The enigmatic fossil arachnid *Kustarachne tenuipes* Scudder, 1890 is a harvestman

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Abstract

Kustarachne tenuipes Scudder, 1890 is the most complete example of a group of enigmatic fossils from the Upper Carboniferous of Mazon Creek, Illinois, USA. Although assigned to a new arachnid order named Kustarachnida Petrunkevitch, 1913, in recent publications these long-legged fossils have been assumed to be misidentified harvestmen (Arachnida: Opiliones). Nevertheless, the original descriptions imply some features which would be unusual for harvestmen, in particular a putative segmented pygidium in a terminal position on the opisthosoma. Detailed re-examination of the type of *K. tenuipes* supports Beall's suggestion that Petrunkevitch's diagnostic characters of Kustarachnida are mostly misinterpretations. *K. tenuipes* does not preserve any unequivocal autapomorphies used to define extant Opiliones, but a combination of features – e.g. a divided carapace with a metapeltidium and a single pair of eyes, slender legs and a large opercular plate behind the leg coxae – are all consistent with it being a harvestman. Indeed in gross morphology it closely resembles various living taxa and reinforces the hypothesis that essentially modern-looking harvestmen existed as early as mid-Palaeozoic times.

Key words: Opiliones, Kustarachnida, Carboniferous, Mazon Creek

INTRODUCTION

Kustarachne tenuipes Scudder, 1890 from the famous Upper Carboniferous Mazon Creek locality in Illinois, USA was originally described as an example of what would now be regarded as the extinct arachnid order Phalangiotarbida. The genus was named after the Czech author Johann Kušta, who described a number of fossil arachnids in the late nineteenth century. Two more species of *Kustarachne* were subsequently described from the same Mazon Creek locality: *K. exstincta* Melander, 1903 (note original spelling, misspelled '*extincta*' in almost all subsequent publications) and *K. sulcata* Melander, 1903. The latter species was later recognised as a ricinuleid (Petrunkevitch 1913) and following Selden (1992) it was referred to a new ricinuleid genus as *Amarixys sulcata*

(Melander, 1903). Another species of *Kustarachne, K. conica* Petrunkevitch, 1913, was also described from Mazon Creek. In this monograph Petrunkevitch (1913) raised *Kustarachne* to a new order, Kustarachnae, eventually modified to Kustarachnida (e.g. Petrunkevitch 1955) to conform to recommendations on nomenclature.

Kustarachnida was diagnosed by Petrunkevitch on a unique combination of characters, including a narrow pedicel between the prosoma and opisthosoma, coxae radiating from a tiny sternum, two eyes on a tubercle, chelate pedipalps in which the coxae are fused together (similar to Thelyphonida and their subchelate pedipalps) and long, slender legs. Petrunkevitch (1949, 1955) placed Kustarachnida close to Thelyphonida (whipscorpions) and Schizomida in the group

Camarostomata, in which the camarostome is the name given to the fused, immovable pedipalpal coxae. After 1955, Kustarachnida was maintained as a distinct order by subsequent authors and some speculative attempts were made to place it in arachnid phylogenies using characters derived from Petrunkevitch's descriptions. For example, van der Hammen (1977) tentatively included Kustarachnida in his group Apatellata with solifuges and pseudoscorpions based on the supposed presence of two trochanters in *Kustarachne* (but see below) while Grasshoff (1978) again placed Kustarachnida close to whipscorpions based on the putative camarostome.

Beall (1986, 1997) criticised Petrunkevitch's conclusions about *Kustarachne* and stated that many of his diagnostic characters were misinterpretations of the fossils, while the combination of triangular coxae, slender legs and a pair of median eyes implied that *Kustarachne* was actually a fossil harvestman (Opiliones). Although no formal redescription or new illustrations of this material have been presented since Petrunkevitch's monographs, Beall's suggestion that these animals are harvestmen has generally been accepted (e.g. Selden 1993a,b; Dunlop 1996; Selden & Dunlop 1998). Nevertheless, explicit autapomorphies of Opiliones have not been identified in *Kustarachne*. As both Beall (1986) and Shultz (1990) have noted, *Kustarachne* is described as having at least one feature which would be unusual for a harvestman – namely a small, segmented pygidium (or postabdomen) at the end of the opisthosoma. Both Scudder's (1890) and Petrunkevitch's (1913, fig. 35) descriptions even imply the presence of a slender, poorly preserved telson in *K. tenuipes*. All known harvestmen have, by contrast, a plate-like anal operculum in this position and lack a telson completely; see e.g. Shultz (2000). The aim of this present study is to re-examine *K. tenuipes* and to see whether it preserves any characters which can resolve its affinities.

MATERIAL AND METHODS

The holotype and only known specimen of *Kustarachne tenuipes* was obtained from the United States National Museum of Natural History, Smithsonian Institution, Washington (USNM 37967). The specimen consists of a part and counterpart. The former is displayed in the museum and was not available for loan, but high-quality digital images of this fossil (Fig. 1A) were provided by Finnegan Marsh (USNM) and an interpretative drawing was prepared from them (Fig. 2A). The fossil harvestman *Nemastomoides longipes* (Petrunkevitch, 1913) was obtained from the Peabody Museum of Natural History, Yale University (YPM 171). This specimen comes from the same Mazon Creek locality as *K. tenuipes* and resembles it in having long, slender legs. The fossils were also compared to extant arachnid material in the collections of the Museum für Naturkunde, Berlin. The types of the other two species of *Kustarachne* were not available for loan at this time. From their descriptions in the literature (Melander 1903; Petrunkevitch 1913) both appear to be rather poorly preserved and their status as distinct species is questionable. Drawings of *K. tenuipes* were prepared with the aid of a *camera lucida* attachment and immersion of the specimen in alcohol proved particularly useful for revealing some details. Descriptions of structures (ridges, tubercles, etc.) refer to their appearance in life. Since the morphology of the fossil supports harvestman affinities (see Discussion) descriptive terminology generally follows that used for Opiliones by Shultz (2000).

Kustarachne tenuipes is preserved as an external mould in an ironstone concretion formed from clay and the iron mineral siderite. The Mazon Creek locality, like much of the Coal Measures, is interpreted as a swampy, deltaic, forest habitat which has been dated as Upper Carboniferous (Westphalian D); Moskovian in alternative stratigraphic schemes. A summary of the geological setting, dating, interpretation of the original environ-

ment and the associated plant and animal fossils can be found in Nitecki (1979) and the early chapters of Shabica & Hay (1997). The fossil has to some extent been compressed dorso-ventally. The part preserves the dorsal surface and the counterpart the ventral surface, respectively. Under alcohol impressions of the original cuticle and its ornament are apparent in places.

RESULTS

Carapace

Petrunkevitch's (1913, fig. 34) original illustration of the carapace, or prosomal dorsal shield, is hopelessly over-simplified and misrepresents the rather large size of the median eyes (Figs. 1A, 2A). More seriously, he did not recognise that the carapace in *Kustarachne tenuipes* essentially comprises two sclerites – recognised here as the fused propeltidium + mesopeltidium and the separate metapel-

tidium – figuring only the anterior part as the entire carapace. In fact the carapace is divided by a distinct procurved sulcus behind the eyes and this posterior sclerite (the metapeltidium) is then followed by the oval opisthosoma (Figs. 1A, 2A). There is also a further groove or sulcus immediately behind the eyes, however this does not extend across the full width of the carapace. This is also seen in living phalangioid harvestmen (Fig. 3) where it represents the original boundary between the fused propeltidium and mesopeltidium (see also Shultz 2000, fig. 1). The propeltidium in the fossil bears depressions, in particular one on the right side, which could conceivably be the ozopores (the openings of the repugnatorial glands), but this interpretation is difficult to confirm. Overall, the carapace has a semicircular outline on its anterior and right lateral sides, but further morphological details are not preserved. Some ventral features
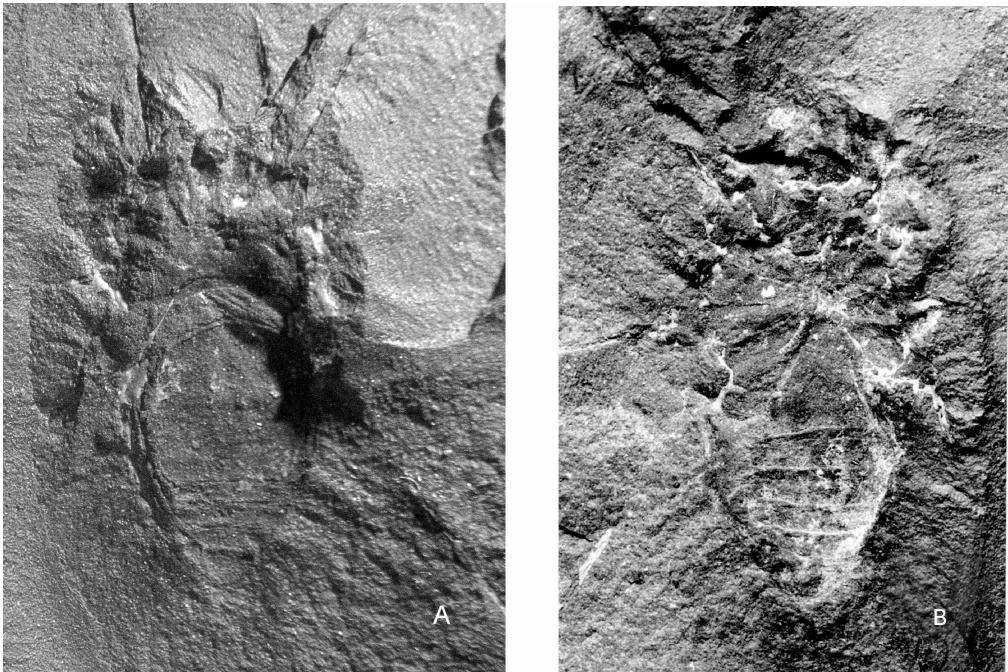

Fig. 1. *Kustarachne tenuipes* Scudder. USNM 37967, an enigmatic fossil arachnid from the Upper Carboniferous (Westphalian D) of Mazon Creek, Grundy County, Illinois, USA. Assigned to the extinct order Kustarachnida by Petrunkevitch (1913), but reinterpreted here as a harvestman (Opiliones). (**A**) Dorsal view. (**B**) Ventral view. Scale bar equals 2 mm.

(subtriangular coxae) appear to be superimposed through onto the carapace while the left margin is poorly preserved and the outline of the carapace here is indistinct.

Chelicerae

The putative ' pedipalps' were originally figured as short appendages, emerging from the camarostome, with four articles, the last two of which formed a chelate claw. In fact these structures are probably the chelicerae (Fig. 2A: ch). Petrunkevitch (1913) appears to have overlooked two slender, pediform, but incomplete elements either side of them (best seen on the ventral surface under alcohol) which are regarded here as the true pedipalps (Fig. 2B: pa). The chelicerae themselves are preserved as a pair of blunt, rounded elements, suggestive of quite robust structures in life. However, the short, stalk-like podomeres and the terminal claw in Petrunkevitch's figures could not be confirmed in this study and it is difficult to determine exactly which cheliceral articles are preserved here.

' Camarostome'

The fused pedipalpal coxae were one of the key features in the original diagnosis of Kustarachnida and the determination of its affinities. There is an approximately triangular region as indicated in Petrunkevitch's illustrations, but its interpretation as a single, fused sclerite covering the mouth region is unconvincing. Preservation in this whole mouth region is poor and clearly outlined features – as compared to the adjacent coxae – are lacking. If Beall (1986) is correct and *K. tenuipes* is regarded as a harvestmen, then there are a series of sclerotised features such as the labium and the coxapophyses (e.g. Shultz 2000) which could potentially be preserved in this region. These coxapophyses are median projections from the coxae of the pedipalps and the first two pairs of legs which help to form a preoral cavity, or stomatheca, in harvestmen. The preservation of the fossil does not allow specific elements in the harvestman scheme to be

identified with any confidence. Given the reinterpretation of the identity and position of the pedipalps (see above), a ' camarostome' *sensu* Petrunkevitch should be regarded as equivocal in *K. tenuipes*. There is no obvious sternum preserved in the fossil between the leg coxae.

Legs

The leg coxae are all approximately the same size and shape and form subtriangular structures. Those on the left side all preserve a distinct, circular pit. Their regularity suggests that the pits may not be artefacts, but the identity and/or function of these structures is unclear. The double trochanters figured by Petrunkevitch are incorrect. The trochanter is a somewhat quadrate element and distal to it the femur begins broadly, but then rapidly narrows into the slender, elongate portion of the leg. This region of narrowing was originally interpreted as a separate, subtriangular podomere, but in fact no podomere boundary is evident between it and the rest of the femur, as is clearly preserved between the coxa and trochanter. A similar narrowing of the proximal region occurs in the legs of at least some extant harvestmen; see e.g. Roewer's (1923, fig. 1053) illustration of *Leiobunum paessleri* Roewer, 1910. The coxae, trochanters and femora preserve an ornament of what would have been fine tubercles in life. The more distal regions of the legs are mostly incomplete and podomere boundaries are difficult to distinguish, but they clearly show their slender, elongate nature. Fold-like lineations along the length of the legs may be due to some degree of post-mortem shrinkage. It is, unfortunately, impossible to tell whether leg II was longest; a characteristic of many extant, ingroup harvestmen.

' Pedicel'

Petrunkevitch (1913) appeared to interpret the presence of a pedicel based on the ventral surface with the triangular plate (see below) narrowing towards the coxal region (Figs. 1B, 2B).
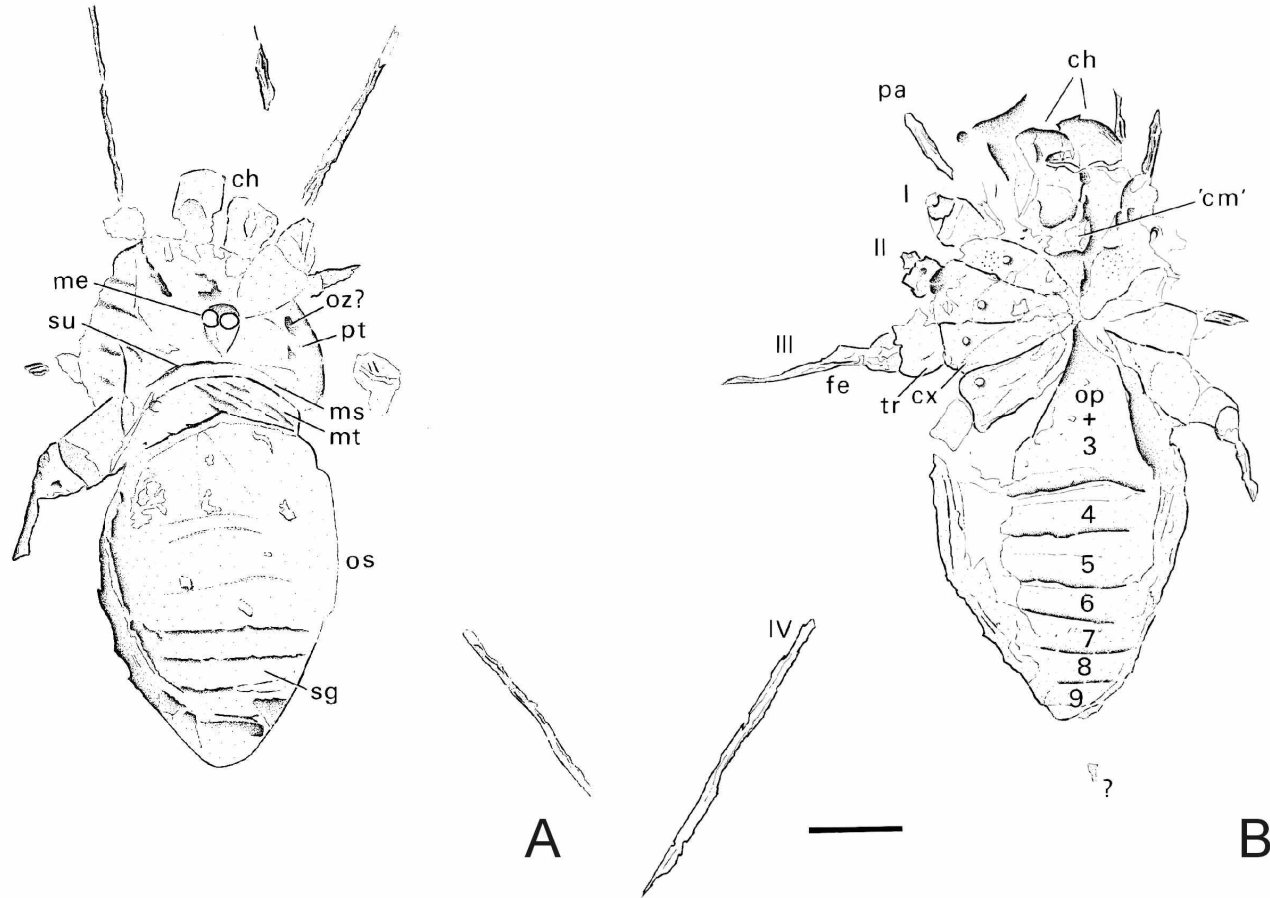
Fig. 2. *Camera lucida* drawing of the specimens shown in Fig. 1. (**A**) Dorsal view. (**B**) Ventral view. Abbreviations: ch = chelicerae; 'cm' = region originally interpreted as the camarostome; cx = coxa (note tubercles); fe = femur; me = median eyes; ms = mesopeltidium of carapace; mt = metapeltidium of carapace; op = operculum; os = opisthosoma; oz? = putative ozopore; pa = pedipalp; pt = propeltidium of carapace; sg = segmented posterior part of opisthosoma; su = sulcus behind median eyes demarcating propeltidium and mesopeltidium; tr = trochanter; opisthosomal sternites tentatively numbered after the scheme of Shultz (2000); legs numbered from I–IV; ? = structure originally interpreted as a telson fragment. Scale bar equals 2 mm.
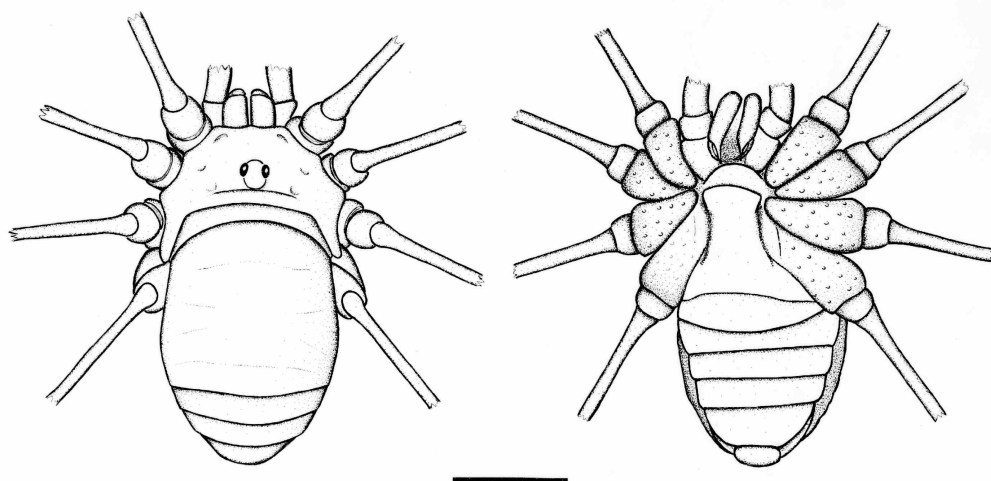
Fig. 3. Comparative drawing of a male of the extant North American harvestman *Leiobunum vittatum* Say. (Opiliones: Palpatores: Eupnoi: Phalangiidae). Drawing made from alcohol-preserved material in the Berlin collection (ZMB 990 from Carolina). Note the striking similarity in gross morphology between this living species and the c. 300 million year old Carboniferous fossil *K. tenuipes*; in particular the divided carapace with an additional sulcus immediately behind the eye tubercle and the dorsal opisthosoma in which the expression of discrete tergites is restricted to the posterior third. Scale bar equals 2 mm.

In contrast, in dorsal view (Figs. 1A, 2A) the prosoma and opisthosoma seem to be broadly joined together through a wide, procurved margin – in the form of a distinct sulcus – which separates the metapeltidium (see above) from the opisthosoma. There is a slight narrowing of the whole body in this region which indicates the division between the two body tagmata. However, this is in no sense the stalk-like pedicel which characterises arachnids like spiders (Araneae) and whipspiders (Amblypygi). Petrunkevitch's pedicel character for *K. tenuipes* is therefore rejected.

Opisthosoma

The opisthosoma is oval in outline, but tapers to a blunt point posteriorly. The dorsal surface of the opisthosoma was illustrated, somewhat inaccurately, by Scudder (1890), but was not figured at all by Petrunkevitch (1913). Dorsally, the anterior region appears to be quite smooth with no distinct pattern of segmentation or other form of ornament. Only towards the posterior end can at least three segments

be distinguished. These have straight posterior margins. Shultz (2000) noted how in many extant harvestmen dorsal segmentation is only recognisable by colour and/or muscle insertion patterns rather than discrete tergal plates. Ventrally, the first sternal element probably represents the operculum plus the next sternite; cf. sternite IX in Shultz (2000, fig. 1). The anterior margin of the operculum thrusts up between the posteriormost leg coxae forming a triangular structure in this region. An area of matrix between this operculum and the coxa on the left side suggests some degree of disarticulation has taken place here. There is no obvious transverse division between the operculum and sternite IX, but in comparison with extant harvestmen, some taxa express this character while other, otherwise similar forms, do not (e.g. figures in Roewer 1923). This large anterior sclerite in *K. tenuipes* is followed by four large sternites, all with straight posterior margins, plus at least two additional segments making up the ill-defined 'pygidum' region (see below). Thus, as in Shultz's (2000) figures

of an extant *Leiobunum*, the fossil *K. tenuipes* appears to show an opisthosoma in which segmentation is poorly expressed dorsally and rather better expressed ventrally.

'Pygidium'

The discretely segmented pygidum shown in the original illustrations is not clearly evident in the fossil, where the posterior outline becomes rather difficult to follow. However, there is a degree of tapering at the posterior end of the opisthosoma. This posterior tapered region does not express strong tagmosis, rather it seems to merge into the outline of the rest of the opisthosoma (Figs. 1B, 2B). It is not a sharply differentiated structure like the pygidiums of arachnids such as whipscorpions, ricinuleids or the extinct trigonotarbids. A true pygidium is thus regarded as equivocal in *K. tenuipes*. Living palpatore harvestmen tend to have a bluntly rounded posterior end to the abdomen, but a tapering posterior end is present in a range of extant species illustrated by Roewer (1923) and, in isolation, this character does not preclude harvestmen affinities for *K. tenuipes*.

'Telson'

There is a small, elongate cuticular element behind the opisthosoma which both Scudder (1890) and Petrunkevitch (1913) recognised (Figs. 1B, 2B). However, it is not in contact with the opisthosoma and does not show annulations like, for example, the telson of whipscorpions. Since there are a number of fragments of plant material distributed randomly throughout the nodule it is quite possible that the 'telson' in *K. tenuipes* is simply a fortuitous piece of plant material located behind the opisthosoma.

DISCUSSION

Explicit autapomorphies of Opiliones (cf. Shultz 1990, p. 32) are equivocal in *Kustarachne tenuipes*. The presence or absence of features such as tracheal openings on the genital segment, a penis and details of the proximal leg

articulations are not preserved. There are structures on the carapace which could be interpreted as the openings of repugnatorial glands (Fig. 2A) – a good harvestman autapomorphy – but they are not wholly convincing. However, as Beall (1986) correctly pointed out, the general shape of *K. tenuipes* is more consistent with it being a harvestman than any other arachnid order.

The key features to note are: (1) a carapace divided into a propeltidium + mesopeltidium and a metapeltidium, (2) a single pair of (large) median eyes, (3) a broad prosoma–opisthosoma junction, (4) long, slender legs, (5) absence of an obvious sternum between the leg coxae, (6) a compact, oval opisthosoma where the segmentation is more distinct posteriorly on the dorsal surface and ventrally in general, and (7) a large ventral plate, or operculum, at the front of the opisthosoma which thrusts up between the last pair of leg coxae. By contrast, many of the characters used by Petrunkevitch (1913, 1949, 1955) to characterise Kustarachnida are either equivocal, i.e. the camarostome and pygidium, or incorrect, i.e. the short, chelate pedipalps, the pedicel and the telson. Beall's (1986, 1997) suggestion that kustarachnids are misidentified harvestmen is therefore strongly supported and further characters in favour of this assessment are presented here.

With respect to its affinities, *Kustarachne tenuipes* is superficially quite similar to *Nemastomoides longipes*, a long-legged fossil with slender coxae from the same Mazon Creek locality, which has always been accepted as a harvestmen (cf. Petrunkevitch 1913). *N. longipes* also lacks unequivocal harvestman autapomorphies (see above) and is recognised as a member of this group simply on its overall appearance. Differences in the proportions of the body suggest that the two genera can probably be maintained as distinct taxa. Specifically, the prosoma in *N. longipes* is somewhat broader relative to its length compared to *K. tenuipes*.

Considering the most recent accounts of harvestman higher systematics (Shultz 1998; Giribet et al. 1999, 2002), *K. tenuipes* preserves few characters which easily resolve its position relative to living Opiliones. Of the three principal groups which are widely recognised, *K. tenuipes* clearly looks more like a palpatore than either a cythophthalmid, in which the legs are short and the median eyes are absent, or a laniatore, where the pedipalps are typically massive and subraptorial, the last pair of legs are often noticeably enlarged and the body can be highly ornamented with spines and tubercles. Palpatores is usually divided into two tribes, Eupnoi and Dyspnoi and the monophyly (Shultz 1998) or paraphyly (Giribet et al. 1999, 2002) of the palpatores is currently the subject of active debate. Although *K. tenuipes* cannot easily be placed on the diagnostic characters used for Recent taxa, in terms of the dorsal morphology and slender legs it is remarkably consistent in its gross morphology with living phalangioids (Eupnoi); see e.g. various illustrations in Roewer (1923) or the *Leiobunum* (Family Gagrelliidae) used by Shultz (2000) in his morphological investigations. A drawing of a modern harvestman, *Leiobunum vittatum*, is included here (Fig. 3) for comparison.

Alternatively, *K. tenuipes* can be compared to extant members of the Nemastomatidae (Dyspnoi), which also express a similar gross morphology. Some Recent dyspnoids again have tergites only expressed in the posterior part of the opisthosoma. However, the overall body of nemastomatids tends to be rather more compact with little or no tagmosis between the prosoma and opisthosoma and a tendency – at least in some living taxa – for the various carapace sclerites to fuse together. In this context, *K. tenuipes* is rather more phalangioid-like in expressing the divided carapace and a clear narrowing between the two body tagmata (Figs. 2-3).

In conclusion, as other authors have suggested (Beall, 1986, 1997; Selden 1993a,b; Dunlop 1996), Kustarachnida should not be treated as a separate arachnid order, but should be included among the opilionids. It is difficult to integrate *K. tenuipes* into the systematics of living taxa since explicit apomorphies of modern higher taxa are not clearly preserved. Nevertheless, it appears most similar in overall appearance to a modern phalangioid. By comparison, an unnamed fossil from the Lower Carboniferous of Scotland (Wood et al. 1985), has not been assigned to a group (Selden 1993a), but is also remarkably modern-looking with a small, rounded body and long slender legs. An older, undescribed harvestman from the Early Devonian Rhynie chert locality in Scotland also looks like it can be assigned to an extant clade (Dunlop *et al.* 2003). All this material, including *K. tenuipes*, implies that harvestmen are a very ancient group and that anatomically modern forms existed as early as the mid Palaeozoic.

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