

# Brachyceran assemblages (Insecta: Diptera) as indicators of terrestrial palaeoenvironments in the Late Mesozoic

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## Introduction

Brachyceran flies are characterized by their high diversity, rapid evolution, broad distribution and rather frequent occurrence in fine-grained lacustrine sediments and in fossilised resins, but rarely in marine deposits. The diversification of brachyceran Diptera started during the Early Jurassic and continued successfully over the Middle–Late Jurassic, Cretaceous and the Cainozoic (Blagoderov *et al.* 2002). The confinement of brachyceran fly taxa to particular deposits, regions and time intervals make these flies useful in biostratigraphy and correlation of non-marine deposits. Indeed, several levels can be traced during the Jurassic and Cretaceous, where brachyceran faunas changed considerably. The stratigraphic position of these levels is sometimes unclear, and their confident correlation with units and boundaries of the International Stratigraphic Chart (Ogg *et al.* 2008) is not always possible. Alternatively, the composition of Mesozoic brachyceran faunas seems to be partially influenced by changing local or regional palaeoenvironments. Although there are some extinct families, most are extant. This presents an opportunity to use presumed ecological characteristics of their representatives for reconstructing palaeoenvironments at sites of their burial (e.g. Coram *et al.* 2000).

## Material

Over 1000 brachyceran compression fossils and inclusions in fossilised resins from more than 60 Jurassic and Cretaceous localities worldwide have been examined (Figs 1, 2). Assemblages from the following oryctocoenoses (revealed death assemblages) have been considered the most representative and have been analysed numerically for the purpose of this study (Fig. 3): Karatau-Mikhailovka (southern Kazakhstan; Callovian–Kimmeridgian), ‘basalmost Cretaceous of Mongolia’ (several localities of similar age), Purbeck and Wealden (England; Berriasian–Barremian), Baissa (Transbaikalia; Valanginian–Hauterivian), Bon-Tsagaan (Mongolia; Barremian–Aptian), Obeshchayushchiy (Russian northern Far East; Cenomanian), Orapa (Botswana; Cenomanian–Turonian). Brief characteristics of localities and further references are provided elsewhere (Rayner *et al.* 1996; Zherikhin *et al.* 1999; Mostovski & Martínez-Delclòs 2000; Mostovski *et al.* 2000; Rasnitsyn & Quicke 2002; Brothers & Rasnitsyn 2003; Gernon *et al.* 2009). The figured specimens are deposited in the collections of the

Paleontological Institute, Russian Academy of Sciences, Moscow (PIN), and the Bernard Price Institute for Palaeontological Research, University of Witwatersrand, Johannesburg (BP).

## Results

### Karatau-Mikhailovka

This locality yielded almost 500 identifiable remains of brachyceran flies that belong to the following families (Fig. 3A): Stratiomyidae (5 specimens or 1.1% of the total assemblage), Xylomyidae (1/0.2%), Xylophagidae *sensu lato* (66/13.9%), Rhagionidae (246/51.7%), Rhagionemepididae (28/5.9%), ?Vermileonidae (1/0.2%), Archisargidae (22/4.6%), Eremochaetidae (5/1.1%), Kovalevicsargidae (4/0.8%), Therevidae (37/7.8%), Asilidae (4/0.8%), Asiloidea fam. indet. (21/4.4%), Apystomyiidae (1/0.2%), Nemestrinidae (17/3.6%), Rhagionemestriidae (1/0.2%), Acroceridae (4/0.8%), Hilarimorphidae (1/0.2%), Scenopinidae (2/0.4%), Empididae: Protempidinae (9/1.9%), Eomyiidae (1/0.2%).

### ‘Basalmost Cretaceous of Mongolia’

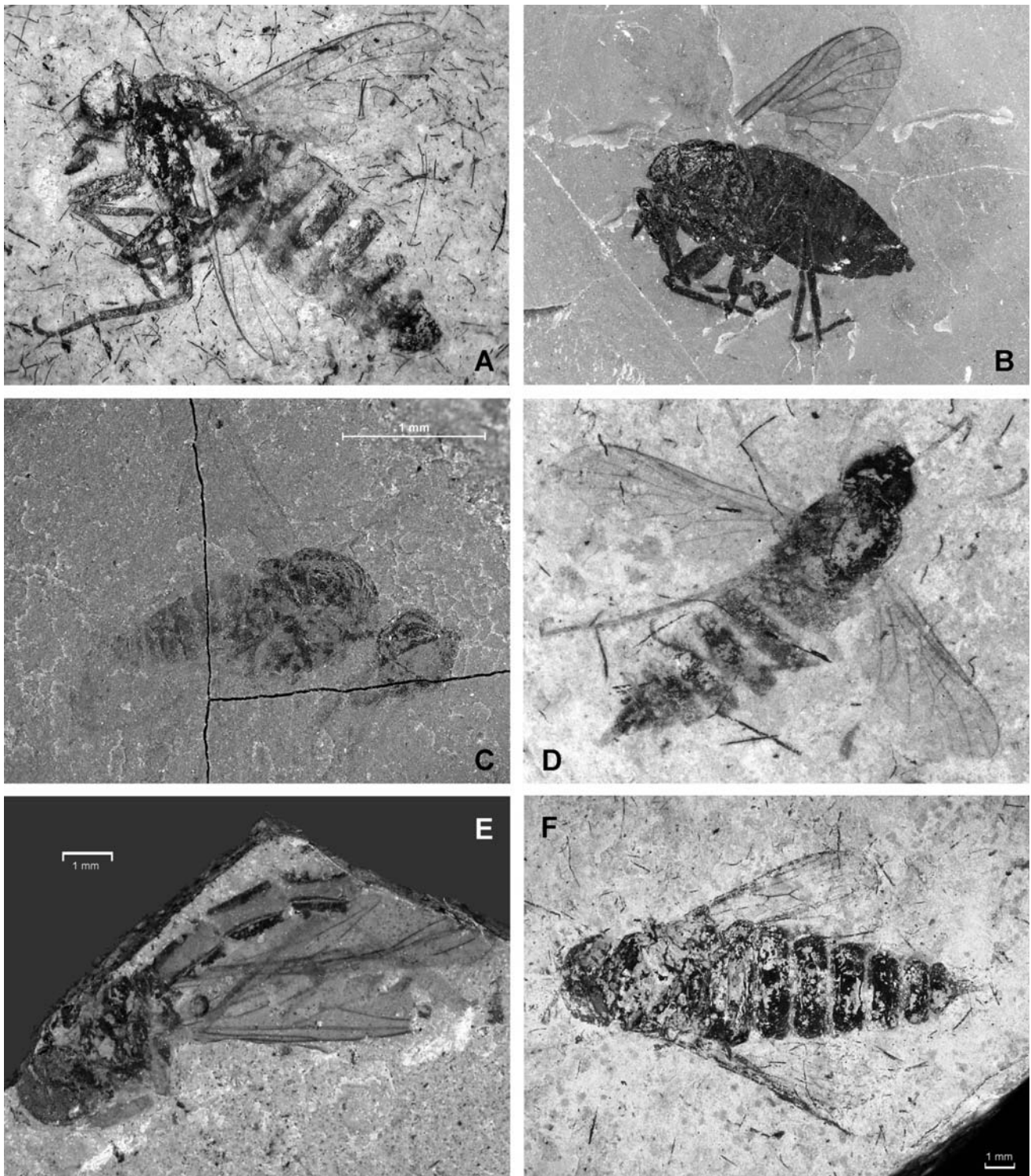
Several localities of a presumably similar age are listed under this name: Gurvan-Erenii-Nuru (10 Rhagionidae, 3 Eremochaetidae, 1 Bombyliidae, 3 Empididae), Hotont (1 Empididae), Hara-Hutul (1 Rhagionidae, 1 Therevidae, 1 Asiloidea indet., 9 Empididae), Manlay (1 Eremochaetidae, 1 Stratiomyidae), Myangad (1 Rhagionidae), Tsagaan-Tsav (2 Empididae), Ulaan-Tolgoy (1 Empididae). If assemblages from these localities are taken as one, the families’ contributions are as follows (Fig. 3B): Stratiomyidae, 2.8%; Rhagionidae, 33.3%; Eremochaetidae, 11.1%; Bombyliidae, 2.8%; Empididae, 44.4%; Therevidae, 2.8%; Asiloidea indet. 2.8%.

### Purbeck and Wealden

Purbeck and Wealden deposits of southern England yielded 51 identifiable brachyceran specimens. Deposits of the Lulworth Formation (Lower Purbeck) consisted of a depauperate assemblage consisting of Rhagionidae (2 specimens/33.3%), Athericidae (1/16.7%), Rhagionemestriidae (2/33.3%), and Empididae (1/16.7%). The Durlston Formation (Middle Purbeck) yielded Rhagionidae (11 specimens/61.1%), Tabanidae (1/5.6%), Empididae (5/27.8%), Opetiidae (1/5.6%). The Lower Weald Clay of England yielded Xylophagidae (1/4.8%), Rhagionidae (4/19%), Athericidae (1/4.8%), Empididae (15/71.4%); whereas the Upper Weald Clay brought Rhagionidae (2/33.3%), Athericidae (2/33.3%), Rhagionemestriidae (1/16.7%), Empididae (1/16.7%).

### Baissa

This Lower Cretaceous Lagerstätten was sampled bed by bed (Zherikhin *et al.* 1999), and revealed a rich brachyceran fauna (221 specimens) (Fig. 3C): Stratiomyidae (6/2.7%), Rhagionidae (25/11.3%), Vermileonidae (1/0.5%), Tabanidae (1/0.5%), Athericidae (1/0.5%), Eremochaetidae (9/4.1%), Nemestrinidae (5/2.3%), ?Bombyliidae (2/0.9%), Mydidae (6/2.7%), Therevidae (1/0.5%), Asilidae (6/2.7%),



**Figure 1.** Compression fossils of Mesozoic brachyceran flies. **A**, *Protorhagio ponomarenkoi* Mostovski, 2008 (Rhagionidae), holotype PIN-2239/2182, Middle–Upper Jurassic of Karatau, Kazakhstan; **B**, *Palaeoarthroteles mesozoicus* Kovalev & Mostovski, 1997 (Rhagionidae), PIN-3063/1436, Upper Jurassic or Lower Cretaceous of Daya, Transbaikalia; **C**, Rhagionidae indet., BP/2/26852, Upper Cretaceous of Orapa, Botswana; **D**, *Probolbomyia modesta* Ussatchov, 1968 (Rhagionempididae), PIN-1789/120, Middle–Upper Jurassic of Karatau, Kazakhstan; **E**, *Eremomukha (Eremocreta) cf. sorosi* Mostovski, 1997 (Eremochaetidae), PIN-4210/5212, Lower Cretaceous of Baissa, Transbaikalia; **F**, *Archinemestrius litigiosus* Mostovski, 1998 (Nemestrinidae), holotype PIN-2784/79, Middle–Upper Jurassic of Karatau, Kazakhstan.

Asiloidea fam. indet. (5/2.3%), Hilarimorphidae (3/1.4%), Empididae (90/40.7%), Platypezidae (30/13.6%), Ironomyiidae: Sinolestinae (29/13.1%), ?Sciadoceridae (1/0.5%).

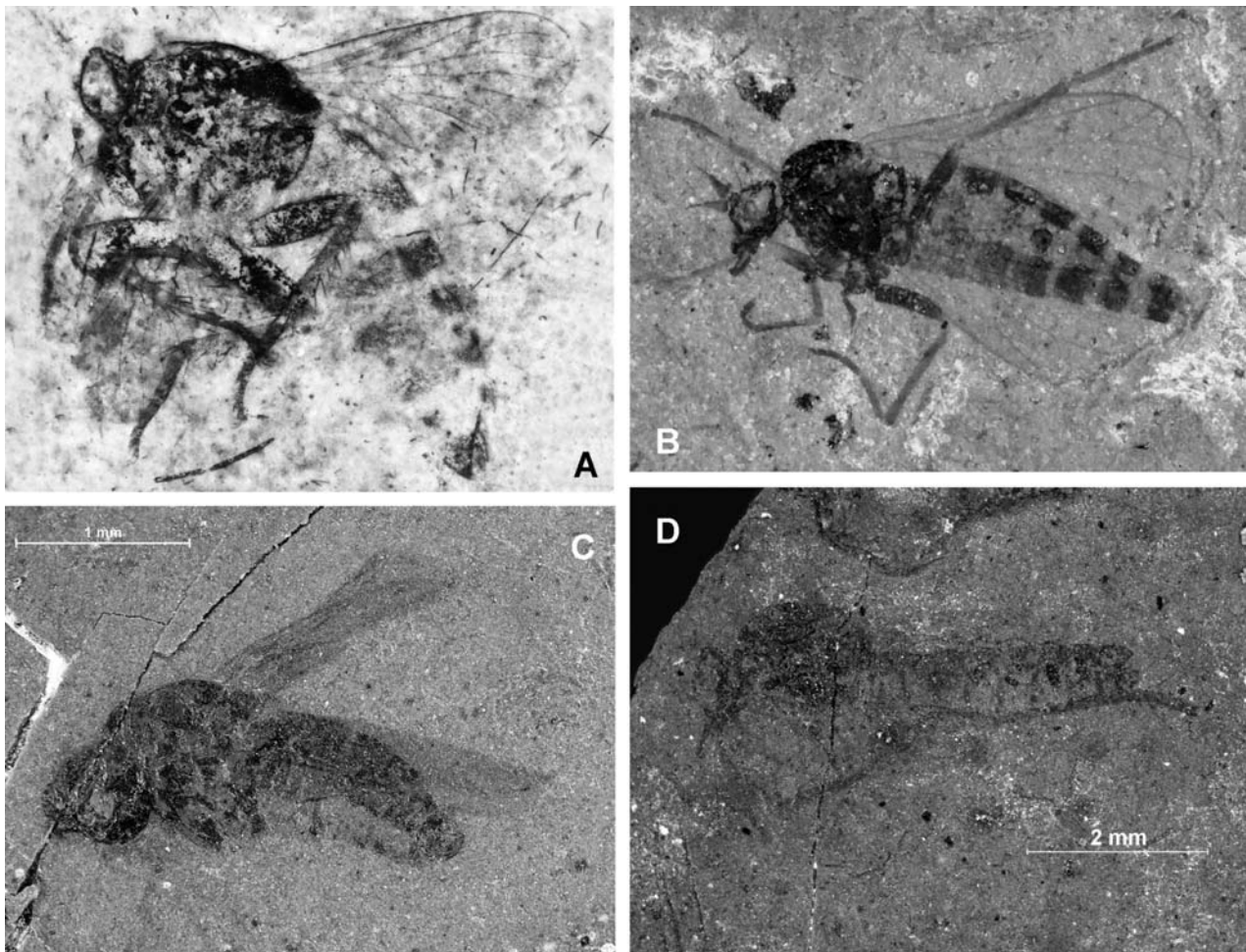
#### Bon-Tsagaan

This locality yielded 49 identifiable brachyceran specimens. The following brachycerans were found (Fig. 3D): Rhagionidae (7/14.3%), Eremochaetidae (3/6.1%), Rhagio-

nemestriidae (1/2%), ?Bombyliidae (1/2%), Therevidae (2/4.1%), ?Mydidae (4/8.2%), Asiloidea fam. indet. (1/2%), Empididae (6/12.2%), Platypezidae (9/18.5%), Ironomyiidae: Sinolestinae (15/30.6%).

#### Obeshchayushchiy

Cenomanian deposits of this locality yielded the following brachyceran assemblage (89 specimens) (Fig. 3E):



**Figure 2.** Compression fossils of Mesozoic brachyceran flies. **A**, *Rhagiophryne bianalis* Rohdendorf, 1964 (Therevidae), PIN-2997/3490, Middle–Upper Jurassic of Karatau, Kazakhstan; **B**, Empididae indet., PIN-4210/6375, Lower Cretaceous of Baissa, Transbaikalia; **C**, Empididae indet., BP/2/26872, Upper Cretaceous of Orapa, Botswana; **D**, Empididae indet., BP/2/25974, Upper Cretaceous of Orapa, Botswana.

Stratiomyidae (4/4.5%), Rhagionidae (3/3.4%), Asiloidea (5/5.6%), Empididae (39/43.8%), Platypezidae (3/3.4%), Ironomyiidae: Sinolestinae (27/30.3%), Platypezoidea indet. (7/7.9%), Phoridae: Prioriphorinae (1/1.1%).

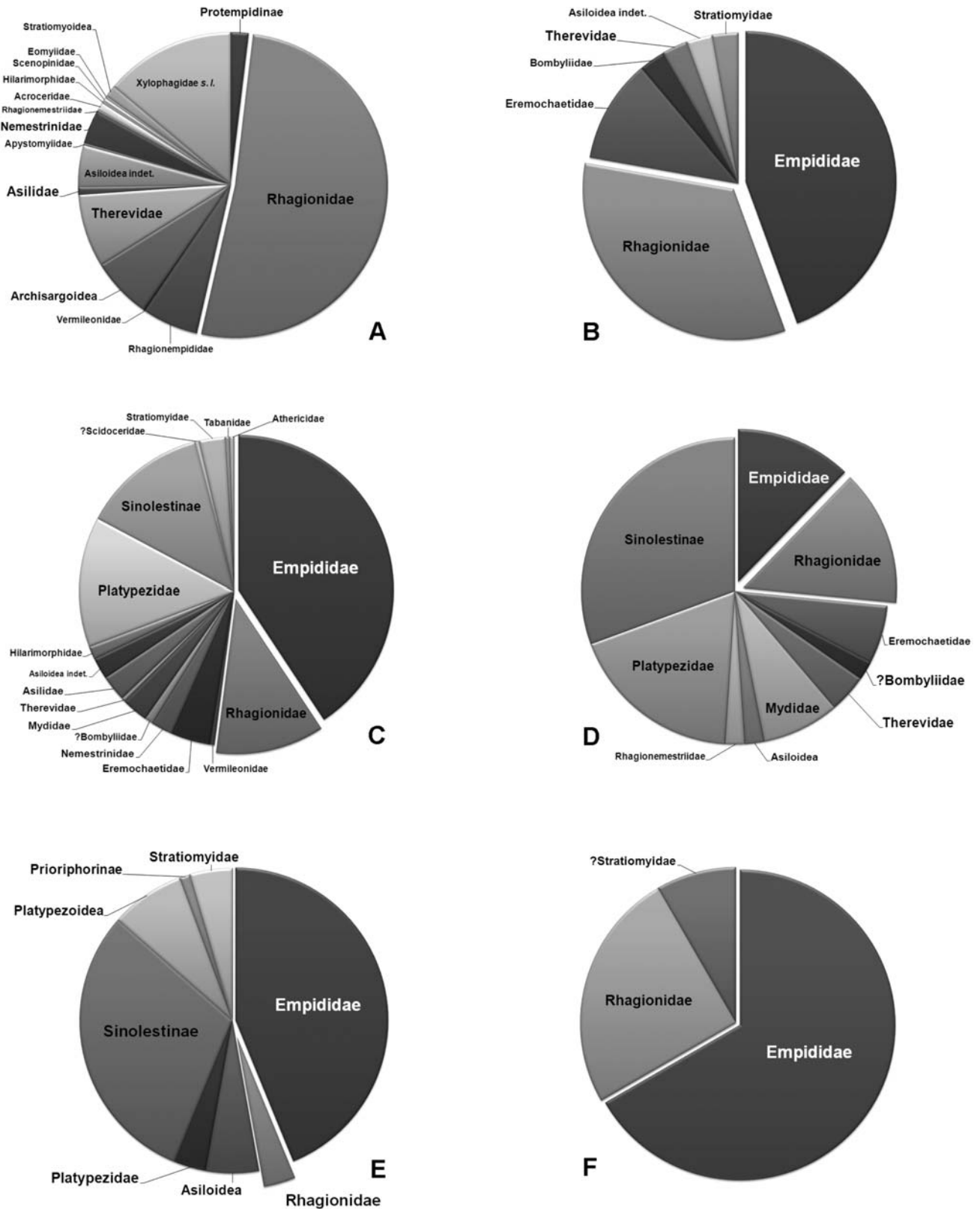
#### Orapa

This is the only southern African Upper Cretaceous locality that has yielded a rich insect assemblage. Brachyceran flies are, however, scarce (12 specimens, Fig. 3F) and represented by almost only two families, Rhagionidae (3 specimens/25%; Fig. 1C) and Empididae (8/66.7%; Figs 2C, 2D), with one poorly preserved impression possibly belonging to Stratiomyidae (8.3%).

#### Discussion and conclusions

The above assemblages clearly differ from each other in their taxonomic composition and ratios of particular families. The Jurassic Karatau assemblage is distinctive in a high number of extinct families and the dominance of Rhagionidae; the rhagionids are exceptionally diverse and represented by archaic forms (Fig. 1A). The relative abundance of stiletto flies (Therevidae, 7.8%) (Fig. 2A) supports a reconstruction of a warm to hot and (semi)arid climate at that time; this is also confirmed by a minor share of Empididae, although they are represented in this locality

by extinct Protempidinae which climatic preferences are uncertain. All other assemblages belong to a more advanced 'empidid' type, with the share of this family varying from 12–67%. The diversification of Empididae, as well as the appearance and diversification of Platypezidae and Ironomyiidae (Sinolestinae), are characteristics of the Cretaceous stage of dipteran evolution. Extant Empididae are predators; it has been noted that members of this family generally prefer mesic local environments, even in regions with generally arid or semi-arid climate (e.g. Smith 1969; Chvála 1983). Having assumed that ecological preferences of empidids have remained largely unchanged, their ratio in various assemblages was used to establish a relative humidity in corresponding palaeoenvironments. The first attempt to employ empidids in palaeoreconstructions for Purbeck and Wealden deposits, Baissa, Bon-Tsagaan and Obeshchayushchiy was made elsewhere (Coram *et al.* 2000). It has been shown that the empidid ratio increases in localities or during periods when warm and humid climate prevailed based on other studies. Empidids also dominate the Orapa assemblage (Figs 2C, 2D), although the latter is extremely poor in brachyceran fossils. However, this fully supports a previous reconstruction of a wet climate in the central Botswana at the beginning of the Late Cretaceous (Waters 1990; Rayner *et al.* 1991). The brachyceran assemblage of the basalmost



**Figure 3.** Composition of brachyceran assemblages in some Mesozoic localities. A, Callovian–Kimmeridgian Karabastau Formation of Karatau; B, 'basalmost Cretaceous of Mongolia'; C, Lower Cretaceous Zaza Formation of Baissa; D, Barremian–Aptian Hurilt Beds of the Bon-Tsagaan Group; E, Cenomanian Ola Formation of Obeshchayushchiy; F, Cenomanian–Turonian of Orapa.

Cretaceous of Mongolia is remarkable for its unusually high (for Cretaceous) share of Rhagionidae (33.3%), while Empididae still dominate (44.4%). Apparently, the rhagionids did not immediately lose their dominant position with the transition over the Jurassic/Cretaceous boundary. The high proportion of empidids suggests humid

conditions near burial sites, which supports general palaeogeographic reconstructions (Zharkov *et al.* 1998).

Data collected at the Baissa locality all for reconstruction of the environmental conditions during the development of the palaeolake. Two main terrestrial insect fossil assemblages are recognized, one being restricted to the middle

part of the section (Beds 25 to 13) and another occurring in the lower part of the section and reappearing in the uppermost beds. Some aquatic insects demonstrate a similar distributional pattern. The mid-section assemblage is more diverse and enriched in more thermophilous taxa, and a warming episode during the deposition of the middle part of the section was postulated (Zherikhin *et al.* 1999). While empidids (Fig. 2B) constitute 40.7% of the total brachyceran assemblage in Baissa, their distribution in different parts of the section varies substantially. The family constitutes 34% in the the assemblage of the 'cold' beds (39–27 and 9–2), whereas it reaches 41% in the 'warm'-bed assemblage, with a maximum of 46% in Bed 22. Such a distribution suggests the transition from drier conditions to more humid environments during the history of the palaeolake. (The uppermost part – Beds 9–2 – is separated from the rest of the section by a fault, and its correct correlation remains debatable.) This interpretation contradicts data obtained from studies on cockroaches (Vršanský *et al.* 2002), where more warm and (semi)arid conditions were postulated for Beds 25–13 of the Baissa sequence. However, representatives of the family Empididae seem to be more sensitive to changes of humidity than to ambient temperatures, unlike cockroaches.

Other brachyceran flies do not show such strong climatic preferences, but may be indicative of other aspects of palaeoenvironments. Thus, long proboscis flies like Nemestrinidae (Fig. 1F) and Mydidae could act as pollinators (Labandeira *et al.* 2007). Parasitic flies were represented in the Late Mesozoic by the Archisargidae, Eremochaetidae, Acroceridae, Apystomyiidae, Bombyliidae *sensu lato*, and Nemestrinidae. Many Archisargidae and Eremochaetidae (Fig. 1E) had a contrasting colour pattern, apparently were good fliers capable of hovering, and possessed a needle-like ovipositor; representatives of extinct Nemestrinidae demonstrate shortened and elongated ovipositor, which suggests a broad spectrum of their hosts. Cretaceous flat-footed flies (Platypezidae) apparently were connected with fungi, like their modern representatives. Quite diverse Cretaceous Sinolestinae have been assigned to Ironomyiidae with some reservations; they share varying portions of the total dipteran fauna based on locality, which suggest a still unknown factor that might influenced their distribution. Rare were presumed haematophagous flies represented by Tabanidae, Athericidae and, possibly, some Rhagionidae; all dipterans with mouthparts adapted for bloodsucking are unknown before the Early Cretaceous (Lukashevich & Mostovski 2003). Ancient Asilidae show a remarkable general resemblance to present-day robber flies, which are predatory and prefer open, often dry landscapes. Extant Acroceridae are parasites of spiders, and an extreme rarity of acrocerids in the palaeontological record correlates well with the utmost rarity of spider compression fossils (Selden *et al.* 2009), although both phenomena can be explained taphonomically.

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## REFERENCES

- BLAGODEROV, V.A., LUKASHEVICH, E.D. & MOSTOVSKI, M.B. 2002. Order Diptera Linne, 1758. The true flies (= Muscida Laicharting, 1781), 227–240. In: Rasnitsyn, A.P. & Quick, D.L.J. (eds), *History of Insects*. Dordrecht, Kluwer Academic Publishers.
- BROTHERS, D.J. & RASNITSYN, A.P. 2003. Diversity of Hymenoptera and other insects in the Late Cretaceous (Turonian) deposits at Orapa, Botswana: a preliminary review. *African Entomology* **11**(2), 221–226.
- CHVÁLA, M. 1983. The Empidoidea (Diptera) of Fennoscandia and Denmark. II. General Part. The families Hybotidae, Atelestidae and Microphoridae. *Fauna Entomologica Scandinavica* **12**, 1–279.
- CORAM, R., JARZEMBOWSKI, E.A. & MOSTOVSKI, M.B. 2000. Two rare eremoneuran flies (Diptera: Empididae and Opetiidae) from the Purbeck Limestone Group. *Paleontological Journal* **34**(Suppl. 3), S370–S373.
- GERNON, T.M., FIELD, M. & SPARKS, R.S.J. 2009. Depositional processes in a kimberlite crater: the Upper Cretaceous Orapa South Pipe (Botswana). *Sedimentology* **56**, 623–643.
- LABANDEIRA, C.C., KVAČEK, J. & MOSTOVSKI, M.B. 2007. Pollination drops, pollen, and insect pollination of Mesozoic gymnosperms. *Taxon* **56**(3), 663–695.
- LUKASHEVICH, E.D. & MOSTOVSKI, M.B. 2003. Haematophagous insects in the paleontological record. *Paleontological Journal* **38**(2), 153–161.
- MOSTOVSKI, M.B., JARZEMBOWSKI, E.A., CORAM, R. & ANSORGE, J. 2000. Curious snipe-flies (Diptera, Rhagionidae) from the Purbeck of Dorset, the Wealden of the Weald and the Lower Cretaceous of Spain and Transbaikalia. *Proceedings of the Geologists' Association* **111**, 153–160.
- MOSTOVSKI, M.B. & MARTÍNEZ-DELCLÓS, X. 2000. New Nemestrinoidea (Diptera: Brachycera) from the Upper Jurassic–Lower Cretaceous of Eurasia, taxonomy and palaeobiology. *Entomological Problems* **31**(2), 137–148.
- OGG, J.G., OGG, G. & GRADSTEIN, F.M. 2008. *The Concise Geologic Time Scale*. Cambridge, UK, Cambridge University Press.
- RAYNER, R.J., BAMFORD, M.K., DIPPENAAR-SCHOEMAN, D.J., MCKAY, I.J., OBERPRIELER, R.G. & WATERS, S.B. 1996. Cretaceous fossils from the Orapa Diamond Mine. *Palaentologia africana* **33**, 55–65.
- RAYNER, R.J., WATERS, S.B., MCKAY, I.J., DOBBS, P.N. & SHAW, A.L. 1991. The mid-Cretaceous palaeoenvironment of central southern Africa (Orapa, Botswana). *Palaeoecology, Palaeoecology* **88**(1–2), 147–156.
- RASNITSYN, A.P. & QUICKE, D.L.J. (eds) 2002. *The History of Insects*. Dordrecht, Kluwer Academic Publishers.
- SELDEN, P.A., ANDERSON, H.M. & ANDERSON, J.M. 2009. A review of the fossil record of spiders (Araneae) with special reference to Africa, and description of a new specimen from the Triassic Molteno Formation of South Africa. *African Invertebrates* **50**(1), 105–116.
- SMITH, K.G.V. 1969. The Empididae of Southern Africa. *Annals of the Natal Museum* **19**, 1–342.
- VRŠANSKÝ, P., MOSTOVSKI, M.B., BAZYLEV, B.A. & BUGDAEVA, E. 2002. Early Cretaceous climate changes suggested on the basis of cockroach wing variations. In: Proceedings of the XVII Congress of the Carpathian-Balkan Geological Association, Bratislava, September 1–4, 2002. *Geologica Carpathica* **53**(Spec. issue), 1–5. Online at: [http://www.geologicacarthica.sk/special/V/Vrsansky\\_etal.pdf](http://www.geologicacarthica.sk/special/V/Vrsansky_etal.pdf)
- WATERS, S. 1990. *Cretaceous Diptera from Orapa, Botswana*. Unpublished Ph.D. thesis, University of Witwatersrand, Johannesburg.
- ZHARKOV, M.A., MURDMAA, I.O. & FILATOVA, N.I. 1998. Paleogeography of the Berriasian–Barremian Ages of the Early Cretaceous. *Stratigraphy and Geological Correlation* **6**(1), 47–69.
- ZHERIKHIN, V.V., MOSTOVSKI, M.B., VRŠANSKÝ, P., BLAGODEROV, V.A. & LUKASHEVICH, E.D. 1999. The unique Lower Cretaceous locality of Baissa and other contemporaneous insect-bearing sites in North and West Transbaikalia. In: *Proceedings of the First Palaeontological Conference, Moscow, 1998*, 185–192. Bratislava, AMBA Projects.