

A review of the North American species of *Oropsylla* Wagner and Ioff, 1926 (Siphonaptera: Ceratophyllidae: Ceratophyllinae)

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ABSTRACT: The North American species of the flea genus *Oropsylla* are reviewed and their host/parasite relationships and distribution are discussed, as well as their role in the maintenance and transmission of sylvatic plague. Keys to the subgenera and species are presented and illustrations of their diagnostic characteristics are included. *Journal of Vector Ecology* 27(2): 184-206. 2002.

Keyword Index: *Oropsylla*, distribution, vector relationships, plague.

INTRODUCTION

Oropsylla. Wagner and Ioff, 1926, Vestn. Mikrobiol. Epidemiol. Parazitol. 5: 86, (Russian), 113 (German). Generitype: *Ceratophyllus silantiewi* Wagner, 1898 by designation.

The classification followed here is essentially that of Smit (1983) but the 12 species of the subgenus *Thrassis* have been excluded and will be treated later as members of a full genus. In the subgenus *Oropsylla*, the species *O. ilovaiskii* Wagner and Ioff, 1926 and *O. tapina* Peus, 1977 are not included because they are extralimital to the area under consideration and *O. eatoni* Hubbard, 1954 is considered to be a junior synonym of *O. arctomys*. In the subgenus *Opisocrostis* the subspecies *O. tuberculatus cynomuris* (Jellison 1939) is included in the account of the nominate species, but no additional nomenclatural action has been taken. Therefore, in this study the genus includes 4 subgenera and 12 species.

Members of this genus are principally ectoparasites of sciurid rodents. Only 2 species, both belonging to the nominate subgenus, appear to be specific to marmots or woodchucks and the remaining taxa prefer a broad range of ground squirrel species of the genus *Spermophilus*. As might be expected, most species have also been taken on a number of rodents sharing ground squirrel habitat, as well as ground squirrel predators.

In North America these are western fleas and only 2 species have been taken east of the Mississippi River. One is a parasite of the woodchuck, *Marmota monax*, whose range extends from the eastern coast of North America, northwest to Alaska. The other is specific to

Spermophilus franklinii and *S. tridecemlineatus*, whose ranges extend from northwest Indiana, Illinois, Missouri and Kansas, northwest to central Alberta. For the most part, the remaining species are partial to semiarid regions which tend to support large populations of ground squirrels and such areas tend to occur most commonly in the western part of North America.

It has long been known that members of this and some other ceratophyllid genera are involved in the maintenance of sylvatic plague in natural populations of rodents. A number of plague-positive collections have been demonstrated in many laboratory studies and species that may be poor vectors may still be effective because of their large numbers. Rodent to rodent transmission may depend on nothing more than the flea's contaminated mouthparts. In a recent study by Suntsov and Suntsova (2000a), the authors describe a mechanism whereby *Yersinia pestis*, the causative agent of plague, could have evolved from a strain of *Y. pseudotuberculosis* via the parasitic larvae of *O. silantiewi* feeding on communally hibernating marmots (probably *Marmota sibirica*) inhabiting the pebble steppes of Mongolia. It is from this general area that the plague organism is thought to have been acquired by humans, probably by marmot hunters.

The genus *Oropsylla* differs from related taxa by the possession of the following combination of characters. A frontal tubercle is always evident although it may be almost invisible, especially in the nominate subgenus. The frontal setal row may be missing in a few individuals, usually females, but is commonly present and consists of 1 to 3 setae. The ocular row is always of

3 setae and the eyes are always present, normal in size and heavily pigmented, although somewhat reduced in *O. silantiewi*. There is no postocular seta. At least a few of the setae arising on the antennal pedicel extend beyond the apex of the clavus in all females and also in the males of the subgenus *Hubbardipsylla*. The apices of the labial palpi extend beyond the foretrochanter in all species and in some almost the entire terminal segment may extend beyond the trochanter.

A pronotal ctenidium is always present and the longest teeth are greater than half the dorsal length of the pronotum. The metathorax possesses a well-developed pleural rod and the metepisternum bears a conspicuous, dome-shaped squamulum on its cephalic margin. A seta adjoining the forefemoral guard seta is well developed and is greater than half the length of the guard seta.

The basal abdominal sternite is usually either bare or bears a lateral patch of small setae, depending on the subgenus. Abdominal tergite I usually bears at least a pair of marginal spinelets, although these may be minute

or even absent in some individuals. There are 2 or 3 antesensilial setae per side depending on the sex and the species. In males with 3, the middle seta is well developed and bordered above and below by minute setulae. In males with only 2, the lower setule has been lost. In females all setae are well developed, although they tend to be subequal in length. There are 1 or 2 acetabular setae depending on the species, and the apex of the aedeagal apodeme is with or without a tendril.

In females, the shape of the caudal margin of st VII varies with the species, as does the ratio of the dimensions of the spermathecal bulga and hilla. The hilla bears a conspicuous apical papilla only in members of the nominate subgenus.

The 12 distribution maps are based on the distribution records of Hopla (1965), Holland (1949, 1985), Haddow et al. (1983), plus specimens in the United States Museum of Natural History and the Lewis collections. Individual dots may represent more than one collection in some cases.

Key to the subgenera of *Oropsylla*

(Modified from Smit, 1983)

- 1 Basal abdominal sternum with a patch (rarely only 1 or 2) of lateral setae often extending onto the upper anterior half 2
 Basal abdominal sternum usually bare, at most with 1 or 2 setae arising on the lower half (sometimes in about the middle of the sternite) 3
- 2 Frontal row consisting of 1 ventral and 1 or 2 dorsal setae. Male lower minute antesensilial seta absent; st VIII long and narrow, extending apically in a long, filamentous vexillum the apex of which is split (Figures 33-36). Female ductus bursae fairly long, with a thin wall; bursa copulatrix with a small but distinct semi-circular sclerotization around the orifice of the ductus obturatus (western North America, on ground squirrels) (*Opisocrostitis*)
 Frontal row of only 1 very small ventral seta which may be absent. Male lower minute antesensilial seta present; st VIII of medium length with a curved apical vexillum with an entire apex (Figures 31-32). Female ductus bursae short with a relatively thick wall; bursa copulatrix without a dark sclerotization (western North America, on ground squirrels and prairie dogs) (*Hubbardipsylla*)
- 3 Male movable process long, slender and curved cephalad (Figure 6); st VIII reduced and without setae (Figure 24); apical portion of distal arm of st IX expanded (Figure 18). Female spermatheca with ventral constriction between the bulga and hilla, the latter without an apical papilla (Figure 42); anal stylet usually with 1 long preapical seta and lacking a dorsal seta (western U.S.A. and Mexico on ground squirrels) (*Diamanus*)
 Male movable process shaped otherwise; st VIII with a narrow apex bearing 2 or 3 long setae (Figures 19-23); apical portion of distal arm of st IX not expanded (Figures 13-17). Female bulga pyriform or oval; hilla slightly longer than bulga and bearing a conspicuous apical papilla (Figures 37-41); anal stylet with 2 to 4 lateral, subapical setae (northern half of North America, Europe and Asia, on ground squirrels and marmots) (*Oropsylla*)

Subgenus (*Oropsylla*) Wagner and Ioff, 1926

Members of this subgenus share the following characters. A frontal tubercle is present but minute in both sexes. A frontal setal row of at least 1 seta is present. At least a few setae arising on the antennal pedicel extend beyond the apex of the clavus. The apices of the labial palpi extend well beyond the foretrochanter. There are usually small marginal spinelets on the metanotum and the basal abdominal sternite bears no lateral setae.

Males in this subgenus share the following characters. In 3 of the 5 species the movable process extends beyond the apex of the fixed process of the clasper. There is one acetabular seta in 2 species, and 2 in the remaining 3. The apex of st VIII is unmodified but bears 2 or 3 long terminal setae. The apical half of the distal arm of st IX is not expanded and does not bear

any spiniforms. The aedeagal crochet is acuminate apically, with subparallel margins. There are usually 3 antesensilial setae with the laterals very much reduced and only the medial well developed. However, in the few males of *O. (Or.) silantiewi* available to me, the outer lateral seta appears to be lost completely and there is no alveolus present. This is true of material from Afghanistan (1), Russia (3) and China (2). The apex of the aedeagal apodeme bears a slight tendril. In females the caudal margin of st VII is variable. The spermathecal bulga is oval or subspherical and the hilla is about as long as the longest dimension of the bulga and bears a conspicuous apical papilla. There are 3 antesensilial setae per side of unequal length. The anal stylet bears 2 to 4 subapical lateral setae.

There are 5 North American species in this subgenus and they may be separated with the following key.

Key to the North American species of *Oropsylla* (*Oropsylla*)
(Modified from Holland, 1985)

- 1 Males normally with 1 acetabular seta per side, apex of movable process extending beyond the apex of the fixed process (Figures 2, 4); st VII of female with a rounded caudal lobe subtended by a shallow sinus, hilla and bulga of spermatheca of equal length (Figures 38, 40) 2
 - 2 Males normally with 2 acetabular setae per side; apex of movable process not, or only barely, extending beyond apex of fixed process; st VII of female with a rounded marginal angle but no sinus below it; hilla of spermatheca longer than bulga 3
 - 2 Male movable process ~2X as long as wide, its apex projecting well beyond the apex of the acuminate fixed process (Figure 2); female usually with 4 antesensilial setae per side; caudal margin of st. VII with rounded marginal lobe subtended by a shallow sinus; spermathecal hilla as long as the longest dimension of the oval bulga (Figure 38) (northern North America from New England, PA, IN, IL, CO and MT, north to MB, SK, AB, BC and AK, primarily as a parasite of the woodchuck, *Marmota monax*) **arctomys**
 - Male movable process < 2X as long as wide, its apex not projecting far beyond the apex of the fixed process (Figure 4); females usually with 3 antesensilial setae; caudal margin of st VII with a slightly more pronounced sinus than in the preceding species (Figure 40) (normally a parasite of *Spermophilus richardsoni* in SD, MT, SK and AB) **rupestris**
 - 3 Movable process of male pointed apically and extending beyond the apex of the gently pointed fixed process (Figure 3); caudal margin of female st VII straight vertically below a smoothly rounded angle (Figure 39) (a parasite of various species of *Spermophilus* in the west from NM and MT, and north to AK) **idahoensis**
 - Movable process of male relatively blunt apically and not extending beyond the apex of the broadly rounded fixed process; caudal margin of fixed process with a distinct concavity above the acetabular setae (Figures 1, 5); caudal margin of female st VII with a pronounced angle, below which the margin is relatively straight (Figures 37, 41) 4
 - 4 Eye reduced; labial palpi long, extending beyond the apex of the trochanter by almost a full segment; spines of pronotal comb relatively short and widely spaced (on *Marmota broweri* in northern Alaska, plus many Asian records) **silantiewi**
 - Eye of normal size; labial palpi shorter; pronotal comb of normal proportions, the teeth closer together (on *Spermophilus parryii* in the High Arctic) **alaskensis**
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***Oropsylla (Oropsylla) alaskensis* (Baker, 1904)**
(Figures 1, 13, 19, 37) (Map 1)

Ceratophyllus alaskensis. Baker, 1904b, Proc. U. S. Nat. Mus. 27(1361): 394. USA, Alaska, North Slope Division, Point Barrow, 71.22N 156.30W, from *Spermophilus parryi*, 27.VI.1898, McElhaney leg. Lectotype ♂ and allotype ♀ designated by Adams and Lewis, 1995: 4. USNM No. 6903.

Oropsylla elana. Jordan, 1929b, Novit. Zool. 35: 160, pl. 8, Figures 7, 8. China, bank of Sungari River opposite Harbin [=Charbin], 47.42N 132.30E, from *Spermophilus* sp., VI.1928, H. M. Jettmar leg. Holotype ♀ BMNH. Synonymized by Smit, 1967: 100.

Oropsylla silantiewi asiatica. Wagner, 1930b, Annu. Mus. Zool. Acad. Imp. Sci. St. Petersburg (1929) 30: 543, figs. 1-10. USSR, NE Yakutskaya, ASSR, mouth of the Kolyma River, ~68.30N 162.00E, from *Spermophilus undulatus*, no date or collector. Two syntype females in ZMUH without numbers according to Smit and Wright, 1965: 12. Synonymized by Smit, 1967: 100.

Oropsylla stejneri. Jordan, 1937, Novit. Zool. 40: 287, Figure 17. USSR, Eastern Siberia, East Cape, 66.05N 169.40E, no host, date or collector. Holotype ♀ by monotypy BMNH. Synonymized by Smit, 1967: 100.

Males of this species are characterized by the presence of 2 acetabular bristles, the apex of the relatively blunt movable process only approximating the apex of the broadly rounded fixed process and the spines in the pronotal comb of normal proportions and spacing. Females are not particularly distinctive although the spermatheca is of medium size (similar to *O. silantiewi*) and the dorsal margin of st VII forms a distinct rounded angle before descending ventrad.

There are relatively few references to this species in the literature. Jellison (1945), in his study of North American *Oropsylla*, cited 1 male and 7 female specimens available for him to examine, all from the Northwest Territories of Canada. Although some of the material came from predators, he stated that this was probably a parasite of Parry's ground squirrel (*Spermophilus parryi*). He also mentioned another incompletely documented female in the collection of the USNM from the Alaska-Yukon border north of the Arctic Circle. Holland (1949) indicated that so little was known of this species that little could be said concerning its

distribution and host affinities, but that it was probably closely associated with ground squirrels of the *Citellus* (= *Spermophilus*) *parryi* group. Ioff and Scaloni (1954), in their discussion of *O. asiatica* (= *O. alaskensis*) in Siberia, posited that the flea was a parasite of *C. undulatus* and was known from many districts in Asia (Yakutsk, Kolyma, Kamchatka, Eastern Mys, Transbaikalia, Cisbaikalia, Krasnoyarsk, Tuva, southeast Altai, Dzhungarian Alatau, Mongolia and Manchuria). They also suggested that Baker's name probably had priority over *O. asiatica*.

Hopla (1965) reported 360 specimens from 39 positive collections of *S. undulatus*. Recent studies cited in Nowak (1999), though including both *S. parryi* and *S. undulatus* in the spermophilid subgenus *Urocitellus*, relegate the latter to southern Siberia, eastern Kazakhstan, Mongolia and northern China, and the former to northeastern Siberia and northwestern Alaska. Hopla (1965) also agrees that this flea is restricted to the parts of its host's range that are truly Arctic. However, he went on to point out that collections from central-eastern Alaska, in the vicinity of Fort Yukon and Circle Hot Springs, came from cleared areas of the taiga at low elevations. He also said that his most southerly record of this flea came from Dry Creek, and in this area some hosts harbored both this species and *O. (Or.) idahoensis*.

Little is known concerning the biology of *O. (Or.) alaskensis*. Hopla (1965) said that records from Ogotoruk Creek were of special significance since they came from hosts taken 15 minutes to an hour after emerging from hibernation. These hosts were much more heavily infested than those collected at any other time. Dissected females from these collections did not show well-developed eggs, and generally eggs were not found before the middle of June in specimens from the Yukon and Circle Hot Springs. Neither Haas et al. (1982) nor Holland (1985) address the biology of the species beyond commentary on host associations and distribution.

***Oropsylla (Oropsylla) arctomys* (Baker, 1904)**
(Figures 2, 14, 20, 38) (Map 2)

Ceratophyllus arctomys. Baker, 1904b, Proc. U. S. Nat. Mus. 27(1361): 411, pl. XXII, figs. 1-6. USA, New York, Madison County, Peterboro, 43.00N 75.40W, from *Marmota monax*, 9.VII.1900, G. S. Miller leg. Lectotype ♂ and allotype ♀ designated by Adams and Lewis, 1995: 6. USNM No. 6916.

Aethopsylla septentrionalis. Stewart and Holland, 1940, Can. Entomol. 72: 41, Figures 1-2. Canada, British Columbia, Wigwam Mine, ~35 km S. Revelstoke, ~51.42N 118.12W, from *Marmota*

monax, 21.V.1939, E. R. Buckell leg. Holotype ♀ in CNCI, No. 4986. Synonymized by Jellison, 1945: 90.

Oropsylla eatoni. Hubbard, 1954, Entomol. News 65: 173, 1 unnumbered figure USA, Washington, Jefferson County, Olympic National Park, ~47.49N 123.42W, from *Marmota olympus*, 12.VIII.1951, C. A. Hubbard leg. Holotype ♂ and allotype ♀ USNM No. 104617. **New Synonymy.**

Males of this species may be distinguished from other members of the subgenus by the broad movable process which is ~2X as long as wide and which extends well beyond the rather pointed apex of the fixed process and by the presence of only 1 acetabular seta. Females possess a larger than usual spermatheca and the caudal margin of st VII usually has at least a slight shallow concavity in its caudal margin below the dorsal angle.

Due to its extensive range, this species figures prominently in the literature dealing with the North American oropsylline fauna. It is a specific parasite of the woodchuck, *Marmota monax*, but in areas where this host does not occur it has been taken on *M. caligata* and *M. flaviventris*. There are also many published records from predators such as *Canis latrans*, *Martes americana*, *Taxidea taxus*, *Urocyon cinereoargenteus* and *Vulpes vulpes*, as well as mammals using woodchuck burrows such as *Sylvilagus floridanus*. As usual, little or nothing has been published concerning the biology of the species. Since its preferred host is not social, as are most species of *Marmota*, it must be assumed that flea infestation is accomplished via sibling/parent contact or during the brief period when the sexes are in contact during mating. Although not well documented, following are observations made on a captive woodchuck in central Iowa.

A number of years ago, a colleague obtained a live woodchuck that he kept in captivity and ultimately went into hibernation. When he acquired the animal, a cursory inspection did not reveal that it was infested with fleas, although admittedly he did not inspect the animal thoroughly. It is not clear whether an artificial burrow was constructed or whether the animal simply hibernated in its cage. In any case, when the woodchuck emerged from hibernation both it and the nesting material were heavily infested with fleas, some of which were brought for identification. Obviously there must have been a few gravid females present initially for such an infestation to occur. According to Svendsen (1999), *M. monax* is a true hibernator in that it curls into a ball with its nose resting on its lower abdomen, its head covered by the hindlegs and tail. During hibernation the heartbeat slows

to ~4 beats per minute and the body temperature drops from 32°C to the ambient temperature of the hibernaculum. Such conditions would seem to be inimical for flea reproduction and development. This subject will be revisited under the account for *O. (Or.) silantiewi*.

***Oropsylla (Oropsylla) idahoensis* (Baker, 1904)**
(Figures 3, 15, 21, 39) (Map 4)

Ceratophyllus idahoensis. Baker, 1904b, Proc. U. S. Nat. Mus. 27(1361): 413, pl. XVII, figs. 1-6. USA, Idaho, Latah County, Moscow, 46.44N 117.00W, from *Spermophilus columbianus*, 1.V.[no year], J. M. Aldrich leg. Lectotype ♂ and allotype ♀ designated by Adams and Lewis, 1995: 19. USNM No. 6918.

Ceratophyllus poeantis. Rothschild, 1905, Novit. Zool. 12: 155, pl. VIII, Figure 22. Canada, Alberta, Banff, 51.10N 115.34W, from "mountain chipmunk", 9.VII.1899, G. F. Dippie leg. Lectotype ♂ BMNH, designated by Smit and Wright, 1978: 37. Synonymized by Jordan, 1929b: 32.

Ceratophyllus bertholfi. C. Fox, 1927, Trans. Am. Entomol. Soc. 53: 211. USA, Alaska, Nagai Island, 55.10N 160.00W, from *Spermophilus parryi*, VI. 1909, collector not given. Holotype ♂ USNM No. 40355. Synonymized by Jordan, 1933b: 74.

Males of this species may be distinguished by their relatively small genitalia. The movable process is rather pointed apically and extends beyond the apex of the fixed process which is rounded apically. Two acetabular setae are present. Females have a relatively small spermatheca and the caudal margin of st VII is either straight or slightly convex below the rounded dorsal angle.

Jellison (1945), following Hubbard (1941), concluded that the preferred host of this flea was *Spermophilus lateralis*. This conclusion was based on the observation that this host always had fleas of this species, though seldom did it host other species. A review of the literature suggests quite the contrary. Indeed, among North American *Oropsylla* species *O. (Or.) idahoensis* seems the most catholic with respect to host preference. It has been reported from at least 54 host species, including 5 birds. Four of the latter were raptors, and the fifth was a woodpecker. In addition to the many small cricetine and microtine host records, this species has been reported from 4 species of *Cynomys*, 14 species of *Spermophilus*, 6 species of *Tamias* and 3 species of tree squirrels and its range extends beyond that of *S.*

lateralis. This is not to suggest that these are preferred hosts but the records lend little support to claims of strict host preference.

Hopla (1965) reported *S. undulatus* (= *S. parryii*) in Alaska as its preferred host, though he also cited collections from *Ochotona collaris* and *Tamiasciurus hudsonicus*. Haas et al. (1982) reported 4 pairs from 2 nests of *Microtus oeconomus*, and Haas et al. (1978) reported collections from *S. parryii* from east-central Alaska. Holland (1985) lists a number of collections from British Columbia, Yukon Territory and Alaska. Again, little is known of the biology of this species.

***Oropsylla (Oropsylla) rupestris* (Jordan, 1929)**
(Figures 4, 16, 22, 40) (Map 4)

Ceratophyllus rupestris. Jordan, 1929b, Novit. Zool. 35: 32. Canada, Alberta, Calgary, 51.50N 114.05W, from *Mustela frenata*, 1911, G. F. Dippie leg. Holotype ♂ BMNH.

This is the other member of the subgenus in which the males have a single acetabular seta. Other male characteristics include a movable process that is < 2X as long as wide, its apex not extending beyond the apex of the fixed process. Females of this species also have a relatively smaller spermatheca and the caudal margin of st VII tends to be at least slightly concave below the rounded dorsal angle.

Our map number 4 is a composite of the maps in Traub et al. (1983) and Holland (1985) and shows this species to be restricted to MT and ND in the United States, and AB, SK and MB, plus a single verified record from YK, in Canada. However, Baird and Saunders (1992) indicate that there is material of this species in the collection of the USNM from OR, WA, UT, AZ, CO and WY, as well as BC in Canada. There are also literature records from ND (Jellison, 1945; Kinzel and Larson, 1973; Larson, 1997) and from ID by Baird and Saunders (1992).

Although evidently specific to *S. columbianus*, there are literature records from 12 other host species. Jellison (1945) questioned the identifications of material from what was then known as *Citellus richardsonii elegans* (= *Spermophilus elegans*) from Madison and Beaverhead counties in MT, and all collections from this host in WY, stating that they were *O. (Or.) idahoensis*. As with other members of the subgenus, little is known about the biology of this species.

***Oropsylla (Oropsylla) silantiewi* (Wagner, 1898)**
(Figures 5, 17, 23, 41) (Map 5)

Ceratophyllus silantiewi. Wagner, 1898, Trudy Russk. Entomol. Obsch. 31: 574, pl. VIII, Figure 12. USSR, Voroneshskaya Gouvnorate, Stein-Steppe [Stone Steppe?], from *Marmota bobac*, 8.VII.1895, A. Silantiew leg. Lectotype ♂ designated by Smit and Wright, 1965: 40. ZMUH No. 2518.

Ceratophyllus crassus. Jordan and Rothschild, 1911, Proc. Zool. Soc. Lond. 2: 374, Figure 111. China, Gansu Province, Old Tauchow [untraced], 2743 m, from *Marmota himalayana*, 1908, M. P. Anderson. Lectotype ♀ BMNH, designated by Smit and Wright, 1978: 14. Synonymized by Smit, 1967: 100.

Paraceras segregatus. Wagner, 1930a, Konowia, 9: 279, 1 figure. USSR, Pamir Mountains, *sine loco*, from *Meles meles*, 1928, collector not given. Holotype ♂ ZMAS. Provisionally synonymized by Ioff and Scaloni, 1954: 256. Listed as a synonym by Smit, 1967: 100.

Oropsylla silantiewi weisskei. Wagner, 1936, Z. Parasitenk. 8: 338, Figure 8. Mongolia, *sine loco*, from *Marmota* sp., no date, Weisske leg. Lectotype ♂ NHMW, designated by Smit and Wright, 1965: 47. Synonymized by Wagner, 1938: 11.

Both sexes of this Arctic species are characterized by the possession of a reduced eye, labial palpi which extend beyond the apex of the trochanter by almost the terminal segment and teeth in the pronotal ctenidium that are both shortened and wider-spaced than in other species. In addition, males have a movable process that is rather blunt apically and does not extend beyond the apex of the rounded fixed process. Females have an intermediately sized spermatheca (along with *O. (Or.) alaskensis*) and the caudal margin may be relatively straight or slightly convex on the dorsal margin and subtended by a shallow sinus.

Until 1963 this species was only known from a large portion of central and eastern Asia. Ioff and Scaloni (1954) listed its range as "from the Donskoi and Cisvolga steppes in the west to the Pacific Ocean in the east, and from the Cisural steppes and Kamchatka in the north to the Tyan-Shan and the Himalayas in the south," where it parasitizes various species of marmots. In 1963 *Oropsylla* specimens were taken from *Marmota broweri* at Peters Lake in the Eastern Brooks Range of northern Alaska. These were subsequently determined to be *O. (Or.) silantiewi* by the late George Holland. Additional

specimens were later taken from the same host species at Chandler Lake and in the Ukukminilagat Valley in the central Brooks Range. These collections were published in Rausch and Rausch (1971). While these records have been noted in subsequent publications, I am not aware of additional collections from Alaska.

Because most marmot species reside in high altitudes and/or latitudes, the colder months are spent in profound hibernation during which the temperature, metabolism and heart rate are greatly reduced. Such rigorous environmental conditions might be expected to have a stultifying effect on the fleas of these hosts. Students of the Siphonaptera have frequently observed that some flea species evidently remain in the nest of the host when the latter departs to forage and thus are seldom collected on the body of the host. These have been referred to in the literature as "nest" fleas, but little serious effort has been made to explain the underlying reasons for this condition. It stands to reason that the rarity of these species is exacerbated when the hosts are in a torpor in their underground retreats for 6 to 8 months of the year. This condition occurs in many marmots, ground squirrels and their fleas.

As early as the 1940's, Russian plague control workers in Transbaikalia observed concentrations of empty flea cocoons on the tails and hindlegs of marmots which had recently emerged from hibernation. No significance was attached to this until it was observed that at least some larvae of *O. silantiewi* were parasites in the mouth and nostrils of their dormant hosts. This has been considered to be "primordial" parasitism by many Russian workers (Vovchinskaya and Olovina, 1946; Ryabov, 1946; Zhovtyi and Peshkov, 1958; Zhovtyi and Prokopen, 1958; Zhovtyi, 1970) and is interpreted as a relatively recent evolutionary phenomenon that is still evolving. That this information has been used in the construction of a theory deriving the plague organism, *Yersinia pestis* from *Y. pseudotuberculosis*, a common intestinal inhabitant of rodents, is beyond the purview of this study. However, the sequence of events in the developmental cycle of the fleas is instructive in how the larvae survive under such inclement conditions and may preview a similar developmental cycle for fleas on some North American mammals.

Suntsov and Suntsova (2000a,b) have described the sequence of events as they evidently take place in the developmental cycle of this species in eastern Siberia and northern Mongolia. In these areas the soil freezes very deeply due to the continental climate, low winter temperatures and little or no snow cover. Hibernacula of *Marmota sibirica*, which hibernate communally, have nest chambers of 1.5 to 2.2 meters below the surface. At

these depths the ground is frozen by early January in Tuva and February in Transbaikalia and is not completely thawed until the following June or July. Therefore marmot nests are frozen for 4 to 6 months. In these nests the marmots remain in relatively uninterrupted dormancy from January to at least early April. Females of *O. (Or.) silantiewi* deposit their eggs on the hibernating marmots where the larvae feed on dander and the feces of the adult fleas. While moving through the pelage of the host, some larvae enter the oral cavity where they feed on blood by abrading the mucous membranes and tongue. Such larvae tend to be larger, have a well-developed fat body and show red blood in their gut. When ready to pupate, the larvae leave the oral cavity and spin their cocoons in the pelage close to the rodent's mouth. Due to the sleeping position of the host, with nose touching the base of the tail between the hindlegs, most of the cocoons are attached in this area.

Whether such a life cycle as described above occurs in Alaska remains to be demonstrated. As far as is known, *O. (Or.) silantiewi* has only been collected on *Marmota broweri* in North America and little is known about its biology. Hoffman (1999) indicates that the Siberian black-capped marmot (*Marmota camtschatica*) digs winter burrows of 100 meters or more in length and penetrates deep into the ground below the permafrost. Hibernating in unfrozen soil could alter the larval behavior in the nest, but if *Marmota broweri* mirrors its Siberian counterpart it is unlikely that its hibernacula will ever be excavated.

Subgenus *Diamanus* Jordan, 1933b

This monotypic subgenus possesses the following characters. The frontal tubercle is small and inconspicuous in both sexes. The frontal setal row is frequently absent, but when present it usually consists of a single small seta. At least a few setae arising on the antennal pedicel extend beyond the apex of the clavus in females. The apices of the labial palpi extend well beyond the foretrochanter in both sexes. The metanotum usually bears a few marginal spinelets and the basal abdominal sternite lacks lateral setae. Males also possess the following characters. The crescentric movable process extends over and well beyond the apex of the oval fixed process of the clasper. There are 2 acetabular setae per side. Sternite VIII is reduced, triangular and without setae. The apex of the distal arm of st IX is expanded but lacks spiniform setae. The aedeagal crochet is acuminate in lateral view. There are 3 antesensorial setae present, the laterals much reduced. The apex of the aedeagal apodeme bears a long tendril. In females the caudal margin of st VIII is straight

vertically. The spermathecal bulga is spherical and set off from the apapillate hilla by a pronounced constriction. The hilla is more than twice the length of the bulga. There are 2 unequal antesensilial setae per side and the anal stylet bears only 1 subapical lateral seta.

***Oropsylla (Diamanus) montana* (Baker, 1895)**
(Figures 6, 18, 24, 42) (Map 6)

Pulex montanus. Baker, 1895, Can. Entomol. 27: 132, no figure. USA, Colorado, Larimer County, foothills W Fort Collins, Arboles, 37.02N 107.24W, from *Sciurus aberti*, 11.IX.1892, J. D. Stannard leg. Lectotype ♂ and allolectotype ♀ designated by Adams and Lewis, 1995: 24. USNM No. 7240.

Ceratophyllus acutus. Baker, 1904a, Invert. Pacifica 1: 40, no figure. USA, California, Santa Clara County, Palo Alto, Stanford University, 37.26N 122.10W, from *Spermophilus* sp., no date, V. Kellogg leg. Holotype ♂ allotype ♀, Essig Museum, University of California, Berkeley. Lectotype ♂ BMNH, designated by Smit and Wright, 1978: 3. Synonymized by Jordan, 1929b: 31.

Ceratophyllus mandarinus. Jordan and Rothschild, 1911, Proc. Zool. Soc. Lond. 2: 375, figs. 112-113. China, Shaanxi Province, Yu-lin-fu, 38.18N 109.45E, 1219 m, from *Spermophilus citellus*, 1908, M. P. Anderson leg. Lectotype ♂ BMNH, designated by Smit and Wright, 1978: 30. Synonymized by Lewis, 1988: 141.

Diamanus hopkinsi. Vargas, 1955, Rev. Inst. Salubr. Enferm. Trop. Mex. 15: 15, pl. I, Figure 2; pl. II, Figure 2; pl. III, Figure 2; pl. IV, Figure 3; pl. V, fig A; pl. VI. USA, Utah, Salt Lake County, Parlay Canyon, from a squirrel, 28.II.1932, H. B. Stafford leg. Holotype ♂ allotype ♀ slide No. 6362, Instituto Salubridad Enfermedades Tropicales, Mexico, D. F. Synonymized by Stark, 1958: 141.

The characters that set this subgenus off from its relatives also serve to characterize the single species assigned here.

Haddow et al. (1983) list this as a western species. Its range extends west from Colorado and New Mexico to the coast, and south from Washington and Idaho to central Mexico where it occurs in rocky, open terrain from near sea level to ~2500m. Although *Spermophilus variegatus* and *S. beecheyi* are listed as the preferred hosts, a review of the literature reveals that it has been taken on at least 61 species of hosts. In addition to the

non-sciurid hosts, the following genera and species of squirrels host this flea, sometimes in enormous numbers. Numbers of host species are given in parentheses after the host genus: *Ammospermophilus* (3); *Cynomys* (2); *Marmota* (1); *Sciurus* (3); *Spermophilus* (9) and *Tamias* (6).

This is one of the 20 or so species of fleas that have been colonized in the laboratory. Transmission studies have shown that on average only about 20% of individuals become infected with plague when feeding on diseased hosts and of these only about 10% transmit the disease to healthy guinea pigs. Therefore, the species is not a very effective vector based on studies by Eskey and Haas (1940), Wheeler and Douglas (1941, 1945) and Burroughs (1947), though Wheeler and Douglas reported more success than the other authors. However, even poor vectors can maintain the disease in wild host populations if they are present in large numbers.

Metzger and Rust (2001) discuss some of the interesting biological and behavioral characteristics of this species.

Subgenus ***Hubbardipsylla*** Smit, 1983

The 2 species assigned to this subgenus share the following characters in common. The frontal tubercle is small but obvious in both sexes. The frontal setal row is frequently absent, but when present consists of 1 small marginal seta. Some of the setae arising on the antennal pedicel extend beyond the apex of the clavus in both sexes. The apices of the labial palpi reach the apex of the foretrochanter but do not extend far beyond it. Marginal spinelets of the metanotum are well developed with 4 to 6 per side. Basal abdominal sternite has a patch of small lateral setae. In males the apex of the movable process does not extend beyond the apex of the fixed process of the clasper. There are 2 acetabular setae per side. The apex of st VIII is terminated by a short, terminal projection that is not fimbriated. The apex of the distal arm of st. IX is not expanded but bears 1 or 2 small spiniforms. Crochet of the aedeagus is triangular in lateral view. The apex of the aedeagal apodeme is terminated by a long tendril and there are 3 antesensilial setae per side. In females the caudal margin of st VII bears a lobe subtended by a sinus. The apapillate spermatheca is ~1.5X as long as the longest dimension of the roughly spherical bulga. There are 2 antesensilial setae per side and the anal stylet bears 1 lateral, subapical seta.

***Oropsylla (Hubbardipsylla) oregonensis* (Good and Prince, 1939)**
(Figures 7, 25, 31, 47) (Map 7)

Key to the species of *Oropsylla* (*Hubbardipsylla*)

- 1 Apex of male movable process almost extending to the broad tip of the fixed process (Figure 7); fixed process clavate apically; apex of distal arm of st IX with subparallel margins and bearing 1 spiniform seta at its tip (Figure 25); caudal margin of female st VII with a long lobe subtended by a deep sinus subtended by another long lobe (Figure 43). (WA, OR, ID, CA, on *Spermophilus beldingi*, *S. columbianus* and *S. townsendii*) ***oregonensis***
- Apex of male movable process not nearly reaching the tip of the fixed process (Figure 8); fixed process elongated apically; apex of distal arm of st IX tapering to a rounded point and with 2 spiniforms at its tip (Figure 26); caudal margin of female st VII with a short dorsal lobe, subtended by a relatively shallow sinus, subtended by a longer, broader lobe (Figure 47). (WA, OR, on *Spermophilus townsendii* and *S. washingtoni*) ***washingtonensis***

Opisocrostitis oregonensis. Good and Prince, 1939, Publ. Hlth. Rep. Wash. 54: 1687. USA, Oregon, Baker County, 13 km S. Baker, 44.46N 117.50W from *Spermophilus beldingi*, 24.IV.1938, E. C. Parkinson et al., leg. Holotype ♂ and allotype ♀ USNM No. 104666.

In males of this species the pointed apex of the movable process reaches the apex of the clavate fixed process which bears a broad, shallow concavity on its caudal margin. The apex of the distal arm of st IX is somewhat broader than in the following species and bears a single small spiniform in addition to a number of small spinelets. In females the caudal margin of st VII bears 2 long lobes separated by a deep median sinus.

Aside from the standard bibliographic references there is little mention of this taxon since its description. Hubbard (1950) recorded it from Vya County, NV; Jellison and Senger (1976) from Baker County, OR; Zielinski (1984) from Nevada County, CA; Schwan and Corwin (1987) from Modoc County, CA and Baird and Saunders (1992) from 5 counties in ID. Though the species seems not to have been associated with plague in the literature, it seems likely that this and the next species play much the same role in nature as *O. (Op.) hirsuta*, *labis* and *tuberculata*. The range of *O. (Op.) bruneri* does not extend into areas where plague is endemic.

Preferred hosts of this species appear to be *Spermophilus beldingi*, *S. columbianus* and *S. townsendii*.

Oropsylla* (*Hubbardipsylla*) *washingtonensis (Good and Prince, 1939)
(Figures 8, 26, 32, 47) (Map 8)

Opisocrostitis washingtonensis. Good and Prince, 1939, Publ. Hlth. Rep. Wash. 54: 1691. USA, Washington, Adams County, 3.2 km E Lind,

46.59N 118.38W, from *Spermophilus townsendii*, 7.III.1938 L. J. Hughes et al. leg. Holotype ♂ and allotype ♀ USNM No. 104698.

As usual, the diagnostic characters separating the 2 members of this subgenus are sexual. In males the apex of the movable process does not reach the apex of the fixed process and the latter is more triangular, with subparallel margins and a round-pointed apex below which is a pronounced but relatively narrow concavity. The apex of the distal arm of st IX is narrower than in the preceding species and bears a pair of small spiniforms at its tip in addition to a number of spinules. In females the margin of st VII projects caudad bears a small dorsal lobe subtended by a shallow sinus which in turn is subtended by a slightly longer caudoventral lobe.

Much the same can be said of this species as of the preceding taxon. If anything, this species has an even more restricted distribution and is restricted to WA and OR. Except for the part of the type series from OR all published records known to me are from WA. They include Svihla (1941); Bacon (1953); Clanton et al. (1971); O'Farrell (1975) and Jellison and Senger (1976).

Although not stated by Haddow et al. (1983) the preferred hosts of this flea appear to be *Spermophilus townsendii* and *S. washingtoni*.

Subgenus *Opisocrostitis* Jordan, 1933b

The 4 species in this subgenus share the following characters. Frontal tubercle inconspicuous to pronounced, especially in some males, arising lower on the frons in females. The frontal setal row is usually present and consists of 1 to 3 setae which are sometimes minute. At least a few of the setae arising on the antennal pedicel of females extend beyond the apex of the clavus. Apices of the labial palpi extend beyond the foretrochanter by almost an entire terminal segment.

Marginal spinelets present on the metanotum, usually more numerous in females. Basal abdominal sternite with a patch of small, lateral setae. In males the movable process of the clasper extends beyond the fixed process, frequently by half or more of its length. There are 2 acetabular bristles per side except in *O. (Op.) bruneri* which has only 1. Sternite VIII terminated by a long, membranous projection that is slightly fimbriated at its apex. The apex of the distal arm of st IX is neither

expanded nor does it bear spiniform setae. Aedeagal crochet acuminate apically, its apex flexed downward. Three of the 4 species lack any sign of an apical tendril on the aedeagal apodeme. Two antesensilial setae per side. In females the contours of st VII are variable. The apapillate spermathecal hilla is usually ~2X the length of the longest dimension of the spermathecal bulga. Usually 2 antesensilial setae per side and the anal stylet bears 1 to 4 lateral, subapical setae.

Key to the species of *Oropsylla (Opisocrostis)*

- 1 Apex of fixed process of male clasper flexed caudad, its caudal margin slightly concave; movable process crescentric, apex only extending slightly beyond the fixed process (Figure 12); caudal margin of female st VII with a bluntly pointed lobe subtended by a relatively deep, broad sinus (Figure 48) (including *O. t. cynomuris* this species ranges from southern BC, AB and SK, south to CA, CO and NM on various species of *Spermophilus* and *Cynomys*) **tuberculata**
Half or more of the male movable process extending beyond the apex of the fixed process; caudal margin of female st VII either entire or with a shorter lobe and shallower sinus 2
 - 2 Apex of movable process of male flexed caudad, ~8X as long as wide at its widest point (Figure 11); caudal margin of female st VII with a blunt or roundly pointed lobe subtended by a relatively narrow sinus and rounded ventral lobe (Figure 45) (BC, AB and SK, south to UT, east to ND and west to OR, on *Spermophilus richardsonii*) **labis**
Apex of the straight movable process extending far beyond the apex of the fixed process; caudal margin of female st VII nearly straight vertically, lacking a distinct lobe or sinus 3
 - 3 Movable process of male clasper 4-5X as long as wide at its widest point, its caudal margin distinctly concave (Figure 10); 2 acetabular setae of unequal length; caudal margin of female st VII forming a rounded dorsal angle before descending, straight or slightly concave (Figure 44) (MT and SD south to AZ, NM, TX and OK, on *Cynomys* species) **hirsuta**
Male clasper with movable process only 3X as long as wide at its widest point, its caudal margin convex (Figure 9); only 1 long acetabular seta; caudal margin of female st VII forming a much more smoothly rounded dorsal angle before descending, straight or slightly convex (Figure 36) (IN, IL, WI and IA, northwest to SK and AB, on *Spermophilus franklinii* and *S. tridecemlineatus*) **bruneri**
-

***Oropsylla (Opisocrostis) bruneri* (Baker, 1895)**
(Figures 9, 27, 33, 46) (Map 9)

Pulex bruneri. Baker, 1895, Can. Entomol. 27: 132, no figures. USA, Iowa, Story County, Ames, 42.02N 93.33W on *Spermophilus tridecemlineatus*, 22.IV.1886, collector not given. Lectotype ♂ designated by Adams and Lewis, 1995: 8. USNM No. 10932.

Ceratophyllus saundersi. Jordan, 1933a, Entomologist 66: 16. Canada, Saskatchewan, SK, 52.10N 106.49W, from *Spermophilus richardsoni*, 1931, J.G. Saunders leg. Holotype ♂ BMNH. Synonymized by Holland, 1952: 71.

Male diagnostic characters in this species include the straight movable process, about half of which extends beyond the blunt apex of the fixed process that bears a single acetabular seta. Further, the movable process is ~3X as long as wide at its widest point and its caudal margin is convex. Neither st VIII nor IX are particularly diagnostic. In females the caudal margin of st VII is entire, as it is in *O. (Op.) hirsuta*, but the dorsal angle is more rounded and less pronounced in *O. (Op.) bruneri*.

Collection records indicate that this is a primary parasite of *Spermophilus franklinii* and *S. tridecemlineatus*. However, it is reported from at least 33 host mammals. Sciurid hosts include 5 species of

ground squirrels; 1 prairie dog; 1 marmot; 2 species of chipmunk; 2 of flying squirrels and 3 of tree squirrels. The remaining hosts are mostly rodents that share habitat with ground squirrels and prairie dogs.

***Oropsylla (Opisocrostis) hirsuta* (Baker, 1895)**
(Figures 10, 28, 34, 49) (Map 10)

Pulex hirsutus. Baker, 1895, Can. Entomol. 27: 130. USA, Colorado, Larimer County, Stove Prairie, ~40.35N 105.20W, from *Cynomys ludovicianus*, 31.VII.1892, C. P. Gillette leg. Lectotype ♀ BMNH, designated by Smit and Wright, 1978: 23.

Male diagnostic characters include a movable process that is 4-5X as long as wide at its widest point and with its caudal margin distinctly concave. There are 2 acetabular bristles in this species, one of which is noticeably shorter than the other. Sternites VIII and IX are not particularly diagnostic, although the distal arm of the former is widest apically, a character shared with *O. (Op.) bruneri*. As previously indicated, the contours of the caudal margin of st VII in females are similar to those of *O. (Op.) bruneri*, but in this species the angle formed between the dorsal and caudal margins is usually somewhat more pronounced.

This is the subgeneritype for this group of species. Primarily a parasite of prairie dogs, there are literature records from *Cynomys gunnesoni*, *leucurus*, *ludovicianus* and *parvidens*. However, the species has been taken on at least 22 host species, among them *Marmota flaviventris* and 5 species of *Spermophilus*. Haddow et al. (1983) indicate that it occurs from 700-3,000m in plains, plateaus and other grassy habitats.

The literature suggests that this species is not a particularly good vector of plague. However, Eskey and Haas (1940) concluded that at least *C. gunnesoni zuniensis* constituted a definitive reservoir in the mountainous areas in southwestern United States, at least in prairie dogs belonging to the white-tailed subgenus *Leucocrossuromys*.

***Oropsylla (Opisocrostis) labis* (Jordan and Rothschild, 1922)**
(Figures 11, 29, 35, 45) (Map 11)

Ceratophyllus labis. Jordan and Rothschild, 1922, Ectoparasites I: 275, Figure 267. Canada, Alberta, Calgary, 51.05N 114.05W, from *Mustela frenata*, 1911, G. F. Dippie leg. Lectotype ♂ BMNH, designated by Smit and Wright, 1978: 27.

Both males and females are distinctive in this species. Males possess a long, boot-shaped movable process, the apical third of which is flexed caudad. The fixed process is blunt apically and usually bears a slight concavity below the fovea. There are 2 acetabular bristles of equal length. Again, st VIII and IX are not particularly diagnostic, although the distal arm of st IX is widest in the middle, a character shared with *O. (Op.) tuberculata*. In females the contours of st VII characteristically involve a small, blunt to rounded dorsal lobe subtended by a small sinus, below which is a broad, rounded lobe which does not extend beyond the apex of the dorsal lobe.

This is a parasite of ground squirrels. Haddow et al. (1983) suggest that its preferred host is *Spermophilus richardsonii*, but there are records from at least 6 other members of this genus, as well as other sciurid genera including *Ammospermophilus*, *Cynomys*, *Marmota* and *Tamias*. Including predator records this flea has been taken on at least 23 mammalian host species.

The literature suggests that this may be a major vector of plague in some populations of ground squirrels and other hosts. Eskey and Haas (1940) show percentages of infection as high as 52% in one of their exposure experiments and all but one of the other experiments yielded percentages in the teens, thirties and forties.

***Oropsylla (Opisocrostis) tuberculata* (Baker, 1904)**
(Figures 12, 30, 36, 48) (Map 12)

Ceratophyllus tuberculatus. Baker, 1904b, Proc. U. S. Nat. Mus. 27: 393. USA, Idaho, Latah County, Moscow, 46.44N 117.00W, from *Spermophilus columbianus*, date not give, J. M. Aldrich leg. Holotype ♀ and syntype ♂ USNM No. 6902.

Opisocrostis tuberculatus cynomuris. Jellison, 1939, Publ. Hlth. Rep. Wash. 54: 843., 1 unnumbered plate. USA, Montana, Broadwater County, Jefferson Canyon, *sine loco*, from *Cynomys ludovicianus*, 22.III.1934, W. L. Jellison leg. Holotype ♀ USNM No 104609.

Opisocrostis ornatus. I. Fox, 1940, Proc. Entomol. Soc. Wash. 42: 67, pl. 9, fig. 8. USA, Colorado, Saguache County, *sine loco*, from *Cynomys gunnisoni*, 26.VI.1926, S. C. McCampbell leg. Holotype ♂ USNM No. 53588. A junior synonym of *O. t. cynomuris* according to Jellison, 1947: 65.

Males of both taxa included here may be separated from other members of the subgenus by the crescentic movable process and the distinctly concave caudal

margin of the fixed process. Jellison's illustrations accompanying the description show the female of the nominate subspecies as being smaller, having a smaller spermatheca and a sharper lobe on the caudal margin of st VII, subtended by a deeper sinus. The drawings are not accompanied by an indication of the degree of magnification and size alone is not generally considered to be a valid taxonomic criterion for separating taxa in the Siphonaptera.

When taken together, the 2 taxa considered here are known from 13 species of *Spermophilus* and 4 species of *Cynomys*, as well as a few other squirrel species, and there are a few records from *Marmota flaviventris* in addition to predator records. There are also records from *Speotyto cunicularia*, the burrowing owl that uses prairie dog burrows as retreats. Strictly speaking, the nominate subspecies is typically associated with ground squirrels, while *O. (Op.) t. cynomuris* parasitizes prairie dogs. Intraspecific variation in all species in this genus is so great that it seems highly unlikely that there is a valid reason for separating the two taxa. However, much additional collecting is required before a reasonable appraisal of their distinctness can be reached.

Although this species is included, along with other members of the genus, among ceratophyllids that transmit plague in wild rodents, it does not rank particularly high among the most common vectors. Eskey and Haas (1940) include it among those species that transmitted plague experimentally in the laboratory. From their data it seems that *C. gunnesoni* and *C. ludivicianus* are the 2 most important hosts, but they indicate that the species was one of the two least selective with respect to host preference.

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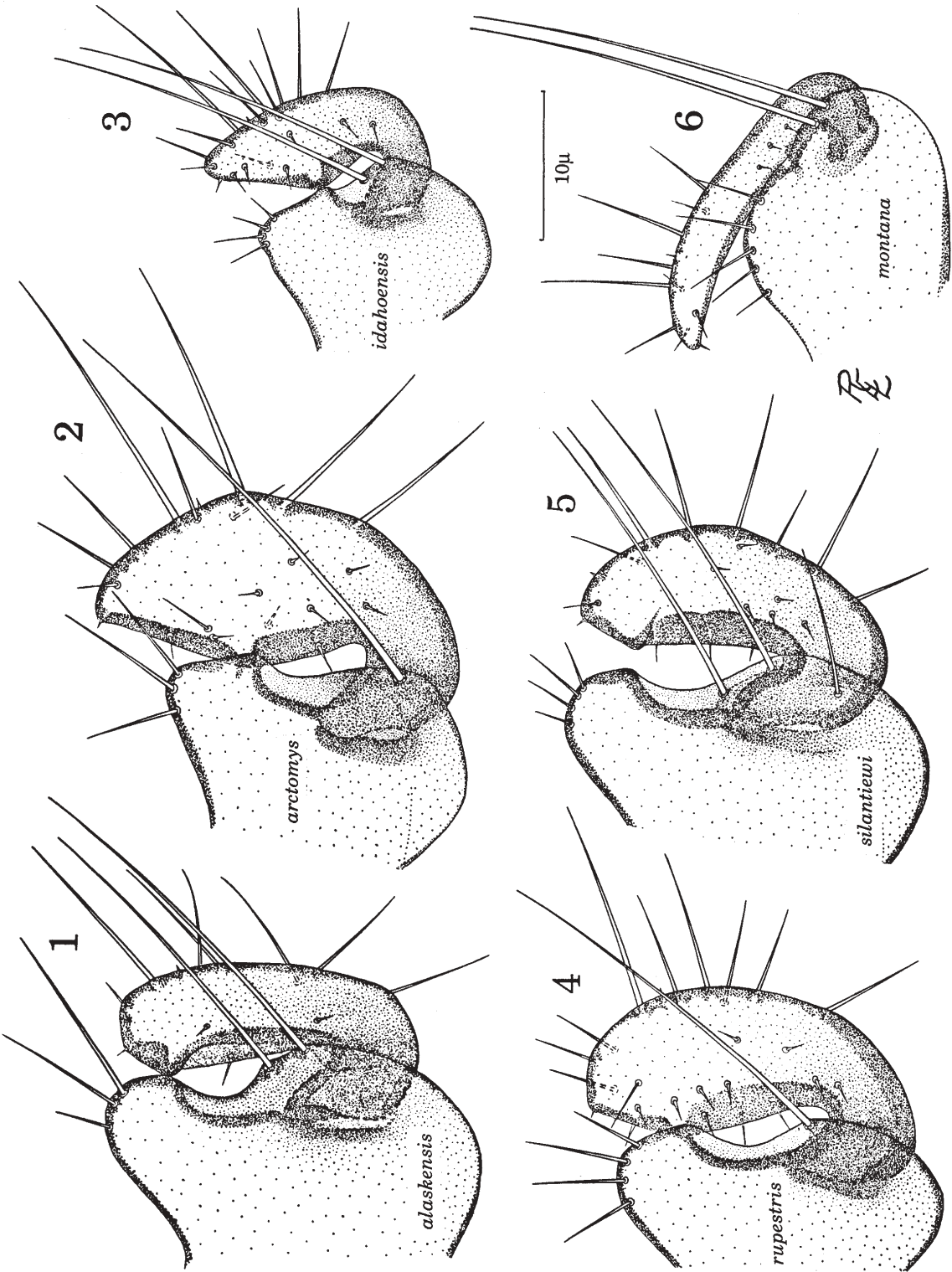
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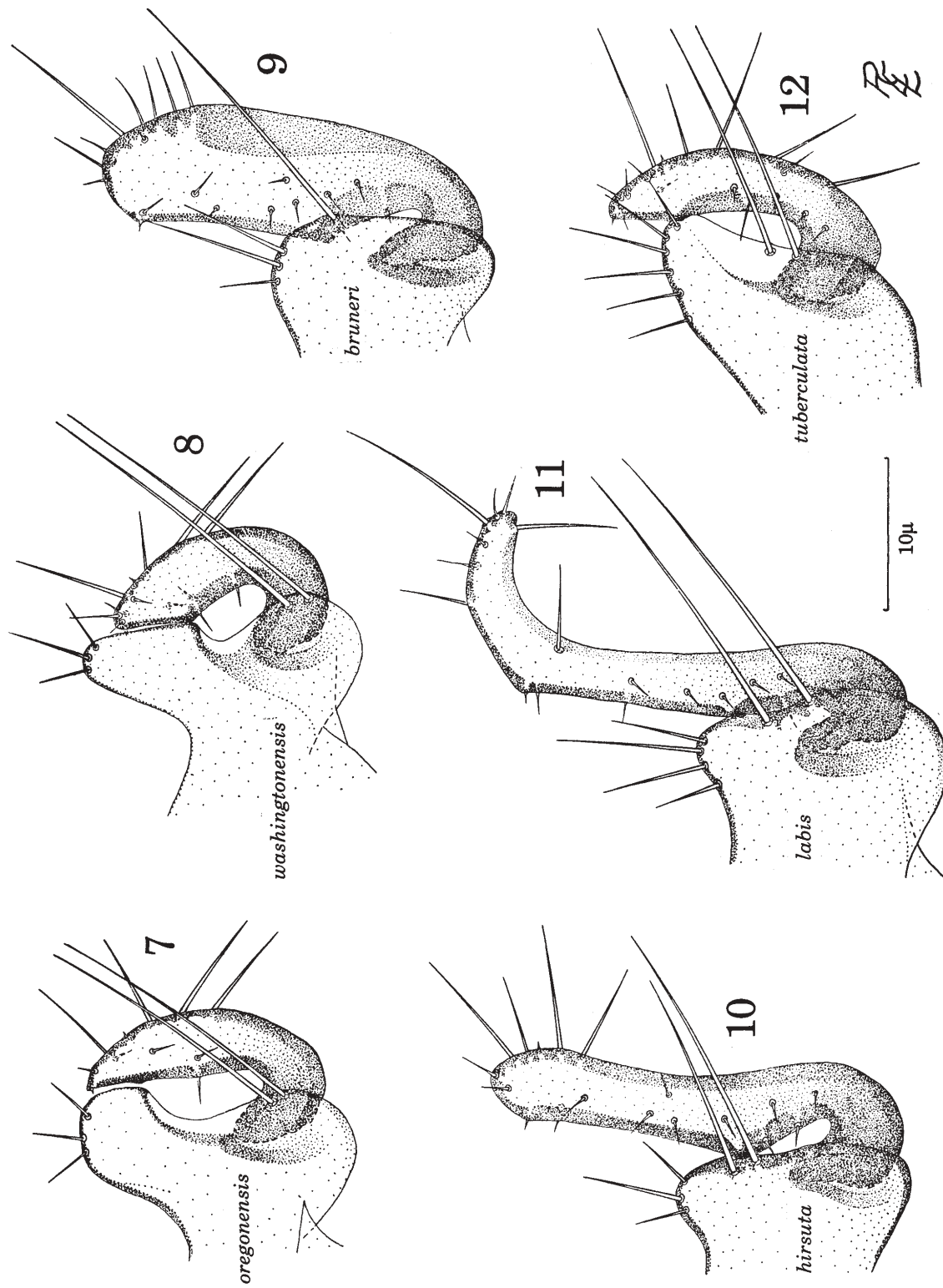
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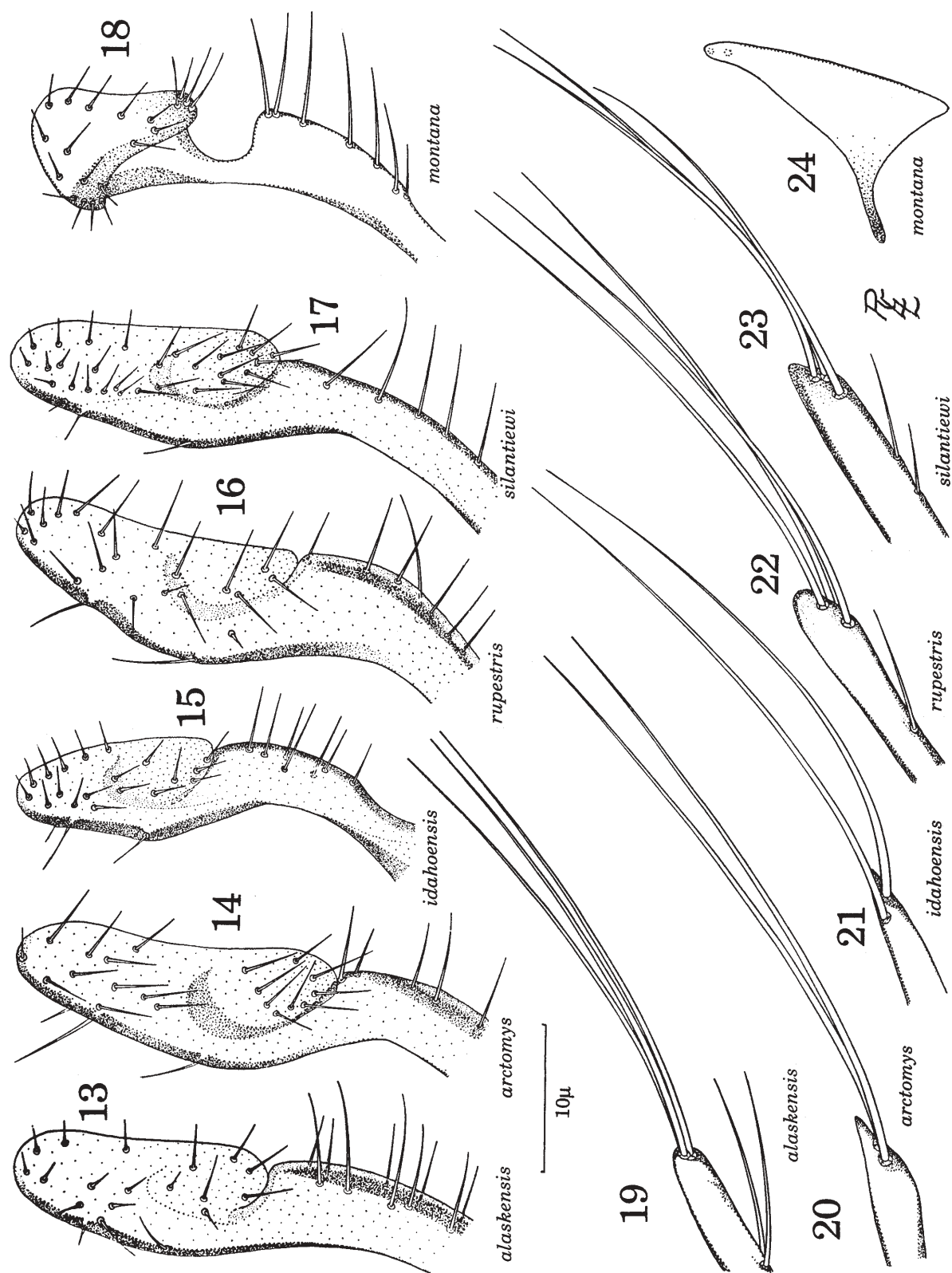
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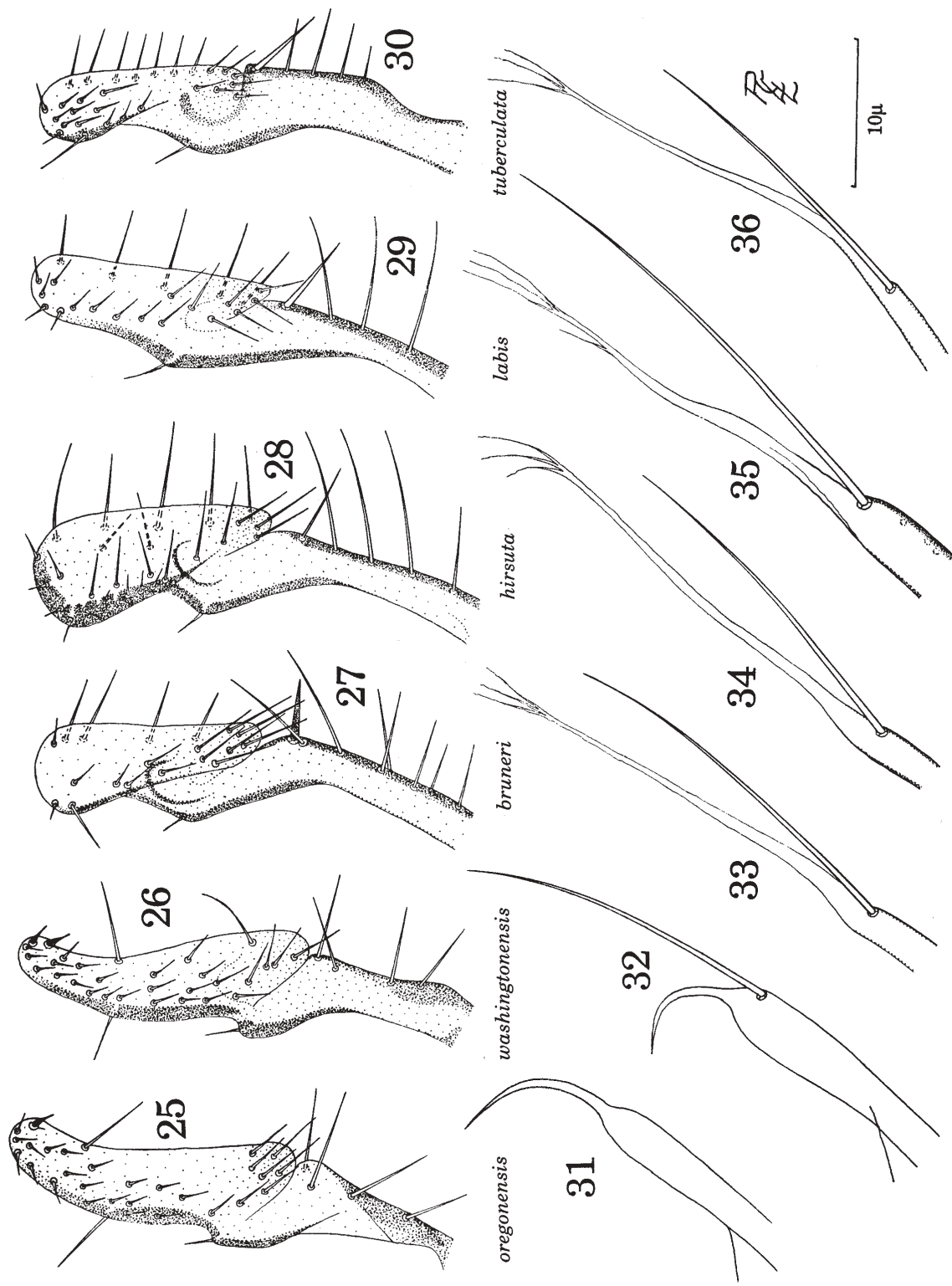
Figures 1-6. Fixed and movable processes of male claspers in *Oropsylla* (*Oropsylla*) and *O.* (*Diamanus*) species.



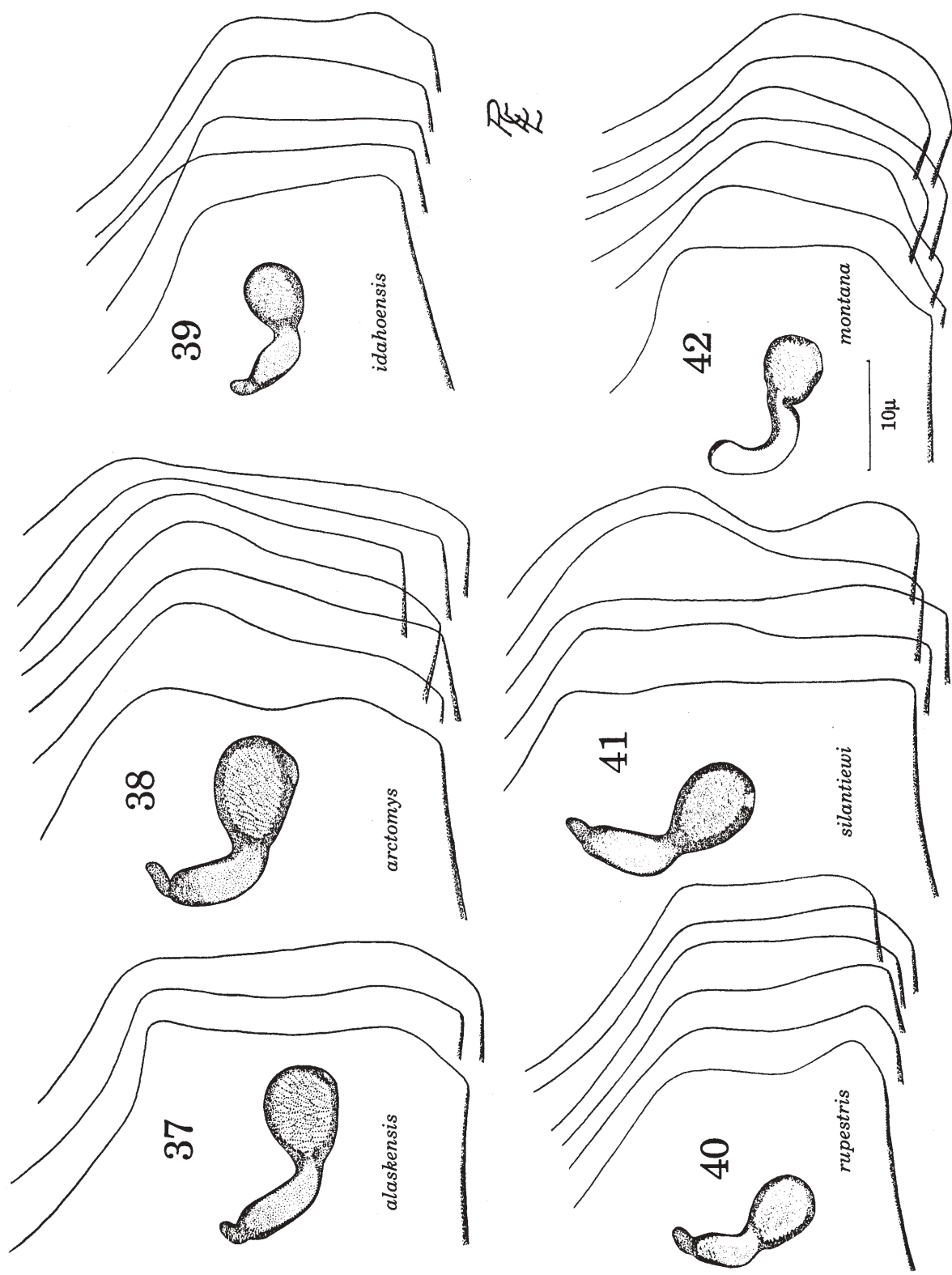
Figures 7-12. Fixed and movable processes of male claspers in *Opisylla* (*Hubbardipsylla*) and *O. (Opisocrostitis)* species.



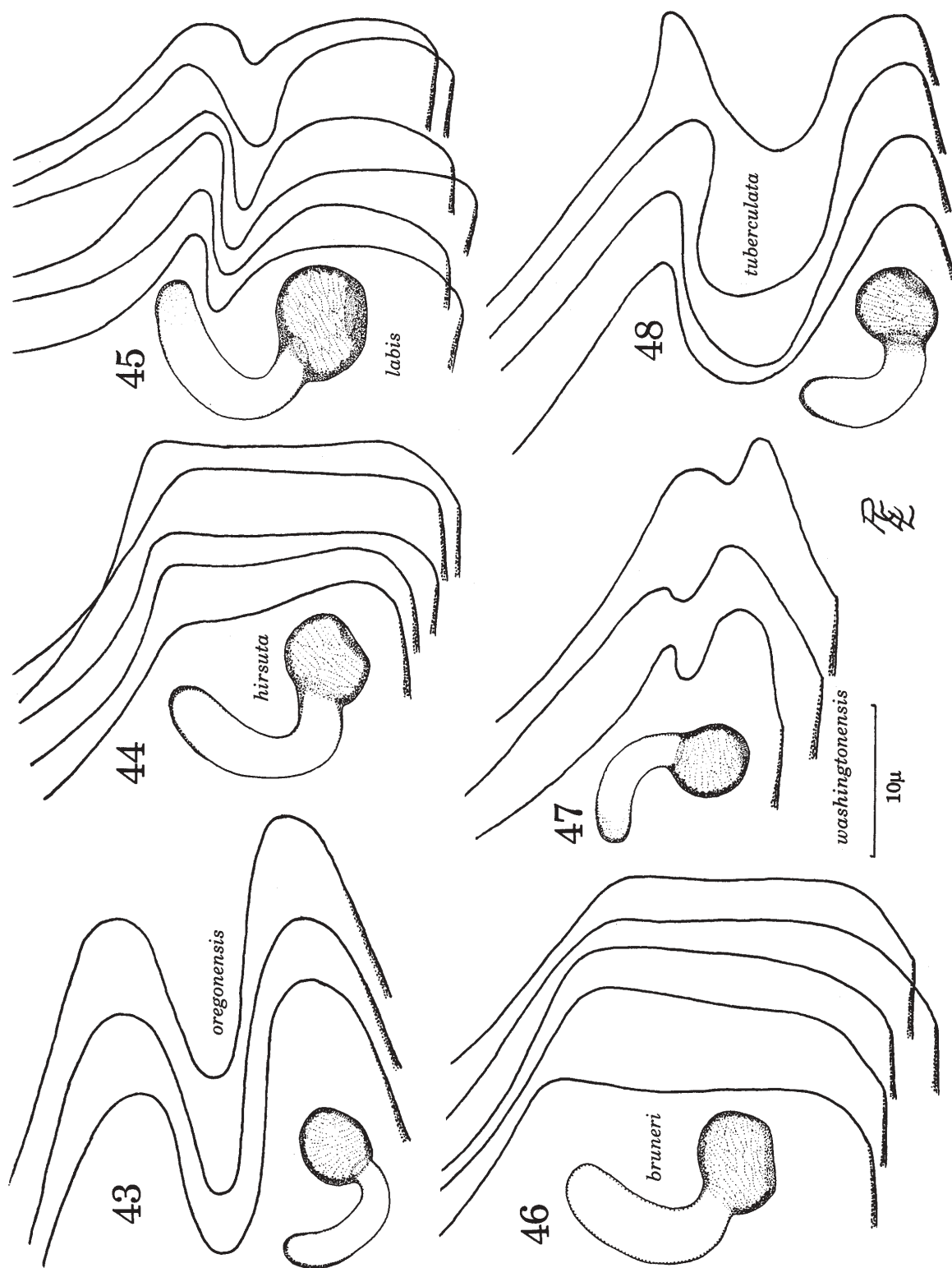
Figures 13-24. Apices of male sternites VIII and IX in *Oropsylla* (*Oropsylla*) and *O. (Diamanus)* species.



Figures 25-36. Apices of male sternites VIII and IX in *Oropsylla* (*Hubbardipsylla*) and *O. (Opisocrostis)* species.



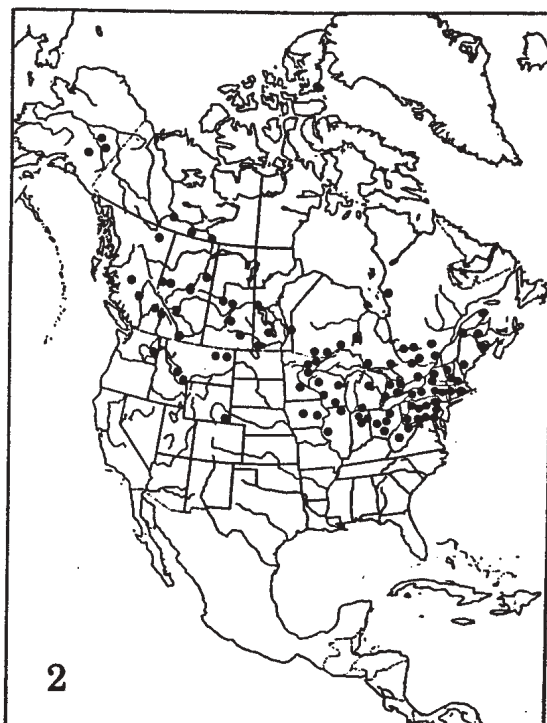
Figures 37-42. Spermathecae and contours of sternite VII in females of *Oropsylla* (*Oropsylla*) and *O. (Diamanus)* species.



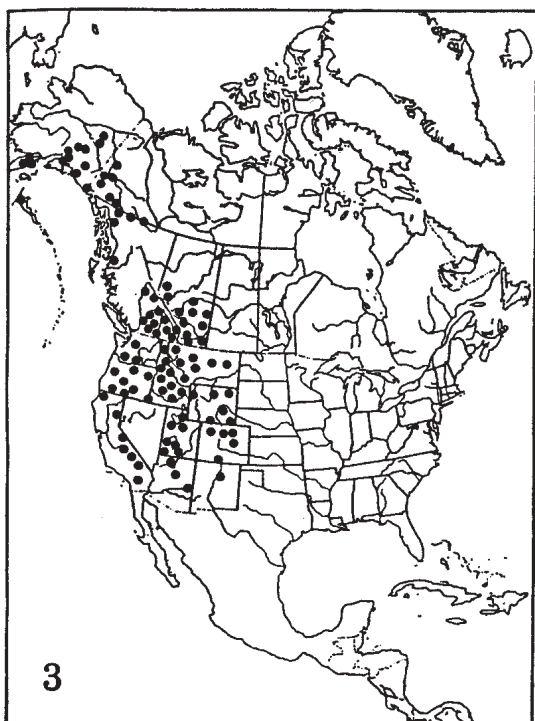
Figures 43-48. Spermathecae and contours of sternite VII in females of *Oropsylla* (*Hubbardipsylla*) and *O. (Opisocrostis)* species.



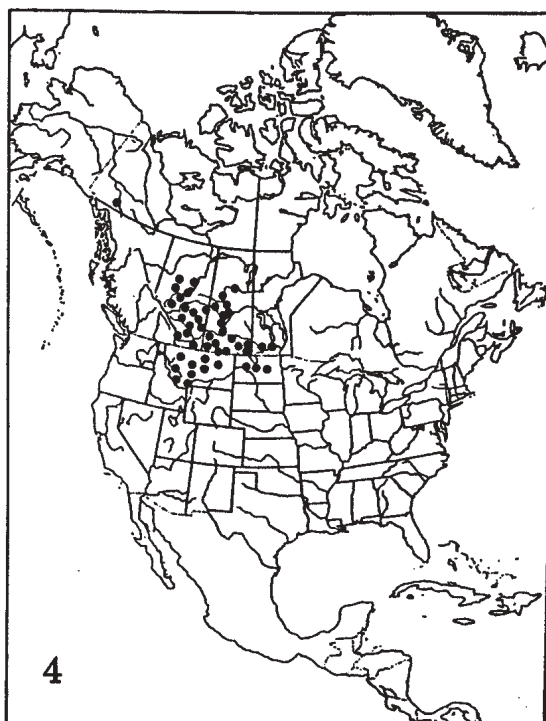
Oropsylla (Oropsylla) alaskensis (Baker, 1904)



Oropsylla (Oropsylla) arctomys (Baker, 1904)



Oropsylla (Oropsylla) idahoensis (Baker, 1904)



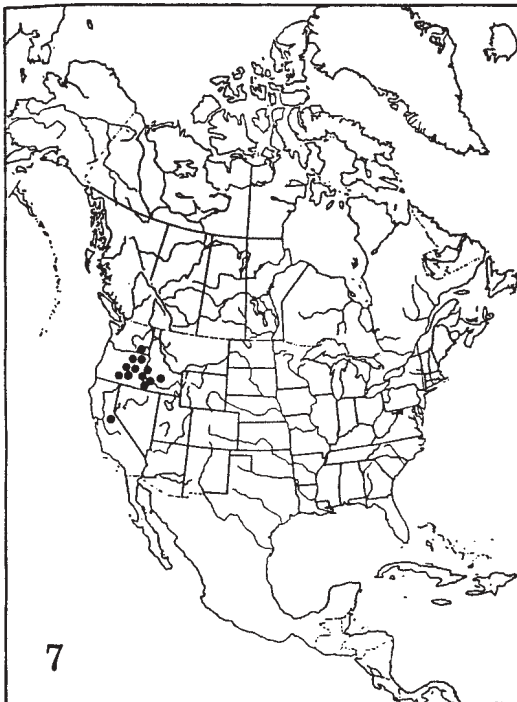
Oropsylla (Oropsylla) rupestris (Jordan, 1929)



Oropsylla (Oropsylla) silantiewi (Wagner, 1898)



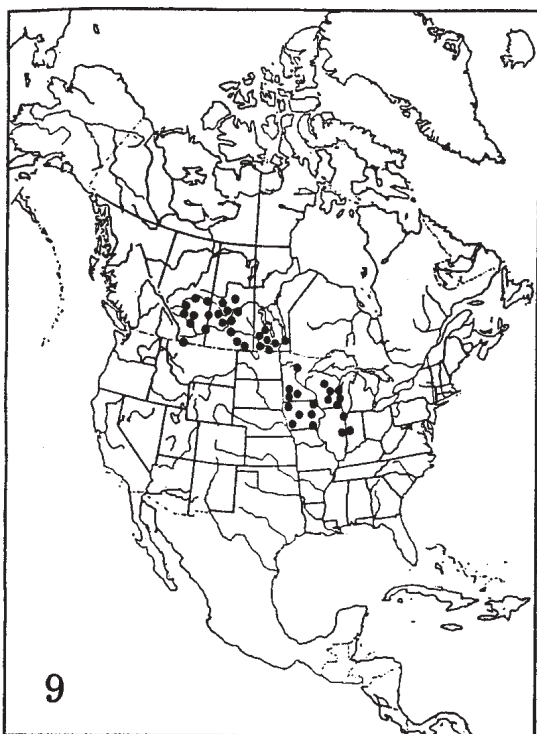
Oropsylla (Diamanus) montana (Baker, 1895)



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



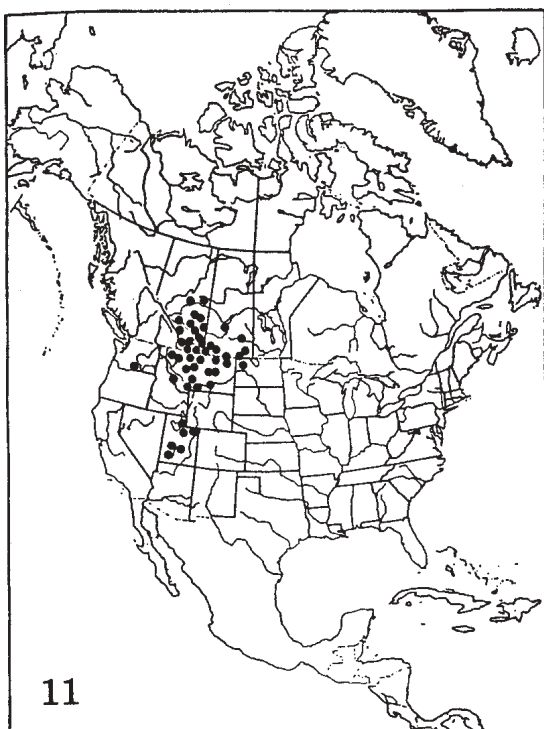
Oropsylla (Hubbardipsylla) washingtonensis (Good & Prince, 1939)



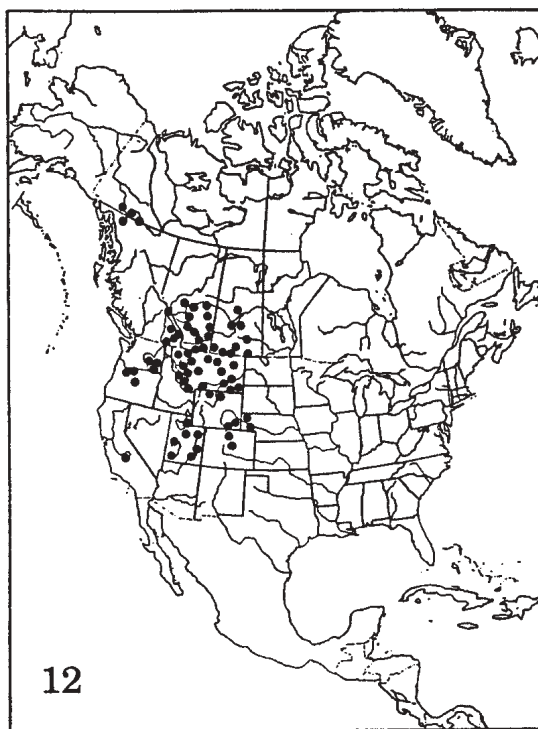
Oropsylla (Opisocrostis) bruneri (Baker, 1895)



Oropsylla (Opisocrostis) hirsuta (Baker, 1895)



Oropsylla (Opisocrostis) labis (J. & R., 1922)



Oropsylla (Opisocrostis) tuberculata (Baker, 1904)