

## THE LATEST ON THE OLDEST

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### INTRODUCTION

In 2008, Helen Read and I wrote a short piece for the *Bulletin* about the discovery of the oldest fossil myriapod (and the oldest demonstrably air-breathing animal), the millipede *Pneumodesmus newmani* Wilson, 2004, from mid-Silurian strata (c. 427 Ma) of Stonehaven, Scotland (Selden & Read, 2008). Last year, a team of geochronologists from the University of Texas at Austin restudied the evidence for the age of the rocks at Stonehaven, using radioisotope data from zircon crystals in the beds surrounding those containing the millipedes, and concluded that they were rather younger than previously thought: early Devonian (c. 414 Ma) in age, or some 13 million years younger (Suarez *et al.*, 2017). This finding removes the title of oldest myriapod from *Pneumodesmus*. So what, now, is the oldest known myriapod and the oldest air-breathing animal?

### STONEHAVEN

First, some background. The intertidal rocks exposed on the shore at Cowie Harbour, north of Stonehaven, Aberdeenshire, consist of a series of conglomerates, sandstones, and siltstones, dipping steeply (in some place overturned), and closed by faults and igneous dykes. The millipede fossils occur in the so-called Cowie Harbour Fish Bed, part of the Cowie Harbour Siltstone Member, in the middle of the foreshore (Figs. 1, 2). The Stonehaven sequence lies about 500 m south of the great Highland Boundary Fault, which runs from here, south-west across Scotland, through Loch Lomond, across the middle of the Isle of Arran, and thence to Ulster and Connemara. Unsurprisingly, the age of this isolated patch of contorted rocks has been disputed for many years.

The Stonehaven sequence, which forms the lowest part of the Old Red Sandstone sequence in Scotland, was originally thought to be latest Silurian (Přídolí) age, based on the aquatic arthropod and fish fossils found there and correlation with similar faunas in Norway (Campbell, 1913). Later work on the Norwegian faunas, however, suggested that both these and the Stonehaven succession might be older, middle Silurian in age (Hanken & Størmer, 1975). A mid-Silurian age was later confirmed by palynological studies (Marshall, 1991; Wellman, 1993) on plant spores from inland sites thought to be part of the Stonehaven Group. So, when Wilson & Anderson (2004) described *Pneumodesmus*, with its clearly visible spiracles, from the Cowie Harbour Fish Bed, it had good claim to be the oldest known land animal, and oldest myriapod. Wilson & Anderson (2004) actually described three millipedes from the Cowie Harbour Fish Bed: *Albadesmus almondi*, *Pneumodesmus newmani* and *Cowiedesmus eroticopodus*, but only *Pneumodesmus* could be demonstrably shown to be an air-breather, and hence the oldest land animal.

That was until last year, when a team at the University of Texas at Austin led by Danny Stöckli investigated the radiometric age of tiny zircon crystals found in the strata either side of the fish bed (Suarez *et al.* 2017). Using U-Pb Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICP-MS), they measured the ratio of  $^{238}\text{U}$ - $^{206}\text{Pb}$  isotopes, and found that they gave dates of  $413.7\pm 4.4$  Ma for a volcanic ash below the fish bed and  $414.3\pm 7.1$  Ma for the sandstone immediately overlying the



**Figure 1: General view of Cowie Harbour, Stonehaven, Aberdeenshire, looking north-east.** The Devonian Cowie Harbour Group form the foreshore exposures, beyond which the cliffs of Slug Head to Garron Point are composed of the older Highland Border Complex which abut the Highland Boundary Fault.



**Figure 2: Cowie Harbour foreshore looking east.** Information board giving details of the fossil bed and its millipedes. The fossil bed lies just beyond the inlet.

fish bed. These dates equate to the Lower Devonian (Lochkovian). They pointed out that the palynological samples of Marshall (1991) and Wellman (1993) come from outcrops isolated from Cowie Harbour by faults, so might not be equivalent.

Since the new dating was published, Shillito & Davies (2017) described some new trace fossils (shallow burrows) from Cowie Harbour, in beds below the Cowie Harbour Siltstone Member which contains *Pneumodesmus*. The burrows were not attributed to millipedes, and the trace fossil assemblage is typical of those found in terrestrial sediments of Siluro-Devonian times after the initial terrestrialization of arthropods but prior to the Devonian radiation of land animals as shown by trace fossil diversity (Buatois *et al.*, 1998; Minter *et al.*, 2017). Hence, Shillito & Davies (2017) suggested that the inland exposures near Stonehaven dated by palynology represent an older, unrelated, formation, and that the fossil-bearing strata exposed in Cowie Harbour were deposited during early Lochkovian times.

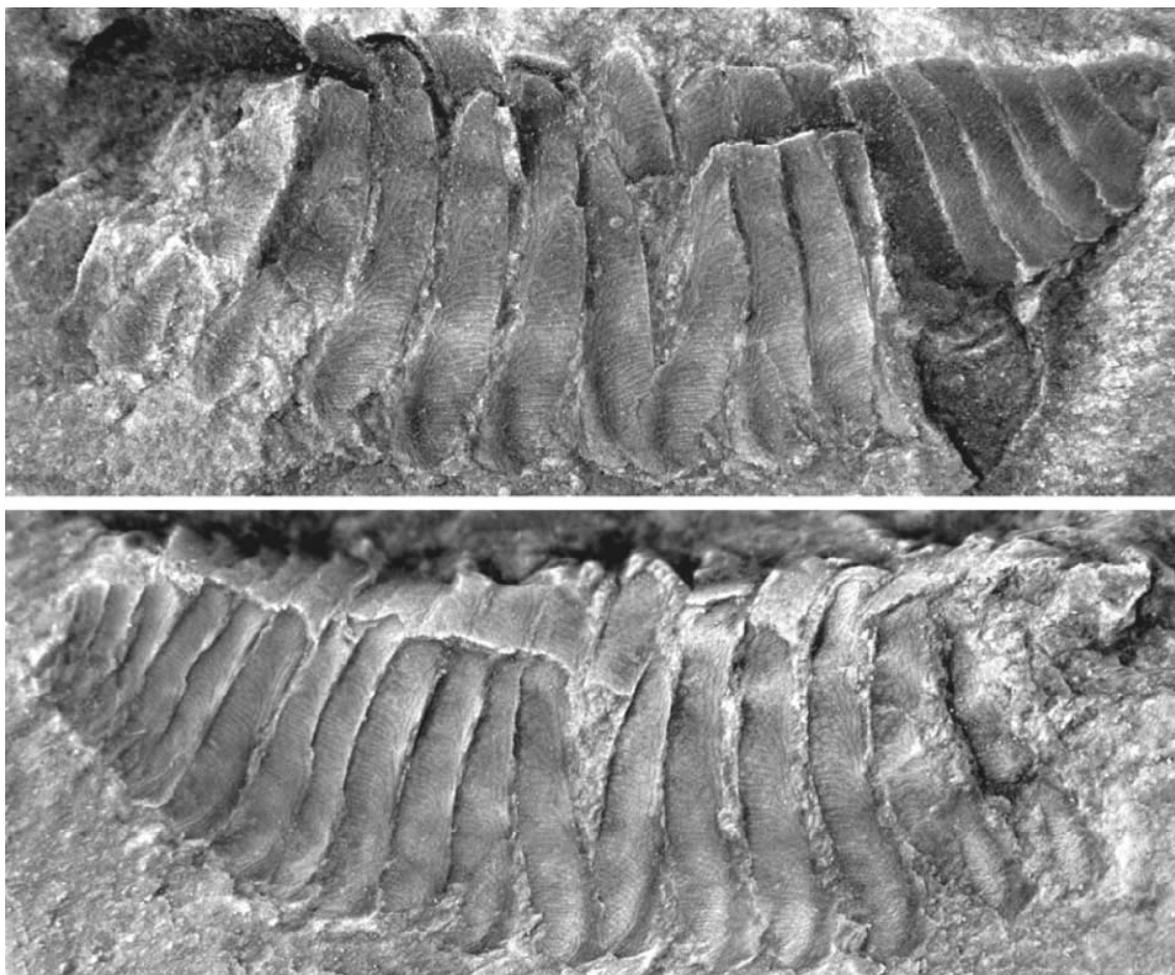
### THE OLDEST MYRIAPOD

Now that *Pneumodesmus* appears to have lost its title to the oldest land animal in the fossil record, what is the oldest, and what is the oldest myriapod? We can discount the enigmatic fossil *Cambropodus* Robison, 1990 from the Cambrian of Utah. This specimen is more likely to be a lobopod rather than an arthropod, if it is an animal at all. Regarding land animals, the problem is that they need to show some sort of terrestrial adaptation; for all we know, the oldest myriapod might have been aquatic. Fossil trackways indicating that aquatic animals hauled themselves out of the water and across subaerially exposed sediments date back to the latest Cambrian (*c.* 488 Ma: MacNaughton *et al.*, 2002), but whether these animals were habitually terrestrial or were aquatic animals sprinting from one pool to another to survive desiccation is not clear. Moreover, evidence for the sediment being exposed to the air (e.g. mud cracks) does not necessarily tell us whether the tracks were made under water and then exposed, or the mud was already drying and cracking when the trackway was made (Braddy, 2004). Nevertheless, a Cambro-Ordovician origin of terrestrial animals was suggested by Rota-Stabelli *et al.* (2013) using molecular clock analyses of extant Ecdysozoa. Many of the early Paleozoic trackways have been ascribed to myriapod-like animals, but it would be unwise to accept them as explicit evidence for the existence of myriapods as we know them. It is conceivable that there were other extinct arthropods around at this time with multiple limbs capable of leaving such impressions (see reviews in Wilson, 2006; Dunlop *et al.*, 2013). Another kind of trace fossil, coprolites, occur in rocks of late Silurian age near Ludlow, Shropshire, which have been attributed to detritivorous animals, probably millipedes (Edwards *et al.*, 1995).

Body fossils of terrestrial animals include scorpions from rocks of middle and late Silurian age (*c.* 430–420 Ma), e.g. *Dolichophonus loudonensis* Laurie, 1899 from the Pentland Hills near Edinburgh, is the oldest known arachnid (Wolfe *et al.*, 2016), and is about the same age as the Stonehaven fossils were before they were shown to be younger. However, there is some discussion about whether early scorpions were aquatic or terrestrial (see discussions in Selden & Jeram, 1989; Scholtz & Kamenz, 2006; Kühl *et al.*, 2012) because some early scorpion fossils show features of aquatic relatives such as eurypterids (sea scorpions), e.g. digitigrade tarsi. So, the earliest fossils which show book lungs and other features which are unequivocally related to terrestrial life are from the locality of Ludford Lane, Shropshire, in rock of late Silurian (Přídolí) age (Jeram *et al.*, 1990). This fauna includes scutigermorph centipedes and eoarthroleurid millipedes (Selden, 2016).

However, while they do not show air-breathing spiracles, the oldest known myriapods do still come from mid-Silurian rocks in Scotland (Wilson, 2005). In this paper, Wilson described two new genera and species of Palaeozoic millipedes, *Zosterogrammus stichostethus* and *Casiogrammus ichthyeros*,

from the Upper Carboniferous locality of Mazon Creek, Illinois, and the Hagshaw Hills (Middle Silurian: Wenlock) of Scotland, respectively. Together with *Purkynia lata* Frič, 1899, from the Upper Carboniferous locality of Nýřany, Czech Republic these millipedes, were placed in the new order Zosterogrammida, which are characterized by trunk rings consisting of an arched diplotergite, a pair of free ventral diplopleurites, and a pair of free ventral sternites (Wilson, 2005). The oldest of these millipedes, *Casiogrammus ichthyeros*, was used as a calibration point in a phylogenomic analysis of the Myriapoda Tree of Life in a recent paper by Fernández *et al.* (2018). *Casiogrammus* (Fig. 3) was first mentioned as a possible millipede by Rolfe (1980), and it is recognized as such simply for possessing a regular series of similar tergites. It somewhat resembles the rather short, broad polyzoniids.



**Figure 3: The oldest known myriapod, *Casiogrammus ichthyeros* Wilson, 2005.**

Top: part; bottom: counterpart.

The Hagshaw Hills, south-west of Glasgow in Lanarkshire, consist of an inlier of older, harder Silurian rocks poking through the younger, softer surrounding Carboniferous strata of the Midland Valley of Scotland. The Fish Bed Formation in the Hagshaw Hills is dated by palynology to early Wenlock (*c.* 430–433 Ma) age (Wellman & Richardson, 1993), and is famous for its diverse fauna of non-marine jawless fish together with eurypterids; apart from the millipede, no other terrestrial arthropods are known from the formation, though some plant fragments occur (Rolfe, 1961, 1992; Ritchie, 1968). The beds were most likely deposited in a relatively permanent lacustrine setting (Wellman & Richardson, 1993).

While *Pneumodesmus newmani* might have lost its status as the oldest myriapod, it remains the oldest known animal showing spiracles for air breathing. Moreover, the oldest known land animal (probably, even though it lacks spiracles), *Casiogrammus*, is also a millipede. These records will remain until more fossils are discovered or the ages of the strata in which they are found are revised. Watch this space!

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