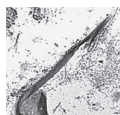


A new Devonian harvestman from the Rhynie chert (Arachnida: Opiliones)

ERIK TIHELKA, LI TIAN & CHENYANG CAI



With over 6,600 described species, harvestmen represent a morphologically and ecologically diverse group of arachnids with a cosmopolitan distribution. Although members of the order Opiliones are believed to have been among some of the earliest terrestrial arthropods, the Palaeozoic fossil record of harvestmen is sparse. Herein, a new harvestman, *Devonopilio hutchinsoni* gen. et sp. nov., is described based on a penis preserved in Lower Devonian Rhynie chert from Aberdeenshire, Scotland (Pragian, ca. 407 Ma). Together with *Eophalangium sheari*, another Early Devonian harvestman known from the Rhynie chert, the new species represents the earliest member of the order Opiliones in the fossil record and one of the oldest terrestrial animals. The new species differs significantly from *E. sheari* in penis morphology, indicating that harvestmen began to diversify before the Early Devonian. • Key words: harvestmen, Opiliones, new species, genitalia, mating system, Palaeozoic, palaeoecology.

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Harvestmen represent an ancient and morphologically diverse lineage of arachnids and probably belonged among the first terrestrial animals (Garwood & Edgecombe 2011, Dunlop *et al.* 2013). Over 6,600 living species have been described to date from across the world, highlighting their status as one of the most successful arachnid orders (Kury 2017). Opiliones exhibit a wide diversity of body plans but most species, at least in the northern hemisphere, can be recognised by a rounded body with a fused prosoma and opisthosoma, and very long legs that gave these charismatic arachnids their name in many of the world's languages (Shultz & Pinto-da-Rocha 2007). Unlike other arachnids, harvestmen produce a repugnatorial substance from their prosomatic glands, lack book lungs, have tracheae opening on the genital area, feed by ingesting their food whole without the use of pre-oral digestion, and most taxa transfer spermatozoa through an eversible penis that can be extended by specialised protractor muscles or haemolymph pressure (Fig. 1). They are an important component of virtually all terrestrial biomes inhabiting spaces under rocks and in bark, dense vegetation, soil, leaf litter, and even subterrestrial habitats such as caves. Most species are generalist predators and scavengers feeding on other arthropods, vertebrate carcasses, fungi, and fruit

(Shultz & Pinto-da-Rocha 2007, Macías-Ordóñez *et al.* 2010, Dunlop & Penney 2012).

The fossil record of Opiliones is very sparse with only a handful of extinct species known since the Palaeozoic (Dunlop & Penney 2012). The exceptional rarity of harvestmen fossils may be in part due to their terrestrial lifestyle and delicate bodies with a poorly mineralized exoskeleton (Dunlop *et al.* 2008). Consequently, most fossil species are known from various Cenozoic amber deposits (Dunlop & Mitov 2009). Only seven Palaeozoic Opiliones have been described to date and, with the exception of one species, all originate from the Carboniferous Coal Measures (Dunlop & Penney 2012). The earliest known harvestman, *Eophalangium sheari*, was described based on remarkably well-preserved fragments of three individuals in Lower Devonian Rhynie chert (Dunlop *et al.* 2003a, b). These fossils preserve the oldest arthropod trachea which indicate that *E. sheari* lived on land. Given the strikingly modern body plan of Devonian and Carboniferous opiliones (Dunlop *et al.* 2003b, Garwood *et al.* 2011), Dunlop (2007) suggested that harvestmen may have originated in the Silurian or even earlier. Recent calibrated phylogenies placed the origin of Opiliones into the Silurian (ca 425 Ma, Fernández *et al.* 2017) or even

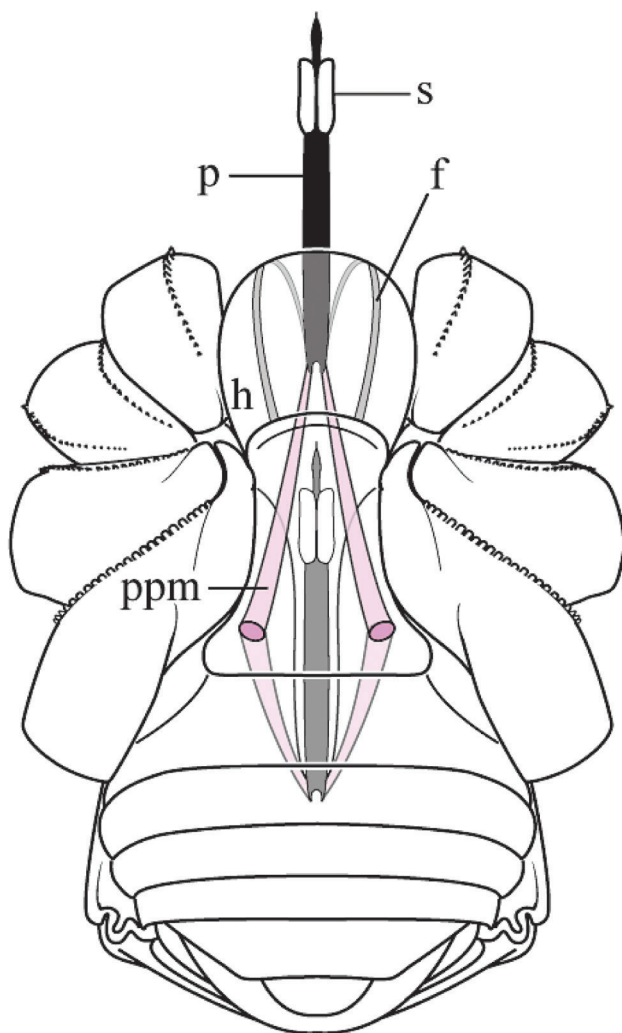


Figure 1. Schematic representation of a penis of the extant harvestman *Leiobunum verrucosum* (Sclerosomatidae) in ventral view in retracted and extended positions. Adapted from Burns & Shultz (2015). Abbreviations: f – fultura; h – hematocha; p – penis; s – nuptial gift sac; ppm – penis protractor muscle.

as far back as the Ordovician (470–420 Ma, Sharma & Giribet 2014).

Here, a new harvestman is described from Lower Devonian Rhynie chert in Aberdeenshire, Scotland. Together with *E. sheari*, the new species represents the earliest known harvestman.

Methods

The Rhynie chert Lagerstätte is an exceptional Early Devonian deposit of world-wide significance that preserves probably the oldest terrestrial ecosystem (Edwards *et al.* 2017). In addition to its age, many Rhynie chert fossils exhibit an extraordinary level of detail including soft

tissue preservation down to the cellular level, offering a unique insight into the morphology and palaeoecology of the earliest organisms to colonise land. The cherts originate from near the village of Rhynie in Aberdeenshire, Scotland and a second unit known as Windyfield chert is located within a kilometre distance (Fayers & Trewin 2003). Radiometric analyses indicate that the chert formed approximately 407 Ma (Mark *et al.* 2013), a finding consistent with palynomorph evidence (Wellman 2006). The organisms were preserved by silica-rich waters in the proximity of ancient hot springs (Rice *et al.* 2002). Trewin (1990) characterised the Rhynie palaeoenvironment surrounding the hot springs as an “alluvial plain with shallow ephemeral pools which bordered a river”. The Rhynie chert was discovered more than a hundred years ago (Mackie 1914) and since then yielded diverse bacteria, algae, fungi, plants, and animals including the earliest nematodes and mites, and the earliest fossil record of herbivory and fungal symbiosis (Edwards *et al.* 2017, Dunlop & Garwood 2017).

The type specimen is preserved on a slide-mounted thin section prepared by the palaeontological preparator Walter Hemingway in 1924 and currently deposited in the Geological Collections of the Bristol Museum and Art Gallery (BRSGM). The specimen was studied using a Bresser Advance ICD stereomicroscope and a Leica DM2000 transmitted light microscope. Drawings were prepared based on microphotographs in Inkscape. The nomenclatural acts introduced herein are registered under ZooBank publication LSID urn:lsid:zoobank.org:pub:A6E67DA8-6F1F-4C2E-8C9D-0F7E938D6677.

Systematic palaeontology

While the specimen dealt with herein is indeed fragmentary, most named Rhynie arthropods, including *Rhyniognatha*, are likewise known only from incomplete specimens, which is somewhat unavoidable given the nature of the chert. In each case, a formal taxon name is practical for separating the specimens from other clearly morphologically distinct individuals. Because the present fossil clearly differs from the previously described *E. sheari*, we choose to propose a new formal taxon name.

Order Opiliones

Family *incertae sedis*

Genus *Devonopilio* gen. nov.

LSID. – urn:lsid:zoobank.org:act:4440D43F-BCEC-4BBD-ACD1-1C0E22FB4C43

Type and only species. – *Devonopilio hutchinsoni* sp. nov.

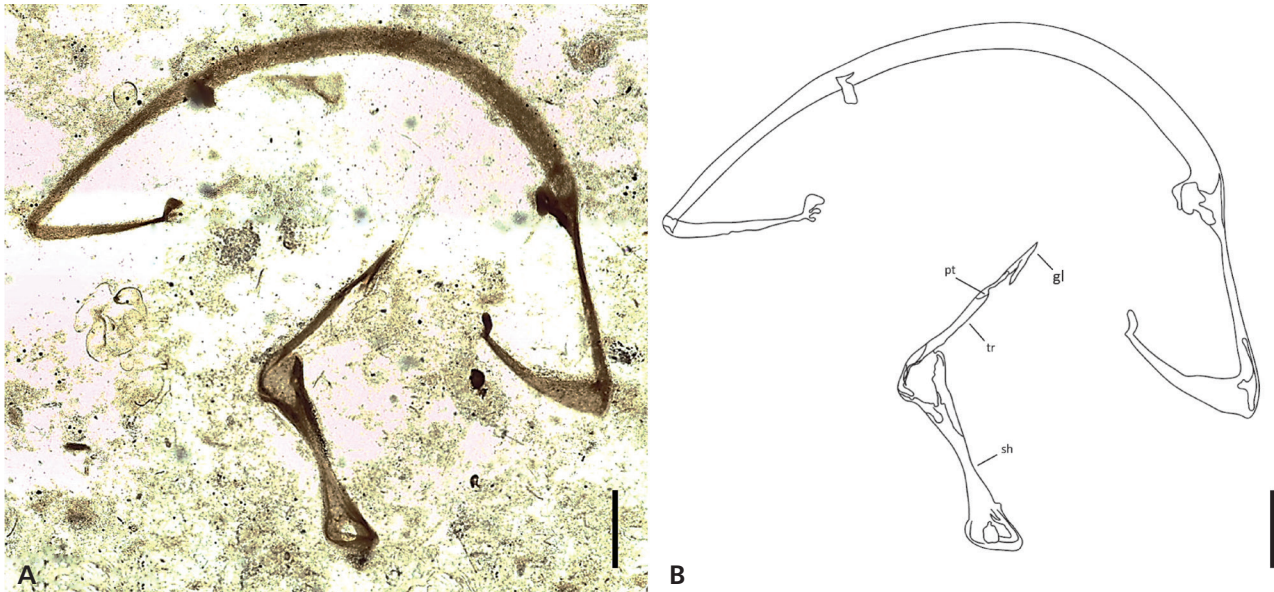


Figure 2. Holotype of *Devonopilio hutchinsoni* gen. et sp. nov. • A – penis with sheath and protractor muscle under a transmitted light microscope. • B – interpretative line drawing. Scale bar = 200 μ m. Abbreviations: gl – glans; pt – penis tendon; sh – sheath; tr – truncus.

Etymology. – Generic name derived from the age of the fossil and the Latin “*opilio*”, the root word of Opiliones. The gender is neutral.

Diagnosis. – Penis straight, with the section connecting it to sheath very thin and sclerotised. Penis truncus narrowest at base, the rest equally wide, with a single tendon located anteromedially. Penis apex with an acute lateral expansion. Penis sheath narrowest medially, slightly longer than penis.

***Devonopilio hutchinsoni* sp. nov.**

Figure 2

LSID. – urn:lsid:zoobank.org:act:9729879C-C04D-4366-BF0D-246093293EE2

Holotype. – Slide Db7365, single isolated penis with associated cuticular fragments.

Type horizon and locality. – Lower Devonian (Pragian) Rhynie chert, Rhynie Cherts Unit of the Windyfield Shales Member, Dryden Flags Formation, Aberdeenshire, Scotland.

Etymology. – The species is named in honour of Deborah Hutchinson, palaeontologist and curator of the Geological Collections of the Bristol Museum and Art Gallery.

Diagnosis. – As for the genus.

Description. – Penis sheath elongate, 0.57 mm long, 0.14 mm wide at broadest point, 1.1 times longer than penis and 5.6 times wider than penis at broadest point. Base and

apex somewhat rounded and darkened, sclerotised. Base with a small circular hole.

Penis slender, lanceolate, not curved, 0.47 mm long and 0.05 mm wide at broadest point. The basal part of the penis consists of a slender truncus (length 3.39 mm, width 0.01 mm) narrowest apically and attached medially to the sheath by a thin expansion, then equally wide. The truncus is sclerotised basally. A darkened band present anteromedially is herein interpreted as a tendon. The apical part of the penis is lanceolate, the glans narrows sharply towards the apex. The apex is darkened, most likely indicating sclerotization, similarly to modern harvestmen (Shultz 2000).

Remarks. – The species is represented by just a single penis associated with several unidentifiable fragments. The interpretation of structure sh (Fig. 2) as the penis sheath is supported by it being connected to the penis truncus. Although the penis sheath in modern harvestmen is not heavily sclerotised, the structure in the present specimen is similar in outline to the penis sheaths in some extant harvestmen (Wijnhoven 2013).

An indeterminate bundled structure is present to the left of the penis sheath. An approximately semi-circular structure is also present above the penis. It is unlikely that this structure represents muscle tissue associated with the penis as Rhynie chert only preserves cuticle-lined structures such as appendages, tendons, lungs, and trachea. It is more probable that these fragments represent the remains of the arachnid’s body wall sectioned during the preparation of the specimen or perhaps muscle insertion plaques that were involved in movement of the legs (Wijnhoven 2013).

Discussion

Systematic position of Rhynie chert harvestmen

The cylindrical elongate structure preserved on slide Db7365 and consisting of a wider basal part and a narrower apical part connected by a narrow joint is herein interpreted as an opilione penis and penis sheath. The structure of the harvestmen penis is rather unique among arthropods and no other arachnid possesses a similar reproductive organ (Bennett & Townsend 2013). The specimen clearly does not represent an opilione ovipositor, as these tend to be apically bifurcate and those in Cyphophthalmi and the majority of Eupnoi are composed of segment-like rings (Martens *et al.* 1981, Shultz & Pinto-da-Rocha 2007). The specimen likewise is not a limb as indicated by the characteristic glans and narrow joint connecting the sheath and the penis. A potentially significant feature of *D. hutchinsoni* gen. et sp. nov. is the basally very thin penis which appears to be rare in opiliones (Macías-Ordóñez *et al.* 2010). The specimen can be easily differentiated from the penis of *Eophalangium sheari*, the only other Devonian harvestmen, by the truncus slender and equally wide throughout, the presence of a single penis tendon, and apex with an acute lateral expansion, lending it a spear-like appearance.

When described, *E. sheari* was tentatively placed into the suborder Eupnoi by Dunlop *et al.* (2003). A phylogenetically significant character discernible in the *E. sheari* penis is the presence of two lateral darkened bands in the penis shaft that were interpreted as tendons, as a result of which the species was treated as a crown-Eupnoi by subsequent workers (Sharma & Giribet 2011, Giribet *et al.* 2012). A later phylogenetic study placed *E. sheari* was in a polytomy with members of Phalangida by Garwood & Dunlop (2014). Garwood *et al.* (2014) identified *E. sheari* as a stem-group cyphophthalmid and placed it into the extinct suborder Tetrophthalmi.

The penis of *D. hutchinsoni* gen. et sp. nov. is clearly divided into a truncus and a glans. This suggests that it could not have belonged to a member of Cyphophthalmi as these harvestmen have an undivided spermatopositor (Giribet *et al.* 2002). The penis also has a darkened anteromedial portion which likely represents a tendon. This would further exclude Troguloidea, which have a penis with two muscles; Laniatores, Gonyleptoidea and Oncopodoidea have a hydraulic-operated glans and completely lack male genital musculature. A single penis tendon is present in the extant superfamilies Ischyropsalidoidea, Phalangioidea, and Travunioidea (Giribet *et al.* 2002, Dunlop *et al.* 2003b). The precise affinity of *D. hutchinsoni* gen. et sp. nov. with any of these taxa cannot be affirmed until other more informative body remains are discovered in the future. As such, *D. hutchinsoni* gen. et sp. nov. is provisionally treated

as Opiliones *incertae sedis*. However, the penis morphology suggests that *D. hutchinsoni* gen. et sp. nov. and *E. sheari* were not closely related and would be placed into two different superfamilies if they were treated as extant taxa. As such, the erection of a new genus for the present fossil is clearly justified. The wide disparity in penis morphologies in the only two known Early Devonian harvestmen suggests that the order began to diversify well before this time.

Palaeoecology

The Chelicerata probably originated in the Cambrian as a group of aquatic arthropods, perhaps similar to modern sea spiders and horseshoe crabs (Dunlop 2010). In basal chelicerates, reproduction likely took place externally as is the case in modern marine arachnids. In extant terrestrial scorpions and pseudoscorpions a fertilisation is also achieved by the male laying a spermatophore on the substrate (Ghilarov 1958). The discovery of preserved intromittent organs in Rhynie chert Opiliones suggests that harvestmen in the Early Devonian were capable of internal fertilization on land without the need to lay spermatophores in water or on the substrate, implying that they were terrestrial.

Some recent harvestmen employ a “solicitous” mating strategy whereby the distal portion of the penis bears a sac that delivers a nuptial gift to the female’s mouth prior to copulation. The precise role of this behaviour is unknown, but the female appears to feed on the nuptial secretion and in some cases rejects the male by running away after feeding on the substance (Gwynne 2008). In contrary, harvestmen employing “antagonistic” mating strategies evolved penises without nuptial gift sacs and apparently penetrate the females by force. Correspondingly, females of these “antagonistic” species often possess sclerotized pregenital defences (Burns *et al.* 2013, Fowler-Finn *et al.* 2014). A phylogenetic analysis of leiobunine harvestmen showed that the presence of a sac is the ancestral condition in this lineage (Burns & Shultz 2015). *Devonopilio hutchinsoni* gen. et sp. nov. lacks a penile sac suggesting that a nuptial gift was probably not delivered to the female, but given our still very incomplete understanding of harvestmen reproductive behaviours (Machado & Macías-Ordóñez 2010) inferences for this extinct species are difficult to make.

Conclusions

Devonopilio hutchinsoni gen. et sp. nov. is described from 407-million-year-old Rhynie chert from Aberdeenshire, Scotland. Alongside *Eophalangium sheari*, *D. hutchinsoni* gen. et sp. nov. is the oldest harvestmen in the fossil

record. The present study thus adds a second harvestman to the Rhynie chert fauna, indicating that at least two reproductively isolated harvestman species co-occurred in the Rhynie hot spring palaeoenvironment in a relatively short geological time interval. If the two fossils were treated as modern taxa, they would be placed into two different superfamilies or suborders on the basis of penis musculature. Our finding indicates a higher morphological disparity in Devonian harvestmen than previously thought.

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