Two laniatorid harvestmen (Opiliones: Cladonychiidae) from Eocene Baltic amber

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Two laniatorid harvestmen (Opiliones: Cladonychiidae) from Eocene Baltic amber

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Abstract. Two new specimens of laniatorid harvestmen (Opiliones: Laniatores) from Eocene (ca. 44–49 Ma) Baltic amber are described. One is clearly adult and assignable to *Proholoscotolemon nemastomoides* (Koch & Berendt, 1854) from the family Cladonychiidae. The second, smaller, specimen is treated as cf. *Proholoscotolemon* sp., but probably represents a juvenile instar of *P. nemastomoides* and allows us to infer at least part of the ontogenetic sequence for Baltic amber laniatorids. The juvenile differs from the adult in the relative size of the body, weaker pedipalpal spination and the absence of tarsomeres subdividing the tarsi at the ends of the legs. Of particular note is the presence of unbranched claws at the tips of legs III–IV. This was unexpected given that juveniles of extant cladonychiids usually have four to six branches on these claws; a condition also thought to be plesiomorphic for this, and some related families.

Keywords: fossil, juvenile, Lutetian, Laniatores, ontogeny

Zusammenfassung. Zwei Weberknechte (Opiliones: Laniatores: Cladonychiidae) aus Baltischem Bernstein (Eozän). Zwei neue Klauenkanker (Opiliones: Laniatores) aus dem Baltischen Bernstein des Eozäns (ca. 44–49 Mio) werden beschrieben. Ein deutlich adultes Tier kann der Art *Proholoscotolemon nemastomoides* (Koch & Berendt, 1854) aus der Familie Cladonychiidae zugeordnet werden. Ein zweites, kleineres Tier wird als cf. *Proholoscotolemon* sp. eingeordnet und ist wahrscheinlich ein Jungtier von *P. nemastomoides*. Dies erlaubt uns, die Ontogenese von Laniatores aus dem Baltischen Bernstein teilweise zu dokumentieren. Das Jungtier unterscheidet sich vom erwachsenen Tier in der relativen Größe des Körpers, in der geringeren Anzahl der Pedipalpendornen und in der Abwesenheit von Tarsomeren, welche die Tarsen an den Beinenden unterteilen. Eine Besonderheit sind die unverzweigten Krallen an den Beinspitzen III-IV. Dies ist ungewöhnlich, da Jungtiere von lebenden Cladonychiiden normalerweise vier bis sechs Zähnchen an den Krallen tragen; ein Merkmal, das für diese und einige verwandte Familien als plesiomorph angesehen wurde.

Laniatores (armoured harvestmen) is the most diverse suborder of Opiliones, with over 4200 living species (Kury 2017). These sometimes large and often spiny and/or tuberculate harvestmen are very rare as fossils. Six species are currently known from the fossil record (Dunlop et al. 2019) including one species described from Burmese amber (ca. 100 Ma), one in Baltic amber (ca. 44–49 Ma) and four in Dominican Republic amber (ca. 16 Ma). Noticeable at all of these deposits so far is the lack of fossil juveniles. Most of our recent knowledge about the development of harvestmen was summarized by Gnaspini (2007), who drew on earlier studies from the 1950s and 1970s. Comprehensive information about the ontogenetic series of modern laniatorids is primarily known from a few Neotropical species (e.g. Gnaspini 1995, Townsend et al. 2009), but Juberthie (1964) provided data for the European species *Scotolemon lespesi* Lucas, 1860 from the family Phalangodidae.

Here we describe a new specimen of the previously reported Baltic amber laniatorid *Proholoscotolemon nemastomoides* (Koch & Berendt, 1854) from the family Cladonychiidae, together with a juvenile assigned here to cf. *Proholoscotolemon* sp. which could well be an immature stage of Koch & Berendt's species. Previous interpretations of *P. nemastomoides* were reviewed by Ubick & Dunlop (2005). In brief, the amber fossil was originally placed in a South American genus. The body of the holotype is largely obscured by a white film, but the pedipalps and distal parts of the legs are better preserved and allowed Ubick & Dunlop (2005) to establish a new, extinct genus, probably closely related to the European *Holoscotolemon* Roewer, 1915 (Cladonychiidae). The new juvenile fossil reveals, for the first time, data about the ontogenetic series of extinct laniatorids.

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Material and methods

The two specimens studied here originate from the private collection of Jörg Wunderlich, and bear the repository numbers CJW BBF2568 (adult) and CJW BBF2545 (juvenile). Neither required further preparation or polishing and both were immersed in water to reduce refraction and photographed using a Leica Z16 APO A stereomicroscope running the software package Leica Application Suite. Stacks of ca. 15–20 images were combined using Helicon Focus 6 and edited for brightness and contrast using Adobe Photoshop CS5. Interpretative drawings were made on a Leica M205C stereomicroscope with a camera lucida attachment, whereby some setae or tubercles were occasionally omitted to enhance visibility of important characteristics. All measurements are in millimetres. Measured lengths may show some deviations due to the three-dimensional position of the inclusions within the amber matrix and average values are marked with an asterisk (*). Fossils were compared to extant harvestmen in the collection of the Museum für Naturkunde Berlin – primarily *Holoscotolemon jaqueti* Roewer, 1915 (Cladonychiidae) and *Scotolemon terricola* Simon, 1872 (Phalangodidae) – to the type of the amber species *P. nemastomoides* (Berendt collection, Museum für Naturkunde Berlin), as well as the literature on extinct and Recent species (Koch & Berendt 1854, Ubick & Dunlop 2005, Briggs & Ubick 2007).

Baltic amber is by some margin the most intensively studied fossil resin deposit and an overview of its age, geological setting and the plant and animal groups recovered here can be found in Weitschat & Wichard (2010). The sediments hosting the amber are conventionally dated to the Lutetian stage of the Eocene (e.g. Wolfe et al. 2016) or ca. 44–49 Ma. At that time Europe consisted of several landmasses, with the Baltic amber forest perhaps belonging to a more northerly area (Dunlop et al. 2018: Fig. 1). A tropical to subtropical forest ecosystem has been inferred, dominated by an extremely warm and humid climate cumulating in the so-called Eocene Optimum at ca. 49 Ma. Several animal groups usually associated with warmer climates, of which laniatorid harvestmen are one example, are thus present in Baltic amber even though they are no longer present in north-central Europe today. Possible source trees for the resin which formed Baltic amber are araucarians, cedars or umbrella pines.

Taxonomy

Order Opiliones Sundevall, 1833
Suborder Laniatores Thorell, 1876
Family Cladonychiidae Hadži, 1935

***Proholoscotolemon nemastomoides* (Koch & Berendt, 1854)**
(Fig. 1a-c)

Material. CJW BBF2568, from Baltic amber (Eocene: Lutetian).

Description. Body pear-shaped, slightly granulated especially posteriorly; length (including free tergites) 2.27, prosoma width 1.32, opisthosoma width 1.82. Ocularium low and oval (length 0.27, width 0.41) with median eyes centrally on the prosoma. Chelicerae relatively long and robust; proximal segment length 0.59*, hand equivocal. Pedipalps raptorial with several long, thick spines. Trochanter with single ventral spine; femur with three dorsal, two mesal and four ectal spines; patella with two mesal spines; tibia with four pairs of lateral spines (from base to apex: two long, two short); tarsus with three pairs of lateral spines (from base to apex: two long, one short). Pedipalp claw shorter than tarsus and slightly curved. Pedipalp article lengths: trochanter 0.43, femur 0.91, patella 0.64, tibia 0.68, tarsus 0.64, claw 0.41; total (trochanter–tarsus) 3.48.

Legs elongate (leg II longest) and smooth. Tarsi subdivided into tarsomeres; terminating in one claw on tarsi I–II and two claws with a single insertion on tarsi III–IV (Fig. 1b: inset). Tarsal claws III–IV smooth, with relatively long base and widely separated prongs. Tarsal formula (i.e. tarsomere counts) 4:11:6:8. Leg I trochanter 0.20, femur 0.86, patella 0.45, tibia 0.95, metatarsus 0.95*, tarsus 0.82; total (trochanter–tarsus) 4.23. Leg II trochanter 0.36, femur 1.84, patella 0.50, tibia 1.50*, metatarsus 1.66, tarsus 1.86; total (trochanter–tarsus) 7.72. Leg III trochanter 0.27, femur 1.14, patella 0.54, tibia 1.00, metatarsus 1.04*, tarsus 0.82; total (trochanter–tarsus) 4.81. Leg IV trochanter 0.32, femur 1.23, patella 0.54, tibia 1.14, metatarsus 1.82, tarsus 1.14; total (trochanter–tarsus) 6.51. Ventral region equivocal; completely covered with white emulsion.

Remarks. CJW BB F2568 is evidently an adult laniatorid due to the presence of large, strongly spined pedipalps and its high tarsomere count. It closely resembles the known Baltic amber species *Proholoscotolemon nemastomoides*, redescribed by Ubick & Dunlop (2005), particularly in terms of the number and position of the pedipalp spines and the observed claw pattern: smooth tarsal claws of legs III–IV with widely separated prongs and a relatively long base (Fig 1b: inset). Our new fossil has a slightly higher tarsomere count compared to previously described material, but on other characters CJW BB F2568 can be referred with some confidence to *P. nemastomoides*.

Koch & Berendt (1854) originally assigned the Baltic amber species to the Neotropical genus *Gonyleptes* Kirby, 1819 which belongs to the infraorder Grassatores. This makes little biogeographical sense; although in fairness *Gonyleptes* was the first living laniatorid genus to be described and there were relatively few genera known in the mid-nineteenth century. The Y-shaped claw on tarsi III–IV of at least the adult fossils clearly supports their referral to the other infraorder: Insidiatores. The habitus of the amber fossils is very similar to the extant *Holoscotolemon* Roewer, 1915 and *Proholoscotolemon nemastomoides* has been proposed as the sister-group, or perhaps even ancestral, to this modern southern European genus. Regarding familial placement, Ubick & Dunlop (2005) transferred *P. nemastomoides* to Cladonychiidae. This family was subsequently downgraded to a subfamily of Travuniidae by Kury et al. (2014), but recent revision by Derkarabetian et al. (2018) accepted Cladonychiidae as a valid family group name and explicitly listed the Baltic amber genus within it. The position of the low ocularium, the long and robust chelicerae, the heavily spined pedipalps and the shape of tarsal claws III-IV in the fossils are all consistent with cladonychiids. Other families of Insidiatores often bear complex claws on tarsi III–IV

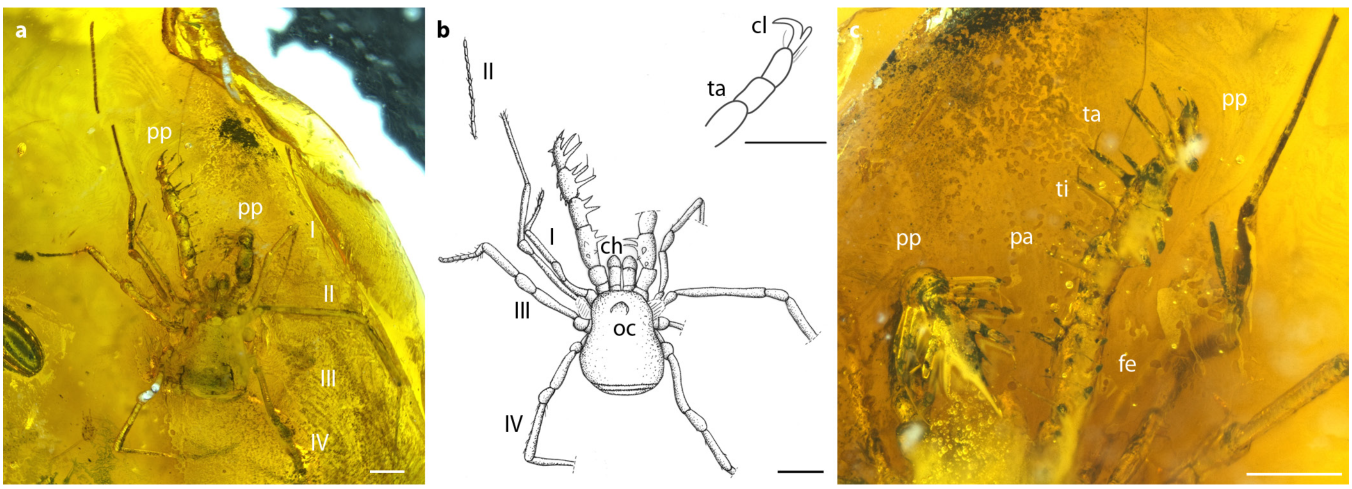

Fig. 1: *Proholoscotolemon nemastomoides* (Koch & Berendt, 1854, CJW BB F2568): **a.** dorsal overview; **b.** camera lucida drawing; (inset: detail of claws on tarsus III showing the single insertion); **c.** close-up of the pedipalps in ventral view. Abbreviations: ch – chelicerae, cl – claw, fe – femur, oc – ocularium, pa – patella, pp – pedipalp, ta – tarsus, ti – tibia. Legs numbered from I–IV. Scale bars 1 mm (inset of b: 0.2 mm)

with additional side branches (see also Discussion), whereas the amber specimen bears simpler claws without side branches (Ubick & Dunlop 2005).

***Proholoscotolemon* sp.** (Fig. 2a-d)

Material. CJW BB F2545 from Baltic amber (Eocene: Lutetian).

Description. Body slightly '8'-shaped and smooth, length 0.49, prosoma width 0.47, opisthosoma width 0.35. Separation between prosoma and opisthosoma indistinct. Ocularium slightly elevated, located near anterior border, eyes placed laterally on ocularium (length 0.053, width 0.12). Chelicerae slender, without spines; proximal segment length 0.15, projecting forward, hand length 0.20 with short fixed and movable fingers, lengths of fingers 0.10. Pedipalps raptorial, with several long spines plus few smaller setae. Trochanter smooth; femur with single mesal spine; patella with single mesal spine; tibia with single mesal spine and tarsus with three pairs of lateral spines (from base to apex: one long, two short). Pedipalp claw shorter than tarsus and curved. Pedipalp article lengths: trochanter 0.10, femur 0.19, patella 0.06, tibia 0.13, tarsus 0.25, claw 0.10; total (trochanter–tarsus) 0.73.

Legs elongate (leg II longest); setose and spiny with metatarsi bearing pair of spines distally (Fig. 2a). Tarsi not subdivided into tarsomeres; one claw on tarsi I–II, two claws with single insertion on tarsi III–IV. Leg length: Leg I trochanter 0.09, femur 0.30, patella 0.10, tibia 0.24, metatarsus 0.26*, tarsus 0.35*; total (trochanter–tarsus) 1.34. Leg II trochanter 0.12, femur 0.53, patella 0.17, tibia 0.47, metatarsus 0.46, tarsus 0.70; total (trochanter–tarsus) 2.45. Leg III trochanter 0.12, femur 0.30, patella 0.16, tibia 0.26, metatarsus 0.32, tarsus 0.33; total (trochanter–tarsus) 1.49. Leg IV trochanter 0.12, femur 0.47, patella 0.17, tibia 0.35, metatarsus 0.53, tarsus 0.40; total (trochanter–tarsus) 2.04. Ventral region equivocal, partially obscured by detritus.

Remarks. With a body length of less than half a millimetre, CJW BB F2545 is noticeably smaller than the previously described Baltic amber laniatorids with body lengths of ca. 2–3 mm (Ubick & Dunlop 2005, see also above) and is evidently a juvenile due to the absence of any subdivision of the leg tarsi into tarsomeres. The position of the ocularium, the already large pedipalps bearing spines and the form of the chelicerae are consistent with it being a cladonychiid, and we strongly suspect that it could be a juvenile instar of *Proholoscotolemon nemastomoides*. Since we lack a full ontogenetic sequence for this species, and cannot rule out the possibility that more than one species of laniatorid was present in the Baltic amber forest, we place this second fossil as cf. *Proholoscotolemon* sp.

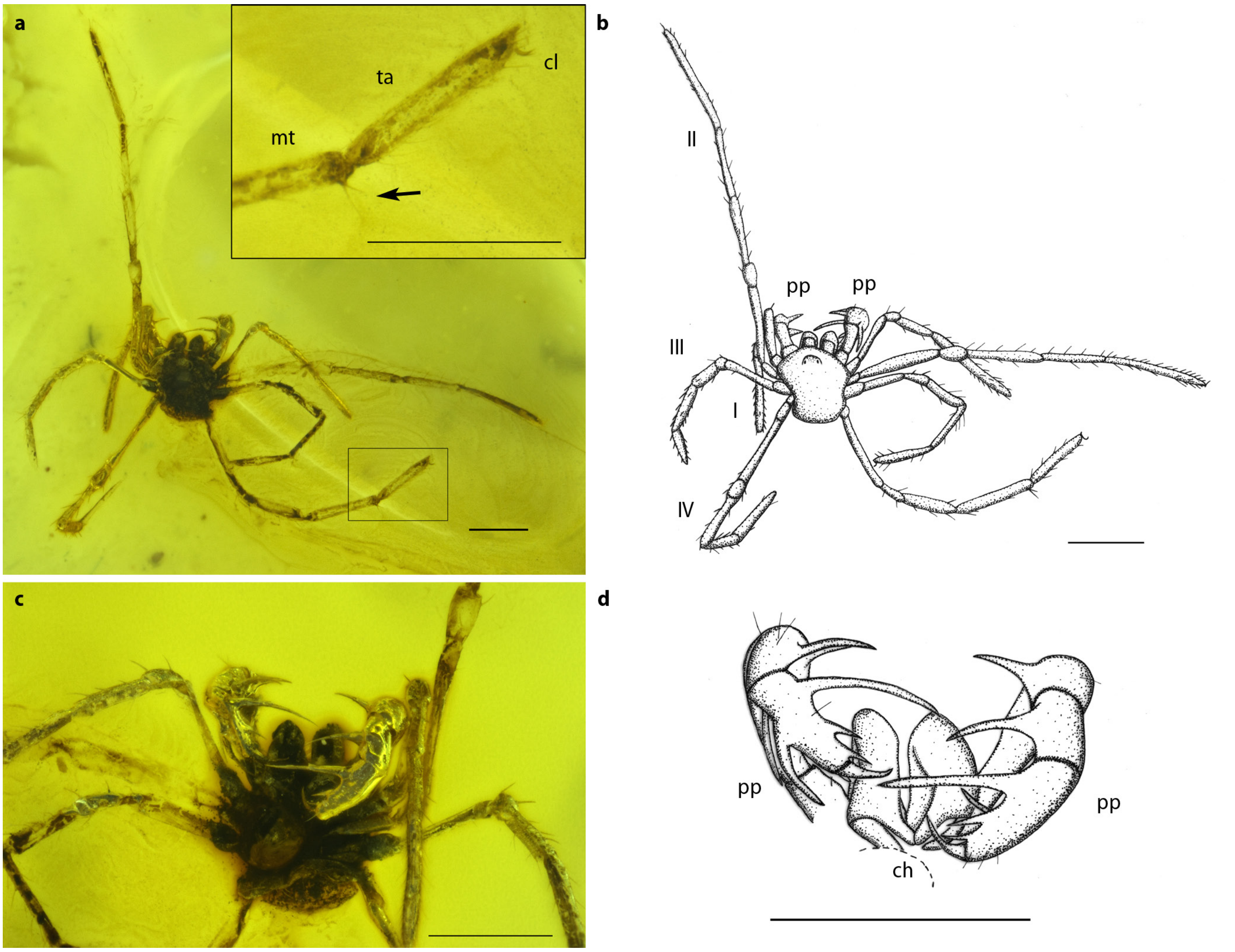

Fig. 2: cf. *Proholoscotolemon* sp. (CJW BB F2545): **a.** dorsal view; **b.** camera lucida drawing; **c.** close-up of the chelicerae and pedipalps in ventral view; **d.** camera lucida drawing of the chelicerae and pedipalps. Abbreviations: ch – chelicerae, cl – claw, mt – metatarsus, oc – ocularium, pp – pedipalp, ta – tarsus. Legs numbered from I–IV. Scale bars 0.5 mm

Discussion

Postembryonic development has been documented for only a few modern harvestman (reviewed by Gnaspini 2007), with a proposed sequence of egg, larvae, up to eight nymphs (the last called the subadult), plus an adult. In living laniatorids the main ontogenetic changes are an increase in the armature of the pedipalps and increasing numbers of tarsomeres (e.g. Gnaspini 2007, Townsend et al. 2009). These trends are reflected in the juvenile fossil described here. Its body is rather small and rounded in relation to the legs, and there are no signs of free tergites at the back of the opisthosoma as would be expected in the eventual *scutum magnum* condition. The position and form of the ocularium and chelicerae in the juvenile fossil are almost identical to that in the adult amber laniatorids. The juvenile already has spiny pedipalps, but the exact number of spines differs on each limb article compared to the adult. The juvenile bears one to eight spines less per article of the pedipalp, except on the tarsus where the number of spines is similar to the adult condition. The tarsus is undivided which together with the weak pedipalp spination and the fact that the body length is less than a quarter of the probable adult length may hint that this is an earlier juvenile stage as opposed to a late stage or subadult. We are not aware of any detailed comparative studies covering all immature life stages within Cladonychiidae, but an illustration of the pedipalp (with almost no spination) in a juvenile European harvestman *Scotolemon lespesi* Lucas, 1860 from the Grassatores family Phalangodidae by Juberthie (1964: fig. 27) suggests that the amber fossil may be at a later stage rather than a recently hatched juvenile.

Of particular interest is the condition of the legs and their claws. The juvenile described here (CJW BB F2545) shows strong leg spination, with a regular spine pattern on all metatarsi. By contrast, the putative adult bears mostly smooth legs with only small, sparse setae on the tarsi. We are not aware of reports of legs being spinier in juvenile laniatorids as compared to adults. Another unexpected detail relates to the tarsal claws. The smooth, unbranched claws of legs III–IV of the juvenile in amber are somewhat similar to the adult condition, although it should be stressed that the claws in the adult are essentially branched and Y-shaped. By contrast, modern juveniles of cladonychiids (and some other insidiatorid families) usually bear complex claws on legs III–IV with four to six side branches (Ubick & Dunlop 2005, Briggs & Ubick 2007): the family name Cladonychiidae literally means "branched claw". The presence of these side-branches, retained in at least the juvenile stages of Insidiatores, has been used to infer that this is a plesiomorphic condition for these harvestmen. An immature Eocene cladonychiid which does not have side branches on its claws may draw this hypothesis into question.

Alternatively, if it is the juvenile of *Proholoscotolemon nemastomoides* it may be possible to define the fossil genus on having the unusual character of unbranched claws on legs III and IV throughout its life cycle. We should also entertain the possibility that the paired claws in the amber juvenile are fused at the base – in which case they could be considered branched – or that if the claws are separate at the base then the fossil may instead belong to Grassatores. The available resolution of the fossil does not allow us to investigate this further. It would also be useful to have comparative studies into claw ontogeny in the probably closely-related modern genus *Holoscotolemon*, but this data is not currently available in the literature.

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