Insects from the Upper Miocene Grubstake Formation of Alaska

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ABSTRACT

Well-preserved insect wings are reported in weakly consolidated lacustrine shale from the Grubstake Formation, Upper Miocene of Suntrana Creek, central Alaska. $^{40}Ar/^{39}Ar$ dating of an immediately overlying volcanic ash indicates an age of slightly more than 6.7 ± 0.1 Ma, or approximately one million years before the opening of the Bering land bridge. The insects include four genera and two subfamilies of ants (Hymenoptera: Formicidae: Myrmicinae and Dolichoderinae), a species of Ichneumonidae (Hymenoptera), three genera and families of flies (Diptera: Chironomidae [genus indet.], Bibionidae [*Bibio*] and Lonchaeidae [*Dasiops*]), and the elytra of curculionid and carabid beetles. Extant distributions of the flies and possibly the ichneumonid include northerly latitudes around Suntrana. The ants are attributable to the extant genera *Dolichoderus* or *Tapinoma* (Dolichoderinae), *Solenopsis* or *Erebomyrma* (Myrmicinae), as well as *Veromessor* and *Novomessor* (Myrmicinae), indicating extensive biogeographic contraction to more southern latitudes of North America today. These finds are consistent with evidence from a slightly younger deposit from the uppermost Miocene (5.7 Ma) of the Seward Peninsula, Alaska. Implications are discussed regarding the differential effects of climate change and land bridges on the dispersal of various insect taxa.

INTRODUCTION

Despite an area of 570,374 square miles and remarkably varied geology, Alaska boasts few reports thus far of Tertiary insects. While there are actually more than 30 sites throughout Alaska where insects from the Quaternary (1.64 Ma to present) have been excavated (summarized by Elias, 1994), very few Tertiary deposits are known, and only one significant Cretaceous deposit is known, which is based on several minute insects in Late Cretaceous amber from the Arctic Coastal Plain (Hurd et al., 1958; Langenheim et al., 1960; Usinger and Smith, 1957; Muesebeck, 1963). The largest deposit of

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Tertiary insects is the so-called Lava Camp site from near Deering, northern Seward Peninsula, a Late Miocene assemblage of well-preserved remains of a flood plain forest (Hopkins et al., 1971; Matthews, 1970, 1976, 1977, 1978). These authors reported mega-fossil plants, several dozen pollen types, and various orders of arthropods in 15 families and nearly 100 species. The flora was identifiable to generic and often to species/species-group levels, and was dominated by spruce (*Picea*) and birch (*Betula*), with at least 10 species of conifers. Well-sclerotized arthropods were preserved as original cuticular remains, albeit completely disarticulated, including, for example, beetle elytra and pronota (e.g., Matthews, 1970, 1976), oribatid mite carapaces, and even some sclerotized portions of male beetle genitalia (the last being highly useful for comparison to modern species). Flight wings were not preserved. Elias and Matthews (2002) reviewed Late Tertiary fossil Coleoptera from northern Alaska and the Canadian high Arctic, and discussed the paleoclimatic implications.

Here we report another occurrence of fossil insects from Alaska, recently discovered in lacustrine shales from the basal Grubstake Formation of Suntrana Creek in central Alaska. This deposit is overlain by a volcanic ash that recently has been dated to 6.7 ± 0.1 Ma, or Late Miocene (see below). Like most compression fossil insects, these are preserved as wings only, but with a venation sufficiently well preserved to allow identification to family and generic levels. Studies of complete, finely preserved insects in Early to mid-Miocene amber (20–15 Ma; Iturralde-Vinent and MacPhee, 1996) from the Dominican Republic indicate that remarkably modern taxa existed at that time, some two-thirds of the species belonging to extant genera (Grimaldi, 1995, unpubl.). Some studies of insects in Dominican amber, in fact, have revealed species extremely similar to modern species (e.g., Krishna and Grimaldi, 1991; Kathirithamby and Grimaldi, 1993), and the great proportion of species in the Late Tertiary (latest Miocene through Pliocene) of the Western Hemisphere Arctic appears to be Recent species (Elias and Matthews, 2002). Thus, Late Miocene insects have little value for

understanding the phylogeny of insects, though they are germane to issues on the lifespan of species as well as biogeography. Insect remains as young as the Pleistocene and Quaternary, in fact, often indicate extensive range contractions, and have provided abundant data on paleoclimatic fluctuations (Coope, 1962, 1970, 1973, 1995). Grimaldi (1992) and Grimaldi and Engel (2005) discussed as well the implications of extralimital fossils for biogeographic hypotheses. The ants preserved in these new Alaskan collections reveal extensive biogeographic contractions, and the insects collectively contribute paleoclimatological data for Alaska during a time period of considerable significance, namely just prior to opening of the Bering land bridge and mixing of the Arctic and North Pacific oceans.

The Deposit

The locality is at Suntrana Creek, a northern tributary of Healy Creek, about 4.8 km above the junction of the latter with the Nenana River near the town of Healy in central Alaska (63°51′N, 148°58′W) (fig. 1). A description of the general geology was provided by Wahrhaftig (1987). The insect specimens occurred in a gray, weakly consolidated, poorly stratified lacustrine shale less than one meter below a prominent white volcanic ash 10 meters above the base of the Grubstake Formation, uppermost unit of the Usibelli Group (fig. 1). Exact derivation of specimens in the shale sequence is uncertain, because specimens were rare and could be found only by removing and splitting weathered shale fragments. Repeated attempts to collect additional specimens were not very successful, probably because the exposure was actively undercut by the creek and yielded relatively fresh material that did not readily split along weak bedding planes to reveal the insect remains. Future collecting will rely on the availability of weathered, unearthed matrix.

The overlying volcanic ash has been correlated (Wahrhaftig et al., 1969) with the Tatlanika Creek ashes 60 km northeast of the Suntrana locality. At Suntrana the ash is not air-fall material, but was transported as sediment by rivers and streams into a broad, shallow lake. Recent $^{40}Ar/^{39}Ar$ dating of
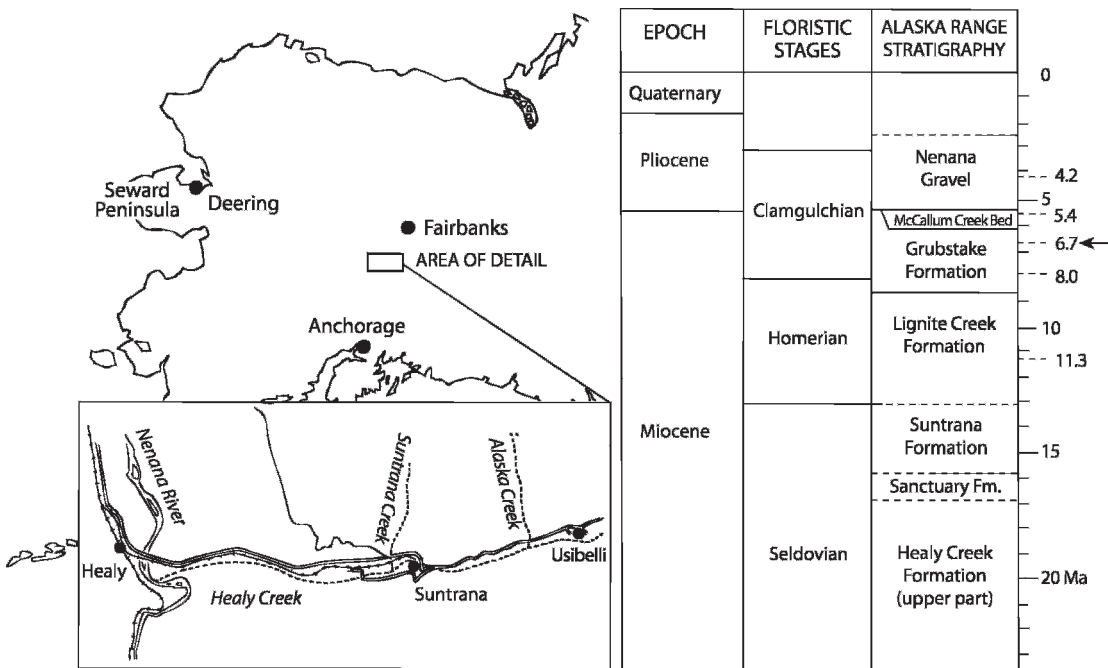
Fig. 1.   Maps showing location of Grubstake Formation where insect fossils were collected, along with a generalized Late Tertiary stratigraphy of the area. Ages with decimal points are radiometric age controls (see Triplehorn et al., 1999). Arrow indicates approximate level of fossil insects.

biotite, hornblende, and plagioclase from the Tatlanika ash gives a weighted mean mineral age of 6.7 ± 0.1 Ma (Triplehorn et al., 1999), which indicates a Late Miocene age for the underlying insect fauna.

The Insects

Thirty-two isolated insect wings were preserved as dark brown, brittle membranous remains on the matrix (e.g., figs. 2, 4, 6, 7). They appear to have some original cuticle, since they are dark brown with a degree of relief and shine, typical of wings and other external cuticular parts of insects. To facilitate observation in some cases, 70% ethanol was applied to the surface to increase the contrast between the veins and remaining areas. Venation was illustrated with a drawing tube on a Zeiss SV-8 stereomicroscope. For two specimens the preservation did not allow identification; a third specimen (UAF-GS8) had some venation preserved, but lack of resolution of the branching precludes unambiguous identification (it appears to be a chironomoid or some other

nematoceran Diptera). Specimens are deposited in the University of Alaska, Fairbanks Museum of Paleontology, for which UAF numbers (GS [Grubstake]1 to GS32) are provided.

Order HYMENOPTERA Linnaeus, 1758

Family Formicidae Latreille, 1802

The wings of alate ants are the most common insect remains from Suntrana, with a total of 22 ant forewings out of 30 identifiable insect specimens. Represented are three genera, possibly three species, of myrmicines and a species of dolichoderine. In discussion of wing venation the terminology used is that presented in Hölldobler and Wilson (1990), as labeled in figure 3. Creighton (1950) served as the primary reference for identification to genus and summaries of extant distributions.

Subfamily Dolichoderinae Forel

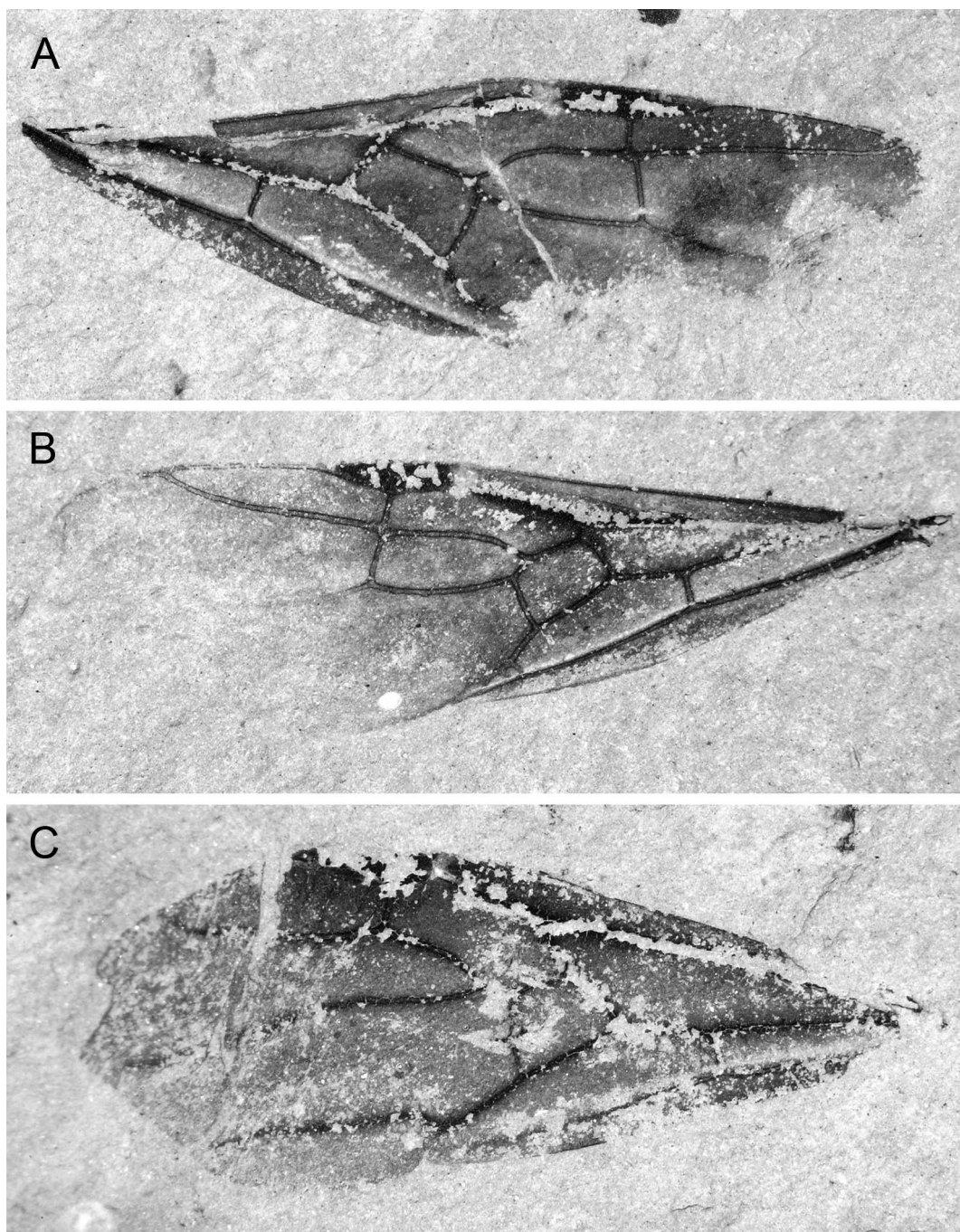SPECIMENS: The myrmicine wings are distinguished from the dolichoderine wing based

Fig. 2.   Photomicrographs of ant forewings. A–B. Dolichoderinae: *Dolichoderus/Tapinoma:* **A.** UAF-GS1; **B.** UAF-GS20. **C.** *Solenopsis/Erebomyrma:* UAF-GS19.

on lack of a second submarginal cell; a discoidal cell that is small and trapezoidal in shape; and presence of a deep first submarginal cell. Specimens UAF-GS1 and GS20 (figs. 2, 3) very closely resembles *Dolichoderus* (*Hypoclinea*) Mayr and *Tapinoma* Foerster by the existence of 1st and 2nd submarginal cells and a discoidal cell, as well as by their relative shapes and positions (Brown and Nutting, 1949; Creighton, 1950). The fossil differs from these two genera by the absence of a short vein connecting the 1st discoidal cell and R+Sc. Wing length is estimated to be 8 to 8.5 mm (tip of wing is lost).

DISCUSSION: There are approximately 20 species of dolichoderine ants in North America belonging to seven genera: *Dolichoderus* Lund, *Dorymyrmex* Mayr, *Forelius* Emery, *Linepithema* Mayr, *Liometopum* Mayr, *Tapinoma* Foerster, and *Technomyrmex* Mayr (Bolton, 1994; Creighton, 1950). These are distributed mostly in the southern part of the U.S., and only one species extends to Manitoba, the northernmost distribution of the subfamily in North America. Extant *Dolichoderus* and *Tapinoma* extend at best to the southernmost border of Canada. *Dolichoderus* appears to have been widespread in the geological record, having been reported from the Miocene of Idaho (Lewis et al., 1990a), Washington state (Lewis et al., 1990b), Dominican Republic (Wilson, 1985), and China (Zhang, 1989; Zhang et al., 1994), from the Oligocene of Colorado (Carpenter, 1930), France (Théobald, 1937a, b), England (Cockerell, 1915), and in Eocene Baltic amber (Wheeler, 1914). *Tapinoma* does not have such an extensive fossil record, and is recorded only in Miocene amber from the Dominican Republic (Wilson, 1985) and Sicily (Kohring and Schlüter, 1989), as compressions from the Miocene of China (Zhang, 1989), and in Eocene amber from Rovno, Ukraine (http://edna. palass-hosting.org/search.php).

Subfamily Myrmicinae Lepeletier de Saint Fargeau

Species 1

SPECIMENS: Specimens UAF-GS2, 4, 5, and 19 (figs. 2, 3) have submarginal and discoidal cells that are similar in size and position to those in the formicine genera

Formica and *Lasius*. In these two genera, however, the apical forking of veins Rs-M is distal to the 1st radial cell. The fossils, in fact, are most similar to the myrmecine genera *Solenopsis* Westwood and *Erebomyrma* Wheeler in also having Rs-M emerge from the middle of the ventral wall of the 1st submarginal cell. The fossils can be ascribed in or near these two myrmicine genera with confidence.

DISCUSSION: In North America there are approximately 15 species of *Solenopsis* (many more in the neotropics); only two species extend to southernmost Canada (*S. molesta* [Say] and *S. texana* Emery. *Solenopsis molesta* is an extremely minute ant, 1.0–1.5 mm body length, much smaller than the fossils (6–7.5 mm estimated wing lengths, based on incomplete specimens). *Erebomyrma* consists of one extant species (*E. longi* Wheeler), known only from Texas. *Solenopsis* has been reported from the Oligocene of France (Théobald, 1937a, b), Miocene of Croatia (Pongrácz, 1928), and Miocene amber of the Dominican Republic (Wilson, 1985), but not reported from the prolific uppermost Eocene volcanic shales of Florissant, Colorado (Carpenter, 1930). *Erebomyrma* has been reported from the Oligocene of Aix-en-Provence, France (Théobald, 1937a,b), but many of the insect fossils from this deposit require revision.

Species 2 (*Aphaenogaster* sp.)

SPECIMENS: UAF-GS23 and UAF-GS24 (figs. 4, 5) are partial forewings with an estimated length of approximately 10 mm. They are most similar to species formerly assigned to *Novomessor* Emery (now in *Aphaenogaster* Mayr), based on the lack of a discoidal and 2nd submarginal cell, and the fact that the (apical) Rs and M veins converge proximally at the tip of the 1st marginal cell (there is no stem to Rs and M), forming an X. The fossils are rather large ants, similar in size to modern species of the genus. The fossil differs from at least *A. albisetosus* (Mayr) because the 1st submarginal cell is not as long and slender.

DISCUSSION: There are two extant North American species of *Aphaenogaster* formerly assigned to *Novomessor*: *albisetosus* (Mayr), which ranges from southwestern Texas to
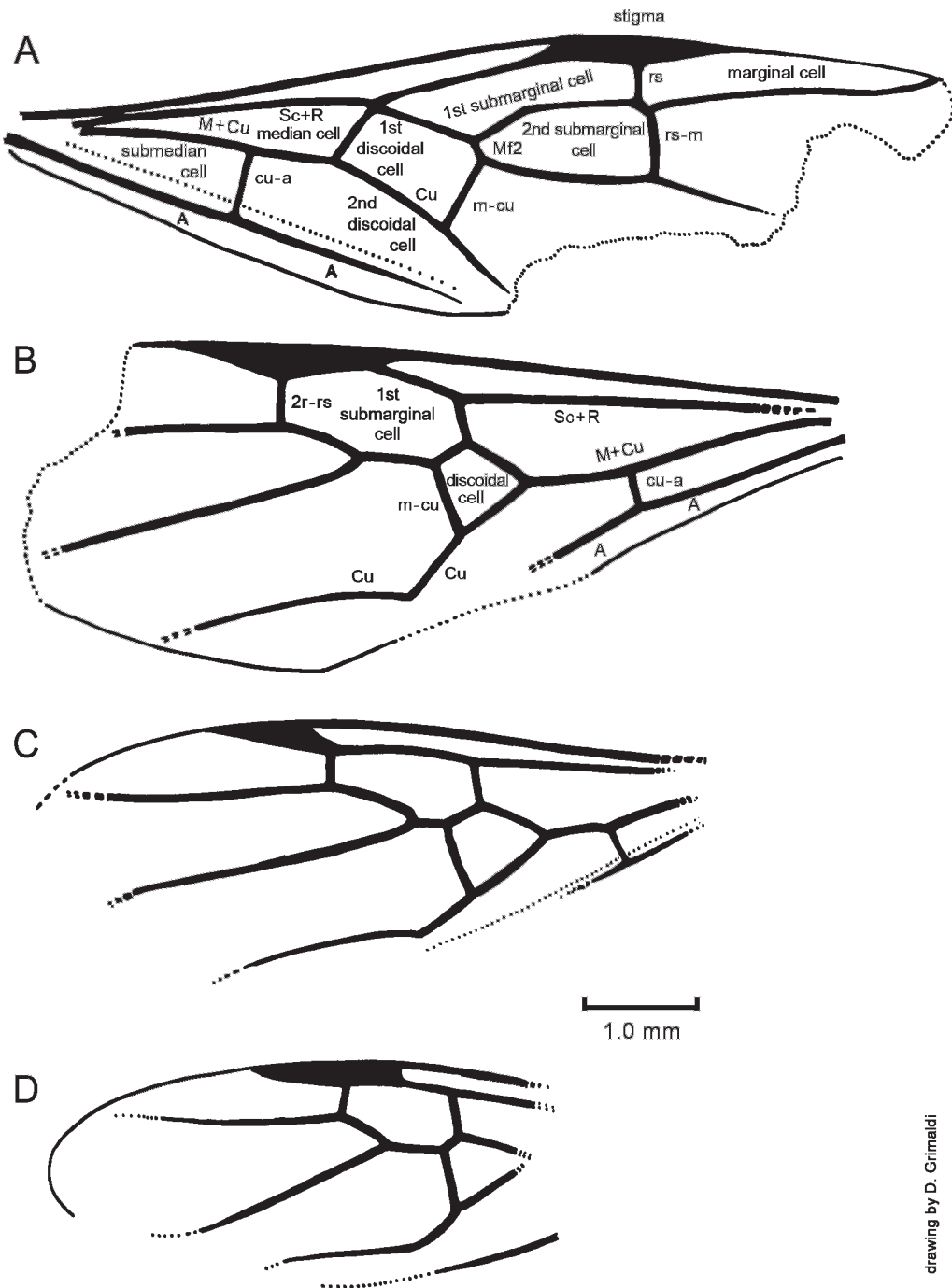
Fig. 3. Camera lucida drawings of ant forewings: **A.** UAF-GS1 (Dolichoderinae: *Dolichoderus/Tapinoma*). B–D: Myrmicinae sp. 1 (*Solenopsis/Erebomyrma*). **B.** UAF-GS2. **C.** UAF-GS4. **D.** UAF-GS5. All to the same scale.
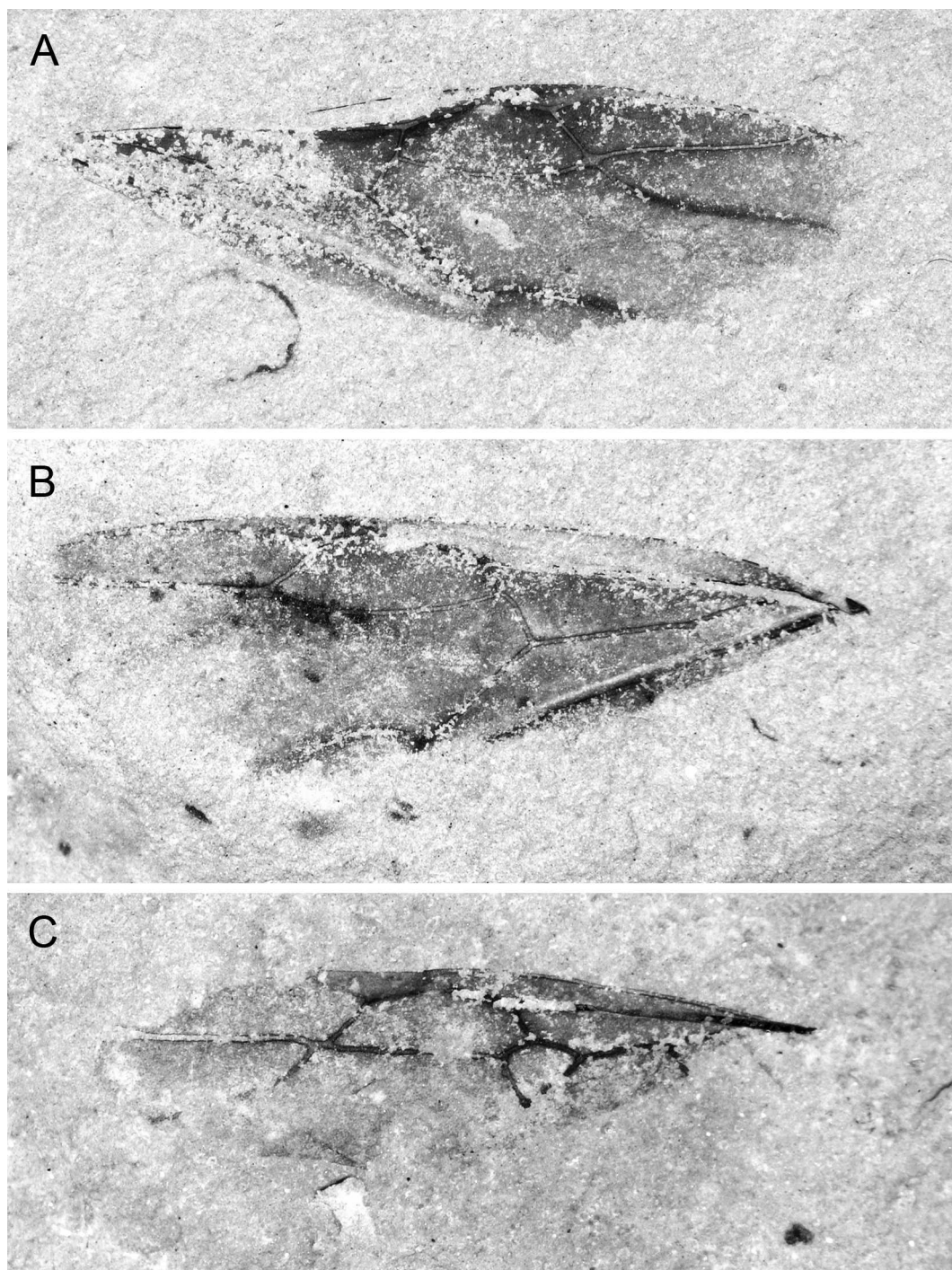
Fig. 4.   Photomicrographs of ant forewings. A, B: *Aphaenogaster* sp. **A.** UAF-GS23. **B.** UAF-GS24. **C.** UAF-GS25, *Messor* (*Veromessor*) sp.
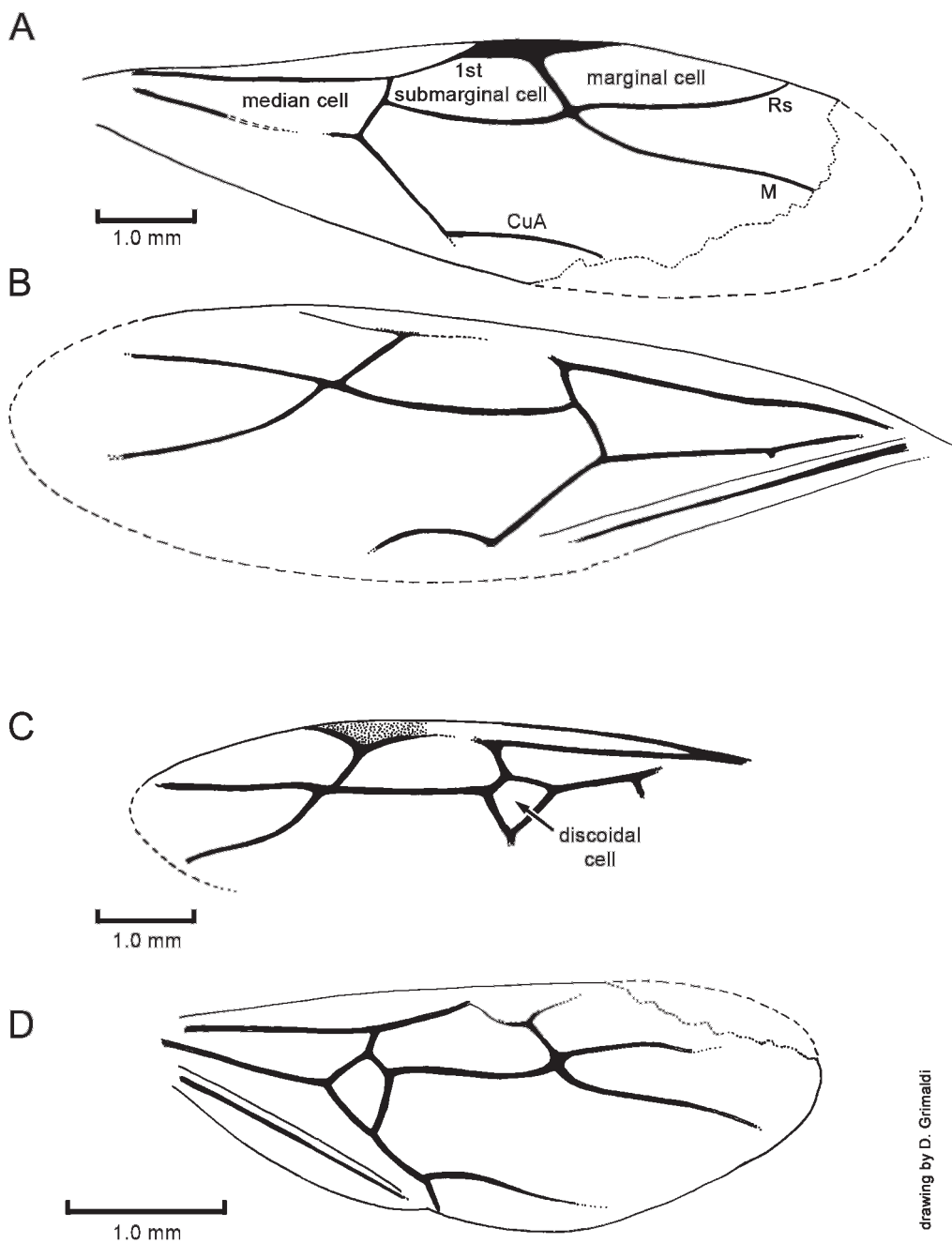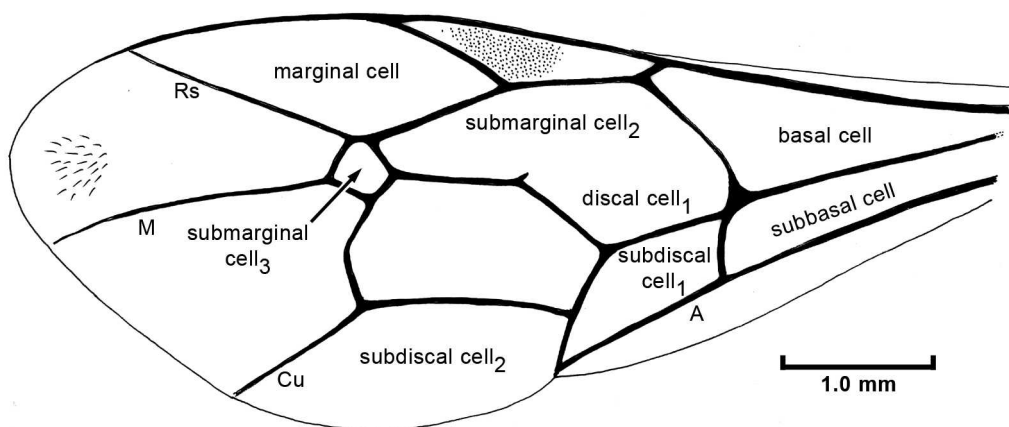
Fig. 5. Camera lucida drawings of ant forewings. A, B: *Aphaenogaster* sp. **A.** UAF-GS23 (A, B to same scale). **B.** UAF-GS24. C, D: *Messor* (*Veromessor*) sp. **C.** UAF-GS25. **D.** UAF-GS11.
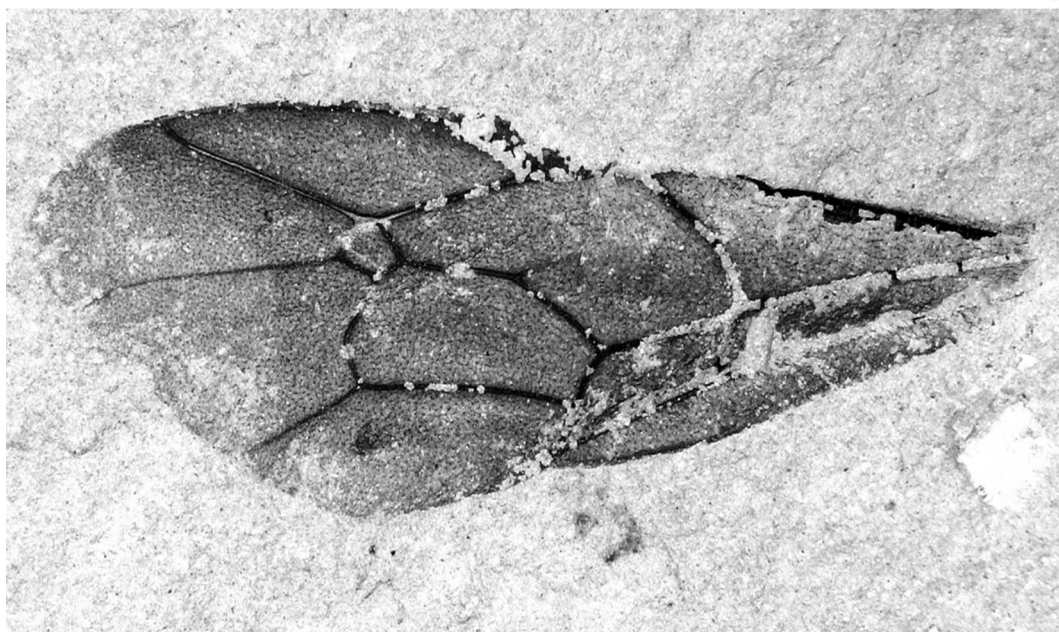
Fig. 6. Camera lucida drawing and photomicrograph of Ichneumonidae forewing, UAF-GS12, cf. *Brachypimpla*.

southern Arizona; and *cockerelli* (E. André), found in Mexico, western Texas, and southern Arizona. They are abundant, desert-dwelling ants that are omnivorous and nest in the ground.

Species 3 (*Messor* sp.)

SPECIMENS: UAF-GS25 and UAF-GS11 (figs. 4, 5) are virtually complete forewings with estimated lengths of approximately 5–7 mm.

They are most similar to the North American species of *Messor* Forel formerly assigned to the genus *Veromessor* Forel, based on the presence of a discoidal and 1st submarginal cell, no 2nd submarginal cell, and the fact that the (apical) R and M veins converge proximally at the tip of the 1st marginal cell (there is barely a stem to R and M), virtually forming an X. The fossil differs from at least *M. andrei* (Mayr) based on the smaller discal cell and veins R and M not as divergent.
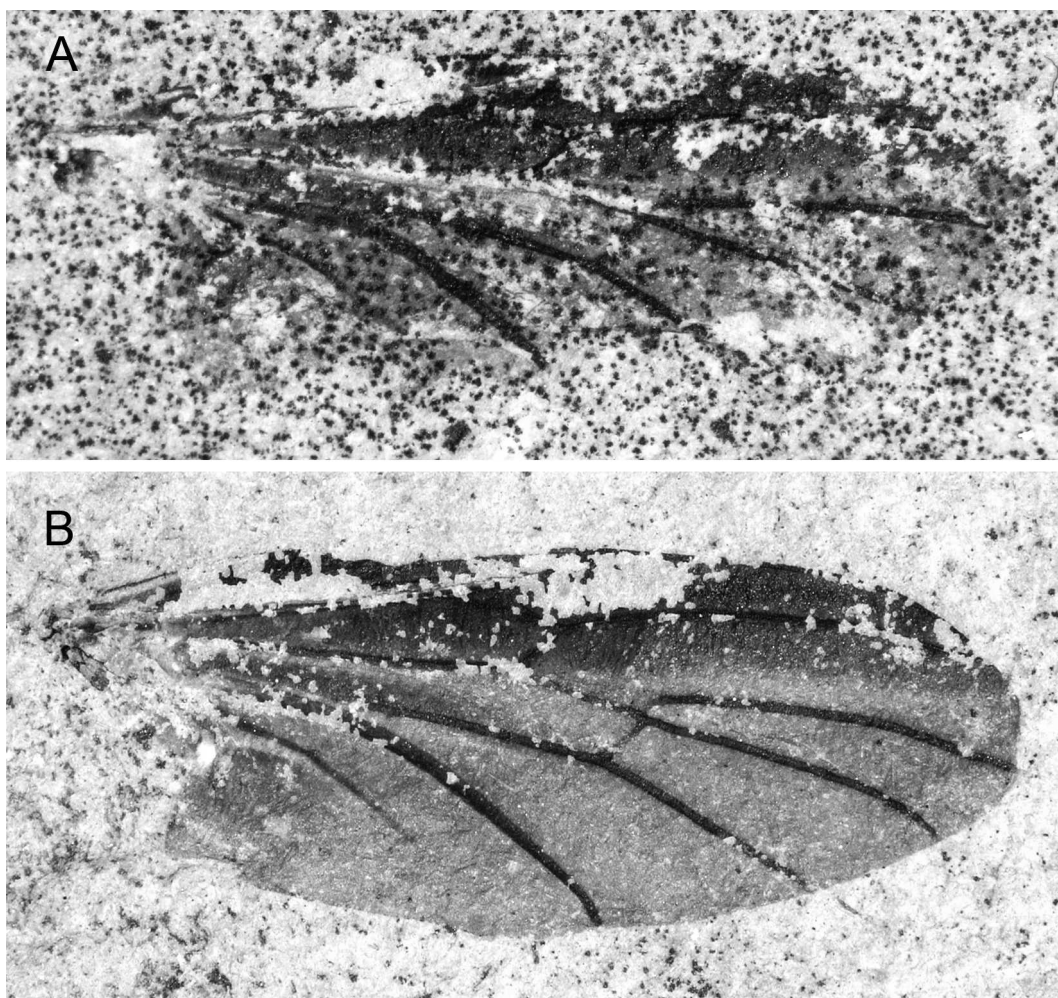
Fig. 7.　Photomicrographs of Bibionidae (*Bibio*) wings. **A.** UAF-GS6. **B.** UAF-GS7.

DISCUSSION: There are five extant species of *Messor* (*Veromessor*) ants, three of which occur exclusively in California or immediate vicinity. The other two are *M. lobognathus* (Andrews) from Colorado, and *M. andrei* (Mayr)—the most widespread species—from California into Oregon, Nevada, and southwestern Arizona. They are desert-dwelling, seed-harvesting ants that build mounds.

Family Ichneumonidae Latreille, 1802

The ichneumonids, or ichneumon flies, are a very large cosmopolitan family (some 60,000 species globally) of parasitoid wasps, which victimize the larvae principally of Lepidoptera, symphytan Hymenoptera, and Coleoptera. Their geological record begins in the Cretaceous, but a great diversity of fossils occurs in various Tertiary deposits (a catalog of those genera with fossil species is in Carpenter, 1992). Given the overwhelming diversity of ichneumonids, identification of their fossils (particularly ones where just a wing remains) would be daunting without comprehensive work like the series of monographs on the North American ichneumonids by Townes et al. and published in *Memoirs of the American Entomological Institute*, which served as reference for the present study. Fortunately, ichneumonid wing venation

(fig. 6) varies sufficiently to distinguish some genera on this basis alone. Significant variation includes presence/absence and size/shape of the small, third submarginal cell (smc3; shape of the second submarginal—discal cell (smc2-dc), and whether there are vein spurs within this cell; shape and size of the first subdiscal cell (sdc1), etc.

Ichneumonid wing UAF-GS12 is similar to that of several genera each in the subfamilies Pimplinae, Cryptinae, and Tryphoninae. Among the Pimplinae, genera with the fossil wing venation include *Atractogaster* Kriechbaumer, *Cenodontis* Townes, *Flavopimpla* Betrem, and *Paraperithous* Haupt. These genera have the small but distinctive spur formed from the angle of vein M+1m-cu that projects into the large smc2-dc1 cell, a distinctive bend in vein 2m-cu, and vein cu-a with its apex slanted distally. However, in *Atractogaster* cell sm3 is significantly smaller than in the fossil, and in all these genera the marginal and dc2 cells are narrower and the basal and subbasal cells significantly longer.

In the Tryphoninae the two genera *Erromenus* Holmgren and *Monoblastus* Hartig are very similar to the fossil. *Erromenus* has 26 species, including six that extend into northern Alaska. All species of *Monoblastus* occur in the United States and southern Canada. In these genera cell smc3 is smaller, the marginal cell is narrower, and cell dc2 is squatter than in the fossil, and there are breaks in the cells that surround many of the cells and no spur projecting into cell smc2-dc.

The cryptine genera *Brachypimpla* Strobl and *Pygocryptus* have wing-cell proportions and shapes most similar to those of the fossil, but in the latter the basal and subbasal cells are longer. *Pygocryptus* has four species in North America, found throughout the U.S., with the distribution of one species (*P. grandis* Thomson) reaching southern Alaska. *Brachypimpla* has two species, which are Palearctic and Asian: *B. brachyura* Strobl (Europe) and *B. latipetiolator* Uchida (Japan). In these the two distal veins M and Cu1 are evanescent, and there are spots of weakness in the veins surrounding cells smc3 and dc2. With these exceptions, the wing venation of the fossil is most similar to *Brachypimpla*. If indeed related to the living species of *Brachypimpla*, it would imply a faunal connection between central Alaska and Eurasia, which would correspond to the known presence of the Bering land bridge at the time. In lieu of an exhaustive morphometric analysis of the venation of UAF-GS12 and the genera of ichneumonids discussed above it would be premature to make any biogeographic conclusions.

Order DIPTERA Linnaeus, 1758

Family Bibionidae Newman, 1835

Genus *Bibio* Geoffrey, 1762

SPECIMENS: Both specimens, UAF-GS6, 7 (figs. 7, 8), are well preserved, with intact venation, and the dark, fuscous membrane of the wing preserved. The very dark, heavily sclerotized stigma at the apex of vein R_1 was apparently not preserved (probably retained on the obverse of each specimen, which was not available). However, even the gradation in fuscous coloration is preserved (best in specimen UAF-GS7), being darkest on the costal third of the wing. Specimen UAF-GS6 has the membrane finely crenulate, which may be just preservational. The wings are 5.5 and 6.0 mm long.

DISCUSSION: The latest revision of the extant North American bibionids was by Hardy (1945), in which he included 51 species of the genus *Bibio*; he later mentioned (Hardy, 1981) that there were 53 Nearctic species. There are an approximately equal number of Palearctic species. There are at least a dozen species of *Bibio* whose distributions extend into Canada (generally to Alberta and Manitoba), and Hardy recorded four species of *Bibio* from Alaska: *B. fumipennis* Walker, *B. inaequalis* Loew, *B. labradorensis* Johnson, and *B. tenellus* Hardy. Wing venation rarely distinguishes species in this genus, and the fossil wings are very similar to living species with one possible exception: the base of vein CuA_2 appears separate from the base of CuA_1, instead of being connected by a fork at about midlength. Since a small knob on CuA_1 occurs where the fork would normally occur, it is almost certain that this venational difference is merely preservational. Thus, the *Bibio* fossils indicate that the present distribution of the genus in Alaska extended at least to the Late Miocene.
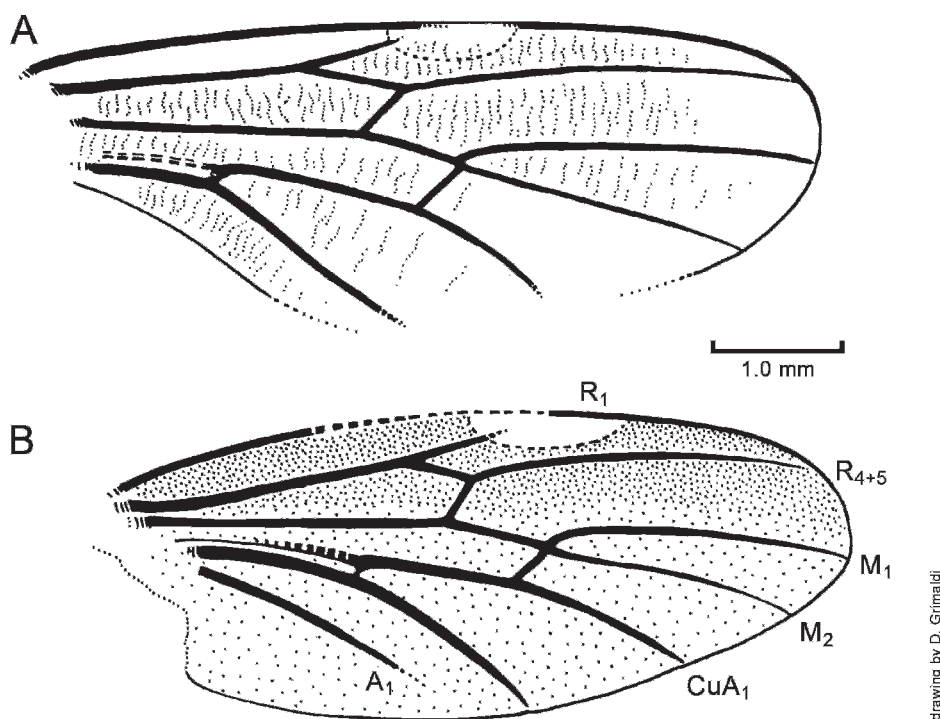
Fig. 8.   Camera lucida drawings of Bibionidae (*Bibio*) wings **A.** UAF-GS6. **B.** UAF-GS7.

Bibionids are an ancient group, with definitive fossils first occurring in the Cretaceous (a Triassic record is incorrect). Nearly 350 names have been attributed to Tertiary bibionids of the Northern Hemisphere (summarized by Evenhuis, 1994). There are nearly 130 species names of Tertiary *Bibio* alone, from the Pliocene through Eocene of the Northern Hemisphere. Eleven North American fossil *Bibio* are reported, all except two from the Oligocene of Florissant; the other two are from the Miocene Latah Formation of Idaho (Lewis, 1969; Lewis et al., 1990a, b). Fitzgerald (1999) described and redescribed several additional Tertiary bibionids, although none are *Bibio*.

Family Lonchaeidae Rondani, 1856

Genus *Dasiops* Rondani, 1856

SPECIMENS: Specimens UAF-GS9 and UAF-GS26 (figs. 9, 10) are complete and well-preserved wings, 3.5 mm and 5.6 mm long. The wings are so well preserved that even the fine veins that comprise the tiny basal cells are intact.

DISCUSSION: The general facies of the wing is typical of the "higher" (Cyclorrhaphan) flies, among which the wing venation is rather conservative. Some cyclorrhaphan families with extremely distinctive wing features can be immediately dismissed, such as many of the muscoids (the wing does not have a large calypter), Agromyzidae, Chloropidae, Sphaeroceridae, many of the tephritoids, etc. Among all other North American cyclorrhaphan genera, these two wings bear closest resemblance to *Dasiops* (Lonchaeidae). This is based on: overall shape of the wing, the large subcostal cell, completeness and close proximity of veins Sc and R_1, closed basal cells bm and cup, and a definite but incomplete vein A_1+CuA_2. Lonchaeids in general have a rather well-developed calypter for "acalyptrate" flies, but it is possible that some of this region of the wing is not preserved in the fossils. The venation of the two specimens is virtually identical, the only (slight) differences being that the crossveins (r-m and m-cu) in UAF-GS26 are slightly closer to each other, the apex of R_{4+5} is slightly more curved toward
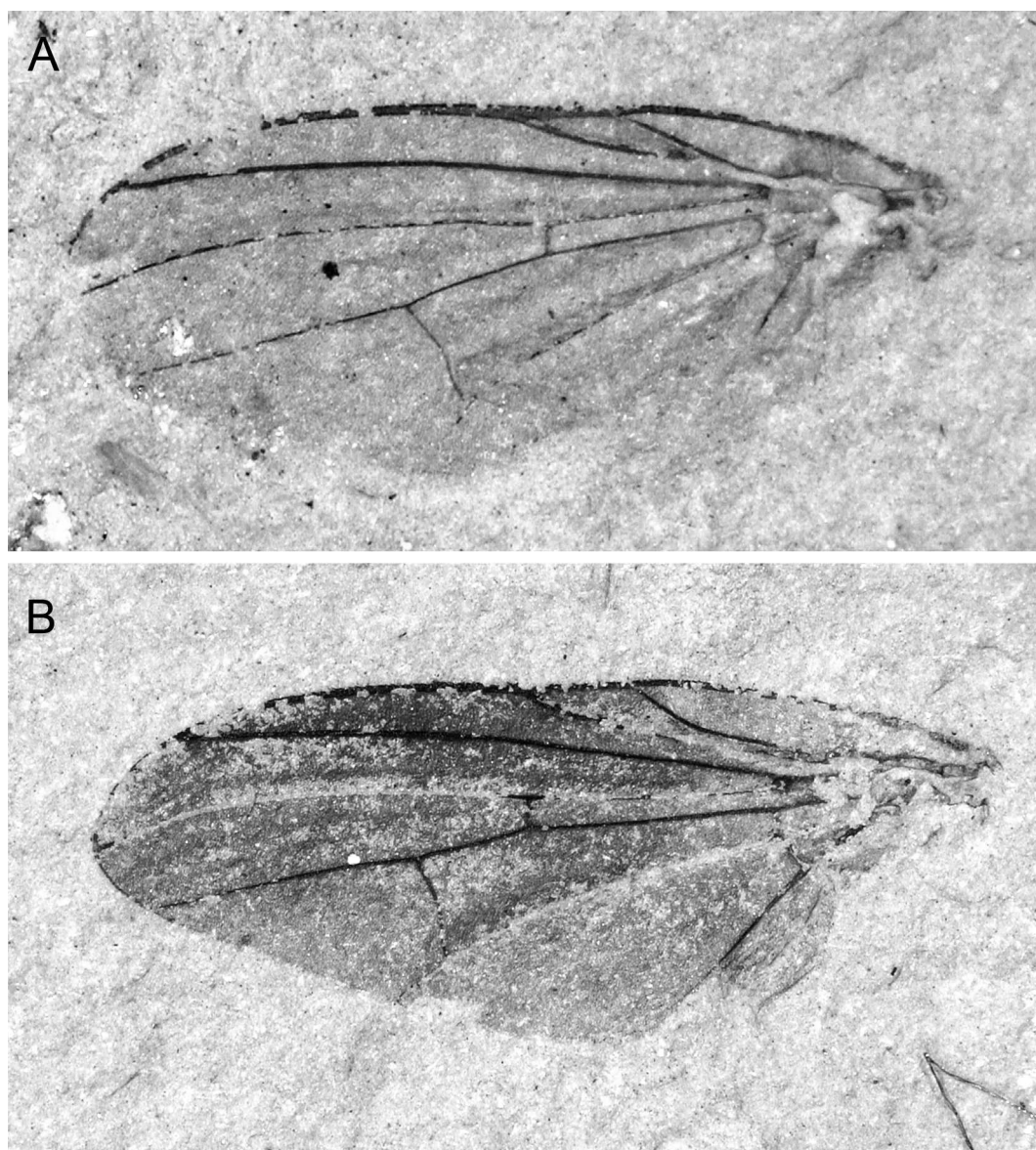
Fig. 9.   Photomicrographs of Lonchaeidae (cf. *Dasiops*) wings. **A.** UAF-GS9. **B.** UAF-GS26.

the apex of M, and the trailing edge of the wing in the distal half is slightly narrower (the tip is narrower). The wing of UAF-GS26 is significantly larger than UAF-GS9 by some 60%, which is extreme for intraspecific variation in acalyptrate flies. Thus, there are probably two species of lonchaeids.

The only account for North America of the genus *Dasiops* are descriptions of new species by McAlpine (1964). The work unfortunately

was not a revision, but some cursory distributional data can be gleaned from it. *Dasiops* is distributed throughout North America with more than 50 species, some of which extend into the Yukon Territory and Northwest Territories of Canada. Seven species are recorded from Alaska: *borealis* McAlpine, *criddlei* McA., *lineelus* McA., *anepsiosus* McA., *hastulatus* McA., and *penealbiceps* McA. (the last three in the *albiceps* group).

A

0.5 mm

B

R_1 Sc

R_{2+3}

h

r-m   br

bm

cup

R_{4+5}

M

m-cu

alula

CuA_1
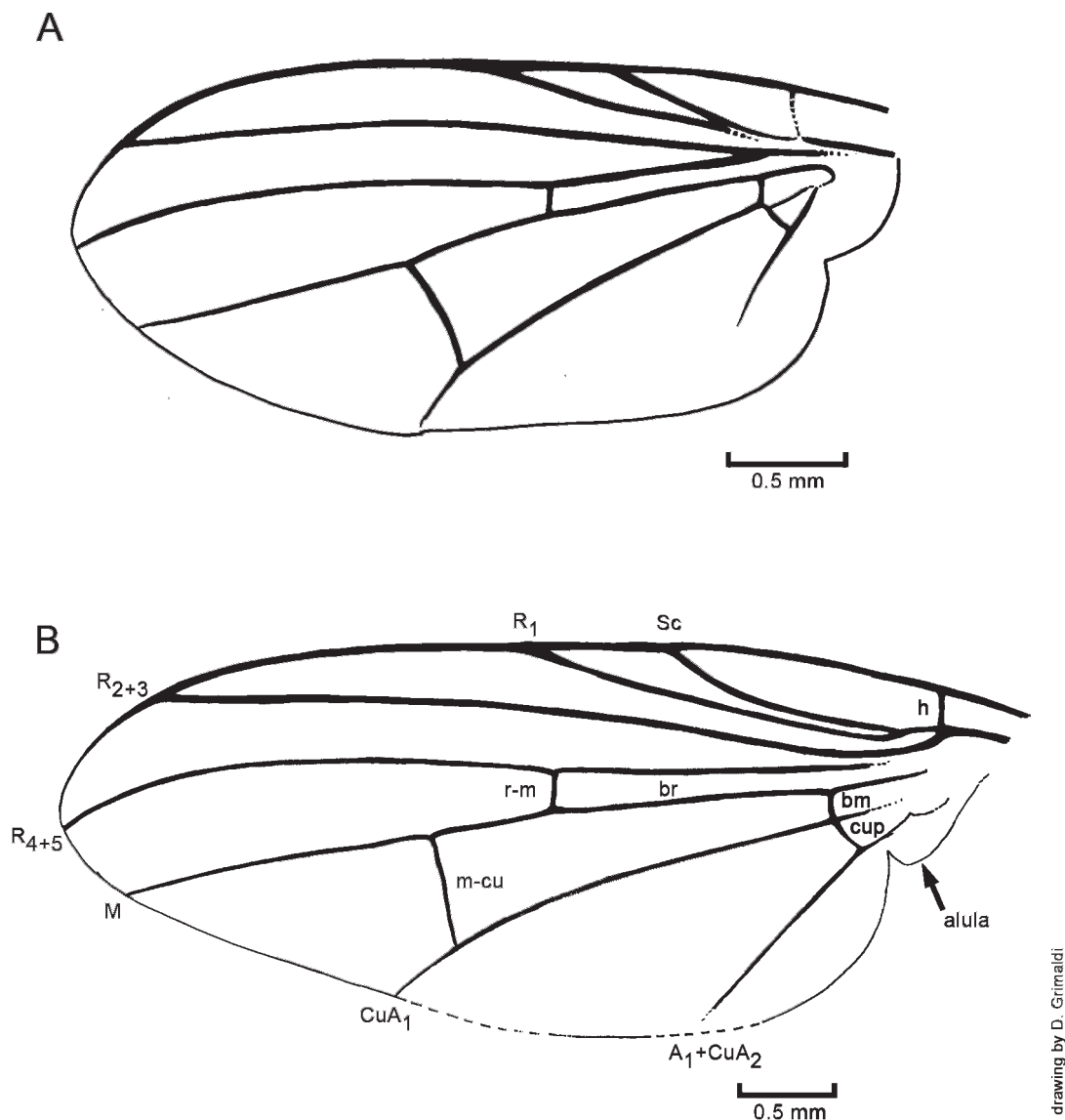
A_1+CuA_2

0.5 mm

drawing by D. Grimaldi

Fig. 10.   Camera lucida drawings of Lonchaeidae (cf. *Dasiops*) wings. **A.** UAF-GS 9. **B.** UAF-GS26.

Species of the genus are not differentiated on the basis of wing venation. According to McAlpine, many species of *Dasiops* breed under the bark of dead or dying conifer trees, usually those attacked by bark beetles (Curculionidae: Scolytinae). Biogeography of this genus is similar to *Bibio*.

The only other, putative fossil lonchaeids to have been described are in Baltic amber (Hennig, 1967), *Glaesolonchea electrica* Hennig and *Morgea mcalpinei* Hennig. However, both have been found to belong to the Pallopteridae (Morge, 1967; McAlpine, 1981). The Alaskan fossil would be the only fossil lonchaeid.

Order COLEOPTERA Linnaeus, 1758

Two taxa of beetles are represented only by a specimen each and for which only the elytra remain (fig. 11). They are both approximately 5 mm in length and have well-developed

striae, but the elytra are distinctly different in structure and thus indicative of two distinct taxa. UAF-GS33 consists of both elytra, which strongly taper to an apical point; the elytra have significant relief, suggesting that the beetle's body was somewhat dome-shaped. Specimen UAF-GS34 consists of just the left elytron, lateral and medial margins of which are parallel to nearly so, and the elytron is quite flat. Specimen UAF-GS33 is a weevil (family Curculionidae) and UAF-GS34 is a ground beetle (family Carabidae) (identifications courtesy of S. A. Elias, personal commun.).

DISCUSSION

The Bering Strait was closed for much of the Cenozoic and even the Late Cretaceous, allowing an interchange of Palearctic and Nearctic biota. In a scenario opposite that of the Panamanian isthmus, which closed approximately three million years ago (allowing an interchange of long isolated South American biota into Central and North America, and vice versa), the Bering Strait opened approximately 5.4–5.5 Ma. This is partly revealed, for example, by the oldest occurrence in the North Pacific of the marine bivalve *Astarte*, in the Milky River Formation near Port Moller on the Alaskan Peninsula (Marinkovich et al., 2002), which was dated by means of diatoms (Gladenkov et al., 2002). This genus occurred only in the Arctic Ocean when the Bering Strait was closed. Thus, the insect outcrop reported here from the Grubstake Formation is approximately one million years older than the opening of the Bering Strait, and presumably the biota of Alaska of the time reflected this interchange. The only suggestion from our study of such interchange is the ichneumonid wasp, which appears most similar to the Palearctic genus *Brachypimpla*. However, this identification is based on venational subtleties and needs to be very rigorously tested.

Palynologically, the lower units of the Usibelli Group (e.g., Suntrana Formation, ca. 13–16 Ma [fig. 1]) indicated warm temperate conditions similar to those presently in the northeastern U.S. and northeastern China (e.g., a mean annual temperature [MAT] of 9°

C: Leopold and Liu, 1994; White and Ager, 1994), then the climate cooled during the period of deposition of the Lignite Creek and Grubstake Formations (Leopold and Liu, 1994). According to Wolfe (1994) MAT during the Grubstake was approximately 3° C; Leopold and Liu (1994) indicated approximately 5° C. Elias and Matthews (2002), using an extensive sample of fossil beetles, calculated T_{max} (mean summer temperatures) between 5.7 and 2 Ma of 12.4° to 13.8° C—significantly warmer than present. Seasonal ice was apparently present during the deposition of the Grubstake, based on the presence of 1–2 cm ''drop stones'' present in the outcrop (D. Triplehorn, personal obs.), which would have been deposited by float ice. Also, during the deposition of the Grubstake the flora was dominated by coniferous forest (Wolfe, 1994), similar to conditions today. This paleoenvironment is corroborated by the fossil Diptera in our study, though the fossil ants from this deposit and the slightly younger deposit in Deering indicate warmer and drier conditions.

The study by Hopkins et al. (1971) was of a relatively diverse assemblage of plants and arthropods from near Deering, Alaska, on the Seward Peninsula, originally stated to be Early Pliocene based on earlier chronology. Dating of basalt in that study indicated an age of 5.7 ± 0.2 Ma, or Late Miocene. Although approximately one million years younger than the Grubstake, the Deering deposit indicates a very similar paleoenvironment to the Grubstake. Deering today is within tundra, but many of the Late Miocene plant taxa from there have modern distributions whose northernmost distribution extends to southern Alaska or even more southerly. These taxa included *Larix*, *Tsuga heterophylla*-type, *Chamaecyparis*, *Symphoricarpos*, and *Corylus*; other taxa, like *Picea* and *Betula*, have extant distributions found not far from Deering. Arthropods showed a more mixed biogeographic pattern similar to that of the Grubstake. Some carabid beetles in their study, like the Diptera in our study, had distributions encompassing the vicinities of the fossil sites, like *Carabus* cf. *truncaticollis* Eschsholtz, *Pterostichus* (*Lyperopherus*), and *P.* (*Cryobius*). Some of the beetles, however, revealed northern extinctions, specifically
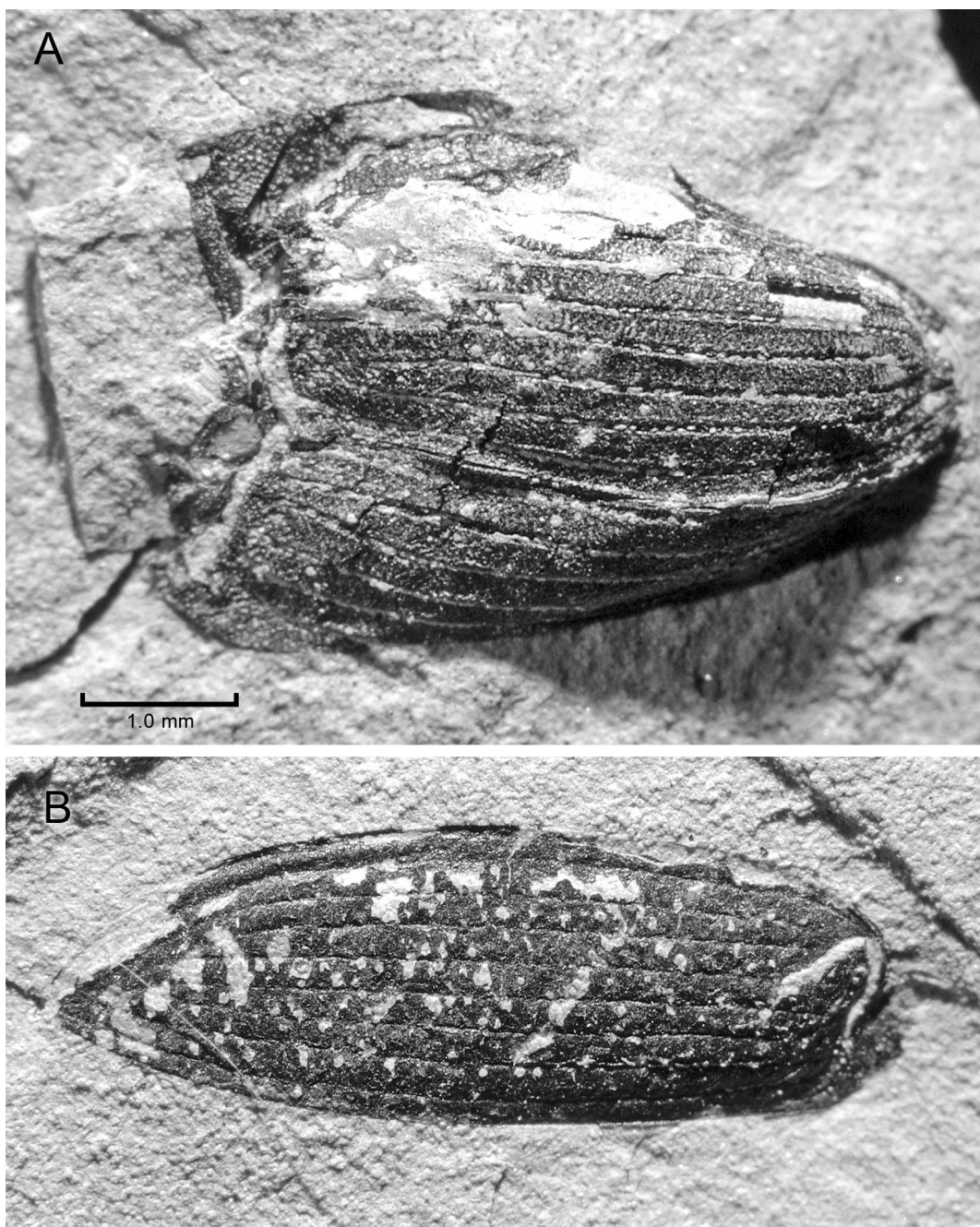
Fig. 11. Photomicrographs of beetle elytra. **A.** UAF-GS33: family Curculionidae. **B.** UAF-GS34: family Carabidae. (Both to the same scale.)

Pterostichus cf. *covinus* Dejean and *Georyssus* sp. The two genera of ants reported in Hopkins et al. (1971) included "relatively abundant" *Leptothorax* Mayr (Myrmicinae), the 30 North American species of which have extant distributions that are largely south of 50°N latitude. The other genus found at Deering, *Camponotus*, is very speciose. Other than one species extending to southern Alaska (*Camponotus herculeanus*), the genus generally extends at best to southern Canada. Greater susceptibility of the ants to climatic changes also reveals the pitfalls of estimating paleoclimatic changes using only one or a few taxa.

The ants from Suntrana and Lava Camp (Deering) outcrops indicate significant northern extinctions, in contrast to the other insect taxa from these two studies, which raise questions on how climate change can differentially and dramatically affect the composition of biological communities and thus the functioning of ecosystems. The species diversity and biomass of ants is maximal in the tropical river basins of the world (particularly the Amazon and Orinoco basins), and ants are well known to become scarce at higher latitudes and altitudes. In tropical montane regions, for example, ant abundance and diversity drops dramatically after approximately 2,000 m altitude, and they drop out entirely in higher montane forests that are constantly cool and wet. Thus, while it is little surprise that the Late Miocene ants from Alaska display greater distributional contraction from extant distributions relative to the other insects, the magnitude of the contraction is unexpected, as was their abundance (more than two-thirds of the insect specimens). Given the profound effects that ants have in tropical and even temperate ecosystems—as soil movers, consumers, predators, plant dispersers, protectors of symbiotic hemipterans (Hölldobler and Wilson, 1990)—their extirpation from any area will have significant impact. The composition of any biological community is an ebb and flow of species, some of which may be transient but nonetheless ecologically very significant.

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