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archipolypodan millipede
from the Carboniferous of the Netherlands
with unusually long tergites

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A new species of possible archipolypodan millipede from the Carboniferous of the Netherlands with unusually long tergites

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ABSTRACT

Millipedes have a long evolutionary history, with the oldest presumed fossils of Diplopoda de Blainville *in* Gervais, 1844 being from the Silurian and the first definite fossil record originating from Devonian deposits. The phylogeny of Diplopoda is not fully resolved yet, especially not concerning fossil representatives. At the same time, already in the Palaeozoic millipedes showed quite a morphological and presumably also ecological variety. We describe here a new species of a Carboniferous millipede from the Westphalian A of the Netherlands, *Lauravolsella willemeni* n. gen., n. sp., a possible representative of Archipolypoda (†Archipolypoda Scudder, 1882). The species is based on a single specimen, preserved with part and counterpart, which both show a three-dimensional preservation. The specimen has unusually long tergites, in normal life position covering most of the following segment. These long tergites might have been beneficial when performing defensive enrolling. In extant millipedes, enrolling is usually facilitated by softer areas between the sternites, allowing for a certain degree of ventral compression. In the new fossil, the sclerotic sternites occupy the entire length of the ventral side of the segment, not allowing for any type of compression. The new fossil therefore demonstrates another solution for the mechanical challenges during enrolment and increases the morphological diversity of Carboniferous millipedes.

KEY WORDS

Myriapoda,
Diplopoda,
Archipolypoda,
stereo imaging,
new genus,
new species.

RÉSUMÉ

Une nouvelle espèce de millipède archipolypode du Carbonifère des Pays-Bas avec des tergites inhabituellement longs.

Les millipèdes ont une longue histoire évolutive, les plus anciens fossiles présumés de Diplopoda de Blainville *in* Gervais, 1844 datant du Silurien et le premier fossile défini provenant de dépôts dévoniens. La phylogénie des diplopodes n'est pas encore totalement résolue, en particulier en ce qui concerne les représentants fossiles. En même temps, dès le Paléozoïque, les mille-pattes présentaient une grande variété morphologique et probablement aussi écologique. Nous décrivons ici une nouvelle espèce de mille-pattes carbonifères du Westphalien A des Pays-Bas, *Lauravolsella willemeni* n. gen., n. sp., un représentant possible d'Archipolypoda (†Archipolypoda Scudder, 1882). L'espèce est basée sur un seul spécimen, préservé avec une partie et une contrepartie, qui montrent toutes deux une préservation tridimensionnelle. Le spécimen a des tergites inhabituellement longs, en position de vie normale couvrant la majeure partie du segment suivant. Ces longs tergites auraient pu être utiles lors de l'enroulement défensif. Chez les millipèdes existants, l'enroulement est généralement facilité par des zones plus souples entre les sternites, permettant un certain degré de compression ventrale. Dans le nouveau fossile, les sternites sclérosés occupent toute la longueur de la face ventrale du segment, ne permettant aucun type de compression. Le nouveau fossile démontre donc une autre solution pour les défis mécaniques lors de l'enroulement et augmente la diversité morphologique des millipèdes du Carbonifère.

MOTS CLÉS
Myriapoda,
Diplopoda,
Archipolypoda,
imagerie stéréo,
genre nouveau,
espèce nouvelle.

INTRODUCTION

Diplopoda de Blainville *in* Gervais, 1844, the group of millipedes, may not be as species-rich as beetles, flies or moths, but with more than 10 000 formally described species in the extant fauna, it is still one of the more diverse lineages in Euarthropoda. Furthermore, millipedes represent important components of the soil and leaf-litter fauna, by this fulfilling important eco-system functions.

The group Diplopoda has a long evolutionary history; the oldest fossils supposed to be millipedes are known from the Silurian (Almond & Lawson 1985; Wilson & Anderson 2004; Wilson 2005a; Shear & Edgecombe 2010: 183); definite representatives of the group are known from the Devonian (Shear 1998: 123). All older fossils of millipede-type appearance (e.g. Budd *et al.* 2001) could not be identified as representatives of Diplopoda more reliably. This also applies to some fossils that are contemporary with true millipedes (Tesakov & Alekseev 1992; Edgecombe 2015a).

The phylogeny of Diplopoda has not been well reconstructed so far, many conflicting hypotheses have been put forward (Shear & Edgecombe 2010: 179, 180; Edgecombe 2015b). Furthermore, most of the phylogenetic reconstructions include only extant representatives. Interpreting fossils in this frame remains still very challenging.

This challenge is especially true for Palaeozoic representatives. Most of the relatively numerous Palaeozoic specimens have been interpreted as representatives of the group Archipolypoda (†Archipolypoda Scudder, 1882). Representatives of Archipolypoda, together with their contemporary relatives, seem to have played an important role in the past, being central components of the Palaeozoic terrestrial fauna. We know quite some details about the biology of some of these animals based on rather complete specimens (e.g. Wilson 2005a, b,

2006a, b; Wilson & Hannibal 2005; Wilson *et al.* 2005); others remain known only from rather fragmentary pieces (e.g. Shear 1993; Hannibal & Krzemiński 2005; Hannibal & May 2021).

Some of the more complete Palaeozoic millipedes, for example, are known to have been able to fully enrol into a tightly closed ball armed with spines, supposedly for defensive purposes (Hannibal & Feldmann 1981; Racheboeuf *et al.* 2004). While such a morphology and behaviour are well known in the extant fauna (e.g. pill bugs, false sand crab larvae, mantis shrimp larvae), this behaviour has likely evolved independently in these Palaeozoic forms, like in other lineages of Euarthropoda (Haug & Haug 2014; Rudolf *et al.* 2016).

While it is well known that many extant millipedes have specialised appendages, most Palaeozoic ones have rather uniform appendages. Still some seem to have possessed already differentiated appendages on the trunk (Hannibal 1995).

Even some interaction between individuals is known for Palaeozoic millipedes. Several small-sized specimens have been preserved in close proximity, indicating an aggregation behaviour of these animals (Wilson 2006a). As the different finds demonstrate, millipedes in the later Palaeozoic already show quite a variety, from a number of deposits from all over the world.

Studies on fossils of Euarthropoda from the Carboniferous of the Netherlands are so far scarce. Pruvost (1927) published an isolated Namurian insect wing from a borehole near Gulpen, southern Limburg, the Netherlands. Laurentiaux (1950) described seven more winged insects from diverse coal mines of southern Limburg. Another new insect wing from the Westphalian A of the “Laura” mine was documented by Brauckmann & Gröning (1996). Laurentiaux-Vieira & Laurentiaux (1961) described a new whip scorpion (Thelyphonida Latreille, 1804; Arachnida Cuvier, 1812), whereas Steur &

Van Houtem (2012) reported on a representative of Trigonotarbida (Arachnida), both from the Westphalian A. In the study of Van der Heide (1951) all then known Carboniferous fossils of Euarthropoda (excluding scorpions and insects) of southern Limburg were listed, including many fragments of *Arthropleura* (†*Arthropleura* Meyer, 1854 – a presumed representative of Myriapoda Latreille, 1802) and an indefinite remain of another possible representative of Myriapoda.

We here report a new fossil millipede from the Carboniferous of the Netherlands. The specimen was collected in 2011 on the Westphalian A dumps of the former “Laura” coal mine in Eyselshoven, southern Limburg.

MATERIAL AND METHODS

MATERIAL

In the focus of the study is a single specimen, MAB13859A/B. It is preserved as part and counterpart. The specimen was found in 2011 by a private collector (Mr. Geert Willemen, Middelbeers, the Netherlands) in the coal mine dump of mine “Laura” near Eyselshoven in Southern Limburg, the Netherlands. Accordingly, the fossil is of lowermost Westphalian age (about 313–304 million years before present), being part of the upper Carboniferous and Pennsylvanian. The specimen is deposited in the Oertijmmuseum, Boxtel, the Netherlands.

For comparison, a millipede from the Pleistocene was documented, ROMIP32380. The label of the specimen stated that it was determined as *Fontaria corrugata* (for a discussion on the validity of this name, see Hoffman 1957). It was found in Whitchurch Township, York County, Ontario. The specimen is deposited at the Royal Ontario Museum, Toronto, Canada.

DOCUMENTATION METHODS

Many Carboniferous fossils of the group Euarthropoda are challenging to be documented with minimum artefacts. A major challenge is the proper differentiation between the information provided by the relief and the colour (Haug *et al.* 2012a, 2015; Hörnig *et al.* 2018). The standard method of using oblique light is not well suited for such an approach. Even, shadow-free lighting provides a good access to the colour information, while stereo imaging provides an independent access to the relief. Stereo images can be produced directly from a specimen by recording two images from two slightly differing angles (Haug *et al.* 2012a, b, 2015; Hörnig *et al.* 2018). It is often necessary for stereo images to document the entire specimen with one image instead of applying composite imaging (Haug *et al.* 2011a), as stitching (merging) of stereo images to a panorama can lead to severe artefacts in depth perception.

The specimen at hand is very elongate, documenting it with a single image for a stereo image would have led to a rather low resolution. Yet, there are alternatives to physical stereo images. Instead, it is possible to extract a surface information of a specimen by depth from defocus (Haug *et al.* 2011b, 2012b, 2013a, b) and produce stereo images from the virtual surfaces resulting from these.

Part and counterpart of the specimen were documented as a composite image (Haug *et al.* 2011a) on a Keyence VHX-6000 digital microscope, under cross-polarised light and unpolarised ring light (Haug *et al.* 2019). Several exposure times were combined (HDR, cf. Haug *et al.* 2013c). Based on depth from defocus, a surface was calculated. Of this, stereo images were produced.

The specimen for comparison was documented as a physical stereo image. The camera used was a Canon EOS Rebel T3i with a MP-E 65 mm lens.

SYSTEMATICS

Myriapoda Latreille, 1802
Diplopoda de Blainville *in* Gervais, 1844
†Archipolypoda Scudder, 1882

Lauravolsella n. gen.

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DERIVATION OF NAME. — A combination of Laura, the name of the former colliery at Eyselshoven, and the Latin word for forceps alluding to the shape of the anal region.

TYPE SPECIES. — *Lauravolsella willemeni* n. gen., n. sp.

DIAGNOSIS. — As for the type species as it is monotypic.

Lauravolsella willemeni n. gen., n. sp. (Figs 1; 2; 4)

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DERIVATION OF NAME. — After the surname of the collector.

HOLOTYPE. — MAB13859A/B.

TYPE LOCALITY AND AGE. — Coal mine dump of mine “Laura” near Eyselshoven in Southern Limburg, the Netherlands, lowermost Westphalian (Westphalian A).

DIAGNOSIS. — Elongate millipede with 20 diplosegments. Each diplosegment with a posteriorly drawn out diplotergites, three times the length of the ventral region of each diplosegment.

DESCRIPTION

Elongate specimen, longer than wide, at least 4.5 times, total length *c.* 40 mm (Figs 1; 2). Mostly ventral details accessible. Subdivision into discrete units apparent: one anterior region, a series of 20 sub-similar units, and a terminal end. The segmented appearance of the body indicates that the specimen is a representative of Euarthropoda; representatives of this group have a body usually differentiated into an anterior head and a posterior trunk.

Anterior region not well preserved with many details, therefore remains partly unclear. It is wider than long. Possibly this



FIG. 1. — New millipede *Lauravolsella willemeni* n. gen., n. sp., MAB13859A/B: **A, B**, part B; **A**, cross-polarised light; **B**, reflected light under ring illumination; **C**, part A, reflected light under ring illumination. Scale bars: 3 mm.

region represents the original head region and some trunk segments. The anterior edge of this region is gently rounded, further posterior elevations and depressions may represent remains of original mouthparts. Alternatively, the elevated region (Fig. 2C marked green) may represent the not well preserved head, and the depression (Fig. 2C marked cyan) may represent a not well delineated trunk segment. At least one pair of insertion areas of presumably locomotory (ambulatory) appendages is apparent at the posterior part of the anterior region. These are most likely arising from a trunk segment, not well delineated from the rest of the anterior region.

All of the following 20 units are subsimilar in appearance (Figs 1; 2A-C). Each unit is wider than long, about four times. Medially a sternal sclerite is apparent, occupying about 20% of the area. The sternal sclerite is deeply subdivided into two equal parts, an anterior one and a posterior one, by a distinct groove (Fig. 2D). Along the groove, four evenly spaced pores are apparent. Adjacent to the sternal sclerites insertion areas of appendages or proximal parts of appendages are apparent, two pairs per unit. These insertions/proximal parts are of similar dimensions as an anterior/posterior part of a sternal sclerite. Further later-

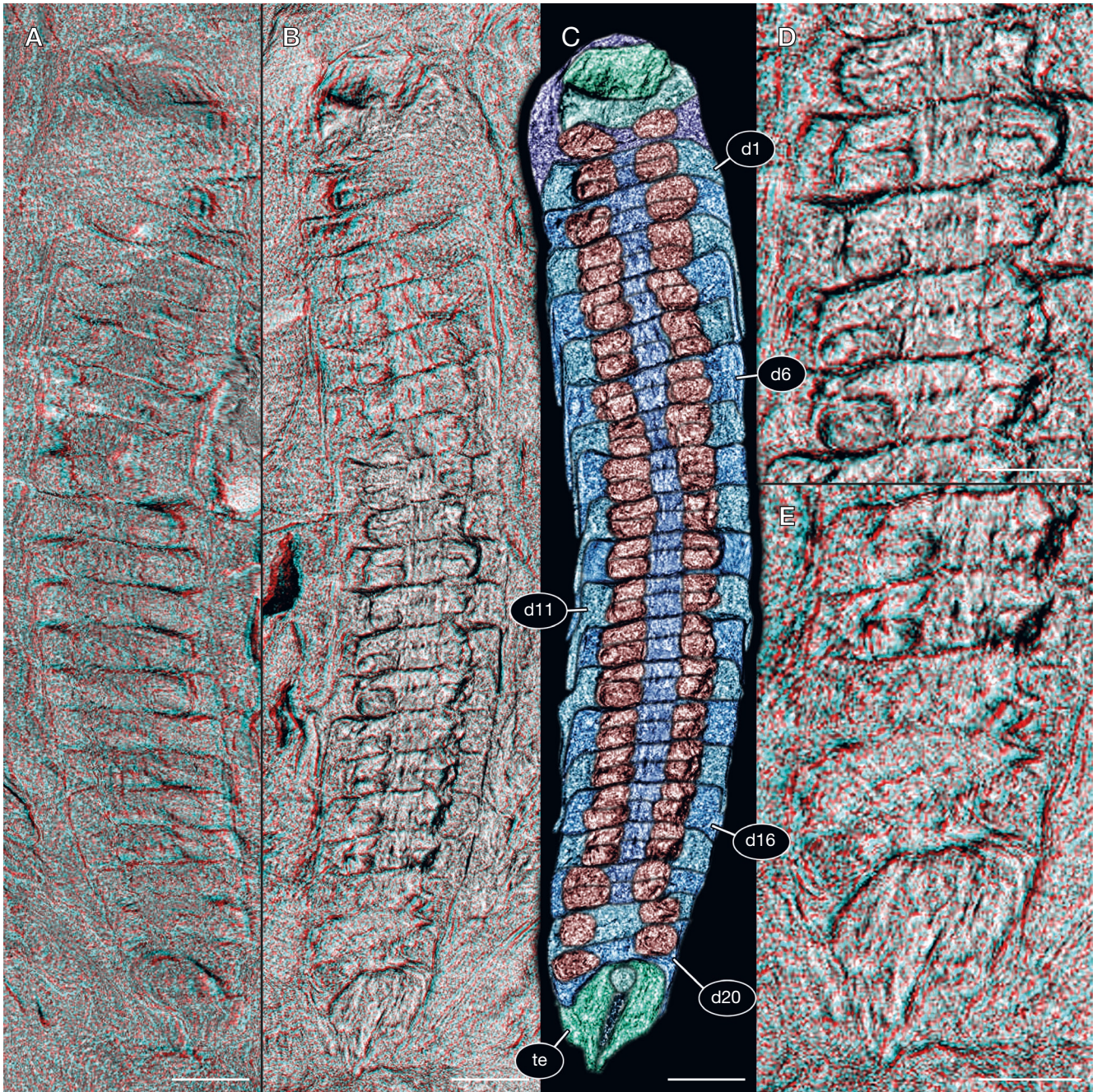


FIG. 2. — New millipede *Lauravolsella willemeni* n. gen., n. sp., MAB13859A/B: **A**, stereo image of part A; **B**, stereo image of part B; **C**, colour-marked version of B; **D**, **E**, stereo images of details of part B; **D**, trunk region showing the leg insertions and sternal sclerites; **E**, terminal end. Abbreviations: **d1-d20**, diplosegments 1-20; **te**, trunk end. Scale bars: A-C, 3 mm; D, E, 2 mm.

ally smooth region. Far lateral parts of the dorsal region of the unit visible in some of the units. More elongated than ventral region, up to three times.

Further posterior units slightly more slender. Very posterior ones slightly backwards curved, partly surrounding the posterior end.

Terminal end drop-shaped with tip facing backwards, slightly longer than wide (Fig. 2E). Three distinct sclerites apparent; antero-median sclerite small circular; other sclerites elongate left and right (symmetrically similar), anteriorly surrounding

the small sclerite, posteriorly leaving an elongate triangular gap between them.

DISCUSSION

THE NEW FOSSIL: A REPRESENTATIVE OF THE LINEAGE OF DIPLOPODA

The fossil is unfortunately incompletely preserved in several aspects. Only the very proximal parts of the appendages are

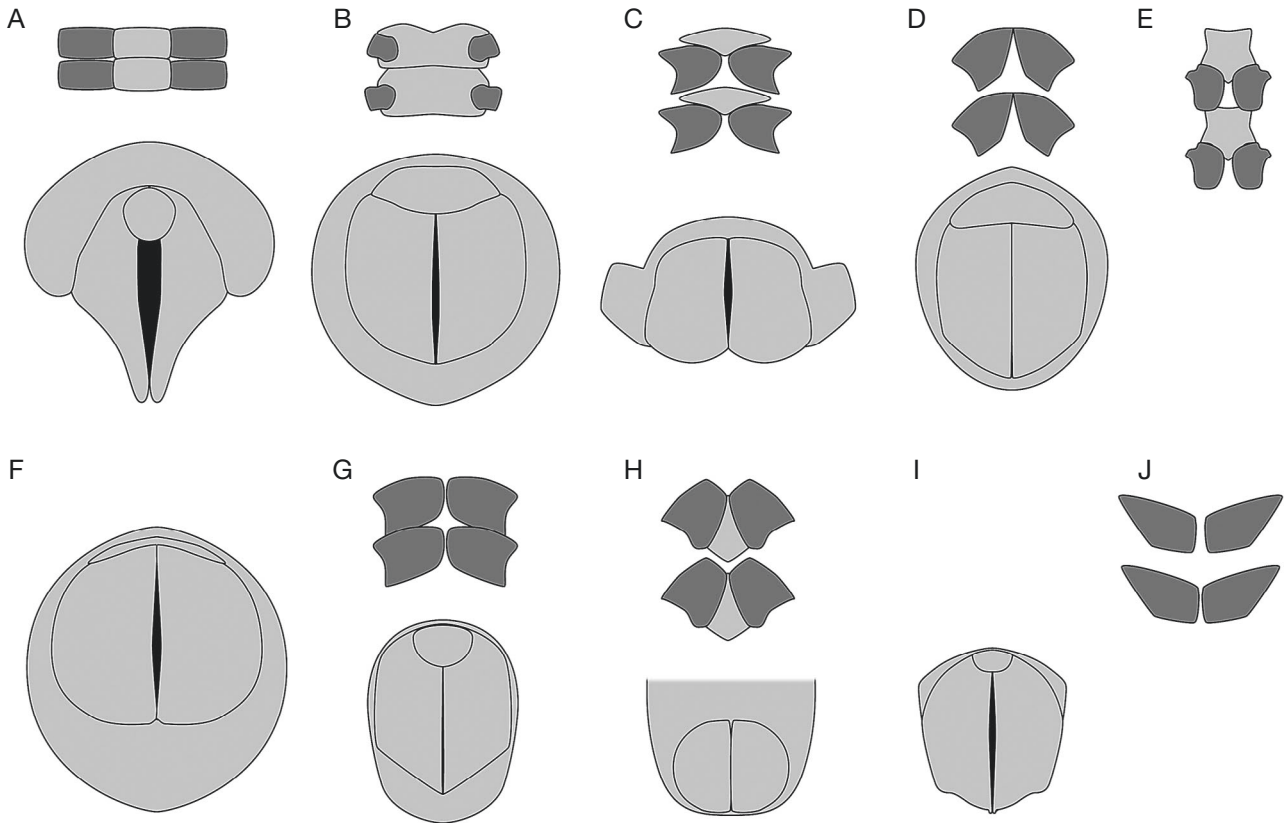


FIG. 3. — Schematic representations of the proximal leg arrangement (upper rows, proximal leg element in **darker grey**, sternite in **lighter grey**) and anal region (lower rows): **A**, new fossil; **B**, Polydesmida Leach, 1815 (based on Gilgado *et al.* 2015: fig. 10D); **C**, Polyxenida Lucas, 1840 (based on Huynh & Veenstra 2018: fig. 6B); **D**, Spirostreptida Brandt, 1833 (based on Likhitrakarn *et al.* 2018: fig. 5O, U); **E**, Siphonophorida Newport, 1844 (based on Marek *et al.* 2012: fig. 23); **F**, Julida Leach, 1814 (Reboleira & Enghoff 2018: fig. 3C); **G**, Callipodida Pocock, 1894 (based on Liu & Tian 2015: fig. 5); **H**, Platydesmida Cook, 1895 (based on Shorter *et al.* 2018: fig. 5D); **I**, Stemmiulida Pocock, 1894 (based on Mauriès *et al.* 2010: fig. 7); **J**, Glomerida Leach, 1814 (based on Antić & Makarov 2021: fig. 1C).

accessible, and especially the anterior body region does not provide many details. Yet, the proximal leg region as well as the terminal end is already quite informative.

As described above, two pairs of appendages correspond to a single tergite in the here described fossil. This arrangement is a diplosegment in the wider sense, as for example known in Pauropoda. In Diplopoda, the diplosegments are further derived into a single structure (diplosegments *sensu stricto*). While diplosegments are known in different lineages of Euarthropoda (e.g. in Scutigermorpha or in certain fossil representatives, e.g. †*Sinoburius lunaris* Hou, Ramsköld & Bergström, 1991; Schmidt *et al.* 2021), diplosegments along (almost) the entire body occur only in Pauropoda and Diplopoda (e.g. Sierwald & Bond 2007; Janssen 2011; Koch 2015). Unfortunately, the anterior body region of the new fossil is not well preserved; in millipedes, we should expect three single segments instead of diplosegments after the head region. While these are not apparent in the fossil, the preservation well explains this lack.

A further structural similarity of the fossil to extant representatives of Diplopoda is the arrangement of the anal region. There are two prominent anal vales (“paraprocts”) and an anterior smaller sclerite (“ventral scale”, “hypoproct”) delimiting the anal opening. Such an arrangement is well apparent in the fossil. It seems that in other lineages of Myriapoda such an arrangement is not developed. Especially in Pauropoda,

no such prominent arrangement of sclerites around the anus is present (Tiegs 1947: 278, text fig. 24A; Scheller 1988: 12, fig. 6; Bu 2020: 56, fig. 1G).

All these observations support the interpretation of the new fossil as a representative of Diplopoda or at least as a derivative of the lineage towards the group (“stem-lineage”). As pointed out, the majority of Carboniferous millipede fossils have so far been interpreted as representatives of the group Archipolypoda. Archipolypoda is characterised by the presence of paired pores on the sternites, often with valve-like structures closing these. Also the new fossil has distinct openings in the sternites, making it likely that the fossil is also a representative of Archipolypoda. Still, it has some morphological details that appear quite unique among the Palaeozoic fossils, such as the very long posteriorly elongated tergites. In addition, it possesses features shared with different extant ingroups of Diplopoda. We briefly highlight some of these.

CHARACTER DISTRIBUTION WITHIN DIPLOPODA

Two aspects are very apparent in the new fossil (Fig. 3A):

- the sclerite anterior to the anus (“ventral scale”, “hypoproct”) is rather small, more or less circular;
- the proximal leg elements are in quite some distance to each other, between them is a distinct sternite.

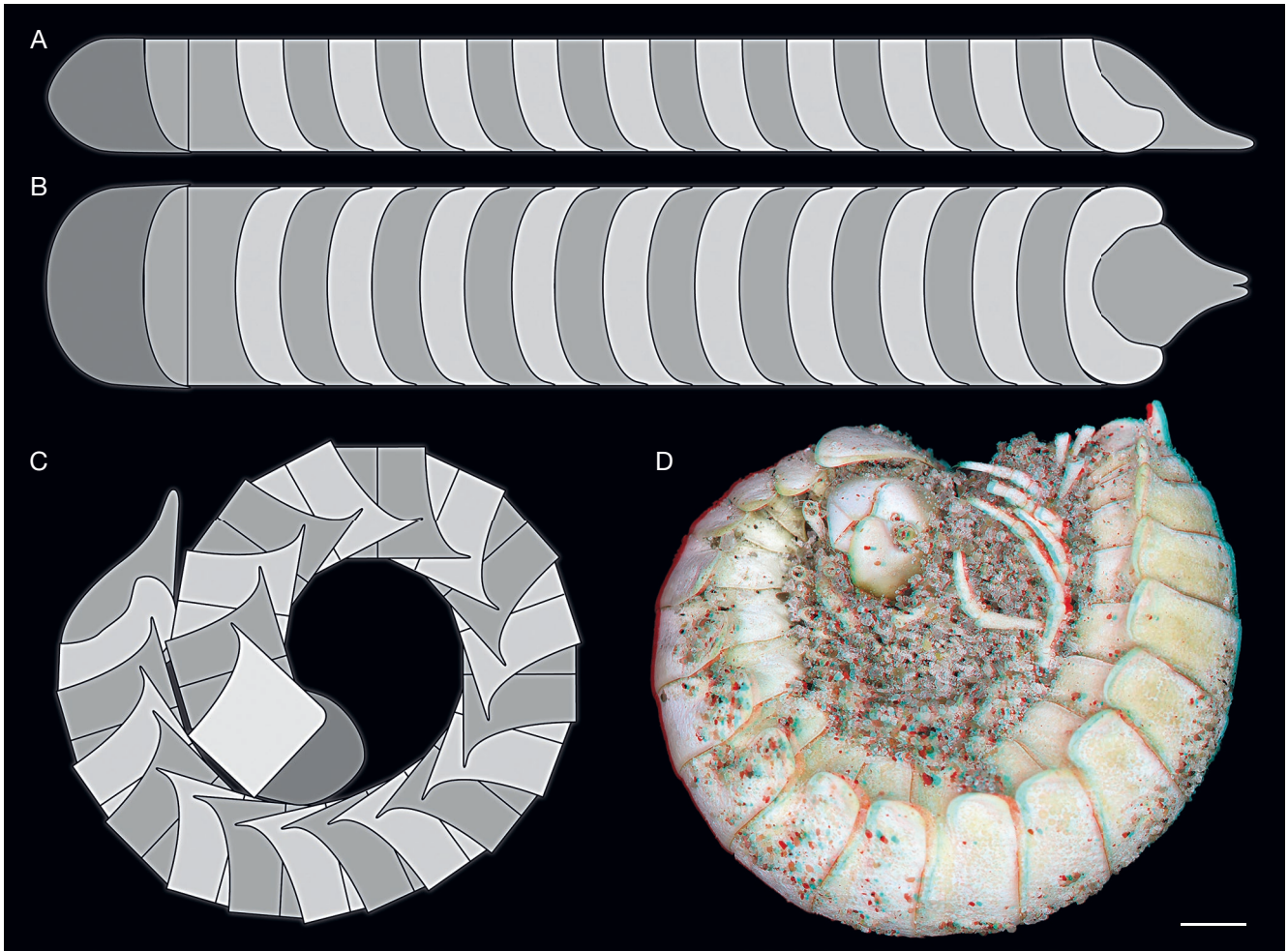


FIG. 4. — Schematic restorations of new millipede *Lauravolsella willemeni* n. gen., n. sp. and comparison: **A**, restoration in lateral view; **B**, restoration in dorsal view; **C**, supposed enrolment posture; **D**, partly enrolled millipede from the Pleistocene for comparison of posture, red-cyan stereo image of ROMIP32380. Scale bar: 2 mm.

Among extant ingroups of Diplopoda, a small sclerite anterior to the anus occurs, for example in representatives of Callipodida Pocock, 1894 (Liu & Tian 2015: 126, fig. 5) (Fig. 3G) and Stemmiulida Pocock, 1894 (Mauriès *et al.* 2010: 75, fig. 7) (Fig. 3I). In other ingroups of Diplopoda, the sclerite anterior to the anus is either not apparent, as in representatives of Polyxenida Lucas, 1840 (Huynh & Veenstra 2018: 143, fig. 6B) (Fig. 3C) or Platydesmida Cook, 1895 (Shorter *et al.* 2018: 30, fig. 5D) (Fig. 3H), or the sclerite is quite broad as in representatives of Polydesmida Leach, 1815 (Gilgado *et al.* 2015: 27, fig. 10D) (Fig. 3B), Spirostreptida Brandt, 1833 (Likhitrakarn *et al.* 2018: 65, fig. 5U) (Fig. 3D), Julida Leach, 1814 (Reboleira & Eng-hoff 2018: 97, fig. 3C) (Fig. 3F), or Chordeumatida Pocock, 1894 (Reboleira *et al.* 2018: 4, fig. 1D).

In most ingroups of Diplopoda, the insertions of the left and right legs are very close to each other, with almost no distance between them and often without a distinct sternite or a rather concealed one as in representatives of Callipodida (Liu & Tian 2015: 126, fig. 5) (Fig. 3G), Glomerida Leach, 1814 (Antić & Makarov 2021: 396, fig. 1C) (Fig. 3J), Spiro-streptida (Likhitrakarn *et al.* 2018: 65, fig. 5O) (Fig. 3D), or Spirobolida Bollman, 1893 (Wesener *et al.* 2009: 31, fig. 16A).

If a more prominent sternite is present in cases in which the legs are close to each other, it may be positioned anterior to the legs as in representatives of Polyxenida (Huynh & Veenstra 2018: fig. 6B) (Fig. 3C), Siphonophorida Newport, 1844 (Marek *et al.* 2012: 94, fig. 23) (Fig. 3E), or Chordeumatida (Reboleira *et al.* 2018: 4, fig. 1B). Alternatively, it may be positioned more posteriorly, “squeezed” in between from posterior as in representatives of Platydesmida (Shorter *et al.* 2018: 30, fig. 5D) (Fig. 3H). A broader sternite region between leg insertions, as in the fossil, is present in representatives of Polydesmida (Golovatch *et al.* 2013: 38, fig. 14G; Gilgado *et al.* 2015: 27, fig. 10D) (Fig. 3B).

In other Palaeozoic millipedes, prominent sternite regions seem to be present, yet the details of the leg insertions remain unclear for some specimens (e.g. Almond & Lawson 1985: 231, fig. 2). In some known representatives of Archipolypoda, the sclerite anterior to the anus is quite broad (Wilson 2005b: 1099, text fig. 3), unlike in the new fossil. Similar to the new fossil, in other representatives of Archipolypoda the region between the leg insertion seems very wide (Wilson 2005b: 1099, text fig. 2). Different from the new fossil, it appears separated into two halves by a distinct median groove.

Overall, the new fossil shows a mixture of features characteristic for Archipolypoda, of specialisations of its own, but also of some features seen in different extant millipedes. Apparently, convergent evolution seems to have been common within millipedes.

FUNCTIONAL ASPECTS OF THE NEW FOSSIL

The strongly posteriorly drawn out (diplo-)tergites of the diplosegments appear quite special on a first glance. Yet, it seems that there is indeed a functional explanation for these structures.

Some millipedes can perform a fully enclosed enrolment (e.g. Glomerida: Antić & Makarov 2021: 398, fig. 3; 405, fig. 9H; Sphaerotheriida: Wesener & Sierwald 2005: 597, fig. 63; Wesener & Koenig 2016: 19, fig. 11C, E-H; 20, fig. 12A, C-E, G; 21, fig. 13A; 22, fig. 14A, B, F-H; some forms of Polydesmida: Golovatch 2003: 48, fig. 24) likely for defensive purposes. Also many millipedes that cannot fully enroll perform a less tightly closed spiral type of enrolment (e.g. Sierwald & Bond 2007: 404, fig. 2C, I; Wesener *et al.* 2009: 32, fig. 17; 67, fig. 37B, C; Shorter *et al.* 2018: 25, fig. 1D).

Enrolling is not a simple task: the dorsal side of the body needs to be stretched, the ventral side to be compressed. For the latter there is often a distance between the sternites with softer membrane (e.g. Golovatch 2003: 56, fig. 46; Golovatch *et al.* 2013: 58, fig. 30H).

In the new fossil, there is apparently no distance between the sternal sclerites, no compression is possible here. Enrolling would be limited to the dorsal stretching. Strong stretching would expose soft membranous areas, if the diplotergites would be of a normal length. The strongly elongated diplotergites hence will most likely provide protection when enrolling.

For estimating how such a posture could look like we need to assume certain aspects of the body which are not directly accessible: the height of the body was assumed as being equal to the width of the appendage insertions (Fig. 4A), as many enrolling millipedes indeed have a body that is relatively high. The exact shape of the posterior edge of the diplotergite was assumed to be slightly concave (Fig. 4B). We assumed maximum tilting for adjacent segments until the anterior edge of the posterior segment was still covered by the drawn out diplotergite of the anterior segment. Based on these assumptions the animal could have enrolled quite effectively (Fig. 4C *vs.* 4D). We also assumed the presence of a collum which allows to fold the head further inwards. It is indeed possible that part of the anterior region of the fossil represents the collum.

Overall, it seems quite likely that the elongated diplotergites served for protection in conjunction with an enrolment behaviour. Yet, no real extant counterpart of such an arrangement is known.

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