

# A Revision of the Nemestrinid Flies (Diptera, Nemestrinidae) Described by Rohdendorf, and a Deascription of New Taxa of the Nemestrinidae from the Upper Jurassic of Kazakhstan

M. B. Mostovski

*Paleontological Institute, Russian Academy of Sciences, ul. Profsoyuznaya 123, 117647 Moscow, Russia*

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**Abstract**—Nemestrinid flies described by Rohdendorf from the Upper Jurassic locality of Karatau (southern Kazakhstan) are revised. *Aenigmestrinus mirabilis* gen. et sp. nov., *Archinemestrius mimas* sp. nov., *A. litigiosus* sp. nov., *Protonemestrius rohdendorfi* sp. nov., and *P. rasnitsyni* sp. nov. are described from the same locality. *Protonemestrius longinasus* Rohd. is synonymized as *P. martynovi* Rohd. The taxonomic position and biology of Jurassic nemestrinids are briefly discussed.

## INTRODUCTION

Fossil representatives of the family Nemestrinidae are known from several localities of various ages in Russia, Kazakhstan, Mongolia, Western Europe and North America. Rohdendorf (1968) described from the Upper Jurassic of the Karatau Range, South Kazakhstan (Chimkent Region, Chayan District, locality nr. the village of Mikhailovka; Upper Jurassic, Karabastau Formation) six species of nemestrinid flies in three genera. He placed two of them in a separate subfamily, the Archinemestrinae. These taxa were characterized mainly on the basis of wing venation. Revision of the types, and study of new material enable a revision of the diagnoses to include essential features such as details of the female genitalia and proboscis structure. The genera *Archinemestrius* and *Protonemestrius* differ significantly in these characters, but should obviously be left in the same subfamily, although the diagnosis is difficult. Most probably this subfamily also includes a monobasic genus *Aenigmestrinus* gen. nov. Despite the wing venation of the type specimen of *A. mirabilis* it seems more derived relative to that of two other genera (radial sector branches and first medial vein entering anterior wing margin, supernumerary crossveins), the genus could be close to *Protonemestrius* on account of the presence of three spherical spermathecae in the female and the weakly modified cerci.

This combination of three spherical spermathecae and weakly modified cerci observed in *Protonemestrius* and *Aenigmestrinus* is a plesiomorphic state relative to all the other nemestrinids (including those fossil taxa for which the structure of reproductive organs is known). In modern nemestrinids two spermathecae are present (Teskey, 1981). In members of the genus *Protonemestrius* the face is swollen, the proboscis is elongate (at least in some species), the phragma is not formed as a separate wing vein, vein reticulation is

absent, the first metatarsomere is no shorter than the others combined, and only  $R_5$  vein enters the wing margin before the wing tip. If the opinion of Bernardi (1973) on the polarity of the primitive and derived character states (he considered the long proboscis primitive) is accepted, the genus *Protonemestrius* would seem to be very archaic, perhaps closest to the base of nemestrinid lineage. An alternative opinion (Zaitsev, 1992) on the short proboscis of ‘anthraxoid’ type as inceptual for the Bombylioidea seems to be more substantiated. If so, this genus is not very generalized. In members of the genus *Archinemestrius* the vein  $R_5$  terminates behind the wing tip, and the first metatarsomere is longer than the others combined. However, the presence of only two oval spermathecae, an elongate ensiform ovipositor, and  $R_{4+5}$  and  $M_{1+2}$  sometimes fused for a considerable distance show that this genus could not be ancestral to other nemestrinids. Such a mosaic of apomorphic and plesiomorphic character states is not rare in fossil forms and consequently Nemestrinidae is not an exception.

One more genus, *Eohirmoneura* was reasonably assigned by Rohdendorf to an extant subfamily Hirmoneurinae. My re-examining of the holotype of *Eohirmoneura carpenteri* Rohd., 1968 showed that unlike in the original description, the diagonal vein is clearly extended to the wing margin. Besides the type locality, the genus *Eohirmoneura* is recorded in the Lower Cretaceous of Spain (Montsech locality). It is possible that *Eohirmoneura* is only a subgenus of the genus *Hirmoneura* Meigen, 1820.

From the paleoenvironmental analysis of the Karatau locality (Polyanskii, Doludenko, 1978; Kirichkova, Doludenko, 1996) and morphological study of fossil nemestrinids some very general conclusions on their biology may be made. The adult flies with perfect flying abilities apparently inhabited, like modern nemestrinids, the dry open, well insulated biotops. They could

presumably feed at the bennettite 'flowers' sucking (with their long proboscis) or licking the liquid exudates. They could also act as pollinators for these plants. The quite large pollen of Bennettitales could be carried between the hairs covering the nemestrinid body. Paleobotanists believe that at least some bennettites could already have acquired entomophily and have reported some peculiar organs capable of functioning as nectaries (Meyen, 1986; Krassilov, 1989). The diversity of the female genitalia (cerci) indicates quite a broad host range of Jurassic nemestrinids, although it is still impossible to state any host association reliably. Modern hirmoneurines parasitize on beetles of the family Scarabaeidae (Bernardi, 1973). Other nemestrinids parasitize the egg clusters and the adult body of the orthopteran family Acrididae (Léonide, 1964a, b). Hence, one can not exclude members of the *Eohirmonera* as parasites of the Scarabaeidae, and other Jurassic nemestrinids as parasites of the Locustopseidae, an extinct analogue of acridids.

The type material on the taxa described is housed in the collection of the Paleontological Institute of the Russian Academy of Sciences (PIN).

## SYSTEMATIC PALEONTOLOGY

### Family Nemestrinidae Macquart, 1834

#### Subfamily Archinemestriinae Rohdendorf, 1968

**Diagnosis.** Wing phragma represented by pigmented section of membrane. First medial vein ending posterior to wing tip, if at anterior wing margin, than three spherical spermathecae. Supernumerary crossveins usually absent.

**Composition.** *Archinemestrius* Rohd., *Protonemestrius* Rohd., *Aenigmestrinus* gen. nov.

#### Genus *Archinemestrius* Rohdendorf, 1968

*Archinemestrius*: Rohdendorf, 1968, p. 181; Bernardi, 1973, p. 237; 1975, p. 48; Zaitsev, 1992, p. 101.

*Archinemestrius*: Rohdendorf, 1968, p. 182 (incorrect original spelling).

**Type species.** *Archinemestrius karatavicus* Rohdendorf, 1968; Upper Jurassic; Kazakhstan.

**Diagnosis.** Head hemispherical. Costal vein running around wing, becoming distinctly thinner beyond  $R_5$  or  $M_1$ , thickest between Sc and  $R_4$ . Costal margin of subcostal cell shorter or longer than that of first radial cell.  $R_5$  ending at or just behind wing tip.  $R_{4+5}$  and  $M_{1+2}$  connected with crossvein *rm* or fused for some distance. Anal cell open. Supernumerary crossveins absent. Alula narrow. First metatarsomere longer than four others combined. Two oval pigmented spermathecae. Cerci relatively long and narrow.

**Composition.** Type species and two new ones.

#### *Archinemestrius karatavicus* Rohdendorf, 1968

*Archinemestrius karatavicus*: Rohdendorf, 1968, p. 182

**Holotype.** PIN, no. 2066/2066, incompletely preserved male (part and counterpart); Karatau-Mikhailovka locality; Karabastau Formation.

**Diagnosis** (Fig. 1a). Costal margin of subcostal cell short.  $R_{4+5}$  forked at the level of  $R_1$  apex.  $R_{4+5}$  and  $M_{1+2}$  drawn together by very short crossvein or fused for very short distance.  $M_{2+3}$  stem continued into  $M_3$  smoothly or with slight bend. Cerci nearly thrice as long as wide at base.

**Measurements**, mm: spec. no. 2784/621: body length (excluding ovipositor), 11; wing width, 1.9.

**Remarks.** Insufficient preservation of the holotype precludes tracing the structure of the antennae beyond doubt. So far as visible the third segment is quite large, with a stick-shaped arista that is as long as the third segment itself and possibly subdivided basally.

**Material.** Besides the holotype, spec. no. 2784/621, a well preserved female from the same locality.

#### *Archinemestrius mimas* Mostovski, sp. nov.

**Etymology.** After one of the Gigants.

**Holotype.** PIN, no. 2997/3496, a moderately preserved female (part and counterpart); Karatau-Mikhailovka locality; Karabastau Formation.

**Description** (Figs. 1b–1f). This is a large, quite dark fly with pale legs. The third antennal segment is rounded conical, at least apically with minute hairs. The arista is as long as the third segment, two-segmented, its basal segment 3.5 times shorter and slightly wider than the distal one, bearing minute hairs. The  $R_{4+5}$  is forked slightly proximad of the  $R_1$  apex. The  $R_{4+5}$  and  $M_{1+2}$  are connected with a crossvein. The  $M_{2+3}$  stem continues into the  $M_3$  with a bend. The *mcu* crossvein connects the CuA to  $M_{3+4}$  stem. The phragma is developed as a feebly pigmented fold. The halter has a dark club and pale stalk. The pro- and mesotibiae are slightly incrassate towards the apices. The hind legs are clearly shorter than the abdomen. The cerci are 2.3 times as long as wide at the base.

**Measurements**, mm: body length (excluding ovipositor), 16; head diameter, 3.8; wing length, 10; wing width, 2.7.

**Comparison.** Distinct from *A. karatavicus* in the shorter cerci, longer *rm*, and the bend between  $M_{2+3}$  and  $M_3$ .

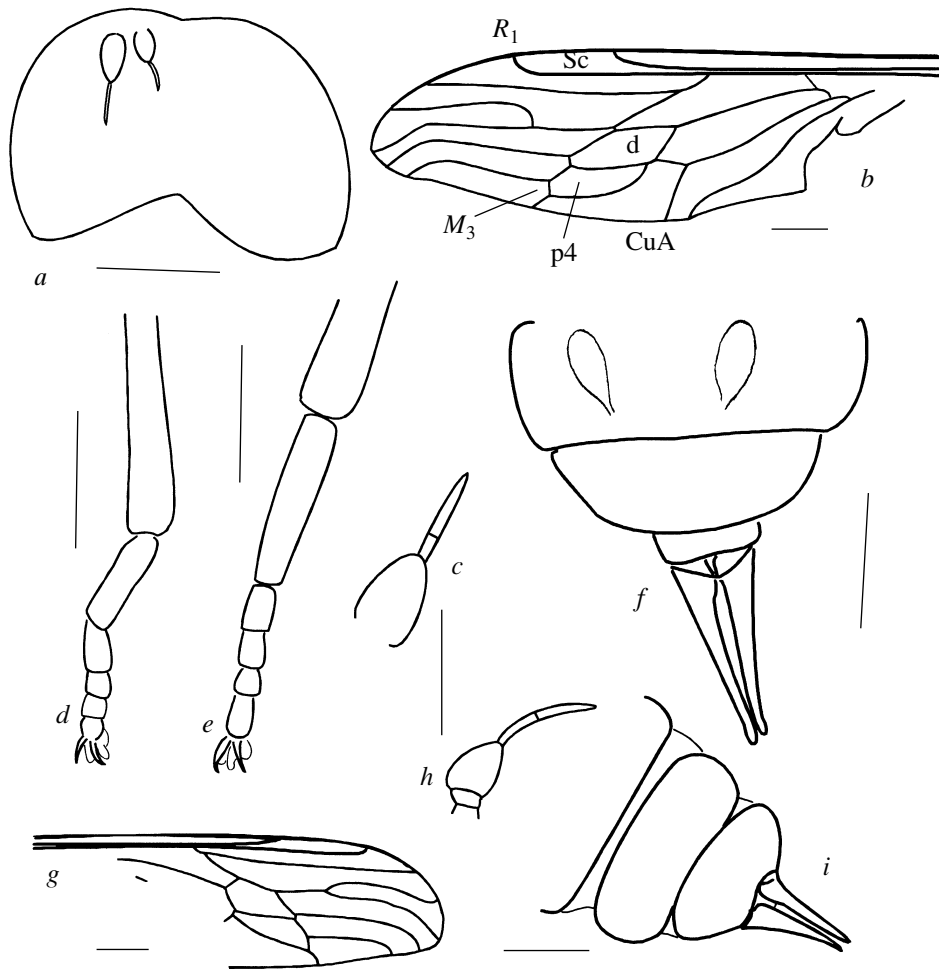
**Material.** Holotype.

#### *Archinemestrius litigiosus* Mostovski, sp. nov.

**Etymology.** Latin *litigiosus* (disputable).

**Holotype.** PIN, no. 2784/79, a well preserved female (part and counterpart); Karatau-Mikhailovka locality; Karabastau Formation.

**Description** (Figs. 1g–1i). This is a large, dark fly. The head diameter is equal to the thorax width. The



**Fig. 1.** Species of the genus *Archinemestrius*: (a) *A. karatavicus* Rohdendorf, holotype PIN, no. 2066/2066, head; (b–f) *A. mimas* sp. nov., holotype PIN, no. 2997/3496, female: (b) wing, (c) antenna, (d) mid leg, (e) hind leg, (f) abdominal apex; (g–i) *A. litigosus* sp. nov., holotype PIN, no. 2784/79, female: (g) wing, (h) antenna, (i) abdominal apex. Scale bar 0.5 mm in Figs. 1c and 1h, 1 mm in others.

occiput is feebly convex. The eyes are separated by a narrow frons. The third antennal segment is rounded conical. The arista is 1.5 times longer than the third segment, two-segmented, its basal segment is a little shorter and no wider than the distal one. The costal margin of the subcostal cell Sc is quite long.  $R_{4+5}$  is forked far proximad of the  $R_1$  apex.  $R_{4+5}$  and  $M_{1+2}$  are fused for a considerable distance. The  $M_{2+3}$  stem directly continues with the  $M_3$ . The *mcu* crossvein connects CuA to  $M_4$ . The cerci are twice as long as wide at the base.

**Measurements**, mm: body length (excluding ovipositor), 12.5–14.5; head diameter, 3–3.2; wing length, 7.4–8; wing width, 1.8–2.3.

**Comparison.** Distinct from the other species in the quite long fusion of  $R_{4+5}$  with  $M_{1+2}$ , *mcu* joining  $M_4$ , shorter cerci, and more proximal  $R_{4+5}$  fork relative to  $R_1$  apex. Moreover, distinct from the type species in the larger size, and from *A. mimas* in the smaller size, longer arista, and  $M_{2+3}$  smoothly continuing onto  $M_3$ .

**Remarks.** The specimen no. 2904/1608 is distinct from the holotype in the arista structure (its basal segment almost thrice shorter and slightly thicker than the distal one) and greater body length, but insufficient preservation precludes its description as a separate species.

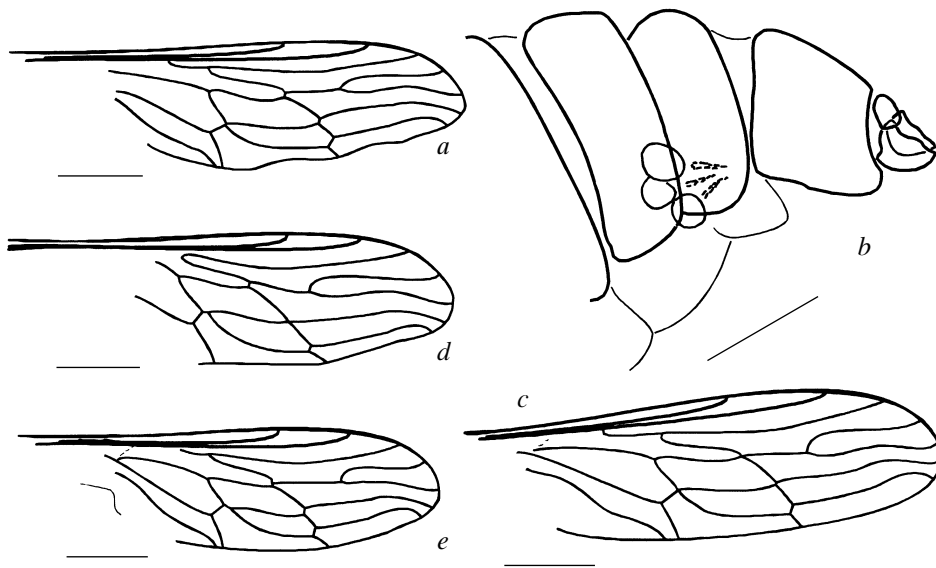
**Material.** Besides the holotype, a paratype PIN, no. 2997/3539(3542) (part and counterpart), and possibly spec. no. 2904/1608, both poorly preserved females from the same locality.

#### Genus *Protonemestrius* Rohdendorf, 1968

*Protonemestrius* Rohdendorf, 1968, p. 182; Bernardi, 1973, p. 238; 1975, p. 48; Zaitsev, 1992, p. 101.

**Type species.** *Protonemestrius martynovi* Rohdendorf, 1968; Upper Jurassic; Kazakhstan.

**Diagnosis.** Head hemispherical or very slightly flattened in anteroposterior direction. Occiput convex. Frons broader in female than in male. Male ommatidia of two types: anteriorly larger, otherwise small. Face



**Fig. 2.** Species of the genus *Protonemestrius*: (a–c) *P. martynovi* Rohdendorf: (a) holotype PIN, no. 2239/2160, wing; (b) specimen no. 2904/1559, abdominal apex; (c) wing of same; (d) *P. bequaerti* Rohdendorf, holotype PIN, no. 2066/2056, wing; (e) *P. handlirschi* Rohdendorf, holotype PIN, no. 2066/1464, wing. Scale bar 1 mm.

convex. Proboscis elongate. Costal vein running around wing, becoming distinctly thinner beyond  $R_5$  or  $M_1$ , thickest between Sc and  $R_4$ . Costal margin of subcostal cell longer than that of first radial cell.  $R_5$  ending at or just before wing tip.  $R_{4+5}$  and  $M_{1+2}$  connected with crossvein *rm* or fused in a point. Anal cell open. Supernumerary crossveins absent. Alula narrow. First metatarsomere as long as or scarcely longer than four others combined. Three spherical pigmented spermathecae. Cerci of ovipositor short.

**Composition.** *P. martynovi* Rohd., 1968 (= *P. longinasus* Rohd., 1968, syn. nov.), *P. bequaerti* Rohd., 1968, *P. handlirschi* Rohd., 1968, *P. rohdendorfi* sp. nov., *P. rasnitsyni* sp. nov.

**Comparison.** Distinct from the genus *Archinemestrius* in the three spherical spermathecae and  $R_5$  never ending behind the wing tip.

**Remarks.** Up to now the elongate proboscis is known only in *P. martynovi* and *P. rohdendorfi*.

***Protonemestrius martynovi* Rohdendorf, 1968**

*Protonemestrius martynovi*: Rohdendorf, 1968, p. 183

*Protonemestrius longinasus*: Rohdendorf, 1968, p. 186 (syn. nov.)

**Holotype.** PIN, no. 2239/2160, moderately preserved ?male (part and counterpart); Karatau-Mikhailovka locality; Karabastau Formation.

**Diagnosis** (Figs. 2a–2c).  $R_{4+5}$  is forked slightly proximad of  $R_1$  apex. The d + p4 cell is not narrow. Distal  $M_3$  section (penultimate section of diagonal vein) equal to or little shorter than last section of diagonal vein. Angles between  $M_{2+3}$  and  $M_3$ , and between  $M_3$  and  $M_{3+4}$  are nearly  $90^\circ$ . Fourth posteromarginal cell is not wide. Cerci as long as wide at base.

**Measurements**, mm: body length, 9.5–10.5; wing length, 6–7.6.

**Remarks.** Wing venation is sometimes quite variable in nemestrinids (see e.g., Timon-David and Léonide, 1968). Re-examination of the type material and study of the new material indicates that the characters listed as diagnostic in the original description, in our opinion, cannot be used for separation of *P. martynovi* and *P. longinasus*. Hence, these species are synonymized.

**Material.** Besides the type material, specimen no. 2904/1559, a moderately preserved female from the same locality.

***Protonemestrius bequaerti* Rohdendorf, 1968**

*Protonemestrius bequaerti*: Rohdendorf, 1968, p. 185

**Holotype.** PIN, no. 2066/2056, moderately preserved female; Karatau-Mikhailovka locality; Karabastau Formation.

**Diagnosis** (Fig. 2d).  $R_{4+5}$  forked far proximad of the  $R_1$  apex. d + p4 cell narrow. Distal  $M_3$  section much (4 times) shorter than last section of diagonal vein. Angles between  $M_{2+3}$  and  $M_3$ , and between  $M_3$  and  $M_{3+4}$  are nearly  $90^\circ$ . Fourth posteromarginal cell not wide. Cerci are scarcely longer than wide at base.

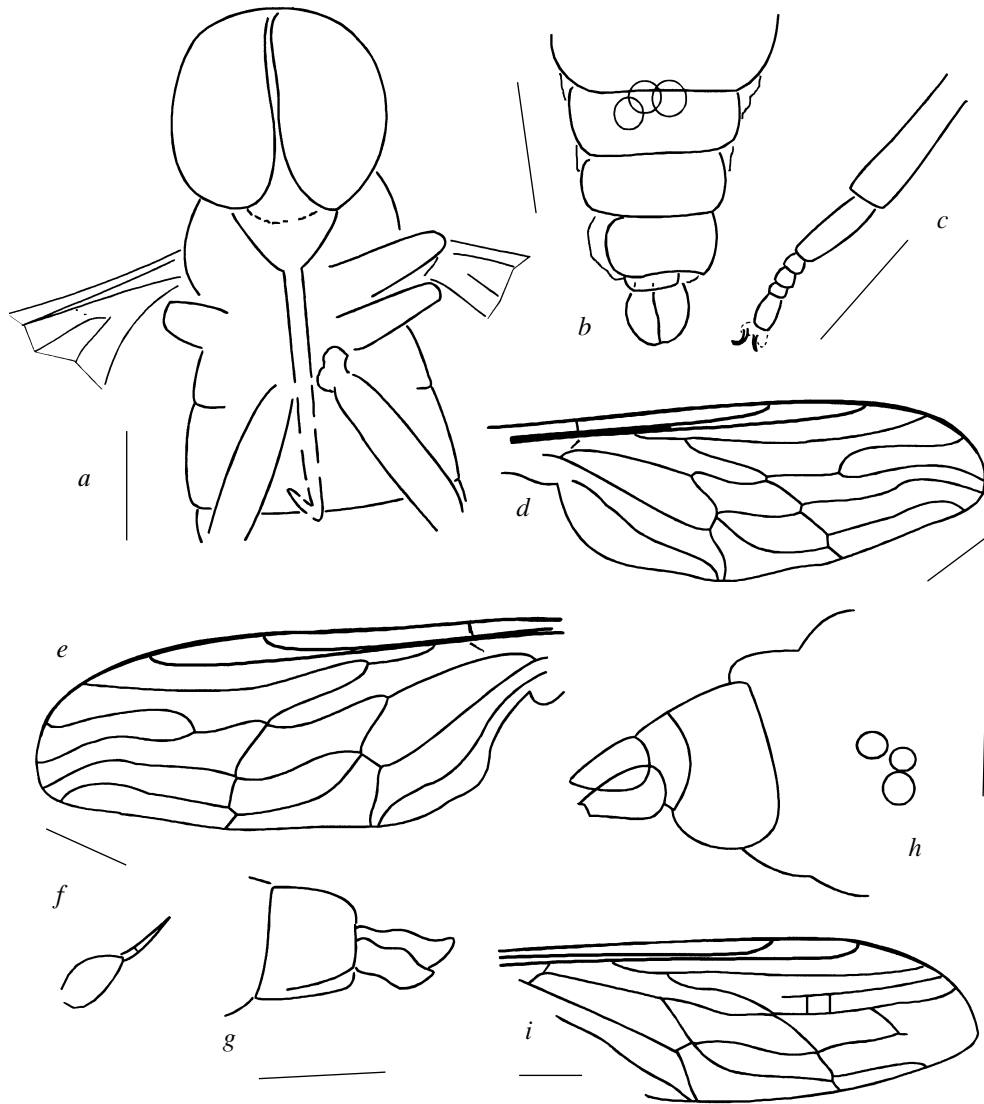
**Measurements**, mm: wing length, 5.7.

**Material.** Holotype.

***Protonemestrius handlirschi* Rohdendorf, 1968**

*Protonemestrius handlirschi*: Rohdendorf, 1968, p. 184

**Holotype.** PIN, no. 2066/1464, moderately preserved fly; Karatau-Mikhailovka locality; Karabastau Formation.



**Fig. 3.** New species of Upper Jurassic nemestrinids: (a–d) *Protonemestrius rohdendorfi* sp. nov., holotype PIN, no. 2784/73: (a) forebody, (b) abdominal apex, (c) apex of metatibia with tarsus, (d) wing; (e–g) *P. rasnitsyni* sp. nov., holotype PIN, no. 2554/908: (e) wing, (f) antenna, (g) abdominal apex; (h–i) *Aenigmestrius mirabilis* sp. nov., holotype PIN, no. 2904/1562: (h) abdominal apex, (i) wing. Scale bar 0.5 mm in Fig. 3f, 1 mm in others.

**Diagnosis** (Fig. 2e).  $R_{4+5}$  is forked level with  $R_1$  apex.  $d + p4$  cell rather narrow. Distal  $M_3$  section 2.5 times shorter than last section of diagonal vein. Angle between  $M_{2+3}$  and  $M_3$  obtuse, that between  $M_3$  and  $M_{3+4}$  nearly  $90^\circ$ . Fourth posteromarginal cell not wide.

**Measurements**, mm: wing length, 5.3.

**Material**. Holotype.

*Protonemestrius rohdendorfi* Mostovski, sp. nov.

**Etymology**. To the memory of paleoentomologist, Prof. B.B. Rohdendorf.

**Holotype**. PIN, no. 2784/73, rather well preserved female (part and counterpart); Karatau-Mikhailovka locality; Karabastau Formation.

**Description** (Fig. 3a–3d). A medium-sized, dark fly, with the abdomen a little paler than the thorax. The head is as wide as the thorax. The eyes are nearly holoptic. The face is swollen; the proboscis is long, and the scutellum small.  $R_1$  was sparse, exceedingly minute bristles.  $R_{4+5}$  is forked proximad of the  $R_1$  apex. The  $d + p4$  cell is not narrow,  $p4$  is a little wider than  $d$ . The distal  $M_3$  section is considerably (3.5–4 times) shorter than the last section of the diagonal vein.  $R_5$  is twice longer than the RS3 section. The angles between  $M_{2+3}$  and  $M_3$ , and between  $M_3$  and  $M_{3+4}$  greatly exceed a right angle. The fourth posteromarginal cell is wide and not narrower than the discal cell. The phragma is developed as a well pigmented fold. The hind legs are a little longer than the abdomen. The metatibiae are equal to and 1.5 times narrower than the femora, scarcely

incrassate at their apices. The first metatarsomere is as long as the four others combined. The cerci are not attenuated apically, as long as or slightly shorter than width at the base.

**Measurements**, mm: body length, 9.5; head diameter, 2.5; wing length, 6; wing width, 2.1.

**Comparison.** From the other species distinct in the p4 wider than the discal cell. Moreover, distinct from *P. handlirschi* in the  $R_{4+5}$  fork displaced basad, from *P. bequaerti* in the wider d + p4 cell, from *P. martynovi* in the larger angles between  $M_{2+3}$  and  $M_3$  and between  $M_3$  and  $M_{3+4}$ .

**Material.** Holotype.

*Protonemestrius rasnitsyni* Mostovski, sp. nov.

**Etymology.** After paleontologist, Prof. A.P. Rasnitsyn.

**Holotype.** PIN, no. 2554/908, rather well preserved female (part and counterpart); Karatau-Mikhailovka locality; Karabastau Formation.

**Description** (Fig. 3e–3g). A quite large, dark fly, with the abdomen and legs a little paler than thorax, and the last abdominal tergite dark. The third antennal segment is rounded conical. The arista is nearly 1.5 times longer than the third segment, its basal segment twice shorter than the distal one.  $R_{4+5}$  is forked proximad of the  $R_1$  apex. The d + p4 cell is not narrow. The distal  $M_3$  section is slightly less than twice shorter than the last section of the diagonal vein. The  $R_5$  is 2.3 times longer than the RS3 section. The angle between  $M_{2+3}$  and  $M_3$  exceeds  $90^\circ$ , that between  $M_3$  and  $M_{3+4}$  is  $90^\circ$ . The fourth posteromarginal cell is narrower than the discal cell. The phragma is developed as a pigmented fold. The hind legs are shorter than the abdomen. The metatibiae are slightly longer and 1.5 times narrower than the femora. The first metatarsomere is as long as the four others combined. The cerci are attenuate apically, curved, longer than wide at the base.

**Measurements**, mm: body length (excluding ovipositor), 14; wing length, 7.5; wing width, 2.4.

**Comparison.** From the other species distinct in the larger size and different shape of cerci (from those species for which their structure is known). Moreover, distinct from *P. handlirschi* in the  $R_{4+5}$  fork displaced basad and wider d + p4 cell, from *P. bequaerti* in the wider d + p4 cell, from *P. martynovi* in the larger angle between  $M_{2+3}$  and  $M_3$ , from *P. rohdendorfi* in the p4 distinctly narrower than the discal cell.

**Material.** Holotype.

**Genus *Aenigmestrinus* Mostovski, gen. nov.**

**Etymology.** From Latin *aenigma* (puzzle) and the genus *Nemestrinus*.

**Type species.** *Aenigmestrinus mirabilis* sp. nov.

**Diagnosis.** Head hemispherical. Costal vein becoming thinner before wing tip, almost untraceable

along posterior wing margin (if it extends around the wing at all). Costal margin of subcostal cell scarcely longer than that of first radial cell. Radial sector branches and at least  $M_1$  entering wing margin before wing tip.  $R_{4+5}$  and  $M_{1+2}$  fused in a point. Anal cell open. Supernumerary crossveins developed. Three spherical pigmented spermathecae. Cerci of ovipositor short.

**Composition.** Type species.

**Comparison.** Distinct from two other genera in the radial sector branches and  $M_1$  entering anterior wing margin, and in addition from the genus *Archinemestrius* in the three spherical spermathecae and short cerci, and from *Protonemestrius* in the presence of supernumerary crossveins.

*Aenigmestrinus mirabilis* Mostovski, sp. nov.

**Etymology.** Latin *mirabilis* (wonderful).

**Holotype.** PIN, no. 2904/1562, moderately preserved female (part and counterpart); Karatau-Mikhailovka locality; Karabastau Formation.

**Description** (Figs. 3h and 3i). A quite large, dark fly, with legs a little paler than body. The body is densely covered with short hairs. The  $R_4$  base is free. The crossveins could appear between  $R_4$  and  $R_5$ . Other crossveins between  $R_5$  and  $M_1$  and between  $M_1$  and  $M_2$  form a type of second diagonal vein, possibly not extending to the wing margin. The phragma is developed as a well pigmented and possibly sclerotized fold. The cerci are subconical, scarcely longer than their combined width at the base. The hind legs are as long as the abdomen.

**Measurements**, mm: body length (excluding ovipositor), 13; wing length, 8.5; wing width, 2.5.

**Remarks.** In specimen no. 2997/941 tentatively assigned to *A. mirabilis*, the arista is composed of three segments, the basal one being shortest.

**Material.** Holotype, and presumably, specimen no. 2997/941, a female (wings and legs not preserved).

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