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First confirmation of spongillaflies (Neuroptera: Sisyridae) from the Cretaceous

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ABSTRACT

New fossil spongillaflies (Neuroptera: Sisyridae) are described from Upper Cretaceous (Santonian) Taimyr amber of northern Siberia: *Prosisyrina sukachevae* gen. et sp. nov. from the Yantardakh locality, and *Prosisyrina* sp. from the Ugolyak locality. These are the first confident sisyrid occurrences in the Mesozoic. *Prosisyrina* gen. nov. is most closely related to the extant tropical genus *Sisyrina*, and to a lesser extent the Eocene *Paleosisyra*. The fossil records of Sisyridae, freshwater sponges and bryozoans are reviewed, and their associations discussed. These Santonian Taimyr sisyrids reasonably imply the possible presence of Spongillina in fresh water near these localities, although freshwater sponges are yet not recorded from the Mesozoic of Eurasia.

1. Introduction

Spongillaflies (Sisyridae) today constitute a small family of little more than 70 extant species in four genera distributed world-wide (Oswald, 2013). Their larvae are aquatic, associated with freshwater sponges and bryozoans (Parfin and Gurney, 1956; Tjeder, 1957; Weissmair, 1994, 1999, 2005).

Sisyrids are considered to be one of the most ancient taxa among extant Neuroptera, and so their position among basal families recovered in many phylogenies of the order is quite reasonable (e.g., Haring and Aspöck, 2004; Winterton et al., 2010; Yang et al., 2012). The family is sometimes even considered as sister to remaining Neuroptera (Zimmermann et al., 2011; Randolf et al., 2013, 2014). Their wing venation is most similar to that of some Permian representatives of Permithonidae (e.g., see Martynov, 1933). Nevertheless, fossil sisyrids were hitherto confidently known only from a few localities of the European Cenozoic (i.e., Oise amber, Baltic amber, Bembridge Mals, and Murat, see below), and in general they are very rare at these localities, except for Oise amber (Cockerell, 1917; Jarzembowski, 1980; Wichard and Weitschat, 1996, 2004; Nel and Jarzembowski, 1997; Erichson and Weitschat, 2000; Nel et al., 2003; Scheven, 2004; Weitschat and Wichard, 1998; Wichard, 2005; Wichard et al., 2009).

There are two records of Sisyridae from the Mesozoic, but neither are confirmed as members of the family. A first-instar larva was recorded from the Upper Cretaceous Taimyr locality at Yantardakh (Zherikhin, 1978), but it has never been illustrated or described. Unfortunately, this fossil is now lost (I.D. Sukacheva, pers. comm.). The second is a poorly-preserved adult from the upper Aptian Crato Formation of Brazil, described as ‘Sisyridae? gen. et sp. indet.’ (Martins-Neto, 1992) and later named *Cratosisyrops gonzagai* Martins-Neto, 1997. Unfortunately, the preserved characters of this specimen as described and illustrated by Martins-Neto (1992, Fig. 2) do not allow a confident family determination, and therefore we do not consider this species to belong to the Sisyridae until the holotype is re-examined.

Here, we describe two specimens that we assign to the new genus *Prosisyrina* gen. nov., which belong to Sisyridae with certainty (one represents a new species, the other is not assigned to a species) from the Upper Cretaceous (Santonian) amber localities Yantardakh and Ugolyak in northern Siberia.

2. Material and methods

This study is based on two sisyrid specimens from Upper Cretaceous Taimyr amber (one from the Yandardakh locality, the other from Ugolyak). Both amber pieces were small, about 7 mm

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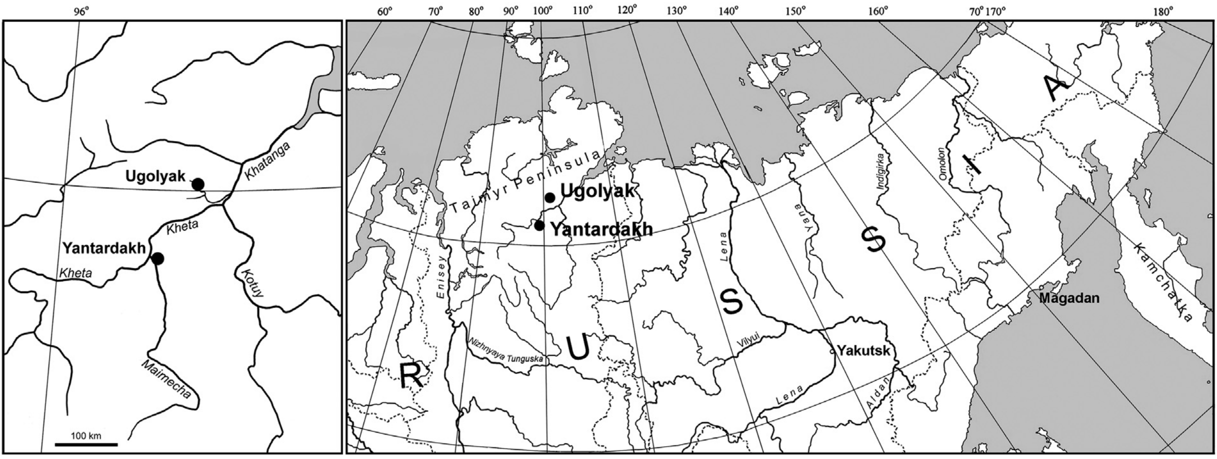

Fig. 1. Maps showing the location of the Taimyr amber localities Yantardakh [71°18′26.54″N E99°33′46.51″E] and Ugolyak [72°1′47.07″N 101°19′47.53″E].

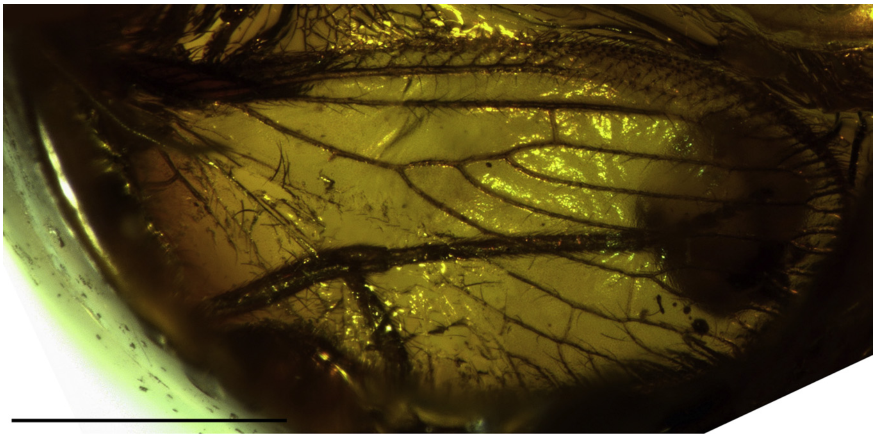

Fig. 2. *Prosisyrina sukachevae* sp. nov., holotype PIN 3311/2145, specimen as preserved. Scale bar represents 1 mm.

long and 4 mm in diameter before cutting. They contain dipteran syninclusions: the piece from Yandardakh includes an adult (male) of Chironomidae (Orthocladiinae), and that from Ugolyak an adult of Hybotidae. Both are housed in the Paleontological Institute of the Russian Academy of Sciences (PIN).

Photographs were taken by E.E. Perkovsky and V. Yu. Nazarenko using a Leica M16 stereomicroscope, and by A.P. Rasnitsyn and D.E. Shcherbakov using a Leica M165 stereomicroscope and an attached Leica DFC 425 digital camera. Line drawings were prepared by V.N. Makarkin using Adobe Photoshop CS3.

The venational terminology in general follows Kukalová-Peck and Lawrence (2004) in the interpretation of Yang et al. (2012, 2014). Terminology of wing spaces and details of venation (e.g., veinlets) follows Oswald (1993).

Abbreviations: AA1 to AA2, first to second branches of anterior anal vein; CuA, anterior cubitus; CuP, posterior cubitus; MA and MP, anterior and posterior branches of media; RA, anterior radius; RP, posterior sector; RP1, proximal-most branch of RP; ScP, subcosta posterior.

3. Localities

There are a number of amber localities of the Kheta Formation occurring in the Taimyr Peninsula, northern Siberia (e.g., Romanikha, Isaevskiy, Sokolovskiy, Yantardakh, Ugolyak) (Zherikhin, 1978; Zherikhin and Eskov, 1999). The Yantardakh locality is richest of them, with nearly 6000 inclusions collected to date. The locality is a cliff on the right bank of the Maimecha River three km upstream from its confluence with the Kheta River (Yantardakh Mountain, about 200 m long and 30 m high [71°18′26.54″N E99°33′46.51″E]) (Fig. 1). Amber pieces were collected in 1970 and 1971 by V V. Zherikhin and I.D. Sukacheva from coal-bearing sands, which form a layer more than 1 m high stretching for 200 m at approximately 15 m above water level (Zherikhin and Sukacheva, 1973); and in 2012 by E A. Sidorchuk, D.S. Kopylov and D.D. Vorontsov from coal-bearing sands within 1 m above water level (E.A. Sidorchuk, pers. comm.).

The Ugolyak locality [72°1′47.07″N 101°19′47.53″E] is located on the left bank of the Severnyi Ugolyak River, 9.5 km upstream from its mouth, a tributary of the Ugolyak River, a left tributary of the Khatanga River. Amber pieces were collected from this locality in 1977 by I.D. Sukacheva.

The age of the Kheta Formation is Coniacian-Santonian according to Saks et al. (1959). All amber from the Yantardakh locality has been found in the upper horizons of the formation, and is therefore thought to be Santonian (Zherikhin, 1978) or even upper Santonian based on the presence of marine bivalves of the genus *Inoceramus* Sowerby, 1814 (e.g., *I. patootensis* de Loriol, 1893 and

I. patootensis cf. *angustus* Beyenburg, 1936) in the overlying (upper Santonian-lower Campanian) Mutino formation (Saks et al., 1959; Zherikhin and Sukacheva, 1973; Zherikhin and Eskov, 1999). The Mutino Formation conformably overlays the amber-bearing horizon without visible breaks (Rasnitsyn, 1980). However, since the Mutino Formation lies above the amber-bearing horizon of the Kheta Formation, this does not allow the lower amber horizon to be considered late Santonian with certainty. The Ugolyak locality was considered by Zherikhin and Eskov (1999) slightly younger, possibly even younger than Santonian, based on the presence of the oldest known syrphid fly. However, it actually belongs to some Empidoidea or Platypezidae (G.V. Popov, pers. comm.), casting this assumption in doubt.

A warm-temperate, humid climate is reconstructed for the Mutino and Turonian/Coniacian Ledyanaya formations that overlies and underlies the Kheta Formation, respectively (Golovneva, 2012). Inclusions of these Taimyr localities are hypothesized to be rapidly buried in deltaic sediments and reflect the fauna that inhabited immediately along the river bank (Zherikhin and Sinitshenkova, 2002).

4. Systematic palaeontology

Order: Neuroptera Linnaeus, 1758.

Family: Sisyridae Banks, 1905.

Genus *Prosisyrina* gen. nov.

Type and only species. *Prosisyrina sukachevae* sp. nov.

Derivation of name. From the Greek *pro*, before, and *Sisyrina*, a genus-group name, referring to its similarity to this extant genus. Gender feminine.

Diagnosis. May be easily distinguished from other genera of Sisyridae by a combination of the following character states: (1) maxillary palpus fusiform, narrowed basally [broadened basally in *Sisyra* Burmeister, 1839, *Paleosisyra* Nel et al., 2003, *Sisyrina* Banks, 1939]; in hind wing, (2) costal space not narrowed medially [more or less clearly narrowed medially in other genera except *Paleosisyra*]; (3) complete outer series of gradate crossveins present [absent in *Sisyra*]; (4) ScP, RA distally widely separated [convergent distally or fused in *Paleosisyra*]; (6) 1r-m long, entering RP far from origin of RP1, but in distal part of length from origin of RP to origin of RP1 [very long, entering RP near origin of RP1 in *Paleosisyra*; or short, entering RP in proximal part of length from origin of RP to origin of RP1 in *Sisyra*, *Sisyrina*, *Sisyborina* Monserrat, 1981 (if present)]; (7) 1r-m entering M proximad fork of Cu [much distad in *Climacia* McLachlan, 1869].

Prosisyrina sukachevae sp. nov.

Figs. 2–4.

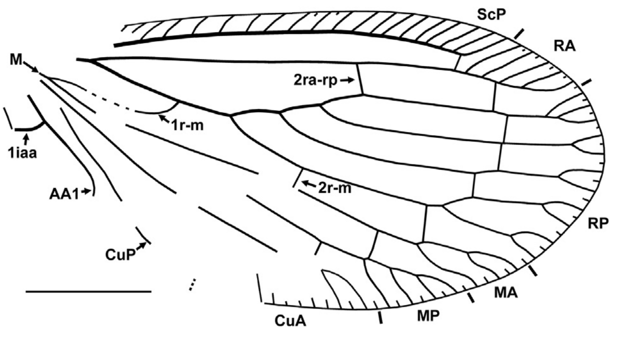

Fig. 3. *Prosisyrina sukachevae* sp. nov., hind wing venation of the holotype PIN 3311/2145. Scale bar represents 0.5 mm.

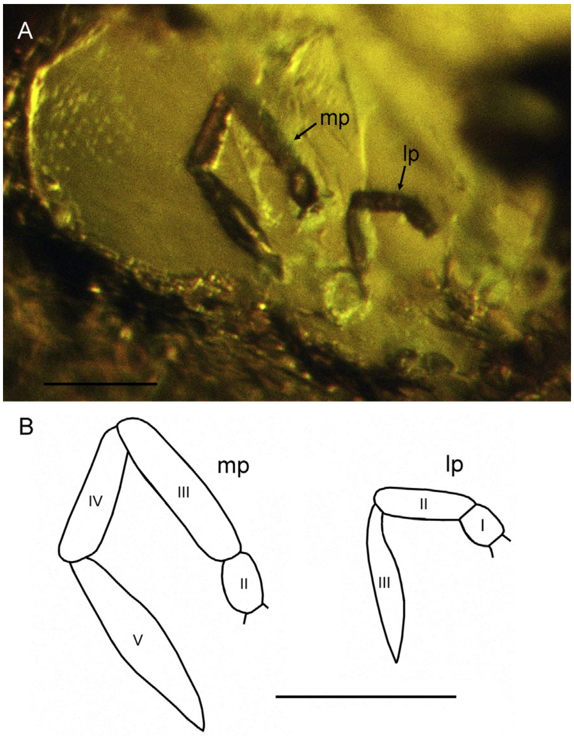

Fig. 4. *Prosisyrina sukachevae* sp. nov., holotype PIN 3311/2145. A, head as preserved. B, drawing of maxillary (mp) and labial (lp) palps. I–V, number of segment. Scale bars represent 0.1 mm.

Derivation of name. The specific epithet is from the surname of Irina D. Sukacheva [Sukatsheva], in recognition of her contributions to the study of Taimyr amber.

Material. Holotype PIN 3311/2145, collected in 2012 by the expedition of PIN. A very incomplete specimen in amber: the head is missing, but its impression is preserved; a nearly complete maxillary palpus and a labial palpus; seven segments of left antennal flagellum located far from the head; a basal fragment of a forewing; a nearly complete hind wing; a complete right fore leg, left and right mid legs, right hind leg. Syninclusion: PIN 3311/2146, a male non-biting midge (Diptera: Chironomidae: Orthocladiinae).

Locality and horizon. Russia: Krasnoyarsk Krai: Taymyrsky Dolgano-Nenetsky District: Taimyr Peninsula: right bank of the Maimecha River 3 km upstream of its confluence with the Kheta River (a left source of the Khatanga River), Yantardakh Mountain (Yantardakh locality). Upper Cretaceous, Santonian (Kheta Formation).

Description. Head preserved as pale impression mainly showing large eyes. Seven flagellomeres of left antenna preserved: three flagellomeres more rounded, four oblong. Maxillary palpus probably five-segmented: basal segment not preserved; second segment very short, dilated medially; third long, slender; fourth slender, about 0.7 length of third; terminal segment longest, fusiform, widest medially, with acute apex. Labial pulpus three-segmented: basal segment rather short, dilated medially; second segment elongate; terminal segment longest, rather narrow, nearly fusiform, with acute apex. Mesothoracic femur nearly equal mesothoracic tibia in length; metathoracic trochanter rather long. Metathoracic femur slightly stouter than metathoracic tibia, about 0.7 its length. Metathoracic tibia slender, presumptive apical false spurs (see *Remarks*) not detected. Relative length of metathoracic tarsomeres: 3.1–1.6–1.3–1–1.6. Basal part of tibia, apex of femur of metathoracic legs appear without colour patterning.

Forewing. Basal portion of costal space narrowed basad; five preserved basal subcostal veinlets simple, closely spaced, oblique.

Hind wing ca. 2.5 mm, 1.1 wide. Costal space rather broad in general, broadened toward wing apex, not narrowed medially. Subcostal veinlets simple, bent to wing apex. ScP stout, joins margin well before wing apex. Subcostal space broad, medially wider than costal space; only one (distal) crossvein detected. RA nearly straight, enter margin before wing apex, with four simple distal branches (veinlets). RA space very broad in proximal half (broadest at origin of RP1), moderately broad in distal half; with two crossveins equal in length (2ra-rp, 3ra-rp). Anterior trace of RP shallowly forked distally with three short branches; three pectinate branches proximad 2ra-rp. RP1 forked at outer gradate series; each branch shallowly forked distally; RP2, RP3 shallowly forked distally. Basal radio-median brace (1 m-r) very long, strongly sigmoid; poorly discernible, especially medially. Fork of M not preserved, probably approximately at level of RP1 origin. MA twice pectinately forked distally. MP with three pectinate branches distally. Fork of Cu not clearly preserved, probably distad place where 1r-m joins M. CuA incomplete, with four preserved pectinate branches (at least five branches assumed in life). CuP long, simple or at most with shallow terminal fork (distal part poorly preserved). AA1 incompletely preserved, apparently simple. AA2 fragmentarily discernible. Crossvein between AA1, AA2 (1iaa) very long, stout, slightly curved. Two series of gradate crossveins present: inner represented by single crossvein (2r-m); outer complete, consisting of seven crossveins (from RA to CuA). Trichiation on veins, wing margins scarce, rather long. Trichosors prominent along entire margins, except for proximal part of costal margin. Wing membrane hyaline; without colour pattern.

Remarks. Previously, it has been widely accepted that tibial spurs are present in Sisyridae; in particular, each metathoracic leg was thought to have two distal spurs (e.g., Killington, 1936; Parfin and Gurney, 1956). However, Vshivkova and Makarkin (2010) found that the metathoracic tibiae of at least *Climacia areolaris* (Hagen, 1861) have no true spurs. Instead, this species possesses two socketed spines (falsicalcarae, or false spurs) which differ from tibial spurs in having longitudinal ridges and by the absence any scattered spinules (Vshivkova and Makarkin, 2010, Fig. 43). Unfortunately, it is impossibly to discern such fine details in these two amber specimens, and, therefore, it is unclear if these are true or false spurs. No other Neuroptera families are known to have such false tibial spurs.

Prosisyrina sp.

Fig. 5.

Material. Specimen PIN 3631/11, collected in 1977 by I.D. Sukacheva. An incomplete, poorly preserved specimen in amber (head and thorax with incomplete antennae and legs, and fragmentary wings). Syninclusion: PIN 3631/12, an adult fly (Diptera: Hybotidae), cut into a separate piece (partially destroyed).

Locality and horizon. Russia: Krasnoyarsk Krai: Taymyrsky Dolgano-Nenetsky District: Taimyr Peninsula: left bank of the Severnyi Ugolyak River 9.5 km upstream from its mouth (Ugolyak locality), a tributary of the Ugolyak River, a left tributary of the Khatanga River. Upper Cretaceous, Santonian (Kheta Formation).

Description. Most of visible head capsule occupied by large eyes; postocular lobe absent as preserved. Antennae incomplete; scapus broad, 0.07 mm long, 0.065 mm wide; all flagellomeres broadly oval; proximal flagellomeres 0.04 mm long, 0.03 mm wide. Terminal segment of maxillary palps fusiform, with acute apex. Prothorax appears very short. Mesothorax covered with long setae. Legs: prothoracic coxa long; mesothoracic femur nearly equal mesothoracic tibia in length; mesobasitarsus nearly as long as two next tarsomeres together; fourth tarsomere of mesotarsus very short, nearly as long as wide; metathoracic femur slightly stouter than metathoracic tibia, about 0.7 its length; presumptive apical false spurs of metathoracic tibia slender, pale.

Forewing. Costal space narrowed basally; moderately broad medially. All preserved subcostal veinlets simple, rather strongly bent to wing apex in proximal portion of costal space.

Hind wing. MA, MP partially preserved; fork of M not preserved. CuA pectinately forked with four preserved branches. Preserved posterior margin with short trichosors in cubital space.

Remarks. Due to its incompleteness, we do not assign specimen PIN 3631/11 to any species. The structure of the maxillary palps and the preserved venation indicate that this specimen belongs to the genus *Prosisyrina*.

5. Discussion

5.1. Comparative morphological analysis of *Prosisyrina*

The family Sisyridae includes six genera, two extinct (*Prosisyrina* gen. nov. from the Upper Cretaceous of northern Siberia, and *Paleosisyra* with two named species from the European Eocene), and four extant: the nearly cosmopolitan *Sisyra* (47 extant species), known also from the upper Miocene; *Climacia* (22 species) restricted to the New World, from Canada (Ontario and Quebec) to Chile; *Sisyborina* (two species) from tropical Africa; and *Sisyrina* (three species) from tropical Asia (southern India, Hainan in southern China) and Australia (northern Queensland) (Oswald, 2013; Monserrat and Duelli, 2014; Forteath et al., 2015). The validity of *Sisyborina* is in need of confirmation as its venation is very similar to that of *Sisyrina*.

The terminal segment of the maxillary palpus is basally dilated in *Sisyra*, *Paleosisyra*, and *Sisyrina* (see Parfin and Gurney, 1956, Figs. 7A; I; Nel et al., 2003, Fig. 7), whereas this is fusiform in *Prosisyrina* gen. nov. The maxillary palpus of *Climacia* is in general similarly constructed as in the new genus; its terminal segment is also medially dilated. The maxillary palpus of *Sisyborina* is not described.

The terminal segment of the labial palpus in *Prosisyrina* gen. nov. is elongate, fusiform, and strongly differs from that of the genera *Sisyra*, *Paleosisyra*, and *Climacia*. In these three genera the terminal segment is broad and triangular, an apomorphic state at the family level (Parfin and Gurney, 1956, Figs. 7B; H; Nel et al., 2003, Fig. 7). The labial palpi of *Sisyborina* and *Sisyrina* are not described. The fusiform shape of the labial palpus in *Prosisyrina* gen. nov. is obviously a plesiomorphic state at the family level.

In general, the hind wing venation of *Prosisyrina* gen. nov. is clearly more similar to that of *Sisyrina*, *Paleosisyra* and *Sisyborina* than that of *Climacia*. Its venation even resembles that of *Sisyra*, despite the absence in the latter of an outer gradate series of crossveins. In *Climacia*, ScP and RA are distally fused; MP is simple in the vast majority of species (very rarely once forked); 1r-m joins M much distad the fork of Cu; M is forked distad the origin of RP1 (see Parfin and Gurney, 1956; pl. 2, Figs. 1–9; Flint, 1998, Figs. 34–39; Monserrat, 2005, Fig. 1). All of these character states are strongly different from those of *Prosisyrina* gen. nov.

The basally dilated RA space of *Prosisyrina* gen. nov. is more similar to that of *Sisyborina*, *Sisyrina* and *Sisyra* than to the narrower RA space of *Paleosisyra*.

ScP and RA are widely spaced distally in *Prosisyrina* gen. nov., *Sisyborina* and *Sisyrina*, and fused in *Paleosisyra*.

MP in *Sisyrina* and *Sisyborina* is once forked, e.g., in *Sisyrina qiong* (Yang and Gao, 2002) (based on the photograph of the holotype) and *Sisyborina marlieri* (Tjeder, 1976, Fig. 1). Sometimes, the anterior branch is shallowly forked again, e.g., *Sisyrina nirvana* Banks, 1939 (Parfin and Gurney, 1956; pl. 1, Fig. 7) and *Sisyborina scitula* Flint (Flint, 2012, Fig. 9). MP of *Paleosisyra* is dichotomously forked (Nel et al., 2003, Fig. 7; Wichard et al., 2009, Fig. 07.06a). MP of *Sisyra* varies among species from once forked (e.g., Tjeder, 1957, Fig. 139) to dichotomously forked (e.g., Flint, 2012, Fig. 8). Therefore, MP with few pectinate branches in *Prosisyrina* gen. nov. is unique in the family.

CuA bears three to four pectinate branches in *Sisyrina* (Parfin and Gurney, 1956; pl. 1, Fig. 7; pers. obs.), four to five in *Sisyborina* (Tjeder, 1976, Fig. 1; Flint, 2012, Fig. 9), and five to seven in *Paleosisyra* (Nel et al., 2003, Figs. 5 and 6). CuA in *Sisyra* varies among species from three to six. Therefore, the structure of CuA in *Prosisyrina* gen. nov is usual for the family.

The crossvein 1r-m in the hind wing of *Prosisyrina* gen. nov is very poorly visible for most of its length; only its portion near RP is clearly discernible. This crossvein is probably similarly constructed in all species of *Sisyrina*. It is weak (‘evanescent’ in Smithers' terminology) in *S. tropica* Smithers, 1973 (p. 20), and not figured in *S. qiong* (see Yang and Gao, 2002, Fig. 5a). Actually, it is present in the holotype of *S. qiong* (X.Y. Liu, pers. comm.). However, only its part near RP is clearly discernible, other parts are very poorly visible as in *Prosisyrina* gen. nov. 1r-m is present as a short basal vein in the paratype of *S. nirvana*. In that specimen, only the portion of 1r-m near RP is well discernible (see Parfin and Gurney, 1956; pl. 1, Fig. 7). In general, *S. nirvana* and *S. qiong* have very similar venation. This crossvein appears to be also very short or very poorly visible in both species of *Sisyborina*; at least it is not shown in drawings of these species (Tjeder, 1976, Fig. 1; Flint, 2012, Fig. 9).

The long crossvein 1r-m of *Prosisyrina* gen. nov is similar in length to that of *Paleosisyra*. In other genera this crossvein is markedly shorter or strongly short.

In summary, the above analysis indicates that the Santonian genus *Prosisyrina* gen. nov. is most closely related to the extant tropical genus *Sisyrina*, and to a lesser extent to the Eocene *Paleosisyra*. It is noteworthy that this new genus is much less similar to the two genera whose species may today occur in temperate to cold regions, *Sisyra* and *Climacia*.

5.2. *Fossil Sisyridae*

The fossil record of Sisyridae is poorly known, with only four named species, including the one named here (Table 1).

Prosisyrina sukachevae sp. nov. and *Prosisyrina* sp. from Santonian Taimyr amber are the only sisyrids confidently known from the Mesozoic. An undescribed sisyrid larva from the same amber (Zherikhin, 1978) may belong to this genus. Of the character states of *Prosisyrina* gen. nov., only the few-pectinate MP in the hind wing does not occur in younger Sisyridae. Otherwise, its hind wing venation is typical for modern sisyrids.

Eocene sisyrids are rather common, and all restricted to Europe. These are mostly known from the lowest Eocene Oise amber (France), but also from upper Eocene Baltic amber and the uppermost Eocene Bembridge Marls (southern England).

Paleosisyra eocenica Nel et al., 2003 is the most abundant Neuroptera species in Oise amber, with more than 25 specimens collected. It is mainly represented by female specimens; only one male is known (A. Nel, pers. comm.). The genus *Paleosisyra* differs from all other sisyrid genera mainly by the presence of an inner gradate series of crossveins in the forewing.

More than ten specimens are known from Baltic amber (including unreported sisyrids in private collections). One species has been described based on three specimens, i.e., *Paleosisyra electrobaltica* Wichard in Wichard et al., 2009. It differs from *P. eocenica* only in few details of the venation and in shape of the terminal segment of the maxillary palpus. All known adult specimens from Baltic amber whose characters are well discernible most probably belong to the genus *Paleosisyra* (i.e., Weitschat and Wichard, 1998; pl. 54b, c; Erichson and Weitschat, 2000, Fig. 44; Scheven, 2004; two Figs. on p. 73).

Two specimens are known from the uppermost Eocene Bembridge Marls of the Isle of Wight (southern England). One specimen is a small fragment of a wing described as *Sisyra* (?) *disrupta* Cockerell, 1917. Judging from the size (estimated wing length about

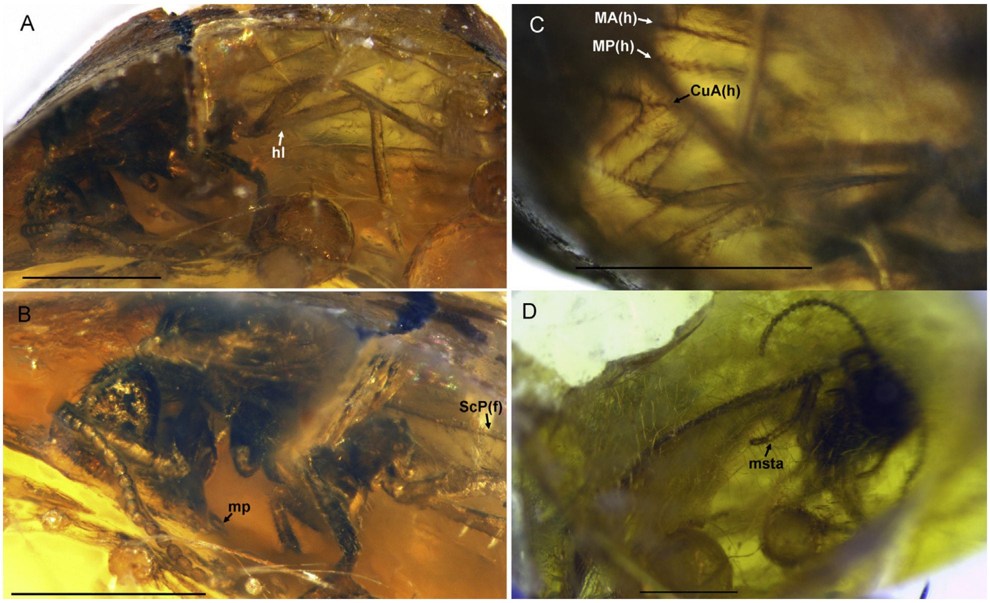

Fig. 5. *Prosisyrina* sp., specimen PIN 3631/11. A, specimen as preserved. B, head and thorax. C, fragment of right hind wing. D, specimen from frontal view. CuA(h), hind wing cubitus anterior; hl, hind legs; mp, maxillary palp; MA(h) and MP(h), hind wing media anterior and posterior; msta, mesotarsus; ScA(f), forewing subcosta anterior. Scale bars represent 0.5 mm.

Table 1
A list of known fossil Sisyridae. The specimens marked by an asterisk are determined by us based on photographs and drawings.

Species	Series/Stage	Locality	References
Prosisyrina sp. [adult]	Upper Cretaceous, Santonian	Ugolyak, Taimyr amber	This paper
Prosisyrina sukachevae gen. et sp. nov. [adult]	Upper Cretaceous, Santonian	Yantardakh, Taimyr amber	This paper
Sisyridae sp. [larva]	Upper Cretaceous, Santonian	Yantardakh, Taimyr amber	Zherikhin, 1978, p. 64
Paleosisyra eocenica Nel et al., 2003 [>25 adults]	lower Eocene	Oise amber, France	Nel et al., 2003, Figs. 1–8
Paleosisyra electrobaltica Wichard in Wichard et al., 2009 [three adults]	upper Eocene	Baltic amber	Weitschat and Wichard, 1998, pl. 54a; Wichard, 2005, Fig. 6; Wichard and Weitschat, 2004, Figs. on pp. 15, 136; Wichard et al., 2009, Figs. 07.05–06; Weitschat and Wichard, 2010, Fig. 11E
**Paleosisyra* sp. [adult]	upper Eocene	Baltic amber	Scheven, 2004, Fig. on p. 73 (right upper)
**Paleosisyra* sp. [adult]	upper Eocene	Baltic amber	Scheven, 2004, Fig. on p. 73 (middle lower)
**Paleosisyra* sp. [adult]	upper Eocene	Baltic amber	Wichard and Weitschat, 1996, pl. 9, Fig. (upper); Weitschat and Wichard, 1998, pl. 54b, c
**Paleosisyra* sp. [adult]	upper Eocene	Baltic amber	Erichson and Weitschat, 2000, Fig. 44
Sisyridae sp. [larva]	upper Eocene	Baltic amber	Wichard et al., 2009, Fig. 07.07a–c
Sisyridae sp. [larva]	upper Eocene	Baltic amber	Weitschat and Wichard, 2010, Fig. 11F
**Paleosisyra* sp. [adult]	uppermost Eocene	Bembridge Marls, England	Jarzembowski, 1980, Fig. 27
?‘*Sisyra*’ (?) *disrupta* Cockerell, 1917 [adult]	uppermost Eocene	Bembridge Marls, England	Cockerell, 1917, pl. 31, Fig. 13
Sisyra sp. [adult]	uppermost Miocene	Murat, France	Nel and Jarzembowski, 1997, Fig. 1

5 mm) it may well be a sisyrid, but the available venation is not fully characteristic of the family. In particular, two branches of RP are simple or nearly simple in *S. disrupta*, whereas all branches of RP are forked in all known species of Sisyridae. Therefore, further examination of the holotype is needed to confirm its assignment to this family. At least, its assignment to the genus *Sisyra* is very doubtful.

The other specimen from the Bembridge Marls is an incomplete forewing folded longitudinally (Jarzembowski, 1980, Fig. 27). It belongs to Sisyridae with certainty, but it is unnamed. Judging from its size (about 4.5 mm) and preserved venation, it is most probably a species of *Paleosisyra*. This assignment is supported by the presence of two character states characteristic of this genus: ScP is probably fused with RA (at least its morphology is very similar to that of the *Paleosisyra* species), and the inner gradate series anterior to MA consists of three crossveins. The latter condition does not occur in other sisyrid genera.

The single sisyrid specimen known from the Neogene is from the uppermost Miocene of the Murat (Sainte-Reine) locality in France (Nel and Jarzembowski, 1997). It is an incomplete forewing, the venation of which clearly indicates that it belongs to the genus *Sisyra*. This determination is supported in particular by the absence of an outer gradate series of crossveins. Nel and Jarzembowski (1997) assigned this unnamed species to the *Sisyra vicaria* species group because of the presence three ra-rp crossveins. The extant *Sisyra nigra* (Retzius, 1783), the only species distributed in both Europe and North America, belongs also to this species group.

ScP and RA are shown to be fused distally in this Murat species. In most extant species of *Sisyra*, however, these veins are distally widely separated (e.g., Parfin and Gurney, 1956; pl. 1, Figs. 1 and 2; Tjeder, 1957, Fig. 139; Penny, 2002, Fig. 660; Flint, 2012, Fig. 8). Rarely, ScP is bent distally towards RA and connected by short crossveins (e.g., Parfin and Gurney, 1956; pl. 1, Fig. 3); this condition occurs in particular in *Sisyra nigra*. The latter condition is sometimes drawn as ScP and RA being fused (e.g., Parfin and Gurney, 1956, Fig. 10 of the same species shown in their photo, pl. 1, Fig. 3) with ScP and RA connecting by a short crossveins. Therefore, a fusion of ScP and RA is necessary to confirm in *Sisyra* and in general in Sisyridae (including *Paleosisyra*).

5.3. *The association of Sisyridae with freshwater sponges and bryozoans*

The larvae of all extant species of Sisyridae are aquatic, inhabiting a variety of freshwater bodies (ponds, lakes, rivers). Those species whose biology is known have an obligatory association with freshwater sponges of the family Spongillidae, without host-predator specificity (e.g., Old, 1933; Killington, 1936; Brown, 1952; Parfin and Gurney, 1956; Weissmair, 1994, 1999, 2005). Sisyrid larvae also feed on bryozoans with a gelatinous ectoderm (e.g., *Cristatella mucedo* (Cuvier, 1798), *Hyalinella punctata* (Hancock, 1850)) which form mixed colonies together with sponges *Spongilla* Lamarck, 1816 and *Ephydatia* Lamouroux, 1816; however, the larvae distinctly prefer sponges (Weissmair, 2005). Moreover, Brown (1952) believed that sisyrid larvae (at least those of *Climacia*) do not feed on bryozoans even if they occur on them.

Judging from their morphology, the larvae of Sisyridae are able to feed only on sedentary or immobile prey (such as sponges and bryozoans); their long, straight, and very thin mouthparts are not suitable for capturing moving prey. It is very probable that this association is ancient, as comparison of Baltic amber and extant larvae shows that general larval morphology in this family appears unchanged since at least the late Eocene (see Wichard et al., 2009, Figs. 07.07a–c). Therefore, we can reasonably assume that the biology of Sisyridae has also not changed since then, and that the presence of fossil sisyrids indicates a presence of freshwater sponges or (with lower probability) gelatinous species of bryozoans.

Sponges (phylum Porifera) and bryozoans (phylum Bryozoa) are ancient groups, mostly marine, who appeared long before insects (Massard and Geimer, 2008; Van Soest et al., 2012). All freshwater sponges belong to the suborder Spongillina, which all inhabit fresh water (order Haplosclerida) (Manconi and Pronzato, 2002). Freshwater bryozoans belong to the class Phylactolaemata (exclusively freshwater) and the order Ctenostomatida of the class Gymnolaemata (Massard and Geimer, 2008). Unlike marine taxa, they lack calcareous (mineralized) skeletons (Taylor, 2005).

Extant freshwater sponges and bryozoans occur on all continents except Antarctica, and live in all types of water bodies (ponds, lakes, rivers, estuaries) (Manconi and Pronzato, 2008; Massard and Geimer, 2008). In general, their global distribution is in accord with the distribution of extant Sisyridae.

Fossil freshwater bryozoans are rarely found, and all of them belong to Phylactolaemata (Massard and Geimer, 2008). The oldest known plumatellid species are from the Upper Permian of Siberia and Kazakhstan (Vinogradov, 1995), but species of Plumatellidae are not gelatinous, as sisyrids feed on, but are of the branching tubular type. The oldest known gelatinous species (Pectinatellidae) are from the Upper Triassic Molteno Formation (South Africa); these statoblasts formed mass occurrences (Kohring and Pint, 2005).

Fossil freshwater sponges occur very rarely in the Paleozoic and Mesozoic (Pisera et al., 2013). The oldest known fossil freshwater sponge spicules are found from the Breitenbach Formation (Upper Carboniferous) in the Saar-Nahe basin, Germany (Schindler et al., 2008). The authors assigned these spicules to Spongillina, interpreting them as belonging to lacustrine deposits. However, Schultze (2009) believes that these sponges might be from both marine and freshwater deposits, as the composition of that faunal assemblage is not decisive. Incomplete preservation of these spicules do not allow determination if they belong to Spongillina. This finding may be the oldest record of the suborder, continuously inhabiting fresh water to modern times; or of some other group that invaded fresh water and soon went extinct, with the Mesozoic to Recent freshwater sponges a result of a separate event invasion of fresh water by other taxa (A. Pisera, pers. comm.).

The oldest described freshwater sponge of the family Spongillidae was found in the Upper Jurassic Morrison Formation, Colorado (Dunagan, 1999). Two species are known from the Lower Cretaceous (Aptian) of the Argentinian Patagonia; a species of the monotypic family Paleospongillidae (Spongillina), and a species of the genus *Spongilla* which is closely related to widely distributed extant species *S. alba* Carter, 1849 (Ott and Volkheimer, 1972; Volkmer-Ribeiro and Reitner, 1991). One species of Spongillidae is known from the Berriasian Purbeck Limestone Group of England (Young, 1878), although Clements (1967, p. 43) considered these assumed sponge spicules "as being silicified pseudomorphs after lenticular gypsum crystals". This finding would be especially important as the neuropteran species *Epimesoberotha parva* Jepson et al., 2012 described from the Purbeck might turn out to be a sisyrid (VM, pers. obs.). Freshwater sponges are not yet recorded from the Upper Cretaceous of Eurasia. However, the occurrence of sisyrids in the Santonian of northern Asia reported in this paper allows a reasonable assumption of the presence of some Spongillina in fresh water near the Taimyr localities of Yantardakh and Ugolyak (in a relatively large potamal river as assumed by Zherikhin and Sinitshenkova, 2002).

The vast majority of fossil sisyrids belong to the genus *Paleosisyra*, currently known only from the Eocene of Europe. However, there are no Eocene localities where freshwater sponges and sisyrids are known to have co-occurred. Freshwater sponges are generally more common in Tertiary localities, particular in the Eocene (Pisera and Sáez, 2003), but sponges are not found in the lowest Eocene Oise amber and related amber-bearing deposits (A. Nel, pers. comm.) where sisyrids are most abundant, nor in Baltic amber. Although sponge spicules are present in the Prussian Formation, from which the majority of the Baltic amber pieces are originated (Ivanik, 2003), these belong to marine sponges, as this formation is considered as deposited on a river delta extending into salt water. In contrast, freshwater sponges are represented by several species of Spongillidae in the Middle European Eocene localities of Messel Pit and Eckfeld Maar (e.g., Müller et al., 1982; Gruber, 1994; Richter and Wuttke, 1999) from where sisyrids are unknown; but this may also be explained in part by taphonomic reasons (at least concerning Messel Pit). Notably, the Messel endemic genus *Lutetiospongilla* Richter and Wuttke, 1999 is most closely related to the extant tropical genus *Radiospongilla* Penney and Racek, 1968 (Richter and Wuttke, 1999). A highly diversified assemblage of freshwater sponge spicules has been recently discovered from the Middle Eocene lacustrine deposits of the Giraffe locality in northern Canada, with at least eight species (mostly undescribed yet) of three families (Pisera et al., 2014). Of these, one described species belongs to the extant Afrotropical genus of Potamolepidae (Pisera et al., 2013); the majority of specimens most probably belong to the extant species *Ephydatia facunda* Weltner, 1895 from Central and South America; the genera *Paleospongilla* (Ott and Volkheimer, 1972), *Radiospongilla* and *Spongilla* are also recorded (Pisera et al., 2014). The Eocene was characterized by equable climate with low temperature seasonality that reached into highest latitudes (in particular, northern Canada), and a mixture of plant and animal taxa in localities today characteristic of both temperate and tropical conditions (Archibald et al., 2010, 2013). This might also be applied to freshwater ecosystems.

The structure of Eocene lacustrine ecosystems greatly differs from Neogene and Recent, in particular, by uneven flow of nutrients into the lakes and the scarcity of benthic angiosperm macrophytes due to light deficiency caused by plankton blooms and floating algal-bacterial mats (Zherikhin and Sinitshenkova, 2002; Ponomarenko, 1996, 2007, 2010a, b). The abundance of *Paleosisyra* in the lowest Eocene Oise amber shows that this genus was adapted to a climate of paratropical (megathermal) mean annual temperatures found there at that time. Specimens of *Paleosisyra* are less common in the mesothermal Bembridge Marls and Baltic amber. The profound changes in the structure of freshwater ecosystems seen beginning in the end of Eocene (Ponomarenko, 2007, 2010a, b) may have led to the extinction of the genus. The only known Miocene sisyrid species is confidently assigned to the extant genus *Sisyra*, perhaps better adapted to Neogene freshwater ecosystems with the abundance of aquatic macrophytes.

6. Conclusion

The Late Cretaceous specimens of Sisyridae described in this paper do not especially differ from extant members of the family. In general, all known fossil sisyrids resemble modern species in their general appearance and wing venation, which form a rather homogenous family. Assuming that the biology of Sisyridae, specifically the association of their larvae with freshwater sponges, has been stable, the occurrences of the Santonian Taimyr sisyrids would imply that some Spongillina in fresh water near these localities should be present, although freshwater sponges are yet not recorded from the Mesozoic of Eurasia. Moreover, the occurrences of certain freshwater sponges in Upper Jurassic and Lower Cretaceous strata (and may be older) indicate that possible sisyrid larvae from this interval would have had suitable food resources.

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