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REINTERPRETATION OF THE SILURIAN SCORPION *PROSCORPIUS OSBORNI* (WHITFIELD): INTEGRATING DATA FROM PALAEOZOIC AND RECENT SCORPIONS

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Abstract: The morphology of the Late Silurian (Přídolí) scorpion *Proscorpius osborni* (Whitfield, 1885*a*) (Arachnida: Scorpiones), from the Phelps Member of the Fiddlers Green Formation of New York, the 'Bertie Waterlime' of earlier stratigraphic schemes, is revised based on studies of new and existing material (a total of 32 specimens). Previous reports of four cheliceral articles, gnathobasic coxae, a labium and gill slits in *P. osborni* can be dismissed. However, we confirm the presence of both median and compound lateral eyes, a pair of tarsal claws, albeit on a more digitigrade foot compared to that of modern scorpions, more than five ventral mesosomal sclerites and a fairly modern pattern of metasomal (i.e. tail) carinae. The co-occurring *Archaeophonus eurypteroides* Kjellesvig-Waering, 1966 and *Stoermeroscorpio delicatus* Kjellesvig-Waering, 1986 are regarded as junior synonyms of *P. osborni*. Fossil scorpion higher systematics is plagued by a plethora of unnecessary and largely monotypic higher taxa and we draw on the results of Jeram's cladistic analysis from 1998 to synonymize formally a series of families and superfamilies with Proscorpiidae Scudder, 1885.

Key words: Scorpiones, morphology, terrestrialisation, 'Bertie Waterlime', USA.

Scorpions have one of the most complete palaeontological records of any arachnid order. The fossil examples are significant for their distinction between the stem group and the crown. Over 100 fossil species are currently recognised: 97 listed in Fet *et al.* (2000) plus a handful described subsequently. Remarkably, the majority of these (more than 80) are Palaeozoic in age. The scorpion fossil record appears, therefore, to be heavily biased towards these older taxa. Part of the reason for this may be that scorpion cuticle is more readily preserved than that of other non-mineralised arthropods, such that scorpions are recovered more frequently in the widespread Silurian–Carboniferous localities yielding brackish and/or terrestrial arthropods; see Jeram (2001) for further discussion. One of the oldest and most celebrated of these early fossils is *Proscorpius osborni* (Whitfield, 1885*a*) from the late Silurian (*c.* 418 Ma) 'Bertie Waterlime' of New York. *Proscorpius* is neither the oldest geologically nor (according to Jeram 1998) the most basal scorpion. It is, however, one of best known (see synonymy list) thanks to numerous well-preserved specimens (cf. Kjellesvig-Waering 1966, 1986), and has often been illustrated as a classic example of a primitive scorpion (e.g. Werner 1934; Sissom 1990; Weygoldt 1998; Dunlop and Braddy 2001; Farley 2001). In this study, we examined new material of this important species recently accessioned into the collections of the Peabody Museum, Yale University and the American Museum of Natural History. We re-examined the original type material and the types of two further species from the same locality, which we interpret as junior synonyms of *P. osborni*. Collectively, we examined a total of 32 specimens, the single largest suite of specimens of an extinct scorpion species.

The monograph of Kjellesvig-Waering (1986) remains the most significant publication on fossil scorpions in the past 20 years. Although presenting a comprehensive and detailed account of the fossil scorpions known until that date, invaluable for tracking down citations and type material, Kjellesvig-Waering's revision suffers from two major drawbacks. First, it was compiled posthumously, such that in places the author's ideas had to be inferred by the editors and important observations in the text are often unsupported by the figures (see below), which tend to be interpretative line drawings rather than

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photographs. Second, a typological classification was presented with a surfeit of (often monotypic) higher taxa based on a limited set of characters. This resulted in a clumsy, 'top-heavy' system of mutually exclusive families and superfamilies with relatively low information content; see further comments in Fet *et al.* (2000, p. 554). Attempts to address this problem cladistically were undertaken by Stockwell (1989) and Jeram (1998). However, Stockwell's (1989) analysis and revised classification were based on an untested assumption that the fossil genera recognised by Kjellesvig-Waering (1986) were monophyletic (Prendini 2000, 2001). Stockwell's work was never formally published, although it is often cited as if it were. Jeram's (1998) analysis, which did not make this assumption of monophyly, demonstrated that many of Kjellesvig-Waering's (1986) groups collapse when additional characters are considered. Jeram thus informally recognised a series of genera and families as plesions approaching the crown group (Orthosterni).

Even within the crown group, scorpion higher systematics is the subject of active controversy (Soleglad and Fet 2003; Prendini and Wheeler 2005; Fet and Soleglad 2005). One of the points to emerge from this debate is the potential role of fossils for polarising characters in modern clades. In this context it is also worth noting Farley's (2005) observation that the early developmental stages of some extant scorpions appear to recapitulate morphology otherwise seen only in fossil taxa. Part of the problem with integrating fossil and Recent data arises because the oldest scorpions were described using decidedly different characters and terminology, typically sharing more in common with those developed for the extinct Eurypterida, than with those used to describe modern scorpions. Our intention in this contribution is to use *P. osborni* as an example of how fossil scorpions can be described and scored for integrative studies, a methodology that we hope can be applied to other extinct species in the future. In a broader context, fossil scorpions are intimately associated with various major conflicts in arachnid evolution. Two particular examples are (1) a putative harvestman (Opiliones) and scorpion clade (e.g. Shultz 2000), based in part on a preoral tube, or stomotheca, formed from coxapophyses projecting from the limb bases, and (2) whether book lungs have a single derivation (Scholtz and Kamenz 2006) or multiple origins (Dunlop and Webster 1999). *P. osborni* contributes to both debates by, supposedly, preserving gnathobasic coxae (i.e. it appears to lack the stomotheca) and gill slits (implying aquatic scorpions and multiple lung origins). Our examination of new and existing fossil material offers us the opportunity to reassess the validity of these, and other, characters and their relevance for understanding early scorpion evolution.

PREVIOUS WORK

Proscorpius osborni was first described by Whitfield (1885*a*) from a single specimen collected in 1882 by A. O. Osborn from the 'Bertie Waterlime' north-west of New York City, NY, USA. Originally placed in *Palaeophonus* Thorell and Lindström, 1884 (erected in the previous year for a Swedish Silurian scorpion), Whitfield (1885*b*) subsequently created a new genus, *Proscorpius* Whitfield, 1885*b*, for the American species, differentiating it from *Palaeophonus* primarily on the presence of paired claws on the walking legs, rather than a single tarsal spine as described for *Palaeophonus*. Scudder (1885) proposed the subfamily Proscorpionini for *Proscorpius*, placing it in Eoscorpionidae, an otherwise Carboniferous family. Thorell (1886), based solely on the published photograph, reinterpreted Whitfield's (1885*a*) holotype and rejected the claim of paired tarsal claws, to which Whitfield (1886) was forced to offer an exasperated defence. Clarke and Ruedemann (1912, pl. 88) reproduced both Whitfield's original figure and a new interpretative drawing. Elements of the pectines, comb-like sensory organs on the underside of the opisthosoma, were reported for the first time. Petrunkevitch (1949) re-illustrated the holotype of *P. osborni* and synonymized *Proscorpius* with *Palaeophonus* based on the earlier criticisms of Whitfield's tarsal interpretation. However, in subsequent studies (Petrunkevitch 1953, 1955) he returned the species to *Proscorpius*, redefining it on various body proportions; see Kjellesvig-Waering (1966) for further details.

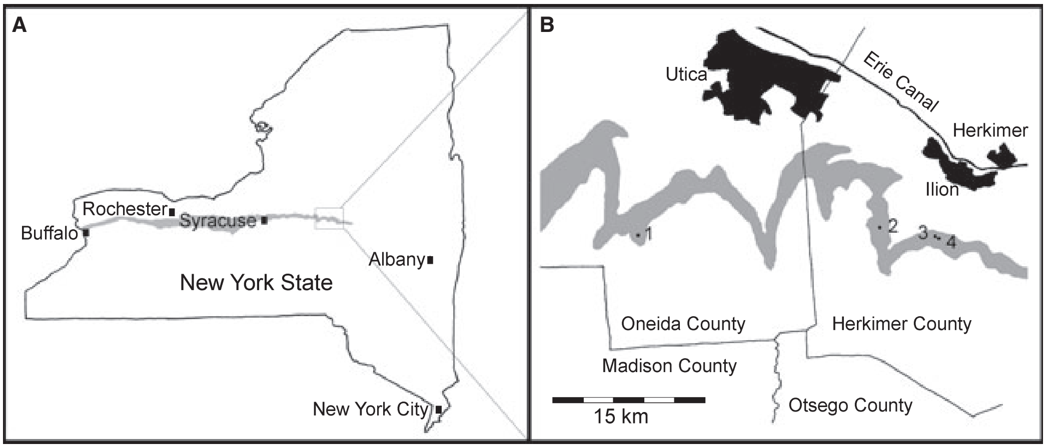
Kjellesvig-Waering (1966) offered a substantial revision of *Proscorpius*, including a rediagnosis, based on an examination of the holotype and additional 'Bertie Waterlime' material. Scudder's subfamily was raised to familial status, Proscorpionidae, later emended to Proscorpiidae. A new genus and species, *Archaeophonus eurypteroides* Kjellesvig-Waering, 1966 from the same locality was also introduced (see 'Systematic palaeontology'). In his subsequent monograph, Kjellesvig-Waering (1986) described in detail six new specimens of *P. osborni*, all from the private collection of Samuel Ciurca (now housed at the Peabody Museum, Yale University). He introduced several significant characters for *P. osborni*, some of which seem atypical for scorpions and underline the need for careful description and unambiguous illustrations. These include the presence of four cheliceral articles, gill slits, a labium slotting into a notch at the front of an oval sternum, and gnathobasic teeth on the first leg coxae. Finally, a third co-occurring species was erected, *Stoermeroscorpio delicatus* Kjellesvig-Waering, 1986, considered sufficiently unique to warrant its own superfamily (see 'Systematic palaeontology').

MATERIAL AND METHODS

The holotype of *Proscorpius osborni* and a second specimen (labelled 'hypotype') are deposited in the American Museum of Natural History (AMNH), the holotype of *Archaeophonus eurypteroides* is in the New York State Museum (NYSM), and the holotype of *Stoermeroscorpio delicatus* is in the Peabody Museum, Yale University (YPM). The Samuel Ciurca material mentioned above, comprising 14 specimens, was recently acquired by the YPM and new repository numbers are listed below under 'Systematic palaeontology'. A further 13 specimens from the named collection of Allan Langheinrich, Illion, New York, were recently accessioned in the permanent collection of the AMNH. For completeness, we have also listed specimens in the Buffalo Museum of Science (BMS) and previous repository numbers of the Cornell University Geological Museum (CUGM) collections, now in the NYSM. Specimens were photographed using a Microptics$^{\mathrm{TM}}$ ML-1000 digital photomicrography system, illustrated with a camera lucida on a Leica MZ16 stereoscope and compared to extant material in the collections of our respective institutions. Measurements, recorded in mm (Table 1), were taken with an ocular micrometer.

GEOLOGICAL SETTING

The material described here all originates from the Phelps Member of the Fiddlers Green Formation of the Bertie Group (Ciurca 1973). The Bertie Group is particularly renowned for the numerous eurypterid horizons it contains and the entire group facies is commonly referred to as the 'Bertie Waterlime' and dated as Late Silurian (Přídolí, *c.* 418 Ma). The entire Bertie Group is a 15–18-m-thick sequence of limestones, dolomitic limestones and evaporites in western and central New York State, USA (see Text-fig. 1A) and south-eastern Ontario, Canada. The stratigraphic sections and the fossil content suggest that it was deposited in a near-shore marine setting, but the evaporites and casts of halite pseudomorphs with sides of up to 30 cm suggest the environment was far from normal marine; hypersalinity must have prevailed throughout most of the depositional history of the Bertie Group (Ciurca and Hamell 1994) and probably retarded bacterial growth. Mud-cracked horizons suggest that parts of the group were occasionally subaerially exposed. It is even conceivable that preservation of eurypterid and scorpion cuticles were promoted by the elevated salinity levels, as their chitinous cuticle is usually prone to degradation by chitinophosphatic bacteria. The Phelps Member, from which the scorpions have been recovered, is a widespread unit throughout the area where the Bertie Group is found. Curiously, the scorpions that have been found thus far originate from only four localities, all of which are geographically within 30 km of each other and close to Utica, NY (Text-fig. 1B, 1–4). The holotype comes from Forge Hollow, close to Waterville (Text-fig. 1B, 1). One specimen comes from the area around Jerusalem Hill (Text-fig. 1B, 2) and the remaining specimens come from an area between Elizabethtown and Spinnerville (Text-fig. 1B, 3–4). Rare, early terrestrial plants like *Cooksonia* sp. also occur in these localities (at least in those that are well sampled) and we cannot, therefore, exclude the possibility that the scorpions are derived from a terrestrial habitat, although the evidence is still inconclusive. Faunal data capable of indicating the original habitat of these scorpions remain to be analysed.

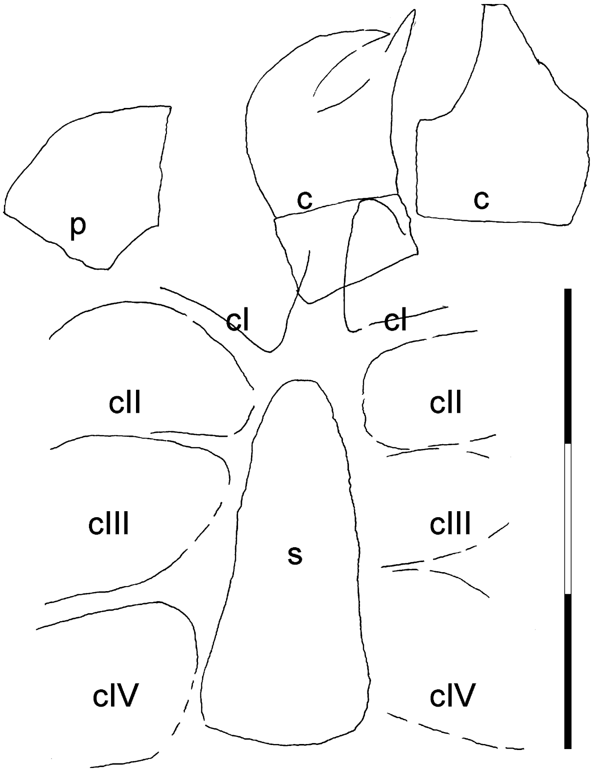


TEXT-FIG. 1. Map of the localities yielding specimens of *Proscorpius osborni* (Whitfield, 1885*a*). A, New York State with the outcrop belt of the Bertie Group marked in grey. B, area around Utica enlarged, again with the outcrop belt in grey, showing four localities yielding *P. osborni* fossils. 1, Forge Hollow (1 specimen); 2, opposite Litchfield Town Hall (1 specimen); 3, Allan Langheinrich Quarry (13 specimens recognized herein); 4, Passage Gulf (17 specimens recognized herein).

MORPHOLOGICAL INTERPRETATION

Chelicerae

The classic interpretation of Chelicerata depicts chelicerae as being composed of three articles, termed in scorpions (Shultz 2007) the protomerite, deuteromerite and tritomerite; reduced to two articles as an apomorphic condition in groups such as spiders. There are, however, published exceptions. If Pycnogonida (sea spiders) are accepted as *bona fide* chelicerates, then one Early Devonian form has been described with five cheliceral articles (Bergström *et al.* 1980) and there is at least one extant species with four (Helfer and Schlottke 1935, fig. 22); although the polarity of this character within the crown group merits further investigation. Kjellesvig-Waering (1964, text-fig. 11) reported four cheliceral articles in pterygotid eurypterid fossils. This isolated observation should be treated with caution because the accompanying plate illustrating this feature is unconvincing. A more plausible explanation was suggested by Størmer (in Selden 1984) in which this ‘extra’ proximal article actually represents internal tendons exposed only because the fossils represent moults. All Recent scorpions possess three cheliceral articles, but Kjellesvig-Waering (1986, p. 40, specimens I and VI) described four in *P. osborni* and several other putatively basal taxa, including *S. delicatus*. Indeed, he went so far as to claim (p. 16) that *all* Palaeozoic scorpions he had studied had four cheliceral articles and numbered them on his interpretative drawings accordingly. Our examinations of the original specimens studied by Kjellesvig-Waering, and new material of *P. osborni* indicated that two cheliceral articles are definitely present (i.e. the fixed and movable finger) and that there was probably a third, more proximal, article as in all extant scorpions (Text-fig. 2; Pl. 1, fig. 3; Pl. 3, fig. 3). We have found no explicit evidence for four articles in any of the available material. We cannot exclude the possibility that some fossil taxa do genuinely have four, but this must be demonstrated by careful inspection and illustration. We suspect that Kjellesvig-Waering tended to identify questionable features in a minority of specimens and then assume their presence in other material, perhaps over-interpreting cracks and folds as genuine article boundaries.



TEXT-FIG. 2. *Proscorpius osborni.* Camera lucida illustration of coxo-sternal region of YPM 208121. Abbreviations: ch, chelicerae; cI, coxa first leg; cII, coxa second leg; cIII, coxa third leg; cIV, coxa fourth leg; p, pedipalp podomeres; s, sternum. Scale bar increments are 1 mm.

Coxapophyses and ‘gnathobases’

Modern scorpions are liquid feeders with a preoral tube formed (in part) from prominent coxal projections variously referred to as the endites, coxapophyses, maxillary or mesal lobes (Farley 2001). These contribute towards the stomotheca, defined by Shultz (2000, p. 436) as ‘a preoral chamber…formed laterally by the pedipalpal coxae and ventrally by extensions of the first and to a lesser extent, second pedal coxae…’. This arrangement is also evident in harvestmen (Opiliones), and was proposed as a potential synapomorphy for (Opiliones + Scorpiones) by Shultz (1990, 2000). Nevertheless, well-developed coxal extensions forming a preoral tube are *not* apparent in various early fossil scorpions (Weygoldt 1998; Dunlop and Webster 1999; Dunlop and Braddy 2001; Farley 2001) raising the question of whether a stomotheca really is part of the scorpion groundplan, or a homoplastic development shared with harvestmen, perhaps associated with terrestrial adaptations for feeding. Jeram (1998) cautioned that the presence or absence of coxapophyses is ambiguous in some early taxa whose preservation renders this region equivocal, but resolved their presence as an apomorphic character (his character 23) appearing *within* the stem group and defining a more derived clade of scorpions.

Instead of coxapophyses, Kjellesvig-Waering (1986, p. 48, specimen VI) claimed that *P. osborni* retained mesal gnathobases on the coxae of the first pair of walking legs, similar to the gnathobases of horseshoe crabs (Xiphosura) and the extinct eurypterids (see especially Selden 1981). If functional, this would imply a mode of feeding in an early scorpion involving preoral maceration of food and thus a feeding style more typical of aquatic chelicerates. This report of gnathobases has been recycled elsewhere in the literature (Jeram 2001; Dunlop and Braddy 2001), but unfortunately they are not at all apparent in the relevant illustration (Kjellesvig-Waering 1986, text-fig. 12B). Our examination of the specimen illustrated by Kjellesvig-Waering (YPM 208121) and other specimens in the AMNH collection failed to resolve gnathobases in this expected position. Indeed, it proved difficult to see much detail in this region. We conclude that the observation is erroneous. We are unaware of any other fossil scorpion with demonstrably gnathobasic appendages. Furthermore, there is no indication, in the material available, of prominent coxapophyses forming a preoral tube in *P. osborni*. The coxae of the second leg abut towards the anterior third of the sternum, and show no visible coxapophyses. The coxae of the first leg are very poorly preserved, but appear in close approximation to each other in front of the sternum, are not fused together, and lack explicit, anteriorly projecting coxapophyses. A rudimentary precursor to the coxapophyses may be present on the first coxa (see Text-fig. 2), but these are very difficult to observe because they are overlapped by elements of the chelicerae and pedipalps. The method of feeding in these scorpions therefore remains enigmatic.

Labium

In ventral view, modern scorpions do not express an obvious labium (= tritosternum in some terminologies) forming the lower lip of the mouth. The labium has thus been considered absent in Scorpiones and interpreted as a plesiomorphic character state in several cladistic analyses (e.g. Shultz 1990, character 10). Classic morphological studies (e.g. Werner 1934, fig. 13; Kästner 1941, fig. 125), identified a tiny, postoral sclerite in front of the sternum in scorpions, but hidden in ventral view by the coxapophyses. It has been suggested that this could be homologous with the tritosternum of other arachnids, although Shultz (2007, fig. 2B), who described this sclerite and its musculature and functional morphology in some detail, did not make this assumption. In contrast, Kjellesvig-Waering (1986, p. 48, specimen VI, now YPM 208121) described a sternum in *P. osborni* bearing a notch-like invagination at the anterior margin, into which a small, diamond-shaped sclerite fits (see especially his fig. 12A–B). This was also interpreted as the labium. As with the gnathobases (see above) we were unable to confirm the presence of such a labium in *P. osborni* (Text-fig. 2), particularly in the well-preserved sternum alluded to below (Pl. 1, fig. 2). Again, Kjellesvig-Waering's observation is questionable.

Sternum

Related to the putative gnathobases and labium, the coxo-sternal region in general played a key role in Kjellesvig-Waering's (1986) classification (especially his text-figs 110–113). *Proscorpius osborni* was illustrated with an oval sternum (Kjellesvig-Waering's text-figs 12, 111A), tapering slightly anteriorly towards the putative labium and surrounded by a series of fairly simple coxae, those of leg 1 to some extent coming together, but not fused, in front of the sternum. The coxo-sternal region thus appeared rather like that of a modern spider. In contrast, we observed the sternum of *P. osborni* to be subtriangular (Text-fig 2; Pl. 1, fig. 2), and without a labium (see above), which is significant given that a pentagonal sternum is traditionally regarded as plesiomorphic (e.g. Petrunkevitch 1916; Lamoral 1980; Stockwell 1989) among modern scorpions, with a triangular sternum considered more derived. We do see a faint division demarcating the anterior third of the sternum (Pl. 1, fig. 2), which may be genuine as it also seems to be present in the probably related *Waeringoscorpio hefteri* Størmer, 1970.

Eyes

Whitfield (1885*a*, *b*) identified both median and lateral ocular tubercles at the front of the carapace. Frič (1904), working from photographs, claimed to see two further impressions near the back of the carapace which he interpreted as the true median eyes. Thus, Clarke and Ruedemann (1912, text-fig. 83) recognised a rather bizarre morphology with lateral eyes on the carapace margin, *lateral* eyes also extending onto a median ocular tubercle at the front of the carapace, and a pair of median eyes towards the back of the carapace. We see no structures resembling eyes in this posterior position on the holotype. Petrunkevitch (1949) refused to accept that *P. osborni* preserved *any* evidence of eyes, but this is a common theme throughout his monograph in which most fossil arachnids were interpreted as blind, despite much evidence to the contrary. Kjellesvig-Waering (1966, 1986) offered a more plausible interpretation of the eyes of *P. osborni*, according to which there are (as Whitfield suggested) two pairs of eyes, the first compound in nature like those of horseshoe crabs or eurypterids, at the anterolateral corners of the carapace, and a pair of small median eyes (ocelli) on a prominent tubercle at the front of the carapace. We studied two specimens, AMNH (Pl. 1, fig. 5) and YPM 209823, which support this interpretation, and the retention of large, multi-faceted lateral eyes is a genuine character and one of the key differences between early stem-group scorpions and the crown-group in which the compound eyes are reduced to a series of between 1–5 pairs of lateral ocelli.

Legs and tarsi

The early, often acrimonious, debate about the number of tarsal claws in *P. osborni* was reviewed by Clarke and Ruedemann (1912) and Kjellesvig-Waering (1966). Further discoveries largely exonerated Whitfield's (1885*b*) position and we can also confirm that the tarsal claws (= apotele or ungues) in *P. osborni* are paired (Pl. 2, fig. 2), and in fact not unlike the condition in modern scorpions. The use of this character to differentiate *Proscorpius* from other Silurian genera with more pointed, 'crab-like' legs seems justified. Interestingly, the telotarsus of *P. osborni* does differ from that of modern scorpions in being longer than the basitarsus and implies an animal that did not use the typical plantigrade stance seen in modern scorpions in which the whole tarsus is placed flat on the substrate. Størmer (1976) and Selden and Jeram (1989) suggested that early scorpions adopted instead a digitigrade stance, with only the tips of the tarsus on the substrate, and cited this as possible evidence for an aquatic habitat.

Abdominal plates and 'gills'

The holotype of *P. osborni* has a prominent crack running through it. An initial point of debate was whether, as Whitfield (1885*b*, 1886) claimed, it expressed the ventral opisthosomal surface to the right of this crack. Whitfield argued that these were sternites and that they lacked an obvious spiracular opening for book lungs. Most subsequent authors (e.g. Thorell 1886; Pocock 1901; Frič 1904; Clarke and Ruedemann 1912; Petrunkevitch 1949) disputed this and maintained that the right-hand side of the holotype merely showed the underside of the tergites. Frič (1904), again working only from photographs, claimed to see 'oval bodies' corresponding to lung sacs, but this could not be confirmed by later authors, including us. Kjellesvig-Waering (1966) alluded to 'openings' at the posterior edges of the abdominal plates of *P. osborni*, and subsequently identified a putative gill slit, *c.* 1 mm across, in one specimen (Kjellesvig-Waering 1986, p. 46, specimen IV, now YPM 208125). We were unable to detect the slit in this specimen (Pl. 2, fig. 1) or other, better preserved material (AMNH: Pl. 1, fig. 1; Pl. 3, figs 1, 4–5) showing the underside of the opisthosoma. In YPM 208125 (Pl. 2, fig. 1), the darker patch identified by Kjellesvig-Waering (1986) as a gill slit is in fact an area where three sternites and tergites overlap, not two as more commonly seen.

A fundamental problem with Kjellesvig-Waering's scheme is that slits in the cuticle do not logically equate to gills, and implicitly an aquatic lifestyle. Even if a narrow, slit-like opening *could* be found, this would appear on the face of it to be far better evidence for a lung spiracle in a terrestrial animal than for an opening for a gill; see e.g. Scholtz and Kamenz (2006) for illustrations of spiracles in Recent arachnids. Unequivocal gills, homologous with those of horseshoe crabs, have yet to be demonstrated in a fossil scorpion (see 'Discussion'). Intuitively, one might expect the entire operculum of a gilled scorpion to form a movable flap and to be open along its entire posterior margin, as in horseshoe crabs and, presumably, eurypterids (cf. Manning and Dunlop 1995). The fact that we observe no openings whatsoever on the ventral surface in *P. osborni* (i.e. no spiracles either within, or marginal on, the ventral sclerites) could be taken as support for flap-like abdominal plates (or opercula) covering gills. However, we would caution that in, for example, whip spiders (Amblypygi) and whip scorpions (Uropygi), the spiracles are effectively hidden in ventral view (see also Scholtz and Kamenz 2006, fig. 2a) and the actual openings are tucked slightly beneath the preceding operculum.

One further observation of considerable significance, which we can confirm here, is that *P. osborni* has at least six, possibly seven, ventral sclerites in the mesosoma. Modern scorpions have only five, four of which bear the paired book lungs. Because of the appendicular origin of the lungs, the relevant four scorpion 'sternites' have been alternatively interpreted as sutured-on abdominal plates, perhaps incorporating elements of the original true sternite which lay above the plate; see Jeram (2001, fig. 16.2) for a hypothesis demonstrating how this might have happened. Jeram (1998, character 5) regarded the loss of one

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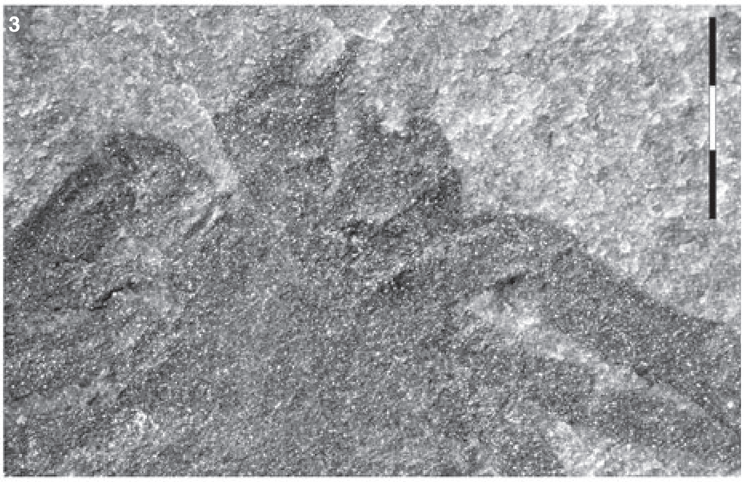
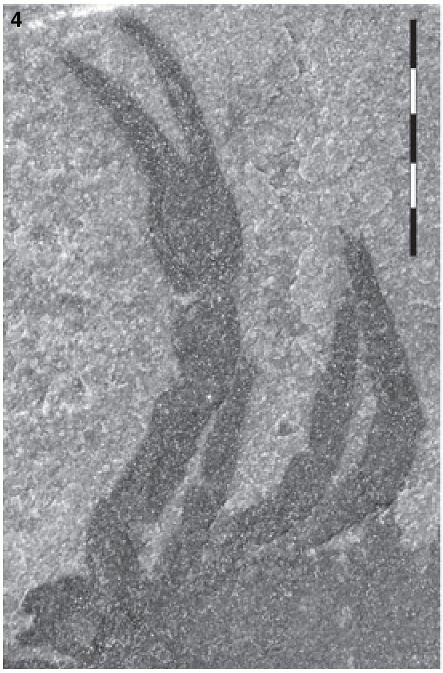
EXPLANATION OF PLATE 1

Figs 1–5. *Proscorpius osborni*. 1, AL 2 (AMNH), almost complete individual. 2, AL 10b (AMNH), well-preserved coxo-sternal region. 3, AL 1 (AMNH), well-preserved chelicerae. 4, AL 1 (AMNH), complete pedipalp and walking legs. 5, AL unnumbered (AMNH), compound lateral eyes and median ocular tubercle. All from the Phelps Member, Fiddlers Green Formation, Bertie Group. Scale bar increments are 1 mm.

PLATE 1





DUNLOP *et al.*, *Proscorpius*

of these abdominal plates as characterising a derived clade, primarily comprising the so-called mesoscorpions plus the crown-group. Exactly how the 'extra' abdominal plate (or plates!) fit into the ground-pattern of early scorpion morphology remains an area for investigation and reflects a long debate about whether scorpions fundamentally have 12 or 13 somites in the opisthosoma and/or whether the pectines belong to the genital or the postgenital segment; see e.g. Dunlop and Webster (1999) for further comments and reviews of the older literature.

This debate now seems largely settled, based on two recent lines of evidence. Using patterns of gene expression, Simonnet *et al.* (2006) recognised 13 opisthosomal segments in a Recent scorpion; beginning with (1) a pregenital segment, (2) a genital segment and (3) the postgenital pectine-bearing segment; with the lungs borne on the subsequent segments 4–7. In a detailed examination of skeletomuscular anatomy, Shultz (2007, fig. 6) also recognized 13 opisthosomal segments, including a highly-reduced first segment, and the same distribution of the genital opening (2), pectines (3) and lungs (segments 4–7). Perhaps the 'missing' abdominal plate retained in basal fossil scorpions belongs to segment 3 (the pectinal segment) and originally underlay the pectines (but see below), although further discussion would be speculative at this stage.

The larger number of ventral sclerites in the fossil scorpions is reminiscent of the condition found in eurypterids. They also have six dorsal mesosomal sclerites, but the ventral side is more complex (Dunlop and Webster 1999). Posteriorly, four pairs of medially divided 'sternites', or abdominal plates, are all possibly covering respiratory structures. In front of these, the genital operculum is found, and is visibly sutured. In the most derived swimming forms, there are only two segments present in the operculum, but in the walking forms and in basal swimming forms, an additional anterior segment is found (Tetlie and Braddy 2004). This is evidence that eurypterids had (like scorpions) a groundplan with 13 somites in their opisthosoma.

Pectines

Pectines are important sensory organs in scorpions and traditionally represent one of the most obvious autapomorphies for the group. They were not fully described from *P. osborni* until the monograph of Kjellesvig-Waering (1986, pp. 46–47). Curiously, we see no evidence of pectines on *any* of the specimens, including the three alluded to by Kjellesvig-Waering (1986), although many of the specimens are ventrally exposed and quite well preserved. Perhaps they were reduced or became disarticulated? An alternative, albeit controversial, explanation would be that there was an early grade of scorpion organisation in which pectines had not evolved. Pectines do seem to be present in the Scottish Silurian species *Allopalaeophonus caledonicus* Hunter, 1886; see especially Peach (1885, p. 297), Pocock (1901, pl. 19) and Kjellesvig-Waering (1986). However, recent study by JAD of new and existing material of *Waeringoscorpio*, a genus probably related to *Proscorpius* (see 'Systematic palaeontology'), found pectines here to be equivocal; this may support the idea that proscorpiids really did lack these structures. Of the remaining proscorpiid genera, only one, *Pseudoarchaeoctonus* Kjellesvig-Waering, 1986 has been described with a hint of pectines (cf. his text-fig. 22), although in fairness some of the others are known only from incomplete and/or dorsally preserved specimens. It is also worth noting that three fossil scorpions (two Devonian: *Branchioscorpio richardsoni* Kjellesvig-Waering, 1986 and *Waeringoscorpio hefteri*; and one Carboniferous: ?*Cyclophthalmus sibiricus* Novojilov and Størmer, 1963) have been described as possessing a pectinal region with knob-like or elongate features somewhat resembling the genital appendage of eurypterids. However, all were described by eurypterid workers, and require confirmation.

Carinae

The scorpion body is characteristically ornamented with series of raised linear ridges, typically in the form of rows of granulation called keels or carinae. While we see no evidence of carinae on the carapace of *P. osborni*, the last mesosomal tergite bears a pair of longitudinal carinae, whereas the corresponding sternite bears two pairs (Pl. 2, fig. 3). The latter character also occurs sporadically in Recent scorpions where it may well be plesiomorphic (Prendini 2000). There is also a series of paired carinae on the metasoma (or tail) which appear to represent the dorsosubmedian, dorsolateral, ventrosubmedian, ventrolateral and (perhaps) median lateral carinae (e.g. Pl. 2,

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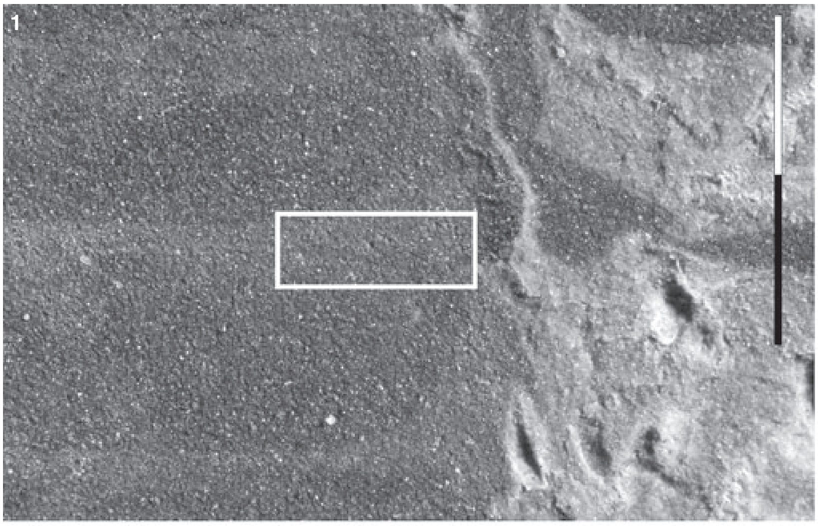
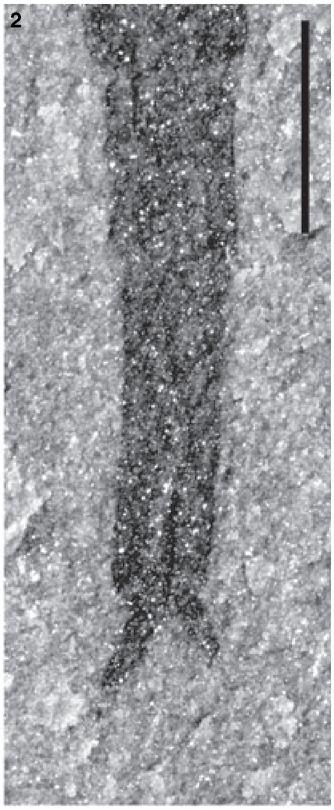
EXPLANATION OF PLATE 2

Figs 1–5. *Proscorpius osborni*. 1, YPM 208125, the so-called 'gill slit' of Kjellesvig-Waering (inset) is just three overlapping cuticular elements. 2, AL 2 (AMNH), clearly showing paired tarsal claws. 3, YPM 212926, sternite VII with paired carinae. 4, YPM 208125, carinae on metasomal segments. 5, AL 1 (AMNH), carinae on metasomal segments. All from the Phelps Member, Fiddlers Green Formation, Bertie Group. Scale bar increments are 1 mm.

PLATE 2





figs 3–5). If this interpretation is correct it would match the basic pattern of ten carinae seen in modern scorpions and suggest that this feature arose very early in scorpion evolution and has remained more or less the same ever since. Several carinae matching those of Recent scorpions are also evident on the pedipalps of *P. osborni*. However, the full complement of pedipalp carinae in *P. osborni* is difficult to discern with confidence.

MODE OF LIFE

Whitfield (1885*b*) was the first author to postulate that Silurian scorpions may have been aquatic, a proposal quickly rejected by Thorell (1886) and later by (among others) Petrunkevitch (1949), who regarded the supposed absence of spiracles for book lungs as equivocal. Yet both Pocock (1901) and Clarke and Ruedemann (1912) raised an important point, widely ignored by those who have challenged the notion of aquatic scorpions, that it is hard to explain why scorpions are the *only* terrestrial arthropods to be deposited, well preserved and fully articulated, in near-shore environments, often among other taxa whose aquatic (if not marine) nature is indisputable. Indeed, many later workers accepted an aquatic habitat for the most basal scorpions (Kjellesvig-Waering 1986; Selden and Jeram 1989; Jeram 1998, 2001). Yet doubts remain (e.g. Weygoldt 1998), not least because the morphological evidence for an aquatic habitat is indirect and typically emphasises the absence of a preoral tube for preoral digestion on land and 'crab-like' legs in some, but by no means all (see 'Morphological interpretation'), early scorpions. Furthermore, unequivocal gills have yet to be recorded from any fossil scorpion. Those illustrated by Størmer (1970) extend well beyond the body wall and may not be homologous with the book lungs of modern scorpions. Others postulated by Kjellesvig-Waering (1986, pls 6–8) turned out to be part of an arthropleurid millipede (Shear and Selden 1995). This debate was also recently brought back into focus by Scholtz and Kamenz's (2006) detailed study of the ultrastructure of scorpion book lungs, which emphasised their extreme similarity to the book lungs of spiders and their near relatives. *Proscorpion osborni* exhibits some slight differences in tarsal morphology compared to Recent species and lacks an obvious preoral tube formed from coxapophyses and, apparently, lacks gill slits and pectines. Unfortunately, these observations fail to provide unambiguous morphological evidence for a particular mode of life.

SYSTEMATIC PALAEONTOLOGY

Plesion (Family) PROSCORPIIDAE Scudder, 1885

1885 Proscorpionini Scudder, p. 739.
1949 Archaeoctonidae Petrunkevitch, p. 137.
1966 Proscorpionidae Scudder; nom. trans. Kjellesvig-Waering, p. 361.
1970 Waeringoscorpionidae Størmer, p. 336.
1986 Archaeoctonoidea Petrunkevitch; nom. trans. Kjellesvig-Waering, p. 66.
1986 Hydroscorpiidae Kjellesvig-Waering, p. 63.
1986 Labrioscorpionidae Kjellesvig-Waering, p. 52.
1986 Proscorpiidae Scudder; nom. trans. Kjellesvig-Waering, p. 39.
1986 Proscorpioidea Scudder, 1885; Kjellesvig-Waering, p. 39.
1986 Stoermeroscorpionidae Kjellesvig-Waering, p. 53.
1986 Stoermeroscorpionoidea Kjellesvig-Waering, p. 53.
1986 Proscorpiidae Scudder; Jeram, p. 25.

Type genus. Proscorpius Whitfield, 1885*b*.

Included genera. Archaeoctonus Pocock, 1911; *Hydroscorpius* Kjellesvig-Waering, 1986; *Labriscorpio* Leary, 1980; *Pseudoarchaeoctonus* Kjellesvig-Waering, 1986; *Waeringoscorpio* Størmer, 1970.

Stratigraphical and geographical range. Late Silurian (Přídolí)–Early Carboniferous (Viséan) of Europe and North America.

Emended diagnosis. Fossil scorpions in which all leg coxae, including those of leg 1, surround and abut a fairly large subtriangular sternum; leg 1 coxae of other scorpions tend to be separated from the sternum by the leg 2 coxae. (Emended from Jeram 1998.)

Remarks. The cladogram of Jeram (1998) recovered a monophyletic group of the above-mentioned genera, united in his analysis primarily by the shape of the coxo-sternal region. Unfortunately the explicit diagnostic character proposed in Jeram's (p. 28) text, i.e. only the first pair of

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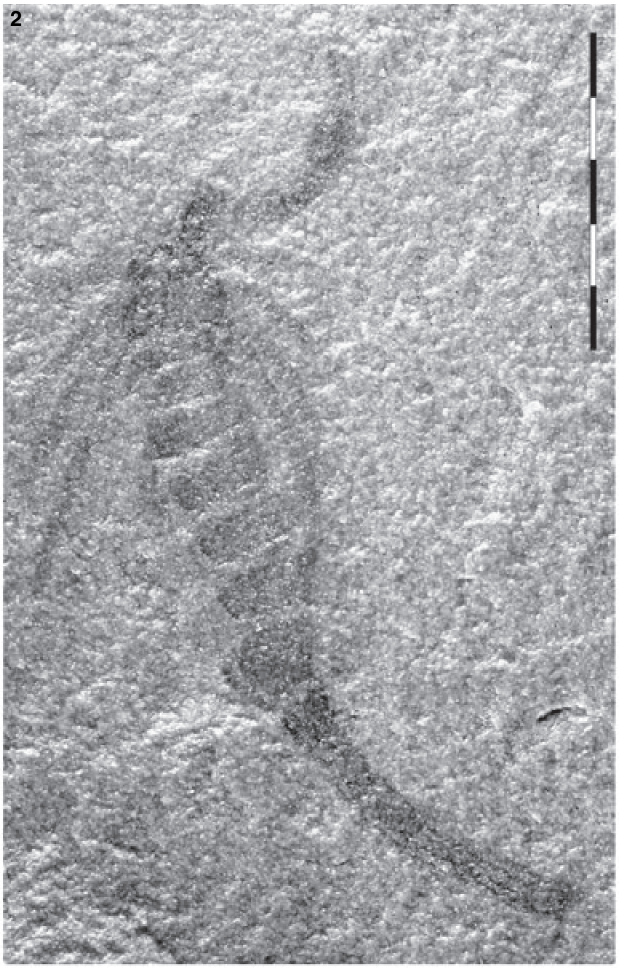
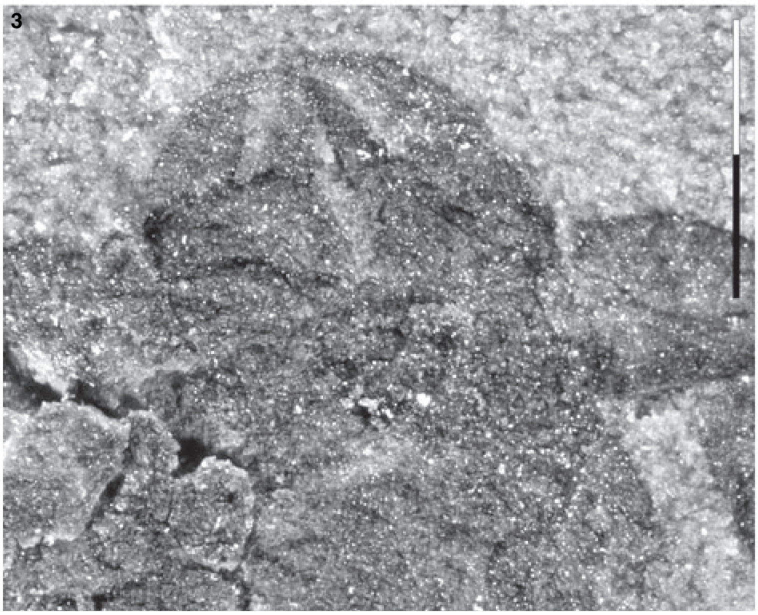
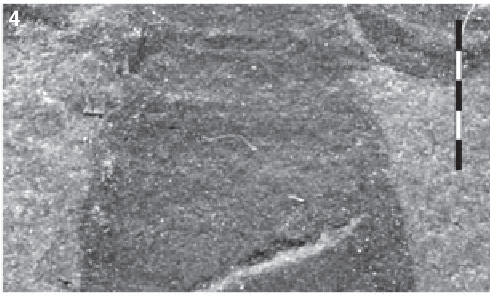
EXPLANATION OF PLATE 3

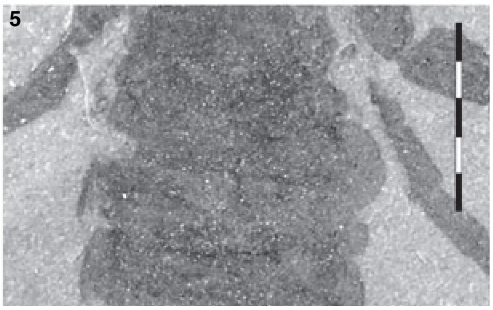
Figs 1–5. *Proscorpius osborni*. 1, AL 3 (AMNH), almost complete individual. 2, YPM 206692, juvenile specimen (holotype of *Stoermeroscorpio delicatus*). 3, AL 2 (AMNH), well preserved chelicerae. 4, AL 1 (AMNH), ventral mesosoma without evidence of pectines. 5, AL 2 (AMNH), ventral mesosoma without evidence of pectines. All from the Phelps Member, Fiddlers Green Formation, Bertie Group. Scale bar increments are 1 mm.

PLATE 3









legs meeting in front of the sternum, cannot be adequately observed in *P. osborni*. As noted in the discussion of gnathobases (above), the first leg coxae are poorly preserved in this species and their mesal morphology (separate and toothed or abutting one other) remains equivocal. Instead we draw on character 22 in Jeram's (1998) cladogram for our emended diagnosis: the first pair of coxae remaining more or less in contact with the sternum. We concede that this character might be plesiomorphic, or form part of a trend towards development of the modern coxo-sternal configuration, but at least based on published illustrations of other Silurian scorpions, such as *Allopalaeophonus caledonicus*, the first leg coxae appear to be more anteriorly situated with respect to the sternum, as is also the case in more derived and Recent scorpion taxa.

Proscorpiidae *sensu* Jeram (1998) is to some extent equivalent to the superfamily Proscorpioidea *sensu* Kjellesvig-Waering (1986) or Palaeoscorpiones *sensu* Stockwell (1989). Despite effectively collapsing various families and superfamilies, Jeram (1998) did not formally synonymize them. Fet *et al.* (2000) therefore retained Kjellesig-Waering's nomenclature in their catalogue. In the interests of establishing a more workable higher classification for Palaeozoic scorpions we take this opportunity to formalise Jeram's (1998) mostly convincing results. We recognise the higher taxa listed above, most of which contain only a single species, as junior synonyms of Proscorpiidae, the oldest available name. We concede that Proscorpiidae may represent a grade rather than a clade. However, we do not believe that a meaningful classification was achieved by placing each species in a monotypic family. In order to simplify the higher classification of Palaeozoic scorpions, we recommend first synonymizing obviously redundant higher categories and then reconstructing monophyletic groups using available names, based on cladistic analysis and unequivocal autapomorphies. Two further proscorpiid genera listed by Jeram (1998), *Archaeophonus* Kjellesvig-Waering, 1966 and *Stoermeroscorpio* Kjellesvig-Waering, 1986, were created to accommodate single species, both of which are interpreted here as synonyms of *Proscorpius osborni* (see below).

Genus PROSCORPIUS Whitfield, 1885*b*

Type and only species. Palaeophonus osborni Whitfield, 1885*a*, by original designation.

Stratigraphical range and distribution. Late Silurian (Přídolí) of New York, USA.

Emended diagnosis. Distinguished from all other extant and extinct scorpions by the following character combination: a pair of large, compound eyes situated anterolaterally, one on each side of carapace, and a median ocular tubercle with two ocelli situated anteromedially between them; leg telotarsi noticeably longer than basitarsi, implying a digitigrade stance, with laterodistal lobes truncated, pair of short, unequal ungues and very short dactyl evident; tibial and tarsal (pedal) spurs absent; sternum subtriangular, external aspect flat, without a concave region or median furrow; sternite VII with distinct pairs of ventrosubmedian and ventrolateral carinae; pectines and spiracles (respiratory stigmata) apparently absent; metasomal segments I–IV with up to ten carinae; telson without subaculear tubercle. (Emended from Kjellesvig-Waering 1986.)

Proscorpius osborni (Whitfield, 1885*a*)
Plates 1–3; Text-figures 2–3

1885*a* *Palaeophonus osborni* n. sp. Whitfield, p. 88, 1 fig.
1885*b* *Proscorpius osborni* (Whitfield); Whitfield, pp. 181–187, pl. 20.
1885 *Proscorpius osborni* (Whitfield); Scudder, p. 739, fig. 915a.
1886 *Proscorpius osborni* (Whitfield); Scudder, p. 28.
1886 *Proscorpius osbornei* [*sic*] (Whitfield); Thorell, p. 269.
1886 *Proscorpius osborni* (Whitfield); Whitfield, p. 216.
1889 *Proscorpius osborni* (Whitfield); Miller, p. 571.
1890 *Proscorpius osborni* (Whitfield); Lesley, pp. 773–774, figs (unnumbered?).
1891 *Palaeophonus osborni* Whitfield; Scudder, p. 28.
1899 *Proscorpius osborni* (Whitfield); Laurie, p. 577.
1901 *Proscorpius osborni* (Whitfield); Pocock, p. 309.
1904 *Proscorpius osborni* (Whitfield); Frič, p. 65, fig. 81.
1907 *Proscorpius osborni* (Whitfield); Frič, p. 6, pl. 3.
1912 *Proscorpius osborni* (Whitfield); Clarke and Ruedemann, pp. 387–400, pl. 86, text-figs 81–83.
1913 *Proscorpius osborni* (Whitfield); Petrunkevitch, p. 32.
1934 *Proscorpius osborni* (Whitfield); Werner, p. 258, fig. 313.
1944 *Proscorpius osborni* (Whitfield); Lehmann, p. 177.
1949 *Palaeophonus osborni* Whitfield; Petrunkevitch, pp. 129–131, fig. 189.
1953 *Proscorpius osborni* (Whitfield); Petrunkevitch, p. 12, fig. 118.
1954 *Proscorpius osborni* (Whitfield); Kjellesvig-Waering, p. 485.
1955 *Proscorpius osborni* (Whitfield); Petrunkevitch, p. 70, figs 38 (3), 39 (A).
1966 *Archaeophonus eurypteroides* n. sp. Kjellesvig-Waering, pp. 373–375, pl. 42, fig. 1; pl. 43, figs 1, 5; text-figs 5–10.
1966 *Proscorpius osborni* (Whitfield); Kjellesvig-Waering, pp. 361–373, pl. 42, figs 2–3; pl. 43, figs 2–4; pl. 44; text-figs 1–4, 11–18.
1986 *Archaeophonus eurypteroides* Kjellesvig-Waering; Kjellesvig-Waering, pp. 50–52, text-fig. 14.

1986 *Proscorpius osborni* (Whitfield); Kjellesvig-Waering, pp. 39–48, pl. 1, text-figs 6–13, 111A.
1986 *Stoermeroscorpio delicatus* n. sp. Kjellesvig-Waering, pp. 53–56, text-figs 15–16.
1993 *Archaeophonus eurypteroides* Kjellesvig-Waering; Selden, p. 303.
1993 *Proscorpius osborni* (Whitfield); Selden, p. 303.
1993 *Stoermeroscorpio delicatus* Kjellesvig-Waering; Selden, p. 303.
1998 *Proscorpius osborni* (Whitfield); Weygoldt, pp. 71–72, fig. 9a.
1998 *Stoermeroscorpio delicatus* Kjellesvig-Waering; Weygoldt, p. 71.
2000 *Archaeophonus eurypteroides* Kjellesvig-Waering; Fet *et al*., p. 573.
2000 *Proscorpius osborni* (Whitfield); Fet *et al*., p. 573.
2000 *Stoermeroscorpio delicatus* Kjellesvig-Waering; Fet *et al*., p. 576.
2001 *Proscorpius osborni* (Whitfield); Dunlop and Braddy, p. 6, fig. 4.
2001 *Proscorpius osborni* (Whitfield); Farley, p. 16, fig. 2.2.
2005 *Proscorpius osborni* (Whitfield); Farley, p. 22.

Holotype. AMNH 2257.

Type locality and horizon. Waterville (= Forge Hollow), Oneida County, New York, USA. Phelps Member, Fiddlers Green Formation, Bertie Group (‘Bertie Waterlime’). Late Silurian, Přídolí.

Additional material. AMNH 28385, BMS E25162 (= CIURCA 031966-1), NYSM 12947 (= former CUGM 41109; holotype of *A. eurypteroides*), 12948 (= former CUGM 41973), YPM 206691 (= CIURCA 062065-1; paratype of *A. eurypteroides*), 206692 (= CIURCA 041771-1–2; holotype of *S. delicatus*), 208121 (= CIURCA 040668-1), 208125 (= CIURCA 041771-1), 208126 (= CIURCA 040564), 208127 (= CIURCA 072868-9B), 208129–208131, 209823 (= CIURCA 042570-1A), 212926–212928 and 213707, AMNH (= AL1–12, and one AL unnumbered). All from the ‘Bertie Waterlime’.

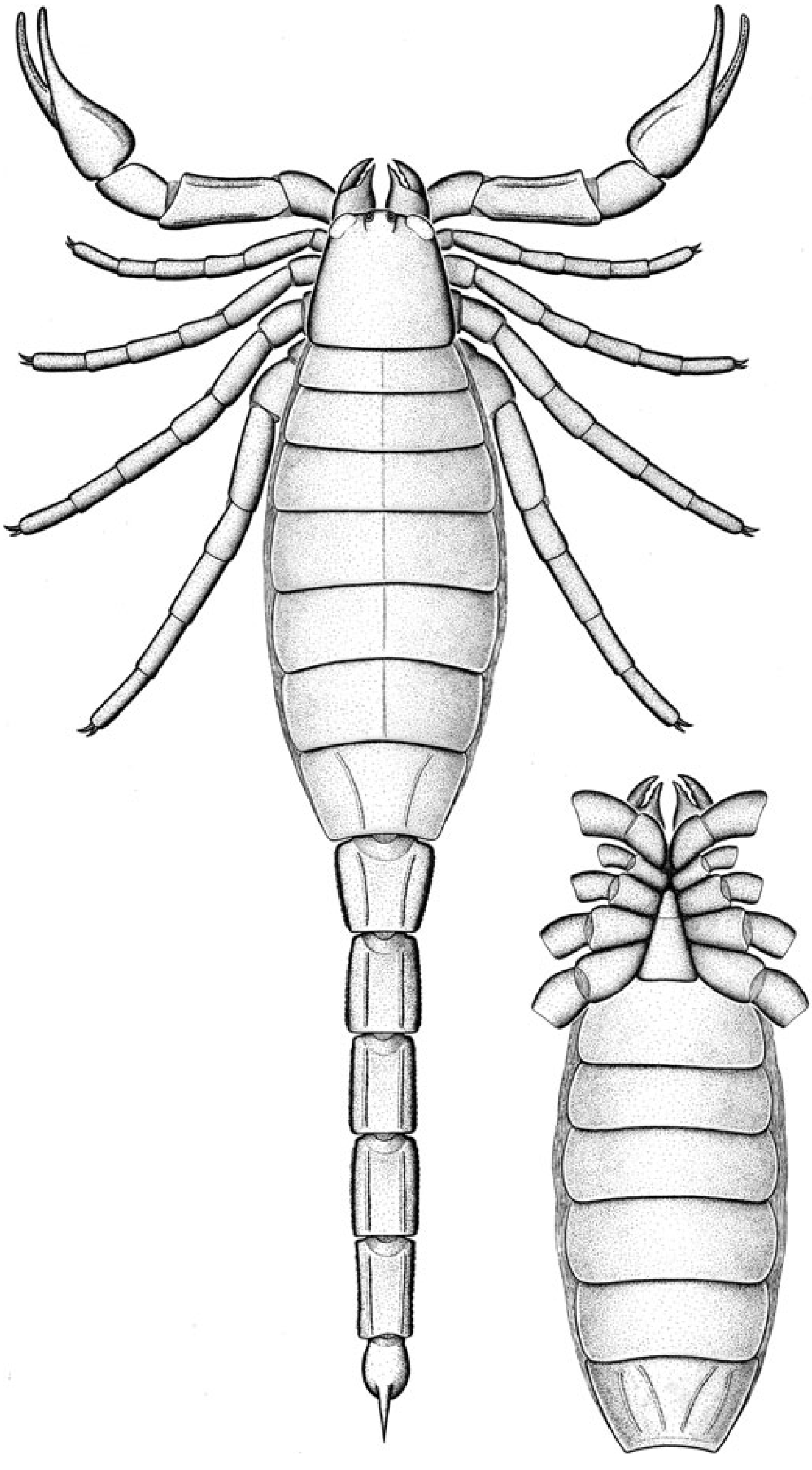
Diagnosis. As for the genus.

Description. Scorpions of small to average size, total length, 13–41.3 mm (mean, 28.3 mm; n = 8; Table 1). Pair of three-articled chelicerae, each with distinct fixed and movable fingers, armed with teeth, situated anterior to carapace, as in Recent scorpions. Carapace anterior margin procurved, length 2.4–4.0 mm (mean, 3.6 mm; n = 8; Table 1). Pair of large, compound eyes situated anterolaterally, one on each side of carapace, and a median ocular tubercle with two ocelli situated anteromedially between them. Posterior carapace margin almost straight. No carapacial sulci or sutures evident. Carapacial surfaces matt, no coarse macrosculpture discernible, and apilose, macrosetae not evident. Pair of six-articled pedipalps, each comprising coxa, trochanter, femur, patella, tibia (chela manus) and tarsus (movable finger), as in Recent scorpions, connected to prosoma beneath carapace. Pedipalp length, 4.2–13.2 mm (mean, 8.6 mm; n = 7; Table 1). Pedipalps each with distinct dorsal, ventral, internal and external surfaces. Pedipalp surfaces in some cases clearly demarcated by carinae (e.g. dorsointernal carina of femur and ventroexternal carina of chela manus), as in Recent scorpions. Dentate margins of chela fixed and movable fingers each with median denticle row. Pedipalp (Pl. 1, fig. 4) surfaces matt, no other surface macrosculpture discernible, and apilose, macrosetae and trichobothria not evident.

Four pairs of ten-articled legs, each comprising coxa, trochanter, femur, patella, tibia, basitarsus, telotarsus, apotele, pair of ungues (lateral tarsal claws) and very short dactyl (median tarsal claw), as in Recent scorpions, connected to prosoma beneath carapace. Legs progressively increasing in length, leg I, 4.1–5 mm (mean, 4.5 mm; n = 2; Table 1); II, 5.3–7 mm (mean, 6.2 mm; n = 2); III, 6–9.5 mm (mean, 7.3 mm; n = 4); IV, 9.1–11 mm (mean, 10 mm; n = 4). Legs with distinct prolateral and retrolateral surfaces, as in Recent scorpions. Leg surfaces matt, no carinae or coarse macrosculpture discernible, and apilose, macrosetae not evident along margins. Retrolateral margins of tibia and basitarsi without obvious tibial or tarsal (pedal) spurs (cf. description of Kjellesvig-Waering, 1986). Telotarsi noticeably longer than basitarsi, unlike Recent scorpions, suggesting a digitigrade stance in life, with laterodistal lobes truncated as in most Recent scorpions. Telotarsi each with raised ventromedian region (spinules?), barely discernible. Pair of short, weakly curved ungues evident on all telotarsi, as in Recent scorpions. Ungues unequal in length, with prolateral ungue noticeably longer than retrolateral ungue, especially on legs III and IV. Dactyl very small and difficult to observe. Maxillary lobes (coxapophyses), gnathobases and labium not discernible. Sternum distinctly subtriangular, as in buthoid scorpions, external aspect flat, without a concave region or median furrow.

Seven tergites (I–VII) visible, as in Recent scorpions. Combined length of tergites, 5.2–16.2 mm (mean, 11.2 mm; n = 8; Table 1). Tergites I–VI, each with weak median carina, VII with distinct pair of submedian carinae almost reaching posterior edge of segment, as in many Recent scorpions. At least six sternites (II–VII) visible in several specimens, unlike Recent scorpions. Sternites acarinate, VII with distinct pairs of ventrosubmedian and ventrolateral carinae (i.e. four carinae), as in many Recent scorpions. Tergite and sternite surfaces matt, no coarse macrosculpture discernible, and apilose, macrosetae not evident along margins. No pectines, genital opercula, genital papillae or spiracles (respiratory stigmata) evident, even on well-preserved specimens.

Metasoma with five clearly defined segments, as in Recent scorpions, progressively increasing in length, but decreasing in width, terminating in a narrow telson (narrower than metasomal segment V). Combined length of metasomal segments and telson, 5.4–21.5 mm (mean, 13.9 mm; n = 8; Table 1). Up to ten carinae evident on metasomal segments I–IV, as in most Recent scorpions, with paired dorsosubmedian, dorsolateral, ventrolateral, and ventrosubmedian carinae especially distinct in many specimens. Median lateral carinae more difficult to discern owing to the orientation of specimens (most of which are positioned horizontally upwards or downwards). Presence of paired ventrosubmedian or single ventromedian carina on metasomal segment V unclear. Telson vesicle dorsal surface flattened, ventral surface convex, terminating in a gently curved aculeus, without a subaculear tubercle ventrally. Surfaces of metasoma



TEXT-FIG 3. Idealized reconstruction of *Proscorpius osborni* in dorsal and ventral views based on a composite of the available material. The shape and position of the pedipalpal coxae are hypothetical and derived somewhat from the probably related *Waeringoscorpio*. In modern (and many fossil) scorpions a pair of genital opercula followed by the pectines would be expected immediately behind the sternum. We reiterate that we found no evidence of these structures, despite numerous appropriately preserved specimens, and thus exclude these features from our reconstruction with some reservations (see text for details). Setae on the limbs and body were probably present, but have also not been included here to avoid introducing preconceptions about possible macrosetal and/or trichobothrial patterns.

and telson matt, no coarse macrosculpture discernible, and apilose, macrosetae not evident.

Remarks. In Jeram's (1998, figs 1–2) cladogram the three 'Bertie Waterlime' genera, *Proscorpius*, *Archaeophonus* and *Stoermeroscorpio*, resolved together as a trichotomy with 100 per cent support. We consider these taxa to be conspecific based on re-examination of the holotypes for the present study, and synonymize them accordingly.

TABLE 1. Meristic data for eight specimens of *Proscorpius osborni* (Whitfield, 1885), including the holotype (AMNH 2257), and the holotype of *Stoermeroscorpio delicatus* Kjellesvig-Waering, 1986, syn. nov. (YPM 206692).

Specimen:	Collection Number	AMNH 2257	AMNH 28385	AMNH AL	AMNH AL	AMNH AL	YPM 206692	YPM 208121	YPM 208125
Carapace:	Length	4		3.9	3.9	4.0	2.4	3.4	3.55
Chela:	Maximum width		1.2		1.85				
Chela:	Maximum height			1.9					
Chela:	Length	5.45	4.4	3.9	5.5	5.9	1.9	4.5	4.2
Chela:	Length of movable finger						0.85	2.4	
Patella:	Maximum width			1.45	1.45	1.4	0.5		
Patella:	Length			2.6	1.8	2.3	0.7		1.3
Femur:	Maximum width			1.2	1.6	1.4	0.45		
Femur:	Length			3.2	3.1	3.1	0.9		2.1
Trochanter:	Length			2.1	1.8	1.95	0.7		1.1
Pedipalp:	Total length (including trochanter)	5.45	4.4	11.8	12.2	13.25	4.2		8.7
Leg I:	Total length			5.0					4.1
Leg II:	Total length			5.3		7.0			
Leg III:	Total length			6.0	7.0	9.5			6.8
Leg IV:	Total length			10.4	9.7	11.0			9.1
Mesosoma:	Total length(tergites)	16.2	6.7	15.95	10.7	14.7	5.2	11.2	9
Mesosoma:	Tergite I length	1.2		1.45	0.7				
Mesosoma:	Tergite II length	1.6		1.8	1.0				1.1
Mesosoma:	Tergite III length	2.0	1.0	2.0	1.3			1.3	1.5
Mesosoma:	Tergite IV length	2.3	1.2	2.1	1.4		0.8	1.5	1.5
Mesosoma:	Tergite V length	2.5	1.2	1.9	1.8		0.8	1.7	1.5
Mesosoma:	Tergite VI length	2.6	1.4	2.8	1.9		0.9	2.5	1.1
Mesosoma:	Tergite VII length	4.0	1.9	3.9	2.6		1.3	2.7	2
Mesosoma:	Tergite maximum width	8.3	4.7	9.45		9.2	2.7	6.43	5.2
Metasoma I:	Maximum width	3.0	1.9	3.2	2.8	2.8	0.9	1.5	1.7
Metasoma I:	Length	3.4	2.0	3.4	2.4	2.9	1	2.2	1.95
Metasoma II:	Maximum width	2.5	1.7	2.8	2.4	2.5	0.7	1.4	1.8
Metasoma II:	Length	3.0	2.4	3.8	2.75	3.9	0.9	2.3	2.5
Metasoma III:	Maximum width	2.2	1.65	2.6	2.3	1.9	0.65	1.4	1.55
Metasoma III:	Length	3.2	2.7	4.0	2.9	3.0	0.9	2.3	2.45
Metasoma IV:	Maximum width	2.1	1.55	2.4	2.2		0.6	1.4	1.2
Metasoma IV:	Length	3.0	2.5	3.65	3.0	3.5	0.95	2.8	2.5
Metasoma V:	Maximum width			2.25	1.7		0.6	1.35	1.1
Metasoma V:	Length			4.0	3.1	3.0	0.75	2.4	2.2
Telson:	Maximum height			1.1		1.2	0.45		1.15
Telson:	Total length			2.65	2.8	3.1	0.9		2.5
Metasoma:	Total length	12.6	9.6	21.5	16.95	19.4	5.4	12	14.1
Total length:	Prosoma+mesosoma+metasoma	32.8	16.3	41.35	31.55	38.1	13	26.6	26.65

Kjellesvig-Waering (1966, 1986) differentiated the somewhat smaller *Archaeophonus eurypteroides* from *P. osborni* on the grounds of a quadrate carapace with large lateral eyes, shorter abdominal tergites and, explicitly, a double trochanter in the last pair of walking legs. The latter character would be unique among all scorpions, extinct or extant, but could not be confirmed in our studies. In general, we suspect that the holotype of *A. eurypteroides* is nothing more than a juvenile *P. osborni*, with the slight differences in body proportions being ontogenetic rather than taxonomic in origin. In support of this, it is well documented among eurypterids (e.g. Andrews *et al.* 1974; Brower and Veinus 1978) that juveniles have proportionately larger compound lateral eyes. The second specimen of *A. eurypteroides* reported by Kjellesvig-Waering (1986, pp. 50–51, fig. 14) does not express a very large eye as in the original description. This rounded feature is actually the trochanter of the pedipalp.

Kjellesvig-Waering (1986) characterised the third 'Bertie Waterlime' species, *Stoermeroscorpio delicatus* (Pl. 3, fig. 2), by a first pair of coxae meeting in front of an elongate pentagonal sternum, poorly developed maxillary lobes, and a fourth pair of coxae abutting the genital opercular plates. The holotype of *S. delicatus* is, in all observable respects, similar to specimens of *P. osborni*, except its small size. None of the characters suggested as differentiating it from *P. osborni* is preserved in sufficient detail to justify a separate species, much less a separate superfamily! The outline of the sternum and most of the coxae are indistinct, while the maxillary lobes of the anterior coxae, the position of the posterior coxae compared to the sternum, and the pectines reported by Kjellesvig-Waering cannot be observed. We believe *S. delicatus* and its delicate features are best interpreted as a juvenile *P. osborni*.

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