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New fossil Sisyridae and Nevrorthidae (Insecta: Neuroptera) from Eocene Baltic amber and Upper Miocene of France

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Neuroptera, Nevrorthidae, Sisyridae, *Sisyra*, *Rophalis*, new diagnosis, fossil, Upper Eocene, Upper Miocene, Baltic amber, diatomaceous palaeolake, France

Abstract. A new species of *Sisyra* is described but not named from the Upper Miocene of France. The study of a new find of *Rophalis relicta* Hagen, 1856 from Baltic amber (Upper Eocene) shows that it is not a sisyrid but a nevrorthid; however, the genital apparatus of the genus *Rophalis* is atypical of this family compared with Recent genera.

INTRODUCTION

Nevrorthidae and Sisyridae are considered to be very rare in the fossil record. One Baltic amber species, *Rophalis relicta*, was described by Hagen (1856) in a distinct fossil subgenus *Rophalis* of the extant genus *Sisyra* Burmeister, 1839. He also described another species *Sisyra amissa*, also from Baltic amber. Krüger (1923a,b), who erroneously attributed the subgenus *Rhophalis* [sic] to Erichson (1842), elevated it to generic rank, gave a short redescription of *R. relicta* and provisionally attributed *Sisyra amissa* to the genus *Rophalis*.

MacLeod (1970) mentioned the presence of twenty-four specimens of Nevrorthidae and Sisyridae in the Hagen collection of Baltic amber in the Museum of Comparative Zoology, Harvard University. This material remains undescribed. Jarzembowski (1980) described an impression of a fossil forewing of Sisyridae close to *Sisyra* from the Palaeogene of the Isle of Wight (UK). Schumann & Wendt (1989) listed a fossil sisyrid (*Sisyra* sp.?) in Miocene Saxonian amber (Bitterfeld District, Germany). Martins-Neto & Vulcano (1990) and Martins-Neto (1994) indicated the presence of undescribed Sisyridae in the Lower Cretaceous Crato Formation (Bacia do Araripe, northeast Brazil). Monserrat (1977) did not list fossils in his world list of Nevrorthidae and Sisyridae. However, the genus *Rophalis* was revised by Parfin & Gurney (1956) but on the basis of the figures by Hagen (loc. cit.). Nevrorthidae have been treated as a family by Zwick (1967), although considered as a tribe by Nakahara (1915) and a subfamily of Sisyridae by Nakahara (1958), who revised them in detail.

We have recently discovered a fossil forewing of Sisyridae in the Upper Miocene of Cantal (France) and have also had the opportunity to study a very fine specimen of Baltic amber Nevrorthidae in the Esben-Petersen collection, Munich Museum of Natural History, Germany.

We mainly follow Aspöck et al. (1980, Figs 79 and 82) for the interpretation of wing venation in Nevrorthidae and Sisyridae.

TAXONOMIC ACCOUNT OF THE FOSSILS

Family Sisyridae Handlirsch, 1906
Genus *Sisyra* Burmeister, 1839
Sisyra vicaria species group
Sisyra sp. indet.

MATERIAL. Specimen No. MNHN-LP-R. 55173, leg. A. Nel, coll. Paleontology Laboratory, National Museum of Natural History, Paris.

STRATIGRAPHY. Upper Miocene, Upper Messinian, circa 5.5 m.y. before present.

LOCALITY. Diatomaceous palaeolake in an ancient maar outcrop at Sainte-Reine (Celite-France), alt. 1,100 m, near Murat, Cantal, France.

DESCRIPTION. Only the distal two-thirds of a forewing preserved (Fig. 1). Length of fragment, 5.8 mm; probable length of wing, 6.1 mm; width, 2.1 mm. Proximal part of costal area not very well preserved, only seven crossveins visible between the base and the pterostigmal area, all simple; width of costal area between C and ScP, 0.2 mm. A dark pterostigmal area clearly visible between C and ScP, 3.8 mm from the wing base, which is crossed by seven or eight crossveins. ScP and RA are clearly fused 5.0 mm distad of the wing base and 1.2 mm basad of the wing apex. ScP + RA short with four very short, simple branches reaching the costal margin. ScP and RA widely separated before fusion; width of area between ScP and RA, 0.2 mm. RA and RP + MA separate 1.2 mm from wing base and 4.8 mm basad of wing apex. Common stem of RP + MA is 0.4 mm long. MA long, simple, bifurcates 1.6 mm before posterior wing margin; each fork of MA branched as shown in Fig. 1. One crossvein between MA and RP just distad of first branch of RP, no crossveins between branches of RP. RP with three long, straight branches. Three crossveins between RA and RP, the area between RA and RP 0.2 mm wide. Base of MP not preserved but very close to base of RP + MA. MP divides into two long branches MP1 and MP2, 0.9 mm distad of its base. One crossvein between MA and MP, just distad of the first fork of MP. MP1 is longer than MP2 and has two main branches, each forked. MP2 with two main branches, but costal one simple. Bases of Cu, CuA and CuP are not preserved, but CuA with four short posterior branches and CuP long, simple vein parallel to CuA. Anal area not preserved.

DISCUSSION. This forewing is clearly a sisyrid, the venation being nearly identical to that of Recent taxa in this family.

Recent Sisyridae are divided into four genera, *Climacia* MacLachlan, 1869; *Sisyra* Burmeister, 1839; *Sisyrina* Banks, 1939; and *Sisyborina* Monserrat, 1981. Vein RP with two main forks, both well basad of the pterostigma, and fusion of RA and ScP plus the lack of any outer crossvein in the forewing preclude any relationship with *Climacia*, *Sisyrina* and *Sisyborina* (Parfin & Gurney, 1956; Carpenter, 1940; Tjeder, 1976; Monserrat, 1981). The new fossil clearly belongs to *Sisyra* and especially the *S. vicaria* group sensu Parfin & Gurney which is characterized by a forewing with three radial crossveins between RA and RP. This fossil is difficult to compare with Recent species

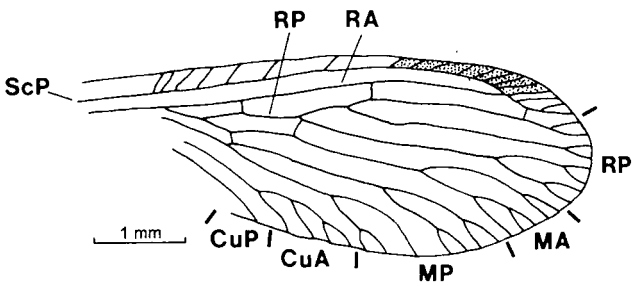

Fig. 1. Forewing venation of *Sisyra* sp. indet., spec. No. MNHN-LP-R. 55173.

in the genus, because of the lack of body and genital parts. We therefore refer it to *Sisyra* sp. undetermined.

Sisyra is a cosmopolitan genus and its discovery in the Upper Miocene of France is not surprising. Recent *Sisyra* larvae are parasitic on freshwater sponges, which are present in the sediment at Sainte-Reine.

Family Nevrorthidae Nakahara, 1958

Genus *Rophalis* Hagen, 1856, nov. sit. (not in Sisyridae)

Rhophalis [sic] Erichson, 1842, error of Krüger, 1923.

TYPE SPECIES. *Rophalis relicta* Hagen, 1856 (monobasic).

Krüger (1923a, b) tentatively attributed another species to the genus *Rophalis*, *R.* (?) *amissa* (Hagen, 1856), whose exact position remains uncertain as discussed below. Krüger erroneously attributed the genus *Rophalis* to Erichson (1842) but the latter author did not say anything concerning this genus. Parfin & Gurney (1956) considered that Erichson only produced an unpublished manuscript and Hagen (1856, Pl. 7, Fig. 25) reproduced Erichson's original figure. Spahr (1992) also noted that the attribution to Erichson is an error and refers to Hagen (1856).

NEW DIAGNOSIS. Venation very similar to that of the Recent genus *Nevrorthus* but differing from all Recent genera in the male genital structures as follows. 10th tergum with two distinct lateral lobes; "Gonarcus-Parameren-Koxopodite-Komplex" (sensu Aspöck et al., 1980) without any visible denticulate paramere and formed by two simple, long arcuate claspers with two long, sharp coxopodites and a reduced aedeagus; 9th sternum without median process but two sharp, long, straight lateral spine-like processes.

Rophalis relicta (Hagen, 1856)

(Figs 2–4)

Sisyra relicta Erichson: Hagen, 1854: 228 (nomen nudum); Handlirsch, 1906: 908.

Sisyra (*Rophalis*) *relicta* Hagen (in Berendt, Pictet-Baraban & Hagen), 1856: 87, Pl. 7, Fig. 25, Pl. 8, Fig. 19.

Rophalis relicta (Hagen): Hagen, 1866: 459; Parfin & Gurney, 1956: 522, 523–524; Jarzembowski, 1980: 261 (listed); Spahr, 1992: 75 (list).

Rhophalis relicta Erichson: Krüger, 1923a: 52–58, 62 (redescription, diagnosis); Krüger, 1923b: 83–84; Larsson, 1978: 86 (cit.); Keilbach, 1982: 284 (list).

REMARKS. The holotype was not designated but Krüger (1923a, b) indicated that the type series is located in the Museum of Danzig (two specimens in coll. Menge and one in coll. Helm). Krüger indicated that the figure of Hagen (1856) of *R. relicta* is on Pl. 7, Fig. 25. He added erroneously that the figure of another specimen from Hagen's collection was on Pl. 8, Fig. 18 and that of *R.* (?) *amissa* on Pl. 8, Fig. 19, but Hagen actually figured *Hemerobius moestus* on Pl. 8, Fig. 18, *R. relicta* on Pl. 8, Fig. 19 and *R.* (?) *amissa* on Pl. 8, Fig. 20.

Parfin & Gurney (1956) thought that the type material was lost, destroyed during the second world war. However, Keilbach (1982) supposed that a fragment of the specimen figured in Hagen (1856, Pl. 7, Fig. 25) is preserved in the collection "Menge u. Helm PD. coll. NPB". We had the opportunity to examine a very fine new specimen (No. I-40, Museum of Munich) attributable to *R. relicta* which is described below.

GEOLOGICAL AGE. Late Eocene, Baltic amber.

LOCALITY DEPOSIT. The exact location of the outcrop is unknown.

DESCRIPTION. A nearly complete specimen in a very clear small piece of amber. The four wings and abdomen with genitalia are clearly visible.

Forewing length, 5.3 mm; width, 1.6 mm. Costal area (between ScP and C) clearly widened 1.0 mm distad of wing base; 0.3 mm wide at widest point and 0.1 mm wide at

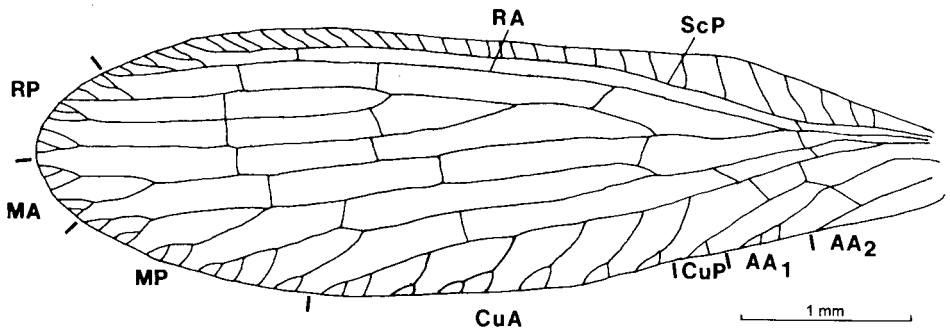

Fig. 2. *Rophalis relicta* Hagen, 1856, specimen I-40 Munich Museum, forewing.

narrowest point. Costal crossveins all simple, numerous, numbering thirty-two between the wing base and the apex of ScP. Area between ScP and RA 0.1 mm wide in widest part and 0.05 mm wide in narrowest part, with a small crossvein nearly opposite the base of RP + MA and another distally, 0.7 mm basad of apex of ScP. ScP and RA never fused and ScP not atrophied distally. RA with three small bifurcate distal branches. RP + MA begins 0.8 mm distad of wing base. MA separates from RP 0.8 mm distally of base of RP + MA; MA long simple, nearly straight vein, bifurcate near distal end, each branch with three terminal branchlets. RP with three long and nearly straight branches, each with terminal branchlets. Three crossveins between RA and RP, the proximal one distinctly oblique. Two irregular rows of gradate crossveins in area between branches of RP and MA: outer gradate crossveins proximal relative to forks of MA and MP1. Base of MP 0.5 mm distad of wing base. Basal crossvein between RP + MA and MP is clearly visible just basad of base of RP + MA; 0.1 mm long. MP forked into MP1 and MP2 1.2 mm distad of its base. MP1 long and straight with two branches 2.3 mm distad of its base. Area between RP + MA, MA and MP1 divided into four long cells; area between MP1 and MP2 divided into two long cells by a single crossvein. MP2 bifurcate 1.8 mm distad of its base. Cu and MP strongly approximated at their bases. Cu divided into CuA and CuP 0.5 mm distad of its base. CuA long with six parallel posterior branches, each forked once or twice. One small, closed quadrangular cell, 0.3 mm long and 0.1 mm wide and one broad posteriorly-open cell between CuA and CuP. CuP 0.9 mm long, bifurcate near posterior wing margin. Vein

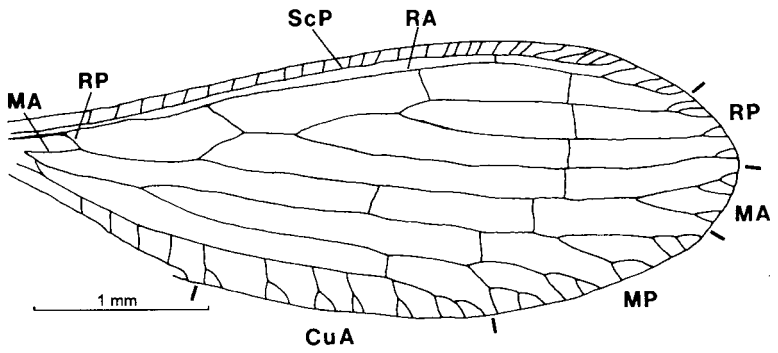

Fig. 3. *Rophalis relicta* Hagen, 1856, specimen I-40 Munich Museum, hindwing.

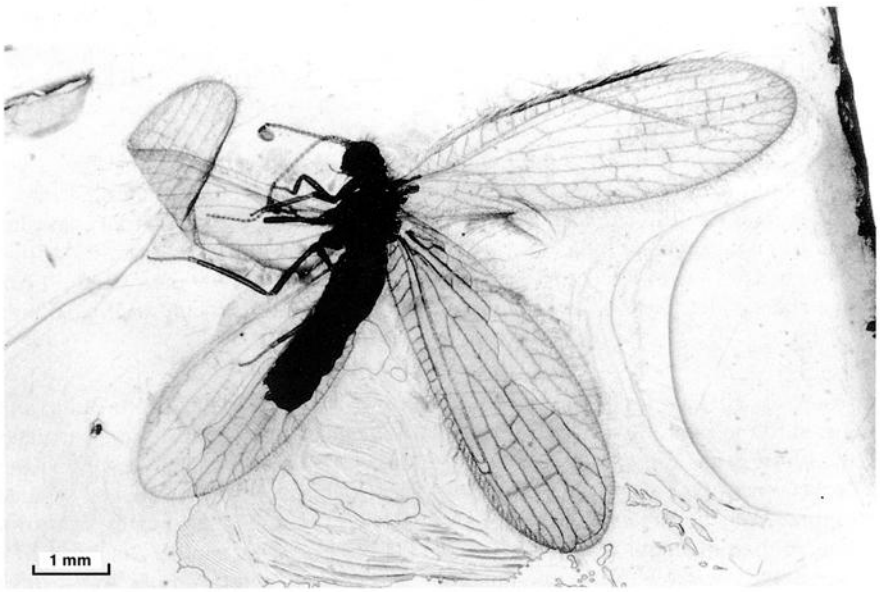

Fig. 4. *Rophalis relicta* Hagen, 1856, specimen I-40. Photograph (courtesy of J. Boudinnot).

AA1 long and with three branches near posterior wing margin; AA2 shorter, simple. One crossvein between CuP and AA1 and between AA1 and AA2. Vein AP not visible. Two rows of 0.2 mm long macrotrichia along the whole wing margin and along all main veins. One nygma clearly visible in the area between RP and MA.

Hindwing length, 4.4 mm; width, 1.6 mm. Costal area (between C and ScP) never widened and distinctly narrower than that of forewing, 0.07 mm wide, with about thirty simple crossveins between wing base and end of ScP. Area between ScP and RA also narrower than that of forewing, 0.05 mm wide. ScP not fused with RA nor atrophied. A small crossvein between ScP and RA, 0.8 mm basad of the end of ScP. RA branched very near to its end. Base of RP 0.3 mm from wing base. Free part of RP (before fusion with MA) very short, 0.1 mm long. Fused portion of RP + MA 0.7 mm long, RP and MA separating distally. RP with three simple branches, each forked very near to its end. Area between RP and RA very broad, 0.3 mm wide, with three crossveins, the proximal one distinctly oblique. MA a long, straight vein, bifurcate 0.5 mm before its end. Area between branches of RP and MA with one row of crossveins, rather well aligned. MP bifurcate 0.7 mm from wing base. MP1 and MP2 bifurcate very near to their apex. Two crossveins between MP1 and MA and one crossvein between MP1 and MP2 and between MP2 and CuA. CuA long, nearly parallel with posterior wing margin, with ten short posterior branches, the five more distal ones bifurcate. CuP and the anal veins not preserved.

GENITAL APPENDAGES. Clearly those of a male nevrorthid. Tenth tergum (sensu Nakahara, 1958, = Ektoprokte sensu Aspöck et al., 1980) is a broad subquadrate plate, 0.3 mm long and 0.3 mm wide, extending well over the genital organs, with two distinct lateral lobes, each 0.1 mm long. The "Gonarcus-Parameren-Koxopodite-Komplex" (sensu Aspöck et al., 1980, = 10th sternum sensu Nakahara, 1958) is simple without any visible denticulate

paramere; but formed by two simple arcuate claspers, each about 0.3 mm long, without any apical tooth. The coxopodite is sharp and elongate, 0.4 mm long. No visible gonarcus arch (sensu Nakahara, 1958) between the two claspers. Aedeagus not visible, reduced or absent. The 9th sternum without median process but with two sharp, straight, lateral spine-like processes, 0.2 mm long.

BODY DETAILS. Head length, 0.3 mm; width, 0.6 mm. Head distinctly transverse. Eye diameter, 0.2 mm; distance between the eyes, 0.2 mm. Antenna length, about 2.4 mm; antenna not ciliate, moniliform with 36 segments. No visible ocelli. Maxillary and labial palpi with terminal segment long, narrow, cylindrical to midpoint, then tapering distinctly and acutely to apex, as in Recent *Nevrorthus* spp. Thorax length, 0.9 mm; width, 0.7 mm. Legs long and slender. Tarsi with 5 segments. Abdomen length, 2.6 mm; width, 0.5 mm.

DISCUSSION

PREVIOUS WORKS. Two fossil species have been previously described from Baltic amber and referred to the same fossil genus (*Rophalis relicta* and *Rophalis amissa*). The diagnosis of the fossil genus *Rophalis* proposed by Krüger (1923a–b) is based on wing venation characters (numerous and simple crossveins in the costal area; RA and ScP well separated; RP with three branches; branches of RP, MA, MP and CuA bifurcate apically; two rows of crossveins in the radial area). Parfin & Gurney (1956: 523) gave another diagnosis of *Rophalis*, apparently without examining the type material: "Numerous costal cross-veins before pterostigma; Sc not appearing coalesced with R1, but running free to margin in both wings; Rs of forewing and hindwing with two main forks far proximal to the pterostigma; inner and outer gradate series of cross-veins present in both forewing and hindwing.... Maxillary and labial palpi with terminal segment long, narrow, and acute." They add that "the venation of the fossil *Rophalis*... appears to be strikingly similar to that of the present-day *Neurorthus*". Indeed, the figures of the fore- and hindwing venation of Hagen (1856, Pl. 7, Fig. 25; Pl. 8, Fig. 19) of the two described specimens of "*Sisyra* (*Rophalis*) *relicta*" show very few differences from the venation of Recent Nevrorthidae, especially *Nevrorthus*: in those specimens of *R. relicta*, the fore- and hindwing outer gradate crossveins are better aligned than in *Nevrorthus* and the forewing costal area appears less broadened near the wing base. Thus, the published wing venation of *Rophalis* provided insufficient generic characterisation.

Furthermore, nothing was known about the male genitalia of "*Sisyra* (*Rophalis*) *relicta*". In consequence, the genus *Rophalis* remained poorly defined.

NEW MATERIAL. The venational characters of this fossil are very similar to those of Recent Nevrorthidae. On wing venational grounds, the fossil resembles *Nipponeurorthus* Nakahara, 1958 (six known East Palaearctic species) because the first branches of RP and MP are forked distad of the outer gradate crossveins in the hindwing, and resembles *Nevrorthus* Costa, 1863 (four known West Palaearctic species, Aspöck & Aspöck, 1983) because of the simple costal crossveins in the forewing. In contrast, *Austroneurorthus* Nakahara, 1958 (one species in Australia) has the costal crossveins partially forked in the forewing and the first branch of RP and MP in the hindwing forked basad of the outer gradate crossveins. However, the genital organs differ greatly from those of Recent *Nevrorthus* spp. because they lack any denticulate parameres and any prominent central processes on the 9th sternum. They differ from *Austroneurorthus* because of the latter character and the non-bilobed claspers of the "Gonarcus-Parameren-Koxopodite-Komplex". The reduced central process of the 9th sternum is very similar to that of *Nipponeurorthus*, but the lack of any apical spine on the claspers of the "Gonarcus-Parameren-

Koxopodite-Komplex" is very different from this extant genus, as is the presence of a long pair of coxopodites.

Thus, this fossil cannot be included in any of the three Recent genera of Nevrorthidae. In the absence of phylogenetic revision of this family, it is impossible to polarize the genitalia characters in Nevrorthidae. At present, all that can be said about the fossil is that it seems to be related to *Nevrorthus* and *Nipponeurorthus*, especially to the latter, from the general appearance of the genitalia.

Venation of specimen I-40 is very similar to that of the two specimens of *R. relicta* figured in Hagen (1856, Pl. 7, Fig. 25; Pl. 8, Fig. 19). The only differences are in the number of crossveins between RA and RP, between MP1 and MP2 and between MP2 and CuA (see Table 1). These differences are very small and cannot justify generic or specific separation between the three fossils. Thus, we propose to attribute specimen I-40 to *Rophalis relicta*. As the genitalia characters of specimen I-40 are well preserved, it is possible to propose a new diagnosis of the genus and species (see above).

TABLE 1. *R. relicta*: venational differences between the syntype specimens in Hagen (1856) and I-40.

Specimen	cr MP1/MP2 fw	cr CuA/MP2 fw	cr RA/RP fw	cr RA/RP hw
Hag. Pl. 7, Fig. 25	1	1	2	2
Hag. Pl. 8, Fig. 19	2	1	3	3
Munich, I-40	1	2	3	3

cr MP1/MP2 fw – number of crossveins between MP1 and MP2 (forewing); cr CuA/MP2 fw – number of crossveins between CuA and MP2 (forewing); cr RA/RP fw – number of crossveins between RA and RP (forewing); cr RA/RP hw – number of crossveins between RA and RP (hindwing).

Other species of *Rophalis*: *Rophalis* (?) *amissa* differs from *R. relicta* in the following features (only the hindwing of *R.* (?) *amissa* was figured): the outer gradate crossveins are less aligned in *R.* (?) *amissa* than in *R. relicta*; *R.* (?) *amissa* has stronger but less numerous posterior branches of CuA than *R. relicta*; the two veins MP1 and MP2 are bifurcate in *R. relicta* and pectinate in *R.* (?) *amissa*; the hindwing of *R.* (?) *amissa* is narrower than that of *R. relicta*.

These differences are greater than those between Hagen's *R. relicta* and specimen I-40, but it remains impossible to be sure of the exact status of *R.* (?) *amissa* because of the lack of any information concerning the genitalia of this species. The location of its holotype is unknown.

CONCLUSION

Even if the wing venation of Sisyridae and Nevrorthidae looks rather similar, these families are considered to be phylogenetically unrelated, i.e. Nevrorthidae (Nevrorthiformia) are the sister-group of Myrmeleontiformia and (Nevrorthidae + Myrmeleontiformia) is the sister-group of Hemerobiiformia (Aspöck, 1992). Sisyridae were considered by Aspöck (1992) as the sister-group of Osmylidae. However, in the most recent approach (Aspöck, 1995), the Sisyridae are interpreted as the sister-group of all other Hemerobiiformia. Thus, the presence of true Sisyridae and Nevrorthidae in the Upper Eocene is not surprising because Myrmeleontiformia are well known from the Lower Cretaceous (Brazil, Spain, etc.) and present in the Upper Jurassic (Germany). The phylogenetic studies of Sisyridae and Nevrorthidae remain to be undertaken and should integrate the fossil taxa, especially the distinctive Baltic amber genus *Rophalis*.

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