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A Pulcid Flea in Miocene Amber from the Dominican Republic (Insecta: Siphonaptera: Pulicidae)*

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ABSTRACT

A new species of flea, *Pulex larimerius*, is described on the basis of a complete female specimen in Miocene amber from the Dominican Republic. Although at least eight other, exceptionally rare fleas are known from Dominican amber, the ones that have been studied all belong to the Rhopalopsyllidae. The specimen described here is unique as the only known fossil in the Pulicidae;

its genus is found throughout the Western Hemisphere and contains one species known to be a cosmopolitan pest. The six described, extant species of *Pulex* feed on a great variety of mammalian hosts, and even a species of bird. The presence of five strands of hair in the amber with the flea virtually confirms the mammalian host of the fossil.

INTRODUCTION

Amber is renowned for the exquisite preservation of small organisms that became entrapped in it millions of years ago when it was sticky resin. Most life forms in amber had habits (based on inference from modern relatives) for which we would expect entrap-

ment in tree resin: midges that swarmed too close to the tree trunk, ants that scurried along the tree trunk, stingless bees that harvested the resin for their nests. As one might expect, ectoparasitic arthropods are extremely rare in amber, as they are in any fossil

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deposit. We report one such exceptional fossil here, in lower Miocene amber from the Dominican Republic.

Fossil fleas, or presumed fleas, have been previously reported from Baltic amber as well as several sedimentary deposits. *Palaeopsylla klebsiana* Dampf, 1911, and *Palaeopsylla dissimilis* Peus, 1968, were described from Baltic amber. According to Larsson (1978) and Poinar (1992, 1995b), these two species belong to the family Hystrihopsyllidae, but *Palaeopsylla*, a primitive genus with 49 living species, is now assigned to the hystrihopsyllid family Ctenophthalmidae. The species in this genus are mainly parasites of insectivores and are restricted to the Palearctic Region. Fleas in Baltic and Dominican amber are the only known Tertiary fossils, although there are five Cretaceous taxa that are presumptive fleas or perhaps closely related to the order Siphonaptera (Lewis and Grimaldi, in prep.).

Dominican amber is known for the great variety of organisms preserved in it, perhaps even more diverse than the Oligocene/Eocene Baltic amber that has been studied for centuries (Larsson, 1978). The age of Dominican amber has been unnecessarily confused. An Oligocene and Eocene age (30–40 Ma) has been given by Poinar (1992, 1995a, 1995b), but stratigraphic information indicates that this amber is actually Miocene (Grimaldi, 1995; Iturralde-Vinent and MacPhee, 1996). Fossils belonging to 24 orders of insects are known from Dominican amber, including such small and rare orders as Zoraptera (Poinar, 1992; Grimaldi, unpubl.). No mallophagan or anopluran lice have been found thus far, nor have bird and bat flies (Hippoboscidae, Nycteribiidae, and Streblidae), but extremely rare ticks occur in this amber (Poinar, 1992; Grimaldi, 1996) and even rarer are the fleas.

Poinar (1992) mentioned three fleas studied by R. Traub, all of which are reported to belong to the Rhopalopsyllidae; two in the Traub collection, the other in the United States National Museum, Smithsonian Institution. Since then, Poinar reported (1995b) another rhopalopsyllid, identified by R. E. Lewis as *Rhopalopsyllus* sp. That specimen is in Poinar's personal collection. There are at least four more unstudied specimens: one

in the Staatlichmuseum für Naturkunde, Stuttgart (photo in Grimaldi, 1996: 115) and the other three in private collections. These appear to be rhopalopsyllids as well. Poinar (1992) reported, based on unpublished work by Traub, that even though most extant rhopalopsyllids feed on rodents and marsupials, morphological features of the three specimens studied by Traub indicate that they were bird parasites. The only living members of this family that are avian ectoparasites belong to the genus *Parapsyllus*, most of which are found on burrow-nesting sea birds in the Southern Hemisphere. A few specimens of *Listronius robertsonianus* (Jordan, 1938) have been taken from penguin nests in the Falkland Islands. Poinar (1995b) later changed his view, arguing that the Dominican amber rhopalopsyllids had capromyid rodent hosts.

Birds did exist in the Dominican amber forests, and various rare feather inclusions have been reported by Poinar (1992) and Grimaldi (1996). In fact, one feather in the Smithsonian collection has been identified, on the basis of microscopic features of the barbules, to be from a piculet woodpecker (Laybourn et al., 1994).

An incredible aspect of the piece of amber we are reporting on here is the presence of five strands of fine hair, obviously of mammalian origin. Although this is not definitive proof that the hair came from the host of the flea, the conclusion is unavoidable, based on the taxonomic position of the fossil and the probability of its preservation. Fleas are extremely rare in Dominican amber, with only eight specimens known from approximately 300,000 pieces of amber ($1:30,000$ or $1:3 \times 10^4$). Hair is also very rare in amber. One of us (Grimaldi) has found only three pieces containing hair in approximately 100,000 pieces of amber screened over the last ten years ($1:30,000$ or $1:3 \times 10^4$). The likelihood of a flea and hair strands being captured simultaneously, *by chance alone*, is inconceivably remote: approximately 1 in 10^8 . Surely this fossil flea fed on a mammal, which would make it the only known fossil flea preserved with remnants of its host.

SYSTEMATICS

Genus *Pulex*

Pulex. Linnaeus, 1758. Syst. Nat., 10th ed., I: 614 (in Europa, America).

TYPE SPECIES: *P. irritans* Linnaeus, 1758, by subsequent designation by Baker, 1904.

GENERIC DIAGNOSIS: Anterior margin of head smoothly rounded or slightly angled, frontal tubercle absent or inconspicuous. Eye present, reduced in *P. sinoculus*, never sinuate or with an internal sinus. Antennal clavus asymmetrical, its dorsal margin foleaceous. Labial palpi four-segmented. Some species with vestigial genal comb of one or two spines per side. Pronotal comb absent. Mesothoracic pleural rod absent. Metanotum and first abdominal tergite of about equal length dorsally, or the former slightly longer than the latter. Spiracle of metepimeron larger than abdominal spiracles. Tarsal segment V of all legs with four pairs of lateral plantar bristles, the space between pairs three and four wider than that between pairs one and two and two and three. Inner surface of hind-coxae with row or patch of short, spiniform bristles. Sensillum with 14 pits per side. Bulga of female spermatheca globular. Not all of these characters are visible in the fossil specimen.

COMMENTS: The flea specimen we describe here is unusual in that it not only belongs to the Pulicidae, it is also a member of an extant genus: *Pulex*. This genus is indigenous to the Western Hemisphere, with one species, *P. irritans*, found throughout the world. It is sometimes divided into two subgenera, each with three species. The species of (*Juxtapulex*) are *P. alvarezi* Barrera, 1955, from the Central American tapir (*Perissodactyla*); *P. echidnophagoides* (Wagner, 1933) from southern Costa Rica from armadillos (*Xenarthra*), and *P. porcinus* Jordan and Rothschild, 1923, from southern Texas and Mexico from peccaries (*Artiodactyla*).

The nominate subgenus, to which this fossil species is assigned because it lacks an angular frons or any sign of a frontal tubercle (characters found in members of the other subgenus), contains *P. sinoculus* Traub, 1950, from Guatemala from pocket gophers (*Rodentia*) and the *P. irritans/simulans* complex. The taxonomic history of *P. irritans* and *P. simulans* is somewhat confused. Until Baker erected *P. simulans* in 1895, all North American records were assigned to *P. irritans*. Jordan and Rothschild (1908) synonymized *P. simulans* with *P. irritans* and it was

not until 1958 that the name was finally resurrected by Smit. From 1908 to 1958 all North American collections were assigned to *P. irritans*. Though the two species are practically impossible to separate in the females and differences in the males are virtually cryptic, they do show some differences in host preferences that allow us to at least speculate about the true nature of the records reported during the 50 years that *P. simulans* was not acknowledged to be a valid species.

First, *P. simulans* is restricted to the Western Hemisphere where it is known from Florida, west and north to southern Alberta and British Columbia in North America, south to the northern half of Brazil and northern Chile in South America. Haas and Wilson (1967) reported this species from Hawaii. It parasitizes a broad range of hosts (*Didelphis* [*Didelphimorphia*], *Canis*, *Mephitis*, and *Urocyon* [*Carnivora*] *Spermophilus* [*Rodentia*], and *Odocoileus* [*Artiodactyla*]) but it seems to be primarily a parasite of prairie dogs (*Cynomys* [*Rodentia*]) and other burrow-dwelling hosts. It occurs at the lower elevations in Central and South America and is replaced by *P. irritans* at higher altitudes, as pointed out by Hopla (1980), but sufficient material to analyze the distribution is not available at this time. Both Hopla (1980) and Smit ([formerly curator of Siphonaptera at the British Museum of Natural History] personal communication. to Lewis) are of the opinion that this is a complex genus and that there are a number of undescribed South American species allied to *P. simulans* that must be studied before it can be accurately delineated.

Pulex irritans is also certainly native to the Western Hemisphere and there it is sympatric with *P. simulans* except in much of northeastern North America and southern South America where *P. simulans* has not been taken. *Pulex irritans* has been transported to other parts of the world via human agencies, but *P. simulans* evidently has not. In some parts of the world *P. irritans* is most common on large, hole-dwelling hosts such as foxes, porcupines, and badgers, and sometimes it becomes a pest of domestic animals. While definitely a parasite of mammals, a population of this species parasitizes the burrowing owl (*Speotyto cunicularia*) from southern British Columbia to northern Utah,

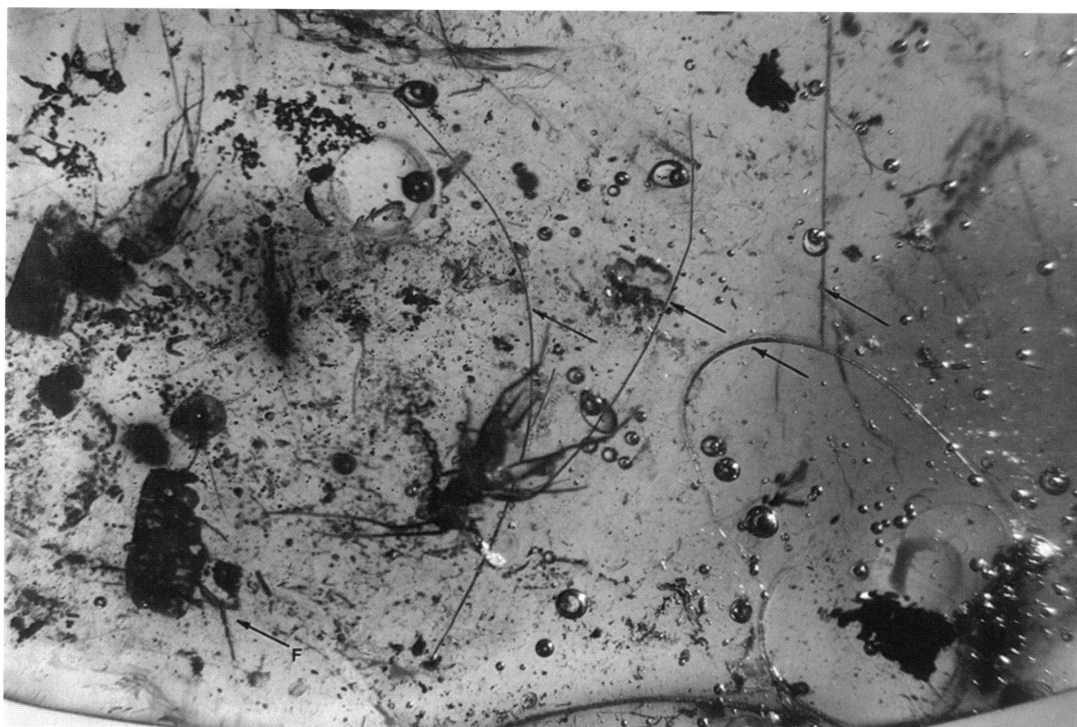


Fig. 1. Photograph of AMNH DR-14-1140, showing most inclusions, particularly the strands of hair (arrows) and the flea (arrow with F).

and western Montana and Wyoming to eastern Washington and Oregon. Hopla (1980) found the species to be remarkably homogeneous morphologically in spite of its broad distribution. However, because of its distribution, it has been reported from a multitude of hosts, most of them probably accidental associations.

Hopla (1980) discussed the genus in detail, especially the host associations and zoogeography of the *Pulex irritans/simulans* complex.

***Pulex (Pulex) larimerius*, new species**

Figures 1, 2

HOLOTYPE: Female, AMNH DR-14-1140.

ETYMOLOGY: Named in honor of Roy and Maria Larimer, who donated the specimen to the AMNH because of its scientific value.

DIAGNOSIS: Anterior margin of head smoothly rounded and lacking a frontal tubercle. Interantennal suture (falx) present. Antennal clavus asymmetrical (though missing from left side and distorted on right). Eye

present and conspicuous, but somewhat reduced in diameter, resembling that of *P. sinoculus*. Labial palpi stiff and sclerotized, their basal segmentation obscured. Mesothorax without internal pleural rods. Metanotum slightly longer dorsally than abdominal tergum I. Tarsal segment V of all legs with four pairs of lateral plantar setae, the distal pair somewhat more delicate than the proximal three pairs. Tarsal claws of all legs long, slender, and bearing a slender basal tooth. All abdominal tergites and most sternites with a single row of long setae. No visible tergal spinelets. One long antesensorial seta per side. Sensillum small, convex, and with a well-developed anterior collar.

DESCRIPTION: Body length ~2.19 mm.

Head. Head capsule smoothly rounded, its frontal and occipital margins separated by narrow but well-defined falx. Frontal tubercle absent. Eye well developed but somewhat reduced in diameter compared to other members of the subgenus except *P. sinoculus*. Three setae in ocular row but no evidence of

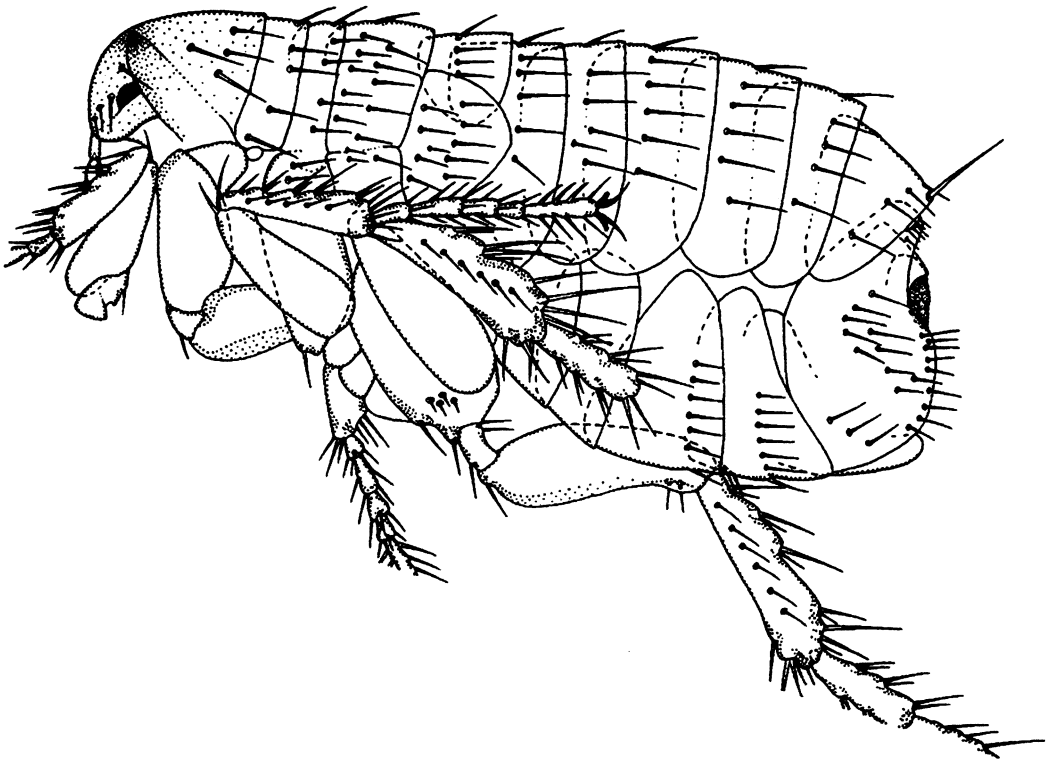


Fig. 2. **Top:** Photomicrograph of flea in AMNH DR-14-1140. **Bottom:** Illustration of flea.

a genal spine. Antennal fossa deep, one side containing a shriveled antenna with an asymmetrical clavus. One long seta per side about midway along the dorsal margin of the antennal fossa. Both frontal and occipital areas of head capsule punctate. Occipital setal row of three long bristles per side, not extending over dorsal margin of head. Maxillary lobe triangular, its palpus four-segmented. Labial palpi stiff, sclerotized, their basal segmentation obscured, but with a least four visible segments, the terminal segment about twice the length of the other visible segments. **Thorax.** Pronotum with five or six setae per side in a single continuous row over dorsum. Prosternosome bare. Mesonotum also with a continuous row of five or six long setae per side. Mesepisternum with two, and mesepimeron with four long setae per side. Metanotum with six long setae per side preceded by two irregular rows of shorter bristles but lacking marginal spinelets. Metepisternum bare, but metepimeron with ten long bristles arranged in two irregular rows of five each. **Legs.** Outer surface of forecoxa with a number of oblique rows of setae, most of which are missing. Foretrochanter and forefemur distinct but bare. Foretibia with about four notches in dorsal margin bearing pairs of long setae, the longest in apical notch extending about half way to the apex of foretarsal segment II. All tarsi five-segmented. Foretarsal segments I and IV shortest, about as long as wide, segment III slightly longer, segment II still longer, and segment V the longest, with four visible pairs of lateral plantar setae, the apical pair much smaller than the other three pairs and spaced as is typical for the genus. Foretarsus terminated by pair of long, thin, tarsal claws (ungues) each with a long, thin, basal tooth. Dorsal margin of midtibia with five notches bearing paired, long setae. Midtarsal segments subequal in length, segments I and IV slightly longer than wide, segment III about twice as long as wide, segment II about three times as long as wide, and segment V slightly longer, with chaetotaxy and unguis as described for foretarsus. Hindcoxae with three or four mildly spiniform bristles apically on inner surface. Dorsal margin of hindtibia with five notches bearing paired long setae, as well as a submarginal row of six fine setae on outer

surface. Longest seta in apical notch extending about $\frac{3}{4}$ distance to apex of hindtarsal segment I. Hindtarsal segment IV hardly as long as wide, segment III slightly longer than wide, segments II and V about equal in length and segment I the longest. The longest apical seta of segment I extends beyond the apex of segment II, that of segment III extends beyond the apex of segment IV, and segment V bears the chaetotaxy as described for the other legs. **Unmodified Abdominal Segments.** Abdominal tergum I with four setae per side in a single row. Terga II–VI with five or six setae per side, also in a single row. Tergum VII with one row of about four long setae and one antesensilial seta per side on its caudal margin. Tergum VIII with about 12 setae per side on its outer surface and another 8 to 10 setae per side along its caudal margin. Sterna III–VII with a single row of four to six setae per side. Caudal margin of sternum VII slightly concave and sternum VIII triangular. **Genital Segments.** Sensillum small, slightly convex dorsally, with a well-developed anterior collar, but the number of pits cannot be determined (14 is normal for the family). The anal stylets, spermatheca, and genital ducts are not visible.

REMARKS

Fleas are usually described from material mounted on microscope slides and are thus only examined in one aspect. However, amber fossils can be manipulated in ways that reveal structures in more than one aspect. Therefore, it should be understood that the accompanying drawing is a composite of both sides of the specimen rather than an illustration of one side.

The amber in which the specimen is preserved is a flat, oval piece, 21 mm long \times 12 mm wide and 4 mm thick, containing the following inclusions: the flea, tiny pyritic crystals (≤ 20 μ m diameter) scattered throughout two fracture planes that parallel the surface (the flea is immediately under one of these planes); cleared/skeletonized phorid fly; decayed, exoskeletal remains of unidentifiable insects; two very tiny (0.35 mm) wingless hexapods, probably neanurid or onychiurid collembolans (a furcula is absent); a nymphal oecanthine (tree) cricket; several

insect fecal pellets and particulate debris; and five strands of fine hair (the longest and most complete is 9.65 mm long and 50 μ m thick).

COMMENTS

Because this flea belongs to an extant genus, and the piece of amber has hair in it, questions of the authenticity of the amber may arise. The piece is unquestionably authentic Dominican amber, based on a variety of features and circumstances. The other inclusions in the amber, their state of preservation, the fact that a hot needle touched to the surface produces a resinous smell, not like burning plastic, and that the piece fluoresces under long-wave UV light, all attest to its authenticity. Also, the piece was discovered among a group of approximately 1000 small pieces of Dominican amber and was not being sold under any pretense.

DISCUSSION

MAMMALS CONTEMPORANEOUS WITH DOMINICAN AMBER

The host of this flea was certainly mammalian. There are several other specimens of Dominican amber containing hematophagous vertebrate parasites preserved with remains of their host. Piece number DR-12-857 in the AMNH contains a tick belonging to the ixodid genus *Amblyomma* with two complete strands of short, fine, stiff hair. There is a remarkable specimen in the Stuttgart collection (DO-5514-M) containing a small swarm of phlebotomine sandflies with approximately 10 strands of hair and debris, probably from a mammal nest. Most of the female sandflies are replete, probably from a blood meal. A photograph of a portion of the piece is shown in Grimaldi (1996: 114). Microscopic features of the hairs in these two pieces have yet to be studied. An argasid tick was reported in a piece of Dominican amber with a probable mammalian scat (Poinar, 1995a).

Hair has been previously reported from Dominican and even Mexican amber (Poinar, 1988, 1992; Poinar and Columbus, 1992). One piece from Costa Collection in Puerta Plata, Dominican Republic (plate 3 in Poinar, 1992) contains a clump of numerous fine hairs. The presence of a mite belonging to

the family Atopomelidae suggests that the hairs belonged to a rodent. The bulk of the New World, Northern Hemisphere species of these mites are parasites of capromyid rodents, although one is known from a species of *Solenodon*, and others from New World monkeys that are now extinct in the Caribbean basin (B. M. O'Connor, personal commun.). The amber described in the other report (Poinar and Columbus, 1992) contains 40 strands of hair and an adhesive grass spikelet to which one of the strands is attached. The cuticular pattern of the hair suggested to these authors that it came from a carnivore. Poinar (1992) mentioned that although some mammals (certain bats and sloths) have distinctive hair structure, identification of hair in amber is problematic. Indeed, variation among hairs from the same individual of many mammals is known to encompass the variation seen among various mammalian orders (Brunner and Coman, 1974; Debrot et al., 1982). Recently, extremely well-preserved hair in late Paleocene coprolites from Mongolia was reported by Meng and Wyss (1996). The hairs were preserved with the skeletal remains of the multituberculate, *Lambdopsalis*, to which they presumably belonged. This hair is very similar to that of modern mammals, indicating that evolutionary changes in the fine structure of mammal hair is extremely conservative. The multituberculates are the most primitive clade of extinct mammals and originated in the Triassic.

The best evidence for a mammal contemporaneous with Dominican amber was reported by MacPhee and Grimaldi (1996). Skeletal remains of an insectivore were found in a piece of amber recovered directly from the La Toca amber mines near Santiago, Dominican Republic, by Grimaldi. The specimen, AMNH DR-14-627, consists of six thoracic vertebrae with portions of four ribs still articulated. The vertebrae are very similar to those of certain insectivores such as the Caribbean endemic solenodontids, *Solenodon* and *Nesophontes*. Unfortunately, no hair is preserved in the piece of amber.

Despite claims that "no findings of fossil mammals older than 10,000 BP [occur] in Hispaniola" (Poinar, 1995b), fossil evidence does exist for Miocene land mammals in

Puerto Rico and Cuba, and thus they must have occurred in Hispaniola as well. The mammals are a megalonychid sloth from the Miocene of Cuba (and another possible one from the Oligocene of Puerto Rico), and a capromyid rodent and platyrrhine primate, also from the Miocene of Cuba (MacPhee and Iturralde-Vinent, 1994, 1995).

SYSTEMATIC AND EVOLUTIONARY SIGNIFICANCE OF A LOWER MIOCENE PULICID

As indicated earlier, our understanding of the composition of the genus *Pulex* is far from complete and large collections of material from Central and South America are required before the alpha taxonomy of this genus can be thoroughly known. Material to support such a study is not presently available. However, the Pulicidae is thought by most pulicologists to be an advanced family compared to most others in the order and quite distinct, in spite of the diversity reflected in its current subfamily classification. *Pulex* is the type genus for both the Pulicinae and the tribe Pulicini, and the six recognized

species are remarkably similar in their morphology, in spite of their diverse host preferences. This is particularly the case in the females, which show only cryptic differences between the species. Although internal structures such as the genital ducts and spermatheca cannot be seen in this fossil, its external morphology is remarkable for its similarity to females of living species, indicating that little morphological evolution has taken place in the genus since the Miocene. (Whether this is viewed as a primitive or derived condition is a matter for conjecture.)

As noted, all of the fossil fleas previously known to date from Dominican amber have belonged to the predominantly Neotropical family Rhopalopsyllidae, most members of which are parasites of small rodents. The origin and New World distribution of species of *Pulex* certainly would favor the presence of pulicid fleas in Dominican amber. Their host preferences for larger animals probably prevented them from coming into contact with the plant resins from which amber ultimately developed.

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