Evolutionary Systematics 2 2018, 31–44 | DOI 10.3897/evolsyst.2.22581

PENSOFT.

EVOLUTIONARY
SYSTEMATICS

Arachnids in Bitterfeld amber: A unique fauna of fossils from the heart of Europe or simply old friends?

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http://zoobank.org/8A229449-E56E-4566-877F-76E75F90667C

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Received 28 November 2017
Accepted 16 February 2018
Published 26 March 2018

Academic editor:
Martin Husemann

Key Words

Arachnida
Fossil
Palaeogene
Sachsen-Anhalt
Faunal comparison

Abstract

Bitterfeld amber, sometimes referred to as Saxon or Saxonian amber, is a potentially significant but poorly known source of arthropod data for the Palaeogene of northern Europe. An important aspect is a long-standing controversy about the age of this amber: namely whether it is equivalent to, and perhaps merely a southerly extension of, the better-known Baltic amber, or whether it is a unique and geological younger deposit sampling a different fauna. Here, we briefly review the Bitterfeld arachnids with particular emphasis on how these data could be used to elucidate the age of this deposit. Five arachnid orders have been recorded from Bitterfeld amber: spiders (Araneae), acariform mites (Acariformes), parasitiform mites (Parasitiformes), harvestmen (Opiliones) and pseudoscorpions (Pseudoscorpiones). This is a lower diversity than Baltic amber, where scorpions (Scorpiones) and camel spiders (Solifugae) have also been recorded. Spiders are the most comprehensively studied group, with more than 75 described species. Other groups such as pseudoscorpions and mites appear to be very diverse, but are virtually undescribed. Morphological overlap is apparent in the arachnid fauna and 40 species are currently shared between Baltic and Bitterfeld amber whilst 50 species are unique to the Bitterfeld deposit. At the family level overlap is even higher, but in all groups Baltic amber appears more diverse than Bitterfeld. This overlap may be interpreted as evidence for temporal conspecifity of the Baltic and Bitterfeld ambers, albeit with the Bitterfeld and Baltic ambers possibly representing independent localities within a larger Eocene European amber area which also included the Rovno amber from the Ukraine. However, caution should be exercised because the taxonomic foundation for such assumptions is far from comprehensive, most of the material remains to be studied in detail using modern techniques of morphological reconstruction. There are further issues with date estimates because some arachnid groups show extraordinary morphological stasis over time, even at species level, which may bias the analyses available. Here, we review the available knowledge on Bitterfeld arachnids and discuss how a detailed assessment of this fauna, and other arthropod taxa, could be generated. Several natural history museums – including Hamburg and Berlin – as well as private collectors host major assemblages of Bitterfeld fossils which may help to clarify the debate about the age and provenance of the material, and the extent to which (morpho)-species were maintained both over geographical distances and potentially geological time.

Introduction

Bitterfeld amber originates from near the town of the same name in the eastern state of Sachsen-Anhalt in Germany. It is sometimes referred to as Saxon or Saxonian amber. For general overviews see, e.g., Kosmowska-Ceranowicz and Krumbiegel (1989), Krumbiegel (1997), Weitschat (1997), Knuth et al. (2002), Wimmer et al. (2009) and Dunlop (2010). The presence of amber in this region has been known for a long time, but scientific study of its inclusions together with their geological setting only really began with collections made during the time of the German Democratic Republic (GDR) (see History). Several groups of plants and arthropods have been recovered from Bitterfeld amber (e.g. Weitschat 2008), including fossil species shared with the better known Baltic amber as well as unique Bitterfeld taxa. Thus, one of the key questions about Bitterfeld amber is whether it shares the same Eocene age as Baltic amber and other ambers, such as Rovno amber from the Ukraine. Indeed, some authors proposed that Bitterfeld is merely a southerly outcrop of the wider Baltic amber forest (e.g. Szwedo and Sontag 2013) and refer to Bitterfeld amber as “Tertiary Baltic amber forest incl. the Bitterfeld deposit” (e.g. Wunderlich 2004b).

Alternative hypothesis stressed the uniqueness of the Bitterfeld deposit, dating its inclusions to a younger Oligocene or even Miocene age. Geochemical data now clearly indicate that Bitterfeld and Baltic amber are *not* identical (e.g. Wolfe et al. 2016). This debate is not entirely trivial as it impacts on questions about how long plant and arthropod species, or their wider lineages, could survive essentially unchanged in the Cenozoic of northern Europe and help to evaluate apparent cases of morphological stasis in a temporal context. Here, we review these issues with particular focus on our specialist group, the arachnids, and draw attention to the presence of previously undescribed Bitterfeld material in public and private collections which may help to answer these questions about the composition, age and distribution of the fauna. We also discuss the state of knowledge concerning the Bitterfeld fossils and how this fauna could be studied in greater depth to evaluate whether the two ambers are the same age, but also to improve our understanding of evolutionary processes of European arthropod faunas more generally.

History. Early reports of ‘Saxon’ amber were reviewed by Kosmowska-Ceranowicz and Krumbiegel (1989) and Krumbiegel (1997) and date back to at least the 17th century. Several localities around Halle an der Saale – now belonging to the federal states of Saxony or Saxony-Anhalt – were known to have produced amber, pieces of which were occasionally referred to as ‘Honigsteine’ [honey stones]. Some ended up in the curiosity cabinets of the local gentry, and in the late 19th century Saxon amber was even used for pipe heads or cigarette tips.

Most of the current Bitterfeld amber material (see also Geological Setting) originates from a former opencast ‘Braunkohle’ mine at Goitsche near Bitterfeld; a historical overview of which can be found in Liehmann (1997). Surveys of the site began in the 1920s with mining planned for the 1940s before being interrupted by the war. Afterwards, activities resumed and the necessary canal and railway links were put in place. Proper mining began in the 1950s under the auspices of the GDR and utilized three main areas or ‘Baufelder’. During the 1970s the ‘Volkseigener Betrieb Ostseeschmuck’ of the GDR – in other words, the publically owned Baltic sea jewelry organization – based in Ribnitz-Damgarten had difficulties obtaining sufficient raw amber from Russia for their jewelry production. In 1974 the ‘VEB Ostseeschmuck’ were made aware of the presence of amber deposits at Goitsche, specifically in ‘Baufeld IIIa’, and by 1975 they had come to an arrangement with the local ‘Braunkohlenkombinat’, or BKK, at Bitterfeld to actively mine it; see also Führmann (1975) for details. This work was initially done by hand, but still yielded more than 1000 kg of raw amber in 1975. In successive years the process was automatized – the amber being washed out of the sediment – resulting in larger yields, such that by the 1980s between 20,000 up to almost 50,000 kg of amber was being recovered per year.

During this time, it also became apparent that, like Baltic amber, Bitterfeld amber also contained animal and plant inclusions. Many specimens were transferred from Ribnitz-Damgarten to the Museum für Naturkunde Berlin (W. Mey, pers. comm.), and further co-operations with the Geiseltal Museum in Halle and the Museum of the Earth in Warsaw were undertaken (Krumbiegel 1997). The arthropod inclusions in Berlin were passed onto the relevant (zoological) curators for identification, leading to initial reports on the fauna by Barthel and Hetzer (1982) and Schumann and Wendt (1989). Early descriptions of individual insect groups included beetles (Hieke and Pietrzeniuk 1984), wasps (Sorg 1986), bugs (Koteja 1986) and caddis flies (Mey 1988). Amber mining ceased in 1990, around the time of German reunification, and after the mine was flooded. The original locality is no longer accessible, having been deliberately flooded in 1998 as part of a larger landscape restoration project to form the ‘Große Goitzschesee’ the north-eastern part of the so-called the ‘Bernsteinsee’ or amber lake. Today, several museums in Germany hold quite significant collections of Bitterfeld amber which were purchased or donated by private collectors. Hunting for amber pieces in Bitterfeld was also a hobby for many naturalists over time (Gröhn 2012), thus there are many additional fossils in private collections that are potentially available for study.

Geological setting and dating controversy. “Bitterfeld amber” originates from Lagerstätten in Eastern Germany, of which the Goitzsche Lagerstätte is the most important (see above). Stratigraphically, the horizons comprising amber pieces are of Upper Oligocene Age (Chattian, 23.0–28.1 Ma; Knuth et al. 2002; Blumenstengel 2004) or Lower Miocene according to earlier publications (e.g., Barthel and Hetzer 1982, see below), but the age of the amber itself could be significantly older. Paleobiologists commonly agree that the arthropod assemblages in Bitterfeld amber are very similar to those in Baltic amber (e.g. Wunderlich 2004a–r; Weitschat and Wichard 2010; Szwedo and Sontag 2013). The term “Baltic amber” is commonly used for succinite from deposits around the Gulf of Gdańsk (Fig. 1). This amber probably originates from Eocene members of the Sciadopityaceae (e.g. Wolfe et al. 2009; Wolfe et al. 2016) or – as also discussed for Bitterfeld amber by Yamamoto et al. (2016) – the Pinaceae (e.g. Mosini and Samperi 1985, Wolfe et al. 2016). Possibly, the amber has been reworked and redeposited in several regions, for example, around Rovno (Ukraine; Fig. 1) and, as discussed here, near Bitterfeld in Germany (Fig. 1); see also Szwedo and Sontag (2013).

While both Baltic and Bitterfeld amber consist of succinite, their chemical signatures differ (Vávra 2008). Röschmann (2008) suggested that both amber types derive from geographically separated forest types, which would be in accordance with the early to middle Eocene palaeogeography (Fig. 1). Similarly, Wolfe et al. (2016) suggested, based on detailed geochemical tests, that both Bitterfeld and Baltic amber are of the same Eocene age, but of different source areas. Unfortunately, the latter authors seem to show a figure with Miocene paleogeography (Wolfe et al. 2016, fig. 6 therein) to indicate the position of the forests during the Eocene. Based on other authors (e.g. Popov et al. 2004, Denk and Grimm 2009, Wimmer et al. 2009, and Szwedo and Sontag 2013), it can be concluded that the Bitterfeld area was positioned at the northern coast of the Bohemian High during the Eocene, between 49 and 48°N, south of the connection between the North Sea and the Eocene Turan Sea. The region of Rovno was also situated at the south of this marine connection, but farther eastwards, and was probably part of the Volhynian High (Popov et al. 2004). The region of Gdańsk was situated at the south coast of the Russian Land, at the other side of the sea arm connecting the North and the Turan Sea, at ~50°N. This sea arm probably closed during the Oligocene (e.g. Popov et al. 2004). Wimmer et al. (2009) discussed the fact that a transport of amber from the Gdańsk region to the Bitterfeld Lagerstätte is unlikely and proposed that former paleogeographic studies and examinations of inclusions are necessary.

In general, the age of any given amber is notoriously difficult to determine because the amber pieces themselves cannot be dated, only the sediments in which they are found. The option to use sporomorphs, particularly pollen, to biostratigraphically date amber pieces is hampered since they cannot easily be extracted from amber, which may explain that there are not yet many related studies for both Baltic and Bitterfeld amber. The question remains: Has older amber become reworked into younger strata? This is a particular problem at Bitterfeld, such that as mentioned above, three alternative ages can be gleaned from the contemporary literature: namely Eocene (e.g. Szwedo and Sontag 2013), Oligocene (e.g. Bartel et al. 2015) or Miocene (e.g. Rikkinen and Poinar 2000). In

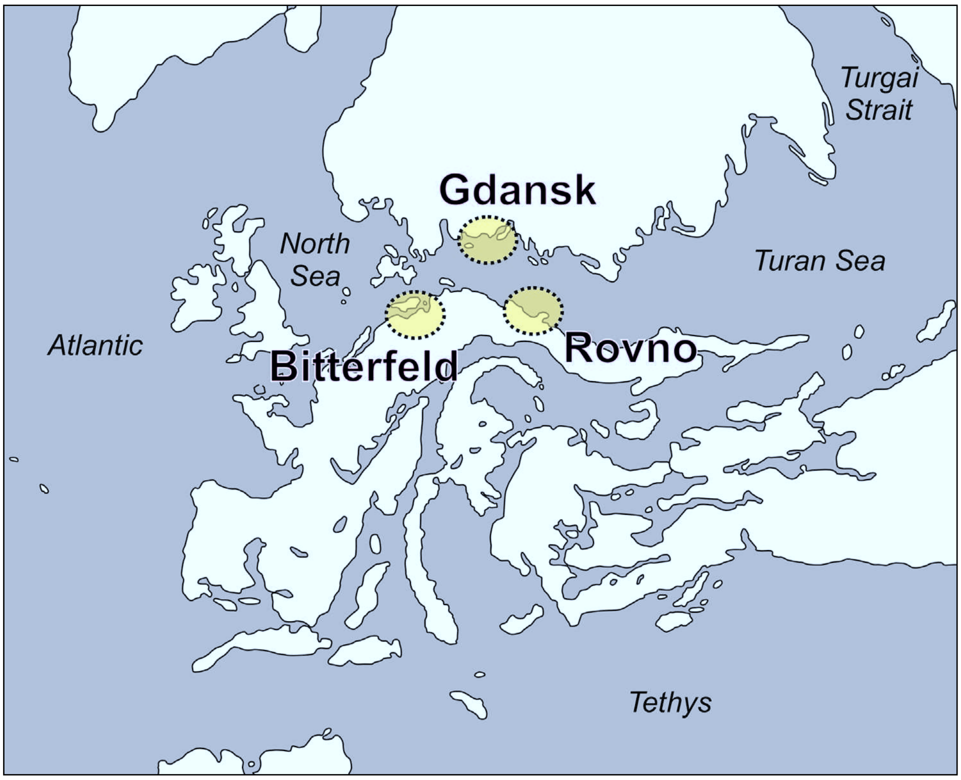

Figure 1. Paleogeographic map of Europe during the early to middle Eocene. Yellow areas indicate the position of the present-day amber Lagerstätten at Bitterfeld, Gdansk and Rovno. Modified after Popov et al. 2004, Denk and Grimm 2009, Blakey 2011, Szwedo and Sontag 2013, and Wolfe et al. 2016.

other words, the amber could be as old as 49 Ma or as young as 20 Ma. A lot can happen in twenty-nine million years and the true age of the Bitterfeld inclusions is relevant to questions such as the palaeoclimate and ecology of the original forest environment. Based on published estimates, the amber could have been deposited during a warm phase not long after the Palaeocene-Eocene Thermal Maximum (ca. 55 Ma, e.g. Westerhold et al. 2009) with mean annual temperatures in Central Europe of ~22 °C (as reconstructed for the Eocene Messel Lagerstätte by Grein et al. 2011), or at a cooler time during the Oligocene/Miocene (e.g. Larsson et al. 2010). The dating controversy can essentially be summarized as pitting evidence from the geological setting – which tends to support a younger date – against evidence from the fossils which includes numerous examples of species shared with Baltic amber. This in turn could imply that the ambers are the same (Eocene) age, and perhaps even sampled the same fauna and environment.

The earliest works on the inclusions (e.g. Barthel and Hetzer 1982) dated Bitterfeld amber to the Miocene, with an absolute date of ca. 22 Ma. Initial descriptions of both plant and animal species generally accepted this Miocene date, and it was still being used in the late 1990s by authors such as Röschmann and Mohrig (1995) and Jähnichen (1998). However, doubts were raised even at the time of the first scientific studies and a brief survey of the spiders by Wunderlich (1983) is the first paper we are aware of which postulated that Bitterfeld amber is simply an older (Eocene) resin reworked into younger sediments. Several subsequent authors have expressed similar views, see especially Weitschat (1997). All of them large based their interpretations on the presence of species common to both Baltic and Bitterfeld amber (see also Table 1).

As pointed out by Szwedo and Sontag (2013), if Bitterfeld and Baltic amber *are* the same age there is a risk that authors may have overlooked similar forms in Baltic amber and described Bitterfeld taxa as different and new under the assumption that they were considerably younger. In this scenario ‘endemic’ Bitterfeld taxa may eventually turn out to be synonyms of Baltic species. At the same time, the arguments for conspecific taxa proving that the ambers are the same age are also underlain by an assumption: namely that (morpho)species do not remain static over several million years. Without independent data on how long, geologically, a particular species can survive there is a risk of both camps falling back on circular arguments: identical species in different ambers indicate deposits of a similar age, or identical species in different ambers indicate stable, long-lived morphotypes inhabiting the Palaeogene of north–central Europe.

Table 1. Summary of the forty species of arachnid described from both Bitterfeld and Baltic amber. Sequence of families largely follows the most recent phylogenetic hypotheses.

Taxon	**Source reference**
OPILIONES	
CADDIDAE	
1. *Caddo dentipalpus* (C. L. Koch & Berendt, 1854)	Dunlop and Mitov (2009)
PHALANGIIDAE	
2. *Dicranopalpus ramiger* (C. L. Koch & Berendt, 1854)	Dunlop and Mitov (2009)
3. *Lacinius bizleyi* Mitov, Dunlop & Penney, 2015	Mitov et al. (2015)
SCLEROSOMATIDAE	
4. *Leiobunum longipes* Menge in Koch & Berendt, 1854	Dunlop and Mitov (2009)
NEMASTOMATIDAE	
5. ?*Histricostoma tuberculatum* (C. L. Koch & Berendt, 1854)	Dunlop and Mitov (2009)
PSEUDOSCORPIONES	
CHEIRIDIIDAE	
6. *Cheiridium hartmanni* (Menge in Koch & Berendt, 1854)	Judson *in* Weitschat (2008)
ACARIFORMES	
SMARIDIDAE	
7. *Fessonia grabenhorsti* Barthel et al., 2015	Bartel et al. (2015)
8. *Fessonia wunderlichi* Bartel et al., 2015	Bartel et al. (2015)
ARANEAE	
DIPLURIDAE	
9. *Clostes priscus* Menge, 1869	Wunderlich (2004a)
TELEMIDAE	
10. ?*Telema moritzi* Wunderlich, 2004b	Wunderlich (2004b)
SEGESTRIIDAE	
11. *Vetsegestria quinquespinosa* Wunderlich, 2004b	Wunderlich (2004b)
OONOPIDAE	
12. *Orchestina* (*Baltorchestina*) *brevis* Wunderlich, 2008a	Wunderlich (2008a)
CYATHOLIPIDAE	
13. *Balticolipus kruemmeri* Wunderlich, 2004j	Wunderlich (2004j)
14. *Succinilipus abditus* Wunderlich, 2004j	Wunderlich (2004j)
SYNOTAXIDAE	
15. *Acrometa cristata* Petrunkevitch, 1942	Wunderlich (2004k)
16. *Succinitaxus brevis* Wunderlich, 2004k	Wunderlich (2004k)
THERIDIIDAE	
17. *Balticoridion dubium* Wunderlich, 2008b	Wunderlich (2008b)
18. *Episinus balticus* Marusik & Penney, 2004	Wunderlich (2008b)
19. *Euryopis bitterfeldensis* Wunderlich, 2008b	Wunderlich (2008b)
20. *Euryopis streyi* Wunderlich, 2008b	Wunderlich (2008b)
21. *Hirsutipalpus varipes* Wunderlich, 2008b	Wunderlich (2008b)
22. *Kochiuridion scutatum* Wunderlich, 2008b	Wunderlich (2008b)
23. *Lasaeola infulata* (C. L. Koch & Berendt, 1854)	Wunderlich (2008b)
24. *Spinitharinus bulbosus* Wunderlich, 2008b	Wunderlich (2008b)
25. *Spinitharinus cheliceratus* Wunderlich, 2008b	Wunderlich (2008b)
26. *Succinobertus adjacens* Wunderlich, 2008b	Wunderlich (2008b)
27. *Ulesanis ovalis* Wunderlich, 2008b	Wunderlich (2008b)
28. *Ulesanis parva* Wunderlich, 2008b	Wunderlich (2008b)
29. *Unispinatoda aculeata* Wunderlich, 2008b	Wunderlich (2008b)
ANAPIDAE (see notes on Comaromidae in text)	
30. *Balticoroma ernstorum* Wunderlich, 2004h	Wunderlich (2004h)
31. *Balticoroma gracilipes* Wunderlich 2004h	Wunderlich (2004h)
32. *Balticoroma serafinorum* Wunderlich, 2004h	Wunderlich (2004h)

Materials and methods

Raw data on arachnid species numbers were drawn from the summary lists by Dunlop et al. (2017) and Harms and

Taxon	Source reference
33. *Flagellanapis voigti* Wunderlich, 2004h	Wunderlich (2004h)
34. *Saxonanapis grabenhorsti* Wunderlich, 2004h	Wunderlich (2004h)
MYSMENIDAE	
35. *Eomysmenopsis spinipes* Wunderlich, 2004h	Wunderlich (2004h)
36. *Mysmena groehni* Wunderlich, 2004h	Wunderlich (2004h)
ZOROPSIDAE	
37. *Succiniropsis kutscheri* Wunderlich, 2004o	Wunderlich (2004o)
HAHNIIDAE	
38. *Cymbiohahnia parens* Wunderlich, 2004n	Wunderlich (2004n)
DICTYNIDAE	
39. *Balticocryphoeca curvitarsis* Wunderlich, 2004n	Wunderlich (2004n)
LIOCRANIDAE	
40. *Apostenus bigibber* Wunderlich, 2004q	Wunderlich (2004q)

Dunlop (2017) together with the relevant primary literature. Specimens used for digital imaging were obtained from the Palaeontological Collections of the CeNak Hamburg, the Palaeontology Department of the Zoological Museum in Berlin, and the Private Collection Grabenhorst. Amber fossils were imaged using a BK Plus Lab System by Dun Inc. with integrated Canon camera, macrolenses (65 mm and 100 mm) and stacked using Zerene Stacker, which is the default software for the BK System. The specimens were immersed in baby oil (Penaten Pflegeöl, Johnson and Johnson GmbH) to improve the refractive index, and were imaged using Canon EOS 5D and Canon MP-E 65 mm lenses, which are integrated into the BK system. The images were edited in Adobe Photoshop CS6.

Several previous studies have imaged Baltic amber inclusions using computer tomography (μ-CT), including Henderickx et al. (2006) and Henderickx and Boone (2014) for pseudoscorpions, and Dunlop et al. (2011, 2012) for spiders and acariform mites respectively. Other authors have used the more powerful synchrotron radiation (SR-μCT) to study arachnids in amber, such as Heetoff et al. (2009) for an oribatid mite in Dominican amber and Saupe et al. (2012) for spiders from French and Spanish amber. As part of our review, we also wanted to explicitly test whether Bitterfeld amber inclusions are amenable to imaging using the synchroton, as this approach often yields very high quality sets of morphological characters directly comparable to modern species. In this context two Bitterfeld pseudoscorpion fossils were scanned using SR-μCT, conducted at the beamline P05 of the storage ring PETRA III (Deutsches Elektronen-Synchrotron — DESY, Hamburg, Germany) operated by Helmholtz-Zentrum Geesthacht (Haibel et al. 2010; Greving et al. 2014; Wilde et al. 2016). Amber pieces were mounted on a beamline standard sample-stubs with plasticine and imaged using attenuation contrast (Greving et al. 2014). The photon energy applied was 25 keV. A total of 1200 radiographic projections were recorded at equal steps between 0 and π. The tomographic reconstruction algorithm "gridrec" was used to yield 32-bit floating point image stacks with isotropic voxel size of 2.42 μm.

Results

Arachnid fossils in Bitterfeld amber are actually not so rare and five of the nine orders that occur naturally in Europe today have been recorded: spiders (Araneae), acariform mites (Acariformes), parasitiform mites (Parasitiformes), pseudoscorpions (Pseudoscorpiones), and harvestmen (Opiliones) (Fig. 2). By contrast, scorpions (Scorpiones), palpigrades (Palpigradi), schizomids (Schizomida) and camel spiders (Solifugae) are not currently known from Bitterfeld amber, although both scorpions and camel spiders are known from Baltic amber (Dunlop et al. 2004; Dunlop and Klann 2009; Lourenço 2016). There are particularly significant collections of spiders, for which more than 75 fossil species have been described, most of them in recent years by Jörg Wunderlich (Tables 1–2) who referred to an "Eocene Bitterfeld amber forest" (e.g. Wunderlich 2017, p. 16). This species number is still negligible compared to the better-known and longer studied Baltic amber, from which hundreds of fossil species have been reported (see Discussion). The harvestmen fauna has been reviewed in some detail, but the mites and pseudoscorpion fossils from Bitterfeld have barely been documented. In the sections below, we briefly review individual groups, before discussing similarities and differences compared to other amber faunas in Europe. In the Discussion we then proceed with remarks on innovative methods that could lead to a more detailed assessment of this fauna.

Harvestmen. The harvestmen fauna in Bitterfeld amber was described by Dunlop and Mitov (2009). Five species are shared between Baltic and Bitterfeld ambers, whilst three additional species are presently unique to Bitterfeld. Again, the age of Bitterfeld amber is critical for an assessment of this fauna because the findings would indicate evolutionary stasis of species over extraordinary long time-periods depending on whether Bitterfeld amber is of Eocene or Oligocene age. Such an example of stasis appeared possible in that one of the Bitterfeld amber harvestmen in the eupnoid genus *Lacinius* (Fig. 2b) was initially considered indistinguishable from an extant species (Dunlop and Mitov 2009), however this same taxon was later found in Baltic amber too and placed in a new (extinct) species based on slight differences compared to its living relatives (Mitov et al. 2015). A mite harvestmen belonging to the suborder Cyphophthalami has also been recorded from the genus *Siro* (Fig. 2a), which occurs today in North America and Europe (Dunlop and Giribet 2003). Another *Siro* species is known from Baltic amber (Dunlop and Mitov 2011). Some of the recovered harvestmen are interesting from a biogeographic perspective. The distinctive, large-eyed *Caddo* does not occur in Europe today, with extant species restricted to the Americas, Japan, and former Gondwanan landmasses such as Australia. Cyphophthalmids also do not occur in northern Europe nowadays and seem to prefer warmer climates in southern Europe.

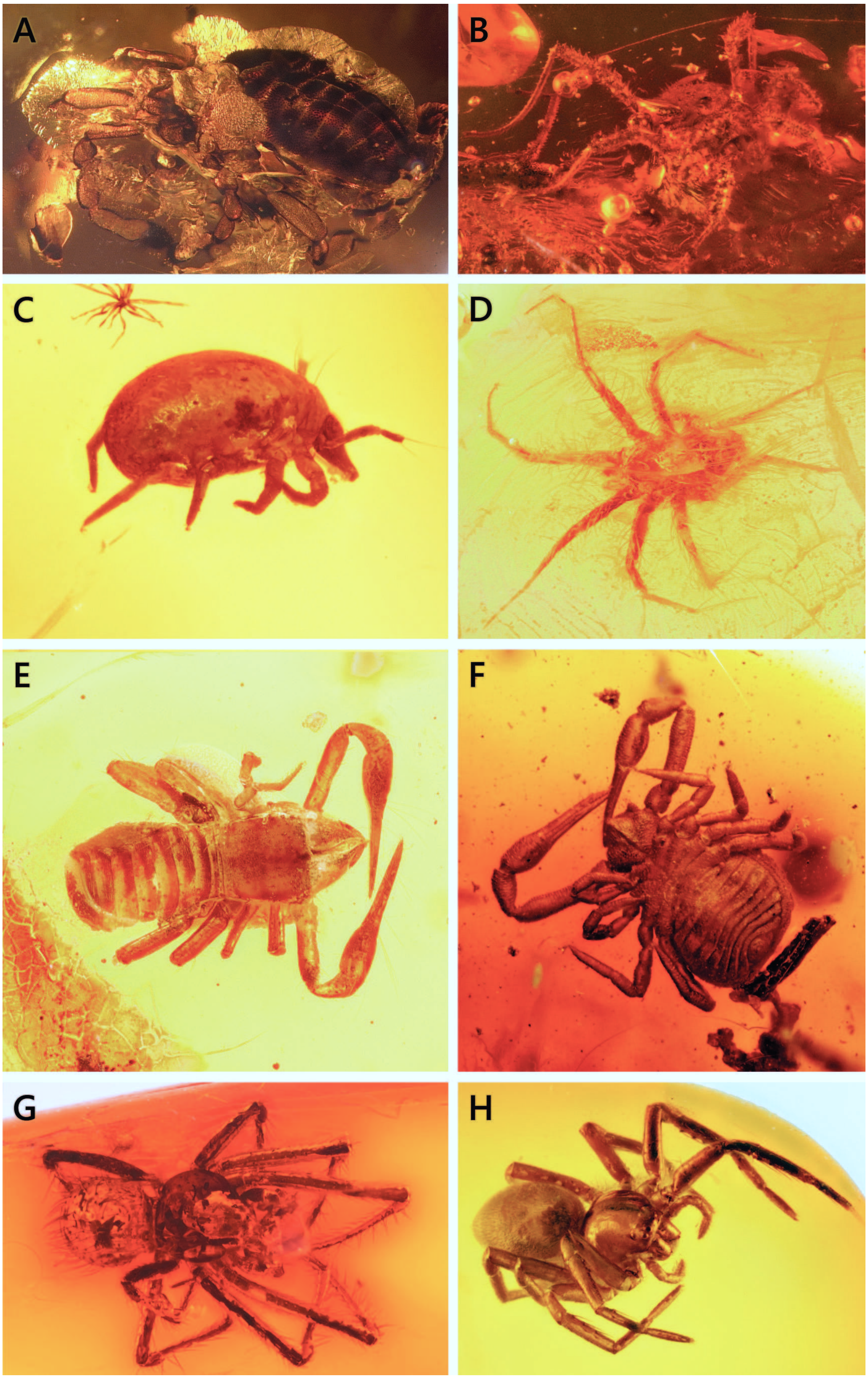

Figure 2. Examples of arachnids preserved in Bitterfeld amber. **A**) harvestman *Siro platypedibus* (Museum für Naturkunde Berlin Coll, No. MB.A. 1086); **B**) ?*Lacinius erinaceus* (Museum für Naturkunde Berlin Coll. No. MB.A. 1661); **C)** undescribed mite species (CeNak Coll. No. BIBS00265); **D)** a second undescribed mite species (CeNak Coll. No. BIBS00244); **E**) undescribed pseudoscorpion in the family Chthoniidae (Grabenhorst Coll. No. PS-6); **F**) first record of the family Pseudogarypidae in Bitterfeld amber (Grabenhorst Coll. No. PS-17); **G**) undescribed crab spider in the family Thomisidae (CeNak Coll. No.BIBS0433); **H)** a second undescribed crab spider in the family Thomisidae (CeNak Coll. No. BIBS0481).

Table 2. The fifty arachnid species so far restricted only to Bitterfeld amber. † indicates an extinct family; sequence of families phylogenetic as above.

Taxon	Source reference
OPILIONES	
SIRONIDAE	
1. *Siro platypedibus* Dunlop & Giribet, 2003	Dunlop and Giribet (2003)
PHALANGIIDAE	
2. *Amilenus deltshevi* Dunlop & Mitov, 2009	Dunlop and Mitov (2009)
NEMASTOMATIDAE	
3. ?*Mitostoma gruberi* Dunlop & Mitov, 2009	Dunlop and Mitov (2009)
ARANEAE	
PHOLCIDAE	
4. *Paraspermophora bitterfeldensis* Wunderlich, 2004b	Wunderlich (2004b)
SEGESTRIIDAE	
5. *Ariadna defuncta* Wunderlich, 2004b	Wunderlich (2004b)
LEPTONETIDAE	
6. *Eoleptoneta curvata* Wunderlich, 2004b	Wunderlich (2004b)
7. *Eoleptoneta kutscheri* Wunderlich, 1991	Wunderlich (1991)
OONOPIDAE	
8. *Orchestina (Baltorchestina) angulata* Wunderlich, 2012	Wunderlich (2011, 2012)
9. *Orchestina (Baltorchestina) bitterfeldensis* Wunderlich, 2008a	Wunderlich (2008a)
10. ?*Stenoonops rugosus* Wunderlich, 2004b	Wunderlich (2004b)
ARCHAEIDAE	
11. ?*Archaea bitterfeldensis* Wunderlich, 2004c	Wunderlich (2004c)
12. *Saxonarchaea dentata* Wunderlich, 2004c	Wunderlich (2004c)
13. *Saxonarchaea diabolica* Wunderlich, 2004c	Wunderlich (2004c)
SPATIATORIDAE†	
14. *Spatiator bitterfeldensis* Wunderlich, 2017	Wunderlich (2017)
ULOBORIDAE	
15. *Hyptiomopes bitterfeldensis* Wunderlich, 2004d	Wunderlich (2004d)
CYATHOLIPIDAE	
16. *Spinilipus bispinosus* Wunderlich, 2004f	Wunderlich (2004f)
17. *Spinilipus curvatus* Wunderlich, 2004f	Wunderlich (2004f)
18. *Succinilipus aspinosus* Wunderlich, 2004f	Wunderlich (2004f)
19. *Succinilipus saxoniensis* Wunderlich, 1993	Wunderlich (1993)
20. *Succinilipus similis* Wunderlich, 2004f	Wunderlich (2004f)
SYNOTAXIDAE	
21. *Chelicerinus abnormis* Wunderlich, 2008a	Wunderlich (2008a)
22. *Cornuanandrus bifurcatus* Wunderlich, 2004k	Wunderlich (2004k)
23. *Cornuanandrus bitterfeldensis* Wunderlich, 2004k	Wunderlich (2004k)
24. *Eosynotaxus bitterfeldensis* Wunderlich, 2004k	Wunderlich (2004k)
NESTICIDAE	
25. *Eopopino rudloffi* Wunderlich, 2004l	Wunderlich (2004l)
THERIDIIDAE	
26. *Lasaeola bitterfeldensis* Wunderlich, 2008b	Wunderlich (2008b)
27. ?*Lasaeola sigillata* Wunderlich, 2008b	Wunderlich (2008b)
THERIDIOSOMATIDAE	
28. *Eotheridiosoma tuber* Wunderlich, 2004g	Wunderlich (2004g)
29. *Eotheridiosoma volutum* Wunderlich, 2004g	Wunderlich (2004g)
30. *Spinitheridiosoma bispinosum* Wunderlich, 2004g	Wunderlich (2004g)
ANAPIDAE	
31. *Balticonopsis bitterfeldensis* Wunderlich, 2004h	Wunderlich (2004h)
32. *Balticonopsis ludwigi* Wunderlich, 2017	Wunderlich (2017)
PROTHERIDIIDAE†	
33. *Protheridion bitterfeldensis* Wunderlich, 2004i	Wunderlich (2004i)
LINYPHIIDAE	
34. *Custodela acutula* Wunderlich, 2004m	Wunderlich (2004m)
35. *Custodela bispina* Wunderlich, 2004m	Wunderlich (2004m)
36. *Custodela bispinosa* Wunderlich, 2004m	Wunderlich (2004m)
37. *Custodela curvata* Wunderlich, 2004m	Wunderlich (2004m)
38. *Custodela femurspinosa* Wunderlich, 2004m	Wunderlich (2004m)
39. ?*Custodela parva* Wunderlich, 2004m	Wunderlich (2004m)
40. *Custodela stridulans* Wunderlich, 2004m	Wunderlich (2004m)
41. *Custodelela hamata* Wunderlich, 2004m	Wunderlich (2004m)
42. *Paralabulla bitterfeldensis* Wunderlich, 2004m	Wunderlich (2004m)
TETRAGNATHIDAE	
43. *Anameta distenda* Wunderlich, 2004e	Wunderlich (2004e)
ARANEIDAE	
44. *Eonephila bitterfeldensis* Wunderlich, 2004f	Wunderlich (2004f)
45. *Eustaloides bitterfeldensis* (Wunderlich, 2004e)	Wunderlich (2004e)
DICTYNIDAE	
46. *Eocryphoeca bitterfeldensis* Wunderlich, 2004n	Wunderlich (2004n)
47. *Mastigusa bitterfeldensis* Wunderlich, 2004n	Wunderlich (2004n)
48. *Mastigusa magnibulbus* Wunderlich, 2004n	Wunderlich (2004n)
EPHALMATORIDAE†	
49. *Ephalmator bitterfeldensis* Wunderlich, 2004o	Wunderlich (2004p)
SALTICIDAE	
50. *Almolinus bitterfeldensis* Wunderlich, 2004r	Wunderlich (2004r)

In detail (see also Table 1) five species of harvestman (Opiliones) are found in both ambers. These consist of one species each from the eupnoid genera *Caddo* (Caddidae), *Dicranopalpus* and *Lacinius* (both Phalangiidae) and *Leiobunum* (Sclerosomatidae), and one from the dyspnoid genus *Histricostoma* (Nemastomatidae) (Dunlop and Mitov 2009; Mitov et al. 2015). Unique Bitterfeld elements (Table 2) comprise one cyphophthlamid in the genus *Siro* (Sironidae), one eupnoid in *Amilenus* (Phalangiidae) and one dyspnoid in *Mitostoma* (Nemastomatidae) (Dunlop and Giribet 2003; Dunlop and Mitov 2009).

Pseudoscorpions. Pseudoscorpions in Bitterfeld amber are likely to represent a diverse fauna which, to date, remains largely undocumented. The fossil history of pseudoscorpions was recently reviewed by Harms and Dunlop (2017) and a total of 49 fossil species in 16 families are currently recognised, of which the majority (34 species in 12 families) were described from Baltic amber. Our preliminary assessment of the Bitterfeld pseudoscorpions suggests that at least nine families are present: Chthoniidae, Tridenchthoniidae, Pseudogarypidae, Neobisiidae, Geogarypidae, Cheiridiidae, Chernetidae, Cheliferidae, and Withiidae. No specimens of Lechytiidae, Feaellidae and Garypinidae have been observed at Bitterfeld so far, although these families do occur in Baltic amber. In contrast to Baltic amber where bark-dwelling taxa are clearly dominant, there seems to be an even representation of ground-dwelling (e.g. Chthoniidae, Geogarypidae) and bark taxa (e.g. Chernetidae, Cheliferidae) by numbers. The families Chthoniidae, Cheiridiidae and Geogarypidae are represented by many fossils at Bitterfeld, and at least the chthoniid fauna seems to be diverse which is interesting given that only two fossil species have been described from Baltic amber (Fig. 2e).

We note that no pseudoscorpion species have yet been formally described from Bitterfeld amber and it is not known whether the samples in various collections represent new species, species that are already known from Baltic and/or Rovno amber, or a mix of both. A shared Baltic/Bitterfeld pseudoscorpion (Pseudoscorpiones) *Cheiridium hartmanni* (Cheiridiidae) was listed by Weitschat (2008), although we have not been able to confirm the source of this record of an established Baltic species in Bitterfeld amber from the primary literature and it appears to be a pers. comm. from Mark Judson. Geogarypidae are known from Baltic amber with three species one of which, *Geogarypus garskii*, has also been described from Rovno amber but not Bitterfeld amber. Some of the Bitterfeld pseudoscorpions are currently identified as Baltic amber species in the collections but these identifications rely on historical descriptions that are often poor and these samples could just as well represent distinct species pending detailed taxonomic analyses. As the preservation of many Bitterfeld samples does not allow for a detailed study (e.g. the amber is too dark to see the trichobothria, or artefacts are present), new methods need to be applied for detailed studies, such as Synchotron microtomography (e.g. Henderickx et al. 2012; Henderickx and Boone 2016). Such studies are particularly valuable for putative new species, such as many of the smaller chthoniids (Fig. 4a), but also those that are interesting in a wider perspective, such as the Pseudogarypidae (Figs 2f, 4b). This family is reported here for the first time from Bitterfeld amber and occurs today only in North America and Tasmania (Harvey 2013), although fossils are common in Baltic amber from which five species have been described. One of these species, *Pseudogarypus minor,* has also been reported from Rovno amber, but methods other than conventional light microscopy need to be applied to check if the Bitterfeld sample belongs to any of the described fossil species. Such work is currently being undertaken. Also preserved in amber are some key fossils that highlight aspects of paleoecology and biology, such as prey-interactions and breeding behaviour (Fig. 3b), that provide insights into paleoenvironments and the animals that lived in those environments.

Mites. The mite fauna preserved in Bitterfeld amber appears diverse, both at the generic and species level, and for both of the mite groups that are currently suggested by molecular analyses (Parasitiformes and Acariformes). Two species of smaridid mites in the parasitengonid genus *Fessonia* have been described (Table 1) which also occur in Baltic amber (Bartel et al. 2015). Fossils potentially belonging to Mesostigmata (Parasitiformes) and Oribatida (Acariformes) have also been observed, but not formally described (Dunlop 2010). Fragments of Labidostomatidae in the prostigmate mite fauna (Acariformes) have been noted, but again not formally described (Sidorchuk and Bertrand, 2013). The probably basal parasitiform mite taxon Opilioacariformes has been described from Baltic amber (Dunlop et al. 2004) but no specimens are known yet from Bitterfeld. The same is true for ticks as the most commonly known group in the Parasitiformes: rare Baltic records, but none from Bitterfeld. No further data are currently available and we have to conclude that both Acariformes and Parasitiformes are likely to represent a diverse, but currently unexplored, fauna. In lieu of formal descriptions, the implications of the mite data for questions of dating and biogeography remain open.

Spiders. As noted above, the vast majority of the fossil arachnids in Bitterfeld amber are spiders (e.g. Fig. 2g, h). More than 75 species in 26 families have been described, almost exclusively by Jörg Wunderlich across several papers and monographs (Wunderlich 1983, 1991, 1993, 2004a–r, 2008a–b, 2012, 2017). Published records include members of three extinct spider families recorded from Bitterfeld material, although the status of these families – Spatiatoridae†, Protheridiidae† and Ephalmatoridae† – has

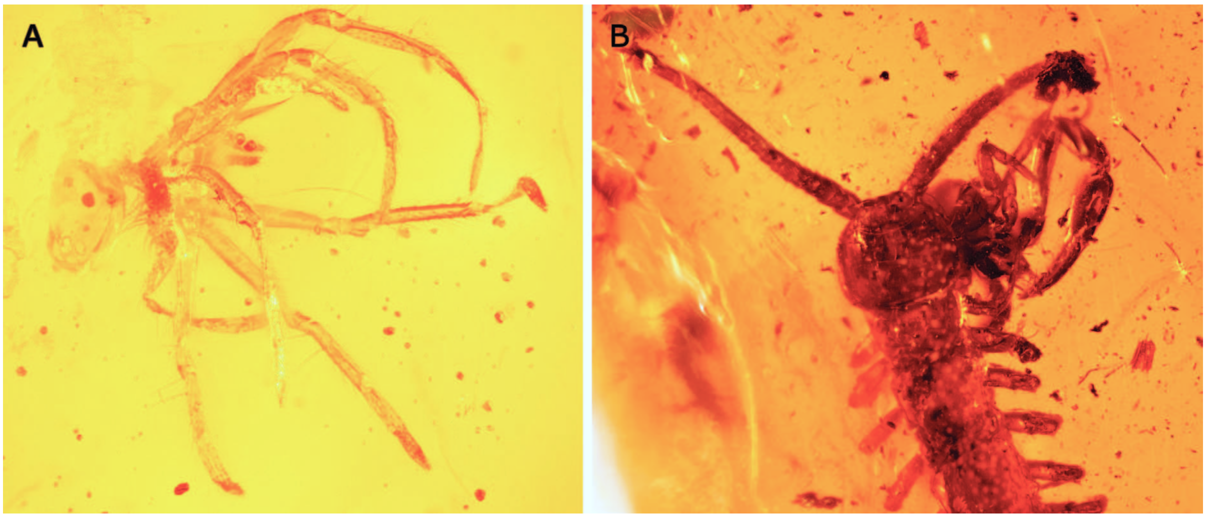

Figure 3. Examples of behavioral traits preserved in Bitterfeld amber: **A**) complete spider exuvia of an unidentified species (CeNak Coll. No. BIBS0514); and **B**) evidence of a lithobiomorph centipede preying on a pseudoscorpion (Grabenhorst Coll. No. My-1).

not been tested using cladistic methods. The mygalomorph spider fauna at Bitterfeld is currently poor (Wunderlich 2004a), with only one species shared with Baltic amber. It belongs to the curtain-web spiders (Dipluridae) which are absent in Europe today, but speciose across several continents in the southern hemisphere. There is a diverse leaf-litter fauna comprising oonopids, hahniids, anapids, mysmenids and zoropsids (e.g. Wunderlich 2004h, 2008a, 2017). Since amber is fossilised tree resin, typical elements of the 'bark' fauna are present such as Segestriidae (Wunderlich 2004b), but the diversity of the web building spiders is certainly highest, with several species of linyphiids (Wunderlich 2004m) and theridiids (Wunderlich 2008b), plus further species in the Tetragnathidae (Wunderlich 2004e) and Uloboridae (Wunderlich 2004d). True orb-weavers (Araneidae) seem comparatively rare (Wunderlich 2004e–f). Wolf spiders (Lycosidae), crab spiders (Thomisidae) and nursery web spiders (Pisauridae) are absent; all groups that are diverse in European ecosystems today. Their absence may be due to their typical lifestyles, which are not associated with trees. A high proportion of species seems to be shared with Baltic amber (Table 1) although it needs to be emphasised that a critical morphological assessment for many of the described Bitterfeld species is lacking, and that the descriptions for many species are insufficient to test for conspecifity. In some groups, species are not shared at all, such as in the linyphiids and theridiosomatid with species unique to Bitterfeld amber (Wunderlich 2004g, m) (see also Table 2) or vice versa. The relationships of many species to Rovno amber fossils are also uncertain.

Some of the described spiders are of considerable biogeographical interest such as the pelican spiders (Archaeidae) (Wunderlich 2004c) and cyatholipid spiders (Cyatholipidae) (Wunderlich 2004j). These families occur today only in disjunctive distributions across the Southern Hemisphere but are diverse in Bitterfeld (and Baltic) ambers with numerous species. Others, such as the Leptonetidae and Telemidae (Wunderlich 1991, 2004b), do not occur in north–central Europe today but are still present in southern Europe, up into France, and in Asia. These taxa may have suffered range retraction since the Neogene, contracting to known fauna refugia such as the Balkans and the Iberian Peninsula (e.g. Schmitt and Varga 2012). Although probably the best documented of the Bitterfeld arachnids at species level, the spider fauna is also the most problematic for a number of reasons. First, there has been no attempt to discriminate Baltic and Bitterfeld ambers in the past and both faunas have generally been treated in unison by taxonomists, implying *a priori* that they are identical. Second, the descriptions of many of the fossil spiders are problematic. Historical records from Baltic amber may be very brief and unreliably illustrated. In other cases higher taxa were raised without a strong underlying phylogenetic analysis. For example, the three extinct families noted above are currently diagnosed (Wunderlich 2004i, p) on characters such as clypeal and leg ratios, or patterns of spination, which are not clearly expressed as apomorphies. An evaluation of Bitterfeld spider faunas compared to those present in Baltic or Rovno amber cannot be undertaken at species level at this stage pending detailed revisions, and we need to fall back to the family level where identifications are relatively reliable. Here, the faunas certainly overlap and many families and genera are shared (Table 1).

In detail, thirty-two spider species have been described from both Baltic and Bitterfeld amber. Among the mygalomorph spiders there is one common species in the ge-

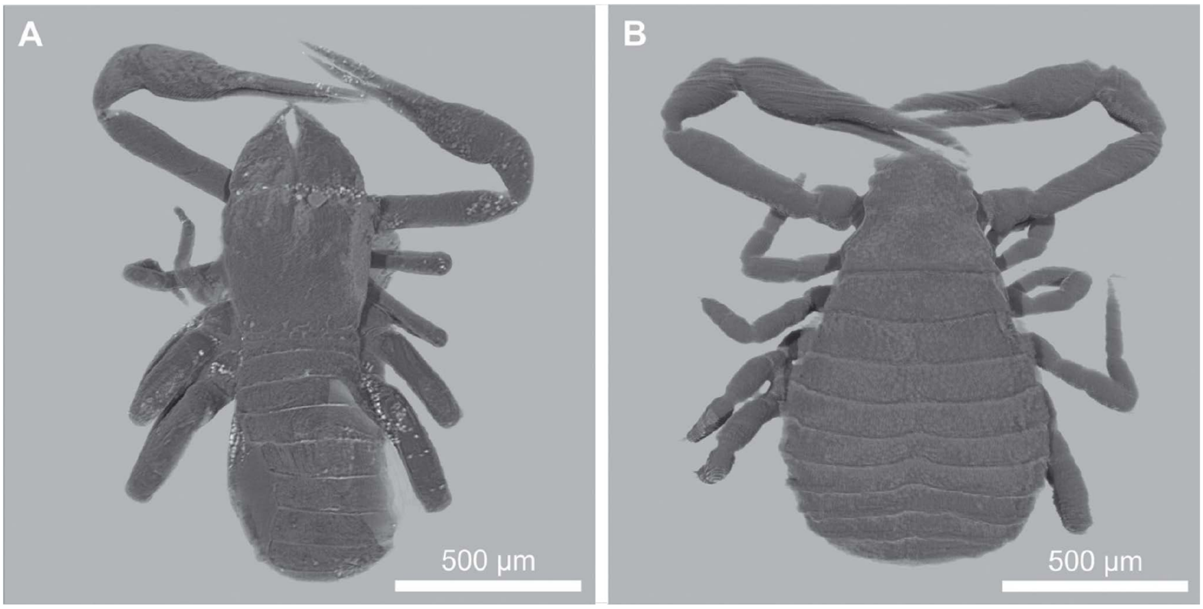

Figure 4. The Bitterfeld amber pseudoscorpions shown in Figs 2E–F imaged this time using synchrotron-based microtomography; these are the first Bitterfeld arachnid fossils to be examined using this technique. **A)** Chthoniidae (Grabenhorst Coll. No. PS-6); **B)** Pseudogarypidae (Grabenhorst Coll. No. PS-17). In the PDF click on the image to access an interactive 3D model.

nus *Clostes* (Dipluridae). For Synspermiata there is one shared species in *Telema* (Telemidae), one in *Vetsegestria* (Segestriidae) and one *Orchestina* (Onopidae). Among entelegyne spiders, there is one common *Balticolipus* and one *Succinilipus* (both Cyatholipidae), one *Acrometa* and one *Succinitaxus* (both Synotaxidae). There is one *Balticoridion*, one *Episinus*, two *Euryopis*, one *Hirsutipalpus*, one *Kochiuridion*, one *Lasaeola*, two *Spinitharinus*, one *Succinobertus*, two *Ulesanis*, and one *Unispinatoda* (all Theridiidae). There is one shared *Flagellanapis* and one *Saxonanapis*, three *Balticoroma* (all Anapidae; although Wunderlich recognised a family Comaromidae including *Balticoroma*), and one *Eomysmenopsis* and one Mysmena (both Mysmenidae). In the derived 'RTA clade' group there is one *Succiniropsis* (Zoropsidae), one *Cymbiohahnia* (Hahniidae), one *Balticocryphoeca* (Dictynidae), and one *Apostenus* (Liocranidae).

By contrast the forty-seven unique endemic spiders taxa (Table 2) include for Synspermiata one *Paraspermophora* (Pholcidae), one *Ariadna* (Segestriidae) and two *Orchestina* and one *Stenoonops* (both Oonopidae). For entelygyne spiders the following taxa are reported: two species in the genus *Eoleptoneta* (Leptonetidae), one *Archaea* and two species in the Bitterfeld endemic genus *Saxonarchaea* (Archaeidae), one species in the genus *Spatiator* of the extinct family Spatiatoridae, one species in the Bitterfeld endemic genus *Hyptiomopes* (Uloboridae), two *Spinilipus* and three *Succinilipus* (both Cyatholipidae), one *Chelicerinus*, two *Cornuanandrus* and one *Eosynotaxus* (all Synotaxidae), one *Eopopino* (Nesticidae), two *Lasaeola* (Theridiidae), one *Eotheridiosoma* and one *Spinitheridiosoma* (both Theridiosomatidae), two *Balticonopsis* (Anapidae), one *Protheridion* (the extinct family Protheridiidae), seven *Custodela*, one in the Bitterfeld endemic *Custodelela* and one *Paralabulla* (all Linyphiidae), one *Anameta* (Tetragnathidae), one *Eonephila* and one *Eustaloides* (both Araneidae). For the RTA clade there is one *Eocryphoeca* and two *Mastigusa* (both Dictynidae), one *Ephalmator* (the extinct family Ephalmatoridae) and one *Almolinus* (Salticidae). Additional taxonomic information may be derived from a diverse spectrum of partially or entirely preserved exuvia that could be identified to family level (Fig. 3a).

Discussion

In the last comprehensive survey of the faunal overlap between the two ambers, Weitschat (2008) listed a grand total of 167 species (plants and arthropods) shared between the Baltic – in his table "Samland" – and Bitterfeld deposits. For plants these consisted of eight liverworts, seven mosses and one flowering plant. He also documented twenty-six shared species of spiders (Araneae), one pseudoscorpion (Pseudoscorpiones) and two millipedes (Diplopoda); his list is in strong contrast to the revised arachnid data of forty-two species above. For insects, he listed three common stick insects (Phasmida), one gladiator (Mantophasmatodea), two termites (Isoptera), three bugs (Heteroptera), twenty-three thrips (Thysanoptera), seven barklice (Psocoptera), eight scale insects (Coccina), nine aphids (Aphidina), one scorpionfly (Mecoptera), three lacewings (Neuroptera), eleven hymenopterans (Hymenoptera), and fifty-one flies and midges (Diptera).

Since Weitschat's publication, other authors have commented on the insect fauna in particular to argue that the two ambers contain the same fauna. For example, Szwedo and Sontag (2013) reviewed the biting midges (Ceratopogonidae) from the three European amber deposits and found them highly similar although the Bitterfeld fauna was less diverse, however their study was founded on the assumption that "…there is no doubt that amber from Bitterfeld is contemporaneous with Baltic amber…" which may have biased the interpretation. Wichard (2013) studied aquatic insects and found "wide-reaching similarities" between the amber faunas, but also exercised caution because most of the Bitterfeld taxa are currently undescribed and need to be studied in detail.

Unfortunately, there are no comprehensive published summaries of the number of endemic Bitterfeld insect species for comparison, but in contrast to the similarities observed by some authors, Alekseev and Grzymala (2015) described nine tenebrionid beetles from Baltic and Bitterfeld amber but did not find any shared species between both deposits. Bukejs et al. (2016) provided a checklist of beetle species described from Bitterfeld amber and found some species to be shared, although other species (and genera) are unique to Bitterfeld (Lyubarsky and Perovsky 2017). In summary, most palaeoentomological studies suggested at strong similarities between Baltic and Bitterfeld ambers, but also noted that taxonomic knowledge is still very fragmentary. Since there are limited data about how long species can stay morphologically unchanged in the insect fauna, this still does not provide more than an indication that both ambers are of the same age.

Geographical distinctness. The most comprehensive study assessing geochemical data was presented by Wolfe et al. (2016). These authors found differences in the geochemical properties and argued that both ambers may be overlapping in time, but may represent paleolatitudinal differences with sources originating from the northern (Baltic) and southern (Bitterfeld) margins of the Paleogene North Sea. If this is true, the arthropod fauna of both ambers may be seen as a mix of widely distributed taxa on several landmasses in the Paleogene of Europe that were bisected by substantial bodies of water, but perhaps also of more narrowly distributed taxa that were found at lower latitudes than their Baltic amber relatives. The Bitterfeld fauna is still of significance then because it represents a snapshot of arthropod diversity with unique fossils that perhaps thrived under slightly warmer climates and perhaps a different vegetation. In any case, a detailed and comprehensive study is necessary to evaluate and compare these hypotheses.

The arachnid data from Bitterfeld amber certainly supports the insect data as Bitterfeld amber appears to have a lower arthropod diversity compared to Baltic amber, although both deposits may still be more diverse than the still rather poorly-known Rovno amber (Szwedo and Sontag 2013). Putting our arachnid data into a wider context, the forty shared and fifty endemic species of Bitterfeld arachnids documented so far (Tables 1–2) are in contrast to a total species count of 899 arachnids – eleven scorpions, sixteen harvestmen, thirty-two pseudoscorpions, one camel spider, four parasitiform mites, 104 acariform mites and 731 spiders – from all three northern European ambers (Baltic, Bitterfeld and Rovno); data from Dunlop et al. (2017). In other words, about 4.5 % of the arachnids (and also 4.4 % of the spiders) are shared species, while 5.6 % (and 6.4 % of the spiders) are Bitterfeld endemics. Although fossils have been widely used to support the hypothesis that Bitterfeld amber is merely a southerly extension of Baltic amber, the species counts for Arachnida actually record (slightly) more unique Bitterfeld faunal elements than common Baltic and Bitterfeld ones.

Yet before drawing too many conclusions, we need to keep several points in mind. First, Baltic amber has been collected and surveyed for more than 200 years and the sheer volume of amber and specimens available is much greater than the inclusions recovered from Bitterfeld. This inevitable collecting bias means that a richer Baltic amber fauna might be expected anyway, and also means that we must bear in mind that perhaps not all potential shared (or endemic) taxa for the Bitterfeld amber have been recorded. Second, at least half of the described Baltic/Bitterfeld amber spider species originated from a single author, Jörg Wunderlich, who often defined taxa based on minor differences. Thus, we suspect that the species diversity of at least the spiders may have been over-estimated, which would probably increase the relative percentages of both the shared and endemic species, but revisions of the described material are required to test this. Third, while shared taxa may be consistent with the hypothesis that we are sampling a common fauna, we lack independent data for whether (morpho)species can remain stable for millions of years and also to what extent they were geographically widespread during the Paleogene. Finally, we note that Bitterfeld amber has been considered by many workers as ‘just another’ deposit of Baltic amber and only relatively recently has its distinct nature been recognised. This means that many specimens (and potentially species) that actually come from Bitterfeld amber are currently mislabelled or misplaced in collections as Baltic amber taxa and need to be retrieved for further study.

New material. Significant collections of Bitterfeld arachnids (and other arthropods) are present in several museums in Germany and additional material is present in private collections which has never been studied in greater depth and, to a large degree, is unknown and undocumented. The spider fauna is moderately well documented, but needs to be reanalysed as noted above. Many additional specimens are also awaiting study, e.g. in the collections of the Berlin and Hamburg Museums of Natural History. The harvestmen fauna is well studied but many more fossils have become available since the last comprehensive review (Dunlop and Mitov 2009) and additional species can be expected. The pseudoscorpion and mite faunas lie essentially bare. While not much can be said about the mites at present, other than that they are abundant with several hundred specimens, the lack of any pseudoscorpion descriptions from Bitterfeld is notable because the Baltic amber pseudoscorpion fauna is very well documented (Harms and Dunlop 2017) and yields about two-thirds of the global fossil diversity for this taxon. As with other arthropod groups, there seem to be some shared morphospecies, but also a number of unique taxa in the chthoniid and neobisiid fauna which may support the hypothesis of a partly distinct status for Bitterfeld versus Baltic amber; irrespective of whether this reflects geographical or temporal differences. Some of this material is also interesting from a biological or ecological perspective because it illustrates the biotic interactions and/or the ecology of invertebrates that once lived in the amber forests (Fig. 3). For example, Fig. 3A shows a rare case of a centipede preying on a pseudoscorpion in amber and there are similar notable examples in the spider and mite fauna. Similarly, we note the presence of the pseudoscorpion family Pseudogarypidae in this amber although this family is only found today in North America and Tasmania (Harvey and Stahlavsky 2009).

Future work. The identification of both fossil and living arachnids often relies on minute characters which can be hard to discern in amber fossils, such as chaetotaxy, trichobothria composition or the fine structure of male spider’s pedipalps. In general, the better the descriptions the more useful the data for comparative studies will be. Over the past couple of decades image stacking has improved the quality of photographs of amber inclusions, but the real breakthrough has been the application of tomography. We demonstrate here, using the example of two pseudoscorpions (Figure 4), that Bitterfeld amber inclusions can also be imaged using synchrotron-based microtomography. Synchrotron-based study have proved to be extremely useful in the taxonomic identification and detailed description of amber fossils (e.g. Henderickx and Boone 2014, 2016; Henderickx et al. 2012) and helped to describe Baltic and Rovno amber fossil in greater detail than ever before. Whilst such methods have not yet been applied in great detail, our next step will be to apply this technology to key taxa from both Baltic and Bitterfeld amber, with the aim of recovering sufficient morphological characters to test whether the arachnids here are conspecific. This in turn should help us determine whether similar-looking elements do in fact represent a unique and independent fauna or whether they are just ‘old friends’ which are assignable to the same, morphologically-defined, species.

Conflict of interest

This manuscript was reviewed externally by two reviewers. All authors declare that there is no conflict of interest.

Acknowledgements

We thank Manfred Barthel and Wolfram Mey (both Berlin) for discussions of the history of work at this site and Gerhard Schmiedl and Marc Theodor (both Hamburg) for animating discussion. We also thank Carsten Gröhn (Hamburg) and Heiner Grabenhorst (Wienhausen) for supplying Baltic and Bitterfeld amber fossils for scientific study, and Nadine Dupérrè (Hamburg) for assistance with curating this material. Thanks to our student assistents for supporting the synchrotron-based microtomography. The Deutsche Forschungsgemeinschaft funded the digitization of the amber collection at the University of Hamburg (Project KO3944/4-1). Jörg Wunderlich and an anonymous reviewer provided helpful comments on an earlier version of the typescript.

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