1993

A comparative study of the aedeagal structure in the Ceratophyllidae (Siphonaptera)

Fatimah Abang

Iowa State University

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A comparative study of the aedeagal structure in the
Ceratophyllidae (Siphonaptera)

Abang, Fatimah, Ph.D.

Iowa State University, 1993
A comparative study of the aedeagal structure in the Ceratophyllidae (Siphonaptera)

by

Fatimah Abang

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1993
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INTRODUCTION

Taxonomic studies in insects usually have been based on comparative structural characters of the skeletal anatomy. However, in attempting the classification of the order Siphonaptera, very severe problems are encountered in the interpretation of these characters in terms of phylogenetic relationships (Mardon, 1978). Traub (1980) saw this as largely due to the occurrence of parallel or convergent evolution, where these morphological characteristics were subject to adaptive modifications due to direct environmental factors. Questions of phylogeny are obscured by parallelism and convergence (Holland, 1964). The occurrence of parallel and convergent evolution lead to difficulty in determining the difference between true synapomorphies and resemblances due to convergent evolution. However, in the case of the Siphonaptera, most authors (Jordan, 1947, Traub, 1950; Mardon, 1978) agreed that the male genitalia remain unaltered from parallel or convergent evolution, and therefore they serve as a useful guide to suprageneric relations.

In spite of the stable characteristic of the male genitalia, comparative studies of the aedeagus to assess its taxonomic value are among aspects of pulicology that have received relatively little attention. As suggested by Traub
(1950), comparative studies of the aedeagus have been neglected for various reasons. Among these he cited the difficulty in determining certain structural details. Additionally, he pointed out that other characters have been considered adequate for taxonomic purposes, while many features of the aedeagal morphology are not yet understood. In supporting the taxonomic value of the flea aedeagus, Mardon (1978) emphasized that, where other characters are beyond interpretation in our present state of knowledge, the genitalic characters should be regarded as of overriding importance.

Except for Traub (1950) and Mardon (1978), most papers on flea taxonomy include little or no reference to the aedeagus. Traub, in many of his publications subsequent to 1950 has continued to treat the aedeagus in some detail, developing specialized terms for its many components. The most recent study involving flea genitalia is that of Cheetham (1988) on the male genitalia and phylogeny in the Pulicoidea, a superfamily only distantly related to the Ceratophyllidae.

Apart from Traub (1950) and Traub et al (1983), descriptions of the aedeagal structure in most genera of the Ceratophyllidae are unavailable in the literature. It is hoped that information obtained during the present study will contribute materially to our understanding of phylogenetic
relationships within the family.

The primary purpose of this study is to describe and present a comparative morphology of the aedeagus in the Ceratophyllidae, illustrated by one or more species of each available genus. Additional objectives are as follows: First, to emphasize the practicability of using the aedeagus for taxonomic purposes. Second, to provide an initial hypothesis as to the phylogeny of the taxa treated, based principally on characters of the aedeagus, which can provide a framework of future hypotheses based on additional comparative data. Third, to discuss the geographical distribution of the genera in relation to the inferred relationships.
LITERATURE REVIEW

History of the Study of the Aedeagus

Our knowledge of the male genital organs of fleas dates back to Rosel von Rosenhof (1749). A brief history of contributions dealing with the male genitalia of fleas was given by Sharif (1945). However, according to Traub (1950), these are mostly morphological papers that do not deal with the aedeagus.

In his treatment of the comparative structure of the aedeagus of Siphonaptera from Mexico and Central America, Traub (1950) included a brief history of the study of the aedeagus. Other earlier workers whose names deserve to be mentioned are Minchin (1915), Pavlovsky (1926), Patton and Evans (1929), Jordan (1939), Wagner (1940), Sharif (1945), Snodgrass (1946), Peus (1955), Holland (1955) and Gunther (1961). Much of our knowledge of the flea aedeagus, however, is attributed to Snodgrass (1946), who, in his classical work on the skeletal anatomy of fleas, described and illustrated nine genera of North American fleas based upon dissected preserved specimens. A detailed general description of the intromittent organ or phallosome, including the aedeagus is included and illustrated in this work. Contributions to our knowledge of the aedeagus are also found in the excellent work
of Traub (1950) and his numerous subsequent studies on flea taxonomy, in which he includes the aedeagus.

Structure of the Aedeagus

The phallosome, or intromittent organ, is by far the most prominent structure of the male flea. Its size is relatively large, occupying perhaps a third or more of the abdominal cavity (Cheetham, 1988). It can be divided into an external part, the aedeagus which bears a large basal apodeme (aedeagal apodeme) and an internal part, the endophallus which is invaginated in the aedeagus. It also extends forward into the basal portion of the abdomen, turning upward anteriorly and receiving the ejaculatory duct at its proximal.

The phallosome of fleas is the most complex genital apparatus of all insects (Peus, 1956; Humphries, 1967). The following description of the male flea genitalia is based on Snodgrass (1946) and Traub (1950). It is intended as an initial overview to familiarize readers with the interpretation and terminology applied to this organ. The terminology closely follows that of Traub (1950) and Rothschild and Traub (1971). For this section, as an aid to understanding the structure of the aedeagus, the reader should refer to Fig. 1.

The aedeagus. The aedeagus arises from the aedeagal
pouch (aep) which lines the cavity formed between the ventral anal sclerite and the ninth sternum.

The basal wall of the pouch (pw) can at times be seen in cleared specimens and serves to separate the aedeagus from the aedeagal apodeme (aea).

The apical part of the aedeagus is often cylindrical and expanded but it may be deeply invaginated, forming a large, hollow endchamber to a varying extent, generally wide open or expanded dorsally and also open to a lesser degree ventrally. The aperture is flanked laterally by various projections or lobes; typically there is a single median dorsal lobe (mdl) of variable shape and a pair of broad lateral lobes (latl). The median dorsal lobe (mdl) may be simple, bifid, flared and convoluted, divided into several lobes or otherwise modified. In some species, there is a distinct sclerite on each side of the median dorsal lobe (amdl). The lateral lobes are short and apical in some genera, while in others they may be long, arising as far cephalad as the fulcrum (ful). They may be relatively weakly or well sclerotized; sometimes their surfaces are ridged. At times, the lateral lobes are fused on each side with the ventral margins of the aedeagal pouch.

The endchamber of the aedeagus contains an aedeagal inner tube, arising from the inner wall of the cavity and usually a pair of movable hooks, or crochets (cr) arising from the
lateral walls. The inner tube of the aedeagus is formed by the invagination of the tube apex, and it leads directly to the endophallus. The inner tube varies in shape and in length in different fleas and is usually confined to the endchamber of the aedeagus, but in some species it extends far out of the latter.

The sclerotized inner wall of the tube is continued below the wall of the endchamber and usually forms a thickened basal part of the tube, which is supported by the fulcrum (ful), arising from the middle plate or middle lamina (mlam) of the apodeme. The sclerotized sheath of the inner tube is often highly modified. The armature may consist of dorsal, ventral or lateral bulges (ait) or of stout flanking sclerites. Apically the fulcrum usually consists of a pair of latero-ventral, convex lobes and a pair of more dorsal, mesal subquadrate lobes. In some species, there is a pair of irregular or acuminate dorsal lobes. Between these lobes is a sclerite that arises from near the floor of the aedeagus and extends dorsad of the fulcrum; the dorsal margin of this sclerite is strongly sclerotized and flanged, usually crescentic in shape. Often only the crescentic dorsal margin is visible and Traub (1950) named this the crescent sclerite (csc). The dorsal margin of the crescent sclerite seems to form the roof of what Sharif (1945) called the sperm-pumping
apparatus.

According to Snodgrass (1946), the crochets are typically flat, hook-shaped structures with their points directed posteriorly. They are highly variable in shape and size. In some species they are reduced to a pair of small plates, and in others they appear to be absent. In the case of the ceratophyllids, however, the crochets are always present, and there is a stout, short, peg-shaped sclerotization, or paxillus (pax) near the point of articulation. The paxillus may be variable in size and shape.

The aedeagal apodeme consists of three plates or laminae; a pair of arched lateral plates (l1am) that are joined dorsally and a middle lamina (m1am) that extends apicad to form the fulcrum supporting the inner tube. All three plates are joined on the dorsal line (Peus, 1956). The lateral plates (l1am) in some species continue forward along the median dorsal lobe (md1) as acuminate projections called the dorsal extensions of lateral lamina (dex1am).

The endophallus. The endophallus is the lumen within the phallosome and is bounded dorso-laterally by the aedeagal apodeme and ventrally by the ventral intramural rod (virga ventralis). It is a direct continuation of the inner wall of the aedeagal inner tube and encloses the true penis.

Within the endophallus are two rod-like structures of
variable length and shape, one lying more or less above the other. These are the dorsal (dpr) and ventral penis rods (vpr). They are visible in cleared fleas and Traub (1950) pointed out that the extent of coiling is a useful taxonomic character. Above the penis rods is the penis, which is usually only faintly discernible in cleared specimens. The penis is actually the inner tube within the endophallus. 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.

The endophallus of the flea is a highly complex structure. Externally, it is a thin-walled, cylindrical sack that extends cephalad from about the base of the fulcrum to the proximal end of the penis rods. If the rods are coiled, as in some species, the sack follows the convolutions. This sack cannot be seen in cleared specimens. Two intramural rods strengthen the sack, the short dorsal intramural rod and the longer ventral intramural rod. Peus (1956) proposed the use of the terms "virga dorsalis" and "virga ventralis" of the endophallus, respectively, for the intramural rods. Arising from these rods are muscles that encircle the endophallus. Paralleling the ventral curvature, but free from it, is the third apodemal rod. In the ceratophyllids, this rod arises from the angle of the ninth sternum (Traub, 1950).
Fig. 1: *Ceratophyllus (Ceratophyllus) gallinae* (Schrank, 1803)
Lateral view of the phallosome. Scale line = 0.05mm
MATERIALS AND METHODS

Although aedeagal characters frequently can be seen in specimens prepared and mounted in the usual manner, study of the aedeagus is most satisfactorily done through dissections where the aedeagus is removed and mounted separately.

The genera and number of species evaluated in this study is shown in Table 1. Specimens available for this study came from various sources: The Lewis Collection, Iowa State University, Ames, Iowa; the British Museum (Natural History), London; Dr. Nixon A. Wilson, University of Northern Iowa, Cedar Falls; Dr. R. L. C. Pilgrim, University of Canterbury, Christchurch, Canterbury, New Zealand; Dr. D. S. (Woody) Horning, Jr., The Macleay Museum, The University of Sydney, New South Wales, Australia. These specimens had been preserved in 70\% ethanol for a period of time. Cheetham (1988) noted that an 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 more easily accomplished.

Specimens were cleared in potassium hydroxide (KOH). The dissected aedeagus and sternite IX were transferred to acid water for 5-10 minutes and dehydrated in absolute ethanol. After immersion in xylene for a few minutes, they were mounted
in Canada balsam.

All dissections were done in KOH with the aid of a dissecting microscope at a magnification of 40x, using minuten nadeln mounted on wooden sticks and extra fine forceps. One dissected aedeagus was mounted laterally while another was mounted dorsally on the same slide. For dorsal mounts, pieces of broken cover slip were used to hold the aedeagus in the proper position. Photomicrographs were taken with a Zeiss photomicroscope using Kodak TMAX.

Specimens studied have been deposited in the Lewis Collection. Ultimate deposition will be in the Field Museum of Natural History, Chicago, Illinois.
HIGHER CLASSIFICATION OF THE CERATOPHYLLIDAE

The family Ceratophyllidae currently contains 515 species and subspecies and constitutes 22.5% of all the taxa presently assigned to the order (Lewis, 1990). This family is almost restricted to the Northern Hemisphere, being poorly represented on southern continents. The few taxa that occur on southern continents show no sign of austral faunal links, all clearly having Holarctic roots (Traub & Rothschild, 1983).

The taxonomy of the Ceratophyllidae has been problematic, and some of the species have had a convoluted nomenclatural history. To date, there is no nomenclatural reference for this family comparable to the "Catalogue of the Rothschild Collection of Fleas" series for the other families of Siphonaptera. However, Lewis (1990) is a valuable and indispensable guide to the nomenclatural references for this family.

Two major earlier attempts at classification of the ceratophyllid genera are those of Ioff (1936) and Wagner (1939). In Ioff's classification, the ceratophyllid genera known at that time were placed in six tribes, the Tarsopsyllini, the Paracerini, the Oropsyllini, the Ceratophyllini, the Amphaliini and the Foxellini. Wagner (1939) put them in seven tribes, the Tarsopsyllini, the
Paracerini, the Oropsyllini, the Ceratophyllini, the Dasypyllini, the Orchopiini and the Citellophilini.

The higher classification of the Ceratophyllidae was reviewed by Lewis (1990). The name was applied as a subfamily or some other category until Holland (1949) elevated it to familial status. In it he included four subfamilies, the Ceratophyllinae, the Leptopsyllinae, the Amphipsyllinae and the Dolichopsyllinae. The Leptopsyllinae, Amphipsyllinae and Dolichopsyllinae are now treated as subfamilies of the Leptopsyllidae. In Smart (1956), Jordan listed only the nominate subfamily in his classification of the Ceratophyllidae. However, the provisional list of genera and subgenera of the order given by Hopkins & Rothschild (1953) also included the Foxellinae. Holland (1964) also listed these two subfamilies. Stark (1970) in dealing with the North American genus **Thrassia**, listed three subfamilies, the Oropsyllinae, Dactylopsyllinae and Ceratophyllinae. Stark's Dactylopsyllinae was the equivalent of the Foxellinae and was based on the fact that *Dactylopsylla* Jordan, 1929 has priority over *Foxella* Wagner, 1929. Today this subfamily contains three genera, *Foxella*, *Spicata* and the nominate genus.

Smit (1973) suggested the superfamily Ceratophylloidea should include the Ceratophyllidae, Leptopsyllidae, Ischnopsyllidae and Ancistropsyllidae. However, his 1982
classification included the Xiphiopsyllidae and reduced the Leptopsyllidae to a subfamily of the Ceratophyllidae. Traub et al (1983) appear to concur with Smit's (1973) concept of the Ceratophylloidea.

As far as the taxonomy and phylogeny of the order Siphonaptera is concerned, the other large families include fleas that are so diverse morphologically that a hierarchy has been established in the scheme of classification (Traub, 1983). However, in marked contrast to the situation in the other families, the ceratophyllids are such a homogeneous group that no such decisions have been made for them (Traub & Rothschild, 1983).

According to Lewis (1990), the status of the name Ceratophyllidae has remained relatively stable for the past 40 years. The subfamilies Leptopsyllinae and Amphipsyllinae have usually been placed in a separate family, the Leptopsyllidae, and the Ceratophyllidae have been treated as a family without subfamilies or have been divided into the Ceratophyllinae and Foxellinae. Smit (manuscript prepared in the 1970's) in Traub et al (1983) did not employ subfamilies. However, Lewis (1990) feels that Smit's 1982 work may better reflect his final thoughts on the proper classification of the family. Holland (1985) employed the subfamilies Ceratophyllinae and Foxellinae. Lewis and Lewis (1985) did not employ
subfamilies, although they are inclined to agree that the
gopher-infesting genera *Foxella, Dactylopsylla* and *Spicata* do seem to form a distinct taxonomic unit.

The most current suprageneric classification of the Ceratophyllidae is as shown in Table 1 which is modified from that of Lewis (1993). In this classification, the Ceratophyllidae is divided into two subfamilies, the Ceratophyllinae and the Dactylopsyllinae, consisting of forty-one and three genera, respectively.

Among major structural characters that define the Ceratophyllidae as stated by Smit (1983) are as follows: genal ctenidium absent; eye never sinuate, it can be vestigial; interantennal suture absent; sensillum of claval flagellomeres 4-6, T-shaped (except for *Glaciopsyllus*); male sternum VIII narrow or vestigial; male telomere with 4 or 5 setae along posterior margin; male distal arm of sternum IX modified in about middle or apical third to form a ventral bay or lateral pouch for reception of paxillus; crochets with paxillus, except in *Paraceras* while it is greatly reduced in *Jellisonia*.

On the basis of the aedeagal structure, according to Traub (1950), the following can be generalized as the aedeagal characters of the Ceratophyllidae. The aedeagal pouch is relatively short and its extent is usually marked by the proximal spur. The latero-ventral margins of the pouch are
Table 1. Present classification of the Ceratophyllidae

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<tr>
<th>Subfamily</th>
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sometimes sclerotized. The endchamber is usually covered by the large lateral lobes, which are usually convex and extend from near pouch wall to near the apex of the median dorsal lobe. The lateral lobes are variable in shape. The crochets are very large, extending distad of the endchamber and with articulation which permits much freedom of movement. The median dorsal lobe is often simple or bifid, but in some species it is highly modified. The sclerotized inner tube is short, usually vertical and often with specialized armatures.

The major characters used in separating the Dactylopsyllinae from the rest of the ceratophyllids are as follows: the eyes of the dactylopsylline fleas are vestigial or virtually absent and unpigmented as compared to the ceratophylline fleas; ocular row with 4-8 setae; squamulum of metepisternum poorly developed or absent and the outer side of the mid and hind femur are very densely striated. Apart from that, the dactylopsylline fleas are exclusively Nearctic in distribution and are only known to parasitize pocket gophers.

Results of the present study suggest the following systematic arrangement of the forty-four taxa studied. The Ceratophyllidae is here considered to contain four subfamilies: the Tarsopsyllinae, Oropsyllinae, Dactylopsyllinae and Ceratophyllinae. The Ceratophyllinae is further divided into two tribes, the Ceratophyllini and the
Nosopsyllini. Genera with aedeagal characters of uncertain resemblances with the remainder of the ceratophyllids are grouped as insertae sedis.

Aedeagal Structure in the Ceratophyllidae

Descriptions of the Genera

insertae sedis

Figs. 2-7.

Genus Smitipsylla Lewis, 1971

Fig. 2.

This genus is represented by two very similar species that parasitize flying squirrels in the mountains of Nepal and West Bengal, India.

Smitipsylla maseri Lewis, 1971

Aedeagal apodeme with region cephalad of fulcrum about 6X as long as broad at maximum width; apodeme long and broad, cephalic end much broader than distal end; apodeme slightly upturned toward cephalic end. Dorsal extension of lateral laminae very broad with a short acuminate apex. Apical appendage absent. True neck not apparent, covered by alate lobe. Proximal spur short. Aedeagal pouch arising from level
of proximal spur; wall of aedegal pouch with ventral margin slightly convex, well sclerotized and ascending dorsad below penis rods till it meets lateral lobes. A late lobes of aedeagal apodeme immediately above dorsal penis rod, broad; ventral margin almost straight. Median dorsal lobe fairly long and well sclerotized; apex rounded and simple; apical sclerite of median dorsal lobe absent. Ford's sclerite present. Distal-lateral lobes prominent as large paired structures. Lateral lobes well-developed, extending from apical sclerite of median dorsal lobe; caudal margin slightly convex; caudo-ventral margin almost straight while proximoventral margin strongly convex. Crochets reduced, very different from other species; far ventrad and mesad to endchamber in position; caudal margin well sclerotized, convex and produced into a narrow acuminate proximo-ventral projection; proximo-ventral margin weakly sclerotized and concave. Paxillus short and broad, slightly barrel-shaped, near caudo-ventral angle. Sclerotized inner tube complex, apex dilated with a prominent hook. Dorsal armature of inner tube produced into a long, curved, finger-like projection; ventral armature thick and very broad, bilobed. Fulcrum not that prominent when compared to other genera; latero-ventral lobes broad-based, and apex long and narrow; dorsal median projection well sclerotized, long and broad, extending to apex
of median dorsal lobe; medial lobes slightly curved dorsally; long and flattened distally. Crescent sclerite small, short and broad; satellite sclerite very small, short and broad; central sclerite reduced to a thin, narrow strip. Penis rods short and uncoiled.

Taxa

*maseri* Lewis, 1971
*prodigiosa* Smit, 1975.

Genus *Paraceras* Wagner, 1916

Fig. 3.

Currently there are 11 named taxa assigned to this genus, at least three of which are junior synonyms (Lewis, 1990). *Paraceras* species are associated either with squirrels or carnivores in the Palaearctic Region, with one species known from Java. An undescribed species is common on montane indigenous rats in Malaya, and another has been found on a squirrel in northern Thailand (Traub et al, 1983).
Paraceras melis (Walker, 1856)

Aedeagal apodeme cephalad of fulcrum 4.7X as long as broad at maximum width; apodeme short and broad, region immediately posterior to fulcrum very much constricted for approximately the distal one-third of apodeme, the remaining two-thirds subequally broad (apodeme very much different from that of other ceratophyllids); lateral laminae with a proximo-ventral flap-like projection; median lamina broad proximally and strongly constricted distally, forming a long neck. Dorsal extension of lateral laminae absent or not prominent. Apical appendage long and thick, longer than penis rods. Neck very long and constricted. Alate lobe long and narrow. Proximal spur short. Wall of aedeagal pouch weakly sclerotized, extending from below neck to base of fulcrum; ventral margin slightly convex. Median dorsal lobe with a long, straight, heavily sclerotized dorsal margin; apical sclerite absent. Ford's sclerite present. Lateral lobes large, extending from one-third median dorsal lobe to below ventral penis rods; caudal margin fairly straight with a convex caudo-ventral edge and an almost biconvex ventral margin: lower lobe smaller than upper lobe. Crochets long and narrow with middle region very much constricted and well sclerotized; caudal region expanded and club-shaped while proximal region produced into a narrow, acuminate, ventrally
directed projection. Sclerotized inner tube long and almost horizontal, confined to endchamber; fistula long; apex not expanded; dorsal armature expanded into a long, proximal, arm-like process, flask-like with a flattened base and high neck; ventral armature subequal to dorsal arm but directed in opposite direction. Fulcrum with latero-ventral lobes almost uniform, not strongly curved, with apex acuminate; dorsal median projection long and narrow, finger-like; medial lobe broad, with a bulbous apex. Crescent sclerite very long and narrow; satellite sclerite similar to crescent sclerite but shorter; central sclerite closely associated with floor of aedeagus which is long and narrow and strongly curved downwards. Penis rods short and uncoiled, shorter than apical appendage.

Comments: Overall very much different from other ceratophyllid taxa; aedeagus proper rectangular in shape, standing at 45 degrees in position to aedeagal apodeme; endchamber broad and rectangular in shape.

Taxa:

*brevimanubrium* Li & Huang, 1979
*crispum* (Jordan & Rothschild, 1911)
*hamatum* Jordan, 1939
*javanicum* (Ewing, 1924)
Genus *Aenigmopsylla* Ioff, 1950

This is a monotypic genus that is associated with squirrels in the Primorsk region of the Russian Federation and in Japan.

*Aenigmopsylla grodekovi* Schevsky, 1950

Aedeagus with region of apodeme anterior to fulcrum about 6.5X as long as broad at maximum width. Aedeagal apodeme almost subequal throughout except posterior to proximal spur and toward apex where ventral margin curves upward; dorsal and ventral margin, otherwise almost straight. Apical appendage very short. Proximal spur very short, almost reduced to a stump. Neck present. Wall of aedeagal pouch well sclerotized, arising from level of proximal spur, descending
and forming a slightly convex proximo-ventral margin, then extending into a straight, thickened margin of posterior half, until meeting base of lateral lobes. Median dorsal lobe not well sclerotized compared to other parts, with short margin, slightly convex; apical sclerite of median dorsal absent. Ford's sclerite present. Lateral lobes relatively small compared to the rest of aedeagus; dorsal margin straight and thickened; caudal margin almost straight and vertical; ventral margin not that prominent. Crochets well developed, long, straight and narrow, directed caudad; shaped like a shoe with a flattened heel; length about one third that of aedeagal apodeme; surface lamellate. Paxillus at ventro-proximal end of crochet, broadly bowl-shaped. Sclerotized inner tube complex, with a conspicuous small hook at the apex; inner tube produced into a broadly based fistula, narrowing as it curves ventrad; dorso-caudal margin of sclerotized inner tube serrated; anterior dorsal arm produced into an irregularly shaped, long projection with vertical base. Ventral armature of inner tube well sclerotized, long and broad, standing at 45 degrees to aedeagus with broad concave apex. Fulcrum with a short, acuminate fulcral brim (not prominent). Crescent sclerite long and flattened, prominently dorsal in position, its dorsal margin slightly convex. Satellite sclerite very narrow and thin; central sclerite very narrow and thin, close
to fulcral medial lobe. Medial lobe of fulcrum long and broad, with acuminate apex. Latero-ventral lobes of fulcrum long and broad, slightly curved and with a slightly acuminate apex. Dorsal median projection absent. Penis rods uncoiled, but curved, with ventral penis rod curving ventrad; ventral rod longer than dorsal rod.

Genus Amphalius Jordan, 1933

Fig. 5.

There are four species in the genus, with eleven subspecies. All are essentially specific parasites of Ochotona from central Asia and China.

Amphalius runatus runatus
(Jordan & Rothschild, 1923)

Ford's sclerite present. Lateral lobes with ventral margin slightly convex, almost straight and caudal margin convex. Crochets almost as long as endchamber but narrower, with a small tongue-like projection; crochets ventral in position and mesal to aedeagus; dorsal margin slightly concave with apex produced into a convex projection; paxillus prominent, near proximal end of crochets. Sclerotized inner tube short and extending slightly out of endchamber; fistula exceptionally long, twisted, and extending far distad; length of fistula 6.5X that of aedeagal apodeme; apex expanded, almost flat and flanked by a thick ovate sclerite; hook small and short. Armature of inner tube complex. Fulcrum with latero-ventral lobes weakly sclerotized, long and narrow with a curved apex; dorsal median projection long and broad, extending along median dorsal lobe almost to apex; medial lobe long and narrow. Crescent sclerite large and broad; satellite sclerite prominent, long and narrow; central sclerite also long and narrow. Penis rods coiled more than 360 degrees. Ventral penis rod extremely thick and well sclerotized.

Taxa:

*clarus clarus* (Jordan & Rothschild, 1922)
*clarus kunlunensis* Yu & Wang, 1981
*clarus tianshanensis* Yu, Yie & Xie, 1987
manosus Li, 1979
runatus runatus (Jordan & Rothschild, 1923)
runatus necopinus (Jordan, 1925)
spirataenius spirataenius Liu, Wu & Wu, 1966
spirataenius badongensis Li, Xie & Yang, 1980
spiraetaenius digingensis Li, Xie & Yang, 1980
spirataenius heishuensis Wang, Shen & Zhai, 1983
spirataenius qinghaiensis Li, Xie & Yang, 1980

Genus Glaciopsyllus Smit & Dunnet, 1962

Fig. 6.

This genus is monotypic. Glaciopsyllus antarcticus is a parasite of sea birds, known from localities both on the mainland of Antarctica and adjacent islands.

Glaciopsyllus antarcticus Smit & Dunnet, 1962

Aedeagus with region of aedeagal apodem cephalad of fulcrum 8X as long as broad at maximum width; apodeme large and broad. Lateral laminae prominent; dorsal extension of lateral laminae large and well developed, extending to below median dorsal lobe. Median lamina consistent in breadth except for tapered proximal end. Apical appendage short. Neck short and broad, not apparent, covered by alate lobe.
Alate lobe crossing over neck, very broad, about two-fifths of apodeme; ventral margin extending slightly below level of median lamina. Proximal spur prominent. Aedeagal pouch short, arising from below proximal spur and diverging dorsad to fuse with lateral lobes. Median dorsal lobe simple, dorsal margin straight. Apical sclerite of median dorsal lobe undeveloped (not prominent). Ford's sclerite present. Lateral lobes large with ventral margin folded. Crochets subrectangular, distal end more acuminate; paxillus large and elongate, near two-thirds proximo-ventral angle of crochets. Endchamber complicated and heavily sclerotized. Filamentous and semimembranous structure extending over most of endchamber (especially distally) and proximal of crochets. Sclerotized inner tube relatively long and vertical in position and projecting slightly from endchamber; apex of sclerotized inner tube expanded and flattened but with straight margin bearing thornlike dorso-distal armature. Fistula long, broad and semimembranous, extending to level of crochets. Dorsal armature of inner tube prominent, rectangular in shape, broad and thick; ventral armature well-sclerotized and prominent. Fulcrum with latero-ventral lobes fairly broad, apex not curved; dorsal median projection very broad and prominent, extending over endchamber and sclerotized inner tube; medial lobe broad, ovate with pointed apex. Crescent sclerite narrow
but prominent; satellite sclerite almost as long as crescent sclerite; central sclerite not prominent. Ventral penis rods short and coiled less than 360 degrees; dorsal penis rod not coiled.

Genus *Macrostylophora* Ewing, 1939  

Fig. 7

This genus currently consists of 38 taxa, all primarily ectoparasites of sciurid rodents in southeast Asia.

*Macrostylophora hastata* (Jordan & Rothschild, 1921)

Aedeagal apodeme cephalad of fulcrum 7.5X as long as broad at maximum width; shape of apodeme slightly different from others, dorsal margin slightly convex toward caudal end and concave proximally; ventral margin vise versa. Lateral laminae extend dorsally as small, convex, flap-like structures with serrated margins toward caudal end; extending over neck. Apical appendage short and slightly curled. Neck not apparent, covered by a dorsal spur-like structure, with lobed projection at proximal end and serrated dorsal margin toward distal end. Dorsal extension of lateral laminae different from others, with a broad base and long acuminate apex. Alate lobe short and broad. Proximal spur not prominent. Aedeagal
pouch large and prominent, weakly sclerotized and lamellate, except ventral margin; ventral margin of wall of aedeagal pouch very well sclerotized. Median dorsal lobe well sclerotized, almost straight; apical sclerite of median dorsal lobe small, well developed and arising ventrad. Lateral lobes large and well developed; caudal margin slightly irregularly convex; ventral margin convex. Crochets large; base broad, triangular with short, broad, slightly curved and subtruncate tongue-like projection; paxillus large, near three-fourths proximo-ventral angle of crochets, almost barrel-shaped but with both margins slightly convex. Sclerotized inner tube large and prominent, almost vertical; apex not expanded and convex; hook small; fistula curving ventrad following band of inner tube; band of inner tube flanked by spiculate structures; dorsal armature of inner tube broad, irregularly-shaped projections at cephalic end; ventral armature not prominent. Fulcrum with latero-ventral lobes long, narrow and weakly sclerotized; dorsal median projection very broad, slightly curved and well sclerotized; medial lobe broad and closely associated with floor of aedeagus and central sclerite; floor long and narrow, reaching below satellite sclerite. Crescent sclerite consistently broad and long; satellite sclerite like crescent sclerite but shorter, about one-third of crescent sclerite; central sclerite slightly
narrow and curved dorsally. Penis rods thick, short and slightly curved.

Taxa:

abazhouensis Liu, Liu & Zhai, 1981
aeretesites Li, Chen & Wei, 1974
angustihamula Li, Zhang & Zeng, 1988
bispiniforma bispiniforma Li, Hsieh & Yang, 1976
bispiniforma gongshanensis Gong & Xie, 1990
borneensis (Jordan, 1926)
conjiangensis Li & Huang, 1979
cuiae cuiae Liu, Wu & Yu, 1964
cuiae jiangkouensis Li & Huang, 1979
euteles (Jordan & Rothschild, 1911)
exilia Li, Wang & Hsieh, 1964
fimbriata (Jordan & Rothschild, 1921)
furcata Shi, Liu & Wu, 1985
gansuensis Zhang & Ma, 1982
hastata hastata (Jordan & Rothschild, 1921)
hastata hainanensis Liu & Pan, 1986
hastata malayensis Traub, 1950
hastata menghaiensis Li, Wang & Hsieh, 1964
hastata nepali Traub, 1950
hastata sikkimensis (Jordan & Rothschild, 1922)
hastata tonkinensis Jordan, 1939
hebeiensis Liu, Wu & Chang, 1979
heinrichi Jordan, 1939
idonea (Rothschild, 1919)
levis (Jordan & Rothschild, 1922)
liae Wang, 1957
luchunensis Huang, 1980
lupata lupata (Jordan & Rothschild, 1921)
lupata bamana Jordan, 1939
microcopia Li, Chen & Wei, 1974
nandanensis Li, Zeng & Zeng, 1987
paoshanensis Li & Yan, 1980
phillipsi (Jordan, 1925)
pilata (Jordan & Rothschild, 1922)
probata (Jordan & Rothschild, 1922)
sodalis (Rothschild, 1919)
trispinosa (Liu, 1939)
uncinalis Jordan, 1939
Subfamily Tarsopsyllinae

Figs. 8-12.

Genus *Tarsopsylla* Wagner, 1927

Fig. 8.

This monotypic genus contains two subspecies, one from North America and the other from Eurasia. They are ectoparasites of squirrels.

*Tarsopsylla octodecimdentata coloradensis* (Baker, 1895)

Aedeagal apodeme cephalad of fulcrum 9X as long as broad at maximum width; apodeme long and narrow with dorsal margin straight and ventral margin convex toward apex. Dorsal extension of lateral laminae short and broad with an acuminate apex. Apical appendage very short. True neck not apparent, covered by alate lobe. Alate lobe not evenly convex with a steeper caudal margin. Proximal spur not prominent. Wall of aedeagal pouch extending from below proximal spur to below base of fulcrum with proximal margin straight, curving disto-ventrally; ventral margin slightly convex. Median dorsal lobe short and straight with apical sclerite well developed. Lateral lobes extending from below median dorsal lobe to below base of fulcrum where it is joined by aedeagal pouch; ventral portion irregular in shape with a sharp ventral projection.
Crochets small and more ventrad from fulcrum; dorsal margin descending toward caudal margin, margin slightly straight, curving into a convex ventral margin, then recurving toward proximo-ventral, slightly concave before produced into an acuminate, thorn-like projection at midway; remainder of ventral margin concave; paxillus short and broad; upper margin slightly concave and lower margin convex. Sclerotized inner tube small and vertical with short fistula; apex expanded with large, prominent hook. Dorsal armature simple, produced into a small, acuminate, hook-like structure; ventral armature long and broad. Fulcrum with latero-ventral lobe short and narrow with a concave apex; dorsal median projection long, extending to apex of median dorsal lobe, broad at base and narrower apically; medial lobe short, curved dorsally with irregular dorsal margin. Crescent sclerite slightly expanded distally with a long, narrow proximal end; satellite sclerite narrow and irregular; central sclerite immediately below crescent sclerite, also narrow. Penis rods fairly thick and coiled less than 360 degrees.

Taxa:
octodecimdentata octodecimdentata (Kolenati, 1863)
octodecimdentata coloradensis (Baker, 1895)
Genus *Myoxopsylla* Wagner, 1927

Fig. 9.

This genus contains three species, all of which are parasites of muscardinid rodents in the Palaearctic Region.

*Myoxopsylla* (*Myoxopsylla*) *laverani*  
(Rothschild, 1911)

Aedeagus with region of aedeagal apodeme cephalad of fulcrum about 5.7X as long as broad at maximum width; region closer to fulcrum short and very much constricted while that toward the proximal end much broader. Dorsal extension of lateral laminae long and prominent. Apical appendage absent. Neck relatively long and narrow. Proximal spur absent. Wall of aedeagal pouch extending from below proximal spur to below fulcrum. Median dorsal lobe short, as in *Foxella*; dorsal margin fairly straight with apex angled and produced into a long apical sclerite of median dorsal lobe, pointing ventrad. Lateral lobes extending over fulcrum and sclerotized inner tube; caudal margin straight, then angled and directed proximad into a straight ventral margin extending one-third the length of lateral lobes; remainder of ventral margin convex to below fulcrum; proximal margin slightly concave. Crochets prominent, toothed, triangular, with curved, thorn-like projection, tip pointing ventrad; dorsal base of
projection produced into a short, proximally-directed projection (toothlike); paxillus sack-shaped, near proximo-ventral. Sclerotized inner tube short and confined to endchamber; part of tube folded and curved ventrad; apex with somewhat spiculate structure; fistula absent; dorsal armature of inner tube thin, flanking over apex of sclerotized inner tube with a small proximal lobe; also with flap-like structure; ventral armature greatly expanded but apex narrower. Fulcrum with latero-ventral lobes broad at base and apex narrow, not strongly curved; dorsal median projection long and broad, extending to apex of median dorsal lobe; medial lobe long and narrow, apex curving ventrad. Crescent sclerite fairly long and narrow, almost directly adjoined to satellite sclerite; satellite sclerite also fairly long and narrow; central sclerite prominent but narrow. Ventral penis rod coiled about 180 degrees; dorsal penis rod uncoiled.

Taxa:
Subgenus (Myoxopsylla) Wagner, 1927
laverani (Rothschild, 1911)
Subgenus (Miriampsylla) Peus, 1977
dryomydis Peus, 1977
jordani Ioff & Argyropulo, 1934
Genus *Orchopeas* Jordan, 1933

Fig. 10.

This Nearctic genus currently contains 20 taxa that parasitize rodents, although a number of them were originally described from predators.

*Orchopeas leucopus* (Baker, 1904)

The following description is based on Traub (1950).

Aedeagal apodeme consisting of a relatively narrow middle lamina that becomes deeply concave near fulcrum, and two lateral laminae that are produced into a dorsal pointed spur at the level of the fulcrum. Other elements of lateral laminae extending apicad as a thin, straight sclerotization, but true dorsal extension of lateral laminae absent. Region of apodeme cephalad of fulcrum relatively long, more than six times as long as broad at maximum width and about three times the distance from base of fulcrum to apex of median dorsal lobe. Apex of apodeme slightly upturned but apical appendage absent. Median dorsal lobe evenly convex, apically acuminate. Apical sclerite of median dorsal lobe represented by a semimembranous structure. Lateral lobes extremely reduced, apparently represented as a semimembranous, short, spiculose lobe near base of crochets. Crochets beak-shaped, large, extending well apicad of median dorsal lobe, somewhat longer
than broad; ventral margin slightly concave, dorso-caudal margin slightly sinuate, apex pointed; a lateral paxillus with an expanded base. Wall of aedeagal pouch sclerotized, arising at base of proximal spur, ventrally strongly convex and then extending apicad to fulcrum. Dorsal spur of lateral laminae associated with aedeagal pouch wall. Neck region not apparent because of development of dorsal spur of lateral laminae. Armature of sclerotized sheath of inner tube reduced to a lateral micro-tubercle. Sclerotized inner tube subrectangular and almost vertical. Apex of sclerotized inner tube subtruncate and expanded, with a recurved cephalic process and an acuminate caudal process which apparently is accompanied by an extension of the inner tube, the caudal process thus appearing bifid. Apical sclerites of inner tube absent. Fulcrum and ventral intramural rod as in Oropsylla (Diamanus) montanus. Penis rods not coiled.

Comments: The important features in this genus are as follows: Development of proximal spur, and of dorsal spur of lateral lobe, reduction of dorsal extension of lateral laminae and of true lateral lobes. Single median dorsal lobe. Well developed, large, beak-shaped crochets. Strongly convex ventral margin of sclerotized wall of aedeagal pouch. Subvertical, short, unsegmented, sclerotized inner tube with reduced armature and expanded apex. Inner tube projecting
slightly distad. Penis rods not coiled, not expanded apically.

Taxa:

*caedens caedens* (Jordan, 1925)
*caedens durus* (Jordan, 1929)
*dieteri* (C. Fox, 1929)
*fulleri* Traub, 1950
*howardi howardi* (Baker, 1895)
*howardi bolivari* Barrera, 1955
*howardi texensis* Eads, 1950
*labiatus* (Baker, 1904)
*latens* (Jordan, 1925)
*leucopus* (Baker, 1904)
*neotomae* Augustson, 1943
*nepos* (Rothschild, 1905)
*sexdentatus sexdentatus* (Baker, 1904)
*sexdentatus agilis* (Rothschild, 1905)
*sexdentatus cascadensis* Jordan, 1939
*sexdentatus firemani* Hubbard, 1955
*sexdentatus intermedius* Hubbard, 1943
*sexdentatus nevadensis* (Jordan, 1929)
*sexdentatus pennsylvanicus* (Jordan, 1928)
*sexdentatus schisintus* (Jordan, 1929)
Genus *Opisodasys* Jordan, 1933

Figs. 11 & 12.

This genus is currently represented by nine taxa which are associated with sciurid rodents. They are wholly Nearctic in distribution.

*Opisodasys* (*Opisodasys*) *pseudarctomys* (Baker, 1904)

Aedeagus with region of aedeagal apodeme cephalad of fulcrum 7X as long as broad at maximum width; apodeme with one third of the proximal end curved dorsad. Dorsal extension of lateral laminae large and prominent with pointed apex. Apical appendage short. Neck not that apparent, crossed over by alate lobe. Alate lobe with margin evenly convex. Proximal spur much longer than apical appendage. Aedeagal pouch extending from below proximal spur to below fulcrum; wall of aedeagal pouch with ventral margin straight. Median dorsal lobe short with straight margin; apical sclerite of median dorsal lobe well developed, with V-shaped hook directed ventrad. Lateral lobes with caudal margin slightly convex; ventral margin angulate, disto-ventral margin slightly convex and proximo-ventral margin produced into a blunt projection. Crochets elongate and well sclerotized with a much narrower distal end, with horn-like projection and a rather broad, square base; paxillus near two-thirds proximo-ventral end.
Sclerotized inner tube complex with a relatively long, well developed fistula, extending proximo-ventrally. Apex of sclerotized inner tube expanded with prominent hook. Sclerotized inner tube confined to endchamber. Dorsal armature of inner tube long and hooklike, directed proximad; crescent sclerite prominent, short and broad with cephalic end narrower, distal end broader; satellite sclerite as a narrow thin strip; central sclerite very close to crescent sclerite in position. Fulcral latero-ventral lobes curved with a bulbous apex; medial lobe broad with subtruncate apex; dorsal median projection short and acuminate. Penis rods relatively short, coiled less than 360 degrees.

Opisodasys (Oxypylla) keeni keeni (Baker, 1896)

Aedeagus with region of aedeagal apodeme cephalad of fulcrum 9X as long as broad at maximum width; apodeme with both ventral and dorsal margins slightly convex and upturned proximad. Dorsal extension of lateral laminae long and broad, extending to the acuminate apex of median dorsal lobe. Apical appendage short. Neck not apparent, covered by alate lobe. Proximal spur absent. Wall of aedeagal pouch not that prominent, weakly sclerotized. Median dorsal lobe short and straight; apical sclerite of median dorsal lobe flared with sclerite well developed, irregularly shaped and directed
ventrad. Lateral lobes well developed; caudal margin fairly convex, descending into a concave margin proximoventrally which extends into a broad, tongue-like ventral margin below fulcrum level. Crochets weakly sclerotized, especially dorsal margin; apex produced into an acuminate, hook-like projection pointing caudo-ventrad. Sclerotized inner tube with fistula curving ventrad; apex expanded and concave with hook present; dorsal armature of inner tube complicated with sclerotized irregular sclerites. Fulcrum with latero-ventral lobes short and broad, not strongly curved, with rounded apex; dorsal median projection fairly long and narrow; medial lobe long and broad, recurving proximad. Crescent sclerite long and fairly broad but not well sclerotized; satellite sclerite thin and not prominent; central sclerite long and flattened, curving ventrad. Penis rods short and curled; ventral rod longer than dorsal.

Comments: Apex of endchamber covered with semimembranous structure.

Taxa:

Subgenus (Opisodasyx) Jordan, 1933

cosmicomys (Baker, 1904)

vesperalis (Jordan, 1929)
Subgenus (Oxypsylla) Smit, 1983

*keeni* (Baker, 1896)

*nesiota* Augustson, 1941

Subgenus (Sciropsylla) Dampf, 1942

*enoplus* (Rothschild, 1909)

*hollandi* Traub, 1947

*perotensis* Dampf, 1942

*robustus* *robustus* (Jordan, 1925)

*robustus mexicanus* Dampf, 1942

Subfamily Dactylopsyllinae

Genus *Foxella* Wagner, 1929

Fig. 13.

This exclusively Nearctic genus consists of 14 taxa. They are ectoparasites of pocket gophers in the western two-thirds of North America.

*Foxella* (*Foxella*) *ignota ignota* (Baker, 1895)

Aedeagal apodeme cephalad of fulcrum about 4.5X as long as broad at maximum width; apodeme long and narrow, much narrower at distal one-third and broadening toward proximal end; dorsal margin irregular proximally. Dorsal extension of lateral laminae short and acuminate, not reaching aedeagus
proper. Apical appendage short and curled. Neck present. Alate lobe present, extending to cephalic end of median dorsal lobe. Proximal spur present. Aedeagal pouch short, arising from level of proximal spur, curving ventrad at level of median lamina and then diverging dorsally to base of fulcrum. Median dorsal lobe simple and unflared, apex subtruncate; apical sclerite of median dorsal lobe present. Lateral lobes well developed, extending from median dorsal lobe over sclerotized inner tube and fulcrum, ventral margin convex and extending well ventrad of penis rods. Endchamber expanded, measured from ventral margin of lateral lobe to dorsal margin of median dorsal lobe, somewhat more than twice as broad as aedeagalar apodeme. Crochets large, extending far distad of endchamber; dorsal margin concave and diverging disto-ventrally, producing an acuminate projection; first half of ventral margin concave, remainder straight or flattened; paxillus near three-fourths proximo-ventral angle of crochets, slightly bulbous shaped. Sclerotized inner tube vertical, short, with complicated armature; apex modified; dorsal armature of inner tube irregularly-shaped; ventral armature broad. Fulcrum with latero-ventral lobes narrow, short and slightly curved; dorsal median projection present, long and narrow; medial lobe broad with an acuminate apex. Crescent sclerite prominent and well developed with proximal end
broader than distal end; satellite sclerite thin and not prominent; central sclerite well sclerotized, much larger than satellite sclerite. Penis rods coiled more than 360 degrees.

Comments: Aedeagus fundamentally similar to that of other ceratophyllids but the sclerotized sheath of the inner tube is highly modified (Traub, 1950). Fulcrum much as in Plusaetis.

Taxa:

Subgenus (Foxella) Wagner, 1929

*ignota ignota* (Baker, 1895)
*ignota albertensis* (Jordan & Rothschild, 1915)
*ignota apachina* (C. Fox, 1914)
*ignota arizonensis* Hubbard, 1947
*ignota chapmani* Hubbard, 1958
*ignota clantoni* Hubbard, 1949
*ignota coufferi* Augustson, 1942
*ignota franciscana* (Rothschild, 1910)
*ignota omissa* Prince, 1945
*ignota recula* (Jordan & Rothschild, 1915)
*ignota utahensis* Wagner, 1936

Subgenus (Afoxella) Smit, 1983

*hooqstraali* Traub, 1950

*macgregori* Barrera, 1953
mexicana I. Fox, 1939

Subfamily Oropsyllinae

Figs. 14-20.

Genus Oropsylla Wagner & Ioff, 1926

Figs. 14-18.

Currently divided into four subgenera (5 of Smit, 1983, in Traub et al) plus Thrassis, which is currently accepted as a separate genus, the 16 species are parasites of marmots and ground squirrels. They are mainly Nearctic in distribution, but two are known from Central Asia, and one was recently described from central Turkey.

Oropsylla (Oropsylla) arctomys (Baker, 1904)

Aedeagal apodeme cephalad of fulcrum about 5.3X as long as broad at maximum width; apodeme broad, broadest at proximal seven-tenths, proximal end almost flattened. Dorsal extension of lateral laminae extends over aedeagus, subacute and somewhat proximad of fulcrum. Apical appendage present; not particularly long but longer than proximal spur. Neck not apparent. Wall of aedeagal pouch arising at level of proximal spur, curving apicad to base of lateral lobe; mid-ventral margin concave, the remainder somewhat convex. Median dorsal
lobe long and fairly straight dorsally; apical sclerite of median dorsal lobe absent. Lateral lobes large and well developed, extending from level of median dorsal lobe to below fulcrum; ventral margin convex, caudal margin slightly sinuate. Crochets large, almost as broad as aedeagal apodeme at maximum and about as long as dorsal margin of median dorsal lobe; dorsal and caudal margins produced apically as a tongue-like extension, recurved ventrally. Endchamber large, expanded dorsally. Sclerotized inner tube directed almost vertically and confined to endchamber. Apical sclerites absent, hook present, broad and large. Armature of inner tube highly specialized, consisting of dorsal and ventral arms; dorsal armature angled dorsally with a hook-like process directed apico-proximally. Fulcrum with latero-ventral lobes typically curved; medial lobe as in O. (D) montana, broad and subovate; dorsal median projection prominent, as in O. (D) montana but broader. Crescent sclerite well developed, short and broad, more or less hemispherical in shape; satellite reduced to a long, very thin strip. Penis rods long and coiled more than 360 degrees.
The following description is based on Traub (1950).

**Oropsylla (Diamanus) montana** (Baker, 1895)

Aedeagal apodeme consists of the well-sclerotized middle lamina which terminates in the fulcrum, and the lateral laminae (difficult to see in cleared specimens) which extend apicad to base of fulcrum. Apodeme broadest at proximal fourth; region cephalad of fulcrum about 4X as long as broad; a long apical appendage and a much shorter proximal spur. Neck short and thick. Wall of aedeagal pouch arising at level of proximal spur, extending ventrad of penis rods and then curving apicad to base of lateral lobes. Endchamber relatively short, distance from base of fulcrum to tip of median dorsal lobe less than half the length of aedeagal apodeme. Median dorsal lobe long, fairly straight dorsally, produced apically into a short hook and then recurved ventrad; apical sclerite of median dorsal lobe short and curved on each side. Lateral lobes greatly developed, extending from an area ventrad and proximad of fulcrum to apex of median dorsal lobe; ventral margin convex, caudal margin deeply sinuate; dorsal extension of lateral laminae extending over aedeagus, subacute, somewhat narrowed proximad of fulcrum, forming a short thick neck. Crochets very well developed, almost as broad as aedeagal apodeme at maximum and about as long as dorsal margin of median dorsal lobe; dorsal and caudal margins
produced apically as a tongue-like extension, as long as remainder of crochet, almost as broad as long at maximum; paxillus at ventral third. Sclerotized inner tube very short, consisting of one sclerite, truncate and located between the armature arms, directed almost vertically; apical sclerites absent. Armature of inner tube highly specialized consisting of a dorsal and ventral arm, dorsal arm angled dorsally and directed apicad and at the end of that extension, a caudal process at right angles; ventral arm with a narrow apical process. Fulcrum consists of the typical curved latero-ventral sclerite; medial lobe subglobular; dorsal median projection a short, narrow, thin strip. Crescent sclerite short but well-developed; satellite sclerite a short sclerotized strip; central sclerite long and thin. Penis rods very long, not expanded proximally, coiled into more than one complete turn, almost with a second complete turn.

**Oropsylla (Hubbardipsylla) oregonensis**  
(Good & Prince, 1939)

Aedeagal apodeme cephalad of fulcrum about 3X as long as broad at maximum width; aedeagus much narrower toward fulcrum, with both dorsal and ventral margins almost straight, and broader proximally, with both margins convex. Dorsal extension of lateral laminae not prominent. Apical appendage
long and curled. Neck short, crossed by alate lobe. Alate lobe short with ventral margin evenly convex. Proximal spur shorter than apical appendage. Wall of aedeagal pouch arising at level of proximal spur, ventral margin extending to level of penis rods and then curving dorso-apicad to base of lateral lobes. Median dorsal lobe as in Oropsylla (Diamanus) montana but not apically produced into a short hook; apical sclerite of median dorsal lobe long and convex. Lateral lobes well-developed, extending over sclerotized inner tube and fulcrum; caudal margin sinuate (as in Diamanus), ventral margin strongly convex. Crochets ovate, somewhat leaf-like, with a sharp apex; crochets almost as broad as aedeagal apodeme at maximum; paxillus elongate. Sclerotized inner tube complicated and vertical; apex convex, hook small but prominent; fistula long, extending caudad and curving ventrad with convex ventral margin; dorsal armature of inner tube broad and irregularly shaped; ventral armature long and broad, with ventral portion somewhat ovate. Fulcrum prominent as in others with latero-ventral lobes broad but not as strongly curved as in (Diamanus); dorsal median projection long and narrow, extending dorsad to median dorsal lobe, somewhat parallel to median dorsal lobe and dorsal extensions of lateral laminae; fulcral medial lobe subglobular and trilobed. Crescent sclerite short and broad, hemispherical but not well
sclerotized; satellite sclerite not that prominent; central sclerite thin and narrow. Penis rods coiled more than 360 degrees.

Comments: Fistula is absent in other species of *Oropsylla* except in the subgenus *Hubbardipsylla*.

*Oropsylla (Opisocrostis) bruneri* (Baker, 1895)

Aedeagal apodeme short and broad with region cephalad of fulcrum about 4.5X as long as broad at maximum width; dorsal margin fairly straight, ventral margin convex. Dorsal extension of lateral laminae broad but narrowing at apex along median dorsal lobe. Apical appendage absent. Neck not apparent, covered by alate lobe. Alate lobe extending over neck. Wall of aedeagal pouch arising from level of proximal spur, convex ventrally, diverging to meet ventral margin of lateral lobes. Median dorsal lobes with dorsal margin straight; apical sclerite of median dorsal lobe absent. Lateral lobes extending over endchamber; upper caudal margin almost straight, curving in slightly before becoming slightly convex throughout ventral margin. Crochets slightly shorter than in *O. (O) arctomys*; dorsal margin slightly straight, with a sharp acuminate distal projection; caudal margin strongly concave and curving into a short straight ventral margin where paxillus lies; paxillus stout. Sclerotized inner tube with
apex complicated, expanded, cup shaped, facing proximad; inner tube confined to endchamber. Dorsal armature of inner tube with a short rugged sclerite; ventral armature a broad rectangular sclerite. Fulcrum with latero-ventral lobe curved with broad base; medial lobe as in O. (D) montana; dorsal median projection a very thin strip, extending to median dorsal lobe. Crescent sclerite very narrow, almost reduced to a thin strip; satellite sclerite very prominent, almost the same size as crescent sclerite; central sclerite fairly prominent. Penis rods short.

Oropsylla (Opisocrostis) tuberculata (Baker, 1904)

Aedeagal apodeme cephalad of fulcrum about 3X as long as broad at maximum width; apodeme broad proximally to base of fulcrum where it is strongly constricted. Dorsal extension of lateral laminae present. Apical appendage absent. Neck not apparent, covered by alate lobe. Alate lobe with ventral margin convex. Wall of aedeagal pouch extending to below neck, ventral margin almost straight before diverging and extending to lateral lobes below fulcral latero-ventral lobes. Proximal spur not prominent. Median dorsal lobe with dorsal margin simple and straight; apical sclerite of median dorsal lobe present but not prominent. Lateral lobes well developed, large, extending over endchamber; ventral margin convex,
produced into a short ventral projection; caudal projection slightly concave. Crochets almost a rounded barrel shaped, with a long sharp tongue-like projection. Endchamber broad, slightly expanded dorsally. Sclerotized inner tube with a complex apex, dilated and produced into a sharp hook-like structure; inner tube much confined to endchamber. Dorsal armature of inner tube complex; ventral armature broad but weakly sclerotized. Fulcrum with latero-ventral lobes broad with a long base but distal arm slightly larger than O.(Q) bruneri; medial lobe broad; dorsal median projection relatively long and broad with acuminate apex. Crescent sclerite prominent; satellite sclerite broad but smaller than crescent sclerite; central sclerite present. Penis rods coiled more than 360 degrees.

Taxa:

Subgenus (Oropsylla) Wagner & Ioff, 1926

alaskensis (Baker, 1904)
arctomys (Baker, 1904)
eatoni Hubbard, 1954
idahoensis (Baker, 1904)
ilovaiskii Wagner & Ioff, 1926
rupestris (Jordan, 1929)
silantiewi (Wagner, 1898)
**tapina** Peus, 1977

**Subgenus (Diamanus) Jordan, 1933**

**montana** (Baker, 1895)

Subgenus **(Hubbardipsylla) Smit, 1983**

**oregonensis** (Good & Prince, 1939)

**washingtonensis** (Good & Prince, 1939)

Subgenus **(Opisocrostis) Jordan, 1933**

**bruneri** (Baker, 1895)

**hirsuta** (Baker, 1895)

**labis** (Jordan & Rothschild, 1922)

**tuberculata tuberculata** (Baker, 1904)

**tuberculata cynomuris** (Jellison, 1939)

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**Genus Thrassis** Jordan, 1933

Figs. 19-20.

This exclusively Nearctic genus is currently represented by 11 species, which Stark, 1970 divided into 29 named taxa, depending on distribution and host preferences. They are associated with terrestrial squirrels, but two taxa are specific to species of **Lagurus** and **Dipodomys**.
Thrassis acamantis acamantis (Rothschild, 1905)

Aedeagal apodeme cephalad of fulcrum 4.5X as long as broad at maximum width; apodeme large and broad, broadest at three-fourths proximad. Dorsal extension of lateral laminae broad based with sharp, tapered apex directed dorsad. Apical appendage absent. Neck present. Alate lobe long and broad. Proximal spur present. Wall of aedeagal pouch extending from below neck to below base of fulcral latero-ventral lobes to base of lateral lobes. Median dorsal lobe with dorsal margin somewhat straight, with lateral extension of median dorsal lobe; apical sclerite of median dorsal lobe semimembranous. Lateral lobes not extending over sclerotized inner tube; prominent, angled with caudal margin produced into a blunt angle while ventral margin strongly produced into a long, sharp, hook-like projection. Crochets large, extending well apicad of median dorsal lobe; somewhat narrow with dorsal margin convex and ventral margin sinuate or concave; apex recurved and acuminate; paxillus bulbous, near three-fourths proximo-ventral portion. Sclerotized inner tube short without fistula; apex of sclerotized inner tube expanded. Dorsal armature of inner tube produced into a broad sclerite with a tapered or thorn-like apex; ventral armature as a thick sclerite. Fulcrum with latero-ventral lobes prominently curved; dorsal median projection long with a broad base and an
acuminate apex; medial lobe broad, as in *T. francisi*. Crescent sclerite prominent, relatively broad; satellite sclerite very narrow; central sclerite prominent. Penis rods coiled more than 360 degrees.

**Thrassis francisi francisi** (C. Fox, 1927)

Aedeagal apodeme cephalad of fulcrum about 4X as long as broad at maximum width; apodeme large and broad, broadest at three-fourths proximal end. Dorsal extension of lateral laminae short with acuminate apex. Apical appendage absent. Neck present, crossed by alate lobe. Alate lobe long and broad with ventral margin convex. Proximal spur present. Wall of aedeagal pouch extending from below alate lobe to ventral projection of lateral lobe, ventral margin convex. Median dorsal lobe long with margin almost straight; apical sclerite of median dorsal lobe semimembranous. Lateral lobes extending over fulcrum, caudal margin convex; ventral projection of lateral lobe very short and blunt, below fulcral latero-ventral lobes in position. Crochets relatively long and broader than those of *T. acamantis*; projection not tongue-like, slightly narrow at base and broaded toward apex; paxillus near five-sevenths proximo-ventral angle of crochets. Sclerotized inner tube long with apex expanded and bowl-shaped, hook present; fistula absent. Dorsal armature of
inner tube complex, produced into a large, ovate lobe; ventral armature a very thick sclerite. Fulcrum with latero-ventral lobes prominent and typically curved with a narrower apex; dorsal median projection long, relatively broad and well sclerotized with margins irregular; medial lobe broad with curved apex. Crescent sclerite long and prominent with broad proximal end and acuminate caudal tip; satellite sclerite prominent and narrow; central sclerite also prominent and narrow. Penis rods with ventral rod coiled more than 360 degrees and dorsal rod uncoiled.

Taxa:

acamantis acamantis (Rothschild, 1905)
acamantis howelli (Jordan, 1925)
acamantis medius Stark, 1970
acamantis pristinus Stark, 1957
acamantis utahensis Wagner, 1936
aridis aridis Prince, 1944
aridis arcuatus Stark, 1957
aridis campestris Prince, 1944
aridis hoffmani (Hubbard, 1949)
arizonensis (Baker, 1898)
augustsoni Hubbard, 1949
bachi bacchi (Rothschild, 1905)
bacchi caducus (Jordan, 1930)
bacchi consimilis Stark, 1957
bacchi gladiolus (Jordan, 1925)
bacchi johnsoni Hubbard, 1949
bacchi pansus (Jordan, 1925)
bacchi setosis Prince, 1944
fotus (Jordan, 1925)
francisi francisi (C. Fox, 1927)
francisi barnesi Stark, 1970
francisi rockwoodi Hubbard, 1942
francisi sierrae Stark, 1970
pandorae pandorae Jellison, 1937
pandorae jellisoni Hubbard, 1940
petiolatus (Baker, 1904)
spenceri spenceri Wagner, 1936
apenseri alpinus Stark, 1957
stanfordi Wagner, 1936
Subfamily Ceratophyllinae Dampf, 1908
Figs. 21-35.
Genus *Citellophilus* Wagner, 1934
Fig. 21.

This Palaearctic genus consists of 20 currently recognized taxa. They are specific parasites of ground squirrels and marmots.

*Citellophilus sungaris sungaris* (Jordan, 1929)

Aedeagus with region of aedeagal apodeme about 4.4X as long as broad at maximum width; apodeme short and broad, broader toward proximal end. Dorsal extension of lateral laminae relative short. Apical appendage short and curled. Neck absent. Alate lobe short. Proximal spur short and curled. Wall of aedeagal pouch broad, extending from below proximal spur to below fulcrum. Median dorsal lobe long, dorsal margin almost straight, its apex bifid; apical sclerite of median dorsal lobe flared. Lateral lobes extending over sclerotized inner tube and fulcrum; caudal margin concave and ventral margin slightly convex. Crochets small, weakly sclerotized dorsally; triangular in shape; distal margin produced into a short, blunt projection; paxillus cylindrical with a straight ventral margin and a round dorsal margin. Sclerotized inner tube small and narrow, confined to
end chamber, with apex slightly expanded, hook present; inner tube extended as fistula; apex modified but simple compared to other species in the genus; dorsal armature of inner tube produced into ventrally-directed, hook-like structures. Fulcrum with latero-ventral lobes long and narrow and not strongly curved; dorsal median projection absent; medial lobe long and prominent, strongly convex dorsally with acuminate apex; floor very prominent and strongly convex dorsally, concave ventrally. Crescent sclerite long and weakly sclerotized dorsally; satellite sclerite short and broad; central sclerite immediately above fulcral medial lobe. Penis rods coiled, ventral rod coiled 1.25X; dorsal rod coiled less than 360 degrees.

Taxa:

*altaicus* (Ioff, 1936)

*gracilis* (Mikulin, 1957)

*ienissejensis* (Wagner, 1902)

*lebedewi lebedewi* (Wagner, 1933)

*lebedewi princeps* (Ioff, 1946)

*martinoi martinoi* (Wagner & Ioff, 1926)

*martinoi rotundus* Rosicky, 1956

*menzbieri* (Ioff, 1950)

*relicticola* (Fedina, 1946)
simplex simplex (Wagner, 1902)
simplex rosickyi Cyprich, 1989
sungaris sungaris (Jordan, 1939)
sungaris lobatschevi Cyprich, Kiefer & Krumpal, 1985
tesquorum tesquorum (Wagner, 1898)
tesquorum ciscaucasicus (Ioff, 1936)
tesquorum mongolicus (Jordan & Rothschild, 1911)
tesquorum transvolgensis (Ioff, 1936)
transcaucasicus (Ioff & Agyropulo, 1934)
trispinus (Wagner & Ioff, 1926)
ullus (Mikulin, 1957)

Genus Callopsylla Wagner, 1934
Figs. 22-23.

This genus currently contains 29 taxa, known exclusively from the Palaearctic region, mainly associated with small rodents.

Callopsylla (Callopsylla) caspia
(Ioff & Agyropulo, 1934)

Aedeagus with region of aedeagal apodeme cephalad of fulcrum 4.5X as long as broad at maximum width; apodeme broad and short, narrow immediately posterior to fulcrum and broader
toward apex; dorsal extension of lateral laminae almost broad, short and acuminate; dorsal margin convex dorsally. Apical appendage not prominent. Neck not prominent, covered by alate lobe. Alate lobe wider than that of C. waterstoni, crossing base of fulcrum. Proximal spur longer than apical appendage. Wall of aedeagal pouch extending to median dorsal lobe. Median dorsal lobe bifid; apical sclerite of median dorsal lobe well sclerotized, thick and broad. Lateral lobes weakly sclerotized and extending ventrad. Crochets weakly sclerotized, dorsal margin irregularly concave, projecting caudad; tongue-like projection blunt, recurved ventrally. Sclerotized inner tube slightly vertical, simple, with a strongly convex dorsal margin, especially toward apex; apex slightly expanded with short hook; inner tube extended as fistula: a simple tube curving ventrad and becoming ringed in a manner reminiscent of a trachea; dorsal armature of inner tube simple, with a short hook-like sclerite projecting cephalad; ventral armature thick and broad. Fulcrum with latero-ventral lobes curved, long and broad, with bulging apex, recurving ventrad; dorsal median projection long and narrow, curved with a broad base; medial lobe as in C. waterstoni. Crescent sclerite long and broader toward caudal end, dorsal margin convex; satellite sclerite small and hardly prominent; central sclerite very narrow, long and well
developed. Penis rods long, uncoiled but curled; ventral penis slightly longer than dorsal rod.

**Callopsylla (Orneacus) waterstoni** (Jordan, 1925)

Aedeagal apodeme cephalad of fulcrum 6.5X as long as broad at maximum width; apodeme with proximal end broader toward proximal and narrower toward distal end. Dorsal extension of lateral laminae broad, dome-shaped, well sclerotized and extending over neck. Apical appendage short and thick. Neck not apparent, covered by alate lobe and dorsal extension of lateral laminae. Alate lobe with proximal margin slanting and ventral margin straight. Proximal spur longer than apical appendage. Wall of aedeagal pouch short, ventral margin recurved toward caudal end. Median dorsal lobe long and convex, apex bifid and well sclerotized; apical sclerite of median dorsal lobe well developed, convex, curving ventrad to level of fistula. Lateral lobes extending over sclerotized inner tube to below fulcrum, caudal margin slightly convex, almost straight; ventral margin convex. Crochets small with large paxillus and fairly long, tongue-like projection which curves ventrad; paxillus large and well developed. Sclerotized inner tube large, broad at base and narrower at apex; hook not well developed and fistula very short; dorsal armature of inner
tube well developed, broad, bulbous and curved; ventral armature well developed, longer and broad. Fulcrum with latero-ventral lobes broad (shorter than C. caspia), curved with dilated apex; dorsal median projection well developed, the first half broad but the other half reduced to a very thin, long, thread-like sclerite; medial lobe well developed, broad, with acuminate apex. Crescent sclerite very broad with dorsal margin prominently convex; satellite sclerite very small; central sclerite thin; floor of aedeagus broad and long, weakly sclerotized but prominent. Penis rods thick, curled but not coiled.

Taxa:

Subgenus (Callopsylla) Wagner, 1934

arcuata Ge, Wang & Ma, 1988
caspia caspia (Ioff & Argyropulo, 1934)
caspia fragilis (Mikulin, 1953)
caspia gaiskii (Vovchinskaya, 1950)
caspia tiflovi Wagner, 1936
changduensis (Liu, Wu & Wu, 1966)
digitata Cai, Wu & Liu, 1984
dolabella Smit & Rosicky, 1976
dolabris (Jordan & Rothschild, 1911)
forfica Wu, Chen & Liu, 1981
kazbegiensis Goncharov, 1980
kozlovi (Wagner, 1928)
lagomys (Wagner, 1898)
liui Li, Wu & Yang, 1989
longispina Zhang & Yu, 1988
mygala (Lewis, 1971)
petaurista Tsai, Wu & Liu, 1974
saxatilis (Ioff & Argyropulo, 1934)
sparsilis sparsilis (Jordan & Rothschild, 1922)
sparsilis atallahi (Lewis, 1971)
streeti Lewis, 1973
yui Ye & Jiang, 1990

Subgenus (Geminopsylla) Beaucournu & Aeschlimann, 1985
beishanensis Wu, Ni & Wu, 1986
gemina (Ioff, 1946)
gypaetina Peus, 1978

Subgenus (Orneacus) Jordan, 1937
oreinus (Jordan, 1937)
waterstoni (Jordan, 1925)

Subgenus (Paracallopsylla) Ioff, 1936
kaznakovi (Wagner, 1928)

Subgenus (Typhlocallopsylla) Ioff, 1936
semenovi (Ioff, 1936)
Genus *Malaraeus* Jordan, 1933

Fig. 24.

This genus is represented by three species that occur in the more or less arid regions of western North America, mainly as parasites of species of *Peromyscus*.

*Malaraeus sinomus* (Jordan, 1925)

Aedeagus with region of aedeagal apodeme cephalad of fulcrum 9X as long as broad at maximum width; apodeme long and narrow, broadest at seven-ninths proximal end with apex of apodeme slightly narrowed. Dorsal extension of lateral laminae absent. Short apical appendage present. Neck present but short. Dorsal spur absent. Alate lobe present but not that prominent. Proximal spur prominent. Aedeagal pouch prominent, weakly sclerotized and arising from level of proximal spur; ventral margin fairly straight, extending to base of lateral lobes. Median dorsal lobe fairly straight, short and bifid apically; apical sclerite of median dorsal lobe simple. Lateral lobes large and well developed; caudal margin slightly concave but mostly straight, curving ventro-proximad into a straight margin below neck level, where it is produced into an acuminate distal end before it recurves to meet the wall of aedeagal pouch. Crochets large but weakly sclerotized with dorsal margin straight and caudal margin
convex, narrowing towards proximo-ventral apex; paxillus wide but shallow-ovate, saucer-shaped. Sclerotized inner tube simple, short and vertical; apex simple with inner tube extended into a short fistula; dorsal armature large, broad and hook-like; ventral armature long and broad. Fulcrum with latero-ventral lobes broad with apex bulging or club-shaped; dorsal median projection narrow but well developed, extending along the length of median dorsal lobe; medial lobe broad and short. Crescent sclerite broad, with proximal end long and narrow, distal end shorter; satellite sclerite narrow with a hook-like proximal end; central sclerite long and thin. Ventral penis rod long and curled, dorsal rod shorter but not curled.

Taxa:

eremicus (Baker, 1904)
sinomus (Jordan, 1925)
telchinus (Rothschild, 1905)

Genus Amalaraeus Ioff, 1936

Fig. 25.

Amalaraeus is a Holarctic genus of Microtine fleas occurring primarily in mountainous and boreal areas.
Amalaraeus dissimilis dissimilis (Jordan, 1938)

Aedeagus with region of aedeagal apodeme cephalad of fulcrum about 5X as long as broad at maximum width; apodeme broadest at seven-tenths proximad and most constricted at three-tenths proximad; dorsal margin convex between apical appendage and proximal spur and concave posterior to proximal spur, ascending until it meets base of median dorsal lobe. Dorsal extension of lateral laminae short and narrow with acuminate apex. Apical appendage reduced to a short stump. True neck absent as in Dasypsyllus. Proximal spur present. Aedeagal pouch arising from level of proximal spur, descending as a straight margin slanting towards caudal; dorsal margin somewhat convex to base of proximal spur, ventral margin straight, then ascending until meeting base of lateral lobes immediately below posterior portion of fulcrum; posterior 2/3 of wall of aedeagal apodeme well sclerotized, remaining one-third membranous. Median dorsal lobe straight, well sclerotized and bifid, as in Dasypsyllus; apical sclerite of median dorsal lobe absent. Ford's sclerite present. Lateral lobes very large and well developed, extending from median dorsal lobe ventrad, caudal margin irregular, slightly concave, ventral portion produced into a broad, tongue-like projection, ridged projection. Crochets slightly twisted, dagger-shaped; paxillus near one-third posterior; region
immediately above paxillus produced into a somewhat rounded semimembranous area. Endchamber compact and complicated. Sclerotized inner tube short, vertical and heavily sclerotized; sclerites above sclerotized inner tube complicated; apex expanded and convex with inner tube produced into a short fistula; armature of inner tube complex, produced into a large, broad, rounded, armlike structure; dorsal armature produced into a broad, vertical, flask-like structure. Fulcrum with latero-ventral lobes short and fairly broad with apex truncate; dorsal median projection absent; medial lobe long, narrow and recurved, with apex directed proximad bulging slightly. Crescent sclerite broad and short; satellite sclerite narrow; central sclerite long, narrow and curved. Penis rods relatively short; ventral rod curved, longer than dorsal rod.

Taxa:

*andersoni andersoni* (Rothschild, 1908)  
*andersoni ioffi* (Darskaya, 1949)  
*arvicolae* (Ioff, 1948)  
*dissimilis dissimilis* (Jordan, 1938)  
*dissimilis angularis* (Tsai, Wu & Liu, 1974)  
*dissimilis angulatus* (Violovich, 1961)  
*dissimilis athabascae* (Holland, 1952)
**Genus *Amaradix* Smit, 1983**

Fig. 26.

There are two species in this genus, primarily associated with wood rats in western North America.

*Amaradix bitterrootensis bitterrootensis*  
*(Dunn, 1923)*

Aedeagal apodeme long and narrow, 5.7X as long as broad at maximum width. Alate lobe present, large, with dorsal margin almost straight and ventral margin convex. Dorsal extension of lateral laminae short, broad and acuminate.
Apical appendage very short. Neck absent, covered by alate lobe. Aedeagal pouch as in others, ventral margin extending ventrad to level of penis rods, convex, curving apicad to base of lateral lobes. Proximal spur short. Median dorsal lobe slightly convex and bifid apically; apical sclerite of median dorsal lobe well developed, produced into a broad, convex band, curving ventrad. Lateral lobes well developed, extending from median dorsal lobe to below base of fulcrum; caudal margin convex, curving ventrad into a fairly straight ventral margin with proximo-ventral margin turning dorsad at almost a right angle, where it joins aedeagal pouch wall. Crochets large and prominent, parallel with aedeagal apodeme; proximal margin deeply sinuate ascending dorso-caudal into a convex margin. Distal region extended into a long tongue-like projection; ventral margin of tongue deeply sinuate; proximo-ventral margin slightly straight; paxillus broad, at proximo-ventral of crochets. Sclerotized inner tube confined to endchamber; apex of sclerotized inner tube slightly expanded, with prominent hook; fistula long and broad, extending ventrad. Dorsal armature of inner tube projecting dorso-caudad, distal-end acuminate. Fulcrum with broad, curved latero-ventral lobes; apex blunt; dorsal median projection short and broad; medial lobes long and broad with apex curved ventrally. Crescent sclerite long and narrow; satellite
sclerite long and narrow, almost as long as crescent sclerite; central sclerite long and very thin. Penis rods long and curved, not coiled.

**Taxa:**

*bitterrootensis* *bitterrootensis* (Dunn, 1923)

*bitterrootensis* *vonfintelis* (Prince, 1959)

*euphorbae* (Rothschild, 1905)

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**Genus *Dasypsyllus* Baker, 1905**

*Fig. 27.*

There are eleven taxa assigned to this genus of bird-fleas, belonging to three subgenera (Smit, 1976a:65). The genus is known from the Holarctic, Neotropical and Oriental Regions.

*Dasypsyllus* (*Dasypsyllus*) *gallinulae* *gallinulae* (Dale, 1878)

Aedeagus with region of aedeagal apodeme cephalad of fulcrum 12X as long as broad at maximum width; apodeme long and very narrow with both median lamina and lateral laminae prominent. Dorsal extension of lateral laminae very narrow. Apical appendage present. True neck absent. Alate lobe not
that prominent, extending to level of median lamina. Proximal spur present and fairly short. Aedeagal pouch very prominent, arising at level of proximal spur; ventral margin strongly convex. Basal wall of aedeagal pouch arising at level of base of proximal spur; ventral margin slightly convex and extending to level of fulcrum. Median dorsal lobe apically bifid, (not curved as in Ceratophyllum) projecting ventrad medially; apical sclerite of median dorsal lobe absent. Lateral lobes well developed, extending on each side as a slightly sinuate, mainly convex lobe from apex of pouch wall to apex of median dorsal lobe. Crochets very large, more than half as broad as endchamber and almost twice as long as broad; dorsal and ventral margin concave; apex oblique but subtruncate; paxillus near proximo-ventral angle, barrel-shaped. Sclerotized inner tube complicated with apex well expanded. Fistula long, curving ventrad to below base of crochet. Armature of sclerotized sheath of inner tube specialized, consisting of a relatively long, horizontal, acuminate sclerite roughly paralleling the stout, slightly arched apex of the sclerotized inner tube. Fulcrum of same basal sclerites as in Q. (Diamanus) montana. Crescent sclerite and related sclerites well developed. Penis rods long but uncoiled.

Comments: Significant characters in this species, as pointed out by Traub(1950) are the following: Presence of apical
appendage and proximal spur. Narrow dorsal extension of lateral laminae. Well developed lateral lobes that are independent of wall of aedeagal pouch and that extend to apex of median dorsal lobe. Conspicuous basal wall of aedeagal pouch arising at level of proximal spur. Very long crochets extending far distad of endchamber. Sclerotized inner tube with complicated armature and apex. A long sclerotized band of inner tube and extra-aedeagal semi-membranous tube present. Penis rods not coiled. Traub (1950) pointed out that the affinities with Ceratophyllus s. lat are obvious.

Taxa:

Subgenus (Dasypsyllus) Baker, 1905
gallinulæ gallinulæ (Dale, 1878)
gallinulæ klossi (Rothschild, 1919)
gallinulæ perpinnatus (Baker, 1904)

Subgenus (Avesopsylla) I. Fox & Anduze, 1947
lasius lasius (Rothschild, 1909)
lasius venezuelensis (I. Fox & Anduze, 1947)

Subgenus (Neornipsyllus) Smit, 1976
aemulus Jordan, 1933
araucanus (Jordan & Rothschild, 1920)
comatus Jordan, 1933
ctenopius (Jordan & Rothschild, 1920)
plumosissimus Smit, 1976
steinegeri (Jordan, 1929)

Genus Ceratophyllus Curtis, 1832
Figs. 28-33.

This genus is a very large group currently consisting of 62 named species and 17 subspecies. The hosts of the subgenus Ceratophyllus tend to nest in habitats that coincidentally are also frequented by mammals (for example, tree holes, burrows, rocks banks, etc.), and this presumably was a factor in the evolutionary transfer of the ancestral (Ceratophyllus) from mammals to birds (Traub et al, 1983). The species are overwhelmingly boreal in distribution. None have been described from the Oriental, Australian, Wallacian or Ethiopian Regions.

The following descriptions are based on specimens of C. (C.) farreni, C.(C.) gallinae, C. (C.) hirundinis, C. (A.) ciliatus , C.(E.) garei and C.(M.) sciurorum. Traub (1950) gave the aedeagal descriptions of C. (C.) riparius Jordan & Rothschild, 1920, which have been compared with dissections of the above-mentioned species.
**Ceratophyllum** (*Ceratophyllum*) farreni farreni
Rothschild, 1905

Aedeagal apodeme long and very narrow, 7X as long as broad at maximum width. Apodeme narrowed cephalad of base of fulcrum, forming a short neck. Dorsal extension of lateral laminae very short and narrow. Apical appendage long and coiled about 270 degrees over apodeme. Proximal spur not prominent. Dorsal spur present. Wall of aedeagal pouch arising far cephalad beyond alate lobe and beneath lateral lobes, parallel in position; ventral margin straight proximally, diverging, then fusing with lateral lobes. Median dorsal lobe bifid apically, apices close together (as compared to *C. hirundinis* where they are widely separated), long and almost flat or straight. Lateral lobes extending over sclerotized inner tube and fulcrum; caudal margin weakly sclerotized, somewhat convex; ventral margin convex. Crochets very long, 1.5X as long as endchamber; almost parallel in position to aedeagal apodeme; dorsal margin slightly convex; distal end produced into a long proximo-ventral projection with ventral margin concave; crochets proximally associated with somewhat filamentous, membranous structure. Sclerotized sheath of inner tube vertical and confined to endchamber; apex expanded, somewhat concave, with hooklike structures. Armature of inner tube very prominent; dorsal armature with
irregular ventral margin and hook-shaped proximal end. Ventral armature present as a thick band. Inner tube remarkable in being extended as a fistula; fistula short, not ringed but pigmented and extending ventrad. Fulcrum with club-shaped latero-ventral lobes which are not curved; dorsal median projection much shorter compared to others in the genus; medial lobe with an angulate distal end, somewhat spear-shaped. Crescent sclerite broad with prominently convex dorsal margin; satellite sclerite prominent; central sclerite very small, nearer to crescent sclerite. Penis rods very long, coiled proximally more than 360 degrees.

Comments: Endchamber and crochets covered with semimembranous and filamentous structure.

**Ceratophyllus** (*Ceratophyllus*) **gallinae**  
(Schrank, 1803)

Aedeagal apodeme long and narrow, region cephalad of fulcrum about 7X as long as broad at maximum width; apodeme somewhat consistent in shape except at proximal end where the ventral margin of the median lamina curves upwards. Dorsal extension of lateral laminae present, but very narrow. Apical appendage long and coiled about 270 degrees. Neck not apparent, covered by alate lobe and dorsal extension of lateral laminae. Dorsal spur prominent, triangular in shape.
Proximal spur present. Aedeagal pouch not obvious; wall of aedeagal pouch arising as far cephalad as proximal spur and not fused with lateral lobes but extending caudad, close to apex of sclerotized inner tube. Distal part of endchamber covered by a filamentous membrane. Median dorsal lobe bifid apically, apices fairly close to each other, that is, almost C-shaped but shorter than in Q. farreni. Apical sclerite of median dorsal lobe absent. Lateral lobes very obvious and large, posterior extending over neck, caudad to a third of aedeagal apodeme. Crochets very long and larger than endchamber, somewhat flask shaped, long and narrow apically, acuminate and slightly arched; paxillus elongated, near three-fourths proximo-ventrad angle of crochets. Sclerotized inner tube extending slightly from endchamber; fistula long and thin; apex expanded and concave; dorsal armature of inner tube reduced to a subapical, lobed expansion on cephalic portion; ventral armature prominent, thick and long. Fulcrum with latero-ventral lobes long and thin, not as curved as in Q. (Diamanus) montana; dorsal median projection long, broad at base but reduced to threadlike distal end; medial lobe just below central sclerite, almost subrectangular in shape. Crescent sclerite thick and well developed, dorsal margin truly convex; satellite sclerite thin and narrow; central sclerite well sclerotized with proximal end bulbous. Penis
rods coiled about 180 degrees.

**Ceratophyllus (Ceratophyllus) hirundinis** (Curtis, 1826)

Aedeagal apodeme long and narrow, region cephalad of base of fulcrum about 6X as long as broad at maximum width, more than 3X the distance from base of fulcrum to apex of median dorsal lobe. Dorsal extension of lateral laminae present but very narrow. Apical appendage very long. Neck not prominent, covered by alate lobe. Alate lobe extending to level of apodeme, covering one-fourth distal apodeme. Proximal spur present. Wall of aedeagal pouch not arising as far cephalad as proximal spur; ventral margin on each side proximally straight but recurved, not fused with lateral lobes. Median dorsal lobe bifid apically, apices widely separated; apical sclerite of median dorsal lobe absent. Lateral lobes large. Crochets very long, larger than endchamber; somewhat flask-shaped, long and narrow apically, acuminate and slightly arched, proximally expanded, with margins somewhat rounded. Sclerotized inner tube confined to endchamber; smaller than **C. (Amonopsyllus) ciliatus** and **C. (Emmareus) garei**; apex expanded and concave; fistula present, curving proximo-ventrad; dorsal armature of inner tube less lobed than that of **C. gallinae** and **C. farreni**; ventral armature prominent. Fulcrum with latero-
ventral lobes slightly curved; dorsal median projection long and broad, not threadlike; medial lobe well-developed, broad and cylindrical. Crescent sclerite with crescent long and well developed; satellite sclerite smaller; central sclerite thin. Penis rods very long and coiled proximally more than 360 degrees.

*Ceratophyllum (Amonopsyllus) ciliatus protinus*
*Jordan, 1929*

Aedeagal apodeme long and narrow, region of apodeme cephalad of fulcrum 9X as long as broad at maximum width; apodeme with dorsal margin very slightly convex overall, much broader proximally and narrowing toward fulcrum. Dorsal extension of lateral laminae reduced. Apical appendage short and curled. Neck very prominent, relatively long and narrow. Proximal spur not prominent. Alate lobe and dorsal spur absent. Aedeagal pouch similar to others; wall of aedeagal pouch fairly straight and joining lateral lobes at base. Median dorsal lobe bifid, margin well sclerotized; apical sclerite of median dorsal lobe absent. Lateral lobes prominent with straight margin. Crochets as in other species in the genus but more ventrad in position; large, with tongue-like projection curving ventrad; paxillus barrel-shaped, near proximo-ventral angle. Sclerotized inner tube extending out
of end chamber; fistula relatively long and prominent, curving ventrad; hook short. Band of inner tube present and broad. Dorsal armature of inner tube lobed, with two long, vertical projections dorsally; ventral armature long and broad. Fulcrum with latero-ventral lobes fairly long and narrow, apex slightly curved and bulbous; long, and well sclerotized dorsal median projection extending along median dorsal lobe; medial lobe weakly sclerotized and truncate. Crescent sclerite long with uneven shape, proximal region broader than caudal part; satellite sclerite short and broad, about one-fifth of crescent sclerite; central sclerite present. Penis rods uncoiled, thicker than in other species in the genus.

Ceratophyllus (Emmareus) garei Rothschild, 1902

Aedeagus with region of aedeagal apodeme cephalad of fulcrum about 7X as long as broad at maximum width. Dorsal extension of lateral laminae long and narrow, broad from one third proximal to proximal end; apex acuminate; median lamina slightly convex dorsally with ventral margin straight. Apical appendage relatively long and curled. True neck not apparent, covered by alate lobe. Alate lobe extends dorsally into a strong, convex margin, extending over fulcrum. Proximal spur long and very prominent, diverging below fulcrum and joining base of lateral lobes. Aedeagal pouch extends
from proximal spur, ventral margin straight. Median dorsal lobe bifid apically, relatively shorter than other species in the genus; apical sclerite of median dorsal lobe absent. Lateral lobes extending over sclerotized inner tube and fulcrum; margin convex. Crochets longer than endchamber, shape typical of the genus, with stout bulbous paxillus. Sclerotized inner tube extending slightly out of endchamber; fistula short; apex greatly expanded and lunar shaped; broader than C. (A) ciliatus. Dorsal armature of inner tube rugged, irregular shaped but shorter than C. (A) ciliatus; ventral armature broad and simple. Fulcrum with sclerites similar to others. Penis rods coiled about 270 degrees.

**Ceratophyllum (Monopsyllus) sciurorum sciurorum**  
(Schrank, 1803)

Aedeagus with region of aedeagal apodeme cephalad of fulcrum about 7X as long as broad at maximum width; apodeme broad throughout with ventral margin convex. Apical appendage long and curled. Neck not apparent, covered by alate lobe. Alate lobe broad and extending over neck. Dorsal spur present but smaller than in other species. Proximal spur absent. Aedeagal pouch as in other species in the genus; wall of aedeagal pouch not prominent. Median dorsal lobe bifid; apical sclerite of median dorsal lobe absent. Lateral lobes
large, broad, with convex ventral margin. Crochets more ventral in position, with tongue-like projection acuminate and shorter; ventral margin wavy; paxillus elongate and cylindrical in shape. Sclerotized inner tube with prominent fistula, projecting ventrad and diverging cephalad; apex broad, lunar-shaped with dorsal margin strongly concave; dorsal armature of inner tube narrow and irregularly shaped; ventral armature long and narrow. Fulcrum with latero-ventral lobes long and narrow, flat with curved apex; dorsal median projection prominent, long and thin but base broad; medial lobe arising at level of floor of capsule, short, flat and convex proximally. Crescent sclerite long and broad, with true crescent shape; satellite sclerite very small; central sclerite present; Penis rods thick and coiled one complete turn.

Comments: As pointed out by Traub (1950), important characters in this genus are: Development of apical appendage and proximal spur. Reduction of dorsal extension of lateral laminae. Fusion of the very well-developed lateral lobes with the latero-apical walls of the aedeagal pouch. Proximal origin of the lateral lobes. Median dorsal lobe apically bifid. Very large crochets that are longer than endchamber, apically curved and acuminate. Vertical sclerotized inner tube with apex expanded. Inner tube developed as a very long
semimembranous fistula. Absence of apical sclerite of median dorsal lobe, vesicle and apical sclerites of inner tube.

Taxa:

Subgenus *(Ceratophyllus)* Curtis, 1832

affinis affinis Nordberg, 1935
affinis neglectus Smit, 1958
altus Tipton & Mendez, 1966
arcuegens Holland, 1952
calderwoodi Holland, 1979
caliotes Jordan, 1937
celsus celsus Jordan, 1936
celsus apricus Jordan, 1939
chutsaensis Liu & WU, 1962
coaquilensis Eads, 1956
delichoni Nordberg, 1935
enefdei enefdei Ioff, 1950
enefdei tianschani Kunitskaya, 1968
farreni farreni Rothschild, 1905
farreni chaoi Smit & Allan, 1955
fringillae (Walker, 1856)
gallinae (Schrank, 1803)
gilvus Jordan & Rothschild, 1922
hirundinis (Curtis, 1926)
idius Jordan & Rothschild, 1920

lari Holland, 1951

maculatus Wagner, 1927

nanshanensis Tsai, Pan & Liu, 1980

niger C. Fox, 1908

olsufjevi Scalon & Violovich, 1961

orites Jordan, 1937

pelecani Augustson, 1942

petrochelidoni Wagner, 1936

phrillinae Smit, 1976

picatilis Cai & Wu, 1988

pullatus Jordan & Rothschild, 1920

ginghaiensis Zhang & Ma, 1985

rauschi Holland, 1960

rossittensis rossittensis Dampf, 1913

rossittensis swansoni Liu, 1935

rusticus Wagner, 1903

sclerapicalis Tsai, Wu & Liu, 1974

scopulorum Holland, 1952

sinicus Jordan, 1932

styx styx Rothschild, 1900

styx concinnus Scalon, 1977

styx freyi Nordberg, 1935

styx jordani Smit, 1955
styx riparius Jordan & Rothschild, 1920

titicacensis Smit, 1978

tribulis Jordan, 1926

vagabundus vagabundus (Boheman, 1866)
vagabundus alpestris Jordan, 1926
vagabundus insularis Rothschild, 1906

Subgenus (Amonopsyllus) Wagner, 1938

ciliatus ciliatus Baker, 1904

Subgenus (Celeophilus) Smit, 1983

adustus Jordan, 1932

zhovtyi Emel'yanova & Goncharov, 1966

Subgenus (Emmareus) Smit, 1983

borealis Rothschild, 1907

chasteli Beaucournu Monnat & Launay, 1982

columbae (Gervais, 1844)
diffinis Jordan, 1925

fionnus Usher, 1968

frigoris Darskaya, 1950

garei Rothschild, 1902

hayoromo Jameson & Sakaguti, 1959

igii Darskaya & Shiranovich, 1971
liae Wu & Li, 1990

spinosus Wagner, 1903

Subgenus (Monopsyllus) Kolenati, 1857

anisus Rothschild, 1907

argus Rothschild, 1908

fenqi (Liu, Xie & Wang, 1986)

forficus (Cai & Wu, 1987)

hamutus (Cai & Wu, 1987)

indages Rothschild, 1908

paradoxus Scalon, 1950

sciurorum sciurorum (Schrank, 1803)

sciurorum asiaticus Ioff, 1936

vison Baker, 1904

vamane (Sakaguti & Nakagawa, 1960)

Subgenus (Rosickiyana) Smit, 1972

lunatus lunatus Jordan & Rothschild, 1920

lunatus tundrensis Holland, 1945

Genus Aetheca Smit, 1983

Fig. 34.

This genus consists of two species, both of which are parasites primarily of deer mice of the genus Peromyscus of the Nearctic region.
Aetheca wagneri (Baker, 1904)

Aedeagus with portion of apodeme cephalad of fulcrum about 7X as long as broad at maximum width; apodeme with cephalic end slightly tilted upwards, dorsal margin convex and ventral margin slightly biconvex. Dorsal extension of lateral lamina prominent, long and narrow, almost reaching apex of sclerotized inner tube. Apical appendage long and coiled, slightly more than 360 degrees. Neck absent. Alate lobe long and broad. Proximal spur present. Dorsal spur absent. Aedeagal pouch short, extending just below neck; ventral margin arising from level of median lamina. Median dorsal lobe bifid; its apex prominent, well sclerotized and flared, curving ventrad; apical sclerite well developed. Lateral lobes well developed, extending over sclerotized inner tube and fulcrum; caudal margin convex; ventral margin also convex with proximal end slightly sinuate. Crochets with tongue-like projections, narrower than aedeagal apodeme at maximum width; crochets weakly sclerotized dorsally; paxillus short, somewhat bowl-shaped. Endchamber prominent with sclerotized structures very well developed. Sclerotized inner tube confined to endchamber; apex expanded; inner tube extended as fistula which extends ventrad and curves proximad; hook prominent. Dorsal armature of inner tube produced into lobe-like projections; ventral armature much broader and well
sclerotized. Fulcrum with latero-ventral lobes relatively short, base broad and apex narrower and slightly curved upwards; dorsal median projection short, narrow and truncate; medial lobe broad at base and narrowing to apex which is reduced to a long, sharp structure curving disto-ventrad. Crescent sclerite well developed, broad with cephalic end narrower than distal end; satellite sclerite prominent, also broad but smaller than crescent sclerite (half the length of crescent sclerite); central sclerite long and narrow. Penis rods coiled more than 360 degrees.

Taxa:

**thamba** (Jordan, 1929)

**wagneri** (Baker, 1904)

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**Genus Jellisonia** Traub, 1944

*Fig. 35.*

This genus consists of twelve species which are restricted to southern Texas through the montane regions of Mexico and Central America. They are mainly associates of *Peromyscus* species and related small rodents (Lewis, 1990).
**Jellisonia bullisi** (Augustson, 1944)

Aedeagus with region of aedeagal apodeme cephalad of fulcrum 6.7X as long as broad at maximum width; apodeme fairly long and narrow and almost uniform throughout, that is, the region cephalad of proximal spur subequal to region apicad of fulcrum. Dorsal extension of lateral laminae well developed, long and narrow. Apical appendage short. Neck absent. Alate lobe present. Proximal spur shorter than apical appendage. Aedeagal pouch extending from below proximal spur, proximal margin almost straight, ventral margin curving dorsad to below fulcrum. Median dorsal lobe short and apically bifid, apical sclerite of median dorsal lobe present. Lateral lobes well developed and large; caudal margin convex; ventral margin almost straight and meeting aedeagal pouch at proximo-ventral margin. Crochets large, extending far apicad of endchamber with apex rugged and micromucronate. Sclerotized inner tube short and vertical; apex extended with hooklike structure prominent; fistula long and thick. Armature of inner tube highly specialized; dorsal armature hooklike and directed proximally; ventral armature broad and prominent. Fulcrum with latero-ventral lobes curved, long and narrow with blunt apex; dorsal median projection present, short with a sharp apex; medial lobe with a sharp apex. Crescent sclerite curved and broad; satellite sclerite small and narrow; central
sclerite narrow. Penis rods long, thick and coiled less than a complete 360 degrees; dorsal penis rod much shorter than ventral rod.

Taxa:

*amadoi* Ponce, 1988  
*bonia* Traub & Johnson, 1952  
*bullisi* (Augustson, 1944)  
*dybasi* Traub, 1950  
*gravi* Hubbard, 1958  
*guerrerensis* Morales, 1990  
*hayesi hayesi* Traub, 1950  
*hayesi breviloba* Traub, 1950  
*ironsi* (Eads, 1947)  
*johnsonae* Tipton & Mendez, 1961  
*klotzi* Traub, 1944  
*mexicana* Ponce, 1988  
*wisemani* Eads, 1951

Genus *Eumolpianus* Smit, 1983  

Fig. 36.

This genus is composed of eight taxa, all of which are ectoparasites of small rodents in western North America.
**Eumolpianus eumolpi eumolpi** (Rothschild, 1905)

Aedeagal apodeme narrow, region cephalad of fulcrum about 7X as long as broad at maximum width, with a fairly straight proximal end. Dorsal extension of lateral laminae narrow at base and broadening midway distally, where it narrows again near apex; weakly sclerotized distally. Apical appendage present. Proximal spur relative long. Neck absent. Alate lobe absent. Wall of aedeagal pouch extending from below proximal spur to fulcrum. Median dorsal lobe with dorsal margin almost straight; apex rounded and well sclerotized; apical sclerite of median dorsal lobe present. Lateral lobes not that prominent, extending over sclerotized inner tube and fulcrum. Crochets large, weakly sclerotized, with short tongue-like dorsal projection and flap-like folded caudal margin; crochets lying oblique to aedeagus, not projecting apically beyond aedeagus; paxillus small, cylindrical or cup-shaped in shape. Sclerotized inner tube with apex slightly expanded; fistula present, extending downward and curving ventrad below base of fulcrum and then recurving caudad and dorsad; fistula long with hook present at base, partially sclerotized but ringed; apex slightly expanded; sclerotized inner tube slightly extending beyond endchamber. Dorsal armature of inner tube simple, not produced into a projection or lobe and reduced to a sclerotized band; ventral armature
long and narrow. Fulcrum with latero-ventral lobes broad at base, narrow and not strongly curved; dorsal median projection present, very narrow with lobed base; medial lobes broad, almost tear-shaped. Crescent sclerite large and prominent, almost triangular in shape, dorsal margin almost straight; satellite sclerite broad; central sclerite very narrow, not that prominent. Penis rods coiled less than 360 degrees.

Taxa:

**cyrturus** (Jordan, 1929)

**eumolpi eumolpi** (Rothschild, 1905)

**eumolpi americanus** (Hubbard, 1950)

**eutamiadis** (Augustson, 1942)

**fornacis** (Jordan, 1937)

**orarius** (Johnson, 1961)

**polumus** (Traub & Johnson, 1952)

**wallowensis** (Hubbard, 1950)

Genus **Megabothris** Jordan, 1933

Figs. 38-39.

There are 21 described taxa assigned to this Holarctic genus. They are ectoparasites primarily of microtine rodents, particularly voles. One species parasitises chipmunks, and
another is found on mustelids in boreal North America.

**Megabothris (Megabothris) calcarifer** (Wagner, 1913)

Aedeagal apodeme long and narrow, with region cephalad of fulcrum 9X as long as broad at maximum width; apodeme with straight proximal end. Lateral laminae prominent, strongly convex ventrally and flatten below proximal spur, extending into a thick dorsal extension of lateral laminae. Apical appendage relatively long, thick and curved at 180 degrees. Neck absent. Alate lobe present. Proximal spur present. Dorsal spur absent. Aedeagal pouch short, arising from level of proximal spur, extending from below proximal spur to below fulcrum. Median dorsal lobe short and straight; apical sclerite of median dorsal lobe weakly sclerotized. Lateral lobes prominent, extending over sclerotized inner tube and fulcrum. Crochets rectangular with caudal margin concave and ventral margin almost straight; paxillus weakly wrinkled, C-shaped, near proximo-ventral angle. Sclerotized inner tube very long with part of tube extending beyond endchamber; projecting portion of tube spiculose and filamentous; apex with well developed hook-like structures curving caudad; ventral and dorsal armature of inner tube simple. Fulcrum with latero-ventral lobes long and broad, slightly curved; medial lobes long and narrow; dorsal median projection long
and narrow. Crescent sclerite long and broad; satellite sclerite slightly thicker, almost triangular. Penis rods thick, ventral rod coiled 3/4X (270 degrees), dorsal penis rod coiled about 1/2X (180 degrees).

Comments: Different from other species in having tube extending beyond endchamber.

**Megabothris (Amegabothris) abantis**
(Rothschild, 1905)

Aedeagal apodeme long and narrow, with region cephalad of fulcrum about 6.5X as long as broad at maximum width; apodeme long and narrow. Dorsal extension of lateral laminae fairly long with acuminate apex. Apical appendage long and curled. Neck absent. Alate lobe present. Proximal spur long and thick, shorter than apical appendage. Basal wall of aedeagal pouch short and well sclerotized, arising at level of proximal spur; ventral margin slightly convex, diverging at a right angle dorsad where it meets lateral lobes. Median dorsal lobe short and simple with apical sclerite well developed. Lateral lobes prominent with strongly convex margin. Crochets with a short, dagger-shaped projection, directed ventrad; paxillus stout. Much of endchamber and crochets covered by large filamentous lobe. Sclerotized inner tube with short fistula; dorsal armature with sharp,
acuminate, cephalic projection; ventral armature long and broad. Fulcrum with latero-ventral lobes fairly long and narrow and slightly curved; dorsal median projection absent; medial lobes very broad and short, extending from base of fulcrum to base of fulcral latero-ventral lobes. Crescent sclerite very long and thin, length almost a third of aedeagus proper; satellite sclerite short and broad, dome-shaped; central sclerite long and thin; floor almost as long as crescent sclerite. Penis rods long and thick, coiled almost 360 degrees.

Taxa:

Subgenus *Megabothris* Jordan, 1933

*acercus* (Jordan, 1925)

*asio asio* (Baker, 1904)

*asio gregsoni* Holland, 1950

*asio megacolpus* (Jordan, 1929)

*beljaevi* (Emel'yanova, 1966)

*bispinosus* (Sychevskiy, 1960)

*calcarifer* (Wagner, 1913)

*sinensis* Dou & Ji, 1979

*sokolovi* (Gershkovich, 1953)

*walkeri* (Rothschild, 1902)
Subgenus *(Amegabothris)* Smit, 1983

*abantis* (Rothschild, 1905)

*clantoni* Hubbard, 1949

*groenlandicus* (Wahlgren, 1903)

*lucifer* (Rothschild, 1905)

*quirini* (Rothschild, 1905)

Subgenus *(Gebiella)* Smit, 1983

*advenarius advenarius* (Wagner, 1930)

*advenarius mantchuricus* Dou & Ji, 1979

*rectangulatus* (Wahlgren, 1903)

*turbidus* (Rothschild, 1909)

Subgenus *(Kueichen lipsylla)* Smit, 1983

*atrox* (Jordan, 1925)

*rhipisoides* Li & Wang, 1964

Genus *Plusaetis* Smit, 1983

Fig. 37.

This recently erected genus is composed of 14 taxa. They are parasites of small rodents from Arizona and New Mexico, through Central America to Colombia and Ecuador.
Plusaetis sibynus sibynus (Jordan, 1925)

Aedeagal apodeme cephalad of fulcrum 4X as long as broad at maximum width; aedeagal apodeme broadest at six-tenths proximal end. Dorsal extension of lateral laminae absent. Apical appendage long. Neck short and broad. Alate lobe extending to level of neck. Proximal spur present. Wall of aedeagal pouch weakly sclerotized, arising at base of proximal spur and extending to base of lateral lobes. Median dorsal lobe curved and acuminate; apical sclerite absent. Lateral lobes somewhat narrower, apical margin more sinuate, ventral margin convex. Crochets broad and subrectangular; paxillus near two-thirds proximo-ventral angle, more ventral in position. Sclerotized inner tube with apex flattened and expanded; thick, hook-like projection present; fistula present, extending far distad; dorsal armature of inner tube produced into acuminate projections; ventral armature prominent as a long and fairly thick band. Fulcrum with latero-ventral lobes very prominent, broad at base and narrowed apically with a blunt apex; dorsal median projection well sclerotized, short and narrow; medial lobe somewhat triangular in shape and almost vertical in position. Crescent sclerite narrow; satellite sclerite short but broader than crescent sclerite; central sclerite not prominent, more dorsal in position. Penis rods fairly long and thick, coiled more
than 360 degrees.

Taxa:

apollinaris (Jordan & Rothschild, 1921)
asetus (Traub, 1950)
azte
cus (Barrera, 1954)
dolens dolens (Jordan & Rothschild, 1914)
dolens quintanus (Jordan, 1931)
equatoris (Jordan, 1933)
mathesoni (Traub, 1950)
parus (Traub, 1950)
ponsi (Barrera, 1955)
sibynus sibynus (Jordan, 1925)
sibynus jordani (Barrera, 1955)
smithi (Johnson, 1954)
soberoni (Barrera, 1958)
vermiformis (Traub, 1950)

Genus Nosopsyllus Jordan, 1933
Figs. 40-45

This large genus consists of 74 currently recognized taxa. They are mainly native to the Palaearctic Region (except for one species from Sub-Saharan Africa). However, two
of them are of cosmopolitan distribution due to human transport. Four subgenera are presently recognized, two of them being monotypic.

**Nosopsyllus** (*Nosopsyllus*) *fasciatus* (Bosc, 1800)

The following description is based on Traub (1950):

Aedeagal apodeme about four times as long as broad at maximum width. Dorsal extension of lateral laminae prominent, fairly broad at base and covering dorsal margin of constricted area or neck. Portion of aedeagus distad of base of fulcrum less than half of length of apodeme. Median dorsal lobe short, acuminate. Apical sclerite of median dorsal lobe well developed. Lateral lobes convex, extending from fulcrum to apex of median dorsal lobe. Crochets large, relatively weakly sclerotized, especially dorsally; a short truncate dorsal lobe; paxillus near proximo-ventral angle. Basal wall of aedeagal pouch arising at level of base of proximal spur and near origin of ventral convexity of middle lamina and then extending to fulcrum. Proximal spur present. Armature of sclerotised sheath of inner tube specialized, consisting of two conspicuous lobular sclerotizations on cephalic margin. Apex of sclerotized inner tube subtruncate, expanded as much as lobes of sheath. Lateral sclerotizations of inner tube very long. Inner tube extended as a long narrow sclerotized
band which curves ventrad and cephalad to base of apodemal strut and then is further extended as a semimembranous extra-aedeagal tube which is recurved and continues caudad past base of crochets. Fulcrum with long curved latero-ventral lobes and a stouter, more dorsal, longer medial lobe. Two crescentric sclerites dorsad of fulcrum, the uppermost probably associated with armature of sclerotized sheath of inner tube, the lower the true crescent sclerite. Ventral intramural rod and dorsal intramural rod present. Penis rods coiled more than 360 degrees.

**Nosopsyllus (Nosopsyllus) londiniensis londiniensis** (Rothschild, 1903)

Aedeagal apodeme cephalad of base of fulcrum to base of apical appendage about 5X as long as broad at maximum width. Dorsal extension of lateral laminae not prominent, fairly broad at base and covering dorsal margin of neck region. Apical appendage long. Neck not apparent, covered by alate lobe. Alate lobe with ventral margin broadly convex and prominently serrated. Proximal spur present. Aedeagal pouch as in *N. (N) fasciatus*. Median dorsal lobe short and acuminate with apical sclerite well developed. Lateral lobes extending from fulcrum to apex of median dorsal lobe; caudal margin almost straight. Crochets large, relatively weakly
sclerotized, especially dorsally; a long truncate dorsal lobe; paxillus elongate, but shorter than that of N. (N) *fasciatus*, near proximo-ventral angle of crochets. Sclerotized inner tube with a long prominent fistula, extending straight ventrad and curving cephalad to below base of fulcrum. Dorsal armature of inner tube consisting of two lobular sclerotizations on cephalic margin, hook-shaped; lateral sclerotization of inner tube very long, thick dorsally and thinning ventrally. Fulcrum with latero-ventral lobes strongly curved, V-shaped; dorsal median projection short with a broad base; medial lobes stouter. Crescent sclerite prominent and thick; satellite sclerite long and thin; central sclerite also prominent. Penis rods fully coiled.

Comments: Dorsal extension of lateral laminae prominent; penis rods fully coiled; fistula very long and prominent. Median dorsal lobe short and acuminate with well developed apical sclerite.

*Nosopsyllus* (*Nosopsyllus*) *simla*  
*(Jordan & Rothschild, 1921)*

Aedeagal apodeme cephalad of fulcrum to base of apical appendage about 4.5X as long as broad at maximum width. Dorsal extension of lateral laminae fairly broad at base, prominent, with acuminate apex. Apical appendage present,
shorter than that of N. (N) fasciatus. Neck not apparent, covered by alate lobe. Alate lobe squarish in shape with ventral margin almost flattened. Proximal spur present. Aedeagal pouch extends from below proximal spur parallel to alate lobe, ventral margin straight, then angled upward caudally to below base of fulcrum. Median dorsal lobe short and acuminate with well developed apical sclerite. Lateral lobes extending from median dorsal lobe to fulcrum. Crochets relatively weakly sclerotized, very short, truncate; dorsal lobe curving ventrad; paxillus elongate, near proximo-ventral fourth of crochets. Sclerotized inner tube with fistula, long, thick and prominent, ear-like shaped, curving ventrad to below apex of fulcral latero-ventral lobes. Sclerotized inner tube confined to endchamber, with apex expanded but not as in N. londiniensis and N. fasciatus; lateral sclerotization of inner tube not as heavy as in N. londiniensis, with a broad, well sclerotized patch dorsally and a sharp well sclerotized but thin ventral end. Dorsal armature of inner tube produced into a broad, weakly sclerotized, flap-like lobe. Fulcrum with latero-ventral lobes not as strongly curved as in N. londiniensis; dorsal median projection not well sclerotized; medial lobes almost crescent-shaped, long and broad. Crescent sclerite long and thin, not as broad as in N. londiniensis; satellite sclerite a fairly thin stump, not prominent; central
sclerite also thin. Penis rods coiled more than once.

Comments: Aedeagus prominently covered by semimembranous structure.

**Nosopsyllus (Nosopsyllus) tamilanus**

(Jordan & Rothschild, 1921)

Aedeagal apodeme cephalad to base of fulcrum about 5.5X as long as broad at maximum width; apodeme with dorsal margin slightly convex and ventral margin fairly straight. Dorsal extension of lateral laminae long and prominent with acuminate apex, base not that broad. Apical appendage very long, much longer than that of *N. fasciatus*. Neck not apparent, covered by alate lobe. Alate lobe fairly broad with ventral margin equally convex. Proximal spur fairly long. Aedeagal pouch extends from below level of proximal spur, parallel with alate lobe. Median dorsal lobe short and acuminate (similar to other species in this genus); apical sclerite of median dorsal lobe well developed. Lateral lobes not apparent, extending over sclerotized inner tube and fulcrum. Crochets as in other species in this genus, weakly sclerotized dorsally; consisting of subtruncate lobes, hook recurved ventrad; paxillus elongate as in others. Sclerotized inner tube close to *N. fasciatus*, extending slightly from endchamber; lateral sclerotization of inner tube is a fairly thin strip; fistula as in *N. simla*. 
Fulcrum with latero-ventral lobes prominent and curved; dorsal median projection short, broad-based with acuminate apex; medial lobes broad, almost vertical in position. Crescent sclerite not that crescentric in shape; satellite sclerite small but prominent; central sclerite curved and narrow. Penis rods coiled 180 degrees.

**Nosopsyllus** (Gerbillophilus)*iranus theodori*
Smit, 1960

Aedeagal apodeme cephalad of base of fulcrum about 6.5X as long as broad at maximum width. Dorsal extension of lateral laminae prominent. Apical appendage fairly long and broad, spiral-like. Neck as in others, not apparent, covered by alate lobe. Alate lobe sharply convex disto-ventrally, crossing over neck. Proximal spur long. Wall of aedeagal pouch short and convex. Median dorsal lobe acuminate. Lateral lobes large, extending over sclerotized inner tube and fulcrum, caudal margin convex. Crochets large, covered by filamentous, membranous structure, with distal end acuminate and very much curved ventrally; paxillus elongate, near one-third proximo-ventral angle of crochets. Sclerotized inner tube with long fistula, curving ventrad and recurving proximad until below level of fulcral latero-ventral lobes; band of inner tube long, almost reaching level of fulcral latero-
ventral lobes; dorsal armature of inner tube as an acuminate projection. Fulcrum with lobes similar to others; dorsal median projection broad. Crescent sclerite very prominent, more dorsal in position; satellite sclerite thin, rod-like; central sclerite apparent, similar to crescent sclerite. Penis rods fully coiled, characteristic of Nosopsyllus.

**Nosopsyllus (Penicus) geneatus** Traub, 1963

Aedeagal apodeme cephalad of base of fulcrum about 5.5X as long as broad at maximum width; aedeagal apodeme long and narrow. Dorsal extension of lateral laminae broad and almost horizontal. Apical appendage very long and curled. Neck not apparent, covered by alate lobe. Alate lobe with ventral margin evenly convex, as in *N. (N) tamilanus*. Proximal spur relatively long. Aedeagal pouch extending from level of proximal spur, ventral margin convex. Median dorsal lobe short and acuminate, apical sclerite of median dorsal lobe present. Lateral lobes not prominent, extending over sclerotized inner tube and fulcrum, caudal margin convex. Crochets weakly sclerotized, tongue-like projection, much smaller, pointing distad, paxillus cylindrical near proximo-ventral. Sclerotized inner tube with fistula extending out of endchamber; band of inner tube present; dorsal armature of inner tube different from subgenus Gerbillophilus except
knobbed/lobed cephalic end. Fulcrum with latero-ventral lobes slightly curved, short and narrow and base much broader; dorsal median projection with broad base and acuminate apex; medial lobe more ventrad in position, broad with acuminate apex. Penis rods very much coiled, that is coiled more than once.

Comment: This species is somewhat close to N. (N.) tamilyanus.

Taxa:

Subgenus (Nosopsyllus) Jordan, 1933

aegaeus Peus, 1978
alladinis (Rothschild, 1904)
arctus (Jordan & Rothschild, 1921)
argutus (Jordan & Rothschild, 1921)
atlantis Jordan, 1937
barbarus (Jordan & Rothschild, 1912)
ceylonensis Smit, 1953
chayuensis Wang & Liu, 1981
consimilis (Wagner, 1898)
durii Hubbard, 1956
elongatus elongatus Li & Shen, 1963
elongatus longchuanensis Li, Xie & Wu, 1990
elongatus puerensis Li, Xie & Yu, 1990
*Elongatus* yanshanensis Li, Xie & Luo, 1990

*Farahae* Farhang-Azad, 1973

*Fasciatus* (Bosc, 1800)

*Fidus* (Jordan & Rothschild, 1915)

*Incisus* (Jordan & Rothschild, 1913)

*Londiniensis londiniensis* (Rothschild, 1903)

*Londiniensis declivus* Traub, 1963

*Medus* Jordan, 1938

*Mikulini* (Kunitskaya & Kunitskaya, 1961)

*Mokrzeckyi* (Wagner, 1916)

*Nicanus* Jordan, 1937

*Nilgiriensis* (Jordan & Rothschild, 1921)

*Philippovi philippovi* (Zagniborodova & Mikulin, 1957)

*Philippovi rashtii* Farhang-Azad, 1970

*Punensis* (Jordan & Rothschild, 1921)

*Punjabensis* (Jordan & Rothschild, 1921)

*Sarinus sarinus* (Jordan & Rothschild, 1921)

*Sarinus aryanus* Smit, 1960

*Sarinus parthius* Smit, 1960

*Simla* (Jordan & Rothschild, 1921)

*Sincerus* (Jordan & Rothschild, 1921)

*Tamilanus* (Jordan & Rothschild, 1921)

*Vauceli* Klein, 1963

*Wualis wualis* Jordan, 1941
wualis boseensis Li & Pan, 1990
wualis diadongensis Li, Xie & Yang, 1990
wualis leizhouensis Li, Huang & Liu, 1986
wualis rongjiangensis Li & Huang, 1990

Subgenus (Gerbillophilus) Wagner, 1934

abramovi (Ioff, 1946)
afghanus Peus, 1957
apicoprominus Tsai, Wu & Liu, 1974
aralis aralis (Argyropulo, 1946)
aralis tschu (Shiranovich, 1946)
baltazardi Farhang-Azad, 1970
bunnii Hubbard, 1956
eremicus Lewis, 1973
garamanticus Beaucournu & Launay, 1988
henlevi henlevi (Rothschild, 1904)
henlevi israelicus Smit, 1960
henlevi mauritanicus (Jordan & Rothschild, 1912)
iranus iranus Wagner & Argyropulo, 1934
iranus attenuatus Smit, 1960
iranus theodori Smit, 1960
laeviceps laeviceps (Wagner, 1909)
laeviceps acer (Mikulin, 1957)
laeviceps consors (Rothschild, 1913)
laeviceps ellobii (Wagner, 1933)
laeviceps kuzenkovi (Yagubians, 1953)
maurus maurus (Jordan & Rothschild, 1912)
maurus angustus Beaucournu & Launay, 1988
monstrosus (Wagner, 1928)
oranus (Jordan, 1931)
pringlei Hubbard, 1956
pumilionis Smit, 1960
tersus (Jordan & Rothschild, 1915)
turkmenicus turkmenicus (Vlasov & Ioff, 1937)
turkmenicus altisetus (Ioff, 1950)
vlasovi (Ioff, 1937)
ziarus Klein, 1963

Subgenus (Nosinius) Smit, 1960

sinaiensis Smit, 1960

Subgenus (Penicus) Traub, 1963

geneatus Traub, 1963
Illustrations

Abbreviations Used in the Figures

aea: aedeagal apodeme
aep: aedeagal pouch
ait: armature of sclerotized inner tube
allo: alate lobes of aedeagal apodeme
amdl: apical sclerite of median dorsal lobe
apapp: apical appendage (of median lamina)
apsit: apex of sclerotized inner tube
bit: band of inner tube
censc: central sclerite
csc: crescent sclerite
cr: crochet
dar: dorsal armature (of sclerotized inner tube)
dexlam: dorsal extension of lateral lamina
dll: disto-lateral lobes
ds: dorsal spur
ec: endchamber
Fsc: Ford's sclerite
fis: fistula
ful: fulcrum
fulb: fulcral brim
fuldmp: fulcral dorsal median projection
fulll: fulcral latero-ventral lobes
fulml: fulcral medial lobes
llam: lateral lamina
latl: lateral lobes
lit: lateral sclerotization of inner tube
mdl: median dorsal lobe
mlam: median lamina
nk: neck
pax: paxillus
pr: penis rods
dpr: dorsal penis rod
vpr: ventral penis rod
ps: proximal spur
pvllam: proximo-ventral projection of lateral laminae
satsc: satellite sclerite
sit: sclerotized inner tube
var: ventral armature (of sclerotized inner tube)
Fig. 2:  *Smitipsylla maseri* Lewis, 1971
Lateral view of the aedeagus. Scale line = 0.05mm

Fig. 3:  *Paraceras melis* (Walker, 1856)
Lateral view of the aedeagus. Scale line = 0.05mm
Fig. 4: **Aenigmopsylla grodekovi** Sychevsky, 1950
Lateral view of the aedeagus. Scale line = 0.05mm

Fig. 5: **Amphalius runatus** (Jordan & Rothschild, 1923)
Lateral view of the aedeagus. Scale line = 0.05mm
Fig. 6: \textbf{Glaciopsyllus antarcticus} Smit & Dunnet, 1962
Lateral view of the aedeagus. Scale line = 0.05mm

Fig. 7: \textbf{Macrostylophora hastata} (Jordan & Rothschild, 1921)
Lateral view of the aedeagus. Scale line = 0.05mm
Fig. 8: *Tarsopsylla octodecimdentata coloradensis* (Baker, 1895)

Lateral view of the aedeagus. Scale line = 0.05mm

Fig. 9: *Myoxopsylla (Myoxopsylla) laverani* (Rothschild, 1911)

Lateral view of the aedeagus. Scale line = 0.05mm
Fig. 10: *Orchopeas leucopus* (Baker, 1904)
Lateral view of the aedeagus. Scale line = 0.025mm

Fig. 11: *Opisodasys (Opisodasys) pseudarctomys* (Baker, 1904)
Lateral view of the aedeagus. Scale line = 0.05mm
Fig. 12: *Opisodasys (Oxypsylla) keeni* (Baker, 1896)
Lateral view of the aedeagus. Scale line = 0.05mm

Fig. 13: *Foxella (Foxella) ignota* (Baker, 1895)
Lateral view of the aedeagus. Scale line = 0.05mm
Fig. 14: *Oropsylla (Oropsylla) arctomys* (Baker, 1904)  
Lateral view of the aedeagus. Scale line = 0.05mm

Fig. 15: *Oropsylla (Opisocrostis) tuberculata* (Baker, 1904)  
Lateral view of the aedeagus. Scale line = 0.05mm
Fig. 16: **Oropsylla (Hubbardipsylla) oregonensis** (Good & Prince, 1939)

Lateral view of the aedeagus. Scale line = 0.05mm

Fig. 17: **Oropsylla (Diamanus) montana** (Baker, 1895)

Lateral view of the aedeagus. Scale line = 0.05mm
Fig. 18: *Oropylla (Opisocrostis) bruneri* (Baker, 1895)
Lateral view of the aedeagus. Scale line = 0.05mm

Fig. 19: *Thrassis acamantis* (Rothschild, 1905)
Lateral view of the aedeagus. Scale line = 0.05mm
Fig. 20: *Thrassis francisi* (C. Fox, 1927)
Lateral view of the aedeagus. Scale line = 0.05mm

Fig. 21: *Citellophilus sungarica* (Jordan, 1929)
Lateral view of the aedeagus. Scale line = 0.05mm
Fig. 22: *Callopsylla (Callopsylla) caspia* (Ioff & Argyropulo, 1934)
Lateral view of the aedeagus. Scale line = 0.05mm

Fig. 23: *Callopsylla (Ornaecus) waterstoni* (Jordan, 1935)
Lateral view of the aedeagus. Scale line = 0.05mm
Fig. 24: **Malaraeus sinomus** (Jordan, 1935)

Lateral view of the aedeagus. Scale line = 0.05mm

Fig. 25: **Amalaraeus dissimilis** (Jordan, 1938)

Lateral view of the aedeagus. Scale line = 0.05mm
Fig. 26: *Amaradix bitterrootensis* (Dunn, 1923)
Lateral view of the aedeagus. Scale line = 0.05mm

Fig. 27: *Dasypsyllus (Dasypsyllus) gallinulae* (Dale, 1878)
Lateral view of the aedeagus. Scale line = 0.05mm
Fig. 28: *Ceratophyllus (Ceratophyllus) farreni* Rothschild, 1905

Lateral view of the aedeagus. Scale line = 0.05mm

Fig. 29: *Ceratophyllus (Ceratophyllus) gallinae* (Schrank, 1803)

Lateral view of the aedeagus. Scale line = 0.05mm
Fig. 30: *Ceratophyllus* (*Ceratophyllus*) *hirundinis*  
(Curtis, 1826)  
Lateral view of the aedeagus. Scale line = 0.05mm

Fig. 31: *Ceratophyllus* (*Amonopsyllus*) *ciliatus protinus*  
Jordan, 1929  
Lateral view of the aedeagus. Scale line = 0.05mm
Fig. 32: *Ceratophyllus* (*Emmareus*) *garei* Rothschild, 1902
Lateral view of the aedeagus. Scale line = 0.05mm

Fig. 33: *Ceratophyllus* (*Monopsyllus*) *sciurorum*
(Schrank, 1803)
Lateral view of the aedeagus. Scale line = 0.05mm
Fig. 34: *Aetheca wagneri* (Baker, 1904)
Lateral view of the aedeagus. Scale line = 0.05mm

Fig. 35: *Jellisonia bullisi* (Augustson, 1944)
Lateral view of the aedeagus. Scale line = 0.05mm
Fig. 36: *Eumolpianus eumolpi* (Rothschild, 1905)
Lateral view of the aedeagus. Scale line = 0.05mm

Fig. 37: *Plusaetis sibynus* (Jordan, 1925)
Lateral view of the aedeagus. Scale line = 0.025mm
Fig. 38: *Megabothris (Megabothris) calcarifer* (Wagner, 1913)

Lateral view of the aedeagus. Scale line = 0.05mm

Fig. 39: *Megabothris (Ameqabothris) abantis* (Rothschild, 1905)

Lateral view of the aedeagus. Scale line = 0.05mm
Fig. 40: **Nosopsyllus (Gerbillophilus) iranus theodori**
*Smit, 1960*

Lateral view of the aedeagus. Scale line = 0.05mm

Fig. 41: **Nosopsyllus (Nosopsyllus) fasciatus** (Bosc, 1800)

Lateral view of the aedeagus. Scale line = 0.05mm
Fig. 42: *Nosopsyllus (Nosopsyllus) simla* (Jordan & Rothschild, 1921)
Lateral view of the aedeagus. Scale line = 0.05mm

Fig. 43: *Nosopsyllus (Nosopsyllus) tamlanu* (Jordan & Rothschild, 1921)
Lateral view of the aedeagus. Scale line = 0.05mm
Fig. 44: *Nosopsyllus (Penicus) geneatus* Traub, 1963

Lateral view of the aedeagus. Scale line = 0.05mm

Fig. 45: *Nosopsyllus (Nosopsyllus) londiniensis* (Rothschild, 1903)

Lateral view of the aedeagus. Scale line = 0.05mm
DISCUSSION

The Aedeagus as a Taxonomic Aid in Classification.

The weighting of genital characters in classification has been discussed by Mardon (1978). Differences in opinion regarding the practicability of using genitalia as a taxonomic aid still persist among systematists. The genitalia are not preferred by many systematists for use at the generic level, either because features that apply to both sexes are preferable or because of the opinion that the genitalia are of value only in determining species (Traub, 1980). In the case of the Ceratophyllidae, results of the present study show that recognition and classification of various genera is possible by studying the characters of the aedeagi. The ceratophyllid aedeagus is obviously a specialized and variable apparatus as compared to the remarkably uniform non-genitalic structure of the ceratophyllid fleas. Without consideration of the structure of the aedeagus, it has been difficult to establish a hierarchical classification for this family. The diversity of the ceratophyllid aedeagus makes it a useful character to separate members of the Ceratophyllidae and makes possible a further classification of the family. Therefore, in the case of the Ceratophyllidae, the aedeagus serves as an indispensable taxonomic aid. However, it is well to remember
that a classification system based solely on one sex is limited in the sense that assignment of the opposite sex is not possible employing the same system.

Character Analysis and Outline of the Inferred Relationships of the Ceratophyllidae.

The ceratophyllid aedeagi are variable and quite reliably characteristic of each taxon. The following aedeagal characters have been observed to occur within the Ceratophyllidae: The neck is either present (Aenigmopsylla, Paraceras, Myoxopsylla, Oropsylla, Thrassis, Foxella, Plusaetis, Malaraeus and some Ceratophyllus) or absent. The proximal spur is present (except in Tarsopsylla, Myoxopsylla, some Opisodasy and Macrostylophora). The apical appendage is present (except in Smitipsylla, Myoxopsylla, Orchopeas and Thrassis). The alate lobe is present (except in Myoxopsylla, Eumolpianus and Amalaraeus). The median dorsal lobe is often single and simple but at times, bifid (as in Citellophilus, Callopsylla, Malaraeus, Amaradix, Amalaraeus, Dasypyllus, Ceratophyllus, Aetheca and Jellisonia). The endchamber is totally covered by the large lateral lobes which are usually convex from near pouch wall to near apex of median dorsal lobe (except in Smitipsylla, Aenigmopsylla, and Orchopeas). The crochets are large and well developed (except in Smitipsylla,
Paraceras, Aenigmopsylla and Amphalius) and parallel to the aedeagal apodeme in position (except in Smitipsylla, Paraceras and Eumolpianus). The sclerotized inner tube is short and usually vertical with complex armature. A fistula is almost always present (except in Smitipsylla, Myoxopsylla, Oropsylla, Thrassis and Foxella) and this can vary considerably in structure, thickness and length. The paxillus is always present (except in Paraceras where it is totally absent and almost so in Jellisonia).

Based on this comparative study of the aedeagal structure in the Ceratophyllidae, a systematic arrangement of the family is suggested here, as shown in Table 3. This family can be divided into four subfamilies: 1. Tarsopsyllinae, 2. Oropsyllinae, 3. Dactylopsyllinae, 4. Ceratophyllinae. The Ceratophyllinae can be further divided into two tribes, the Ceratophyllini and the Nosopsyllini.

As far as character evolution within the family is concerned, at this point, it is difficult to ascertain the primitive or derived state of all the characters studied. This is due to the fact that a detailed comparative knowledge of the phallosome or of the aedeagus, in particular, in all the siphonapteran families is not available. Comparative knowledge of the aedeagus of all the siphonapteran families is necessary in order to trace the pattern of the characters,
being either widely distributed, reduced, lost or derived within the order. Without observing these trends, it is impossible to trace character evolution within a group. However, certain speculations can be made on the basis of the following points: Traub & Rothschild (1983) speculated that the Ceratophyllidae is the most advanced, recently evolved and highly developed group in the Siphonaptera on the basis of historical biogeographic and host data. Besides that, on the basis of the genitalic features, the Ceratophyllidae lack many primitive genitalic features as seen in the more ancient families (Traub & Rothschild, 1983).

In the classification system proposed here, subfamily rank is assigned because of the distinct structural dissimilarities between groups within the family.

Aedeagal characters involved in the discussion are shown in Table 2. For the discussion of the inferred relationships of the Ceratophyllidae, the reader is referred to the dendrogram showing the relationships within the Ceratophyllidae (Fig. 46), and the proposed suprageneric classification of the twenty-six genera of the Ceratophyllidae studied (Table 3). The dendrogram was created using MacClade, Version 3 (Maddison & Maddison, 1992). However, cladistic analysis of the group using MacClade, Version 3, could not be done at this point in the study.
Table 2. The aedeagal characters used in the inferred relationships of the Ceratophyllidae

<table>
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<th>Genus</th>
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<td>Crochet position. Oblique or vertical (A) or more or less horizontal or parallel with the aedeagal apodeme (B).</td>
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<td>Apex of sclerotized inner tube. Expanded (A) or not expanded (B).</td>
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Table 2 (continued)

(15) Armature of sclerotized inner tube. Simple (S) or complex (C).

(16) Fistula. Present (+) or absent (-).

(17) Fulcral dorsal median projection. Present (+) or absent (-).

(18) Fulcral brim. Present (+) or absent (-).

(19) Lateral lobes. Large and extending entirely over the endchamber (A) or reduced and not totally covering the endchamber (B).

(20) The degree of coiling of the penis rods. <1/4-<1/2 coil (A); 1/2-1 coil (B); 1 coil (C); 1-2 coils (D) or 1/2-1-2-3 coils (E).

(21) Paxillus. Present (A), very much reduced (B) or totally absent (C).
Fig. 46: The inferred relationships of the Ceratophyllidae
Table 3. Proposed suprageneric classification of twenty-six of the forty-four genera in the Ceratophyllidae

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1. Tarsopsyllinae

The tarsopsylline genera are united by the presence of a short, simple median dorsal lobe that has an angled apex. Its apical sclerite is well sclerotized and especially well developed in *Myoxopsylla*, where it is long and projects ventrally. Apart from that, the aedeagal apodeme is usually narrow and slender and curves upward, toward the anterior. The crochets are large and well developed, with the apical part projecting posteriorly. This projection can be sharp and with or without "toothed structure". Most of the genera in this subfamily have penis rods that are coiled less than 360 degrees, that is, between one half and one complete coil.

On the basis of the gross modification of the aedeagus, the members of this subfamily do not seem to have close affinities. However, they can be united on the basis of the aedeagal characters mentioned above, since they do not deviate much from each other in these characters. An interesting point to note here is that there is great diversity in the aedeagal structure of *Opisodasys*. This was also noted by Ioff (1936), who pointed out that such diversity could cause one to doubt that all the species assigned here belong to the same genus. However, the placement of these taxa in separate subgenera, as they are presently, is satisfactory to accommodate this diversity. This subfamily is here considered
as more primitive, when compared to the Oropsyllinae, based on the structure of the penis rods. Coiled penis rods are a common phenomenon in the Ceratophyllidae. As Traub & Rothschild (1983) noted, this is rarely so in the more primitive siphonapteran families. It is speculated here that the more coiled the penis rods are, the more advanced the group is. Coiled penis rods are commonly observed in the Ceratophyllinae.

2. Oropsyllinae

This subfamily contains the genera Oropsylla and Thrassis. It is characterized by the distinctive shape and position of the crochets, which are fairly large, each with a tongue-like projection pointing posteriorly. The projections vary much intragenerically. The crochets are mesad to the endchamber in position. Apart from that, they also have well developed lateral lobes that extend ventrad from the endchamber. However, they are variable in shape, either extending as sharp, ventral projections or simply as broad lobes extending ventrad. Additional distinctive characters that are shared among members of this group are the absence of a fistula and the presence of a neck. However, the evolutionary status of the combination of the absence and presence of the fistula and the neck among the Ceratophyllidae is difficult to determine at this point. This group is
entirely Nearctic in range, except for two species of *Oropsylla* known from Central Asia and central Turkey. The Tarsopsyllinae also has members that are Nearctic in distribution, while some of them are Palaearctic.

3. **Dactylopsyllinae**

*Foxella* is traditionally placed in this subfamily together with *Dactylopsylla* and *Spicata*. Specimens of these two genera were not available for this study. However, based on Smit's (1983) illustrations of *Dactylopsylla* and *Spicata*, it is observed that the aedeagi of both genera are similar to that of *Foxella* in that the endchamber is dorsally expanded and the sclerotized inner tube lacks a fistula. Based on this, *Dactylopsylla* and *Spicata* are placed here, together with *Foxella*.

Members of this subfamily are obviously closest to the Oropsyllinae, especially in the shape of the crochets and in the absence of the fistula. However, they also deviate enough to clearly emphasize their distinctness and are placed in a subfamily of their own. A distinctive character that separates them from the Oropsyllinae, and also from the other members of the family, is the dorsally expanded endchamber. The endchamber is not expanded in the other subfamilies. Ioff (1936) noted that, on the basis of many characteristics, especially non-genitalic, the Dactylopsyllinae show their
origin from the same root as the Oropsyllinae. However, in view of a number of other characteristics, he considered it unfeasible to combine Foxella with the Oropsylline fleas. The affinities between the Oropsyllinae and the Dactylopsyllinae may also be seen from the similar geographical distribution that they share. Both subfamilies are distributed mainly in the Nearctic Region.

4. Ceratophyllinae:

Of all the taxa in the Ceratophyllidae, this group is here considered as the most difficult group to separate. It consists of various types of fleas. However, although the structure of the aedeagi is variable, they do not seem to deviate from the general body plan of a typical "ceratophyllloid" aedeagus when compared to members of the first three subfamilies. Members of this group can be characterized by aedeagal characters that are also characteristic of the family Ceratophyllidae. This subfamily is here considered to be the most advanced group in the family. From the comparison among members of this subfamily and the remainder of the ceratophyllid genera, it appears that members of this group show more diversity in aedeagal structure and are grouped in this subfamily on the basis of a combination of the following aedeagal characters: The proximal spur and the apical appendage are always present.
The lateral lobes are large and extend over the endchamber. The sclerotized inner tube is short and vertical, mostly with complex armature. A tanned fistula is always present. Traub & Rothschild (1983) presumed the function of the fistula as serving to reinforced and guide the penis rods. The median dorsal lobe is either simple or bifid. The penis rods are coiled, and the coiling can reach up to three times a full coil as in *Nosopsyllus*.

The Ceratophyllinae is further divisible into subgroups that are designated here as the tribes Ceratophyllini and the Nosopsyllini. They differ principally on the nature of the median dorsal lobe.

4(i) Ceratophyllini

This tribe, which consists of *Citellophilus, Callopsylla, Malaraeus, Amalaraeus, Amaradix, Dasypsyllus, Ceratophyllus, Aetheca* and *Jellisonia*, exhibits a bifid median dorsal lobe. A bifid median dorsal lobe can be interpreted as a derived state in the Ceratophyllidae. The armature of the sclerotized inner tube is complex except in *Jellisonia*, where it is simple.

Within this group, it is observed that *Citellophilus* and *Callopsylla* are more closely related to each other and distinct from the rest of the Ceratophyllini in some characteristics of the aedeagus. The aedeagal apodemes are
fundamentally similar, narrowing immediately before the fulcrum and broadening anteriorly. Another important character that these two genera share is a fairly large aedeagal pouch when compared to the smaller ones in the remaining genera.

On the basis of the presence of a neck, *Malaraeus* is closer to the Oropsyllinae than the rest of the ceratophylline genera. *Amalaraeus* is here considered as close to *Amaradix* based on the large, well developed crochets and lateral lobes which are also well developed, with the ventral part of the lobes expanding ventrad beyond the endchamber. However, based on the presence of the Ford's sclerite, *Amalaraeus* is here considered as a less advanced group. The aedeagi of *Amaradix* and *Dasysyllus* share a similar, well sclerotized median dorsal lobe and its well developed apical sclerite. *Dasysyllus* can be further related to *Ceratophyllus*. The affinity between the aedeagi of *Dasysyllus* and *Ceratophyllus* lies in the well developed crochets, which are normally parallel in position with the aedeagal apodeme. In both genera, the aedeagus proper is much narrower when compared to that of the other genera. *Aetheca* shows some affinities with *Jellisonia* in having a fundamentally similar form of the sclerotized inner tube and lateral lobes, which extend ventrad of the endchamber beyond the levels of the penis rods.
4(ii) Nosopsyllini.

The median dorsal lobe of the members of the Nosopsyllini is not bifid. However, although simple, it can be variously modified.

In the classification scheme presented here, four genera are placed in the Nosopsyllini. These are Eumolpianus, Megabothris, Plusaetis and Nosopsyllus. The aedeagus of Eumolpianus approaches that of Megabothris in having a simple armature of the sclerotized inner tube. Megabothris can be further considered to be related to Plusaetis due to the absence of the apical sclerite of the median dorsal lobe. The similarity of the aedeagus in Plusaetis and Nosopsyllus, however, lies in the similarity of the median dorsal lobe which, is acuminate, and the fully coiled penis rods.

The species in the genus Nosopsyllus are considered here to be the most specialized in the Ceratophyllidae. They can be readily recognized by the fully coiled penis rods, the rounded aedeagus proper, a fairly long and prominent fistula and the large bulbous crochets, which, although variable and reliably species-specific, still share the common morphology which can be simply referred to as the "nosopsylloid" type of crochets.

The geographic and host distributions of the Ceratophyllidae have been extensively treated by Haddow et al
The Ceratophyllinae are mainly Nearctic, with the exception of the following: *Ceratophyllus* is boreal in distribution while *Citellophilus*, *Callopsylla* and *Nosopsyllus* are Palaearctic. *Amalaraeus* has a Holarctic distribution similar to *Megabothris* and some *Dasypsyllus*. The remaining *Dasypsyllus* are distributed in the Neotropical and Oriental regions.

As far as geographical distribution is concerned, the more advanced members of the Ceratophyllidae, as suggested here, are widely distributed in the Northern Hemisphere and poorly represented in the Southern Hemisphere.

5. *insertae sedis*

This group consists of six genera: *Smitipsylla*, *Paraceras*, *Aenigmopsylla*, *Amphalius*, *Glaciopsyllus* and *Macrostylophora*. The relationships among these genera are not clear. However, they are grouped together in this systematic arrangement based on the fact that they do not possess clear resemblances with the remaining ceratophyllid genera. In this group, some of the aedeagal structures deviate to a great degree from the basic ceratophyllid aedeagus. Members of this heterogeneous group could be either closely related to the family sister group, the Leptopsyllidae or they could be specialized and deviant to such an extent that it is not easy to uncover its relationships with the rest of the genera in
the family. As far as geographical distribution is concerned, members of this group are variously distributed as explained in the section on the descriptions of the genera.

*Smitipsylla* is definitely a member of the Ceratophyllidae. However, its aedeagus is of the type found in the Leptopsyllidae, a more primitive family with close ties to the Ceratophyllidae. Among the distinctive characters of the aedeagus in *Smitipsylla* is the presence of the disto-lateral lobes, which is unique in the Ceratophyllidae. The median dorsal lobe is long, simple and convex with the apex lobed and rounded. The apical median dorsal lobe is absent. The lateral lobes are well defined but reduced and not totally covering the endchamber. The crochets are very much reduced with an oblique orientation, that is, lying alongside the caudo-ventral margin of the aedeagus, as opposed to the position of the crochets of the remaining ceratophyllid genera, which is normally parallel to the aedeagal apodeme. The aedeagal apodeme projects almost at 45 degrees to the aedeagus proper.

The presence of the disto-lateral lobes is unique in the Ceratophyllidae. These lobes are absent in the rest of the ceratophyllids examined during this study, except in *Oropsylla (Diamanus) montana*. However, in *O. (D) montana*, they are not as well developed as in *Smitipsylla*. Rothschild & Traub
(1971) defined the disto-lateral lobes as especially well developed in the Leptopsyllidae. With this information, the loss of the disto-lateral lobes in the Ceratophyllidae could be hypothesized as a derived state, and therefore the presence of the disto-lateral lobe in Smîtîpsylla could be considered as primitive, being widely-distributed in the Leptopsyllidae. Another character that Smîtîpsylla is likely to have shared with the leptopsyllids is the presence of Ford's sclerite. However, the presence of this character in the specimens studied is not easily demonstrated. The sclerite discussed here is considered to be Ford's sclerite because it does not fit the definition of the apical sclerite of the median dorsal lobe (Rothschild & Traub, 1971). Ford's sclerite is considered to be well-developed in the more primitive families, such as the Leptopsyllidae and the Pygiopsyllidae. On this basis, it can be hypothesized that Ford's sclerite may have been lost in the evolution of the Ceratophyllidae. It is likely that the reduction or absence of this structure in the Ceratophyllidae is a derived rather than an ancestral state.

Based on the presence of the disto-lateral lobes and Ford's sclerite, it is assumed that Smîtîpsylla is a close relative of the Leptopsyllidae. However, having those aedeagal characters shared between a leptopsyllid and a ceratophyllid, besides being a primitive ceratophyllid,
Smitipsylla can also be interpreted as a transitional form or intermediate genus that links the Leptopsyllidae to the Ceratophyllidae.

Two other genera with the aedeagi very distinct from other members of the Ceratophyllidae are Paraceras and Amphalius. Paraceras has an aedeagus that differs to a great degree from the basic plan of the ceratophylloid aedeagus. The distinctness and complexities of the aedeagus of Paraceras pose problems of interpretation. Paraceras is unique and distinct from the remaining ceratophyllids in the following: The median dorsal lobe is fairly long and slightly concave with the apex as a fingerlike projection flanked by the Ford's sclerite. The aedeagus proper is fundamentally rectangular and oblique in position with very much reduced crochets that lie alongside the caudal margin of the aedeagus. It is also distinct from the remaining ceratophyllids in the absence of the paxillus that is evidently present and well developed in all the ceratophyllid genera, except being very much reduced in Jellisonia. The neck region is exceptionally long and very much constricted when compared to the other genera. The sclerotized inner tube is long with well defined armlike armature. The girdle is strongly sclerotized, whereas in the remaining ceratophyllid genera, this is not apparent. The apodeme is very much different from that of other
ceratophyllids, being very much constricted near the base of
the fulcrum and subequally broad toward the posterior.
Another unique character among the ceratophyllid aedeagi is
the structure of the lateral laminae which have prominent
proximo-ventral flap-like projections. In addition, the
apical appendage is fairly thick and well sclerotized.

The reduction of the crochets and the absence of the
paxillus suggest two possibilities. One, that there are
strong affinities between Paraceras and the more primitive
Leptopsyllidae. Or two, it is likely that the reduction of
the crochets and the absence of the paxillus in the
Ceratophyllidae are a derived condition, rather than an
ancestral character state, since they are well developed in
nearly all other members of the family. This could lead to
the conclusion reached by Ioff (1936) that Paraceras is a
genus that is specialized and deviant from other genera in the
Ceratophyllidae.

Amphalius differs distinctly from the other genera in
having an extremely long, thick, twisted fistula. Apart
from that, it may also be distinguished from the remaining
ceratophyllids in the following: The median dorsal lobe is
simple, slightly convex, with a tapered apex. The crochets
are fundamentally different from the normal ceratophyllid
crochets in that they are ventral in position and mesal to
aedeagus. The paxillus is extremely elongate. The sclerites of the endchamber are not well defined. The ventral penis rod is unusually thicker than any other ceratophyllid. The aedeagal apodeme is much broader when compared to the other ceratophyllids, with its apex curved upwards. Like Paraceras, Amphalius shares no close resemblance with the other ceratophyllids in the aedeagal characters mentioned above. Its relationships with the other genera in the Ceratophyllidae are difficult to determine. However, Amphalius does not deviate much from the basic ceratophylloid aedeagal body plan. The occurrence of the above-mentioned structures may be modified character states, which have been derived from the basic ceratophylloid aedeagus. On this basis, it is likely that Amphalius is probably also just another specialized ceratophyllid genus. However, like the other genera discussed so far, Amphalius is included in this group because its relationship with the rest of the Ceratophyllidae is not clear and difficult to determine at this point.

A distinctive character that readily distinguishes Aenigmopsylla from other genera in the Ceratophyllidae is the reduced, long, straight and narrow crochets, lying horizontally, but more ventrad to the endchamber. Goncharov (1981) included this character state along with other non-
genitalic characters in recognizing the subfamily Aenigmopsyllinae in his classification of the Ceratophyllidae. Apart from the crochets being distinctive, the apex of the median dorsal lobe is slightly curved. Ford's sclerite is present and well defined. Based on Rothschild & Traub's (1983) terminology of Ford's sclerite, the presence of this character, at this point, could be interpreted as primitive, since it is shared with the leptopsyllids. The reduced lateral lobes is another feature which is not common in the Ceratophyllidae, where they are well developed. Another feature of the aedeagus of Aenigmopsylla which distinguishes it from the other ceratophyllid genera is the absence of the fulcral dorsal median projection and instead, the presence of a short spur-like structure which could be the fulcral brim. Similar to the previously mentioned genera, the relationship between Aenigmopsylla and the remainder of the Ceratophyllidae is not clear. For this reason, it is placed here.

In contrast to Smitipsylla, Paraceras, Amphalius and Aenigmopsylla, the aedeagus of Glaciopsyllus does not deviate much from the general plan of a typical ceratophyllloid aedeagus. However, it can still be immediately separated from the rest of the Ceratophyllidae in having fairly large lateral lobes with the ventral margin somewhat weakly folded. In comparison to the endchamber, the crochets are small and
subrectangular in shape and mesad to the endchamber in position. Another uncommon ceratophyllid character is the presence of Ford's sclerite which is interpreted here as a primitive state.

_Macrostylophora_ is one of the largest genera in the family with a number of undescribed species. It is not an easy group to place among the ceratophyllid genera, but it is here grouped alongside the above mentioned genera on the same grounds as applied to the previously discussed genera. That is, no clear resemblances exist with the other members of the Ceratophyllidae. However, based on the short, simple and apically-angled median dorsal lobe and its well developed apical sclerite, _Macrostylophora_ approaches the Tarsopsyllinae. It is unusual in that the proximal spur is not apparent. A dorsal spur-like structure may be present but this differs extremely in structure from that of _Ceratophyllus, Orchopeas_ and in some _Opisodasyx_.

CONCLUSIONS

The aedeagi of the ceratophyllid genera are complex structures. This complexity at times makes the description and comparison of structures within this group more easily recognized than previously appreciated. However, this does not mean that the aedeagus is a failure as a taxonomic tool. One is still able to recognize the distinctness of each genus and the similarities shared by members within a group. The complexity of the structure of the aedeagus and the lack of understanding in the function and morphology of this structure still permits the aedeagus to be utilized as a taxonomic aid in the study of such a homogeneous group as the Ceratophyllidae.


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