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The earliest record of terrestrial animals in Gondwana: A scorpion from the Famennian (Late Devonian) Witpoort Formation of South Africa

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ABSTRACT

The new genus and species, *Gondwanascorpio emzantsiensis*, are described in Scorpiones *incertae sedis* on the basis of fragments from the Famennian (Late Devonian) Waterloo Farm locality near Grahamstown, Eastern Cape, South Africa. This finding adds to the sparse record of Late Devonian scorpion taxa and provides the first evidence of Palaeozoic scorpions from Gondwana. Material includes a complete chela with associated patella as well as a telson with associated metasomal segment V, resembling those of the Mesoscorpionina. This is the first record of a scorpion occurring at high latitudes. Its close resemblance to contemporary taxa from Laurasia and China is consistent with evidence from the type locality for increasingly uniform terrestrial ecosystems by the end of the Devonian, characterised by cosmopolitan plant genera such as the progymnosperm tree *Archaeopteris*. In part, this may reflect increasing proximity between Laurasia and Gondwana towards the end of the Devonian. These specimens also provide the earliest record of terrestrial animals in Gondwana.

KEY WORDS: Scorpiones, Mesoscorpionina, Late Devonian, Famennian, Gondwana, South Africa, Waterloo Farm, chela, high palaeolatitude, new taxa, terrestrialisation.

INTRODUCTION

Modern scorpions are an abundant group generally occurring in tropical and warm temperate regions worldwide, although examples are known from cold high altitude environments in Patagonia. They are not known to occur naturally at latitudes higher than 50 degrees (Polis 1990). Scorpions are extremely conservative organisms that occur in the fossil record from the early Silurian period (Størmer 1977; Dunlop & Selden 2013) and are believed to have been an entirely terrestrial clade (e.g. Scholtz & Kamenz 2006; Dunlop *et al.* 2008; Kühl *et al.* 2012), with the exception of Devonian *Waeringoscorpio* Størmer, 1970 which may have been secondarily aquatic (Kühl *et al.* 2012).

Early scorpions were classically considered to have been aquatic and probably marine (e.g. Rolfe & Beckett 1984; Kjellesvig-Waering 1986; Polis 1990), all Silurian examples having been recovered from marginal marine lagoonal sediments (Jeram 1998). Terrestrialisation was believed to have occurred early in their history, probably during the Devonian period, with allegedly aquatic Proscorpiidae coexisting with terrestrial Mesoscorpionina and 'palaeosterns' until the early Carboniferous (Jeram 1998).

Evidence for terrestriality in mesoscorpions was provided by demonstration of booklungs in *Pulmonoscorpius* Jeram, 1994 from early Carboniferous strata of East Kirkton in Scotland (Jeram 1990, 1994). The presence of an oral tube (floored by the coxal apophyses) in structurally similar *Pulmonoscorpius*, *Petaloscorpio* Kjellesvig-Waering, 1986 and *Hubeiscorpio* Walossek, Li & Brauckmann, 1990 (Walossek *et al*. 1990) was considered indicative that the mesoscorpion clade that they comprise was terrestrial (Jeram 1998).

The view that basal scorpions were not terrestrial and that terrestrialisation occurred in scorpions independently of other Arachnida (Selden & Jeram 1989) carried the im-

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plication that the Araneae are not monophyletic (Scholtz & Kamenz 2006). This has been strongly refuted by Scholtz and Kamenz (2006) who argue that booklungs are an apomorphy of Araneae, that the Araneae are monophyletic and that they resulted from a single terrestrialisation event in their common stem lineage. This implies that all fossil scorpions were primarily terrestrial. Scholtz and Kamenz (2006) argue that several other arachnid characters such as trichobothria, slit-sense organs, endodermal malphigian tubules, and extra-intestinal digestion can be interpreted as apomorphic arachnid adaptations to land (Scholtz & Kamenz 2006).

Support for this view comes from the redescription of a number of apparently basal taxa. Dunlop *et al.* (2008) re-examined the oldest (Late Silurian) members of the Proscorpiidae, viz. *Proscorpius* Whitfield, 1885 (Whitfield 1885*a*, *b*), *Archaeophonus* Kjellesvig-Waering, 1966 and *Stoermeroscorpio* Kjellesvig-Waering, 1986, and synonomised them under *Proscorpius*. They refuted evidence for gill openings and found no structural evidence to support an aquatic lifestyle. They assert that no definite evidence for internal gills or any unambiguously aquatic character has ever been unequivocally demonstrated in a fossil scorpion (Dunlop *et al.* 2008).

Palaeoscorpius devonicus Lehmann, 1944 from the Lower Devonian Hunsrück Slate Lagerstätte in Germany has also been re-investigated (Kühl *et al.* 2012). This key fossil was formerly interpreted as the most basal member of the Scorpiones and as one of the order's most likely candidates for an aquatic mode of life (Jeram 1998). New imagery was obtained using radiography, X-ray micro-tomography, and CT scanning techniques. Layered internal mesosomal organs were located and interpreted as probable book lungs (Kühl *et al.* 2012). Kühl *et al.* (2012) note that much of the argument for *Palaeoscorpius* Lehmann, 1944 being marine was based on the belief that the Hunsrück Slate was of deep marine origin. Conversely, recent studies of the palaeoenvironment suggest that the 'Hunsrück Sea' was part of an intrashelf basin close to the shore, into which terrestrial plants were periodically washed. Terrestrial material was likewise preserved in the lagoonal deposits that have yielded other early scorpions (Kühl *et al.* 2012). After reviewing all evidence Kühl *et al.* (2012) conclude that *Palaeoscorpius* was most likely to have been terrestrial. They also note that this provides strong evidence for arachnid monophyly and a single shared terrestrial arachnid ancestor. Highly unusual Lower Devonian *Waeringoscorpio* may have been secondarily aquatic as its unique filamentous external organs strongly resemble the tracheal gills of (secondarily) aquatic insects (Poschmann *et al*. 2008; Kühl *et al.* 2012).

Scorpion evolution is patchily represented in the fossil record due to the poor preservation potential of scorpions, particularly in terrestrial environments. Only 16 species, commonly represented by single specimens, of Silurian and Devonian scorpions were recognised in 15 genera by Jeram (1998). Of these, two Silurian genera and species have subsequently fallen away (Dunlop *et al*. 2008). All but one genus, *Hubeiscorpio*, have been recovered from European and North American strata (Sissom 1990), that at the time of their deposition formed a continuous land mass, Laurasia. Both Laurasia and China situated within tropical to subtropical latitudes during the Silurian and Devonian (Scotese & Mckerrow 1990; Mitchell *et al*. 2012).

Only two occurrences of scorpion fossils have been recorded from the Late Devonian (Jeram 1996, 1998). These are *Petaloscorpio bureaui* Kjellesvig-Waering, 1986 from the Frasnian Escuminac Formation of Canada (Jeram 1996) and *Hubeiscorpio gracilitarsus*

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Walossek, Li & Brauckmann, 1990 from the Frasnian of China (Walossek *et al*. 1990). Cladistic analysis of scorpions (Jeram 1998) places these two species as sister groups within the clade Mesoscorpionina, together with early Carboniferous *Pulmonoscorpius* (*Acanthoscorpius* Kjellesvig-Waering, 1986 having been subsequently removed from the Scorpiones (Legg *et al*. 2009)). The Mesoscorpionina form the sister group of late Carboniferous *Palaeopisthacanthus* Petrunkevitch, 1913, the earliest member of the crown group (Jeram 1998). Legg *et al*. (2009), however, suggest that mesoscorpions may be paraphyletic with regard to the crown group.

MATERIAL AND METHODS

New material consists of fragments recovered from the Witpoort Formation (Witteberg Group, Cape Supergroup) Waterloo Farm locality near Grahamstown, South Africa. This locality consists of black carbonaceous shale derived from anaerobic mud deposited in a back-barrier marginal marine lagoonal estuary (Gess & Hiller 1995*a*). Organic remains accumulated in this setting include those of algae (Gess & Hiller 1995*b*; Hiller & Gess 1996), terrestrial plants (Gess & Hiller 1995*a*; Anderson *et al*. 1995) and fish (Gess & Hiller 1995*a*; Long *et al*. 1997; Gess 2001; Gess *et al*. 2006). Invertebrate remains include those of small smooth-shelled bivalves, ostracods, conchostacans, and a eurypterid (Gess & Hiller 1995*a*). All fossil material consists of near two-dimensional compressions in which all original tissues have been replaced by secondary metamorphic mica. This has largely been altered to chlorite during uplift (Gess & Hiller 1995*a*).

The Witpoort Formation strata at Waterloo Farm were deposited towards the end of the Famennian age of the Late Devonian period, approximately 360 million years ago.

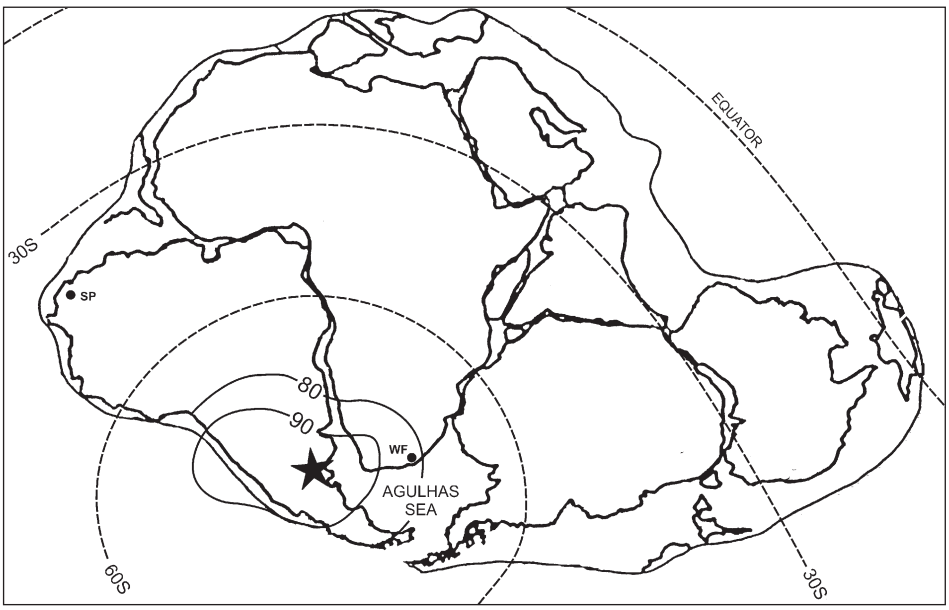


Fig. 1. Gondwanan reconstruction with position of the South Pole (star), main latitudes reconstructed for Late Devonian/Early Carboniferous (modified after Scotese & Barrett 1990), and the position of the Waterloo Farm (WF).

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The Waterloo Farm estuary formed along the shoreline of the intracontinental Agulhas Sea, apparently within fifteen degrees of the south pole (Scotese & McKerrow 1990; Scotese & Barrett 1990; Mitchell *et al*. 2012) (Fig. 1).

Scorpion fragments, including a pedipalp chela articulating with a patella (Fig. 2A, B) and a telson attached to a metasomal segment V (Fig. 2C, D) have been recovered. The telson is slightly damaged where it has been compressed together with small plant fragments.

TAXONOMY

Order Scorpiones *incertae sedis*

Genus **Gondwanascorpio** gen. n.

Etymology: From Gondwana and Latin *scorpio* (scorpion). Masculine gender.

Type species: *Gondwanascorpio emzantsiensis* sp. n.

Diagnosis: The manus of the chela approximately equals the patella in length (character 11, Jeram 1998). Rami of the chela are very elongate, exceeding twice the length of the manus (character 13, Jeram 1998). Elongation of the manus and rami of the chela have been proposed as apomorphies helping to define the Mesoscorpionina together with crown group scorpions (Jeram 1998). Identification as a member of the Mesoscorpionina would, however, be incautious on the basis of only two characters. The gripping surfaces of the rami are crenulated, with crenulation peaks on the two rami arranged in an alternating pattern. There are 6 crenulations on the free ramus and probably 6 on the fixed ramus, though these are proximally more subdued. Notably the chela closely resembles that of *Pulmonoscorpius*, although the rami of the latter do not appear to be markedly crenulate. Comparison with Late Devonian genera is limited by lack of pedipalps in the type specimen of *Hubeiscorpio* and their incomplete preservation in *Petaloscorpio*. The pedipalp chelae of *Petaloscorpio* are also elongate, although no further

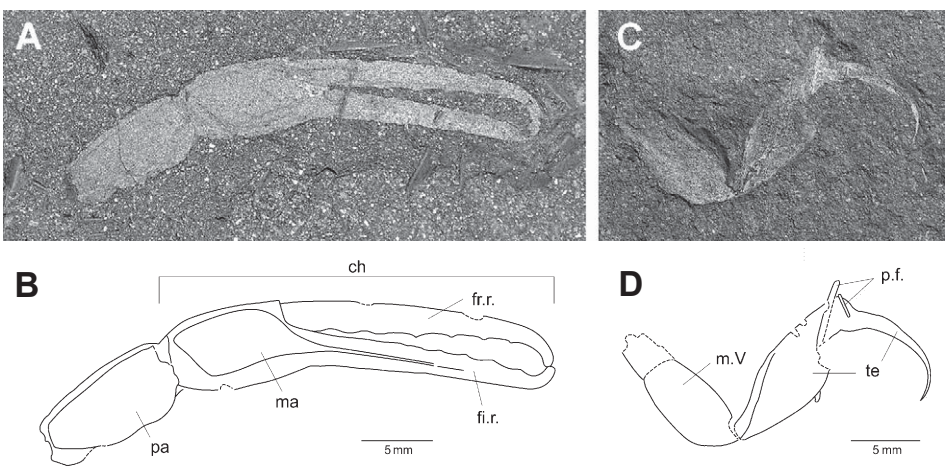


Fig. 2. *Gondwanascorpio emzantsiensis* gen. & sp. n.: (A, B) holotype AM5700, general appearance and details of pedipalp chela articulating with patella, (C, D) paratype AM5701, general appearance and details of telson and metasomal segment V. Abbreviations: ch – chela, fi.r. – fixed ramus, fr.r. – free ramus, ma – manus, pa – patella, m.V – metasomal segment V, p.f. – plant fragments, te – telson.

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details have been described or illustrated. The telson of *Gondwanascorpio* resembles that of *Pulmonoscorpius*. Due to the fragmentary nature of the new material and paucity of knowledge of Palaeozoic scorpions the material is unidentifiable beyond Scorpiones *incertae sedis*. Close affinity to known Late Devonian and Early Carboniferous mesoscorpionine genera, particularly *Pulmonoscorpius*, is, however, probable.

Gondwanascorpio emzantsiensis sp. n.

Fig. 2

Etymology: From genitive of isiXhosa *umZantsi* (south), which is sometimes used for South Africa.

Description:

Complete chela 25 mm long.

Holotype: AM7500 SOUTH AFRICA: *Eastern Cape*: Waterloo Farm, 33°19'23.97"S 26°32'13.05"E; Late Devonian, Famennian, Cape Supergroup, Witteberg Group, Witpoort Formation.

Paratype: AM7501, same locality and strata as holotype.

DISCUSSION

This represents the first record of a Palaeozoic scorpion from Gondwana. It is extremely unusual in that it has been recovered from rocks apparently deposited at a far higher latitude than that at which modern or fossil scorpions are known to have occurred. This may reflect amelioration of climatic gradients towards the end of the Devonian (Streel *et al*. 2000).

The presence of a scorpion in Gondwana, similar to Laurasian taxa, is consistent with growing evidence for globally comparable terrestrial ecosystems by the end of the Devonian. These were characterised by cosmopolitan plant genera such as the progymnosperm tree *Archaeopteris*, which has also been described from Waterloo Farm (Anderson *et al*. 1995). A breakdown in disparity between Gondwanan and Laurasian marginal marine ecosystems towards the end of the Devonian has previously been noted, possibly caused by increasing proximity of Laurasia to Gondwana (Young 1987).

Gondwanascorpio is the oldest known terrestrial animal from Gondwana. The only other putative terrestrial animal reported from the Devonian of Gondwana were tergites of *Maldybulakia* Tesakov & Alekseev, 1998 from Australia (Edgecombe 1998*a*, *b*). Having at first been described from Kazakhstan as *Lophodesmus*, *Maldybulakia* was originally considered to most probably represent a type of myriapod (Tesakov & Alekseev 1992). It has subsequently been demonstrated that *Maldybulakia* most likely represents remains of an aquatic xiphosuran (Anderson *et al.* 1998; Edgecombe 2004).

The next oldest records of terrestrial animals from southern Africa are insects from the Early Permian Whitehill Formation (Ecca Group, Karoo Supergroup) (McLachlan & Anderson 1977) that was deposited approximately 90 million years later (Fildani *et al*. 2007). This remarkable gap in the regional fossil record is partially accounted for by a tectonically related 30 million year depositional hiatus, which began around 330 million years ago and was followed by a period of approximately 10 million years of deposition of the Dwyka Group (Karoo Supergroup) glacial diamictites. These resulted from southern Africa's passage over the South Pole during the Carboniferous and the consequent glaciation of most of Gondwana (Catuneanu *et al*. 2005).

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REFERENCES

Anderson, H.M., Hiller, N. & Gess, R.W. 1995. *Archaeopteris* (Progymnospermopsida) from the Devonian of southern Africa. *Botanical Journal of the Linnean Society* **117**: 305–320.

Anderson, L.I., Poschmann, M. & Brauckmann, C. 1998. On the Emsian (Lower Devonian) arthropods of the Rhenish Slate Mountains: 2. The synziphosurine *Willwerathia*. *Paläontologische Zeitschrift* **72**: 325–336.

Catuneanu, O., Wopfner, H., Eriksson, P.G., Cairncross, B., Rubidge, B.S., Smith, R.M.H. & Hancox, P.J. 2005. The Karoo basins of south-central Africa. *Journal of African Earth Sciences* **43**: 211–253.

Dunlop, J.A. & Selden, P.A. 2013. Scorpion fragments from the Silurian of Powys, Wales. *Arachnology* **16** (1): 27–32.

Dunlop, J.A., Tetlie, O.E. & Prendini, L. 2008. Reinterpretation of the Silurian scorpion *Proscorpius osborni* (Whitfield): integrating data from Palaeozoic and recent scorpions. *Palaeontology* **51** (2): 303–320.

Edgecombe, G.D. 1998*a*. Devonian terrestrial arthropods from Gondwana. *Nature* **394**: 172–175.

———1998*b*. Early myriapodous arthropods from Australia: *Maldybulakia* from the Devonian of New South Wales. *Records of the Australian Museum* **50** (3): 293–313.

———2004. Morphological data, extant Myriopoda, and the myriopod stem group. *Contributions to Zoology* **73** (3): 207–241.

Fildani, A., Drinkwater, N.J., Weislogel, A., McHargue, T., Hodgson, D.M. & Flint, S.S. 2007. Age controls on the Tanqua and Laingsburg deep-water systems: New insights on the evolution and sedimentary fill of the Karoo Basin. *Journal of Sedimentary Research* **77**: 901–908.

Gess, R.W. 2001. A new species of *Diplacanthus* from the Late Devonian (Famennian) of South Africa. *Annales de Paléontologie* **87**: 49–60.

Gess, R.W. & Hiller, N. 1995*a*. A preliminary catalogue of fossil algal, plant, arthropod, and fish remains from a Late Devonian black shale near Grahamstown, South Africa. *Annals of the Cape Provincial Museums (Natural History)* **19**: 225–304.

———1995*b*. Late Devonian charophytes from the Witteberg Group, South Africa. *Review of Palaeobotany and Palynology* **89**: 417–428.

Gess, R.W., Coates, M.I. & Rubidge, B.S. 2006. A lamprey from the Devonian period of South Africa. *Nature* **443**: 981–984.

Hiller, N. & Gess, R.W. 1996. Marine algal remains from the Upper Devonian of South Africa. *Review of Palaeobotany and Palynology* **91**: 143–149.

Jeram, A.J. 1990. Book-lungs in a Lower Carboniferous scorpion. *Nature* **343**: 360–361.

———1994 (1993). Scorpions from the Visean of East Kirkton, West Lothian, Scotland, with a revision of the infraorder Mesoscorpionina. *Transactions of the Royal Society of Edinburgh*: *Earth Sciences* **84**: 283–299.

———1996. Chelicerata from the Escuminac Formation. *In*: Schultze, H.-P. & Cloutier, R., eds, *Devonian Fishes and Plants of Miguasha, Quebec, Canada*. Munich: Dr Friedrich Pfeil, pp. 103–111.

———1998. Phylogeny, classification and evolution of Silurian and Devonian scorpions. *In*: Selden, P.A., ed., *Proceedings of the 17th European Colloquium of Arachnology, Edinburgh, 1997*. Burnham Beeches: The British Arachnological Society, pp. 17–31.

Kjellesvig-Waering, E.N. 1966. Silurian scorpions of New York. *Journal of Paleontology* **40**: 359–375.

———1986. A restudy of the fossil Scorpionida of the world. *Palaeontographica americana* **55**: 1–287.

Kühl, G., Bergmann, A., Dunlop, J.A., Garwood, R.J. & Rust, J. 2012. Redescription and palaeobiology of *Palaeoscorpius devonicus* Lehmann, 1944 from the Lower Devonian Hunsrück Slate of Germany. *Palaeontology* **55**: 775–787.

Legg, D.A., Braddy, S.J. & Dunlop, J.A. 2009. The supposed scorpion *Acanthoscorpio mucronatus* Kjellesvig-Waering, recognized as a juvenile eurypterid and its implications for scorpion systematics.

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Progressive Palaeontology, Programme and Abstracts. Birmingham, UK: The Palaeontological Association & University of Birmingham, p. 19.

Lehmann, W.H. 1944. *Palaeoscorpius devonicus* n. g. n. sp., ein Skorpion aus dem rheinischen Unterdevon. *Neues Jahrbuch für Paläontologie, Monatshefte B* **7/9**: 177–185.

Long, J.A., Anderson, M.E., Gess, R.W. & Hiller, N. 1997. New placoderm fishes from the Late Devonian of South Africa. *Journal of Vertebrate Palaeontology* **17**: 253–268.

McLachlan, I.R. & Anderson, A.M. 1977. Fossil insect wings from the Early Permian White Band Formation, South Africa. *Palaeontologia africana* **20**: 83–86.

Mitchell, R.N., Kilian, T.M. & Evans, D.A.D. 2012. Supercontinent cycles and the calculation of palaeolongitude in deep time. *Nature* **482**: 208–211.

Petrunkevitch, A.I. 1913. A monograph of the terrestrial Palaeozoic Arachnida of North America. *Transactions of the Connecticut Academy of Arts and Sciences* **18**: 1–137.

Polis, G.A. 1990. Introduction. *In*: Polis, G.A., ed., *The Biology of Scorpions*. Stanford: Stanford University Press, pp. 1–8.

Poschmann, M., Dunlop, J.A., Kamenz, C. & Scholtz, G. 2008. The Lower Devonian scorpion *Waeringoscorpio* and the respiratory nature of its filamentous structures, with the description of a new species from the Westerwald area, Germany. *Paläontologische Zeitschrift* **82**: 418–436.

Rolfe, W.D.I. & Beckett, C.M. 1984. Autecology of Silurian Xiphosurida, Scorpionida, and Phyllocarida. *Special Papers in Palaeontology* **32**: 27–37.

Scholtz, G. & Kamenz, C. 2006. The book lungs of Scorpiones and Tetrapulmonata (Chelicerata, Arachnida): Evidence for homology and a single terrestrialisation event of a common arachnid ancestor. *Zoology* **109**: 2–13.

Scotese, C.R. & Barrett, S.F. 1990. Gondwana's movement over the south Pole during the Palaeozoic: evidence from lithological indicators of climate. *In*: McKerrow, W.S. & Scottese, C.R., eds, *Palaeozoic palaeogeography and biogeography*. *Memoirs of the Geological Society of London* **12**: 75–86.

Scotese, C.R. & McKerrow, W.S. 1990. Revised world maps and introduction. *In*: McKerrow, W.S. & Scotese, C.R., eds, *Palaeozoic palaeogeography and biogeography*. *Memoirs of the Geological Society of London* **12**: 1–21.

Selden, P.A. & Jeram, A.J. 1989. Palaeophysiology of terrestrialisation in Chelicerata. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **80**: 303–310.

Sissom, W.D. 1990. Systematics, Biogeography and Palaeontology. *In*: Polis, G.A., ed., *The Biology of Scorpions*. Stanford: Stanford University Press, pp. 64–160.

Størmer, L. 1970. Arthropods from the Lower Devonian (Lower Emsian) of Alken-an-der-Mosel, Germany. Part 1. Arachnida. *Senchenbergiana Lethaia* **51**: 335–369.

———1977. Arthropod invasion of land during Late Silurian and Devonian times. *Science* **197**: 1362–1364.

Streel, M., Caputo, M.V., Loboziak, S. & Melo, G. 2000. Late Frasnian–Famennian climates based on palynomorph analyses and the question of the Late Devonian glaciations. *Earth Science Reviews* **52**: 121–173.

Tesakov, A.S. & Alekseev, A.S. 1992. Myriapod-like arthropods from the Lower Devonian of central Kazakhstan. *Paleontological Journal* **26**: 18–23.

———1998. *Maldybulakia* – new name for *Lophodesmus* Tesakov & Alekseev, 1992 (Arthropoda). *Paleontological Journal* **32**: 49.

Walossek, D., Li, C.-S. & Brauckmann, C. 1990. A scorpion from the Upper Devonian of Hubei Province, China (Arachnida, Scorpionida). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **3**: 169–180.

Whitfield, R.P. 1885*a*. An American Silurian scorpion (*Palaeophonus osborni*). *Science* **6**: 87.

———1885*b*. On a fossil scorpion from the Silurian rocks of America. *Bulletin of the American Museum of Natural History* **6**: 181–190.

Young, G.C. 1987. Devonian palaeontological data and the Armorica problem. *Palaeogeography, Palaeoclimatology, Palaeoecology* **60**: 283–304.

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