A new species of Laniatores (Arachnida: Opiliones) from Eocene Baltic amber with notes on the evolution of Insidiatores

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Abstract. Two new laniatoreans from Eocene Baltic amber are described. *Baltonychia obscura* gen. et sp. nov. represents the first fossil Laniatores with a peltonychium on tarsus III–IV, implying that its closest living relatives are likely members of the extant families Cladonychiidae or Travuniidae. A second fossil is described as Insidiatores indet. as its preservation does not allow further assignment. Both fossils are substantially different to the so far only known Baltic amber laniatorean species *Proholoscotolemon nemastomoides* (Koch & Berendt, 1854), and suggest a more diverse Laniatores fauna in the Eocene of north-central Europe. The evolutionary history of the infraorder Insidiatores and their development into troglomorphic species is discussed.

Keywords: Baltic amber, Eocene, Insidiatores, Laniatores

Zusammenfassung. Eine neue Art der Krallenweberknechte (Arachnida: Opiliones: Laniatores) aus dem baltischen Bernstein des Eozäns, mit Anmerkungen zur Evolution der Insidatores. Zwei neue Krallenweberknechte aus dem baltischen Bernstein des Eozäns werden beschrieben. *Baltonychia obscura* gen. et sp. nov. repräsentiert den ersten fossilen Krallenweberknecht mit einem Peltonychium an den Tarsen III–IV, wodurch sich die noch lebenden Familien Cladonychiidae oder Travuniidae als mögliche nächste Verwandte herausstellen. Ein zweites Fossil wird als Insidatores indet. beschrieben, da seine Erhaltung keine genauere Bestimmung erlaubt. Beide Fossilien heben sich deutlich von der zuvor einzigen bekannten fossilen Krallenweberknechtart aus baltischem Bernstein, *Proholoscotolemon nemastomoides* (Koch & Berendt, 1854), ab, was eine deutlich diversere Krallenweberknechtfauna während des Eozäns in Nord-Mittel Europa vermuten lässt. Die evolutionäre Geschichte der Infraordnung Insidatores und ihre mögliche Entwicklung in Höhlenbewohnern wird diskutiert.

Of the four living suborders within the harvestmen (Arachnida: Opiliones), Laniatores is by far the most diverse today with over 4200 described species. In this sense, they represent almost two thirds of the total harvestman diversity (Kury 2017, Kury et al. 2021). The presence of large, raptorial pedipalps often combined with strongly developed body and/or leg armature, as well as two terminal (or single and branched) claws on legs III and IV, clearly distinguishes laniatoreans from the other three living harvestman suborders. Because of this ornamentation, they are also sometimes referred to as armoured harvestmen. Based on their claw morphology Laniatores can be further subdivided into two Infraorders: Insidiatores with a single claw on legs III and IV bearing smaller distal branches, and Grassatores with two claws on legs III and IV which have separate insertions (Shultz & Pinto-da-Rocha 2007).

The largest part of the extant Laniatores fauna can be found today in tropical regions such as South and Central America or Southeast Asia. Holarctic laniatoreans are noticeably less species-rich and can usually be found under rocks and logs, leaf litter or in caves (Pinto-da-Rocha et al. 2007). Europe, in particular, is sparsely inhabited, with only a few species belonging to the relatively widespread families Cladonychiidae and Phalangodidae, and the rarer, more geographically restricted families Buemarinoidae and Travuniidae. European laniatoreans tend to be restricted today to more southern/Mediterranean regions across an area from northern Spain to Croatia (Derkarabetian et al. 2018); often from karst habitats, as reviewed by Ubick & Ozimec (2019 and references therein).

The modern diversity of Laniatores is not reflected in their current fossil record, presumably in part because of a lack of suitable fossil localities in regions where these animals are abundant today. Both molecular phylogenies (e.g. Sharma & Giribet 2011) and the fossil records of the harvestman suborders Eupnoi and Dyspnoi, both of which are known from the Carboniferous (Garwood et al. 2011), predict that Laniatores should have been present in the Palaeozoic. However, the youngest records so far are mid-Cretaceous (Selden et al. 2016). Fifteen fossil laniatorean species have been described in total and all of these are amber inclusions. Four are known from Miocene Dominican amber, one from Eocene Baltic amber and ten from mid-Cretaceous Burmese amber (Dunlop et al. 2020, Bartel et al. 2021, Bartel et al. in press and references therein). Here, we describe two new laniatorean fossils from European Baltic amber. Of the four families found in Europe today, Cladonychiidae has already been recorded (Ubick & Dunlop 2005, Bartel & Dunlop 2019), and we can now report the first Baltic amber Laniatores with a peltonychium. Thus, indicating potential affinities to the families Travuniidae or Cladonychiidae.

Material and methods

Two specimens from Eocene Baltic amber were available for study. One originates from the private collection of Jonas Damzen (Vilnius, Lithuania), the other from the private collection of Jörg Wunderlich (CJW; Hirschberg, Germany). The specimen from Jonas Damzen is now deposited in the Museum für Naturkunde, Berlin (repository number 4453) under the acronym MB.A. for Museum Berlin, Arthropoda.

Both inclusions were photographed using a Zeiss Axioscope 5 and a Zeiss Discovery V8. Stacks of 20–60 images were made at different focal planes and subsequently combined using Helicon Focus 7. Final corrections regarding brightness and contrast were made in Adobe Photoshop 2022. Interpretative pencil drawings were created using a

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Leica M205C stereomicroscope with a camera lucida attachment. Last, but not least, these were digitally redrawn following Coleman (2003, 2018) in Adobe Illustrator 2022 using a Wacom Intuos graphic tablet. The dorsal body of specimen MB.A.4453 (Fig. 1a) was photographed by Jonas Damzen and his original image is used with his permission. Since the drawings are not based on the photographs, there are some differences in orientation.

All measurements are given in mm and may be slight approximations due to the three-dimensional position of the amber specimens within the amber matrix. Both fossils were compared with extant laniatoreans available in the collection of the Museum für Naturkunde, Berlin, as well as with previously described fossil species (see Introduction).

Abbreviations. cx = coxa, fe = femur, L = length, mt = metatarsus, pa = patella, ta = tarsus, ti = tibia, tr = trochanter, W = width.

Systematic palaeontology
Order Opiliones Sundevall, 1833
Suborder Laniatores Thorell, 1876

Remarks. The fossils described herein can reliably be identified as members of the suborder Laniatores, mainly based on the presence of relatively large, raptorial pedipalps and their unique claw morphology (where visible). Potential familial affinities are separately discussed below.

Superfamily Travunioidea Absolon & Kratochvíl, 1932
Family Incertae sedis

Remarks. MB.A.4453 (Fig. 1a-d) probably represents a juvenile due to its rather small size and low tarsomere count. Nevertheless, the habitus and claw morphology of this specimen are of particular interest, as these are clearly different to the previously known Baltic amber species *Proholoscotolemon nemastomoides* (Koch & Berendt, 1854). Originally placed in a gonyleptid genus, this species was later transferred to an extant phalangodid genus, *Scotolemon* Lucas, 1861 by Staręga (1976, 2002), which makes more biogeographical sense for a Holarctic fossil (Lucas 1861). It was formally redescribed, transferred to Cladonychiidae and assigned to an extinct genus by Ubick & Dunlop (2005). A juvenile assignable to this species was later documented by Bartel & Dunlop (2019), allowing some comparisons to be made across different developmental stages.

The body habitus of our new fossil is more subtrapezoidal compared to the more hourglass-shaped outline of *P. nemastomoides* (Fig. 1a-b). Additionally, the claws on legs III and IV of the new fossil are very different. In *P. nemastomoides* the claw bears two side branches on a single prong. By contrast, the new specimen bears a peltonychium with at least 3–4 side branches on each side (Fig. 1c-d). This arrangement is typical for some living members of the superfamily Travunioidea, especially in taxa that are highly troglomorphic cave obligates (see discussion in Derkarabetian et al. 2018). However, it should be noted that some Triaenonychoidea can express similar structures, for example *Picunchenops spelaeus* Maury, 1988 (Triaenonychidae) from Argentina, some *Lomanella* Pocock, 1903 (Lomanellidae) from Australia, and *Synthetonychia* For-

ster, 1954 (Synthetonychiidae) from New Zealand, although in the latter genus the structure was called a "synthetonychium" (Forster 1954, Maury 1988, Pocock 1903, Hunt & Hickman 1993). This convergence on the peltonychial form has been suggested to be a result of neotenic processes (Hunt & Hickman 1993), although formal developmental studies have not been conducted.

An additional complication is the fact that the hind claws of most Insidiatores can be highly homoplastic at all taxonomic levels, even showing variation within the same species (Derkarabetian et al. 2018). Especially in the early stages of development, claws of different Insidiatores families can appear similar. For example, Briggs (1969: figs 39-40) figured some claws of cladonychiid juveniles and among these the claws of *Erebomaster acanthina* Crosby & Bishop, 1924 which also somewhat resemble those of our fossil (Crosby & Bishop 1924). However, the latter bears an additional arolium, typical for juveniles, which is absent in the amber specimen. Claws of juveniles without an arolium were figured by, e.g., Suzuki (1975: fig. 1A-D) for the Japanese genus *Yuria* Suzuki, 1964 (incertae sedis in Travunioidea; Derkarabetian et al. 2018), while adults have a peltonychium.

Given that the Opiliones fauna present in the Baltic (and Bitterfeld) amber deposits is unequivocally northern temperate in its affinities, the new amber specimen can be confidently assigned to the either the superfamily Travunioidea or potentially Buemarinoidae (Insidiatores, Triaenonychoidea). The recently described relictual family Buemarinoidae Karaman, 2019 (Insidiatores, Triaenonychoidea) includes two species from caves in central Europe (Karaman 2019). Adult buemarinoids do not possess a peltonychium, but juveniles of one European species for which juveniles were available, *Turonychus fadriquei* Derkarabetian, Prieto & Giribet, 2021, do possess a peltonychium (Derkarabetian et al. 2021). While Buemarinoidae is a possibility based on morphology, multiple reasons suggest why Travunioidea is more likely. First, in Europe travunioids occur at much higher latitudes than buemarinoids in the present day, which are restricted to caves in more arid regions of the Mediterranean (Spain and Sardinia). This difference in geographic distribution likely held through geologic time. Relatedly, and second, buemarinoids as a family are an ancient relictual lineage, composed of four geographically restricted monotypic genera found in the eastern United States (*Fumontana* Shear, 1977), Mediterranean (*Buemarinoa* Roewer, 1956 and *Turonychus* Derkarabetian, Prieto & Giribet, 2021) and Madagascar (*Flavonuncia* Lawrence, 1959) (Lawrence 1959, Roewer 1956, Shear 1977, Derkarabetian et al. 2021).

Within Travunioidea, confidence at the family level decreases because it is possibly an immature specimen for which the most distinctive feature is a tarsal claw character. However, two families are clearly possible: Cladonychiidae, which today are widespread across the mountainous regions of central and southern Europe and Travuniidae, which are rare cave-obligate taxa currently found in the Balkan Peninsula of south-eastern Europe. Within the European Cladonychiidae, the fossil is more similar to the genus *Peltonychia* Roewer, 1935 (Roewer 1935). *Peltonychia* possesses tarsal claws in the form of a peltonychium in adults, while *Holoscotolemon* Roewer, 1915 does not (Roewer 1915). Important to note here is Roewer's drawing of a tarsal claw for a juvenile of *Peltonychia*
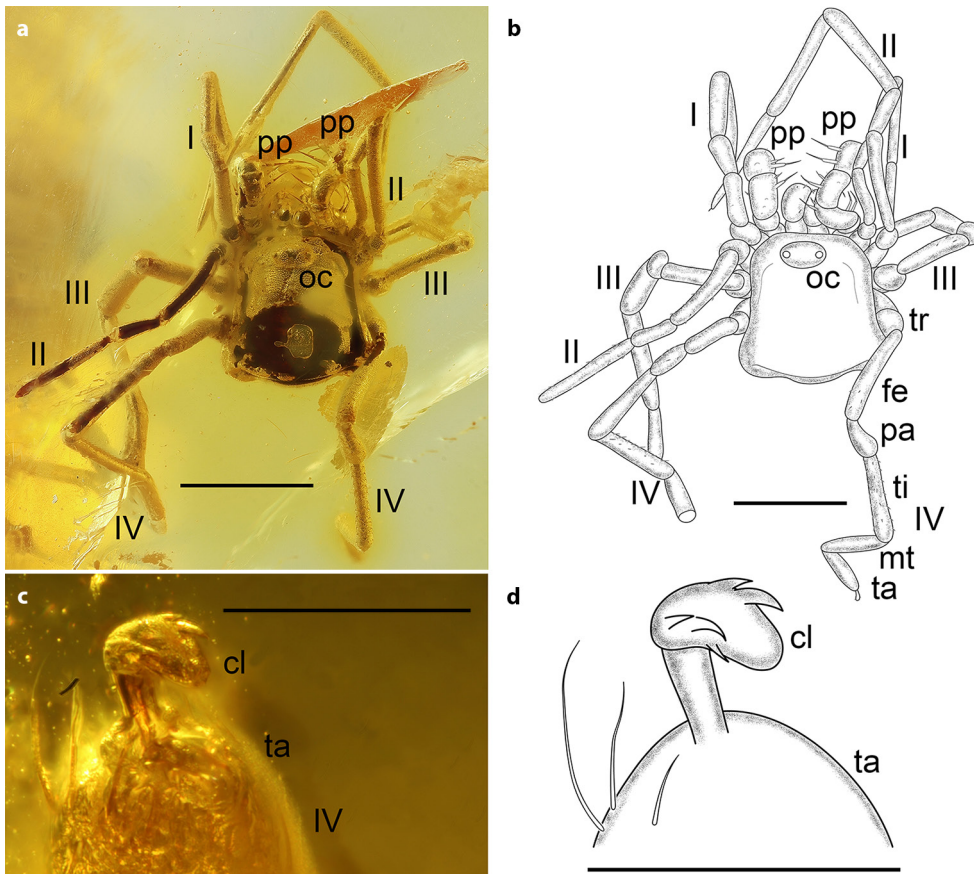
Fig. 1: *Baltonychia obscura* gen. et sp. nov., holotype: MB.A.4453. **a.** dorsal overview (photo: Jonas Damzen); **b.** camera lucida drawing of Fig. 1a; **c.** close-up of claw IV; **d.** camera lucida drawing of Fig 1c. Abbreviations: cl, claw; fe, femur; mt, metatarsus; oc, ocular tubercle; pa, patella; pp, pedipalp; ta, tarsus; ti, tibia; tr, trochanter. Legs numbered from I–IV. Scale bars = 1 mm (a, b) and 0.1 mm (c, d) (photo 1b-d: Christian Bartel)

clavigera Roewer, 1935 which clearly shows an arolium and is not in the form of a peltonychium (Roewer 1935: fig. 3). Additionally, this fossil has small tubercles on the dorsal surface of the pedipalpal femur, similar to *Peltonychia*, while *Holoscotolemon* species tend to have more developed spines (Roewer 1915). Multiple species of *Travunia* Absolon, 1920 (Travuniidae) were described as juveniles and possess a peltonychium (Absolon 1920, Kratochvíl 1937).

The new amber fossil could thus represent a lineage related, or ancestral to, the modern genus *Peltonychia*, or an ancestral surface-living Travuniidae, from a time prior to the family becoming restricted to cave habitats. Considering the homoplastic nature of the tarsal claw as a taxonomic character, the associated reluctance for modern opilionologists to rely on tarsal claw morphology, difficulty in assigning even some extant juveniles to genera, and the relative rarity of descriptions of juveniles in some taxa, assignment of this specimen to a family with confidence is difficult. As such, we leave this specimen at Travunioidea. Nevertheless, based on its unique appearance compared to *P. nemastomoides* and given its possibly ancestral status, we place this fossil in a new genus and species.

Baltonychia gen. nov.
urn:lsid:zoobank.org:act:46A5D55A-7E9C-4986-B30C-5729596B9D9B

Type species. *Baltonychia obscura* gen. et sp. nov.
Etymology. Named after a combination from Baltic amber and the peltonychium.
Diagnosis. Can be distinguished from *Proholoscotolemon nemastomoides* Koch & Berendt, 1854 by a small subtrapezoidal body, a very large and wide ocular tubercle and by the presence of a peltonychium with at least 3–4 side branches on tarsus III–IV.

Baltonychia obscura gen. et sp. nov. (Fig. 1a-d)
urn:lsid:zoobank.org:act:3BDBFE65-78FA-415F-934D-76238E3518E9

Holotype. MB.A.4453 (ex coll. Jonas Damzen, JDC11158).
Type-locality. Baltic amber. Palaeogene, Eocene (Late Lutetian–Early Priabonian).
Etymology. Named from the Latin adjective obscurus (obscure), which has probable Greek origin. It refers to its uncertain familial affinities. Gender feminine.
Diagnosis. As for the genus.
Description. Body subtrapezoidal and completely covered with fine granules dorsally, L 1.37, anterior W 1.09, maximum posterior W 1.35. Dorsal segments equivocal. Ocular tubercle very large and wide, oval and granulated, with lateral eye lenses, L 0.06, W 0.07. Ocular tubercle located near the anterior border. Chelicerae rather large and robust. Chelicerae proximal segment covered with at least three thicker setae. Chelicerae proximal segment L 0.35, chelicerae hand and fingers equivocal. Pedipalps longer than body, robust and raptorial. Pedipalp femur with two large ventral setiferous tubercles proximally, two mesal setiferous tubercles distally (a small one in front of a larger one) and one small ectal spine. Femur additionally covered with a few tubercles. Pedipalp patella with two mesal setiferous tubercles (one of medium size and a large one) and one larger ventral spine. Patella also covered with tubercles, granules and two very small spines dorsally. Pedipalp tibia with two very large mesal setiferous tubercles and 1–2 ectal setiferous tubercles. Pedipalp tarsus with two smaller setiferous tubercles

distally and 1–2 larger setiferous tubercles proximally on each side. Tarsus ends in a somewhat curved claw, L 0.14. Pedipalp length: tr 0.12, fe 0.46, pa 0.37, ti 0.30, ta 0.23, total (tr–ta) 1.48. Legs moderately long (leg II longest) and granulated. Leg tibiae I–IV with larger sometimes setiferous granules. Leg tarsi I–IV potentially subdivided, all ending in a single claw. Claw III and IV modified in form of a peltonychium with at least 3–4 side branches on each side of the median prong. Tarsal formula: 2+;2+;1–2;1–2. Leg length: Leg I cx ?, tr 0.21, fe 0.51, pa 0.37, ti 0.58, mt 0.74, ta 0.66, total (tr–ta) 3.07; Leg II cx ?, tr 0.26, fe 0.93, pa 0.42, ti 0.93, mt 1.00, ta 1.05, total (tr–ta) 4.59; Leg III cx ?, tr 0.23, fe 0.72, pa 0.28, ti 0.67, mt 0.98, ta 0.91, total (tr–ta) 3.79; Leg IV cx ?, tr 0.21, fe 0.93, pa 0.35, ti 0.81, mt 0.70, ta 0.58, total (tr–ta) 3.58. Ventral characters obscured.

Family Insidiatores indet

Remarks. CJW BBF2290 (Fig. 2a-d) could be an adult or the penultimate instar of a laniatorean, as the body is relatively large and the pedipalps seem to be well developed. The habitus of this fossil, with its strongly-armed pedipalps, is similar to modern members of the superfamily Travunioidea and to the previously known Baltic amber species *Proholoscotolemon nemastomoides*. The latter bears a comparable number of spines on the pedipalp, femur and patella, but its body appears to be more hourglass-shaped than the body of this new fossil (Bartel & Dunlop 2019). Unfortunately, most of the important characters, like the number of leg tarsomeres or the claw morphology, are not preserved in this new amber specimen and thus it is not possible to properly ascertain its affinities. Nevertheless, we suggest the possibility that this fossil could represent a new species of Baltic amber laniatorean, due to the fact that its body appears to be more compact and more

granulated. This in turn might indicate a closer relationship to modern members of the family Paranonychidae, the European cladonychiid genus *Peltonychia* or even to American genera within Cladonychiidae and Cryptomastridae. For now, we refer the fossil to Insidiatores indet. and offer a short description which can be used for comparison in future studies.
Material. CJW BBF2290 from Baltic amber. Palaeogene, Eocene (Late Lutetian–Early Priabonian).
Description. Body pear-shaped and completely granulated dorsally, L 2.07, anterior W 1.36, maximum posterior W 1.96. Dorsal segments fused into scutum magnum. Rounded and relatively low ocular tubercle removed from the anterior border with lateral eye lenses, L 0.33, W 0.36, eye lens diameter 0.06. Chelicerae moderately large and sparsely covered with tubercles on the proximal segment. Chelicerae proximal segment L 0.43. Pedipalps robust and raptorial. Pedipalp femur bearing larger tubercles and 1–2 large mesal spines distally. Pedipalp patella also bearing a large tubercle and two mesal spines. Pedipalp length: fe 0.73, pa 0.40, ti ?, ta ?. Legs incomplete, relatively long, rather slender and sparsely granulated. Claws not visible.
Ventral characters equivocal.

Discussion
Fossil laniatoreans in Baltic amber are extremely rare and only a few specimens have been formally described (Koch & Berendt 1854, Ubick & Dunlop 2005, Bartel & Dunlop 2019, this study). At the same time, they have considerable potential to reveal new insights into the evolution and biogeographical history of this otherwise predominantly tropical harvestman suborder. The infraorder Insidiatores is of particular interest as its two superfamilies, Travunioidea and Triaenonychoidea (minus the relictual Buemarinoidae), have a disjunct distribution today being found in the temperate regions of the north-
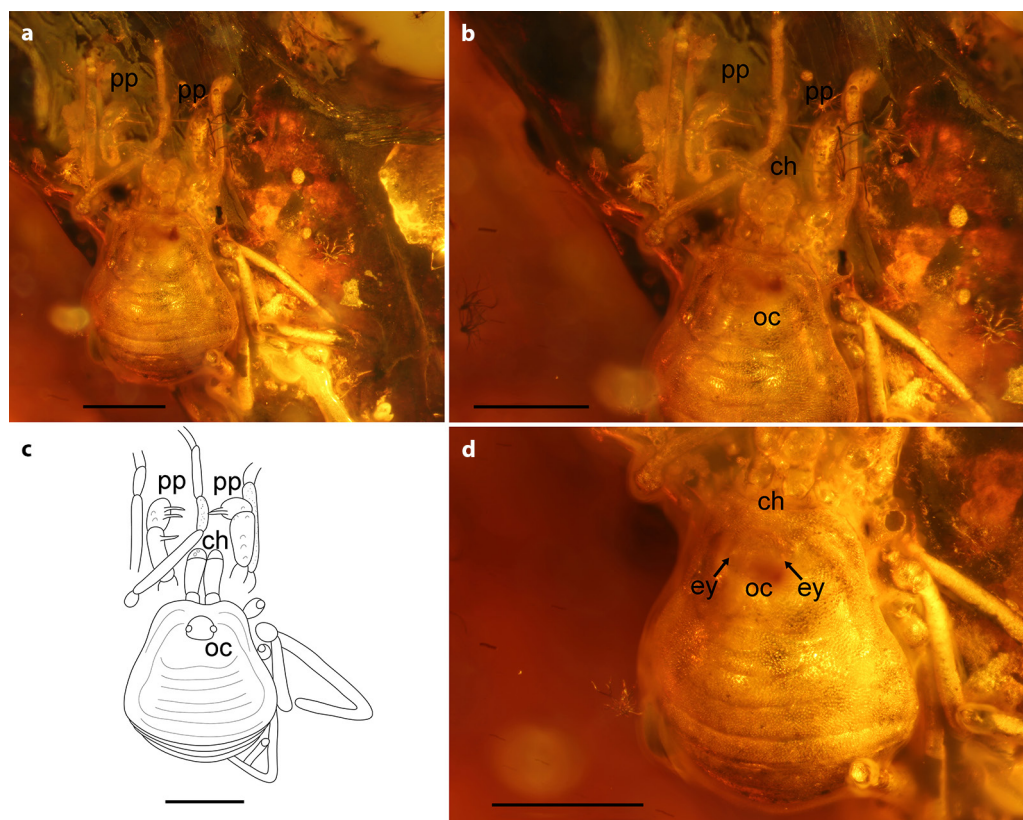

Fig. 2: Insidiatores indet., CJW BBF2290. **a.** dorsal overview; **b.** close up of the chelicerae and pedipalps in dorsal view; **c.** camera lucida drawing of Fig. 2a; **d.** Close-up of the dorsal body, eye lenses arrowed. Abbreviations: ch, chelicerae; ey, eye lens; oc, ocular tubercle; pp, pedipalp. Scale bars = 1 mm (Photo: Christian Bartel)

ern and southern hemispheres respectively (Derkarabetian et al. 2018, 2021). As noted above, all Baltic amber laniatoreans appear to be travunioids which would be expected from a biogeographical perspective and indicates that the superfamily was present in Europe by at least the Eocene.

The sparse modern Laniatores fauna of Europe adds further impetus to the importance of analysing fossil specimens. Even allowing for some tectonic shifts since the Eocene, Baltic amber was deposited further north than the distribution ranges of any modern European Laniatores. A similar situation has been observed in mite harvestmen (the suborder Cyphophthalmi) which are found in more southern parts of Europe today, but at one stage occurred further north as indicated by their presence in both Bitterfeld (Dunlop & Giribet 2003) and Baltic amber (Dunlop & Mitov 2011). Among other arachnids, Baltic amber camel spiders (Solifugae) also occurred further north than the European distribution ranges of their living relatives (Dunlop et al. 2004, Dunlop & Klann 2009) and some genera of pseudoscorpions (Pseudoscorpiones) found in European ambers are restricted today to the Mediterranean basin (Harms & Dunlop 2017).

The Eocene climate of northern Europe is also presumed to have been somewhat warmer than today, albeit not tropical, which may have allowed many groups to be more widespread in Europe at this time (Sadowski et al. 2017). Repopulation of the more northern regions of Europe can be observed in many extant arachnid taxa like e.g. the European wasp spider, *Argiope bruennichi* (Scopoli, 1772) and the venomous yellow sac spider *Cheiracanthium punctorium* Villers, 1789 (Krehenwinkel & Tautz 2013, Krehenwinkel et al. 2016). This phenomenon can also be observed in *Trichonephila sexpunctata* (Giebel, 1867), which is restricted to south-western South America (Bartoleti et al. 2017, Giebel 1867). The reasons for these range expansions are manifold. The ongoing global warming and adaptive genetic changes contribute only partially to this very complex system, as discussed in more detail by Krehenwinkel et al. (2016).

Both newly described fossils demonstrate that the Laniatores fauna of Europe during the Eocene was more diverse than the single species described by Koch & Berendt (1854). Especially, *Baltonychia obscura* gen. et sp. nov., might reveal new information about the evolutionary history of European Insidiatores, despite its enigmatic familial affinities. If the fossil represents an ancestral form of the family Travuniidae, it could indicate that early members of this family lived outside of caves and retained a well-developed ocularium. Decreasing global temperatures after the Eocene may have led to a range shift towards today's more southern distribution, while some lineages might have adapted to caves as a new, possibly refugial, habitat. In fact, Travunioidea are well represented in caves, with seven genera being entirely cave-obligate, and multiple genera including both surface and cave-adapted species or populations where cave invasion and subsequent adaptation can be a common phenomenon (e.g. Derkarabetian et al. 2010).

The assignment of fossil F2290 is less clear. However, its affinities could lie with one of the extant North American laniatorean genera based on its overall habitus; a distribution pattern which already has precedent among the harvestmen. In a wider sense, Baltic amber seems to preserve an essentially Holarctic harvestman fauna, potentially supported by the presence of putative land bridges allowing migration between

North America and Eurasia after the Cretaceous, evidence for which has been published for vertebrates and plants (see e.g. Bai et al. 2018, Graham 2018). Already known examples of harvestmen found in Baltic amber that are restricted today to East Asia and/or North America include the genera *Caddo* Banks, 1892, *Eumesosoma* Cokendolpher, 1980 and *Protolophus* Banks, 1893 (see e.g. Elsaka et al. 2019). Further fossil laniatorean specimens preserving more somatic characters would undoubtedly help to test these hypotheses and perhaps contribute towards a reconstruction of the evolutionary history of Laniatores in Europe.

References

Absolon K 1920 O mikrofotografování neprůhledných drobných předmětů. Druhé sdělení [On microphotographing of opaque small objects. 2nd part]. – Časopis moravského musea zemského, Brno 17-19 [1918-1920]: 582-601 [in Czech]

Bai B, Wang YQ & Meng J 2018 The divergence and dispersal of early perissodactyls as evidenced by early Eocene equids from Asia. – Communications Biology 1 (115): 1-10 – doi: 10.1038/s42003-018-0116-5

Banks N 1892 A new genus of Phalangiidae. – Proceedings of the Entomological Society of Washington 2(2): 249-250

Banks N 1893 The Phalanginae of the United States. – The Canadian Entomologist 25: 205-211 – doi: 10.4039/Ent25205-8

Bartel C & Dunlop JA 2019 Two laniatorid harvestmen (Opiliones: Cladonychiidae) from Eocene Baltic amber. – Arachnologische Mitteilungen 58: 9-12 – doi: 10.30963/aramit5804

Bartel C, Dunlop JA, Sharma PP, Selden PA, Ren D & Shih C 2021 Laniatorean harvestmen (Arachnida: Opilliones) from mid-Cretaceous Burmese amber. – Cretaceous Research 119: 1-15 – doi: 10.1016/j.cretres.2020.104703

Bartel C, Dunlop JA, Sharma PP, Selden PA, Tarasov PE, Ren D & Shih C in press Four new Laniatorean harvestmen (Arachnida: Opilliones) from mid-Cretaceous Burmese amber. – Palaeoworld in press – doi: 10.1016/j.palwor.2022.06.006

Briggs TS 1969 A new Holarctic family of laniatorid phalangids (Opiliones). – Pan Pacific Entomologist 45: 35-50

Coleman CO 2003 "Digital inking": How to make perfect line drawings on computers. – Organisms, Diversity & Evolution 3: 303-304 – doi: 10.1078/1439-6092-00081

Coleman CO 2018 Shadings in digital taxonomic drawings. – Zoosystematics and Evolution 94: 529-533 – doi: 10.3897/zse.94.28624

Crosby CR & Bishop SC 1924 Notes on the Opiliones of the southeastern United States with descriptions of new species. – Journal of the Elisha Mitchell Scientific Society 40 (1/2): 8-26

Derkarabetian S, Steinmann DB & Hedin M 2010 Repeated and time-correlated morphological convergence in cave-dwelling harvestmen (Opiliones, Laniatores) from montane western North America. – PLoS One 5 (e10388): 1-13 – doi: 10.1371/journal.pone.0010388

Derkarabetian S, Starrett J, Tsurusaki N, Ubick D, Castillo S & Hedin M 2018 A stable phylogenomic classification of Travunioidea (Arachnida, Opiliones, Laniatores) based on sequence capture of ultraconserved elements. – Zookeys 760: 1-36 – doi: 10.3897/zookeys.760.24937

Derkarabetian S, Baker CM, Prieto C, Hedin M & Giribet G 2021 Phylogenomic reevaluation of Triaenonychoidea (Opiliones, La-

niatores), and systematics of Triaenonychidae, including two new families. – Invertebrate Systematics 35: 133-157 – doi: 10.1071/is20047

Dunlop JA & Giribet G 2003 The first fossil cyphophthalmid (Arachnida, Opiliones) from Bitterfeld amber, Germany. – Journal of Arachnology 31: 371-378 – doi: 10.1636/h03-03

Dunlop JA & Klann AE 2009 A second camel spider (Arachnida: Solifugae) from Baltic amber. – Acta Geologica Polonica 59: 39-44

Dunlop JA & Mitov PG 2011 The first fossil cyphophthalmid harvestman from Baltic amber. – Arachnologische Mitteilungen 40: 47-54 – doi: 10.5431/aramit4006

Dunlop JA, Wunderlich J & Poinar GO jr 2004 The first fossil opilioacariform mite (Acari: Opilioacariformes) and the first Baltic amber camel spider (Solifugae). – Transactions of the Royal Society of Edinburgh: Earth Sciences 94: 261-273 – doi: 10.1017/s0263593303000178

Dunlop JA, Penney D & Jekel D 2020 A summary list of fossil spiders and their relatives. – World Spider Catalog, version 20.5. – Internet: http://wsc.nmbe.ch (18. Jul. 2022) – doi: 10.24436/2

Elsaka M, Mitov PG & Dunlop JA 2019 New fossil harvestmen (Arachnida: Opiliones) in the Hoffeins amber collection. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 292/2: 155-169 – doi: 10.1127/njgpa/2019/0815

Forster RR 1954 The New Zealand harvestmen (suborder Laniatores). – Canterbury Museum Bulletin, Christchurch 2: 1-329

Garwood RJ, Dunlop JA, Giribet G & Sutton MD 2011 Anatomically modern Carboniferous harvestmen demonstrate early cladogenesis and stasis in Opiliones. – Nature Communications 2 (444): 1-7 – doi: 10.1038/ncomms1458

Giebel CG 1867 Neue Spinne, *Nephila sexpunctata*, von Mendoza. – Zeitschrift für die Gesammten Naturwissenschaften 30: 325-326.

Graham A 2018 The role of land bridges, ancient environments, and migrations in the assembly of the North American flora. – Journal of Systematics and Evolution 56: 405-429 – doi: 10.1111/jse.12302

Harms D & Dunlop JA 2017 The fossil history of pseudoscorpions (Arachnida: Pseudoscorpiones). – Fossil Record 20: 215-238 – doi: 10.5194/fr-20-215-2017

Hunt GS & Hickman JL 1993 A revision of the genus *Lomanella* Pocock and its implications for family level classification in the Travunioidea (Arachnida: Opiliones: Triaenonychidae). – Records of the Australian Museum, Sydney 45: 81-119. – doi: 10.3853/j.0067-1975.45.1993.131

Karaman I 2019 A redescription and family placement of *Buemarinoa patrizii* Roewer, 1956 (Opiliones), Laniatores, Triaenonychidae). – Biologica Serbica 41: 67-77.

Koch CL & Berendt GC 1854 Die im Bernstein befindlichen Myriapoden, Arachniden und Apteren der Vorwelt. In: Berendt GC (ed.) Die in Bernstein befindlichen organischen Reste der Vorwelt gesammelt in Verbindung mit mehreren bearbeitetet und herausgegeben von Dr. Georg Carl Berendt zu Danzig. 1. Nicolai, Berlin. 124 pp. – doi: 10.5962/bhl.title.51864

Kratochvíl J 1937 *Lola insularis* nov. gen. nov. spec. (fam. Phalangodidae) a *Travunia* (?) *jandai* nov. spec. (fam. Travuniidae), dva noví jeskynní sekáči z jihodalmatinských ostrovů [*Lola insularis* nov. gen. nov. spec. (fam. Phalangodidae) et *Travunia* (?) *jandai* nov. spec. (fam. Travuniidae), deux opilions cavernicoles nouveaux des îles de la Dalmatie méridionale]. – Entomologické Listy [Folia Entomologica], Brno 1: 44-54 [in French]

Krehenwinkel H & Tautz D 2013 Northern range expansion of European populations of the wasp spider *Argiope bruennichi* is associated with global warming-correlated genetic admixture and population-specific temperature adaptations. – Molecular Ecology 22: 2232-2248 – doi: 10.1111/mec.12223

Krehenwinkel H, Rödder D, Naparus-Aljancic M & Kuntner M 2016 Rapid genetic and ecological differentiation during the northern range expansion of the venomous yellow sac spider *Cheiracanthium punctorium* in Europe. – Evolutionary Applications 9: 1229-1240 – doi: 10.1111/eva.12392

Kury AB 2017 Classification of Opiliones. Museu Nacional/UFRJ website. – Internet: http://www.museunacional.ufrj.br/mndi/Aracnologia/opiliones.html (14. Jul. 2022)

Kury AB, Mendes AC, Cardoso L, Kury MS, Granado AA, Giribet G, Cruz-López JA & Longhorn SJ 2021. World Catalogue of Opiliones. In: Bánki O, Roskov Y, Döring M, Ower G, Vandepitte L, Hobern D, Remsen D, Schalk P, DeWalt RE, Keping M, Miller J, Orrell T, Aalbu R, Adlard R, Adriaenssens EM, Aedo C, Aescht E, Akkari N, Alexander S, et al., Catalogue of Life Checklist (Version 2021-03-23) – doi: 10.48580/dfp3-4pt

Lawrence RF 1959 Arachnides-Opilions. – Faune de Madagascar, Publications de L'Institut de Recherche Scientifique Tananarive Tsimbazaza 9: 1-121

Lucas PH 1861 Observations sur un genre nouvelle d'Arachnide Trachéenne (*Scotolemon lespesii*) qui habite les grottes de l'Ariége. – Annales de la Société Entomologique de France 8: 973-983.

Maury EA 1988 Triaenonychidae sudamericanos V. Un nuevo genero de Opiliones cavernicolas de la Patagonia (Opiliones, Laniatores). – Mémoires de Biospéologie, Moulis 15: 117-131

Pinto-da-Rocha R, Machado G & Giribet G 2007 Harvestmen: The Biology of Opiliones. Harvard University Press, Cambridge. 597 pp. – doi: 10.4159/9780674276833

Pocock RI 1903 On some new harvest-spiders of the order Opiliones from the southern continents. – Proceedings of the Zoological Society of London 72 (II, 2, 1902): 392-413

Roewer CF 1915 106 neue Opilioniden. – Archiv für Naturgeschichte, Berlin, Abt. A, Original-Arbeiten 81 (3): 1-152

Roewer CF 1935 Opiliones. Fünfte Serie, zugleich eine Revision aller bisher bekannten Europäischen Laniatores. Biospeologica. LXII. – Archives de zoologie expérimentale et générale, Paris 78 (1): 1-96

Roewer CF 1956 Cavernicole Arachniden aus Sardinien II. – Fragmenta Entomologica, Roma 2 (9): 97-104

Sadowski EM, Schmidt AR, Seyfullah LJ & Kunzmann L 2017 Conifers of the 'Baltic amber forest' and their palaeoecological significance. – Stapfia 106: 1-73

Selden PA, Dunlop JA, Giribet G, Zhang W & Ren D 2016 The oldest armoured harvestmen (Arachnida: Opiliones: Laniatores), from Upper Cretaceous Myanmar amber. – Cretaceous Research 65: 206-212 – doi: 10.1016/j.cretres.2016.05.004

Sharma PP & Giribet G 2011 The evolutionary and biogeographic history of the armoured harvestmen – Laniatores phylogeny based on ten molecular markers, with the description of two new families of Opiliones (Arachnida). – Invertebrate Systematics 25: 106-142 – doi: 10.1071/is11002

Shear WA 1977 *Fumontana deprehendor*, n. gen., n. sp., the first triaenonychid opilionid from eastern North America (Opiliones: Laniatores: Triaenonychidae). – Journal of Arachnology 3: 177-183

Shultz JW & Pinto-da-Rocha R 2007 Morphology and Functional Anatomy. In: Pinto-da-Rocha R, Machado G & Giribet G (eds.) Harvestmen: The Biology of Opiliones. Harvard University Press, Cambridge. pp. 14-61 – doi: 10.4159/9780674276833

Suzuki S 1975 The harvestmen of Family Travuniidae from Japan (Travunoidea, Opiliones, Arachnida). – Journal of Science of Hiroshima University (Series B, Division 1) 26: 53-63

Staręga W 1976 Opiliones, Kosarze (Arachnoidea). Polska Akademia Nauk, Warszawa. 97 pp.

Staręga W 2002 Baltic amber harvestmen (Opiliones) from Polish collections. – Annales Zoologici 52: 601-604

Ubick D & Dunlop JA 2005 On the placement of the Baltic amber harvestman *Gonyleptes nemastomoides* Koch & Berendt, 1854, with notes on the phylogeny of Cladonychiidae (Opiliones, Laniatores, Travunioidea). – Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe 8: 75-82 – doi: 10.1002/mmng.200410005

Ubick D & Ozimec R 2019 A new critically endangered species of the harvestman genus *Lola* Kratochvíl, 1937 (Opiliones: Laniatores: Phalangodidae) from the Dalmatian karst, with notes on troglomorphy in European phalangodids. – Journal of Arachnology 47: 142-153 – doi: 10.1636/0161-8202-47.1.142