

***Paleoculicis minutus* (Diptera: Culicidae) n. gen., n. sp.,  
from Cretaceous Canadian amber ,  
with a summary of described fossil mosquitoes**

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ABSTRACT

A new genus and species of fossil mosquito (Diptera: Culicidae) is described from Canadian Cretaceous amber, thus providing the first undeniable record of this group from the Cretaceous Period. *Paleoculicis minutus* n.gen., n.sp. can be separated from extant culicids by features of the head, thorax, and abdomen. *Paleoculicis* has closer affinities to the Culicinae than to the Anophelinae or Toxorhynchitinae. If *P. minutus* fed on blood, a range of vertebrates (including dinosaurs) were potential hosts some 79 million years ago. A review of previous descriptions of fossil mosquitoes is presented. Many cannot be confidently assigned to the Culicidae, while others are extant species in copal. Only a minority of them can be regarded as true Culicidae, all of which are reported from Tertiary deposits.

*Keywords:* Fossil mosquitos. *Paleoculicis minutus*. Culicidae. Canadian amber.

RESUMEN

Se describe un nuevo género y especie de mosquito (Diptera: Culicidae) del ámbar del Cretácico de Canadá, que aporta el primer registro irrefutable de este grupo en el período Cretácico. *Paleoculicis minutus* n.gen., n.sp. puede ser diferenciado de los culcideos existentes por caracteres de la cabeza, tórax y abdomen. *Paleoculicis* tiene estrechas afinidades con los Culicinae, así como con los Anophelinae o los Toxorhynchitinae. Si *Paleoculicis minutus* se alimentaba de sangre, un amplio grupo de vertebrados (incluidos los dinosaurios) fueron huéspedes potenciales hace unos 79 millones de años. Se presenta la revisión de los mosquitos fósiles descritos con anterioridad. Algunos no pueden ser asignados de manera segura a los Culicidae, mientras que otras son especies actuales encontradas en el copal. Sólo una minoría de ellos pueden ser considerados como verdaderos Culicidae, los cuales se relacionan con depósitos del Terciario.

*Palabras clave:* Mosquitos fósiles. *Paleoculicis minutus*. Culicidae. Ambar canadiense.

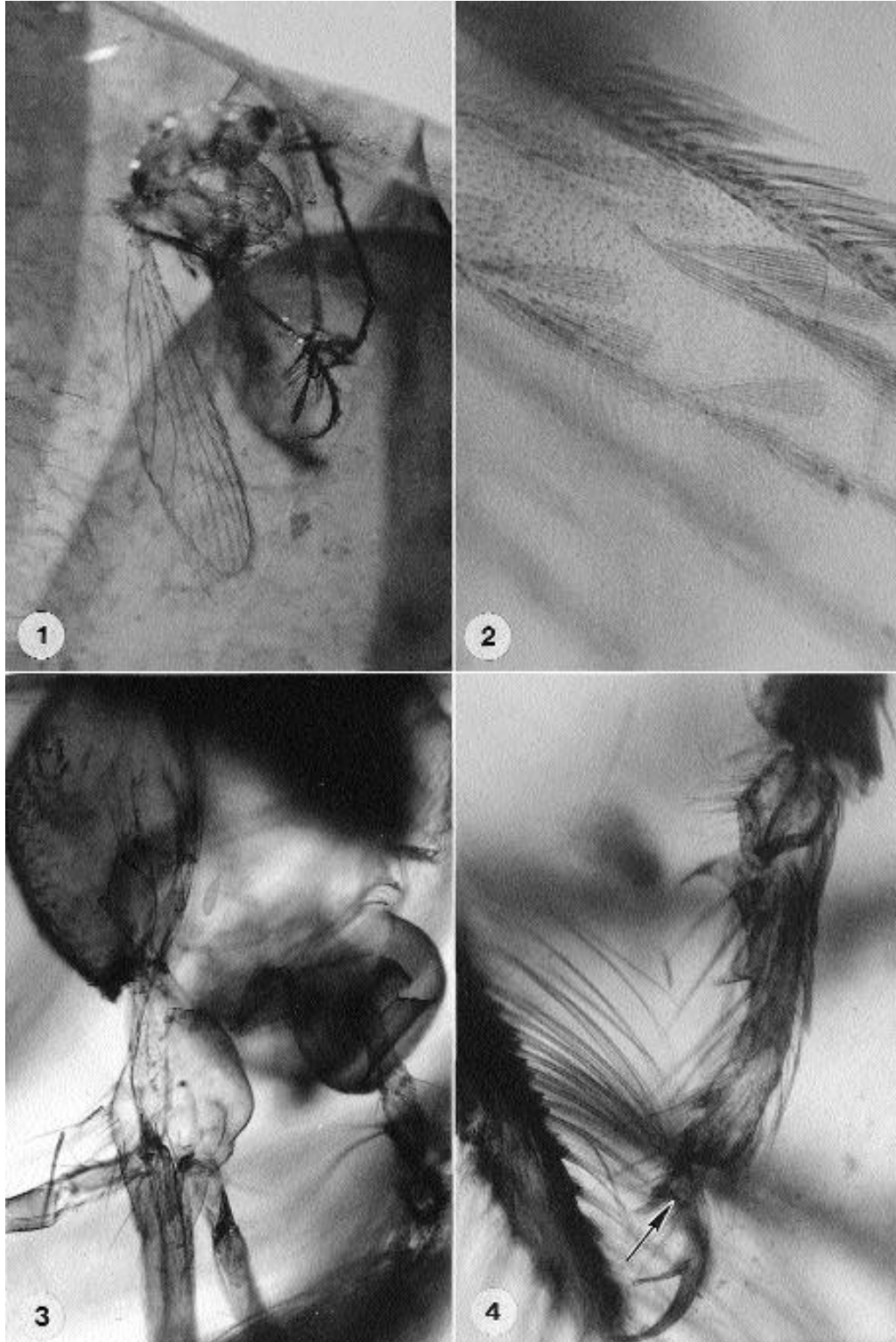


Figure 1. *Paleoculicis minutus* n.gen., n.sp. in Canadian Cretaceous amber (RTMP 95.73.1). 1.- Entire male specimen; 2.- Scales on wing veins; 3.- Portion of head showing pedicel, compound eyes, and clypeus; 4.- Terminal tarsal segments and claws on foreleg (arrow shows spur on smaller posterior claw).

## INTRODUCTION

Canadian Cretaceous amber is an important source of very interesting fossils, ranging from Protozoa (Legg, 1942) and bird feathers (Pike, 1995) to unique parasitic associations (Poinar et al., 1997). Canadian amber occurs in two separate locations, Cedar Lake in Manitoba and Grassy Lake in Alberta (Poinar, 1992). A taphonomic study described the various types of amber found in these deposits (Pike, 1995). Careful analyses indicated that the Cedar Lake amber originated from Alberta where the amber was washed out of sedimentary layers lining the beds of the Saskatchewan River and deposited in Cedar Lake. Thus the amber from both sources is presently thought to originate from the same general deposits, to be the same age, and to be formed by the same araucarian trees (Lambert et al., 1990). Amber sediments occur in the Foremost Formation of the Judith River Group. This formation comprises a portion of the Campanian which ranges in age from 76.5 to 79.5 million years (Eberth and Hamblin, 1993).

While studying the inclusions in these deposits, one of us (T.P) noted a small nematoceran that belonged to the Culicidae. Further examination revealed that the specimen was a unique male mosquito that could not be placed in any known genus. The present study describes this fossil, discusses its implications, and provides a summary of the described fossil mosquitoes.

## MATERIALS AND METHODS

The amber containing the fossil mosquito had been embedded in bioplastic and polished down to a thin section several millimeters thick. This technique not only preserves the specimen but allows it to be viewed in detail under the compound microscope, a necessity when working with such small, rare fossils. Thus far, after approximately five years, the medium has remained clear and unchanged. The amber was orange with darker, somewhat parallel, undulating lines that probably represent the borders of sequential resin flows. Drawings were made with the aid of a camera lucida, and photographs were taken with a Nikon Orthophot microscope.

## RESULTS

Careful examination of the fossil mosquito revealed the following characters that place this specimen in the family Culicidae: 1) long, narrow wings with typical

mosquito venation, 2) well-developed palpus characteristic of male mosquitoes, 3) no ocelli, 4) evidence of a long proboscis, and 5) numerous scales on the wing veins, wing margins, and legs. Since it can not be placed in any existing genus of Culicidae, the specimen is described below in a new genus. Morphological terminology follows McAlpine et al. (1981) in large part.

**Order:** Diptera LINNAEUS, 1758

**Family:** Culicidae BILLBERG, 1820

GENUS *Paleoculicis* n.gen.

Figures 1 - 2

*Diagnosis:* Distinguished by the combination of: 1) vertex of head with erect scales piliform, 2) katepisternum with about 36 bristles in broad band of 2-3 vertical rows that extend entire height of sclerite, 3) lower mesepimeron with 2 strong bristles, 4) scutellum rounded, 5) pleuron and abdomen without scales, and 6) vein Sc with bristles at base ventrally; and by the following unique characteristics (apomorphies): 1) compound eye with large facets and 2) gonocoxites with strong spicules.

*Paleoculicis minutus* n.sp.

*Description:* Adult male with body and both wings present. Size minute, length from clypeus to tip of abdomen approximately 3.0 mm. Head: Structures incomplete, with top portion obscured by bubble; proboscis obviously elongate, but only basal portion present; antennae missing but one palpus complete; vertex with erect piliform scales lacking striae posteriorly, erect piliform scales with striae anteriorly, and striated decumbent scales near eyes; compound eyes appearing to have fewer and larger facets in relation to size of head than extant culicids; eye facets slightly irregular, measuring approximately 32  $\mu\text{m}$  by 25  $\mu\text{m}$ ; lower postocular setae 2, long, strong; clypeus smaller than pedicel, width = 128  $\mu\text{m}$ , without scales or setae; basal portion of proboscis slender, with dark scales and several setae at base ventrally; palpus long, uniformly dark-scaled, no banding obvious, 5-segmented; combined palpomeres 2-3 comprising 0.59 total length of palpus, palpomere 4 comprising 0.16 length, with numerous long, strong bristles; palpomere 5 comprising 0.17 length, swollen in distal half, with fewer, shorter and finer bristles; palpomere 3 gradually enlarged toward apex, with long bristles at apex ventrally; antenna with pedicel greatly enlarged, width = 158  $\mu\text{m}$ , without setae or scales; flagellum strongly plumose (only basal 2 flagellomeres present, but long bristles of additional fla-

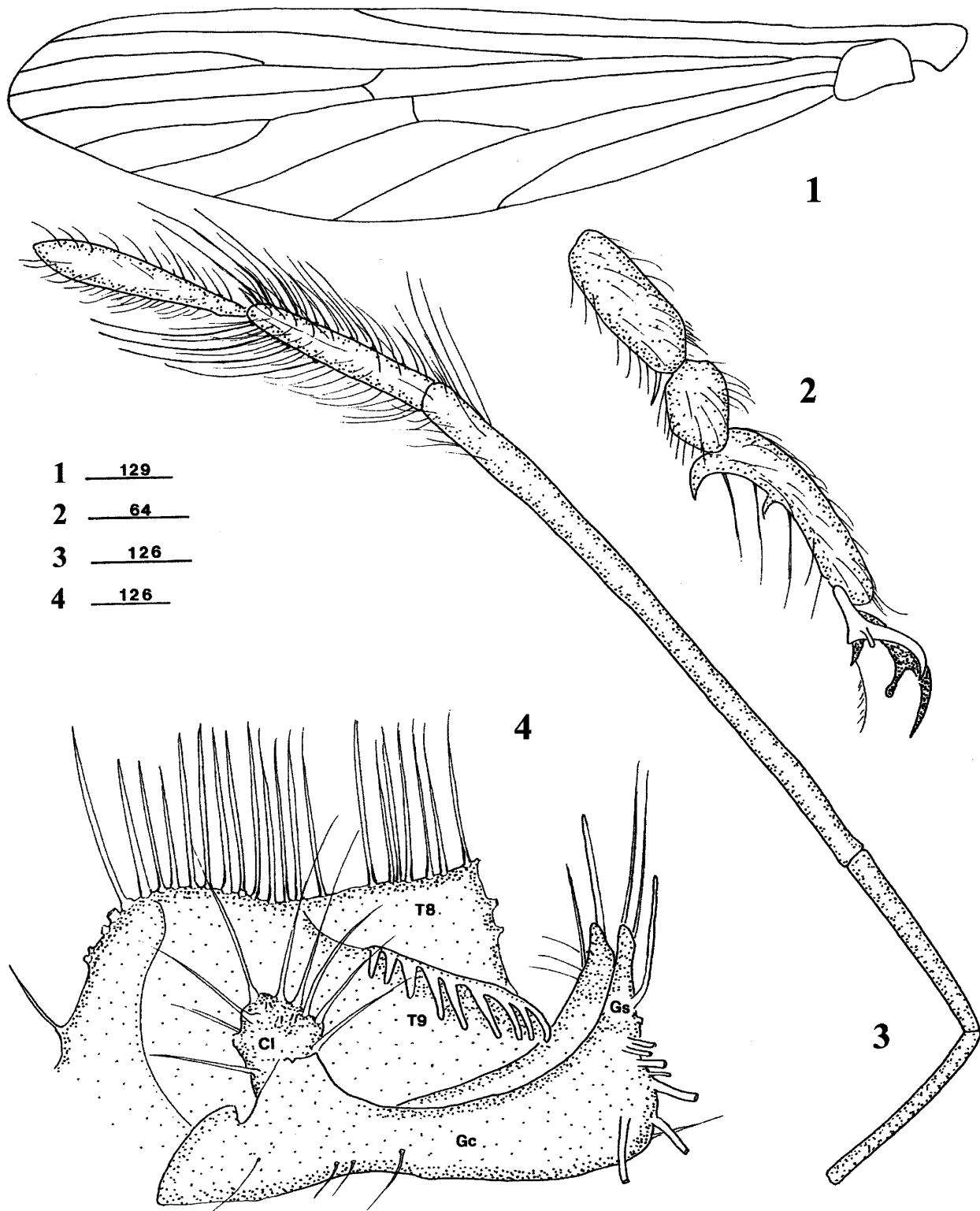


Figure 2. *Paleoculicis minutus* n.gen., n.sp. in Canadian Cretaceous amber (RTMP 95.73.1). 1.- wing venation (scales omitted). 2.- Terminal portion of left foreleg showing unequal claws and empodium. 3.- Palpus (scales omitted). 4.- Male genitalia; T 8- eighth abdominal tergite; T 9- ninth abdominal tergite; Cl- claspette; Gc- gonocoxite; Gs- gonostylus. Values in bar lines are in micrometers.

gellomeres present in amber); flagellomere 1 with scales; flagellomere 2 short. Thorax: Scutum largely obscured by bubble, but with supraalar bristles and alveoli of prescutellar bristles evident; scutellum apparently round, with a uniform row of bristles on posterior edge; mediotergite without setae; antepronota not clearly seen, but apparently small and well separated, with numerous alveoli and at least 1 erect scale; postpronotum and paratergite not visible; spiracular and postspiracular areas apparently without setae; prealar area not separated from katepisternum by distinct suture; katepisternum with about 36 bristles in broad band of 2-3 vertical rows extending entire height of sclerite; proepisternum with at least 3 alveoli; prealar setae or alveoli 12; meron large, its upper edge distinctly above base of hind coxa; mesepimeron with 12 upper setae, 2 strong lower anterior bristles and 2-3 posterior setae; pleuron apparently without scales. Legs: Both forelegs present; mid- and hindlegs missing beyond coxae; forefemur L = 901  $\mu\text{m}$ ; tarsomeres L = 1 = 838  $\mu\text{m}$ ; 2 = 183  $\mu\text{m}$ ; 3 = 110  $\mu\text{m}$ ; 4 = 61  $\mu\text{m}$ ; 5 = 148  $\mu\text{m}$ ; forecoxa with few scales and numerous bristles; foreleg completely brown scaled, no pattern or ornamentation visible; forefemur not swollen; foretarsomere 5 much longer than tarsomere 4, its plantar surface with setose swelling at base, several long, strong bristles, and 1 short, spiniform seta near middle; claws paired, enlarged, unequal; larger anterior claw with sharp basal tooth and long, blunt submedian tooth; smaller posterior claw with short basal spur projecting laterally; pulvillus apparently not developed; empodium present, its basal sclerite subquadrate, its filament long-spiculate. Wing: L = 2.1 mm, with typical culicid venation and scalation; microtrichia distinct; membrane not infuscated, banding absent; plume scales of veins narrow, symmetrical; vein Sc with single row of bristles at base ventrally; stem vein without dorsal bristles; veins RS and R 4+5 without basal spurs; cell  $r_2$  2.3 times longer than its stem; cell M slightly longer than its stem; crossveins without scales, r-m distad of m-cu; vein CuP without scales at base ventrally; vein A long, reaching wing margin far distad of level of fork of CuA; posterior margin of wing with fringe of long scales; alula with numerous closely-spaced setae; upper calypter with long row of marginal bristles. Abdomen: Tergites and sternites with vestiture of long bristles, without scales; tergite 8 with very numerous long bristles; genitalia distorted, impossible to see clearly and interpret with certainty; tergite 9 (?) with single undivided row of 9 very strong spiniform setae; gonocoxite apparently with few setae, but with very strong spicules distally; claspette (?) a large rounded lobe with at least 9 bristles, some long, near base of gonocoxite; gonostylus (?) subapical, very small, short, slender, with very long, strong spicules,

most of which appear to be broken off; phallosome and proctiger not visible.

*Type specimen:* RTMP 95.73.1; holotype male deposited in the Royal Tyrrell Museum of Paleontology in Drumheller, Alberta, Canada.

*Type locality:* Near village of Grassy Lake, Alberta. Exact co-ordinates are in file at the Royal Museum of Paleontology and available to qualified investigators.

*Occurrence:* Foremost Formation, Campanian, Upper Cretaceous.

*Etymology:* Species name "minutus" based on the small size of the specimen.

*Discussion:* *Paleoculicis* can be separated from extant genera of Culicidae by the characters listed in the diagnosis. It is not possible to place *Paleoculicis* into the classification of extant Culicidae because many characters of the single male specimen cannot be observed and characteristics of the female and immatures are totally unknown. Although the rounded scutellum and scaleless abdomen of *Paleoculicis* are characters found in the extant anopheline genera *Anopheles* and *Bironella*, many features of *Paleoculicis* — such as the presence of numerous bristles in a broad vertical band on the katepisternum, the presence of strong lower mesepimeral bristles, the presence of bristles at the base of the subcostal vein ventrally, and the presence of setae on the alula of the wing — argue against a relationship with those genera. Additionally, the form of the male palpus (palpomeres 4 and 5 relatively slender, not swollen to form a club) and foretarsus (with paired claws rather than a single claw) are unlike the usual development of these features in *Anopheles*. The rounded scutellum and scaleless abdomen of *Anopheles* have usually been interpreted as plesiomorphic characters (Belkin, 1968). Their occurrence in *Paleoculicis* supports this hypothesis.

Among extant mosquitoes, the presence of numerous bristles on the lower surface of the wing at the base of the subcostal vein is known in the genera *Culiseta* and *Opifex* and the subgenera *Nothoskusea* of *Aedes* (females only), *Austromansonia* of *Coquillettidia* (Belkin, 1968), and a few species of *Coquillettidia* s. s. (Marks, 1974). As noted in more detail below, the occurrence of bristles at the base of the subcostal vein ventrally has been interpreted as a plesiomorphic character.

The genitalia of a male mosquito typically provide numerous valuable taxonomic characteristics. Unfortu-

<u>Species</u>	<u>Age and location</u>	<u>Reference , notes</u>
<b>Recent</b>		
<i>Aedes ciliaris</i> (LINNAEUS)	Copal, Sweden	Linnaeus, 1767; Bloch, 1776; <i>nomen dubium</i> (Natvig, 1948); possibly same as <i>Aedes cinereus</i> MEIGEN (Edwards, 1932; Natvig, 1948).
<i>Culex flavus</i> GISTL	Copal, Brazil	Gistel, 1831
<i>Culex loewi</i> GIEBEL	Copal, Africa	Giebel, 1862; this is <i>Toxorhynchites brevipalpis</i> THEBALD 1901 (an extant species); <i>loewi</i> has been suppressed by the International Commission on Zoological Nomenclature (Opinion 1213) (Melville, 1982).
<i>Culex tanzaniae</i>	Copal, Tanzania	Capasso, 1991; <i>nomen nudum</i>
<b>Tertiary</b>		
<i>Aedes petrifactellus</i> (COCKERELL)	Oligocene, Isle of Wight, England	Cockerell, 1915; synonym of <i>A. protolepis</i> (Cock.) (Edwards, 1923).
<i>Aedes protolepis</i> (COCKERELL)	Oligocene, Isle of Wight, England	Cockerell, 1915
<i>Anopheles? rottensis</i> STATZ	Oligocene, Rott, Germany	Statz, 1944
<i>Culex damnatorum</i> SCUDDER	Eocene, Green River, Wyoming	Scudder, 1890
<i>Culex erikae</i> SZAD. AND SZAD.	Eocene, Poland	Szadziewski and Szadziewska, 1985
<i>Culex pipiens</i> LINNAEUS	Eocene, Poland	Keilbach, 1982; <i>Culex pipiens</i> is a recent species and further studies of the fossil may show it to be <i>C. erikae</i> or an undescribed species
<i>Culex proavitus</i> SCUDDER	Eocene, Fossil Canyon, Utah	Scudder, 1877; a psychodid (Edwards, 1923)
<i>Culex protorhinus</i> COCKERELL	Oligocene, Isle of Wight, England	Cockerell, 1915; generic position doubtful (Edwards, 1932)
<i>Culex vectensis</i> EDWARDS	Oligocene, Isle of Wight, England	Edwards, 1923
<i>Culex winchesteri</i> COCKERELL	Eocene, Cathedral Bluffs, Colorado	Cockerell, 1919
<i>Culicites tertiaris</i> HEYDEN	Upper Oligocene, Germany	Von Heyden, 1862; a chaoborid (Edwards, 1923)
<i>Mansonia cockerelli</i> (EDWARDS)	Oligocene, Isle of Wight, England	Edwards, 1923
<i>Mansonia martinii</i> STATZ	Oligocene, Rott, Germany	Statz, 1944
<i>Mansonia varivestita</i> STATZ	Oligocene, Rott, Germany	Statz, 1944
<i>Neoculicites arvenensis</i> (PITON)	Oligocene, Lac Chambon, France	Piton, 1936; Evenhuis, 1994
<i>Neoculicites ceyx</i> (HEYDEN)	Upper Oligocene, Germany	Von Heyden, 1870; possibly an <i>Aedes</i> (Edwards, 1923); Evenhuis, 1994
<i>Neoculicites depereti</i> (MEUNIER)	Upper Oligocene, Aix, France	Meunier, 1917; Evenhuis, 1994

<b>Mesozoic</b>		
<i>Amblylexis gibberata</i> BODE	Jurassic, Germany	Bode, 1953; none of the genera by Bode listed here are considered assignable to family by Carpenter (1992), and none were considered to be Culicidae by Knight and Stone (1977)
<i>Amianta eurycephala</i> BODE	Jurassic, Germany	Bode, 1953
<i>Amphipromeca acuta</i> BODE	Jurassic, Germany	Bode, 1953
<i>Apistogrypotes inflexa</i> BODE	Jurassic, Germany	Bode, 1953
<i>Asioculicus damiaoensis</i> HONG	Jurassic-Cretaceous, China	Anonymous, 1976; not a mosquito (present study)
<i>Asioculicus longipodus</i> HONG AND WANG	Cretaceous, China	Anonymous, 1976; not a mosquito (present study)
<i>Chironomaptera gregaria</i> (GRAGAU)	Cretaceous, China	Kalugina, 1980; family assignment doubtful (Carpenter, 1992); listed as a Chaoboridae (Evenhuis, 1994)
<i>Culex fossilis</i> BRODIE	Jurassic, England	Brodie, 1845; a chironomid (Edwards, 1923)
<i>Cormophora arucaiformis</i> BODE	Jurassic, Germany	Bode, 1953
<i>Culiciscolex gibberatus</i> BODE	Jurassic, Germany	Bode, 1953
<i>Cyrtomides maculatus</i> BODE	Jurassic, Germany	Bode, 1953
<i>Ellipes laesa</i> BODE	Jurassic, Germany	Bode, 1953
<i>Epidocampe retrocrassata</i> BODE	Jurassic, Germany	Bode, 1953
<i>Propexis incerta</i> BODE	Jurassic, Germany	Bode, 1953
<i>Rhopaloscolex brevis</i> BODE	Jurassic, Germany	Bode, 1953
<i>R. longus</i> BODE	Jurassic, Germany	Bode, 1953
<i>Sphallonymphites decuratus</i> BODE	Jurassic, Germany	Bode, 1953

Table 1. Fossils described as mosquitoes

nately, the tip of the abdomen of the holotype of *Paleoculicis minutus* is so folded, twisted, and flattened that a complete description and accurate interpretation of the genitalia are not possible. However, even the incomplete description and sketch of the genitalia we have provided do show some unusual characteristics. Deeply embedded in the structures at the tip of the abdomen, and scarcely visible, is a single row of nine very strong spiniform setae. We believe these are most likely borne on tergite 9. While no extant mosquito has exactly this arrangement or development of setae on tergite 9, some *Tripteroides* have very strong spiniform setae on paired tergite 9 lobes, and some *Trichoprosopon* have a single median tergite 9 lobe bearing multiple rows of weaker spiniform setae. Near one end of what we interpret to be a gonocoxite is a large, rounded lobe bearing at least 9 bristles. We believe this lobe is most likely a claspette near the

base of the gonocoxite. Many extant species of *Aedes* have claspettes bearing numerous setae at their apex. Alternatively, the rounded lobe near the base of the gonocoxite could be interpreted as a tergite 9 lobe and the single row of strong spiniform setae would then have to be borne on a more anterior abdominal segment, such as segment 8. Such an interpretation is not out of the question since some extant species of *Culiseta* have smaller spiniform setae on the caudal margin of tergite 8 of the male. However, we prefer the interpretation of the rounded lobe as a claspette rather than a tergite 9 lobe because its bristles are longer and more spreading than the bristles normally found on tergite 9 lobes of male mosquitoes. The only obviously paired structures we can discern on the genitalia are a pair of short projections at nearly a right angle to the long axis of what we have considered to be a gonocoxite. These are at the opposite end of the

gonocoxite from what we consider to be the claspette, so we interpret each as being a gonostylus. If this interpretation is correct, then the gonostylus is unusually small and does not bear the apical spiniform that occurs in most male mosquitoes. The figure of the genitalia shows the gonostylus to be fused to the gonocoxite, but we doubt that these structures are actually fused. The specimen is too darkened in this area for this to be seen clearly at this time. One of the most unusual features of the genitalia is the development of what appear to be strong spicules on the gonocoxite and gonostylus. Most of these are short, with the free end abruptly truncate, thus giving the appearance of having been broken off. The presence of such strong, and possibly long, spicules on the gonocoxite and gonostylus is a unique development in the Culicidae. We have not been able to see any structures identifiable as the phallosome or proctiger. We believe we would be able to see some evidence of a strongly sclerotized paraproct or strongly sclerotized paraproct teeth if either were present. Since we have not been able to discern them, the proctiger may be membranous, as it is in extant species of *Anopheles*, *Uranotaenia*, and *Aedeomyia*.

Mosquitoes have traditionally been divided into three subfamilies, the Anophelinae, Toxorhynchitinae, and Culicinae (Belkin, 1968). If this classification is accepted for the sake of argument, then *Paleoculicis* appears to be closer to the Culicinae than the other subfamilies. As already noted, many characteristics of *Paleoculicis* argue against it being an anopheline mosquito. We do not believe there is any reason to hypothesize a relationship between *Paleoculicis* and *Toxorhynchites* since there are no similarities between these genera other than a rounded scutellum. The rounded scutellum and scaleless pleuron and abdomen of *Paleoculicis* would be unique characters in the Culicinae. These characteristics along with the uniquely developed large facets of the compound eye and strong spicules on the gonocoxite might be evidence that *Paleoculicis* represents another major lineage of the family, one without extant species.

Belkin (1968) considered the aedine mosquitoes *Opifex*, *Aedes* (*Nothoskusea*), and *Aedes* (*Halaedes*) to be derivatives of a single phyletic line in which many primitive characteristics of mosquitoes had been retained by one or more of the extant species. Among these characters he included a broad interocular space, the strong development of the scape of the antenna, the presence of spicules on the outer surface of the claws of females, the presence of numerous bristles at the base of the subcostal vein ventrally, and the strong development

of bristles and poor development of scales on the head, thorax, and abdomen. The occurrence of bristles at the base of the subcostal vein ventrally, the occurrence of piliform erect scales (rather than the typical widened and forked or toothed erect scales) on the head, the occurrence of numerous bristles on the pleuron, and the absence of scales on the pleuron and abdomen in *Paleoculicis* lend support to the hypothesis that these are plesiomorphic characteristics. However, if Belkin is wrong in his polarization of these characteristics, then their occurrence in *Paleoculicis* suggests the possibility that this genus is an aedine mosquito. If a claspette is actually present on the gonocoxite of *Paleoculicis*, then the hypothesis that *Paleoculicis* is an aedine mosquito is further supported.

The recent phylogenetic analysis of the Culicidae by Harbach and Kitching (1998) provides no help in placing *Paleoculicis* because many of the characteristics used by Harbach and Kitching are unknown for *Paleoculicis*, because of extensive homoplasy in many of the characters used to classify mosquitoes, and because of the general methodology used by these authors.

The antenna of many, but not all, male mosquitoes is an auditory receptor used to detect the flight tone of the female. The pedicel of *Paleoculicis minutus* is greatly enlarged and there is evidence that the flagellum is strongly plumose, thus suggesting that the antenna of *P. minutus* was an auditory receptor, and suggesting moreover that mating took place in swarms.

The portion of the proboscis of the holotype of *Paleoculicis minutus* that remains is similar in all respects to the basal portion of the proboscis of extant species of mosquitoes. We describe the pleuron and abdomen of *Paleoculicis minutus* as not having scales, and we do not believe scales were ever present. The large number of bristles still in place on the pleuron and the abdomen argues against the scales having been removed by abrasion, and we can not envision any process that could have preferentially removed scales from these parts of the body, but left them on the top of the head, palpus, proboscis, legs, and wings.

## FOSSIL MOSQUITOES

Edwards (1923) stated "The origin and phylogenetic history of the Culicidae must go back well into the Mesozoic Era; and, from the small size and fragile nature of the insects, it is probably too much to hope that we can ever obtain much direct palaeontological evidence on



these matters.” The present specimen confirms Edward’s idea about a Mesozoic origin of the Culicidae and clearly is the oldest described specimen that can be confidently placed in the family Culicidae as well as being the first described mosquito from the Mesozoic period. Citations of fossil mosquitoes have been presented by Evenhuis (1994), Labandeira (1994), Carpenter (1992), Edwards (1923, 1932) and Poinar (1992). None of the four citations listed by Labandeira (1994) as Cretaceous Culicidae are in actuality descriptions of members of the family Culicidae and they need not be considered further here. All of the available descriptions that do deal with actual or possible Culicidae are listed in Table 1 under the categories of Recent, Tertiary and Mesozoic records. Reports of non-described fossil mosquitoes are not included in the table. There are no reports of mosquito fossils from the Paleozoic. While a number of descriptions pertain to Mesozoic fossils, none can be confidently assigned to the Culicidae. All of the descriptions of Bode (1953) are based on larval and pupal remains and we agree with Carpenter (1992) that they are too poorly preserved to permit assignment to any family. *Asioculicus damiaoensis* HONG from the late Jurassic-early Cretaceous of China and *A. longipodus* HONG AND WANG from the lower Cretaceous of China were placed in the Culicidae by their describers (in Anonymous, 1976). However, these insects are not mosquitoes. *Asioculicus* is described as having 3 ocelli and 15-segmented filamentous antennae; either character excludes the genus from the Culicidae. Moreover, *Asioculicus longipodus* is described as having a 10-segmented abdomen, which also argues against its placement in the Culicidae. Of all the fossil “mosquitoes” described or proposed since 1767 (Table 1), only 12, all from the Tertiary, appear to be reliable records (extinct species that are not synonyms of other fossil culicids, do not belong to other insect groups, and are not in copal). None of these 12 can be assigned to *Paleoculicis*.

One of the problems today, as in the past, is with insects in copal (semi-fossilized resin) thought to be in amber or material dated as Pliocene or Pleistocene in age. The copal deposits in Colombia, Madagascar, Kenya, and Tanzania have been carbon dated from 25 to 400 years old and there is no evidence that any of these deposits extends back even to the Pliocene although the material is often sold as amber, even by knowledgeable entomologists at national entomological meetings. Anyone intending to describe biota from copal deposits should have carbon dating performed on a portion of the piece. Fairly reliable dates can be obtained up to at least 50,000 years using this technique.

The presence of mosquitoes in the Mesozoic Era raises some interesting questions regarding possible hosts and vector relationships. During the Campanian in southern Alberta, all of the known groups of vertebrates were present (Wood et al., 1988) and within the coal seams from which the amber nodule was collected are dinosaur remains. Feathers in the amber testify to a wide range of avifauna existing at that period (Pike, 1995). Since it is likely that *P. minutus* was a blood-sucker, then possible terrestrial hosts would include multituberculates, monotremes, marsupials, lizards, snakes, turtles, crocodylians, eosuchans, and the first placentals as well as representatives of the Dinosauria. Extant mosquitoes transmit a wide range of micro-organisms, including viruses, protozoans, and nematodes. Such vector relationships might have been established by the Mesozoic.

#### ACKNOWLEDGMENTS

Thanks are extended to Philippe Rossignol for providing the senior author with pertinent literature, Xuan-Li Yao for translating the description of the genus *Asioculicus* HONG, and Roberta Poinar for offering suggestions on the manuscript.

#### REFERENCES

- Anonymous, 1976. Paleontological atlas of north China, Part of Inner Mongolia. Vol.2. Geology Publishing House, Beijing (in Chinese), 261 p.
- Belkin, J.N., 1968. Mosquito Studies (Diptera, Culicidae). VII. The Culicidae of New Zealand. Contrib. Am. Entomol. Inst. (Ann Arbor), 3(1), 1-182.
- Bloch, M.E., 1776. Beitrag zur Naturgeschichte des Kopals. Besch. Ges.Naturforsch., Freunde Berlin, 2, 91-96.
- Bode, A., 1953. Die Insektenfauna des ostniedersaechsischen oberen Lias. Palaeontographica, 103A, 1-375.
- Brodie, P.B., 1845. A history of the fossil insects of the secondary rocks of England. J. van Voorst, London, 130 p.
- Capasso, L., 1991. Fossil mosquitoes and the spread of infectious diseases in man’s ancestors. J. Paleopathol., 3, 171-201.
- Carpenter, F.M., 1992. Volume 4: Superclass Hexapoda. In: Treatise on Invertebrate Paleontology. Part R, Arthropoda 4. (Volume 2). Geological Society of America, Boulder, Colorado, & University of Kansas, Lawrence, Kansas, 279-655.
- Cockerell, T.D.A., 1915. British fossil insects. Proc. U. S. Nat. Mus., 49, 469-499.
- Cockerell, T.D.A., 1919. The oldest mosquitoes. Nature, 103, 44.
- Eberth, D.A., Hamblin, A.P., 1993. Tectonic, stratigraphic, and sedimentological significance of a regional discontinuity in

- the Judith River Group (Belly River Wedge) of southern Alberta, Saskatchewan and northern Montana. *Can. J. Earth Sci.*, 30, 174-200.
- Edwards, F.W., 1923. Oligocene mosquitoes in the British Museum; with a summary of our present knowledge concerning fossil Culicidae. *Q. J. Geol. Soc. Lond.*, 79, 139-155.
- Edwards, F.W., 1932. Diptera. Fam. Culicidae. In Wytzman, P., *Genera Insectorum. Fascicle 194.* Brussels, Desmet-Verteneuil, 258 p.
- Evenhuis, N.L., 1994. *Catalogue of the fossil flies of the World.* Leiden, Backhuys Publishers, 600 p.
- Giebel, C.G.A., 1862. Wirbeltier- und Insektenreste im Bernstein. *Z. Ges. Naturwiss.*, 20, 311-321.
- Gistel, J., 1831. Kerfe in Copal eingeschlossen. *Isis (Oken's)*, 24(3), 247-248.
- Harbach, R.E., Kitching, I.J., 1998. Phylogeny and classification of the Culicidae (Diptera). *Syst. Entomol.*, 23, 327-370.
- von Heyden, C.H.G., 1862. Gliederthiere aus der Braunkohle des Niederrhein's, der Wetterau und der Rohn. *Palaeontographica*, 10, 62-82.
- von Heyden, L., 1870. Fossile Dipteren aus der Braunkohle von Rott im Siebengebirge. *Palaeontographica*, 17, 237-266.
- Kalugina, N. S., 1980. [Mosquitoes of the Chaoboridae and Chironomidae from the Lower Cretaceous deposits of Lake Manlay]. *Tr. Sovmest. Sov.-Mongol. Paleontol. Ekped.*, 13, 62-65. [In Russian.]
- Keilbach, R., 1982. Bibliographie und liste der Arten Tierischer Einschlüsse in fossilen Harzen sowie ihrer Aufbewahrungsart. Teil 1-2. *Dtsch. Entomol. Z. (N. F.)*, 29, 129-286, 301-491.
- Knight, K.L., Stone, A., 1977. A catalog of the mosquitoes of the world (Diptera: Culicidae). Second Edition. *Thomas Say Found.*, 6, 1-611.
- Labandeira, C.C., 1994. A compendium of fossil insect families. *Milw. Public Mus. Contrib. Biol. Geol.*, 88, 1-71.
- Lambert, J.B., Frye, J.S., Poinar, Jr., G.O., 1990. Analysis of North American amber by carbon-13 NMR spectroscopy. *Geoarchaeology*, 5, 43-52.
- Legg, W.M., 1942. Collection, preparation and statistical study of fossil insects from Chemawinitite. Senior thesis, Department of Biology, Princeton University, 66 p.
- Linnaeus, C., 1767. *Systema naturae per regna tria naturae.* Edition 12, revised, Holmiae. Vol. 1, Pt 2, 533-1327.
- Marks, E.N., 1974. Notes on some taxonomic characters of Culicidae. *Mosq. Syst.*, 6, 211-213.
- McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R., Wood, D.M., (Coods.) 1981. *Manual of Nearctic Diptera.* Vol. 1. Ottawa, Ontario, Canada, Biosystematics Research Institute (Research Branch Agriculture Canada, Monogr. No. 27). 674 p.
- Melville, R.V., 1982. Opinion 1213; *Toxorhynchites brevipalpis* Theobald, 1901 (Insecta, Diptera): Conserved. *Bull. Zool. Nomencl.*, 39, 122-123.
- Meunier, F., 1917. Sur quelques insectes des lignites de l'Aquitainien de Rott, Sept Montagnes (Preusse rhénane). *Verh. K. Akad. Wetenskap.*, (II) 20, 3-17.
- Natvig, L.R., 1948. Contributions to the knowledge of the Danish and Fennoscandian mosquitoes: Culicini. *Nor. Entomol. Tidsskr.*, Suppl. 1, 1-567.
- Pike, E.M., 1995. Amber taphonomy and the Grassy Lake, Alberta amber fauna. Doctoral thesis, The University of Calgary, Alberta. 264 p.
- Poinar, Jr., G.O., 1992. *Life in amber.* Stanford University Press, Stanford, CA. 350 p.
- Poinar, Jr., G.O., Krantz, G.W., Boucet, A.J., Pike, T.M., 1997. A unique Mesozoic parasitic association. *Naturwissenschaften*, 84, 321-322.
- Scudder, S.H., 1877. The first discovered traces of fossil insects in the American tertiaries. *Bull. U.S. Geol. Geogr. Surv. Terr.*, 3 (4), 741-762.
- Scudder, S.H., 1890. The Tertiary insects of North America. *Rep. U.S. Geol. Surv. Terr.*, 13, 1-734.
- Statz, G., 1944. Neue Dipteren (Nematocera) aus dem Oberoligocän von Rott. V. Familie Culicidae (Stechmücke). *Palaeontographica*, (A) 95, 108-121.
- Szadziewski, R., Szadziewska, M.M., 1985. *Culex erikae* n.sp. (Diptera, Culicidae) from the Baltic amber. *Polsk. Pismo. Entomol.*, 55, 513-518.
- Wood, J.M., Thomas, R.G., Visser, J., 1988. Fluvial processes and vertebrate taphonomy: Upper Cretaceous Judith River Formation, south-central Dinosaur Park, Alberta, Canada. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 66, 127-143.