

The oldest species of the relic extant genus *Mesochria* from Eocene Fushun amber of China (Diptera: Anisopodidae: Mycetobiinae)

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ABSTRACT

A new species – *Mesochria fani* Szadziewski and Szwedo sp. nov. – is described from Eocene Fushun amber. This is the oldest record of the genus *Mesochria*, which includes 10 extant species living in the tropics of the Oriental and Afrotropical regions. Fossil records of the genus from Miocene Dominican amber (20 Ma) and Eocene Fushun amber (50 Ma) indicate that this extant group is relictual, and that during its evolution it had a wider, pantropical distribution.

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INTRODUCTION

Nematoceran dipterans of the family Anisopodidae Knab, 1912 (wood gnats, window-gnats) are common flies in forests, feeding on flowers or sap exuding from trees. They are found on all continents except Antarctica; they are less numerous on islands. Adults are small to medium-sized (usually

4-12 mm), with a small, rounded head and short mouthparts. The compound eyes are dichoptic or holoptic. Ocelli are present and form an equilateral triangle. The slender antennae with 14 flagellomeres vary from relatively short to longer than the head and thorax together. The wings are wide, with two or three median branches, sometimes with distinct stigma. The legs are relatively long,

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with distinct tibial spurs. Larvae are saprophagous, usually living in decaying or fermenting organic matter. The family Anisopodidae comprises 25 genera with 196 species, including several described fossil taxa (Oosterbroek, 2006; Thompson, 2006; Pape et al., 2011; Lukashevich, 2012). With the transferral of Eopleciidae Rohdendorf, 1946 and Sinotendipedidae Hong and Wang, 1990 to Anisopodidae (Ansorge and Krzemiński, 1995; Pape et al., 2011), as well as the genus *Tega* Blagoderov et al., 1993 from Cramptonomyidae Hennig, 1969 (Lukashevich, 2012), the fossil record of this family is represented by 18 fossil genera, 3 extant genera and 47 species (Evenhuis, 2014). The internal subdivisions of Anisopodidae are still a matter of discussion (Amorim and Grimaldi, 2006; Oosterbroek, 2006; Thompson, 2006; Pape et al., 2011; Lukashevich, 2012).

The oldest fossil of the Anisopodidae – *Mesorhyphus rhaeticus* Rohdendorf, 1962 – comes from the Ak-Bulak-Say locality, Sogyuty, near Lake Issyk-Kul, Dzhil Formation, Kyrgyzstan, which is aged Hettangian/Sinemurian, Early Jurassic (Rohdendorf, 1962; Rasnitsyn and Zherikhin, 2002; PaleoBioDB, 2016). Various extinct genera are reported from Jurassic and Cretaceous deposits of Asia and Europe (Evenhuis, 1994, 2014). A few species are known from Eocene Baltic amber, but also from sedimentary deposits in England and North America (Evenhuis, 1994, 2014). The Miocene record consists of findings in fossil resins of the New World, as well as in sedimentary deposits from North America and Europe (Evenhuis, 1994, 2014). The general chronological and stratigraphic distribution pattern of Anisopodidae illustrates its long and complicated evolutionary history.

Some enigmatic taxa placed in Anisopodidae (= Rhyphidae Newman, 1834) were described from Fushun amber by Hong (1981). A new genus and new species – *Caloneura plectilis* Hong, 1981 – was proposed, with a strange wing venation, resulting from its misinterpretation, as one wing overlapped the other one (Hong, 1981, p. 91, figures 96 and 97-IV). Subsequently, Evenhuis (1994, 2014) replaced the preoccupied generic name with *Hongocaloneura* Evenhuis, 1994: 282 and transferred it to unplaced nematocerous flies. Hong (2002) claimed that his interpretation of the wing venation was correct and established the new family Hongocaloneuridae Hong, 2002 in the Anisopodoidea Knab, 1912. Later, Zhang (2007) commented that the wing venation of *Hongocaloneura plectilis*, with four branches of M, had never been reported among known Diptera. Another

taxon ascribed to Anisopodidae from Fushun amber – *Eoanisopodites fushunensis* Hong, 2002 – appears to be an unavailable name, as this species was proposed after 1999 without any mention of the type depository (ICZN, 1999; Evenhuis, 2014).

The traditional subfamily Mycetobiinae Crampton, 1924 is often treated as a separate family Mycetobiidae of worldwide distribution, with 5 genera and about 20 extant species. Members of the subfamily are robust, small flies, 4–7 mm long, with a transparent wing membrane, d-cell absent, and an M vein with 2 branches. The head has three ocelli arranged in a triangle on the frons. The antennae are relatively short, with 14 flagellomeres. The proboscis is well-developed, and the 4-segmented palpus short. The thorax is convex. The claws are similar on all the legs; the small, simple, empodium is reduced. Larvae usually are found in moist habitats, in rotting or fermenting organic matter, and are common in exuding tree-sap and rot holes (Krivosheina, 1997; Oosterbroek, 2006; Thompson, 2006).

The purpose of the present paper is to describe the oldest species of the extant genus *Mesochria* Enderlein, 1910, from early Eocene Fushun amber. The only fossil species of *Mesochria* known so far was reported from Miocene Dominican amber (Grimaldi, 1991).

MATERIAL AND METHODS

The Fushun amber specimen comes from the layers of the West Opencast Coalmine (Xilutian Opencast Coalmine). The West Opencast Coalmine (41°50' N, 123°54' E), located to the south of Fushun City, Liaoning Province, China (Figure 1.1), is the largest opencast coalmine in Asia, but after more than 110 years of mining, it is now exhausted and being reclaimed (Figure 1.3, 1.4). The coal and oil shales are found in a relatively small east–west-trending exposure of Mesozoic and Cenozoic sedimentary and volcanic rocks surrounded by Precambrian terrain consisting mainly of granitic gneiss (Johnson, 1990; Wu et al., 2002). These continental sequences consist of swampy to fluvio-deltaic and tuffaceous sediments that were deposited in the basin during the early Palaeogene (Hong et al., 1980; Johnson, 1990; Yang and Li, 1997; Wu et al., 2002). The mining district in the Fushun basin contains the Palaeocene Laohutai and Lizigou formations and the Eocene Guchengzi, Jijuntun, Xilutian, and Gengjiajie formations (Figure 1.2). The amber-bearing Eocene Guchengzi Formation includes thick coal beds intercalated with

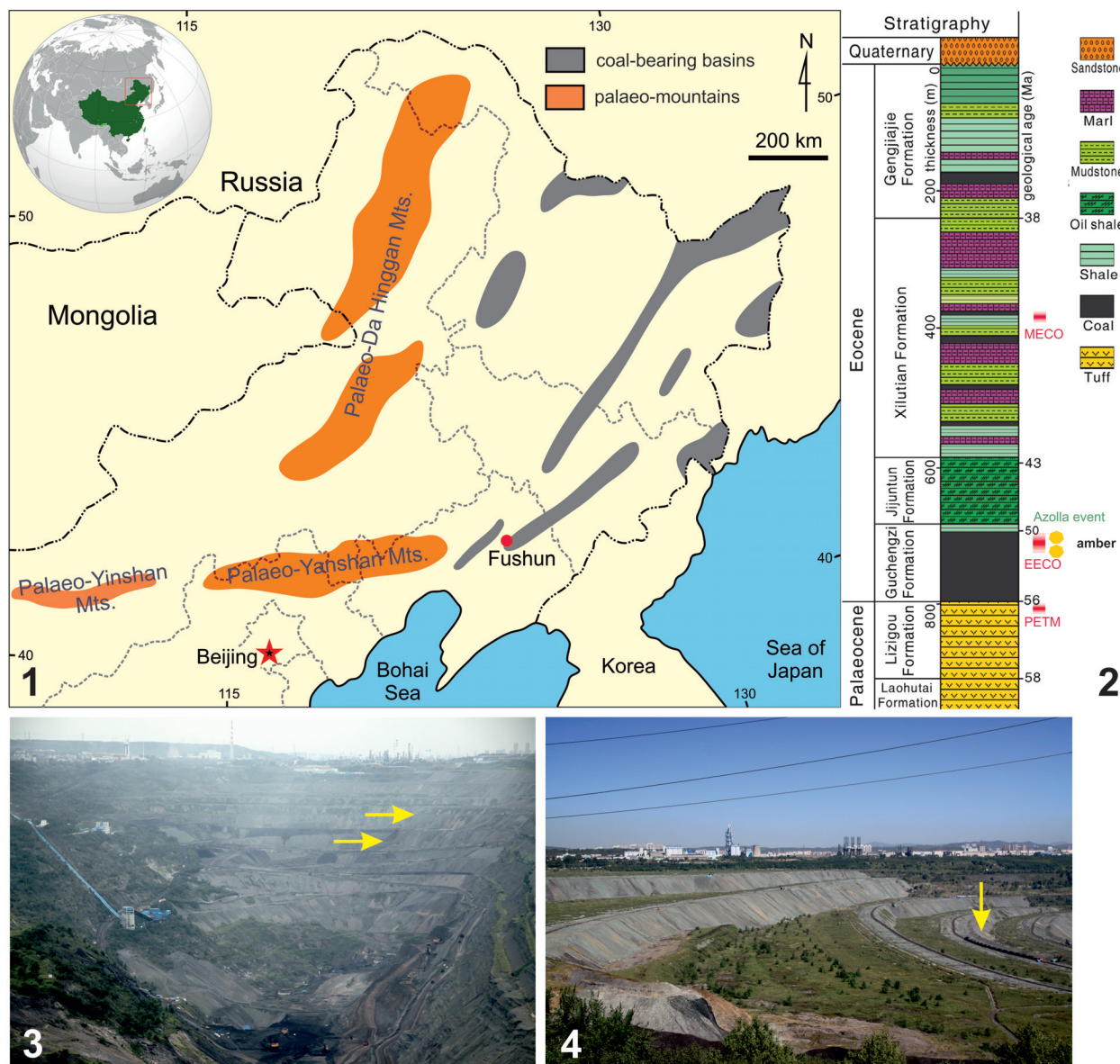


FIGURE 1. **1**, Fushun fossil site location and palaeogeographic setting of north-eastern China during the Eocene; Palaeotopographic reconstruction after Wang H. (1995); **2**, stratigraphic sequence of the West Opencast Coalmine. The yellow heptagons indicate amber-bearing layers in upper section of the Guchengzi Formation. PETM – Palaeocene-Eocene Thermal Maximum (approximately 55 Ma); EECO – Early Eocene Climatic Optimum (51–53 Ma); MECO – Middle Eocene Climatic Optimum (approximately 41.5 Ma); **3**, View of the West Opencast Coalmine, from the east, 3 September 2013; arrows indicate amber-bearing strata; **4**, View of reclamation works in the West Opencast Coalmine from the west, 5 September 2014.

carbonaceous shale (Wu et al., 2001; Meng et al., 2012, Wang, B. et al., 2014).

The West Opencast Coalmine was the largest amber deposit in China. The Fushun amber-bearing strata were the middle and upper coal beds of the Guchengzi Formation, assigned to an early-middle Ypresian age (51–55 Ma) and constrained by the palaeofloras (Wang, Q. et al., 2010; Quan et

al., 2011), palaeomagnetic considerations and isotopic dating (Zhao et al., 1994; Quan et al., 2011). The palaeoclimate in the early Eocene in Fushun is reconstructed as moist subtropical, with variability in seasonal precipitation (very probably a monsoonal system), with dry and wet seasons (Quan et al., 2011, 2012; Wang, D., et al. 2013). The estimated mean annual temperature varied between

15–21°C; the coldest month mean temperature varied between 9–14°C and the warmest month mean temperature varied between 19–25°C. The mean annual precipitation is estimated as having varied between 650–1500 mm (Wang, Q. et al., 2010; Quan et al., 2011, 2012). These estimations concerns Guchengzi Formation and are based on floral elements (palynofloras) preserved with use of the principle of coexistence approach (CA; Mosbrugger and Utescher, 1997) based on the concept of “nearest living relative (NLR) philosophy”; Quan et al. (2012) deals also with leaf physiognomical analyses for the reconstructions and habitat conditions discussed. The climate was slightly cooler than that of coeval Europe (Mosbrugger et al., 2005; Zachos et al., 2008, Wang, Q. et al., 2010).

The colour of Fushun amber could vary from honey, light yellow, transparent, through various varieties of orange, cherry and cognac, translucent to opaque, patchy and non-transparent forms of dappled earth-amber. This variety is also related to the depositional conditions. The amber pieces are usually small, seldom longer than 10 cm. Fushun amber is naturally autoclaved as the amber-bearing coal deposits were affected by a massive intrusion of basic magmas in the Oligocene (Wu et al., 2000; Wang, X. et al., 2001) so that the amber was heated during diagenesis, like Burmese amber (Shi et al., 2012). The Fourier transform infrared (FTIR) spectrum of Fushun amber shows characteristics of cupressaceous-araucarian resins (Tappert et al., 2013), which suggest Cupressaceae (especially *Metasequoia*) as the mother plant of the resin. Fragments of *Metasequoia* are not only the most common plant inclusions in Fushun amber but also very frequent as compressions in the amber-bearing and succeeding layers, supporting this interpretation (Wang, B. et al., 2014).

Fushun amber contains a diverse, well-preserved fossil arthropod fauna and abundant botanical and other inclusions such as leaves, fungi and even mammalian hairs. In addition, some microinclusions, such as palynomorphs and testate amoebae, are frequently found in Fushun amber (Wang, B. et al., 2011, 2014). Arthropod inclusions cover an impressive array, including 22 orders and more than 80 families (Wang, B. et al., 2011, 2014).

The piece of amber under scrutiny here comes from the collections of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. Fresh amber coated in thick coal dust was ground and polished manually with a series of wet silicon carbide abrasive papers to remove the opaque surface and to mini-

mize light reflections during further investigation. The specimen was examined under Olympus SZ11 and SZ12 stereomicroscopes and an Olympus BX43 microscope. Photographs were taken with a Nikon DXM1200 digital camera connected to the above stereomicroscopes and with a Zeiss Discovery V20 system.

According to Recommendation 40A of the Code (ICZN, 1999) the name of family is correctly cited as ‘Anisopodidae Knab, 1912’. We follow here the proposition by Thompson (2006) to treat *Mesochria* (including *Neomesochria* Amorim and Tozoni, 1994) in the traditional concept as defined by the fusion of wing veins R_{2+3} to R_1 . Morphological terms are adopted from Thompson (2006).

SYSTEMATIC PALAEOLOGY

Order DIPTERA Linnaeus, 1758
 Suborder NEMATOCERA Duméril, 1805
 Infraorder BIBIONOMORPHA Hennig, 1954
 Family ANISOPODIDAE Knab, 1912
 Subfamily MYCETOBIIINAE Crampton, 1924
 Genus MESOCHRIA Enderlein, 1910

Type species. *Mesochria scottiana* Enderlein, 1910: 65, by original designation.

Mesochria fani Szadziewski and Szwedo sp. nov.
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Etymology. The specific name is dedicated to Mr. Yong Fan, the director of the Fushun Amber Institute, in recognition of his important contribution to the study of Fushun amber.

Material examined. Holotype male, NIGP156988, Fushun amber. Deposited in the collections of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. Specimen is slightly distorted and carbonized, due to preservation conditions of amber (Wu et al., 2000; Wang, X. et al., 2001), i.e., natural heating (autoclaving) in the deposit, which is often affecting amber inclusions from Fushun.

Diagnosis. The species is characteristic in having well-developed anal veins, the median fork much longer than the basal stem, the costal vein extending one third of the way between apices R_{4+5} and M_1 , and the mid leg with two tibial spurs. Fossil *M. neotropica* from Dominican amber differs in having the median fork slightly shorter than the basal stem, the costal vein ending halfway between R_{4+5} and M_1 , no anal veins, and the mid leg with one tibial spur. Both fossil species are much smaller than extant members of the genus.

Description. Male. Body dark, altered in amber, length 4.1 mm. Natural colours not preserved. Left mid leg separated from thorax more robust than unnaturally slender right leg (Figure 2.1, 2.5). Distal flagellomeres missing, lost during preparation.

Head barely visible (Figure 2.3). Eyes bare, very probably touching or narrowly separated. Ocelli on raised tubercle present. Antenna apparently with 14 more or less cylindrical flagellomeres. Proboscis (Figure 2.3.) short. Palpus 4-segmented, with distal three segments well visible. Fourth palpal segment cylindrical with evenly pointed apex, 4 times longer than third one (Figure 2.3, 2.4).

Scutum barely preserved. Scutellum bearing 4 marginal bristles.

Wing typical of the genus (Figure 2.2, 2.7): length measured from base 2.9 mm. Wing membrane hyaline. Costal vein distinctly extending one third of the way between apices R_{4+5} and M_1 . Subcostal vein bare, ending in C slightly proximal to base of radius. Radial sector R_s setose. Veins R_1 and R_{2+3} convergent, contiguous apically. Median fork distinctly longer than basal stem (1.8 times). Cross veins complete. Two distinct anal veins present.

Fore and hind tibiae with single apical spur. Mid tibia with two apical spurs. Hind tibia with distinct tibial comb composed of dense row of setae. Claws small, equal, apices bifid; empodium absent. Measurements are given in Table 1.

Male genitalia barely visible (Figure 2.5, 2.6). Gonocoxites large, fused. Cerci well developed, long.

Female unknown.

Age and occurrence. Early Eocene, Guchengzi Formation, Fushun amber. Xilutian coal mine, Fushun, Liaoning, China (41.8° N, 123.9° E; palaeocoordinates 43.5° N, 116.0° E).

DISCUSSION

The male of the new species is very similar to the female of fossil *Mesochria neotropica* Grimaldi, 1991 from Miocene Dominican amber. The colouration cannot be used for identification as it is not preserved in inclusions from Fushun amber. The only differences are in the wing venation and in the numbers of tibial spurs on the mid leg (see diagnosis). Extant species are distinctly larger with wing lengths over 4.0 mm. Both fossil species are smaller with wing lengths from 2.9 to 3.1 mm.

The clear definition and unambiguous set of character of the *Mesochria* Enderlein and related genera are still far from resolution. The generic key of Thompson and Rogers (1992) gave the features of all modern genera placed in the family at that

time. Later, the genus *Neomesochria* Amorim and Tozoni, 1994 was proposed combining number of New World and New Caledonia species of the genus *Mycetobia* Meigen, 1818, comprising also the fossil *Mesochria neotropica* Grimaldi, 1991. This statement was argued by Thompson (2006), as according to his opinion the genus *Neomesochria* lacks any synapomorphy, and the only known to that date *Mesochria neotropica* venation characters, i.e., terminal R_{2+3} fused to R_1 , places it clearly in the genus *Mesochria*. Number of species are known exclusively from type specimens with very brief and/or incomplete descriptions. The constituting features of the genus *Mesochria* are: terminal R_{2+3} fused to R_1 , M two-branched; discal cell absent, metatibia with apical comb, and additionally, contiguous state of the male eyes (Michelsen, 1999; Thompson, 2006). The other distinguishing features are based on coloration of particular elements of body, but these data are lacking for some modern species (Thompson, 2006). Very little is known on the biology of *Mesochria*. The stout hooks on the 8th abdominal segment are present as five pairs in *Mesochria* (Thompson, 2006); pupal skin of *Mesochria medicorum* Edwards, 1928b, was obtained from rotting banana fibre in Ghana (Edwards, 1928b; Keilin and Tate, 1940). Its sister-group, *Mycetobia* is saprophagous and live in fermenting saps runs or slime fluxes from wounds in trees or in tree holes (Keilin, 1919; Keilin and Tate, 1940; Krivosheina, 1997).

Ten extant species of *Mesochria* are known from Fiji (*M. schlingeri* Thompson, 2006; *M. vulgaris* Thompson, 2006), Samoa (*M. buxtoniana* Edwards, 1928a), Java (*M. cinctipes* de Meijere, 1913), Borneo (*M. intermedia* Edwards, 1931), Madagascar (*M. sylvatica* Stuckenberg, 1961; *M. griveaudi* Stuckenberg, 1961), the Seychelles (*M. scottiana* Enderlein, 1910), Ghana (*M. medicorum* Edwards, 1928b) and the Democratic Republic of Congo (Zaire) (*M. congoensis* Tolle, 1956) – Figure 3. During the Palaeogene and Neogene the genus was more widely distributed, in the lower Eocene it was present in North China (*M. fani*, present report) and in the Miocene in the Caribbean Region (*M. neotropica* Grimaldi, 1991). The genus *Mesochria* was exemplified as illustrating the tropical Gondwanan track (Matile, 1990) with sporadic “recent extensions” into the Holarctic (Amorim and Pires, 1996; Cranston, 2005). The tropical Gondwanan track (Matile, 1990) was proposed for explanation of Gondwanan distributions of groups, which phylogenies are concordant with subsequent breakups of Gondwanan landmasses

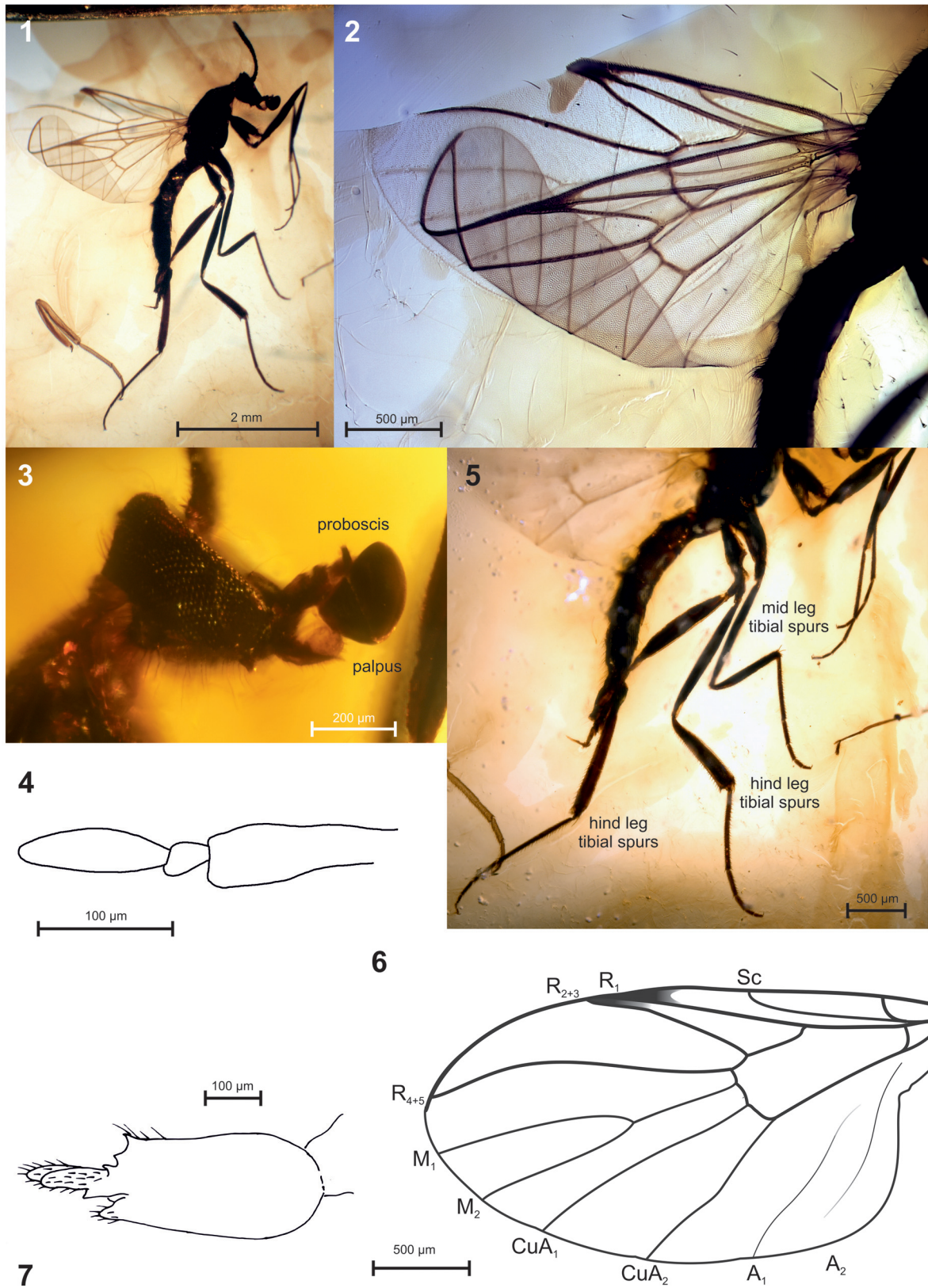


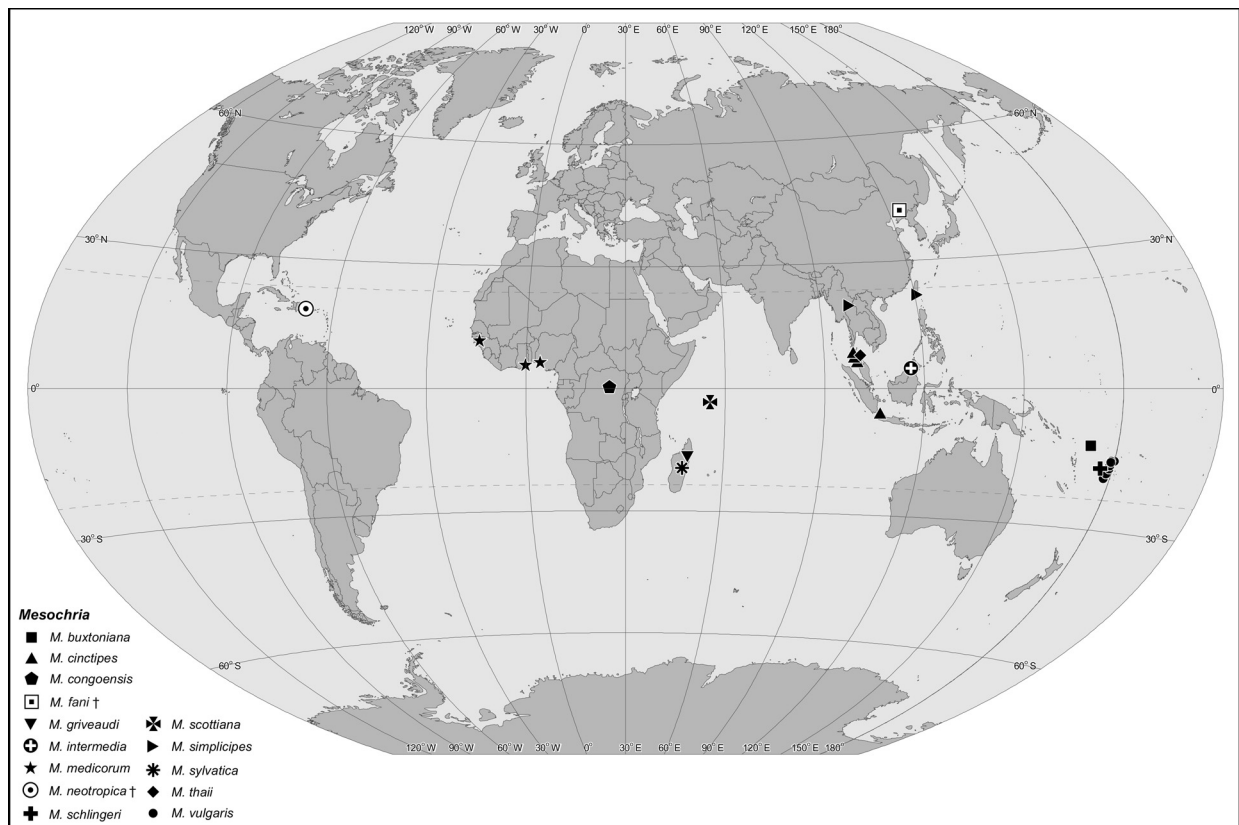
FIGURE 2. Holotype male of *Mesochria fani* Szadziewski and Szwedo, sp. nov. **1**, habitus, lateral aspect; **2**, wings; **3**, mouthparts; **4**, palpus; **5**, legs; **6**, wing reconstructed; **7**, genitalia, lateral aspect.

TABLE 1. Length measurements of legs (in mm). TR (ta1/ta2) – tarsal ratio; fe – femur; ti – tibia; ta1-ta5 – tarsomeres 1-5.

	TR	fe	ti	ta1	ta2	ta3	ta4	ta5
Fore leg	2.8	0.90	0.95	0.61	0.22	0.15	0.09	0.09
Mid leg	2.7	1.00	0.88	0.60	0.22	0.16	0.09	0.09
Hind leg	3.1	1.18	1.37	0.81	0.26	0.16	0.09	0.09

(dated minimally to the early Cretaceous). In fact, this track, was recognized earlier by Harrison (1928), a perceptive early adopter of the Wegener paradigm. Vast majority of the extinct Anisopodidae is known exclusively from the Northern Hemisphere, since the early Jurassic to the Pleistocene (Evenhuis 1994, 2014). Within the Anisopodidae, as Matile (1990) and Amorim and Pires (1996) observed, extant members have fossil material from the northern hemisphere, but tropical Gondwanan track is seen in the pairs of sister genera *Eogaster* (Afro-Oriental)/*Olbogaster* (Neotropical), and *Mesochria* (Afro-Oriental)/*Neomesochria* (Neotropical/Australian). The problem of so-called Gondwanan taxa was widely discussed (Eskov,

1992; Sanmartín and Ronquist, 2004; McCarthy et al., 2007), with various explanations given. Vicariance and long distance dispersion events are allopatry based, geographical explanations for the process of speciation and, although both had a role in the diversification of lineages, often are treated as exclusive alternative models (Crisp et al., 2011; Gillespie et al., 2012). The present finding of the oldest species of *Mesochria* from the early Eocene of the Northern Hemisphere challenges tropical Gondwanan track hypothesis (Matile, 1990). We believe, the present distribution of *Mesochria* could result from its long history, with both vicariance and long dispersal events. More mechanisms could be involved in explanation of their distribution and

**FIGURE 3.** Geographical distribution of fossil and extant species of the genus *Mesochria*.

presence of the known fossils. The most rates of taxa formation are observed in such locations in which the struggle for existence against abiotic factors is reduced, as proposed by concepts of zonal stratification (Zherikhin, 1978) and phytospreading (Meyen, 1987a, 1987b), which are the extensions of Darlington's "equatorial pump" concept (Darlington, 1957, 1959). The model of the "tropical pump" assumes that formation of the new taxa is restricted mainly to the tropical equatorial zone, and proliferated descendants oust the ancestors to the extratropical regions. The concept of zonal stratification assumes that due to deterioration of more uniform climatic and ecological conditions of the late Cretaceous-early Palaeogene times and re-organisation of biosphere, with separation and differentiation of bioclimatic zones numerous late Mesozoic and early Cenozoic taxa gone extinct (Zherikhin, 1978; Eskov, 1996). The phenomenon of phytospreading (Meyen, 1987a, 1987b; Eskov, 1996) is not so much geographic as ecological in nature. It assumes that the newly formed taxa follow by anisotropic propagation ("spreading") from regions of the world where the climatic conditions are most into regions with harsher abiotic conditions. The late Mesozoic and early Cenozoic were characterised by weak climatic zonality (Gornitz, 2009), which resulted in intermittent and ceasing operation of "equatorial pump" mechanism (Eskov, 1995, 1996), and increasing role of second-rank gradients (humid-arid, lowland-highland, etc.), enabling the phytospreading mechanism operant in the regime of Dobruskina's (1982) diffuse centres of speciation. This could trigger the diversification of *Mesochria*. Subsequent, late Palaeogene and early Neogene transition from azonal to zonal epoch, establishment of a new climatic regime and biotic reorganization, resulting in concentration of Mesozoic-Palaeogene relics in the tropical and subtropical zones.

All the modern species of the genus *Mesochria* are present within the belt with mean annual temperature above 25°C and with mean annual precipitation over 1600 mm (Peel et al., 2007; CCKP, 2015; SAGE, 2015). The new species comes from the amberiferous layers of the Guchengzi Formation. The reconstructed Mean Annual Temperature for these layers are 15.2–15.6°C for the middle and 17.9–21.1°C for the upper; Mean Annual Precipitation 1035–1362 mm for the middle and 897–1355 mm for the upper (Quan et al., 2011, 2012). However, some recent species were reported from more elevated areas, where local MAT and MAP values could be

decreased and better correspond to the conditions reconstructed for the Early Eocene Fushun area. Most of the amber specimens were found in the upper layer of the Guchengzi Formation, according to Quan et al. (2012) these strata were deposited during the Early Eocene warming period. In our opinion, presence of fossil *Mesochria* in Fushun amber corroborates the hypothesis on subtropical climate, or at least fluctuation of climate during the terminal early Eocene as already suggested by Quan et al. (2012).

Despite of scarcity of biological data on *Mesochria*, its biological and environmental requirements, limited recent distribution and fossil record some explanations on its evolutionary history can be presented. In our opinion the distributional pattern of the modern *Mesochria* resulted from concentration of relictual descendants of late Mesozoic-Palaeogene forms in the tropical and subtropical zones. Both vicariance and long distance dispersal events, as well as other evolutionary mechanisms probably shaped the long history of this relictual genus, which, with present finding could be traced back to early Eocene times.

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