Millipedes from the Grès à Voltzia, Triassic of France, with comments on Mesozoic millipedes (Diplopoda: Helminthomorpha: Eugnatha)

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Abstract

Hannibaliulus wilsonae, n. gen., n. sp. is described from a series of ten specimens from the early Triassic Grès à Voltzia Lagerstätte of north-east France. The best specimens (holotype and paratype) show a probably equal number of around 44 diplosegments. The affinities of the new species appear to be with the Order Callipodida, but clear apomorphies of that order are not observable on the specimens, both of which appear to be female. Other records of Mesozoic diplopods are briefly discussed and evaluated.

Key words

Callipodida, fossil, Lagerstätte

Introduction

While millipede (Diplopoda) fossils from the Carboniferous document a diverse and probably abundant fauna, Mesozoic examples are much rarer; only two, or possibly three, species having been described from the entire era. Thus, the discovery of well-preserved millipedes from the famed Fossil-Lagerstätte of Grès à Voltzia, France, merits documentation and description. The two specimens described below as *Hannibaliulus wilsonae,* n. gen., n. sp., are rather modern in appearance, but in the absence of any

clear apomorphies it is not possible to assign them to a previously known fossil or living order or family.

Geological setting

The sediments bearing the fossils, the Grès à meules, form the lower part of the Grès à Voltzia, which belongs to the upper part of the Buntsandstein, of early Triassic (Anisian) age (Fig. 1). Three facies have been recognized in the Grès à meules Formation (Gall 1971, 1983, 1985): a) thick lenses of fine-grained sandstone, grey or pink but most often multicoloured, containing land plant debris and stegocephalian bone fragments; b) green or red silt/clay lenses, generally composed of a succession of laminae each a few millimetres thick, with well preserved fossils of aquatic and terrestrial organisms; c) beds of calcareous sandstone with a sparse marine fauna.

The millipedes come from the clay lenses (facies b), in which the associated fauna includes terrestrial scorpions, spiders, and insects. An aquatic fauna occurs in the same beds, represented by medusoids, annelids, *Lingula*, bivalves, limulids, crustaceans, and fish. Land plants are also abundant, comprising horsetails, ferns, and gymnosperms (*Voltzia*). Some animals (e.g. *Lingula*, bivalves) are preserved in life position. Many arthropods (limulids, crustaceans) show, in the same horizon, different larval stages, adults, and moults. Clutches of insect eggs, coprolites, and trace fossils are also present. The biota is rich in individuals but poor in species (Gall 1971, 1983, 1985).
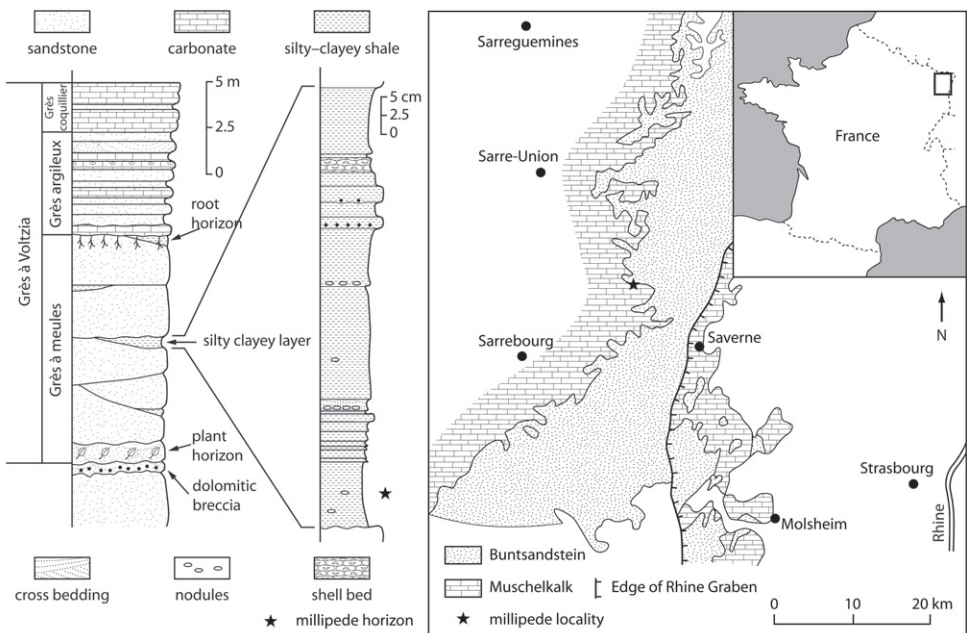

Figure 1. Location map and stratigraphic occurrence of the Grès à Voltzia millipede locality in the Triassic rocks of north-east France.

Palaeoecology

Evidence from the sediments and fossils points to a deltaic sedimentary environment (Gall 1971, 1983). The sandstone facies corresponds to point bars deposited in strongly sinuous channels; the clay lenses represent the settling of fine material in brackish ponds; the calcareous sandstone results from brief incursions of sea water during storms. The palaeogeographical position for the localities, in the subtropics near the eastern edge of Pangaea, together with the red-beds and the xeromorphic nature of the land flora (Gall 1983), suggest a semi-arid climate in the region. However, the low-lying, deltaic situation suggests that aridity was not severe locally. The climate was probably seasonal; the pools filling during the wet season and evaporating as the dry season approached. Eventually, the pools where the clay lenses were deposited became shallower and dried out completely. This is supported by the presence of desiccation cracks, reptile footprints, salt pseudomorphs, and land plants in life position at the top of each clay lens. Also, moving upwards through each lens a transition from aquatic to terrestrial biota is observable (Gall 1983).

The excellent preservation of the terrestrial biota in the clay lens facies, the low energy of deposition, and the presence of *in situ* plant roots indicate that these organisms lived immediately in the neighbourhood of the water bodies. No evidence conflicts with the conclusions of Gall (1971, 1983) that the aquatic fauna lived and died *in situ* (i.e. it is autochthonous) and that the preserved terrestrial fossils crawled or fell from the adjacent terrestrial environment to their place of entombment. There is no evidence of drifting of the fossils by water currents. The kinds of plants and animals present, particularly the presence of *Lingula* in situ, together with the impoverished species diversity, strongly suggest a brackish water community. The euryhaline fauna is typical of transitional environments: lagoons, pools, and swamps between land and sea and the dwarfed nature of the stenohaline marine forms supports this (Gall 1983). Such a fauna is adapted to fluctuating conditions of salinity, oxygenation, desiccation, etc. The composition of such restricted communities shows a striking continuity during the course of Earth history.

The millipedes evidently inhabited the margins of the stagnant pools where a sparse vegetation dominated by bushes of *Voltzia*, and reed beds formed by horsetails (*Schizoneura, Equisetites*), grew. The specimens described here represent the only known species of diplopod living in this Triassic landscape.

Taphonomy

Drying-up of the pools led to the death of the aquatic fauna. The abundance of estheriids is significant in that these crustaceans are adapted to swift completion of their life cycle in temporary water bodies. Regular high evaporation rates of the water bodies also favoured deoxygenation, consequent mass mortality of the aquatic fauna, and the rapid proliferation of microbial films. Such films may have shielded the carcasses from scavenging activity and created, by production of mucus, a closed environment inhibit-

ing the decomposition of organic material. Later, the deposition of a new detrital load (clay, silt) buried the microbial films and the organisms (Gall 1990).

The millipede specimens described below may either have been washed as carcasses into a pool, or fallen in and drowned there. It is unlikely the specimens represent moults, since these animals quickly consume their shed exoskeletons to recycle calcium; fresh millipede moults are usually headless and split down the mid-dorsal line. The specimens are relaxed and extended, not curled in a spiral, and appear to have undergone minimal decay. It may also be possible that in the process of scavenging organic matter left after one drying cycle of the pool, the millipedes were overwhelmed and buried when flooding refilled the basin. The millipedes are preserved flattened by sediment compaction in most cases, and as brown organic cuticle. The two nearly complete specimens (MYR1a,b; MYR10a,b) are extended and preserved in lateral view. Other specimens (see list below) consist of either isolated series of tergites, or cross sections. Small pieces of cuticle are preserved on and just within the fine clayrock. Splitting of the rock has resulted in part of each specimen being preserved on one slab, and part on another. Part and counterpart correspond to left and right in most cases. In most specimens, some of the cuticle has fallen away leaving an external mould; this is particularly the case with the legs.

Material and methods

All the millipede specimens come from localities numbered 238, in the Bust–Hangviller region as described in Gall (1971). The specimens are labelled as follows: MYR1a,b, 238; MYR2a, 238C; MYR3a,b, 238A; MYR4, 238; MYR5, 238B; MYR6, 238D/C; MYR7a,b, 238A/B; MYR8a,b, 238B; MYR9a,b, ?; MYR10a,b, 238A. Whilst data are lacking for MYR9a,b, it is reasonable to assume it also came from the 238 localities because all the other specimens originate from there, and its preservation is similar to that of the others. Specimens were studied, drawn and photographed on a Wild M7S stereomicroscope using a Nikon D1X digital camera and drawing tube. Digital manipulation of photographs and drawings was done on an Apple PowerBook G4 using Vuescan 7 scanning software (www.hamrick.com), Adobe Photoshop 7 and Adobe Illustrator 10 under OS X.

Description of specimens

?Superorder Nematophora Verhoeff, 1913
?Order Callipodida Pocock, 1894

Genus *Hannibaliulus*, n. gen.

Type species: *Hannibaliulus wilsonae*, n. sp., by monotypy.
    Diagnosis: Collum small, not covering head, metazonites of the pleurotergites smooth, with a distinct transverse depression and ventrolateral rebordered flange; ozopores absent

(?); sternites probably free from pleurotergites; eyepatches with numerous ocelli; about 43–44 trunk segments; epiproct rounded, about 1.5 times longer than wide.

Occurrence: Grès à meules formation, lower part of the Grès à Voltzia, which belongs to the upper part of the Buntsandstein, of early Triassic (Anisian) age, in the Bust–Hangviller region of the Vosges mountains, north-east France (see Gall 1971 for details).

Etymology: The generic name honours Dr Joseph Hannibal of the Cleveland Museum of Natural History, Ohio, in recognition of his many contributions to the study of fossil myriapods.

Discussion: The rebordered, free ventrolateral margins of the pleurotergites imply that the sternites and pleurotergites are not fused, as they are in juliform millipedes. Cylindrical diplosegments with free sternites occur in several millipede superorders; however, the large eyepatches and high segment count rule out any of these except the Nematophora (comprising the orders Chordeumatida, Callipodida, and Stemmiulida). All Nematophora have a mid-dorsal suture on each trunk segment save the collum (the legless first segment). Because of the lateral preservation of our material we are unable to observe this character on the holotype and paratype, but another specimen (Myr2a), preserved in dorsal view, shows evidence for such a suture (Fig. 8). Among the nematophoran orders, the specimens seem closest in form to the order Callipodida. The large eyepatches rule out assignment to the extant order Stemmiulida, in which the eyes consist of one or two large, single stemmata. Chordeumatida have fixed segment numbers ranging from 26 to 32, as well as distinctive segmental setae we think may have been preserved, if originally present. Callipodida, as well as Chordeumatida, also have a prominent pair of epiproctal spinnerets, and given the condition and orientation of our material these should be visible, but they are not. Callipodida do not have fixed segment numbers, but adults always have more than 32. Unlike chordeumatidans, callipodidans have prominent ozopores laterally on all metazonites from the fifth rearward, and these were not observed on our specimens. Of course it is entirely possible that Triassic millipedes may have had combinations of characters not seen in living forms, or that *Hannibaliulus wilsonae* is a representative of a stem lineage of Nematophora, which may have originated in the late Carboniferous or earlier (Hannibal 2000, Wilson 2006).

While Wilson (2006) argued for early cladogenesis in the Diplopoda, and placed the origin of the Nematophora in the late Carboniferous, this was based on the occurrence of *Hexacontasoma* Hannibal 2000, which, while it may possibly be related to the Callipodida, has no visible synapomorphies of that group. Assigning millipede fossils to extant orders is a difficult business because the apomorphies of those orders are rarely visible in fossils. Many millipede fossils show juliform body structure, but that does not mean that they are necessarily related to existing julimorph orders; convergence in body structure is a frequent phenomenon among millipedes. For example, on the basis of short series of body segments it would not be possible to differentiate a cylindrical, paranota-less polydesmidan (of which there are many) from a julidan. The orders Polydesmida and Julida are not closely related.

Hannibaliulus wilsonae, n. sp.
Figs 2-8

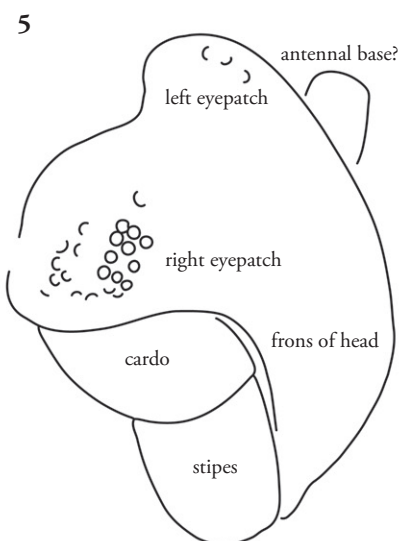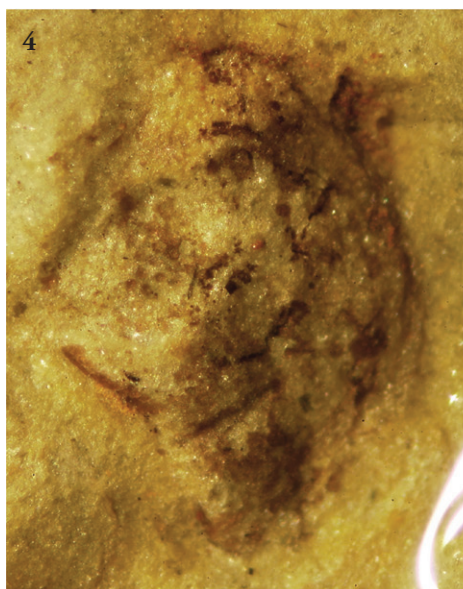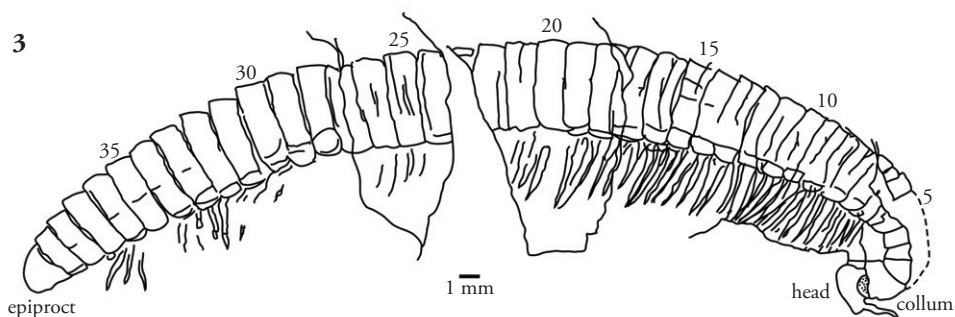*Diagnosis and occurrence*: As for the genus.

Etymology: The species epithet recognizes the important and ground-breaking contributions of Dr Heather M. Wilson to palaeomyriapodology.

Description: Length of holotype, 52.92 mm, of paratype, 56.24 mm. Greatest widths, 4.63 mm and 3.88 mm, respectively. Forty to 44 trunk segments, including collum and epiproct. Pleurotergites consisting of prozonites and metazonites, prozonites hardly visible, telescoped into preceding metazonites. Metazonites divided by wide, shallow transverse depression into anterior and posterior parts, ventral margins strongly rebordered. Ozopores not detected, segmental setae and epiproctal spinnerets not detected. Collum not covering head. Epiproct longer than penultimate diplosegment, posteriorly rounded. Legs consisting of the usual seven podomeres, relatively long. Head broadly rounded, bearing two eyepatches with multiple ocelli; cardo and stipes of massive mandible preserved.

Types: Holotype part and counterpart MYR1a,b; paratype part and counterpart MYR10a,b, deposited in the Laboratorie de Géologie et de Paléontologie, Université Louis Pasteur, Strasbourg, France.
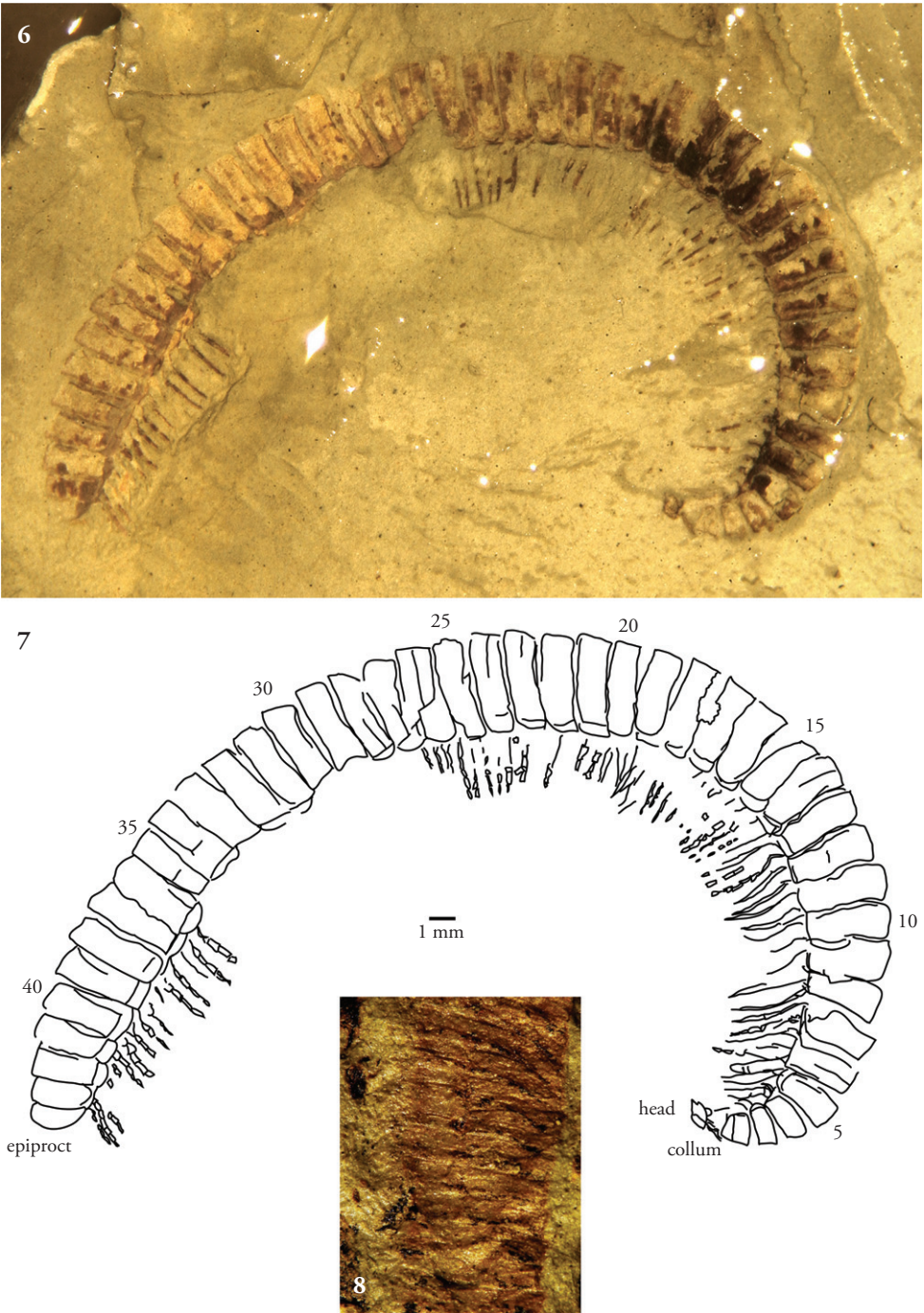
Other material: MYR2a, MYR3a,b, MYR4, MYR5, MYR6, MYR7a,b, MYR8a,b, MYR9a,b, all with the same locality, horizon and repository.

Discussion: The interpretation of the apparent separate ventral sclerites associated with some diplotergites on the holotype is difficult. Hoffman (1963) interpreted roughly similar Carboniferous specimens of xyloiulids as having been crushed by compression so that the broken-off lower portion of the diplotergite appeared to be a separate sclerite. Kraus (1974), on the other hand, in an interpretation accepted by Wilson and Hannibal (2005), thought them to be separate pleurites. While Kraus (1974) did not argue extensively for his interpretation, Wilson & Hannibal (2005) carried out experiments on extant species with free pleurites which showed that the key points were consistent patterns of separation, occasional overlap of the pleurites and diplotergites, and a lack of continuity between the two of such features as rebordered margins. Further, among Wilson and Hannibal's specimens were some with ventral preservation which clearly showed the separate pleurites. Since we are unable to demonstrate any of these features from our specimens, we fall back on Hoffman's hypothesis of the crushing and breaking of ventral flanges of at least some of the diplotergites. In some diplosegments on the holotype, the entire metazonite seems continuous, and in others, a ventral portion is separate. Preserved at a slightly different angle, there is no suggestion of free pleurites on the paratype. While the breaks occur at almost the same level in each diplosegment, their jagged margins and the lack of rebordering dorsal to the break speaks against free pleurites, though, as in spirobolidans, there could have been a suture at that level which produced a line of weakness along which breakage could easily occur. We remain open to other interpretations, and any new material may help to solve this problem. The rebordering of the flanges, however, shows clearly that there

Figures 2-3. *Hannibaliulus wilsonae*, gen. et sp. nov.: 2. holotype part MYR1a, dry. 3. explanatory drawing of holotype part.

Figures 4-5. *Hannibaliulus wilsonae*, gen. et sp. nov.: 4. holotype counterpart MYR1b head, under alcohol. 5. explanatory drawing of holotype counterpart head.

Figures 6-7. *Hannibaliulus wilsonae*, gen. et sp. nov.: 6. paratype part MYR10a, under alcohol. 7. explanatory drawing of paratype part.

Figure 8. *Hannibaliulus wilsonae*, gen. et sp. nov.: specimen MYR2a, under alcohol; dorsoventrally compressed specimen showing position of mid-dorsal suture.

must have been free sternites and the living animals did not exhibit complete rings as seen in Polydesmida and Julida. Specimen MYR2a consists of several segments from the posterior end of another individual, seen in dorsal view and crushed. The consistently broken midline speaks for a mid-dorsal suture in this species (Fig. 8).

The nearly identical numbers of trunk segments in both specimens (40–44), given the possibility of counting errors on broken and damaged specimens, raises the possibility that both specimens are adults and that the number of trunk segments may have been fixed at some figure around 44 (or the two similar counts may merely be coincidence). Further evidence of adulthood is the fact that the last diplosegment anterior to the epiproct bears legs; in juvenile millipedes there is usually one or a series of legless diplosegments anterior to the epiproct. If the specimens are adults, both are females, since none of the legs in the anterior portion of the body are modified as gonopods.

Discussion

Millipedes (Diplopoda) were among the first animals on land, and indeed may have been the very first. Trace fossils attributed to diplopods have been described from Cambro-Ordovician and Ordovician strata (Retallack & Feakes 1987, Johnson et al. 1994, Retallack 2001, MacNaughton et al. 2002). These trace fossils have been cogently reviewed by Wilson (2006), who raised serious questions, particularly about the burrows described by Retallack (2001). However, the Borrowdale Volcanic Group traces, of Ordovician (Llandeilo-Caradoc) age, described by Johnson et al. (1994) are consistent with traces made experimentally using some living millipede species. The first millipede body fossils occur in the Silurian Stonehaven Group of Scotland (Wilson & Anderson 2004), which may be Wenlock in age (Almond 1985, Wilson & Anderson 2004). Well-preserved and well-described specimens are known from Devonian rocks (Almond 1985, Shear et al. 1996, Wilson 2006) of Britain, the USA, and Canada.

A greater range of morphotypes of millipedes than seen today may have lived in late Carboniferous coal forests, though helminthomorph types have existed since at least Silurian times [for reviews of the myriapod fossil record and phylogenesis, see Shear (1997) and Wilson (2006)]. The Permian Period, however, is virtually a blank as far as fossil millipedes are concerned, though insects are well represented. Hannibal (2006) has briefly mentioned Lower Permian millipede fossils from fissure fills in southwest Oklahoma, USA, but these specimens remain undescribed. Thus we find that there is a very long time gap between the relatively abundant and well-studied Carboniferous fauna and the few known Mesozoic specimens—a time gap which includes the Permo-Triassic extinction event.

Mesozoic millipedes are rare and poorly known. Only *Tomiulus angulatus* Martynov, 1936 has been described from the Triassic, *Decorotergum warrenae* Jell, 1983 from the Jurassic, and *Gobiulus sabulosus* Dzik, 1975 from the Cretaceous. Thus the discovery of new specimens of Triassic millipedes represents a significant step forward in understanding diplopod evolution, particularly as it occurred after the Permo-Triassic extinction event.

Tomiulus angulatus was redescribed in detail by Dzik (1981). The specimen comes from the Olenkian of the Babiy Kamin' Gorge of the Tom' River, Siberia (Martynov 1936, Dzik 1981). The Olenkian is roughly equivalent to the upper Scythian, about 245 myo. The two specimens, which may be parts of the same individual, consist of 15 and about 16 diplosegments respectively. The state of preservation is such that the only possibly significant feature visible is the terraced sculpture of the pro- and metazonites (Dzik 1981). Dzik's reconstruction of the diplosegments (fig. 2) is unusual and shows an infolding of the posterior margin of each metazonite that completely covers the following prozonite; in other words, a double layer of metazonital cuticle overlying the prozonite. Such a segment structure is unknown from any millipede, living or fossil, and is not supported by the photographs provided (Dzik's fig. 1). The terraced sculpture of the metazonites resembles that of members of the extinct family Xyloiulidae, to which he assigned the species. Hoffman (1963) considered the Carboniferous xyloiulids to be basal spirobolidans, nonetheless describing the putative gonopods in one specimen of *Plagiascetus lateralis* Hoffman as conforming to a "spirostreptoid" pattern. But the two orders Spirobolida and Spirostreptida are not closely related. Despite all this confusion, all that *T. angulatus* really has in common with the xyloiulids is tergal ornament—which would be considered a highly unreliable character for family assignment in living millipedes. So the question as to whether the xyloiulids, as a clade of Palaeozoic diplopods, survived the Permo-Triassic crisis remains open.

Jell (1983) described *Decorotergum warrenae* from the early Jurassic of Australia, based on poorly preserved and very partial remains of what does appear to be a diplopod, showing smooth prozonites and metazonites with a transverse furrow. However, at most 12 segments are preserved, and it is not clear from the photographs if these are from the posterior or anterior end, or from the middle of the body. Jell (1983) considered the alternatives of assigning the fossil to the Order Amnylispedida, or the Order Polydesmida, but neither is convincing. The material requires restudy.

Gobiulus sabulosus was also described by Dzik (1975), from 13 specimens, including two heads, found in the Barun Goyot Formation, Khulsan, in the Gobi Desert of Mongolia. The age is thought to be middle Campanian, about 77 myo. Dzik (1975) interpreted this species as a member of the extant order Spirobolida, and tentatively assigned it to the living Family Atopetholidae. Dzik (1975) stated that the atopetholids are to be found in Central America, the tropical regions of Asia, and in North and South Africa. However, Atopetholidae is an endemic North American family, not known to occur south of México City (Hoffman & Orcutt 1960, Hoffman 1999). The specimens show none of the currently recognized synapomorphies of atopetholids. Dzik (1975) reconstructed the gnathochilarium and collum of the species in an unusual manner, showing the gula, or gnathochilarial sternite, as a broad, triangular sclerite extending anteriorly nearly to the distal end of the mentum. Such a structure does not occur in any spirobolidan family, nor indeed anywhere in the Diplopoda. It is certainly not, as Dzik (1975) maintained, characteristic of the Atopetholidae. The photographs of the specimen are too unclear to determine if such a reconstruction is supported. However, assignment of *Gobiulus sabulosus* to the order Spirobolida is not

unreasonable, based on general appearance, the small, fixed, but unfused sternites, the median frontal suture of the head and the short lateral margins of the collum.

Another possible Mesozoic millipede, *?Xylobius mexicanus* Mullerried, 1942, was dismissed by Dzik (1975) as having no affinity to millipedes. However, we are not so sure; the photograph in the original article shows an S-shaped structure, tapering slightly at either end, and made up of even-sized divisions (about 52 or 53, according to the text) which, at the possible anterior end of the fossil, show longitudinal striations. The photograph is not clearly reproduced and only an examination of the specimen, the whereabouts of which are not known, would resolve its position. The stratigraphic position of this fossil is also in doubt; Mullerried (1942) admitting the possibility of a stratigraphic range from Jurassic to mid-Cretaceous.

Hannibaliulus wilsonae therefore represents only the fourth or fifth definitively known occurrence of the Class Diplopoda from the entire Mesozoic. Our specimens of *H. wilsonae* are quite similar in general appearance to members of the extinct order Pleurojulida, described by Wilson & Hannibal (2005). However, we cannot verify that our specimens had separate pleurites and indeed think that was not the case. As the ordinal name suggests, pleurojulidans, while resembling juliforms, differed from them in having free pleurites. If further *Voltzia* specimens allow the verification of separate pleurites, this would imply that members of Pleurojulida, now known from the Westphalian D of the Czech Republic, survived the entire Permian and the Permo-Triassic extinction.

Acknowledgments

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