



# An interesting new species of Sisyridae (Neuroptera) from the Upper Cretaceous Taimyr amber



Vladimir N. Makarkin <sup>a</sup>, Evgeny E. Perkovsky <sup>b,\*</sup>

<sup>a</sup> Institute of Biology and Soil Sciences, Far East Branch of the Russian Academy of Sciences, Vladivostok, 960022, Russia

<sup>b</sup> Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, ul. Bogdana Khmel'nitskogo 15, Kiev, 01601, Ukraine

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## ABSTRACT

*Prosisyrina sphinga* sp. nov. (Neuroptera: Sisyridae) is described from Upper Cretaceous (Santonian) Taimyr amber of northern Siberia (Yantardakh locality). The new species is preliminary assigned to this Cretaceous genus, mainly based on character states of the maxillary palpus and the hind wing vein M and crossvein 1r-m, and the presumable absence of tibial false spurs. However, the structure of the costal space and the RP branching in the hind wing indicate that it may belong to a new, closely related genus. The discovery of this second species from the locality might suggest that sisyrids were usual members of the Santonian riparian biocenoses of northern Siberia.

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## 1. Introduction

The small neuropteran family Sisyridae (spongilla-flies) includes little more than 70 extant species in four genera distributed worldwide (Oswald, 2015). Their specialized aquatic larvae feed on freshwater sponges and bryozoans (Parfin and Gurney, 1956; Weissmair, 1994, 2005). The family is of great phylogenetic importance, as the venation of some of its members is most similar to that of the Permian Permithonidae.

The fossil record of the family is very poor, known mainly from the Cenozoic with four described species from four European localities, i.e., the earliest Eocene Oise amber, the late Eocene Baltic amber, the latest Eocene Bembridge Marls, and the Miocene locality at Murat in France (Cockerell, 1917; Nel and Jarzembowski, 1997; Nel et al., 2003; Wichard et al., 2009). The occurrence of Sisyridae in the Cretaceous was only recently confirmed when two specimens were described from Santonian Taimyr amber of northern Siberia, i.e., *Prosisyrina sukachevae* Perkovsky and Makarkin, 2015 from the Yantardakh locality, and *Prosisyrina* sp. from the Ugolyak locality (Perkovsky and Makarkin, 2015). The earlier reports of Sisyridae from the Mesozoic are not confirmed yet as members of this family, i.e., a larva from the Upper Cretaceous of the Taimyr

amber (Zherikhin, 1978) and an adult from the Lower Cretaceous Crato Formation of Brazil (Martins-Neto, 1992, 1997).

In this paper, we describe a remarkable male of a new sisyrid species from the Santonian Taimyr Yantardakh locality, which we preliminarily assign to *Prosisyrina* Perkovsky & Makarkin, 2015.

## 2. Material and methods

This study is based on a single sisyrid specimen embedded in a piece of Upper Cretaceous Taimyr amber from the Yantardakh locality. Its location, stratigraphy and age were considered by Perkovsky and Makarkin (2015) and Rasnitsyn et al. (2016). The amber piece is small, about 6.5 mm long and 2.8 mm in diameter before cutting. The specimen is housed in the Paleontological Institute of the Russian Academy of Sciences (PIN).

Photographs were taken by A.P. Rasnitsyn using a Leica M165 stereomicroscope and an attached Leica DFC 425 digital camera, by V.Yu. Nazarenko using a Leica M165 stereomicroscope, and by V.M. Loktionov using a SteREO Discovery.V12 stereomicroscope. Line drawings were prepared by the first author using Adobe Photoshop CS3.

The venational terminology in general follows Kukulová-Peck and Lawrence (2004) in the interpretation of Yang et al. (2012 and 2014). Terminology of wing spaces and details of venation (e.g., veinlets) follows Oswald (1993). Terminology of genitalia follows Aspöck and Aspöck (2008).

\* Corresponding author.

E-mail address: [perkovsk@gmail.com](mailto:perkovsk@gmail.com) (E.E. Perkovsky).

All taxonomic acts established in the present work have been registered in ZooBank LSID (see below), together with the electronic publication urn:lsid:zoobank.org:pub:0E478011-3802-4A5F-8578-0AA59FD461A3.

Abbreviations: 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. Crossveins are designated by the longitudinal veins to which they connect, and are numbered in sequence from

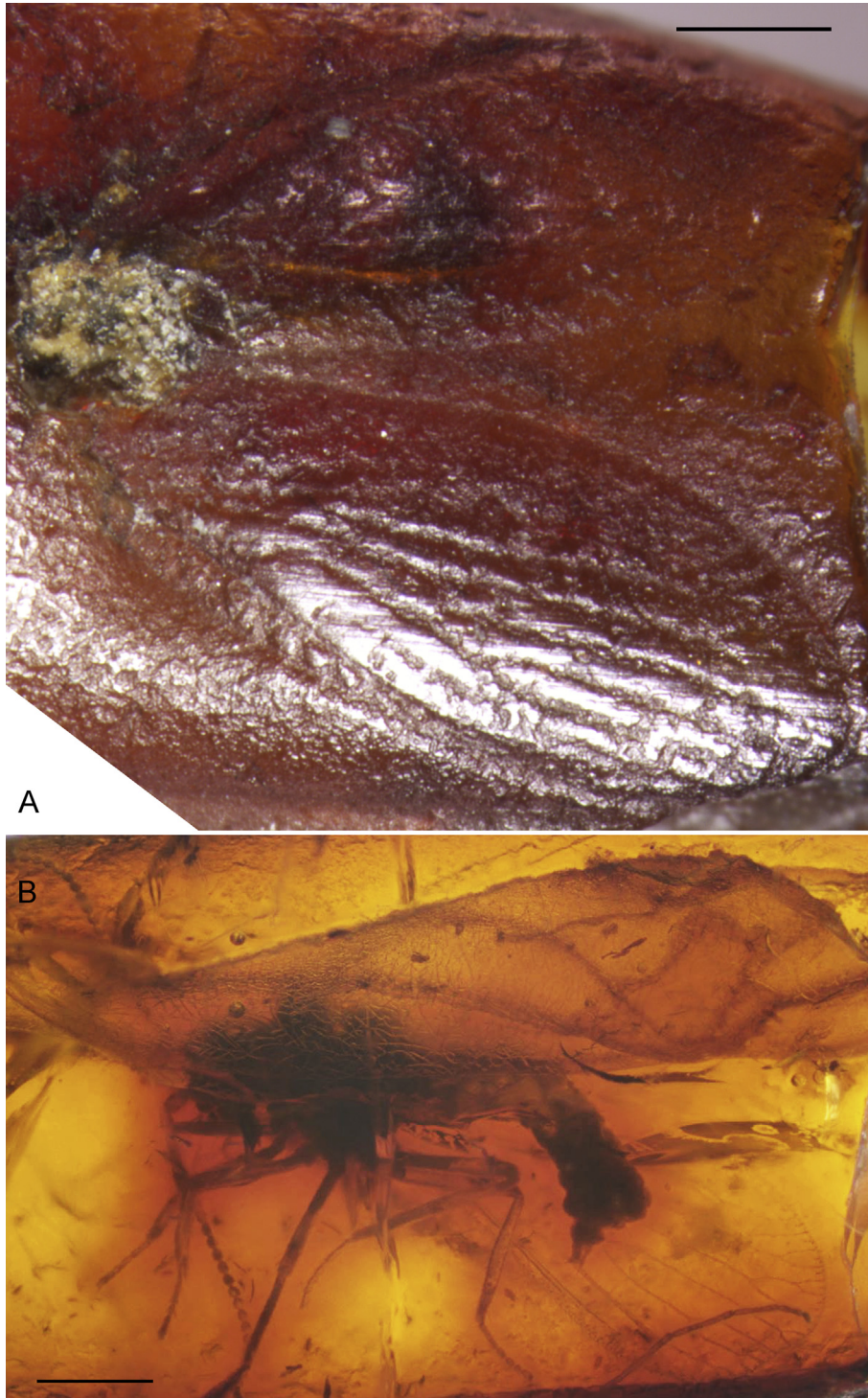
the wing base, e.g., 2scp-r, second (distal-most) crossvein connecting ScP and RA; 1r-m, basal crossvein between R/RP and M.

### 3. Systematic palaeontology

Order: Neuroptera [Linnaeus, 1758](#)

Family: Sisyridae [Banks, 1905](#)

Genus *Prosisyrina* Perkovsky & Makarkin, 2015



**Fig. 1.** *Prosisyrina sphinga* sp. nov., holotype PIN 3311/2525, specimen as preserved. A, dorsal view. B, lateral view. Scale bars represent 0.5 mm.

***Prosisyrina sphinga* sp. nov.**

(urn:lsid:zoobank.org:act:3DC578D5-76D9-4839-8AA1-70A212A5D132)

Figs. 1–5

**Derivation of name.** From the Latin noun *sphinga*, sphinx (in the Greek mythology, a monster with a lion's body and a woman's head who asks riddles), referring to difficulties in generic placement of the species.

**Material.** Holotype PIN 3311/2525, collected in 2012 during a PIN expedition. A slightly incomplete and poorly preserved specimen in amber: dorsal parts of the head, thorax, and forewings lay upon the amber surface, and are partly destroyed, or their details are very poorly discernible; antennae, hind wings are incompletely preserved or partly poorly visible; all legs are complete. Syninclusion: Diptera, Nematocera (destroyed).

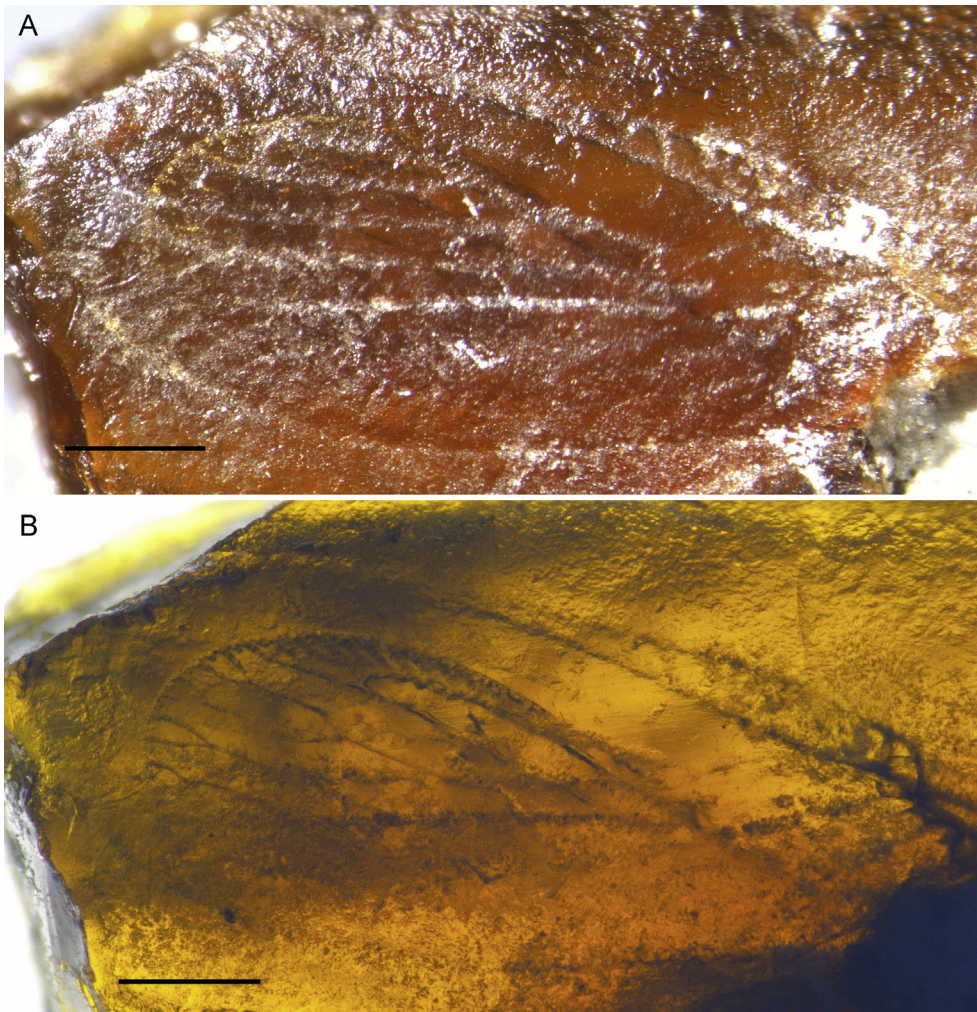
**Locality and horizon.** Russia: Krasnoyarskiy Krai: Taimyrsky (Dolgano-Nenetsky) District: Taimyr Peninsula: right bank of the Maimecha River in 3 km upstream from its confluence with the Kheta River (a left tributary of the Khatanga River), Yantardakh Hill (Yantardakh locality) [71.307222°N, 99.562778°E] (see [Perkovsky and Makarkin, 2015](#), fig. 1). Upper Cretaceous, Santonian (Kheta Formation).

**Diagnosis.** May be easily distinguished from *Prosisyrina sukachevae* by the following hind wing character states: (1) two branches of RP originating proximad 2ra-rp, one branch far distad 2ra-rp [all three branches originate proximad 2ra-rp in *P. sukachevae*]; and (2) crossvein 1r-m entering RP in proximal half of length from origin of RP to origin of RP1 [in distal half in *P. sukachevae*].

**Description.** Male. Head capsule poorly preserved; only large eyes well discernible. Antennae incomplete, poorly preserved; scapus large, nearly twice as long as wide ([Fig. 3](#)); pedicellus remarkably larger than proximal flagellomeres, elongated, slightly dilated towards apex; preserved flagellomeres longer than wide. Distal four segments of maxillary palps preserved: second segment appears short; third to fifth segments elongate, nearly equal in length; terminal (fifth) segment probably fusiform, widest medially (incompletely visible). Labial palps not detected.

All legs rather slender, covered with fine rather short setae. Tibial apical false spurs on all legs not detected (i.e., absent or extremely short). Relative length of metatarsal tarsomeres: 3.7–1.5–1.3–1–1.5.

Distal abdominal segments rather well preserved ([Fig. 4B,C](#)). Tergite 8 of normal generalized shape, rather broad. Tergite 9 narrow laterally, dilated dorsally; not fused with ectoproct, but these



**Fig. 2.** *Prosisyrina sphinga* sp. nov., holotype PIN 3311/2525. A, left forewing. B, left hind wing. Scale bars represent 0.5 mm.

closely approach laterally. Tergite 10 (ectoproct) probably narrow dorsally, more or less rounded laterally; callus cerci not discernible. Paired gonocoxites 9 small, rounded, with several long fine setae; placed laterally, i.e., spaced far from each other. Sternite 8 relatively broad, rounded ventrally. Sternite 9 very large, strongly extending; broad basally, narrowed apically with two terminal strong setae.

Forewing ca. 3.3 mm long, 1.3 mm wide. Costal space relatively narrow; widest approximately at proximal 1/5 of wing length. Preserved subcostal veinlets simple, becoming more widely spaced towards distal part of wing. Subcostal space broad. RA space slightly narrower than subcostal space, with two detected crossveins (3ra-rp, 4ra-rp). RP with three long branches, all originating proximad 3ra-rp. RP1 originated near origin RP, forked distally (incompletely preserved); preserved RP2, RP3 simple. Fork of M not discernible; MA nearly straight before distal forking. Other venation indistinctly discernible.

Hind wing ca. 2.2 mm long as preserved (estimated complete length ca. 2.5 mm), 1.2 mm wide. Costal space in general narrow, slightly narrowed medially. Subcostal veinlets simple, strongly oblique, rather widely spaced. ScP entering margin well before wing apex, rather strongly curved proximad 2scp-r. RA nearly straight, entering margin before wing apex, with four simple distal veinlets in right wing, and two veinlets (one forked) in left wing. Subcostal space broad, appearing dilated distad; crossveins not detected except distal. RA space broad, especially proximad 2ra-rp. RP with two branches before 2ra-rp, one far after. Stem of RP once forked distally. RP1 twice dichotomously forked. RP2 once forked distally. RP3 simple (right wing), one once forked distally (left wing). Crossvein 1r-m clearly visible for almost entire length under lighting at some angle; long, entering RP at proximal half of length from origin of RP to origin of RP1. M dividing into MA, MP basally compared with other sisyrids, opposite distal end of 1r-m in proximal half of length from origin of RP to origin of RP1. MA with two distal pectinate branches. MP pectinate, with three distal branches. CuA pectinate, with four preserved simple branches. Outer gradate series complete, consisting of six crossveins from RA to CuA. Of inner gradate series, only 2ra-rp detected. Trichosors prominent along entire preserved margins, except for proximal part of costal margin where these indistinct.

#### 4. Discussion

The discovery of the new species of Sisyridae from the Upper Cretaceous Taimyr Peninsula locality at Yantardakh is noteworthy. From this locality, the other adult specimen (i.e., the holotype of *Prosisyrina sukachevae*) and a presumed sisyrid larva are also known (Zherikhin, 1978; Perkovsky and Makarkin, 2015). This is currently the only fossil locality from which more than one species of sisyrid has been described. A third adult sisyrid specimen (*Prosisyrina* sp.) was found at the nearby Taimyr Peninsula locality of Ugolyak (Perkovsky and Makarkin, 2015). This might suggest that sisyrids were usual members of the Santonian riparian biocenoses of northern Siberia, living adjacent to the river bank as suggested by Zherikhin and Sinitschenkova (2002).

The holotype of *Prosisyrina sphinga* sp. n. is incompletely preserved, especially its head, thorax and forewings. Nonetheless, the male genitalia of the new species are rather well discernible, and allow comparison among genera. This is the second known record of a male fossil sisyrid; the first was the early Eocene *Paleosisyrina eocenica* Nel et al., 2003. Unfortunately, the holotype of *Prosisyrina sukachevae* lacks its abdomen, and some of its hind wing character states quite strongly differ from those of *Prosisyrina sphinga* sp. n. As a result, it is rather unclear if the new species belongs to *Prosisyrina* or to a new genus. However, we argue below that it is more

appropriate to preliminarily assign the new species to *Prosisyrina* than to create a new genus to accommodate it, as significant characters of the new species are in general similar to those of *Prosisyrina*.

The maxillary palpus of the new species appears very similar to that of *Prosisyrina sukachevae*, although it is poorly visible (Fig. 3). Its distal segment is relatively slender, probably fusiform. However, this condition is plesiomorphic in the family (see other details in Perkovsky and Makarkin, 2015). Other preserved characters of the head, antennae, thorax, and legs are not particularly diagnostic of genera. However, *Prosisyrina sphinga* sp. n. is similar to *P. sukachevae* by the presumable absence of tibial false spurs (at least these have not been detected).

The ninth tergite in the new species is generalized at the order level. This condition is apomorphically derived in other genera. In *Climacia* McLachlan, 1869, it is mediodorsally divided into two elongated lateral halves (Parfin and Gurney, 1956). In *Sisyra* Burmeister, 1839, it is more strongly derived, represented by a pair of small lateral sclerites (e.g., Tjeder, 1957, fig. 149). In *Sisyborina* Monserrat, 1981, these lateral sclerites are fully fused with the ectoprocts (Tjeder, 1976, figs. 3, 4). The structure of this tergite in *Sisyra* Banks, 1939 and *Paleosisyrina* Nel et al., 2003 is not clear.

The tenth tergite is entire in the new species, and probably in all Sisyridae except *Climacia*, in which it is divided mediodorsally into two lateral plates (ectoprocts) (Parfin and Gurney, 1956). In general, the structure of 10th tergite in *Prosisyrina sphinga* sp. n. is similar to that of *Sisyra* and *Sisyborina*, and it is, therefore, not useful in generic determination.

The structure of the ninth sternite of *Prosisyrina sphinga* sp. n. is most similar to that of the extant Afrotropical genus *Sisyborina*, especially *S. scitula* Flint, 2012 (Flint, 2012, figs. 5, 7). In these species, the ninth sternite is very prominent, of similar shape, and with two bunches of strong terminal setae (one bunch contains five

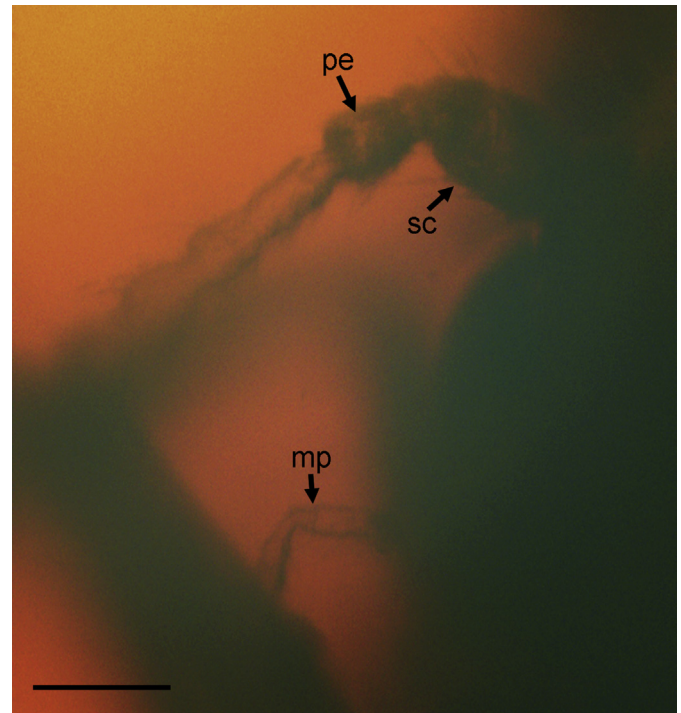
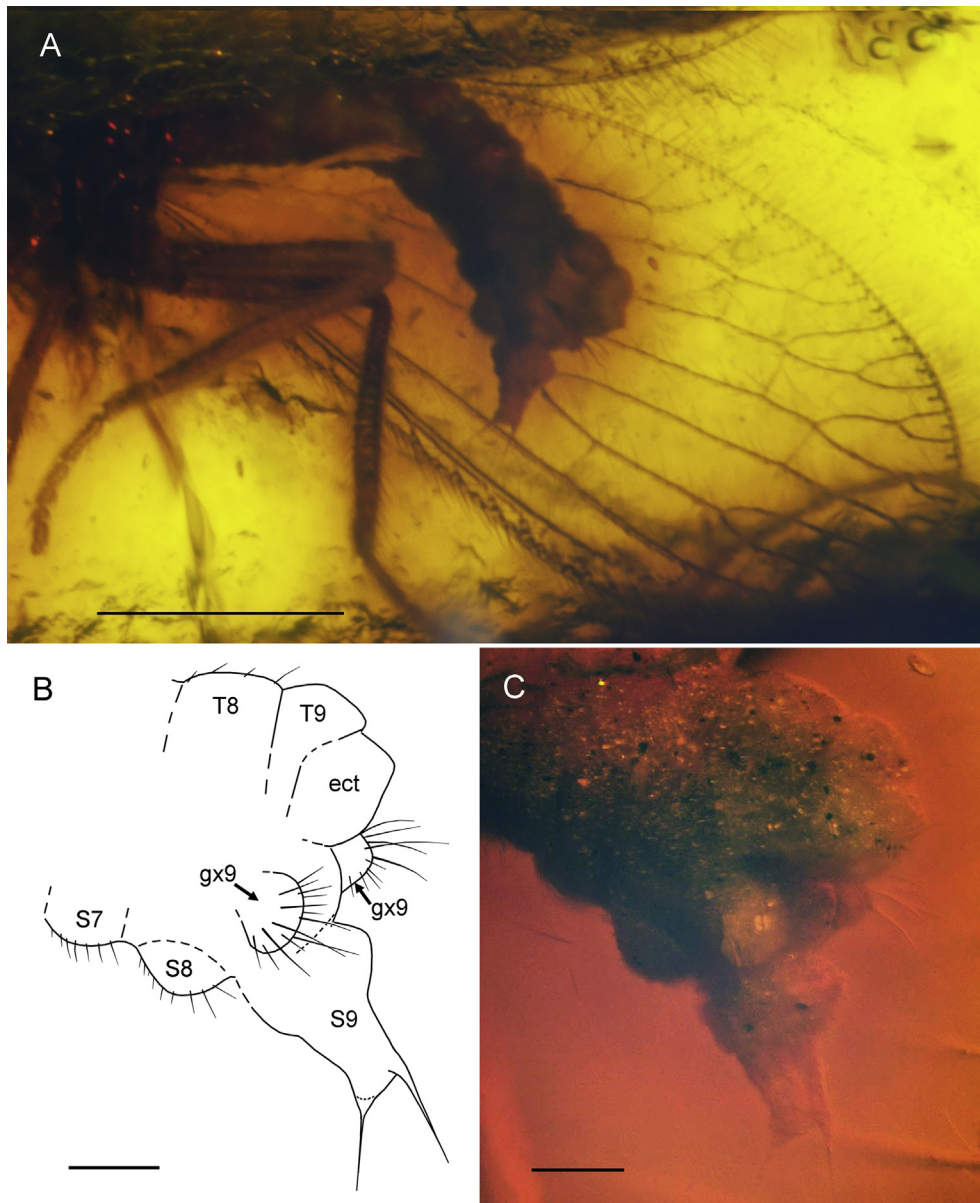


Fig. 3. *Prosisyrina sphinga* sp. nov., holotype PIN 3311/2525, proximal portion of left antenna and maxillary palpus. Abbreviations: pe, pedicellus; mp, maxillary palpus; sc, scapus. Scale bar represents 0.1 mm.



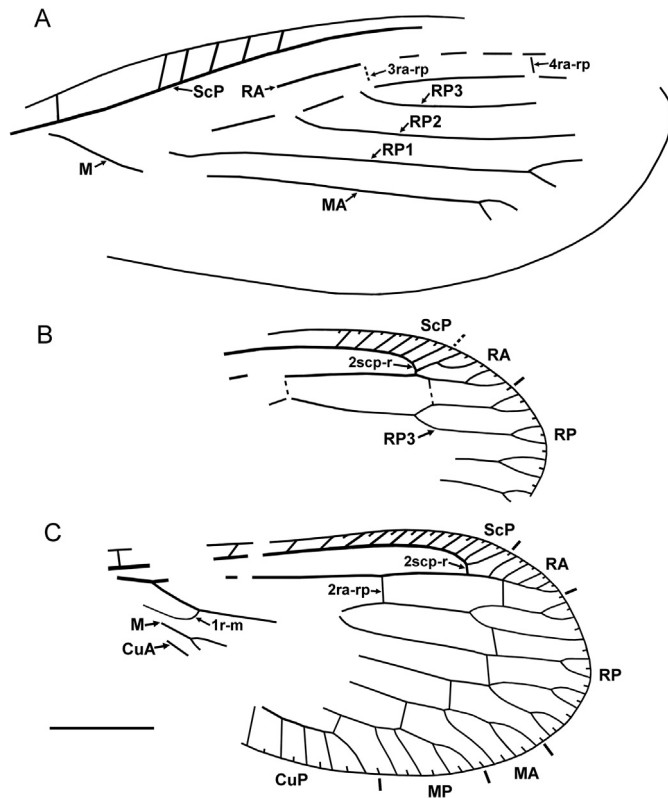
**Fig. 4.** *Prosisyrina sphinga* sp. nov., holotype PIN 3311/2525. A, abdomen and right hind wing. B, latero-caudal view of apex of abdomen (line drawing). C, same (photograph). Abbreviations: ect, ectoptroct; gx9, gonocoxites 9; pe, pedicellus; sc, scapus; S7 to S9, 7th to 9th sternites; T8, T9, 8th, 9th tergites. Scale bars represent 0.5 mm (A), 0.1 mm (B, C).

setae in *S. scitula*, and one in *P. sphinga*). Another species of this genus – *Sisyborina marlieri* (Tjeder, 1976) – also bears this long and prominent ninth sternite, but without caudal processes or strong setae (Tjeder, 1976, figs. 3, 5). In other extant genera, this sternite is relatively short, including in *Sisyryna qiong* Yang & Gao, 2002 (Yang and Gao, 2002, fig. 5c), the only species of the genus where it is described; at least, it is not prominent and without caudal processes. In the early Eocene *Paleosisyryna eocenica*, it is similarly “large and appearing terminal ventrally, but with no posterior processes” (Nel et al., 2003, p. 114). All the known specimens of *Paleosisyryna electrobaltica* Wichard in Wichard et al., 2009 from Baltic amber are females.

Gonocoxites 9 (entoprocesses of Tjeder, 1957, 1976, claspers of Parfin and Gurney, 1956, Smithers, 1973; coxopodites of Nel et al., 2003, Flint, 2012; tenth sternum of Penny, 1981) in the new species are extremely short for the family and appear weakly sclerotized. This paired structure in the extant *Sisyryna*, *Sisyryna*, and

*Sisyborina* is heavily sclerotized, long to very long, prominent, and often has dentate projections or setae (e.g., Smithers, 1973, figs. 1, 2; Tjeder, 1976, fig. 3; Flint, 2012, figs. 1–6). In *Paleosisyryna eocenica*, gonocoxites 9 are also long, each “furnished with setae and denticles in their inner side” (Nel et al., 2003, p. 114, fig. 8). In *Climacia*, gonocoxites 9 are elongated but not prominent, with a series of denticles along caudal margin (Parfin and Gurney, 1956; Penny, 1981). Therefore, the structure of gonocoxites 9 in this new species (and presumably the genus *Prosisyrina*) is unique within Sisyryidae.

The forewings of the new species are poorly preserved, but their discernible venation is generally similar to that of all known genera (except *Climacia*) in that in particular three branches of RP are long and originate proximad 3ra-rp (Figs. 2A and 5A). In *Climacia*, one to two branches of RP are originated proximad 3ra-rp (see Parfin and Gurney, 1956, pl. 2, figs. 1–9, pl. 3, figs. 1, 2; Penny, 1981, figs. 2–4; Monserrat, 2005, fig. 1). Therefore, based solely on forewing



**Fig. 5.** *Prosisyrina sphinga* sp. nov., wing venation of the holotype PIN 3311/2525. A, left forewing. B, left hind wing (both converted to standard view, with apex to the right). C, right hind wing. Scale bar represents 0.5 mm (all to scale).

characters, the new species could be attributed to any known genus except *Climacia*.

The hind wings are better preserved, and provide more characters for generic determination. Of these, the branching of RP is most interesting, i.e., two long branches originating before 2ra-rp, and another, relatively short one after. This configuration is found only in one other species, *Climacia chilleana* Parfin & Gurney, 1956 (Parfin and Gurney, 1956, pl. 3, fig. 2), although one RP branch originating before 2ra-rp is characteristic of most other species of *Climacia*. In other genera, there are three long branches of RP all originating proximad 2ra-rp. The only known exception is *Sisyra qiong* Yang & Gao, 2002, in which RP3 is rather long, but its origin is located somewhat distad 2ra-rp (pers. obs.). It is quite obvious that a similar branching of RP in *Prosisyrina sphinga* and *Climacia chilleana* evolved convergently, as these species are strongly different in other characters.

The new species is also characterized by its basal forking of M, i.e., opposite the proximal half of the length from the origin of RP to the origin of RP1, and probably proximad the proximal branch of CuA (this can be inferred from preserved venation, although this portion of the wing is not visible). A similar basal forking is found only in the Eocene genera *Paleosisyra*. In this genus, M is forked clearly proximad the proximal branch of CuA, and approximately opposite the mid-point of the length from the origin of RP to the origin of RP1 (see Nel et al., 2003, fig. 5; Scheven, 2004, right upper fig. on p. 73; Wichard et al., 2009, fig. 07.05b). In other genera (i.e., *Sisyra*, *Sisyra*, and *Sisyborina*) M is forked in the distal half of the length from the origin of RP to the origin of RP1, and at most opposite the proximal branch of CuA (in most species, distad the proximal branch of CuA), and very distally in *Climacia*. The fork of M in *Prosisyrina sukachevae* is not preserved, but its preserved

venation indicates that this fork may be also basal, at the same level that in the new species.

The basal crossvein 1r-m in *Prosisyrina sphinga* sp. n. is relatively long, only slightly shorter than that of *P. sukachevae*. It is clearly discernible for its entire visible length, whereas in *P. sukachevae* this crossvein is very poorly visible for most of its length. Crossvein 1r-m is markedly shorter in all extant sisyrids, and longer in *Paleosisyra*. Therefore, a *Prosisyrina* generic affinity of the new species is most probable, based on this character.

The hind wing costal space of the new species is similar to that of many extant species in that it is slightly narrowed medially (very narrow medially in others) unlike *P. sukachevae*, in which this space is not narrowed medially.

The subcostal veinlets of *Prosisyrina sphinga* sp. n. are spaced more obliquely and more widely than those of *P. sukachevae*. Those veinlets appear to be also widely spaced (but not so obliquely) in most extant species. In this respect, the configuration of its subcostal veinlets is more similar to that of most species of all extant genera than it is to species of the two fossil genera, especially *Prosisyrina sukachevae* and *Paleosisyra eocenica*.

In summary, it is clear that the species herein described certainly does not belong to *Sisyra* and *Climacia*, based on the characters of its genitalia and wing venation, and it cannot be assigned to *Paleosisyra*, *Sisyra*, or *Sisyborina* based on male genitalia. Therefore, the new species may theoretically belong to *Prosisyrina*, or to a new genus. We prefer to assign it to *Prosisyrina* as its characters are in general similar to those of that genus (namely, the structure of the maxillary palpus, the hind wing M and 1r-m, and the presumable absence of tibial false spurs). However, there is still a probability that this species belongs to a new, closely related genus. This is implied in particular from the structure of the costal space and the manner of RP branching in the hind wing. Unfortunately, both *Prosisyrina sukachevae* and *P. sphinga* sp. n. can be compared only by their hind wing, hind leg, and maxillary palpus character states. Other characters are missing in the fossil of *P. sukachevae*, or not detected in that of *P. sphinga* sp. n. Therefore, we refrain from establishing a new genus for this new species until more complete specimens of both or either of these species are found.

## 5. Conclusion

The discovery of this new sisyrid species from the Upper Cretaceous Taimyr amber is important, whether it belongs to *Prosisyrina* or to a new, closely related genus. It provides the possibility for the first time to study the male genitalia of Cretaceous sisyrids in more or less detail. Also, the finding of three specimens belonging to two species in Taimyr amber might suggest that sisyrids were common and diverse, at least in the Santonian riparian biocenoses of northern Siberia. Based on this, we may reasonably presume that new taxa of the Mesozoic Sisyridae will most likely be found in future.

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## References

- Aspöck, U., Aspöck, H., 2008. Phylogenetic relevance of the genital sclerites of Neuropterida (Insecta: Holometabola). *Systematic Entomology* 33, 97–127.
- Banks, N., 1905. A revision of the Nearctic Hemerobiidae. *Transactions of the American Entomological Society* 32, 21–51.
- Banks, N., 1939. New genera and species of neuropteroid insects. *Bulletin of the Museum of Comparative Zoology* 85, 439–504.
- Burmeister, H.C.C., 1839. *Handbuch der Entomologie. Zweiter Band. Besondere Entomologie. Zweite Abtheilung. Kaukerfe. Gymnognatha. (Zweite Hälfte; vulgo Neuroptera)*. Theod. Chr. Friedr. Enslin, Berlin i–xii + 757–1050 pp.
- Cockerell, T.D.A., 1917. New Tertiary insects. *Proceedings of the United States National Museum* 52, 373–384.
- Flint Jr., O.S., 2012. New species, records, and a synonymy of African Sisyridae (Neuroptera). *Insecta Mundi* 0223, 1–6.
- Kukalová-Peck, J., Lawrence, J.F., 2004. Relationships among coleopteran suborders and major endoneopteran lineages: evidence from hind wing characters. *European Journal of Entomology* 101, 95–144.
- Linnaeus, C., 1758. *Systema naturae per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis* (10th ed. vol. 1). Holmiae: Salvii. 824 pp.
- Martins-Neto, R.G., 1992. Neurópteros (Insecta, Planipennia) da Formação Santana (Cretáceo Inferior) Bacia do Araripe, Nordeste do Brasil. V. – Aspectos filogenéticos, paleoecológicos, paleobiogeográficos e descrição de novos taxa. *Anais da Academia Brasileira de Ciências* 64, 117–148.
- Martins-Neto, R.G., 1997. Neurópteros (Insecta, Planipennia) da Formação Santana (Cretáceo Inferior), Bacia do Araripe, nordeste do Brasil. X – Descrição de novos táxons (Chrysopidae, Babinskaiidae, Myrmeleontidae, Ascalaphidae e Psychopidae). *Revista Universidade de Guarulhos, Série Ciências Exatas e Tecnológicas* 2 (4), 68–83.
- McLachlan, R., 1869. New species, &c., of Hemerobiina; with synonymic notes (first series). *Entomologists Monthly Magazine* 6, 21–27.
- Monserrat, V.J., 1981. Sobre los Sisiridos de la Región Oriental (Neuroptera, Planipennia, Sisyridae). *EOS: Revista Española de Entomología* 57, 165–186.
- Monserrat, V.J., 2005. Nuevos datos sobre algunas pequeñas familias de neurópteros (Insecta: Neuroptera: Nevrothidae, Osmylidae, Sisyridae, Dilaridae). *Heteropterus: Revista de Entomología* 5, 1–26.
- Nel, A., Jarzembowski, E., 1997. New fossil Sisyridae and Nevrothidae (Insecta: Neuroptera) from Eocene Baltic amber and Upper Miocene of France. *European Journal of Entomology* 94, 287–294.
- Nel, A., Menier, J.-J., Waller, A., Hodebert, G., de Plöég, G., 2003. New fossil spongillaflies from the lowermost Eocene amber of France (Insecta, Neuroptera, Sisyridae). *Geodiversitas* 25, 109–117.
- Oswald, J.D., 1993. Revision and cladistic analysis of the world genera of the family Hemerobiidae (Insecta: Neuroptera). *Journal of New York Entomological Society* 101, 143–299.
- Oswald, J.D., 2015. *Neuropterida Species of the World. Version 4.0*. Available from: <http://lacewing.tamu.edu/SpeciesCatalog/Main> (accessed 10.12.15.).
- Parfin, S.I., Gurney, A.B., 1956. The spongilla-flies, with special reference to those of the western hemisphere (Sisyridae, Neuroptera). *Proceedings of the United States National Museum* 105, 421–529.
- Penny, N.D., 1981. Neuroptera of the Amazon Basin. Part 1. Sisyridae. *Acta Amazonica* 11, 157–169.
- Perkovsky, E.E., Makarkin, V.N., 2015. First confirmation of spongillaflies (Neuroptera: Sisyridae) from the Cretaceous. *Cretaceous Research* 56, 363–371.
- Rasnitsyn, A.P., Bashkuev, A.S., Kopylov, D.S., Lukashevich, E.D., Ponomarenko, A.G., Popov, Yu.A., Rasnitsyn, D.A., Ryzhkova, O.V., Sidorchuk, E.A., Sukatsheva, I.D., Vorontsov, D.D., 2016. Sequence and scale of changes in the terrestrial biota during the Cretaceous (based on materials from fossil resins). *Cretaceous Research* 61, 234–255.
- Scheven, J., 2004. *Bernstein-Einschlüsse: Eine untergegangene Welt bezeugt die Schöpfung. Erinnerungen an die Welt vor der Sintflut*. Kuratorium Lebendige Vorwelt, Hofheim a.T., 160 pp.
- Smithers, C.N., 1973. A new species and new records of Sisyridae (Neuroptera) from Australia. *Australian Entomological Magazine* 1, 19–22.
- Tjeder, B., 1957. Neuroptera-Planipennia. The lace-wings of Southern Africa. 1. Introduction and families Coniopterygidae, Sisyridae, and Osmylidae. In: Hanström, B., Brinck, P., Rudebec, G. (Eds.), *South African Animal Life*, vol. 4. Swedish Natural Science Research Council, Stockholm, pp. 95–188.
- Tjeder, B., 1976. *Sisyrida marlieri* n. sp. from Zaïre and Nigeria, the first representative of the genus in Africa (Neuroptera: Sisyridae). *Entomologica Scandinavica* 7, 207–210.
- Weissmair, W., 1994. Eidonomie und Ökologie zweier europäischer Schwammfliegen-Arten (Neuroptera: Sisyridae). *Entomologia Generalis* 18, 261–272.
- Weissmair, W., 2005. Schwammhafte (Insekta: Neuroptera: Sisyridae) – Parasiten der Moostiere (Bryozoa). *Denisia* 16, 299–304.
- Wichard, W., Gröhn, C., Seredysz, F., 2009. Aquatic Insects in Baltic Amber. Was-serinsekten im Baltischen Bernstein. Verlag Kessel, Remagen, 336 pp.
- Yang, C.K., Gao, M.Y., 2002. Neuroptera: Sisyridae. In: Huang, F.S. (Ed.), *Forest insects of Hainan*. Science Press, Beijing, pp. 286–289 (in Chinese, English summary).
- Yang, Q., Makarkin, V.N., Winterton, S.L., Khramov, A.V., Ren, D., 2012. A remarkable new family of Jurassic insects (Neuroptera) with primitive wing venation and its phylogenetic position in Neuropterida. *PLoS One* 7 (9), e44762.
- Yang, Q., Makarkin, V.N., Ren, D., 2014. Two new species of Kalligramma Walther (Neuroptera: Kalligrammatidae) from the Middle Jurassic of China. *Annals of the Entomological Society of America* 107, 917–925.
- Zherikhin, V.V., 1978. Development and Changes in Cretaceous and Cainozoic Faunistic Complexes (Tracheates and Chelicerates). Nauka Press, Moscow, 200 pp. (in Russian).
- Zherikhin, V.V., Sinitschenkova, N.D., 2002. Ecological history of the aquatic insects. Cretaceous. In: Rasnitsyn, A.P., Quicke, D.L.J. (Eds.), *History of Insects*. Kluwer Academic Publishers, Dordrecht, Boston, London, pp. 400–417.