



## Spongillaflies (Neuroptera, Sisyridae) in Baltic amber

WILFRIED WICHARD<sup>1,4</sup>, SONJA WEDMANN<sup>2,4</sup> & THOMAS WEITERSCHAN<sup>3</sup>

<sup>1</sup>University of Koeln, Institute of Biology, Gronewaldstrasse 2, D-50931 Koeln, Germany

<sup>2</sup>Senckenberg Forschungsstation Grube Messel, Markstrasse 35, D-64409 Messel, Germany

<sup>3</sup>Forsteler Strasse 1, D-64739 Höchst Odw., Germany

<sup>4</sup>Corresponding authors. E-mail: [wichard@uni-koeln.de](mailto:wichard@uni-koeln.de); [sonja.wedmann@senckenberg.de](mailto:sonja.wedmann@senckenberg.de)

### Abstract

Two spongillafly species are described and illustrated from Eocene Baltic amber: *Paleosisyra minor* n. sp. and *Paleosisyra electrobaltica* Wichard *et al.*, 2009; the latter species was described based on a female and is now re-described in consideration of the male genitalia of two new male specimens. Extant Sisyridae comprise few species, and their fossil record is very scarce.

**Key words:** Eocene, *Paleosisyra*, fossil sisyrid larvae, amphibious Neuroptera

### Introduction

Neuroptera is a predominantly terrestrial insect order with about 6000 described species and 18 families. The larvae of some Osmylidae go occasionally underwater and forage for submerged food. Only two neuropteran families, Sisyridae and Neurorthidae, are amphibious and have aquatic larval and pupal stages. The family Sisyridae contains about 70 living species and five extant genera: *Sisyra* Burmeister, 1839 (worldwide distributed), *Sisyrina* Banks, 1939 (Asia, Australia), *Sisyrella* Banks, 1913 (Japan), *Sisyborina* Monserrat, 1981 (Africa) and *Climacia* McLachlan, 1869 (America). Their life cycles have been described e.g. by Parfin & Gurney (1956), Weissmair (1999, 2005) and Hölzel & Weissmair 2002. Extant sisyrid larvae live in fresh water colonies of sponges or Bryozoa, on which the larvae feed.

At present, *Paradoxosisyra groehni* Makarkin, 2016 is the oldest fossil sisyrid specimen from the Cretaceous (lowest Cenomanian) Burmese amber and assigned to the new subfamily Paradoxosisyrinae, which is characterized by enormously long siphonate mouthparts and very long and slender hind legs (Makarkin 2016). Further spongillafly species, *Prosisyrina sukachevae* Perkovsky & Makarkin, 2015 and *Prosisyrina sphinga* Perkovsky & Makarkin, 2016, are found in Cretaceous (Santonian) Taymir amber. Fossil sisyrid larvae (Wichard *et al.* 2009) and further two species of the extinct genus *Paleosisyra* are known from the Eocene: *P. eocenica* Nel *et al.*, 2003 of the French Oise amber and *P. electrobaltica* Wichard *et al.*, 2009 from the Baltic amber. *Paleosisyra eocenica* is now re-described based on new male specimens and a third species *Paleosisyra minor* n. sp. was recently found in Baltic amber and is described in this paper.

### Material and methods

The fossil spongillafly specimens are enclosed in Eocene Baltic amber. The specimens were examined under a Leica M5 or MZ12.5 dissecting microscope (Leica, Wetzlar, Germany). Photographs were taken using a Leica stereomicroscope M 420 Apozoom in combination with Canon EOS 600D, EOS utility software and the Zerene Stacker software, incident and transmitted light used simultaneously. All images were edited with Adobe Photoshop CS4.

The wing venation terminology in general follows Kukalova-Peck & Lawrence (2004) using the venation abbreviations in text and figures: A—Analis (here: 1A, 2A, 3A); CuA—Cubitus Anterior; CuP - Cubitus Posterior;

MA - Media Anterior; MP - Media Posterior; R - Radius; RA - Radius Anterior; RP - Radius Posterior and RP1, RP2, RP3, RP 4, RP3+4—subordinate branches of Radius Posterior (sequence sensu Kukalova-Peck & Lawrence 2004); Sc—Subcosta. Following Oswald (1993) the forewing cross-veins are arranged in more or less aligned gradate series. These series are numerically designated 1 to 4 starting at the base of the wing: 1—basal, 2—inner, 3—middle and 4—outer gradate series. The terminology of the genitalia generally follows that of Aspöck & Aspöck (2008): e—ectoproct of 10<sup>th</sup> tergite, gx9—gonocoxite of 9<sup>th</sup> segment, S9—9<sup>th</sup> segment.

## Systematic palaeontology

### Order Neuroptera Linnaeus, 1758

### Family Sisyridae Banks, 1905

### Genus *Paleosisyra* Nel, Menier, Waller, Hodebert & de Ploeg, 2003

Type species: *Paleosisyra eocenica* Nel, Menier, Waller, Hodebert & de Ploeg, 2003

**Diagnosis** (modified from Nel *et al.*, 2003): The genus *Paleosisyra* is characterised by a combination of the following traits: 1. the fusion of subcosta Sc and radial vein RA at wing apex below the pterostigma region of fore- and hind wings, 2. complete outer gradate cross-veins series present in fore- and hindwings, 3. in hindwings a basal sinusoid cross-vein rpma-mp entering RP+MA close to the dichotomous branch in RP and in MA, and 4. the triangular-shaped terminal segments of labial and maxillary palps. Moreover, male genitalia with a pair of movable, sclerotised gonocoxites (claspers); female genitalia with the gonapophysis lateralis tapered and strongly curved dorsad. The species of *Paleosisyra* are separated by the variable wing venation and predominantly by the outer male genitalia. The extinct species differ significantly from all extant Sisyridae species in the hindwings by the conjunction of cross-vein rpma-mp with the apical part of RP+MA - instead of the basal part of RP+MA. *Paleosisyra* is an extinct Eocene sisyrid genus.

### *Paleosisyra minor* n. sp.

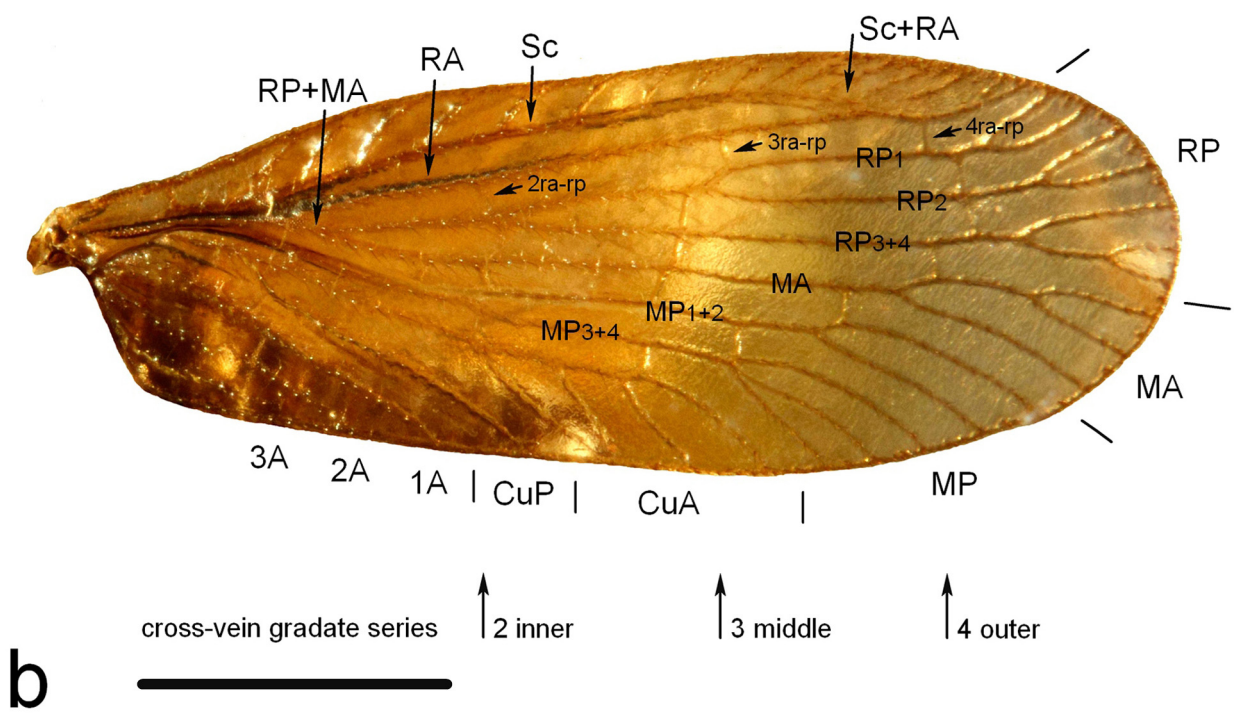
Figs. 1–2

**Holotype.** Male, deposited in the Senckenberg Forschungsinstitut und Naturmuseum, coll-no. SMF Be 2519 (ex coll. Weiterschan no. 1551). The specimen is embedded in a very small piece of amber; it is well preserved, in dorsal view the hindwings are largely covered by the forewings, in ventral view the right fore- and hindwing are distorted and partially covered by thin air films; male genitalia are poorly preserved.

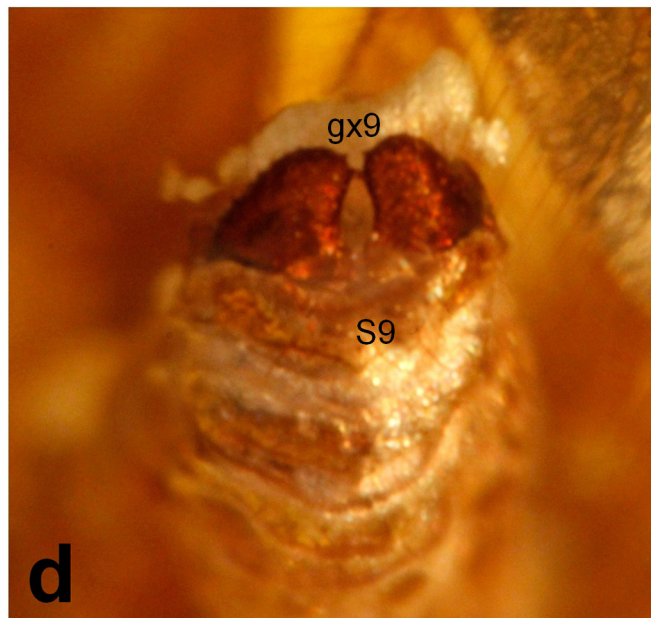
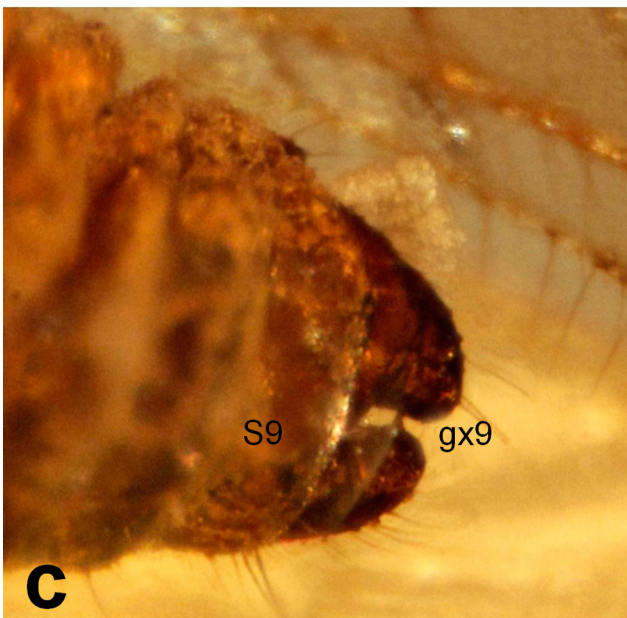
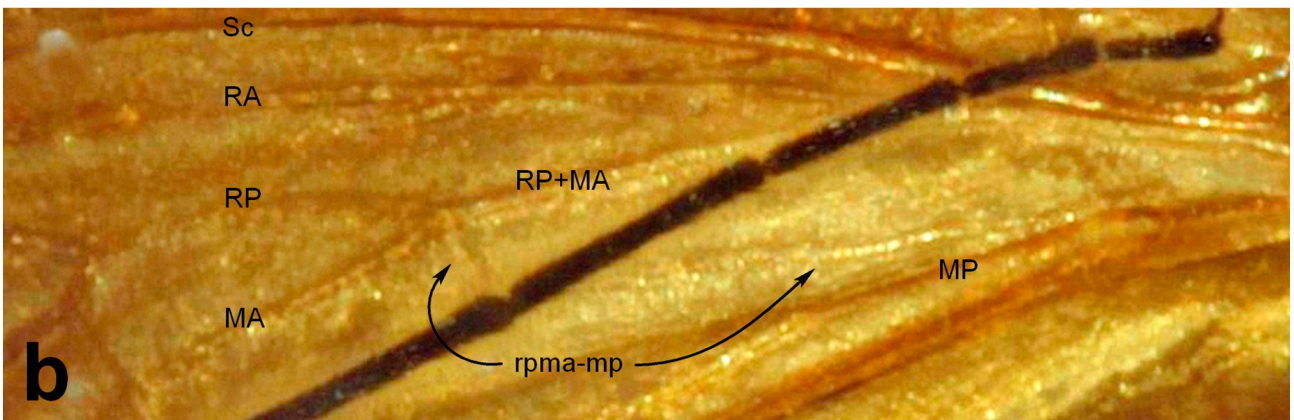
**Etymology.** The species *minor* (latin: small) is named after its small size (forewing length 3.5 mm), smaller than *P. electrobaltica* (forewing length 4–5 mm) and *P. eocenica* (forewing length 5.2 mm)

**Diagnosis.** *Paleosisyra minor* n. sp. comes with the traits of genus *Paleosisyra* and differs from *P. eocenica* and *P. electrobaltica* mainly by the male genitalia. The coxopodits are stocky and almost hemispherical, compared to the elongate and digitiform coxopodits of *P. electrobaltica* and to the “long” coxopodits of *P. eocenica*. The forewing venation is characterised by the 3-branched RP in contrast to the 4-branched RP in *P. eocenica* and *P. electrobaltica*. Three gradate series of cross-veins can be discerned (Fig. 1b). The apical cross-veins are arranged in a more or less aligned outer gradate series. In the forewing of *Paleosisyra minor* n. sp., CuA runs to the wing margin with only two terminal branches and a final terminal fork. In the hindwing the sinusoid cross-vein rpma-mp originates from MP and enters RP+MA directly at the dichotomous branch (Fig. 2b).

**Description.** *Head* (Fig. 1a): Antenna filamentous, two-thirds of the length of the forewings. Scapus distinctly larger than the other segments; pedicellus smaller, basally narrow and distally globular. The following 29 flagellomeres slightly longer than wide and approximately cylindrical. Maxillary palp 5-segmented, with first, second and fourth segments shorter than the third; terminal segment triangular in dorsal view, twice as long as the third, broadest at base, narrowed and tapered at apex. Labial palps with third terminal segment enlarged, flattened, triangle-shaped, the second segment smaller than the terminal and than the narrow first segments. Dorsal region of the head capsule (vertex) slightly convex, on both sides large compound eyes well visible.



**FIGURE 1.** *Paleosisyra minor* n. sp. (holotype, deposited in the Senckenberg Forschungsinstitut und Naturmuseum, coll-no. SMF Be 2519). a—male in dorsal view; right forewing apically distorted, left forewing length 3.5 mm. b—left forewing, scale bar = 1 mm, labelling see material and methods.



**FIGURE 2.** *Paleosisyra minor* n. sp. (holotype, deposited in the Senckenberg Forschungsinstitut und Naturmuseum, coll-no. SMF Be 2519). a—male in ventral view. b—hindwing venation. c—male genitalia in ventral view. d—male genitalia in ventrodistal view.

*Forewing* (Fig. 1b): Length 3.5 mm; membrane hyaline; costal area widened, costal cross-veins all simple, about 14 before the apical fusion between Sc and RA; subcostal area between Sc and RA with subcostal cross-vein sc-ra below the 2<sup>nd</sup> costal cross-vein and above the dichotomous branch of RA and RP+MA, then followed by the dichotomous branch in RP and in MA below the 3<sup>rd</sup> costal cross-vein.

Between RA and RP cross-vein 2ra-rp just placed basally of the dichotomous branch of RP in RP1+2 and RP3+4. The dichotomous branch of RP1+2 in RP1 and RP2 is located close to the next cross-vein 3ra-rp; RP3+4 unbranched, simple; RP 3-branched (RP1, RP2, RP3+4), all 3 branches apically with short terminal forks. MA simple, divided apically into two short terminal branches; MP midway with dichotomous branch MP1+2 and MP3+4, both divided apically into two or three terminal branches. CuA and CuP separated from wing base; CuA running parallel to margin with two terminal branches and finally a terminal fork; CuP simple. Anal veins 1A to 3A all simple, running separately to anal margin.

The area between RA and RP has three cross-veins: 2ra-rp, 3ra-rp and 4ra-rp. Cross-vein 2ra-rp participates in the inner cross-vein gradate series. Crossvein 3ra-rp is connected to the middle cross-vein gradate series. The outer cross-vein gradate series consists of cross-veins running along the furcation of the terminal branches at the apical wing margin, including cross-vein 4ra-rp of the area between RA and RP.

*Hindwing* (Fig. 2a): Costal cross-veins all simple and numerous before the apical fusion of Sc and RA; subcostal area between Sc and RA with a basal cross-vein. At wing base the stem of R hypothetically present and fused with MA; subsequently follows the dichotomous branch with RA and RP+MA; then MA separating from RP. Sinusoid cross-vein rpma-mp originating basally of MP and entering apically RP+MA directly at the dichotomous branch with separated RP and MA (Fig. 2b). RP 2-branched, separated in RP1+2 and RP 3+4, all of them with terminal forks. MA and MP simple, with terminal forks. CuA with terminal branches, CuP simple. Anal veins (1A, 2A, 3A) simple, running separately to anal margin. Apical cross-veins forming an outer gradate series.

*Male genitalia* (Fig. 2c, d): The outer genital structures are poorly preserved. The ectoproct is horseshoe-shaped but largely covered by a white reflecting air film (verlumpt), the gonocoxites (cp) heavily sclerotized, stocky and almost hemispherical; their inner sides slightly concave, apparently with a spacer to keep apart the gonocoxites. Ninth sternite (S9) slightly sclerotized, V-shaped, wide angled, without any posterior processes.

### ***Paleosisyra electrobaltica* Wichard, Gröhn & Seredszus, 2009**

Figs. 3–4

**Holotype.** Female, embedded in Eocene Baltic amber, deposited in the Geologisch-Paläontologisches Museum of the University of Hamburg, Inv.-No.: GPIMH 4522 (ex coll. Gröhn 6997).

**Additional description.** *Paleosisyra electrobaltica* Wichard *et al.*, 2009 was described on base of a female and is now re-described in consideration of the male genitalia of two new male specimens, described as:

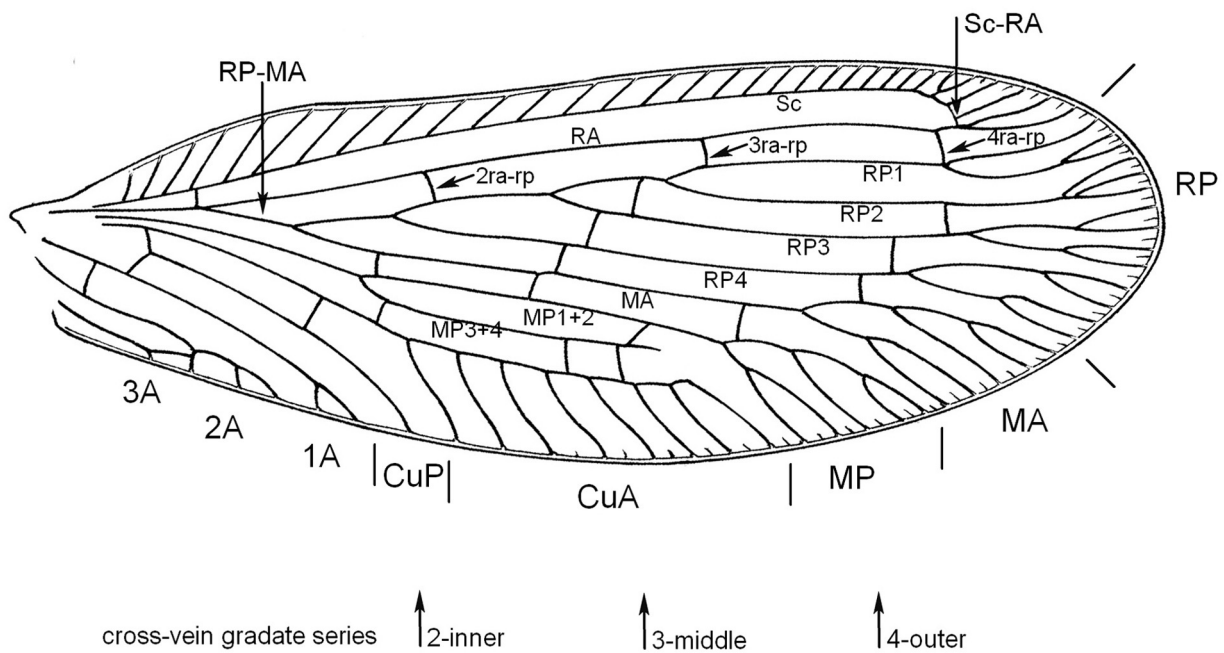
**Paratype 1:** Male, embedded in Eocene Baltic amber, deposited in coll. W. Wichard, well preserved, in lateral view male genitalia partially covered with a white reflecting air film (verlumpt).

**Paratype 2:** Male, embedded in Eocene Baltic amber, deposited in coll. T. Weiterschan, coll-no. 1380, well preserved, male genitalia in lateral view.

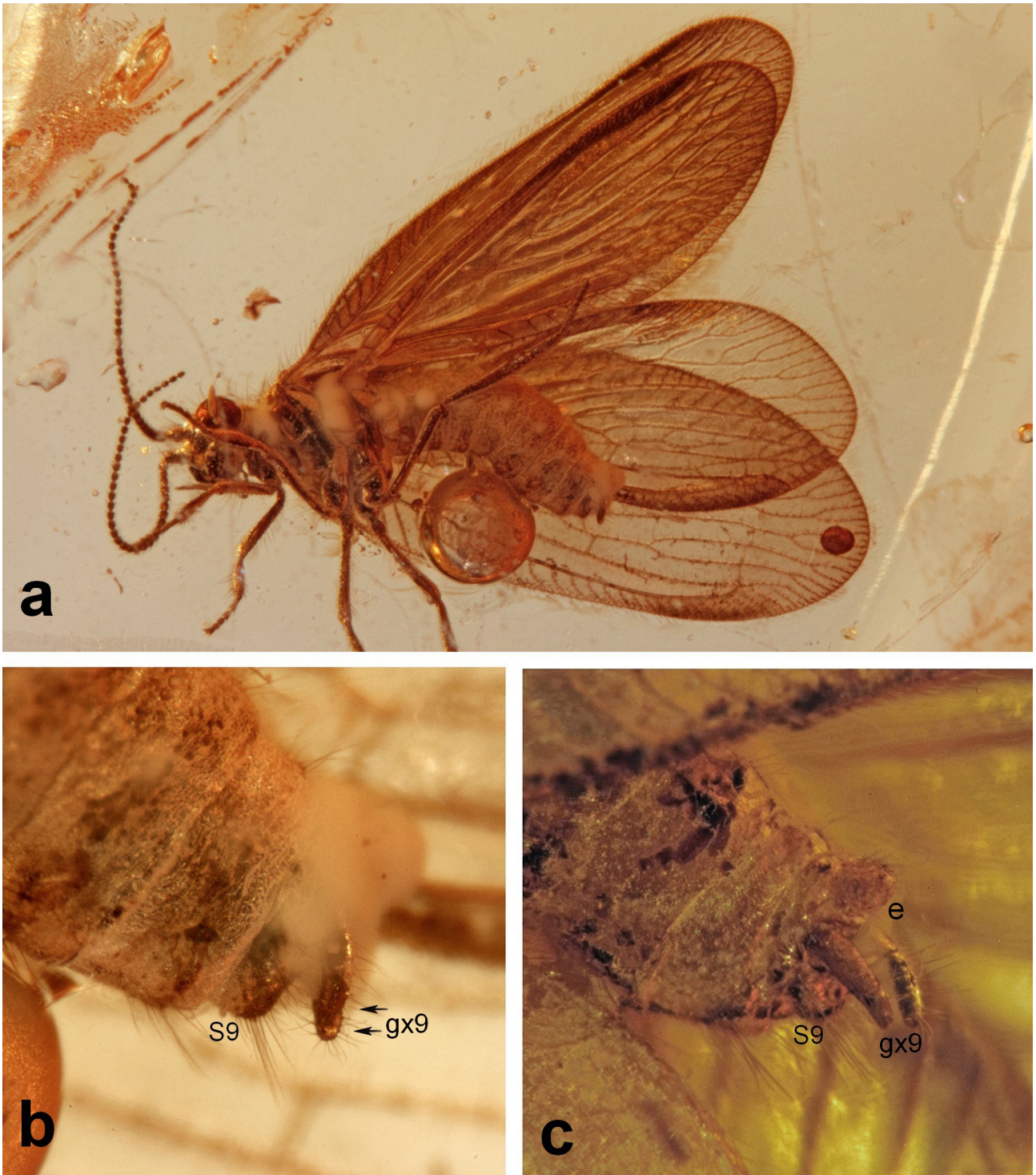
**Diagnosis.** *Paleosisyra electrobaltica* Wichard *et al.*, 2009 comes with the traits of the genus *Paleosisyra* and differs from *P. minor* n. sp. by the coxopodites which are elongate and digitiform, slightly curved ventrad. Compared with the description of the “long” coxopodites of *P. eocenica* Nel *et al.*, 2003 the elongate and digitiform coxopodites of *P. electrobaltica* do not currently allow a significant differentiation. In the forewing of *P. electrobaltica* RP is 4-branched. The apical cross-veins are arranged in a more or less aligned outer gradate series. CuA is running to the wing margin with 5-6 terminal branches and finally a terminal fork. In the hindwing the sinusoid cross-vein rpma-mp originates basally from MP and enters RP+MA apically close to the dichotomous branch. The residual distance to the dichotomous branch is a little longer than in *P. eocenica* and *P. minor* and distinctly shorter than in the Cretaceous *Prosisyrina sukachevae*.

**Description.** *Head* (Fig. 3a, 4a): Antenna filamentous, about two-thirds of the length of the forewings. Scapus distinctly larger than the other segments; pedicellus smaller, basally narrow and distally globular. The following 36 flagellomeres slightly longer than wide and approximately cylindrical. Maxillary palp 5-segmented, with first, second and fourth segments shorter than the third; terminal segment triangular in dorsal view, twice as long as the

third, broadest at base, narrowed and tapered at apex. Labial palps with third terminal segment enlarged, flattened, triangle shaped, the second segment smaller than the terminal and the narrow first segments.



**FIGURE 3.** *Paleosisyra electrobaltica* Wichard *et al.*, 2009 (female holotype, deposited in the Geologisch-Paläontologisches Museum of the University of Hamburg, Inv.-No.: GPIMH 4522). a—female in dorsal view, forewing length 5 mm. b—drawing of forewing, scale bar = 1 mm, labelling see material and methods.



**FIGURE 4.** *Paleosisyra electrobaltica* Wichard *et al.*, 2009 (male paratypes). a—male, paratype no. 1, deposited in coll. W. Wichard, ventrolateral view, forewing length 4.5 mm. b—male genitalia, paratype no. 1, deposited in coll. W. Wichard. c—male genitalia, paratype no. 2, deposited in coll. T. Weiterschan.

*Forewing* (Fig. 3b): Length 4.5 (male)–5 (female) mm; membrane hyaline; costal area widened, costal cross-veins all simple, about 29 cross-veins before the apical fusion between Sc and RA; subcostal area between Sc and RA with a basal cross-vein, sc-ra, below the bifurcation of RA and RP+MA; then followed by the separating of RP+MA in RP and MA. RP is 4-branched, RP4, RP3, RP2 and RP1 separating in a row from RP, all branches apically with short terminal forks. MA simple, divided apically into several terminal branches; MP forking midway into two branches MP1+2 and MP3+4, both divided apically into short terminal branches. CuA and CuP separated

at wing base; CuA running to margin with 5-6 terminal branches and a terminal fork; CuP simple. Anal veins (1A, 2A, 3A) all simple and ending in short terminal forks at wing margin. Forewing with basal (sc-ra), inner, middle and outer cross-vein gradate series. It is noteworthy that the wing venation is highly variable, in particular the cross-veins vary in presence and location and e.g. MP is incomplete on the right forewing of the female holotype (Fig. 3b).

*Hindwing* (Fig. 4a): Length about 3.8 mm (male); membrane hyaline. Costal cross-veins simple and numerous before the apical fusion of Sc and RA; subcostal area between Sc and RA with basal cross-vein sc-ra. At wing base the stem of R is hypothetically fused with MA along a short distance; following the dichotomous branch with RA and RP+MA. Sinusoid cross-vein rpma-mp originating basally of MP and entering apically RP+MA, thereafter MA separating from RP. RP is 3-branched; RP3 and RP1+2 separating in a row from RP; RP1+2 dichotomously branched into RP1 and RP2, all branches apically with short terminal forks. MA and MP simple, divided apically into several terminal branches. CuA with terminal branches, CuP simple. Anal veins (1A, 2A, 3A) simple, running separately to anal margin. Apical cross-veins forming an outer gradate series.

*Male genitalia* (Fig. 4b, c): The outer genital structures are poorly preserved, partially covered by a white film (verlumpt). The dorsal ectoproct (e) bulblike in lateral view. Gonocoxite (gx9) elongate, digitiform, at apex rounded, slightly curved medioventrad. Ninth sternite (S9) slightly sclerotized and slightly pre-bulged, in lateral view. Outer male genitalia loosely hairy; setae at ninth sternite longer than setae at ectoproct and gonocoxite.

*Female genitalia*: Tenth tergite dorsally forming a small and sclerotized ectoproct. Ninth tergite, in lateral view, bulky and rounded, at its base broad, apically slightly tapered, bearing the gonapophysis lateralis, which is elongate and at apex pointed, strongly curved dorsad. Ventrally the subgenital plate formed by two parallel slim plates.

### Key to the species in the genus *Paleosisyra*

- 1 In forewing radius posterior 3-branched ..... *P. minor* n. sp.
- In forewing radius posterior 4-branched ..... 2
- 2 In male genitalia ectoproct bulbous, coxopodite digitiform, curved ventrad ..... *P. electrobaltica*
- In male genitalia ectoproct broader than long, coxopodite long, straight. .... *P. eocenica*

### Discussion

Sisyrid larvae live mostly in freshwater colonies of sponges, on which they feed. This way of life is realised today and was in existence very probably in the Eocene (principle of actualism). The fossil record of sisyrid larvae (Wichard *et al.*, 2009) and of the two here presented extinct species in Baltic amber indicates the presence of sponges (Porifera, Spongillidae) in fresh water within the so-called Eocene “amber forest”, even though sponges are not yet recorded from Baltic amber.

The study by Winterton *et al.* (2010) places the origin of the sisyrid lineage into the first half of the Mesozoic, so the group may be quite old. The combination of the scarce fossil record and the relatively few extant species of Sisyridae might indicate that this family was never very diverse, perhaps due to its specialized life style.

### Acknowledgements

We thank two anonymous reviewers for their comments on the manuscript.

### References

- Aspöck, U. & Aspöck, H. (2008) Phylogenetic relevance of the genital sclerites of Neuropterida (Insecta: Holometabola). *Systematic Entomology*, 33, 97–127.  
<http://dx.doi.org/10.1111/j.1365-3113.2007.00396.x>
- Banks, N. (1905) A revision of the Nearctic Hemerobiidae. *Transactions of the American Entomological Society*, 32, 21–51.
- Banks, N. (1913) Synopses and descriptions of exotic Neuroptera. *Transactions of the American Entomological Society*, 39,



201–242.

- 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, xii + 294 pp. [pp. i–xii + 757–1050]
- Hölzel, H. & Weissmar, W. (2002) Insecta: Neuroptera. *Süßwasserfauna von Mitteleuropa*, 16, 31–86.
- Kukalova-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.  
<http://dx.doi.org/10.14411/eje.2004.018>
- Linnaeus, C. (1758) *Systema naturae per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Vol. 1. 10<sup>th</sup> Edition*, Salvii, Holmiae, 824 pp.
- Makarkin, V.N. (2016) Enormously long, siphonate mouthparts of a new, oldest known spongillafly (Neuroptera: Sisyridae) from Burmese amber imply nectarivory or hematophagy. *Cretaceous Research*. [in press]  
<http://dx.doi.org/10.1016/j.cretres.2016.04.007>
- Makarkin, V.N. & Perkovsky, E.E. (2016) An interesting new species of Sisyridae (Neuroptera) from the Upper Cretaceous Taimyr amber. *Cretaceous Research*, 63, 170–176.  
<http://dx.doi.org/10.1016/j.cretres.2016.03.010>
- McLachlan, R. (1869) New species, &c., of Hemerobiina; with synonymic notes (first series). *Entomologist's Monthly Magazine*, 6, 21–27.
- Monserat, V. J. (1981) Sobre los Sisiridos de la Región Oriental (Neuroptera, Planipennia, Sisyridae). *EOS: Revista Española de Entomología*, 57, 165–186.
- Nel, A., Menier, J.J., Waller, A., Hodebert, G. & de Ploeg, G. (2003) New fossil spongillafly 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 the New York Entomological Society*, 101, 143–299.
- 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.  
<http://dx.doi.org/10.5479/si.00963801.105-3360.421>
- Perkovsky, E.E. & Makarkin, V.N. (2015) First confirmation of spongillafly (Neuroptera: Sisyridae) from the Cretaceous. *Cretaceous Research*, 56, 363–371.  
<http://dx.doi.org/10.1016/j.cretres.2015.06.003>
- Weissmair, W. (1999) Präimaginale Stadien, Biologie und Ethologie der europäischen Sisyridae (Neuroptera: Neuroptera). *Stapfia*, 60, 101–128.
- Weissmair, W. (2005) Schwammhafte (Insecta: Neuroptera: Sisyridae)—Parasiten der Moostiere (Bryozoa). *Denisia*, 16, 299–304.
- Wichard, W., Gröhn, C. & Seredusz, F. (2009) *Aquatic Insects in Baltic Amber*. Kessel Verlag, Remagen, 336 pp.
- Winterton, S.L., Hardy, N.B. & Wiegmann, B.M. (2010) On wings of lace: phylogeny and Bayesian divergence time estimates of Neuropterida (Insecta) based on morphological and molecular data. *Systematic Entomology*, 35, 349–378.  
<http://dx.doi.org/10.1111/j.1365-3113.2010.00521.x>