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THE MESOZOIC FAMILY ARCHIZELMIRIDAE (DIPTERA: INSECTA)

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ABSTRACT—A nematocerous fly family known previously only from one species and specimen from the Upper Jurassic of Karatau, Kazakhstan, Archizelmiridae is expanded here to include additional records preserved as compression fossils and ones in amber. The compressions are from the Upper Jurassic of Shar-Teg, Mongolia and Lower Cretaceous of Baissa, Transbaikal, with a new species, *Archizelmira baissa*, from Baissa. Particularly significant are three finely preserved new species and genera in ambers from the Cretaceous Period: *Zelmiarcha lebanensis* (Lebanon: Lower Aptian), *Archimelzira americana* (New Jersey: Turonian), and *Burmazelmira aristica* (Burma [Myanmar]: mid-Cretaceous). The latter two species interestingly possess stylate antennae, those of *Burmazelmira* being the only aristate antennae in the order Diptera outside the suborder Brachycera. A cladogram is presented for the relationships among archizelmirid species, cladistic rank of which correlates with stratigraphic age. Transformation series of the antennal flagellum in Archizelmiridae corresponds with one recently hypothesized for the Brachycera, wherein the style and arista are derived from the apical flagellomere(s). The family appears to be a member of the extant group Sciaroidea, which includes fungus gnats and gall midges, though precise relationships remain unclear.

INTRODUCTION

CRETACEOUS AMBERS FROM throughout the Northern Hemisphere have yielded a great diversity of insects, large percentages of these being nematocerous Diptera. These deposits include amber from western Canada (Campanian), New Jersey USA (Turonian), Taymyr peninsula of northern Siberia (Santonian, some Cenomanian), Lebanon and Jordan (Neocomian), northern Spain (Aptian), France (Cenomanian), and Japan (Aptian) (reviewed in Grimaldi, 1996). Age of amber from northern Burma (Myanmar) has been equivocal, previously thought to be Eocene or even Miocene (e.g., Grimaldi, 1996). Recent study and restudy of historical material at the Natural History Museum in London (NHML) reveals several exclusively Cretaceous insect taxa in Burmese amber (Rasnitsyn and Ross, 2000; Zherikhin and Ross, 2000), indicating its probable Cretaceous age. A biostratigraphic account of Burmese amber, based on the systematics of insect inclusions in newly excavated material, is also provided by Grimaldi et al. (2002). That study suggests, in fact, that the Burmese amber may be as old as Cenomanian. Among that new material is an interesting Mesozoic taxon, which we treat herein.

Our first encounter with an archizelmirid was a single specimen found by the senior author from among nearly 2000 inclusions in amber from central New Jersey. It was originally thought to be a highly modified sciarid, except for the unusual flagellum and peculiarities of the venation. Then, several years later, a series of venationally similar midges in Lebanese amber were sent to the authors from Dr. Dany Azar (Musée d'histoire naturelle, Paris). Plesiomorphic morphology of the older Lebanese specimens indicated they were not sciarids. Later, a series of very interesting specimens with a highly modified, aristate antenna was found by the senior author in Burmese amber among material recently acquired by the AMNH. These had the distinctive venation of the other specimens, but, again, taxonomic identities remained uncertain. Lastly, compression fossils examined by V.B. from several Jurassic and Cretaceous Eurasian sites had a venation quite similar to that of *Archizelmira kazachstanica* Rohdendorf, 1962, as well as to those flies in amber. Rohdendorf described the genus, for which a new family was designated, based on a rather incomplete specimen from the famously diverse insect Lagerstätte from the Upper Jurassic of Karatau, Kazakhstan. Thus, with a name in precedence, and affinities now known on the basis of well-preserved amber material, we can provide a detailed report of the formerly poorly known Mesozoic midges in the family Archizelmiridae.

This study is an example as to how the fine preservation in amber can significantly extend the understanding of phylogenetic affinities, well beyond what is possible with compression fossils. Although thousands of nematocerous fly inclusions occur in Cretaceous ambers from western Canada, northern Siberia, and Spain, no archizelmirids have yet been found in them.

COLLECTIONS, GEOLOGICAL SETTINGS, AND METHODS

Compression fossil specimens were borrowed from the Arthropoda Laboratory of the Paleontological Institute, Moscow (PIN). These include ten new specimens from the Kimmeridgian of Karatau, Kazakhastan. Also, three specimens from the Upper Jurassic of Shar-Teg, Mongolia were studied, as were two specimens from the Valanginian-Barremian of Baissa, Transbaikal. For each of these deposits more than 20,000 insect specimens were collected, so Archizelmiridae represent a small fraction of each paleofauna.

Amber material is deposited in two collections. Lebanese amber specimens are from the Azar collection, courtesy of Dr. Dany Azar, Department of Entomology, National Museum of Natural History, Paris. Specimens in New Jersey and Burmese amber are in the Division of Invertebrate Zoology (Entomology), American Museum of Natural History. There have been recent comprehensive treatments of the taphonomy, stratigraphy, and diversity of fossil inclusions for each of these ambers.

Amber from the Lower Cretaceous of the Middle East ''Levantine Belt'' occurs throughout central Lebanon, northern Israel, and parts of Jordan. Lebanese amber is treated extensively by Azar (2000). All Lebanese amber is Lower Cretaceous, except for one outcrop [from Ghiné: Upper Jurassic (which is not fossiliferous)]; ages vary considerably among the Cretaceous outcrops. The Lebanese amber Archizelmiridae studied here all derive from Hammana, attributed to the Lower Aptian (Azar, 2000). Botanical source appears to be the extinct conifer family Cheirolepidiaceae, based on chemistry of the amber and association with vegetative and reproductive macrofossil remains. Diptera comprise 58 percent of all organismal inclusions in amber from Hammana, of which there are 18 specimens among several thousand that belong to a new genus of Archizelmiridae described here. Amber from New Jersey was treated extensively in a recent volume (Grimaldi, 2000); its stratigraphy and taphonomy was presented by Grimaldi et al. (2000). The outcrop of highly fossiliferous amber from New Jersey is from the South Amboy Fire Clay (Turonian), of Old Crossman's pits (''White Oaks'' site), Sayreville, Middlesex County. Botanical source appears to be Cupressaceae sensu lato, also based on amber chemistry and direct association with wood and cone scales. Diptera comprise 34 percent of all organisms in the Sayreville amber, only one specimen of which is an archizelmirid.

Lastly, Burmese amber historically and recently derives from the northern Myanmar state of Kachin. Until recently, the only collection of Burmese amber fossils was one consisting of 1,200 inclusions in the Natural History Museum, London, assembled between 1905–1910. Recent restudy of the inclusions in that collection indicate that the material is Cretaceous, as based on the presence of Serphitidae and several other families of insects restricted to the Cretaceous (Rasnitsyn and Ross, 2000). Confusion over the putative Tertiary age derives from the fact that Burmese amber was redeposited in Miocene deposits (Zherikhin and Ross, 2000). In 2000, the AMNH received 150 kgs. of newly excavated amber from near Myitkyina, Kachin, Myanmar. This material yielded a diverse array of organisms, recently summarized by Grimaldi et al. (2002). Among the organisms found were various new records of genera and families of insects that corroborate the Cretaceous age of Burmese amber, and in fact suggest an age of approximately Cenomanian. This age corresponds with Cenomanian-aged exposures near the Kachin amber outcrops (Zherikhin and Ross, 2000), which have yet to be examined for amber but which are likely to have been the source of Burmese amber. Botanical source of Burmese amber is unknown, but almost certainly was coniferous. Diptera comprise 42 percent of all Burmese amber inclusions in the AMNH collection, but only seven specimens were Archizelmiridae. No archizelmirids occur in the NHM collection. Based on preservation in amber and in sediments, Archizelmiridae were apparently rare in the Upper Mesozoic.

Amber specimens were prepared according to the procedures outlined in Nascimbene and Silverstein (2000). This involved embedding the brittle Cretaceous amber in epoxy under vacuum, then trimming with a diamond wheel and grinding and polishing flat surfaces that optimize views of particularly important structures. Specimens were studied with a Zeiss SV8 (up to 68×) and a Leitz Wetzlar stereomicroscope (up to 144×), and a Zeiss compound microscope (up to 400×). With thin, flat preparations, amber pieces can be mounted on a microscope slide and studied under a compound scope using standard transmitted light and intense reflected light from a fiber optic lamp. This allows visualizing minute structures, such as of the antenna and pretarsus.

Terminology for wing venation is controversial, though we have generally followed McAlpine (1981) as a standard reference. The main disparity between this reference and what several of us are interpreting concerns the homology of radial veins. Here, in accordance with McAlpine (1981), the apically branched veins of Rs are identified as R_{2+3} and R_{4+5}, though basal Bibionomorpha (e.g., Triassic Vimrhyphidae and Mesozoic Protorhyphidae) have R_{2+3} originating before r-m and R_{4+5} distal to r-m. In most Sciaroidea and Bibionidae there is a single branch of Rs. Thus, what we call R_{2+3} can also be interpreted as R_4 or even Rs_3 and what is called R_{4+5} can be interpreted as R_5.

SYSTEMATIC PALEONTOLOGY

Class INSECTA Linnaeus, 1758
Order DIPTERA Linnaeus, 1758
Family ARCHIZELMIRIDAE Rohdendorf, 1962

Diagnosis.—(emended from Rohdendorf) Jurassic and Cretaceous Diptera with large, dichoptic eyes and no dorso-ventral differentiation of facets, where eyes have been preserved; plesiomorphically with 14 moniliform flagellomeres, apomorphically reduced to an antennal style or even an apical arista. Body gracile where known; legs long, tibiae with 1:2:2 small apical spurs; coxae relatively long. Wing venation very distinctive: Veins C and R are dark, other veins very light; C ends at apex of R_{4+5} or slightly beyond (but not extended to apex of M_1); R vein field generally narrow, with short, oblique or transverse base of RS; bases of M_{1+2}, CuA_1, and CuA_2 nearly parallel, attached to posterior wall of large basal cell partially formed by vein composed of r-m and m-cu. Anal vein incomplete, short; anal lobe of variable size, but generally large.

Type genus.—*Archizelmira* Rohdendorf, 1962, by original designation.

Genus ARCHIZELMIRA Rohdendorf, 1962

Type species.—*A. kazachstanica* Rohdendorf, 1962: 326 (1991: 473, fig. 1040).

Diagnosis.—(emended from Rohdendorf, based on re-examination of holotype of *A. kazachstanica* and new material from the type and other localities) Wing membrane with microtrichia only; R_1 long, extended to level of or slightly past base of fork of R_{2+3}-$R_{4+5.}$ Point of Rs joining R_1 distal to point where Rs joins M. R_{2+3} and R_{4+5} apically branched, forking just beyond middle of the Rs vein; R_{2+3} connecting to C close to R_1. Sc vein reduced and incomplete (not reaching to C).

Discussion.—The compression fossil species (*Archizelmira*) have a venation that is plesiomorphic to that of the species preserved in amber, notably the distal fork of R. The backwards slope of Rs and the very weak development of Sc are certainly apomorphic for *Archizelmira*. In the amber fossil genera Sc is as thick and sclerotized as the C and R veins, so if Sc was present in the compression fossil taxa (*Archizelmira* spp.) it would very likely have been preserved, though this is not certain.

ARCHIZELMIRA KAZACHSTANICA Rohdendorf, 1962
Figures 1.1–1.4, 2–4, 5.1

Diagnosis.—Distinguished from *Archizelmira baissa*, n. sp. on the basis of Rs lying at a wide angle in relation to the axis of R (approximately 65–70°); apex of R_1 reaching level of base of apical fork of R or significantly beyond; CuA_2 gently curved, such that the smallest distance between CuA_2 and CuA_1 is barely less than the length of m-cu.

Type.—Holotype, PIN SAGU-17, Upper Jurassic, Karatau (Kimmeridgian). Examined (Figs. 2.1, 3). Though SAGU-17 is labelled as the holotype, specimen PIN 2997/3284 (Fig. 4.2) is most similar to the specimen figured by Rohdendorf.

Other material examined.—KAZAKHSTAN: Chimkent, Karatau: PIN 2066/2077±, 2239/2029, 2239/2030 (Fig. 2.4), 2239/2031 (Fig. 2.6 [habitus photo]; Fig. 4.1 [wing]), 2239/2034 (Fig. 4.4: antenna), 2997/3284 (Fig. 4.2 [wing]), 2997/3216 (Fig. 4.5 [tibial spurs]), 2997/4774. MONGOLIA: Shar-Teg: PIN 4270/2244 (Fig. 1.4: wing), 4270/2243± (Figs. 1.3 [photo of wing], 4.3 [drawing of wing]), PIN 4270/2242±. Venation of specimens from Karatau and Shar-Teg are indistinguishable, although some of the wings are considerably different in size. In specimen PIN 2239/2034 one antenna is sufficiently well preserved to observe 14 flagellomeres, which are virtually moniliform (Fig. 4.4)—definitely without the differentiation of articles seen in the amber fossil taxa. Also, PIN 2997/3216 reveals a pair of well-developed tibial spurs (lengths almost three times the width of the basitarsus), although it is unclear to which pair of tibiae these belong (Fig. 4.5). Preservation of the Karatau and Baissa material are similar, being a greyish shale laced with silvery filaments of plant fibers and reddish and yellowish flecks of minerals. The insects are preserved as brownish films; in the best specimens microtrichia can be preserved. Observation is far better with the surface wet with ethanol, which improves contrast between the image and matrix, and reduces irregularity of the matrix. Most specimens are completely articulated bodies. In contrast, the Shar-Teg specimens are wing imprints only, but the matrix

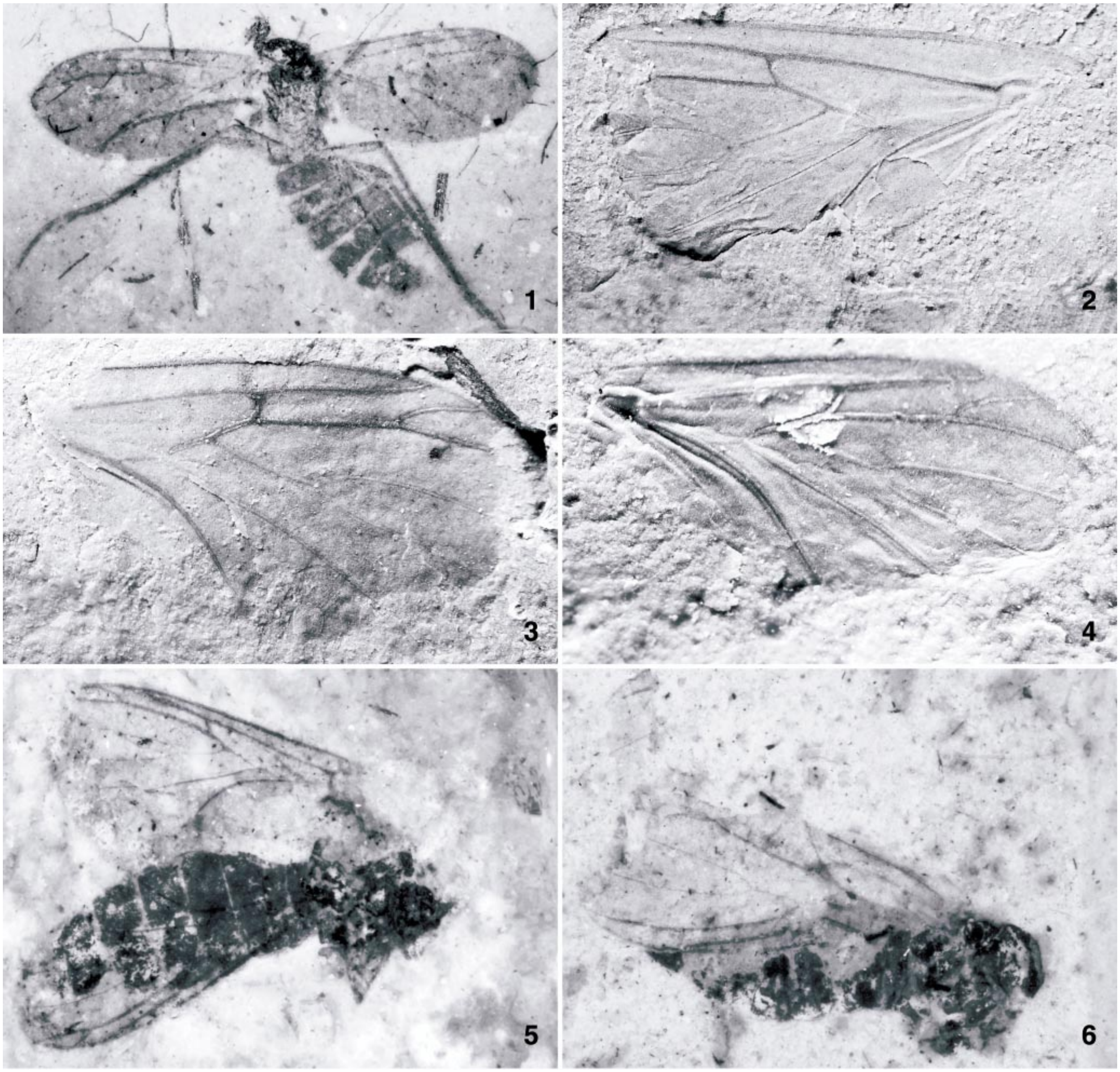


FIGURE *1*—Photomicrographs of compression fossil *Archizelmira* species. *1, A. kazachstanica* (PIN 2997/3284), from Karatau, Kazachstan; *2–4, A. kazachstanica* from Shar-Teg, Mongolia, *2,* PIN 4270/2242, *3,* PIN 4270/2243, *4.* PIN 4270/2244; *5, 6, A. baissa*, new species, from Baissa, Transbaikal, *5,* holotype, PIN 3064/9039, *6,* PIN 3064/9918. For size measurements see Table 1.

is a very fine grained mudstone that has preserved veins with excellent resolution and relief. Use of ethanol actually reduces visibility of the Shar-Teg specimens.

Discussion.—Based on our study of the type specimen and better preserved material from Karatau and Shar-Teg, there are significant inaccuracies with Rohdendorf's illustration and description of the species. *Archizelmira kazachstanica* does not possess a complete Sc, nor veins within the large basal cell, an incomplete M_2, or a reduced anal lobe. In fact, there are fewer preserved features in the type specimen than shown by Rohdendorf, including the apices of R_{2+3} and R_{4+5}, M_1 and M_2. The holotype was originally covered with Canada Balsam for possibly 40 years. Its surface had become heavily crazed, making it impossible to examine the specimen, so the balsam was removed with xylene. This may have affected the preservation, though not so much to have resulted in a venation so disparate with Rohdendorf's illustration. The specimen was kept uncoated.

ARCHIZELMIRA BAISSA new species

Figures 1.5, 1.6, 5.2

Diagnosis.—Distinguished from *Archizelmira kazachstanica* on the basis of Rs lying at a slightly more acute angle in relation

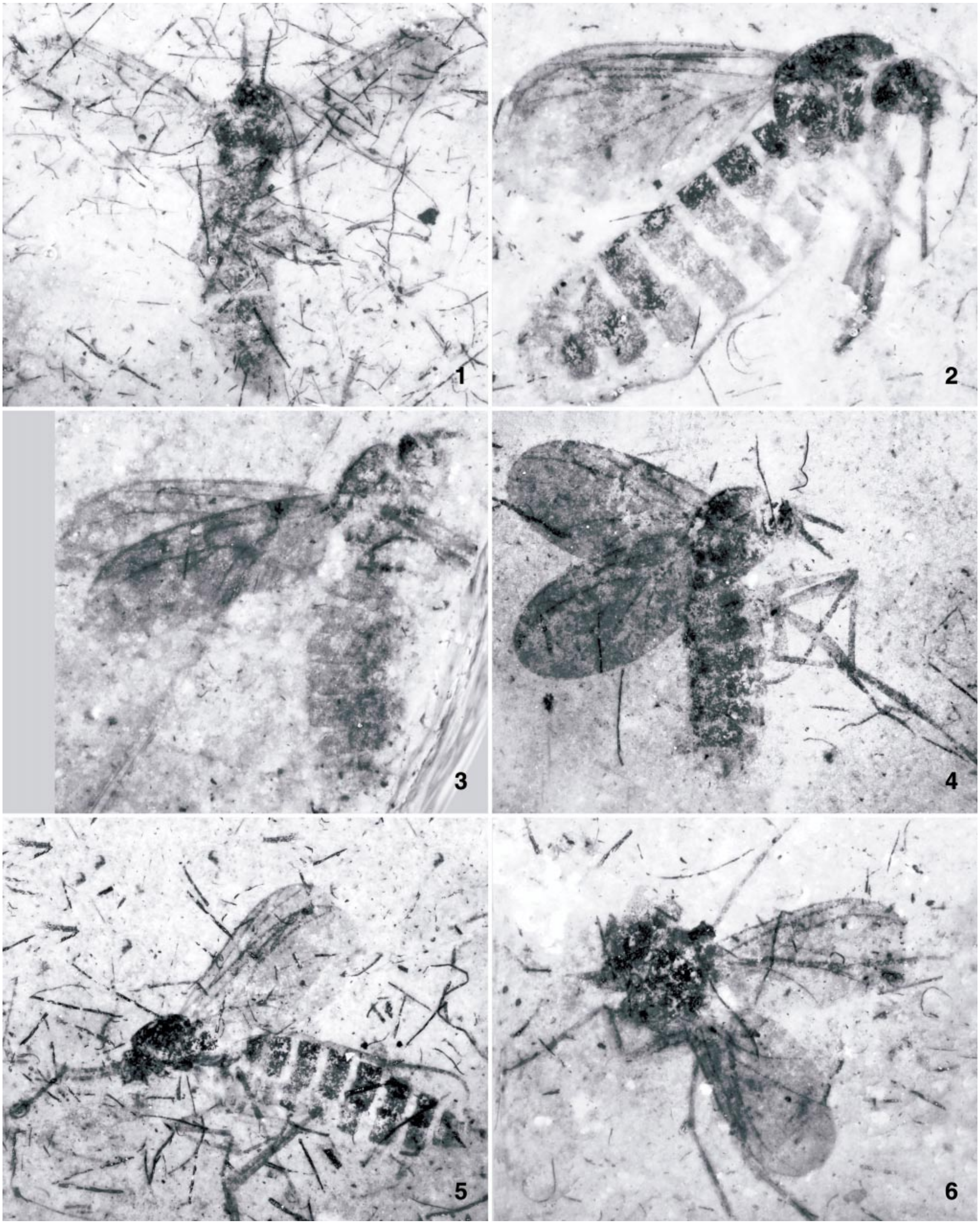


FIGURE 2—Photomicrographs of *Archizelmira kazachstanica*, all from Karatau, Kazachstan. *1,* Holotype (PIN SAGU-17); *2,* PIN 2066/2077; *3,* PIN 2239/2029; *4,* PIN 2239/2030; *5,* PIN 2239/3147; *6,* PIN 2239/2031.

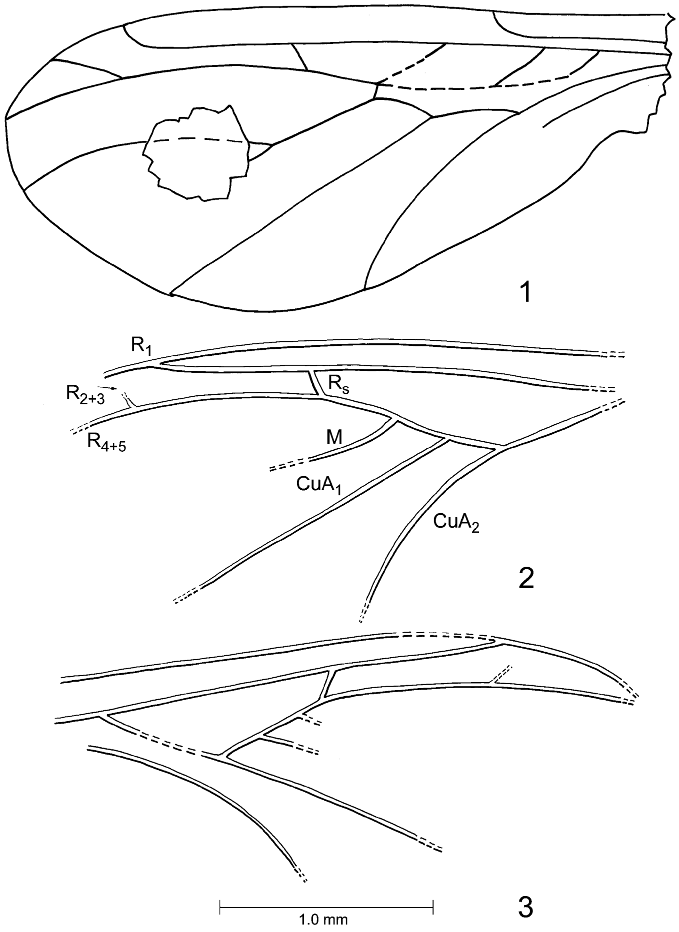


FIGURE 3—*Archizelmira kazachstanica* wing venation. *1,* Original figure of wing and venation of holotype of *A. kazachstanica* (redrawn from Rohdendorf, 1962); *2, 3,* wings and venation of *A. kazachstanica* holotype, re-examined.

to the axis of R (approximately 45°), and slightly shorter; apex of R_1 not quite reaching level of base of apical fork of R; CuA_2 strongly curved, such that the minimum distance between CuA_2 and CuA_1 along their lengths approaches 0.30× the length of m-cu.

Etymology.—From Baissa, the type locality.

Type.—Holotype, Russia: Transbaikal: Baissa, PIN 3064/9039 (Fig. 1.5 [photo, partial habitus]; Fig. 5.2 [wing fragment]). Paratype: PIN 3064/9918± (Fig. 1.6 [photo]).

Occurrence.—Known only from the Early Cretaceous of Baissa, Transbaikal.

Genus ZELMIARCHA new genus

Type species.—*Zelmiarcha lebanensis*, new species.

Diagnosis.—Eyes bare, face with extensive membranous areas; antenna with 14 flagellomeres evenly tapered apicad to fine point; R_1 end of Rs slanted proximad; R_{2+3} lost; R_{4+5} and C meet considerably before apex of C. Flagellomeres 1–8 each with pair of sharp scales on opposite sides. Known only from Lebanese amber.

Etymology.—An anagrammatic spelling of *Archizelmira*.

ZELMIARCHA LEBANENSIS new species
Figures 6.1–6.5, 8

Diagnosis.—As for genus.

Description.—HEAD: Eyes bare, large, occupying entire lateral surface of head, not dichoptic in male; no dorso-ventral differentiation of facets. Three ocelli present, not on a distinct protuberance; vertex with scattered short setulae. Palpus with three short segments visible (a fourth, small basal segment may exist), apical one about half the width of others. Labellum small, a fine V-shaped sclerite (probably the labrum) present; clypeus isolated, flat, quadrate. Face ventrally with short, broad carina and thin sclerotized median strip; small sclerotized lobe connected to base of antenna; otherwise, face largely membranous [best seen in Az567 (Fig. 8.4)]. Antenna with 14 flagellomeres, gradually tapered in width distad; apical flagellomere quite fine, bearing pair of fine, stiff setulae. Flagellomeres setulose, pedicel bulbous, with single, preapical whorl of fine setulae; scape slightly longer than pedicel. Each of flagellomeres 1–8 with pair of tooth-like scales; scales on opposite sides of each flagellomere. These scales have no appearance of being sensilla. Cervical region fairly long. THORAX: Scutum with two rows of dorsocentrals, two rows of acrostichals (best seen in specimen Az566); approximately three setae on postpronotal lobe, six to seven in notopleural area; six on scutellum. Scutum relatively flat, not domed. Pleura as figured (Fig. 8.1). Coxae relatively long, length approximately three times the width, with ventral row of setae. Legs long, slender; tibiae with short apical spurs: one foretibial spur, two midtibial, two hindtibial. Hind femur is thickest leg segment. Wing: C and R veins dark, other veins light. Sc incomplete, short h vein present near base; R_1 straight, basal half with ca. 10 fine setae. Short Rs near mid length of wing, nearly perpendicular to longitudinal veins, R_1 end directed slightly proximad. R_{4+5} meets C well before C ends distant from apex of M_1. Large basal cell formed by R, Rs, r-m, m-cu and base of CuA_1 and CuA veins. Bases of M and CuA veins nearly equidistant, parallel; M forked, CuA_1 and CuA_2 simple, the latter curved, not sinuous. CuP very short, apex reaching approximately to level base of A_1. Anal lobe well developed, but not as large is in other species. ABDOMEN: fairly long and slender. Male genitalia with very stout gonocoxa and gonostylus, apex of latter with single small apical tooth.

Etymology.—From Lebanon.

Types.—All from Azar Collection, in Natural History Museum, Paris, from: LEBANON: Hammana (Lower Aptian). Specimens Az569, A571 (Fig. 6.4), and Az574 are embedded in epoxy. Holotype: ♂, Az566 (Fig. 6.1), very well preserved specimen in a clear yellow piece that was cut square 4 × 5 × 1 mm and polished. Paratypes: Az201 containing 1♂ and 1 specimen of unknown sex, a clear yellow piece mounted on a slide with Canada Balsam; Az565 (Fig. 6.2), containing 1.5 specimens, complete one disarticulated, possibly ♂, but well preserved, in a clear yellow piece 7 × 9 × 2 mm; Az567 (Fig. 6.3), an extremely well preserved ♂ in a piece of clear yellow amber that is uncut and unpolished, 12 × 9 × 2 mm; Az571 (Fig. 6.4), 2♂♂ in a clear yellow piece 5 × 6 × 2 mm also containing a ♂ ceratopogonid; Az573, a ♂ in fair condition, in an irregular, semipolished piece of clear yellow and deep red amber; Az575 (Fig. 6.5), 2♂♂ in a clear yellow piece 9 × 6 × 4 mm; Az576, a ♂ in a clear yellow piece of amber with some dark planes, 6 × 3 × 3 mm; Az577, ♂ in uncut yellow piece 10 × 8 × 4 mm; Az578 (sex unknown) in yellow uncut piece 10 × 5 × 4 mm.

Occurrence.—Known only from Lebanese amber.

Discussion.—The three genera preserved in amber represent a monophyletic group on the basis of loss of vein R_{2+3}. Also, there is differentiation of flagellomeres in this group, with flagellomeres gradually or dramatically narrowed apicad. *Zelmiarcha* is the sister group to the other two genera, having the antennal articles least differentiated and lacking a vein CuA_2 that is sinuous.

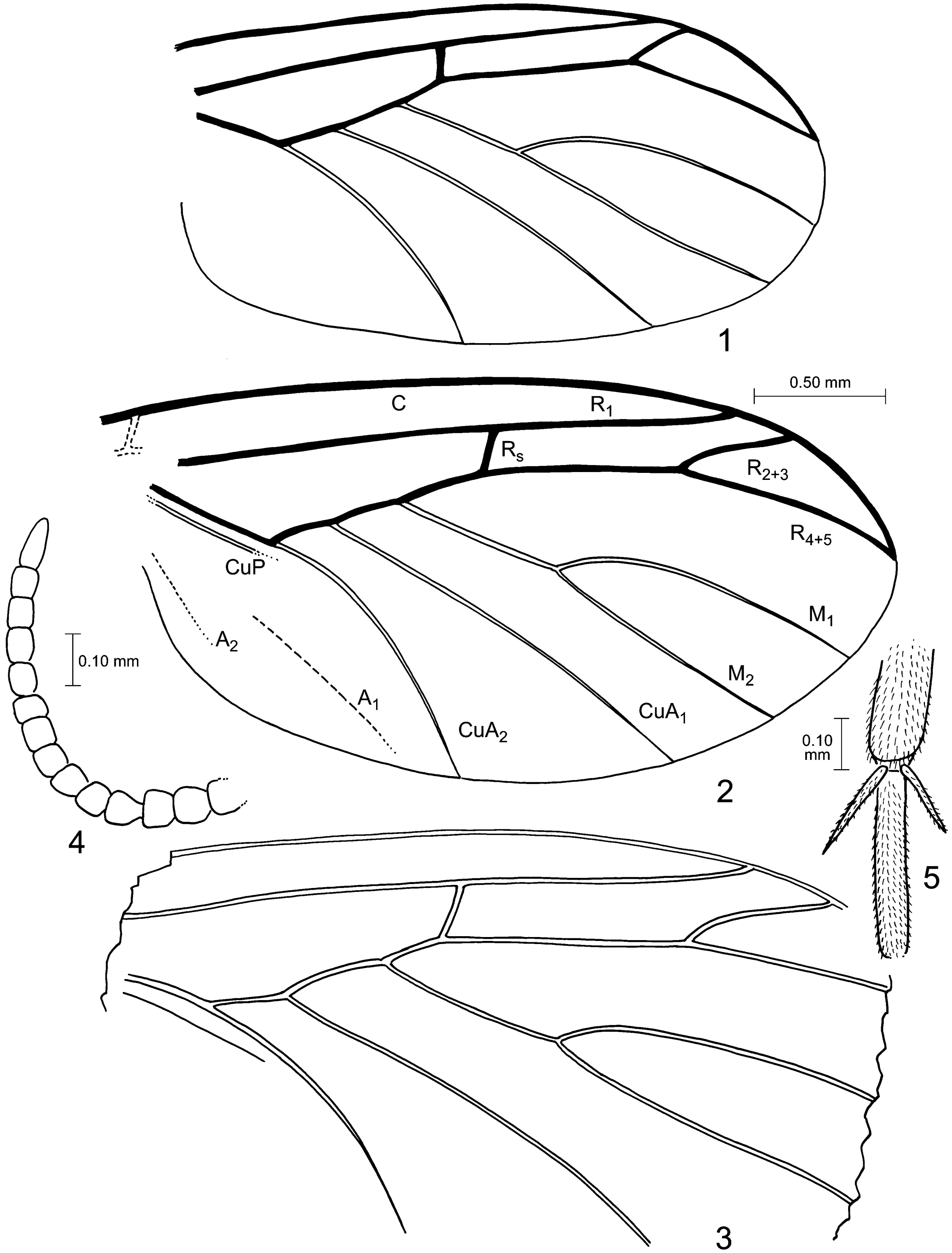


FIGURE 4—Wings and venation of new specimens of *A. kazachstanica* from Karatau, Kazachstan (*1, 2, 4, 5*) and Shar-Teg, Mongolia (*3*). *1,* Wing, PIN 2239/2031; *2,* wing, PIN 2997/3284; *3,* wing, PIN 4270/2243; *4,* antenna, PIN 2239/2034; *5,* tibial spurs, PIN 2997/3216.

Genus ARCHIMELZIRA new genus

Type species.—*Archimelzira americana* new species.

Diagnosis.—Antennal flagellum distinctly modified, where flagellomeres 3–11 are approximately one-half the width of the basal two flagellomeres, and flagellomere 11 is a fine, elongate style. CuA_2 kinked; bases of CuA_1 and CuA_2 very close and near base of wing, near level of crossvein h; m-cu very long. Rs extremely short.

Etymology.—An anagram of *Archizelmira*.

ARCHIMELZIRA AMERICANA new species

Figures 6.6, 9

Diagnosis.—As for genus.

Description.—Most of head and pleura obscured by milky froth of microscopic bubbles. Antennae well exposed, revealing 11 flagellomeres. Flagellomeres 1 and 2 cup-shaped, with 2 apparently

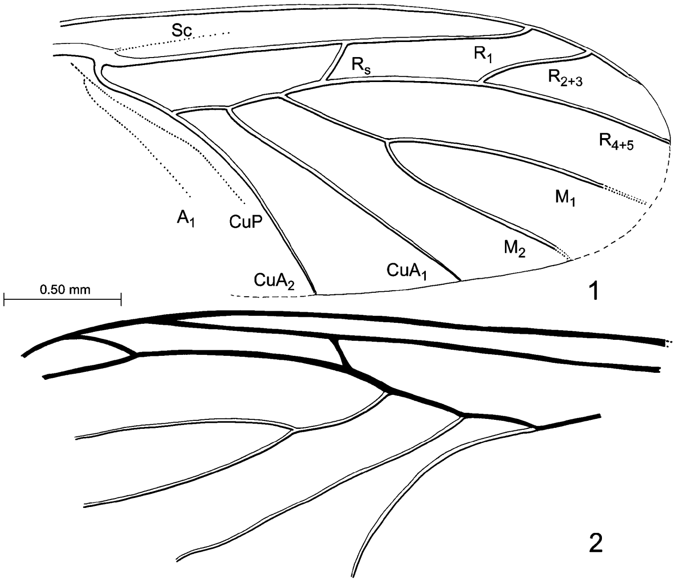


FIGURE 5—Wings of *Archizelmira* species. *1, Archizelmira kazachstanica,* from Shar-Teg, Mongolia (PIN 4270/2244); *2,* Holotype wing and venation of *Archizelmira baissa* n. sp. (PIN 3064/9039).

recessed half-way into 1; segments 3–11 half or less the width of flagellomeres 1 and 2. Flagellomeres 9 and 10 slightly narrower and longer than preceding segments; flagellomere 11 with small bulbous base abruptly narrowed to fine, setulose style. Length of flagellomere 11 equal nearly to length of all preceding segments. THORAX: Scutum visible, relatively broad, slightly arched, with apparently single row of acrostichal setulae and indeterminate number of larger dorsocentrals posteriorly. Scutellum with two transverse rows of approximately 6 stiff, fine setae each, one row near posterior margin of scutum. Lengths of scutellar setae approximately equal to length of scutellum. Legs with 1:2:2 tibial spurs. Wing: Vein C ends midway between apices of R_{4+5} and M_1. Space between C and R_1 relatively deep; Sc barely perceptible. Rs very short, situated close to where R and M fork. Space between R_{4+5} and R_1 very narrow; both veins with row of fine trichia. CuA_1 extremely straight, fine; CuA_2 kinked in distal half; bases of CuA_1 and CuA_2 join r-m very basally, near level of crossvein h. Anal lobe well developed. ABDOMEN: Relatively short compared to other genera. Genitalia: Male with stout gonocoxa and stout gonostylus (width of latter nearly equal to length); apex of gonostylus with sclerotized apical tooth.

Etymology.—Referring to an American representative of the family.

Type.—Holotype and unique specimen, AMNH NJ-258, collected by Keith Luzzi at the White Oaks (Old Crossman's) clay pits, Sayreville Township, Middlesex Co., New Jersey, U.S.A (South Amboy Fire Clay, Raritan Formation [Turonian: Grimaldi et al., 2000]).

Occurrence.—Known only from the Late Cretaceous of New Jersey.

Discussion.—The wing venation of this species is more divergent than all other archizelmirids, due to the extreme costalization of the radial veins, the very short Rs crossvein, the extreme basal forking of CuA, and the kinked CuA_2. Differentiation of the flagellomeres, structure of the male genitalia, costalization of R veins, forked M, and a kinked CuA_2 indicate this unusual fly is in the Archizelmiridae.

Genus BURMAZELMIRA new genus

Type species.—*Burmazelmira aristica*, new species.

Diagnosis.—Venation most similar to *Archizelmira* and *Zelmiarcha* but plesiomorphically with CuP and A_1 better developed and Sc reaching nearly to Rs. Eyes with dense, short interfacetal setulae. Antennae highly autapomorphic, with basal 12 flagellomeres fused into cone, and apical flagellomere (possibly two) long and aristate.

Etymology.—Referring to the former name of the country of Myanmar.

BURMAZELMIRA ARISTICA new species

Figures 6.7, 6.8, 7.1–7.3, 10

Diagnosis.—As for genus.

Description.—HEAD: Eyes large, occupying entire lateral surface of head; dichoptic, without dorso-ventral differentiation of facets, with dense interfacetal setulae (length of setula approximately equal to diameter of facet). Three ocelli present, not on a prominent mound; between ocelli are ca. 10 fine setae, length of several three times the diameter of ocellus. Mouthparts with labellum well developed; palpus well developed, with three segments, apical palpomere equal to length of proximal palpomere but one-half the width. Antenna with long, narrow scape (length ca. three times the width); pedicel large, scoop-shaped, with row of short, stiff setae on distal rim. Flagellomeres highly differentiated: basal 12 flagellomeres greatly fused into a thick cone-shaped structure (faint annuli discernable under high magnification), with dense, fine microtrichia. Base of fused basal flagellomeres with a long, narrow condyle inserted into the apex of the pedicel. Apical segment—presumably the apical flagellomere—very long, whip-like (an arista), without pubescence. Cervix elongate. THORAX: Pleura: See Fig. 10.8. Legs: Long, slender, with fore:mid:hind tibial spurs 1:2:2. Fore tibia with apical comb of approximately 10 fine setae. Wing: C and R veins dark; others light. Sc fairly long, abruptly ended just proximal to level of Rs crossvein. Vein C ends at apex of R_{4+5}, ending is distant from apex of M_1. R_1 with row of evenly-spaced setulae along most of its length. CuA_2 slightly sinuous. CuP and A_1 well developed, but abruptly incomplete, lengths more than half the distance from wing base to margin. Anal lobe large, slightly projecting; alula and "squama thoracicalis" also present. ABDOMEN: Genitalia: Male with gonocoxa fairly narrow; gonostylus approximately equal in thickness, with apical pair of tooth-like spines pointing mediad.

Etymology.—Referring to the unique antenna.

Type.—Holotype: AMNH Bu178 (Fig. 6.8), Paratypes: AMNH Bu194 (Fig. 6.7), Bu398, Bu400, Bu491 (also contains 1 Psychodidae, 2 Ceratopogonidae, 2 Psocoptera, 1 Berothidae, 1 Araneae), Bu492, Bu493, Bu565W (Fig. 7.4).

Occurrence.—Known only from the Upper Cretaceous of Myanmar.

Discussion.—The highly modified antennae and sinuous CuA_2 vein indicates that *Burmazelmira* and *Archimelzira* (in New Jersey amber) are sister groups, and each of these genera have acquired separate autapomorphies.

DISCUSSION

Relationships among families. Monophyly of the Archizelmiridae still requires rigorous proof, but with the data at hand there is no serious doubt about this. Morphology also indicates a close relationship with the Sciaroidea, a group containing the living families Sciaridae, Mycetophilidae, Bolitophilidae, Keroplatidae, Ditomyiidae, Lygistorrhinidae, Manotidae, and Cecidomyiidae. The point where Rs meets R_{4+5} basal to the R_1-Rs juncture—as occurs in *Archizelmira*—is a unique feature in the Sciaroidea. Another apomorphic feature of the Archizelmiridae is the almost

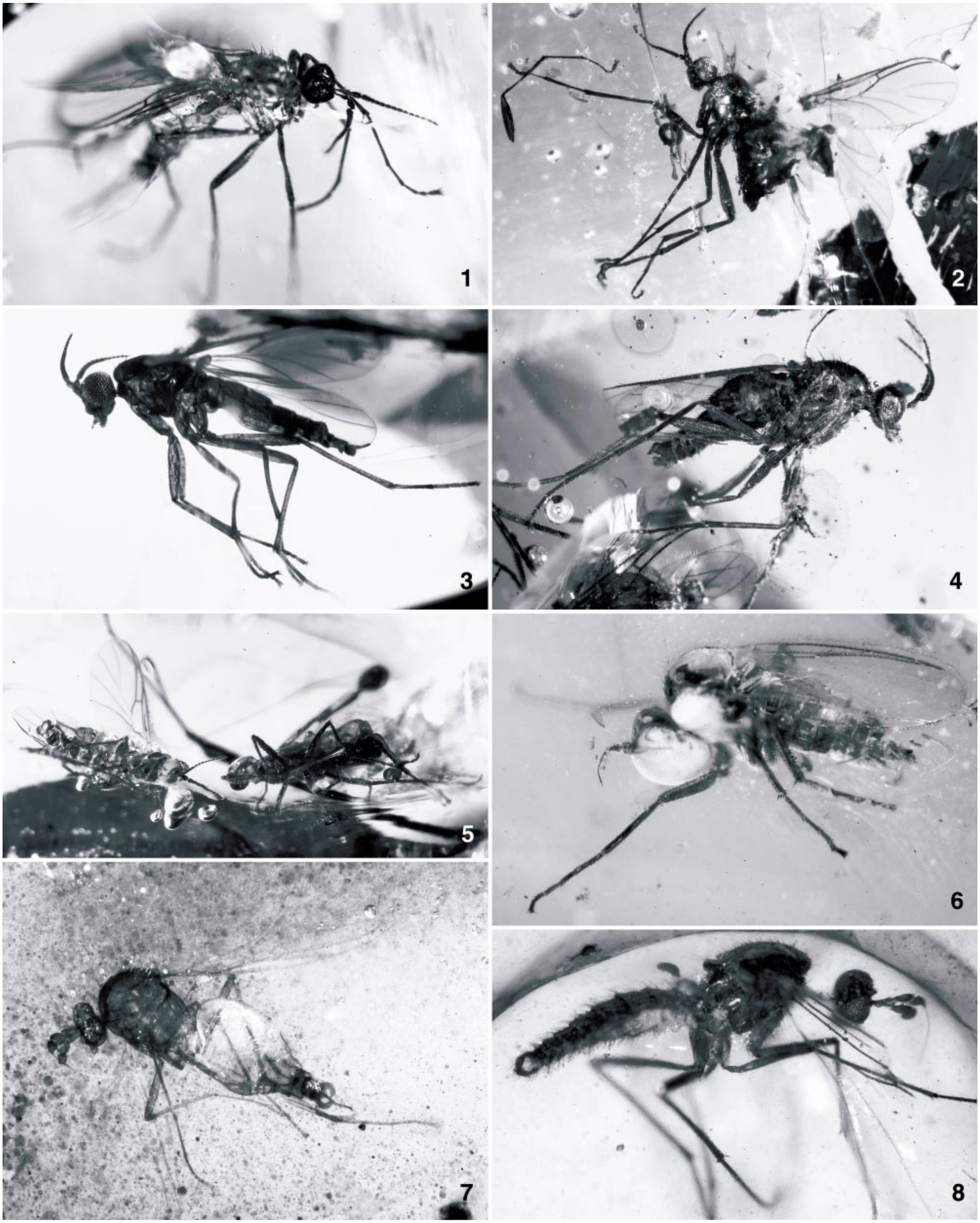


FIGURE 6—Photomicrographs of Archizelmiridae in Cretaceous ambers. *1–5*, *Zelmiarcha lebanensis*, n. gen. and sp., in Lebanese amber; *1*, Az566, *2*, Az564, *3*, Az567, *4*, Az571, *5*, Az575; *6*, *Archimelzira americana* n. gen. and sp., holotype in New Jersey amber (AMNH NJ258); *7–8*, *Burmazelmira aristica* n. gen. and sp. in Burmese amber, *7*, AMNH Bu194, *8*, holotype, AMNH Bu178.

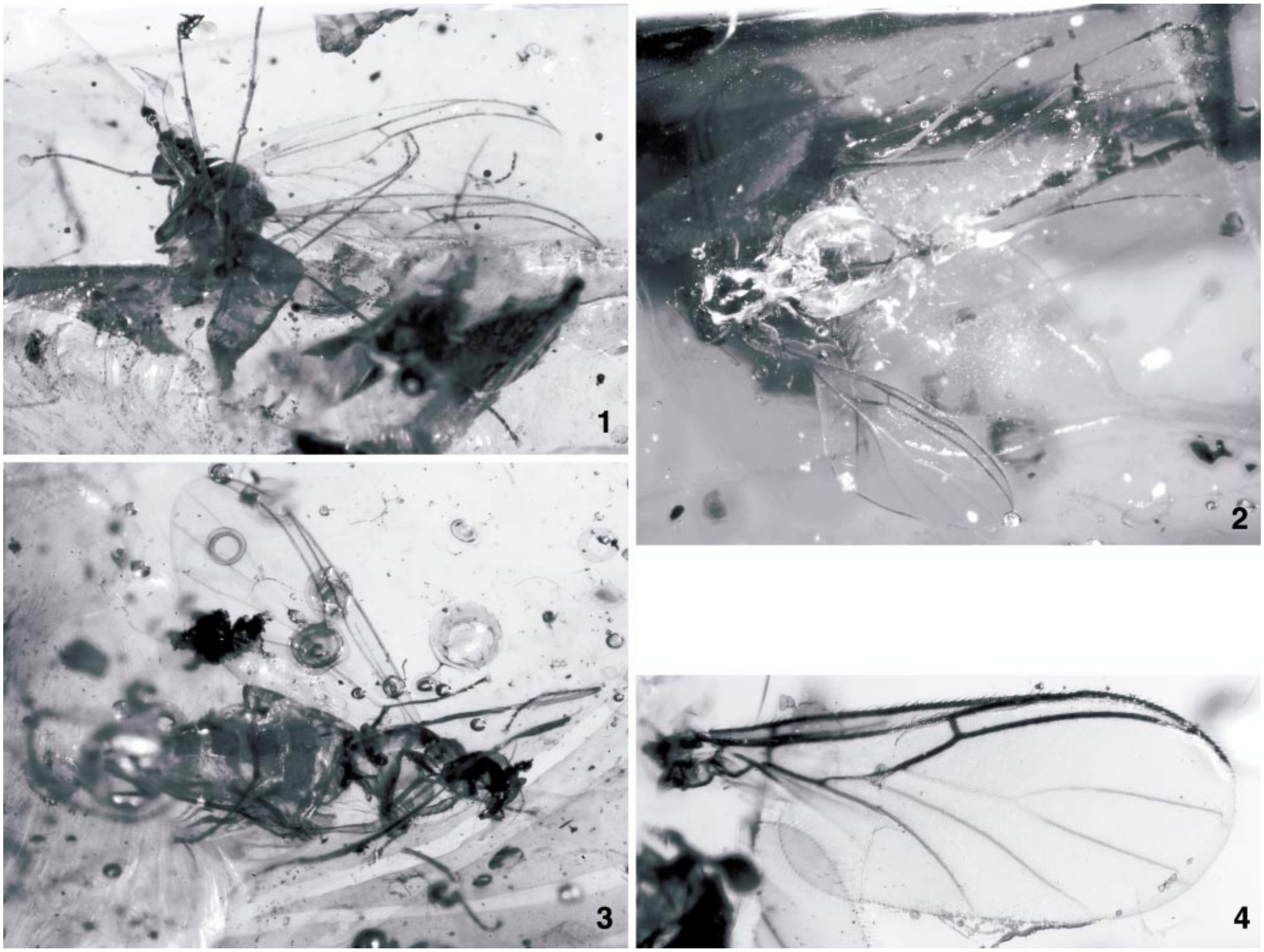


FIGURE 7—Photomicrographs of *Burmazelmira aristica* in Burmese amber (*1–3*) and *Zelmiarcha* in Lebanese amber (*4*). *4, Zelmiarcha lebanensis*, Az564 (wing).

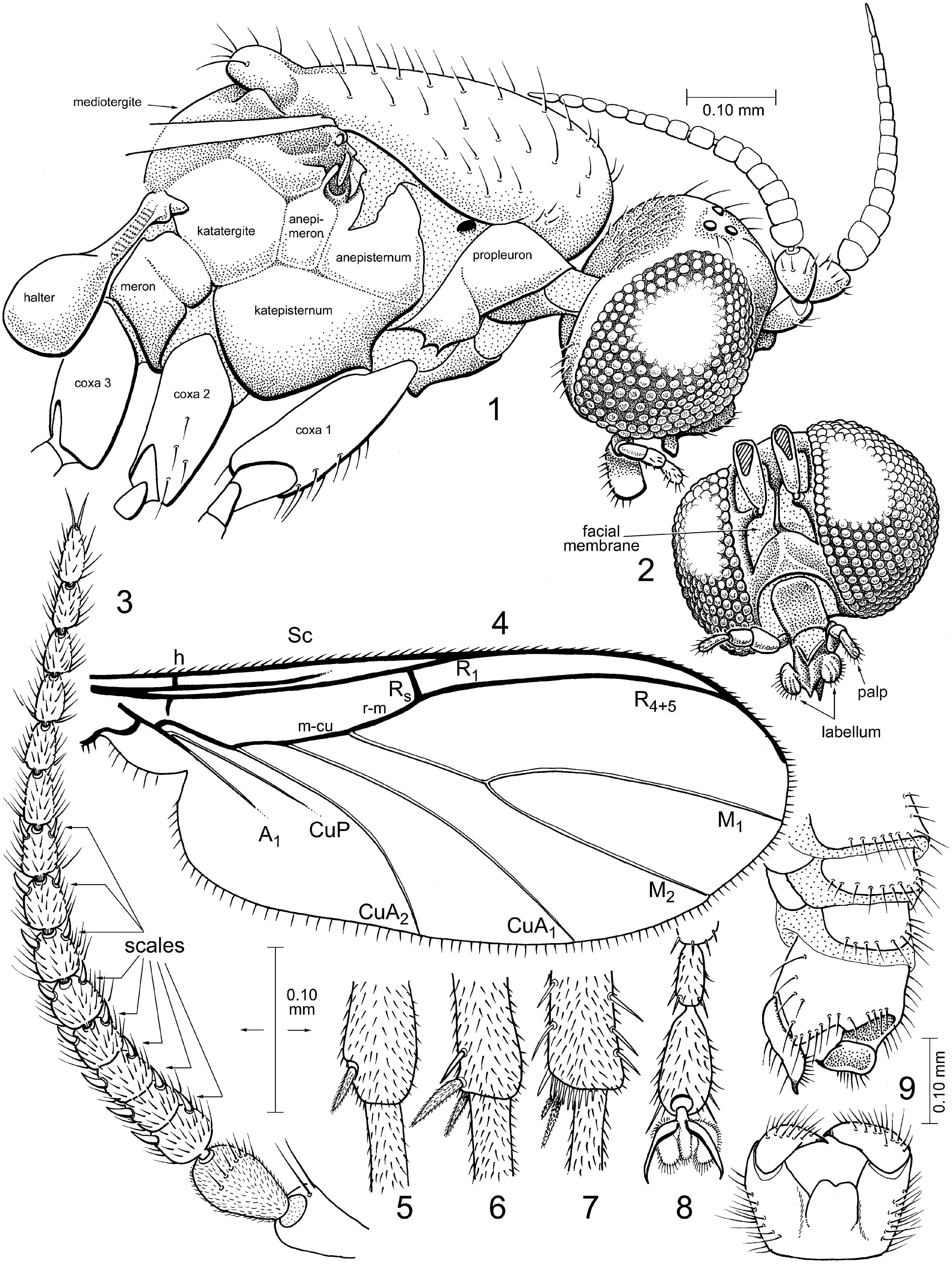
longitudinal position of r-m. Even though the Sciaridae and some Keroplatidae (e.g., *Macrocera*) also possess this feature, the shape of the thoracic sclerites in the Archizelmiridae, as discussed below, are good indicators that Archizelmiridae is close to the Bolitophilidae, Ditomyiidae, and other Sciaroidea. The absence of a complete M, connecting M_{1+2} to the base of the wing, likewise indicates placement of the family in the Sciaroidea (Amorim, 1993; Matile, 1990). Many features of the Archizelmiridae are plesiomorphic and uninformative within the superfamily, such as the number of flagellomeres, the presence of tibial spurs, and the shape of the gonocoxites and gonostyli (see, for example, Matile, 1990).

The possibility of a close relationship with the Sciaridae is raised by the extreme cubital displacement towards the base of the wing in the New Jersey amber genus *Archimelzira*. However, antennal structure indicates that this genus is a derived member of the Archizelmiridae, and the wing venation of *Archizelmira*, *Zelmiarcha*, and *Burmazelmira* is most similar to that of *Heterotricha* Loew and other basal genera of Sciaroidea (Fig. 11). In classifications of the sciaroids, *Heterotricha* has been mobile: placed in the Bolitophilidae, Diadocidiidae, and Sciaridae. Hence, the basal displacement of the cubital veins of *Archimelzira* is convergent with Sciaridae and basal Cecidomyiidae like *Catotricha* Edwards, 1938.

The thoracic pleura of Archizelmiridae, visible in some of the amber fossils, provide additional clues about relationships. The plesiomorphic condition of the ventral part of the thorax in the Bibionomorpha has a mesepimeron that is quite wide, which is a state that is retained in the Cecidomyiidae and Sciaridae. Most basal genera of these families have a typical L-shaped mesepimeron. In other Sciaroidea families the ventral half of the mesepimeron is more slender or, as in many genera, completely obliterated by the fusion of the katepisternum and the metepisternum.

→

FIGURE 8—*Zelmiarcha lebanensis*, n. gen. and sp., from Lower Aptian of Lebanon. *1*, Head and thorax (Az 576); *2*, head, oblique frontal view (Az 567); *3*, antenna (Az 565); *4*, wing (Az 565); *5, 6, 7*, apices of fore, mid, and hind tibiae, respectively, showing spurs (Az565); *8*, pretarsus (Az565); *9*, male genitalia (Az571), showing ventral view (male 1) and dorsal view (male 2).


mediotergite
0.10 mm
katatergite
anepi-
meron
anepisternum
propleuron
halter
meron
katepisternum
coxa 3
coxa 2
coxa 1
1
facial
membrane
2
palp
labellum
3
Sc
4
h
R_1
R_s
r-m
R_{4+5}
m-cu
A_1
CuP
M_1
M_2
CuA_2
CuA_1
scales
0.10
mm
5
6
7
8
9
0.10 mm

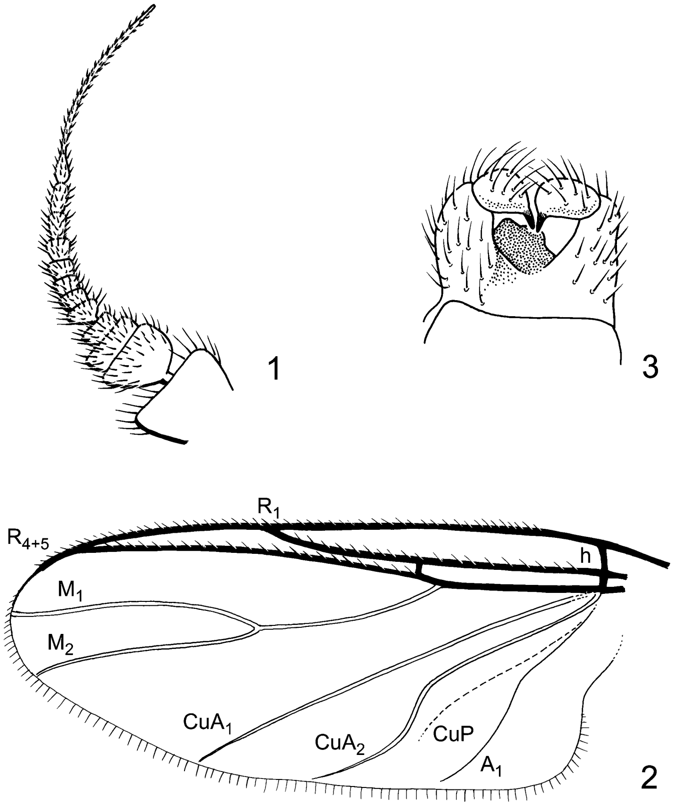


FIGURE 9—*Archimelzira americana* n. gen. and sp., from Turonian amber of New Jersey (holotype, AMNH NJ258). *1,* Antenna; *2,* wing; *3,* male genitalia, ventral view.

The Archizelmiridae have the mesepimeron restricted to the dorsal part of the pleura (Fig. 8.1), indicating that these genera definitely do not belong in the Sciaridae.

Another source of evidence is the mediotergite. In Bibionidae, Cecidomyiidae and Sciaridae, the length of the mediotergite is short (perhaps apomorphic), while in Dityomyiidae and Bolitophilidae it is elongated and straight (perhaps plesiomorphic), and in Keroplatidae and Mycetophilidae it is folded, with the laterotergite projected laterally (certainly apomorphic). In the Archizelmiridae the mediotergite resembles the condition seen in Ditomyiidae and Bolitophilidae, with a long and unfolded sclerite. This evidence suggests a homoplasious similarity in the wing venation of Archizelmiridae and Sciaridae, and that this extinct family is not among the higher Sciaroidea. Pulvilli complicate the situation further. The amber fossil Archizelmiridae have well developed pulvilli (e.g., Figs. 8.8, 10.4), which are found only in Sciaridae among the sciaroids (these are present but less developed in Cecidomyiidae). A detailed study of the pulvillus is warranted to determine if this structure is homologous or convergent between archizelmirids and sciarids. A more precise indication of the position of the Archizelmiridae will depend on resolving relationships among the families of Sciaroidea, especially the positions of Bolitophilidae, *Heterotricha, Ohakunea* Tonnoir and Edwards, and related basal genera.

The highly modified antenna of some archizelmirids is autapomorphic within the Bibionomorpha, and even all nematocerous Diptera, so this is uninformative concerning familial relationships. Some reduction of the mouthparts in Archizelmiridae is shared with various clades in the Keroplatidae and Mycetophilidae, but appears to be plesiomorphic at the family level.

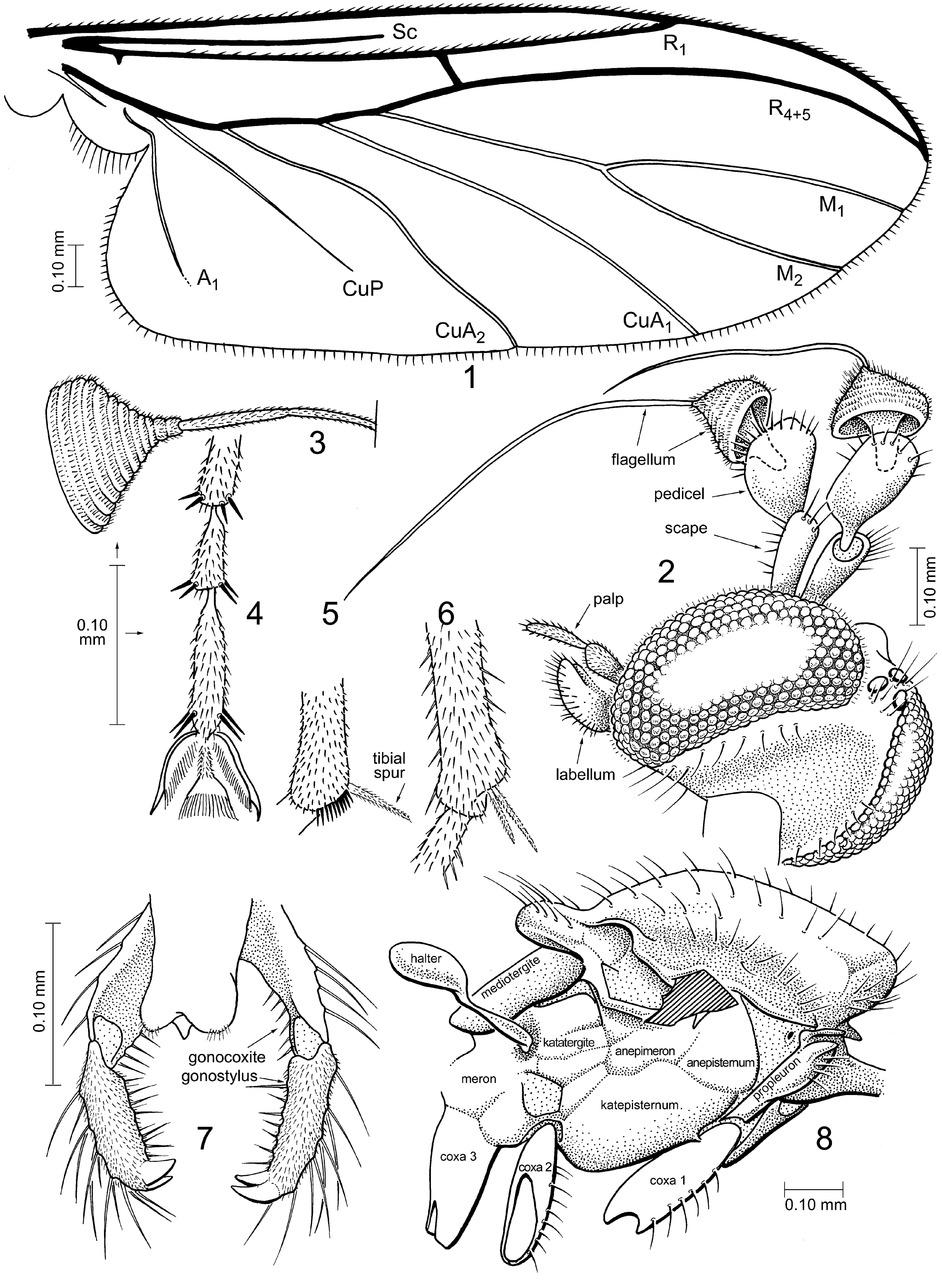
Based on material far better preserved than was available to Rohdendorf (1962), it appears that the Archizelmiridae is a basal clade of the Sciaroidea. Based on some wing features, archizelmirids could even be assigned close to the Bolitophilidae, but this alone can be misleading about phylogenetic relationships. The wings of extant basal sciaroids, like *Heterotricha*, an undescribed genus from Japan, *Pterogymnus* Freeman and especially *Rhynchoheterotricha* Freeman (these latter two in the Sciaridae), are quite similar to that of Archizelmiridae (Fig. 11). Many of the higher Bibionomorpha described to date from the Mesozoic also appear to be basal sciaroids, but their precise relationships will remain unclear without a greatly needed study of relationships among living and extinct genera.

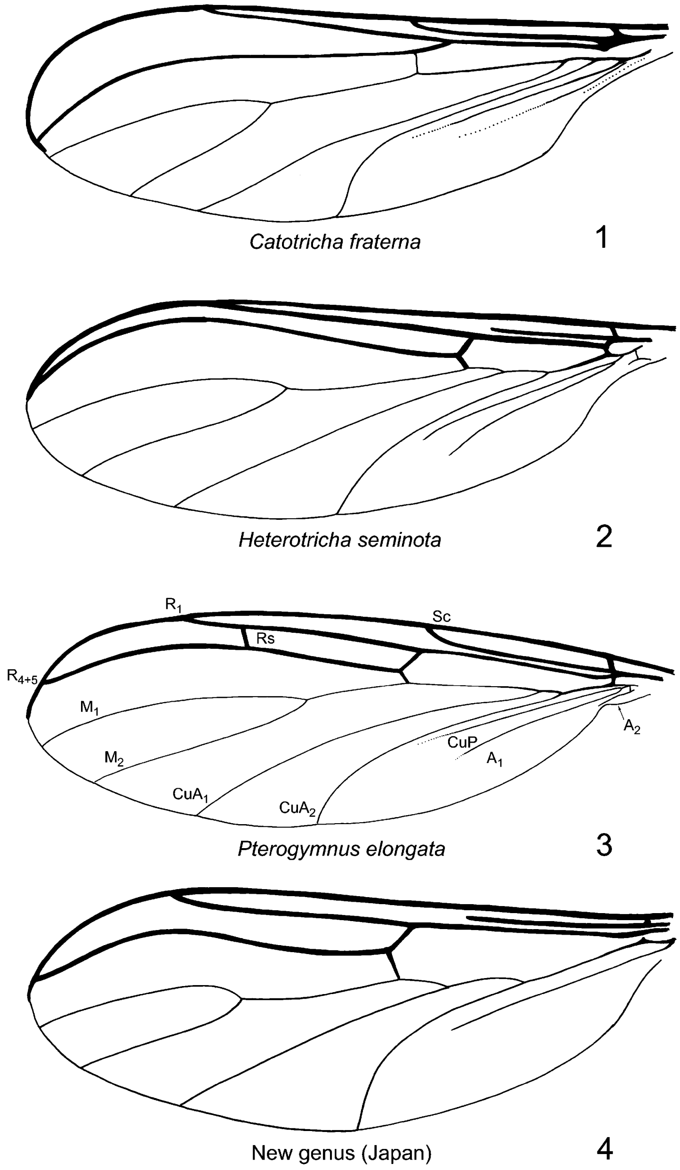
Relationships among genera of Archizelmiridae.—For each character discussed below the apomorphic condition is discussed first, then the plesiomorphic condition. The relatively few characters are all in agreement with each other and no characters were found to be homoplasious, so the single resulting cladogram did not require computer parsimony analysis.

1. Vein Rs has a direction of slant with the junction point of Rs and R_1 distal to the juncture point of Rs and r-m. Plesiomorphically the Rs-R_1 juncture point is considerably proximal to the Rs-rm juncture point, as is found in the Ditomyiidae, Bolitophilidae, Keroplatidae, and other primitive genera of the Sciaroidea. This feature is synapomorphic for *Archizelmira kazachstanica* and *A. baissa*.
2. Vein r-m long, and in line with m-cu: synapomorphic for *Archizelmira*, *Zelmiarcha*, and *Burmazelmira*. The derived nature of various other features of *Archimelzira* in New Jersey amber indicates that the short Rs vein perpendicular to the stem of R is derived, so the position of r-m in line with m-cu is synapomorphic for the family Archizelmiridae. Vein r-m takes various positions among basal genera of sciaroids, particularly a perpendicular position in *Symmerus*, Diadocidiidae, and *Palaeoplatyura*. R-m is nearly horizontal, in cases in line with m-cu, in Sciaridae and in various clades of Mycetophilidae s.s., such as *Azana*, *Docosia*, *Greenomyia*, Gnoristini, and Leiinae. The Sciaridae have a very basal (proximal) origin of Cu, which appears independently derived from the condition in Archizelmiridae.
3. Vein R_{2+3} lost. Presence of this vein is clearly in the groundplan of the Bibionomorpha. Amorim (1993) interpreted this vein as R_4. R_{2+3} is also lost in basal Sciaridae, all Cecidomyiidae, basal Diadocidiidae, in Bolitophilidae, some Keroplatidae, and some Mycetophilidae. *Archizelmira* retains R_{2+3}, and loss of the vein is clearly synapomorphic for the other three genera in the family.
4. Apex of R_1 is extended at best to the level of the base of fork of M_1–M_2. This feature is found in the three genera preserved in amber. Plesiomorphically, the apex of R_1 is extended well past the level of the M_1–M_2 fork, as is found in *Archizelmira* and basal genera of various families in Sciaroidea (e.g., Fig. 11).

→

FIGURE 10—*Burmazelmira aristica* n. gen. and sp., from Cretaceous (?Cenomanian) of northern Myanmar. *1,* Wing; *2,* head, posterolateral view; *3,* detail of antenna; *4,* pretarsus; *5, 6,* apices of fore and hind tibiae, respectively; *7,* male genitalia (dorsal view); *8,* lateral view of thorax, AMNH Bu178.


Sc
R1
R4+5
M1
M2
CuA1
CuA2
CuP
A1
0.10 mm
1
3
flagellum
pedicel
scape
2
0.10 mm
palp
labellum
0.10 mm
4
5
6
tibial spur
7
0.10 mm
gonocoxite
gonostylus
halter
mediotergite
katatergite
anepimeron
anepisternum
meron
katepisternum
propleuron
coxa 3
coxa 2
coxa 1
8
0.10 mm



Catotricha fraterna 1

Heterotricha seminota 2

Pterogymnus elongata 3

New genus (Japan) 4

FIGURE *11*—Wing venation of extant primitive genera from several families of sciaroid flies, which have a plesiomorphic resemblance to the venation of Archizelmiridae.

5. Flagellomeres are distinctly differentiated, with the basal segments thicker and slightly longer, and the apical segments tapered to a point or a hair-like process and slightly to greatly longer. This feature is synapomorphic for all three genera preserved in amber, the least modified of which is *Zelmiarcha* in Lebanese amber (see character 6). Plesiomorphically there is very little differentiation between the apical and basal segments, as in most nematocerous flies.
6. This is a further modification of character 5, being an extreme narrowing of distal flagellomere(s) into a hair-like structure (an arista). In *Burmazelmira* all pre-apical flagellomeres are compacted into a conical structure with ring-like annulations; the apical flagellomere is long, fine, and whip-like. *Archimelzira* in New Jersey amber has flagellomeres 5 and distad very narrow, with the apical one long and fine. Its antenna is further modified by the loss of flagellomeres, possessing 11 instead of 14.

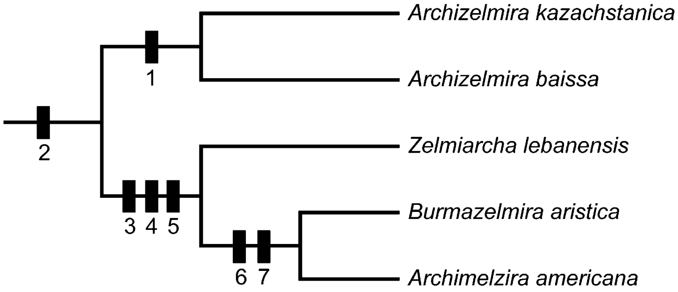


FIGURE *12*—Cladogram of archizelmirid genera and species. Numbers refer to characters described in the text.

7. Vein CuA_2 is synapomorphically sinuous in *Burmazelmira* and in the New Jersey amber *Archimelzira* (this also occurs, convergently, in some leiine Mycetophilidae). Plesiomorphically, this vein is straight or curved, as in *Archizelmira*, *Zelmiarcha*, and most other sciaroids.

CONCLUSIONS

Relationships among the four genera of Archizelmiridae are easily deciphered: *Archimelzira* (New Jersey amber) and *Burmazelmira* (Burmese amber) are sister genera, *Zelmiarcha* (Lebanese amber) is the sister group to *Archimelzira* + *Burmazelmira*, and *Archizelmira* (Eurasian compressions) is the most basal lineage. There is a single cladogram (Fig. 12) for the data. The loss of R_{2+3} (character 3), together with another modification of the radial sector (character 4), indicate monophyly of the genera in amber. The shape of the flagellum (character 6) and CuA_2 (character 7) clearly link *Archimelzira* and *Burmazelmira*. The considerable differences between the cubital fork area of *Archimelzira* and the other three genera (which are similar to the living genus *Rhynchoheterotricha*), suggests a convergent development in this feature between *Archimelzira* and other sciaroid flies.

Phylogenetic relationships correlate with stratigraphic occurrence. The most plesiomorphic lineage, *Archizelmira*, occurs from the Upper Jurassic (Kimmeridgian) to Lower Cretaceous (Valanginian-Barremian). The clade of amber genera, defined by characters 3–5, has its earliest occurrence in the Lower Aptian (*Zelmiarcha*). The most recently derived lineage is comprised of *Archimelzira* and *Burmazelmira*, these genera of which are Turonian and putatively Cenomanian (Grimaldi et al., 2001), respectively. Progressive morphological specialization from the Upper Jurassic to the Upper Cretaceous, and lack of Tertiary records, suggest that the Archizelmiridae became extinct by the end of the Cretaceous or early Tertiary.

Morphological transformation of the antenna also correlates with stratigraphic occurrence. The oldest genus, *Archizelmira*, possesses a generalized nematoceran flagellum with moniliform segments (Fig. 4.4). The next oldest genus, *Zelmiarcha*, has slight differentiation of flagellomeres (Fig. 8.1, 8.4), and the pair of most recently derived genera (*Archimelzira* and *Burmazelmira*) have an extremely modified antennal flagellum (Figs. 9.1 and 10.3). Interestingly, this unique situation corresponds exactly to the hypothesis recently proposed by Stuckenberg (1999) for the evolution of the flagellum in brachyceran Diptera. Using several independent transformation series of flagellomere structure in various Vermileonidae, he concluded that the fine, elongate, terminal style seen in many Brachycera, and the arista seen in Eremoneura, represents the apical flagellomere. In other words, there has been extreme consolidation and/or loss of preapical flagellomeres, not the apical ones. This same transformation series occurs in the Archizelmiridae. Additionally, there is co-occurrence in the Archizelmiridae and some other fly families of antennal reduction

TABLE *1*—Measurements of Archizelmiridae (in mm).

				Leg segment lengths			
Species-specimen	Body L.	Wing L.	Thorax L.	Coxa	Fore Femur	Tibia	Hind femur
Archizelmira kazachstanica:							
PIN 2997/3216	2.35	2.48	—	—	—	—	—
PIN 2239/2030	4.03	3.08	—	—	—	—	—
PIN 2997/4774	—	2.32	—	—	—	—	—
PIN 2066/2077	4.75	2.98	—	—	—	—	—
PIN 2239/2034	4.11	3.20	—	—	—	—	—
PIN 2997/3147	3.16	2.89	—	—	—	—	—
PIN 2239/2029	3.19	2.65	—	—	—	—	—
PIN 4230/2244	—	2.74	—	—	—	—	—
PIN 4270/2242	—	3.46	—	—	—	—	—
PIN 4270/2243	—	3.56	—	—	—	—	—
Archizelmira baissa:							
PIN 3064/9039*	—	3.25	—	—	—	—	—
PIN 3064/9918	—	3.37	—	—	—	—	—
Zelmiarcha lebanensis:							
Az201	1.17	1.28	0.33	—	—	—	—
Az566*	1.42	1.31	—	—	0.42	0.53	0.53
Az565	1.34	1.32	0.49	0.25	0.47	0.59	0.53
Az567	—	1.26	—	—	—	—	—
Az569	1.14	1.30	0.37	—	0.32	0.43	0.53
Az571	1.62	1.36	0.43	0.28	0.51	0.49	0.60
Az573	1.30	1.25	0.45	—	—	—	—
Az575	1.30	1.11	0.46	—	—	—	—
Az576	1.78	1.36	0.49	0.26	0.40	—	0.55
Archimelzira americanus:							
AMNH NJ258*	1.71	1.44	0.49	—	0.44	0.42	0.57
Burmazelmira aristica:							
AMNH Bu178*	2.25	1.81	0.66	0.29	0.53	0.56	0.69
AMNH Bu194	2.33	2.08	0.61	—	0.45	0.56	0.72
AMNH Bu491	1.61	2.05	—	—	0.46	0.59	0.59
AMNH Bu492	2.49	2.09	0.82	—	—	—	—
AMNH Bu493	—	2.31	0.66	—	0.51	0.51	—

* Holotypes.

and wing vein costalization (costalization is the crowding and sclerotization of the radial veins, with veins M and Cu light, well separated, and few in number). Among living Diptera this is found in the Simuliidae (blackflies), Synneuridae and Scatopsidae (scavenger flies), and many Brachycera. Correlated trends in these structures are probably functional, related to flight and sensory ability.

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