A brief review of brachycerous flies (Diptera, Brachycera) in the Mesozoic, with descriptions of some curious taxa

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MOSTOVSKI, M.B. 1999. A brief review of brachycerous flies (Diptera, Brachycera) in the Mesozoic, with descriptions of some curious taxa. In: AMBA/AM/PFICM98/1.99: 103-110. Brachycerous flies from Mesozoic deposits are reviewed. New taxa of Stratiomyidae (Beridinae), Xylomyidae, Xylophagidae (Coenomyiinae) and Empididae (Protempidinae) are described from the Jurassic of Kazakhstan and Mongolia, and from the Lower Cretaceous of Spain.

Key words: Diptera, Brachycera, Mesozoic, evolution, new taxa.

Fossils of brachycerous flies have been recorded in deposits of all continents except for the Antarctic (EVENHUIS, 1994). The palaeontological record of brachycerans begins in the Early-Middle Triassic (KRZEMINSKI, 1998). The earliest brachyceran is represented by an isolated wing from the Early-Middle Triassic deposits in France; it possesses the most generalized venation. In the Early Jurassic, not later than the Sinemurian, the flies diverged into Stratiomyomorpha and Asilomorpha. The first Stratiomyomorpha belonging to the family Oligophrynidae have been found in both Europe (ANSORGE & KRZEMINSKI, 1994) and Asia (ROHDENDORF, 1962). The position of the family Alinkidae described from the Upper Triassic of North America and originally placed within Brachycera (KRZEMINSKI, 1992) remains debatable (SHCHERBAKOV et al., 1995).

Rapid radiation of the brachycerous flies started in the Toarcian or so. Representatives of at least four lineages (Tabanoidea, Xylophagoidea, Nemestrinoidea and Empidoidea) are recorded in Toarcian deposits of Grimmen, Germany. Both Nemestrinoidea and Empidoidea are represented by extinct subfamilies, Archinemestriinae and Protempidinae respectively. Diverse Rhagionidae are widespread and found in Laurasian (ANSORGE, 1996; KOVALEV, 1981) and Gondwanan deposits. Archisargoidea, another lineage of brachyceran, are recorded since the Early-Middle Jurassic of China (HONG, 1983).

In the Middle and Late Jurassic brachycerous flies diverged into many families, i.e. Apystomyiidae?, Archocyrtidae, Asilidae, Eremochaetidae, Hilarimorphidae, Kovalevisargidae, Mythicomyiidae, Nemestrinidae Hirmoneurinae, Protapioceridae, Rhagionempididae, Scenopinidae, Stratiomyidae, Tabanidae, Therevidae, Vermileonidae?, Xylomyidae, Xylophagidae, Coenomiinae. The family Eomyiidae erected by ROHDENDORF (1962) for his monobasic genus known only from a single poorly preserved specimen from the Jurassic deposits in Kazakhstan. Its true familial placement is still not clear. Another enigmatic family is Palaeophoridae with the single monobasic genus included. Re-examination of *Palaeophora ancestrix* (ROHD., 1938) holotype confirmed HENNIG's (1954) opinion that this fly is not close to phorids. Vermileonidae from the Middle-Upper Jurassic/Lower Cretaceous seem to be rather plesiomorphic if compared with the recent representatives of the family. Nevertheless, such an early separation from rhagionid-like ancestor is supported by analysis of the male genitalia muscles of recent vermileonids (OVTSHINNIKOVA, 1997).

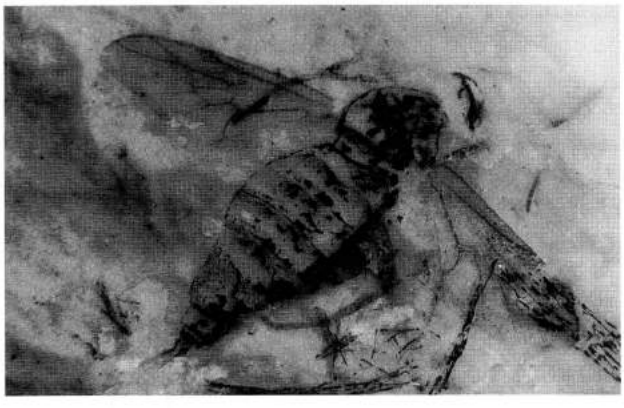
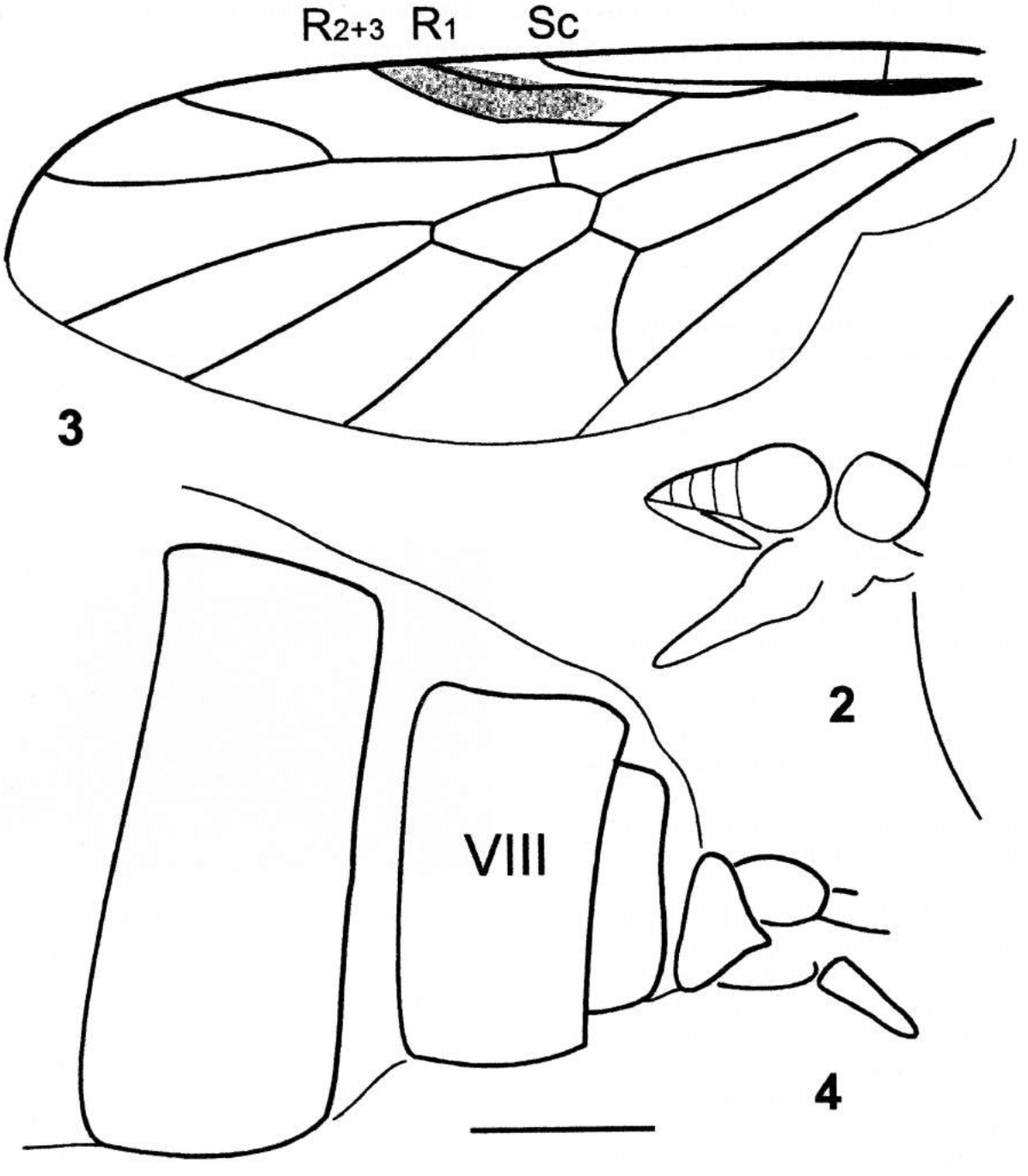


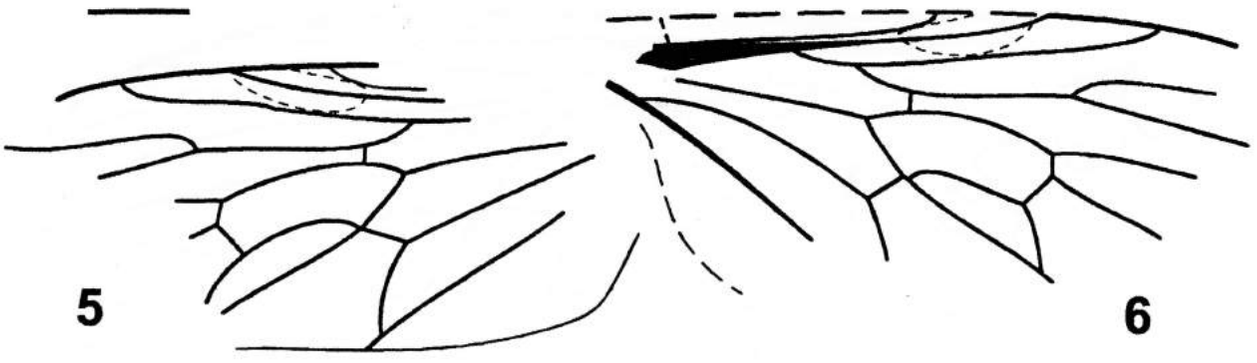
Fig. 1: *Montsecia martinezdelclosi* sp. nov., holotype UB, LP-043-XMD-A/B, - impression as it appears (x 20).



Figs 2 - 4: *Montsecia martinezdelclosi* sp. nov., holotype UB, LP-043-XMD-A/B. 2 - antennae; 3 - wing; 4 - tip of abdomen. Scale bar 0.5 mm in all figures.

Brachycerous flies form about 10% of the non-aquatic Diptera, and extinct families up to 30% in the assemblage of the most comprehensive Karabastau Formation (the upper Callovian - Kimmeridgian) in the southern Kazakhstan. The Rhagionidae are dominant in Jurassic oryctocenoses and may form more than 52% of all Brachycera. Primitive forms with annulated antennal flagellum dominate among rhagionids.

The transition from Jurassic to Cretaceous assemblages was accompanied by the appearance and disappearance of high-ranking taxa, and was obviously asynchronous. The fauna of the Yixian Formation includes both typically Jurassic and Cretaceous elements, i.e. *Protonemestrius*, Protempidinae, eremochaetids of nominative subfamily, and Tabanidae, *Protapiocera* respectively. *Protonemestrius*, *Palaepangonius*, *Eopangonius*,



Figs. 5, 6: *Xylomya? shcherbakovi* sp. nov., holotype PI 2784/131, left and right wings respectively.

Protapiocera are supposed to be connected with plants possessing flower-like organs as pollinators and nectar-feeders (MOSTOVSKI, 1998; REN, 1998). The age of the Yixian Formation is supposed to be the latest Jurassic (REN et al., 1997), though the Early Cretaceous age can not be excluded (SMITH et al., 1995). The fauna of Turga Formation comprises both Eremochaetinae and Platypezoidea beside to Rhagionidae and true Empididae, whereas absolute dating allow us to adopt the Early Cretaceous age of Turga deposits (136-126 Myr, Dr E. TRUSOVA pers. comm.).

Brachyceran assemblages of an Early Cretaceous type are known mainly from Eurasia and South America (Brazil). The percentage of brachycerous flies among the non-aquatic Diptera rose to 30% (in the locality of Baissa), whilst that of extinct families fell to 6.7 - 16%. The Phoromorpha and advanced Empididae were dominant, and Rhagionidae became more advanced and more similar to the recent forms. The Platypezidae are found in Lower Cretaceous deposits of Europe (the Middle Purbeck beds in England) and Asia (China, Mongolia and Transbaikalia), whereas Ironomyiidae (Sinolestinae) are recorded only in the Lower Cretaceous of Asia (MOSTOVSKI, 1995a, b). Eremochaetinae were substituted by more advanced Eremomukhinae (MOSTOVSKI, 1997). The horseflies were not rare in the Early Cretaceous. Several specimens of the Tabanidae are found in Gondwanan (Brazil) (MARTINS-NETO & KUCERA-SANTOS, 1994) and Laurasian (England, Spain) deposits (CORAM et al., 1995). Early and Late Cretaceous faunas can only be separated with difficulty. Assemblages of the latter are known from Europe, Asia and North America, mainly from fossil resins. A few brachycerous flies (empidids and a ?tabanid) have also been found in South Africa. The Empididae are dominant (up to 45% of Brachycera) and the Phoromorpha subdominant. The subfamily Prioriphorinae (Phoridae) is characteristic of the Late Cretaceous (BROWN & PIKE, 1990; MOSTOVSKI, 1996; 1999 GRIMALDI & CUMMING, 1999). The transition between these faunas seems to occur not later than in the Aptian-Albian. Brachyceran assemblage of Alavese amber in Spain (Middle Aptian-Lower Albian) demonstrates advanced features, i.e. a large amount of empidids with admixture of Rhagionidae, Prioriphorinae and Eremochaetidae (ARILLO & MOSTOVSKI, in press). Eremochaetids from Alavese and New Jersey ambers (GRIMALDI & CUMMING, 1999) may be allocated to a new subfamily of their own. The Syrphoidea and Schizophora appeared in the Santonian-Maastrichtian, but they were extremely rare.

The brachycerous faunas were more advanced in the Mesozoic when compared with insect faunas as a whole. The percentage of extinct families is less than that among other Insecta in the Late Mesozoic (RASNITSYN, 1988).

Descriptions

The type specimens of the species described below are housed in the University of Barcelona, Spain (UB) and Paleontological Institute, Russia (PI).

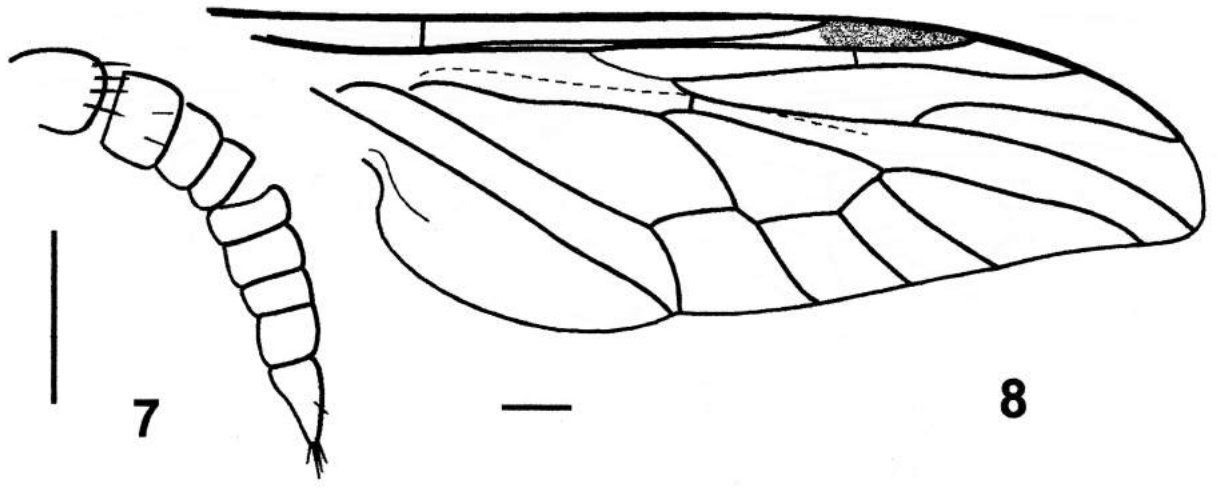
Stratiomyidae

Beridinae

Montsecia gen. nov.

Type species. *Montsecia martinezdelclosi* sp. nov.

Diagnosis. Length of scape and pedicel subequal to their width. Pedicel broader than scape.



Figs. 7, 8: *Ganeopteromyia calypso* sp. nov., holotype PI 2066/1419. 6 - antenna; 7 - wing.

Flagellum unclear annulated, as broad as pedicel at base. Scutellum without spines. Abdomen little broader than thorax, more or less elongated. Cerci two-segmented, distal segment not shorter than basal, rather thin.

Composition. Monobasic.

Comparison. Differs from all other Beridinae except *Allognosta* Osten Sacken in scutellum without spines. Differs from *Allognosta* in longer and thinner distal segment of cerci and unclear annulation of antennal flagellum.

Remarks. Soldier-flies of the subfamily Beridinae are considered to be the most primitive among Stratiomyidae. Beridinae are recorded in Jurassic and Cretaceous deposits of Europe and Asia (Karabastau Formation, Zaza Formation (the Neocomian of Transbaikalia), Ola Formation (the Senomanian - Turonian of Russian Far East)). Numerous larvae from the locality of Montsec were allocated to Stratiomyidae (WHALLEY & JARZEMBOWSKI, 1985).

Etymology. From the type locality.

Montsecia martinezdelclosi sp. nov.

Type locality and horizon. Lerida Province, Spain; Calcaires a charophytes du Montsec Formation.

Holotype UB LP-043-XMD-A/B, part and counterpart of well-preserved female from La Pedrera outcrop.

Description. Flies with dark body and legs paler, body length 5 mm (Fig. 1). Head not broader than thorax, slightly flattened antero-posteriorly. Antennae longer than head. Flagellum 2.5 times as long as scape and pedicel combined (Fig. 2). Basal ring of flagellum distinct. Flagellum stick-like apically. Thorax covered with rare fine hairs. Legs slender with short hairs. Costal vein ends near wing tip (Fig. 3). Costal section between R2+3 and R1 shorter than that between R1 and Sc. Anal lobe and alula weakly developed. Wing membrane densely microtrichose. Pterostigma well developed. Wing length 3 mm, width 1.1 mm. Abdominal segments covered with rare fine hairs. X tergite triangular, slightly concave at hind margins (Fig. 4). Basal segment of cercus barrel-shaped with hairs longer than those on abdominal segments. Hairs on distal segment of cercus shorter.

Etymology. In honour of Spain paleoentomologist Dr X. MARTINEZ-DELCLOS.

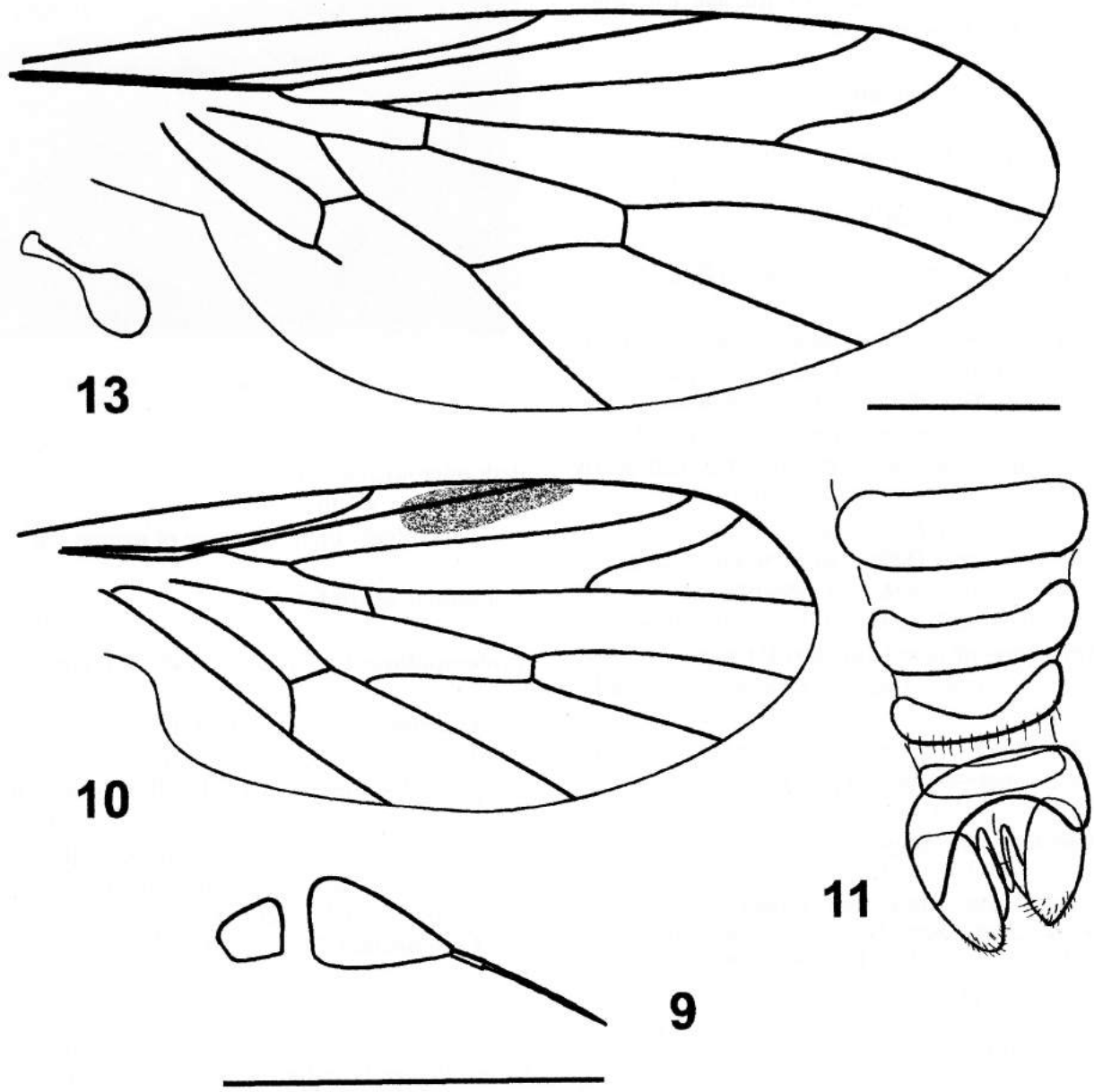
Xylomyidae (= Solvidae)

Xylomya? shcherbakovi sp. nov.

Type locality and horizon. Karatau locality, southern Kazakhstan; Middle - Upper Jurassic, Karabastau Formation.

Holotype PI 2784/131, incomplete body with wings.

Description. Pale-brown coloured flies of moderate size, body length approx. 5 mm. Hind femora not modified, unarmed. R1 terminates little basal of fork of R4+5 and tip of discal cell (Figs. 5, 6). R4+5 fork not broad. Costal sections between Sc and R1, and R1 and R2+3 subequal. RS originates at midlength of anterior basal cell. rm in basal quarter of discal cell. Discal cell 1.5 times as broad as m3 cell. M1 nearly straight. mcu 2.25 times as long as rm, runs to basal part of M3+4 at point or just before M3+4 fork. Anal cell petiolate. Wing membrane



Figs. 9-11, 13: New fossil Empididae. 9-11 - *Homalocnemimus abjugatus* sp. nov., holotype PI 2997/996(1002). 9 - antenna; 10 - wing; 11 - male terminalia; 13 - *Protoreogeton admirabilis* sp. nov., holotype PI 3791/2859 - wing and halter.

entirly microtrichose, veins without any hairs or setae. Pterostigma pale, but distinct. Wing length approx. 3 mm, width 1.1 mm.

Comparison. Differs from other species of the genus *Xylomya* (including those known from the Baltic amber (HENNIG, 1967)) in the point of origin of RS, presence of pale pterostigma, absence from basal portion of M4. Differs from *X. inornata* Melander from the Oligocene of Florissant in smaller size and body paler.

Remarks. The new species can not be identified as *Xylomya* undoubtedly, because the structure of palpi, genitalia are still unknown as well as some other features. *X.? shcherbakovi* similar to species of the genus *Dialysis* WALKER (?=*Napemyia* WEBB) in wing venation generally, but differs in shorter R1 and longer costal section between R1 and R2+3. The new species differs from *Zhangsolva cupressa* (ZHANG) (Xylophagidae, Pantophthalminae ?=Zhangsolvidae NAGATOMI ET YANG) in longer fork of R4+5 which is not broad, nearly straight M1, and smaller size; differs from species of Rachiceridae with similar venation in transverse rm in the basal quarter of discal cell, broader discal cell, and longer costal section between R1 and R2+3.

Etymology. In honour of Russian paleoentomologist Dr D. SHCHERBAKOV.

Xylophagidae sensu lato

Coenomyiinae WESTWOOD, 1840

Ganeopteromyia gen. nov.

Type species. *Ganeopteromyia calypso* sp. nov.

Diagnosis. Flagellum tapered, subdivided into eight homonomous rings. Basal ring is equal to pedicel in width. Tips of R1 and R2+3 not drawn together. R4 not much curved. Transverse rm basad of Sc tip. Discal cell broadened distally. Anal cell nearly closed.

Composition. Monobasic.

Comparison. Differs from recent *Coenomyia* LATREILLE, *Anacanthaspis* ROEDER, *Arthropeas* LOEW, *Odontosabula* MATSUMURA in basal position of rm, shape of discal cell and R4 more smoothly curved. Differs from the two former also in smaller pedicel.

Etymology. From γανορ Greek – beauty, πτερυξ Greek - wing, and μυια Greek - fly.

***Ganeopteromyia calypso* sp. nov.**

Type locality and horizon. Karatau locality, southern Kazakhstan; Middle-Upper Jurassic, Karabastau Formation.

Holotype PI 2066/1419, impression of wing, antennae and body fragments.

Description. Body light brown, femora little darker. Thorax, legs and abdomen covered with rather dense and long dark hairs. Pedicel bears rather long hairs apically (Fig. 7). Flagellum with rare hairs and fascicle of long hairs at tip. Costal vein circumambient, thickened anteriorly (Fig. 8). Costal sections Sc-R1 and R1-R2+3 are subequal. Base of R and R1 with rare setae from above, not longer than those at costal vein. RS stem weakly sclerotized. RS2 thrice shorter RS1. Short transverse vein between R1 and R2+3 beneath pterostigma. rm at very base of discal cell. Basal section of M3+4 much longer than that of M1+2. Distal section of M3+4 short. M1 hardly sinuate, M2, M3 ? M4 parallel, slightly arched backward. mcu nearly parallel to hind margin of wing. Posterior basal cell longer and broader than anterior one. Anal lobe well developed. Dark brown, nearly black pterostigma between Sc and R1 tips. Wing membrane densely covered with dark microtrichiae. Alula not well developed. Wing length 7 mm, width 2 mm.

Fig. 12: *Protoreogeton admirabilis* sp. nov., holotype PI 3791/2859. 12 - impression as it appears (x 23).

Etymology. From the name of nymph Calypso.

Empididae sensu lato

Protempidinae USSATCHOV, 1968, stat. nov.

Diagnosis. Proboscis short. Fore legs not elongated. Costal vein circumambient. Subcostal vein complete. R4 present. Discal cell present. Three medial veins. Anal cell always closed, very long or shorter, but CuA never recurrent. Hypopygium symmetrical. Gonopods two-segmented. Basimers not fused. Male genitalia seem to be not complex.

Composition. *Protempis* USSATCHOV, *Helempis* REN, *Homalocnemimus* gen. nov., *Protoreogeton* gen. nov.

Remark. The structure of prosternum is not known in details, but it appears to be weakly developed.

***Homalocnemimus* gen. nov.**

Type species. *Homalocnemimus abjugatus* sp. nov.

Diagnosis. First flegellomere conical, 2 times as long as broad (Fig. 9). Arista stick-like, as long as first flagellomere, with short basal subsegment. Intermedial vein long, runs into M3+4 at level of rm. Anal cell with long petiole. Axillar lobe moderately developed. Male genitalia not modified.

Composition. Monobasic.

Comparison. Differs from *Protempis* in first flagellomere shorter, arista and intermedial vein longer. Differs from *Helempis* in general habitus and intermedial vein longer.

Remarks. The new genus is similar in the wing venation to the recent *Homalocnemis* PHILIPPI from the southern Hemisphere, but differs in first flagellomere shorter and male genitalia not modified. Insufficiently preserved specimens PI 2066/1597 and 2997/4762 may be also allocated to this genus.

Etymology. From the genus Homalocnemis and μτμορ Greek - imitator.

Homalocnemimus abjugatus sp. nov.

Type locality and horizon. Karatau locality, southern Kazakhstan; Middle-Upper Jurassic, Karabastau Formation.

Holotype PI 2997/996(1002), part and counterpart of well preserved male. Paratypes PI 2239/2172, 2554/1131, 2997/3457, 2997/3492, males.

Description. Small (2.8-3.3 mm) dark flies, antennae and legs light brown. R5 ends at wing tip (Fig. 10). Medial veins nearly straight. Pterostigma pale, mainly below R1. Wing length 2.0-2.2 mm, width 0.8-0.9 mm. Length of V - VIII tergites diminish gradually (Fig. 11). VI tergite with trapezoid incision and VII tergite with broad triangle incision at fore margin, the latter with hairs at hind margin. VIII tergite parallel-sided. Rear margin of epandrium semi-rounded. Basimers oval in shape from above, with rather straight upper and strongly convex lower margin in profile, 2 times as long as broad, with rather long robust hairs in apical third. Distimers 1.5 times as long as basimers, little thickened, articulated with basimers in end of second third of latter.

Etymology. From abjugatus Latin - divorced.

Protoreogeton gen. nov.

Type species. *Protoreogeton admirabilis* sp. nov.

Diagnosis. First flagellomere elongated conical, 2.3 times as long as broad. Arista 1.5 times as short as first flagellomere, with short basal segment. Intermedial vein not long, runs into M3+4 distad of rm (Fig. 13). Anal cell rather short, but CuA not recurrent. CuP incomplete. Axillar lobe poorly developed. Male genitalia not enlarged.

Composition. Monobasic.

Comparison. Differs from other protempidine genera in much shorter anal cell.

Etymology. From the genus Oreogeton.

Protoreogeton admirabilis sp. nov.

Type locality and horizon. Bakhar locality, Bayan-Hongor Aymag, Mongolia; Middle Jurassic, Ortsag beds of Bakhar Group.

Holotype PI 3791/2859, part and counterpart of male from 208/4 outcrop.

Description. Small (3.7 mm) dark flies (Fig. 12). R5 ends just behind wing tip. M1 arched forward. Posterior basal cell shorter. Pterostigma very pale, below R1. Halters pale brown. Wing length 2.8 mm, width 1.1 mm.

Etymology. From admirabilis Latin - admirable.

Acknowledgments

I would like to express my sincere thanks to all my collegues from Arthropods Laboratory (PI), Dr E. TRUSOVA (St.-Petersburg, Russia), Dr B. STUCKENBERG (Pietermaritzburg, South Africa) for practical help and fruitful consultations. I am grateful to Dr J. ANSORGE (Greifswald, Germany), Dr A. ARILLO (Madrid, Spain), Mr R. CORAM (Swanage, UK), Dr D. GRIMALDI (New York, USA), Dr E. JARZEMBOWSKI (Maidstone, UK), Dr W. KRZEMINSKI (Krakow, Poland), Dr X. MARTINEZ-DELCLOS (Barselona, Spain), Dr A. NEL (Paris, France), Mr A. ROSS (London, UK) for loan specimens and providing helpful information about fossils of brachycerous flies. I am much indebt to Mrs T. OUDATCHINA for technical assistance. This study was supported financially by the ISF grant a97-181, the Geologists' Association (UK), ESF Project "Fossil Insects" and Paleontological Society (USA, PalSIRP, grant ? RGO-638 (B) via CRDF).

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