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On the problematic placement of the fossil arthropod *Devonopilio hutchinsoni* in Opiliones (Arachnida)

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Harvestmen (Arachnida: Opiliones) were among the earliest terrestrial arthropods but their unmineralized exoskeletons are scarce and often fragmentary as fossils (Palencia *et al.* 2019). Consequently, the discovery and interpretations of fossil harvestmen from the early Palaeozoic can have disproportionate effects on the understanding of evolution in Opiliones. Recently, *Devonopilio hutchinsoni* Tihelka, Tian & Cai, 2020, was described as a new fossil harvestman from the well-known Rhynie chert deposits of Scotland, an important source of information on freshwater and terrestrial ecosystems of the early Devonian (Tihelka *et al.* 2020). This species would be one of the earliest records of harvestmen. The description was based on a single slide showing fragments of arthropod cuticle, which Tihelka *et al.* interpreted as a harvestmen penis and unspecified associated body parts. As specialists on harvestman morphology and systematics, we were intrigued by these conclusions. However, based on the material presented by Tihelka *et al*. we find no compelling evidence supporting the proposal that the specimen is a harvestman.

The Rhynie chert deposit (see an excellent overview in Garwood *et al*. 2020) contains exquisitely preserved, unequivocal members of the Opiliones crown-group (Dunlop *et al*. 2003, 2004) which offer direct evidence that terrestrial harvestmen have existed since at least the early Devonian (Pragian) (407.6+2.2Ma) (Edwards *et al*. 2018). The first harvestman species described from the Rhynie chert was *Eophalangium sheari* Dunlop, Anderson, Kerp & Hass, 2004 based on three fossil specimens, two male and one female (Dunlop *et al*. 2004). The fossils were remarkably well preserved and contained a huge amount of morphological information from external and internal morphology, which revealed an extraordinary degree of morphological stasis in Opiliones. The presence of an obvious tracheal system provides strong evidence that *E. sheari* was a terrestrial animal, and the well-preserved male and female genitalia were surprisingly modern. In fact, *Eophalangium sheari* provides the oldest example of a penis in a terrestrial animal (Dunlop *et al*. 2003) and thereby shows that the evolutionary innovation of direct sperm transfer (*i.e.*, guaranteeing that gametes interact without contact with the external environment) appeared early in arthropod terrestrialization.

As the earliest unambiguous example of a harvestman, *E. sheari* is extremely important for understanding the evolutionary history of Opiliones. The species was originally placed in the suborder Eupnoi (Dunlop *et al*. 2004) but was later transferred by Garwood, Sharma, Dunlop & Giribet (2014) to the newly proposed plesion suborder Tetrophthalmi along with a Carboniferous species, *Hastocularis argus* Garwood, Sharma, Dunlop & Giribet, 2014. The phylogenetic status and position of Tetrophthalmi remains unclear, with recent studies regarding it as a stem group of Cyphophthalmi or placing it within a basal polytomy (Tetrophthalmi + Cyphophthalmi + Phalangida) (Garwood *et al*. 2017; Wang *et al*. 2018). Despite this topological instability (expected due to the large amount of missing data in the fossil taxa) the results point to the existence of at least three major lineages of Opiliones in the early Devonian. Therefore, it is reasonable to expect the discovery of additional Devonian harvestmen.

Tihelka *et al*. (2020) seemed to have fulfilled that expectation with the description of *Devonopilio hutchinsoni* (Fig. 1). They placed the fossil in the arachnid Order Opiliones based on a "...cylindrical elongate structure … consisting of a wider basal part and a narrower apical part connected by a narrow joint...", which they identified as an opilionid penis sheath and penis shaft, respectively (Tihelka *et al*. 2020). Their taxonomic diagnosis and description were based solely on the interpretation of these structures. Other fragments in the preparation were treated as unidentifiable and not included in the taxonomic description, although they were considered parts of the same animal.

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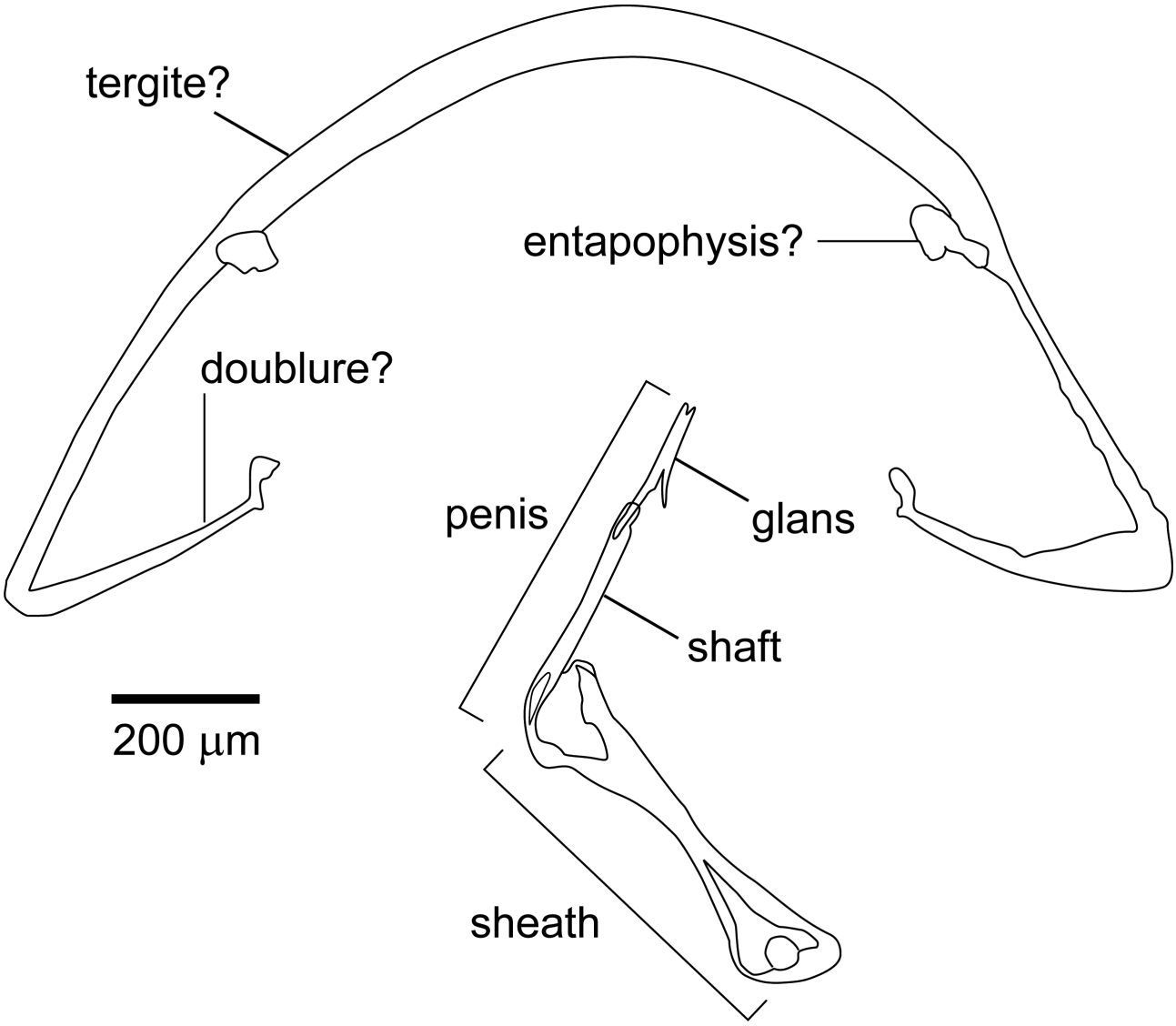

FIGURE 1. Drawing of the only specimen of the proposed Devonian harvestman, *Devonopilio hutchinsoni*, redrawn from photo in Tihelka *et al*. (2020). The penis and shaft are based on interpretations by Tihelka *et al*. but are rejected here. Tihelka *et al*. did not interpret the structure that we have proposed as a cross section of a tergite in an undetermined arthropod.

Herein, we challenge the conclusions reached by Tihelka *et al*. (2020) through a critical analysis of the morphological interpretations made by these authors. Most importantly, the structures that they interpreted as a harvestman penis could not function in the same way as in extant harvestmen. The supposed penis sheath was heavily sclerotized, which is inconsistent with the mechanical role of this structure in harvestmen. The sheath allows the penis shaft to be freely extended during mating and retracted during other times. In its resting (inverted) position the sheath serves as the wall of the pregenital chamber (Shultz & Pinto-da-Rocha, 2007). During mating the sheath is protruded (everted) by muscles and hemolymph pressure and is often visible externally as a translucent balloon-like structure. Consequently, the sheath must be elastic, flexible and weakly chitinized (Fig. 2) to permit the movements that protrude the penis from, and return it to, the pregenital chamber. A heavily sclerotized sheath is functionally incompatible with penis eversion and would prevent copulation. In contrast, the penis must be sclerotized (Fig. 2) or otherwise stiffened in order to enter the female's pregenital chamber to access the seminal receptacles within the retracted ovipositor. Therefore, two contiguous, cylindrical, heavily sclerotized structures cannot be considered characteristic of a harvestman penis and penis sheath. In contrast, pregenital chambers with weakly chitinized and flexible walls can be clearly observed in a male and the female of *Eophalangium sheari* (Dunlop *et al*. 2004, figs 3b and 5c).

It is noteworthy that Tihelka *et al*. (2020) acknowledged that the penis sheath in modern harvestmen is not heavily sclerotized yet maintained their interpretation because the fossil penis sheath was similar in outline to those of some

extant harvestmen. In fact, the outline of the supposed penis sheath of *D. hutchinsoni* superficially resembles the outline of penis sheaths illustrated in Wijnhoven (2013), a resemblance reinforced by the outline of the elastic stiffening rods or fulturae (Wijnhoven 2013, fig. 14B). But it is important to note that the penis sheath drawn in Wijnhoven (2013) depicts sheath morphology in a retracted penis, that is, a penis resting inside the body. In *D. hutchinsoni* the penis is external to the penis sheath, not inside it (Tihelka *et al*. 2020) (Fig. 1), which is only possible when the penis is everted. When everted, the wall of the pregenital chamber is exposed except in the proximal region of the sheath (Fig. 3). Furthermore, the posterior (proximal) end of the penis has a continuous circumferential attachment with the sheath, thereby allowing hemolymph, nerves, tracheae, etc. to pass from the body to the everted penis. Neither condition is observed in the sclerites of *D. hutchinsoni* that Tihelka *et al*. regard as a harvestman penis.

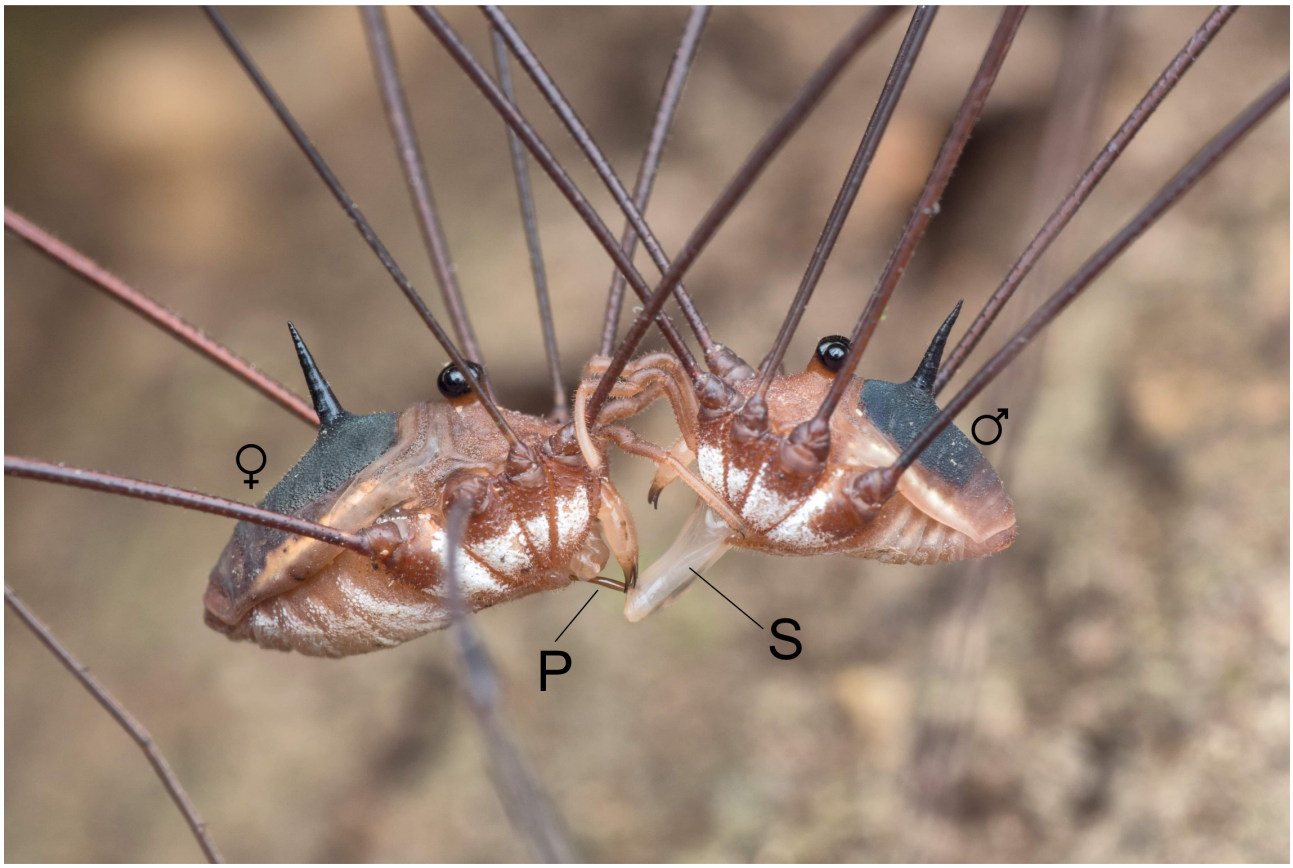

FIGURE 2. Female and male Gagrellinae (Opiliones: Eupnoi: Sclerosomatidae) in copula. P: penis, S: penis sheath, ♀: female, ♂: male. Photo courtesy of Melvyn Yeo, taken in Johor, Malaysia.

If the structure highlighted by Tihelka *et al*. (2020) is not a harvestman penis, the question remains as to what it is. The large crescent-shaped structure associated with the purported penis (Fig. 1) offers a possibility. It is clearly a bilaterally symmetrical structure, which suggests that it is part of a cuticular body wall that was sectioned transversely. In fact, the object is very similar to the cross section of an arthropod tergite with one median and two lateral regions, with possible entapophyses projecting from the junction of medial and each lateral region, as well as pronounced lateral doublures extending medially from the lateral tergal regions. While we cannot reliably assign such a tergite to a specific taxon, its arrangement is consistent with that of certain arthropods, such as crustaceans or euthycarcinoids, that are already known to occur in the Rhynie chert and associated deposits. In fact, the shape of the dorsal surface and the putative entapophyses seems to match the morphology of *Heterocrania rhyniensis* (Hirst & Maulik, 1926) (see Hirst & Maulik 1926, fig. 1A; Anderson & Trewin 2003, fig. 15B) but the issue should be addressed by workers more familiar with Rhynie chert arthropods. In contrast, the tergites of known harvestmen do not have large lateral doublures or tergal entapophyses.

If our interpretation is correct, the "penis" has a nearly mid-ventral position with respect to the tergite, a region that would likely be occupied by ventral sclerites, such as sternites and appendages. Tihelka *et al*. (2020) explicitly dismissed the idea that these structures are appendages, but this view appears to rely on the assumption that the appendages would be sufficiently complete to be readily identified. However, the fossil is contained within a section mounted on a microscope slide, and it is very unlikely that an appendage (or a penis) would be oriented in such a way as to fall exactly within

the transverse plane of the section. It is more likely that the sclerites are fragments of ventral cuticular structures, such as appendages, that happened to be broken and sectioned in such a way that they bear a vague resemblance to a harvestman penis. Whatever structures are contained within the fossil, it is very doubtful that they represent a morphologically and functionally unique example of an isolated penis from an early harvestman. We conclude that *Eophalangium sheari* remains the only harvestman known from the Rhynie chert.

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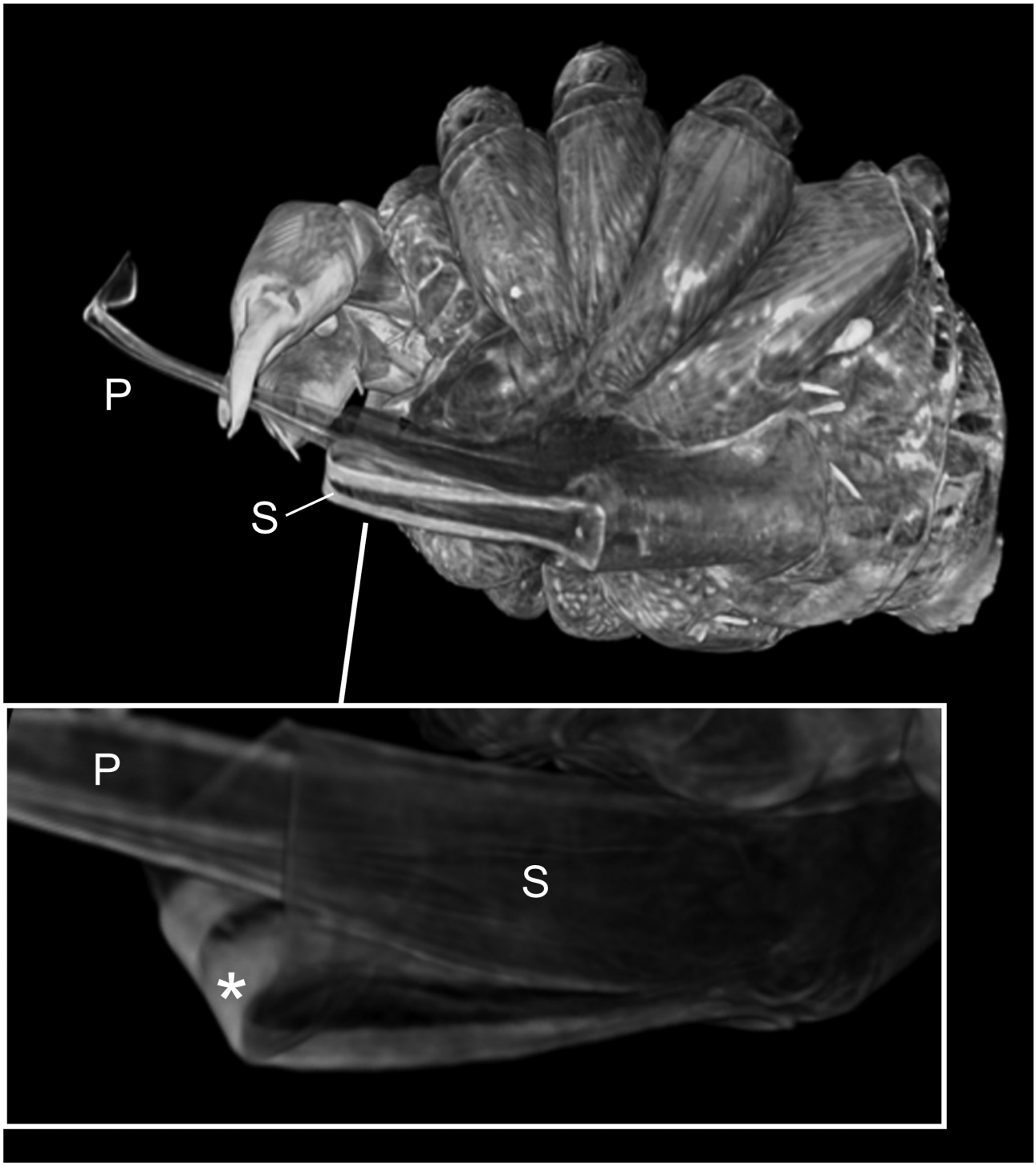

FIGURE 3. MicroCT images of a male of *Phalangium opilio* (Opiliones: Eupnoi: Phalangiidae) with everted penis, latero-ventral view. Inset shows detail of penis sheath, latero-dorsal view. P: penis, S: penis sheath, Asterisk marks the loop of the proximal region of the sheath when the penis is everted. MicroCT images courtesy of Rachel Werneck.

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