

Pseudoscorpions in Bitterfeld Amber – a survey

With 15 figures and 4 tables

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Kurzfassung

AHRENS, J.; HARMS, D.; DUNLOP, J.A. & KOTTHOFF, U.: Pseudoskorpione im Bitterfelder Bernstein – Eine Übersicht

Bernstein aus der Gegend von Bitterfeld in Deutschland ist eine wichtige Quelle für paläobiologische Daten für das Paläogen Mitteleuropas. Zahlreiche Invertebratenarten sind in diesem Bernstein überliefert, aber für viele fehlt noch eine formale Beschreibung und Dokumentation. In dieser Studie geben wir einen ersten Überblick über die Pseudoskorpionfauna des Bitterfelder Bernsteins. Alle verfügbaren Exemplare aus Museums- und Privatsammlungen wurden auf Familienniveau identifiziert und wenn möglich Morphotypen zugeordnet, die vermutlich Arten repräsentieren. Für jeden dieser Morphotypen wurde ein repräsentativer Vertreter photographiert, um einen Katalog der gesamten Vergesellschaftung zu erstellen und die morphologische Diversität der Bitterfelder Pseudoskorpion-Fauna zu dokumentieren. Insgesamt wurden elf Familien und 32 Morphotypen identifiziert. Von einer Ausnahme abgesehen sind alle Bitterfelder Familien bereits aus anderen paläogenen Bernsteinvorkommen bekannt, insbesondere aus Baltischem Bernstein, beinhalten aber vermutlich neue Arten, die näher untersucht werden müssen. Der erste fossile Nachweis der Familie Pseudotyranochthoniidae wird vorgestellt, dieser ist von besonderer biogeographischer Bedeutung. Weiterhin konnten einige bemerkenswerte ökologische Interaktionen in den Bitterfelder Stücken nachgewiesen werden: phoretisches Verhalten und Interaktion mit Prädatoren. Die analysierten Bernsteininkluden implizieren eine paläogene mitteleuropäische Pseudoskorpion-Vergesellschaftung, die die heutige an Diversität auf Familienniveau und wohl auch auf Artniveau weit übertrifft. Sie ist insgesamt eher vergleichbar mit heutigen Faunen warm-temperierter/mediterraner Biome und indiziert somit eher wärmeres Klima.

Schlüsselwörter: Arachnida, Eozän, Fossilien, Mooskorpione, Paläontologie, Pseudoskorpione, Succinit

Abstract

Amber from the Bitterfeld area in Germany is a significant source of paleobiological data for the Paleogene of central Europe. Rich invertebrate communities have been preserved in this amber but most species remain to be documented and described. In this study, we provide the first inventory of the pseudoscorpion fauna from Bitterfeld amber. All available specimens from both museum and private collections were identified to family level and assigned to morphotypes (= putative species) where possible. From each morphotype one representative specimen was photographed in order to

catalogue the entire collection and document the Bitterfeld community in its morphological diversity. Overall, eleven families and 32 morphotypes were identified. All but one family are known from other Paleogene ambers in Europe (especially Baltic amber) but there are a number of putative new species that warrant detailed taxonomic study. The first fossil record of the family Pseudotyranchothoniidae is established here which has significant biogeographical implications. We further present remarkable ecological interactions preserved in Bitterfeld amber, i.e. phoretic behaviour and interactions with other invertebrate predators. Overall, the fossils suggest a diverse community, richer than that found in central Europe today, both at the species and family level. It reflects much warmer climate, similar to the faunas found in warm-temperate or Mediterranean biomes of the world today.

Keywords: arachnida, Eocene, false scorpions, fossils, paleontology, pseudoscorpiones, succinite

1 Introduction

Amber is fossilized plant resin and found in many geological deposits across the world (RAGAZZI & SCHMIDT 2011). Such resins are an invaluable source of preserved animal and plant material between the Carboniferous (the oldest ambers, BRAY & ANDERSON 2009) to the Neogene (youngest ambers, RAGAZZI & SCHMIDT 2011). Often it is amber inclusions, as opposed to compression fossils, which provide the first record of a given animal group. In some cases even patterns of behavior or the interaction of animals have been preserved (POINAR 2010). Amber inclusions can also provide information on the paleoenvironment and paleoclimates at a given time because the preserved specimens often have extant relatives with known biological or ecological characteristics. Dating amber directly is difficult because stratigraphic analysis of the embedding sediment is used to give minimal ages for the deposition of ambers, but very often the amber has been reworked or relocated since its formation and may be found in strata that are younger and/or unrelated to the original amber habitats (POINAR 2010; RAGAZZI & SCHMIDT 2011). Therefore, the identification and comparison of inclusions such as plant remains or arthropods between ambers or between amber and other fossil sources is often used to estimate the timing and duration of amber deposition.

Ambers can be classified according to their chemical composition and origin. The most common amber in Europe is succinite which is derived from polymer resins and contains a high percentage of succinic acids (ANDERSON et al. 1992). Several sources of succinite are known, but the most common is Baltic amber from the Gulf of Gdańsk. This amber probably formed during the Eocene from resin of the plant families *Sciadopityaceae* or *Pinaceae* (WOLFE et al. 2016), plants that probably formed a common “Baltic amber forest” that stretched along the margins of the North Sea during the Paleogene (SADOWSKI et al. 2017). Succinite has also accumulated in the Rovno region (Ukraine) where it probably originated from conifers growing in the Ukrainian Crystalline Rock Massif in a subtropical climate (PERKOVSKY et al. 2007). A third large deposit of succinite is found near Bitterfeld (Saxony-Anhalt, Germany). Bitterfeld amber, also sometimes referred to as Saxonian amber, originates from a former open-cast “Braunkohle” (brown coal) mine at Goitzsche. There have been numerous overviews on this amber type, among them articles by KNUTH et al. (2002), WIMMER et al. (2009), and DUNLOP (2010).

One pending question is that of age: Bitterfeld amber may just be another deposit of Baltic amber and thus also of Eocene age, but it could alternatively be much younger. Some authors have even suggested Miocene origins, about 20 million years younger than Baltic amber.

What we do know is that the Bitterfeld amber is embedded in horizons of Upper Oligocene age, but there is evidence that the amber is older and was reworked into those horizons later (FUHRMANN 2004). SZWEDO & SONTAG (2013) suggested that all three common succinite ambers (Baltic, Rovno and Bitterfeld) are of the same age and originated in different regions of the same amber forest, while WOLFE et al. (2016) argued that Bitterfeld and Baltic amber are not synonymous and geochemically divergent. Considering the Early to Middle Eocene paleogeography (Fig. 1), the latter hypothesis is appealing but we must also consider the possibility that all three amber types could have originated over long time periods, perhaps millions of years, and thus under changing geographic and climatic conditions. Herein, we use an age estimation of 49 Ma for Bitterfeld and Baltic amber, but compare e.g. SADOWSKI et al. (2017) for younger age estimations (e.g. late Eocene). Recently, DUNLOP et al. (2018) reviewed arachnids from Bitterfeld amber and pointed out that previously undescribed Bitterfeld material in public and private collections may help to assess the relation between Bitterfeld amber and the other Paleogene amber types. In this context, we carried out the first comprehensive survey on pseudoscorpions from Bitterfeld amber.

Pseudoscorpions (Arachnida: Pseudoscorpiones) are especially suitable for paleobiological investigations because they are an old arachnid lineage (Fig. 2) with origins in the Devonian (SHEAR et al. 1989) and diverse in many amber types across the world (HARMS & DUNLOP 2017). Pseudoscorpions are small reddish to black or brown arachnids with body lengths of up to seven millimeters (WEYGOLDT 1966). They resemble the better-known scorpions, but lack

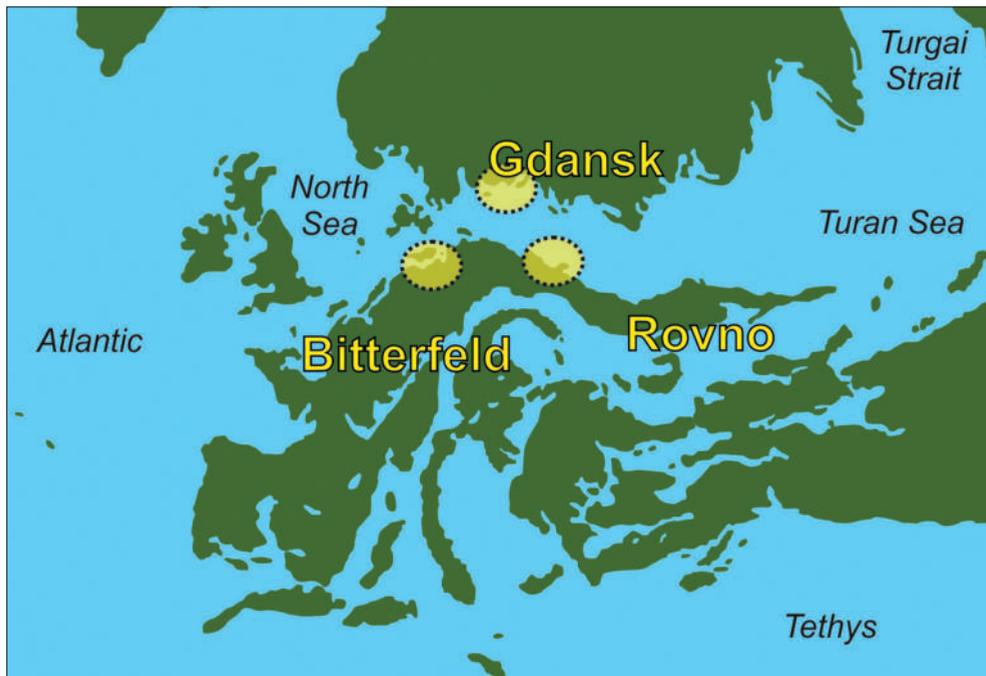


Fig. 1: Paleogeographic map of Europe during the Early to Middle Eocene. Yellow areas mark the estimated Eocene positions of the amber deposits of Bitterfeld, Gdańsk, and Rovno. Modified after POPOV et al. (2004), DENK & GRIMM (2009), BLAKEY (2011), SZWEDO & SONTAG (2013), WOLFE et al. (2016), and DUNLOP et al. (2018).

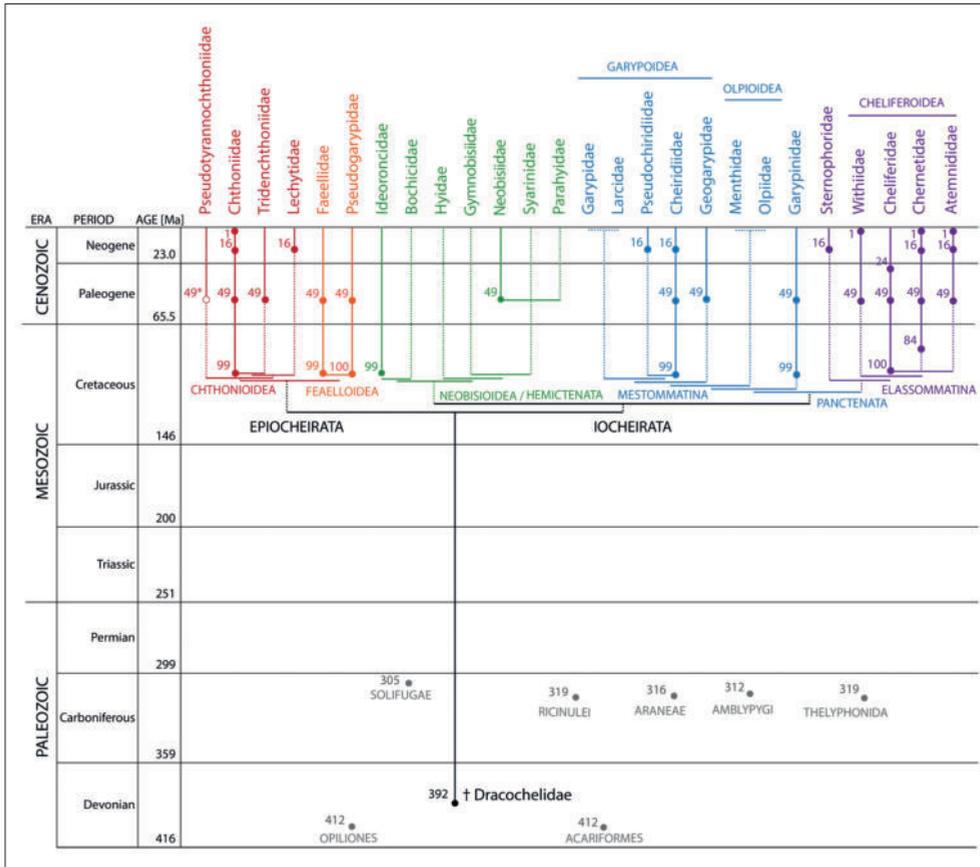


Fig. 2: Evolutionary time tree for pseudoscorpions. Families with a fossil record are given as solid lines and those without a fossil record as dotted lines. Key fossils for each family are indicated by circles and an age estimate is provided (e.g. Ideonocidae, 99 million years before present). For comparison maximum age estimates for other arachnid groups are given. The first fossil record of a member of the Pseudotyranochthoniidae (marked with *) is discussed in the text. Figure modified from HARMS & DUNLOP (2017).

the tail and the sting (Fig. 3). The fossil history of pseudoscorpions was recently summarized (by HARMS & DUNLOP (2017), who offered reasons why these animals are potentially useful for paleobiological and paleoenvironmental research, such as their specific habitat and climate requirements which have probably changed little over time. Overall 26 families containing roughly 3.700 species of pseudoscorpions are recognized today (HARVEY 2013) and most of these families evolved long before the Paleogene (HARMS & DUNLOP 2017). The fossil record is sparser but comprises 49 described species from 16 families. Of these, 32 fossil species (12 families) were described from Baltic amber and two species are shared between Baltic amber and Rovno amber (HARMS & DUNLOP 2017). The Bitterfeld fauna has not been documented so far, although this amber source also contains a very diverse pseudoscorpion fauna with many specimens in both private and public collections. In an early overview of the arthropods present in Bitterfeld amber SCHUMANN & WENDT (1989) reported a single pseudoscorpion, but this specimen was not identified to species level and no collection number was given.

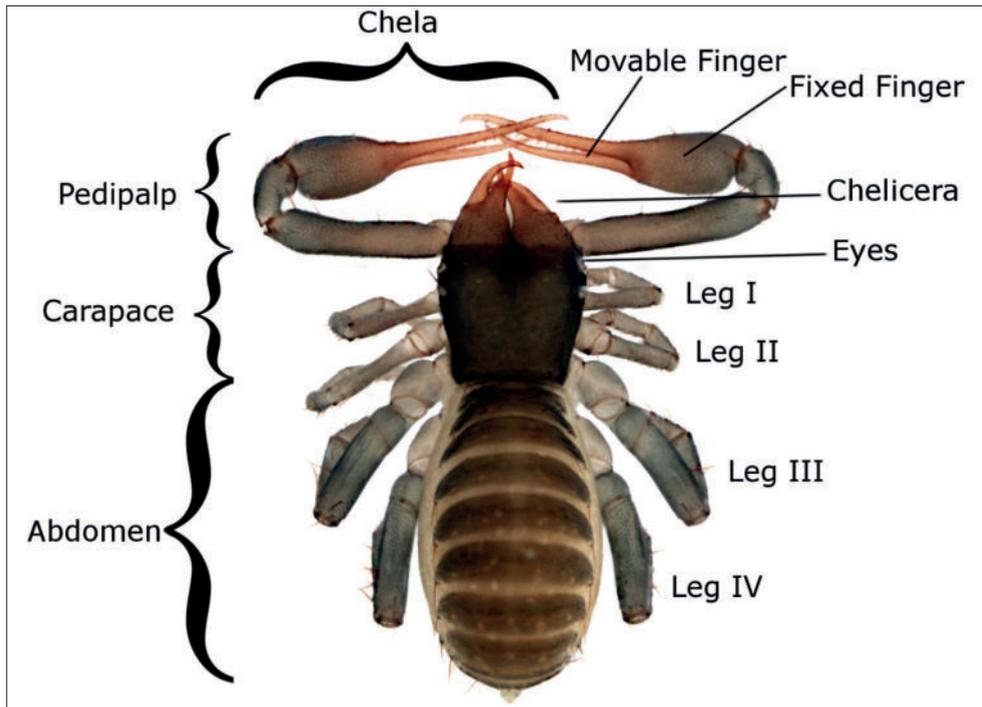


Fig. 3: Pseudoscorpion morphology. Undescribed species of *Pseudotyranochthonius* (family Pseudotyranochthoniidae) from south-western Australia.

Here, we provide a checklist of the pseudoscorpion taxa present in Bitterfeld amber, their repositories, and preliminary taxonomic identifications as a baseline for a forthcoming detailed taxonomic revision. We also provide a photographic atlas of these amber fossils, in the hope of facilitating proper family identification by amber researchers based on the photos and the literature cited herein. We also point out some fossils that are of specific interest (e.g. for their biogeography) and illustrate biological interactions of pseudoscorpions with other arthropods. Finally, we provide some basic comparisons with the much better studied Baltic amber and point out similarities (and differences) between the documented amber pseudoscorpion faunas.

2 Materials and methods

The paleontological collection of the Center for Natural History (CeNak) at the University of Hamburg houses a large amber collection that comprises both Bitterfeld and Baltic amber fossils (objects from Bitterfeld abbreviated with BIBSXXXXX). Additional material was sourced from the paleontological collections of the Museum für Naturkunde Berlin (abbreviated MBAXXXX), the Naturkundemuseum Mauritianum Altenburg (abbreviated BiXXXX, collection Walter Ludwig, WORSCHESCH 2017), the Museum für Geologie Göttingen (abbreviated 2XXXX), as well as from the private collectors Heinrich Grabenhorst, (abbreviated PS-XX and MY-X), Carsten Gröhn (abbreviated S XXXX), and Michael Steiner (Freie Universität Berlin, abbreviated BitXXX), and, via Ivo Rappsilber, from the Goitzsche

Bernstein GmbH (abbreviated T-S-PS-XX, collected during 2016/2017). In case of the material from the Goitzsche Bernstein GmbH, probably 90% of the collected material originates from the “Friedersdorfer Bernsteinschluff” (RAPPSILBER & WENDEL 2019). Generally, we can be sure that the analyzed pieces of “Bitterfeld amber” indeed originate from the region of Bitterfeld, though there may be a small remaining risk that in older collections Bitterfeld and Baltic amber has been mixed. However, even then, it would be much more probable that Bitterfeld amber was labeled as “Baltic amber”, not vice versa.

A Leica M165 C stereo microscope was used for sorting and morphological study. Determination was done to family level first and putative species within the families were identified afterwards using standard taxonomic features (body length and ratios, number and position of eyes, shape and setation of carapace and abdomen, length and shape of palpal hands, presence of venom glands in palpal fingers, etc.) and the family keys and available taxonomic literature for pseudoscorpions (BEIER 1932a, 1932b, 1963; HARVEY 1992; MAHNERT 2004; LEGG & FARR-COX 2016). The classification and nomenclature for families follows BENAVIDES et al. (2019). We excluded 23 specimens from the analysis because they were either juvenile and/or poorly preserved. In general, we refer here to putative species within the families as “morphotypes” because detailed descriptions/measurements and differential diagnoses would be required to establish proper species concepts and to formally name the taxa. As such, our recognition of morphotypes represents a first step towards a comprehensive taxonomic documentation of this fauna, which is beyond the scope of this initial survey. Within each family, morphotypes are ordered alphabetically from the most common morph (starting with *a*) to singletons. All measurements of morphotypes are given in mm and measurements are given in the form of length × width; size (body length) is given as length of carapace + length of abdomen. Information about diversity, distributions, and putative climatic preferences were sourced from HARVEY (2013).

Imaging of specimens was carried out with a Canon EOS 7D Mark II camera with a microscopic lens (5x magnification), or with a Canon EOS 5D Mark III camera with 65 mm lens and 4x magnification, mounted on a custom-made BK Plus Lab System by Dun, Inc. Zerene Stacker was used to generate stacked images. Images were provided with scale bars and compiled into plates in Adobe Photoshop CS6 (ADOBE 2008). Light sources were directed through a semi-transparent filter to prevent light reflection by the amber surface. To prevent optical distortion, amber pieces were immersed in baby oil (e.g. ‘Penaten Pflegeöl’, Johnson and Johnson GmbH) and coated in epoxy to seal cracks and gaps.

3 Results

HARVEY (1992) divided the pseudoscorpions into two suborders: the Epiocheirata (pseudoscorpions without venom glands) and Iocheirata (pseudoscorpions with venom glands). Whilst the Iocheirata was recovered as monophyletic in recent molecular analyses (MURIENNE et al. 2008, HARVEY et al. 2016, BENAVIDES et al. 2019), the Epiocheirata is paraphyletic and now comprises two suborders that lack venom glands: Heterosphyronida CHAMBERLIN, 1929 (families Chthoniidae DADAY, 1889 and Pseudotyranochthoniidae BEIER, 1932) and Atoposphyronida HARVEY, 2019 (Feaellidae ELLINGSEN, 1906 and Pseudogarypidae CHAMBERLIN, 1923). All three main lineages are present in Bitterfeld amber (Tab. 1), but Iocheirata are the most diverse and common lineage. They also comprise the bark-dwelling taxa, which are more likely to become trapped in resin, whereas Heterosphyronida

and Atoposphyronida comprise leaf litter and soil-dwelling animals. Eleven of the currently recognized 26 pseudoscorpion families are recognized here from Bitterfeld amber (Tab. 2). An overview of specimen counts and assigned morphotypes is presented in Tab. 1. Overall, 109 pieces of Bitterfeld amber were examined; 86 contained pseudoscorpions that could be assigned to a family with some room for error (Tab. 3: list of examined pieces; Tab. 4: differentiating characteristics for families and morphotypes).

Tab. 1: Numbers of specimen and assumed morphotypes per family found in Bitterfeld amber

suborder	superfamily	family	no. of specimens	no. of morphotypes
Epiocheirata	Chthonioidea	Chthoniidae	17	4
		Pseudotyranochthoniidae	1	1
	Fealloidea	Pseudogarypidae	2	1
Iochairata	Cheiridioidea	Cheiridiidae	14	3
	Cheliferoidea	Atemnidae	2	2
		Cheliferidae	14	7
		Chernetidae	9	4
		Withiidae	2	1
	Garypoidea	Garypininae	1	1
		Geogarypidae	16	4
	Neobisioidea	Neobisiidae	6	4

Tab. 2: Number of species per family found in Baltic amber (HARMS & DUNLOP 2017) in comparison to assumed morphotype in Bitterfeld amber; note that this table follows the subdivision into Epiocheirata and Iodicheirata (HARVEY, 1992), but that Epiocheirata are considered a paraphyletic group according to newer analyses (e.g. BENAVIDES et al., 2019).

suborder	superfamily	family	no. species (Baltic)	no. morphotypes (Bitterfeld)
Epiocheirata	Chthonioidea	Chthoniidae	2	4
		Pseudotyranochthoniidae	-	1
		Tridenchthoniidae	1	-
	Fealloidea	Pseudogarypidae	5	1
		Feallidae	1	-
Iodicheirata	Cheiridioidea	Cheiridiidae	1	3
	Cheliferoidea	Atemnidae	1	2
		Cheliferidae	10	7
		Chernetidae	2	4
		Withiidae	1	1
	Garypoidea	Garypininae	1	1
		Geogarypidae	3	4
	Neobisioidea	Neobisiidae	4	4
TOTAL			32	32

Tab. 3: Full list of all amber pieces examined for this study, with assignment to families and morphotypes

Collection-No.	Owner	Family	Morphotype
MBA547	Geol. Paläontol. Museum Berlin	Atemnidae	a
PS-18	Heinrich Grabenhorst	Atemnidae	b
Bi1456	Naturkundemuseum Mauritianum Altenburg	Cheiridiidae	b
Bi1460	Naturkundemuseum Mauritianum Altenburg	Cheiridiidae	a
Bi2265	Naturkundemuseum Mauritianum Altenburg	Cheiridiidae	b
Bi2267	Naturkundemuseum Mauritianum Altenburg	Cheiridiidae	a
Bit16	Christian Neumann	Cheiridiidae	a
PS-15	Heinrich Grabenhorst	Cheiridiidae	a
PS-19	Heinrich Grabenhorst	Cheiridiidae	a
PS-26	Heinrich Grabenhorst	Cheiridiidae	
PS-3	Heinrich Grabenhorst	Cheiridiidae	a
PS-7	Heinrich Grabenhorst	Cheiridiidae	c
PS-9	Heinrich Grabenhorst	Cheiridiidae	
T-S-PS-10	Ivo Rappsilber	Cheiridiidae	b
T-S-PS-4	Ivo Rappsilber	Cheiridiidae	b
T-S-PS-6	Ivo Rappsilber	Cheiridiidae	b
23779	Museum für Geologie Göttingen	Cheliferidae	Electrochelifer-a
23781	Museum für Geologie Göttingen	Cheliferidae	b
23785	Museum für Geologie Göttingen	Cheliferidae	e
23828	Museum für Geologie Göttingen	Cheliferidae	a
29614	Museum für Geologie Göttingen	Cheliferidae	d
Bi2266	Naturkundemuseum Mauritianum Altenburg	Cheliferidae	Electrochelifer-a
BIBS0224	Universität Hamburg	Cheliferidae	b
BIBS0225	Universität Hamburg	Cheliferidae	b
MBA1157	Geol. Paläontol. Museum Berlin	Cheliferidae	c

Tab. 3: Continuation

Collection-No.	Owner	Family	Morphotype
MBA545	Geol. Paläontol. Museum Berlin	Cheliferidae	Electrochelifer-a
MBA550.1-2	Geol. Paläontol. Museum Berlin	Cheliferidae	Electrochelifer-b
T-S-PS-1	Goitzsche Bernstein GmbH	Cheliferidae	a
T-S-PS-7	Goitzsche Bernstein GmbH	Cheliferidae	a
T-S-PS-9	Goitzsche Bernstein GmbH	Cheliferidae	a
Bi1448	Naturkundemuseum Mauritianum Altenburg	Chernetidae	
Bi1450	Naturkundemuseum Mauritianum Altenburg	Chernetidae	b
Bi1457	Naturkundemuseum Mauritianum Altenburg	Chernetidae	a
Bi1461	Naturkundemuseum Mauritianum Altenburg	Chernetidae	
Bi1465	Naturkundemuseum Mauritianum Altenburg	Chernetidae	
MBA1153	Geol. Paläontol. Museum Berlin	Chernetidae	d
MBA1158	Geol. Paläontol. Museum Berlin	Chernetidae	a
MBA1165	Geol. Paläontol. Museum Berlin	Chernetidae	
T-S-PS-2	Goitzsche Bernstein GmbH	Chernetidae	c
23738	Museum für Geologie Göttingen	Chthoniidae	b
23776	Museum für Geologie Göttingen	Chthoniidae	b
Bi1454	Naturkundemuseum Mauritianum Altenburg	Chthoniidae	
Bi1455	Naturkundemuseum Mauritianum Altenburg	Chthoniidae	

Tab. 3: Continuation

Collection-No.	Owner	Family	Morphotype
Bi1459	Naturkundemuseum Mauritianum Altenburg	Chthoniidae	
Bi2264	Naturkundemuseum Mauritianum Altenburg	Chthoniidae	
BIBS0222	Universität Hamburg	Chthoniidae	
Bit96	Christian Neumann	Chthoniidae	a
MBA1155a	Geol. Paläontol. Museum Berlin	Chthoniidae	a
MBA549	Geol. Paläontol. Museum Berlin	Chthoniidae	b
PS-1	Heinrich Grabenhorst	Chthoniidae	a
PS-11	Heinrich Grabenhorst	Chthoniidae	
PS-14	Heinrich Grabenhorst	Chthoniidae	a
PS-21	Heinrich Grabenhorst	Chthoniidae	c
PS-27	Heinrich Grabenhorst	Chthoniidae	d
PS-6	Heinrich Grabenhorst	Chthoniidae	a
T-S-PS-3	Goitzsche Bernstein GmbH	Chthoniidae	b
Bi1453	Naturkundemuseum Mauritianum Altenburg	Garypinidae	
23780	Museum für Geologie Göttingen	Geogarypidae	b
23851	Museum für Geologie Göttingen	Geogarypidae	a
Bi1451	Naturkundemuseum Mauritianum Altenburg	Geogarypidae	c
Bi2263	Naturkundemuseum Mauritianum Altenburg	Geogarypidae	
BIBS0217	Universität Hamburg	Geogarypidae	a
BIBS0218	Universität Hamburg	Geogarypidae	a
BIBS0219	Universität Hamburg	Geogarypidae	c
BIBS0223	Universität Hamburg	Geogarypidae	
BIBS0226	Universität Hamburg	Geogarypidae	
MBA1152	Geol. Paläontol. Museum Berlin	Geogarypidae	
MBA1178	Geol. Paläontol. Museum Berlin	Geogarypidae	d
PS-20	Heinrich Grabenhorst	Geogarypidae	a
PS-23	Heinrich Grabenhorst	Geogarypidae	

Tab. 3: Continuation

Collection-No.	Owner	Family	Morphotype
PS-25	Heinrich Grabenhorst	Geogarypidae	
PS-8	Heinrich Grabenhorst	Geogarypidae	a
S 3946	Carsten Gröhn	Geogarypidae	b
23777	Museum für Geologie Göttingen	Neobisidae	
Bi1449	Naturkundemuseum Mauritianum Altenburg	Neobisidae	a
Bi1452	Naturkundemuseum Mauritianum Altenburg	Neobisidae	
BIBS0221	Universität Hamburg	Neobisidae	
MBA1150	Geol. Paläontol. Museum Berlin	Neobisidae	
MBA1151	Geol. Paläontol. Museum Berlin	Neobisidae	d
MBA1159a	Geol. Paläontol. Museum Berlin	Neobisidae	b
PS-12	Heinrich Grabenhorst	Neobisidae	c
MBA548	Geol. Paläontol. Museum Berlin	Pseudogarypidae	a
PS-17	Heinrich Grabenhorst	Pseudogarypidae	a
23850	Museum für Geologie Göttingen	Pseudotyranochthoniidae	a
BIBS0216	Universität Hamburg	Withidae	
PS-4	Heinrich Grabenhorst	Withidae	
23782	Museum für Geologie Göttingen		
23783	Museum für Geologie Göttingen		
23784	Museum für Geologie Göttingen		
23786	Museum für Geologie Göttingen		
Bi1458	Naturkundemuseum Mauritianum Altenburg		
Bi1462	Naturkundemuseum Mauritianum Altenburg		
Bi1463	Naturkundemuseum Mauritianum Altenburg		

Tab. 3: Continuation

Collection-No.	Owner	Family	Morphotype
Bi1464	Naturkundemuseum Mauritianum Altenburg		
Bi1466	Naturkundemuseum Mauritianum Altenburg		
BIBS0220	Universität Hamburg		
Bit335	FU Berlin		
MBA1156	Geol. Paläontol. Museum Berlin		
My-1	Heinrich Grabenhorst		
PS-10	Heinrich Grabenhorst		
PS-16	Heinrich Grabenhorst		
PS-2	Heinrich Grabenhorst		
PS-22	Heinrich Grabenhorst		
PS-24	Heinrich Grabenhorst		
PS-28	Heinrich Grabenhorst		
PS-5	Heinrich Grabenhorst		
S 291	Carsten Gröhn		
T-S-PS-5	Goitzsche Bernstein GmbH		
T-S-PS-8	Goitzsche Bernstein GmbH		

Tab. 4: Overview on found morphotypes of pseudoscorpions in Bitterfeld amber. Differentiating characteristics and measurements given. Measurements are given in mm and follow the from length \times width, for carapace (c), abdomen (a), and pedipalpal hands (p) respectively. Size is given as length of carapace + length of abdomen

family	morpho- type	numberof specimens	differentiating- characteristics	measurements	size	collection- numbers
Chthoniidae	a	5	carapace wider than long, long palpal hands, abdomen 1.5 times longer than wide	c: 0.35×0.43 a: 0.58×0.38 p: 0.71×0.10	0.93	<i>Bit96,</i> <i>MBA1155a,</i> <i>PS-1, PS-</i> <i>14, PS-6</i>
Chthoniidae	b	4	carapace as wide as long, abdomen twice as long as wide	c: 0.37×0.33 a: 0.75×0.35 p: 0.65×0.15	1.12	<i>23738,</i> <i>23776,</i> <i>MBA549,</i> <i>T-S-PS-3</i>
Chthoniidae	c	1	carapace as wide as long, pedipalpal hands shorter, abdomen 1.5 times longer than wide	c: 0.34×0.34 a: 0.58×0.4 p: 0.62×0.13	0.92	<i>PS-21</i>

Tab. 4: Continuation

family	morpho- type	number of specimens	differentiating- characteristics	measurements	size	collection- numbers
Chthoniidae	d	1	smaller than all other morphotypes	c: 0.18×0.16 a: 0.17×0.12 p: 0.22×0.06	0.35	<i>PS-27</i>
Pseudotyranochthoniidae	a	1	carapace and abdomen roughly as wide as long	c: 0.30×0.36 a: 0.50×0.46 p: 0.66×0.16	0.80	<i>23850</i>
Pseudogarypidae	a	2	tear-shaped, abdomen 3x wider than carapace	c: 0.50×0.45 a: 1.53×1.36 p: 0.91×0.24	2.03	<i>PS-17 (juvenile), MBA548</i>
Cheiridiidae	a	6	biggest morphotype, carapace 1.5 times wider than long	c: 0.18×0.26 a: 0.58×0.49 p: 0.31×0.10	0.76	<i>Bi1460, Bi2267 (juvenile), Bit16, PS-15, PS-19, PS-3</i>
Cheiridiidae	b	5	smaller, carapace more than twice as wide as long	c: 0.08×0.19 a: 0.41×0.37 p: 0.24×0.08	0.49	<i>Bi1456, Bi2265, T-S-PS-10, T-S-PS-4, T-S-PS-6</i>
Cheiridiidae	c	1	smaller, carapace 1.5 times wider than long	c: 0.10×0.14 a: 0.41×0.30 p: 0.22×0.08	0.51	<i>PS-7</i>
Atemnidae	a	1	smaller, abdomen twice as long as wide, carapace slightly longer than wide	c: 0.77×0.61 a: 1.46×0.72 p: 1.04×0.44	2.23	<i>MBA547</i>
Atemnidae	b	1	bigger, abdomen 1.5 times longer than wide, carapace slightly wider than long	c: 0.90×0.98 a: 2.16×1.42 p: 1.04×0.44	3.06	<i>PS-18</i>
Cheliferidae	a	4	small, abdomen with 10 spatulate setae on each tergite, carapace grained with two furrows and about 20 setae	c: 0.73×0.67 a: 0.85×0.93 p: 1.00×0.36	1.58	<i>T-S-PS-7, T-S-PS-9, T-S-PS-1 (juvenile), 23828 (juvenile)</i>

Tab. 4: Continuation

family	morpho- type	number of specimens	differentiating- characteristics	measurements	size	collection- numbers
Cheliferidae	b	3	smaller, very short fingers, abdomen nearly 1.5 times longer than wide, few thickened setae on abdomen	c: 0.81×0.64 a: 1.50×0.94 p: 0.87×0.24	2.31	23781 (juvenile?), BIBS0224, BIBS0225 (juvenile)
Cheliferidae	c	1	biggest morphotype, carapace as long as wide, abdomen slightly longer than wide	c: 0.69×0.66 a: 1.01×0.73 p: 1.12×0.26	1.70	MBA1157
Cheliferidae	d	1	smaller, abdomen slightly longer than wide, carapace with furrow, two eyes, abdomen with thick setae	c: 0.69×0.66 a: 1.01×0.73 p: 1.12×0.26	1.70	29614
Cheliferidae	e	1	slightly smaller than <i>a</i> and <i>c</i> , abdomen as wide as long	c: 0.59×0.64 a: 0.87×0.81 p: 0.87×0.19	1.46	23785
Cheliferidae	El-a	3	(modified leg I), abdomen 1.5 times longer than wide, long setae on last tergite, claws slightly less bent	c: not possible a: 1.38×0.89 p: 1.10×0.30		23779, Bi2266 (juvenile), MBA545
Cheliferidae	El-b	1	(modified leg I), abdomen nearly as wide as long, pedipalpal finger more bent than El-a	c: 0.53×0.55 a: 0.88×0.83 p: 0.93×0.27	1.41	MBA550.1-2
Chernetidae	a	2	biggest morphotype, carapace as long as wide, abdomen wider than long	c: 1.00×0.98 a: 0.92×1.23 p: 1.20×0.40	1.92	Bi1457, MBA1158
Chernetidae	b	1	small, carapace grained with one median furrow and without setae (two eyes)	c: 0.56×0.47 a: 0.83×0.73 p: 0.75×0.20	1.39	Bi1450

Tab. 4: Continuation

family	morpho-type	number of specimens	differentiating-characteristics	measurements	size	collection-numbers
Chernetidae	c	1	small like <i>a</i> and <i>c</i> , but with thicker (not spatulate) setae on abdomen	c: 0.43×0.40 a: 0.68×0.54 p: 0.73×0.21	1.11	<i>T-S-PS-2</i> (juvenile)
Chernetidae	d	1	carapace twice as broad as wide, palpal hands only 1.5 times longer than wide	c: 0.37×0.67 a: missing p: 0.54×0.34		<i>MBA 1153</i>
Withiidae	?	2	carapace as long as wide and abdomen 1.5 times longer than wide	c: 0.67×0.68 a: 1.31×0.86 p: 1.10×0.28	1.98	<i>BIBS0216</i> , <i>PS-4</i>
Garypinidae		1	only half of the specimen visible, abdomen longer than wide, carapace roughly as long as wide	c: $0.39 \times ?$ a: $1.00 \times ?$ p: $0.61 \times ?$	1.39	<i>Bi1453</i>
Geogarypidae	a	4	second biggest, carapace and abdomen as long as wide, but eyes on bump (highly granulated)	c: 0.70×0.65 a: 1.01×1.01 p: 1.12×0.27	1.71	<i>23851</i> , <i>BIBS0217</i> , <i>BIBS0218</i> , <i>PS-20</i>
Geogarypidae	b	2	small, carapace and abdomen as long as wide, no bump on carapace, claws slightly bent	c: 0.45×0.46 a: 0.62×0.62 p: 0.67×0.14	1.07	<i>S 3946</i> , <i>23780</i>
Geogarypidae	c	2	small, carapace as long as wide, abdomen slightly longer than wide, (highly granulated, eyes on bump, bend claws)	c: 0.49×0.54 a: 0.63×0.72 p: 0.82×0.22	1.12	<i>BIBS0219</i> , <i>Bi1451</i>
Geogarypidae	d	1	biggest, carapace and abdomen slightly wider than long	c: 0.81×0.95 a: 1.16×1.38 p: 1.60×0.44	1.97	<i>MBA1178</i>
Neobisiidae	a	1	big (2.43), carapace as long as wide, abdomen nearly twice as long as wide	c: 0.89×0.74 a: 1.54×0.80 p: 1.65×0.52	2.43	<i>Bi1449</i>

Tab. 4: Continuation

family	morpho- type	numberof specimens	differentiating- characteristics	measurements	size	collection- numbers
Neobisiidae	b	1	big (2.54), carapace and abdomen twice as long as wide	c: 0.89×0.55 a: 1.65×0.78 p: 1.14×0.42	2.54	<i>MBA1159a</i>
Neobisiidae	c	1	big (2.35), carapace twice as long as wide, abdomen probably more than twice as long as wide	c: 0.85×0.50 a: at least 1.50×0.66 p: 1.37×0.25	at leas 2.35	<i>PS-12</i>
Neobisiidae	d	1	biggest (2.58,) compact, roundish, abdomen and carapace only 1.5 times longer than wide	c: 1.28×0.76 a: 1.30×0.76 p: 1.02×0.34	2.58	<i>MBA1151</i> (<i>deuto-</i> <i>nymph</i>)

3.1 Suborder Heterosphyronida CHAMBERLIN, 1929

Four extant families were recognized until recently (Chthoniidae DADAY, 1889; Lechtyiidae CHAMBERLIN, 1929; Pseudotyranochthoniidae Judson, 1992 and Tridenchthoniidae BALZAN, 1893) but the Lechtyiidae and Tridenchthoniidae are now considered subfamilies of the Chthoniidae (BENAVIDES et al. 2019). Two families are present in Bitterfeld amber: Chthoniidae (17 fossils, 4 morphotypes), and Pseudotyranochthoniidae (1 specimen). Tridenchthoniinae (known from Baltic amber) is not present in the Bitterfeld amber collections we examined. Lechtyiinae is not known from any of the succinite ambers. All taxa are essentially leaf-litter fauna and not generally found under tree bark or other deciduous habitats (e.g. animal nests).

Family Chthoniidae DADAY 1889

This family of pseudoscorpions can be recognized in amber by virtue of the large chelicerae and the fusion of the metatarsi and tarsi in legs I and II; features that are shared only with the Pseudotyranochthoniidae BEIER, 1932. From this family, Chthoniids can be distinguished by the medial position of trichobothria *ib* and *isb* on the dorsal side of the chelal hand (Fig. 4, arrow) whereas in the Pseudotyranochthoniidae they are situated distal at the base of the fixed finger. In juvenile specimens only one trichobothrium is present in this position.

The specimens in Bitterfeld amber cluster according to body length body ratios. The most abundant morphotype (morphotype *a*) yielded five specimens which could be distinguished from other morphotypes by a carapace that is only slightly wider than long (0.35×0.43) and the long palpal hands (0.71×0.17). Four specimens were assigned to morphotype *b* and have a carapace that is nearly as wide as long (0.37×0.33). One specimen was assigned to morphotype *c*, also characterized by a subquadratic carapace (0.34×0.34), but with a smaller

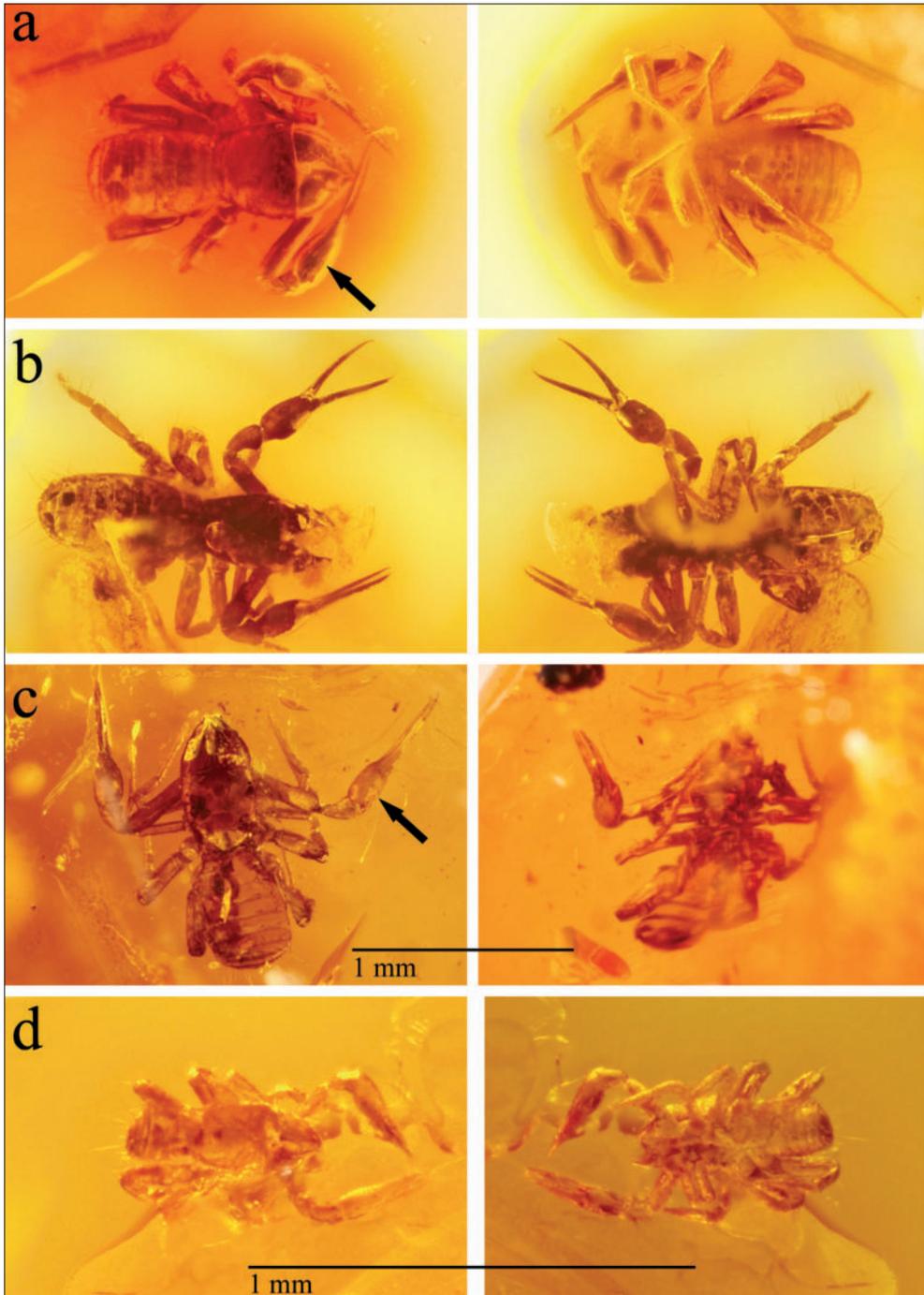


Fig. 4: Diversity of Chthoniidae found in Bitterfeld amber. a: MBA1155, morphotype *a*. b: MBA549, morphotype *b*. c: PS-21, morphotype *c*. d: PS-27, morphotype *d*. Scale bar for a, b, c is the same. Dorsal views are given on the left side and ventral views are on the right side.

body length and shorter pedipalps. Morphotype *d* was represented by a single specimen and differed from all others by its very small size (0.35) despite being adult. Six specimens could not be assigned to any of the morphotypes because they were poorly preserved or barely visible in the amber.

Family Pseudotyranochthoniidae JUDSON, 1992

Pseudotyranochthoniidae share many characteristics of Chthoniidae, but differ by the distal position of trichobothria *ib* and *isb* on the chelal hand (e.g. HARMS 2013, HARMS & HARVEY 2013). The present specimen (carapace: 0.30×0.36 , abdomen: 0.50×0.46 , Fig. 5) represents the first fossil record of this family and has considerable biogeographical implications. This family is extinct in Europe today and the closest records are from the central Asia (*Centrochthonius* BEIER, 1931), east Asia (*Allochthonius* CHAMBERLIN, 1929) and the western USA (*Pseudotyranochthonius* BEIER, 1932). The amber specimen requires detailed taxonomic assessment.

3.2 Suborder Atoposphyronida HARVEY, 2019.

This suborder comprises two families with distributions that exclude each other today: the Pseudogarypidae CHAMBERLIN, 1923 are present in temperate North America with six species and the Feaellidae occur only in warm habitats of the Southern Hemisphere. Interestingly, both families are present alongside each other in Baltic amber (HARMS & DUNLOP 2017) and the Pseudogarypidae CHAMBERLIN, 1923 is also known from Rovno amber. Members of both families can easily be distinguished from other pseudoscorpions by the presence of anterior protuberances or large tubercles at the anterior margin of the carapace, and the flat and broad abdomen. Pseudogarypidae today have been collected under bark and flat rocks in shaded forest habitats, and in caves.

Family Pseudogarypidae CHAMBERLIN, 1923

The present specimen provides the first record of this family in Bitterfeld amber. Additional fossil species are present in Baltic amber (5 species) and Rovno amber (1) and this family was obviously widespread in Europe during the Eocene, but is now extinct in Eurasia. The present specimen (carapace 0.50×0.45 , Fig. 6) may be conspecific with *Pseudogarypus minor* BEIER, 1947 known from both Baltic and Rovno amber (HENDERICKX et al. 2013) pending further analysis.

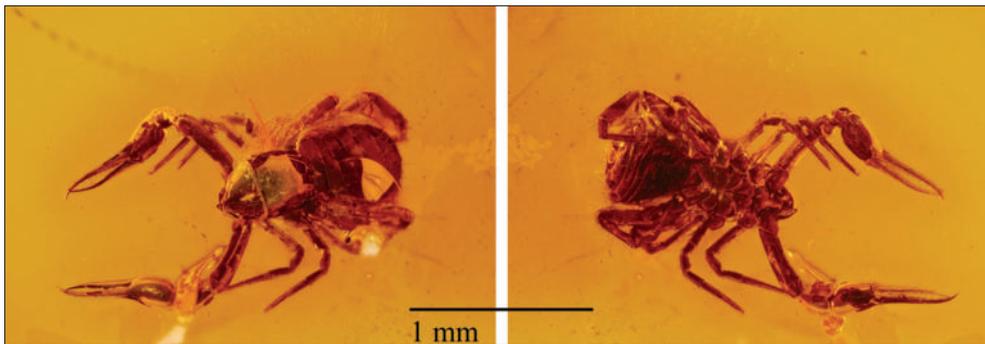


Fig. 5: First fossil record of Pseudotyranochthoniidae (Göttingen Collection no. 23850). Dorsal view (left) and ventral view (right side).

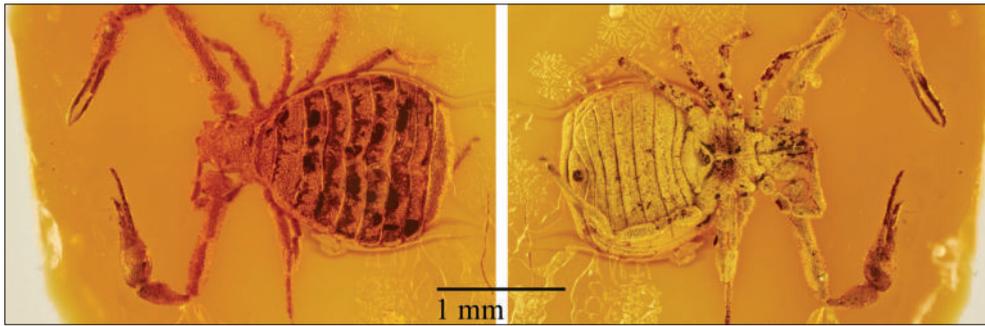


Fig. 6: *Pseudogarypus* in Bitterfeld amber (MBA 548). Dorsal view (left) and ventral view (right side).

3.3 Suborder Icocheirata HARVEY, 1992

This suborder is defined by the presence of a venom apparatus in one or both pedipalp fingers and includes groups that are common under tree bark and rocks, but also ephemeral habitats (e.g. animal nests) and leaf litter and/or soil biota. The Icocheirata are ecologically and morphologically the most diverse lineage of pseudoscorpions. Several families in this suborder are known to contain phoretic species, i.e. animals that hitchhike on other animals to disperse between habitats. The Bitterfeld material contains 26 morphotypes in eight extant families.

Family Atemnidae KISHIDA, 1929

This family includes medium-sized to large (>5 mm) pseudoscorpions with a venom gland in the fixed chelal finger, but not the movable finger. In amber, these pseudoscorpions may be distinguished by having a rather elongate and ‘worm-like’ abdomen, small chelicerae, robust pedipalps, and a subrectangular carapace with eyes near the anterior margin. Two morphotypes are represented in Bitterfeld amber by singleton species, see Fig. 7. Morphotype *a* is smaller (2.23) with a slightly longer than wider carapace (0.77×0.61) and morphotype *b* is significantly larger (3.06) and with a carapace that is slightly wider than long (0.90×0.98). One species is known from Baltic amber, but none from Rovno amber (HARMS & DUNLOP 2017).

Family Cheiridiidae HANSEN, 1894

This family includes very small (1–2 mm in body length) pseudoscorpions that are usually found under rocks or tree bark, but have also been found in bird nests. Many recent species are widely distributed and known to use phoresy as a means of dispersal. The highest diversity in the recent fauna is in warm climates, but some species are also found in temperate regions. We distinguish three different morphotypes among the specimens assigned to this family (Fig. 8). All morphotypes have a granulated cuticula, a triangular carapace, and a rounded to ovate abdomen. Six specimens (5 adult, 1 juvenile) were assigned to morphotype *a*. This type is comparatively large (0.76) and is characterized by a carapace that is nearly 1.5 times wider than long (0.18×0.26). Morphotype *b* (4 specimens) is smaller (0.49) and the carapace is more than twice as wide as long (0.08×0.19). Only one specimen was assigned to morphotype *c*. It resembles type *a* with the carapace being 1.5 times wider than long (0.10×0.14), but is smaller (0.51) and has less pronounced furrows between the segments on the abdomen. This specimen may be a juvenile of type *a*. Two specimens could not be assigned to a morphotype because they were damaged. Overall, this family is quite common in Bitterfeld amber and it is worth noting that it is more common than in Baltic amber (one described species) and Rovno amber (no records).

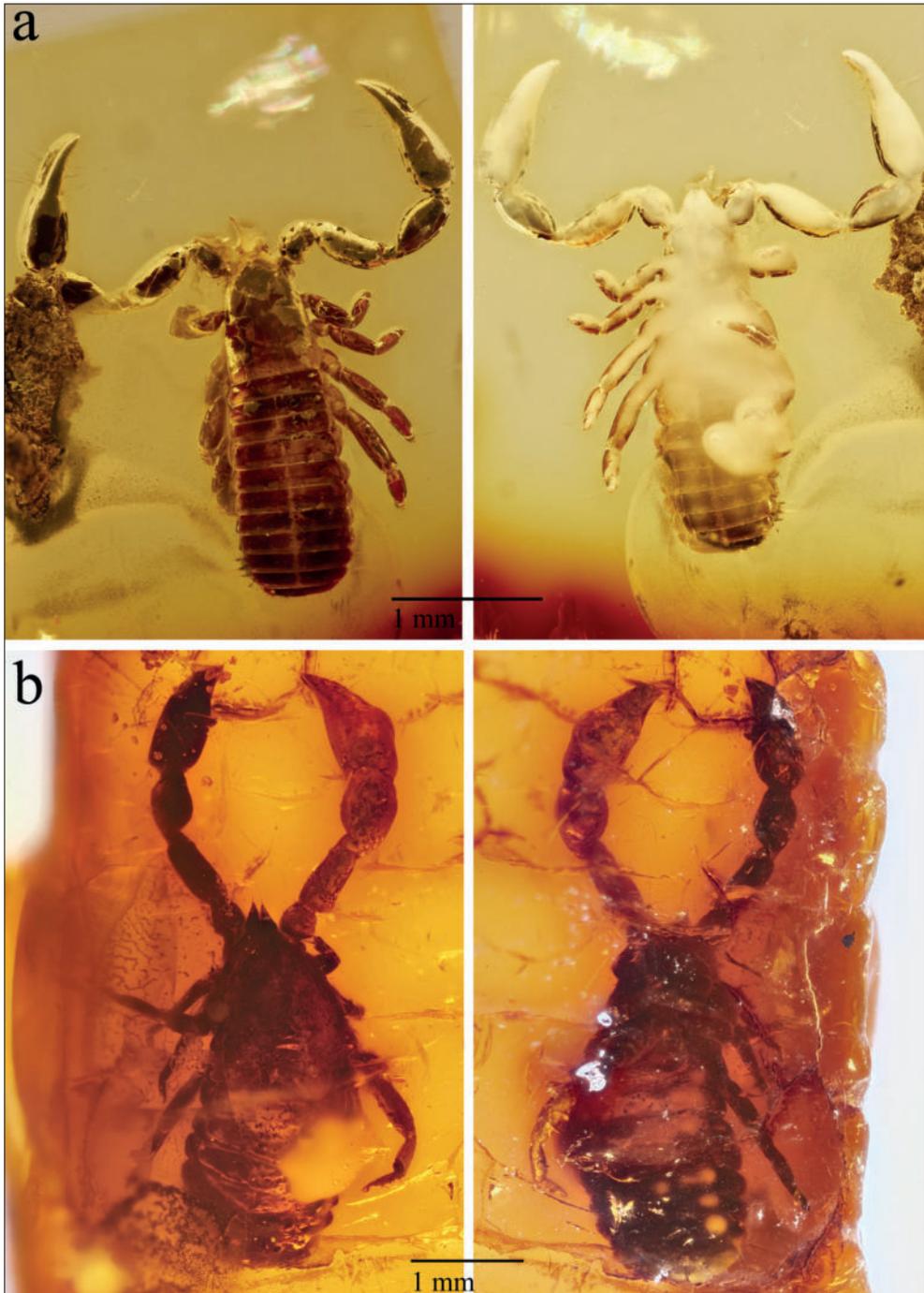


Fig. 7: Diversity of Atemnidae found in Bitterfeld amber. a: MBA547, morphotype *a*. b: PS-18, morphotype *b*. Dorsal view on left side, ventral view on right side.

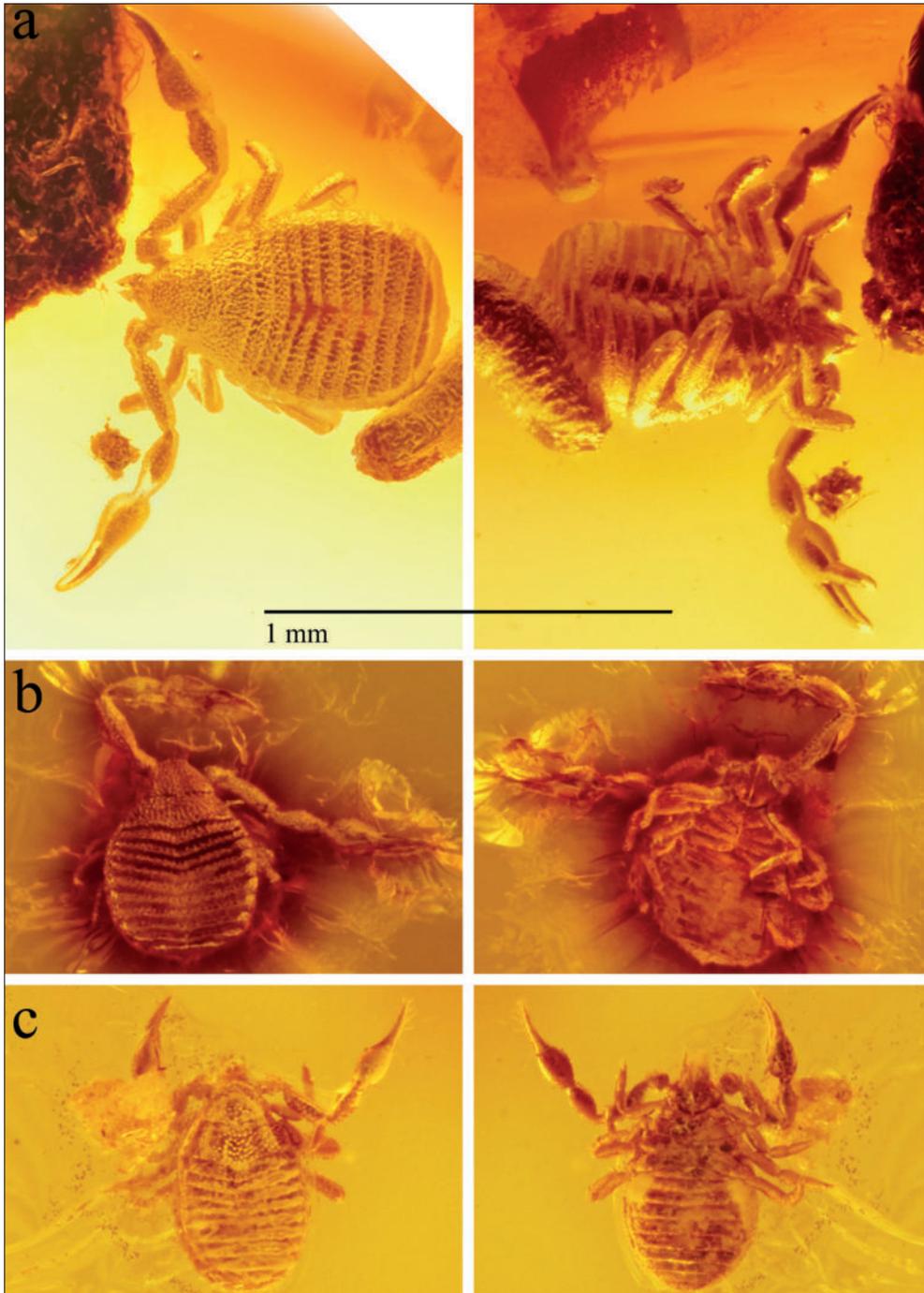


Fig. 8: Diversity of Cheiridiidae found in Bitterfeld amber. a: PS-3, morphotype *a*. b: Bi2265, morphotype *b*. c: PS-7, morphotype *c*. Scale bar given for all specimen. Dorsal view on left side, ventral view on right side.

Family Cheliferidae Risso, 1827

This family is similar to Atemnidae in general appearance (subrectangular carapace and eyes near the anterior margin; palpal femur without trichobothria in basal half, femur/patella junction of leg I and II oblique), but the venom apparatus is found in both fingers (HARVEY 1992) and the animals are stouter and the abdomen not as long. Most cheliferids are phoretic and use a variety of insects to disperse between habitats. Many species also live under tree bark. The family is common in all amber types and present here at Bitterfeld too with at least five morphotypes. Of notable interest is the presence of the genus *Electrochelifer* BEIER, 1937 – an extinct genus which is also known from Baltic amber with five species. Males in this genus are characterized by a thickened tarsus I that often has additional protuberances that are species-characteristic (e.g. Fig. 9, arrow) (BEIER 1937, DASHDAMIROV 2007).

Two morphotypes of *Electrochelifer* were distinguished here: type *a* (3 specimens, including one juvenile) with a body length of 1.58 and long setae on the last tergite, and type *b* which is smaller (body length 1.41) and lacks these setae. Five additional morphotypes were also identified that do not belong to this genus (Fig. 10). Cheliferidae morphotype *a* (4 specimens, one probably juvenile) is relatively small (body length 1.58, probably longer, since the abdomen is bent upwards) and has spatulate setae on the abdomen, as well as median furrows on the carapace (0.73 long \times 0.67 wide). Morphotype *b* (3 specimens, body length 1.68) with very short pedipalp fingers (0.33 – slightly less than a third of the length of the palpal hand) and few thick setae on the abdomen; morphotype *c* with a body length of 3.51, type *d* with a body length of 1.7 and a carapace with furrows, and type *e* which is considerably smaller (1.46). Morphotypes *c*, *d*, and *e* were each represented by a single specimen.

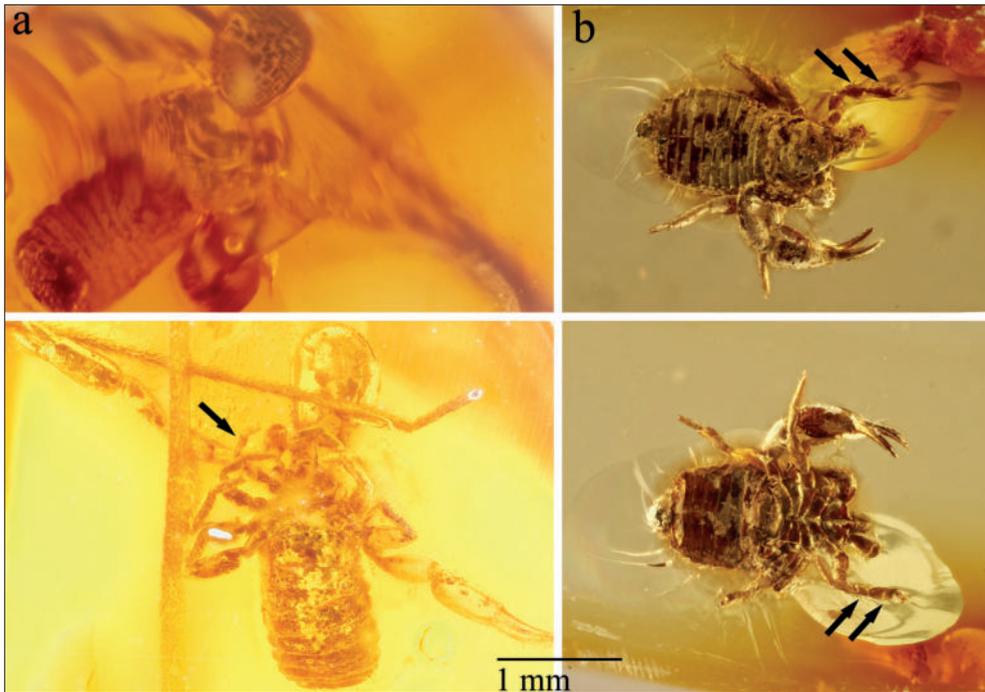


Fig. 9: Morphotypes of *Electrochelifer* (Cheliferidae) found in Bitterfeld amber. a: 23779, morphotype *Electrochelifera*, phoretic on insect leg. b: MBA55.1-20, morphotype *Electrocheliferb*. Scale bar given for both specimens. Arrows indicate the modified tarsus (and tibia) I. Dorsal view above, ventral view below.

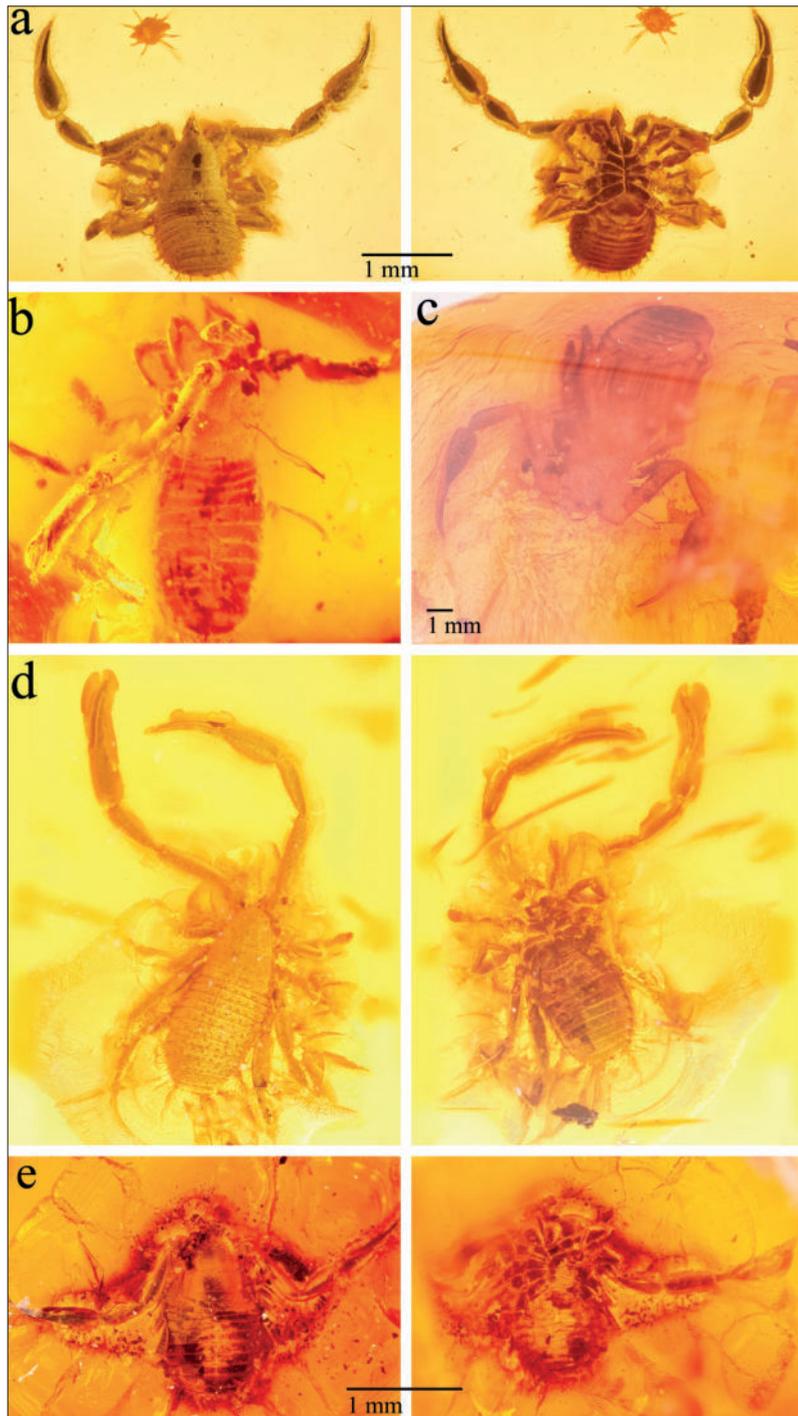


Fig. 10: Diversity of Cheliferidae (without *Electrochelifer*) found in Bitterfeld amber. a: T-S-PS-7 morphotype *a*, b: BIBS0224 dorsal view, morphotype *b*. c: MBA1157 dorsal view, morphotype *c*. d: 29614, morphotype *d*. e: 23785, morphotype *e*. Scale bar for b, d, e is the same. Dorsal view on left side, ventral view on right side.

Family Chernetidae MENGE, 1855

Chernetidae are similar to Atemnidae and Cheliferidae, but can be differentiated by the presence of a venom apparatus only in the movable finger, and at least one accessory tooth in their fingers (HARVEY 1992). Four morphotypes were found in this family, see Fig. 11. Morphotype *a* (2 specimens) is considerably larger (2.92). Morphotype *b* (1 specimen; 1.34) lacks setae on the carapace and has one median furrow only. Morphotype *c* (1 specimen), was quite small (1.11) and had simple setae on the abdomen. The only specimen of morphotype *d* lacks an abdomen, but the carapace is much wider than long (0.37×0.67) and the palpal hand is broad and 1.5 times longer than wide (0.54×0.34). No picture is given due to the poor preservation of this specimen. Four additional specimens in this family were juveniles, damaged or covered in white emulsion. They could not be assigned to any morphotype.

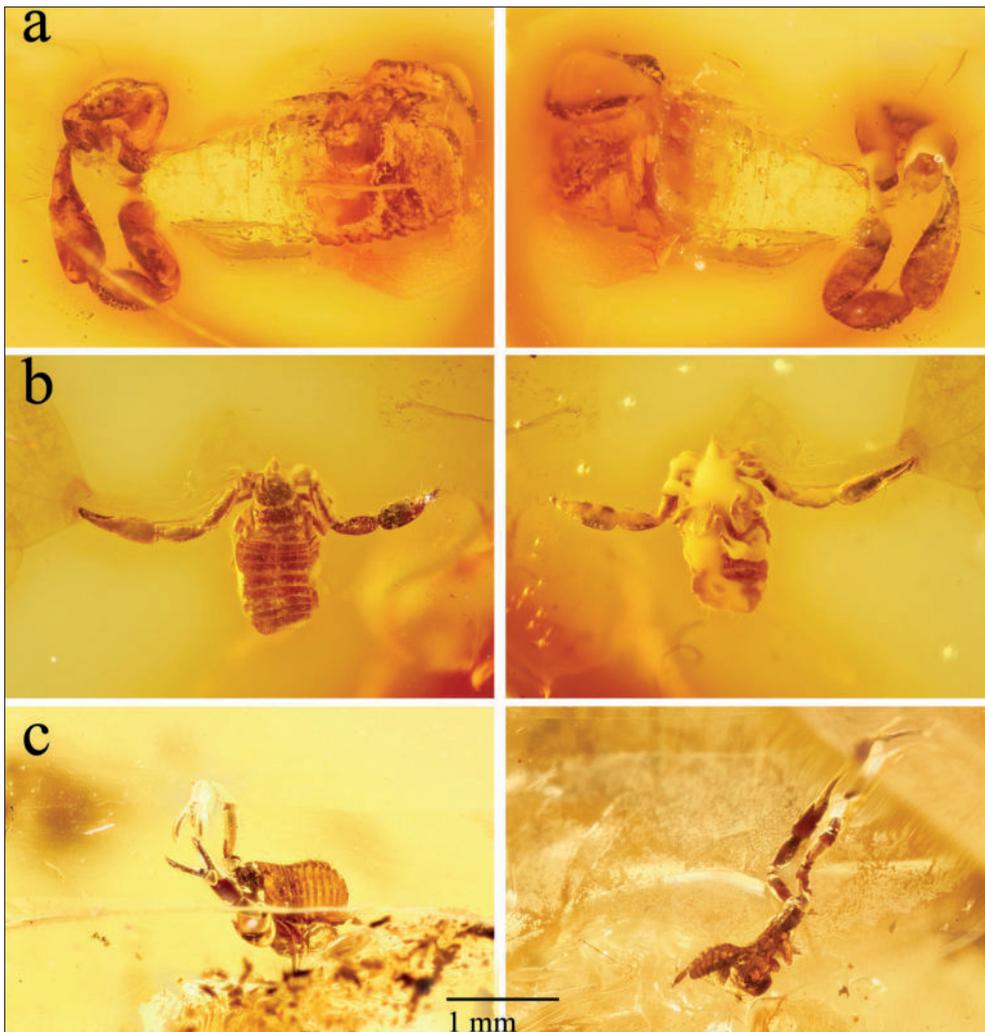


Fig. 11: Diversity of Chernetidae found in Bitterfeld amber. a: MBA1158, morphotype *a*. b: Bi1450 morphotype *b*. c: T-S-PS-2, morphotype *c*. Scale bar given for all specimen. It was not possible to take an image of morphotype *d*, due to impurities in the amber piece. Dorsal view on left side, ventral view on right side. Note that the ventral view is given instead of a lateral view in Figure 11c.

Family Garypinidae JUDSON, 1992

Garypinidae have a slender appearance and are medium-sized pseudoscorpions. At least some of the tergites of the abdomen are divided and the carapace has four eyes near the anterior margin. One fossil garypinid was found in the Bitterfeld collections (Fig. 12) but could not be identified further due to poor preservation. One species has been described from Baltic amber, but none from Rovno amber.

Family Geogarypidae CHAMBERLIN, 1930

This is amongst the more common families of pseudoscorpions found in Bitterfeld amber and can easily be diagnosed by the rectangular carapace with a granulate cuticle and four eyes that are situated on a mound and removed from the anterior margin. The animals are quite flat and may possess dark colour patches on the abdominal tergites, even in amber. Geogarypids can be found today under rocks, tree bark and other sheltered habitats. They are moderately common in Baltic amber (3 described species) and Rovno amber (1 species). Four morphotypes are also present in Bitterfeld amber (Fig. 13). Morphotype *a* is represented by four specimens and quite large (1.71). It is characterized by a carapace that is roughly as long as wide (0.70×0.65), and the eyes are situated on a distinct mound. Morphotype *b* (2 specimens) is smaller (1.07), the eye mound less pronounced, and the carapace is roughly as long as wide (0.45×0.46). Morphotype *c* (2 specimens) is similar in size to type *b* (1.12), but the eyes are positioned on a distinct mound. Morphotype *d* (1 specimen) is much larger (1.97) and with a carapace that is slightly wider than long (0.81×0.95). Six additional specimens could not be identified further.

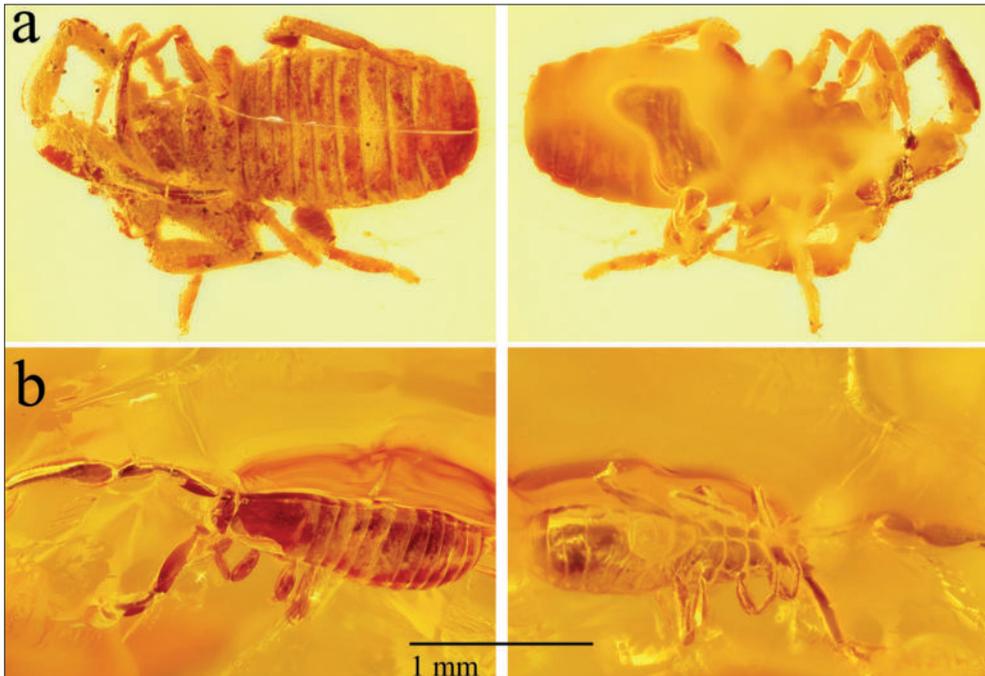


Fig. 12: a: Withiid found in Bitterfeld amber (PS-4). b: Garypinid found in Bitterfeld amber (Bi1453). Scale bar given for both specimens. Dorsal view on left side, ventral view on right side.

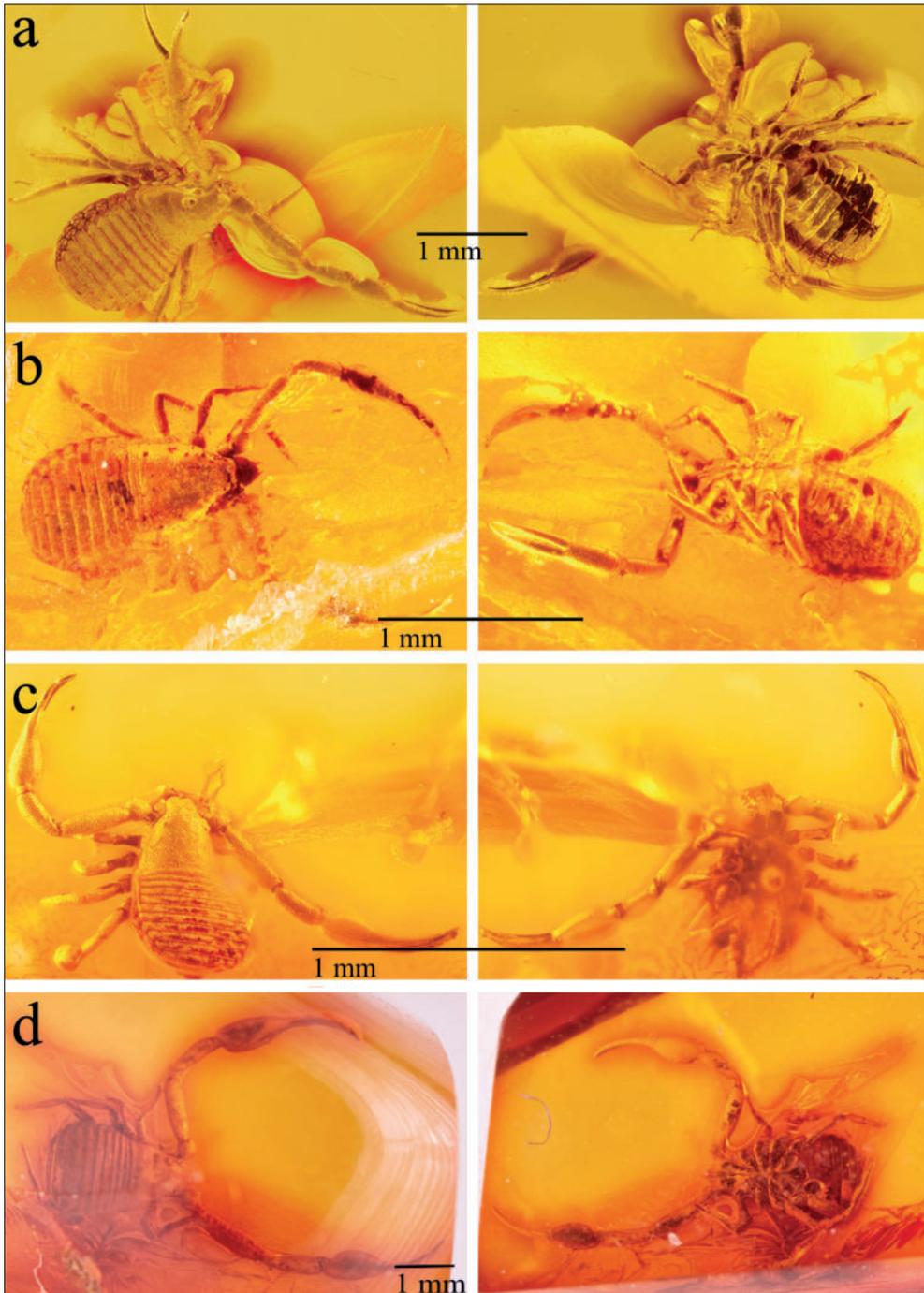


Fig. 13: Diversity of Geogarypidae found in Bitterfeld amber. a: 23851, morphotype *a*. b: 23780, morphotype *b*. c: Bi1451, morphotype *c*. d: MBA1178, morphotype *d*. Dorsal view on left side, ventral view on right side.

Family Neobisiidae CHAMBERLIN, 1930

This is the most common lineage of pseudoscorpions in temperate regions of the Palearctic today and its species are typically found in leaf litter, topsoil and caves. No neobisiids are known to be phoretic today, which sets them apart from the other families of the Icocheirata that are present in Bitterfeld amber. Many species today are also dispersal-restricted and have rather small distribution ranges. Four morphotypes were distinguished in Bitterfeld amber (Fig.14). Morphotype *a* (2.43 in body length) can be differentiated by a carapace that is roughly as long as wide (0.89×0.74). Morphotype *b* is similar in size (2.54), but the carapace is almost twice as long as wide (0.89×0.55). Morphotype *c* is smaller than *b* (2.35), has a very slender carapace (0.85×0.50) and very long chelal hands. Morphotype *d* is a nymph, but probably a distinct species because of unique carapace ratios (1.28×0.76). The remaining six specimens could not be identified further.

Family Withiidae CHAMBERLIN, 1931

This family is characterized by glandular setae on the ventral surface of the abdomen, and femur/patella junctions of leg I and II that are perpendicular and not oblique (HARVEY 1992). One specimen in the Bitterfeld collections may belong to this family, see Fig. 12. The carapace is as long as wide (0.67×0.68).

3.4 Syninclusions

In some pieces syninclusions were found, namely a mite (in piece Bi2266, with Cheliferidae, morphotype *Electrochelifer-a*), a spider (piece PS-25, with Geogarypidae, no morphotype assigned), and a springtail (Collembola) and biting midge (Ceratopogonidae; in amber piece S 3946, with Geogarypidae, morphotype *b*). Some fossils also demonstrate direct evidence of ecological interactions in the Bitterfeld amber forest. One pseudoscorpion specimen is entangled in a spider web, but the ventral side is covered in white emulsion (Piece PS-4, Fig. 15b). A phoretic specimen of *Electrochelifer* (morphotype *a*, Cheliferidae) was also found holding onto an insect leg (Piece 23778, Fig. 15a). As only the leg of the insect is preserved, it could not be determined further. A remarkable predator–prey interaction is illustrated here by a centipede feeding on a pseudoscorpion (Piece MY-1, Fig. 15c). The pseudoscorpion could not be identified to family level because several body parts had already been consumed by the centipede and were missing.

4 Discussion

4.1 Comparative diversity patterns and taxonomic composition

Embedding of organisms in amber is often selective (e.g. RAGAZZI & SCHMIDT 2011) and depends on both the mobility and preferred microhabitat of the animals that were enclosed in the tree resin. The composition and number of taxa is thus always biased and only partially reflects the actual paleodiversity in a given habitat. Concerning pseudoscorpions, BEIER (1937) noted a strong bias towards bark-dwelling taxa for Baltic amber, explainable by their adjacency to the resin source, while litter-dwelling taxa were comparatively rare, and cave dwelling taxa were not documented at all. The Bitterfeld pseudoscorpion fauna does not show such a bias: 23 specimens (11 morphotypes) belonged to families that can be

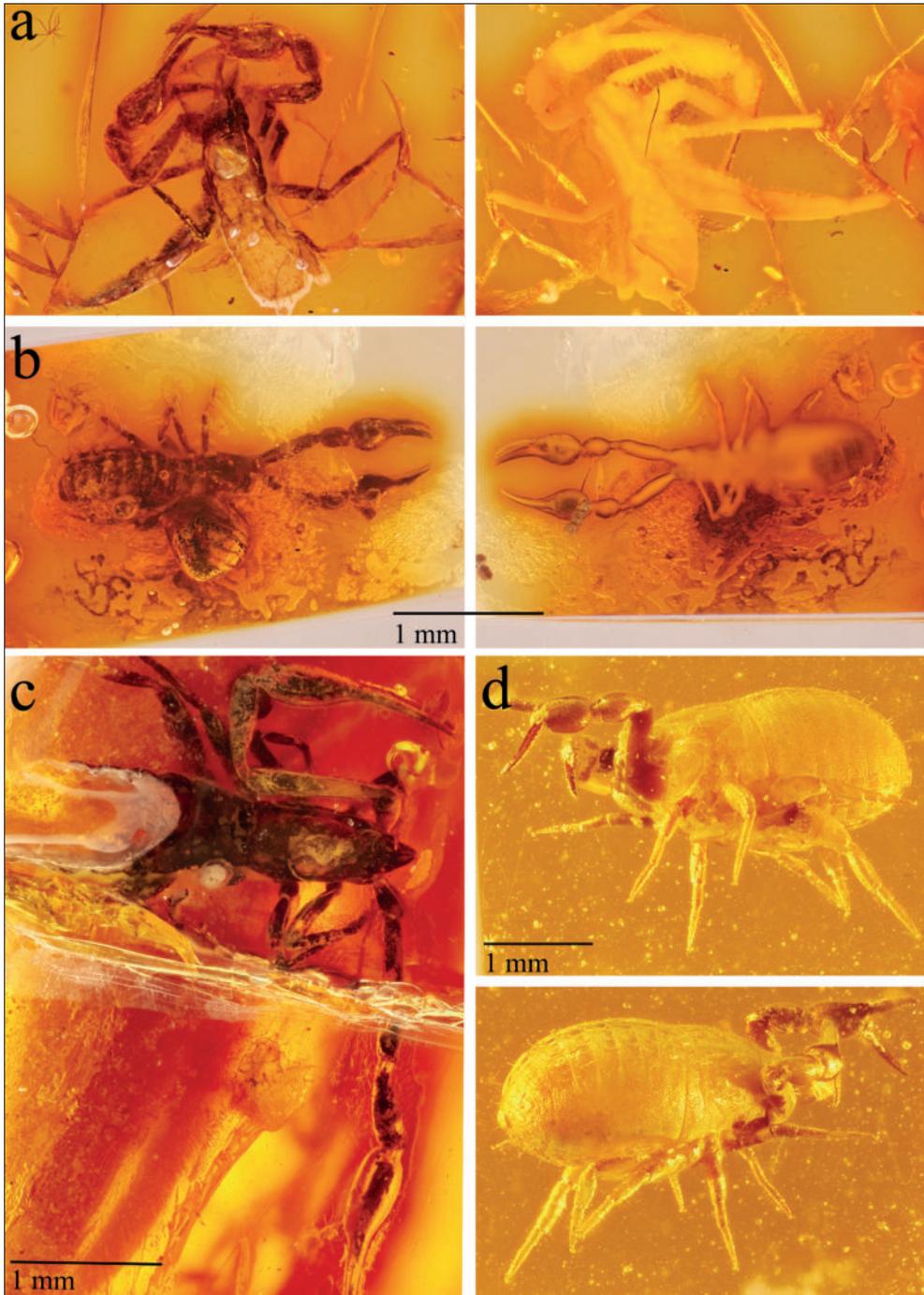


Fig. 14: Diversity of Neobisiidae found in Bitterfeld amber. a: Bi1449, morphotype *a*. b: MBA1159, morphotype *b*. c: PS-12, morphotype *c*. d: MBA1151, morphotype *d*. Scale bar for a and b is the same. Dorsal view on left side, ventral view on right side. Note that lateral views are given in Fig. 13d

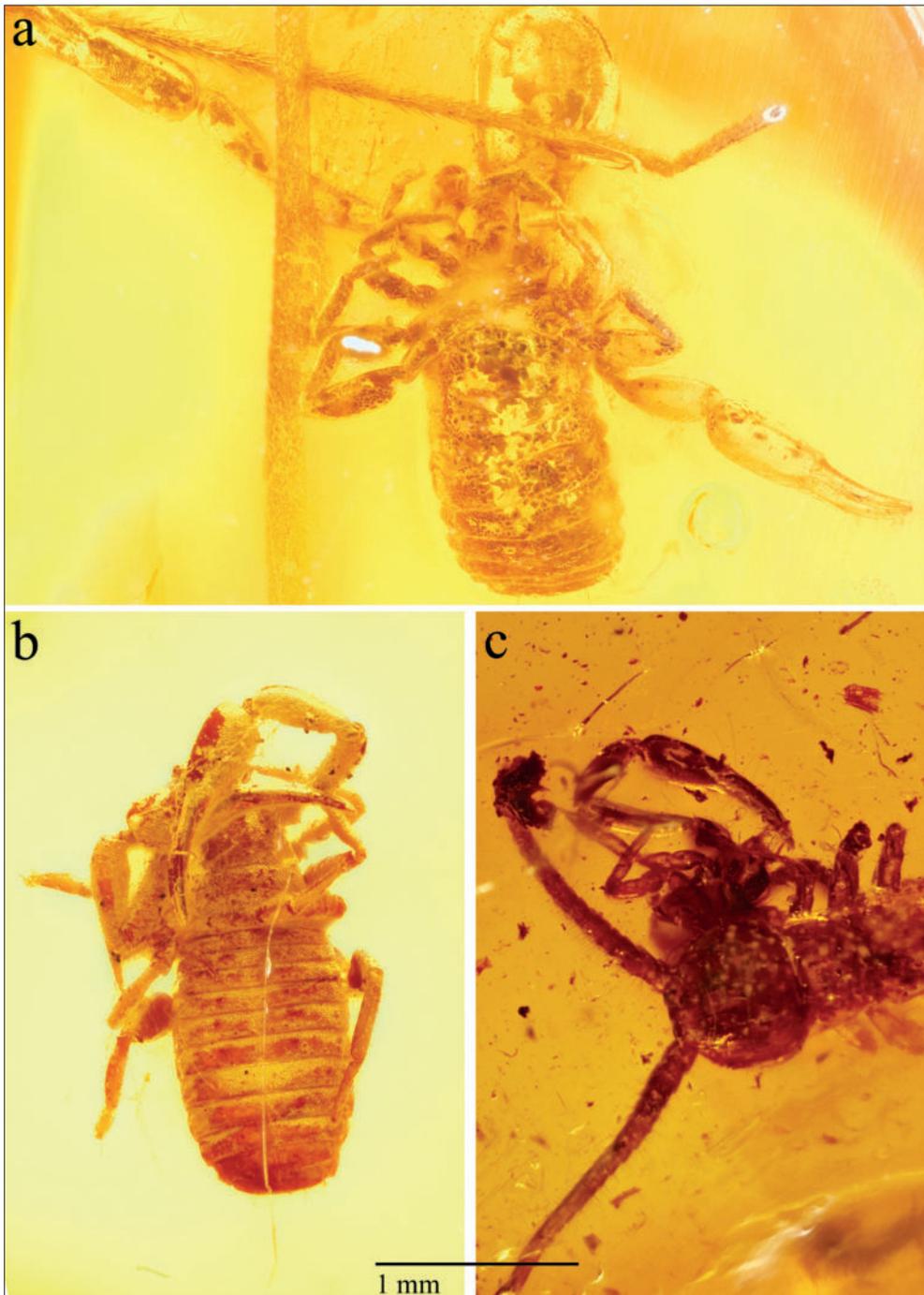


Fig. 15: Ecological interactions of pseudoscorpions found in Bitterfeld amber. a: 23779, *Electrochelifer* (morphotype *a*, Cheliferidae) phoretic on the leg of a putative Nematocera (ventral), b: PS-4 (Withiidae) entangled in spider webs (dorsal). c: MY-1, centipede feeding on a pseudoscorpion (dorsal view).

found under tree bark and above-ground habitats (i.e. the families Atemnidae, Chernetidae, Cheliferidae), but there were also many specimens that belong to typical leaf litter elements (i.e. Chthoniidae, Pseudogarypidae, Neobisiidae; 27 specimens and 9 morphotypes). We do not know why the Bitterfeld deposit preserved so many specimens from leaf litter, but this amber type does seem to better represent the taxonomic diversity of a fossil pseudoscorpion community at a given time and place. This community was remarkably diverse and, with 11 families, is considerably richer than the diversity we find in central Germany today (8 families) and includes lineages that are now extinct in Europe (e.g. Pseudogarypidae, Pseudotyranochthoniidae), those that are still present today in southern Europe but not central Europe (e.g. Geogarypidae, Garypinidae), and those that have broad present-day distributions with species in many climates throughout the Palearctic (e.g. Neobisiidae, Cheliferidae).

Generally, pseudoscorpion species numbers in Bitterfeld amber (32 assigned morphotypes) and Baltic amber (32 described species) seem to be similar based on this study, even though Baltic amber has been studied for more than a century and a half and the source area of Baltic amber is much larger. Both ambers also share the same pseudoscorpion families, including those that are not found in central or northern Europe today (see above). The only difference at family level between both ambers is the absence of the subfamily Tridenchthoniinae in Bitterfeld amber although a single species has been described from Baltic amber (HARMS & DUNLOP 2017), and the new record of the family Pseudotyranochthoniidae in Bitterfeld amber. Both ambers include groups that are nowadays restricted to temperate and mesic forest refugia in North America (e.g. Pseudogarypidae), but also those that prefer mediterranean or even tropical climates today (e.g. Geogarypidae, Garypinidae). As such, the pseudoscorpion data are comparable with those for spiders that also include a number of taxa that are now extinct in Europe and found in warmer climates today, alongside those that are still present in central Europe. Rovno amber is comparatively poor in pseudoscorpion species number and only two fossils have been described so far (*Pseudogarypus minor* BEIER, 1947; *Geogarypus gorskii* HENDERICKX, 2005; HENDERICKX et al. 2012, 2013): both of which are also present in Baltic amber. Despite similarities in species numbers and family composition between the three amber types, there are differences at the species level. In some families, the Bitterfeld samples may belong to species that have already been described from Baltic amber (e.g. *Pseudogarypus minor* in the Pseudogarypidae, species of *Electrochelifer* in the family Cheliferidae and *Geogarypus* in the Geogarypidae: but see DASHDAMIROV (2007) and HENDERICKX & PERKOVSKY (2012), although a detailed taxonomic analysis is required to test if these species are indeed shared between ambers and widespread, or represent separate species that are perhaps very similar in morphology but still distinguishable. In other families (e.g. Chthoniidae, Neobisiidae and Garypinidae) the Bitterfeld taxa are certainly unique and have not been recognized amongst the Baltic and Rovno amber collections we studied. It is worth adding that these families include a high proportion of range-restricted species today.

Several conclusions may be drawn from the data available: First, the pseudoscorpion faunas from all three ambers are taxonomically similar at the family level, but provisionally show some degree of endemism at the species level pending formal description of the Bitterfeld taxa. Second, the Bitterfeld and Baltic amber faunas both include lineages that live in temperate mesic forest refugia, but also those that are restricted to warmer climates today. This is somewhat puzzling and may indicate changes in climatic preference in some pseudoscorpion lineages over time, the overall complexity of the European paleobiota which allowed for co-existence of lineages with differing ecological requirements, or a longer time of amber

deposition and shifts in temperature during this period from warm to cooler. Third, the data do not support the hypothesis that Bitterfeld amber is significantly younger than Baltic amber because both deposits share very similar faunas (and perhaps even some common species). Conversely, this deposit is not Baltic amber either and obviously supported a certain degree of endemism in some families. Overall, the data are most in line with the hypothesis that the succinate ambers were geographically separated and represent different facets of invertebrate communities across a more or less common Eocene amber forest, irrespective of some differences in the timing of deposition. The recent notion by WOLFE et al. (2016) that Bitterfeld and Baltic ambers are chemically different does not refute this hypothesis either, because the tree resin that formed the amber could have originated from different plant species that grew at these fossil sites during the Eocene. The pseudoscorpion fauna at Bitterfeld may thus reflect a slightly different forest type (and perhaps local climates) than those near the Baltic Sea: perhaps comparable to differences that occur today between the flora and fauna in Northern Germany and those found in Southern Germany.

4.2 Biogeographical and ecosystem implications

This study has some biogeographical implications but also adds more data to the puzzle of re-constructing European ecosystems. The Bitterfeld fauna includes two lineages that are today extinct in Europe. The Pseudogarypidae is amongst the most basal lineages of pseudoscorpions (BENNAVIDES et al. 2019) and is present in all European succinate ambers with at least four species (HARMS & DUNLOP 2017). The closest relatives are six species that are found today in warm-temperate forests in the eastern and western USA (HARVEY & ŠTÁHLAVSKÝ 2010; HARVEY 2013). Similarly, the first record of the Pseudotyranochthoniidae highlights similar patterns because recent relatives occur today in warm temperate forests of the western USA and eastern Asia (HARMS & HARVEY 2013). The most recent and certainly most comprehensive analysis of plant fossils in Baltic amber (SADOWSKI et al. 2017) concluded that the Baltic amber flora indicates a warm-temperate paleoclimate and affinities to extant warm-temperate to temperate floras of East Asia and North America, but not subtropical or tropical conditions. The closest analogue today may be the extensive conifer forests in the western USA. The data for these two pseudoscorpion lineages (Pseudogarypidae and Pseudotyranochthoniidae), of which one was also found in Baltic amber, provide evidence for SADOWSKI et al.'s hypotheses (2017) based on invertebrate data, but also point to excessive extinction events in Europe since the late Eocene. Other examples are also present in the harvestman faunas (DUNLOP et al. 2018, ELSAKA et al. 2019), in particular the genera *Caddo*, *Protolophus* and *Eumesosoma* and fit into a pattern of European ambers hosting several arachnid taxa which may originally have been Holarctic in their distribution, but are otherwise known today only from Asia and/or North America.

A somewhat contradictory picture arises though from several pseudoscorpion lineages that occur today in Mediterranean refugia across Europe, such as the Geogarypidae, Garypinidae, Cheiridiidae and some genera in the Neobisiidae. These lineages survived in Europe since the Eocene, but based on the fossil data, retracted to the well-known refugia in Europe (the Balkans, the Iberian Peninsula and Italy: e.g. SCHMITT 2007, Fig. 2), but are also found in even more southern distributions (tropical or subtropical climates) today rather than warm temperate habitats. Climate preferences can change over time and rainfall regimes in Europe during the Eocene were certainly very different from what they are today. Plant-based data from the middle Eocene Messel Formation, ~300 km SW of the Bitterfeld deposit, imply a paratropical climate with much higher annual precipitation values than today (e.g. GREIN et

al. 2011). Certainly, the warm temperate Eocene forest supported a pseudoscorpion fauna that was diverse and unique, with lineages that became extinct, those that retracted to more southerly latitudes (e.g. Mediterranean refugia) and those that were able to survive and even diversify (e.g. Neobisiidae). As such, the Eocene fauna of European pseudoscorpions does not have a similar match in the world today, but is similar in patterning and diversification signatures to the Eocene spider and harvestmen faunas in Europe that is also very diverse and illustrates the same three response patterns (extinction, retraction and post-Eocene diversification) (e.g. DUNLOP & MITOV 2007, DUNLOP et al. 2018).

Other implications may arise for our understanding of European paleogeography. The Bitterfeld and Rovno amber forests may have been separated from the Baltic forest by the North Sea and the Turan Seas (See Fig. 1). If this is true, one might expect differences in taxa that are dispersal-restricted, but not in those that are dispersal prone between the three succinite deposits. The occurrence of common or highly similar *Electrochelifer* (Cheliferiidae) and Chernetidae species in all deposits is not problematic in this context because species in these families are often phoretic and have wide distribution ranges (e.g. OPATOVA & ŠŤÁHLAVSKÝ 2018), but the occurrence of common species in the dispersal-restricted leaf litter fauna (e.g. *Pseudogarypus minor*) is unexpected. A detailed study of the leaf-litter fauna of pseudoscorpions (e.g. Chthoniidae, Neobisiidae, Pseudogarypidae) and other lineages that are dispersal-restricted (e.g. Pseudogarypidae) is warranted to test the hypothesis of spatial partitioning of amber forests imposed by Eocene paleogeography.

4.3 Ecological interactions

The predator-prey interaction of a centipede feeding on a pseudoscorpion (MY-1, 15) is the first fossil evidence of such behavior. It is known that centipedes feed on various small arthropods, thus preying on pseudoscorpions is not surprising (EDGECOMBE & GIRIBET 2007), but direct evidence can now be provided here. Entrapment in resin may have been fast in many cases such as this one because the centipede showed no signs of escape attempts. Similar assumptions can be made about the *Electrochelifer* sp. (morphotype *a*, Cheliferidae, No. 23779, Fig. 15) that was preserved phoretic on a putative midge (Nematocera). Other cases of phoresy have been recorded in fossil pseudoscorpions (e.g. BEIER 1947, JUDSON 2003, POINAR et al. 1998) and such behaviors were obviously already common in the Paleogene pseudoscorpion faunas and displayed by several families. The origins of phoresy in pseudoscorpions presumably lie in Mesozoic ambers (e.g. the Cretaceous Myanmar amber). Another interesting interaction is that of spiders feeding on pseudoscorpions. The entangled pseudoscorpions belong to the bark fauna, but the spider has unfortunately not been preserved.

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6 References

- ADOBE. (2008): Adobe Photoshop CS6.
- ANDERSON, K.B.; WINANS, R.E. & BOTTO, R.E. (1992): The nature and fate of natural resins in the geosphere-II. Identification, classification and nomenclature of resinites. – *Organic Geochemistry* **18** (6): 829–841.
- BEIER, M. (1932a): Pseudoscorpionidea I, Subord. Chthoniinea et Neobisiinea. – Walter de Gruyter & Co, Berlin, Leipzig.
- BEIER, M. (1932b): Pseudoscorpionidea II, Cheliferinea. – Walter de Gruyter & Co, Berlin, Leipzig.
- BEIER, M. (1937): Pseudoscorpione aus dem Baltischen Bernstein. – *Festschrift für Prof. Embrik Strand* **2**: 302–316.
- BEIER, M. (1947): Pseudoskorpione im Baltischen Bernstein und die Untersuchung von Bernstein-Einschlüssen. – *Mikroskopie* **1**: 188–199.
- BEIER, M. (1963): Ordnung Pseudoscorpionidea (Afterskorpione). – *Bestimmungstab. Bodenf. Europas* (Vol. 1). – Akademie-Verlag, Berlin.
- BENAVIDES, L.R.; COSGROVE, J.G.; HARVEY, M.S. & GIRIBET, G. (2019): Phylogenomic interrogation resolves the backbone of the Pseudoscorpiones Tree of Life. – *Molecular Phylogenetics and Evolution*. [<https://doi.org/10.1016/j.ympev.2019.05.023>] accessed: 22.07.2019.
- BLAKEY, R. (2011): Global Paleogeography. [<https://deephimemaps.com>] accessed: 22.07.2019.
- BRAY, P.S. & ANDERSON, K.B. (2009): Identification of Carboniferous (320 Million Years Old) Class Ic Amber. – *Science* **326**: 132–134.
- DASHDAMIROV, S. (2007): A new species of false scorpion from Baltic amber with a redescription of *Electrochelifer balticus* BEIER, 1955 and remarks on some fossil Cheliferidae (Arachnida: Chelonethida). – *Acta Biologica Benrodis* **14**: 1–14.
- DENK, T., & GRIMM, G.W. (2009): The biogeographic history of beech trees. – *Review of Palaeobotany and Palynology* **158** (1–2): 83–100.
- DUNLOP, J.A. & MITOV, P.C. (2007): Fossil harvestmen (Arachnida, Opiliones) from Bitterfeld amber. *ZooKeys* **16**: 347–375.
- DUNLOP, J.A. (2010). Bitterfeld amber. – In: PENNEY, D. (ed.): *Biodiversity of fossils in amber from the major world deposits*. – Siri Scientific Press, Manchester: 57–68.
- DUNLOP, J.A.; KOTHOFF, U.; HAMMEL, J.; AHRENS, J. & HARMS, D. (2018): Arachnids in Bitterfeld amber: A unique fauna of fossils from the heart of Europe or simply old friends? – *Evolutionary Systematics* **2** (1): 32–44.
- EDGEcombe, G.D. & GIRIBET, G. (2007): Evolutionary Biology of Centipedes (Myriapoda: Chilopoda). – *Annual Review of Entomology* **52** (1): 151–170.
- ELSAKA, M.; MITOV, P.G. & DUNLOP, J.A. (2019): New fossil harvestmen (Arachnida: Opiliones) in the HOFFEINS amber collection. – *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen* **292** (2): 155–169.
- FUHRMANN, R. (2004): Entstehung, Entdeckung und Erkundung der Bernsteinlagerstätte Bitterfeld. – *Exkursionsführer und Veröffentlichungen der Gesellschaft für Geowissenschaften* **224**: 25–37.
- GREIN, M.; UTESCHER, T.; WILDE, V. & ROTH-NEBELSICK, A. (2011): Reconstruction of the middle Eocene climate of Messel using palaeobotanical data. – *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **260** (3): 305–318.
- HARMS, D. (2013): A new species of *Pseudotyranochthonius* Beier (Pseudoscorpiones: Pseudotyranochthoniidae) from the Warrumbungle Range, New South Wales. – *Memoirs of the Queensland Museum* **58**: 112–123.

- HARMS, D. & HARVEY, M.S. (2013): Review of the cave-dwelling species of *Pseudotyranochthonius* Beier (Arachnida: Pseudoscorpiones: Pseudotyranochthoniidae) from mainland Australia, with description of two troglobitic species. – *Australian Journal of Entomology* **5**: 129–143.
- HARMS, D. & DUNLOP, J.A. (2017): The fossil history of pseudoscorpions (Arachnida: Pseudoscorpiones). – *Mitteilungen aus dem Museum für Naturkunde in Berlin. Fossil Record* **20** (2): 215.
- HARVEY, M. S. (1992): The Phylogeny and Classification of the Pseudoscorpionida. – *Invertebrate Taxonomy* **6** (6): 1373–1435.
- HARVEY, M.S. (2013): Pseudoscorpions of the World, Version 3.0. [<http://museum.wa.gov.au/catalogues-beta/pseudoscorpions>] accessed: 22.07.2019
- HARVEY, M. S. & ŠTÁHLAVSKÝ, F. (2010): A review of the pseudoscorpion genus *Oreolpium* (Pseudoscorpiones: Garypinidae), with remarks on the composition of the Garypinidae and on pseudoscorpions with bipolar distributions. – *Journal of Arachnology* **38** (2): 294–308.
- HARVEY, M.S.; HUEY, J.A.; HILLYER, M.J.; MCINTYRE, E. & GIRIBET, G. (2016): The first troglobitic species of Gymnobiidae (Pseudoscorpiones: Neobisioidea), from Table Mountain (Western Cape Province, South Africa) and its phylogenetic position. – *Invertebrate Systematics* **30** (1): 75–85.
- HENDERICKX, H. & PERKOVSKY, E. (2012): The first geogarypid (Pseudoscorpiones, Geogarypidae) in Rovno Amber (Ukraine). – *Vestnik zoologii* **46** (3): 273–276.
- HENDERICKX, H.; PERKOVSKY, E.E.; VAN HOOREBEKE, L. & BOONE, M. (2013): The first pseudogarypid in Rovno amber (Ukraine) (Pseudoscorpiones: Pseudogarypidae). – *Phegea* **41** (4): 90–92.
- JUDSON, M.L.I. (2003): Baltic amber fossil of *Garypinus electri* BEIER provides first evidence of phoresy in the pseudoscorpion family Garypinidae (Arachnida: Chelonethi). – *Arthropoda Selecta Special Is* (1): 127–131.
- KNUTH, G.; KOCH, T.; RAPPSILBER, I. & VOLLAND, L. (2002): Concerning amber in the Bitterfeld region – geological and genetic aspects. – *Hallesches Jahrbuch für Geowissenschaften* **24**: 35–46.
- LEGG, G. & FARR-COX, F. (2016): Illustrated key to the British false scorpions (Pseudoscorpions). – Field Studies Council AIDGAP Guides, Vol. OP173.
- MAHNERT, V. (2004): Die Pseudoskorpione Österreichs (Arachnida, Pseudoscorpiones), Vol. 14.
- MURIENNE, J.; HARVEY, M.S. & GIRIBET, G. (2008): First molecular phylogeny of the major clades of Pseudoscorpiones (Arthropoda: Chelicerata). – *Molecular phylogenetics and evolution* **49** (1): 179–184.
- OPATOVA, V. & ŠTÁHLAVSKÝ, F. (2018): Phoretic or not? Phylogeography of the pseudoscorpion *Chernes hahnii* (Pseudoscorpiones: Chernetidae). – *Journal of Arachnology* **46** (1): 104–113.
- PERKOVSKY, E.E.; RASNITSYN, A.P.; VLASKIN, A.P. & TARASCHUK, M.V. (2007): A comparative analysis of the Baltic and Rovno amber arthropod faunas: representative samples. – *African Invertebrates* **48** (1): 229–245.
- POINAR, J.G. (2010): Insects in Amber. – *Annual review of entomology* **38** (1): 145–159.
- POINAR, J.G.; CURCIC, B.P. M. & COKENDOLPHER, J.C. (1998): Arthropod phoresy involving pseudoscorpions in the past and present. – *Acta Arachnologica* **47** (2): 79–96.
- POPOV, S.V.; RÖGL, F.; ROZANOV, A.Y.; STEININGER, F.F.; SHCHERBA, I.G. & KOVAC, M. (2004): Lithological-paleogeographic maps of Paratethys – 10 maps late Eocene to pliocene. Schweizerbart Science Publishers, Stuttgart.
- RAGAZZI, E. & SCHMIDT, A.R. (2011): Amber. – In: *Encyclopedia of Geobiology*. – Springer, Netherlands.
- RAPPSILBER, I. & WENDEL, A. (2019): Bernsteinengewinnung aus dem Bernsteinsee bei Bitterfeld und erste wissenschaftliche Ergebnisse. – *Mauritiana* **37**: 87–112.
- SADOWSKI, E.-M.; SCHMIDT, A.R.; SEYFULLAH, L.J. & KUNZMANN, L. (2017): Conifers of the "Baltic Amber Forest" and Their Palaeoecological Significance. – *Land Oberösterreich, Oberösterreichisches Landesmuseum*.

- SCHMITT, T. (2007): Molecular biogeography of Europe: Pleistocene cycles and postglacial trends. – *Frontiers in Zoology* **4**: 11.
- SCHUMANN, H. & WENDT, H. (1989): Zur Kenntnis der tierischen Inkluden des Sächsischen Bernsteins. – *Deutsche Entomologische Zeitschrift* **36** (1–3): 33–44.
- SHEAR, W.A.; SCHAWALLER, W. & BONAMO, P.M. (1989): Record of Palaeozoic Pseudoscorpions. – *Nature* **341**: 527–529.
- SZWEDO, J. & SONTAG, E. (2013): The flies (Diptera) say that amber from the Gulf of Gdańsk, Bitterfeld and Rovno is the same Baltic amber. – *Polish Journal of Entomology / Polskie Pismo Entomologiczne* **82** (4): 379–388.
- WEYGOLDT, D.P. (1966): Moos- und Bücherskorpione. – *Die Neue Brehm-Bücherei* **365**, A. Ziemsen Verlag, Wittenberg Lutherstadt.
- WIMMER, R.; RASCHER, J.; KRUMBIEGEL, G.; RAPPSILBER, I. & STANDKE, G. (2009): Bitterfelder Bernstein – ein fossiles Harz und seine geologische Geschichte. – *Geowissenschaftliche Mitteilungen, GMIT* **38**: 15.
- WOLFE, A.P.; MCKELLAR, R.C.; TAPPERT, R.; SODHI, R.N.S. & MUEHLENBACHS, K. (2016): Bitterfeld amber is not Baltic amber: Three geochemical tests and further constraints on the botanical affinities of succinite. – *Review of Palaeobotany and Palynology* **225**: 21–32.
- WORSCHESCH, K. (2017): „Forscher, Sammler, Sammlungen: Lebenswerke von privat – gesichert im Museum.“ Erwerb bedeutender Sammlungen durch das Mauritianum in den letzten 10 Jahren. – *Mauritiana* **32**: 17–34.

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