to median, fused with fulcral area above lateral fulcral lobes. Penis rods heavy, short, not much curved above aedeagal apodem; similar in size and shape; Apodemal rod very stout, somewhat longer than aedeagal apodeme. Capsule area compact, lateral lobes heavy, broadly fused to median lobe; median lobe triangular in lateral view; tectum small, flat. Suspensory sclerites present, may be difficult to see; proximal spur present, dorsad of tectum. Inner tube simple, smoothly tapered to distal end; vesicle large with strong dorsal process. Aedeagal sheath with strong ventral connection to apodemal rod; lateral lobes present, sclerotized; apex pointed; crochet probably single; spiculose membrane of end chamber present.

Comments

The group does not display great diversity. The periphthallic structures are similar in general to those in the cheopis-group. The manubrium is long, P1 is small to very small, P3 hyaline. SS bears a row of heavy setae near the posterior margin, and these may be numerous and very heavy in some species. SS is generally large and broad medially. The group has been well reviewed by Haeselbarth (1964).
There are 15 species in this taxon, ranked as a species group within *Xenopsylla*. The group merits elevation to generic status. They range from N. Africa through Xinjiang Province, PRC, and mainly parasitize cricetids. As defined here the group contains *X. gratiosa* which is a parasite of *Puffinus* reported from the Canary Islands. *Xenopsylla gratiosa* was given species group status by Hopkins and Rothschild (1953).

*Xenopsylla conformis conformis* (Wagner, 1903)

LC #11606; Iran.

Periphallic Structures: 9T apodeme absent. Manubrium short, tapered apically. P1 0.7X as long as manubrium, 3X as long as broad. P2 subequal in length and breadth to P1, internal apodeme absent; P3 large, appearing as extension of base of manubrium; subequal in length and breadth to P1. Parameral bridge not well developed. 8T and 8S unmodified. Distal arm 9S large, broad, subequal in length to aedeagus, closely associated at base with apodemal rod; Proximal arm hyaline, reduced, arising distad of most proximal portion of distal arm.

Phallosome: Median lamina constricted basally, arched medially, flared and rounded proximally, 4X as long as width at broadest point, 1.8X length of aedeagus. Penis rods similar in
shape and length, not curled over aedeagal apodeme; apodemal rod well developed, extending beyond aedeagal apodeme. Capsule area compact, at angle to long axis of aedeagal apodeme; lateral fulcral lobes long, extending considerably beyond median lobe; tectum large, straight, extending distad of median lobe. Suspensory sclerites not strong if present; proximal spur present, not usually well defined. Inner tube strongly decurved distally, with prominent dorsal knob at midpoint; proximal process small; vesicle large, strong ventrally; distal end with spiculose spiral striations. Aedeagal sheath large, trumpet shaped distally, flaring dorsally, with wings flanking inner tube; S-shaped thickenings of wings present.

Comments

This is a homogeneous assemblage characterized by the following features: short manubrium, broad Pl in most species, short penis rods, a teardrop shaped aedeagal apodeme with constricted neck, a compressed fulcral area, decurved, tapering inner tube with spiculose terminal vestment, bell-shaped and detached dorsal aedeagal sheath, latero-ventral wings usually with lateral thickenings. In many species in the group, there is a spiculose area at the inner base of the wings. This is particularly noticeable in X. gerbilli gerbilli. Suspensory sclerites or proximal spur generally present, but weak. Distal arm 95 closely associated with apodemal rod; proximal arms
present, hyaline, reduced, not fused with girdle.

The structure of the 9th sternum and detailed resemblances of the aedeagus indicate the close affinities between *Synosternus* and this group. In particular, the presence of the spiculose area at the inner base of the wings in both groups argues for their status as sister taxa.

*Xenopsylla gratiosa* has been distinguished from the *conformis*-group solely on the basis of tarsal and femoral chaetotaxy. These characters are adaptations peculiar to bird fleas (Traub, 1972b). On the basis of genitalic characters the species is indistinguishable from species of the *conformis*-group and should be included in it since it is likely a sister taxon to some part of that group.

*Xenopsylla gratiosa* Jordan and Rothschild, 1923

*LC; Greece.*

Periphallic Structures: Pygidial plate reduced, not as much as in *X. conformis*, 9T apodeme absent. Manubrium short. P1 0.6X length of manubrium. P2 subequal in length to P1, 0.5X as broad. P3 slightly broader than P1, 0.75X as long as P1. Parameral bridge membranous. 8T, 8S unmodified. 8S distal arm broad, associated at base with apodemal rod.

Phallosome: Median lamina teardrop shaped, constricted basally, flared, rounded proximally, 4+X as long as broad at broadest measure, 1.6X length of aedeagus. Penis rods similar in
length, upper rod expanded proximally, apodemal rod well
developed; **v**irga ventralis nearly length of aedeagal apodeme.
Capsule area compact; lateral lobes long, median lobe distally
knobbed; tectum straight, shifted distally. Suspensory sclerites
present, weak. Inner tube strongly decurved distally, with
prominent spiral toothed striations over distal half; vesicle
large with strong dorsal process. Aedeagal sheath large,
trumpet-like, apex pointed; lateral wings large.

8. Species group: **erilli**

Plate 45, Fig. 139.

The 2 species in this group are parasites of squirrels of
the Ethiopian region. They have traditionally been considered a
species group within *Xenopsylla*, but merit the rank of genus.

*Xenopsylla erilli* (Rothschild, 1904).

BM(NH), paralectotype; Cape Colony.

Periphallic Structures: ST apodeme absent. Manubrium
short, tapering gradually, blunt apically. P1 0.75X length of
manubrium, 5.7X as long as broad. P2 2X as broad as long, and
slightly longer than P1; P3 short, broad basally. Parameral
bridge indistinct. ST,SS unmodified. Distal arm SS even breadth
over length, approximately same length as aedeagus. Proximal arm
broad basally, attached distad of proximal point of distal arm.

Phallosome: Median lamina constricted basally, flared
slightly proximally, 6X as long as broad at broadest point, 1.6X length of aedeagus. Penis rods short, not curling above aedeagal apodeme; apodemal rod well developed, shorter than penis rods. Capsule area compact, lateral lobes slightly longer than median, median rounded distally; tectum arched, extending beyond median lobe; Proximal spur may be visible as membrane, suspensory sclerites weak or absent. Inner tube decurved distally with prominent dorsal tooth; vesicle large. Aedeagal sheath not strongly tanned, attached only basally, median dorsal lobe pointed dorsally, ribs continuous with lateral lobes. Wings large, elongate ellipsoidal.

Comments

These species are quite similar. The aedeagal sheath and elongate wings are characteristic for the group. *Xenopsylla cryptonella* has a spiculose membrane at the distal end of the inner tube, and a much more heavily developed girdle and wing base.
Xenopsylla (s.l.): Species List
Arranged according to proposed group limits
Species may be arranged alphabetically or geographically

1. cheopis-group:
a. cheopis subgroup:
  acomydis Reus, 1977
  aequiseta Enderlein, 1901
  bantorum Jordan, 1938
  cheopis Rothschild, 1903
b. astia subgroup:
pestanai Ribeiro, 1975
  versuta Jordan, 1925
  nubica Rothschild, 1903
  dipodilli Smit, 1960
  nesokiae Ioff, 1946
  astia Rothschild, 1911
  hussai Sharif, 1930
  nesiotes (J. & R., 1908)
papuensis Jordan, 1933
  vexabilis Jordan, 1925
  australiaca Mardon & Dunnett 1971

2. trispinis-group:
moucheti Smit, 1958
  trispinis Waterston, 1911

3. nilotica-group:
coppensi Beaucornu, Houin & Rodhain 1970
  debilis Jordan, 1925
  difficilis Jordan, 1925
  humilis Jordan, 1925
  jorgei Ribeiro, 1975
  mulleri De Meillon, 1947
  nilotica (J. & R., 1908)
  orientalis Marcus, de Meillon & Davis, 1960
  raybouldi Hubbard, 1963
  silvai Ribeiro, 1975
  tangenykensis Marcus, de Meillon & Davis, 1960
  trifaria de Meillon, 1930

4. eridos-group:
aridos Rothschild, 1904
  frayi de Meillon, 1937
  geldenhuysj de Meillon, 1949
  hipponax de Meillon, 1942
  occidentalis de Meillon, 1938
  philoxera Hopkins, 1949
5. *brasiliensis*-group:

- angolensis Ribeiro, 1975
- bechuanae de Meillon, 1947
- crinita J. & R., 1922
- syngenesis Jordan, 1937
- torta (J. & R., 1908)

- *brasiliensis* (Baker, 1904)
- cornigera Smit, 1956
- hamula Jordan, 1925
- morgandaviesi Hubbard, 1963
- robertsi Jordan, 1936
- zumpti Haeselbarth, 1963

- georychi (C. Fox, 1914)
- graingeri Smit, 1956

- sarodes sarodes Jordan, 1937
- sarodes manyarensis Hubbard, 1963
- sarodes serengetiensis Hubbard, 1963
- scopulifer (Rothschild, 1905)

6. *hiruta*-group:

- *hiruta* hirsuta Ingram, 1928
- *hiruta* multiseta Haeselbarth, 1964
- *hiruta* placida de Meillon & Hardy, 1951
- lobengulae de Meillon, 1930
- sulcata Ingram, 1928

- demeilloni Haeselbarth, 1964
- davisi de Meillon, 1940
- petteri Lumaret, 1962

7. *conformis*-group:

- *bianci* Smit, 1957
- *cunicularia* Smit, 1957
- *ramesis* (Rothschild, 1904)
- *taractes* J. & R., 1913

- *buxtoni* Jordan, 1949
- *conformis conformis* (Wagner, 1903)
- *conformis dipodes* Ioff, 1953
- *conformis mycerini* (Rothschild, 1904)
- *gerbilli gerbilli* (Wagner, 1903)
- *gerbilli caspica* Ioff, 1950
- *gerbilli minax* Jordan, 1926
- *hirtipes* Rothschild, 1913
magdalinae Ioff, 1935
nuttalli Ioff, 1930
persica Ioff, 1946
skrjabini Ioff, 1930
regis (Rothschild, 1903)
tarimensis Yu & Wang, 1979

gratiosa J. & R., 1923

8. erilli-group:
cryptonella de Meillon & Hardy, 1954
erilli (Rothschild, 1904)
Synosternus Jordan, 1925
Plates 48 - 52.

The six species of this genus parasitize a wide range of mammalian hosts. The group is distributed from Africa, through Central Asia to India.

**Synosternus pallidus** (Taschenberg, 1880)

LC #7839; Afghanistan.
Plates 48 - 50.

Periphallic Structures: ST apodeme absent. Manubrium long, tapered proximally. P1 4x as long as broad, more than 1.8x as long as manubrium, shaped as in *X. cheopis*, internal apodeme absent. P2 similar in shape to P1, 0.6x as long as broad. Parameral bridge formed near base of inner apodeme of P2. ST, 8S unmodified. Distal arm 9S thin, as long as aedeagus and closely associated with base of apodomal rod and lateral area of girdle; broad basally, tapering and upcurved distally. Proximal arm hyaline, attached to distal arm distad of proximal end of latter.

Phallosome: Aedeagal apodeme teardrop shaped overall, constricted basally, 4.5x as long as broad at broadest point, approx. 2.25x as long as aedeagus. Lateral laminae hyaline, not fused with lateral fulcral lobes. Penis rods usually curved through 90 degrees. Apodomal rod stout. Capsule region compressed, lateral fulcral lobes thick, curvature shallow; median lobe relatively large, dorsal margin swollen distally,
tectum arched. Y-sclerite bifid. Suspensory sclerites absent. Inner tube with strong walls and proximal process; of constant breadth over proximal 2/3, distal 1/3 smaller, tapered, upcurved, with dorsal tubercle; ventral surface spined; conspicuous brush present ventral to distal end of tube. Vesicle strong. Ribs small, lying laterad of capsule, continuous with median dorsal lobe of aedeagus. Lateral wings present, projecting freely from sheath near base of inner tube. Crochets absent. Small area of minute spicules on inner face of base of wings. Median dorsal lobe of sheath pointed apically, freely detached from inner tube along length.

M29 may be present and inserted on tubercle of inner tube.

Notes on Function

Occasional specimens found with the genitalia everted provide a clue as to the mechanism of these remarkable structures. The lateral wings are seen to swing open and downward, while the unsheathed brush hangs freely. Extension of the lateral wings is probably produced by contraction of M25-26 operating on a hinge-like mechanism at their base in a manner reminiscent of that seen in Ctenocephalides species, though the hinge operation here is less clear. Contraction of M29 may serve to vibrate the brush during copulation in a manner analogous to the vibration of the flaps of the clasper lobe described for Archaeopsylla.
Comments

*Synosternus pallidus*, *S. caffer*, *S. burtoni* and *S. somalicus* are probably all quite similar (not all of these were available for this study), though there is variation in the periphallic structures. *Synosternus longispinus* and *S. cleopatrae* exhibit features which set them apart from the above species.

*Synosternus longispinus* (Wagner, 1893)

LC #7787; Afghanistan.

Plate 51, Fig. 153.

Manubrium fused rigidly to pygidial plate. P1, P2 very narrow and long, subequal in length, more than 2x as long as P3. P3 setose. Aedeagal apodeme very long and thin, 15x as long as broad at broadest point. Lateral fulcral lobes very stout, broadly fused with median lamina proximally, and with inner tube distally; median lobe reduced, dorsal margin hook-like in lateral view. Proximal end inner tube greatly thickened and expanded dorsally; distal end upcurved with spiculose membrane as in *S. cleopatrae*. Median dorsal lobe aedeagus large; wings hyaline, reduced in length. 9S large, sinuous, as long as aedeagus; closely associated with base of apodemal rod and girdle; proximal arm apparently absent, or hyaline.
Synosternus cleopatrae cleopatrae (Rothschild, 1903)

LC #15286; Jordan.

Plate 51, Figs. 154, 155; Plate 52.

Manubrium and pygidial plate more rigidly fused than in S. pallidus. P2 proportionately longer, P3 proportionately narrower. Suspensory sclerites present but weak. Aedegal apodeme generally as S. pallidus, but decurved basally. Lateral laminae fused with lateral fulcral lobes. Inner tube strongly arched, and with thicker walls proximally than S. pallidus, distal tubercle large, unique; spiculose membrane of end chamber large, bag-like. Ribs appear weak in lateral view, but are actually strong and quite wide when seen from above; lateral wings present, broader than in S. pallidus, with S-shaped thickening when seen in lateral view. Distal arm SS simple, as long as aedeagus, closely associated with base of apodemal rod. Proximal arm broad basally, not arising from proximal end of distal arm.

Comments

Synosternus pallidus is a good representative for the genus since it exhibits the major characters. Synosternus pallidus, S. caffer and probably S. somalicus and S. burtoni form a natural group based on clasper and manubrium structure as well as the basic form of the phallosome. The 9th sternum in the genus is closely associated with the apodemal rod and girdle, and though
the proximal arm is present primitively as in *S. cleopatrae*, it is reduced or absent in the other members of the genus.

*Synosternus pallidus* apparently exhibits an intermediate condition in which the proximal arm is present, but is detached entirely from the distal arm. The bracing function of the distal arm is taken over by the lateral areas of the girdle; this is particularly clear in *S. longispinus*. *Synosternus longispinus* is quite unique in the structure of the periphallic organs and differs from all other members of the genus in the extreme hypertrophy of the inner tube and in the reduction of the wings.

*Synosternus cleopatrae* exhibits the basic structure of the periphallic organs characteristic of the genus and the basic characters of the phallosome are similar: the hypertrophy of the inner tube, the presence of lateral wings and the development of the spiculose membrane of the end chamber. This species is, however, the most important in the genus from the point of view of classification. The striking similarities between the phallosome of *S. cleopatrae* and that of members of the *conformis*-group of *Xenopsylla* provided the key to the arrangement suggested here. Thus *S. cleopatrae* likely represents a primitive state for this genus, the other species representing elongated versions of this.

**Taxa:**
- *burtoni* Marcus and DeMeillon, 1960
- *caffer* (J. & R., 1923)
- *cleopatrae cleopatrae* (Rothschild, 1903)
The five species in the genus are found solely on the island of Madagascar. The hosts are rodents and other small mammals.

**Synopsyllus fonquerniei** Wagner & Roubaud, 1932

Plate 53.

Periphallic Structures: ST apodeme absent. Manubrium long, thin. P1 fan-like, 1.6x as long as broad. 0.25x as long as manubrium. P2 slightly longer than P1, blade-like. P3 indistinct, ventral to P1, P2. Parameral bridge formed by membrane connecting well developed internal apodeme of P2. S8 with row of long, stout setae, ST unmodified. Distal arm S8 sinuous, tapering distally.

Phallosome: Aedeagal apodeme more or less rectangular, 3.5x as long as broad at base, slightly longer than aedeagus; median lamina may be absent. Penis rods barely curving 180 degrees over aedeagal apodeme. Apodemal rod very stout, constricted basally. Lateral fulcral lobes possibly fused with lateral laminae, sharply angled, tapering distally. Median lobe short, broad, fused with dorsally extended median lamina. Capsule small,

Comments

Species other than S. fonquernei were not available for study, and analysis of the genus is based on illustrations in the literature. Those provided by Klein (1964, 1965a,b) are especially clear. Variation occurs most notably in the shape of P1, and in the basal breadth of the aedeagal apodeme and thus in the height of the ribs above the capsule area. Both measures are quite variable. Among S. fonquernei, S. smiti, S. girardi and S. estradei, the breadth of the apodeme is positively correlated with the breadth of P1. However S. robici exhibits a very narrow apodeme and a very wide clasper lobe. These measures are both smallest in S. estradei, increasing in S. smiti and are largest of all in S. fonquernei and S. girardi. In S. robici the supratectal space is small as that in S. estradei, but P1 is
quite broad and triangular. These relations combined with the fact that the phallosomes of S. fonquernei and S. girardi do not seem out of place in relation to other genera in the subfamily suggest that S. estradei is the primitive form for the genus. Thus a broad P1 is probably a derived character of the genus, rather than a primitive character similar to that seen in the Archaeopsyllinae for instance, as suggested by Hopkins and Rothschild (1953).

Good derived genital characters may be restricted to the inner tube armature, but more species would need to be studied in detail. It is difficult to tell from the material at hand but the median lamina appears to be absent in S. fonquernei, and Klein's illustrations suggest that this may be true for the genus as a whole. If so, this would be a good derived character, shared only with Echidnophaga, which is unrelated to this group. The genus shares with the hirsuta-group of Xenopsylla the loss or reduction of the metasternal/metaepisternal suture, and both have heavy setae on 8S.

Taxa:
estradei Klein, 1984
fonquernei Wagner & Roubaud, 1932
girardi Klein, 1966
robici Klein, 1966
smiti Lumaret, 1962
Parapulex Wagner, 1910

Plate 54.

Both species in the group are parasites of spiny mice of the genus Acomys. Parapulex chephrenis is mainly Palearctic, P. echinatus is from the Ethiopian region.

Parapulex chephrenis (Rothschild, 1903)

LC #15475; Saudi Arabia.

Periphallic Structures: 9T apodeme absent. Manubrium thin. P1, P2 membranous at base. P1 short, conical, less than 3x as long as broad at base, less than 0.4x as long as manubrium. P2 1.8x as long as P1, nearly equal in breadth. P3 small, pointed in lateral view. Parameral bridge membranous, internal apodeme P2 reduced. 8T, 8S unmodified. Distal arm 9S broad, paddle-like, as long as aedeagus and closely associated with apodemal rod; proximal arm sinuous, very thin.

Phallosome: Aedeagal apodeme thin, constricted basally, more than 11x as long as broad at broadest point, 1.9x as long as aedeagus. Penis rods short, not much curved over aedeagal apodeme. Apodemal rod stout. Lateral fulcral lobes with ventro-proximal projection, fused with median lamina; median lobe large, Knob-like, tectum arched, strong. Proximal spur may be visible as dorsal membrane. Inner tube distinctive with very large proximo-dorsal expansion, tapering to thin, upcurved distal end. Ribs strong, angular, close to capsule. Median dorsal lobe
of sheath truncate, shorter than inner tube; lateral wings large, elongate, acuminate distally. Ventral membrane of sheath produced and thickened ventral to tip of inner tube.

Comments

Genitalic differences between the two species are minimal. Distal arm 98 larger in P. echinatus, wings less pointed. The genus is unique in the shape of the inner tube and in the overall form of the body and the presence of spiniform setae.

Taxa:
chephrenis (Rothschild, 1903)
echinatus Smit, 1956

Procaviopsylla Jordan, 1925

Plate 55, Fig. 162; Plate 56.

The six species in the genus are all parasites of hyraxes of the Ethiopian region.
Procaviopsylla divergens J. & R., 1908

LC #15589: S. Africa.

Periphallic Structures: 9T apodeme reduced to small projection. Manubrium short, thin. P1, P2 subequal, membranous at base; P1 more than 4x as long as broad, 0.6x as long as manubrium. Apodeme of P2 reduced. P3 hyaline, broadly rounded. Parameral bridge strengthened with central thickenings near the base of P3 which are likely origins of M23. Distal arm 95 large, expanded distally, not as long as aedeagus, apex slightly acuminate; proximal arm broad, blunt dorsally.

Phallosome: Aedeagal apodeme 5.0x as long as broad at broadest point, constricted basally, 1.5x as long as aedeagus. Median lamina thickened at dorsal and ventral margins, lateral laminae hyaline. Penis rods short, not much longer than aedeagal apodeme. Apodemal rod stout. Lateral fulcral lobes fused with lateral laminae, strong, broadly curving. Median lobe dorsal margin strong, curved. Tectum arched, distal to median fulcral lobe. Suspensory sclerites weak or absent. Inner tube large, expanded proximally, with dorsal dome, distal end with dorsal tooth, apex constricted. Vesicle large. Ribs strong, widely flaring laterally; median dorsal lobe broad, blunt; lateral lobes wide. Lateral wings elongate ellipsoid. Accessory lobe of wings present, appearing as claw shaped sclerotization, medial to wings.
Comments

There is some question as to whether *P. creusae* and *P. divergens* are actually different species. They are said to be synhospitalic (Hopkins and Rothschild, 1953), and are very close anatomically. The above description is based on a single specimen identified as *creusae*, but which exhibits a mix of characters. The basic genital anatomy of the genus is quite uniform in any case. Variations may occur in the angle between the aedeagal apodeme and the aedeagus, the degree of curvature of the lateral fulcral lobes, the degree of sclerotization of the accessory lobes of the wings, the extent of the proximal expansion of the inner tube and the shape of the distal arm of *SS*, as well as the shapes and relative sizes of the clasper lobes.

Distinctions in the genital anatomy between *Procaviopsylla* and *Pariodontis* is of a degree which could well be considered to delimit species within a genus. However the body form in *Pariodontis* is radically different from that in *Procaviopsylla*. This situation in which the genital anatomy is very close while the fascies are so remote is unique in the Pulicoidea.

Taxa:

*angolensis* Jordan, 1925  
*creusae* (J. & R., 1904)  
*divergens* (J. & R., 1908)  
*isidis* (Rothschild, 1903)  
*procaviae* (Fox, 1914)  
*spinifex spinifex* Jordan, 1936  
*spinifex cabrali* Ribiero 1975
Pariodontis Jordan & Rothschild, 1908

Plate 55, Fig. 163.

There are two species in the genus, *P. riggenbachii*, with 3 subspecies, and *P. subjugis*. All are mainly parasites of Old World porcupines.

*Pariodontis riggenbachii riggenbachii* (Rothschild, 1904)

LC #9093; Ethiopia.

Periphalic Structures: ST apodeme reduced to small projection on either side of 10T. Manubrium stout, 10x as long as broad. P1, P2 membranous at base. P1 more than 9x as long as broad, 0.7x as long as manubrium. P2 slightly shorter and broader than P1. P3 broad, setose. Parameral bridge associated with development of base of P3, internal apodeme P2 very short. Distal arm SS large, expanded distally, as long as aedeagus.

Phallosoma: Aedeagal apodeme strongly constricted, decurved at base, 5x as long as broad at broadest point, 1.7x as long as aedeagus. Median lamina thickened at dorsal and ventral margins. Penis rods very short, not curving over aedeagal apodeme. Apodemal rod stout, about as long as rods. Lateral fulcral lobes fused with median lamina, broadly curved; median lobe strong, projecting distally. Tectum small, tanned portion continuous with inner tube dorsally. Suspensory sclerites absent. Inner tube expanded basally with dorsal dome and strong proximal projections, slightly decurved distally. Vesicle strongly
margined. Ribs well developed, arched, flaring widely laterally; sheath with large, blunt median dorsal lobe, lateral lobes large. Wings not apparent in available material; accessory sclerite apparently present as in Procaviopsylla. M25-26 inserts near distal end of accessory sclerite.

Comments

The group is homogeneous and differences between P. r. riggenbachi and P. subjugis are not pronounced. Pariodontis subjugis bears large sclerotizations medial to base of P3, probably serving as insertions for M23 as well as forming the parameral bridge. This association of P3 with the bridge is primitive for the genus. The distal arm of 9S is reduced in P. subjugis.

Taxa:
riggenbachi riggenbachi (Rothschild, 1904)
riggenbachi turkestanica Dubinin, 1947
riggenbachi werneckii Costa Lima, 1940
subjugis Jordan, 1925
Genus X

Plate 55, Fig. 164.

This genus is known from a single male in the British Museum(NH) Collection, and will be described in a later paper. It was collected in Tanganyika on Otomys angoniensis.

Periphallic Structures: Apodeme 9T present, elongate triangular in lateral view. Manubrium thin, rod-like, not broadly fused with apodeme. P1, P2 subequal in length. P1 more than 5.5X as long as broad. P2 slightly broader than P1. Apodeme P2 short. P3 triangular, large, broadly fused with base of manubrium, bearing single tooth-like spiniform ventro-medially. Distal arm 9S as long as aedeagus, broad basally, tapering distally.

Phallosome: Aedeagal apodeme 10X as long as broad, 3X as long as aedeagus; constricted basally, smoothly tapering and upcurved apically, ending in filiform projection. Ventral margin median lamina strong, lateral laminae hyaline. Penis rods curving 360 degrees over apodeme. Apodemal rod well developed. Lateral fulcral lobes apparently fused with lateral laminae; thin, broadly curved. Median dorsal lobe dorsal margin strong, curved. Suspensory sclerites absent. Inner tube large, expanded proximally with dorsal dome; strong walls over proximal 2/3; proximal projections prominent; smoothly tapering overall. Vesicle large, strongly margined. Ribs developed laterally into small pads lying dorsad of lateral fulcral lobes; sheath tapered
distally, pointed at dorsal apex. Lateral lobes indistinct, wings not clearly discernible; accessory lobes apparently absent.

Comments

The body of this species is xenopsylline in general fascies. The genitalic anatomy places it with *Procaviopsylla* and *Pariodontis* though it clearly differs from both. The presence of g7T is unusual among Xenopsyllinae and is considered to be a reversion; traces of it occur in *Procaviopsylla* and *Pariodontis* as well. The filiform apex of the aedeagal apodeme is a derived character of this genus, but is also found in the eridos-group of *Xenopsylla*. The pad-like development of the ribs and the absence of accessory lobes also set the genus apart from its closest relatives.

*Puiicellia* Smit, 1964.

The male of this genus is unknown.
SPILOPSYLLINAE Oudemans, 1909

Plates 57 - 64.

There are twelve species and six subspecies in six genera in this largely New World group. The hosts are mostly lagomorphs and their predators. Two genera infest ground nesting sea birds, and are evidently derived from rabbit infesting ancestors.

Cediopsylla Jordan, 1925

Plates 57 - 61.

The four species and two subspecies in this genus are parasites of New World rabbits and hares.

Cediopsylla inaequalis interrupta (Baker, 1895)

LC #12574; Oregon.

Periphallic Structures: 9T apodeme large, constricted medially. Manubrium broadly fused basally with 9T apodeme, elongate triangular, blunt proximally. P1 very large, bilobed; dorsal lobe 1.7x as long as broad at broadest point, 1.2x as long as manubrium, triangular, distal spiniform present; ventral lobe 0.66x as long as dorsal, distal margin truncate. Parameral bridge as membranous connection between strong internal apodemes of P1, strongly curved ventrad in lateral view. Short lateral
lobes of anal sternum present. P2, P3 forming pincers, less than 0.5x as long as P1, approximately equal in length. P2 slightly broader, P3 sharply elbowed near basal third. 8T with lateral margins slightly thickened near 8th tergal tracheal trunk, seen as tooth or spur. 8S modified by presence of small medio-ventral paired lobes with basal setae. 9S distal arm large, expanded, nearly as long as aedeagus, broad basally, constricted medially, expanded distally with flared lateral lobes, large heavy setae along ventral margin medially. Musculature: M12: origin dorso-lateral margin 9T apodeme, insertion near latero-ventral margin pygidial plate. M15: origin distal end manubrium, insertion proximal arm 9S. M16-17: origin distal end manubrium, insertion near lateral wall aedeagal pouch. M20: origin dorso-proximal margin 9T apodeme, insertion near base P2. M21: origin dorsal margin manubrium, insertion near base P2. M22: origin dorsal margin P1, insertion near base P3. M23: origin proximal end aedeagal apodeme, insertion ventral margin manubrial base, near base of P3.

Phallosome: Aedeagal apodeme narrow, of constant breadth, 7.5x as long as broad at broadest point, 4.5x as long as aedeagus. Lateral laminae hyaline, not fused with fulcrum. Small dorso-proximal fin present. Penis rods curling 180 degrees over aedeagal apodeme; apodemal rod well developed, nearly as long as penis rods. Fulcrum large, appended from median lamina, lateral fulcral lobes thin, broadly curved, median lobe broad.
tectum small, slightly arched. Lateral shafts prominent. Suspensory sclerites absent. Inner tube with proximal projection strongly fused with lateral fulcral lobes; tube simple, shallowly S-curved distally with large proximally directed dorsal tooth. Vesicle prominent with strong dorsal projection. Aedeagal sheath lacking scaffolding; proximal lobes of lateral walls projecting latero-dorsally, medial hooks projecting latero-ventrally, distal latero-ventral lobes and large bifid hood. Ford's sclerite present, large, strongly arched in lateral view; crochets large, broad, palmate, lying ventro-distally to apex of inner tube. Musculature: M25-26: origin proximal end aedeagal apodeme, insertion near base of crochets. M28: absent(?).

Notes on Function

The distal arm of SS couples with the ventro-lateral hooks of the aedeagal sheath, and SS and the aedeagus no doubt move as a unit. It is possible that SS assists in the protrusion of the aedeagus, thus explaining the apparent loss of M24.

Comments

Variation between the subspecies of C. inaequalis and C. simplex is not especially marked. Most notable are differences in the width of the aedeagal apodeme, the shape of the crochets and Ford's sclerite, it is bifid in C. simplex, and of the distal arm of SS and ventral lobe of SS.
Cediopsylla spillmani was not included in the material under study, but the genitalia are said by Jordan (1930) to be close to C. simplex. The genitalia of C. tepolita are well illustrated by Barrera (1967). Further study is necessary before definitive statements can be made, but the apparent absence or reduction of the crochets, along with the reduction of the ventral lobes of PI suggest close affinities between C. tepolita and Spilopsyllus cuniculi. It may be that C. tepolita and S. cuniculi should be regarded as one subgenus of an expanded Spilopsyllus, the remaining species of Cediopsylla constituting the other.

Taxa:
inæqualis inæqualis (Baker, 1895)
inæqualis interrupta Jordan, 1925
simplex (Baker, 1895)
spillmani Jordan, 1930
tepolita Barrera, 1967

Spilopsyllus Baker, 1905
Plate 62, Fig. 183

This genus is represented by a single species, S. cuniculi, which parasitizes Old World rabbits of the European and N. Mediterranean regions of the Palaearctic.

Spilopsyllus cuniculi (Dale, 1898)

LC #6009; Ireland.

This species is quite close in general structure to Cediopsylla.
Periphallic Structures: 9T apodeme longest medially. Manubrium broadly fused to 9T apodeme, tapered proximally. PI bilobed, dorsal lobe approximately as long as broad at broadest point, oval in lateral view, approximately equal in length to manubrium; ventral lobe small, truncate; large internal apodeme curving sharply ventrad. P2, P3 forming pincers approximately 0.33x as long as P1, blunt. Lateral process anal sternum present. ST spur present. 8S not lobed as in Cediopsylla but with strong spines at ventro-distal margin. Distal arm 9S simple, long, thin.

Phallosome: Aedeagal apodeme thin, 6x as long as broad at broadest point, 1.5x as long as aedeagus; lateral laminae hyaline, not fused with fulcrum; small dorso-proximal fin present. Penis rods curling 180 degrees over aedeagal apodeme; apodemal rod well developed, nearly as long as penis rods. Fulcrum with lateral lobes broadly curved, median lobe with strong dorsal margin; tectum small, slightly arched. Suspensory sclerites absent. Inner tube simple, broad, tapering distally, proximal projection fused with lateral fulcral lobes. Vesicle with strong ventral margin. Aedeagal sheath without scaffolding, probably with lateral wings present proximally; hood large, truncate with spinous area ventro-distally; crochets small, appearing as tanned spots ventro-distal to apex inner tube.
Comments

*Spilopsyllus* is quite close anatomically to *Cediopsylla* and the genitalia differ to a degree similar to that which divides *Pulex* and *Juxtapulex*. This is especially true given the presence of *Cediopsylla spillmani* in that genus. It is likely that *Spilopsyllus* and *Cediopsylla* should be treated as congeneric (see discussion under *Cediopsylla*).

*Actenopsylla* Jordan & Rothschild, 1923

Plate 62, Fig. 104.

The genus is monotypic, known from *A. suavis*, a parasite of puffins, petrels and aukslets from the Pacific coast of North America.

*Actenopsylla suavis* J. & R., 1923

LC #15275; California.

Periphallic Structures: 9T apodeme quite long dorsally, constricted ventrally. Manubrium broadly fused basally, elongate triangular. P1 large, broadly rectangular, equal in length to manubrium, 1.5x as long as broad; spiniform present distally. P2 reduced, elongate teardrop-shaped, narrowing distally, P3 as long as P1, broadly S-shaped. Lateral process anal sternum present. 8T spur present. 8S with deep lateral cleft producing triangular ventral lobe and rounded dorsal lobe. 8S distal arm with
elaborate lobes and hyaline fringe ventrally; proximal arm strong.

Phallosome: Aedeagal apodeme stout, less than 4x as long as broad at broadest point, 1.3X as long as aedeagus; small fin present dorso-proximally. Lateral laminae hyaline, not fused with fulcrum. Penis rods curling 180 degrees over aedeagal apodeme; apodemal rod well developed, nearly as long as rods. Median lamina with dorsal bay cephalad of fulcrum; median lamina stalked. Lateral fulcral lobes thin, long. Median fulcral lobe with thickened dorsal margin and strong dorsal fork. Crescent sclerite arched. Proximal spur present but weak. Inner tube simple, tapering and broadly decurved distally with minute spicules over distal 1/2. Vesicle strongly margined. Aedeagal sheath broad, constricted somewhat medially; lateral lobes present as in Cedipsylla; ventral membrane extensive; crochets large, ovoid in lateral view, lying dorso-lateral to apex inner tube.

Ornithopsylla Rothschild, 1908

Plate 62, Fig. 185.

The genus is monotypic; O. laetitiae is a parasite of petrels in the British Isles.
Ornithopsylla laetitiae Rothschild, 1908

LC #6951; Great Britian.

Periphallic Structures: ST apodeme quite large, long dorsally and ventrally. Process of anal sternum present. Manubrium thick, blunt, very broad basally, strongly upcurved proximally. P1 bilobed, dorsal lobe very broad, slightly longer than broad, somewhat longer than manubrium, spiniform present distally; ventral lobe approximately 0.66x as long as dorsal, strongly rounded ventral margin. P2 greatly reduced, P3 nearly as long as P1, 6x as long as broad. ST with weak spur. SS deeply cleft laterally and with large ventral medial lobe. SS distal arm large, much expanded medially, acuminate distally. Very large scimitar shaped spiniform associated with anal tergum.

Phallosome: Aedeagal apodeme less than 4x as long as broad, 1.6x as long as aedeagus. Lateral laminae hyaline, not fused to fulcrum; median lamina stalked. Penis rods curled nearly 360 degrees over aedeagus; apodemal rod nearly as long. Lateral fulcral lobes straight, thin; median lobe nearly as long as lateral, strong dorsal margin, proximal knob present, tectum arched. Inner tube simple, with small dorsal tooth distally, articulated with lateral fulcral lobes proximally. Vesicle large. Aedeagal sheath simple, broad basally, truncate distally; crochets small, ventro-distal to apex of inner tube.
Comments

The species is closest to Actenopsylla in general fascies, although the genitalic characters are quite distinct.

Euhoplopsyllus Ewing, 1940

Plate 63, Fig. 186; Plate 64.

The genus contains three species, one of which, E. glacialis, is widely distributed and consists of six subspecies. The group is probably of Nearctic origin (Holland, 1964) but subspecies of E. glacialis range from Greenland to Central America and west to Afghanistan, while E. andensis and E. manconis are South American.

Euhoplopsyllus glacialis foxi (Ewing, 1924)

LC #12189; California.

Periphallic Structures: ST large, expanded dorsally, constricted medially. Manubrium broad basally, short, upcurved, truncate proximally. P1 bilobed, dorsal lobe with two processes: upper process short, quadrate more than 2x as long as broad; ventral process long, finger like, with heavy spiniform apically. Ventral lobe P1 reduced, triangular, broadly fused with base of manubrium. P2 absent. P3 strong, slightly longer than ventral process of P1, expanded somewhat distally. Small triangular process at base of anal sternum. ST tooth present. SS deeply
cleft laterally, ventral medial lobe setose, triangular in lateral view. 9S proximal arm strong, wide; distal arm large, as long as aedeagus, expanded and rounded distally.

Phallosome: Aedeagal apodeme thin, 8x as long as broad at broadest point, 1.7x as long as aedeagus. Lateral laminae hyaline, median lamina stalked at fulcrum, dorsal bay present. Penis rods curling 180 degrees over aedeagal apodeme; apodemal rod stout. Lateral fulcral lobes long, not much curved, median lobe with strongly margined distally directed dorsal fork. Tectum flat. Inner tube simple, tapering, decurved distally; articulated with lateral fulcral lobes; crochets indeterminate, not evident externally (see Plate 64).

Musculature: M29: apparently present, insertion on projection at dorsal margin of inner tube, just distal to crescent sclerite.

Comments

The male of E. andensis is unknown. Euhoplopsyllus manconis was not seen, but Jordan's illustration of the clasper (Hopkins and Rothschild, 1953) indicates that it is close to the species described here.

Taxa:
glacialis

Taschenberg, 1880

glacialis affinis

Baker, 1904

glacialis exoticus

J. & R., 1923

glacialis foxi

Ewing, 1924

glacialis lynx

Baker, 1904

glacialis profugus

Jordan, 1925
andensis (Jordan, 1933)
manconis (Jordan, 1950)

**Hoplopyllus** Baker, 1905

Plate 63, Fig. 187.

Both species in the genus are parasites of North American hares and ground squirrels.

**Hoplopyllus anomalus** (Baker, 1904)

LC #5710; Arizona.

Periphallic Structures: 9T apodeme longest medially.

Manubrium thin, angled sharply ventrad. P1 bilobed, upper lobe large, broadly oval, about as broad as long, 0.6x as long as manubrium; spiniform present at apex of dorsal margin; internal apodeme sharply angled ventrad. Small ventral lobe P1 present. P2 greatly reduced. P3 finger-like, about as long as P1, upcurved, truncate distally. Lateral projection of anal sternum present. 8T tooth reduced or absent. 8S probably not cleft.

8S simple, distal arm 0.75x as long as aedeagus.

Phallosome: Aedeagal apodeme 6x as long as broad, 1.5x as long as aedeagus, rounded distally. Lateral laminae hyaline, not fused with fulcrum. Penis rods curled nearly 180 degrees over aedeagal apodeme; apodemal rod stout, nearly as long as penis rods. Lateral fulcral lobes sharply angled, median lobe with strong dorsal margin; tectum may be fused with tooth proximally

Comments

**Hoplopyllus pectinatus** exhibits several characters which differ considerably from *H. anomalus*. This species was not available for the study, and the comparison is based on the drawings of Barrera (1967). The following characters of *H. pectinatus* are those which vary greatly from *H. anomalus*.

**Periphallic Structures:** ST apodema constricted medially; manubrium broad, sharply upcurved. P2 reduced or absent. P3 longer than in *H. anomalus*. Distal arm 3S large, as long as aedeagus, ventral margin rounded, hyaline fringe associated with 3S according to Barrera.

**Phallosome:** Aedeagal apodeme with dorso-proximal fin. Inner tube with large dorsal tooth, distal end of tube very sharply curved ventrad; crochet shifted proximally, thus still lying near ventral margin apex inner tube. Median dorsal lobe of sheath pointed, upturned.

The species differ a good deal in several aedeagal structures, but these differences themselves do not raise doubts about their inclusion in one genus. The periphallic structures
however are more puzzling. The 9T and manubrium of *H. anomalus* is unique whereas those in *H. pectinatus* are very like the arrangement found in *Euhoplopsyllus* and *Ornithopsylla*. The 9S and P3 as well are nearer *Euhoplopsyllus* than to *H. anomalus*, while P1 resembles that in *H. anomalus*.

*Taxa:*

*anomalus* (Baker, 1904)
*pectinatus* Barrera, 1967
PULICINAE Billberg, 1820

Plates 65 - 76.

As understood here the subfamily contains 4 genera, represented by 30 species. Pulicine fleas occur in both the New World and the Old World, and infest a variety of hosts.

Pulex Linnaeus, 1758

Plates 65 - 73.

There are six species in the genus, all from the New World. They frequent a wide range of hosts. The genus includes the so-called "human flea", Pulex irritans, which is described and illustrated here in some detail, as the representative species for the subfamily. Juxtapulex Wagner, 1933 is here considered a subgenus of Pulex, following Barrera (1955) and Hopla (1980).

Pulex irritans Linnaeus 1758

LC #6136; Lebanon.

Periphallic Structures: Apparent limits of pygidial plate greatly reduced, very narrow; 9T apodeme well developed, short dorsally, expanded in length ventrally and broadly fused with manubrium. P1 very large, forming ovoid flap covering P2, P3 0.8x as long as manubrium, 1.25x as long as broad. Manubrium

Phallosome: Aedeagal apodeme thin, slightly expanded proximally, 7.5x as long as broad at base, 1.5x as long as aedeagus. Lateral laminae hyaline, fused basally with median lamina near dorsal margin of latter, large proximo-dorsal fin present. Penis rods very long, curving nearly 540 degrees over aedeagus (apparently always offset laterally to left side of aedeagal apodeme). Apodemal rod nearly as long as penis rods. Capsule region small; lateral fulcral lobes fused with median lamina. Sharply angled; median lobe small, tectum small, flat. Proximal spur and suspensory sclerites lacking. Inner tube long, thin, tapering smoothly to distal end, dorsal wall thickened, proximal process strong, fused with lateral fulcral lobe; distal

Notes on Function

A very rare slide mount of a copulating pair was available for study (Fig. 210: Collection of Col. R. Traub). Though it is possible that positions shifted during fixation, no obvious disruption was observed.

The pincers formed of P2 and P3 apparently act on the posterior margin of sternum 7 of the female (not actually grasped in the specimen). The insertion of the muscles which act on the base of the pincers is not clear. I suspect that P2 bears one direct insertion (M20) and is articulated in such a way that the movement of P3 (which bears M21 and M22) acts to move P2 as well.
The action of the aedeagus was unexpected. Ford's sclerite is found to be extremely mobile, and curls ventrally to lie alongside the inner tube, and is seen, perhaps coincidentally, to press against the spiculose ventral membrane, forcing it outward against the female tissues. The crochets have been drawn inward, lying now turned and laterad of the inner tube. The pseudocrochets rotate on their long axis, the flaps now directed ventrally.

Assuming that these conditions approximate those found naturally in copulating pairs, the function of the various lobes is still fairly obscure. The pseudo-crochets apparently act to lock the aedeagus in place and perhaps help expand the vaginal opening. Ford's sclerite and the crochets seem to act more directly on the aedeagal tip than on any structure of the female. Ford's sclerite may serve to press the ventral membrane to the vaginal tissue thus anchoring the aedeagus, but this may only be a secondary function. The crochets perhaps act with Ford's sclerite to guide the penis rods, but this is not at all clear. It may be that the true crochets in *Ctenocephalides* serve a similar function.

M26 acts on both Ford's sclerite and the crochets, and the pseudo-crochets are moved only indirectly. It is this aspect of the musculature which has led to homologizing the dorsal structures with the crochets in other genera, contrary to Traub (1950) who designated them pseudo-crochets. Thus, on this view,
the more ventral flaps are the pseudo-crochets (crochets of Traub). The muscle here designated M25 has been found thus far only in *Pulex* and the homology is uncertain, but seems the most likely. The function of this muscle is not obvious. Its contraction would seem to serve only to raise the distal end of the aedeagus, in which action it would be aided by M29 which inserts on the inner tube. It may be noted that this pivot action of the inner tube thus produced would seem to be hindered by the fusion of the lateral fulcral lobes with the proximal process of the inner tube.

The extent and structure of the spiculose ventral membrane suggests some anchoring function during copulation, and perhaps stimulation of the female as well. It is possible that hemolymph pressure is used to expand this membrane and thus produce contact with the female tissues.

*Pulex* is divided into two subgenera, *Pulex* (*Pulex*) and *Pulex* (*Juxtapulex*) (Barrera, 1955 and Hopla, 1980). These taxa are readily distinguished on the basis of the male genitalia alone, and all species are easily recognized with the exception of *Pulex* (*P.*) *simulans*.
This species is sympatric with *P. irritans* over much of the latter's Nearctic and Neotropical range (Hopla, 1980). There has been some disagreement over the taxonomic status of *P. simulans*. It is separable from *P. irritans* anatomically only on the basis of the shape of Ford's sclerite and the outline of the pseudocrochet. These characters exhibit a range of variation within each species, and as shown for *P. irritans* above, the pseudocrochet is quite movable and its outline is dependent upon its orientation. Thus care must be taken in using this as a character. *Pulex simulans* generally has a smaller Ford's sclerite and the pseudocrochet is smaller and more proximal.

*Pulex (Pulex) sinoculus* Traub, 1950

LC #6256, paratype; Guatemala.

Plate 73, Fig. 215.

Periphallic structures: very close to *P. irritans*, manubrium more narrow, origin M23 more developed, articulation of P3 more distinct.

Phallosome: Median lamina aedeagal apodeme somewhat narrower than *P. irritans*, lateral laminae narrow, and fused more proximally. Major differences with *P. irritans* occur at the terminal end of the aedeagus. Median dorsal lobe with prominent dorsal thickening, Ford's sclerite much reduced, more distally
articulated and not covered by lateral lobes; crochet with sclerotized basal articulation. Pseudocrochet large, prominent, long, with reduced median flap.

**Pulex (Juxtapulex)**

**Pulex (Juxtapulex) echiophagoides** (Wagner, 1933)

LC #6249; Panama.

Plate 73, Fig. 212.

Periphallic Structures: Manubrium longer, thinner than *P. irritans*. PI reduced in breadth by about 2/3, though dorsal margin much the same shape as in *P. irritans*. P2, P3 similar in shape to those in *P. irritans* though less than 0.5x as long as PI. ST with larger spur than *P. irritans*.

Phallosome: Inner tube with angular dorsal projections along nearly entire length. Ford's sclerite small, with decurved, pointed apex; crochets not heavily tanned, but tendon clearly visible; pseudocrochets very large, broad proximally with tapered hook distally. Median dorsal lobe pointed apically, curving dorso-proximally.

**Pulex (Juxtapulex) porcinus** J. & R., 1923

LC #11092; Texas.

Plate 73, Fig. 213.

Periphallic structures: P2, P3 proportionately somewhat
shorter, more blunt than *P. echidnophagoides*, otherwise very similar.

Phallosome: similar to above -- dorsal projection of inner tube much less developed; crochets and pseudocrochets less obvious, smaller. Ford's sclerite reduced or absent.

*Pulex (Juxtapulex) alvarezi* Barrera, 1955

Traub Collection.

Plate 73, Fig. 214.

Periphallic Structures: as above.

Phallosome: Dorsal wall of aedeagal sheath heavily tanned, obscuring possible projections of inner tube; Ford's sclerite blunt; crochet large, well developed, pseudocrochet small.

Comments

The subgenera are distinctly divisible on the basis of the male genitalia. P1 is reduced in breadth by 2/3 in *Juxtapulex*. *Pulex (J.) alvarezi* retains phallosome characters of *Pulex (Pulex)*, but *P. (J.) echidnophagoides* and *P. (J.) porcinus* show ornamentation of the inner tube, expansion of the pseudocrochets and reduction in the tanning of the crochets. It is possible that *P. (J.) echidnophagoides* is a derived form of *P. (J.) porcinus*, judging by the further hypertrophy of the inner tube and pseudocrochet.
Taxa:

_Pulex_ (Pulex)
- _irritans_ L., 1758
- _simulans_ Baker, 1895
- _sinoculus_ Traub, 1950

_Pulex_ (Juxtapulex)
- _alvarezi_ Barrera, 1955
- _porcinus_ J. & R., 1923
- _echidnophagoides_ (Wagner, 1933)

_Echidnophaga_ Olliff, 1886

Plates 74, 75.

The genus is composed of 21 species. They inhabit the Australian, Palearctic and Ethiopian regions, and frequent a wide range of hosts. _Echidnophaga gallinacea_, on which the generic description is based, is cosmopolitan as a result of human transport.

_Echidnophaga gallinacea_ (Westwood, 1875)

LC #13057; Egypt.

Plate 74, Fig. 218; Plate 75.

Periphallic Structures: Pygidial plate much reduced; 8T apodeme large, long dorsally, reduced and shortened ventrally. Manubrium long, thin, rod-like. P1 of uniform width, blunt distally, 0.45x as long as manubrium, 3.25x as long as broad at base. P2, P3 forming pincers, width of both together at base equal to width of base of P1, P2, P3 approx. 0.5x length of P1. Parameral bridge entirely membranous. 8T spur present. Distal
arm 9S as long as aedeagus, of even width throughout; proximal arm simple; arms nearly equal in length. Musculature: identical to that seen in P. irritans.

Phallosome: Aedeagal apodeme 7.5x as long as broad at base, 2x as long as aedeagus, lateral laminae hyaline; median lamina consisting of small longitudinal ridge, probably without ventral lamella; shallow dorsal fin present, apex of apodeme upturned. Penis rods short, not much longer than aedeagal apodeme. Capsule area large, tectum broadly domed, continuous distally with inner tube; lateral fulcral lobes broadly curved, median lobe small, indistinct. Suspensory sclerites absent. Inner tube simple, tapering smoothly to tip; vesicle large, circular. Aedeagal sheath bullet shaped, broad at base, blunt distally. Median dorsal lobe bifid; crochets wide with pointed tooth; structures at distal end of runners may represent pseudocrochets; lateral lobes present; Ford's sclerite bifid.

Comments

Echidnophaga gallinacea is representative of the majority of species. Smit (1967) has remarked that the males of this genus are on the whole less diagnostic than the females. Of the species available for study E. aethiops, E. murina, E. myrmecobii and E. oschaninni are virtually indistinguishable from one another and from E. gallinacea, on the basis of genitalic characters alone, and this despite the wide geographic range.
represented (E. myrmecobii is Australian, E. oschaninni from Central Asia, E. aethiops Ethiopian and E. murina Mediterranean). On the basis of illustrations of the claspers in the original descriptions of the species not seen in the study, it is not expected that any will exhibit great divergence from this pattern, although Jordan (1925) states that E. tarda is "between gallinacea and bradyta", and significant variation is seen in this species and in E. larina as described below.

The genus is generally very regular in anatomy with the exception of E. larina and E. bradyta. Echidnophaga larina departs from the gallinacea-group by virtue of hypertrophy of the aedeagal sheath, as well as by an exaggeration of the clasper characteristics. Echidnophaga bradyta exhibits its own radical changes in the clasper apparatus and carries the sheath hypertrophy to an extreme. Although E. bradyta is very distinctive, its link to other members of the genus is clear when E. larina is regarded as an intermediate form.

Echidnophaga larina J. & R., 1906

LC #13057; Egypt.
Plate 74, Fig. 218

Periphallic Structures: 9T apodeme very long dorsally, sharply narrowing ventrally. Manubrium at sharp angle to P1, forming acute angle with 9T apodeme. P1 large, 4x as long as broad, about as long as manubrium. P1 with large internal
apodeme, probably associated with parameral bridge. P2, P3 relatively large, nearly as long as P1; forming pincers. P3 with distal end upcurved. 8T spur present. 9S highly modified, L-shaped in lateral view, distal arms flanking phallosome. 8S divided medially to accommodate 9S.

Phallosome: Aedeagal apodeme 8x as long as broad, 1.7x as long as aedeagus, lateral laminae hyaline. Suspensory sclerites lacking. Apodemal rod stout, connecting to well defined girdle; runners distinct. Apex of sheath with diverse lobes, homologies obscure.

The phallosome of *E. larina* is fundamentally similar to *E. gallinacea*, the differences due entirely to hypertrophy of the structures of the aedeagal sheath. This phenomenon is carried to a further extreme in *E. bradyta*.

**Echidnophaga bradyta J. & R., 1906**

LC: Orange Free State.

Plate 74, Fig. 219.

Periphallic structures: 9T apodeme greatly expanded distally, broad and long. Manubrium sharply curved proximally, forming acute angle with 9T apodeme. P1 very large, triangular, broad and blunt distally, as long as manubrium. P2, P3 highly modified, 0.5x length of P1. P2 triangular, P3 thin, clubbed distally.

Phallosome: Aedeagal apodeme 7x as long as broad at base.
Median lamina with strong central core, dorsal fin extending length of apodeme; lateral laminae hyaline. Apodemal rod very stout. Aedeagal sheath extremely hypertrophied, heavily tanned; girdle, ribs, runners very strong, homologies of other parts obscure.

Taxa:
- aethiops J. & R., 1906
- ambulans ambulans M. Rothschild, 1936
- ambulans inepta M. Rothschild, 1936
- aranka J. & R., 1906
- bradyta J. & R., 1906
- calabyi Mardon & Dunnett, 1971
- cornuta Wagner, 1936
- eyrei Mardon & Dunnett, 1971
- gallinacea (Westwood, 1875)
- larina J. & R., 1906
- liopus J. & R., 1906
- macronychia J. & R., 1906
- murina (Tiraboschi, 1903)
- myrmecobia Rothschild, 1909
- oschanini Wagner, 1930
- ochotona Li, 1957
- octotricha Mardon & Dunnet, 1971
- perilis Jordan, 1925
- popovi Ioff & Argropulo, 1934
- tarda Jordan, 1925
- tenerifensis Gil Collado, Rodriguez Rodriguez & Zapatero Ramos, 1982
- tiscadea Smit, 1967
**Neotunga Smit, 1962**

Plate 76, Fig. 222.

This taxon contains two species. Originally described from a female *N. euloidea* from an East African pangolin, the genus was later enlarged by the transfer of *Echidnophaga inexpectata* (Smit and Wright, 1978). The latter species is known from both sexes and infests warthogs in Kenya and the Sudan.

**Neotunga inexpectata** (Smit, 1950)

BM(NH); Kenya.

Periphallic Structures: 9T apodeme large, expanded dorsally, reduced ventrally. Manubrium broad, upcurved and expanded proximally. P1 thin, broadly decurved, 4.5x as long as broad at broadest point, 0.86x as long as manubrium. P2. P3 forming pincers, relatively very long, as long as P1. 8T spur present. SS distal arm thin, about as long as aedeagus.

Phallosome: Aedeagal apodeme long, thin, more than 12x as long as broad at base; lateral laminae hyaline. Penis rods short, not much longer than aedeagus. Capsule area small, inner tube simple, tapered distally. Median dorsal lobe hooked at apex, bifid. Paired latero-dorsal lobes may represent crochets, or Ford's sclerite.
Comments

Although the available material is in poor condition, it is clear that Neotunga is closely allied to the gallinacea group of Echidnophaga. When originally described from the female N. euloidea, the genus was said to exhibit characters that place it as an intermediate between Tungidae and Pulicidae (Smit, 1962b). For a discussion of this point and the concomitant changes in classification see the discussion in section IV below.

Taxa:
- euloidea Smit, 1962
- inexpectata (Smit, 1950)

**Delopsylla Jordan, 1926**

Plate 76, Fig. 223.

The genus is monotypic. *D. crassipes* is a parasite of the Spring Hare in East Africa.

**Delopsylla crassipes Jordan, 1926**

B.M.(NH)↑ Kenya.

Periphallic Structures: 9T apodeme large, expanded in length both dorsally and ventrally. Manubrium thin, straight, at right angle to margin of 9T apodeme. P2, P3 forming pincers, approx. 0.5x as long as P1, P3 slightly longer than P2. 8T spur present. Distal arms 9S widely separated basally, lying laterad of aedeagus, tapering to thin apex, longer than aedeagus.
Phallosome: Aedeagal apodeme large, 5x as long as broad at broadest point, 2x as long as aedeagus. Proximal dorsal fin present. Lateral laminae hyaline. Penis rods short, not much longer than aedeagus. Lateral fulcral lobes modified into heavily tanned plates; tectum knob-like, fused with inner tube distally. Suspensory sclerites absent. Inner tube small, semi-circular. Aedeagal sheath with runners, modified girdle attaching to lateral ridge formed of hypertrophied ribs. Crochets tricornered, tooth-like; pseudocrochets present. Ford’s sclerite absent; sheath with dorso-medial plate.

Comments

**Delopsylla** is most closely related to *Echidnophaga* on the basis of general facies and periphallic anatomy, and to *E. larina* and *E. bradyta* in particular on the basis of phallosome structures. All 3 taxa share similar hypertrophy of the aedeagal sheath, especially the runners, girdle and ribs.
HECTOPSyllINAE Baker, 1904

Plates 77 - 81.

This Neotropical group contains two genera, Hectopsyilla, with ten species, mostly parasites of small rodents, and Rhynchopsyllus, with two species, both parasites of bats. The male genitalia are most unique, and those of H. psittaci are representative of the tribe. The species is a bird parasite.

Hectopsyilla Frauenfeld, 1860

Hectopsyilla psittaci Frauenfeld, 1860

LC #15591; California.

Plates 77, 78, 79, Figs. 231, 232; Plate 80.

Periphallic Structures: Pygidial plate greatly reduced, 3T apodeme absent. Pi roughly trapezoidal, broad basally. Manubrium unique, short, 2x as broad as long, with dorsal and ventral projections (M1 and M2 of Hopkins and Rothschild, 1953), fused dorso-caudally with ventral margin of pygidial plate. Parameral bridge entirely membranous. P2, P3 small, less than 0.5x as long as P1, forming pincers. P2 fixed, P3 moveable. Distal arms 3S greatly hypertrophied and expanded into 3 large membranous lobes; proximal arm with very large flat lobe.

Phallosome: Aedeagal apodeme 2.33x as long as broad at broadest point, 1.4 x as long as aedeagus. Deep dorsal fold present from ventral edge of which median lamina is produced. Median lamina extended into long tubular stalk bearing fulcrum distally. Lateral laminae large, ventral margin thickened, fused dorsally and ventrally with base of aedeagal sheath. Penis rods very short, not curling over aedeagal apodeme; virga ventralis approximately 0.5x as long as rods, broad distally. Apodemal rod greatly reduced, originating near base of SS, about as long as longest penis rod. Fulcral lobes borne by stalk-like extension of median lamina; lateral lobes very reduced, median thick, straight. Tectum membranous, continuous distally with inner tube. Lateral shafts large, strong, "canoe-shaped". Inner tube broad proximally, tapering to simple tube, surrounded by tanned cuticle where tube projects to exterior of aedeagus; exterior portion simple, slightly tapered and decurved. Vesicle reduced
to membrane surrounding end of virga ventralis. Aedeagal sheath broad at base, continuous basally with lateral laminae; dorsal longitudinal struts heavily tanned. Median dorsal lobe blunt. Ford's sclerite present. Crochets large, heavily tanned, surrounding sclerotization complex; ventral pseudocrochet present, pointed apically. End chamber with cuticular hairs. 

Musculature: M25-26: origin proximal end lateral laminae, insertion near base of crochets. These muscle bundles are very large and conspicuous in section and probably insert at two different places on the inner tube armature. M29: (probably present) origin along dorsal inner wall of aedeagal apodeme, insertion near lateral walls of capsule at base of inner tube. A single thin tendon apparently represents this muscle distally.

Notes on Function

The short rods and the long external projection of the inner tube suggest that sperm is transferred by means of the pumping action of the capsule. The enlarged capsule and lateral shafts support this. M29 may assist in this function. The very heavy musculature of the aedeagus implies an important anchoring role for the structures of the end chamber.

Comments

The manubrial plate may be either a fusion product of the ST apodeme and the true manubrium or a development of the manubrium
alone. Lack of muscle insertions on P1 complicates the assignment of homology to this structure. If the manubrial plate is a fusion product of the 9T apodeme and the true manubrium then \textit{Hectopsylla} can be regarded as an intermediate stage in the production of a structure such as found in \textit{Tunga}. These matters are treated in the discussion.

The clasper apparatus is fundamentally the same in all known species, though variation in the shape of the lobes occurs.

Similar degrees of variation occur in the anatomy of the phallosome, with \textit{H. gemina} perhaps representing the most radical departure. \textit{Hectopsylla stomis} is noteworthy for the extreme hypertrophy of the ninth sternal lobes and the great expansion and thickening of the eighth sternum.

\textbf{Taxa:}

\textit{broscus} J. & R., 1906
\textit{coniger} J. & R., 1906
\textit{cypha} Jordan, 1942
\textit{eskeyi} Jordan, 1933
\textit{gemia} Jordan, 1939
\textit{gracilis} Mahnert, 1902
\textit{Knighti} Traub & Gammons 1950
\textit{psittaci} Frauenfeld, 1860
\textit{stomis} Jordan, 1925
\textit{suarezii} C. Fox, 1929

\textbf{Rhynchopsyllus Haller, 1880}

This genus contains two species, the male is known only from \textit{R. megastigmata}. Specimens of these were not available for study, but the single illustration of the male genitalia (Tipton...
& Mendez, 1966) clearly indicates the close affinity between
Hectopsylla and this genus. There would seem to be only a single
significant character separating the two and that is the lack of
SS lobes in Rhynchopsyllus.
There are nine species in the genus. They are mostly parasites of small rodents or South American edentates. The distribution of the genus is disjunct, six species from the New World and two from the Manchurian subregion of the Palaearctic. *Tunga penetrans* has been spread from the Neotropics to West Africa by human activities. The genus does not exhibit much anatomical variation and *T. monositus* is representative. The males are very small fleas with highly modified genitalia.

*Tunga monositus* Barnes & Radovsky, 1969

LC #1255; Baja California.

Plate 82, Figs. 242 - 244. Plate 83, 84, Fig. 249.

The male genitalia have been well reviewed in the original description.

Periphallic Structures: Pygidial plate reduced to sensillum and anal sclerites; ST apodeme absent. Clasper apparatus highly modified: Pincers with dorsal lobe fixed and fused with simple manubriual arm, ventral moveable process. Clasper arm hinged dorsally to lower edge of pygidial plate.

Phallosome: Aedeagus very large in relation to abdomen, divided into two sections by medial hinge. Distal segment somewhat shorter than proximal. Aedeagal apodeme short and broad, 2x as long as broad at broadest point. Lateral laminae hyaline, free from capsule area; median lamina strong forming rod-like stalk from which fulcral lobes project. Penis rods very short, not as long as aedegal apodeme. Lateral fulcral lobes broad basally, membranous distally, median lobe long, arched upward. Lateral shafts of capsule very large ("canoe-shaped lateral struts" of Barnes and Radovsky, 1969). Tectum broadly domed, fused with dorsal wall of inner tube distally. Inner tube very broad proximally, rapidly tapering to membranous tube at hinge. Vesicle reduced to small membranous area proximal to
ventral thickening of inner tube. Virga ventralis present. Apodemal rod greatly reduced, difficult to discern distally, arising just ventral to hinge joint, proceeding proximally to curl slightly beyond aedeagal apodeme. Aedeagal sheath divided between the two arms of aedeagus: ribs prominent, continuous proximally with lateral laminae, narrowing distally to form main dorsal strut of proximal arm of aedeagus, terminal knob forming hinge joint. Distal portion of sheath contains continuation of inner tube which is simple and acuminate distally, extending length of sheath. Distal arm of sheath quadripartite, with lateral and median lobes flanking inner tube. Musculature: M25-26: origin lateral laminae, insertion obscure, presumably proximal end of median lobes (crochets). M29: origin inner dorsal margin of ribs, insertion near lateral walls of inner tube dorsal to vesicle area (homology uncertain). Muscles of hinge: muscle bundle here may be derived from sternal muscles of segment 7 or 8.

Notes on Function

Female tungids are subcutaneous parasites, burrowing head first into the host. Copulation occurs after the female has embedded, and the male must introit through the opening in the host's skin through which the terminalia of the female communicate with the exterior (Geigy and Suter, 1960; Barnes & Radovsky, 1969). The unique development of the aedeagus is
associated with the mode of copulation this necessitates (see Geigy and Suter, 1960). The distal arm of the aedeagus can swing ventrally 90 degrees to the plane of the aedeagal apodeme.

The shortened penis rods imply that sperm transport occurs via the inner tube. The large capsule and strong lateral shafts are consistent with the notion that sperm and seminal fluid pumping actually occurs in tungids. It is possible that M29 aids in this process.

Comments

The highly unusual genitalic anatomy of tungids is explained by their unusual mode of copulation.

M22 in related fleas originates on the large P1 and inserts as here. This might suggest that the dorsal lobe here represents P1 and the ventral P3. However the shape of the pincers in Tunga is very like that formed by P2 and P3 in other relatives of this group and the simplest assumption is no doubt that P1 has atrophied and the origin of M22 shifted onto P2. In Hectopsylla P2 is fixed and indicates the kind of intermediate that would have to occur. These points will be discussed elsewhere.

The median lobes of the distal end of the aedeagus have been referred to the crochets (Barnes and Radovsky, 1969), and this is likely. Johnson (1957) has identified runners and pseudocrochets in T. penetrans but this is probably ill-advised because of the great degree of modification.
Smit (1962a) divided the genus into two species groups. The members of the primitive *caecata*-group containing *T. monositus* are primarily parasites of cricetid rodents (Barnes and Radovsky, 1968). The members of the derived *penetrans*-group are parasites of South American edentates (*T. penetrans* itself mainly infests suids and humans). General morphological differences are given by Barnes and Radovsky. Genitalic differences are not pronounced, concerning primarily the proportions of the various parts. Wang (1976) gave the oriental species, *T. caecigena*, and *T. calida* the status of subgenus. This does not conflict with the grouping of Smit (1962a), since it is not unlikely that they are sister species.

**Taxa:**

**caecata-group:**
- *caecata* (Enderlein, 1901)
- *caecigena* J. & R., 1921
- *callida* Li & Chin, 1957
- *libis* Smit, 1962
- *monositus* Barnes & Radovsky, 1969

**penetrans-group:**
- *bondari* Wagner, 1932
- *penetrans* L., 1758
- *terasma* Jordan, 1937
- *travassosi* Pinto & Dreyfus, 1927
The present study has revealed the extraordinary uniqueness of the genitalia in this genus. It is suggested that this, along with the consequent uncertainty as to the suprageneric placement of this genus is sufficient grounds for elevating the group to the rank of subfamily.

**Moeopsyllinae**

Plates 85, 86.

This aberrant genus is represented by the single species *M. sjoestedi*, a parasite of wart hogs in East Africa.

**Moeopsylla Rothschild, 1908**

This aberrant genus is represented by the single species *M. sjoestedi*, a parasite of wart hogs in East Africa.

**Moeopsylla sjoestedi** Rothschild, 1908

B.M.(NH); Uganda.

Periphallic organs: 9T apodeme long and narrow. Manubrium stout, widely separated from 9T apodeme. P1 dorso-ventrally flattened, 0.6x length of manubrium, more than 7x as long as broad in lateral view. P2 short, knob-like, 0.33x as long as P1. P3 absent as such, perhaps represented by ventro-distal lobe of manubrial base. Parameral bridge as lightly sclerotized arch between bases of P2. 9S very broad at base, tapering distally with small upcurved terminal hook.

**Phallosome:** This structure is extremely peculiar and
requires special description. Aedeagal apodeme 5x as long as broad at broadest point, constricted strongly basally; dorsal bay present over basal 2/3. Lateral laminae fused with lateral fulcral lobes; median fulcral lobe continuous with median lamella; fulcral region thus supported on stalk of aedeagal apodeme. Penis rods short, not much curved over aedeagal apodeme. Apodemal rod very stout, longer than rods. Capsule relatively very small, lateral fulcral lobes greatly expanded, as broad as entire capsule area, fused broadly with proximal end of inner tube; crescent sclerite small. Inner tube bulbous basally, vesicle present, though much reduced. Suspensory sclerites lacking. Inner tube is reflexed, doubling back on itself. At the point of the first turn, there is a large, dorsal projection. The tube proceeds cephalad and fits into the dorsal bay of the aedeagal apodeme. The inner tube then again reverses direction to describe a broad arch over the entire phallosome, terminating at a point distal to the previous distal-most extension. The aedeagal sheath is present, but highly modified, having shifted cephalad; large, arching ribs are present over the capsule area, extending from a point far proximad on the aedeagal apodeme and terminating distally in blunt lateral walls from which the proximal end of the inner tube projects. Very large lateral lobes, broadly elliptical in shape, occur dorsad of the ribs; they are closely appressed to each other along their dorsal margin, and are in close association with the distal end of the
inner tube. Crochet-like musculated structures are present at the ventro-distal end of the lobes. The apparent crochets are long and knife-like with a median articulation. The muscles which insert on these structures are apparently homologous in origin with M25-26.

Notes On Function

The single specimen which was dissected for examination, and a further slide mount with the elliptical lobes separated, suggest that a clasping function has been taken on by the lobes and the crochets. The inner tube appears freely separable from the elliptical lobes, but its mode of protraction, if any, is unknown. No possible homologues of M29 were observed which might serve to move this structure. The presence of short penis rods is puzzling, and sperm transfer is apparently accomplished via the exceedingly long inner tube. One might thus expect a well developed capsule for the pumping of sperm, but this is not the case, the capsule area being considerably reduced in size. The distal arms of 9S are extrudable and the arms separable much as seen in Synosternus pallidus. Examination of specimens in copulo would be enlightening.

Comments

Despite the radical departure from the usual anatomy, homologies can be ascertained. The capsule region and the
Aedeagal apodeme remain essentially unchanged. The inner tube and aedeagal sheath are the structures which have altered so dramatically, but even here ribs and crochets can be discerned. The ribs are very large and have shifted far cephalad from their usual positions. The presence of crochets at the distal ends of the elliptical lobes suggests that these latter are homologues of the distal lateral walls of the aedeagal sheath which have again shifted dorso-proximally to the ribs which now lie below them.

The periphallie structures bear no relation to the genera within the Pulicinae where this genus has been placed, but neither are they very similar to those in other groups. They most resemble those found in the Archaeopsyllinae. *Moeopsylla* has been placed within the Pulicinae on the basis of non-genitalic characters, notably its general facies, lack of ctendia, the lack of a mesopleural rod. It will be argued below that although it shares certain characters of the phallosome with Tunginae it is probably best to place it as the sister group of the Archaeopsyllinae + Xenopsyllinae with the rank of subfamily.
2. Summary of Selected Genital Musculature:  
Comparison among the Pulicoid Subfamilies

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(1): either M23 or M24  
(2): divided in this genus.
IV. DISCUSSION

1. Outline of a Phylogeny of the Pulicoidea

A. Comments on Method

Prior to the presentation of suggestions for a phylogeny and classification of these taxa, it is appropriate to present some indication of the underlying assumptions concerning the nature of a proper classification.

The aim of systematics is the explanation of the order underlying the diversity of species. The purpose of a classification is to mirror in some sense the patterns of relationship among the included taxa. These relationships exist on several levels and therefore "closeness of relation" is not a simple concept.

Ambiguities arise because evolution proceeds through the action of two separate processes: reproduction and selection. Reproduction results in genealogy pure and simple, if we discount random effects such as drift for the moment, and it proceeds irrespective of the action of the second process. The effects of selection vary in magnitude over time and space. The independence of these processes results in the circumstances that produce the basic ambiguities: 1. organisms with no recent genealogical connections can be very similar phenotypically, and 2. organisms that are very dissimilar phenotypically may have recent genealogical connections. Since organisms may be
meaningfully conceived as related in these two different senses, a proper classification will mirror both, in so far as possible.

A complete understanding of the ecology and evolution of a group of organisms requires both recognition of the degree and kind of anatomical and behavioral variation present (a phenotypic map of the taxon), and the discovery of the phylogenetic connections among the subordinate taxa (a genotypic map, in other words, a phylogenetic tree). A complete systematic account of any group must present a delimitation and description of the various kinds of taxa included as well as an hypothesis about the nature of their historical relationships. Classifications only form a part of such a complete account and as such provide only the framework for the organization of information about the taxon, and the details must be filled in explicitly by the systematist. It is well to remember that a classification as such is always made more intelligible and useful with reference to the whole of the revisionary study of which it is a part.

The distinction should be made between SYSTEMATIC taxa used in the classification of the group, and PHYLOGENETIC taxa which are entirely congruent with the branching pattern based solely on derived characters. These latter taxa need not be formally named or used in the classification, but an explicit hypothesis of phylogeny is necessary to unify and judge the coherence of any general statements about the taxon.

Historically, the original biological taxa were systematic
taxa that were defined wholly typologically. Since the acceptance of an evolutionary explanation of the "naturalness" of such groupings as a result of common descent, systematic taxa are no longer defined with reference to an ideal type, but with implicit reference to historical relations, and the natural groups are understood to be necessarily monophyletic. But, however linear history may be in the abstract, and when considered as pure genealogy, the traces of evolution consist of clusters of organisms recognizable according to degree of resemblance. Typological classifications are not faulty because patterns do not exist in nature, but because they fail in their explanations of them. On the other hand, entirely genealogical classifications obscure the phenotypic map which is the primary datum of biology. Proper systematic classifications therefore can be regarded as standing midway between purely idealistic/typological classifications on the one hand, and entirely historical/genealogical classifications on the other. Both of the extremes leave important aspects of the interrelationships among the organisms out of account. The first is excessively abstract because it is ahistorical, and life is not; the second because it refuses to explicitly acknowledge the "types" we find in the world. A proper classification should recognize both phenotype and genotype in so far as possible.

Systematic taxa are traditionally, and properly, established with reference to some notion of anatomical type and are
delimited by degree of phenotypic difference. These criteria tend to impart a stability and ease of use to the classification which are not generally possible if strictly phylogenetic principles are used.

Ranking of taxa should not be proposed on the basis of hypotheses of phylogeny which are not generally accepted by workers in the group as this only contributes to instability, and obscures the morphological map in any case. Systematic taxa are less subject to dispute when they are based on anatomy. A conservative approach should be followed when new taxa are erected. Paraphyletic taxa are in principle acceptable, since these may help reveal the degree of variation in "Kinds" of organisms. Such taxa do not directly contradict the genealogy, though they do not reveal it entirely. When paraphyletic taxa are erected or their existence suspected, it is of great importance that the information implicit in these systematic ranks be accompanied by explicit accounts of the presumed phylogeny as well, since both aspects of the history of the taxon are of equal importance. Paraphyletic groupings should be accompanied by an account of the characters which delineate the monophyletic groups. Polyphyletic taxa are not in principle acceptable since these actively contradict the presumed phylogeny.

There are parallels between the historical development of systematics as a science, and the actual practice of the
taxonomist in the encounter with a new group of organisms. The nature of the approach one must take is logically constrained to mirror the history of systematics. Faced with the plurality of organisms in a group, analysis must begin somewhere, and must of necessity rest on unanalyzed assumptions. One must begin by grouping purely typologically in a provisional way. Some kind of initial order is produced. Then, and only then, can one begin to ask the historical question as to whether the proposed taxa are monophyletic. It is at this point that one explicitly searches for derived characters. This search requires the hypothesis of a sister group, which primitively, and logically speaking, is proposed typologically. In practice one must accept the results of earlier studies, at least provisionally. Thus the logical requirement for an unanalyzed sister group is fulfilled. At the same time one gets a previous analysis "gratis" by accepting the judgements of earlier workers.

Monophyletic taxa can only be recognized by the presence of derived characters. Groups cannot be established on the basis of primitive characters. The latter may reveal common ancestry, but the level of the taxon in which they are united is not thereby determined. Each systematic taxon should be based on a set of derived characters which allow recognition of the members included at that level.

The fulfillment of this simple requirement is made problematic by the occurrence of convergence, parallelism and
reversals in the historical pattern of character distributions. Thus the taxa are not to be DEFINED by their derived characters, since certain included taxa may lack them, or exhibit characters which are indicative of membership in other taxa of the same rank. There are two possible solutions to the problem of discovering the branching patterns in the face of such ambiguities. One may opt for methods of parsimony, and assume that those arrangements which minimize convergence are most likely to be true. This requires that one have several characters to analyze, and that one assume that parsimony in evolution has in fact occurred. If convergence and parallelism are rampant, then parsimony methods may be misleading. Alternatively, one may minimize the problem by the weighting of characters. Those which seem least likely to be convergent are taken as the keys to the true phylogeny. Such characters are those which are unique and highly divergent, which are complex in nature, which are thought to be least apt to be the result of environmental influences, or show stability at the level in question.

I believe that character weighting, especially in a group as fundamentally uniform and constrained by the requirements of the environment as are fleas, is an indispensable tool in the reconstruction of the history of the organisms. Among the Siphonaptera there are numerous instances of convergence in chaetotaxy as a result of life on similar hosts (Traub, 1980a).
Thus combs and spines and the like are very poor indicators of phylogeny. A similar situation obtains with regard to thoracic anatomy since the ecology of the animal is related to its ability to jump, and thus to its thoracic structure. The general fascies of the animal may also be strongly tied to the nature of the host, as will be suggested below.

This entire study is based on an assumption of the utility of character weighting. The male genitalia are a rich potential source of characters and can serve as excellent indicators of relationship for the following reasons: 1. They are extremely complicated structures, with at least two major, developmentally separate components, the periphallic organs and the phallosome itself. They thus provide many different characters and character states. 2. They are generally very species specific and in many cases are the only structures which can adequately serve in the recognition of species and subspecies. They are traditionally used as characters important in the establishment of genera. 3. The range of variation of these structures within the Pulicoidea is far greater than the variation in any other characters in either male or female fleas. 4. They are apparently not directly subject to environmental influences associated with the nature of the host and its habits, and therefore are uncoupled to some degree at least from the external determinants of the anatomy of the organisms. Such characters which are relatively unconstrained may be expected to reveal
patterns of variation which are based more on the internal and
developmental characteristics of the organisms, and therefore to
be more revealing of historical relations than characters
determined directly by environmental accidents.

The phylogeny presented below is the first explicitly
proposed for the Pulicoidea. Prior classifications have divided
the taxon into groups of various ranks, but have given no very
definite justifications for the arrangements, nor has "degree of
relatedness" been discussed at all. It is important to recognize
that the cladogram which follows is presented as an hypothesis.
Whether any particular relationships suggested are accepted by
workers in the group is of less concern than that this framework
provide the basis for critical discussion about relations within
the group. If some of these suggested relations are in error,
and surely they are, then I hope at least to have provided
definite arguments which may be criticized, and a framework for
new theories. It is particularly important that workers on a
taxon give explicit explanations for proposed classifications so
that all the results of their studies will be available to future
workers.

Further work especially needs to be done on the
non-genitalic characters of the male, as well as on all aspects
of the female anatomy. Additional study of the male genitalia is
required for many groups, and more extensive use of the scanning
electron microscope would be very helpful. A better
understanding of biogeography and host relationships would also be helpful. Some of the phylogenetic taxa suggested here are probably well founded, others are very provisional.

The Pulicoidea is a very heterogeneous taxon. Of particular concern is my inability to discern any derived genitalic characters for the group as a whole. It is possible that a close study of the other families in the order will reveal such characters, but at least for the time being the group must be regarded as monophyletic on the basis of non-genitalic characters alone. I have of necessity taken at face value the belief of Jordan, cited by Hopkins and Rothschild (1953) and Holland (1964) that the sister group of the pulicids is the rest of the Siphonaptera in toto. It is therefore assumed that the Pulicoidea is not paraphyletic with respect to the rest of the fleas. In establishing a set of characters to be understood as primitive for this taxon I have tried to use those which are widespread within the other families and which they share with at least some of the pulicids.
B. Cladogram and Key to the Characters
Genitalic Characters
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1. High level characters. May be subject to reversals at lower levels.

201 Manubrium fused, broad
201' Manubrium free, rod-like
202 ST apodeme broadly continuous with manubrium
202' ST apodeme separate from manubrium; or vestigial
202" ST apodeme absent
203 P1 fused, not articulated
203' P1 movable, articulated basally
203" P1 reduced
204 Clasper with single, distal movable process
204' P2 present at base of P1
204" P3 developed from base of manubrium
204a Pincers present; upper lobe fixed
204a' Upper lobe articulated, movable
204b Upper lobe reduced, pincer lost
205 Parameral bridge associated with P1
205' Parameral bridge associated with P2
205" Parameral bridge associated with base of P3; apodeme P2 reduced
206 Suspensory sclerites present
206' Absent
207 M12 present/ M13 absent
207' M12 absent/ M13 present
208 Trichoid sensillum at base of clasper lobes
208' Trichoid sensillum absent
209 Aedeagal sheath with scaffold
209a Aedeagal sheath tubular
210 Crochets small, reduced
210' Crochets large, lateral bodies
211 Aedeagal wings present
211' Aedeagal wings lost
211a Wings with S-shaped lateral elements
211b Elongate lateral wings
212 Thermastromorph superstructure
213 Spiculose membrane of end chamber
213' Lost

2. Middle level characters. May be subject to reversals.

101 BS with ventral thickening
102 Periphallic structures alike
103 P3 setose
104 Armature & ventral process inner tube
105 Tripartite armature inner tube
106 8S setae
107 8S dorsal arm w/ non-proximal attachment
108 P3 less fused (except cryptonella)
109 aed sheath free along lateral margins
110 phallosome similar (note aedeagal apodeme)
111 P3 with large Knob at base
112 phallosome similar
113 accessory lobe of wings
114 distal end inner tube recessed
115 distal end inner tube elongated
116 vesicle reduced or absent
117 stalked fulcrum
118 echinophagoid phallosome
119 hypertrophied aedeagal sheath
120 Ford's sclerite present
121 hypertrophied penis rods
122 P1 with spiniform setae
123 P1 bilobed
124 P1 reduced
125 process of anal sternum present
126 P3 enlarged
127 lobe of 8S present
127' reduced
128 manubrium broad, upcurved
129 aedeagal sheath greatly altered

3. Lowest level characters. Unique to individual genera.

001 P2 elongate
002 spiculose membrane of aedeagal pouch
003 P1 with hyaline fringe
004 lateral laminae fused with lat fulcral lobes
005 periphallie structures; phallosome
006 distal end inner tube?
007 hypertrophied inner tube
008 spiral spicules at end of inner tube
009 inner tube unique
010 sheath unique
011 filamentous aed apodeme
012 Tunga: choose character
013 Moepsylla: choose character
014 similar genitalia
015 ventrodistal spines of sheath
016 8S hyaline fringe
Non-genitalic characters

1. Higher level characters.
   A combs present; genal and ctenidial
   A' absent
   B mesopleural rod present
   B' absent
   C xenopsylline body form
   C' absent; associated with host switch

2. Lower level.
   D metasternal/episternal suture lost
   E Hypertrophied mouthparts/Neosomic female
   F echidnophagoid head and fascies
   F' loss associated with change of habit
C. Relationships among pulicid fleas

i. Introduction

The taxa included within Pulicoidea present a wide range of systematic and anatomical variety. While there are 15 genera containing 3 or fewer species, *Xenopsylla* as traditionally understood contains 83 species and subspecies. There are some suprageneric groupings which are quite homogeneous anatomically (*Xenopsyllinae* for example), and yet genera such as *Tunga* and *Moeopsylla* stand so far apart from any others as to make their relations most problematic. Thus the taxonomist finds here sources of confusion and difficulty at both extremes. Among some groups, characters are seemingly too similar to allow for discrimination of groups and judgement of primitive and derived states. Among others the gaps are so great that while there is no question about which characters are derived, it is not easy to say what the precursors were like.

In the following pages, I will discuss the derived characters of each of the phylogenetic taxa suggested, as well as give some indication as to the nature of the similarities which unite the systematic taxa as they have traditionally been arranged. The characters are primarily those of the male genitalia, but non-genitalic characters have been used occasionally either because of a lack of genitalic ones, or
because they are judged to be of such fundamental significance that they must be mentioned. In general only those primitive characters which are subject to later alteration are discussed. The failure to mention a character which is clearly primitive only indicates that it has no significance in this discussion. Often in the case of individual genera only a single derived character has been included in the cladogram. This does not necessarily mean that no others are present, and others may be found in the discussion of the genus. In those cases where no derived characters can be found to distinguish two or more taxa, the strong possibility exists that the taxa involved may be paraphyletic. These cases are discussed individually.

One of the virtues of erecting a hypothetical phylogeny is that it allows discussion of data concerning host associations and biogeography in a meaningful fashion. Such data are discussed here to some extent, in cases where they and the phylogeny are felt to be reciprocally illuminating.

ii. The Traditional Taxonomy of the Pulicoidea

The basic arrangement (Hopkins and Rothschild, 1953) had been to divide the group into two families, the Pulicidae and the Tungidae. The former contained four subfamilies, the Archaeopsyllinae, the Xenopsyllinae, the Pulicinæ and the Spilopsyllinae. The latter contained Tunginæ and Hectopsyllinae. The discovery of Neotunga prompted Hopkins and
Rothschild (1966) to reduce Tungidae and Pulicidae as then
defined to subfamilies within an enlarged Pulicidae, since the
genus was said to destroy the sharp boundaries between the
families. A discussion of this is included below. The former
subfamilies thus are given tribal status in this classification.
The primary differences between Tunginae and Pulicinae lie in the
variations in size and habits as well as in the characters used
in the key (the presence of spiniform setae on the hind coxae and
the number of sensillal pits present). Smit (1982) has recently
proposed another arrangement. Here Tungidae and Pulicidae are
elevated to family status again, but Tungidae now contains only
the genus Tunga, and Neotunginae and Hectopsyllinae are included
among the other pulicid subfamilies. Although all of these
classifications are accompanied by descriptions of the included
taxa and/or by keys for their analysis, no analyses are given to
allow the reader to discover precisely the reasoning behind the
proposed arrangements and only the most experienced readers are
likely to be able to assess the adequacy of the proposals.

The arrangement of systematic taxa suggested here is as
follows. Taxa of pulicid fleas are best divided at subfamily
rank, though it should be noted that one of these taxa may be
paraphyletic. The subfamilies then are Archaeopsyllinae,
Xenopsyllinae, Spilopsyllinae, Pulicinae, Tunginae,
Hectopsyllinae and Moeopsyllinae. Major deviations from
traditional arrangements are covered in detail below, but to
anticipate, they include the following: the breakup of
*Xenopsylla*, a reassessment of *Neotunga*, and the recognition of
the wholly aberrant nature of *Moeopsylla* and concomitant
questions as to its placement.

iii. Character Analysis and the Relations among the Taxa

As an aid to understanding the relationships as they are
explained below the reader should refer to the cladogram and Key
to the derived characters. For ease of reference the characters
have been arranged in 3 groups. Those at the 200 level are
characters which are important at the highest levels of the
included taxa. Characters numbered 001 and so on, are those
which are restricted to a single genus. Numbers in the 100
series are intermediate in range. No absolute significance is
attributed to these assignments. In addition, prime (') and
double-prime (") notation when appended to a given number denote
derived states of that character. Alternate states of the same
character may be denoted by a lower case letter (e.g., 204 and
204a). These notations are described in the Key to the
characters. In the discussion below, characters which are
restricted to individual genera will not normally be discussed,
and the interested reader may consult the section on the genera
above for further details.
Primitive Characters

The following genitalic conditions are widespread among the families of Siphonaptera and are here considered primitive for the pulicids: The manubrium is broadly fused to the 9th tergal apodeme and to the base of the pygidial plate, and is immovable, so that the manubrium and the apodeme together form a single fused structure arching over the terminalia. The body of the clasper (P1) is not articulated with the manubrial base but is broad basally, and fused with it. There is a single distal moveable process (P2), which articulates with the clasper body. The bases of the clasper lobes are united medially to form a more or less sclerotized arch (parameral bridge) dorsal to the aedeagal pouch. In addition to the above, the following may be added, though here the reasoning is more conjectural. The crochets may have been present, but not as large lateral bodies. This may be a derived pulicid character, but comparative work on the other families is needed. Also musculus tergoparaproctalis (M12) and musculus epiproctoparaproctalis (M13) would likely have been present, but their occurrence is known with certainty only for certain of the species which Günther (1961) studied.

Currently, knowledge of primitive characters of the phallosome itself is limited to those universal structural features which are obviously common to all fleas. Because detailed comparative knowledge of this structure in all families is not available, derived characters have not been proposed. For
example, it has been stated that Ford's sclerite is common in
primitive families (Traub and Rothschild, 1983), and though this
may certainly be true, it is not known to which group(s) this may
apply, and the fact that only four genera of pulicids are known
to possess this structure suggests that it may not be primitive
at this level.

Two primitive nongenitalic characters which are important
for this study are the presence of combs, both genal and
tenidial, and the presence of the mesopleural rod.

The Major Divisions

The Pulicoidea is divisible into two major groups which are
designated Rhipimorpha and Thermastromorpha. They differ
principally in the basic structure of the clasper mechanism.
Rhipimorpha (fr. Gk. rhipis: fan) primitively exhibits a broad,
basally articulated outer clasper lobe (P1), and the distal
process (P2) has shifted to the basal area of P1. The rhipimorph
phalosome is characterized by the presence of the scaffold-like
structure of the aedeagal sheath. This group contains the
Archaeopsyllinae, the Xenopsyllinae, and perhaps the
Moeopsyllinae. The group is entirely Old World in range, all of
the species being Ethiopian or Palaearctic.

Thermastromorpha (fr. Gk. thermastros: pincer) is
characterized by the presence of a pincer mechanism formed by the
two inner clasper lobes, usually designated P2 and P3 for the
upper and lower lobes respectively. The aedeagal sheath is basically tubular. The included major taxa are the Pulicinae, Spilopsyllinae, Tunginae, and Hectopsyllinae. These fleas are inhabitants of both the Old and New Worlds. This wide distribution coupled with the great diversity of anatomies represented, suggests that this may be the older of the two major divisions.

Rhipimorpha

The major derived genitalic characters are the articulated, paddle or fan shaped outer lobe of the clasper (P1), the basally located moveable process (P2), and the presence of the scaffold-like supports of the aedeagal sheath. This latter character is not as obvious and definitive as the others and is more subject to reversal. The scaffold is a result of the differential tanning of the sheath into rod-like areas, especially along the ribs, girdle and runners as well as along the lateral areas of the sheath. This kind of development is seen very clearly in Ctenocephalides and to a lesser extent in Xenopsylla cheopis and allied species. Hypertrophy of these structures is seen in Centetipsylla. An actual scaffold is difficult to discern in many species, and may in fact be lacking in them. I still believe that such a structure is widespread enough to be included as a derived character, at least as the basic form for the group. As will be discussed again below, this
contrasts with the tubular form of the sheath common in
Thermastromorpha as exemplified by Pulex and Cediopsylla.

Although based on very little information, the absence of
M12 is suggested as a possible derived character. It is absent
in Ctenocephalides and in Xenopsylla cheopis, but present in
those Thermastromorpha dissected.

Suspensory sclerites are evident in many rhipimorph genera,
and are especially well developed in archaeopsyllines (except
apparently Centetipsylla). They seem to be absent or at best
very weak in all Thermastromorpha. Where any development of the
dorsal pouch wall is evident in the latter it takes the form of a
proximal spur.

Finally there is a character hypothesized as primitive here
which is very important in the analysis of the relationships
between the Archaeopsyllinae and the Xenopsyllinae. All four
Archaeopsylline genera have a distinctive trichoid sensillum at
the base of the clasper lobes. This character occurs in no other
genera. Either it is a character primitive to the Rhipimorpha
and lost in the Xenopsyllinae, or the Archaeopsyllinae are in
fact holophyletic (i.e., not paraphyletic as suggested here).
The conflicting characters which suggest that the
Archaeopsyllinae is paraphyletic involve the periphallic organs.
Xenopsyllines share with Archaeopsylla and Ctenocephalides the
unfused, rod-like manubrium and the disjunction of the base of
the manubrium from the 9th tergal apodeme. The rod-like
manubrium never occurs elsewhere among the pulicids. In addition, the state of the 9th tergal apodeme in Archaeopsylla and Ctenocephalides can be interpreted as intermediate between a fully fused manubrium and the complete absence of the apodeme of tergum 9 characteristic of nearly all the Xenopsyllinae. There are only a few cases in the Xenopsyllinae in which these characters are even slightly reversed. The manubrium tends to be fused in some species of Synosternus, though it is still rod-like, and the 9th tergal apodeme tends to reappear as a small projection only in Procaviopsylla, Pariodontis and Genus X. Thus the uniqueness and stability of these characters lead to the suggestion that the trichoid sensillum may be primitive and not a derived character of the Archaeopsyllinae, and that it has been lost in the Xenopsyllinae. This loss would seem to be consistent with the reduced size and strength of PI characteristic of that group.

Further, there may be a character of the phallosome which unites the Archaeopsyllinae with the Xenopsyllinae. Both Ctenocephalides and Aphropsylla possess lateral wings which derive from the lateral lobes of the aedeagal sheath as well as crochets. Within the Xenopsyllinae there are two groups, as we shall see, one of which has a developed crochet, the other, developed wings. If the wings in Ctenocephalides and Aphropsylla are homologous with those in Synosternus, for example, then again, Archaeopsyllinae is paraphyletic. I think there is good
reason to believe they are: they are both developments of the lateral lobes of the aedeagus, they both seem to function by lateral extension, and they both seem to be articulated and musculated in a similar manner. One argument against this is that it requires that the primitive condition has been lost in both *Centetipsylla* and *Archaeopsylla* since neither of these have discernible wings.

If one denies this arrangement, then the periphallic characters must have arisen independently in the two subfamilies, and any stages intermediate between the primitive state and that in the *Xenopsyllinae* are no longer extant. Also one must hold that the wings in the *Archaeopsyllinae* and in the *Xenopsyllinae* are independently acquired as well.

**Archaeopsyllinae**

If this group is holophyletic, such a judgement can be based only on the common possession of the trichoid sensillum at the base of the clasper lobes. Within the group, *Centetipsylla* and *Aphropsylla* are related by the very large lateral crochets in both genera. This characteristic is rare in the pulicids, but occurs also in *Cediopsylla* and *Hectopsylla* and in certain members of the *brasiliensis*-group of *Xenopsylla*. They also share a ventral development of the 9th sternum which is no doubt derived at this level, but also occurs in one form or another in thermastromorph genera.
Centetipsylla itself is quite distinct among archaeopsyllines in having lost the heavy suspensory sclerites, and in the possession of spiniform setae on P1 (a character which is universal among Spilopsyllinae).

Archaeopsylla is characterized by the hyaline fringe of P1 discussed earlier. This genus also possess a muscle at the base of P1 which could be a homologue of M22, which otherwise appears only in the Thermastromorpha. This could be the reappearance of the ancestral condition, or a new development associated with the vibratory function of the clasper and the hyaline fringe.

Ctenocephalides is unusual in that the lateral laminae are strongly margined ventrally and are broadly fused with the lateral fulcral lobes. This is known elsewhere in the pulicids only in Synosternus cleopatrae, Procaviopsylla and perhaps Synopsyllus. Günther (1961) proposed a theory of the evolutionary development of the phallosome, based on a comparison of Ctenocephalides canis and Hystrichopsylla talpae, which depends upon a condition such as this being primitive. In Hystrichopsylla the fulcrum is in its entirety supported by the median lamina or an extension of it and the lateral laminae are fused with the wall of the aedeagal pouch. Günther holds this to be the derived condition. In most pulicids the lateral laminae are not connected with the lateral lobes, but the full range of forms is exhibited, from that seen in Ctenocephalides to the situation on Tunga where the fulcrum is borne on a stalk of the
median lamina. Günther's argument seems sound enough, and clearly the extreme condition in *Tunga* is derived among the pulicids, but there is no real evidence to show that really large, supportive lateral laminae are primitive for this group.

**Xenopsyllinae**

This subfamily is characterized by several derived features which involve reduction or loss of primitive characters. The apodeme of tergum 9 is completely absent in nearly all species, and appears in very reduced form only in three closely related genera. The outer clasper lobe is reduced significantly in size in the great majority of species, and is only enlarged in some *Synopsyllus* and members of the *conformis*-group of *Xenopsylla*. The trichoid sensillum proposed as primitive above has been lost, likely in accord with the reduction of P1. Suspensory sclerites are rarely well developed, and their appearance in the *brasiliensis*-group is to be interpreted as a reacquisition.

Two new characters appear in this group: A third lobe of the clasper apparatus, designated P3, is present ventrally or medio-ventrally to P2 and seems to be derived from the distal area of the base of the manubrium. In addition most members of this group have some sort of spiculose membrane of the end chamber. This may be associated with the distal end of the inner tube alone, or may be more extensive. This kind of elaboration exists elsewhere, as far as is known, only in *Pulex irritans* and
in *Hectopsylla*. It is almost certainly absent in other
Rhipimorpha.

Noteworthy also is the complete absence of combs in the
Xenopsyllinae. This reduction has occurred independently in the
Pulicinae on this view.

There is another character which should be mentioned,
although its distribution is not known. The Y-sclerite is now
known to be bifid distally only in certain members of this group.
They are: *Xenopsylla cheopis*, *X. versuta*, *X. eridos*, *Synosternus*
pallidus and probably *S. cleopatrae*, and in *Procaviopsylla*
divergens.

A striking characteristic of the group as a whole is evident
when the variation in genitalic anatomy is compared with the
uniformity in general body form among the genera. *Xenopsylla*
(s.l.), *Synosternus*, *Synopsyllus*, Genus X and *Procaviopsylla* all
share what may be called the "xenopsylline" body form, and
deviations from this may be interpreted as a result of host
associations. Thus it is suggested that this body form itself is
a primitive character of the group. If this is accepted, then
the proposed dismantling of *Xenopsylla* (s.l.) seems less radical.

There are two major lineages in the Xenopsyllinae, the
*Xenopsylla* (s.s.)/ *Synopsyllus* group (Group I.), and the
*Synosternus*/*Procaviopsylla* group (Group II).
Group I

In these species, the internal apodeme of P2 is well developed and forms the lateral portion of the parameral bridge. PI is without an apodeme. The wings are lost, and only the crochet remains, though it may be accompanied by a relatively complex armature. It is characteristic of this group that while the periphallic structures as a whole are very much alike, and are very similar to the anatomy seen in *Xenopsylla cheopis*, the phallosome varies quite widely. This uniformity of the periphallic structures along with the wide gaps in the anatomy of the phallosome among the four main groups of *Xenopsylla* and *Synopsyllus* make determination of the relations among them very difficult.

The *cheopis/trispinis* complex is united by the similar structure of the armature of the inner tube, and the presence of a distinctive ventral process just distal to the vesicle. These species have apparently lost the spiculose membrane of the end chamber. There is difficulty in determining a derived character set to differentiate these two groups, and it is thus quite possible that the *cheopis*-group is paraphyletic, *X. trispinis* having a common ancestor with some subgroup within it.

The *nilotica*-group is also potentially paraphyletic. It is united with the *eridos*-group by the distinctive tripartite armature of the inner tube. As pointed out earlier however, the only character defining the *eridos*-group is the presence of
hypertrophied penis rods, and a tendency in this direction is evidenced by *X. nilotica* itself.

The *brasiliensis*-group is easily recognized by the presence of a strongly developed P2, and by the general outline of the phallosome. In this group the suspensory sclerites also reappear, and are quite well developed. This very well defined group provides an example of one of the reasons phylogenies can be so hard to determine. The nature of the crochets would seem to be a fairly good character at a suprageneric level, but here we find some species with very large and conspicuous claw-like crochets, and others which seem to lack them entirely. This kind of gap in the anatomies within a small, well defined group, in a character that one might expect to be constant, indicates that any generalizations are to be viewed with some scepticism.

*Synosternus* is not easy to place, but is put alongside the *hirsuta*-group here on the basis of the common possession of large setae on the 8th sternum in both groups and by the absence or reduction of the metasternal/metepisternal suture in both. This latter character also occurs in *Synosternus*, but genitalic characters have been given priority here because of their greater complexity. Derived genitalic characters of *Synopsyllus* may include the vestiture of the distal end of the inner tube, but more species would need to be studied in detail. The *hirsuta*-group shows many primitive characters and good derived genitalic features have not been found.
Group II

In these species the crochets are absent and the lateral wings of the sheath are developed in their place. The parameral bridge is associated with the base of P3 and there is no internal apodeme of P2. P3 is setose in all species, while it is bare in Group I. The bare condition is probably primitive, setae appearing after the development of the lobe itself. There are two subgroups, IIa and IIb.

Further studies need to be done on the structure of the wings in these species. It is assumed here that the accessory lobes of the wings in *Procaviopsylla* and *Parodontis* are homologues of the S-shaped sclerites in the wings of species in subgroup IIa.

In subgroup IIa, P3 is comparatively freely attached at the base (except in *X. cryptonella* in the *erilli*-group). The dorsal portion of the aedeagal sheath is free along the lateral margin, only connecting basally. The proximal arm of the 9th sternum does not fuse with the distal arm terminally, so that the latter bears a projection pointing cephalad.

*Synosternus* and the *conformis*-group of *Xenopsylla* (s.l.) are united on the basis of the great similarity in the phallosomes of *S. cleopatrae* and members of the latter group. The remarkable similarities in details strongly suggest this arrangement. This means that *S. cleopatrae* exhibits the primitive condition in the
genus and that the conditions seen in S. pallidus etc. are derived (see generic description of Synosternus).

The affinities of Parapulex are not clear. It is here placed with the erilli-group on the basis of the apparently very similar lateral wings of the aedeagal sheath. On this interpretation, the very distinct body form and setation of Parapulex are to be regarded as being adaptations to the spiny mice (Acomys) which are the primary hosts of this flea. It is well known that fleas with spiny hosts tend to have large, widely spaced setae (Traub, 1972b). The primitive xenopsylline body form has been lost, as well as the spiculose membrane of the end chamber. The inner tube of this species is most distinctive.

Subgroup IIb. is quite well founded. Here we find the reappearance in a reduced form, of the 9th tergal apodeme. The phallosome is very similar in all these species, and they share a distinct cuticular enlargement at the base of P3 which is probably a further development of the parameral bridge structure, and which here at least, serves as the insertion for M23. It is difficult to analyze the relations among these three taxa, but in spite of the need for more detailed dissections it is suggested that Procaviopsylla and Pariodontis be placed together as the sister group of Genus X since they appear to share an accessory lobe of the lateral wings absent in that taxon. Pariodontis and Procaviopsylla are notable because they represent the only case in the pulicids where genitalic relations between two genera are
so clear while the general body forms are so different. As was suggested for *Parapulex* this is probably the result of a host switch. *Procaviopsylla* retains the xenopsylline body form, and the species are parasites of hyraxes. *Pariodontis* can be viewed as a larger, more elongate variation of the former, with large stout setae over the entire body. This would seem to correlate well with its life on porcupines.

In summary, the rationale for the rearrangement of the taxa formerly included in *Xenopsylla* is that the xenopsylline body form is a primitive character for the subfamily, and cannot be used to distinguish derived taxa. The characters of the male genitalia clearly suggest that at least with respect to *Synosternus*, *Xenopsylla* is paraphyletic, and that the *conformis-* and *erilli-* groups are very distinct from the rest of those included in *Xenopsylla*. The apparent distance between *X. erilli* and *X. conformis* and the other genera in the subfamily is best explained by the adaptations of the latter to very different hosts.
Thermastromorpha

The primary derived character setting this group apart is the presence of a distinctive pincer mechanism formed from the two inner clasper lobes. The hypothesized ancestral state for the pulicids is the presence of a single, distal moveable process, which is represented by P2 in the Rhipimorpha. A third lobe in Rhipimorpha is restricted to the Xenopsyllinae, and no pincer mechanism is present. The homologies of the various clasper lobes will be discussed below.

The two other characters suggested as derived for the group are less convincing, but are suggestive of close relation. The aedeagal sheath in these species tends to be tubular, in contrast to the scaffolded sheath present in Rhipimorpha. This is well illustrated by Cedipsylla inaequalis interrupta, Pulex irritans and Hectosylla psittaci. The sheath here is a unified tubular structure without distinct ribs, runners or girdle. In this view, the other species are derivative from this form. Exceptions occur. Delopsylla, Echidnophaga larina and E. bradyta exhibit a very hypertrophied and derived sheath which includes characters of the scaffold seen in Rhipimorpha, but this is to be regarded as a result of hypertrophy and not indicative of close relation.

There is, also, a "thermastromorph" superstructure, the prime attribute of which is the presence of a suprafulcral ridge,
formed by the portion of the median lamina just dorsad of the median fulcral lobe. This results in a tendency for the fulcrum to be borne on a stalk. This peculiarity is seen in its most reduced state in *Pulex* and *Cediopsylla*, and carried to the greatest extreme in *Tunga*, and *Hectopsylla*. As will be discussed below, it is also present in *Moeopsylla*.

It is also possible that these species have lost M13 and retained M12, in a reversal of the pattern suggested for the *Rhipimorpha*, though again this is based upon slim evidence.

In contrast to the *Rhipimorpha*, species in the *Thermastromorpha* exhibit a very wide range of anatomies, and gaps between taxa may be great. Consequently the relations among the taxa are more obscure. Ranking of the included taxa has been disputed. The status of *Tunginae* and *Hectopsyllinae* will be discussed below. They here are treated as subfamilies. They are very distinct anatomically, but on the view presented here, represent subtaxa within the *Thermastromorpha*.

**Spilopsyllinae**

The relations among members of this subfamily are not clear, although its monophyletic status seems well established. These genera all have a bilobed P1, except *Europsyllus*, and this is easily interpreted as derived. All have spiniform setae on P1, a distinct process of the anal sternum is present and the 8th sternum bears a midventral lobe.
Given these characters common to the group as a whole, it is difficult to find significant derived characters for the taxon *Cediopsylla* + *Spilopsyllus*. The genitalia do not depart in any great degree from the basic form. These genera are indistinguishable on the basis of nongenitalic characters. *Spilopsyllus cuniculi* is easily distinguished from most *Cediopsylla* species in having spine-like projections on the ventrodistal portion of the aedeagal sheath, having a reduced crochet, and in lacking Ford's sclerite. Characters apparently present in *Cediopsylla tepolita* (not seen during this study) suggest that *Spilopsyllus* and *Cediopsylla* are best regarded as congeneric. Barrera's (1967) drawings indicate that *C. tepolita* possesses Ford's sclerite and reduced crochets, thus representing an intermediate between *Cediopsylla* and *Spilopsyllus*. The presence of large claw-like crochets is interpreted here as a derived character, the primitive Thermastromorpha having small crochets. Thus the state seen in *C. tepolita* and *S. cuniculi* is primitive, and that in the North American species, derived.

The remaining spilopsylline genera are united by the common enlargement of P3 and by the loss of the clasping mechanism and concomitant reduction in the size of P2. Beyond this it is difficult to ascertain relations because of conflicts among the few clearly derived characters present. The unusual manubrium shared by *Hoplopsyllus*, *Euhoplopsyllus* and *Ornithopsylla* would seem to unite these. On the basis of Barrera's drawings of *H.*
pectinatus, there is some question as to whether it should be
considered congeneric with H. anomalus. On the basis of the
periphallie structures H. anomalus does not belong in this
assemblage. Actenopsylla shares with Ornithopsylla the complete
loss of P2, and with Euhoplopsyilus the presence of a dorsal bay
of the aedeagal apodeme just proximal to the fulcrum, as well as
a prominent distally projecting suprafulcral ridge. These
conflicting characters along with the marked degree of difference
among the phallosomes in these genera make relations impossible
to establish on the basis of the present knowledge of the
genitalia in this group in particular scanning electron
microscope studies might be useful.

Pulicinae

The Pulicinae itself, though comparatively homogeneous, is
not well defined on the basis of characters which are surely
derived. A possible candidate is the recessed distal end of the
inner tube. The overall similarities in the structure of the
periphallic organs among these species is perhaps a good derived
character, but this is made problematic by the resemblances
between the anatomies of Pulex and Cediopsylla. It is not
possible to say what the ancestral periphallic organs were like,
but the structure seen in Pulex would seem to be a good candidate
for the kind of anatomy from which Pulicinae and Spilopsyllinae
alike were derived. This cannot, therefore, be used to describe
the Pulicinae.

*Pulex* itself is easily recognized by the elongate penis rods and the presence of Ford's sclerite. This genus probably also possesses a spiculose membrane of the endchamber, though it has been seen only in *P. irritans* with certainty.

The echidnophagoid species make up the remainder of this subgroup. They are united by the presence of an "echidnophagoid phallosome", which is more easily recognized than described. *Echidnophaga* is interpreted as paraphyletic on this view, some species having departed more than others from a supposed echidnophagan ancestor. *Delopsylla, E. larina* and *E. bradyta* all are distinguished by the hypertrophy of the aedeagal sheath, which is clearly derived directly from the kind of structure found in normal echidnophagans. The phallosome of *E. bradyta* is best interpreted as a further hypertrophy of the structures found in *E. larina*, and so is another rare example of a "morphoseries" in the pulicids.

Derived genitalic characters are not found in *Echidnophaga* exclusive of *larina* and *bradyta*, and this group is probably paraphyletic with respect to *Neotunga*. The latter is unquestionably echidnophagoid, and the unusual features the genus exhibits are certainly associated with its mode of life rather than indicative of phylogeny. The phallosome in the only available specimens is not well preserved, but clearly reveals a structure very like that seen in *Echidnophaga*, including the
bifid dorsal aedeagal sheath and bifid dorsal sclerite, which may represent either Ford's sclerite or the paired crochets. 

Neotunga will be discussed in relation to the higher classification of the Tunginae below.

Tunginae and Hectopsyllinae

The species included here are among the most interesting of the pulicids and they differ greatly in anatomy from all other groups. The apodeme of tergum 9 is absent in Tunga and greatly altered in Hectopsyilla. In both, the upper lobe of the pincer mechanism is immobile. The distal end of the inner tube is elongate, the vesicle is reduced or absent and the fulcrum is borne upon a long stalk extending from the median lamina. The aedeagal sheath is greatly modified in both genera, but in strikingly different ways. All species are without combs and the mesopleural rod is absent.

Tunginae

The question which has arisen as to the classification of Tunga is whether it deserves the rank of family or subfamily. As discussed earlier, Hopkins and Rothschild (1953) opted for family status. In 1971 they suggested that the discovery of Neotunga, "so annexant between Tungidae and Pulicidae", requires the demotion of these as then defined to subfamilies within an expanded Pulicidae.
The females of both *Tunga* and *Neotunga* are sessile, neosomic, parasites. As we have seen, *Neotunga* belongs within the Pulicidae as it was then defined. It is in fact closely allied to *Echidnophaga*. The similarities between this genus and *Tunga* are entirely due to convergent evolution. Thus, insofar as ranking is to be based on divergent anatomy and behavior, *Tunga* is no longer so completely isolated, and its demotion to subfamily rank is justified. However, this by itself says nothing about the phylogenetic relations between the two genera. Hopkins and Rothschild (1966) go on to make the puzzling statement "The old belief that *Tunga* and *Echidnophaga* are close relatives is apparently correct, though the characters on which it is based are almost wholly adaptive and of little phylogenetic significance." They seem to feel that *Neotunga* is echidnophagan, but do not say so explicitly. If they hold that the characters relating *Echidnophaga* + *Neotunga* and *Tunga* are "wholly adaptive and of little phylogenetic significance" then on what basis do they assert that they are close relatives? The relationships proposed here are perhaps not satisfactory, but they do at least make an explicit attempt to indicate the nature of the "close relation" between these taxa.

In sum, the Tungidae and Pulicidae are not sister taxa. On this ground alone, one could deny the tungids family status. In addition, the life style of *Neotunga* is clearly an example of convergent evolution, and although it stands in some respects as
an anatomical intermediate between the tungids and the pulicids, it clearly belongs in the genus Echidnophaga. Thus the "degree of difference" argument for giving the tungids family status dissappears, as pointed out by Hopkins and Rothschild (1966). They should be treated as a subfamily.

Hectopsyllinae

These genera are not very distinct and perhaps Hectopsylla is paraphyletic. In any case they are anatomically very distinct from all other fleas. They are certainly thermastrnomorph however, and their relationship to Tunga is fairly clear, on the basis of features of the phallosome as described above, although the two genera have taken separate paths. In Tunga the aedeagal sheath has become long and thin, probably in response to its behavioral peculiarities, while in Hectopsylla the sheath has enlarged to become tubular and quite separate from the underlying superstructure. The periphallal structures are a puzzle, but the homologies of the musculature suggest that the apodeme of tergum 9 is represented by the upper lobe of the "manubrium" and the manubrium proper by the lower lobe.

As to the question of rank, the Hectopsyllinae is surely holophyletic, and exhibits a degree of difference from the other higher taxa at least equal to that which separates the other subfamilies, and so on both counts merits this rank.
Moeopsyllinae

*Moeopsylla sjoestedi* is the most aberrant and puzzling of the pulicid fleas. There are two tentative placements which have seemed to me at one time or another to merit consideration. The genus has been included in the Pulicinae, and shares with the members of that group the lack of a mesopleural rod and genal and pronotal combs. The genitalic characters bear no apparent relation to any seen in the Pulicinae. There are, however, certain similarities between the phallosome in *Moeopsylla*, and that seen in *Tunga*.

In both genera, the aedeagal sheath has greatly enlarged ribs. These are fused to the aedeagal apodeme in *Tunga* and detached from it in *Moeopsylla*. The lateral sheath membranes are produced into large elliptical lobes with crochets associated with the distal ends, and the inner tube in both genera is greatly elongate. It is possible that these are convergent developments originating from very different precursors, since in each case the parts are clearly homologous with normal components of the aedeagus and a unique common ancestor is not necessarily required in explanation. It is possible that they share an ancestor with a reduced 9th tergal apodeme, this structure having been lost entirely in *Tunga*, and reduced in *Moeopsylla*.

If we regard these characters of the phallosome as necessarily derived from a common ancestor, then an alternative phylogeny of the Thermastromorpha is suggested. The absence of
combs and of the mesopleural rod become the derived characters of Pulicinae + Tunginae + Hectopsyllinae. The sister group to this taxon is then the Spilopsyllinae. The Tunginae + Hectopsyllinae then could be the sister group of Pulicinae. These would be united by the same characters discussed above with the additional possibility that they share an ancestor with a reduced 9th tergal apodeme which has been lost in Tunga, reduced in Moeopsylla and modified greatly in Hectopsylla. In this scheme the similarities between the pincer apparatus in Pulex and Cediopsylla must be viewed as primitive for the Thermastromorpha, or as independently acquired. This is not particularly satisfactory, since an alternate view is more coherent. This will be treated below in the discussion of clasper lobe homologies.

Placing Tunga and Moeopsylla together would perhaps throw some light on the disjunct distribution of Tunga. If that genus had a common ancestor with the Ethiopian Moeopsylla then it would support the argument that Tunga was once more widespread in the tropics than it is today. Moeopsylla could be regarded as an aberrant offshoot of the tungids which has evolved in isolation in Africa.

The argument for the affinity of Moeopsylla with Tunga amounts to this: the combs are absent, but this is also a characteristic of the Xenopsyllinae, the mesopleural rod is absent, and there seems to be a relationship between the very highly derived phallosome in Tunga and Hectopsylla and that seen
in *Moeopsylla*, although each is quite distinct.

On the other hand, it must be acknowledged that *Moeopsylla* belongs in the Thermastromorpha only if we ignore the basic form of the periphalline structures. P3 is absent entirely, there is no vestige of a pincer apparatus, and the apodeme of the 9th tergum is present in a divided state. All of these conditions, as well as the location and shapes of P1 and P2, suggest affinities with Archaeopsyllinae. The only character of the phallosome that is reminiscent of Rhipimorpha is the nature of the enlarged ribs. These are very like a hypertrophied version of those seen in *Ctenocephalides*.

On the whole, it is perhaps best to ignore the nongenitalic characters of this genus and regard the apparent relations with the phallosome in Tunginae as independent developments. *Moeopsylla* then falls within the Rhipimorpha and its sister group is the Archaeopsyllinae + Xenopsyllinae.

This flea also exhibits a character which is found in no other pulicid, but which may be a character of the ancestral flea. The parameral bridge in *M. sjoestedi* is in the form of a sclerotized arch somewhat like that in *Hystrichopsylla talpae* ( Günther, 1961).

In summary, *Moeopsylla sjoestedi* may be a relict of a much larger group having relatively little affinity with recent pulicids as we know them, or, it may represent an aberrant offshoot of the ancestral tungid line that has evolved in
isolation from the remaining members of that group.

2. Homologies of Some Structures of the Male Genitalia

A. The Clasper Lobes

The phylogenetic scheme laid out here was initially formulated without any particularly detailed analyses of the homologies of the clasper lobes. Rather, the presence or absence of pincers, and the general form of the periphallie organs was considered, in comparison to proposed primitive states. Now that this work has been done, and a framework for discussion has been proposed, it remains to analyze explicitly the possible significance of this arrangement for the detailed homologies of the structures.

The clasper lobes within the Pulicoidea exhibit a great deal of variation. In this work, the nomenclature of Hopkins and Rothschild (1953) has generally been adopted (P1, P2 and P3) in order to minimize confusion in the discussion of these taxa. It remains to be judged how far these structures are comparable among the taxa.

The basic assumption is that the outer clasper lobe, P1 is the homologue of the body of the clasper in other families. There can be no real doubt about this based on position and function alone. These structures are fused with the manubrium,
the 9th tergal apodeme and the base of the pygidial plate in all fleas.

Questions arise with respect to the remaining lobes. The basic arrangement in most other siphonapteran families is the presence of a moveable process more or less distally on the body of the main clasper lobe. Smit (1970) and Günther (1961) consider the moveable process the telomere, and the body of the clasper the basimere, based on the belief that these structures are homologous with primitive appendages of the genital segments. This type of arrangement has been accepted as primitive for the pulicids in this analysis. Günther, basing his conclusions on Ctenocephalides canis, decided that P2 in this genus represents the ancestral telomere which has shifted proximally. The view accepted here is that P2 in the Archaeopsyllinae represents this moveable process in other fleas, and that the possession of two clasper lobes in some form is the original condition.

If Thermastromorhpa and Rhipimorpha split before the appearance of a third clasper lobe, as its absence in Archaeopsyllinae suggests, then such a third lobe, however designated, need not be homologous in the two divisions. The xenopsylline P3 is a product of the extension of the region where the manubrium, the pygidial plate, and the bases of P1 and P2 coalesce. Though there is considerable variation in the shape and strength of this lobe, there is no reason to doubt the homology within this subfamily.
The situation in Thermastromorpha is more complex. Here the dorsal inner lobe is usually designated P2, and the lower pincer lobe P3, but which of these actually represents the original moveable process? Two observations suggest that the lower lobe (P3) is the primitive process. This is in agreement with Smit (1930) who designates the upper pincer lobe in Thermastromorpha the pseudotelomere. Dissections and manipulations of preserved specimens of *Pulex irritans* and *Cediopsylla inaequalis interrupta* indicate that the hinge mechanism at the base of the pincers is such that movement of one is directly tied mechanically to the movement of the other. The exact location of muscle insertions in such minute structures is impossible to determine, but I believe that it is possible that the muscles concerned (M20, 21 & 22) may primarily insert on the lower lobe (P3) and that the upper is moved indirectly. Certainly it seems that the lower lobe accepts most, if not all, of the insertions. Secondly, the condition in *Hectopsylla* is suggestive. Here the upper lobe is entirely immobile and the lower lobe moveable. It is possible that this represents retention of, or reversion to, the primitive state for the Thermastromorpha. This also has implications for the condition in *Tunga*. As pointed out earlier, it is most likely that the pincers in *Tunga* are homologues of the pincers in the rest of the Thermastromorpha and that it is P1 that has been lost. Thus *Tunga*, with the immovable upper lobe of the pincer, also represents the primitive condition of the pincers. If this
is so, then the upper lobe would have first become moveable indirectly in the course of evolution, and only then perhaps directly connected to a muscle. This could have happened twice: once in the Pulicinae and once in the Spilopsyllinae. In that case the absence of combs and of the mesopleural rod is a derived character of the Pulicinae + Tunginae + Hectopsyllinae. Alternatively, given the great similarities between the claspers in Cedopsylla and Pulex, this moveable upper lobe could be regarded as a derived character uniting the Pulicinae and the Spilopsyllinae.

In light of the above, it seems most likely that the lower lobe of the pincer (P3) in these species represents the primitive moveable process, and is thus homologous with P2 in the Rhipimorpha. The upper lobe (P2) in Thermastromorpha is a new structure, with no counterpart in the rhipimorphs.

Further, there is evidence of a relationship between P3 in the Xenopsyllinae and the lower lobe of P1 in the Spilopsyllinae. Smit (1980) discusses certain abnormalities in the development of the male genitalia in Spilopsyllus cuniculi. In the specimen concerned, the products of the primary phallic rudiments have not moved into their normal positions and consequently the 9th and 10th terga have developed independently of the phallosome and those components of the clasper which are derived from the phallic rudiments. The manubrium, both lobes of the pincer, and the major, upper lobe of P1 are all missing. There is a setose
lobe appended ventrally from the pygidial plate which Smit refers to the lower lobe of P1 in this species. There seems little doubt that this is the proper homology. If, as Smit suggests, P3 in the Xenopsyllinae is a product of the tergal elements and not of the primary phallic lobes, then the lower lobe of P1 in the Spilopsyllinae and P3 in the Xenopsyllinae are developmental homologues. It was suggested above that the xenopsylline P3 is derived from the basal area of the pygidial plate and manubrium, and thus Smit's proposal has merit. It will not be possible to know with certainty whether this is true until a similar teratum is known from the xenopsyllines since the anatomical techniques for determining the developmental origin of these structures are too crude to answer the question. If these structures were to turn out to be derived from similar tergal elements, it would not necessarily alter the present view of phylogenetic relations. The extent of tergal elements in the periphallic organs of the primitive pulicid are not known, nor are they for the Archaeopsyllinae. They are likely restricted to the area near the base of the pygidial plate, and certainly do not form any major lobes of the clasper in archaeopsyllines. It is possible that an extension of these elements occurred twice, once in Spilopsyllinae and once in Xenopsyllinae. In neither case are the resulting structures supplied with muscle insertions, and they seem to be restricted to secondary mechanical and sensory functions in both cases. It seems most simple to assume that no
such structures were present in the ancestral pulicid, especially since they are absent in the Archaeopsyllinae, a group which seems to exhibit the least derived clasper structures.

B. The Crochets

The term crochet was first used by Snodgrass (1946). He described them as "moveable hooks... arising from the lateral walls [of the end chamber]". Each was said to be the insertion for a single long muscle which runs along the entire length of the aedeagal apodeme. These structures are extremely variable in pulicids and are absent entirely in some groups. There has been a certain amount of confusion concerning the nomenclature of the armature of the inner tube in pulicids. The conclusions drawn during this study have been discussed for each of the genera above, but it may be useful to summarize here.

The muscles which extend to the membranes of the end chamber are probably present in all pulicids (M25-26). Their insertions are not always distinct, and they may end in membranes of uncertain extent. The term crochet should be restricted, insofar as possible, to laterally located structures which are directly moved by the tendon of these muscles. This is not a problem in many cases. Those taxa which are difficult to assess are mentioned below.

Ctenocephalides has both crochets and lateral wings. The crochets are difficult to see in mounted material, but are
hook-like and do arise from the lateral walls of the end chamber. The wings are secondary and are derived from the lateral external walls of the sheath.

In the Xenopsyllinae one group has retained the crochets and many here have developed the associated armature to such an extent that use of the term "crochet" is unwise. The other group has apparently lost the crochet entirely and the lateral wings are developed instead. They bear the insertion of M25-26 but should not be designated crochets.

Most thermastromorphs do not present a problem. *Pulex irritans* bears terminal crochets which lie laterad of the distal end of the inner tube, and also have more ventral pseudocrochets, which have been mislabeled by some workers.

The nature of the crochets in some of the spilopsyllines is still unclear, and requires further study.

Crochets cannot be identified with certainty in *Tunga*, thought they are, surprisingly, quite clear and provide good landmarks in *Moeopsylla*.

The term "pseudocrochet" may be useful within a particular genus, but given the great variety of structures of the armature of the inner tube within the family as a whole, it is not wise to attempt to standardize its usage.

Throughout this work, reference has been made to the structure forming the roof of the capsule since this provides a convenient landmark when analyzing the phalosome. Rothschild
and Traub (1971) have devoted considerable space to the
description of this structure in various families of fleas. They
propose a variety of terms to describe the various portions of
the roof of the capsule, which, as a whole is called the'
tectum', following Jordan (1941). They have found it useful to
distinguish a pair of crescent sclerites, a central sclerite and
a satellite sclerite. During the course of this study it has not
been found necessary to make such distinctions for the pulicid
taxa, and they have therefore been avoided. The tectum is nearly
always visible in lateral view as a crescentic "sclerite" lying
dorsad of the median fulcral lobe. Among the taxa studied, there
is no indication that this is a true sclerite, or that it is a
paired structure. Therefore the commonly used term "crescent
sclerite" has not been used, preference being given to the
general term "tectum".
GENERAL SUMMARY

The male genitalia of fleas are among the most elaborate known. The details of structure and the mode of function are not well understood. The great diversity of genitalic form displayed within the Siphonaptera provides a rich source of characters for studies of the phylogenetic relations among taxa in the order.

This work is divided into two parts. In the first, the results of an investigation of the pupal development and adult anatomy of the male genitalia of *Xenopsylla cheopis* (Rothschild, 1903) are presented. This analysis serves as a basis for the descriptions of the genitalia in the 24 genera for which the males are known, which form the bulk of the second part. This comparative study results in conclusions concerning the relationships among the taxa which are presented in the form of a cladogram for the pulicoid genera. This is the first cladogram presented for the pulicids.

The genitalic anatomy of male pulicid fleas, while showing great diversity within the group, and somewhat less overall complexity than is exhibited by certain other families of fleas, is shown to be identical in basic structure and musculature with that reported in other families. Pupal development of the genitalic rudiments is comparable in all essentials to that reported for ceratophyllid fleas and is consistent with the general pattern of development described for the panorpoid...
complex as a whole.

The adult anatomy of the genitalia of male X. cheopis consists of two major elements, the phallosome and the clasper apparatus. These are described in some detail, including aspects of the musculature which prove useful in phylogenetic comparisons.

The major results of the comparative study in Part II are as follows:

The division of the Pulicoidea into the Pulicidae and the Tungidae is not tenable. The major division is based on clasper anatomy and is between the Rhipimorpha (fr. Gk.: fan) and the Thermastromorpha (fr. Gk.: pincer). The Rhipimorpha is predominantly restricted to the New World, the Thermastromorpha to the Old. The genus Neotunga, supposedly annectant between the Tungidae and the Pulicidae, is clearly not closely allied to the tungids, but represents a case of convergent evolution. The Tunginae is best understood as the sister group to the Hectopsyllinae.

The existing subfamilies are all likely monophyletic with the possible exception of the Archaeopsyllinae which may be paraphyletic with respect to the Xenopsyllinae.

The large genus Xenopsylla as usually understood is polyphyletic and should be broken into three separate genera.

The monotypic genus Moeopsylla exhibits a very aberrant genitalic anatomy, and should be transferred from the Pulicinae.
and elevated to the rank of subfamily. This new taxon, Moeopsyllinae, is of uncertain affinities, but is treated here as the sister group of the Archaeopsyllinae + Xenopsyllinae.

During the course of this study a new genus was discovered in material from the British Museum, and will be described in a later paper. The taxon is a member of the Xenopsyllinae and is allied with Procauropsylla and Pariodontis.
Literature Cited


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## Appendix I
### Pulicidae: Species List with Hosts and Distribution

#### Archaeopsyllinae

<table>
<thead>
<tr>
<th>Species</th>
<th>Hosts</th>
<th>Distribution</th>
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<tbody>
<tr>
<td><em>Ctenocephalides</em></td>
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</tr>
<tr>
<td>arabicus (Jordan, 1925)</td>
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<td>chabaudi Beaucornu &amp; Bain, 1982</td>
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#### Archaeopsylla Dampf. 1908

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<tr>
<td>erinacei erinacei (Bouché, 1835)</td>
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<tr>
<td></td>
<td>Manchurian</td>
</tr>
</tbody>
</table>

#### Centetipsylla Jordan 1925

<table>
<thead>
<tr>
<th>Species</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>madagascariensis (Rothschild, 1908)</td>
<td>tenrecs</td>
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<tr>
<td></td>
<td>Madagascar</td>
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</table>

#### Aphropsylla Jordan, 1932

<table>
<thead>
<tr>
<th>Species</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>conversa (J. &amp; R., 1913)</td>
<td>Lophiomys, Dendrohyrax,</td>
</tr>
<tr>
<td></td>
<td>E. Afr.</td>
</tr>
<tr>
<td>wollastoni (Rothschild, 1908)</td>
<td>&quot;rodent&quot;</td>
</tr>
<tr>
<td></td>
<td>Uganda</td>
</tr>
</tbody>
</table>
Nesolagobius J. & R., 1922

*callosus* J. & R., 1922

Nesolagus Sumatra

**XENOPSYLLINAE**

*Xenopsylla* Glinkiewicz, 1907

1. *cheopis* group
   a. *cheopis* subgroup:
      - *acomydis* Peus, 1977
      - *sequisetosa* (Enderlein, 1901)
      - *bantorum* Jordan, 1930

   Acomys, Nesioetes

   Cyprus

   W. Afr.

   field rats/predators

   E. Afr.

   Yemen

   Cosm.

   b. *astia* subgroup: (arranged geographically):
      - *pestanai* Ribeiro, 1975
      - *versuta* Jordan, 1925
      - *nubica* (Rothschild, 1903)
      - *dipodilli* Smit, 1960
      - *nesokiae* Ioff, 1946
      - *astia* Rothschild, 1911
      - *hussaini* Sharif, 1930
      - *nesioetes* (J. & R., 1908)
      - *papuensis* (Jordan, 1933)
      - *vaaxabilis* Jordan, 1925

   Lemmiscomys Aethomys

   Angora

   Sciuridae, Gliridae

   S. & C. Afr.

   Muridae Praomys

   Muridae

   Aliactaga, Jaculus

   Palearctic

   Ethiopian

   Mammals

   Dead Sea

   Ethiopian

   Turkmenva

   Indian

   Palaeartic

   N. India

   S. Java

   New Guinea

   Australia

   Hawaii

   australiaca Mardon & Dunnett 1971

   Rattus, Mus, etc.

   Australia

2. *trispinis* group
   - *mouschat* Smit, 1950
   - *trispinis* Waterston, 1911

   Picathartes

   Petrochelidon

   Cameroon

   S. Afr.

3. *nilotica* group
   - *coppensi* Beaucornu, Houin & Rodhain 1970
   - *debilis* Jordan, 1925
   - *difficilis* Jordan, 1925
   - *humilis* Jordan, 1925
   - *jorgei* Ribeiro, 1975
   - *mulier* de Meillon, 1947
   - *nilotica* (J. & R., 1908)
   - *orientalis* Marcus, de Meillon & Davis, 1960
   - *raybouldi* Hubbard, 1963

   Tatera

   Tatera

   Tatera

   Tatera

   Tatera

   Tatera

   Tatera

   Tatera

   Tatera

   Ethiopia

   E. Afr.

   E. Afr.

   E. Afr.

   Angola

   Kalahari

   E. Afr.

   Mozambique

   Tanzania
4. eridos group

- Tatera, Parotomys, S. Afr.
- Otomys
- Saccostomus
- Saccostomus
- Muridae
- Tatera, Graphiurus
- C. Afr.
- Cricetomys etc.
- E. Afr.
- Graphiurus, Thamnomys
- Cape Prov.
- Cryptomys
- Angola
- Thallomys
- Kenya
- Acomys, Lemniscomys
- Tanzania
- Saccostomus
- Kenya.
- Tatera
- Aethomys, Praomys
- S. Afr.
- Rattus, Lemniscomys
- Kenya
- Paraxerus, Thamnomys
- Thallomys, Aethomys

5. brasiliensis group

- Tatera, Parotomys, S. Afr.
- Otomys
- Saccostomus
- Saccostomus
- Muridae
- Tatera, Graphiurus
- C. Afr.
- Cricetomys etc.
- E. Afr.
- Graphiurus, Thamnomys
- Cape Prov.
- Cryptomys
- Angola
- Thallomys
- Kenya
- Acomys, Lemniscomys
- Tanzania
- Saccostomus
- Kenya.
- Tatera
- Aethomys, Praomys
- S. Afr.
- Rattus, Lemniscomys
- Kenya
- Paraxerus, Thamnomys
- Thallomys, Aethomys

6. hirsuta group

- Tatera, Parotomys, S. Afr.
- Otomys
- Saccostomus
- Saccostomus
- Muridae
- Tatera, Graphiurus
- C. Afr.
- Cricetomys etc.
- E. Afr.
- Graphiurus, Thamnomys
- Cape Prov.
- Cryptomys
- Angola
- Thallomys
- Kenya
- Acomys, Lemniscomys
- Tanzania
- Saccostomus
- Kenya.
- Tatera
- Aethomys, Praomys
- S. Afr.
- Rattus, Lemniscomys
- Kenya
- Paraxerus, Thamnomys
- Thallomys, Aethomys
### 7. conformis group

<table>
<thead>
<tr>
<th>Name</th>
<th>Synonym</th>
<th>Description</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>blanci Smit, 1957</td>
<td><em>Mus</em></td>
<td>Morocco</td>
<td>N. Iran</td>
</tr>
<tr>
<td>buxtoni Jordan, 1949</td>
<td><em>gerbillines</em></td>
<td>Morrocco</td>
<td>C. Asia</td>
</tr>
<tr>
<td>conformis conformis (Wagner, 1903)</td>
<td><em>gerbillines</em></td>
<td>Morrocco</td>
<td>C. Asia</td>
</tr>
<tr>
<td>conformis dipodes Ioff, 1953</td>
<td><em>gerbillines</em></td>
<td>Turkestan-Transcaspia</td>
<td>(as above)</td>
</tr>
<tr>
<td>conformis mycerini (Rothschild, 1904)</td>
<td><em>gerbillines</em></td>
<td>Turkestan-Transcaspia</td>
<td>(as above)</td>
</tr>
<tr>
<td>cunicularis Smit, 1957</td>
<td><em>Oryctolagus</em></td>
<td>Morocco</td>
<td>Tunisia</td>
</tr>
<tr>
<td>gerbilli caspica Ioff, 1950</td>
<td><em>gerbillines</em></td>
<td>Afghanistan-Turkmeniya</td>
<td>Afghanistan-Turkmeniya</td>
</tr>
<tr>
<td>gerbilli minax Jordan, 1926</td>
<td><em>gerbillines</em></td>
<td>Pakistan</td>
<td>S. Turkmeniya</td>
</tr>
<tr>
<td>gratiosa J. &amp; R., 1923</td>
<td><em>Puffinus</em></td>
<td>Morrocco</td>
<td>E. Iran</td>
</tr>
<tr>
<td>hirtipes Rothschild, 1913</td>
<td><em>gerbillines</em></td>
<td>Afghanistan-Turkmeniya</td>
<td>Afghanis-Turkmeniya</td>
</tr>
<tr>
<td>magdalinae Ioff, 1935</td>
<td><em>Ellobius, Nesokia</em></td>
<td>Morrocco</td>
<td>E. Iran</td>
</tr>
<tr>
<td>nutteri Ioff, 1930</td>
<td><em>gerbillines</em></td>
<td>Afghanistan-Turkmeniya</td>
<td>S. Turkmeniya</td>
</tr>
<tr>
<td>persica Ioff, 1946</td>
<td><em>Meriones</em></td>
<td>Morrocco</td>
<td>E. Iran</td>
</tr>
<tr>
<td>ramesis (Rothschild, 1904)</td>
<td><em>gerbillines</em></td>
<td>Morrocco</td>
<td>S. Turkmeniya</td>
</tr>
<tr>
<td>skrjabinii Ioff, 1930</td>
<td><em>gerbillines</em></td>
<td>Morrocco</td>
<td>S. Turkmeniya</td>
</tr>
<tr>
<td>regis (Rothschild, 1903)</td>
<td><em>Meriones, Rhombomys</em></td>
<td>Morocco</td>
<td>E. Iran</td>
</tr>
<tr>
<td>taractes J. &amp; R., 1913</td>
<td><em>gerbillines</em></td>
<td>Morocco</td>
<td>E. Iran</td>
</tr>
<tr>
<td>tarimensis Yu &amp; Wang, 1979</td>
<td><em>Dipus</em></td>
<td>Morocco</td>
<td>E. Iran</td>
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</table>

### 8. erilli group

<table>
<thead>
<tr>
<th>Name</th>
<th>Synonym</th>
<th>Description</th>
<th>Location</th>
</tr>
</thead>
</table>

**Synosternus** (Jordan, 1925)

<table>
<thead>
<tr>
<th>Name</th>
<th>Synonym</th>
<th>Description</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>burtoni Marcus and DeMeillon, 1960</td>
<td><em>Herpestes, Xerus</em></td>
<td>Somalia</td>
<td>Somalia</td>
</tr>
<tr>
<td>cleopatrae cleopatrae (Rothschild, 1903)</td>
<td><em>gerbillines</em></td>
<td>W. Afr.</td>
<td>W. Pak.</td>
</tr>
<tr>
<td>cleopatrae pyramidalis (Rothschild, 1904)</td>
<td><em>gerbillines</em></td>
<td>W. Afr.</td>
<td>W. Pak.</td>
</tr>
<tr>
<td>longispinus (Wagner, 1889)</td>
<td><em>carnivores, hedgehogs</em></td>
<td>C. Asia</td>
<td>C. Asia</td>
</tr>
<tr>
<td>pallidus (Taschenburg, 1890)</td>
<td><em>carnivores, insectivores</em></td>
<td>C. Afr.</td>
<td>Medit. - Afgh. - C. Asia-India</td>
</tr>
<tr>
<td>robustus Murzakhmetova, 1969</td>
<td><em>carnivores, hedgehogs</em></td>
<td>C. Asia</td>
<td>C. Asia</td>
</tr>
</tbody>
</table>
somalicus (J. & R., 1908) Xerus Somalia, Kenya, Tanzania, Uganda

Synopsyllus Wagner & Roubaud, 1932

estradaj Klein, 1964 rodents, small mammals Madagascar
fonquernei Wagner & Roubaud, 1932 Rodents, small mammals Madagascar
 girardj Klein, 1966 rodents, small mammals Madagascar
roberti Klein, 1966 rodents, small mammals Madagascar
smiti Lumaret, 1962 rodents, small mammals Madagascar

Parapulex Wagner, 1910

chephrenis (Rothschild, 1903) Acomys Egypt, Sudan, Ethiopia Israel, Jordan
 echinatus Smit, 1956 Acomys, gerbillines Kenya, Tanzania

Procaviopsylla Jordan, 1925

angolensis Jordan, 1925 Procavia Ethiopian
 creusae (J. & R., 1904) Procavia Ethiopian
 divergens (J. & R., 1906) Procavia Ethiopian
 isidis (Rothschild, 1903) Procavia Ethiopian
 procaviacae (Fox, 1914) Procavia Ethiopian
 spinifex spinifex (Jordan, 1936) Procavia Ethiopian
 spinifex cabrali Ribiero 1975 Heterohyrax Ethiopian

Pariodontis J. & R., 1908

riggenbachiriggenbach (Rothschild, 1904) Hystrix E. & S. Afr. + Morocco
 riggenbachiturkestanica Dubinin, 1947 Hystrix Turkestan
 riggenbachiwerneki Costa Lima, 1940 Hystrix Indian
 subjugis Jordan, 1925 Hystrix Indo-Chinese
 Indo-Malayan

Genus X

D. sp. Otomys Tanganyika
231

**Pulicella Smit, 1964**

*macrotheca Smit, 1964* Rattus Nyasaland

**SPILOPSYLLINAE**

*Cedioptila* Jordan, 1925


*simplex* (Baker, 1895) rabbits, hares E.N. America

*spillmanii* Jordan, 1930 rabbits, hares Ecuador

*tepolita* Barrera, 1957 rabbits, hares Mexico

**Spilopsyllus** Baker, 1895

*cuniculi* (Dale, 1878) Oryctolagus Palearctic

**Actenopsylla** J. & R., 1923

*suavis* J. & R., 1923 Puffins, petrels, auklets Pac. coast N. Amer.

**Ornithopsylla** Rothschild, 1908

*laetitiae* Rothschild, 1908 Puffinus puffinus Britain

**Euhoplopsyllus** Ewing, 1940

*andensis* (Jordan, 1933) Thomasomys Ecuador

*exoticus* (J. & R., 1923) rabbits, sm. mammals Panama

*glacialis glacialis* (Taschenberg, 1880) rabbits, predators Canada

*glacialis affinis* (Baker, 1904) hares, rabbits Rocky Mts., Californian

*glacialis foxi* (Ewing, 1924) hares, rabbits, Citellus Subreg.

*glacialis lynx* (Baker, 1904) Lynx N.U.S., Canada

*glacialis proflatus* (Jordan, 1925) hares Central Asia
manconis (Jordan, 1950) Sylvilagus Peru

Hoplopsyllus Baker, 1905

anomalus (Baker, 1904) squirrels, hares S.W. U.S. - N. Mex.
pectinatus Barrera, 1967 Romerolagus diazi Mexico

PULICINAE

Pulex (Pulex) Linnaeus, 1758

irritans L., 1758 pigs, carnivores, man Cosmopolitan
simulans Baker, 1895 deer, carnivores, rodents Pac. N.W. - Panama
sinoculus Traub, 1950 Sciurus, Orthogeomys Guatemala

Pulex (Juxtapulex)

alvarezi Barrera, 1955 Dasypus Costa Rica
porcinus J. & R., 1923 Tapirella Mexico
echidnophagoides (Wagner, 1933) peccaries S.W. U.S.- N.Mex.

Echidnophaga Olliff, 1886
(arranged geographically)

gallinacea (Westwood, 1875) various Cosmop.
murina (Tiraboschi, 1903) Mus, Rattus Mediterr.
tarda Jordan, 1925 carnivores Ethiopia

popovi Ioff & Argyropulo, 1934 carnivores Armen., Iran

oschanini Wagner, 1930 Rhombomys Cen. Asia
ochotona Li, 1957 pikas China
tiscades Smit, 1967 Allactaga Mongolia

ambulans ambulans M. Roths., 1936 Tachyglossus N.S.W., E. Austr.
ambulans inepta M. Roths., 1936 Tachyglossus (as above)
aranka J. & R., 1906  
Bettongia  
W. Australia

calabyi Mardon & Dunnett, 1971  
wombats  
S. Australia

cornuta Wagner, 1936  
wombats  
S. Australia

evrei Mardon & Dunnett, 1971  
wombats  
S. Australia

liopus J. & R., 1906  
various  
W. Australia

macronychia J. & R., 1906  
Bettongia  
W. Australia

myrmecobii Rothschild, 1909  
Trichosurus, Oryctolagus  
Australia

octotricha Mardon & Dunnet, 1971  
wombats  
Australia

perilis Jordan, 1925  
various  
W. Australia

Neotunga Smit, 1962

euloidea Smit, 1962  
Manis  
Rhodesia

inexpectata  
(Smit, 1950)  
Phacochoerus  
Kenya, Sudan

Delopsylla Jordan, 1926

crassipes Jordan, 1926  
Pedetes capensis  
Kenya

HECTOPSyllinae

Hectopsylla von Frauenfeld, 1860

broscus J. & R., 1906  
Conepatus  
Chilean

conger J. & R., 1906  
Conepatus  
Chilean

cypha Jordan, 1942  
Microcavia, Octomys  
Chilean

eskevi Jordan, 1933  
rats, Cavia  
Chilean

gemina Jordan, 1939  
Microcavia, Octomys, Graomyis  
Chilean

gracilis Mahnert, 1882  
Ellipomodontia  
Chilean

knuthi Traub & Gammons, 1950  
swift  
Mexico

psittaci von Frauenfeld, 1860  
chickens, owls,  
Psittacus

stomis Jordan, 1925  
birds, Mephitis, Lagostomus  
Chilean

suarezi C. Fox, 1929  
Cavia, Rattus  
Chilean

Rhynchopsyllus Haller, 1880

megastigmata Traub & Gammons, 1950  
bats  
Peru

pulex Haller, 1880  
bats  
S. America

(male not known)
TUNIGINAE

**Tungia Jarocki, 1838**

1. *caecata*-group

<table>
<thead>
<tr>
<th>Species</th>
<th>Hosts</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>caecata</em> (Enderlein, 1901)</td>
<td><em>Rattus, Mus</em></td>
<td>Brazil</td>
</tr>
<tr>
<td><em>caecigena</em> J. &amp; R., 1921</td>
<td><em>Rattus, Mus</em></td>
<td>China, Japan</td>
</tr>
<tr>
<td></td>
<td><em>Apodemus, Eothenomys</em></td>
<td>China</td>
</tr>
<tr>
<td><em>callida</em> Li &amp; Chin, 1957</td>
<td>(as above)</td>
<td>China</td>
</tr>
<tr>
<td><em>libis</em> Smit, 1962</td>
<td><em>Akodon</em></td>
<td>Ecuador, Chile</td>
</tr>
<tr>
<td><em>monositus</em> Barnes &amp; Radovsky, 1969</td>
<td><em>Peromyscus</em></td>
<td>Baja Calif.</td>
</tr>
</tbody>
</table>

2. *penetrans*-group

<table>
<thead>
<tr>
<th>Species</th>
<th>Hosts</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>penetrans</em> Wagner, 1932</td>
<td><em>Tamandua, Carjama</em></td>
<td>Brazil</td>
</tr>
<tr>
<td></td>
<td><em>various</em></td>
<td>S. U.S.-Paraguay</td>
</tr>
<tr>
<td><em>terasma</em> Jordan, 1937</td>
<td><em>Cabassous</em></td>
<td>Brazil</td>
</tr>
<tr>
<td><em>travassosi</em> Pinto &amp; Dreyfus, 1927</td>
<td><em>Tatusia</em></td>
<td>Brazil</td>
</tr>
</tbody>
</table>

MOEOPSISYLLINAE

**Moeopsylla Rothschild, 1908**

<table>
<thead>
<tr>
<th>Species</th>
<th>Hosts</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>sjoestedti</em> Rothschild, 1908</td>
<td><em>Phacochoerus</em></td>
<td>E. Afr.</td>
</tr>
</tbody>
</table>
Appendix II:  
*Menopsylla* (s.l.) Species List  
Arranged alphabetically according to species placement in Hopkins and Rothschild (1953) or original descriptions

1. *brasiliensis*-group - 22 taxa  
   - angolensis Ribeiro, 1975  
   - bechuanæ de Meillon, 1947  
   - brasiliensis (Baker, 1904)  
   - cornigera Smit, 1956  
   - crinita J. & R., 1922  
   - georychi (C. Fox, 1914)  
   - graingeri Smit, 1956  
   - hamula Jordan, 1925  
   - jorgei Ribeiro, 1975  
   - morgandaviesi Hubbard, 1963  
   - mulleri de Meillon, 1947  
   - orientalis Marcus, de Meillon & Davis, 1960  
   - raybouldi Hubbard, 1963  
   - robertsi Jordan, 1936  
   - sarodes sarodes Jordan, 1937  
   - sarodes manyarensis Hubbard, 1963  
   - sarodes serengetiensis Hubbard, 1963  
   - scopulifer (Roths., 1905)  
   - syngenis Jordan, 1937  
   - trifaria de Meillon, 1930  
   - zumpti Haeselbarth, 1963

2. *cheopis*-group - 25 taxa  
   - acomydis Peus, 1977  
   - aequiseta (Enderlein, 1901)  
   - astia Rothschild, 1911  
   - australiaca Mardon & Dunnett 1971  
   - bantorum Jordan, 1938  
   - cheopis (Rothschild, 1903)  
   - dipodilli Smit, 1960  
   - eridos (Rothschild, 1904)  
   - frasi de Meillon, 1937  
   - geidenhuysi de Meillon, 1949  
   - hipponax de Meillon, 1942  
   - hussaini Sharif, 1937  
   - nesiotes (J. & R., 1900)  
   - nesokiae Ioff, 1946  
   - nubica (Rothschild, 1903)  
   - occidentalis de Meillon, 1938  
   - papuensis (Jordan, 1933)  
   - pestanai Ribeiro, 1975  
   - philoxera Hopkins, 1949
phyllomae de Meillon, 1934
piriej Ingram, 1929
silvai Ribeiro, 1975
tanganyikensis Marcus, de Meillon & Davis, 1960
versuta Jordan, 1925
 vexabilis Jordan, 1925

3. conformis-group - 18 taxa
blanci Smit, 1957
buxtoni Jordan, 1949
conformis conformis (Wagner, 1903)
conformis dipodis Ioff, 1953
conformis mycerini (Rothschild, 1904)
cunicularis Smit, 1957
gerbilli gerbilli (Wagner, 1903)
gerbilli caspica Ioff, 1950
gerbilli minax Jordan, 1926
hirtipes Rothschild, 1913
magdalinae Ioff, 1935
nuttalli Ioff, 1930
persica Ioff, 1946
ramesis (Rothschild, 1904)
regis (Rothschild, 1903)
skrjabini Ioff, 1930
taractes J. & R., 1913
tarinensis Yu & Wang, 1979

4. erilli-group - 2 taxa
cryptonella de Meillon & Hardy, 1954
erilli (Rothschild, 1904)

5. gratiosa-group
gratiosa J. & R., 1923

6. hirsuta-group - 8 taxa
demelloni Haesebarth, 1964
davisi de Meillon, 1940
hirsuta hirsuta Ingram, 1929
hirsuta multiseta Haesebarth, 1964
hirsuta placida de Meillon & Hardy, 1951
lobengulae de Meillon, 1930
petteri Lumaret, 1962
sulcata Ingram, 1926

7. nilotica-group - 5 taxa
coppensii Beaucornu, Houin & Rodhain 1970
debilis Jordan, 1925
difficilis Jordan, 1925
humilis Jordan, 1925
nilotica (J. & R., 1908)
9. *trispinis*-group
   *moucheti* Smit. 1958
   *trispinis* Waterston, 1911
   female only.
Appendix III: Solutions and Techniques

1. Bouin's Dubosq-Brasil:
   150cc 80% Ethanol
   60cc 40% formaldehyde
   15cc glacial acetic acid
   1gm picric acid
   Specimens were immersed live at 35-45 degrees Celsius for 24 hours, and stored in the fixative until embedded.

2. Karnowsky's Fixative Variation:
   12.5ml 0.2M cacodylate buffer, pH 7.3
   7.5ml 10% formaldehyde made up from paraformaldehyde
   3.7ml 25% glutaraldehyde
   0.0125gm picric acid

3. Zalokar's Method:
   Animals were immersed in a mixture of 50% heptane and 50% glutaraldehyde at 25 degrees Celsius for 1-2 hours with occasional shaking, then dehydrated to 70% ethanol for storage.

4. Ito and Vinson Variation:
   This procedure requires a change to maleate buffer and secondary post-fixation in uranyl acetate. No visible
improvement was found over the simpler Karnowsky technique.

5. Chatton's Eosin Y/Light Green Stain:

Solution A

95% ethanol .............100gm
Light Green ..............1gm
Eosin-Y ..................2gm
(dissolve with occasional shaking for several days).

Solution B

5% acetic acid in absolute ethanol.

6. Eggs of *Ctenocephalides felis* were treated as follows (after Zalokar):

1. dechorionated in 50% commercial bleach less than 5 min.
2. washed in 3 changes of phosphate buffer, pH 7.4, 15 min. each.
3. fixed in 25% gluteraldehyde in heptane: 15-20 mins. with occasional vigorous shaking.
4. buffer wash.
5. immersed in Pronase (6 units/mg.), 0.25g/6ml for 10-14 mins.
6. buffer wash.
7. postfixed in 1% osmium tetroxide for 2-24 hrs.
8. buffer wash.
9. acetone dehydration.
10. embedded in Medcast resin, at least 24 hrs. for each change of resin solution.
A comparative study of the male genitalia in the Pulicoidea
(Siphonaptera)

by

Thomas Bigelow Cheatham

Volume 2 of 2

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of the
Requirements for the Degree of
DOCTOR OF PHILOSOPHY

Major: Entomology

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Abbreviations used in the figures

aa: aedeagal apodeme
ac: anal cone
acclb: accessory lobe
aed: aedeagus
ag: accessory gland
an: anus
ans: anal strut
apb: antepygidial bristle
ar: apodemal rod
as: aedeagal sheath
at9: apodeme of tergum 9
br: brush
c: capsule
cl: clasper lobe
cr: crochet
cu: cuticle
dfl: dorsal fork (of median fulcral lobe)
dl: dorsal lobe (of aedeagus)
dls: dorsal longitudinal strut
drn: dorsal branch of the runner
eb: ejaculatory bulb
ec: end chamber
ed: ejaculatory duct
enph: endophallus
epd: epididymis
fg: foregut
fn: fin (of aedeagal apodeme)
fp: fringe of penis
Fs: Ford's sclerite
g: girdle
hd: hood
hf: hyaline fringe
hk: hook
inv: invagination
L1(L2): L1 and L2 - dorsal and ventral lobes of P1
lf1: lateral fulcral lobe
ll: lateral lamina (of aedeagal apodeme)
llb: lateral lobe of the aedeagal sheath
lpr: lower penis rod
lsc: lateral shaft of the capsule
lu: lumen
m( ): muscle number
man: manubrium
mem: membrane
mes: mesomere
mf1: median fulcral lobe
ml: median lamina (of aedeagal apodeme)
mlb: median lobe of the aedeagus
PART I

PLATES 1 - 27
(Unless otherwise noted, all illustrations are of *Xenopsylla cheopis*)

PLATE 1

Schematic representation of generalized genitalia

Fig. 1: Components of the superstructure of a generalized aedeagus in their relative positions

Fig. 2: Complete aedeagus, including schematic transverse section at the level of the aedeagal apodeme

Fig. 3: Relative position of generalized periphallic structures. The coordinate system superimposed upon the aedeagal apodeme and the curve of the penis rods indicates the approximate orientation used in Part II in describing the length of the penis rods in various genera in terms of the number of degrees of curvature
PLATE 2

Fig. 4: Longitudinal section of the embryo of *Ctenocephalides felis felis* Bouché, illustrating primary segmentation. Scale line = 0.10mm

Fig. 5: Longitudinal section of the first instar larva of *Xenopsylla cheopis*. Segment 11 is represented by the paired anal struts, one of which is partly seen in this section. Scale line = 0.25mm
PLATE 3

Fig. 6: Ventral and lateral views of the terminal abdominal segments of the third instar larva showing the primary phallic lobes. The specimen represented ventrally in the second, and laterally in the third illustration is at a slightly later stage of development, and the parameres have begun to shift dorsally. Scale line = 0.1mm.

Fig. 7: Schematic representation of a longitudinal section through the developing phallosome in the pupa. The aedeagal apodeme (aa) and the apodemal rod (ar) develop as invaginations. The capsule (c) and the vesicle (v) are both formed as invaginations within the lumen of the genitalic mass. The penis (p) is an evagination of the proximal end of the lumen.

Fig. 8: Lateral view of the terminalia of a male pupa showing the outline of the pupal cuticle and the form of the underlying cuticular structures of the early pharate adult. Compare with Fig. 14. Scale line for Fig. 8 and Fig. 9 = 0.2mm.

Fig. 9: Lateral view of late pharate adult terminalia, pupal cuticle removed. Compare with Fig. 41.
Plate 4

Longitudinal sections of larval terminalia

Fig. 10: Median longitudinal section of terminal segments of an early third instar larva illustrating the position of the phallic rudiment (phr). Note the position of the intersegmental muscle (m9), for comparison with that in Fig. 12. Scale line = 0.1mm

Fig. 11: Higher magnification of phallic rudiment (same specimen as in Fig. 10, section slightly mesad of the former). The large mass of cells probably represents the mesomere, and the thin ventral arm, the paramere. Scale line = 0.05mm

Fig. 12: Terminal segments of a third instar larva at a slightly later stage. The developing tissue has begun to withdraw from the larval cuticle in the area around the phallic rudiment. The lobes of pupal sternum 9 have begun to form (s9) and m9 loops into the body cavity as the rudiment enlarges and withdraws. Scale line = 0.1mm

Fig. 13: Third instar larva. Ectodermal invagination in the region of the tergum of abdominal segment 10 and the anal strut. (See text). Scale line = 0.05mm
PLATE 5

Pupal terminalia. Scale lines = 0.1mm

Fig. 14: Scanning electron micrograph of pupal terminalia. Note the reduction of the eighth tergum. The external lobes of the parameres at this stage bear little relation to the final position of the clasper lobes in the adult, and are much smaller.

Figs. 15 & 16: Median longitudinal sections of the pupal terminalia. These specimens are at approximately the same stage of development. Note here, and in Fig. 17 the origin of the penis rods (pr) from the lateral walls of the lumen of the genitalic mass. Note the terminal cap (tc) from which the sensillium and at least the dorsal portion of the adult anal cone develop.

Fig. 17: Longitudinal section through the terminalia of the early pharate adult. The penis (p) with the central ejaculatory duct and the forming penis rods (pr) are clearly visible.

Fig. 18: Longitudinal section of pupal terminalia. This section is taken laterad of the median plane and the developing lateral fulcral lobe (lf1) can be seen, as well as the differentiating sensillium.

Fig. 19: Same specimen as in Fig. 18. This more lateral section shows the characteristic closing apparatus of the abdominal spiracles, here associated with the eighth abdominal segment.
Frontal sections of pupal terminalia. Scale lines = 0.05mm

Fig. 20: The lumen (lu) of the genitalic mass is evident, as are the developing paired vasa deferentia (vd) and the accessory glands.

Fig. 21: Same specimen as in Fig. 20, section more dorsal. Note the single clasper lobe on either side. Tissue of the end chamber, perhaps including that which will produce the crotchets (cr), is visible.

Fig. 22: Same specimen as above, more dorsal section, which just includes the parameral bridge.

Fig. 23: This specimen is at a later stage of development than that in the other figures of this plate. This plane of section corresponds roughly to that of Fig. 22. Notice the longitudinal division of the clasper lobe rudiments, which apparently gives rise to the clasper lobes of the adult. There is no apparent subsegmentation along the proximo-distal axis. The parameral bridge is now well developed.
PLATE 7

Transverse sections of pupal terminalia. Figs. 24 - 31 are in proximal to distal order. Scale lines = 0.05mm unless otherwise indicated.

Fig. 24: Rudimentary tissues of the paired vasa efferentia (ve) connecting the testes to the four lobes of the accessory glands (ag). There appear to be four vasa efferentia since they loop before ending in the accessory glands. The paired vasa deferentia (vd) connect the accessory glands with the ejaculatory bulb (not seen in this series). Scale line = 0.025mm

Figs. 25 & 26: The rectal papillae (rp) are visible, as well as the vasa deferentia (vd) and the proximal end of the genitalic mass.

Fig. 27: The aedeagal apodeme (aa) arises as a deep, dorso-ventrally flattened invagination with a central lumen, which is visible here.

Fig. 28: Noteworthy here is the appearance of the apodemal rod (ar), invaginated as is the aedeagal apodeme. Notice the developing penis rods (pr) which appear to form as evaginations along the inner wall of the lumen of the genital mass. Compare with Figs. 16 & 17.

Fig. 29: The clasper lobe has begun to divide longitudinally and is here visible with two separate processes (Compare Fig. 23). The distal arms of sternum 9 appear here and in the next two figures.

Fig. 30: The dorsal lobe of the aedeagus (dl) is continuous dorsally in the adult, but apparently arises by the union of two lateral arms.

Fig. 31: The original parameres (par) are still present as an empty shell of pupal cuticle.
PLATE 8

Transverse sections of terminalia of early pharate adult. Although much of the abdominal content was not preserved intact in this specimen, the genitalic components remain. Figures 32 to 39 are in proximal to distal order. Compare to figures in Plate 7. Compare with Plates 16 & 17 for adult structures. Scale lines = 0.1mm

Fig. 32: Notable here is the separation of the penis rods from the endophallus wall

Fig. 33: Here the circular cross section of the endophallus wall is clearly evident ventrad of the laminae of the aedeagal apodeme

Fig. 34: This section is just distal to the end of the tissue of the penis itself

Fig. 35: The sensillia setae are visible near the top of this photograph

Fig. 36: The three clasper lobes of the adult are separated by this stage of development

Fig. 37: The elements of the sensillium are evident at the top of the specimen here

Fig. 38: Here the endchamber (ec) can be seen to open into the space between the pupal and adult cuticle

Fig. 39: This most distal section shows the presence of the parameres as now empty casts formed of the pupal cuticle
PLATE 9

Fig. 40: Lateral view of the phallosome and external terminalia. Compare especially with Figs. 41, 42 & 45. Scale line = 0.1mm.
PLATE 10

Scanning electron micrographs of the adult terminalia. Scale lines = 0.1mm

Fig. 41: Lateral view of terminalia of a late pharate adult with the pupal cuticle removed. A remnant of the pupal cuticle is visible above the sensillum.

Fig. 42: Dorso-caudal view of a similar specimen.
PLATE 11

Periphalic structures of the adult. Scale line = approx. 0.1mm

Fig. 43: Mesal view of the pygidial plate and clasper apparatus

Fig. 44: Ventral view of the clasper apparatus
Lateral aspect of the adult phallosome. Scale lines = 0.1mm

Fig. 45: Scanning electron micrograph of the phallosome showing external cuticular structure of the aedeagus and surface muscles of the internal portion of the phallosome

Fig. 46: Light micrograph of the cuticular structures of the phallosome
PLATE 13

Fig. 47: Lateral view of the cuticular structures of the aedeagus. Focal plane approximately median. Compare especially with Figs. 48-52 & 61-64. Scale line = 0.05mm
PLATE 14

Cuticular structures of the aedeagus

Figs. 48 & 49: Lateral view of the aedeagus, external and internal cuticular structures, respectively. Scale line = 0.1mm

Fig. 50: Ventral view of the capsule/fulcrum complex. Scale line = 0.05mm

Fig. 51: Dorsal view of the aedeagus showing the muscles of the crotch and inner tube. Scale line = 0.1mm

Fig. 52: Ventral view of the aedeagus emphasizing external cuticular structures. Scale line = 0.1mm
PLATE 15

Fig. 53: Median longitudinal section through terminalia of late pharate adult. Scale line = 0.1mm
PLATE 16

Transverse sections through adult phallosome, continued onto PLATE 17. Labeled to illustrate principal muscles and cuticular structures. It is not claimed that all the muscles identified by Günther (1961) have been exhaustively traced. Figures 54 to 60 are in proximal to distal order. Scale line for all figures = 0.05mm
PLATE 17

Figs. 58 - 60: The maze-like patterns underlying the Y-sclerite are sections through the penis rods which have a complex structure at this level. (See PLATE 22)

Fig. 60: Note the lateral membrane (mem) of the Y-sclerite which isolates the penis rods from the lumen of the inner tube
PLATE 18

Lateral views of cuticular structures of the dissected phallosome

Fig. 61: Aedeagal sheath, including the apodemal rod, which arises as an invagination at the base of the sheath. The tendons of the sheath muscles (M26-27 and M29) are just visible ventral to the ribs (r). Compare with Fig. 46. Scale line = 0.1mm

Fig. 62: The distal portion of the superstructure with the sheath removed. The sheath and the superstructure are connected via the ribs at the point indicated here by the arrow. Compare with Figs. 64 & 67. Scale line = 0.25mm
PLATE 19

Cuticular structures of the aedeagus

Fig. 63: Ventral view of the aedeagus. Compare with Fig. 52. Scale line = 0.05mm

Fig. 64: Dorsal view of superstructure, vesicle removed. Scale as above. Compare Figs. 62 & 67
PLATE 20

Cuticular structures of the aedeagus

Fig. 65: Ventral view of the capsule and fulcrum. Compare with Fig. 50. Scale line = 0.05mm

Fig. 66: Dorsal view of the vesicle including distal end of virga ventralis. Compare with Figs. 68 & 70. Scale line = 0.025mm
PLATE 21

Scanning electron micrographs of elements of the superstructure

Fig. 67: Ventrolateral view of the distal end of the superstructure with the vesicle removed. Scale line = 0.05mm

Fig. 68: Dorsal view of the vesicle and virga ventralis. Scale as above

Fig. 69: Higher magnification of the proximal end of the structure in Fig. 68. The cuticular spines arise from the endophallus membrane. Scale line = 0.01mm

Fig. 70: Higher magnification of the vesicle in Fig. 68. Scale line as above
The penis rods

Fig. 71: Lateral view of *Xenopsylla cheopis* with penis rods extended. Scale line = 0.1mm

Fig. 72: Penis and penis rods. The lower rod is indicated by the arrows. Scale as above

Fig. 73: Scanning electron micrograph of the distal end of the upper rod. Scale line = 0.025mm

Fig. 74: Scanning electron micrograph of the distal end of the lower rod. Scale as above
PLATE 23

Fine structure of some cuticular elements of the phallosome

Fig. 75: Transmission electron micrograph of a transverse section through the upper and lower penis rods (upr, lpr) at approximately the level of Fig. 54. The cuticular spines of the endophallus are seen here in cross section. Compare Fig. 69. Notice that the cuticular structure of the rods is not laminar as is the case in cuticular structures which arise as invaginations. Compare Figs. 76 & 77. Scale line = 2 microns

Fig. 76: Transmission electron micrograph of transverse section through the median lamina of the adeagal apodeme. Scale line = 1 micron

Fig. 77: Transmission electron micrograph of the apodema rod. Scale line = 1 micron
The Penis

Fig. 78: Transverse section through the penis at a level somewhat proximal to that of Fig. 54. The lumen of the ejaculatory duct (ed), a trachaeal branch (tr) and numerous nuclei (nu) are visible. Scale line = 10 microns

Fig. 79: Transmission electron micrograph of transverse section of the penis depicting the central tissue. Tracheoles within their tracheoblast cells are common among the simple cells of this tissue. The lumen of the ejaculatory duct (lu) is just visible to the upper right. Scale line = 1 micron
The Penis (continued)

Fig. 80: Transmission electron micrograph as in Fig. 79, but depicting the outer cuticular boundary of the penis (cu). A cuticular spine of the virga ventralis is visible in section, as are numerous fleshy projections of the fringe of the penis (fp). Scale line = 0.5 microns

Figs. 81 & 82: Scanning electron micrographs of the dorsal surface of the penis. Although the tissue has shrunken during processing, the general character of the surface is evident, and includes finger-like fringed folds, here called the fringes of the penis. Scale line Fig. 81 = 10 microns, Fig. 82 = 2.5 microns
Fig. 83: Transverse section through the adult abdomen showing the arrangement of the phallosome, vasa deferentia (vd), testes (tes) and epididymis (epd). Scale line = 0.05mm

Fig. 84: Longitudinal section of the testis of a late pharate adult showing the wave-like arrangement of the sperm bundles. Scale line = 0.05mm

Fig. 85: Distal end of the testis of a late pupa with the testicular plug (tes p) in place. Scale line = 0.025mm

Fig. 86: Longitudinal section through the ejaculatory bulb. The vasa deferentia are to the right. Scale line = 0.025mm
PLATE 27

Fig. 87: Transmission electron micrograph of the vas deferens of a pharate adult. Scale line = 2.5 microns

Figs. 88 & 89: Transmission electron micrographs of transverse sections through sperm tails in the late pharate adult. Scale line Fig. 88 = 1 micron, Fig. 89 = 0.5 microns
PART II

PLATES 28 - 86

ARCHAEOPSyllINAE: PLATES 28 - 39

PLATE 28

Terminalia of Ctenocephalides felis felis (Bouché, 1835)
Scale lines = 0.05 mm

Fig. 90: Adult male terminalia of C. felis. Lateral lobes and wings of the aedeagus somewhat elevated.

Fig. 91: Higher magnification of similar specimen with lateral lobes in relaxed position.
PLATE 29

Periphallic structures of C. felis felis
Scale lines = 0.1mm

Fig. 92: Median view of the periphallic structures

Fig. 93: Ventral view of the structures depicted above, muscles removed
PLATE 30

Fig. 94: Lateral view of the phallosome of C. felis felis. Scale = 0.1mm
PLATE 31

Cuticular structures of the aedeagus of C. felis felis
Scale lines = 0.05mm

Fig. 95: Ventral view of the aedeagus of C. felis felis. Focal plane approximately medial

Fig. 96: Dorsal view of the aedeagus. Focal plane at level of ribs
PLATE 32

Cuticular structures of the aedeagal sheath of *Ctenocephalides felis felis*

Scale line approx. = 0.1mm

Compare Plates 28, 30 & 31

Fig. 97: Lateral view of aedeagal sheath

Fig. 98: As above, lateral lobes extended

Fig. 99: As above, rods everted

Fig. 100: Dorso-lateral view

Fig. 101: Dorsal view

Fig. 102: Ventral view
PLATE 33

Longitudinal sections of the phallosome of Ctenocephalides orientis (Jordan, 1925)
Scale = 0.05mm

Fig. 103: Median longitudinal section of the phallosome

Fig. 104: Longitudinal section of same specimen as Fig. 103, slightly laterad of median plane. Notice the strong connection between the lateral lamina (1l) and the lateral fulcral lobe (1fl). This section also reveals the flexible joint between the lateral fulcral lobe and the proximal portion of the inner tube.
PLATE 34

Transverse sections of the phallosome of *Ctenocephalides orientis*
Figs. 105-108 arranged in proximal to distal order
Scale lines = 0.05mm

Fig. 105: Section through the aedeagal apodeme

Fig. 106: Structures of the capsule and fulcrum. Notice the lumen at the center of the ribs in this area

Fig. 107: Section through the distal end of the capsule and the vesicle

Fig. 108: Section through the distal portion of the aedeagus
PLATE 35

Structures of the phallosome of *Ctenocephalides orientis*, dissected
Scale line = approx. 0.05mm

Fig. 109: Dorsal and ventral views of the capsule

Fig. 110: Ventral view of the capsule, fulcrum and Y-sclerite

Fig. 111: Dorsal view of the Y-sclerite

Fig. 112: Lateral view of the superstructure with the aedeagal sheath removed to illustrate the muscles of the crochets

Fig. 113: Ventral view of the vesicle and virga ventralis
PLATE 36

Ctenocephalides: Variations in the aedeagus
Scale line = 0.1mm

Fig. 114: C. felis felis
Fig. 115: C. canis
Fig. 116: C. arabicus multispinosis
Fig. 117: C. orientis
Fig. 118: C. connatus
PLATE 37

Terminalia of *Archaeopsylla erinacei maura* J. & R., 1912
Scale line = 0.1 mm

Fig. 119: Lateral view of the outer clasper lobe

Fig. 120: Median view of the terminalia with the left clasper lobes removed
PLATE 38

Terminalia of *Archaeopsylla erinacei* maure J. & R., 1912

Fig. 121: Ventro-caudal view of specimen in Fig. 120. Scale line = 0.025mm

Fig. 122: Lateral view of male abdomen, abdominal tergites and sternites removed. Scale line = 0.01mm
PLATE 39

Genitalic structures of Archaeopsyllinae
Scale lines = 0.1mm

Fig. 123: Archaeopsylla erinacei maura. Lateral view of
genitalic structures; ventral view of periphallic structures;
lateral view of phallosome

Fig. 124: Centetipsylla madagascariensis (Rothschild, 1900)

Fig. 125: Aphropsylla conversa (J. & R., 1913)
PLATE 40

Xenopsylla astia Rothschild, 1911

Fig. 126: The adult terminalia. Scale line = 0.025mm

Fig. 127: Lateral view of the aedeagus. Scale line = 0.05mm
Plate 41

Genitalia of Xenopsyllinae

Fig. 128: Phallosome of *Xenopsylla nubica* (Rothschild, 1903). Scale line = 0.10mm

Fig. 129: Aedeagus of *Xenopsylla versuta* Jordan, 1925. Dorsal view. Scale line = 0.025mm
PLATE 42

Genitalia of Xenopsyllinae

Scale lines: phallosomes = 0.1mm; periphallic structures = 0.05mm

Fig. 130: Xenopsylla trispinig Waterston, 1911

Fig. 131: Xenopsylla nilotica (J. & R., 1908). Components of the tripartite armature of the inner tube are indicated by the numerals (see text)

Fig. 132: Xenopsylla eridos (Rothschild, 1904)
Xenopsylla eridos (Rothschild, 1904)

Fig. 133: Lateral view of the phallosome. Scale line = 0.1mm

Fig. 134: The aedeagus. The components of the armature of the inner tube are indicated by numerals. Notice that the smaller of the two penis rods can be seen passing through the folds of the larger here, in the area just dorsal of the runner (rn). Scale line = 0.05mm
PLATE 44

Genitalia of Xenopsyllinae
Scale lines: phallosomes = 0.1mm; periphallic structures = 0.05mm

Fig. 135: *Xenopsylla brasiliensis* (Baker, 1904)

Fig. 136: *Xenopsylla hirsuta hirsuta* Ingram, 1928
PLATE 45

Genitalia of Xenopsyllinae
Scale lines = 0.1mm

Fig. 137: *Xenopsylla conformis conformis* (Wagner, 1903)
Fig. 138: *Xenopsylla gratiosa* J. & R., 1923
Fig. 139: *Xenopsylla erilli* (Rothschild, 1904)
PLATE 46

*Xenopsylla conformis mycerini* (Rothschild, 1904)

Fig. 140: The adult terminalia. Scale line = 0.05mm

Fig. 141: Phallosome. Scale line = 0.1mm
PLATE 47

*Xenopsylla conformis mycerini* (Rothschild, 1904)

Fig. 142: Adult terminalia. Scale = 0.05mm

Fig. 143: As above. Scale = 0.025mm
Synosternus pallidus (Taschenburg, 1880)

Fig. 144: Phallosome and brush everted. Compare Plate 50. Scale line = 0.05mm
Fig. 145: Clasper apparatus. Scale as above
Fig. 146: Ventral view of clasper apparatus. Scale as above
Fig. 147: Phallosome. Scale line = 0.1mm
Synosternus pallidus (Taschenburg, 1880)
Scale lines = 0.05mm

Fig. 148: Adult terminalia

Fig. 149: Dorsal view of phallosome. Focal plane approximately median
PLATE 50

_Synosternus pallidus_ (Taschenburg, 1880)
Scale lines = 0.05mm

Fig. 150: Lateral view of everted phallosome, brush exposed
Fig. 151: Everted phallosome, brush retracted
Genitalia of *Synosternus*

Fig. 152: *Synosternus caffer* (J. & R., 1923). Scale line = 0.1mm

Fig. 153: *Synosternus longispinus* (Wagner, 1883). Scale as above

Fig. 154: *Synosternus cleopatrae cleopatrae* (Rothschild, 1903). Phallosome. Scale as above

Fig. 155: *Synosternus cleopatrae cleopatrae*. Ventral and lateral views of the clasper apparatus. Scale lines = 0.05mm
Plate 52

*Synosternus cleopatrae cleopatrae* (Rothschild, 1903)
Scale lines = 0.05mm

Fig. 156: Lateral view of aedeagus

Fig. 157: Terminalia
PLATE 53

Synopsyllus fonquerniei Wagner & Roubaud, 1932
Scale lines = 0.1mm

Fig. 158: Phallosome and clasper

Fig. 159: Aedeagus
Parapulex chephrensis (Rothschild, 1903)
Scale lines = 0.05mm

Fig. 160: Phallosome and clasper
Fig. 161: Aedeagus
PLATE 55
Genitalia of Xenopsyllinae
Scale lines = 0.1mm

Fig. 162: Procaviopsylla creusae (Rothschild, 1904)
Fig. 163: Pariodontis riggenbachi riggenbachi (Rothschild, 1904)
Fig. 164: Genus X
PLATE 56

*Procaviopsylla creusae* (Rothschild, 1904)
Scale lines = 0.05 mm

Fig. 165: Lateral view of the aedeagus

Fig. 166: Dorsal view of the aedeagus. Focal plane approximately medial; the wings are not clearly visible at this focal plane
Cediopsylla inaequalis interrupta Jordan, 1925
Scale lines = 0.1mm

Fig. 167: Lateral view of the terminalia, lateral lobe of sternum 8 removed from left side. Note the dorsal and ventral lobes of P1

Fig. 168: Latero-caudal view of aedeagus and distal lobes of sternum 9
PLATE 58

*Cediopsylla inaequalis interrupta* Jordan, 1925
Scale line = 0.1mm

Fig. 169: Lateral view of periphallic structures. L1 and L2 are respectively, the dorsal and ventral lobes of P1. M22 would not actually be visible since it lies within the body of P1.

Fig. 170: Medial view of periphallic structures. The process of the anal sclerites (pas) is not shown in this drawing.

Fig. 171: Ventral view of periphallic structures.
PLATE 59

*Cediopsylla inaequalis interrupta* Jordan, 1925
Phallosome
Scale lines = 0.1mm

Fig. 172: Schematic lateral view

Fig. 173: Lateral view of cleared specimen. The ejaculatory bulb (eb) and some of the muscles are visible
PLATE 60

_Cadiopsylla inaequalis interrupta_ Jordan, 1925
The aedeagal sheath
Scale line = 0.1mm

**Fig. 174:** Lateral view of the sheath. Also shown is the sclerotized inner tube as it appears when dissected out

**Fig. 175:** Dorsal view of the sheath

**Fig. 176:** Ventral view of the sheath. The small sclerite which lies below the crochets is easily removed and is illustrated to the right
PLATE 61

*Cediopsylla inaequalis interrupta* Jordan, 1925
Transverse sections of the phallosome

Figs. 177-182 are arranged in proximal to distal order
Scale lines = 0.05mm

**Fig. 177:** The proximal fin (fn) is visible here

**Fig. 178:** Notice the circular invagination (inv) of the aedeagal apodeme. This may be mistaken in lateral view for a proximal spur

**Fig. 179:** Here the connection between the median lamina and the lateral fulcral lobes is clearly seen

**Fig. 180:** Note particularly the proximal lobes of the sheath (prlb). The arrangement of the other components is as expected

**Fig. 181:** Note the hooks (hk)

**Fig. 182:** Ford's sclerite is a single lobe in this species
PLATE 62

Genitalia of Spilopsyllinae
Scale lines = 0.1mm

Fig. 183: *Spilopsyllus cuniculi* (Dale, 1878)

Fig. 184: *Actenopsylla suavis* J. & R., 1923

Fig. 185: *Ornithopsylla laetitiae* Rothschild, 1908
PLATE 63

Genitalia of Spilopsyllinae
Scale lines = 0.1mm

Fig. 186: *Euhoplopsyllus glacialis foxi* (Ewing, 1924)

Fig. 187: *Hoplopsyllus anomalus* (Baker, 1904)
PLATE 64

Terminalia of *Euholopsyllus glacialis foxi* (Ewing, 1924)
Scale lines = 0.05 mm

Fig. 188: Latero-caudal view of terminalia

Fig. 189: Dorsal view of different specimen. Note the positions of the arms of s9 in the two figures
PLATE 65

Pulex irritans L., 1758
Scale lines = 0.1mm

Fig. 190: Caudal view of the terminalia

Fig. 191: Latero-caudal view of terminalia, left clasper lobes removed
PLATE 66

Pulex irritans L., 1758
Periphallic structures
Scale line = 0.1mm

Fig. 192: Lateral view. M22 would not be visible since it lies within P1

Fig. 193: Medial view. M22 would not be visible

Fig. 194: Ventral view of cuticular structures
PLATE 87

Puilex irritans L., 1758
Phallosome
Scale lines = 0.1mm

Fig. 195: Schematic lateral view. Compare with Cediopsylla

Fig. 196: Lateral view of phallosome
PLATE 68

\textit{Pulex irritans} L., 1758
Aedeagus
Scale line = 0.05mm

Fig. 197: Lateral view of aedeagus

Fig. 198: Ventral view. Focal plane approximately medial
**PLATE 69**

*Pulex irritans* L., 1758

Aedeagus

Scale line = approx. 0.1mm

Fig. 199: Lateral view of aedeagus

Fig. 200: Schematic diagram illustrating the relation of the distal end of the inner tube to the distal membranes which surround it

Fig. 201: Ventral view of the aedeagus

Fig. 202: Schematic ventral view of the superstructure, with the vesicle removed. The arrow indicates the opening through which the penis rods pass. The Y-sclerite lies just dorsal to this opening, and its tongue fits into the slot, closing off the inner tube lumen from the endophallus proper
Pulex irritans L., 1758

Fig. 203: Latero-ventral view of aedeagus illustrating the spiculose ventral membrane. Scale line = 0.05mm

Fig. 204: Higher magnification of the ventral membrane. Scale line = 0.01mm
Plate 71

Pulex irritans L., 1758
Transverse sections of the phallosome
Figs. 205 - 209 arranged in proximal to distal order

Fig. 205: Section through the aedeagal apodeme. Notice that the virga ventralis and the ventral wall of the endophallus are clearly distinct here. Scale line = 0.05mm

Fig. 206: Section through area just proximal to fulcrum region. Scale line = 0.01mm

Fig. 207: Section through proximal end of capsule/fulcrum region. Notice that the capsule is here folded laterad of the median fulcrum lobe (mf1). Scale line as above

Fig. 208: Section through the region of the vesicle. Scale line = 0.05mm

Fig. 209: Section through the shaft of the aedeagus. Scale line as Fig. 208
**PLATE 72**

*Pulex irritans* L., 1758

**Fig. 210**: Pair in copula. (Slide from the collection of R. Traub). Female is on the right. Notice the positions of the pseudocrochets and Ford's sclerite. Scale line = 0.1mm

**Fig. 211**: Schematic lateral view of the aedeagus showing the internal musculature. Scale line = 0.1mm
Plate 73

Genitalia of Pulex
Scale lines = 0.1mm

Fig. 212: Pulex (Juxtapulex) echidnophagoides (Wagner, 1933)
Fig. 213: Pulex (Juxtapulex) porcinus J. & R., 1923
Fig. 214: Pulex (Juxtapulex) alvarezi Barrera, 1955
Fig. 215: Pulex sinocus Traub, 1950
Genitalia of *Echidnophaga*
Scale lines = 0.1mm

Fig. 216: *Echidnophaga gallinacea* (Westwood, 1875). Lateral and ventral views of clasper apparatus, and phallosome

Fig. 217: *Echidnophaga larina* J. & R., 1906

Fig. 218: *Echidnophaga bradyta* J. & R., 1906
PLATE 75

Echidnophaga gallinacea (Westwood, 1875)

Fig. 219: Lateral view of the phallosome. Scale line = 0.05mm

Fig. 220: Caudal view of the phallosome. Scale line = 0.025mm

Fig. 221: Latero-caudal view of the phallosome. Scale line = 0.025mm
Genitalia of Pulicinae

Fig. 222: *Neotunga inexpectata* Smith, 1962. Scale lines: periphallie structures = 0.05mm; phallosome = 0.1mm

Fig. 223: *Delopsylla crassipes* Jordan, 1926. Scale line = 0.1mm
HECTOPSylliINae

Plates 77 - 81

Plate 77

Hectopsylla psittaci Frauenfeld, 1880

Fig. 224: Lateral view of periphallic structures. Scale line = 0.05 mm

Fig. 225: Medial view of periphallic structures. Scale approximately as above

Fig. 226: Lateral view of phallosome. Scale = 0.1 mm

Fig. 227: Lateral view of sternum 9. Distal lobes are to the right. (Compare Figs. 230 & 232). Scale line = 0.1 mm

Fig. 228: Caudal view of distal end of phallosome. Scale line = 0.05 mm
PLATE 78

Hectopsylla psittaci Frauenfeld, 1860
Scale line = 0.1 mm

Fig. 229: Lateral view of phallosome

Fig. 230: Lateral view of male terminalia. Note distal lobes of sternum 9
Genitalia of Hectopsyllinae

Fig. 231: Transverse section of the endophallus of *Hectopsylla psittaci*, showing trichoid sensillae (trs). See text discussion, Part I. Scale line = 0.01mm

Fig. 232: Caudal view of the distal lobes of sternum 9, *Hectopsylla psittaci*. Scale line = 0.1mm

Fig. 233: Lateral view of the terminalia of *Hectopsylla stomis* Jordan, 1925. Note the strong sclerotization of s9
Hectopsylla psittaci Frauenfeld. 1860.

Transverse sections of the phallosome. Figs. 234 - 237 are arranged in proximal to distal order.

Scale lines = 0.05mm

Fig. 234: The dorsal bay of the aedeagal apodeme is visible at the top. Notice that here the median lamina (ml) and the stalk of the fulcrum (stf) are separate.

Fig. 235: This section is just proximal to the main lumen of the capsule. Note the large lateral shafts of the capsule (lsc) and the small lateral fulcral lobes (lfl).

Fig. 236: The dorsal longitudinal struts (dls) are chitinous structures which are separate from the wall of the sheath at this level. Note the highly developed muscles of the sheath.

Fig. 237: This section passes through the sheath near its distal end.
PLATE 81

Hectopsyilla: Variations in the aedeagus

Fig. 238: Hectopsyilla suarezi C. Fox, 1929
Fig. 239: Hectopsyilla stomis Jordan, 1925
Fig. 240: Hectopsyilla cypha Jordan, 1942
Fig. 241: Hectopsyilla gemina Jordan, 1939
Genitalia of Tunginae

Fig. 242: Lateral view of the terminalia of Tunga monositus
Barnes & Radovsky, 1968. Compare with Figs. 244 & 246-249. Scale line = 0.1mm

Fig. 243: Dorsal view of aedeagus of Tunga monositus. Scale line as above

Fig. 244: Caudal view of terminalia of Tunga monositus. Scale line = 0.05mm

Fig. 245: Lateral view of terminalia of Tunga penetrans
(Linnaeus, 1758). The aedeagus is everted and twisted so that the dorsal side faces the viewer. Scale line = 0.1mm
PLATE 83

_Tungia monositus_ Barnes & Radovsky, 1969

Fig. 246: Lateral view of terminalia. Scale line = 0.1mm

Fig. 247: Lateral view of clasper apparatus. Scale line = 0.05mm

Fig. 248: Lateral view of the capsule/fulcrum area. Scale as above
PLATE 84

Genitalia of Tunginae
Scale lines = 0.1mm

Fig. 249: Phallosome of *Tunga monositus*

Fig. 250: Terminalia of *Tunga penetrans*. Notice the different proportions of the ribs (r) and the fulcral stalk (stf)
PLATE 85

Moeopsylla sjoestedti J. & R., 1908
Scale lines = 0.1mm

Fig. 251: Lateral view of periphallic structures
Fig. 252: Ventral view of periphallic structures
Fig. 253: Crochets -- lateral (upper) and medial (lower) views
Fig. 254: Lateral view of phallosome
Moeopsylla sjoestedti J. & R., 1908
Scale lines = 0.1mm

Fig. 255: Lateral view of distal end of phallosome

Fig. 256: Lateral view of terminalia, aedeagus everted. Note that the lateral lobes are separable

Fig. 257: Lateral view of the terminalia. The distal end of s9 is broken on the left side

Fig. 258: Latero-caudal view of specimen in previous figure