

New Nemestrinoidea (Diptera: Brachycera) from the Upper Jurassic – Lower Cretaceous of Eurasia, taxonomy and palaeobiology

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MOSTOVSKI, M.B. & MARTÍNEZ-DELCLÓS, X. 2000. New Nemestrinoidea (Diptera: Brachycera) from the Upper Jurassic – Lower Cretaceous of Eurasia, taxonomy and palaeobiology. *Entomol. Probl.* 31(2): 137 - 148. – New nemestrinoids belonging to the families Rhagionemestriidae and Nemestrinidae from the Jurassic deposits of the Southern Kazakhstan and Germany and Lower Cretaceous deposits of Spain, Russia, and Mongolia are described. The authors argued including the Heterostominae in the Rhagionemestriidae; and the latter is considered as a connecting link between Xylophagidae and Nemestrinidae. The Nemestrinoidea and Nemestrinidae themselves demonstrate high taxonomic diversity since the Middle – Upper Jurassic although members of the families Rhagionemestriidae and Nemestrinidae appeared in the Lower Jurassic for the first time. Both extinct Archinemestriinae and extant Hirmoneurinae are known since the Jurassic, while Nemestrininae came into palaeontological record in the Lower Cretaceous. Fossil nemestrinids, at least those with long proboscis, are postulated to be connected with bennettites or angiosperms as nectar-feeders and possibly pollinators.

Key words: Diptera, Nemestrinoidea, Jurassic, Lower Cretaceous, Europe, Asia, new taxa, palaeobiology.

Introduction

The superfamily Nemestrinoidea includes three families, Rhagionemestriidae, Nemestrinidae, and Acroceridae, although the family Bombyliidae may be also considered as a member of this superfamily (e.g. OVTSHINIKOVA 1998). Acroceridae include small- to moderately-sized flies found world-wide except oceanic islands; and all known species are internal parasites of spiders. The fossils of Acroceridae are found mainly in Cenozoic ambers (EVENHUIS 1994). Two Mesozoic impressions were also allocated to this family (USSATCHOV 1968; NARTSHUK 1996), although their true placement remains disputable (MOSTOVSKI 1997a).

Nemestrinidae, commonly called tangle-veined flies, is a virtually cosmopolitan group of brachycerous flies consisting of about 300 species in over 20 genera. The first and the most ancient undoubted nemestrinid fly belonging to the extinct subfamily Archinemestriinae was found in Liassic deposits of Germany (Dr. J. ANSORGE pers. comm.). The fossil record of Archinemestriinae shows them to be most diversified in the Middle – Late Jurassic. Representatives of nine Archinemestriinae species are recorded in the deposits of the Karabastau Formation in southern Kazakhstan (MOSTOVSKI 1998). Hirmoneurinae are also known since the Jurassic (HANDLIRSCH 1906-1908; ROHDENDORF 1968) while Nemestrininae are believed to appear only in the Early Cretaceous.

Rhagionemestriidae was originally erected as a subfamily within Nemestrinidae for the single monobasic genus from the Jurassic of Kazakhstan (USSATCHOV 1968).

BERNARDI (1973a) questioned the familial placement of *Rhagionemestrius rapidus* USSATCHOV, and NAGATOMI & YANG (1998) correctly raised the rank of the subfamily. Regarding taxa included in this family see under the section **Systematic palaeontology**.

Material and Methods

Localities studied

Karatau. The famous locality of Karatau (Karatau-Mikhailovka) is situated in the Karatau Mountain Ridge, Chimkent Region, Southern Kazakhstan. The continental deposits of the Karabastau Formation yield more than 18 000 remains of diverse insects, a lot of plants, fishes, and conchostracans. Gastropods, ostracods, and spiders are not common. A salamander, five species of reptiles, and a feather belonging to a bird or a dinosaur have been described from the same beds (DOLUDENKO et al. 1990). Numerous plant remains are represented in Karatau mainly by bennettites, conifers, pteridophytes, and cycadophytes as well as Equisetales, Caytoniales, Ginkgoales, Cycadales, and Czekanowskiales. Judging from the plant assemblage and a spore-pollen complex analysis, the age of the Karabastau Fm. may be assigned to the Callovian – Kimmeridgian (KIRICHKOVA & DOLUDENKO 1996). There are representatives of 19 insect orders, with beetles, true flies, bugs, and cockroaches predominating (PANFILOV 1968; DOLUDENKO et al. 1990).

Brachycerous flies are exceptionally diverse in the fauna of Karatau. There are representatives of the families

Stratiomyidae, Xylomyidae, Rhagionidae, Rhagionempididae, Xylophagidae, Therevidae, Asilidae, Archisargidae, Eremochaetidae, Kovalevisargidae, Nemestrinidae, Acroceridae Archocyrtrinae, Empididae Protempidinae, and such rare (in the palaeontological record) families as Hilarimorphidae, Scenopinidae, Apystomyiidae, and ?Vermileonidae.

Nemestrinoidea are relatively abundant in the deposits of the Karabastau Fm. and are represented by all three families, i.e. Rhagionemestriidae, Acroceridae, and Nemestrinidae. The latter is the most diverse. Ten nemestrinid species in four genera belonging to both Archinemestriinae and Hirmonneurinae have been described so far (ROHDENDORF 1968; MOSTOVSKI 1998). Nemestrinoids form 4.8 per cent of Brachycera. Archinemestriine genus *Protonemestrius* have been also found in deposits of the Yixian Formation in the north-eastern China (REN 1998a), which is Tithonian (REN et al. 1997), Hauterivian – Aptian (SMITH et al., 1995), or Barremian (SWISHER et al., 1999) in age¹.

Baissa. The unique locality of Baissa is the richest insect-bearing site among more than a hundred sites currently known in Transbaikalia. The beds are exposed at the left bank of the Vitim River, 40 km downstream of the mouth of the Zaza River. Deposits of the Zaza Formation are represented in this locality by conglomerates, sandstones and siltstones interbedded by clays, marls, and limestones. About 20 000 remains representing 25 insect orders, a lot of pelecipods and gastropods, ostracods and conchostacans, also spiders, harvestmen, fishes, bird feathers as well as unique freshwater bryozoan colony and bird or pterosaur bones have been found in Baissa (ZHERIKHIN et al., in press). The faunistic assemblage of Baissa may be referred to “Ephemeropsis-Coptoclava” type (ZHERIKHIN 1978). Its characteristic components are osteoglossomorph fish *Lycoptera*, mayfly *Ephemeropsis*, water beetle *Coptoclava* and phyllopod *Bairdestheria*. The age of the Zaza Fm. is accepted by geologists and palaeozoologists as Neocomian or Early Neocomian (e.g. MARTINSON 1961; ZHERIKHIN 1978; RASNITSYN et al. 1998), but palaeobotanists do not reject its Barremian – Aptian age (e.g. VAKHRAMEEV & KOTOVA 1977). The climate in the Early Neocomian is supposed to be humid and temperate to warm for the latitudes in question (ZHARKOV et al., 1998), although there are some lithological evidences in favour of semiarid climate in this region (LIAMINA 1980).

Brachycerous flies are represented by the families Stratiomyidae, Rhagionidae, Nemestrinidae, Bombyliidae, Hilarimorphidae, Apioceridae, Therevidae, Asilidae, Vermileonidae?, Eremochaetidae, Empididae belonging to extant subfamilies Hybotinae and Oreogtoninae, Platypezidae, Ironomyiidae Sinolestinae, and Sciadoceridae. The flies of Baissa display some similarity with those from the Yixian Fm. and also with the Middle Purbeck Beds and Wealden of the southern England (MOSTOVSKI & VRSANSKY 1998).

Numerous plant remains are represented in Baissa mainly by conifers with an admixture of ginkgoaceous plants and Czekanowskiales and equisetaceous plants, pteridophytes, bennettites, and angiosperms. The plant

assemblage shows similarity with those of the Hurilt Beds of the Bon-Tsagaan Group in Mongolia and of the Yixian Fm. (Dr. E. BUGDAEVA pers. comm.).

La Cabrua & la Pedrera de Meir. The localities of La Cabrua and la Pedrera de Meir are situated in the Montsec Range, to the south of Pyrenees, in Catalonia, Northeast of Spain. The continental deposits of “Calcaires Charophytes du Montsec” Formation yield more than 3000 remains of diverse insects. Plants and other arthropods (ostracods, crustaceans, and spiders) are also found yet not common. Three species of frogs, two lacertilians and a crocodile, feathers and birds (SANZ et al. 1997) have been described from these limestones (MARTÍNEZ-DELCLÓS 1985). Numerous plant remains, mainly Equisetales, Filicales, Cycadofilicales, Caytoniales, Coniferales, Ginkgoales, Bennettiales, Cycadales, and Ranales, are represented in Montsec beds. Abundant bryophytes (BLANC-LOUVEL & BARALE 1983) and some charophytes are also found. The age of these lithographic limestones is Berriasian – Valanginian based on ostracods (BRENNER et al. 1974), or latest Hauterivian – early Barremian based on charophytes according to other authors (ANSORGE 1993; MARTÍN-CLOSAS & LÓPEZ-MORÓN 1995).

There are representatives of 13 insect orders, with beetles and cockroaches as terrestrial and mayfly nymphs as aquatic dominating (MARTÍNEZ-DELCLÓS & NEL 1995). Brachycerous flies are not diverse in these outcrops and belong to the families Stratiomyidae, Nemestrinidae, Rhagionemestriidae, Rhagionidae, and Empididae (WHALLEY & JARZEMBOWSKI 1985; ANSORGE 1991; MOSTOVSKI in press; MOSTOVSKI & MARTÍNEZ-DELCLÓS this work). It is noteworthy that soldier-flies are represented by a single adult fly and numerous larvae.

Las Hoyas. The Las Hoyas outcrop belongs to Las Hoyas Sub-Basin which is located in the southern part of the “Serranía de Cuenca” (South-western Iberian Mountain Range, Spain). The continental deposits of La Huérguina Formation yield more than 2500 individuals in 13 insect orders. Aquatic Heteroptera (MARTÍNEZ-DELCLÓS et al. 1995) and terrestrial beetles and neuropterans are the most abundant groups. Plants have not been studied yet, but remains of Filicales, Bennettiales, Caytoniales, Coniferales, Gnetales, and possible Angiospermae have been found. Bryophytes and charophytes are well represented (SANZ et al. 1988; MARTÍN-CLOSAS & DIÉGUEZ 1998). Based on the charophytes and ostracods record, the limestones of Las Hoyas are of Late Barremian age. Eight families of fishes, three families of amphibians (frogs, salamanders, and salamander-like albanerpetonids), turtles, lacertilians, crocodylomorphs, dinosaurs, and birds are found (MELÉNDEZ 1995).

Brachycerous flies are scarce and are represented by larvae of Stratiomyidae, an adult of Nemestrinidae, two specimens of Tabanidae, and a destroyed specimen of Therevidae.

Bon-Tsagaan. The locality of Bon-Tsagaan is the richest Lower Cretaceous fossil-bearing site in Mongolia. It is situated in Central Mongolia, Bayanhongor Aimak, 5 km to the south of Bon-Tsagaan Lake (Bon-Tsagaan-Nuur). The geology of this area and the stratigraphy of

¹The late Early Cretaceous age of insect-bearing beds of the Yixian Fm. seems to be better argued, however.

Lower Cretaceous deposits in Central Mongolia, and the Bon-Tsagaan Group in particular, were described thoroughly by SINITSА (1993). Numerous molluscs, ostracods, fishes, birds and pterosaurs occur in the Hurilt Beds of the Bon-Tsagaan Group (ibid.). More than 10 000 insect specimens collected represent 15 orders, with Coleoptera, Homoptera, Blattodea, and Heteroptera dominating and subdominating. Remains of osteoglossomorph fish *Lycoptera* and *Coptoclava* beetles are rather common. Conchostracans are rare. Diverse plants were studied by KRASSILOV (1982). The age of the Bon-Tsagaan Group seems to be restricted to the Barremian – Aptian. There is evidence in favour of a warm and arid climate (SINITSА, 1993).

Brachycerous flies are not diverse in the locality of Bon-Tsagaan, and are represented only by Rhagionidae, Eremochaetidae, Rhagionemestriidae, ?Bombyliidae, true Empididae, Therevidae, ?Apioceridae, Platypezidae and Ironomyiidae Sinolestinae.

The material studied are housed in the following Museum and Institutions: PI – Paleontological Institute, Moscow; UB – Universitat de Barcelona; LH – Universidad Autónoma de Madrid; MNHN – National Museum of Natural History, Paris, Institut d'Estudis Ilerdencs. There is one more specimen of Nemestrinidae in the collection of UB besides those described below (LC-040-EP), but its taxonomic position can not be clarified due to its poor condition. Wing abbreviation mainly follows SHCHERBAKOV et al. (1995).

Systematic palaeontology

Rhagionemestriidae USSATCHOV, 1968

Diagnosis. Costal vein circumambient, becomes thinner beyond R_4 or wing apex. R_1 rather long. Medial spar of wing is represented by either convex R_5 and fold running along RS, R_{4+5} and M_1 beyond r-m (in this case R_{2+3} is curved, and terminates near R_1 tip) or diagonal vein, which is not formed of M_3 (R_{2+3} is straight, otherwise tips of R_1 and R_{2+3} are not approaching). Anal cell open or closed.

Subfamilies included. The family includes two subfamilies, Rhagionemestriinae and Heterostominae.

Discussion. We recognise two subfamilies within this family, Rhagionemestriinae and Heterostominae. The nominative subfamily includes two tribes, Rhagionemestriini and Exeretoneurini. The subfamily Heterostominae comprises the tribes of Heterostomini and Sinonemestriini. *Sinonemestrius tuanwangensis* HONG & WANG was described from Lower Cretaceous Laiyang Formation in the northeastern China and was originally placed in the family Nemestrinidae (HONG & WANG, 1990), obviously judging from the specific position of the veins R_4 , R_5 , M_1 and M_2 terminating near the wing tip. Nevertheless the short R_1 , relatively short and arched R_{2+3} ending at R_1 tip, and the absence of the so-called "diagonal" vein should prevent one from putting this genus in Nemestrinidae. In some features *Sinonemestrius* resembles the genus *Heterostomus* BIGOT (arched R_{2+3} terminating at R_1 tip, sigmoidal R_4 , shape of discal cell) or *Exeretoneura* MACQUART (curved in different ways R_{2+3} , R_4 , R_5 , M_1 , the ten-

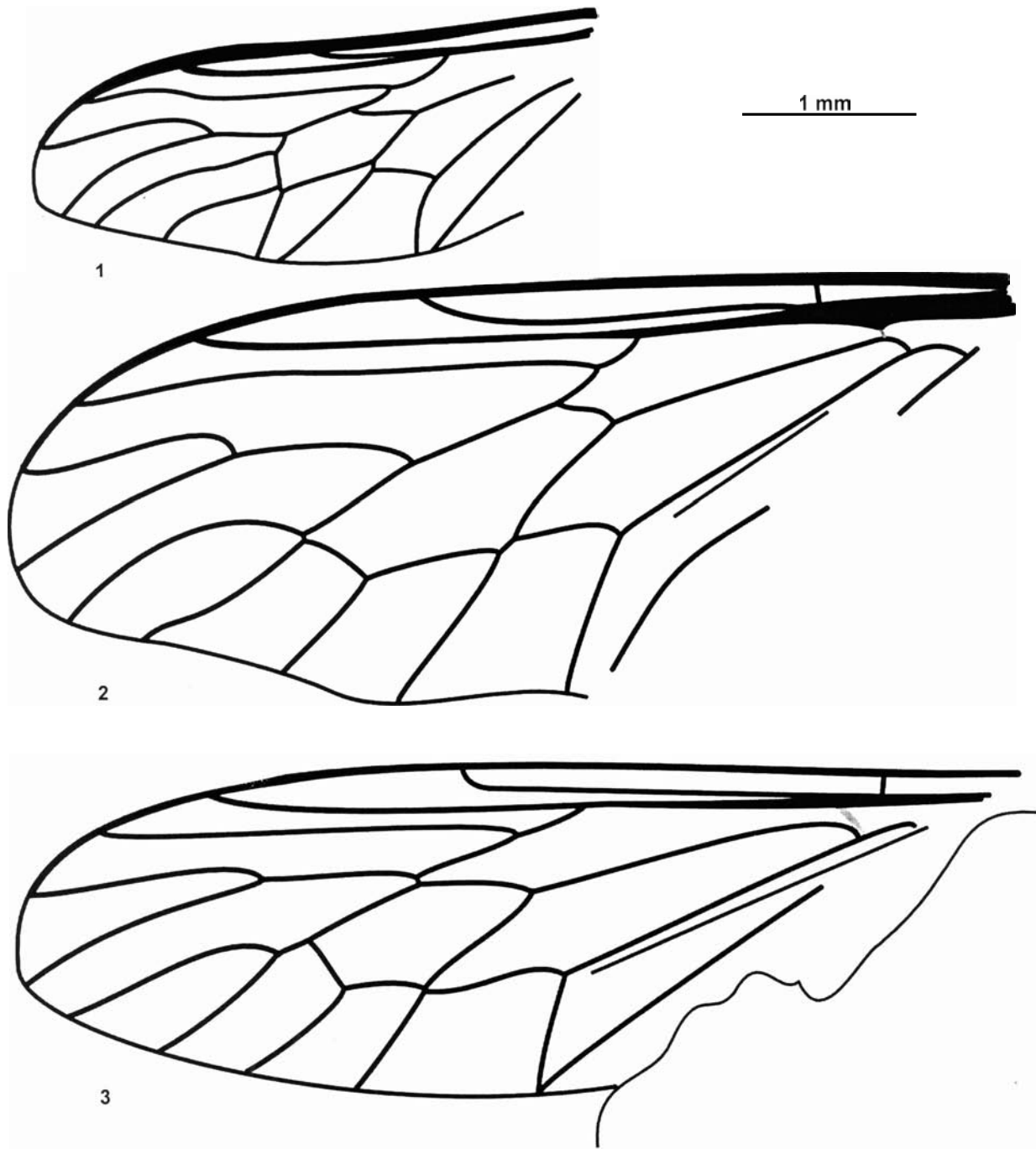
dency to shift veins tips to the fore margin of wing, petiolate p_4 and opened anal cell). *Exeretoneura* had been included in Nemestrinidae until NAGATOMI (1977) erected a new family for this genus. Later he argued in favour of closeness of *Exeretoneura* and *Heterostomus*, based on studying the male genitalia and some other features, and considered them as belonging to Xylophagidae s. l. as subfamilies (NAGATOMI, 1984, 1985, 1992). Investigation of folds in wings of *Coenomyia ferruginea* (SCOPOLI), *Heterostomus curvipalpis* BIGOT, *Exeretoneura maculipennis* MACQUART, and another fossil species of *Sinonemestrius* from the Lower Wealden Clay in England provides more evidence for to their taxonomic position (JARZEMBOWSKI & MOSTOVSKI, 1999). The condition observed in *C. ferruginea* and *H. curvipalpis* (R_5 convexity and convex fold, forming the extra supporting spar (ENNOS, 1989), distad of r-m running along M_{1+2}) seems to be similar to that of *Exeretoneura* and Nemestrinidae: the spar coincides with the diagonal vein composed of RS, R_{4+5} , M_{1+2} (and often fusion of two the latter, replacing r-m), and M_2 (in *Exeretoneura*, *Nagatomukha* gen.nov., and *Iberomosca* gen.nov.) or M_{2+3} and M_{3+4} (in Nemestrinidae). In *Sinonemestrius* the spar is represented by a strong convex fold running between radial and medial sectors (along RS and R_{4+5} proximad of r-m, and distad of r-m along M_{1+2}), i. e. it looks even more similar to that of *Coenomyia* than to that of *Heterostomus* (does not coincide with any part of R_{4+5}). However, the Nemestrinoidea (excluding Bombyliidae) retaining pulvilliform empodium are often placed in the lower Brachycera (NAGATOMI 1992) as phylogenetically independent from Asiloidea etc. If so, *Sinonemestrius* plus *Heterostomus* and *Exeretoneura* (differing from true nemestrinids in primitive antennal structure and other plesiomorphies) plus Rhagionemestriini, on the other hand, could be a link between Xylophagidae and Nemestrinidae. Such a peculiar position of *Exeretoneura* is supported by the structure of the male genitalia musculature (Dr. O.G. OVTSHINNIKOVA, pers. comm.). The larva of *Exeretoneura* and its biology are similar to those of Coenomyiinae (PALMER & YEATES 1998). NAGATOMI and YANG (1998) put the genus *Sinonemestrius* in a family of its own and depicted sister-group relationships between Sinonemestriidae and Nemestrinidae, based only on the specific position of veins M_1 and M_2 . It seems more reasonable to assign tribal rank to the former. The most ancient member of Sinonemestriini is found in the Lower Jurassic of Germany (Dr. J. ANSORGE pers. comm.).

Rhagionemestriinae

Diagnosis. Medial spar of wing is formed with diagonal vein composed of RS, R_{4+5} , M_{1+2} beyond r-m, or fused $R_{4+5}+M_{1+2}$ and rest of $M_{1+2}+M_2$ (rarely M_1).

Tribes included. The subfamily includes two tribes, Rhagionemestriini and Exeretoneurini.

Remarks. Partly fused R_{4+5} and M_{1+2} occur also in Eremochaetidae, in some Acroceridae and Nemestrinidae. Nevertheless the fork of R_{4+5} is greatly reduced or entirely absent in Eremochaetidae, and the anal lobe is somewhat reduced as well (e.g. MOSTOVSKI, 1997b).



Figs 1 - 3 Wings of Rhagionemestriini: 1) *Rhagionemestrius rapidus* USSATCHOV, 1968; 2) *Nagatomukha karabas* sp.nov.; 3) *Iberomosca ponomarenkoi* sp.nov.

Rhagionemestriini

Type genus. *Rhagionemestrius* USSATCHOV, 1968; Middle - Upper Jurassic; Kazakhstan.

Diagnosis. R_{2+3} straight, tip not approaching R_1 . R_5 runs into wing margin beyond apex. Fourth posterior cell open.

Genera included. *Rhagionemestrius* and *Nagatomukha* gen.nov. from the Jurassic of Kazakhstan, and *Iberomosca* gen.nov. from the Lower Cretaceous of Spain and Mongolia.

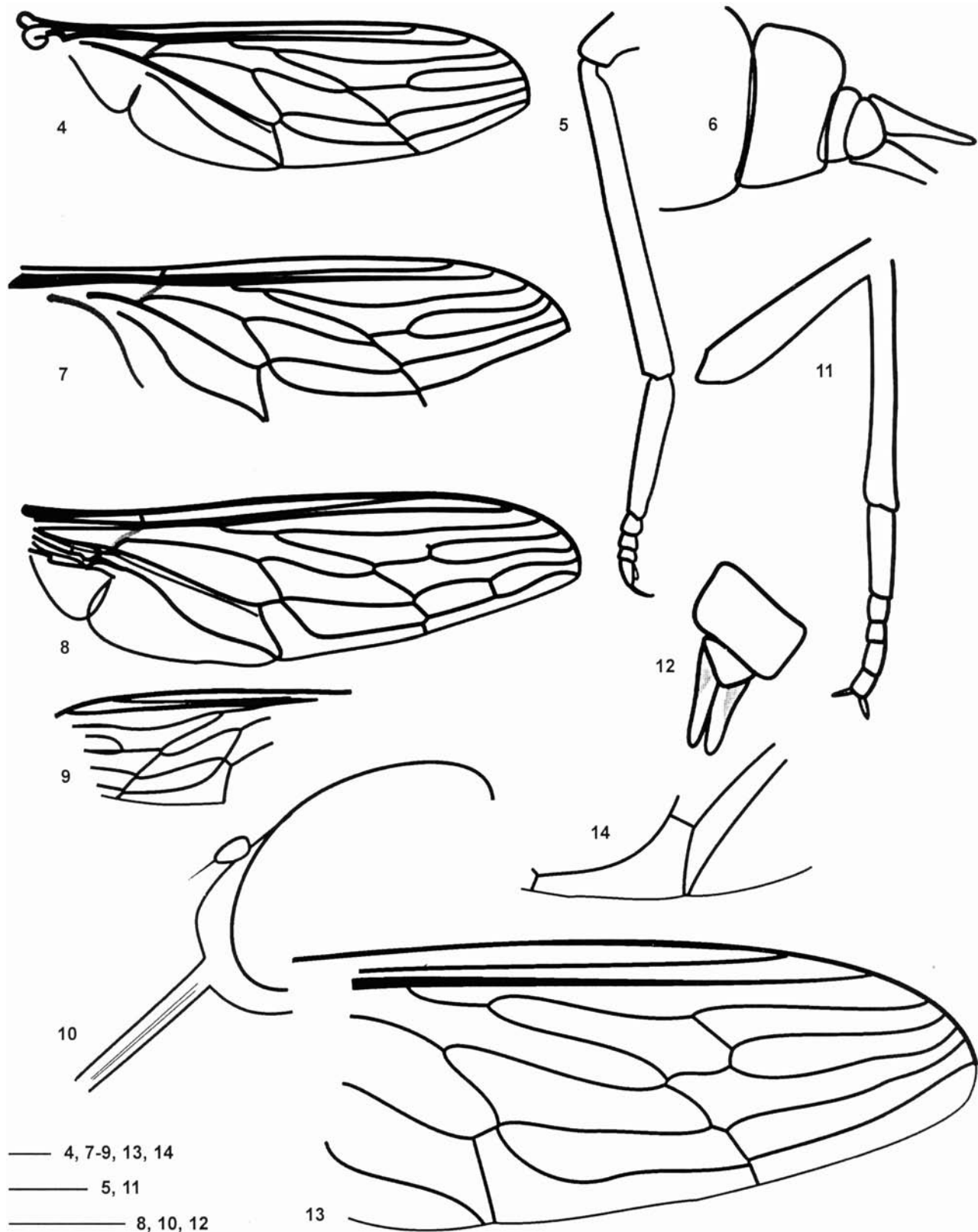
Remark. We restudied the holotype of *Rh. rapidus*

USSATCHOV, 1968, kept in the PI and discovered that C, Sc, and R_1 are not thickened as much as figured in the original paper, and the part of the wing blade between C and R_1 is not sclerotized. In fact, the costal vein becomes thinner beyond R_4 (Fig. 1).

Nagatomukha gen.nov.

Type species. *Nagatomukha karabas* sp.nov.; Middle - Upper Jurassic of Kazakhstan.

Diagnosis. RS_1 and RS_2 subequal. Transverse r-m



Figs 4 - 14 Details of fossil Nemestrinidae: 4 - 6) *Hirmoneura* (*Hirmoneura*?) *richterae* sp.nov., holotype: 4) wing; 5) hind leg; 6) tip of the abdomen; 7) *H. (H.?) elenae* sp.nov., wing; 8) *H. (Eohirmoneura) neli* sp.nov., wing; 9 - 12) *Prosoeca (Palembolus) saxea* sp.nov.: 9) wing fragment; 10) head in profile; 11) hind leg; 12) tip of the abdomen; 13) *Nemestrinus?* *incertus* sp.nov., holotype, wing; 14) *Nemestrinidae* incertae sedis, In. 44361, wing fragment. Scale bars: 1 mm.

absent, R_{4+5} and M_{1+2} fused. Basal part of M_2 very short. Diagonal vein is formed of RS, R_{4+5} , fused R_{4+5} and M_{1+2} , M_{1+2} beyond fusion, and M_2 . Anterior basal cell shorter

than posterior one. Discal cell elongated. Anal cell open.

Species included. Monobasic.

Comparison. The new genus differs from *Rha-*

gionemestrius in M_2 forming distal part of the diagonal vein, also in shorter R_5 , d elongated, discal cell longer, and ba shorter.

Etymology. The genus is named in honour of eminent Japanese dipterologist Dr. Akira NAGATOMI.

Nagatomukha karabas sp.nov.

Material examined. Holotype PI 206612024, part and counterpart of wings, and fragments of abdominal segments and tarsus, Kazakhstan, the locality of Karatau-Mikhailovka, Karabastau Fm.

Description (Figs 2, 15). RS_3 less than 1.5 times shorter than R_5 . The latter terminates just beyond wing apex. M_1 arched forwards. M_1 and M_2 parallel. Transverse m-cu between M_{3+4} and CuA. Tarsi pale, densely covered with light silky hairs. Claws wide, nearly parallel, strongly curved, with basal half light and apical half black. Abdominal tergites covered very short dark hairs and with dark contrast pattern.

Measurements, mm. Wing length 5.5, wing width 2.6.

Etymology. The species name is derived from Karabastau Formation.

Iberomosca gen.nov.

Type species. *Iberomosca kakoeima* sp.nov.; Lower Cretaceous of Spain.

Diagnosis. RS_1 shorter than RS_2 . Short transverse r-m present. Diagonal vein is formed of RS, R_{4+5} , M_{1+2} beyond r-m, and M_2 . Basal cells equal or nearly so. Discal cell not elongated. Transverse m-cu rather long, sigmoid. Anal cell closed, with point stalk.

Species included. Type species and *I. ponomarenkoi* sp.nov. from the Lower Cretaceous of Mongolia.

Comparison. The new genus differs from the other genera in presence of r-m, additionally from *Rhagionemestrius* in M_2 forming the diagonal vein distally, and from *Nagatomukha* gen.nov. in shorter discal cell and equal basal cells.

Etymology. Generic name is derived from Iberia, pre-Roman name of Spain, and *mosca* "fly" in Spanish.

Iberomosca kakoeima sp.nov.

Material examined. Holotype UB LC-34-EP a/b, part and counterpart of wings and body fragments, Spain, La Cabrera outcrop, Lower Cretaceous, "Calcaires i charophytes du Montsec" Fm.

Description (Fig. 16). Body and legs more or less light, rather densely covered with hairs. At least one tibia with wide transverse band. Dark elongated pterostigma above R_1 . RS_1 and RS_2 equal, RS_3 1.5 times as long as RS_2 . R_4 nearly straight. R_{4+5} and M_{1+2} angled at r-m. Transverse r-m just before discal cell mid-length. Basal sections of M_{1+2} and M_{3+4} subequal. M_1 nearly straight. M_2 slightly arched backwards. Intermedial vein connects M_3 with point of bifurcation M_{1+2} . Basal section of M_4

very short. Phragma at wing base distinct but poorly sclerotized. Distal portion of CuA arched. Anal lobe and alula poorly developed.

Measurements, mm. Wing length 6, wing width 1.9.

Etymology. Specific name is derived from *kakoeima* "poorly dressed" in Greek.

Iberomosca ponomarenkoi sp.nov.

Material examined. Holotype PI 355913786, impression of isolated wing, Mongolia, the locality of Bon-Tsagaan, outcrop 35, Hurilt Beds of Bon-Tsagaan Group.

Description (Fig. 3). RS_1 little shorter than RS_2 , RS_3 1.5 times as long as RS_2 . R_4 nearly straight. R_{4+5} and M_{1+2} angled at r-m. Transverse r-m just before discal cell mid-length. Basal section of M_{1+2} little shorter than that of M_{3+4} . M_{1+2} fork with long petiole. Posterior basal cell little longer and wider than anterior one. M_2 slightly arched backwards. Basal section of M_4 very short or entirely absent. Phragma at wing base distinct but not heavily sclerotized. Distal portion of CuA nearly straight. Wing membrane microtrichose. Pterostigma absent.

Measurements, mm. Wing length 6.4, wing width 2.

Comparison. *I. ponomarenkoi* sp.nov. differs from *I. kakoeima* sp.nov. in M_{1+2} fork petiolate, posterior basal cell longer and wider, distal portion of CuA nearly straight, and absence of pterostigma.

Etymology. The species is named in honour of eminent Russian palaeoentomologist Dr. A.G. PONOMARENKO.

Nemestrinidae MACQUART, 1834

Wing venation in nemestrinids is rather unstable (e.g. TIMON-DAVID & LEONIDE, 1968), so it is difficult to apply its features to separate species or even genera. It is necessary to keep in mind that any placement based only on venation may be somewhat incorrect. An excellent condition of the flies from Spanish localities is pure luck and allows one to avoid taxonomic inaccuracies.

Hirmoneurinae

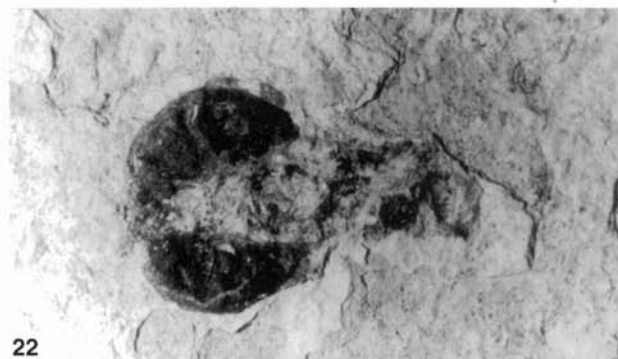
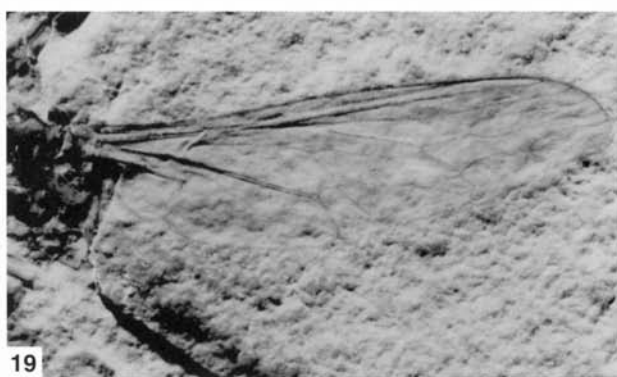
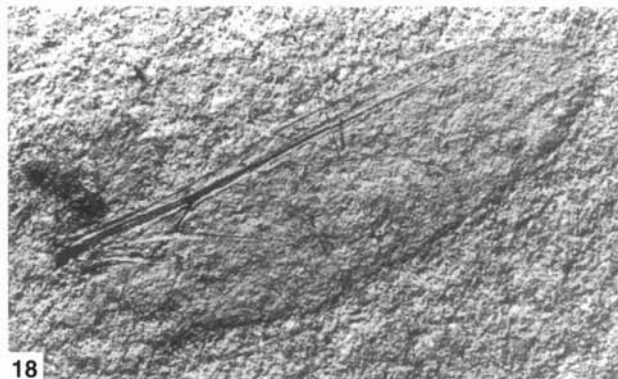
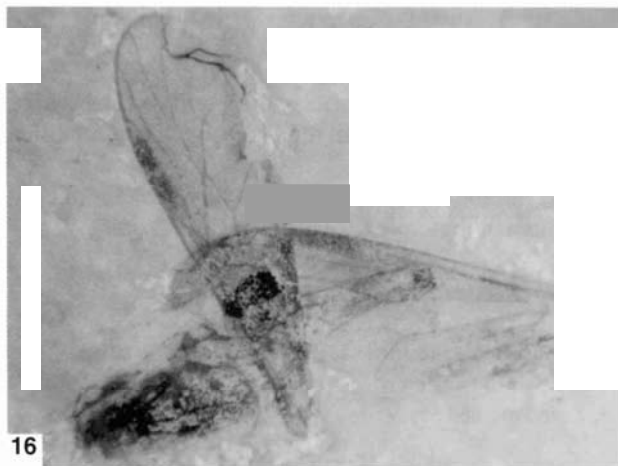
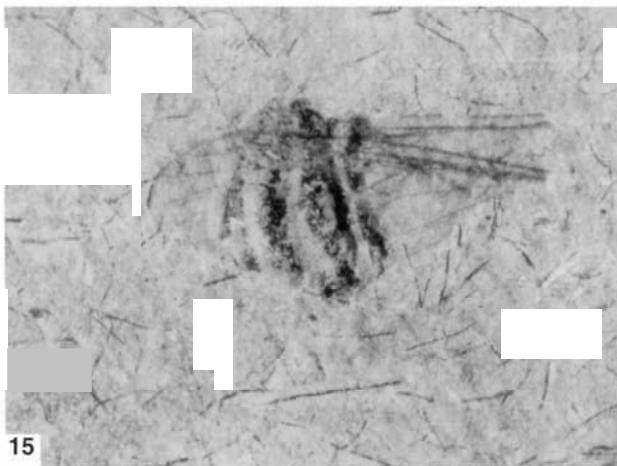
Hirmoneura MEIGEN, 1820

Hirmoneura (Hirmoneura?) richterae sp.nov.

Diptero de la familia de los Nemestrinidos: LACASA-RUIZ & MARTÍNEZ-DELCLÒS, 1986: 222, pl. 1, fig. 4.

Material examined. Holotype MNHN B48822 NB, female without head, right wing and some legs, Spain, La Pedrera outcrop, Lower Cretaceous, "Calcaires i charophytes du Montsec" Fm. Additional material. UB LC-2721-IEI-A/B, sex unknown (La Cabrera outcrop), LC-1964-IEI-NB, female (La Cabrera outcrop), LP-0022-IEI/G-A/B, sex unknown (La Pedrera outcrop).

Description (Figs 4–6, 17). Large flies, body entirely dark. Body covered with short hairs, more silky on tho-



Figs 15 - 22 New fossil Nemestrinoidea: 15) *Nagatomukha karabas* sp.nov.; 16) *Iberomosca kakoeima* sp.nov.; 17) *Hirmonaura* (*Hirmonaura*?) *richterae* sp.nov., specimen UB LC-2721-IEI; 18) *H.* (*H.*?) *elenae* sp.nov.; 19) *H.* (*Eohirmonaura*) *neli* sp.nov.; 20) *Prosoeca* (*Palembolus*) *saxea* sp.nov.; 21, 22) *Nemestrinus*? *incertus* sp.nov., (21) holotype, (22) specimen PI 3064/9690.

rax. Last abdominal tergite and cerci covered with extremely short hairs. Head as broad as thorax, little flattened. Eyes bare. Transverse r-m before apical fourth of discal

cell. Discal cell broader than fourth posterior cell. Anal cell narrowly open or nearly closed. First tarsomere of hind leg twice as long as other four combined. Three

spherical spermathecae and their ducts well pigmented.

Measurements, mm. Body length 12–15, wing length 9.5–10.5, wing width 2.8–3.2.

Comparison. The species differs from some living species in first tarsomere of hind leg longer, non-modified spermathecae.

Etymology. The species is named in honour of eminent Russian dipterologist Dr. V.A. RICHTER.

Hirmoneura (Hirmoneura?) *elenae* sp.nov.

Material examined. Holotype PI 421016381, part and counterpart of isolated wing, Transbaikalia, the locality of Baisa, Zaza Fm., bed 31.

Description (Figs 7, 18). Subcostal vein long, terminates distad of diagonal vein tip. RS_2 3.1 times as long as RS_3 . Transverse r-m in apical fourth of discal cell. M_{1+2} smoothly curved before m-m. M_4 smoothly curved backwards. CuP strongly curved rearwards. Anal cell as broad as, or even broader than, posterior basal cell, with maximal width at mid-length. Distinct sclerotized fold behind CuP. Alula broad.

Measurements, mm. Wing length 13.5, wing width 3.9.

Comparison. H. (H.?) *elenae* sp.nov. differs from H. (H.?) *richterae* sp.nov. in longer RS_2 , in broader anal cell, r-m shifted far distad of discal cell mid-length, and in larger size.

Etymology. The species is named in honour of Russian palaeontologist Elena D. LUKASHEVICH, the collector of the holotype.

Subgenus Eohirmoneura ROHDENDORF, 1968, stat.nov.

Type species. *Eohirmoneura carpenteri* ROHDENDORF, 1968; Middle – Upper Jurassic, Kazakhstan.

Diagnosis. R_4 with short stub just after bifurcation or R_4 angled. M_2 runs backwards before wing margin. Additional cross vein between M_1 and M_2 present. Fourth posterior cell somewhat widened in basal portion. Diagonal vein complete, zigzag shaped. Anal cell closed or nearly so.

Species included. H. (Eohirmoneura) *neli* sp.nov. besides the type species.

Comparison. Eohirmoneura differs from the subgenus Hirmoneurites COCKERELL from the Oligocene of the USA in incomplete cross vein between R_{2+3} and R_4 , M_2 bent apically. It differs from nominative subgenus in the shape of the diagonal vein and short stub at R_4 .

Hirmoneura (Eohirmoneura) *neli* sp.nov.

Diptero adulte, famille des Nemestrinidae: MARTÍNEZ-DELCLÒS & RUIZ DE LOIZAGA, 1993: 199, pl. 1, fig. 10.

Material examined. Holotype MNHN B48821 AIB, well preserved impression of wing, and partly thorax and legs, Spain, La Pedrera outcrop, Lower Cretaceous, "Calcaires à charophytes du Montsec" Fm.

Description (Figs 8, 19). Large flies with dark thorax, base of abdomen and legs except for apical tarsomeres which are paler. R_{4+5} fork more or less symmetrical in its base, R_4 without sudden break. Cell p_4 narrows distally, M_4 strongly curved. CuP sigmoid, anal cell widens at mid-length. Alula broad and short. Thorax, first abdominal tergites and at least femora covered with short hairs.

Measurements, mm. Wing length 14, wing width 4.

Comparison. The new species differs from H. (E.) *carpenteri* in R_{4+5} fork more or less symmetrical, R_4 smoothly curved, M_4 strongly curved, anal cell widened at mid-length, and larger in size.

Etymology. The species is named in honour of French palaeontologist Dr. A. NEL.

Nemestrininae

Prosoeca SCHINER, 1867

Prosoeca (Palembolus) *saxea* sp.nov.

Material examined. Holotype LH ADR-0040-IB, impression of well preserved female, Spain, the locality of Las Hoyas, Lower Cretaceous, Barremian. The type specimen is from the collection of Mr. Armando Díaz-Romeral, Museo de Cuenca (Cuenca, Spain) and is deposited in the Unidad de Paleontología, Universidad Autónoma de Madrid.

Description (Figs 9–12, 20). Large dark flies, fore and mid tibiae and tarsi paler, thorax almost black. Eyes bare. Face slightly prominent in profile. Proboscis obviously long, at least as long as head. Palps light brown, clavate. Third antennal segment oval-shaped, arista as long as third segment. Subcostal vein relatively short, terminates at level of R_{4+5} bifurcation and diagonal vein tip, or so. RS_2 2 times as long as RS_3 and RS_1 . Transverse r-m before apical fourth of discal cell. Discal cell rather long and narrow, as broad as fourth posterior cell, or so. M_4 markedly curved backwards. First tarsomere of hind leg as long as other four combined.

Measurements, mm. Body length 12, wing length 7.8, wing width 2.6.

Comparison. The species differs from *P. (Palembolus) florigerus* (SCUDDER) in Sc and RS_2 shorter. Sc terminates far beyond both R_{4+5} bifurcation and diagonal vein tip in *P. (P.) florigerus*. M_4 is more strongly curved in the new species.

Discussion. In the key to world genera (BERNARDI 1973b) the new species easily runs to the genus *Prosoeca*. The distribution of the genus *Prosoeca* is restricted now to South Africa. The fossil species *Palembolus florigerus* described from the Oligocene of the USA (SCUDDER, 1878) was also transferred here and considered as a subgenus (BEQUAERT & CARPENTER 1936). However BERNARDI (1973b) preferred to keep *Palembolus* as a separate genus, based only on zoogeographical evidence. Both *P. (P.) florigerus* and *P. (P.) saxea* sp.nov. differ from other species of the genus in their quite prominent face, although *P. (P.) saxea* sp.nov. resembles them in wing venation. The genus *Florinemestrius* described

from the Yixian Fm. (REN 1998a) also runs to the genus *Prosoeca*. Meantime *Florinemestrius* differs from the subgenus *Palembolus* in having a face that is not prominent and at the same time differs from the nominative subgenus in the head being as broad as the thorax and the legs slender. Additional transverse veins occur neither in *Palembolus* nor in *Prosoeca* s. str. On balance, one should keep *Florinemestrius* as a separate genus closely related to *Prosoeca*.

Etymology. Specific name is derived from *saxea* "stony" in Latin.

Nemestrinus LATREILLE, 1802

Nemestrinus? incertus sp.nov.

Material examined. Holotype PI 3064/9929, part and counterpart of wing without basal portion, Transbaikalia, the locality of Baissa, Lower Cretaceous, Zaza Fm., bed 31. Additional material. PI 3064/9690, impression of head with fragments of antennae and proboscis from the same locality and bed.

Description (Figs 13, 21, 22). Frons dark, densely covered with short hairs. Frons above antennae 0.2 times as broad as head, becomes wider upwards. Third antennal segment bulb-like. Length of second and third antennal segments combined equal to that of frons above antennae. Clypeal swelling covered with short hairs. Proboscis long. At least fore tibiae covered with short black robust hairs. Transverse r-m very short. $M_{1+2}+M_3$ stalk little longer than r-m. Free part of M_3 very short. M_4 strongly curved backwards at base, then runs nearly parallel to hind margin of wing.

Measurements, mm. Head diameter 5, wing length near 14, wing width 5.

Remark. The proper position of the new species is unknown. The wing venation resembles that of some species of *Nemestrinus* lacking reticulation (e.g. *N. caucasicus* (FISCHER)) although characters available do not allow one to compare this species with living ones.

Etymology. Specific name is derived from *incertus* "doubtful" in Latin.

Nemestrinidae incertae sedis

There is one more specimen of nemestrinid flies from the Solnhofen locality (Blumenberg near Eichstatt, Bavaria, Germany, Tithonian) found in the collection of the British Museum of Natural History (part and counterpart, In. 44361). This is the second record of *Nemestrinidae* from the Upper Jurassic of Germany (HANDLIRSCH 1906-08; ANSORGE & MOSTOVSKI in press). The specimen is a nearly complete fly with a broad stout body, the head is hemispherical, as broad as the thorax and the abdomen is densely covered with short hairs. Body length is 15 mm, wing length is approximately 10.5 mm. It is impossible to assign this specimen to any known genus or even subfamily, due to its poor condition. However, it differs from *Prohirmoneura jurassica* HANDLIRSCH described from the same locality and other fossil nemestrinids in the form of its anal cell (Fig. 14). The anal cell may resemble

those of some bee flies, but the last medial vein running in its distal portion parallel to the hind margin of the wing and the presence of the tip of diagonal vein prove the placement of the specimen in question within Nemestrinidae. Only two undoubted brachycerans have been found in Solnhofen, and both of them are nemestrinids. It is remarkable and might be explained just by sampling bias, although there is only one true fly (PI 107211) that most probably belongs to Nemestrinidae collected in the basalmost Lower Cretaceous deposits of the south-eastern Mongolian locality of Tushilge-Uul, near Sainshand.

Biological and palaeobiological inferences

Adults of extant nemestrinids can be found hovering, feeding on flowers or resting in the sun. Generally, tangle-veined flies inhabit arid and semi-arid hot areas. Their larvae are internal parasites of either grasshoppers or scarabaeid beetles, and usually take one year to develop (e.g. LEONIDE 1964a, b; BERNARDI 1973b). The first instar is planidial and searches out the host. The larvae pass through four instars before pupating.

It has been established that some of the ancient nemestrinids possessed the long proboscis. These are *Protonemestrius*, *Florinemestrius*, *Prosoeca* subgen. *Palembolus*, and *Nemestrinus? incertus* sp.nov. Judging from the prominent face, or expressed clypeal swelling in some nemestrinids the cibarial pump was well developed. The flies could presumably feed at the bennettite "flowers" or angiosperm flowers, sucking or licking the liquid exudates (MOSTOVSKI 1998; REN 1998b; REN & HONG 1998). Palaeobotanists believe that at least some bennettites could already have acquired entomophily; and they have reported some peculiar organs capable of functioning as nectaries (MEYEN 1986; KRASSILOV 1989). The flies could also act as pollinators for these plants. The quite large pollen of Bennettitales could be carried between the hairs covering the nemestrinid body. It is necessary to point out that some other Mesozoic flies could be connected with flower-bearing plants. These are Apioceridae from the localities of Baissa, Bon-Tsagaan, and Khetana in the Russian Far East, and the Yixian Fm., Tabanidae from the Middle Purbeck Beds, Las Hoyas, Yixian Fm., Baissa, and Crato Fm. in Brazil, and scarce Bombyliidae. Theoretically, various Jurassic and Cretaceous Archisargoidea cannot be excluded from this list.

Regarding the family Rhagionemestriidae, biological data are scarce and insufficient. The only species of the genus *Heterostomus* is known from Chile, four species of *Exeretoneura* are found in Australia and Tasmania. The biology and immature stages of *Heterostomus* are not known. As mentioned above, the larva of *Exeretoneura* and its biology are similar to those of Coenomyiinae (PALMER & YEATES 1998). Fossil Rhagionemestriidae were obviously able to hover judging from the wing blade structure.

Acknowledgements

The authors would like to express sincere thanks to Dr. A. NEL (MNHN), Dr. D. GRIMALDI (American Muse-

um of Natural History, New York), Mr A.J. Ross (British Museum of Natural History, London), Mr **Armando DIAZ-ROMERAL** (Museo de Cuenca, Cuenca) for loan fossil specimens, Dr. A.L. OZEROV (Zoological Museum of Moscow State University) for loan recent material in his care for comparative study, and Dr. J. ANSORGE (Institut für Geologische Wissenschaften, Greifswald) for information about some fossil Nemestrinoidea. The senior author is also grateful to Dr. V.A. RICHTER (Zoological Institute, St.-Petersburg) and Dr. D.E. SHCHERBAKOV (PI) for fruitful discussions and consultations. Expeditions to the locality of **Baissa** were arranged in 1997 and 1998 by Mr P. VRSANSKY (Comenius University, Bratislava) under the projects EURUS'97 and AMBA supported by the UNESCO. The authors are much obliged to photographer A. MAZIN (PI), Mrs. T. OUDATCHINA (MOSCOW), and Mr P. VRSANSKY for technical assistance. The study was financially supported by DGES-0061 I to XMD; Paleontological Society (PaSIRP, USA, grant via the U.S. CRDF for the FSU no. RGO-822-7) and Federal Central Programme for Science and Technology (project 4) and Russian Academy of Sciences, to MBM, and ESF Project "Fossil Insects" to both authors.

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Manuscript received: 15. 3. 2000