Curious snipe-flies (Diptera: Rhagionidae) from the Purbeck of Dorset, the Wealden of the Weald and the Lower Cretaceous of Spain and Transbaikalia

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MOSTOVSKI, M. B., JARZEMBOWSKI, E. A., CORAM, R. A. & 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. Four new Lower Cretaceous species of the rhagionid genus *Ptiolinites* are described: *Ptiolinites heidiae* sp. nov. and *P. raypearcei* sp. nov. from southern England, *P. almuthae* sp. nov. from Spain and *P. oudatchinae* sp. nov. from northern Transbaikalia. Re-evaluation of the antennal structure allows us to assign *Ptiolinites* to the subfamily Rhagioninae.

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1. INTRODUCTION

The Rhagionidae (snipe-flies) is one of the most ancient families of brachycerous flies. Snipe-flies originated near the Early–Middle Triassic boundary and were rather rare during the Triassic and Early Jurassic (Krzemiński, 1998; Mostovski, in press). The abundance and taxonomic diversity of rhagionids increased dramatically in the Middle–Late Jurassic. For example, the family forms up to 52% of the brachyceran assemblage of the Karabastau Formation at the famous Asian locality of Karatau, which is Callovian–Kimmeridgian in age (Polyansky & Doludenko, 1978; Kirichkova & Doludenko, 1996). The diversity and abundance of snipe-flies decreased gradually during the Cretaceous Period. The Rhagionidae are reported in both the Purbeck and the Wealden in southern England (Jarzembowski, 1984; Jarzembowski & Coram, 1997). To date, eleven specimens have been found in Clements' Bed DB175 (Clements, 1993) in the Durlston Formation (Upper Berriasian) of Durlston Bay in Dorset and two specimens in the Soft Cockle beds (Lulworth Formation, Lower Berriasian) of the same locality. Four specimens of Rhagionidae have been collected from the Wealden at Clockhouse Brickworks, Capel, Surrey (late Hauterivian, Lower Weald Clay) and two from Smokejacks Brickworks, Ockley, Surrey (early Barremian, Upper Weald Clay). Five species in three genera occur in the Purbeck and Wealden deposits. Four specimens from Clements' Bed DB175 and three from Clockhouse Brickworks have been identified as belonging to new species of the genus *Ptiolinites*, originally described from the Lower Cretaceous of Mongolia.

The lacustrine Zaza Formation of the Lower Cretaceous locality of Baissa in Transbaikalia (53° 18′ N, 112° 5′ E) has produced twenty-five rhagionid specimens to date, representing 11% of the brachyceran assemblage. The distinctive wing venation and other characters of a specimen found recently at Baissa (project EURUS '97) allow us to assign it to *Ptiolinites*. The British Lower Cretaceous insects are usually disarticulated but intact at Baissa, and this specimen is no exception.

Finally, the Lower Cretaceous lithographic limestones of Sierra del Montsec, northeastern Spain (42° 0′ N, 0° 57′ E) have yielded several fossil Brachycera, including a distinctive rhagionid specimen referable to *Ptiolinites*, described below.

Biological data on Recent rhagionids are scarce. Adults tend to frequent fairly dense vegetation and are predacious, mainly on other insects. Larvae of the cosmopolitan genera *Chrysopilus* and *Rhagio* are predators, those of some species of *Chrysopilus* are also aquatic (Thomas, 1978). The genera *Ptiolina* and *Spania* are Holarctic, and their immature stages are thought to be associated with liverworts (Nartshuk, 1995).

2. FOSSIL LOCALITIES

The geology of the rhagionid-bearing Weald Clay localities has been summarized already in the *Proceedings*

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by Jarzembowski (1991). The insects occur in scour fills and other well-cemented lithologies. The disarticulated remains are thought to have been washed into the Wealden sub-basin during the wet season by rivers flowing south from the Londinian uplands. The palaeoclimate is considered to have been subtropical/ warm temperate and generally more humid after the dry phase represented by the Purbeck Beds (Jarzembowski, 1995). The Purbeck insect beds were deposited in brackish or hypersaline conditions and hence lack the freshwater faunal elements, such as mayflies (Ephemeroptera), that occur at Baissa. The productive Clements' Bed DB175 in the Middle Purbeck of Durlston Bay was deposited in a lagoonal environment with stromatolites on mudflats (Andrews, 1986).

The lithographic limestones of the Sierra del Montsec are intercalated within littoral charophytic limestones as the pelagic facies of a limnic/lacustrine environment. The carbonate mud, particle size about 3 μm, was deposited in the deepest parts of a fresh or brackish water lagoon without direct connection to the epicontinental sea. Originally an Upper Berriasian–Lower Valanginian age was proposed for the lithographic limestones (Brenner, Goldmacher & Schroeder, 1974; Lacasa-Ruiz & Martínez-Delclòs, 1986; Fregenal-Martínez, Martínez-Delclòs, Meléndez & Ruiz de Loizaga, 1992). However, after recording utricles of the charophyte *Atopochara trivolvis triquetra* Grambast, 1968, Ansorge (1993a) suggested a Lower Barremian age. This suggestion has recently been supported by Martín-Closas & López-Morón (1995). The rich and well preserved insect fauna of Montsec consists of autochthonous/parautochthonous aquatic insect larvae and allochthonous terrestrial insects. Representatives of fourteen insect orders have been recorded to date.

Baissa is the richest insect-bearing site among more than a hundred now known in Transbaikalia. The deposits of the Zaza Formation are mainly sandstones and siltstones interbedded with clays, marls, limestones, sideritic clays and phosphates. Representatives of twenty-five insect orders have been found, mainly in the marls, as well as many bivalves, gastropods, ostracods, conchostracans and a unique freshwater bryozoan colony. In addition there are spiders, harvestmen, fishes and bird feathers and bones. The absence of reptile remains, frequent in the Purbeck and Wealden, is of taphonomic interest. The faunistic assemblage at Baissa is of the *Ephemeropsis–Coptoclava* type (Zherikhin, 1978). Its characteristic members are the osteoglossomorph fish *Lycoptera*, the mayfly *Ephemeropsis*, water beetle *Coptoclava* and conchostracan *Bairdestheria*. The brachyceran assemblage at Baissa shares some taxa with the Yixian Formation of northeastern China which is of Late Jurassic or Early Cretaceous age (Tithonian according to Ren, Guo, Lu, Ji, Tang & Jing, 1997; Barremian according to Swisher, Wang, Wang, Xu & Wang, 1999). Numerous plant remains are also found at Baissa. These are mainly conifers, with some ginkgoaceous plants and czekanowskiales, and rare horsetails, pteridophytes, bennettitales and proangiosperms. The plant assemblage resembles that of the Hurilt Beds of the Bon-Tsagaan Group in Mongolia, and the Yixian Formation (Dr E. Bugdaeva, pers. comm.). The age of the Zaza Formation is accepted by geologists and palaeozoologists as Neocomian or Early Neocomian (e.g. Martinson, 1961; Kolesnikov, 1964; Zherikhin, 1978; Skoblo & Liamina, 1990; Rasnitsyn, Jarzembowski & Ross, 1998), but palaeobotanists have not excluded a Barremian–Aptian age (Vakhrameev & Kotova, 1977). The Transbaikalian climate in the Early Neocomian is supposed to have been rather warm and humid (Allen, 1998; Zharkov, Murdmaa & Filatova, 1998) though there is some lithological evidence of semi-arid conditions in the region of the Vitim River in Early Cretaceous times (Liamina, 1980).

3. SYSTEMATIC DESCRIPTIONS

Specimens studied are kept in the following Museums and Institutions: MNEMG – Maidstone Museum & Art Gallery, Maidstone; NHM – Natural History Museum, London; FGWG – Institut für Geologische Wissenschaften, Greifswald; PI – Palaeontological Institute, Moscow.

Vein abbreviations follow Shcherbakov, Lukashevich & Blagoderov (1995).

Family RHAGIONIDAE Latreille, 1802

Subfamily RHAGIONINAE Latreille, 1802

Genus PTILOLINITES Kovalev, 1986

Type species

Ptiolinites cretaceus Kovalev, 1986; Lower Cretaceous, Mongolia.

Diagnosis

Head hemispherical. Eyes holoptic in male. First flagellomere of antenna symmetrically rounded with rather long and thin terminal arista. Costal vein circumambient, becoming thinner beyond R5. Costal area between R1 and R2+3 longer than that between Sc and R1. M1 and M2 arise from the discal cell on a common stalk, or diverge at intermedial (*im*) crossvein. R2+3 sinuate. Anal cell closed or nearly so. Pterostigma present but may be very pale. Legs slender. Three spherical sclerotised spermathecae in female. Male genitalia small.

Other included species: *P. heidiae* sp. nov., *P. raypearcei* sp. nov., *P. almuthae* sp. nov. and *P. oudatchinae* sp. nov.

Discussion

The genus *Ptiolinites*, from the Lower Cretaceous Gurvan–Eren Formation of Myangad in West Mongolia, was described by Kovalev (1986) who considered it to be practically identical to the Recent genus *Ptiolina* Zetterstedt within the subfamily Spaniinae, separating the

two genera simply because of the inadequate preservation of the fossil. However, his placement of *Ptiolinites* is erroneous. The arista in the holotype of *P. cretaceus* is evidently incomplete and thus appears to be short and *Ptiolina*-like. However, the first flagellomere (the third antennal segment) of the type specimen is undoubtedly more rounded than suggested by Kovalev's figure (1986, fig. 115). The arista should be longer and articulated with the first flagellomere, and vein R2+3 is distinctly sinuate. The arista is comparatively long in the new specimens from Baissa and Montsec. It is thus possible to transfer this genus to the subfamily Rhagioninae, though tibial spurs were probably reduced. Nevertheless, the exact position of *Ptiolinites* and its relationship with other genera is still unclear because we lack data on the fine structure of both male and female genitalia, amongst other characters. Within the Rhagioninae, *Ptiolinites* differs from the Recent genus *Chrysopilus* Macquart in its sinuate R2+3, from the Recent genus *Rhagio* Fabricius in its closed anal cell and vein M1+2 arising from the discal cell mainly by a common stalk. *Ptiolinites* shares with the Recent genus *Alloleptis* Nagatomi & Saigusa (Nagatomi, 1982) a common stem to M1 and M2, but has a longer anal cell. It differs from the fossil genus *Scelorhagio* Zhang, Zhang & Li, 1993, from the Lower Cretaceous Laiyang Formation of China, in its sinuate R2+3 and M1+2 arising from the discal cell by a common stalk. The venation of *Ptiolinites* is very similar to that of the fossil genus *Palaeobrachyceron* Kovalev, 1981, recorded from the Lower–Middle Jurassic of Siberia (Kovalev, 1981) and Lower Jurassic of Germany (Ansorge, 1996). However *Ptiolinites* differs from this genus in its aristate antennae, hemispherical head and unenlarged maxillary palps. The recently described *Paleochrysopilus* Grimaldi & Cumming, 1999, from Lower Cretaceous Lebanese amber, shares with *Ptiolinites* a common stalk to M1+2 but has a less sinuous R2+3 and incomplete base to vein M.

The wing venation in some Recent rhagionids is quite variable. Additional transverse veins and absence of the intermedial crossvein occur occasionally in *Chrysopilus*, *Ptiolina* and *Spania*. The intermedial crossvein may shift basally or distally so that M1 and M2 arise from the discal cell independently or by a common stalk. Such variations may occur in different populations of the same species, or even in males and females of the same population. In addition, significant differences may be found in the left and right wings of the same specimen (Szilády, 1934). There is also sexual dimorphism in body size in some species of snipe-flies. We have considered these factors when assigning the fossil material to new species.

Ptiolinites heidiae sp. nov.

Figs. 1, 2.

Diagnosis

R4+5 bifurcate distad of intermedial crossvein. Fork R4+5 not broadened distally. M1 and M2 arise from the discal cell by a common stalk. Discal cell rather broad. Basal section of M4 absent (i.e. M4 meets discal cell directly, rather than meeting crossvein *m-cu*).

Fig. 1. *Ptiolinites heidiae* sp. nov. Holotype MNEMG 1999.21; length of body 2.8 mm.

Derivation of name

After Mrs Heidi Coram, the collector of the holotype.

Description

Wing length 2.7–2.8 mm, wing width 1–1.2 mm. Estimated body length 2.8 mm.

Body dark. R4+5 bifurcate distad of intermedial crossvein. RS2 (section of vein between base of R2+3 and crossvein *r-m*) shorter or equal to RS3 (section of vein between crossvein *r-m* and base of R4). Costal area between R4 and R5 shorter than the section between R5 and M1. Crossvein *r-m* before midlength of discal cell. Stalk M1+2 beyond discal cell shorter than intermedial crossvein. Discal cell 2.5 to 3 times as long as broad. Crossvein *m-cu* originates before M3+4 fork or at the

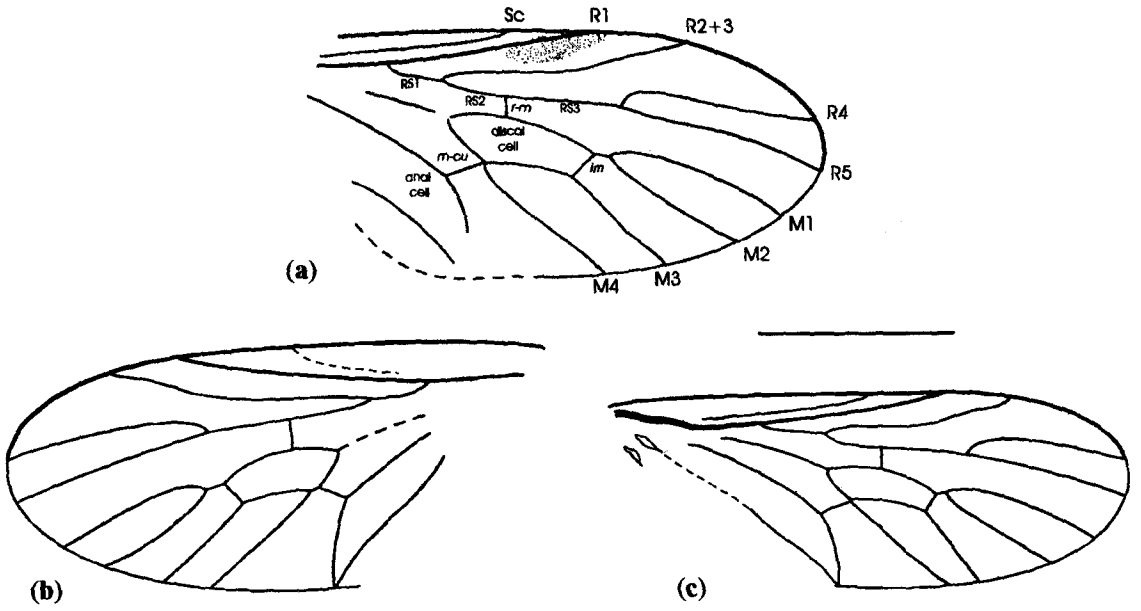

Fig. 2. *Ptiolinites heidiae* sp. nov. Wing venation. (**a**) Holotype, MNEMG 1999.21, showing vein abbreviations as used in text; (**b**) paratype MNEMG 1999.22; (**c**) paratype MNEMG 1999.23. Scale bar here and elsewhere 1.0 mm.

point of bifurcation. Anal cell with point stalk. Pterostigma faint.

Material

Holotype: MNEMG 1999.21, incomplete body with one wing, presumably male. Paratypes: MNEMG 1999.22, MNEMG 1999.23, Coram coll., wings.

Horizon and locality

Purbeck Limestone Group, Durlston Formation (Middle

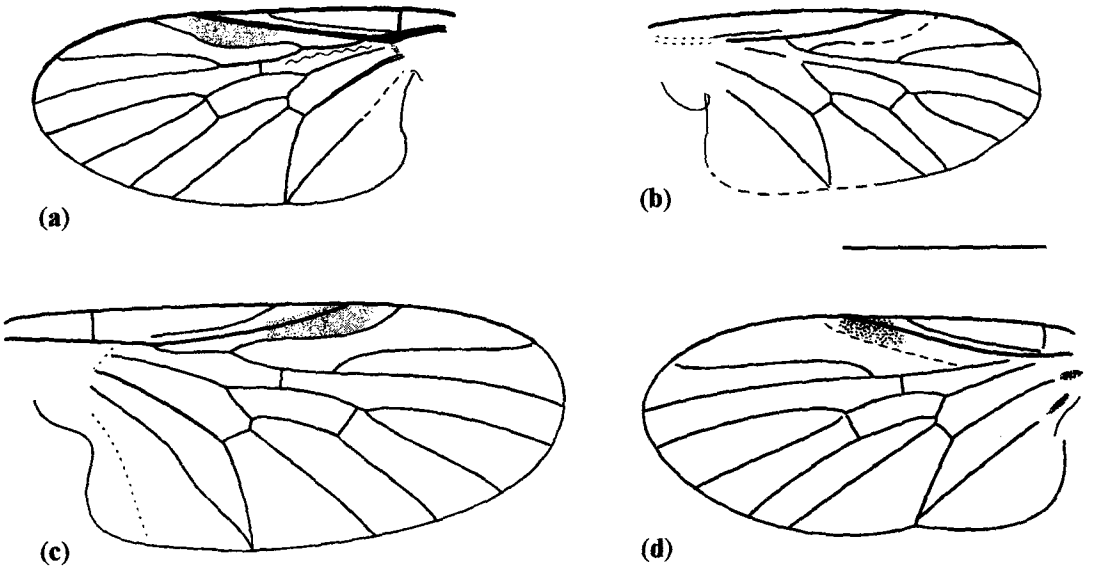

Fig. 3. *Ptiolinites raypearcei* sp. nov. Wing venation. (**a**) Holotype MNEMG 1999.18 (wavy line represents fold); (**b**) paratype MNEMG 1999.24; (**c**) paratype NHM In.64633; (**d**) paratype MNEMG 1999.37.

Purbeck Beds), Clements' Bed DB175, Upper Berriasian, Durlston Bay, Swanage, Dorset. National Grid Reference SZ 038784.

Ptiolinites raypearcei sp. nov.

Fig. 3.

Jarzembowski, 1984: p. 89, fig. 50 [photograph].
Jarzembowski, 1987: p. 290, fig. 12.16.
Evenhuis, 1994: p. 295.

Diagnosis

R4+5 bifurcate basad of intermedial crossvein. Fork R4+5 broadened distally. M1 and M2 arise from discal cell by common stalk or intermedial crossvein originates at the point of bifurcation. Discal cell narrow. Basal section of M4 present.

Derivation of name

After the late Dr Raymond Pearce of Headington, Oxford.

Description

Wing length 1.9–2.8 mm, wing width 0.8–1.2 mm. R1 with row of fine short setae. R4+5 bifurcate basad of intermedial crossvein. RS2 longer or equal to RS3. Costal area between R4 and R5 longer than the section between R5 and M1. Crossvein *r-m* before midlength of discal cell. Stalk M1+2 beyond discal cell much shorter than intermedial crossvein. Discal cell approx. 4 times as long as broad. Basal section of M4 rather long, comparable in length to stalk M1+2 beyond discal cell, or longer. Anal cell with point stalk or with very short petiole. Convex fold developed between RS and M base. Pterostigma faint. Wing membrane with microtrichia.

Material

Holotype: MNEMG 1999.18, wing, Jarzembowski coll. Paratypes: MNEMG 1999.24, Coram coll.; NHM In.64633, MNEMG 1999.37, Jarzembowski coll., wings.

Horizons and localities

Holotype and paratypes NHM In.64633, MNEMG 1999.37: Lower Weald Clay, Clockhouse Brickworks, Capel, Surrey, National Grid reference TQ 175385. Paratype: MNEMG 1999.24: Purbeck Limestone Group, Durlston Formation (Middle Purbeck beds), Clements' Bed DB175, Upper Berriasian, Durlston Bay, Swanage, Dorset, National Grid Reference SZ 038784.

Ptiolinites almuthae sp. nov.

Figs 4, 5.

Ansorge, 1991: pp 58-59, fig. 52; pl. 5, fig. 8.
Ansorge, 1993b, p. 33, fig. 6.

Diagnosis

R2+3 strongly curved. R4+5 bifurcate basad of intermedial crossvein. M1 and M2 arise from the discal cell by a long common stalk. Discal cell rather broad. Basal section of M4 absent.

Derivation of name

The species is named after Ms Almuth Barz.

Description

Wing length approx. 1.5 mm, wing width 0.7 mm. Length of body impression 2.8 mm. Estimated body length in life 2.1 mm.*

Thorax and legs dark, nearly black, abdomen paler. First flagellomere dark, symmetrical, with a terminal rather long and thin arista which seems to be segmented. Frons with several fine hairs. Legs covered with very short dark hairs. R4+5 bifurcates basad of intermedial crossvein. Crossvein *r-m* before midlength of discal cell. M1 and M2 originate from discal cell with a common stalk which is at least as long as the intermedial crossvein. Discal cell approx. 3.3 times long as broad. Crossvein *m-cu* originates before the point of bifurcation of M3 and M4. Anal cell with point stalk. Pterostigma absent. Wing membrane with microtrichia. Two visible well-sclerotised spherical spermathecae.

Fig. 4. *Ptiolinites almuthae* sp. nov. Holotype FGWG 137; length of body 2.8 mm.

* The difference in size between actual and estimated body length is due to postmortem extension of the intersegmental membranes.

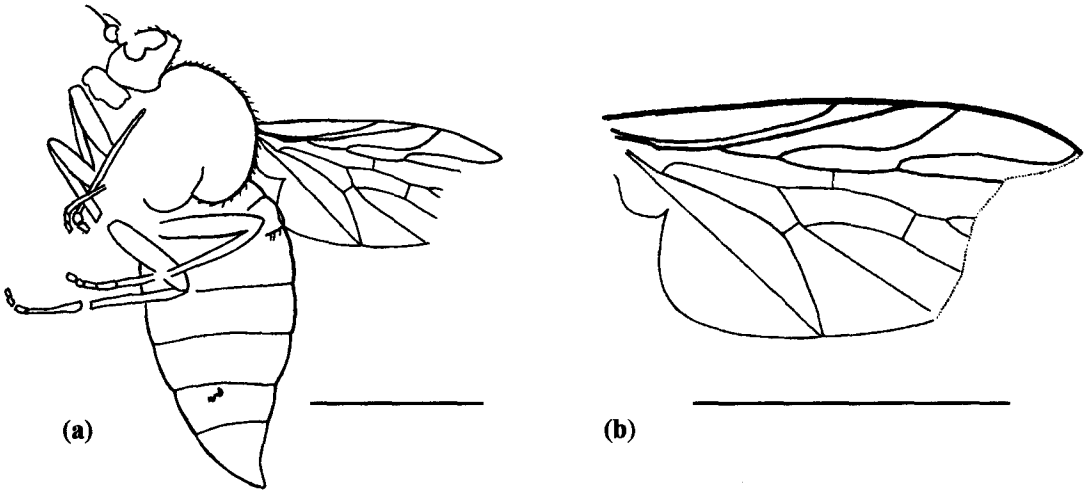

Fig. 5. *Ptiolinites almuthae* sp. nov. (**a**) Holotype FGWG 137, body as preserved; (**b**) holotype wing venation.

Material

Holotype: FGWG 137, impression of female.

Horizon and locality

Lower Cretaceous, La Cabrua locality near Santa Maria de Meia, Sierra del Montsec, Lérida Province, Spain (42° 0′ N, 0° 57′ E).

Ptiolinites oudatchinae sp. nov.

Fig. 6.

Diagnosis

R4+5 bifurcate at the level of intermedial crossvein or a little basad. Fork R4+5 not broadened distally. Intermedial crossvein originates at the point of bifurcation of M1 and M2. Discal cell narrow. Basal section of M4 absent.

Derivation of name

After Mrs T. Oudatchina, the collector of the holotype.

Description

Wing length 2.0 mm, wing width 0.9 mm. Length of body impression 3.3 mm. Estimated body length in life 2.6 mm. Thorax dark, legs and abdomen pale. Maxillary palps not enlarged, dark, with a few very delicate hairs apically. First flagellomere pale, symmetrical, with a terminal rather long and thin arista. Face with several fine hairs. Legs covered with very short dark hairs. R1 with row of

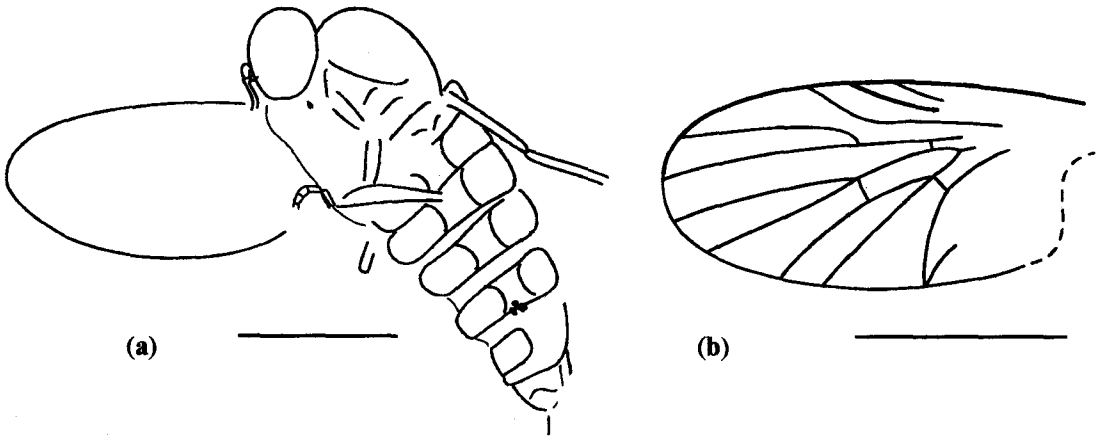

Fig. 6. *Ptiolinites oudatchinae* sp. nov. (**a**) Holotype PI 4210/5216, body as preserved; (**b**) holotype wing venation.

fine short setae. R4+5 bifurcates at the level of the intermedial crossvein or a little basad. Costal area between R4 and R5 shorter than between R5 and M1. Crossvein *r-m* far before midlength of discal cell. M1 and M2 originate from discal cell without any stalk. Discal cell 4 times as long as broad. Crossvein *m-cu* originates at the point of bifurcation of M3 and M4. Anal cell with point stalk. Pterostigma very pale and faint. Wing membrane with microtrichia. Three small, well sclerotized spherical spermathecae.

Material

Holotype: PI 4210/5216, part and counterpart of incomplete female.

Horizon and locality

Neocomian, Zaza Formation, bed 31, left bank of Vitim River *c.* 40 km downstream of the mouth of the Zaza River, Baissa, Transbaikalia (53° 18′ N, 112° 5′ E).

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REFERENCES

ALLEN, P. 1998. Purbeck–Wealden (early Cretaceous) climates. *Proceedings of the Geologists' Association,* **109**, 197–236.

ANDREWS, J. E. 1986 (for 1985). Algal laminae with calcite pseudomorphs after gypsum from the Middle Purbeck of Durlston Bay, Dorset. *Proceedings of the Dorset Natural History & Archaeological Society*, **107**, 187–189.

ANSORGE, J. 1991. 'Zur Sedimentologie und Paläontologie des unterkretazischen Plattenkalkaufschlusses "La Cabrua" (Sierra del Montsec; Provinz Lerida, NE-Spanien) unter besonderer Berücksichtigung der fossilen Insekten.' Diploma thesis, University of Greifswald.

—— 1993a. Bemerkenswerte Lebensspuren und *?Cretosphex catalunicus* n. sp. (Insecta; Hymenoptera) aus den unterkretazischen Plattenkalken del Sierra del Montsec (Provinz Lerida, NE-Spain). *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, **190**, 19–35.

—— 1993b. Insektenfundstellen im Oberen Lias und der Unterkreide. *Natur und Museum*, **123**, Frankfurt am Main, 31–34.

—— 1996. Insecten aus dem oberen Lias von Grimmen (Vorpommern, Norddeutschland). *Neue Paleontologische Abhandlungen*, **2**, 1–132.

BRENNER, P., GOLDMACHER, W. & SCHROEDER, R. 1974. Ostrakoden und Alter der Plattenkalke von Rubies (Sierra del Monsech, Prov. Lérida, N.E.-Spanien). *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, **8**, 513–524.

CLEMENTS, R. G. 1993 (for 1992). Type-section of the Purbeck Limestone Group, Durlston Bay, Swanage, Dorset. *Proceedings of the Dorset Natural History & Archaeological Society*, **114**, 181–206.

EVENHUIS, N. L. 1994. *Catalogue of the fossil flies of the world (Insecta: Diptera)*. Backhuys, Leiden.

FREGENAL-MARTÍNEZ, M., MARTÍNEZ-DELCLÒS, X., MELÉNDEZ, N. & RUIZ DE LOIZAGA, M. J. 1992. Lower Cretaceous lake deposits from la sierra del Montsec la Cabrua fossil site, Pyrenees. In (Catalan, J. & Pretus, J. Ll.; eds) *XXV SIL Congress, Barcelona, Aug. 21–27.* Mid-Congress Excursions, 12-1–12-10.

GRIMALDI, D. & CUMMING, J. 1999. Brachyceran Diptera in Cretaceous ambers and Mesozoic diversification of the Eremoneura. *Bulletin of the American Museum of Natural History*, **239**, New York.

JARZEMBOWSKI, E. A. 1984. Early Cretaceous insects from southern England. *Modern Geology*, **9**, 71–93.

—— 1987. 'Early Cretaceous insects from southern England.' PhD thesis, University of Reading.

—— 1991. The Weald Clay of the Weald: report of 1988/9 Field Meetings. *Proceedings of the Geologists' Association*, **102**, 83–92.

—— 1995. Early Cretaceous insect faunas and palaeo-environment. *Cretaceous Research*, **16**, 681–693.

—— & CORAM, R. 1997 (for 1996). New fossil insect records from the Purbeck of Dorset and the Wealden of the Weald. *Proceedings of the Dorset Natural History & Archaeological Society*, **118**, 119–124.

KIRICHKOVA, A. I. & DOLUDENKO, M. P. 1996. New data on phytostratigraphy of the Jurassic deposits of Kazakhstan. *Stratigraphy and Geological Correlation*, **4**, 35–52 [in Russian].

KOLESNIKOV, C. M. 1964. Stratigraphy of the continental Cretaceous of Transbaikalia. *Trudy Limnologicheskogo Instituta SO AN SSSR [Proceedings of the Limnological Institute of the Siberian Branch of the Academy of Sciences, USSR]*, **4**, 5–138.

KOVALEV, V. G. 1981. The most ancient representatives of brachycerous flies from the Jurassic of Siberia. *Paleontologicheskiy Zhurnal [Paleontological Journal]*, **3**, 85–101 [in Russian].

—— 1986. Bibionomorpha et Asilomorpha. In: Insects in the Early Cretaceous ecosystems of West Mongolia. *Transactions of the Joint Soviet–Mongolian Palaeontological Expedition*, **28**, 127–154 [in Russian].

KRZEMIŃSKI, W. 1998. Origin and the first stages of evolution of the Diptera Brachycera. In (Ismay, J. W.; ed.) *Abstracts Volume, 4th International Congress of Dipterology, Oxford*, 113–114.

LACASA-RUIZ, A. & MARTÍNEZ-DELCLÒS, X. 1986. Fauna y Flora de los yacimentos Neocomienses del Montsec (Prov. Lérida). *Paleontologia y evolución*, **20**, 215–223.

LIAMINA, N. A. 1980. 'Stratigraphy and genetic types of Lower Cretaceous deposits in depressions to the South of the Vitim plateau.' PhD thesis, Irkutsk [in Russian].

MARTÍN-CLOSAS, C. & LÓPEZ-MORÓN, N. 1995. The charophyte flora. In (Martínez-Delclòs, X.; ed.) *International*

Symposium on Lithographic Limestones. Field trip guide book, Leida, 29–31.

MARTINSON, G. G. 1961. The Mesozoic and Cenozoic molluscs from continental deposits of the Siberian platform, Transbaikalia and Mongolia. *Trudy Baikalskoi limnologicheskoi stantsii AN SSSR [Proceedings of the Baikal Limnological Station of the AS, USSR]*, **19**, 1–332.

MOSTOVSKI, M. B. in press. A brief review of brachycerous flies (Diptera, Brachycera) in the Mesozoic with descriptions of some curious taxa. *Entomological Problems*.

NAGATOMI, A. 1982. The genera of Rhagionidae. *Journal of Natural History*, **16**, 31–70.

NARTSHUK, E. P. 1995. Taxonomic and faunistic data on the Rhagionidae (Diptera, Brachycera) of the northern Palaearctic. *Acta Zoologica Fennica*, **199**, 17–24.

POLYANSKY, B. V. & DOLUDENKO, M. P. 1978. On sedimentogenesis of the Upper Jurassic flyschoid deposits of the Karatau Mountain Ridge (southern Kazakhstan). *Lithology and Mineral Resources*, **3**, 78–88 [in Russian].

RASNITSYN, A. P., JARZEMBOWSKI, E. A. & ROSS, A. J. 1998. Wasps (Insecta: Vespida = Hymenoptera) from the Purbeck and Wealden (Lower Cretaceous) of southern England and their biostratigraphical and palaeoenvironmental significance. *Cretaceous Research*, **19**, 329–391.

REN, D., GUO, Z., LU, L., JI, S., TANG, F. & JING, Y. 1997. A further contribution to our knowledge of the Upper Jurassic Yixian Formation in western Liaoning. *Geological Review*, **43**, 449–459 [in Chinese].

SHCHERBAKOV, D. E., LUKASHEVICH, E. D. & BLAGODEROV, V. A. 1995. Triassic Diptera and initial radiation of the order. *International Journal of Dipterological Research*, **6**, 75–115.

SKOBLO, V. M. & LIAMINA, N. A. 1990. The continental Cretaceous of Transbaikalia, and the problems of intra- and interregional correlation. In (Krassilov, V. A.; ed.) *The continental Cretaceous of the USSR*. Far Eastern Branch of the USSR Academy of Sciences, Vladivostok, 85–90 [in Russian].

SWISHER, C. C., WANG, Y.-Q., WANG, X.-L., XU, X. & WANG, Y. 1999. Cretaceous age for the feathered dinosaurs of Liaoning, China. *Nature*, **400**, 58–61.

SZILÁDY, Z. 1934. Die Palaearktischen Rhagioniden. *Annales Musei Nationalis Hungarici*, **28**, 229–270.

THOMAS, A. G. B. 1978. Diptères torrenticoles peu connus: V. Les Rhagionidae (genre *Chrysopilus*) du sud de la France (Brachycera, Orthorrhapha). *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **114**, 305–331.

VAKHRAMEEV, V. A. & KOTOVA, I. Z. 1977. Ancient angiosperms and associated plants from the Lower Cretaceous deposits of Transbaikalia. *Paleontologicheskiy Zhurnal [Paleontological Journal]*, **4**, 101–109 [in Russian].

ZHANG, J., ZHANG, S. & LI, L. 1993. Mesozoic gadflies (Insecta: Diptera). *Acta Palaeontologica Sinica*, **32**, 662–672.

ZHARKOV, M. A., MURDMAA, I. O. & FILATOVA, N. I. 1998. Paleogeography of the Berriasian–Barremian stages of the Early Cretaceous. *Stratigraphy and Geological Correlation*, **6**, 49–72 [in Russian].

ZHERIKHIN, V. V. 1978. *Evolution and changes in the Cretaceous and Cenozoic faunistic assemblages*. Nauka, Moscow [in Russian].

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