New fossil spongilla-flies from the lowermost Eocene amber of France (Insecta, Neuroptera, Sisyridae)

André NEL
Jean-Jacques MENIER
Alain WALLER
Gilbert HODEBERT
Gaël DE PLOËG
Département Histoire de la Terre, Muséum national d'Histoire naturelle,
et CNRS UMR 8569,
Bâtiment d'Entomologie,
45 rue Buffon, F-75231 Paris cedex 05 (France)
anel@mnhn.fr
menier@mnhn.fr

Nel A., Menier J.-J., Waller A., Hodebert G. & De Ploëg G. 2003. — New fossil spongilla-flies from the lowermost Eocene amber of France (Insecta, Neuroptera, Sisyridae). *Geodiversitas* 25 (1) : 109-117.

ABSTRACT
A critical list of the fossil Sisyridae is proposed. The new sisyrid genus and species *Paleosisyra eocenica* n. gen., n. sp. is described from the lowermost Eocene amber of the Paris basin. Its relationships within the family are discussed in a first phylogenetic analysis of the Sisyridae. It falls as sister genus of the recent genus *Sisyra* Burmeister, 1839 and had probably a similar chorology. Some specimens of *P. eocenica* n. gen., n. sp. are covered by pollen, suggesting that it lived on flowers, as for the recent *Sisyra*. Also, the male specimens of *P. eocenica* n. gen., n. sp. are clearly less frequent than the female, as for the recent *Sisyra*. This taxon is the oldest accurate record of the Sisyridae.

KEY WORDS
Insecta,
Neuroptera,
Sisyridae,
Paleosisyra eocenica n. gen., n. sp.,
amber,
lowermost Eocene,
Paris basin,
France,
phylogenetic analysis,
new genus,
new species.

RÉSUMÉ
Nouveaux Sisyridae fossiles de l'ambre éocène inférieur de France (Insecta, Neuroptera).
Une liste critique des Sisyridae fossiles connus est proposée. Les nouveaux genre et espèce de Sisyridae *Paleosisyra eocenica* n. gen., n. sp. sont décrits de l'ambre éocène basal du Bassin de Paris. Ses affinités dans cette famille sont discutées dans une première analyse phylogénétique des Sisyridae. *Paleosisyra* n. gen. est le genre frère de *Sisyra* Burmeister, 1839 et avait probablement une chorologie similaire. Des spécimens de *P. eocenica* n. gen., n. sp. sont couverts de pollen, suggérant une alimentation au dépend de fleurs, comme pour les *Sisyra* modernes. Les mâles de *P. eocenica* n. gen., n. sp. semblent nettement plus rares que les femelles, comme chez les *Sisyra* actuels. Il s'agit du plus ancien Sisyridae décrit.

MOTS CLÉS
Insecta,
Neuroptera,
Sisyridae,
Paleosisyra eocenica n. gen., n. sp.,
ambre,
Éocène basal,
Bassin de Paris,
France,
analyse phylogénétique,
nouveau genre,
nouvelle espèce.

INTRODUCTION

The Sisyridae Handlirsch, 1906 is a small family, with only five extant genera, i.e. *Climacia* McLachlan, 1869 (Nearctic and Neotropical), *Sisyra* Burmeister, 1839 (Cosmopolitan), *Sisyrella* Banks, 1913 (Japan), *Sisyrina* Banks, 1939 (India), and *Sisyborina* Montserrat, 1981 (Afrotropical region) (Carpenter 1940; Tjeder 1976; Monserrat 1977, 1981). Sisyridae strongly resemble the Nevrorthidae Nakahara, 1915 in their wing venation. After Monserrat (1977), the family Nevrorthidae comprises three extant genera, i.e. *Austroneurorthus* Nakahara, 1958 (Australia), *Nevrorthus* Costa, 1863 (Palaearctic), and *Nipponeurorthus* Nakahara, 1958 (Eastern Asia), and the Baltic amber genus *Rophalis* Hagen, 1856. The fossil record of both families is very scarce.

Schlüter (1986), in his list of fossil Neuroptera, indicated that the Sisyridae are known from the Cretaceous, without any indication of literature.

The only Mesozoic described taxon, *Cratosisyrops gongazai* Martins-Neto, 1997 (revised in Martins-Neto 2000) (Lower Cretaceous, Santana Formation, north-eastern Brazil) was first figured and described by Martins-Neto (1992) as a "Sisyridae? gen. et sp. indet.". Martins-Neto (1997) gave the following diagnostic characters: small size; great eyes; oval wings; forewing Sc and R very close to each other, connected distally by a small cross-vein; MA forks near the base of the wing; RP with five branches; CuA pectinated; CuP bifurcated. Martins-Neto (1997) attributed this fossil taxon to the Sisyridae with some doubt and compared it to the genus *Sibithone* Ponomarenko, 1984 (in the fossil family Mesithonidae Panfilov, 1980). After the description and original figure of the type specimen, as proposed by Martins-Neto, it is not possible to attribute this taxon to a precise family. It could be related to Sisyridae, Nevrorthidae, or even Dilaridae Handlirsch, 1906.

Jarzembowski (1980) described an impression of the fore- and hindwing of a fossil Sisyridae from the upper Eocene of the Isle of Wight (UK). Its wing venation is "closest to the extant genus *Sisyra*". The preserved parts of the wing venation strongly resemble to that of *Paleosisyra* n. gen., but also to *Nevrorthus*.

Wichard & Weitschat (1996: fig. 9) figured two adult specimens from the Baltic amber that they attributed to "*Sisyra* (*Rophalis*) div. spec. – Sisyridae". The specimen figured in their "Tafel 9" (lower photograph) is clearly a *Rophalis* sp. because it has its forewing veins Sc and R not distally joined, but with a small cross-vein between them. It is very similar to the specimen of *Rophalis relicta* Hagen, 1856 described in the Nevrorthidae by Nel & Jarzembowski (1997). Wichard & Weitschat (1996: fig. 10) figured a larva they attributed to a "*Neurorthus* spec. – Neurorthidae". This larva could be that of *Rophalis* and would confirm the presence of the family Nevrorthidae in the Baltic amber. The specimen figured in the upper photograph of their "Tafel 9" is not a *Rophalis* sp. Interestingly, it is very similar to *Paleosisyra eocenica* n. gen., n. sp. (especially in its forewing veins Sc and RA which are distally joined, without any cross-vein between them, it has numerous cross-veins in the costal area, etc.). It seems to be a female specimen because of the presence of genital appendages very similar to those of *Paleosisyra eocenica* n. gen., n. sp.

Weitschat & Wichard (1998: fig. 54a) also figured a female adult specimen from Baltic amber they attribute to "?*Rophalis* sp.". The genital appendages of this specimen correspond to those of a Sisyridae and its wing venation to that of *Paleosisyra* n. gen., especially in the presence of a very short fusion of MA with RP in hindwing (see below). All these specimens probably belong to this genus, but a direct revision of these specimens will be necessary before any systematic attribution.

Schumann & Wendt (1989) mentioned a fossil Sisyridae from the Saxonian amber (Miocene, Germany).

Nel & Jarzembowski (1997) revised the Baltic amber genus *Rophalis* Hagen, 1856 and attributed it to the Nevrorthidae. They also described a *Sisyra* sp. indet. (upper Miocene of the Centre of France).

The present new species is the oldest accurate Sisyridae. We follow Aspöck *et al.* (1980) in their interpretation of genitalia characters and wing venation of Sisyridae, and Parfin & Gurney (1956) in their nomenclature of the body structures.

ABBREVIATIONS

1st m	first cross-vein between MA and MP;
1st, 2nd, 3rd r	cross-veins between R and RP;
A1, 2, 3	anal veins;
cp	coxopodites;
CuA	cubitus anterior;
CuP	cubitus posterior;
epr	ectoprocte;
gl	"gonapophyses latérales";
M	median vein;
MA	media anterior;
MP	media posterior;
R	radial vein;
RP	radius posterior;
RA	radius anterior;
Sc	subcosta.

SYSTEMATICS

Order NEUROPTERA Handlirsch, 1908
Family SISYRIDAE Handlirsch, 1906

Genus *Paleosisyra* n. gen.

TYPE SPECIES. — *Paleosisyra eocenica* n. gen., n. sp.

ETYMOLOGY. — After Paleo and the genus *Sisyra*.

DIAGNOSIS. — *Paleosisyra* n. gen. has three characters absent in all extant Sisyridae, i.e. very short fusion of MA with RP in hindwing; prothoracic epimeron and episternum well defined and broad, with a furrow between them; two strong spurs on prothoracic legs (unlike the unique spur of the legs of the extant Sisyridae, after Parfin & Gurney 1956). It has also a unique combination of characters: last segment of labial and maxillary palpi triangular; mesonotum with scutellum having a broad apex; Sc and R clearly coalescent at apex of wing below the pterostigma in fore- and hindwing; costal cross-veins all simple, numerous in fore- and hindwing; series of outer and inner gradate cross-veins in fore- and hindwing; anal veins A3 distally fused with A2, not running to anal margin; in male genitalia, a pair of long movable heavily sclerotized claspers, furnished with setae and denticles in their inner side; male parameres very small compared to claspers; female genital gl long and narrow, with the apex strongly curved.

Paleosisyra eocenica n. sp.
(Figs 1-8)

TYPE MATERIAL. — Holotype male specimen PA 2789 (1/8), with eight adult Diptera: Chironomidae and a Ephemeroptera in the same piece of amber. Female allotype specimen PA 156 (1/2), female paratype specimens PA 11, PA 52 (1/5), PA 157 (1/5), PA 2329, PA 2478 (1/2) and (2/2), PA 2493 (1/2), PA 2812, PA 3921, PA 4144, PA 4864, PA 5368, PA 5374, PA 5603. All specimens in collection De Ploëg and Indivision Langlois-Meurine, deposited in Muséum national d'Histoire naturelle, Paris. Specimens collected in Le Quesnoy all bear the letter PA for Paris (meaning Paris basin); the following number is the ordinal number in the collection.

ETYMOLOGY. — After the age of the amber locality.

TYPE LOCALITY. — Le Quesnoy, Chevrière, region of Creil, Oise department, France.

GEOLOGICAL AGE. — Lowermost Eocene, Sparnacian, level MP7 of the mammal fauna of Dormaal. We could demonstrate that the amber is autochthonous and very different from the Baltic amber in age, chemical composition and origin (Nel *et al.* 1999).

STATE OF PRESERVATION OF THE MATERIAL. — Specimen PA 2789 (1/8): nearly complete in a very clear piece of amber. The upper surfaces of the thorax and abdomen are partly destroyed. Specimen PA 156 (1/2): complete in a very clear piece of amber, together with a small insect. Specimens PA 11, PA 2478 (1/2 and 2/2), PA 2493 (1/2), PA 2812, PA 5368, and PA 5603: complete in very clear pieces of amber. Specimen PA 2329: complete covered with pollen. Specimens PA 157 (1/5), PA 4144, PA 4864, and PA 5374: head and thorax partly destroyed. Specimen PA 3921: apical parts of four wings.

DESCRIPTION

It is based on all specimens. The characters only visible on one specimen are indicated.

Head

Antenna with 36 segments, two whorls of setae on all but the basal segment, on which the setae are irregularly arranged; basal antennal segment larger than the others; clypeus and labrum not clearly visible; maxillary palpi with first, second and fourth segments shorter than the third, which is about one time and a half as long, terminal segment triangular in dorsal view, twice as long as the third, broadest at base, narrowed and tapered to a point

FIG. 1. — *Paleosisyra eocenica* n. gen., n. sp., specimen PA 2478 (1/2). Scale bar: 1 mm.

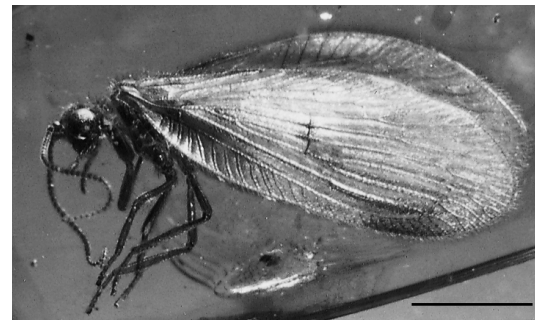

FIG. 2. — *Paleosisyra eocenica* n. gen., n. sp., specimen PA 2329. Scale bar: 1 mm.

at apex (Fig. 7); labium not visible, except for labial palpi, with third terminal segment greatly enlarged, flattened, triangle shaped and very wide at base, the second small and subcylindrical, the first one time and a half the length of the second, and narrowed proximally; clypeus and labrum with anterior margins almost straight; labrum about three times as broad as long (visible on specimen PA 156, 1/2).

Thorax

Pronotum with a strong median furrow, laterally extended but not overlapping the cervicales and dorsal portion of pleural sclerites; laterocervicales (*sensu* Parfin & Gurney 1956) large and prominent; prothoracic epimeron and episternum well defined and broad, with a furrow between them, unlike in extant *Sisyra* and *Climacia*, in which these sclerites are "reduced and united to almost form a single plate" (Parfin & Gurney 1956); numerous long and strong setae on pronotum and pleural sclerites; caudal indentation of posterior margin of metepimeron weak, less pronounced than in *Sisyra* (visible on specimen PA 157, 1/5); mesonotum with scutellum having a broad apex, similar to that of *Sisyra* (visible on specimen PA 2493, 1/2); metanotum and metascutellum not visible, hidden under the hindwings.

Legs

Metathoracic pair longer than meso- and prothoracic pairs; coxae and trochanter similar to those of extant Sisyridae (Parfin & Gurney 1956); two spurs on prothoracic leg, disposed one in front of the other; two spurs on mesothoracic and metathoracic legs, one beside the other; tarsi five-segmented; the metatarsus the longest, the fourth the shortest; the fifth bearing a pair of curved, simple claws, with a broad ventral empodium between, as for extant Sisyridae.

Forewing (Fig. 3)

Length 5.2 mm; width 2.0 mm; membrane hyaline, with pterostigma slightly darker; costal area widened 1.4 mm distal of wing base, 0.4 mm wide at widest point and 0.2 mm wide at narrowest point; costal cross-veins all simple, numerous, about 26 before pterostigma and 14 in the pterostigma before the apical fusion between Sc and R; subcostal area between Sc and R, 0.2 mm wide; only one basal subcostal cross-vein, below the fourth costal cross-vein; Sc and R clearly coalescent at apex of wing below the pterostigma; RP + MA separating off from R 0.8 mm from base; RP separating from MA 0.2 mm distally; basal of the first cross-vein (1st r *sensu* Parfin & Gurney 1956) between R and RP; three cross-veins in the area between R and RP; the first basal fork of RP is just basal of 1st r, only at the 27% of the wing length, instead of 40% in *Sisyra vicaria* (Walker, 1853) and 70% in *Climacia areolaris* (Hagen, 1861); a cross-vein aligned with the 1st r between MA and first posterior branch of RP; distance between the first and the second fork of RP 1.2 mm, longer than in *Sisyra*); the second fork of RP is at the 50% of the wing length and

the third fork slightly distally, at the 60% of the wing length; MA divided into two branches 0.6 mm basal of level of junction between Sc and R; MP forking into two branches 0.5 mm distal of separation of RP and MA, below the first fork of RP; the two branches of MP with terminal forks basal of level of junction between Sc and R; CuA and CuP separated 0.7 mm from wing base; CuA with four main branches, organized in two groups, not parallel and of different length; CuP simple; A1 with one marginal forking; A2 simple; A3 distally fused with A2, not running to anal margin (specimen PA 156, 1/2); three radio-medial cross-veins between RP and MA; two medial cross-veins between MA and MP; two medio-cubital cross-veins between MP and CuA; one cubital cross-vein between CuA and CuP; one cubito-anal cross-vein between CuP and A1; one anal cross-vein between A1 and A2; one inner series of three gradate cross-veins, not exactly aligned with 2nd r; one outer series of five gradate cross-veins, included the 3rd r.

Hindwing (Figs 4-6)

Length 3.9 mm; width 1.9 mm; membrane hyaline, with pterostigma slightly darker; costal area not widened, 0.1 mm wide at widest point; costal cross-veins all simple, numerous, about 18 before pterostigma and eight in the pterostigma before the apical fusion of Sc and R; subcostal area between Sc and R, 0.6 mm wide; no basal subcostal cross-vein; Sc and R clearly coalescent at apex of wing below the pterostigma; RP separating off from R 0.7 mm from base; MA separating off from MP 0.2 mm from base of M and fused with RP 0.7 mm distally; MA and RP are fused for a very short distance, MA separating from RP again 0.03 mm distally, 0.4 mm basal of first cross-vein (1st m *sensu* Parfin & Gurney 1956) between MA and MP; cross-vein 1st r between R and RP well distal (0.4 mm) of first basal fork of RP, and about 0.2 mm distal of level of 1st m; two cross-veins in the area between R and RP; cross-vein 2nd r just distal of the point of coalescence of Sc and R; distance between the first and the second fork of RP, 0.3 mm; MP forking basal of point of separation of RP from MA; costal

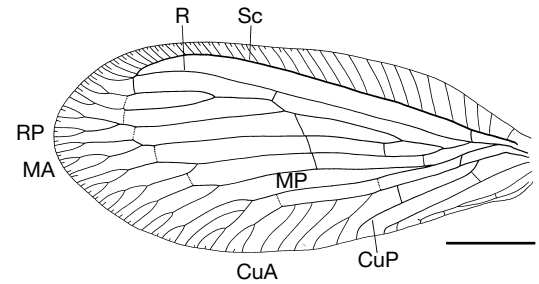

FIG. 3. — *Paleosisyra eocenica* n. gen., n. sp., specimen PA 2478 (1/2), forewing. Abbreviations: **CuA**, cubitus anterior; **CuP**, cubitus posterior; **MA**, media anterior; **MP**, media posterior; **R**, radial vein; **RP**, radius posterior; **Sc**, subcosta. Scale bar: 1 mm.

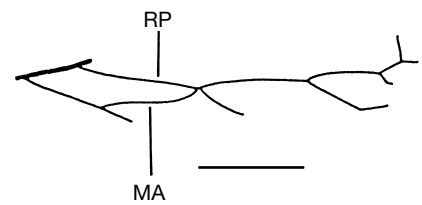

FIG. 4. — *Paleosisyra eocenica* n. gen., n. sp., specimen PA 2478 (1/2), left hindwing, area of the bases of M and RP. Abbreviations: **MA**, media anterior; **RP**, radius posterior. Scale bar: 0.5 mm.

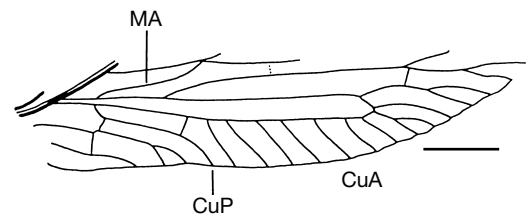

FIG. 5. — *Paleosisyra eocenica* n. gen., n. sp., specimen PA 2478 (1/2), posterior part of right hindwing. Abbreviations: **CuA**, cubitus anterior; **CuP**, cubitus posterior; **MA**, media anterior. Scale bar: 0.5 mm.

branch of MP with terminal fork basal of level of point of coalescence of Sc and R; CuA and CuP separating near base of wing; CuA long parallel to posterior wing margin, with seven or eight simple parallel posterior branches; CuP simple; A1 simple or with a short marginal fork; A2 simple; one series of seven outer scalariform cross-veins; two cross-veins between MA and MP; one cross-vein between the two branches of MP, one

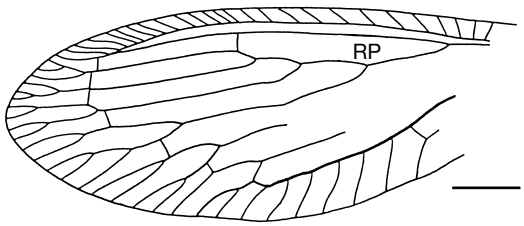

FIG. 6. — *Paleosisyra eocenica* n. gen., n. sp., specimen PA 2478 (1/2), left hindwing in dorsal view. Abbreviation: **RP**, radius posterior. Scale bar: 0.5 mm.

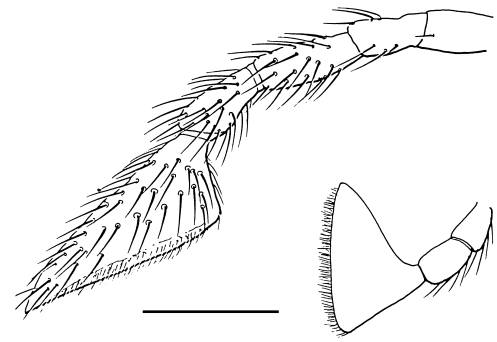

FIG. 7. — *Paleosisyra eocenica* n. gen., n. sp., specimen PA 2478 (1/2), labial and maxillary palpi. Scale bar: 0.1 mm.

between MP and CuA, one between CuA and CuP, one between CuP and A1, and one between A1 and A2.

Abdomen

Second and third tergites not sclerotized, appearing as rows of setae; fourth to seventh sclerotized, but small oval; second sternite large, with V-shaped streak; third sternite smaller, rectangular; sternites fourth to seventh also rectangular but smaller than third.

Male genital appendages (specimen PA 2789) (Fig. 8)

They are rather poorly preserved. Eighth and ninth tergites not well preserved; ectoprocte (epr *sensu* Aspöck *et al.* 1980) entire, broader than long; ninth sternite large and appearing terminal ventrally, but with no posterior processes; a pair of long movable heavily sclerotized coxopodites (cp *sensu* Aspöck *et al.* 1980), furnished with setae and denticles in their inner side; parameres very small compared to claspers, hidden under the ectoprocte.

Female genital appendages

Ninth tergite and ectoprocte (epr) as in Fig. 8; gl long and narrow, with the apex strongly curved.

DISCUSSION

After the key of the families of New (1990), *Paleosisyra* n. gen. falls in the Sisyridae because of the following characters: forewing and hindwing of generally similar shape; prothorax not elongated; fore leg not raptorial; antenna filiform, not clubbed; hindwing not broader than forewing near base; true ocelli absent on the head; no vena triplica; veins Sc and R fused near apex of wing; forewing with one single RP; arising from R near base of wing; hindwing CuA long parallel to posterior margin for some distance; the forewing costal cross-veins all simple. Some are forked in Nevrorthidae, after New (1990), but some specimens of *Nevrorthus fallax* (Rambur, 1842) have their costal cross-veins all simple (Nakahara 1958), forewing with only one Sc-R cross-vein.

The habitus and wing venation of Sisyridae and Nevrorthidae are very similar, although the two families are not closely related, after Aspöck (1992).

Paleosisyra n. gen. shares two venational characters with the Nevrorthidae, i.e. presence of two rows of gradate cross-veins in forewing; hindwing coalescence of MA with RP short. Nevertheless, it also differs from the extant and fossil Nevrorthidae in the clearly apically fused veins Sc and R. Outer gradates are also present in *Sisyrina*, *Sisyborina* and *Climacia*. Thus, this character is not sufficient to discriminate between the two families.

The male genital appendages of *Paleosisyra* n. gen. are not of recent nevrorthid-type, i.e. ninth sternite with no long median process, coxopodite very long (Nakahara 1958; Aspöck *et al.* 1980). Also, the female ninth tergite of *Paleosisyra* n. gen. is of sisyrid- rather than nevrorthid-type (Aspöck *et al.* 1980). Therefore,

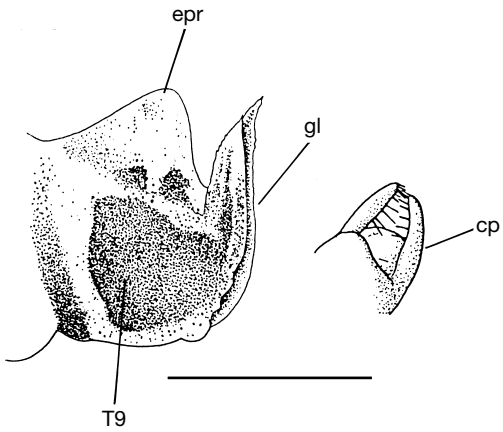

FIG. 8. — *Paleosisyra eocenica* n. gen., n. sp., male genital appendages of specimen PA 2789 and female genital appendages of specimen PA 2478 (1/2). Abbreviations: **cp**, coxopodite; **epr**, ectoprocte (after Aspöck *et al*. 1980); **gl**, lateral gonapophyses; **T9**, 9th tergite. Scale bar: 0.5 mm.

we attribute *Paleosisyra* n. gen. to the Sisyridae rather than Nevrorthidae. *Paleosisyra* n. gen. differs from the fossil genus *Rhopalis* in its Sc and R coalescent apically and its male genital appendages not of nevrorthid-type.

Within this family, after the key of genera, based on wing venation alone, proposed by Parfin & Gurney (1956), the presence of a series of outer gradate cross-veins in fore- and hindwings, and the presence of two main forks in the fore- and hindwing RP would be characteristic of *Sisyrina*. But the Sc clearly distinct in pterostigma and fused with R of *Paleosisyra* n. gen. is not in agreement with an attribution to *Sisyrina*. Furthermore, the A3 distally fused with A2, not running to anal margin is a character typical of *Climacia*, after the key of Parfin & Gurney (1956). Thus, *Paleosisyra* n. gen. does not fall near any of the extant genera, after this key.

Paleosisyra n. gen. and *Sisyra* share several body characters, i.e. the terminal segments of labial and maxillary palpi triangular; caudal indentation of posterior margin of metepimeron weak; mesonotum with scutellum having a broad apex. These characters are not present in *Climacia*. On the contrary, *Paleosisyra* n. gen. shares with *Climacia* some characters absent in *Sisyra*, i.e. pronotum laterally extended; prothoracic latero-cervical sclerites large and prominent. These characters are apparently conflictual to define the relationships of *Paleosisyra* n. gen. with the extant sisyrid genera.

The relative position of Sisyridae and Nevrorthidae has been subject to discussion since a long time (Lestage 1923). Aspöck (1992) considered that the Sisyridae could be the sister group of the Osmylidae but later (1995, 1996), she moved this family to a basal position in the Hemerobiiformia (*sensu* Aspöck 1995), as sister group of all other representative of this group of families. More recently, Aspöck *et al.* (2001) considered the Sisyridae as the sister group of the Coniopterygidae Burmeister, 1839, within Hemerobiiformia.

Sziráki (1996) contradicted these last hypotheses of Aspöck, as he considered that the Nevrorthidae (and Sisyridae) are Osmyloidea Leach, 1895. This last author does not give precisions concerning the relationships between these two families and is not very clear on the synapomorphies supporting their grouping in Osmyloidea. In all her papers, Aspöck (1992, 1995, 1996) and Aspöck *et al.* (2001) considered that the Nevrorthidae are the sister group of the Myrmeleontiformia, the [Nevrorthiformia + Myrmeleontiformia] being the sister group of the Hemerobiiformia. Thus, they would absolutely not be closely related to the Sisyridae, despite of great similarities in their general habitus.

A phylogenetic analysis, based on 12 characters, using *Nevrorthus* as outgroup, was performed using the computer software Paup 3.1.1. One parcimonious topology T = (*Nevrorthus* + (*Climacia* + (*Paleosisyra* n. gen. + *Sisyra*))) was obtained, 18 steps long, consistency index 0.94, consistency index excluding uninformative characters, 0.66, retention index 0.8. The four characters "1", "2", "5", and "13" support the clade (*Paleosisyra* n. gen. + *Sisyra*). Character "8" is convergent between *Sisyra* and *Climacia*. A calculation of the Bremer's indices (Bremer 1994) shows that: 1) the search of the trees of 19 steps or less respects the minimal tree; and 2) the search of the trees of 20 steps gives two trees with a totally unresolved consensus tree. The characters

TABLE 1. — Character states in Sisyridae. List of characters: **1**, terminal segment of maxillary palpi: (**0**), narrow, in dorsal view, more or less cylindrical, broadest at point about third of length, (**1**), triangular in dorsal view, broadest at base, narrowed and tapered to a point at apex; **2**, labial palpi: (**0**), with third terminal segment not enlarged, and not triangle shaped and wide at base, (**1**), with third terminal segment greatly enlarged, flattened, triangle shaped and very wide at base; **3**, pronotum: (**0**), laterally extended to overlap the cervicales and dorsal portion of pleural sclerites, (**1**), laterally extended but not overlapping the cervicales and dorsal portion of pleural sclerites, (**2**), not laterally extended; **4**, laterocervicales of the prothorax: (**0**), large and prominent, (**1**), not large and prominent; **5**, mesonotum with scutellum: (**0**), having a narrow apex, (**1**), having a broad apex; **6**, metascutellum: (**0**), having a narrow apex, (**1**), having a broad apex; **7**, a series of outer gradate cross-veins, in fore- and hindwing: (**0**), present, (**1**), absent; **8**, in the hindwing, media anterior and radial sector are: (**0**), fused for a short distance, (**1**), fused for a long distance; **9**, subcosta and radius are distally: (**0**), separated but with a cross-vein between them, (**1**), coalescent; **10**, the cross-veins in the costal area are: (**0**), numerous, (**1**), few; **11**, the forewing vein 3A reaches distally: (**0**), vein 2A, (**1**), the posterior margin; **12**, in the forewing, the marginal branches of cubitus anterior are: (**0**), well parallel, (**1**), organized in two groups, not parallel and of different length.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Nevrorthus Costa, 1863	0	0	0	0	0	0	0	0	0/1	0	0	0
Sisyra Burmeister, 1839	1	1	2	1	1	1	1	1	0/1	1	1	1
Paleosisyra n. gen.	1	1	1	0	1	?	0	0	1	0	0	1
Climacia McLachlan, 1869	0	0	0	0	0	0	0	1	0,1	0,1	0	0

appear rather congruent, but they are too sparse to be definitively accurate in this proposal of phylogeny. Clearly, further analyses shall be necessary to confirm this hypothesis, also because of the lack of information for potential other outgroups (other Hemerobiiformia) and for other sisyrid genera.

Nevertheless, the hypothesis of a sister group relationships between *Sisyra* and *Paleosisyra* n. gen. is supported by, at least, two unique synapomorphies, i.e. the structures of the labial and maxillary palps. Their general habitus and wing venations are also very similar.

Although other Neuroptera are known from the same outcrop, belonging to the Coniopterygidae, Psychopsidae Tylliard, 1919 and Hemerobiidae Latreille, 1803, *Paleosisyra eocenica* n. gen., n. sp. is the more frequent taxon of this order in the Paris amber (16 specimens for a total collection of about 6000 insects collected), suggesting that the amber was produced near the biota of this insect. The larvae of the extant Sisyridae are aquatic and live in freshwater sponges (Spongillidae), filamentous algae and bryozoans (Parfin & Gurney 1956). The adults seem to live on flowers and probably eat pollen. Interestingly, two specimens of *Paleosisyra eocenica* n. gen., n. sp. were covered with pollen. The ratio male/female is also surprising (one male for 15 female specimens). In the modern *Sisyra* spp., female are also much more frequent than the male (Lerault pers. comm.). These data could suggest that the biology of *Paleosysira* was similar to those of extant Sisyridae, which is also confirmed by its phylogenetic position, close to *Sisyra* (Nel 1997).

Acknowledgements

This paper is the contribution n° 02 to the knowledge of the fauna of the lowermost Eocene amber of the Paris basin. We thank the company Lafarge-Granulat for the help with the sampling of the fossil and the family Langlois-Meurinne for the authorization of working in their property. We also sincerely thank Dr. Wilfried Wichard and Dr. Ulricke Aspöck for their interesting reviewers' comments.

REFERENCES

ASPÖCK U. 1992. — Crucial points in the phylogeny of the Neuroptera (Insecta), *in* CANARD M., ASPÖCK H. & MANSELL M. W. (eds), Current research in Neuropterology. *Proceedings of the Fourth International Symposium on Neuropterology,* Bagnère-de-Luchon, France, 1991, Toulouse, 1992: 63-73.

ASPÖCK U. 1995. — Neue Hypothesen zum System der Neuropterida. *Mitteilungen der Deutschen Gesellschaf fürt Allgemeine Angewandte Entomologie* 10: 633-636.

ASPÖCK U. 1996. — Classification and phylogeny of the Neuropteroidea: An introduction. *Proceedings of the 20th International Congress of Entomology*, Firenze, 25-31 August 1996: 30.

ASPÖCK H., ASPÖCK U. & HÖLZEL H. 1980. — *Die Neuropteren Europas: eine Zusammenfassende Harstellune der Systematik, Okologie und Chorologie der Neuropteroidea Europas*. Goecke und Evers, Krefeld, 2 vols, 495 + 355 p.

ASPÖCK U., PLANT J. D. & NEMESCHKAL H. L. 2001. — Cladistic analysis of Neuroptera and their position within Neuropterida (Insecta: Holometabola: Neuropterida: Neuroptera). *Systematic Entomology* 26: 73-86.

BREMER K. 1994. — Branch support and tree stability. *Cladistics* 10: 295-304.

CARPENTER F. M. 1940. — A revision of the Nearctic Hemerobiidae, Berothidae, Sisyridae, Polystoechotidae and Dilaridae (Neuroptera). *Proceedings of the American Academy of Arts and Sciences* 74: 193-278.

JARZEMBOWSKI E. A. 1980. — Fossil insects from the Bembridge Marls, Paleogene of the Isle of Wight. *Bulletin of the British Museum of Natural History* (A), Geology 33: 237-293.

LESTAGE J. A. 1923. — Où faut-il placer les *Neurorthus* ? (Insecta Planipennia). *Annales de la Société entomologique de Belgique* 63: 65-72.

MARTINS-NETO R. G. 1992. — Neurópteros (Insecta, Planipennia) da Formação Santana (Cretáceo Inferior) bacia do Araripe, Nordeste do Brasil. 5: Aspectos filogenéticos, paleoecológicos, paleobiogeográficos e descrição de novos taxa. *Anais Academia Brasiliera Ciências* 64: 117-148.

MARTINS-NETO R. G. 1997. — Neuroptera (Insecta, Planipennia) from Santana Formation (Lower Cretaceous), Araripe Basin, Northeast Brazil. 10: Description of new taxa (Chrysopidae, Babinskaiidae, Myrmeleontidae, Ascalaphidae and Psychopsidae). *Revista Universidade Guarulhos, Ciências Exatas e Tecnológicas* 2: 68-83.

MARTINS-NETO R. G. 2000. — Remarks on the neuropterofauna (Insecta, Neuroptera) from the Brazilian Cretaceous with keys for the identification of the known taxa. *Acta Geologica Hispanica* 35: 97-118.

MONTSERRAT V. 1977. — A systematic and alphabetic list of *Neurorthidae* and *Sisyridae* (Neuroptera). *Nouvelle Revue d'Entomologie* 7: 91-96.

MONTSERRAT V. 1981. — Sobre los Sisíridos de la Región Oriental (Neuroptera, Planipennia, Sisyridae). *Eos* 57: 165-186.

NAKAHARA W. 1958. — The Neurorthinae, a new subfamily of the Sisyridae. *Mushi* 32: 19-31.

NEL A. 1997. — The probabilistic inference of unknown data in phylogenetic analysis, *in* GRANDCOLAS P. (ed.), The origin of biodiversity in Insects: Phylogenetic tests of evolutionary scenarios. *Mémoires du Muséum national d'Histoire naturelle* 173: 305-327.

NEL A. & JARZEMBOWSKI E. A. 1997. — New fossil Sisyridae and Nevrorthidae (Insecta: Neuroptera) from Eocene Baltic amber and Upper Miocene of France. *European Journal of Entomology* 94: 287-294.

NEL A., DE PLÖEG G., DEJAX J., DUTHEIL D., DE FRANCESCHI D., GHEERBRANT E., GODINOT M., HERVET S., MENIER J.-J., AUGÉ M., BIGNOT G., CAVAGNETTO C., DUFFAUD S., GAUDANT J., HUA S., JOSSANG A., DE LAPPARENT DE BROIN F., POZZI J.-P., PAICHELER J.-C., BOUCHET F. & RAGE J.-C. 1999. — Un gisement sparnacien exceptionnel à plantes, arthropodes et vertébrés (Éocène basal, MP7): Le Quesnoy (Oise, France). *Comptes Rendus de l'Académie des Sciences*, *Sciences de la Terre et des Planètes* 329: 65-72.

NEW T. R. 1990. — Planipennia (lacewings). *Handbook of Zoology* 4 (30): 1-132.

PARFIN S. I. & GURNEY A. B. 1956. — The spongillaflies, with special reference to those of the Western hemisphere (Sisyridae, Neuroptera). *Proceedings of the United States of National Museum* 105: 421-529.

SCHLÜTER TH. 1986. — The fossil Planipennia – a review, *in* GEPP J., ASPÖCK H. & HÖLZEL H. (eds), Recent research in neuropterology. *Proceedings of the 2nd International Symposium on Neuropterology*, Graz, Austria. Symposium held in Hamburg, 1984: 103-111.

SCHUMANN H. & WENDT H. 1989. — Zur Kenntnis der tierischen Inklusen des sächsischen Bernstein. *Deutsches Entomologische Zeitschrift* (N.F.) 36: 33-44.

SZIRÁKI G. 1996. — Female internal genitalia of *Megalithone tillyardi* Riek, 1974 with comments on the systematic position of the neuropterous families (Neuroptera: Ithonidae). *Folia Entomologica Hungarica* 57: 277-284.

TJEDER B. 1976. — *Sisyrina marlieri* n. sp. from Zaire and Nigeria, the first representative of the genus in Africa (Neuroptera: Sisyridae). *Entomologica Scandinavia* 7: 207-210.

WEITSCHAT W. & WICHARD W. 1998. — *Atlas der Pflanzen und Tiere im Baltischen Bernstein*. Pfeil, München, 256 p.

WICHARD W. & WEITSCHAT W. 1996. — Wasserinsekten im Bernstein. Eine paläobiologische Studie. *Entomologische Mitteilungen aus dem Löbbecke Museum + Aquazoo* 4: 1-122.

Submitted on 17 July 2001;
accepted on 23 October 2001.