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A case of pedipalpal regeneration in a fossil harvestman (Arachnida: Opiliones)

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Abstract. The first pedipalpal regeneration observed in a fossil harvestman (Arachnida: Opiliones) is documented in a specimen of *Dicranopalpus ramiger* (Koch & Berendt, 1854) from Eocene Baltic amber (ca. 44–49 Ma). The tibia of the right pedipalp is strongly truncated and shorter than the adjacent patella and its apophysis. Possible reasons for this aberration are discussed. It most likely represents an example of partial tibial regeneration after a traumatic event, while experimental manipulation of the pedipalps of extant phalangiid harvestmen suggests that the observed morphology in the amber fossil is unlikely to be due to autospasy.

Keywords: abnormalities, Baltic amber, *Dicranopalpus*, pedipalps, Phalangiidae, regeneration, teratology

Zusammenfassung. Ein Fall von Pedipalpen-Regeneration bei einem fossilen Weberknecht (Arachnida: Opiliones). Die erste Pedipalpen-Regeneration eines fossilen Weberknechtes (Arachnida: Opiliones) wird anhand von *Dicranopalpus ramiger* (Koch & Berendt, 1854) aus dem Baltischen Bernstein des Eozäns (ca. 44–49 Mio. J.) untersucht. Die Tibia des rechten Pedipalpus ist stark verkürzt und kürzer als die benachbarte Patella mit ihrer Apophyse. Mögliche Gründe für diese Aberration werden diskutiert. Es könnte ein Fall einer teilweisen Regeneration der Tibia nach einer Verletzung sein. Demhingegen deuten Versuche einer experimentellen Manipulation der Pedipalpen heute lebender Phalangiiden darauf hin, dass die beobachtete Morphologie des Bernsteinfossils nicht durch äußere Kraftwirkung hervorgerufen werden kann.

Teratologies are developmental abnormalities, often manifesting as unusual morphologies. These malformations are rare among living organisms and can occasionally be picked up in the fossil record too. Examples among arthropods largely relate to the extinct trilobites (e.g. Owen 1985, Babcock 1993, Fatka et al. 2009, Zamora et al. 2011) and fossils of horseshoe crabs (Bicknell et al. 2018), for which a wealth of material is available yielding these infrequent anomalies. Teratologies have also been mentioned from fossil termites (Engel & Declòs 2010) and dipterans (Tschirnhaus & Hoffeins 2009) preserved in amber. We should note here that teratological changes must be differentiated from injuries or disease-related abnormalities acquired during the animal's lifetime, or the healing processes from such events.

Since individual abnormalities should not be used as taxonomic characters in both living or fossil species, it is important to document such cases and thus avoid false conclusions. The arachnid fossil record is not as rich (both in species and specimens) compared to trilobites or insects. The same is also valid for cases of abnormalities found among fossil arachnids. To our knowledge, malformations among extinct arachnids have only been reported for a handful of amber spiders (e.g. Wunderlich 2004, 2015, Penney 2005), including legs being lost through appendectomy, evidence of limb regeneration through truncated appendages and/or appendage stumps, and abnormalities (outgrowths, thickenings) affecting the legs or pedipalps. Here, we document a first case of an aberrant pedipalp observed in a fossil harvestman, *Dicranopalpus ramiger* (Koch & Berendt, 1854), found in Eocene Baltic amber (ca. 44–49 Ma old).

Material and methods

The specimen under study stems from the private collection of Christel and Hans-Werner Hoffeins (Hamburg, Germany, repository number 118/2). Elsaka et al. (2019: 161) briefly mentioned the fossil and noted its unusual pedipalps, but did not provide any formal description or illustration. The owners plan to deposit their collection of amber harvestmen in the Senckenberg Naturmuseum, Frankfurt am Main (C. Hoffeins pers. comm. 2016). An exact provenance for the material is not available, but many of the Baltic amber inclusions collected in recent years originate from the Kaliningrad region of the Russian Baltic. The Baltic amber forest is thought to have been a warm habitat and is conventionally dated to an Eocene (Lutetian) age of about 44–49 Ma. The harvestman specimen was studied and photographed under a Leica Z16 APO A stereomicroscope and compared to available descriptions of the fossil species (Dunlop 2006, Dunlop & Mitov 2009, and literature therein). Stacks of 20–30 images were created using the software package Leica application suite. These were combined with Helicon Focus 6 and edited for brightness and contrast using Adobe Photoshop CS5 to ensure that all parts of the specimen are visible. The computer-aided illustration was created from the image following the methods of Coleman (2003) with Adobe Illustrator CS2 using a Wacom Intuos graphic tablet.

We also investigated whether extant representatives of Phalangiidae Latreille, 1802 can undergo pedipalpal autospasy, i.e. separation of the appendages at a predetermined weak point through an externally applied force under a perceived imminent threat. For terminology on different types of appendectomy in harvestmen and other arthropods we follow Bliss (1960), Roth & Roth (1984) and Maruzzo et al. (2005). We experimented with 30 specimens of three species of long-legged phalangiids: three males and three females of *Opilio parietinus* (De Geer, 1778), six males and nine females of *Opilio ruzickai* (Šilhavý, 1938), and four males and five females of *Lacinius dentiger* (C. L. Koch, 1847). All were collected from the area of Sofia City and from the West Rhodopa Mountains (6.–23. Oct. 2019, leg. & det. P. Mitov). Potential pedipalpal loss was induced by clamping the tibia of one of the pedipalps with tweezers, leaving the harvestmen hanging

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this way for five minutes, occasionally gently shaking the animal. In addition, after all the legs had been immobilized, one pedipalp was carefully pulled with tweezers for about a minute while the corresponding joint was observed under a binocular stereomicroscope to control the applied force.

Results

Description of the fossil. The fossil harvestman (Fig. 1a), body length ca. 1.64 mm, is preserved as a complete inclusion in a tear-drop shaped piece of amber with dimensions of 39 × 16 × 5 mm. The left pedipalp is normally developed (Fig. 1a) and confirms its identity as *Dicranopalpus ramiger*. This species has been previously recorded from Baltic (Dunlop 2006), Bitterfeld (Dunlop & Mitov 2009) and Rovno amber (Perkovsky et al. 2010), and like modern representatives of the genus (e.g. Wijnhoven 2013) it bears a large, setose apophysis on the mesal side of the pedipalp patella which gives the pedipalps a characteristically bifurcate appearance (Fig. 1a). The most unusual feature of specimen 118/2 is the right pedipalp (Fig. 1b-c). The femur and patella appear normal, and the patella bears the apophysis (length: 0.4 mm). However, the tibia is abnormally truncated to a small (length: 0.3 mm) stub (Fig. 1b: arrow) which is shorter than both the patella and its apophysis and is closed and neatly rounded at the tip.

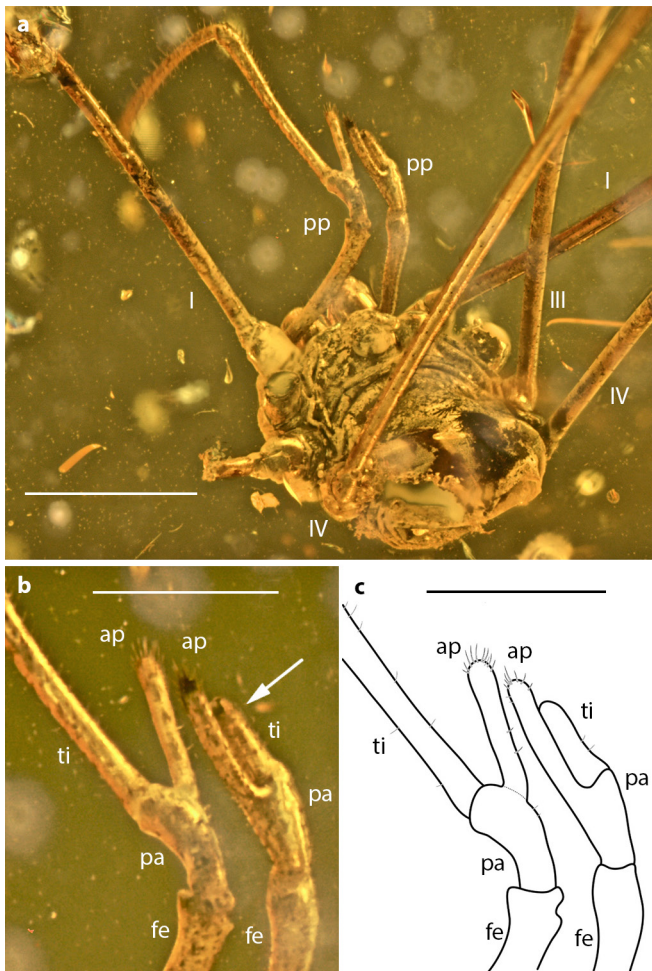


Fig. 1: *Dicranopalpus ramiger* (Koch & Berendt, 1854), Hoffeins collection No. 118/2. **a.** dorsal overview; **b.** close-up of the pedipalps in dorsal view (truncated tibia of the right pedipalps indicated by an arrow); **c.** interpretative drawing of the pedipalps. Abbreviations: ap – patellar apophysis, fe – femur, pa – patella, pp – pedipalps, ti – tibia. Legs numbered. Scale bars: 1 mm (a), 0.5 mm (b-c)

In detail, the stunted (aberrant) tibia has a decreasing diameter towards the tip, usual colour, very sparse chaetotaxy, and is almost four times shorter than the tibia of the normal (left) pedipalp (length: 1.08 mm). The tarsus of the right pedipalp, and its tarsal claw, is thus missing completely. In this case the tibial stump is a terminal article, and its tip is covered only by smooth chitin (apically); a pseudonormal terminal-tibial chaetotaxy is absent, as well as the auxiliary/secondary claw, see for example, notes on post-traumatic leg repair in Novak et al. (2006) and Townsend et al. (2016).

Manipulations. In the experimental manipulations testing whether extant phalangiid harvestmen exhibit a defensive autospasy response in their pedipalps, no pedipalpal loss was observed at all.

Discussion

In a wider context, teratological data on extant harvestmen was reviewed by Juberthie (1963a) and Mitov (1995b), and references therein. Mitov (1995b) recognised three groups of anomalies: (1) those relating to the appendages, (2) to the opisthosomal segmentation, or (3) to the macrosculpture. The new aberrant amber specimen falls into the first category. We are not aware of published records of pedipalp abnormalities in extant *Dicranopalpus* Doleschall, 1852, thus the fossil studied here may represent the first example of this abnormality in this genus.

It is noteworthy that harvestmen featuring abnormal pedipalps occur very rarely in collections of modern material (Mitov 1995b, P. G. Mitov (PGM) pers. obs.). For example, Mitov (1995b) observed truncated pedipalps with reduced segmental composition in living specimens of *Rilaena balcanica* Šilhavý, 1965 (1296 examined specimens) and *Mitopus morio* (Fabricius, 1779) (4193 examined specimens). In each species the abnormality was observed only twice, which represented 0.15% and ca. 0.05% of the number of sampled individuals respectively. Of the total 36413 examined opilionid specimens belonging to numerous species only the four noted above were found to have aberrant pedipalps (Mitov 2000), indicating that this particular aberration is extraordinary rare – occurring in only 1 in about 10000 (or ca. 0.01%) of the sampled individuals.

Examples in the literature of aberrant pedipalps in living harvestmen usually refer to underdeveloped or reduced numbers of segments, although in such cases the tarsus is often present and usually ends in a claw (Suzuki 1958: figs 1-2, Mitov 1995b: fig. 1, PGM pers. obs.). In these cases, when there are reduced segments with developed chaetotaxy and a claw on the corresponding distal segment of the pedipalps, it is very difficult to assess whether these aberrations are caused by an abnormal regeneration after injury, by a healing process after amputation of segments, or are teratologies/malformations as a result of genetic factors, or aberrations acquired during embryonic development. The latter can be induced by various teratogenic factors such as environmental temperature; see e.g. Juberthie (1960, 1961, 1962, 1963a, 1963b, 1964, 1968) as recorded in harvestmen or Napiórkowska & Templin (2018, and references therein) as observed in spiders.

In the fossil described here the missing original claw and the lack of dense and fine chaetotaxy, characteristic of the tarsus (cf. Wolff et al. 2016: fig. 2) suggests that the truncated segment is indeed the tibia (Fig. 1b-c) and not the tarsus. The

presumption here is that the right tibia in the fossil has undergone partial regeneration. Support for this hypothesis is the presence of a distal rounded tip on the terminal tibial trunk with a smooth (newly regenerated) cuticle growth over the distal tip on the terminal stump including the relatively sparse chaetotaxy. These formations, according to Novak et al. (2006) and Townsend et al. (2016), are typical for completely healed wounds and represent the first stage in the cuticular regeneration. In our case, all these features are well recognisable.

Disarticulated limbs are quite common among arachnids preserved in amber, presumably a result of the animal trying to escape the sticky resin. However, harvestmen legs usually separate near the base (Gnaspini & Hara 2007), where at the trochanter–femur junction or near the base of the femur (Roth & Roth 1984). There is often a predetermined zone which allows the animal to detach a trapped or injured limb. We are confident that the observed morphology here is not an appendage which has been freshly broken off distally. A fresh injury is likely to appear sharp-edged (compare with Novak et al. 2006, Townsend et al. 2016) and not rounded as in our case (Fig. 1c), or leaking haemolymph as observed by Penney (2005) in an amber spider with separated limbs. A more likely explanation is post-traumatic repair with clearly developed features that are visible in our specimen (see Novak et al. 2006, Townsend et al. 2016, and comments above).

The original injury may have been caused by a mechanical traumatic event, such as pressure, trampling, falling stones/dead tree branches or a predator attack (probably a bite). Even since the Eocene the typical predators of harvestmen were probably mainly spiders, ants and various vertebrates (frogs, toads, lizards, small insectivorous mammals). Extant predators of harvestmen (Mitov 1995a, Cokendolpher & Mitov 2007, Cook et al. 2013, Klenovšek et al. 2013, Townsend et al. 2016, and references therein) attack harvestmen on the soil and among the leaf-litter, and may also hunt them through the vegetation (e.g. on trees).

Our fossil specimen is so small (with body length less than 2 mm and length of normal pedipalpal tibia approx. 1 mm) that it could easily be ingested by a vertebrate predator. Lizards and amphibians devour whole harvestmen, while insectivores (such as modern shrews) chew them into small pieces (Mitov 1995a, PGM pers. obs. on the stomach contents of various recent vertebrate predators). Our *Dicranopalpus ramiger* fossil could have been attacked by a small invertebrate such as an ant which would have been easily able to cut off a pedipalp with their mandibles (see comments in Mitov 1995a: 71, and Townsend et al. 2016: 10). Another possibility would be injury from a fight against a rival; see e.g. comments on mating behaviour in Edgar (1990: 531).

The present anomaly is unlikely to be due to autospasy, because all known cases of detachment have been observed on harvestman legs, and not their pedipalps (Miller 1977, Roth & Roth 1984, Gnaspini & Hara 2007, Shultz & Pinto-da-Rocha 2007). The experimental manipulation of the pedipalps of extant phalangiid harvestmen (see above) also suggests that the observed morphology in the amber fossil is unlikely to be due to autospasy. For these reasons, we feel it is safe to conclude that at least in this family of Opiliones pedipalpal autospasy is not a typical escape mechanism and is thus unlikely to be responsible for the truncated pedipalp in the fossil. The pedipalps of harvestmen are usually significantly shorter

than the legs, folded close to the front of the body, and are therefore less likely to be grabbed by predators than the much longer legs (especially in phalangiids). The pedipalps are also multifunctional appendages, i.e. they facilitate locomotion, take part in sensorial reactions, prey capture, feeding, courtship and mating behaviour, and in male–male fights (Wolff et al. 2016). Because of this functionality it may be the case that no mechanism has evolved to facilitate pedipalp loss through autospasy.

The smaller diameter of the tibial stump, as compared to the normal tibia (Fig. 1b–c), is consistent with the hypothesis that the observed morphology could be the result of tibial partial regeneration after a traumatic event (i.e. the regenerated surface of the cuticle) occurring at an early developmental stage. This is comparable to the distinctive underdevelopment of the coxae and trochanters which is frequently observed in extant harvestmen with severed legs (Stipberger 1928: 50, Sato & Suzuki 1939: figs 3–4, Gnaspini & Hara 2007, PGM pers. obs.).

In troglidid (suborder Dyspnoi) and cosmetid harvestmen (suborder Laniatores) damaged legs can regenerate to form a rounded stump (Novak et al. 2006, Townsend et al. 2016: figs 8, 10), which is similar to the condition observed in the fossil specimen (see Results). This ability to regenerate limb stumps has only been documented so far in representatives of the above-mentioned families, although it should be cautioned that this phenomenon has not been studied across all harvestmen. At the same time these groups (i.e. troglidids and cosmetids) are also known to be unable to cast off injured legs (Pabst 1953: 44, Townsend et al. 2016: 11). *Dicranopalpus ramiger* belongs to Phalangiidae (suborder Eupnoi). Phalangiid harvestmen are not known to be able to regenerate lost or damaged legs in their entirety, even during subsequent moults (Henking 1888, Stipberger 1928, Savory 1936, 1938, Juberthie 1963a, Roth & Roth 1984, Townsend et al. 2016). The same applies also to the pedipalps of the harvestmen as was experimentally proven by Savory (1936, 1938: 3), who concluded that the pedipalps were not restored when lost.

Dicranopalpus ramiger is one of the most commonly encountered harvestman species in northern European amber. For example, nearly 25% of the harvestman inclusions in the Hoffeins' collection could be assigned to *D. ramiger* (Elsaka et al. 2019, Tab. 1), while in the rich Wunderlich collection (which we are also currently studying) about 15–20% of the specimens are *D. ramiger*. Perkovsky et al. (2010: 126) also remarked that “Thirteen out of 23 (57%) Rovno amber harvestmen (Fig. 6, 9) belong to the species *Dicranopalpus ramiger* (Koch & Berendt) (Phalangiidae), which is not so common in Baltic amber.” This can most likely be explained by the fact that similar to the extant *D. ramosus* (Simon, 1909) which is known to be arboricolous (Noordijk et al. 2007), *D. ramiger* probably also spent a lot of time on trees, in which case it would not be surprising to find it more frequently trapped in resin.

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