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A spiny harvestman (Arachnida: Opiliones) from the Upper Carboniferous of Missouri, USA

Шипастый сенокосец (Arachnida: Opiliones) из позднего карбона Миссури, США

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ABSTRACT. A new fossil harvestman (Arachnida: Opiliones) is described from the Upper Carboniferous Coal Measures of western Missouri, USA. *Echinopustulus samuelnelsoni* gen. et sp.n. is tentatively assigned to the suborder Dyspnoi and shares features with both trogulid and, less convincingly, ceratolasmatid opilionids. This fairly long-legged fossil is only known from the dorsal surface which exhibits a pustulate ornament and a remarkable, autapomorphic, morphology of two pairs of large opisthosomal spines: an anterior, paramedian pair emerging from a single, central tubercle and a posterior pair positioned more laterally. Like the French fossil *Eotrogulus fayoli* Thevenin, 1901, this new material may provide further evidence that the Dyspnoi clade extends back to at least the late Carboniferous (*c*. 300 Ma).

РЕЗЮМЕ. Описан новый ископаемый сенокосец (Arachnida: Opiliones) из верхнекарбоновых углей западного Миссури, США. *Echinopustulus samuelnelsoni* gen. et sp.n., который предварительно отнесен к подотряду Dyspnoi, несет признаки как трогулид, так и в меньшей степени цератолясмид. Это отчетливо длинноногое ископаемое известно только с дорзальной поверхности, на которой имеется пупырчатый орнамент и заметная, аутапорморфная, структура, состоящая из двух пар крупных опистомальных шипов: передней, парамедиальной пары, выходящей из единственного центрального бугорка, и задней пары, расположенной более латерально. Как и ископаемое *Eotrogulus fayoli* Thevenin, 1901 из Франции, новый материал отодвигает находки клады Dyspnoi назад, как минимум до позднего карбона (примерно 300 млн.).

KEY WORDS: fossil, Carboniferous, taxonomy, harvestman, Dyspnoi, new species, USA.
КЛЮЧЕВЫЕ СЛОВА: ископаемое, карбон, таксономия, сенокосец, Dyspnoi, новый вид, США.

Introduction

Fossil harvestmen (Arachnida: Opiliones) are rare. The oldest examples date back to the Early Devonian [Dunlop *et al*., 2003] and a small number of Carboniferous harvestmen have also been described. These come from the Coal Measures of Commentry in France [Thevenin, 1901] and Mazon Creek in the USA [Petrunkevitch, 1913], and from the slightly older east Kirkton site in Scotland [Wood *et al*., 1985]. Restudy of the extinct arachnid order Kustarachnida from Mazon Creek has indicated that these fossils are misidentified harvestmen [Beall, 1986; Dunlop, 2004]. By contrast, the entire Mesozoic has yielded only two incompletely described specimens, while the Tertiary has a much more diverse and better known fauna

including specimens in shales [Cokendolpher & Cokendolpher, 1982] and inclusions in amber [e.g., Cokendolpher & Poinar, 1998; Staręga, 2002; Dunlop & Giribet, 2003]. All four suborders *sensu* Giribet *et al.* [2002] are represented in Tertiary amber and most of these fossils can be assigned to Recent genera.

The Upper Carboniferous harvestman fauna currently consists of the rare Commentry and Mazon Creek forms which can now be divided among three genera: *Eotrogulus* Thevenin, 1901, *Nemastomoides* Thevenin, 1901 and *Kustarachne* Scudder, 1890. The position of these fossils within Opiliones remains problematic. Both *Eotrogulus* and *Nemastomoides* have been included in the superfamily Troguloidea of the suborder Dyspnoi. These two fossil genera were raised to new families by Petrunkevitch [1955]; albeit on questionable characters relating to the coxo-sternal region which should not be part of the harvestman ground pattern. Restudy is required to confirm their familial status and Dunlop [in press] compared both *Kustarachne* and *Nemastomoides* to living Eupnoi; the group which includes the most common 'daddy-long-legs' type of harvestmen.

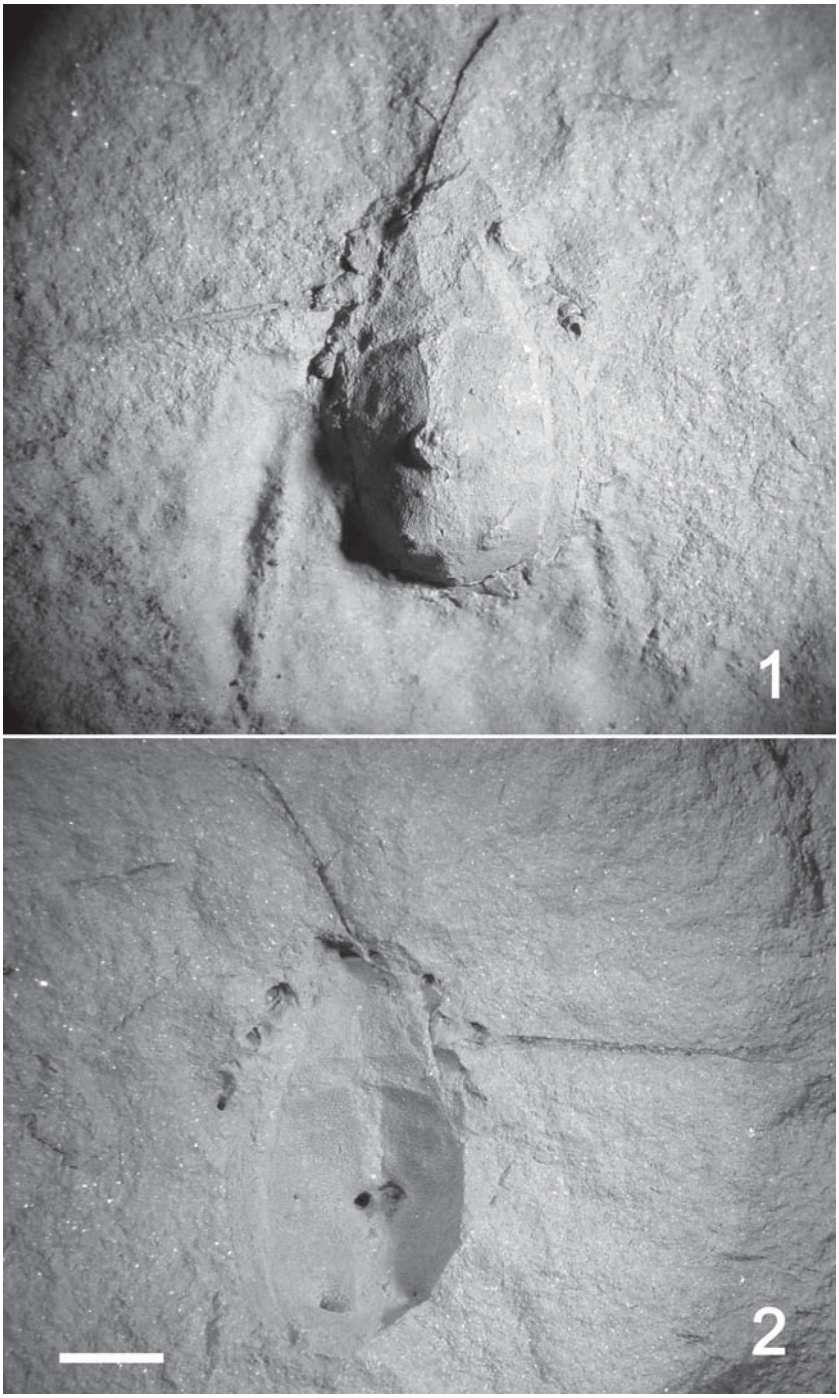
Dyspnoi are fairly abundant and widespread today across the northern hemisphere, although they do tend to be predominantly soil animals and are thus more cryptic than the more familiar Eupnoi. Modern-looking Dyspnoi assignable to the living genus *Nemastoma* have long been known from Tertiary amber [see e.g., Petrunkevitch, 1955], but the only reliable Palaeozoic dyspnoid harvestman is the French fossil *Eotrogulus* from the Coal Measures of Commentry. From its description in the literature *Eotrogulus* looks superficially like a member of the trogulid clade, with a somewhat elongate, lozenge-shaped body in which the opisthosoma is broadly joined to a subtriangular carapace. The legs are quite long and slender, but nowhere near as extreme as in some phalangiid harvestmen. *Eotrogulus* was raised to a new, monotypic family and potentially represents the oldest record of both Troguloidea and Dyspnoi. Unfortunately the status of the holotype is uncertain. The only other fossil trogulid described in the literature is *Trogulus longipes* Haupt, 1956 from the Eocene 'Braunkohl' of Geiseltal in Germany. This incomplete and not very well illustrated fossil is somewhat consistent with a living trogulid in overall shape, but this assignment is difficult to confirm from the description and again the status of the holotype is uncertain.

In this paper a new fossil arachnid is described from the Coal Measures of western Missouri, USA. In overall appearance this spiny specimen is quite different from previously described Carboniferous arachnids and clearly merits a new taxon. It is interpreted as the second example of an Upper Carboniferous dyspnoid harvestman; albeit of uncertain affinities within the Dyspnoi clade.

Material and methods

The fossil was acquired from a private dealer (Charles Isbon) by Dr Elliot Nelson (St Louis, USA), who recognized its significance and made it available for study to the author. The fossil was reportedly collected from private land in western Missouri, USA, but the exact locality could not be traced. It may come from near the town of Windsor. However, a number of sites in western Missouri yield Coal Measure fossils similar to the famous Braidwood section of the Mazon Creek locality [B. Stinchcomb, pers. comm.] and in general these Missouri coal deposits are not as extensive or as well researched as those of Illinois, which include Mazon Creek. The Missouri fossils are preserved in a similar way to Mazon Creek material as impressions in clay-ironstone concretions. The sediments yielding the Missouri concretions belong to the Pleasanton Group, which is dated to upper Middle Pennsylvanian; equivalent to the Upper Carboniferous in European stratigraphy. A summary of the geological setting of this region can be found in Howe [1982].

The fossils were studied under a stereomicroscope with a *camera lucida* attachment used to prepare the drawings. A fine needle was used to prepare the anterior part of the carapace and also to excavate the soft sediment infill from the spines on the back of the opisthosoma. Other Upper Carboniferous harvestmen from Mazon Creek were obtained from the United States National Museum (USNM) and the Peabody Museum, Yale (YPM). Of the non-amber dyspnoid harvestmen, *Eotrogulus fayoli* Thevenin, 1901 was reported from the Museum National



Figs 1–2. *Echinopustulus samuelnelsoni* gen. et sp.n., a new spiny harvestman from the Upper Carboniferous Coal Measures of western Missouri, USA. 1 — part; 2 — counterpart. Scale: 2 mm.

Рис. 1–2. *Echinopustulus samuelnelsoni* gen. et sp.n., новый шипастый сенокосец из верхнекарбоновых углей западного Миссури, США. 1 — основная часть; 2 — обратный отпечаток. Масштаб: 2 мм.

d'Histoire Naturelle (MNHN) in Paris, but could not be traced in the collections during a recent search [A. Rage, pers. comm.]. Similarly, the type of *Trogulus longipes* should be in the Gieseltal Museum in Halle, Germany, but could not be traced [M. Hellmund, pers. comm.]. The fossil material was also compared to extant harvestmen in the zoological collections of the Museum für Naturkunde, Berlin.

Results and discussion

Morphological interpretation

The fossil (Figs 1–4) is preserved in a nodule as a part and counterpart. Both show the dorsal surface of the animal, respectively, in positive and negative relief. The latter preserves more details of the morphology and ornamentation. Descriptions are of the appearance of the animal 'in life'. In overview, this is a small to medium sized arachnid, *c.* 9 mm long, in which the prosoma and opisthosoma are somewhat compact and broadly joined together via a procurved sulcus, with little tagmosis between them. The limb series is incomplete, but is suggestive of long, fairly slender legs. Together, these features strongly imply that this fossil is a harvestman, although (as with existing Carboniferous harvestmen) unequivocal autapomorphies of the order relating to the genitalia and repugnatorial glands cannot be resolved.

Ornament

The general dorsal body surface of both the carapace and opisthosoma is covered with a distinct ornament of fairly dense, tiny pustules. In places their preservation is patchy and they are more apparent on the counterpart (Fig. 4), especially under low angle lighting. They seem to fade out towards the margins of the carapace and they tend to form ring-like patterns around the median tubercle for the anterior spines (see below). This pustulate ornament is absent from a slightly raised, but weakly defined median band, about 0.5 mm wide, which extends from the middle of the carapace down along the length of the opisthosoma where it is interrupted only by the anterior spine tubercle. The legs are not well enough preserved to resolve whether the pustulate ornament continues here too.

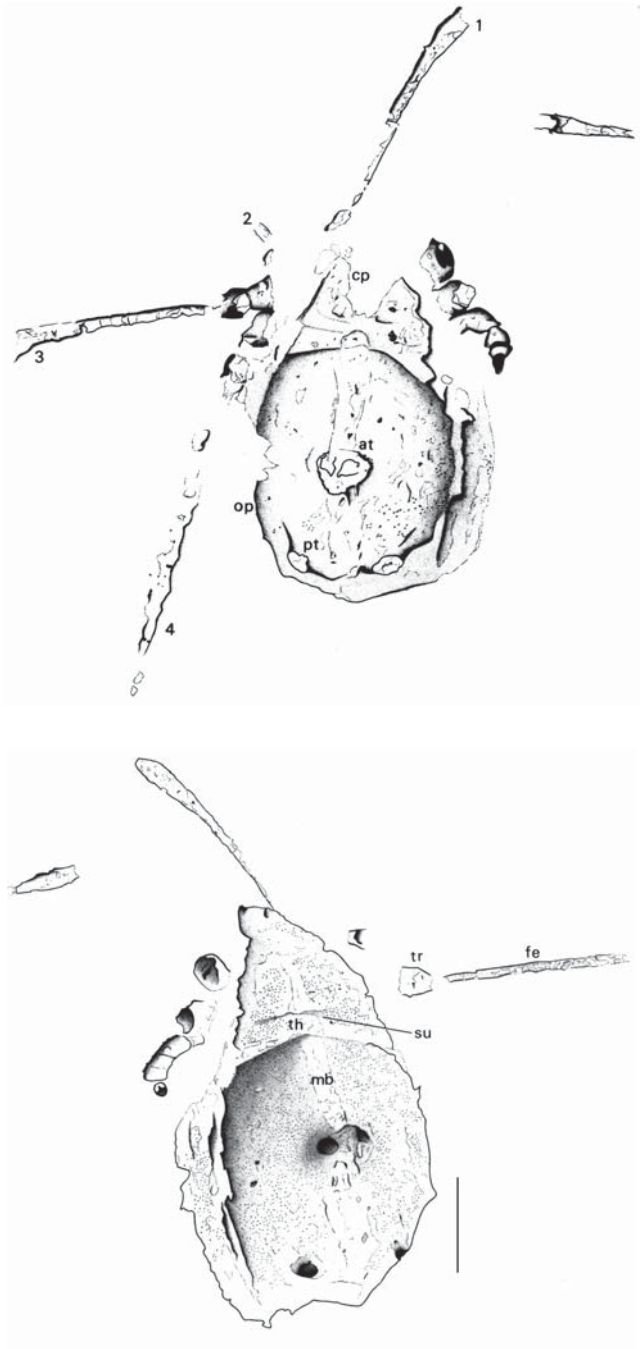
Prosoma

The carapace is subtriangular, but the anterior tip is, unfortunately, not preserved. Excavation of the anterior end failed to reveal structures such as eyes (which remain equivocal) or, for example, the characteristic bilobed 'hood' seen in modern trogulid harvestmen. The carapace expresses a weak division or sulcus towards its posterior end. Although not a separate sclerite, this corresponds to the metapeltidium or last thoracic tergite *sensu* Giribet *et al*. [1999: character 21]. The median band and ornament here have been noted above. The mouthparts and pedipalps are not preserved. The leg series is incomplete and only the proximal podomeres are preserved. They give the impression of slender, rather gracile legs in which the femora widen distally; see the leg 1 femur in particular. The trochanters are quite well preserved as short, somewhat globular podomeres which widen distally.

Opisthosoma

The opisthosoma is the best preserved region. It is oval, about one and a half times as long as wide. It seems to have become splayed out on one side with an irregular margin. This may be a taphonomic effect of compression. Generally, the fossil retains much of the original three-dimensionality. The dorsal side of the opisthosoma is dome-shaped and highly vaulted (Figs 1, 3); considerably more so than the carapace. An important feature of note is the apparent lack of clear tergal divisions along the entire length of the opisthosoma. In the scheme of Giribet *et al*. [2002: character 115] this degree of tergite fusion approaches an apomorphic character state which has been termed the 'scutum magnum'. It should be noted that varying degrees of opisthosomal tergite fusion have been acquired, probably independently, in a number of modern harvestman lineages.

The new fossil preserves another interesting apomorphic feature. The part expresses three raised tubercles on the back of the opisthosoma (Figs 1, 3). The median tubercle occupies a central position on the opisthosoma where it bisects the median band along the back of the animal. This tubercle bears the outline impres-



Figs 3–4. Camera lucida drawings of the specimens shown in Figs 1–2. Abbreviations: at = anterior spine-bearing tubercle; cp = carapace; fe = femur; mb = median band; op = opisthosoma; pt = posterior spine-bearing tubercle; su = sulcus; th = thoracic tergite (or metapeltidium); tr = trochanter. Legs numbered from 1–4. Scale: 2 mm.

Рис. 3–4. Перерисовка экземпляра, показанного на Рис. 1–2, с помощью рисовального аппарата. Сокращения: at = передний бугорок, несущий шип; cp = карапакс; fe = бедро; mb = медиальная полоса; op = опистосома; pt = задний бугорок; несущий шип; su = сулькус; th = торакальный тергит (или метапельтидиум); tr = трохантер. Ноги пронумерованы от 1 до 4. Масштаб: 2 мм.

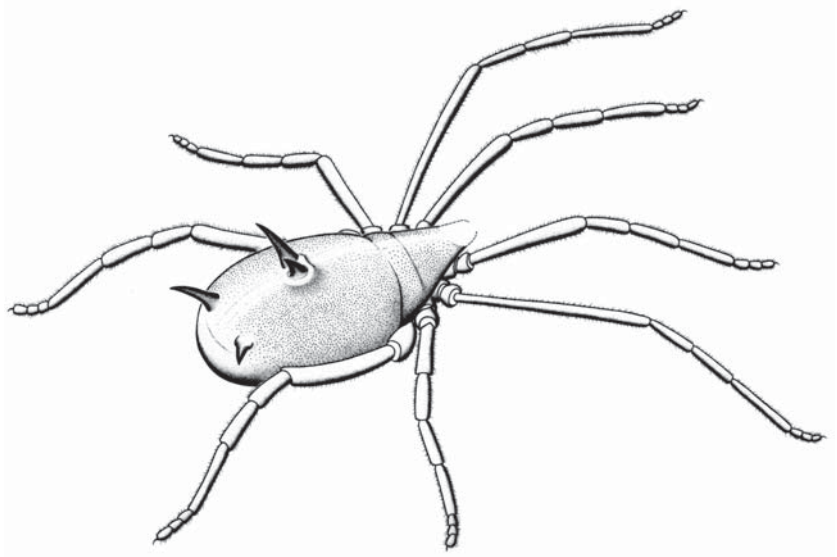


Fig. 5. Sketch reconstruction of the appearance in life of *Echinopustulus samuelnelsoni*. The anterior end of the carapace is unknown and not reconstructed here.

Рис. 5. Схематическая реконструкция внешнего вида *Echinopustulus samuelnelsoni*. Передняя часть карапакса не известна и поэтому не реконструирована.

sions of the bases of two conical, paramedian projections. The other two tubercles are posterolateral on the opisthosoma and again each is clearly the base of a larger, projecting structure. The counterpart (Figs 2, 4) confirms that each of these four bases bore a large spine or thorn. Excavation of the matrix infilling the spines revealed that these tapering structures extend quite deeply into the counterpart and would have been prominent projections on the back of the animal in life. The median pair originating from a single tubercle essentially point upwards while the posterolateral pair project upwards and backwards. They are clearly defensive adaptations increasing the handling time of the animal to potential predators. Spines of various lengths and orientations are seen in a number of harvestman lineages; and are particularly common among the tropical Laniatores. The ventral surface of the fossil is unknown. A reconstruction of the suggested appearance of the animal in life is presented in Fig. 5.

Affinities

This fossil does not unequivocally resemble any particular living harvestman group, but instead preserves a mosaic of characters, some of which are suggestive of particular living taxa (see below). The absence of eyes, pedipalps, and the entire leg series are a hindrance to resolving its affinities, while characters like pustulate cuticle occur in representatives of all major harvestman clades [Roewer, 1923; Martens, 1978]. It is conceivable that there were stem group Palaeozoic harvestmen which differed substantially from living forms and which are not assignable to existing clades. Nevertheless, the modern crown groups of some suborders can be excluded.

The apparent absence of opisthosomal tergites is similar to the situation in the basal cyphophthalmid harvestmen. However, unlike the Missouri fossil, cyphophthalmids do not show any thoracic division of the carapace and they still express segmental divisions of the opisthosoma as transverse furrows. Cyphophthalmids are also typically much smaller (1–3 mm) and the new fossil lacks the characteristic raised openings of the repugnatorial glands (ozophores) on the carapace which are autapomorphic for Cyphophthalmi.

The large thorns on the opisthosoma are reminiscent of spination in many genera of the morphologically diverse laniatores [see figures

in Roewer, 1923]. However, most laniatores (with a few exceptions) express some degree of opisthosomal segmentation. Furthermore, this suborder can be more explicitly excluded since, like cypthopthalmids, laniatores do not express a divided carapace. Protective spines have clearly arisen multiple times among different harvestman clades. Unfortunately the pedipalps in the fossil are equivocal. Large, raptorial pedipalps are a laniatore autapomorphy.

The divided carapace thus supports referral of this fossil to either the suborders Eupnoi or Dyspnoi; see e.g., Giribet *et al*. [1999, 2002] for a discussion of whether these two groups form a monophyletic clade. Intuitively, Eupnoi looks unlikely since the overwhelming majority of eupnoid taxa have a prominent, raised eye tubercle in the middle of the carapace, with a further sulcus dividing the carapace immediately behind the eyes. However, like this fossil, a number of living eupnoids lack external opisthosomal segmentation [e.g., Roewer, 1923]. Significantly, the Missouri fossil shares gross morphological characters with two groups among the Dyspnoi (the Trogulidae and the Ceratolasmatidae) but lacks unequivocal diagnostic characters of either. For this reason it is tentatively assigned to an unresolved, possibly basal, position within Dyspnoi and the two alternative placements are discussed in further detail below.

Trogulidae

Trogulid characters expressed by this fossil include: (a) the overall body shape, which is somewhat elongate with a long, subtriangular carapace, (b) the absence of opisthosomal segmentation (Giribet*et al*. [2002] scored a scutum magnum as present in *Trogulus*), (c) the finely pustulate cuticle ornament, and (d) a median band running along the length of the body [cf. Roewer, 1923: fig. 800]. The lack of an eye tubercle in the middle of the carapace is also consistent with this group, but as noted above excavations of the anterior end of the carapace failed to reveal either eyes or the one unequivocal trogulid autapomorphy: a bilobed projection or hood. That said, the full extent of the carapace could not be revealed within the nodule and from published figures a hood is also equivocal in the putative fossil trogulid*Eotrogulus*. No living trogulid has such prominent opisthosomal spines.

Ceratolasmatidae

The family Ceratolasmatidae was established by Shear [1986]. Ceratolasmatid characters expressed by the Missouri fossil refer primarily to opisthosomal spination. Like the fossil, members of this family have the pustulate ornament and at least one species, *Acuclavella merickeli* Shear, 1986 has a superficially very similar pattern of spination: two anterior spines arising from a single base followed by two more widely separated posterior spines [Shear, 1986: fig. 18]. However, when considered in detail this spination differs from that in the fossil in that the anterior spines in*A. merickeli* arise from the metapeltidium (i.e., the thoracic tergite of the carapace) while those in the fossil are clearly opisthosomal. Similarities to Ceratolasmatidae are further weakened by the fact that these extant harvestmen have a compact body retaining evidence of opisthsomal segmentation posteriorly, a prominent eye tubercle with a large spine and that other species have different patterns of spination [e.g., Shear, 1986: figs 23–29]. Given the likelihood that spination is homoplastic within Opiliones, trogulid affinities for the Missouri fossil look, on balance, more convincing; although explicit autapomorphies of this family are not unequivocally preserved.

Species description

Order Opiliones Sundevall, 1833

Suborder ?Dyspnoi Hansen et Sørensen, 1904

***Echinopustulus* gen.n.**

ETYMOLOGY. Combination of *Echino* and *pustulus* for the spiny and pustulate nature of the body. The gender is masculine.

DIAGNOSIS. Carboniferous harvestmen with a pustulate cuticle bearing two pairs of dorsal spines on an unsegmented opisthosoma. Anterior pair of spines originate close to centre of opisthosoma from a single tubercle; more posterior spines more widely separated.

REMARKS. The new genus reflects the rather unique spiny morphology which is not seen in any other putative Carboniferous harvestman; or indeed any other described Palaeozoic arachnid.

Echinopustulus samuelnelsoni **sp.n.**
Figs 1–5.

MATERIAL. Holotype and only known specimen. Peabody Museum (repository number: YPM 204165), Yale, USA.

ETYMOLOGY. Named at Elliot Nelson's request for his late father, who encouraged his interest in natural history.

DIAGNOSIS. As for the genus.

DISTRIBUTION. Upper Carboniferous Pleasanton Group of western Missouri, USA; possibly near the town of Windsor.

DESCRIPTION. Total preserved body length 8.7 mm. Maximum preserved carapace length 2.8 mm. Carapace subtriangular, basal width 3.4 mm, divided towards posterior end by straight, transverse sulcus. Eyes and pedipalps equivocal. Leg series incomplete, but trochanters bulbous, length *c.* 0.8 mm. Legs long and slender. Leg 1 femur 4.3 mm long. Femur of leg 3 at least 4.1 mm long. Leg 4 indistinct, but slender. Opisthosoma oval, broadly joined to prosoma via a procurved sulcus. Opisthosoma dome-like and highly vaulted; standing about 2 mm proud of the nodule surface in the part. Cuticle splayed out laterally on one opisthosomal margin. Total opisthosoma length 5.9 mm; maximum width 4.3 mm. Dorsal surface of both carapace and opisthosoma ornamented with dense pattern of minute pustules; absent from carapace margins and a weakly defined median band. Median band, width *c*. 0.5 mm, extends some 7 mm along the body from the middle of the carapace down onto the opisthosoma. Opisthosoma bears two pairs of spines preserved as spine bases (diameter *c.* 0.4 mm) on part and as deep holes in counterpart. Anterior pair paramedian, emerging dorsally from a single, centrally positioned, heart-shaped tubercle; diameter *c.* 1.1 mm. Posterior pair emerge postero-laterally at a separation of *c.* 2.0 mm from each other.

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