

The first fossil cyphophthalmid harvestman from Baltic amber

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Abstract: The first fossil cyphophthalmid harvestman (Opiliones: Cyphophthalmi) from Palaeogene (Eocene) Baltic amber is described. This is only the third fossil example of this basal harvestman lineage; the others being from the probably slightly younger Bitterfeld amber and the much older, early Cretaceous, Myanmar (Burmese) amber. Although incomplete and lacking most of the appendages, the new Baltic amber fossil can be identified as a female. The somatic characters preserved, especially spiracle morphology and the coxo-genital region, allow it to be assigned with some confidence to the extant genus *Siro* Latreille, 1796 (Sironidae). This fossil is formally described here as *Siro balticus* **sp. nov.** It resembles modern North American *Siro* species more than modern European ones, and can be distinguished principally on its relatively large size and the outline form of the body.

Keywords: Cyphophthalmi, Eocene, new species, Opiliones, palaeontology, *Siro*, systematics

There are currently 29 valid species of fossil harvestmen (Arachnida: Opiliones) in the literature; see DUNLOP (2007) for an older summary. Since 2007 a further species belonging to Cyphophthalmi has been described from early Cretaceous (ca. 100 Ma) Myanmar (Burmese) amber (POINAR 2008). Long-legged and rather modern-looking Eupnoi material, partially assignable to the extant family Sclerosomatidae, is now known from the mid Jurassic (ca. 160–180 Ma) of Daohugou, Inner Mongolia, China (HUANG et al. 2009). Both records are highly significant given the relative rarity of both Asian fossil arachnids and Mesozoic Arachnida in general. DUNLOP & MITOV (2009) described further specimens belonging to Eupnoi and Dyspnoi in the German Bitterfeld amber; the age of which is controversial, but which may be Oligocene (ca. 24–25 Ma). Some of these records are of species previously recorded from the older (Eocene, ca. 45–50 Ma) Baltic amber. Two further Bitterfeld species were described as new, and one is effectively indistinguishable from, and potentially conspecific with, a living Caucasus harvestman species.

Cyphophthalmids (mite harvestmen) are widely recognised as the most basal lineage of Opiliones (e.g. GIRIBET et al. 2002, 2010: Figs. 9–10) and yet they show the poorest fossil record of any of the major harvestman groups. This may well be a consequence of

the small size and cryptic lifestyle of these superficially mite-like animals, which significantly reduces their potential for fossilisation. While conceding the inherent imprecision in age estimates, the phylogeny of



Figures 1-2: *Siro balticus* sp. nov.; holotype (F2147/BB/CJW). The first record of a fossil mite harvestman (Arachnida: Opiliones: Cyphophthalmi) from Eocene (ca. 45–50 Ma) Baltic amber. – 1: Dorsal view. – 2: Ventral view. Scale bar equals 1.0 mm.

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GIRIBET et al. (2010) predicted a possible diversification age (as opposed to origins) for Cyphophthalmi of ca. 345 Ma (i.e. early Carboniferous). This postdates the oldest known harvestman (probably an eupnoid) which is early Devonian (ca. 410 Ma) in age.

The extant cyphophthalmid fauna currently comprises 168 species (MURIENNE et al. 2010). The first fossil example of a cyphophthalmid, *Siro platypedipus* Dunlop & Giribet, 2003, was described from Bitterfeld amber and assigned to the extant genus *Siro* Latreille, 1796 (Sironidae). A second species, *Palaeosiro burmanicum* Poinar, 2008 was described from Cretaceous Myanmar amber (see above). It was assigned to a new (extinct) genus, also in the family Sironidae, based on the combination of its small size, the presence of type 2 ozophores, round spiracles, and a large sternal gland on the first sternite (POINAR 2008). In terms of biogeography (e.g. BOYER et al. 2007, Fig. 1) its assignment to Sironidae is probably incorrect (Giribet pers. comm.), given that only the family Stylocellidae occurs in this region of SE Asia today. Based on the putative presence of a cuticular lens and microvilli in the ozophores Poinar suggested that these structures may also have functioned as light-sensitive organs, in addition to their function in releasing defensive secretions. A more prosaic interpretation would be that the translucent areas at the ends of the ozophores merely reflect fluid released during the entrapment process.

Here, we report on only the third fossil example of a cyphophthalmid (Figs. 1–3, 5–6). The specimen is incomplete which makes detailed comparisons with other extant and fossil taxa (cf. KARAMAN 2009 and references therein) difficult. However some genus-specific characters can indeed be recovered and we can provisionally assign it to a new species of *Siro*; representing the first record of the genus from Baltic amber.

Material and Methods

The new fossil described here is from the Jörg Wunderlich collection, specimen number F2147/BB/CJW. This material will probably be transferred eventually to the Senckenberg Museum, Frankfurt/Main, Germany, or one of its allied institutions. The specimen lies in a subrectangular block of clear, yellow amber; dimensions ca. 25 × 15 mm. It was extracted from a larger amber piece (number F2159) in order to reveal the ventral surface of the harvestman more clearly.

The fossil was photographed (Figs. 1–2) by taking

sequential series of ca. 10 images at different focal planes through the specimen using a Leica stereomicroscope with the Leica Application Suite software. Stacks of images were assembled into a single final picture using Auto Montage. It was drawn and studied under a stereomicroscope with a *camera lucida* attachment (Fig. 5–6). The fossil was compared to extant cyphophthalmids in the collections of the Museum für Naturkunde Berlin and the personal collection of P.G. Mitov, as well as to the literature; particularly JUBERTHIE (1970), GIRIBET & BOYER (2002) and KARAMAN (2009), from whom the morphological terminology used is largely adopted. Terms for the description of the coxo-genital region are based on HOFFMAN (1963) and VAN DER HAMMEN (1985).

Further data on the distribution of modern genera was retrieved from the catalogue of GIRIBET (2000), now updated online and including numerous images of extant taxa under <<http://giribet.oeb.harvard.edu/Cyphophthalmi/>>. An exact provenance for the new fossil specimen is not recorded, but much of the currently available amber derives from the Kaliningrad region on the Baltic coast of Russia. An exact age for amber is difficult to determine objectively, but Baltic amber is traditionally dated at Paleogene (Eocene), or about 45–50 Ma.

For comparative purposes, a scanning electron micrograph (SEM) photograph of the genital region of a recent cyphophthalmid harvestman is also included here (Fig. 4): 1 female *Cyphophthalmus duricorius* Joseph, 1868: Slovenia, 4 km NW from Postojna, Pivka Jama camp site, under stones in the old pine forest (N 45°48'18.28" E 14°12'16.01", 550–579 m a.s.l.), 16.IX.1989, leg. and det. P. G. MITOV. The SEM study was made at 10–20 kV with a Philips 515 machine. The specimen was sputter-coated with a 300–400 Å gold layer. Further SEMs of the American species *Siro exilis* Hoffman, 1963 were kindly provided by Günther Raspotnik (Figs. 7–8): 1 female *Siro exilis* Hoffman, 1963: West Virginia, Randolph Co., Monongahela National Forest, nr. Bowden; Otter Creek Wilderness trailhead near Alpena Gap, deep litter of mixed riparian forest (red maple, yellow birch, eastern hemlock, white spruce) with dense understory of rhododendron, 930 m a.s.l., 38° 56.505' N, 79° 40.084' W, 13.VI.2006, leg. and det. Roy A. Norton.

The specimen was air-dried, mounted on an aluminium stub and sputtered with gold (AGAR sputtercoater, Gröpl, Tulln, Austria). The SEM study was made at 20 kV with a Philips XL30 ESEM (Philips/

FEI, Vienna, Austria) at high vacuum mode.

Order Opiliones Sundevall, 1833

Suborder Cyphophthalmi Simon, 1879

Family Sironidae Simon, 1879

Genus *Siro* Latreille, 1796

***Siro balticus* sp. nov.**

Material: Holotype ♀ and only known specimen, JÖRG Wunderlich collection, F2147/BB/CJW. From Baltic amber, exact locality not recorded; Paleogene, Eocene.

Diagnosis: Relatively large (length 2.34 mm) fossil *Siro* species, specifically without the projecting rear end typical of modern European forms, and with body proportions differing from those in the – probably more closely related – extant North American species (see Remarks for details).

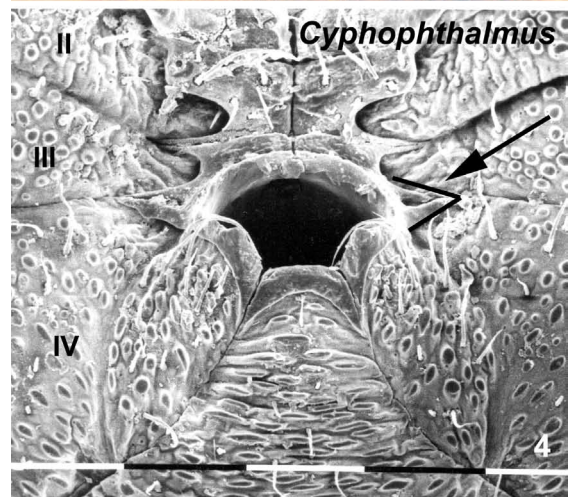
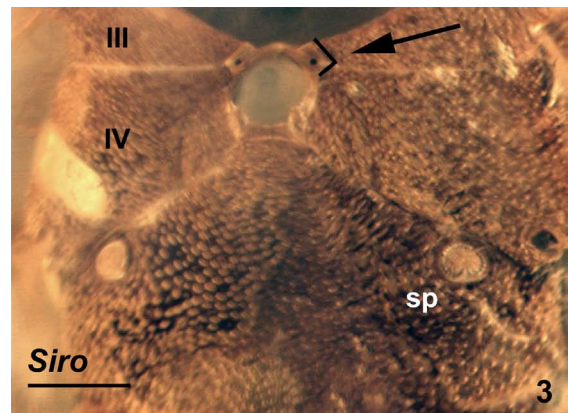
Derivation of name: From Baltic amber and the Baltic region; the source of this material.

Description: Partially complete female specimen preserved in both dorsal (Figs. 1, 5) and ventral view (Figs. 2, 6). All measurements in mm. Body oval; pale brown in colour within the amber, but with darker patches across the body; total length 2.34; maximum prosomal width behind the ozophores 1.33; maximum opisthosomal width 1.34. Length:width ratio 1.75. Distance between front of scutum (i.e. anterior margin of prosoma) to an imaginary line connecting the anterior (front) bases of ozophores 0.23; total width across (and including) ozophores 1.09.

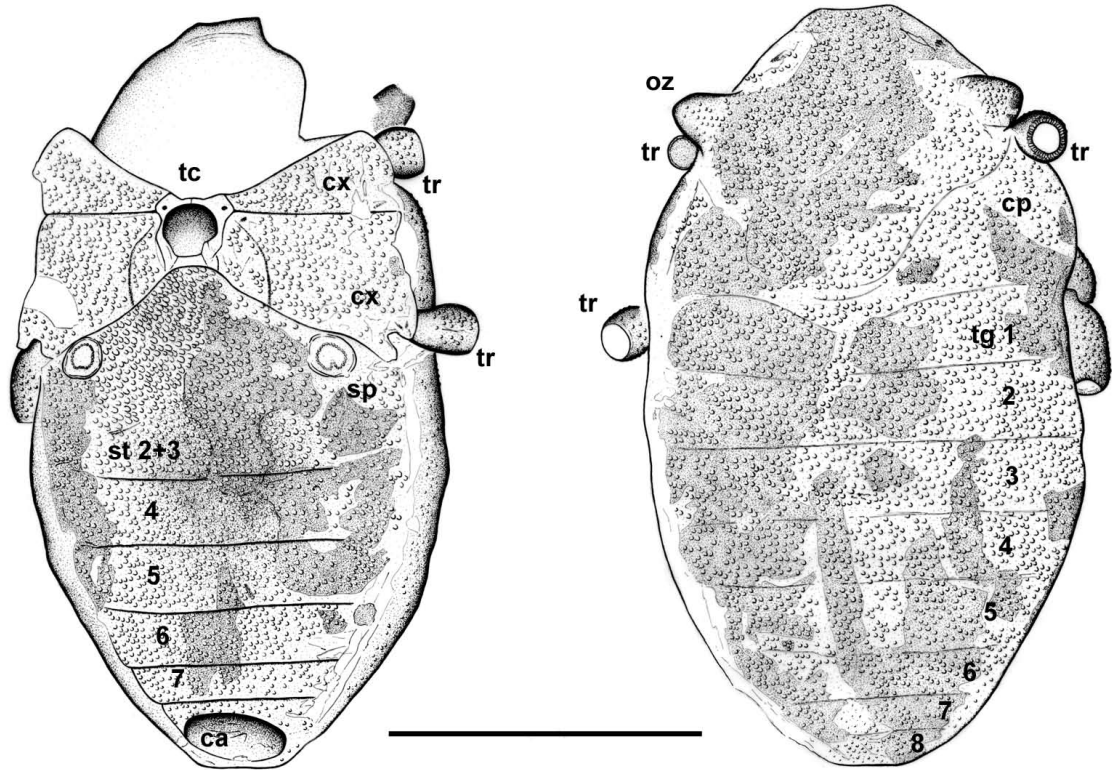
Entire body with pustulate ornament of small, rounded to oval tubercles, generally larger in anterior body regions and smaller posteriorly and on the leg trochanters. Eyes absent. Ozophores conical to slightly pointed and angular, dorsolaterally prominent on the scutum in the type 2 position sensu JUBERTHIE (1970, Fig. 2). Exact position of the ozopore itself – i.e. the opening of the repugnatorial gland – difficult to resolve, but may be terminal. Length of ozophores 0.13; width at base 0.22. Slight bulge to body immediately behind the ozophores. Frontal ridge of scutum (i.e. anterior margin of carapace) slightly recurved. Sulcus beginning immediately behind the ozophores curves down towards the midline and defines a posteriorly deeply recurved anterior area of the body; length 0.84 on the midline. Area behind it incorporates the bulge in the body laterally and is also recurved at the midline, length here 0.12. This region followed by eight, quite clearly defined, tergites all with essentially straight posterior margins. Gaps between tergites lack tuberculation. Anterior four tergites longer, lengths c. 0.2; posterior three are notably shorter, lengths 0.13,

0.11 and 0.12 respectively. Posterior end of opisthosoma bluntly rounded to slightly angular in dorsal view.

Ventral prosomal complex incomplete. Chelicerae, pedipalps, coxae of legs 1–2 and all walking legs beyond the trochanter absent. Conceivably, the missing coxae (I–II, or perhaps II only) were free, i.e. not fused to coxae III–IV; which could explain why the breakage point in the fossil lies between the second and third coxae. Third coxae triangular, coming to a point immediately above the thoracic complex, but not quite reaching the midline. Third trochanter somewhat



Figures 3-4: Details of the thoracic complex region. – **3:** *Siro balticus* sp. nov.; holotype (F2147/BB/CJW). The rounded spiracle (sp) with denticles inside the lumen is a convincing character of the genus *Siro* Latreille, 1796. Coxae numbered. The area between coxal lobes III and IV (i.e. around the coxal pores) has an obtuse, ca. 90°, angle (outlined by black bars: arrowed); another *Siro* character. Scale bar equals 200 µm. – **4:** Same region in a modern cyphophthalmid, *Cyphophthalmus duricorius* Joseph, 1868, SEM. Scale bars equal 100 µm. In *Cyphophthalmus*, by contrast, the area between coxal lobes III and IV has a very acute angle (outlined by black bars: arrowed).



Figures 5-6: Interpretative *camera lucida* drawings of the specimen shown in Figs. 1-2. **5:** Dorsal view. – **6:** Ventral view. Abbreviations: ca = expected site of corona analis, cp = carapace, cx = coxa, oz = ozophore, sp = spiracle, st = sternites 2+3 (subsequent sternites numbered successively), tc = thoracic complex, tg1 = tergite 1 (subsequent tergites numbered successively), tr = trochanter. Scale bar equals 1.0 mm.

rounded and cup-shaped, but details equivocal. Fourth coxae much larger than the third and more quadratic in shape. Distinct suture line originates near the anterolateral corners of the thoracic complex and curves towards the posterior margin of the coxae, bisecting it about a third of the way along its length towards the distal margin. Fourth trochanter emerges from the posterior part of the fourth coxae and is associated with a small, but distinct indent into the coxal margin. Trochanter 4 tubular, longer than wide and with a slightly oval outline, widening distally, length 0.28.

Thoracic complex with the outline of an inverted subtriangular structure, dominated centrally by large genital opening (or gonostome) of the female type (Fig. 3). Gonostome anteriorly with semicircular outline; width 0.17, length 0.16; no genital structures visible within this opening. Thoracic complex flanked laterally by sutured-off part of the fourth coxae, posteriorly by the second sternite and anteriorly (in part) by the third coxae. More anterior elements missing. Thoracic complex divided anteriorly by a short mid-

line sulcus. Either side of this, i.e. on the anterolateral margins of the gonostome, are areas surrounding the coxal pores (= orifices of the coxal glands). Pores themselves clearly visible as small, but distinct holes, diameter 0.0125, lying between coxal lobes III and IV.

Sternites two and three apparently fused into a single, large subtriangular plate, projecting anteriorly between the leg 4 coxae with a procurved and bluntly rounded anterior margin pointing towards the thoracic complex. Tuberculation here heavier, with larger and more oval tubercles. Spiracles present as prominent, round to oval-shaped elements (maximum diameter 0.16) in a lateral position immediately behind the fourth coxae; ring of tiny denticles present within the lumen, expressing – at least on the right side – a distinct invagination towards the centre of the spiracle. No obvious sternal pores, or other structures, located on the midline between the spiracles.

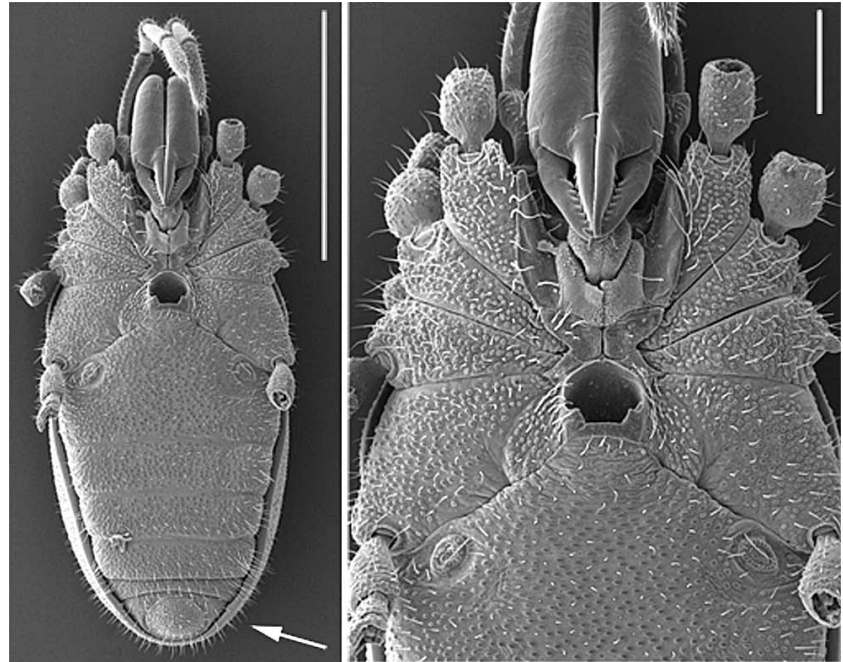
Five sternal elements (presumably sternites 4–8) preserved behind the large, spiracle-bearing sclerite. Sternites 4–7 decrease successively in length: i.e.

0.20, 0.19, 0.16 and 0.10. Sternite 8 forms the anterior border of a fairly large oval opening, width 0.32, which in life would probably have contained the corona analis. Posterior margin of opisthosoma somewhat blunt and rectangular in ventral view; i.e. not smoothly rounded, but details of any specific sclerites here difficult to resolve. In general, tergites slightly wider than sternites and marginal overlap from the overlying tergites can be seen ventrally at the lateral edges of the body.

In cyphophthalmids the form of the gonostome differs between the sexes and this specimen clearly has the female type. Since the gonostome is preserved open (Fig. 3), it must be an adult and is thus clearly a mortality rather than a moult.

Intuitively, the new fossil with its distribution in the Eocene of northern Europe is likely to be a member of Sironidae (see e.g. GIRIBET (2000: Fig. 2) or BOYER et al. (2007: Fig. 1) for distribution maps) because none of the other extant cyphophthalmid families occur in this region today. The fossil is unquestionably modern in appearance and affinities with a number of extant genera need to be considered: i.e. *Siro* Latreille, 1796, *Cyphophthalmus* Joseph, 1868 (re-established by BOYER et al. 2005 for a Balkan radiation; see also KARAMAN 2009 and MURIENNE et al. 2010) and the four Iberian genera most recently investigated by MURIENNE & GIRIBET (2009). These taxa are morphologically rather conservative and appear similar in overall habitus, while a number of taxonomically important details are missing from the new fossil which hinders its unequivocal generic assignment.

KARAMAN (2009: table 1) established a series of characters useful in separating *Siro* from *Cyphophthalmus*. Some of these, such as the number of paired, movable fingers associated with the spermatopositor, the number of anal glands, and the shape of the adenostyle of the tarsal gland apophyses, only occur in males and are thus unhelpful in placing this female



Figures 7-8: Comparative SEM images of a female of the Recent species *Siro exilis* Hoffman, 1963 from the eastern USA. These eastern *Siro* species are thought to be closer to the European fauna than those of the western USA (cf. Shear 1980). **7:** Overview. Scale bar equals 1.0 mm. Note the overall similarity to the fossil *Siro* species in terms of the absence of a projecting rear end (arrowed); a feature usually seen in the (modern) European forms. – **8:** Detail of spiracles and thoracic complex region. Scale bar equals 200 μ m.

fossil. An alternative character (cf. KARAMAN 2009: p. 262) which would have been useful is the shape and structure of the prosomal complex (i.e. the coxal lobes of legs II, immediately in front of the genital opening), but unfortunately this feature is equivocal in the fossil.

A character discussed by KARAMAN (2009) which is preserved is the form of the spiracles and this does offers useful data about the animal's affinities. In *Cyphophthalmus* the spiracles are semicircular, each with a conical cuticular projection on its posterior margin. This is not seen in the fossil, which by contrast (Fig. 3) seems to share a character seen, so far, only in *Siro* and which consists of a more rounded spiracle (of circular type, sensu GIRIBET & BOYER 2002), with denticles inside the lumen (cf. BIVORT & GIRIBET 2004: Fig. 36c, KARAMAN 2009: Figs. 2A–B). For this reason we are confident in our generic assignment of this fossil to *Siro*. In support of this hypothesis we also note that the form and width of the area between coxal lobes III and IV is very different between *Siro* and *Cyphophthalmus* species. Specifically, the endites (= coxapophysis) of coxae III and IV form either an area (around the coxal pores) with a very acute angle

(in *Cyphophthalmus*: Fig. 4) or a right/obtuse angle (in *Siro*: Fig. 3); thus in this context the amber fossil more closely resembles female *Siro* species. For comparative figures of *Siro* see e.g. RAFALSKI (1958: Fig. 7) for *Siro carpaticus* Rafalski, 1956, JUBERTHIE (1967: Fig. 7) for *Siro rubens* Latreille, 1804, and NOVAK & GIRIBET (2006: Figs. 5, 7, 12) for *Siro crassus* Novak & Giribet, 2006. For various *Cyphophthalmus* species we refer also to EISENBEIS & WICHARD (1987: Plate 27, d) (sub *Siro duricorius*), MITOV (1994, Fig. 23) (sub *Siro beschkovi*) or KARAMAN (2008, 2009).

Although incomplete, we feel able to assign this new fossil to its own species. Of particular interest is the posterior end of the body. Females of modern European *Siro* species typically show a projecting rear end (see e.g. figures in JUBERTHIE 1970), whereas the Baltic amber example has a more smoothly rounded back end which thus resembles, the North American *Siro* species (e.g. NEWELL 1943, 1947, HOFFMAN 1963, SHEAR 1980; see also Fig. 7). Conceivably our fossil was part of this (formally Laurasian?) lineage (see Discussion). At 2.34 mm in body length the new fossil sironid is somewhat larger than typical American *Siro* species. Body lengths of females vary from 1.10 mm (in *Siro sonoma* Shear, 1980) to 2.08 mm (in *Siro exilis* Hoffman, 1963 – the largest modern American sironid); see also NEWELL (1943, 1947). The largest European sironid is the epigean *Siro crassus* Novak & Giribet, 2006 in which females reach 2.40–2.61 mm.

Direct comparison with the previously described European amber species, *Siro platypedibus*, is difficult given that the fossils are preserved in completely different orientations. The coxo-genital and anal region of the younger Bitterfeld fossil cannot be resolved. The originally proposed diagnosis was based on its flattened legs; a character which cannot be tested in the Baltic form. In any case this has recently been challenged as a possible artefact by KARAMAN (2009). He noted that limb flattening can occur while making preparations of extant material in various mounting media, and that the amber-forming resin as a similarly concentrated viscose medium could have induced comparable effects. Our new fossil and *S. platypedibus* are, at ca. 2 mm long, similar in overall size. While it may be possible to draw some comparisons based on the profile of the body sculpture in these respective fossils, we currently have little data to argue either for or against the conspecificity of these extinct taxa from the different amber faunas.

Discussion

As noted above, GIRIBET et al. (2010) inferred a basal divergence time for modern cyphophthalmid lineages perhaps as far back as the Carboniferous (ca. 345 Ma); at which time Europe and North America were part of the single palaeocontinent Laurasia. Indeed, SHEAR (1980, p. 4) commented on the strong similarities between some of the (eastern) N. American cyphophthalmids and the European fauna: "... the original divergence took place between the western species and *S[iro] exilis* (Figs. 7–8) plus the European forms. The movement of North America away from Europe and Africa, which resulted in the opening of the present Atlantic Ocean, may account for the separation of *S. exilis* from its European relatives." The hypothesis that the North American *Siro* species are not monophyletic was again supported in a recent study by GIRIBET & SHEAR (2010), who further recovered European affinities for some American taxa under some parameters of analysis and reiterated the idea that *Siro* may be a very ancient genus.

What this implies is, first, that there is no fundamental objection to recovering an American-like *Siro* species from Baltic amber. This lineage may well have been originally distributed more widely across the Palaearctic, and was present in north-central Europe during the presumably warmer conditions associated with the Baltic amber forest. A possible parallel example of this would be the eupnoid harvestman genus *Caddo* Banks, 1892 which was also present in Europe during the early to mid-Paleogene (DUNLOP & MITOV 2009, and references therein), but is absent from the modern European fauna and yet still found today in North America. Second, the opening of the Atlantic began during in the Triassic (ca. 200–250 Ma), and this, in turn, offers a minimum divergence time, based on geological evidence, for a common ancestor of these similar-looking American and European *Siro* species; the latter also including *Siro balticus*.

To reiterate, North America yields *Siro* (cf. GIRIBET & SHEAR 2010), while both *Siro* and *Cyphophthalmus* occur in Europe. In recent studies *Cyphophthalmus* was treated as a specifically Balkan radiation (BOYER et al. 2005, KARAMAN 2009); although we should note that *Siro* has also been reported at least as far south as Slovenia (NOVAK & GIRIBET 2006). Recent work by MURIENNE et al. (2010) inferred a late Cretaceous radiation for *Cyphophthalmus* of ca.

94 Ma and attempted to tie the explosive evolution of its numerous endemic species into the wider geological development of the Balkan Peninsula. Slow rates of evolution for cyphophthalmids in general were postulated by SHEAR (1980) – see also GIRIBET & SHEAR (2010) – and the modern appearance of this amber fossil (cf. Figs. 1–2 and 7–8) compared to extant forms tends to support this supposition: at least for *Siro*. Unfortunately, we still lack Palaeozoic cyphophthalmids which should date from the early phase of their evolution as predicted by molecular analyses.

Acknowledgments

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References

- BANKS N. (1892): A new genus of Phalangidae. – Proceedings of the Entomological Society of Washington 2 (2): 249–251
- BIVORT B.L. DE & G. GIRIBET (2004): A new genus of cyphophthalmid from the Iberian Peninsula with a phylogenetic analysis of the Sironidae (Arachnida: Opiliones: Cyphophthalmi) and a SEM database of external morphology. – Invertebrate Systematics 18: 7–52 – doi: [10.1071/IS03029](https://doi.org/10.1071/IS03029)
- BOYER S.L., I. KARAMAN & G. GIRIBET (2005): The genus *Cyphophthalmus* (Arachnida, Opiliones, Cyphophthalmi) in Europe: a phylogenetic approach to Balkan Peninsula biogeography. – Molecular Phylogenetics and Evolution 36: 554–567 – doi: [10.1016/j.ympev.2005.04.004](https://doi.org/10.1016/j.ympev.2005.04.004)
- BOYER S.L., R.M. CLOUSE, L.R. BENAVIDES, P. SHARMA, P.J. SCHWENDINGER, I. KARUNARATHNA & G. GIRIBET (2007): Biogeography of the world: a case study from cyphophthalmid Opiliones, a globally distributed group of arachnids. – Journal of Biogeography 34: 2070–2085 – doi: [10.1111/j.1365-2699.2007.01755.x](https://doi.org/10.1111/j.1365-2699.2007.01755.x)
- DUNLOP J.A. (2007): Paleontology. In: PINTO-DA-ROCHA R., G. MACHADO & G. GIRIBET (eds): Harvestmen. The biology of Opiliones. Harvard University Press, Cambridge, MA. pp. 247–265
- DUNLOP J.A. & G. GIRIBET (2003): The first fossil cyphophthalmid (Arachnida, Opiliones) from Bitterfeld amber, Germany. – Journal of Arachnology 31: 371–378 – doi: [10.1636/H03-03](https://doi.org/10.1636/H03-03)
- DUNLOP J.A. & P.G. MITOV (2009): Fossil harvestmen (Arachnida: Opiliones) from Bitterfeld amber. – ZooKeys 16: 347–375 – doi: [10.3897/zookeys.16.224](https://doi.org/10.3897/zookeys.16.224)
- EISENBEIS G. & W. WICHARD (1987): Atlas on the biology of soil arthropods. Springer-Verlag, Berlin, Heidelberg, New York, London, Paris, Tokyo. 437 pp.
- GIRIBET G. (2000): Catalogue of the Cyphophthalmi of the world (Arachnida: Opiliones). – Revista Ibérica de Arachnología 2: 49–76
- GIRIBET G. & S.L. BOYER (2002): A cladistic analysis of the cyphophthalmid genera (Opiliones, Cyphophthalmi). – Journal of Arachnology 30: 110–128 – doi: [10.1636/0161-8202\(2002\)030\[0110:ACAOTC\]2.0.CO;2](https://doi.org/10.1636/0161-8202(2002)030[0110:ACAOTC]2.0.CO;2)
- GIRIBET G., G.D. EDGEcombe, W.C. WHEELER & C. BABBITT (2002): Phylogeny and systematic position of Opiliones: a combined analysis of chelicerate relationships using morphological and molecular data. – Cladistics 18: 5–70 – doi: [10.1111/j.1096-0031.2002.tb00140.x](https://doi.org/10.1111/j.1096-0031.2002.tb00140.x)
- GIRIBET G. & W. SHEAR (2010): The genus *Siro* Latreille, 1796 (Opiliones, Cyphophthalmi, Sironidae), in North America with a phylogenetic analysis based on molecular data and the description of four new species. – Bulletin of the Museum of Comparative Zoology 160: 1–33 – doi: [10.3099/0027-4100-160.1.1](https://doi.org/10.3099/0027-4100-160.1.1)
- GIRIBET G., L. VOGT, A. PÉREZ GONZÁLEZ, P. SHARMA & A.B. KURY (2010): A multilocus approach to harvestman (Arachnida: Opiliones) phylogeny with emphasis on biogeography and the systematics of Laniatores. – Cladistics 26: 408–437 – doi: [10.1111/j.1096-0031.2009.00296.x](https://doi.org/10.1111/j.1096-0031.2009.00296.x)
- HAMMEN L. VAN DER (1985): Comparative studies in Chelicerata II. Opilionida. – Zoologische Verhandlungen Leiden 220: 1–60
- HOFFMAN R.L. (1963): A new phalangid of the genus *Siro* from Eastern United States and taxonomic [sic] notes on other American sironids. – Senckenbergiana biologica 44: 129–139
- HUANG D.-Y., P.A. SELDEN & J.A. DUNLOP (2009): Harvestmen (Arachnida: Opiliones) from the Middle Jurassic of China. – Naturwissenschaften 96: 955–962 – doi: [10.1007/s00114-009-0556-3](https://doi.org/10.1007/s00114-009-0556-3)
- JOSEPH G. (1868): *Cyphophthalmus duricorius*, eine neue Arachniden-Gattung aus einer neuen Familie der Arthrogastren-Ordnung entdeckt in der Luëger Grotte in Krain. – Berliner Entomologische Zeitschrift 12: 241–250 – doi: [10.1002/mmnd.18680120208](https://doi.org/10.1002/mmnd.18680120208)
- JUBERTHIE C. (1967): *Siro rubens* (Opiliones, Cyphophthalmi). – Revue d'Écologie et de Biologie du Sol 4: 155–171
- JUBERTHIE C. (1970): Les genres d'Opilions Sironidae (Cyphophthalmes). – Bulletin du Muséum National d'Histoire Naturelles, 2^{ème} Série, 41: 1371–1390

- KARAMAN I.M. (2008): Cyphophthalmi of Serbia (Arachnida, Opiliones). In: PAVIČEVIĆ D. & M. PERREAU (eds): Advances in studies of the fauna of the Balkan Peninsula. Papers dedicated to the memory of Guido Nonveiller. Nature Protection Institute of Serbia, Belgrade. pp. 97-118
- KARAMAN I.M. (2009): The taxonomic status and diversity of Balkan sironids (Opiliones, Cyphophthalmi) with descriptions of twelve new species. – Zoological Journal of the Linnean Society 156: 260-318 – doi: [10.1111/j.1096-3642.2009.00446.x](https://doi.org/10.1111/j.1096-3642.2009.00446.x)
- LATREILLE P.A. (1796): Précis des caractères génériques des insectes, disposés dans un ordre naturel. Prévot, Paris. 201 pp.
- LATREILLE P.A. (1804): Histoire naturelle, générale et particulière, des Crustacés et des Insectes. Vol. 7. F. Dufart, Paris. pp. 144-305
- MITOV P.G. (1994): *Siro beschkovi*, spec. nov. aus Bulgarien. – Spixiana 17: 275-282
- MURIENNE J. & G. GIRIBET (2009): The Iberian Peninsula: ancient history of a hot spot of mite harvestmen (Arachnida: Opiliones: Cyphophthalmi: Sironidae) diversity. – Zoological Journal of the Linnean Society 156: 785-800 – doi: [10.1111/j.1096-3642.2008.00512.x](https://doi.org/10.1111/j.1096-3642.2008.00512.x)
- MURIENNE J., I.M. KARAMAN & G. GIRIBET (2010): Explosive evolution of an ancient group of Cyphophthalmi (Arachnida: Opiliones) in the Balkan Peninsula. – Journal of Biogeography 37: 90-102 – doi: [10.1111/j.1365-2699.2009.02180.x](https://doi.org/10.1111/j.1365-2699.2009.02180.x)
- NEWELL I.M. (1943): A new sironid from North America (Opiliones, Cyphophthalmi, Sironidae). – Transactions of the American Microscopical Society 62: 416-422
- NEWELL I.M. (1947): The rediscovery and clarification of *Siro acaroides* (Ewing) (Opiliones, Cyphophthalmi, Sironidae). – Transactions of the American Microscopical Society 66: 354-365
- NOVAK T. & G. GIRIBET (2006): A new species of Cyphophthalmi (Arachnida, Opiliones, Sironidae) from Eastern Slovenia. – Zootaxa 1330: 27-42
- POINAR G.O. JR (2008): *Palaeosiro burmanicum* n. gen., n. sp., a fossil Cyphophthalmi (Arachnida: Opiliones: Sironidae) in Early Cretaceous Burmese amber. In: MAKAROV S.E. & R.N. DIMITRIJEVIĆ (eds): Advances in Arachnology and Developmental Biology. Papers dedicated to Prof. Dr. Božidar Čurčić. Inst Zool, Belgrade; BAS, Sofia; Fac Life Sci, Vienna; SASA, Belgrade & UNESCO MAB Serbia, Vienna, Belgrade, Sofia. Monographs 12. pp. 267-274
- RAFALSKI J. (1958): A description of *Siro carpaticus* sp. n. with remarks on the morphology and systematics of the Cyphophthalmi (Opiliones). – Acta Zoologica Cracoviensia 2: 521-556
- SHEAR W.A. (1980): A review of the Cyphophthalmi of the United States and Mexico, with a proposed reclassification of the Suborder (Arachnida, Opiliones). – American Museum Novitates 2705: 1-34
- SIMON E. (1879): Les Arachnides de France VII. Contenant les ordres des Chernetes, Scorpiones et Opiliones. Roret, Paris. 332 pp.
- SUNDEVALL J.C. (1833): Conspectus Arachnidium. C. F. Berling, Londini Gothorum. 39 pp.