

***TOXORHYNCHITES (TOXORHYNCHITES) MEXICANUS*, N. SP.
(DIPTERA: CULICIDAE) FROM MEXICAN AMBER: A NEW WORLD
SPECIES WITH OLD WORLD AFFINITIES**

THOMAS J. ZAVORTINK AND GEORGE O. POINAR, JR.

(TJZ) Bohart Museum, Department of Entomology, University of California, One Shields Avenue, Davis, CA 95616, U.S.A. (e-mail: tjzavortink@ucdavis.edu); (GOP) Department of Zoology, Oregon State University, Corvallis, OR 97331, U.S.A. (e-mail: poinarg@science.oregonstate.edu)

Abstract.—A new species of fossil mosquito, *Toxorhynchites (Toxorhynchites) mexicanus*, is described from Mexican amber. This species differs from all extant species of the genus by having a strong bristle posteriorly on the postpronotum and it differs from all species of the subgenus *Toxorhynchites* by having the unique combination of a short *rm* index (1.3) and conspicuous caudal tufts of setae on the abdomen. This is the first record of the Old World subgenus *Toxorhynchites* in the New World.

Key Words: fossil, new species, Mexico, Neotropics, disjunct distribution

Adult mosquitoes of the genus *Toxorhynchites* Theobald are noted for their large size, brilliant coloration, and reflexed proboscis. The more than 90 extant species and subspecies are placed into four subgenera. The genus is primarily tropical in distribution, but with a few species extending into north temperate regions (Japan, southern Siberia, southern Canada). Females are non-haematophagous and oviposit in phytotelmata. Larvae are predaceous, feeding chiefly on other mosquito larvae. For a variety of reasons—the lack of medical importance, the difficulty of associating the sexes because of strong sexual dimorphism, the relative uniformity of the immature stages and of the male genitalia throughout the genus, and the difficulty of obtaining sufficient numbers of specimens to assess variation—the genus is poorly known taxonomically. Further information about

the genus can be found in papers by Steffan and Evenhuis (1981, 1985) and in many of the classic mosquito faunas and catalogs of the past century (Barraud 1934; Belkin 1962; Carpenter and LaCasse 1955; Dyar 1928; Edwards 1922, 1932, 1941; Lane 1953; Lee et al. 1988; Service 1990; Tanaka et al. 1979).

Relatively few fossil mosquitoes have been described from amber. Among these are *Paleoculicis minutus* Poinar, Zavortink, Pike, and Johnston, 2000 from Cretaceous Canadian amber; *Anopheles (Nyssorhynchus) dominicanus* Zavortink and Poinar, 2000, and *Culex malariager* Poinar, 2005 from Tertiary Dominican amber; and the alleged mosquito *Burmaculex antiquus* Borkent and Grimaldi, 2004 from Cretaceous Burmese amber. A synopsis of all described fossil mosquitoes known at the time is given by Poinar et al. (2000).

The mosquito *Culex loewi* Giebel was originally described as a fossil species supposedly embedded in amber (Giebel 1862). Subsequent research has shown, however, that the specimen is in recent gum copal and that it belongs to the extant species *Toxorhynchites brevivalpis* Theobald. The history of this specimen is provided in the request to the International Commission of Zoological Nomenclature to suppress the name *T. loewi* and conserve *T. brevivalpis* (White 1977).

Among fossils from the Isle of Wight provisionally referred to *Culex protorhinus* Cockerell by Edwards (1923) is a male abdomen described as follows: "The eighth segment is very broad, much broader than the hypopygium, and distinctly broader than the seventh segment (thus recalling *Megarhinus* [= *Toxorhynchites*])." This statement by Edwards is the basis for the overstatement by Mattingly (1962): "An Oligocene fossil from the Isle of Wight has also been attributed to it [*Toxorhynchites*] (Edwards 1923)." The true identity of this fossil has not been determined and it has not been formally described.

We take this opportunity to describe a new species of *Toxorhynchites* from Mexican amber. This is the first genuine fossil of the genus to be described. We place the new species in the subgenus *Toxorhynchites*, thereby establishing an early record of the subgenus in the New World. The tree responsible for producing Mexican amber, the legume *Hymenaea mexicana* Poinar and Brown, 2002, also has Old World affinities, with the most closely related living species occurring in Africa.

The amber with the fossil *Toxorhynchites* originated from mines or exposed amber-bearing veins near the village of Simojovel, Chiapas, Mexico. The amber there occurs in a sequence of primarily marine calcareous sandstones, siltstones, and shales with seams of lignite. These deposits extend from the Balumtun

Sandstone (Lower Miocene) to the La Quinta Formation (Upper Oligocene). They are assigned to the planktonic foraminiferal zones represented by *Globigerina ciperoensis* Bolli and *Globorotalia kuglieri* Bolli, Loeblich and Tappan, an interval within zones N3 and N4 of the Cenozoic Planktonic Foraminiferal Zonal Sequence, which has been dated radiometrically at 22.5 to 26 million years (Berggren and Van Couvering 1974). However, since the amber was washed into a coastal lagoon from soils beneath resin-producing trees, these dates provide only a minimum age for it. Further information on Mexican amber may be found in Poinar (1992).

MATERIALS AND METHODS

The piece of amber with the *Toxorhynchites* specimen is roughly trapezoidal in outline, with sides of 40, 15, 20, and 25 mm, a thickness of 5 to 10 mm, and a weight of 5.59 g. It is clear orange yellow in color. In addition to the *Toxorhynchites* mosquito, the amber includes six smaller dipterans, including two small, damaged culicine mosquitoes, and bits of dark brown or black organic debris. The *Toxorhynchites* mosquito is nearly complete, with only the left hind leg missing. The position of the mosquito in the amber precludes a clear view of portions of the head and thorax, and the presence of a thin silvery film over much of the surface of the thorax obscures the distribution of scales and other characters on the scutum and pleuron.

Adults of *Toxorhynchites* and several other genera of diurnal mosquitoes have scales with iridescent or metallic colors that may vary in intensity and hue according to the angle of observation. If scales of the fossil *Toxorhynchites*, as, for example, those at the edges of structures, can be observed by transmitted light, then it can be determined whether they are pigmented or not. The

pigmented ones were probably brown or black and probably displayed two or more of the iridescent colors adjacent to each other in the series varying from blue to blue green, green, bronze, deep golden, copper, and purple. The scales without pigment may have been matte white or may have displayed brilliant metallic silver or gold reflections. We have described some scales of the fossil as dark and some as light, meaning only that they do or do not bear pigment. We have described some scales as having green or purple iridescence, but we do not know what colors they may have displayed in life. First, we do not know how fossilization in amber may have affected the structural colors of the scales, and second, we do not know the complete range of hues the scales may have displayed since most parts of the fossil can be observed in only one orientation.

Observations and photographs were made with a Nikon stereoscopic microscope SMZ 1500 and Nikon Optiphot microscope at magnifications up to 112 \times . Morphological terminology follows McAlpine (1981), Harbach and Knight (1980), and Steffan and Evenhuis (1985).

***Toxorhynchites (Toxorhynchites) mexicanus* Zavortink and Poinar, new species**
(Figs. 1–4)

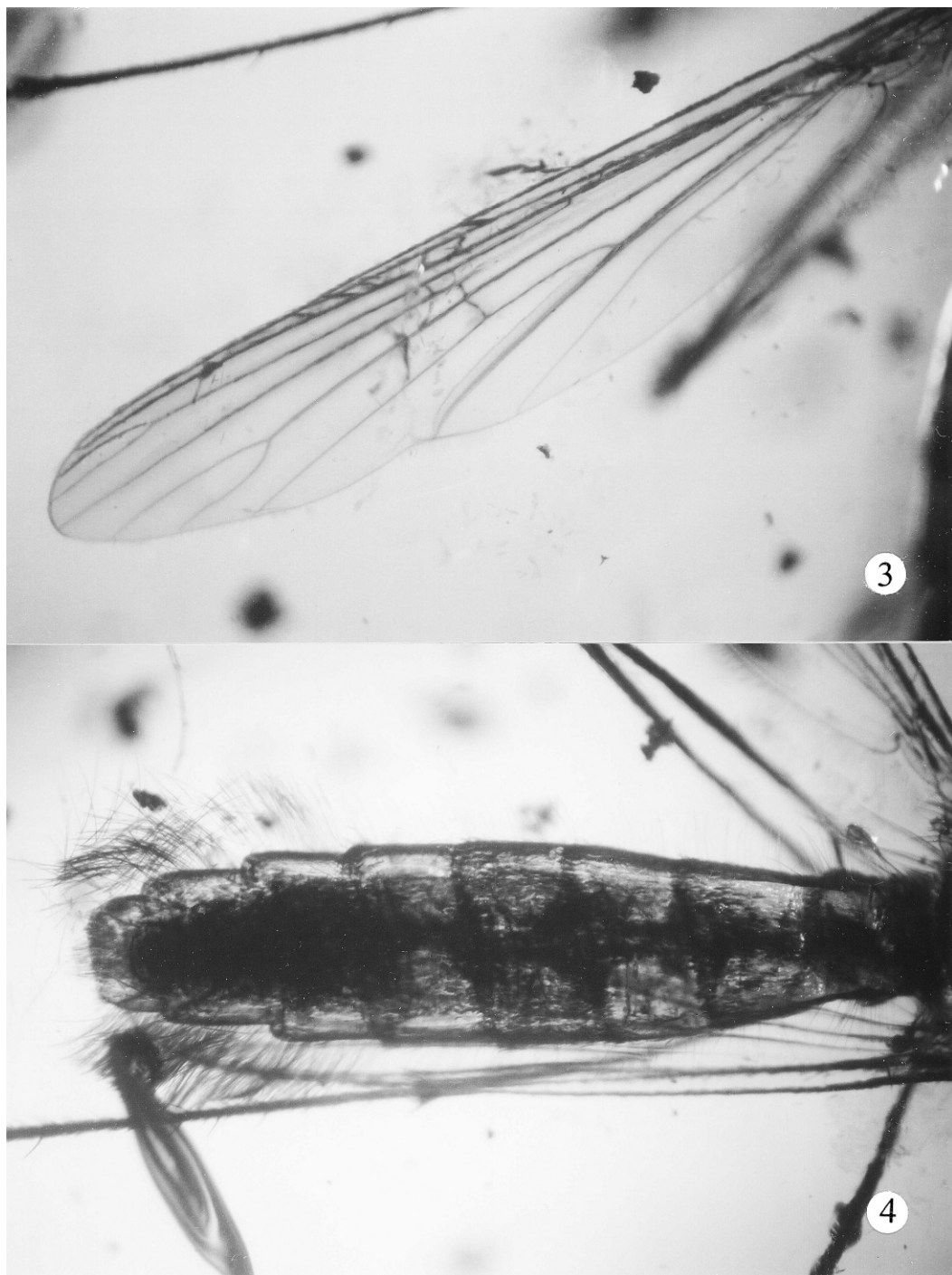
Diagnosis.—This species differs from all extant species of *Toxorhynchites* by possessing a strong bristle posteriorly on the postpronotum. Its short palpus comprised of two obvious palpomeres allies it with Old World species of the genus, from which it can be distinguished by the unique combination of a short rm index (1.3; equals length of the basal spur of wing vein R₄₊₅ from the base of vein R₄₊₅ to crossvein r-m divided by the length of crossvein r-m) and conspicuous caudal tufts of setae on the abdomen (see

Edwards 1922, 1941; Steffan and Evenhuis 1985).

Description of holotype female.—*Wing*: 5.6 mm. *Proboscis*: 5.5 mm. *Forefemur*: 3.3 mm. *Abdomen*: 4.9 mm. *Head* (Fig. 2): Integument dark brown. Eyes contiguous above antennae and ventrally behind proboscis. Top of head with broad flat scales, some in front with dark green iridescence, some in back with purple iridescence; occiput with erect scales posteriorly. Ocular bristles present, at least 5 upper, 1 strong lateral near widest part of head on left side; underside of head with fine bristles. Clypeus overlying base of palpus laterally. Proboscis long, attenuate, curved downward beyond middle; with numerous subbasal bristles; inserted into cavity of head capsule, without collarlike ring at base; labellum long. Palpus short, about 0.2 length of proboscis, slender, with 2 obvious palpomeres, the distal 2.5 length of proximal. Antenna short, about 0.6 length of proboscis; pedicel small, apparently with scales dorsally; flagellar bristles sparse; flagellomere 1 slightly longer than 2, with scales dorsally. *Thorax*: Integument black. Paratergite broad. Anteprenotal lobes large. Meron small, its upper margin in line with base of hindcoxa. Scutum with bristles on anterior promontory, antearlar area, and supraalar area; with broad flat scales, some in posterior fossal area dark with purple iridescence, some in posterior dorsocentral area dark with green iridescence. Scutellum evenly rounded, with even row of marginal bristles or alveoli; with broad flat scales, most apparently with purple iridescence. Anteprenotum with anterior row of numerous large and small bristles; with broad flat scales, some with purple iridescence. Postpronotum with 1 strong bristle posteriorly; with broad flat scales, those in upper posterior part dark with purple iridescence. Pleuron with bristles on upper proepisternum (at least 11), spi-



Figs. 1-2. Holotype female of *Toxorhynchites mexicanus* in Mexican amber. 1, Whole mosquito. 2, Head.



Figs. 3-4. Holotype female of *Toxorhynchites mexicanus* in Mexican amber. 3, Wing. 4, Abdomen.

racular area (at least 12), posterior katepisternum (several, 1 large), prealar knob (at least 22, some long, 2.0–2.5 times length of spiracular bristles), and mesepimeron (at least 13 in upper area and caudal row, apparently 2 strong in lower area). Pleuron with broad flat scales on anteprocoxal membrane, upper proepisternum, katepisternum, and mesepimeron, possibly also on lower proepisternum. *Legs*: Bristles short, stout. Foretarsomeres 4,5 subequal in length. Hindtibia apparently completely dark scaled. All tarsi apparently completely dark scaled. Claws simple, smaller on hindleg. Pulvilli absent. *Wing* (Fig. 3): Long, slender. Small area of membrane around crossvein m-cu slightly infuscated. Scales on anterior veins short, broad. Cell R_2 short, about 0.36 length of vein R_{2+3} . Vein R_s right-angled at base. Vein R_{4+5} right-angled at base and with long, scaled basal spur bearing crossvein r-m; rm index about 1.3. Crossvein m-cu slightly angled. Cell Cu_1 with sclerotized furrow in front of vein Cu_2 leading to angled submarginal thickening. Plical vein strongly marked. Vein 1A long, ending on margin far distad of branching of vein Cu. Stem vein without dorsal bristles. Vein Sc without bristles at base ventrally. Alula and upper calypter with a few very small marginal setae. *Halter*: Knob apparently with pale scales. *Abdomen* (Fig. 4): Integument light brown. Terga dark scaled dorsally, most scales apparently with purple iridescence, but some in middle of tergum II with green iridescence, some on tergum VIII with bright green iridescence; tergum I with very numerous bristles; laterotergite apparently without dense vestiture of scales, its lower area with numerous setae; sides of terga II–VII with pale scales except at apex of each segment; lateral margin of terga VI, VII, and VIII with tufts of long brown or black setae, some of the setae on VIII possibly red. Sterna scaled, color of most

scales not obvious, but scales in basal median triangular patch on sternum IV appear darker than others.

Type material.—HOLOTYPE female in amber, from near Simojovel, Chiapas, Mexico. Accession number D-7-188, deposited in the Poinar amber collection maintained at Oregon State University, Corvallis.

Etymology.—The new species is named for its country of origin.

DISCUSSION

Toxorhynchites mexicanus clearly belongs to the genus *Toxorhynchites*, as shown by the following characteristics: large size; scales of head, thorax, and abdomen broad, flat, and with evidence of iridescent colors; proboscis long, attenuate, reflexed, and inserted into cavity of head capsule, the genae not forming a collarlike ring at its base; posterior margin of scutellum evenly rounded; base of meron in line with base of hindcoxa; cell R_2 of wing short; cell Cu_1 of wing with sclerotized furrow in front of vein Cu_2 leading to an angled submarginal thickening; abdomen completely covered with scales and with conspicuous caudal tufts of setae. The only observed feature of the fossil species that deviates significantly from the condition in extant species of the genus is its possession of a strong bristle located posteriorly on the postpronotum.

Four subgenera of *Toxorhynchites* are recognized: *Afrorhynchus* Ribeiro and *Toxorhynchites s. s.* in the Old World, and *Ankylorhynchus* Lutz and *Lynchiella* Lahille in the New World. The three long-recognized subgenera *Ankylorhynchus*, *Lynchiella*, and *Toxorhynchites* differ from each other in structure of the female palpus and antenna (Edwards 1932). In *Toxorhynchites s. s.*, the palpus of the female is short, only about 0.20–0.25 the length of the proboscis, has only two obvious palpomeres, and is blunt; in *Lynchiella*, the palpus is about 0.67 the

length of the proboscis, comprised of three obvious palpomeres, and blunt; and in *Ankylorhynchus*, the palpus is about as long as the proboscis, has three obvious palpomeres, and is pointed and upturned. *Ankylorhynchus* also differs from the other subgenera in having the antenna of the female subplumose. Relatively recently, some African species (the *lutescens* group of Edwards 1941) were segregated from *Toxorhynchites s. s.* into the subgenus *Afrorhynchus* on the basis of several colorational and male claw and genitalic characters (Ribeiro 1992, 2005).

In *T. mexicanus*, the palpus is short, about 0.2 the length of the proboscis, blunt, comprised of two obvious, relatively slender palpomeres, and the antenna is sparsely plumose. These diagnostic characters place the species into one of the two Old World subgenera, either *Afrorhynchus* or *Toxorhynchites s. s.* Although we cannot discern most of the colorational characters that distinguish these subgenera, we place *T. mexicanus* in the nominal subgenus because those parts of the pleural integument that can be seen are uniformly black (rather than yellow or tan), the hindtibia and hindtarsomere 3 are dark scaled (rather than one or both having a conspicuous white patch or ring), the caudal tufts of setae on terga VI and VII are brown or black (rather than yellow, orange, or red), and the rm index is 1.3 (instead of greater than 2.0). The fossil species does not appear to belong to any of the species groups of *Toxorhynchites s. s.* recognized by Steffan and Evenhuis (1985) and Ribeiro (1991).

Most taxonomic characters of adult *Toxorhynchites* are colorational, with the iridescent or metallic colors of the scales of the head and its appendages (palpus and male flagellomere 1 in particular), the thorax and its appendages (legs especially, but also the wing), and the abdomen (both terga and sterna) being

important. Because it is embedded in amber, we have only limited knowledge of the iridescent and metallic colors of the scales of *T. mexicanus* and therefore we cannot provide additional diagnostic characters for the species based on color. All tarsi of *T. mexicanus* appear to be completely dark scaled, but we cannot be certain that inconspicuous streaks of whitish or bluish scales similar to those that occur on one side of the tarsus in some extant species of the genus are truly absent. The caudal tufts of setae of extant species of *Toxorhynchites* may be white, yellow, orange, red, brown, or black. In *T. mexicanus*, the setae of these tufts are identical in color to the dark scales of the right hindtibia that lies adjacent to the abdomen, leading us to believe that the tufts are brown or black. However, some of the setae of the tufts on segment VIII that have become detached and lie in the amber near the tip of the abdomen have a decided red cast, raising the possibility that the tufts on VIII were partly red in life.

The occurrence of a fossil species of *Toxorhynchites s. s.* in the North American tropics in the mid-Tertiary is an unexpected disjunct distribution. In general, tropical intercontinental disjunctions can have three explanations: vicariance, overland dispersal through the boreotropics, and long-distance chance dispersal across an ocean barrier (Givnish and Renner 2004). We think it highly unlikely that a mosquito like *Toxorhynchites* could have crossed the Atlantic by long-distance dispersal. In his study of the mosquitoes of the South Pacific, Belkin (1962) noted that the majority of mosquitoes do not seem to be able to cross ocean barriers of even a few miles, as shown by their regional differentiation within island groups. The exceptions to this generalization are a few widespread South Pacific species of *Aedes*, *Coquillettidia*, and *Culex* that breed in ground pools in open areas

and that may attain high population densities. According to Belkin, although adults of these species may have been dispersed passively by winds, dispersal of the species may have occurred in the egg stage instead. In the case of *Aedes*, the eggs are laid on damp soil at the edges of breeding sites and once embryonated are resistant to desiccation. When the soil and eggs are dry, it is possible that the eggs could be picked up by strong winds and blown across ocean barriers. In the case of *Coquillettidia* and *Culex*, the eggs are laid in rafts that float on the water surface. It is possible that egg rafts could cling to the feathers or legs of waterfowl and be carried to distant sites through the active flight of the birds. Adults of *Toxorhynchites* are never abundant and are largely restricted to sylvan situations where they rest in protected sites. We do not believe it is likely that an adult *Toxorhynchites* could be picked up by winds and be blown across an extensive ocean barrier. Eggs of *Toxorhynchites* are deposited in phytotelmata, are not resistant to desiccation, and hatch within 40 to 60 h (Steffan and Evenhuis 1981). We do not believe there is any possibility that eggs of *Toxorhynchites* could be blown out of phytotelmata, be transported long distances by the wind, and be redeposited in a habitat suitable for development of the immature stages.

The introduction of exotic species of *Toxorhynchites* to some islands of the South Pacific for biological control of container-breeding mosquitoes and their subsequent discovery on nearby islands have generated speculation on their methods of dispersal. Lever (1943) reported that in the Fiji Islands *Toxorhynchites splendens* (Wiedemann) appeared on Mango Island nine or 10 years after its introduction to Vanuabalavu Island. He believed the insect had crossed the 19 km of open sea between the islands by aerial dispersal aided by the southeast trade wind. Engber et al.

(1978) reported that in the Samoan Islands *Toxorhynchites amboinensis* (Dobleschall) was first collected on Upolu Island 15 years after its introduction to Tutuila Island, which lies 72 km to the southeast. Since the mosquito was largely restricted to the lee side of Upolu where, moreover, several harbors, wharves, and an airport are located, and since its immatures were frequently found in artificial containers (including tires and large drums), the authors believed the mosquito was more likely introduced through commerce than by windblown aerial dispersal.

There are actually two disjunctions of *Toxorhynchites* that need to be explained. The first is the occurrence of the genus in the tropics of both the New and Old Worlds, and the second is the occurrence of the subgenus *Toxorhynchites* in Mexico in the mid-Tertiary. As for the presence of *Toxorhynchites* in the tropics of both hemispheres, we believe that the genus was present in West Gondwanaland before its breakup in the mid-Cretaceous. Subsequent to the breakup, the subgenera *Ankylorhynchus* and *Lynchiella* differentiated in South America during that continent's long period of isolation as an island, and *Afrorhynchus* differentiated in Africa. In this regard, it is undoubtedly significant that today *Ankylorhynchus* occurs only in South America, the majority of species of *Lynchiella* occur only there as well (a few species extend into or are limited to North America and the West Indies), and *Afrorhynchus* is restricted to Africa. We are not the first to invoke vicariance as the explanation for the ampho-Atlantic distribution of *Toxorhynchites*. Nearly 70 years ago, Edwards (1941) stated: "It cannot be a coincidence that the genera and subgenera [of mosquitoes] common to Africa and South America (see p. 450) are those which on morphological grounds are regarded as the most primitive. The explanation seems obvi-

ous, that these groups were present in both regions before the final separation of Africa and South America in cretaceous times." Edwards' list on page 450 includes the genus *Megarhinus* (= *Toxorhynchites*).

Toxorhynchites s. s. is largely restricted to the Afrotropic and Indomalayan ecozones, but with extensions into the eastern Palaearctic and northern Australasian ecozones. The majority of the extant species and species groups occurs in southern Asia. We believe the subgenus or its progenitors dispersed from Africa to Eurasia in the late Cretaceous or Paleocene and radiated there. As for the occurrence of *Toxorhynchites s. s.* in southern North America in the mid-Tertiary, we postulate that it migrated from Eurasia to North America during the Eocene when dispersal routes across the North Atlantic and Beringia existed and tropical climates extended much farther north than today. Some of the characteristics of *T. mexicanus* are found in relatively few modern species of the subgenus. The unusually short and slender palpus, small rm index, and unscaled laterotergite are shared with *Toxorhynchites manicatus* (Edwards) from Japan and Taiwan and the presence of 1 or more strong lateral ocular bristles is shared with *Toxorhynchites christophi* (Portschinsky) from China, Korea, and Siberia and *Toxorhynchites towadensis* (Matsumura) from Japan (Tanaka et al. 1979). We believe these similarities between *T. mexicanus* and modern species of *Toxorhynchites s. s.* that occur at the northern periphery of the distribution of the subgenus in eastern Asia favor the hypothesis of migration of the subgenus into North America through Beringia. Since *Toxorhynchites s. s.* no longer occurs in North America, it obviously became extinct there. We do not know if its extinction was the result of competition with the subgenus *Lynchiella* after the latter spread into North America,

perhaps as recently as the Pliocene when the modern Central American Isthmus formed, or was brought about by other biotic or abiotic factors independent of that event.

ACKNOWLEDGMENTS

We thank Sandra S. Shanks for suggesting improvements to an earlier draft of this manuscript and James E. Pecor for information about species of *Toxorhynchites* in the collection of the National Museum of Natural History, Smithsonian Institution.

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