



## First recorded evidence in the fossil record of snipe flies (Diptera: Rhagionidae) in Cretaceous amber, France

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### ARTICLE INFO

#### Article history:

Received 15 June 2009

Accepted in revised form 4 August 2009

Available online 11 August 2009

#### Keywords:

New species

*Novelaria*

*Chrysopilus*

Amber

Cretaceous

France

### ABSTRACT

*Novelaria*, a new genus of rhagionid of late Albian age with three new species, is the first record of this family from Charentes amber (southwestern France). The new genus is probably closely related to the recent genus *Chrysopilus*. However its relationship with the other fossils in amber is discussed. A key for separation of the new species is provided and the diversity of the family during the Cretaceous is also briefly discussed.

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### 1. Introduction

The Rhagionidae (snipe flies) are represented by 49 genera and about 700 species (Santos, 2008). Nagatomi (1982) and Kerr (2004) proposed the most recent reviews of living genera and phylogenetic analysis. Generally the larvae are predatory and terrestrial, however, the genus *Chrysopilus* (Thomas, 1978; Watson and Dallwitz, 2003) is found in aquatic habitats. Adults are typically found perching on the leaves of plants in the humid forests and woodlands of intertropical areas (Santos and Amorim, 2007).

Rhagionidae is an ancient family, the species *Gallia alsatica* Krzeminski and Krzeminska 2003 (Krzeminski and Krzeminska, 2003) are known from the Triassic of France. Most extinct genera were reviewed by Nagatomi and Yang (1998). The fossil record of Rhagionidae is very large, including unplaced species and genera, more than 40 genera and more than 80 species have already been described (see Table 2).

The Rhagionidae is well represented in amber specimens, particularly the brachyceran families (Haenni, 2003; Sontag, 2003; Perkovski et al., 2007). However, despite the large number of specimens the classification of the Rhagionidae is still far from certain. Nagatomi (1982) recognized four subfamilies: Glutopinae, Rhagioninae, Spaniinae, and Austroleptinae. However, Stuckenberg

(2001) proposed that the Rhagioninae, Spaniinae, and Austroleptinae were families, and within the Rhagionidae he highlighted three subfamilies; the Pagioninae, Pelecorhynchinae, and Bolbomyiinae. Most recently Kerr (2004) proposed four subfamilies for the Rhagionidae, the Spaniinae, Arthroceratinae, Chrysopilinae, and Rhagioninae, and elevated Bolbomyiinae to family level. The same author included a good overview of the history of the classification of the family.

The Archingeay-Les Nouillers amber where these new rhagionid inclusions were discovered has been dated to the Lower Cretaceous, uppermost Albian by Néraudeau et al. (2002). The palaeoenvironment is interpreted as influenced both by marine and freshwater inputs, in a “mangrove”-like habitat based on the invertebrate fauna found which comprises oysters, gastropods and marine bivalves, fossil plants, and on terrestrial and marine vertebrates (Néraudeau et al., 2002,2003; Perrichot, 2005).

### 2. Systematic palaeontology

#### 2.1. Material

The following specimens MNHN ARC226.11, MNHN ARC226.26, MNHN ARC226.38, and MNHN ARC226.41 are included in a piece of amber containing a high number of organisms such as Diptera: Brachycera and Nematocera, Heteroptera: Gerromorpha, Orthoptera: Grylloidea, Psocoptera, Blattodea, Hymenoptera, Lepidoptera, Araneae, and spicules of demospunges. The specimens are housed

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in the Laboratoire de Paléontologie, Muséum national d'Histoire naturelle, Paris. The specimens were embedded in Canada balsam between glass cover slips for study (see Perrichot, 2005, for a full description of the specimen preparation).

## 2.2. Locality and stratigraphic horizon

All the species described are from the Archingeay-Les Nouillers, Charente-Maritime, in southwestern France, dated to the Early Cretaceous, latest Albian (Néraudeau et al., 2002).

Order: Diptera  
 Infraorder: Tabanomorpha  
 Family: Rhagionidae Latreille, 1802  
 Genus *Novelaria* gen.nov.

*Type species.* *Novelaria aetheria* sp. nov., other species. *Novelaria una* sp. nov., *Novelaria magna* sp. nov.

*Derivation of name.* The genus name is derived from the name “Novelariens,” the demonym for the residents of the town of Les Nouillers.

*Diagnosis.* The new genus can be distinguished from all living and extinct genera by the combination of the following characters: presence of a long stalk to fork of M1–M2; vein M3 present, reaching wing margin; M arising clearly from Cu; sinuate R2+3 and close to R1; fork R4+5 basad to intermedial cross-vein; palpus one-segmented; antennal arista arising from first flagellomere centrally and with small basal aristonere; clypeus bulbous; no scale-like thoracic setae; metapleura setose; laterotergite setose; post-spiracular sclerite smooth; macrochaetae of hind tibia present; tibial spurs 1:2:1.

*Novelaria aetheria* sp. nov.  
 Fig. 1A–G

*Derivation of name.* The species name is derived from the Latin word for “eternal” referring to its eternal life as a fossil.

*Diagnosis.* More than two strong setae on fore tibia; four long and strong setae in anterior part of hind tibia; M3 ending almost parallel to M4; cross-vein cu-m almost reaching fork of M3–M4; first four segments of abdomen densely setose.

*Description.* Body: Female. Body length 2.62 mm, wing length about 2.00 mm, length of tibiae: fore 0.7 mm, mid 0.65 mm, hind 0.75 mm.

Head: Broadest width between eyes just above antenna, wide parafacial with some hairs, clypeus ending before antennae, antenna with long arista, flagellomere I and II aristate, thin, flagellomere III drop-shaped (Fig. 1C).

Wing: Costal vein circumambient; sinuate R2+3 and close to R1; R5 straight, R4 arising from R5 with sharp bend at base, fork R4+5 basad of intermedial cross-vein; stalk to fork of M1–M2 longer than cross-vein of discal cell; M arising clearly from CuA; M3 ending almost parallel to M4; cross-vein m-cu almost reaching fork of M3–M4; anal cell petiolate; pterostigma pale from fork RS–R2+3 and reaching wing margin from R1 to R2+3 (Fig. 1B only drawn in part).

Thorax: Mesoprescutum, mesoscutum and mesoscutellum densely setose, metapleura setose (Fig. 1C).

Legs: All legs densely setose; fore tibia with row of at last seven strong setae; mid tibia with nine apical setae strong; hind tibia with four long and strong setae; tibial spurs with following combination 1:2:1; empodium pulvilliform, pulvilli shorter than empodium (Fig. 1D, E and G).

Abdomen: First four abdominal segments densely setose, apical segments bare, abdomen elongated and reduced gradually in size, abdominal segments 5, 6, and 7 rather swollen.

*Material.* Holotype MNHN ARC226.11.

*Novelaria una* sp. nov.

Fig. 2A–F

*Derivation of name.* The species name is derived from the Latin words for “only one” because of the characters: only one tibial spur and one strong seta on fore tibia.

*Diagnosis.* Only one strong seta on fore tibia; a series of about ten strong but short setae on hind tibia; M3 ending almost parallel to M4; cross-vein cu-m arising at 2/3 the length of cu-m behind fork of M3–M4.

*Description.* Body: Female. Body length 2.34 mm, wing length about 2.05 mm, length of tibiae: fore 0.74 mm, mid unknown, hind 0.84 mm.

Head: Broad width between eyes just above antenna, parafacial wide with some setulae, clypeus ending before antennae, antenna with long arista, flagellomere I and II aristate, thin, flagellomere III drop-shaped.

Wing: Costal vein circumambient; sinuate R2+3 and close to R1, R5 straight, R4 arising from R5 with sharp bend at its base, fork R4+5 basad of intermedial cross-vein, stalk to fork of M1–M2 longer than cross-vein of discal cell, M arising clearly from CuA, M3 ending almost parallel to M4, cross-vein m-cu arising at 2/3 length of cu-m behind fork of M3–M4, anal cell petiolate; pterostigma from fork RS–R2+3 and reaching wing margin from Sc to R2+3 (Fig. 2C).

Thorax: Mesoprescutum, mesoscutum, and mesoscutellum densely setose, metapleura lightly setose.

Legs: All legs densely setose, fore tibia with only one strong seta, tibial spurs with following combination 1:2:1, part of mid tibia lost, hind tibia with more than 10 strong setae; empodium pulvilliform, pulvilli shorter than empodium (Fig. 2)D–F.

Abdomen: All segments densely hairy.

*Material.* Holotype MNHN ARC226.36.

*Novelaria magna* sp. nov.

Fig. 3A–G

*Derivation of name.* The species name is derived from the Latin word for “big” because it is the largest species of the genus.

*Diagnosis.* Large body, 3.35 mm long; fore tibia with two strong but short setae; series of about ten strong setae on hind tibia; M3 ending very close to M4; cross-vein cu-m reaching fork of M3–M4; pterostigma from fork RS–R2+3 and reaching wing margin from R1 to R2+3.

*Description.* Body: Female. Body length 3.35 mm, wing length about 2.36 mm, length of tibiae: fore and mid in difficult positions to estimate their length, hind 0.9 mm.

Head: Broadest width between eyes just above antenna, parafacial wide with some setae, clypeus ending before antennae, antenna with long arista, flagellomere I and II aristate, thin, flagellomere III drop-shaped (Fig. 3C).

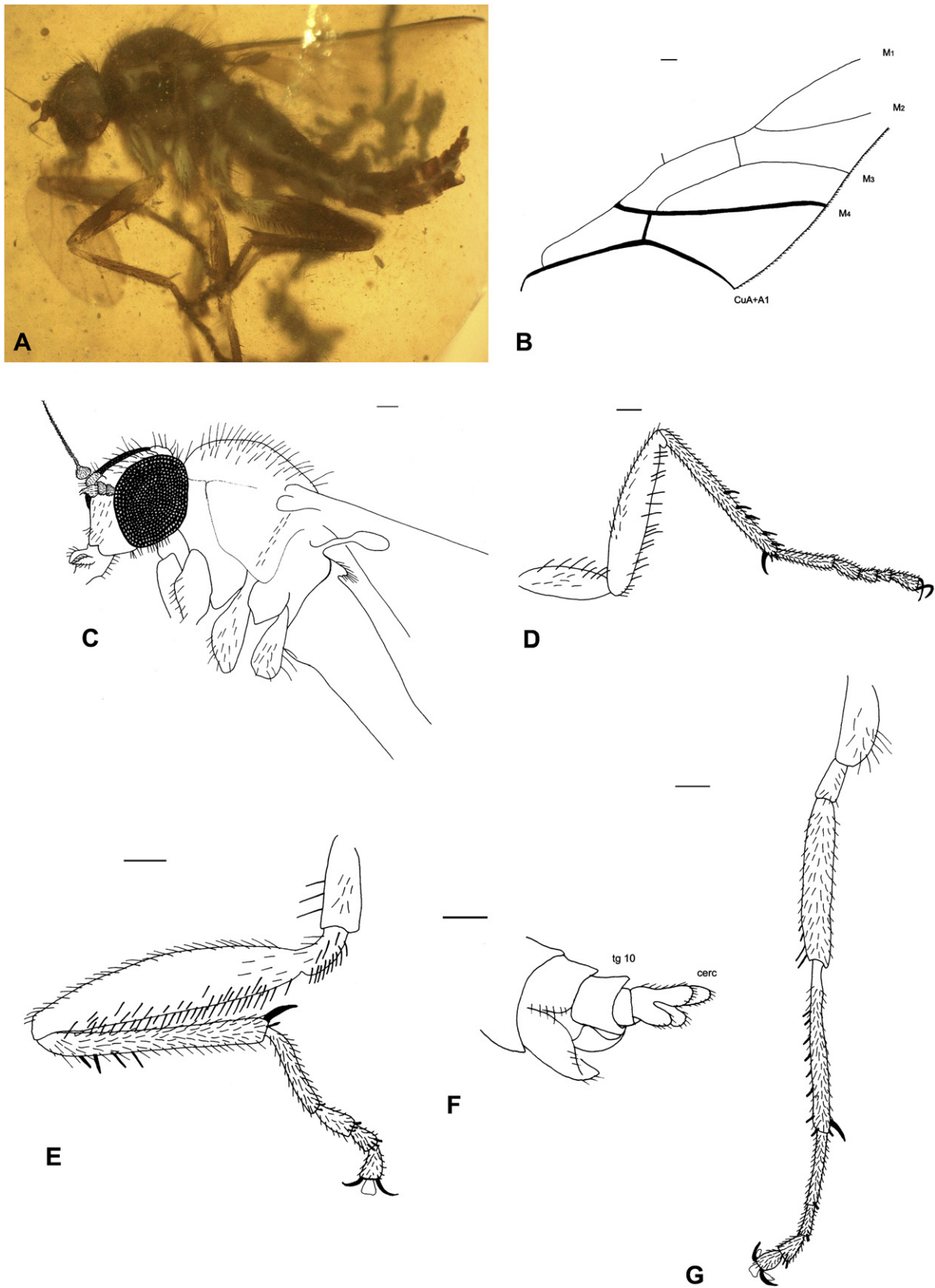
Wing: Costal vein circumambient, thinner beyond R5; sinuate R2+3 and close to R1, R5 straight, R4 arising from R5 with sharp bend at its base, fork R4+5 basad of intermedial cross-vein, stalk to fork of M1–M2 longer than cross-vein of discal cell, M arising clearly from CuA, M3 ending very close to M4, cross-vein m-cu reaching fork of M3–M4; anal cell petiolate; pterostigma pale from fork RS–R2+3 and reaching wing margin from R1 to R2+3 (Fig. 3B).

Thorax: Mesoprescutum, mesoscutum and mesoscutellum densely setose, metapleura densely setose (Fig. 3C).

Legs: All legs densely setose, fore tibia with two strong setae, mid tibia with at last three strong setae, hind tibia with at last 10 strong setae, tibial spurs with the following combination 1:2:1, empodium pulvilliform, pulvilli shorter than empodium (Fig. 3D–F).

Abdomen: All segments densely setose.

*Material.* Holotype MNHN ARC226.38.



**Fig. 1.** A, habitus of *Novelaria aetherius* sp. nov. ARC 226.11; B, part of the wing; C, head and thorax; D, foreleg; E, hind leg; F, female genitalia; G, mid leg. Scale bar represents 0.1 mm.

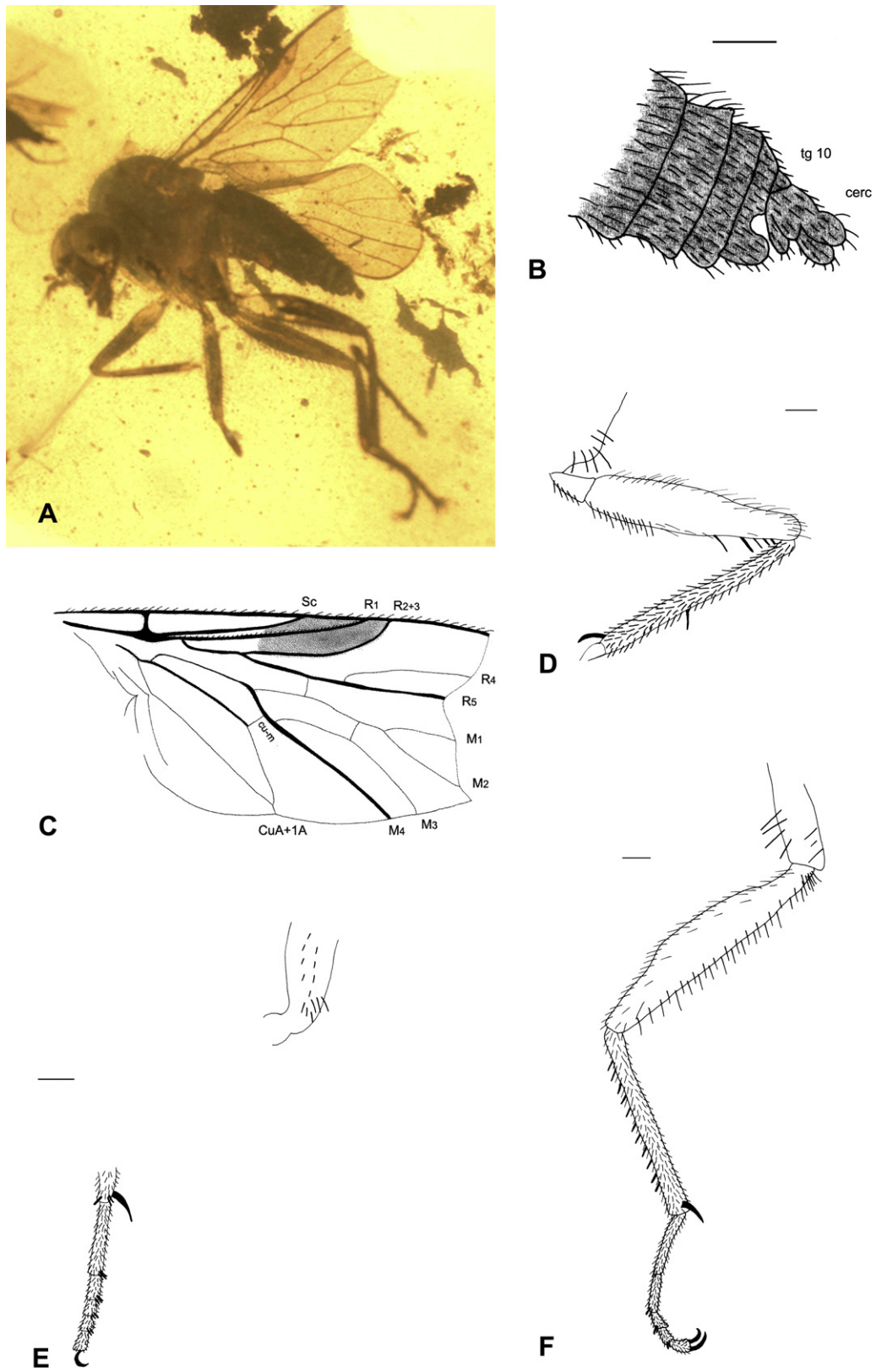


Fig. 2. A, habitus of *Novelaria una* sp. nov. ARC 226.36; B, female genitalia; C, wing; D, fore leg; E, mid leg; F, hind leg. Scale bar represents 0.1 mm.

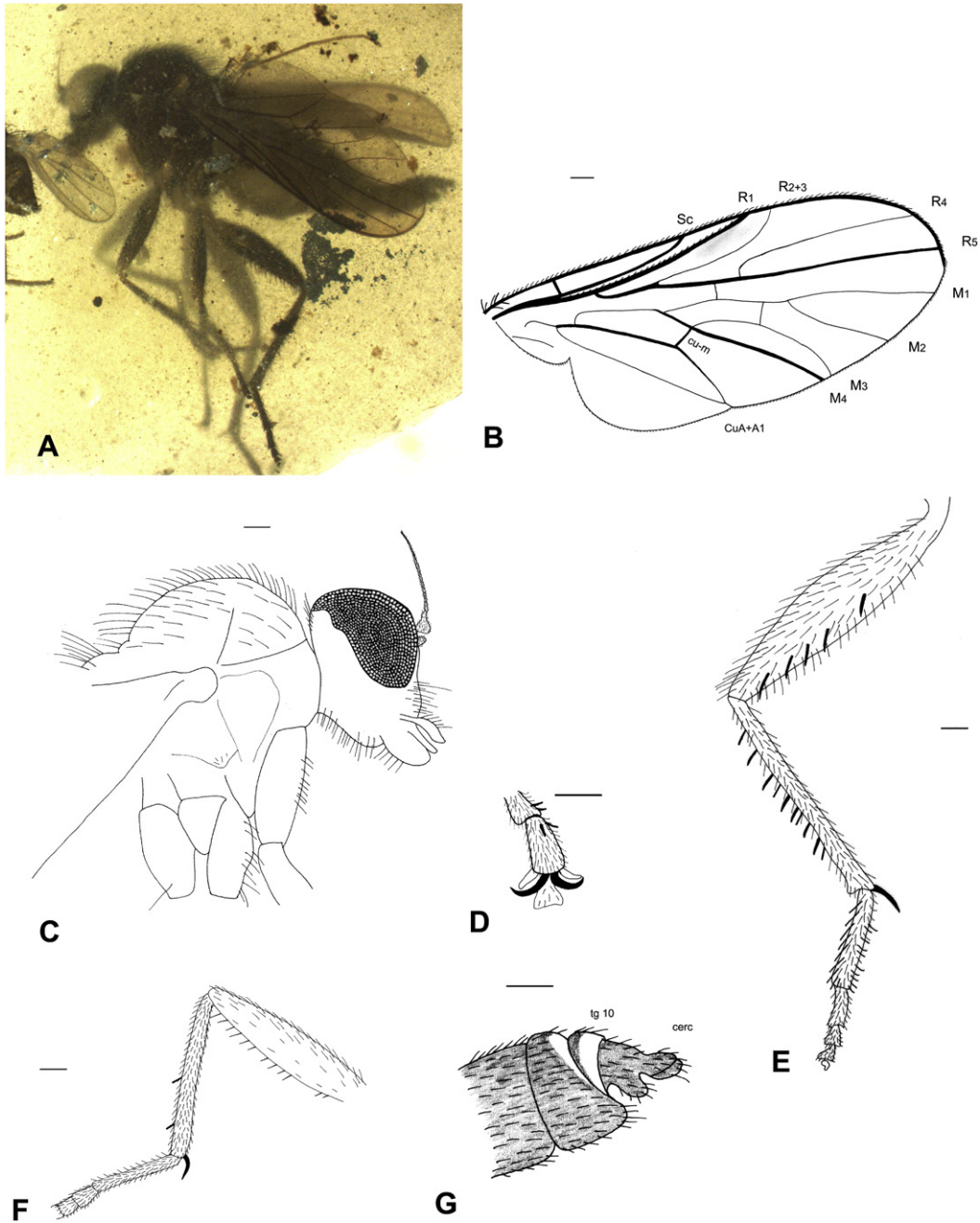


Fig. 3. A, habitus of *Novelaria magna* sp. nov. ARC 226.38; B, wing; C, head and thorax; D, tarsus; E, hind leg; F, mid leg; G, female genitalia. Scale bar represents 0.1 mm.

**3. Key: species of *Novelaria***

- 1. Long strong setae on fore tibia ... 2
  - Short strong seta on fore tibia ... 3
- 2. One strong seta on fore tibia; a series of about ten strong but short setae on hind tibia; M3 ending almost parallel to M4; cross-vein cu-m arising at 2/3 the length of cu-m behind fork of M3-M4. ... *una*
  - More than two strong setae on fore tibia, four long and strong setae in anterior part of hind tibia; M3 ending almost parallel to M4; cross-vein cu-m almost reaching fork of M3-M4; first four segments of abdomen densely setose ... *Aetheria*
- 3. Fore tibia with two strong short setae; series of about ten strong setae on hind tibia; M3 ending very close to M4; cross-

vein cu-m reaching fork of M3-M4; pterostigma from fork RS-R2+3 and reaching wing margin from R1 to R2+3 ... *magna*

**4. Discussion**

According to Nagatomi (1977) *Novelaria* gen. nov. should be assigned to the Rhagionidae because of the following characters: basisternum separated from episternum; vein Rs arising much before base of discal cell; mid-lower part of face swollen; 2nd submarginal cell long and rather narrow; vein 1A straight or nearly so; gena (below the palpus) without a large bulbous protuberance; palpus longer and without an apical pit or a transverse section; alula present; plane of scutellum convex. Nagatomi (1977) also

**Table 1**  
Comparison of the new genus *Novelaria* with the possible closely related genera

	<i>Novelaria</i>	<i>Chrysopilus</i>	<i>Schizella</i>	<i>Stylospania</i>	<i>Paleochrysopilus</i>	<i>Ptiolinites</i>
wings	<ul style="list-style-type: none"> <li>– long stalk to fork of M<sub>1</sub>-M<sub>2</sub></li> <li>– M arising from Cu</li> <li>– distance between apices of R<sub>1</sub> and R<sub>2+3</sub> shorter than that between Sc and R<sub>1</sub></li> <li>– pterostigma present</li> <li>– anal cell petiolate</li> </ul>	<ul style="list-style-type: none"> <li>– normally without stalk fork of M<sub>1</sub>-M<sub>2</sub></li> <li>– M arising from Cu</li> <li>– distance between apices of R<sub>1</sub> and R<sub>2+3</sub> shorter than that between Sc and R<sub>1</sub></li> <li>– pterostigma present</li> <li>– anal cell petiolate</li> </ul>	<ul style="list-style-type: none"> <li>– without stalk fork of M<sub>1</sub>-M<sub>2</sub></li> <li>– wing vein M<sub>3</sub> present</li> <li>– R<sub>1</sub> and R<sub>2+3</sub> close together at wing margin</li> <li>– pterostigma present</li> <li>– Anal cell open</li> </ul>	<ul style="list-style-type: none"> <li>– without stalk fork of M<sub>1</sub>-M<sub>2</sub></li> <li>– wing vein M<sub>3</sub> present</li> <li>– R<sub>1</sub> and R<sub>2+3</sub> close together at wing margin</li> <li>– pterostigma present</li> <li>– anal cell petiolate</li> </ul>	<ul style="list-style-type: none"> <li>– stalk to fork of M<sub>1</sub>-M<sub>2</sub></li> <li>– M incomplete</li> <li>– distance between apices of R<sub>1</sub> and R<sub>2+3</sub> longer than that between Sc and R<sub>1</sub></li> <li>– pterostigma not present</li> <li>– anal cell petiolate</li> </ul>	<ul style="list-style-type: none"> <li>– stalk to fork of M<sub>1</sub>-M<sub>2</sub></li> <li>– M complete?</li> <li>– distance between apices of R<sub>1</sub> and R<sub>2+3</sub> longer than that between Sc and R<sub>1</sub></li> <li>– pterostigma present</li> <li>– anal cell closed or nearly so, but not petiolate</li> </ul>
antenna	arista arising from first flagellomere apically, arista with small basal aristonere	arista arising apically from first flagellomere	arista produced ventrally from first flagellomere	arista produced ventrally from first flagellomere	aristate with small basal aristonere	stylate annulated
legs	empodium pulvilliform tibial spurs 1:2:1	empodium pulvilliform tibial spurs 1:2:1	empodium pulvilliform tibial spurs 1:2:1	empodium pulvilliformtibial spurs 1:2:1	empodium setiform tibial spurs? 1:2:1	? ?

mentioned the presence of tibial spurs with the following possible combinations 0:2:0, 0:2:1, 0:2:2, or 1:2:2 for the family. However the spurs are present at last on the mid tibia and one or two are usually present on the hind tibia (James and Turner, 1981). According to the definition of Stuckenberg (2001) *Novelaria* gen. nov. should be assigned to the Rhagionidae because of the pronounced telescoping of the female post-abdomen; female cerci closely adjacent dorsally; and R<sub>2+3</sub> with curvature beneath pterostigma. However, Zloty et al. (2005) consider the telescoping post-abdomen as a plesiomorphic character.

According to Nagatomi (1982) *Novelaria* probably belongs to the Rhagioninae, the most primitive subfamily of Rhagionidae (Kerr, 2004), because the female cercus is bi-segmented and the two segments are contiguous with each other, the first segment is not dilated; female sternum 9 absent; female tergum 10 well developed; face swollen; and antennal segment 3 with a long arista. According to Stuckenberg (2001) *Novelaria* would be best assigned to the Rhagioninae because the mesothoracic laterotergite is setose; R<sub>4</sub> strongly curved; and R<sub>5</sub> aligned with R<sub>4+5</sub>. Together with three fossil genera, *Paleochrysopilus* Grimaldi and Cumming, 1999, *Ptiolinites* Kovalev, 1986, and *Achrysopilus* Zhang et al., 2008 *Novelaria* share the presence of a stalk to the fork of M<sub>1</sub>-M<sub>2</sub>. However Stuckenberg (2001) mentioned that most probably *Paleochrysopilus* does not belong to the Rhagionidae because of the number of abdominal tergites and the setiform empodium, not typical for the Rhagionidae. *Ptiolinites* have the anal cell closed or nearly so, but not petiolate as it is the case of *Novelaria*. Finally, *Achrysopilus* differ from *Novelaria* by the distance between cross-vein r-m and fork R<sub>4+5</sub>.

*Novelaria* shares with the recent genus *Chrysopilus* (Macquart, 1826) a characteristically short distance between the apices of R<sub>1</sub> and R<sub>2+3</sub>, M arising from Cu, presence of a pterostigma, anal cell petiolate, and in some populations of *Chrysopilus* the stalked M<sub>1+2</sub> (Mostovski, pers. comm., 2009). However the combination of the characters of *Novelaria* indicates conclusively that this is a new genus (see Table 1).

Following the key to the recent rhagionid genera of Kerr (2004), *Novelaria* would fall near the group of three genera *Chrysopilus*, *Schizella*, and *Stylospania* (*Chrysopilinae* Bezzi, 1903 sensu Kerr) based on the following key characters: clypeus bulbous; post-spiracular sclerite smooth; one hind tibial spur; wing vein M<sub>3</sub> present, reaching wing margin; laterotergite setose; macrochaetae of hind tibia present; and palpus one-segmented. Nevertheless

*Novelaria* lacks scale-like thoracic setae with structural colour, which is present in *Chrysopilus* and *Schizella* but not in *Stylospania*. However, *Novelaria* shares with *Chrysopilus* an aristate antenna arising apically from the first flagellomere and not ventrally as found in *Schizella* and *Stylospania*.

Genital characteristics cannot be used in order to distinguish the three different species of *Novelaria* as the rhagionid female post-abdomen is strongly telescopic and contains wide intersegmental membranes greatly increasing the length of abdomen when fully extended (Stuckenberg, 2001). It is likely that the difference in the form and length of abdomen and genitalia could be due to taphonomical bias.

## 5. Conclusions

Mostovski (2000) and Mostovski (2008) suggest that the diversity and abundance of snipe flies were especially great during the Jurassic and gradually decreased during the Cretaceous. However, more and more Cretaceous fossils have since been discovered (see Table 2), e.g., in Spanish amber 10 exemplars from Peñacerrada (Provincia de Álava) and one from San Just (Provincia de Teruel) which are waiting for formal description (Arillo pers. comm., 2009). A further 24 rhagionids from the Lower Cretaceous of Russia are also waiting to be described (Mostovski, 2000). Arillo et al. (2009) also described a species of the genus *Litoleptis* from Spanish amber, and placed it within the family Spaniidae, a family closely related to Rhagionidae (Stuckenberg, 2001) and considered by other authors as a rhagionid subfamily (Wiegmann et al., 2000; Yates, 2002; Kerr, 2004). During the Jurassic to the Eocene, rhagionid fossils are very frequent, suggesting that the family was diverse and widely distributed. However during the Miocene the fossil record decreased notably, at least in the Mexican and Dominican ambers (Solórzano Kraemer pers. obs.).

The decrease of the abundance after the Eocene could be a consequence of the gradual global cooling, which began after the Paleocene-Eocene boundary (Zachos et al., 2001). The palaeoenvironment of the Archingey-Les Nouillers amber can be reconstructed as close to aquatic and sandy biotopes because of the presence of aquatic insects as Gerridae and Mesoveliidae, among other arthropods. In the same piece of amber spicules of demosponges have been found (Girard et al., 2008) indicating the proximity of the tree resin to the marine coast.

**Table 2**

List of rhagionid genera with fossil species (arranged according to geological age), modified and updated from Evenhuis (1994) with the following references: Grimaldi & Cumming (1999), Hong et al. (1992), Mostovski (2000,2008), Mostovski and Jarzembowski (2000), Mostovski (2000), Krzeminski and Krzeminska (2003), Zhang et al. (2006, 2008), Engel and Gross (2008), and Santos (2008)

Genus	No Species	Region	Stratigraphic position
<b>Gallia</b> Krzeminski and Krzeminska, 2003	<i>Gallia alsatica</i> Krzeminski and Krzeminska, 2003	France	Early/Middle Triassic
<b>Palaeobrachyceron</b> Kovalev, 1981	<i>Palaeobrachyceron willmanni</i> Ansoerge, 1996	Germany	Lower Jurassic
<b>Grimmia</b> Ansoerge, 1996	<i>Grimmia baltica</i> Ansoerge, 1996	Germany	Lower Jurassic
<b>Taschigatra</b> Mostovski and Jarzembowski, 2000	<i>Taschigatra bharataya</i> Mostovski and Jarzembowski, 2000	India	Lower Jurassic
	<i>Taschigatra tulyabhijana</i> Mostovski and Jarzembowski, 2000		
<b>Liassobrachyceron</b> Krzeminski & Ansoerge, 2005	<i>Liassobrachyceron kotejai</i> Krzeminski & Ansoerge, 2005	Germany	Lower Jurassic
<b>Ija</b> Kovalev, 1981	<i>Ija problematica</i> Kovalev, 1981	Russia (Siberia)	Middle Jurassic
<b>Palaeobolbomyia</b> Kovalev, 1982	<i>Palaeobolbomyia sibirica</i> Kovalev, 1982	Russia (Siberia)	Middle Jurassic
<b>Kubekovia</b> Kovalev in Kalugina & Kovalev, 1985	<i>Kubekovia accessoria</i> Kovalev in Kalugina & Kovalev, 1985	Russia (Siberia)	Middle Jurassic
<b>Sinorhagio</b> Zhang et al., 2006	<i>Sinorhagio daohugouensis</i> Zhang et al., 2006	Mongolia	Middle Jurassic
<b>Achrysopilus</b> Zhang et al., 2008	<i>Achrysopilus neimenguensis</i> Zhang et al., 2008	Mongolia	Middle Jurassic
<b>Jurabrachyceron</b> Kovalev, 1981	<i>Jurabrachyceron abbreviatum</i> Kovalev, 1981	Russia (Siberia)	Middle/Upper Jurassic
<b>Palaeobrachyceron</b> Kovalev, 1981	<i>Palaeobrachyceron handlirschi</i> Kovalev, 1981	Russia (Siberia)	Middle/Upper Jurassic
	<i>Palaeobrachyceron hennigi</i> Kovalev, 1981		
	<i>Palaeobrachyceron nagatomii</i> Kovalev, 1981		
	<i>Palaeobrachyceron rohdendorfi</i> Kovalev, 1981		
	<i>Palaeobrachyceron steyskali</i> Kovalev, 1981		
<b>*Archirhagio</b> Rohdendorf, 1938	<i>Archirhagio obscurus</i> Rohdendorf, 1938	Kazakhstan	Middle/Upper Jurassic
<b>Palaeobolbomyia</b> Kovalev, 1982	<i>Palaeobolbomyia kazakhstanica</i> Mostovski, 2000	Kazakhstan	Middle/Upper Jurassic
	<i>Palaeobolbomyia devia</i> Mostovski, 2000	China	
	<i>Palaeobolbomyia mongolica</i> Mostovski, 2000	Mongolia	
<b>Palaeostratiomyia</b> Rohdendorf, 1938	<i>Palaeostratiomyia pygmaea</i> Rohdendorf, 1938	Kazakhstan	Middle/Upper Jurassic
<b>Protorhagio</b> Rohdendorf, 1938	<i>Protorhagio capitatus</i> Rohdendorf, 1938	Kazakhstan	Middle/Upper Jurassic
	<i>Protorhagio karataviens</i> Mostovski, 2008		
	<i>Protorhagio ponomarenkoi</i> Mostovski, 2008		
	<i>Protorhagio ruptus</i> Mostovski, 2008		
<b>Palaeobolbomyia</b> Kovalev, 1982	<i>Palaeobolbomyia yakutensis</i> Mostovski, 2000	Russia (Yakutiya)	Upper Jurassic
	<i>Palaeobolbomyia angustalata</i> Mostovski, 2000		
<b>Mesorhagiophryne</b> Hong & Wang, 1990	<i>Mesorhagiophryne incerta</i> Hong & Wang, 1990	China	Upper Jurassic
	<i>Mesorhagiophryne robusta</i> Hong & Wang, 1990		
<b>Mesostratiomyia</b> Hong & Wang, 1990	<i>Mesostratiomyia laiyangensis</i> Hong & Wang, 1990	China	Upper Jurassic
<b>Stratiomyopsis</b> Hong & Wang, 1990	<i>Stratiomyopsis robusta</i> Hong & Wang, 1990	China	Upper Jurassic
<b>Scelorhagio</b> Zhang, 1993	<i>Scelorhagio mecomastigus</i> Zhang, 1993	China	Upper Jurassic
<b>Basilorhagio</b> Ren et al., 1995	<i>Basilorhagio venustus</i> Ren et al., 1995	China	Upper Jurassic
<b>Oiobrachyceron</b> Ren, 1998	<i>Oiobrachyceron limnogenus</i> Ren, 1998	China	Upper Jurassic
<b>Oiobrachyceron</b> Ren, 1998	<i>Oiobrachyceron chinensis</i> Ren, 1998	China	Upper Jurassic
<b>Pauromyia</b> Ren, 1998	<i>Pauromyia oresbia</i> Ren, 1998	China	Upper Jurassic
<b>Arthroteles</b> Bezzi, 1926 (probably <i>Palaeoarthroteles</i> Mostovski pers. comm. 2009)	Unidentified spp.	Russia (Siberia)	Upper Jurassic/Lower Cretaceous
<b>Palaeoarthroteles</b> Kovalev & Mostovski 1997	<i>Palaeoarthroteles mesozoicus</i> Kovalev & Mostovski, 1997	Trasbaikalia	Upper Jurassic/Lower Cretaceous
<b>Ptiolina</b> Zetterstedt, 1842	Unidentified sp. Jarzembowski, 1984	England	Lower Cretaceous
<b>Atherimorpha</b> White, 1914	<i>Atherimorpha festuca</i> Jell & Duncan, 1986	Australia	Lower Cretaceous
<b>Mongolomyia</b> Kovalev, 1986	<i>Mongolomyia latitarsis</i> Kovalev, 1986	Mongolia	Lower Cretaceous
<b>Longhuaia</b> Hong et al., 1992	<i>Longhuaia orientalis</i> Hong et al., 1992	China	Lower Cretaceous
<b>Paleochrysopilus</b> Grimaldi & Cumming, 1999	<i>Paleochrysopilus hirsutus</i> Grimaldi & Cumming, 1999	Lebanon	Lower Cretaceous
<b>Mesobolbomyia</b> Grimaldi & Cumming, 1999	<i>Mesobolbomyia acraei</i> Grimaldi & Cumming, 1999	Lebanon	Lower Cretaceous
<b>Genus A</b> (Grimaldi & Cumming 1999)	Unidentified sp.	Lebanon	Lower Cretaceous
<b>Genus C</b> (Grimaldi & Cumming 1999)	Unidentified sp.	Lebanon	Lower Cretaceous
<b>Genus D</b> (Grimaldi & Cumming 1999)	Unidentified sp.	Lebanon	Lower Cretaceous

(continued on next page)



## Acknowledgements

We thank CNRS (Centre national de la recherche scientifique) for the funds provided for this research. Thanks are due also to Didier Néraudeau and Vincent Perrichot for discussion and who provided the material used for this investigation and to Jonathan Codd for grammar correction. This paper is a contribution to the CNRS ANR program “AMBRACE” (project n BLAN07-1-184190). We are grateful to Thierry Guyot (Univ. La Rochelle) who collected and gave us the piece of amber with the fossils described herein.

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