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A FOSSIL HARVESTMAN (ARACHNIDA, OPILIONES) FROM THE MISSISSIPPIAN OF EAST KIRKTON, SCOTLAND

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ABSTRACT. A fossil harvestman (Arachnida, Opiliones) from the Mississippian (Viséan: Brigantian) of East Kirkton, Scotland is described as *Brigantibunum listoni* new genus and species. At ca. 340 Ma, it represents the second oldest record of Opiliones. Although some details are lacking, this long-legged, small-bodied and rather gracile harvestman is surprisingly modern-looking and appears to show the impression of an annulate ovipositor. Its leg anatomy closely matches that of some living Eupnoi and it is tentatively referred to this clade. Like the newly discovered Rhynie chert harvestmen, it reinforces the idea that modern, crown-group Opiliones can be traced back to at least the mid-Paleozoic.

Keywords: Taxonomy, new species, Viséan, Paleozoic, Eupnoi

Fossil harvestmen (Opiliones) are very rare. Although they are best known from Tertiary ambers (e.g., Cokendolpher & Poinar 1998; Staręga 2002; Dunlop & Giribet 2003), there are also two Mesozoic records (Roger 1946; Jell & Duncan 1986) neither of which have been formally named and the first of which is dubious. Until recently the earliest harvestmen were Pennsylvanian (ca. 300 Ma) fossils from the Coal Measures of Commentry in France (Thevenin 1901) and Mazon Creek in the USA (Petrunkevitch 1913). Restudy of Petrunkevitch's (1913) putative extinct order Kustarachnida has shown that these Mazon Creek arachnids are misidentified harvestmen (Beall 1986, 1997; Dunlop 2004a). Additional Pennsylvanian-aged harvestmen have been collected from Missouri, USA (Dunlop 2004b) and Poland (Maciek Kania, pers. comm., 2004).

The oldest recorded harvestmen are exceptionally preserved, three-dimensional fossils from the Early Devonian (ca. 400 Ma) Rhynie cherts of Scotland (Dunlop et al. 2003, 2004). Provisionally assigned to the Eupnoi clade as *Eophalangium sheari* Dunlop et al. 2004, this exquisite, silicified material displays details of internal structures such as genitalia and trachea, all of which point towards these ancient harvestmen having a very similar gross morphology to living animals. The second oldest harvestman is also rather modern looking and comes from the Mississippian (ca. 340 Ma) of East Kirkton in Scotland (Wood et al. 1985). The East Kirkton harvestman (Figs. 1–3) is preserved in a more typical fashion as a flattened impression and superficially resembles living 'daddy long-legs' forms. In general, Mississippian arachnid fossils are far less common than either Devonian or Pennsylvanian examples (see Dunlop & Rößler 2003 for a review), thus any record from this time period is significant.

The East Kirkton harvestman was briefly mentioned, with a figure, in the original summary paper dealing with the locality (Wood et al. 1985). It has also been noted or listed in some further publications (Smithson 1989; Selden 1993a, b; Clack 1998; Jeram 2001; Dunlop & Rößler 2003; Dunlop 2004a). Here we formally describe and name this important specimen and discuss its significance in the light of other recent fossil harvestman discoveries.

METHODS

The East Kirkton harvestman was borrowed on research loan from the Hunterian Museum,

Glasgow, United Kingdom (GLAHM A2854), where it is customarily on display. The specimen was digitally photographed using a Leica DC100 digital camera mounted on a Leica MZFLIII microscope and drawn using a camera lucida attachment. Adobe Photoshop Limited Edition 5.0 was used to manipulate the digital images. For comparative purposes the type material of *Nemastomoides longipes* (Petrunkevitch 1913) from the Peabody Museum, Yale (YPM 171), *N. depressus* (Petrunkevitch 1913) from the United States National Museum (USNM 37974) and *Kustarachne tenuipes* Scudder 1890 (USNM 37967) was examined, along with *Eophalangium sheari* from Rhynie (held in the University of Munster, Germany) and extant species preserved in the Museum für Naturkunde Berlin.

Geological setting.—The East Kirkton Limestone is a fossil Konservat-Lägerstatte located near Bathgate, West Lothian, Scotland; about 27 km west of Edinburgh. The limestone is the lowest of five which occur within the Bathgate Hills Volcanic Formation. This in turn can be correlated with the lower part of the Brigantian Stage of the Viséan Series of the Mississippian (= Lower Carboniferous in European terminology). The Brigantian Stage spans the time interval 336.0–339.4 Ma. Further details can be found in Rolfe et al. (1994). The East Kirkton locality has also yielded scorpions (Jeram 1994, 2001), myriapods (Shear 1994) and a variety of terrestrial tetrapods including the anthracosaurid *Silvanerpeton miripedes* and the famous stem-amniote *Westlothiana lizziae*; however early insects and arachnid groups like the extinct order Trigonotarbida, which are usually fairly common in terrestrial deposits of this age, are so far absent.

Preservation.—GLAHM A2854 is preserved as a compression fossil on the surface of a thin, grey bed of calcareous tuff. The light red–brown coloration of the harvestman is analogous to that of the scorpion fossils etched from the East Kirkton limestone (Jeram 1994) and suggests that some constituent of the original cuticle still remains, rather than it being a wholly carbonized cuticle. This in turn suggests that chitinoclastic bacteria were excluded from the preservational environment during the formation of the deposit and the arthropod fossils contained therein. The fossil originated from bed 82 (S.P. Wood pers. comm. 2002). Rolfe et al. (1994) identified the combined thickness of bed 81 and bed 82 (with a lateral variation in thickness between 80 and 140 mm) as the same unit which Geikie (1861) named 'bed b'. This unit contains dense accumulations of ostracods on some bedding surfaces as well as charcoalified plant material. This is also the likely source bed of the holotype of *Westlothiana lizziae*. Durant (1994) summarized the likely paleoenvironment in which the sediments exposed in the East Kirkton Quarry were deposited in a shallow lake close to the flanks of an active volcano. Volcanic eruption products including ash and tuffs, were eroded and washed down into the lake. Set against a backdrop of active volcanism in the area in which it formed, it is no surprise that ashy bands, pyroclastic fragments and chemical sediments influenced by hot spring activity dominate the sequence hosting both terrestrial and aquatic plant and animal fossils. Widespread development of limestone formed from stromatolitic algae also point to an unusual physio-chemical environment for the formation of this deposit.

In the fossil's plane of compression at least four elongate and articulated legs are preserved. A thin calcite vein cross-cuts the legs of the fossil (Figs. 1, 2). Close study of the harvestman body suggests that other legs may have broken off prior to preservation. However, it is obvious that such delicate structures, which easily break off in extant animals even while still alive, indicate only a short period of transport into the preservational environment. Perhaps this animal was rafted out onto the open lake on floating vegetation before dropping into the water?

MORPHOLOGICAL INTERPRETATION

Body.—The body (Figs. 1–3) is small and rounded. We suspect it is essentially a dorsolateral to ventro-lateral compression in which the two sides of the body have become superimposed. As is typical for harvestmen, the prosoma and opisthosoma are broadly joined. Features such as eyes or mouthparts are equivocal, even under higher magnification, but the body does come to a slight, angular point on the dorsal side where an eye tubercle might be expected. Low-angle lighting reveals lines on the harvestman body which might correspond to the original opisthosomal segmentation and/or elements of the coxae which

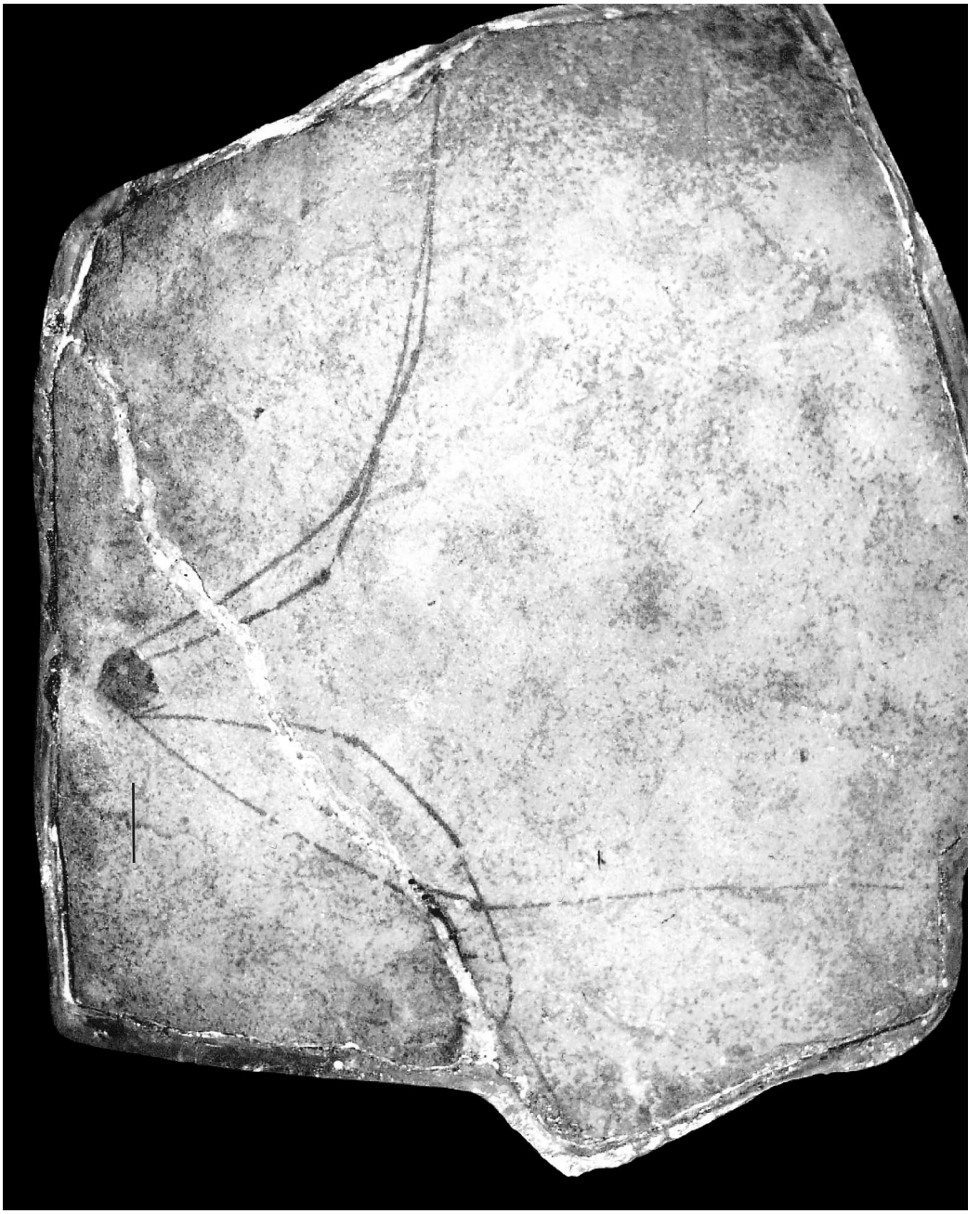

Figure 1.—*Brigantibunum listoni* new genus and species. from the Mississippian (Viséan: Brigantian) of East Kirkton, Scotland. This modern-looking specimen is here tentatively assigned to the Eupnoi clade. Scale bar = 5 mm.

come up the side of the body in many living harvestmen. These lines do not form a clear pattern running the length of the body and in similar-looking extant harvestmen segmentation is generally poorly defined (e.g., Shultz 2000) and may only be betrayed by folds or color patterns on the body surface. The fossil also reveals fine tuberculation on the body where cuticle has been preserved and, while there is some degree of locali-

zation, the tubercles do not define identifiable segments.

Ovipositor.—One intriguing feature is an apparently annulate structure overlaying the left side of the body, which is only clearly visible under high magnification and low angle lighting (Fig. 3). It is associated with original cuticle which tends to suggest it is not an artefact, and at least towards the 'dorsal' end there are rows of tiny circular structures across each annulation which might be tubercles or setal sockets. We tentatively interpret this structure as an ovipositor since its annulate morphology and proportions relative to the body are suggestive of that in a modern eupnoid harvestman (e.g., Shultz 2000). The East Kirkton scorpions preserve respiratory organs (Jeram 1994), which shows that there is the potential at this locality to recover internal features. If this is an ovipositor, it is the second oldest record of internal genitalia, after the one recovered in *Eophalangium sheari* from Rhynie (Dunlop et al. 2003, 2004). It implies that the East Kirkton fossil is a female which probably laid its eggs in the substrate. In living harvestmen the ovipositor is apparently extended through hemolymph pressure (Shultz 2000). Perhaps the ovipositor in the fossil was squeezed out of the body during compression and came to lie across the opisthosoma?

Legs.—Four almost complete legs are preserved, all of which are very long and gracile; up to ca. twelve times the length of the body. A small fragment of either a fifth leg or, perhaps, a pedipalp is also preserved. It is difficult to assign legs unequivocally to their sequence in the body, but the longest leg (which is also the most gracile) is probably leg 2. This leg is longest in most living (non-cyphophthalmid) harvestman and has a more tactile function. Indeed all 4 preserved legs express slightly different femur lengths (see Systematics) and this might indicate that the fossil is essentially a lateral view preserving legs 1–4 on one side of the body; with the corresponding legs from the other side either missing or still within the matrix. A tentative numbering scheme is proposed based on this assumption (Fig. 2).

Discrete podomeres can be recognized, and the basic leg anatomy is a precise match for living eupnoid harvestmen (cf. Shultz 2000). The femur is elongate and slender. It is followed by a very short patella which is slightly thicker than the adjacent podomeres. It forms a distinct and bulbous 'knee'. The tibia is again elongate and slender, widening distally to form a disjunct articulation with the next podomere, the basitarsus. This basitarsus is also long and slender, although the transition to the telotarsus is indistinct. In many living harvestmen the telotarsus is composed of many short tarsomeres. These cannot be resolved in the fossil, but the distal curvature of at least one of the legs (leg 1 in our scheme, see Figs. 1 & 2) implies that it, too, was formed from numerous articulating elements. Claws at the ends of the legs (the apotele) are equivocal.

SYSTEMATIC PALAEONTOLOGY

?Eupnoi Hansen & Sørensen 1904

Remarks.—As noted by Selden (1993a), the East Kirkton fossil is clearly a harvestman, but explicit diagnostic characters of higher taxa within Opiliones are not clearly preserved. Nevertheless, its overall morphology with a 4 mm globular body and long, essentially homogeneous legs is wholly inconsistent with Cyphophthalmi, which are tiny (typically 1–2 mm) with short, stubby legs. Nor does it resemble the more robust Laniatores in which leg 4 is often enlarged and spiny (although not, for example, in oncopodids) and in which prominent, raptorial pedipalps would be expected. This leaves the Palpatores group, the monophyly of which is currently in dispute (compare Shultz 1998 and Giribet et al. 2002). The older Rhynie chert harvestmen preserve convincing eupnoid characters (Dunlop et al. 2003, 2004a), thus both Eupnoi and its putative sister taxon lineage, Dyspnoi sensu Shultz (1998) or (Dyspnoi + Laniatores) sensu Giribet et al. (2002), can be predicted from the Mississippian.

Both the Eupnoi and Dyspnoi clades, which make up the traditional Palpatores group, include long-legged taxa. The extremely long and gracile legs in GLAHM A2854, which are up to about twelve times body length, tend to favor affinities with phalangiid or sclerosomatid harvestmen (Eupnoi), for example members of common eupnoid genera like *Leiobunum* C.L. Koch 1839, *Opilio* Herbst 1798 and *Phalangium* Linnaeus 1758. Among the Recent Dyspnoi, common genera such as

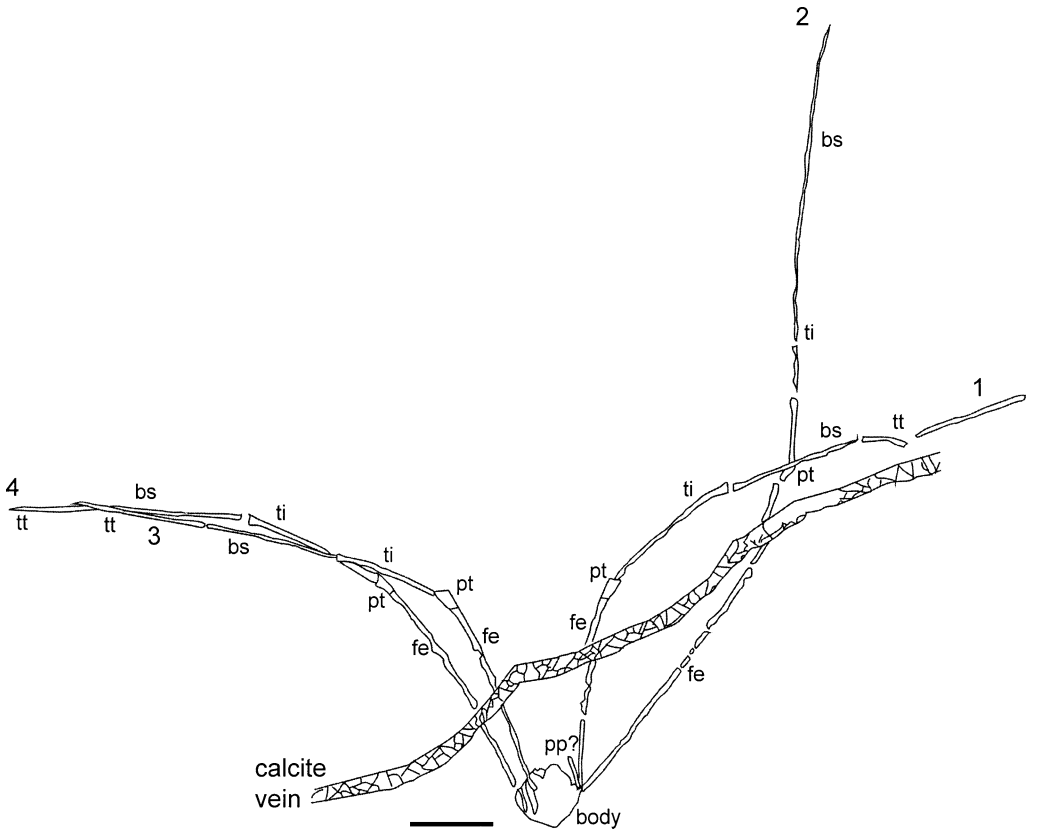

Figure 2.—Interpretative drawing of the specimen shown in Fig. 1. Abbreviations: bs = basitarsus, fe = femur, pp = possibile pedipalp, pt = patella, ti = tibia, tt = telotarsus. Legs tentatively numbered from 1 to 4, with leg 2 longest. Scale bar = 5 mm.

Nemastoma C.L. Koch 1836 and *Dicranolasma* Sørensen 1873 typically have legs which are somewhat shorter in relation to body length. Members of the dyspnoid genus *Mitostoma* Roewer 1951 are closer to GLAHM A2854 in terms of leg lengths. Data from the fairly widespread *M. chrysomelas* (Hermann 1804) in Martens (1978, p. 143) suggests that leg length (13.7 mm) is, at best, about eight times body length (1.7 mm), although in a highly-specialized Alpine cave species like *M. anopthalmum* (Fage 1946) leg length (22.8 mm) can be over fourteen times body length (1.6 mm); data from Martens (1978, p. 149). Clearly leg length is not an ideal character and as noted by Martens, these parameters can vary even within a species and between males and females.

The putative ovipositor also hints at a eupnoid. If our interpretation is correct, this annulate morphology only occurs in Cyphophthalmi (rejected for the reasons outlined above) and Eupnoi (Shultz 1998, 2000; Giribet et al. 2002). However, explicit autapomorphies of Eupnoi cannot be resolved unequivocally in the fossil. The lakeside paleoenvironment is unlikely to have trapped either high mountain and/or cave animals. The long and gracile legs in the fossil are more characteristic for certain phalangiid and sclerosomatid eupnoids, as opposed to the usual range in non-specialist dyspnoids. On these grounds we tentatively assign the East Kirkton fossil to Eupnoi.

Brigantibunum new genus

Type and only species.—*Brigantibunum listoni* new genus and species.

Etymology.—From the Brigantian age of the fossil and the suffix ''bunum'' used in modern genera of small bodied, long-legged harvestmen such as *Leiobunum*.

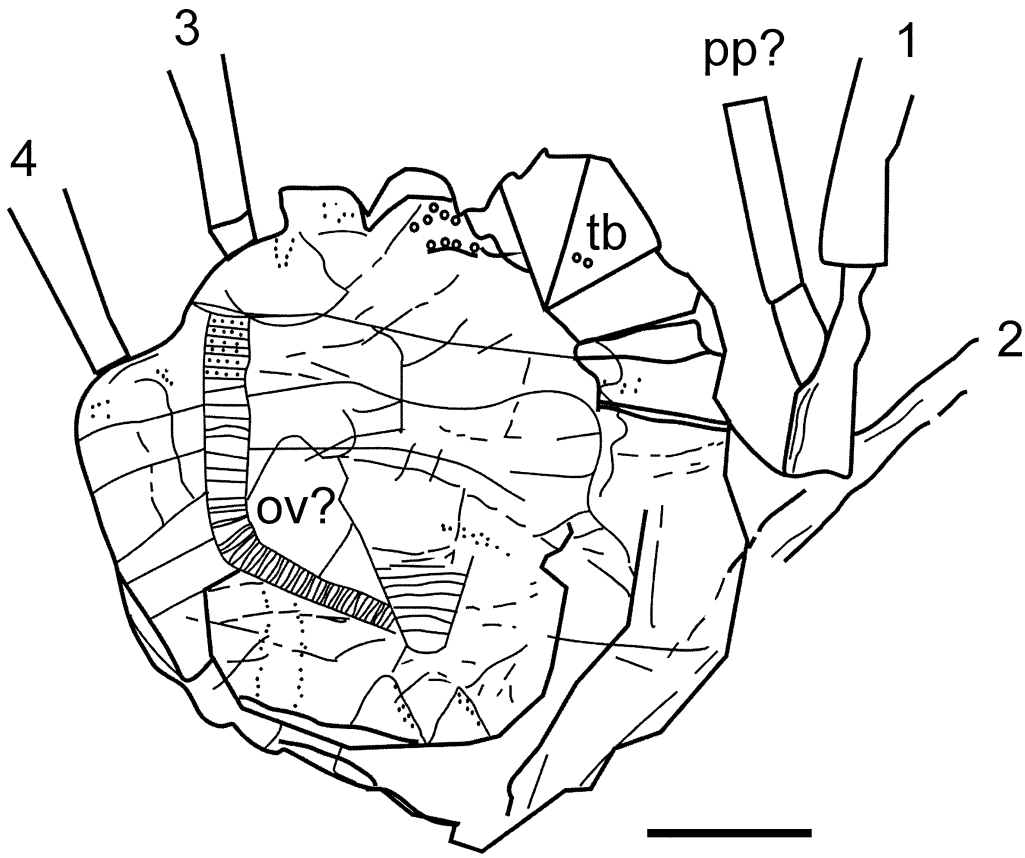

Figure 3.—Detail of the body region under low angle lighting and immersion in alcohol. Abbreviations: ov? = possible annulate ovipositor, tb = tuberculation of cuticle. Leg sequence as in Fig. 2. Scale bar = 1 mm.

Diagnosis.—Extremely gracile Paleozoic harvestman with long, slender legs up to twelve times the length of the small, ovate body. Femora at least two and a half to three times the length of the body.

Remarks.—The *Eophalangium sheari* material from the Devonian of Rhynie, Aberdeenshire, Scotland includes a long-legged specimen. Given the very different modes of preservation, direct comparisons with the East Kirkton fossil are problematic. The three-dimensional Rhynie material yields many characters not testable in the East Kirkton specimen. Furthermore, the (male) Rhynie fossil associated with the long legs is incomplete and the full extent of both the legs and body remains equivocal. Further discoveries may change this interpretation, but we can find no explicit autapomorphies or even reliable ratios of body proportions to argue that the East Kirkton fossil belongs to *Eophalangium* Dunlop et al., 2004.

Among the Pennsylvanian opilionids, our fossil is clearly not congeneric with the putative Commentry troguloid *Eotrogulus fayoli* Thevenin 1901, which is a robust animal with an elongate body and comparatively short legs. This leaves three species of *Kustarachne* Scudder 1890, two of which are rather incomplete and doubtful, and three species of *Nematostomoides* Thevenin 1901; of which *N. depressus* from Mazon Creek is a misidentified phalangiotarbid (Beall 1997; pers. obs.). The East Kirkton fossil appears longer-legged than all these Pennsylvanian forms, although the Mazon Creek specimens are in nodules and the full extent of the legs is, of course, not preserved. In detail, the length of the femur offers a potential diagnostic character and the femora in the East Kirkton fossil are pro-

portionately longer (ca. 3 times body length) than the femora in *Nemastomoides* and *Kustarachne* (ca. 1–2 times body length). Overall, GLAHM A2854 is a unique find and the only record of a Mississippian harvestman. It most closely resembles the Commentry species *N. elaveris* Thevenin 1901, but based on its extreme leg length and gracile appearance we assign it to a new genus diagnosed on the body–femur ratio.

Brigantibunum listoni new species
Figs. 1, 2.

?Earliest known harvestman (Arachnida, Opiliones): Wood et al. 1985: 355–356, fig. 1.

Opilionid or harvestman: Smithson 1989: 676–678; Selden 1993a: 392–393; Selden 1993b: 305–306; Clack 1998: 66–69; Jeram 2001: 374, tabs. 16.1, 16.2; Dunlop & Rößler 2003: 389; Dunlop & Giribet 2003: 371; Dunlop 2004a: 24; 2004b: 67.

Type.—Holotype, from the East Kirkton Quarry, near Bathgate, (27 km west of Edinburgh), West Lothian, Scotland (Grid reference NS 991690), collected by Mr. Stan P. Wood, derived from Unit 82 of the East Kirkton Limestone, West Lothian Oil-Shale Formation, Strathclyde Group, Upper Viséan (Brigantian), Mississipian (= Lower Carboniferous in European stratigraphy) (GLAHM A2854).

Etymology.—For Jeff Liston (University of Glasgow & Hunterian Museum).

Diagnosis.—As for the genus.

Description.—Body small, rounded, ca. 4 mm in diameter. Red–brown cuticle includes fine tuberculation and possible segment/coxal boundaries. Elongate, annulate structure (?ovipositor), length 2.5 mm, curves across body on left side. Small, incomplete limb element (?pedipalp), length 2 mm, projects from body on right side. Four legs preserved, all long, slender and extremely gracile. All legs with different lengths and podomere proportions, tentatively numbered in sequence (see also Morphological interpretation) from longest to shortest: 2 4 1 3. All legs slightly curved, one leg (probably leg 2) distinctly longer; maximum approximate preserved leg lengths as follows. Leg 1: 38 mm, leg 2: 51 mm, leg 3: 34 mm, leg 4: 40 mm. Femora long, lengths as follows. Leg 1: 12 mm, leg 2: 21 mm, leg 3: 11 mm, leg 4: 14 mm. All patellae short, ca. 1.5 mm. Tibiae longer, lengths as follows. Leg 1: 8 mm, leg 2: 14 mm, leg 3: 6 mm, leg 4: 9 mm. Basitarsi lengths as follows. Leg 1: 8 mm, leg 2: unclear, leg 3: 8 mm, leg 4: 9 mm. Telotarsi incomplete, but long and slender.

DISCUSSION

Brigantibunum listoni fits into a developing pattern (e.g., Dunlop et al. 2003, 2004; Dunlop 2004a, b) in which harvestmen appear to have evolved relatively early into recognizable crown-group forms (i.e. animals assignable to clades with Recent representatives) and exhibit a high degree of stasis, with little fundamental change over hundreds of millions of years. Harvestmen with the same basic shape as the East Kirkton fossil, remain common and abundant today; particularly in the northern hemisphere. To put this into context, the oldest crown-group spiders (Selden 1996) are mesotheles (the most basal living spider clade) and are first recorded from the end of the Pennsylvanian. This is some 100 million years after the oldest crown-group harvestmen from Rhynie, which can be assigned to the eupnoids; a somewhat derived clade. It is also worth mentioning that in recent arachnid phylogenies (e.g. Giribet et al. 2002) harvestmen seem to resolve in a fairly basal position (compared to spiders) as part of the so-called Dromopoda clade along with scorpions, pseudoscorpions and solifuges.

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