

REDESCRIPTION OF *SIMULIDIUM PRISCUM* WESTWOOD AND *PSEUDOSIMULIUM HUMIDUM* (BRODIE) (INSECTA: DIPTERA: RHAGIONIDAE) FROM THE PURBECK LIMESTONE GROUP (LOWER CRETACEOUS) OF ENGLAND

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SYNOPSIS The holotype of *Simulidium priscum* Westwood, 1854 has been rediscovered in the collections of The Natural History Museum, London. It is a single wing from the Lulworth Formation (Berriasian) of Durlston Bay, Dorset. *S. priscum* and *Pseudosimulium humidum* (Brodie 1845) from the Lulworth Formation of Wiltshire are redescribed and placed within the Rhagionidae.

KEY WORDS *Simulidium*, *Pseudosimulium*, *Rhagionidae*, *Purbeck*, *Cretaceous*, *England*

INTRODUCTION

Recent work to re-organise and curate the fossil insect collection at The Natural History Museum, London (NHM) has resulted in the discovery of some unlabelled type specimens. In particular those from the Purbeck Limestone Group of England that were originally figured in Brodie (1845) and Westwood (1854) have been re-examined. Brodie and Westwood named some of the specimens and later Giebel (1856) and Handlirsch (1906–08) put names to many of the other figures. The Brodie collection of Purbeck fossil insects consists of about 2000 specimens but only about a quarter of the type and figured specimens had previously been labelled. So far 74 out of the 75 Purbeck specimens figured in Brodie (1845) and about half of the specimens figured in Westwood (1854) have been found (Clifford *et al.* 1994; Ross & Jarzembowski 1996). Continued close examination of the collection should reveal more type and figured specimens although, unfortunately, some (e.g. the type of *Libellulium agrias* Westwood, re-figured in Jarzembowski 1994) are clearly not present. Brodie's collection was purchased by the NHM in 1898, 1 year after his death and 53 years after the publication of his book. During his lifetime as a priest he moved many times

and lived in the counties of Wiltshire, Buckinghamshire, Gloucestershire and Warwickshire (Anon 1992); so it is not surprising that some specimens are missing. It is hoped that they will turn up in another museum.

One of the rediscovered types is that of *Simulidium priscum* Westwood, an enigmatic fly, the systematic placement of which had become the subject of some speculation because the type was presumed lost. Similarly, the placement of another fossil, *Pseudosimulium humidum* Brodie, was uncertain for a long time (Craig 1977). Both these taxa were originally assumed to be allied to *Simulium* (Simuliidae) and later considered to belong to the Ceratopogonidae by some authors. Both families are of medical importance today due to their blood-feeding habits and their fossils are of interest to scientists studying the origins of blood-feeding in insects.

Close examination has revealed that both *S. priscum* and *P. humidum* actually belong to the snipe fly family, the Rhagionidae. They both possess a sinuous Radius (R)₂₊₃ vein, which is one of the rhagionid autapomorphies according to Stuckenberg (2001). This family of predatory flies consists of 23 extant genera with about 530 extant species (Nagatomi 1982). Rhagionids are well represented in the fossil record, however most of them (other than those in

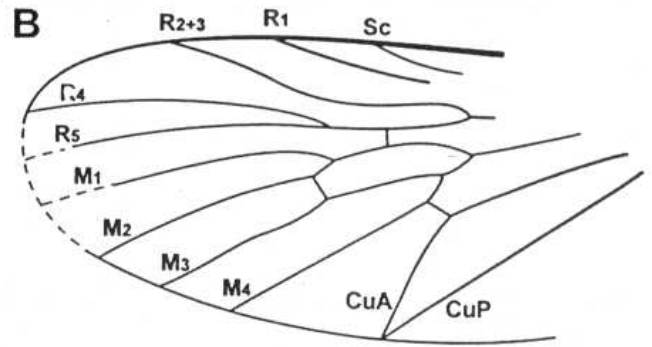
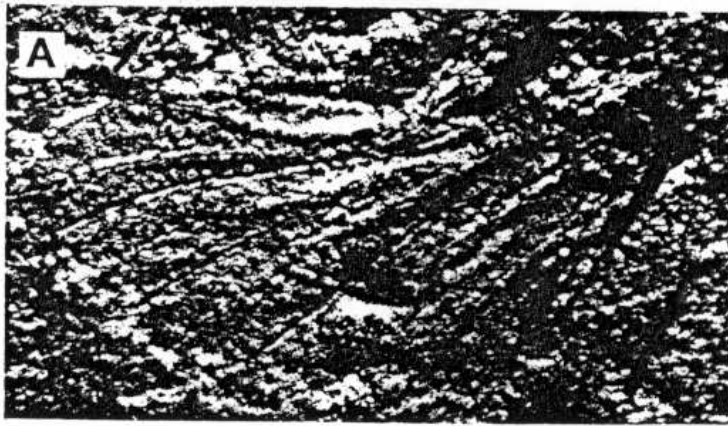


Figure 1 *Simulidium priscum* Westwood, NHM In.59266 (holotype), Lulworth Formation (Berriasian); Durlston Bay, Dorset; Brodie Collection. Length of wing 3.8 mm. A, photograph; B, camera lucida drawing.

amber) still await description. Evenhuis (1994) listed 24 genera and 48 extinct species of rhagionids known from the fossil record, mainly from the Mesozoic, and some other taxa have been recently added (Ansorge 1996; Kovalev & Mostovski 1997; Mostovski 2000; Mostovski & Jarzembowski 2000; Mostovski *et al.* 2000). The oldest are from the Lower Jurassic of Germany and India (Ansorge 1996; Mostovski & Jarzembowski 2000). Mesozoic rhagionids are important for elucidating the phylogeny of flies because this family forms the stem-group of the Brachycera.

SYSTEMATIC DESCRIPTIONS

Genus *SIMULIDIUM* Westwood, 1854

TYPE SPECIES. *Simulidium priscum* Westwood, 1854.

DIAGNOSIS. Vein Radius (R_{2+3}) sinuous, ending at Costa (C) not close to R_1 . Four medial veins. Basal part of Median (M_2) and intermedial cross-vein constitute right angle. Anal cell closed with a point stalk.

OCCURRENCE. Lower Cretaceous (Berriasian) of Dorset, England.

Simulidium priscum Westwood, 1854 (Figs 1A, B, 2)

- 1854 *Simulidium priscum* Westwood: 394, pl. 15, fig. 15.
 1856 *Simulidium priscum* Westwood; Giebel: 229.
 1879 *Simulidium priscum* Westwood; Goss: 142–143.
 1881–85 *Simulidium priscum* Westwood; Scudder in Zittel: 811, fig. 1087.
 1886 *Simulidium priscum* Westwood; Scudder: 93.
 1887 *Simulidium priscum* Westwood; Scudder in Zittel: 812, fig. 1104.
 1891 *Simulidium priscum* Westwood; Scudder: 226.
 1895 *Simulidium priscum* Westwood; Woodward: 392.
 1906–08 *Simulidium priscum* Westwood; Handlirsch: 629, pl. 51, fig. 3.
 1939 *Simulidium priscum* Westwood; Handlirsch: 161.
 1964 *Simulidium priscum* Westwood; Rohdendorf: 240.
 1974 *Simulidium priscum* Westwood; Rohdendorf: 271.
 1986 *Simulidium priscum* Westwood; Crosskey & Taylor: 401.
 1987 *Simulidium priscum* Westwood; Crosskey: 430.

1988 *Simulidium priscum* Westwood; Grogan & Szadziewski: 808–809.

1990 *Simulidium priscum* Westwood; Szadziewski: 231.

1990 *Simulidium priscum* Westwood; Crosskey: 58.

1992 *Simulidium priscum* Westwood; Szadziewski & Schlüter: 73.

1992 *Simulidium priscum* Westwood; Jarzembowski: 179.

1994 *Simulidium priscum* Westwood; Evenhuis: 113, 117.

1995 *Simulidium priscum* Westwood; Borkent: 12, 29, 84.

1996 *Simulidium priscum* Westwood; Szadziewski: 25.

HOLOTYPE. NHM Palaeontology Department In.59266. An isolated wing from the Lulworth Formation (Berriasian) of Durlston Bay, Dorset, England.

DESCRIPTION. Wing rather broad. Length preserved 3.8 mm, total length would have been 4.5 mm. Subcosta (Sc) close to R_1 . Vein R_1 long. Costal sections Sc– R_1 and R_1 – R_{2+3} subequal. RS ($R_{2+3} + R_4 + R_5$) and M stem and R_{4+5} and M_{1+2} forking at the same level. Fork R_{4+5} rather long. R_4 evenly arched. Cross-vein r–m occurs about halfway along the discal cell. M_1 and M_2 slightly divergent; M_2 , M_3 and M_4 subparallel. Discal cell narrow, with both anterior and posterior margins gently curved.

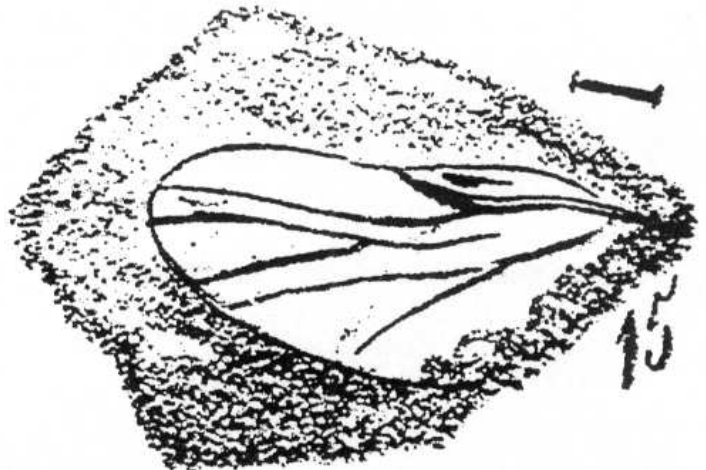


Figure 2 *Simulidium priscum* Westwood; original figure of holotype in Westwood (1854: pl. 15; fig. 15).

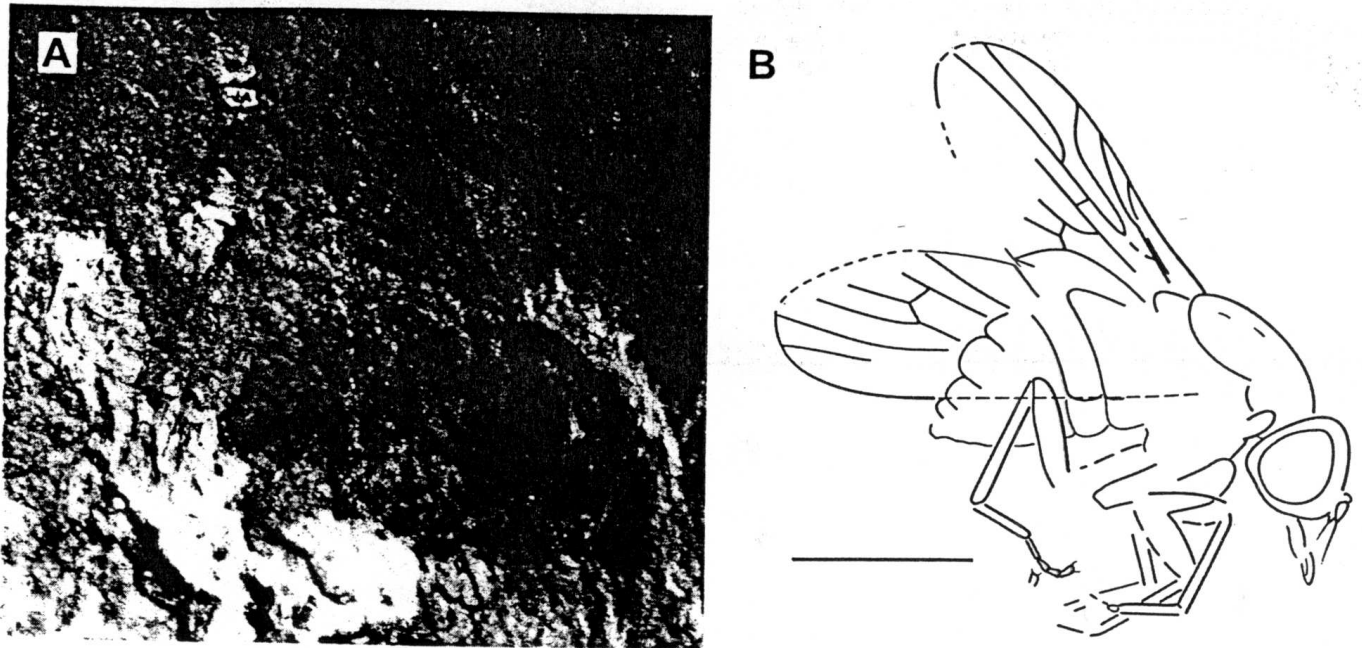


Figure 3 *Pseudosimulium humidum* (Brodie), specimen NHM I.3952 (holotype); Insect Limestone, Lulworth Formation (Berriasian); Dinton, Wiltshire; Brodie Collection. A, photograph; body length 2.6 mm. B, camera lucida drawing; scale bar = 1 mm.

Genus *PSEUDOSIMULIUM* Handlirsch, 1906

TYPE SPECIES. *Simulium? humidum* Brodie, 1845.

DIAGNOSIS. Third antennal segment ovoid, slightly tapered apically. Arista not stylate. R_{2+3} sinuous, ending at costa not close to R_1 . Four medial veins. Anal cell closed with point stalk.

OCCURRENCE. Lower Cretaceous (Berriasian) of Wiltshire, England.

Pseudosimulium humidum (Brodie, 1845) (Figs 3A, B, 4)

- 1845 *Simulium humidum* Brodie: 33, pl. 3, fig. 8.
- 1854 *Simulium humidum* Brodie; Morris: 119.
- 1856 *Simulium humidum* Brodie; Giebel: 229.
- 1879 *Simulium humidum* Brodie; Goss: 145.
- 1886 *Simulium humidum* Brodie; Scudder: 93.
- 1891 *Simulium humidum* Brodie; Scudder: 226.
- 1895 *Simulium humidum* Brodie; Woodward: 392.
- 1904 *Simulidium humidum* Brodie; Meunier: 404.
- 1906–08 *Pseudosimulium humidum* (Brodie); Handlirsch: 631, pl. 51, fig. 10.
- 1939 *Pseudosimulium humidum* (Brodie); Handlirsch: 162.
- 1954 *Pseudosimulium humidum* (Brodie); Hennig: 290.
- 1964 *Pseudosimulium humidum* (Brodie); Rohdendorf: 240.
- 1974 *Pseudosimulium humidum* (Brodie); Rohdendorf: 270.
- 1974 *Pseudosimulium humidum* (Brodie); Rubtzov: 250.
- 1977 *Pseudosimulium humidum* (Brodie); Craig: 175–178.
- 1981 *Pseudosimulium humidum* (Brodie); Peterson: 362.
- 1986 *Pseudosimulium humidum* (Brodie); Crosskey & Taylor: 401.
- 1987 *Pseudosimulium humidum* (Brodie); Crosskey: 430.
- 1988 *Pseudosimulium humidum* (Brodie); Szadziewski: 8.
- 1988 *Pseudosimulium humidum* (Brodie); Grogan & Szadziewski: 808.
- 1990 *Pseudosimulium humidum* (Brodie); Crosskey: 58.

- 1994 *Pseudosimulium humidum* (Brodie); Evenhuis: 288.
- 1995 *Pseudosimulium humidum* (Brodie); Borkent: 84.
- 1996 *Pseudosimulium humidum* (Brodie); Ross & Jarzembowski: i 13, fig. 1 (8).

HOLOTYPE. NHM Palaeontology Department I.3952. Female from the Insect Limestone, Lulworth Formation (Berriasian) of Dinton, Vale of Wardour, Wiltshire, England.

DESCRIPTION. Body compact. Body length 2.6 mm, wing length 2.4 mm. Second and third antennal segments of the same width. Arista approximately two times as long as third antennal segment. Cheeks narrow. Proboscis shorter than head length. Labella not enlarged. Mesonotum with hairs. Sc close to R_1 . Vein R_1 not long. Costal section Sc– R_1 somewhat longer than R_1 – R_{2+3} . RS forking before M stem, R_{4+5}

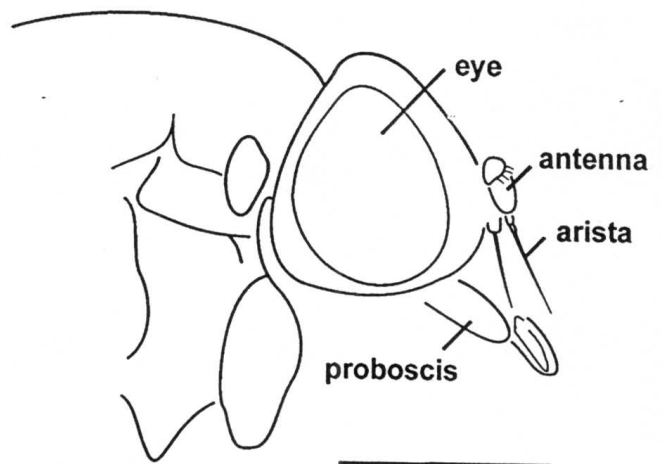


Figure 4 *Pseudosimulium humidum* (Brodie), detail of head of holotype, specimen NHM I.3952; Insect Limestone, Lulworth Formation (Berriasian); Dinton, Wiltshire; Brodie Collection. Scale bar = 0.5 mm.

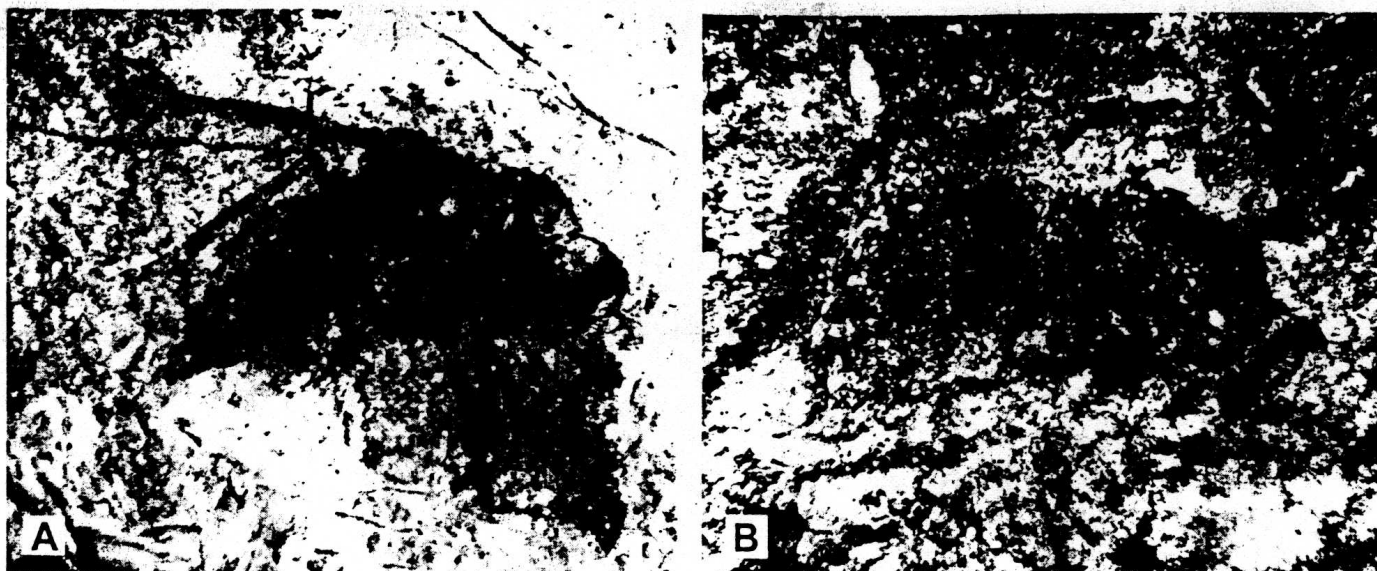


Figure 5 A, *Pseudosimulium* sp., specimen NHM I.3499; Insect Limestone, Lulworth Formation (Berriasian); Dinton, Wiltshire; Brodie Collection. Body length 3.0 mm. B, Indeterminate rhagionid, specimen NHM I.12706; Insect Limestone, Lulworth Formation (Berriasian); Dinton, Wiltshire; Brodie Collection. Body length 2.0 mm.

forking before M_{1+2} . Vein R_4 distinctly sinuous. Cross-vein $r-m$ occurs before midlength of discal cell, roughly at the level of basal part of M_4 . Discal cell rather long, slightly broadened distally. Medial veins subparallel or slightly divergent. Legs slender. At least fore and hind tibiae without apical spurs.

DISCUSSION

The wing impression on specimen In.59266 (Fig. 1A) appears to be the one that was figured and named as *Simulidium priscum* by Westwood (1854) due to the presence of a deep furrow lying anterior to vein R_{2+3} , which can be seen on Westwood's figure (Fig. 2). This is the only Purbeck dipteran at the NHM that displays this feature. Westwood (1854) did not draw the cross-veins, but it is probable that he could not see them because they are faint and only visible under high magnification with low angle lighting.

The specimen was only labelled 'Purbecks' but the growth of salt crystals over the surface of the specimen indicates it came from the coast. The majority of Brodie's Purbeck insects came from inland sites in Wiltshire and from Durlston Bay on the Dorset coast (Brodie 1854), therefore it is extremely likely that this specimen came from Durlston Bay. Westwood (1854) cited the specimen as having been collected from the Middle Purbecks of Durlston Bay, but the lithology of the specimen is a cream limestone containing fusainised plant debris, which is typical of the insect-bearing horizons in the Hard and Soft Cockle beds of the Lulworth Formation (Clements 1993) and which are regarded as Berriasian (Lower Cretaceous) in age (Rasnitsyn *et al.* 1998).

Westwood's (1854) incomplete figure of *Simulidium priscum* resulted in much confusion over the systematic placement of the taxon. Westwood (1854: 384) described it as 'the wing of a small Dipterous insect, apparently allied to *Simulium*' while Scudder in Zittel (1881–85) included *S. priscum* in the Simuliidae (black flies). Handlirsch (1906–08) transferred it to the Bibionidae (march flies) and then

Rohdendorf (1964) transferred it to the extinct Protopleciidae. Rubtsov (1974) doubted that *Simulidium* might be an ancestral simuliid. Grogan & Szadziwski (1988) suggested that *S. priscum* could belong to the Ceratopogonidae (biting midges), which would therefore make it the oldest fossil member of that family. Carpenter (1992) did not include *Simulidium* in his treatise (Clifford *et al.* 1994) while Evenhuis (1994) chose to retain it provisionally under the Protopleciidae following Rohdendorf (1964). The venation of *S. priscum* agrees with the diagnosis for the Rhagionidae and, therefore, the species belongs to that family. Nagatomi (1982) regards the shape of the female terminalia as being important for subfamilial placement. Since this is unknown in *Simulidium* it therefore cannot be placed in a subfamily.

Different opinions on the systematic position of *Pseudosimulium humidum* were summarised by Craig (1977), although generally most previous authors considered it was a simuliid. Craig (1977) rejected its position in the Simuliidae and suggested that it may be a ceratopogonid. Rubtsov (1974) considered that this fossil may belong to the Psychodidae and Kalugina (*in* Kalugina & Kovalev 1985) considered that it may belong to the Eoptychopteridae. The aristate antennae and wing venation indicate that this species belongs instead to the Rhagionidae. There are two similar specimens present in the collection of the Natural History Museum, London. Specimen I.3499 (Fig. 5A) is obviously a snipe fly female, 3.0 mm long, closely resembling the holotype. Unfortunately, although Craig (1977) included it under *P. humidum*, its assignment to this species is not possible due to its incomplete preservation. This specimen provides some important features. At least the hind tibiae appears to be lacking terminal spurs and it probably has three subspherical or somewhat elongated spermathecae that are poorly visible in the abdomen. Specimen I.12706 (Fig. 5B) is labelled '37 *Simulium?*'. Based on the shape of the antennae, wing venation features and its general appearance, this specimen may be included in the Rhagionidae as well. The shape of its antennae and body size is similar

to that of *P. humidum* but there are differences in the wing venation of I.12706, in particular Sc and R₁ are somewhat longer and it has a lower angle between R₁ and R₂₊₃. The specimen is incomplete, which prevents its allocation to either *P. humidum* with certainty or to a new species. The three specimens (I.3499, I.3952 and I.12706) are labelled 'Dinton' and are preserved in a light brown or grey micrite with fragments of fusain. This indicates that they probably came from Brodie's Insect Limestone, which lies below the Cinder Bed, in the Lulworth Formation (Ross & Jarzembowski 1996). The original figure from Brodie (1845) of the holotype is reproduced in Ross & Jarzembowski (1996).

Given that *S. priscum* and *P. humidum* are not ceratopogonids, then the oldest ceratopogonids (biting midges) are known from the Lower Cretaceous in Austrian and Lebanese amber (Szadziewski 1996; Borkent 1997, 2000, 2001), which are probably Hauterivian to Barremian in age. Ceratopogonids are also known from the slightly younger Alava amber (Szadziewski & Arillo 1998).

The comparison and identification of rhagionids described from isolated wings is difficult since wing venation features may vary considerably. However, *S. priscum* has the combination of two characters that separate it from most other rhagionids. These are the closed anal cell and the mutual position of the M₂ base and intermedial cross-vein, forming the right angle or nearly so. The same combination is found in the recent genus *Chrysopilus*, from which *S. priscum* differs in the shape of the vein R₂₊₃.

Scelorhagio mecomastigus Zhang, Zhang & Li 1993 from the Laiyang Formation (Lower Cretaceous) of China is similar to *Pseudosimulium humidum* but differs from it in the slightly larger size and in having the dorso-apical arista, petiolate anal cell and somewhat shorter costal R₁-R₂₊₃ section. The position of the arista is an important feature at the generic level and indicates that *Scelorhagio* is a separate genus.

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